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TAXONOMY AND BIOGEOGRAPHY OF AFRICAN FRUIT BATS (MAMMALIA, MEGACHIROPTERA). 3. THE GENERA *SCOTONYCTERIS* MATSCHIE, 1894, *CASINYCTERIS* THOMAS, 1910, *PTEROPUS* BRISSON, 1762, AND *EIDOLON* RAFINESQUE, 1815

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ABSTRACT

The genera *Scotonycteris* Matschie, 1894, *Casinycteris* Thomas, 1910, *Pteropus* Brisson, 1762 and *Eidolon* Rafinesque, 1815 are characterized. An effort is made to assess the possible relationship between the genera *Scotonycteris* and *Casinycteris*. Within *Scotonycteris zenkeri* Matschie, 1894 a number of geographically disjunct or probably disjunct and morphologically distinct population groups are recognized. The available material of *Scotonycteris ophiodon* Pohle, 1943 suggests that this species may also consist of a number of geographically disjunct and possibly morphologically distinguishable groups. Its distribution shadows that of *S. zenkeri*. The genus *Casinycteris* and the nature and function of its peculiarly shortened bony palate are discussed, in relation to the condition of the postdental palate in *Neopteryx* Hayman, 1946. The genus *Pteropus* and its species inhabiting islands in the western part of the Indian Ocean are treated less extensively than the other African fruit bats. It is shown that subspecific divisions in *P. rufus* E. Geoffroy St.-Hilaire, 1903 cannot be maintained, consequently *P. r. princeps* Andersen, 1908 is synonymized with *P. rufus*. The type locality of *P. seychellensis* Milne Edwards, 1877 is identified as the Island of Marianne — an altogether new locality for the species. *P. s. seychellensis* and *P. s. comorensis* M. J. Nicoll, 1908 are more closely related than formerly recognized, whereas *P. aldabrensis* True, 1893, is more distant and considered a good species instead of a subspecies of *P. seychellensis*. The genus *Eidolon* shows agreement with *Rousettus* Gray, 1821 in brain case deflection and morphology. *E. helvum* (Kerr, 1792) is shown to be practically absent from the Sudan woodland zone south of the Sahara, and most probably from eastern Ethiopia and the Horn of Africa, and only very locally distributed in central East Africa and in most of southern Africa. The alleged monotypy of the genus *Eidolon* is shown to be based on a misinterpretation of the literature. The form described from Madagascar, *Eidolon dupreanum* (Pollen, 1867) is considered an independant species.

INTRODUCTION

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

TAXONOMIC SECTION

Scotonycteris Matschie, 1894

Scotonycteris Matschie, 1894: 200 (type species: *Scotonycteris zenkeri* Matschie, 1894), 1899: 70; Miller, 1907: 64; Andersen, 1912: 563; Eisentraut, 1960b; Rosevaer, 1965: 112; Kuhn, 1968: 170.

Epomophorus; G. G. Simpson, 1945: 54.

Matschie (1894) in his description of *Scotonycteris* was handicapped in trying to place it in relation to other genera because he knew so few: five genera from the Orient and five from Africa — some of these apparently only from their descriptions. His first idea was that because of the combination of a nail on the second finger and the insertion of the wing on the first toe, *Scotonycteris* was related to the Asian genus *Cynopterus* Cuvier, 1824, although he noticed that its low cheek teeth number and the absence of a visible tail marked considerable differences. His second thought was that *Scotonycteris* looked like a small *Epomophorus* Bennett, 1836, with the same reduced number of cheek teeth, the same form of nose, labial groove, ears, length ratios of metacarpals, and the rudimentary tail and narrow tail membrane. It differed, according to Matschie, by the insertion of the wing, by the more strongly curved canines, and the fact that in both jaws the last molar is round and only half the size of the preceding tooth. In 1899, Matschie added that the canines were fang-shaped, separated from the premolars by a diastem, and that the molars were as in *Cynopterus* but rounder. It furthermore differed from that genus by its less degenerated tail membrane. Nevertheless, Matschie listed it near *Cynopterus* and not near *Epomophorus*.

Miller (1907) found the canines to be as in *Epomophorus* and *Hypsignathus* H. Allen, 1861 but relatively larger. He remarked that the larger cheek teeth, except the two flattish lower molars, had obliquely sloping crowns and no distinct crushing surfaces. He pointed out that the skull was not flattened as in *Epomophorus* but resembling that of *Cynopterus*, although with a more compressed anterior rostrum and spatulate premaxillae (instead for tapering above), and that the slender and weak mandibulum was almost exactly as in *Epomophorus*. He noted that externally *Scotonycteris* is also much like *Epomophorus*, except for less developed lips, and concluded that it is rather more closely related to that genus than to *Cynopterus*.

Andersen (1912) agreed with Miller that *Scotonycteris* is connected with epomophorine genera and placed the genus near *Nanonycteris* Matschie, 1899. In his diagnosis he mentioned the short and slender cranial rostrum; the long postdental palate with straight, converging lateral margins; the extension of the upper tooth rows to the ventral margin of the orbital cavity; the short roundish cheek teeth; the insertion of the wing membrane on the first toe; the white markings on the head and the absence of white ear tufts; the small size. In his description he emphasized differences with *Nanonycteris* and, to a lesser extent, *Cynopterus*: premaxillae not tapering above and with deeper alveolar branches; more strongly diverging upper tooth rows; larger diastem between C^1 and P^3, and posterior position of upper cheek teeth row; postdental palate longer and converging; postorbital processes smaller; zygomata more horizontal and standing out more widely owing to broader temporal fossa; mandible stronger. There was no need to differentiate the teeth in *Scotonycteris*, as these are entirely different from any other epomophorine species. Its palate ridges had been figured, but not very distinct, by Matschie (1899, plate 13). Andersen (1912) interpreted this figure and thought the palate ridges to be "easily derived from" those of *Nanonycteris*. Of the external characters, the ears were said to be smaller than in *Nanonycteris*; Andersen further mentioned the rudimentary tail; the well-developed interfemoral membrane; the about 20-23 vertical fasciae of the mesopatagium, the reticulate pattern of the wing membranes, the relatively long thumb and the relatively short metacarpals and long first phalanges of the third and fourth digits compared to those in *Nanonycteris*.

The discovery of *Scotonycteris ophiodon* Pohle, 1943 necessitated a broader concept of the genus. This species is very much larger (up to about 3.5 times the weight of *zenkeri*), its skull is different in a number of ways, and its teeth are less degenerated, showing several characters which are lacking in *zenkeri*. Pohle described the single type specimen in detail, and could compare it directly with the holotype of *zenkeri*. The snout in *ophiodon* would be relatively broader, and its ear and metacarpal of second digit relatively longer than in *zenkeri*. Its fur colours are as in *zenkeri* except that *ophiodon* has whitish hairs at its ear bases; these are much less prominent than in *Epomophorus* and other epauletted genera and could not be detected in the holotype (but that had been in alcohol for 44 years prior to description and Pohle did not trust its colours). The soft palate in *ophiodon* as figured and described by Pohle is less like that in *Nanonycteris* than Andersen had presumed for *zenkeri* (and, *mutatis mutandis*, for the genus). There are six undivided interdental smooth ridges and about 12 postdental serrate ridges, some divided, some not, some complete and others incomplete, with irregular connections between the ridges.

Eisentraut (1960b) did not discuss the characters of the genus because he thought these to have been described sufficiently. Rosevaer (1965: 112) repeated Andersen's idea that *Scotonycteris* is closely related to *Nanonycteris* ("and hence to *Epomophorus* as well"). He mentioned the three-bandedness of the back fur in all *Scotonycteris* specimens he examined: dark at base, whitish in the middle and (lighter or darker) brown at the tips.

Kuhn (1968) described the innervation of the larynx in a modest number of fruit bat species, among which *Scotonycteris zenkeri*, *Epomophorus labiatus* (Temminck, 1837) (as *E. anurus* Heuglin, 1864), *Epomops buettikoferi* (Matschie, 1899) (as *Epomophorus* (*Epomops*) *franqueti buettikoferi*), and *Hypsignathus monstrosus* H. Allen, 1861. He emphasized that the numbers of species and specimens examined were too low to conclude that the nature of this innervation is a taxonomically instructive character in Megachiroptera. It was nevertheless clear to him, on the basis of the distinct differences he found, that *Scotonycteris* should be considered related to the *Epomophorus* group (including the other genera mentioned above) but not as a synonym as Simpson (1945: 54) had suggested.

The various generic characters put forward by the authors cited above can be amended as follows. (For absolute and relative measurements of *Scotonycteris*, see the species' diagnoses and tables 1, 2 and 3). While gsl in *S. zenkeri* is slightly larger, on the average, than in *Nanonycteris veldkampii* (see its diagnosis and table 11 in Bergmans, 1989), its relative rl is smaller, which is according to Andersen's statement. In the large *S. ophiodon*, however, rl is proportionally not very much larger than in *S. zenkeri*, but distinctly smaller than in *Epomophorus* skulls of the same length. Hence, the shortness of the rostrum is a character of the genus which does not indicate a particular relationship with other short-snouted epomophorines. Judging from the widths across upper canines and molars the rostrum in *zenkeri* averages a little slenderer, only at the level of the upper molars, than in the somewhat larger of skulls of *Micropteropus pusillus* (Peters, 1867) (see table 1 in Bergmans, 1989): C^1-C^1 amounts to 21.6-24.8% of the gsl in 13 ♂♂ and to 20.5-24.5% in 12 ♀♀, and M^1-M^1 to 28.4-33.2% in 13 ♂♂ and to 28.8-33.0% in 12 ♀♀. In *ophiodon*, C^1-C^1 amounts to 21.7% of the gsl in 1 ♂ and to 21.5-23.4% in 4 ♀♀, and M^1-M^1 to 36.1% in 1 ♂ and to 34.6-39.7% in 4 ♀♀. Only M^1-M^1 is distinctly larger, proportionally, than in *zenkeri*.

In 12 *zenkeri* ♂♂ ear length varies from 48.1 to 58.1% of the gsl, in 7 ♀♀ from 46.6 to 58.8%; in 1 *ophiodon* ♂ it is 62.8% of the gsl and in 5 ♀♀ it varies from c. 55.4 to 62.3%. This confirms Pohle's observations of relatively longer ears in *ophiodon*.

In 5 *zenkeri* ♂♂ the second metacarpal length is between 47.7 and 53.1% of the fal, in 5♀♀ between 47.5 and 52.1%; in 3 *ophiodon* ♂♂ it varies from 49.3 to 53.0% of the fal and in 3 ♀♀ from the 52.0 to 54.8%. A preliminary conclusion from these few data is that only in *ophiodon* ♀♀ this length is relatively slightly longer than in *zenkeri*; another, that — like in *Epomophorus* — (certain) differences between sexes may be more apparent in large than in small species of *Scotonycteris*.

The palatal ridge pattern in *zenkeri* reflects that in *ophiodon*, although the number of ridges is smaller. There are four (or five, if the elevation at the level of the incisive foramen is included) rather strong, smooth, undivided interdental ridges (the fourth is sometimes divided), and two postdental, more or less serrate ridges of equal strength, all of which are slightly curved forward, and separated from these by a small ridge-less space six or seven weak and denticulate ridges, each consisting of two halves curving backward which may be connected or divided in the middle (see Kuhn, 1962, figs. 1 and 2).

Scotonycteris zenkeri Matschie, 1894

Scotonycteris zenkeri Matschie, 1894: 202 (type locality: Yaoundé), 1899: 71; Andersen, 1912: 567; Cabrera, 1929: 17; Kuhn, 1962; Eisentraut, 1963: 72, 1964: 537; Kuhn, 1965: 326; Coe *et al.*, 1965a: 183; Rosevaer, 1965: 114; Brosset, 1966b: 56, 1966c: 34, 40, 141; Hayman *et al.*, 1966: 21; Kuhn, 1968: 170; Hayman *et al.*, 1971: 5; Bergmans, 1973: 287; Eisentraut, 1973: 36; Bergmans *et al.*, 1974: 35; Vielliard, 1974: 977; Jeffrey, 1975: 955; Coe, 1976: 544; Happold *et al.*, 1978: 77; Emmons *et al.*, 1983; Happold, 1987: 47; Roth *et al.*, 1988: 184.
Scotonycteris bedfordi O. Thomas, 1904: 372 (type locality Fish Town); Miller, 1907: 65.
Casinycteris argynnis (not of O. Thomas, 1910); Schouteden, 1944: 107 (in part: the specimen from Beni); Koopman, 1965: 3 (in part: the specimen from Beni).
Epomophorus zenkeri; Dekeyser, 1955: 108.
Scotonycteris zenkeri occidentalis Hayman, 1947: 503 (type locality: Oda); De Vree, 1971: 32; Hayman *et al.*, 1971: 5; Verschuren, 1977: 616; Wolton *et al.*, 1982: 430, 441.
Scotonycteris zenkeri zenkeri; Aellen, 1952: 39; Eisentraut, 1960b: 299; Rosevaer, 1965: 115; Hayman *et al.*, 1971: 5; Happold *et al.*, 1978: 77; Bergmans, 1979: 178.

Material examined

CAMEROUN. Bipindi: 1 ♀, alc., skull, IV-1898, G. Zenker (ZMB 54390). Bitye: 1 ♀, skull (BMNH 26.11.11.1). Dikume: 1 imm. ♀, 21-II-1967, M. Eisentraut (MAKB 69.460). Eseka: 2 imm. ♀♀, 20-VI-1973, L. W. Robbins (AMNH 236275/76). 7 km E of Kribi: 2 ♀♀, alc. 15/16-IV-1973, J. Prévost (MNHN 1979-343/44). Kupe. 1 imm. ♂, 1 imm. ♀, 23-XI/1-XII-1966, M. Eisentraut (MAKB 69.459,-61). 15 km SE of Mamfe: 1 ♀, 9-XII-1971, L. W. Robbins (AMNH 241018). Meyo Nkoulou: 1 ♀, alc., 27-III-1973, L. W. Robbins (MRAC). Above Mueli: 1 ♀, 1 ♂, 5/16-II-1958, M. Eisentraut (MAKB 61.646/47). Tombel: 1 ♀, alc. (BMNH 66.6274). Tombel Estate: 1 ♀, alc. (BMNH 66.3516). Yaoundé: 1 ♀, alc., skull, ≤ 1894, G. Zenker (holotype of *Scotonycteris zenkeri* Matschie, 1899; ZMB 66533).
(Barombi Kang, Kumba, Lake Barombi (Mbo), Lombe, Malende, Mangamba, Mawutu, 6 km W of Menguemé, Victoria.)
CENTRAL AFRICAN REPUBLIC. La Maboké (by inference): 2 ♂♂, 1 ♀, alc., skulls, 28-V/3-VI-1966, R. Pujol & P. Tesschi (MNHN 1979-399/401).
CONGO. Dimonika: 1 ♂, 1 imm. ♂, 9/10-III-1970, University of Brazzaville (UBRA 1-♂-70-03-10, 7-♂-70-03-09).
EQUATORIAL GUINEA. Nkolentangan: 1 ♀, skull, 6-VIII-1908, Tessmann (ZMB 50004).
FERNANDO POO. Basileo: 1 specimen, skull, H. Schouteden (MRAC 28428). Fish Town: 1 ♀, 2-I-1904, E. Seimund (holotype of *Scotonycteris bedfordi* O. Thomas, 1904; BMNH 4.7.1.28). San Carlos: 5 ♂♂, 2 ♀♀, 1 imm., 2/15-X-1962, M. Eisentraut (64.360/62, -64, -66/71).
GABON. Belinga: 2 ♂♂, 1 ♀, alc., 2 skulls extracted, XII-1962/II-1963, J. Dragesco (ZMA 20.662/64); 1 ♀, alc., skull, 18/22-II-1963, Mission Biologique au Gabon (ZMA 20.659); 1 ♂, alc., skull, VI/VII-1963, Mission Biologique au Gabon (MNHN); 2 ♂♂, alc., skulls, VII-1963, Mission Biologique au Gabon (MNHN; ZMA 20.660); 1♀, 4-II-1964, P. J. H. van Bree (ZMA 7808); 1 specimen, skull, ≤ III-1964 (ZMA 18.270); 1 imm. ♂, alc., III-1964, Mission Biologique au Gabon (ZMA 20.661); 1 ♂, alc., 1 ♂, alc., skull missing, 1 imm. ♂, alc., skull, J. Dragesco (MNHN). Makokou: 1 ♀, alc., 10-XII-1965, Mission Biologique au Gabon (ZMA 20.658).
GHANA. Butre: 1 ♂, 18-I-1968, J. C. Geest (USNM 411614). Chiriso: 1 ♂, 25-I-1968, J. C. Geest (USNM 414023). 6 miles NW of Kade: 1 ♂, 8♀♀, 1 imm. ♀, 29-X/1-XI-1967, H. W. Setzer (USNM 411608/17). Nkawkaw: 2 ♂♂, 10-VIII-1967, B. J. Hayward (USNM 411618/19). Oda: 1 ♀, 1946, G. S. Cansdale (holotype of *Scotonycteris zenkeri occidentalis* Hayman, 1947; BMNH 46.898); 1 ♀, 13-X-1968, J. W. LeDuc (USNM 439884). 32 miles W of Prestea: 3 ♀♀, 1 specimen, 5-I-1968, J. C. Geest (USNM 414018/21). Prince's Town: 4 ♀♀, 23/25-VIII-1967, B. J. Hayward (USNM 411620/23). University of Cape Coast, Cape Coast: 1 ♀, alc. (BMNH 78.2817).
(Kade Agricultural Research Station, 7 miles NE of Kade, Pampramase.)
IVORY COAST. Adiopodoumé: 2 ♂♂, 2 ♀♀, 12/14-VIII-1971, L. W. Robbins (AMNH 239378/81). Banco Forest: 2 ♀♀, 28/30-XI-1968, L. W. Robbins/J. W. LeDuc (USNM 429895, -97); 1 ♂, 30-V-1969, T. J. McIntyre (USNM 467894). Bolo: 1 ♂, 1-II-1973, J. Vissault (ZMA 18.040). Lamto: 1 ♂, 27-II-1970, J. Vissault (ZMA 16.552). Matonguiné: 1 imm. ♀, 18-I-1973, J. Vissault (ZMA 18.039). Niebe: 1 ♂, 26-II-1969, J. W. LeDuc (USNM 46573917). Yapo Sud: 1 ♂, 13-XII-1968, J. W. LeDuc (USNM 429895).
(Tai Forest).
LIBERIA. Grassfield, Mount Nimba: 3 ♂♂, 1 ♀, alc. (BMNH). Iti: 1 ♂, alc., 12-II-1966, J. Verschuren (IRSN 16085). Mount Nimba West: 1 ♂, 1 imm. ♂, 3 ♀♀, 24-

XII-1965/19-III-1966, J. Verschuren (IRSN 16084, -86/88). Sino: 1 ♂, 1 ♀, alc. (BMNH). Tars Town: 1 ♂, 5 ♀♀, 21/29-VIII-1971, D. A. Schlitter (USNM 481683/88). 25 km N of Tchien: 1 ♂, 1-VIII-1971, L. W. Robbins (AMNH 239382). Tokadeh, Mount Nimba: 3 ♂♂, 1 ♀, alc. (BMNH). "Liberia": 1 ♂, skin, 1-VII-1965, J. Verschuren (IRSN 16761).

(Harbel, main Nimba Ridge, Peloken, between Zarobo and Freemanntown).

NIGERIA. Gambari Forest Reserve: 1 ♀, alc., skull, 4-XII-1966, D. C. D. Happold (ZMA 20.702); 6 ♂♂, alc., 2/3-I-1970, D. C. D. Happold (field numbers 1214/15, -17/18, -20/21; collection D. C. D. Happold); 3 ♂♂, alc., 5-I-1973, D. C. D. Happold (field numbers 1614/16; collection D. C. D. Happold). Shasha Forest Reserve: 1 ♀, alc., 1-IV-1971, D. C. D. Happold (field number 1398; collection D. C. D. Happold).

(Oban, Omo Forest Reserve, Sapoba Forest Reserve.)

ZAIRE. Beni: 1 ♀, Bonnevie, (MRAC 3244). Irangi: 1 ♀, 14-XI-1955, J. J. Laarman (RMNH 16326A/26325); 3 ♂♂, alc., I/II-1984, H. Stephan (SMF 65008/10); 1 ♀, 25-V-1964, A. Prigogine (MRAC 32584); 1 ♂, alc., 18-X-1990, W. Bergmans (ZMA 24.197); Kiloboze: 1 ♂, 2-II-1963, A. Prigogine (MRAC 31345).

Diagnosis: A small bat, fal between 45 and 56.4, overall fur colour impression brown to reddish brown intermixed with whitish brown on back; white fur patch dorsally on rostrum and ditto behind eyes; no visible tail; short and anteriorly relatively narrow rostrum; premaxillae well developed; mandibulum quite strong; canines relatively tall; premolars and molars in occlusal view short and roundish; two series of palatal ridges: one of six or seven strong ridges, four or five of which interdental and one or two posterior ones sometimes serrate, and one series of six or seven thin, serrate, postdental ridges. Measurement ranges and ratios taken from all over the species' range:

fal ♂♂ 45.0-55.0 (n = 58);
♀♀ 47.7-56.4 (n = 52).
gsl ♂♂ 24.0-28.6 (n = 26);
♀♀ 24.6-29.1 (n = 38).
cbl ♂♂ 23.5-27.8 (n = 22);
♀♀ 23.8-28.2 (n = 12).
rl ♂♂ 7.7-10.0 (n = 12).
♀♀ 7.7-10.0 (n = 12).
pl ♂♂ 12.9-15.2 (n = 16);
♀♀ 13.0-15.6 (n = 11).
zw ♂♂ 16.1-18.4 (n = 12);
♀♀ 15.8-19.3 (n = 14).
C^1-M^1 ♂♂ 7.9- 9.2 (n = 16);
♀♀ 7.4- 9.4 (n = 14).
W ♂♂ 16 -24 (n = 15);
♀♀ 18 -27 (n = 6).
rl ♂♂ 32.9-34.6% of gsl (n = 15);
♀♀ 30.4-34.3% of gsl (n = 12).
pl ♂♂ 52.5-55.7% of gsl (n = 15);
♀♀ 51.3-55.6% of gsl (n = 11).
zw ♂♂ 63.5-68.7% of gsl (n = 13);
♀♀ 62.3-68.6% of gsl (n = 12).

For a breakdown of measurements per country see table 1. There is some geographical variation in overall size, in the form of the postdental palate, and in the size and position of the cheek teeth, which will be discussed below.

Distribution: Fig. 1.

Related species: The only congeneric species, *S. ophiodon*, is similar in external appearance except that it has (indistinct) white ear tufts at the ear bases, and light-coloured finger joints, but it is much larger, with a fal of 75 or more and without overlap in any dimension. *Casinycteris argynnis* Thomas, 1910 is externally rather similar but slightly larger, with somewhat larger ears, a less clearly defined white fur patch on the muzzle, more conspiciously white lips and cheeks, and yellowish skin on the finger joints (which are brown in *Scotonycteris zenkeri*). *Casinycteris argynnis* differs furthermore in the extreme reduction of its postdental palate.

Remarks

Taxonomy: O. Thomas (1904) described *Scotonycteris bedfordi* as a new species from Fernando Poo, which would differ from the continental *S. zenkeri* mainly by its much smaller ears (11 instead of 17) and a more hairy interfemoral membrane. Andersen (1912) pointed out that the ear in *zenkeri* is not 17 as Matschie (1894) had published, but 12.5 and that *bedfordi* is not distinguishable from *zenkeri*.

Hayman (1947) described the subspecies *occidentalis* from Oda, Ghana, on the basis of its darker fur colour, caused by sepia instead of

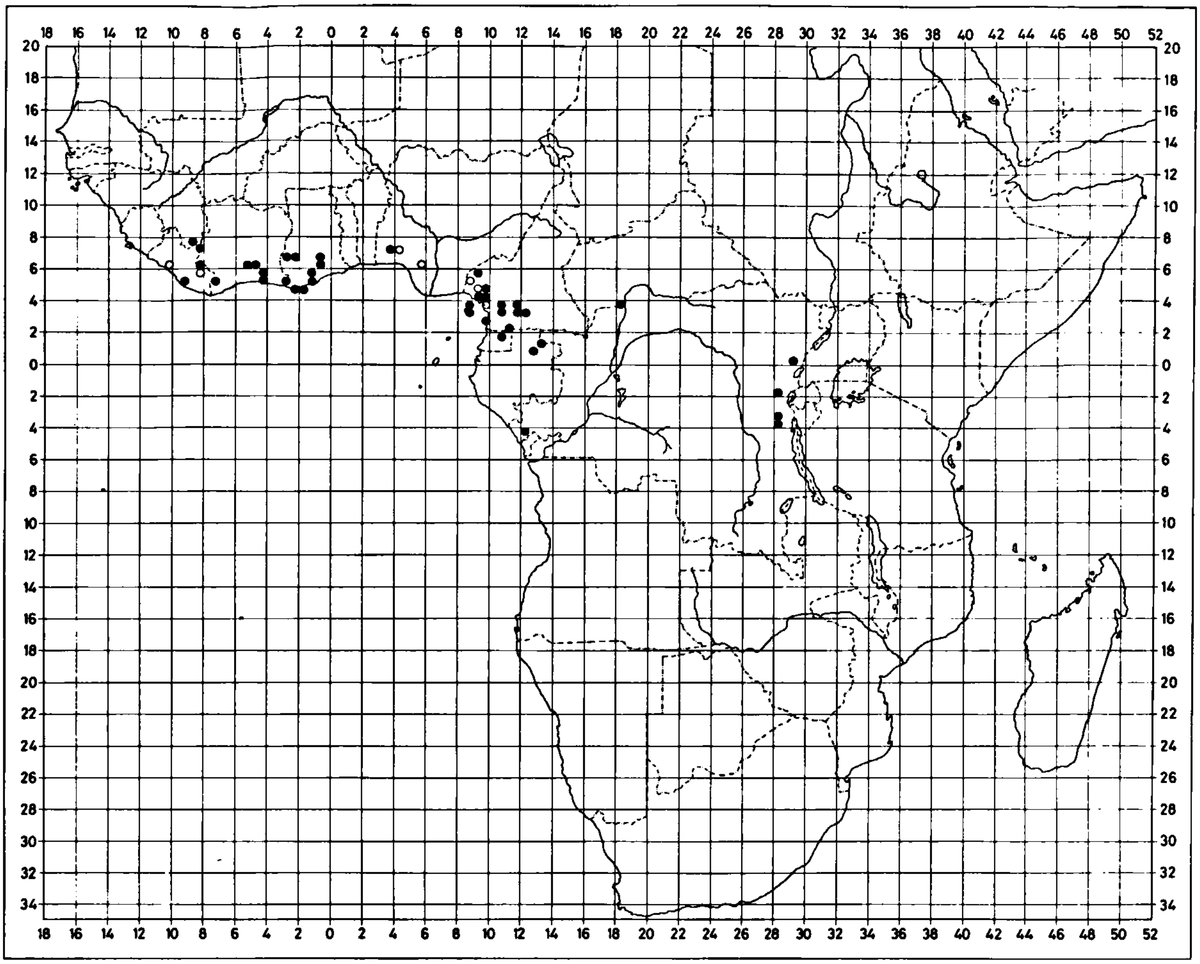

Fig. 1. Distribution of *Scotonycteris zenkeri* Matschie, 1894; black dots: squares from where material has been identified by the author; open circles are based on records in the literature, museum registers and correspondence.

russet or rust-brown hair tips, and darker membranes. Eisentraut (1960b) remarked that more Upper Guinean specimens were needed to establish the taxonomic value of these differences. Kuhn (1962) described an adult and a young specimen from Liberia which agreed with Eisentraut's specimens from Cameroun and concluded that either individual variation or age difference should be held responsible for the characters described by Hayman and hence that *occidentalis* is not tenable. However, Rosevear (1965) observed that in *occidentalis* (of which he could study the type specimen only) the chest and belly are medially much whiter than in typical *zenkeri*, and that this patch is far more sharply defined from the darker brown flanks than in the typical race. Rosevear also published drawings of the postdental palates of both *zenkeri* and *occidentalis* and wrote that in *zenkeri* this has practically straight margins which converge strongly, while in *occidentalis* the margins are distinctly convex and not converging (except for a slight inward curvature posteriorly); in *zenkeri*, moreover, the whole palate is only weakly arched, whereas in *occidentalis* it is strongly arched. De Vree (1971) could confirm these observations for two specimens from Ivory Coast, and added that in *occidentalis* the position of M^1 is less backward than in two specimens from eastern Zaire identified as *zenkeri*, in which M^1 is at the level of the posterior margin of the anterior zygomatic arch insertion. De Vree found no colour differences between the Ivory Coast and Zaire specimens. Bergmans *et al.* (1974) gave a detailed description of the fur in another adult specimen from Ivory Coast, which also agreed with that in typical *zenkeri*. They examined specimens from Gabon and Zaire, and found that the fur characters described by Hayman (1947) and Rosevear (1965) are not restricted to certain regions but instead may occur in western, central and eastern populations, and should thus be considered individual variations. Bergmans *et al.* (1974) confirmed De Vree's observation on the position of M^1 and published drawings of their Ivory Coast specimen and of an East Zaire specimen. These drawings strongly suggest that a backward position of M^1 is related to generally larger teeth dimensions. Happold *et al.* (1978) recorded the first Nigerian specimens and identified these with typical *zenkeri* on the basis of their fur colour and their small size, with an average fal of less than 50. The latter character is clearly erroneous: in their key Happold *et al.* (1978: 124) mention a fal range of 49-55. The present author measured the same series and found a range of 50.0-56.4 (see table 1). Nevertheless, Happold *et al.* have rightly drawn attention to size as another variable character within the species.

When Rosevear (1965) described and illustrated postdental palates of the two subspecific divisions, he used a specimen from Fernando Poo (in fact: the type of *S. bedfordi* O. Thomas, 1904) as representative of typical *zenkeri*. Now that many more specimens are known it appears that this is not correct. The same applies to De Vree's (1971) reference to specimens from eastern Zaire as typical *zenkeri*. The known distribution of the species (fig. 1) shows several large gaps, indicating lack of collecting efforts or successes but in part probably reflecting reality, as there are differences between some of the population groups separated by them. Some of these groups appear to be clearly defined. Although it could be argued to recognize them as subspecies, I prefer to describe them without proposing subspecific divisions yet, as the picture of the species' distribution is incomplete and some groups are hardly represented in collections. Moreover, not all characters are known for each group.

The holotype of *S. zenkeri*, a ♀ in alcohol with extracted skull (ZMB 66533), is rather large (fal 53;7) with a small skull (gsl 25.5, according to Matschie, 1894; premaxillae now missing and length without these 24.7). Its postdental palate has almost straight lateral margins, with a slight inward curvature posteriorly (as mentioned by Rosevear, 1965, for *S. z. occidentalis*). I have not noted, at the time, if the palate is arched in this specimen. Measurements of tooth rows and individual teeth have been published by Andersen (1912); as many teeth are loose now (and some lost) I have not been able to reproduce those measurements. From the alveoli of M^1 however it is clear that this was at about 0.4 mm anterior to the posterior margin of the anterior zygomatic arch insertion.

The holotype of *occidentalis*, a ♀, skin and skull (BMNH 46.898), is of medium overall size (fal 49.9) and has a small skull (gsl 24.6). (Another ♀ from the type locality, in the USNM, has a fal of 54.6 and a gsl of 26.9.) The palate is arched. The lateral margins of the postdental palate are convex, but not as strongly as in the rather coarse sketch in Rosevear (1965, fig. 18b): the difference in this respect with the type of *zenkeri* is quite subtle. Its M^1 is positioned well in front of the margin of the zygoma.

The shape of the lateral margins of the postdental palate in adult specimens is determined by the eventual width of the posterior part of the postdental palate, formed by the palatine bones. At some stage during growth, these fuse with the maxillary bones, which form the antero-lateral parts of the postdental palate, including the anterior part of the lateral margins, which part always tends to converge backward. The wider the palatine bones grow, the more this tendency to converge will be masked. Although there are general geographical differences in the shape of the

Table 1. Selected measurements of *Scotonycteris zenkeri* Matschie, 1894 per country. Countries in an order approximately from west to east.

					♂♂								♀♀				
		fal	gsl	cbl	rl	pl	zw	C^1-M^1	W	fal	gsl	cbl	rl	pl	zw	C^1-M^1	W
Liberia	n	13	2		1	1	1	1		10	5						
	mean	51.1								52.2	25.9						
	min	46.8	25.2		9.1	14.4	17.6	8.4		49.1	25.5						
	max	54.0	≥ 27.4							55.8	26.7						
Ivory Coast	n	7	6	1	2	2	1	2		4	3						
	mean	50.7	26.3							51.4	26.0						
	min	49.5	25.5	25.1	8.6	14.1	17.1	8.3		50.6	25.8						
	max	52.8	26.9		9.7	14.5		8.3		52.2	26.2						
Ghana	n	5	5							17	17	1	1	1	1	1	
	mean	51.3	26.3							52.3	26.6						
	min	50.3	25.5							49.4	24.6	23.8	7.8	13.2	15.8	7.4	
	max	53.6	27.4							55.8	27.9						
Nigeria	n	9	1	1	1	1	1	1	8	2	1	1	1	1	1	1	2
	mean	53.0							22								
	min	50.0	28.6	27.8	9.9	15.2	18.4	8.6	20	55.0	29.1	28.2	10.0	15.6	19.3	9.4	22
	max	55.0							24	56.4							27
Fernando Poo	n	4	5	5	5	5	4	5	5	3	3	3	3	3	3	3	2
	mean	46.0	25.4	24.7	8.5	13.7	16.6	8.4	18.4	48.5	25.7	24.7	8.6	13.6	16.3	8.3	
	min	45.0	24.5	23.7	8.4	12.9	16.2	8.2	16	48.2	25.2	24.2	8.6	13.3	16.0	8.2	19
	max	47.3	25.9	25.3	8.7	14.2	17.0	8.6	22	49.1	26.3	25.1	8.6	13.8	17.0	8.4	19
Cameroun	n	3	1	1	1	1		1	1	8	2	1	1	1	3	2	2
	mean	49.1								49.8					17.5		
	min	48.7	26.0	25.0	8.9	14.2		8.2	16.5	47.7	25.9	25.3	8.4	13.4	17.0	8.2	18
	max	49.2								53.7	26.1				17.9	8.3	19
Central African Republic	n	2	1	1	1	1	1	1		1	1	1	1				
	min	47.1	24.0	23.5	7.9	12.9	16.5	8.3		54.1	24.6	23.8	8.0				
	max	47.9															
Equatorial Guinea	n										1	1	1	1	1	1	
											25.7	25.0	8.5	13.9	16.5	8.6	
Gabon	n	6	3	3	3	3	3	3		4	3	3	3	3	3	3	
	mean	49.4	26.0	25.5	8.7	14.1	16.7	8.4		50.2	25.6	24.4	8.2	13.7	16.9	8.0	
	min	46.3	24.9	24.5	8.3	13.7	16.1	7.9		48.4	25.3	24.0	7.7	13.0	16.8	7.7	
	max	51.8	26.8	26.1	9.0	14.4	17.3	9.2		51.8	25.7	24.7	8.4	14.3	17.1	8.5	
Congo	n	1	1		1	1	1	1									
		47.3	26.4		8.7	14.3	16.8	8.2									
Zaire	n	4	1	1	1	1		1		3	2	1	1	1	2	3	
	mean	50.8								51.9						8.8	
	min	48.0	c.26.0	24.6	8.7	13.9		8.0		49.8	28.0	27.4	9.3	14.7	18.1	8.4	
	max	53.2								55.5	≥28.2				19.1	9.1	

postdental palate margins, there is always a certain amount of individual variation, and the use of the character in taxonomy is not without problems.

The first seemingly coherent group of populations to be considered is that inhabiting western Upper Guinea (Liberia, Ivory Coast and Ghana). It is separated from the second by the Dahomey Gap. The specimens average somewhat larger than those in the populations in Cameroun from where the type of the species originates. The palate varies from moderately to strongly arched; the postdental part is always the most concave. The lateral margins of the postdental palate are 'convex' (as in fig. 2a) to very moderately convex. The teeth are relatively small (fig. 2a; see also fig. 3A in Bergmans *et al.*, 1974), with high and slender upper canines, narrow premolars, and frequently a posteriorly narrowing M^1. Upper premolars and molars have traces of inner cusps only, lower premolars and molars have more distinct inner cusps. The outer cusps in P_4 and, to a lesser extent, M_1 are placed near or at the anterior end of the tooth, which has at most a very narrow anterior basal shelf; these teeth approach P_3 in form, which has a single, posterior, sloping occlusal surface. The distance between M^1 and the margin of the zygoma is relatively large. If subspecific divisions are to be recognized, *occidentalis* is the available name for this group.

The second group is that in western Nigeria, discovered and reported by Happold *et al.* (1978). It is separated from group 1 by the Dahomey Gap and from the next group, inhabiting the Mount Cameroun region (and probably extending into eastern Nigeria) by a barrier yet to be identified — possibly the Niger delta. Available measurements show that here the species reaches its largest dimensions in body and skull measurements. The overlap in fal range with the western Upper Guinea group is considerable, that in gsl range probably less (I have examined only two skulls); and it is averaging more distinctly larger in these ranges than the specimens in southwest Cameroun (and the other nearby group, on Fernando Poo). The postdental palate in the Nigerian specimens is fairly arched, the interdental palate less. The postdental palate margins (see fig. 2b) are converging anteriorly and 'straight' posteriorly. The teeth are relatively large, with high and short (i.e. antero-posteriorly) upper canines, broad premolars, and a roundish M^1. Upper premolars and molars have weak or no inner cusps. P_4 and M_1 have weakly marked inner cusps; their outer cusps are placed more backward than in western Upper Guinea specimens, and there is a larger anterior basal slope or shelf.

The third group inhabits the Mount Cameroun region, adjoining southwest Cameroun (and probably southeast Nigeria), including the species type locality Yaounde, and mainland Equatorial Guinea. It is not clear if there are disjunctions between this part of the species' range and the few known localities in the Central African Republic, Gabon and Congo. Fal and probably also gsl average slightly smaller than in western Upper Guinea and more distinctly smaller than in West Nigeria. The palate is weakly to moderately arched. Behind the inward curvature of the anterior, maxillary part the palate margins are straight, with a posterior inward curvature (see fig. 2c). The teeth are not as elongate as in western Upper Guinea specimens, and smaller than in specimens from West Nigeria and East Zaire. The distance between P^3 and P^4 may be quite large, and M^1 is at some distance from the zygoma margin but slightly closer, on average, than in specimens from western Upper Guinea and West Nigeria. The canines are slender. Upper premolars and molars have weak or no inner cusps. The inner cusp in P_3 may be indistinct or at most weak, in P_4 it is quite distinct in almost all specimens. The outer cusps in the lower cheek teeth are placed backward, as in the West Nigerian specimens, leaving space for an anterior basal slope or shelf. The single specimen known from Mbini (mainland Equatorial Guinea) is similar. Those from northeast Gabon are similar in size, have moderately arched palates with straight to weakly convex postdental margins (fig. 2f). Their teeth are more robust than in the specimens from the Mount Cameroun region. M^1 is placed more backward, its posterior side past the level of the posterior margin of the zygoma insertion. The single adult specimen known from Congo is rather small, has straight postdental palate margins except for the anterior and posterior curvatures, but M^1 is placed well anterior to the zygoma margin level, as in the western Upper Guinea specimens. (I have no other notes on it.) The two males from the Central African Republic have small fals, the female has a large fal, and all three have small gsls. Their teeth (see fig. 2e)

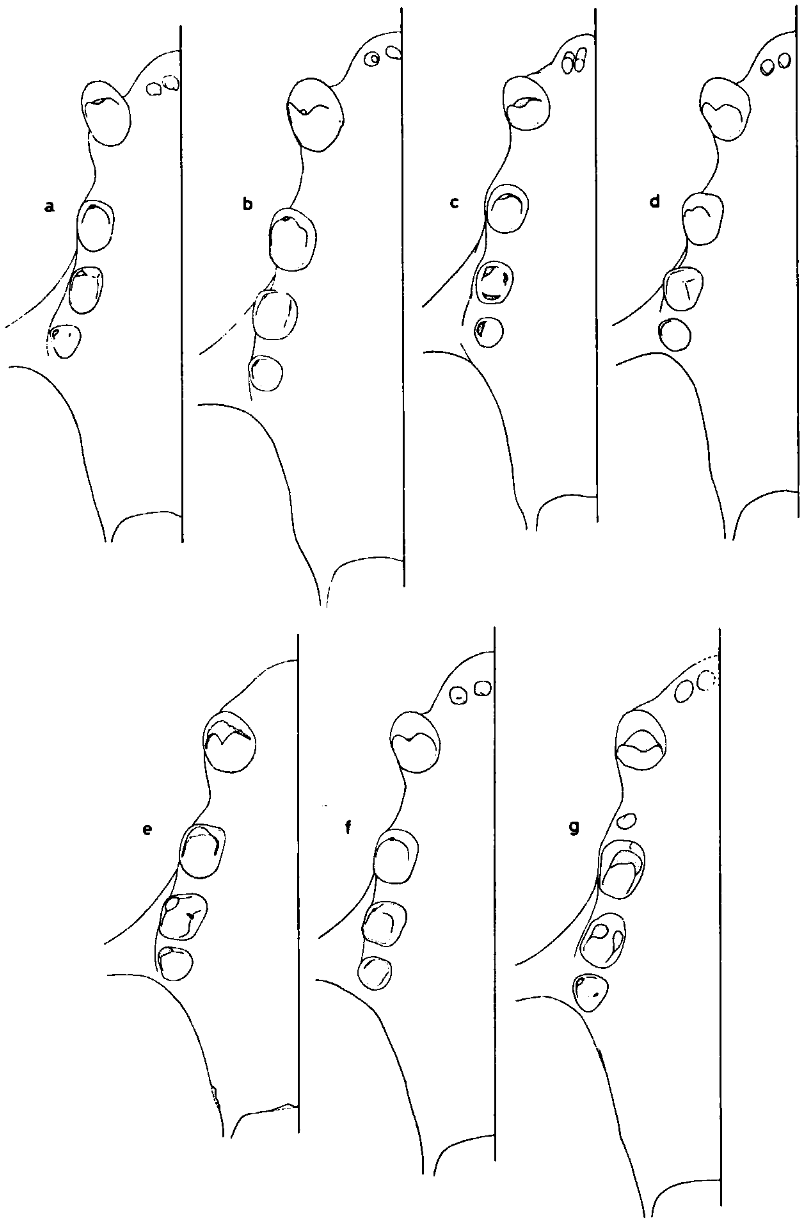

Fig. 2. Ventral view of right hand tooth rows and postdental palate margin in *Scotonycteris zenkeri* Matschie, 1894; worn areas are stippled. a. ♂, from Bolo, Ivory Coast (ZMA 18.040); b. ♀, from Gambari Forest, Nigeria (ZMA 20.702); c. ♂, from Mueli, Cameroun (MAKB 61.647); d. ♀, from San Carlos, Fernando Poo (MAKB 64.370); e. ♂, from La Maboké (by inference), Central African Republic (incisors not preserved, enamel damaged. MNHN CG 1979-400); f. ♀, from Belinga, Gabon (ZMA 20.659); g. ♀, from Kiliza, Zaire (note the extra P^1; MRAC 32584). All specimens have been drawn to the same scale.

are at least as robust as in the specimens from Gabon; the antero-internal orientation of the anterior basal shelf in the upper cheek teeth, connected to a relative backward position of the inner cusps and weakly present in specimens of all groups except perhaps the western Upper Guinea one, is strongest in these specimens, especially in P^4. M^1 is close to the bone margin and its posterior side is past the posterior margin of the zygoma insertion.

The fourth group is restricted to Fernando Poo. To judge from the fal ranges and means the specimens here are averaging smaller than anywhere else. The palate is generally moderately arched, its postdental margins (see fig. 2d) are not strongly converging, with a rather strong posterior curvature, resembling West Nigerian specimens. Premolars and molars are rather short and broad and about equal in size to those in specimens from southwest Cameroun. In most specimens, M^1 is placed distinctly anterior to the posterior margin of the zygoma insertion but in some it is further backward and in one — incidentally the specimen in fig. 2d — its posterior margin is on level with that margin. Inner cusps are absent or at most vestigious in P^3 and M^1 but in P^4 they are rather high in eight out of ten specimens, either somewhat camouflaged by an equally high commissure connecting the inner with the outer cusp, or partly independent by this commissure being lower. Of the lower cheek teeth only P_4 has distinct but small inner cusps. The outer cusp in this tooth is long and anteriorly placed, leaving either little or no place at all for an anterior basal shelf. For the Fernando Poo populations the subspecific name *bedfordi* would be available.

The fifth group inhabits eastern Zaire. The specimens here are as large as those from western Upper Guinea, with gsl probably averaging larger. Their palate varies from weakly (RMNH 26325) to rather strongly (MRAC 32584) convex and has nearly straight postdental margins in which the posterior curvature may be angular (see fig. 2g). The teeth are relatively large. M^1 is placed backward, its posterior side on level with the posterior margin of the zygoma insertion or further backward. C^1 is short, antero-posteriorly. P^4 has a small but distinct inner cusp and a rather large anterior basal shelf. M^1 has a trace of an inner cusp. P_3 has a distinct inner cusp, with or without a commissure between it and the outer cusp. P_4 has a weak inner cusp only.

Whereas the groups from western Upper Guinea, West Nigeria, Fernando Poo and possibly East Zaire (where the extent of the distribution may be larger than known at present) appear to be fairly distinct, the situation in the central part of the species' distribution, i.e. southwest Cameroun and adjoining regions and Central African Republic, Gabon and Congo, is insufficiently known for an overall picture of probable disjunctions in distribution. At this stage, taxonomy seems best restricted to filling the gaps in our knowledge of the species' occurrence and describing the variation thus found.

In the account of *Casinycteris argynnis* O. Thomas, 1910 the differences with *Scotonycteris zenkeri* and vice versa will be discussed in more detail. However, a note on the often reported great external similarity seems in place. *Scotonycteris zenkeri* is smaller, has somewhat smaller and less vertical ears, slightly more laterally directed eyes, not much of an angle between forehead and snout, shorter thumbs, dark instead of contrastingly light finger joints, and different head fur colours and pattern. It has no white tuft at the base of the ears. The oblong white patch on the bridge of the rostrum is sharply defined, whereas in *Casinycteris argynnis* it is less contrasting and less distinct. *S. zenkeri* has been described as having an upper lip narrowly edged with white from angle of mouth to some distance from nostrils (Andersen, 1912). This suggests that apart from the rostral patch, the post-ocular patch and the upper lip edge which are white, the fur of the head is brown. While this may be so in particular specimens, it is not the rule. The brown fur does not in all specimens cover all of the sides of the head. It usually surrounds the eye (it sometimes just separates eye and post-ocular white spot) and borders the white lip area, but it need not continue much further downward. In one specimen (SMF 65009 from Irangi, Zaire), which possibly presents the other extreme of this variation, the whole lower side of the head, below a line connecting mouth angle with posterior ear base, is whitish. From this, three bands of white ascend into the brown: the upper lip edge, a narrow stripe between lip edge and eye (this may be a spot: Coe, 1976), and a band between eye and ear.

The white post-ocular spot in this specimen is the end of this band. In all specimens a rather broad stretch of skin around the mouth, behind nostrils and chin on both upper and lower jaw and extending quite far beyond the mouth angle, is whitish and only sparsely furred with white hairs. In *Casinycteris argynnis*, lips and cheeks are also white. In *Scotonycteris zenkeri*, the white on lips and cheeks is mixed with scattered brown hairs, in *C. argynnis* it is pure white.

Distribution and geographical variation: *Scotonycteris zenkeri* is a typical lowland rain forest species. Of 64 collecting localities, 30 are in Wetter types of the Guineo-Congolian lowland rain forest zone, 13 in Drier types of the same, and 8 in a Mosaic of both (types 1a, 2 and 3, respectively, in White, 1983); 5 are in a Mosaic of lowland rain forest and secondary grassland, 4 on the border of types 1 or 3 with, and 1 within the boundaries of Afromontane vegetation (types 11a and 19a in White, 1983); finally, 1 is in Transitional rain forest, 1 in West African coastal mosaic, and 1 on the border of type 11a with Mangrove (types 4, 15 and 77 in White, 1983). The "montane" or near montane localities are at Mount Cameroun at 600 m (above Mueli; Eisentraut, 1963: 37) at Irangi (850 m), and at Mount Nimba between 500 and 600 m (Coe, 1976), between 500 and 1000 m (Verschuren, 1977), and below 800 m (Wolton *et al.*, 1982). Wolton *et al.* (1982) stated that at Mount Nimba the species was conspicuously absent from higher altitudes (than 800 m).

Because of their possible taxonomical implications, details of the known geographical variation have been given under the caption Taxonomy. When viewed at large, the distribution of the population groups of *Scotonycteris zenkeri* appears to reflect the situation during the late Pleistocene, when lowland forest species were confined to a restricted number of refuges, as discussed by Moreau (1966) and others. The geological history of present distribution patterns of African fruit bats will be reviewed in the general discussion at the end of this series.

Scotonycteris ophiodon Pohle, 1943

Scotonycteris ophiodon Pohle, 1943: 78 (type locality: Bipindi); Aellen, 1952: 39; Novick, 1958; Eisentraut, 1960b: 305, 1963: 73; Coe *et al.*, 1965a: 183; Kuhn, 1965: 326; Rosevear, 1965: 116; Hayman *et al.*, 1971: 5; Bergmans, 1973; Eisentraut, 1973: 36; Coe, 1976: 545; Eisentraut, 1976: 79, 193; Bergmans, 1979: 180; Haiduk *et al.*, 1980: 185, 1981: 226; Hill, 1982: 117; Wolton *et al.*, 1982: 430, 441; Roth *et al.*, 1988: 184.

Scotonycteris ophiodon cansdalei Hayman, 1946: 503; Eisentraut, 1960b: 305-308; Rosevear, 1965: 116-118; Hayman *et al.*, 1971: 5.

Epomophorus ophiodon; Dekeyser, 1955: 108.

Scotonycteris ophiodon ssp.; Rosevear, 1965: 118.

Material examined

CAMEROUN. Bipindi: 1 imm. ♀, alc. (not seen), skull, V-1899, G. Zenker (holotype of *Scotonycteris ophiodon* Pohle, 1943; ZMB 50001). (3 km W of Eseka, Malende, above Mueli.)

CONGO. Dimonika: 1 ♀, 1 imm., 13-III-1972, University of Brazzaville (ZMA 19.715; UBRA 9-♀-72-03-13).

GHANA. Oda: 1 ♀, 24-XII-1945, G. S. Cansdale (holotype of *Scotonycteris ophiodon cansdalei* Hayman, 1946; BMNH 46.229); 32 miles W of Prestea, at 02°28′ W, 05°23′ N: 1 ♀, 5-I-1968, J. C. Geest (USNM 414017).

LIBERIA. Mount Nimba, at Old Mine Road: 3 ♂♂, 1 ♀, 1 imm. ♀, alc., 23-VII/28-VIII-1978, R. J. Wolton (BMNH 79.444/48). Tars Town: 2 ♂♂, 1 ♀, 20/22-VII-1971, D. A. Schlitter (USNM 481679, -81/82).

Diagnosis: A medium-sized fruit bat, fal between 75 and 87.6, overall fur colour impression somewhat reddish light brown; white fur patch dorsally on rostrum and ditto behind eyes; (rather indistinct) white tufts at anterior and posterior ear bases; contrastingly light-coloured finger joints; no visible tail; short rostrum; premaxillae well-developed; mandibulum rather heavy; upper and lower canines very tall and with an inner cusp; third and fourth premolars and first molars tall and pointed, in occlusal view short and roundish, and with very distinct inner cusps; two series of palatal ridges: one of six undivided interdental smooth ridges, and one of about 12 postdental serrate ridges. Measurement ranges and ratios taken from all over the species' range:

fal ♂♂ 74.6-78.7 (n = 6);
♀♀ 75.3-87.6 (n = 6).
gsl ♂♂ 38.0-38.2 (n = 2);

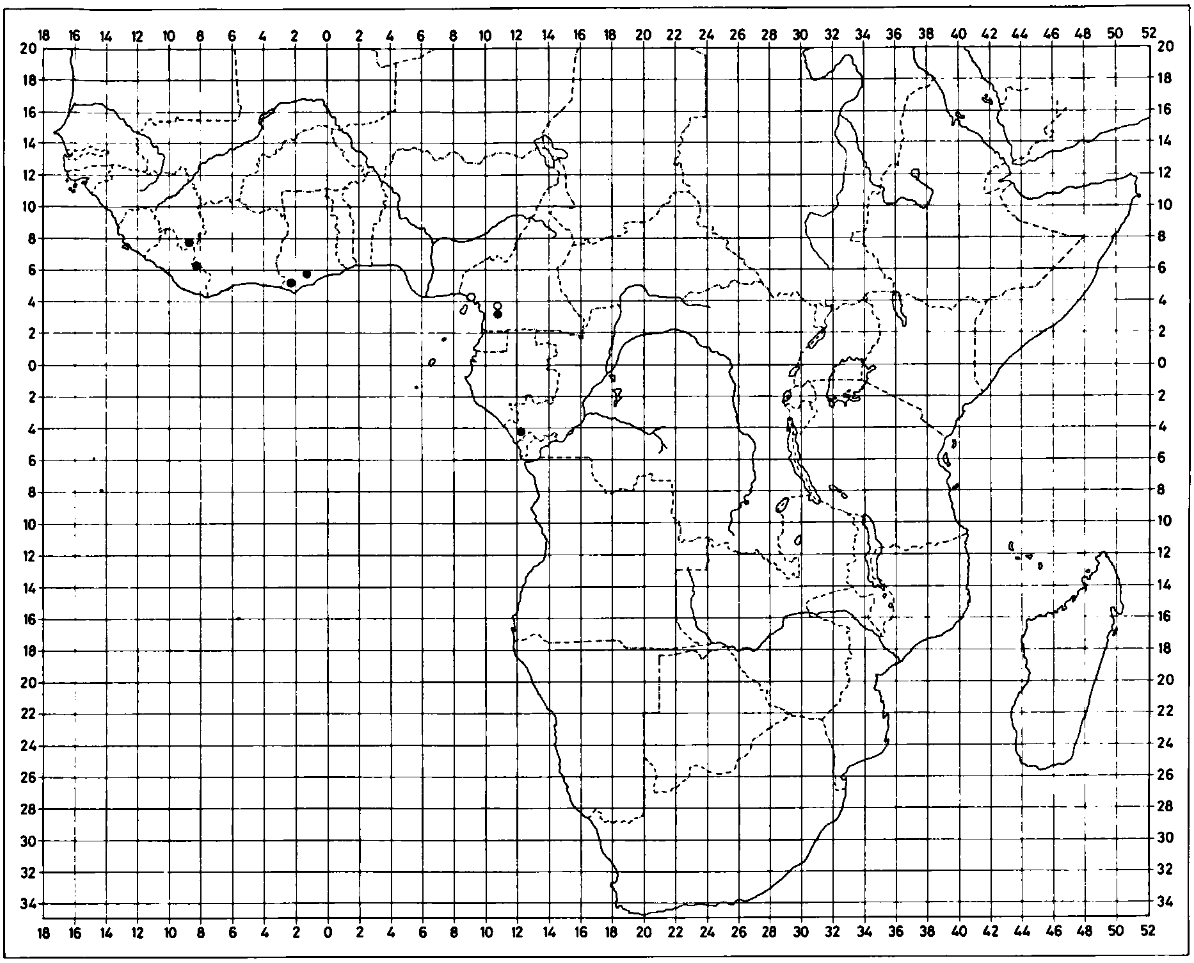

Fig. 3. Distribution of *Scotonycteris ophiodon* Pohle, 1943; black dots: squares from where material has been identified by the author; open circles are based on records in the literature, museum registers and correspondence.

	♀♀	35.3-43.3 (n = 5).
cbl	♂♂	37.4 (n = 1);
	♀♀	34.5-41.8 (n = 4).
rl	♂♂	13.2 (n = 1);
	♀♀	12.2-16.0 (n = 4).
pl	♂♂	22.0 (n = 1);
	♀♀	19.6-25.3 (n = 4).
zw	♂♂	23.3-24.4 (n = 3);
	♀♀	22.6-27.3 (n = 4).
C^1-M^1	♂♂	13.5 (n = 1);
	♀♀	12.0-15.0 (n = 4).
W	♂♂	65 -71 (n = 4);
	♀♀	65 -95 (n = 6).
rl	♂♂	34.7% of gsl (n = 1);
	♀♀	33.2-36.9% of gsl (n = 5).
pl	♂♂	57.9% of gsl (n = 1);
	♀♀	55.2-58.4% of gsl (n = 5).
zw	♂♂	61.6% of gsl (n = 1);
	♀♀	62.3-64.0% of gsl (n = 4).

Specimens from Congo appear to be considerably larger than those from Liberia, Ghana and Cameroun. Those from Cameroun may be intermediate.

Distribution: Fig. 3.

Related species: *Scotonycteris zenkeri* is the only other species in the genus and externally very similar, except that it lacks white ear tufts, is generally somewhat darker with on the back whitish intermixing with the brown, and is very much smaller, with a fal less than 57. *Casinycteris argynnis* is also similar, externally, but has relatively larger and more rounded ears, a less defined white rostral fur patch, more conspicuously white lips and cheeks, and is much smaller, with a fal less than 64; internally the most striking difference lies in the reduction of the postdental palate.

Remarks

Taxonomy: Altogether 19 specimens of this species are known to me, of which only 13 certain adults, from four mutually distant areas: northwest Liberia, southern Ghana, southwest Cameroun, and southwest Congo. Of these, seven are from Liberia and three from Cameroun, and from Ghana and Congo no male specimens are known. This limited material does of course not allow for a sufficient analysis of possible intraspecific differences of taxonomic value. Nevertheless, if the disjunctions in the presently known distribution do reflect reality, such differences are to be expected.

Hayman (1946) based a new subspecies on a female specimen from Ghana, on details of the fur colours (although the type specimen had obviously been discoloured, as related in Pohle's original account) and on some cranial differences which were later rightly recognized as mature states of the immature conditions in the holotype (Eisentraut, 1960b; Rosevear, 1965). Novick (1958) described a specimen from "Liberia" differing in possessing yellow fur patches below the white post-ocular spots and, if compared to the holotype, longer feet and metacarpals and a number of slightly larger skull dimensions. In my experience, measuring the length of the foot in Megachiroptera is not an easy procedure and the results of field measurements as often written on collectors' labels can not be reproduced. Novick measured a foot length in his specimen of 19, which is substantially more than the 14 Pohle (1943) measured in the holotype and the 15 Hayman (1946) copied from the field label of the specimen from Ghana. But Eisentraut (1960b) measured 16, 16, and 17, respectively, as foot length in a ♂, ♀ and subadult ♀ from Mount Cameroun, Coe (1976) measured a foot of 18 in a female specimen from Liberia, and J. C. Geest, who collected the USNM ♀ at 32 miles West of Prestea, Ghana, noted 18 as the length of its foot. These results render Novick's measurement less extreme than he supposed it was. The metacarpal lengths given by Novick are relatively large, even considering that his only values for comparison, the lengths published by Pohle (1943) and Hayman (1946), appear to be rather too small (see table 3). Novick's absolute values (table 2, right hand column) are not exceptional, however, but quite match those of other Liberian specimens. The aberrant measurement, therefore, is the published fal of Novick's specimen. I suspect that it may be too small, possibly due to the way in which the skin has been prepared. The BMNH specimens from Liberia (Mount Nimba) do not show the bright yellow fur patch under the white post-ocular spot. They have been in alcohol for some time, which may have caused some discolouration, but it is not likely that no trace would have been left as the other fur colours are still quite normal (see also Hill, 1982). Moreover, the pictures of a live specimen of the same series published by Wolton *et al.* (1982, pl. V) do suggest there were no such yellow patches. This may indicate that Novick's specimen is not from Mount Nimba but instead representing an unknown locality. Some research into its precise history may yet reveal this.

The adult ♀ from Congo, described and discussed earlier (Bergmans, 1973; 1979), is considerably larger in body and skull dimensions than specimens from the other regions, and its subadult companion is also large (see Bergmans, 1973). From the data in table 3 it appears that ♀♀, as in *Scotonycteris zenkeri*, may reach higher average dimensions than ♂♂. It also seems that specimens from Ghana may not differ much, in size, from Liberian specimens and that those from Cameroun may have slightly larger skulls than their western relatives: gsl varies from 35.3 to 38.2 in

Table 2. Measurements of adult specimens of *Scotonycteris ophiodon* Pohle, 1943 and of the subadult holotype specimen (♀ZMB 50001), per sex and per country; countries in an order from west to east.

sex	?	♂♂						♀♀						
origin	Liberia	Liberia					Cameroun	Liberia		Ghana		Cameroun		Congo
collection	YPM	BMNH	BMNH	BMNH	USNM	USNM	MAKB	BMNH	USNM	BMNH	USNM	ZMB	MAKB	ZMA
Number	9442	79.446	79.447	79.448	481679	481681	#196	79.444	481682	46.229	414017	50001	#211	19.715
preparation	dry	alc.	alc.	alc.	dry	dry		alc.	dry	dry	dry	alc./S.		dry
fal	73.8	78.7	75.0	77.5	76.0	76.7	74.6	75.3	81.4	c.75.5	76.7	75	77.8	87.6
3rd metacarpal	58.5	60.3	56.3	58.6			56.5	56.5		53.8		54	58.6	66.2
4th metacarpal	55.5	57.2	53.5	55.6			51.7	54.7				50	55.1	63.1
5th metacarpal	54.9	57.3	54.8	57.1			52.8	57.0		50.5		51	56.8	64.1
ear length	—	21.4	20.0	21.8			24	20.1		22	23	20.5	25	24
gsl	—				—	38.0	38.2		37.4	35.3	38.2	>35.5	40.2	43.3
cbl	—				—	37.4			37.0	34.5	36.7	34.8		41.8
rl					—	13.2			12.7	12.2	12.7	12.5		16.0
pl					—	22.0			21.8	19.6	21.1	20.6		25.3
cranium width					15.1	15.1	16.0		15.0	14.6	15.0	—	16.3	17.0
iow	7.2				7.0	7.0	7.2		7.2	6.7	6.6	6.3	7.7	7.7
pow					7.7	6.7	7.8		6.6	6.9	6.7	8.8	7.8	7.2
zw	—				23.3	23.4	24.4		23.7	22.6	23.8	—		27.3
mandible length	29.5				28.2	28.5	29.0		29.0	26.8	28.2	26.5	30.3	33.1
mandible height	14									12.8	13.8	11.0		
C^1-C^1	7.8	9.0	8.2	8.8	8.5		8.3	8.4		7.6	8.5	7.2	9.4	10.0
C^1-M^1		13.4	12.5	12.6			13.5	12.0		12.1	12.0	11.9	13.5	15.0
M^1-M^1	13.4						13.8			12.3	13.2	11.9	15.0	17.2
C_1-M_2	11.9	15.4	14.6	14.8			14.9	14.0		13.7	14.0	13.8	15.0	16.9
W							71				69		95	

N.B. Measurements of YPM specimen after Novick (1958), of tooth rows of BMNH Liberian specimens after Hill (1982), of MAKB specimens after Eisentraut (1960b), of body of ZMB specimen after Pohle (1943); ear lengths and weight of dry specimens copied from labels.

Table 3. Metacarpal lengths as percentages of fals in adults of *Scotonycteris ophiodon* Pohle, 1943. The subadult holotype specimen (ZMB 50001) has been included.

sex	?	♂	♂	♂	♂	♀	♀	subad. ♀	♀	♀
country	"Liberia"	Liberia	Liberia	Liberia	Cameroun	Liberia	Ghana	Cameroun	Cameroun	Congo
collection	YPM	BMNH	BMNH	BMNH	MAKB	BMNH	BMNH	ZMB	MAKB	ZMA
number	9442	79.446	79.447	79.448	* 196	79.444	46.229	50001	* 211	19.715
metacarpal 2	58.2[1]	51.3	49.3	53.0		54.6		52		54.8
metacarpal 3	79.2[1]	76.6	75.0	75.6	75.7[2]	75.0	47[3]	72	75.3[2]	75.5
metacarpal 4	75.2[1]	72.6	71.3	71.7	69.3[2]	72.6	71.2[3]	66.7	70.8[2]	72.0
metacarpal 5	74.4[1]	72.8	73.1	73.6	70.8[2]	75.7	66.9[3]	68	73.0[2]	73.2

[1] calculated from Novick's measurements (1958)

[2] calculated from Eisentraut's measurements (1960)

[2] calculated from Hayman's measurements (1946)

Liberian and Ghanese ♀♀, but amounts to 40.2 in a ♀ from Cameroun. But it is beyond doubt that the single known Congolese ♀ represents a population of large-sized individuals which, once their geographical isolation has been assessed, probably deserve subspecific distinction. This isolation, as well as that of the other parts of the known distribution pattern, is not unlikely. Where the species is apparently common this may be established by the usual technique (see Wolton *et al.*, 1982). In spite of this, it has never been discovered in some well-researched forest areas in between the regions of distribution. With regard to the assumed gap between the Camerounese and Congolese populations it is of interest to note here that rather extensive fruit bat collecting and research over a number of years in northeast Gabon, as reported by Brosset (e.g. 1966b), Emmons *et al.* (1983) and others, and to which must be added the collecting results of Dr P. J. H. van Bree in 1963-1964 (unpublished but included in the present series), have never uncovered a specimen of *Scotonycteris ophiodon* — whereas *S. zenkeri* is not uncommon there.

Direct comparison of the Congolese female skull and that of the specimen from Ghana described as *cansdalei* revealed some differences which would not all seem attributable to normal intraspecific variation. The braincase in the Ghanese specimen is relatively higher, ascending strongly just behind the postorbital constriction. Its very low temporal ridges converge and almost meet at the top of the braincase, but continue separately towards the skull constriction at about 5 mm from the supraoccipital ridge, where they fuse into a single ridge. Its supraoccipital ridge is also less pronounced than in the Congolese specimen. In the latter, the braincase is not domed but evenly rounded, and the temporal ridges fuse at its highest point. A domed skull and largely separated temporal ridges are possibly only related to small skull dimensions and not restricted to certain populations.

The bullae in the Ghanese specimen are relatively smaller, with a greater distance between them and the glenoid fossa than in the specimen from Congo. The position of M^1 in the Ghanese specimen is more lingual than in the specimen from Congo, in which it is placed partly outside the line through canine and premolars. This is shown in the distance over M^1-M^1 which is 34.8% of the gsl in the former and 39.7% in the latter specimen. Even in the other, far larger skull from Ghana M^1-M^1 is only 34.5%, which supports that this character may be of taxonomic value. In the adult ♀ from Cameroun M^1-M^1 is 37.3% of the gsl, which is intermediate between the values from Ghana and Congo — just as its skull size. Finally, the secondary or inner cusps of upper and lower canines are much less conspicuously notched in Liberian and Ghanese specimens than in Congolese specimens (see Bergmans, 1979, fig. 4).

Haiduk *et al.* (1980) examined the karyotype of a male of *S. ophiodon* from near Eseka, Cameroun, and established the diploid number as 34 and the fundamental number as 62. They found the karyotype to be distinctive, in several respects, from a number of other African Megachiroptera, including some epomophorines, and on this basis rejected synonymization of *Scotonycteris* with *Epomops* Gray, 1870, as has been proposed by Simpson (1945). One character, a pair of small acrocentric chromosomes, may be shared with the more distant genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899, and *Megaloglossus* Pagenstecher, 1885, but this could not be conclusively demonstrated. Haiduk *et al.* (1981) used differential G- and C-band staining to assess the magnitude of chromosomal variation in *Scotonycteris ophiodon* and seven other African Megachiroptera. This technique allowed for the identification of four times as many rearrangements as standard karyotyping. The G-banded karyotype of *S. ophiodon* now turned out to be unlike any of the other taxa examined, including some epomophorines.To derive it from that of *Myonycteris torquata* (Dobson, 1878) which was used as the standard reference, a much higher number of rearrangements is needed than for any of the other species. However, evolutionary relationships are not implied by these authors, who present their results as a possible sequence of chromosomal events explained in the most parsimonious fashion.

Distribution and geographical variation: The known distribution pattern of *S. ophiodon* curiously shadows that of *S. zenkeri*, be it that it shows larger gaps between fewer collecting localities, and no such localities at all east of 13° E. It is also worth noting that towards the East the pattern adjoins that of *Casinycteris argynnis* (see fig. 4), which comes very close in southern Cameroun but has not yet been found to overlap.

S. ophiodon is a typical inhabitant of the West

African rain forest belt (Eisentraut, 1963). Most localities are in Wetter (32 miles west of Prestea; Bipindi; Eseka; Malende; above Mueli) or Drier (Oda; Dimonika) types of Guineo-Congolian lowland rain forest, or in a mosaic of both (types 1a, 2 and 3, respectively, in White, 1983). At Mount Nimba, Wolton *et al.* (1982) caught nine out of ten specimens between 1000 and 1200 m and remarked on the species' altitudinally distinct distribution. Coe (1976) noted that at about 900 m the rain forest on Mount Nimba gives way to *Parinari* forest (and, locally, tree fern forest), dominated by *Parinari excelsa* Sabine and probably produced by, among other conditions, the dense cloud layers that develop almost daily through the rainy season at this altitude and above. But Wolton *et al.* also caught a specimen at 550 m, and Coe one at 820 m, and in all other regions the species has been collected between 120 m (Oda, Ghana) and somewhat above 600 m (Mueli, Cameroon), and there can be no doubt that *S. ophiodon* is a lowland forest species which at Mount Nimba has developed a habit of living largely above 1000 m — at least during the months (July-September) when Wolton and his party were collecting, and possibly in connection with the condition of certain food species.

If the disjunct distribution will be confirmed by further field research, it will not be easily explained. Earlier, I have discussed some differences between specimens from the various regions which may yet turn out to be of taxonomic value. If they do, they will at the same time indicate mutual isolation of the various (groups of) populations over a considerable stretch of time — as in *Scotonycteris zenkeri* —, to be reviewed in the general discussion at the end of this series.

Casinycteris O. Thomas, 1910

Casinycteris O. Thomas, 1910: 111 (type species: *Casinycteris argynnis* O. Thomas, 1910); Andersen, 1912 568; Hayman, 1946.
Scotonycteris (not of Matschie, 1894); Pohle, 1943: 86.

O. Thomas (1910) based this genus mainly on the markedly shortened postdental palate, "recalling that found in some of the Microchiroptera". By most of its other characters the type and only species, *Casinycteris argynnis* O. Thomas, 1910, would have been assigned to *Scotonycteris* (of which, at the time, only *S. zenkeri* was known). Thomas' diagnosis of *Casinycteris* therefore centres around its differences from *Scotonycteris*. External characters, including colouration, are "precisely as in *Scotonycteris*", Thomas wrote. Only its ears are larger and its wings orange coloured in the fresh state. (About the latter condition in fresh *Scotonycteris* nothing was known.) The palate ends practically at the level of the upper molar; its posterior margin shows two forward incurvations, one in each half, and in the median plane it connects with a long and high vomerine bridge. Thomas' diagnosis included further that compared to *Scotonycteris* the rostrum in *Casinycteris* is relatively shorter, its bony palate more arched mesially, its zygomata are more abruptly expanded and its postorbital processes and cranial ridges more strongly developed; he described the teeth as generally higher, pointed, and shorter and broader than in *Scotonycteris*, with well developed inner cusps.

Apart from the exellent illustrations of skull, teeth, and soft palate Andersen (1912) found little to add. He remarked that the pollex in *Casinycteris* is perhaps relatively shorter than in *Scotonycteris*, that the rostrum is not only shorter but also broader, with a more deeply concave interocular region and a near horizontal profile instead of descending towards the tip of the nasals and an anteriorly more steeply ascending alveolar line, that the braincase is rather broader, the mandibular ramus thicker, and the coronoid process higher, broader and less sloping. Andersen further noted that the canines are conspicuously longer, that the upper canines have a faint vertical groove on the anteromedial surface, that M^1 and M_2 are less reduced and that the inner cusps of P^3, P^4 and P_4 are diverging at the tips. He described the soft palate as with four thick and prominent and one thinner and serrate interdental ridges and a large number of irregular, thin and serrate ridges crowded together on the postdental palate.

Pohle (1943), when describing *Scotonycteris ophiodon*, pointed out that most of the characters of this species are intermediate between those of *S. zenkeri* and *Casinycteris argynnis*. He rejected a solution which, in his opinion, some colleagues might have chosen to the problem of the generic assignment of the new species: to propose a new genus. He agreed with Thomas and Andersen (*op. cit.*) that the shortened postdental palate as a unique character in the Megachiroptera presented the single important diagnostic feature of the genus *Casinycteris* and consequently placed the new species in *Scotonycteris*. But he argued further that the condition of the bony palate in the type specimen of *C. argynnis* might be nothing more than a pathological malformation (a so-called cleft palate). (If Pohle had known the reports by Allen *et al.*, 1917 — and its companion paper by Lang *et al.*, 1917a — and Schwarz, 1920 on the second and third specimens of *Casinycteris argynnis*, respectively, which both matched the palate condition of the type specimen, his remark on the possibly pathological background of this condition would have become redundant). Pohle continued that even if the palate condition in the type specimen of *C. argynnis* would turn out to be the normal one for the species, it would still not justify a separate genus. It would be the expression of a genetic change which occurs, as an anomaly, frequently ("erheblich") throughout the mammalian Class, for which reason it should be interpreted as a relatively simple change and as such of too little importance to serve as the basis for a genus. Pohle went on with the not quite logical remark that if there were no other characters than the short palate, *C. argynnis* could not even stand as a species, and he proposed to synonymize *Casinycteris* with *Scotonycteris*.

Hayman (1946) commented on these views but somehow failed to appreciate the quintessence of Pohle's reasoning: the genetic argument. Hayman rejected the proposed synonymization on the ground that the shortened palate had been established as the normal condition in *C. argynnis* and concluded that the genus must stand.

No other author has discussed the generic allocation of *Casinycteris*. It should perhaps be noted here that G. G. Simpson (1945), who specifically dealt with the criteria applicable in supraspecific mammalian taxonomy and was certainly aware of the possibly relatively simple mutation underlying the reduction of the bony palate in *Casinycteris*, synonymized *Scotonycteris* with *Epomophorus* Bennett, 1836 (regarding it as a subgenus at most: see Simpson, p. 36) but retained *Casinycteris* as an independent genus. Whatever his opinion may have been on the pertinence to phylogenetic taxonomy of the shared characters of *Scotonycteris* and *Casinycteris*, Simpson apartly valued the unique morphology of the palate in *Casinycteris* as highly relevant in that respect.

Some remarks may be added here to explain why in the present paper *Casinycteris* has been maintained as a genus and not as a subgenus or synonym of *Scotonycteris*. I agree with Simpson's implicit statement that differences or similarities in facial fur colour patterns should not be given too much weight, in mammalian taxonomy. Within the Megachiroptera, Andersen (1912) mentioned *Styloctenium wallacei* (Gray, 1866) and *Pteropus personatus* Temminck, 1825 as species with white markings of the head similar to those of the species presently under discussion; a further variant is seen in *Neopteryx frosti* Hayman, 1946 (see fig. 7 in Bergmans *et al.*, 1988). In quite a few mammalian Orders certain species are adorned with rather similar patterns. Brosset (1966c, fig. 13) explained that in *Scotonycteris zenkeri* the light fur patches contribute to the bat's camouflage when it is hiding in the foliage during the day. This may apply also to *S. ophiodon* and *Casinycteris argynnis*, which may have a preference for the same type of roost. For *S. ophiodon* this has been inferred by Eisentraut (1960b). It cannot be exluded that, as in the other species mentioned, the facial patterns of *Scotonycteris* on the one hand and *Casinycteris* on the other have developed independently and are an example of convergence. But because of the other characters shared by the two genera a possible common origin of the patterns cannot be too easily discarded. The bright orange colour and reticulate pattern of the wing membranes in live *Casinycteris argynnis* as mentioned by O. Thomas (1910) are matched by the yellowish-brown (or Sulphin Yellow) and reticulate wings in live adult *Scotonycteris ophiodon* (see the descriptive remarks in Hayman, 1946 and Eisentraut, 1960b). The orange and yellowish colours disappear after death and preparation of the specimens, the reticulate pattern does not. Adult *Scotonycteris zenkeri* have dark brown (Eisentraut, 1960b) or light olive brown membranes (Kuhn, 1962). Field notes on the type specimen of *Casinycteris argynnis* state that the ears, eyelids and muzzle were also bright orange in life (O. Thomas, 1910). Lang *et al.* (1917a) described the nose as dirty pink and ears and wing membranes as yellowish brown. The bare skin of mouth, eyelids and ears in live *S. ophiodon* are dark yellow, according to Hayman (1946). Neither orange nor yellow are preserved in prepared specimens. There appear to be no field notes on the colour of the naked facial parts in *S. zenkeri*. But Eisentraut (1960b), who collected both *Scotonycteris* species and mentioned the yellow in *ophiodon* does not describe anything like it for *zenkeri*, and the pictures of live *zenkeri* in Brosset (1966c) suggest that nose and ears have the same dark colour tone as the flight membranes. In *Casinycteris argynnis* the joints of metacapals with first phalanges and of first and second phalanges of the third, fourth and fifth fingers are contrastingly light — lemon coloured, according to Perret *et al.*, 1956 — in live or fresh specimens (see the picture in Nowak *et al.*, 1983) and in preserved specimens. In *Scotonycteris ophiodon* the mentioned joints are also light in colour, in *S. zenkeri*, to all appearances, they are not. (Since the completion of this paper, the author collected both *Casinycteris argynnis* and *Scotonycteris zenkeri*, at Irangi in East Zaire. In two specimens of *C. argynnis* the skin of the anterior and inner central part of the ear and of the finger joints was light yellow; a narrow band of skin around the eye, interrupted behind by the white postocular spot and continuous in front towards the region around the somewhat darker inner margins of the nostrils, the chin and the anterior part of the wing near the pollex and the two phalanges of the index were light yellowish brown; the wing membranes as a whole were medium brown with a yellowish hue. The margin and upper and posterior parts of the ear were brown, with the upper and posterior rim even blackish brown. In one specimen of *S. zenkeri* all exposed skin parts were rather brown. The very thick and extensible upper lips in *C. argynnis* resemble cheek-pouches and emphasize its short-snoutedness, whereas in *S. zenkeri* the lips are much less specialized.)

As with the colour characters, a number of other characters initially believed to differentiate *Casinycteris* from *Scotonycteris* have lost much of their significance through the discovery of *Scotonycteris ophiodon* which is intermediate in many respects. Yet, it is easily recognized as a less advanced form of *Scotonycteris*. In *Casinycteris*, the orientation of the foramen magnum is rather more horizontal than in *Scotonycteris*, which may be related to a different general posture of the head. In this connection the cervical vertebrae should be examined (see Jepsen, 1970). The vomerine ridge in *Casinycteris* continues as a rather sharp ridge to the level of the anterior sides of the bullae. In *Scotonycteris* there is no ridge; the median part of the vomer is only slightly elevated, and this elevation ends anterior to the end of the pterygoid wings. The rostrum profile in *Casinycteris* is slightly turned-up; in *S. ophiodon* it is rather 'normal', as in *zenkeri*, although relatively higher anteriorly. In *Casinycteris* there is a distinct angle in the lateral profile between rostrum and braincase, in *Scotonycteris* this border is not sharply marked. The front in *Casinycteris* is concave, in *S. ophiodon* it is only slightly so, in *S. zenkeri* it is not. The braincase in *Casinycteris* is strongly rounded, in *S. zenkeri* it is somewhat rounded, and in *S. ophiodon* it is not; in part this may be explained as a juvenile trait persisting more strongly in small species — but only in part, as the difference between *Casinycteris* and *zenkeri* is also large, while *zenkeri* is even smaller. The upper margin of the orbit is strong and rather sharp in *Casinycteris* and inflated and roundish in *Scotonycteris*. The zygomatic arches in *Casinycteris* are standing out more widely, laterally, and run much lower, in lateral view, with the lower margin almost at the level of the alveolar line, than in *Scotonycteris*, in which they are generally more lightly built, and are on level with the infraorbital foramen. Andersen (1912) connected the wide arches with a lateral expansion of the orbito-temporal cavity. The low position observed here contributes to the same effect. The large cavity is most simply explained if the eye is relatively large, but I have noted in alcohol specimens of *Casinycteris* that the eyes are rather more forward-oriented than in *Scotonycteris* (*zenkeri*), which would also necessitate some lateral expansion of the orbital cavity — but this observation is in need of confirmation, preferably by pictures or films of live specimens of both genera.

The following notes were made while comparing the skull of the type of *Casinycteris argynnis* with the skull of the adult specimen of *S. ophiodon* from Congo. The bullae in *Casinycteris* are somewhat oblique, in ventral view, with an antero-internal extension. In the Congo specimen of *S. ophiodon* the bullae are also oblique but in a specimen from Ghana they are not, just as in *S. zenkeri*. The mandible in *Casinycteris* is much as in *S. ophiodon* but even more thickened, with more strongly diverging tooth rows: in projection, the position of P_3 is labial to that of C_1, and that of P_4 labial to that of P_3, while in *S. ophiodon* P_3 slightly overlaps with C_1 and P_4 strongly overlaps with P_3. The morphology of the teeth in *Casinycteris shows* many similarities to that in *S. ophiodon*, although most teeth are relatively shorter, antero-posteriorly, than in that species. The dentition in *S. zenkeri* resembles a strongly reduced state of that in *S. ophiodon*. In *Casinycteris*, the upper incisors are short, as in *S. zenkeri*; in *S. ophiodon* they are long. The upper canine has a faint vertical groove on the antero-medial surface (Andersen, 1912), delineating a weak, smooth inner ridge running from cingulum to tip; in *S. ophiodon* this ridge is conspicuous and notched in some specimens, in *S. zenkeri* it is as weak as in *Casinycteris*. The inner cusps of P^3, P^4 and M^1 in *Casinycteris* are less developed than in *S. ophiodon*. Only in P^4 it has an independant tip; in P^3 it is merged with the outer cusp, in M^1 it is vestigial. In P^4 there is a rudimentary anterior basal shelf, while in *S. ophiodon* this shelf is larger. The lower incisors in *Casinycteris* are long, in both species of *Scotonycteris* they are short. The lower canines in *Casinycteris* are long, as in *S. ophiodon*, but have only vestiges of vertical inner ridges. There are almost no anterior and posterior basal shelves in P_4 and M_1, while in *S. ophiodon* especially the posterior shelves are quite well developed in these teeth. The tips of the cheek teeth in *Casinycteris* are generally slightly forward or vertically directed while in *S. ophiodon* at least those of all premolars weakly reflect the recurved form of the upper canine tips.

The important diagnostic skull characters of *Casinycteris* so far are its up-turned rostrum, its proportionally larger orbital cavity, and its less vertical foramen magnum. Together with the relatively larger ears, these characters are bound to make *Casinycteris* look quite different from both *Scotonycteris* species. The existing pictures (Nowak *et al.*, 1983; Brosset, 1966c; Wolton *et al.*, 1982) confirm this. The published remarks on *C. argynnis* being externally indistinguishable from *S. zenkeri*, e.g. by O. Thomas (1910), are always based on dead and preserved specimens.

A further difference and most crucial to current taxonomic views, is the reduction of the postdental palate. This reduction comes down to the loss of what the palatine bones contribute to the formation of the palate. The posterior edge of the palate is entirely formed by the maxillary bones. In adult *Scotonycteris*, most obviously in examples of *ophiodon*, the palatine section of the palate is somewhat depressed, and the line of depression seems to foreshadow the actual loss in *Casinycteris*. Pohle (1943) may be right that this mutation may involve only a relatively simple genetic change, but whether this justifies taxonomic distinction on genus level or not should also be measured by the resulting condition and its functioning. Moreover, the discovery, in 1946, of *Neopteryx frosti*, which has a vacuity in each half of the palatine part of the palate (see Hayman, 1946), which in three of the four specimens on record interrupt the lateral palate margin and are really indentations instead of foramina (see Bergmans *et al.*, 1988), suggests that the loss of the palatine palate section may well be the result of a series of subsequent mutations instead of one. Pohle's comparison to the cleft palate and its frequent occurrence in mammals is therefore unsatisfactory. Andersen (1912) remarked that the soft palate in *Casinycteris* continues as far backward as in other Megachiroptera (including *Scotonycteris*), and one is tempted to believe that the lack of a bony support may enhance its flexibility and therewith its sucking capacity, which may be advantageous in exploiting particular food sources. Another question is, of course, which functions may be hampered by the reduction of the palate. According to Romer (1966), the origin of the palate in mammals (in fact: the secondary palate if compared to more primitive taxa) can reasonably be associated with the development of the constant body temperature characteristic and the palate is an aid in the maintenance of continuous breathing (practically a necessity) while the mouth is functional in eating. Romer compared mammals with crocodilians and noted that in mammals the bony palate does not extend so far back as that in crocodilians, but is continued by a fold of skin as a "soft palate". Thus, generally speaking, the soft palate may well perform the mentioned, primary functions of the (posterior part of the) bony palate — which it apparently does in *Casinycteris*, like in many other short-palated mammals, such as many Microchiroptera. In this respect it is significant that the ridge pattern on the postdental part of the soft palate in *Casiyncteris* does not differ substantially from that in *Scotonycteris*.

The use of the term reduction implies that I consider this character to be derived (apomorph). The rationale behind this is that no other Recent species of the Megachiroptera shares this character or exhibits some state of its development — except perhaps *Neopteryx frosti*. Negative evidence is presented by the only fossil species in which the skull has been preserved, the Miocene *Archaeopteropus transiens* Meschinelli, 1903. The skull is not in good condition but its describer was aware of the diagnostic value of the morphology of the postdental palate in Megachiroptera (in his differential diagnosis he included "le ossa palatine che si continuano dietro l'ultimo molare, restringendosi lentamente indietro") and at least found no indication that *Archaeopteropus* is atypical in this respect. Although it does not necessarily follow that a non-reduced palate presents the primitive (plesiomorph) state in Megachiroptera (see for a discussion of Dollo's so-called law of irreversibility Simpson, 1945), it certainly is very likely, which should be included in the ongoing discussions of the origin of the Megachiroptera and their position vis-à-vis Microchiroptera.

If the functional effect of the palate reduction in *Casinycteris* is as plain as suggested above, the present valuation of this reduction as the most important diagnostic character of a genus may be disputed. On the other hand, even with our poor and incomplete knowledge of the taxon, *Casinycteris* is easily recognized as distinct, and I prefer to await further information, e.g. on its functional anatomy, before reconsidering its taxonomic position.

Casinycteris argynnis O. Thomas, 1910

Casinycteris argynnis O. Thomas, 1910: 111 (type locality: Bitye); Andersen, 1912: 572; J. A. Allen *et al.*, 1917: 421; Lang *et al.*, 1917: 483, 1917a: 511; Schwarz, 1920: 1054; Hayman, 1946; Schouteden, 1944: 107 (in part: the specimen from Stanleystad); Dekeyser, 1955: 106; Perret *et al.*, 1956: 428; Hayman *et al.*, 1966: 21; Pirlot, 1970; Pirlot *et al.*, 1970; Hayman *et al.*, 1971: 5; Bergmans, 1979: 182; Nowak *et al.*, 1983: 192; Meirte, 1984a.

Scotonycteris argynnis; Pohle, 1943.

Material examined

CAMEROUN. Bitye: 1 ♀, 19-XI-1909, G. L. Bates (holotype specimen of *Casinycteris argynnis* O. Thomas, 1910; BMNH 11.5.5.1). Mang: 2 ♂♂, alc., skulls, 20/26-II-1975, D. Thys van den Audenaerde/Van den Veken (MRAC 75-56-M-81, -98). Meyo-Nkoulou: 2 ♀♀ (1 in alc.), skulls, 24-III-1973, L. W. Robbins & D. Thys van den Audenaerde (MRAC 73-18-M-93, -188).

(Mefo.)

ZAIRE. Bena-Bala: 2 ♀♀, 15-I-1984, Nsankulu Betu (MRAC 84-35-M-1, -2). Boende: 1 ♂, 1 ♀, alc., skulls, 1967, E. P. Lootens (MRAC 38652/53). Irangi: 1 ♀, skin, rostrum and damaged mandibulum, 30-XII-1956, H. Stephan (MRAC 27430); 4 ♂♂, 2 ♀♀, 1 imm. ♀, alc., and 5 ♂♂, 2 ♀♀, rostrum and mandibulum, 11-I/18-II-1984, H. Stephan (SMF 64988/65046, 65052): ? Irangi: 1 ♀, rostrum and mandibulum, (? 12-I-1984), H. Stephan (SMF 69400). Koloka: 1 ♂, alc., skull, VI-1911, H. Schubotz (SMF 6367). Lukonga: 1 ♀, 6-VIII-1979, Nsankulu Betu (MRAC 80-13-M-3). Luluabourg: 2 ♂♂ (1 in alc.), 2 ♀♀ (1 in alc.), skulls, 25-II/18-III-1965, De Roo (MRAC 33347/48, 33411/12). Medje: 1 ♀, 22-IV-1910, H. Lang & J. P. Chapin (AMNH 48751). Stanleyville: 1 imm. ♂, alc., skull, V-1926, H. Schouteden (MRAC 16211). Zaire: 1 ♀, 1984, Nsankulu Betu (MRAC 84-35-M-3).

Diagnosis: A small bat, fal between 49.8 and 63.5; thumb relatively long; relatively large, vertical, rounded ears; overall fur colour impression slightly russet brown, mixed with whitish; white fur patch dorsally on rostrum and ditto behind eyes; fur on lips and cheeks white; white tufts at anterior bases of ears; skin of ears, around eyes, around nostrils, of chin and of anterior part of wing and of finger joints yellow or yellowish brown; no visible tail; short, up-turned rostrum; domed braincase; well-developed premaxillae; zygomatic arches relatively strong, standing out wide laterally, with ventral side practically on level with alveolar line; mandibulum quite strong; upper and lower canines tall; premolars and molars in occlusal view short, broad and subcircular, with inner cusps especially well-developed and separate in P^4, P_3 and P_4; two series of palatal ridges: one of three or four thick and one thin and serrate interdental ridges, and one of up to about 13 to 16 crowded, irregular, thin and serrate postdental ridges. Measurement ranges and ratios taken from all over the species' range:

fal ♂♂ 49.8-54.9 (n = 10);
♀♀ 54.4-63.5 (n = 13).
gsl ♂♂ 23.3-25.7 (n = 4);
♀♀ 25.4-28.0 (n = 11).
cbl ♂♂ 21.8-23.9 (n = 3);
♀♀ 24.0-26.7 (n = 11).
rl ♂♂ 6.0- 7.3 (n = 9);
♀♀ 7.3- 8.4 (n = 15).
pl ♂♂ 7.4- 9.4 (n = 9);
♀♀ 8.8-10.9 (n = 14).
zw ♂♂ 18.3-19.5 (n = 5);
♀♀ 17.9-20.4 (n = 11).
C^1-M^1 ♂♂ 7.1- 8.5 (n = 6);
♀♀ 8.3- 9.3 (n = 12).
W ♂♂ 26 (n = 1);
♀♀ 28.5-33 (n = 3);
rl ♂♂ 28.0-29.3% of gsl (n = 4);
♀♀ 29.1-30.9% of gsl (n = 11).
pl ♂♂ 33.7-36.6% of gsl (n = 4);
♀♀ 36.9-39.7% of gsl (n = 11).
zw ♂♂ 75.9-78.5% of gsl (n = 4);
♀♀ 70.5-75.3% of gsl (n = 11).

For selected measurements per country see table 4. The small number of adult specimens per region prevent a reliable analysis of possible geographical variation.

Distribution: Fig. 4.

Related species: *Scotonycteris zenkeri* is somewhat smaller, with a fal of 45-56.4, but rather similar, with the rostral and postocular white fur patches but without a white tuft at the ear basis. It has no up-turned rostrum, relatively smaller ears, no yellow in its exposed skin parts, zygomatic arches on level with the infraorbital foramen, smaller canines, more simple cheek teeth without separate inner cusps, and an unreduced postdental palate. *Scotonycteris ophiodon* is much larger, with a fal of 75 or more, slightly pointed ears, a rather similar colour pattern, no up-turned rostrum, zygomatic arches on level with the infraorbital foramen, canines with distinct vertical inner ridges, and an unreduced postdental palate.

Remarks

Taxonomy: the taxonomy of the species is very much that of the genus, which has been amply discussed in the preceding pages, with the focus on the nature of the relation with *Scotonycteris*. The up-turned rostrum, wide and low zygomatic arches and reduced postdental palate are considered generic characters. All other characters, such as pertaining to dimen-

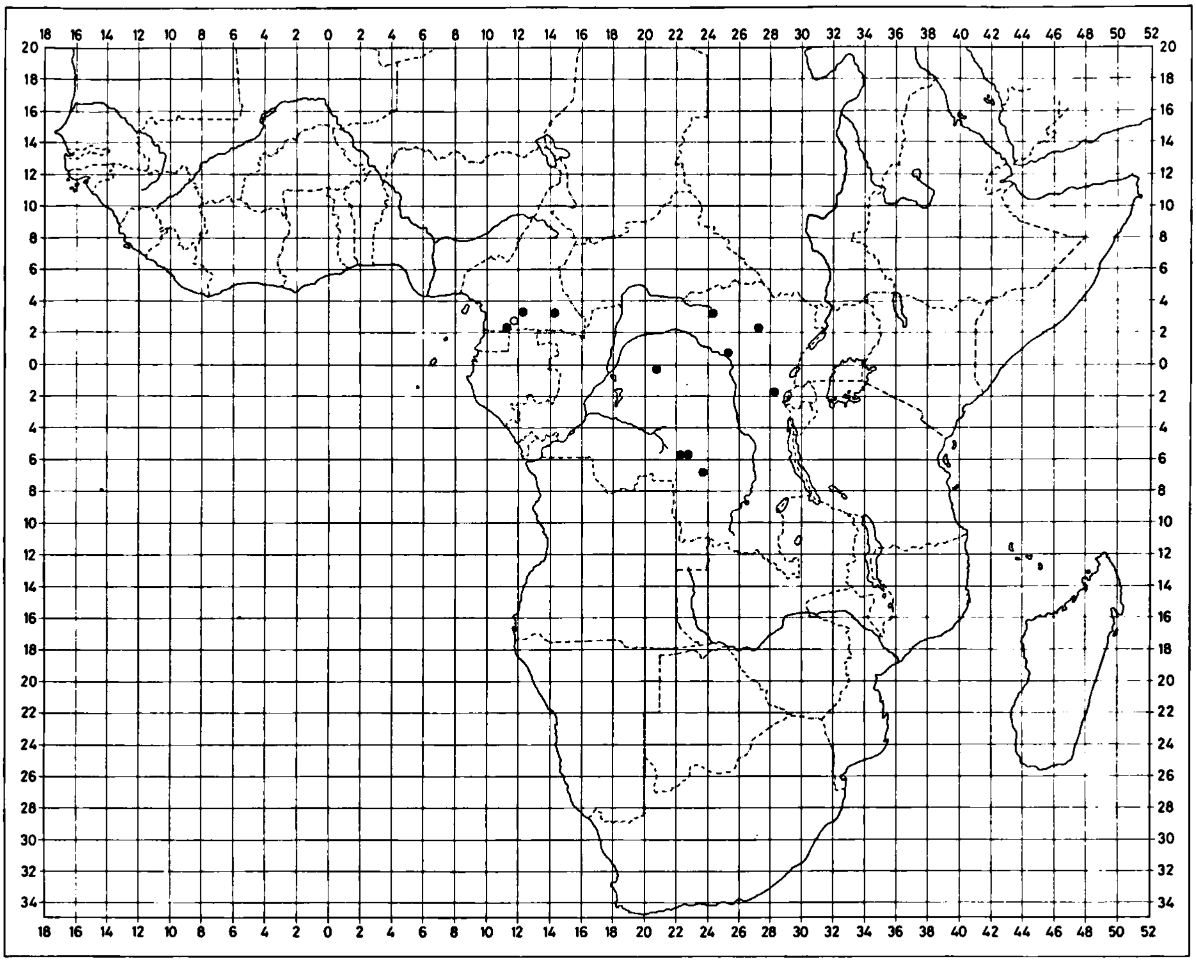

Fig. 4. Distribution of *Casinycteris argynnis* Thomas, 1910; black dots: squares from where material has been identified by the author; open circles are based on records in the literature, museum registers and correspondence.

sions, skin and fur colour, size and form of ears, and dental and soft palate morphology are considered specific characters.

After some seven records and/or descriptions of individual specimens in the literature, Meirte (1984a) was the first to deal with a more substantial series of specimens. In the present report, the number is again considerably extended, but unfortunately the skulls of a number of new specimens have been preserved as rostrums and mandibulums only. Meirte (1984a) suggested that the relatively dark colour of an immature specimen could be due to its having been immersed in alcohol; I am quite sure that it is just the juvenile colouration, as juveniles of fruit bats, and certainly of epomorphorines, are usually darker than their parents. In some specimens, e.g. from Irangi, the rostral white fur patch is less distinct than in *Scotonycteris zenkeri*. On the other hand, the bands along upper and lower lip and the cheek are more conspicuously white, as the skin beneath is nearly white, against yellowish or light brown in *Scotonycteris*, and as there are no intermixing dark hairs, as in *Scotonycteris*. The newly recorded specimens from Irangi (4 ♂♂, fals: 49.8, 51.3, 52.5 and 53.7; 3 ♂♂, rls/pls/mandible lengths: 6.5/8.0/18.2, 6.5/8.1/18.6, and 6.6/7.9/18.7; 3 ♀♀, fals: 57.0, 57.9, 58.1; 2 ♀♀, rls/pls/ mandible

Table 4. Selected measurements of *Casinycteris argynnis* O. Thomas, 1910.

		♂♂								♀♀[1]							
		fal	gsl	cbl	rl	pl	zw	C^1-M^1	W	fal	gsl	cbl	rl	pl	zw	C^1-M^1	W
Cameroun	n	2	2	1	2	2	2	2		4	4	3	3	3	3	3	2
	m									61.3	27.8	26.4	8.3	10.3	19.9	9.1	
	min	53.8	24.9	23.3	7.1	8.4	19.0	8.1		60.0	27.1	26.1	8.1	10.0	19.5	8.9	30
	max	54.2	24.9		7.3	8.9	19.2	8.2		63.5	28.4	26.7	8.4	10.8	20.4	9.3	33
Zaire	n	9[2]	2	2	7	7	3	4	1	11[2]	8	8	12	11	8	9	1
	m	52.5			6.6	8.3	18.9	7.8		58.3	27.0	25.8	7.9	10.0	19.6	8.9	
	min	50.4	23.3	21.8	6.0	7.4	18.3	7.1	26	54.4	25.4	24.0	7.3	8.8	17.9	8.3	28.5
	max	54.9	25.7	23.9	7.2	9.4	19.5	8.5		61.0	27.8	26.6	8.4	10.9	20.3	9.3	

[1] fal and gsl of specimen from Mefo included, copied from Perret *et al.*, 1956

[2] fal of specimen from Boende included, copied from Meirte, 1984

lengths: 7.4/9.0/20.1, 7.4/9.4/20.4) are only slightly smaller than the (immature) ♂ from Stanleyville and the ♀ from Medje, respectively, and the ♂♂ equal the ♂ from Koloka. The 2 ♀♀ from Bena-Bala — the only new locality since Meirte (1984) — have fals of 57.9 and 59.8 and gsls of 27.0 and 27.7, and agree perfectly with the specimens from Lukonga and Luluabourg, also in Kasai. (Specimen MRAC 33411 from Luluabourg, listed as an immature ♀ by Meirte, is an adult ♂. Several of its incisors, both P_1 and the right hand M_2 are missing, but this is not a pattern shown normally by immatures. Moreover, its skull sutures are closed, which proves it to be mature. Maturity, size and undeveloped teats combine to infer its sex as male).

Distribution and geographical variation: The presently known localities may be conveniently divided into four groups: Cameroun (Bitye, Mang, Mefo, Meyo-Nkoulou), northeast Zaire (Irangi, Koloka, Medje, Stanleyville), Boende, and Kasai (Lukonga, Luluabourg, Bena-Bala). Meirte (1984a) noticed that the specimens from Cameroun are large, those from Boende small, and those from Kasai large-skulled. I measured slightly larger fals and gsl (a single specimen) in ♂♂ from Kasai if compared to those from Cameroun, and slightly smaller fals and overlapping gsls in ♀♀ from Kasai if compared to ♀♀ from Cameroun. The ♂♂ from northeast Zaire are smaller than those from Cameroun and Kasai (but their gsls are not known) and the ♀♀ from northeast Zaire overlap in fal range with those from Kasai while the single known gsl is slightly smaller. But these geographically rather distinct areas are undoubtedly inhabited by a number of populations each, and the available numbers of measurements (5 or less per area) do not allow for more than very cautious speculations about geographical variations in size between the areas. And of course there is no reason yet to suppose that the distribution is as discontinuous as it now appears. It may be significant, in this respect, that the species occurs at Boende, in the Swamp forest of Central Zaire (according to White, 1983: type 8) — a vegetation type from where few Megachiroptera are known — and rather central to the other three areas.

Of the 12 localities on record, four are in Wetter and two in Drier types of Guineo-Congolian lowland rain forest, and two in a Mosaic of these (types 1a, 2 and 3 in White, 1983). One is in Transitional rain forest, two are in Swamp forest not far from type 1a, and two are in a Mosaic of Guineo-Congolian rain forest and secondary grassland (types 4, 8 and 11a in White, 1983). Quite obviously, *Casinycteris argynnis* is a species of the lowland rain forest. The SMF series from Irangi confirm Meirte's observation that the species must be locally abundant; this need not contradict its roosting solitary by day, as observed by Lang *et al.* (1917a).

Pteropus Brisson, 1762

Pteropus Brisson, 1762: 13, 153-155 (type species: "*Pteropus rufus aut niger, auriculis brevibus acutisculis*"); Andersen, 1912: 61-79 (identification of type species as *Vespertilio vampyrus niger* Kerr, 1792 = *Pteropus niger* (Kerr, 1792)).

As noted in the general introduction (Bergmans, 1988: 78-79) I have not studied the genus *Pteropus* Brisson, 1792 as extensively as the other genera treated in this series. Almost 90% of the about 60 species currently recognized (see Honacki *et al.*, 1982; Nowak *et al.*, 1983) are extralimital, and a true review of the genus would be out of place here.

Pteropus does not occur on the African mainland and most of the species presently examined inhabit oceanic islands in the western Indian Ocean and cannot be called African in the true, biogeographical sense. Two, however, do inhabit continental islands (Pemba, Mafia) and some of the taxa on the oceanic islands are evidently phylogenetically closely related.

Andersen (1912) was the first reviser of *Pteropus*. After him, no other author has published on the taxonomy of the entire genus. In 1961, Dr H. Felten of the Senckenberg Museum in Frankfurt initiated a series of studies set up to eventually comprise all *Pteropus* species, but pressing other tasks prevented him from fulfilling the project. Nowak *et al.* (1983) mentioned a number of other relevant post-Andersen papers dealing with particular species and more have appeared simultaneously and later in which important mutations were reported (e.g. Musser *et al.*, 1982). The only paper relevant to the taxonomy of the 'African' species was published by Hill (1971).

Andersen (1912) placed *Pteropus* in a special branch of his Rousettine section of Megachiroptera. Of that section, *Rousettus* Gray, 1821 (including *Lissonycteris* Andersen, 1912 as a subgenus), *Eidolon* Rafinesque, 1815 and *Boneia* Jentink, 1879 (considered a synonym of *Rousettus* by the present author (see Bergmans *et al.*, 1988)) formed the Rousettine branch. To this should now also be added the genus *Myonycteris* Matschie, 1899 which Andersen had placed in his Cynopterine section, where it does not belong (e.g. Rosevear, 1965; Hayman *et al.*, 1971). Important diagnostic characters of the Rousettine branch are: the presence of a tail; the third metacarpal being nearly always slightly but distinctly longer than the fourth and fifth; rostrum not shortened (here, *Myonycteris* tends to deviate); palate not particularly narrowed; the occiput being short ("not subtubular"); the simple form of premolars and molars. (A third branch of the Rousettine section, the Dobsonian branch, is entirely restricted to the Philippines, East Indonesia, New Guinea and the Solomon Islands, and northeast Australia, and need not concern us here.) The Pteropine branch, consisting of the genera *Pteropus*, *Acerodon* Jourdan, 1837, *Pteralopex* Thomas, 1888 and *Styloctenium* Matschie, 1899 (and to which should probably be added *Neopteryx* Hayman, 1946) is distinguished by the absence of a tail; the third and fourth metacarpal being nearly always shorter than the fifth; a generally narrowed palate; a more or less subtubular occiput; and often some degree of specialization in premolars and molars. This branch is also essentially non-African, with the exception of the genus *Pteropus* which has somehow populated a number of islands in the Indian Ocean near Africa.

Andersen (1912: 76) divided *Pteropus* into 17 groups "according to their probable natural affinities". (It is certainly possible to ammend Andersen's theories about natural affinities within *Pteropus* but, again, this would involve more or less extensive accounts of many non-African species, from which I prefer to refrain in the present report). Of these 17 groups, the *hypomelanus*, *rufus*, *melanopogon* and *lombocensis* groups have representatives in the African part of the Indian Ocean. Only the *rufus* group is restricted to that region.

As several of the species treated below are exceptional members of their respective groups, in that they do not agree with one or more of the diagnostic characters, I have arranged them in an order not according to their groups but to the chronology of their description.

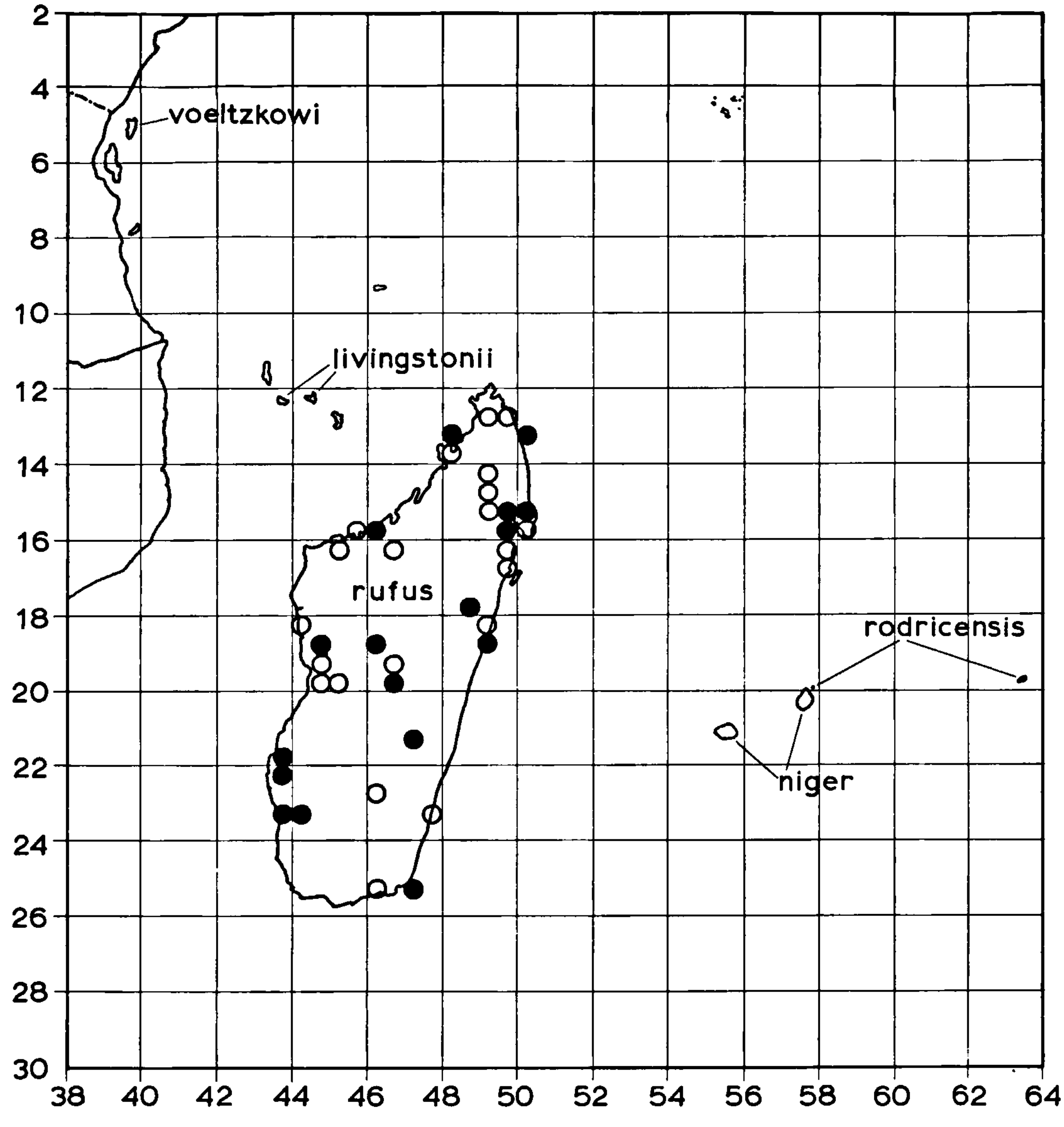

Fig. 5. Distribution of *Pteropus livingstonii* Gray, 1866, *P. niger* (Kerr, 1792), *P. rodricensis* Dobson, 1878, *P. rufus* E. Geoffroy St.-Hilaire, 1803 and *P. voeltzkowi* Matschie, 1909. Only the islands where these species are known to occur or have occurred are indicated (see the text for details) with the exception of *P. rufus* (the only species in Madagascar) for which black dots are based on specimens, identified by the author and open circles are based on records in the literature, museums and correspondence.

Pteropus niger (Kerr, 1792)

Vespertilio vampyrus niger Kerr, 1792: xvii, 90.
Pteropus niger; Andersen, 1912: 215 (designation of Réunion as type locality), 1913: 337; d'Emmerez de Charmoy, 1914*; Lougnon, 1933-1937*; Hayman *et al.*, 1971: 10; Hill, 1971: 574; Temple, 1974; Cheke, 1975*; Jones, 1980*; Cheke *et al.*, 1981: 207, 212; Moutou, 1982: 37; Carroll, 1985: 4.
*) Quoted from Cheke *et al.*, 1981.

Material examined

MAURITIUS. Majastre: 2 imm., 1911, P. Carié (MNHN CC 1958-775/76). Mare au Songes: 27 skeletal fragments (or 7 or more individuals), via Geo Mason (ZMA 16.356). Ravines of Le Réduit: 2 imm ♂♂, 1 ♀, XII-1926, A. d'Emmerez de Charmoy (BMNH 34.7.2.11/13). Rose Hill: 1 ♀, 4-XI-1949, via M. A. Onon (BMNH 62.1919). "Mauritius": 1 ♂, mounted, skull (marked "*Pteropus vulgaris* Geoffr., type"; MNHN, Ancien cabinet, montage 745H + crâne, type (no 154), CG 1990-26); 1 ♂, mounted, skull (RMNH 37213; Jentink, 1887 and 1888: specimen *a* under *Pteropus vulgaris* Geoffroy); 1 imm. "♀", mounted, skull *in situ* (RMNH 37214; Jentink, 1888: specimen *b* under *Pteropus vulgaris* Geoffroy); 1 imm. ♂, 1 imm. specimen, skins only, 1827, J. Andreae/Sitzler (SMF 12.437, 440); 1 ♂ (?), H. Whitely (BMNH 66.1.24.1); 1 ♀, alc., skull fragments, C. Gere (?) (MNHN CG 1873-259); 1 ♂, mounted, skull, P. Deyrolle (MNHN CG 1877-571).
(Bambou Mountains, Black River Gorges, Combo Forest, Montagne Fayence, Montagne du Rempart, River Coignard nr Centre de Flacq, Savanne Range, southern foothills of central plateau.)
"MADAGASCAR": 1 skull, from the MNHN (RMNH 37216; Jentink, 1887: specimen *c* under *Pteropus vulgaris* Geoffroy); 1 ♂, mounted, skull, 1876, C. Mulié (RMNH 37215; Jentink, 1887 and 1888: specimen *d* under *Pteropus vulgaris* Geoffroy).
RÉUNION.
(Réunion.)

Diagnosis: A large fruit bat, fal c. 159-171, gsl 63.8-71.0; with small, pointed ears, length from tip to notch about 21, nearly concealed in the fur; fur of head yellowish or yellowish brown, with dark russet brown on top, from between eyes and ears on backward; a glossy, dark russet brown mantle; back fur buff on the sides and dark brown in a spinal tract of about 30-35 wide and converging backwards; underparts also mainly dark reddish brown; upper side of tibia clothed with buff fur; tail membrane distinct in the middle.

Measurements: Table 5.

Distribution: Fig. 5.

Related species: The only sympatric species, *Pteropus subniger* (Kerr, 1792), now considered extinct, is very much smaller, with a fal less than 100. In the whole region under consideration, only *P. rufus* E. Geoffroy, 1803 and *P. livingstonii* Gray, 1866, both allopatric, are about equal in size, but both have large, exposed ears, entirely different fur colours, with a light mantle and uniformly dark back in *rufus* and only one or two remnant patches of a light mantle and a very dark, blackish back in *livingstonii*.

Remarks

Taxonomy: While Andersen (1912) believed the type specimen to be "not in existence", Moutou (1982) revived hope it might still be. He quoted Rode (1941) who would have listed it among the mammal types in the MNHN, but Moutou himself failed to retrieve it from the collections. In fact, Rode (*op. cit.*) listed what he accepted as the type specimen of *Pteropus vulgaris* E. Geoffroy, 1810 and mentioned, in the section pertaining to that specimen, the name of the species it really represents, and of which *P. vulgaris* is a junior synonym: *Pteropus niger*. (See Andersen, 1912: 221-223 and Rode, 1941: 75 for a discussion of this specimen and the uncertainty regarding its provenance.)

Andersen (1912) could examine ten specimens (in the BMNH, MNHN, RMNH and ZMB collections). Although probably all adults, these specimens were for the most part very old, mounted animals and if their skulls had been extracted these were usually not complete. Notwithstanding the fact that the species is heavily hunted, with as many as around 1000 shot anually even in 1974 (Cheke *et al.*, 1981), hardly any specimen seems to have been preserved and added to a museum collection since Andersen. I have traced only two more adult ♀♀, 6 immatures (some of which pre-

Table 5. Measurements of *Pteropus niger* (Kerr, 1792). Provenance of specimens: see section on material examined.

sex/age	♂ imm.	♂ imm.	♂ imm.	♂ ad.	♂ ad.	♂ ad.	♂ ad.	? ad.	♀/?/ad.	♀ ad.	♀ ad.	♀ ad.	♂ ?/ad.
collection	SMF	BMNH	BMNH	MNHN	RMNH	RMNH	MNHN	RMNH	ZMA	BMNH	BMNH	MNHN	BMNH
number	12.440	34.7. 2.12	34.7. 2.11	1877 -571	37213	37215	1990 -26	37216	16.356b	34.7. 2.13	62. 1919	1873- 259	66.1 24.1
fal	c. 155.5	156.0	159.5	—	c. 160	c. 159	c. 165.5	—	—	160.0		—	156.0
3rd metacarpal				c. 106.2	c. 110.5	c. 109.5	c. 117.5	—	—			107.8	
4th metacarpal				c. 106.7	c. 112.2	c. 107.0	c. 116.8	—	—			104.9	
5th metacarpal				c. 112.0	c. 113.8	—	c. 118.3	—	—			110.9	
ear, tip to notch								—	—			20.8	
gsl		—	—	—	69.3	≥ 70.0	71.7	68.2	—	65.0	66.0	—	66.3
cbl		—	—	—	68.3	68.7	71.0	—	—	63.8	65.2		65.5
rl		24.9	25.1	26.8	27.3	27.0	28.5	25.5	—	25.2	25.0	—	25.8
pl		—	—	38.2	39.5	39.7	40.2	37.8	—	36.0	36.6	—	37.9
cranium width		—	—	23.6	23.5	24.0	22.1	22.9	—	22.3	22.4	—	22.8
iow		9.1	9.0	9.1	9.5	9.6	9.6	9.8	—	9.0	9.9	c. 9.5	9.5
pow		—	7.7	6.8	6.9	7.2	6.4	6.9	—	6.6	7.3	c. 7.0	7.9
zw		—	—	40.2	40.1	39.2	38.8	37.4	—	c.34.2	36.1	—	34.9
mandibular length		52.8	52.6	53.5	54.5	55.0	58.0	53.9	51.4	52.0	51.2	50.9	51.8
mandibular height		c.25	26.0	26.7	26.9	27.6	31.6	26.9	—	26.0	—	≥ 25.5	25.5
C^1-C^1		12.8	—	13.7	14.4	14.0	14.6	13.4	—	12.4	13.1	—	13.4
C^1-M^2		24.7	—	25.4	25.8	26.1	27.0	24.9	—	23.8	25.3	24.7	25.2
M^1-M^1		17.8	—	18.7	19.1	18.5	20.0	18.3	—	17.8	18.7	—	18.4
M^2-M^2			—	17.1	17.7	17.1	19.0	17.3	—			—	
C_1-M_3		28.0	c. 29.0	28.6	29.3	29.8	30.3	28.2	28.1*	27.0	28.0	27.6	28.4

* alveolar length.

Andersen but in a collection he did not visit: the SMF), and a collection of mandibles and other bones and fragments in the ZMA collection. As I did not include the genus *Pteropus* in my studies from the very start and have not checked all collections visited for the presence of *Pteropus* material from the western Indian Ocean, there is undoubtedly more material than I saw, and the account of the species' infraspecific variation will hopefully be amended later. Specimens I have with certainty not seen are those in the ZMB — 2 ♂♂ and 1 ♀ of *Pteropus vulgaris* from Mauritius are mentioned by Matschie, 1899; an unsexed skull in the RMNH — Jentink, 1887, specimen *b* of *Pteropus vulgaris* (specimen *e*, the skull of the mounted juvenile appearing as specimen *c* of *P. vulgaris* in Jentink, 1888, represents *P. subniger*); and the mounted specimen BMNH 44.11.16.4 mentioned by Andersen, 1912: 223.

The data in table 5 show ♂♂ to attain larger body and skull dimensions than ♀♀. Cheke *et al.* (1981) listed fals and weights of four ♀♀ shot in 1974 on the River Coignard near Centre de Flaque (fal/W respectively: 143/380; 147/460; 153/465; 155/520), and fals of specimens in the BMNH (5), the Mauritius Institute in Port Louis, Mauritius (5), and the museum in St. Denis, Réunion (2). By inference one may conclude that all these specimens were considered adult by these authors, although it is not stated how this was established, while some of the BMNH specimens (34.7.2.11/12) are not fully adult and another (BMNH 66.1.24.1), labelled as a ♂, may be either not full-grown or a ♀ (when zw is plotted against gsl it groups with ♀♀ — but of course the data are few). (I have also not seen the one specimen of the four shot ♀♀ of Cheke *et al.*, which was presented to the BMNH, nor of course the other three and the seven older specimens in the Mauritius and Réunion collections). My own data indicate that ♂♂ may become adult when their fal is around 160 (which renders one of 171 as recorded by Andersen, 1912, perfectly likely) and ♀♀ when it is around 150. Cheke *et al.* (1981) record a maximum for ♀♀ of 162. The metacarpal lengths taken from dry specimens are clearly not accurate but nevertheless confirm that the fifth is longer than the third and fourth, as diagnosed for the genus. Specimen MNHN 1873-259 is preserved in alcohol. Its metacarpal lengths are quite accurate, and its ear length (20.8) which appears the first such measurement published for the species will not be much shorter than in life.

Distribution and geographical variation: Cheke *et al.* (1981) studied the species' history and present situation in Mauritius in detail; they also collected detailed data on its former existence in Réunion, where it was exterminated by hunters possibly between 1772 and 1801. Moutou (1982) also wrote on its former occurrence in Réunion. Andersen (1913) identified a subfossil skull from Rodrigues as *P. niger*. There is no other record from that island. Mauritius must have been covered largely with lowland rain forest and *Pteropus niger* may have occurred all over the island. Little natural forest remains today, and the species has decreased accordingly. In Réunion its distribution may have been more restricted as the mountains here are much higher and the forest will have been more diversified or even absent from the higher ranges.

Some old specimens are labelled "Madagascar", and would have been collected at Tamatave (e.g. Dobson, 1878). Jentink (1888) also listed a specimen from "Madagascar". Andersen (1912) rejected these records, suggesting that specimens might have been brought alive from the Mascarenes to Madagascar. All later authors agreed with him. For what it is worth, I wish to mention the small village of Tamatave at about 3 km south-southeast of St.-Paul on the central west coast of Réunion.

Pteropus subniger (Kerr, 1792)

Vespertilio vampyrus subniger Kerr, 1792: xvii, 91.

Pteropus subniger; Andersen, 1912: 164 (designation of Réunion as the type locality); d'Emmerez de Charmoy, 1914*; Lougnon, 1933-1937*; Aellen, 1957: 192; Michel, 1972*; Temple, 1974; Cheke *et al.*, 1981: 209, 212; Moutou, 1982: 38; Carroll, 1985: 4.

Pteropus vulgaris (not of E. Geoffroy St.-Hilaire, 1810); Temminck, 1837: 74, pl. 38 (in part: the mounted juvenile specimen with extracted skull); Jentink, 1887: 252 (in part: specimen *e*), 1888: 138 (in part: specimen *c*).

Pteropus niger (not of (Kerr, 1792)); Andersen, 1912: 216 (in part: the juvenile specimen cited from Temminck, 1837, in the synonymy under *Pteropus vulgaris* E. Geoffroy St.-Hilaire).

* Quoted from Chete *et al.* (1981)

Material examined

MAURITIUS: 1 imm. specimen, mounted, skull (incomplete), ≤ 1837 (RMNH 37217; Jentink, 1887, under *Pteropus vulgaris* Geoffroy, specimen *e* and Jentink, 1888, under *P. vulgaris*, specimen *c*); 1 specimen, ≤ 1866, via H. Whitely (BMNH 66.1.24.2); 1 ♀, alc., skull missing, ≤ 1872 (MNHN 1872-324). (Mare au Songes.)
? RÉUNION: 1 ♂, skin, skull (incomplete), part of skeleton, 1839 (?), M. J. Desjardins (BMNH 34.7.2.60).
LOCALITY UNKNOWN: 1 imm. ♂, skin, skull fragment, "Leyden Mus./86a" (BMNH 37.4.28.31); 1 imm. ♂, skin, skull (damaged), J. Gould (BMNH 43.12.30.13); 1 imm. specimen, skin, skull (incomplete), ≤ 1849, via Parzudaki (BMNH 49.8.23.8); 1 imm. specimen, 1 imm. ♂, skins, skulls (incomplete), < 1856, Tomes Collection (BMNH 7.1.1.257/257bis); 1 imm. (♂?), skin (BMNH; not registered); 1 imm. (♀?), mounted, skull fragments, via Vasseur (MNHN CG 1990-25); 1 specimen, mounted, skull *in situ* (MNHN; not registered).

Diagnosis: A medium-sized fruit bat, fal 95.2-99.2, gsl 44.7-46 (ranges not completely known; measurements of Andersen, 1912 included); cheek teeth exceptionally small for the genus, and very narrow; ears small, ovate, weakly pointed, furred, length from tip to notch about 12, practically hidden in the long fur on the head; fur on top of head, and fur of mantle and on body very long and dense; colour impression of fur on head variable, golden yellowish or darker brown, somewhat grizzled; fur of mantle up to 26.5 in length, colour variable, golden yellowish, orange buff or tawny ochraceous; fur of back up to 26.5 in length, medium brown; ventrally, mantle fur slightly darker than dorsally; fur of breast and belly up to 15-22 in length, medium brown; extreme lower part of back, dorsal and ventral side of tibiae, and anal region clothed with light brownish yellow or buff fur; tail membrane very narrow in the middle.

Measurements: Table 6.

Distribution: Fig. 6.

Related species: The only sympatric species, *Pteropus niger* (Kerr, 1792), is very much larger, with a fal longer than 150 and a gsl of more than 60. That species is moreover at once distinguished by the contrasting dark fur tract on the middle of the back. Of the other species of *Pteropus* in the western Indian Ocean region, none is as small as *subniger*; all have fals of over 120 or even much longer.

Remarks

Taxonomy: I have not examined the ZMB material of *P. subniger*, as listed by Matschie (1899: 30) under *P. rubricollis* E. Geoffroy, a junior synonym: 2 ♂♂ and 1 ♀ from Bourbon (= Réunion) and 1 ♀ and 1 juvenile ♀ from Mauritius; Matschie figured the head and teeth of a young — but, by all appearances, adult — ♀ from Mauritius (pl. 8, figs. 1, 1a-d). Other specimens I have not studied are in the BMNH (Andersen, 1912: 170, the imm specimen listed under *a* and the imm. ♀ from Mauritius no. 66.1. 24.3); the NMW (a reportedly immature specimen from Réunion — but see Cheke *et al.*, 1981: 214 about its origin —, no. 17458); the Musée Zoologique in Strasbourg (a presumably adult ♂, mounted, from Mauritius, labelled "1986, Schneider"; see Aellen, 1957); the FMNH (an adult specimen from Mauritius, apparently acquired through the dealer Ward in New York; see Elliot 1907); the MAKB (skeletal remains, 1914, via G. E. Mason; Dr R. Hutterer, *in lit.*, 31-I-1980); and possibly elsewhere. Together, these specimens form an important part of what has remained of *P. subniger*, which is now generally regarded as extinct, having died out between 1864 and 1873 in Mauritius and around 1860 in Réunion (Temple, 1974; Cheke *et al.*, 1981; Moutou, 1982). (Incidentally, the specimen in Strasbourg, dated 1876 and apparently not known to Cheke *et al.* (1981), may hold a fur-

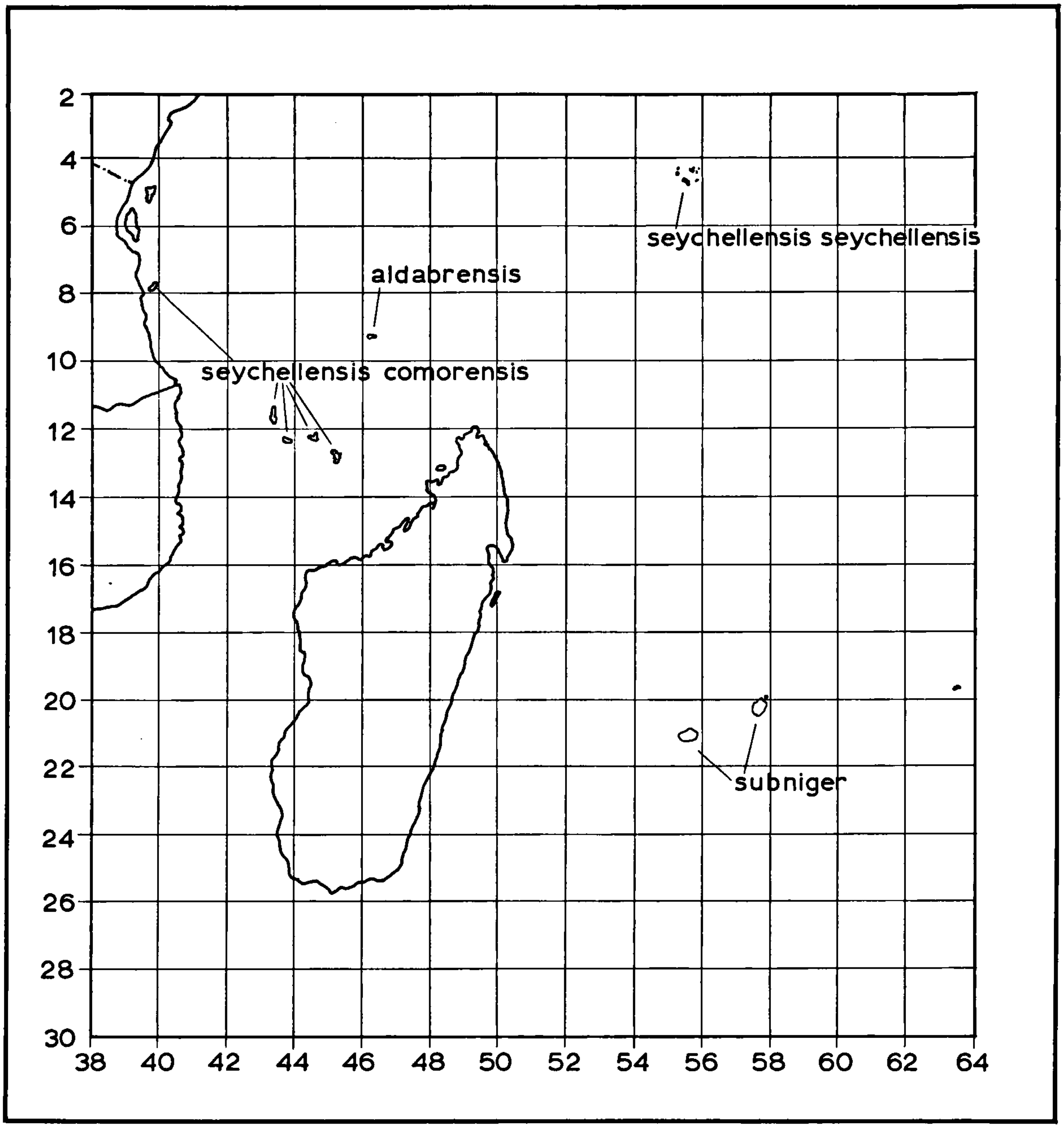

Fig. 6. Distribution of *Pteropus aldabrensis* True 1893, *P. seychellensis seychellensis* Milne-Edwards, 1877, *P. s. comorensis* M. J. Nicoll, 1908 and *P. subniger* (Kerr, 1792). Only the islands where these species are known to occur or have occurred are indicated (see the text for details).

ther clue to the species' time of extinction in Mauritius). On the other hand, the material I examined includes only three sexed adults: a ♂ with an incomplete skull, a ♂ with a skin that cannot be reliably measured, and a ♀ in alcohol of which the skull is missing. Another adult, with a well-preserved skull but less well-prepared skin, is of unknown sex. Andersen (1912), as the only other author who published measurements of this species in an effort to

Table 6. Measurements of *Pteropus subniger* (Kerr, 1792). M = Mauritius, R = Réunion, U = Unknown origin. See text for some other measurements of the only alcohol specimen examined (MNHN 1872-324).

sex/age	♂ ad.	♂*	♂ ad.	♂imm.	♂imm.	♂?/imm.	♀ ad.	♀ ?/ad.	?/ad.	?/imm.**	?/imm.	?/imm.	?/imm.
origin	R?	M	U	U	U	U	M	M	U	M	U	U	U
collection	BMNH		BMNH	BMNH	BMNH	BMNH	MNHN	BMNH	MNHN	RMNH	BMNH	BMNH	MNHN
number	34.7. 2.60		43.12 30.13	37.4 28.31	7.1.1. 257bis	not reg'd.	1872- 324	66.1 24.2	not reg'd.	37217	49.8. 23.8	7.1.1. 257	1990- 25
fal	98.8		93.8?	93.0	93.0	—	98.8	85.3?	99.2	c. 94.5	92.7	91.9	85?
3rd metacarpal	73.5	75	73.6?	65.7	66.0	66.4	72.4	61.7	73.0	c. 71	66.4	66.0	c. 65
4th metacarpal		74.5					71.5		71.8	c. 68.3			c. 61
5th metacarpal		78					75.0		76.3	c. 73			c. 66
ear, tip to notch							12.2						
gsl	≥43.4		45.6	—	—		—	44.7		≥33.0	43.6	>44.7	>40.8
cbl	—		—	—	—		—	42.3		—	—	—	—
rl	17.8		16.1	15.1	15.5		—	15.6		11.0	15.1	16.2	14.3
pl	≥25.5		25.0	22.5	22.7		—	23.4		—	22.5	23.8	21.1
cranium width	—		18.5	—	—		—	18.3		—	—	17.7	—
iow	8.0		6.5	6.7	6.8		—	6.8		6.5	6.5	6.2	5.9
pow	7.4		7.4	7.8	8.3		—	7.5		c. 9.7	8.5	7.4	6.4
zw	—		—	—	—		—	25.6		—	—	23.6	—
mandible length	—		34.4	32.7	32.4		—	32.2		24.3	32.6	32.4	—
mandible height	—		16.0	14.4	14.1		—	15.5		7.1	—	—	—
C^1-C^1	11.5		10.4	10.2	9.9		—	10.1			10.0	9.9	9.9
C^1-M^2	>16.3		16.0	15.4	15.5		—	15.4			14.5	15.3	14.7
M^1-M^1	—		12.5	12.5	12.5		—	12.2			12.6	12.5	—
M^2-M^2			11.3	11.3	11.1		—	10.9			11.3	11.4	
C_1-M_3	18.3		18.3	17.5	17.6		—	17.0			17.0	17.6	17.3

* measurements of specimen in Musée Zoologique, Strasbourg, after Aellen (1957)

** specimen *e* under *Pteropus vulgaris* Geoffroy in Jentink, 1887, and *c* under *P. vulgaris* in Jentink, 1888 analyse its dimensional variation, reported to have examined the ZMB specimens, but unfortunately this is not reflected in his data. Summarizing, neither the literature nor my own data allow for conclusions regarding variation ranges of measurements or the possible extent of sexual dimorphism. As the skins of most specimens have been preserved as mounted specimens or at any event dry, and fals and metacarpals and phalanges are not to be measured in a sufficiently accurate way, it may be useful to mention here some more measurements of the only alcohol specimen I studied, a ♀ from Mauritius in the MNHN, than are listed in table 6 (MNHN CG 1872-324): tail 0; hindfoot (with claws) 32.2; tibia 44.5; 1st finger: metacarpal 12.2, 1st phalanx 20.8, claw 9.0; 2nd finger: metacarpal 54.3, 1st phalanx 9.7, 2nd phalanx 10.1; 3rd finger: metacarpal 72.4, 1st phalanx 46.6, 2nd phalanx 51.7 (stretched: 57.0); 4th finger: metacarpal 71.5, 1st phalanx 39.7, 2nd phalanx 38;9 (stretched: 41.5); 5th finger: metacarpal 75.0, 1st phalanx 31.3, 2nd phalanx 27.1 (stretched: 28.0).

Distribution and geographical variation: *Pteropus subniger* reportedly roosted in hollow trees and "amongst rocks" (see Cheke *et al.*, 1981). It presumably lived in the lowland rain forests in Mauritius and Réunion. In the latter island, towards the end of the species' total destruction, it was probably restricted to altitudes between 1200 and 1600 m (see Moutou, 1982). Its very long and dense fur suggest that the species may have had a preference for cool roosting places, such as the higher altitudes in Réunion, and its reported ability to exploit suitably rocky substrates indicate that it was not dependent on forest or even trees for roosting places. But there are only very few observations, all from a time when the species was already heavily hunted by man, and efforts to reconstruct elements of its ecology must remain highly speculative.

I have no indications that the populations of Mauritius and Réunion were mutually different. This would not be unexpected, and may yet follow from further and more detailed studies of the material preserved.

Pteropus rufus E. Geoffroy St.-Hilaire, 1803

Pteropus rufus E. Geoffroy St.-Hilaire, 1803: 47 (type locality: Madagascar); Andersen, 1912: 202; Dorst, 1947a: 306, 1947b: 82, 1948: 184; Mayoux *et al.*, 1970: 2137; Carroll, 1985: 4; Hickey *et al.*, 1987: 381; Nicoll *et al.*, 1989.

Pteropus rufus rufus; Andersen, 1912: 204; G. M. Allen, 1918: 512; Dorst, 1947a: 307; Hayman *et al.*, 1971: 10; Hill, 1971: 574.

Pteropus rufus princeps Andersen, 1908a: 367 (type locality: Fort Dauphin); Dorst, 1947a: 307, 1947b: 82; Hayman *et al.*, 1971: 10; Hill, 1971: 574.

Pteropus (edwardsi) rufus rufus; Kaudern, 1915: 75.

Material examined

MADAGASCAR (including nearby islets). Amballiala: 1 ♀, mounted head, skull *in situ*, 11-VIII-1865, F. P. L. Pollen & D. C. van Dam (RMNH 37210: Jentink. 1888. specimen *k* under *Pteropus edwardsii* E. Geoffroy St.-Hilaire). Ankiliabo: 1 ♂, alc., 4-V-1898 (MNHN CG 1975-846). Antsiran: 1 ♂, 1 ♀, alc., Alluaud (MNHN CG 1893-469/70). Befandriana: 1 ♂, 22-XI-1929) (MNHN CG 1932-3390). Beroroha: 1 imm. ♂, 1 imm. ♀, VIII-1931, W. F. H. Rosenberg (BMNH 32.7.19.3/4). Betafo: 1 imm. ♂, alc., 25 or 29-X or XI-1906, C. I. Forsyth Major (BMNH 97.9.1.29). Fort Dauphin: 1 ♂, alc., skull, Cloisel (type specimen of *Pteropus rufus princeps* Andersen, 1908; BMNH 91.11.30.10); 1 specimen, skin, 29-III/3-IV-1927 (BMNH 34.7.2.55). Nr Lac Alaotra: 1 imm. ♂, VI-1960, H. A. W. Smit (ZMA 2933). Majunga: 1 ♂ (?), skull, Bastard (MNHN CG 1962-2621); 40 km NW of Maroantsetra: 1 ♀, 31-V-1930, cf. A. L. Rand (AMNH 100487). 20 km SW of Maroantsetra: 1 ♂, 1 imm. ♂, 1 ♀, skull BMNH ♂ missing, 1-, 3- and 10-VI-1930, Mission Zoologique Franco-Anglo-Américaine à Madagascar (= MZFAAM) (MNHN CG 1932-3392; BMNH 35.18.176/77). Maromandia: 2 imm. ♂♂, 1 imm. ♀, 31-VI-1931 and not dated, MZFAAM (MNHN CG 1932-3393; BMNH 35.1.8.171/72). Northwest coast Madagascar: 1 ♂ (?), mounted, skull, 23-VII-1865, F. P. L. Pollen & D. C. van Dam (RMNH 37223; Jentink, 1887, specimen *a* and 1888, specimen *f*, under *Pteropus edwardsii*). Nossi-Bé: 1 imm. ♂, mounted, 30-VII-1865, F. P. L. Pollen & D. C. van Dam (RMNH 37212; Jentink, 1888, specimen *g* under *Pteropus edwardsii*); 2 skulls, skin of one, VII-1975, B. Stequert (ZMA 18.041/42). Nossi Tany Kely: 1 specimen, mounted head, 4-X-1865, F. P. L. Pollen & D. C. van Dam (RMNH 37211; Jentink, 1888, specimen *l* under *Pteropus edwardsii*). Taluky (or Tabiky or Tahilly), west of Ankatoako: 1 imm. ♀, 1 ♀, 1- and 10-XI-1929, MZFAAM (BMNH 35.1.8.175; MNHN CG 1932-3389). Tampina: 5 ♂♂, skulls only, VI-1931, H. Bluntschli (AMNH 17616/20); 1 ♂, alc., 1932, H. Bluntschli (SMF 7026). Tsiandro: 1 ♀, 19-VII-1929, MZFAAM (MNHN CG 1932-3386).

Tsiroanomandidy: 1 ♀, 1 imm. ♀, 16-VI-1929, MZFAAM (BMNH 35.1.8.173; MNHN CG 1932-3387). 80 km E. of Tulear: 1 ♂, 3 ♀♀, 23-X-1929 (BMNH ♀ without date), MZFAAM (MNHN CG 1932-3391 and -?; AMNH 100492; BMNH 35.1.8.174). Tulear region: 1 specimen (RMHN 2386). Vohemar: 1 imm. ♀, skin, skull inside, VII-1907, C. W. Brebner (RMNH 26320); 1 ♀, A. Crossley (BMNH 70.5.5.45). "Madagascar": 1 cf. ♀, skull, 1866, Grandidier (MNHN CG 1962-2619); 2 ♀♀ (BMNH 76.1.31.28/29); 1 imm. ♀, 1 ♀, mounted, skulls (RMNH 37221/22; Jentink, 1887, specimens *c* and *b*, and 1988 specimens *d* and *e*, respectively, under *Pteropus edwardsii*); 2 ♂♂, mounted (RMNH 37218/19; Jentink, 1888, specimens *a* and *b* under *Pteropus edwardsii*); 1 ♀, skin in alc., skull *in situ*, Catat (MNHN CG 1891-170); 1 cf. ♀, skull (MNHN CG 1892-2031); 1 specimen, skull, "Vivarium I-1951" (MNHN CG 1962-2618); 1 cf. ♂, skull (MNHN CG 1962-2620); 1 imm. ♂, alc., skull, 7-VIII-1968, B. Koechlin (MNHN CG 1975-849): 1 specimen, alc., Delacour (MNHN CG 1976-2). "Madagascar?"; 1 ♂, mounted, skull (RMNH 37220; Jentink, 1888, specimen *c* under *Pteropus edwardsii*).
(Ambovombé, Amburvi, Analabe, Analamera, Anjanaharibe-Sud, Ankarafantsika, Berenty, Berevo, ?Farafangana, Fianarantsoa, L. Fiherenana Val., Forêt de Tsimembo, c. 60 km S/150 km inland of Ihosy, ?L'Isalo, Itambelo, ? Lake Itasy, Lokobe, Mahakamby, Mananara, Manombo, Manongarivo, Marojejy, Masoala, Miandrivazo, Mongakatompo, Montagne D'Ambre, Namoroka, Palace Rock, road from Pamantare to Antananario (= Tananarive), upper Siribihina River, Ste. Marie de Marovoay, nr Tamatave, Tsingy de Bemaraha, 20 km E of Tulear.)

Diagnosis: A large fruit bat, fal 153.2-171.0, gsl 66.4-76.0; ears exposed, pointed, length from tip to notch 35.0-38.0; fur of muzzle and face medium brown, lighter to yellowish between and behind eyes and on crown towards mantle, which is light brownish yellow dorsally and orange-yellow on sides of neck and ventrally; fur of back and flanks dark brown, of breast and belly yellowish brown, darker in anal region; tibia practically naked, with at most a scattering of short hairs over the proximal half; tail membrane relatively wide, about 15 in centre. Measurements and ratios taken from all over the species' range:

fal	♂♂	168.2-171.0 (n = 4);
	♀♀	153.8-167.5 (n = 10).
gsl	♂♂	71.7- 76.0 (n = 6);
	♀♀	66.4- 72.3 (n = 8).
cbl	♂♂	70.2- 74.5 (n = 6);
	♀♀	64.0- 70.9 (n = 8).
rl	♂♂	27.0- 29.7 (n = 7);
	♀♀	25.1- 28.3 (n = 12).
pl	♂♂	39.0- 42.0 (n = 7);
	♀♀	36.6- 40.9 (n = 12).
zw	♂♂	40.2- 44.0 (n = 6);
	♀♀	34.5- 39.5 (n = 10).
C^1-M^1	♂♂	26.9- 28.1 (n = 7);
	♀♀	24.8- 28.0 (n = 11).
rl	♂♂	37.7- 39.1% of gsl (n = 6);
	♀♀	37.8- 39.1% of gsl (n = 8).
pl	♂♂	54.9- 55.9% of gsl (n = 6);
	♀♀	55.1- 57.4% of gsl (n = 8).
zw	♂♂	54.2- 59.1% of gsl (n = 5);
	♀♀	51.8- 57.1% of gsl (n = 8).

An immature ♂, fal "14 cm", gsl 65.5, had a weight of 490 g. I have no other data on weights. In size, the species seems not to vary much over its range (see also table 7).

Measurements: Table 7 gives fals and gsls arranged according to latitude. Some measurements which are not part of the diagnosis are discussed under Remarks.

Distribution: Fig. 5.

Related species: All *Pteropus* species in the western Indian Ocean region are allopatric and only *P. niger* and *P. livingstonii* Gray, 1866 attain about the same size. *P. niger* has much smaller ears, a yellowish brown back with a dark spinal tract, and a furred tibia. *P. livingstonii* has large but rounded ears, very dark to blackish fur, a much reduced mantle, and a naked tibia. *P. seychellensis* Milne-Edwards, 1887 and *P. voeltzkowi* Matschie, 1909 both average distinctly smaller (to distinguish them from *rufus* it is most helpful to consider the sexes separately) and have relatively smaller ears; their fur colours differ only little from those of *rufus*, and they have naked tibiae.

Remarks

Taxonomy: Andersen (1908a) based the subspecies *princeps* on a single ♂ from Fort Dauphin, now called Taolanaro, in the extreme southeast of Madagascar. It was considerably larger than the other specimens Andersen

Table 7. Forearm lengths and greatest skull lengths of *Pteropus rufus* E. Geoffroy-St. Hilaire, 1803 arranged according to the latitudes of collecting localities.

		♂♂		♀♀		sex unknown*	
		fals	gsls	fals	gsls	fals	gls
Vohemar	13 22 S			167.5			
Nossi Bé	13 24 S						68.7, 70.4
40 km NW of Maraoantsetra	15 11 S			155.5	66.4		
20 km SW of Maraoantsetra	15 35 S	169.5		162.3			
Majunga	15 40 S						69.2
Tampina	18 30 S	171.0	71.7, 71.8, 74.1, 74.9, 75.4				
Tsiandro	18 42 S			159.8	68.8		
Tsiroanomandidy	18 46 S			153.2	≥66.3		
Ankiliabo	21 41 S	168.2					
Tulear region	23 20 S**				68.3		70.9
Taluky	23 20 S**			159.0	68.4		
80 km E of Tulear	23 20 S**			159.9	68.1, 69.3, 71.0		
Fort Dauphin	25 01 S	170.5	76.0			165.0	

* specimens from Nossi Bé and Tulear region most probably ♀♀

** approximations

knew, and it was thought that the southeastern occurrence was isolated from the northern and central populations. As is apparent from the measurements in the present diagnosis, ♂♂ average distinctly larger in body and skull dimensions than ♀♀, a fact Andersen did not take into account, possibly because he could examine probably only one other adult ♂, from North Madagascar (BMNH 91.11.20.1; alc., skull *in situ*; not studied by me). A series of five male skulls from Tampina at 18°30'S on the central east coast of Madagascar in the AMNH shows that the skull of the type specimen of *princeps* is large but does not deserve taxonomic distinction: its gsl of 76.0 (my measurement) is only slightly larger than the largest of the Tampina five, which run from 71.8 to 75.4. Another ♂ from Tampina (SMF 7026; alc.) has a fal 171.0, which is even slightly larger than that of the type of *princeps* (170.5). Therefore, I consider *P. rufus princeps* as a synonym of *P. rufus*. This conclusion is supported by G. M. Allen's identification (1918) as typical *rufus* of material from 20 km east of Tulear, together with specimens from localities in western central Madagascar. Since Andersen's account (1912), a number of new localities have been discovered where *rufus* occurs, which more or less connect the central and southern parts of its distribution (see fig. 5). Available fal and gsl measurements arranged in an order from North to South (table 7) do not suggest that dimensional disjunctions are to be expected.

The observed sexual dimorphism in skull dimensions, especially the ratio greatest skull length/zygomatic width, may serve to identify with near-certainty the sex of most specimens of unknown or doubtful sex. (Specimen MNHN CG 1932-3391, labelled as a ♂, and the following specimens of unknown sex: MNHN CG 1892-2031 and CG 1962-2619, RMNH 2386, and ZMA 18.401/02, are all very probably ♀♀.)

In five ♀♀ the lengths of metacarpals 3, 4 and 5 were measured; the respective lengths per specimen are: 106.0, 104.4, 108.0; 109.2, 109.5, 113.6; 111.3, 108.8, 112.8; 105.2, 104.6, 109.0; 109.6, 110.5, 114.3. The differences are slight, the third metacarpal is not always longer than the fourth, but the fifth is always longer than the other two.

Distribution and geographical variation: Of the 44 collecting localities I have traced on maps, nine are in Lowland rain forest, wetter types; three in Moist montane forest; one is in a Mosaic of lowland rain forest and secondary grassland; six are in Cultivation and secondary grassland replacing upland and montane forest (types 1b, 5, 11b, and 18 in White, 1983). Five are in Dry deciduous forest;

14 in a Mosaic of dry deciduous forest and secondary grassland; and six in Deciduous thicket (types 7, 22b and 41 in White, 1983). If anything, this data indicates that *P. rufus* may be found in wetter as well as drier forests, and in natural forests as well as cultivation areas. Many specimens will have been collected at their day roosts, and the availability of suitable roosting trees and the absence of disturbance may be important conditions determining where the species spends the day. Like many of its congeners, *P. rufus* has a preference for coastal roosting places, although it has been found far inland in a number of cases (see fig. 5). Its roost may be quite far from where it goes to forage; specimens from coastal islands have been seen to fly towards the coast of Madagascar to feed.

The species' occurrence all over the island, and its regular foraging tours which may vary through the seasons, do not render intraspecific variation very likely.

Pteropus livingstonii Gray, 1866

Pteropus livingstonii Gray, 1866: 66 (type locality: Johanna Island = Anjouan); Cheke *et al.*, 1981: 228; Carroll, 1985: 4; Anonymus, 1989a: 231, 1989b; 232-233.

Pteropus livingstonei; Andersen, 1912: 247; Hayman *et al.*, 1971: 10; Kock, 1978a; Meirte, 1984: 50; Anonymus, 1988: 247.

Material examined

COMORES.

ANJOUAN (or Johanna Island): 1 specimen, skin, incomplete skull, ≤1863, D. Livingstone (holotype specimen of *Pteropus livingstonii* Gray, 1866; BMNH 63.12.11.2); 1 specimen, alc., skull, ≤1886, Humblot (MNHN CG 1886-1533); 3 specimens, mounted, skulls *in situ*, ≤1886, Humblot (MNHN CG 1886-1272/74); 1 "♂", 1 "♀", mounted, incomplete skulls, III-1887, Frank (RMNH 37224/25; Jentink, 1888, specimens *a* and *b*); 1 ♀, 1 specimen, skins, incomplete skulls, Frank (BMNH 88.5.9.1/2); 1 ♀, 1 imm. ♂, VIII-1927, M. Deloye (BMNH 34.7.2.35/36).

(Bambao, nr Dzialandze Lake, between Dindi and Dzialandze Lake.)

MOHÉLI.

(Bangoma, below Col de Méledjélé, between Mirongoni and the Chalet de St. Antoine.)

Diagnosis: A large fruit bat, fal c. 161-172, gsl 69.1-72.4 (ranges not completely known); dentition relatively heavy; ears large, exposed, semicircularly rounded off above, length from notch to tip about 31; fur blackish above and beneath, with a dark russet hue, sprinkled with bright tawny hairs in mantle, on lower back and on flanks; mantle of the same dark colour, dorsally with a transverse band of tawny-tipped hairs, the band up to about 6 cm wide and 1 to 1,5 cm long, antero-posteriorly, or with a patch of such hairs on each shoulder; upper side of tibia largely naked, upper inner side of tibia thickly clothed with fur, as the adjoining tail membrane; tail membrane scarcely developed in centre.

Measurements: Table 8.

Distribution: Fig. 5.

Related species: In the western Indian Ocean region, only *P. niger* and *P. rufus* attain the same dimensions. *P. niger* has small, pointed, non-exposed ears, and a very different colour pattern, *P. rufus* has large but pointed ears and brownish yellow to orange-yellow mantle which strongly contrasts with the dark body fur; both *niger* and *rufus* are allopatric. The only sympatric *Pteropus* species, *P. seychellensis comorensis* Nicoll, 1908 resembles *P. rufus* but is smaller, with a fal of 149.5-157.5, relatively smaller, pointed ears, and a mantle of the same contrasting colour.

Remarks

Taxonomy: Although described in 1866, and reported to be common in the large forests covering the higher altitudes of Anjouan by Humblot who visited the island not much later and collected the MNHN specimens (see Andersen, 1912; Cheke *et al.*, 1981), material of this species in collections has remained scarce. Unfortunately, it is rarely in a good condition. Cheke *et al.* (1981) gave a summary of this material which is, however, not quite correct. The "largest series" collected by Humblot for the MNHN is represented in that collection by four specimens only. Frank must have collected at least five specimens, instead of three, as there

Table 8. Measurements of *Pteropus livingstonii* Gray, 1866. All specimens are from Anjouan.

sex/age collection number	"♂"/ad. RMNH 37224	♂/imm. BMNH 34.7. 2.36	♀/ad. BMNH 88.5. 9.1	♀/ad. BMNH 34.7. 2.35	"♀"/ad. RMNH 37225	?/ad. BMNH 63.12. 11.2	?/ad. MNHN CG 1886 -1533	?/ad. BMNH 88.5. 9.2
fal	c. 172	c. 69	171	168.5	c. 168.5	—	170.7*	161
3rd metacarpal	120.1			119.5	119.9	117	122.7	
4th metacarpal	117.7				116.0		119.1	
5th metacarpal	124.6			125.8	123.3		126.1	
ear, notch to tip							30.3*	
gsl	—	39.4	69.1	72.3	—	—	72.4	—
cbl	—	35.0	—	71.1	—	—	70.4	—
rl	30.3		29.4	29.3	29.1	—	28.9	28.8
pl	41.3		40.6	40.3	41.1	—	39.2	39.1
cranium width	24.2		24.0	23.0	—	—	23.5	—
iow	12.0		12.3	12.1	12.0	12.0	12.1	12.5
pow	9.0		8.9	9.7	—	10.0	9.5	9.0
zygomatic width	39.3	22.0	—	37.7	—	—	38.3	—
mandible length	58.3		58.8	57.4	58.1	57.9	56.4	56.5
mandible height	28.9		29.0	29.9	29.2	29.9	29.9	27.5
C^1-C^1	14.3		14.9	13.9	14.7	—	14.1	14.4
C^1-M^2	30.0		28.6	28.2	28.7	—	28.0	27.3
M^1-M^1	20.4		20.6	21.1	20.6	—	21.2	20.0
M^2-M^2	17.8				17.8	18.3	18.4	
C_1-M_3	33.4		31.5	31.7	32.6	31.2	31.0	31.1

* measurement: courtesey of Mr. M. Tranier

are two in the BMNH, two in the RMNH, and one in the ZMB which were collected by him. I have not studied *Pteropus* in the ZMB and have missed the Frank specimen there and, presumably, the three specimens collected by A. Voeltzkow. With my present data, I cannot say anything conclusive on dimensional ranges or possible sexual dimorphism.

Distribution and geographical variation: Until recently, *Pteropus livingstonii* was thought to be restricted to Anjouan. Cheke *et al.* (1981) published the first observations, in 1975 and 1977, from Mohéli, and suggested that it should also be looked for on Grande Comore. On Anjouan, the species avoids "the lower parts in the vicinity of the sea" but certainly exists above 600 m, but on Mohéli, which reaches a much lower altitude than Anjouan, it was observed at about 600-650 m, 350 m, and below 300 m (Cheke *et al.*, 1981; Anonymous, 1989).

Pteropus rodricensis Dobson, 1878

Pteropus rodricensis Dobson, 1878: 36 (type locality: Rodriguez); Andersen, 1912: 273; Bertuchi, 1923*; Vinson, 1965a*; Vinson, 1965: 251; Cheke, 1974*; Durrell, 1976a, 1976b, 1976c, 1977a, 1977b: 88; Carroll, 1978a, 1978b; Pook, 1978; Carroll, 1979; Jones, 1980*; Carroll, 1981; Cheke *et al.*, 1981: 210, 217; Carroll, 1982a-b, 1984, 1985: 5; Anonymous, 1987; West *et al.*, 1987; Young, 1987.

Pteropus mascarinus Mason, 1907: 220 (type locality: Round Island, near Mauritius); Andersen, 1907a: 351, 1912: 275; Cheke *et al.*, 1981: 210.

Quoted from Cheke *et al.*, 1981.

Material examined

RODRIGUES. Cascade Pigeon: 1 ♂, skin, skull, skeleton, 27-IV-1976, R. Lammers (SMF 54964); 1 ♂, alc., 20-IX-1978, J. Hartley & A. S. Cheke (BMNH 79.155); 1 foetus, 28-IX-1978, J. Hartley & A. S. Cheke (BMNH 79.156); 1 imm. ♀, 1 imm. ♂, alc., skull of ♀, died on 2-I- and 12-VIII-1982, respectively, at Jersey Wildlife Preservation Trust (parents: Cascade Pigeon, IV/V-1976, G. M. Durrell) (ZMA 21.526, 21.880).

"Rodrigues": 1 ♂, alc., skull, 1874, J. Gulliver (BMNH 76.3.11.1; holotype specimen of *Pteropus rodricensis* Dobson, 1878); 2 imm. ♂♂, 1 ♀, 1 imm. ♀, alc., skull of ♀, 1874, J. Gulliver (BMNH 76.3.11.2/5; no. 76.3.11.4 now in the SMF, as no. 44785; three of these, 1 ♂ and 2 ♀♀, are paratype specimens of *Pteropus rodricensis* Dobson, 1878 — see text); 1 ♂, 1 ♀ (skin not seen), 1874, H. H. Slater (BMNH 76.3.15.14/15; paratypes of *Pteropus rodricensis* Dobson, 1878); 1 ♂, skin, ≤VI-1909, H. A. Bellairs (RMNH 37228); 1 imm. ♂, ≤VI-1910, H. A. Bellairs (RMNH 37227); 1♂, 1 imm. ♀, skins, V-1927, F. E. Pickering (BMNH 36.6.24.3, -5); 1 ♂, 1 imm. ♂, 3 ♀♀, 1 imm. ♀, alc., ≤1934, via G. E. Mason, (BMNH 34.7.2.66/67). Jersey Wildlife Preservation Trust Zoological Garden: 1 imm, alc., † 6-VI-1983, given in permanent loan by Dr J. E. Cooper, Royal College of Surgeons, London (ZMA 24.198).
(Anse Mourouk, Baie aux Huitres valley below Jardin Mamzelle.)
ROUND ISLAND: 1 incomplete skull, some bones, 1906, via G. E. Mason (BMNH 25.8.10.1; holotype specimen of *Pteropus mascarinus* Mason, 1907).

Diagnosis: A moderately large fruit bat, fal 121.1-128.4 (according to the literature: up to 133.5), gsl 50.1-52.2 (range not completely known); last upper and lower molars reduced; ears short, nearly hidden in the fur, pointed, length from notch to tip about 22.5; fur on upper and ventral parts dark brown, thinly mixed with long, glossy, yellowish hairs; mantle dorsally orange-yellow to yellowish posteriorly and on the sides, and ventrally orange brown mixed with dark brown; tibia with long fur on proximal half, fur gradually shorter and thinner on distal half; tail membrane very narrow in centre.

fal	♂♂	121.2-125.9	(n = 6);
	♀♀	123.3-128.4	(n = 4).
gsl	♂♂	50.8- 52.2	(n = 2);
	♀♀	50.1	(n = 1).
cbl	♂♂	49.3- 50.9	(n = 2);
	♀♀	48.3	(n = 1).
rl	♂♂	17.8- 19.2	(n = 3);
	♀♀	17.7- 18.1	(n = 2).
pl	♂♂	26.5- 28.1	(n = 3);
	♀♀	26.3- 26.9	(n = 2).
zw	♂♂	28.0- 30.2	(n = 2);
	♀♀	25.9- 28.0	(n = 2).
C^1-M^2	♂♂	18.4- 18.8	(n = 3);
	♀♀	18.0- 18.6	(n = 2).

rl	♂♂	35.0- 36.0% of gsl	(n = 2);
	♀♀	35.3 % of gsl	(n = 1).
pl	♂♂	52.2- 52.5% of gsl	(n = 2);
	♀♀	52.5 % of gsl	(n = 1).
zw	♂♂	55.1 % of gsl	(n = 1);
	♀♀	51.7 % of gsl	(n = 1).

Cheke *et al.* (1981) published maximum fals of 133.5 for ♂♂ and 128 for ♀♀, and weights of 216-295 in 23 ♂♂ and 204-306 in 8 ♀♀ (some of which presumably pregnant).

Distribution: Fig. 6.

Related species: All *Pteropus* species in the western Indian Ocean region are either distinctly smaller, with fals below 110 (*P. subniger*), or larger, with fals of 133 or more (all others); the smallest of these is *P. aldabrensis* True, 1893, which has, however, relatively larger ears, teeth of normal dimensions, a quite different fur colour pattern, and naked tibiae. Presently, all other *Pteropus* species are allopatric with *rodricensis*; only *P. niger* has probably been sympatric in the past. The now extinct *P. subniger* shows the greatest similarity in being small, with small ears, reduced teeth, and haired tibiae, but its body fur has a quite different colour. *P. niger*, geographically nearest, has a fal of c. 159-171, small ears, normally sized teeth, haired tibiae, and a very different colour pattern. Species with dark back fur and bright mantles as in *P. rodricensis*, such as *P. rufus*, *P. seychellensis* Milne-Edwards, 1887 and *P. voeltzkowi* Matschie, 1909 are larger, have large, exposed ears, normal teeth dimensions, and naked tibiae.

Remarks

Taxonomy: Dobson (1878) based his description on seven specimens in the BMNH. He gave a number of body and wing measurements of an adult ♂. Andersen (1912) examined the same series but had located a skin of one of the specimens that had been missed by Dobson (his specimen *f*), and an additional ♂. Andersen listed an adult ♂ as the type of the species. From the accounts of Dobson and Andersen it cannot be ascertained which is the extra ♂

(BMNH 76.3.11.1, -2, or -3). This is of some importance, as it does not belong to the type series. For the present, I accept that it is not the specimen selected by Andersen as the holotype.

Mason (1907) described a new and supposedly extinct species, *Pteropus mascarinus*, on the basis of a skull found on Round Island northeast of Mauritius. Andersen (1907a), who never saw the skull, concluded from the published data that *mascarinus* "must be exceedingly like the now living *Pt. rodricensis*". In 1912 he synonymized *mascarinus* with that species. Cheke *et al.* (1981) confirmed this, upon a re-examination of the "intact adult skull". I found, in 1989, a broken and incomplete skull (but Mason already had to estimate several dimensions) of a nearly but not fully adult animal (as Andersen had expected), from which only a few of the standard measurements could be taken: cranium width 18.3, mandible length 39.8, C_1-M_3 21.8; estimated were gsl 48.5, C^1-M^2 19.9, and M^1-M^1 14.2. These measurements, nor those of its teeth published by Mason (1907) and Andersen (1907a) or their morphology justify recognition of *mascarinus* as distinct from *rodricensis*.

The measurements in the diagnosis suggest that ♀♀ may have longer fals, on average, than ♂♂, but some data in Cheke *et al.* (1981) suggest otherwise: in 23 ♂♂ the fal range was 117-133.5, in 8 ♀♀ it was 116-128. The early morning weight ranges in these specimens was 216-295 for ♂♂ and 204-306 for ♀♀ (some of which presumably pregnant). It is not stated how the maturity of the specimens was established and I doubt if the lower values apply to adults. But the maximal fals and weights will certainly do, and ♂♂ appear to average just a little larger than ♀♀ in size.

Distribution and geographical variation: Cheke *et al.* (1981) summarize what data they could collect on the species' former distribution on Rodriguez. Naturally it declined catastrophically with the extensive clearance of forests between 1955 and 1968, when land use was entirely determined by agricultural 'development'. The reader is referred to their report for more details. Places of known historical occurrence are mentioned under Material examined. The evidence from Round Island may represent the remains of a straggler from Rodrigues rather than anything else.

Pteropus seychellensis Milne-Edwards, 1877

Pteropus seychellensis Milne-Edwards, 1877: 221 (type locality: Seychelles — but see text); Andersen, 1912: 212; Rode, 1941: 76

Pteropus comorensis M. J. Nicoll, 1908: 87, 88, 90 (type locality: Mayotte, Comores); Andersen 1912: 208.

(Further references under the subspecies).

Diagnosis: A large fruit bat, fal 147.1-158.2, gsl 64.7—≤72.7; teeth of normal dimensions; ears pointed, length 29-37; snout blackish; sides and crown of head with golden yellowish or brownish yellow fur; mantle dorsally golden yellowish or orange brown, ventrally somewhat darker, either yellowish and sometimes with a russet hue, or orangy; back fur blackish brown, with or without a variable amount of admixed whitish hairs; fur on underparts essentially dark brown or dark reddish brown, with a variable amount of hairs with yellowish or orange brown tips, especially on the breast; tibia at most thinly haired on proximal half and naked on distal half; tail membrane well developed, in centre about 15 deep.

Distribution: Fig. 6.

Pteropus seychellensis seychellensis Milne-Edwards, 1877

Pteropus seychellensis Milne-Edwards, 1877: 221 (type locality: Seychelles — but see text); Andersen, 1912: 212; Rode, 1941: 76; Hayman *et al.*, 1971: 10; Cook, 1979; Maisels, 1979; Verschuren, 1985.

Pteropus seychellensis seychellensis; Hill, 1971: 574; Racey, 1979; Suttie, 1979; Racey *et al.*, 1984: 607.

Material examined

COUSIN.
(Cousin.)
CURIEUSE.
(Curieuse.)
LA DIGUE: 2 ♂♂, 1 imm., skins, skulls, skeletons, 14/22-V-1979, M. Ackermann/H. Leffler/K. J. Walch/S. Weigelt (SMF 57376/78).

FÉLICITÉ.
(Félicité.)
MAHÉ. Anse au Pins: 1 imm. ♂, alc., 26-V-1980, R. Wilson (RMNH 28733). Cascade Estate: 1 ♂, 28-II-1907, H. P. Thomasset (RMNH 37226). "Mahé": 2 imm., skins only, IV-1940, A. D. Sapsworth (BMNH 48.261/62).
MARIANNE: 1 imm. ♂, mounted, skull (damaged), 1877, Lantz (MNHN CG 1878-1107; paratype specimen of *Pteropus seychellensis* Milne-Edwards, 1877); 1 ♀, mounted, skull, 1877, Lantz (MNHN CG 1878-1110; holotype specimen of *Pteropus seychellensis* Milne-Edwards, 1977).
PRASLIN. Grand Anse: 1 ♂, 2 ♀♀, alc., VIII/IX-1976, C. M. Nicoll & P. P. Evans (BMNH 77.484/86); 2 ♂♂, alc., 18/20-VII-1977, P. A. Racey (BMNH 78.3050/51). "Praslin": 4 (imm.?) ♂♂, 2 (imm.?) ♀♀, skins, incomplete skulls, via Rothschild (BMNH 1939.1326/31); 1 specimen, skin not seen, VII-1909, R. H. Pickwood (SMF 5803); ♂♂, 1 specimen, 18-V-1979, M. Ackermann/H. Leffler/K. J. Walch/S. Weigelt (SMF 57379/81); 9 bones, via G. E. Mason (ZMA 16.713).
(Fond Azore, Au Morne, La Pasquière.)
SILHOUETTE: 1 imm. ♂, mummy (BMNH 73.523). 1 imm., alc. (BMNH 69.5.21.1); 1 (imm.?) ♀, J. S. Gardiner (BMNH 6.3.18.1).
"SEYCHELLES": 1 imm., alc. (BMNH 69.5.21.1); 1 (imm.?) ♀, J. S. Gardiner (BMNH 6.3.18.1).

Diagnosis: A large fruit bat, fal c. 150.5-158.2, gsl 64.7-72.7; ears 30-32; back fur with conspicuous sprinkling of glossy, greyish white hairs, variable in number, most numerous on sides and rump; breast and belly fur hairs dark brown with short ochraceous or yellowish tips; mantle ventrally generally a shade of golden ochraeous, in some specimens with a pale russet hue, not orangy. Further as for the species.

fal	♂♂	c. 150.5- 158.2	(n = 7);
	♀♀	152.6-?155	(n = 2)
gsl	♂♂	66.9-≥72.2	(n = 4);
	♀♀	64.7	(n = 1).
cbl	♂♂	65.7- 65.8	(n = 3);
	♀♀	63.4	(n = 1).
rl	♂♂	25.5- 26.4	(n = 4);
	♀♀	24.7	(n = 1).
pl	♂♂	37.0- 37.8	(n = 4);
	♀♀	35.9	(n = 1).
zw	♂♂	37.5- 38.5	(n = 5);
	♀♀	35.4	(n = 1).
C^1-M^2	♂♂	23.5- 27.1	(n = 5);
	♀♀	23.3	(n = 1).

rl	♂♂	38.4- 39.3% of gsl	(n = 3);
	♀♀	38.2 % of gsl	(n = 1).
pl	♂♂	55.9- 56.3% of gsl	(n = 3);
	♀♀	55.5 % of gsl	(n = 1).
zw	♂♂	56.0- 57.5% of gsl	(n = 3);
	♀♀	54.7 % of gsl	(n = 1).

Racey *et al.* (1984) gave as weights for 6 adult ♂♂ in August/September 479-604 (mean 543) and for 2 adult ♀♀ 450 and 508. For possible variation between the populations of different islands, see the remarks below. Incidentally, the measurements of the single female skull are those of the holotype specimen.

Distribution: Fig. 6.

Related species: From the subspecies *Pteropus seychellensis comorensis* M. J. Nicoll, 1908 the typical race differs in details of the fur colours; it has a much stronger admixture of whitish hairs on back and rump and a darker breast and belly caused by the bright hair tips being relatively shorter. In the region of the western Indian Ocean, only *P. rufus*, *P. aldabrensis* True, 1893 and *P. voeltzkowi* Matschie, 1909 share the combination of the following characters: distinctly exposed, pointed ears, normally sized teeth, a mantle strongly contrasting in colour with that of the back fur, and thinly or partly haired or naked tibiae. *P. rufus* averages distinctly larger in all dimensions, lacks the greyish white hairs on back and rump and has generally brighter coloured underparts. *P. aldabrensis* is absolutely smaller in all dimensions and differs greatly in colours of its fur. *P. voeltzkowi* largely overlaps in body and skull measurements but has relatively smaller ears and differs in details of its fur colours.

Remarks

Taxonomy: Milne-Edwards (1877) did not mention the number of specimens from the "Seychelles" on which he based *P. seychellensis*; nor did he designate a specimen as holotype, or mention a more specific type locality. Andersen (1912) considered four specimens in the MNHN as syntypes (CG 1878-1106, -08/09, and -12); thinking that these all were from Mahé, he fixed Mahé as type locality. Rode

(1941: 76) listed two specimens not seen by Andersen but belonging to the same series, as holotype (CG 1878-1110) and paratype (CG 1878-1107) respectively, and included as other paratypes CG 1878-1106, -1108 and -1109; he also claimed that all these specimens were from Mahé. I was surprised therefore when visiting the MNHN in April 1990 to find evidence that specimen 1110 might originate from Marianne (either on its label or on the underside of its board — I forgot to note that). Mr. M. Tranier kindly consulted the General Catalogue for me, and explained (*in lit.*, 23-VII-1990) that specimens 1106 to 1110 are indeed from Marianne, and 1111 and 1112 from Mahé.

Mayr (1969: 373) suggested that "in cases where the syntypes are from several localities and a previous reviser has already restricted the type locality of the species, a responsible zoologist will give due consideration to this fact in the selection of the lectotype". Mayr (1969: 375) emphasized that, contrary to species, subspecies can often only be identified by adequate population samples. Considering this and the fact that five syntypes are from Marianne and only two from Mahé; that the subspecies' possible variation within the Seychelles has not been analysed; that Andersen (1912) apparently was not aware that three of the four syntypes he had identified as such were not from Mahé but from Marianne; and that Rode (1941) published his selection of a "holotype" — which, of course, should be a lectotype — which is now known to originate from Marianne, lead me to propose here to recognize specimen MNHN CG 1878-1110, a mounted ♀ of which the skull has been extracted since Rode (1941), collected by Lantz on Marianne, as lectotype of *Pteropus seychellensis* Milne-Edwards, 1877, and to fix Marianne Island as the type locality of the species. All other specimens of the same series, i.e. MNHN CG 1878-1106/09 and -1111/12, can safely be accepted as having served Milne-Edwards for his descriptive note (1877) and can be regarded as paralectotypes.

Andersen (1912) published a fal range of 143-154, based on five young adults including the syntypes seen by him, but noted that he suspected the smallest specimen to be not quite full-grown, while the others were "probably full-sized". The mentioned range has nevertheless been copied by Hayman *et al.* (1971), Hill (1971) and Kingdon (1974). It suggests that the typical subspecies averages distinctly smaller, in fal, than *comorensis*. My measurements do however not support this. The smallest fal I measured in the typical subspecies is c. 150.5 in a ♂ from La Digue (SMF 57376); smaller fals may yet be expected in ♀♀. In *comorensis* I measured a minimum of 147.1 in ♂♂ (and one of 151.3 in ♀♀), and I do not think that there will be very appreciable size difference between the two subspecies. The numbers of specimens examined are much too low for an assessment. In this context it should also be borne in mind that there may be differences between populations of islands within the Seychelles between which there is no exchange. It is known that bats from Praslin visit nearby islands to feed (M. E. Nicoll *et al.*, 1981; mrs. drs. C. H. van Duyl, pers. comm., 23-VII-1990, observed bats flying from Praslin to Cousin, in 1986), but trips between Praslin and Mahé or Silhouette will probably be incidental at most.

Distribution and geographical variation: *P. s. seychellensis* is known from all the larger islands of the Seychelles: Mahé, Praslin, Silhouette and La Digue, and also from some smaller ones: Félicité, Curieuse, Marianne and Cousin. Nicoll *et al.* (1981) pointed out that smaller islands within the Praslin group that do not support permanent populations, such as Curieuse, are only visited irregularly, depending on the availability of edible fruit. Inter-island distances within the Praslin group are certainly small enough to be abridged by these bats, and a more or less frequent, be it perhaps modest, gene-flow between the populations of this group may be expected. As already observed, this will probably be different between the Praslin group populations on the one hand, and those of the Mahé group and Silhouette on the other. A more detailed study of the available material is needed to answer this question.

Pteropus seychellensis comorensis M. J. Nicoll, 1908

Pteropus comorensis M. J. Nicoll, 1908: 87, 88, 90 (type locality: Buzi Islet, Mayotte Harbour, Comores; *fide* Moreau *et al.*, 1946: 398); Andersen, 1912: 208; Moreau, 1939: 115; Moreau *et al.*, 1940: 118, 1946: 398; Swynnerton *et al.*, 1951: 287; Hayman *et al.*, 1971: 10; Kingdon, 1974: 140; Pakenham, 1984: 25.

Pteropus seychellensis comorensis; Hill, 1971: Cheke *et al.*, 1981: 225; Meirte, 1984b: 50; Carroll, 1985: 4.

Pteropus livingstonii (not of Gray, 1866); Benson, 1960: 26*; Dahl, 1979b*.

? *Pteropus rufus* (not of E. Geoffroy-St. Hilaire, 1803); Anciaux de Faveaux, 1972*.

* Quoted from Cheke *et al.*, 1981.

Material examined

ANJOUAN: 1 imm., ≤ 1853, J. Barrow (BMNH 53.5.27.1); 1 imm., ≤ 1863, D. Livingstone (BMNH 63.12.11.1); 3 ♂♂, 2 imm. ♂♂, 1 ♀, 1 imm. ♀, ≤ 1877 (BMNH 77.4.2.1/7); 1 ♂, 1 imm. ♀, alc., skulls, 1887, Poulay (NMW 17465/66).

GRANDE COMORE: 1 imm. ♂, 1 ♀, ≤ 1879, J. Kirk (BMNH 79.11.12.5/6); 1 ♂, skin, cf. ≤ 1885, F. Coyler (BMNH 36.6.24.2); 2 ♀♀, ≤ 1886, Humblot (MNHN CG 1886-1408/09). "Grande Comore" (or "Mayotte": on underside of board): 3 ♂♂, 3 specimens, mounted, skulls *in situ*, ≤ 1886 Humblot (MNHN CG 1886-1410, -12/14, 2039/40).

(Boboni, Iconi village, crater of lac Sallé, Moroni, N'Bachile village.)

MAFIA. Kua, Juani Islet: 3 ♂♂, 10-X-1952, G. H. Swynnerton (BMNH 64.1307/09). "Mafia": 1 ♂, skin, skull *in situ*, IX-1938, R. E. Moreau (BMNH 1938.10.24.1). ? Mafia: 1 imm., skull, 1824, W. Bojer (NMW 17459).

MAYOTTE: 1 ♂, 1 ♀, mounted, skull of ♀ *in situ*, 19-V- and 6-VI-1864, F. P. L. Pollen & D. C. van Dam (RMNH 37207/08; Jentink, 1887 specimen *d* (the ♂), 1888 specimens *h, i*, all under *Pteropus edwardsii* Geoffroy, 1810); 2 ♂♂, 2 imm. ♂♂, 1 ad., 1 imm., ≤ 1884, Humblot (MNHN CG 1884-2034, -36/37, -41/43); 3 ♂♂, 2-III-1906, M. J. Nicoll (BMNH 6.6.3.14/16; syntypes of *Pteropus comorensis* M. J. Nicoll, 1908); 1 ♂, alc., skull, ≤ 1906, M. J. Nicoll (SMF 44784; formerly BMNH 6.6.3.17).

(Coconi.)

MOHÉLI: 1 ad., VIII-1862, 1 imm. (skull only), J. Kirk (BMNH 65.10.25.1/1bis).

(Bangoma, Dziani Boundouni.)

"COMORES": 1 imm. ♂, mounted, skull *in situ*, 1880, Frank (RMNH 37209; Jentink, 1888 specimen *j* under *Pteropus edwardsii*).

Diagnosis: A large fruit bat, fal 147.1-157.5, gsl 63.9-68.2; ears 29-37; back fur only very thinly sprinkled with glossy greyish white hairs; breast and belly fur hairs dark brown at base, with long yellowish buff distal ends which almost completely conceal the dark brown colour, except on flanks and in anal region where the bright hair tips are shorter; mantle on sides of neck and foreneck deep orange-buff. Further as for the species.

fal	♂♂	147.1-157.5	(n = 13);
	♀♀	151.3-154.1	(n = 4).
gsl	♂♂	65.2- 68.2	(n = 12);
	♀♀	65.4- 65.6	(n = 2).
cbl	♂♂	63.9- 66.4	(n = 9);
	♀♀	64.1	(n = 1).
rl	♂♂	24.2- 26.0	(n = 13);
	♀♀	24.4- 25.2	(n = 3).
pl	♂♂	35.0- 37.5	(n = 12);
	♀♀	35.9- 36.0	(n = 2).
zw	♂♂	35.7- 39.3	(n = 11);
	♀♀	35.1	(n = 1).
C^1-M^2	♂♂	23.6- 25.4	(n = 14);
	♀♀	24.2- 24.4	(n = 2).
rl	♂♂	37.1- 39.1% of gsl	(n = 9);
	♀♀	37.3- 38.4% of gsl	(n = 2).
pl	♂♂	53.4- 55.4% of gsl	(n = 9);
	♀♀	54.9- 54.9% of gsl	(n = 2).
zw	♂♂	53.2- 59.4% of gsl	(n = 9);
	♀♀	53.5 % of gsl	(n = 1).

For possible variation between the populations of different islands, see the remarks below.

Distribution: Fig. 6.

Related species: From the typical subspecies *P. s. comorensis* differs in the small amount of greyish white hairs in its back fur (except, perhaps, the specimens from Mafia), and in the larger length, and therewith colour dominance, of the bright distal parts of breast and belly hairs. For differences between *comorensis* and other *Pteropus* from the region see the section on related species under the nominate subspecies.

Remarks

Taxonomy: *P. s. comorensis* is probably less different in size from *P. s. seychellensis* than has been suggested by various authors quoting a fal range for the latter from Andersen (1912) which was in part based on immature specimens. In fact, the two may be of about equal size, although, considering that populations should be analysed per island, the numbers of measurements per island are insufficient for an assessment. For the time being, the two can only be distinguished by the gradual differences in fur colours mentioned above, and I fully agree with Hill (1971) that *comorensis* should be regarded as a subspecies of *seychellensis*.

Distribution and geographical variation: *P. s. comorensis* apparently inhabits the four larger islands of the Comores and, in addition, Mafia. The few specimens from the latter island that I have examined, in the BMNH, had rather much grey in their back fur and the position of the Mafia population within the species needs further analysis.

Pteropus aldabrensis True, 1893.

Pteropus aldabrensis True, 1893: 533 (type locality: Aldabra Island); Andersen, 1912: 213; Beamish, 1970: 125*; Hayman *et al.*, 1971: 10.
Pteropus seychellensis aldabrensis; Hill, 1971: 574; Racey *et al.*, 1984; Carroll, 1985: 4; P. Roberts *et al.*, 1989.
Pteropus seychellensis aldabrabensis; Honacki *et al.*, 1982: 124
* Quoted from Cheke *et al.*, 1981.

Material examined

MALABAR.
(Anse Badamier, Anse Malabar.)
SOUTH ISLAND. Takamaka: 1 ♀, 1 imm. ♂, alc., 27-XI-1955 (or '56), J. C. F. Fryer (BMNH 13.2.18.3/4); 1 imm. ♂, alc., 12-II-1968, A. M. Hutson (BMNH 68.934). Takamaka Grove: 3 ♂♂, alc., 14-II-1968, A. M. Hutson (BMNH 68.935/37).
WEST ISLAND. Settlement: 2 ♂♂, 1 imm. ♀, alc., 31-I-1968, A. M. Hutson & J. G. Frazier (BMNH 68.931/33); 1 imm. ♀, alc., 1968, A. M. Hutson & J. G. Frazier (BMNH 68.1090); 1 imm., alc., 6-XII-1972, Royal Society Expedition (BMNH 74.375).
"ALDABRA": 1 ♂, 20-VII-1906, Thibault (BMNH 1939.1333); 1 ♀ (?), 24-IV-1907, H. P. Thomasset (RMNH); 1 ♂, 12-V-1954, Cherbonnier (MNHN CG 1956-637).

Diagnosis: A large species, fal 133.8-140.8, gsl 58.3-58.7 (ranges not completely known); teeth of normal dimensions; ears pointed, length 25-28; snout greyish brown; chin and throat dark brown; cheeks with scattered, short whitish hairs; interocular and temporal regions, crown and occiput with bright ochraeous-yellowish white fur; mantle orange-buff tinged with ochraeous-rufous, shading into deep orange brown on sides of neck and foreneck; back fur hairs with light grey bases and light grey-brown tips mixed with whitish yellow tips and, in some specimens, with black tips, resulting in an overall impression of greenish grey(-brown), palest on rump and femurs; back fur conspicuously sprinkled with glossy greyish white hairs, especially laterally; breast and belly hairs with greyish bases and yellowish to orange brown distal ends which dominate the overall impression; flanks the same, or lighter, depending on the length of the light-coloured hair ends; tibia with fur on proximal half and some scattered hairs on distal half, colour of fur corresponding with that of back fur, sometimes with a reddish hue; tail membrane well developed in centre.

Measurements: Of the adult specimens I examined, most were preserved in alcohol, with the skull *in situ*. In 7 ♂♂ the fal range is 133.8-140.8, 4 others measured by Mr. A. M. Hutson in the field but not collected also fall in this range; in 2 ♀♀ the fals measured 136.0 and ≥ 131.5, respectively. Six ♂♂ had weights of 257-395 (mean c. 305; Mr. A. M. Hutson, *in lit.*, XI-1989). Skull measurements of ♂ BMNH 1939.1333, ♂ MNHN 1956-637 and ♀ (?) RMNH are: gsl >58.5/—/≤58.7; cbl —/—/—; rl 21.4/21.1/21.6; pl 31.3/31.1/32.6; cranium width 20.9/—/21.1; iow 7.6/7.9/7.9; pow 8.8/—/7.3; zw —/31.7/30.0; mandible length 44.7/44.4/45.1; mandible height 20.8/21.9/22.2; C^1-C^1 10.1/10.6/10.5; C^1-M^2 20.9/20.7/21.1; M^1-M^1 14.4/14.0/14.8; M^2-M^2 ?/13.1/—; C_1-M_3 23.4/23.3/23.6, respectively. Andersen (1912) gave measurements of a ♂ (USNM 62061), with a gsl of 58.3, and the other skull dimensions generally slightly larger than those of the skulls I measured.

Distribution: Fig. 6.

Related species: In the region of the western

Indian Ocean, *P. seychellensis* (both subspecies) is the most similar species, but that species is absolutely larger in body and skull measurements and differs in details of its fur colours, especially in its more strongly yellowish head fur and essentially blackish brown back fur. Other similar species are *P. rufus* and *P. voeltzkowi*, which are both still larger and also differ in fur colours. The other *Pteropus* species in the region possess one or more of the following characters distinguishing them from *P. aldabrensis*: rounded ears or small, almost concealed ears; reduced teeth dimensions, blackish mantle fur, and/or a furred tibia. No *Pteropus* species is sympatric with *aldabrensis*.

Remarks

Taxonomy: True (1893) based this species on two ♂♂ which would seem immature by their respective fals of 119 and 117 but adult by the skull measurements in the description (e.g. zw 33.5 and 33.6, and mandible length 44.0 and 45.0 respectively). True's observation that the postorbital processes are united with the zygomatic arches also indicates adultness. I have not examined these specimens (then USNM 20984/36053 and 20985/36054) but they consist of dry skins and skulls and the too small fals are no doubt due to the way of preparation of the skins. (It is not clear to me why Honacki *et al.*, 1982: 124, expressly changed the specific epithet from *aldabrensis* into *aldabrabensis*. True's description was first issued as an "advance sheet" on 14-VII-1893 and later included, as paper 948, in volume 16 of the Proceedings of the USNM for 1893 but published in 1894. I have only access to the latter, which is about *aldabrensis*.)

Andersen (1912) characterized the fur of *aldabrensis* as "in every essential respect like that of *Pt. comorensis* and allied species, save for the very strong admixture of broccoli-brown and wood-brown in the colour of back and rump." The skins I have seen do not support this general notion, nor do some excellent colour slides of *aldabrensis* made by mrs. drs. C. H. van Duyl in July/September 1986 in Aldabra. True (1893) described the head and cheeks of the two syntypes as pale yellow, the hairs of the crown of the head as very pale yellow at the base with darker tips, and the back and extremities as gray-buff. I have described the main head fur as bright ochraceous-yellowish white and the back fur as consisting of hairs with light grey bases and light grey-brown tips mixed with whitish yellow tips and, in some specimens, with black tips, resulting in an overall impression of greenish grey(-brown).

In the account of typical *Pteropus seychellensis* I have already pointed out that since Andersen (1912) a wrong concept of its size, as measured by its fal, has been held ("143-154") which made it nearly continuous with *aldabrensis* ("130-141"). In fact, the ranges are clearly disjunct. The known and here published weights confirm that.

Thirdly, Andersen (1912) mentioned that *aldabrensis* has a relatively broader mesopterygoid fossa than *comorensis*, and suggested that its M^2 and M_3 might be slightly more reduced than in that taxon. He could examine only one specimen of *aldabrensis*, however.

Hill (1971), reviewing the species of Andersen's *Pteropus rufus* group, found no valid reason for maintaining *P. aldabrensis* as a distinct species. I agree that *seychellensis* is by all appearances its nearest living phylogenetic relative but I cannot accept Hill's arguments to synonymize the two. Hill has copied the fal ranges (except that of *aldabrensis*) from Andersen (1912), including the doubtful values for typical *seychellensis*, and failed therefore to recognize the true range of that taxon — which would have revealed that it is disjunct with *aldabrensis* and overlaps (possibly completely) with *comorensis*. Furthermore, Hill does not give a comparative account of the skull morphology or skull measurements of *aldabrensis* (all but one of this species in the BMNH are preserved in alcohol, with the skulls *in situ*) and *seychellensis*. Likewise, he does not comment on Andersen's observation of molar reductions in *aldabrensis*. And finally, Hill's summaries of colour patterns are so succinct that certain differences are left out; head and mantle are not specifically mentioned and the back fur colour is reduced, in his remarks, to some shade of brown with a weaker or stronger sprinkling of silvery grey.

Distribution and geographical variation: *P. aldabrensis* is restricted to the Aldabra atoll, where it may be met with almost everywhere, probably also becaused food sources are limited and exploited intensively (e.g. P. Roberts *et al.*, 1989). In view of the restricted distribution and the species' movements through its range intraspecific variation is not likely to be found.

Pteropus voeltzkowi Matschie, 1909

Pteropus (*Spectrum*) *voeltzkowi* Matschie, 1909: 486 (type locality: Fufuni).

Pteropus voeltzkowi; Andersen, 1912: 818; Aders, 1917: 400; Moreaeu *et al.*, 1940: 118; Swynnerton *et al.*, 1951: 287; Hayman *et al.*, 1971: 10; Hill, 1971: 575; Kingdon, 1974: 140; Meirte, 1984b: 50; Pakenham, 1984: 25; Carroll, 1985: 4; Seehausen, 1990.

Material examined

PEMBA. Chakechake: 1 ♂, 15-IX-1923, A. Loveridge (BMNH 24.3.8.7). Inkoani: 1 ♀, 18-VIII-1923, via A. Loveridge (BMNH 24.3.8.4). Malindini, Barawa (road Weti-Chake): 1 ♂, 1 ♀, 1 imm. ♀, 25-VIII-1954, W. H. R. Lumsden (BMNH 64.893/95). Mbiji, Inkoani: 1 ♂, 1 ♀, 14/18-VIII-1923, via A. Loveridge (BMNH 24.3.8.2/3). Mizi Miombe Hill: 2 ♂♂, 18/20-IV-1939, R. H. W. Pakenham (BMNH 55.163/64). Mkoani: 1 specimen, 24-V-1939, R. H. W. Pakenham (BMNH 55.165). Matanga, Mgogoni: 2 ♂♂, 3 ♀♀, 23/24-VIII-1954, W. H. R. Lumsden (BMNH 64.888/92). Ole: 1 imm. ♂, 1 ♀, 1 imm. ♀ (skin only), 26-VI/26-IX-1923, via A. Loveridge (BMNH 24.3.8.5/6, 24.12.15.5). Tundau...: 1 ♂, skin, 27-VII-1913 (BMNH 13.10.28.1). "Pembla": 2 ♂♂ (1: skin only), 1 ♀ (alc., skull), A. Gunning (BMNH 9.10.14.1, 10.3.24.1/2).
(Fufuni, Jambangome, Kisiwani, Kiwani, Ziwani.)

Diagnosis: A large species, fal 145.6-163.1, gsl 62.8-68.0; teeth of normal dimensions; ears pointed, length c. 26-28; snout dark, with few, scattered hairs; cheeks thinly haired; fur of sides of head, preocular and interocular regions, and crown of head dark brown or reddish orange-brown, mixed with silvery greyish buff hairs, especially on crown; occiput and mantle with dark reddish brown tipped hairs or, in mantle, hairs with brighter orange brown or tawny cinnamon-rufous tips; mantle hair tips on sides of neck and foreneck again deeper reddish brown; fur of back and rump blackish brown with an admixture of a few silvery greyish white hairs or, increasing in number towards rump, dark reddish brown hairs; fur of breast and belly either some tinge of russet or dark brown, darkest on breast and middle of belly and palest on sides of belly, or reddish golden-yellow, passing into brown on lower belly; tibia with some fur on inner side of proximal part, otherwise naked; tail membrane distinct.

fal	♂♂	149.0-163.1 (n = 6);
	♀♀	145.6-158.4 (n = 5).
gsl	♂♂	64.1- 68.0 (n = 8);
	♀♀	62.8- 67.9 (n = 8).
cbl	♂♂	63.1- 67.0 (n = 5);
	♀♀	62.1- 66.9 (n = 4).
rl	♂♂	25.2- 26.7 (n = 8);
	♀♀	24.0- 26.4 (n = 6).
pl	♂♂	36.4- 39.7 (n = 8);
	♀♀	36.4- 39.8 (n = 6).
zw	♂♂	34.9- 38.0 (n = 8);
	♀♀	32.7- 36.3 (n = 6).
C^1-M^2	♂♂	24.4- 26.8 (n = 5);
	♀♀	24.2- 26.4 (n = 6).
W	♂♂	470-610 (n = 3);
	♀♀	430-600 (n = 4).
rl	♂♂	37.9- 39.4% of gsl (n = 8);
	♀♀	37.1- 39.0% of gsl (n = 6).
pl	♂♂	56.0- 58.6% of gsl (n = 8);
	♀♀	56.3- 58.6% of gsl (n = 6).
zw	♂♂	53.0- 57.7% of gsl (n = 8);
	♀♀	49.3- 54.1% of gsl (n = 5).

Distribution: Fig. 5.

Related species: In the western Indian Ocean region, *P. seychellensis* is the most similar species, and largely overlaps in body and skull size. Its ears are relatively larger (but caution is needed here, as most ear measurements were taken by different collectors). In *voeltzkowi*, the length of the upper tooth row and the palatal length appear to average larger than in *seychellensis comorensis* (vis-à-vis the typical subspecies this is as yet less clear). The most striking differences are presented by the fur colours: in *voeltzkowi* the head fur is mainly dark brown or reddish orange-brown, against golden yellowish or brownish yellow in *seychellensis*, and the mantle is also much darker and much more reddish in appearance in *voeltzkowi*. *P. rufus* averages larger in body and skull dimensions but the lower values overlap with the higher in *voeltzkowi*. The ears in *rufus* are relatively larger and its relative palatal length appears to be smaller, on average. *P. rufus* also differs in fur colours; the fur on its head is light brown to yellowish and its mantle is also brownish yellow, dorsally (and orange-yellow only on sides of neck and ventrally). *P. aldabrensis* is absolutely smaller in all measurements and also shows a number of fur colour differences. Other *Pteropus* species in the region differ by one or more of the following characters: rounded instead of pointed ears or small, almost concealed ears; reduced teeth dimensions; blackish mantle fur; a furred tibia.

Remarks

Taxonomy: *Pteropus voeltzkowi* shows strong morphological similarities to *P. seychellensis*, and its most aberrant character from that species is its reddish and dark appearance. Dr. J. E. Hill has considered to relegate it to subspecific rank within *seychellensis*, but has not done so mainly because of this very typical colour pattern (pers. comm., 14-XI-1989). As Pakenham (1984: 26) observed: "*P. voeltzkowi*'s foxy red head, neck and mantle contrast strikingly with other Indian Ocean *Pteropus*." Matschie (1909) wrote that its ears were so short (17-18) as to be almost hidden in the fur. He could examine dry skins only. Collectors in the field measured 25 in one ♂ and 20 in two ♀♀ (Loveridge) and 26, 26, 28 in 3 ♂♂ and 26, 27, and 28 in 3 ♀♀, respectively (Lumsden); although we do not know the circumstances Lumsden's measurements were clearly taken with more accuracy than the others. (The BMNH collection contains two specimens in alcohol, of which I failed to take the ear lengths at the time. These may serve to bring further light in this matter.)

Distribution and geographical variation: *P. voeltzkowi* is restricted to Pemba but has been found over the larger part of the island. According to Pakenham (1984) it often roosts on small islands off Pemba's coasts and flies across at sunset, to forage. Seehausen (1990), who visited Pemba late in 1989, found strong indications that the distribution as pictured by Pakenham (1984) and Carroll (1985) has become largely historical, and he considers the species to be very seriously endangered. Seehausen (*op. cit.*) concluded from interviews with inhabitants of Pemba that the species used to occur in the western parts of the island, which was once covered with rain forest, and not in the eastern, drier parts. The locality "Matanga-Mgogoni" mentioned by Kingdon is based on BMNH specimens labelled "Matanga, Mgogoni, on main road" and should be "along the road between Matangatuani and Mgogoni". In view of the restricted range intraspecific variation is not to be expected.

Eidolon Rafinesque, 1815

Eidolon Rafinesque, 1815: 54; Andersen, 1908b: 432 (designation of *Pteropus stramineus* E. Geoffroy-St. Hilaire, 1803 = *Vespertilio vampyrus helvus* Kerr, 1792 as type species), 1912: 2; Leche, 1921: 40.

Andersen (1908b) revived the genus name *Eidolon* proposed by Rafinesque (1815) for the section "Rousettes à queue" in E. Geoffroy-St. Hilaire (1810), and designated the earliest known species in that section, *Pteropus stramineus* E. Geoffroy-St. Hilaire, 1803 (a junior synonym of *Vespertilio vampyrus helvus* Kerr, 1792) as the type of the genus. Geoffroy-St. Hilaire (1810) did not provide other characters for this section than the possession of a short tail and a generally smaller overall size than the species forming the section of "Rousettes sans queue" (coinciding with *Pteropus*). It is interesting to note here, however, that Geoffroy-St. Hilaire (1810) gave an excellent diagnosis of the present Megachiroptera as a distinct and coherent group within the Chiroptera.

Rafinesque (1815) based his arrangement of the Chiroptera on the writings of earlier authors — in this particular case, of Geoffroy-St. Hilaire. He did not discuss the characters mentioned by those authors, nor did he provide new ones. (Andersen, 1908b, gave an eminent analysis of Rafinesque's section on Megachiroptera, which he quoted *in extenso*).

Peters (1862) proposed the new genus *Pterocyon* for an African species which by its dental formula was like *Pachysoma* E. Geoffroy-St. Hilaire, 1828 (a junior synonym of *Cynopterus* Cuvier, 1824) but in all other characters agreed with *Epomophorus* Bennett, 1836. Peters did not indicate a type for his new species *Pterocyon paleaceus*, but Andersen (1912: 12) pointed out that Peters was renaming *Pteropus stramineus* (i.e. *Eidolon helvum helvum*).

Jentink (1881) described the genus *Leiponyx*, based on a very old specimen without index claws and with many teeth worn away, but nevertheless recognized by Miller (1907: 56) as synonymous with *Pterocyon* (i.e. *Eidolon*). As Jentink concentrated his diagnosis on the clawless index, he mentioned but a few other characters: muzzle as in *Pteropus*; nostrils slightly projecting, rather deeply emarginate between; upper lip with a distinct vertical groove in front; metacarpal of middle finger shorter than index finger; wings from sides of back and from base of first toe; tail short, for its greater part free from membrane; dental formula: upper teeth 2.1.2.2, lower teeth 2.1.3.3.

Matschie (1899) listed *Pterocyon* as a subgenus of *Xantharpyia* Gray, 1843, in which he furthermore included species of *Rousettus* Gray, 1821, *Myonycteris* Matschie, 1899, *Lissonycteris* Andersen, 1912 and a species of *Cynopterus*. As characters of *Xantharpyia* he listed, among others: base of thumb included in flying membrane (as in *Epomophorus*); flying membrane from second toe; snout stretched; third metacarpal about as long as the index; no white ear tufts; dental formula: upper teeth 2.1.3.2, lower teeth 2.1.3.3; males without baculum; males with (possibly only in mating season) round tufts of brushy hairs in foreneck under each ear, connected with glands; seven soft palate ridges (three or four posterior ones divided) and one to four toothed lines at posterior palate margin; plagiopatagium with *Epomophorus*-like distribution of fasciae. The subgenus *Pterocyon* consisted of the species *Pteropus stramineus* and *Pteropus dupreanus* Pollen, 1867 and was distinguished by the length of M_1 (as large as the lengths of M_2 and M_3 together), the number of fasciae of the plagiopatagium (18 or more, against 16 or less in other *Xantharpyia*), and by four (instead of one or two) toothed lines at the posterior palate margin.

Miller (1907) synonymized *Leiponyx* Jentink with *Pterocyon* upon studying the type specimen of its type species, *Leiponyx buettikoferi* Jentink, 1881. He treated *Pterocyon* again as a distinct genus and added as characters the ungrooved, relatively rounded crowns of the lower incisors (as opposed to the condition in *Rousettus*) and the unique morphology of the auditory bullae, the outer portion of which is a prominent lip or short tube surrounding the meatus. Incidentally, Andersen in the same year (1907b) also synonymized *Leiponyx* with *Pterocyon*, rather tentatively as he had not seen the specimen concerned.

Andersen (1907b, 1912) selected the following characters for his diagnosis of *Pterocyon* (in 1907)/*Eidolon* (1912): basicranial axis considerably deflected, alveolar line when projected backward passing through bases of post-tympanic and paroccipital processes; premaxillaries separated in front; rostrum long, its length much greater than the lachrymal width, and front of orbit above posterior half or middle of M^1; palate much broader posteriorly than between canines; tympanic produced externally into a short tubular bony auditory meatus; occiput not elongated and tubular; cutting edges of lower incisors simple (not bifid); P^2 in cross-section twice the size of an upper incisor; M_1 in length equal to M_2 and M_3 together; second digit clawed; membranes from side of back; a short tail.

Thus, the possession of a distinct tail on which the earliest classification of the Megachiroptera rested, has not lost its diagnostic character, although it is shared by a number of genera (in Africa: *Eidolon*, *Rousettus*, *Myonycteris* and *Lissonycteris*). That *Eidolon* would share all diagnostic characters except its dental formula with *Epomophorus*, as Peters (1862) suggested, only holds for its (relatively) long rostrum, its hardly elongated occiput, its clawed second digit, and the place of insertion of the flying membranes (the side of the back). The clawless index and aberrant dental formula in Jentink's diagnosis (1881) are clearly attributable to the involved specimen's old age. The length of the third metacarpal is not in all specimens larger than that of the first digit.

Matschie (1899) listed some characters for *Eidolon* which are clearly not correct: the membrane is inserted on the first toe, not on the second; males do possess a baculum (see Didier, 1965); the glandular hairs are not restricted to the sides of the neck but also cover the foreneck, and they are not restricted to males (Andersen, 1912; Mainoya *et al.*, 1979); the number of fasciae can be as low as 16; the number of toothed lines at the back of the soft palate can be less than four (Andersen, 1912).

Miller met Andersen when travelling in Europe for the preparations of his book (Miller, 1907) and as Andersen published a revision of *Eidolon* (as *Pterocyon*), *Rousettus* and *Myonycteris* in 1907 they will certainly have discussed the characters of these genera. Therefore, it is not clear whether Miller discovered the two characters — a bony auditory meatus and smooth lower incisor cutting edges — he mentioned for *Eidolon* or if Andersen did.

Leche (1921) did not add new generic characters but based his treatment entirely on Andersen (1912).

I have only a few comments on Andersen's diagnosis of 1912. The measure of brain case deflection described by him, and shown in his fig. 1 of the skull of a male from Fernando Poo, is not typical. According to Andersen, the alveolar line when projected backward passes very nearly through the bases of the posttympanic and paraoccipital processes and upper margin of the occipital condyle, but in specimens of both sexes from the West African mainland in the ZMA collection, including one from the type locality Senegal, the deflection is distinctly greater. If compared with Andersen's figure, the brain case is generally more domed and more strongly descending posteriorly. The occiput is slightly elongated and certainly somewhat tubular, although never as strongly tubular as in *Pteropus*. The morphology of the brain case is rather more as in the specimen of *Rousettus* figured by Andersen (1912, fig. 2), of which genus he wrote "brain-case in most species deflected very nearly to the same degree as in *Eidolon*"! The alveolar line in West African mainland *Eidolon*, when projected backward, passes through or above the bases of the mentioned processes and through the occiput, above the occipital condyle. The conclusion must be that either the specimen Andersen selected for his figure is aberrant or the populations from Fernandoo Poo are morphologically different from mainland ones. In this respect it is of interest that Eisentraut (1964) noted that an *Eidolon* population at Sainte Isabelle, Fernando Poo, was probably not migratory. An example of morphological differentiation of Fernando Poo fruit bats from mainland populations is discussed in the account of *Scotonycteris zenkeri*.

Eidolon helvum (Kerr, 1792)

Vespertilio vampyrus helvus Kerr, 1792: xvii, 91 (no locality).
Pteropus stramineus E. Geoffroy-St. Hilaire, 1803; 48.
Pterocyon paleaceus Peters, 1862: 423.
Leiponyx buettikoferi Jentink, 1881: 59.
Pterocyon buettikoferi; Miller, 1907: 56.
Pterocyon helvus; Andersen, 1907b: 504 (designation of Senegal as type locality).
Pterocyon sabaeus Andersen, 1907b: 505 (type locality: Lahej).
Eidolon helvum; Andersen, 1908b: 433, 1912: 8.
Eidolon sabaeum; Andersen, 1912: 15; Sanborn *et al.*, 1953: 234.
Eidolon helvum sabaeum; Eisentraut, 1964: 532; Harrison, 1964: 44.
(Further references under the subspecies).

Diagnosis: A large fruit bat, fal c. 110-133, gsl c. 50.5-58.5; brain case distinctly domed; skull foramina generally relatively large; grizzled

yellowish and dull brown fur, dorsally well demarcated against the dark wings; premaxillae not proclivous; tooth rows diverging backwards; posterior margin of mandibulum distinctly concave below processus articularis; premolars and molars with weak outer and inner ridges and shallow median groove.
Measurement ranges and ratios for the two subspecies combined:

fal in ♂♂ 109 -130.5,
in ♀♀ 111.8-133.2;
gsl in ♂♂ 52.5- 58.6,
♀♀ 50.4- 58.2
rl in ♂♂ 35.3- 39.9% of gsl,
in ♀♀ 36.0- 39.8% of gsl;
pl in ♂♂ 52.6- 59.4% of gsl,
in ♀♀ 52.7- 57.4% of gsl;
zw in ♂♂ 55.7- 62.3% of gsl,
in ♀♀ 55.0- 62.1% of gsl.

Distribution: Fig. 7.

Remarks

To conclude from the nomenclature he used, G. M. Allen (1939a) was the first to consider *Eidolon sabaeum* (Andersen, 1907) as a subspecies of *Eidolon helvum*. This has been followed by a number of later authors on *sabaeum (see* the references in the account of that subspecies). *Eidolon dupreanum* was retained by Allen as an independent species.

Schouteden (1944) claimed that *Eidolon* is a monotypic genus, with *helvum* as its only species, thus suggesting that *dupreanum* would also be a subspecies of *helvum*. Schouteden certainly did not study *dupreanum*, at the time, and his statement must be based on a misinterpretation of the binominal nomenclature used by Sanderson (1940) and/or G. M. Allen *et al.* (1942) for mainland African *Eidolon*.

Eisentraut (1964) took Schouteden's remark for a reasoned taxonomic statement, and Hayman *et al.* (1971) referred to Eisentraut *(op. cit.)* as the originator of the idea that *Eidolon* would be monotypical, and followed him in their widely used identification manual for African Chiroptera.

However, whereas the subspecific rank of *sabaeum* has been adopted by those who, since G. M. Allen's check list of 1939, have studied actual material of that taxon and compared it with specimens of typical *helvum* (Harrison, 1964; Nader, 1985), those who studied material of *dupreanum* and compared that to typical *helvum* material retained *dupreanum* as an independant species (Dietz, 1916; Didier, 1965).

In the following account I have adopted G. M. Allen's (1939) partly implicit concept of the taxonomic divisions within the genus *Eidolon*. Although I must admit that an extensive analysis of *dupreanum* material (for which the opportunity has failed me) may lead to a reappraisal of that species' taxonomic status yet, I cannot agree with procedures in which taxonomic shifts are proposed without a single argument.

Eidolon helvum helvum (Kerr, 1792)

Vespertilio vampyrus helvus Kerr, 1792: xvii, 91 (no locality).
Pterocyon helvus; Andersen, 1907b: 504 (designation of Senegal as type locality); Lönnberg, 1908: 2.
Eidolon helvum; Andersen, 1908b: 433; Dollman, 1908: 545, 1909: 349; Wroughton, 1911: 458; Andersen, 1912: 8; A. Roberts, 1913: 65; J. A. Allen *et al.*, 1917: 414; Lang *et al.*, 1917, 1917a: 497; Wettstein, 1917: 94; Hollister, 1918: 71; Fitzsimons, 1919: 93; Schwarz, 1920: 1052; De Fenis, 1921; De Beaux, 1922b: 365; Loveridge, 1923: 692; Cabrera *et al.*, 1926: 593; Cabrera, 1929: 12; Shortridge, 1934: 47; Mendez, 1937: 64; G. M. Allen, 1939b: 261; Moreau *et al.*, 1940: 118; Hill *et al.*, 1941: 28; Eisentraut, 1942: 249; Krumbiegel, 1942: 339; Eisentraut, 1945: 374; Bramwell, 1947: 57; Radford, 1947: 309; Malbrant *et al.*, 1949: 81; Rousselot, 1950; A. Roberts, 1951: 53; Swynnerton *et al.*, 1951: 15; Aellen, 1952: 23; Malbrant, 1952; Ellerman *et al.*, 1953: 44; Lawrence *et al.*, 1953; Osmaston, 1953; Rosevear, 1953: 81; Bourlière *et al.*, 1955; Dekeyser, 1955: 105; Eisentraut, 1956a: 507; Perret *et al.*, 1956: 428; Aellen, 1957: 191; Benedict, 1957; Eisentraut, 1957a, 1957b: 624, 659; Blancou, 1958: 10; Boulger *et al.*, 1958: 421; Huggel, 1958; Baker *et al.*, 1959; Booth, 1959: 28; Fain, 1959: 1, 4, 10; Harrison, 1959: 219; Sweeney, 1959: 7; Ansell, 1960b: 8; Malzy *et al.*, 1960; Harrison, 1961: 286; Webster, 1961; Jaeger, 1962: 114; Malzy, 1962; Aellen, 1963: 629; Eisentraut, 1963: 57; Hayman, 1963: 95; Morris, 1964; Ogilvie *et al.*, 1964; Vesey-Fitzgerald, 1964: 63; Child, 1965: 78; Didier, 1965:

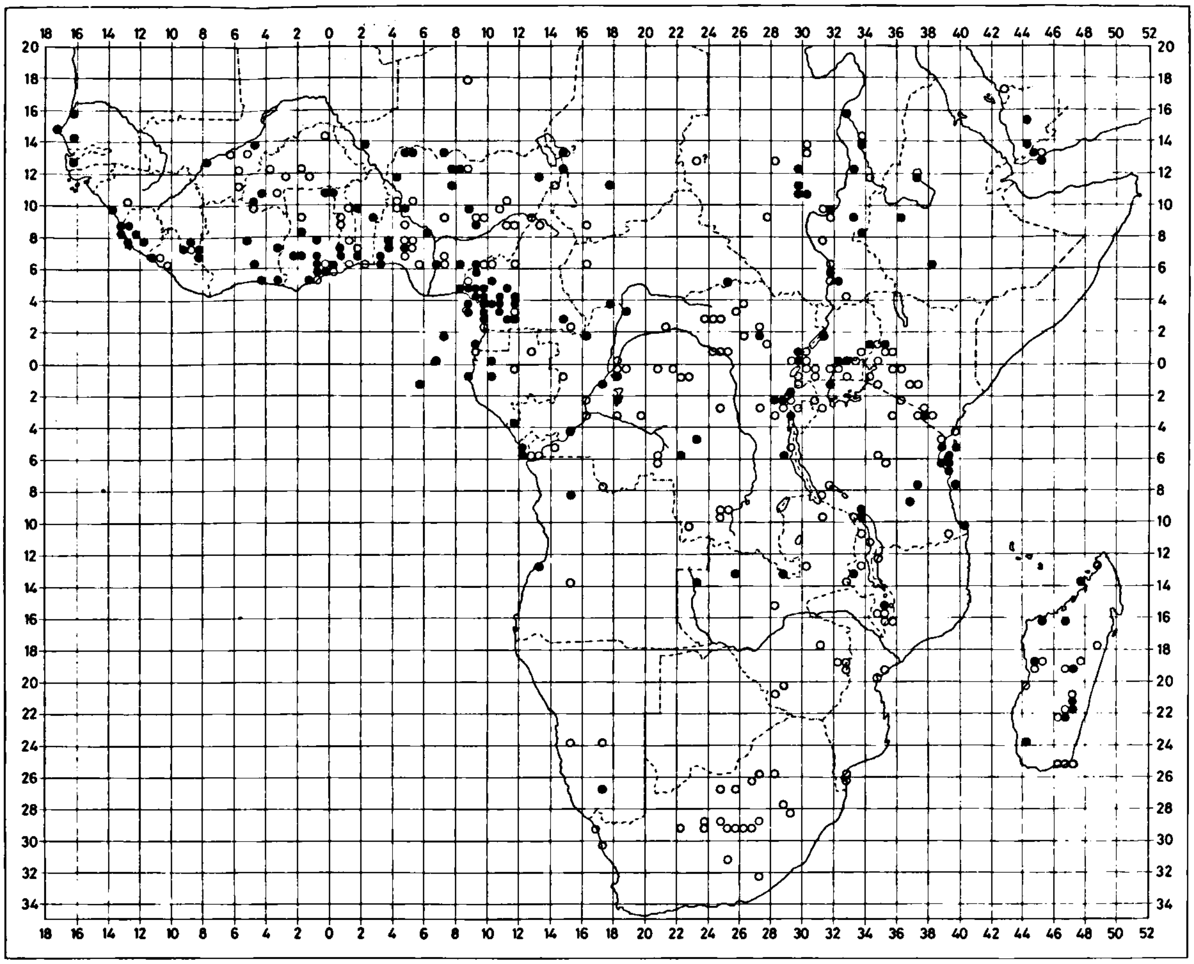

Fig. 7. Distribution of *Eidolon helvum helvum* (Kerr, 1792): on the African mainland; *E. helvum sabaeum* (Andersen, 1907): in the southwest of the Arabian Peninsula; and *E. dupreanum* (Pollen, 1867): in Madagascar. Black dots: squares from where material has been identified by the author; open circles are based on records in the literature, museum registers and correspondence.

335; Huggel-Wolf *et al.*, 1965; Koopman, 1965: 2; Mutere, 1965a, 1965b; Osmaston, 1965; Rosevear, 1965: 68; Aellen, 1966: 69; Brosset, 1966a: 364, 1966b: 52, 1966c: 134; Hayman *et al.*, 1966: 21; Rahm, 1966: 63; Rahm *et al.*, 1966: 13; Ansell, 1967: 2; Blackwell, 1967; Happold, 1967; Mutere, 1967; Rowlatt, 1967; Aellen *et al.*, 1968: 438; Kulzer, 1968; D. I. H. Simpson *et al.*, 1968a, 1968b; Kock, 1969: 11; Kulzer, 1969; Erkert, 1970; Henson, 1970; Niort, 1970: 254; Jones, 1971: 124, 1972; Kock, 1972: 123; Aderounmou, 1973; Fayenuwo *et al.*, 1973; Abobarin, 1974; Adeosun, 1974; Aniedu, 1974; Ansell, 1974: 9; Ayensu, 1974; Bergmans *et al.*, 1974: 20; Halstead, 1974; Kingdon, 1974: 146; Largen *et al.*, 1974: 228; Okon, 1974; Omusun, 1974; Vieillard, 1974: 977; Fenton, 1975; Koopman, 1975: 357; Lynch, 1975: 116, 122; Roer, 1974/1975: 106; Stuart, 1975: 7; Coe, 1976: 542; Fain, 1976; Funmilayo, 1976; Bradbury, 1977: 19; Kallen, 1977: 294; Rasweiler, 1977: 541; Anciaux de Faveaux, 1978: 80; Bergmans, 1978a; Fain, 1978: 176; Funmilayo, 1978; Happold *et al.*, 1978: 72; Kingdon, 1978; Kock, 1978b: 118; Okon, 1978; Funmilayo, 1979; Mainoya *et al.*, 1979; Smithers *et al.*, 1979: 25; Swanepoel *et al.*, 1980: 168; Verschuren, 1980: 2; Marshall *et al.*, 1982: 56; Wolton *et al.*, 1982: 431; Emmons *et al.*, 1983; D. W. Thomas, 1983; Anciaux de Faveaux, 1983: 27; Koch-Weser, 1984: 260; Baeten *et al.*, 1984: 183; Happold, 1984: 272; Ogen-Odoi, 1984: 36; Herselman *et al.*, 1985: 82; Fedden *et al.*, 1986: 183; Happold, 1987: 38; Happold *et al.*, 1987: 350; Roth *et al.*, 1988: 184.

Xantharpyia straminea; Auerbach, 1913.

? *Eidolon helvum*; O. Thomas *et al.*, 1923: 249; Bourbon *et al.*, 1929: 287.

Eidolon; Flower, 1932: 377.

Cynonycteris straminea; Rodhain *et al.*, 1916: 249; Pécaud, 1925; Gromier, 1936: 34.

Eidolon stramineum; G. M. Allen, 1939b: 55, 234.

Eidolon helvum helvum; G. M. Allen, 1939a: 54; Sanderson, 1940: 665; G. M. Allen *et al.*, 1942: 160; Schouteden, 1944: 100; Dekeyser, 1950: 388, 392; Sweeney, 1959: 7; Rahm *et al.*, 1963: 25; Eisentraut, 1964: 531; Kuhn, 1965: 325; Brosset, 1966c: 134; Eisentraut, 1968: 171; Kuhn, 1968: 174; De Vree *et al.*, 1969: 203, 1970: 43; De Vree, 1971: 37; De Vree *et al.*, 1971: 161; Hayman *et al.*, 1971: 11; Eisentraut, 1973: 356, 1973a: 33; Vielliard, 1974: 977; Koopman, 1975: 357; Smithers *et al.*, 1976: 40; Verschuren, 1977: 616; Ansell, 1978: 17; Koopman *et al.*, 1978: 2; Bergmans, 1979: 163; Robbins, 1980: 85; Kock, 1981: 330; Rodgers *et al.*, 1982: 241: Rautenbach, 1982: 31; Bergmans *et al.*, 1983: 118; Feiler, 1984: 75; Pakenham, 1984: 24; Feiler, 1986: 73; Happold, 1987: 38; Ansell *et al.*, 1988: 28; DeFrees *et al.*, 1988.

? *Eidolon helvum*; Coe *et al.*, 1965b.

Material examined

ANGOLA. Benguela: 1 specimen, alc., Monteiro (ZMB 4239). 30 km W of Camatabela: 1 ♂, 1954, G. H. Heinrich (FMNH 81729). Chinchoxo: 1 specimen, alc. (ZMB 5224); 2 imm., Falkenstein (ZMB 10210/11).

(Caconda, Cuillo River, ?Dundo, Lucinda.)

BENIN. Kpodave: 1 specimen (USNM 438859). Soubroukou: 1 specimen (USNM 438857). Tourou: 1 specimen (USNM 421266). "Dahomey": 1 specimen, I-1910, Waterlot (MNHN CG 1911-1531); 2 specimens (BMNH 44.7.4.20, 52.2.22.1).

(Borgou, Ouidah.)

BURKINA FASO. Fo: 1 specimen (USNM 467916). Koutoura: 1 specimen (USNM 467918). Sideradougou: 1 specimen (USNM 467919).

(Boroma, Dedougou, Diebougou, Dori, Ouagadougou, Voko.)

BURUNDI. Bujumbura: 1 ♂, alc., 16-VIII-1976, J. Verschuren (IRSN 19908).

Busiga, Kayanza.)

CAMEROUN. Bafia region: 1 ♂, Tessmann (ZMB 31487). Bana: 1 skin, Glauning (ZMB). Banjun: 1 specimen, 17-IX-1907, Glauning (ZMB). Basho: 1 ?♂, 1 ♀, via Von Oertzen (ZMB). Batanga: 1 imm., A. I. Good (CMNH 2303). Bipindi: 1 ♀, G. Zenker (ZMB 10202); 1 ♀, alc., 14-VI-1906, G. Zenker (ZMB). Buea: 2 specimens, alc., P. Preuss (ZMB 10203/04). Douala: 1 specimen, alc., 15-XII-1913, A. Haas (SMF 5383). Ebolowa: 1 imm. ♀, 5-XI-1952, A. I. Good (FMNH 74232). Edea: 1 ♂, 8-XI-1922, J. A. Reis (FMNH 24247). Eseka: 1 specimen (AMNH 236280); 1 ♀, 13-VII-1974, L. W. Robbins (CMNH 40990). Itoki: 1 ♂, IV-1891, Y. Sjöstedt (ZMB 6943). Kribi: 1 ♀, alc., skull, 21-II-1904, Mann (ZIZM 38192): 1 imm., 17-II-1920, J. A. Reiss (CMNH 5158); 1 imm. ♂, alc., 16-IV-1973, J. Prévost (MNHN CG 1979-321). Kumba: 1 specimen (USNM 511909); 1 specimen, alc. (BMNH). Lolodorf: 1 imm. ♂, 15-X-1937, A. I. Good (CMNH 16059). Mamfe: 1 skull, Mack (ZMB); alc. material (BMNH). Moba: 1 specimen, VI-1901 (ZMB 54703). Mondole Island: 1 specimen (HZM). Mount Manengouba: 1 ♀, 3 imm. ♂♂, 3 imm. ♀♀, 30-XI/3-XII-1973, J. Prévost (MNHN CG 1979-314/20). Ossidinge: 1 ♂, 1 specimen, alc., skulls, 4 specimens, alc., Mansfeld (ZMB 54598, 54602, 54693, 54702, 54935, 54939). Nicolls Island: 1 ♂, 1 imm. ♂, 1 ♀, 2 imm. ♀♀, and 2 specimens in alc., 7/10-II-1938, M. Eisentraut (ZMB 54674, 67046, 93797/801). Sakbayeme: 2 ♂♂, 12-VIII-1931, J. A. Reis (FMNH 43568/69). Sanga Ngoko: 1 skin, 27-XI-1906, Glauning (ZMB). Sangmelima: 1 skin, 13-VIII-1913, H. Rolle (ZMB 18369). Tombel: 1 specimen (HZM). Victoria: 1 imm., alc., P. Preuss (ZMB); 1 imm., alc., skull, 11-II-1899, P. Preuss (ZMB 54940); 1 specimen, alc., XI-1901/II-1902, P. Preuss (ZMB 54657); 1 imm. skull, via E. A. Böttcher (ZMB 92839); 2 specimens (BMNH 36.10.30.1/2). Yaoundé: 1 ♀, G. Zenker (ZMB 10218); 1 imm. ♀, alc., 23-X-1973, J. Prévost (MNHN CG 1979-322).

(Bankim, Batoke, Bimbia, Bota, Campo, Ekona, Foulassi, Great Soppo Forest, Isongo, Makumunu, Metet, Mora, Mouloundou, Obala, Oku Mountains, Poli, along the Sanaga, Sanga, Saxenhof, Ydé.)

CENTRAL AFRICAN REPUBLIC. La Maboké: 1 imm. ♂, alc., 10-XII-1965, R. Pujol (MNHN); 1 imm. ♂, alc., 30-VI-1966, Ndéma (MNHN). Nyam-Nyam: 1 ♂, 2 ♀♀, before 17-VI-1884, via Bohndorff (IRSN 181, 181b, 181j). Semmio: 1 ♂, 1 imm. ♂, 1 skull, 1 skin, via Bohndorff (ZMB 7426/28, 10206).

(Boukoko, between Bozoum and Zemio.)

CHAD. Fort Lamy: 1 ♂, 24-VI-1954. Expedition Laenen (IRSN 12652); 1 specimen, 1954, Colonel de Barmont (MNHN 1956-636). Melfi Mountains: 2 skulls, 20-IV-1911, A. F. M. Herz (SMF 6354/55). Nr Zamia: 1 ♂, Poutrin (MNHN CG 1911-778).

(Moundou.)

CONGO. Brazzaville: 1 specimen (AMNH 120259). Dinguembo: 1 ♂, 2 ♀♀, 6-XII-1972, W. Bergmans (ZMA 15.529/31).

(Ewo, Région du Pool.)

EQUATORIAL GUINEA. Elobey: 1 specimen, 7-VIII-1919, M. M. Escalera (MNCN 20-//-25.7). Elobey District: alc. material (BMNH).

ETHIOPIA. Dag Island, Lake Tana: 1 specimen (BMNH 1937.2.24.2). Gambela region: 2 ♂♂, alc., skulls (SMF 73.35/36). Jikaw: 1 ♀, alc., 23-II-1976, G. Nikolaus (SMNS 29859).

(Bulcha, Didessa, Gambela, Illubabor Province.)

FERNANDO POO. Bantabiri: alc. material (BMNH). Bilelepe: 1 specimen (USNM 141529). Bilelifri: 1 skull (BMNH 4.7.1.14). Santa Isabel: 1 specimen, 15-VI-1919,

M. M. Escalera (MNCN 20-//-25.16). "Fernando Poo": 1 skin, 1852, via W. Cuming (SMF 12.436); 14 skulls (BMNH 4.7.1.12/13, -15, -17/27). (Bissé, Natividad, San Carlos, Santa Isabel.)

GABON. Boukoko: 1 specimen, alc., 1962, F. Petter (MNHN). Cap Lopez: 1 specimen, alc., R. Buchholz (ZMB 4951). Kango: 1 specimen (AMNH 120256). Lambarene: 1 specimen (BMNH 8.6.14.5). "Gabon": 1 specimen (BMNH 74.10.6.3).

(Booué, Libreville, Makokou.)

GAMBIA. "Gambia": 2 specimens (BMNH 39.10.5.8, 66.1.10.2).

GHANA. Aburi: 2 specimens (BMNH 20.5.12.2/3). Achimota: 1 specimen (HZM). 3 miles E of Afegame: 1 ♀, alc., skull, 15-IV-1971, W. F. Rodenburg (RMNH 22958). Ashanti: 1 mounted specimen (RMNH). Bator: 1 specimen (USNM 411807). Gambaga: 1 specimen (USNM 424825). Goaso: 1 specimen, alc. (BMNH). Jukwa: 1 specimen (BMNH 98.10.24.2/3, 64.1270/71). Legon: 1 specimen (USNM 414061). Nkawkaw: 1 specimen (USNM 411806). Oda: 1 ♂, 16-VIII-1946, G. S. Cansdale (FMNH 62249), 1 specimen (USNM 439925). Yabraso: 1 specimen (USNM 424823).

(Accra, Achimota Forest Reserve, Bunso, Elmina, 7 miles NE of Kade, Mole Game Reserve, Shai Hills Game Reserve, Winneba.)

GUINEA. Konakri: 1 specimen, alc. (MNHN CG 1897-974).

(Kindia.)

GUINEA-BISSAU, Bolama Island: 1 imm. ♀, alc., 2-II-1979, J. de Waart (ZMA 20.462).

IVORY COAST. Abidjan Plateau: 25 ♂♂, 1 imm. ♂, 28 ♀♀, 4 imm. ♀♀, 24-II-1973, J. Vissault (ZMA 18.917/74). Adiopodoumé: 9 ♂♂, 1 imm. ♂, 16-IV-1973, J. Vissault (ZMA 18.866/75). "Assinie": 1 specimen, alc. (MNHN). 5 km SE Toumodi: 2 specimens (AMNH 239384/85). Yabrasso: 1 specimen (USNM 467915). (Abidjan, Bouaké, Ferkessedougou, Flampleu, Gopoupleu, Tai Forest.)

KENYA. Lake Victoria: 1 specimen (BMNH 2.7.5.3). Sigor: alc. material (BMNH). "Kenya": 1 specimen (BMNH 46.709).

(W slope Aberdares, Cherangani, Cherangani Mountains, Chyulu Hills, nr Mount Elgon, Kabete, Kaimosi, Kakamega, nr Kapsowar, Kavirondo, Kimingini, nr Kitale, northern shore Lake Natron, Maragoli, nr Mara River, Mbale, Mombasa, Mukumu, nr Nakuru, Ndarugu River, Ruiru, Sabatia, Ugaya Island in Lake Victoria.)

LIBERIA. Bonan: alc. material (BMNH). Buluma: 1 specimen, mounted (RMNH). At full sea nr Cape Palmas: 1 specimen, alc., 8-IV-1915, S. Kiekebusch (ZMB 20528). Mount Nimba West: 1 ♀, alc., 6-II-1966, J. Verschuren (IRSN 16082). Robertsport: 1 specimen, alc., skull, via Ward (USNM 102461). Teayee: alc. material (BMNH). Wreppoosta: 1 pullus, alc. (ZMB 44456; original identification).

(Deaple, Du River, Ganta, Gaple, Harbel, Tokadeh, Mühlenberg-Mission.)

MAFIA. Ngombeni: 1 specimen (BMNH 64.1311).

MALAWI. Between Bangweolo and Lake Nyasa: 1 specimen (BMNH 10.3.14.1). Lisanthu: 1 imm. ♂, alc., 20-III-1982, H. Jachmann (ZMA 21.694). Misuku: 1 specimen (HZM). Mount Malosa: 1 specimen (BMNH 97.10.1.17). Tualosa: 1 specimen (BMNH 97.10.1.14). Zomba: 2 specimens (BMNH 96.10.28.5, 99.6.28.1). "Nyasa": 2 specimens (BMNH 97.10.1.15/16).

(Blantyre, Likomo Island, Ruo River, Tedzani Falls, Viphya Plateau, Zoa Estate; 1134A.)

MALI. Bamako: 1 ♂, 2 imm. ♂♂, 1 ♀, 1958, P. Malzy (MNHN CG 1960-543/46).

(Koutalia, San, Ségou, Sikasso.)

MOZAMBIQUE.

(Reserva do Maputo, nr Vila Manica, nr Vila de Dondo; c. 1935A, c. 2532D, c. 2632B.)

NAMIBIA. Anas-Süd: 1 ♀, 1939, M. Lein-Weber (ZMB 90649). Litembo: 2 ♀♀, 1 imm. ♀, 1 imm., 20-I-1914, Lademann (ZMB 19771, -73, -75, -77, -79).

(Gobabeb, Tsumis.)

NIGER. Maradi: 1 imm. ♂, 1 imm. ♀, 1-I-1941 (MNHN CG 1962-64/65). Niamey: 1 specimen, 9-XI-1965, Blancou (MNHN CG 1970-423).

(Irabellaben.)

NIGERIA. Abulschi: 1 specimen (BMNH 2.11.10.2). Asaba: alc. material (BMNH). 1 mile W of Bichi: 1 specimen (USNM 378782). (Old) Calabar: 1 specimen (BMNH 70.3.29.15). Dada: 1 specimen (USNM 402574). Ibadan: 2 specimens (BMNH 50.169/70); 1 ♀, alc., 4-IV-1966, J. M. (NHMI); 1 specimen (USNM 483195). Ife: 5 ♂♂, 2 ♀♀, 1 imm. ♀, 1975/1976, G. Oderhowho (NMHI); 4 ♂♂, 5 imm. ♂♂, 11 ♀♀, 3 imm. ♀♀, 13-VIII-1976, W. Bergmans (ZMA 18.414/15, 18.466/86). Ikang: 1 imm. ♂, alc., 27-VII-1976, W. Bergmans (ZMA 18.601). Ilobi: 1 specimen, D. R. Rosevear, field number 753/50 (NHMI). Ita: 2 ♂♂, 5 imm. ♂♂, 1 imm. ♀, 17/20-VII-1950, D. R. Rosevear, field numbers 822/50-826/50, 828/50, 830/50, 832/50 (NHMI). Jos: 1 imm. ♂, alc., 27-VI-1976, W. Bergmans (ZMA 18.413); 1 imm. ♂, 1 imm. ♀, alc., VII-1976, Gyamgzi (ZMA 18.575/76); 1 imm., head, alc., VII-1977, P. Beron (ZMA 20.613). Karaduwa: 1 specimen (USNM 402569). Maiduguru: 1 ♂, 1-VII-1948, D. R. Rosevear, field no. 301/48 (NHMI); 3 specimens (BMNH 50.166/68); 1 specimen (HZM). Molai Forest Reserve: 1 specimen (HZM). New Bussa: alc. material (BMNH). 7 miles W of Oyo: 1 specimen (USNM 377102). Panisau: 1 specimen (USNM 402570). 12 miles N of Sokoto: 2 specimens (USNM 378786; HZM). Tangaza: 1 specimen (USNM 402564). 15 miles W of Zaria: 1 specimen (USNM 378785). "N. Nigeria": 3 specimens (BMNH 11.3.24.1/3). "Nigeria": 1 specimen (BMNH 50.171). (Abuja, Akpaka Forest Reserve, Baissa, Basho, nr Benin, Borgu Game Reserve, Enugu Ngwo, Futuk, Gombi, Ijan-Ekiti, Ila, Ilorin, Iyin-Ekiti, Jalingo, Kabwir, Kainji Lake National Park, Kassa, Kontagora, Lagos, Lake Alau, Ntene, Nsukka, Oban, Obubra, Okitipupa, Onitsha, Oshogbo, nr Pandam, Panyam, Wukari, Yakoko, Yola.)

PAGULU. Pagulu: 1 ♀, alc., skull, 11-IX-1911, A. Schultze (SMF 6.356); 1 specimen, skull (BMNH 11.6.12.9); 1 specimen, alc., 1959, Cambridge Expedition (BMNH).

PEMBA. Pemba: 1 ♀, alc., VIII-1964, T. S. Jones (SMF).

(Fundo Island.)

PRINCIPE. Principe: 1 skull, Dohrn (ZMB 3467); 3 skulls (BMNH 4.1.1.2, 11.6.12.7/8).

(Bella Vista.)

RWANDA. Bugarura Island, Lake Kivu: 5 ♂♂, 1 ♀, alc., 27/29-VI-1953, Mission des Lacs K. E. A. (IRSN 10537/42). Mugarura Island, Lake Kivu: 3 ♂♂ (1 skull missing?), 4 ♀♀ (1 skin, 2 skulls missing?), 3 skulls, 25/29-III-1909, Von Stegman & Stein (ZMB).

(Butare, Gisenyi, Nyarutaru, Sifu.)

SÃO TOMÉ. Port São Tomé: 1 specimen (BMNH 11.6.12.10). "São Tomé": 3 specimens (BMNH 4.1.1.1, 07.27.1/2); alc. material, 1971, R. de Naurois (MNHN); 1 specimen (USNM 104534).

(Roça Monte Macaco, Roça Laura, Roça Nova Java.)

SENEGAL. Dakar: 1 specimen (USNM 380220). Fatick: 4 ♂♂, 11 ♀♀, 19-II-1934, F. C. Wonder (FMNH 42242, -45/46, 42700, -07/08, -10, -12). 10 km SE of St. Louis: 1 specimen (USNM 380225). 10 km W of Thies: 1 specimen (USNM 380228). Ziguinchor: 1 specimen (USNM 377815). "Senegal": 1 specimen, skull, skeleton, via Museum Vrolik (ZMA 723); 1 mounted specimen (RMNH); 2 specimens (BMNH 44.1.18.16/17); 1 specimen (IRSN 12.449).

(Rufisque, Sébikotane.)

SIERRA LEONE. Bo: 1 specimen, alc. (BMNH). Bonthe: 2 specimens (BMNH 53.601, 59.200). Freetown: 2 ♂♂, 1 ♀, 1974, E. Bragg (USNM 511987/89). Rokupr: 1 specimen (BMNH 53.35). 100 miles off the coast of Sierra Leone: 1 specimen (BMNH 10.10.21.1). "Sierra Leone": 1 imm. ♀, alc., 12-XII-1928, Hoffmann (ZIZM 42300); 4 specimens (BMNH 11.3.2, 50.1888/89, 53.36).

(Kissey, nr Njala, Yile Island.)

SOMALIA.

(Somaliland.)

SOUTH AFRICA.

(Barberspan, Barkly West, Bedford, ?Campbell, Douglas, Hondeklipbaai, Koegas, Little Namaqualand, Mazelsfontein, Middelburg, Namaqualand, Port Nolloth, Pretoria, Rustenburg, Steynsburg, Steunsdorp, Transvaal, Tylden, Vrijburg, Wildeharthoek.)

SUDAN. Bahr el Abiad: 1 skin, Th. von Heuglin (SMF 12.435). Bahr el Ghazal: 4 specimens (BMNH 8.7.13.1/2, 11.11.25.2/3). Lafoon: 13 specimens (6 in alc.), 23-XI-1949, H. Hoogstraal (FMNH 368861/66, 66535/37, -40/43). Khartoum: 2 specimens (BMNH 3.2.8.1/1a); 1 ♂, alc., 3/10-III-1984, A. Walen (ZMA 22.179). 4 miles N of Malakal: 1 ♂, 27-I-1961, H. Hoogstraal (FMNH 99251). Sennar: 1 mounted specimen (RMNH); 1 ♂, J. J. Prévost (IRSN 180); 1 specimen (BMNH 47.5.27.28/49.8.16.8). "Sudan": 1 ♂, 1 ♀, formaline, skulls, 1912, Hesselboger (SMF); 1 specimen (BMNH 70.1988).

(Aburi, between Abu Suqra and Buqrah, Abu Zabad, along the Blue Nile, Bor, Buram, Chor Loddo, Dilling, Duk, East Equatoria, Eleis, El Obeid, En Nahud, Jebel Beli vian nr Lado, ? Jebel Mara, Kadugli, Kordofan Province, Lado, Madâl, Rheika, Roseires, Shambat, Sîr-Land, Sobat River, Taufikia, Tonga, Tossari, Tuga, Wad Medani.)

TANZANIA. Amani: 2 specimens (BMNH 1937.8.18.3/4). Bagamoyo; 2 ♀♀, Gierra (MNHN CG 1881-290/91). Bukoba District: 1 specimen (BMNH 32.19.9.2). Dar es Salaam: 1 specimen, alc., H. C. Raven (USNM 236955). Kidode: 1 specimen, 30-V-1960, D. L. Harrison (SMF 19.473). Mahenge: 1 specimen (HZM). Mikindani: 1 specimen, alc., 30-III-1966, Th. Anderson (SMF 26.978). Nanguruwe: 1 specimen (HZM). Rutenganio: 1 specimen, alc., before 12-I-1900, Fülleborn (ZMB 54941). Weru Weru River: 2 specimens (BMNH 51.377/78). "Tanzania": 1 specimen (BMNH 64.1312).

(Nr Bihara-Mulo, nr Bombo, W side Lake Natron, nr Magiro, Mahaka, Moshi, nr Mpui, nr Newala, nr Oldeani, East Usambara Mountains).

TOGO. Dapango: 1 ♂, 2 ♀♀, alc., 9-V-1968, J. W. LeDuc (USNM 478561/63); 1 specimen (USNM 437596). Ezimé: 1 specimen (USNM 437598). Konda Tokpli: 4 ♂♂, 9 ♀♀, alc., ?29-XII-1963, P. Niort (MNHN). Palimé: 1 ♂, alc., Miss Duc (MNHN). "Togo": 1 skin, 4-III-1908, Richers (ZMB).

(Adjido, Agadji, Atakpamé, Binaparba, Fazao, Kamina, Korbongou, Lomé, Misahöhé, Namoundjoga, Niamtougou, Odjolo, Tchonou, Tététou, Togoville.)

UGANDA. Budongo Forest: 1 ♂, 2 imm. ♂♂, 1 ♀, 1 imm. ♀, 1/25-VII-1966, J. G. & A. Williams (LACM 51425/29). Buluganya: alc. material (BMNH). Entebbe: 1 ♂, alc., 6-I-1965 (SMF); 1 specimen (ROM 39041). Kampala: 1 ♂ (alc.), 1 ♀, 24-X/8-XII-1964 (SMF); 3 skins (AMNH 184224/26). Karevia: 1 ♀, skull 18-II-1891, Emin Pascha (ZMB 10236). Katalemura: 1 specimen (ROM 40098). Kiuulu: 1 specimen (ROM 38776). Makerere Hill: 1 specimen (ROM 45916); alc. material (BMNH). Malukhu: alc. material (BMNH).

(Bugala Island, Busoga, Bussu, Entebbe Peninsula, Fort Portal, nr Ibanda, Jinja, Kalinzu Forest, Kyembogo Farm, Limaibà, nr Masaka, Mbale, nr Mbarara, Mihunga, Namulusi Island, nr Rukungiri, Mount Ruwenzori.)

ZAIRE. Bomili: 1 ♀, 1 specimen, alc., 1-V-1908, Schubotz (ZMB 54596, -99). Goma: 1 ♀, alc., XII-1987, J. Schoorl (ZMA 24.139). Mouth of Congo: 1 specimen (BMNH 92.5.7.1). Isato: 1 imm. ♂, before 23-XII-1947, A. Henrion (IRSN 13110). Ituri Forest: 1 specimen

(BMNH 7.1.2.8). Kakonda: 1 specimen (AMNH 118868). Katana: 1 specimen (AMNH 180892). 10 km W of Kinshasa: 1 ♂, alc., V. Wallach, 15-IV-1980 (ZMA 21.145). Kisanga: 1 ♀, 1 ♂, 27-X-1948, J. de Wilde (IRSN 12778/79). Kivu: 1 ♀, 1 imm., 11-IX-1935, Mission Babault (MNHN CG 1939-198/99). Leopoldville: 1 specimen, ?1947, A. Henrion (IRSN 12271). Leopold II Lake: 2 specimens (BMNH 27.3.1.47/38). Nr Lupufa River: 1 specimen (BMNH 9.1.3.1). Lukolela: 1 specimen (AMNH 86879). Luluabourg: 3 specimens (BMNH 26.7.6.45/46, 26.11.1.23). Lwiro: 2 ♂♂, 1 imm. ♀, VIII-1955/11-V-1956, J. J. Laarman (RMNH 16356/57, -84). Between Mawambi and Avakubi: 1 specimen, alc. (BMNH). Mbole: 1 specimen (AMNH 119157). Ndama: 1 imm. ♀, 21-VII-1954, C. F. de Wilde (IRSN 17295). Ngerere Lepi: 3 ♂♂, 3 ♀♀, 5/6-I-1943, J. de Wilde (IRSN 12772/77). Tumba Lake: 1 specimen (AMNH 180894).

(Avakubi, Bambesi, Basongo, Berthe Island, Birende, Boendi, Bokalakala, Bokuma, Bokungu, Bolobo, Boma, Bukavu, Bukavu region, Buta, Butembo, Buyumbu, Buzibu, Dilolo, Djamba, Eala, Franz-Jozef Falls, Ibembo, Ikengo, Inkongo, Iyonda, Kabambaie, Kabobo Mountain, Kahungu, Karevia, Kasende, Keseki, Kinda, Kinshasa, Kitundu, Kitutu, Kitwabaluzi, Koteli, Kunungu, Kupelonge, Kwamouth, Lake Kivu, Luebo, Lufira River, Lusanga, Mahagi, Makumbi, Mamvu, Medje, Mondombe, Mongende, Mpe, Muezi Lupungu, Mugarura Island, Mukimbungu, Mukimvika, Mulungu region, Mushunguri, New Beni, Nyambasha, Oshwe, Panga, Rungu, Shabunda, Sierra Leone, Stanleyville, Tondu, Tshikapa, Umangi, Welle River above Bambili, Yangambi, Yokamba, Zambi.)

ZAMBIA. Balovale: 1 specimen (HZM). Kafue: 1 specimen (USNM 297469). Kasempa District: 1 specimen (HZM). "NW Rhodesia": 1 specimen, 1930, H. O. Reade (FMNH 36114).

(Abercorn, Chipata, Kasama, Kasempa, Lusaka, Munali, Ndola, Nyika National Park; 1230C2.)

ZANZIBAR. Grave: 4 specimens (BMNH 19.6.9.6, 20.6.10.4/6). Kebandiko Islands: 1 specimen, alc., skull (ZMB 58209). Tumbatu Island: 1 ♂, 2-VI-1922, E. Hoffman, and 1 ♂ without data (ZMB 93345/46). "Zanzibar": 1 ♂, 1 ♀, 7 specimens, alc., ≤ 1884, Révoil (MNHN CG 1884-515, -18, -22, -26, and not reg'd); 1 ♂, alc., VIII-1964, T. S. Jones (SMF); 5 specimens (BMNH 55.169/73).

(Bat Island.)

ZIMBABWE. Ndola: 2 specimens (BMNH 35.9.1.19/20). (Mashonaland).

Diagnosis: Generally as for the species; fal, gsl and other skull measurements averaging relatively large; width over M^1-M^1 relatively large; P^4, M^1, P_4, M_1 and M_2 relatively narrow. Measurement ranges and ratios from all over the subspecies' range:

fal	♂♂	109.8-130.5	(n = 44),
	♀♀	111.8-133.2	(n = 50);
gsl	♂♂	52.7- 58.6	(n = 46),
	♀♀	52.2- 58.2	(n = 48).
cbl	♂♂	50.7- 56.4	(n = 37),
	♀♀	50.5- 55.8	(n = 38);
rl	♂♂	19.6- 22.4	(n = 34),
	♀♀	19.2- 23.0	(n = 41);
pl	♂♂	28.6- 32.9	(n = 32),
	♀♀	28.0- 32.0	(n = 37);
zw	♂♂	30.5- 35.1	(n = 34),
	♀♀	30.1- 33.9	(n = 34);
C^1-M^2	♂♂	19.3- 22.5	(n = 32),
	♀♀	19.3- 22.8	(n = 35);
W	♂♂	212 -311	(n = 36),
	♀♀	183 -350	(n = 40).
rl	♂♂	35.3- 39.9% of gsl	(n = 30),
	♀♀	36.0- 39.8% of gsl	(n = 32);
pl	♂♂	52.6- 59.4% of gsl	(n = 28),
	♀♀	52.7- 57.4% of gsl	(n = 30);
zw	♂♂	55.7- 62.3% of gsl	(n = 30),
	♀♀	55.0- 62.1% of gsl	(n = 26).

On the African mainland, geographical variation in size is not apparent (but no large series have been examined in detail, except from West Africa). Feiler (1984) described a ♂ from São Tomé with a fall of 111 and a gsl of 52.5 and noted that it was smaller than mainland specimens. Eisentraut (1964) gave a gsl range for four ♂♂ from Fernando Poo of 55.8-58.7, which suggests that this island may harbour rather large-skulled specimens.

Distribution: Fig. 7.

Related species: The allopatric *Eidolon dupreanum* (Pollen, 1867) from Madagascar is evidently closely related but differs in average size and in characters of fur, skull and teeth (and also in its ecology). For details and for a discussion of its taxonomic position vis-à-vis *Eidolon helvum* the reader is referred to the remarks on page 159 and to the account of *Eidolon dupreanum*. The next nearest relatives would be the species of the genus *Rousettus*; these are all distinctly smaller, never yellowish, have their premaxillaries in contact, and lack an auditory meatus and they are also differing in their ecology.

Remarks

Taxonomy: *Pterocyon paleaceus* Peters is frequently dated as from 1861, when on 11 April the name was mentioned in a lecture, but this lecture was only published, as part of a meeting report, in 1862.

With regard to the measurement and weight ranges given in the diagnosis, it should be noted that some earlier authors have published other extremes for some of these. In the case of smaller minima, immature specimens have obviously been included by J. A. Allen *et al.* (1917), Rosevear (1965), Kock (1969) and Jones (1971). Andersen (1912) gave 62.2 as largest gsl and 23.8 as largest C^1-M^2 length; I have not found on what specimen(s) this was based. Jones (1971) gave as maximum W for a ♂ 328.2. Aniedu (1974) collected hundreds of specimens and noted their weights and, of most specimens, fals (in cm). Unfortunately it is not indicated how adultness was assessed; eliminating all specimens with a fal of 11 cm or less and counting only those of which both fal and W are given, the results are as follows: 104 ♂♂ with fals of 11.2-13.4 cm and weights of 197-325, and 112 ♀♀ with fals of 11.2-13.5 cm and weights of 180-340. (These high numbers of specimens from a single colony — that at Ife, Nigeria — call for the calculation of means and standard deviations, but fals are given either with or without decimals and many fals and weights are obviously rounded values.)

The weight range for ♀♀ in my diagnosis can be almost sharply divided into two ranges: all 16 specimens but one weighing less than 270 were not pregnant, and all 24 but one weighing more than 270 were. Aniedu (1974) listed as weights (but no fals) of 126 pregnant ♀♀ 175-365; only two of these were less than 260 (175 and 225, respectively) and the size of the embryo was not given. Omusun (1974) weighed 20 pregnant ♀♀ of the same colony, at Ife. They ranged from 249 (with an embryo of 14) to 357 (with one of 37.6).

Distribution and geographical variation: The overall distribution of *Eidolon helvum helvum* has been suggested to comprise all of sub-Saharan Africa, with the West and Central African forest blocks and a large part of central East Africa as "prime habitat" (DeFrees *et al.*, 1988) or, with inclusion of Central Ethiopia, as "possible 'home' range" (Kingdon, 1974), and the remaining part as migratory range (both sources). These are over-generalizations, which ignore that no records exist for very large parts of the area involved.

There are very few records from the broad belt of Sahel *Acacia* wooded grassland and deciduous bushland which borders the Sahara in the south, i.e. north of the Sudanian woodland zone (types 43 and 29a, respectively, in White, 1983). Exceptions are the records from the extreme northwest of Senegal (10 km southeast of St. Louis), from Irabellaben in the Aïr Mountains in Niger, perhaps near Lake Chad, and various records from Sudan and Ethiopia, where the Sudanian woodland belt is replaced by a mosaic of other vegetation types. The mentioned Senegalese record is reportedly from a river region and it is not far from the Sudanian woodland zone, which curves northward toward the west coast of West Africa. The occurrence of *Eidolon helvum* in the Aïr Mountains, surrounded by Northern Sahel semi-desert grassland and shrubland (type 54a in White, 1983) and even far north of the Sahel *Acacia* wooded grassland and deciduous bushland zone, is of greater interest. Bourbon *et al.* (1929) noted "grandes *Rousettes*" in the Aïr region and Dekeyser (1950) identified 3 specimens collected at Irabellaben as *Eidolon helvum.* He gave some measurements and it appears that his specimens fit the ranges of the typical subspecies. However, the population here is most probably isolated from the main distribution area, and a comparative analysis seems worthwhile. Happold (1984), analysing the small mammal fauna of the Sahara, mentioned *Eidolon helvum* as a migrant into semi-arid regions when fruits are available. But this does not seem the explanation for the species' presence in the Aïr Mountains, which are at about 400 km from the nearest known other collecting localities. I presume that they have been populated by *Eidolon* by chance, like any other island offering sufficiently favourable conditions and that the present population is resident. (I have insufficient data to assume a relict status for the Aïr population. Talbot (1980), describing the climate of the West African Sahel over the past 20,000 years, mentioned an increased humidity after 12,000 B.P. to 4000 B.P. — with an arid interlude from 8000 to 7000 B.P., and supposed that the Aïr region was included in the catchment of the Niger system active during periods of maximum humidity, especially between 12,000 and 8000 B.P. *Eidolon* may well have reached the region then, and stayed on.)

In the Lake Chad region the species may occur at Samia, a small island in a zone of Herbaceous swamp and aquatic vegetation (type 75 in White, 1983) - if this is the Zamia mentioned by Vielliard (1974). N'Djamena, to the south of Lake Chad, is in Edaphic grassland mosaic with communities of *Acacia* and broad-leaves trees (type 63 in White, 1983) but, of course, also with gardens and fruit trees.

In Sudan, most collecting localities are associated with the White Nile and the Blue Nile, which cross a number of different vegetation types but where the species is no doubt attracted and enabled to penetrate as far north as Khartoum by the riverine vegetation and the gardens and orchards of human settlements (compare Kock, 1969). Flower (1932) noted the species to be numerous at Khartoum and south along the Blue Nile. More western localities in Sudan are in "dry savanna" (Koopman, 1975); of these, El Obeid (and Bara north of it, from where sightings of fruit bats have been recorded) are in the zone of Sahel *Acacia* wooded grassland and deciduous bushland, but this zone is rather narrow here, and El Obeid is not far from the easternmost tongue of Sudanian woodland. Again, *Eidolon* is probably attracted by the fruit trees planted here, such as dates at Bara (Kock, 1969). In western Ethiopia *Eidolon* is known from a few localities in Ethiopian woodland (type 29b in White, 1983) and transitions between this and various grassland and wooded grassland types. The southern record in Ethiopia is from Bulcha (specimen USNM 462724; not seen by me), in the zone of East African evergreen and semi-evergreen bushland and thicket, on the border of Afromontane vegetation (types 38 and 19a respectively in White, 1983).

Another very large area from where virtually no *Eidolon* has been recorded is formed by northern and eastern Ethiopia, Djibouti, most of Somalia and the largest (northeastern) part of Kenya, covered with Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket and Somalia-Masai semi-desert grassland and shrubland (types 42 and 54b in White, 1983). The exception is Somalia from where Monticelli (1887) mentioned a specimen (as *Cynonycteris straminea*), but no precise locality. DeFrees *et al.* (1988), quoting this record from Andersen (1907b), interpreted it rather freely as "Somaliland (Somalia, Djibouti, southeastern Ethiopia)", suggesting therewith an immense but largely imaginary extension of the species' distribution. Scaramella (1975) mentioned north Somalia, where it seems he observed the species himself: "Controllato direttamente sia in Yemen che in Somalia." Dr. P. Agnelli (*in lit.*, 22-X-1990) kindly translated this phrase: "Checked both in Yemen and Somalia,", adding, however, that many regard Scaramello's publications as unreliable. I would therefore suggest that the record is in need of confirmation. (In 1975, D. Scaramella, L. F. Russo & F. P. D'Errico published "I mammiferi della Somalia", which does not include anv reference to *Eidolon helvum.*) The north of Somalia is covered with the mentioned vegetation type 54b but has a number of pockets of Mangrove (type 77 in White, 1983) along the coast, and *Eidolon* is most likely to be found there, apart from planted fruit trees and gardens. If the occurrence here is as isolated as it seems, the species may well be represented by the Arabian subspecies *sabaeum* instead of the typical form. Negative evidence for the species' occurrence in northern Somalia is offered by De Beaux

(1922; 1924) who did not list it for the former Italian Somalia. Its absence from the checklist of Somalian mammals by Funaioli *et al.*, 1966, is a further indication.

A third large region where the species is less widespread than has been suggested is central East Africa. Here it is found only around the lakes, in southern Uganda and Kenya and in northern Tanzania, along the Tanzanian coast, and at a few scattered localities in central and eastern Tanzania. Just as in the Horn of Africa, *Eidolon* apparently avoids here the large area of Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (type 42 in White, 1983), which covers most of Kenya and large parts of Tanzania, i.e. southeast of Lake Victoria and a broad belt from the northeast towards Lake Malawi. The species seeks out the forested areas at this belt's edges, such as mountain slopes, and coastal forests such as mangroves. No records are known to me from the entire northern part of Mozambique east of Lake Malawi. The vegetation here (Wetter and Drier Zambezian miombo woodlands; types 25 and 26 in White, 1983) would seem more favourable. West of the Rift, and south of the Central African rain forest block, most records are of individual specimens. In southeast Zaire and in the northern and central parts of Angola and Zambia *Eidolon* has been found mostly in the large areas of Wetter Zambezian miombo woodland. In Malawi, also covered with these woodlands and in the higher parts with Afromontane vegetation (type 19a in White, 1983), a colony of many thousands of specimens is known on the South Viphya Plateau. Ansell *et al.* (1988) emphasize that Malawi should nevertheless not be included in the species' prime habitat as known records have been during the rains (October-April) only; the mentioned colony is present from October to February. The main factor limiting *Eidolon*'s distribution in southern Africa is of course the Kalahari Desert (Kalahari *Acacia* wooded grassland and deciduous bushland, type 44 in White, 1983) and the adjoining Kalahari/Karoo-Namib transition (semi-desert vegetation type 56 in White, 1983). There are no records at all from Angola east of 16° E (except one on the Zairese border), from Namibia north of 25° S or east of 18° E, from all of Botswana (Smithers, 1971), from the northwestern part of Zimbabwe, from the southern half of Mozambique except for some coastal (Mangrove) records, and from large parts of South Africa. In southern Africa *Eidolon* is rarely recorded (Herselman *et al.*, 1985). In South Africa most records are from or from near High Grassveld (type 58 in White, 1983), some are from the Transition from Karoo shrubland to Highveld (type 57b in White, 1983), and some from the east-west zone of Bushy Karoo-Namib shrubland (type 51 in White, 1983) just south of the northern deserts. The most exceptional records are those from coastal northwest South Africa and from Namibia, where specimens have been collected not only in Bushy Karoo-Namib shrubland (Anas-Süd) but also in Succulent Karoo shrubland (Hondeklipbaai), Kalahari/Karoo-Namib transition (Tsumis), and in the Namib Desert (Port Nolloth and Gobabeb) (types 52, 56 and 74 in White, 1983). Some of the southern African records can possibly be linked to the occurrence of populations in Malawi or to the coastal distribution in Tanzania and Mozambique (where the species is bound to be found along the northern coast). Others are possibly of specimens which used riverine vegetation (e.g. *Ficus* spp.) to penetrate into otherwise dry and supposedly hostile land. Human settlements with their gardens and fruit trees and orchards offer further possibilities. But it is difficult to understand the finds in such distant sites in desert surroundings as in Namibia and just south of it, without knowing more precise details of the localities themselves and of their suitable connecting corridors to better inhabitable areas. The species is known to be capable of sustained flight but although it is numerous and the prime island colonizer among African fruit bats, and will certainly occasionally end up in strange places, there may be better explanations than mere random wandering for its excursions. Although to my knowledge no colonies have been reported from

South Africa, most records are from a few areas, e.g. near and west of Bloemfontein. It would seem worthwhile to know more about the origins and habits of the specimens in these areas.

I have tried to show that *Eidolon helvum* has a more intricate distribution pattern than has been suggested by some authors. This applies especially to the species' occurrence outside the West and Central African rain forest blocks. Inside these, there is no obvious preference. Coastal forests often harbour populations, and so do forests bordering rivers, but the species has also been found far from larger waters, in all the types of rain forest White (1983) has distinguished, from sea level to considerable altitudes. Kingdom (1974) mentioned sightings at 2000 m.

Eidolom helvum sabaeum (Andersen, 1907)

Pterocyon sabaeus Andersen, 1907b: 505 (type locality Lahej).
Eidolon sabaeum; Andersen, 1912: 15; Sanborn *et al.*, 1953 234; Rosevear, 1965: 68.
Eidolon stramineum; G. M. Allen, 1939b: 234.
Eidolon helvum sabaeum; Eisentraut, 1964: 532; Harrison, 1964: 44; Hayman *et al.*, 1971: 11; Scaramella, 1975: 375; Nader, 1985; DeFrees *et al.*, 1988: 1.
Eidolon ? sabaeum; Aellen, 1951: 46.
Eidolon helvum ? sabaeum; Heran, 1965.
Eidolon helvum; Harrison, 1972: 626.

Material examined

SAUDI ARABIA.
(Al Shugayri.)
YEMEN. Near Aden: 1 specimen (BMNH 99.11.6.2). Al Jilla: 1 specimen (BMNH 1937.10.18.1). Near Lahadasch: 1 specimen, alc., 9-XI-1892, O. Neumann (ZMB 6596). Lahej: 2 ♀♀, 10-V-1969, E. D. I. Jackson (HZM 22.5507, 23.5508); 6 specimens (BMNH 95.6.1.44/46, 99.3.14.1, 99.11.6.4/5); 1 ♂, 1 imm. ♂, alc. (BMNH). Sana'a: 3 ♂♂, alc. (BMNH). Ta'izz: 1 imm. ♂, 22-XII-1948, P. A. Clancey (HZM 1.818); 1 ♂, 23-I-1951, H. Hoogstraal (FMNH 78061). ("Haadge".)

Diagnosis: Generally as for the species; skull relatively small; on average, fal, gsl and other skull measurements smaller, rostrum slenderer, and P^4, P_4 and molars broader than in the typical subspecies. Measurement ranges and ratios mainly based on Harrison (1964):

fal ♂♂ 109 -124.7 (n = 9),
♀♀ 113.5-124.3 (n = 5);
gsl ♂♂ 52.5- 53.6 (n = 4),
♀♀ 50.4- 53.3 (n = 5);
cbl ♂♂ 49.9- 52.2 (n = 4),
♀♀ 48 - 51.3 (n = 5);
rl ♀♀ 19.6 (n = 1);
pl ♀♀ 28.5 (n = 1);
zw ♂♂ 30.3- 32.4 (n = 4),
♀♀ 29.6- 31.7 (n = 4);
C^1-M^2 ♂♂ 19.5- 20.2 (n = 3),
♀♀ 18.6- 19.5 (n = 3).
rl ♀♀ 38.2 % of gsl (n = 1);
pl ♀♀ 55.5 % of gsl (n = 1);
zw ♂♂ 56.5- 61.0% of gsl (n = 4),
♀♀ 56.2- 61.8% of gsl (n = 4).

Distribution: Fig. 7.

Related species: See under the typical subspecies.

Remarks

Taxonomy: Since G. M. Allen (1939a) classed *sabaeum* as a subspecies of *helvum*, only Harrison (1964) examined and compared a number of specimens and concluded to adopt Allen's view. Nader (1985), reporting on the first specimen from Saudi Arabia, also ranked *sabaeum* as a subspecies of *helvum*. I have not yet had an opportunity to compare a series of *sabaeum* to one of typical *helvum*, but from the data at my disposal and to judge from published data and measurements (see the synonymy; unfortunately, one source has not yet been located: Hayman, 1941, quoted by Harrison, 1964; I tend to agree with the authors mentioned.

Distribution and geographical variation: The known distribution of *sabaeum* is given with the localities mentioned in the section Material examined. It is quite restricted and geographical variation is therefore not to be expected. I have no vegetation map for Yemen but as in the drier parts of *Eidolon*'s African mainland range it will lead a more or less wandering life here and in adjoining Saudi

Arabia, in search of available food. This will also contribute to the supposed lack of geographical variation. If, as put forward in the Remarks on the nominate subspecies, the possible northern Somalian population(s) of *Eidolon helvum* should indeed be found to agree with *sabaeum* rather than *helvum*, the specimens there may show some differentiation from the Arabian ones.

Eidolon dupreanum (Pollen, 1867)

Pteropus dupréanus Pollen, 1867: 419, *in*: Schlegel, 1867 (type locality not mentioned); Schlegel, 1868a: 17, 1868b: 272.
Cynonycteris dupreana; Jentink, 1887: 264, 1888: 152.
Eidolon dupreanum; Andersen, 1912: 7; Dietz, 1916: 152; Grandidier *et al.*, 1932; Rand, 1932: 254; G. M. Allen, 1939a: 54; Dorst, 1947a: 307, 1947b: 82, 1948: 186; Decary, 1950: Eisentraut, 1963: 58; Didier, 1965: 337; Rosevear, 1965: 68.
Eidolon dupreana; Kaudern, 1915: 75.
Eidolon helvum dupreanum; Eisentraut, 1964: 532; Hayman *et al.*, 1971: 11; Koopman, 1975: 360; McHale, 1987: 114; DeFrees *et al.*, 1988: 2.
Eidolon helvum dubreanus; Eisentraut, 1973a: 33.
Eidolon helvum dupraneum; Wilson *et al.*, 1988: 168.
Eidolon helvum; Nicoll *et al.*, 1989.

Material examined

MADAGASCAR. Ampotaka: 1 specimen, Mission Zoologique Franco-Anglo-Américaine à Madagascar (= MZFAAM) (AMNH 100486); 1 ♂, 1 imm. ♂, 25-III-1930, MZFAAM (MNHN CG 1932-3397, -99); 2 specimens, MZFAAM (BMNH 35.1.8.185/86). Andrahaha (? Androbaka) Cave: 1 imm. ♂, 12 imm., cf. 15/19-III-1904, A. Voeltzkow (ZMB 187, 54432, 54783, and unregistered); 2 imm., skulls, 14-XI-1904, A. Voeltzkow (ZMB). Anorontsanga: 1 ♀, 1 imm. ♀, 10/12-I-1931, MZFAAM (MNHN CG 1932-3401/02); 1 specimen, MZFAAM (AMNH 100494); 3 specimens, MZFAAM (BMNH 35.1.8.182/84). Fianarantsoa: 1 specimen, alc., skull, III-1909, G. E. Mason (ZMB 58208). Itambelo: 1 imm. ♂, 1 specimen, 6-VI-1896, C. I. Forsyth Major (FMNH 5648; BMNH 97.9.1.31). Ivohibe (? Ivohihe): 2 ♂♂, 1 imm. ♀, skins, 1 imm. ♂, 14-VIII-1929, MZFAAM (MNHN CG 1932-3395/96, -98, 1932-3403); 1 specimen, MZFAAM (BMNH 35.1.8.181). Mongakatompo: 1 ♀, skin, 1 specimen, 24-V-1929, A. S. Rand (MNHN CG 1932-3400, -04). Namoroka: 1 ♂, skin, 7-III-1931, A. S. Rand & P. A. Du Mont (MNHN CG 1932-3394); 1 specimen, MZFAAM (AMNH 10051). Nossi-Bé: 1 ♀, 1 imm. ♂, mounted, skulls, 17-VIII-1865, D. C. van Dam & F. P. L. Pollen (♀: lectotype specimen of *Pteropus dupreanus* Pollen, 1867, RMNH 37230; ♂: paralectotype specimen of *Pteropus dupreanus* Pollen, 1867, RMNH 37229). Tsiandro: 1 specimen, MZFAAM (AMNH 100489). "Madagascar": 1 specimen, skeleton, 10-XII-1891, Malaurent (IRSN 179); 1 specimen, skin, skull inside, 1907 (RMNH); 1 specimen, alc., X-1938, R. Decary (MNHN); 2 specimens (BMNH 97.9.1.30, 35.1.8.187); 1 ♂, alc. (FMNH 74197); 1 imm. ♂, skin, Bartlett (ZMB 5208).

(Ambositra, Ambovombé, Analabe, Andrahomana, Ankarana Cave, Ankavandra, 18 miles SW of Fianarantsoa, nr Fort Dauphin, 30 km N of Ihosy, Lake Itasy, Lake Alaotra basin, Morondava, Palace Rock, 17 km S of Tananarive, Tananarive, Vinanitelo.)

Diagnosis: A large fruit bat, and, on average, the largest member of the genus; fal 122.9-133.1, gsl 55.8-59.3; braincase only moderately domed; skull foramina generally relatively small; light greyish brown fur; proclivous premaxillae; weakly diverging tooth rows; posterior margin of mandibulum at most very weakly concave below processus articularis; teeth relatively heavy; row of upper incisors sub-semicircular; premolars and molars with robust outer and inner longitudinal ridges and distinct median groove. Measurement ranges and ratios:

fal	♂♂	129.1-133.1	(n = 8),
	♀♀	122.9-129.2	(n = 4);
gsl	♂♂	57.0- 59.3	(n = 5),
	♀♀	55.0- 57.0	(n = 3);
cbl	♂♂	54.5- 57.5	(n = 4),
	♀♀	52.7- 55.0	(n = 3);
rl	♂♂	21.8- 23.3	(n = 5),
	♀♀	21.4	(n = 1);
pl	♂♂	30.0- 31.7	(n = 5),
	♀♀	29.3- 30.3	(n = 2);
zw	♂♂	32.4- 33.8	(n = 4),
	♀♀	31.6- 32.1	(n = 3);
C^1-M^2	♂♂	20.7- 22.2	(n = 5),
	♀♀	17.8- 20.0	(n = 2);
W	♂♂	245-340	(n = 2),
	♀♀	220-330	(n = 4).
rl	♂♂	38.0- 39.3% of gsl	(n = 5),
	♀♀	38.9 % of gsl	(n = 1);
pl	♂♂	52.6- 53.5% of gsl	(n = 4),
	♀♀	53.1- 53.3% of gsl	(n = 2);
zw	♂♂	54.6- 57.9% of gsl	(n = 4),
	♀♀	56.3- 57.5% of gsl	(n = 3).

Collectors' labels of ROM specimens mention field measurements of fals in 3 ♂♂ of 125.4-134.0 and in 4 ♀♀ 117.5-132.0. I have not examined these specimens (only seen their index cards) and do not know if they are all adult. The given weight ranges also apply to these specimens.

Distribution: Fig. 7.

Related species: *Eidolon helvum* is closely related but differs in its smaller average size, in characters of fur, skull and teeth (compare the account of that species), and in ecology. The nearest related other taxa would be *Rousettus* species. These are all smaller, darker in fur, with their premaxillaries in contact, and without an auditory meatus.

Remarks

Taxonomy: G. M. Allen (1939a) noted that F. P. L. Pollen is the author of this species, and not H. Schlegel & F. P. L. Pollen, and that it was published in 1867 and not in 1866, two facts which before and after his observation have been largely neglected (e.g. Andersen, 1912; DeFrees *et al.*, 1988). Schlegel (1867) explicitly mentioned Pollen as the author of this species ("*Pteropus dupréanus*, n. sp., Pollen.") when he inserted a short description in his list of the mammals collected by Pollen and D. C. van Dam in Madagascar. Schlegel's intention is confirmed when he wrote, in a later publication (1868a) "une (...) espèce (...) à laquelle mr. Pollen a conféré l'épithète *Dupreanus*." In this paper, Schlegel gave more details on the species, but stated explicitly that these were taken from a letter by Pollen. As for the year of publication, the first description was published in the volume of the Proceedings of the Zoological Society, London, for 1866, in 1867.

The type locality of the species was not mentioned, in that first description, and would thus be "Madagascar". Jentink (1887) mentioned "Nord-Ouest de Madagascar" as the origin of the two syntype specimens. This can be traced back to Schlegel (1868b) who listed them under that heading. (Schlegel's name is not attached to this list and it can be argued that Van Dam is the author; but as Schlegel had apparently identified all specimens, I assume that he also compiled this list.) However, when examining the syntype specimens, I found a note by the late Dr A. M. Husson, formerly curator of mammals at the RMNH, who had discovered that the female specimen is marked, on the underside of the board of the mounted skin, "Pollen et v. Dam, Nossi-bé, 17.8.1865". The other specimen, a subadult male, being of the same collecting date, can safely be accepted as having been collected together with the female. As the female is adult and well preserved, I select that specimen (RMNH 37320) as the lectotype, the subadult male therewith becoming paralectotype, of *Pteropus dupreanus* Pollen, 1867, and fix Nossi Bé as the type locality.

Andersen (1912) distinguished *dupreanum* from *helvum* on the basis of its (relatively) longer and slenderer cranial rostrum; slightly broader posterior premolars and molars; longer M^1 (conspicuously longer than P^4); comparatively larger P_1 and M_2; longer and more woolly, less adpressed and browner fur; and rather longer metacarpals and phalanges. He could not examine very many specimens. All his measurements except the maximum values for some metacarpals and phalanges, lower leg (with a question mark), foot, and width over C^1-C^1, fall within his ranges for *helvum*. However, all new measurements since Andersen indicate that *dupreanum* averages distinctly larger if measured by fal. Dietz (1916) added that *dupreanum* differs in the morphology of its mandibulum. Whereas in *helvum* the posterior margin between processus articularis and processus angularis shows a strong incurvation, it is practically straight in *dupreanum*; the processus angularis is rather pointed in *helvum* but rounded in *dupreanum*. Comparing both type specimens of *dupreanum* to some *helvum*, I found that in *dupreanum* the premaxillae are clearly more proclivous, with a distinct space between I^2 and C^1 when viewed from lateral, whereas in *helvum* there is hardly or no space. Another difference may be found in the form of the nasalia, which in *dupreanum* are posteriorly slightly convex, in lateral view, and in *helvum* rather linear. The cranial foramina in *dupreanum* are generally smaller in *helvum*; the lachrymal foramen is shallower and the infraorbital foramen is smaller, for instance. The foramen magnum is probably relatively wider than in *helvum*. The brain case in *dupreanum* is less domed, in lateral view, and posteriorly slightly more constricted, than in *helvum*. The teeth rows are less diverging in *dupreanum*. All its teeth are stronger and larger: the upper incisors are 1,5 to 2 times the bulk of those in *helvum*; C^1 is longer antero-posteriorly; P^1 is 1,5 to 2 times the bulk of P^1 in *helvum*; P^3 is not much larger but when seen from lateral, much broader towards its tip; P^4 is slightly shorter but broader, with a higher and thicker inner ridge showing a rudimental inner cusp anterior to the outer cusp, and with a more distinct longitudinal median groove (in *helvum* the two cusps are on level with one another); M^1 has a stronger inner ridge and a more distinct median groove; M^2 is smaller and wider than long, against longer than wide in *helvum*; the lower incisors form a semi-circle, against a more linear row in *helvum*, and are somewhat larger; C_1 is thicker, less curved; P_1 is 1,5 to 2 times the bulk of P_1 in helvum; P_3 is longer, antero-posteriorly, with slightly more of a basal shelf at the back, and in lateral distal view slightly lower but broader towards the tip; P_4 has a distinctly separate inner cusp, in position anterior to the outer cusp, and a rudiment of a second outer cusp, in position anterior to the main outer cusp (in *helvum* there is no inner cusp and no trace of a small anterior outer cusp); M_1 is slightly shorter and broader, with thicker inner and outer ridges; M_2 does not show much differentiation; M_3 is slightly weaker than in *helvum*.

According to labels on the specimens, Voeltzkow collected a series of *Eidolon dupreanum* in the Androhaha (or Androbaka) Cave on the Onilahy River, at 20 km downstream from Tongobory, on 19-III-1904. The late Dr. R. L. Peterson collected the species at various localities, in 1968. Nearly all his specimens were either shot in caves or from a cleft in a cliff (personal communication, X-1977). McHale (1987) identified fruit bats roosting in the entrance chamber of the Cave of Antsiroandoha in the Ankarana Special Reserve as *Eidolon*. This faculty of using a different niche than *Eidolon* on the mainland seems to point at an ecological differentiation which deserves further study.

The above-mentioned morphological differences and the possibly primitive (namely: *Rousettus*-like) roosting ecology together with the apparent geographical isolation lead me to regard *dupreanum* as a species. Further study of a larger material may yet lead to a different opinion.

Distribution and geographical variation: As appears from the map (fig. 7) *Eidolon dupreanum* appears to avoid the eastern coast of Madagascar except in the south. It has been collected in Malagasy dry deciduous forest and in a Mosaic of this forest with secondary grassland (types 7 and 22b in White, 1983), and in Malagasy moist montane forest and in the Cultivation and secondary grassland replacing this forest (types 5 and 18 in White, 1983). It is curious that no specimens appear to have been collected in the Malagasy lowland rain forest: wetter types (type 1b in White, 1983). Intraspecific variation within Madagascar does not seem likely although this has not been examined yet.

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N.B. Only those references have been included which have not already been given in the first and second parts of this series (Bergmans, 1988, 1989). One reference which has inadvertently been omitted from the bibliography in the second part, i.e. Palmeirim *et al.*, 1979, is listed below.

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