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TAXONOMY AND BIOGEOGRAPHY OF AFRICAN FRUIT BATS (MAMMALIA, MEGACHIROPTERA). 2. THE GENERA *MICROPTEROPUS* MATSCHIE, 1899, *EPOMOPS* GRAY, 1870, *HYPSIGNATHUS* H. ALLEN, 1861, *NANONYCTERIS* MATSCHIE, 1899, AND *PLEROTES* ANDERSEN, 1910

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ABSTRACT

The genera *Micropteropus* Matschie, 1899, *Epomops* Gray, 1870, *Hypsignathus* H. Allen, 1861, *Nanonycteris* Matschie, 1899 and *Plerotes* Andersen, 1910 and the species assigned to them are reviewed. All the currently recognized taxa are maintained except subspecific partitions in *Epomops franqueti* (Tomes, 1860). The known characters are reviewed and discussed, and new characters presented, and their possible taxonomical implications mentioned.

Of the skull characters traditionally used to distinguish *Micropteropus* from *Epomophorus* Bennett, 1836 relative rostrum length, relative zygomatic width and the form of the postdental palate are found to be rather in line with the tendencies in that genus. The palatal ridges in both species of *Micropteropus* are less different from those in *Epomophorus* than has generally been claimed but at the same time distinguish those species, as seem to do chromosome morphology (only known for *M. pusillus* (Peters, 1867)) and, probably, the anatomy of the vocalization organs. The original type specimen and locality of *M. pusillus*, disregarded since Andersen (1912) rejected them, are recognized. Within *Epomops*, a typical section is distinguished containing the forest species *franqueti* and *buettikoferi* (Matschie, 1899), while the woodland species *dobsonii* (Bocage, 1889) is considered atypical and possibly not congeneric. For the latter species a neotype is designated. In addition to earlier observed differences, the typical section of *Epomops* differs from *Epomophorus* in the morphology of its pterygoid wings. *Epomops franqueti strepitans* Andersen, 1910 is synonymized with the nominal subspecies as no satisfactory delimitation or transitional zone can be conceived. *E. buettikoferi* is maintained as a species on the basis of several sympatric occurrences with *E. franqueti* but the need for further research is recognized. Pterygoid wing morphology in *Epomops dobsonii* is as in *Epomophorus*, and its postdental palate exhibits transitional characters from typical *Epomops* toward *Epomophorus*; its palatal ridges are atypical and possibly derived from a pattern as in *Epomophorus*. *Hypsignathus monstrosus* H. Allen, 1861 resembles typical *Epomops* in its pterygoid wing morphology and palatal ridge pattern, and is less related to *E. dobsonii* than has been suggested. Some of the generic characters of *Nanonycteris* are rejected as neotenic traits. Several characters of *Nanonycteris veldkampii* (Jentink, 1888) suggest that *Epomops dobsonii* may be its nearest living relative rather than typical *Epomops*. In this small species females are (on average) larger than males in all measurements, which is the reverse of the situation in all larger epomophorines. Yet, males have relatively longer rostrums and larger zygomatic widths. *Plerotes* is confirmed as a genus combining primitive and specialized traits, but certain wing characters claimed to distinguish it are rejected and the need for wet preservation of future specimens is emphasized. *P. anchietae* (de Seabra, 1900) is known from nine specimens, most of which immature. A neotype is designated to replace the lost holotype. New cranial and fur characters are described.

INTRODUCTION

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

TAXONOMIC SECTION

Micropteropus Matschie, 1899

Micropteropus Matschie, 1899: 36, 57 (as subgenus of *Epomophorus* Bennett, 1836; type: *Epomophorus pusillus* Peters, 1867).

Epomophorus Bennett, 1836 (part); Miller, 1907: 65; Simpson, 1945: 54.

Micropteropus; Andersen, 1910: 99; Andersen, 1912: 554; Ellerman *et al.*, 1953: 49; Haiduk *et al.*, 1980; Haiduk *et al.*, 1981.

Matschie (1899) proposed *Micropteropus* as a subgenus of *Epomophorus* (after having decided first that all "Ohrbüschel-Flughunde" should be included in that genus) to accomodate *Epomophorus pusillus*, mainly because of the combination, in that species, of a relatively short snout and an aberrant soft palate. (The relative snout length, measured as the distance between the anterior corner of the eye and the tip of the nose compared to the breadth of the head at the corners of the mouth would be the same as in *Epomops* Gray, 1866.) Andersen (1910) argued that inclusion of *Epomops* and *Micropteropus* in *Epomophorus* would render the latter genus "decidedly the most heterogeneous genus of fruit-bats." He furthermore observed that, with *Epomops* and *Micropteropus* separated, "*Epomophorus* would stand as a perfectly homogeneous group, sharply defined against all other genera of the Epomophorine section, and in the shape of the postdental palate contrasting even with all other genera of Megachiroptera." In 1912 Andersen gave an extensive diagnosis of the genus *Micropteropus*. He emphasized the short and broad rostrum, the relatively broad palate between M^1-M^1 and the abrupt narrowing of the palate behind the zygomatic processes, the fact that the upper tooth row reaches backward nearly to the orbital cavity, the posteriorly depressed postdental palate, the prominent palation rim, and the peculiar soft palate. Some of these characters are obviously related to a shortening of the rostrum if compared to *Epomophorus*, with which only *Micropteropus* shares, in Andersen's view, a "distinctly depressed postdental palate and prominent palation rim." This latter observation contradicts his statement of 1910 that the shape of the postdental palate in *Epomophorus* is unique.

As discussed earlier (Bergmans, 1988), some of the skull characters used by Andersen to characterize *Epomophorus* are related to skull size and may therefore differ substantially between large and small species. This applies particularly to rostrum length, relative zygomatic width, and the measure of depression of the postdental palate. The relative skull measurements of *Micropteropus pusillus* (table 1) are remarkably well in line with those of *Epomophorus* (Bergmans, 1988, table 1). *Micropteropus pusillus* skulls are smaller than the smallest *Epomophorus* skulls (those of *E. minor* Dobson, 1880). Relative rostrum lengths and relative palatal lengths in *Micropteropus pusillus* are generally less and zygomatic widths and widths over M^1-M^1 more than in *E. minor*, which is according to what may be expected for an *Epomophorus* species smaller than *minor*.

Contrary to what Andersen wrote in 1912, the postdental palate in *Micropteropus pusillus* is not depressed; when viewed upside down, it even shows a gentle slope 'upward' toward the posterior margin, which itself is not a "prominent rim" (Andersen, 1912) but only slightly raised. This is quite different from most *Epomophorus* species. In the largest species, *E. gambianus* (Ogilby, 1835), the palate is extremely concave. Postdentally, the lateral and posterior palate margins are broad and nearly vertical. The resulting scooped shape of the postdental palate is stronger in ♂♂ than in ♀♀. In other *Epomophorus* species this shape is weaker as the skulls are smaller. It is still quite pronounced in *E. labiatus* (Temminck, 1837) but much less so in *E. minor*. In the relatively

Table 1. Relative skull measurements in *Micropteropus pusillus* (Peters, 1867) and *Micropteropus intermedius* Hayman, 1963; minimum and maximum values and number of measurements.

	Micropteropus pusillus		*Micropteropus intermedius*	
	♂♂	♀♀	♂	♀♀*
gsl	27.8-30.6 n = 57	26.8-31.0 n = 90	± 33.3 n = 1	32.0-33.3 n = 3
rl as % of gsl	32.3-35.9 n = 51	31.3-34.8 n = 73	± 34.2 n = 1	34.8-35.0 n = 2
pl as % of gsl	50.3-57.3 n = 49	51.9-55.5 n = 65	± 54.7 n = 1	54.0-56.2 n = 3
pl as % of M^1-M^1	150-177 n = 53	146-174 n = 66	± 177 n = 1	168-180 n = 3
zw as % of gsl	60.2-65.9 n = 42	58.1-67.3 n = 65	61.6 n = 1	62.2-62.7 n = 2
C^1-C^1 as % of gsl	19.4-22.3 n = 37	19.0-22.4 n = 53	19.8 n = 1	19.2-21.6 n = 3
M^1-M^1 as % of gsl	32.0-35.7 n = 50	31.5-36.5 n = 66	30.9 n = 1	30.9-32.9 n = 3

* Including measurements of the Banana/Netonna specimen published by Kock (1987).

large *E. wahlbergi* (Sundevall, 1846) the postdental palate is strongly hollow; the posterior margin is even more strongly vertical than in *E. gambianus*. In *E. grandis* (Sanborn, 1950) the postdental palate is only weakly depressed behind the 6th ridge, and its lateral and posterior margins are slightly curved 'upward'.

The other distinguishing character of *Micropteropus* is its typical palatal ridge pattern. Both Matschie (1899) and Andersen (1910; 1912) knew only one species of *Micropteropus*, i.e. *M. pusillus*. Matschie (1899) described its soft palate as bearing no transverse ridges but instead a longitudinal median groove, forked in front, with behind the fork on each side four closely crowded, more or less distinct elevations. Andersen (1912) described the palatum as having five thick and prominent ridges (and two or three inconspicuous thin and serrate ridges close together at the palation rim): first ridge at canines and postcanine diastemas, undivided, hastate, with the point directed backward, and second to fifth ridges divided by a deep groove extending along median line of palate, broadest in front and gradually narrowing posteriorly; thus divided in the middle the ridges form four thick triangular prominences along either border of the groove. Andersen (1912) saw a probable homology between this pattern and that in other epomophorine species, notably *Epomops dobsonii* (Bocage, 1889), which also has five ridges, corresponding in position with those in *M. pusillus*.

Examination of several series of *Micropteropus pusillus* palates *in situ*, preserved in alcohol, has led me to the conclusion that the palatal ridge pattern in that species is less different from that in *Epomophorus* than both Matschie (1899) and Andersen (1912) suggested. The first ridge in *Epomophorus* species is more pointed ("hastate") than Andersen's illustrations (1912: 516) show (compare fig. 2 in Bergmans, 1978). The essential number of ridges in *Micropteropus* — and I agree with Andersen that the elevations represent the halves of medially divided ridges — is six, not five. The separations between the ridges are not always very distinct and in most specimens the ridges 2 and 3 are merged and easily taken for a single ridge. In a number of specimens there is an indistinct

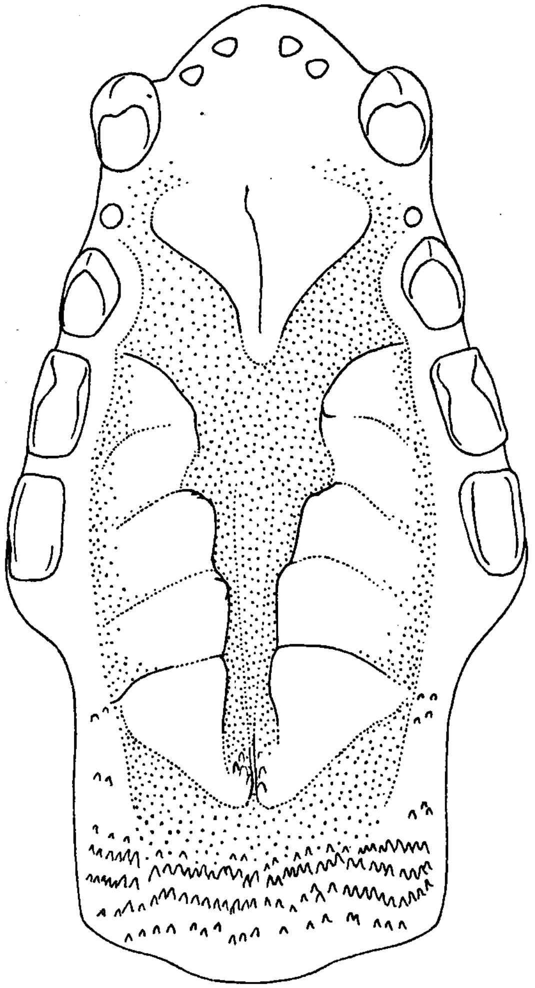

Fig. 1. The soft palate in a ♂ of *Micropteropus pusillus* (Peters, 1867) from Pointe Noire, Congo (ZMA 15.852). (Incidentally, this specimen has two minute P^1.)

separation, or a trace of one, and in some specimens it is a distinct furrow. The separation between ridges 3 and 4 may also be difficult to observe. That between 4 and 5 is usually clearly present and the groove between 5 and 6 is frequently stronger than the others. The sixth ridge is also often more elevated than the other ridges. In a few specimens all ridges except the pair 2 and 3 are separated by weak grooves. Fig. 1 depicts a Congolese specimen (♀, ZMA 15.852, from Pointe Noire, Congo) with a weak linear depression between 2 and 3, while there is no clear connection between 3 and 4 at the border of the median groove. In another specimen (♀, ZMA 15.881, from the same locality) the ridges 3 to 6 are mutually disconnected. The thin and serrate ridges at the palation rim are very irregular and may number up to four (see fig. 1).

In 1963, Hayman described *Micropterus intermedius*. To date, only four specimens of this species have been recorded: 1 ♂ and 3 ♀♀ (for details see the account of the species). The skull of the ♂ (measurements: tables 1 and 3) is slightly shorter than the smallest male skull in *Epomophorus minor* (see table 1 in Bergmans, 1988) and longer than the largest male skull in *Micropteropus pusillus*. It is broken and its measurements are approximations. According to expectation, its relative rostrum and palatal lengths are smaller than in *E. minor* but they are not larger than the maximum values for *M. pusillus*; the relative zygomatic width is larger than in *E. minor* and falls within the lower range of *M. pusillus*, and its relative width over M^1-M^1 is larger than in *E. minor* and smaller than in *M. pusillus*. In *M. intermedius* ♀♀ the skulls are as long as those of the smallest *E. minor* ♀♀, and longer than those of the largest *M. pusillus* ♀♀. Their relative rostrum and palatal lengths are smaller than those in *E. minor* ♀♀ and as large as or slightly more than those in *M. pusillus* ♀♀; their relative zygomatic widths are larger than in *E. minor* ♀♀ and fall within the variation range of *M. pusillus* ♀♀ and relative widths over M^1-M^1 are larger than in *E. minor* and smaller than or overlapping with the lower values for *M. pusillus* ♀♀.

The postdental palate in *M. intermedius* is not depressed but quite like that in *M. pusillus*; its posterior margin and the adjoining, posterior parts of its lateral margins are slightly raised. The soft palate in the type specimen of *M. intermedius* was described by Hayman (1963) as follows: palatal ridges five, the first undivided, the remaining four paired, widely separated anteriorly, converging posteriorly so that the last pair are almost in contact. But the soft palate in *intermedius* is essentially as in *pusillus*. Hayman's own illustration shows that the 'second' ridge actually consists of two fused ridges. The ridges 2/3 to 6 are furthermore not so sharply separated from each other as that drawing suggests. Fig. 4 shows the soft palate of the only other specimen in which it has been preserved. In this specimen, from Luluabourg, Zaire, the ridges 2 and 3 are fused but weak, with only a distinct elevation of 2, on the right side, and slightly stronger and weakly separated from each other on the left side. The ridges 4 to 6 are not the *Epomophorus*-like transverse ridges drawn by Hayman for the type specimen, but rather like the rectangular elevations in *M. pusillus*, most distinct at their antero-internal corner and the adjoining anterior and inner margins, and the combined inner margins at either side forming the border of the median palatal groove. (In both specimens, however, the soft palate has suffered from dehydration and it has become difficult to assess all the details of the original configuration. For further discussion see the account of the species.)

Whereas the skull characters do not warrant generic distinction of *Micropteropus* from *Epomophorus*, the peculiar form of the soft palate in both *pusillus* and *intermedius* suggests a common lineage of these species, and a deviation, at some stage, from the line which has led to modern *Epomophorus*, and seems to justify distinction. In the absence of other distinguishing characters, Matschie's originally proposed subgeneric rank would probably be appropriate. But the results of two different types of recent research imply further differences between the two taxa. Dulic *et al.* (1973) examined karyotypes of *Epomophorus anurus* Heuglin, 1864 (a synonym of *E. labiatus*; see Bergmans, 1988) and *E. wahlbergi.* Peterson *et al.* (1975) studied karyotypes of *E. gambianus crypturus* Peters, 1852 (reported as *E. crypturus* and *E. gambianus* (Ogilby, 1835)) and *E. wahlbergi* (reported under its own name and as *Epomops franqueti* (Tomes, 1860)). Haiduk *et al.* (1980; 1981) described the karyotype and studied G- and C-bands in, among other species, *Micropterapus pusillus.* In their first paper they concluded that chromosomally the genus *Micropteropus* appears to be similar to the genera *Epomops, Hypsignathus* H. Allen, 1861 and *Epomophorus*, but also that *Micropteropus* is chromosomally distinctive compared to *Epomops* and *Hypsignathus.* From the mentioned publications combined it can be concluded that *Micropteropus* differs also from *Epomophorus* in this respect. It has a diploid number (2N) of 35 in ♂♂ (♀♀ were not studied) and a fundamental number (FN) of 64 against 35 and 68 respectively in ♂♂ of *E. gambianus crypturus* and 36 and 68 in *E. wahlbergi* (both sexes); it has 13 pairs of metacentrics and submetacentrics and 3 pairs of subtelocentrics, against 13 and 4 in *E. g. crypturus* and 15 and 3 in *E. wahlbergi*, respectively; finally, in *Micropteropus* ♂♂ the Y chromosome has been involved in one or several rearrangements that resulted in the formation of two Y elements (Haiduk *et al.*, 1981) while there are no Y chromosomes in the ♂♂ of the two *Epomophorus* species examined. Baker (1970) emphasizes that chromosome morphology in bats is an independant character from cranial features and general gross anatomy, and that bat chromosomes seem to evolve at a slow rate when compared to the rate of change in gross anatomical features "on which present phylogeny is constructed". In his opinion, similarities or divergence in karyotypes should therefore receive serious consideration as indicators of degrees of relationship. Although Baker (1970) appears to have studied Microchiroptera and only includes some literature data for Megachiroptera, his statement that cranial features and general gross anatomy in bats are strongly affected by adaptation to different feeding niches and the implication that these characters evolve at a relatively fast rate, may certainly be relevant in studies of Megachiroptera.

Zeller (1984) examined the anatomy of the vocalization organs in *Epomophorus, Epomops* and *Hypsignathus.* These genera possess an enlarged larynx, especially in the males, related to their habit of emitting loud calls during the mating season. These calls are well-known to people living in areas where these genera occur. Notwithstanding its abundance in many areas such calls have been reported for *Micropterapus pusillus* only once: "The males make a shrill ringing note resembling that of other epomophorines" (Kingdon, 1974: 160). Kingdon did not state where and how he assessed that this species was responsible for the observed sound. A preliminary investigation of the anatomy of a male indicates that its larynx is enlarged, possibly to the extent described by Zeller (1984) for *Epomophorus*.

Because of the apparent chromosomal differences and pending more definite results of anatomical research I think that generic rank for *Micropteropus* remains justified.

Micropteropus pusillus (Peters, 1867)

Epomophorus schoënsis (not of (Rüppell, 1842)); Tomes, 1860: 56, 1861: Pl. I figs 4-4a.

Epomophorus pusillus Peters, 1867: 870 (type locality: Yoruba).

Epomophorus (*Micropteropus*) *pusillus*; Matschie, 1899: 57; Rosevear, 1953: 82.

Micropteropus pusillus; Andersen, 1912: 557; J. A. Allen *et al.*, 1917: 421; Lang *et al.*, 1917b: 510; De Beaux, 1922b: 365; Cabrera *et al.*, 1926: 593; Monard, 1939: 54; Sanderson, 1940; Hill *et al.*, 1941: 35; Schouteden, 1944: 106; Malbrant *et al.*, 1949: 84; Sanborn, 1950: 54; Swynnerton *et al.*, 1951: 288; Ellerman *et al.*, 1953: 49; Hayman, 1954: 280; Aellen, 1952: 38; Aellen, 1956: 24; Eisentraut, 1956b: 513, 1957b: 624; Verschuren, 1957: 210; Booth, 1959: 28; Harrison, 1961: 287; Eisentraut, 1963: 71; Hayman, 1963: 97; Didier, 1965: 340; Heim de Balsac, 1965: 314; Koopman, 1965: 3; Kuhn, 1965: 325; Rosevear, 1965: 108; Blackwell, 1966: 247; Brosset, 1966a: 365; Hayman *et al.*, 1966: 27; Orshoven *et al.*, 1966: 187; De Vree *et al.*, 1969: 202; Kock, 1969: 24; De Vree *et al.*, 1970: 42; De Vree, 1971: 37; De Vree *et al.*, 1971: 160; Gallagher *et al.*, 1977: 25; Hayman *et al.*, 1971: 9; Hill *et al.*, 1971: 30; Jones, 1971: 128; Dorst *et al.*, 1972: 394; Jones, 1972; Eisentraut, 1973: 358; Ansell, 1974: 7; Ayensu, 1974; Bergmans *et al.*, 1974: 32; Kingdon, 1974: 159; Largen *et al.*, 1974: 228; Vielliard, 1974: 978; Koopman, 1975: 365; Ansell, 1978: 17; Happold *et al.*, 1978: 76; Koopman *et al.*, 1978: 2; Bergmans, 1979: 175; Haiduk *et al.*, 1980; Robbins, 1980: 85; Haiduk *et al.*, 1981; Kock, 1981: 331; Hutterer *et al.*, 1982: 124; Marshall *et al.*, 1982; Schlitter *et al.*, 1982: 138; Anciaux, 1983: 31; Aggundey *et al.*, 1984: 124 (in part: the record from Meru River, cited from G. M. Allen. 1911. refers to *Epomophorus minor* Dobson, 1880); Koch-Weser, 1984: 264; D. W. Thomas, 1984: 485; D. W. Thomas *et al.*, 1984; Koopman, 1986: 10; Happold, 1987: 45; Hickey *et al.*, 1987; Kock, 1987: 220, 222; Crawford-Cabral, 1989: 13.

Micropterus (sic) *pusillus*; Leleup, 1956: 76.

Nanonycteris veldkampi (not of (Jentink, 1888)); Vielliard, 1974: 977.

Material examined

(Due to time constraints, in a number of cases only the identity of the specimen, or of one of a series, has been assessed, and its/their locality noted. Thus, where data are not mentioned, they are not necessarily lacking.)

ANGOLA. Catete: 3 ♀♀, alc., 21/22-XI-1953, purchased (NMBA 5826/28). Canhoca: 2 skulls (BMNH 4.4.9.9/.10). Chinchoxo: 1 specimen, alc., Falkenstein (ZMB 4802). Dundo: 3 ♀♀, alc., VII-1948/1949, A. de B. Machado (FMNH 66449/51). Malange: 1 specimen, alc., skull, Von Mechow (ZMB 5851). Mukozo: 1 ♂, 3-VI-1953, Hellmich (ZSM 1954/41). Pungo Andongo: 1 specimen, alc., skull not seen, Falkenstein (ZMB 5221). (Dande, Galanga, Loanda).

BENIN. Agouagou: 1 ♀, alc., 12-VIII-1910, Bouet (MNHN 1911-890). "Dahomey": 1 ♂, alc., 24-IV-1912, Waterlot (MNHN 1912-446).

(Bimbereke, Diho, Guéné, Kouandé, Parakou, Segbana.)

BURKINA FASO.

(Djipologo, Koutoura, Nobéré, Po National Park.)

BURUNDI.

(Resha.)

CAMEROUN. 5 km SW of Eseka: 1 specimen (AMNH 236277). Koutaba: 1 ♂, alc., 20-V-1973, J. Prévost (MNHN 1979-242). Kribi: 2 ♂♂, alc., 17-IV-1973, J. Prévost (MNHN 1979-232/33). Lolabé: 1 imm. ♂, 1 imm. ♀, alc., 19-III-1987, A. P. M. van der Zon (ZMA 23.518/19). Mboakon: 1 specimen (AMNH 236278). Mount Manengouba: 1 ♀, alc., 30-XI-1973, J. Prévost (MNHN 1979-221). 14 km S of Ngaoundere: 1 specimen (AMNH 241019). Nkolbisson: 1 ♀, alc., 5-V-1973, J. Prévost (MNHN 1979-239). Ntui: 2 ♂♂, 2 ♀♀, alc., 11-XI-1973, J. Prévost (MNHN 1979-214/17). 55 km NE of Obala: 1 specimen (AMNH 241020). Obala: 1 ♂, 1 specimen, alc., 10-IX-1967, M. Germaine & H. Garcin (MNHN). Tibati: 1 skull (BMNH 23.1.22.8). Yaoundé: 10 ♂♂, 7 ♀♀, alc., 14-II-1973/28-I-1974, J. Prévost (MNHN 1979-225/26, -31, -34, -44/45, -49/51, -53, -55, -57/58, -60, -63, -68, -73). 5 km S of Yoko: 2 ♂♂, alc., 19-I-1974, J. Prévost (MNHN 1979-275/76). 15 km S of Yoko: 1 ♂, 22-I-1974, J. Prévost (MNHN 1979-284).

(2 km E of Bafut, 20 km N of Banyo, 32 km E of Banyo, 30 km ESE of Banyo, Bota, Buea, 10 miles N of Buea: CDD Banana Plantation, Ekona, Garoua, Great Soppo, Isobi, Kribi, Maloko River 5 km N of Ntui, 6 km N of Mayo Darlé, 15 km SSE of Mbouda, Meania, Meng River 6 km NW of Tibati, Metchum River 10 km E of Gwofong, S. Minim, Mpundu-Muyuka 35 miles NE of Buea, Nyasoso, 12 km S/4 km E of Obala, 55 km NE of Obala, Small Soppo, Tinta Valley, Tombel, Victoria, Ydé.)

CENTRAL AFRICAN REPUBLIC. Bangassou: 2 ♂♂, 1 ♀, 2 imm. ♀♀, 12/28-XII-1974, L. W. Robbins (CNHM 40985/89). Bozoum: 1 specimen (AMNH 88438). Kojali River: 1 ♀, Tessmann (ZMB 31942). La Landjia: 1 ♂, XI-1959, H. Gillet (MNHN 1966-172). Probably La Maboké: 1 specimen, 14-V-1966, R. Pujol & P. Teocchi (MNHN). M'Baïki: 1 ♀, 2 ♂♂, 10/12-XII-1974, L. W. Robbins (CNHM 40982/84).

(Goumba-Koumbala confluence, Gounda Camp, Koumbala Camp, Zemio.)

CHAD.

(Sarh.)

CONGO. Material from Bouloungi, Brazzaville, Dimonika, Djambala, Grand Bois, Ile M'Bamou, Lekana, Loandjili, Makaba, Meya, Plateau Konkouya, Pointe Noire, Sibiti. For details see Bergmans, 1979.

EQUATORIAL GUINEA. Ikunde: 6 specimens, alc., skulls of 3, III-1970, F. G. Celo (SMF 37653/58).

ETHIOPIA. Abore: 1 imm. ♂, 6-VI-1976, G. Nikolaus (SMNS 29841). 10 km from Agora: 1 ♀, alc., 14-VI-1968, J. Prévost (MNHN 04049). Didessa: 1 ♂, 1 ♀, 2 imm., alc., 1/2-X-1971, J. Prévost (MNHN 03329/30, -30, -34). Donkam River/Lake Tana: 1 skull (BMNH 28.1.11.6). Donkam River/40 miles S of Lake Tana: 1 skull (BMNH 28.1.11.7). Gambela: 3 ♂♂, 6 ♀♀, 1 specimen, skins and alc., skulls of 3, 22-VI/28-VII-1972, G. Nikolaus (MAKB 73.77/86). 15 km E of Gambela: 1 ♀, 19-II-1976, G. Nikolaus (SMNS 29840). 60 km E of Gambela: 3 ♂♂, 15-II-1976, G. Nikolaus (SMNS 29816/17, -39). Sirba: 2 specimens, alc., skulls (BMNH 70.400/01).

(Bulcha, Bulcha Forest, Didessa River Bridge, Doki River Bridge, Kelam, Tola River.)

GABON. Booué: 2 skulls (BMNH 58.310/11). Franceville: 1 specimen, alc., Schwebish-Thollon (MNHN 1884-582). Kango: 1 specimen, 17-XI-1943, R. Malbrant & A. Maclatchy (AMNH 120265); 2 ♂♂, 2 imm., skins, XII-1943, R. Malbrant & A. Maclatchy (MNHN 1947-212/15). Lambarené: 1 specimen, alc. (MNHN 1896-3435).

GAMBIA. Bathurst: 1 specimen (BMNH 89.3.2.1). 8 miles W of Bathurst: 1 specimen (USNM 77562).

(Walikunda.)

GHANA. Aburi: 1 specimen (BMNH 20.10.28.2). 9 miles NE of Accra: 1 specimen (AMNH 241021). Achimota: 2 specimens (BMNH 65.741; USNM 411634). Aiyikuna: 1 specimen (USNM 411654). Amedzofe: 1 specimen (USNM 411631). Banda: 3 skulls (BMNH 50.1504/06). Bangwon: 1 specimen (USNM 414766). Bator: 1 specimen (USNM 411624). 15 km S of Bimbilla: 1 specimen (AMNH 239383). Chiriso: 1 specimen (USNM 414060). Gambaga: 2 specimens (BMNH 98.10.24.1; USNM 424785). Ghana: 1 imm. ♀ alc., skull, 10-VI-1893, Kurtz (SMNS). Klein Popo: 1 specimen, alc., Linnaea (ZMB 10003). Kumasi: 2 specimens (BMNH 29.5.29.2/.3). Legon: series of specimens (USNM 411674...). Legon Folly: 1 skull (BMNH 65.742). Leklebi Agbesi: 1 specimen (USNM 424796). Mole Game Park: 2 specimens, 11/12-VII-1974, A. N. McWilliam (AMNH 237406/07). Oda: 1 specimen (USNM 439924). Odomi Jongo: 1 specimen (USNM 424766). Parisi: 1 specimen (USNM 414761). Sakpa: 1 specimen (USNM 414767). Sogakofe: 1 skull (BMNH 58.661). Subinja: 1 specimen (USNM 414760). Wulasi: 1 specimen (USNM 424765). Yabraso: 1 specimen (USNM 424776).

(Accra, 60 miles W of Aflao, Akosombo, 1 mile N of Akwamufe, nr Damongo, 15 miles NW of Damongo, Ejura, 7 miles NE of Kade, Larteh Junction, Lovi Camp, Mampong, Nungua, Shai Hills Game Reserve, Tashi.) GUINEA. Kankasili: 18 ♂♀, 35 ♀♀, 15-XI-1966/25-II-1967, J. van Orshoven (ZMA 10.741/42, -63, -65, -67, -69, -71/75, -78, -80/87, -90/94, -96, -98/99; 10.800/02, 04/06, -09, -13, -15/18, -23, -25, -27, -39/40, -42, 47/51, -54, -58). Kouroussa: 1 ♂, 1 imm. ♀, alc., 1903, H. Pobeguin (MNHN 1905-457).

(Boké.)

GUINEA-BISSAU. Bissau: 1 ♂, 23-XII-1926, E. Hintz (ZMB 42517).

(Madiné Boé.)

IVORY COAST. Material from Konankoffikro and Lamto (for details see Bergmans *et al.*, 1974). Bouaké: 1 ♀, formalin, 5-II-1965, D. Parelius (FMNH 99032). Bouna: 1 specimen (USNM 467895). Duékoué: 1 imm. ♂, alc., ORSTOM Adiopodoumé (ZMA 16.719). Fetekro: 1 specimen (USNM 467908). Japo Sud; 1 specimen (USNM 429898). Korhogo: 1 ♀, 28-VIII-1968, J. M. Ailanjian (LACM 51413). Lamto: 1 specimen, alc. (BMNH). Tulé: 1 specimen (USNM 454433).

(Adiopodoumé, Man, Wango-Fitini.)

KENYA. 20 miles SW of Barberton Pool: 1 specimen (USNM 350816).

(South Kavirondo.)

LIBERIA. Grand Bassa: 1 skull (BMNH 8.7.27.2). Nanna Kru: 2 skulls (BMNH 11.11.3.4/.5); 1 specimen, alc. (BMNH).

(Grand Bassa, Grand Cape Mount, Little Cola, Robertsport.)

MALI.

(Bamako.)

NIGERIA. Abeokuta: 2 skulls (BMNH). Afon: 1 specimen (USNM 402528). Asaba: 1 skull (BMNH 92.6.22.1). Bacita: 3 ♂♂, 12 ♀♀, 6 imm. ♀♀, 23-XI-1973/7-I-1974, G. F. Mees (RMNH 23625/40, -46/50). Felele: 1 specimen (USNM 402541). Ibadan: 1 ♀, 12-I-1948, D. R. Rosevear, field number 255/48 (NHMI); 2 ♂♂, 2 ♀♀, 8 imm. ♀♀, 12/16-VI-1965, J. I. Menzies (FMNH 99063/74); 1 imm. ♀, 14-III-1972, D. C. D. Happold, field number B1505 (ZMI); 16 ♂♂, 1 imm. ♂, 38 ♀♀, alc., no collecting dates or collectors (ZMI 49/51, 53/57, 60, 64/65, 69, 71/72, 74, 76/77, 81, 83, 85, 91, 93/96, 99, 99, 100, 102/15, 118, 121/23, 134/35, 139, 141, 143, 148, 156/58, 160, 162); 1 ♀, 2 imm. ♂♂, 5/7-VIII-1976, W. Bergmans (ZMA 19.057/59); 1 specimen (AMNH 204296); 5 skulls (BMNH 61.76/80). Ife: 2 imm. ♂♂, 17/22-VIII-1976, W. Bergmans (ZMA 19.069/70). Igbo-Ora: 1 specimen (USNM 402499). Jos: 1 imm. ♂, 25-VI-1976, W. Bergmans (ZMA 19.034); 8 ♂♂, 5 imm. ♂♂, 29 ♀♀, 15 imm. ♀♀, alc., 13 skulls extracted, 18-IX-1976/VII-1977, P. Beron (ZMA 19.099/132, -36/45, 20.578/90). Kudu: 1 specimen (USNM 402527). Kware: 1 specimen (USNM 402511). 'Lagos': 1 ♀, 1 imm. ♂, alc., skulls, purchased from Gerrard (ZMB 4338, 10046); 1 specimen, alc., skull, purchased (BMNH 72.10.24.6). Makurdi: 1 ♀, alc., 1976/1977, P. Beron (ZMA 19.135). Mkar: 2 imm. ♂♂, 12/13-VII-1976, W. Bergmans (ZMA 19.055/56). Near Oli River: 2 ♀♀, alc., 19-II-1971, D. C. D. Happold, field numbers B1310/11 (ZMUI). Pandam Wildlife Park: 3 ♂♂, 2 imm. ♂♂, 7 ♀♀, 8 imm. ♀♀, 2/7-VII-1976, W. Bergmans (ZMA 19.035/54). Tsanchaga: 1 specimen (USNM 402514). Upper Ogun Ranch: 1 specimen (USNM 402512). Yoruba: 1 imm. ♀, 1862, Mann (SMNS 934); 1 imm. ♀, alc., skull, in or before 1867, Krauss (ZMB 3438; the holotype specimen of *Epomophorus pusillus* Peters, 1867; see under Remarks).

(Agodi, Bida, Egbe, Enugu, Enugu Ridge, Igbetti, Ikoyi, Kaduna, Kagoro, Kainji Lake National Park, Mokwa, New Bussa, Okon, Olokomeji Forest Reserve, Panshanu, Samaru, Shaffini, Yankari, Zaria.)

SENEGAL.

(Bady, Diattacounda.)

SIERRA LEONE.

(Bonthe, Freetown, nr Kabala, Lumley Village, Lunsar, Makeni, Musaia.)

SUDAN. Western foothills of Boma Mountains: 1 ♂, 1 imm. ♂, 1 ♀, 3 imm. ♀♀, 19/24-II-1979, G. Nikolaus (SMNS 29832/35, -51/52). 25 km N of Boro River: 1 ♀, 3 imm. ♀♀, some: alc., 31-III-1979, G. Nikolaus (SMNS 29836/38, -53). Gilo: 1 ♂, 2 ♀♀, 3 imm. ♀♀, some: alc., 4-I/27-II-1978, G. Nikolaus (SMNS 29821/23, -31, -44, -46). Juba: 1 ♂, alc., 13-I-1977, G. Nikolaus (SMNS 29818). Kajiko North: 2 ♂♂, 1 imm. ♂, alc., 16/17-VII-1978, G. Nikolaus (SMNS 29824/26). Kajiko South: 1 imm. ♀, 20-VII-1978, G. Nikolaus (SMNS 29847). 10 km W of Kajo Kaji: 4 ♂♂, 1 imm. ♂, 1 ♀, some: alc., 25-VII-1978, G. Nikolaus (SMNS 29827/30, -48/49). Maridi: 1 ♀, 1 imm. ♀, alc., 7-II-1977, G. Nikolaus (SMNS 29819/20). Raffile: 1 ♀, 13-IX-1978, G. Nikolaus (SMNS 29850). 45 km N of Tambura: 1 ♂, 1 imm. ♂ (alc.), 2-II-1977, G. Nikolaus (SMNS 29842/43). Tapari River: 1 imm. ♀, 15-II-1978, G. Nikolaus (SMNS 29854).

(Agok, Bahr el Ghazal, Bongo, Imurok, Jebel Kau, Kagelu, Kan, Katire, Mbili, Moimoi, Mundri, Nzara, Okaru, Palwar, Rumbek, Torit, Tossari, Wanalerel, Wau, Yambio.)

TANZANIA. Ngoroine: 1 imm. ♀, 1 imm., alc., skull of one, 28-I/II-1894, O. Neumann (ZMB 10052/53).

TOGO. Bismarckburg: 1 ♀, alc., skull, Büttner (ZMB 6756); 1 imm. ♂, alc., Conradt (ZMB 10051). Kete: 1 imm. ♂, alc., Zech (ZMB 10054). Misahöhe: 1 specimen, alc., Baumann (ZMB 10050).

(Adina, Adjido, Agadji, Agomé-Tomegbé, Ahoué-houé, Aledjo, Atakpamé, Apeyemé, Azafi, Binaparba, Borgou, Dedomé, Dzjogbégan, Ebeva, Edifou, Evou, Ezimé, Fazao, Kamina, Kodegbé, Kolokopé, Koutoukpa, Lomnava, Niamtougou, Nuatja, Odjolo, Ounabé, Pagala, Paio, Plateau Akposso, Sansanné-Mango, Tchonou, Témedja, Tététou, Togoville.)

UGANDA. Budongo Forest: 2 ♂♂, 1 imm. ♂, 6 ♀♀, 5 imm. ♀♀, 16-VI/4-VII-1966, J. G. & A. Williams (LACM 51409/12, -15/17, -19/24, 54148); 1 imm. ♀, 9-V-1970, I. Bampton (LACM 36119). (Nr) Entebbe: 2 specimens (FMNH 67860/61). Gulu: 1 specimen (USNM 351199). Kiriamo: 1 skull (BMNH 90.6.8.14). Ntandi: 1 imm. 0, 7-XI-1968, A. Williams (LACM 51414).

(Nr Arua, Bugabo, Bugala Island, Bukasa Island, Bulugeni, Busoga, Bussu, Katalemura, Mbale, 10 miles E of Moyo, Namubali, Namulere, Soroti, Zika.)

ZAIRE. Gangala na Bodio: 1 imm. ♀, alc., 25-V-1948, Mission Hediger-Verschuren (IRSN 11660). Kaswabilenga: 2 ♂♂, 3 imm. ♀♀, 5/7-X-1957, G. F. de Witte (IRSN 10679/83). Kinkole: 1 ♀, 2 imm. ♀♀, alc., 15-VIII-1980, via V. Wallach (ZMA 21.146/48). Luluabourg: 2 skulls (BMNH 26.7.6.60/61). Mboga: 6 skulls (BMNH 30.11.11.70/75). N'soro: 1 skull (BMNH 7.7.8.29).

Parc National de Garamba: 1 ♂, 1 ♀, 1 imm. ♀, alc., 16-XI-1951 and 22-V-1952, Mission de Saeger (IRSN 13521/22).

(Banana/Netonna, Beno, Benza Masola, Boga, Bokalakala, Bokoro, Congo da Lemba, Congo-Nil/Aka, Dedegwa River, Gandi Sunde, Irumu, Kabinda, Kinkole-Pêcheur, Kinshasa, Kwamouth, Kwango, Lubondai-Tshimbulu, Lukolela, Lusanga, Mahagi-Ogondjo, Makengo, Moanda, Mukimbungu, Niangara, Vista, Yema, Zambi, Zongo.)

ZAMBIA.

(Jimbe Stream, Salujinga.)

Diagnosis: The smallest species of the genus, with a fal less than 56, a gsl of 31.0 or less, a C^1-M^1 length of 8.0-10.1, and a soft palate with six thick and prominent ridges, the first whole and the others medially divided, the halves of second and third often mutually united without a clear trace of a separating groove, and the halves of fourth to sixth ridges more or less united to that of the third and to each other, with the groove separating five and six usually most distinct.

Measurement ranges and ratios taken from all over the species range:

fal ♂♂ 46.4-54.7 (n = 149),
♀♀ 49.5-55.7 (n = 201);
gsl ♂♂ 27.8-30.6 (n = 57),
♀♀ 26.8-31.0 (n = 90);
cbl ♂♂ 26.8-29.8 (n = 48),

Table 2. Selected measurements of *Micropteropus pusillus* (Peters, 1867) per country.

		fal	gsl	cbl	rl	zw	C^1-M^1	M^1-M^1	W	fal	gsl	cbl	rl	zw	C^1-M^1	M^1-M^1	W
Angola	n				1	1	1	1		3							
	m									52.3							
	min				9.5	17.4	8.3	9.3		51.3							
	max									52.9							
Benin	n	1								1							
		49.6								51.3							
Cameroun	n	37								19							
	m	50.7								52.3							
	min	48.4								50.5							
	max	54.4								53.5							
Central African Republic	n	5							4	3							2
	m	50.0							29.5	52.5							
	min	48.2							28	51.7							27
	max	51.7							30	53.3							30
Congo	n	25	20	19	21	17	21	21		36	28	23	25	23	24	24	
	m	49.9	29.1	28.2	9.7	18.0	9.0	9.6		51.7	28.5	27.6	9.5	17.8	8.7	9.5	
	min	46.4	27.8	26.8	9.1	16.9	8.6	9.1		49.5	26.8	26.0	8.9	16.7	8.0	9.0	
	max	52.7	30.5	29.5	10.5	18.6	9.6	10.3		54.8	29.4	28.7	10.2	19.1	9.5	9.9	
Ethiopia	n	4	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1
	m	52.7															
	min	50.2	28.8	28.0	9.9	17.6	9.9	9.6	31	52.9	31.0	30.3	11.1	18.0	10.0	9.9	27
	max	54.7								53.8							
Gabon	n	1															
		49.1															
Guinea	n	18	12	7	17	9	16	15		35	26	12	31	23	30	30	
	m	51.4	29.2	28.5	9.8	18.5	9.0	9.9		52.9	28.6	27.7	9.5	17.9	8.8	9.6	
	min	49.3	28.0	27.6	9.2	17.6	8.1	9.4		50.7	27.4	27.1	8.8	17.1	8.5	9.0	
	max	53.1	30.6	29.4	10.6	18.9	9.5	10.1		55.1	29.6	28.5	10.1	18.7	9.2	10.1	
Guinea Bissau	n	1	1														
		51.3	29.0														
Ivory Coast	n	10	9	9	9	8	9	9		4	5	5	4	5	5	4	
	m	51.7	29.6	28.6	10.0	18.4	8.8	9.9		54.1	28.6	27.6	9.6	18.0	8.7	9.7	
	min	49.7	28.3	27.5	9.3	17.9	8.5	9.5		53.0	27.7	26.8	9.3	17.7	8.4	9.4	
	max	54.1	30.5	29.4	10.7	18.9	9.0	10.4		55.2	29.5	28.2	10.0	18.3	9.2	9.8	
Nigeria	n	33	10	8	8	8	8	8	5	86	21	18	18	18	14	14	15
	m	51.1	29.3	28.5	9.8	18.4	9.1	9.9	29.9	52.6	28.9	28.0	9.7	18.1	8.9	9.8	29.8
	min	48.4	27.9	27.4	9.1	18.0	8.6	9.4	27.8	50.1	28.1	27.2	9.3	17.4	7.9	9.4	24.2
	max	53.8	30.3	29.1	10.3	19.0	9.6	10.5	34	55.7	29.7	28.8	10.3	19.1	9.3	10.5	34.0
Sudan	n	10	2	2	2	2	2	2	10	4	3	3	3	3	3	3	4
	m	52.3							30	51.6	28.6	27.9	9.6	18.1	9.2	9.7	28
	min	51.0	29.2	28.3	9.8	17.8	9.4	9.6	24	50.6	27.6	26.9	9.2	17.9	8.5	9.3	20
	max	54.3	30.4	29.8	10.9	18.9	9.7	10.3	35	52.3	29.4	28.6	10.1	18.4	10.1	10.2	32
Togo	n									1							
										51.8							
Uganda	n	2	1	1					1	6	6	6					6
	m									51.7	28.5	27.7					29
	min	50.0	29.6	28.6					28	50.4	28.0	27.0					26
	max	50.5								53.2	29.4	28.6					32
Zaire	n	2	1	1						1							
	min	49.6	27.9	27.3						54.0							
	max	51.5															

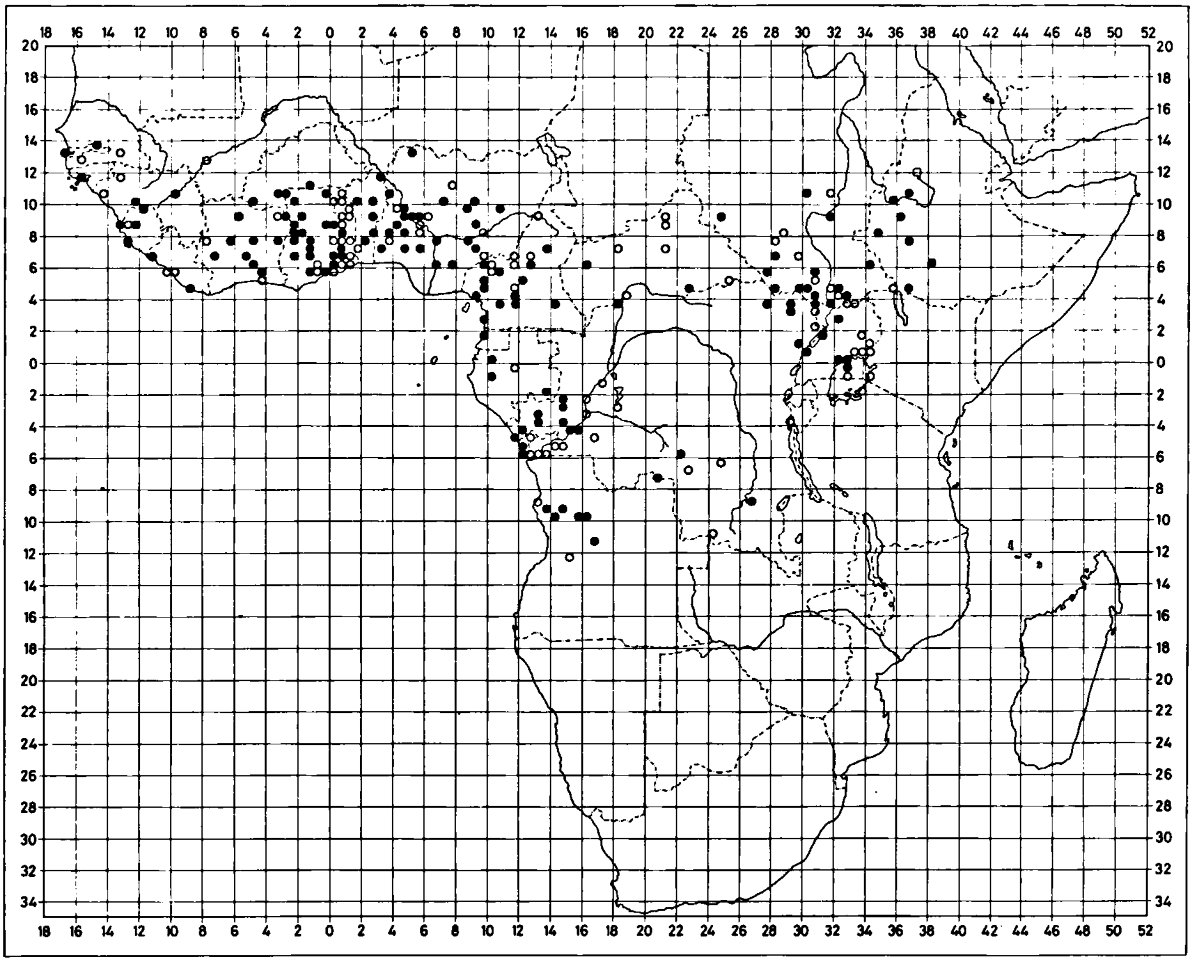

Fig. 2. Distribution of *Micropteropus pusillus* (Peters, 1867). Black dots: squares from which material has been identified by the author. Open circles: records from literature, museum registers and correspondence.
N.B. The localities on the east coast of Lake Victoria are to be regarded with reservation; see the text.

	♀♀	26.0-30.3	(n = 68);
rl	♂♂	9.1-10.9	(n = 59),
	♀♀	8.8-11.1	(n = 82);
zw	♂♂	16.9-19.0	(n = 46),
	♀♀	16.7-19.1	(n = 73);
C^1-M^1	♂♂	8.1- 9.9	(n = 58),
	♀♀	8.0-10.1	(n = 77);
M^1-M^1	♂♂	9.1-10.5	(n = 57),
	♀♀	9.0-10.5	(n = 76);
W	♂♂	24 -35	(n = 21),
	♀♀	20 -34	(n = 28).

Specimens quite uniform throughout the species' range. For a breakdown of measurements per country see table 2.

Distribution: Fig. 2.

Related species: The only other species of the genus, *Micropteropus intermedius*, is larger in most body, skull, and teeth measurements (at least on the average; very few specimens are known), and differs in details of the soft palate. (For teeth measurements of *M. pusillus* see Van Orshoven *et al.*, 1968 — in which paper $P_{3,4}$ and $M_{1,2}$ are called P_3 and $M_{1,2,3}$ — and Bergmans, 1979.)

Remarks

Taxonomy: There is an unsatisfactory situation with regard to the type specimen and type locality of this species. When Peters (1867) named it, he confined himself to the remarks that the ZMB had acquired a specimen from Yoruba which completely matched Tomes' description and figures (1860; 1861) of three specimens — two from Gambia and one from Gabon — which Tomes had identified as *Pteropus schoensis* Rüppell, 1842, and that Tomes' identification was wrong. *Pteropus schoensis*, rightly referred to *Epomophorus* Bennett, 1836 by Tomes (1860), has later been synonymized with *Epomophorus labiatus* (Temminck, 1837) (see Andersen, 1912: 529).

Andersen (1912) judged that Peters' new name *Epomophorus pusillus* hung "on Tomes' description and figures, not on the Yoruba specimen (Berlin Museum no. 3438) incidentally mentioned but not described by Peters." He continued to observe that Tomes' two "cotypes" from Gambia were probably lost, as was the specimen from Gabon which had belonged to the MNHN. Andersen concluded that Gambia should be considered the type locality.

According to Recommendation 73B of the International Code of Zoological Nomenclature a zoologist, basing a new nominal species on specimens before him and who subjectively associates with it specimens that he believes to have been misidentified by another author, should designate his holotype from the former. In the ZMB registers Peters' Yoruba specimen is labelled as type of *Epomophorus pusillus* (Dr R. Angermann, *in lit.*, 15-XI-1988). It does not seem correct to say, as Andersen did, that Peters only mentioned the Yoruba specimen; it is evident that he examined it carefully and compared it with Tomes' description and figures, and also with the actual type specimen of *Pteropus schoensis*: see the introductory remarks and the text on *Epomophorus labiatus* in Peters (1867). In my opinion, one can only conclude that Peters must have thought it superfluous to repeat Tomes' description and illustrations.

Considering all this, I reject Andersen's contention and accept the mentioned specimen from Yoruba (ZMB 3438, an immature female preserved in alcohol, with extracted skull, with the name Krauss on its label) as the holotype and Yoruba, southwest Nigeria, as the type locality of the species. Mr Krauss was probably Dr F. (v.) Krauss (1812-1890), curator of zoology and later director of the Staatliches Museum für Naturkunde in Stuttgart which received, between 1862 and 1883, several small collections of mammals from Adolph Mann at Lagos. One in 1862 was labelled "Yoruba", all the others were labelled "Lagos". The Stuttgart museum still holds one specimen of *Micropteropus pusillus* collected by Mann in 1862 in Yoruba, and I assume that Dr Krauss sent material from this same collection to Peters in Berlin. (Dr F. Dieterlen kindly provided the data on Dr Krauss; *in lit.*, 29-I-1989.)

Distribution and geographical variation: Rosevear (1965) outlined the range of *Micropteropus pusillus* as stretching from Gambia to Tanzania and Angola, mostly in the open woodlands but with some records also from localities in the high forest. The localities presently on record (fig. 2) permit a more detailed analysis. In the north the species remains within the northern limit of the west-east belt of Sudanian and Ethiopian woodlands (types 29a-b in White, 1983). In West Africa some localities approach the latitude of 14° N, in Sudan and Ethiopia it is not known from north of 11° N. The eastern limit of the northern range appears to be set by the Ethiopian highlands, which are only penetrated by way of some low-lying river valleys on the western side and by the central rift valley from the south, where the only known locality, Bulcha Forest, is also the easternmost point of the species' distribution. Towards the south it remains west of the Kenyan/Tanzanian highlands. G. M. Allen (1911) recorded the species, as *Epomophorus pusillus*, from Meru River (c. 00°21'N 37°41'E), a record also included by Harrison (1961), but this is based on misidentified *Epomophorus minor* Dobson, 1880 (Ms M. E. Rutzmoser, *in lit.*, 6-X-1988). (The question mark before the relevant entry in the synonymy of *E. minor* in Bergmans, 1988: 118, can now be deleted.) There are several records from the region north of Lake Victoria. Aggundey *et al.* (1984) recorded USNM material from "Barberton's farm, Kitale"; I noted as collecting locality for specimen USNM 350816 "Kitale 20 mi SW Barberton Pool". This suggests that Kitale stands for Kitale District. Neither Barberton's farm nor Barberton Pool have been located and the record has not been mapped. All other records in this region are from Uganda. The easternmost ones here are from Mbale and Namubali, both at 34°12′E, deposited in the BMNH. There are a few records from east of Lake Victoria. Copley (1950) recorded the species from South Kavirondo (at 00°45′S 34°25′E: Aggundey *et al.*, 1984). I have not seen material evidence for this record (possibly in the museum in Nairobi) and I have mapped it with some reservation. Matschie (1899) recorded the species from "Ngoroine zwischen Victoria-Nyansa und dem Guasso-Nyiro des Massailandes". This was based on two specimens collected by O. Neumann in 1894 at "Ngoroine am unteren Mara, Bezirk Muansa" in Tanzania (ZMB 10052/53). Andersen (1912: 558) quoted this as "Ngoroine, Ngare Dobash" and "the eastern side of Victoria Nyanza (Ngare Dobash)", which seems confusing as Ngare Dobash is probably the same as Engare Dabash at 00°40′S 35°32′E in Kenya (in analogy with Ngare Nyuki = Engare Nanyuki: Aggundey *et al.*, 1984). Swynnerton *et al.* (1951) spelled Ngoroine as Nguruimi, either a tribal area south of the Mara River, between 01°30′ and 02°S and 34°15′ and 35°E and presently overlapping, at its eastern side, with Serengeti National Park, or — more probable — a locality at 01°31′S 33°56′E. I have mapped this locality with some reservation with regard to its correctness. Possibly on the same basis, Swynnerton (1958) listed *Micropteropus pusillus* as occurring in bushland and riverine forest in Serengeti National Park, which to me seems an inadmissable extrapolation.

In the southern part of the species' range it remains within the North Zambesian woodland (type 29c in White, 1983) in northwest Angola, and Wetter Zambesian miombo woodland dominated by *Brachystegia, Julbernardia* and *Isoberlinia* (type 25 in White, 1983) in northeast Angola (in which country, as elsewhere, its occurrence is not necessarily related to the presence, or former presence, of true forest, as supposed by Crawford-Cabral, 1989) and Central and eastern South Zaire and on the northwest Zambian border. (The locality Mukozo is in northwest Angola, according to its original label. I have not traced it, and Crawford-Cabral, 1989 incorrectly referred to a village of the same name in the South.)

Within the outer range limits sketched above, *Micropteropus pusillus* has been collected in a variety of different vegetation types, incidentally very much the same types as listed for *Epomophorus labiatus* by Bergmans (1988, table 5) but in a greater variety because of its much larger range. Although it appears to be a true woodland species it is able, like some *Epomophorus* species — or probably even better — to enter, by way of rivers, roads or other corridors, into other, adjoining types, such as rain and swamp forests and, provided that there is enough food and cover, bushland and edaphic grasslands. For collecting sites within forest boundaries it is often possible to demonstrate a considerable measure of disturbance or interruption of the closed forest cover at the time of capture, such as villages, gardens, logging concessions and river banks. To my knowledge, collecting efforts in undisturbed forest areas have never yielded a single specimen of *Micropterapus pusillus*. Hence, its collecting localities are mostly outside the original West and Central African rain forest blocks.

As table 2 shows, dimensions in the species are quite uniform throughout its range.

Micropteropus intermedius Hayman, 1963

Epomophorus pusillus (not of Peters, 1867); Noack, 1889 206 (in part: specimen SMF 2509).

Micropteropus grandis (not of Sanborn, 1950); Ellerman *et al.*, 1953: 49 (in part: Thysville); Hayman, 1954: 281.

Micropterus (*sic*) *grandis*; Leleup, 1956: 76.

Micropteropus intermedius Hayman, 1963: 100 (type locality: Dundo); Hayman *et al.*, 1966: 27; Hayman *et al.*, 1971: 9; Crawford-Cabral, 1989: 13.

Table 3. Measurements of *Micropteropus intermedius* Hayman, 1963.

	MRAC 22661 ♂ Near Thysville Zaire	BMNH 62.2073 ♀ Dundo, Angola holotype	SMF 2509* ♀ Banana/Netonna Zaire	MRAC 32380 ♀ Luluabourg Zaire
tail length	3	c. 5		
tibia length	23.7	c. 26	25	
foot (with claws)	16.0	c. 18.2	16.8	17.2
ear length	14.8	c. 17.4	14.3	
fal	58.1	63.6	58.3	57.2
3rd metacarpal length	-	45.6	43.4	40.6
5th metacarpal length	41.5	44.3	39.2	39.7
gsl	c. 33.3	33.3	32.2	32.0
cbl	c. 32.5	32.5	31.8	31.2
rl	c. 11.4	11.6		11.2
pl	c. 18.2	18.5	18.1	17.3
cranium width	c. 13.3	13.8		13.4
iow	c. 6.0	6.0	6.6	6.5
pow	c. 8.3	7.9	8.8	9.6
zw	c. 20.5	-	20.2	19.9
mandible length	25.7	26.0	25.35	24.9
mandible height		9.7		9.5
C^1-C^1	6.6	6.4	6.65	6.9
C^1-M^1	c. 10.6	10.2	10.5	10.2
M^1-M^1	c. 10.3	10.3	10.6	10.3
C_1-M_2	11.8	10.4	11.9	11.3
length x width P^3	2.0 x 1.2			2.0 x 1.3
length x width P^4	2.3 x 1.4			2.3 x 1.5
length x width M^1	-			2.2 x 1.4
length x width P_1				0.95 x 0.8
length x width P_3	1.6 x 1.0			1.8 x 1.2
length x width P_4	2.2 x 1.2			2.1 x 1.3
length x width M_1	2.4 x 1.4			2.1 x 1.3
length x width M_2	1.3 x 1.1			1.4 x 1.1

* Measurements copied from Kock, 1987.

Micropteropus pusillus (not of Peters, 1867); Kock, 1969: 24 (in part: SMF 2509).

Micropterus (*sic*) *intermedius*; Kock, 1987: 220.

Material examined

ANGOLA. Dundo: 1 ♀, alc., skull, VI/VII-1953, A. de Barros Machado (BMNH 62.2073; holotype of *Micropteropus intermedius* (Hayman, 1963).

ZAIRE. Luluabourg: 1 ♀, skin, skull in alc., 15-III-1964, J. de Roo (MRAC 32380). Near Thysville, Area of the Cataracts, Cave B13a: 1 ♂, alc., skull, 13-VII-1949, N. Leleup (MRAC 22661).

Diagnosis: The largest of the two known species of the genus, with (in the four specimens on record) a fal of 57.2-63.6, a gsl of 32.0-33.3, a C^1-M^1 length of 10.2-10.6, and a soft palate with six more or less prominent ridges, the first whole and the others medially divided, the halves of the second and especially the third relatively weak and apparently mutually united in part of the specimens, and the halves of the fourth to sixth ridge quite clearly separated from one another.

fal	♂	58.1	(n = 1),
	♀ ♀	57.2-63.6	(n = 3);
gsl	♂	c. 33.3	(n = 1),
	♀ ♀	32.0-33.3	(n = 3);

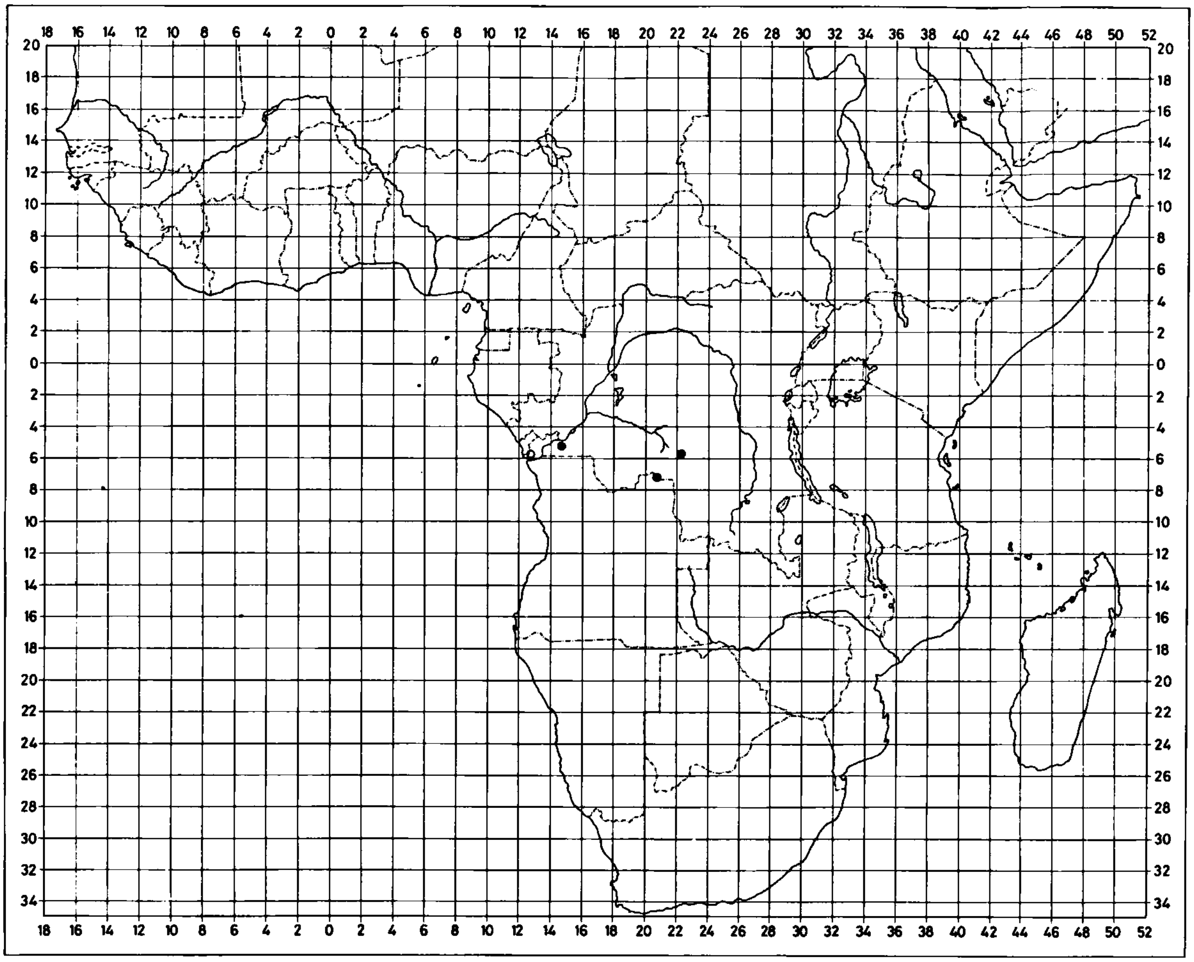

Fig. 3. Distribution of *Micropteropus intermedius* Hayman, 1963. Black dots: squares from where material has been identified by the author. Open circle: record from the literature (but after the completion of this paper also examined by the author).

cbl	♂	c. 32.5	(n = 1),
	♀♀	31.2-32.5	(n = 3);
rl	♂	c. 11.4	(n = 1),
	♀♀	11.2-11.6	(n = 2);
zw	♂	c. 20.5	(n = 1),
	♀♀	19.9-20.2	(n = 2);
C^1-M^1	♂	c. 10.6	(n = 1),
	♀♀	10.2-10.5	(n = 3);
M^1-M^1	♂	c. 10.3	(n = 1),
	♀♀	10.3-10.6	(n = 3).

There is as yet no evidence of geographical variation.

Measurements: Table 3.

Distribution: Fig. 3.

Related species: The only other species of the genus, *Micropteropus pusillus*, is smaller in most body, skull, and tooth dimensions, and differs in details of the soft palate.

Remarks

Taxonomy: The first collected specimen of *Micropteropus intermedius*, reported by Kock (1987), had been in the SMF collection for about a century, identified as *M. pusillus*, before its real identity was discovered. The second specimen collected, from near Thysville, Congo was originally identified as *Micropteropus grandis* Sanborn, 1950 (assigned to *Epomophorus* by the present author; see Bergmans, 1988). These incidents indicate how easily somewhat similarly sized epomophorine species may be taken for one another when the soft palate is not examined carefully (it has neither been preserved in the SMF specimen, nor in the one from near Thysville) or when dimensions are not analysed. When Hayman (1963) described *Micropteropus intermedius*, he characterized it as falling within the body size range of *Epomophorus grandis* but with cranial measurements notably less than in that species and a typical palatal ridge pattern. At that time, two adult specimens of each species were known. Now, there are four of *M. intermedius* and three of *E. grandis* in collections. Available measurements (table 3 in this paper, and table 13 in Bergmans, 1988) strongly suggest that *M. intermedius*, despite overlap in some, averages distinctly smaller in all body dimensions than *E. grandis*. They further indicate that its skull dimensions may be absolutely smaller. The tooth dimensions show some overlap but will probably all average smaller.

If compared to *M. pusillus, M. intermedius* is larger, or will average larger, in practically all measurements. Its palatal ridge pattern serves to distinguish it from both *E. grandis* and *M. pusillus*. It has only been preserved in the type specimen and in the one from Luluabourg, and drawings of both have been published (Hayman, 1963; this paper). Hayman's figure of the type's palate is rather schematical and not quite correct: the first ridge has been drawn as consisting of two halves pointing inward and backward and united at their posterior ends, while in fact it is a single, triangular pad not unlike that in *M. pusillus*; Hayman's 'second ridge' in fact represents the fused second and third ridges; and the two circular halves which in his figure represent the third (= fourth) ridge are in reality rather more longitudinal, transversely, and not as widely separated as suggested.

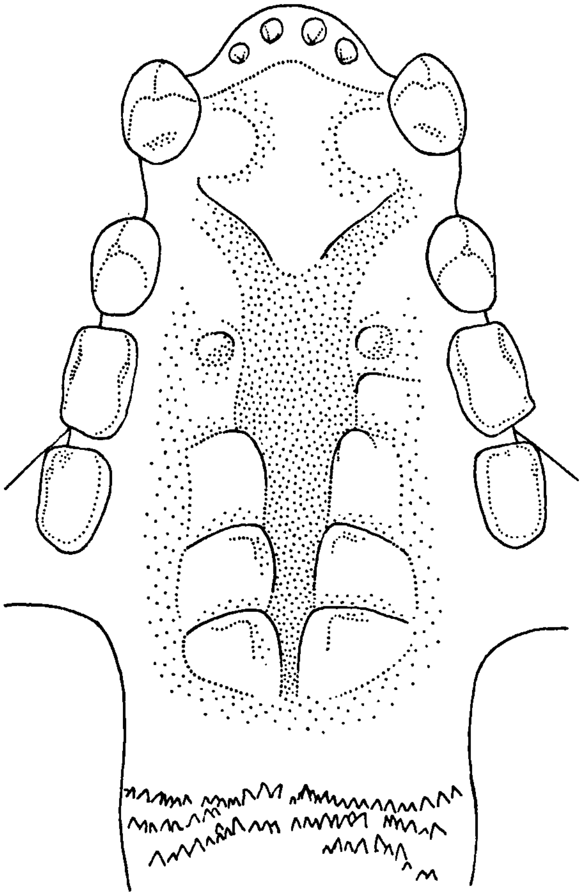

Fig. 4. The soft palate in a ♀ of *Micropteropus intermedius* Hayman, 1963 from Luluabourg, Zaire (MRAC 32.380); the form of the ridges is affected by dehydration (see the text).

The skull of the Luluabourg specimen (collected in 1964) had been preserved dry, with the soft palate *in situ*. In 1978, I put the skull in water for some days to soften the palate, and then in alcohol. The form of the ridges certainly remained affected by dehydration, but less so than before; the thinner parts, such as the labial ends, have suffered particularly and are now mostly indistinct (fig. 4).

In spite of the insufficient concept of the species to be drawn from the available specimens, there is no reason as yet to question its present generic allocation. Further studies should include better preserved soft palates (preferably wet and photographed immediately after collecting), vocal organ anatomy (especially in males), and chromosomal analysis.

Distribution: There is some confusion about the origin of the specimen from near Thysville. Leleup (1956) described it as "Territoire des Cataractes, B13a". B13a is a code for one of a system of caves, in which the specimen was found roosting in a place under a rock near the entrance. (Leleup's conclusion, on this ground, that the species is "troglophile" seems somewhat premature to me.) Heuts *et al.* (1954) mapped this cave on their fig. 8; I calculated that its entrance is about 3.4 km SSE of Thysville, at c. 14°54'E 05°18'S. This same locality has been published, for reasons unexplained, under the name Songolo (Hayman *et al.*, 1971), spelled as Songololo by Kock (1987). Songololo is at 14°05'E 05°40'S and evidently incorrect. (I found two Songolo's: one at 26°44'E 00°58'S, the other at 30°10'E, 01°25'N.)

All four collecting localities are in areas where forest and other, more open vegetation types alternate. Banana/Netonna are in an area of Mangrove (type 77 in White, 1983), bordered by West African coastal mosaic and Mosaic of Guineo-Congolian rain forest and secondary grassland (types 15 and 11a in White, 1983). Both cave B13a near Thysville and Dundo are within the latter type (11a). Luluabourg is located in Guineo-Congolian rain forest: drier types (type 2 in White, 1983), but practically on the border of the same type 11a. *Micropteropus intermedius* most probably remains south of the Central African rain forest block. Whether or not it does occur in the woodlands to the south, which seems more likely, remains to be discovered.

Biology: Although not the subject of this paper, it would seem unwise not to mention two observations pertaining to the species' reproductive biology. The type specimen was pregnant at the time of capture (June/July); the single embryo has a fal of c. 11 and a gsl of c. 14. The ♂ from cave B13a, caught on 13 July, had testes of c. 5.5 in length (measured through the skin).

Epomops Gray, 1866

Epomops Gray, 1866: 65 (type species: *Epomophorus franqueti* Tomes, 1860); Andersen, 1912: 487.

Gray (1866) distinguished his new genus *Epomops*, together with other "Epomophorina" known by him (*Epomophorus* Bennett, 1836 — then still including *Micropteropus* Matschie, 1899 —, and *Hypsignathus* H. Allen, 1861), by the combination of the following characters: 28 teeth, of which 4 upper and 4 lower incisors (the lower not crowded), and 2 upper and 3 lower premolars the first of which "minute, often deciduous"; head elongated, swollen in front; glands on shoulder with a tuft of white hairs. From *Epomophorus* it differed in having a moderate face instead of a very long one, an oval skull with the face much shorter than the brain-case instead of an elongate skull with the face as long as the brain-case, and the upper incisors separate instead of close together. From *Hypsignathus* it differed also in the relative shortness of its snout and in the absence of the swollen nose and chin discs typically of that genus. (It appears that Gray did not know that shoulder tufts are only found in adult ♂♂, and that they are lacking in *Hypsignathus*.)

Dobson (1878) synonymized *Epomops* with *Epomophorus*; at the same time he was the first to notice its aberrant palatal ridge pattern. He based his diagnosis on specimens of *Epomops franqueti* and *Epomops buettikoferi* (Matschie, 1899), which he had all identified as *Epomophorus franqueti* and *Epomophorus comptus* H. Allen, 1861 (a synonym of *E. franqueti*; see Andersen, 1910b). Dobson's conclusions, and his errors, are treated extensively by Andersen (1910b).

Matschie (1899) classified *Epomops* as a subgenus of *Epomophorus*; as differential characters he mentioned the short snout, the larger number of fasciae in the plagiopatagium (at least 36 against at most 32), the even more rudimentary tail, the rather flat postdental palate (instead of a concave one), and an M^1 without an outward curve at the posterior end of the labial side but instead gradually narrowing towards the back side. Matschie recognized as species *E. franqueti, E. dobsonii* Bocage, 1889 and also *E. comptus*. In his differential diagnoses of *franqueti* and *comptus* he repeated the errors of Dobson (*op. cit.*), corrected by Andersen (1910b).

Miller (1907) considered *Epomops* a synonym of *Epomophorus*; his diagnosis of that genus, in which he also included as synonyms *Micropteropus* and *Nanonycteris* Matschie, 1899 has been summarized in Bergmans, 1988 (p. 81).

Andersen (1910b) found himself compelled to disagree with Miller. He pointed out that while in *Epomophorus* the rostrum and palate are unusually narrow and the postdental palate is deeply hollowed out posteriorly, in *Epomops* rostrum and palate are broadened and the postdental palate has preserved the common, i.e. flattened, shape; other differences are to be found in the palatal ridge configuration, with in *Epomophorus* six equally prominent and thick ridges and in *Epomops* only three thick ridges and a set of thin and serrate postdental ridges; finally, Andersen mentioned the hyoid bones and the pharyngeal sacs as different in both genera. The basis for the latter remark had been provided by an anatomical study published by Dobson (1881). On the basis of morphological characters Andersen concluded that *Epomops* is in fact much more closely related to *Hypsignathus* and *Plerotes* Andersen, 1910 than to *Epomophorus*. In 1912 Andersen elaborated the generic characters rather more in relation to the supposedly most primitive living form of Megachiroptera, *Rousettus* Gray, 1821, and to *Hypsignathus* and *Plerotes*, than to *Epomophorus*. Because he now had also included *Epomophorus dobsonii* Bocage, 1889 in *Epomops*, he had to modify his 1910(b) statement on the palatal ridge patterns, as in *dobsonii* there are two prominent postdental ridges and one or a few thin and serrate ridges near the posterior palate margin instead of about five to seven thin and serrate ridges as in *franqueti* and *buettikoferi*. In his description of the genus *Epomophorus*, however, Andersen (1912) compared this almost exclusively with *Epomops*, and a comparison of both accounts yields the following differential characters of *Epomops*: vertical fasciae of mesopatagium 36-47 (against 11-33); metacarpals of digits 2-5 and phalanges of digits 3-5 relatively longer; interdental palatal ridges conspicuously different from postdental ones; bony palate broad and, postdentally, flat; ascending branches of premaxillae tapering almost to a point (instead of equally wide throughout); zygomatic arches weaker, hardly or not vertically expanded in the middle; hyoid bones and arrangement of connected muscles differing in many details; males with two pairs of pharyngeal sacs (instead of one).

Haiduk *et al.* (1980) described the karyotype of *Epomops franqueti*. Those of *Epomophorus gambianus crypturus, E. labiatus* and *E. wahlbergi* were described by Dulic *et al.* (1973) and Peterson *et al.* (1975) — some under incorrect names: see the remarks on p. 93. Males of *Epomophorus wahlbergi* and females of all mentioned species have a diploid number (2N) of 36 and a fundamental number (FN) of 68. Males of *Epomophorus gambianus crypturus* have 2N = 35. Males of *Epomops franqueti* were not examined. Haiduk *et al.* (*op. cit.*) concluded that chromosomally both genera appear to be similar to each other.

Zeller (1984), in his study of the vocal organs of *Epomops, Epomophorus* and *Hypsignathus*, considered *Epomophorus* to be closest to the supposed ancestral condition, *Hypsignathus* furthest away from it, and *Epomops* as intermediate (although developed independantly from *Hypsignathus*). Zeller examined ♂♂ and ♀♀ of — if identified correctly — *Epomophorus labiatus* (the ♀ reported as *anurus*), *Epomops buettikoferi* and *Hypsignathus monstrosus*. He found the larynx to be enlarged in all these species; in ♂♂ of *Epomops* it is considerably larger than in those of *Epomophorus* and partially situated in the thoracic cavity instead of the caudal half of the neck as in *Epomophorus*, while in ♀♀ of *Epomops* it is smaller than in ♂♂ of that genus but larger than in both sexes of *Epomophorus*. Such anatomical differences should certainly play a role in taxonomy but their value as generic characters can only be assessed by further research, involving the other species of

Epomops and *Epomophorus* (and preferably other epomophorines as well).

It should be noted that specimens of the genus *Epomops*, with the possible exception of *E. dobsonii* (Bocage, 1889), do not always conform to all general criteria for adulthood as mentioned in the Introduction (Bergmans, 1988). Male specimens which are clearly adult by all other criteria, with epaulets and worn teeth, may still show incompletely fused skull base sutures; pterygoid and basisphenoid in particular may still be separated by a cartilaginous zone. On the other hand, the skull base sutures may be completely fused and closed in female specimens in which the rostrum has evidently not yet reached its full adult length.

Epomops franqueti (Tomes, 1860)

Epomophorus franqueti Tomes, 1860: 54 (type locality: Gaboon); Didier, 1965: 339; Addy *et al.*, 1978.

Epomops franqueti; Gray, 1866: 65; Andersen, 1912: 494; De Beaux, 1922b: 365; Rode, 1941: 79; Blackwell, 1966: 247, 1967: 79; Brosset, 1966a: 364, 1966b: 54; Jones, 1971: 125, 1972; Eisentraut, 1973: 356; Ayensu, 1974; Kingdon, 1974: 163; Okia, 1974: 462; Vielliard, 1974: 977; Bergmans, 1975; Koopman, 1975: 362; Haiduk *et al.*, 1980, 1981; Bergmans, 1982: 158; Emmons *et al.*, 1983; Koopman, 1986: 10; Happold, 1987: 45 (in part: the ZMA specimens from Pandam Game Reserve are here referred to *Epomops buettikoferi* (Matschie, 1989)); Hickey *et al.*, 1987.

Epomops franqueti franqueti; Andersen, 1912: 497; J. A. Allen *et al.*, 1917: 417; Lang *et al.*, 1917: 500; Schwarz, 1920: 1053; Cabrera *et al.*, 1926: 593; Cabrera, 1929: 15; Sandersen, 1940; Hill *et al.*, 1941: 31; Schouteden, 1944: 103; Malbrant *et al.*, 1949: 81; Swynnerton *et al.*, 1951: 288; Aellen, 1952: 28; Perret *et al.*, 1956: 428; Verschuren, 1957: 196; Novick, 1960: 395; Koopman, 1965: 2; Rosevaer, 1965: 106; Gallagher *et al.*, 1966: 24; Hayman *et al.*, 1966: 24; Aellen *et al.*, 1968: 439; Kock, 1969: 18; Hayman *et al.*, 1971: 8; Ansell, 1978: 16; Bergmans, 1979: 169; Fedden *et al.*, 1986: 182; Feiler, 1986: 70; Crawford-Cabral, 1989: 11.

Epomops franqueti strepitans Andersen, 1910: 106 (type locality: Asaba); Andersen, 1912: 496; Booth, 1959: 28; Rosevaer, 1965: 106; De Vree *et al.*, 1969: 202, 1970: 42, 1971: 160; De Vree, 1971: 35; Hayman *et al.*, 1971: 8; Bergmans *et al.*, 1974: 24; Happold *et al.*, 1978: 75; Robbins, 1980: 85.

Epomophorus (Epomops) franqueti; Rosevaer, 1953: 82.

Epomops franqueti franqueti ⋛ *strepitans*; Eisentraut, 1963: 65.

Material examined

ANGOLA. Canzele: 2 ♂♂, 1 imm. ♀, 7/15-IV-1954, G. Heinrich (FMNH 81621/23). 30 km S of Gabela: 1 ♂, alc., 29-VIII-1954, G. Heinrich (FMNH 84021). Malanje: 1 ♂, alc., skull, Von Mechow (ZMB 10031). (Dundo, Estação Agronomica de Salazar, Ndalatando, Uige.)

BENIN. Kpodave: 1 ♀, 22-VI-1968, C. B. Robbins (USNM 438854).

CAMEROUN. Aqua Town: 1 ♂, alc., R. Buchholtz (ZMB 5002). Bamenda: 1 ♂, 5-IX-1969, R. Glen (ROM 54931). Batanga: 1 imm. ♀, 3-IV-1931, A. I. Good (CMNH 7439); 1 imm. ♀, N H. D. Cox (USNM 114688). Batouri District: 3 ? ♀♀, 1 ♂, 18-X-1933, 5-III-1935, 1-VII-1935, F. G. Merfield (PCMB 644/45, 9, 162); 1 ♂, 1 imm. ♀, F. G. Merfield (BMNH 33.8.4.9/10). 30 km W of Bertoua: 1 ♀, 17-IV-1972, L. W. Robbins (AMNH 241013). Bipindi: 1 ♀, 1 ♂, alc., I- and XII-1898, G. Zenker (ZMB 11280, 54934); 1 imm. ♂, 1 ♀, 12-XI-1907, G. Zenker (ZMB); 1 ♂, alc., G. Zenker (ZMB); 1 ♂, alc., skull, 29-VI-1912 (ZMB). 10 km W of Bipindi: 1 imm. ♂, skull (ROM 56252). Bitye: 1 imm. ♂, 20-X-1912, G. L. Bates (FMNH 29482); 2 ♂♂, 1 ♀, 1 imm. ♀, G. L. Bates (BMNH 9.10.2.2, 11.5.5.2, 23.1.22.6/7). Bota: 10 ♂♂, 7 ♀♀, 6 imm. ♀♀, 1 specimen, 5-XI-1965/26-V-1968, T. S. Jones (ROM 43329, -31/33, -36/37, -39/43, -47, -53/54; 46770, -74, -76/78; 50889, -91/92, -94/95). Buea: 1 imm. ♂, 1 ♂, alc., 2/28-X-1973, J. Prévost (MNHN 1979-198/198bis). 2 km W of Buea Station: 2 ♀♀, 1 ♂, 23/24-IV-1973, V. Ngam (ROM 69002, -05/06). 2 km S of Buea: 1 imm. ♀, 5-V-1973, V. Ngam (ROM 69025). Ekona: 1 ♀, 7-VII-1970, V. Ngam (ROM 58372). Elat: 1 imm. ♀, 29-IV-1913, ? W. E. Johnston (CMNH 2608). Eseka: 1 ♂, 16-VI-1973, L. W. Robbins (AMNH 236258); 1 ♂, 14-VII-1974, L. W. Robbins (AMNH 236259). 6 km SE of Eseka: 2 ♂♂, 1 ♀, 31-V/12-VI-1974, L. W. Robbins (AMNH 236260/61, -63). 7 km N of Eseka: 1 ♀, 3-XI-1972, L. W. Robbins (AMNH 236268). 5 km SW of Eseka: 1 ♂, 3-VII-1974, L. W. Robbins (CMNH 40978). 25 miles S of Garoua: 1 imm., skull, G. L. Bates (BMNH 34.11.22.3). Johan Albrechtshöhe: 1 skull, ? ♂, 12-XI-1899, Conradt (ZMB 54425). 9 km W of Keboko: 1 ♀, 18-I-1970, R. L. Peterson (ROM 55607). Klein Batanga: 1 ♀, alc., I-IV-1909, Kaiser (ZMB). Kounden: 1 ♀, alc., 22-V-1973, J. Prévost (MNHN 1979-195). Koutaba: 2 ♀♀, alc., 19-V-1973, J. Prévost (MNHN 1979-193/94). Kribi: 1 ♂, alc., via Morgen (ZMB 9041); 1 ♂, 1 ♀, 11-IX-1969, R. Glen (ROM 54937, -39); 1 imm. ♂, skull (ROM 56265); 1 ♀, alc., skull, 26-IV-1904, G. Zenker (ZMB 54198). Kribi, Bipindihof: 1 ♀, 1 specimen, skulls, H. Zenker (ZMB 40160/61). Kumba: 3 ♂♂, 4 ♀♀, 12/30-V-1969, V.

Ngam (ROM 51530/32, -34, -36/37, -88); 1 ♀, 1 imm. ♀, 1 ♂, 24/26-X-1975, D. E. Wilson (USNM 511903/05). 15 km S of Kumba: 1 ♀, 1 ♂, 25-I-1970, R. L. Peterson (ROM 55743, -61). Lolodorf: 1 ♀, 8-X-1913, A. I. Good (CMNH 2869); 2 ♀♀, 6/27-XI-1914, A. I. Good (CMNH 3026, 3920); 1 imm. ♂, 1 ♀, 14-V-1918, J. A. Reis (CMNH 4617, -22); 1 ♂, skin, 9-XII-1922, A. I. Good (CMNH 5627); 1 imm. ♂, 1 ♀, 20-VIII-1920, A. I. Good (CMNH 6136/37); 1 ♂, 26-IX-1927, A. I. Good (CMNH 6135); 1 ♀, 1 ♂, 28-I-1936, A. I. Good (CMNH 13172/73); 1 imm. ♀, 8-IV-1938, A. I. Good (CMNH 16060). 40 km N of Lomié: 1 ♂, 18-VI-1970, R. M. Glen & V. N. Ngam (ROM 57147). 12 km SE of Mamfe: 1 ♀, 5-XII-1971, L. W. Robbins (AMNH 241014). 15 km SE of Mamfe: 1 ♀, 9-XII-1971, L. W. Robbins (AMNH 241009). Mangamba, at Mungo River: 1 ♂, 20-XII-1970, V. Ngam (ROM 68920). 15 km SSE of Mbouda: 1 imm., 29-I-1970, R. L. Peterson (ROM 55834). 6 km W of Menguemé, at Soumou River: 3 ♀♀, 14/16-II-1970, R. L. Peterson (ROM 56170, -91; 56203). Mount Manengouba: 1 ♂, 1 imm. ♂, 1 ♀, alc., 30-XI/1-XII-1973, J. Prévost (MNHN 1979-183/85). Mpundu: 1 imm. ♀, 25-VII-1970, V. Ngam (ROM 58372). Muea: 1 ? ♀, 4-VII-1970, V. Ngam (ROM 58339). Above Mueli: 1 imm. ♀, 6-II-1958, M. Eisentraut (USNM 318301). 6 km W of Muenge: 1 ♀, 1 ♂, 16/18-II-1970, R. L. Peterson (ROM 56206, -24). Muyuka: 1 ♀, 23-VIII-1969, R. Glen (ROM 54915); 3 ♀♀, 26/27-VI-1970, V. N. Ngam (ROM 58281, -84, -86). 5 km N of Ntui, at Maloko River: 1 ♀, 11-II-1970, R. L. Peterson (ROM 56127). 7 km N of Ntui: 1 ♂, alc., 11-XI-1973, J. Prévost (MNHN 1979-181). 11 km N of Ntui: 2 ♀♀, alc., 11-XI-1973, J. Prévost (MNHN 1979-179/180). 12 km S, 4 km E of Obala: 2 ♀♀, 20-I/12-II-1970, R. L. Peterson (ROM 55633, 56131). Olangina: 1 ? ♀, 8-VIII-1929 (PCMB PC 143). Sakbayeme: 1 ♂, 7-VIII-1931, J. A. Reis (FMNH 43575). Sangmelima: 1 imm. ♀, 22-V-1933, A. I. Good (CMNH 9508); 1 ♂, 1 ♀, 1 imm. ♂, 21-II/16-V-1934, A. I. Good (CMNH 10312/14). Small Soppo: 1 imm. ♀, 5-V-1973, V. Ngam (ROM 69025). Somalomo: 2 ♂♂, 2 imm. ♂♂, 2 ♀♀, 1 skull, 1 imm., alc., 10/12-II-1987, A. P. M. van der Zon (ZMA 23.525/32); 1 ♂, 2 imm. ♂♂, alc., 18/20-I-1989, A. P. M. van der Zon (ZMA). Tisongo: 1 ♀, 12-XI-1975, D. E. Wilson (USNM 511906). Victoria: 1 ♂, skull; 1 imm., alc., 1 ♂, alc., skull, 1 ♀, skull, cf. 1898/1901, Preuss (ZMB 9040, 67052, 53871/72). Yaoundé: 1 imm. skull, 1 imm. skin, VIII-1897, Von Carnap-Querheim (ZMB 10026, -29); 2 ♀♀, alc., 10-II/4-VI-1986, M. Germain (MNHN); 4 ♂♂, 3 imm. ♂♂, 7 ♀♀, 5 imm. ♀♀, 26-II/27-XI-1973, J. Prévost (MNHN 1979-182, -86/92, -96/97, -99/207). 5 km S of Yoko: 1 ♀, 2 imm. ♀♀, 19/21-I-1974, J. Prévost (MNHN 1979-208/10). Cameroun: 1 ? ♀, skull, Reichenow (ZMB 4785).

(Ambam, Bimbia, Dikome Balue, Douala, Ekundu, Esso song, Foulassi, Idenau, Ikiliwindi, Isobi, Itoki, Konn, Lake Barombi Mbo, Mabeta, Mawutu, Meania, Metet, Mukonje, Ndikinimeki, Ngam, 13 km S of Ngaoundere, Tiko.)

CENTRAL AFRICAN REPUBLIC. Bangui: 1 ♀, 1 imm. ♀, alc., skulls, 5-VIII-1965, A. Chippaux (MNHN). Boukoko: 1 imm., alc., 7-IV-1964, R. Pujol (MNHN). La Maboké: 1 ? ♀, alc., 1966, R. Pujol (MNHN). Zemio: 1 specimen, stuffed, skull (RMNH). Central African Republic: 4 ♂♂, 2 ? ♂♂, 6 imm., alc., 9/27-V-1966, R. Pujol & P. Teocchi, field numbers of 10: 1, 12, 13, 16, 18, 22, 23, 36, 44, 51 (MNHN).

CONGO. All specimens listed in Bergmans, 1979. ZMA 15.647 is a ♂, not a ♀; ZMA 15.642 probably also.

EQUATORIAL GUINEA. Attogondama: 1 imm., skin, 6-II-1913, Escherich (ZMB). Benito River: 1 ♂, alc., Guirol (MNHN 1881-929); 1 imm. ♀, alc., skull, G. L. Bates (BMNH 98.5.4.15). Ekododo: 1 ♂, 24-III-1913, Escherich, field number 160 (ZMB). Elloby: 1 ♀, alc., skull (BMNH 74.10.6.2).

(15 miles from Benito River mouth, Evuenam, Ikunde.)

GABON. Anguanamo, Ngari: 1 ♂, 6-VII-1918, C. R. Aschemeier (USNM 220868). Belinga: 3 imm. ♂♂, 3 ♀♀, 2 imm., alc., XII-1962/II-1963, A. Brosset (MNHN); 1 ♀, alc., skull, XII-1962/II-1963, Mission Biologique au Gabon (ZMA 20.690); 1 imm., alc., skull, 20-VI-1963, Mission Biologique au Gabon (ZMA 20.689); 1 ♂, alc., skull, 25-VI-1963, Mission Biologique au Gabon, and 1 imm. ♂, data probably the same (ZMA 20.687/88); 1 ♂, alc., skull, 31-I-1964, P. J. H. van Bree (ZMA 7947). ? Belinga: 1 ♂, 2 ♀♀, alc., I-1963, A. Brosset (MNHN); 1 ♂, 1 ♀, alc., VI/VII-1963, A. Brosset (MNHN). Booué: 1 ♀, R. Malbrant & A. Maclatchy (MNHN 1947-210). Como River: 1 ♀, G. L. Bates (BMNH 97.7.1.3). Dongila: 1 ♀, alc., skull, R. Buchholz (ZMB 4956). Fernan Vaz: 2 imm., alc. (FMNH 73821, -23). ? Lac Zedée, Ogoué: 1 ♀, ? 2-XII-1875, M. Marche (MNHN 1876-2041). Makokou: 2 ♂♂, 1 imm. ♂, 25-VII-1963, Mission Biologique au Gabon (ZMA 20.691/93); 2 imm. ♀♀, 2 ♂♂, 1 ♀, alc., skulls, 7/8-XII-1963, P. J. H. van Bree (ZMA 7930/31, -43/45); 3 ♂♂, alc., skulls, XII-1963, Mission Biologique au Gabon (ZMA 20.694/96); 7 ♂♂, 9 imm. ♂♂, 7 imm. ♀♀, skulls, 10-XII-1963/5-I-1964, P. J. H. van Bree (ZMA 6818/40); 1 ♀, 1 imm. ♂, alc., skulls, 12/14-II-1964, Mission Biologique au Gabon (ZMA 20.697/98); 2 ♂♂, 3 imm. ♂♂, 1 imm., 25-VII-1963/25-II-1964, A. Brosset (MNHN); 1 imm. ♂, alc., skull, 15-XI-1965, Mission Biologique au Gabon (ZMA 20.699). ? Makokou: 1 ♂, 1 imm., 1963/1964, A. Brosset (MNHN). Mouïla: 1 ♀, 8-VII-1948, A. Maclatchy (MNHN 1949-308). Mitzic: 1 ♂, 1 imm. ♂, 1 ♀, 1 imm. ♀, 1957, G. N. Davies/Cambs West African Expedition (BMNH 58.306/09).

(Kango.)

GHANA. Aburi Hills, 1 imm. ♂, 31-VII-1967, B. J. Hayward (USNM 411530). 9 miles E of Accra: 1 ♀, 17-IX-1971, L. W. Robbins (AMNH 241012). Amedzofe: 1 ♀, 30-VIII-1967, B. J. Hayward (USNM 411598). Bator: 1 imm. ♀, 16-VII-1967, B. J. Hayward (USNM

411597). 1 mile N of Berekuso: 5 ♂♂, 3 ♀♀, 9/16-X-1967, J. C. Geest/J. W. LeDuc/C. B. Robbins (USNM 411534/41). Bibianaha: 1 imm. ♀, alc., skull (BMNH 12.8.27.1). Butre: 22 ♂♂, 4 imm. ♂♂, 12 ♀♀, 2 imm. ♀♀, 17/22-I-1968, J. C. Geest (USNM 413919/21, -28/29, -31, -35/48, -51, -56, -58, -64, -66, 68/70, -73, -76, -79/80, -86, -89, -98; 414002, -10, -12/13, -15). Fanti: 1 imm. ♂, Sharpe (ZMB 4477). Kade: 1 ♀, 28-X-1967, C. B. Robbins (USNM 411468). 6 miles NW of Kade: 2 ♂♂, 1 imm. ♂, 5 ♀♀, 5 imm. ♀♀, 1/2-XI-1967, H. W. Setzer (USNM 411545/57). 6 miles N of Kade: 2 ♀♀, 29-III-1968, J. C. Geest (USNM ....54, -59). 7 miles NE of Kade: 12 ♂♂, 12 ♀♀, 5 imm. ♀♀, 1-VIII/30-IX-1965, C. J. Ralph (ROM 36633/39, -50, -52/55, -57/59, -61/63, -65/69, -72/75). Kete: 1 ♀, alc., skull, Graf von Zech (ZMB 8945). Klein Popo: 1 imm. ♂, alc., Linnaea (ZMB 10004). Kumasi: (identification questionable) 1 imm. ♂, 15-V-1961, D. H. Barry (BMNH 65.740). Legon: imm. ♀, 4-IX-1965, C. J. Ralph (USNM 36656); 3 ♂♂, 15 ♀♀, 6 imm. ♀♀, 20-VII/8-XII-1967, J. C. Geest/B. J. Hayward/C. B. Robbins/H. W. Setzer (USNM 411334, -97; 411501/17, -58; 413875/76, -81/82); 1 ♀, 24-IX-1968, R. E. Vaden (USNM 439865); 1 ♀, 7-X-1968, L. W. Robbins (USNM 439903). Leklebi Agbesia: 1 ♂, 30-VI-1968, J. C. Geest (USNM 424757). Nkawkaw: 3 ♂♂, 5 imm. ♂♂, 7 ♀♀, 4 imm. ♀♀, 5-VIII/9-X-1967, J. C. Geest/B. J. Hayward (USNM 411518/29, -31/33, -59/62). Oda: 16 ♂♂, 1 imm. ♂, 3 ♀♀, 11/15-X-1968, R. E. Vaden/H. W. Setzer/J. W. LeDuc/L. W. Robbins (USNM 439851, -55/56, 58/63, -66/69, -71/74, -77, 82/83). Odomi Jongo: 3 ♂♂, 2 ♀♀, 17/22-VI-1968, J. C. Geest (USNM 424742, -47/48, -51, -53). Prince's Town: 2 ♀♀, 26-VIII-1967, B. J. Hayward (USNM 411599/600). St. George d'Elmina: 1 ♀, alc., skull (ZMA 1626). Subinja: 4 ♂♂, 5 ♀♀, 21/24-II-1968, J. C. Geest (USNM 414740, -42/45, -47/48, -50/51). Tafo: 1 ♂, 28-VII-1961 (BMNH 62.247). Ghana: 1 ♂, skull (ZMB 2620).

(Achimota, Akosombo, Akwam, Akwamufe, Boti Falls, Lilidze Mountain Range.)

IVORY COAST. Abidjan: 1 imm. ♀, 24-VI-1965, D. Parelius (FMNH 99030). Adiopodoumé: 14 ♂♂, 4 imm. ♂♂, 19 ♀♀, 5 imm. ♀♀, 5 imm. (2: skulls only; 2: skins only; 12: alc., 11 skulls extracted), 1963/1972, ORSTOM (ZMA 16.746/58, 16.813, 17.312/19; AMNH 239376/77; others: MNHN). Banco Forest: 3 ♀♀, 29/30-XI-1968, J. W. LeDuc/L. W. Robbins (USNM 429879/80, -83). Lamto: 1 imm. ♀, alc., skull, 30-V-1964, L. Bellier (ZMA 16.745).

NIGERIA. Abonnema: 1 ♂, 1 imm. ♂, 1 ♀, Ansorge (BMNH 2.11.2.4/6). Agege: 1 imm. ♂, alc., skull, 28/29-VIII-1976, W. Bergmans (ZMA 19.098). Akpaka Forest Reserve: 1 ♀, 22-XI-1952, D. R. Rosevear, 970/52 (NHMI). Asaba: 1 ♂, alc., skull (BMNH 95.5.3;6). (Old) Calabar: 1 ♂, 1 ♀, Robb (BMNH 80.7.21.1, -3); 1 ♂, alc., skull, 23-VII-1976, W. Bergmans (ZMA 19.031). Ibadan: 1 ♀, 4-III-1952 (NHMI); 1 ♂, 21-XI-1959, F. C. Sibley (AMNH 204293); 1 ♂, 1 imm. ♂, 1 imm. ♀, F. C. Sibley (BMNH 61.82/84); 1 imm., 1-I-1963, P. Ward (ZMI); 1 ♂, 6 ♀♀, 4 imm. ♀♀, 1 specimen, 8/17-VI-1965, J. Menzies (FMNH 99051/62); 1 ♀, XII-1965, H. J. Herbert (USNM); 5 ♂♂, 11 ♀♀, 14-IX-1966/15-IV-1968, S. B. Akpan/H. W. Setzer (USNM 402339; 402455, -58/61, -76, -79/81; 483187/92); 1 ♂, 2 ♀♀, 1 imm. ♀, 4/5-VIII-1976, W. Bergmans (ZMA 19.032/33, -88/89); 5 ♂♂, 3 imm. ♂♂, 12 ♀♀, 3 specimens, alc. (ZMI 1/2, 4, 7, 9, 10, 13/14, 18/22, 25/26, 28/30, 33/34, 39, 53). Ife: 4 ♂♂, 4 ♀♀, 10 imm., alc., 1975/1976, G. Oderhowho (NHMI); 1 ♀, alc., skull, 21/22-VIII-1976, W. Bergmans (ZMA 19.097). Igbo-Ora: 1 ♂, 3 ♀♀, 23/26-X-1966, H. W. Setzer/J. C. Geest (USNM 402465, -67/69). Lagos: 1 ♂, alc., skull, Salmin (ZMB 3649); 1 ♂, 1-IV-1952, D. R. Rosevear 943/52 (NHMI). Oban: 1 ♂, P. A. Talbot (BMNH 10.6.1.8). Odukpani: 1 imm. ♀, 24/25-VII-1976, W. Bergmans (ZMA 19.087). Sapoba: 1 ♂, 3 ♀♀, 10/15-VII-1966, H. J. Herbert (USNM 379501, -03, -05/06). Umuahia: 1 specimen (BMNH 46.282).

(Igbo-Oloyin, Mamu River Forest Reserve, Nikrowa, N'ko, Obubra, Olokomeji Forest Reserve, Omo Forest Reserve, Onitsha, Owerri Province.)

SUDAN. Kajiko North: 2 ♀♀, 3 imm. ♀♀, 16/17-VII-1978, G. Nikolaus (SMNS 29897/99, 29900, -02). Kajiko South: 1 ♀, 18-VII-1978, G. Nikolaus (SMNS 29901).

(Rumbek.)

TANZANIA.

(Bukoba, Rubondo.)

TOGO. Ezime: 1 imm. ♀, 2-VII-1968, J. W. LeDuc (USNM 437591). Kadjamba: 1 ♂, skin, 21-XII-1912, A. F. von Mecklenburg/W. Bruch (ZMB). Misahöhe: 1 imm. ♀, alc., skull, 1-VII-1904, Smend (ZMB 50003).

(Adina, Adjido, Agadji, Agomé-Tomegbé, Ahoué-houé, Atakpamé, Azafi, Dedomé, Dzjogbégan, Ebeva, Edifou, Ezimé, Fazao, Grand Popo, Klouto, Koutoukpa, Odjolo, Plateau Akposso, Tétetou.)

UGANDA. Budongo Forest: 2 imm. ♀♀, 13/16-X-1963, WFVZ (LACM 31773/74); 1 imm. ♀, alc., skull, 12-VII-1965, A. Starrett (LACM 19630); 1 ♂, 1 imm. ♂, 7 ♀♀, 16-VI/8-VII-1966, J. G. & A. Williams (LACM 51497/505); 1 ♂, 17-IX-1966, J. G. Williams (ROM 40155); 3 ♂♂, 1 ♀, 1 imm. ♀, 3/22-VI-1968, J. G. Williams (ROM 46443/44, 46511, 46654); 2 ♂♂, 1 imm. ♂, 2 ♀♀, 4 imm. ♀♀, 3 specimens, 5/26-V-1970, I. Bampton (LACM 36102, -04/07, -09/13, -15/16). Ishasha River: 1 imm. ♂, 1 imm. ♀, 28-VI/27-VIII-1962, S. Keith (AMNH 189476/77). Ithama Mine: 1 ♂, 2 ♀♀, 1 imm., 26-III-1967/3-VII-1969, A. L. Archer/R. Glen/A. Williams (LACM 35507, 51506/08). Kalinzu Forest: 1 ♀, 30-X-1969, A. Williams (LACM 35666). Kibale Forest: 2 ♂♂, 1 ♀, 6-XI/3-XII-1966, R. Glen & A. Williams (LACM 51495/96, 51625). Malabigambo Forest: 1 ♂, 2 ♀♀, 27-I/15-II-1968, A. L. Archer (LACM 51509/11). Mongiro: 1 ♂, 1 ♀, 4/11-XI-1968, R. Glen (LACM 51492, -94). Mwela: 2 ♂♂, 3 ♀♀, 30-XI/15-XII-1967, A. L. Archer (LACM 51474/76,

-78/79). Ntandi: 4 ♂♂, 2 imm. ♂♂, 4 ♀♀, 2 imm. ♀♀, 16/29-VI-1967, A. L. Archer/R. Glen/A. Williams (LACM 51480/91); 1 ♂, 8-XI-1968, A. Williams (LACM 51493).
(Bugabo, Bugala Island, nr Buloba, nr Bundibugyo, Entebbe, Entebbe Peninsula, nr 40 km ESE of Port Portal, Hakitengya, nr Kahunge, nr Kanungu, nr 15 km SSW of Karongo, Katalemura, Katera, nr Kayunga, nr Kijura, nr Kyabazala, Lunyo, Masaka, nr 20 km NW of Masindi, nr Mubende, nr Munteme, nr Nakasajja, nr Ndeke, nr 10 km NE of Ndeke, Nyabirongo, Zika.)
ZAIRE. Beni: 1 imm. ♂, skull, IX-1910, R. Grauer (NMW 4879). Fort Beni: 1 ♂, R. E. Deut (BMNH 6.12.4.59). Gangala-na-Bodio: 1 imm. ♂, alc., 31-V-1948, Mission Hediger-Verschuren (IRSN 11659). Inkongo: 1 ♂ (BMNH 17.1.21.2). Irangi: 1 ♂, 1 specimen, alc., skulls, 16-III/17-VIII-1964, P. Kunkel (SMF 31834/35). Ituri River, 40 miles SW of Irumu: 1 ♀, 2 imm. ♀♀ (BMNH 30.11.11.66/68). Kimpoko: 1 imm., 22-VI-1979, Mutashiya Tsh. Ng. (NMW 25774). Kinshasa: 1 ♀, 21-IV-1964, J. van Orshoven (ZMA 11.169). Koloka: 1 specimen, alc., skull, VI-1911, H. Schubotz (SMF 6357). Kyn-vitumbi: 1 imm., 15-VII-1946, J. de Wilde (IRSN 13326). Lukolela: 1 imm. ♂, 25-VII-1930, F. Edson (AMNH 86765). Luluabourg: 1 imm., 19-I-1925 (NMBA 3801/7696); 1 imm. ♀, 11-I-1964, A. E. M. de Roo (AMNH 207739); 1 ♂, R. Callewaert (BMNH 26.7.6.56). Mambaka: 1 ♀ (BMNH 14.4.8.2). Medje: 1 specimen, C. Christy (BMNH 19.5.8.9). Mistandunga: 1 ♂, 1 ♀, 23-VII-1930, F. Edson (AMNH 86766/67). Moera: 1 imm. ♀, VII-1910, R. Grauer (NMW 4878). Mutsora: 1 ♀, 4-IV-1951, R. Christiaens (IRSN 13327). Pidigala Nord: 1 ♂, alc., 23-IV-1952, Mission De Saeger (IRSN 13501). Stanleyville: 1 ♂, Christy (BMNH 14.4.8.1). Teturi: 1 ♂, 2 imm., 6-II-1947/15-III-1948, J. & D. Hiernaux (IRSN 7044, 7052/53). Tingasi: 1 ♂, V-1882, Emin Pasha (BMNH 87.12.1.26).
(Aba, Alipango, Avakubi, Babeke, Bafuka, Bambesa, Basongo, Befale, Bikoro, Boangi, Boendi, Bokuma, Bokungu, Boma, Bumba, Buta, Congo da Lemba, Dungu, Eala, Epulu, Faradje, Gemena, Ibembo, Ikela, Irumi, Ituri Forest, Kamituga, Katende falls, Keseki, Kin-Gombé (Kimpoko), Kisingani, Koteli, Kunungu, Lubumbashi, Luebo, Mawambi, Mongbwalu, Mutwanga, Niangara, Niapu, Panga, Paulis, Penge, Pilipili, Poko, Rutshuru, Rungu, Semliki River, Stanleyville, Tshopo falls, Weko Forest, Yakuluku, Yangambi, Zobia.)
ZAMBIA.
(Abercorn.)

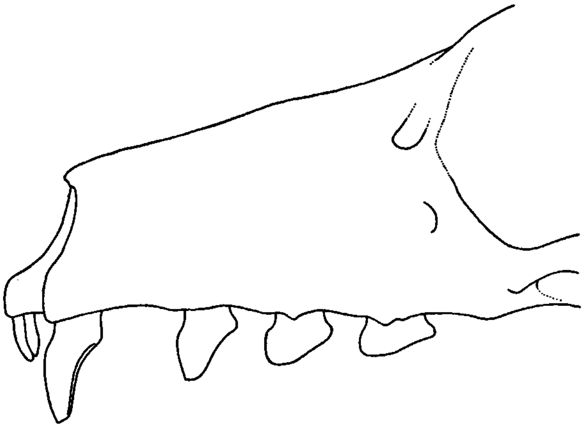

Fig. 5. Rostrum profile of *Epomops franqueti* (Tomes, 1860) from Adiopodoumé, Ivory Coast (ZMA 16.752); sex uncertain, probably ♂.

Fig. 6. *Epomops franqueti* (Tomes, 1860): caudal end of right pterygoid wing. (Specimen from Adiopodoumé, Ivory Coast, ZMA 16.752; probably a ♂.)

Diagnosis: Skull relatively short, dorsal profile of rostrum (fig. 5) slightly concave or straight, or very rarely slightly convex; rostrum and palate relatively short, palate rather weakly concave from side to side and antero-posteriorly; zygoma long, without distinct postorbital process; pterygoid wings extending to tympanic bullae and curled outward posteriorly, forming a cavity (fig. 6); tooth rows not excessively short; a high incidence of deciduous second upper incisors; soft palate with, from front to back, three thick and five to eight rather thin ridges, with the third thick ridge usually undivided in the middle and the thin ridges rather narrowly divided in the middle (the pos-

Table 4. Forearm lengths, greatest skull lengths and weights of *Epomops franqueti* (Tomes, 1860) per country. Order of countries approximately from west to east.

			♂♂			♀♀	
		fal	gsl	W	fal	gsl	W
Ivory Coast	n	13	10	8	20	11	8
	m	86.2	46.2	102	79.9	40.3	72
	min	84.0	44.4	92	76.5	37.8	61
	max	88.9	48.7	115	84.3	41.9	81
Ghana	n	61	63	12	58	60	11
	m	87.9	46.9	126.7	82.2	42.2	94.5
	min	83.5	43.3	110	77.0	38.6	88
	max	93.9	49.9	140	87.1	45.3	102
Togo	n	1					
		89					
Benin	n				1	1	
					82.7	41.3	
Nigeria	n	16	13	3	30	23	7
	m	90.3	47.5	130.7	83.6	42.4	94.2
	min	85.8	45.4	119	79.1	40.2	90
	max	95.1	50.6	142	88.5	44.5	110
Cameroun	n	35	33	9	51	44	
	m	94.9	49.6	133.8	88.5	44.4	
	min	90.0	46.8	110	82.7	41.9	
	max	100.0	53.3	145	94.1	47.0	
Equatorial Guinea	n					1	
						44.6	
Gabon	n	14	13	8	11	5	2
	m	96.3	50.8	131	90.8	45.2	
	min	89.9	48.8	98	88.0	42.9	89
	max	100.9	52.1	159	93.8	46.6	115
Congo	n	9	6		17	11	
	m	93.5	49.4		88.3	44.5	
	min	90.0	47.4		84.2	42.6	
	max	97.4	51.4		93.7	46.6	
Angola	n	3	3				
	m	c. 95.9	49.6				
	min	c. 93	49.3				
	max	97.8	49.9				
Central African Republic	n	4			1	1	
	m	98.2					
	min	97.4			85.5	43.9	
	max	99.6					
Zaire	n	4	3		3	4	
	m	95.2	50.3		88.2	44.5	
	min	91.7	48.1		84.8	43.3	
	max	97.6	51.9		93.6	46.2	

table 4 continued

Sudan	n				3	1	3
	m				91.6		123
	min				88.5	46.7	120
	max				96.4		130
Uganda	n	20	17	15	21	22	16
	m	95.7	51.1	146.9	89.6	45.7	109.5
	min	92.3	49.9	130	85.7	44.0	94
	max	99.1	52.4	172	93.5	47.8	128

terior ones often undivided) and finely serrate, the halves of the anterior three or four thin ridges somewhat convex towards the front, the posterior ones about straight or weakly concave, with a single central curve or angle pointing forward.

Measurement ranges and ratios taken from all over the species' range:

fal	♂♂	83.5-100.9	(n = 178),
	♀♀	76.5- 96.4	(n = 216);
gsl	♂♂	43.7- 53.3	(n = 160),
	♀♀	37.8- 47.8	(n = 184);
cbl	♂♂	43.7- 52.2	(n = 46),
	♀♀	36.3- 47.0	(n = 56);
rl	♂♂	17.3- 21.6	(n = 30),
	♀♀	13.8- 18.4	(n = 26)
pl	♂♂	24.4- 30.2	(n = 27),
	♀♀	20.4- 26.2	(n = 26);
zw	♂♂	25.8- 30.0	(n = 45),
	♀♀	21.2- 27.8	(n = 52);
C^1-M^1	♂♂	14.7- 17.9	(n = 43),
	♀♀	12.2- 16.5	(n = 54);
W	♂♂	92 -172	(n = 47),
	♀♀	61 -130	(n = 45);
rl	♂♂	38.7- 42.7% of gsl	(n = 30),
	♀♀	37.0- 40.4% of gsl	(n = 26);
pl	♂♂	54.2- 59.0% of gsl	(n = 27),
	♀♀	53.1- 56.7% of gsl	(n = 26);
zw	♂♂	52.6- 59.2% of gsl	(n = 42),
	♀♀	54.9- 60.4% of gsl	(n = 52).

Specimens are larger in the Central African part of the species' range. For a breakdown of size ranges per country see table 4.

Distribution: Fig. 7.

Related species: Epomops buettikoferi (Matschie, 1899) is very similar but averages larger in all measurements where it is sympatric (see table 8); its dorsal rostrum profile is often slightly convex, its rostrum and palate are relatively longer, its second upper incisors usually not deciduous, its third palatal ridge is usually distinctly divided, and its thin palatal ridges are morphologically different. *Epomops dobsonii* (Bocage, 1889) differs in the morphology of its pterygoid wings and soft palate.

Remarks

Taxonomy: The type specimen of *Epomophorus franqueti* Tomes, 1860 was collected by Dr Franquet of the French Imperial Navy in "Gaboon" (Tomes, 1860). It is a mounted adult ♂ (MNHN A 107) with extracted skull (Muséum d'Anatomie Comparée, Paris, A 6767) (Andersen, 1912). Tomes (1860) gave some measurements which Andersen (1912) confirmed (e.g. fal 95.25; length from extremity of nasal bones to occipital crest 48.7; length from extremity of nasal bones to front of orbit 19.5; breadth across zygomatic arches 29.6). I have not examined the type but it is clearly consistent with specimens from Gabon I measured.

Andersen (1912) was the first author who examined a larger series, of altogether 46 specimens. He divided the species into two subspecies: a smaller western one, ranging from Ghana to Calabar in southeast Nigeria, and a larger "eastern and southern" one, ranging from Calabar east to Lake Victoria and south to Angola. He measured five adult ♂♂ and two adult ♀♀ of the western subspecies *strepitans*,

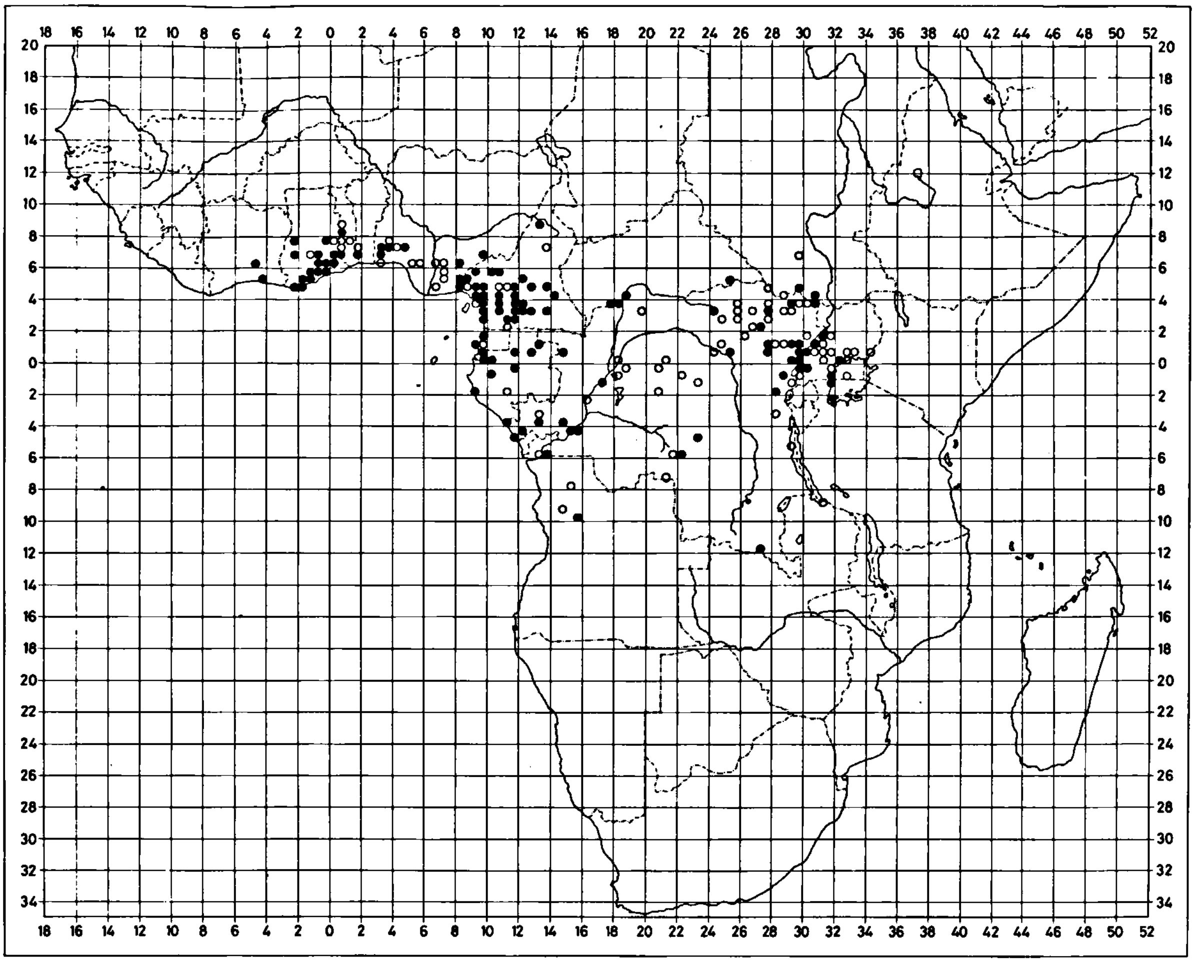

Fig. 7. Distribution of *Epomops franqueti* (Tomes, 1860). Black dots: squares from where material has been identified by the author. Open circles: records from literature, museum registers and correspondence.

and nine adult ♂♂ and eight adult ♀♀ of the eastern *franqueti*: small numbers if the distribution area is taken into account. The ♂♂ of *strepitans* in his series were just slightly smaller than the ♂♂ of *franqueti* and in the ♀♀ of both the dimensions overlap. Only few later authors have commented on this subdivision. Sanderson (1940) identified a specimen from Nko (= N'ko, Obubra Division, about 125 km north of Calabar) as typical *franqueti*. In combination with Calabar itself, this would imply that the Cross River may represent the dividing line between the two subspecies. Aellen (1952) listed all specimens from Cameroun, either reported in the literature or examined by himself, as typical *franqueti*. Eisentraut (1963) mentioned the Cross River as an approximation of the supposed dividing line, but the measurements in his large series from Cameroun Mountain (see table 6) clearly connected the subspecific ranges given by Andersen (1912): the fal ranges in ♂♂ and ♀♀ include Andersen's ranges for *strepitans* but also the lower halves of the ranges for typical *franqueti*, the gsl range in Eisentraut's ♂♂ does the same and that in his ♀♀ just overlaps with Andersen's maximum for *strepitans* and falls completely within his range for *franqueti*. Eisentraut concluded that the Mount Cameroun ♂♂ were more like *strepitans* while the ♀♀ resembled *franqueti*, and sug-

Table 5. Annotated data from the literature on *Epomops franqueti* (Tomes, 1860) which add to the ranges given in table 4; order of countries as in that table.

		♂♂			♀♀		source	remarks
	fal	gsl	W	fal	gsl	W		
Ivory Coast		*40.9*-48.7			37.8-*45.3*		Bergmans *et al.*, 1974	*In italics*: mistakes*
Cameroun	85.7-93.0	46.3-50.2		82.0-88.6			Eisentraut, 1963	
Equatorial Guinea	95						De Beaux, 1929	
Equatorial Guinea	92.6-97.4	49.0-51.0		88.4-94.8	43.4-*51.2*		Jones, 1971	*In italics*: must be a ♂
Gabon		(46)-*58*	125			85	Brosset, 1966b	gsl: mistake*; Ws: means
Congo	*86.2*-97.4				43.3-*49.3*		Bergmans, 1979	*In italics*: mistakes*
Angola			105			84	Novick, 1960	
Angola	92			85-92			Feiler, 1986	
Zaire		51 -52.5					J. A. Allen *et al.*, 1917	
Zaire				81			Verschuren, 1957	Probably immature
Zaire	93-102						Koopman, 1975	

* mistakes in Bergmans *et al.*, 1974 and Bergmans, 1979 due to wrong age and sex assessments; mistake in Brosset, 1966b no doubt due to an error in reading or printing.

gested that the Mount Cameroun region might represent a transition zone of the two subspecies. Rosevear (1965) could examine more material from west of the Cross River and suggested that the dividing line would lie further west and possibly coincide with the lower Niger.

While it is clear that West African specimens average smaller in body and skull measurements than Central African ones (see tables 4 and 5) it is not possible, in my opinion, to delimit subspecific ranges. From Ivory Coast to Nigeria the dimensions appear to increase clinally. In table 6 measurements of Nigerian specimens are listed in groups divided by the lower Niger and Cross rivers; those from Mount Cameroun as given by Eisentraut (1963) are added. The fal range of the male series from Ibadan is almost exactly the same as that in the series from Mount Cameroun—the Ibadan ♀♀ average slightly lower than the Mount Cameroun ones. The fals in Ife ♂♂ and ♀♀ appear to average even larger than in Mount Cameroun specimens. The phenomenon of population-specific ranges found for various *Epomophorus* species (Bergmans, 1988) may also play a role here. Gsls average smaller in both ♂♂ and ♀♀ west of the Cross River if compared to those east and south of it—but apart from the Ibadan series all samples are very small, and so are the differences shown.

If subspecies are to be recognized, it will not be possible to define their ranges without recognizing a considerable zone of transition, and the underlying data remains very meagre. As the species' range is most probably continuous, additional data from Cameroun and further east and south may be expected, moreover, to demonstrate a continuation of the clinal change in dimensions. For these reasons it seems that there is not much sense in maintaining any subspecific division for the present, and I consider the subspecies *strepitans* Andersen, 1910 a synonym of the nominate form.

As Andersen remarked (1912: 489), I^2 is often deciduous. In 94 specimens I examined in this respect, 36 had no I^2 on either side and in 13 this tooth was absent on one side; there is neither a clear connection with age nor with sex, but there appears to be one with geography. The incidence of lost I^2 is highest in Central African specimens. Of 40 specimens from Gabon, 17 have no I^2 and five have only one; of 24 specimens in Ivory Coast, five have no I^2 and five have an I^2 on one side.

The soft palate has been studied in 280 specimens. In 247 the third thick ridge was

Table 6. Forearm lengths, greatest skull lengths and weights of *Epomops franqueti* (Tomes, 1860) from Nigerian localities and from Mount Cameroun, arranged in an order from west to east. Measurements between brackets are of nearly adult specimens. I = west of the lower Niger; II = between lower Niger and Cross; III = east of Cross; IV = Mount Cameroun (data copied from Eisentraut, 1963).

			♂♂			♀♀	
		fal	gsl	W	fal	gsl	W
I	Igbo-Ora	90.8	46.4		81.5-85.0 n = 3 m = 83.5	42.3	
	Agege	(81.6)	(42.4)	(81)			
	Lagos	90.9	47.1				
	Ibadan	85.8-93.1 n = 9 m = 89.4	46.7-48.0 n = 7 m = 47.4	119-131 n = 2	79.6-86.5 n = 22 m = 83.4	40.2-44.2 n = 17 m = 42.0	85-110 n = 6 m = 94
	Omo Forest Reserve				87.9*		91*
	Ife	86.0-95.1 n = 4 m = 91.7			81.0-88.5 n = 4 m = 86.0	43.2	95
	Sapoba		49.1		(81*)	43.0-44.5 n = 3 m = 43.8	(74*)
II	Asaba		47.3				
	Akpaka Forest Reserve				79.1		
	Abonema					≥41	
	Umuahia		47.0**				
III	Oban		(45.4)				
	Odukpani				(79.6)	(44.1)	(76)
	Calabar	91.8	46.0-50.6 n = 2	142		43.5	
IV	Mount Cameroun	85.7-93.0 n = 10 m = 89.0	46.3-50.2 n = 10 m = 48.3		82.0-88.6 n = 10 m = 85.7	43.5-45.9 n = 8 m = 44.5	

* data from ROM files; ** specimen BMNH 46.282, labelled as ♀

undivided in the middle, although notched in ten, and in 33 (12%) it was divided. The highest incidence of divided third ridges was found in Ivory Coast (15 out of 40 specimens), a 'medium' incidence in Ghana (3 out of 23) and Nigeria (9 out of 64), and the lowest in Cameroun (1 out of 68), Gabon (4 out of 44) and Congo (0 out of 25). De Vree (1971) observed that the third ridge in *Epomops buettikoferi* is sometimes only narrowly divided, contrary to the normal wide division in that species but quite similar to *E. franqueti* specimens with a divided ridge. Kuhn (1965) recorded a *buettikoferi* ♂ from Liberia with an undivided third ridge, and Wolton *et al.* (1982) found a ♂ and a ♀ with undivided third ridges, also in Liberia. De Vree (1971) observed also a difference in the general aspect of the soft palates of some *buettikoferi* specimens from Ivory Coast and Liberia on the one hand and a large collection of *franqueti* from Togo on the other (see also Bergmans *et al.*, 1974). The median gap dividing the fourth interdental and the postdental ridges is relatively wider in *buettikoferi*, and the serrated halves of ridges four to seven in that species are usually characterized by one large ‘tooth’, while in *franqueti* all the ridge teeth are of about equal size and rather smaller than those in *buettikoferi*.

The configuration of the palatal ridges presents one of the few differential characters by which *franqueti* and *buettikoferi* may be distinguished. Especially in the area of sympatry (compare figs. 7 and 13) sometimes specimens are found which appear to be somewhat intermediate in that character. While it is obvious that the two species are very similar and phylogenetically probably closely related, rendering hybridisation a possible explanation, dimensional data from the area of sympatry confirm the occurrence of two distinct taxa (compare Bergmans *et al.*, 1974).

Distribution and geographical variation: *Epomops franqueti* is essentially a species of the Guineo-Congolian lowland rain forest, occurring in both the wetter and drier types (types 1a and 2 in White, 1983). It ranges from eastern Upper Guinea (eastern Ivory Coast and Ghana) to the whole of Lower Guinea (classification of Moreau, 1963). It appears to avoid the West African coastal mosaic and the mangrove forests (types 15 and 77 in White, 1983). Within the forest belt it does probably not enter the large area of Swamp forest in northeast Congo and adjacent Zaire (type 8 in White, 1983)—but few collectors have worked that area. On the continental side of the rain forests, the species occurs in the various mosaics of rain forest with woodland and grassland, and has occasionally been collected in Sudanian woodland with abundant *Isoberlinia* (Togo, Sudan) and Wetter Zambezian miombo woodland dominated by *Brachystegia*, *Julbernardia* and *Isoberlinia* (Zaire, Angola, Zambia) (types 27 and 25 in White, 1983). In East Zaire it has been collected in Afromontane vegetation (type 19a in White, 1983). De Seabra (1909) recorded the species from Moçamedes at the Angolan coast, but this is in an outlier of the Namib desert and quite far from suitable natural habitat; I presume that his evidence originated from a distant inland place and have not mapped Moçamedes (Crawford-Cabral, 1989, independantly reached the same conclusion).

Part of the geographical variation has been dealt with in the discussion of the intraspecific taxonomy. Larger series have been examined from few regions only. West African specimens show an increase in average dimensions from Ivory Coast to Cameroun. From Cameroun towards the south, no further change is apparent. In the eastern part of the species' range, dimensions are probably slightly larger again (compare table 4).

Epomops dobsonii (Bocage, 1889)

Epomophorus dobsonii Bocage, 1889: 1 (type locality Quindumbo).

Epomops dobsonii; Andersen, 1912: 500; Hill *et al.*, 1941: 33; Hill, 1941: 82; Schouteden, 1944: 103; Harrison, 1959: 220; Ansell, 1960b: 9; Hayman, 1963: 95; Hayman *et al.*, 1966: 24 (in part: specimen 1811b from Kanzenze represents *Epomophorus*); Ansell, 1967: 3; Smithers, 1968: 28; Hayman *et al.*, 1971: 8; Smithers, 1971: 55; Ansell, 1978: 17; Bergmans, 1979a: 239; Anciaux de Faveaux, 1983: 31; Bergmans *et al.*, 1983: 119; Smithers, 1983: 60; Meester *et al.*, 1986: 27; Happold *et al.*, 1987: 351; Ansell *et al.*, 1988: 351; Crawford-Cabral, 1989: 11.

Material examined

ANGOLA. Nr Bailundo: 1 imm., skull, 30-XII-1907, F. C. Wellman (BMNH 8.2.12.2). Calunda: 1 imm. ♂, alc., via Dundo Museum (BMNH 63.1013). Chitau: 1 ♂, skin, skull, collected 27-II-1933 by the Phipps Bradley Expedition, field number 902, at c. 1500 m (4930′) (neotype of *Epomops dobsonii* (Bocage, 1889), designated in this paper; AMNH 88068); 4 ♂♂, 4 ♀♀, 6-II/6-III-1933, Phipps Bradley Expedition (AMNH 88067/68, -73, -83, -85/87, -90/91). Hanha: 1 imm. ♀, mounted, skull extracted but not traced, 1895, J. d'Anchieta (MLZA 474b; “syntypo T117”). Kalonga: 1 ♂, 30-IX-1904, W. J. Ansorge (BMNH 5.5.9.3). Mount Moco: 2 imm. ♀♀, alc., 9/10-X-1954, G. Heinrich (FMNH 84030/31). Mount Soque: 1 ♂, 1 imm. ♂, 3 ♀♀, 1 imm. ♀, 3 specimens, alc., 25/28-VIII-1954, G. Heinrich (FMNH 84022/29, -32). Quindumbo: 1 ♂, mounted, skull extracted but not traced, 1887, J. d'Anchieta (holotype “T 116” of *Epomophorus dobsonii* Bocage, 1889; MLZA). (Alto Chicapa, Dondi, Gabela, Galanga.)

BOTSWANA.
(Kasane.)

MALAWI. Administration Camp, Kasungu National Park: 1 ♂, alc., skull, 24-I-1982, H. Jachmann (ZMA 21.689). Lifupa: 1 imm. ♀, alc., 9-I-1982, H. Jachmann (ZMA 21.688). Lisanthu: 1 imm. ♀, alc., skull, 7-III-1982, H. Jachmann (ZMA 21.692). Livingstonia: 1 ♂, alc. (BMNH 34.6.4.1). Rocky outcrop, Kasungu

National Park: 1 ♀, 1 imm. ♀, alc., 21/22-II-1982, H. Jachmann (ZMA 21.690/91).
(Zomba.)

RWANDA. Rubona: 1 ♂, 21-XII-1966, M. Anciaux de Faveaux (IRSN 16037).

TANZANIA. Kibwele: 1 ♂, alc., skull, 5-I-1983, T. C. E. Congdon (SMF 62863); 1 imm. ♂, alc., skull, 19-II-1983, K. Beakbane (SMF 66945). Tabora: 1 ♂, alc., skull, 1-III-1911, (via) G. Diesener (ZMB).

ZAIRE. Elizabethville: 1 ♀, 1930, via H. J. Brédo (IRSN 6280); 1 imm. ♀, alc., 12-I-1956, M. Anciaux de Faveaux (BMNH 57.432); 1 ♀, alc., skull, 1930, H. J. Brédo (ZMA 20.163). Kambove: 1 imm. ♂, 6-II-1907, S. A. Neave (BMNH 7.12.13.1). Kanzenze: 1 ♀, ≤V-1939, via R. P. Lefébure (IRSN 1811). Lusinga: 1 imm., 1941/1943, R. Grauvet (IRSN 10678); 1 ♂, 3 imm. ♂♂, 1 ♀, skeletons of 3, skins of 2, skulls, 3/19-I-1948, G. F. de Witte (IRSN 10666, -68/69, -74/75). Mulima: 1 ♀, 17-XII-1947, G. F. de Witte (IRSN 10664).
(Kasende, Katentania, Mwera.)

ZAMBIA. Abercorn: 1 ♀, alc., 1951, H. J. Brédo (IRSN 13109); 3 ♂♂, 3 ♀♀, 1954/1958, L. D. E. F. Vesey-Fitzgerald (HZM 1.1953, 2.2081, 3.2460, 4.2465, 7.3031, 8.3032); 2 ♂♂, 1 ♀, 3 imm. ♀♀, 2/10-IV-1964, cf. L. D. E. F. Vesey-Fitzgerald (BMNH 66.5402/07). Balovale: 1 ♀, 8-X-1938, T. D. Carter (AMNH 115821). Chavuma area: 1 ♀, 3-III-1959, W. F. H. Ansell (HZM 6.2862). Chipengali area: 1 ♂, 2 specimens, cf. 1963, V. J. Wilson (BMNH 66.5473/75). Kabompo District at 24 37 E, 13 05 S: 1 ♂, 14-XI-1959, W. F. H. Ansell (HZM 2.2801). Kafue River at 27 18 E, 12 18 S: 1 ♀, 23-II-1963, A. J. Tree (FMNH 96267). Ndola: 1 ♂ (BMNH 26.12.1.3). Sakeji Stream: 1 imm. ♀, 24-VI-1973, W. F. H. Ansell (ROM 73961). South Lueti River: 1 imm., 30-XI-1961, M. A. Traylor (FMNH 95213).
(Fort Jameson, Kabompo, Kafue River at 27 23 E/14 05 S, Kasama, Lusaka, Mindolo Dam, Mwekera, Salujinga; 1127C2, 1227A4, 1332B2.)

Fig. 8. Rostrum profile of a ♂ of *Epomops dobsonii* (Bocage, 1889) from Chitau, Angola (the neotype specimen; AMNH 88068).

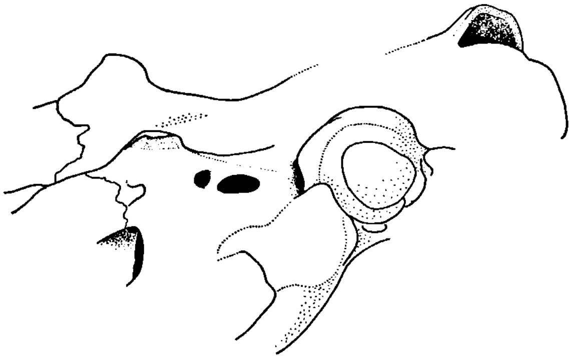

Fig. 9. *Epomops dobsonii* (Bocage, 1889): caudal end of right pterygoid wing. (Specimen: ♂ from Chitau, Angola; neotype specimen, AMNH 88068).

Diagnosis: Skull length intermediate between *Epomops franqueti* and *E. buettikoferi*; dorsal profile of rostrum convex (fig. 8), rostrum relatively long; zygoma relatively short, with low anterior insertion and moderate but distinct postorbital process; palate strongly concave from side to side and antero-posteriorly; posterior part of postdental palate with slightly raised lateral margins and thickened caudal margin; pterygoid wings raised, curling outward only slightly, ending anterior to tympanic bullae (fig. 9); tooth rows short, posterior third of jaws edentulous; no deciduous incisors; soft palate with five thick ridges, two of which postdental, and three or four thin and serrate ridges near posterior margin; second thick ridge bifurcate at extremities, fourth and fifth each with two large triangular projections pointing forward.

Measurement ranges and ratios taken from all over the species' range:

fal	♂♂	84.0-91.5	(n = 16),
	♀♀	80.4-88.3	(n = 15);
gsl	♂♂	52.4-55.3	(n = 14),
	♀♀	45.6-49.4	(n = 13);
cbl	♂♂	52.7-54.7	(n = 5),
	♀♀	45.3-48.4	(n = 8);
rl	♂♂	24.5-25.4	(n = 5),
	♀♀	19.7-21.2	(n = 7),
pl	♂♂	30.1-31.6	(n = 5),
	♀♀	25.7-27.5	(n = 8);
zw	♂♂	25.2-26.9	(n = 6),
	♀♀	23.6-25.4	(n = 7);

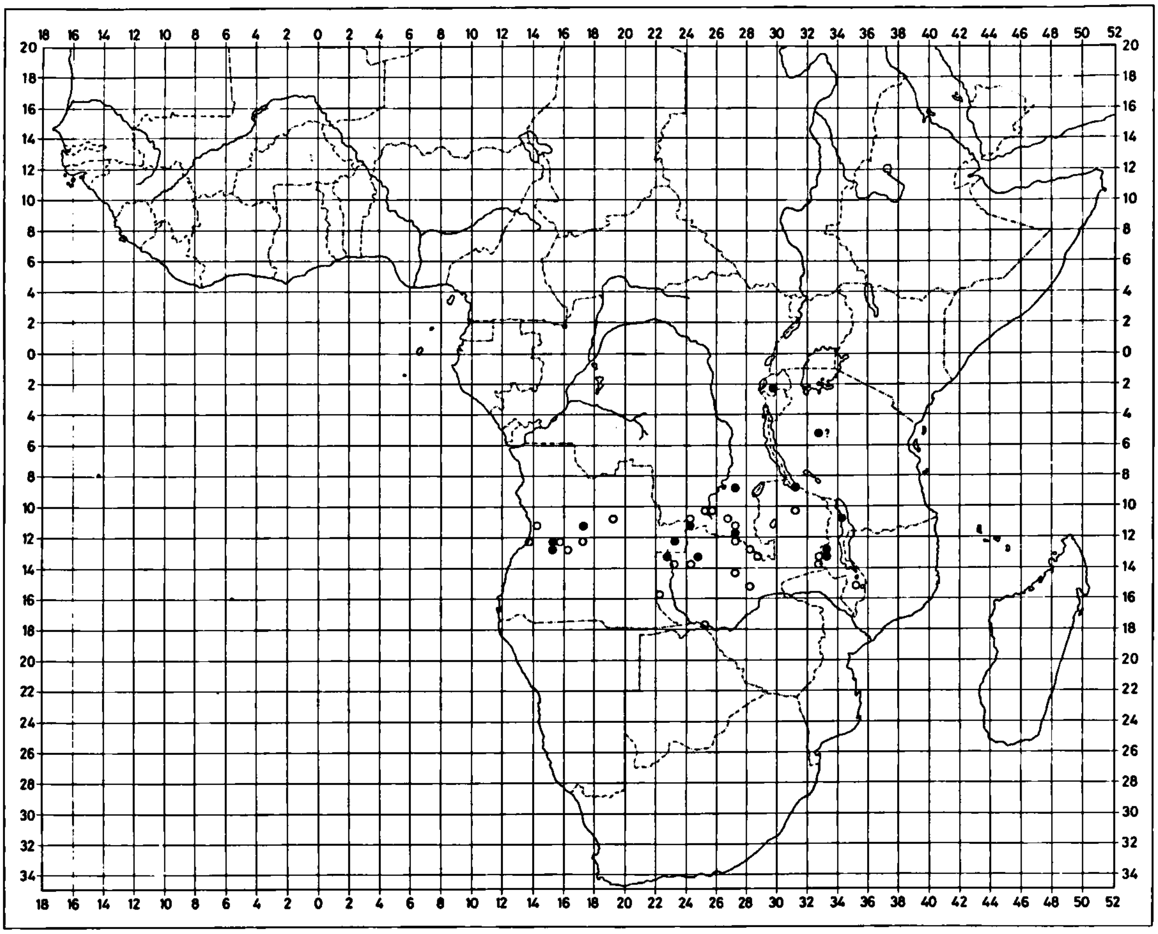

Fig. 10. Distribution of *Epomops dobsonii* (Bocage, 1889). Black dots: squares from where material has been identified by the author. N.B. Kibwele, at 35°13′E 08°36′S in Tanzania, should be added; see the text. Open circles: records from literature, museum registers and correspondence.

C^1-M^1	♂♂	14.5-16.7 (n = 7),
	♀♀	13.6-14.6 (n = 8);
rl	♂♂	45.7-46.8% of gsl (n = 5),
	♀♀	42.6-44.7% of gsl (n = 7);
pl	♂♂	55.9-57.4% of gsl (n = 5),
	♀♀	55.5-59.3% of gsl (n = 8);
zw	♂♂	46.8-50.0% of gsl (n = 5),
	♀♀	50.4-53.6% of gsl (n = 7).

A male specimen from Livingstonia, Malawi (BMNH 34.6.4.1) has a fal of 93.5. From the limited number of specimens measured, geographical variation in dimensions is not apparent. For measurements per country see table 7.

Distribution: Fig. 10.

Related species: Epomops franqueti and *E. buettikoferi* can easily be distinguished by their palatal ridge patterns and pterygoid wing morphology. *Epomophorus* species in general, and also the sympatric *E. angolensis* and *E. gambianus crypturus*, have relatively longer palates, relatively longer tooth rows, and six in stead of five thick palatal ridges.

Remarks

Taxonomy: In December 1975 I visited the Museu e Laboratório Zoológico e Antropológico (Museu Bocage) in Lisbon and examined type material of *Epomophorus dobsonii*. Of the holotype, a male from Quindumbo, Angola, only the mounted skin appeared to be still present—its skull could not be traced. There was another mounted skin without skull, of a female from Hanha, Angola which was labelled as syntype; however, its label mentioned the year 1895, and it must have been the specimen collected by J. d'Anchieta in that year and described by Bocage in 1896. Bocage did not mention any specimen but the holotype, in his original description (1889), but on the contrary emphasized that the holotype was the sole representative of the species then in his possession.

In March 1978 the Museu Bocage was hit by a great fire, which destroyed most of its collections and library (Palmeirim *et al.*, 1979). The type specimens of the African fruit bat species described by J. V. Barboza du Bocage and A. F. de Seabra and all other African Megachiroptera then present in the museum were also lost in this disaster (Dr J. M. Palmeirim, *in lit.*, 25-I-1981; Dr J. Crawford-Cabral, *in lit.*, 23-II-1981).

Bocage (1889) compared the type specimen to one of *Epomophorus angolensis* Gray, 1870 from the same locality (identified as *E. gambianus* by Bocage). He found the two species to be of about equal overall dimensions but in *dobsonii* the head was shorter and the fur colour more uniform and darker than in *angolensis*. He further noted that the first phalange of the fourth finger was relatively longer in *dobsonii* and that its palatal ridges were quite different. He gave an accurate illustration of the soft palate and described it well: the first ridge behind the canines, with a notch in the middle and pointing backward further than in *angolensis*; the second between P^3 and P^4, bifurcate at either extremity, the two branches ending at the two teeth mentioned; the third just before M^1, and rather like the fifth in *angolensis* (i.e. a slightly curved ridge, divided in the middle); the fourth behind M^1, flattened, with a free anterior margin with two triangular projections pointing forward; the fifth directly behind the fourth, with about the same form but somewhat smaller; posteriorly, Bocage's illustration shows three complete, thin, serrate ridges and a fourth which is centrally widely divided — the third of these thin ridges pointing sharply forward in the middle.

Andersen (1912) included the species in *Epomops*, on grounds which in my opinion are not very convincing and some of which are not tenable. His first reason must have been the form of the postdental palate. This is strongly concave with raised margins in large species of *Epomophorus*, especially in the males, and less concave without raised margins and flattening towards the margins in *Epomops*. *Epomops dobsonii*, however, presents transitional traits in this respect. Its palate is strongly concave, gradually rising from its greatest depth between the last upper molars towards the posterior margin; posteriorly, the lateral margins of the postdental palate are slightly raised; the posterior margin is thickened, and curved inward and slightly raised at either side of the median plane, all of which is not so in *Epomops franqueti* and *E. buettikoferi*. The palatal ridge pattern in *dobsonii* constitutes another character that Andersen thought to resemble that in *Epomops* rather than *Epomophorus*. He studied dry material of one adult and two immature specimens (of which at least one without soft palate: BMNH 8.2.12.2), and neither his short description nor his illustration is fully accurate. The first ridge is described as "slightly hastate" (not in the account of *Epomops* but in that of *Micropteropus pusillus*: Andersen, 1912: 557) and figured accordingly, approaching the state of this character in *Epomops franqueti* and *E. buettikoferi*. The second ridge, quite thick in the real and in Bocage's figure, appears as very thin in Andersen's; both its position and its bifurcate ends suggest its representing a fusion of what in an earlier state were two ridges (possible homologues of the second and third ridges in *Epomophorus*). The fourth and fifth ridges are described by Andersen (1912: 489, 494) as "thick and triangularly prominent", as "thinner" than the anterior three, and as "two pairs of prominent, triangular ridges", respectively. His figure (31C, p. 489) shows the fourth ridge whole and the fifth as if divided in the middle. In the alcohol specimens I have examined, both ridges are whole and undivided, with or without one or a few small additional projections between the two large ones. Finally, Andersen (same pages) wrote about "one or two" and "one or a few" thin, serrate ridges near the posterior edge of the palate. In the alcohol specimens I have examined there are three of these ridges (the third pointing forward in the middle, its point interrupting the second) and in some, as in the holotype, lateral parts of a fourth.

If it can be agreed that the second ridge is a fusion of a second and third in an earlier state, the soft palate has derived from one with six thick ridges, two of which postdental, and three or four thin ridges: a pattern as in *Epomophorus* rather than *Epomops*.

Andersen furthermore pointed out that the cranial characters in *Epomops dobsonii* would be essentially as in *E. buettikoferi* and that *dobsonii* would even be "probably a southern representative of *E. buettikoferi*, with peculiarly modified palate-ridges and somewhat weaker dentition." There is, however, at least one cranial character in which *dobsonii* is consistent with *Epomophorus* and not with *Epomops*, and this must have escaped Andersen's attention. As included in the diagnoses of all three *Epomops* species, and shown in figs. 6, 9 and 12, the form of the pterygoid wing serves to distinguish *dobsonii* from both *buettikoferi* and *franqueti*. In *dobsonii* it is rather high, curling outward only weakly, and ending at some distance anterior to the tympanic bulla. In both other species it remains lower, curls outward rather strongly, and continues to meet the tympanic bulla at its antero-internal side; just caudal of the oval foramen it curls so far outward as to touch the base of the skull, enclosing a space, widening towards the tympanic bulla. I have not found a description of this structure in the general osteological literature (Flower, 1885; Romer, 1962; Grassé, 1967; Moore, 1981) and its possible function is not known to me. Although in some other genera of African Megachiroptera the pterygoid wing also extends towards the tympanic bulla (*Rousettus* Gray, 1821; *Lissonycteris* Andersen, 1912; *Myonycteris* Matschie, 1899), this extension is never raised and curled outward, but rather a low ridge. In *Pteropus* Brisson, 1762, *Eidolon* Rafinesque, 1815, *Megaloglossus* Pagenstecher, 1885 and in the epomophorine genera *Epomophorus*, *Nanonycteris*, *Scotonycteris* Matschie, 1894 and *Casinycteris* Thomas, 1910 the wing gradually looses height as it continues backward and always ends well before the tympanic bulla. In *Micropteropus* and *Plerotes* (fig. 18c) this ridge appears to be slightly inflated and only in the latter genus does reach the bulla. The condition described for *Epomops franqueti* and *E. buettikoferi*, however, is found in only one other genus of African Megachiroptera, i.e. *Hypsignathus*. This seems to add to the arguments in favour of a close phyletic relationship of that genus to typical *Epomops* (i.e. *franqueti* and *buettikoferi*), and strengthen the idea that *Epomops dobsonii* is possibly not well placed in *Epomops*.

My reasons for maintaining its allocation in that genus are that the species is not a typical representative of *Epomophorus* either, nor, for that matter, of one of the other epomophorine genera that have been described, and that before a shift in its taxonomic position can be proposed other characters, in particular the anatomy of its vocal organs, should be examined and compared to those of the other epomophorine species — including a number for which this anatomy has also not yet been studied.

In view of the questionable taxonomic position of the species and the complex and as yet insufficiently established taxonomy of the group of epomophorine species as a whole, it is desirable to designate a neotype specimen. As such, I have selected an adult male specimen, skin and skull, collected 27-II-1933 at Chitau, 4930′ (1503 m), Angola by the Phipps-Bradley Expedition, field number 902, in the American Museum of Natural History, New York (AMNH 88068). Quindumbo (or Chindumbo), the original type locality, was placed by Hill *et al.*, 1941 at 15°05′E 12°30′S, which according to my maps (Times Atlas; and Main

Table 7. Ranges of selected measurements of *Epomops dobsonii* (Bocage, 1889) per country.

					♂♂							♀♀			
		fal	gsl	cbl	rl	pl	zw	C^1-M^1	fal	gsl	cbl	rl	pl	zw	C^1-M^1
Angola	n	7	6	1	1	1	1	1	5	4					
	m	86.7	53.4						83.4	46.7					
	min	84.0	52.4	53.3	24.8	30.3	27.0	16.3	82.0	45.6					
	max	90.5	54.8						84.2	47.5					
Malawi	n	1	1	1	1	1	1	1	1						
		89.9	53.6	53.7	25.1	30.1	26.4	16.1	88.3						
Rwanda	n	1	1	1	1	1	1	1							
		90.5	-	-	-	-	26.6	-							
Tanzania	n	1	1	1	1	1	1	1							
		91.5	55.3	54.5	25.4	31.6	26.6	16.7*							
Zaire	n	1	1	1	1	1	1	1	4	3	3	3	3	3	4
	m								81.8	46.1	45.7	21.0	25.9	23.9	14.0
	min	85.0*	-	-	-	-	25.2	14.5	80.3	45.6	45.3	20.0	25.7	23.6	13.6
	max								83.7	46.8	46.1	22.0	26.1	24.6	14.2
Zambia	n	3	5	2	2	2	2	3	5	6	5	5	5	4	4
	m	86.5	54.0						83.0	47.1	46.3	20.2	26.7	24.8	14.1
	min	84.2	53.0	53.3	24.7	30.8	25.8	14.9	80.4	45.9	45.4	19.7	25.8	23.9	13.8
	max	87.7	55.1	54.7	25.2	30.9	26.9	16.2	86.5	49.4	48.4	21.2	27.5	25.4	14.6

* approximated

Administration of Geodesy and Cartography under the Council of Ministers of the USSR, 1987) is on the most elevated part (2000-2600 m) of the western Angolan plateau, in western Huambo. (To judge from the altitude, I presume that the location may have been in one of the valleys in the area.) (Since the completion of this paper, I received Crawford-Cabral's paper of 1989, in which several of Hill *et al.*'s coordinates, among which those of Quindumbo, are replaced by others. Chindumbo is at 14°56'E 12°28'S, between 1350 and 1450 m.) There are but a few other records from this area: the material from Galanga recorded by Bocage (1898) was also lost in the Lisbon museum fire; the specimen from Bailundo recorded by Andersen (1912) is a juvenile; the single specimen from Dondi recorded by Hill (1941) is an adult ♀ (skin, skull, 30-VI-1936, K. H. Prior, MVZ 88694); the skull has the left zygomatic arch broken, and a small amount of the right occipital bone is missing (Dr W. Z. Lidicker, Jr, *in lit.* 12-VII-1989). From near the margins of the plateau some more *dobsonii* localities are known. Among these, Chitau stands out because it is represented by a series of 25 specimens, nine of which adult, in the AMNH collection.

The measurements of the neotype specimen (also partly included in table 7) are: fal 86.4, third metacarpal length 63.0, fourth metacarpal length 56.4, fifth metacarpal length 62.2; gsl 53.7, cbl 53.3, rl 24.8, pl 30.3, cranium width 18.0, iow 7.5, pow 10.5, zw 27.0, C^1-C^1 10.5, C^1-M^1 16.3, M^1-M^1 14.7; mandibulum length 42.7, mandibulum height 15.1, C$_1$-M$_2$ 17.7; length x width C^1 3.0 x 2.15, P^3 2.5 x 1.8, P^4 2.8 x 1.65, M^1 2.75 x 1.5, C$_1$ 1.9 x 1.9, P$_1$ 1.2 x 1.2, P$_3$ 2.3 x 1.75, P$_4$ 2.55 x 1.6, M$_1$ 2.75 x 1.45, M$_2$ 1.6 x 1.3.

Distribution and geographical variation: All but two of the localities are in a west-east belt between 8° and 18°S and all are west of 36°E. The exceptions are Rubona in Rwanda and Tabora in Tanzania, which will be discussed later. The two main distribution areas seem to be in West and Central Angola, and Zambia and adjoining southeast Zaire, Malawi (where the species has recently been found at Zomba: Dr. N. J. van Strien, pers. comm., 29-VII-1989) and the extreme North of Zimbabwe. In these areas, the species is largely restricted to woodland vegetations: 20 out of 42 localities (47.6%) are in Wetter Zambezian miombo woodland (dominated by *Brachystegia*, *Julbernardia* and *Isoberlinia*) (type 25 in White, 1983), and eight others are either in this or in an adjoining type nearby or a mosaic of both. The species appears to be restricted by the belts of shrubland and desert vegetations lining the Atlantic coast in the West, by the Lower Guinea rain forest block in the North, and by drier vegetation such as the Mosaic of Zambezian dry deciduous forest and secondary grassland, and the Drier Zambezian miombo woodland (dominated by *Brachystegia* and *Julbernardia*) (types 22a and 26 in White, 1983) to the South, southeast, and East. The species' apparent preference for woodland habitats presents an ecological argument to relate it to *Epomophorus* rather than *Epomops*. Hanha, from where Bocage (1896) recorded the species, is in the Bushy Karoo-Namib shrubland (type 51 in White, 1983) but at c. 15 km from the North Zambezian woodland (type 29c in White, 1983) which somewhat further east gives way to the mentioned Wetter Zambezian miombo woodland preferred by the species, and the specimen may have come from this hinterland. To the northeast, the species seems to occur in western Tanzania and in Rwanda. Bergmans (1979a) recorded a specimen from Tabora, Tanzania, which he located at 32°50'E 05°02'S. Since then, three other Tabora's in Tanzania were found: two are near the border with Zambia (at 32°38'E 08°43'S and c. 32°58'E 09°03'S, respectively) and in the Wetter Zambezian miombo woodland, and therefore more likely candidates than the third, at c. 36°55'E 10°45'S, and than the well-known city of Tabora chosen by Bergmans in 1979(a), which are both in the Drier Zambezian miombo woodland (dominated by *Brachystegia* and *Julbernardia*) (type 26 in White, 1983).

Note added in proof: Since the completion of this article, I found two Tanzanian specimens of *Epomops dobsonii* collected at Kibwele (35°13'E 08°36' S), in the SMF collection. This locality is in Afromontane vegetation at 1890 m, and suggests that the species is to be expected in the broad stretch of Wetter Zambezian woodland (type 25 in White, 1983) bordering almost the entire eastern shore of Lake Malawi.

More to the west in Tanzania the Wetter Zambezian miombo woodland stretches northward to Lake Victoria: a possible corridor to Rwanda, where one specimen has been collected at Rubona in the Mosaic of *Brachystegia bakerana* and edaphic grassland (type 45 in White, 1983); this specimen, an adult ♂, consists of a skin and an incomplete skull and was labelled as *Epomophorus* cf. *crypturus*. Its gsl is >51.0 (being the length without the missing premaxillae) and its fal is 90.5. Two other epomophorines are to be considered: *Epomophorus gambianus (crypturus)* and *Epomops franqueti*; other species of the same size class are not to be expected here. However, neither palate morphology nor C^1-M^1 length are as in those species; the palate is strongly concave and postdentally quite broad (14.5, anterior to the zygomata), without a raised posterior margin, which margin is concave at either side of the median plane. All teeth are missing but over the alveoles the upper teeth row measures 14.3 (over the cingulae it may have been 15.5), leaving at least a third of the jaw edentulous. In addition to this, the cranium is rather broad (18.1) and the iow (7.0) and pow (10.3) are also as in *E. dobsonii*.

Some data suggest that eastern populations may be characterized by slightly heavier dentition, but the numbers of measurements for the various regions are too small to be conclusive on this point.

Epomops buettikoferi (Matschie, 1899)

Epomophorus buettikoferi Matschie, 1899: 45 (type locality Schieffelinsville).

Epomops buettikoferi; Andersen, 1910: 105; Andersen, 1912: 499; van Orshoven *et al.*, 1968: 182, Hayman *et al.*, 1971: 8; De Vree, 1971: 34; Bergmans *et al.*, 1974: 29; Bergmans, 1975; Coe, 1976: 543; Verschuren, 1977: 617; Bergmans, 1982: 158; Wolton *et al.*, 1982: 429; D. W. Thomas, 1984; D. W. Thomas *et al.*, 1984; Zeller, 1984: 215.

Epomophorus (Epomops) franqueti buettikoferi; Kuhn, 1965 325, 1968: 171; Püscher, 1972.

Material examined

GHANA. Ahiriso: 6 ♀♀, 25/28-I-1968, J. C. Geest (USNM 414003/05,-07/08). Bimpong Forest Reserve: 1 ♀, alc. (BMNH 66.6241). Butre: 9 ♂♂, 7 ♀♀, 17/22-I-1968, J. C. Geest (USNM 413911, -14, -17, -22/23, -27, -32/34, -49/50, -60, -65, -67, 414000/01). Jukwa: 7 ♂♂, 7 imm. ♂♂, 7 ♀♀, 7 imnm. ♀♀, 17/21-VIII-1967, B. J. Hayward (USNM 411563/86, -90, -92/93, -96). 6 miles N of Kade: 1 ♀, 29-III-1968, J. C. Geest (USNM 414752). Kumasi: 1 ♀, alc., 1928, via G. Heizmann (NMBA 4108); 1 ♀, 15-V-1961, D. H. Barry (BMNH 65.739); 2 ♀♀, 3-XI-1964, F. R. Allison (BMNH 65.684/85); 2 ♂♂, 2 ♀♀ (skulls only), 29-III/2-VII-1965, D. H. Barry (BMNH 66.6209/12). Legon: 1 ♀, 1-XII-1967, J. C. Geest (USNM 411328). Oda: 1 imm. ♀, 3-VI-1946, G. S. Cansdale (FMNH 55764). 32 miles W of Prestea: 5 ♂♂, 4 imm. ♂♂, 10 ♀♀, 7/12-I-1968, J. C. Geest (USNM 413887/88, -92/99, 413900/08). Takoradi: 1 ♂, 2 ♀♀ (1: alc., 1: skull only), 2-IV/30-V-1965, D. H. Barry (BMNH 66.6215/17). Ghana: 1 ♀, A. M. Mackilligin (BMNH 8.8.6.11).
(7 miles NE of Kade, Kuwari, Sewhi Wiaso.)

GUINEA. Kankasili: 3 ♂♂, 8 ♀♀ (2: skulls only; 2: skins only), 1 skin and 1 imm., 15-XI-1966/1-III-1967, J. van Orshoven (ZMA 10.733, 10.866/68, -70, -72/73, -75, -77, -79, -83, -85/86).

IVORY COAST. Adiopodoumé: 1 imm. ♀, 11-VIII-1970, ORSTOM (ZMA 17.275); 1 ♂, alc., 16-XI-1970, ORSTOM (ZMB). Adzopé: 2 ♂♂, 3 ♀♀, 1 imm. ♀, 4 imm., 8-III-1971, J. Vissault (ZMA 17.295/99; others: MNHN). Ahierémou: 1 ♂, 4 ♀♀, 3 imm., 22/25-XI-1972, J. Vissault (ZMA 17.300/03; others: MNHN). Banco Forest: 1 ♀, 30-XI-1969, L. W. Robbins (USNM 429884). Blékoum: 2 ♀♀, 21-I-1969, J. W. LeDuc (USNM 429885/86). Bolo: 1 ♂, 1 imm. ♂, 2 ♀♀, 1 imm. ♀, 31-I/2-II-1973, J. Vissault (ZMA 17.304/05; others MNHN). Diala: 1 ♀, 12-II-1969, J. W. LeDuc (USNM 429844). Gueboua: 1 ♂, 25-XI-1970, ORSTOM (ZMA 17.273). Guitri: 1 ♂, ♀, 8-VI-1969, T. J. McIntyre/L. W. Robbins (USNM 467872, -79). Konankoffikro: 4 ♂♂, 15 ♀♀, 1 imm., (2: skulls only), IX-1970, ORSTOM (ZMA 17.084/93; others: MNHN). Lamto: 23 ♂♂, 2 ? ♂♂, 1 imm. ♂, 2 imm. ? ♂♂, 3 ♀♀, 1 imm. ♀, (5: alc., skull), 1964/1970, ORSTOM (ZMA 17.257/65, -68/72; others: MNHN) and J. W. LeDuc/L. W. Robbins (USNM 465740/43). Matonguiné: 1 ♂, 2 ♀♀, 20/21-I-1973, J. Vissault (MNHN). Niebe: 2 imm. ♂♂, 1 ♀ (skin only), 1 ♀, 27-II/26-IX-1969, ORSTOM (MNHN) and J. W. LeDuc/L. W. Robbins (USNM 465735/36, -38). Soubre: 1 ♂, 15-V-1969, T. J. McIntyre (USNM 467876). Toumodi: 1 ♂, 1 ♀, 19-VIII-1971, L. W. Robbins (AMNH 239367/68). Yapo-Sud: 2 ♀♀, 1 imm. ♀, XII-1968, J. W. LeDuc (USNM 429888, -91/92). Ivory Coast: 3 ? ♂♂ (skulls), 3 ? ♀♀ (2: skulls, 1: skin), ORSTOM (ZMA 17.307; others: MNHN).
(Abidjan, ? 33 km W of Korhogo, Toyébli.)

LIBERIA. Cape Palmas: 1 ♀, alc., skull, Th. R. Steele (USNM 38189). Du Queah River or Du River: 1 ♀, 5-II-1944, H. H. Burgess (AMNH 167541). Grand Bassa: 1 ♂, alc., skull, A. McCloy (BMNH 8.7.27.1). Harbel: 1 ♀ (AMNH 204449); 2 ♂♂, 19-VII-1963, A. E. Weyer (AMNH 207007/08); 1 ♂, alc., skull (LACM 19584). Iti: 1 imm. ♂, alc., 8-II-1966, J. Verschuren (IRSN 16101). Mount Coffee: 1 imm. ♂, alc., skull, 1-III-1897, R. P. Currie (USNM 83798). Mount Nimba: 2 imm. ♂♂, alc., 7 ♀♀ (6: alc.), 1 imm. ♀, 1965/1966, J. Verschuren (IRSN 16093/103); 1 ♂, 1 imm. ♂, 1 imm. ♀, 2-V/19-VII-1966, M. J. Coe (BMNH 67.1433/35). Mühlenburg-Mission: 1 imm. ♂, alc., skull, 19-X-1880, J. Büttikofer/C. F. Sala (RMNH 19638). Schieffelinsville: 1 ♂. alc., skull, F. X. Stämpfli (holotype of *Epomophorus buettikoferi* Matschie, 1899; RMNH); 1 ♀, alc., skull, 11-I-1887, J. Büttikofer/C. F. Sala (RMNH 19639). St. Paul's River: 1 imm. ♀, alc., skull, VI-1892, O. F. Cook (USNM 37892). Tappita: 1 specimen, 1960, H. Himmelheber (SMF 20063). Tars Town: 3 ♂♂, 1 imm. ♂, 3 ♀♀, 2/19-VII-1971, D. A. Schlitter (USNM 467872/77); 1 ♀, 1-VIII-1971, L. W. Robbins (AMNH 239365). Yekepa: 2 imm. ♂♂, 23/25-VII-1965, J. Verschuren (IRSN).
(Bavia, Bendu, Deaple, ? Grand Lapin, Gwene Town, Pelokehn, Robertsport, Salayea, Soforé-Place, Teaye.)

NIGERIA. Arusua: 1 ♂, 2 ♀♀ (1: alc., skull), 8/9-VII-1976, W. Bergmans (ZMA 19.084/86). Ife: 2 ♂♂, 1 imm. ♂, 2 ♀♀, 2 imm. ♀♀, alc., skulls, 14/17-VIII-1976, W. Bergmans (ZMA 19.090/96). Ilesha: 1 ♂, 24-VIII-1963, (HZM 2.4229). Pandam Wildlife Park: 1 imm. ♂, 1 ♀, 1 imm. ♀, alc., skulls, 2/4-VII-1976, W. Bergmans (ZMA 19.081/83).

SIERRA LEONE. Bo: 1 ♀, VI-1961, A. Todd (HZM 1.3483). Freetown: 1 ♂, alc., skull, 23-IX-1886, Swoboda (NMW 17.866). Njala: 3 ♂♂, 1 ♀, alc., skulls, T. S. Jones (BMNH 59.201/04). Sierra Leone: 1 ♂, alc., skull, Royal Army Medical College (BMNH 9.1.4.4); 1 ♀, alc., skull (BMNH 66.22.1).
(Bonthe, Lumley Village, Lunsar, Mount Aureol.)

Diagnosis: Skull relatively long, dorsal profile of rostrum straight or somewhat convex (fig. 11); rostrum and palate relatively long, palate rather strongly concave from side to side and anteroposteriorly; zygoma long, without distinct postorbital process; pterygoid wings extending

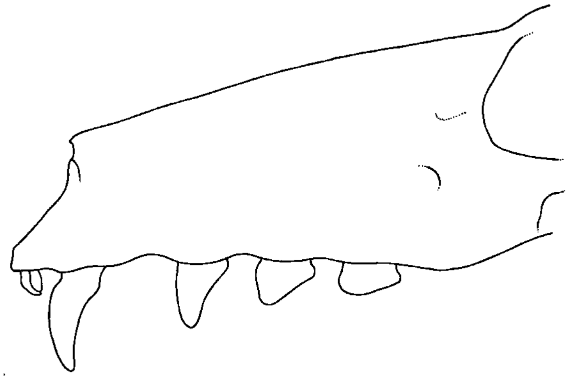

Fig. 11. Rostrum profile of a ♂ of *Epomops buettikoferi* (Matschie, 1899) from Lamto, Ivory Coast (ZMA 17.271).

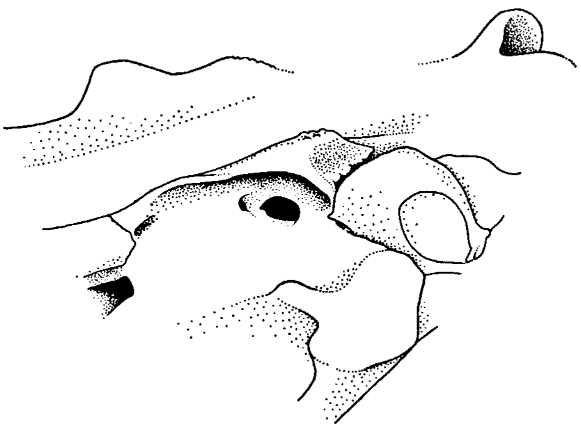

Fig. 12. *Epomops buettikoferi* (Matschie, 1899): caudal end of right pterygoid wing. (Specimen: ♂ from Lamto, Ivory Coast; ZMA 17.271.)

to tympanic bullae and curled outward posteriorly, forming a cavity (fig. 12); tooth rows rather short; second upper incisors rarely deciduous; soft palate with, from front to back, three thick and five to eight rather thin ridges, with the third thick ridge usually widely divided in the middle (very rarely undivided), the thin ridges irregularly serrated (with forward pointing teeth), the first five centrally divided by a wide groove narrowing posteriorly, the posterior ones undivided; the halves of the first thin ridge shortest, angular, consisting of one large tooth and very few small ones each; the halves of the second to fourth or fifth thin ridges also angular, dominated by a single central tooth each, but with more additional small teeth; the posterior ridges more finely serrated, and often slightly curved or angulated — pointing forward — in the middle.

Measurement ranges and ratios taken from all over the species' range:

fal	♂♂	88.6-102.2	(n = 67),
	♀♀	82.4- 95.0	(n = 89);
gsl	♂♂	50.9- 61.0	(n = 60),
	♀♀	45.8- 52.9	(n = 86);
cbl	♂♂	52.5- 59.4	(n = 25),
	♀♀	47.0- 51.8	(n = 29);
rl	♂♂	22.7- 28.5	(n = 31),
	♀♀	17.7- 23.5	(n = 37);
pl	♂♂	30.0- 36.7	(n = 26),
	♀♀	27.0- 31.2	(n = 30);
zw	♂♂	27.0- 30.3	(n = 33),
	♀♀	23.9- 27.3	(n = 30);
C^1-M^1	♂♂	17.2- 20.3	(n = 36),
	♀♀	14.9- 17.9	(n = 42);
W	♂♂	133 -198	(n = 8),
	♀♀	94 -132	(n = 12);
rl	♂♂	43.6- 47.6% of gsl	(n = 25),
	♀♀	41.1- 44.4% of gsl	(n = 31);
pl	♂♂	58.5- 61.7% of gsl	(n = 22),
	♀♀	56.6- 60.4% of gsl	(n = 25);
zw	♂♂	47.0- 53.4% of gsl	(n = 26),
	♀♀	47.3- 55.7% of gsl	(n = 26).

Specimens largest in the western part of the species' range, and smallest in the eastern part. For size classes per country see table 8.

Distribution: Fig. 13.

Related species: Epomops franqueti is very similar but averages smaller in all measurements where it is sympatric (see table 8); its dorsal rostrum profile is often concave, its rostrum and palate are relatively shorter, its second upper incisors are frequently deciduous, its third palatal ridge is usually not divided, and its thin palatal ridges are morphologically different. *Epomops dobsonii* averages smaller and differs in morphology of pterygoid wings and of soft palatal ridges.

Remarks

Taxonomy: When Matschie (1899) described *Epomophorus buettikoferi* he did so on the basis of

Table 8. Forearm lengths, greatest skull lengths and weights of *Epomops buettikoferi* (Matschie, 1899) per country. Order of countries approximately from west to east.

		♂♂			♀♀		
		fal	gsl	W	fal	gsl	W
Guinea	n	3			4	1	
	m	95.2			89.5		
	min	94.1			87.8	49.0	
	max	96.2			90.8		
Sierra Leone	n	1	3		2	3	1
	m		57.1			49.7	
	min	101	57.8		86.4	48.5	94
	max		59.0		90.4	50.4	
Liberia	n	2	6		13	8	
	m		59.2		89.8	50.3	
	min	97.9	57.9		87.4	49.0	
	max	99.7	61.0		92.9	52.0	
Ivory Coast	n	37	27	4	30	31	6
	m	97.6	58.2	169	90.0	50.5	109.5
	min	92.9	55.0	145	83.4	48.2	100
	max	102.2	60.2	198	95.0	52.9	132
Ghana	n	21	21	1	35	38	
	m	93.8	54.5		88.1	49.1	
	min	88.6	50.9	146	82.4	45.8	
	max	102.1	58.8		92.1	51.7	
Nigeria	n	4	4	3	5	5	5
	m	93.9	53.8	148	88.6	48.6	116
	min	92.4	52.6	133	85.5	48.3	107
	max	97.4	54.6	162	92.7	49.1	125

size. He had not seen the single specimen he assigned to it but relied on the data published by Jentink (1888a). Andersen (1910) found it to represent a distinct species of *Epomops*, with "its true characters (...) entirely different from those given by Matschie". (Matschie had considered *Epomops* a subgenus of *Epomophorus*.) It is ironic that, apart from the important and correct assigment to another genus, *buettikoferi* should now be distinguished from its nearest living relative, *franqueti*, mainly on the basis of size. The other diagnostic characters put forward by Andersen are to some extent subject to variation which typically diminishes the morphological distance to *franqueti*, rendering it extremely difficult sometimes to identify particular single specimens, especially when they are not full-grown. This is probably also true for some of the differential characters mentioned in the present paper: the relatively greater length of rostrum and palate are no doubt related to the greater absolute length of the skull. Some authors (Kuhn, 1965; Püscher, 1972) have suggested that *buettikoferi* should be considered a subspecies of *franqueti*, but they offered no arguments on this point, which demonstrates a gross underestimation of the problem involved. Others (Rosevear, 1965; Hayman *et al.*, 1971; De Vree, 1971; Bergmans *et al.*, 1974; Bergmans, 1975 and 1982) have stressed the co-existence in West Africa of two species of *Epomops*, and also their partial

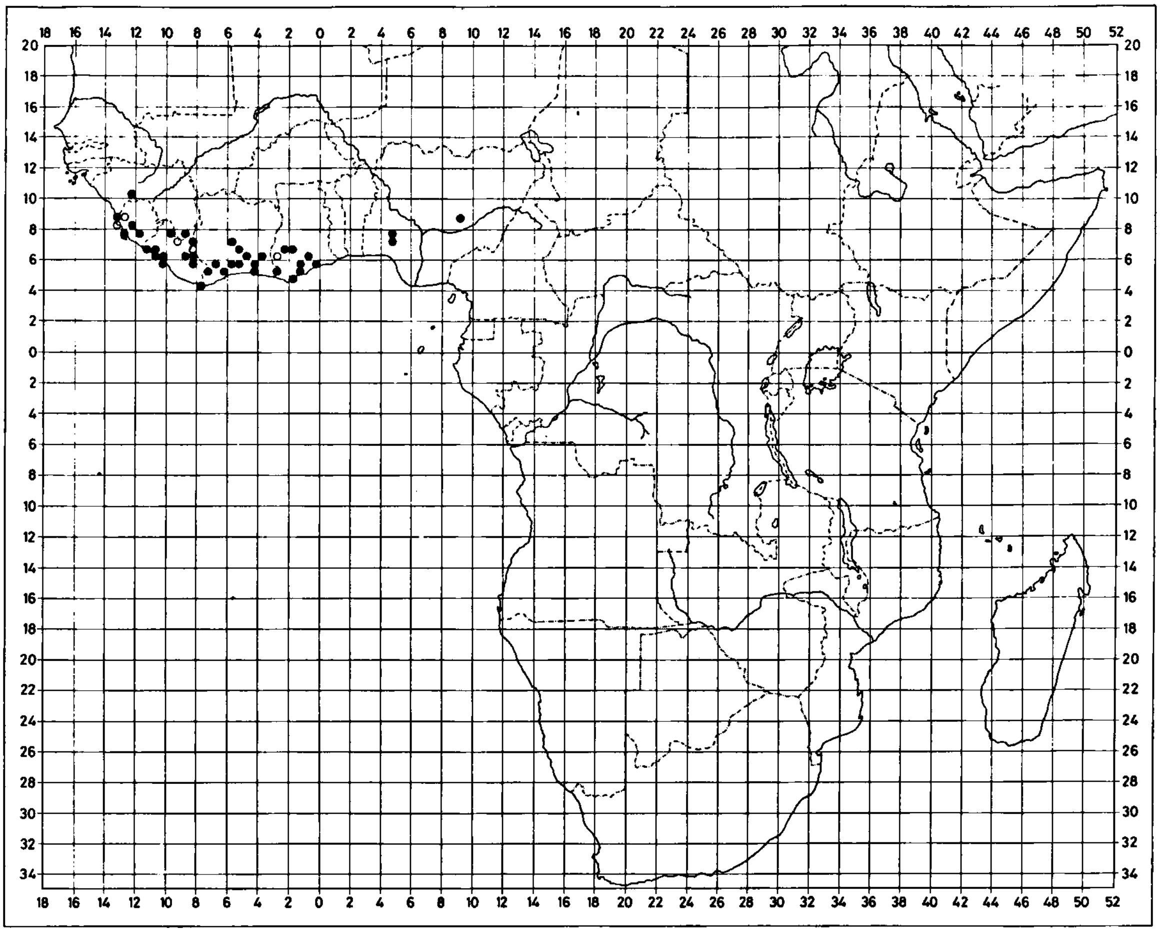

Fig. 13. Distribution of *Epomops buettikoferi* (Matschie, 1899). Black dots: squares from where material has been identified by the author. Open circles: records from literature, museum registers and correspondence.

overlap in distribution. De Vree (1971) pointed out that the palatal ridge configuration in *buettikoferi* from Ivory Coast is different from that in *franqueti* from Togo, and in his postscriptum he mentioned to have examined the first *franqueti* specimens from Ivory Coast — apparently with palatal ridges as in the Togo specimens and moreover from a locality from where he also recorded *buettikoferi*: Adiopodoumé. Unfortunately, De Vree did not discuss body or skull dimensions. Bergmans *et al.* (1974) examined larger series of both species from Ivory Coast: 27 specimens of *franqueti* and 66 of *buettikoferi*. Recent re-examination of the ZMA part of this material revealed that some of the specimens are probably sexed wrongly — dry skins do often not allow for an easy check — and that in some cases skins and skulls are incorrectly allotted to the same specimen; on top of this, a more critical age assessment (a result of many more years in fruit bat taxonomy) brought on another small shift in the appreciation of this series. Nevertheless, the main conclusion of Bergmans *et al.* (1974), further elaborated in Bergmans (1975), namely that there are, in Ivory Coast and in Ghana, two distinct size classes of *Epomops*, identifyable with *buettikoferi* and *franqueti*, respectively, remains valid.

In 1982 Bergmans assigned a number of Nigerian *Epomops* specimens to *buettikoferi*. Its

Table 9. Size and weight of *Epomops buettikoferi* (Matschie, 1899) and *Epomops franqueti* (Tomes, 1860) in countries of sympatry. Available data for Togo and Benin included.

		♂♂						♀♀					
		buettikoferi			*franqueti*			*buettikoferi*			*franqueti*		
		fal	gsl	W	fal	gsl	W	fal	gsl	W	fal	gsl	W
Ivory Coast	n	37	27	4	13	10	8	30	31	6	20	11	8
	m	97.6	58.2	169	86.2	46.2	102	90.0	50.5	109.5	79.9	40.3	72
	min	92.9	55.0	145	84.0	44.4	92	83.4	48.2	100	76.5	37.8	61
	max	102.2	60.0	198	88.9	48.7	115	95.0	52.9	132	84.3	41.9	81
Ghana	n	21	21	1	60	62	12	35	38		58	60	11
	m	93.8	54.5		87.9	47.0	126.7	88.1	49.1		82.2	42.2	94.5
	min	88.6	50.9	146	83.5	43.7	110	82.4	45.8		77.0	38.6	88
	max	102.1	58.8		93.9	49.9	140	92.1	51.7		87.1	45.3	102
Togo	n				1								
					89								
Benin	n										1	1	
											82.7	41.3	
Nigeria	n	4	4	3	16	13	3	5	5	5	30	23	7
	m	93.9	53.8	148	90.3	47.5	130.7	88.6	48.6	116	83.6	42.4	94.2
	min	92.4	52.6	133	85.8	45.4	119	85.5	48.3	107	79.1	40.2	90
	max	97.4	54.6	162	95.1	50.6	142	92.7	49.1	125	88.5	44.5	110

occurrence in that country had been alluded to by Hayman *et al.* (1971). Happold (1987), in his commendable work on Nigerian mammals, has not included *Epomops buettikoferi*; he listed the specimens from Ilesha (HZM) and Pandam Game Reserve (ZMA) referred to *buettikoferi* by Bergmans (1982) under *franqueti*, but did not include their measurements in the ranges given for that species. In a foot-note he remarked that there is some evidence for the occurrence of *buettikoferi* in Nigeria but that more specimens are required to ascertain either this or that *franqueti* "shows a greater range of variation than is known at present". (His reference here to Bergmans, 1977 is erroneous.) If Happold would have included the *Epomops* measurements of Bergmans (1982) and if he would have considered the sexes separately, his conclusion would probably have been different.

In table 9, dimensions of *buettikoferi* and *franqueti* from countries of sympatry are compared. The numbers of Nigerian *buettikoferi* are low, and the specimens involved are smaller than typical specimens (compare table 8). In fact they agree reasonably well with specimens from Ghana. The difference between Nigerian *buettikoferi* and *franqueti* (which latter species reaches relatively large dimensions in Nigeria: see the discussion of its intraspecific variation) is most apparent in skull dimensions. Especially the female gsl range in *buettikoferi* of 48.3-49.1 (n = 5) is convincingly disjunct with that of 40.2-44.5 in 23 Nigerian *franqueti*, but the male gsl ranges, 52.6-54.6 (n = 4) and 45.4-50.6 (n = 13), respectively, are also covering, between them, a variation of some 9 mm: rather too much for one species within a rather restricted area.

Rosevear (1953) wrote that *buettikoferi* and *franqueti* had recently been found to meet at Kumasi in Ghana. There is ample material in the BMNH, where he worked, which can be identified with *buettikoferi* on the basis of size alone (see the section on material examined). The identity of an immature ♂ labelled as *franqueti* (BMNH 65.740) is less certain, however. In all these specimens, the soft palate has not been preserved. A more detailed study of this material (including some other specimens in alcohol), for which I had no opportunity yet, is necessary to answer the question of sympatry at Kumasi. Other *Epomops* material from Kumasi is in the NMBA (no. 4108, adult ♀, alc., fal 83.6, gsl about 46, palatal ridges as in *buettikoferi*) and in the ROM (no. 56520, ♀, alc., fal 88.6, not examined).

De Vree (1971) recorded both *buettikoferi* and *franqueti* from Adiopodoumé in Ivory Coast. Of the first, he figured the soft palate; of the second, he only mentioned its find and it must be inferred that it was also identified by its palatal ridge pattern. Bergmans *et al.* (1974) confirmed the sympatry at Adiopodoumé and mentioned Lamto in Ivory Coast as a further site of sympatry; they examined a large series of *franqueti* from Adiopodoumé, but only three *buettikoferi*. One of the latter (ORSTOM A 8298) was later re-identified as *franqueti* (Bergmans, 1975: 149) (I now suspect that its skin and skull do not belong together), but the others are clearly *buettikoferi*, both by palatal ridges and size: a ♂, alc., fal 96.7, gsl c. 60 (ORSTOM A8756, now in the ZMB) and an immature ♀, fal 90.2, gsl ≥47.5 (ORSTOM A8362, now ZMA 17.275). From Lamto, there was a large series of unmistakable *buettikoferi* but only one immature ♀, with fal 74.0 and gsl 39.1, identified as *franqueti* on the basis of its undivided third palatal ridge and small molars (M^1 length 2.7). This is, of course, meagre evidence, the more so because its fourth and fifth palatal ridges resemble those of *buettikoferi*. Dr D. W. Thomas, who netted fruit bats at Lamto for a whole year, never caught a single specimen of *franqueti* (personal communication, 22-VII-1981).

Bergmans (1975) mentioned Abidjan in Ivory Coast as a *buettikoferi* locality. The notes on which this was based are lost, unfortunately. Later, I noted two collections containing *Epomops* material from Abidjan: FMNH (no. 99030) and BMNH (material in alcohol), both labelled as *franqueti*. I have not examined this material but do not exclude that Abidjan may also harbour both species.

Bergmans (1982), reporting on *Epomops* from Nigeria, recorded both *franqueti* and *buettikoferi* from Ife. Of three adult ♀♀ collected in the arboretrum on the campus of the University of Ife, at Ife, one (ZMA 19.097) had a fal of 81.0 and a gsl of 43.2 and represents *franqueti*, while the two others (ZMA 19.093, -95) had falls of 90.9 and 92.7 and gsls of 48.2 and 49.1, respectively, and were identified as *buettikoferi*.

In the present paper several other localities where the two species are sympatric are recorded. In the USNM there is a large *Epomops* collection from Ivory Coast and from Ghana in which all specimens have been labelled as *franqueti*, but which contains quite some *buettikoferi*. Of four adult ♀♀ from Banco Forest, Ivory Coast (USNM 429879/80, -83/83) three had fals of 77.7, 78.6 and 81.8, respectively (their skulls were damaged) and one had a fal of 88.4, a gsl of 51.3 and an M^1 length of c. 3.6, and clearly represents *buettikoferi*. Material from Butre, Ghana also contains both species; 22 ♂♂ have fals of 83.7-90.7 (mean 87.6), gsls of 43.7-49.9 (mean 46.9), and 25 (including immatures) have M^1 lengths of c. 2.6-3.3 (mean 3.0), and 12 ♀♀ have fals of 79.4-85.2 (mean 82.4), gsls of 40.5-44.2 (mean 42.1), and (n = 13) M^1 lengths of c. 2.7-3.1 (mean 2.8), and are here assigned to *franqueti*; 9 ♂♂ have fals of 89.9-93.9 (mean 91.7), gsls of 50.9-56.6 (mean 52.8), and M^1 lengths of 3.1-3.4 (mean 3.3), and 7 ♀♀ have fals of 87.4-91.8 (mean 89.3), gsls of 48.6-50.0 (mean 49.2) and (n = 6) M^1 lengths of 3.0-3.3 (mean 3.2) and are presently assigned to *buettikoferi*. From the Kade area, Ghana, there are 4 ♂♂ with fals of c. 85.6-88.9 and 13 ♂♂ with gsls of 46.2-48.3 (mean 47.2), and 7 ♀♀ with fals of 80.0-86.9 (mean 83.2) and 16 ♀♀ with gsls of 40.9-43.6 (mean 42.3), all assigned to *franqueti*, and there is one ♀ with a fal of 89.8 and a gsl of 48.9 which is assigned to *buettikoferi*. From Legon, Ghana, there are 3 ♂♂ with fals of 87.9-88.5 (mean 88.3) and gsls of 45.6-48.0 (mean 46.5) and 16 ♀♀ with fals of 77.2-83.8 (mean 81.7) and gsls of 39.9-43.5 (mean 41.9), which represent *franqueti*, and one ♀ with a fal of 84.8 and a gsl of 51.7, which is identified as *buettikoferi*. From Oda, Ghana, *franqueti* is represented in the USNM by 16 ♂♂ with fals of 83.7-90.7 (mean 87.7) and (n = 9) gsls of 45.8-48.9 (mean 47.2) and 3 ♀♀ with fals of 82.1-83.6 (mean 82.8) and (n = 1) a gsl of 41.7. If specimen FMNH 55764 is a ♀, as its label says, it represents *buettikoferi*: it is immature, has a fal of 85.6, a gsl of 45.5, and an M^1 of 3.2.

Although some of these examples appear to leave no doubt that the two taxa live side by side (while others rest on meagre evidence and need further study), it cannot be denied that the taxonomic separation of the two is complicated by the geographical size variation in both species and by the intermediate state of the palatal ridge configuration in a number of specimens. *Epomops franqueti* diminishes in size from Cameroun to Ivory Coast. *Epomops buettikoferi* decreases in dimensions from west to east; it is largest west of Ghana and smallest towards eastern Ghana and in Nigeria. In the latter two countries the two species overlap per sex in overall dimensions and for correct identification it is fundamental to measure skull dimensions.

The atypical soft palates are not restricted to the (known) area of distributional overlap. The third ridge may be only narrowly divided or undivided in *buettikoferi* far west of that area, and the post-third ridges intermediate between this species and *franqueti* where *franqueti* has not been collected. Kuhn (1965) and Wolton *et al.* (1982) recorded *buettikoferi* with undivided third ridges from Liberia.

The 13 Nigerian *Epomops* specimens in the ZMA assigned to *buettikoferi* were collected in two areas. Seven are from Ife, where the species is sympatric with *franqueti*; of these, one has a divided third ridge and typical post-third ridges, three have notched third ridges and intermediate post-third ridges, and two have undivided, un-notched ridges and also intermediate post-third ridges (the seventh is a neonatus). The other six are from Arusa and Pandam, both in the Pandam Game Reserve; in two of these the third ridge is broadly divided and the other ridges are also typical, in three others it is narrowly divided with typical post-third ridges in two and intermediate ridges in one, and in one it is undivided with intermediate post-third ridges.

Although intermediate ridge patterns are suggestive of intergradation between the two species, the two different size classes found to be sympatric in several localities over a large area in West Africa are not. Ranking *buettikoferi* as a subspecies of *franqueti* (Kuhn, 1965; Püscher, 1972), or even as a synonym as Happold suggested (1987: 348) when listing *franqueti* for Sierra Leone and Liberia, seems highly premature.

Distribution and geographical variation: *Epomops buettikoferi* is an inhabitant of the wetter and drier types of the Guineo-Congolian lowland rain forests of the western Upper Guinea forest block and the adjoining Mosaic of lowland rain forest and secondary grassland (types 1a, 2, 3 and 11a in White, 1983), with some possibly isolated occurrences in the eastern Upper Guinea region (the Nigerian localities). In Sierra Leone and coastal Liberia the mentioned Mosaic is the predominant type, in Ivory Coast the wetter rain forest, and in Ghana the drier types. Only exceptionally have specimens been collected outside (but never really far away from) these types. Njala in Sierra Leone is in a tongue of Swamp forest (type 8 in White, 1983) surrounded by the rain forest/grassland Mosaic. Bonthe and possibly Mount Aureol in Sierra Leone and Bendu and Robertsport in Liberia are in or at the coastal zone of Mangrove forest (type 77 in White, 1983). A detailed analysis on a smaller scale revealed that, in the Mount Nimba area, *Epomops buettikoferi* was caught mostly in areas of secondary bush or cultivated land, in preference to primary rain forest; it was rarely caught within the closed forest but did occur in the fringes (Wolton *et al.*, 1982).

Hypsignathus H. Allen, 1861

Hypsignathus H. Allen, 1861: 156 (type species: *Hypsignathus monstrosus* H. Allen, 1861); Miller, 1907: 67; Andersen, 1912: 501; Rosevear, 1965: 88; Zeller, 1984.

Epomophorus (*Hypsignathus*); Dobson, 1878: 5, 6; Matschie, 1899: 35, 42.

H. Allen (1861) described this genus in the same paper as *Epomophorus comptus* n. sp., a junior synonym of *Epomops franqueti* (Tomes, 1860), and *Pteropus mollipilosus* n. sp., a junior synonym of *Eidolon helvum* (Kerr, 1792). We may safely assume, therefore, that he compared *Hypsignathus* with the genera represented by those species, although his description mentions "*Pteropus*" only. He characterized the genus (in fact: the male representative of the type species which formed his basis) by the possession of a large head with a humped nose, cutaneous expansions of the skin of the snout, the backward position of the wings, the articulation of the incisors: the lower closing in front of the upper, a high and facially broad skull occasioned by the development of the nasal bones, a relatively small cranium, parietal and occipital ridges, a deeply arched palatum, a short upper tooth row, a low coronoid process, and lower fourth premolar and first and second molar assuming the carnivorous type.

Dobson (1878) and Matschie (1899) mentioned as differential characters of *Hypsignathus*, which they classed as a subgenus of *Epomophorus* Bennett, 1836, the absence of shoulder pouches and tufts, the cutaneous muzzle folds, the high rostrum (Matschie), and the distinct external molar cusps (Dobson). Miller (1907) elevated *Hypsignathus* again to the genus rank on the basis of its peculiarities, especially those of the teeth: P^4, M^1, P_4, M_1 and M_2 with inner ridge much more developed than in *Epomophorus* and median furrow correspondingly deepened, and outer ridge of M_1 and M_2 divided into two distinct blunt cusps. Miller also mentioned the paired air-sacs extending from the extremity of the muzzle to halfway between eyes and ears. Andersen (1912) differentiated *Hypsignathus* largely on the basis of its enlarged cranial rostrum (especially in the male), the articulation of its incisors, the relatively complicated morphology of the (lower) molars, and the integumentary folds of the upper lip, and added the specific number of vertebrae (15 thoracic, 3 lumbar and 0 postsacral, against 13, 4 and 2 respectively in *Epomops*) and, besides the paired maxillary air sac, two pairs of pharyngeal air-sacs. The latter character would be shared with *Epomops* (*franqueti*) but Andersen's statement is obviously a lapsus as Dobson (1881), who published an anatomical study on the subject, wrote that in *Hypsignathus* there are no posterior pharyngeal air-sacs, so there is only one pair, as opposed to *Epomops franqueti*. The remark by Rosevear (1965), who followed Andersen (1912) in recognizing generic differences between *Epomops* and *Epomophorus*, that *Hypsignathus* is related to *Epomophorus*, must also be erroneous, as its affinities are clearly to *Epomops* (compare Andersen, 1912, who moreover pointed out that its affinities to *Epomophorus* are more remote).

Kuhn (1968) examined the innervation of the larynx in, among other fruit bats, *Epomops buettikoferi* (as *Epomophorus*), *Epomophorus labiatus* (as *anurus*), and *Hypsignathus monstrosus*, and found that in these species the larynx was served by the Nervus laryngeus cranialis, as opposed to the Nervus laryngeus caudalis in the other species examined — of which only *Scotonycteris zenkeri* Matschie, 1894, as a supposed relative, is of interest here. Although Kuhn found distinct differences between *Hypsignathus, Epomops* and *Epomophorus*, it appears that he does not attach taxonomic value to those differences per se.

Zeller (1984) found essential differences in the degree of development of the larynx and in the associated topography of the thoracic organs between the same three genera and postulated that *Hypsignathus* is further from *Epomophorus* than is *Epomops*.

Hypsignathus monstrosus H. Allen, 1861

Hypsignathus monstrosus H. Allen, 1861: 157 (type locality: "West Africa"); Andersen, 1910: 99; Andersen, 1912: 506 (specification of type locality as "Gaboon"); J. A. Allen *et al.*, 1917: 418; Lang *et al.*, 1917a; Lang *et al.*, 1917: 502; Cabrera *et al.*, 1926: 593; Cabrera, 1929: 14; Duke, 1934; Mertens, 1938; Sanderson, 1940; Krumbiegel, 1942: 338; Schouteden, 1944: 104 (in part: material from Congo da Lemba belongs to *Epomops franqueti*); Malbrant *et al.*, 1949: 82; Sanborn, 1950: 53; Aellen, 1952: 30; Eisentraut, 1956: 513; Perret *et al.*, 1956: 428; Benedict, 1957; Eisentraut, 1957: 624, 659; Novick, 1960: 395; Fleetwood, 1962: 203; Eisentraut, 1963: 69; Hayman, 1963: 95; Rahm *et al.*, 1963: 27; Didier, 1965: 341; Koopman, 1965: 3; Kuhn, 1965: 326; Rosevear, 1965: 89; Hayman *et al.*, 1966: 25 (in part: specimen MRAC 492 from Congo da Lemba belongs to *Epomops franqueti*; specimen MRAC 20560, from Bonoala, is erroneously reported as from Bokuma); Rahm, 1966: 63; Schneider *et al.*, 1967; Kuhn, 1968: 173; Van Deusen, 1968; Hayman *et al.*, 1971: 5; Jones, 1971: 125; Bergmans *et al.*, 1974: 23; Kingdon, 1974: 167; Jeffrey, 1975: 955; Koopman, 1975: 362; Verschuren, 1977: 617; Coe, 1976: 544; Bradbury, 1977; Happold *et al.*, 1978: 73; Koopman *et al.*, 1978: 2; Bergmans, 1979: 169; Robbins, 1980: 85; Haiduk *et al.*, 1980, 1981; Wolton *et al.*, 1982: 431; Emmons *et al.*, 1983; Nowak *et al.*, 1983: 187; Aggundey *et al.*, 1984: 123; Zeller, 1984: 209; Fedden *et al.*, 1986: 181; Feiler, 1986: 66; Koopman, 1986: 10; Hickey *et al.*, 1987; Roth *et al.*, 1988: 184; Crawford-Cabral, 1989: 11.

[? *Hypsignathus monstrosus*]; Dybowski, 1893: 132-133.
Epomophorus (*Hypsignathus*) *monstrosus*; Rosevear, 1953: 82.
Hypsygnathus monstrosus; Brosset, 1966a: 364, 1966b: 53.
? *Hypsignathus monstrosus*; Stoppard *et al.*, 1967.

Material examined

ANGOLA. Dundo: 1 ♂, alc., VII-1948, A. de Barros Machado (FMNH 66435). 30 km S of Gabela: 1 ♀, 25-VII-1954, G. Heinrich (FMNH 83588). Angola: 2 imm. ♂♂, alc., 1954, G. Heinrich (FMNH 81726/27).
(30 km W of Camabatela, Estação Agronómica de Salazar, Ndalatando, Uige.)
BURKINA FASO. Fo: 1 imm. ♀, 11-VI-1969, R. E. Vaden (USNM 467882). Orodara: 1 imm. ♀, 19-VI-1969, R. E. Vaden (USNM 467883). Sideradougou: 2 ♂♂, 1 ♀, 29/30-VI-1969, R. E. Vaden (USNM 467887, -91/92).
CAMEROUN. Alen: 1 ♂, alc., 20-III-1973, L. W. Robbins (MRAC). Bafut: 1 ♀, 1-II-1970, R. L. Peterson (ROM 55884). Balue Mountains: 1 imm. ♀, skull, 1 skull, 2 mandibles, Konietzko (ZMB). Bamumbo: 1 ♂, I. T. Sanderson (BMNH 48.601). Bibundi: 1 ♀ (?), 1891, Y. Sjöstedt (NRS 67); 1 ♀, Y. Sjöstedt (ZMB 6942); 3 ♂♂, 1 ♀, alc., skulls, 16-II- and 16-VII-1911, M. Retzlaff (ZIZM 39203, -65); 1 imm. ♂, alc., 2-III-1913, Wenke (ZIZM 39529). Bipindi: 1 ♂, IX-1898, G. Zenker (ZMB 54410); 1 imm. ♀, alc., 6-XII-1901 (?), G. Zenker (ZMB); 1 ♂, 1 ♀, 1 imm., 12-XI-1907 (?), G. Zenker (ZMB); 1 imm., 28-XII-1910 (?), G. Zenker (ZMB); 1 imm. ♂, G. Zenker (ZMB). 10 km W of Bipindi: 1 imm. ♂, 19-II-1970, R. L. Peterson (ROM 56249). Bonge: 1 imm. ♂, Y. Sjöstedt (ZMB 7043). Boteke: 1 ♂, 2 imm. ♂♂ (?), 12/18-V-1973, V. N. Ngam (ROM 69054/55, -67). Eseka: 1 ♀, 23-VI-1974, L. W. Robbins (CMNH 40981). 5 km SW of Eseka: 1 imm. ♀, 29-VI-1974, L. W. Robbins (AMNH 236271). Great Soppo Forest: 1 ♂, 25-III-1970, V. N. Ngam (ROM 56909). Isongo: 1 ♂, alc., skull, 2-XII-1914, M. Retzlaff (ZIZM 40000). 9 km N of Kiribi: 1 ♂, 21-II-1970, R. L. Peterson (ROM 56264). Kribi: 1 ♂, G. Zenker (ZMB 40163); 1 imm. ♂, 11-IX-1969, R. Glen (ROM 54941). Kumba: 1♂, 3 imm. ♂♂, 1 ♀, 1 embryo, 13-V/2-VI-1969, V. Ngam (ROM 51533, -42, -61, -82, -87, -93). Metet: 1 ♂, 20-VIII-1936, S. E. Johnson (AMNH 114208). Obala: 1 ♂, 11-III-1933, F. G. Merfield (PCMB 270). 12 km S, 4 km E of Obala: 1 imm. ♀, 20-I-1970, R. L. Peterson (ROM 55629); 1 ♂, 1 imm. ♀ (skeleton), 12/13-II-1970, R. L. Peterson (ROM 56132, -59). Small Soppo: 1 ♀, 5-V-1973, V. N Ngam (ROM 69024). Somalomo: 1 ♂, alc., 11-II-1987, A. P. M. van der Zon (ZMA 23.520). Soumou River: 1 ♂, 14-II-1970, R. L. Peterson (ROM 56169). Victoria: 8 ♂♂, 4 imm. ♂♂, 2 imm. ♀♀, 2 imm., (some specimens incomplete), 1898/1902, P. Preuss (ZMB 54200, -04/07; 54600/01, -04; 54696, -98; 6 without number); 1 skin, 13-II-1906, Strunk (ZMB). Yaunde: 1 imm., skin, G. Zenker (ZMB 9010); 1 imm., Haberer (ZMB 54697); 1 imm. ♀, alc., 23-XI-1973, J. Prévost (MNHN 1979-313). Cameroun: 1 ♂, alc., skull, 28-X-1937, R. Mertens (SMF 7101).
(Bimbia, Boulou tribal region, Diouma, Ekundu, Itoki, Lake Koto Barombi, Lomié, Mamfe, Mount Cameroun, Mueli, N'dian, Ngam, Okoiyong, Sakbayeme, Tinta.)
CENTRAL AFRICAN REPUBLIC. Bangui: 1 ♂, alc., 13/27-XI-1965, A. Chippaux (MNHN); 1 ♀, alc., skull, 1965, A. Chippaux (MNHN). Boukoko Kôbo: 1 ♀, 1 imm., alc., 3-II-1964 (MNHN). Nola region: 1 ♂, skin, XI-1929 (MNHN 1931-846). Zemio: 1 ♀, skin, ≤ 1884, via Bohndorff (IRSN 184).
CONGO. Odzala: 1 ♂, 1 ♀, X-1963, A. Descarpentries/A. Villiers (MNHN 1975-803/04). Congo: 1 ♀, alc., Ballay (MNHN 1883-30); 1 ♂, 3 specimens, alc., M. de Brazza (MNHN 1886-135/38); 1 ♀, alc., J. P. Adam (MNHN 1975-805).
(Liranga?)
EQUATORIAL GUINEA. Benito: 1 skull (BMNH 1939.3736). Benito River, 15 miles from mouth: 2 ♂♂, 1 ♀, G. L. Bates (BMNH 98.10.7.2, 99.7.22.1/2). Noja region: 1 ♀, skin, Escherich (ZMB). Spanish Guinea: 1 pullus, alc., 20-XII-1913, Escherich (ZMB).
(Eloby Island, Cape S. John, Ikunde.)
FERNANDO POO. Basoulo East: 3 ♂♂, 12/19-V-1929, J. G. Correia (AMNH 90226/28). Santa Isabel: 1 specimen, 1 imm. ♂, cf. 20-IX-1919 (MNCN 20//25.3, 20//25.4). Fernando Poo: 1 ♂, skin, 1 imm., 1936, Bisthegy (NMW B4781/82).
(Mongola, San Carlos.)
GABON. Belinga: 3 ♀♀, alc., XII-1962/II-1963, Mission Biologique au Gabon (ZMA 20.681, -83, -85); 1 ♂, 3 ♀♀, 1 imm. ♀, 1 specimen, XII-1962/III-1963, Mission Biologique au Gabon (MNHN); 1 ♂, alc., skull, I-1963, J. Dragesco (ZMA 20.684); 1 ♂, 2 ♀♀, 1 imm. ♀, 28-I/11-II-1964, P. J. H. van Bree (ZMA 7798/7801). Dongila: 1 ♀, alc., R. Buchholz (ZMB 4955). Makokou: 1 ♂, alc., 1962, Mission Biologique au Gabon (ZMA 20.686). Nehali: 1 ♂, W. J. Ansorge (BMNH 8.6.14.6).

Ogoué: 1 specimen, alc., M. Marche (MNHN, 1876-20-40?). Rembo Kotou: 1 specimen, alc., C. R. Aschemeier (USNM 220894). Gabon: 1 ♂, alc., skull, Schilling (ZMB).

(Avil Nyabe, Bawaka, Edzuameyen, Eyameyong, 100 miles W of M'Bigou, Mékambo, Mekob, Mouianze-Ivindo confluence, Ovan, Tsetü, Yokob.)

? GAMBIA. Gambia: 1 imm. ♀, via Gerrard (BMNH 76.7.21.1).

GHANA. Berekuso: 2 ♀♀, 5-XI-1967, J. C. Geest (USNM 411602, -04). Bunso: 1 imm. ♂, 1 ♀, 5-V-1973, P. Neugebauer (NMW 15948/49). Butre: 1 ♂, 2 ♀♀, 17/21-I-1968, J. C. Geest (USNM 414014/16). 6 miles NW of Kade: 2 ♂♂, 1 ♀, 31-X/2-XI-1967, H. W. Setzer (USNM 414005/07). 6 miles N of Kade: 1 ♂, 29-III-1968, J. C. Geest (USNM 424758). 7 miles NE of Kade: 1 imm. ♀, 13-VIII-1965, C. J. Ralph (ROM 36647). Kumasi: 1 ♀, 1 imm. ♀, 12-VI-1964 and 18-VI-1966, Allison (BMNH 64.1272, 66.5576); 1 ♀, 11-IV-1965, D. H. Barry (BMNH 66.6207). Leklebi Agbesia: 2 ♂♂, 27/29-VI-1968, J. C. Geest (USNM 424763/64). Oda: 1 ♂, 2 imm. ♀♀, 7-XII-1945/29-IV-1946, G. S. Cansdale (FMNH 54438, 54725, 55763); 1 ♀, G. S. Cansdale (BMNH 46.372). Odomi Jongo: 1 ♂, 21-VI-1968, J. C. Geest (USNM 424761). 32 miles W of Prestea: 3 imm., 10/13-I-1968, J. C. Geest (USNM 414010/12). Sefwi Asemparaye: alc. material (BMNH). Subinja: 1 ♂, 1 ♀, 21/22-II-1968, J. C. Geest (USNM 414782/83).

(Ajemera, Brongahafo, Koforidua, Krokosua Hills, Pampramase.)

IVORY COAST. Abidjan: alc. material (BMNH). Adiopodoumé: 1 ♀, 1 imm. ♀, 1-X-1971, L. W. Robbins (AMNH 241016/17); 4 ♂♂, 4 ♀♀, 18/19-IV-1972, ORSTOM (ZMA 16.525/26, -28; others: MNHN); 1 imm. ♀, 3-XI-1972, J. Vissault (ZMA 18.878); 3 ♀♀, 16-IV-1973, J. Vissault (ZMA 18.863/65). Ahieremou: 1 imm. ♂, 1 imm. ? ♀, 25-XI-1972, J. Vissault (ZMA 18.876/77). Banco Forest: 1 ♀, 30-XI-1968, J. W. LeDuc (USNM 429893). Lamto: 1 ♂, 1 imm. ♀, 20-II-1972, ORSTOM (ZMA 16.527, -29). Sassandra River: 11 ♂♂ (2: skins only), 2 ♀♀, 17/19-II-1969, L. W. Robbins/J. W. LeDuc (USNM 465745/46, -48/50, -52, -54/57, -60; ZMA 16.523/24). Siénso: 1 ♀, 14-III-1969, J. W. LeDuc (USNM 465761). 10 miles WNW of Soubre: 1 ♀, 13-VI-1969, L. W. Robbins (USNM 467881).

KENYA.

(Kaimosi, Kakamega Forest, Shikusa.)

LIBERIA. Mount Nimba: 1 imm. ♀, skin, 2-VIII-1965, J. Verschuren (IRSN 16743); 1 ♀, alc., 6-II-1966, J. Verschuren (IRSN 16083); 2 ♀♀, 14/20-VII-1966, McCoe (BMNH 67.1431/32). Robertsfield Airport, Monrovia: 1 imm., 11/12-X-1971, via R. J. Businк (ZMA 14.576).

(Du River, Gaple, Junk River, Kpeaple, Schieffelinsville, Teayee, Tokadeh.)

NIGERIA. 1,5 miles E of Aguleri: 1 ♂, 24-II-1966, H. J. Herbert (USNM 377098). Akpaka Forest Reserve: 1 ♀, 19-XII-1952, D. R. Rosevear, field no. 984/52 (NHMI). Benin: 1 imm. ♀, alc., skull, H. H. Squire (BMNH 4.8.28.1). Felele: 1 ♂, J. C. Geest (USNM 402563). Ibadan: 1 ♀, 2 imm, ♀♀, 1 imm. skin, 4-IV-1949/11-VIII-1951, D. R. Rosevear, field no.'s 703/49, 704/49, 754/50, 904/51 (NHMI); 1 ♀, VI-1961, K. D. Taylor (BMNH 62.246); 1 imm. ♂, 1 imm. ♀, 9-VI-1965, J. I. Menzies (FMNH 99080/81); 2 imm. ♀♀ (1: alc.), 4/5-VIII-1976, W. Bergmans (ZMA 18.599/600). Ife: 1 ♀, 1975/1976, G. Oderhowho (NHMI). Igbo-Ora: 1 ♀, 25-X-1966, H. W. Setzer (USNM 402561). Kwa River: 1 ♂, P. A. Talbot (BMNH 10.6.1.6). Lagos: 1 imm. ♂, A. S. Pearse (BMNH 26.11.24.2). Oban: 1 imm. ♂, P. A. Talbot (BMNH 10.6.67). Topo Island: 1 ♀, alc., 30-III-1966, "J.M.", field no. 130 (NHMI). Nigeria: 1 ♂, skull, Forest Department no. 651 (NHMI).

((Old) Calabar, N'ko, Onitsha Province.)

SIERRA LEONE. Mount Aureol: 1 ♀, 20-II-1970, S. Cousins/D. Pitt (ROM 56489).

(Freetown.)

SUDAN. Li Rangu: 1 ♂, 3-V-1948, R. Alison (USNM 317903).

(Bangangai Forest.)

TOGO. Ezimé: 1 ♀, 2-VII-1968, J. W. LeDuc (USNM 437594). Misahöhe: 1 ♂, 1 imm. ♂, alc., Baumann (ZMB 9008/09). Palimé: 3 ♂♂, Miss Duc (MNHN).

UGANDA. Budongo Forest: 1 ♀, 22-VI-1966, J. G. & A. Williams (LACM 51401); 1 imm. ♀, 22-VI-1968, Shortt/Williams (ROM 46655). Entebbe: alc. material (BMNH). Itama area: 1 ♀, 27-III-1967, A. Williams (LACM 51402); 1 ♀, 21-VI-1969, R. Glen (LACM 35482). Kampala: 1 imm. ♀, 6-VII-1961, P. Cook (HZM 1.3518). Kibale Forest: 1 ♂, 2 ♀♀, 3/11-XII-1966, R. Glen/A. Williams (LACM 51406/08). Ntandi: 3 ♀♀, 16/17-VI-1967 and 3-XII-1968, R. Glen/A. Williams (LACM 51403, 51504/05).

(Nr Bulamagi, Butiti, Bwamba Forest, South Mabira Forest, nr 20 km NW of Masindi, nr Ndeke, nr Sempaya.)

ZAIRE. Nr Angu: 1 ♀, 22-IV-1906, Alexander Gosling Expedition (BMNH 7.7.8.23). Arebi: 2 ♀♀, 1 imm., 19-VII-1925, H. Schouteden (MRAC 8499/501). Avakubi: 5 ♂♂, 1 ♀, 23-XII-1913/18-V-1914, H. Lang/J. P. Chapin (AMNH 48636/39, -48/49); 1 imm. ♀, 11-V-1914, H. Lang/J. P. Chapin (MRAC 12.376); 1 skin (NMW 18282). Bafwabaka: 2 ♂♂ (1: skin only), 1 imm. ♂, 2 ♀♀, 2-V-1910, H. Lang/J. P. Chapin (AMNH 48631, -54; FMNH 43873; MRAC 12360). Bamanya: 1 ♀, 16-IV-1952, P. Hulstaert/R. P. Leonet (MRAC 21689). Bambesa: 1 ♀, skull, 29-V-1938, Vrijdagh (MRAC 14796). Bambu: 1 ♂, skull, I-1948, D. Hiernaux (IRSN 7037). Bela: 1 imm., skull, 14-IV-1947, J. Hiernaux (IRSN 7040). Beni: 1 imm. ♀, 1-V-1921, N. Gyldenstolpe (NRS 1-387); 1 imm. ♂, 25-X-1926 (AMNH 82529). Boendi: 1 ♂, alc., R. P. Wijnands (MRAC 15949). Bokuma: 1 imm., 22-X-1950, R. P. Lootens (MRAC 20397). Bokungu: 1 imm., 2-XII-1948, L. Dupuis (MRAC 18693); 2 imm., 1949, L. Dupuis

(MRAC 18817: mismatched; 18818). Bolafa: 2 ♂♂ (1: skin only), 1 ♀, 1 imm. ♀, 2 imm. skins, V-1956, Stevenart (MRAC 25841/46). Bonoala: 1 ♂, skull, R. P. Lootens (MRAC 20560). Buta: 5 ♀♀, 1 imm. ♀, (3: skulls only), 1 imm., VI-1934/VI-1936, R. F. Hulsebaut (MRAC 12563/64, 12671, 13379/80, 17320/21). Butembo: 1 imm. ♂, alc., IV-1956, P. Dyleff/Van der Meersche (MRAC 23956). Eala: 3 imm. ♂♂ (1: alc., 2: skins), 2 ♀♀, 4/5-I-1921, H. Schouteden (MRAC 6524, -24a, -27/28, -31); 1 imm. ♀, alc., 1921, Verlaine (MRAC 16215). Epulu: 1 ♂, 1 imm. ♂, 1 ♀, 1 imm. skin, 21/24-IX-1956, M. Poll (MRAC 25596/99); 1 ♀, 3 imm. ♀♀, 1 imm. (alc.), IX-1956, M. Poll (MRAC 27645/49); 2 ♀♀, skins, 4-III-1957, H. Stephan (MRAC 27417/18); 1 imm. ♂, 2 ♀♀ (1: skull only), 4-III/17-V-1957 (MRAC 26609/11). Equateur: 1 specimen, alc., 1921, Verlaine (MRAC 38239). Eringeti Forest: 1 imm. ♀, 19-IX-1949, J. de Wilde (IRSN 12945). Ibembo: 2 ♂♂, 1 imm. ♂ (alc.), 1 imm., 10-IX-1949/20-XII-1951, R. F. Hutsebaut (MRAC 19527, 19620, 20744, 21714); 1 skull, Rodhain (MRAC 7642). Ikengo: 1 imm. skin, 15-II-1921, H. Schouteden (MRAC 6529). Inongo: 1 ♀, alc., 1-X-1945, J. Gustin (MRAC 18124). Kamituga: 1 ♀, 2-VIII-1954, A. Prigogine (MRAC 23422); 1 ♀, skull, 10-VI-1964, A. Prigogine (MRAC 32855). Kasai: 3 skulls, 1 imm. skull, Compagnie du Kasaï (MRAC 738, 738a-c). Kasongo: 1 imm., alc., 1959/1960, P. Benoit (MRAC 31106). Kilo: 1 ♀, alc. (MRAC 10775). Kilomamensa: 1 ♂, Pilette (MRAC 6143). Kindu: 1 skin, Grauer (ZMB A4809). Kisala: 1 ♀, skin, mandibulum, 16-X-1920, H. Schouteden (MRAC 6530). "Km 104": 1 ♀, 11-III-1957, J. J. Laarman (RMNH 16346). Koteli: 1 ♂, 2-I-1925, H. Schouteden (MRAC 8784). Kunungu: 2 ♀♀, H. Schouteden (MRAC 14169, 15509). Lesse: 1 imm., 4-XI-1913, Bonnevie (MRAC 3236). Lisala: 1 imm., received 19-I-1929, Babilon (MRAC 9574); 1 skull, Babilon (MRAC 9575). Lobi: 1 ♂, 19-II-1906, Alexander Gosling Expedition (BMNH 7.7.8.21). Lower Congo: 1 ♀, skin, H. E. Laman (NRS 4-18). Luebo: 1 ♀, 26-VIII-1921, H. Schouteden (MRAC 6525). Lukolela: 1 specimen, VIII-1923, J. Ghesquière (MRAC 7038); 2 imm. ♂♂, 2 ♀♀, 6/31-VIII-1930, F. Edson/J. P. Chapin (AMNH 86761/64); 1 imm. ♂, 31-VII-1931, Lecocq (MRAC 11736). Luluabourg: 1 ♀, R. Callewaert (BMNH 26.7.6.48). Lukoi River: 1 imm. ♀, D. Fraser (BMNH 27.3.1.17). Mpe: 1 ♀, alc., Maes (MRAC 2662). Ndwa: 1 ♀, 1 imm. ♀, 1938/1939, H. Schouteden (MRAC 15421/22). Nepoko River: 2 ♂♂, heads, alc., L. Henrion (MRAC 18137). Paulis: 1 imm., 4-V-1951, Abbeloos (MRAC 20510). Penge: 1 ♂, 21-IV-1914 (MRAC 48642). Stanleyville: 1 ♀, 18-VIII-1909, H. Lang/J. P. Chapin (AMNH 48629); 1 ♀, 16-XII-1914, H. Lang/J. P. Chapin (AMNH 48652). Tingasi: 1 ♀, 1 imm. ♀ (skull), 29-X-1883, Emin Pasha (BMNH 87.12.1.24/25). Tondu: 1 ♂, skull, 19-II-1921, H. Schouteden (MRAC 7784). Tsuapa District: 1 imm. ♀, skull, received 25-IX-1951, A. Meynen (IRSN 15188). Yakolele: 2 ♂♂, 2 imm. ♂♂, 1 imm., 26-VI/28-VIII-1953, L. Dupuis (MRAC 21889/90, 21911/13). Yangambi: 1 imm., 18-IX-1939, Vrijdagh (MRAC 17238); 1 ♀, 25-X-1947, R. Germain (IRSN 6984); 1 ♂, skin, 7-VIII-1951, L. Toussaint (IRSN 12944). Island in Congo opposite Yangambi: 1 ♂, alc., 1938, V. van Straelen (IRSN 5941). Zobia: 1 ♂, 1 imm. ♂, 1 ♀, 1 imm., received 18-IV-1946, Van Woensel (IRSN 6963/66).

(Abimva, Bambili, Bomili region, Bondo Mabe, Bongala, Buhengara, Bumbu, Bunyakiri, Chagala, Dungu, Ilebo, Irangi, Kilo-Mines, Kingoyi, Libenge, Lwiro, Mabali, Mbali, New Beni, Niangara, Yalosemba.)

Diagnosis: The largest of African fruit bat species and the only one with projecting skin folds on its muzzle; skull large; rostrum excessively heavy, anteriorly very high, and laterally compressed in males, less so in females, and relatively long in both sexes; premaxillae broad; palate concave from side to side and antero-posteriorly; postdental palate without raised margins; zygoma long, with or without a small postorbital process; pterygoid wings extending to tympanic bullae and curled outward posteriorly, forming a cavity; teeth spaced; outer ridge of M_1 bilobed or trilobed, that of M_2 bilobed; soft palate with three thick and undivided interdental ridges and about eight thin and serrate postdental ridges, frequently irregular and occasionnally divided in the middle. Measurement ranges and ratios taken from all over the species' range:

fal	♂♂	120.3-138.6 (n = 80),
	♀♀	111.8-127.4 (n = 65);
gsl	♂♂	67.9- 74.0 (n = 69),
	♀♀	56.8- 63.8 (n = 45);
cbl	♂♂	67.0- 72.3 (n = 23),
	♀♀	56.8- 63.3 (n = 23);
rl	♂♂	33.0- 37.7 (n = 19),
	♀♀	25.0- 29.8 (n = 35);
pl	♂♂	39.6- 44.6 (n = 14),
	♀♀	32.1- 36.5 (n = 33);
zw	♂♂	32.9- 38.7 (n = 25),
	♀♀	31.6- 34.7 (n = 19);
C^1-M^1	♂♂	21.8- 24.7 (n = 29),
	♀♀	18.4- 21.2 (n = 36);
W	♂♂	290 -419 (n = 8),
	♀♀	207 -302 (n = 13);
rl	♂♂	48.6- 51.8% of gsl (n = 13),
	♀♀	43.2- 47.5% of gsl (n = 21);

Table 10. Ranges of selected measurements of *Hypsignathus monstrosus* H. Allen, 1861 per country.

		♂♂								♀♀							
		fal	gsl	cbl	rl	pl	zw	C^1-M^1	W	fal	gsl	cbl	rl	pl	zw	C^1-M^1	W
Angola	n	1								1							1
		124.3								119.4							302
Burkina Faso	n	2	2								1						
	min	128.9	68.5								59.4						
	max	133.2	71.4														
Cameroun	n	19	18	11	4		12	13	3	5	2		1			1	1
	m	133.3	71.0	70.4	36.1		36.6	23.5	391	120.6							
	min	127.5	67.6	68.2	34.6		35.2	22.3	355	116.9	59.1		26.3			19.9	250
	max	138.6	73.2	72.3	37.5		38.1	24.7	419	122.5	60.6						
Central African Republic	n	1							1	2							
	min	135.5							392	119.6							
	max									122.6							
Congo	n	2	1	1	1	1	1	1		3	1	1	1	1		1	
	m									119.0							
	min	128.3	67.9	67.4	33.0	39.6	34.9	22.5		117.5	59.8	59.2	27.1	34.1		19.9	
	max	137.5								121.7							
Equatorial Guinea	n		3							1							
	m		72.0														
	min		70.8							122.0							
	max		72.9														
Fernando Poo	n	2	3														
	m		72.3														
	min	130.7	71.5														
	max	± 136	73.0														
Gabon	n	4	3	2	1	1	2	2	1	9	2	2	2	2	2	2	2
	m	132.6	70.4							120.9							
	min	128.9	68.1	67.0	33.8	40.0	35.6	21.8	290	118.4	59.9	59.3	26.8	33.9	32.6	19.7	207
	max	134.2	72.2	70.5			37.8	22.6		125.7	61.4	61.2	28.4	35.1	33.2	21.2	246
Ghana	n	8	8	1					1	7	7	1				1	1
	m	133.7	70.5							119.3	59.7						
	min	125.6	68.6	68.6					370	115.5	58.1	60.8				20.8	270
	max	138.3	73.1							127.4	62.2						
Ivory Coast	n	15	14	4	4	4	4	4		7	8	4	4	5	3	6	
	m	130.6	70.2	68.8	35.1	41.2	35.3	22.8		122.3	60.1	59.8	27.6	34.2	32.3	20.5	
	min	120.3	69.0	68.4	34.5	40.8	32.9	22.2		116.9	58.2	57.7	26.3	33.4	32.0	19.6	
	max	135.8	71.2	69.9	35.7	41.5	36.1	23.5		127.4	62.7	62.2	29.8	35.1	32.8	21.2	
Liberia	n								2		2						3
	m																232
	min								374		57.2						208
	max								412		59.9						256
Nigeria	n	2	3							3	2		2	2	2	1	
	m		71.4							114.8							
	min	124.7	71.0							111.8	57.3		25.6	32.5	32.1	20.3	
	max	129.1	71.6							118.6	58.8		27.2	33.7	32.1		
Uganda	n	1								6	5	5	6	6	5	6	5
	m									116.6	60.0	59.3	27.3	34.1	33.2	20.4	253
	min	137.2*								114.3	59.6	58.5	26.9	32.9	32.5	19.6	219
	max									120.3	61.0	60.5	28.0	35.4	34.1	21.0	270

table 10 continued

Sierra Leone	n								1						
									115.1						
Sudan	n	1	1												
		132.0	69.9												
Togo	n	4													
	m	129.6													
	min	124.1													
	max	134.4													
Zaire	n	18	13	4	9	8	6	9	19	16	10	18	17	7	18
	m	134.0	72.1	70.4	36.2	42.9	37.4	23.2	120.3	60.3	59.4	27.5	34.3	32.9	20.1
	min	128.7	69.7	68.9	34.6	41.7	36.4	22.5	113.2	58.0	56.8	25.0	32.1	31.6	18.4
	max	137.0	74.0	71.7	37.7	44.6	38.7	24.5	125.3	63.8	63.3	29.5	36.5	34.7	21.1

* collector's measurement

pl ♂♂ 58.3- 61.2% of gsl (n = 10),
♀♀ 55.5- 58.5% of gsl (n = 21);
zw ♂♂ 47.7- 54.0% of gsl (n = 23),
♀♀ 52.3- 57.0% of gsl (n = 15).

Bradbury (1977) measured fals and weights of a large number of adult ♂♂ and ♀♀ at one site in Northeast Gabon: 87 ♂♂ had fals of 134 ± 3 and 83 ♀♀ fals of 120 ± 3; 91♂♂ weighed 420 ± 1 and 74 ♀♀ 234 ± 19 (variations are standard variations). There appears to be no appreciable geographical variation in dimensions. For a breakdown of size ranges per country see table 10.

Distribution: Fig. 14.

Related species: Epomops buettikoferi and *Epomops franqueti* present the greatest morphological similarity but are both much smaller and without projecting skin folds on the muzzle. The rostrum in these species is much less developed and their cheek teeth are more simple. Adult *Epomops* males have shoulder pouches and tufts, which are lacking in *Hypsignathus.*

Remarks

Taxonomy: A number of similarities of *Hypsignathus monstrosus* to *Epomops* have been noted by Andersen (1912). Its karyotype could not be distinguished from that of *Epomops franqueti* but in G- and C-bands it differs in two aspects (Haiduk *et al.*, 1980, 1981). The pterygoid wing morphology as discussed in the account of *Epomops dobsonii* (p. 119) is a further character shared by *Hypsignathus monstrosus* and typical *Epomops*, i.e. *franqueti* and *buettikoferi*. The exceptional development of the larynx in *Hypsignathus monstrosus*, entering the thoracic cavity ventrally and, in males, nearly filling up the upper and middle mediastinum and reaching caudally to the diaphragm, and the associated cranio-dorsal curvation of the trachea also distinguish *Hypsignathus* from typical *Epomops.* According to Zeller (1984), who studied and described the anatomy of the vocal organs in these genera and in *Epomophorus*, "the different topography of the thoracic organs demonstrates, that the enlargement of the larynx took place independantly in both genera." The anatomy of *Epomops dobsonii* has not been described and I suspect that it may be found to differ from both *Hypsignathus* and typical *Epomops* and possibly agree rather with the less abnormal condition described for *Epomophorus labiatus* (including *anurus*) by Zeller.

Andersen (1912) described the palate ridges (fig. 15) as very similar to those of *Epomops* and postulated that *E. dobsonii* would exhibit a transitional stage from *E. franqueti* toward *Hypsignathus.* His observations are based on dried palates, in which the ridges have lost much of their original volume and form. The first and second ridges in *Hypsignathus* are very thick,

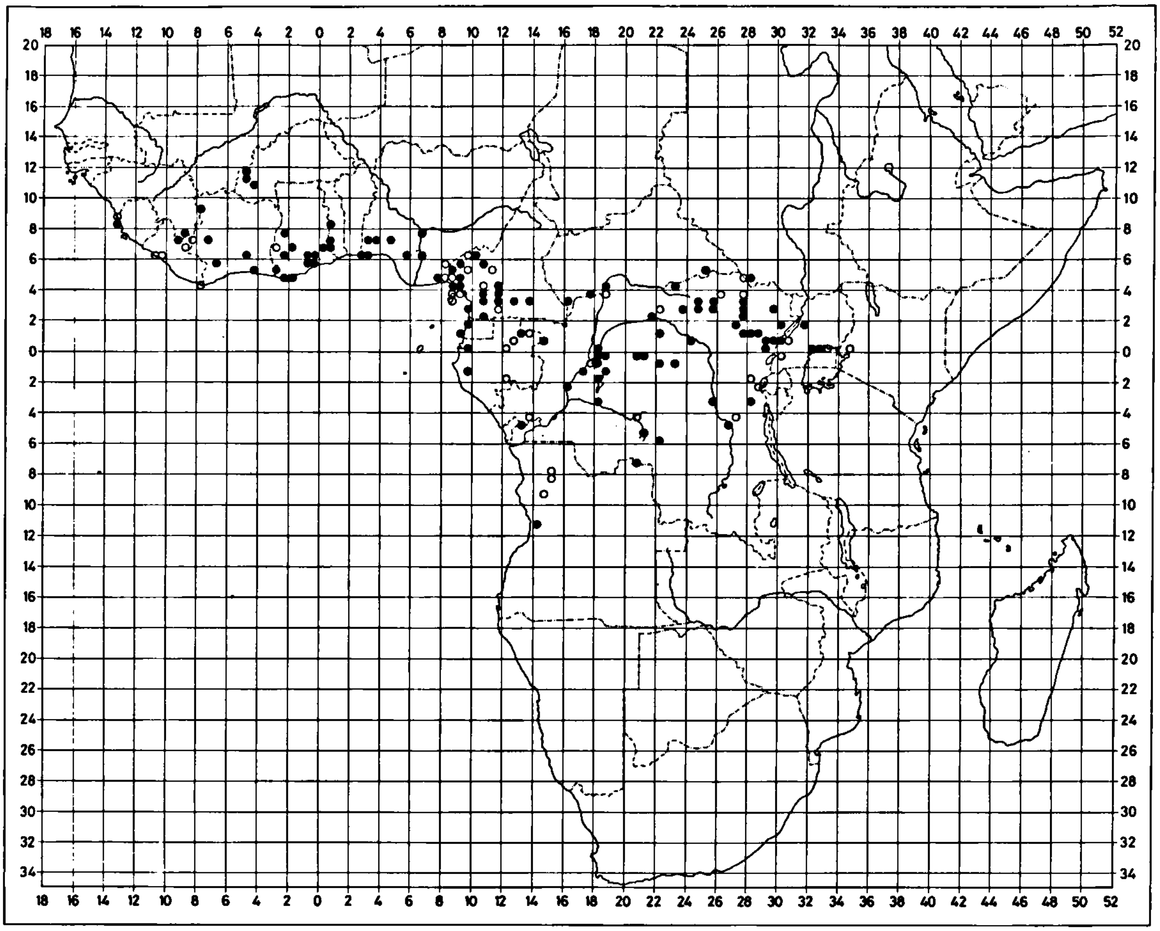

Fig. 14. Distribution of *Hypsignathus monstrosus* H. Allen, 1861. Black dots: squares from where material has been identified by the author. Open circles: records from literature, museum registers and correspondence.

with yet thicker extremities. The third ridge is much thinner, its anterior side often with a small median projection, but also with thicker extremities. In ridge four these extremities appear to have become the only solid parts, cushion-like, in an otherwise thin and weakly serrated ridge, interrupted or nearly so in the slightly concave middle; the two thick parts may each bear a tooth-like anterior projection. The fifth ridge resembles the fourth but the thick parts are weaker, the median part is slightly convex, and the serrations are much more distinct. The sixth to tenth or eleventh ridges are convex or angular, irregular, medially interrupted or not, and finely and sharply serrated. The pattern is reminiscent of that in typical *Epomops*, i.e. *franqueti* and *buettikoferi*, the ridges one to five more of the latter in the thick cushion-like and sometimes dented parts and the others more of *franqueti*. Ridges four and five only vaguely resemble those in *E. dobsonii*, in which these ridges are much more prominent and placed further backward (it has been suggested in the account of that species that they actually represent the original ridges five and six).

Distribution and geographical variation: *Hypsignathus monstrosus* is a species of the moist forest but has occasionally been found also outside the original West and Central African rain forest blocks. It occurs in both Wetter and Drier types of Guineo-Congolian

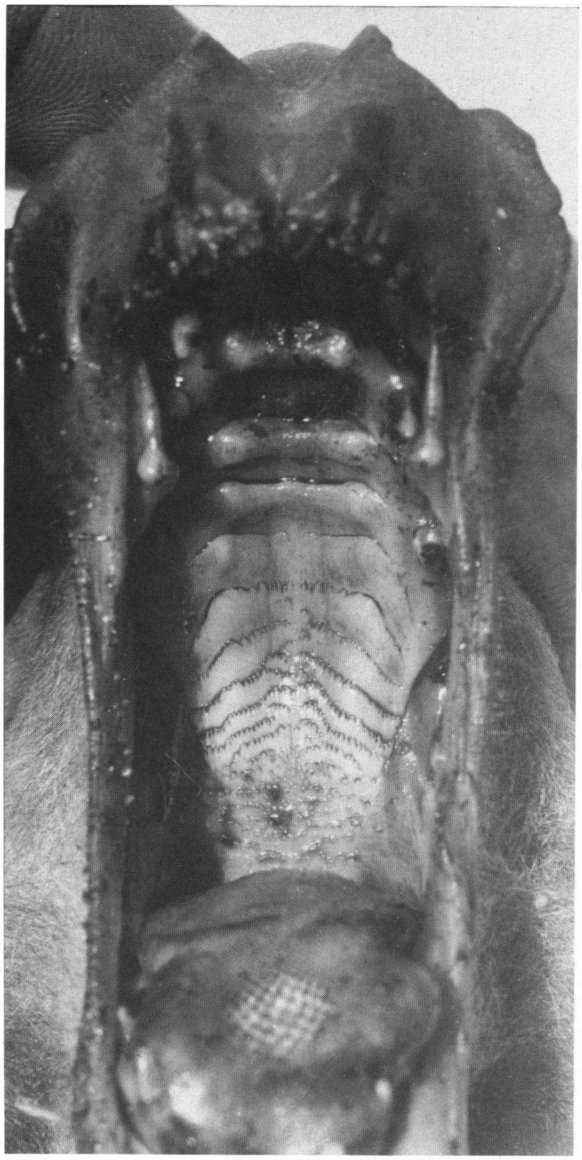

Fig. 15. Soft palate of a ♂ of *Hypsignathus monstrosus* H Allen, 1861 from Lamto, Ivory Coast (ZMA 16.527) Courtesy Mr. J. Vissault.

lowland rain forest and in the Mosaic of both, and, for example in northwestern Zaire, also in Swamp forest and in the Mosaic of that type with the lowland rain forest (types 1a, 2, 3, 8 and 9 in White, 1983). In many instances, *Hypsignathus monstrosus* has been caught in the Mosaic of Guineo-Congolian lowland rain forest and secondary grassland which borders the rain forest in many places (type 11a in White, 1983). Some records are from Afromontane vegetation (type 19a in White, 1983): Mount Nimba in Liberia, Lake Kivu area in eastern Zaire, and Manera Forest in Ethiopia (Andral *et al.*, 1968). The latter locality is highly isolated from the main distribution area and the record itself is not very convincing. Andral *et al.* (1968) caught 140 bats and sent them to two institutes for identification, the East African Virus Research Institute in Entebbe, and the MNHN in Paris. The list of names, five in all, does not betray taxonomical expertise (and I never found one of their specimens in the MNHN), and I seriously doubt if *Hypsignathus monstrosus* was collected in Manera Forest. Consequently I have refrained from mapping this locality.

Another type of forest from where the species has been recorded is Mangrove (type 77 in White, 1983); the only example I know is from Calabar in southeast Nigeria.

A small number of records is from woodlands. In Ivory Coast, Burkina Faso and Ghana *Hypsignathus* has been collected in Sudanian woodland with abundant *Isoberlinia*, and in Burkina Faso also in Sudanian undifferentiated woodland (types 27 and 29a in White, 1983). In Angola it was taken in Wetter Zambezian miombo woodland (dominated by *Brachystegia, Julbernardia* and *Isoberlinia*) and in or near North Zambezian undifferentiated woodland (types 25 and 29c in White, 1983).

The northernmost West African localities, in Burkina Faso, were described by Koopman *et al.* (1978) as in "riverine forest, tree and tree-shrub savannas, and (...) a tree in a village." It is highly probable that riverine forests serve as passage ways into woodland areas. In this respect, Rosevear (1965) noted that *Hypsignathus* was found in fringing forests and forest remnants. In actual rain forest, riparian trees seem to be preferred as roosting and reproduction sites (Jentink, 1888; Brosset, 1966b; Bradbury, 1977), while foraging apparently takes place also in surrounding areas of secondary growth and in old plantations (Jeffrey, 1975; Bradbury, 1977). In Ibadan, Nigeria, the present author netted two specimens in the rich garden of the Botanical Institute of the University of Ibadan.

The suggestion by Bergmans *et al.* (1974) that in Zaire male specimens might reach larger dimensions than in Ivory Coast would seem to be confirmed by the data in table 10. However, most localities are represented in collections by only one or a few specimens and next to nothing is known about the possible variation in dimensions between nearby populations. The material available from Ivory Coast may coincidentally represent populations of small-sized individuals. In this respect it is significant, perhaps, that the size range of male specimens from Ghana is nearer to that of Zaire than of Ivory Coast specimens.

Nanonycteris Matschie, 1899

Nanonycteris Matschie, 1899: 36, 58 (as subgenus of *Epomophorus* Bennett, 1836; type: *Epomophorus veldkampii* Jentink, 1888)
Epomophorus (in part); Miller, 1907: 65.
Nanonycteris; Andersen, 1912: 559; Rosevear, 1965: 110.

Jentink (1888), in his description of *Epomophorus veldkampii*, mentioned its external similarity to *Micropteropus pusillus* and emphasized its typical palatal ridge pattern as distinguishing character. Matschie (1899) thought that *Epomophorus veldkampii* was like "*Epomophorus* s. str." in the build of its head with, compared with *Micropteropus pusillus*, a narrower snout (distance between anterior eye corner and tip of nose much greater than width of head at mouth corners), and its plagiopatagium, but overall much smaller, and like *Epomops* in the form of its bony palate. On the other hand, he mentioned the relative shortness of its upper tooth row, with the last molar reaching only to the level of the anterior margin of the foramen infraorbitale, and the peculiar palatal ridge pattern to distinguish it from both, and proposed *Nanonycteris* as a subgenus of *Epomophorus* (*Epomops* was also considered a subgenus of that genus, by Matschie) to accomodate *Epomophorus veldkampii.* Miller (1907), who had no opportunity to examine the species himself, ranked *Nanonycteris* as a synonym of *Epomophorus.* Andersen (1912) raised it to generic rank. He put forward as diagnostic characters its small size, its short and narrow cranial rostrum, its broad and posteriorly flattened postdental palate without prominent rim, its short upper tooth rows, and its palatal ridge pattern. He compared the genus mainly with *Micropteropus*, which has a distinctly broader rostrum and interdental palate but narrowed postdental palate, longer tooth rows, and entirely different palatal ridges. The brain case in *Nanonycteris* is rounder than in *Micropteropus*, its zygomata are slenderer and standing out less far, and its mandibulum, especially at the coronoid, is weaker. Because of all this, Andersen found it difficult to believe in any very close relationship between *Nanonycteris* and *Micropteropus*, and rather assumed a connection with *Epomops* because of bony and soft palate morphology. Rosevear (1965) added that in *Nanonycteris* the tooth rows diverge less than in *Micropteropus*, which follows also, of course, from the narrowness of its cranial rostrum referred to by Andersen (1912).

Some of the cranial characters considered as diagnostic for the genus by Andersen (1912), i.e. the round brain case, the zygomata being slender and rather close to the skull, and the weak mandibulum, are neotenic, and although their diagnostic value in the identification of the species *Nanonycteris veldkampii* is beyond doubt, their use in the differential diagnosis of a genus does not seem appropriate. (Some species of the fruit bat genus *Rousettus* show similar characters, while others do not.)

Jentink (1888a) described the palatal ridge pattern in *Epomophorus veldkampii.* Matschie (1899), in his diagnosis of *Nanonycteris*, mentioned the aberrant pattern but did not deal with it at great length. Andersen described it in some more detail and figured it (1912; fig. 41). (Rosevear's illustration, 1965: fig. 13b, has obviously been drawn after Andersen's.) The pattern is not easily associated with one of the patterns known from other epomophorine genera. Andersen thought it to be connected with that in *Epomops*. Here, Andersen referred to typical *Epomops*, i.e. *franqueti*.

The short tooth rows, the concave and actually slightly thickened posterior margin of the bony palate, the 'normal' morphology of the pterygoid wing, and maybe also the development of (predominantly) postdental palatal ridges with thick and prominent central portions, would suggest that *Nanonycteris veldkampii*'s affinities lie with *Epomops dobsonii* rather than with *E. franqueti*. As for *E. dobsonii*, the anatomy of the vocal organs of *Nanonycteris* has also not yet been described. Their morphology and topography should certainly be included in further taxonomic discussions of epomophorine genera.

Nanonycteris veldkampii (Jentink, 1888)

Epomophorus veldkampii Jentink, 1888a: 51 (type locality Buluma, Fisherman Lake), 1888: 138; Rosevear, 1953 22.

Epomophorus (*Nanonycteris*) *veldkampii*; Matschie, 1899: 59.

Nanonycteris veldkampii; Andersen, 1912: 562; Sanderson, 1940; Aellen, 1952: 39; H. G. Baker *et al.*, 1957, 1959; Booth, 1959: 29; Harris *et al.*, 1959; Eisentraut, 1963: 72; Kuhn, 1965: 325; Rosevear, 1965: 111; van Orshoven *et al.*, 1968: 189; De Vree *et al.*, 1969: 203, 1970: 42, 1971: 161; De Vree, 1971: 37; Hayman *et al.*, 1971: 9; Eisentraut, 1973: 36; Ayensu, 1974; Bergmans *et al.*, 1974: 33; Jeffrey, 1975: 955; Coe, 1976: 543; Verschuren, 1977: 618; Happold *et al.*, 1978: 76; Bergmans, 1982: 157; Marshall *et al.*, 1982; Wolton *et al.*, 1982: 425; D. W. Thomas, 1983; Fedden *et al.*, 1986: 182; Happold, 1987: 46; Hickey *et al.*, 1987; Roth *et al.*, 1988.

Material examined

CAMEROUN. Bota: 1 specimen (BMNH 67.1728). Mamfe: 2 specimens (BMNH 48.605/06). 7 km N of Ntui: 1 ♀, alc., 11-XI-1973, J. Prévost (MNHN 1979-311). 5 km S of Yoko: 1 imm. ♀, alc., 19-I-1974, J. Prévost (MNHN 1979-312).

(Buea, 10 miles N of Buea, Kumba, S of Mamfe, 15 km SE of Mamfe, Mount Cameroun, Mukonje, Nyasoso, Tombel, Victoria.)

CENTRAL AFRICAN REPUBLIC. Bangui: 1 specimen, Allyn? (LACM 19928).

GHANA. Accra: 1 imm. ♂, alc. (ZMB 4061). Achimota: alc. material (BMNH). Bator: 3 ♂♂, 1 imm. ♂, 1 ♀, 1 imm. ♀, 16-VII-1967, B. J. Hayward (USNM 411788, -90/94). Begoro: 1 imm. ♂, alc., skull, 1881, Mohr (SMNS 1780). Bibianaha: 1 specimen (BMNH 12.2.27.1). By Motel, Mole National Park: alc. material (BMNH). Gambaga: 1 ♂, 9-V-1968, J. C. Geest (USNM 424821). Gukstenar: alc. material (BMNH 72.185). Kradji: 1 imm., alc., Baumann (ZMB 10039). Kumasi: 5 specimens (BMNH 66.6192/96). Legon: 1 ♂, 1 imm. ♂, 4 ♀♀, 1 imm. ♀, 1 skull, 15-VII/27-IX-1967, B. J. Hayward/J. W. LeDuc (USNM 411796, -98, 411800/05). Mole National Park: alc. material (BMNH). Takoradi: 4 specimens (BMNH 66.6199/202). Yabraso: 5 ♂♂, 2 imm. ♂♂, 5 ♀♀, 8/12-IV-1968, J. C. Geest (USNM 424798, 424800, -05/13, -15/16).

(Akosombo, Ashanti, Doyum/Shai Hills Game Reserve, Elmina, 7 miles NE of Kade, Kete, Krokosua Hills, Loni/Damango, Lovi, Mole National Park nr Headquarters, Pampramase, Sanole Hotelcamp 15 miles NW of Damongo, Sefwi Asemparaye, Shai Hills.)

GUINEA. Kankasili: 4 ♀♀ (1: alc.), 1 embryo (alc.), 15-XI-1966/1-III-1967, J. van Orshoven (ZMA 10.734, -36, -40, -44, 10.865). Macenta: 1 specimen, alc., 1920, Chabaneau, field no. 373 (MNHN).

IVORY COAST. Abidjan: alc. material (BMNH). Adiopodoumé: 1 imm. ♀, alc., 22-XII-1966, ORSTOM (ZMA 16.647); 8 ♂♂ (1: alc.), 6 ♀♀ (1: alc.), 1 imm., 15-V/16-XI-1970, J. Vissault (ZMA 16.648/52, -54/55; others: MNHN); 1 specimen, 28-IX-1972, J. Vissault (ZMA 18.044). Adzopé: 2 ♀♀, 8-III-1971, J. Vissault (ZMA 16.646; MNHN). Bolo: 1 specimen, 2-II-1973, J. Vissault (ZMA 18.046). 25 km N of Bouaké: 1 imm. ♂, 29-X-1971, L. W. Robbins (AMNH 241024). Douna: 1 imm. ♀, 1-VII-1969, L. W. Robbins (USNM 467914). Kong: 1 ♂, 19-V-1969, L. W. Robbins (USNM 454434). Lamto: 2 ♂♂, 3-X-1970, J. Vissault (ZMA 16.653; MNHN). Matonguiné: 1 specimen, 21-I-1973, J. Vissault (ZMA 18.045). Ivory Coast: 3 ♀♀, 1970/1973, J. Vissault (ZMA 18.047/49).

(Tai Forest, Wango-Fitini.)

LIBERIA. Buluma: 1 ♀, alc., skull, 19-IV-1881, J. Büttikofer/C. F. Sala (holotype of *Epomophorus veldkampii* Jentink, 1888; RMNH 20400). Iti: 1 ♂, 3 ♀♀, alc., 10/18-II-1966, J. Verschuren (IRSN 16051, -62, -66/67). Mount Nimba East: 1 ♂, 2 ♀♀, alc., 2/4-II-1966, J. Verschuren (IRSN 16050, -59, -78). Mount Nimba West: 4 ♂♂ (alc.), 4 imm. ♂♂ (alc.), 18 ♀♀ (17: alc.), 7 imm. ♀♀ (4: alc.), 18-XII-1965/21-III-1966, J. Verschuren (IRSN 16044/47, -49, -52/58, -60/61, -63/65, -68/76, -79/81).

NIGERIA. Calabar: 1 imm. ♂ (alc.), 1 imm. ♀, alc., skull, 30-VII/1-VIII-1976, W. Bergmans (ZMA 18.608/09). Ibadan: 1 specimen, I-1950, D. R. Rosevear, field no. 746/50 (NMHI); 1 ♀, 4-XII-1959, F. C. Sibley (AMNH 204297); 1 imm., 1-I-1963, P. Ward (ZMUI); 1 ♂, alc., 5-VI-1964 (NMHI); 1 ♂ (ZMUI; 140). Ife: 1 ♂, 1975/76, G. Oderhowho (NHMI). Jos: 1 imm. ♂, 1 ♀, 1 imm., alc., VII-1977, P. Beron (ZMA 20.575/77). Oban: 1 specimen (BMNH 10.6.1.48). Pandam: 1 imm. ♀, alc., skull, 1/2-VII-1976, W. Bergmans (ZMA 18.607). Shasha Forest Reserve: 2 ♂♂, 1 ♀, 1 imm.,

Table 11. Ranges of selected measurements of *Nanonycteris veldkampii* (Jentink, 1888) per country.

		♂♂								♀♀							
		fal	gsl	cbl	rl	pl	zw	C^1-M^1	W*	fal	gsl	cbl	rl	pl	zw	C^1-M^1	W*
Cameroun	n									1							1
										50.2							25
Ghana	n	10	10						1	10	8						3
	m	47.1	25.8							49.3	25.9						26
	min	44.3	25.0						21	45.2	24.1						24
	max	48.2	26.5							51.5	27.1						27
Guinea	n									4	1	1	3	3	1	3	
	m									49.6			9.0	12.4		7.2	
	min									47.0	26.2	24.6	8.4	12.0	14.9	7.0	
	max									51.4			9.6	13.1		7.6	
Ivory Coast	n	11	9	8	9	1	7	9		6	7	4	7	4	6	7	
	m	46.4	25.4	23.3	8.7		14.9	7.0		49.9	25.9	24.9	9.1	13.0	14.9	7.3	
	min	45.0	23.6	21.9	8.0	11.3	14.7	6.8		47.1	24.3	23.9	8.7	12.5	14.5	6.9	
	max	49.4	26.8	24.0	9.1		15.3	7.3		53.2	27.1	25.6	9.4	13.4	15.3	7.7	
Liberia	n	5								23	1	1				1	
	m	47.6								50.1							
	min	46.1								46.4	25.9	24.3				7.7	
	max	49.4								53.4							
Nigeria	n	5							1	2	1						1
	m	46.5								50.0							
	min	45.6							19	49.1	26.1						23
	max	47.8								51.5							

* For weights see also the remarks in the Diagnosis.

1/2-IV-1971, D. C. D. Happold (ZMUI; 138, B 1387/88, B 1402).

(Igangan Forest Reserve, Lagos, Mokwa, Nikrowa, Sapoba Forest Reserve, Shaffini, Shagunu.)

SIERRA LEONE. Bo: 1 specimen, alc., skull (BMNH 62.301).

TOGO. Bismarckburg: 1 imm. ♀, alc., skull, Conradt (ZMB 10041). Misahöhe: 2 imm. ♀♀, alc., Baumann (ZMB 7546, 10043).

(Adina, Adjido, Agadji, Aledjo, Atakpamé, Dedomé, Ebeva, Edifou, Evou, Ezimé, Fazao, Kamina, Koutoukpa, Lomnava, Odjolo, Paio, Plateau Akposso, Tchonou, Témedja, Tététou, Togoville.)

Diagnosis: The smallest of all epomophorine bats with white hair tufts at the ear bases and epaulets in males, with a fal of at most 50 in males and 54 in females, a gsl of about 27 or less, a C^1-M^1 length of 6.8-7.7, a short and slender snout, and a palatal ridge pattern with from front to back 3 whole ridges, 1 whole or narrowly divided ridge, 4 to 5 medially notched ridges with thick and prominent central portions and very thin, backward directed serrate lateral parts, and 3 or 4 thin serrate ridges without prominent central portions. Measurement ranges and ratios taken from all over the species' range:

fal	♂♂	44.3-49.4 (n = 31),
	♀♀	45.2-53.4 (n = 47);
gsl	♂♂	23.6-26.8 (n = 19),
	♀♀	24.1-27.1 (n = 18);
cbl	♂♂	21.9-24.0 (n = 8),
	♀♀	23.9-25.6 (n = 6);
rl	♂♂	8.0- 9.1 (n = 9),
	♀♀	8.4- 9.6 (n = 10);
pl	♂♂	11.3 (n = 1),
	♀♀	12.0-13.4 (n = 7);
zw	♂♂	14.7-15.3 (n = 7),
	♀♀	14.5-15.3 (n = 7);
C^1-M^1	♂♂	6.8- 7.3 (n = 9),
	♀♀	6.9- 7.7 (n = 11);

W ♂♂ 19 -21 (n = 2),
♀♀ 23 -27 (n = 5).
rl ♂♂ 33.6-35.3% of gsl (n = 9),
♀♀ 34.0-36.6% of gsl (n = 8);
pl ♂♂ 47.9% of gsl (n = 1),
♀♀ 48.3-51.0% of gsl (n = 5);
zw ♂♂ 57.0-59.4% of gsl (n = 7),
♀♀ 55.4-59.7% of gsl (n = 6).

For a breakdown of measurements see table 11. The data are too few to allow for assessment of possible geographical variation in measurements. Literature data are not always easy to use as the sexes may be lumped and criteria for age assessment are seldom given. Jeffrey (1975) gave as W for 7 ♂♂ 18-28 (m 22) and for 8 ♀♀ 17-30 (m 24); Coe (1976) for 17 ♂♂ 16-23 (m 19.7) and for ♀♀ 18-35 (n ? and m 23); Happold *et al.* (1978) gave 19-33 as range for 24 specimens. Marshall *et al.* (1982) gave a fal range for 50 adult ♂♂ of 44-51 (m 47.5) and for 64 adult ♀♀ one of 46-54 (m 50.2); for 52 adult ♂♂ a W range of 17-26 (m 20.6) and for 55 adult ♀♀ one of 16-28 (m 22.6); all specimens were from Mole National Park, Ghana. Fedden *et al.* (1986) gave as W range 18.1-25.3 for 2 ♂♂ and 1 pregnant ♀.

Distribution: Fig. 16.

Related species: No known living fruit bat species appears to be closely related to *Nanonycteris veldkampii*. Confusion with the often sympatric *Micropteropus pusillus* is possible. However, a glance at the soft palate suffices to tell both species apart, and to the experienced field worker the difference in rostral dimensions is obvious.

Remarks

Taxonomy: The caption of Jentink's paper in which the description of *Epomophorus veldkampii* appeared (1888a) included the date "December 1887", which must have misled Andersen (1912) and several later authors who believed 1887 to be the year of publication of the species. Jentink's paper, the first note in Volume X of Notes from the Leyden Museum, was issued together with the second and third notes, in April 1888, however. Jentink did not mention the date of collection of the holotype in his description but included it in his systematic catalogue of the RMNH collections (1888): 19-IV-1881.

Nanonycteris veldkampii is not very numerous in collections and when visiting those I have been inclined, moreover, to give low priority to its study, as it represents such an unquestionable taxon. For those reasons, the diagnosis and table 11 contain fewer data than nevertheless would have been desirable. Conclusions based on these data therefore bear the mark of preliminarity, and are in need of a more solid foundation. Having said that, I wish to mention two phenomena. The first is that ♀♀ appear to be larger than ♂♂ in both body and skull measurements. This would be in line with an observation to be drawn from the measurements given for the epomophorine species treated hitherto in this series. In the larger species, ♂♂ are always distinctly larger than ♀♀, usually on the average but in some cases, e.g. skull size in *Hypsignathus monstrosus*, even absolutely. With size, this tendency diminishes. In a relatively small species like *Epomophorus minor* the differences have become very small. In the still smaller *Micropteropus pusillus*, ♂♂ have slightly smaller fals than ♀♀ and on the average about equal gsls. In *Nanonycteris veldkampii* an inevitable barrier seems to have been crossed and the tendency seems to be reversed.

The second observation is that in spite of their skulls averaging smaller than those of ♀♀, ♂♂ of *Nanonycteris veldkampii* show one male character in relative skull measurements: zw in ♂♂ amounts to higher percentages, on average, than in ♀♀.

Andersen's description (1912) of the palatal ridge pattern was based on a few specimens and rather concise, and is amended here. The first ridge is either straight or slightly hastate. Ridges 2 to 4 are usually straight in their median portions but curve backwards at their extremities. Going from front to back, the straight median part becomes shorter from the third ridge on. In the fourth, it is intermediate

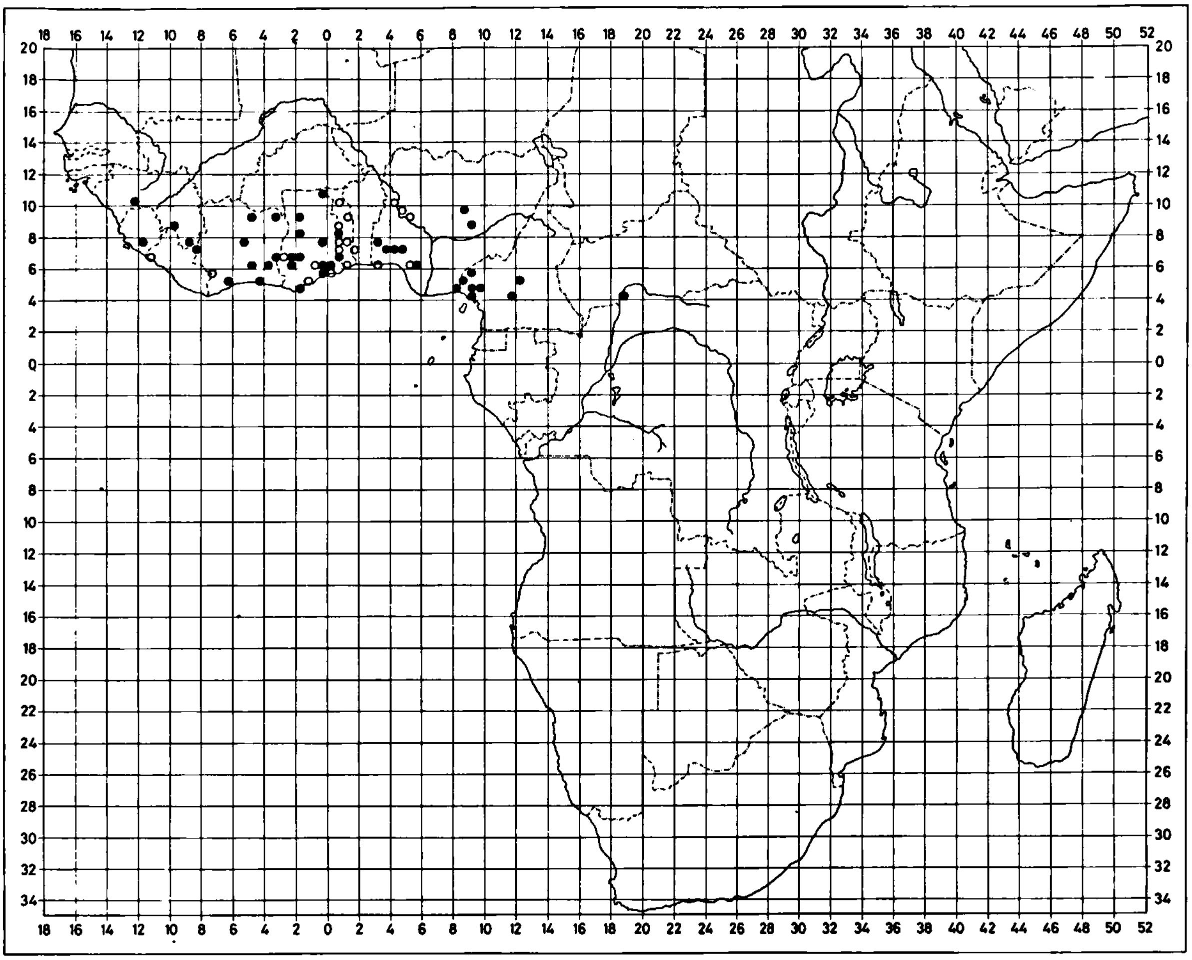

Fig. 16. Distribution of *Nanonycteris veldkampii* (Jentink, 1888). Black dots: squares from where material has been identified by the author. Open circles: records from literature, museum registers and correspondence.

between that in the third and fifth ridges. The thin lateral portions of the fourth ridge are long and reach relatively further backwards. Ridge four is also intermediate between the third and fifth in two other respects; it is either whole (as in ZMA 16.647 from Adiopodoumé), notched (as in ZMA 10.744 from Kankasili) or very narrowly divided (Jentink, 1888a; Andersen, 1912; ZMA 18.607 from Pandam and 18.608 from Calabar), and it may be very weakly serrate (ZMA 18.607). All authors but Rosevear, 1965 describe ridges 5 to 8, or 9, as divided in the middle but in fact they are only notched: the thick median parts of these ridges are continuous and only their protruding anterior margins are indented in the middle. Their serrate lateral parts — of which an ocassional one may be missing — run sideward and backward. The following ridges, 9 or 10 to 13, are serrate and reflect the general form of the preceding ones but become weaker and less curved, the last one running almost parallel to the weakly concave posterior margin of the bony palate.

Not the number but the form of the ridges 5 to 8, or 9, with their thick and undivided but indented median part and vestigial lateral parts is possibly (partly) homologous with that of the two thick postdental ridges in *Epomops dobsonii*.

In *Nanonycteris* this configuration is supported by the corresponding form of the bony palate, with a longitudinal median elevation and shallow depressions, underneath the lateral parts of ridges 3 to 8 or 9, at either side. At its posterior end the bony palate is slightly elevated again and the end of the depressions is marked by ridge 10. The posterior palate margin is curved inward and slightly thickened.

Distribution and geographical variation: In an earlier paper (Bergmans, 1982) the limits of the distribution at large have been discussed. The westernmost locality on record is Kankasili in Guinea and the easternmost Bangui in the Central African Republic. No records are known from south of 4° N, and the species is thus not known to occur in Zaire or Congo as some older and since corrected reports would have it and as was erroneously repeated as recently as 1982 by Honacki *et al.* The Bangui specimen (LACM 19928) is not well labelled and a further record from there would be welcome. The presently reported MNHN specimens collected by Dr J. Prévost near Ntui and Yoko are the first Cameroun records from considerably east of the established occurrence in the Mount Cameroun region and as such add to the probability of Bangui as part of the species' range.

Nanonycteris veldkampii is generally considered a species of the lowland rain forest in West and northwestern Central Africa (e.g. Sanderson, 1940; Verschuren, 1977) which has also been found in Guinea Savanne (Baker *et al.*, 1957) and which in Ivory Coast has been shown to migrate annually into this vegetation zone and even into the southern Sudanese savanne (at Wango-Fitini) — which would be type 27, Sudanian woodland with abundant *Isoberlinia*, in White's nomenclature (1983) adopted in this series — (Thomas, 1983). A number of collecting localities listed in the present account are also within this vegetation zone: Douna and Kong in the Ivory Coast; Damango, Gambaga, Loni, Lovi and Mole National Park (see also Marshall *et al.*, 1982) in Ghana; Aledjo, Bismarckburg (= Yege), Fazao, Lomnava, Odjolo, Paio, Tchonou and Témedja in Togo; and Jos, Shaffini and Shagunu in Nigeria.

Of the 92 collecting localities recorded here, 43 (46.7%) are in wetter (15) or drier (20) types of Guineo-Congolian lowland rain forest, on the border of the wetter type with Swamp forest (3), in a Mosaic of both wetter and drier types (3), or in Mangrove (2) (types 1a, 2, 3, 8 and 77 in White, 1983); 8 (8.7%) are in border areas of the former with the following types; 21 (22.8%) are in Mosaic of Guineo-Congolian lowland rain forest and secondary grassland (12), the same mosaic with *Isoberlinia* woodland (3), in West African coastal mosaic (2), or in or at Afromontane vegetation (4) (types 11a, 12, 15 and 19a in White, 1983); 19 (20.6%) are in Sudanian woodland with abundant *Isoberlinia* (17), on the border of this with Jos Plateau mosaic (1), or in Sudanian undifferentiated woodland with islands of *Isoberlinia* (1) (types 27, 30 and 32 in White, 1983); and 1 could not be located. The species' association with forest is obvious, but so are its wanderings into woodland zones, and populations in isolated forest patches should probably not too easily be considered as relics. Happold *et al.* (1978) recorded it from the rain forest zone but also from forest relics in the savanna and from forested areas close to the Niger River. The species is also known to adapt to cultivated areas. Baker *et al.* (1957) reported on its visits to a tree plantation. Eisentraut (1973a) mentioned its occurrence in an open plantation and in a botanic garden in a city. Jeffrey (1975) found it in food farm areas and secondary bush. Fedden *et al.* (1986) netted it at fruiting guava trees in a cultivated area. The present author collected it in a large and poorly planted garden in Calabar.

Nanonycteris veldkampii is known from many places at or near sea level up to 1200 m (on Mount Nimba; Verschuren, 1977).

Bergmans *et al.* (1974) noted that in Ivory Coast specimens the teeth appeared longer and narrower than in those from Guinea reported by van Orshoven *et al.* (1968). As already observed, the present data are insufficient to assess possible geographical variation in dimensions. From what is known, however, and in the light of its largely continuous distribution and its apparent mobility, it is likely that such variation, if it exists, will be very limited.

Plerotes Andersen, 1910

Plerotes Andersen, 1910a: 97, 1910b: 99, 1912: 483.

Andersen (1910a) based the genus *Plerotes* on 11 characters, differentiating it from its supposedly nearest ally, *Epomops*. From *Epomophorus*, to which the type and still only species had originally been assigned, it differs essentially in having a flattened postdental palate instead of one with raised margins. Andersen's 11 characters are the following:

— The presence of P^1 and M_3, resulting in an unusual dental formula within the epomophorine genera. Later authors have emphasized that the number of teeth in *Plerotes* is variable: the second specimen known, described by G. M. Allen (1945) had no M_3; Harrison (1960) described a specimen with only one pair of upper incisors (and referred to Schouteden who in various publications had mentioned as number of upper cheek teeth 3 or 4 and of lower cheek teeth 5 or 6 — but that author based this on the descriptions of the type specimen and on a specimen of *Epomophorus*, as Hayman *et al.*, 1966, discovered); Hayman *et al.* (1966) reported a specimen with alveoli for M^2, and another which lacked M_3 on one side. In a specimen recorded by Crawford-Cabral (1989) and described in the following pages, there is no M_3 on either side.

The optional presence of certain upper incisors is possibly somehow connected with the relatively large width of the anterior part of the rostrum. (It is not clear which incisors are missing in Harrison's specimen; the position of the remaining pair is intermediate between the normal positions of I^1 and I^2, which are moreover morphologically identical.) The premaxillae in *Plerotes* are separated in front (as a consequence of the widened rostrum?) and will have lost in strength for the support of upper incisors. Andersen (1912) somehow failed to mention the separated premaxillae but his illustration of the holotype skull is unequivocal on this point. In the specimen figured in the present paper the separation is also visible (fig. 18c). The upper incisors are minute and have probably lost all or most of their original function. It is not unlikely that the absence of one or two upper incisors will be a recurring phenomenon in *Plerotes*. In this respect an interesting parallel is offered by *Rousettus bidens* (Jentink, 1879), an otherwise very different species of North Sulawesi. In that species too, the anterior rostrum is relatively broad, the premaxillae are separated, the upper incisors are small and their number varies from 2 to 4 (Bergmans *et al.*, 1988). As upper incisors in other epomophorine bats are usually small to very small, their characteristics in *Plerotes* should probably be appreciated as presenting an expectable further stage in a trend than a ground for generic distinction.

P^1 in *Plerotes* is rudimentary. In other epomophorine species it has been lost and its presence in an occasional specimen is exceptional (e.g. the specimen of *Micropteropus pusillus* in fig. 1).

Hayman *et al.* (1966) mentioned alveoli for M^2 in one specimen (IRSN 10686). I found open alveoli in the right, and closed alveoli in the left half of the mandible of this specimen. It is an immature ♂, and it does not seem likely that it had M^2.

An optional M_3 is a character shared by the African genus *Myonycteris* Matschie, 1899 in which it is present in the species *torquata* (Dobson, 1878) and *brachycephala* (Bocage, 1889) and absent in *M. relicta* Bergmans, 1980, and by the Sulawesian *Eonycteris spelaea rosenbergii* (Jentink, 1889) (see Bergmans *et al.*, 1988).

— The second to fifth characters differentiating *Plerotes* from *Epomops* as summed up by Andersen (1910a), apply to the weakness of the dentition on the whole and to the simple form of the cheek-teeth, with extremely small incisors, and low, long and narrow premolars and molars without cusps and with only traces of longitudinal grooves. This does not apply to P^1, P_1 and M^3 which are rudimentary (Andersen, 1912).

— The sixth to eleventh characters include the unusual large width of the palate, with M^1-M^1 larger than C^1-M^1 (against smaller in *Epomops*); the strong braincase deflection; the simple palatal ridges, resembling those in rousettines rather than epomophorines; the length of the second metacarpal (less than half the fal, against much more than this in *Epomops*), the fourth metacarpal being the longest (the third in *Epomops*), and the second phalanx of the third digit being about as long as the third metacarpal (against much shorter than this in *Epomops*); the extremely narrow interfemoral membrane and the absence of a calcar; and the low number of vertical fasciae of the mesopatagium (7 or 8 against 36-47 in *Epomops*).

No author after Andersen has found reason to discuss the generic status of *Plerotes*. The genus indeed possesses a unique combination of characters. As Andersen (1912: liii) pointed out, it is primitive in its dental formula and palatal ridge configuration, but highly specialized in a number of other characters, notably the delicate morphology of skull and teeth — which are most probably adaptations to a very specific trophic niche.

It is unfortunate that none of the few known representatives of *Plerotes* has been preserved in spirit. There are only skins and skulls (and some in a not too good condition), and many taxonomically probably useful morphological and anatomical characters cannot be examined. Harrison (1960) described its tongue, which is not of the macroglossine type as G. M. Allen (1945) had expected, but of the normal, short epomophorine type. Andersen (1910a, 1912) put much emphasis on the relative lengths of metacarpals and phalanges but even these measurements, when taken from dry skins (or a mounted specimen, as the one Andersen examined), are not really reliable as these very thin bones are easily deformed during the drying process. Andersen's data on these bones are doubtful (compare table 12, and the remarks in the species' account) and as yet not acceptable as evidence for specific — let alone generic — peculiarities.

Plerotes anchietae (de Seabra, 1900)

Epomophorus n. sp., de Seabra, 1898: 166.

Epomophorus anchietae de Seabra, 1900: 116 (type locality: Galanga).

Plerotes anchietae; Andersen, 1910a: 97, 1912: 486; Hill *et al.*, 1941: 30; G. M. Allen, 1945; Ellerman *et al.*, 1953: 46; Ansell, 1960b: 9; Harrison, 1960: 68 (in part: the specimen from Abercorn); Hayman *et al.*. 1966: 28 (in part: the Panda specimen represents *Epomophorus*); Hayman *et al.*, 1971: 6; Kingdon, 1974: 165; Ansell, 1978: 16; Feiler, 1986: 72; Crawford-Cabral, 1989: 10.

Nanonycteris veldkampii (not of Jentink, 1888); Frechkop, 1954.

Plerotes ancheilae; Murray *et al.*, 1975: 673, 676.

Material examined

ANGOLA. Chitau: 1 specimen, 12-I-1931, R. & L. Boulton (CMNH 6971). Dande: 1 imm. ♀, 8-XII-1959, J. V. Santos (neotype of *Plerotes anchietae* (de Seabra, 1900), designated in this paper; Centro de Zoologia, Instituto de Investigaçao Científica Tropical, Lisbon, No. 31-59026); Galanga: 1 ♀, mounted specimen, skull in alcohol, 1893, J. d'Anchieta (holotype of *Epomophorus anchietae* de Seabra, 1900; MLZA 481a).
(Mussende.)

ZAIRE. Lusinga: 1 specimen, skin, 10-XII-1947, Mission G. F. de Witte (IRSN 10685); 1 specimen, skin, calvarium, 14-I-1948, Mission G. F. de Witte (IRSN 10686).

ZAMBIA. Abercorn: 1 imm. ♂, 29-IX-1958, L. D. E. Vesey-Fitzgerald (HZM 1.3049).
(Kasama.)

Diagnosis: A small epomophorine bat, with whitish hair tufts at the ear bases (adult males unknown: their possession of epaulets unconfirmed), a fal in ♂♂ of probably at least about 48 and in two ♀♀ (one of which slightly subadult) 49.4-52.5, a gsl in ♂♂ of probably at least 27 and in two ♀♀ (one of which slightly subadult) 26.8-29.5, C^1-M^1 in ♂♂ probably over 7.5 and in two ♀♀ (one slightly subadult) 7.2-8.2; an extremely narrow interfemoral membrane; a broad and low rostrum, a roundish and deflected braincase, a weak mandibulum and strongly reduced cheek-teeth; simple palatal ridges, the first four curved and undivided, the posterior four serrated and more or less divided in the middle (an occasional trace of a ninth ridge).

Measurements: Table 12.

Table 12. Measurements of *Plerotes anchietae* (de Seabra, 1900).

		neotype	holotype						
country	Angola	Angola	Angola	Angola	Angola	Zaire	Zaire	Zambia	Zambia
locality	Chitau	Dande	Galanga	Mussende	Mussende	Lusinga	Lusinga	Abercorn	Kasama
sex/age	imm. "♀"	imm. "♀"	ad. ♀	"♀"	"♂"	imm. "♂"	imm. "♂"	imm. ♂	imm./?
collection	CMNH 6971	IICT 31-59026	MLZA 481a	UAL 6735	UAL 6734	IRSN 10685	IRSN 10686	HZM 1.3049	BMNH 63.45
HB	87		95	76	96			83	
T	0			0	0				
E	17		15	17	17			18	
tibia			24	20	20				
HF (c.u.)	19		10					12.8	
fal	48.2	49.4	52.5	50	50	48.9	45.3	48.7	48
pollex			22					20	
1st digit: metacarpal		7.8							
1st phalanx		11.7							
2nd digit: metacarpal	24.8	24.4	23.5	25	26			21.1	
1st phalanx		5.8	6.5						
3rd digit: metacarpal	34.9	35.2	36	35	34			32.6	
1st phalanx	25.3	24.6	27.5	28	28				
2nd phalanx	30.7	30.3	35	33	26				
4th digit: metacarpal	34.9	33.6	37	34	34			30.2	
1st phalanx		19.9	22						
2nd phalanx		16.5	20.5						
5th digit: metacarpal	34.4	34.0	36.5	35	35			32.1	
1st phalanx		17.1	19.5						
2nd phalanx		14.6	16.5						
gsl	>26.3	26.8	29.5				25.1	27.0	28.4
cbl		25.5	28.5	—	28.0		23.6	25.9	27.1
rl		10.2	11.6				8.6	9.7	10.5
pl		13.7	15.8				12.7	14.9	14.5
cranium width	12.0	11.3	12.4				12.0	12.0	
iow	4.7	4.5	5.1				4.2	4.6	4.7
pow	7.8	7.2	8.3				7.8	8.3	8.5
mastoid width	10.7			9.9	10.2		10.9	10.8	11.1
zw		13.8	—	—	16.2		—	13.6	15.2
mandible length	21.0	20.5	22.1				—	20.3	
mandible height		5.7					—	5.7	
C^1-C^1		6.1	6.7				6.2	6.0	6.5
C^1-M^1	7.6	7.2	8.2	8.6	8.6		7.1	7.45	7.4
M^1-M^1	7.9	7.5	9.0	7.9	8.8		7.8	7.8	8.5
C_1-M_2	8.9	8.5							
C_1-M_3			10.5					9.6	10.3
length x width of:									
C^1		2.0 x 1.05							
P^1		0.25 x 0.15	0.4 x 0.4						
P^3	1.6 x 1.7	1.6 x 0.65	1.5 x 0.9						
P^4	1.8 x 0.75	1.65 x 0.75	1.7 x 0.8						
M^1	1.4 x 0.7	1.4 x 0.75	1.3 x 0.7						
C_1		1.1 x 1.5							
P_1		0.6 x 0.6	0.5 x 0.5						
P_3		1.25 x 0.8	1.2 x 0.7						
P_4	1.5 x 0.7	1.4 x 0.75	1.6 x 0.8						
M_1	1.4 x 0.65	1.6 x 0.65	1.6 x 0.7						
M_2	1.0 x 0.5	1.0 x 0.6	1.2 x 0.6						
M_3			0.6 x 0.5						

Notes. Wing bones, mastoid width, M^1-M^1 and teeth of Chitau specimen after Hill *et al.* (1941). Body holotype after de Seabra (1900) and wing bones and P^1 and P_1 after Andersen (1912). Mussende specimens after Feiler (1986). Mastoid width Lusinga specimen 10686 after Hayman *et al.* (1966). Abercorn specimen: body and wing measurements, except 3rd metacarpal, and zygomatic and mastoid widths after Harrison (1960). Kasama specimen: after Hayman *et al.* (1966).

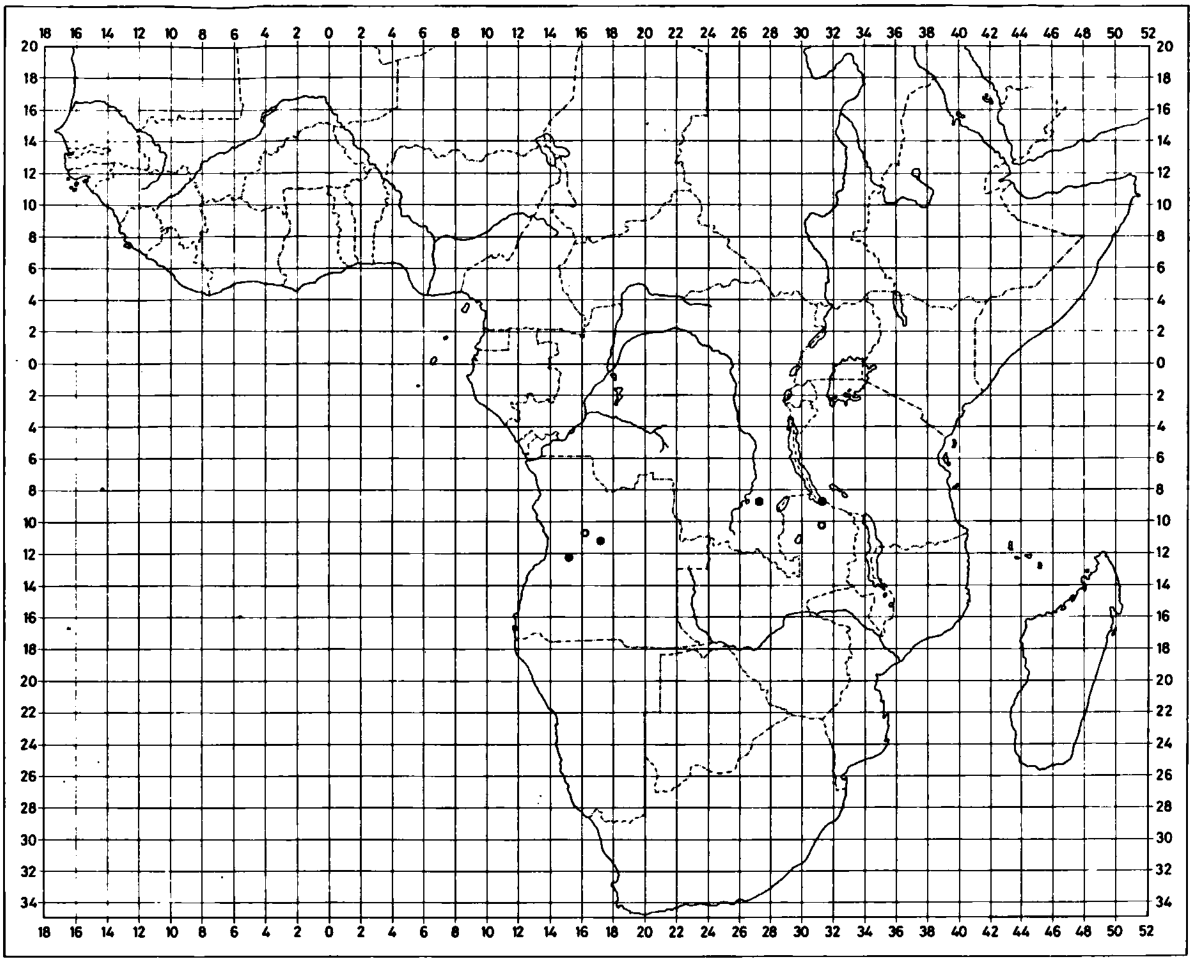

Fig. 17. Distribution of *Plerotes anchietae* (de Seabra, 1900). Black dots: squares from where material has been identified by the author; open circles: records from literature.

Distribution: Fig. 17.

Related species: Of the known epomophorines no species closely approaches *Plerotes anchietae* in characters. Of about the same size and bearing a superficial resemblance are the widely allopatric *Nanonycteris veldkampii* and the at least partly sympatric *Micropteropus pusillus* and *M. intermedius*, but these are at once distinguished by their more extensive interfemoral membrane and their very different palatal ridge patterns.

Remarks

Taxonomy: To my knowledge, altogether nine specimens of *Plerotes anchietae* have been collected. Their appearance in the literature, however, is somewhat confusing. Some, but not all have received due attention.

The holotype, from Galanga, Angola, was recorded by de Seabra prior to his description of the species (1898, 1900). Andersen (1910a) based the genus *Plerotes* on this specimen and described it in full in 1912; after him, the present author was probably the first and the last person to study it, in 1975, before it was destroyed in the fire referred to in the account of *Epomops dobsonii* (see p. 118).

Hill *et al.* (1941) described the second known specimen, from Chitau, Angola, but mixed their account with notes on the type specimen.

In fact a note on the Chitau specimen had already been written by G. M. Allen; this was only published, however, in 1945 when it had been found among his papers by Miss Barbara Lawrence, some time after his death.

The third specimen, from Abercorn, Zambia, was mentioned by Ansell (1960b) prior to its description by Harrison (1960).

Hayman *et al.* (1966) identified two further specimens, from Lusinga, Zaire. These had been published before, by Frechkop (1954), as *Nanonycteris veldkampii* (which caused several later authors to include Zaire in the range of that species). Hayman *et al.* recorded some measurements.

The sixth specimen, from Kasama, Zambia was also reported by Hayman *et al.* (1966). A further specimen, from Likasi, Zaire, would be in the MRAC collection (Hayman *et. al.*, 1966) but according to Dr. W. van Neer (*in lit.*, 14-IX-1989) no specimen from Likasi, or Jadothville, in that collection has been identified as *Plerotes anchietae.*

The seventh and eighth specimens, from Mussende, Angola were studied and described by Feiler (1986).

The ninth specimen, from Dande, Angola, was recorded by Crawford-Cabral (1989) and will be described in the present paper.

Some erroneous records have also been published. Schouteden (1944, and in other papers) had identified a specimen from Congo da Lemba in Lower Congo, Zaire as a probable *Plerotes anchietae.* As it was an *Epomophorus*, as Hayman *et al.* (1966) discovered, the number of cheek-teeth (3 upper and 5 lower) mentioned by Schouteden has confused later authors (e.g. Harrison, 1960) with regard to the variability of the dental formula in *Plerotes.* Hayman *et al.* (1966) mentioned a specimen from Panda, Zaire, in the MRAC (26210); they did not give any details. An examination of the specimen revealed it to represent *Epomophorus* (immature, probably *minor*).

Of the nine specimens on record, only one — the lost holotype — can presently with certainty be regarded as fully adult. Of the other specimens which could be examined, their alleged sex is difficult to confirm and they do not add to our knowledge of the species' adult dimensions. The Chitau specimen was recorded as a subadult ♂ by Hill *et al.* (1941) and as "an adult female, although labeled a male" by G. M. Allen (1945). But its skull sutures are incompletely fused (see also Allen's illustrations) and it is clearly immature; its nipples are flat and there is no other easy way to assess its sex; its premaxillae are missing. The specimen from Abercorn is a nearly adult ♂, with still visible skull base sutures and without epaulets (although it is not yet known if adult ♂♂ develop epaulets). Both specimens from Lusinga are labelled as ♂; of IRSN 10686 I have seen a skin and skull without mandibulum (although there should be a fragment: see Hayman *et al.*, 1966), of IRSN 10685 a skin only. Hayman *et al.* (1966) identified them as immature on the basis of open epiphyses in the wings and, for IRSN 10686, on the presence of thin and pointed upper incisors, identified as milk incisors. The skull of this specimen is nevertheless nearly full-grown. The Kasama specimen is a subadult of apparently unknown sex (Hayman *et al.*, 1966). The Mussende specimens in the collection of the University of Angola in Luanda as recorded by Feiler (1986) are difficult to interpret; the reported sexes will have been copied from the labels but possible sex-confirming characters and age are not discussed. The Dande specimen is a ♀, according to its label, but not fully adult and with flat nipples, and its sex is therefore not certain. (Immature fruit bats are frequently wrongly sexed and the sex stated on their labels should never be taken for granted.)

In the light of our poor knowledge of the taxonomy, of specific and secondary sexual characters, and of intraspecific variation, it is desirable to designate a substitute for the lost holotype. As neotype I have chosen a subadult "♀", skin and skull, collected at Dande, Angola, on 8-XII-1959 by Mr. Jaime V. Santos and now in the Centro de Zoologica of the Instituto de Investigaçao Científica Tropical in Lisboa, Portugal (as IICI 31-59026). The skin of this specimen is in good condition, except that the right wing membrane is torn in one place; its skull is in perfect condition, with the dried soft palate *in situ*. Traces of some skull sutures are visible, notably of that between vomer and sphenoid. Its teeth are practically unworn but spaced as in the holotype (Andersen, 1912: 484, fig. 28), except perhaps a slightly smaller space between P^3 and P^4 (its rl is 20.6% of its gsl, against 22.1% in the holotype). Its finger joints appear to be not completely ossified. Its nipples are flat. Its measurements are included in table 12 and various aspects of its skull, including the soft palate, are given in figs. 18a-d.

This specimen and the collected data on some others allow for some additions to earlier descriptions and for a critical assessment of certain statements by Andersen (1910a, 1912). Although Andersen (1912) described the rostrum in the holotype as "low and very broad, dorsal profile conspicuously descending postero-anteriorly", his illustration hardly shows this. In the neotype the rostrum also tapers towards the front and is very much lower at the level of the canines than near the orbit. (The anterior part of the nasals in the neotype may have collapsed a little in the drying process, but if so this is of little significance to anterior rostrum height.) The premaxillae are separated in front. The braincase is domed and rounded, and strikingly bulging just anterior of the mandibular glenoid, practically covering the anterior pterygoideal foramen when viewed from the side. The zygomatic arches, missing in the holotype, are low and very slender, with two distinct angles at the jugal junctures when viewed from the side (and easily distorted during preparation, as on the right side in the neotype). The orbit is relatively large. The auditory bullae, missing in the holotype, are of rather normal proportions (i.e. relatively about the same as in other epomophorines — but this is admittedly difficult to measure). The foramen lacrymale is very small and, in lateral view, partly covered by a sheat of bone. The foramen infraorbitale is also rather small. There is a very small foramen supraorbitale. Both the optic foramen and the anterior pterygoideal foramen are rather small and oriented towards the front; this is related to the morphology of the braincase in this region, referred to above. Foramen rotundum and foramen ovale, when viewed from below, are partly covered by a thin bony ridge. The processus coronoideus, missing in the holotype, is slender but not as low as Andersen (1912) presumed.

Andersen's redescription of the holotype (1912) is short, as the then sole representative of the species had also served for his more extensive descriptions of the genus (1910a, 1912). The relative measurements of the holotype's wing bones are discussed in those descriptions. The metacarpal of the second digit would be "much less" than half the fal, Andersen's measurements being 23.5 and 53. From the collected measurements in table 12 it is clear that, although some of the specimens may not have reached adult wing bone ratios, Andersen's measurements must be regarded with reservation. (Incidentally, Harrison (1960) gave 21.1 as length of the second metacarpal in the Abercorn specimen but his illustrations show this to be an error.) Andersen also stated that of the metacarpals the fourth is the longest (his measurement of 27 in the table on p. 510 in Andersen, 1912 should read 37, as can be calculated from the table with wing indices on p. 485). Again, this is not confirmed by the other available measurements. Doubt seems also justified with regard to his claim that the length of the second phalanx of the third digit would be subequal to that of the metacarpal of that digit (the measurement of this phalanx in the Mussende "male" in Feiler, 1986 can hardly be correct).

Some other statements by Andersen on bodily characters, such as the form of the ear, should be read with reservation and need to be checked against future specimens preserved in spirit.

De Seabra (1900) described the fur colour as slightly yellowish grey (on the breast a little more yellowish), with the exception of the white ear tufts and dark spots around the eyes and stretching toward the nostrils without reaching

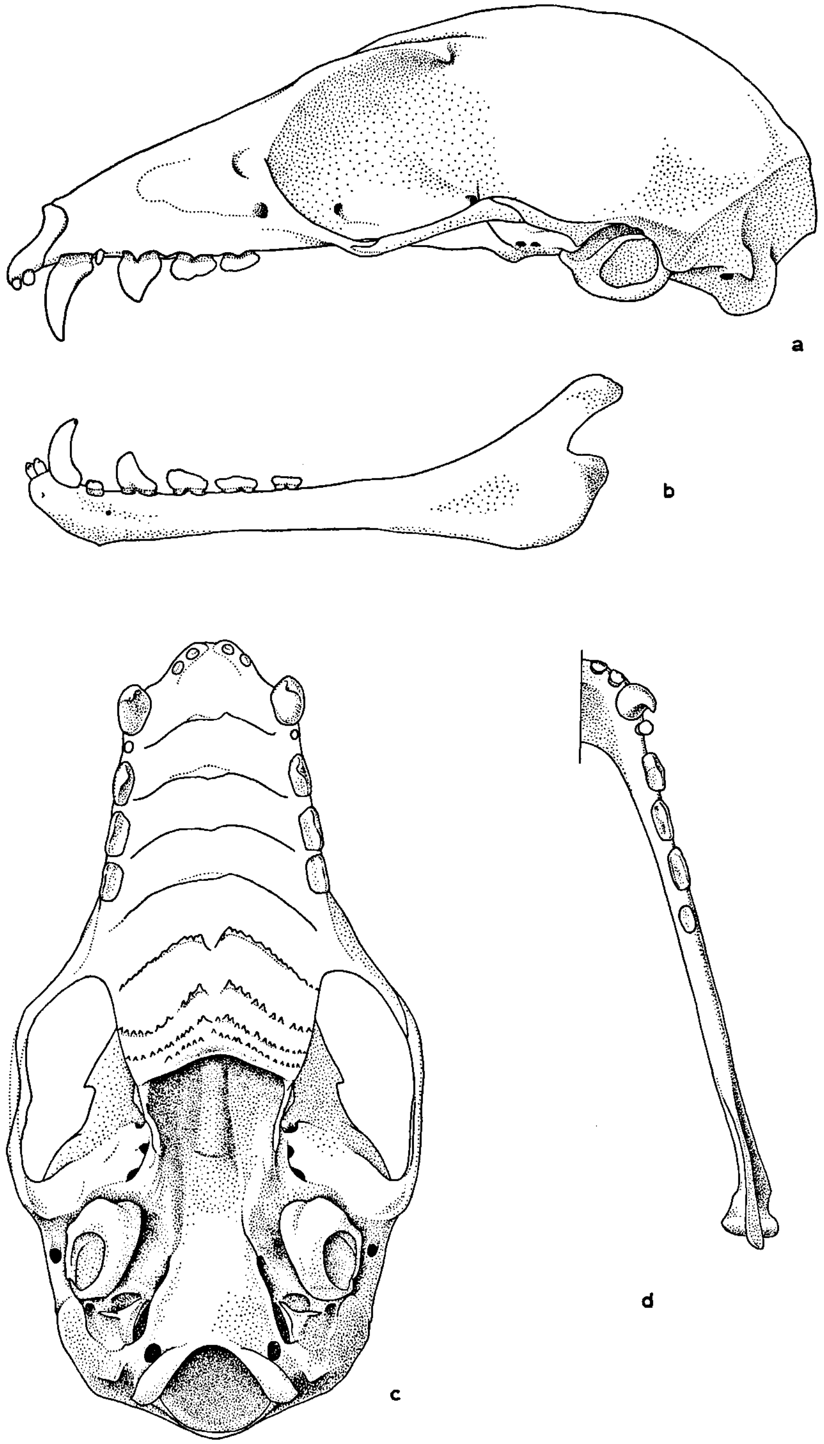

Fig. 18. Skull of neotype specimen of *Plerotes anchietae* (de Seabra, 1900); a: left aspect of skull; b: left aspect of mandible; c: basal aspect of skull, with dried soft palate in situ and masking the margins of the postdental bony palate; d: dorsal aspect of right half of mandible.

these. Andersen (1912) described the fur colours of the back as "brownish isabella with greyish white or creamy white bases to the hairs" and those of the underparts as "much lighter, greyish drab". He did not describe the fur on the head. Harrison (1960) also only described the fur on back and underparts. The fur of the neotype specimen is in a much better condition than that of the holotype when I saw it. No previous author has mentioned the distinct moustache of stiff, backward directed, yellowish white hairs along the upper lip behind the nostril and tapering to some point anterior to the angle of the mouth, or the chin-beard of the same colour, with a bristle of a few rows of hairs right behind the chin pad followed by backward directed hairs extending to near the mouth angle. The specimen has the narrow, darker (reddish) brown rings around the eyes mentioned by de Seabra, and on either side the band of the same colour running from the eye towards the nostril, ending where it meets the whitish moustache. The stiff moustache and beard hairs will no doubt function as carriers of pollen — if *Plerotes* is a visitor of flowers, which seems very likely. The back fur is about as Andersen (1912) described it, with the whitish hair bases causing the fur to look a bit ruffled. Chin — behind the beard —, throat, breast, belly and flanks are covered with thin, long, soft hairs; these are lighter than the back fur, although again slightly darker on the flanks and somewhat yellowish in the centre of the belly, but darkest at their bases.

Distribution and geographical variation: All collecting localities are within the Wetter Zambezian miombo woodland (dominated by *Brachystegia, Julbernardia* and *Isoberlinia*) (type 25 in White, 1983) with the possible exception of Kasama in Zambia which is in the Mosaic of Zambezian dry evergreen forest and wetter miombo woodland (type 21 in White, 1983). *Plerotes anchietae* is an apparent woodland species, occupying the centres, as it seems, of both general distribution areas of *Epomops dobsonii* (see fig. 10). Crawford-Cabral (1989) noted that the four Angolan localities are all on the Angolan Plateau. Of one, Chitau, the label states the collecting altitude as just under 1500 m (4900′); both Dande and Mussende are between 1000 and 1500 m and Galanga (for which Crawford-Cabral gives slightly different coordinates than the here followed Hill *et al.*, 1941) is between 1500 and 2000 m. Crawford-Cabral (*op. cit.*) suspects that much of the present distribution of forest species in West Angola may be explained by the possible southward advance of rain forest during the last pluvial, which left behind spread forests on the higher altitudes (see his fig. 3). For true forest species as *Megaloglossus woermanni* Pagenstecher, 1885 and *Hypsignathus monstrosus* this may well be true but *Micropteropus pusillus* and *Epomophorus wahlbergi* (Sundevall, 1846) are no true forest species and will rather have moved with their home woodlands and forest edges as these were forced southwards by the same climatic changes that set the forests in movement. *Plerotes anchietae* may rather belong with them than with forest species although it is much more specialized, which may be (part of) an explanation for its restricted distribution, possibly connected with that of certain food plants.

In the eastern part of its known range Kasama is between 1000 and 1500 m, Abercorn is on the border of the 1000-1500 and 1500-2000 m ranges, and Lusinga is at 1760 m. This seems to confirm the (sub)montane habitat preference — but many lowland Megachiroptera occur well over 1500 m and more data are needed for a good assessment.

If *Plerotes anchietae* does inhabit, as it now seems, two geographically widely separated areas, intraspecific variation may be expected. As yet the material is too restricted to say more than that.

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