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## TAXONOMY AND BIOGEOGRAPHY OF AFRICAN FRUIT BATS (MAMMALIA, MEGACHIROPTERA). 1. GENERAL INTRODUCTION; MATERIAL AND METHODS; RESULTS: THE GENUS *EPOMOPHORUS* BENNETT, 1836

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### ABSTRACT

This first part of a revision of African fruit bats contains a short general Introduction and a section Materials and Methods, both pertaining to all parts — as are the first remarks under Results —, and a study of the genus *Epomophorus* Bennett, 1836. Prior important descriptions of *Epomophorus* are reviewed and current concepts of the generic characters relative rostrum length; relative palatal length; depression of postdental palate; palatal ridge pattern; and sexual dimorphism are modified. Of all problematical taxa within the genus type specimens have been examined. The following six species are retained: *Epomophorus angolensis* Gray, 1870; *E. gambianus* (Ogilby, 1835); *E. grandis* (Sanborn, 1950); *E. labiatus* (Temminck, 1837); *E. minor* Dobson, 1880; *E. wahlbergi* (Sundevall, 1846). On morphological and distributional grounds *E. crypturus* Peters, 1852 and *E. pousarguesi* Trouessart, 1904 are ranked as subspecies of *E. gambianus*. The holotype and only known adult specimen of *E. reii* Aellen, 1950 is considered an aberrant specimen of *E. g. gambianus*, and *E. reii* is synonymized with that species. On allometric grounds *E. gambianus parvus* Ansell, 1960 is considered a synonym of *E. gambianus crypturus*. Based on an examination of the type specimen, the skull of which is figured for the first time, arguments are put forward for a new concept of *E. labiatus*, deviating considerably from the standard set by Andersen in 1912. Its type locality is changed from "Sennar" into the original "Abyssinia" again. *E. anurus* is synonymized with *E. labiatus* and denied the subspecific status granted to it by other authors. The geographical variation of size within *E. wahlbergi* is analyzed and as a result subspecific divisions on the basis of differences in size are rejected as untenable. Hence *E. wahlbergi haldemani* (Hallowell, 1846) is considered a synonym of *E. wahlbergi*. As *E. minor* is apparently sympatric with *E. labiatus* in several areas, it is treated as specifically distinct from that species. It is made clear, nevertheless, that their mutual distinctness may not hold throughout their shared distribution area. Examination of the skull characters and soft palate has led to the transfer of *Micropteropus grandis* Sanborn, 1950 to the genus *Epomophorus*. The distribution patterns of all species are critically assessed and associated with the vegetation types distinguished by White (1983). For the first time, pan-African distribution maps, including many new records, are given for all species and subspecies.

### INTRODUCTION

Fruit bats (Megachiroptera) are found in the tropics and subtropics of the old world. Presently, about 165 species are recognized

(Honacki *et al.*, 1982; Ziegler, 1982; Smith *et al.*, 1983; Heaney *et al.*, 1984; Rozendaal, 1984; Bergmans *et al.*, 1985). The last comprehensive systematic review of fruit bats is the work by Andersen (1912). Even at that time, a

total of 955 pages was needed to record what was known about taxonomy and distribution of the 186 species then recognized. Andersen's work is still a most important reference work for the subject. Almost all genera listed by him are still accepted today, notwithstanding the extensive synonymizations proposed by Simpson (1945). Of the African genera, only *Stenonycteris* and *Lissonycteris*, both proposed as subgenera by Andersen, 1912 to accommodate certain species of *Rousettus* Gray, 1821 and raised to generic rank by certain later authors, are the subject of some controversy with regard to their validity as such.

Since Andersen, our knowledge of the intraspecific variation of many species has been greatly augmented. As a result, quite a few species recognized by him have been synonymized with others, or at most retained as subspecies. On the other hand, a fair number of new species has also been proposed. Although our present knowledge would justify a new effort similar to Andersen's *magnum opus*, this will probably never be undertaken, as it would amount to a series of several volumes, whose publication would not be feasible.

The present paper is the first in a small series reviewing the taxonomy and distribution of the African Megachiroptera, building on, and sometimes contradicting, Andersen's work on the basis of the many new specimens and other data which have been collected since.

## MATERIAL AND METHODS

This section applies to all parts of the forthcoming series of papers. Specimens have been examined and measured from many museum collections, a survey of which is given at the end of this section. Each species account in the taxonomic section contains a standardized enumeration of the material involved. Specimens are listed per country, in an alphabetic order. Unless otherwise stated, specimens are adult and consist of dry skins and skulls. Other data preferably include collecting locality and date, collector(s), collection, and

registration number; when these data are incomplete this does not necessarily reflect reality — specimens are sometimes incompletely labelled and there has not always been sufficient time, during visits in collections, to consult registers for missing data. In the enumerations of specimens, published collecting localities from where no specimens have been examined by the present author are listed between brackets at the end of each country entry. See Ansell, 1978: 3 and fig. J, for an explanation of the grid code system in use in southern Africa.

Although the enumerations are quite lengthy in a number of cases, it was thought that they should be included to enable reproduction of the results, as they indicate which specimens have been examined and identified by the author. Moreover, they indicate which collections are important with regard to certain species or regions, they give due credit to collectors, and, in combination with the gazetteer to be published in the last part of this series, enable more precise mapping than feasible in the present pan-African presentation of species' distributions.

Specimens and skulls have been measured to the nearest 0.1 mm with vernier callipers, teeth to the nearest 0.05 mm with a stereomicroscope with micrometer disc. The designation of teeth follows Andersen (1912: xxvii-xxviii). All measurements are given in mm. Weights have been copied from collectors' labels and are given in g. Only adult specimens have been used when establishing variation ranges of measurements, except for those of teeth which can also be measured in immatures.

Adulthood of specimens, in the sense of their being full-grown, has been determined using various parameters. From the author's experience, fused and ossified skull base sutures (between pterygoid and basisphenoid, and between basisphenoid and basioccipital bones) offer one of the most reliable criteria for adulthood — given that the skull usually is the only part of the skeleton available for measuring. The measure of ossification of the phalanges at the finger joints, which is a hun-

dred per cent in adults, is another useful character, but not always easy to observe. In males, the development of secondary sexual characters such as collars and epaulets generally only occur in full-grown specimens. Contrarily, pregnancy and developed mammae do occur in subadult females (Bergmans, 1979b). Excessive tooth wear, also observable in spirit specimens with the skull *in situ*, is never found in other than older adult specimens. (One should always bear in mind that broken teeth, such as canines, are occasionally found in young, immature specimens.) In most, if not all, fruit bat species there is a difference in fur colours between immature and adult specimens.

Immature specimens are usually rather dull if compared to adults; in quite a few species the fur of immatures is interspersed with greyish hairs. Another means to detect immaturity are the ratios between certain proportions. Megachiroptera are born with proportionally rather large feet, for instance, and an experienced observer recognizes specimens as immature by their 'too large' feet. Some useful characters to assess adulthood are restricted to certain taxa; in males of the genus *Epomophorus* Bennett, 1836 the relative length of the snout is distinctly larger in adults than in immatures.

Definitions of measurements as taken by the present author are as follows.

*Head and body length:* The distance from tip of snout across back to base of tail. Because heads of Megachiroptera cannot be laid back this length is measured with a thread laid on the specimen and following the distance.

*Tail length:* The length of the external tail.

*Tibia length:* The distance between the two extremes of the tibia *in situ*, as far as can be ascertained in wholly preserved specimens.

*Foot length:* The distance from the 'back' side of the heel to the most distal point of the claws.

*Ear length:* The distance between the most proximal point of the basal notch and the tip.

*Forearm length:* The length of the forearm *in situ*, including the joints with the upper arm and hand; in order to standardize results and to minimize the contributions of the joints, the elbow and wrist are bent so that both upper arm

and metacarpals are lying against the forearm (as much as possible, without forcing them).

*Metacarpal length:* The length of the metacarpal *in situ*, from the top of the wrist to the most distal point of the metacarpal.

*Greatest skull length:* The distance between prosthion and opisthocranium. The opisthocranium or most caudal point of the skull can be situated either on the occipital region of the braincase, or in the median plane on the line connecting the most caudal points of the condyli occipitales, or on the sagittal/occipital crest.

*Condylbasal length:* The distance between prosthion and the intersection of the median plane and the line connecting the most caudal points of the condyli occipitales.

*Rostrum length:* The distance between prosthion and the most anterior point of the orbit margin. This way of measuring the rostrum length is preferred to measuring between the most distal point of the nasal bones and anterior orbit margin.

*Palatal length:* The distance between prosthion and the intersection of the tangent of the middle of the caudal margin of the palatum and the median plane.

*Cranium width:* The width of the actual braincase above the caudal insertions of the zygomatic arches. This measurement is not very exact.

*Interorbital width:* The distance between the innermost points of the interorbital constriction of the skull roof.

*Postorbital width:* The distance between the innermost points of the postorbital constriction of the skull roof.

*Zygomatic width:* The distance between the most distal points of both zygomatic arches.

*Mandible length:* The distance between the most distal point of the ramus and the most proximal point of the processus articularis.

*Mandible height:* The perpendicular height of the mandible when laid on a flat surface, from that surface to the highest tip of the processus coronoideus.

Teeth rows, widths over teeth, and teeth have been measured over the cingula. Teeth lengths have been measured approximately in line with

the orientation of the teeth row involved, and teeth widths perpendicular to these lengths.

No attempt has been made yet at a phylogenetic analysis of the group of taxa involved. As Haiduk *et al.* (1984), who carried out chromosomal banding studies in a limited number of African species, noted "a suitable outgroup for the Megachiroptera has not yet been found". This still holds true. The very place of the taxon Megachiroptera, traditionally regarded as a Suborder of the Order Chiroptera, is the subject of renewed discussions (Pettigrew, 1986; Martin, 1986). It is felt that the subject is beyond the scope of the present work. It should focus on the assessment of systematically and evolutionary potentially useful characters other than, and in addition to, those which can be examined in museum specimens and on which genus and species taxonomy is based. It should, in the author's opinion, also take into account the non-African Megachiroptera, which comprise four fifths of the whole Suborder, including two subfamilies not found in Africa.

The order of genera in the taxonomic section of the Results is as follows:

Pteropodinae

*Epomophorus* Bennett, 1836

*Micropteropus* Matschie, 1899

*Epomops* Gray, 1870

*Hypsignathus* H. Allen, 1861

*Nanonycteris* Matschie, 1899

*Plerotes* Andersen, 1910

*Scotoonycteris* Matschie, 1894

*Casinycteris* Thomas, 1910

*Pteropus* Brisson, 1762

*Eidolon* Rafinesque, 1815

*Rousettus* Gray, 1821

*Lissonycteris* Andersen, 1912

*Myonycteris* Matschie, 1899

Macroglossinae

*Megaloglossus* Pagenstecher, 1885.

The arrangement of supraspecific taxa is in agreement with Hayman *et al.* (1971). Within polytypic genera species are dealt with in chronological order of description, with the exception of *Epomophorus* in which the morphologically allied species of the *gambianus*

group (*sensu* Andersen, 1912), *i.e.* *gambianus* (Ogilby, 1835), *labiatus* (Temminck, 1837), *angolensis* Gray, 1870 and *minor* Dobson, 1880 have been arranged accordingly.

Each species account consists of the same elements. In the synonymies no attempt at completeness is made. Unless of crucial or other relevant significance, references already listed by Andersen (1912) have been omitted. The listed references either contain sufficient details for an identification check or record material also examined by the present author. The synonymies are followed by an enumeration of material examined, arranged per country or island. For practical reasons country names are kept short; for biogeographical reasons important islands are listed independently.

Other details pertaining to this section have been given in the earlier paragraph on material. The diagnoses that follow are differential in the first place, including ranges and, if essential, ratios of some important measurements, and a short note summarizing geographic variation. Tables provide (known) measurement ranges per country. Distribution maps are given for all species. The mapping unit is the 'square' formed by whole and half degrees latitude and longitude. Localities of specimens identified by the author are shown as black dots, those collected from literature, collection registers and correspondence as open circles. In a paragraph on related species the most apparent differences with the phenotypically nearest species are summarized. The final section of each species account are the remarks, discussing the taxonomy of the species, its distribution in relation to environmental parameters such as vegetation types and altitude, and geographical variation.

All drawings have been made by the author, those of specimens with suitable drawing equipment, unless otherwise stated.

The larger part of the series will consist of the taxonomic section. Although the genus *Pteropus* has not been studied as extensively as the others (because of its Asian 'background', its absence on the African mainland, and its poor representation in the author's basic study collection in the Zoölogisch Museum in Amsterdam), it will

be included for the sake of completeness. The extralimital distributions of *Eidolon helvum* (Kerr, 1792) and *Rousettus aegyptiacus* (E. Geoffroy, 1810), will receive the same treatment as their African distributions. The series will be concluded by a part containing a key to African Megachiroptera, a general discussion, acknowledgements, and a gazetteer.

Throughout the series, the following abbreviations have been used.

alc. = alcohol; cbl = condylobasal length; fal(s) = forearm length(s); gsl(s) = greatest skull length(s); imm. = immature; iow = interorbital width; l M<sup>1</sup> = length of M<sup>1</sup>; m = mean; min = minimum; max = maximum; n = number; nr = near; rl = rostrum length; pl = palatal length; pow = postorbital width; W = weight; zw = zygomatic width.

AMNH = American Museum of Natural History, New York; AMS = Australian Museum, Sydney; BMNH = British Museum (Natural History), London; CAS = California Academy of Sciences, San Francisco; CMNH = Carnegie Museum of Natural History, Pittsburgh; FMNH = Field Museum of Natural History, Chicago; HZM = Harrison Zoological Museum, Sevenoaks; IRSN = Institut Royal des Sciences Naturelles de Belgique, Brussels; LACM = Los Angeles County Museum of Natural History, Los Angeles; LER = Laboratoire Emile Roubaud, Brazzaville; MAKB = Museum Alexander Koenig, Bonn; MHNC = Musée d'Histoire Naturelle, La Chaux-de-Fonds; MLZA = Museu e Laboratório Zoológico e Antropológico, Lisbon; MNCN = Museo Nacional de Ciencias Naturales, Madrid; MNHN = Muséum National d'Histoire Naturelle, Paris; MRAC = Musée Royal de l'Afrique Centrale, Tervuren; MVZ = Museum of Vertebrate Zoology, Berkeley; NHMI = Natural History Museum, University of Ife, Ife; NMBA = Naturhistorisches Museum, Basel; NMW = Naturhistorisches Museum, Wien; PCMB = Powell Cotton Museum, Birchington; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden; ROM = Royal Ontario Museum, Toronto; SMF = Senckenberg Museum, Frankfurt; SMNS = Staatliches Museum für Naturkunde, Stuttgart; SMTD = Staatliches Museum für Tierkunde, Dresden; UBRA = Laboratoire de Zoologie, Université de Brazzaville, Brazzaville; UMB = Uebersee-Museum, Bremen; USNM = United States National Museum, Washington; ZIZM = Zoologisches Institut und Zoologisches Museum, Hamburg; ZMA = Zoologisch Museum, Amsterdam; ZMB = Zoologisches Museum, Berlin; ZMUI = Zoology Museum, University of Ibadan, Ibadan; ZSBS = Zoologische Sammlung des Bayerischen Staates, München.

## RESULTS

In fig. 1 all the locality data of African Megachiroptera collected during the course of this study have been combined (except those from north of 20° N and part of the extralimital data of *Pteropus* Brisson, 1762 and *Rousettus aegyptiacus* (E. Geoffroy, 1810), which will be given with the accounts of the species). The picture reflects successful collecting activities in the dotted squares. All other conclusions one would like to draw from it are somewhat tentative.

Even the dots may represent a single collected specimen only and hence the fruit bats of a dotted square may still be as good as unknown. Of course, the enumerations of specimens examined, in the following species accounts, in combination with the gazetteer to be published in the last part, allow for more refined analyses for those interested in particular regions or squares. On the other hand, a white square does not necessarily imply that no fruit bat collecting has ever been carried out there. Such activities are not always successful, especially in Africa (see Findley *et al.*, 1983), and apart from that my data are, of course, not complete. Nevertheless, the map certainly indicates areas which have been intensively collected over the years, and gives some indirect proof of generally little or poorly collected regions.

## TAXONOMIC SECTION

Pteropodidae

Pteropodinae

### *Epomophorus* Bennett, 1836

*Epomophorus* Bennett, 1836: 149 (type species: *Epomophorus gambianus* (Ogilby, 1835)); Andersen, 1912: 514

The original description of the genus is very brief. Bennett observed that a "Pteropine Bat", obtained from the neighbourhood of the river Gambia, possessed shoulder tufts of white hairs, and a possible backward position of the wings. The latter character could be an artefact,

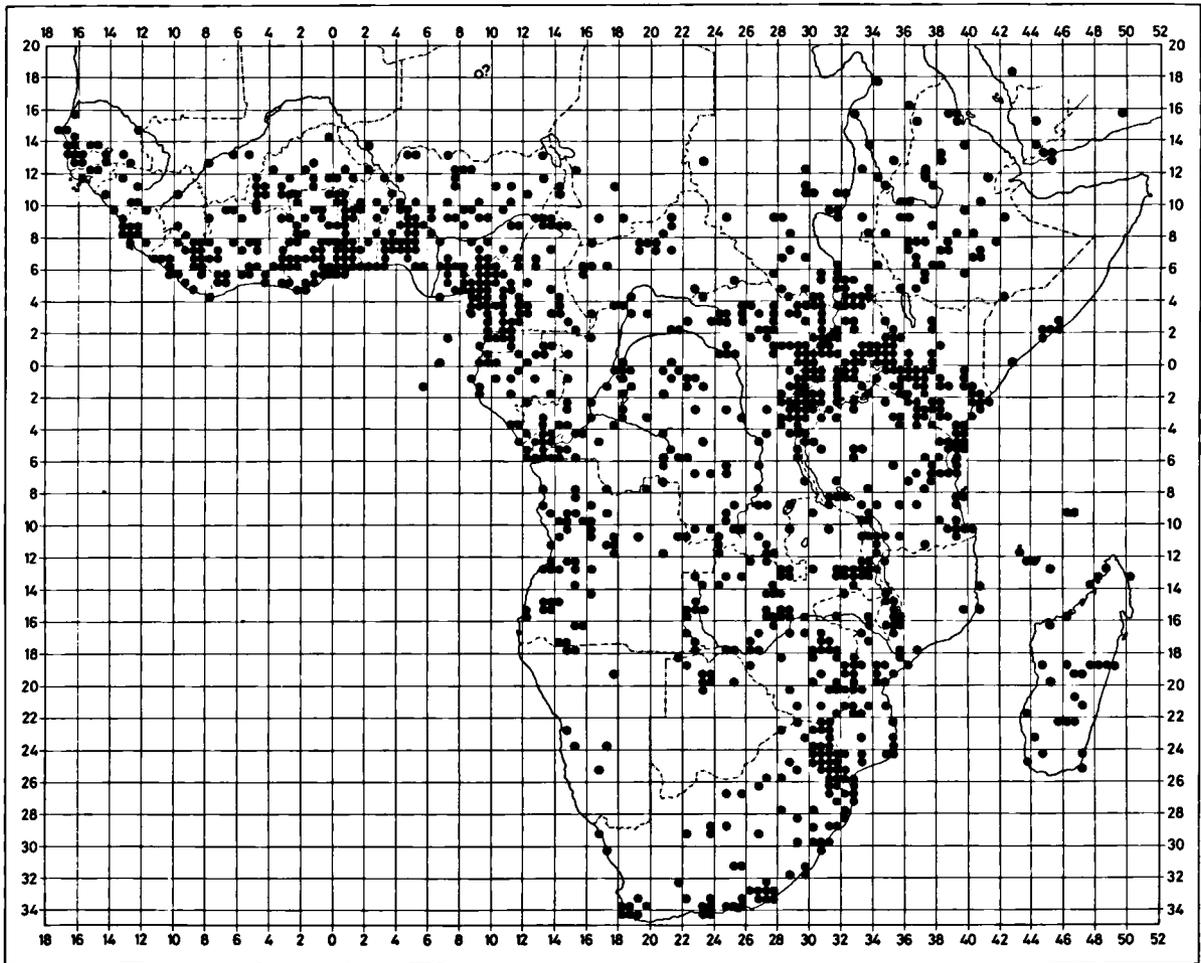


Fig. 1. Distribution of Megachiroptera in Africa south of 20° N and west of 52° E, based on specimens in collections and some few pertinent sightings.

liable to distortion to which the dry skin might have been subjected during preparation, and Bennett hesitated to propose the new genus name *Epomophorus* “definitively until he had an opportunity of examining a specimen preserved in spirit”. The dry specimen at his disposal formed part of a series which one year earlier had provided Ogilby (1835) with the basis for his description of *Pteropus gambianus* and *P. macrocephalus* (the ♀♀ and ♂♂ of *Epomophorus gambianus*, respectively). Ogilby drew attention to the atypical dentition, with only 3 upper and 5 lower cheek teeth, if compared to other fruit bats, which to him appeared to indicate a new subgenus or even genus. He did not describe

the skull and somehow failed to mention the white shoulder tufts in the ♂. In 1841 Bennett again drew attention to the tentative character of his diagnosis, and illustrated his account with a drawing of the whole animal and with one of its hair structure.

Only much later, in 1860, Tomes gave a first extensive description of the genus *Epomophorus*, known to him by *E. gambianus* (as *E. macrocephalus* and *E. gambianus*, the latter including *E. crypturus* Peters, 1852 — which name in Tomes’ work of 1860 covered specimens of *E. wahlbergi* (Sundevall, 1846) as well: Andersen, 1912: 519); *E. pusillus* Peters, 1867 (identified by Tomes as *E. schoensis* (Ruep-

pell, 1842) — a synonym of *E. labiatus* Temminck (1837)); and *E. franqueti* Tomes, 1860, on which Gray (1866) based the genus *Epomops*. Tomes diagnosed *Epomophorus* as having broad wings, expanded fingers, long thumbs half enclosed in the antibrachial membrane, the latter maintaining its full breadth from side of body to carpus; backward positioned wings, wing membranes from side of body and extending to base of toes and more or less translucent and strongly marked with lines and papillae; enlarged lips; small ears; rudimentary tail; moderate feet; short and unicoloured hairs, white tufts at bases of ear margins, white or yellow shoulder tufts in ♂♂ of “some of the species”; fragile skull with relatively long facial portion in large species and large cranial portion in small ones, a small and backward-directed supra-orbital process, zygoma without dorsal process, relatively large auditory bullae, a posteriorly but very slightly curved palate whose hinder margin has the appearance of a transverse ridge more or less raised from the level of the palate; a thin and weak mandible with narrow rami, a weak processus angularis, little modification for muscle attachment in the posterior part, and a processus coronoideus with an easily descending anterior side; 3 upper and 5 lower cheek teeth, P<sup>2</sup> (= P<sup>3</sup>) and P<sub>2</sub> (= P<sub>3</sub>) prominent as canines (a very small P<sup>1</sup> (= P<sup>2</sup>) would possibly be present in immature specimens and be lost at a more advanced stage), and small and feebly developed molars.

Dobson (1878) included *Hypsignathus* Allen, 1861 as a subgenus and *Epomops* as a synonym of *Epomophorus*, and based his concept of the latter on *E. gambianus* (as *macrocephalus* and *gambianus*); *E. labiatus*, the type of which appeared to him an example of an immature individual of a small variety of *E. gambianus*; *Epomops franqueti* (as *Epomophorus franqueti* and *E. comptus* Allen, 1861 — a synonym of *Epomops franqueti*); *E. pusillus*; and *E. wahlbergi* (identified as *E. labiatus*; see Andersen, 1912: 519). He mentioned only a few characters that had not or incompletely been described by Tomes (1860): second finger with claw, third metacarpal length equal to or shorter than second finger,

wing membrane from base or back of second toe, skull not as vaulted as in other fruit bats, bony palate much vaulted behind, premaxillary bones united in front.

Miller (1907) treated *Epomops*, *Micropteropus* Matschie, 1899, *Nanonycteris* Matschie, 1899 as synonyms, without stating his reasons. The species Miller assigned to *Epomophorus* were *gambianus* (as *gambianus* and *macrocephalus*), *crypturus*, *labiatus*, *minor*, *pusillus*, *wahlbergi* (as *wahlbergi* and *neumanni* Matschie, 1899), *Epomops franqueti* (as *franqueti* and *comptus*), *Epomops buettikoferi* (Matschie, 1899) (as *franqueti*, from Liberia), and *Epomops dobsonii* Bocage, 1899. Miller compared *Epomophorus* mainly with *Pteropus* Brisson, 1762 and *Cynopterus* Cuvier, 1825. Important characters put forward by him were: skull broad and flattened, depth of braincase usually little more than half its width, braincase never strongly deflected, occipital region slightly deflected and not tubular, alveolar line projected backwards usually passing through auditory bulla and occipital condyle; premaxillaries barely united anteriorly; canines small, weak, without anterior furrow, secondary cusps or ridges; premolars and molars smaller than in *Pteropus*, with relatively smaller cusps and ridges; spaces between C<sup>1</sup> and P<sup>3</sup> and between P<sup>3</sup> and P<sup>4</sup> relatively larger than in *Pteropus*.

Andersen, in his general account of plastic characters of Megachiroptera (1912: xix-xlvii), emphasized for the epomophorine section as a whole that it is the only section of fruit bats in which more essential modifications of the system of palatal ridges occur: “...in that section, and in that only, nearly every genus has its own peculiar form and arrangement of the palate ridges, and in some cases (*Epomops*, *Epomophorus*) even the species may be identified from the characters of their soft palate...”. (The last remark of course also applies to a number of species of other epomophorine genera.) As another special phenomenon Andersen mentioned the unusually high development in many genera of secondary sexual differences: with in ♂♂ a larger average body and skull size, a stronger lengthening of

the rostrum (with the peculiar enlargement of the rostrum and large cutaneous folds in *Hypsignathus* H. Allen, 1861), brighter fur colours, shoulder pouches and tufts in most genera, and in some genera (*Epomops*, *Hypsignathus*, *Epomophorus*) pharyngeal air-sacs and enlargement of the larynx.

Andersen's description of the genus *Epomophorus* (1912: 514-517) includes the more useful of all characters put forward by his predecessors, extended by his own observations. It may be summarized as follows: skull with long and narrow rostrum and palate; ascending branches of premaxillae of equal breadth throughout; dental formula with 3 upper and 5 lower cheek teeth; palate deeply depressed in front of the high and prominent palation border; six thick and prominent palate ridges, the four anterior ridges undivided (second to fourth often notched in the middle), fifth and sixth distinctly separated at middle; characteristic morphology of hyoid bones and related muscles; mesopatagium with 11-33 vertical fasciae; metacarpals, and phalanges of digits 3, 4 and 5, relatively short (if compared to *Epomops*); adult ♂♂ with shoulder pouches and erectable hair tufts; ♂♂ with a small pharyngeal sac; ♂♂ of all species except *labiatus* and *minor* averaging considerably larger than ♀♀.

Some of Andersen's diagnostic remarks need modification. The rostrum and palate are particularly long and narrow in the larger species, especially in the ♂♂, except *wahlbergi*, and much less so in the ♀♀ of those species and in both sexes of *wahlbergi*, *minor* and *grandis* (see table 1). The measure of depression of the postdental palate is not equal in all species, and strongest in the larger ones (*gambianus*, *angolensis*, *labiatus* and *wahlbergi*). In the smaller species *minor* and *grandis* it approaches *Micropteropus* Matschie, 1899. The second to fourth palatal ridges are narrowly divided in adult specimens of one species, *E. grandis*. In *labiatus* and *minor* ♂♂ average larger than ♀♀ although sexual size dimorphism becomes less significant with smaller overall size. (Of *grandis*

too few specimens are known yet for an assessment of possible size dimorphism.)

Within the genus, Andersen (1912: 520) distinguished two groups: the *wahlbergi* group characterized by the possession of only one postdental palatal ridge and of 22-33 vertical fasciae of the mesopatagium, with as only species *E. wahlbergi*; and the *gambianus* group, with two postdental palatal ridges and 11-24 vertical fasciae, and divided into two subgroups, one with the fourth palatal ridge midway between the third and the fifth (*gambianus*, *crypturus*, *anurus*, *labiatus* and *minor*) and one with the fourth ridge much nearer the third than the fifth (*angolensis* and *pousarguesi*). These subdivisions, which possibly reflect phylogenetic relationships, also need some adjustments. In the smaller specimens of *labiatus* and *minor* (and in *grandis*) the fifth palatal ridge is not completely postdental but usually on level with the posterior sides of the upper molars (M<sup>1</sup>) — as in certain specimens of *wahlbergi* the fifth ridge may not be entirely interdental but partly postdental. Andersen's concept of the palatal ridge pattern in *pousarguesi* was wrong; it is as in typical *gambianus* (see Bergmans, 1978) and should be grouped with that species. In this paper, it is regarded as a subspecies of *gambianus*, as is *crypturus*, while *anurus* is synonymized with *labiatus*. The description of *grandis* has been published long after Andersen's work, and adds to the variation within the genus. It shows similarities to the broad-skulled *wahlbergi*, but should probably form a group on its own.

Table 1 gives gsls and a number of relative skull measurements for all species and subspecies of *Epomophorus* presently regarded as valid. The species *minor*, *labiatus* and *gambianus* with its differently sized subspecies form a corresponding series. Of the other three, *grandis* has a relatively large zygomatic width and a relatively short palate, *angolensis* has a relatively long rostrum and short palate, and *wahlbergi* has a relatively large zygomatic width and a relatively short rostrum and palate.

In the following species accounts the order is

Table 1. Relative skull measurements in species of *Epomophorus* Bennett, 1836; minimum and maximum values and number of measurements.

	<i>grandis</i>	<i>minor</i>	<i>labiatus</i>	<i>gambianus</i> <i>crypturus</i>	<i>gambianus</i> <i>gambianus</i>	<i>gambianus</i> <i>pousarguesi</i>	<i>angolensis</i>	<i>wahlbergi</i>
♂♂ gsl	35.4-36.7 n = 2	33.7-41.5 n = 96	40.2-51.0 n = 69	51.8-55.7 n = 47	53.3-62.5 n = 203	63.6 n = 1	56.4-60.0 n = 2	44.4-57.3 n = 122
rl as % of gsl	37.0-37.3 n = 2	36.5-41.0 n = 50	39.6-43.3 n = 35	43.7-45.4 n = 10	43.6-47.2 n = 19	46.7 n = 1	47.0-48.0 n = 2	37.7-42.8 n = 16
pl as % of gsl	56.9-57.1 n = 2	57.1-62.5 n = 50	60.1-64.3 n = 29	63.0-65.3 n = 10	65.2-67.7 n = 16	67.6 n = 1	62.3-62.6 n = 2	54.6-60.7 n = 14
pl as % of M <sup>1</sup> -M <sup>1</sup>	180-185 n = 2	191-239 n = 47	211-250 n = 25	238-264 n = 10	251-285 n = 15	257.5 n = 1	225-243 n = 3	201-216 n = 14
zw as % of gsl	56.7-61.0 n = 2	52.0-59.2 n = 71	49.0-56.0 n = 36	46.8-51.7 n = 21	45.5-50.3 n = 30	49.1 n = 1	45.7 n = 1	50.6-57.7 n = 52
C <sup>1</sup> -C <sup>1</sup> as % of gsl	19.1-19.5 n = 2	18.0-21.8 n = 44	17.4-20.8 n = 29	17.8-20.0 n = 16	16.7-18.3 n = 11	17.8 n = 1	16.7-16.7 n = 2	18.5-21.2 n = 13
M <sup>1</sup> -M <sup>1</sup> as % of gsl	30.8-31.6 n = 2	25.8-30.5 n = 47	25.7-29.0 n = 26	24.7-27.4 n = 17	24.0-26.5 n = 14	26.3 n = 1	≤25.7-27.5 n = 2	26.2-29.8 n = 14
♀♀ gsl	36.4 n = 1	32.0-39.5 n = 59	36.8-44.9 n = 62	44.0-48.8 n = 34	46.1-55.4 n = 269	54.4-56.8 n = 3	49.6- ±50.6 n = 3	41.0-49.3 n = 155
rl as % of gsl	36.5 n = 1	35.1-39.1 n = 32	38.0-41.5 n = 37	41.1-42.7 n = 10	41.5-45.6 n = 25	44.4-45.0 n = 2	44.5- ±45.3 n = 3	37.2-41.3 n = 37
pl as % of gsl	55.5 n = 1	57.0-62.7 n = 31	57.6-63.0 n = 30	60.7-64.0 n = 10	63.1-66.9 n = 23	63.8-66.4 n = 3	59.7-60.7 n = 4	57.4-62.4 n = 33
pl as % of M <sup>1</sup> -M <sup>1</sup>	176 n = 1	184-228 n = 29	195-250 n = 31	214-248 n = 12	221-262 n = 19	238-250 n = 3	215-240 n = 4	184-210 n = 28
zw as % of gsl	59.9 n = 1	53.9-60.9 n = 47	51.2-57.1 n = 35	50.9-55.8 n = 23	48.3-53.9 n = 35	47.7-50.5 n = 3	50.5 n = 1	52.3-59.6 n = 70
C <sup>1</sup> -C <sup>1</sup> as % of gsl	20.6 n = 1	17.2-23.5 n = 27	17.7-21.6 n = 30	18.3-20.7 n = 16	17.3-19.0 n = 13	17.5-17.8 n = 3	±16.6-17.9 n = 3	18.8-22.6 n = 32
M <sup>1</sup> -M <sup>1</sup> as % of gsl	31.6 n = 1	27.0-31.2 n = 31	26.5-30.0 n = 25	25.4-29.5 n = 16	24.8-29.2 n = 17	25.8-27.4 n = 3	±25.3-28.2 n = 3	28.1-32.1 n = 30

according to these groupings: first comes the *gambianus* group, then *angolensis*, *wahlbergi* and *grandis*.

### *Epomophorus gambianus* (Ogilby, 1835)

*Pteropus gambianus* Ogilby, 1835: 100 (type locality: Gambia).

*Epomophorus gambianus*; Andersen, 1912: 538-542.

*Epomophorus crypturus* Peters, 1852: 26 (type locality: Tete); Andersen, 1912: 535-537. New synonymy.

*Epomophorus pousarguesi* Trouessart, 1904: 55 (type locality: Grande Brousse between Yabanda and Mpoko); Andersen, 1912: 543; Bergmans, 1978b: 683. New synonymy.

*Epomophorus reii* Aellen, 1950: 559 (type locality: Rei Bouba). New synonymy.

(Further references under the subspecies.)

**Diagnosis:** The largest, typical species of the genus, with a relatively long rostrum and palate, a relatively narrow zygomatic width, the fourth palatal ridge halfway between the third

and fifth, and two postdental ridges. Measurement ranges and ratios for the three subspecies combined:

fal	in ♂♂	80-100,
	in ♀♀	75-95;
gsl	in ♂♂	51-64,
	in ♀♀	44-57;
rl	in ♂♂	43.6-47.2% of gsl,
	in ♀♀	41.1-45.6% of gsl;
pl	in ♂♂	63.0-67.7% of gsl,
	in ♀♀	60.7-66.9% of gsl;
zw	in ♂♂	46.8-51.7% of gsl,
	in ♀♀	47.7-55.8% of gsl.

*Distribution:* Fig. 2.

***Epomophorus gambianus gambianus* (Ogilby, 1835)**

*Pteropus gambianus* Ogilby, 1835: 100 (type locality: Gambia).

*Epomophorus gambianus*; Andersen, 1912: 538; O. Thomas, 1912: 270; Schwarz, 1915: 59; Braestrup, 1935: 86; Monard, 1939: 52; Rousselot, 1950: 233; Booth, 1959: 28; Rosevear, 1965: 94 (in part: not the specimens mentioned from the Congolese Republic, Northern Rhodesia and Gaboon); Van Orshoven *et al.*, 1968: 182; Hayman *et al.*, 1971: 7 (in part: not the specimens from Katanga, Zambia and Rhodesia); Dorst *et al.*, 1972: 396; Eisentraut, 1973:356; Ayensu, 1974: 702; Largen *et al.*, 1974: 227; Eisentraut, 1975: 78; Jeffrey, 1975: 955; Koopman, 1975: 364; Poché, 1975: 41; Happold *et al.*, 1978: 74; Kock, 1978: 119;

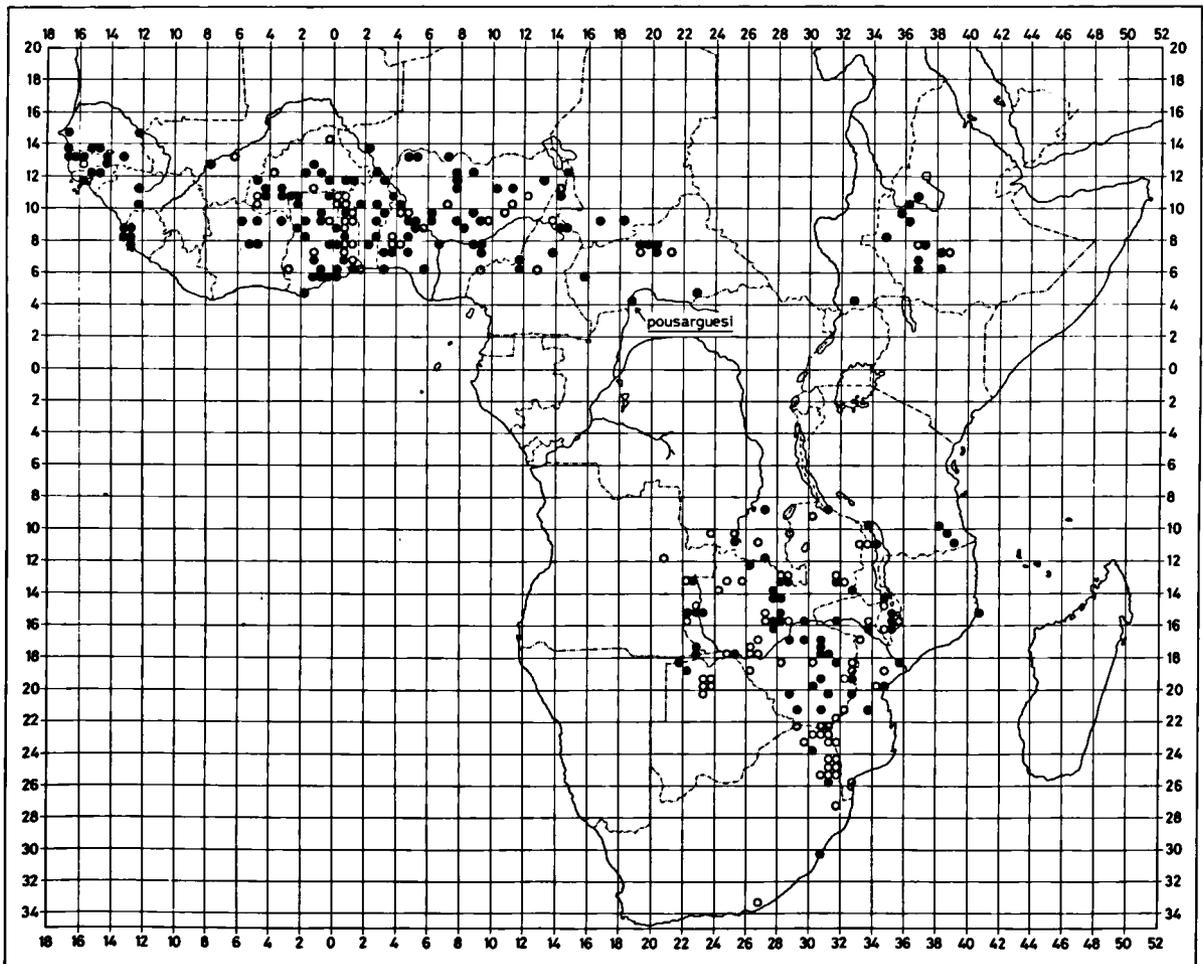


Fig. 2. Distribution of *Epomophorus gambianus* (Ogilby, 1835): north of 4° N, the nominate subspecies; at Bangui *E. g. pousarguesi* Trouessart, 1904; south of 8° S, *E. g. crypturus* Peters, 1852. Black dots: squares from which material has been identified by the author. Open circles: records from literature, museum registers, and correspondence.

Koopman *et al.*, 1978: 2; Robbins, 1980: 85; Marshall *et al.*, 1982; Schlitter *et al.*, 1982: 138 (in part: the specimen quoted from De Pousargues is in fact the holotype of *Epomophorus pousarguesi* Trouessart, 1904); Koch-Weser, 1984: 261.

*Epomophorus reii* Aellen, 1950: 559 (type locality: Rei Bouba); Aellen, 1952: 35; Baud, 1977: 203.

? *Epomophorus anurus* (not of Heuglin, 1864); Thomas *et al.*, 1921: 1; Rosevear, 1965: 100; Happold, 1987: 43; Adam *et al.*, 1972: 59.

*Epomophorus* sp.; Hill *et al.*, 1971: 29.

### Material examined

BENIN. Bimbereke: 4 ♂♂, 2 imm. ♂♂, 3 ♀♀, 4 imm. ♀♀, 19-I-1968, J. W. LeDuc (USNM 421183-95), 2 ♂♂, 2 imm. ♂♂, 2 ♀♀, 20-I-1968, C. B. Robbins (USNM 421196-201). Diho: 1 ♀, 2 imm. ♀♀, 14- and 16-I-1968, J. W. LeDuc, C. B. Robbins (USNM 421180-82). Guéné: 5 ♂♂, 6 imm. ♂♂, 12 ♀♀, 7 imm. ♀♀, 13-I-1968, J. W. LeDuc/C. B. Robbins (USNM 421202/31). Kouande: 3 ♂♂, 7 ♀♀, 26/27-IV-1968, J. W. LeDuc/C. B. Robbins (USNM 438844/53). Nikki: 3 ♂♂, 1 ♀, 19- and 23-II-1968, C. B. Robbins (USNM 421238/41). Parakou: 1 ♂, 3 imm. ♂♂, 7 ♀♀, 27-, 28- and 29-II-1968, J. W. LeDuc/C. B. Robbins (USNM 421242/52); 1 imm. ♂, *alc.*, 1-XI-1986, I. van Woersem (ZMA 23.121). Segbana: 1 ♂, 3 imm. ♂♂, 1 ♀, 1 imm. ♀, 13-II-1968, C. B. Robbins (USNM 421232/37). Zizonkamé: 1 ♀, 18-IV-1968, J. W. LeDuc (USNM 438843).

BURKINA FASO. Arly: 1 imm. ♂, 1 imm. ♀, 13-XI-1968, R. E. Vaden (USNM 450473; ZMA 16.531). Bobo Dioulasso: 1 specimen, *alc.*, V-1966, Hamon (MNHN). Boussouma: 1 imm. ♂, 1 ♀, 1 imm. ♀, 12- and 13-II-1969, R. E. Vaden (USNM 452716/18). Cella: 2 ♂♂, 1 ♀, 15-III-1969, R. E. Vaden (USNM 452719/23). Djipologo: 2 ♀♀, 9-VII-1969, R. E. Vaden (USNM 467807/8). Fo: 9 ♂♂, 1 imm. ♂, 8 ♀♀, 2 imm. ♀♀, 11- and 14-VI-1969, R. E. Vaden (USNM 467821/22, -24, -27/28, -30/31, -49, -51, -53, -57/8, -61, -63, -65, -68/71, 467911). Founzan: 8 ♂♂, 5 ♀♀, 13/17-V-1969, R. E. Vaden (USNM 454444, -46/50, -52/53, -55, -59/60, -62, -64). Koutoura: 2 ♂♂, 8 ♀♀, 23- and 25-VI-1969, R. E. Vaden (USNM 467765/72, -74, -76). Natiaboani: 4 ♂♂, 14-XII-1968, R. E. Vaden (USNM 450474/6; ZMA 16.530). Nazinga: 1 ♀, *alc.*, V-1988, M. van der Wal (ZMA 23.535). Ouagadougou: 6 ♂♂, 2 imm. ♂♂, 2 ♀♀, 9 imm. ♀♀, 15- and 16-I-1969, 27-IV-1969, R. E. Vaden (USNM 452692/5, -697/704, 06/08, -13; 454436, -38/39). Ougarou: 3 ♂♂, 10 ♀♀, 1 imm. ♀, 23/25-III-1969, R. E. Vaden (USNM 452724, -26/30, -32/33, -35/39, -41). Sideradougou: 13 ♂♂, 4 ♀♀, 30-VI/1-VII-1969, R. E. Vaden (USNM 467781, -83, -85/90, -92/95, -97, -99, 467803/04, 06).

(Banfora, Dedougou, Diomga, nr Nobéré, Oradara, Pigahiri, Po National Park.)

CAMEROON. 30 km ESE of Banyo: 4 ♂♂, 1 imm. ♂, 5 ♀♀, 4/5-II-1970, R. L. Peterson (ROM 55913/22). 4 km N of Mayo Darle: 3 ♂♂, 4 ♀♀, 4-II-1970, R. L. Peterson (ROM 55901/05, -13/14). Mayo Vaimba: 1 imm. ♂, *alc.*, 4-II-1986, A. P. M. van der Zon (ZMA 23.067); Meng River, 6 km N of Tibati: 1 ♂, 2 imm. ♂♂, 1 ♀, 6 imm. ♀♀, 7-II-1970, R. L. Peterson (ROM 55997/56001, -04/07, 56068). Meng River, 6 km NW of Tibati: 1 ♂, 1 ♀, 3 imm. ♀♀, 7/8-II-1970, R. L. Peterson (ROM 55996, 56062/63, -69/70). 14 km S of Ngaoundere: 1 imm. ♂, 2 ♀♀, 6/7-IV-1972, L. W. Robbins (AMNH 241006, -07/08). Rei Bouba: 1 ♀, 1 imm. ♀, 13-IX-1947. "MSS Cameroun" (MNHC 32-8-970: holotype *Epomophorus reii* Aellen, 1950; MNHC 32-8-969: paratype of same). Tibati: 4 ♂♂, 1 imm. ♂, 2 ♀♀, 2 imm ♀♀, 20-V/13-VI-1947 (MHNC 32-8-953/61).

(Maroua, Mora, Pitoa.)

CENTRAL AFRICAN REPUBLIC. Bamingui: 1 imm. ♀, 18-VI-1979, C. A. Spinage (BMNH 79.2028); 1 imm. ♂, 7-IV-1980, C. A. Spinage (BMNH 81.228). Bangassou: 1 imm. ♀, 27-XII-1974, L. W. Robbins (CNHM 40972). Buar: 1 ♀, no date, Tessmann (ZMB 31489). Kaja Nze: 1 imm. ♂, 27-XII-1981, C. A. Spinage (BMNH 83.285). Njia: 1 ♂, 1912-1913, Houy (ZMB 20854).

(Badingua, Bamingui-Bangoran National Park, Bouala, Bozoum (?), Crampel, Koumbala Camp, Ndélé.)

CHAD. Guidari: 4 ♂♂, 2 imm. ♂♂, 8 ♀♀, 1 imm. ♀, 2/3-VI-1952, T. D. Carter/W. Weber (AMNH 165835/39, -43/46, -48/50; USNM 301932/34).

(N'Djamena.)

ETHIOPIA. 10 km from Agaro, road to Jima: 1 ♂, 2 imm. ♂♂, *alc.*, skulls, 11- and 14-VI-1968 (MNHN 1972-478). Azir River mouth: 1 imm. ♀, 21-VIII-1968, P. Morris (BMNH 70.399). Bulcha: 2 imm. ♂♂, 29-I-1976, 1 ♂, *alc.*, 4-II-1976, G. Nikolaus (SMNS 29.855/57); 1 ♂, 1 imm. ♂, 5 ♀♀, *alc.*, skulls of adults, J. S. Ash (USNM 497495, -99, 497502/04, -09, -13). Bulcha Forest: 1 ♂, 2 ♀♀, *alc.*, 4/13-VI-1971, J. S. Ash (BMNH 72.502/04). Didessa River: 1 ♂, III-1970, M. J. Lagen (*p.*) (one of series BMNH 71.2412/17). Djala: 1 imm. ♀, 1-II-1901, Neumann (ZMB). Djiren, Jima: 1 ♀, 1-IV-1901, Neumann (ZMB). Doki River: 1 ♂, skin, 14-IV-1976, G. Nikolaus (SMNS 29879). Gambela: 2 ♂♂, 2 ♀♀, *alc.*, skulls, 1972/73, J. S. Ash (USNM 497514/15, 520890/01). 15 km E of Gambela: 1 ♂, 1 imm. ♀, *alc.*, 19/20-II-1976, G. Nikolaus (SMNS 29857/58). Gimbi: 1 imm. ♀, *alc.*, 26-IX-1971 (MNHN). Manera Forest: 1 ♂, *alc.*, skull, 1964, Andral (MNHN).

(Domkam River, Lake Awasa (east shore), Sidamo.)

GAMBIA. Basse: 1 ♀, A. P. Buxton (BMNH 49.458). 8 miles W of Bathurst: 2 ♀♀, 2 imm. ♀♀, 13/15-I-1966, R. M. Davis (USNM 377553/56). Brikama Bar: 1 ♀, 1 imm. ♀, 26-VII-1977, I. P. Brownlow (HZM 8.8989, 24.9005). "Gambia": 1 ♂, skin, D. Rendall (BMNH 7.1.1.232); 4 ♀♀, 1 imm. ♀, D. Rendall (BMNH 7.1.1.233: holotype specimen of *Pteropus gambianus* Ogilby,

1835; BMNH 74a-c/124b-d and 7.1.1.231: paratypes of same). Keneba: 1 imm. ♀, 13-VII-1977, I. P. Brownlow (HZM 16.8997). 10 miles SE of Kuntaur: 1 ♀, skin (BMNH 49.459). Kudang: 3 ♂♂, 2 imm. ♂♂, 16-II-1966, R. M. Davis (USNM 377557/61). Toniataba: 1 ♀, 1 imm. ♀, 10-VI-1966, R. M. Davis (USNM 379355/56). Walikunda: 5 ♂♂, 4 imm. ♂♂, 5 ♀♀, 2 imm. ♀♀, 25/26-VII-1977, I. P. Brownlow (HZM 6.8987, 7.8988, 9.8990/15.8996, 17.8998/23.9004).

GHANA. Accra: 1 ♂, alc., skull, Reichenow (ZMB 4784). 9 miles NE of Accra: 2 ♂♂, 17-IX-1971, L. W. Robbins (AMNH 241010/11). Achimota: 3 ♂♂, 5 ♀♀, 18-X/14-XI-1967, J. C. Geest/J. W. LeDuc/C. B. Robbins/H. W. Setzer (USNM 411451, -53, -56, -60, -62, -64/66). Aiyikuma: 7 ♂♂, 10 imm. ♂♂, 16 ♀♀, 15 imm. ♀♀, 11-XI-1967, J. C. Geest/H. W. Setzer (USNM 411239/86). Bangwon: 1 ♀, 13-III-1968, J. C. Geest (USNM 414730). Bator: 1 imm. ♂, 16-VII-1967, B. J. Hayward (USNM 411489). Bimbilla: 1 ♀, alc., skull, 20-XII-1900, Mischlich (ZMB 53896). 15 miles S of Bimbilla: 3 ♂♂, 2 ♀♀, 3/4-IX-1971, L. W. Robbins (AMNH 239353/55, -60/61). Doyum: 2 ♂♂, 2 ♀♀, 16-XI-1967, H. W. Setzer (USNM 411483/84, -86, -88). Gambaga: 8 ♀♀, 9/11-V-1968, J. C. Geest (USNM 424708/11, -15/16, -18/19). Ho: 1 ♂, 1 ♀, alc., skulls, ♂: 17-VI-1904, F. Schröder (ZMB 54195, 54592). 7 miles NE of Kade: 2 imm. ♂♂, 4 ♀♀, 1 imm. ♀, 3-VIII/29-IX-1965, C. J. Ralph (ROM 36624/26, -29/32). Keta: 2 ♂♂, 4 ♀♀, 31-VIII-1967, B. J. Hayward (USNM 411490, -93, -95, -97/99). Kete Krachi: 1 ♂, 1 imm. ♂, 2 ♀♀, alc., skulls, 20-VI-1899, Graf Zech (ZMB 53875, 54361, -65, 54518); 1 ♂, skull, Graf Zech (ZMB 67065). Legon: 5 ♂♂, 3 ♀♀, 4 imm. ♀♀, 22-VII/6-IX-1965, C. J. Ralph (ROM 35804/09, 36620/23, -27); 47 ♂♂, 47 ♀♀, 20-VII/9-XII-1967, J. C. Geest/B. J. Hayward/J. W. LeDuc/C. B. Robbins/H. W. Setzer (USNM 411287/88, -92; 411300/02, -04/08, -12, -17/18, -20, -22, -25, -29, -35, -37/38, -42/45, -48/49, -52, -55, -57/58, -65/66, -69, -74, -81/83, -85/87, -89, -92/94; 411400/02, -04, -08/09, -12/13, -15/17, -21, -23, -25, -27/28, -30/32, -36, -74, -76; 413808/09, -15, -19, -25/27, -33/34, -38/40, -42, -46/47, -53/54, -57, -60, -64/66, -69, -72/74, -85); 10 ♂♂, 6 ♀♀, 23-IX/7-X-1968, L. W. Robbins/R. E. Vaden (USNM 439846/48), -92, -94, -97/98, 439900/02, -04/06, -08, -10, -12). Naboga: 2 ♂♂, 1 ♀, 15/23-IV-1968, J. C. Geest (USNM 424692/93, -95; skin 424692 mismatched). Odomi Jongo: 2 ♂♂, 1 ♀, 18/21-VI-1968, J. C. Geest (USNM 424737/39). Parisi: 1 ♂, 4 ♀♀, 29-II/1-III-1968, J. C. Geest (USNM 414698, 414701, -04/06). Pulima: 8 ♂♂, 12 ♀♀, 5/7-III-1968, J. C. Geest (USNM 414707, -09, -11/13, -16, -18/19, -22, -24/26, -28/29, -33/37, -39). Sakpa: 2 ♀♀, 17-III-1968, J. C. Geest (USNM 414731/32). Shishe: 4 ♂♂, 3 ♀♀, 6-V-1968, J. C. Geest (USNM 424700, -02, -04/06). Tamale: 4 ♂♂, 1 ♀, 3 imm. ♀♀, 10-V-1973, P. Neugebauer (NMW 15951/58); 16 adult and 6 imm. skulls, 10-V-1973, P. Neugebauer (NMW 15965/70, -72/74, -78/80, ZMA 18.129/38).

Wulasi: 3 ♂♂, 6 ♀♀, 16/20-V-1968, J. C. Geest (USNM 424722/24, -27, -29, -32, -34/36).

(Aburi, Ejura, Juaso-Kuwasi, Kintampo, Larteh Junction, Lawra, Mole Game Reserve, Nuango Road, Nungua, Oda, Sekondi, Sefwi Wiawso, Shai Hills Game Reserve.)

GUINEA. Kankasili: 1 ♀, 15-XI-1966/1-III-1967, J. van Orshoven (ZMA 10.743). Pita area: 1 ♂, alc., 27-VII-1910, Le Pobéguin (MNHN 1911-1718).

GUINEA-BISSAU. Bolama: 1 ♂, mounted, 1883, D. da Costa (MLZA T118; probable holotype of *Epomophorus guineensis* Bocage, 1898). Contubo-el: 1 ♂, 2 ♀♀, 2 imm. ♀♀, 2/3-I-1938, A. Monard (MHNC 32-8-964/68). Mansoa: 1 ♀, 12-XII-1937, A. Monard (MHNC 32-8-963). Sama: 1 ♂, skin, 20-I-1938, A. Monard (MHNC 32-8-962).

IVORY COAST. Bouaké: 3 ♂♂, 12/13-II-1965, D. Parelus (FMNH 99035/37). Bouna: 2 ♂♂, 4 ♀♀, 2/5-VII-1969, T. J. McIntyre/L. W. Robbins (USNM 467835, -37, -41/42, -44/45). ? Bowako: 1 imm. ♀, 29-I-1965, D. Parelus (FMNH 99034). Fetekro: 3 imm. specimens, 16-VII-1969, T. J. McIntyre (USNM 467846/48). Kong: 1 ♀, 17-V-1969, J. W. LeDuc (USNM 454435). Korhogo: 1 imm. ♀, 18-VI-1964, D. Parelus (FMNH 99031); 1 ♂, 28-VIII-1968, M. Ailanjian (LACM 51301). 8 km S of Korhogo: 1 ♂, 30-VIII-1968, M. Ailanjian (LACM).

(Wango-Fitini.)

LIBERIA.

(Kpeable (?))

MALI. Bamako: 4 ♂♂, 3 ♀♀, 2 imm. specimens, II-1936, P. Rode (MNHN 1936-1492/99, -1500); 1 imm. ♂, 1 imm. ♀, 1958, P. Malzy (MNHN 1960-547/48); 1 imm. ♂, 1959, P. Malzy (MNHN 1966-175). Sotuba: 5 ♂♂, 3 imm. ♂♂, 12 ♀♀, 4 imm. ♀♀, 6-III/11-IV-1934, F. C. Wonder (FMNH 42209/17, 42224/25, -27/30, W.713-X, W.714-X, W.716-X, W.717-X, W.768-X, W.770-X, W.771-X, W.772-X, W.774-X). "Sotuba and Moribadougou": 1 ♂, 7 ♀♀, 1 imm. ♀, alc., III/IV-1934, F. C. Wonder (FMNH 42232/40).

(Ségou.)

NIGER. Niamey: 1 ♀, 3-XI-1965, (L?) Blancou (MNHN 1970-422); 2 ♀♀, 1 specimen, alc., no date, (L?) Blancou (MNHN). Park W.: 1 imm. ♀, 16-III-1977, S. Kosten (ZMA 19.182).

(Maradi.)

NIGERIA. Abeokuta: 1 ♀, 10-III-1960 (HZM 38.5234); 1 imm. ♀, 14-III-1960, G. Brown (HZM 2.3174). Afon: 3 ♂♂, 9 ♀♀, 4 imm. ♀♀, 9/10-V-1967, J. C. Geest (USNM 402412/18, -21/29). Arusua: 3 imm. ♂♂, 1 ♀, 8/9-VIII-1976, W. Bergmans (ZMA 18.589/92). Bacita: 3 ♀♀, 1 imm. ♀, 9-XI/21-XII-1973, G. F. Mees (RMNH 23623/24, -45, -51). Darazo: 1 imm. ♀, 25-III-1949, D. R. Rosevear, field number 467/49 (NHMI). Darazo Forest Reserve: 1 ♂, 1 imm. ♀, 26-III/1-IV-1949, D. R. Rosevear, field numbers 488/49, 469/49 (NHMI). Ejigbo: 1 ♂, 18-XII-1972, D. C. D. Happold, field number 1608

(BMNH). Felele: 1 ♂, 4 ♀♀, 17/19-V-1967, J. C. Geest (USNM 402441, -44/47). Fika: 1 ♀, 23-V-1966, H. J. Herbert (USNM 378766). Ibadan: 1 ♀, 1 imm. ♀, 13-X/27-XI-1947, D. R. Rosevear, field numbers 44/47, 93/47 (NHMI; BMNH 50.172); 1 ♀, 16-XI-1959, F. C. Sibley (AMNH 204294); 1 imm. ♀, alc., 24-XII-1960, F. C. Sibley (BMNH 62.444); 3 ♂♂, 3 ♀♀, 28-IV-1966/2-II-1967, H. J. Herbert/S. B. Akpan/H. W. Setzer (USNM 378770, 402329/30, -38, -42); 2 ♀♀, 26-V- and 15-X-1967, S. B. Akpan (USNM 402449, 483175); 1 ♂, 1 ♀, 12/15-VI-1965, J. I. Menzies (FMNH 99076, -78); 1 ♂, 1 ♀, alc., 10/28-III-1972, D. C. D. Happold, field numbers 1503, 1542 (BMNH); 2 ♂♂, alc., 1/5-V-1975, D. C. D. Happold, field numbers 1-78, 1-86 (BMNH); 4 ♂♂, 4 imm. ♂♂, 6 ♀♀, 3 imm. ♀♀, before or in 1976, ?R. H. Parker/J. Fagbohunmi (ZMUI 17, 27, 27, 35/38, 41, 126/33, 155); 1 imm. ♂, 2 ♀♀, 4/8-VIII-1976, W. Bergmans (ZMA 18.596/98). Ife: 3 ♀♀, frozen, 1975/76, G. Oderhowho (NHMI). Igbo-Ora: 1 ♂, 1 ♀, 21/23-X-1966, J. C. Geest/H. W. Setzer (USNM 402344, -48). Ikoyi: 1 ♂, 3 imm. ♀♀, 3-VII-1975/11-V-1976, I. Brownlow (HZM 2.8205, 3.8204, 4.8347, 5.8348). Jebba: 1 ♀, alc. (BMNH 99.8.24.10). Jos: 1 ♂, 4 imm. ♂♂, 7 ♀♀, 8 imm. ♀♀, 20-IX-1976/VII-1977, P. Beron (ZMA 19.071/75, -77/80, 19.133/34, 20.601/07, -14/15). Kano: 1 ♀, alc., skull, 1979, H. Grick (HZM 26.10128). Karaduwa: 5 ♀♀, 14-I-1967, J. C. Geest (USNM 402373/75, -78/79). Kudu: 4 ♂♂, 6 ♀♀, 4/5-III-1967, J. C. Geest (USNM 402393/94, -96, -98/99, 402400, -02/03, -05/06). Lagos: 1 ♂, Salmin (ZMB 3413). Lake Alau: 1 ♂, 5-VII-1978, A. Ford (HZM 25.9671). Mada River, 3 miles E of Gudi: 1 ♂, 1 ♀, 12/18-III-1967, J. C. Geest (USNM 402407/08). Maiduguri: 1 imm. ♀, 27-VI-1948, D. R. Rosevear, field number 297/48 (NHMI); 1 imm. ♀, 27-VI-1948, D. R. Rosevear, field number 298/48 (BMNH 50.173). Makurdi: 1 imm. ♂, alc., skull, 1976/77, P. Beron (ZMA 19.076). Mkar: 2 imm. ♂♂, 1 ♀, 12-VII-1976, W. Bergmans (ZMA 18.593/95). Nagaruta Forest Reserve: 1 ♀, 2-VIII-1962 (BMNH 64.47). New Bussa: 2 ♂♂, alc., 18/20-X-1969, D. C. D. Happold, field numbers 1425, 1435 (BMNH). "Nigeria" (exact data lost): 2 imm. ♂♂, 2 ♀♀, 1 imm. ♀, II/VII-1977, P. Beron (ZMA 20.608/12). Oli River: 1 ♂, alc., 15-III-1972, D. C. D. Happold, field number 1688 (BMNH). Ologomo: 2 ♀♀, 27-II-1949, D. R. Rosevear, field numbers 453/49, 454/49 (NHMI). Pandam Wildlife Park: 7 ♂♂, 3 imm. ♂♂, 2 imm. ♀♀, 3/7-VII-1976, W. Bergmans (ZMA 18.577/88). Panisau: 1 ♂, 4 ♀♀, 24-I-1967, J. C. Geest (USNM 402381/83, -88/89). Panyam Fish Farm: 1 ♀, 1 imm. ♀, 11/13-IV-1967, J. C. Geest (USNM 402410/11). Parmiso: 1 imm. ♀, skin, 19-XII-1919, A. Buchanan (BMNH 21.2.11.1). Shaffini: 2 imm. ♂♂, 1 ♀, alc., 20-X-1969, D. C. D. Happold, field numbers B1437, B1440, B1447 (ZMUI). Shagunu: 1 ♀, 2 imm. ♀♀, alc., XII-1965, field numbers 124/26 (NHMI). Sokoto: 1 ♂, 1-II-1959 (HZM 1.2871). 12 miles N of Sokoto: 1 imm. ♂, 1 ♀, 9-V-1966, H. J. Herbert

(USNM 378773/74). Tangaza: 3 ♂♂, 2 ♀♀, 2/4-XII-1966, J. C. Geest (USNM 402362/66). Tsanchaga: 3 ♀♀, 8-I-1967, J. C. Geest (USNM 402367/68, -70). Upper Ogun Game Reserve: 1 ♂, 4-III-1973, D. C. D. Happold, field number 1628 (BMNH). 15 miles N of Zaria: 2 ♂♂, 25/27-IV-1966, H. J. Herbert (USNM 378766/67). Zungeru: ♂, 1 ♀, 26-V-1966, H. J. Herbert (USNM 378776, 485836).

(Benin, Bida, nr Biu, Borgu Game Reserve, Gombe, Kabwir, Kainji Lake National Park, Mokwa, Okon, Oli River, Oyo, nr Pankshin, Panyam, Samuru, Yankari.) SENEGAL. Dialakoto: 7 ♂♂, 1 imm. ♂, 3 ♀♀, 3 in alc., 5/10-V-1966, R. M. Davis (USNM 379093, -96/98, 379100/02, -05, 381321/23). Missirah Saloum: 1 ♂, 2 imm. ♂♂, 6 ♀♀, alc., IV/V-1977, J. Verschuren (IRSN 19910). Nieri River: 1 ♂, F. R. Roberts (p.) (BMNH 11.7.22.1). Thies: 1 ♂, skull, 1 imm. ♀, skin, 1 imm. ♀, skull, 20-VI/30-X-1908, Riggenbach (ZMB A.109, A.109, -).

(Bakel, Diattacounda.)

SIERRA LEONE. Bonthe: 1 ♀, 26-VIII-1948, T. S. Jones (ROM 51049).

(Aberdeen Village, Freetown, Kent, Kisse, Lunsar, Murray Town, Salt Pan, York.)

SUDAN. Gilo: 2 imm. ♀♀, 1 in alc., 8/10-IV-1978, G. Nikolaus (SMNS 29865, -86). Talanga Forest: 1 ♂, alc., 2-VII-1978, G. Nikolaus (SMNS 29854).

(Nzara (?), Sennar (?))

TOGO. Gbatope: 1 ♂, 2 ♀♀, 28-VI-1968, C. B. Robbins (USNM 437585, -88/89). Kadjamba: 2 skulls "zu A119.13", 21-XII-1912, Herzog A. F. von Mecklenburg (ZMB 54423, -27); 3 imm. skins, 21-XII-1912, Herzog A. F. von Mecklenburg/W. Bruch (ZMB). Kunjuruma: 1 ♂, alc., skull, 1 ♂, 1 ♀, skulls, Baumann (ZMB 10009/10, 10170). Lomé: 3 imm. ♀♀, skins/one skull, 16-IV-1914, L. Keilhack (ZMB 17815/17). Napa-ire: 1 ♂, alc., skull, 19-XII-1900, Mischlich (ZMB 54197). Oti: 1 imm. ♀, alc., skull (ZMB 54362). Pagala: 1 ♂, 1 ♀, 29/31-V-1968, J. W. LeDuc (USNM 437581, -83).

(Adina, Adjido, Agadji, Aledjo, Atakpamé, Azafi, Binaparba, Borgou, Dedomé, Ebeva, Edifou, Evou, Ezimé, Fazao, Grand Popo, Kamina, Kodegbé, Kolokopé, Koutoukpa, Lomnava, Namoundjoga, Nanergou, Niamtougou, Odjolo, Ounabé, Paio, Pogan, Porto Séguro, Sansanné-Mango, Tchonou, Témédja, Togoville.)

*Diagnosis:* As for the species, but with the following measurement ranges and ratios:

fal	♂♂	81.7-95.1 (n = 270),
	♀♀	76.2-90.3 (n = 350);
gsl	♂♂	53.3-62.5 (n = 203),
	♀♀	46.1-55.4 (n = 269);
cbl	♂♂	53.1-61.5 (n = 36),
	♀♀	46.2-54.4 (n = 40);

rl ♂♂ 24.4-28.3 (n = 23),  
 ♀♀ 19.8-24.5 (n = 28);  
 zw ♂♂ 26.1-29.0 (n = 34),  
 ♀♀ 24.1-27.1 (n = 36);  
 C<sup>1</sup>-M<sup>1</sup> ♂♂ 18.8-22.0 (n = 30),  
 ♀♀ 16.5-22.6 (n = 36);  
 W ♂♂ 96 -155 (n = 33),  
 ♀♀ 86.5-130 (n = 24);  
 rl ♂♂ 43.6-47.2% of gsl,  
 ♀♀ 41.5-45.6% of gsl;

pl ♂♂ 65.2-67.7% of gsl,  
 ♀♀ 63.1-66.9% of gsl;  
 zw ♂♂ 45.5-50.3% of gsl,  
 ♀♀ 48.3-53.9% of gsl.

Specimens smallest in western part of range and, on the average, larger towards the east. For a breakdown of measurement ranges per country see table 2.

*Distribution:* Fig. 2.

Table 2. Ranges of selected measurements of *Epomophorus gambianus gambianus* (Ogilby, 1835) per country, arranged in an order from west to east.

		♂♂						♀♀							
		fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	W	fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	W
Gambia	n	9	8	5		5	5		15	8	7	3	7	10	
	m	86.4	54.2	53.9		26.4	19.2		81.3	48.5	48.1	22.0	25.0	17.7	
	min	83.4	53.3	53.1		26.1	18.8		79.6	46.6	46.5	21.3	24.4	16.5	
	max	90.8	55.0	54.8		26.8	19.6		85.0	49.8	49.3	22.6	25.6	19.7	
Senegal	n	8	5	1	1	1	1		9	3					
	m	86.0	55.4						83.1	48.7					
	min	82.1	53.9	53.9	24.4	26.7	20.9		78.0	47.5					
	max	89.6	57.0						86.0	49.7					
Guinea-Bissau	n	2	1		1	1	1		1	2	2	2	1	3	
	m													17.7	
	min	82.0	55.4		25.5	27.8	19.0		85.7	47.3	47.0	20.3	25.0	17.4	
	max	83.5								48.8	48.6	21.6		18.0	
Guinea	n	1							1			1	1	1	
	m	89.3							83.9			21.5	25.7	18.4	
Sierra Leone	n								1	1					
	m								85.1	51.3					
Mali	n	9	6	4	4	4	4		10	9	1	1	1	1	
	m	86.2	56.7	56.4	25.5	27.2	20.5		84.0	48.9					
	min	81.7	55.3	55.3	24.4	26.5	19.7		80.9	46.1	49.8	21.8	25.7	18.2	
	max	89.0	57.7	57.2	26.3	28.1	21.0		88.5	50.6					
Ivory Coast	n	5	2	2		2	1		5	5					
	m	89.7							85.4	52.8					
	min	89.0	58.1	58.4		28.2	20.8		83.1	51.1					
	max	90.4	58.2	58.9		28.9			88.3	55.4					
Burkina Faso	n	45	27		1		1	1	46	29					
	m	88.9	58.9						84.1	51.0					
	min	83.6	55.8		25.9		21.7	96	77.0	48.7					
	max	92.5	61.6						89.2	53.3					
Ghana	n	105	99	6	4	4	4	8	119	106		1		1	3
	m	88.5	59.1	58.7	26.8	28.1	20.8	132	82.7	50.8					97
	min	82.3	56.3	57.4	25.7	27.3	19.7	110	76.2	48.0		22.0		17.4	92
	max	95.1	62.5	60.4	27.9	29.0	22.0	155	90.3	53.7					104
Togo	n	6	3	2	4	3			5	6	5	2	3	2	
	m	88.3	59.9		27.4	28.4			84.6	51.3	51.2		26.1		
	min	81.7	57.8	57.8	25.7	27.8			80.0	49.6	49.6	21.7	25.9	19.3	
	max	91.4	61.7	60.3	28.3	28.9			87.4	53.6	53.4	23.7	26.3	22.6	

		♂♂							♀♀						
		fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	W	fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	W
Benin	n	18	15						34	30					
	m	88.7	59.9						82.8	51.0					
	min	85.6	56.9						76.3	49.2					
	max	93.9	61.9						86.6	54.8					
Niger	n								1						
									78.8						
Nigeria	n	38	24	8	4	8	8	13	71	52	18	17	19	14	7
	m	88.7	59.0	58.2	27.0	27.4	20.6	121	83.6	51.0	50.2	22.1	25.7	18.3	93
	min	83.4	55.6	55.6	25.3	26.1	19.7	99	76.3	47.7	47.2	19.8	24.4	17.1	86.5
	max	94.5	62.4	60.6	28.3	28.0	21.3	148	88.5	53.7	54.4	24.5	27.1	19.5	102
Cameroun	n	10	7	4	4	3	3	9	15	6	1	1	1	2	13
	m	89.9	58.7	58.9	27.3	27.5	20.4	138	85.4	50.8					111
	min	85.3	57.6	57.6	26.3	27.0	20.2	115	79.3	49.7	50.9	22.6	25.6	17.9	95
	max	92.0	60.3	60.3	28.3	28.3	20.5	150	90.0	51.5				18.1	130
Chad	n	3	2						5	6					
	m	89.7							84.6	51.1					
	min	86.2	58.3						82.9	49.7					
	max	93.3	59.0						85.5	53.1					
Central African Republic*	n	1							3	2	1	1			
	m								88.0						
	min	86.8							87.8	51.4	51.2	22.2			
	max								88.1	55.9					
Sudan	n	1													
		89.6													
Ethiopia	n	9	4	4		3	2	2	10	5	5		3	2	
	m	89.4	58.8	58.7		27.3			83.0	49.7	49.6		24.5		
	min	84.7	56.4	56.4		26.9	19.4	120	81.5	46.4	46.2		24.1	17.7	
	max	92.8	61.5	61.5		27.7	20.3	135	85.7	52.2	52.1		25.5	18.0	

\* Measurements of three ♀♀ from the Central African Republic by Dr D. Kock (*in lit.*, 31-I-1978).

*Related species:* *Epomophorus labiatus* (Temminck, 1837), a predominantly eastern species with which *E. g. gambianus* is sympatric in northeast Nigeria, north Cameroun, southern Sudan and western and central Ethiopia, averages smaller in all body and skull measurements. The *gsl* in *labiatus* is absolutely smaller in both sexes. There is a slight overlap in fall in ♀♀. As far as the evidence goes, however, *labiatus* is absolutely smaller than typical *gambianus* in areas of sympatry (compare tables 2 and 4). From the rather few available specimens of the allopatric *Epomophorus angolensis* Gray, 1870 from western Angola and Namibia this species appears to be similar in size to typical *gambianus*, but has a relatively slightly longer rostrum and a relatively shorter

palate (see table 1), and differs in palatal ridge pattern (fourth ridge nearer to third than fifth, instead of halfway between them).

#### Remarks

**Taxonomy:** The taxonomic status of typical *Epomophorus gambianus* has been stable since its description (Ogilby, 1835) and subsequent allocation to the genus *Epomophorus* soon thereafter (Gray, 1838, quoted by Andersen, 1912: 538; not traced by the present author). Andersen (1912) gives a thorough account of its taxonomical history, which was marked by a number of persistent synonyms, wrong concepts and misidentifications. Andersen had examined 50 specimens of typical *gambianus*

(including immature ones) and based his diagnosis largely on a comparison with the evidently closely related *Epomophorus crypturus* Peters, 1852, from southern Africa: *gambianus* being "Similar to *E. crypturus*, but larger and with relatively longer rostrum and palate" (Andersen, 1912: 539). This diagnosis is essentially right but an examination of the much larger numbers of specimens which are now available has shown that the dimensional variation in typical *gambianus* includes much of that in *crypturus* and that the relative lengths of both rostrum and palate are functions of the overall skull size rather than specific characters (see table 1). For this reason, *crypturus* is here regarded as a subspecies of *gambianus*, and *gambianus sensu lato* has been diagnosed primarily to enable differentiation from *Epomophorus labiatus*.

Distribution and geographical variation: Andersen (1912) examined specimens of *E. g. gambianus* from localities all through its known range: Senegal, Gambia, Sierra Leone, Ghana, Togo, Nigeria and Ethiopia. He also mentioned specimens from Sennar, Sudan (cited by Koopman, 1975) but these are of uncertain origin (Kock, 1969: 24). Sennar is located in what White (1983) classified as Sahel *Acacia* wooded grassland and deciduous bushland, a vegetation type from which the species appears to be absent throughout. Rosevear (1965) suggested that the species' distribution would be continuous from Senegal to Nigeria (cited by Hayman *et al.*, 1971) and from there across the continent to Sudan and Ethiopia, but this was not based on material evidence. In fact, the known distribution shows some very considerable disjunctions. Rosevear further mentioned examples in the BMNH collection from "the Gaboon coast" which I have not been able to locate. The only *Epomophorus* species from the coast of Gabon (and from all of that country, for that matter) appears to be *E. wahlbergi* (Sundevall, 1846) (for details see the section on examined material under that species). As *E. g. gambianus* has not been recorded from southeast coastal Nigeria, nor from coastal Cameroun or Equatorial Guinea, and *E. wahlbergi* does not occur in the faunal

regions which were known to Rosevear, it is not unlikely that he took examples of *wahlbergi* for *gambianus*. BMNH mammalogists Hayman & Hill (1971) did not include Gabon in the range of *gambianus*, which supports this presumption.

The aforementioned belt of Sahel *Acacia* wooded grassland and deciduous bushland apparently poses the northern limit to the species' dispersion. Most collecting localities are in Sudanian woodland, either with abundant *Isobertinia* or undifferentiated, and in areas with a forest/grassland mosaic (types 27, 29a, 30 and 11a in White, 1983). The forest/grassland mosaic is the main vegetation type bordering the original rain forest belt. There are some records from forest areas: from drier types of Guineo-Congolian rain forest in Ghana and from mangrove forest (types 2 and 77 in White, 1983). Rosevear (1965) referred to BMNH specimens from the "closed rain forest south-west of Kumasi". I have not seen those specimens. It has rather occurred to me, when examining fruit bat collections, that *E. gambianus* is rarely collected together with forest fruit bat species. From my field observations in Nigeria I would conclude that *E. gambianus* is a woodland species which does not avoid forest edges and which will probably quite easily colonize areas in the original rain forest belt where the forest has been destroyed. The mangrove sites where the species has been collected are all quite near the forest/grassland mosaic, where the forest edge niche is of course amply represented. It should also be borne in mind that much of the mangrove forests have been cleared to make way for agricultural 'development', and hence for species like *E. gambianus*. It is unlikely that the species' alleged occurrence in rain forest will hold against the results of an analysis of the extent of rain forest related to dates and localities of capture. The forest/grassland mosaic borders the West African coast from Dakar in Senegal to the Liberian/Ivory Coast border and from Elmina in Ghana to the Benin/Nigerian border (the so-called Dahomey Gap) and here *E. gambianus* may reach the coast—although it does hardly penetrate the narrow belts of this type between rain forest

blocks and the coast; where there was or still is rain forest or swamp forest (type 8 in White, 1983) this has formed or still forms the southern limit of its range. This accounts for its absence in much of Sierra Leone, Liberia, southern Ivory Coast, southwest Ghana, and most of southern Nigeria.

There is no satisfactory explanation for the large disjunction in the distribution between 8° and 12° W; it appears as if in this part of Africa the species largely avoids altitudes above 500 m. (Kuhn, 1965, recorded *E. gambianus* from Kpeapele in Liberia, but it is not clear on what evidence this was based.) Apart from the mountain ranges northeast of Mount Cameroon, the map (fig. 2) suggests a further disjunction in southwest Chad and the western Central African Republic. However, few successful collecting efforts have been made in those regions (compare fig. 1). Between 23° E in the eastern Central African Republic and 32° E in southern Sudan a third distributional gap may exist. Some collecting has been carried out here but the fruit bat fauna is certainly not well-known and considering the vegetation types — essentially the same as in West Africa — *gambianus* will probably be discovered yet. The populations in south Sudan and in Ethiopia show no apparent differences from their western relatives, which supports this hypothesis. At the same time, they inhabit quite aberrant vegetation types: Ethiopian woodland; transitions from this to Ethiopian *Acacia* deciduous bushland and wooded grassland; Afromontane vegetation; East African evergreen and semi-evergreen bushland and thicket; and in the central Ethiopian rift possibly Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (types 29b, 35, 19a, 38 and 42 respectively, in White, 1983).

As table 2 shows, dimensional variation in typical *gambianus* is very restricted. From Gambia towards Ivory Coast there is a slight increase in body size (as expressed in fal) in both sexes. From Ivory Coast eastwards this measurement does not vary much. Skull size increases from Gambia to Ghana in ♂♂ and to Ivory Coast in ♀♀ but also remains quite

steady from there on eastward. The smallest specimens of the typical subspecies are thus found in and near Gambia, from where the type series was procured.

In 1950, Aellen described *Epomophorus reii* from Rei Bouba in Cameroun. The species was based on an adult ♀ and two juvenile specimens. I have examined both the holotype and the larger paratype specimen (also a ♀). Both have been preserved as skins and skulls. Aellen compared *reii* with *E. gambianus* and *E. angolensis*. He gave as fal of the holotype 82. As the upper arms have not been preserved, this measurement can only be estimated. My estimate is 82.2 or more, which indicates a body size as in typical *gambianus* ♀♀ (fal range 76.2-90.3). According to Aellen, *reii* would differ from *gambianus* in a number of skull characters: its zygomatic width being larger than half the gsl, instead of smaller; its palatal length 2.2 times M<sup>1</sup>-M<sup>1</sup>, instead of 2.25-2.33 times; M<sup>1</sup>-M<sup>1</sup> larger than length of postdental palate instead of smaller; and a smaller ratio rostrum length/C<sup>1</sup>-M<sup>1</sup> length (1.05 instead of 1.14-1.17). Aellen had only Andersen's (1912) description of *gambianus* as reference for that species. Andersen gave measurement ranges for seven adult female skulls, originating from Gambia to Ethiopia and thus hardly reflecting possible variation within individual populations. Of zygomatic widths he gave one example only. In the type of *reii*, the right zygomatic arch is incomplete. Its estimated zygomatic width is 25.6, which is 50.5% of its gsl of 50.7. In 35 typical *gambianus* ♀♀ I measured a range of 48.3-53.9% of the gsl (see table 1). The palatal length in the type of *reii*, 32.8 or 254.3% of its M<sup>1</sup>-M<sup>1</sup> width of 12.9, also falls within the range of 221.0-262.0% measured in typical *gambianus* (table 1). Aellen (1950: 562) probably measured what Rosevear (1965: 364) indicated as palatal length, but I do not think that comparison of that measurement will lead to another result. I have likewise not measured postdental palatal length in typical *gambianus*. Direct comparison of the skull of the type of *reii* with a large number of *gambianus* skulls however, showed that *reii* falls within the variation

of *gambianus* also in this respect. The same applies to the ratio rostrum length/C<sup>1</sup>-M<sup>1</sup> length. The small sample size available to Andersen (1912) is clearly insufficient to serve as reference for *gambianus*. Aellen's calculations of relative measurements, such as the relation between rostrum and upper tooth row lengths, based on Andersen's data, are moreover not quite correct. Andersen gave measurement ranges, and Aellen related the given minimum rostrum length to the given minimum C<sup>1</sup>-M<sup>1</sup> length, and likewise the given maxima. But, however logical it may seem, the smallest measurements are not always found in the smallest skull, and the same goes for the large extremes.

*E. reii* furthermore differs from *gambianus* in its palatal ridge pattern, with as most important difference that the fourth ridge is nearer to the third than to the fifth instead of about halfway between these two. Aellen's only data on the pattern in *gambianus* was Andersen's illustration (1912: 516). Unfortunately, the soft palate of the type of *reii* has not been preserved (nor that of the paratype examined by the present author, but this would not be conclusive, due to its immaturity). Through careful examination of the bony palate, which often shows slight elevations underneath the soft ridges (especially the back ones), the configuration of the ridges may be partly inferred. The visible bony ridge supports in the type of *reii* are shown in fig. 3. The indicated positions of the fourth, fifth and sixth ridges should be fairly accurate, those of the second and third can not be determined unequivocally. The fourth to sixth ridges will have been as in typical *gambianus*, in which the fourth is usually slightly more forward than in Andersen's figure and crossing the line connecting the posterior sides of both P<sup>4</sup> (compare Bergmans, 1978, fig. 2), and in which the proportions of the fifth ridge are quite variable, influencing its distance to the fourth and sixth (*op.cit.*). The third ridge in the type of *reii* appears to have been placed relatively backward, and the second again as in typical *gambianus*. This leaves us with a single specimen of *Epomophorus*, collected in a region inhabited

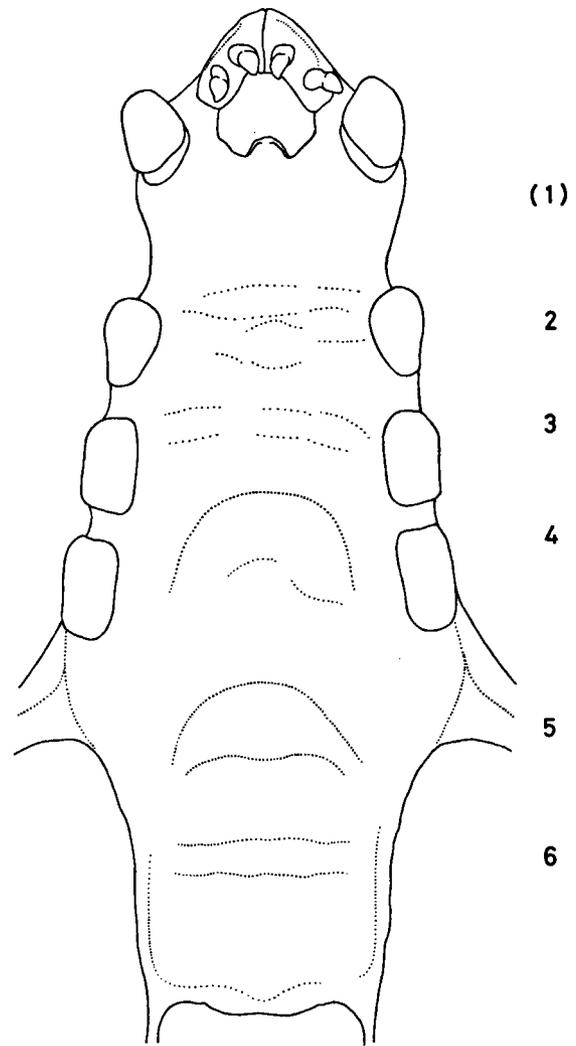


Fig. 3. Palatum of the holotype specimen of *Epomophorus reii* Aellen, 1950 (= *E. gambianus gambianus* (Ogilby, 1835)). Dotted lines indicate elevations corresponding with ridges on the soft palate (which has not been preserved); there is no elevation at the level of ridge 1, and the position of the vestigial elevations underneath ridges 2 and 3 is equivocal.

by *E. gambianus* (see also Eisentraut, 1973: 1975) and agreeing with this in all its characters except for a slightly dispositioned palatal ridge. I therefore consider *Epomophorus reii* Aellen, 1950 as a synonym of *Epomophorus gambianus gambianus* (Ogilby, 1835). Aellen (1950) also compared *reii* with *Epomophorus angolensis* Gray, 1870. As this species and its differences from *gambianus* are dealt with elsewhere in this paper, there is no need to reflect on them in this place.

**Epomophorus gambianus crypturus** Peters, 1852 — New combination

*Epomophorus crypturus* Peters, 1852: 26 (type locality: Tete); Andersen, 1912: 535; Kershaw, 1922a: 100, 1922b: 178; Loveridge, 1922: 43; Schouteden, 1944: 105; Roberts, 1951: 57; Sweeney, 1959: 8; Harrison, 1959: 222; Ansell, 1960a: 164, 1960b: 11; Hayman, 1963: 97; Morris, 1964: 73; Pienaar, 1964: 8; Hayman *et al.*, 1966 (in part; specimens MRAC 2767, IRSN 10677 and IRSN 13326 are *Rousettus aegyptiacus* (E. Geoffroy, 1810), *Epomophorus labiatus* (Temminck, 1837), and *Epomops franqueti* (Tomes, 1860), respectively); Koopman, 1966: 156; Hayman *et al.*, 1971: 7; Smithers, 1971: 54; Ansell *et al.*, 1973: 30; Meester, 1973: 138; Peterson *et al.*, 1975: 2; Smithers *et al.*, 1976: 40; Ansell, 1978: 17; Rautenbach, 1982: 30; Anciaux de Faveaux, 1983: 30; Herselman *et al.*, 1985: 79; Hapold *et al.*, 1987: 348 (in part: the specimen from Kasungu National Park is *Epomophorus labiatus* (Temminck, 1837)); Ansell *et al.*, 1988: 27 (in part: the specimen from Kasungu National Park is *Epomophorus labiatus* (Temminck, 1837)).

*Epomophorus angolensis* (not of Gray, 1870); Jameson, 1909: 468.

*Epomophorus gambianus*; Hayman, 1954: 281; ? Didier, 1965: 338 (in part: specimen MNHN C.G. 1.(13) from "Rhodésie"); Hayman *et al.*, 1966: 7 (in part: specimen IRSN 186b is *Epomophorus wahlbergi* (Sundevall, 1846)); Fenton, 1975: 14; Peterson *et al.*, 1975: 4; Archer, 1977: 145; D. W. Thomas *et al.*, 1978: 403; Anciaux de Faveaux, 1983: 30.

*Epomophorus gambianus parvus* Ansell, 1960a: 160 (type locality: Balovale District; corrected into Chingi by Ansell, 1978: 17); Ansell, 1960b: 11; Koopman, 1966: 156; Ansell, 1978: 17. New synonymy.

*Epomophorus crypturus parvus*; Meester *et al.*, 1986: 27.

**Material examined**

ANGOLA. Lac Calundo: 1 ♂, alc., skull (BMNH 63.1024). Luiana Camp: 1 ♀, 1 imm. ♀, alc., skulls, 1 imm., alc., IX-1964, J. K. Doust (CMNH 40476/78). BOTSWANA. Maun: 3 ♂♂, 1 imm. ♀, 23/25-V-1930, Vernay-Lang (FMNH 38489/92); 1 imm. ♀, 29-XII-1955, Zumpt (SMNS 5034). Shakawe: 1 ♀, 5-X-1950, T. Larson (AMNH 168102); 1 ♂, 21-II-1964, R. H. Smithers (HZM 27.4238); 10 ♂♂, 2 imm. ♂♂, 2 imm. ♀♀, 4/9-V-1967, S. W. Goussard/T. N. Liversedge (USNM 425248/54, -57/63). Xugana: 1 ♀, alc., skull (not seen), 23-XI-1975, A. L. Archer *et al.* (USNM 518607). (Chobe River, Kasane, Kwaai River, Sepopa, Shorobe; 1923C4.) MALAWI. Cape Maclear: 1 ♂, 31-V-1975, L. W. Robbins (CMNH). Cholo: 1 imm. ♀, R. C. Wood (p.) (BMNH 22.12.17.3). Karonga: 1 imm., II/IV-1956, R. H. Oram (HZM 4.2199). Likabula: 1 ♀, 26-VI-1946, H.

E. Anthony (AMNH 161852). Zomba: 3 imm. ♀♀, alc., skulls, H. H. Johnston (p.) (BMNH 94.1.25.23, 94.6.7.1., 95.12.7.2).

(Blantyre, Chikwawa, Lichenya, Livingstonia, Liwonde, Ruu River (?), Thondwe, Zoa Estate; 1434D.)

MOZAMBIQUE. Lumbo: 4 ♀♀, 1 imm. ♀, 20-VII-1918, A. Loveridge (BMNH 22.7.17.24/28). Mague: 4 ♂♂, 2 imm. ♂♂, 1 imm., 5 imm. ♀♀, 20/23-VIII-1964, H. J. Herbert (USNM 365123/34). Masembeti: 1 imm.♂, C. D. Rudd (p.) (BMNH 7.6.2.10). Shupanga: 1 ♂, skull, J. Kirk (p.) (BMNH 64.1.9.6). Tete: 3 ♀♀, 1 imm. ♀, 1 imm., 2 in alc. (1 skull missing) and 2 skulls only, W. C. H. Peters (ZMB 355; 553 = holotype of *Epomophorus crypturus* Peters, 1852, alc., skull missing; 10018; 10078; 10080); 2 imm. ♀♀, B. Alexander (p.)/C. D. Rudd (BMNH 99.8.3.2, 8.4.3.8). Near Tete: 1 imm.♂, B. Alexander (p.) (BMNH 99.8.3.1). 30 miles NW of Zinave: 1 ♂, alc. (not seen), skull, 12-X-1968, R. G. van Gelder (AMNH 216400).

(Beira, Incomati River (?), 30 miles N of Tete; 1633B, 1633C, 1832D, 1934C, 2032B, 2131D, 2132A, 2133B, 2231A.)

NAMIBIA. Nampini: 1 ♂, 1 imm. ♂, 9-VIII-1949, N. P. Arends (AMNH 146782, -84). (1724C.)

TANZANIA. Liwale: 1 ♀, 1 imm. ♂, 11-XII-1951, C. J. P. Ionides (HZM 2.1347, 3.1359); 1 imm. ♂, 9-XI-1958, C. J. P. Ionides (HZM 39.6343); 1 ♂, 27-I-1953, G. H. Swynnerton *et al.* (BMNH 64.1333). Nachingwea: 1 ♂, 1 imm. ♂, 1 ♀, 1 imm. ♀, 2 imm., 19-X-1958, A. F. Rees (HZM 9.2790, 10.2791, 11.2792, 12.2793, 33.4822, 34.4823). Newala: 2 ♂♂, 2 ♀♀, 2 imm., skull material, 27-XII-1959 and 12-XI-1960 (HZM 32.4746, 35.5231, 36.5232, 37.5233, 40.6650, 41.6651).

ZAIRE. Dikulwe River: 1 ♀, S. A. Neave (p.) (BMNH 7.12.13.2). Jadotville: 1 imm. ♀, 6-XII-1959, M. Anciaux de Faveaux (IRSN 14595). Kakanda: 1 ♀, alc. (BMNH 55.136). Kakontwa: 1 imm. ♂, 1 ♀, alc., 17-I-1961, M. Anciaux de Faveaux (IRSN, ♀: 14597). Kanzenze: 1 imm. ♀, 14-VII-1947, R. P. Lefebure (IRSN 13.107); 1 imm., 28-XI-1948, N. LeLeup (BMNH 54.786). Kasapa: 2 ♂♂, 2 imm. ♂♂, 1 ♀, 22-VIII-1969, J. Poelman (p.) (IRSN 18779/80, 18841/42, unreg.). Lubumbashi: ♂, alc., 26-III-1966, X. Misonne (IRSN 17207). Mulima: 1 ♂, 28-VI-1949, G. F. de Witte (IRSN 10665).

(Kasaji, Kasenga, Likasi, Lusinga, Mabwe (?), Sakania.)

ZAMBIA. Broken Hill: 1 ♂, alc. (BMNH). Chavuma area: 1 imm. ♂, 1-III-1959, W. F. H. Ansell (HZM); 1♂, 3-III-1959, W. F. H. Ansell (BMNH 59.610; holotype of *Epomophorus gambianus parvus* Ansell, 1960). Chilanga: 1 imm., 15-I-1963, V. J. Wilson (AMNH 218964); 1 imm.♀, 26-VI-1963, C. W. Benson (BMNH 66.5414). Chilwa Island: 1 imm. ♂, W. Ansell (BMNH 55.1061). Chipata: 1 imm. ♂, G. Lancaster (BMNH 37.12.8.1). Kalabo: 5 ♂♂, 1 imm. ♂, 2 ♀♀, 4-V-1965/16-IX-1966, M. Japp/W. F. H. Ansell (BMNH 66.5415, -24/26,

68.992/95). Limulunga: 1 ♀, T. D. Carter (AMNH 115820). Luanshya: 1 ♂, skin, 23-XI-1948, T. Larson (AMNH 168098); 1 ♂, skull, T. Larson (AMNH 169161; probably of AMNH 168098); 1 ♂, 17-I-1949, T. Larson (AMNH 168099); 2 imm. ♂♂, 5/12-I-1957, W. F. H. Ansell (HZM 7.2542, 8.2543). Lusaka: 1 ♂, 1 imm. ♂, 11/17-V-1963, V. J. Wilson (AMNH 218965/66); 1 imm. ♀, 3-VIII-1965, W. F. H. Ansell (BMNH 66.5416); 1 ♂, 1 imm. ♀, 1 imm. ♂, 19-II-1966, 24-XII-1966, 2-I-1967, T. P. Farrell (HZM 29.4707, 30.4727, 31.4740). Machiya Ferry: 1 ♀, 25-VIII-1963, A. J. Tree *et al.* (BMNH 66.5423). Magoye Research Station: 1 ♂, VI-1974, B. Wells (HZM 42.7597). Mazabuka: 2 imm. ♂♂, 2 ♀♀, W. F. H. Ansell (BMNH 55.1055/58); 4 imm. ♂♂, 1 ♀, 2 imm. ♀♀, 20-XII-1966 and 3/6-I-1967, J. McLeod (BMNH 68.113/14, -17/21). Mfuwe Game Camp: 1 imm. ♂, 29-III-1964, W. F. H. Ansell (p.) (BMNH 66.5417); 3 ♂♂, 28-XII-1966, 21/27-VII-1967, R. J. Dowsett (BMNH 68.112, 68.990/91). Ndola: 1 ♂, 1 imm., 8-V-1956, 22-IV-1957, W. F. H. Ansell (HZM 5.2229, 6.2541). Pwira Pan: 5 ♀♀, 17/18-VIII-1963, A. J. Tree *et al.* (BMNH 66.5418/22). Sihole: 3 ♀♀, 1 imm. ♀, 5/8-XII-1961, M. A. Traylor (FMNH 95208/11). Sikongo: 4 ♂♂, 18/20-XI-1961, M. A. Traylor (FMNH 95205/07, -12). Solwezi: 1 ♂, W. F. H. Ansell (BMNH 55.1054).

(Abercorn, Kabompo District at 13°05'S 24°37'E., Kabulonga Dam, Kalomo, Kasempa, nr Kazungula, Lisikili Lake, Lochinvar Ranch House, Mongu, Mpokoroso, Muyombe, Naleza, Nyika National Park at 10°35'S 33°40'E, Nyika Rest House; 1028B3, 1228C3, 1228D1, 1231D4, 1322B1, 1323C1, 1324C1, 1328A2, 1331B2, 1331B3, 1332A3, 1422D3, 1522C1, 1527D3, 1528C2, 1528D1, 1626D3.)

ZIMBABWE. Balla Balla: 1 ♂, alc., 13-VI-1980, S. G. Sowler (Sowler collection). Bulawayo: 1 ♀, 17-X-1924, J. Durrant (HZM 1.376). Chipinga: 1 ♀, alc. (BMNH 66.6154). 10 km NW of Concession: 1 imm. ♀, 15-VI-1975, L. W. Robbins (CNHM 40973); Cyrene: 1 ♂, 27-IV-1976 (HZM 43.8376). Henderson Research Station: 1 ♂, 1 ♀, 11/13-X-1967, S. W. Goussard (USNM 425266/67). 6 km E of Kariba: 3 ♀♀, 15-VI-1975, L. W. Robbins (CMNH 40974/76). Kazungula: 1 ♂, 2 ♀♀, 25-IX-1931, Vernay-Lang (FMNH 38493/95). Near Marandellas: 1 ♂, 1 ♀, 14-XII-1970, National Museum of Rhodesia (ZMA 19.804/05). Near Miami: 1 ♀, 29-XI-1961, Mitchell (HZM 18.3929). 18 miles W of Norton: 1 imm. ♂, 22-IX-1961, A. C. Kemp (HZM 15.3882). Nuanetsi Ranch: 1 ♂, alc., skull, 3 ♀♀, 27-V-1972, R. L. Peterson *et al.* (ROM 64899, 64910/11, -22). Retreat Farm: 3 ♂♂, 1 imm. ♂, 1 ♀, skins not seen, cf. 27-V/2-VI-1972, R. L. Peterson *et al.* (ROM 64987/88, -96/97, 65004). "Rhodesia": 2 ♂♂, alc., 22-VI-1910, Ellenberger (MNHN). Salisbury: 1 imm. ♀, 3-II-1961, R. Smithers (ROM 33777); 1 imm. ♂, 13-X-1961, G. L. Guy (FMNH 95143); 1 ♀, skin not seen, 6-X-1961, R. N. Smithers (AMNH 213043); 1 ♂, skin not seen, 1 imm. ♀, 20-X-1961, R. N. Smithers (AMNH 213044; HZM

16.3912); 2 ♂♂, 31-X-1961, G. L. Guy (USNM 368602; ROM 33778: skin possibly mismatched); 1 ♀, alc., skull, probably 31-X-1961, probably G. L. Guy (ROM 64517); 1 ♀, 30-III-1962, R. N. Smithers (AMNH 213041); 1 ♂, 1 ♀, 14/17-VII-1962, A. P. Shone (HZM 17.3928, 19.3938); 1 ♀, 27-VII-1963, R. N. Smithers (AMNH 213045); 1 ♂, 1 ♀, 20-X-1963, H. R. Smithers (HZM 23.3969, 26.3972); 1 ♀, 24-IV-1964, P. Scott-Martin, 1 imm. ♀, VII-1967, D. Ward (USNM 368603/04); 1 ♂, 11-V-1965, Hickmans Loure (USNM 382642); 1 ♀, 20-X-1966 (MNHN 1969-35); 1 ♂, 26-V-1967 (MNHN 1969-34); 1 imm., 23-IV-1965, R. N. Smithers (AMNH 21304). Selukwe Reserve: 1 ♂, skull, 4-II-1957, R. H. R. Stevenson (AMNH 180374). Umluli River: 1 imm. ♀, G. A. K. Marshall (p.) (BMNH 96.5.18.1). Umtali: 1 (♂?), skull, skin (mismatched?), D. G. Broadley (HZM 14.3706); Umvukwes: 1 ♀, 8-XII-1964, B. P. Mammal Survey (USNM). Umvuma: 2 ♂♂, 1 specimen: 5-I-1964, G. W. Begg (HZM 22.3968, 24.3970). Zambesi-Chewore junction: 1 ♂, 20-VIII-1962, 1 ♀, 24-VIII-1968, G. L. Guy (HZM 20.3939, 21.3940).

(Chirinda, Deteema, Gadzima, Hostes Nicolle Institute for Wildlife Research, Inyanga, Limpopo-Shashi River confluence, Wankie National Park at 17°48'S 26°57'E, Nampini, Shumba, West Nicholson; 1725C4.)

SOUTH AFRICA. 14 km NW of Barberton: 1 ♀, 22-XI-1975, L. W. Robbins (CNHM 40965). 48 km NE of Shepstone: 2 ♂♂ (one: a skeleton), 3 ♀♀ (one: alc., one: a skeleton), 2-XII-1975, L. W. Robbins (CNHM 40966/70). Tzaneen: 1 ♂, VI/VII-1907?, H. L. Jameson (BMNH 9.3.2.3).

(Crocodile River, Crocodile Bridge, Durban, Dzungwini, Grahamstown, Greefswald, Hectorspruit, Klaserie-Olifants River confluence, Komati River, Letaba, Levubu River nr confluence with Limpopo, Madimbo, Malelane, Matukwatadam, Nelspruit, nr Newington, Othawa, Pirie, Pongola, Port Elizabeth (?), Pretoriuskop, Punda Milia, 10 miles W of Punda Milia, Shinghidzi, Sibasa, Soutpansberg, Ten Bosch Estates, Tshokwane, Uzumbe River valley.)

*Diagnosis:* As for the species, but with the following measurement ranges and ratios:

fal	♂♂	80.0-88.4 (n = 51),
	♀♀	75.0-83.2 (n = 40);
gsl	♂♂	51.8-55.7 (n = 47),
	♀♀	44.0-48.8 (n = 34);
cbl	♂♂	51.1-55.3 (n = 21),
	♀♀	44.0-48.2 (n = 19);
rl	♂♂	22.6-24.9 (n = 15),
	♀♀	18.0-20.8 (n = 18);
zw	♂♂	25.5-27.4 (n = 25),
	♀♀	23.5-25.7 (n = 31);
C <sup>1</sup> -M <sup>1</sup>	♂♂	16.7-19.5 (n = 31),
	♀♀	14.7-16.9 (n = 27);

W ♂♂ 91.0-139.6 (n = 11),  
 ♀♀ 56 -100 (n = 13);  
 rl ♂♂ 43.7-45.4% of gsl,  
 ♀♀ 41.1-42.7% of gsl;  
 pl ♂♂ 63.0-65.3% of gsl,  
 ♀♀ 60.7-64.0% of gsl;  
 zw ♂♂ 46.8-51.7% of gsl,  
 ♀♀ 50.9-55.8% of gsl.

in fal and no overlap in gsl, cbl and rl. Measurement ranges almost completely overlapping with those of the typical subspecies but all minima lower and all maxima very distinctly lower. Possibly some geographic variation in size, with slightly smaller specimens in the southwest of the distribution area (= northern Botswana) and larger ones towards the northeast and east. For a breakdown of measurement ranges per country see table 3.

*Distribution:* Fig. 2.

Sexual dimorphism relatively strongly pronounced, much more than in the typical subspecies, with little overlap between the sexes

Table 3. Ranges of selected measurements of *Epomophorus gambianus crypturus* Peters, 1852, per country.

		♂♂						♀♀							
		fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	W	fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	W
Angola	n						1								
							18.5								
Botswana	n	15	10	2		3	2	1	1						
	m	83.2	53.2			26.2									
	min	80.0	52.3	54.2		25.5	16.9	75.5	46.6						
	max	86.8	54.9	54.9		26.6	19.5								
Malawi	n							1	1						
								78.6	46.6						
Mozambique	n	3	3		1	1		2	1	2	5	4	4		
	m	86.5	52.5								19.6	24.4	15.5		
	min	85.4	52.0		24.0	26.7		80.2	45.4	45.1	18.8	24.2	15.0		
	max	87.4	53.0					80.3		47.2	20.4	24.8	16.1		
Namibia	n		1												
			55.3												
Tanzania	n	2	1	1	1	2	4	2	3	3		3	4		
	m						18.1		46.4	46.0		24.2	16.4		
	min	82.8	52.5	52.5	24.9	26.3	17.6	77.4	45.7	45.6		23.8	16.1		
	max	85.1				26.7	18.7	79.3	47.3	46.7		24.5	16.9		
Zaire	n	4	3	3	3	1	3	4	2	2	2	2	2		
	m	85.0	53.8	53.8	24.2		18.2	79.4							
	min	84.7	53.2	53.2	23.9	26.2	18.1	77.6	45.9	45.6	19.0	23.6	15.0		
	max	85.9	54.1	54.1	24.5		18.3	80.1	46.3	45.7	19.2	24.6	15.9		
Zambia	n	15	14	7	8	9	13	5	14	10	5	9	11	9	4
	m	85.2	53.7	54.0	24.3	26.9	18.3	112	80.0	45.9	45.6	19.4	24.5	15.6	72
	min	82.5	52.4	52.4	23.2	25.9	16.7	99	76.8	44.3	44.0	18.4	23.5	14.7	56
	max	88.4	55.4	55.3	24.9	27.4	19.4	136	82.8	48.8	48.2	20.8	25.7	16.8	83
Zimbabwe	n	9	12	6	1	7	7	4	14	13	7	1	9	6	5
	m	85.0	53.9	53.5		26.1	18.2	113	77.6	45.9	45.9		24.6	16.2	82
	min	82.7	51.9	51.1	23.5	25.5	17.0	91	75.0	44.0	44.5	18.8	23.8	15.8	72
	max	88.4	55.7	54.6		26.6	19.3	140	81.5	47.4	47.1		25.4	16.8	98
South Africa	n	3	3	2	1	1	1	2	2	2	1				4
	m	84.2	53.3												95
	min	81.8	51.8	51.4	22.6	26.1	18.3	126	82.5	46.8	46.5				89
	max	88.4	54.4	53.8				130	82.5	47.3					100

*Related species:* These have been discussed under the typical subspecies, but some remarks on their position vis-à-vis *E. g. crypturus* are in order. *E. labiatus* is possibly sympatric in southern Tanzania and in Malawi. In Tanzania it is smaller in all measurements (compare table 4), although the southern populations are hardly known and may consist of relatively large specimens if compared to other Tanzanian populations. (They may be related to the geographically much nearer populations in Malawi rather than the more northern Tanzanian ones.) From Malawi very few adult specimens of either species have been reported but available data indicate a distinct dimensional gap (see Bergmans *et al.*, 1983, who recorded the first Malawian *labiatus*, as *anurus*). The allopatric *Epomophorus angolensis* is distinctly larger than *E. gambianus crypturus*. There is some overlap in fal and possibly also in gsl (to be expected in ♀♀). It has a relatively longer rostrum and shorter palate, however, and differs in palatal ridge pattern, with the fourth ridge nearer to the third than the fifth, instead of halfway between these.

#### Remarks

**Taxonomy:** As follows from the entries in the synonymy, several earlier authors have identified *crypturus* as *gambianus*. Their reasons are not always clear. Hayman (1954) recorded specimens from Kanzenze and Kasaji in southeastern Zaire as the first *gambianus* from that country. He did not discuss why he identified these (partly even immature) specimens as such and not as *crypturus* and he certainly did not propose the synonymy of *crypturus* with *gambianus*. Didier (1965) mentioned *gambianus* from "Rhodesie" in the MNHN; this may concern the 2 ♂♂ from Zimbabwe listed under material examined, collected 22-VI-1910 by Ellenberger. In a compilation on the bats of Zaire, Rwanda and Burundi (Hayman *et al.*, 1966) both taxa figure as species; the measurement ranges in the key in this work are roughly copied from Andersen (1912), with the result that those given for *gambianus* apply to the

nominate subspecies from north of 4° N and not to the specimens from southern Zaire listed under *gambianus*, which will all key out as *crypturus*. Although these authors apparently knew Ansell's Mammals of Northern Rhodesia (1960b), they failed to make mention of *gambianus parvus*.

Ansell (1960a) described this subspecies from northern Zimbabwe and southern Zaire, based on specimens including one identified by Hayman (1954) as *gambianus*. He diagnosed it as differing from the nominate race by "the markedly smaller size of the male, and also, apparently, by lack of size discrepancy between the sexes." In his description Ansell remarked that the lack of sexual size dimorphism needed to be confirmed by more material of females, as he had seen only one ♀ (and 4 ♂♂). From *crypturus* the new *gambianus parvus* would differ "in the proportions of the median palate, and postdental palate, to M<sup>1</sup>-M<sup>1</sup> width; orbit-tip of nasals to C-M<sup>1</sup>; and zygomatic width to total length, and in having the front of the orbit well behind the level of M<sup>1</sup>" (Ansell, 1960a: 162). In the state of these characters, which are all related to the measure of lengthening of the rostrum and thus, as I have emphasized before, to the absolute skull length, *E. g. parvus* would agree with the appreciably larger *E. g. gambianus* and not with the equally sized *E. crypturus*. At the time of his description, Ansell had no access to a sufficient comparison collection. His only information on typical *gambianus* appears to have been Andersen's (1912) account. Although he rightly identified some of his specimens as *gambianus*, an examination of more extensive material would have led to the conclusion that in relative skull proportions these specimens agreed with *crypturus* rather than with nominate *gambianus* as described by Andersen (who incidentally had only rather large skulls at his disposal).

Koopman (1966) identified two specimens from Luanshya in Zambia and two others from Nampini, Zimbabwe as *E. g. parvus*, pointing out their more slender rostrum if compared to *crypturus* and their small size if compared to nominate *gambianus*. Archer (1977) identified

some specimens from Botswana as *E. gambianus*, apparently without examination of skull characters, D. W. Thomas *et al.* (1978) did so with specimens from Zimbabwe, and Anciaux de Faveaux (1983) mentioned both *gambianus* and *crypturus* from southern Zaire. Other unreasoned records of *gambianus* from Zimbabwe (Fenton, 1975; Peterson *et al.*, 1975) were later corrected and the specimens assigned to *crypturus* (see footnote in Ansell, 1978: 17).

In 1978 Ansell expressed his doubts about the validity of *parvus*. Since its description only ♂♂ had been collected which were ascribable to *parvus*, all ♀♀ keying out as *crypturus*, and

Ansell suggested that *gambianus* (*parvus*) and *crypturus* could prove to be conspecific if adequate series of properly sexed adult skulls would become available for analysis. Apparently on that ground, but without reference to Ansell's work, or new arguments, Koopman (in Honacki *et al.*, 1982) included *parvus* in *crypturus*. For the present study, I collected both gsl and rl measurements of 10 ♂♂ and 11 ♀♀. In fig. 4 gsl is plotted against rl expressed as percentage of gsl. More frequently, I measured both gsl and zw of the same skull: in fig. 4 gsl is also plotted against zw expressed as percentage of gsl, for 22 ♂♂ and 23 ♀♀. In these

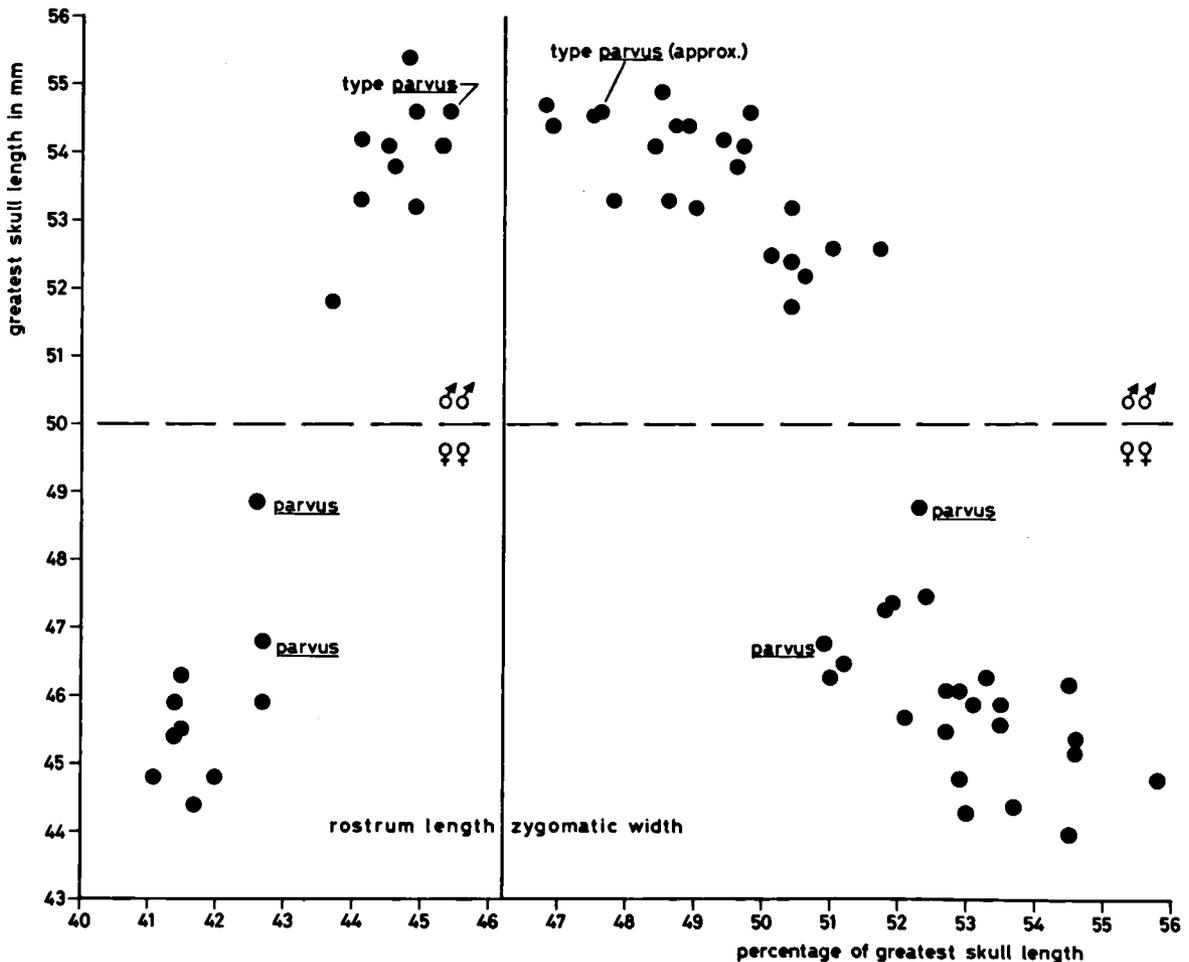


Fig. 4. *Epomophorus gambianus crypturus* Peters, 1852: ratios between greatest skull length and rostrum length as percentage of greatest skull length, and between greatest skull length and zygomatic width as percentage of greatest skull length. The holotype specimen of *E. g. parvus* Ansell, 1960 (considered a synonym of *E. g. crypturus*) and some other specimens found in collections labelled as *parvus*, are indicated.

series the type of *parvus* and some other specimens identified as *parvus* by Ansell are included and indicated as such. Some conclusions are obvious: the relative length of the rostrum increases with increasing skull length, while the relative zygomatic width decreases with increasing skull length. The type of *parvus* had a relatively large skull, which accounts for its 'slender' rostrum and narrow zygomatic width, but it is clearly consistent with the other specimens. The two ♀♀ identified as *parvus* (BMNH 66.5422 from Pwira Pan and BMNH 66.5423 from Machiya Ferry, both in Zambia) are also large specimens, one possessing the maximum skull length in ♀♀, but they also fit in with the variation shown by the other specimens. The mean value of the 34 female gsl measurements with a total range of 44.0-48.8 (see p. 94) is 46.0. In other relative skull measurements the two ♀♀ also remain within the variation to be expected for *crypturus*. The following values are of the type of *parvus* and the ♀♀ BMNH 66.5422 and 66.5423, respectively:

palatal length as			
percentage of gsl	65.2	63.5	63.0
palatal length as			
percentage of M <sup>1</sup> -M <sup>1</sup>	263.7	246.0	247.9
C <sup>1</sup> -C <sup>1</sup> as percentage			
of gsl	17.8	19.1	18.4
M <sup>1</sup> -M <sup>1</sup> as percentage			
of gsl	24.7	25.8	25.4

Summarizing, *parvus* appears to be based on misinterpreted allometries in the skull in *crypturus*.

Koopman (1966) suggested that *anurus* could be a subspecies of *crypturus*. Kock (1969) ranked *anurus* as a subspecies of *labiatus*, and Koopman (1975) was inclined to agree with this alliance. On different grounds I conclude that *anurus* should be regarded as a mere synonym of *labiatus*, without taxonomic status (this paper). Unless a complicated pattern of genetic relationships is conceived, this implies that *labiatus* ("anurus") cannot be a subspecies of *crypturus* (*gambianus*), as *labiatus* and *gambianus* are sympatric in North Cameroon, South Sudan, and Ethiopia. As there are no indications of possible

interbreeding of *labiatus* and *crypturus*, there is no need for speculations (compare the remarks on *Epomophorus labiatus* in relation to *E. minor* on pp. 114-118). Happold *et al.* (1987) tentatively included the Malawian specimens identified as *anurus* (= *labiatus*) by Bergmans *et al.* (1983) in *crypturus*. They were followed in this by Ansell *et al.* (1988). The adult ♂ concerned had a fal of 77.1 and a gsl of 47.1; the other, almost adult ♂ had a fal of 77.4. In fal these specimens approach *crypturus*, but the gsl is much too small, as appears from the range for this measurement in the diagnosis (with as minimum value in 47 adult skulls 51.8), and I see no reason for re-allocation of these specimens. The measurement ranges given by Happold *et al.* (1987) apparently include many immature specimens and have little value in this discussion.

Distribution and geographical variation: *E. g. crypturus* appears to be restricted to the various types of woodland of tropical and subtropical East Africa south of about 8° S. Aggundey *et al.* (1984) quoted a record of *E. crypturus* from as far north as Mombasa by Peters (1877b), but this was based on a specimen of *E. wahlbergi* (Sundevall, 1846) as Andersen (1912: 523) observed. *E. crypturus* seems to avoid Zambesian *Acacia* deciduous bushland and wooded grassland (type 35a in White, 1983) as much as the nominate subspecies avoids the Ethiopian equivalent of this vegetation. Smithers (1971) believed that *crypturus* may penetrate drier regions by way of riverine woodlands, as specimens had been found in fig trees (*Ficus* sp.), and some notes on collectors' labels support this idea.

In the north the distribution limit may be dictated by the occurrence of the Mosaic of Guineo-Congolese lowland rainforest and secondary grassland (type 11a in White, 1983) in Zaire — although forest edges are a likely habitat and *crypturus* may still be discovered here —, and possibly by the mountain ranges marking the border between Zimbabwe and Tanzania — although *crypturus* has been found in southeastern Tanzania and may still be encountered in the southwest of this country. In

the west and southwest, drier types of vegetation, in casu the mentioned Zambesian *Acacia* deciduous bushland and wooded grassland in eastern Angola and in Botswana and the Kalahari *Acacia* wooded grassland and deciduous bushland in Botswana (type 44 in White, 1983) appear to prevent *crypturus* from dispersion. In the south, *crypturus* remains east of the extensive region of highveld grassland (type 58 in White, 1983) in the Transvaal. The eastern border of its distribution here and in northeast Mozambique cannot be correlated with changes in vegetation or other natural phenomena, and it is probably just poorly known. Smithers *et al.* (1976) could map relatively few fruit bat localities in Mozambique; the northeast of this country is a virtual blank in this respect (compare also fig. 1).

The known localities cannot be correlated with a particular range of altitudes but in many cases *crypturus* inhabits areas with considerable relief. The records from at or near the coast and other documented collecting heights range from about sea level to 2185 m (this latter record reported by Ansell *et al.*, 1973). Comparison of collecting localities with a contour map learns that most specimens have been collected at altitudes between 500 and 1500 m.

The available measurements (table 3) suggest that some geographic variation in dimensions may exist. Specimens from Botswana are somewhat smaller, on the average, than those from Zambia, Zimbabwe and, possibly, Mozambique and South Africa. Smithers (1971) gives as weights for 15 ♂♂ from Botswana 91.0-118.0 g (mean 103.4), which seems to confirm their relative small size if compared to the data from the mentioned other countries (table 3).

### ***Epomophorus gambianus pousarguesi* Trouessart, 1904 — New combination**

*Epomophorus pousarguesi* Trouessart, 1904: 55 (type locality: Grande Brousse between Yabanda and Mpoko); Bergmans, 1978: 681; Schlitter *et al.*, 1982: 151 (in part: only the specimen from between Mpoko (near Makorou) and Yabanda — not Yobanda — and from Bangui; there is no solid record from the Poste de la Mission Haut Kemo — which is not "at Bangui").

*Epomophorus gambianus*; Schlitter *et al.*, 1982: 138 (in part the specimen cited from De Pousargues, 1897).

#### *Material examined*

CENTRAL AFRICAN REPUBLIC. Along the track between Mpoko (near Makorou) and Yabanda: 1 ♀, 5/11-XII-1891, J. Dybowski (holotype of *Epomophorus pousarguesi* Trouessart, 1904; MNHN 1899-1020). Bangui: 1 ♂, 2 ♀♀, alc., skulls, 27-XI-1965, A. Chipaux (MNHN: 1 ♂, 1 ♀; ZMA 18.097: 1 ♀).

*Diagnosis:* As for the species but with the following measurement ranges and ratios:

fal	♂	100.0, ♀♀	91 -94.8 (n = 3);
gsl	♂	63.6, ♀♀	54.4-56.8 (n = 3);
cbl	♂	63.6, ♀♀	54.0-56.1 (n = 2);
rl	♂	29.7, ♀♀	24.5-25.2 (n = 2);
zw	♂	31.2, ♀♀	26.5-28.7 (n = 3);
C <sup>1</sup> -M <sup>1</sup>	♂	23.2, ♀♀	19.2-19.4 (n = 3);
W		♀♀	145 (n = 1);
rl	♂	46.7% of gsl,	♀♀ 44.4-45.0% of
		gsl;	
pl	♂	67.6% of gsl,	♀♀ 63.8-66.4% of
		gsl;	
zw	♂	49.1% of gsl,	♀♀ 47.7-50.5% of
		gsl.	

Measurement ranges largely unknown but apparently the largest subspecies.

*Distribution:* Fig. 2.

*Related species:* See this section under the nominate subspecies. It is not known if *E. g. pousarguesi* is sympatric with other species of the genus.

#### *Remarks*

*Taxonomy:* In an earlier paper (Bergmans, 1978) I argued that the only character distinguishing *pousarguesi* from *gambianus* is the larger size of the former. I retained it as a species because at that time my understanding of the distribution pattern of *gambianus* was still very incomplete. I assumed that it would be much more widespread in this part of Africa and could not conceive *pousarguesi* as a marginal and essentially allopatric population of *gambianus*. Even now, I am not quite prepared to agree with Schlitter *et al.* (1982) that *gambianus*

is widespread in the Central African Republic. There are only a few records and still fewer reasoned identifications. But, although there are still very few records of *gambianus* from between 15° and 32° E, there are virtually no records from the Central African lowland rainforest (south of about 4° to 4°30' N). This is much in line with what we know of the species' preference for vegetation types, and it follows that *pousarguesi* represents indeed a marginal and probably even isolated population, for which because of its aberrant measurements subspecific rank within *gambianus* seems appropriate.

It may be useful to give an account here of the records of *Epomophorus gambianus* for the Central African Republic. Schwarz (1915) mentioned two specimens from Njia, between Gore in Chad on the border with the Republic and the Nana Barya River. It is not clear in which of the two countries Njia should be located but as Gore was the starting point of the expedition Schwarz dealt with, and the Pama River to the south the end, it is more probably in the Republic. One of the two specimens, noted but not measured by me in the SMF, is labelled "Ngia-Fl.", which may indicate the Nya River on the border just west of Gore. Dr D. Kock gave for this adult ♀ (alc., skull, XI-1912, R. Houy, SMF 5823) a fal of 88.1 and a gsl of 55.9; in fal it agrees with the typical subspecies, in gsl it is slightly larger and widens the existing overlap between the ♀♀ of both subspecies (Kock, *in lit.*, 31-I-1978). The other specimen, labelled "Ngia" only (ZMB 20854), is a young adult ♂ with a fal of 86.8 and a broken skull (gsl possibly about 57.5). In 1920, Schwarz mentioned specimens from Fort Crampel (which I have not found in collections) and Badingua. There are two ♀♀ from Badingua in the SMF, with fals of 87.8 and 88.0, respectively (Dr D. Kock, *in lit.*, 31-I-1978). Blancou (1958) recorded *E. pousarguesi* from Bozoum. Some material collected by him is in the AMNH but I have not seen any evidence for this record. As will appear from the following, Bozoum is more likely inhabited by typical *gambianus*, and for the present I reject

Blancou's *pousarguesi* record. His record, in the same paper, of *gambianus* from Ndélé is more likely correct, but I have not come across specimens from there in collections. Schlitter *et al.* (1982) recorded *gambianus* from Bangassou and Koumbala Camp. I examined the single ♀ specimen from Bangassou (CMNH 40972) and cannot agree that it is adult, as these authors claimed. Their identification may be right but as Bangassou may also be inhabited by *pousarguesi*, I prefer to await further material from that area. The ZMB collection contains an adult ♀ (fal about 84, gsl 51.4) from Bouar, which clearly represents typical *gambianus*, as do three specimens in the BMNH collection: an adult ♂ from Kaja Nze (gsl about 54.4), a subadult ♂ from Bamingui-Bangoran National Park at 7°55' N, 19°26' E (gsl 53.9), and a subadult ♀ from Bamingui (gsl 49.6).

Summarizing, in the Central African Republic *E. g. gambianus* is known from two or three areas: the west (Bouar, Njia, and possibly Bozoum), the central north (Badingua, Bamingui; Bamingui-Bangora National Park; Kaja Nze; Koumbala; and possibly Crampel and Ndélé); and possibly the central southeast (Bangassou). *E. g. pousarguesi* is known with certainty only from along the track between Mpoko (near Makorou) and Yabanda, and from Bangui. The only existing, conceivable physical barrier separating the two subspecies at least sufficiently effectively to allow for a sustained dimensional difference is the watershed (altitude between 500 and 1000 m) between the basins of the Chari and Oubangui rivers. Of the localities mentioned, however, the location of Bouar does not fit this hypothesis, and would call for another explanation (for instance, a discontinuity in distribution). It furthermore implies that the type locality would be on the Oubangui side of the watershed, which would practically restrict it to Yabanda itself (see Bergmans, 1978, fig. 1). It moreover suggests that Bangassou would lie in the *pousarguesi* area. Another factor that may play a role is a difference in habitat preference. Yabanda, Bangui and Bangassou are in the west-east belt of Mosaic of Guineo-Congolian lowland rain

forest and secondary grassland (type 11a in White, 1983), but so is Bouar. All other localities are in the belt of Sudanian woodland with abundant *Isobertinia* (type 27 in White, 1983). However, in West Africa typical *gambianus* is found in both these vegetation types. In conclusion, it is not unlikely that geohistorical changes, and ensuing climatological and vegetational changes, rather than recent conditions are at the basis of the original separation of the two subspecies.

### ***Epomophorus labiatus* (Temminck, 1837)**

*Pteropus labiatus* Temminck, 1837: 83 (type locality Abyssinia).

*Epomophorus labiatus*; Tomes, 1860: 55; Tomes, 1861: 11; Jentink, 1887: 251; Jentink, 1888: 137; Andersen, 1912: 529-531 (in part: possibly only the type specimen; see the remarks below).

*Epomophorus anurus* Heuglin, 1864: 12; Andersen, 1912: 532-535; Dollman, 1914b: 308; Verschuren, 1957: 199; Rahm *et al.*, 1963: 27; Hill *et al.*, 1971: 29; Bergmans *et al.*, 1983: 118; Baeten *et al.*, 1984: 184.

? *Epomophorus labiatus minor*; G. M. Allen *et al.*, 1936: 45 (locality suggestive of *labiatus* rather than *Epomophorus minor* Dobson, 1880).

*Epomophorus crypturus* (not of Peters, 1852); Hayman *et al.*, 1966: 23 (in part: specimen IRSN 10677 from "Kilwezi"—the label reads Kilubwezi); Happold *et al.*, 1987: 348 (in part: the specimens from Kasungu National Park); Ansell *et al.*, 1988: 27 (in part: the specimens from Kasungu National Park).

*Epomophorus labiatus anurus*; Kock, 1969: 18-24; Largen *et al.*, 1974: 227 (in part: specimens from near Ghinir are *Epomophorus minor* Dobson, 1880).

*Epomophorus labiatus labiatus*; Largen *et al.*, 1974: 226-227.

*Epomophorus gambianus* (not of Ogilby, 1835); Tuttle, 1986: 540-558.

### *Material examined*

(Other locality records not listed unless identification unequivocal.)

BURUNDI. Bujumbura: 4 ♀♀, alc., VIII-1976, J. Verschuren (IRSN 19909); 12 ♂♂, 5 ♀♀, alc., 12/21-XI-1978, F. C. Roest (IRSN). Kigamba: 8 ♂♂, 11 ♀♀, alc., 15-VII-1976, J. Verschuren (IRSN 19900, 19902).

CHAD.

(Maïlao.)

CONGO. Pointe Noire: 1 ♀, 29-XI-1972, W. Bergmans (ZMA 15.667).

ETHIOPIA. "Abyssinia": 1 imm. ♀, mounted, skull, P.-E. Botta (lectotype of *Epomophorus labiatus* (Temminck, 1837); RMNH; Jentink, 1887, specimen *b*; 1888,

specimen *c*). Aisaita: 6 ♂♂, 4 ♀♀, alc., J. S. Ash (USNM 462683/85, -90/92, 462704, -08, -10/11). Azir River mouth: 2 imm. ♀♀, alc., skulls, 21-VIII-1968, P. Morris (BMNH 70.397/98). Bahadu: 1 ♀, alc., skull (USNM 497491). Bahr dar Giorgis: 1 ♂, alc., 4-VI-1922, J. P. Mitchell (BMNH 23.3.26.1). Bellegas Valley: 1 ♂, Th. von Heuglin (NMW 18300). Bulcha: 1 ♂, I-1974, J. S. Ash (USNM 462688); 1 ♂, 4-II-1976, G. Nikolaus (SMNS 29878). Bulcha Forest: 3 ♂♂, alc. (BMNH). Gondar: 2 ♂♂ (BMNH 60.137/38). Keren: 1 ♀, 1 imm.♂, alc., skulls, 1909, G. Ceconi (ZMB 67067/68). Koka: 1 imm. (♀ ?), 16-X-1973, J. S. Ash (USNM 462682). Lake Awasa: 1 ♂, alc., skull, 2-IX-1973, H. Rupp (ZMA 17.343). Lake Tana: 1 ♀, alc., skull, X-1967, Schüz (SMNS 17489). Makale: 1 specimen, skull, 18-I-1976, J. S. Ash (USNM 521056). Shifra: 2 ♀♀ (one: alc.), 7/9-V-1976, G. Nikolaus (SMNS 29860, 29880). Sidamo, Bulcha Forest: 1 (♀ ?), skull, 13-XII-1969, M. J. Largen (BMNH 71.2410).

(Gofa, Simien.)

KENYA. Barberton's Farm: 2 ♂♂, 1 ♀, 26/31-VII-1963, R. E. Mumford (USNM 350809/10, -12). Kakamega Forest: 3 ♂♂, 3 ♀♀, 27-I-1971, J. G. Williams (ROM 65993/97, 66000). Kibwezi: 1 imm. ♀, 25-I-1950, E. M. Queeny (AMNH 184472). Kirui: 1 ♂, R. Kemp (BMNH 10.4.1.4). Kitale and 12 miles W of Kitale: 15 ♂♂, 16 ♀♀, 24-VII/13-VIII-1968, B. J. Hayward (USNM 436420/24, -26/35, -43/44, -46/50, -56/57, -59/62, -64/66). 15 km W of Kitale: 1 ♂, alc., skull (ROM 42958). Kongelai escarpment: 1 ♀, 22-VII-1964, J. G. Williams (LACM 51442); 2 ♀♀, 23-XII-1965, J. G. Williams (ROM 40196/97). 3 miles S of Kongelai escarpment: 4 ♂♂, 1 ♀, 2/3-VIII-1968, B. J. Hayward (USNM 436436/40). Mitunbur: 1 ♀, 11-XII-1965, J. G. Williams (ROM 38250). Mount Elgon (Kenya or Uganda): 1 ♀, R. Kemp (BMNH 10.4.1.5). Rondo Forest: 1 ♀, 2 ♂♂, I-1972, R. L. Peterson & R. Glen (ROM 63887/89). Simbi: 1 ♂, alc. (BMNH). 30 miles E of Tororo: 3 ♂♂, 1 ♀, 23/24-V-1965, A. E. & J. G. Williams (ROM 36228/30, -32). Turkwell: 2 ♂♂, skins (BMNH 93.2.3.4, -6).

(Lamu.)

MALAWI. Lisanthu: 1 ♂, alc., skull, 19-III-1982, H. Jachmann (ZMA 21.693b).

NIGERIA. Malamfatori: 1 ♂, alc., 1968, J. Fagbohunmi and party (ZMUI).

RWANDA. Gisenye: 1 ♂, 5-VII-1927, J. P. Chapin *et al.* (AMNH 82377). Musha: 1 ♂, 25-III-1968, M. Anciaux de Faveaux (IRSN 16023). Rubona: 3 ♂♂, 4 ♀♀, 18-I/27-XII-1966, M. Anciaux de Faveaux (IRSN 15481, 16024, -26, -29/30, -35).

(Bugarama, Butare, Karama, Kayonza, Kibuye, Kigali, Mabanza, Murunda, Nyakibanda, Nyamata, Nyundo, Rukira.)

SUDAN. Boma Mountains, western foothills: 1 ♂, alc., 23-II-1979, G. Nikolaus (SMNS 29874). Boro River (25 km north): 1 ♀, 31-III-1979, G. Nikolaus (SMNS 29893).

Buram: 5 ♂♂, 2 ♀♀, 1 specimen, alc. and/or skulls, 26-I/3-III-1965, D. Kock (SMF 33039/40, -42, -48, -56/57, 33156/57). Dad Majok: 1 imm. ♂, 1 imm. (♀ ?), 29-III-1907, A. L. Butler (BMNH 8.4.2.1/2). Didinga Mountains, western foothills: 2 ♂♂, alc., 5/7-II-1979, G. Nikolaus (SMNS 29872). Gilo: 1 ♀, 4-I-1978, G. Nikolaus (SMNS 29885). Ikotos: 1 imm. ♀, 4 imm. ♂♂, 16-II/5-V-1950, J. S. Owen, H. Hoogstraal (FMNH 67161, 67314/7). Jebel Maba: 1 ♀, via A. L. Butler (BMNH 11.11.25.4). Kadugli: 2 ♀♀, (1: alc.), skulls, 2-IX-1962 and 13-III-1963, D. Kock (SMF 33054, 33154). Kagelu: 1 ♀, 18-XI-1940, J. G. Myers (AMNH 118581). Kajo Kaji (10 km west): 3 ♀♀ (1 in alc.), 25-VII-1978, G. Nikolaus (SMNS 29866, -89/90). Kapoeta: 1 ♂, alc., 17-XII-1977, G. Nikolaus (SMNS 29864). Kapoeta (40 miles west): 1 imm. ♀, 15-XII-1977, G. Nikolaus (SMNS 29883). Kassala: 1 ♀, 27-XI-1972, H. Hoogstraal & M. N. Kaiser (FMNH 105578). Maridi: 1 ♂, alc., 1 imm. ♀, 7-VIII-1978, G. Nikolaus (SMNS 29870, 29892). Mount Korobe: 1 ♂, 1 ♀ (alc.), 27-VII-1978, G. Nikolaus (SMNS 29869, -91). Nagishot: 1 ♀, 31-XII-1977, G. Nikolaus (SMNS 29884). Raffile/Sue River: 1 imm. ♂, alc., 13-IX-1978, G. Nikolaus (SMNS 29871). Riki River: 1 ♀, alc., 5-IV-1979, G. Nikolaus (SMNS 29875). Tonj: 2 ♂♂ (1: alc.), 21/22-I-1977, G. Nikolaus (SMNS 29862, -81). Torit: 5 ♂♂, 2 ♀♀, 22-X-1949/24-I-1950, H. Hoogstraal (FMNH 66546, -49/51, -53, -55, -57). Torit (80 km E): 2 ♀♀ (1: alc.), 13-XII-1977, G. Nikolaus (SMNS 29863, -82). Zalingi: 1 ♀, 14-IV-1964, M. El Rayah (ROM).

(Mbili, Mundri, Ngohalima, Ngosulugu, Raffili, Raga, Wau.)

TANZANIA. Handajega: 1 ♂, 7-X-1960, via J. Plisnier (IRSN 15633). Kasulu: 1 ♀, via C. H. B. Grant (BMNH 22.8.25.1). Kibarra: 2 imm. ♂♂, 2 imm. ♀♀, alc., 25/26-VIII-1985, P. C. Goudswaard (ZMA 22.718/21). Kigoma: 1 ♂, alc. (BMNH). Mazwa: 1 ♀, alc., skull, 10/11-IX-1983, R. Luttk (ZMA 22.249). Minziro: 3 ♂♂, 14-II-1968, 1 ♀, A. L. Archer (LACM 61461/4). Mwanza: 10 ♂♂, 8 ♀♀, alc., skulls, 28/29-I/XII-1983, R. Luttk, and 11-II/26-III-1985, P. C. Goudswaard (ZMA 22.241, -43, -46/48, -50/51, 22.424, -27/30, -33/35, -43, 22.517, -22). Tabora: 5 ♂♂, 1 ♀, via Swaythling, 9-XII-1918, A. Loveridge, without date, A. Loveridge, and 30-VIII-1963 (3 specimens), respectively (BMNH -, -, 22.7.17.20; LACM 31763/5). Ugano: 1 ♀, 24-VI-1938 (NMW B5112). Ukora Island: 1 ♂, 1 ♀, III-1953, A. Smith (BMNH 64.1334/5). Ussuwi: 6 ♂♂, skins, skulls of 2, 4 specimens, skulls possibly of the 6 ♂♂, probably all of 1907, Grauer (ZMB 54413/17, -21, and without numbers).

UGANDA. Amudat: 1 ♂, 6-VIII-1968, B. J. Hayward (USNM 436442). Budongo Forest: 2 ♂♂, 1 ♀, 6/27-VI-1966, J. G. & A. Williams (ROM 46475; LACM 51458/9). Buhuru: 1 ♀, alc., skull, 1911, R. Kmunke (NMW 17862). Bukalasa: 3 ♂♂, 2 ♀♀, alc. (BMNH). Bwamba Forest: 1 ♂, 13-IX-1958, P. Martin (LACM 19532). Entebbe: 1 ♂, alc., 29-II-1907, Schlüter (ZMB

A5.08); 2 ♂♂, alc. (BMNH). Kampala: 4 ♂♂, 1 ♀, 21/22-XII-1909, E. A. Mearns, J. A. Loring (USNM 164905, -07, -10/11, -13). Katera: 2 ♂♂, cf. 11/15-II-1962, A. L. Archer (LACM 51460/65). Masindi: 2 ♂♂, 28-IX-1957, 15-X-1958 (BMNH 66.3599, 66.3601); 1 ♀, 22-III-1927, J. T. Zimmer (FMNH 29431). Mbale: 3 ♀♀, alc., 11-III/5-IV-1965 (BMNH 65.1058/062). Mengo: 1 ♂, 10-XII-1897, F. J. Jackson (BMNH 99.8.4.2). Mongiro, Bwamba Forest: 3 ♂♂, 1 ♀, X-1957, 19/20-VII-1963, 16-XI-1968, 'WVZ', R. Glen (LACM 31761, -67/68, 51454). Moroto: 1 ♂, 31-III-1966, A. C. Brooks (BMNH 66.3602). Mount Moroto: 1 ♂, W. P. Lowe (BMNH 13.10.18.9). Namulere: 1 ♀, alc. (BMNH 64.61). Namubali: 5 ♂♂, 2 ♀♀, alc. (BMNH 65.1058/62; -). Ngongera: 1 ♂, 7 ♀♀, alc., skulls of 6, 29-III-1970, J. D. Hawkins & J. van Vegten (ZMA 13.355, -57, -60/62, -65, -67, -69). Ntandi, Bwamba Forest: 4 imm. ♀♀, 25-VI-1967, 9/15-XI-1968, A. Williams, R. Glen (LACM 51446/8, 51453). Ntorako (15 miles south): 1 imm. ♀, 1-VIII-1963, 'WVZ' (LACM 31766). Pajule: 1 ♂, alc. (BMNH). Port Alice: 1 specimen, alc., skull (BMNH 1.8.9.91). Ruwenzori: 2 ♂♂, 2 ♀♀, 11-III/17-VII-1906, R. E. Dent (BMNH 6.12.4.7/10). Soweh Island: 1 ♂, skull, 15-I-1891, Emin Pasha (ZMB 54426).

ZAIRE. Baraka: 1 ♂, 3 imm. ♂♂, alc., 16-IV-1947, Mission Biologique du Lac Tanganika (IRSN 9061); 1 ♂, 1 ♀, alc. (BMNH). Fataki (region): 2 ♂♂, alc., 1948, via J. Verschuren (IRSN 18528). Gangala na Bodio: 2 ♂♂, 22-XI-1947, via M. Micha, 1 ♀, alc., 9-IV-1948, Mission Hediger-Verschuren (IRSN 12934/5, 11658). Parc National de Garamba (various sites): 4 ♂♂ (1 in alc.), 4 ♀♀, 1-III-1951/2-IV-1952, Mission de Saeger (IRSN 13506/08, -10, -12/13, -16, -19). Kahungu: 1 ♂, 14-X-1963, F. Dieterlen (SMNS 7289). Kilubwezi: 1 ♀, 6-VIII-1948, G. F. de Witte (IRSN 10677). Kiriamo: 1 imm. ♂, Emin Pasha (BMNH). Kirimba: 1 ♀, skull, 18-I-1892, Stuhlmann (ZMB 10027). Lwiro: 1 ♀, 28-XI-1964, cf. F. Dieterlen (SMNS 7290). Nyakaliba: 1 ♂, 10-II-1954, G. F. de Witte (IRSN 17293). Rutshuru: 1 ♂, alc., 10-I-1938, Mission S. Frechkop (IRSN 4787). Uvira: 3 ♀♀ (2: alc., skulls), II-1910, R. Grauer (NMW 4880) and 20-V-1955, E. Baker (USNM 301713/14).

*Diagnosis:* A medium-sized, typical species of the genus, with the fourth palatal ridge halfway between the third and fifth, and two postdental ridges — although in small specimens the first of these two may be partly interdental —; a relatively short rostrum and palate; a relatively large zygomatic width. Measurement ranges and ratios taken from specimens from all over the species' range:

fal ♂♂ 66.7-80.3 (n = 145),  
♀♀ 64.8-78.3 (n = 108);

gsl ♂♂ 40.2-51.0 (n = 69),  
 ♀♀ 36.8-44.9 (n = 62);  
 cbl ♂♂ 40.0-48.4 (n = 44),  
 ♀♀ 37.0-43.9 (n = 39);  
 rl ♂♂ 16.1-20.6 (n = 33),  
 ♀♀ 14.4-18.1 (n = 36);  
 zw ♂♂ 21.6-25.3 (n = 43),  
 ♀♀ 20.0-24.0 (n = 36);  
 C<sup>1</sup>-M<sup>1</sup> ♂♂ 13.5-17.8 (n = 45),  
 ♀♀ 13.3-16.0 (n = 39);  
 M<sup>1</sup> ♂♂ 2.7- 3.9 (n = 44),  
 ♀♀ 2.6- 3.8 (n = 49);  
 W ♂♂ 54-99 (n = 23),  
 ♀♀ 51-81 (n = 21);  
 rl ♂♂ 39.6-43.3% of gsl,

♀♀ 38.0-41.5% of gsl;  
 pl ♂♂ 60.1-64.3% of gsl,  
 ♀♀ 57.6-63.0% of gsl;  
 zw ♂♂ 49.0-56.0% of gsl,  
 ♀♀ 51.2-57.1% of gsl.

Dimensions of specimens largest in southwestern Sudan and northeastern Zaire, smallest in western Kenya and northwestern Tanzania. Table 4 gives a breakdown of measurement ranges per country.

*Distribution:* Fig. 5.

*Related species:* In the southern and largely disjunct *Epomophorus gambianus crypturus* the ♂♂ are absolutely larger and the ♀♀ average

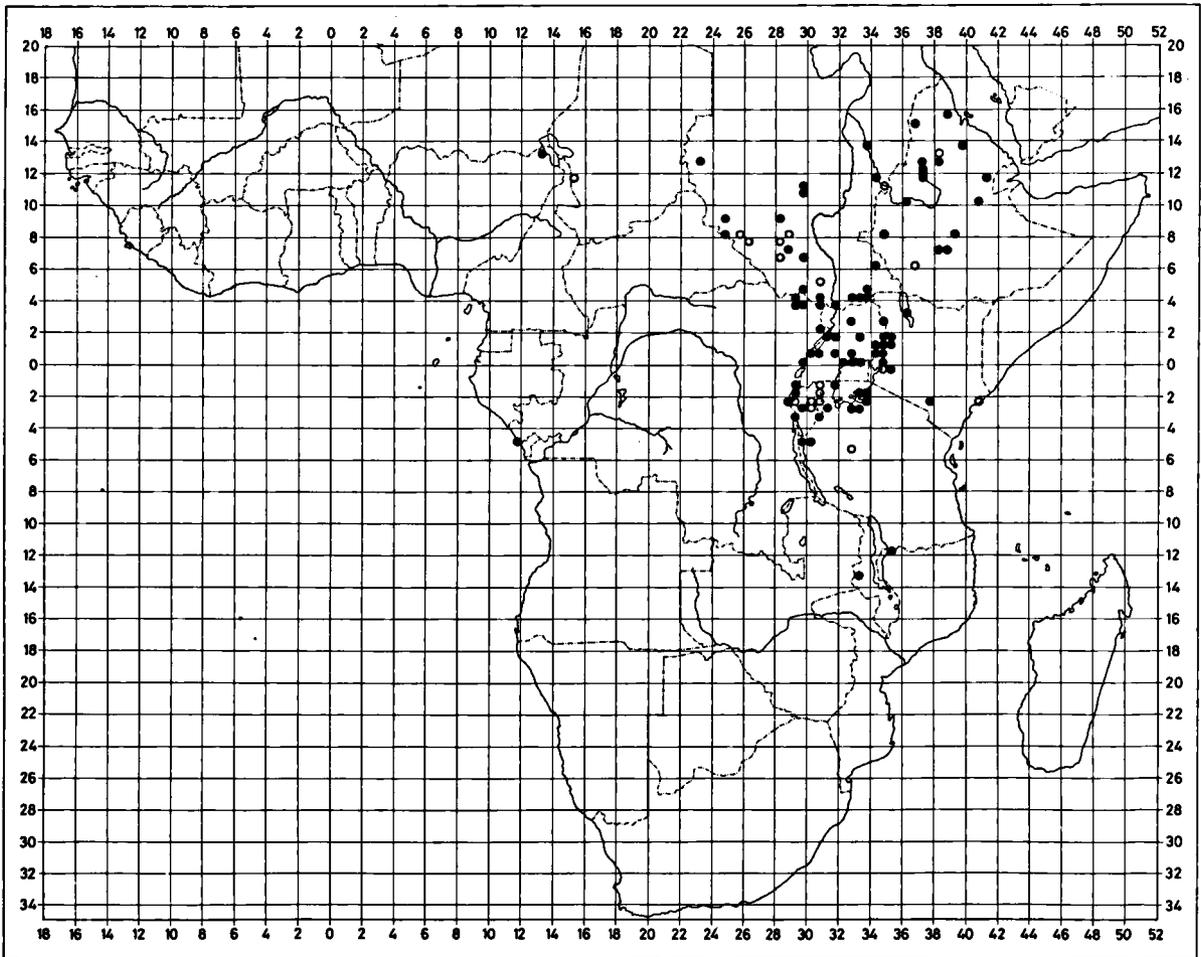


Fig. 5. Distribution of *Epomophorus labiatus* (Temminck, 1837). Black dots: squares from which material has been identified by the author. Open circles: records from literature and correspondence.

Table 4. Ranges of selected measurements of *Epomophorus labiatus* (Temminck, 1837) per country.

		♂♂					♀♀						
		fal	gsl	zw	C <sup>1</sup> -M <sup>1</sup>	I M <sup>1</sup>	W	fal	gsl	zw	C <sup>1</sup> -M <sup>1</sup>	I M <sup>1</sup>	W
Burundi	n	20						17					
	m	72.3						69.8					
	min	68.6						66.7					
	max	75.3						72.4					
Chad*	n	1											
		77	51.0	24.9	17.8								
Congo	n							1	1	1	1	1	
								69.1	39.1	23.0	14.0	2.8	
Ethiopia	n	14	6	4	5	11		8	3	2	3	8	2
	m	70.9	43.6	23.5	15.9	3.2		69.2	40.1	21.6	14.6	3.25	55
	min	66.1	41.3	22.9	14.7	2.8		66.8	37.8	21.0	13.9	2.6	53
	max	78.6	46.6	23.7	17.1	3.9		74.1	43.4	22.3	16.0	3.8	57
Kenya	n	29	22		1	1	4	27	23			1	3
	m	72.6	46.4		15.6	3.35	80	69.5	40.8			3.5	66
	min	66.7	45.5				75	67.1	36.8				56
	max	78.2	48.6				84	73.0	43.0				75
Malawi	n	1	1	1	1								
		77.1	47.1	23.6	16.35								
Nigeria	n	1											
		78.0											
Uganda	n	33	13	13	14	10	8	22	11	9	9	8	8
	m	73.4	46.2	23.5	15.9	3.0	76.5	71.5	42.0	22.7	14.7	3.2	68
	min	70.0	44.1	21.9	14.6	2.7	65	66.7	40.2	20.6	13.6	2.8	61
	max	77.2	48.6	24.9	16.6	3.3	92	75.5	44.0	23.9	15.5	3.8	81
Rwanda	n	1	2	2	3			2		1	2		
	m				14.3								
	min	71.4	40.8	22.0	13.9			65.5		20.6	13.7		
	max		42.6	22.5	14.7			67			13.7		
Sudan	n	11	6	4	4	10	6	8	9	6	9	21	7
	m	74.4	46.3	24.4	16.4	3.3	76.5	73.1	41.8	22.4	14.5	3.1	65
	min	68.3	44.2	24.0	15.7	3.0	63	68.3	39.5	21.3	13.5	2.6	58
	max	80.0	48.3	25.3	17.1	3.7	99	77.4	44.9	24.0	15.4	3.7	70
Tanzania	n	22	6	17	12	9	5	15	10	12	9	10	1
	m	70.3	42.4	22.6	14.4	3.0	64	68.0	39.0	21.2	13.6	2.9	51
	min	67.9	40.2	21.6	13.5	2.8	54	64.8	38.1	20.0	13.3	2.65	
	max	73.9	46.2	24.2	15.1	3.15	70	72.1	40.7	22.4	14.8	3.1	
Zaire	n	11	2	1	4	3		7	5	5	6		
	m	76.4			16.4	3.0		73.7	42.0	23.0	14.5		
	min	73.3	43.1	22.9	15.0	2.8		70.8	40.0	22.1	13.6		
	max	80.3	46.5		17.1	3.3		78.3	43.6	24.0	16.0		

\* Measurements Chad specimen copied from Vielliard, 1974.

larger in all dimensions, and in the predominantly eastern *E. minor* Dobson, 1880 both ♂♂ and ♀♀ average distinctly smaller in all measurements than *E. labiatus*. (See also the remarks below.)

#### Remarks

Taxonomy: Temminck (1837) based the description of this species on two specimens, a ♂ and a ♀. He figured the ♂ with fully developed

epaulets, and the heads of both specimens. His only measurements are of total length, wing span and fal, respectively "4 pouces 1 ou 2 lignes" (110.25 or 112.5), "15 pouces" (405), and "2 pouces 4 lignes" (63). It is not stated which measurement pertains to which specimen. Tomes (1861) examined both specimens and published some external measurements of the "nearly, if not quite adult" ♂, which had a fal of 63.5 and a head length of 46.6; the ♀ was thought to represent "quite a young example of some larger species...".

Only 16 years later, Jentink listed the latter as the only type specimen still present in the RMNH collection (1887: 251, specimen *b*; 1888: 137, specimen *c*). Andersen (1912: 530) consequently referred to this specimen as the type of the species, and although no later student of *Epomophorus* seems to have examined it and it has played no role in the development of epomophorine taxonomy as yet, I propose here to follow Andersen and consider it as the lecto-type specimen of *Pteropus labiatus*, because the other specimen has apparently been lost. However, this entails an unexpected and important consequence. Whereas it is very likely, from the combination of its adulthood (epaulets!) and fal of 63.5, that the ♂ syntype specimen represented what is currently known as *Epomophorus minor* Dobson, 1880 and its continued existence would have rendered *minor* a synonym of *labiatus* (as it was by far the better specimen to serve as type — although its provenance was unknown), the remaining ♀ is different. Tomes (1861) was right in his remark that it belongs to a larger species and it is curious that Andersen neglected this observation. Andersen's concept of the species has been the guideline for many later authors and, in my opinion, the source of much confusion in the taxonomy of the smaller epomophorines.

The six important adult specimens used by Andersen were: a mounted ♂, with skull *in situ*, from Sennar (MNHN A110); an odd skull from Sennar (MNHN A6780), apparently identified by Andersen as a ♂, a young adult ♂ in spirit, with extracted skull, from Roseires (BMNH

8.4.17.3); a mounted ♂, with skull, from "Abyssinia", originally from the Rüppell collection (RMNH); a mounted ♂, with skull, from Let Marefia (MNHN 1885-189); a mounted ♀, with skull *in situ*, from Sennar (MNHN A111). For teeth measurements Andersen used the following six specimens: the ♀ type specimen; the odd skull from Sennar (MNHN 6780); two ♂♂ (one immature) from Roseires (BMNH 8.4.17.2/3); the ♂ from Let Marefia (MNHN 1885-189); and one unsexed specimen from "Shoa" (SMF 4370).

Thus, forearm and other body measurements were taken from one spirit and four mounted specimens. As forearms in mounted specimens are usually not to be measured accurately, Andersen's range of 62-66.5 for four ♂♂ and the length of 66 for one ♀ are not very reliable. He further measured four male skulls only, but nevertheless concluded that "sexual difference in size [is] none or quite inconspicuous", an idea that has persisted into our time (e.g. Hayman *et al.*, 1971). I have not seen all the specimens used by Andersen (1912) but do not expect them to reveal much which cannot be gleaned from Andersen's remarks. Of all later authors, only Harrison (1959) seems to have analysed Andersen's description of *labiatus* in some detail. He measured teeth in three specimens from Roseires in the BMNH (certainly including two of Andersen's), as since Andersen's work teeth measurements were regarded as one of the crucial characters by which *labiatus* could be distinguished from *minor*, but could not reproduce Andersen's values; Harrison's maximum values for P<sup>3</sup>, P<sup>4</sup> and M<sup>1</sup> lengths are even less than Andersen's minimum values.

The localities in Andersen's series fall into two groups: Sennar and Roseires in central eastern Sudan, and Let Marefia, Shoa and Abyssinia in Ethiopia. Abyssinia includes an area where *minor* is also found. (Largen *et al.*, 1974, mentioned *minor* also from Let Marefia.) But it should be noted that some of Andersen's specimens are of inexact or even doubtful origin. First, there is the change, by Andersen, of the type locality "Abbyssinia" into Sennar.

Sennar is much more exact, as locality, but outside Abyssinia. It has not been made clear why Temminck would have made such a mistake. Dr M. Tranier of the MNHN kindly informed me, *in lit.*, 15-X-1987, that according to the registers of that institution Paul-Emile Botta, French consul at Djeddah, Arabia, sent two series of small mammals to Paris: specimens from Egypt and Sudan in 1834, and from Arabia in 1837. Among the first were three fruit bats "with pendulous lips" from Sennar. There were still three such specimens in Paris when Andersen visited the MNHN, and consequently Botta must have collected more specimens, and possibly in other localities, than would appear from the registers of that museum. I therefore propose here to change the type locality of *E. labiatus* back into the original "Abyssinia" again. Second, the Roseires specimens came to the BMNH via a zoo, a wayside station that not often bothered about exact natural origins of specimens. Third, of course, indications like Shoa and Abyssinia are far too general, as we now know, to include specimens so labelled in an analysis of *Epomophorus* taxonomy in this part of Africa.

Andersen's minimum of 62 for male fal is not consistent with any other data I collected for *labiatus*, but very much smaller. This may be due, in part, to the impossibility of properly measuring fals in mounted specimens. But if it approaches the correct value, it indicates *minor*. Andersen's only spirit specimen, a ♂ from Roseires, will certainly have had a fal in the range of 62-66.5; I have only seen its skull, which has a gsl of 37.65 and a cbl of 36.65, and in my opinion the specimen represents *minor*. Andersen's range for male gsl, 37.2-39.7, also indicates *minor* rather than *labiatus*. Andersen's teeth measurements for *labiatus* are somehow too large (Harrison, 1959). They include those of the type specimen, which I have also measured. The lengths of P<sup>3</sup>, P<sup>4</sup> and M<sup>1</sup> (2.79, 2.84 and 3.67, respectively) are within the ranges given by Andersen and greater than Harrison's values for three specimens from Roseires (which, to judge from those measurements, may all three represent *minor*.)

At present it is not feasible to solve all the problems inherent to Andersen's published concept of *labiatus*. It seems useful, however, to point them out here, because many later workers have adopted it. Allen *et al.* (1936) based their conclusion that *minor* is a subspecies of *labiatus* on that concept, and were followed in this by many others (e.g. Moreau *et al.*, 1940; Swynnerton *et al.*, 1951; Ellerman *et al.*, 1953; Lawrence *et al.*, 1953; Harrison, 1959, 1961; Ansell, 1960b, 1967; Kulzer, 1962a; Funaioli *et al.*, 1966; Hayman *et al.*, 1966; Koopman, 1966; Funaioli *et al.*, 1968; Hayman *et al.*, 1971). Recent authors frequently refer to the important contribution of Hayman *et al.* (1971) to the identification manual for African mammals, where *labiatus*, including *minor*, is discriminated from other species of *Epomophorus* by a forearm length range copied directly from Andersen (1912).

Kock (1969), dealing with a rather large series of *Epomophorus* from two localities in a restricted area in southern central Sudan, was the first author who realized that *E. labiatus* is a larger species than had been generally accepted. From the dimensions of his own specimens compared to those of some *minor* specimens from Ethiopia and Tanzania and to other data on *minor* in the literature (especially Harrison, 1959) he concluded that *labiatus* and *minor* are distinct species. Also on the basis of those dimensions, which he considered intermediate between those of typical *E. anurus* Heuglin, 1864 and *E. labiatus*, Kock concluded that *anurus* and *labiatus* are only parts of a cline, with smaller specimens in the northeast (including Sennar, as type locality of *labiatus*) and larger ones in the south of Sudan (including Bongo, as type locality of *anurus*), and he ranked them accordingly as subspecies of *labiatus*. Specific distinctness of *minor* from *labiatus* is also the opinion of Largen *et al.*, 1974; Ansell, 1978; Bergmans *et al.*, 1983; Aggundey *et al.*, 1984; Baeten *et al.*, 1984; and Haiduk *et al.*, 1984. Largen *et al.* (1974) followed Kock (1969) in considering *anurus* a subspecies of *labiatus*. Kingdon (1974), who wrote about an "*Epomophorus gambianus* complex" and refrain-

ed from treating any of the forms of this complex as an independent species, mentioned populations from coastal Kenya and southwestern Tanzania which are intermediate between *anurus* and *labiatus* (*sensu* Hayman *et al.*, 1971, thus including *minor*). In 1978 Kingdon recognized *labiatus* (including *minor*) and *anurus* as species, suspecting that *labiatus* “differentiated from *E. anurus* in north-east Africa during a very dry period and later spread, interdigitating with *E. anurus*, in a complex overlap pattern.” Koopman (1975) agreed with Kock (1969) that *labiatus* is allied with *anurus* rather than *minor*, although he thought there was still considerable uncertainty. Aggundey *et al.* (1984) listed *anurus* as a subspecies of *labiatus*. McLellan (1986) recognized “the most common of the pteropodid bats in southern Sudan” easily as *labiatus* and apparently followed Koopman’s suggestion — but not his reservation — of considering *anurus* a synonym. She found *minor* to be easily separable, and sympatrical with *labiatus* in several localities.

Kock’s (1969) analysis of *labiatus* (*i.c.* *labiatus anurus*) from Buram and Kadugli in southern central Sudan is unfortunate in that it is based on few complete adult specimens, the remainder being either damaged (skulls) or immature, as recent re-examination of most of his material by the present author revealed. Kock’s ranges for body and skull measurements are therefore biased towards too low values. He gave 62.5-75.9 as forearm length range in six ♂♂, and 61.5-74.2 as that in 14 ♀♀; and 35.9-46.9 as skull length range in four ♂♂, and 35.9-44.8 as that range in 7 ♀♀. Such ranges would be extraordinary in any fruit bat population and the lower values were clearly taken from immatures. I measured nine ♂♂ of Kock’s series (there are a few more specimens than he listed), three with skulls only, and found two adults with fals of 73.9 and 76.1, and altogether four adult skulls with gsls of 42.8 without premaxillae, about 44.2 (broken), 45.75, and 46.7. (A fifth specimen, SMF 33156, would according to its label be a ♀ but I think it is a ♂; I only saw the skull, which measured 44.1.) I further measured 14 ♀♀ of

Kock’s series and found only four adults, of one a skull only and two with cleaned but broken skulls; fals are 72.2, 72.5 and 74.6 and gsls 40.3, about 41, and  $\geq 41.85$ .

Koopman (1975), who also included this material in his studies, apparently drew the same conclusion with regard to the ♂♂. For 16 adult ♂♂ from Sudan he gave a fal range of 71-75. However, he most probably mixed immature or *minor* ♀♀ with adult *labiatus* ♀♀ when calculating a fal range of 62-74 ( $n = 33$ ). As cbl Koopman gave a range of 42.4-47.0 for nine adult ♂♂ and 38.7-43.8 for six adult ♀♀. He did not identify any of his Sudanese *Epomophorus* as *minor*. McLellan (1986) gave as fal range in ten adult ♂♂ 75-81 and in four adult ♀♀ 70-74 (against 64-66 in two adult ♂♂ and 62-67 in two adult ♀♀ of *minor*, in part from the same southern Sudanese localities). Her high values for ♂♂ will be due, in part, to the fact that she measured them in the field. But they also seem to point at a phenomenon observed earlier by Kingdon (1974) and of importance in taxonomy, namely that measurement ranges within a species vary geographically and characterize local populations rather than the species over a large part (or all) of its range. Some isolation of local populations may play a role, but if there is seasonality in reproduction, dimensional characteristics may be related to local conditions such as climate and food availability and indeed vary with time (compare Ransome, 1987). (In this respect it would be interesting to sample adult fals of a given population over a number of years—which can be done without sacrificing specimens.)

In synonymizing *anurus* with *labiatus* Kock (1969) used the size classes proposed by Andersen (1912): *labiatus* with forearm lengths of 62-66.5 in ♂♂ and 66 in one ♀ (but no important sexual difference), and *anurus* with forearm lengths of 71.5-78 in ♂♂ and 66.5-74 in ♀♀. Kock’s measurements of his own series (62.5-75.9 in ♂♂ and 61.5-74.2 in ♀♀) seemed to unite those ranges. But, adults in Kock’s material are clearly referable to what Andersen called *anurus*.

However, Andersen's data on adult *labiatus* fal are doubtful. All more recent and well-labelled material of smaller *Epomophorus* from Sudan falls into either one of two size classes: a larger one more or less consistent with Andersen's *anurus* class (fal 68.3-81 in ♂♂ — including McLellan's range —, and 68.3-77.4 in ♀♀; gsl 44.2-48.3 in ♂♂ and 39.5-44.9 in ♀♀, data of all Sudanese samples combined), and a smaller for which I have only McLellan's (1986) data and those on one of the Roseires specimens (BMNH 8.4.17.3 — assuming it is from Roseires) (fal in two ♂♂ 64-66, in two ♀♀ 62-67; gsl in Roseires ♂ 37.65; cbl in two ♂♂ 36.65-37.5 and in three ♀♀ 34.2-37.5) and which McLellan also identified as *minor*. The estimated gsl of the immature lectotype of *labiatus* is 35 or more, and far from adult size. The distance between C<sup>1</sup> and P<sup>3</sup> in adult *Epomophorus* is at least equal to the length of C<sup>1</sup>, the distances C<sub>1</sub>-P<sub>1</sub> and P<sub>1</sub>-P<sub>3</sub> are rather great,

and premolars and molars are generally well apart, all of which is clearly not so in the lectotype specimen (figs. 6a-d). All this being so, and the teeth measurements taken into account, there can be no doubt that this specimen represents the larger class size.

This implies that *labiatus* is a larger species than Andersen (1912) thought it was (and that his concept of this species was partly based on *minor* specimens — possibly all but the lectotype!) and that *Epomophorus anurus* Heuglin, 1864 is a synonym of *labiatus*. There appears to be no reason, moreover, to retain *anurus* as a subspecies of *labiatus*, as Kock proposed. (Figs. 7a-b give an idea of the skull of the male syntype of *E. anurus*.)

Distribution and geographical variation: In dimensions, *Epomophorus labiatus* is far from uniform throughout its range. Study of larger samples of single populations — conceived here as assemblages inhabiting different

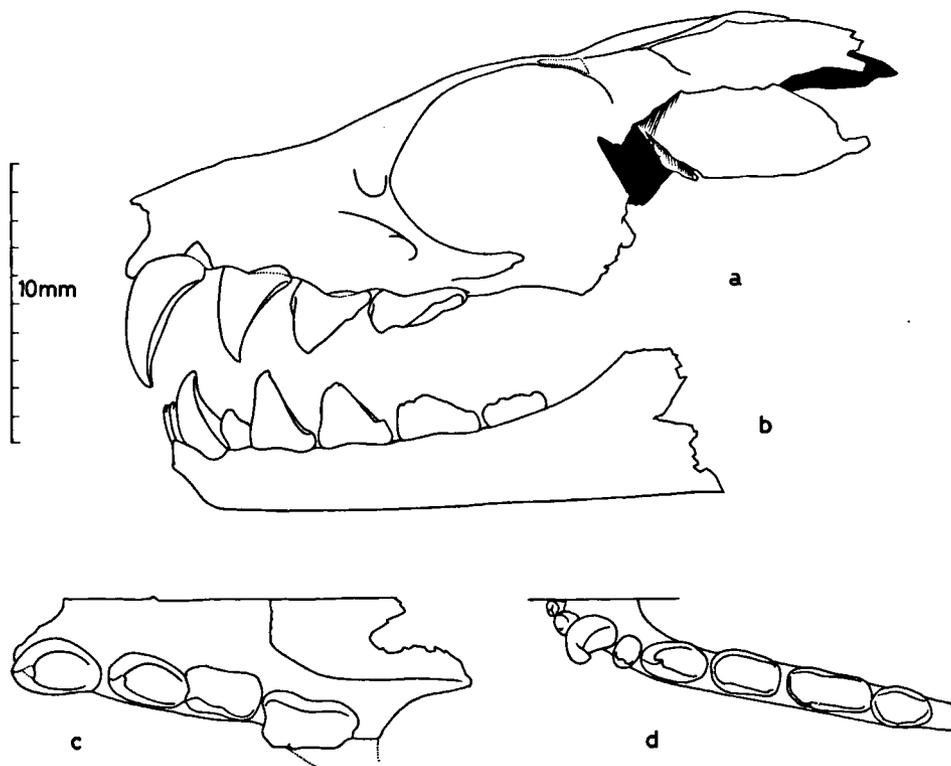


Fig. 6. Lectotype specimen of *Epomophorus labiatus* (Temminck, 1837) (RMNH); a: left aspect of skull; b: left aspect of mandible; c: ventral aspect of right upper tooth row; d: dorsal aspect of left lower tooth row. Scale applies to all figures.

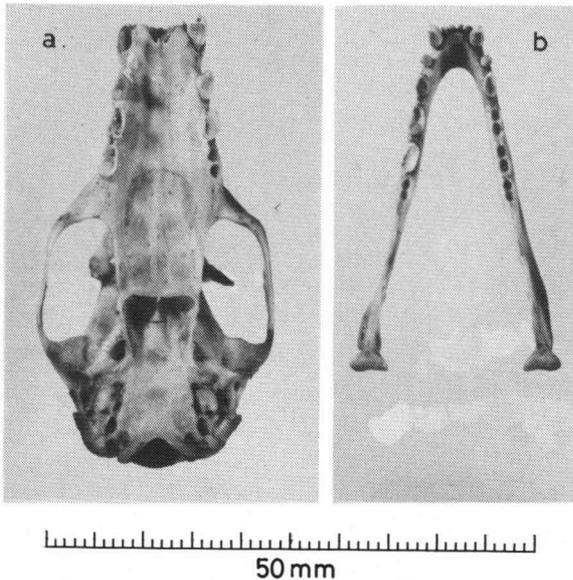


Fig. 7. Male syntype specimen of *Epomophorus anurus* Heuglin, 1864 (SMNS 1090) (= *E. labiatus* (Temminck, 1837)); a. ventral aspect of skull; b. dorsal aspect of mandible. Photographs courtesy of Dr F. Dieterlen.

areas with apparently restricted gene flow between them — invariably leads to the conclusion that variation of body and skull dimensions within a population is rather restricted if compared to the species as a whole. As a result, there may be distinct differences in measurement ranges between populations, even of relatively close localities. Superimposed is a more large-scale geographic variation in size. Before giving some examples to illustrate both local and overall variation it seems useful to give an outline of the species' distribution as known at present.

The distribution map (fig. 5) is based on material examined by the author and on those locality data in the literature accompanied by sufficient data to allow for an identification check. This seems the best procedure as, apart from problems through mix-ups of *labiatus* and *minor*, it has not been possible in most cases to infer which species concepts authors have applied. Specimens identified as “*labiatus minor*” have frequently been referred to as *labiatus*, while they possibly do represent *minor*. Furthermore, some authors have not quite

appreciated the problems involved in determining the age of specimens and have published records of certain species, based in reality on immature specimens of larger species. Altogether, localities have only been taken from Andersen, 1912; G. M. Allen, 1914; J. A. Allen *et al.*, 1917; Rahm *et al.*, 1963; Vielliard, 1974; Baeten *et al.*, 1984; and McLellan, 1986.

Most records of *Epomophorus labiatus* are from the central East African lake area and south Sudan, and the species appears to be quite common in much of southern Sudan and western Ethiopia. In East Africa it is replaced by *minor* over most of the lower regions between the Ethiopian and central highlands and the coast, and there seems to be little overlap in distribution with that species. In Ethiopia, *labiatus* penetrates as far eastward as the central rift valley, from where I have seen specimens from Aisaita, Bahadu, Koka, Lake Awasa, and Bulcha. The MNHN specimens from 7 km of Ghinir, east of the rift valley, reported as *labiatus* by Dorst *et al.*, 1972, and as *labiatus anurus* by Largen *et al.*, 1974 are unmistakably *minor*: an adult ♂ has a fal of 61.5, and two adult ♀♀ have fals of 60.7 and 61.3.

From a broad belt in the dry north of Kenya, west and east of Lake Turkana, no other *Epomophorus* specimens are known to me than two *labiatus* ♂♂ from Turkwell. From southern Kenya there are a few records indicating that here *labiatus* intrudes the eastern lowlands. Some of those records are reliable, others need careful re-examination. Peters (1880) recorded the species from Malindi; his specimen formed part of the series described as *Epomophorus stuhlmanni* by Matschie (1899), which Andersen (1912) considered a synonym of *Epomophorus wahlbergi haldemani* (Hallowell, 1846). Dollman (1914a) recorded *E. anurus* from Sebaki River, but failed to state what led him to this identification. Whitaker *et al.* (1978) recorded *labiatus* from near Tiwi and Aggundey *et al.* (1984) recorded the species from Patta Island but both records need confirmation as no data on specific characters were provided. Aggundey *et al.* (1984) listed Kibwezi as *labiatus* locality. This was based on a ♀ (AMNH 184472),

nearly adult, with a fal of 71.8 and a gsl of 40.8, which in 1977 I also identified as *labiatus* and which Dr K. F. Koopman has kindly re-examined and also identified as such (*in lit.*, 29-XII-1987). Ms. L. J. McLellan (*in lit.*, 16-IX- and 9-X-1987) mentioned a ♀ with a fal of 70 from Lamu, which she had identified as *labiatus* as it had two postdental palatal ridges.

From the material I have examined there appears to be a large gap between the populations of northwest Tanzania and the two records from South Tanzania and Malawi. The first is based on an adult ♀ from Ugano (NMW B5112) and the second on 2 ♂♂ from Kasungu National Park (ZMA 21.693a/b; identified as *anurus* by Bergmans *et al.*, 1983). Another rather southern record, from Keyberg in Zaire, recorded by Hayman *et al.* (1966) is based on an immature ♀ in spirit with the skull *in situ* (IRSN 13106) and is therefore not reliable.

*Epomophorus labiatus* seems largely to avoid the rain forests of the Zaire basin, although Hayman *et al.*, 1966 record it (as *anurus*) from Panga and Bokungu; I have not seen those specimens (MRAC 9139 and 18844) and not mapped them. An isolated locality is Pointe Noire in Congo, from where a single specimen has been assigned to *labiatus* (see Bergmans, 1979). North of the rain forest of the Zaire basin the species has also been recorded from several localities outside its present centre of distribution, all towards the west. Two ♀♀ from 25 km north of Boro River (SMNS 29893/4, the latter a subadult; fal 77.4/76.7, gsl 44.3/43.6, respectively) and one from Zalingei (ROM; fal 74.0, gsl about 42.6), both in southwestern Sudan, are here assigned to *labiatus*.

There are no definite records from the Central African Republic. Blancou (1936) suggested to have observed what may have been *labiatus* (as *anurus*) at several localities in Ouham Pende in the west of this country. It is not indicated if he collected any specimens — I have not come across them in collections — and his allegations remain to be confirmed. Schlitter *et al.* (1982), reporting on bats of the Central African Republic, quoted Schwarz (1920) and

Kock (1969) who recorded the species from the Middle Chari River. Of course, this locality is too inexact to be mapped but I would rather place it in Chad than in the Central African Republic.

Rosevear (1965) recorded 3 specimens (as *anurus*) from Maiduguri, Farniso and Ibadan in Nigeria. The one from Farniso (or Parniso) was published earlier by Thomas *et al.* (1921), as *Epomophorus anurus*. Rosevear did not give data on these individuals — his measurement ranges for the species are the — enlarged — ranges given by Andersen (1912). The specimens are in the BMNH. The one from Maiduguri (BMNH 50.173), a skin and skull, collected by D. R. Rosevear on 27-VI-1948 is labelled as a ♂ but has no epaulets; its almost completely fused skull base sutures show it to be subadult or young adult. It has a fal of  $\geq 78.5$  (its upper arms are missing) and a gsl of about 47 (its premaxillae are missing). If it is a ♂, it probably represents *labiatus*; the alternative would be *Epomophorus gambianus* (Ogilby, 1835), of which Nigerian ♂♂ have a fal range of 85.5-94.0 (n = 10) and a gsl range of 55.6-62.4 (n = 24). But the rostrum is not typically long as in ♂♂ and instead of epaulets there are other aberrant hairs, long and slightly wavy, both characters of ♀♀. If it is a ♀, it approaches the lower limits of the measurement ranges in Nigerian *gambianus* ♀♀: fal 80.4-87.9 (n = 16) and gsl 47.7-53.7 (n = 51). Unfortunately, the specimen's sex cannot be checked on the skin, which is damaged in that region. (A specimen from Lake Alau, near Maiduguri, collected by A. Ford on 5-VII-1978 and now in the HZM collection — no. 25.9671 — is an adult ♂ with a fal of 86.9 and a gsl of 55.6, and is assigned to *gambianus*.) The specimen from Farniso (BMNH 21.2.11.1) was collected by A. Buchanan on 19-XII-1919. I have seen its skin only. It is labelled as a ♀ and has a fal of 75.5. Both its fur colour and the developmental stage of its finger joints indicate that the specimen is immature. If it is a ♀, it probably represents *gambianus*. (There are some adult specimens from Panisau in the USNM — no.'s 402381/3, -8/9 — which are all *gambianus*.)

The specimen from Ibadan (BMNH 50.172) was collected by D. R. Rosevear on 27-XI-1947. It consists of a skin (fal. 70.7) and a broken skull (gsl about 38.8) and is clearly juvenile, with  $M^1$  and  $M_2$  in the process of emerging. Happold (1987) questions its identification and so do I. All adult *Epomophorus* from Ibadan that I have examined are *gambianus*. An unpublished specimen from Ibadan identified as *labiatus* (*i.e.* *anurus*) was collected on 24-XII-1960 by F. C. Sibley (BMNH 62.444). In my opinion, it is an immature *gambianus* (fal 74.3). Another Nigerian specimen identified as *labiatus* was collected on 3-VII-1975 by I. Brownlow at Ikoyi, Lagos (HZM 2.8205). It is a ♀ (fal 77.3, gsl 43.9) with incompletely fused skull base sutures; other specimens from Ikoyi include an adult ♂ (HZM 4.8347; fal 86.7, gsl 58.4) of *gambianus*. Happold (1987) mentions Darazo as a further Nigerian locality, from where *labiatus* material would rest in the NHMI (Happold's NHI). The only specimen from Darazo I have found in that collection (in 1976) is an adult ♂, skin and broken skull, collected by D. R. Rosevear on 1-IV-1949. According to its field label its fal was 90 and Rosevear had identified it as *gambianus*. I measured its fal as 85.5 (whatever it was, originally, it was longer than this) and found no reason to change its original identification.

The only unquestionable Nigerian *labiatus* that I have seen was collected by J. Fagbohunmi and party at Malamfatori (collecting date not stated) and is deposited in the ZMUI. Of eight spirit specimens, with skulls *in situ*, only one, a ♂, was adult (epaulets; fal 78.0, length of head about 50).

Finally, Adam *et al.* (1972) recorded a series of *labiatus* (as *anurus*) from Bandia and Saboya in western Senegal. They stated their eight specimens to be adult and gave a number of measurements. From these it appears that both fal and gsl ranges in the 3 ♂♂ of the series (all from Bandia) are unusually large (70-80.5 and 43.2-48.4, respectively) while their palatal lengths ("crâne: longueur au palais"; see the table on page 61 in their paper), if measured as defined by Rosevear (1965: 367), are unusually

short: 53-56% of the gsl, against 61-64% in 12 adult ♂♂ from Sudan, Ethiopia, Uganda and Malawi. From the large fal and gsl ranges I gather that at least the smallest specimen may be immature (although the smallest fal and gsl are not attributed to the same animal; inadvertent exchange of skins and skulls during preparation does not seem unlikely), and from the small palatal lengths that all specimens may be immature. The spectacular lengthening of the rostrum in ♂♂ of the *Epomophorus* section is one of the last growth processes to take place before specimens become full-grown. If the specimens are immature, they may represent *E. gambianus*. If at least some of them are mature, they possibly represent a quite distinct population. The series has probably been deposited with ORSTOM in Dakar. Efforts to trace and borrow it, however, have not been successful. Pending re-examination of the series, I prefer to regard its identification as uncertain and to not introduce the localities on the map.

After this critical exercise a picture of the species' (known) distribution emerges (fig. 5) with as probably most striking aspect the eastern border of the present centre of distribution, coinciding rather sharply with the eastern Rift Valley in Ethiopia and Kenya and deviating from this towards the west in the area south and southeast of Lake Victoria. The western border of this central area coincides with the western Rift Valley along the eastern Zairese border, fanning out towards the north-west north of Lake Albert. The species appears largely to avoid the lower coastal plains in the east and the equally low Congo basin in the west, although of course the isolated Lamu Island lies at sea level and some other unspecified localities will also lie relatively low, and the species does intrude the Upper Nile basin in the north — although not the Sudds, as far as we know. Collectors' notes on labels include many collecting altitudes, ranging from 610 to 1920 m (2000-6200').

The isolated localities on the map may represent disjunct parts of the overall distribution. Published accounts of *Epomophorus* distribution in the areas separating them from what is envis-

aged here as the present centre of distribution do contain little evidence of possible connecting populations. Kingdon's (1974: 1978) surveys of East African *Epomophorus* distributions, especially of the "gambianus complex" species, are rather more conceptual than based on material evidence. I have seen very few fruit bat specimens from Central Tanzania in collections (see fig. 1) and Kingdon's more detailed fruit bat distribution maps (1974: 130, 134, 137, 147, 157, and 161) confirm that, while collecting efforts and observations have been made there (compare his other maps), relatively few fruit bats were involved. Therefore, the isolation of the Malawian and South Tanzanian populations becomes more likely.

For the West Congolese population the same is possibly true. Hayman *et al.* (1966: Plates I-III) have mapped rather many Zairese bat collecting localities in the adjoining Lower Zaire district, among which one, Congo da Lemba, for "*Epomophorus labiatus minor*" based on a single specimen (MRAC 408) which may or may not be an immature *labiatus* (I have not seen it), and not a single one for "*Epomophorus anurus*". The nearest localities for both, as mapped by these authors, are more than 1000 km towards the east and northeast.

Malamfatori in Nigeria is possibly less isolated from the centre of distribution. Very few fruit bat collecting efforts seem to have been made in the belt between 10° and 14° N between this locality and western Sudan (fig. 1), and *labiatus* may still be found to occur there. Westward from Malamfatori more samples of *Epomophorus* have been collected in this belt. Apart from the unsatisfactory Nigerian and Senegalese records of "*anurus*" dealt with earlier, specimens have invariably been identified as *gambianus* and as far as the published data go this seems quite right.

In *Epomophorus* samples from this belt encountered in collections, I have moreover never found anything but *gambianus*. If Adam *et al.* (1972) collected *labiatus* in western Senegal, the population there would appear to be isolated from the northeast Nigerian one.

It may logically be assumed that at one time

or other the isolates have been in contact somehow with the present centre of distribution. As *labiatus* is entirely dependant on vegetation for food and predominantly also for shelter (some have been observed to roost under roofs), changes in vegetation should be considered first when searching for causes of the fragmentation of the species' distribution. Moreau (1966) held man-induced changes in Africa's vegetation, through the use of fire, the spreading of domestic animals, and the cultivation of ever larger stretches of land, largely responsible for changes observed in the distributions of certain bird species. These changes have affected the savanna and drier vegetation types in the first place, and as *labiatus* is essentially an inhabitant of such types (see below) it has most probably also been affected.

At the time of writing, I have traced 67 *labiatus* localities. These can be associated with the vegetation types distinguished by White (1983) as in Table 5. (When reading this table, it should be kept in mind that some of the distributional data are based on old records, collected in times when the African vegetation had not yet come down to the degraded levels of today.)

Dimensional variation: The extent of dimensional variation as indicated in the diagnosis of the species is never observed in a single population. Especially skull size appears to be rather restricted within a population. There are not many series of adult specimens from single localities in collections but some examples follow here. From 12 miles west of Kitale, Kenya, 15 ♂♂ have a fal range of 69.9-78.2 and (n = 12) a gsl range of 45.5-48.6; 16 ♀♀ from that locality have a fal range of 67.4-72.4 and (n = 13) a gsl range of 39.6-43.0. Ten ♂♂ from Mwanza, Tanzania, have a fal range of 67.9-71.8 and a gsl range of 41.5-44.1; eight ♀♀ from Mwanza have a fal range of 64.8-68.9 and (n = 7) a gsl range of 38.1-39.1. Near Mwanza in Lake Victoria lies Ukora Island, from where a ♂ has a fal of 71.8 and a gsl of 46.2, and a ♀ a fal of 68.8 and a gsl of 40.6, suggesting higher average measurements in this nearby population.

Table 5. Collecting localities of *Epomophorus labiatus* (Temminck, 1837) and associated vegetation types according to White, 1983.

Category	Vegetation type	Nigeria	Chad	Sudan	Ethiopia	Congo	Zaire	Uganda	Kenya	Rwanda	Burundi	Tanzania	Malawi
Forests	1. Guineo-Congolian rain forest: drier types								1				
Forest transitions & mosaics	2. Mosaic of Guineo-Congolian rain forest and secondary grassland					1	2	2	4				
	3. Afromontane vegetation				2		1		1	6	1	2	
Woodland	4. Wetter Zambezi miombo woodland (dominated by <i>Brachystegia</i> , <i>Julbernardia</i> and <i>Isobertinia</i> )							2					1
	5. Drier Zambezi miombo woodland (dominated by <i>Brachystegia</i> and <i>Julbernardia</i> )												1
	6. Sudanian woodland with abundant <i>Isobertinia</i>				4								
	7. Sudanian woodland				2			1					
	8. Ethiopian woodland					3							
Woodland mosaics & transitions	9. Transition from Ethiopian woodland to <i>Acacia</i> deciduous bushland and wooded grassland				5								
Bushland & thicket	10. Somalia-Masai <i>Acacia-Commiphora</i> deciduous bushland and thicket				1	3		2					2
	11. Sahel <i>Acacia</i> wooded grassland and deciduous bushland		1		1								
Bushland & thicket mosaics	12. Mosaic of East African evergreen bushland and secondary <i>Acacia</i> wooded grassland									10	1		
Semi-desert vegetation	13. Northern Sahel semi-desert grassland and shrubland				2								
Grassland	14. Edaphic grassland in the Upper Nile basin				1								
Edaphic grassland mosaics	15. With communities of <i>Acacia</i> and broad-leaved trees				1								
	16. With semi-aquatic vegetation					1							
Desert	17. Regs, hamadas, wadis				1								

Apart from local and regional variation, certain trends affecting the species over all of its known range may be noted. Although, on the whole, few measurements of adult specimens are available, seemingly typical specimens —

that is, in my opinion, as explained earlier, concurring in size with material from southern central Sudan — have been collected at several localities in the central Ethiopian rift; in Ethiopia west of the central rift; in southern

central, eastern and southeastern Sudan; in Uganda; and in western Kenya. Although, again, available samples are very limited, there is some evidence that measurement ranges in populations from western and southwest Sudan and northeast Zaire average slightly higher than in the typical specimens referred to above. The type specimens of *Epomophorus anurus*, from Bongo, Sudan, belong here: according to Andersen (1912), a ♂ with a fal of 78 and a gsl of 48.8 (see figs. 7a-b; I estimated a gsl of about 47) and a ♀ with a fal of 74. The single specimens from Chad and Nigeria are suggestive of still higher average measurements in these more western populations.

Other odd specimens, from Congo, coastal Kenya (a ♀ with a fal of 70) and Malawi fit in with the Sudanese ranges. In the case of Malawi it should be noted that this population is separated from others with larger measurements by Tanzanian populations with atypically smaller measurements. Relatively small individuals are found in northwest (Gondar) and northeast (Aisaita; Shifra) Ethiopia, and possibly also at some localities in the central rift in Ethiopia (Bahadu; Koka) from where I

have seen single or immature specimens only, and in northwest Tanzania. These populations have given rise to problems regarding the distinctness of *labiatus* and *minor*, and to ideas concerning subspecific divisions within *labiatus*.

To start with the question of *labiatus* vis-à-vis *minor*, Andersen's conviction that these species hardly differed in body or skull size and that the differences in teeth dimensions offered the best distinguishing characters has focused later attention almost entirely on teeth measurements. As we now know, typical *labiatus* is rather larger than typical *minor*, and it may seem like forcing an open door to say that larger specimens (here: two morphologically closely similar species combined) usually do have larger teeth than smaller ones, and atypically small *labiatus* (as hypothetical atypically large *minor*) are bound to have intermediately sized teeth and thus to obscure the picture. But in my opinion it is not correct to compare absolute teeth sizes of two differently sized species. Table 6 gives M<sup>1</sup> length as a percentage of cbl for all *labiatus* and *minor* specimens of which I took those two measurements. Although most numbers are

Table 6. M<sup>1</sup> lengths as percentages of condylobasal lengths in *Epomophorus labiatus* (Temminck, 1837) and *E. minor* Dobson, 1880.

	<i>E. labiatus</i>				<i>E. minor</i>			
	♂♂		♀♀		♂♂		♀♀	
	n	range	n	range	n	range	n	range
Congo			1	7.1				
Ethiopia	5	6.8-8.4	1	8.6	25	7.0-8.4	14	7.0-8.6
Kenya	1	7.3			4	7.3-7.9	1	7.9
Uganda	3	6.1-7.5	6	7.4-8.9				
Sudan	4	7.1-7.7	9	7.4-8.6	1	8.5		
Tanzania	5	6.8-7.5	5	7.1-8.3	10	6.4-8.1	5	7.0-8.4
Zambia					1	7.9		
Zanzibar*					1	7.7		

\* subadult (holotype specimen)

small, some conclusions are evident. First, ♀♀ have only slightly smaller teeth but distinctly shorter skulls than ♂♂, hence their relative M<sup>1</sup> lengths are larger, on the average, and deserve separate treatment. Second, the variation ranges are sometimes considerable, reflecting in part the absolute ranges as given in Tables 4 and 8. Third, the ranges of *labiatus* and *minor* show sufficient overlap to cast doubt on the usefulness of relative M<sup>1</sup> length (and most probably other teeth measurements) as distinguishing character between these two species.

The remaining character commonly used to distinguish *labiatus* and *minor* is body size as reflected in fal ranges. Over their respective areas both species show considerable variation in this measurement and when all measurements are combined the smallest *labiatus* overlap with the largest *minor* (in both sexes). The same is true for the greatest skull length and other skull measurements and weights. If fals are plotted against gsls, the values found for *labiatus* are even in direct line with those of *minor* (in both sexes); and with a given fal, the majority of ♂♂ have larger greatest skull lengths than ♀♀, to about the same extent in both species. All this seems well in favour of the notion that *minor* is a small subspecies of *labiatus*. Their mutually largely exclusive distribution patterns, as construed by the present author (figs. 5 and 8), would also seem to fit in with this view.

In reality, however, the relation between *labiatus* and *minor* is much more complicated than that. McLellan (1986) identified both species from four localities in southwestern Sudan. Another area of sympatry may exist in southern and coastal Kenya. Baeten *et al.*, 1984, recorded both species (*labiatus* as *anurus*) from six localities in Rwanda, stating that they were "always caught together" and that *labiatus* (i.e. *anurus*) is "clearly larger" (unfortunately, no measurements are given). In Malawi, *labiatus* (reported as *anurus*) and *minor* are sympatric at Lisanthu in Kasungu National Park (Bergmans *et al.*, 1983). There are indications, moreover, that in several other regions along

the 'borderline' between *labiatus* and *minor* the two approach each other closely, or actually meet, without there being evidence of interbreeding (i.e. dimensional gradients).

One of those areas is the central rift in Ethiopia. North of this rift, at Aisaita, 6 ♂♂ have a fal range of 66.1-71.1 (mean 68.7) and head lengths of about 42.5-43.8, and 4 ♀♀ have a fal range of 66.8-71.0 (mean 68.6) and head lengths of about 38.4-39.8; these specimens are assigned to *labiatus* (compare overall Ethiopian *minor* measurement ranges in table 8). Thirteen ♂♂ from Bahadu, with a fal range of 58.7-63.6 (mean 61.3) and a gsl range (n = 11) of 33.8-36.8 (mean 35.2), and eight ♀♀ with a fal range of 59.0-61.7 (mean 60.6) and a gsl range of 32.6-33.6 (mean 33.2), are assigned to *minor*. A young adult ♀ from the same locality, fal 67.5 and gsl 38.1, is assigned to *labiatus*. Ten ♂♂ from Koka, fal range (n = 9) 60.9-64.8 (mean 62.7) and gsl range (n = 9) 35.3-36.7 (mean 36.0), and 14 ♀♀, fal range 59.7-64.0 (mean 61.8) and gsl range (n = 6) 33.3-36.0 (mean = 34.3), are assigned to *minor*. An immature ♀ from Koka, fal 68.8, is identified as *labiatus*. Nine ♂♂ from (Lake) Abiata, fal range 60.8-66.6 (mean 62.0) and gsl range (n = 8) 34.9-37.9 (mean 36.0) are assigned to *minor*. One ♂ from the rather nearby Lake Awasa (separated from Abiata by a narrow height), fal 73.5 and gsl 46.2, clearly represents *labiatus*. Another area where *labiatus* and *minor* approach each other is at, and east of, the Kenyan-Ugandese border, between about 0° and 2°30' N. Specimens from Moroto and Mount Moroto, Amudat or Anudat, Kongelai, Mitunbur, 12 miles west of Kitale, Kirui, 30 miles east of Tororo, Rondo Forest, Kakamega and Simbi represent *labiatus*, while specimens from Amudat or Anudat, Mitunbur, Kanyangaren, Turkwell Gorge, Amaler, Sigor, the northeast base of Cherangani Mountains, Kerio Valley and Solai Valley represent *minor*.

Table 7 gives numbers and fal and gsl ranges of specimens from these localities. Only few specimens may possibly give rise to the assumption of interbreeding. The larger ♂ from Amudat clearly belongs to *labiatus* and the ♀

Table 7. Forearm length and greatest skull length in *Epomophorus labiatus* (Temminck, 1837) and *E. minor* Dobson, 1880 near the Kenyan-Ugandese border.

Collecting localities (collecting altitudes*)	<i>labiatus</i>				<i>minor</i>			
	♂♂		♀♀		♂♂		♀♀	
	n	fal range (mean)	n	gsl range (mean)	n	fal range (mean)	n	gsl range (mean)
Moroto (1370) and Mount Moroto (1500-3000)	2	70.0-72.2	1	44.1				
Amudat (1370)	1	72.8	1	44.6	1	66.4	1	39.1
Kongelai (1370-1676)	4	67.6-70.6 (69.1)	4	40.4-42.9 (41.5)	3	67.1-70.3 (68.4)	3	36.88-40.9 (38.6)
12 miles W of Kitale (1890-1920)	15	69.9-78.2 (72.8)	11	45.5-48.6 (46.6)	16	67.4-72.4 (69.7)	13	39.6-43.0 (41.5)
Kirui	1	73.9	1	46.1				
30 miles east of Tororo (1524)	3	70.0-75.9 (73.1)	3	44.9-47.0 (45.9)	1	73.0	1	42.5
Rondo Forest (1524)	2	73.4-74.3	2	46.3-46.5	1	69.1	1	41.2
Kakamega Forest (1524)	3	70.1-74.0 (72.4)	3	45.0-47.7 (46.3)	3	68.0-71.0 (69.8)	3	38.2-41.8 (40.5)
Simbi (914-1524)	1	73.8						
Kanyangaren (914-1524)					1	62.4	1	36.7
Korau (610)					4	60.2-64.3 (62.0)	1	35.6
Turkwell Gorge (945)							2	60.3-60.7
Amaler (762)							2	60.0-62.0
Sigor (762-1219)					19	59.7-66.1 (62.4)	12	33.7-36.7 (35.4)
							5	58.8-62.5 (60.3)
Cherangani Mountains base at Wei Wei River (927)					8	59.0-63.6 (61.3)	7	34.8-36.7 (35.9)
							7	58.3-64.2 (61.4)
Kerio Valley (914)					2	59.7-60.3	2	34.8-36.6
Solai Valley (1951)					1	57.0		

\* Altitudes copied from labels except those of Mount Moroto, Simbi, Kanyangaren and Sigor, which were taken from maps.

from this locality to *minor*; the smaller ♂ has a large gsl for *minor* but its fal is small and if put in *labiatus*, its gsl would render the local range of this measurement in that species extraordinarily large. The specimens from each of the other localities clearly belong to either the larger (*labiatus*), or the smaller (*minor*) size class. The specimens from Kongelai are rather small if compared to the other *labiatus* samples but for the present I consider them as representing a small variant of that species rather than interbreeding populations as they are larger than the *minor* specimens considered here and overlap with the *labiatus* ranges except that of gsl in

♂♂. It should be noted, on the other hand, that the geographic position of Kongelai is in between the (as far as known) exclusive *minor* localities in the lower regions north and east of the Cherangani Mountains and the Elgeyo escarpment, and the ditto *labiatus* localities in the higher regions to the west of those heights. In this area, *minor* sticks to its preference for lower altitudes, while *labiatus* is ambiguous, avoiding much of the *minor* habitat (with the exception of Amudat) and inhabiting adjoining higher altitudes, to come down to the lower ranges usually only where *minor* is absent, i.e. to the west of the mentioned heights. East of them,

Solai Valley may then offer an exceptional example of the opposite: *minor* advancing uphill as far as 1950 m, in the assumed absence of *labiatus*.

Towards the south, across the Tanzanian border, *labiatus* remains west — and *minor* east — of the continuing heights and mountains which here separate the east side of the Serengeti Plain from the Eastern Rift, and north of about 5° S. Still further south, *minor* passes the Eastern Rift system and penetrates western Tanzania. Near that latitude then, encounters between the two species may here be expected. Identification of the few and small samples from this zone is complicated by the relatively small size of *labiatus* in northwest Tanzania (e.g. the sample from Mwanza; see p. 112) and the relatively large size of *minor* here if compared to more eastern and northern populations. An example: 6 ♂♂ from Tabora have a fal range (n = 5) of 68.0-71.6 (mean 70.2) and a gsl range (n = 5) of 40.2-41.6 (mean 40.8); one ♀ has a fal of 68.8 and a gsl of 37.7. From the nearby Igalula and Igonda, 4 ♀♀ have a fal range of 61.3-64 (mean 62.5) and a gsl range (n = 3) of 35.6-36.9 (mean 36.2). For the present, I have assigned the Tabora specimens to *labiatus* and the others to *minor*. However, the Tabora specimens are even smaller in skull dimensions than the small *labiatus* specimens from Mwanza at Lake Victoria (see p. 112), and show overlap in skull measurements with *minor* specimens from Kilosa, Morogoro, and Kissaki.

Our understanding of the relation between *labiatus* and *minor* is still unsatisfactory. If in any part of East Africa interbreeding between the two, and hence their conspecificity, would be suggested by the occurring phenotypes, it is in western Tanzania. But the available samples are too restricted and too fragmentary, while in other areas where *labiatus* and *minor* are sympatric (e.g. in the adjacent Rwanda) they appear to behave as independent species. If all the populations assigned here to *labiatus* do represent a single species, and if those assigned to *minor* are likewise a (different) specific entity, the suggested phenomenon of geographical dif-

ferences in behaviour towards one another (ranging from no apparent interaction to interbreeding) may possibly be explained by assuming a common ancestor and the existence of geographical variation in genotype in one or both species, allowing for interbreeding in some areas, and further complicated by geographical variation in ecological preferences (compare the situation in the so-called green frog complex in Europe (e.g. Berger, 1973; Tunner, 1973)).

In Ugano, south Tanzania, an adult ♀ (NMW B5112) was collected with a fal of at least 73.5 (upper arm not preserved) and a gsl of more than 41.2 (occiput missing); in other skull measurements it agrees with typical *labiatus*. An adult ♂ from Ugano (NMW 19831) has a fal of 61.5 and a skull length (without premaxillae) of 35.0, and clearly represents *minor*. Easily separable specimens of both species from western central Malawi were described (*labiatus* as *anurus*) by Bergmans *et al.*, 1983.

Notwithstanding its extensive distribution, with several isolated occurrences, valid intraspecific divisions of *labiatus* have not yet been proposed. Kock (1969), who considered *anurus* a large subspecies of *labiatus*, did not elaborate the geography of this division; typical *labiatus* should be looked for in Sennar and probably to the north and east of this locality, and the supposedly larger *anurus* in the Nuba Mountains and more westward. I have concluded earlier that typical *labiatus* must be about as large as *anurus* and that the latter does not deserve subspecific rank. Kock did not examine the type specimen but derived his concept of *labiatus* from the literature and from some specimens from northeastern Sudan and northern Ethiopia which were smaller than his Nuba Mountain specimens (see p. 106). In Largen *et al.* (1974) “*labiatus labiatus*” localities were mapped in Ethiopia north of 12° N (and in Let Marefia but this is based on Andersen’s (1912) identification of specimen MNHN 1885-189, which in my opinion must represent *minor*), and “*labiatus anurus*” in Ethiopia south of this latitude. Kock’s typical *labiatus* from eastern Sudan were the two BMNH specimens from

Roseires which I think are *minor* and a single *labiatus* ♀ from Jebel Maba of which I only saw the skull (broken; gsl 39.3 or more). Largen *et al.* (1974) mapped seven localities for typical *labiatus* in north Ethiopia west of the central rift but left the identification of the specimens from five of those localities "open to doubt". I have also examined odd specimens from the region concerned, including some from those localities. A ♂ from Bellegaz Valley (1830 m) has a gsl of 43.7 (fal unmeasurable) and two ♂♂ from Gondar (2200 m) have fals of 68.3 and 70.2 and gsls of 41.3 and 41.5, respectively. A ♂ from Bahr dar Giorgis (1850 m) has a fal of 73.4. A ♀ from Kassala (500-1000 m), just across the Sudanese border, has a gsl of 39.5. A ♀ from Keren (1400 m) has a fal of 69.7 and a gsl of 39.1. A ♀ from Lake Tana (1830 m) has a fal of 74.1 and a gsl of 43.4. An unsexed skull from Makale (1500-2000 m) measures 42.2 in length.

These few data are of course insufficient for a thorough analysis but they may be taken to indicate probable differences in measurement ranges between populations, like everywhere else, and also that some will average lower than Kock's (1969) Nuba Mountains population(s) (see p. 107) while others may agree with those. But it should be noted that the numbers of adult specimens from the Nuba Mountains as well as from other, more southern Sudanese populations are about as small as from the Ethiopian ones considered here.

The problematical position of *labiatus* with regard to *minor* and our as yet restricted knowledge of geographical and local variation in *labiatus* for the present prevent meaningful intraspecific subdivisions to be made.

### ***Epomophorus minor* Dobson, 1880**

*Epomophorus minor* Dobson, 1880: 715 (type locality: Zan-zibar); O. Thomas, 1890: 446 (in part: specimens from Bagamoyo); Andersen, 1912: 531-532; Dollman, 1914b: 308; Loveridge, 1922: 43 (in part: specimens from Dar es Salaam and Morogoro); De Beaux, 1924: 152; Kock, 1969: 20; Largen *et al.*, 1974: 225; Ansell, 1978: 16; Bergmans *et al.*, 1983: 119; Aggundey *et al.*, 1984: 124 (in part: specimens from Turkwell, Kitale, 12 miles west of Kitale, and probably also Kaimosi, are

*Epomophorus labiatus* (Temminck, 1837)); Baeten *et al.*, 1984: 184; Haiduk *et al.*, 1984: 1; McLellan, 1986: 4; Happold *et al.*, 1987: 349; Ansell *et al.*, 1988: 27.

? *Epomophorus pusillus* (not of Peters, 1867); G. M. Allen, 1911: 322.

*Epomophorus labiatus* (not of Temminck, 1837); Andersen, 1912: 529-531 (in part: specimens from Roseires, Let Marefia, and probably those from Abyssinia and Shoa); Lanza, 1961: 170; Dorst *et al.*, 1972: 395 (in part: the specimens from 7 km from Ghinir).

*Epomophorus anurus* (not of Heuglin, 1864); De Beaux, 1922: 22.

*Epomophorus labiatus minor*; Swynnerton *et al.*, 1951: 287 (in part: BMNH specimens from Tabora and Kasulu here referred to *Epomophorus labiatus* (Temminck, 1837); ZMB specimens from Ujiji, quoted from Andersen, 1912, are too immature for identification); Aellen, 1957: 193; Eisentraut, 1958: 19; Harrison, 1959: 221 (in part: BMNH specimens from Tabora and Kasulu here referred to *Epomophorus labiatus* (Temminck, 1837); ZMB specimens from Ujiji, quoted from Andersen, 1912, are too immature for identification); Ansell, 1960b: 10; Harrison, 1961: 287 (in part: material from Kaimosi probably represents *Epomophorus labiatus* (Temminck, 1837)); Kulzer, 1962a: 164-181; Hayman *et al.*, 1966: 23 (identifications of individual specimens need confirmation); Koopman, 1966: 156; Ansell, 1967: 4; Funaioli *et al.*, 1968: 199; Hayman *et al.*, 1971: 7 (in part; compare description of distribution with concept in present work).

*Epomophorus labiatus anurus* (not of Heuglin, 1864); Largen *et al.*, 1974: 227 (in part: the specimens from 7 km from Ghinir).

### *Material examined*

ETHIOPIA. Abiata: 5 ♂♂, 1 ♀, alc., skulls, X-1971, J. S. Ash (USNM 497521, 497523/7). Abore: 1 ♂, alc., skull, 1 imm. ♀, alc., 6-VI-1976, G. Nikolaus (SMNS 29895/6). Awash: 1 ♂, skin, 31-IX-1914 (BMNH 39.1345). Bahadu: 13 ♂♂, 8 ♀♀, alc., skulls, 1 imm. ♀, alc., J. S. Ash (USNM 497529, -31, -32, -35/37, -42/43, -47/48, -50, -76, -78, -80/81, -83, -85/87); 20-I-1971, M. J. Largen (BMNH 71.2427/8); 3/7-V-1971, M. J. Largen (ZMA 17.344). Daroli: 1 ♂, alc., skull, 9-III-1901, Von Erlanger (ZMB 67063). Errer River at bridge Jiggiga road: 1 ♀, skull, 6-I-1964, R. H. Ingersol (MVZ 141882). Errer Valley, 500 m east of bridge Jiggiga road: 1 ♂, skull, 12-XII-1962, R. H. Ingersol (MVZ: 141881). 7 km from Ghinir: 1 ♂, 2 ♀♀, 3 imm. ♀♀, alc., 17/18-II-1971, J. Prévost (MNHN). C. 70 km southwest of Gidole: 1 (imm.?) ♀, alc. (BMNH). Harar: 1 (imm.?) ♀, alc., VII-1906, E. Szántó (NMW 15.204). Koka: 10 ♂♂, 2 imm. ♂♂, 14 ♀♀, 1 imm. ♀, alc., skulls of 15, J. S. Ash (USNM 462697, -699, -703, 497551, -54/57, -62/64, -67, -69/73, -75); D. A. Schlitter (CMNH 74220); R. Traub (CMNH 74196, -98/99, 74200, 74200, -207, -212, -219).

Lake Abiata, east shore: 3 ♂♂, 1 imm. ♂, skulls, 17/27-X-1970, M. J. Largen (BMNH 71.2420/21, -23, -25); 4 ♂♂, alc. (BMNH; probably partly the same specimens); 1 ♀, alc., (BMNH), 1 imm. ♀, alc., skull, 21-X-1970, M. J. Largen (BMNH 71.2422). Sidam-Bale bridge: 6 ♂♂, 2 ♀♀, alc. (BMNH). Sof Omar: 1 ♀, alc. (BMNH). (Farri.)

KENYA. Amaler: 2 ♀♀, 16-XII-1965, A. E. Williams (ROM 40195, 40256). Cherangani Mountains, northeast base, at Wei Wei River: 8 ♂♂, 3 imm. ♂♂, 7 ♀♀, 7 imm. ♀♀, 17/21-IX-1969, K. E. Stager, Cheney East Africa Expedition (LACM 36477/501). 1 mile north of Guaso Nyiro River bridge: 12 ♂♂, 1 ♀, alc. (ROM 71348/59, 71392). Southern Guaso Nyiro: 1 ♀, W. P. Selae (?) (BMNH 13.10.18.10). Isiolo: 1 ♀, 3-XI-1963, "I. M./WFVZ 6" (LACM 31769). Kanyangaren: 2 ♂♂, alc., skulls, 4-IX-1970, I. R. Aggundey (ZMA 19.834/5). Kerio Valley: 2 ♂♂, 9-X-1963, "WFVZ 10" (LACM 31752, -54). Kinna: 4 imm. ♂♂, 1 ♀, 2 imm. ♀♀, 23/24-VI-1973, National Museum Nairobi (LACM 45640/44); 23-VI-1973, M. J. Sutton (ROM 71079, ...). Korau: 1 ♂, 1 ♀, 4-VII-1965, J. Jones (ROM 36223/4); 3 ♂♂, alc. (ROM 66049, -51, -53). Guaso Nyiro River, near Magadi: 4 ♂♂, 1 imm. ♂, 1 ♀, 3 imm. ♀♀, 2/3-VII-1964, J. G. Williams (LACM 51430, -32/34, -34, -37/40). Magadi: 1 ♂, 1 imm. ♀, 14-IX-1958, S. N. Greenberg African Collection (CAS 11906/7), 3 ♂♂, 4/6-VII-1973, M. J. Sutton (ROM 71100/02). Masabubu: 1 ♀, 26-VI-1960, R. H. Pine (AMNH 187268). Mitunbur: 1 imm. ♀, 11-XII-1965, J. G. Williams (ROM 38265). Mount Nyiro, west base: 1 imm. ♂, 4-VI-1968, K. E. Stager (LACM 51318). River Olebortoto: 1 ♂, 1 imm. ♂, 1 ♀, 14-IX-1969, A. N. Start (BMNH 75.2407/9). Sigor: 1 ♂, ♀, 10-III-1964, J. G. Williams (LACM 51431, -35); 5 ♂♂, 1 ♀, 2 imm. ♀♀, 1-VI/11-XII-1965, J. G. Williams (ROM 36218/22, 38262/63); 3 ♂♂, 7/21-VII-1966, A. E. Williams (ROM 40250/51, -57); 1 ♂, 21-X-1966, J. D. Start (BMNH 75.2405); 1 ♂, 22-VIII-1967, A. N. Start (BMNH 75.2406); 1 ♂, skull, 7-V-1970, J. W. Wright (MVZ 142033); 6 ♂♂, 3 ♀♀, alc. (BMNH). Solai Valley: 1 ♂, 4 ♀♀, alc. (ROM 66316/8, 66341/2). Turkwell Gorge: 2 ♀♀, alc. (ROM 65507/8).

MALAWI. Cape Maclear: 2 ♂♂, 1 ♀, 2 imm. ♀♀, 30/31-V-1975, L. W. Robbins (CMNH 409758/62). Karonga: 2 ♂♂, 4 ♀♀, cf. 4-I-1956/9-XII-1957, R. H. Oram (HZM 9.1926, 12.2198, 13.2204, 20.2621, 21.2638, 22.2639); 1 ♂, 1 ♀, alc. (BMNH). Kasungu National Park Administration Camp: 1 ♂, 25-I-1982, H. Jachmann (ZMA 21.677). Lingadzi River Valley house: 1 ♂, 20-II-1982, H. Jachmann (ZMA 21.678). Lisanthu: 5 ♂♂, 2 imm. ♂♂, 6/13-III-1982, H. Jachmann (ZMA 21.680/86). Nkhotakota: 4 ♀♀, 11/14-VIII-1946, H. E. Anthony (AMNH 161853, -56/58). (Kamuzu Academy, Kausi, Livingstonia, Monkey Bay, Nchalo, Nkhotakota, Thondwe, Vitanda, Zomba; 1232D, 1233A, 1233C, 1332D, 1635B).

#### RWANDA.

(Gisenyi, Kibuye, Kigali, Mabanza, Murunda, Nyundo.) SOMALIA. Dowa: 1 ♀, alc. (BMNH).

(Afgoi, Dolo, Genale, Libsoma farm.)

SUDAN. Roseires: 2 imm. ♂♂, skulls, IX-1907, S. S. Flower (via Egyptian Government Zoological Gardens) (BMNH 8.4.17.2/3).

(Mbilli, Mundri, Raffile/Sue River, Wau.)

TANZANIA. Arusha: 2 ♂♂, 24-II-1956, H. Hoogstraal (FMNH 86017/18); 1 ♂, 1 ♀, alc., 24-XII-1956, H. Hoogstraal & M. N. Kaiser (FMNH 86509/10). Bagamoyo: 1 imm. ♂, 1 imm. ♀, 20-II-1890, Emin Pasha (BMNH 90.6.8.12/13); 1 ♀, alc., skull, Fischer (ZMB 5601); 6 ♂♂, 4 ♀♀, skulls, 1960, H. W. P. van Barneveld (RMNH). Chimala: 2 ♂♂, 1 ♀, 22-X-1952, S. Knipper (SMNS 5606/8). Dar es Salaam: 1 imm. ♂, alc., skull (ZMB); 3 ♂♂, 1 imm. ♂, A. Loveridge (BMNH 22.7.17.22/23, ...); 1 ♂, alc. (Kagera, Dar es Salaam; BMNH); 2 imm. ♀♀, 29-III- and 30-IV-1983, R. Luttkik (ZMA 22.236/7). Igalula: 1 ♀, 7-V-1959, A. F. Rees (HZM 25.2973). Igonda: 1 ♀, skin, 26-X-1882, R. Böhm and 2 ♀♀, R. Böhm (ZMB 9966, 10022, -24). Kafukola: 2 ♂♂, 13-VII- and 16-VIII-1955, S. A. D. Robertson (HZM 8.1887; BMNH 56.387); 2 ♂♂, 6-VI- and 6-VIII-1956, S. A. D. Robertson (HZM 17.2358, 14.2351); 1 ♀, 25-IV-1958, L. D. E. F. Vesey-Fitzgerald (HZM 29.3063). Kalembo: 1 ♀, 10-IV-1956, S. A. D. Robertson (HZM 16.2355). Kawe: 2 ♂♂, 6-I-1965, A. Williams (LACM 31759, 40338). Kidugallo: 1 ♂, 7-XII-1957, Th. Andersen (SMNS 5980). Kilosa: 1 imm. ♀, 31-X-1926, J. T. Zimmer (FMNH 29430); 2 ♂♂, 8-V-1923, A. Loveridge (BMNH 24.1.1.8/9); 1 ♀, 1 ♂, 17-I-1959 and 19-XII-1958, A. F. Rees (HZM 24.2779, 24.2830). Kissaki: 2 ♂♂, A. Buchanan (BMNH 21.12.4.1/2). Lake Manyara: 1 ♀, 16-III-1958 (BMNH 69.20). Lake Natron, west side: 2 ♀♀, 1 imm. ♀, 22-VIII-1964, P. Leakey (BMNH 75.2402/4). Magugu: 1 ♀, 3-VIII-1960, J. Popp (ZSM 1960/405). Mbeya: 1 ♂, skin (BMNH 68.73). Mikindani: 1 imm. ♂, K. Schilling (ZMB 54513). Mohorro: 1 ♂, alc., skull, 25-V-1901, F. Langheld (ZMB). Morogoro: 13 ♂♂ (5: skins only), cf. 22/27-XI-1918, A. Loveridge (BMNH 22.7.17.10/15, 2.4.1.1.10, and 5 without numbers; USNM 297468); 1 ♀, via Swaythling (BMNH 22.7.17.21). Mto-wa-mbu: 1 ♀, 2 imm. ♀♀, 3-VII-1937, Uthmöller & Bohmann (ZSM 1937/210, -212/213). Mwaya: 1 ♂, 8-IX-1949, O. Milton (BMNH 51.379). Pangani Falls: 1 ♀, 13-V-1897 (ZMB 54791). Rukwa: 1 ♀, 16-IV-1954, L. D. E. F. Vesey-Fitzgerald (HZM 3.1796). Songea: 1 specimen, alc. (BMNH). Tanga: 1 ♂, 1 ♀, 7-III- and 28-VII-1963, I. Bampton (USNM 351176, -78); 1 ♂, 4 ♀♀, 28-VII/1-IX-1963, "WFVZ" (LACM 31753, -55/57, -59). Tukuyu: 1 ♂, 29-VIII-1964, C. J. P. Ionides (HZM 31.4020). Turiani: 2 ♂♂, 1 ♀, 25-XI-1950, C. E. Cade (FMNH 77487/9). Ugano: 1 ♂, 1935/6, H. Zerny (NMW 19831). Ujiji: 1 imm. ♀, Hösemann (ZMB 10100).

Utengule: 2 ♂♂, 26-X-1938, W. Jörgens (ZMB 60915/6).

(Kisarawe.)

UGANDA. Amudat: 1 ♂, 1 ♀, 5-VIII-1968, B. J. Hayward (USNM 436488/89).

ZAIRE. Albertville: 1 ♂, alc. (BMNH 55.1191); 2 imm. ♂♂, alc., 4-III- and 15-VI-1947, Mission hydrobiologique du Lac Tanganika (IRSN 9065/6). Mulongo: 1 ♂, 30-X-1974, M. D. Callagher (HZM 32.7869).

(Lake Mweru.)

ZAMBIA. Abercorn: 1 ♂, 3 ♀♀, 5-I-1953, 24-IV-1954, 14-XI-1958, 1-XII-1958, L. D. E. F. Fesey-Fitzgerald (HZM 1.1444, 4.1797, 26.3052, 27.3053). Jumbe: 1 ♂, 18-I-1964, R. J. Dowsett (AMNH 207412). Kalambo Falls: 1 imm. ♂, C. S. Holliday (cf. HZM). Mfuwe Camp: 1 ♂, 1 imm. ♂, 2 imm. ♀♀, 29/30-III-1964, W. F. H. Ansell (BMNH 66.5408/11). Mwanya area: 1 ♀, W. F. H. Ansell (BMNH 65.365). Nsadzu: 1 imm. ♀, via D. Gordon Lancaster (BMNH 37.12.8.2). (Chipata, Jumbe, Kasama, Lundazi, Mpulungu, Nsefu Game Camp, Teleka.)

ZANZIBAR. Zanzibar: 1 ♂, alc., skull, received in exchange from G. E. Dobson (holotype specimen; BMNH 79.9.12.4); 1 ♀, alc., skull, G. E. Dobson (ZMB 5550); 1 ♀, received 24-VI-1881, via De Ville (IRSN 1878).

*Diagnosis:* A small-sized, typical species of the genus, with the fourth palatal ridge halfway between the third and fifth and essentially two postdental palatal ridges — in smaller specimens, the fifth ridge may be partly interdental; a relatively short rostrum and palate; a relatively large zygomatic width. Measurement ranges and ratios taken from specimens from all over the species' range:

fal	♂♂	57.0-68.9	(n = 152),
	♀♀	54.1-67.6	(n = 83);
gsl	♂♂	33.7-41.5	(n = 96),
	♀♀	32.0-39.5	(n = 59);
cbl	♂♂	33.0-40.8	(n = 78),
	♀♀	31.0-39.0	(n = 50);
rl	♂♂	12.6-16.4	(n = 55),
	♀♀	11.2-16.0	(n = 34);
zw	♂♂	19.0-22.0	(n = 82),
	♀♀	18.9-21.6	(n = 48);
C <sup>1</sup> -M <sup>1</sup>	♂♂	11.5-14.8	(n = 83),
	♀♀	10.9-13.3	(n = 50);
M <sup>1</sup>	♂♂	2.35- 3.25	(n = 58),
	♀♀	2.25- 3.2	(n = 40);
W	♂♂	32-58	(n = 29),
	♀♀	25 -62	(n = 19);

rl	♂♂	36.5-41.0% of gsl,
	♀♀	35.1-39.1% of gsl;
pl	♂♂	57.1-62.5% of gsl,
	♀♀	57.0-62.7% of gsl;
zw	♂♂	52.0-59.2% of gsl,
	♀♀	53.9-60.9% of gsl.

Specimens smallest in eastern Ethiopia, southern Somalia, and Kenya, and largest in eastern central and southwest Tanzania and adjacent Zambia and Malawi. Table 8 gives a breakdown of measurement ranges per country.

*Distribution:* Fig. 8.

*Related species:* The generally more western *E. labiatus*, in which both ♂♂ and ♀♀ average distinctly larger in all measurements than *E. minor*. See for the relation between these two species also the remarks under both.

#### Remarks

*Taxonomy:* *Epomophorus minor* is the smallest typical species of the genus and on species level the only taxonomic question is its position in relation to the first larger species, *E. labiatus*. In the discussion on that species, I have extensively dealt with this problem and for many details the reader may be referred to that section. In short, Andersen's (1912) authoritative account of *E. labiatus*, which has served as the conceptual basis for many later authors on that species, appears to be based on specimens of both *E. labiatus* and *E. minor*, and Andersen thought that *minor* differed from *labiatus* almost exclusively by its weaker dentition. In fact, *minor* averages considerably smaller than *labiatus* in all measurements. Many authors using Andersen's diagnoses put *minor* down as a subspecies of *labiatus*. It was believed that their ranges were allopatric, with intergrades occurring in the border zone. However, in several regions the two appear to occur side by side (Malawi: Bergmans *et al.*, 1983; Rwanda: Baeten *et al.*, 1984; Sudan: McLellan, 1986), which of course indicates specific difference. Other regions, especially western Tanzania, harbour populations of, in my present opinion,

Table 8. Ranges of selected measurements of *Epomophorus minor* Dobson, 1880 per country.

		♂♂						♀♀					
		fal	gsl	zw	C <sup>1</sup> -M <sup>1</sup>	LM <sup>1</sup>	W	fal	gsl	zw	C <sup>1</sup> -M <sup>1</sup>	LM <sup>1</sup>	W
Ethiopia	n	40	31	29	30	26	1	26	16	15	15	17	
	m	62.5	35.6	20.1	12.2	2.6	37	61.5	33.8	19.7	11.6	2.5	
	min	58.7	33.8	19.0	11.5	2.4		59.0	32.6	19.0	11.0	2.3	
	max	67.3	37.9	21.0	13.2	2.9		64.0	36.0	20.7	12.2	2.8	
Kenya	n	59	30	20	21	8	21	26	16	12	10	2	12
	m	62.35	35.9	20.1	12.4	2.7	43	60.25	33.6	19.5	11.5		38
	min	57.0	33.7	19.0	11.9	2.5	32	54.1	32.0	18.9	10.9	2.5	25
	max	66.1	37.6	21.1	13.8	2.9	58	64.2	36.1	21.1	12.2	2.6	46
Malawi	n	10	6	5	5		2	4	3	2	2		1
	m	63.6	38.3	20.7	13.1			61.4	35.4				38
	min	59.8	35.4	19.9	12.9		37	59.9	35.0	19.5	12.1		
	max	66.2	39.3	21.2	13.4		38	62.9	36.0	19.8	12.7		
Sudan	n					2							
	min					3.1							
	max					3.25							
Rwanda	n											2	
	min											2.5	
	max											2.8	
Somalia*							64.2						
Tanzania	n	35	25	26	24	19	3	19	20	15	18	15	6
	m	65.3	39.7	21.2	13.6	2.75	51	62.8	36.3	20.4	12.4	2.8	44
	min	58.1	37.8	20.4	12.8	2.35	46	60.3	34.3	19.5	11.7	2.25	33
	max	68.9	41.5	22.0	14.8	3.1	55	67.6	39.5	21.6	13.3	3.2	62
Zaire	n	2	1	1	1								
	min	62.2	40.1	21.7	13.4								
	max	66.1											
Zambia	n	3	3	1	2	2		4	3	3	4	4	
	m	66.7	38.8	20.4				63.8	35.5	19.5	12.2	2.55	
	min	66.0	37.5		13.1	2.7		63.1	34.8	19.3	11.7	2.5	
	max	67.0	39.8		13.4	2.9		65.3	36.2	19.7	12.8	2.6	
Zanzibar	n					1		2	1	1	1		
	min					2.7		62.5	35.3	20.5	12.5		
	max							62.7					

\* Lanza (1961) gave for the gsl of 4 adult ♂♂ from Somalia 34.8-35.9 (mean 35.5) and for 8 adult ♀♀ from Somalia a gsl range of 31.8-34.0 (mean 33.0) (all reported as *Epomophorus labiatus* (Temminck, 1837)).

atypically small *labiatus*, which some may wish to consider as intergrades. These certainly do complicate matters, and the two may eventually be found to behave as independent species in one region and to intergrade in another (as has been found for green frog species in Europe).

Distribution and geographical variation: *E. minor* is a species from woodlands, savanna areas with forest patches, bushlands, and even drier vegetation types. In northwest

Ethiopia and North Somalia it has been collected in Somalia-Masai semi-desert grassland (type 54 in White, 1983). In eastern Somalia and Kenya the species is found in Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket and in the Kenyan highlands in a Mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland (types 42 and 45 in White, 1983). In eastern Sudan *E. minor* occurs in the Transition from Ethiopian

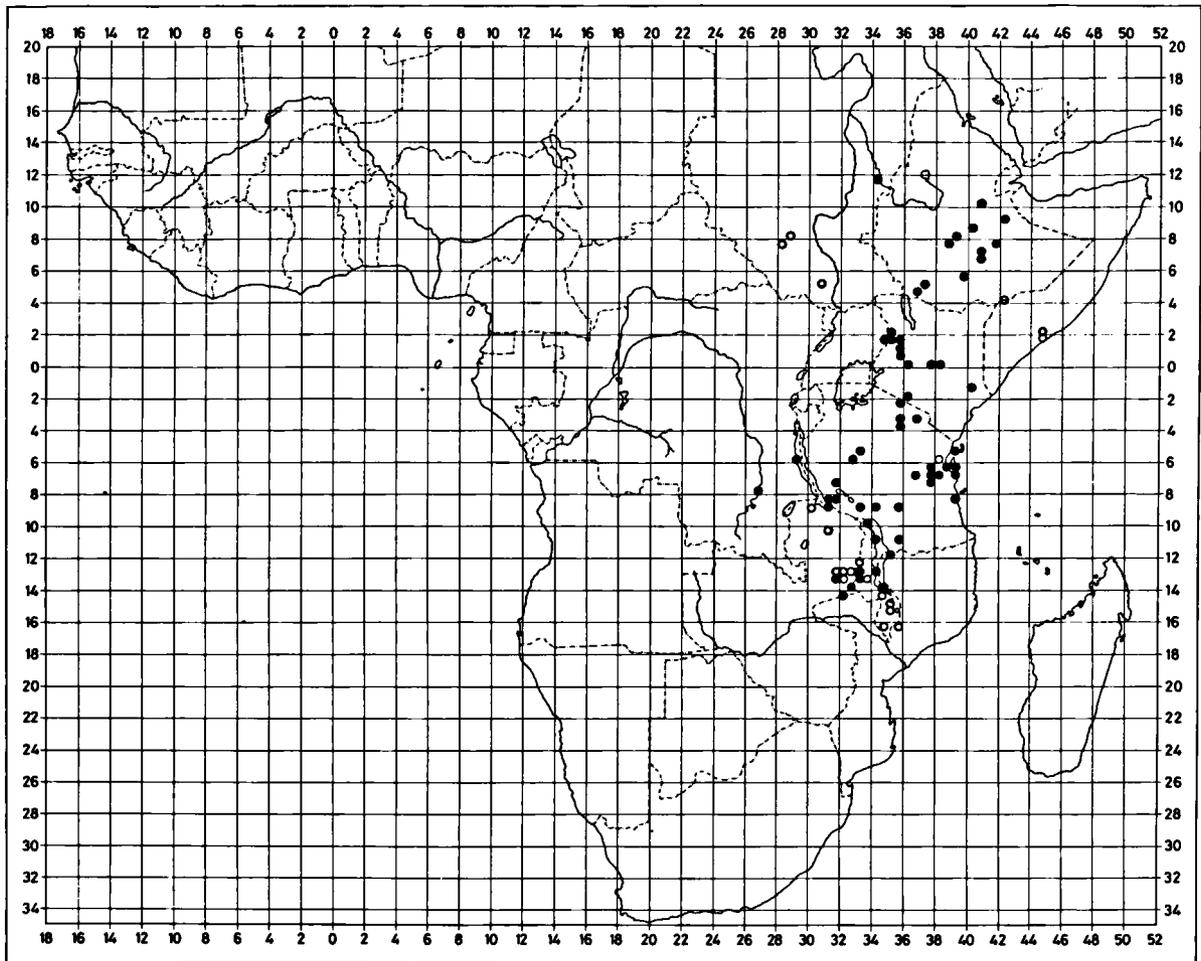


Fig. 8. Distribution of *Epomophorus minor* Dobson, 1880. Black dots: squares from which material has been identified by the author. Open circles: records from literature.

woodland to *Acacia* deciduous bushland and wooded grassland and in southern Sudan in Sudanian woodland with abundant *Isberlinia* (types 35b and 27 in White, 1983).

More towards the south, collecting localities are in Wetter (South Tanzania, Malawi, Zaire) and Drier (Central and South Tanzania) Zambesian miombo woodlands, and in Malawi also in North Zambesian woodland (types 25, 26 and 29c in White, 1983). In eastern and southern Tanzania the species is found in the Forest patches in East African coastal mosaic and in the Mangrove zone (types 16a and 77 in White, 1983). Marginal localities are in or near Afromontane vegetation: Harar in Ethiopia

and northern Lake Tanganyika in Zaire (type 19a in White, 1983).

In fact, there is not much difference in habitat preference between *E. minor* and *E. labiatus*, except the general difference in altitude, and *minor*'s choice is much the same as that of *Epomophorus wahlbergi* (Sundevall, 1846).

The geographical variation of *E. minor* has been summarized in the diagnosis.

#### **Epomophorus angolensis Gray, 1870**

*Epomophorus macrocephalus* var. *angolensis* Gray, 1870: 125 (type locality: Angola).

*Epomophorus angolensis*; Matschie, 1899: 47 (in part: specimens from Benguela, Moçâmedes; others: uncer-

tain); Andersen, 1912: 542 (specification of type locality as Benguela); Monard, 1935: 33; Shortridge, 1934: 43; Hill *et al.*, 1941: 34; Hayman, 1963: 97; Kock, 1969: 19; Smithers, 1983: 56; Feiler, 1986: 67; Meester *et al.*, 1986: 27.

#### Material examined

ANGOLA. "Angola": 1 imm., alc., via Lisbon Museum (ZMB 3632). Benguela: 1 imm. ♂, alc., skull, J. J. Monteiro (BMNH 64.8.16.1; holotype of *Epomophorus angolensis* Gray); 1 imm. ♀, alc., skull, J. J. Monteiro (p.) (BMNH 64.8.16.2); 2 ♂♂, alc., skulls, 1 imm., alc., J. J. Monteiro (cf. via Sclater) (ZMB 4238, 10012/10068, 10013). Chitau: 1 imm. ♀, 2-III-1933, Phipps, Bradley Expedition (AMNH 88071). Concordia, Cumbira, Omombolo: 1 imm. ♀, 25-V-1928, J. H. Wilhelm (ZMB 41802). Hanha: 2 imm. ♀♀, 15/16-V-1925, Lang Boulton, Vernay Angola Expedition (AMNH 85520, -23). Huila: 6 imm. ♂♂, 3 ♀♀, 4 imm. ♀♀, 30-XI/2-XII-1954, G. H. Heinrich (FMNH 83590/91, 84035/41, -43/46). Loanda: 1 imm. ♀, alc., skull, VIII-1900/III-1901, Heim (ZMB 54932).

(Ambriz, Cubango, Fazenda Bumbo at Humpata, Fazenda Cacanda nr Bibala, Lubango, Moçâmedes, Mupa, Quipungo, Quiteve, Tchivinguiro.)

NAMIBIA. Cunene River: 1 imm. ♂, G. C. Shortridge (BMNH 25.12.4.3). Odongwa: 1 ♀, 1 imm. ♀, G. C. Shortridge (BMNH 25.12.4.8/9). Otjimbimbi (or Otjumbumbi): 1 ♂, skin (skull not seen), G. C. Shortridge (BMNH 25.12.4.2). "Swakopmund": 1 ♂, 1 imm. ♂, 1 ♀, Higgins (ZMB 3603/10069, 3885/10071, 3886/10078). Tshimhaka: 1 specimen, skin, 25-VII-1927, G. C. Shortridge (BMNH 28.9.11.61). Ukualukasi: 2 ♀♀, 1 ♀ (?), 24-IX-1924, G. C. Shortridge (BMNH 25.12.4.4/6).

**Diagnosis:** A large species of the genus, only slightly smaller than typical *Epomophorus gambianus*, characterized by the position of the fourth palatal ridge: nearer to the third than to the fifth, with two postdental palatal ridges, a relatively long rostrum and a relatively short palate.

fal	♂♂	85.2-93.9 (n = 4),
	♀♀	81.1-85.5 (n = 9);
gsl	♂♂	56.4-60.0 (n = 2),
	♀♀	49.6-50.6 (n = 3);
cbl	♂♂	56.4-60.0 (n = 2),
	♀♀	49.3-50.1 (n = 3);
rl	♂♂	26.5-28.8 (n = 3),
	♀♀	22.2-22.5 (n = 4);
zw	♂♂	27.4 (n = 1),
	♀♀	25.1 (n = 1);

C <sup>1</sup> -M <sup>1</sup>	♂♂	20.4-21.6 (n = 2),
	♀♀	17.0-17.9 (n = 6);
rl	♂♂	47.0-48.0% of gsl,
	♀♀	44.5- ± 45.3% of gsl;
pl	♂♂	62.3-62.6% of gsl,
	♀♀	59.7-60.7% of gsl;
zw	♂♂	45.7% of gsl,
	♀♀	50.5% of gsl.

For measurements of individual specimens see table 9.

**Distribution:** Fig. 9. The liability of Swakopmund as collecting locality has been questioned by Shortridge (1934); it has not been mapped. See also under Remarks.

**Related species:** *Epomophorus gambianus* has a relatively shorter rostrum and longer palate, and its fourth palatal ridge is at equal distances from the third and fifth. Its southern African subspecies *crypturus*, which is known from the east Angolan border on eastward, averages smaller in all body and skull measurements.

#### Remarks

**Taxonomy:** After *E. gambianus pousarguesi* and *E. grandis* (Sanborn, 1950), *E. angolensis* is the rarest representative of the genus in collections. This is undoubtedly due to its restricted distribution in a part of Africa which is not often visited by collectors. Of the known specimens, very few are adult, and the dimensional variation of the species is incompletely known. Very few authors have published measurements (Andersen, 1912; Monard, 1935; Hayman, 1963; Feiler, 1986). Feiler (1986) gave ranges of a number of measurements in 23 specimens (which are in the National Museum at Lubango: Dr A. Feiler, *in lit.*, 9-VI-1988), but unfortunately, as he remarked himself, there are "Verschiedenheiten in den Massen, die (...) wenig wahrscheinlich sind." I am convinced that the measurements are correct but I presume that the series of ♀♀ contains a number of immature specimens, possibly of both sexes.

Inclusion of some earlier published measurements in the ranges cited in the

Table 9. Measurements of *Epomophorus angolensis* Gray, 1870.

	Angola					Namibia				
	BMNH	ZMB	ZMB	ZMB	ZMB	FMNH	FMNH	BMNH	BMNH	BMNH
	64.8.16.1	4238	10068	10069	10071	83590	83591	25.12.4.4	25.12.4.5	25.12.4.8
	holotype			/3603	/3885					
	♂ imm.	♂	♂	♂	♂	♀	♀	♀	♀	♀
	Benguela	Benguela	Benguela	"Swakopmund"		Huila	Huila	Ukualukasi		Odongwa
fal	89.4	91.6	91.0	84.9	85.2	83.7	85.5	83.0	81.1	83.4
gsl	± 54*	56.4	60.0	—	—	± 50.6**	± 50.6**	≥ 49.4	49.6	—
cbl	± 53.7	56.4	60.0	—	—	± 50.1	± 49.8	—	49.3	—
rl	± 25.0	26.5	28.8	—	28.0	22.9	22.5	22.1	22.3	—
pl	± 33.0	35.3	37.4	—	36.2	30.7	30.2	29.7	30.1	—
cranium width	17.4	17.6	17.2	—	—	17.2	16.6	—	16.7	17.0
iow	7.7	8.1	8.5	7.4	8.6	7.4	7.3	7.3	7.4	7.1
pow	10.7	11.1	9.8	9.6	9.0	10.7	—	—	10.3	9.9
zw	± 26.0	—	27.4	—	—	—	—	—	25.1	—
mandible length	43.6	—	49.5	—	48.1	41.0	41.4	39.9	39.5	40.7
mandible height	16.3	—	16.0	15.4	17.4	14.4	14.4	14.8	14.3	15.5
width over C <sup>1</sup> -C <sup>1</sup>	9.2	9.4	10.0	—	—	8.4	8.6	8.9	8.9	8.7
C <sup>1</sup> -M <sup>1</sup>	18.8	—	21.6	17.0	20.4	17.5	17.5	17.1	17.2	17.9
M <sup>1</sup> -M <sup>1</sup>	13.9	≥ 14.5	16.5	13.9	16.1	12.8	13.2	13.6	14.0	13.5
C <sub>1</sub> -M <sub>2</sub>	20.8	—	23.3	—	22.4	18.7	19.0	19.0	19.3	19.8
length P <sup>3</sup>	2.9									
P <sup>4</sup>	3.3									
M <sup>1</sup>	3.4							3.3	3.3	3.3

\* without premaxilla

\*\* skulls with fractures

diagnosis would enlarge gsl in ♂♂ to 56.4-61.5 (although this larger maximum value, published by Andersen, 1912 must be of a skull also seen by the present author); it would enlarge gsl in ♀♀ to 48-52 (after Monard, 1935 — who's smallest of 3 ♀♀, with a fal of 75 and a gsl of 46.5, was almost certainly immature); and it would enlarge fal in ♂♂ to 85.2-95 (this new maximum value quoted from Feiler, 1986 — whose largest ♂ measurements will certainly be correct).

Distribution and geographical variation: The distribution of *E. angolensis* is restricted to western Angola and northern Namibia. In Angola, it remains west and south of the Mosaic of Guineo-Congolian lowland rain forest and secondary grassland and Edaphic and secondary grassland on Kalahari Sand (types 11a and 60 in White, 1983) and largely north of the Mosaic of Zambebian dry deciduous forest and secondary grassland (type

22a in White, 1983) in the south. The species has been collected chiefly in the central block of Wetter Zambebian miombo woodland, the northwestern stretch of North Zambebian woodland, and the southwestern area of *Colophospermum mopane* woodland and scrub woodland — with which it just crosses the Namibian border — (types 25, 29c and 28 in White, 1983). Some old records are from the Bushy Karoo Namib scrubland (at Benguela) and from the Namib desert (at Moçâmedes and Swakopmund) (types 51 and 74 in White, 1983). Shortridge (1934) thought that the Swakopmund specimens may have come from a more inland place; this may be true for those from Benguela and Moçâmedes as well. I have included them in the map because they are quite near the distribution area of the species, while Swakopmund is far outside that area — of course, as far as known. In eastern Angola *E. angolensis* appears to be halted by the extensive

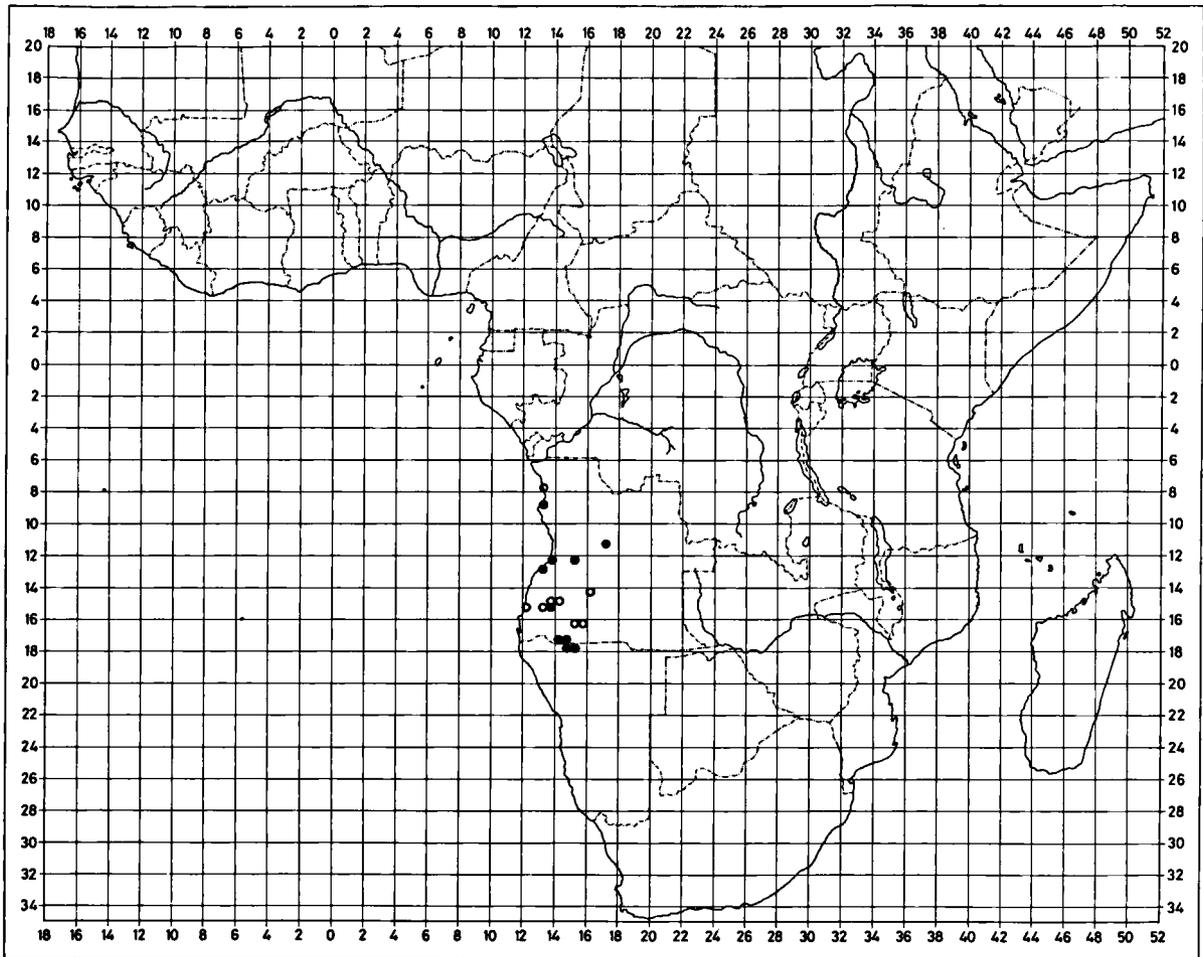


Fig. 9. Distribution of *Epomophorus angolensis* Gray, 1870. Black dots: squares from which material has been identified by the author. Open circles: records from literature and correspondence.

region of Mosaic of *Brachystegia bakerana* thicket and edaphic grassland (type 47 in White, 1983). The western border of this vegetation type, in which no other Megachiroptera have been collected either, runs from about 10°30' S 22°E, where it approaches the northern vegetative limit of the species, to the southwest at about 16°S, 16°E.

In theory, the species could penetrate into Katanga through a corridor of Wetter Zambesian miombo woodland at 10°30' S, 22°E, although in this region this type is interspersed with the probably less suitable Zambesian dry evergreen forest (type 6 in White, 1983). In Katanga, *E. angolensis* is replaced by *E. gam-*

*bianus crvbturus*. The relatively restricted and in itself continuous distribution area of *E. angolensis* render geographic variation unlikely, but I have seen too few specimens to be able to confirm this idea.

#### ***Epomophorus wahlbergi* (Sundevall, 1846)**

*Pteropus wahlbergi* Sundevall, 1846: 118 ("Prope Portenatal et in Caffraria interiore occisus.").

*Pteropus haldemani* Hallowell, 1846: 52 ("West Africa").

*Epomophorus wahlbergi*; Peters, 1867: 869; Andersen, 1912: 521-529 (selection of type and designation of type locality: ♂, mounted, skull, Naturhistoriska Riksmuseet, Stockholm 1040, collected by J. Wahlberg, 27-XI-1843, at the Tugela River); Lönnberg, 1912: 47; Kershaw, 1922b: 178; Loveridge, 1922:

43; Funaiola *et al.*, 1968: 199; Lanza, 1961: 170; Morris, 1964: 73; Kingdon, 1974: 157; Peterson *et al.*, 1975: 2; O'Shea *et al.*, 1980: 490; Smithers, 1983: 55; Fenton *et al.*, 1985: 461; Herselman *et al.*, 1985: 79; Happold *et al.*, 1987: 350.

*Epomophorus neumanni* Matschie, 1899: 50 (in part: specimens from Mombasa, Malindi, Takaungu); G. M. Allen, 1911: 322.

*Epomophorus wahlbergi haldemani*; Andersen, 1912: 522; J. A. Allen *et al.*, 1917: 421; Lang *et al.*, 1917: 509; Hollister, 1918: 71; De Beaux, 1924: 152; Cabrera *et al.*, 1926: 593; Cabrera, 1929: 16; Moreau *et al.*, 1940: 125; Hill *et al.*, 1941: 33; Schoutedden, 1944: 106; Malbrant *et al.*, 1949: 83; Sanborn, 1950: 54; Swynnerton *et al.*, 1951: 287; Aellen, 1957: 193; Eisentraut, 1958: 20; Ansell, 1960a: 164; Ansell, 1960b: 10; Harrison, 1961: 287; Novick, 1960: 395; Kulzer, 1962a: 165; Kulzer, 1962b: 123; Hayman, 1963: 95; Koopman, 1965: 3; Hayman *et al.*, 1966: 24 (in part: MRAC 20278 is a shrew); Ansell, 1967: 4; Ansell, 1978: 16; Bergmans, 1979: 173; Aggundey *et al.*, 1984: 123; Feiler, 1986: 67.

*Epomophorus wahlbergi wahlbergi*; Andersen, 1912: 526; St. Leger, 1932: 957; Moreau *et al.*, 1940: 125; Roberts, 1951: 57; Swynnerton *et al.*, 1951: 287; Aellen, 1957: 193; Sweeney, 1959: 8; Ansell, 1960b: 10; Harrison, 1961: 287; Pienaar, 1964: 9; Ansell, 1967: 4; Smithers *et al.*, 1976: 39; Dulic *et al.*, 1977: 232; Ansell, 1978: 16; Rautenbach, 1982: 29; Ansell *et al.*, 1988: 27.

*Epomophorus gambianus* (not of Ogilby, 1835); Malbrant *et al.*, 1949: 83; ? Didier, 1965: 338 (in part: specimens MNHN 13-13 and 1885-367 from "Congo"); Hayman *et al.*, 1966: 23 (in part: specimen IRSN 186b from Landana).

*Epomophorus crypturus* (not of Peters, 1852); Peters, 1877b 913; Aggundey *et al.*, 1984: 123.

### Material examined

ANGOLA. Benguela: 1 ♀, alc., J. J. Monteiro (ZMB 4240). Cassai: 1 ♂, R. H. Smithers, 8-II-1965 (HZM 15.4236). Chinchoxo: 2 ♂♂, alc., skulls, 1 imm. ♂, alc., 1 ♀, Falkenstein (ZMB 4801, 9974, -76/77). Chitau: 1 ♀, 9-VIII-1925, Lang Boulton (AMNH 85519). Dundo (or Dondo): 1 imm. ♂, alc., 23-I-1955, G. H. Heinrich (FMNH 84051). Duque de Bragança (25 km N, 15 km E): 1 imm. ♀, 1954, G. H. Heinrich (FMNH 81725). Landana: 1 specimen (IRSN 186b). Luhanda: 1 ♂, 1 imm. ♂, 1 imm. ♀, 18/20-VI-1954, G. H. Heinrich (FMNH 81606/08). Malange (Malanje): 2 ♀♀, alc. (not seen), skulls, Von Mechow (ZMB 9969, 9971). Mount Moco: 1 ♀, 3-X-1954, G. H. Heinrich (FMNH 83589). (Ambacca, Cabuta, Caconda, Calulo, Carlo, Cubicula, (Rio) Cuillo, Dando, Luanda, Lubango, Luchingue River, Massano de Amorim, Missongue, Moçâmedes, Mulundu, Mussende, Noqui, Novo Redondo, Pungo Andongo, Quimbango, Quimdumbo, Quissange, Serra de Seles, Uige.)

BURUNDI. Near Bulaganya: 1 ♂, 1 ♀, alc. (BMNH). Kigamba: 1 imm. ♂, 15-VII-1976, J. Verschuren (IRSN 19928).

CAMEROUN. Cf. Aqua Town (Douala): 1 imm. ♂, alc. (not seen by present author), skull, before 1895, Reichenow (ZMB 4786).

CONGO. Pointe Noire: 1 ♂, 3 imm. ♂♂, 4 ♀♀, 2 imm. ♀♀, 1 imm., (6 specimens: alc., adults: skulls), 6-XI/14-XII-1972, W. Bergmans (ZMA 15.541/50, 15.666).

? EQUATORIAL GUINEA. Alen: 1 ♀, (skull not seen), XII-1906, Tessmann (ZMB).

? ETHIOPIA. "Abyssinien": 1 ♂, Th. von Heuglin (NMW 18301). "Abyssinia": 1 ♀, skull, purchased (Verreaux) (BMNH 49.8.16.5/47.7.8.25).

GABON. Cape Lopez: 1 ♂, 10-II-1915, H. Lang & J. P. Chapin (AMNH 48662). Fernan Vaz: 3 ♂♂, 3 ♀♀, alc. (FMNH 73812, -16/19, -24). Franceville: 1 specimen, alc., Schwebisch & Thollon (MNHN 1884-583). Lac Anengué: 1 ♂, 1 (imm.?) ♂, alc., skulls, Roux (MNHN 1950-877). Omboué: 8 ♂♂, 1 imm. ♂, 6 ♀♀, 1 imm. ♀, 5-VII/12-X-1917, C. R. Aschemeier (USNM 218490, 218950, -53/55, -57, -62, -64, -66, -69, -71, -76, 219077/80).

KENYA. Athi River: 1 ♀, 2-VII-1968, B. J. Hayward (USNM 436386). Arabuko-Sokoke District: 1 imm. ♀, 17-V-1973, J. M. K. Ithia (LACM 45639). Arabuko-Sokoke Forest: 3 imm. ♂♂, 15/16-V-1973, J. N. Kyongo/J. Ithia (LACM 45636/38); 1 ♂, 3 ♀♀, 1 imm. ♀, alc., skulls, 5/12-X-1979, W. & E. Bergmans (ZMA 20.844/48). Bodhai, Boni Forest: 1 imm. ♀, 11-III-1973, K. Stager (LACM 42802). Bura: 1 ♂, 8 ♀♀, 4 imm. ♀♀, 9/20-III-1963, Knudsen-Machris Expedition (LACM 19778, -81/82, 19944/53). Daren: 1 imm. ♀, 24-VI-1965, A. Starrett (LACM 19631). Donyo Sabuk: 1 ♀, R. L. Peterson & Glen (ROM 63882). Garissa: 1 ♀, 22-I-1961, P. Martin (LACM 19535). Gedeh: 1 imm. ♂, 1 ♀, 5/6-V-1973, J. M. K. Ithia (LACM 45633/34). Inyokoni: 2 ♂♂, 1 imm. ♂, 4/6-XII-1976, R. Kyongo (RMNH). Kairuni: 1 imm. ♀, 20-IX-1973, K. E. Stager (LACM 45632). Kakamega: 1 ♀, 25-IX-1959, C. J. P. Ionides (HZM 9.3080); 1 ♀, 23-VII-1963, R. E. Mumford (USNM 350807); 1 ♀, 1-VIII-1963, D. A. Zimmerman (USNM 350808). Kakamega Forest: 1 imm. ♂, 24-XII-1962, J. Williams (LACM 19537); 6 ♀♀, 1 imm. ♀, (7 skins, 6 skulls), IX-1968, R. Glen (ROM 50472, -78, -90, 50518, -21/22, -47); 2 ♀♀, 1 imm. ♀, 14/27-I-1971, J. G. Williams (ROM 65991/92, -99); 1 ♀, 23-VII-1972, J. Ithia (LACM 42831). Kamuani: 1 ♀, 22-III-1970, J. Ithia (LACM 36057). Karen: 2 ♂♂, 1 ♀, 29-VI-1968, B. J. Hayward (USNM 436383/85). Kiambu: 1 ♂, 15-VIII-1951, D. Witter (CAS 12196). 4 miles NW of Kiambu: 1 ♂, 20-V-1973, R. H. Seed (ROM 68104). Kiboko: 1 ♂, 4 ♀♀, 6/13-VII-1968, B. J. Hayward (USNM 436387, -91/93, 436404); 1 ♀, alc., 28-IX-1975, K. F. Koopman (AMNH 237323). Kibwezi: 1 ♂, 3 ♀♀, 12-VII-1968, B. J. Hayward (USNM 436397/99, 436403). Kichaka Simba: 4 ♂♂, 2 imm. ♂♂, 3 imm. ♀♀, 20/26-V-1972, J. N. Kyongo (LACM 40157/65). Kikoko: 2 ♂♂, 2 imm.

♂♂, 2 ♀♀, 13/16-XII-1977, R. Kyongo (RMNH). Kilifi: 1 ♀, 20-IV-1960, B. Walker (CAS 12549); 1 imm. ♂, 20-VIII-1963, 'native' (USNM 350815); 1 ♀, 17-VIII-1965, J. G. Williams (ROM 36225); 2 imm. ♀♀, 24/25-I-1968, J. G. Williams (LACM 51467, -73). Kitale: 1 ♂, 2-VIII-1963, R. E. Mumford (USNM 350813); 6 ♂♂, 24-VII/1-VIII-1968, B. J. Hayward (USNM 436405/06, -08, -10, -12/13). 12 miles W of Kitale: 4 ♂♂, 27-VII/10-VIII-1968, B. J. Hayward (USNM 436411, -14/16). Kiuu: 1 imm. ♂, 7 ♀♀, 1 imm. ♀, 12/27-I-1966, D. Sillu (ROM 38369/76). Kwale: 7 ♂♂, 3 imm. ♂♂, 3 imm. male skins, 7 ♀♀ (skulls of 4), 5 imm. ♀♀ (skulls of 3), 12-V/16-XII-1977, R. Kyongo (RMNH); 3 ♂♂, 1 imm. ♂, 8 ♀♀, 1 imm. ♀, alc., skulls of adults, 26/27-X-1979, W. & E. Bergmans (ZMA 20.868/80). Kyamunyuu: 1 ♀, 20-VIII-1968 (LACM 36476). Kyanguli area: 1 ♀, imm. ♀, 24-III-1970, J. Ithia (LACM 36058/59). Lake Paradise, Mount Marsabit: 4 ♂♂, 1 imm. ♂, 1 ♀ (skin only), 5 imm. ♀♀, 22/30-VI-1971, K. E. Stager (LACM 40141/51). Lamu: 1 imm. ♂, alc., 18-II-1982, A. Walen (ZMA 21.708). Langata: 1 ♂, 7-VII-1965, J. G. Williams (ROM 36226). Lion Hill: 1 imm. ♂, alc., skull, 30-X-1979, W. & E. Bergmans (ZMA 20.881). Lukore, Mkanda River: 1 imm. ♂, alc., 23-II-1982, A. Walen (ZMA 21.709). Lukore area: 1 imm. ♂, 2 ♀♀, 2 imm. ♀♀, 19/28-XI-1970 (1: no date), J. Ithia (LACM 37881/83, 45629). Machakos: 1 ♀, 1-XI-1963, W. F. V. Z (LACM 31743). Machorra, Taita Hills: 1 ♀, 14-XI-1911, E. Heller (USNM 182653). Makandara Forest: 4 ♂♂, 2 ♀♀, alc., skulls, 3 imm. ♂♂, alc., 17/26-X-1979, W. & E. Bergmans (ZMA 20.855/63). Makeri: 2 ♂♂, 1 ♀, 13-XII-1962, S. Keith (AMNH 206678, -80/81). Makindu: 1 ♀ (ROM 63804). Malindi: 1 imm. ♂, alc., Fischer (ZMB 5597); 2 ♀♀, (18-)XII-1954, J. P. Fowler (USNM 301519, HZM 6.2489); 8 ♂♂, 7 ♀♀, 17/18-VIII-1960, R. H. Pine (AMNH 187270, -73/82, -84/87). Mara River: 1 ♂, 10-II-1973, J. G. Williams (ROM 68434). Masabubu: 1 ♂, 23-VI-1960, R. H. Pine (AMNH 187267). Mbero Hills: 1 ♀, 4-X-1973, J. Eger & E. Glen (ROM 71427). Mbero Rocks: 1 ♀, 12-VII-1968, J. Ithia (LACM 36774). Mida: 1 ♀, 12-V-1973, J. N. Kyongo (LACM 45635). Mkanda River: 2 ♂♂, 3 imm. ♀♀, 10/19-XI-1970, J. Ithia (LACM 37876/80). Molo: 1 imm. ♀, 7-X-1963, "W. F. V. Z" (LACM 31742). Mombasa: 1 ♂, 1 ♀, 1 specimen, alc., J. M. Hildebrandt (ZMB 5081, 5428, 9967); 1 ♂, skin, Hirsch (ZMB 11379); 1 ♀, 26-III-1926, J. P. Chapin (AMNH 82525). Msambweni: 1 mummy, 23-XI-1987, W. Bergmans (ZMA 23.466). Mukanda River (Bridge Mukanda 2): 1 ♂, 1 ♀, alc., skulls, 26-II-1982, A. Walen (ZMA 21.710/11). Muumandu: 1 ♀, 12-V-1977, R. Kyongo (RMNH). Muumangu Forest: 4 imm. ♂♂, 5 ♀♀, 5 imm. ♀♀, 5 imm. ♀♀, (skulls of 2), 2-XI/9-XII-1977, R. Kyongo (RMNH). Mwingi: 1 imm. ♀, 11-IV-1972, J. N. Kyongo (LACM 40166). Nairobi: 1 ♂, 12-V-1959, J. Williams (LACM 19534); 2 ♀♀, 3/12-VI-1963, J. G. Williams (USNM 350801, -06); 1 ♀, 1-II-1967, Sillu (ROM 41795); 9 adults, 11 imm., sex unknown, skulls, 18-V/3-VI-1967, W. J. Hamilton (MVZ 137005/24); 2 ♂♂, 17-V-1969, G. Kirkham (ROM 59262/63); 1 imm. ♀ (USNM 350814). Nakuru: 1 ♀, 20-VIII-1968, B. J. Hayward (USNM 436417). Namanga: 1 ♂, 10-XII-(?)1952, J. G. Williams (HZM 4.1394); 1 imm. ♀, 8-II-1950, E. M. Queen African Expedition (AMNH 184473); 2 ♂♂, 1 imm. ♀, J. G. Williams (HZM 3.1384, 4.1394, 5.1409). Ngaranyiru: 1 ♂, 1 imm. ♂, 1 ♀, 23-VII-1973, M. J. Sutton (ROM 71118, -20/21). Ngong: 2 ♂♂, 1 ♀, 29-VI/1-VII-1963, J. G. Williams (USNM 350802, -04/05). Ngong Hills: 2 ♂♂, 1 imm. ♂, 3 ♀♀, 2 imm. ♀♀, alc., skulls of 7, 18-I-1982, A. Walen (ZMA 21.700/07). Nyeri: 1 ♂, 3-IX-1957, J. P. Fowler (HZM). Shimba Hills: 1 imm. ♂, 7-X-1965, D. M. Sillu (ROM 36698); 2 ♂♂, 4 ♀♀, 2 imm. ♀♀, 19/25-XI-1966, D. M. Sillu (ROM 41785/88, -91/94). Shimba Hills settlement, Mukanda River: 2 ♂♂, 2 ♀♀, 2 imm. ♀♀, 1/18-XI-1970, J. Ithia (LACM 37870/71, -71, -73/75). Songhor, Tinderet Forest: 1 ♂, 3-I-1960, M. Ellis (HZM 8.3061). Takaungu: 1 ? ♂, 3 ♀♀, 2 imm. ♀♀, alc. (of 5), skulls, 54364 and 54366 4-IX-1901, Thomas (ZMB 53873, -97, 54364, -66/67; skins and skulls of 53873 and -97 mismatched); 1 ♂, 15-VIII-1965, A. E. Williams (ROM 36227); 4 ♂♂, 1 imm. ♂, 26-I-1968, A. Williams (LACM 51468/72). Talek River, near Talek Gate: 1 ♂, alc., skull, 26-I-1982, A. Walen (ZMA 21.752). Tarla's Dam: 1 imm. ♂, 1 ♀, 17/26-VIII-1966, A. E. Williams (ROM 40283/84). Tiwi Beach: 2 ♂♂, 4-III-1969, J. Parker (ROM 59265/66); 3 ♀♀, alc., skulls, 1 imm. ♀, alc., 19/20-X-1979, W. & E. Bergmans (ZMA 20.864/67). Utwani Forest, Witu: 1 ♀, 19-XII-1962, S. Keith (AMNH 206683). Waa: 2 imm. ♀♀, 25-X-1963, W. F. V. Z (LACM 31745, -72). Watamu: 1 ♂, 9 ♀♀, 4 imm. ♀♀, 12 in alc., skulls of 9, 1/7-X-1979, W. & E. Bergmans (ZMA 20.824/37). Witu Forest: 3 imm. ♂♂, 2 ♀♀, 1 imm. ♀, 11-III-1973, K. Stager (LACM 42800/01, -03/06). (Baricho, Cherangani Mountains, Chyulu Hills, Diani, Mount Elgon, near Embu, Endau Mountain, Edebeess, Garabani, Hunters Lodge, Kabete, nr Kapenguria, Karura Forest, Kericho, Kijabe, Kikambala, Kipini, Kitui, nr Kom, Kongelai escarpment, Lake Naivasha, nr Limuru, upper Luazomele River, Masalani, Meru River, nr Mumias, Murango, S of Nandi Hills, Narok, Nyandarua, Olebortoto River, Ol Messoti, Ruaraka, Wei Wei River, Smara, Taita, Tinderet Forest, Tsavo Swamp, Uaso Nyiro River bridge, nr Vipingo, Yala River.) MALAWI. Cholo: *Epomophorus? wahlbergi*, 1 ♀, skin only, 13-II-1928, R. C. Wood (CMNH 6375). (Chikwawa, Chiromo, Karonga, Mandala, Blantyre, Zoa Estate, Zomba; 0933C, 1233B, 1434B, 1635B.) MOZAMBIQUE. Beira: 1 ♂, 4 ♀♀, VIII-1969, Robsory (ROM 51096/99, 51102). 10 km N of Beira: 1 ♀, 30-X-1964, R. M. Davis (USNM 365135). 20 miles N of Beira: 1 ♀, 21-IX-1962, R. W. Rankins (HZM 16.4237). Chimongo: 3 ♂♂, 23-II-1964, R. E. Cole (USNM 351989/91). Jangamo: 1 ♂, 2 ♀♀, 14-IV-1964, R. E. Cole (USNM 352000/01, -03). Lalana Luli: 1 ♀, 28-V-

1925, Müller-Thalman (ZSM 1925-3006). Luabo: 1 ♀, 26-IV-1970, P. Smith (HZM 24.5924). Massangena: 1 ♀, 7-II-1964, R. E. Cole (USNM 351986). 2 km S of Massingana: 2 ♀♀, 11-IV-1964, R. E. Cole (USNM 351995, -98). Moamba: 1 ♂, 12-III-1964, R. E. Cole (USNM 351994). Naamacha: 1 imm. ♀, 10-X-1964, M. Baddeley (ROM 51109). Panda: 7 ♂♂, 21-IV-1964, R. E. Cole (USNM 352004/10). Posto Inhaca: 1 ♂, 2 ♀♀, 18-I-1964, R. E. Cole (USNM 351979/80, -82). Tette: 1 imm. ♂, alc., W. C. H. Peters (ZMB 10020). (Inhambane, Lacerdonia, Magué, Maqué, Quelimane, Vila Machado District; 1531D, 1735D, 1832B, 1832D, 1834C, 1932D, 1934D, 1935A, 2032B, 2132A, 2133B, 2134B, 2235A, 2323A, 2432A, 2433C, 2434B, 2435B, 2531D, 2532C, 2632B, 3532C.)

PEMBA ISLAND. Mwitiku, Michiwini: 1 specimen, alc. (BMNH).

TANZANIA. Ambangulu: 1 ♂, 1 imm. ♂, alc., skulls, 2 imm., alc., 8-III-1899, Martienssen (ZMB 54593, -95, 54662, 67064). 6 miles S of Arusha: 1 ♀, 24-VII-1956, H. Hoogstraal (FMNH 86019). Bagamoyo: 1 ♂, skull, 1 ♀, 1960/1961, H. W. P. van Barneveld (RMNH). Bunduki: 1 ♂, 4 ♀♀, (1: alc.), 1 imm. ♀, skull, 9/15-I-1964, K. E. Stager (LACM 19684/85, 55311/14). Dar es Salaam: 1 imm. ♂, 1882, R. Pachinger (NMW 17864); 1 specimen, VIII-1897, F. X. Mayer (NMW 17863); 4 ♀♀, 14-VIII-1926, J. T. Zimmer (FMNH 27282/85); 1 ♀, 22-X-1935, H. Dinkelacker (SMNS 3175); 1 ♀, 3 imm. ♀♀, (2: skulls only), Stuhlmann (ZMB A5677, 9990/91, -98); 2 imm. ♂♂, 1 ♀, alc., skulls (ZMB 54208/10). Lake Duluti: 1 ♂, 3-VII-1973, C. H. D. Clarke (ROM 69186). Lembeni: 2 imm. ♂♂, 2 ♀♀, 3 imm. ♀♀, 23-VIII/17-XII-1957, Th. Andersen (SMNS 5973/79). Lindi: 1 imm., Tülleborn (ZMB 9252). Liwale: 1 ♀, skull, XI-1958, C. J. P. Ionides (HZM 25.6344). Lukoga: 1 ♂, 1 ♀, 6-IX/4-X-1961, A. F. Rees (HZM 13.4022, 14.4056). Masimani: 1 ♀, skull, IX-1899, Schillings (ZMB 54420). Mikindani: 1 ♂, alc., skull, 14-I-1910, Grote (ZMB 67053). Mlalo. *Epomophorus ? wahlbergi*, 1 ♂, skin only, 19-X-1906, Korstow Roehl (ZMB). Moshi: 1 imm., alc., O. Neumann (ZMB 9986); *Epomophorus ? wahlbergi*, 1 imm., mummy, 17-IV-1921, H. C. Raven (USNM 238035). Mto-wa-umbu: 1 imm. ♀, 3-VII-1937, Uthmöller & Bohmann (ZSBS 1937/221). Nashallo: 1 ♀, 1 imm., 9-IX-1952, G. Zink (SMNS 4163, -67). Rondo: 1 ♂, 11-II-1959, C. J. P. Ionides (HZM 7.2900). Rubondo: 1 imm. ♀ (ROM 56533). Tanga: 1 specimen, alc., Gierra (MNHN 1897-1510); 1 ♀, 1 imm. ♀, 18-VII-1963, I. Bampton (USNM 351173, -79); 1 imm. ♀, 1-IX-1963, I. Bampton (ROM 68475); 4 ♀♀, 2 imm. ♀♀, 1 specimen, 1-XI-1963, WFVZ (LACM 31744, -46/51); 1 imm. ♀, 12-IV-1964, J. G. Williams (LACM 51444); 1 ♀, 1-VI-1964, J. G. Williams (ROM 38274). Tendaguru: 1 imm., alc., skull, 7-II-1912, Janensch (ZMB 54196). Tengeru: 1 ♀, 20-VII-1953, G. H. Swynnerton (AMNH 179288). Ukambesi (or Ukambari, or Kitui Ukamba): 1 ♂, 1 ♀, 1 imm. ♀ (skull only), 1 imm., J. M. Hildebrandt (ZMB

5380/83). Usangi: 1 ♂, 1 imm. ♂, 2 imm. ♀♀, 27/30-V-1952, G. Zink (SMNS 4161/62, -64/65). Ushindo: 1 ♂, skull, 19-I-1894, Stuhlmann (ZMB A5675). Vikundo (or Vikindo): 1 ♂, 2 ? ♀♀, 3 imm., skulls (skin of 1), Stuhlmann (ZMB 9978/82, -89). (Amani, nr Bulongwa, Engare Nairobi, nr Fungoni, Ikoma, nr Iringa, nr Kahé, nr Kilwa Kivinje, Lake Manyara, Malala, Matengo Hills, nr Mbeya, nr Mbuguni, nr Mlowa, nr Mount Meru, Msingi, nr Mtwara, nr Newala, nr Ngomba, ? Niam-Niam, nr Nyoni, Oldonyo Sambu, nr Sanya Juu, Tunduru, Usa River.)

ZAIRE. Banana: 1 ♂, 1 ♀, 1 imm., alc., skull of ♂, 9-V-1910, A. Gruvel (MNHN 1911-1565). Gandajika: 1 imm. 1 ♀, X-1948, P. de Francquen (IRSN 13.108). Kabanga: 1 ♂, skin, 12-I-1952, L. Spaute (IRSN 13.329). Kananga (as Luluabourg): 1 ♀, 23-XI-1922, R. Callewaert (AMNH 86255); 2 ♀♀, 26-XI-1922 (MNHN 1960-3859/60); 1 imm., 31-III-1924 (NMBA 3800, 7695). 1 ♀, 30-XI-1924, R. Callewaert (AMNH 86251); 1 ♀, 1-II-1964, A. E. M. de Roo (AMNH 207736).

(Boma, Congo da Lemba, Kanzenze, Kilinga, Lubondai-Tshimbulu, Lubumbashi, Lusanga, Moanda, Mulongo, Ndota, Netonna, Rutshuru, Tshikapa.)

ZAMBIA. Kanyale Stream: 1 ♀, 30-VII-1973, P. H. D. Ansell (ROM 73960). Naleza: *Epomophorus ? wahlbergi*, 1 ♂, skin, 7-X-1969, W. Sheppe (CAS 15102). Zambesi Rapids, Ikelenge: 1 ♀, 17-I-1965, R. H. Smithers (HZM 18.4368). (Abercorn, Chingi, Chipata, Chowo Forest, near Kabwe, Kasempa, Mongu, Ndola, Nyika National Park, Salujinga, Solwezi; 1124A3, 1127C2, 1322B1, 1327D4.)

ZANZIBAR. Kokotoni: 1 imm. ♂, 1 ♀, alc., A. Voeltzkow (ZMB A.76a07); 1 ♂, alc., no skull, VII/XI-1889, A. Voeltzkow (NMW 17496). "Zanzibar": 3 imm. ♂♂, alc., via De Ville (IRSN 187, 187B); 2 ♂♂, alc., O. Neumann (ZMB 10001/02); 1 ♀, 1 imm. ♀, alc., skull of adult, Stuhlmann (ZMB 9996, 10000); 1 imm., alc., Wessel (ZMB 2957). (Chuaka, Kizankazi, Mojon.)

ZIMBABWE. Chirinda Forest: 1 ♀, 27-IX-1967, H. W. Setzer (USNM 425264). Henderson Research Station: *Epomophorus ? wahlbergi*, 1 imm. ♂, 13-X-1967, S. W. Goussard (USNM 425265). Retreat Farm: 1 ♀, 1-VI-1972, R. L. Peterson *et al.* (ROM 64978). Sabi-Lundi confluence: 1 ♂, 15-I-1968, T. Liversedge (ROM 470239). Umtali: 1 ♀, 19-VI-1960, R. H. Smithers (HZM 10.3237); 1 ♂, 12-XII-1960, R. H. Smithers (HZM 11.3448); 1 ♂, 19-III-1962 (HZM 12.3705); 1 ♀, 23-V-1972, R. L. Peterson *et al.* (ROM 64837). (Chikwarakwara, Hostes Nicolle Institute of Wildlife Research, "Mashonaland", Salisbury, Shilo; 1730D, 1731A, 1831B, 1832C, 1931D, 1932D, 2132A, 2230B, 2231A.)

SOUTH AFRICA. 14 miles N of Barberton: 2 ♂♂, 13-X-1969, S. J. Liversedge (USNM 468324/25). Carter's Nurseries: 2 skulls (HZM 26.6528/29). Durban: 1 ♂,

1871, Schlüter (SMNS 1432); 1 ♂, Schlüter (ZMB 3917); 1 imm. ♂, 17-III-1955, M. Baddeley (ROM 41707); 1 ♀, alc., skull, Hahn (ZMB 10016). Grahamstown: 1 ?♀, alc., skull, 1900, Albany Museum (USNM 113455); 1 ♂, alc. skull (ZMB 10014). Hlatikulu: 2 ♀♀, 7-IV-1969, M. Baddeley (ROM 51105, -07). King William's Town: 1 ♂, 4-IV-1938, T. D. Carter (AMNH 115818); 1 imm. ♀, 29-V-1944, Kaffrarian Museum (HZM 20.4726). Makatini Flats: 1 ♀, 30-XI-1961, M. Baddeley (ROM 41708). Nelspruit: 1 imm., 1949, Zumpt (SMNS 6726); 1 ♂, 25-IV-1953, Zumpt (SMNS 5033). Pietermaritzburg: 1 ♂, 1-XI-1950, H. Friedman (USNM 292064); 1 imm. ♂, 20-XI-1950, 1 ♂, VI-1951, P. A. Clancey (HZM 1.1115, 2.1295). Port Elizabeth: 1 ♂, 1 imm. ?♀, 29-VI/1-VII-1940, J. A. Pringle (HZM 19.4725, 21.4737); 1 specimen, 5-VI-1965, Port Elizabeth Museum (HZM 22.4738). Port St. Johns: 1 specimen, skull, Bachmann (ZMB 9742). Pretoria District: 1 ♂, V-1927, A. K. Haagner (FMNH 38136). Stockenström: 1 ♂, 6-XI-1953, N. P. Arends (AMNH 185379). Umkomaas: 3 ♀♀, 1 imm. ♀, alc., skulls of 2, 30-X-1979/9-V-1980, S. G. Sowler (ZMA 21.156/59). Unterlumi: 1 imm. ♀, alc., V. Schuck (USNM 198679). Van Staaden River Pass: 2 ♂♂, 26-IV-1949, T. Larson (AMNH 168100/01). 11 miles W of Witrivier: 1 ♀, 11-XII-1966, I. L. Rautenbach (AMNH 381537).

(Alice, Althorpe, Balossi, Bedford, Blaney, Eshowe, George's Valley, Farm Narina, Gladstone, Greefswald, Hans Merenbley Nature Reserve, Harmony Block, Hectorspruit, Itala Nature Reserve, Kcurbooms Reserve, Komatipoort, Lake Sibayi, Letsitele, Levuvhu Hippo Pool, Loskopdam, Louis Tricherdt, Malelane, Malta Farm, Malvern, Marone, Matukwatadam, Mbabane, Mossel Bay, Naboomspruit, 11 km N of Newington, Ngoye Forest, Niambunana, Ofcolaco, Pafuri, Peddie, Pirie, Pongola, Pretoria, Schagen, Soutpansberg, Steynsdorp, Sweet Home, The Downs, Tricherdtsdal, Tshaneni, Tugela River, Tzaneen, Umtata, Uzumbe River valley, Walmer, Weenen.)

**Diagnosis:** The only species of the genus with the fourth palatal ridge nearer to the third than to the fifth and only one postdental palatal ridge; a relatively short rostrum and palate; a relatively large zygomatic width. Body and skull dimensions geographically strongly variable. Measurement ranges and ratios taken from specimens from all over the species' range:

fal	♂♂ 72.3-94.9 (n = 133), ♀♀ 67.7-87.5 (n = 184);
gsl	♂♂ 44.4-57.3 (n = 122), ♀♀ 41.0-49.3 (n = 155);
cb1	♂♂ 44.3-57.3 (n = 64), ♀♀ 40.6-49.1 (n = 86);

rl	♂♂ 18.6-23.4 (n = 17), ♀♀ 15.5-20.0 (n = 40);
zw	♂♂ 24.6-29.0 (n = 58), ♀♀ 22.9-27.4 (n = 80);
C <sup>1</sup> -M <sup>1</sup>	♂♂ 15.7-18.9 (n = 37), ♀♀ 14.0-17.4 (n = 53);
W	♂♂ 60 -124 (n = 45), ♀♀ 54 -125 (n = 78);
rl	♂♂ 37.7-42.8% of gsl, ♀♀ 37.2-41.3% of gsl;
pl	♂♂ 54.6-60.7% of gsl, ♀♀ 57.4-62.4% of gsl;
zw	in ♂♂ 50.6-57.7% of gsl, ♀♀ 52.3-59.6% of gsl.

For a breakdown of measurement ranges per country see table 10.

**Distribution:** Fig. 10.

**Related species:** *Epomophorus wahlbergi* is sympatric or probably so with other species of the genus over much of its range: with *E. angolensis* in Angola, with *E. labiatus* in parts of Uganda, Burundi, (Rwanda?), Kenya and Tanzania, with *E. minor* in parts of Somalia, Kenya and Tanzania, in southeast Zaire, western Zambia and Malawi, and with *E. gambianus crypturus* in southeast Zaire, Zambia, southeast Tanzania, Zimbabwe, Mozambique and northeast South Africa. With *angolensis* and *gambianus crypturus* it shows a large overlap in dimensions, with *labiatus* only a small overlap, while it is always larger than *minor*. From all species it differs in some relative proportions of the skull (see table 1) and in having one postdental palatal ridge instead of two (or, in a few exceptional cases, one postdental and one partly interdental).

#### Remarks

**Taxonomy:** When Andersen (1912) synonymized *Pteropus haldemani* Hallowell, 1846 with *Pteropus wahlbergi* Sundevall, 1846 he retained it as a subspecies because of its smaller averaging skull, teeth and external dimensions. This applied particularly to the male skull, which in *wahlbergi* ranged from 52 to 55.5 in gsl (n = 12) and in *haldemani* from 47 to 51 (n = 7). The nominate subspecies' range Andersen

Table 10. Ranges of selected measurements of *Epomophorus wahlbergi* (Sundevall, 1846) per country.

		♂♂							♀♀								
		fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	1M <sup>1</sup>	W	fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	1M <sup>1</sup>	W
Angola	n	3	4	3		2	3		3	5	2		2	2			
	mean		49.6	50.2			17.5										
	min	± 80	47.3	49.8		26.7	17.0		± 78	43.2	43.9		24.9	15.3			
	max	87.1	51.0	50.9		28.2	18.0		81.1	≥ 45	44.2		25.9	15.5			
Congo	n	1	1	1	1	1	1	2	5	5	5	5	5	5	5		
	mean								80.4	46.3	46.2	18.7	25.4	16.3	3.45		
	min	81.9	48.9	48.9	19.8	27.2	17.3	3.5	78.5	46.0	45.7	18.1	24.8	16.2	3.4		
	max							3.6	82.5	46.7	46.7	19.2	25.9	16.4	3.6		
Gabon	n	14	5						8	4							
	mean	81.3	49.1						78.7	45.2							
	min	78.0	48.5						76.8	43.4							
	max	84.2	50.0						81.1	46.7							
Kenya*	n	82	75	42	12	40	18	12	43	116	96	58	26	55	29	24	68
	mean	80.4	49.6	49.3	20.2	26.5	17.1	3.65	92	76.3	43.9	43.3	16.8	24.3	15.0	3.4	77
	min	72.3	44.4	44.3	18.6	24.6	15.7	3.3	60	67.7	41.0	40.6	15.5	22.9	14.0	2.9	54
	max	89.0	53.1	53.1	21.3	28.8	18.3	4.25	114	87.5	49.3	49.1	18.6	27.2	16.2	3.75	125
Mozambique	n	14	10						14	10	1	1	1	2	1		
	mean	86.6	53.2						82.5	46.5							
	min	81.8	50.9						79.4	42.8	47.3	17.5	25.3	16.2	3.9		
	max	94.9	55.7						86.1	48.6				17.1			
Tanzania	n	5	10	9	3	8	7	1	2	16	19	14	6	13	8	5	4
	mean	83.2	52.2	52.4	21.7	28.3	18.2			81.0	46.4	46.5	18.4	26.0	16.5	3.7	72
	min	81.0	49.9	50.0	20.6	26.6	17.3	4.0	78	77.6	43.1	44.6	17.4	25.2	15.5	3.4	67
	max	86.3	55.0	55.0	23.4	29.0	18.9		124	86.0	47.5	46.9	18.9	26.9	17.0	3.9	78
Zaire	n	1	1					1		6	4						
	mean									81.8	46.3						
	min	83.0	53.2					3.6		79.5	44.9						
	max									84.9	47.5						
Zambia	n								1	2	1		1	1			1
	min								80.8	44.5	44.6		24.8	15.5			94
	max									44.8							
Zanzibar	n	1	2	2		1	2		1		1			1			
	min	89.9	49.3	49.3		27.1	16.9		80.2		45.6			16.1			
	max		50.3	50.0			17.3										
Zimbabwe	n	3	3	2		2	2		4	4			1	1			2
	mean	85.9	52.3						82.5	45.9							
	min	84.3	51.5	51.5		27.8	17.7		79.6	44.7			25.9	16.4			80
	max	88.5	53.5	51.9		28.7	18.1		85.1	46.8							85
South Africa	n	9	10	4	1	3	4		9	6	4	2	2	4	2		3
	mean	86.4	53.7	54.3		28.4	17.7		82.9	47.4	47.6			17.1			94
	min	83.7	51.2	52.2	21.6	27.9	17.3		77.4	45.5	46.7	19.7	26.7	16.9	3.75		87
	max	88.7	57.3	57.3		29.0	18.3		85.7	48.9	48.9	20.0	27.4	17.4	3.9		102

\* See table 12 for a breakdown into geographical subranges.

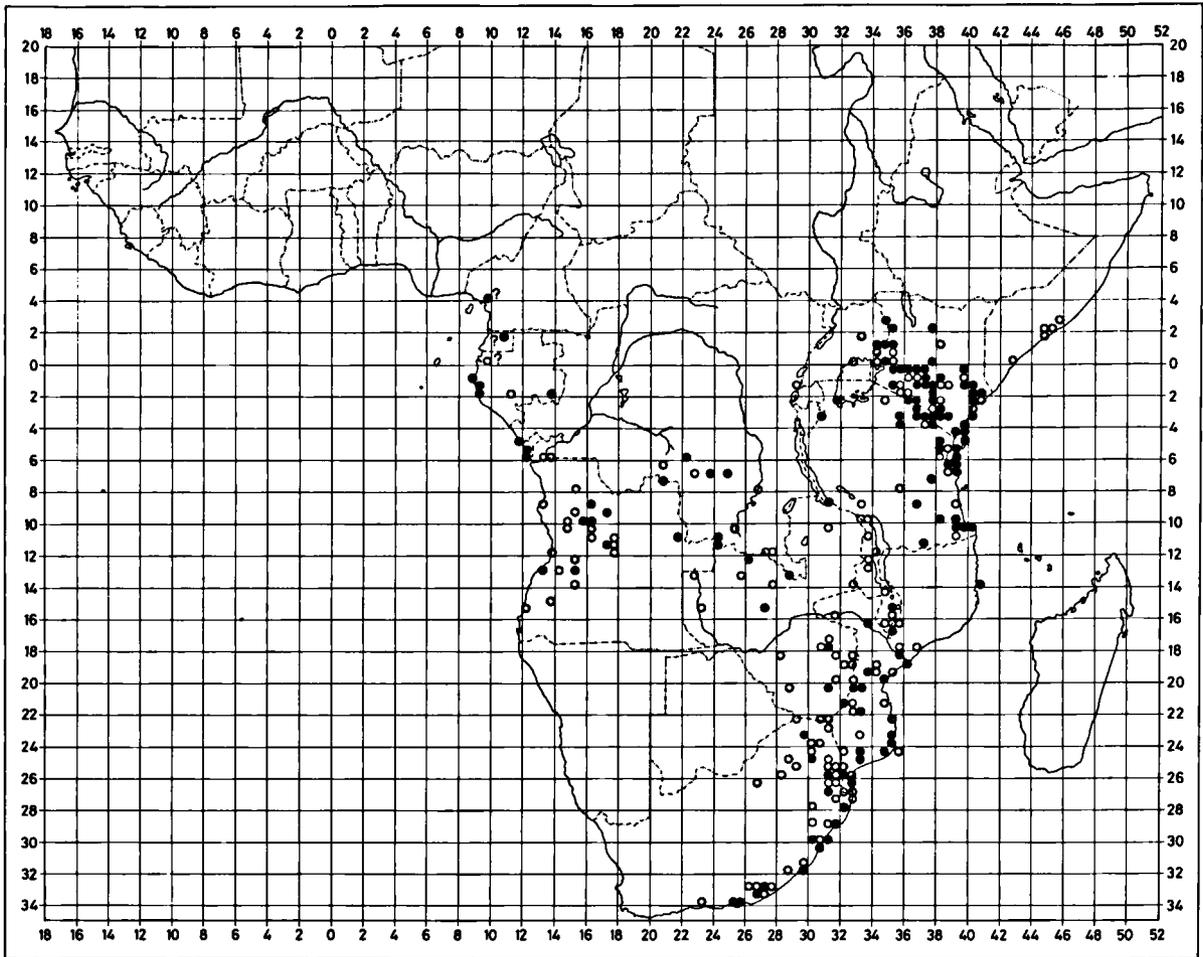


Fig. 10. Distribution of *Epomophorus wahlbergi* (Sundevall, 1846). Black dots: squares from which material has been identified by the author. Open circles: records from literature, museum registers, and correspondence.

(1912: 522) described as “from southern British East Africa to eastern Cape Colony”, that of *haldemani* as “essentially western (Cameroons to Benguela), but extends through the Congo Valley east to British and northern German East Africa, where it meets *E. w. wahlbergi*...” It is not at once clear what was meant with “the Congo Valley” as there were no specimens from the actual Congo basin among Andersen’s material. In fact, his western and eastern localities were separated by an enormous gap. Only the specimens from Dondo in northeast Angola suggested that the populations in the two regions might be connected. In the section on *haldemani*, Andersen (1912: 524) described

its range as “east through the Welle River district (Niam-Niam)”. The basis for this idea, which itself must have led to his remark on “the Congo Valley”, was a specimen from Zémio in the southeastern Central African Republic. But this locality is separated from the western populations by a very large area of uninterrupted rain and swamp forests which appear unsuitable habitat for this species. Apparently, Andersen had not realized that *wahlbergi* is not found in moist forests, and some specimens he knew from “the Cameroons” and “Gaboon” must have misled him here.

In theory, Zémio may be connected with the eastern populations via the wide band of

Guineo-Congolian lowland rain forest and secondary grassland mosaic (type 11a in White, 1983) in which Zémio itself is located and which runs eastward almost to Lake Albert and from there southward to Lake Edward, on the Zairese-Ugandese border. From south of Lake Edward, the species has been recorded from Rutshuru (Hayman *et al.*, 1966). However, in spite of considerable collecting efforts in north-east Zaire (compare fig. 1) the species has never been discovered there. The Zémio specimen was bought from the trader Bohndorff (Jentink, 1885: 35) and to me its origin is doubtful. (See also below, under Distribution and geographical variation.) The two subspecific ranges as conceived by Andersen are remarkable in that they cross each other. "In British and German East Africa it (= *haldemani*) meets and occurs together with (...) *E. w. wahlbergi*" (Andersen, 1912: 524), or "In the equatorial regions of this area it (= nominate *wahlbergi*) occurs together with *haldemani*" (Andersen, 1912: 527). But if one maps the localities mentioned by Andersen for both subspecies it becomes apparent that not only they "occur together" but that even their ranges cross, with the small *haldemani* exclusively occupying the Kenyan coast (Malindi, Takaungu and Mombasa), after 'passing' a north-south range of the large *wahlbergi* (Smara, Fort Hall, Moshi). Somewhat further south, both subspecies would occur together (in Zanzibar and at Dar es Salaam).

Later authors have added to this complex pattern. De Beaux (1924) assigned specimens from coastal Somalia to *haldemani*. Cabrera *et al.* (1926) did so with material from Luluabourg in central southern Zaire. Schoutedden (1944) probably based his outline of the subspecies' distribution in Zaire (Lower Congo, and eastward to Kasai) on that record. Hayman *et al.* (1966) listed all Zaire specimens under *haldemani*, including several from Katanga, one from Rutshuru, and one from the northern Ibembo (the latter apparently with a wrong collection number: that of a shrew). Moreau *et al.* (1940: 125) wrote to have found both subspecies in Zanzibar and thought that there existed "a zone of intergrades" on the neighbouring

mainland, the Tanzanian specimens being mostly *wahlbergi* and the Kenyan specimens mostly *haldemani*. In their list of Tanzanian mammals, Swynnerton *et al.* (1951) stated *wahlbergi* to be recorded from Dar es Salaam, Vikindu and Lindi, and to be "generally distributed throughout Liwale and Mikindani Districts; occasional in Kilwa District; Pemba and Zanzibar Islands", and recorded *haldemani* from Engare Nairobi and Old Moshi, both near Mount Kilimanjaro. The mentioned *wahlbergi* Districts and Lindi are in the southeast of the country. According to these authors, intergrades would occur in Zanzibar and Pemba. Eisentraut (1958) identified specimens from near Mount Kilimanjaro (Nashallo and Msingi) also as *haldemani*. Kulzer (1962a) recorded *haldemani* from Lembeni, about 60 km southeast of Moshi. Harrison (1961), in his checklist of Kenyan bats, added a number of new records for both subspecies to the ones already published for that country.

Mapping of all those localities leads to a confusing picture, with in addition to the ideas forwarded by Andersen (1912) *wahlbergi* at the northern coast (Lamu) and both *wahlbergi* and *haldemani* in the highlands, and with Namanga on the Tanzanian border as a third locality where both would occur side by side. Aggundey *et al.* (1984) assigned all Kenyan specimens which had ever been reported to *haldemani*, at the same time stating that "the relationship in East Africa between the nominate subspecies and the more western and smaller *E. w. haldemani* requires additional study." Ansell (1960a, b; 1967; 1978) provisionally identified specimens from northwestern Zambia as *haldemani* and those from northeastern Zambia as *wahlbergi*. As the synonymy (p. 125) shows, a number of authors did not identify their specimens on the level of subspecies, while others dealt with samples of either typical *wahlbergi* or *haldemani* populations. Some published measurements add to the ranges given in table 10, and are here quoted in table 11.

Unless some complicated pattern of migration and subsequent alternate occupation of certain regions is assumed, for which I see no

Table 11. Some measurements of *E. w. wahlbergi* (Sundevall, 1846) and *E. w. haldemani* (Hallowell, 1846) quoted from the literature.

country	subspecies	♂♂						♀♀						source
		fal			gsl			fal			gsl			
		n	min-max	mean										
Angola	<i>haldemani</i>							1	82.6		1	43.3		Hill <i>et al.</i> , 1941*
	„	16	77 -89.1					9	76.0-85.5					Sanborn, 1950
	„	14	82 -88	84				21	72 -83	78				Hayman, 1963
	„	17	70 -85					25	71 -83	77				Feiler, 1986**
Malawi	—	9	81.0-90.0	86.8				23	73.0-90.0	82.7				Happold <i>et al.</i> , 1987**
West Zambia	<i>haldemani</i>							4	c.76-82		2	42.6-44.6		Ansell, 1960a; 1967***
East Zambia	<i>wahlbergi</i>	1	88.6		1	50.3								Ansell, 1967
Somalia	—				8	45.4-51.8	49.4				8	40.4-44.0	41.7	Lanza, 1961
Tanzania	<i>haldemani</i>							4	76.3-78.3	77.2				Kulzer, 1962a
South Africa	<i>wahlbergi</i>	16	79 -92	84				10	68 -85	77.7				Rautenbach, 1982**
Southern Africa	—	3	81 -85	84				8	68 -85	78				Smithers, 1983**

\* Specimen reported as ♂; fal and gsl in 1977 79.2 and 43.2, respectively.

\*\* Some of these ranges almost certainly include immature specimens.

\*\*\* Subspecific identification provisional.

reason yet, sympatry of two subspecies cannot be accepted. The alleged coexistence of two subspecies in some localities is certainly based on insufficient knowledge of the possible variation of characters within single populations. Likewise, crossing of two subspecific ranges is only conceivable in the event of separation in time. The first question to be addressed is if the coastal populations in Somalia, Kenya and northern Tanzania are indeed congruent with those in the regions west and southwest of the Central African rain forest block identified as *haldemani*. An analysis of my data on Kenyan specimens confirms that the coastal specimens are smaller, on the average, than the inland ones; specimens from the Tana River plains agree with those from the coast rather than with those from the inlands, while a small sample from Lake Paradise, Marsabit consists of exceptionally small specimens. In table 12 measurements of Kenyan specimens have been arranged accordingly. Kenyan lowland ♂♂ have almost the same gsl range as ♂♂ from Angola, Congo and Gabon (in Kenyan ♀♀ it averages slightly lower) but to judge from the fal range they are generally smaller (and so are

the ♀♀). Available M<sup>1</sup> lengths (tables 10 and 12) suggest that the cheek teeth in Kenyan lowland specimens are smaller, on the average, than in specimens from Angola, Congo and Gabon. This seems to be confirmed by the slightly larger C<sup>1</sup>-M<sup>1</sup> lengths in the latter. My preliminary conclusion is that there is no reason to assume a common origin for the populations in Angola, Congo and Gabon on the one hand, and in the Kenyan lowlands on the other.

Although there are only few series from single Kenyan localities, it is evident that within the highland and lowland categories, populations may show distinct differences in size. The largest highland specimens are known from Kitale, Kakamega, Kakamega Forest and Songhor; the smallest from Kiu, Kiboko, and Makindu. The largest lowland specimens are from Kwale and the Shimba Hills, and the smallest from Arabuko-Sokoke Forest, Kilifi, Malindi, Witu and Witu Forest. No clear patterns of geographical variation (e.g. of clinal nature) arise yet and the only conclusion at this stage is that individual populations may be characterized by certain dimensions, and that this does not offer a solid basis for taxonomic

Table 12. Ranges of selected measurements of *Epomophorus wahlbergi* (Sundevall, 1846) from Kenya divided into three geographical categories: highlands (1000 m and upwards); lowlands (coastal zone and Tana River plains); and Marsabit area.

	♂♂									♀♀							W	1 M <sup>1</sup>
	fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	l M <sup>1</sup>	W	fal	gsl	cbl	rl	zw	C <sup>1</sup> -M <sup>1</sup>	l M <sup>1</sup>			
highlands	n	32	30	11		9	7	2	7	51	35	9	1	11	2	1	21	18
	mean	83.1	51.0	50.7		27.3	17.4		104	78.8	45.2	45.5		25.7			88	3.75
	min	77.1	49.3	49.3		26.6	15.9	4.0	97	73.6	42.0	43.8	18.6	24.4	15.7	3.6	73	3.45
	max	89.0	53.1	53.1		28.8	18.3	4.25	114	87.5	49.3	49.1		27.2	16.2		125	4.2
lowlands	n	46	41	27	12	27	11	10	33	65	61	49	25	44	27	23	47	
	mean	78.9	49.1	49.3	20.2	26.4	16.9	3.55	91	74.4	43.1	42.9	16.7	24.0	14.9	3.4	72	
	min	72.3	47.1	47.0	18.6	24.6	15.7	3.3	60	67.7	41.0	40.6	15.5	22.9	14.0	2.9	54	
	max	85.1	51.7	51.7	21.3	27.6	17.9	3.9	102	80.1	45.2	45.3	17.2	25.7	15.6	3.75	98	
Marsabit	n	4	4	4		4			3									
	mean	76.5	45.4	45.4		25.5			78									
	min	76.0	44.4	44.3		24.9			73									
	max	77.0	45.8	45.8		25.7			82									

\* unsexed specimens from Nairobi.

(subspecific) distinctions. The apparent geographical gap between Kenyan highland and lowland populations (see fig. 11), if reflecting the real situation and not merely the distribution of collecting activities, may account for the differences of those two groups at large. The Marsabit sample may represent an isolated and rather dwarfed population, but shows leanings toward the specimens from some coastal Somalian localities reported by Lanza (1961; see table 11).

The differences between the two named subspecies *wahlbergi* and *haldemani* as defined by Andersen (1912) are only slightly diminished by the data in table 10, but this modest result is at least partly due to the restricted material (particularly of ♂♂) available from most regions and especially from the Zairese and Zambian populations which connect the western and eastern ranges. In fal, and in gsl in ♀♀, the differences between the two are not substantial. The important distinction lies in male skull size. The gsl range in ♂♂ from Gabon, Congo and Angola (47.3-51.0) overlaps with the ranges in both Kenya lowland and highland categories (47.1-51.7 and 49.3-53.1, respectively) and Tanzania (49.9-55.0), while the latter two ranges overlap amply with those

known for Mozambique (50.9-55.7) and South Africa (51.2-57.3). Data on more specimens from regions which are now poorly represented are likely to augment these range overlaps. I do not have sufficient data on teeth measurements of southern African specimens. Those of ♀♀ indicate that in this respect specimens from west and east and specimens from east and south, overlap. These overlaps will most probably prove to be larger when more data become available.

Size variations within *Epomophorus wahlbergi s.l.* appear to be of a clinal nature and at present the recognition of subspecies does not seem the appropriate way to explain them (see also the remark in Hayman *et al.*, 1971: 7). In addition, there may be regional and local variations, as in Kenya. These are also in need of further research. With regard to body size there appear to be tendencies to an increase with altitude and with latitude, and an ecological explanation, maybe according to Bergmann's rule, should be considered.

Distribution and geographical variation: The northwestern part of the species' distribution is not well established. Matschie (1895) mentioned material of *Epomophorus gambianus* from Aqua Town (a quarter of Douala).

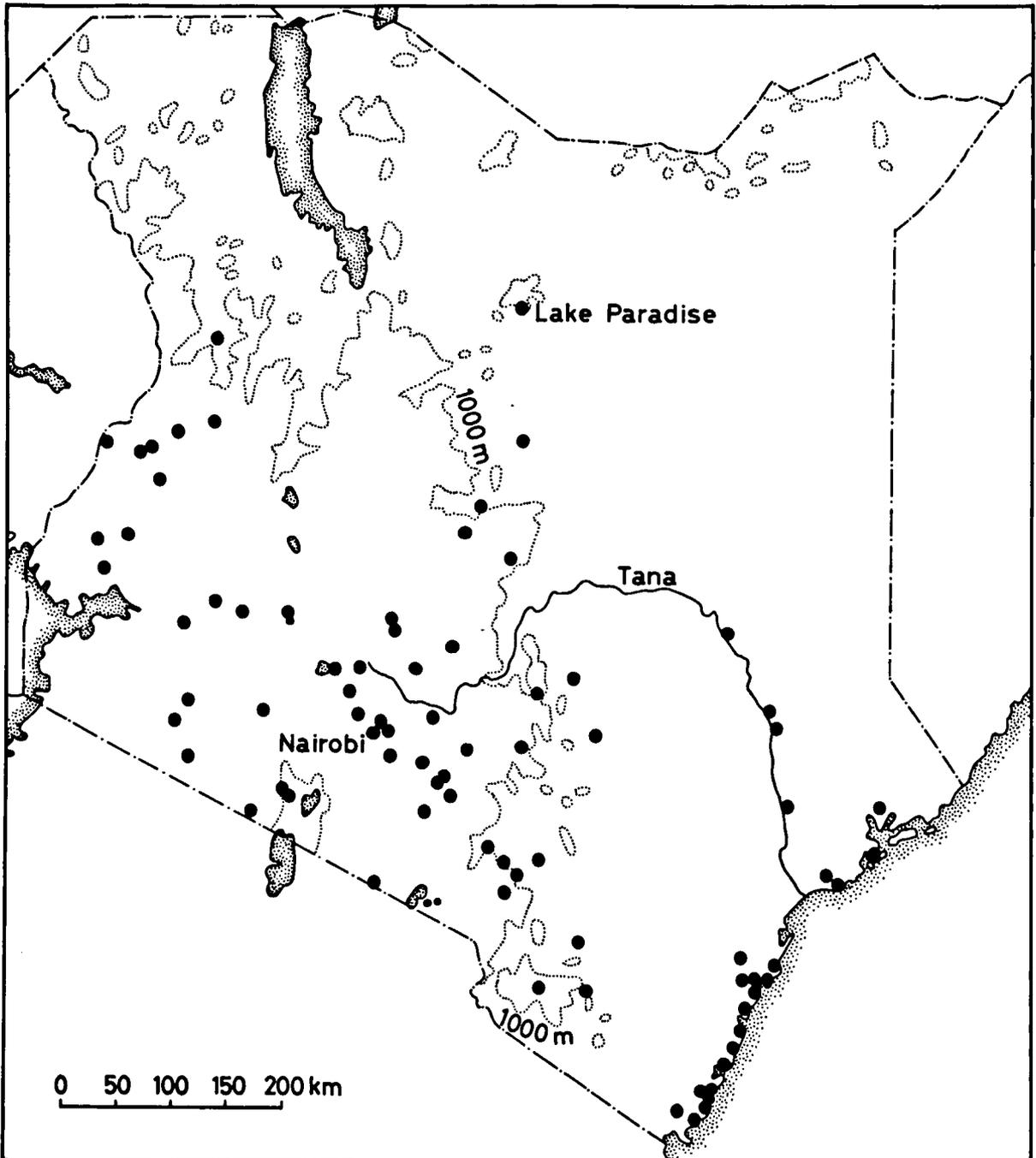


Fig. 11. Collecting localities of *Epomophorus wahlbergi* (Sundevall, 1846) in Kenya, to show the possible disjunction between highland and lowland populations.

In 1899 Matschie included this specimen in his new species *E. zenkeri* and described its origin now as "Kamerun-Delta". Andersen (1912) synonymized *E. zenkeri* with *E. wahlbergi* and

examined this specimen along with the other types, referring to it as from "the Cameroons". It is a nearly adult ♂ (ZMB 4786) of which I have only studied the skull, labelled

“Kamerun” (gsl 46.8, cbl 46.4, C<sup>1</sup>-M<sup>1</sup> 16.8). Cabrera (1903) recorded *E. gambianus* from Rio Muni; I have not seen this specimen in the MNCN, but according to Andersen (1912: 523) it represents *E. wahlbergi*. In the ZMB collection I examined the skin of a ♀ collected by Tessmann in December 1906 at Alen, Equatorial Guinea (not registered; field number 30), labelled “*E. aff. zenkeri*”. The specimen had developed nipples and a fal of 84.5; its skull should also be present but could not be found. From Gabon, Peters (1877a) recorded *Epomophorus macrocephalus* (= *E. gambianus*) for Donguila. Andersen (1912: 523) thought that this could have been *wahlbergi* (but listed the reference also under *Hypsognathus monstrosus* H. Allen, 1861; Andersen, 1912: 507). The species is known with certainty from some other localities in Gabon, from Pointe Noire in Congo, and from near the mouth of the Zaire River. Bergmans (1979) hypothesized that the species would prefer woodland savannas and penetrate with these into the forest zone. It was noted that the localities in this part of Africa are in or at stretches of woodland savanna cutting through the forest from the south. If the record from Aqua Town is correct, *E. wahlbergi* apparently also disperses along the coast, possibly making use of the many coastal settlements and gardens as stepping stones. Aqua Town, Donguila, Cape Lopez, Lac Anengué and Fernan Vaz are all in the Mangrove zone (type 77 in White, 1983). At the mouth of the Zaire River, but also in Kenya, Tanzania and Mozambique, the species is found in mangrove forests. (In East Africa, however, the hinterland of such forests never consists of lowland rain forest.) Only Alen, in Rio Muni, is located within the Mosaic of wetter and drier types of Guineo-Congolian lowland rain forest (type 3 in White, 1983) and would present an exception (if its identity is correct).

In the taxonomical remarks I have already expressed my doubts about the origin of the specimen said to come from Zémio, because of the apparent isolation of this locality, which one would expect to be connected by other finds

with the eastern populations. There are also two specimens labelled “Abyssinia”: an adult ♂ with a fal of 87.9 and a badly damaged skull but with its soft palate preserved and confirming its identity, collected halfway the 19th century by Th. von Heuglin (NMW 18301), and a stuffed ♀ with skull, purchased before or in 1847 from Verreaux (BMNH 47.7.8.25; 49.8.16.5). Andersen (1912: 524-525) considered the origin of Verreaux’ specimen as uncertain. Largen *et al.* (1974), who examined all Ethiopian bats in the BMNH, do not mention it and do not list *E. wahlbergi* for Ethiopia. It seems worthwhile to search Von Heuglin’s itineraries for the possible origin of his specimen. The occurrence of isolated populations in southern Ethiopia is not unlikely. Marsabit in nearby northern Kenya, an area of Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket, with a core of Mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland, surrounded on all sides by Somalia-Masai semi-desert grassland and shrubland (types 42, 45 and 54b in White, 1983, respectively), seems to support such an isolated population. Types 42 and 45 are dominant where the species occurs in the Kenyan highlands.

Another example may be the small coastal range in Somalia, although here the original vegetation cover (type 42) is continuous to Kenyan parts of the species’ range, and its distribution may just be poorly known. Apart from the vegetation types already mentioned, the vast majority of collecting sites of *E. wahlbergi* is located either in Woodlands (types 25, 26, 28 and 29c-e in White, 1983) or in Forest transitions and mosaics (types 11a, 16a-c, 19a, and 20 or 24).

The geographical variation within the species has been dealt with in the notes on its taxonomy.

***Epomophorus grandis* (Sanborn, 1950) —  
New combination**

*Micropteropus grandis* Sanborn, 1950: 55 (Dundo);  
Hayman, 1963: 97; Bergmans, 1979: 174.

*Material examined:*

ANGOLA. Dundo: 1 ♀, alc. (including soft palate and tongue), skull, IX-1948, A. de Barros Machado (holotype of *Micropteropus grandis*; FMNH 66433); 1 imm. ♂, alc., IX-1948, A. de Barros Machado (young of holotype; FMNH 66434); 1 ♂, alc., skull (BMNH 63.1025).  
 CONGO. Pointe Noire: 1 ♂, 20-XII-1972, W. Bergmans (ZMA 15.535).

*Diagnosis:* A small species with a relatively large zygomatic width and a relatively short, posteriorly wide palate; the second to sixth palatal ridges interrupted in the middle; the fifth palatal ridge on level with the posterior sides of the last upper molars (M<sup>1</sup>).

*Measurements:* Table 13.

*Distribution:* Fig. 12.

*Related species:* In body and skull size the few known examples of *E. grandis* fall within the size ranges of *E. minor*, but from this and from the larger — and at Pointe Noire: sympatric — *E. labiatus* it differs by its relatively broad skull and posterior palate and by its interrupted second to fourth palatal ridges. From *labiatus* it differs by its smaller skull dimensions.

*Remarks*

*Taxonomy:* Sanborn (1950) wrote that in characters *Micropteropus grandis* was “like *Micropteropus pusillus* but much larger and with six palate ridges arranged differently than in

Table 13. Measurements of *Epomophorus grandis* (Sanborn, 1950)

	FMNH 66434 ♀ Dundo, Angola holotype	BMNH 63.1025 ♂ Dundo, Angola	ZMA 15.535 ♂ Pointe Noire, Congo
head and body length			99 **
tail length	7.5		3.8
tibia length	28.2	27.3	28.7**
foot (with claws)	19.6	18.1	18
ear length	± 16	17.3	17.5
fal	65.8	62.8	62.3**
3rd metacarpal length	49.8	45.4	43.2
5th metacarpal length	46.9	43.2	41
gsl	36.4	36.7	35.4
cbl	35.3	36.1	34.8
rl	13.3	13.7	13.1
pl	20.2	20.9	20.2
cranium width	14.5	14.4	14.3
iow	6.3	6.3	6.0
pow	8.8	9.4	9.0
zw	21.8	20.8	21.6
mandible length	28.6	28.7	28.3
mandible height		10.2	10.4
C <sup>1</sup> -C <sup>1</sup>	7.5	7.0	6.9
C <sup>1</sup> -M <sup>1</sup>	12.3	12.3	11.8
M <sup>1</sup> -M <sup>1</sup>	11.5	11.3	11.2
C <sub>1</sub> -M <sub>2</sub>	13.5	13.7	13.1
length x width P <sup>3</sup>	2.3 x 1.3*	2.0 x 1.5	2.25 x 1.25
length x width P <sup>4</sup>	2.5 x 1.4*	2.5 x 1.7	2.4 x 1.5
length x width M <sup>1</sup>	2.3 x 1.4*	2.8 x 1.7	2.6 x 1.5

\* measured with vernier callipers

\*\* field measurements

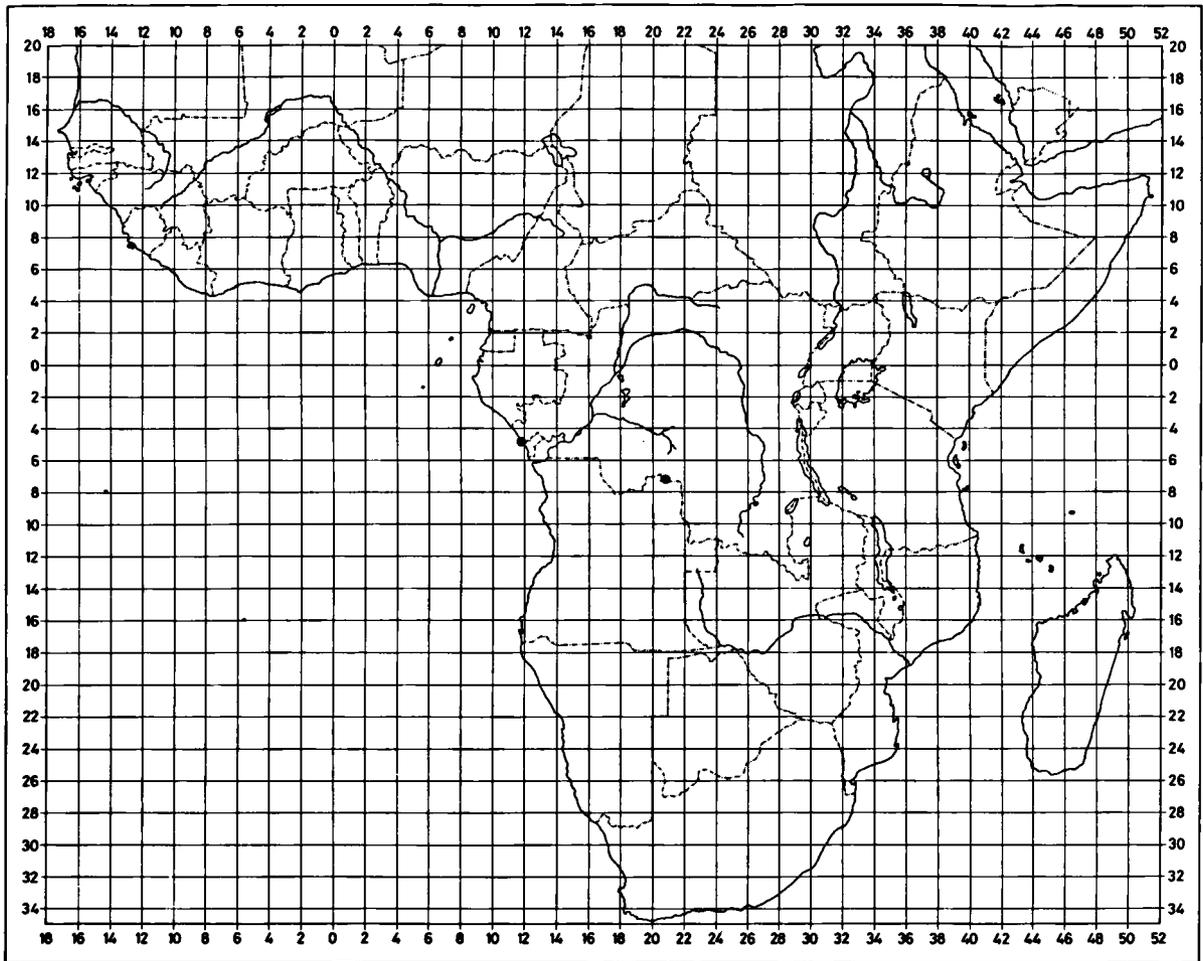


Fig. 12. Distribution of *Epomophorus grandis* (Sanborn, 1950). Black dots: squares from which material has been identified by the author.

*pusillus*." He wrote further that its skull was "like that of *pusillus* but much larger; palate not so wide relatively and tooth rows not so divergent posteriorly; in other characters, shape, teeth, etc., as in *pusillus*." And he finally remarked that "The palate ridges in this new species (...) show an approach to the partially paired ridges in *Epomops*." It is remarkable that he left out any comparative remark on *Epomophorus*, as the excellent picture of the holotype specimen shows an animal very much like a small representative of that genus, while its palatal ridge pattern is much nearer to that in *Epomophorus* than any other genus (Sanborn,

1950: figs 2-3). Hayman (1963), in his description of *Micropteropus intermedius*, rightly pointed out that "The new form, *M. intermedius*, is quite clearly intermediate between *M. pusillus* and *M. grandis*, and one effect of its discovery is that the generic distinction of *Micropteropus*, as defined by Andersen (1912), is no longer so clearly recognisable as compared with *Epomophorus*. The strong shortening of the rostrum in the type species of the genus, *M. pusillus*, is not matched in either *M. grandis* or *M. intermedius*, in both of which the rostrum is longer in relation to total skull length, and the highly specialised palatal ridges of *M. pusillus* lead, in

*M. grandis* and *M. intermedius*, to a type which, while still peculiar, is approaching that found in *Epomophorus*.”

Hayman (1963) described a further specimen of *M. grandis*, collected at the type locality Dundo. It was a ♂ without epaulets but otherwise full-grown. His very clear pictures (Hayman, 1963: figs 4-5) again show an *Epomophorus*-like animal rather than a *Micropteropus*. Bergmans (1979b) described a third adult specimen, a young adult ♂ from the Congo coast at Pointe Noire, without questioning its generic allocation.

The taxon *Micropteropus* was originally proposed as a subgenus of *Epomophorus* by Matschie (1899), to accommodate *E. pusillus* Peters, 1867. Matschie (1899) equally considered as subgenera of that genus *Hypsignathus* Allen, 1861, *Epomops* Gray, 1866, and *Nanonycteris* Matschie, 1899. The typical subgenus *Epomophorus* comprised, in Matschie's view, the then recognized *Epomophorus* species (including some that later have been synonymized with others), and also what we now call *Epomops buetikoferi* (Matschie, 1899); in the subgenus *Epomops*, Matschie included (of the species still regarded as valid) *Epomophorus franqueti* Tomes, 1860 and *E. dobsonii* Bocage, 1889. The characters which would distinguish *Micropteropus* from *Epomophorus* would, according to Matschie, be the following. Smaller body size, with fal not exceeding 60. An even more rudimentary tail. A short rostrum, with the distance between anterior eye corner and tip of nose in *Micropteropus* about equal to the width of the head at the mouth corners, and in *Epomophorus* much greater than this width. A rather flat postdental palate, against a somewhat depressed postdental palate in *Epomophorus*. Soft palatal ridge configuration in *Micropteropus* with a longitudinal, anteriorly bifurcated median groove with at both sides, closely together, four elevations (“Höcker”), instead of transverse ridges as in *Epomophorus*.

In 1910 Andersen suggested generic status for *Micropteropus*, because of its very short rostrum. In 1912 he elaborated this view, and distinguished *Micropteropus* from *Epomophorus* by

the following characters (partly not explicitly stated, but implicit in his descriptions and illustrations). Small body size (fal not greater than about 53, against at least 60 in *Epomophorus*). Small rostrum length (front of orbit to tip of nasals), less than or subequal to the lachrymal width (across lower edges of lachrymal foramina), against much greater than this width in *Epomophorus*. Bony palate relatively broad between the first upper molars and abruptly narrowed behind the zygomatic processes and posteriorly depressed (in *Epomophorus* the bony palate long and narrow, not abruptly narrowed behind the zygomatic processes, and posteriorly deeply depressed). Palatal ridge configuration with five thick and prominent ridges in *Micropteropus*, the second to fifth of which divided by a deep groove, against six in *Epomophorus* of which only the fifth and sixth divided by a narrow interruption. Backward extension of maxillary tooth row, nearly to the orbital cavity (seen from ventral side) in *Micropteropus* and remaining well in front of this in *Epomophorus*. Summarizing, all characters pertain to overall size, rostrum length, and form of bony and soft palate.

At present there appear to be sufficient reasons to retain *Micropteropus* as a genus, separate from *Epomophorus*, for the type species *pusillus* and for *M. intermedius*. These reasons will be further discussed in the account of *Micropteropus* in part 2 of this series. I see no good reason, however, to regard *Micropteropus grandis* Hayman as different from *Epomophorus*. In fal and absolute and relative skull dimensions the three known adult specimens closely approach or overlap with those in *E. minor* (tables 1, 8, and 13). Its rostrum and palate are longer, relatively, than in *E. wahlbergi*. In both sexes, the relative width of the palate at the level of the first upper molars ( $M^1-M^1$  as % of gsl) is larger than the maximum values for that width, i.e. of the smallest individuals, in *E. minor*, while its gsl is even longer than in those specimens. In the ♂♂, this width is even slightly larger than in the broad-skulled *E. wahlbergi*. In the ♂ from Pointe Noire the rostrum (here: front of orbit to tip of nasals) is

larger than the lachrymal width (11.7 against 9.5) and as such quite in line with other *Epomophorus* specimens of its size. The narrowing of the bony palate behind the upper tooth row is very gradual in the long-snouted large species and becomes more abrupt in species with shorter rostra, in which the farther backward extending upper tooth rows leave little space for the process.

Although the relative large  $M^1$ - $M^1$  width may serve to distinguish *E. grandis* from other species of the genus, it hardly adds to the variation accepted for the genus as a whole and certainly would not seem to justify the allocation of *grandis* to another genus.

One of the most important differences between *Micropteropus* and *Epomophorus* is found in the palatal ridge patterns. Matschie's (1899) and Andersen's (1912) descriptions have been quoted already. The first ridge in *Micropteropus* is strongly hastate, pointing backward, and the remaining ridges are divided by a deep central groove. In *Epomophorus* the first ridge is triangular but not hastate, and of the others only the last two are narrowly divided in the middle. I have examined the soft palate of all four *grandis* specimens on record. In the type it has been detached from the skull and preserved in spirit. Fig. 13 was drawn of the soft palate put back in place (unfortunately with no other equipment than vernier callipers, squared paper, and some drawing experience). As was already evident from Sanborn's (1950) original figure (also included in Hayman, 1963), the first ridge is not hastate, the central dividing grooves of ridges 2, 3 and 4 are narrow, and ridges 5 and 6 are as in *Epomophorus*. In the somewhat dehydrated palate the halves of ridges 2 and 3 show traces of connections in the centre. In ridge 4 this is not apparent. In the young of the type, a ♂ with milk dentition, a fal of 45.8 and a head length of 28.3, the soft palate has been left *in situ* in the spirit specimen. Ridge 1 is notched in the middle and the ridges 2, 3 and 4 are not divided in the middle but at most very weakly notched. In the second adult specimen, described and figured by Hayman (1963), the soft palate has been left *in situ* and

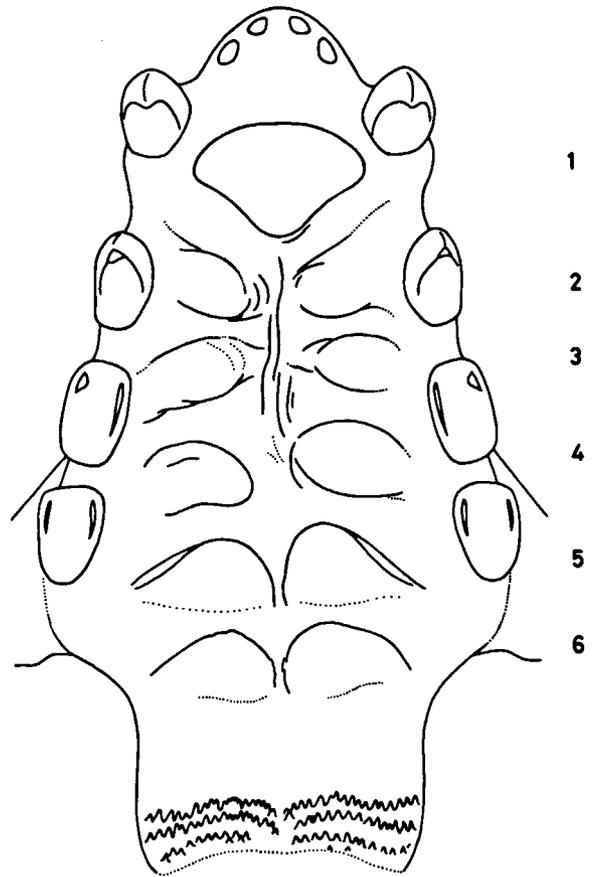


Fig. 13. Holotype specimen of *Epomophorus grandis* (Sanborn, 1950) (FMNH 66433); ventral aspect of rostrum with soft palate *in situ*.

the extracted skull has been preserved in alcohol. Hayman's picture (1963, fig. 5) shows that ridge 1 is not hastate and quite as in *Epomophorus*, and that although the ridges 2, 3 and 4 each consist of two crescent-shaped halves, the separation between those halves is incomplete or weak in 2, distinct but narrow in 3, and apparently incomplete in 4. The ridges 5 and 6 are again as in *Epomophorus*. After years in alcohol, the palate is also dehydrated and the pattern has become less distinct, but it is still evident that 2, 3 and 4 are only weakly disconnected in the middle. In the fourth specimen, the ♂ from Pointe Noire, the soft palate has been dried with the skull and later softened in water. Position and morphology of the ridges were recognized as similar to those in the type

(Bergmans, 1979). The ridges 2, 3 and 4 are divided in the middle, but in all three the halves also show traces of weak connections.

To conclude, it appears that in *grandis* the ridges 2, 3 and 4 are not divided in juveniles and become rather weakly divided in adults. This is essentially different from the situation in *Micropteropus pusillus*, in which juveniles possess the same ridge configuration as adults. In typical *Epomophorus* central longitudinal notches in these ridges are not uncommon (see also Andersen, 1912: 516, on this phenomenon). In morphology, the ridge pattern in *grandis* resembles that in *Epomophorus* much more than that in typical *Micropteropus*.

The above considerations on size, skull dimensions and soft palate have led me to consider *grandis* as a species of *Epomophorus*.

Distribution and geographical variation: *E. grandis* is only known from the type locality Dundo in northeast Angola and Pointe Noire at the Congolese coast. Hayman quoted Dr A. de Barros Machado on the zoogeography of northeast Angola, which is inhabited by "elements of both the Guinea-Congo and Zambesian-Rhodesian faunas. This situation is accounted for by the fact that the district as a whole consists of a gentle slope to the northward of the typical Rhodesian-type savannah, deeply intersected by the numerous northward flowing rivers draining the region towards the lower Kasai and hence to the Congo. The courses of these rivers are marked by long narrow strips of gallery forest extending like long fingers from the Congo rain forests of the north deep into the savannah region" (Hayman, 1963: 85).

Bergmans (1979: 168, fig. 2) described and figured the locality where he collected the Congolese specimen: a small fringe of palms (*Borassus* sp.) and shrubs along the beach. According to White (1983), both Dundo and Pointe Noire are located in his type 11a, Mosaic of Guineo-Congolian lowland rain forest and secondary grassland. It is of course speculative to envision the species' overall distribution. The fact that it has never been collected in the rain forests to the north is in accordance with what may be expected for an *Epomophorus*

species. It will more probably be found yet in the various types of woodland to the south.

Bergmans (1979) described some differences he found between the Pointe Noire specimen and the type. Some of these may be related to a difference in age, others probably reflect normal intraspecific variation. Further specimens are needed to assess their nature.

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