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TAXONOMY AND BIOGEOGRAPHY OF AFRICAN FRUIT BATS (MAMMALIA, MEGACHIROPTERA).

4. THE GENUS *ROUSETTUS* GRAY, 1821

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ABSTRACT

The concept of the genus *Rousettus* Gray, 1821 as established by Andersen (1912) is revised to accommodate *R. madagascariensis* Grandidier, 1929, *R. obliuivus* Kock, 1978 and *R. spinalatus* Bergmans & Hill, 1980, and to reflect the following mutations. Following Bergmans *et al.* (1988), the genus *Boneia* Jentink, 1879 is treated as a synonym of *Rousettus*, which adds to that genus the species *B. bidens* Jentink, 1879. The subgenus *Stenonycteris* Andersen, 1912 is considered a synonym of *Rousettus*, and the subgenus *Lissonycteris* Andersen, 1912 a full genus, to be reviewed in the next part of this series. All African *Rousettus* species are characterized and their distributions, including many new records, and geographical variation are analyzed. Following Eisentraut (1960), *R. egyptiacus* (É. Geoffroy-St. Hilaire, 1810) is divided into four, geographically disjunct, subspecies: *egyptiacus* from southern Egypt northward to and along the Mediterranean coast, including Cyprus, into southern Turkey; *leachii* (Smith, 1829) from southern Sudan and Ethiopia through East Africa to the Cape; *unicolor* (Gray, 1870) from northwest Angola to the Mount Cameroun region and from there to Senegal; and the extralimital *arabicus* Anderson & de Winton, 1902 from the southern half of the Arabian Peninsula to southern Iran and Pakistan (*arabicus* records from East Ethiopia are thought to be based on small-skulled *leachii*). All four subspecies are shown to vary geographically. The differences between *arabicus* and *R. leschenaultii* (Desmarest, 1820), which both inhabit Pakistan, are discussed at length. Notwithstanding several recent publications, *Rousettus lanosus* O. Thomas, 1906 is considered very distinct from *Rousettus madagascariensis*. Its scattered highland distribution has given rise to appreciable geographic variation. Three rough divisions are described but for the present no subspecies are recognized: East Zaïre, adjoining Uganda and (probably) Rwanda; (probably) West Ethiopia, South Sudan, East Uganda and Kenyan highlands; and Northeast Tanzania to Malawi. The Malawi records are the first for that country. Of *R. madagascariensis*, many new specimens have come to light, and its diagnosis is adapted accordingly. Its association, as a subspecies, with *R. lanosus* by some recent authors is based on a misinterpretation of its original description and other literature, and rejected as untenable. Its differences from *R. obliuivus* are described in detail for the first time. Some previously unrecorded specimens of *R. obliuivus* are reported. It is suggested that sexual dimorphism may be at least partly responsible for the "geographic" variation noted by Kock (1978).

INTRODUCTION

For a general introduction to the series of which this paper forms the fourth part, the reader is referred to the first part (Bergmans, 1988), which also contains a section Material and Methods.

TAXONOMIC SECTION

Rousettus Gray, 1821

Rousettus Gray, 1821: 299 (type species: *Pteropus egyptiacus* É. Geoffroy-St. Hilaire, 1810); Palmer, 1898: 112; Matschie, 1899: viii, 65 (in part: excluding *Pterocyon* Peters, 1862, *Myonycteris* Matschie, 1899, and *Cynonycteris brachycephala* Bocage, 1889); Andersen, 1907 b: 505; Miller, 1907: 54 (in part: not *Myonycteris* Matschie, 1899); Andersen, 1912: 16 (in part: excluding *Lissonycteris* Andersen, 1912); Leche, 1921: 40; Kulzer, 1979; Corbet *et al.*, 1991: 40.

Boneia Jentink, 1879: 117 (type species: *Boneia bidens* Jentink, 1879); Miller, 1907: 61; Andersen, 1912: 55; Leche, 1921: 40; Corbet *et al.*, 1991: 41.

Stenonycteris Andersen, 1912: 23 (type species: *Rousettus lanosus* O. Thomas, 1906); Leche, 1921: 41; Kingdon, 1974: 117, 124.

The genus name *Rousettus* Gray, 1821 has long gone unnoticed. Several subsequent synonyms were based either on the type species, *R. egyptiacus* (É. Geoffroy-St. Hilaire, 1810) or on very close relatives or other species, even by Gray himself, until *Rousettus* was revived by Palmer, in 1898. Both Miller (1907) and Andersen (1907b, 1912) gave synonymies. Miller included *Myonycteris* Matschie, 1899, proposed as a subgenus of *Rousettus* to accommodate *Cynonycteris torquata* Dobson, 1878 and *C. angolensis* Bocage, 1898. Andersen (1912) considered *Myonycteris* an independent genus, which is followed here, but separated *C. angolensis* from it and proposed a new subgenus of *Rousettus* for this species, i.e. *Lissonycteris*. Several later authors have argued that *Lissonycteris* should stand as a genus, which view is also held by the present author, and will be elaborated in the next part of this series.

This difference of opinion with Andersen; the addition, after 1912, of several new species to the genus (*R. madagascariensis* Grandidier, 1929; *R.*

obliviosus Kock, 1978; *R. spinalatus* Bergmans & Hill, 1980); and the synonymization with *Rousettus* of the genus *Boneia* Jentink, 1879 (with a single species, *B. bidens* Jentink, 1879) by Bergmans *et al.*, 1988, necessitate a revision of the concept of *Rousettus* as formulated by Andersen (1912: 16-23). (An analysis of the pre-Andersen developmental history of the concept of *Rousettus* will not be attempted here. Andersen (1912), in his synonymies and historical sections on genus and species, provided all the references and summaries of the important ones. But the original publications of *Rousettus* and some of its synonyms contain no descriptions and the descriptions of some other synonyms are very brief and equivocal, while most include other taxa. The meant analysis would therefore focus on bibliographical facts more than anything else and it seems much wiser to accept Andersen's description of the genus as the authoritative one, in which all earlier accounts have been sufficiently considered.) The present account of African Megachiroptera is not the appropriate place for a revision of the entire genus *Rousettus* as the fundament for a new genus concept. In the mean time, available knowledge of the species involved, including the five extralimital ones presently recognized, allows for the following amendments of Andersen's diagnosis and descriptive notes:

General shape of skull as in *Eidolon*, but braincase deflection variable (the alveolar line projected backward passing through upper part of occipital condyle or upper margin of foramen magnum or level with median part of occipital ridge), and the tympanic without bony auditory meatus; rostrum rather long (length greater than lachrymal width) and, in the larger species, broad; front of orbit vertically above middle or posterior half of M^1 ; premaxillaries separated or in contact, in some taxa co-ossified in a minority of specimens. Incisors 2/2-2/2 but I^1 often deciduous in *bidens*; lower incisors (when unworn) bifid except, probably, in *bidens*; cheek-teeth normally 5/6 (P^1 deciduous in *leschenaultii seminudus* Gray, 1870 and *amplexicaudatus brachyotis* (Dobson, 1877)); P^1 sub-equal in bulk to an upper incisor; M_1 shorter than M_2 and M_3 combined. Second digit clawed; membrane insertion

variable: from sides of back or (in *spinalatus*) from the spinal line; a short but distinct tail; forearm length 65-107 mm. Palatal ridge formula $4 + 3 + 1$ (exceptionally $3 + 4 + 1$), $4 + 4 + 1$ (sometimes $4 + 4/3 + 1$ or $4 + 3/4 + 1$; for an explanation of this notation see Eisentraut, 1960), or $4 + 3 + 1/2$ (sometimes $4 + 3 + 2/3$) (in *bidens*).

A revision of the entire genus should also include a reassessment of proposed subgeneric divisions. Removing *Lissonycteris* from *Rousettus* leaves us with the subgenera *Rousettus* and *Stenonycteris* Andersen, 1912 and, as suggested recently by Corbet *et al.* (1991), *Boneia*. *Stenonycteris* was distinguished mainly on the basis of its relatively strong brain-case deflection and excessively narrow cheek-teeth. Leche (1921) thought that *Stenonycteris* was only slightly less different from typical *Rousettus* than were *Boneia* and *Lissonycteris*, and all three would deserve generic rank. Describing a series of *Rousettus madagascariensis*, Bergmans (1977a) argued that this species is intermediate between typical *Rousettus* and *Stenonycteris* in all morphological characters except the narrowness of its cheek-teeth which would place it in the latter, if one would wish to maintain that. If I understand him well, Kock (1978a), describing *Rousettus obliviosus*, observed that a strong brain-case deflection is not necessarily a primitive character and thus of uncertain value in phylogenetic assessments such as the recognition of subgeneric divisions. Bergmans (1977a) considered brain-case deflection as a neotenic character, weakened but persisting in adults of *madagascariensis* (and most strongly so in the smallest individuals). *Rousettus bidens*, with a fal of 94.3-103.5, a gsl of 43.8-46.3 and weights of 150-194 one of the largest species of the genus (see Bergmans *et al.*, 1988), has a strongly deflected brain-case but is otherwise quite different from *Stenonycteris*, which indicates that adult brain-case deflection may indeed be an adaptation developed independently in various strains of *Rousettus*. On grounds not stated but most probably these morphological considerations Corbet *et al.* (1991) synonymized *Stenonycteris* with *Rousettus*. (They retained *Boneia* as a subgenus for reasons stated by Corbet *et al.* in 1992 and to be discussed in the next part of this series.) Kingdon (1974)

introduced a different class of characters to distinguish *Stenonycteris* from *Rousettus*: a different wing posture when roosting, different foreclaw use and locomotion when clambering about, and shape, posture and movements of the ear. He therewith subscribed to the views of Lawrence *et al.* (1963) who used, among others, behavioural and locomotory characters to separate *Lissonycteris* from *Rousettus*. Kingdon considered *Stenonycteris* also as a genus on its own.

I fully agree that patterns of behaviour and locomotion should be given full consideration in phylogenetic reconstructions. But whereas the separation of *Lissonycteris* appears to be justified on other grounds (to be dealt with under that genus in the next part of this series), there is as yet no solid basis for subgeneric divisions within *Rousettus*. Only Andersen (1912) has compared all *Rousettus* species (then known) - a prerequisite for the appreciation of possible meaningful subgroupings. The known differences between *Boneia* and *Rousettus* were thought to be of a gradual nature (Bergmans *et al.*, 1988), and as far as *Stenonycteris* is concerned, the apparent distinctions from *Rousettus egyptiacus* as observed by Kingdon (1974) relate to characters which are as yet of unknown state in the majority of other *Rousettus* species. (The account of the genus *Lissonycteris* in the next part of this series will include an analysis of many morphological characters in *Rousettus* species as well.) To a lesser extent, this also holds for the faculty of acoustic orientation. Among Megachiroptera, this has been found only in *Rousettus*. It has so far been established in the species *egyptiacus*, *amplexicaudatus* (É. Geoffroy-St. Hilaire, 1810) and *leschenaultii* (Desmarest, 1820) (as *seminudus* Gray, 1870) (Möhres *et al.*, 1956; Novick, 1958a). Notwithstanding Kock's (1972) assertion of the opposite, Kingdon (1974) made it plausible that *R. lanosus* Thomas, 1906 also orients acoustically. Payne *et al.* (1985) implied this for *R. spinalatus* when they wrote that this species lives in dark caves, while Bergmans *et al.* (1988) reported on the cave-dwelling habits of *R. bidens* and *R. celebensis*. *R. madagascariensis* also roosts in caves (this paper). Kulzer (1979) said that other cave inhabiting fruit bat genera use partly lighted caves only.

Novick (1958a) found that *Eonycteris* Dobson, 1873, as one of those genera, orients visually, and may find its way through the dark by memory or by random noise and echoes. Gould (1988) suggested that they might use the clapping sounds of their wings. In the diagnoses in the following species accounts those differential characters have been selected which when used in combination allow for the discrimination of the African forms here considered. Some extralimital species are very distinct and cannot possibly be taken for any of the African ones, but some others possess morphological similarities to certain African species. *Rousettus leschenaultii* resembles *R. egyptiacus* and *R. obliuosus*; *R. amplexicaudatus* is not always easy to distinguish from *leschenaultii* and may thus also be confused with these. However, an extensive treatment of extralimital species would not be in place here. Specimens of known origin need not present identification problems, except, perhaps, specimens from Pakistan, where *egyptiacus* 'meets' *leschenaultii*. This matter will be discussed in the account of *R. e. arabicus* Anderson & de Winton, 1902.

***Rousettus egyptiacus* (É. Geoffroy - St. Hilaire, 1810)**

Pteropus Egyptiacus E. Geoffroy-St. Hilaire, 1810: 96 (type locality: the great Pyramid, Lower Egypt - i.e. at Giza); the specific epithet has later been corrected and changed into *egyptiacus* by its author (see foot-note in Andersen, 1912: 29), but this correction is considered an unjustified emendation by Corbet *et al.*, 1992.

Pteropus Leachii Smith, 1829: 433 (type locality: Cape Town).

Eleutherura unicolor Gray, 1870: 117 (type locality: Gaboon).

Rousettus arabicus Anderson & de Winton, 1902: 86, 88, 90 (type locality: Aden).

Rousettus aegyptiacus; Andersen, 1912: 29; G.M. Allen, 1939a: 62; Rode, 1941: 80; Ellerman *et al.*, 1953: 45; Kulzer, 1956; Möhres *et al.*, 1956: 2; Griffin *et al.*, 1958; Bar-Yosef *et al.*, 1966; Kock, 1969: 16; S. Erkert, 1970; Pirlot, 1970; Pirlot *et al.*, 1970; Lane *et al.*, 1971; Norberg, 1972; Brown, 1973; Kingdon, 1974: 128; Suthers *et al.*, 1980; K.D. Jürgens *et al.*, 1981; H.G. Erkert, 1982; Kleinschmidt *et al.*, 1982; Happold, 1984: 272; Dobat *et al.*, 1985: 297; Hickey *et al.*, 1987; S. P. Thomas, 1987: 90; Bergmans *et al.*, 1988: 11; Bernard, 1988; Norberg, 1989: 205.

Rousettus aegyptiacus; Lang *et al.*, 1917: 480, 481.

Cynonycteris aegyptiacus; Wood Jones, 1917.

Rousettus egyptiacus; Mendez, 1937: 63; Corbet *et al.*, 1992: 67.

Rousettus aegyptiacus occidentalis Eisentraut, 1960a: 231 (type locality: Mueli).

Rousettus aegyptiacus; Brosset, 1966c: 131.

Rousettus aegyptiacus ssp.; Feiler, 1984: 75.

(Further references under the subspecies.)

Diagnosis: A medium-sized short-furred fruit bat, on average the largest species of the genus in Africa, total fal range 82.1-106.3 (minimum in Africa 85.7); brain-case only very moderately deflected, alveolar line straight, if projected back-ward passing near or through upper part of occipital condyle; widths of P³, P⁴, M¹, P₃, P₄ and M₁ more than half their lengths; wing from back of first toe or interspace between first and second toe; dorsal side of tibia practically naked, with very short and thinly spread hairs only. Measurement ranges and ratios for subspecies combined:

fal	♂♂	85.7 - 106.3,
	♀♀	82.1 - 101.7;
gsl	♂♂	38.8 - 46.6,
	♀♀	38.0 - 45.8;
rl	♂♂	35.6 - 39.1% of gsl,
	♀♀	35.0 - 38.8% of gsl;
C ¹ -C ¹	♂♂	18.3 - 22.3% of gsl,
	♀♀	18.8 - 21.6% of gsl;
M ² -M ²	♂♂	27.9 - 32.1% of gsl,
	♀♀	28.1 - 32.9% of gsl.

Distribution: Figs. 1 and 2.

Remarks

Andersen (1912) distinguished three forms within what is presently considered *Rousettus egyptiacus*: *R. egyptiacus*, *R. leachii* and *R. arabicus*. His *R. egyptiacus* included the typical subspecies and Gray's *Eleutherura unicolor*. In his diagnoses the sexes are not separated. According to his key, *egyptiacus* and *leachii* differ from *arabicus* in the greater length of their tibiae (40-45.5 against 37-39.5) and their rounded (against attenuated)

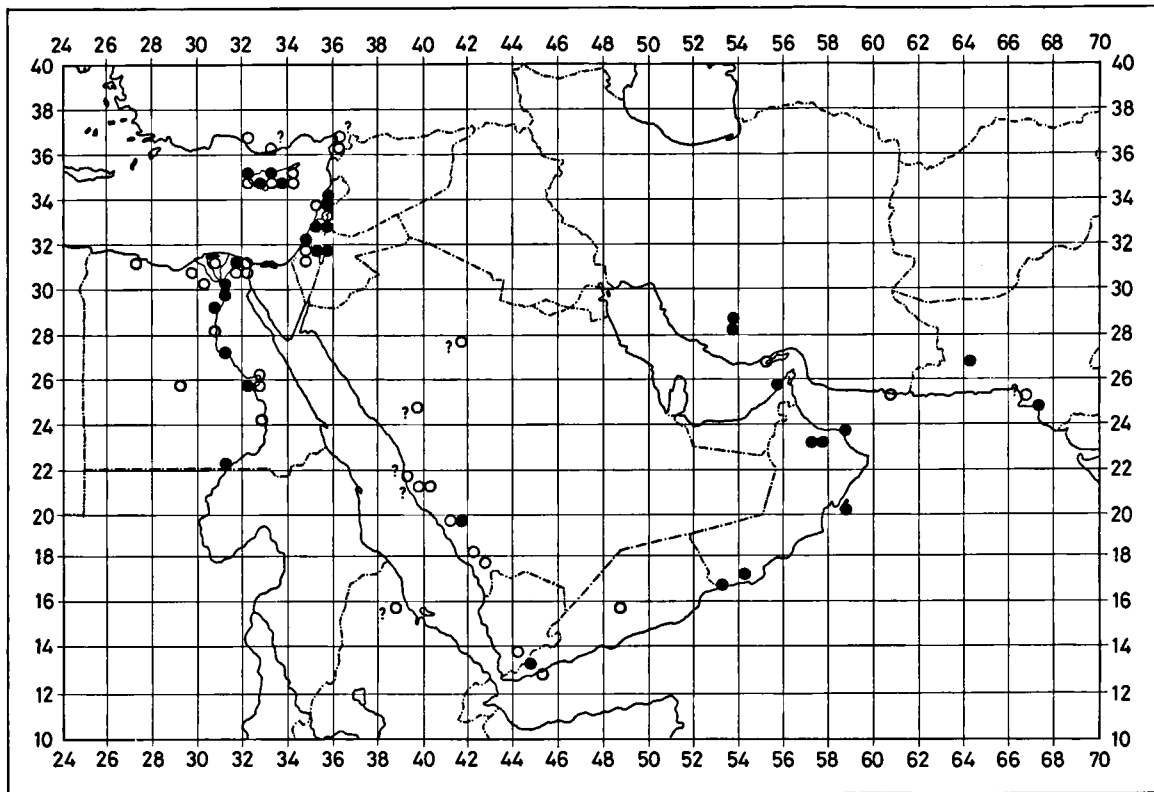


Fig. 1. Distribution of *Rousettus egyptiacus* (É. Geoffroy-St. Hilaire, 1810): West of 38° E and north of 20° N, the nominate subspecies; east of 38° E in the Arabian Peninsula and eastward: *R. e. arabicus* Anderson & de Winton, 1902 (question-marked localities indicate observations of "*Rousettus* sp." and are in need of confirmation); the single Ethiopian record on this map probably represents *R. e. leachii* (Smith, 1829). Black dots: squares from which material has been identified by the author. Open circles: records from literature, museum registers, and correspondence.

ear tips; *egyptiacus* differs from *leachii* in having a larger skull (43.6-46.7 against 40.5-43.8), a heavier rostrum, a palatal ridge pattern of 4 + 4 + 1 (against 4 + 3 + 1; with some variation in both). From his species accounts it further appears that, due to a more developed frontal region in *egyptiacus* the interorbital width is larger than the postorbital width while in *leachii* the latter is almost always larger than the interorbital width; the temporal ridges unite into a sagittal crest at a more distal point in *egyptiacus* than in *leachii*, and often remain separate in the latter; the coronoid process of the mandibulum is higher and the angular portion stronger and more projecting in *egyptiacus* than in *leachii*; and the teeth in *egyptiacus*

are averaging markedly larger than in *leachii*. Andersen differentiated *arabicus* also mainly from *leachii*, which he used as a standard instead of the typical species: the skull in *arabicus* is smaller than in *leachii* (38.7-41.8 against 40.5-43.8), the rostrum shorter (13-13.6 against 13.8-15.2) and the teeth are smaller (the molars narrower) than in *leachii*; the palatal ridge pattern in *arabicus* is mostly as in *egyptiacus* but sometimes as in *leachii*.

The first reviser after Andersen was Eisentraut (1960a). He followed Ellerman *et al.* (1953) in ranking *leachii* as subspecies of *egyptiacus* and considered *arabicus* also as a race of that species. He further proposed a new subspecies, *occidentalis*, for specimens from West Africa (from Senegal to

Gabon). He noted that Andersen (1912) had synonymized *unicolor* with typical *egyptiacus* on wrong grounds but did not use the name *unicolor* for the West African subspecies. Like Andersen, he did not separate the sexes in his analysis. He took the typical subspecies as standard and his diagnoses deviated from Andersen's on some points: *egyptiacus* has a fal of 88.2-96.5; is large-headed, with a wide and high rostrum; co-ossified premaxillaries in a minority of old specimens only (6 out of 22); interorbital width usually larger than postorbital width (in 15 out of 18 specimens); a distinct sagittal crest in most old specimens (in 17 out of 22); a relatively small angle between mandibular ramus and coronoid process (121°-132°); strongly developed dentition, with broad molars; a palatal ridge pattern of 4 + 3 + 1 with in most specimens at least the beginning of an additional ridge behind the sixth: 4 + 3/4 + 1 (or, when further developed, 4 + 4/3 + 1 and when complete 4 + 4 + 1). *R. leachii* has a fal of 87.8-96.2, averaging slightly smaller in body measurements than *egyptiacus*; a smaller head than *egyptiacus*, with a more delicately built skull and a slenderer rostrum (Eisentraut did not state if premaxillaries are co-ossified or not); a relatively small interorbital width (smaller than postorbital width in 5 out of 7 specimens); no sagittal crest, and separated temporal ridges in most specimens; a larger angle between mandibular ramus and coronoid process (132°-142°) than *egyptiacus*; weaker dentition than in *egyptiacus*, with narrower molars; a palatal ridge pattern of 4 + 3 + 1 in one specimen and 4 + 4 + 1 in another. *R. arabicus* averages smaller in all measurements than the other subspecies although there is considerable overlap in size. Eisentraut could study only two specimens and did not give a full analysis; no remarks were made on premaxillaries, inter- and postorbital widths, and sagittal crest. Mentioned are: A relatively small angle between mandibular ramus and coronoid process (128°); strongly developed dentition with broad and, in some cases, relatively long molars (Eisentraut pointed out here that Andersen erroneously described the dentition of *arabicus* as weaker and its molars as narrower than in *leachii*; in some cases the molars may be slightly narrower than in *egyptiacus*); a palatal

ridge pattern of 4 + 3 + 1 with parts of an extra ridge behind the sixth. *R. e. occidentalis* averages larger than typical *egyptiacus*, has a fal of 86.5-102, an average skull size intermediate between *egyptiacus* and *leachii*; a rostrum also intermediate between those two subspecies; rarely co-ossified premaxillaries; an interorbital width mostly as in *leachii*; smaller than postorbital width in 14, equal to it in 11, and larger than it in 4 specimens; a strong sagittal crest in 5, a weak crest in 5, and no crest at all in 21 out of 31 specimens; an angle between mandibular ramus and coronoid process which is intermediate between *egyptiacus* and *leachii* (129°-140°; mean 33.5°); dentition weaker than in *egyptiacus*, with narrower molars, more as in *leachii*; a palatal ridge pattern of 4 + 3 + 1 in 44 out of 61 specimens (with the fourth divided in 5 specimens, which could thus be described as 3 + 4 + 1 - but the division is narrow and difficult to interpret as indicative of a change, as the present author has observed), 4 + 3/4 + 1 in 11, 4 + 4/3 + 1 in 5, and 4 + 4 + 1 in 1.

Eisentraut (1960a) observed that some specimens from Gabon averaged somewhat larger than the types of *occidentalis* from Cameroun, while specimens from more western regions (Senegal to Ivory Coast) were somewhat smaller. Koopman (1966) considered *occidentalis* a synonym of *unicolor*, "the oldest name for the west African subspecies", without referring to Eisentraut's observations. Bergmans (1979) studied specimens from Congo which confirmed Eisentraut's findings; as the variation seemed modest and clinal he agreed with Koopman that all populations from Senegal to Cameroun and from there to Angola (i.e. west of 16 E) should be assigned to the same subspecies, *unicolor*.

In the following accounts I have maintained the four subspecies. Where necessary and possible, their diagnoses are completed and amended. The differences between them are slight but obvious and indicate independent lines of development in all four, while their known distribution areas are disjunct.

(Note: Juste *et al.*, 1993 have published two new subspecies of *Rousettus egyptiacus*, from the islands of Principe and São Tomé respectively, in the Zoological Journal of the Linnean Society.)

Rousettus egyptiacus egyptiacus

(É. Geoffroy - St. Hilaire, 1810)

Pteropus Egyptiacus É. Geoffroy- St. Hilaire, 1810: 96 (type locality: the great Pyramid, Lower Egypt - i.e. at Giza).

Rousettus aegyptiacus; Bonhote, 1909: 788; Andersen, 1912: 29; G.M. Allen, 1939a: 62 (in part), 1939b: 234, 282; Ellerman *et al.*, 1951: 92 (in part); Sanborn *et al.*, 1955; Kulzer, 1958: 375, 1960: 240, 1961: 219; Kaisila, 1966; Lehmann, 1966: 258; Storch, 1968; Atallah, 1970; Harrison, 1972: 626; Madkour, 1976; Atallah, 1977: 286; Kumerloev, 1976a: 84, 1976b: 170; Kock *et al.*, 1979: 68; Wassif *et al.*, 1984; Makin, 1989: 405, 1990; Opstaele, 1990: 16; Churcher, 1991.

Rousettus egyptiacus; Flower, 1932: 376; Setzer, 1952: 346; Lewis *et al.*, 1962: 474; Kuhn, 1968.

Rousettus aegyptiacus; Dor, 1947: 50.

Rousettus aegyptiacus aegyptiacus; Ellerman *et al.*, 1953: 46 (in part); Eisentraut, 1960a: 222; Maser, 1966; Hayman *et al.*, 1971: 11; Gaisler *et al.*, 1972: 4; Koopman, 1975: 361; Eisentraut, 1976: 74; Spitzenberger, 1979: 440; Qumsiyeh, 1980: 37, 1985: 13; Qumsiyeh *et al.*, 1986: 140; Korine *et al.*, 1990; Harrison *et al.*, 1991: 24.

Rousettus aegyptiacus aegyptiacus; Hoogstraal, 1962: 145.

Rousettus (Rousettus) aegyptiacus aegyptiacus; Anciaux de Favéaux, 1978a: 460 (in part: the specimens from Egypt); Kock, 1978a: 206.

Material examined

CYPRUS. Apsiou: 1 imm. ♂, 1 ♀, alc., skulls, 30-III-1973, F. Spitzenberger (ZMA 22.124/25). Konkia: 4 specimens, alc., 21-IV-1913, G. Cecconi (ZMB). Some km S of Lachi: 6 ♂♂, 1 ♀, 2 imm. ♀♀, 15/16-V-1985, J. van Wingerde (ZMA 22.902/10). Larnaka: 1 specimen, G. Cecconi (USNM 123303). Nicosia: 3 specimens (BMNH 3.12.4.3/.4, -.6). "Cyprus": 4 specimens (BMNH 79.10.16.5/.6, 99.7.2.1/.2); 1 ♀, 1 imm. ♂, 2 specimens, alc., Rolle (ZMB 10248/51).

(Akrotiri, Ayia Napa, nr Ayioa Epikritos, Bellapais, Episkopi Bay, Famagusta, between Klepini and Pentadactylos, Ktema, Lachi, Paralimni, Polis, Prastiou, between Pyla and Troulli, Trozina, Yermasoyia Reservoir.)

EGYPT. Abu Simbel (temple): 1 specimen, 21-I-1963, L.D. Brongersma (RMNH 17668). Nr Assiut: alc. material (BMNH). Cairo, Abbassia: 1 ♂, 1975, K. Wassif (ZMA 22.162). Cairo, Citadel: 4 ♂♂, 2 imm. ♂♂, 3 ♀♀, 1 imm. ♀, 1 imm., alc., 20-VIII/2-X-1952, H. Hoogstraal (FMNH 80748/58). Cairo, Maade: alc. material (BMNH). Cairo, Mohammed Ali Mosque: 1 ♂, 1 ♀, 3-V-1951, H. Hoogstraal (FMNH 78591/92). Cairo, Sultan Hassan Mosque: 4 ♂♂, 2 imm. ♂♂, 2 ♀♀, 1 imm., 22-VI-1959, H. Hoogstraal (FMNH 90461/62, 12189, 31390/95); 1 ♂, 1 ♀, H. Hoogstraal (FMNH 89707/08); 5 ♂♂, 14 ♀♀, ages not

assessed, 10-VII-1963 (SMF 22643/61); 2 ♂♂, 1 imm. ♂, 3 ♀♀, 1 imm. ♀, alc., skulls of adults, 7-I-1984, A. Walen (ZMA 22.205/11). Cairo: 1 imm. ♂, alc., no skull, 1888, Stuhlmann (ZIZM 22062); 1 ♀, alc., 10-VII-1931 (SMF 12035); 6 specimens, alc., E. Kulzer (SMF 25778/79, 25861/64: captive bred); 3 specimens (BMNH 3.12.8.1, -.3/.4); alc. material (BMNH); 1 specimen (USNM 312121). Cairo region: 1 ♂, alc., 6-VI-1880, Mook (NMW 15203). Damietta: alc. material (BMNH). El Mansuriya: 1 ♀, 1 imm. ♀, alc., 28-V-1951, H. Hoogstraal (FMNH 79163/164). El Walidiya: 3 ♂♂, 2-IV-1957, H. Hoogstraal/M. N. Kaiser (FMNH 87766/68). Gezira Island: 1 specimen (USNM 282381). (El) Giza: 1 ♂, 1 ♀, alc., 27-V-1953, H. Hoogstraal (FMNH 85521/22); 4 specimens (BMNH 9.7.1.1/.4); alc. material (BMNH). Nr Luxor (Kurna and Grand Hotel ruins): 8 ♂♂, 1 ♀, 1 specimen, alc., 21/26-III-1938, H. Nelson (FMNH 47772/81).

Mahallet el Kebir: alc. material, J. Anderson (BMNH). Medinet el Fayum: 1 ♀, alc., skull, 1893, R. H. Brown (ZMA 16.668). "Egypt": 1 ♂, 1829, via museum at Frankfurt (SMNS 3608); 1 ♂, 1851, von Müller (SMNS 426); a small series, 1-VI-1852, Th. von Heuglin (NMW); 3 specimens, alc., Letourneau (MNHN CG 1880-2039/40); 6 specimens (BMNH 39a/f); 1 ♀, alc., 3 skulls, 4 mounted specimens (RMNH); 2 skulls, 2 specimens (1 in alc.), 3 skins (SMF 892/93, 1314, 12232, 12444, -79, -83); 1 ♀, skin, von Sack (ZMB 348); 3 specimens, alc. (ZMB 10252/54).

(Aswan, Burg el Arab, Delta Barrage Gardens, Dumyât, El Aiyat, El Faiyûm, El Karnak, El Minya, El Tell el Kebîr, El Zamalik, Fuah, Ismâiliya, Mataria, Matrûh, Nigm, Port Said, Q'asr, Qina, Thebe, Wâdi el Natrûn.)

ISRAEL. Herzliyya Cave, Mount Carmel: 1 imm. ♀, 9-VI-1968, E. Shor (NMW 13535). Jaffa: 1 imm. ♀, 2 ♂♂, alc., skulls, Aharoni (ZMB 53866/68). Jerusalem: 1 imm. ♂, alc., 5-II-1950, G. Haas (FMNH 75788); 1 ♀, alc., skull, 17-X-1958 (SMF 20526). Mount Carmel: 1 specimen, alc., skull (SMF 18988). Ofer Cave: 16 adult, 3 imm., skulls, mostly incomplete, sex unknown, 22-X-1988, S.G. Sowler (fumigation victims; ZMA 23.911/29). Tabgha: 1 skin, 4-I-1912, E. Schmitz (ZMB). ? Tel Aviv: 2 ♀♀, 1951, E. Sochurek (NMW 8379, 17905). "Palestine": 1 ♂ (ZMB 53869); 1 ♂, 1 imm. ♂, alc., via M. Dor (MNHN CG 1948-500, 1951-1).

(Between Bertovia and Tel-Chai: in owl pellets, Dan, Hayonim cave: Pleistocene remains, Me'arath Hateamim nr Hartuv, Rehobot, Wadi Kurn at Acre.)

JORDAN. Jericho: 1 skin (ZMB).

(Al-Mahhattah, Amman, El Hamma.)

LEBANON. Antilyas: 1 specimen (BMNH 22.7.6.10); 1 imm. ♂, 19-III-1960, J. E. Stencil (FMNH 99555). Beirut River Cave: 1 specimen (BMNH 61.392). Maam el Tien Cave: 1 ♀, 2 imm. ♀♀, 1 imm. ♂, alc., 1955, C.A. Reed (FMNH 84501, -12/13, -16). Mount Lebanon: 1 specimen (BMNH 94.5.7.2).

(Amchîte, Beirut, Beit Meri, Hazmieh, Jahmour, Junieh, Lebanon Cave, Mogharet Saleh, Ras Beirut, Roman

aqueduct 2 km E of Hazmieh, Saida, Tripoli.)
 SYRIA. Zerka River: 1 ♀, alc., skull, 1886 (SMF 11913).
 TURKEY. "Turkey": subfossil remains (BMNH 67.616).
 (Alanya, Antakya, Antalya, Bedirge region, Dermustlu Koy, Gülnar, Harbiye, ? Iskenderun.)

Diagnosis: Generally as for the species, but the least specialized of the subspecies, with on average a large skull, broad rostrum and interorbital region, a sagittal crest in most old specimens, a small angle between mandibular ramus and coronoid process, and strong cheek-teeth.

The following measurement ranges and ratios are from all over the subspecies' range (the specimens of unknown sex are the series from Ofer Cave, Israel):

fal	♂♂	87.1 - 101.4	(n = 37),
	♀♀	86.0 - 100.3	(n = 22);
tibia	♂♂	41.4 - 45.6	(n = 8),
	♀♀	41.1 - 42.6	(n = 6);
ear	♂♂	18.3 - 21.7	(n = 6),
	♀♀	20.0 - 21.4	(n = 4);
gsl	♂♂	43.4 - 46.2	(n = 12),
	♀♀	41.2 - 44.2	(n = 9),
	?	42.0 - 42.7	(n = 2);
rl	♂♂	16.3 - 17.0	(n = 9),
	♀♀	14.8 - 16.6	(n = 6);
iow	♂♂	8.5 - 9.9	(n = 9),
	♀♀	8.0 - 8.6	(n = 6),
	?	7.5 - 8.7	(n = 16);
pow	♂♂	7.7 - 8.6	(n = 9),
	♀♀	7.1 - 8.4	(n = 6),
	?	7.2 - 8.4	(n = 16);
zw	♂♂	26.2 - 29.1	(n = 10),
	♀♀	24.9 - 27.0	(n = 6),
	?	25.4 - 27.2	(n = 13);
C ¹ -M ²	♂♂	17.0 - 18.2	(n = 9),
	♀♀	16.1 - 16.8	(n = 4),
	?	15.9	(n = 1);
C ₁ -M ₃	♂♂	17.2 - 19.7	(n = 7),
	♀♀	17.2 - 18.2	(n = 4);
M ¹ length	♂♂	3.3 - 3.45	(n = 7),
	♀♀	3.1 - 3.45	(n = 6),
	?	3.2 - 3.5	(n = 3);
M ¹ width	♂♂	2.1 - 2.3	(n = 7),
	♀♀	2.0 - 2.15	(n = 6),
	?	2.1 - 2.3	(n = 3);

W	♀♀	112	(n = 1);
rl	♂♂	36.8 - 37.9	ofgsl (n = 7),
	♀♀	35.0 - 37.6	of gsl (n = 6);
C ¹ -C ¹	♂♂	20.4 - 21.3	of gsl (n = 5),
	♀♀	20.6 - 21.5	of gsl (n = 4),
	?	19.2%	of gsl (n = 1);
M ² -M ²	♂♂	28.2 - 30.2%	of gsl (n = 5),
	♀♀	29.3 - 30.8%	of gsl (n = 4),
	?	29.8%	of gsl (n = 1).

Setzer (1952) found smaller skulls (gsl male 41.8, ♀ 39.2) in specimens from Gezira Island, Cairo. Spitzenberger (1979), in her excellent account of a large series from Cyprus, found smaller minimum dimensions in male skulls (e.g. gsl 41.6, iow 7.9, C¹-M² 15.6) and larger size ranges in ♀♀ (gsl 40.4-44.9; iow 7.5-9.0, C¹-M² 15.4 - 16.9); she published a weight range for 66 males of 135-175. Gaisler *et al.* (1972) gave a weight range of 125-170.5 in 8 ♂♂, of 89.5-151 in 3 ♀♀ and 101.5-162 in 3 pregnant ♀♀ - all from Egypt. Especially ♀ specimens from Cyprus appear to average somewhat larger than those from Egypt (fal range, including literature data, 89.0-100.3 against 84-97.0); from other areas the numbers of available adult specimens are insufficient for an assessment of geographical variation.

Distribution: Fig. 1.

Related species: In large parts of its distribution area *Rousettus egyptiacus* is the only representative of its genus and not easily confused with other species. It has no white facial markings or ear tufts, which distinguishes it from all epomophorines. Its possession of an externally distinct tail is shared by three other genera only: *Eidolon* Rafinesque, 1815 with larger dimensions (fal 109.8-133.2, gsl 52.2-58.6), a partly straw-coloured fur (against dull or dark but never bright in *Rousettus egyptiacus*), separated premaxillaries, and a bony auditory meatus; *Myonycteris* Matschie, 1899 with smaller species (fal 54.9-75.1, gsl 30.1-39.2), dense fur, a less deflected brain-case, on average a relatively shorter rostrum, wings from second toe, a dorsally partly or wholly furred tibia, and a band of thick hairs on neck sides and foreneck in males;

Lissonycteris Andersen, 1912, with smaller body measurements (fal 67.8-88.0, gsl 36.6-46.4), long and dense fur, a less deflected brain-case, squarish cheek-teeth, wings from second toe, a dorsally furred tibia, and a band of thick hairs on neck sides and foreneck in males.

In parts of East Africa, *Rousettus lanosus* is sympatric. This species has long fur, dorsally furred tibiae, somewhat smaller average size (fal 85.3-95.0, gsl 39.4-44.8), a strongly deflected brain-case, narrow cheek-teeth and wings usually inserted at the second toe.

In Pakistan *R. egyptiacus arabicus* occurs together with *R. leschenaultii*. They have both been recorded in Karachi but are possibly largely allopatric. *R. leschenaultii* in this region is smaller, on average, and has relatively shorter wings. The differences between the two species have not yet been sufficiently analysed, through lack of material, and the reader is referred to the section on *R. egyptiacus arabicus*, where under Remarks and in tables 4 and 5 available data are given and discussed.

Remarks

Taxonomy: There is a slight but distinct sexual size dimorphism, with ♂♂ averaging larger than ♀♀. Measurement ranges should therefore include either male or ♀♀ values. The fal ranges (87.1-101.4 in ♂♂, 86.0-100.3 in ♀♀) show an extension when compared with the range given by Eisentraut (1960a). The dominant palatal ridge pattern is 4 + 4 + 1 (5 out of 14 specimens) with its derivatives 4 + 3/4 + 1 (5 specimens) and 4 + 4/3 + 1 (1 specimen); other patterns are 4 + 3 + 1 (2 specimens) and 4 + 3/5 + 1 (1 specimen). In the latter specimen there are additional, incomplete 6th and 8th ridges. As for the other characters of this subspecies, Eisentraut's diagnosis (1960a) is apt and sufficient.

Distribution and geographical variation: After its discovery in the Antakya region in southern Turkey in the 1950s, *R. e. egyptiacus* has been recorded from two other Turkish localities. Kinzelbach (1986) saw a stuffed specimen in a shop in Alanya in 1975, which had reportedly been shot near that town.

The owner did not want to sell it and two years later both bat and shop had disappeared. Dr P.J.H. van Bree also observed a stuffed specimen of the same species in a shop in Alanya in 1979 (pers. comm., VII-1979) but unfortunately the shop was closed. Kinzelbach (1986) mentioned an observation of a "gigantic bat, obviously a fruit bat" near Gülnar, in 1986. Dr R. Geldiay, in a letter to Dr van Bree (27-VIII-1979), wrote that the cultivation of fruits like apples, tangerines, oranges and bananas had become common south of the Taurus Mountains, from Hatay westward to Finike (at 30°08' E). This has probably paved the road for *Rousettus* from the Antakya region, although immigration from Cyprus should also be considered a possible source of the species near Alanya. (Dr V. Calandra told the present author about stories referring to gigantic bats which she heard in southern Sicily (pers. comm., 20-VIII-1987). Hufnagl (1972) wrote that "fruit bats have been found on some Mediterranean islands and one even in Mostar, Yugoslavia." He gave no further details.)

Fitzinger (1869: 81) recorded that [Th.] Kotschy discovered the species in Syria. The origin of his material (neither in the NMW, nor located elsewhere yet) or observations is most probably Beirut, or somewhere near it, in present-day Lebanon (Dr F. Spitzenberger, *in lit.*, 17-X-1991). Seabra (1898a) recorded a specimen from Syria in the MLZA collection. Both Matschie (1899) and Andersen (1912) referred to the latter record (and Andersen also to the former), and Kock's contention that they did not refer to material evidence is therefore incorrect (Kock, 1969). Kock himself published a record from Zerka River, Syria, based on specimen SMF 11913 collected there in 1886 by a Dr Schumacher. Later, Kock *et al.* (1979) discovered that this specimen is not from Syria but from Jordan. Jordan has a Zerqua or Zarqa River (Harrison *et al.*, 1991 and Times Atlas, respectively) and the species' occurrence there is perfectly likely. The problem with the Syrian records is their age. The name "Syria" covered a different region then from that which it does now (compare Anderson *et al.*, 1902: 87.) Nevertheless, *Rousettus* may still be discovered in the Mediter-

anean section of present-day Syria (but probably not at the Ouadi Zergane or Zarqua Suyu River in that country, at 40° 22' E, 36° 55' N - my initial identification of Zerka River).

According to Kinzelbach (1986) the species would now also occur in Sinai, following the cultivation of *Ficus* species.

Nader (1975) identified 17 specimens from Tayif, Saudi Arabia, as *R. e. egyptiacus*. However, while the fal ranges in this series (88-95 in 6 ♂♂, 85-93 in 6 ♀♀) overlap with the lower values in the typical subspecies they perfectly fit the ranges known for *arabicus*, and their skull dimensions (gsl 38.8-42.1 in 6 ♂♂ and 38.9-40.5 in 5 ♀♀) demonstrate that they should be referred to that subspecies.

In Egypt, the typical subspecies appears to reach its southern limit in Africa. Kulzer (1958) observed the species at Aswân and Maser (1966) identified Aswân specimens as *R. e. egyptiacus*. Subsequently, Aswân has been considered its southernmost locality (Kock, 1969; Koopman, 1975). A specimen collected on 21-I-1963 at Abu Simbel (RMNH 17668) proves that the species occurs, or has occurred, at least 200 km more to the south. Old references to the species' occurrence in "Nubia" (quoted by Andersen, 1912; Kock, 1969), which were never supported by material evidence, are becoming more plausible with this record. Records from more southern Sudanese localities are treated under *R. e. leachii*.

R. e. egyptiacus appears to be very flexible in its two main ecological requirements: caves for day-roosting and food trees. It has most probably occurred in (parts of) its present distribution area at least from Pleistocene times onwards, as a Pleistocene record from Hayonim Cave, Israel (Bar-Yosef *et al.*, 1966), subfossil remains from Turkey (BMNH) and the c. 4000 years old wall paintings at Beni Hasan, Egypt (G. M. Allen, 1939b, fig. 2) suggest. The species has been quick to exploit man-made cave-like habitats such as chambers in pyramids and temples, mosques, and buildings of lesser stature. And it readily exploits a variety of cultivated exotic fruits. Almost all reports on the typical subspecies refer to these two faculties and hardly ever to its occurrence in particular natural caves or its for-

aging in wild trees. In Lebanon, Lewis *et al.* (1962) observed a preference for the coastal plains and the Lebanon mountains, which they thought to be almost certainly correlated with the availability of food. A largely similar pattern appears to be found in the whole of the East-Mediterranean coastal region, and may develop in southern Turkey as well. In Egypt, the subspecies is restricted to the Nile valley and delta and some few oases. Several authors mention its consumption of *Ficus* species, mostly figs but in one instance also leaves (Anderson *et al.*, 1902; Flower, 1932; Lewis *et al.*, 1962; Atallah, 1977; Kinzelbach, 1986), and Spitzenberger (1979) recorded shoots of *Morus alba* and fruits of *Ceratonia siliqua* as part of the diet. As these tree genera naturally occur in the African Mediterranean and/or West Asian regions, these observations probably relate to the subspecies' customary natural food. A reconstruction of its natural, i.e. prehistorical distribution pattern should certainly start with one of the contemporaneous forests and their composition.

***Rousettus egyptiacus leachii* (Smith, 1829)**

Pteropus Leachii Smith, 1829: 433 (type locality: Cape).

? *Rousettus aegyptiacus*; Senna, 1905: 256; Andersen, 1912: 30 (in part: the specimen from Erythrea).

Rousettus leachii; Andersen, 1912: 25; Lönnberg, 1917: 47; Fitzsimons, 1919: 91; Loveridge, 1923: 692; Flower, 1931: 160; G.M. Allen *et al.*, 193: 45; Friant, 1951; Zuckerman, 1953: 836; Eisentraut, 1958: 18; Kulzer, 1958: 377; Fain, 1959: 4; Theodor, 1968: 321.

Rousettus lanosus kempi (not of Thomas, 1909); Granvik, 1924 9 (at least in part: see text).

Rousettus collaris; Cowles, 1936: 122.

Rousettus leachii; G.M. Allen, 1939a: 62; Moreau *et al.*, 1940: 118; A. Roberts, 1951: 55; Lawrence *et al.*, 1953: 17; Kulzer, 1959: 15; Hoogstraal, 1960: 359; Lombard, 1962; Didier, 1965: 341.

Rousettus (Rousettus) leachi; Schouten, 1944: 102; Leleup, 1956: 75.

Rousettus aegyptiacus leachi; Ellerman *et al.*, 1953: 46; Harrison, 1959: 222; Ansell, 1960b: 8; Eisentraut, 1960a: 230; Kulzer, 1962b: 116; J. D. Jurgens, 1963; Hayman *et al.*, 1966 (in part: not the specimens from Tamba-tamba and Thysville); Koopman, 1966: 155; Ansell, 1967: 2, 28; Verschuren, 1967; Ansell, 1969: 5; Niort, 1970: 256; Hayman *et al.*, 1971: 11; Anciaux de Faveaux, 1972: 82; Dulic *et al.*, 1973: 232; Koopman, 1975: 360; Anciaux de

- Faveaux, 1976; Eisentraut, 1976: 75; Jacobsen *et al.*, 1976; Smithers *et al.*, 1976: 41; Dulic *et al.*, 1977: 232; Ansell, 1978: 18; Fain, 1978: 176; Herzig-Straschil *et al.*, 1978; Smithers *et al.*, 1979: 26; Rautenbach, 1982: 31; Smithers, 1983: 63; Dobat *et al.*, 1985: 297; Happold *et al.*, 1987: 352.
- Rousettus (Rousettus) aegyptiacus*; Leleup, 1956: 75 (in part: the specimens from Kakontwe); Cunningham-van Someren, 1972b: 24; Baeten *et al.*, 1984: 185.
- Rousettus aegyptiacus leachii*; Ansell, 1957: 536; Pakenham, 1984: 26; Ansell *et al.*, 1988: 28.
- Rousettus aegyptiacus*; Griffin *et al.*, 1958; Novick, 1958a: 445; Sweeney, 1959: 7; Lawrence *et al.*, 1963; Rahm *et al.*, 1963: 26; Williams, 1966; Mutere, 1968; Simpson *et al.*, 1968a, b; Spinage, 1968; Cunningham-van Someren, 1972a: 9, 1979; Start, 1972; Mutere, 1973; Kingdon, 1974: 128 (in part); Largen *et al.*, 1974: 228 (in part: not the specimens from 10 km from Agaro and from Ghimbibi); Fenton, 1975; Keegan, 1975; Robinson, 1976: 149; Addy *et al.*, 1978, 1979; Baranga, 1978; D.W. Thomas *et al.*, 1978; Suthers, 1978; van der Westhuyzen, 1978a, b; Whitaker *et al.*, 1978; Keegan, 1979; Mainoya *et al.*, 1979; Rautenbach *et al.*, 1979: 83; Baranga, 1980; Keegan *et al.*, 1980; McWilliam, 1980a: 4, 1980b: 4; Haiduk *et al.*, 1981; Baranga, 1982; Herselman *et al.*, 1985: 81; Hutton, 1986: 227; Koopman, 1986: 10; Bernard, 1988; Bojarski *et al.*, 1988; Braack, 1989; Happold *et al.*, 1989, 1990: 564.
- Epomophorus crypturus* (not of Peters, 1852); Hayman *et al.*, 1966: 23 (in part: the specimen from Pempéré).
- ? *Rousettus aegyptiacus arabicus* (not of Anderson & de Winton, 1902); Hayman *et al.*, 1971: 11.
- Rousettus (Rousettus) aegyptiacus leachi*; Anciaux de Faveaux, 1972: 84, 1978a: 459; Kock, 1978a: 207.
- Rousettus aegyptiacus aegyptiacus*; Dorst *et al.*, 1972 (in part: not the specimens from 10 km from Agaro and from Ghimbibi).
- Rousettus (Lissonycteris) angolensis* (not of Bocage, 1898); Hayman *et al.*, 1966: 30 (in part: specimens from Beni and possibly from Rutshuru); Verschuren, 1980: 6; Kock, 1981 (in part: the record cited from Verschuren, on page 329).
- Rousettus (Rousettus) aegyptiacus leachii*; Kock, 1981: 330; Aggundey *et al.*, 1984: 122.
- Rousettus (Stenonycteris) lanosus kempi* (not of Thomas, 1909); Aggundey *et al.*, 1984: 122 (in part: at least some of the specimens quoted from Granvik, 1924).
- seen), skulls, 2/11-XII-1969, M.J. Largen (BMNH 71.2438/39). Didessa River: 1 ♀, 1 specimen, alc., 1970 (SMF 41830/31). Gambela: 1 ♀, alc., skull, 6-VIII-1972 (SMF 44837). 15 km E of Gambela: 2 imm. ♂♂, 19/20-II-1976, G. Nikolaus (SMNS 29799, 29808). Gojeb River: 1 ♂, alc., skull, 17-VIII-1973, H. Rupp (SMF 45116). Jimma: 1 ♂, alc., skull, 4-VIII-1973 (SMF 44867). Koffolé: 1 ♀, alc., skull, 21-IV-1968 (MNHN CG 1972-481). Lake Abaya, west shore: 1 ♀, 1 imm., 30-IV/7-V-1968 (MNHN CG 1972-480). "Ethiopia": 2 specimens (BMNH 71.2438/39). "Abessinien": ? 1 ♂ embryo, alc., 31-X-1900, Schrader (ZMB 54903).
- (Addi Sciaddi, Arba Minch, Barzata Cave, Bulcha, Didessa, Gololcha, Illubabor Province, Koka, Lake Abiata, Sof Omar.)
- KENYA. Bahati: 9 specimens (AMNH 184437/45). Cha Simba: 4 ♂♂, 3 ♀, skins in alc., skulls, 1980/1981, F. Spitzenberger (NMW; field numbers 369/75). Cherangani Mountains, NE base, at Wei Wei River: 6 ♂♂, 1 imm., ♂, 2 ♀♀, 3 imm. ♀♀, 17/19-IX-1969, K.E. Stager (LACM 36462/73). Diani Forest: 1 fem, alc., skull, 17-IX-1979, W. & E. Bergmans (ZMA 20.895). Gedeh: 1 imm. ♂, 5-V-1973, J.N. Kyongo (LACM 45627). Kibwezi: 1 imm. ♂, alc., 8-XII-1908, Schettler (ZMB). Kitum(u) Cave: 2 ♂♂, 3 imm. ♂♂, 7 ♀♀, 3 imm. ♀♀, skins in alc., skulls, 25-XII-1980, F. Spitzenberger (NMW; field numbers 41/55); 1 ♂, 1 ♀, alc., 3 skulls, 1 skeleton, 1971 (SMF 40640/41, -50/51, -65). Kongelai Escarpment: 1 imm. ♂, 22-VII-1964, J. G. Williams (LACM 51543). Lake Baringo Escarpment: 1 imm. ♂, 2 imm. ♀♀, 14-VII-1964, J. G. Williams (LACM 51540/42). Makandara Forest: 1 imm. ♂, alc., 16-X-1979, W. & E. Bergmans, (ZMA 20.894). Maragot: 1 specimen (USNM 436377). Mida: 1 imm. ♂, 12-V-1973, J.M. Kithia (LACM 45628). Mount Elgon: 2 ♂♂, 29-V-1920, H. Granvik (NRS 125, 129); 3 specimens (as from Elgon Caves) (AMNH 30774/76). Mukanda River, bridge Mukanda 2: 1 ♂, 1 ♀, alc., skulls, 26-II-1982, A. Walen (ZMA 21.698/99). Ngong Hills, below Westwood Park Hotel: 1 ♂, alc., skull, 18-I-1982, A. Walen (ZMA 21.697). Shimoni Cave: 1 ♂, 1 ♀, 1 imm., alc., 16-V-1971 (SMF 40637/39). Sokoke Forest: 1 ♂, 4 ♀♀, alc., skulls of 4, 10/11-X-1979, W. & E. Bergmans (ZMA 20.889/93). Subukia: 1 ♂, 2 imm. ♂♂, 3 ♀♀, 1 imm. ♀, alc., 24-VIII-1956, H. Hoogstraal/M. N. Kaiser (FMNH 86514/20). Tiwi Beach: 1 ♀, alc., 19-X-1979, W. & E. Bergmans (ZMA 20.896). Ukunda: 1 imm. ♀, 26-X-1970, Kyongo (LACM 37783). Vipingo Cave: 1 specimen (USNM 350795); (as from 22 miles N of Mombasa) 1 ♀, alc., skull, 12-VIII-1965, A. Starret (LACM). Watamu: 7 ♀♀, alc., skulls of 6, 2/7-X-1979, W. & E. Bergmans (ZMA 20.882/88). "Kenya": 1 imm., alc., Babault (MNHN).
- (Nr Amboseli, Baringo, Chyulu Hills, (01) Donyo Sabuk, nr Gononi, Kakamega, Kampi ya Samaki, Karen, nr Kargi, nr Kilaguni, Lake Baringo, nr Magutuni, nr Mara River, c. 30 miles N of Mida, Nairobi, nr Naivasha, Nakuru, Narok, Ngombeni, Saboti, nr Samburu, nr Sigor, Uaso Nyiro River Bridge.)

Material examined

BURUNDI. Bujumbura: 1 ♂, alc., VIII-1976, J. Verschuren (IRSN 19903).

(Gihanga, Kayanza, Nyanza-Lac, Resha, Rumonge.)

ETHIOPIA. Baro: 1 ♀, alc., 15-II-1976, G. Nikolaus (SMNS 29798). Bulcha Forest: 1 ♀, 1 imm. ♂, alc. (not

MAFIA. Kua, Juani Islet: 2 specimens (BMNH 64.1313/14).

MALAWI. Lengwe National Park: 1 ♂, 2 ♀♀, 1 imm. ♀, VI/VII-1988, N. J. van Strien (collection N. J. van Strien; field numbers 198/99, 203/04).

(Likabula River, Mlolo, Nchalo, Ngabu, 1535D, 1635A, 1635B.)

MOZAMBIQUE.

(Chimezi, Inhambane, Revue-Boze River Junction, 1832B, 1832D, 1833C, 2033A, 2335C.)

PEMBA. Fundo Island: alc. material (BMNH). Maziwanguombe: alc. material (BMNH).

(Micheweni, Msuka.)

RWANDA. Gisenyi: 1 ♂, 3 imm. ♂♂, 2 imm. ♀♀, 15-VII and 13-X-1980, alc., skulls, H.H. de Iongh (ZMA 21.243/47, 21.364). Ruhengeri: 1 ♂, 1 ♀, 8-VI-1966, M. Anciaux de Faveaux (IRSN 15485); 1 ♂, 1 imm. ♂, 4 ♀♀, 2 imm. ♀♀, alc., skulls, 15-X-1980, H.H. de Iongh (ZMA 21.248/55).

(Bugurama, Kibuye, Kitabi, Nyamata, Nyundo, Rukira, Tamira, Uwinka.)

SOUTH AFRICA. Amanzimtoti: 1 ♂, alc., skull, 3-VIII-1979, S. Sowler (ZMA 21.155). Bat's Cave: 2 ♂♂, 1 ♀, 1 imm. ♀, alc., skulls of 2, 26-IV-1979, P. Swanepoel & L.R. Wingate (ZMA 20.708/11). Cape (of Good Hope): 2 skins, skull of 1, 1835 and 1837 (SMF 12430, -32); 1 specimen (BMNH 43.12.7.21); 6 mounted specimens, 1 in alc., 1 skeleton and skull, 4 skulls (RMNH); 1 ♂, skin, skull in situ, 1 imm., 1837, von Ludwig (SMNS 5, 4002); 1 ♂, 1 ♀, 1 specimen, skulls, 1 imm. ♂, alc., Mundt (ZMB 350/51, AM782, 2553). Cape Town: 6 specimens (BMNH 37.4.28.33/.34, -.38, -.40, -.67, 75.8.9.1). Knysna: 8 specimens (BMNH 5.5.7.5/.12). Matlapitsi Cave: 4 ♂♂, 1 imm. ♂, 4 ♀♀, 1 imm. ♀, alc., skulls of 4, 4-VIII-1979, B. Fratcher (ZMA 21.015/19, -59/63). Pirie Forest: 1 specimen (AMNH 146781). Stellenbosch Flats: 2 specimens, 10-XI-1951 (SMF 11349/50). Tafelberg: 8 specimens, alc., 1961 (SMF 22015/22).

(Amabele, Barberton, Bean-se-bos, Bedford, Bloukrans River area, Die Hel, Durban, East London, Grahamstown, Helderberg, Ismont Crevasse, Keurbooms Reserve, King William's Town, Krakeel River, Langkloof, Lanner Gorge Cave, Letsitele, Levuvhu Hippo Pool, Malta Farm, Mganduli, Nahoon Point, Natal, Pafuri, Patensie, Pirie, ca 55 km NNE of Port Elizabeth, Port Shepstone, Robertson, Simuwana's Rangers Post, Skeleton Cave, Stellenbosch, St. Lucia, nr mouth of Storm River, Swartberg, Swellendam, The Downs, Twee Riviere, Uzumbe River valley, Winterhoek Mountains, Wynberg.)

SUDAN. Imatong Mountains: 1 ♂, alc., 31-XII-1952, J.S. Owen (FMNH 81546). Jebel Goumia: 1 ♂, 11 ♀♀, alc., skulls of 2, 31-XII-1952, J.S. Owen (FMNH 74154/62, -64/66). ? Khartoum: 1 ♂, skin, skull *in situ*, 1857, F. Kolenati (SMNS 674). Talanga Forest: 1 ♀, alc., 1-VII-1978, G. Nikolaus (SMNS 29805).

(Bejudah-Steppe, Gilo, Lokwi, district of Sennar, White

Nile.)

TANZANIA. Bukoba: 1 ♂, 1 ♀, skulls, Ermin Pascha (ZMB 10233/34). Bwanga-Bukoba: 1 imm. ♂, 1 imm. ♀, 4 specimens, alc., skull of 1, A.F. zu Mecklenburg (ZMB 54199/200). Kibata: 1 ♂, 1 ♀, alc., 30-I-1912, Bickel (SMNS 2874/75). Kulumuzi Caves: 1 imm., alc., VI-1905, Y. Sjöstedt (MNHN CG 1913-22); 2 imm., alc., 11-VI-1909, M. Allnaud (MNHN CG 1911-726), and 4 imm., alc., same data (MNHN, not reg'd). Makoa: 5 ♀♀, 5 imm. ♀♀, 20/21-I-1952, G. Zink (SMNS 4151/60). Pangani: 1 imm. ♀, Gerrard (ZMB). Siga Caves: 1 imm. ♀, 2 imm., skull of 1, 1 specimen, alc., II-1893 (or '95), O. Neumann (ZMB 10226, -28, -31). (Nr) Tanga: 2 ♂♂, 2 ♀♀, Gierra (MNHN CG 1895-390/93); 1 ♂, 1 imm. ♀, alc., Martienssen (ZMB 10128, -30); 1 imm. ♀, alc., skull, 12-VII-1907, Y. Sjöstedt (ZMB 54369).

(Bagilo, nr Bugomara, Dar-es-Salaam, Kiziba, nr Kwa Kuchinia, nr Minziro, nr Morogoro, Moshi, nr Ndutu, nr Oldeani, southern part of Ruana National Park.)

UGANDA. Bundimusuba: 1 ♂, 26-XI-1968, R. Glen (LACM 51539). Bwamba Forest: 1 ♂, XI-1957, "WVZ" (LACM 31780). Kibale Forest: 1 ♂, 3-XII-1966, R. Glen & A. Williams (LACM 51512). Lake Nabugabo: 2 specimens (BMNH 34.6.2.2/.3). Mount Elgon: 6 specimens (BMNH 10.4.1.8, 24.6.10.1, 25.10.19.1, -.3/.5). Ntandi: 1 ♂, 1 ♀, 1 specimen, 14-VI-1967, 29-X- and 15-XI-1968, R. Glen/A. Williams (LACM 51513/14, -38). Ruhizha area: 1 ♀, 11-III-1967, A. C. Archer (LACM 51544).

(Bukakata, Bulago, nr Bushenyi, Busüga, nr Buwayo, Entebbe, Entebbe Peninsula, Fort Portal, nr Ibanda, Impenetrable Forest, nr Jinja, nr Kampala, nr Kanungu, Kasokera, nr Kisoro, Kyema, nr Kyenjojo, Maramagambo Forest, Masaka, Masaka District, nr Masindi, nr Mbale, nr Munteme, nr Murchison Falls, nr Oboia, Ruwenzori Mountains, Sipi, nr Toro, nr Tororo, Zika.)

ZAIRE. Butembo region: 1 ♀, 31-VII-1947, J. Hiernaux (IRSN 7054). Jadotville: 2 ♂♂, alc., 6/18-XII-1959, M. Anciaux de Faveaux (IRSN 14600/01). Jolohafiri: 1 ♀, skull, 30-VII-1947, J. Hiernaux (IRSN 7063). Kadjuju: 1 imm., alc., 10-VII-1933, G. Babault (MNHN). Kakonda: 1 ♂ (AMNH 118865). Kakondo: 1 ♂, 1 imm. ♂, alc., 1 ♀, 1 imm., skulls, XII-1946, F. Hendricks (IRSN 13114, 13283/84); 1 ♀, 1 specimen (AMNH 180897/98). Kasua: alc. material (BMNH). Katana: 7 ♂♂, 1 ♀, 1 imm. ♀, 1956, J. Laarman (RMNH 16347/55), 1 ♂, J. Laarman (RMNH 16401); 1 specimen, alc., skull, 30-V-1963 (SMF 31823); 1 specimen (AMNH 180901). Kivu: 1 ♂, 1 imm. ♂, 24-XII-1946, F. Hendricks (IRSN 12932/33); 1 specimen, alc., 19-VII-1964 (SMF 31824). Kyniamahura: 1 imm. ♂, 1 ♀, alc., 7-V-1938, S. Frenchkop (IRSN 4784/85). Lwiro: 2 specimens, alc., skulls, 2-VI-1964 and 22-VI-1965 (SMF 31821/22); 2 specimens, alc., 1965, P. Kunkel (SMF 25859/60); 1 specimen (USNM 301694). Mahyusa Cave: 2 specimens (BMNH 58.647/48). Mayna-Moto stream: 1 ♂, 22-VIII-1949, J. de Wilde (IRSN 12930). Mont Hoyo: 1 ♂, alc., 2 imm. ♂♂, 2 ♀♀, 1 imm. ♀, 12-VIII-1947, J.

Hiernaux (IRSN 7057/61, 7474). Mutsora: 1 ♂, 27-IX-1949, J. de Wilde (IRSN 12931). Nyamabere: 3 ♀♀, 7-I-1947, G. van Cools (IRSN 12871/73). Ruvara: 1 imm. ♂, 2-IV-1950, J. de Wilde (IRSN 12929). (Beni, Bushushu, Butembo, Djemba, Eaux Chaudes at Katana, Kakontwe, Kalimabenge, Kalomoni, Kasyo, Kilo-Mines, Mufunga, Mugaba, Mulungu region, Murambi, Nyambasha, Parc National Albert, Pempéré, Cave of Pempéré, Rumoka, Rutshuru.) ZAMBIA. Chipangwe Cave: 1 imm. ♀, 24-IX-1967, W. Sheppe (CAS 15101); 1 ♀, 1-IX-1971, T. Osborne (CAS 16162). Mfuwe: 1 specimen (BMNH 68.111). (Chilanga, Leopard's Hill Cave, Lusaka, Mfuwe Game Camp, Mkwisi, Reitfontein, 1528B3, 1528C1, 1528C2, 1528D1.) ZANZIBAR. Zanzibar: 1 ♂, alc., skull, 7-X-1895 (ZMB). ZIMBABWE. (Chikupa Cave area, Chikwarakwara, Haroni/Lusitu Rivers confluence, Hostes Nicolle Institute for Wildlife Research, Inyanga, Mutema Sabi River, Retreat Farm.)

Diagnosis: Generally as for the species. If compared to the typical subspecies, skull less strongly built and on average slightly smaller, rostrum laterally compressed and dorsally more strongly tapering towards the distal end, premaxillae more slender and usually not co-ossified, interorbital width averaging slightly smaller and postorbital width somewhat larger, sagittal crest lacking or at most very low, mandibular ramus lower and its angle with the coronoid process larger, coronoid process narrower and shorter, angular process not projecting backwards, and cheek-teeth narrower - except first premolars. The following measurement ranges and ratios are from all over the subspecies' range:

fa	♂♂	87.2 - 106.3	(n = 51),
	♀♀	85.7 - 101.3	(n = 71);
tibia	♂♂	42.2 - 44.6	(n = 7),
	♀♀	38.1 - 45.7	(n = 22);
ear	♂♂	19.3 - 21.4	(n = 8),
	♀♀	19.4 - 21.9	(n = 22);
gsl	♂♂	42.1 - 45.7	(n = 36),
	♀♀	38.3 - 43.9	(n = 43);
rl	♂♂	15.4 - 17.4	(n = 32),
	♀♀	14.6 - 16.6	(n = 36);
iow	♂♂	7.6 - 9.1	(n = 34),
	♀♀	7.4 - 9.0	(n = 37);
pow	♂♂	7.6 - 9.4	(n = 34),

zw	♀♀	7.7 - 10.3	(n = 37);
	♂♂	24.2 - 28.9	(n = 33),
C ¹ -M ²	♀♀	24.0 - 27.3	(n = 38);
	♂♂	15.2 - 17.3	(n = 35),
C ₁ -M ₃	♀♀	14.4 - 17.1	(n = 40);
	♂♂	17.1 - 19.2	(n = 29),
M ¹ length	♀♀	16.7 - 18.7	(n = 33);
	♂♂	2.75 - 3.1	(n = 22),
M ¹ width	♀♀	2.6 - 3.3	(n = 18);
	♂♂	1.6 - 2.2	(n = 22),
W	♀♀	1.6 - 2.2	(n = 18);
	♂♂	111 - 166	(n = 23),
rl	♀♀	100 - 155	(n = 19),
	♂♂	35.6 - 38.9% of gsl	(n = 32),
C ¹ -C ¹	♀♀	35.7 - 38.8% of gsl	(n = 36);
	♂♂	19.7 - 22.3% of gsl	(n = 23),
M ² -M ²	♀♀	18.9 - 21.5% of gsl	(n = 34);
	♂♂	27.9 - 31.9% of gsl	(n = 30),
	♀♀	28.1 - 32.9% of gsl	(n = 32).

Koopman (1975) gave 90 as minimum fal in Sudanese ♂♂ and 91 as minimum in ♀♀ from that country. Rautenbach (1982) gave fal ranges of 84-100 in 5 males and 92-98 in 5 ♀♀ from the Transvaal in South Africa. There appears to be some slight variation in average size, with smaller dimensions in southern Africa, in the Tanzanian and Kenyan Coastal regions and in Ethiopia, and somewhat larger sized specimens around the central Rift Valley from eastern Zaïre to western Kenya and northeast Tanzania. The largest specimen on record is a ♂ from Bujumbura in Burundi, with a fal of 106.3. For a breakdown of measurements per country see table 1.

Measurements: Table 1.

Distribution: Fig. 2.

Related species: See the account of the typical subspecies.

Remarks

Taxonomy: The diagnostic trends, a weaker skull and weaker dentition than in the typical subspecies, apply to all populations of *leachii* and therewith justify its separation as a subspecies, but there is quite some variation within *leachii*

Table 1. Ranges of selected measurements of *Rousettus aegyptiacus leachii* (Smith, 1829) per country.

		fal	tibia	ear	gsl	rl	iow	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ₁ - M ₃	M ¹ length	W width
Burundi	♂♂ n	1													
		106.3													
Ethiopia	♀♀ n	3		1											1
	mean	92.5													
	min	92.0		22											130
	max	92.8													
Kenya	♂♂ n	18	1	1	15	13	15	15	13	13	13	13	11	5	5
	mean	94.6			42.8	16.1	8.5	8.7	26.0	8.9	12.9	16.5	18.2	2.9	1.8
	min	87.2	44.6	20.1	40.1	15.4	7.6	7.6	24.2	8.5	12.3	15.7	17.1	2.7	1.6
	max	99.7			44.0	17.1	9.0	9.5	27.0	9.8	13.6	17.3	19.2	3.0	2.0
	♀♀ n	28	13	13	18	18	19	19	17	19	18	18	18	8	8
	mean	94.4	43.7	20.4	42.2	15.0	8.2	8.7	25.2	8.5	12.6	16.2	17.7	2.95	1.9
	min	87.8	41.3	19.4	41.0	14.9	7.5	7.7	24.2	7.9	12.1	15.3	16.7	2.8	1.8
	max	98.5	47.7	21.9	43.9	16.9	8.9	10.3	26.4	8.8	13.3	17.0	18.4	3.3	2.2
Malawi	♂♂ n	1			1	1	1	1	1	1	1	1	1	1	1
		96.1			43.0	16.0	8.2	7.7	26.4	9.0	13.1	16.5	18.1	2.95	1.9
	♀♀ n	2			2	2	2	2	2	2	1	1	1	1	1
	min	91.4			41.8	15.4	8.0	8.3	26.0	8.6	13.2	16.0	17.7	3.05	1.9
	max	95.1			42.7	15.7	8.2	8.4	26.2	9.2					
Rwanda	♂♂ n	3	2	2	2	2	2	2	2	2	2	2	2	5	5
	mean	95.3												3.0	2.0
	min	92.8	42.6	20.8	43.1	16.4	8.2	9.0	25.5	8.7	12.9	16.1	17.6	2.9	1.9
	max	96.9	42.7	21.4	44.4	16.7	8.2	9.2	27.1	8.8	13.6	17.1	18.7	3.1	2.1
	♀♀ n	5	4	4	4	4	4	4	4	4	4	4	4	6	6
	mean	97.2	42.9	20.9	41.5	15.1	8.0	8.8	25.6	8.5	12.9	16.1	17.7	2.95	2.05
	min	95.0	41.4	20.2	40.9	14.6	7.5	8.5	24.3	8.3	12.5	15.7	16.9	2.8	2.0
	max	99.9	44.3	21.9	41.9	15.5	8.5	9.2	26.7	8.8	13.6	17.1	18.7	3.1	2.1
South Africa	♂♂ n	7	4	5	4	4	4	4	3	3	3	4	3	2	2
	mean	95.7	44.5	20.5	43.6	16.45	8.5	8.75	26.9	8.9	13.2	16.7	18.6		
	min	93.4	42.2	19.3	42.6	16.0	7.8	8.2	26.3	8.6	12.5	16.3	18.3	3.0	2.0
	max	97.6	42.9	21.0	44.3	17.0	9.1	9.2	27.5	9.2	14.0	17.2	19.0	3.1	2.2
	♀♀ n	5	4	4	4	3	3	3	2	2	2	3	2	2	2
	mean	89.9	39.4	20.25	42.0	15.55	8.2	8.6				16.0			
	min	85.5	38.1	19.7	41.3	15.4	8.0	8.3	25.0	8.0	12.3	15.9	17.4	2.9	1.6
	max	94.1	41.0	21.4	42.3	15.8	8.4	9.0	25.7	8.0	12.4	16.2	17.7	2.95	2.0
Sudan	♂♂ n	2													
	min	96.0													
	max	100.0													
	♀♀ n	11													
	mean	96.7													
	min	93.8													
	max	99.9													

Table 1, continued.

		fal	tibia	ear	gsl	rl	iow	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ₁ - M ₃	M ¹ length	W width
Tanza- nia	♂♂ n	3							1			1			
	mean	93.9							27.2			15.7			
	min	91.7													
	max	97.8													
	♀♀ n	7			5	5	5	5	6	5	4	5	4		
	mean	94.0			42.0	15.9	8.1	8.7	24.9	8.4	12.4	15.6	17.7		
	min	90.5			40.2	15.2	7.6	8.3	24.0	8.1	12.2	14.4	17.2		
	max	97.7			42.9	16.6	8.5	9.5	25.6	8.8	12.6	16.7	18.3		
Uganda	♂♂ n	4			4	4	4	4	4	4	4	4			
	mean	96.4			43.1	16.0	8.75	8.55	27.1	9.05	13.0	16.7	18.1		2
	min	93.7			42.4	15.6	8.3	7.6	25.4	8.6	12.3	15.9	17.5		
	max	99.3			43.9	16.4	9.0	9.4	28.0	9.5	13.5	17.3	18.6		111
	♀♀ n	2			2	2	2	2	2	2	2	2			135
	min	95.1			42.5	15.3	8.2	9.1	25.8	8.2	12.9	15.8	17.5		1
	max	95.6			42.7	15.7	9.0	9.3	26.3	8.9	13.0	16.3	17.5		125
Zaire east of 26°C	♂♂ n	11			10	8	8	8	9		7	10	8	8	8
	mean	96.4			43.6	16.5	8.5	8.1	27.7		13.0	16.2	18.1	3.0	1.9
	min	92.1			42.3	15.9	8.2	7.6	25.5		12.2	15.2	17.2	2.8	1.7
	max	100.6			45.7	17.4	8.9	8.4	29.2		13.6	16.8	19.0	3.1	2.0
	♀♀ n	7			4	2	2	2	4	1	2	6	2	1	1
	mean	96.8			42.6				26.5			15.9			
	min	93.4			41.9	15.4	7.4	8.3	25.4	8.2	12.1	15.3	17.0	2.6	1.8
	max	101.3			43.1	15.8	8.0	9.0	27.3		12.7	16.5	17.7		
Zambia	♀♀ n	1			1				1			1			
		85.7			41.3				24.4			16.4			
Zanzibar	♂♂ n	1													
		95.3													

which would be worth an analysis when larger series from the various regions of its distribution area have become available. To Eisentraut's (1960a) differential diagnosis of *leachii* as summarized in the species' account the following observations might be added. As ♂♂ average larger than ♀♀ in fal and nearly all skull dimensions, the sexes should be treated separately in taxonomic accounts. It may be advisable furthermore to not compare the dimensions of *leachii* as a whole to those of *egyptiacus*; as a whole, *leachii* averages smaller, but the mentioned maximum fal is larger than the maximum in *egyptiacus*. The premaxil-

laries in *leachii* (not mentioned by Eisentraut, 1960a) are usually not co-ossified: they are in 1 out of 32 ZMA skulls, in 12 they are not, in 12 they are probably not (the observation being hampered by the *in situ* dried soft palate) and in 7 it could not be assessed (for the same reason). Proportionally, rl in *leachii* (35.6-38.9% of gsl) is not visibly longer than in *egyptiacus* (35.0-37.9%), while the widths over C¹-C¹ and M²-M² are also inappropriate to quantify the slenderness of the rostrum in *leachii*. But dorsal to the level of the palate it is more compressed and in lateral profile it tapers towards the front more strongly. The

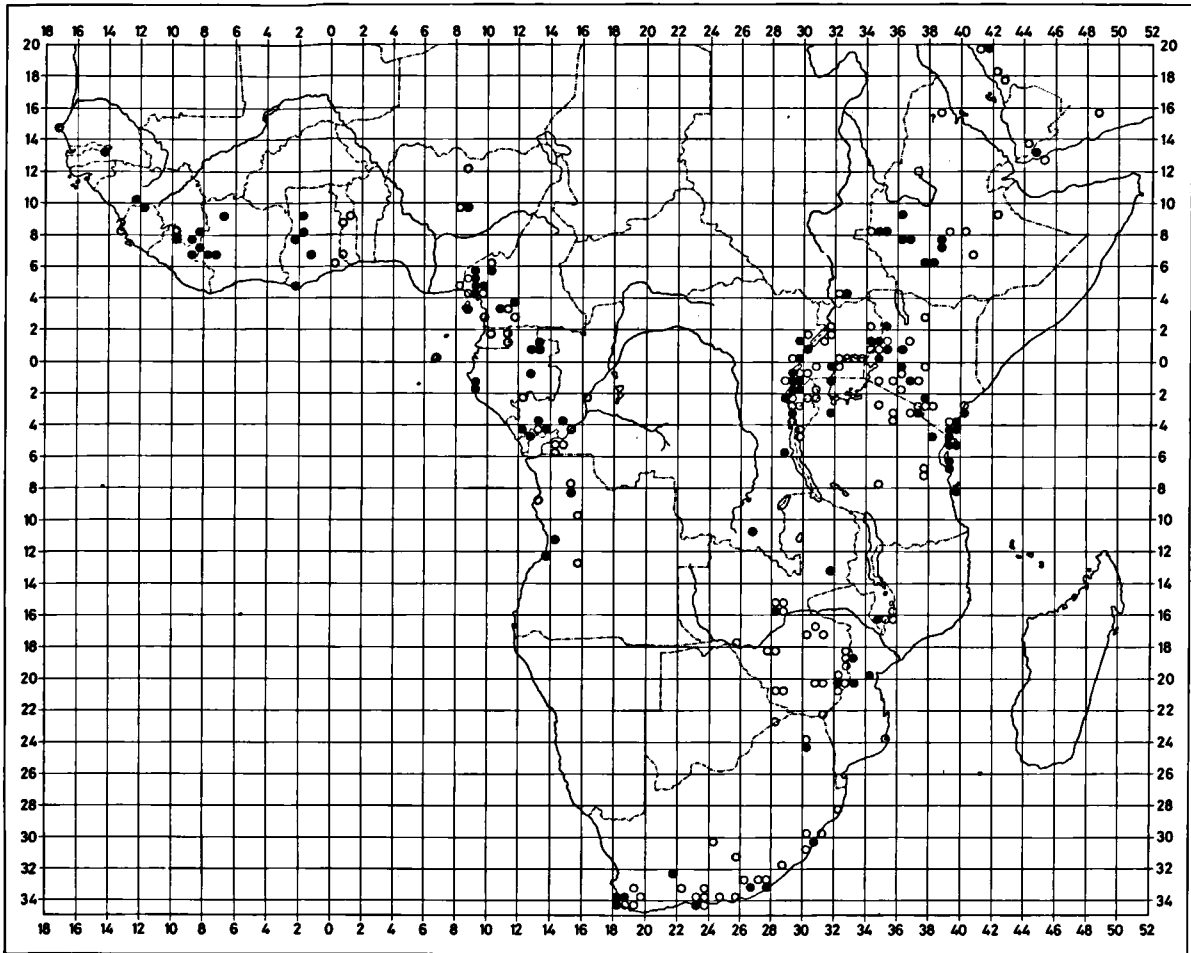


Fig. 2. Distribution of *Rousettus egyptiacus* (É. Geoffroy-St. Hilaire, 1810): West of 17° E, *R. e. unicolor* (Gray, 1870); east of 17° E, except the Arabian Peninsula, *R. e. leachii* (Smith, 1829) (specimens from eastern Ethiopia with reservation; see the Remarks). Black dots: squares from which material has been identified by the author. Open circles: records from literature, museum registers, and correspondence.

larger angle between mandibular ramus and coronoid process is related to a larger deflection of the posterior part of the mandibulum as such (and this to the measure of brain-case deflection), resulting also in the orientation of the angular process being downward rather than backward. The dominant palatal ridge pattern is 4 + 3 + 1 (25 out of 34 specimens), which confirms Andersen's observations (1912). In 6 specimens it is 3 + 4 + 1, in 2 it is 4 + 3/4 + 1, and in 1 it is 4 + 3/5 + 1 (with parts of additional ridges behind the normal 5th and 6th).

Distribution and geographical variation: There are some doubtful reports

on the occurrence of *R. egyptiacus* from in between the established distribution areas of the subspecies *egyptiacus* and *leachii*. Kock (1969) cited Dr R. Hartmann who travelled in Sudan in 1859-1860 and mentioned Nubia, the Baiyuda Desert (as "Bejudah-Steppe") and the Sennar region as parts of the distribution area. According to Kock these reports are not based on observations by Hartmann himself and cannot be trusted. The discovery of the species at Abu Simbel (see the account of the typical subspecies) however, lends some support to its alleged presence in Nubia; presently, western and central Nubia are Absolute Desert (type 67 in White, 1983) and there

are virtually no oases, but there is the Nile. Its borders here are irrigated and used for various cultures and should offer opportunities for dispersal, provided that appropriate roosting places are available in sufficient frequency. The Baiyuda Desert may be a similar case. Then there is a specimen in the SMNS, collected in 1857 by F. Kolenati and doubtfully labelled Khartoum. It is a stuffed skin with the skull *in situ* and thus as yet of unknown subspecific identity. (I have not mapped it.) The only fruit bat known with certainty from Khartoum is *Eidolon helvum helvum* (Kerr, 1792), a species apparently able to penetrate here from the south. This suggests that if *R. egyptiacus* occurs here, *R. e. leachii* may be the more likely candidate. This assumption receives some further support from the palaeobotanical study by Wickens (1982), who collected evidence for a wet and warm early to middle Holocene in central Sudan, and for a drier climate from about middle Holocene times onwards, with a progressive shift southwards of the rainfall, vegetation and faunal zones. From Sennar, both *Eidolon helvum* and *Epomophorus labiatus* (Temminck, 1837) are known. The nearest known *R. egyptiacus* locality is Didessa in western Ethiopia, connected with Sennar by the Didessa River and the Blue Nile.

In 1900, a specimen of *R. egyptiacus* was collected at Addi Sciaddi, east of Keren, in northern Eritrea (Senna, 1905). It may still exist, possibly in the Museo di Napoli. Addi Sciaddi is associated with the western part of the Ethiopian plateau, where *leachii* is widespread in the south, and on the map the specimen is provisionally included in that subspecies.

Hayman *et al.* (1971) reported on an AMNH specimen of *R. egyptiacus* from Harar in eastern Ethiopia which Dr K. F. Koopman had referred to *R. e. arabicus*. Largen *et al.* (1974) listed a number of Ethiopian specimens as *R. e. leachii* and a number as *R. e. ssp.*, and wrote that the former is found in the west and *R. e. arabicus* in the east of Ethiopia but that the geographical limits had yet to be determined, a subject then under review by Dr J. E. Hill. (Their inclusion in *leachii* of a specimen from Gololcha must be erroneous.) Some BMNH labels show that Dr Hill did reinvestigate

Ethiopian *R. egyptiacus*: spirit specimens from Bulcha Forest, Didessa River (at 36°09' E, 09°02' N) and Lake Abiata have been referred to *arabicus*, one from Arba Minch has remained without subspecific name. Didessa River is in the west of the country, while Lake Abiata and Bulcha Forest are in the Central Rift - as is Arba Minch. However, only a few skulls could be examined: a ♀ and an immature ♂ from Bulcha Forest (BMNH 71.2438/39), and the results are preliminary. The skulls have been re-examined for the present study. The ♀♀ has a gsl of 38.3, which is small if compared with 'normal' *leachii* ♀♀ (gsl range 40.2-43.9), and the subadult ♂ has a gsl of 38.4. The teeth of these specimens, however, are not larger than in Kenyan specimens from Mount Elgon and Baringo in the BMNH collection. Although in these small skulls the teeth are relatively large, resulting in an *arabicus*-like configuration, my present understanding is that the affinity of these specimens is with *leachii* rather than *arabicus*. A further analysis, which depends on the availability of skull material, may yet reveal that the Central Rift divides western large-skulled *leachii* from eastern small-skulled *arabicus*, in which case the skulls examined would probably represent intergrades and more typical *arabicus* should be found in more eastern localities. But if lower average skull dimensions turn out to be the main difference, inclusion in *leachii* would possibly be more appropriate.

Specimens from the Kenyan coastal region (ZMA specimens from Diani Forest, Makandara Forest, Mukanda River, Sokoke Forest, Tiwi Beach and Watamu) are essentially like those from the South African coastal region (ZMA specimens from Bat's Cave and Amanzimtoti). In this light, Eisentraut's (1960a) use of specimens from northeast Tanzania for his diagnosis of *leachii* is quite legitimate. However, specimens from the western Rift Valley (ZMA specimens from Gisenyi and Ruhengeri in Rwanda) and the Kenyan highlands (ZMA specimen from the Ngong Hills) differ from East and South African coastal specimens in having slightly smaller average teeth dimensions. Canines are laterally more flattened, upper molars and premolars are narrower and shorter (except P¹ and, in part of the

specimens, P³ and M²), P₁ is larger but other lower premolars and molars are narrower and shorter, especially M₂. These differences are worthy of checking on a larger material. They appear to reflect the west-east division in Ethiopia discussed above, although eastern Ethiopian populations are highland populations themselves, and are not known to be connected with coastal ones.

The distribution of *leachii* appears to be determined by the presence of suitable caves for roosting rather than by vegetation types. Nearly all collecting localities are in or near areas with considerable relief, such as mountains, rocks and cliff coasts, and many specimens have been taken directly from caves. There are few records from the mountainous parts of central and southwest Tanzania, northern Zambia and Malawi, and none from northwest Mozambique, where *leachii* may be expected to occur. To my knowledge, *leachii* has not yet been found to exploit man-made structures but it certainly forages on cultivated tree fruits and to that end invades villages and towns. It is known to bridge considerable distances between roosts and foraging areas (D. W. Thomas *et al.*, 1978; McWilliam, 1980b). Out of 221 traceable collecting localities only 4 are in true forest: Drier types of Guineo-Congolian rain forest (type 2 in White, 1983) and 6 in Mangrove (type 77 in White, 1983); 93 are in forest transitions and mosaics, notably 52 localities in Undifferentiated Afromontane vegetation (type 19a in White, 1983), 21 in East African coastal mosaic and 20 in Mosaic of Guineo-Congolian rain forest and secondary grassland (types 16 and 11 in White, 1983), with another 31 localities on the borders of types 11, 16 or 19 with one of the other types to be mentioned below. In the southern parts of its distribution, *leachii* has been found in nearly all types of woodland (altogether 34 localities; types 25-29b/d in White, 1983); bushland and thicket (18 localities; some in types 38 and 39 but 14 in type 42 in White, 1983: Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket); Mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland (14 localities; type 45 in White, 1983); Cape shrubland (11 localities; type 50 in

White, 1983); and very few in other types or on borders between two of the types mentioned.

R. e. leachii has been collected from sea level up to more than 2500 m: Koffolé, Ethiopia, 2500 m; Saboti, Kenya, 1950 m; Uwinka, Rwanda, 2512 m; Jebel Goumia, Sudan, 1980 m; Ruhizha area, Uganda, 2070-2440 m; Mugaba, Zaïre, 2200 m.

Note: Granvik (1924) published on a series of 23 specimens from a cave at 2440 m on the Kenyan side of Mount Elgon, which he had identified as *Rousettus lanosus kempi* Thomas, 1909. By courtesy of Dr K. Edelstam I have been enabled to examine two specimens of this series and found them to represent *R. e. leachii*. As *R. lanosus* is known from Mount Elgon, it is just possible that the series contains both species.

***Rousettus aegyptiacus unicolor* (Gray, 1870)**

Eleutherura unicolor Gray, 1870: 117 (type locality: Gaboon).

Rousettus aegyptiacus; Andersen, 1912: 29 (in part: the specimens from Angola and Gaboon); Cabrera, 1929: 13; Sanborn, 1936: 107; G. M. Allen, 1939a: 62 (in part); Sanderson, 1940: 666; Hill *et al.*, 1941: 29; Malbrant *et al.*, 1949: 84; Ellerman *et al.*, 1951: 92 (in part); Aellen, 1952: 26; Booth, 1959: 29; Strinati, 1960; Brosset, 1966c: 88, 1966d: 169; J.-P. Adam *et al.*, 1967: 220; van Orshoven *et al.*, 1968: 179; Jones, 1971: 125; Kock, 1973; Marshall *et al.*, 1982: 56; Emmons *et al.*, 1983; Dowsett *et al.*, 1991: 255.

Rousettus aegyptiacus; Mendez, 1937 (in part: the specimen from Fernando Poo).

Rousettus (Rousettus) aegyptiacus; Schouteden, 1944: 102; Rosevear, 1953: 83; Leleup, 1956: 75 (in part: the specimens from Territoire des Cataractes in Bas-Congo).

Rousettus aegyptiacus occidentalis Eisentraut, 1960a: 231 (type locality: Mueli); Aellen, 1963: 630; Eisentraut, 1963: 59, 1964: 532; Rosevear, 1965: 83; Coe, 1976: 546; Baud, 1977: 203; Verschuren, 1984: 101.

Rousettus aegyptiacus unicolor Koopman, 1966: 155; Aellen *et al.*, 1968: 438; De Vree *et al.*, 1969: 203, 1970: 43; Hayman *et al.*, 1971: 11; Eisentraut, 1973a: 33; J.-P. Adam *et al.*, 1974; Bergmans *et al.*, 1974: 21; Eisentraut, 1976: 75; Baud, 1977: 203; Bergmans, 1979: 165; Wolton *et al.*, 1982: 428; Fedden *et al.*, 1986: 184; Feiler, 1986: 73; Happold, 1987: 41; Bergmans *et al.*, 1988: 11; Crawford-Cabral, 1989: 10.

Rousettus aegyptiacus occidentalis; Brosset, 1966a: 363, 1966b: 52.

Rousettus aegyptiacus leachi 'not of (Smith, 1829)); Hayman *et al.*, 1966: 29 (in part: the specimens from Tamba-tamba

and Thysville).
Rousettus (Rousettus) aegyptiacus occidentalis; Verschuren, 1977: 618.
Rousettus (Rousettus) aegyptiacus unicolor; Anciaux de Faveaux, 1978a: 459; Kock, 1978a: 207.

Material examined

ANGOLA. Benguela: 1 imm. ♀, skull, before 30-IX-1930, Blazer (RMNH 2535). Canzele: 1 imm. ♂, alc., 1954, Blazer (RMNH 81728). 30 km S of Gabela: 3 ♂♂ (2 in alc.), 27-VIII-1954, G. Heinrich (FMNH 83592, 84033/34). Hanha: 1 specimen (AMNH 85518). N'kuta: 1 imm. ♂, alc., skull, VI-1911, W. I. Ansorge (ZMB). "Angola": 1 specimen (BMNH 4.4.9.2). (Luanda, Pungo Andongo, Quindumbo, Uige.)
 CAMEROUN. 14 km E of Bamenda: 10 specimens (AMNH 240988/97). Bipindihof: 2 specimens, alc., G. Zenker (ZMB 54691, -99). Buea: 1 imm. ♂, 2 ♀♀, 21-VI/15-VII-1934, R. & L. Boulton (FMNH 42584/86). Lobe: 1 specimen (BMNH 60.52). Lolodorf: 1 ♂, 15-VI-1918, 1 ♂, 29-VII-1929, J. A. Reis (CMNH 4637, 3928). Northern Mount Cameroun: 1 specimen (USNM 318299). Victoria: 1 ♂, alc., skull, 1907 (SMF 28287); 1 specimen, alc., Strunk (ZMB 54700). Yaoundé: 1 ♀, alc., skull, G. Zenker (ZMB 10239); 2 imm. ♂♂, 7 imm. ♀♀, alc., 5-III/11-IV-1973, J. Prévost (MNHN CG 1979-334/42). "Cameroun": 6 ♂♂, 1 ♀, 11 specimens, alc. (MNHN). (Bafut, Bibundi, 10 km W of Bipindi, Bota, Boteke, 10 miles N of Buea, Debundscha, Ekona, Great Soppo at Buea, Idenau, Isobi, Kribi, 14 km N of Kribi, Kumba, Lake Barombi, 20 miles N of Lolodorf, Mamfe, Mangamba Big Farm, Meye, Mount Cameroun, Mueli, 6 km W of Muege, Muyuka, Ongoo, Pinda Hill Cave at Lolodorf, Sangmelima, Small Soppo, Tiko, Tombel.)
 CONGO. Dimonika: 1 ♂, 1 ♀, alc., skulls, 17/22-I-1964, A. Descarpentries & A. Villiers (MNHN CG 1975-801/02); 1 imm. ♂, skull, 8-III-1970, Université de Brazzaville (UBRA 1-♂-8-03-70); 3 ♂♂, 1 imm. ♂, 1 ♀, 1 imm., 13/14-III-1972, Université de Brazzaville (UBRA 1-, 3-, 7-♂-72-03-13, and unregistered). Grand Bois: 1 ♀, formalin, 25-V-1972, Université de Brazzaville (UBRA). Kila N'Tari cave: 1 imm. ♂, alc., skull, 25-V-1960, Tauflieb (MNHN CG 1975-794); 2 ♂♂, 4 imm., II-1963, Laboratoire Emile Roubaud (LER 214). Makaba: 2 imm., formalin, 12-III-1970, Université de Brazzaville (UBRA). Meya: 1 imm., formalin, 19-V-1972, Université de Brazzaville (UBRA). "Congo": 1 ♀, formalin (UBRA); 1 ♀, formalin, 13-III-1972, Université de Brazzaville (probably from Dimonika; UBRA). (Brazzaville, Dibakouélé, Divenié, Loudima-Kimongo, Massif de Bangou, Mouyondzi, Sibiti.)
 EQUATORIAL GUINEA. (Akassi, Engong, Moka, Mokula, Mount Bong.)

FERNANDO POO. Moka: 1 specimen (AMNH 206953). "Fernando Poo": 1 specimen (MNCN 1.008). (San Carlos.)
 GABON. Angoué Lake: 1 specimen, alc., Roux (MNHN CG 1950-825). Batouala: 1 ♂, 1 imm. ♂, 1 ♀, 1 imm., alc., skulls, 22/26-VII-1963, Mission Biologique au Gabon (MNHN; ZMA 20.665/66). Bélinga: 1 ♂, alc., skull, 9-XII-1962, Mission Biologique au Gabon (ZMA 20.667); 2 ♂♂, 2 imm. ♂♂, 1 ♀, alc., XII-1962/II-1963, Mission Biologique au Gabon (MNHN); 3 ♂♂, 1 imm. ♂, 1 ♀, 1 imm., alc., skulls of 4, II/III-1963, Mission Biologique au Gabon (MNHN; ZMA 20.668, -75/78); 1 specimen, 1 imm., skulls, VII/VIII-1963, Mission Biologique au Gabon (ZMA 20.679/80); 1 imm. ♂, 1963, Mission Biologique au Gabon (MNHN); 1 ♂, 3 imm. ♂♂, 3 ♀♀, 1 imm. ♀, alc., skulls of 6, XII-1963/II-1964, P. J. H. van Bree (ZMA 6841, 7928/29, -32, -46, -48, 8703/04, 22.123). Lastoursville: 1 imm., 25-IV-1945, R. Malbrant & A. Maclatchy (MNHN CG 1947-216). ? Makokou: 6 specimens (MNHN). (Fernan Faz, Pahou.)
 GAMBIA. Basse: 1 specimen (BMNH 49.462).
 GHANA. 1 mile W of Agogo: 1 specimen (BMNH 61.1594). NE of Konkoni: 1 specimen, alc. (BMNH). Kumasi: 2 specimens (BMNH 50.1502/03). Prince's Town: 1 specimen (USNM 411238). Subinja: 1 specimen (USNM 414689). Yabroso: 1 specimen (USNM 424659). (Krobo Hill, nr Headquarters Mole Game Reserve.)
 GUINEA. Fouta Djallon: 1 ♀, alc., 27-VII-1910, Pobeguine (MNHN CG 1911-1719). Kankasili: 1 ♀, 1 specimen, 15-XI-1966/1-III-1967, J. van Orshoven (ZMA 10.739, 10.876). Seredou: 1 ♀, alc., skull, 18-XII-1959, J. Roche (MNHN CG 1970-463). (Zié Cave at Mount Nimba.)
 IVORY COAST. ? Bolo: 1 skull, 1972/73, J. Vissault (ZMA 19.273). 2 km S of Boundiali: 2 imm. ♂♂, 1 imm. ♀, 23-VII-1970, M. Ailoujian (LACM 33030/31, ...). Duékoué: 1 ♂, 1 ♀, 3-III-1969, J. W. LeDuc/L. W. Robbins (ZMA 16.532; MNHN); 1 specimen (USNM 465680). Kahin: 1 specimen (USNM 465720). Matonguiné: 3 ♂♂, 2 imm. ♂♂, 2 ♀♀, 1 imm. ♀, skins, skulls; 10 ♂♂, 6 imm. ♂♂, 10 ♀♀, skins only; 23 adult specimens, 15 imm., skulls only; 17/21-I-1973, J. Vissault (ZMA 18.879/916, 18.979/83, -87/93, 18.998/19.012, -14/16, -18/21, -23).
 LIBERIA. Bagalumu, Lofa, Mount Nimba: alc. material (BMNH). Cassava Farm/Banana Plantation, Mount Nimba: alc. material (BMNH). Iti: 2 ♂♂, 5 ♀♀, 1 imm. ♀, alc., 12/15-II- and 4-III-1966, J. Verschuren (IRSN 16109/11, -13/15). Iti Rivière: 1 imm. ♂, alc., 31-I-1966, J. Verschuren (IRSN 16106). Mount Nimba: 1 ♂, 1 ♀, 1 imm. ♀, alc., 30-XI/1-XII-1965, J. Verschuren (IRSN 16104/05, -18). Nimba East: 1 imm. ♀, alc., 2-II-1966, J. Verschuren (IRSN 16107). Nimba West: 1 ♂, 1 imm. ♂, 1 imm. ♀, alc., 7-II/2-III-1966, J. Verschuren (IRSN 16.108, -12, 16.757). Old Ridge Road, Mount Nimba: alc. material (BMNH). Yekepa: 1 ♂, 2 ♀♀, alc., 8/23-VII-1965, J.

Verschuren (IRSN 16746/48).

NIGERIA. Jos: 3 ♂♂, 1 ♀, (2 in alc.), 25- and 28/29-VI-1976, W. Bergmans (ZMA 18.406/09).

(N of Calabar, Kagoro, Kano, Oban.)

SENEGAL. "Senegal": 1 specimen, mounted (RMNH); 1 ♂, skin, skull *in situ*, received 25-VII-1932 (ex-collection de Selys-Longchamps; IRSN 12.452).

(Dakar, rocky islands of La Madeleine.)

SIERRA LEONE. Musaia: 2 specimens and alc. material (BMNH).

(Fourah Bay College at Freetown, Mount Aureol.)

TOGO.

(Aledjo, Fazao, Misahohe.)

ZAIRE.

(Banza-Nfinda cave nr Thysville, Kunungu, Mukimbungu, Tamba-tamba cave nr Thysville.)

Diagnosis: Generally as for the species. If compared to the subspecies *egyptiacus* and *leachii*: fal on average slightly larger, mainly through higher minimum values; skull on average somewhat smaller and less strongly built than in *egyptiacus* and about the same size as but stronger than in *leachii*, rostrum usually slightly narrower than in *egyptiacus* but stronger than in *leachii*, with a larger relative width over M²-M² than in both, premaxillae slender and rarely co-ossified; in ♂♂, interorbital width averaging smaller than in *egyptiacus*, in both sexes postorbital width averaging larger than in the nominate form, much as in *leachii*; in ♂♂, iow either larger or smaller than pow, in ♀♀ more often smaller; sagittal crest rarely present, mandibular ramus slightly weaker than in *egyptiacus* and its angle with the coronoid process larger, coronoid process usually shorter and somewhat narrower than in *egyptiacus*, angular process not projecting backwards as in *egyptiacus*; built of mandibulum, as of skull, generally somewhat stronger than in *leachii*; cheek-teeth generally narrower and shorter than in *egyptiacus*, much as in *leachii*. The following measurement ranges and ratios are from all over the subspecies' range:

fal	♂♂	91.3 - 102.1	(n = 46),
	♀♀	90.3 - 106.3	(n = 38);
tibia	♂♂	42.0 - 46.6	(n = 6),
	♀♀	40.8 - 45.8	(n = 4);
ear	♂♂	17.8 - 22.0	(n = 6),
	♀♀	18.0 - 22.7	(n = 5);

gsl	♂♂	42.6 - 45.2	(l = 13),
	♀♀	39.8 - 44.0	(n = 10),
	?	39.7 - 45.6	(n = 24);
rl	♂♂	15.9 - 17.3	(n = 13),
	♀♀	14.5 - 16.9	(n = 10),
	?	14.6 - 17.3	(n = 23);
iow	♂♂	7.7 - 9.5	(n = 13),
	♀♀	7.4 - 8.6	(n = 11),
	?	7.2 - 9.4	(n = 23);
pow	♂♂	7.7 - 9.5	(n = 13),
	♀♀	7.6 - 9.4	(n = 11),
	?	7.5 - 9.8	(n = 24);
zw	♂♂	24.7 - 28.6	(n = 13),
	♀♀	23.6 - 26.2	(n = 9),
	?	24.6 - 28.0	(n = 22);
C ¹ -M ²	♂♂	16.5 - 18.2	(n = 13),
	♀♀	15.1 - 17.4	(n = 8),
	?	15.8 - 17.8	(n = 22);
C ₁ -M ₃	♂♂	18.1 - 19.4	(n = 13),
	♀♀	17.0 - 18.9	(n = 11),
	?	15.8 - 19.2	(n = 23);
M ¹ length	♂♂	2.7 - 3.3	(n = 15),
	♀♀	2.7 - 3.0	(n = 5),
	?	2.7 - 3.2	(n = 39);
M ¹ width	♂♂	1.8 - 2.2	(n = 15),
	♀♀	1.8 - 1.9	(n = 5),
	?	1.8 - 2.15	(n = 39);
W	♂♂	110 - 168	(n = 18)
	♀♀	100 - 140	(n = 19);
rl	♂♂	36.1 - 39.1% of gsl	(n = 10),
	♀♀	35.8 - 38.5% of gsl	(n = 7),
	?	35.8 - 38.4% of gsl	(n = 23);
C ¹ -C ¹	♂♂	18.3 - 22.3% of gsl	(n = 10),
	♀♀	18.8 - 21.6% of gsl	(n = 6),
	?	18.6 - 22.4% of gsl	(n = 22);
M ² -M ²	♂♂	29.5 - 32.1% of gsl	(n = 11),
	♀♀	30.4 - 32.6% of gsl	(n = 5),
	?	29.2 - 34.3% of gsl	(n = 21).

Data in the literature are often not specified per sex and in some cases include immature specimens, and are of little use in the present diagnosis. The maximum fal value, 106.3 in a female from Congo (see Bergmans, 1979) is matched by the maximum of 106 in an unsexed series from Gabon reported by Brosset (1966b). Eisentraut (1960a) measured a maximum gsl of 46.5 in an unsexed series of 4 specimens from Gabon. This

is probably a male. Jones (1971) gave 46.4 as gsl for a male from Rio Muni, Equatorial Guinea (the other 4 specimens listed by him are immature). Feiler (1986) measured a zw of 30.0 in a male from Angola. Wolton *et al.* (1982) gave 195 as maximum W in a series of ♂ from Liberia.

Specimens from Senegal to Nigeria are slightly smaller in body and skull dimensions, on average, than those from southern Cameroun to Angola, but the ranges largely overlap. Specimens from the Mount Cameroun area are intermediate.

Measurements: Table 2.

Distribution: Fig. 2.

Related species: See the account of the typical subspecies.

Remarks

Taxonomy: Eisentraut (1960a) based his new subspecies *occidentalis* on 83 specimens from the Mount Cameroun region, 9 from Senegal, Guinea and Ivory Coast, 1 from southern Cameroun and 4 from Gabon. The holotype was from Mount Cameroun. Koopman (1966) synonymized *occidentalis* with *unicolor*. Bergmans (1979) confirmed Eisentraut's observation that specimens from southern Cameroun and Gabon - to which he added Congo, and to which Rio Muni, western Zaïre and northern Angola are tentatively added here - have larger average body, skull and teeth measurements than typical *occidentalis*. The variation from southern Congo to Mount Cameroun seems clinal and the differences are modest, and Eisentraut's large series from Mount Cameroun connects this line with the more western populations. It seems best, therefore, to unite all West African and western Central African populations in *unicolor*, with *occidentalis* as a synonym. When the present diagnosis are compared, it emerges that *unicolor* has far more in common with *leachii* than with *egyptiacus*. It differs from *leachii* mainly in its higher average fal, slightly stronger skull, somewhat stronger rostrum, and larger width over M²-M², but it shares with *leachii* and not with *egyptiacus* a general weakening of skull and mandible built. This may

be related to a greater variety of available food species in the *unicolor* and *leachii* areas if compared to the relatively harsher (natural) environments where the nominate form and *arabicus* are found. The dominant palatal ridge pattern in *unicolor* is 4 + 3 + 1, with some variation, as in *leachii*. The fourth ridge may be narrowly divided, and (parts of) an extra ridge may appear in the central group.

Distribution and geographical variation: West of the Mount Cameroun region, the rather few and scattered collecting localities hardly indicate a pattern. South of it, more localities are known, and suggest a continuous distribution, with concentrations at and near mountains and other areas with caves.

Of the 111 traceable *unicolor* localities, 34 are in Guineo-Congolian Lowland rain forest: wetter types, 12 in drier types of the same, and 1 in Mosaic of these two (types 1a, 2 and 3 in White, 1983); 21 are in Mosaic of Lowland rain forest and secondary grassland, 1 is in Mangrove, and 3 are on the border of two of the mentioned types. Only 5 are in Undifferentiated Afromontane vegetation (type 19a in White, 1983) and 9 on the border of that type with type 3 or 11a, and only 11 in one of the Woodland types (25, 27, 29a, 29c in White, 1983). Finally, 1 is in the Jos Plateau mosaic and 2 are in Bushy Karoo-Namib shrubland (types 32 and 51 in White, 1983). Thus, *unicolor* is often found in forests (including Mangrove; 54% of the localities) and forest transitions and mosaics (32%). As with *leachii*, known roosts of *unicolor* are all in caves, and the availability of caves again seems to be the first decisive factor for the possible presence of *Rousettus egyptiacus* in a given area, regardless of vegetation types (provided that foraging areas are within reach).

Table 2 Ranges of selected measurements of *Rousettus egyptiacus unicolor* (Gray, 1870) per country.

			fal	tibia	ear	gsl	rl	iow	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ₁ - M ₃	M ¹ length	W width
Angola	♂♂	n	3													
		mean	97.5													
		min	93.7													
		max	102.0													
Cameroun	♂♂	n	7			1										
		mean	94.8													
		min	92.1			45.1										
		max	98.8													
	♀♀	n	3													
		mean	97.1													
		min	92.9													
		max	101.7													
Congo	♂♂	n	6	1	1	2	2	2	2	2	1	2	2	2	5	5
		mean	97.9											2.95	2.0	
		min	93.9	45	20	44.1	16.3	8.2	8.4	25.5	9.0	13.3	16.8	18.6	2.7	1.8
		max	100.7			44.2	16.5	8.7	9.5	27.9		13.6	17.1	18.8	3.3	2.1
	♀♀	n	3	1	1	1	1	1	1	1	1	1	1	1	1	1
		mean	100.3													
		min	93.9	41	19	43.8	16.3	7.8	9.2	25.7	9.1	13.3	17.0	18.9	3.0	1.9
		max	106.3													
Gabon	♂♂	n	7	3	3	4	3	3	3	4	3	3	3	3	7	7
		mean	96.6	44.7	19.3	43.9	16.0	8.2	8.1	27.0	9.1	13.3	16.8	18.55	3.1	2.0
		min	92.2	43.6	17.8	43.0	15.9	7.7	7.7	25.7	8.5	12.9	16.5	18.5	2.9	1.9
		max	99.0	46.6	21.8	44.3	16.1	8.6	8.3	28.1	9.8	13.9	17.2	18.6	3.3	2.2
	♀♀	n	5	3	4	3	4	4	4	2	4	2	2	3	1	1
		mean	96.8	44.6	20.5	42.9	16.0	8.25	8.7		9.0			18.3		
		min	94.7	43.6	19.0	42.2	15.1	8.1	8.2	25.0	8.7	13.1	16.3	17.9	3.0	1.9
		max	99.8	45.8	22.7	43.9	16.9	8.6	9.1	25.1	9.4	13.5	17.4	18.7		
	?	n				1	1	2	2	1	2	1	1	2	3	3
		mean													2.9	2.0
		min				41.9	15.7	8.0	7.7	26.6	8.9	13.1	16.3	17.6	2.7	1.9
		max						8.3	8.0		9.9			19.2	3.0	2.1
Guinea	♂♂	n	1			1	1	1	1	1	1	1	1	1		
			97.7			--	16.9	8.9	8.5	28.0	10.1	13.9	16.9	18.1		
	♀♀	n	3			1	1	1	1	1	1	1	1	1	1	1
		mean	94.7													
		min	91.7			44.0	16.8	8.1	8.4	26.2	8.6	12.4	16.7	18.5	2.7	1.9
		max	97.8													130
	?	n													6	6
		mean													2.9	1.9
		min													2.8	1.8
		max													3.1	2.0

Table 2, continued.

Table 2, continued.

		fal	tibia	ear	gsl	rl	iow	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ₁ - M ₃	M ¹ length	W width		
Ivory Coast	♂♂	n	12	14	11	4	4	4	4	4	4	4	4	2	2	13	
		mean	95.7	44.5	22	43.7	16.8	8.3	8.4	26.3	9.0	13.6	16.85	18.65			129
		min	91.3	40	20	42.6	16.4	8.0	7.8	24.7	7.8	13.2	16.5	18.4	2.9	1.8	116
		max	102.1	47	24	44.3	17.3	8.6	8.8	27.7	9.5	14.0	17.0	18.8	3.0	1.9	158
	♀♀	n	13	12	11	3	3	3	3	3	2	3	3	3	2	2	12
		mean	94.0	43	21	42.4	15.4	8.0	9.1	25.1		13.3	16.2	17.8			116
		min	90.3	41	19	39.8	14.5	8.1	8.6	23.6	8.2	12.3	15.1	17.0	2.7	1.8	100
		max	100.8	45	22	43.9	16.9	8.6	9.4	26.1	9.3	14.2	16.8	18.4	2.8	1.9	140
	?	n				22	22	21	22	21	21	20	20	21	30	30	
		mean				42.9	16.0	8.1	8.5	26.0	8.9	13.1	16.8	18.4	3.0	1.95	
		min				39.7	14.6	7.2	7.5	24.3	8.0	12.2	16.0	17.0	2.7	1.8	
		max				45.6	17.3	9.4	9.8	28.0	10.1	14.3	17.8	19.5	3.2	2.15	
Liberia	♂♂	n	5				1	1	1	1	1	1	1			2	
		mean	96.0														
		min	95.0				16.1	7.8	8.5	--	8.4	13.6	17.0	18.5			110
		max	97.0														128
	♀♀	n	8				1	2	2	2	2	1	1	2			5
		mean	93.7														117
		min	91.3				15.7	7.7	7.6	24.7	8.1	13.4	16.8	18.1			108
		max	96.8					7.9	8.3	25.2	9.7			18.5			128
Nigeria	♂♂	n	3	3	3	2	2	2	2	2	2	2	2	1	1	3	
		mean	98.9	43.0	21.5												148
		min	98.1	42.0	21.2	43.9	16.3	8.3	8.7	26.6	9.5	13.6	16.9	19.0	3.0	2.2	130
		max	99.6	44.1	22.0	45.2	16.7	9.5	9.3	28.6	9.9	14.5	18.2	19.4			168
	♀♀	n	1	1	1												1
			96.1	40.8	18.0												132
Senegal	♂♂	n	1														
		c.92															

***Rousettus egyptiacus arabicus* Anderson & de Winton, 1902**

Rousettus arabicus Andersen & de Winton, 1902: 86, 88, 90 (type locality: Aden); Andersen, 1907b: 502, 507, 1912: 33 (in part: not the specimens from Mukkle Hills reported by Murray, 1884; see the text); Ellerman *et al.*, 1951: 92; Siddiqi, 1961: 102.

Rousettus aegyptiacus arabicus; Eisentraut, 1960a: 229; Harrison, 1964: 49; Hayman *et al.*, 1971: 11; Scaramella, 1975: 375; T.J. Roberts, 1977: 33 (in part: see text); Kock *et al.*, 1979: 69; DeBlase, 1980: 41; Harrison, 1980: 390; Harrison *et al.*, 1991: 24.

? *Rousettus* sp.; Yaman, 1966: 268, 270.

Rousettus aegyptiacus; Nader, 1974: 20, 1978: 174.

Rousettus aegyptiacus aegyptiacus; Nader, 1975: 332.

Rousettus (Rousettus) aegyptiacus aegyptiacus; Anciaux de Favcaux, 1978a: 460 (in part: the specimens from Aden).

Material examined

IRAN. Ahmad Mahmoudi Juyum: 1 ♂, 1 imm. ♀, 1-I-1963, D. M. Lay (FMNH 96456/57). 4 km WSW of Jahrom: 4 ♂♂ (1: alc.), 1 imm. ♂, 1 ♀, 2 imm. ♀♀, 31-XII-1962/1-I-1963, D. M. Lay (FMNH 96447/50, -52/53, -59/60). 3.3 miles SW of Jahrom: 1 ♂, 12-XI-1968, W. S. & J. K. Street Expedition to Turkey (FMNH 111008). (Baluchistan, Namakdun at south coast of Qeshm Island, Tiss.)

OMAN. Nr Al Tabaqah, Wadi Sahtani: 1 ♂, 4-V-1981, M. D. Gallagher (HZM 107.11626). Jabal Dhawi: 2 ♂♂, alc.,

skull of one, 1-V-1979, Saif Ali Salim Al Katheri (ZMA 20.515/16). Khadafri Plateau, Jebel Qamr: 3 ♂♂, 2 ♀♀, 2 imm. ♀♀ (1 in alc.), 27-IX-1976, M. D. Gallagher (HZM 87.8587/93.8593); 1 ♀, 30-IX-1977, M. D. Gallagher (HZM 98.9145). Masirah Island: 1 ♂, 3-IX-1977, M. D. Gallagher (HZM 102.9245). Muscat: alc. material (BMNH). 'Ulyah, Wadi Bani Karus: 1 ♂, 7-XII-1984, D. L. Harrison/M. D. Gallagher (HZM 110.15243). Wadi Darbat, Jabal Qara: 1 ♂, 1 ♀ (alc.), 21-X-1977, P. G. White/T. Rogers, M. D. Gallagher (HZM 97.9144, 101.9148). Upper Wadi Halfayn, Jabal Akhdar: 1 specimen, S, skeleton, 14-II-1980, D. P. Mallon (HZM 105.10634). Wadi Sahtan: 1 ♂, 19-III-1979, M. D. Gallagher/J. Ros (HZM 104.10054). Wadi Sayq: 2 ♂♂, 1 ♀, 25/27-IX-1977, M. D. Gallagher (HZM 95.9142, 96.9143, 99.9146). PAKISTAN. Karachi: 2 ♂♂, C. B. Tyeshurst (BMNH 20.1.17.1/.2); alc. material (BMNH). Panjgur: 2 ♂♂, 1 ♀, 11-I-1918, J. E. B. Hotson (FMNH 82620/22); 3 ♂♂, 3 ♀♀, J. E. Hotson (BMNH 19.11.7.1/.6).

(? Clifton, Lak Bidok, ? Makli Hills.)

SAUDI ARABIA. Wadi Khaytan: 2 imm. ♀♀ (1 in alc.), III- and 1-V-1984, D. Lickfold (HZM 109.14487, 112.17717).

(Abha-Raydah escarpment, Al Baha escarpment, Al Maski, ? Hayel, ? Jeddah, ? Medina, ? Mekka, Tayif.)

UNITED ARAB EMIRATES. Ras el Khaimah: 1 imm. specimen, S, skeleton, 24-III-1972, M. D. Gallagher (HZM 84.6660).

YEMEN. Lahej: 1 ♂, 1 ♀, 21-III-1895, J. W. Yerbury (BMNH 95.6.1.48/49); 2 ♂♂, 1 ♀, 1 imm. ♀, A. B. Percival/W. Dodson (BMNH 99.11.6.6/.9); alc. material (BMNH); 1 ♀, 30-VII-1971 and 1 imm. ♂, 20-V-1972, A. K. Nasher (HZM 85.7193, 86.7194).

(Aden, nr Aden, "Alturbam", Saiun, Taizz.)

Roussettus leschenaultii (Desmarest, 1820), comparative material:

PAKISTAN. Malir: 1 mummy, 6-III-1965, J.A. Anderson (AMNH 217287). 2 miles NE of Malir City: 2 ♂♂, 1 imm. ♂, 10 ♀♀, 5 imm. ♀♀, skins (not seen), skulls (mostly incomplete, with loose teeth), 31-V-1972, D. Walton (BMNH 73.666/75, -77/78, -80/85). Lahore: 2 ♂♂, 2 ♀♀, skins (not seen), skulls, 16-XI-1966 and 2-II-1968, T. J. Roberts (BMNH 67.1104/06, 69.484).

INDIA, specimens in the Természettudományi Múzeum Allattára, Budapest, measured by drs. G.H. Glas. Khaneri Caves, cave 1 (nr Bombay): 1 ♂, 1 imm. ♀, 9-VII-1967, G. Topál (field numbers 530, 533). Parvati Cave, Poona: 3 ♂♂, 8 ♀♀, 1 imm. ♀, 5-VIII-1967, G. Topál (field numbers 587, -93, -95/96, -98/99, 601, -03/04).

Diagnosis: Generally as for the species. If compared to the other three subspecies, averaging distinctly smaller in all body and skull dimen-

sions; tibia on average possibly relatively slightly shorter; rostrum much as in *leachii*, with lateral sides converging towards dorsal side more than in *egyptiacus*, nasalia relatively narrow, dorsal side of rostrum tapering towards the distal end; premaxillae rarely co-ossified; in both sexes, interorbital width larger than postorbital width in roughly two thirds of the specimens - in the others the widths are equal or the situation is reversed; sagittal crest absent, in ♂♂ a very low ridge may be present instead; occipital crest rather weak; infra-orbital foramen frequently divided by a thin bony septum; mandibular ramus not weaker than in *egyptiacus*, its angle with the coronoid process not much larger, the process itself not weaker or shorter, angular process projecting backward as in *egyptiacus*, teeth rows converging from back to front more strongly than in *egyptiacus*; teeth relatively large, averaging only very little smaller (mostly: narrower) than in *egyptiacus*. The following measurement ranges and ratios are from all over the subspecies' range:

fal	♂♂	85.7 - 94.4	(n = 25),
	♀♀	79.9 - 91.2	(n = 10);
tibia	♂♂	38.7 - 39.7	(n = 2);
	♀♀	19.0 - 22.2	(n = 12);
ear	♂♂	19.1 - 23.0	(n = 7);
	♀♀	38.7 - 42.7	(n = 24),
gsl	♂♂	38.0 - 41.0	(n = 10);
	♀♀	13.8 - 16.3	(n = 18),
rl	♂♂	13.2 - 14.8	(n = 9);
	♀♀	7.2 - 8.7	(n = 17),
iow	♂♂	7.2 - 8.8	(n = 10);
	♀♀	6.6 - 8.4	(n = 17),
pow	♂♂	6.2 - 7.9	(n = 10);
	♀♀	23.9 - 26.1	(n = 18),
zw	♂♂	22.8 - 25.1	(n = 10);
	♀♀	15.1 - 16.7	(n = 19),
C ¹ -M ²	♂♂	14.6 - 15.6	(n = 6);
	♀♀	16.6 - 17.9	(n = 19),
C ₁ -M ₃	♂♂	16.0 - 17.3	(n = 7);
	♀♀	2.8 - 3.6*	(n = 19),
M ¹ length	♂♂	2.6 - 3.0*	(n = 11);
	♀♀	1.6 - 2.1*	(n = 19),
M ¹ width	♂♂	1.5 - 1.9*	(n = 11);
	♀♀	98.5 - 128.0	(n = 3);
W	♂♂		

rl	♂♂	35.3 - 38.2% of gsl (n= 16),
	♀♀	34.3 - 36.1% of gsl (n= 9);
C ¹ -C ¹	♂♂	19.5 - 20.7% of gsl (n= 17),
	♀♀	18.9 - 20.5% of gsl (n= 8);
M ² -M ²	♂♂	28.7 - 31.8% of gsl (n= 16),
	♀♀	29.3 - 32.3% of gsl (n= 6).

* approximate measurements

Specimens in the Arabian Peninsula may attain slightly larger average dimensions than those in Iran and Pakistan. For a breakdown of measurements see table 3.

Distribution: Fig. 1.

Related species: See the account of the typical subspecies.

Remarks

Taxonomy: When Anderson *et al.* (1902) described *Rousettus arabicus*, they compared it with a number of other *Rousettus* species, notably *egyptiacus* and *leachii* - as *R. collaris* (Illiger, 1815), an old and incorrect name (see Andersen, 1912: 28) - and the largely Asiatic species *R. leschenaultii* and *R. amplexicaudatus*. The differences of *arabicus* with other African *Rousettus*, including extralimital typical *egyptiacus*, have been described by Anderson *et al.* (1902) and Andersen (1907b, 1912). Some of the characters used by these authors to distinguish *arabicus* are difficult or impossible to substantiate when a larger material is examined. They used some absolute size differences but these are to be expected in a generally smaller subspecies. E.g. proportionally the rostrum is not shorter in *arabicus* than in *leachii* or the others, and not narrower (slenderer) than in *leachii*: compare the relative widths over C¹-C¹ and M²-M² in the diagnoses. The relative length of the tibia (and possibly the foot) may average slightly lower but this should be assessed in a larger fresh or spirit material. The form of the ear, according to Anderson *et al.* (1902) more pointed and with less convex borders than in *egyptiacus* and broader than in *leachii*, is another character which at present is difficult to assess and should be examined in a larger fresh or spirit material.

The specimens from Tayif in Saudi Arabia, identified as typical *egyptiacus* by Nader (1975), should on the basis of the measurements published by that author be allocated to *arabicus*. The fal ranges (88-95 in 6 ♂♂, 85-93 in 6 ♀♀) nearly completely overlap with those in both *egyptiacus* and *arabicus*, but the gsl ranges (38.8-42.1 in 6 ♂♂, 38.9-40.5 in 5 ♀♀) are distinctly below those in *egyptiacus* and agree with those in *arabicus*. This placement certainly agrees better with the known Arabian distribution patterns of both subspecies (Harrison *et al.*, 1991; this paper). The differences between *arabicus* and *leschenaultii* have never yet been dealt with sufficiently. *R. leschenaultii* replaces *arabicus* in Asia from East Pakistan towards the east. It is the only extralimital (i.e. non-African) species that needs to be considered in the present context, *amplexicaudatus* being found only much further to the east (see Rookmaaker *et al.*, 1981). Anderson *et al.* (1902) examined a series of *leschenaultii* from Nepal and noted that these had similar ears to those of *arabicus* (including specimens from Aden and Karachi), but considerably longer tails, strikingly different skulls, smaller teeth, and a narrow and elongate M₃ (against more rounded in *arabicus*). They did not elaborate the skull differences. Andersen (1907b) used the length of the pollex and the length of the 2nd phalanx of the 3rd digit to differentiate the two: a pollex (with claw) of ≥ 30 and a phalanx of ≥ 50.5 indicating *arabicus* and a pollex of ≤ 30 and a phalanx of ≤ 47.2 *leschenaultii*. He used the same material as Anderson *et al.* (1902), plus a specimen of *arabicus* from Muscat. In his diagnoses, Andersen wrote that *leschenaultii* is allied to *arabicus*, but "smaller, with the muzzle shorter and slenderer, the tip of the ears not attenuated, the pollex markedly shorter, wings shorter, especially the first and second phalanx of the third digit, and the foot smaller. Forearm 80.5-87.5 mm." In 1912 Andersen gave as measurements for *arabicus* and, added here between brackets, *leschenaultii*: pollex 30-33 (26.5-29.5), fal 87-96 (80.5-87.5), 1st and 2nd phalanx of 3rd digit 37-39.8 and 50.5-56.5 (33.8-36.8 and 41-46.2). He introduced as differential characters the relative length of the first finger (if fal is put at 1000, the index is 361 in *arabicus* and 335 in

Table 3. Ranges of selected measurements of *Rousettus egyptiacus arabicus* Anderson & de Winton, 1902 per country *

		fal	tibia	ear	gsl	rl	iow	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ₁ - M ₃	M ¹ length	W width
Iran	♂♂	n	4		5										3
		mean	89.3		40.4										114.2
		min	86.2		39.5										98.5
		max	92.5		41.9										128.0
	♀♀	n	1												
			87.4												
	♂♂	n	11	2	10	11	11	10	11	11	11	11	11	11	11
		mean	90.4		20.3	41.5	15.2	8.1	7.4	25.3	8.4	12.5	16.0	17.3	3.1
		min	87.8	38.7	19.0	40.2	14.5	7.6	6.6	24.3	8.1	12.0	15.4	16.8	2.9
		max	93.2	39.7	22.2	42.6	16.3	8.6	8.0	26.1	8.7	13.0	16.7	17.8	3.6
	♀♀	n	4		5	5	5	5	5	5	5	5	4	5	5
		mean	88.6		20.1	39.5	13.8	7.5	7.1	23.7	7.95	12.0	15.25	16.45	2.85
		min	86.3		19.1	39.0	13.5	7.2	6.2	23.0	7.7	11.6	15.0	16.0	2.7
		max	91.2		21.5	40.1	14.1	7.9	7.5	24.1	8.0	12.7	15.6	16.9	3.0
	?	n			1	1	1	1	1	1	1	1	1	1	1
					41.0	15.1	7.3	7.4	24.3	7.9	12.0	15.9	16.8	3.1	1.9
Pakistan	♂♂	n	7		2	5	4	5	4	4	5	3	5	5	5
		mean	89.0			41.5	14.8	7.8	7.7	24.7	8.1	12.5	16.2	17.5	3.2
		min	85.7		20	40.5	14.4	7.2	7.2	24.4	8.0	12.0	15.9	17.2	c.2.8
		max	91.3		22	42.7	15.1	8.7	8.4	24.9	8.2	12.8	16.5	17.9	3.5
	♀♀	n	4		1	3	2	3	3	3	1			1	
		mean	87.1			39.4		8.0	7.7	24.3					
		min	82.6		22	39.0	13.7	7.5	7.5	23.8	8.0			17.3	
		max	90.2			41.0	14.8	8.8	7.9	25.1					
	♀♀	n													
	Saudi Arabia	n												2	2
		min												2.7	1.7
	max													3.0	1.9
United Arab Emirates	?	n												1	1
														3.0	1.8
Yemen	♂♂	n	3		3	3	2	2	3	3	3	3	3	3	3
		mean	91.6		39.9	14.2			24.5	8.0	11.9	15.6	17.0	2.95	1.85
		min	87.7		38.7	13.8	7.4	7.4	23.9	7.9	11.6	15.1	16.6	2.9	1.7
		max	94.4		41.1	14.5	7.5	7.9	25.2	8.2	12.4	16.2	17.3	3.1	2.1
	♀♀	n	1		1	2	2	2	2	2	1	1	2	4	4
		mean												2.75	1.75
		min	79.9		23	38.0	13.2	7.4	7.4	22.8	7.2	11.6	14.6	16.0	2.6
		max				40.5	14.4	7.4	7.8	24.0	7.8		16.6	2.9	1.8
	♀♀	n													

* Most M¹ measurements have been taken with callipers: the M¹ ranges are approximations.

Table 4. Forearm lengths and greatest skull lengths in *Rousettus egyptiacus arabicus* Anderson & de Winton, 1902 and *Rousettus leschenaultii* (Desmarest, 1820) in Pakistan and further to the east.

<i>Rousettus egyptiacus arabicus</i>					<i>Rousettus leschenaultii</i>				
		Panjgur		Karachi		Malir		Lahore	
		n	min - max	n	min - max	n	min - max	n	min - max
♂♂	fal	5	85.7 - 91.3	2	89.4 - 89.6				
	gsl	4	41.3 - 42.7	2	> 40 - 40.5	1	37.3	2	39.6 - 40.6
♀♀	fal	4	82.6 - 90.2						
	gsl	3	39.0 - 41.0			4	36.1 - 37.6	2	36.6 - 38.4
?	fal					6	75.2 - 82.9		
	gsl					6	36.2 - 38.2		

<i>Rousettus leschenaultii</i> (continued)									
		Bombay region		Northeast India		Indo-China		Indonesia	
		n	min - max	n	min - max	n	min - max	n	min - max
♂♂	fal	4	83.0 - 88.0	3	78.7 - 87.0	4	77.5 - 85.6	20	84.0 - 96.3
	gsl	4	37.5 - 39.4	3	37.1 - 38.9	2	39.1 - 39.7	16	40.3 - 43.6
♀♀	fal	8	79.2 - 83.3	6	77.2 - 84.2	7	77.0 - 80.8	15	85.2 - 91.2
	gsl	7	35.0 - 36.7	4	35.4 - 37.8	2	37.8 - 38.0	53	38.8 - 42.5
?	fal								
	gsl					1	40.1		

Note: Data unsexed specimens Malir after Kock, 1978a; data Bombay region courtesy of Dr. G. Topál, Budapest and drs G.H. Glas, Arnhem; data Northeast India, Indo-China and Indonesia from files.

leschenaultii) and of the wing as expressed in the index of the 2nd phalanx of the 3rd digit (601 in *arabicus* and 521 in *leschenaultii*). (In fact, these values apply to *Rousettus egyptiacus* sensu lato and to various Asiatic forms of *Rousettus*, including *leschenaultii*, respectively; see the table in Andersen, 1912: 20.) Siddiqi (1961), dealing with the mammals of Pakistan, copied Andersen's (1907b) measurements of pollex and 2nd phalanx of 3rd digit to distinguish *arabicus* and *leschenaultii*. He also labelled individual measurements of 5 specimens of *arabicus* from Panjgur and Karachi in Pakistan and of 5 specimens of *leschenaultii* from Bengal and Burma, which allow for calculation of the mentioned indices; the pollex index range in *arabicus* is 357-381 (mean 369) and in *leschenaultii* 319-364 (mean 334), the index of the 2nd phalanx of the 3rd digit in *arabicus* is 617-654 (mean 637), in *leschenaultii* 522-551 (mean 536). Walton (1974) identified new speci-

mens from Karachi (from University Road near Karachi University) and from 2 miles northeast of Malir City as *R. leschenaultii*. From his measurements it is clear that relatively small bats were involved (mean fal 81; mean W in ♂♂ 82, in ♀♀ 75). It appears that the single specimen from Karachi, a mummified female, is not included in these values. Walton thought these to be the first *leschenaultii* recorded for Pakistan and suggested to check the identities of previously reported *arabicus* from that country (Karachi, Panjgur and Lahore - the latter quoted from Siddiqi, 1969, a source inaccessible to the present author). Murray (1884), however, published data on a specimen from Muklee Hills or Clifton, identified as *amplexicaudatus*, which is clearly a *leschenaultii* (fal 85.1, pollex 25.4, index pollex 298, 2nd phalanx of 3rd digit 47.0, index of this phalanx 552). T. J. Roberts (1977), like Siddiqi (1961), copied Andersen's (1907b) values

for pollex length and length of 2nd phalanx of 3rd digit to discriminate the two species (erroneously stating that *leschenaultii* has a phalanx of ≤ 40 , which should be ≤ 50). He somehow decided that all southern Pakistan *Rousettus* (Panjgur, Makli Hills, Lak Bidok, Karachi/Clifton, and Malir; Lak Bidok quoted from a source not available to the present author: Eates, 1968) must be referred to *arabicus* and all north-eastern Pakistan specimens to *leschenaultii* (Malakand Pass, Vale of Peshawar, Muzaffarabad, Sialkot District, and Lahore; localities quoted from Mirza, 1968 and Siddiqi, 1969, which have not been seen by the present author). He mentioned the following characters to describe *leschenaultii*: compared to *arabicus*, it is slightly smaller on average; it has a more rufescent tone to the dorsal fur; a much more distinct collar of radiating hairs on lower neck and shoulder region, consisting of hairs with pale bases; a pollex of up to 26, with the claw 4; and a small vestigial tail. He gave some field measurement ranges and means for both species which are, unfortunately, useless: the age of the specimens is not specified, the sexes are not separate, *leschenaultii* appears to be larger than *arabicus* (head and body length 120-145 against 105-134), contradictory to his diagnosis, and the pollex is up to 26 in both. Kock (1978a) measured 6 specimens of unknown sex from Malir (AMNH 217280/83, -85, -88), which he had identified as *leschenaultii*: fal 75.2-82.9, pollex 23.2-24.5 ($n = 4$), gsl 36.2-38.2, iow 7.1-8.2, pow 7.9-8.6, C^1-C^1 6.8-7.7, M^2-M^2 10.3-11.7 C^1-M^2 13.4-14.1, C_1-M_3 14.7-16.0, M^1 length 2.44-2.88, and M^1 width 1.44-1.68. Kock *et al.* (1979) stressed that Walton (1974) had found only *leschenaultii* in Karachi and Malir and that Kock (1978a) had also identified Malir specimens as such. They agreed with Walton that the recorded distribution of *egyptiacus arabicus* in Pakistan is doubtful. Nevertheless their own map copies Robert's (1977) and includes Karachi and Malir.

It is of interest to note here that Dulic *et al.* (1973) established some chromosomal differences between Ugandan specimens of *R. egyptiacus leachii* and Indian specimens of *R. leschenaultii*. In relation to the question of the identity of *arabicus*

vis-à-vis *leschenaultii* further chromosomal research may be a promising area.

Summarizing, *leschenaultii* is an altogether smaller bat, with a different fur colour and more distinct collar, shorter wings, longer tail, shorter and slenderer muzzle, smaller teeth, and an elongate instead of roundish M_3 , and possibly differs further from *arabicus* in chromosomal morphology. (See the account of the genus *Lissonycteris* in the next part of this series for an analysis of a number of *Rousettus* characters.)

Size ranges of both *arabicus* and *leschenaultii* and their possible variation in the region are not well-known. In *arabicus* there appears to be a light tendency towards smaller size in its more eastern populations (e.g. fal in ♂♂ from Saudi Arabia 88-95, Yemen 87.7-94.4, Oman 87.8-93.2, Iran 86.2-92.5, and Panjgur in western Pakistan 85.7-91.3; Nader, 1975 and table 3). Dimensions in *leschenaultii* are also quite variable over its range (see Rookmaaker *et al.*, 1981) and populations in adjoining western India show some overlap with *arabicus* (see Table 4). The same may be expected for populations in eastern (and northern) Pakistan. The data available to me - rather many from east of Pakistan but only skull measurements of a few specimens from Malir and Lahore (see Table 5) - suggest that in the region involved *leschenaultii* averages smaller than *arabicus*. Three *arabicus* ♂♂ from Iran had weights of 98.5-128.0 (mean 114.2). Walton (1974) gave 82 as average weight of 4 ♂♂ and 75 as that of 4 ♀♀ of *leschenaultii* from 2 miles northeast of Malir. (T. J. Roberts, 1977, gave 78.2 as average weight of 10 adults from Malir identified as *arabicus* - which are undoubtedly *leschenaultii*). Fal ranges in 7 *arabicus* ♂♂ and 4 ♀♀ from Pakistan are 85.7-91.3 and 82.6-90.2, respectively. According to Walton (1974) the average fal in 4 ♂♂ and 4 ♀♀ of *leschenaultii* from Pakistan is 81; the range will then be about 76-86, which fairly agrees with the range measured in 9 specimens from Poona, India (77.7-84.8; see Table 5). T. J. Roberts (1977) gave 79 as average fal in 11 specimens from the Malakand Pass and Lahore, both in North Pakistan, most probably rightly identified as *leschenaultii*.

In Pakistan, 5 *arabicus* ♂♂ have a gsl range of

40.5-42.7, against one of 37.3-40.6 in 3 *leschenaultii* ♂♂; 3 *arabicus* ♀♀ have a gsl range of 39.0-41.0 against one of 36.1-38.4 in 6 *leschenaultii* ♀♀. However, these ranges are composed of values from various localities and moreover certainly incomplete, and range overlaps are to be expected.

The relative wing proportion as measured by the index of the 2nd phalanx of the 3rd digit appears to be an important differential character deserving further study in the region, as the data quoted earlier from Siddiqi (1961) strongly suggest. (In 46 specimens of *leschenaultii* from north-east India to Bali this index varies from 443 to 586, with a majority of 38 between 480 and 550.)

The length of the tail is quite variable in *Rousettus* species and the remark by Anderson *et al.* (1902) that it would be "considerably longer" in *leschenaultii* than in *arabicus* is not supported by the evidence. Andersen (1912) already gave ranges of 13-17.5 and 9-17, respectively.

Comparing skulls of *arabicus* from Karachi and Panjgur with skulls of *leschenaultii* from Malir and Lahore in the BMNH collection I noted the following relative differences: the skull of *arabicus* is slightly more robust, less deflected, its rostrum broader (especially anteriorly), its teeth are larger, and the distance between M² and the margin of the palate where it passes into the rear of the zygomatic arch insertion is distinctly shorter (c. 0.4 in *arabicus* BMNH 19.11.7.1 from Panjgur against 1.8 in *leschenaultii* BMNH 73.667 from 2 miles northeast of Malir City). Unfortunately, the material did not allow many relevant measurements to be taken.

R. arabicus is known from Karachi and *R. leschenaultii* too (Walton, 1974). The latter has also been reported from Malir, 10 miles east of Karachi, and from 2 miles northeast of Malir. The actual size of the area of sympatry is of interest, as is the relation between the two species: co-existence, ecological or competitive separation, and so on. (It is unfortunate that Murray, 1884, who described a specimen of *leschenaultii*, did not state from where it originated: Mukkle Hills or Clifton.)

Distribution and geographical variation: Regarding the African scope of

the present series, *arabicus* is extralimital. It has been reported once from eastern Ethiopia (Hayman *et al.*, 1971) but pending an analysis of a larger material I consider this allocation as uncertain and refer all Ethiopian specimens to *leachii* (see my remarks on that subspecies). The known distribution of *arabicus* is very patchy. A number of new collecting localities have become known only recently (Harrison, 1980; Harrison *et al.*, 1991; this paper) and more may be expected. Nevertheless, food resources for *Rousettus* in this part of the world are geographically restricted and the pattern will most probably remain patchy. Indeed, some authors have, by inference or explicitly, indicated the apparent rareness of *arabicus* in areas searched by them (T. J. Roberts, 1977, for Pakistan - part of his observations concern *leschenaultii*: see above; DeBlase, 1980, for Iran). However, apart from a possible slight decrease in size from west to east, distinct morphological differentiation between (groups of) populations is not apparent. Of course, the material from many localities is very limited. But in part this supposed uniformity may be due to the species' ability - in these regions probably also a necessity - to fly large distances between roosts and foraging grounds. This mobility, and also the active following of the spreading of fruit tree plantations, is certainly strongly suggested by Yaman (1966), who listed species causing damage to fruit trees in Saudi Arabia in certain parts of the year; a fruit bat identified as *Rousettus* sp. is reported to feed on dates at Hayel, Medinah, Mekah and Taif in June-August, on pomegranate at Medinah, Mekah and Taif in summer, and on grape vine "countrywide" in summer. Nader (1975) identified fruit bats from Tayif as *R. egyptiacus* and believed to have observed the same species in Jeddah. As it is known from several Saudi-Arabian localities in the relatively narrow lowland zone bordering the Red Sea and in the adjoining Asir Mountain range (from south to north: Al Maski, Abhā, Wadi Khaytan, Al Baha and Tayif), the coastal zone being an important area for fruit tree cultivation (Yaman, 1966), its occurrence at Mecca and Jiddah is perfectly likely. Medina, at about 125 km from this zone, is an important agricultural centre itself (Yaman, 1966) and on the border of extensive lava fields

Table 5. Ranges of selected measurements of *Rousettus leschenaultii* (Desmarest, 1820) from Pakistan and western India*

		fal	tibia	ear	tail	gsl	cbl	rl	low	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ¹ - M ₃
2 miles NE of Malir City, Pakistan	♂♂ n					1	1	1	2	2	1				
	min					37.3	36.7	13.7	7.7	7.8	22.5				
	max								7.8	8.9					
	♀♀ n					4	4	3	10	10	6	1		1	2
	mean					36.7	35.3	13.2	7.3	8.4	22.35				
	min					36.1	34.9	13.0	6.8	7.7	21.9	7.0		13.3	15.1
	max					37.6	36.2	13.5	8.2	8.9	23.4				15.7
Lahore, Pakistan	♂♂ n					2	2	2	2	2	2				
	min					39.6	38.0	14.4	7.8	8.0	24.4				
	max					40.6	38.8	15.2	7.9	9.4	24.8				
	♀♀ n					2	2	2	2	2	2	1	1	1	1
	min					36.6	35.2	12.4	7.0	7.8	21.8	6.8	10.7	13.8	15.7
	max					38.4	36.9	13.6	7.4	8.8	22.4				
Khaneri Caves nr Bombay, India	♂♂ n	1	1	1	1	1	1				1			1	
		77.1	40.2	16.8	12.0	37.5	36.0				21.0			14.2	
Parvati Cave, Poona, India	♂♂ n	3	2	3	2	3	3				3			3	
	mean	83.9		20.0		38.6	37.1				22.6			14.7	
	min	83.3	41.5	19.4	12.1	37.9	36.4				21.8			14.2	
	max	84.8	41.8	20.4	13.4	39.4	38.0				23.9			15.1	
	♀♀ n	6	8	8	4	7	7				8			8	
	mean	79.75	37.7	20.1	12.4	36.2	34.8				21.8			13.5	
	min	77.7	36.6	19.1	11.0	35.0	33.7				21.0			13.1	
	max	81.2	39.4	20.9	14.9	36.7	35.4				22.8			14.0	

M¹
length width

2 miles NE of Malir City, Pakistan	♂♂ n	1	1
		2.5	1.6
Lahore, Pakistan	♀♀ n	1	1
	min	2.4	1.4
	max		

* Measurements of Indian specimens courtesy
drs G.H. Glas

(Times atlas) which are likely to offer ample suitable roosting caves. Ha'il is more difficult to envisage as *Rousettus* habitat, unless suitable stepping stones connect it with either Medina or some as yet unknown locality on the Persian Gulf Coast. But it may also be comparable to the isolated occurrences in Iran and Pakistan, which should probably be considered as relicts from times when there was still more forest cover (cf. Harrison, 1964: 3).

With regard to the Red Sea coastal zone it should be noted that *Eidolon helvum* (Kerr, 1792), already known from the southwest corner of the Arabian Peninsula and from Al Shugayri in Saudi Arabia just across the border from Yemen, has recently been reported from as far

north as the Al Baha escarpment (Harrison *et al.*, 1991). This species is also known to cover considerable distances when foraging and although it will probably have more difficulties than *Rousettus* in finding permanent roosting places, it should be expected in other than the known localities.

***Rousettus lanosus* O. Thomas, 1906**

Rousettus lanosus O. Thomas, 1906: 137 (type locality: Ruwenzori East, at 13000'; amended by Hayman *et al.*, 1966: 30: "Mubuku valley, Uganda, 13000'"); Andersen, 1907b: 503, 511; Lönnberg, 1908a: 6; G. M. Allen, 1939a: 62; ? Poll, 1939: 35 (an MRAC specimen from Rutshuru; not mentioned by Hayman *et al.*, 1966; not seen by the present author); Dorst, 1947a: 307; Ryberg, 1947: 40; Theodor, 1955: 227; Benedict, 1957: 332; Hayman *et al.*, 1971: 12 (in part: not including Madagascar); Kock, 1972: 125; Bergmans, 1977a: 71; Kock, 1978a: 209 (in part: not including Madagascar); Whitaker *et al.*, 1978: 634; Bergmans, 1982: 161; Rodgers *et al.*, 1982: 241; Verschuren, 1984: 101; Koopman, 1986: 10.

Rousettus kempfi O. Thomas, 1909: 543 (type locality: Kirui, Mount Elgon at 6000'; corrected and amended into "Kirui's, southern foothills of Mount Elgon, Kenya Colony" by Moreau *et al.*, 1946; further specified as "Twere (Kirui's), south slopes of Mt. Elgon (...), (ca 00 46 N, 34 37 E)" by Swynnerton *et al.*, 1951); G. M. Allen, 1939a: 62; Moreau *et al.*, 1946: 398; Dorst, 1947a: 307; ? Kulzer, 1958: 377; Bergmans, 1977a: 71.

Rousettus (Stenonycteris) lanosus; Andersen, 1912: 49, 813; Schouteden, 1944: 102 (in part: the specimen from foot of Ruwenzori; others not mentioned by Hayman *et al.*, 1966: 31, nor seen by the present author); Hayman *et al.*, 1966: 31; Baeten *et al.*, 1984: 185 (in part: not including Madagascar).

Rousettus (Stenonycteris) kempfi; Andersen, 1912: 813; Swynnerton *et al.*, 1951: 286.

Rousettus leachi; ? Loveridge, 1923: 692; G. M. Allen *et al.*, 1927: 413; ? Theodor, 1968: 321.

Rousettus lanosus kempfi; ? Granvik, 1924: 9 (at most in part; see the text); G. M. Allen *et al.*, 1936: 45; Largen *et al.*, 1974: 230; Eisentraut, 1976: 75; Theodor, 1979: 679.

Rousettus (Stenonycteris) lanosus kempfi; Harrison, 1961: 287; Hayman *et al.*, 1971: 12; Kock, 1978a: 207; Aggundey *et al.*, 1984: 122.

Rousettus (Lissonycteris) angolensis (not of (Bocage, 1898)); Hayman *et al.*, 1966: 30 (in part: specimens MRAC 23674 and 23676 from Butembo, and possibly specimen 9904a from Kabalo: see text).

Rousettus (Stenonycteris) lanosus lanosus; Hayman *et al.*, 1971: 12; Kock, 1978a: 207.

Stenonycteris lanosus; Kingdon, 1974: 134 (in part: not including Madagascar).

Material examined

ETHIOPIA. "Shoa": 1 imm., W. Cornwallis Harris (BMNH 61.2.30.6).

(Afallo, Beletta Forest, Dorsey.)

KENYA. Kairuni: 3 ♂♂, 3 ♀♀, 1 imm. ♀, 20-IX-1973, K. E. Stager (LACM 45617/23). Kakamega Forest: 2 ♂♂ (1: skin only), 2 ♀♀ (1: skull only), IX-1968, R. Glen (ROM 50537/38, -42/43). Kiege Hill: 1 imm. ♀, 10-V-1955, W. G. Dyson (HZM 1.2015). Kiptaget River: 1 ♂, 1 imm. ♂, 1 imm. ♀, 28-III-1968, A. E. Williams (ROM 48719/21). Kyanbym (? Kianbu): 1 imm. ♂, skull (broken) (BMNH 19.4.17.1). Nr Limuru: 3 ♂♂, 2 imm. ♀♀, 4-I-1962, D. Ferrow (LACM 19527/31). Makingeny Cave: 3 imm. ♂♂, 2 ♀♀, 1 imm. ♀, 1980/81, F. Spitzenberger (field numbers 64/69; NMW). Menengai Crater: 2 ♂♂, 3 ♀♀, 1 imm. ♀, 8-VI-1948, and 1 ♂, 1 ♀, without date, H. Hoogstraal and party (FMNH 82227, 85448/51, USNM 317893/94); 1 ♂, 1 ♀, 2 imm. ♀♀, 9-VI-1963, R. E. Mumford (USNM 350779/82); 1 ♂, 4 ♀♀, 31-VIII-1965, A. N. Start (BMNH 75.2422/26); 2 ♂♂, 1 imm. ♂, 3 ♀♀, 5 imm. ♀♀, 23-VII-1968, B. J. Hayward (USNM 436366/76); 1 ♂, 2 imm. ♂♂, 3 ♀♀, 1 imm. ♀, 22-I-1979, A. Walen (ZMA 20.426/32). Nakuru jail cave: 3 ♂♂, 1 ♀, skins (skulls not seen), 3-I-1981, F. Spitzenberger (field numbers 195/99; NMW).

(Kathama Kangundo Escarpment, Kirui's, Mount Elgon, ? nr Naivasha.)

MALAWI. Misuku-Mugheze Mission: 1 ♂, 2 imm. ♂♂, 3 ♀♀, 21-VI-1990, N. J. van Strien (collection Van Strien; ZMA 24.573/74). Nkhata Bay: 1 ♀, 25-XII-1989, N. J. van Strien (collection Van Strien).

RWANDA. (Kanyamiheto, Kinigi, Murunda, Uwinka.)

SUDAN. Gilo: 2 ♂♂, 4 imm. ♂♂, 4 ♀♀, 1 imm. ♀, 5/7-I-1978, 4/10-IV-1978 and 6-X-1978, G. Nikolaus (SMNS 29801, -03/04, -07, -09/15).

TANZANIA. Bagilo: 1 imm. ♂, 6-V-1922, A. Loveridge (USNM 268761); 1 ♂, 1 ♀, 20-IX-1926, A. Loveridge (FMNH 34185/86). Isongo: 1 ♂, 3 ♀♀, 6 imm. ♀♀, 25/28-II-1960, A. F. Rees/D. L. Harrison (HZM 5.3129/12.3146; SMF 19471/72). Mahenge: 3 ♂♂, 1 imm. ♀ (skull), 1 broken skull, 28/29-VIII-1959 and 24-III-1964, A. F. Rees (HZM 2.3034/4.3036; BMNH 64.852/53).

(Elton Plateau, Kibonoto, West Usambaras.)

UGANDA. Bwindi Swamp: 1 ♂, 1 imm. ♂, 4 ♀♀, 2 imm., 20-III-1967, R. Glen (LACM 51534/36, -45/49). Fort Portal: 1 ♂, 27-I-1967, J. G. Williams (ROM 41781). Itama Mine area: 1 ♂, 1 imm. ♂, 1 imm. ♀, 4-VI-1969, R. Glen (LACM 35504/06). Mount Egon: 1 imm. ♀, 16-IX-1909, R. Kemp (paratype of *Rousettus kempfi* O. Thomas, 1909; BMNH 10.4.1.7); 2 skulls (BMNH 34.4.1.1/.2). Old Kalongi: 1 ♂, skin and skull, 7 ♀♀, 1 imm. ♀, alc., 1/8-II-1925, E. Heller (FMNH 26234/37, 30572/77); 1 ♂, 22-XII-1926, J. P. Chapin (AMNH 82526). Ruhizha: 1 ♀, 19-VI-1971, J. Kingdon (HZM 13.6491). Ruwenzori East: 1 imm. ♀ (skin not seen), 13-III-1906, R. Dent (BMNH 6.12.4.11).

ZAIRE. Butago Valley: 2 ♀♀, 1 imm. ♀, 24-XII-1926, J. P. Chapin (AMNH 82380, 82527/28). Butembo: 3 ♂♂, 31-I/21-II-1956, P. Dyleff (MRAC 23553, 23674, -76). Ishibiti: 1 ♀, 28-XII-1963, A. E. M. de Roo (AMNH 207735). Kabira: 1 ♂, 19-III-1959, U. Rahm (MRAC 28025). Kalonge: 1 imm. ♂, 2 ♀♀, 26/28-I- and 22-II-1953, G. F. de Witte (IRSN 17299, 37116/17). Lamya Valley: 1 imm. ♀, 16-XI-1945, J. de Wilde (IRSN 12928). Lwiro: 2 specimens, alc., skulls, 8-IX-1963 and 23-X-1965, P. Kunkel (SMF 31829/30). Murambi: 1 ♂, 6-XII-1954, G. F. de Witte (MRAC 37119). Mutsora: 1 ♀, skin only, 13-VIII-1949, J. de Wilde (IRSN 12927). Nyabiondo: 2 imm. ♂♂, 2 ♀♀, 27-XII-1990/1-I-1991, J.-P. Lubula Bulambo & N. Masumbuko Kamitongo (ZMA 24.344/47). Nyakakumbi, Mugaba Cave: 1 ♀, 1 imm. ♀, 19-VII-1962, A. Elbl (USNM 375232 /33). Ruwenzori (foot): 1 ♂, skin only, 1925, via H. Schouteden (MRAC 9904a). (Kabalo, Kikura, Lake Marion, Lamara, Lwiro, ? Rutshuru.)

Diagnosis: A medium-sized, dorsally long-furred fruit bat, fal 85.3-95.0; skull delicately built, premaxillaries produced forward, not co-ossified; brain-case strongly deflected, alveolar line projected backward passing through middle or upper half of supraoccipital, postorbital width larger than interorbital width; zygomatic arches extremely slender; cheek-teeth narrow, width of large premolars and molars equal to or slightly more than half their lengths; wings from back of second toe (incidentally from between first and second toe); dorsal side of tibia furred; palatal ridges usually 4 + 3 + 1. Measurement ranges and ratios from all over the species' range:

fal	♂♂	85.3 - 93.3	(n = 31),
	♀♀	85.6 - 95.0	(n = 40);
gsl	♂♂	41.1 - 44.8	(n = 26),
	♀♀	39.4 - 43.7	(n = 34);
rl	♂♂	15.6 - 17.9	(n = 27),
	♀♀	15.3 - 17.6	(n = 35);
iow	♂♂	7.2 - 8.8	(n = 29),
	♀♀	7.0 - 8.7	(n = 36);
pow	♂♂	8.5 - 10.5	(n = 29),
	♀♀	8.1 - 11.1	(n = 37);
zw	♂♂	23.4 - 26.6	(n = 27);
	♀♀	22.3 - 25.6	(n = 30);
C ¹ -C ¹	♂♂	8.5 - 10.0	(n = 27),
	♀♀	7.9 - 9.8	(n = 35);
M ² -M ²	♂♂	11.3 - 13.2	(n = 22),
	♀♀	10.9 - 13.2	(n = 26);

C ¹ -M ²	♂♂	13.8 - 15.7	(n = 25),
	♀♀	13.5 - 15.6	(n = 30);
C ₁ -M ₃	♂♂	15.1 - 17.8	(n = 27),
	♀♀	15.5 - 17.5	(n = 32);
M ¹ length	♂♂	2.1 - 2.45	(n = 3),
	♀♀	2.15 - 2.5	(n = 5);
M ¹ width	♂♂	1.1 - 1.45	(n = 11),
	♀♀	1.0 - 1.5	(n = 17);
W	♂♂	102 - 140	(n = 11),
	♀♀	94 - 162	(n = 20);
rl	♂♂	37.9 - 41.1% of gsl	(n = 26),
	♀♀	38.0 - 41.1% of gsl	(n = 34);
C ₁ -C ₁	♂♂	20.0 - 23.0% of gsl	(n = 25),
	♀♀	19.7 - 22.4% of gsl	(n = 31);
M ₂ -M ₂	♂♂	26.2 - 30.4% of gsl	(n = 21),
	♀♀	27.1 - 31.3% of gsl	(n = 23).

The female weight range can be subdivided into one of 94-127 for 15 non-pregnant and one of 120-162 for 5 pregnant ♀♀. Specimens from Zaïre, West Uganda (and most probably Rwanda) have narrower cheek-teeth, on average, than specimens from Ethiopia, Sudan, East Uganda, Kenya, Tanzania and Malawi. Other geographical variation to be discussed under Remarks. Table 6 gives a breakdown of measurement ranges per country.

Distribution: Fig. 3.

Related species: *Rousettus egyptiacus* is sympatric with *R. lanosus* over most of its range. This species is short-furred, averages somewhat larger (in East Africa: fal 85.7-106.3, gsl 38.3-45.7), has a stronger and only moderately deflected skull, stronger teeth, wings usually from the first toe, and dorsally naked tibiae.

Some differences between *R. lanosus* and more distant species may be derived from the paragraph on related species in the account of *R. egyptiacus egyptiacus*. Both *R. madagascariensis* (fal 66.0-76.2, gsl 34.1-37.6) and *R. obliviosus* (fal 70.3-76.6, gsl 33.5-36.7) are extralimital, absolutely smaller, and have dorsally naked tibiae.

Remarks

Taxonomy: As outlined in the introductory notes on the genus *Rousettus*, it is not possible to

clearly define the subgenus *Stenonycteris* Andersen, 1912. An assessment of possible subgeneric divisions is beyond the scope of the present series. The same applies to the recognition of *Stenonycteris* as a genus on its own as has been suggested, in passing as it were, by Leche (1921) and endorsed by Kingdon (1974).

Several authors (Hayman *et al.*, 1971; Kingdon, 1974; Kock, 1978a; Baeten *et al.*, 1984) hold that *Rousettus lanosus* sensu lato inhabits not only East African mountain ranges but also Madagascar. In their view, *Rousettus madagascariensis* is only a subspecies of *R. lanosus*. It is of interest to trace the origin of this idea. Dorst (1947a) wrote that *R. madagascariensis*, which he knew from its original description only, "shows affinities with the continental forms *R. kempi* Thomas and *R. lanosus* Thomas, through the flattening of the brain-case: the skull profile is indeed rectilinear from the nostrils to the top of the brain-case. It differs from them especially by its smaller size (forearm: 65 mm); it is the smallest species of the genus" (translation: W. B.). The straight skull profile from the anterior tip of the nasals to the top of the brain-case is suggested by the original drawing in Grandidier (1929), who also emphasized it in his text. See also Grandidier *et al.*, 1932. But the illustration is peculiar because it does not show the interruption of this profile by the slightly bulging interorbital sinuses which are present in *madagascariensis* (compare fig. 2 in Bergmans, 1977a) and in *lanosus* (see fig. 3 in Andersen, 1912). A straight or nearly straight anterior dorsal skull profile is shared with typical *Rousettus* (i.e. *egyptiacus*) as well (compare fig. 2 in Andersen, 1912) and a useless character in the present context. The other character mentioned by Dorst, small size (fal 65), is much more important because it is far beyond the range of *lanosus*. The procedure followed by Hayman *et al.* (1971) who based the synonymy on a few stray remarks derived from a detailed description without consulting this in the first place does not seem correct. They moreover quoted Dorst rather too freely when stipulating that this author had noted that "its affinities are with *kempi* and *lanosus* and that the chief difference lies in the smaller size...". Their further remark that more material

would be needed to confirm or reject this allocation suggests that Dorst had synonymized *madagascariensis* with *lanosus*, which he had not. Of their followers, only Kock (1978a) consulted Grandidier (1929) but failed to conclude that *madagascariensis* is different from *lanosus* on a specific level, misled by the too narrow teeth in the original figures (Dr D. Kock, *in lit.*, 7-IX-1976) and not counting obvious differences in size and proportions.

Meanwhile, the patchy distribution of *Rousettus lanosus* is complicated enough. The apparent isolation of groups of populations has given rise to several local, or regional, morphological developments. The first to be discovered was the slightly stronger dentition in specimens from Mount Elgon if compared to the typical specimens from Ruwenzori. O. Thomas (1909) based a new species, *Rousettus kempi*, on this difference (and a slight difference in fur colour). Granvik (1924) ranked *kempi* as a subspecies of *lanosus*. He did not provide arguments and re-examination of two of his 23 specimens from Mount Elgon revealed that they were *Rousettus egyptiacus leachii*. G. M. Allen *et al.* (1936) reported on *R. lanosus kempi* from Mount Elgon, stating that *kempi* "is only a very slightly differentiated race". With the notable exception of G. M. Allen himself (1939a), who somehow listed *kempi* again as a full species, subspecific status for *kempi* has been accepted (or specific status denied) by most students of specimens from beyond the typical *lanosus* range, i.e. East Zaïre, adjoining West Uganda, and probably Rwanda (Hayman *et al.*, 1971; Kingdon, 1974; Largen *et al.*, 1974; Eisentraut, 1976; Kock, 1978a; Theodor, 1979; Bergmans, 1982; Rodgers *et al.*, 1982; Aggundey *et al.*, 1984; Baeten *et al.*, 1984). Thus, specimens from Ethiopia, Sudan, Kenya and Tanzania (see G. M. Allen *et al.*, 1936) were all assigned to or associated with *R. lanosus kempi*. And as far as teeth dimensions are concerned, specimens from Malawi also agree with *kempi* rather than *lanosus*. For these first records for Malawi I am much indebted to Dr N. J. van Strien.

Andersen (1912) published teeth measurements of the type specimens of both *lanosus* and *kempi* (the latter unfortunately mixed with a specimen

Table 6. Ranges of selected measurements of *Rousettus lanosus* O. Thomas, 1906, per country. Order of countries chosen to reflect trends of geographical variation (see the text).

			fal	gsl	rl	iow	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ₁ - M ₃	M ¹ length	width	W T
Zaire	♂♂	n	4	2	3	4	4	3	4	2	4	4	2	2	
		mean	88.4		16.6	7.8	9.4	24.1	8.85		14.4	16.2			
		min	85.3	41.9	15.8	7.2	8.5	23.8	8.8	11.3	13.8	15.1	2.1	1.1	
		max	92.5	42.6	17.5	8.5	10.0	24.7	8.9	c.11.8	15.0	16.8	2.4	1.2	
	♂♂	n	5	5	5	5	5	5	4	2	2	4	1	1	2
		mean	92.3	42.2	17.0	7.5	9.8	23.4	8.6			16.0			
		min	90.0	41.0	16.5	7.0	9.2	22.9	8.3	11.3	14.0	15.6	2.15	1.3	120
		max	95.0	43.1	17.6	8.1	10.8	23.8	8.9	11.7	14.7	16.3			162
	?	n		2											
		min		40.3											
		max		42.6											
West Uganda	♂♂	n	4	5	5	5	5	5	5	1	2	5			3
		mean	90.8	42.5	17.1	8.0	9.3	24.5	9.0			16.8			c.127
		min	88.0	41.2	16.7	7.8	8.8	23.9	8.7	11.5	14.4	16.2			115
		max	92.0	43.9	17.7	8.3	9.7	25.4	9.2		15.6	17.8			135
	♀♀	n	11	9	9	9	9	5	8	5	6	6		1	5
		mean	90.5	41.9	16.9	7.6	9.5	23.0	8.6	11.4	14.4	16.2		1.2	126
		min	87.6	39.6	15.9	7.1	8.8	22.3	8.3	10.9	14.0	15.6			99
		max	94.1	43.5	17.5	8.2	10.4	24.7	9.0	11.7	15.0	17.0			142
	♂♂	n	1	1	1	1	1	1	1	1	1	1			1
		mean	88.3	42.0	16.1	7.5	9.2	24.0	8.9	11.8	14.1	16.3			112
		min													
		max													
Sudan	♀♀	n	1	3	3	3	3	3	3	2	3	3			4
		mean		39.8	15.6	7.7	9.0	23.0	8.1		14.1	15.7			100
		min	90.0	39.4	15.3	7.5	8.1	22.7	7.9	12.3	14.0	15.5			94
		max		40.6	15.9	7.9	10.1	23.4	8.3	12.7	14.3	16.0			115
	♂♂	n	17	13	13	14	14	13	13	13	13	13		1	7
		mean	89.8	42.7	16.9	7.7	9.2	25.0	8.9	12.2	14.9	16.8			123
		min	86.6	41.1	15.6	7.4	8.5	23.4	8.5	11.6	14.1	16.1		1.1	102
		max	93.3	44.0	17.7	8.2	10.0	26.0	9.4	13.2	15.7	17.8			140
	♀♀	n	15	12	12	13	14	11	13	11	12	13	1	4	9
		mean	88.8	41.7	16.5	7.5	9.4	23.8	8.5	12.0	14.6	16.5		1.3	113
		min	85.6	40.1	15.5	7.1	8.4	23.0	8.1	11.4	14.0	15.7	2.5	1.2	100
		max	92.0	43.7	17.5	8.4	10.0	25.1	9.1	12.8	15.6	17.3		1.4	125
Tanzania	♂♂	n	4	4	4	4	4	4	3	4	4	3			3
		mean	89.9	43.5	17.4	8.5	9.9	26.2	9.7	12.8	15.1	17.0		1.23	
		min	88.7	42.5	16.5	8.3	9.6	25.6	9.5	12.4	14.4	16.3		1.2	
		max	92.8	44.8	17.9	8.8	10.5	26.6	9.9	13.1	15.6	17.6		1.3	
	♀♀	n	4	2	3	3	3	3	4	3	4	3			8
		mean	89.7		17.3	8.2	10.6	25.2	9.2	12.8	14.5	16.3		1.2	
		min	85.9	43.3	17.3	7.9	10.4	24.8	8.6	12.6	13.5	15.5		1.0	
		max	93.5	43.7	17.4	8.7	10.9	25.6	9.8	13.2	15.3	17.2		1.3	

Table 6, continued.

		fal	gsl	rl	iow	pow	zw	C ¹ - C ¹	M ² - M ²	C ¹ - M ²	C ₁ - M ₃	M ¹ length	width	W
Malawi	♂♂ n	1	1	1	1	1	1	1	1	1	1	1	1	
		91.4	44.0	17.5	8.2	9.7	25.7	10.0	12.8	14.8	17.1	2.45	1.45	
	♀♀ n	3	3	3	3	3	3	3	3	3	3	3	3	
	mean	92.0	43.5	17.4	8.0	10.4	25.0	9.5	12.8	14.9	17.0	2.5	1.4	
	min	91.3	43.4	17.3	7.9	10.0	24.7	9.4	12.7	14.7	16.5	2.5	1.35	
	max	92.9	43.5	17.5	8.1	11.1	25.2	9.6	13.0	15.2	17.5	2.5	1.5	

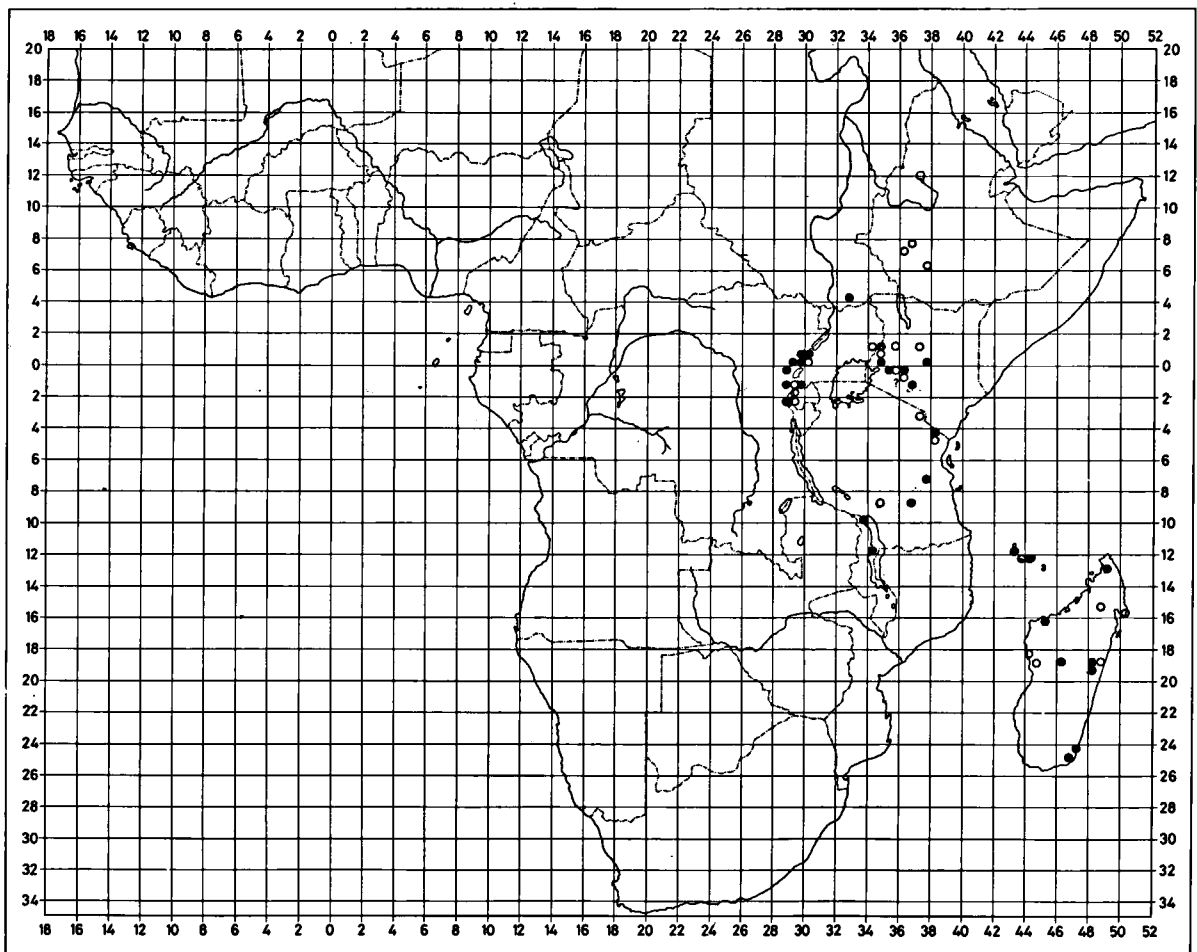


Fig. 3. Distribution of *Rousettus lanosus* O. Thomas, 1906: African mainland; *Rousettus madagascariensis* Grandidier, 1929: Madagascar; and *Rousettus obliviosus* Kock, 1978: Comores. Black dots: squares from which material has been identified by the author. Open circles: records from literature, museum registers, and correspondence.

Table 7. Measurements of teeth in *Rousettus lanosus* O. Thomas, 1906: length x width, measured over the cingula.

Country		Zaire			Kenya		
Locality Specimen	Kabira MRAC ¹ 28025	Nyabiondo ZMA 24.346		Butembo MRAC ¹ 23553	Menengai ZMA 20.428		Menengai ZMA 20.431
Sex	♂	♀		♂	♂		♀
C ¹		2.2 x 1.5			2.3 x 1.45		2.2 x 1.6
P ¹		0.8 x 0.7			0.7 x 0.6		0.7 x 0.65
P ³	2.6 x 1.3	2.35 x 1.3		2.3 x 1.2	2.4 x 1.3		2.3 x 1.2
P ⁴	2.7 x 1.4	2.55 x 1.35		2.4 x 1.3	2.9 x 1.45		2.65 x 1.45
M ¹	2.4 x 1.2 ³	2.15 x 1.3		2.1 x 1.1	2.55 x 1.45		2.5 x 1.35
M ²	1.2 x 0.8 ³	1.35 x 0.95		1.2 x 0.8	1.45 x 1.1		1.3 x 1.0
C ₁		1.6 x 1.5			1.8 x 1.6		1.6 x 1.5
P ₁		1.35 x 0.95			1.6 x 1.0		1.45 x 1.2
P ₃	2.1 x 1.1	1.9 x 1.1		1.9 x 1.0	2.15 x 1.2		2.0 x 1.2
P ₄	2.4 x 1.3	2.2 x 1.2		2.1 x 1.2	2.45 x 1.2		2.4 x 1.3
M ₁	2.6 x 1.2	2.3 x 1.2		2.3 x 1.0	2.7 x 1.35		2.7 x 1.35
M ₂	1.7 x 1.1	1.5 x 1.05		1.5 x 0.8	1.8 x 1.2		1.75 x 1.2
M ₃	1.3 x 0.9	1.3 x 0.8		1.1 x 0.8	1.45 x 1.0		1.35 x 1.05

Country		Malawi			
Locality Specimen	Misuku ² v. Strien Coll.	Misuku ² v. Strien Coll.	Misuku ² v. Strien Coll.	Misuku ² v. Strien Coll.	Nkhata Bay v. Strien Coll.
Sex	♂	♂	♀	♀	♀
C ¹					
P ¹					
P ³					
P ⁴	2.7 x 1.35	2.85 x 1.45	2.6 x 1.35	2.8 x 1.45	2.95 x 1.5
M ¹	2.45 x 1.45	2.6 x 1.45	2.5 x 1.35	2.5 x 1.35	2.5 x 1.5
M ²	1.45 x 1.05	1.35 x 1.1	1.5 x 0.95	1.45 x 1.05	1.5 x 1.1

¹ MRAC specimens: calliper measurements; ² Misuku-Mughese Mission; ³ teeth very worn.

from Shoa). Largest are the differences in length in P⁴ (0.3-0.5 mm), M¹ (0.2-0.6), P₄ (cf. 0.3), and M₁ (0.2-0.4), and in width in M¹ (0.3-0.4), M² (0.4-0.6), and M₁ (0.3-0.4). Table 7 gives some of my more accurate teeth measurements. Of the Zairese specimens the one from Kabira agrees with typical *lanosus*, while the other two show a tendency towards still smaller lengths. The examples from Kenya, which would represent *kempi* (Hayman *et al.*, 1971; Aggundey *et al.*, 1984), have generally shorter and narrower cheek-teeth than the types of *kempi* (with the possible exception of

M₃ length). The specimens from Malawi tend to agree with those from Menengai, Kenya. To these observations may be added that specimens from Gilo, Sudan, also agree more or less with those from Menengai: P⁴ and M¹ are somewhat shorter in some specimens, while at the same time canines and first upper and lower molars are slightly more robust (Bergmans, 1982). Summarizing, the whole eastern arc of *lanosus* populations, from Ethiopia via South Sudan over East Uganda, Kenya and Tanzania to Malawi, differs from the western arc (Zaire, West Uganda

Table 8. Relative widths over cingula of C^1-C^1 and M^2-M^2 in *Rousettus lanosus* O. Thomas, 1906 per country.

		East Zaïre				West Uganda				Sudan			
		n	min	-	max	n	min	-	max	n	min	-	max
gsl	♂♂	2	41.9	-	42.6	5	41.2	-	43.9	1			42.0
	♀♀	5	41.0	-	43.1	9	39.6	-	43.5	3	39.4	-	40.6
C^1-C^1 as % of gsl	♂♂	2	20.65	-	21.0	5	20.7	-	21.8	1			21.2
	♀♀	4	20.0	-	20.8	8	19.8	-	21.4	3	20.05	-	20.75
M^2-M^2 as % of gsl	♂♂	1		c.	28.1	1			26.2	1			28.1
	♀♀	2	27.3	-	27.4	5	27.1	-	28.0	2	31.2	-	31.3
		Kenya				Tanzania				Malawi			
		n	min	-	max	n	min	-	max	n	min	-	max
gsl	♂♂	13	41.1	-	44.0	4	42.5	-	44.8	1			44.0
	♀♀	16	39.4	-	43.7	2	43.3	-	43.7	3	43.4	-	43.5
C^1-C^1 as % of gsl	♂♂	13	20.0	-	22.15	3	22.1	-	23.05	1			22.7
	♀♀	16	19.7	-	21.4	1			22.4	3	21.6	-	22.05
M^2-M^2 as % of gsl	♂♂	13	27.85	-	30.0	4	28.2	-	30.45	1			29.1
	♀♀	14	28.2	-	31.3	2	28.8	-	30.5	3	29.2	-	29.95

and, probably, Rwanda) in larger teeth dimensions. But there is overlap between the arcs, and there are appreciable differences between the groups of populations which together constitute the eastern arc.

And there are other variables which interfere with a simple east-west divide. (As with teeth dimensions, the numbers of data per highland area or mountain range are restricted.) In some respects, the specimens from Sudan and Kenya (and thus, possibly Ethiopia) appear to be intermediate between those of the western arc and those of (the remainder of) the eastern arc. Western arc specimens have slightly smaller skulls, on average, than those of the eastern arc except Sudan and Kenya. The same applies to the relative width over C^1-C^1 . Specimens of the western arc also have relatively small M^2-M^2 widths. In this, specimens from Sudan and Kenya agree with those from Tanzania and Malawi. (The discussed measurements are listed in Table 8.) Next to typical *lanosus* (western arc) and *kempi* (Mount Elgon and, with some variation, Sudan, Kenya and possibly Ethiopia) one

could consider the populations from Tanzania and Malawi to represent a third subspecies, characterized by the combination of a relatively large skull, a wide rostrum, possibly a different palatal ridge pattern (4 + 4 + 1, in Malawi specimens), and large teeth. But at the present stage I prefer not to distinguish any subspecies, as they would still be only weakly defined and as much more variation may be expected to come to light when the species and its distribution become better known.

Distribution and geographical variation: In Ethiopia, *lanosus* is known from the plateau west of the Central Rift only. The few known localities are all south of the Abbai River (or Blue Nile). Between this plateau and the chain of mountains along the borders of Sudan with Uganda, where the species is known from the Imatong Mountains, and of Uganda and Kenya, where it has been found at Mount Elgon (and further east), the vast Turkana depression with the Lotagipi Swamp and Lake Turkana must present an insurmountable barrier for this species. Its occurrence at some of the

mountains between Imatong and Elgon is to be expected - provided that there is forest. Between the Imatong Mountains and the collecting localities at Ruwenzori and the nearly continuous mountain ranges and their outliers in the border region of Zaïre and its eastern neighbours, the very broad peneplain of the Bahr el Jebel or Albert Nile will constitute a barrier. The species should be looked for, however, in the Blue Mountains west of Lake Albert. In Kenya, the distribution of *lanosus* appears to be continuous from Mount Elgon to Mount Kenya (i.e. the nearby Kiega Hill) and Nairobi (i.e. Limuru and Kiambu). The southern extension of the Kenyan Highlands east of Lake Magadi and, in Tanzania, east and south of Lake Natron and southwest of Lake Manyara, have, to my knowledge, hardly been searched for fruit bats and *Rousettus lanosus* may certainly be expected here, where forests have persisted. Rodgers *et al.* (1982) and Lovett (1990) indicated montane forest at Ngorongoro and Hanang, in this region. The eastern arc of the distribution pattern is continued through eastern Tanzania, including Kilimanjaro (Kibonoto), West Usambaras (Isongo), Uluguru Mountains (Bagilo), Mahenge (at a mere 1067 m), and the Elton Plateau. Kingdon (1974) mapped four localities in Tanzania, one of which suggests that he found the species in the Uzungwa Mountains (near Iringa). It may of course also be expected in other forested mountain islands in this chain: Meru perhaps, the Para ranges, the East Usambaras, the Nguru and Ukaguru Mountains, and some smaller ones (see Lovett, 1990 for a map). The arc is further continued into Malawi, where *lanosus* has been collected near the Misuku-Mughese Mission on the Mughese Hill in the extreme northwest and at Nkhata Bay, at 11°37' S at the coast of Lake Malawi.

Of the 54 traceable collecting localities 32 lie in Undifferentiated Afromontane vegetation (59%; type 19a in White, 1983), 3 others probably also, and 10 on the border of this type and another; 4 are in Mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland (type 45 in White, 1983), and 1 in each of the following types: Drier types of Guineo-

Congolian rain forest, Wetter Zambezian miombo woodland (dominated by *Brachystegia*, *Fulberardia* and *Isoberlinia*), Drier Zambezian miombo woodland (dominated by *Brachystegia* and *Isoberlinia*), East African evergreen and semi-evergreen bushland and thicket, and Somalia-Masai *Acacia*-*Commiphora* deciduous bushland and thicket (types 2, 25, 26, 38 and 42, respectively, in White, 1983). Altogether 83% of the localities are in or associated with montane vegetation. The known collecting altitudes for *R. lanosus*, 950-3977 m (Bergmans, 1977a; Kock, 1978a), are extended through the find at Nkhata Bay in Malawi, which is at 500 m. But of the 44 known altitudes only two are below 1000 m, 5 between 1000 and 1500 m, 18 or 19 between 1500 and 2000 m, 13 between 2000 and 2500 m, 2 between 2500 and 3000 m, and 3 between 3500 and 4000 m. In conclusion, *R. lanosus* is largely but not strictly montane.

To explain the present discontinuous montane distribution, Kingdon (1974) conjectured that *lanosus* might represent "an early population of cave-dwelling bats that has been displaced in all but the coldest habitats by the superior *Rousettus aegyptiacus*." This would imply that *lanosus* as such is not of montane origin. The species' most striking specializations appear to be the weakening of its skull and teeth, which must be related to a particular diet, i.e. food plant species (see also Andersen, 1912: 23). At the (tree) species level, Afromontane rain forest (a section of the mentioned type 19a in White, 1983) is almost completely different from Guineo-Congolian lowland rain forest. This apparently also applies to other montane forest types *vis-à-vis* this and other lowland forest types. It is plausible, therefore, that *lanosus* evolved in - or with - one of these presently montane forest types, and was not driven there by a competitive relative. Its occurrence on many mutually widely separated mountains and mountain ranges should probably be explained by the hypothesis which Moreau (1966) put forward in relation to East African montane forest birds showing similar scattered distributions. During various colder periods of the Pleistocene, and for the last time only 25,000-18,000 years ago, montane climate conditions reigned over large parts

of lowland Africa, and were continuous from Ethiopia to Angola and the Cape Province. During such periods the distribution of what is now montane vegetation, and its zoocoenosis (including such species as *Rousettus lanosus*), could gradually expand to eventually cover much of lowland East Africa, to be thrown back on remaining islands of high altitude offering suitable climatic conditions during warmer periods such as the Present. Indeed, the collective flora of the "Afromontane archipelago-like regional centre of endemism", including all the mountainous areas here considered, shows a remarkable continuity and uniformity (White, 1983).

Rousettus egyptiacus has not necessarily been absent in East Africa during the Pleistocene, but its movements have probably been the reverse of those assumed here for *R. lanosus*: the colder periods will have forced it into a marginal existence or even exclusively to the lowest regions, at the coast, while withdrawals of *lanosus* to higher altitudes will have been followed by new advances of *egyptiacus*. If competition between the two has ever been - or still is - the case, it will be restricted to altitudinal zones of overlap, and probably rather for caves than for food. In East Africa, *egyptiacus* has occasionally been collected at considerable heights, up to 2512 m (at Uwinka, Rwanda), and potentially there is ample chance for the two species to meet. However, not many localities - eight, to my knowledge, have yielded both species and the two are known to occur not far from one another in only a few other areas. There is only one published instance of actual cave-sharing, in the cave under the Sipi Falls on Mount Elgon (G. M. Allen *et al.*, 1936; Kingdon, 1974). My preliminary conclusion is that differences in ecological preferences keep the two species largely, but not categorically separated.

In the section on taxonomy three geographical groups of populations have been distinguished: those of the western arc (Zaire, West Uganda, and probably Rwanda), the northern part of the eastern arc (East Uganda, Kenya, Sudan, and probably Ethiopia), and the southern part of the eastern arc (Tanzania, Malawi). If the process of skull and teeth degeneration is considered a progressive trend, the most advanced *lanosus* inhabit

the western arc, intermediate forms the second region, and the most conservative the third. This suggests that *lanosus* may be of southern origin and that it has first dispersed towards the northern part of the eastern arc, and from there on to the western arc. Movements within each of the three regions must have been more frequent than between them. It may be of significance in this context that many of the eastern arc mountains and highlands are of Pliocene age, whereas those of the western arc (Ruwendzori, Virungas) reached their present heights only during the Pleistocene.

***Rousettus madagascariensis* Grandidier, 1929**

Rousettus madagascariensis Grandidier, 1929: 91 (type locality: surroundings of Beforona); Grandidier *et al.*, 1932; Dorst, 1947a: 307, 1947b: 82; ? Decary, 1950; Jobling, 1952: 132; Theodor, 1955: 207; Bergmans, 1977a; Honacki *et al.*, 1982: 126; Meirte, 1987; Bergmans *et al.*, 1988: 10; Nicoll *et al.*, 1989: 58, 84, 217; Pont *et al.*, 1990.

Rousettus (Stenonycteris) madagascariensis; G. M. Allen, 1939a: 63.

Rousettus (Stenonycteris) lanosus madagascariensis; Hayman *et al.*, 1971: 12.

Stenonycteris lanosus (not of (O. Thomas, 1906)); Kingdon, 1974: 134 (in part: the record from Madagascar).

Rousettus lanosus (not of O. Thomas, 1906); Largen *et al.*, 1974: 255 (in part: the records from Madagascar).

Rousettus lanosus madagascariensis; Kock, 1978a: 205; Cheke *et al.*, 1981: 231.

Rousettus (Stenonycteris) lanosus (not of O. Thomas, 1906); Baeten *et al.*, 1984: 185 (in part: the record from Madagascar).

Rousettus (Rousettus) madagascariensis; Corbet *et al.*, 1991: 41.

Material examined

Grotte de l'Ankarana: 1 ♀, alc., skull, 1924, Mr Waterlot (MNHN). Bevato: 1 imm. ♀, alc., skull, 10-VI-1930, R. Archbold/A. L. Rand/P. A. Du Mont (MNHN CG 1975-800); possibly from the same locality, date and collectors: 1 ♂, 2 ♀♀, 1 imm. ♀ (MNHN CG 1975-795, -798/799, ZMA 19.312). 8 miles NE of Fort Dauphin: 2 ♂♂, 1 imm. ♂, 3 ♀♀, 1 imm. ♀, 15/16-VI-1968, A. E. Williams (ROM 46919/25). Mananteina: 2 ♂♂, 1 ♀, 28-XI-1948, H. Hoogstraal/R. Alison (FMNH 85229/30, USNM 317899). Mandramondronta River: 1 imm. ♀, 15-VI-1968, A. E. Williams (ROM 46918). Namoroka: 1 imm. ♀, alc., 6-III-

1931, A. L. Rand/P. A. Du Mont (MNHN CG 1975-797). Perinet (in part: 990 m): 3 ♂♂, 1 imm. ♂, 1 ♀, 2 imm. ♀♀, 3rd week III-1967 and 24-IV-1967, R. L. Peterson/J. G. Williams/R. Glen (ROM 42038/41, 42130/32); (800 m): 6 ♂♂, 1 ♀, IV/V-1969, R. Bénédicte (ROM 51114/20). 8 km S of Perinet: 12 ♂♂ (of which 2 in alc., 1 skeleton), 7 imm. ♂♂ (5 in alc., 1 skeleton), 2 ♀♀ (1 in alc.), 9 imm. ♀♀ (6 in alc.), 23-IV-1967, R. L. Peterson/J. G. Williams/R. Glen (ROM 42007/36). "Madagascar": 2 ♂♂, 5 ♀♀, 1 imm. ♀, no date, R. Decary (MNHN CG 1975-785/92); 1 imm. ♂ (MNHN CG 1912-45).

(Antsalova, nr Beforona, Forêt de Tsimembo, Masoala Peninsula, Réserve Naturelle Intégrale de Maroejy, Réserve Spéciale d'Ankarana, Réserve Naturelle Intégrale du Tsingy de Bemaraha.)

Diagnosis: A small-sized, normally furred fruit bat, fal range 66.0-76.2; skull delicately built, premaxillae produced forward, not co-ossified; brain-case moderately deflected, alveolar line projected backward passing through upper part of, or just above, condylus occipitalis or just above the foramen magnum; postorbital width larger than interorbital width in most specimens; supraoccipital crest low; zygomatic arches slender; cheek-teeth relatively narrow, with the widths of premolars and molars about equal to or slightly more than half their lengths, except M² and M₃ in which the width is distinctly larger; wings from between 1st and 2nd toe; dorsal side of tibia practically naked; palatal ridges 4 + 3 + 1. Measurement ranges and ratios from all over the species' range:

fal	♂♂	67.3 - 76.0	(n = 28),
	♀♀	66.0 - 76.2	(n = 13);
gsl	♂♂	34.1 - 38.2	(n = 25),
	♀♀	34.4 - 37.6	(n = 11);
rl	♂♂	12.5 - 14.4	(n = 3),
	♀♀	13.0 - 14.8	(n = 7);
iow	♂♂	6.2 - 7.6	(n = 27),
	♀♀	6.2 - 7.3	(n = 11);
pow	♂♂	6.1 - 8.2	(n = 27),
	♀♀	6.8 - 8.3	(n = 10);
zw	♂♂	19.7 - 22.6	(n = 26),
	♀♀	18.6 - 21.0	(n = 7);
C ¹ -C ¹	♂♂	6.8 - 7.7	(n = 26),
	♀♀	6.4 - 7.3	(n = 11);
M ² -M ²	♂♂	9.6 - 11.0	(n = 26),
	♀♀	9.6 - 10.8	(n = 11);

C ¹ -M ²	♂♂	12.8 - 14.4	(n = 27),
	♀♀	12.7 - 14.5	(n = 11);
C ₁ -M ₃	♂♂	14.0 - 15.8	(n = 27),
	♀♀	14.2 - 16.3	(n = 11);
M ¹ length	♂♂	2.25 - 2.4	(n = 2),
	♀♀	2.2 - 2.3	(n = 4);
M ¹ width	♂♂	1.3 - 1.4	(n = 2),
	♀♀	1.3 - 1.4	(n = 4);
W	♂♂	60.0 - 83.0	(n = 16),
	♀♀	44.0 - 61.0	(n = 4);
rl	♂♂	36.5 - 38.7% of gsl	(n = 3),
	♀♀	37.1 - 39.4% of gsl	(n = 7);
C ¹ -C ¹	♂♂	19.0 - 20.9% of gsl	(n = 25),
	♀♀	18.2 - 20.5% of gsl	(n = 11);
M ² -M ²	♂♂	25.9 - 29.3% of gsl	(n = 25),
	♀♀	27.0 - 29.4% of gsl	(n = 11).

These ranges and ratios are for a large part based on measurements of ROM specimens as taken by the late Dr R. L. Peterson, who was considering a report on this important new material when the present author published a note on newly discovered specimens in the MNHN (Bergmans, 1977a). Dr Peterson then abandoned his plan because this would have led to a near duplication, and kindly made his data available, which is gratefully acknowledged here. Grandidier (1929) measured a fal of 65 and a zw of 23 in the holotype specimen, a male, his other measurements of its skull falling within the ranges given above. Pont *et al.* (1990) gave as maximum fal in ♂♂ 77.2 and as minimum weight in ♂♂ 59; their other measurements possibly all apply to juvenile and subadult specimens. (The available data on ♂♂ suggest some slight geographical variation but unfortunately some crucial ones are without locality.)

Distribution: Fig. 3.

Related species: *Rousettus obliuissus* from the Comores is about similar in size (its fal on average probably somewhat longer, its skull on average somewhat smaller), but has a more strongly built skull with a broader rostrum and a stronger brain-case deflection, distinctly stronger teeth - especially P₁, and other premolars and molars. *Rousettus lanosus* of the East African mainland shares a delicate skull built and narrow cheek-teeth, but its skull shows a strong brain-case

deflection and the species is absolutely larger (fal 85.3-95.0, gsl 39.4-44.8), with long fur and dorsally furred tibiae.

Remarks

Taxonomy: Subgeneric divisions including *Stenonycteris* used by many authors to distinguish certain *Rousettus* species are not recognized here for reasons indicated in the introductory notes on the genus.

The year of publication of *Rousettus madagascariensis* is often cited as 1928 but Tome XI of the Bulletin de l'Académie Malgache, Nouvelle Série, for 1928, in which it appeared, was published in 1929. The type specimen, an adult male, was collected in 1917 near the village of Beforona for the Académie Malgache. Presently, it forms part of the Grandidier Collection acquired for the Museum of Comparative Zoology in Cambridge, Massachusetts in January 1947 (as no. MCZ 45432; Ms M. E. Rutzmoser, *in lit.*, 18-XI-1988). Hayman *et al.* (1971) and several followers considered *madagascariensis* a subspecies of *R. lanosus*. The origin of this mistaken idea, countered by Bergmans (1977a) but adhered to by Kock (1978a) and Baeten *et al.* (1984), has been dealt with in the account of *R. lanosus*. *R. madagascariensis* differs from that species in absolute size, ear form, length and distribution of fur, wing insertion, measure of brain-case deflection, angle between mandibular ramus and coronoid process, teeth morphology and dimensions, and ecology (Bergmans, 1977a; this paper). The following observations on its differences from *R. obliviosus* are largely based on the direct comparison of two specimens only (ZMA 19.312 and 20.903).

R. madagascariensis has a more delicately built skull, more protruding premaxillae and upper canines, a narrower rostrum, thinner zygomatic arches, a less deflected brain-case, a narrower palate and more strongly diverging tooth-rows, a sudden (instead of gradual) narrowing of the postdental palate where it passes into the pterygoid wings, a slightly larger distance between pterygoid wing and foramen ovale, slightly

longer glenoid fossae, slightly smaller bullae, a higher foramen magnum, a weaker mandibular ramus, a shorter coronoid process, lower but more pointed canines, smaller P₁, similarly formed but narrower upper and lower canines and third and fourth premolars and first molars, and a larger distance between M² and posterior margin of anterior zygomatic arch insertion. (See also the account of the genus *Lissonycteris* in the next part of this series.)

Distribution and geographical variation: Most vegetation types of Madagascar cover, or did cover, belts running parallel to the north-south axis of the island (White, 1983; Nicoll *et al.*, 1989). A notable exception is the Malagasy deciduous thicket and its Mosaic with secondary grassland (types 41 and 46 in White, 1983), which cover the southwest coast and a large part of the southern tip of the island - except the extreme southeast. This area is also notable for the absence, as far as known, of *Rousettus madagascariensis*. The species has been found in all other major types: Malagasy lowland rain forest: wetter types (Beforona; Masoala Pensinsula); Malagasy moist montane forest (Perinet; 8 km south of Perinet); Malagasy dry deciduous forest (Ankarana; Tsimembo; Tsingy de Bemaraha); and in Malagasy mosaic of lowland rain forest and secondary grassland (8 miles northeast of Fort Dauphin; Mananteneina; Mandramondronta River); Malagasy cultivation and secondary grassland replacing upland and montane forest (Antsalova); and Malagasy mosaic of dry deciduous forest and secondary grassland (Bevato; Namoroka) (types 1b, 5, 7, 11b, 18 and 22b in White, 1983). Pont *et al.* (1990) caught the species "near a river and in a clearing in peripheral forest/plantation". Bergmans' conclusion (1977a) that the species inhabits all lower, forested areas along the coast, can now be adjusted. It is apparently restricted to forests, both moist and dry, and mosaics of these forests with secondary vegetation; it is not restricted to coastal areas, and it occurs from sea level up to an altitude of at least 990 m (near Perinet).

The series from 8 km south of Perinet (ROM 42007/36) was taken in a forest cave, where about 350 animals roosted. After the specimen

from the Grotte (= Cave) de l'Ankarana, this is further evidence that this *Rousettus* species also roosts in caves and is thus likely to possess the faculty of echolocation. Pont *et al.* (1990) noted that the species is "occasionally caught from its cave roosts and eaten" but this remark seems not to be based on original observations. The measure of availability of suitable caves will no doubt influence its distribution pattern and its foraging movements. This may explain that it has been collected in nearly all vegetation types.

There are not many dimensional data per locality (except Perinet) and these data are not sufficient to conclude on geographical variation.

Dr M. E. Nicoll, to whom I owe the records from Ankarana, Masoala Peninsula, and Antsaholova, noted that the species seems to be at least locally common (*in lit.*, 14-III-1989). This was confirmed for a locality in the Marojejy reserve by Pont *et al.* (1990).

***Rousettus obliviosus* Kock, 1978**

Rousettus (Rousettus) obliviosus Kock, 1978a: 208 (type locality: cave near Boboni); Corbet *et al.*, 1991: 41.

Rousettus obliviosus; Cheke *et al.*, 1981: 231; Honacki *et al.*, 1982: 126; Meirte, 1984b: 51; Carroll, 1985: 5; Meirte, 1987: 21.

Material examined

ANJOUAN. Centre de Bambao: 1 specimen, skin only, 10-X-1903, A. Voeltzkow (field number 86; ZMB). "Anjouan": 1 imm. ♀, alc., skull, 11-X-1903, A. Voeltzkow (paratype specimen of *Rousettus obliviosus* Kock, 1978; field number 94; ex-ZMB 58196; ZMA 20.903); 1 ♀, skin only, 11-X-1903, A. Voeltzkow (field number 96; ZMB). No locality but probably Anjouan: 1 ♂, skin only, A. Voeltzkow (field number 93; ZMB). No locality but probably Anjouan or Grand Comoro: 2 skulls, A. Voeltzkow (ZMB).

GRAND COMORO. Cave near Boboni: 1 ♂, alc. (skull not seen), 3-VIII-1903, A. Voeltzkow (holotype specimen of *Rousettus obliviosus* Kock, 1978; ZMB 58207). "Grand Comoro": 3 ♂♂, alc. (skulls not seen), 21-XII-1903, A. Voeltzkow (paratype specimens of *Rousettus obliviosus* Kock, 1978; ZMB 58203, -05/06); 2 specimens, skins only, A. Voeltzkow (field numbers 60, 65; ZMB).

MOHELI.

(1 km north of Fomboni.)

Diagnosis: A small-sized, normally furred fruit bat, fal range 70.3-76.6, skull of normal solid built, premaxillae not co-ossified, brain-case strongly deflected, alveolar line projected backward passing through occiput above foramen magnum, postorbital width larger than interorbital width in most specimens, supra-occipital crest well-developed, cheek-teeth of normal shape and proportions, with the widths of larger cheek-teeth larger than half their lengths, P₁ relatively large, wings from base of second toe, dorsal side of tibia naked, palatal ridge pattern normally 4 + 3 + 1. Measurement ranges and ratios from specimens from Anjouan and Grand Comoro, mainly based on Kock (1978a):

fal	♂♂	71.0 - 76.6	(n = 6),
	♀♀	70.3 - 74.4	(n = 4);
gsl	♂♂	34.7 - 36.7	(n = 4),
	♀♀	33.5 - 33.5	(n = 2);
iow	♂♂	7.0 - 7.8	(n = 5),
	♀♀	6.7 - 7.3	(n = 3);
pow	♂♂	7.3 - 8.1	(n = 5),
	♀♀	7.5 - 8.0	(n = 3);
zw	♂♂	20.4 - 21.8	(n = 4),
	♀♀	19.6 - 20.2	(n = 3);
C ¹ -C ¹	♂♂	6.6 - 7.1	(n = 5),
	♀♀	6.1 - 6.3	(n = 3);
M ² -M ²	♂♂	10.0 - 10.4	(n = 5),
	♀♀	9.7 - 9.9	(n = 3);
C ¹ -M ²	♂♂	12.5 - 13.2	(n = 5),
	♀♀	12.2 - 12.6	(n = 3);
C ₁ -M ₃	♂♂	14.0 - 14.9	(n = 5),
	♀♀	13.6 - 13.8	(n = 3);
M ¹ length	♂♂	2.5 - 2.7	(n = 5),
	♀♀	2.5 - 2.6	(n = 3);
M ¹ width	♂♂	1.4 - 1.55	(n = 5),
	♀♀	1.4 - 1.5	(n = 3);
C ¹ -C ¹	♂♂	18.5 - 20.3% of gsl	(n = 4),
	♀♀	18.2 - 18.8% of gsl	(n = 2);
M ² -M ²	♂♂	28.0 - 29.7% of gsl	(n = 4),
	♀♀	28.9 - 29.5% of gsl	(n = 2).

For reasons to be discussed, the fal ranges are given with some reservation. The few available data are insufficient to assess possible variation between the populations of the three islands.

Distribution: Fig. 3.

Related species: Of the African species *Rousettus* *egyptiacus* appears to be the nearest relative. But *obliviosus* is smaller in all its dimensions, has a much more strongly deflected brain-case and a smaller anterior rostrum height. *R. madagascariensis* is about similar in size but has a more delicately built skull, with a narrower rostrum and a much weaker brain-case deflection, and distinctly narrower cheek-teeth. Of the extralimital species of the genus, *R. leschenaultii* has populations of similar-sized individuals, such as those in Northwest India and East Pakistan (see Table 5). Kock (1978a) listed a number of differences. Meirte (1987) suggested that the relation between the two species should be reinvestigated.

Remarks

T a x o n o m y: The type series of *obliviosus* consists of 13 specimens: 1 adult ♀, 3 "subad.-ad." ♀♀, 1 immature ♀, and 1 immature of unknown sex from Anjouan, and 5 adult ♂♂ and 2 adult ♀♀ from Grand Comoro (Kock, 1978). I have not been able to examine much of this series. Of the three "subad.-ad." ♀♀, one (ZMB 58196; now ZMA 20.903) is clearly immature; to judge from Table 1 in Kock (1978a), listing three specimens from Anjouan, the other two should then be adult.

Some skull measurements taken by me fairly matched those originally taken and published by Kock (1978a) and stored, per individual specimen, in the SMF card index, but some fal measurements did not. My values are somewhat higher. The maxima in the ranges here given were measured by me, the minima by Kock. I presume the latter also would be higher if measured by me. The maxima are both from specimens belonging to the same series as the types but found by me in the ZMB sometime after the description of *obliviosus*, in April 1979 (see the section Material examined).

D i s t r i b u t i o n a n d g e o g r a p h i c a l v a r i a t i o n: The type series, collected in 1875 (?) and 1903 (see Cheke *et al.*, 1981), originated from Grand Comoro and Anjouan. Cheke *et al.*

(1981) did not sight the species on any of the four Comores in 1975 and 1977 and somewhat prematurely concluded that "whether it still survives is not clear". The USNM holds a specimen collected on 11-XI-1979 by K.B. Kverno at 1 km north of Fomboni on Mohéli. Meirte (1984b) related that a Belgian expedition collected 46 specimens in the Comores in 1981 and 1983; Mohéli is the only island mentioned, but the species was also collected on Grand Comoro, and on both islands the species appears to be common (dr. D. Meirte, in lit., 13-II-1990). Some preliminary results were published (Meirte, 1987). Meirte concluded that *Rousettus obliviosus* is a distinct species with a relatively long tail and rather squarish teeth, and only little sexual dimorphism. He could not distinguish between specimens from the different islands on a subspecific level. He suggested a closer relationship with *leschenaultii*, implying "a possible migration pattern also found in the avifauna of the Comores." Since 1984, the MRAC had acquired quite a few more specimens: Meirte (1987) mentioned 64 examples.

Kock (1978a) did not separate the sexes in his measurements. He remarked that "slight size differences between the populations of Grand Comoro and Anjouan islands, the latter tending to be smaller in some skull dimensions, do not yet justify the recognition of subspecies." However, from the measurement ranges per sex it is clear that *Rousettus obliviosus* forms no exception to the phenomenon of sexual dimorphism in *Rousettus* (and other Megachiroptera, for that matter). And as Kock had only (3) adult ♀♀ from Anjouan, and mostly ♂♂ (5, against 2 ♀♀) from Grand Comoro, sexual dimorphism should have been part of the explanation for the observed variation. Nevertheless, some variation between the different island populations does not seem entirely unlikely.

All four Comoros are covered with Zanzibar-Inhambane coastal mosaic (type 16a in White, 1983). Much of the forest, especially in the lower regions, has been destroyed. In parts of the remaining forest the undergrowth has been replaced by banana plantations. The large series captured by the Belgian expedition indicates that

the species, which most probably is a lowland forest species, has been able to adapt itself to the changing environment thus far.

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