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# TAXONOMY AND BIOGEOGRAPHY OF AFRICAN FRUIT BATS (MAMMALIA, MEGACHIROPTERA). 5. THE GENERA *LISSONYCTERIS* ANDERSEN, 1912, *MYONYCTERIS* MATSCHIE, 1899 AND *MEGALOGLOSSUS* PAGENSTECHER, 1885; GENERAL REMARKS AND CONCLUSIONS; ANNEX: KEY TO ALL SPECIES

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## ABSTRACT

This is the last part in a series comprising all Megachiroptera known from mainland Africa and its islands. The concept of the genus *Lissonycteris* Andersen, 1912 is reviewed and adapted. For the first time, its differential characters *vis-à-vis* the genera *Rousettus* Gray, 1821, and *Myonycteris* Matschie, 1899 as described in the literature have been checked against material of all the species involved. As a consequence, a number of these characters are considered of no taxonomic value and have not been retained, while some new differential characters are described. *Lissonycteris* and *Myonycteris* are considered different from *Rousettus* on generic level, while *Lissonycteris* and *Myonycteris* are more closely related to one another than each of these to *Rousettus*. New observations on all African and extralimital species of *Rousettus* are reported and the retention of *Boneia* Jentink, 1879 as a subgenus by Corbet *et al.* (1991, 1992) is rejected. *Lissonycteris* is considered a monotypic genus, with as single species the polytypic *L. angolensis* (Bocage, 1898). The subspecies *angolensis*, *smithii* (O. Thomas, 1908) and *ruwenzorii* (Eisentraut, 1965) are recognized, and two new subspecies, *petraea* and *goliath*, are described. *Myonycteris* consists of three species, *torquata* (Dobson, 1878), *brachycephala* (Bocage, 1889) and *relicta* Bergmans, 1980. Their present taxonomy is conform earlier reports (Bergmans, 1976, 1980a). *M. torquata* is considered a monotypical species. *M. relicta* is reported from Zimbabwe for the first time, extending its known distribution 1400 km southwards. Following Kirsch *et al.* (1995) and Springer *et al* (1995), the subfamily Macroglossinae is considered a synonym of the subfamily Pteropodinae. The taxonomy and distribution of *Megaloglossus woermanni* Pagenstecher, 1885 are reviewed. In a final section, general remarks and conclusions are presented on the supraspecific taxonomy of the Megachiroptera and a classification is proposed which includes the raise to subfamily rank of the Rousettinae and Epomophorinae and the recognition of the new tribes Scotonycterini and Plerotini; some recent publications bearing on African species taxonomy are reviewed; and an appraisal is made of the distribution patterns found throughout this series. A vicariance model is proposed to explain the occurrence in Asia and Africa of both *Pteropus* Brisson, 1762 and *Rousettus* Gray, 1821. For woodland species, the regions SE Tchad/E Central African Republic/W Sudan; N half of Tanzania; and E Angola/adjoining Zaïre have been identified as having (had) a barrier effect on dispersal. For forest species, important divides appear to be in the regions Volta River/Dahomey Gap; SE Nigeria; C and S Gabon; C Zaïre, from N to S; the Western Rift system; several barriers in E Africa. Finally, an illustrated key to all African Megachiroptera is given, primarily based on externally visible characters and designed for use in the field.

## INTRODUCTION

For a general introduction to the series of which this paper forms the fifth part, the reader is referred to the first part (Bergmans, 1988), which also contains a section Materials and Methods, including the abbreviations used. (Most often used are fal = forearm length, and gsl = greatest skull length.) The gazetteer of African fruit bat localities announced in the first part of this series has been completed but, for financial reasons, will be produced separately, and is available on request.

## TAXONOMIC SECTION

### **Lissonycteris** Andersen, 1912

*Lissonycteris* Andersen, 1912: 23, 814 (as subgenus of *Rousettus* Gray, 1821; type species: *Cynonycteris angolensis* Bocage, 1898); Leche, 1921: 41; Benedict, 1957: 292, 300; Koopman, 1975: 361, 1994: 20.

*Lissonycteris* (as a genus); Schwarz, 1920; Novick, 1958a: 445-457; Lawrence *et al.*, 1963; Rosevear, 1965: 79, 84; Kingdon, 1974: 124; Bergmans, 1980: 179; Haiduk *et al.*, 1980: 187, 1981, 1984; Kirsch *et al.*, 1995; Springer *et al.*, 1995.

Andersen (1907b) included *Cynonycteris angolensis* Bocage, 1898 in *Rousettus* Gray, 1821. A few years later, he proposed the subgenus *Lissonycteris* for what he called the "most aberrant species of *Rousettus*" (Andersen, 1912: 23, 53). He compared it with the following species of typical *Rousettus*: *egyptiacus*, *amplexicaudatus*, *celebensis*, and *leschenaultii* (all but *celebensis* still under more than one species name). As diagnostic characters of *Lissonycteris* Andersen mentioned its only slight brain-case deflection (against moderate in *Rousettus* sensu stricto); the ossification of the premaxillaries (which he found only exceptionally in old specimens of one typical *Rousettus* species); the peculiar, subquadrate outlines of the cheek-teeth (against oblong in *Rousettus*); the extreme reduction of $P_1$ (against a less strong reduction in *Rousettus*); the attachment of the wing to the second toe (to the first toe in *Rousettus*); the distinct 'antitragal' lobe (small and rounded in *Rousettus*); the long and silky fur (against short in *Rousettus* - except *R. celebensis*). In his Addenda and Corrigenda, Andersen (1912: 814-815) added, on the basis of the species *Rousettus smithi* O. Thomas, 1908 not previously considered by him and also representing *Lissonycteris*, that *Lissonycteris* would probably be considered a genus, distinct from *Rousettus*, by future systematists. He added some diagnostic characters: the flattening of the posterior braincase (which with the only slight deflection gives the skull in profile a rather striking resemblance to that of *Epomophorus* Bennett, 1836); the lesser height of the rostrum; the thin ascending branches of the premaxillae; the more inflated frontal sinuses; the relatively longer postdental palate; the different morphology of the cheek-teeth, with their outer and inner ridges much more cusp-like, shorter antero-posteriorly, and higher vertically, those in $P_4$ separated (against fused in *Rousettus*) and those of $M_1$, $M_2$ and $M_3$ even slightly diverging above; the reduction of $M^1$ (smaller than $P^4$, larger than this in *Rousettus*); the shortness of the tibia; and the conspicuously greater lengths of the fingers.

Schwarz (1920) listed *Lissonycteris* as a genus, without further comment.

Leche (1921) pointed out that Andersen's analysis of the exceptional position *vis-à-vis* typical *Rousettus* would justify its raise to generic rank.

Benedict (1957) found that the form of the hair scales in *Lissonycteris* is more similar to that in the *Epomophorus* section (sensu Andersen, 1912) than that in the *Rousettus* section. She also observed that while typical *Rousettus* has conspicuous overhair, *Lissonycteris* lacks overhair entirely (and *Stenonycteris* has sparse overhair).

Novick (1958a) treated *Lissonycteris* as a genus, referring to Novick and Lawrence, 1958, a paper which appeared, however, only in 1963 and with Lawrence as the first author. Novick (1958a) added to the arguments the fact that *Lissonycteris* orients visually and lacks the faculty of acoustic orientation found in at least three species of typical *Rousettus*, i.e. *egyptiacus*, *leschenaultii* (as *seminudus*), and *amplexicaudatus*.

Lawrence *et al.* (1963) re-examined the generic status and relationships of typical *Rousettus* and *Lissonycteris*, prompted by differences in non-flight locomotion and orientation observed between live specimens of both. Their observations include the following: *Rousettus* inhabits dimly lit caves with large entrances and sheltered retreats, where they hang in large clusters along the walls or ceiling, by their hind feet and with their backs to the wall, the wings folded at their sides. There is no general observation on cave type or colony size of *Lissonycteris* in this paper but one remark is of importance. While Novick (1958a: 445) suggested that, like *Rousettus*, *Lissonycteris* was captured "from large cave-dwelling colonies", Lawrence *et al.* mentioned that only a single wild colony of about 20 *Lissonycteris* was observed. *Lissonycteris* always roosts hanging free from the ceiling of the cave. *Rousettus* uses all four limbs in entering and leaving crevices: its feet and its wrists in walking, and its thumbs in climbing vertically or even upside down along irregular surfaces or branches. To this purpose, it is able to fold its wings considerably. *Lissonycteris* never uses its wings for locomotion other than flight. It would therefore also never enter crevices to roost. It is not able to fold its wings as tight as *Rousettus*. It does not land on horizontal surfaces and, when forced to, shows awkward and incompetent movements only, while at least in captivity *Rousettus* frequently crawls. *Rousettus* occasionally uses its wrists and thumbs to readjust morsels of fruit in its mouth and only on one occasion was seen using its hind foot claws to manipulate food in its mouth. *Lissonycteris* regularly uses its hind feet for handling its food, but rarely its wrists or thumbs; it grasps fruit with its teeth and then brings a foot down to its mouth to hold the bulk with widely spread toes and, after having bitten off a morsel, holds the remainder against its chest or abdomen, frequently wholly or partly covered by its wings. *Rousettus* never seems to store fruit in its cheeks or to fly with any in its mouth, but generally stays to eat at the food source. It seems to swallow fruit fibers together with the juice. *Lissonycteris* tends to hold food in its cheeks and carry food to its roost, and after having expressed and swallowed the juice will drop the bolus of fiber.

To these differences in ecology, roosting posture and behaviour, limb use, and feeding behaviour Lawrence *et al.* (1963) added the following morphological differences (in part quoted from the diagnosis of *Myonycteris* in Andersen, 1912): In *Lissonycteris* and *Myonycteris*, compared with *Rousettus*, the facial axis is less deflected, the orbits are larger, the nostrils are more prominent, the calcar is weaker, the wings are relatively larger (metacarpal and first phalanx of fifth digit conspicuously longer than forearm in *Lissonycteris*, about equal to it in *Myonycteris*, and much shorter in *Rousettus*); the attachment of the wing near the middle of the first phalanx of the second toe (in *Myonycteris*: ditto; in *Rousettus* usually between metatarsals one and two, sometimes near the basis of the first phalanges, often well proximal to this); the odontoid papillae bordering the lips: rather high and pointed, forming a single row extending from the angle of the mouth forward about to the canines (in *Myonycteris*: ditto, with a poorly defined second row on the upper lip; in *Rousettus*: a reduced single row of small papillae); the palatal ridge pattern, with nearly straight ridges 1-3, a divided ridge 4, and somewhat converging ridges 4-7 in *Lissonycteris* and *Myonycteris* (more bowed forward, usually undivided, and more parallel, respectively, in *Rousettus*); furthermore, *Lissonycteris* and *Myonycteris* have a shorter, less robust tail, longer, denser fur on the notopatagium and the proximal dorsal surface of the tibia, a smaller foot with a webbed basal quarter to third of the first phalanges, slenderer claws, and an extensive patch of glandular fur on the throat of adult males. Lawrence *et al.* (1963) also mentioned a number of cranial and dental characters distinguishing *Lissonycteris* and *Myonycteris* from *Rousettus*: a relatively long anterior skull part (from the tips of the premaxillaries to behind the postorbital processes) as compared with both brain-case length (from behind the postorbital processes) and its bulk; a slender rostrum, with posteriorly depressed nasals; greatly developed lateral frontal sinuses; raised posterior orbital margins; a concave interorbital region; an elongated and flattened posterior brain-case; a larger orbit, with a sharper edged antero-ventral border, plate-like where it is pierced by the infraorbital canal; different shape and spacing of the teeth; a different occlusion pattern.

Kingdon (1974) referred to Lawrence *et al.* (1963) and suggested that the separation between *Lissonycteris* and *Rousettus* (and *Stenonycteris*, which he also regarded as a genus) may be more ancient than the radiation of other fruit bat genera. He added that all three occupy distinct ecological niches, which he considered an important criterion for the recognition of genera. In Kingdon's vision, *Lissonycteris* would represent a primitive type of fruit bat, roosting very much as ancestral forms, in hollow trees and well-lit caves. (On one occasion, Kingdon captured a specimen roosting in dense undergrowth in montane forest.) The ancestors of modern *Rousettus* (and *Stenonycteris*) developed a way to echolocate and could then exploit the darker parts of caves. They could afford to remain conservative because no other fruit bat followed them there. (This is true for present-day Africa and Madagascar, but not for large parts of Southeast Asia, where *Eonycteris* Dobson, 1873 forms large dark-cave colonies - unless this is also a rousettine bat. See the general remarks and conclusions. W.B.) Apart from the difference in roosting sites between *Lissonycteris* and the others, Kingdon did not elaborate the ecological niche differences.

Koopman (1975), following Rosevear (1965) in regarding *Lissonycteris* as monotypic, put forward that many of the cranial and dental characters mentioned by Lawrence *et al.* (1963) by which *Lissonycteris* (and *Myonycteris*) differ from *Rousettus* do not hold when all *Rousettus* species are examined. He regarded only the following as reliable: the dish-faced appearance of the interorbital region; the larger orbit; the orbital rim; and the relatively large lateral frontal sinuses. All these characters he supposed to be related to the larger size of the eye, which in turn may be related to the absence of echolocation (Koopman, 1975). Koopman therefore retained *Lissonycteris* as a subgenus of *Rousettus*, also in his recent survey of bat systematics (Koopman, 1994).

Bergmans (1980) mentioned the narrowing of the anterior palate, resulting in the tooth-rows being curved inward, and the relative heaviness of $P_4$ as characters of both *Lissonycteris* and *Myonycteris* and not found in *Rousettus*.

Haiduk *et al.* (1980) studied the standard karyotype of *Lissonycteris angolensis* and found a diploid number (2n) of 36 and a fundamental number (FN) of 66. They expressed some doubt whether Dulic *et al.* (1973), who published a 2n of 36 and an FN of 68 for *Rousettus egyptiacus*, would not be mistaken. In 1981, Haiduk *et al.* examined the latter species themselves, and found the same values for 2n and FN as in *Lissonycteris angolensis.* They did find differences, however, in the G-bands. *L. angolensis* shows a polymorphism in pair 1 which is not shared by *R. egyptiacus.* The latter species has two pericentric inversions in pair 1 which are not found in *L. angolensis.* The species were both compared with *Myonycteris torquata* (Dobson, 1878), which differs from *L. angolensis* only in having a different polymorphism in pair 1. In their schematic presentation of chromosomal evolution Haiduk *et al.* (1981) grouped *Lissonycteris angolensis* with *Myonycteris torquata,* while *Rousettus egyptiacus* is placed at some distance. But they emphasized that this arrangement does not imply evolutionary relationships and merely represents a possible sequence of chromosomal events.

From the above as well as from the synonymies under the species and subspecies it is clear that at present two opinions on the systematic position of *Lissonycteris* are diagonally opposed: its placement as a subgenus in the genus *Rousettus* and its placement as a genus on its own. However, many authors appear to base their opinion solely on that of others and seem not to be aware of views opposing theirs. For this reason, the comments below are very detailed. For these comments, ZMA material of *Lissonycteris* has been compared with material of *Myonycteris torquata* and *M. relicta* and all nine currently recognized *Rousettus* species, all in the same collection except *M. relicta* (which is no. 62472 in the Natural History Museum in Bulawayo, Zimbabwe - NHMBZ). Material of African species is listed in the species accounts in the present series (Bergmans, 1994; this paper). Extralimital material of *Rousettus* is listed in Rookmaaker *et al.* (1981) and Bergmans *et al.* (1988) except: *R. leschenaultii* from Koira, Orissa, India (ZMA 20.492/97); Khab No Koi and Tab Kwang, both in Thailand (ZMA 21.669 /70); and *R. spinalatus* from Batu Timbang, Sabah, Malaysia (ZMA 23.132/33). Of *Myonycteris brachycephala* (Bocage, 1889), detailed skull drawings were available (Andersen, 1912; this paper, figs. 7a-d), and of *M. relicta* Bergmans, 1980, slides of skull and skin of the holotype specimen and a newly discovered specimen from Zimbabwe (this paper). The following specimens have been used to calculate relative measurements: *Lissonycteris angolensis,* ♂ from Pointe Noire, Congo (ZMA 15.537); *Myonycteris torquata*, ♂ from Pointe Noire (ZMA 15.423); *M. relicta*, ♀ from Haroni-Lusitu confluence, Zimbab-we (NHMBZ 62472); *Rousettus egyptiacus*, ♂ from Cairo, Egypt (ZMA 22.205); *R. amplexicaudatus*, ♂ from Ambon, Indonesia (ZMA 21.442); *R. bidens*, ♂ from Imandi market, Indonesia (ZMA 22.759); *R. celebensis*, ♂ from Kuala Navusu, Indonesia (ZMA 18.571); *R. lanosus*, ♂ from Menengai, Kenya (ZMA 20.428); *R. leschenaultii*, ♀ from Koira, India (ZMA 20.497) and a ♂ from Bogor, Indonesia (ZMA 16.656); *R. madagascariensis*, ♀ from Bevato of Namoroka, Madagascar (ZMA 19.312); *R. obliviosus*, imm. ♀ from Anjouan, Comores (ZMA 20.903); *R. spinalatus*, ♂ from Batu Timbang, Malaysia (ZMA 23.132).

### *Skull*

Andersen (1912) measured brain-case deflection by projecting the upper alveolar line backward and noting where the projection cuts the occipital region. In all *Rousettus* species, the alveolar line is relatively straight. In *Lissonycteris* and *Myonycteris* it is not, and its projection is a dubious affair. The present author has compared deflection by placing the skull, with the mandible *in situ*, on an even surface, resting it on the mandibular ramus excluding the projecting angular process (this has to sink into the surface); the relative distance between the occipital condylae and the surface is a measure for the deflection. (A still better method would be to measure the angle between facial axis and basicranial axis on lateral view photographs.) It appeared that there is little brain-case deflection in *Lissonycteris*, *Myonycteris*, *Rousettus egyptiacus* and *R. leschenaultii*, moderate deflection in *R. amplexicaudatus* and *R. spinalatus*, while in all other *Rousettus* species it is strong. As a character to distinguish these genera, brain-case deflection has no apparent value. (See also the account of *Rousettus* in Bergmans, 1994.)

The anterior part of the skull in *Lissonycteris* (see Lawrence *et al.*, 1963) is relatively longer than in all *Rousettus* species except *lanosus* and *madagascariensis*, and *Myonycteris torquata*. However, this relation is difficult to ascertain; one has to work with projected lengths, with skulls showing different measures of deflection.

The "flattening" of the posterior brain-case in *Lissonycteris* is, in fact, the dorsal component of a constriction of the skull somewhat behind the posterior insertion of the zygomatic arch. This constriction is also present in *Myonycteris* and, to a variable extent, *Rousettus*. In *Rousettus*, the actual constriction is generally not as distinct, while in most species the deflection of the brain-case tends to mask it still more. Nevertheless, the posterior brain-case in *Lissonycteris* and *Myonycteris* is relatively low. This can be assessed by comparing the relative occipital heights (the distance, in the median plane, between the occipital ridge and the ventral margin of the foramen magnum - or the line connecting the most ventral points of the occipital condyles, related to gsl, or brain-case length). Only in *Rousettus bidens* the occipital height is as low as in the two other genera.

The elongation of the brain-case was measured by Lawrence *et al.* (1963) by comparing the distance from the bottom of the occipital condyles to the top of the occipital crest with the distance from the postglenoid process to the back of the condyle. In *Lissonycteris* and *Myonycteris* they found that the first distance was smaller than the second, in *Rousettus* it was larger than this or equal to it. As has just been pointed out, the relative occipital height in the first two genera is lower than in all *Rousettus* species but *bidens*, and it does not seem to offer the best means to establish brain-case elongation. Moreover, it proved impossible to reproduce all of the findings of Lawrence *et al.* (1963). The first distance was found to be smaller than the second in *Lissonycteris* (with a difference of 2.4), *Myonycteris torquata* (1.8), and all *Rousettus* species (2.8 in *bidens* and 0.2-1.4 in the others) except *obliviosus* and some *leschenaultii shortridgei*, in which the first distance was larger than the second (0.7 and 0.2, respectively). The postglenoid process is an ill-defined process and the different results may well be caused by a different method of measuring a distance from that process to another point. But the calculated value must be considered a doubtful measure of brain-case elongation anyhow. When calculating the percentage of cbl of the brain-case length (measured from the median point on the connecting line between the dorsal ends of the distinct grooves in the orbits that mark the anterior limit of the brain-case proper, to the posteriormost

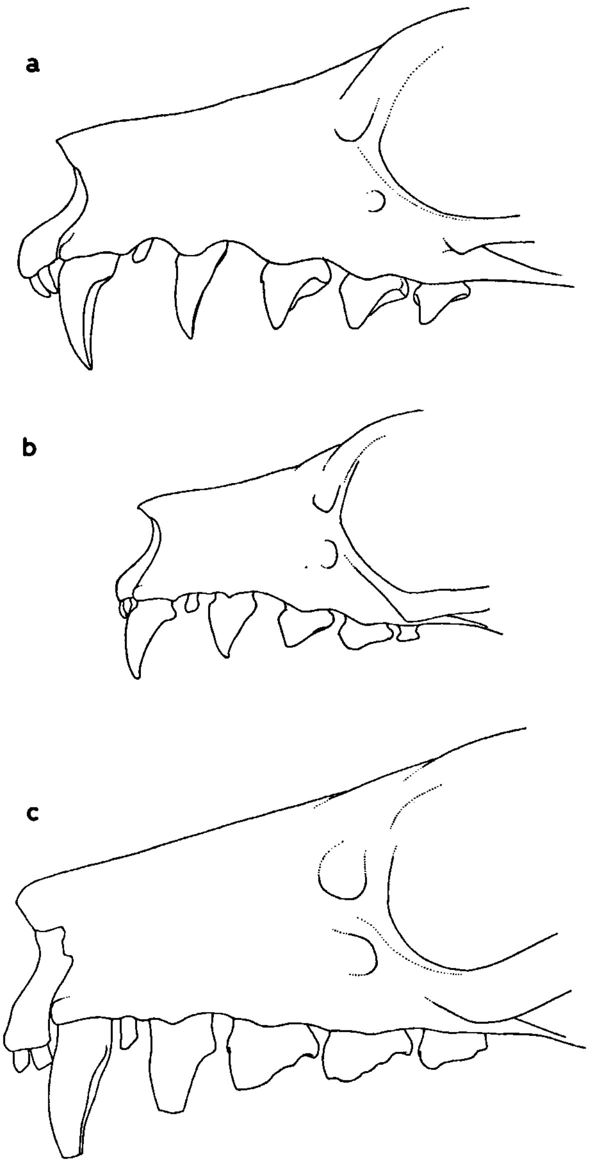

Fig. 1. Rostra. Lateral view of a: *Lissonycteris angolensis angolensis* (Bocage, 1889), ♂ from Pointe Noire, Congo (ZMA 15.537); b: *Myonycteris torquata* (Dobson, 1878), ♂ from Pointe Noire, Congo (ZMA 15.423); c: *Rousettus egyptiacus egyptiacus* (É. Geoffroy-St. Hilaire, 1810), ♂ from Cairo, Egypt (ZMA 22.205).

point on the occiput), *Lissonycteris* has a slightly shorter brain-case than all *Rousettus* species (59.7% of cbl, against 61.6-68.8% in *Rousettus*; *Myonycteris torquata*: 65.1%). It is difficult, however, to determine the anterior measuring point reliably, and the difference found is minimal.

A typical characteristic not noted before is that the upper alveolar line in *Lissonycteris* and *Myonycteris* changes in level and direction between $P^3$ and $P^4$. This brings on a different shape of the rostrum if compared with *Rousettus*, with a low distal part with nearly parallel dorsal side and lateroventral margin anterior to $P^4$ (figs. 1a-c). The mandibular alveolar line does not correspond to this level change but remains rather straight, and the resulting local divergence accomodates the relatively high premolars and anterior molars.

Lawrence *et al.* (1963) drew attention to the characteristic occlusion pattern in *Lissonycteris* and *Myonycteris*, with alternating $P^3$ and $P_3$ and with $P^3$ and $P^4$ barely occluding with $P_4$. To this may be added that $P_4$ has shifted outward, as far as $P^3$. In *Lissonycteris* this pattern is very distinct and in *Myonycteris torquata* it is essentially the same. In *M. brachycephala* and *relicta* these teeth are relatively heavier and not as distant from one another. These species do, however, show the same trend toward widely spaced anterior cheek-teeth. In *Rousettus* species none of the above characters is found. The third premolars are slender but not as thin as in *Lissonycteris*; moreover, they are nearer to each other ($P^3/P_3$) and nearer to $C^1$ ($P_3$) and $P_4$ ($P^3$). The fourth premolars are relatively heavier, less pointed, and longer than those in *Lissonycteris* and occlude with each other and with $P^3$ ($P_4$) and $M_1$ ($P^4$).

The relative anterior rostrum height in *Lissonycteris* and *Myonycteris* is smaller than in all *Rousettus* species except *madagascariensis* and *obliviosus*. In *madagascariensis* this height is even smaller than in *Lissonycteris*. Lawrence *et al.* (1963) noted that in *Lissonycteris* and in *Myonycteris* the nasals are depressed posteriorly, while in *Rousettus* they are not. This contributes to a relatively low posterior rostrum in the former two genera (figs. 1a-b), although it is difficult to quantify.

The anterior palate is slightly narrowed in *Lissonycteris*, and somewhat more in *Myonycteris*; the upper tooth-rows appear to be constricted from $P^3$ on forward. In most *Rousettus* the tooth-rows are converging but straight, except in *amplexicaudatus* in which they are also a bit concave and in *R. bidens* in which they are straight but hardly converging.

In all *Lissonycteris* specimens the premaxillae are co-ossified, in *Rousettus* species except the odd old *R. e. egyptiacus* and in *Myonycteris torquata* they are not. In the holotype specimen of *M. relicta* they are not, but in a specimen from Zimbabwe they are. The ascending branches of the premaxillae are of a generally heavier built in *Rousettus* than in *Lissonycteris* and *Myonycteris* (fig. 1a-c), but in some species the difference is trivial or non-existant (e.g. *R. spinalatus*).

Andersen (1912: 814) wrote that *Lissonycteris* has a relatively longer postdental palate than typical *Rousettus*. Of the species Andersen examined, only *R. celebensis* has a convincingly shorter postdental palate (related to cbl and pl). In *R. egyptiacus* and *R. leschenaultii shortridgei* its relative length is about equal to, or slightly larger than, that in *Lissonycteris*, in *R. amplexicaudatus* and typical *R. leschenaultii* about equal or slightly shorter. *R. lanosus* and *R. madagascariensis* have relatively longer postdental palates, and *obliviosus* and *spinalatus* have relatively shorter ones than *Lissonycteris*. In *R. bidens* it is somewhat shorter if related to cbl but longer if related to pl.

To judge from the external appearance, the lateral frontal sinuses in *Lissonycteris* and *Myonycteris* are more inflated than the medial ones. This is accentuated by the low rostrum. In *Rousettus egyptiacus* and typical *leschenaultii* the sinuses are much less pronounced, at least externally, but the lateral pair is slightly more inflated. In *R. bidens* the lateral pair is prominent, the medial pair less. In *R. lanosus* the lateral pair is also the most prominent but the difference with the medial pair is less than in *R. bidens*. In *R. madagascariensis*, *obliviosus*, *leschenaultii shortridgei* and *spinalatus* the two pairs of sinuses are about equally inflated. In *R. amplexicaudatus* and *celebensis* the medial pair tends to be more inflated than the lateral pair.

The interorbital skull roof in *Lissonycteris* and *Myonycteris* is slightly concave. In *Rousettus bidens* it is very weakly concave. In *R. egyptiacus* males it is weakly concave, in females and in both sexes of *R. amplexicaudatus* and *leschenaultii* it is flat to weakly convex. In *R. celebensis* it is about flat. In *R. lanosus*, *madagascariensis*, *obliviosus* and *spinalatus* it is slightly convex.

There appears to be no objective way to measure the relative size of the orbit. Lawrence *et al.* (1963) took its diameter parallel to the antero-rostral margin and related it to the lachrymal width. But the lachrymal width itself is not without interspecific variation. In *Lissonycteris* and *Myonycteris*, where the orbit was found to be largest, the rostrum is relatively low and narrow, while in most *Rousettus* species it is not (exceptions are *R. madagascariensis* and some *R. amplexicaudatus*). Presently, the distance was measured between a point directly beneath the postorbital process and the approximate opposite, deepest point of the caudal side of the zygomatic arch, and related to cbl and to brain-case length (bcl; measured as described above). According to this method, *Myonycteris torquata* has the relatively largest orbit (29.5% of cbl; 45.3% of bcl). In two examples of *M. relicta* it is 25.0 and 26.3% of cbl, respectively (bcl not available). On *M. brachycephala* there are no data, but measurements in Andersen (1912: 584) indicate that the relative size of the orbit is also smaller than in *M. torquata*. In *Rousettus* relative orbit size also varies: *R. leschenaultii shortridgei* has the largest (25.5% of cbl; 40.8% of bcl) and *R. celebensis* the smallest (22.3% of cbl; 34.0% of bcl). *Lissonycteris* (23.7% of cbl; 39.7% of bcl) falls within the variation range of *Rousettus*, although the bcl percentage is among the highest.

The antero-ventral border of the orbit is a rather thin and sharp-edged rim in *Lissonycteris* and *Myonycteris*, but not much less so in *Rousettus leschenaultii* and *madagascariensis*. The anterior part of the zygomatic arch is generally flatter in the former two genera, and rounder (in section) in most *Rousettus* (not in typical *leschenaultii*). As the root of the arch widens towards the skull, the length of the infra-orbital canal rather depends on the angle under which this root joins the skull. This angle varies but I have found no convincing differences between the genera.

The posterior zygomatic arch insertion in *Lissonycteris* and *Myonycteris* is more distal than in most *Rousettus* species, as dorsal skull views show. In strongly deflected skulls the position of the glenoid fossa in relation to the tympanic bulla offers a better means to check this. However, *R. amplexicaudatus*, *bidens* and *spinalatus* do not differ very much, in this respect, from the other two genera.

### *Dentition*

The larger premolars and molars in *Lissonycteris* are relatively short, antero-posteriorly, squarish in outline, and with large interstices, especially between canines and premolars. In *Rousettus* these teeth are essentially oblong, even though quite broad and nearly squarish in some species (*bidens*, *spinalatus*), with smaller interstices - except *lanosus*, with its reduced dentition. In *Myonycteris*, *torquata* comes nearest to *Lissonycteris* (see Andersen, 1912, fig. 47), *brachycephala* resembles *Lissonycteris* in teeth outlines but its teeth are large and hence the interdental spaces small (Andersen, 1912, fig. 47; this paper, fig. 7a-d), and *relicta* has relatively long teeth but nevertheless shows the same tendency towards larger interstices as *torquata* (Bergmans, 1980, figs. 1-2). Andersen's (1912) remark that in *Myonycteris* both upper and lower fourth premolars and first molars are shorter than in *Rousettus* do not apply to *M. relicta*.

In *Lissonycteris* and *Myonycteris torquata* and *brachycephala* $C^1$ has a different form and orientation than in *Rousettus*. In the former, it is relatively lower, more strongly hook-shaped, with a rudimentary postero-basal shelf; the postero-internal side is directed backward rather than inward. In *Rousettus* it is high, without postero-basal shelf, and laterally more or less depressed (with nearly flat labial and lingual sides in *amplexicaudatus*, *bidens* and *celebensis*); the postero-internal side is directed inward rather than backward. In *Myonycteris relicta* it is low, but its orientation and postero-basal details are rather as in *Rousettus*.

The basal outline of $P^3$ in *Lissonycteris* is rather symmetrical, short, sub-oval. Its postero-internal side is directed backward. Its tip is pointed and placed labially. It has no postero-basal shelf. In *Myonycteris torquata* it is shorter, and in all three *Myonycteris* species the tip is more lingual and there is a weak postero-basal shelf. In *Rousettus egyptiacus* $P^3$ has a different basal outline, with a much narrower posterior side. Its tip is less pointed and placed more inward, and there is a rudiment of a second, internal cusp on the internal keel running from tip to base. In other *Rousettus* species the basal outline of $P^3$ is essentially the same, except *lanosus* and *madagascariensis* in which $P^3$ is laterally depressed, and *bidens* in which it is not narrowed. *R. bidens* is the only other species with a - weak but distinct - inner cusp; in this species, the main cusp is placed more toward the labial side, and the anterior and posterior upper surfaces are not directed lingually but forward and backward, respectively.

$P^4$ in *Lissonycteris* is squarish in outline, has a distinct outer and a distinct inner cusp, both slightly anterior to the middle and mutually connected by a concave loph, and a distinct but weak postero-basal ledge. In *Myonycteris torquata* and *M. brachycephala*, $P^4$ is more rectangular and has weaker, lower cusps, a weak antero-basal and still weaker postero-basal ledge. In *M. torquata* the anterior surface has a weak longitudinal ridge and there is a rudiment of what appears an antero-internal cusp. In *M. relicta*, the outer cusp is low but distinct, the inner is a mere vault in the inner ridge; the whole tooth is placed rather obliquely in the row, with its anterior side directed inward. In *Rousettus egyptiacus* $P^4$ is relatively longer, with stronger outer and inner ridges and forward-placed cusps; the distinct but low outer cusp forms part of the outer ridge; the inner cusp is a much lower but thicker part of the inner ridge, opposite the outer cusp. The inner ridge shows a vestigial antero-internal cusp and a low but distinct postero-internal cusp. In other *Rousettus* species $P^4$ is essentially the same. In *R. leschenaultii* the inner cusp is placed more forward. The cusps may be somewhat weaker (*amplexicaudatus*, *leschenaultii*, *madagascariensis*, *obliviosus*) to very weak, with little or no further diversification of the inner ridge (*bidens*, *celebensis*, *lanosus*, *spinalatus*). In *R. spinalatus* $P^4$ is very broad.

In *Lissonycteris*, $M^1$ is a weakened version of $P^4$, and $M^2$ a further weakened form of $M^1$. $M^1$ has a very weak inner cusp which is scarcely higher than its commissure with the outer cusp. The outer cusp in $M^2$ tends to point forward. In *Myonycteris*, $M^1$ is also a weakened form of $P^4$. $M^2$ is very small, roundish, with a ridge all around but without cusps. In *Rousettus egyptiacus* $M^1$ also resembles a weak $P^4$ although it may be a trifle longer. The main cusps are placed near the front, the inner cusp at the antero-internal corner. There is an equally-sized postero-internal cusp. In $M^2$ the outer cusp is weak, there is only a vestigial antero-internal cusp, and a more pronounced postero-internal cusp. In *R. leschenaultii*, *madagascariensis* and *obliviosus* these molars are essentially as in *R. egyptiacus*. In *R. amplexicaudatus* they are further degenerated, with low ($M^1$) or no ($M^2$) inner cusps. In the other *Rousettus* species they are also less differentiated, to various extents.

The lower incisors are bilobed in *Lissonycteris*, *Myonycteris* and most *Rousettus*. In *M. torquata* this is less distinct in $I_2$. In *R. lanosus* the lobes are weak, in *R. spinalatus* they are vestigial, in *R. bidens* they are lacking. In all three genera there is little size difference between $I_1$ and $I_2$, except in *R. bidens*, in which $I_2$ is three to four times the bulk of $I_1$.

In *Lissonycteris*, $C_1$ is a low, outward-pointing simple tooth, scarcely higher than $P_3$; there is a slight angle between antero-external and antero-internal faces, a distinct vertical ridge with at its posterior side a parallel groove between antero-external and posterior faces, and a rudimental postero-basal shelf. In *Myonycteris torquata* $C_1$ is relatively smaller, less outward-directed, with none of the characters mentioned further for *Lissonycteris*. In *M. brachycephala* $C_1$ is lower than $P_3$; in both this species and *M. relicta* $C_1$ is relatively simple but has a narrow postero-basal shelf. In *Rousettus egyptiacus* $C_1$ is relatively much bulkier, especially in width, than in *Lissonycteris*. It is clearly higher than $P_3$ and has all the characters mentioned for *Lissonycteris*, be it less pronounced. In the other *Rousettus* species, those characters are present to a varying extent, but usually weaker than in *R. egyptiacus*. In *R. amplexicaudatus* the postero-basal shelf is practically lacking. In *R. bidens* $C_1$ has turned outward: what in other species is the antero-external face has become the external face, and other faces have shifted accordingly. Its basis is clearly longer than wide. Its tip is strongly bent outward. In *R. celebensis*, $C_1$ is quite similar.

$P_1$ is very small, with a distinct outer cusp, in *Lissonycteris*. It is slightly larger in surface but not very different in shape in *Myonycteris torquata* and *brachycephala*, about 1.5 times larger in *M. relicta*, and much larger and variable in shape in *Rousettus*: 3-4 times in *madagascariensis*, 4-5 times in *egyptiacus*, *amplexicaudatus*, *lanosus*, typical *leschenaultii*, *obliviosus* and *spinalatus*, and about 6-7.5 times in *bidens* and *celebensis*. In all *Rousettus species* $P_1$ has a distinct outer cusp and is about as wide as long in all species except *bidens*, *celebensis* and *madagascariensis* in which it is distinctly longer than wide.

$P_3$ in *Lissonycteris* is a relatively simple, rather blunt-tipped, short tooth, with the rounded anterior side thickened at its base, its almost flat posterior side turned slightly outward, and a narrow postero-basal shelf. In *Myonycteris* it is relatively lower than in *Lissonycteris*, with its tip a bit more backward, and a wider postero-basal shelf. In *Rousettus egyptiacus* it is relatively heavier and lower than in *Lissonycteris*, with a weakly keeled and more strongly recurved anterior side, a slightly inward-directed posterior side, and a wider postero-basal shelf with a ledge which is thickened at the postero-internal corner. In most other *Rousettus* species it is much the same but laterally depressed, lower, and usually less differentiated.

$P_4$ in *Lissonycteris* is the largest of the cheek-teeth, longer than $P_3$ and longer but hardly broader than $M_1$. It has a broad, blunt outer cusp just before the middle, and an inner ridge ending in a rather high, somewhat transverse, free-tipped inner cusp, anterior to the outer cusp and connected with it by a concave commissure. The tooth is narrowed anteriorly, thickened at its anterior base, and ends in a weak postero-basal ledge. In *Myonycteris torquata* $P_4$ is relatively large, longer and broader than both $P_3$ and $M_1$. Morphologically it is a much weakened version of $P_4$ in *Lissonycteris*; it is lower and little differentiated, with the inner cusp reduced to a mere ‘shoulder’ in the inner ridge where it curves inward and upward to join the outer ridge and cusp. In *M. brachycephala* $P_4$ is also the largest tooth of the row and morphologically much as in *Lissonycteris*, with diverging outer and inner cusps. In *M. relicta* $P_4$ is the largest of all teeth, long (antero-posteriorly), with a broad outer cusp and no inner cusp. In *Rousettus egyptiacus* $P_4$ is broader than $P_3$ and slightly broader than $M_1$ but neither in this nor in other species of *Rousettus* it is particularly large. In *R. egyptiacus* it is a heavy, sub-rectangular tooth with thick outer and inner ridges, a broad blunt outer cusp placed near the anterior end, the inner ridge bending inward and forming a shoulder before joining the outer cusp. The posterior surface is strongly concave. In other *Rousettus* species, $P_4$ varies on this pattern. In most, outer and inner ridges and cusps are reduced in height if compared to *egyptiacus*, in some the cusps are placed more backward (especially in *bidens* and *madagascariensis*, but also in *lanosus* and, to a lesser extent, in some others). In *R. bidens*, *celebensis*, *madagascariensis* and *spinalatus* the whole tooth is very low, and the cusps are largely rudimentary.

The first to third lower molars in *Lissonycteris* are sub-rectangular in outline, all have outer and inner ridges, passing into anterior and posterior ridges. The broad, blunt outer cusps are placed anterior to the middle ($M_1$) or at the middle ($M_2$, $M_3$), and decrease in height with the overall size of the teeth, from $M_1$ to $M_3$. The inner cusps are reduced to broad upward curves of the inner ridges. The upper surfaces are flat except for the outer quarter which slopes upward to the outer cusp. In $M_1$ a distinct ridge runs from the cusp tip to halfway its inner face, in $M_2$ and $M_3$ there are less pronounced to vestigial ridges. The outer cusps in $M_2$ and $M_3$ lean outward. In *Myonycteris torquata* $M_1$ is more oblong than in *Lissonycteris*. Its low outer cusp and the upward curve in the inner ridge are placed near the anterior side. The ridges and cusp are less sharp than in *Lissonycteris*. $M_2$ and $M_3$ are sub-rectangular, $M_2$ slightly narrowing towards the back, with a ridge all around. The outer ridge is slightly higher than the inner but there are no cusps. In *M. brachycephala* these molars are about the same, only wider. In *M. relicta* $M_1$ is long, narrow, and low, with the outer ridge higher than the inner, a trace of an antero-median outer cusp and of a commissure to the lingual ridge. $M_2$ is not differentiated. There is no $M_3$. In *Rousettus egyptiacus* $M_1$-$M_3$ are heavy, oblong, relatively high teeth with thick ridges all around but for tiny incurvations at the short sides in $M_1$ and $M_2$, the outer ridge somewhat higher than the inner, and both ridges highest at the anterior side but without real cusps. The upper surfaces are concave. $M_1$ is the largest, $M_3$ the shortest tooth. Other *Rousettus* species have the same bath-tub type teeth or less differentiated to degenerated forms thereof. In *R. bidens* they are almost flat, without ridges, and vestiges of cusps only in $M_1$. In *R. celebensis* they are low, with concave surfaces, $M_1$ and $M_2$ with or without traces of cusps. In *R. spinalatus* these molars are approaching those of *bidens* in shape.

### *Bacula*

Bacula are subject to age and (possibly) individual variation (Martin, 1978). As the available samples of the genera under discussion are small, the conclusions must be preliminary. The bacula of adult *Lissonycteris* and *Myonycteris* appear to be morphologically related, while African mainland *Rousettus* (i. e. *egyptiacus* and *lanosus*) are more distant (figs. 2a-f). The shape in *R. egyptiacus* (fig. 2e) is very simple. It has been figured earlier by Harrison (1964; *R. e. arabicus*), Didier (1965; *R. e. leachii*) and Madkour (1976; typical subspecies). The specimens of Harrison and Madkour both show a small proximal incurvation but otherwise agree fairly well with the present specimen. Didier's specimen is less slender but equally simple. Most apparent in these *egyptiacus* bacula is the almost complete absence of digital lateral wing-like projections. The baculum of *R. lanosus* has small wings (fig. 2f); the figured specimen is fully adult and this may be the ultimate adult condition. Krutzsch (1959; 1962) described and figured bacula of *R. a. amplexicaudatus* (in 1959 as *R. a. brachyotis* (Dobson, 1877) and in 1962 as *R. a. minor* (Dobson, 1873)), *R. a. infumatus* (Gray, 1870) (as *R. a. amplexicaudatus*), and *R. leschenaultii shortridgei*. Bhatnagar (1967) described and figured a baculum of typical *leschenaultii* from North Malacca, Agrawal *et al.* (1973) did so for specimens of *amplexicaudatus* from India or Burma and *leschenaultii* from India, and Martin (1978) gave descriptions and figures of bacula of a juvenile and three adult typical *leschenaultii*, the adults of different ages, from the same North-Malaccan locality as Bhatnagar's specimen. *R. amplexicaudatus* has wing-like projections of variable size, possibly connected with age, and a proximal incurvation in two of the three figured specimens. According to Martin (1978), *R. l. leschenaultii* exhibits age and individual variation; with age the baculum becomes larger and develops distal head and proximal wings, but in one of his two oldest specimens it is an undifferentiated oblong bone, not unlike those of *R. l. shortridgei* and *R. l. leschenaultii* figured by Krutzsch (1962) and Bhatnagar (1967), respectively - which by their size are also adult specimens -, and, indeed, not unlike the known examples of *R. egyptiacus*. (It can not be excluded that Martin's winged specimens represent *amplexicaudatus* instead of *leschenaultii*, as both species occur in northern Malacca; this would explain the extreme variation encountered by him and which appears to be quite exception-

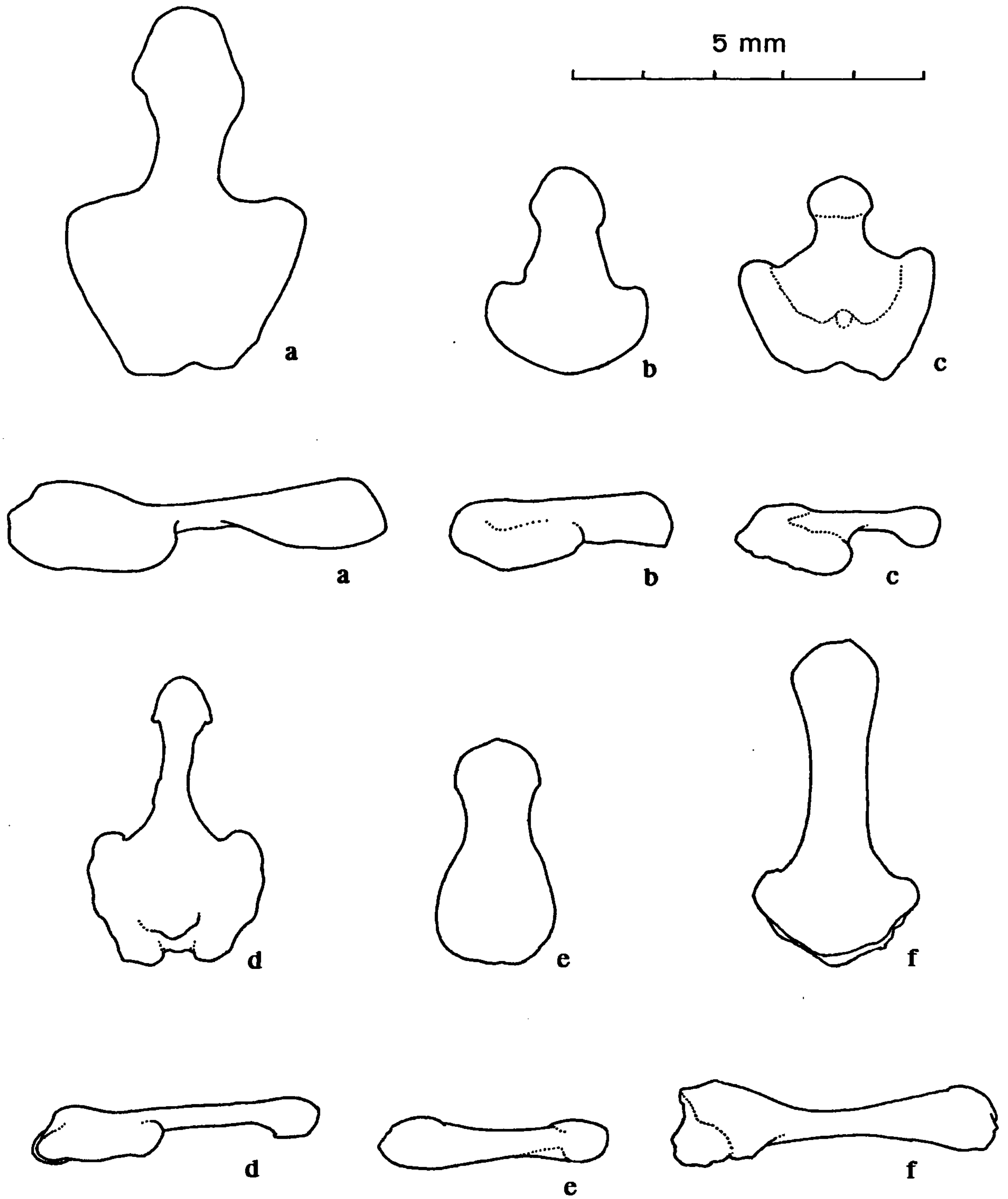

Fig. 2. Bacula. Upper figures a-f: dorsal views, with digital side at the top; lower figures a-f: lateral views, from the right side. a: *Lissonycteris angolensis angolensis* (Bocage, 1889), young adult from Odukpani, Nigeria (ZMA 18.614); b: *Myonycteris torquata* (Dobson, 1878), young adult from Belinga, Gabon (ZMA 20.649); c: *Myonycteris torquata* (Dobson, 1878), adult from Bolo, Ivory Coast (ZMA 16.963); d: *Myonycteris relicta* Bergmans, 1980, adult from Ambangulu, Tanzania (paratype specimen; ZMB 54936); e: *Rousettus egyptiacus egyptiacus* (É. Geoffroy-St. Hilaire, 1810), young adult from Belinga, Gabon (ZMA 7946); f: *Rousettus lanosus* O. Thomas, 1906, adult from Menengai, Kenya (ZMA 20.428). Scale applies to all figures.

al within a species. The baculum of *leschenaultii* as figured by Agrawal *et al.*, 1973, has a relatively broad ovoid proximal part.) In the known winged bacula of *Rousettus* the wings are more proximal, and hence the shafts longer, than in *Lissonycteris*. In an adult specimen of *Myonycteris torquata* (fig. 2c) the other extreme is found, with only a rudimentary shaft. In *M. relicta* (fig. 2d) the wings resemble those of *M. torquata* but the shaft is thinner and as long as in *Rousettus amplexicaudatus*.

### *Ears*

The ear conchs in *Lissonycteris* and *Myonycteris* are relatively thin and delicate; the basis of the anterior ear margin is thickened, and above it the anterior margin is partly turned back; the 'antitragal' lobe is angular and pointed; the margins and the tip of the conchs are naked but for very few single short hairs. In nearly all *Rousettus* species the ear conchs are rather fleshy; the basal half or more of the anterior margin and in some species also the lower posterior margin - in *lanosus* even the whole margin - is thickened; the "antitragal" lobe is thick and rounded off or, in *amplexicaudatus* and *spinalatus*, somewhat angular and turned outward; in *egyptiacus*, *amplexicaudatus*, *leschenaultii*, *obliviosus* and *madagascariensis* the ear conch is wholly or partly covered with numerous very short hairs, especially the margins; in *celebensis* and *lanosus* there are few hairs and in *spinalatus* practically none. The overall exception in ear conch characters is *R. bidens*: this species agrees with *Lissonycteris* and *Myonycteris* in all aspects mentioned.

### *Nostrils and chin pads*

Within *Rousettus*, there is variation in the measure of tubularity of the nostrils, in the groove in between the nostrils, and in the distance of these to the lips. I have not found that *Lissonycteris* or *Myonycteris* are exceptional in any way. The same applies to the shape and relative size of the chin pad.

### *Wings*

Andersen (1912) and Lawrence *et al.* (1963) pointed out that *Lissonycteris* has longer fingers, and thus larger (more "developed" wings) than *Rousettus*. *Myonycteris* would be intermediary. Andersen (1912: 20) compared *Lissonycteris* with *Rousettus* only, and stated that the indices of pollex, second digit, and third metacarpal (i. e. the values of their lengths when fal is put at 1000) are larger than in *Rousettus*; his values for *Myonycteris torquata* (including all forms distinguished by him) lead to intermediate indices in this species. He furthermore wrote that the second finger in *Lissonycteris* is longer than the third metacarpal, and that in the fifth finger the second phalanx is longer, as a rule, than the first. Lawrence *et al.* (1963) compared the combined lengths of metacarpal and first phalanx in fingers three to five to the fal; in *Lissonycteris* they would be longer, in *Myonycteris* subequal, and in *Rousettus* shorter (or in finger three somewhat longer and in finger four subequal). In table 1 all these measurements and indices are given for up to 5 specimens of all species concerned. (Lawrence *et al.*, 1963, did not list their material, but they certainly did not consider all species.) From this table the following conclusions can be drawn. First, there are relatively large variation ranges in the lengths of particular finger bones. Therefore, the ranges found will not be complete and the conclusions somewhat tentative. *Lissonycteris* and *Myonycteris* have relatively longer thumbs, on average, than *Rousettus*. *M. brachycephala* appears to have the longest, followed by *Lissonycteris*, *M. torquata* and *M. relicta*. Of *Rousettus*, the species *celebensis*, *lanosus*, *bidens* and possibly *madagascariensis* have the longest thumbs, *celebensis* overlapping with *Lissonycteris* and the others with *Myonycteris*. *R. egyptiacus*, and probably *R. obliviosus* (see Kock, 1978a), also slightly overlap with the smaller values in *Myonycteris*; *R. amplexicaudatus* and *leschenaultii* have shorter thumbs, and *spinalatus* has the shortest, none of these approaching *Myonycteris*. The index of the second finger (claw included) is 755-805 in *Lissonycteris*, 718-777 in *Myonycteris*, and 555-703 in *Rousettus*. This digit is longer than the third metacarpal in the first two genera and shorter than this in most *Rousettus*; in *R. bidens* and *leschenaultii* it is slightly shorter or longer, in *celebensis* and *madagascariensis* it is clearly longer.

Table 1. Digit lengths and indices and tibia length index in *Lissonycteris* Anderen, 1912, *Myonycteris* Matschie, 1899, and *Rousettus* Gray, 1821. Abbreviations: c.u. = claw included; m = metacarpal; Mad. = Madagascar; p = phalanx. (For detailed origin of specimens see the text.)

| Species, specimen, sex, origin | fal | pollex index c.u. | digit 2 length c.u. | digit 2 index c.u. | digit 3 length m+p1 | m 3 index | digit 4 length m+p1 | digit 5 length m+p1 | digit 5 length p1 | digit 5 length p2 | tibia index |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *L. angolensis*, ZMA 16.535, ♂, Ivory Coast | 73.5 | 441 | 57.1 | 777 | 90.1 | 740 | 75.4 | 71.0 | 21.8 | 24.4 | 448 |
| - ZMA 18.610, ♂, East Nigeria | 79.5 | 445 | 61.7 | 776 | 98.5 | 746 | 82.9 | 76.9 | 23.2 | 27.2 | 430 |
| - ZMA 18.611, ♂, East Nigeria | 77.7 | 457 | 58.7 | 755 | 97.9 | 739 | 83.0 | 76.6 | 23.6 | 28.6 | 454 |
| - ZMA 24.560, ♂, East Zaïre | 77.4 | 450 | 62.3 | 805 | 96.4 | 731 | 83.2 | 81.0 | 26.0 | 28.1 | 427 |
| *M. torquata*, ZMA 20.649, ♂, Gabon | 62.7 | 415 | 46.4 | 740 | 71.8 | 676 | 60.1 | 59.2 | 19.0 | 20.6 | 383 |
| - ZMA 20.650, ♂, Gabon | 58.8 | 434 | 45.1 | 767 | 65.4 | 682 | 59.6 | 55.7 | 16.3 | 17.5 | 391 |
| - ZMA 20.652, ♀, Gabon | 63.7 | 427 | 48.0 | 754 | 78.9 | 728 | 66.4 | 64.0 | 20.0 | 22.2 | 375 |
| - ZMA 20.654, ♀, Gabon | 60.7 | 395 | 44.0 | 725 | 70.2 | 682 | 59.4 | 56.5 | 17.9 | 19.4 | 366 |
| - ZMA 24.568, ♂, East Zaïre | 55.7 | 449 | 43.3 | 777 | 67.5 | 718 | 57.9 | 54.7 | 16.7 | 20.8 | 415 |
| *M. brachycephala*, SMTD 14030, ♂[1], Sao Tomé | 58.5 |  | 44.4 | 759 | 69.5 | 708 | 58.9 | 56.6 | 17.6 | 19.1 |  |
| - SNMS 41801, Sao Tomé | 62.0 | 465 | 46.3 | 747 | 74.5 | 721 | 63.3 | 61.0 | 19.0 | 20.2 | ± 379 |
| - SNMS 41802[1], Sao Tomé | 63.4 | 426 | 48.8 | 770 | 73.2 | 696 | 62.7 | 60.4 | 19.1 | 22.0 | 426 |
| *M. relicta*, RMNH 27909, ♂, Kenya | 69.3 | 430 | 51.7 | 746 | 81.9 | 714 | 71.1 | 67.9 | 21.9 | 25.0 | 385 |
| - ZMB 54937, ♀, Tanzania | 75.1 | 426 | 55.7 | 742 | 89.1 | 710 | 77.3 | 76.0 | 24.3 | 28.6 | 390 |
| - LACM 19517, ♀, Tanzania | 69.4 | 411 | 49.8 | 718 | 79.4 | 680 | 77.0 | 66.1 | 21.0 | 23.2 | 382 |
| - CMNH 57685[2], ♀, Tanzania | 65.9 |  |  |  | 77.5 | 698 | 69.6 | 65.3 | 20.8 |  | 396 |
| - NHMBZ 62472, ♀, Zimbabwe | 69.4 |  | 50.6 |  | 82.2 |  | 70.6 | 68.6 | 22.0 | 24.0 |  |
| *R. egyptiacus*, ZMA 22.205, ♂, Egypt | 95.8 | 402 | 66.3 | 692 | 110.2 | 701 | 97.1 | 93.4 | 30.3 | 28.4 | 425 |
| - ZMA 22.206, ♂, Egypt | 93.1 | 395 | 61.5 | 661 | 102.2 | 675 | 91.6 | 87.6 | 28.6 | 28.0 | 456 |
| - ZMA 22.208, ♀, Egypt | 96.2 | 378 | 65.5 | 681 | 109.3 | 696 | 97.4 | 93.4 | 30.0 | 28.9 | 416 |
| *R. amplexicaudatus*, ZMA 22.509, ♂, Bali | 79.2 | 347 | 48.0 | 606 | 81.3 | 634 | 72.8 | 69.4 | 20.5 | 25.4 | 423 |
| - ZMA 22.510, ♂, Bali | 78.4 | 367 | 48.1 | 614 | 84.1 | 662 | 73.4 | 70.7 | 21.1 | 26.7 | 455 |
| - ZMA 22.511, ♂, Bali | 74.3 | 369 | 46.3 | 623 | 78.6 | 637 | 69.3 | 65.3 | 20.9 | 24.8 | 456 |
| *R. bidens*, ZMA 22.759, ♂, Sulawesi | 99.4 | 414 | 68.8 | 692 | 117.3 | 688 | 103.1 | 95.0 | 28.0 | 37.7 | 536 |
| - ZMA 22.760, ♂, Sulawesi | 97.5 | 404 | 67.4 | 691 | 112.2 | 686 | 100.5 | 92.4 | 25.3 | 32.2 | 544 |
| - ZMA 22.761, ♀, Sulawesi | 98.3 | 403 | 66.6 | 678 | 116.3 | 701 | 105.9 | 96.8 | 27.2 | 30.8 | 541 |
| *R. celebensis*, ZMA 22.137, ♀, Sulawesi | 74.2 | 442 | 52.2 | 703 | 85.4 | 671 | 73.6 | 70.6 | 21.8 | 25.0 | 467 |
| - ZMA 22.219, ♂, Sulawesi | 77.9 | 420 | 51.7 | 664 | 87.9 | 653 | 75.4 | 71.1 | 21.6 | 27.3 | 483 |
| - ZMA 22.222, ♀, Sulawesi | 74.5 | 443 | 51.0 | 685 | 85.1 | 670 | 70.8 | 68.4 | 19.9 | 28.4 | 466 |
| *R. lanosus*, ZMA 20.428, ♂, Kenya | 92.0 | 398 | 59.5 | 647 | 104.7 | 688 | 92.3 | 88.1 | 27.4 | 31.9 | 453 |
| - ZMA 24.344, ♀, East Zaïre | 94.0 | 410 | 61.2 | 651 | 101.9 | 668 | 87.0 | 84.6 | 27.3 | 34.7 | 468 |
| - ZMA 24.346, ♀, East Zaïre | 90.0 | 429 | 59.9 | 666 | 99.1 | 669 | 88.3 | 83.0 | 27.5 | 32.6 | 447 |
| *R. leschenaultii*, ZMA 20.494, ♂, East India | 86.7 | 355 | 52.9 | 610 | 93.4 | 661 | 84.8 | 79.9 | 26.8 | 28.4 | 465 |
| - ZMA 20.496, ♀, East India | 78.5 | 357 | 51.0 | 650 | 81.5 | 628 | 75.5 | 71.6 | 23.6 | 22.8 | 456 |
| - ZMA 20.497, ♀, East India | 84.0 | 354 | 54.3 | 646 | 90.8 | 655 | 82.4 | 78.9 | 26.7 | 26.6 | 467 |
| *R. madagascariensis*, ZMA 19.132, ♀, Mad. | 68.5 | 400 | 48.3 | 705 | 75.4 | 672 | 70.5 | 65.4 | 21.0 | 19.3 | 464 |
| - ROM 46919[3], ♂, Mad. | 73.4 |  |  |  | 79.4 | 661 | 72.7 | 68.9 | 22.0 | 18.0 | 465 |
| - ROM 46920[3], ♂, Mad. | 71.6 |  |  |  | 77.7 | 666 | 69.0 | 65.4 | 21.5 | 20.1 | 450 |
| *R. obliviosus*, ZMA 20.903, ♀[1], Anjouan | 72.2 | 389 | 47.4 | 656 | 78.6 | 666 | 69.2 | 66.0 | 20.8 | 23.8 | 485 |
| *R. spinalatus*, NMW 24112, ♀, Sumatra | 80.6 | 316 |  |  | 78.9 | 599 | 70.8 | 68.0 | 21.6 | 23.5 | 391 |
| - ZMA 23.132, ♂, Borneo | 88.7 | 325 | 49.2 | 555 | 86.7 | 608 | 77.5 | 75.0 | 23.0 | 27.6 | 399 |
| - ZMA 23.133, ♀, Borneo | 83.6 | 317 | 47.5 | 568 | 80.3 | 603 | 71.8 | 69.6 | 21.2 | 22.2 | 388 |
| - ZRCS[4] 7188, ♀, Borneo | 89.3 | 290 |  |  | 82.2 | 573 | 73.1 | 70.0 | 22.5 | 26.5 | 386 |

[1]) nearly adult; [2]) data from Schlitter *et al.*, 1981; [3]) data from Dr. R. L. Peterson; [4]) Zoological Reference Collection, University of Singapore, Singapore

The index of metacarpal plus first phalanx of the third finger is 1226-1260 in *Lissonycteris*, 1112-1239 in *Myonycteris*, and 920-1180 in *Rousettus*. In all *Rousettus* except *spinalatus* this length exceeds the fal; the maximum is found in *R. bidens*, due to its long first phalanx. The same index of the fourth finger is 1026-1075 in *Lissonycteris*, 959-1110 in *Myonycteris*, and 819-1077 in *Rousettus*. In *Myonycteris torquata* this length is slightly smaller or larger than the fal. In *Rousettus* it is slightly longer than the fal in *bidens*, subequal to the fal in *egyptiacus* and *madagascariensis*, subequal to or slightly shorther than the fal in *celebensis*, *lanosus*, *leschenaultii* and *obliviosus*, and clearly shorter in *amplexicaudatus* and *spinalatus*. The index of metacarpal plus first phalanx of the fifth finger is 966-1047 in *Lissonycteris*, 931-1012 in *Myonycteris*, and 784-985 in *Rousettus*. The length is clearly shorter than the fal in *R. spinalatus* (index 784-846) and *amplexicaudatus* (876-902), and only slightly so in *egyptiacus* (941-975) and *bidens* (948-985). The second finger is distinctly longer than the third metacarpal in *Lissonycteris* and *Myonycteris*, slightly longer than this in *Rousettus celebensis* and *madagascariensis*, slightly longer or shorter in *R. bidens* and *leschenaultii*, and shorter in all other *Rousettus*. The second phalanx of the fifth finger is longer than its first phalanx in *Lissonycteris*, *Myonycteris* and all *Rousettus* except *madagascariensis*.

### *Tibia*

According to Andersen (1912) this would be much shorter in *Lissonycteris* than in *Rousettus*. However, he compared absolute lengths. The tibia index is 427-454 in *Lissonycteris*, 366-426 in *Myonycteris*, and 386-544 in *Rousettus*. In *R. egyptiacus*, *amplexicaudatus* and *lanosus*, relative tibia length does not differ much from that in *Lissonycteris*; only in *R. spinalatus* it is distinctly smaller than in that genus, and in all other *Rousettus* it is from slightly to much larger, with a maximum in *bidens*.

### *Foot*

The foot length in *Lissonycteris* and *Myonycteris* would be smaller than in *Rousettus*, the claws more slender, and the webbing more extensive. The foot length index is 258-311 in *Lissonycteris*, 252-290 in *Myonycteris*, and 212-337 in *Rousettus*. In *R. amplexicaudatus*, *leschenaultii* and *spinalatus* it is lower, in *R. egyptiacus*, *lanosus*, *madagascariensis*, and possibly *obliviosus* it averages lower, and in *R. bidens* it averages higher than in *Lissonycteris*. Direct comparison shows that the claws in *Lissonycteris* (and *Myonycteris*) are relatively smaller and slenderer than in all *Rousettus* species except *madagascariensis*. J.-P. Adam *et al.* (1974) distinguished *Lissonycteris* from *R. egyptiacus* in the field by its slender foot claws. In *Lissonycteris*, the basal quarter to half of the toes are webbed, in *Myonycteris* the basal third to half. In *Rousettus*, there is no webbing in *celebensis* and *obliviosus*, and only rudimentary webbing in the other species.

### *Wing insertion*

According to Andersen (1912) and Lawrence *et al.* (1963) the wing is attached to the second toe, near the middle of the first phalanx, in *Lissonycteris* and *Myonycteris*, and to the first toe (Andersen) or between metatarsals 1 and 2, near the bases of phalanges 1 and 2 or well proximal to these (Lawrence *et al.*) in *Rousettus*. The place of attachment in *Lissonycteris* varies from one to two thirds from the basis of the first phalanx of the second toe, in a specimen of *M. relicta* (the holotype) it is inserted at a third from the basis, and in *Myonycteris torquata* from one half to three quarters from this. In *Rousettus* it is variable. Only in two available (ZMA) specimens of *spinalatus* is the wing exclusively associated with the first toe, inserted at the basis of the first metatarsal. In *R. egyptiacus*, *amplexicaudatus*, and *leschenaultii* it may be inserted at or near the basis of the first toe or in between the first and second toes, in *leschenaultii* also at a fifth of the metatarsal length from the toe basis, and in *amplexicaudatus* at half this length from the toe basis. In *R. lanosus* it is inserted on the inside of the first toe basis or on the second metatarsal at a fifth of its length from the toe basis. In the single available specimens of *R. madagascariensis* and *obliviosus* the wing is attached to the outer side of the second metatarsal, in the first species at a third of its length from the toe basis, in the second at half its length from there. In *R. bidens* the wing is attached halfway to the second metatarsal, or in between metatarsals 1 and 2.

### *Calcar*

This would be more delicate in *Lissonycteris* and *Myonycteris* than in *Rousettus* (Lawrence *et al.*, 1963). It is generally thicker, or broader, in *Rousettus* if compared to the other genera, but the difference is minimal.

### *External penis*

No systematic survey has been done on relative external penis length as possible generic character but a preliminary impression is that in *Rousettus* this length may be larger than in the other two genera.

### *Odontoid papillae*

Lawrence *et al.* (1963) remarked that in *Lissonycteris* the odontoid papillae are rather high and pointed, extending from the angle of the mouth to about the canines; in *Myonycteris* they would be about the same, with in some instances a poorly defined second upper row toward the angle of the mouth; and in *Rousettus* these authors found small papillae, reduced in extent and size, in single rows. In general, their findings can be confirmed. However, it should be pointed out that these papillae are in fact the knotty or pointed projections in between indentations of ridges along the inside of the lips. These ridges do not extend anteriorly behind nose and chin pads. In *Lissonycteris* the anterior two fifths of the upper ridge is narrow, with few papillae (or rather tubercles). The posterior part of the upper ridge has numerous indentations and the alternating papillae vary in size and height. Near the angle of the mouth they are longest. Here, a shallow groove runs between lip and ridge. The anterior sixth of the ridge along the lower lip is without indentations, the papillae on the remainder are much as on the upper ridge. Between lower ridge and lip runs a groove from the angle of the mouth over two thirds of the distance to the chin pad. In life, both upper and lower papillae are directed horizontally inward, and rest against teeth and gums. The indentations continue as narrow folds, towards the lips but also on the inside of the mouth, where they go upward and bend backward or, from the lower ridge, downward and backward. Together, papillae and folds may function in, respectively, holding and guiding the juice passing through the teeth from fruit morsels chewn and pressed between tongue and palate. In *Myonycteris torquata* the indentations are deeper and the papillae longer and more pointed than in *Lissonycteris*. Otherwise there are no differences, except that in one of the specimens examined there is a longitudinal groove dividing some of the upper papillae near the mouth angle into two. This may represent what Lawrence *et al.* (1963) interpreted as two rows. In all *Rousettus* species the papillae are much reduced. In *R. egyptiacus* and *leschenaultii* the upper ridge has a few weak indentations in the anterior half, is interrupted halfway, and has a number of short papillae, some with two tips, behind this interruption. These papillae diminish in size towards the angle of the mouth. The lower ridge has only short, inward and downward directed papillae on its posterior half, some with more than one tip, and also petering out towards the mouth angle. In *R. obliviosus* and *spinalatus* there are small papillae on the posterior upper and lower ridge halves; in *R. madagascariensis* too, but they are less numerous and still smaller. In *R. amplexicaudatus* the reduction is yet more advanced (or the development less far) with the papillae stopping short well before the angle of the mouth. In *R. bidens*, *celebensis* and *lanosus* the ridges bear no papillae and have at most a few weak indentations and tubercles.

### *Palatal ridges*

Andersen (1912) emphasized the numbers of ridges in the three genera, Lawrence *et al.* (1963) their morphology. The number of ridges is expressed in a formula indicating, from front to back, three groups: undivided ridges, ridges divided midway, and thin serrated ridges near the posterior end of the palate. Ridges of the median group, especially the posterior ones, are usually also more or less serrated. For *Lissonycteris* this formula is normally 3 + 4 + 2 (Bocage, 1892, fig. 2; Seabra, 1898b, Pl. 1 fig. 9; Andersen, 1912; Veiga-Ferreira, 1948, fig. 2a - not 2d; Eisentraut, 1963, fig. 19; Lawrence *et al.*, 1963; Happold *et al.*, 1978, fig. 3B). Andersen (1912) mentioned one specimen (out of four) with the formula 4 + 3 + 2. Veiga-Ferreira (1948) gave the formula as 3 + 1 + 3 + 2, indicating that (only) the first ridge of the median group is wholly interdental. Eisentraut (1963) pointed out that the sixth ridge can be irregular, incomplete, or even absent, resulting in the formula 3 + 3 + 2. Lawrence *et al.* (1963) observed that the third group sometimes consisted of three instead of two (poorly defined) ridges. Present results agree with the above. For *Myonycteris torquata* the normal formula is also 3 + 4 + 2 (Eisentraut, 1963, fig. 20; De Vree, 1971, fig. 3). Andersen (1912) examined one specimen only, which later turned out to be aberrant (4 + 3 + 2). De Vree (1971) observed that the thin ridges of the third group are often narrowly divided in the middle. Of 70 specimens examined by the present author, 58 agree with the formula 3 + 4 + 2; 5 have 4 + 3 + 2 ridges, 1 has 2 + 5 + 2, 2 have 4 + 4 + 2, 1 has 3 + 5 + 2, 2 have 3 + 3 + 2, and 1 has 3 + 3 + 1 ridges. For *M. brachycephala*, Bocage (1898) illustrated what was left of the soft palate in the holotype specimen, revealing a pattern of 4 + 3 + ? A photograph of a recently collected specimen, kindly made available by Dr A. Feiler, shows a pattern of 4 + 3 + 2. The pattern in two specimens of *M. relicta* is 3 + 3 + 2; in one of these specimens, there are remnants of an extra ridge between the fifth and sixth.

The dominant pattern in most *Rousettus* species is 4 + 3 + 1. Exceptions are typical *R. egyptiacus* with 4 + 4 + 1, *R. bidens* with 4 + 3 + 2, and *R. spinalatus* with 3 + 4 + 1. *Rousettus* species are also subject to considerable variation in this pattern, which for the African species is described in the species accounts.

In general, the intraspecific variation comes down to one or two more ridges (often, extra ridges are represented by fragments only), one or two less (only in one specimen - of *M. torquata* - the posterior group was reduced from two to one ridge), or a shift between the ridge numbers in the anterior group of whole ridges and the median group with divided ridges. When these shifts (often arbitrarily, because 'whole' ridges are often notched in the middle, while 'divided' ridges are often only very narrowly divided) are neglected and the first two groups combined, *Lissonycteris* has a simplified formula of 7 + 2 (exceptionally 7 + 3); *Myonycteris* one of 7 + 2 or (*relicta*) 6 + 2; and *Rousettus* one of 7 + 1 (the bulk), 7 + 2 (*bidens*), or 8 + 1 (mostly typical *egyptiacus*). An aberrant specimen of *Lissonycteris* from Cameroon shows how the formula 7 + 2 may transform into 8 + 1, or, of course, *vice versa* (fig. 3): ridge 8 has moved away from ridge 9 and is intermediate in form between ridges 7 and 9.

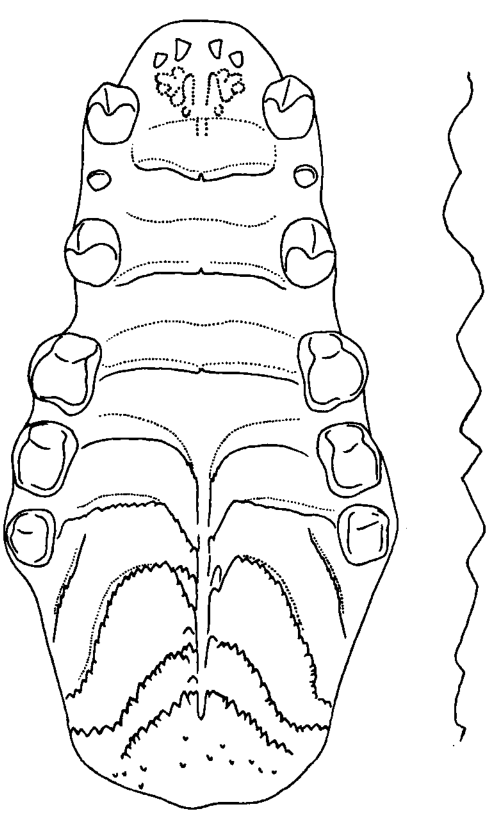

Fig. 3. Soft palate of *Lissonycteris angolensis angolensis* (Bocage, 1889) from Cameroun (collected by De Grelin, no other data; MNHN, not registered). The line on the right represents a profile, taken at about halfway the median line and the teeth (it does not cut through the reduced sixth ridge).

Lawrence *et al.* (1963) observed that the first three ridges in *Rousettus* are more bowed forward than in *Lissonycteris* and *Myonycteris*, that ridges 4 and 5 in the latter two genera have recurved inner ends, and that their ridges 4 to 7 converge somewhat at their medial ends. However, these observations do hardly hold as useful generic distinctions. In *Rousettus leschenaultii* the first three ridges are either as in *Lissonycteris*, or even slightly less bowed, or somewhat more. In typical *R. egyptiacus*, from Egypt and Cyprus, they are as weakly bowed as in *Lissonycteris*, and in *R. amplexicaudatus* too, or only very slightly more. In *R. egyptiacus arabicus*, *celebensis*, *madagascariensis*, *oblivíosus* and *spinalatus* they are slightly more curved. Only in *R. egyptiacus leachii*, *e. unicolor*, *bidens* and *lanosus* they are distinctly more curved. In all *Rousettus* species the median group ridges 5 and 6, and in some cases 7, have at least weakly but often distinctly recurved inner ends (as have 'median group' divided ridges in many other fruit bat genera than those discussed here). In some *Rousettus* species the last two ridges of the median group may show a slight tendency to converge. But also in many *Lissonycteris* and *Myonycteris* convergence of these ridges is weak at most (e.g. Eisentraut, 1963, fig. 19 and De Vree, 1971, fig. 3).

### *Fur*

Andersen described the fur of *Lissonycteris angolensis* from Angola, Northeast Zaïre and West Uganda as long and silky; in his Addenda he observed that the fur in specimens from Sierra Leone and West Nigeria was considerably shorter. The fur in *Myonycteris torquata* was also described by him as silky, and as short on breast and belly. In *Rousettus*, Andersen found the fur to be short in all species but *celebensis*. Hair length as such varies considerably, in the genera under discussion, and does not seem to have diagnostic value above the species level. The silkyness, however, will be determined to a large extent by the morphology of the individual hairs. Benedict (1957) examined and figured body hair structure in *Rousettus amplexicaudatus* and *R. lanosus*, and body and "gland" hair structure in *Lissonycteris angolensis* (as *Rousettus*) and *Myonycteris torquata* (as *M. wroughtoni* Andersen, 1908). Ruff hairs in males she considered as gland hairs. She found that *Lissonycteris* and *Myonycteris* do not possess underhair but only overhair, while *Rousettus* has both types. In hair scale form, she wrote, *Lissonycteris angolensis* "is more similar to that of the *Epomophorus* section than to the *Rousettus* section to which Andersen assigns it", and *Myonycteris torquata*, which she treated as a species in the *Cynopterus* section (where Andersen, 1912, had put it) has hair scales which are "virtually indistinguishable from those of the *Epomophorus* section", and quite different from others in the *Cynopterus* section. Although at least many males of *Rousettus amplexicaudatus* have specialized hairs in two tufts on the sides of the neck, Benedict did not describe those. Mainoya *et al.* (1979) examined the skin patches where such specialized hairs grow in *Rousettus egyptiacus*, *Lissonycteris angolensis* (as *Rousettus*), and *Eidolon helvum* (Kerr, 1792). They found that whereas in *Rousettus* and *Eidolon* the skin contains sebacious glands or gland alveoli in association with hair follicles, the skin in *Lissonycteris* contains almost no glandular tissue. These authors suggested a visual rather than olfactory function for the ruff hairs in *Lissonycteris* males. Kingdon (1974), however, observed that glandular activity probably is seasonal. Full development of these glands may then coincide with the gonad cycle. In Uganda, Kingdon caught a male with large testes and a sticky ruff in September. Anciaux de Faveaux (1978) analysed reproductive data from East Zaïre and Rwanda and found evidence for two cycles per year. His data were few, however, and Verschuren (1977) and Wolton *et al.* (1982) collected data at Mount Nimba which appear to cast doubt on true seasonality in that region. Fedden *et al.* (1986) observed that many specimens were sticky from fig consumption. Hickey *et al.* (1987) examined mid-dorsal and "glandular" hairs in *R. egyptiacus*, *L. angolensis* (as *Rousettus*), *Myonycteris torquata* and a number of epomophorine and other bats. They did not refer to the findings of Mainoya *et al.* (1979) and wrote about gland (or scent-dispersing) hairs in all species just mentioned. In *Rousettus egyptiacus*, the body and gland hairs were of the same size and shape. In *Lissonycteris* and *Myonycteris* the ruff hairs exhibited "the most spectacular" differences. They had larger diameters and the scales were more divergent than in body hairs, giving them a pine-cone appearance. (In the epomophorines examined, some also showed differences between "gland" and body hair, to various extents, and some did not.) Figs. 4a-n show hairs of *Lissonycteris* and *Myonycteris* species. The relative sizes are given in the caption. The top two rows depict body and ruff hair of *M. relicta*. Its body hair resembles that of *M. torquata* (pl. 25 fig. t in Benedict, 1957; fig. 2c in Hickey *et al.*, 1987). The first picture, e, of the ruff hair shows the transition from the basal shaft, which is of normal diameter, to the much thicker part characteristic of the ruff hairs in this genus. Picture f shows the maximum ruff hair

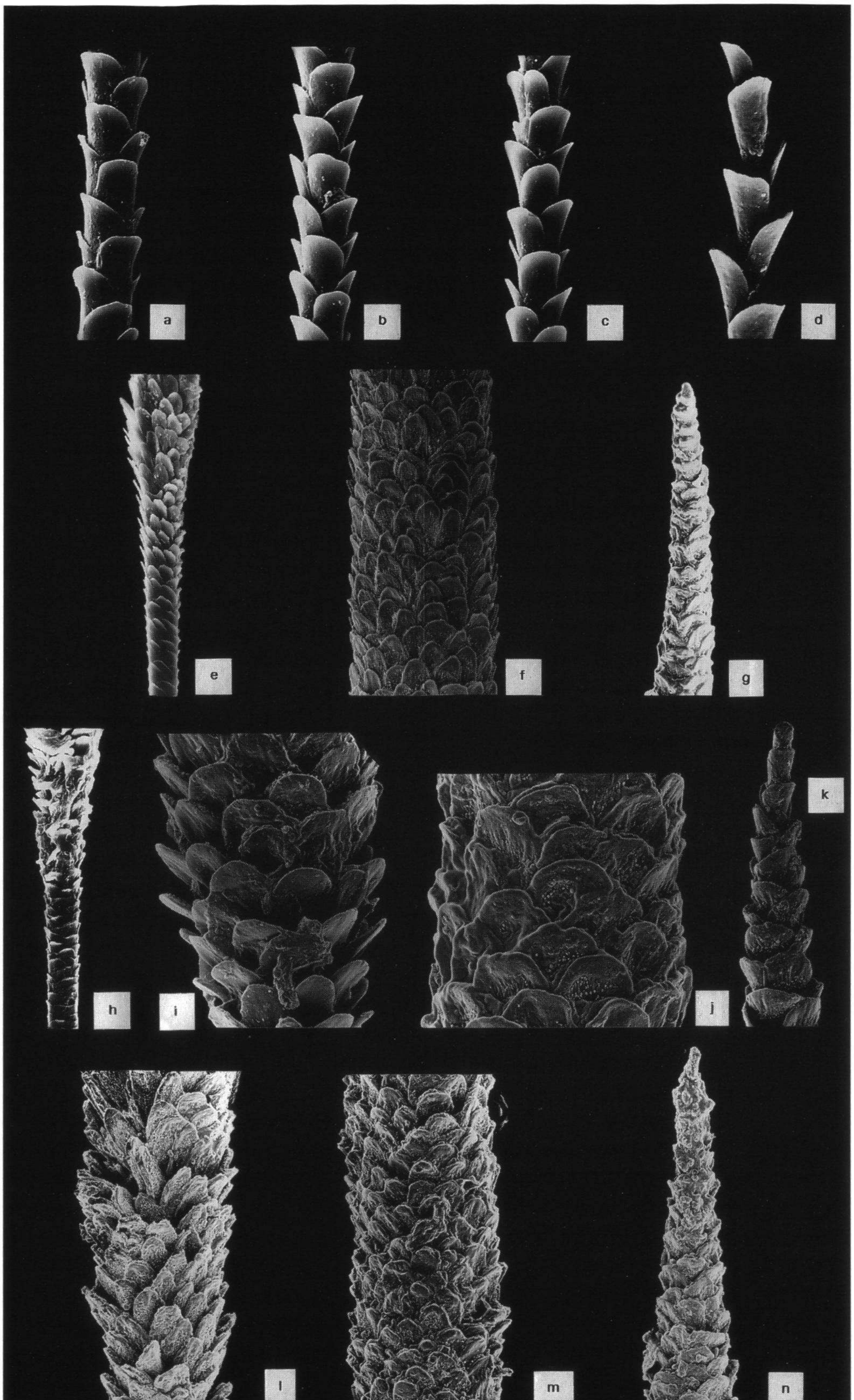
a
b
c
d
e
f
g
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Fig. 4. Hair scale forms; r.e.f. = relative enlargement factor.
4a-d: *Myonycteris relicta* Bergmans, 1980, ♂ from Ambangulu, Tanzania (paratype specimen; ZMB 54396); a: mid-dorsal hair, middle (r.e.f. 22), b: ditto, halfway middle and tip (r.e.f. 22), c: ditto, near tip (r.e.f. 22), d: ditto, tip (r.e.f. 44).
4 e-g: *Myonycteris relicta* Bergmans, 1980, ♂ from Mukanda River, Kenya (holotype specimen, RMNH 27909); e: ruff hair, near basis (r.e.f. not calculated), f: ditto, halfway basis and middle (r.e.f. not calculated), g: ditto, tip; (r.e.f. not calculated).
4h-k: *Myonycteris torquata* (Dobson, 1878), ♂ from Belinga, Gabon (ZMA 20.655); h: ruff hair, basis (r.e.f. 11), i: ditto, near basis (r.e.f. 20), j: ditto, middle (r.e.f. 20), k: ditto, tip (r.e.f. 14).
4l-n: *Lissonycteris angolensis smithii* (O. Thomas, 1908), ♂ from Lamto, Ivory Coast (ZMA 16.535); l: ruff hair, a quarter from basis (r.e.f. 9), m: ditto, middle (r.e.f. 9), n: ditto, tip (r.e.f. 9), those of *M. relicta* ruff hair by Mr. D. Platvoet.
SEM photographs by Dr. E. S. W. Weinberg.

width, and g the tapering tip. Pictures h-k depict a ruff hair of *M. torquata*: the transition from basal shaft to the thick part and three views of the latter, showing the pine-cone like scales (i), the thickest middle part (j), and the tapering tip (k) (see also pl. 28 figs. a-c in Benedict, 1957, and fig. 2d in Hickey *et al.*, 1987). From the literature and the present pictures it appears that the ruff hairs in the two *Myonycteris* species resemble each other; the basal shaft in *relicta* is perhaps somewhat thinner, and the tip slightly less slender. The bottom row shows a ruff hair of *Lissonycteris angolensis smithi* (O. Thomas, 1908). The scales are smaller and more numerous than in *Myonycteris torquata* (compare l with i and m with j - but note the different enlargement factors), but not essentially different in form. Lawrence *et al.* (1963) commented on the distribution of fur in the three genera, stating that *Lissonycteris* and *Myonycteris* have longer, denser fur on notopatagium and proximal dorsal surface of tibiae than *Rousettus*. Although several *Rousettus* species have short body fur (*egyptiacus* - with variation between subspecies -, *amplexicaudatus*, *bidens*, *leschenaultii*, *spinalatus*), some have fur of intermediate length (*madagascariensis*, *obliviosus*), long dorsal fur (*lanosus*), or generally long and dense fur, also covering noto-patagium and tibiae (*celebensis*). Lawrence *et al.* further pointed out that *Rousettus* males lack the ruff of thick hairs present in *Lissonycteris* and *Myonycteris*. But in most, if not all, *Rousettus* species adult males have two small areas of specialized hairs, at the sides of the neck (I have no data on this character in *madagascariensis* and *obliviosus*). These hairs may be thick and coarse (*amplexicaudatus*, *celebensis*, *lanosus*, *spinalatus*) or only slightly thicker than the surrounding body hairs, sometimes shorter than these (*bidens*), sometimes longer (*leschenaultii*).

### Physiology

*Lissonycteris* orients entirely visually (Novick, 1958 a), and for all we know, *Myonycteris* does the same. *Lissonycteris* has been found to roost in caves but never in the dark parts. (The remark by Fedden *et al.*, 1986, that *Lissonycteris* can echo-locate is unfounded.) *Myonycteris* has never been found in caves. *M. torquata* roosts solitarily in trees; specimens have been observed hanging from branches and in banana trees, at modest heights (Brosset, 1966c). Various *Rousettus* species have been shown to orient visually and acoustically. The other species have not yet been examined on this point but some of them are known to roost in caves, as summarized in the account of the genus *Rousettus* in Bergmans (1994).

### Ecology

Most ecological notes concerning *Lissonycteris* relate either to places where it has been found roosting, or to colony numbers. Both are different from what is known about *Rousettus*. Eisentraut (1942) described some coastal caves in Cameroon, which were in fact open tunnels, in one of which he observed a small number (but at least 17) of *Lissonycteris* females and immatures, hanging in one heap. Hayman (1954) reported on specimens from Togo, collected from hollow trees; according to their collector, A. H. Booth, this would be a common roosting place for the species. Eisentraut (1956a) observed small numbers of *Lissonycteris* in the highest places in a subterranean cave in Cameroon. In another cave nearby the species roosted near a vertical shaft through which daylight entered. In these and two other caves in the area Eisentraut found at most a few dozen specimens per cave. Leleup (1956) estimated a colony in a cave near Thysville, Zaïre, at about 3000 specimens. In this cave system, *Rousettus egyptiacus* also roosted, and as Leleup's report is the only one mentioning a large number, confusion with that species appears most likely. Eisentraut *et al.* (1957) collected specimens in Guinea which roosted near the entrances of two caves where daylight could enter. Novick (1958a) observed a colony of *Lissonycteris* in a cave in East Zaïre and wrote that cave-inhabiting Megachiroptera other than *Rousettus* do not seem to occupy totally dark caves or possibly make use of favourable lighting conditions to enter and leave, or orient by memory or by random noise and echoes. Rosevear (1965) wrote that *Lissonycteris* concregates in usually small colonies of up to 50 specimens. Eisentraut (1973a) mentioned to have found *Lissonycteris* in Fernando Poo in recesses of protruding rocks - next to nearly all caves visited there. J.-P. Adam *et al.* (1974) wrote that in the 17 caves in Congo where they studied the species, in seven of which they also found *Rousettus egyptiacus*, *Lissonycteris* always occupied relatively light parts of the cave: entrance porches, rooms with collapsed roofs or other openings to daylight, and galleries open at both sides, while *Rousettus* always inhabited the deeper parts. This spatial separation was convincingly reflected in their parasitological findings. Nevertheless, these authors also related that exceptionally the two species would be found in the same cave zone. In those cases, *Lissonycteris* would keep to the periphery of the *Rousettus* colony. The largest number of *Lissonycteris* encountered by J.-P. Adam *et al.* in any cave was about a hundred. More often there were only a few individuals, and these would never aggregate in a real colony but remain isolated, thought to be attracted to the same cave merely by its favourable conditions. Kingdon (1974) once found a solitary specimen roosting in undergrowth in montane forest. Happold *et al.* (1978) found 35 to 40 individuals in a cave in West Nigeria, clustered together in two groups at about 20 m from the entrance. Koopman *et al.* (1978) reported on a specimen taken in a hut, in Burkina Faso. Bergmans (1979) obtained two specimens which had been roosting under packs of dead palm fronds hanging down the stem (probably of *Hyphaene guineensis*; see Dowsett *et al.*, 1991). Brosset (1984) recorded small colonies of the species in a number of mine galleries at Mount Nimba. In this region, *Lissonycteris* and *Rousettus* appear to be altitudinally separated, with the first occurring mostly above 1000 m and the latter at lower altitudes (Verschuren, 1977; Wolton *et al.*, 1982; Brosset, 1984). Koch-Weser (1984) found 30-40 *Lissonycteris* in a subterranean bunker in Burkina Faso, hanging near a small opening through which daylight entered. The present author collected two sexually inactive males and a nursing female in a forest area in southeastern Nigeria, from a colony of maybe 15 specimens in an open, tunnel-like space between huge limestone rocks. The bats were hanging at a height of about 6 m, not in clusters but by themselves. From many of the above and a few other, less detailed accounts (Lawrence *et al.*, 1963; F. Adam *et al.*, 1972; Schlitter *et al.*, 1982; Fedden *et al.*, 1986) it is evident that *Lissonycteris* often roosts in real caves, contrary to what Kock (1972) wrote, but that it selects the lighter parts. Although it is generally known that *Rousettus* species may form very large cave colonies, there are few accounts of actual colony size. For the species sympatric with *Lissonycteris*, *R. egyptiacus* and *R. lanosus*, the following has been published. Eisentraut (1963) estimated a colony of *egyptiacus* in Cameroon at about a thousand individuals. Rosevear (1965) mentioned a colony of tens of thousands of *egyptiacus* in Uganda - although it was not certain that no other species were involved too. Baranga (1980) collected large numbers (700) from Ugan-dan caves at Lake Victoria. The largest known colony appears to be the one described by McWilliam (1980b), who estimated that a cave at the Kenyan coast (shown by him to the present author in 1979) contained 50,000 specimens of *egyptiacus*. The only reference to numbers of individuals in *lanosus* colonies is made by Kingdon (1974), who observed several hundred in a mine adit in Uganda. *Myonycteris* species have never been found to roost in caves. For all we know, they do not live in colonies. (Their lack of Nycteribiidae is but one indication.) Again, little is known of the movements of the species considered. Wolton *et al.* (1982) concluded that *Lissonyc-teris* and *Myonycteris torquata* prefer the closed forest and its fringes, while *Rousettus egyptiacus* was trapped mostly in young secondary bush or cultivated land. However, Cosson (in prep.) conducted the first study in Africa of the occurrence of fruit bats in the canopy level, and found that *Myonycteris torquata* is very common in the canopy in the Campo Faunal Reserve in southwest Cameroun.

### *Other possible generic differences*

Lawrence *et al.* (1963) observed that in hanging posture, non-flight locomotion, and feeding habits *Lissonycteris* differs from *Rousettus.* A picture of *Myonycteris torquata* (Brosset, 1966c, fig. 53) suggests that this species, like *Lissonycteris*, can not fold its wings as tight as *Rousettus.* (In specimens of *M. torquata* and *M. relicta* preserved in spirit it is likewise impossible to fold the wings as in *Rousettus* without damaging them.) Related skeletal and muscular anatomy should be examined in the species concerned to establish the taxonomic value of this difference. J.-P. Adam *et al.* (1974) remarked that *Lissonycteris* are very much calmer, among themselves, than are *Rousettus egyptiacus.* In translation they wrote: "In the cages of *Lissonycteris* one never observes the 'discussions' so frequent in those of *Rousettus egyptiacus*; *Lissonycteris* is a gentle animal which one can perfectly handle with bare hands... with some precautions." Behaviour should of course be studied in the field as well. Calm behaviour will probably be related to the essentially non-gregarious roosting - just as the squabbling among *Rousettus* (which the present author was able to observe in *R. egyptiacus* in Kenya and in *R. leschenaultii shortridgei* in Bali, Indonesia) wll be related to its hanging shoulder to shoulder.

### *Parasites*

Several authors have indicated that *Lissonycteris*, *Myonycteris*, and *Rousettus* have specific ecto- and endoparasites (e.g. J.-P. Adam *et al.*, 1974; Wolton *et al.*, 1982). For example, no Nycteribiidae have been described from *Myonycteris*, while *Lissonycteris* is often infested with these flies, but with other species than is *Rousettus.* A comparative analysis of host-parasite relations may provide new evolutionary arguments for the relations of the bat genera under discussion.

### *Summary*

Summarizing, and leaving out findings not including or not yet established for all species considered, *Lissonycteris* differs from *Rousettus* in its much more specialized rostrum; its co-ossified premaxillae; its relatively short brain-case; its more specialized, differently formed, much more widely spaced cheek-teeth; its broader wing (through relatively longer first to third, and averagingly longer fourth and fifth fingers); its webbed toes; its more developed odontoid papillae; and its possession of a ruff of very aberrant hairs in males. It furthermore differs from many (probably all) *Rousettus* in its hair scale morphology; its karyotype and chromosomal evolution; its lack of acoustic orientation, and its related roosting and parasitological ecology; its roosting posture and locomotory behaviour and - probably - underlying anatomy; and its social behaviour. (After writing up these conclusions, the author's attention was drawn to a very recent publication by Kirsch *et al.* (1995), who on the basis of DNA hybridization experiments concluded that *Lissonycteris* is not a part of *Rousettus*, but associated with *Megaloglossus* Pagenstecher, 1885, and separated from *Rousettus* by *Epomophorus* Bennett, 1836.)

From *Myonycteris*, *Lissonycteris* differs in the slightly larger relative length of its rostrum and its probably related smaller relative brain-case length; its more pronounced spacing of cheek-teeth; its coossified premaxillae; its relatively smaller orbit; in many details of its dental morphology; its wing development, with averagingly larger relative lengths of second, third and fifth fingers; its relatively longer tibiae; its roosting ecology.

It can be argued that the differentiation between *Lissonycteris* and *Myonycteris* appears insufficient for generic separation, and that the former should be considered a synonym of the latter, but the foregoing account has shown that many of the characters considered are not yet, or at most poorly known for the two less common *Myonycteris* species, and the meant rearrangement would seem premature. (See in this context also the papers of Peterson *et al.*, 1995 and Juste *et al.*, in prep., which were received long after writing the above and are reviewed in the General remarks and conclusions at the end of this paper.)

On these grounds, I presently prefer to maintain both as genera. Some authors who have classified *Lissonycteris* as a subgenus of *Rousettus*, or have suggested to rank *Myonycteris* as such, have tended to concentrate on apparent similarities, without realizing that a number of those are equally shared by many other fruit bat genera too. A good example is the aberrant throat or neck fur in males. As Quay (1969) pointed out, nearly all male Pteropodidae possess some form of modified hair in that region: shoulder tufts, neck tufts, epaulets, ruffs, mantles, or patches of longer or differently coloured hair. In this light, the fact that many if not all *Rousettus* males have or may have neck tufts instead of a ruff rather discriminates this genus from *Lissonycteris* and *Myonycteris* than that it would link it to them.

Corbet *et al.* (1992) retained *Boneia* Jentink, 1879 as a subgenus to accomodate *Rousettus bidens*, on the basis of differences stated in their table 44. The differences can be divided into four groups: 1) overall size, as measured by fal; 2) functioning of premaxillaries, as measured by the strength of their connection; 3) strength of mandible, as measured by height of coronoid process; 4) teeth morphology and measure of degeneration. When all *Rousettus* species are considered, several of these differences do not hold:

Ad 1) Fal in *Boneia* is larger than 90 and would be smaller than 90 in *Rousettus* (Corbet *et al.*, 1992). However, *R. egyptiacus* and *leschenaultii* do attain fals over 95 and overlap or even surpass the range in *bidens* (*R. e. leachii* and *R. e. unicolor*; see Bergmans, 1994). These species are themselves absolutely larger than some of the other species retained in typical *Rousettus* by Corbet *et al.* (1992). In the opinion of the present author, differences in size are not appropriate as supraspecific character within *Rousettus*.

Ad 2) The premaxillaries are indeed connected in all *Rousettus* species but *bidens*.

Ad 3) The coronoid process is low in *bidens* and would be high in *Rousettus* (Corbet *et al.*, 1992). In fact, relative coronoid height, measured as mandibular height and expressed as percentage of mandibular length varies much within *Rousettus* s.l. In *lanosus*, it is smaller, on average, than in *bidens*; the lower values in *madagascariensis*, *egyptiacus leachii*, *e. unicolor*, *celebensis*, *amplexicaudatus* and *leschenaultii leschenaultii* overlap with the range found in *bidens*. Only in *leschenaultii shortridgei*, *spinalatus*, *egyptiacus egyptiacus* and *e. arabicus* no overlap was found. (Of *obliviosus*, no good coronoid measurements are available.) If compared to gsl, the mandibular height range in *bidens* overlaps completely with the variation in *lanosus*, while that in *madagascariensis* partly overlaps in range.

Ad 4) The number of upper incisors in *bidens* is essentially as in other *Rousettus*, and the frequent loss of $I^1$ in *bidens* does not qualify as a character of taxonomic value (see also Bergmans *et al.*, 1988). The anterior side of $C^1$ is grooved in *bidens* and would be smooth in other *Rousettus* (Corbet *et al.*, 1992). However, smooth anterior $C^1$ sides are found only in *egyptiacus* and *leschenaultii*, while stronger or weaker grooves, positioned rather antero-internally due to the orientation of the tooth, are to be found in *R. amplexicaudatus*, *celebensis*, *lanosus*, *madagascariensis*, *obliviosus*, and *spinalatus*. The basal length of $C^1$, related to that of $P^4$, is larger in *bidens* than in other *Rousettus* (Corbet *et al.*, 1992). A laterally depressed and seemingly long $C^1$ as found in *bidens* is also found in *amplexicaudatus* and *celebensis*; its length relative to that of $P^4$ rather indicates a short $P^4$. Corbet *et al.* (1992) further mentioned morphological differences in $P^3$, $P^4$, $P_3$, and $P_4$, which are low and flat in *bidens* and would be high and with strong surface ridges in other *Rousettus*. The reader is referred to the earlier account on teeth in this paper, from which it is clear that this statement applies mostly to *R. egyptiacus* but does not hold when all *Rousettus* species are compared. Finally, Corbet *et al.* (1992) mention the relatively large surface and height of $I_2$ relative to $I_1$ in *bidens*; in other *Rousettus*, $I_2$ is also larger than $I_1$, but only very moderatley so.

Summarizing, unique characters in *Rousettus bidens* are its disconnected premaxillae and relatively large $I_2$; the other characters mentioned by

Corbet *et al.* (1992) show a range of states all through the genus, without absolute differences between *bidens* and the other species. In the present author's opinion, the mentioned differential characters are of specific rather than subgeneric value. Some other *Rousettus* species also possess rather exceptional characters, and subgeneric divisioning should be based on a broader analysis, including those characters.

### **Lissonycteris angolensis** (Bocage, 1898)

*Cynonycteris angolensis* Bocage, 1898: 133, 138 (type locality: Pungo Andongo).
*Rousettus angolensis*; Andersen, 1907b: 503, 510; Eisentraut, 1965; Kock, 1973; Mainoya *et al.*, 1979; Honacki *et al.*, 1982: 126; Smithers, 1983: 64; Dobat *et al.*, 1985; Hickey *et al.*, 1987: 383.
*Rousettus smithii* O. Thomas, 1908: 375 (type locality: Sierra Leone).
*Rousettus (Lissonycteris) angolensis*; Andersen, 1912: 51; Leche, 1921: 41; Benedict, 1957: 292; Hayman *et al.*, 1971: 12; Meester *et al.*, 1986: 30; Corbet *et al.*, 1991: 41.
*Rousettus (Lissonycteris) crypticola* Cabrera, 1920: 106 (type locality: Fernando Poo).
*Lissonycteris angolensis*; Schwarz, 1920: 1046; Novick, 1958a; Lawrence *et al.*, 1963; Eisentraut, 1976: 75; Haiduk *et al.*, 1980, 1981.
*Rousettus angolensis ruwenzorii* Eisentraut, 1965: 3 (type locality: Ruwenzori East).
(Further references under the subspecies.)

*Diagnosis*: A rather small to medium-sized, densely furred fruit bat, with a fal range of 67.8-89.6; an only slightly deflected brain-case; a relatively long, anteriorly narrow and low rostrum, with coossified premaxillae; a distinct level change in the upper alveolar line; widely spaced cheek-teeth of which especially $P^4$ and $M^1$ are squarish in outline; broad wings, inserted at the second toe; partially webbed toes; a palatal ridge pattern of 3 + 4 + 2 (occasionally 4 + 3 + 2; exceptionally another variant); a ruff of specialized hairs in adult males.

Measurement ranges and ratios for the subspecies combined:

| | | |
|---|---|---|
| fal | ♂♂ | 68.4 - 87.5, |
| | ♀♀ | 67.8 - 89.6; |
| gsl | ♂♂ | 37.0 - 46.0, |
| | ♀♀ | 36.6 - 45.8; |
| rl | ♂♂ | 33.9 - 39.2% of gsl, |
| | ♀♀ | 33.8 - 38.5% of gsl; |
| $C^1$-$C^1$ | ♂♂ | 17.7 - 20.6% of gsl, |
| | ♀♀ | 18.2 - 20.6% of gsl; |
| $M^2$-$M^2$ | ♂♂ | 27.9 - 32.2% of gsl, |
| | ♀♀ | 28.2 - 33.0% of gsl. |

*Distribution:* Fig. 5.

*Remarks*

O. Thomas (1908) distinguished *Rousettus smithii* from Sierra Leone from typical *R. angolensis* by the following characters: it was smaller, the skull was narrower and more lightly built, $M^2$ and $M_3$ were relatively smaller, its ears were narrower, and the fur was shorter and not extending further than the proximal half of the tibiae. Andersen (1912: 814) treated *smithii* as "a perfectly distinct species". Cabrera (1920) described *Rousettus (Lissonycteris) crypticola* on the basis of a single specimen from Fernando Poo, with equally minor differences: its rostrum would be shorter than in *angolensis*, with the anterior orbit rim on level with the $P^4/M^1$ interstice, its $P_1$ larger (two times a lower incisor in surface), and its tibiae furred only partly, as in *smithii*. Frechkop (1954) thought that both *smithii* and *crypticola* were certainly only subspecies of *angolensis*, and Eisentraut (1960a, 1963) and Hayman (1960), who could not confirm the shorter rostrum and larger $P_1$ in *crypticola*, agreed with him - both even doubting if *crypticola* would be taxonomically valid at all. In 1964, Eisentraut could examine 37 specimens of *Lissonycteris* from Fernando Poo and found that in measurements (fal 70-77, mean 73.2; gsl 38.9-41.0, mean 40.2) they largely overlapped with 20 typical *angolensis* from Mount Cameroon on the opposite mainland (fal 72.0-81.4, mean 77.5; gsl 39.5-42.2, mean 40.7). Pointing out that the difference was appreciable but small, Eisentraut ranked *crypticola* as a synonym of *angolensis*. In his revision of the genus *Lissonycteris*, Eisentraut (1965) recognized a single species, *angolensis*, with three subspecies: *angolensis*, *smithii*, and the new and relatively large *ruwenzorii* from Mount Ruwenzorii.

Although Eisentraut's analysis is very useful,

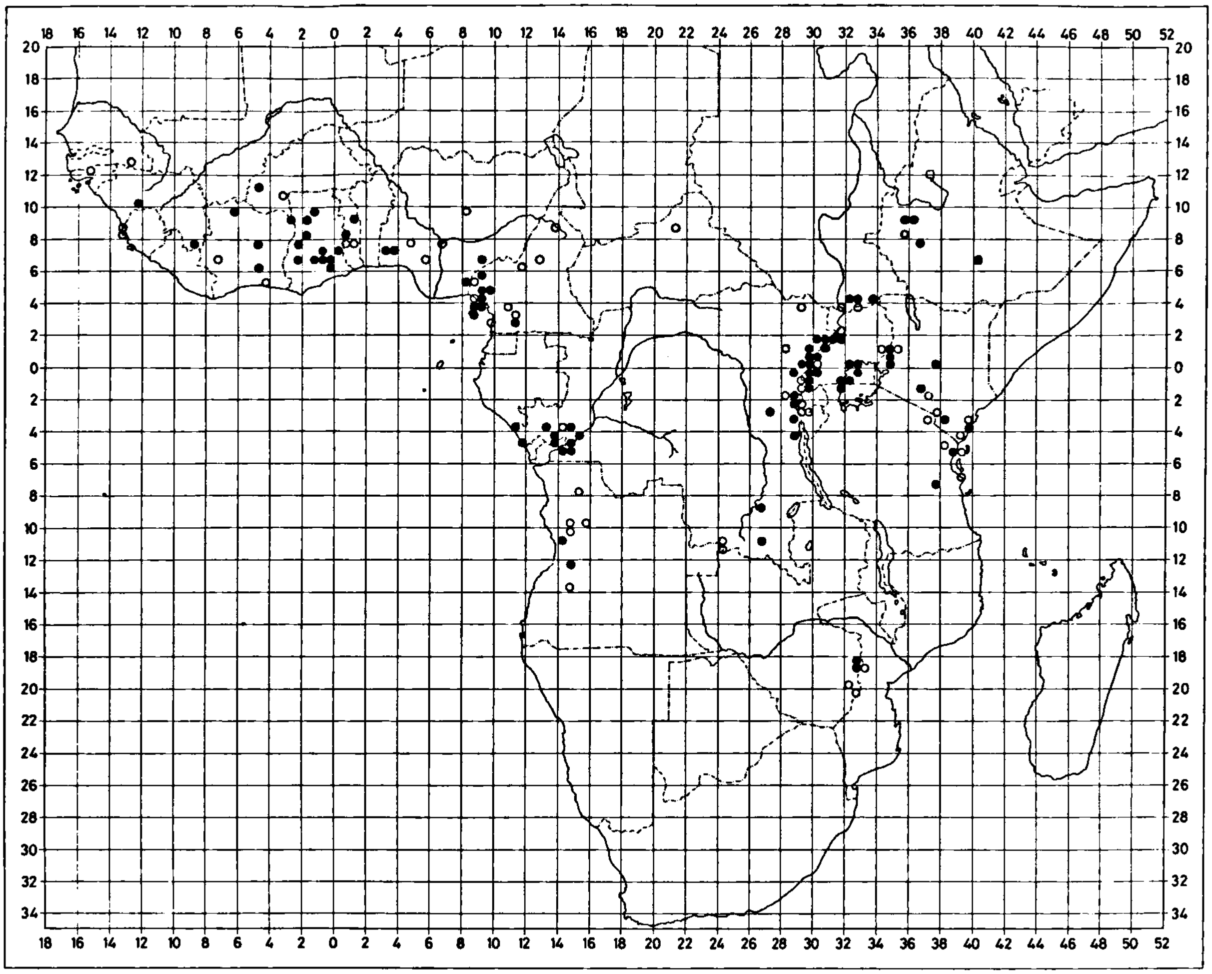

Fig. 5. Distribution of *Lissonycteris angolensis* (Bocage, 1889): Between 4 E and 22 E, the nominate subspecies; west of 2 E, *L. a. smithii* (O. Thomas, 1908) (and between 2 and 4 E, or further E, a possible transition area); east of 22 E and between 6 N and 12 S, *L. a. ruwenzorii* Eisentraut, 1965; east of 34 E and north of 6 N, *L. a. petraea* n. ssp.; east of 30 E and south of 16 S, *L. a. goliath* n. ssp. Black dots: squares from which material has been idntified by the author. Open circles: records from literature and correspondence.

and the recognition of one, polytypic species has been generally acknowledged, some problems with regard to its intraspecific taxonomy remain to be solved.

Since Eisentraut's revision (1965), many more *Lissonycteris* localities have been published, and the presently known distribution (fig. 5) allows for a reappraisal of intraspecific divisions. The pattern shows a number of gaps which in most cases appear to separate distinct (groups of) populations. The available data on *Lissonycteris* do not cover all discrete groups evenly but, with due caution, the following conclusions can be drawn. Typical *angolensis* occurs in Angola, western Zaïre, southern Congo (and possibly southern Gabon). The transition area between these and the more western *smithii* populations is thought to cover a part of southwestern Nigeria. Following Eisentraut (1964), Fernando Poo is included in the range of typical *angolensis*, although measurement averages are relatively low and skulls are slightly different, with relatively wide rostra (measured over $C^1$-$C^1$ and $M^2$-$M^2$).

So far, central Zaïre has not yielded any *Lissonycteris*. The records from the Central African Republic and southeast Zaïre nevertheless suggest the possibility of connections between 'western' and 'eastern' *Lissonycteris*. Taxonomically, these connections are as yet of unknown significance, as populations from eastern Zaïre and further to the east, usually assigned to *ruwenzorii*, are generally quite distinct from western populations. Within the East African region at large, the northernmost populations, from Ethiopia, are not conformable to *ruwenzorii* or to one of the other described forms and are described below as a new subspecies. The southernmost populations, in the border area of Zimbabwe and Mozambique, are also distinct from *ruwenzorii* and the other subspecies and ranked below as a further distinct subspecies.

In the literature, sexual dimorphism in *Lissonycteris angolensis* has not yet been examined. Tables 2-6 show that male skulls average slightly larger than female skulls, while females have longer forearms, on average, than males.

### Lissonycteris angolensis angolensis
(Bocage, 1898)

*Cynonycteris angolensis* Bocage, 1898: 133, 138 (type locality: Pungo Andongo).

*Rousettus angolensis*; Andersen, 1907b: 511 (in part: records from Angola and Cameroun); Cabrera, 1929: 13; Hill *et al.*, 1941: 29; Eisentraut, 1942: 254; Malbrant *et al.*, 1949: 84; Aellen, 1952: 27; Eisentraut, 1956a: 509, 1957: 624, 659; Schlitter *et al.*, 1982: 139; Happold, 1987: 41 (in part: possibly not the USNM material from Filele; see text); Dowsett *et al.*, 1991: 259.

*Rousettus (Lissonycteris) angolensis*; Andersen, 1912: 53 (in part: records trom Angola and Cameroun); G. M. Allen, 1939a: 63 (in part: records from Angola and Cameroun); Schouteden, 1944: 102 (in part: specimens from Banga, Kinkamba and Leopoldstad); Ellerman *et al.*, 1953: 46 (in part: records from Angola and Cameroun); Frechkop, 1954: 11; Hayman, 1954: 278 (in part: records from Bosafinda and Thysville); Leleup, 1956: 76; Hayman *et al.*, 1966: 30 (in part: the specimens from Barafinda, Kimbemba and Thysville, and possibly not those from Kabalo and Rutshuru); Koopman, 1994: 20.

*Rousettus (Lissonycteris) crypticola* Cabrera, 1920: 106 (type locality: San Fernando Cave, Basilé), 1929: 14; G. M. Allen, 1939a: 63; Frechkop, 1954: 11.

*Lissonycteris angolensis*; Schwarz, 1920: 1046; Rosevear, 1965: 84; Brosset, 1966c: 133; Happold *et al.*, 1978: 73; Hutterer *et al.*, 1982: 123; Crawford-Cabral, 1989: 10.

*Rousettus (Lissonycteris) smithii*; G. M. Allen, 1939a: 63 (in part: records from southern Nigeria); Rosevear, 1953: 83.

*Rousettus (Lissonycteris) angolensis angolensis*; Frechkop, 1954: 11; Hayman *et al.*, 1971: 12 (in part: not the records from Rhodesia); Smithers *et al.*, 1979: 27 (in part: not the material from Haroni/Lusitu River confluence); Koopman, 1994: 20 (in part: not the record from Zimbabwe).

*Rousettus (Lissonycteris) angolensis crypticola*; Hayman, 1960: 62.

*Rousettus angolensis angolensis*; Eisentraut, 1963: 60, 1964: 533, 1965: 1; Smithers *et al.*, 1976: 42; Schlitter *et al.*, 1982: 139; Smithers, 1983: 65 (in part: not the records from Zimbabwe and Mozambique); Fedden *et al.*, 1986: 184; Happold, 1987: 42 (in part: specimens from Ipole and Obudu).

*Rousettus angolensis crypticola*; Eisentraut, 1963: 61.

*Lissonycteris angolensis angolensis*; Rosevear, 1965: 85; Ansell, 1967: 2; Aellen *et al.*, 1968: 438; Eisentraut, 1973a: 34; J.-P. Adam *et al.*, 1974: 149; Ansell, 1974: 9, 1978: 18; Happold *et al.* 1978: 73; Bergmans, 1979: 167; Feiler, 1986: 73.

*Lissonycteris angolensis crypticola*; Rosevear, 1965: 87.

#### *Material examined*

ANGOLA. Congulu: 4 skulls (BMNH 35.1.6.8/.11). Quibula: 1 ♀, mounted (skull not seen), 1891, J. d'Anchieta ("T 113, sintipo?"; MLZA); 1 imm., mounted, skull inside, J. d'Anchieta ("T113, sintipo?"; MLZA).

(Amboin, Cabuta, Cahata, Calulo, Congolo, Hanha, Pungo Andongo, Uige.)

CAMEROUN. Bimbia: 3 imm. ♂♂, 7 ♀♀, 5 imm. ♀♀, 4-II-1938, M. Eisentraut (ZMB 93792/95 and unregistered). Nr Bokwango: 1 skull (BMNH 68.879). Buea: 1 ♂, 4 imm. ♂♂, 2 ♀♀, 3 imm. ♀♀, 2/30-X-1973, J. Prévost (MNHN CG 1979-324/33). Nr Buea: 6 skulls (BMNH 68.873/78). 15 km SE of Mamfe: 1 ♀, 7-XII-1971, L. W. Robbins (AMNH 240986). Man-o-War: 1 ♀, alc. (BMNH). Melan: 1 ♂, 1 ♀, 16-I-1953, A. I. Good (FMNH 74237/38). Mount Manengouba: 1 ♀, alc., 4/5-IX-1978, J. Prévost (MNHN CG 1979-323). Mukonje: 1 ♀, alc. (BMNH). Saxenhof Estate: 1 ♀, alc. (BMNH). Son Jem: 2 ♂♂, 1 imm. ♂, 1 ♀, 16-IX-1931, J. A. Reis (FMNH 43571/74). Tombel: 1 ♂, 21-II-1938, M. Eisentraut (ZMB 93796); 1 imm., alc. (BMNH). "Cameroun": 1 ♀, alc., skull, de Grelin (MNHN).

(Bibundi, Bonge, Dikume, Ebolowa, Ekona, Eseka, Great Soppo, Korup Reserve, Kribi, Kumba, Kupe, Lake Barombi, Mamfe, Mayo Darlé, nr Minim, Muenge, N'dian, Nyasoso, Rumpi Mountains.)

CENTRAL AFRICAN REPUBLIC.

(Goumba-Koumbala confluence.)

CONGO. The material listed by Bergmans (1979).

EQUATORIAL GUINEA.

("Guinée espagnole".)

FERNANDO POO. Basileo: 1 ♀, skin (skull not seen), 26-VII-1919, D. Manuel M. de la Escalera (holotype specimen of *Rousettus (Lissonycteris) crypticola* Cabrera, 1920; MNCN 20-

II-25-5). Moka: 1 specimen, II-1964, Aurelio Bosilio (AMNH 206954). Santa Isabel: 2 skulls (BMNH 60.242/43); 2 ♀♀, alc., skulls, IX-1959, Cambridge Annobon Expedition (BMNH).
(Mongola, Refugio, San Carlos.)
NIGERIA. Obudu: 1 specimen, alc., D. C. D. Happold (BMNH 76.1837). Odukpani: 1 ♂, alc., 6-XII-1970, T. S. Jones (BMNH 71.933); 3 ♂♂ (2: alc., skulls), 1 ♀, 1 imm. ♀ (alc.), 21-VII-1976, W. Bergmans (ZMA 18.610/14).
(? Filele - see the text; Ipole, Kagoro, Sapoba Forest Reserve.)
WEST ZAIRE. Barafinda, cave B 13: 4 ♀♀, 3 imm. ♀♀, 15-VI-1949, N. Leleup (MRAC 22504/10). Bosafinda, cave B 18: 1 ♂, 2 ♀♀, alc., 15-VI-1949, N. Leleup (BMNH). Kimbemba (Luozi): 1 ♂, alc., IX-1936, Schwetz (MRAC 13701); 1 imm. ♂, alc., 1965, De Roo (MRAC 33568). Kinshasa: 1 ♀, received in 1926, H. Schouteden (MRAC 15760). Thysville: 1 ♂, 1936, Schwetz (MRAC 13689). Thysville, cave B 13a: 1 ♀, 1 ♂, 23-V- and 17-VIII-1949, N. Leleup (MRAC 22503, 22671); cave B. B. R.: 1 ♂, 17-VIII-1949, N. Leleup (MRAC 22672).
(Kinkamba.)

*Diagnosis*: As for the species, with the following measurements.

| | | | |
|---|---|---|---|
| fal | ♂♂ | 72.0 - 81.3 | (n = 16), |
| | ♀♀ | 72.2 - 83.0 | (n = 28); |
| gsl | ♂♂ | 38.7 - 42.1 | (n = 8), |
| | ♀♀ | 38.7 - 41.7 | (n = 12); |
| rl | ♂♂ | 14.3 - 16.0 | (n = 8), |
| | ♀♀ | 14.5 - 15.1 | (n = 7); |
| iow | ♂♂ | 6.5 - 7.4 | (n = 10), |
| | ♀♀ | 6.3 - 7.1 | (n = 8); |
| pow | ♂♂ | 7.5 - 8.6 | (n = 10), |
| | ♀♀ | 7.4 - 9.4 | (n = 9); |
| zw | ♂♂ | 22.8 - 25.0 | (n = 9), |
| | ♀♀ | 22.6 - 24.1 | (n = 9); |
| $C^1$-$C^1$ | ♂♂ | 7.7 - 8.4 | (n = 10), |
| | ♀♀ | 7.4 - 8.1 | (n = 8); |
| $M^2$-$M^2$ | ♂♂ | 12.0 - 12.8 | (n = 9), |
| | ♀♀ | 11.6 - 12.8 | (n = 9); |
| $C^1$-$M^2$ | ♂♂ | 14.7 - 16.4 | (n = 10), |
| | ♀♀ | 15.0 - 17.2 | (n = 11); |
| $C_1$-$M_3$ | ♂♂ | 16.1 - 17.8 | (n = 9), |
| | ♀♀ | 16.3 - 17.7 | (n = 9); |
| W | ♂♂ | 67 - 84.5 | (n = 9), |
| | ♀♀ | 72 - 87 | (n = 9); |
| rl | ♂♂ | 35.7 - 39.2% of gsl | (n = 8), |
| | ♀♀ | 35.8 - 37.9% of gsl | (n = 7); |
| $C^1$-$C^1$ | ♂♂ | 18.3 - 20.4% of gsl | (n = 8), |
| | ♀♀ | 18.2 - 20.2% of gsl | (n = 6); |
| $M^2$-$M^2$ | ♂♂ | 29.6 - 31.7% of gsl | (n = 8), |
| | ♀♀ | 28.2 - 31.2% of gsl | (n = 7). |

The weights of females are of a non-pregnant specimen (72), a non-pregnant specimen suckling a large young (76.5), pregnant specimens (78, 79, 80, 85, 87), and probably pregnant specimens (83, 85). The subspecies' known range shows a large gap between 3° S and 2° N, and the northern populations differ slightly from the southern ones.

*Measurements:* See for some additional measurements table 1.

*Distribution:* Fig. 5.

*Related species*: *Lissonycteris angolensis* has no congeners. Morphologically, *Myonycteris* species are most closely related. They are smaller: West and Central African *M. torquata* with a fal range of 54.9-67.1 and a gsl range of 30.1-30.2-35.8 (*M. brachycephala* from Sao Tomé probably not much different), and east African *M. relicta* with a fal range of 65.9-75.1 and a gsl range of 35.5-39.2; *Myonycteris* has less specialized, oblong teeth, relatively narrower wings, and shorter tibiae. *M. relicta* has no $M_3$. Of the superficially similar species of the genus *Rousettus* the species *egyptiacus* and, in East Africa, *lanosus* are sympatric. They are both larger than *Lissonycteris*: the sympatric subspecies of *egyptiacus*, *unicolor* and *leachii*, with a fal range of 85.7-106.3 and a gsl range of 38.3-45.7, narrowly spaced oblong cheek teeth, dorsally practically naked tibiae, and adult males without ruff; *lanosus* with a fal range of 85.3-95.0, a gsl range of 39.4-44.8, a strongly deflected brain-case, very narrow oblong teeth, and adult males without ruff.

### *Remarks*

Taxonomy: Before his formal description of the species in 1898, Bocage reported on the (Angolan) type series in 1892 and mentioned then to have an adult ♀ from Pungo-Andongo, a young ♂ from Cahata, and several individuals of both sexes from Quibula. In the first paper he gave measurements of an adult ♀, possibly the one from Pungo-Andongo, and in the second he repeated these (with some alterations) and added those of a ♂. In neither article he mentioned that adult ♂♂ have aberrant ruff hairs, although in

1898 he wrote, without attaching these notes to a specific specimen or sex, that the hairs on either side of the head, the throat, and the ventral side of the neck are distinctly longer than those on breast and belly. Andersen (1912: 51), and after him Hollister (1918: 70), implicitly fixed the type locality as Pungo Andongo, and therewith Bocage's single adult ♀ from that village as holotype specimen. Andersen listed one of the syntypes, an immature ♀ from Quibula, as present in the BMNH (in spirit, skull extracted; 97.8.6.1). This must be the specimen Bocage had sent to Mr. Oldfield Thomas of that museum, to have it compared directly with the type of *Myonycteris torquata* (Dobson, 1878) (Bocage, 1898).

In 1975 the present author visited the MLZA in Lisboa and found only two specimens of Bocage's original series: a mounted adult ♀ without skull (fal c. 82) and a mounted juvenile with its skull inside, both collected in 1891 by José d'Anchieta at Quibula. Both were marked "sintipo? T113". These were certainly syntypes. At the time, the MLZA collection was not in good order and the other syntype specimens may still have been present somewhere. If all type specimens except the one in the BMNH have indeed remained in the MLZA, which is most probable, they have been destroyed in a fire in 1978 (Bergmans, 1989: 118), rendering the BMNH specimen the only syntype left.

Distribution and geographical variation: *Lissonycteris angolensis angolensis* occurs from central west and northwest Angola over the most western part of Zaïre and southern Congo towards - mainly southwestern - Cameroun, Fernando Poo and eastern Nigeria. It has not been found yet in Gabon or Equatorial Guinea. In Nigeria, it meets with the subspecies *smithii* (see below). There are few specimens from central Nigeria, central Cameroun and the northern Central African Republic and their subspecific identity, which is probably *angolensis*, needs further analysis.

To judge from the vegetation types in the region (White, 1983), it can be assumed that the Angolan populations are essentially continuous with the ones in southern Congo and adjoining Zaïre. (Northwest Angola has hardly been searched for Chiroptera: Bergmans, 1988, fig. 1; Crawford-Cabral, 1989, fig. 1.) Therefore, ZMA specimens from Pointe Noire in southwest Congo have presently been considered as representative for the typical subspecies. However, specimens from north of 2 N°, in Cameroun, south-eastern Nigeria, and Fernando Poo are slightly different from the Congolese ones, with relatively slightly higher (and in Fernando Poo specimens also wider) rostrum and brain-case, suggesting that the 'Gabonese gap' in the known distribution might reflect a reality. However, in body and skull size, and in relative stoutness of skull build, Southeast Nigerian and Camerounese specimens largely agree with those from Congo, West Zaïre and Angola. Those from Fernando Poo average smaller in size, but remain practically within the lower range values. There appears to be a slight difference in their rostrum width as measured over upper canines and molars but following Eisentraut (1965) they are not considered taxonomically distinct. In dental morphology, these northern specimens are intermediate between typical *angolensis* and the western subspecies *smithii*, which has relatively smaller and slightly less differentiated teeth. In *angolensis*, $I^1$ is narrower and less bent, $C^1$ has a broader postero-basal shelf, $P^3$ is more obtuse, $P^4$ is longer with less vertical cusps and a higher inner cusp, $M^1$ is longer with a higher inner cusp, and $M^2$ is longer; $C_1$ is wider with a broader postero-basal shelf, $P_3$ is more obtuse, $P_4$ has less vertical more diverging and about equally high cusps, and $M_1$-$M_3$ are longer and more strongly differentiated.

The limit or transition area between the nominate subspecies and *smithii* is not yet fully clear. Andersen (1912: 814) identified a specimen from "South Nigeria (western province)" as *smithii*. Hayman (1954) and Eisentraut (1965) followed this. The latter author observed that *smithii* increases in size from Guinea Bissau to West Nigeria, but he also suggested that there may be some clear limit between this and the typical subspecies when he wrote that in Cameroun typical *angolensis* ("die sich anschliessende Nominatrasse") takes over. But is there a clear limit? Happold *et al.* (1978) reported on a series from Ipole, West Nigeria, which they judged to be closest to *smithii* in most respects although the total skull length was more typical of *angolensis*. These authors identified a specimen from Obudu, east Nigeria, as *angolensis*. Their Ipole series existed of 22 specimens, 20 of which ♀♀, for which they gave a fal range of 66-81, a gsl range of 38-43, and a W range of 54-92 (all ranges indicating that the smaller specimens will not have been adult). The maximum values are certainly indicative of *angolensis*. In 1987 Happold repeated that the western Nigerian subspecies is probably *smithii* and that the specimen from Obudu belongs to *angolensis*. He also mapped records from central and central southern Nigeria - Kagoro, Filele and Sapobi Forest Reserve but did not comment on the subspecific identity f these specimens (Happold's record from Filele is based on USNM material. In this collection I only identified *Myonycteris torquata* from Filele. Happold did not list that - it is just possible that he took it for *Lissonycteris*.) To judge from published measurements (fal ♂♂ 70, 73, ♀♀ 70, 73, 75; gsl ♂ 38.8, ♀♀ 38.3, 38.8) specimens from Togo represent *smithii* (Hayman, 1954). Three specimens from Idere (HZM) and two from Igbo-Ora (USNM) in West Nigeria West of Ipole measured by the present author are much the same: fal 3 ♂♂ >67, 70.5, 71.3, 1 ♀ 73.0; gsl 3 ♂♂ 37.7, 38.2, ≥38.4, W 1 ♂ 62, 1 ♀ 65, and assigned here to *smithii*, as is - provisionally - the specimen from nearby Ibadan of which unfortunately no measurements are available. There is no obvious barrier between Idere/Igbo-Ora/(Ibadan) and Ipole. If Ipole specimens may attain measurements as large as Happold *et al.* (1978) indicate, we must assume a large transition area of *smithii* and *angolensis*, comprising all of southern Nigeria and part of Cameroun, with typical large size found as far west as Ipole but at the same time *smithii* dimensions in western Nigeria and dental traits of *smithii* eastward into Cameroun.

Until now, the limits between the nominate and eastern subspecies appear to be rather clear: in a large gap between 16° and 24° E and south of 8° N no specimens have been collected. However, north of 8° N 4 specimens have been netted in the north of the Central African Republic (Schlitter *et al.*, 1982). These authors assigned them to the typical form rather than *R. a. ruwenzorii* on the basis of their size: fal 1 ♂ 74.4, 1 ♀ 75.1. As presently understood, these measurements are not decisive. The difference between *angolensis* and *ruwenzorii* is found in average skull size rather than in forearm length, and further study - and preferably: further specimens from the Central African Republic region - are needed to assess the taxonomic position of the species' representatives here.

The typical subspecies has been found in forests and in forest transitions and mosaics, and to a lesser extent in woodlands (types according to White, 1983; followed by number of collecting localities): Guineo-Congolian lowland rain forest: wetter types (type 1a; 23); ditto: drier types (type 2; 3); mosaic of types 1a and 2 (type 3; 1); Mosaic of lowland rain forest and secondary grassland (type 11a; 18); Afromontane undifferentiated vegetation (type 19a; 4); Wetter Zambezian miombo woodland (type 25; 5); Sudanian woodland with abundant *Isoberlinia* (type 27; 1); Sudanian undifferentiated woodland (type 29a; 1); and North Zambezian undifferentiated woodland (type 29c; 3).

### **Lissonycteris angolensis smithii** (O. Thomas, 1908)

*Xantharpyia (Myonycteris) angolensis*; Matschie, 1899: 64 (in part: the specimen from Togo).

*Rousettus angolensis*; Andersen, 1907b: 511 (in part: records from Togo).

*Rousettus smithii* O. Thomas, 1908: 375 (type locality: Sierra Leone); G. M. Allen, 1939a: 63 (in part: records from Sierra Leone to Togo).

*Rousettus (Lissonycteris) angolensis smithi*; Andersen, 1912: 53 (in part: records from Togo); Frechkop 1954: 11; Hayman *et al.*, 1971: 12; Verschuren, 1977: 618; Koopman, 1994: 20.

*Rousettus (Lissonycteris) smithi;* Andersen, 1912: 814; G. M. Allen, 1939a: 63; Hayman, 1954: 278.

*Lissonycteris smithii*; Schwartz, 1920: 1048.

*Rousettus (Lyssonycteris) angolensis*; Veiga-Ferreira, 1948: 63.

*Rousettus smithi*; Eisentraut *et al.*, 1957: 326.

*Rousettus angolensis smithi*; Eisentraut, 1963: 61, 1965: 1; Koopman *et al.*, 1978: 2; Happold, 1987: 42 (in part: the specimens from Idere and Igbo-Ora).

*Lissonycteris angolensis smithi*; Rosevear, 1965: 84, 86; Orshoven *et al.*, 1968: 181; De Vree *et al.*, 1969: 203, 1970: 43; De Vree, 1971: 38; Bergmans *et al.*, 1974: 38; Happold *et al.*, 1978: 73; Robbins, 1980: 85; Wolton *et al.*, 1982: 426; Brosset, 1984: 546; Koch-Weser, 1984: 263.

*Lyssonycteris angolensis smithi*; F. Adam *et al.*, 1972: 61.

*Lissonycteris angolensis*; Coe, 1976: 546; Marshall *et al.*, 1982: 56.

*Material examined*

BURKINA FASO. Oradora: 1 ♂, 1 imm. ♀, 17- and 19-IV-1969, R. E. Vaden (USNM 467761/62).
(Diebougou.)
GHANA. Agogo: 2 skulls (BMNH 65.744/45). 7 miles west of Daboya: 3 skulls (BMNH 65.560/62). Javiefe: 1 skull (BMNH 65.746). Leklebi Agbesia: 2 ♂♂, 2 ♀♀, 26-VI-1968, J. C. Geest (USNM 424685, -88/90). Mole National Park: alc. material (BMNH). Nkawnkaw: 2 ♂♂, 11/12-VIII-1967, B. J. Hayward (USNM 411838/39). Odomi Jongo: 2 ♂♂, 1 imm. ♂, 5 ♀♀, 1 imm. ♀, 1 specimen, 17/23-VI-1967, J. C. Geest (USNM 424661, -63, -65/70, -76/77). Subinja: 1 ♂, 24-II-1968, J. C. Geest (USNM 414695). Todzi: 2 skulls (BMNH 65.747, 66.14). Yabraso: 1 ♀, 11-IV-1968, J. C. Geest (USNM 424660).
(Abdomasi, Babiani, Boti Falls, Wenchi.)
GUINEA. Kankasili: 2 ♀♀, 15-XI-1966/1-III-1967, J. van Orshoven (ZMA 10.735, -38).
(Darsalam, plateau de Salung nr Nyembaro.)
GUINEA BISSAO.
(Mansoa.)
IVORY COAST. Bouna: 1 ♀, 5-VII-1969, L. W. Robbins (USNM 467711). Fetekro: 7 ♂♂, 21 ♀♀, 18-VII-1969, T. J. McIntyre/L. W. Robbins (USNM 467718/20, -23/27, -34/36, -39/42, -44/48, -50, -52/55, -57, -59/60). Lamto 1 ♂, alc., skull, 26-VI-1964, J. Vissault (ZMA 16.535); 1 ♂, 29-I-1969, J. W. LeDuc (USNM 465727); 1 ♂, 1 ♀, 1/2-VII-1970, J. Vissault (MNHN); 1 ♂, 27-VIII-1970, J. Vissault (ZMA 16.533). Yama: 4 ♂♂, 4 ♀♀, 20-3-1969, J. W. LeDuc/J. Vissault (ZMA 16.534; USNM 465727/34). "Ivory Coast: 2 ♂♂, 1 imm., 1972/73, J. Vissault (ZMA 18.050/52).
(Adiopodoumé, Duékoué.)
LIBERIA. Nimba East: 2 ♂♂, 1 imm. ♂, 2 ♀♀, alc., 1/4-II-1966, J. Verschuren (IRSN 16116/20, 16756). Nimba West: 1 ♀, 1 imm. ♀, alc., 27-II/12-III-1966, J. Verschuren (IRSN 16121, 16755). South of Mount Richard Molard: 1 ♀, 7-I-1966, J. Verschuren (IRSN 16119). "Liberia": 3 ♂♂, 1 ?♂, 2 ♀♀, 24-VII/XII-1965, J. Verschuren (IRSN 16749/54).
(Mount Nimba: Cassave Farm, Banana Plantation, Grassfield, and Old Mine Road.)
NIGERIA. Ibadan: 1 ♀, no data (ZMUI 144). Idere: 1 ♂, 1 ♀, 1 imm. ♀, 29-I-1964, M. Skirron (HZM 1.4139, 2.4140, 3.4141). Igbo-Ora: 1 ♂, 1 ♀, 24/25-X-1966, H. W. Setzer (USNM 402314/15). "South Nigeria (Western Province)": 1 ♂, skull, 1908, A. E. Kitson (BMNH 8.10.25.1).
SENEGAL.
(Ebarak.)
SIERRA LEONE.
(Lumley Village, Mount Aureol, "Sierra Leone".)
TOGO. Akenim: 1 ♀, skin only, 19-VII-1954, A. H. Booth (MRAC 23.719); 3 specimens, A. H. Booth (BMNH 55.370/72). Bismarckburg: 1 ♀, 2 imm., alc., skulls, Büttner (ZMB 6758/60). Papase: 1 specimen (BMNH 53.728). Pewa: 1 ♂, 25-V-1968, J. W. LeDuc (USNM 437590).
(Adjido, Ahoué-houé, Aledjo, Atakpamé, Odjolo.)

*Diagnosis:* As for the species but averaging small in body and skull dimensions, with measurements as listed below; with less extensively webbed toes; and with relatively small and little differentiated teeth.

| | | | |
|---|---|---|---|
| fal | ♂♂ | 68.4 - 75.2 | (n = 29), |
| | ♀♀ | 67.8 - 77.7 | (n = 45); |
| gsl | ♂♂ | 37.0 - 39.7 | (n = 24), |
| | ♀♀ | 36.6 - 40.1 | (n = 28); |
| rl | ♂♂ | 13.0 - 14.5 | (n = 6), |
| | ♀♀ | 12.9 - 14.2 | (n = 6); |
| iow | ♂♂ | 5.8 - 6.4 | (n = 6), |
| | ♀♀ | 5.7 - 6.2 | (n = 5); |
| pow | ♂♂ | 8.0 - 8.7 | (n = 6), |
| | ♀♀ | 6.9 - 8.1 | (n = 5); |
| zw | ♂♂ | 20.1 - 22.2 | (n = 5), |
| | ♀♀ | 20.5 - 22.6 | (n = 6); |
| $C^1$-$C^1$ | ♂♂ | 7.2 - 7.8 | (n = 6), |
| | ♀♀ | 6.8 - 7.7 | (n = 5); |
| $M^2$-$M^2$ | ♂♂ | 10.7 - 11.7 | (n = 6), |
| | ♀♀ | 10.4 - 12.2 | (n = 5); |
| $C^1$-$M^2$ | ♂♂ | 13.9 - 15.0 | (n = 7), |
| | ♀♀ | 13.9 - 14.6 | (n = 6); |
| $C_1$-$M_3$ | ♂♂ | 15.5 - 16.4 | (n = 6), |
| | ♀♀ | 15.5 - 15.9 | (n = 5); |
| W | ♂♂ | 6 - 65 | (n = 2), |
| | ♀♀ | 60 - 72 | (n = 4); |
| rl | ♂♂ | 33.9 - 37.9% of gsl | (n = 6), |
| | ♀♀ | 33.8 - 36.2% of gsl | (n = 3); |
| $C^1$-$C^1$ | ♂♂ | 18.6 - 20.4% of gsl | (n = 5), |
| | ♀♀ | 19.3 - 20.2% of gsl | (n = 2); |
| $M^2$-$M^2$ | ♂♂ | 27.9 - 30.6% of gsl | (n = 6), |
| | ♀♀ | 29.7 - 31.9% of gsl | (n = 3). |

From the literature, some minor range extensions may be added: a fal of 66.7 in a ♂ from Guinea-Bissau (Veiga-Ferreira, 1948), one of 66 in a ♀ from Guinea (Eisentraut *et al.*, 1957); a gsl of 36.7 in a ♂ from Senegal (F. Adam *et al.*, 1972) and one of 36.4 in a ♀ from Guinea (Eisentraut *et al.*, 1957). The ranges given by Coe (1976) for a small series from Mount Nimba obviously include wrongly identified specimens of other species (fals of 86 in ♂♂ and of 83 in ♀♀) and are useless. Wolton *et al.* (1982), also on specimens from Mount Nimba, probably included immature specimens in their fal range for ♂♂; they noted as W in 84 ♂♂ 45-75 (mean 64.4; again indicating inclusion of immatures), in 28 ♀♀ 54-78, and in 46 pregnant ♀♀ 51-85.5.

*Measurements:* For some additional measurements the reader is referred to table 1.

*Distribution:* Fig. 5.

*Related species:* See the account of the typical subspecies.

*Remarks*

Taxonomy: O. Thomas (1908) gave as important characters distinguishing *Rousettus smithii* from *R. angolensis*: smaller size; narrower and more lightly built skull, with zygomata less widely expanded; fur shorter, extending to proximal half only of tibiae; ears narrower; teeth smaller, similar in relative proportions with the exception that $M^2$ and $M_3$ are much smaller, about one-third instead of one-half the size of $M^1$ and $M_2$, respectively. Andersen (1912: 814) did not add to this, and neither did Eisentraut (1965).

On the whole, *smithii* does never attain the maximum dimensions of *angolensis*. The skull in *smithii* appears to be more delicate than in *angolensis*, and its brain-case deflection is slightly stronger, which, as a neotenic character, may be connected with its smaller size. The zygomatic width is clearly a function of skull length, becoming relatively smaller with skull growth (shown, incidentally, by Eisentraut, 1965, in his fig. 2), and has no true taxonomic value. Remarkably, this allometry has also been found for *Epomophorus gambianus* (see Bergmans, 1988: 98).

Differences in fur length and distribution do exist between *Lissonycteris* populations from different regions but do not coincide with subspecific divisions. ZMA specimens from Guinea, Ivory Coast and East Nigeria (the latter assigned to the typical subspecies) have the fur relatively short and more thinly to near absent on the proximal half of the tibiae, and always leaving the distal half practically naked. The two ZMA specimens from Congo, the one from East Zaïre, and the one from Ethiopia (representing the subspecies *angolensis*, *ruwenzorii*, and *petraea*, respectively) have more dense fur, extending on three to four fifths of the tibiae. Specimens from Zimbabwe, to be described as a new subspecies below, have dense, long fur, extending on the tibiae nearly to the feet. The Congo specimens roosted in palms practically on the beach, the Zaïre specimen is from a higher altitude, and the Zimbabwe specimens are from 18° to 20° S, so climatic conditions may have an influence here.

O. Thomas' (1908) observation on the narrow ear in *smithii* when compared to *angolensis* was based on one adult spirit specimen of *smithii* and the dry skins of six adults of what we now call *ruwenzorii* (see lists of BMNH specimens in Andersen, 1912). Some measurements on spirit specimens by the present author only indicate that ear width is 12-14 throughout the species and that, apart from some individual variation within populations, specimens of larger subspecies have relatively slightly larger ears.

The webbing between the toes in *Lissonycteris* appears to be somewhat less developed in *smithii* than in *angolensis*.

Other differences are to be found in the teeth. If compared to the typical subspecies, $I^1$ in *smithii* is wider and more strongly bent backward; $C^1$ has less of a postero-basal shelf; $P^3$ is more pointed; $P^4$ is shorter antero-posteriorly and has more vertical cusps, with the inner cusp lower; $M^1$ is shorter and has a lower inner cusp; $M^2$ is shorter. $C_1$ is narrower, with less of a postero-basal shelf; $P_3$ is more pointed; $P_4$ has more vertical cusps standing closer together, the inner one lower; $M_1$, $M_2$ and $M_3$ are shorter and less differentiated.

Distribution and geographical variation: There are not very many samples of *smithii* in collections but they suggest that the subspecies may be found quite evenly distributed through the West African forest zone from Senegal and Guinea-Bissau to West Nigeria and, to a lesser extent, its woodlands. The species has not yet been recorded for Gambia, Mali and Benin. Of 41 localities, 15 are in forest, 16 in forest mosaics and transitions, and 10 in woodlands or, according to the classification by White (1983): 2 are in wetter types of Guineo-Congolian Lowland rain forest (type 1a), 9 in drier types of same (type 2), 2 in a mixture of these (type 3) and 2 in Mangrove (type 77); 15 are in Mosaic of Guineo-Congolean Lowland rain forest and secondary grassland (type 11a) and 1 is in Undifferentiated Afromontane vegetation (type 19a); 9 are in Sudanian woodland with abundant *Isoberlinia* (type 27) and 1 is in Undifferentiated Sudanian woodland (type 29a).

Eisentraut (1965), in his observations on *smithii*, concentrated on differences in size, and observed a gradual increase in size in *smithii/angolensis* from west to east. However, the few data at his disposal do not allow for more than the conclusion that specimens from extreme western Africa (Guinea-Bissau, Guinea, Sierra Leone) probably average slightly smaller than specimens from Togo (which in turn are smaller than specimens from Cameroon but these do not represent *smithii*). The data presently at hand are still few, but do not yet confirm a clinal change in size either. In the region from Guinea-Bissau to Togo, the largest specimens (fal 69.8-75.2 in 5 ♂♂ and 67.8-77.7 in 6 ♀♀, gsl 39.7 in 1 ♂) have now been found at Mount Nimba in Liberia, while gsl in ♀♀ in Ivory Coast attains 40.1. It may well be that, instead of a clinal change, within particular populations such as on Mount Nimba larger average dimensions are developed than in others.

## **Lissonycteris angolensis ruwenzorii** (Eisentraut, 1965)

*Rousettus angolensis*; Andersen, 1907b: 511 (in part: records from Ruwenzori and German East Africa); Hollister, 1918: 70; De Beaux, 1922: 364; Koopman, 1975: 361; Rodgers *et al.*, 1982: 241; Koopman, 1986: 10.

*Rousettus (Lissonycteris) angolensis*; Andersen, 1912: 53 (in part: records from Ruwenzori and german East Africa); G. M. Allen *et al.*, 1936: 44; G. M. Allen, 1939a: 63 (in part: specimens from Kenya and Tanzania); G. M. Allen *et al.*, 1942: 160; Schouteden, 1944: 102 (in part: specimens from Kodja, Mongbwalu, Mulungu, Ruwenzori); Swynnerton *et al.*, 1951: 287; Ellerman *et al.*, 1953: 46 (in part: specimens from Kenya and Tan-zania); Frechkop, 1954: 11; Hayman, 1954: 278 (in part: record from Mt. Wago); Harrison, 1961: 287; Hayman *et al.*, 1966: 30 (in part: not the specimens from Barafin-da, Beni, no.'s 23674 and 23676 from Butembo, Kimbemba, and Thysville, and possibly not those from Kabalo and Rutshuru); Verschuren, 1967; D. I. H. Simpson *et al.*, 1968b; Koopman, 1975: 362; Kock, 1981: 330.

*Lissonycteris angolensis*; Novick, 1958a; Lawrence *et al.*, 1963; Anciaux de Faveaux, 1972: 85; Kingdon, 1974: 137; Anciaux de Faveaux, 1976, 1978: 458; Ansell, 1978: 18; Baeten *et al.*, 1984: 185.

*Rousettus angolensis ruwenzorii* Eisentraut, 1965: 3 (type locality: Ruwenzorii East); Koopman, 1975: 361.

*Lissonycteris angolensis angolensis*; Ansell, 1967: 2, 1974: 9, 1978: 18.

*Rousettus (Lissonycteris) angolensis angolensis*; Hayman *et al.*, 1971: 12 (in part: records from Zambia and Rhodesia).

*Rousettus (Lissonycteris) angolensis ruwenzorii*; Hayman *et al.*, 1971: 12; Aggundey *et al.*, 1984: 122; Koopman, 1994: 20.

### *Material examined*

KENYA. Barberton Cave: 1 ♀, 7-II-1959, J. Williams (LACM 19516); 1 ♂, 1 ♀, 25/29-VII-1963, R. E. M. Mumford (USNM 35070, -94). Chepkelele: 1 ♂, 4 ♀♀, alc., 31-XII-1980, F. Spitzenberger (field numbers 166/170; NMW). Kairuni: 2 ♂♂, 1 imm. ♂, 19/20-IX-1973, K. E. Stager (LACM 45624/26). Kakamega: 1 ♂, 19-VIII-1958, J. D. L. Fleetwood (HZM 12.2707). Kakamega Forest: 1 ♂, VII-1959, J. G. Williams (LACM 19518); 1 ♂, VI-1961, J. G. Williams (LACM 51516); 5 ♂♂, 1 ♀, 1 imm. ♀, (24-)XII-1962, P. Martin/R. Glen (LACM 19520/26); alc. material (BMNH). Kakamega Mine: 2 ♂♂, 2 ♀♀, 21-VII-1963, R. E. M. Mumford (USNM 350783/84, -86/87). Karura Forest: 1 ♂, 1-VIII-1958, F. D. L. Fleetwood (HZM 13.2708). Kipsiryori Cave: 1 ♂ (pullus), 6 ♀♀, alc., 29-XII-1980, F. Spitzenberger (field numbers 116/122); NMW). Lirandha Hill: 4 ♂♂, 3 ♀♀, 15-XII-1956, J. G. Williams (HZM 5.2280, 6.2356, 7.2357, 8.2359, 9.2364, 10.2366, 11.2367). Mount Elgon, southeast slopes: 3 ♀♀, 2 imm. ♀♀, 2-V-1953, J. G. Williams (HZM 1.1907, 2.1908, 3.2274, 4.2275, 14.2960). Nabonga Cave: 2 ♀♀, alc., skull of one, 30-XII-1980, F. Spitzenberger (field numbers 159/160; NMW). Ngangao Forest: 1 ♀, 21-VIII-1965, A. D. Forbes-Watson (USNM 375887). Nyunga ya Mawe Cave: 2 ♀♀, alc., 30-XII-1980, F. Spitzenberger (field numbers 127/128; NMW). 3 miles southeast of Saboti: 4 ♀♀, 25-VII-1968, B. J. Hayward (USNM 436379/82).

(Arabuko Sokoke Forest, Cherengani Hills, Chyulu Hills, Kabolet River, Kichakasimba, Kimini Caves, Kimmilli area, 20 miles southwest of Kitale, Markwijit, Mneneka blow holes, east side of Mount Elgon, south of Mount Elgon, Muumando, Tarla's Dam, west of Pokot Escarpment.)

RWANDA.

(Gisovu, Ntango, Ruta Bansugera, Uwinka.)

SUDAN. Katire: 1 imm. ♂, alc., G. Nikolaus (SMNS 29802). Loki (or Lokwi): 1 ♂, 1 imm. ♂, 3 ♀♀, alc., 9-II/17-III-1951, J. S. Owen (FMNH 182112/16). Lokwi: 5 ♂♂, 4 ♀♀, 1 imm. ♀, 2 specimens, (1: skull only; 4: alc.), 9-II/12-XI-1951, J. S. Owen (FMNH 78212, 79577/87). Nagishot: 1 ♂, alc., G. Nikolaus (SMNS 29800). Sunnat: 1 ♀, 22-II-

1950, H. Hoogstraal (FMNH 67162). Talanga Forest: 1 ♂, 1 ♀, 2 imm. ♀♀, (3: alc.), 17-VI-1950, J. S. Owen (FMNH 68042/44, 77606); 1 ♀, alc., 2-VII-1978, G. Nikolaus (SMNS 29806).

(Gilo, Isore, Logot.)

TANZANIA. Amani Forest: 1 ♂, 6-X-1962, S. Keith (AMNH 206670). Bukoba: 1 skull, Emin Pascha (ZMB 10246). Bunduki: 2 ♂♂, skins, 1 ♀, skull, 11/15-I-1964, K. E. Stager (LACM 19686, 51636, 55003). Kwamkoro: 1 ♀, alc., skull, 17-VI-1908, Vossler (ZMB). Nr Lwandani Cave: 4 imm. ♂♂, 4 imm. ♀♀, alc., 9/11-I-1981, F. Spitzenberger (field numbers 303, 342/346, 357/358; NMW).

(Kibongoto, Kisarawe, Magrotto, Tanga, East Usambara Mountains.)

UGANDA. Budongo: 1 imm. ♀, alc., skull, 7-VII-1965, A. Starret (LACM 19628). Budongo Forest: 1 imm. ♂, 11-X-1963, WFVZ-2 (LACM 31776); 4 ♂♂, 1 imm. ♂, 2 ♀♀, 2 imm. ♀♀, 16/30-VI-1966, J. G. & A. Williams (LACM 51521/29); 1 ♂, 3 ♀♀, 1 imm. ♀, 30-IV/11-V-1970, I. Bampton (LACM 36103, -08, -14, -17/18). Bukasa Island: 2 specimens, plus alc. material (BMNH 71.957/58 and unregistered). Nr Bulago: 1 ♂, alc. (BMNH). Bwindi area: 1 ♂, 29-V-1969, A. Williams (LACM 35491). Bwindi Swamp: 1 ♂, 2 ♀♀, 1 imm. ♀, 19/20-III-1967, R. Glen (LACM 51605/08). Entebbe: 1 ♀, alc. (BMNH). Impenetrable Forest: 1 ♀, 1 imm. ♀, 8/11-III-1967, A. L. Archer (LACM 51550, 51601). Ishasha River: 1 ♀, S. Keith (AMNH 189475). Itama area: 1 ♂, 4 ♀♀, 4 imm. ♀♀, 4/21-VI-1969, R. Glen/A. Williams (LACM 35493/97, -99/500, -02/03). Itama mine (area): 4 ♂♂, 5 ♀♀, 2 specimens, 26/31-III- and 2-IV-1967, A. L. Archer/A. Williams (LACM 51609/16, -18/20; unregistered). Kalinzu Forest: 2 ♂♂, 1 ♀, 31-X-1969, R. Glen (LACM 35667/69). Kampala: 1 specimen, alc., XII-1964 (SMF 23677). Kayonza Forest: 1 imm. ♂, 2 ♀♀, VII-1958, WFVZ (LACM 31777/79). Kibale Forest: 7 ♂♂, 2 imm. ♀♀, 5/28-XI-1966, R. Glen/A. Williams (LACM 51621/24, -31/35). Kinyala Estate: 2 ♂♂, 2 ♀♀, alc. (BMNH). ? Kita Melira: 1 imm. (AMNH 189473). Kwapur Cave: 1 ♂, 1 ♀, 1 imm., alc. (BMNH). Malabigambo Forest: 4 ♂♂, 1 imm., 27-I/3-II-1968, A. L. Archer (LACM 51626/30). Mwana Island: 1 imm. ♂, game warden, alc. (BMNH). Mwela: 1 ♂, 2 ♀♀, 1 imm. ♀, 10-XII-1967, A. L. Archer (LACM 51530/33). Ntandi: 2 ♂♂, 17-VII-1967, A. L. Archer/A. Williams (LACM 51517/18); 1 ♀, 1 imm. ♀, 31-X/15-XI-1968, R. Glen (LACM 51515, -19). West of Ntandi: 2 ♀♀, 20-XI-1968, A. Williams/R. Glen (LACM 51520, -37). Ruhizha: 1 ♂, 4 ♀♀, 4 imm. ♀♀, 10/21-V-1969, A. Williams (LACM 35483/90, 35501). Ruhizha area: 2 ♂♂, 1 ♀, 19-III-1967, A. Williams (LACM 51602/04); 1 ♂, 1 ♀, 2/5-VI-1969, R. Glen (LACM 35492, -98). Ruwenzori East: 4 ♂♂, 3 ♀♀, 3/14-III-1906, R. E. Dent (USNM 172916; MRAC 933a-c, 934a-c); 5 specimens (paratype specimens of *Rousettus angolensis ruwenzorii* Eisentraut, 1965; BMNH 6.12.4.2/.6); 1 ♂, 2 ♀♀, alc. (BMNH).

(Butandiga, Dwaji Island, Kinyala, Maiba Island, Mobuku Valley, Sambiye River.)

EAST ZAIRE. Butembo area: 1 ♀, 1 specimen, alc., 1955 and ?, Dyleff (MRAC 23449, 26435). Djugu Forest: 1 imm., 1952, A. Fain (MRAC 23151). Itombwe: 1 ♂, alc., 10-IX-1957, N. Leleup (MRAC 26706). Jaima: 1 specimen (BMNH 7.7.8.24). Kabambi: 1 ♀, 17-VIII-1947, J. Hiernaux (IRSN 7055). Kahuzi: 1 ♀, 2 specimens, alc., skulls, 16-X-1965 and 20/21-IV-1966, P. Kunkel (SMF 31818/20). Kalumbu Cave: 1 imm. ♂, 1 ♀ (alc.), 1-XII-1957 and ?, M. Anciaux de Faveaux (MRAC 27592/93). Kilo-Mines: 4 ♂♂, 1 ♀, 20-IV-1949, J. Hiernaux (MRAC 19090/94). Lubango: 1 ♀, skin, 25-V-1950, A. Prigogine (MRAC 20691). Lusilubi Valley: 1 ♂, 12-VIII-1946, J. de Wilde (IRSN 13328). Lutunguru: 2 ♀♀, 30-III/5-IV-1949, 2 ♂♂, 6-VII and 4-VIII-1949, and 1 ♀, 16-II-1952, A. Prigogine (MRAC 18862/63, 19052/53, 20820). Lwana: 1 ♀, alc., 19-IV-1992, N. Masumbuko Kamitongo (ZMA 24.560). Lwiro: 1 ♂, 1 specimen, 28-V-1964 and VII-1965, P. Kunkel (SMF 31816/17). Matupi Cave: 1 imm. ♀, alc., 4-VIII-1955, G. F. de Witte (MRAC 37118). Miki-Kamituga: 1 ♀, 20-VIII-1954, A. Prigogine (MRAC 23423). Mongbwalu: 1 ♂, 14-VIII-1939, Janssens (MRAC 15759). Mont Hoyo (cave): 1 ♀, 17-VIII-1947, J. Hiernaux (IRSN 7065); 1 ♂, 1 ♀, 1 specimen, 4-V-1955, W. L. Schmitt/E. W. Baker (USNM 301703, -05/06); 3 ♂♂, 19-IX-1955, J. P. Chapin (AMNH 180902, -04/05). Mont Wago: 1 ♂, A. Fain (MRAC 20804); 2 ♂♂, 1952, A. Fain (MRAC 21436/37). Munoi: 1 ♀, 1 imm. ♀, 14-VI-1948, G. F. de Witte (IRSN 10662/63). Pelenge: 1 ♂, 1 ♀, 4-VI-1947, G. F. de Witte (IRSN 10660/61). Shabunda: 1 ♀, 16-VIII-1952, P. G. Vercammen (MRAC 23177).

(Beshokwe, Djelube River, Irangi, Kabolela, Katanda, Kodja, between Mawambi and Avakubi, Mount Muvo, Mulungu,

? Rutshuru, Saliboko.)

ZAMBIA.

(Sakeji, Salujinga.)

*Diagnosis*: As for the species but on average slightly larger than the typical subspecies in bodily dimensions as measured by fal, and especially in skull size, and with the following measurement ranges.

| | | | |
|---|---|---|---|
| fal | ♂♂ | 72.3 - 84.4 | (n = 91), |
| | ♀♀ | 72.8 - 83.0 | (n = 86); |
| gsl | ♂♂ | 39.3 - 43.8 | (n = 57), |
| | ♀♀ | 39.1 - 43.2 | (n = 58); |
| rl | ♂♂ | 14.8 - 16.2 | (n = 16), |
| | ♀♀ | 14.4 - 16.5 | (n = 14); |
| iow | ♂♂ | 6.3 - 7.9 | (n = 20), |
| | ♀♀ | 5.6 - 7.4 | (n = 19); |
| pow | ♂♂ | 7.2 - 9.3 | (n = 20), |

| | | | |
|---|---|---|---|
| | ♀♀ | 6.7 - 9.4 | (n = 20); |
| zw | ♂♂ | 22.8 - 26.7 | (n = 50), |
| | ♀♀ | 22.3 - 25.8 | (n = 46); |
| $C^1$-$C^1$ | ♂♂ | 7.7 - 8.7 | (n = 17), |
| | ♀♀ | 7.6 - 8.8 | (n = 16); |
| $M^2$-$M^2$ | ♂♂ | 12.1 - 13.6 | (n = 15), |
| | ♀♀ | 12.5 - 13.7 | (n = 14); |
| $C^1$-$M^2$ | ♂♂ | 14.7 - 16.7 | (n = 55), |
| | ♀♀ | 13.9 - 16.5 | (n = 53); |
| $C_1$-$M_3$ | ♂♂ | 17.0 - 18.5 | (n = 12), |
| | ♀♀ | 16.7 - 18.2 | (n = 15); |
| W | ♂♂ | 66 - 97 | (n = 35), |
| | ♀♀ | 65 -100 | (n = 43); |
| rl | ♂♂ | 36.5 - 38.2% of gsl | (n = 11), |
| | ♀♀ | 36.0 - 38.5% of gsl | (n = 11); |
| $C^1$-$C^1$ | ♂♂ | 18.8 - 20.6% of gsl | (n = 10), |
| | ♀♀ | 18.8 - 20.6% of gsl | (n = 11); |
| $M^2$-$M^2$ | ♂♂ | 28.8 - 32.2% of gsl | (n = 9), |
| | ♀♀ | 30.0 - 33.0% of gsl | (n = 11). |

Within *L. a. ruwenzorii*, there is not much variation, except that specimens from Sudan appear to have larger fals, on average, than those from more southern populations.

*Measurements:* For some additional measurements see table 1.

*Distribution:* Fig. 5.

*Related species:* See the account of the typical subspecies.

*Remarks*

Taxonomy: Eisentraut (1965) distinguished *L. a. ruwenzorii* on the basis of its larger skull and teeth dimensions and by the length of its fur, which was greater than in the specimens of *angolensis* and *smithii* he had before him.

The difference in average skull size has turned out somewhat less dramatic than Eisentraut concluded from his material. The type series came from rather high on Mount Ruwenzori (1575 m) and its fur length may be an adaptation to the lower temperatures at this altitude. (A possible difference may yet be found in the index of the second digit, which is relatively large in a specimen from Lwana, East Zaïre (table 1) but has not been measured in other spirit specimens of *ruwenzorii*.) *L. a. ruwenzorii* and *L. a. angolensis* are more similar to one another than either of these to one of the other subspecies.

Distribution and geographical variation: The most northern occurrence of *Lissonycteris angolensis ruwenzorii* is in the mountain range in southern Sudan. Going from there, it is found along the mountain ranges along the Western Rift towards the north tip of Lake Tanganyika, with a few known occurrences in Zaïre west of this range and some in southeast Zaïre and adjoining extreme northwest Zambia. Ansell (1978), in his thorough account of Zambian mammals, did not expect the species to occur further south in Zambia. A record from about 50-100 km south of Lake Tanganyika mapped but not dicussed by Kingdon (1974) has not been included by Ansell (1978) and has been left out in fig. 5 as well. Some localities near the Ugandan northwest coast of Lake Victoria and some of its islands are possibly connected with the Western Rift populations. Departing again from southern Sudan, the subspecies is found also along the eastern border of Uganda (although no specimens are known from the northern half of this border), from the Kenyan highlands (from where there may also be a connection with populations along the north and northwest coasts of Lake Victoria), and along the border with Tanzania towards the coast. In Tanzania, it is known as far south as Bunduki in the Uluguru Mountains. It may be expected to be found on other forested massifs of the eastern arc (compare the distributions of *Rousettus lanosus* O. Thomas, 1906 mapped as fig. 3 in Bergmans, 1994 and of *Myonycteris relicta* Bergmans, 1980 mapped in fig. 6 in the present paper).

Of 97 localities where the subspecies has been found, 15 are in forests: 8 in Drier types of Guineo-Congolian rain forest, 3 in Wetter types of the same, 2 in Transitional rain forest, 1 in Swamp forest, and 1 in Mangrove (types 2, 1a, 4, 8 and 77 in White, 1977); 62 are in forest transitions and mosaics: 34 in Undifferentiated Afromontane vegetation, 22 in Mosaic of Guineo-Congolian rain forest and secondary grassland, 6 in East African coastal mosaic (Zanzibar-Inhambane: 5, and Forest patches: 1) (types 19a, 11a, 16b and 16a in White, 1983); 13 are in bushland and thickets: 12 in Mosaic of East African evergreen bushland and secondary *Acacia* woodland, and 1 on the border of this and Somalia-Masai

*Acacia-Commiphora* deciduous bushland and thicket (types 45 and 42 in White, 1983); 5 are in woodlands: 2 in Wetter Zambezian miombo woodland (dominated by *Brachystegia*, *Julbernardia* and *Isoberlinia*), 2 in Sudanian woodland with abundant *Isoberlinia*, and 1 in Undifferentiated Sudanian woodland (types 25, 27 and 29a in White, 1983); and 2 in Mosaic of wetter Zambezian woodland and secondary grassland (type 31 in White, 1983).

### **Lissonycteris angolensis petraea** n. ssp.

*Rousettus aegyptiacus aegyptiacus* (not of E. Geoffroy-St. Hilaire, 1810); Dorst *et al.*, 1972: 394 (in part: the specimens from 10 km from Agaro and from Ghimbi).

*Rousettus aegyptiacus* (not of E. Geoffroy-St. Hilaire, 1810); Largen *et al.*, 1974: 228 (in part: the records from 10 km from Agaro and from Ghimbi).

*Rousettus angolensis*; Largen *et al.*, 1974: 229, 255.

*Rousettus angolensis ruwenzorii*; Largen *et al.*, 1974: 230.

#### *Material examined*

ETHIOPIA. Holotype specimen: 1 ♂, alc., skull, 10/13-VI-1968, 10 km from Agaro, at the road to Jimma, J. Dorst and party (MNHN CG 1972-482; field number 4017); paratype specimens: 5 ♂♂, 2 imm. ♂♂, 1 ♀, 2 imm. ♀♀, alc., skulls, same data as holotype specimen (MNHN CG 1972-482, field numbers 4018/19, -24, -27, -32, -44/46, -51 and ZMA 25.180, field number 4050).
Other material: Didessa River: 1 ♀, 2 ♂♂, alc. (BMNH 71.2446/47, 72.638). Ghimbi: 1 imm. ♂, 2 imm. ♀♀, alc., 27/30-IX-1971, J. Dorst and party (MNHN CG 1984-2074/76). Nur Moha-med Cave: alc. material (BMNH).

#### *Referred material (not examined)*

ETHIOPIA. Didessa: 2 specimens, alc., I-1972, J. S. Ash (USNM 497488/89); 1 specimen, 25-I-1973, J. S. Ash (USNM 497490).
(Doki River Bridge.)

*Diagnosis:* As for the species, but with small average body and skull dimensions, with a fal range in 8 ♂♂ of 72.7-76.3 (mean 74.2) and in 2 ♀♀ 71.7-73.5, and a gsl range in 6 ♂♂ of 38.5-41.3 (mean 39.7), and (antero-posteriorly) short and low canines and cheek teeth, the latter with relatively long outer ridges.
Compared with *L. a. angolensis* and *L. a. ruwenzorii*, smaller average body and skull dimensions and (antero-posteriorly) relatively shorter upper canines and shorter and lower upper cheek teeth with longer and more diverging outer cusps, or ridges, and $P^4$ and $M^1$ more squarish; larger lower cheek teeth equally low and also with relatively long outer cusps. Compared with *L. a. smithii*, slightly larger in average body and skull dimensions, upper incisors narrower and not sharply curved backward, upper and lower cheek teeth with relatively long outer cusps, $P^4$ with a well-developed inner cusp.

*Measurements:* Table 2. Some ratios are:
rl ♂♂ 37.1 - 38.3% of gsl (n = 6);
$C^1$-$C^1$ ♂♂ 17.9 - 18.7% of gsl (n = 5);
$M^2$-$M^2$ ♂♂ 27.3 - 30.5% of gsl (n = 5).

*Distribution:* Fig. 5.

*Related species:* See the account of the typical subspecies.

#### *Remarks*

Taxonomy: The Ethiopian populations of *L. angolensis* are geographically nearest to those in South Sudan, at a distance of about 600 km, identified as *L. a. ruwenzorii* and including the largest specimens of that subspecies: the fal range in 8 ♂♂ is 76.5-84.4 and in 8 ♀♀ 76.5-80.9; the gsl is c. 41.2 in 1 ♂ and 40.1-41.3 in 3 ♀♀.
The next nearest subspecies is *L. a. angolensis*, possibly represented at about 1500 km to the West, in the northern Central African Republic (fal of 1 ♂ 74.4, of 1 ♀ 75.1; Schlitter *et al.*, 1982), and still further west in Cameroun where specimens average larger (fal range in 4 ♂♂ 73.4-80.0 and in 12 ♀♀ 74.5-83.0; gsl in 1 ♂ 42.1 and in 4 ♀♀ 38.7-40.5) and, like *ruwenzorii*, differ in teeth morphology. In overall size *L. a. petraea* comes nearest to *L. a. smithii*, but it is separated from this by *L. a. angolensis* and differs in teeth morphology. The cheek teeth in the new subspecies show specific trends in their development. They are relatively weak by being shorter and lower, and at the same time retain long outer ridges (or cusps) instead of the short, more pointed cusps in the other sub-

Table 2. Selected measurements of type specimens of *Lissonycteris angolensis petraea* new subspecies, from 10 km from Agaro, at the road to Jimma, Ethiopia.

| | ♂♂ | | | | | | ♀ |
|---|---|---|---|---|---|---|---|
| | holotype MNHN 1972-482/4017 | | paratypes MNHN 1972-482/#4018-51 ZMA 25.180 | | | | paratype MNHN 1972-482/4019 |
| | | n | mean | min | - | max | |
| fal | 72.7 | 5 | 75.0 | 72.1 | - | 76.3 | 71.7 |
| E | 20.3 | 5 | 20.4 | 19.9 | - | 21.4 | 20.7 |
| HF | 20.8 | 5 | 20.5 | 18.6 | - | 22.0 | 19.8 |
| tibia | 32.0 | 5 | 32.0 | 31.4 | - | 32.5 | 31.4 |
| 3rd metacarpal | 54.6 | 5 | 56.1 | 55.0 | - | 56.5 | 52.0 |
| 5th metacarpal | 53.4 | 5 | 53.8 | 53.2 | - | 54.4 | 51.3 |
| gsl | 38.9 | 5 | 39.8 | 38.5 | - | 41.3 | — |
| cbl | 37.4 | 5 | 38.8 | 37.6 | - | 40.2 | — |
| rl | 14.5 | 5 | 14.9 | 14.3 | - | 15.4 | — |
| pl | 21.4 | 5 | 21.4 | 20.6 | - | 21.9 | — |
| mandible length | 30.0 | 5 | 30.8 | 29.5 | - | 31.6 | — |
| cranium width | 14.6 | 5 | 15.1 | 14.5 | - | 15.7 | — |
| iob | 6.0 | 5 | 6.7 | 6.5 | - | 7.0 | — |
| pob | 7.6 | 5 | 8.2 | 7.5 | - | 9.0 | — |
| zw | 22.3 | 4 | 23.0 | 22.1 | - | 23.3 | — |
| $C^1$-$C^1$ | 7.1 | 4 | 7.4 | 7.1 | - | 7.6 | — |
| $C^1$-$M^2$ | 14.7 | 5 | 14.9 | 14.5 | - | 15.3 | — |
| $M^2$-$M^2$ | 11.2 | 4 | 11.8 | 11.3 | - | 12.3 | — |
| $C_1$-$M_3$ | 16.2 | 5 | 16.4 | 16.0 | - | 16.7 | — |
| $P^3$ length | 2.1 | 6 | 2.25 | 2.1 | - | 2.5 | — |
| width | 1.65 | 6 | 1.7 | 1.6 | - | 1.8 | — |
| $P^4$ length | 2.3 | 6 | 2.6 | 2.4 | - | 2.8 | — |
| width | 1.9 | 6 | 2.1 | 1.9 | - | 2.25 | — |
| $M^1$ length | 2.4 | 6 | 2.35 | 2.1 | - | 2.6 | — |
| width | 1.9 | 6 | 1.9 | 1.75 | - | 2.1 | — |

species, and the inner cusp in $P^4$ is less obsolete than in *smithii*. The overall weakening of the dentition may indicate that this subspecies represents an old branch of the species, while the long outer ridges, which are probably a primitive character, may have persisted as an adaptation to specific food sources.

The palatal ridge pattern in *petraea* is 3 + 4 + 2 in nine, and 4 + 3 + 2 in two (including the holotype) out of 11 specimens. The sixth ridge is much reduced in two specimens. The specimen with field number 4018 has an $M^3$ measuring 0.9 x 0.95 on the left side, and the one with number 4024 an $M_4$ of 1.0 x 0.9 on the right side.

Distribution and geographical variation: The six known localities are all in or near montane rain forest in the southern Ethiopian highlands, at both sides of the Central Rift, with altitudes between 1190 and 2600 m (only of Doki River Bridge no altitude is known). Of the six localities, three are in East African evergreen and semi-evergreen bushland and thicket, two in

Undifferentiated Afromontane vegetation, and one in Undifferentiated Ethiopian woodland (types 38, 19a and 29b in White, 1983). The distribution area is separated from the areas of the subspecies *ruwenzorii* and *angolensis* by less favourable and probably uninhabitable vegetation types: towards the west mainly by a Transition from undifferentiated Ethiopian woodland to *Acacia* deciduous bushland and wooded grassland, and Edaphic grassland in the Upper Nile basin (types 35b and 61 in White, 1983), and towards the south mainly by Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (type 42 in White, 1983).

With the exception of the type series, the samples are insufficient to establish possible geographical variation.

Four specimens were infested with typical examples of the nycteribiid fly *Dipseliopoda biannulata* (Oldroyd, 1953).

*Etymology:* The new subspecies has been named in honour of Dr. Peter J. H. van Bree, former Curator of Mammalogy of the Institute for Systematics and Population Biology (Zoölogisch Museum) of the University of Amsterdam, under whose guidance the author laid the basis for his studies of African fruit bats. The names Peter and *petraea* are both derived from the Greek *petra*, in its meaning of rock in the metaphorical sense of a solid and trustworthy basis, but also referring to the subspecies' apparent confinement to the tormented relief of the Ethiopian plateau.

### **Lissonycteris angolensis goliath** n. ssp.

*Rousettus (Lissonycteris) angolensis*; Harrison, 1960: 65, 1961: 287; Meester *et al.*, 1986: 30.
*Rousettus angolensis*; Fenton, 1975; Hutton, 1986: 227.
*Rousettus angolensis angolensis*; Smithers *et al.*, 1976: 42, 1983: 65 (in part: records from Zimbabwe and Mozambique).
*Rousettus (Lissonycteris) angolensis angolensis*; Hayman *et al.*, 1971: 12 (in part: records from Rhodesia); Smithers *et al.*, 1979: 27 (in part: not the record from the Haroni/Lusitu River confluence); Koopman, 1994: 20 (in part: the record from Zimbabwe).

*Material examined*

ZIMBABWE. Holotype specimen: 1 ♀, skin, skull, 19-III-1970, Gleneagles, Inyanga, collected by M. Stuart Irwin and party (NHMBZ 59831; field number T1854); paratype specimens: 4 ♂♂, 1 imm. ♂, 2 ♀♀, 1 imm. ♀, skins, skulls, same data as for holotype specimen (HZM 16.7321, field number GNA/MP 1; NHMBZ 59826/29, -32/33 & ZMA 24.719, field numbers T1848/50, -52/53, -55/56).
Other material: Umtali: 1 ♂, skin, skull, 18-VI-1960, R. H. Smithers (HZM 15.3219).

*Referred material (not examined)*

MOZAMBIQUE.
(Western boundary of Vila Pery District, 1832Bd, 1832Dc, 1833Cc.)
ZIMBABWE.
(Birchenough Bridge at Sabi River.)

*Diagnosis:* As for the species, but with large body, skull, and teeth dimensions, with fal ranges of 81.9-87.5 in 4 ♂♂ and 82.1-89.6 in 3 ♀♀ and gsl ranges of ≥43.3-46.0 in 4 ♂♂ and ≥42.2-45.8 in 3 ♀♀, and (antero-posteriorly) long cheek teeth with rather distinct heels anterior and posterior to the outer cusps.

*Measurements:* Table 3. Some ratios are:

| | | | |
|---|---|---|---|
| rl | ♂♂ | 37.2 - 38.0% of gsl | (n = 2), |
| | ♀♀ | 38.2% of gsl | (n = 1); |
| $C^1$-$C^1$ | ♂♂ | 17.4 - 20.4% of gsl | (n = 2), |
| | ♀♀ | 19.0% of gsl | (n = 1); |
| $M^2$-$M^2$ | ♂♂ | 29.1 - 30.1% of gsl | (n = 2), |
| | ♀♀ | 29.4% of gsl | (n = 1). |

*Distribution:* Fig. 5.

*Related species:* See the account of the typical subspecies.

*Remarks*

Taxonomy: The seven known localities are all in or near the border area of Zimbabwe and Mozambique, between 18 and 20 30 S and at a distance of about 1000 km from the nearest known populations of *L. a. ruwenzorii.* Ansell (1967, 1974) recorded representatives of the species, here included in *ruwenzorii*, from extreme northwest Zambia and, in 1978 the same author remarked that, apart from northeast Zambia it was perhaps unlikely to occur elsewhere in the

Table 3. Selected measurements of type specimens of *Lissonycteris angolensis goliath* new subspecies, from Gleneagles (Estate) and a specimen from Umtali (NHMBZ 59826/33; ZMA 24.719; HZM 15.3219, 16.7321); mc = metacarpal length; mand = mandible length; cran = cranium width.

| | ♂♂ Gleneagles | | | ♂ Umtali | ♀♀ Gleneagles | | |
|---|---|---|---|---|---|---|---|
| | n | mean | min - max | | holotype NHMBZ 59831 | NHMBZ 59830 | NHMBZ 59832 |
| fal | 3 | 84.7 | 81.9 - 87.5 | c.82 | 89.6 | 82.1 | 83.8 |
| HF | 4 | 24.4 | 23.6 - 25.1 | | 22.5 | 23.9 | 23.4 |
| 3rd mc | 4 | 61.3 | 57.9 - 64.5 | 60.2 | 64.2 | 61.6 | 58.8 |
| 5th mc | 4 | 57.6 | 54.0 - 59.7 | 57.3 | 60.8 | 57.6 | 60.8 |
| gsl | 3 | | ≥43.3 - ≥45.3 | 46.0 | 45.8 | ≥42.3 | ≥42.2 |
| cbl | 2 | | 42.0 - 44.3 | 45.0 | 44.5 | — | 41.5 |
| rl | 3 | 16.8 | 16.2 - 17.2 | 17.5 | 17.5 | 16.1 | 16.0 |
| pl | 3 | 24.4 | 23.6 - 25.7 | 25.5 | 25.1 | 23.1 | 22.9 |
| mand | 3 | 34.5 | 33.9 - 35.2 | 35.3 | 35.0 | 33.0 | 33.0 |
| cran | 4 | 17.0 | 16.6 - 17.7 | 17.5 | 16.7 | 16.3 | 16.3 |
| iow | 4 | 8.0 | 7.0 - 8.6 | 7.1 | 7.3 | 7.1 | 7.4 |
| pow | 4 | 9.1 | 8.8 - 9.4 | 8.6 | 8.0 | 7.2 | 9.0 |
| zw | 3 | 26.1 | 24.6 - 27.9 | 26.6 | 26.0 | 25.7 | 25.7 |
| $C^1$-$C^1$ | 4 | 8.7 | 8.4 - 8.9 | 8.0 | 8.7 | 8.5 | 8.3 |
| $C^1$-$M^2$ | 4 | 16.5 | 16.3 - 17.0 | 16.5 | 17.6 | 16.6 | 15.6 |
| $M^2$-$M^2$ | 3 | 13.3 | 13.1 - 13.6 | 13.4 | 13.5 | 13.5 | 13.1 |
| $C_1$-$M_3$ | 4 | 18.4 | 18.2 - 18.8 | | 19.6 | 18.3 | 17.2 |
| $P^3$ length | 5 | 2.5 | 2.25- 2.65 | 2.9 | 2.8 | 2.65 | 2.75 |
| width | 5 | 2.0 | 1.9 - 2.0 | 1.9 | 2.15 | 2.15 | 2.1 |
| $P^4$ length | 5 | 3.2 | 3.1 - 3.3 | 3.3 | 3.3 | 3.25 | 2.9 |
| width | 5 | 2.4 | 2.25- 2.6 | 2.25 | 2.5 | 2.65 | 2.6 |
| $M^1$ length | 5 | 2.9 | 2.8 - 3.0 | 2.8 | 3.0 | 3.15 | 2.8 |
| width | 5 | 2.3 | 2.1 - 2.5 | 2.1 | 2.5 | 2.4 | 2.5 |

country. Other *ruwenzorii* specimens are known from southeast Zaïre (fig. 5). With fal ranges of 72.3-84.4 in ♂♂ and 72.8-83.0 in ♀♀ and gsl ranges of 39.3-43.8 in ♂♂ and 39.1-43.2 in ♀♀, *ruwenzorii* averages very distinctly smaller than *goliath*. No fruit bats have been recorded from the northeast zone of Zimbabwe (Bergmans, 1988, fig. 1), and the new subspecies' characteristics strongly suggest its prolonged isolation from the Central and East African populations of *angolensis*. Apart from its larger size, its premolars and molars, especially $P^3$, $P^4$, $M^1$ and $P_4$, $M_1$ and $M_2$, are relatively longer, with in lateral view more distinct heels anterior and posterior to the outer cusps, which themselves are relatively obtuse. The difference in size between $M^1$ and $M^2$ is generally smaller than in the smaller subspecies *smithii* and *petraea*. As a consequence of the longer cheek teeth, the interstices between them are relatively short.

Harrison (1960), who described the first specimen of *Lissonycteris angolensis* from this region, already remarked on its exceptional size when compared to specimens from Kenya, and refrained from describing a new subspecies only because of the limited material. Smithers *et al.* (1979) gave some rounded measurements of specimens from Zimbabwe but did not comment on them.

The palatal ridge pattern has been preserved only in the specimen from Umtali and is typically 3 + 4 + 2.

Distribution and geographical variation: Harrison recorded a specimen from Umtali (= Mutare; square code 1832Dc, or 1832D3), Zimbabwe. Smithers *et al.* (1976) recorded specimens from along the western boundary of Vila Pery District in Mozambique. They did not mention specific localities (nor where their specimens have been deposited), but on their map the squares 1832Bd, 1832Dc, 1833Cc and 2032Bb have been marked. (From the localities mentioned in their gazetteer, only Machipanda corresponds with 1832Dc and Chemezi with 1833Cc.) Smithers *et al.* (1979) added Birchenough Bridge on Sabi River (1932Cd) and Gleneagles (1832Bd), both in Zimbabwe, as collecting localities for *Lissonycteris angolensis*. They also mentioned material from the Haroni/Lusitu River, but this actually represents *Myonycteris relicta* Bergmans, 1980 (see present paper).

The distribution appears to be confined to the escarpment region in the border area of Zimbabwe and Mozambique, between 17 and 21 S, with known occurences from between 200 and 500 m (Birchenough Bridge) to 1800 m (Gleneagles). Smithers *et al.* (1979) reported that the specimen from Umtali had been taken in an old, established suburban garden with trees and shrubs, where it was feeding on guavas among many *Epomophorus wahlbergi* (Sundevall, 1846), but that two of the other localities were associated with evergreen forest (one of these probably the Haroni/Lusitu River confluence from where the species was incorrectly recorded). According to White (1983) the localities are all associated with forest mosaics, forest transitions or woodland: 2 are in Undifferentiated Afromontane vegetation (type 19a), 1 is in Drier Zambezian miombo woodland (dominated by *Brachystegia* and *Julbernardia*) (type 26), 1 in *Colophospermum* mopane woodland and scrub woodland (type 28), and 3 in either type 19a, or 16, or 26, in which 16(a) is East African Zanzibar-Inhambane coastal mosaic. Its restricted distribution would suggest that geographical variation within this subspecies is unlikely.

*Etymology:* The specific epithet *goliath* has been chosen in honour of Dr. David L. Harrison, who would have 'mastered' this Goliath long ago if he had had more specimens. Of course, it also refers to the subspecies' exceptionally large dimensions.

## **Myonycteris** Matschie, 1899

*Myonycteris* Matschie, 1899: 61, 63 (as a subgenus of *Xantharpyia* Gray, 1843; type species *Cynonycteris torquata* Dobson, 1878); Andersen, 1907b: 511, 1912: 576; Lawrence *et al.*, 1963; Rosevear, 1965: 119; Bergmans, 1976, 1980a: 172.

*Phygetis* Andersen, 1912: 579; Bergmans, 1976; Koopman, 1994: 21.

*Phylletis*; Juste *et al.*, 1993: 222.

As Andersen (1912) explained, *Myonycteris* was originally described by Matschie (1899) as a subgenus of *Xantharpyia* Gray, 1843, including two species, *M. torquata* Dobson, 1878 and *M. angolensis* (Bocage, 1898). The former species, though not known to Matschie from personal inspection, was fixed as type of the "subgenus", but the diagnosis of the subgenus was based on the latter species, which however was recognized as belonging to the genus *Rousettus* Gray, 1821 by Andersen (1912) and which is treated as an independant genus by the present author. The first clear diagnosis of *Myonycteris* was compiled by Andersen (1912) and, together with the earlier account of the genus *Lissonycteris* in the present paper, in which this is differentiated from *Rousettus* and *Myonycteris*, served as the basis for the following short description.

A genus of small to rather small fruit bats, with a total fal range of 54.9-75.1 (three species known); an only very slightly deflected, low braincase; large orbits; premaxillae seldom co-ossified; a specialized rostrum with a more or less distinct level change in the alveolar line; relatively large orbits; oblong cheek teeth with relatively heavy $P^4$ and $P_4$ and reduced or absent $M_3$; broad wings, inserted at second toe; relatively short tibiae; partially webbed toes; palatal ridge pattern normally 3 + 4 + 2, 4 + 3 + 2, or 3 + 3 + 2; a ruff of specialized hairs in adult males. Measurement ranges and ratios for the species combined:

| | |
|---|---|
| fal | 54.9 - 75.1; |
| gsl | 30.2 - 39.2; |
| rl | 10.1 - 15.1; |
| $C^1$-$C^1$ | 5.8 - 7.8; |
| $M^2$-$M^2$ | 7.6 - 10.5. |

Andersen (1912) classified *Myonycteris* as a member of his *Cynopterus* section, but Simpson (1945) classed it as a synonym of *Rousettus* Gray, 1821. Lawrence *et al.* (1963) argued that *Myonycteris* and *Lissonycteris* are narrowly related and pointed out the distinctness of a myonycterine section, containing these two genera, from both the cynopterine and rousettine sections, and stressed that the myonycterine section is more closely related to the epomophorine section. The genus *Myonycteris* was revised by Bergmans (1976). He synonymized the subgenus *Phygetis* Andersen, 1912 with *Myonycteris* and recognized two species, *M. torquata* (Dobson, 1878) and *M. brachycephala* (Bocage, 1889). In 1980 he described a third species, *M. relicta.* Koopman (1994) retained the subgenus *Phygetis.*

### **Myonycteris torquata** (Dobson, 1878)

*Cynonycteris torquata* Dobson, 1878: 71, 76 (type locality: Angola; restricted to the "Lower Cuanza Region" by Bergmans, 1976, and further to the area of Golungo Alto by Crawford-Cabral, 1989); Jentink, 1888a: 52.

*Xantharpyia (Myonycteris) torquata*; Matschie, 1899: 64.

*Rousettus torquatus*; Miller, 1907: 54.

*Myonycteris collaris*; Andersen, 1907b: 512 (in part: not including Sao Tomé).

*Myonycteris wroughtoni* Andersen, 1908c: 450 (type locality: River Likandi), 1912: 580 (spelling of type locality name ammended: River Likati); J. A. Allen *et al.*, 1917: 422; Lang *et al.*, 1917: 511; Schouteden, 1944: 107; Benedict, 1957: 353; Verschuren, 1957: 213; Eisentraut, 1963: 64; Koopman, 1965: 4; Brosset, 1966a: 366, 1966c: 134; Hayman *et al.*, 1966: 29; Verschuren, 1967; Bergmans, 1976: 190.

*Myonycteris leptodon* Andersen, 1908c: 450 (type locality: Sierra Leone), 1912: 580; Rosevear, 1965: 121; Bergmans, 1976: 190.

*Myonycteris (Myonycteris) torquata*; Andersen, 1912: 581; Koopman, 1994: 21.

*Myonycteris torquata*; Hill *et al.*, 1941: 30; Schouteden, 1944: 107; Eisentraut, 1963: 63; Rosevear, 1965: 120; Brosset, 1966a: 366, 1966b: 58, 1966c: 134; Ansell, 1967: 3; Mumford, 1970; Jones, 1971: 129; Bergmans *et al.*, 1974: 39; Vielliard, 1974: 977; Jeffrey, 1975: 955; Bergmans, 1976: 190; Gallagher *et al.*, 1977: 25; Ansell, 1978: 18; Happold *et al.*, 1978: 121; Bergmans, 1979: 168, 1980; Haiduk *et al.*, 1980, 1981; Honacki *et al.*, 1982: 118; Hutterer *et al.*, 1976: 124; Marshall *et al.*, 1982: 56; Schlitter *et al.*, 1982: 152; Emmons *et al.*, 1983; Hill, 1983: 56; D. W. Thomas, 1983: 2269; Dobat *et al.*, 1985; Happold, 1987: 47; Hickey *et al.*, 1987; Roth *et al.*, 1988: 184; Crawford-Cabral, 1989: 10; Koopman, 1989: 2; Dowsett *et al.*, 1991: 255; Mickleburgh *et al.*, 1992: 80; Heller *et al.* (1994: 7); Juste *et al.*, 1994a: 275; Cosson (in press).

*Myonycteris torquatus*; Krumbiegel, 1942: 340; Eisentraut, 1964: 535.

*Myonycteris torquata leptodon*; Kuhn, 1965: 325; De Vree *et al.*, 1969: 204, 1971: 161; De Vree, 1971: 38; Coe, 1976: 542; Verschuren, 1977: 619; Wolton *et al.*, 1982: 423.

*Myonycteris (Myonycteris) torquata torquata*; Hayman *et al.*, 1971: 12; Koopman, 1994: 21.

*Myonycteris (Myonycteris) torquata leptodon*; Hayman *et al.*, 1971: 12; Koopman, 1994: 21.

*Myonycteris (Myonycteris) torquata wroughtoni*; Hayman *et al.*, 1971: 12; Koopman, 1994: 21.

*Myonycteris torquatus torquatus*; Eisentraut, 1973a: 34.

*Myonycteris torquata wroughtoni*; Kingdon, 1974: 139.

*Myonycteris torquate*; Kityo, 1993: 24.

#### *Material examined*

ANGOLA. "Angola": 1 ♂, alc., skull, 1853-1860, F. Welwitsch (lectotype specimen of *Cynonycteris torquata* Dobson, 1878; BMNH 66.1.20.4).

CAMEROUN. 30 km W of Bertoua: 8 ♀♀ (1: alc.), 1 imm. ♀, 19/23-IV-1972, L. W. Robbins (AMNH 240998/1005, 241093). Bitye: 1 ♂, 1 ♀, no date & 13-X-1910, G. L. Bates (BMNH 13.9.12.2/11.5.5.3). Ebolowa: 1 imm. ♂, alc., skull, 1913, G. Schwab (AMNH 54426). Eseka: 1 ♂, 2 ♀♀, 16/24-VI-1973, L. W. Robbins (AMNH 236236/37, -39). 5 km SW of Eseka: 11 ♂♂, 1 imm. ♂, 5 ♀♀, 3 imm. ♀♀, 16-VI/4-VII-1973, 28-VI/5-VII-1974, L. W. Robbins and party (AMNH 236240/46, -48/52; CMNH 40949/51, -53/57); 6 km SE of Eseka: 1 ♂, 1 ♀, 31-V-1974, L. W. Robbins (AMNH 236253/54). Kanyol: 1 ♂, skin, 16-VI-1932, F. G. Merfield (BMNH 33.8.4.19). Koutaba: 1 ♀, alc., 20-V-1973, J. Prévost (MNHN CG 1979-292). Lolodorf: 1 ♂, 20-III-1914, J. A. Reis (CMNH 3651). Mey Joss: 1 specimen, 11-VII-1932, F. G. Merfield (BMNH 33.8.4.20). Ngobilo: 1 imm., 11-IX-1931, J. A. Reis (FMNH 43576).

Ntui: 1 imm., alc., 11-XI-1973, J. Prévost (MNHN CG 1979-285). Obala: 1 imm., 2-V-1933, F. G. Merfield (PCMB 514). Yaoundé: 8 ♂♂, 5 imm. ♂♂, 7 ♀♀, 4 imm. ♀♀, alc., 28-II/21-X-1973, J. Prévost (MNHN CG 1979-286/91, -293/310). "Cameroun": 1 ♂, alc., skull, Strickland (BMNH 50.8.29.1).

(Bota, 2 km W of Buea, Campo Faunal Reserve, Isobi, Kumba, Lake Barombi, 40 km N of Lomié, Marienberg, S of Minim, Mueli, Mukonje, Ngaoundere, Tote Tea Forest nr Buea.)

CENTRAL AFRICAN REPUBLIC. La Maboké: 10 ♂♂ (7: alc., skulls of 7), 23 ♀♀ (17: alc., skulls of 17), 11 imm. ♀♀, spring 1966, 10/28-V-1966, R. Pujol/P. Teocchi, and VII-1968, Quentin (MNHN CG 1972-654/97).

(Bamingui-Bangoran National Park.)

CONGO. Dimonika: 7 ♀♀ (2: formol), 5 specimens (2: formol), 8-III/14-VI-1970 and 10/13-III-1972 (UBRA). Makaba: 2 specimens, formol, 12-III-1970 and 12-III-1972 (UBRA). Odzala: 1 imm. ♀, alc., skull, 1-XI-1963, A. Descarpentries & A. Villiers (MNHN). Pointe Noire: 1 ♂, 28-XI-1972, W. Bergmans (ZMA 15.423). Sibiti: 1 ♀, alc., skull, 25-XI-1963, A. Descarpentries/A. Villiers (MNHN). "Congo": 1 specimen, formol, 13-III-1972 (UBRA).

(Bena, ? Brazzaville, Koubotchi, col du Mont Bamba.)

EQUATORIAL GUINEA.

(Ikunde.)

FERNANDO POO. Musola: 1 ? ♀, skin, 9-IX-1939, H. Eidman (ZMB 58892).

GABON. Belinga: 10 ♂♂, 3 imm. ♂♂, 7 ♀♀, 2 imm. ♀♀, XII-1962/III-1964, J. Dragesco/Mission Biologique au Gabon (MNHN; ZMA 20.649/57); 1 ♀, alc., 1-II-1964, P. J. H. van Bree (ZMA 7802); ? Belinga: 1 ♀, 3-XII-1962, Mission Biologique au Gabon (MNHN). Bengoué: 1 imm. ♂, 28-III-1964, Mission Biologique au Gabon (ZMA 20.648). Makokou: 1 imm. ♂, 1 ♀, 1 imm. ♀, 1/2-XII-1965, Mission Biologique au gabon (MNHN; ZMA 20.647).

(? Ntyonga.)

GHANA. Aburi: 1 ♂, alc., Mission Dieterlin (NMBA). 6 miles N of Kade: 5 ♂♂, 1 ♀, 29-III-1968, J. C. Geest (USNM 414785/89, -91). Kumasi: 3 ♂♂, 2 imm. ♂♂, 1 ♀, 3 imm. ♀♀, 29-IV/23-VI-1965, D. H. Barry (BMNH 65.6220/27, 65.743). 32 miles W of Prestea: 2 ♂♂, 7 imm. ♂♂, 9 ♀♀, 9 imm. ♀♀, 7/13-I-1968, J. C. Geest (USNM 413755/64, -70/74, -80/84, -90/94, 413803/04).

(Akosombo, Bia tributaries North Forest Reserve, Bimpong Forest Reserve, Kade, 7 miles NE of Kade, Krokosua Hills, Kumawu, Legon, Mole Game Reserve, Pampramase, Sefwi Asemparaye, Sefwi Wiawso.)

GUINEA. Kouroussa: 1 imm. ♀, alc., skull, ≤ 1902, Pobeguin (MNHN CG 1902-21). Mont Richard Molard: 1 ♀, 7-I-1966, J. Verschuren (IRSN 16848).

IVORY COAST. Banco Forest: 1 ♀, 29-V-1969, L. W. Robbins (USNM 467878). Bolo: 4 ♂♂ (2 without skulls), 3 ♀♀, 2 imm. ♀♀, 2 imm. (1: skin only), 31-I/2-II-1973, J. Vissault (ZMA 16.960/65; MNHN). Lamto: 5 ♂♂ (3: alc., skulls of 3), 3 ♀♀ (alc., skulls of 2), 2 imm. ♀♀ (alc., one without skull), 14-V/5-VI-1964, L. Bellier (ZMA 16.941/46; MNHN); 11 ♂♂, 2 imm. ♂♂, 3 ♀♀, 8 imm. ♀♀, 27-V/6-XII-1970, J. Vissault (ZMA 16.947/59; MNHN). Saubre: 1 ♀, 14-VI-1969, L. W. Robbins (USNM 467764). "Ivory Coast": 1 ♂, 3 skulls, 2 imm., ORSTOM (MNHN).

(Adiopodoumé, Tai Forest, Wango-Fitini.)

LIBERIA. Mount Nimba: 6 ♂♂, 2 imm. ♂♂, 4 ♀♀, 3 imm. ♀♀, 14/19-VII-1966, M. J. Coe (BMNH 67.1436/50); 48 ♂♂, 82 ♀♀, alc., 16 skins, 12 skulls, from various locations on Mount Nimba, XII-1965/III-1966, J. Verschuren (IRSN 16798/99, 16800/29, -31/47, -49/99, 16910/28). Schieffelinsville: 1 ♂, 14-VIII-1884, F. X. Stampfli (RMNH 17359). Tars Town ("25 km N of Tchien"): 1 ♂, 2 ♀♀, 31-VII/1-VIII-1971, L. W. Robbins (AMNH 239350/52).

(Bagalugu (Lofa), Douoba, Grassfield, Iti, Juarzon, Old Mine Road, Pelokehn, Salayea, Saniquellie, Sino, Teaye, Zigida.)

NIGERIA. Felele: 1 ♂, 19-V-1967, J. C. Geest (USNM 402316). Ibadan: 1 ♂, XII-1965, H. J. Herbert (USNM 377094); 1 ♂, 1 imm. ♂, 1 imm. ♀, cf. X/XI-1966, J. Menzies (BMNH; NHMI); 2 ♂♂ (1: alc.), 5-XI-1966 & 21-V-1967, J. C. Geest (BMNH; USNM 402317). Sapoba: 1 ♀, alc., D. C. D. Happold (BMNH).

SIERRA LEONE. "Sierra Leone": 1 ♂, ≤ 1891, J. Hickman (holotype specimen of *Myonycteris leptodon* Andersen, 1908; BMNH 91.2.13.1).

UGANDA. Bwamba Forest: 1 ♀, XI-1957, "WFVZ 28" (LACM 31775). Mwela, Bugoma Forest: 2 ♂♂, 1 imm. ♀, 10-XII-1967, A. L. Archer (LACM 51637/39). Ntandi: 1 imm., 27-VII-1967, A. L. Archer (LACM 51640).

ZAIRE. Congo-Nil-Aka: 1 ♂, 20-V-1952, Mission H. de Saeger (MRAC 13525). Gangala-na-Bodio: 1 imm. ♂, 11-V-1948, Mission Hediger-Verschuren (MRAC 11657). Kamikoni: 1 ♀, 17-V-1960 (IRSN 1.694). Kananga (Luluabourg): 2 ♂♂, 1-IV-1965, De Roo (MRAC 33413/14). Karambi: 1 imm. ♀, alc., 4-IV-1992, N. Masumbuko Kamitongo (ZMA 24.567). Kinshasa: 3 ♂♂, 10-I/2-V-1962, A. F. de Bont (MRAC 31197/99); 1 imm., 2-V-1964, J. van Orshoven (ZMA 11.163). Kumbi: 2 ♂♂, alc., 7-XII-1993, N. Masumbuko Kamitongo (ZMA 24.896/97). Likati (River): 2 ♂♂, 18-IV-1906, Alexander-Gosling expedition (holotype and paratype specimens of *Myonycteris wroughtoni* Andersen, 1908; BMNH 7.7.8.25/.26). Lwana: 1 ♂, alc., 12/20-IV-1992, N. Masumbuko Kamitongo (ZMA 24.568). Medje: 1 ♂, 2 ♀♀, 1 imm. ♀, 16-IV-1910/4-IV-1914, H. Lang/J. P. Chapin (AMNH 48752/55).

"Near Congo": 1 imm., ≤ 1870, Currer (paralectotype of *Cynonycteris torquata* Dobson, 1878; BMNH 43.9.27.2).

(Nr Babeke, Irangi, Scieri Forest 30 km SW of Kindu.)

ZAMBIA. Salujinga: 2 ♂♂, 15-XI-1964, C. W. Benson (BMNH 65.534/35).

*Diagnosis:* A small member of the genus, inhabiting the forests of West and Central Africa, with a fal range of 54.9-67.1 and a gsl range of 30.2-35.8; relatively weak and simple dentition, with strongly reduced $P^1$, $M^2$ and $M_2$ and outer and inner of ridge $P_4$ fused anteriorly; a palatal ridge pattern of 3 + 4 + 2 (but variants not exceptional).

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

| | | | |
|---|---|---|---|
| fal | ♂♂ | 55.7 - 65.4 | (n = 97), |
| | ♀♀ | 54.9 - 67.1 | (n = 86); |
| gsl | ♂♂ | 30.6 - 35.8 | (n = 65), |
| | ♀♀ | 30.2 - 35.2 | (n = 58); |
| rl | ♂♂ | 10.3 - 12.9 | (n = 61), |
| | ♀♀ | 10.1 - 12.7 | (n = 56); |
| iow | ♂♂ | 4.9 - 7.8 | (n = 60), |
| | ♀♀ | 4.8 - 6.6 | (n = 57); |
| pow | ♂♂ | 6.1 - 9.6 | (n = 59), |
| | ♀♀ | 6.1 - 9.6 | (n = 57); |
| zw | ♂♂ | 18.3 - 21.6 | (n = 47), |
| | ♀♀ | 18.2 - 21.3 | (n = 48); |
| $C^1$-$C^1$ | ♂♂ | 5.9 - 7.3 | (n = 50), |
| | ♀♀ | 5.8 - 7.8 | (n = 35) |
| $M^2$-$M^2$ | ♂♂ | 8.0 - 10.0 | (n = 57), |
| | ♀♀ | 7.6 - 10.1 | (n = 47); |
| $C^1$-$M^2$ | ♂♂ | 11.3 - 13.3 | (n = 59), |
| | ♀♀ | 11.0 - 12.9 | (n = 53); |
| $C_1$-$M_3$ | ♂♂ | 12.3 - 14.7 | (n = 58), |
| | ♀♀ | 12.2 - 14.4 | (n = 53); |
| W | ♂♂ | 27 - 51 | (n = 48), |
| | ♀♀ | 31 - 60 | (n = 32); |
| rl | ♂♂ | 31.9 - 36.8% of gsl | (n = 52), |
| | ♀♀ | 32.2 - 36.6% of gsl | (n = 68); |
| $C^1$-$C^1$ | ♂♂ | 17.3 - 22.6% of gsl | (n = 44), |
| | ♀♀ | 18.4 - 23.6% of gsl | (n = 30); |
| $M^2$-$M^2$ | ♂♂ | 24.0 - 31.6% of gsl | (n = 52), |
| | ♀♀ | 23.5 - 30.1% of gsl | (n = 42). |

The weight range for ♀♀ includes at least 5 pregnant specimens with weights of 33, 36, 45, 45 and 54.

*Measurements:* For some additional measurements see table 1.

*Distribution:* Fig. 6.

*Related species: Myonycteris brachycephala* differs in having a stronger skull and heavier and more differentiated cheek teeth. *M. relicta* is larger, with a fal range of 65.9-75.1 and a gsl range of 35.5-39.2, and lacks $M_3$. All subspecies of *Lissonycteris angolensis* are larger, with combined fal ranges of 67.8-88.0 and gsl ranges of 36.4-46.4, and have squarish $P^4$ and $M^1$ and much less reduced last molars. The superficially resembling species of *Rousettus* are also larger, the sympatric *R. egyptiacus* subspecies and *R. lanosus* having fals above 85 and gsls above 38.

*Remarks*

Taxonomy: *Myonycteris torquata* includes *M. wroughtoni* described from northeastern Zaïre and *M. leptodon* described from Sierra Leone, previously retained as subspecies by many authors, but thought to be untenable as such by Bergmans (1976), who concluded the following: "*wroughtoni* differs mainly from *torquata* by somewhat larger absolute greatest skull length (averages in the two sexes 0.9 and 1.2 mm higher) and absolute forearm length (averages 1.6 and 1.7 mm higher), and by a larger relative $M^2$ length (...); *leptodon* differs from *torquata* by larger absolute greatest skull length (averages 1 and 1.2 mm higher) and absolute forearm length (averages 0.8 and 1 mm higher), by very slightly larger relative rostrum length and interorbital width, by somewhat smaller relative lengths of $P^4$, $M^1$ and possibly $P_4$ and $M_1$, by larger relative $M^2$ length, and possibly by smaller relative ear length and larger relative metacarpal length; *leptodon* differs from *wroughtoni* by smaller absolute forearm length (average 0.6 and 0.9 mm lower), by slightly larger relative interorbital width, possibly by smaller relative lengths of $P^4$, $M^1$, $P_4$ and $M_1$, by larger relative $M_2$ length and possibly by smaller relative ear length." Bergmans (1976) concluded that several of Andersen's (1908, 1912) observations regarding specific differences between *torquata*, *wroughtoni* and *leptodon* do not hold, while those that, to a certain degree, could be confirmed, were insufficient as differential characters to warrant the recognition of subspecific divisions within *M. torquata*, and proposed to synonymize *wroughtoni* and *leptodon* with *torquata*. Koopman (1994) retained them as subspecies.

From an analysis of the collector's travels Bergmans (1976) had concluded that the holotype specimen of *M. torquata* had been collected in northwest Angola, in the "Lower Cuanza Region" (north of the lower Cuanza River).

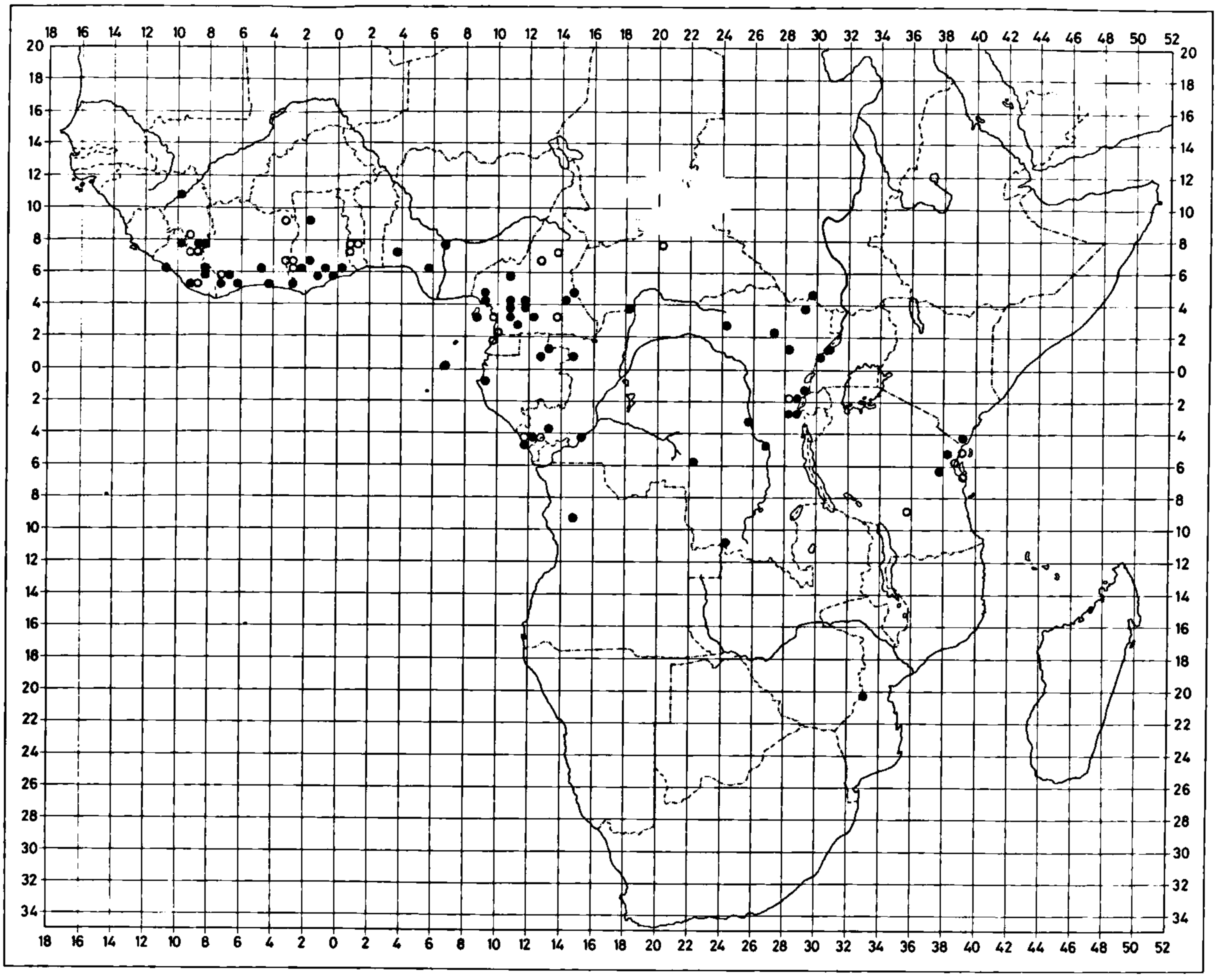

Fig. 6. Distribution of *Myonycteris* Matschie, 1899. African mainland west of 32 E and Fernando Poo: *M. torquata* (Dobson, 1878); Sao Tomé: *M. brachycephala* (Bocage, 1889); African mainland east of 32 E: *M. relicta* Bergmans, 1980. Black dots: squares from which material has been identified by the author. Open circles: records from literature and correspondence.

Crawford-Cabral (1989), having first-hand knowledge of the region, proposed the area of the village of Golungo Alto in this region as the most probable collecting site, as it is situated in the southern part of the "medium moist" Dembo Forest. As this is the only area where the collector passed through vegetation of type 11a in White (1983), Mosaic of Guineo-Congolian lowland rain forest and secondary grassland, all other areas being woodlands or drier types, this conclusion is here supported. The collecting date then becomes IX-1854/11-X-1856.

Distribution and geographical variation: Since Bergmans' revision of the genus and its distribution (1976), *M. torquata* has been collected from many new localities. The species' distribution appears to be continuous from Guinea to Central Nigeria and possibly to Cameroun. The Nigerian gap has been reduced but no specimens are known from east of the Niger. Juste *et al.* (1994a) confirmed the species' occurrence in Bioko Island (formerly Fernando Poo). In Cameroun the species is found all through the forest zone, with extensions into Equatorial Guinea, Gabon and the Central African Republic. There may be a gap between the North-Gabonese and Congolese/Angolan populations, and there are still not many localities known which tend to connect all the mentioned areas with those in east and southeast

Zaïre. In Bergmans (1976), collecting localities have been plotted on the then available vegetation map of Africa (Keay, 1959). Most were in "moist forest at low and medium altitudes" and in the surrounding "forest-savanne mosaic and woodlands" and "savannas, relatively moist types". The highest collecting altitude known was 800 m. For the present paper, 93 collecting localities could be located with sufficient accuracy to determine vegetation types according to White (1983): 29 are in Guineo-Congolian lowland rain forest: wetter types, 28 in drier types of the same, and 9 in Mosaic of these two (types 1a, 2 and 3, respectively); 2 are in transitional rain forest (type 4), 16 in Mosaic of Guineo-Congolian lowland rain forest and secondary grassland (type 11a), 3 in Undifferentiated Afromontane vegetation (19a); and 1 is in Wetter Zambezian miombo woodland (dominated by *Brachystegia, Julbernardia* and *Isoberlinia*), 4 are in Sudanian woodland with abundant *Isoberlinia*, and 1 is in Undifferentiated Sudanian woodland (types 25, 27 and 29a, respectively). The 6 finds in woodlands, some of which are very near forest or forest mosaic types, may be connected with annual migratory movements as discovered for *M. torquata* in Ivory Coast by D. W. Thomas (1983). A recent observation by Cosson (in press) may shed some light on the relative rarity of this species in ground level mist net catches. In southwest Cameroun he caught many specimens in the canopy between 15 and 30 m.

### **Myonycteris brachycephala** (Bocage, 1889)

*Cynonycteris brachycephala* Bocage, 1889a: 197-198 (type locality: St. Thomé), 1898: 138, 1905: 66.

*Cynonycteris brachycephalus*; Seabra, 1898b: 170.

*Xantharpyia (Xantharpyia) brachycephala*; Matschie, 1899: 65, 66.

*Myonycteris collaris*; Andersen, 1907b: 512 (in part: the specimen from Sao Tomé).

*Rousettus brachycephala*; Miller, 1907: 54.

*Myonycteris (Phygetis) brachycephala*; Andersen, 1912: 582; Hayman *et al.*, 1971: 13; Koopman, 1994: 21.

*Myonycteris brachycephala*; Bergmans, 1976, 1980: 173; Honacki *et al.*, 1982: 118; Feiler, 1984: 76; Mickleburgh *et al.*, 1992: 79; Juste *et al.*, 1993.

*Material examined*

SAO TOME. Cascata: 1 adult, skin, skull, 1 imm., alc., skull, IX-1989, J. Haft (SNMS 41801/02). "Sao Tomé": 1 ♀, mounted specimen, skull (not seen), 1868, F. Newton/Pires (holotype specimen of *Cynonycteris brachycephala* Bocage, 1889; MLZA 449a/"Holotipo T 114"); 1 imm. ♂, 9-VI-1983, A. Feiler (SMTD B 14030).

*Diagnosis:* A small member of the genus, confined to the island of Sao Tomé, with a known fal range of 62.0-64.2 (3 specimens) and a known gsl of 33.4; relatively strong and differentiated dentition, with rather strongly reduced $P^1$, $M^2$ and $M_3$, and $P_4$ with widely separated outer and inner ridges; a palatal ridge pattern of 4 + 3 + 2 (one example known). All known specimens have developed only 1 lower inner incisor.

*Measurements:* Table 4. See also table 1. Some ratios (of the few subadult and adult specimens in table 4, sexes combined) are: rl 31.7-34.8% gsl; $C^1$-$C^1$ 18.5-19.7% of gsl; $M^2$-$M^2$ 26.3-31.0% of gsl.

*Distribution:* Fig. 6.

*Related species: Myonycteris torquata* differs in having a weaker skull and weaker, rather simple teeth. *M. relicta* is probably considerably larger, with a fal range of 65.9-75.1 and a gsl range of 35.5-39.2, and lacks $M_3$. *Lissonycteris angolensis* is larger, with a forearm length range of 67.8-88.0 and a gsl range of 36.4-46.4, and has squarish $P^4$ and $M^1$ and less reduced last molars. The sympatric and superficially slightly resembling *Rousettus egyptiacus tomensis* Juste & Ibañez, 1993 is larger, having a mean fal of 99.9 ± 1.79 and a mean gsl of 45.0 ± 0.51.

*Remarks*

Taxonomy: Andersen's (1912) account of *M. brachycephala* and its differential characters of skull and dentition were based on the holotype specimen only. Bergmans (1976), who had to rely on Andersen's account as the skull could not be traced in the MLZA in 1975, quoted as most important: "Skull in general aspect and even in size very similar to that of *M. wroughtoni*, but postdental palate dictinctly narrower and with lateral margins more rapidly converging antero-posteri-

Table 4. Selected measurements of *Myonycteris brachycephala* Bocage, 1889.

| | ♀<br>MLZA<br>449a<br>holotype | subad. ♂<br>SMTD<br>B14030 | "♂"<br>SMNS<br>41801 | subad."♀"<br>SMNS<br>41802 |
|---|---|---|---|---|
| fal | 64.2 | 58.5 | 62.0 | 63.4 |
| HF | | 15** | 15** | 16.0 |
| 3rd mc | 44.4 | 41.4 | 44.7 | 44.1 |
| 5th mc | 41* | 39.0 | 42.0 | 41.3 |
| gsl | 34* | 31.0 | 33.4 | 32.8 |
| cbl | | 30.0 | 32.2 | 31.8 |
| rl | | 10.8 | 10.6 | |
| pl | | 16.6 | 17.3 | |
| mand | 25.7* | 22.7 | 24.5 | |
| cran | 13.7* | 12.9 | 13.0 | |
| iow | 6.8* | 5.5 | 6.2 | |
| pow | | 6.6 | 5.6 | |
| zw | 19.8* | — | 20.6 | 20.4 |
| $C^1$-$C^1$ | 6.7* | 6.1 | 6.3 | 6.1 |
| $C^1$-$M^2$ | 12.8* | 11.8 | 12.1 | |
| $M^2$-$M^2$ | | 9.6 | 8.8 | |
| $C_1$-$M_3$ | 13.6* | 12.8 | 13.4 | |
| $P^3$ length | 2.6* | 2.5 | | |
| width | 1.9* | 1.9 | | |
| $P^4$ length | 2.9* | 3.0 | | |
| width | 2.1* | 2.25 | | |
| $M^1$ length | 2.6* | 2.65 | | |
| width | 1.9* | 2.1 | | |

* After Andersen (1912); ** field measurements

orly, inter-orbital region broader, and (no doubt owing to the much heavier dentition) temporal ridges fused in median line to form a low sagittal crest, zygomatic arches deeper and more strongly curved upward posteriorly (stronger fascia temporalis), coronoid process higher and broader, and angular process more prominently developed." On the dentition in *brachycephala* Andersen (1912) wrote that, in comparison with *torquata, wroughtoni* and *leptodon*, the canines are shorter ($C^1$ barely exceeding $P^3$ in height, $C_1$ conspicuously lower than $P_3$); upper and lower cheek teeth are much larger and with considerably higher and sharper cusps; outer and inner ridges of $P^3$ are obscurely separated (instead of fused) and both raised as conical cusps; the inner ridge in $P^4$ is similarly conical; and the antero-internal base of $P^4$ is more prominent and edge-like.

A direct comparison of the skull of the second known specimen, a subadult ♂ (SMTD B 14030; see figs. 7a-d), with a (near) typical specimen of *M. torquata* (ZMA 15.423 from Pointe Noire, Congo) yielded the following. In *brachycephala* the dorsal side of the rostrum, i.e. of the nasals, is nearly convex and posteriorly higher; the postorbital foramen is dorsally very small; the postorbital process is narrow from base to tip (not unlike *torquata* specimens from Ivory Coast); the skull is less constricted posteriorly; the orbit is smaller; the foramen lachrymale is smaller and the foramen infra-orbitale is placed more backward; the pterygoid wings (both broken) appear to be curved inward more strongly; $C^1$-$M^3$ is longer, with the posterior side of $M^2$ level with the posterior side of the anterior zygomatic arch insertion (in *M. torquata* this is halfway $M^3$); the mandibular ramus is thicker, its symphysis longer, its coronoid process more vertical and longer. In this and in the two SMNS specimens (SMNS 41801/02; registered as ♂ and ♀ but possibly ♀ and ♂, respectively) there are only three lower incisors; in all three, the right $I_1$ appears to be lacking, its place annexed by its left counterpart. They agree with what Andersen (1912: 577) described for the holotype. Juste *et al.* (1993) elaborately described and discussed the same phenomenon in a first report on 19 specimens collected in 1988 and 1989.

Distribution and geographical variation: White (1983) did not include the island in his vegetation study, but in a short note on birds (Anonymus, 1987) the vegetation of both Principe and Sao Tomé is characterized as follows: "... the range of vegetation types is enormous (...) - from mist forest in the south to acacias and baobabs 50 km north. Most of the forest on the lowlands and north-facing highland slopes had been converted to (...) plantations...". The same author also noted: "...an area of some 200 sq km of untouched rainforest in the centre and southwest of Sao Tomé has most likely never

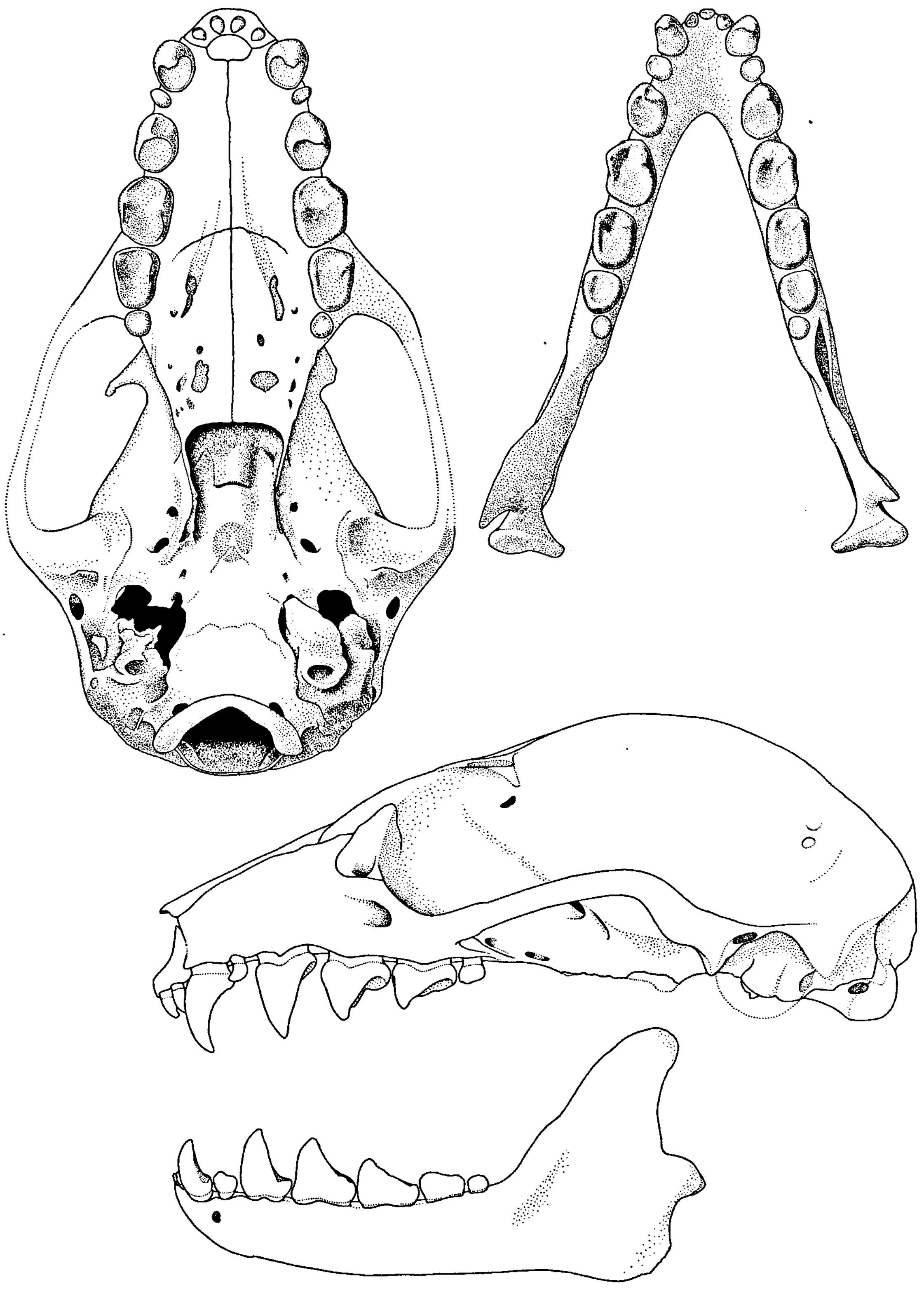

Fig. 7. Skull a nearly adult ♂ of *Myonycteris brachycephala* (Bocage, 1889) from Sao Tomé (SMTD B14030). Stippled areas of palatum not completely ossified; zygomatic arches partly 'restored'; auditory regions, left lateral postdental palate margins, pterygoid wings, and right coronoid process damaged and incomplete.

been explored ornithologically." and "On both islands the widespread abandonment of the plantations since independence has permitted the regeneration of large areas of secondary vegetation at all altitudes." Sayer *et al.* (1992) compiled available knowledge on the forest on the island and described its progressive destruction. Their map confirms the anonymous report quoted above. Feiler (1984) wrote that the second specimen of *Myonycteris brachycephala* had been collected at an altitude of about 800 m in an original forest area. Nadler *et al.* (1993) mapped Cascata, locality of the two SMNS specimens, in the northwest of the island, just north of the mountain Pico de Sao Tomé. Sayer *et al.* (1992) indicated remnants of lowland forests there, and the spot is also close to montane forest. Dr. J. Juste (*in lit.*, 12-VII-1990) mentioned that the species had been caught in montane forest at 1300 m, and in a cocoa plantation at 300 m. From his collected data (on the 19 specimens mentioned before) he concluded that the species prefers the forested mountain zones but may be found to live in plantation areas, and avoids the coastal zone and the northern - dry - part of the island.

It is not likely that within an island of only 847 km$^2$ taxonomical variation has developed.

## **Myonycteris relicta** Bergmans, 1980

*Rousettus angolensis angolensis*; Smithers *et al.*, 1976: 42 (in part the record mapped in square 2033B).
*Rousettus (Lissonycteris) angolensis angolensis*; Smithers *et al.*, 1979: 27 (in part: the material from Haroni/Lusitu River confluence).
*Myonycteris relicta* Bergmans, 1980a: 173 (type locality: Mukanda River, Lukore area, Shimba Hills), 1980b: 96; Schlitter *et al.*, 1981: 385; Honacki *et al.*, 1982: 118; Aggundey *et al.*, 1984: 122; Mickleburgh *et al.*, 1992: 79.
*Myonycteris (Myonycteris) relicta*; Koopman, 1994: 21.

### *Material examined*

KENYA. Mukanda River, Lukore area, Shimba Hills: 1 ♂, 30-VII-1978, R. N. Kyongo (holotype specimen of *Myonycteris relicta* Bergmans, 1980; RMNH 27909).
(Mwele Forest.)
TANZANIA. Ambangulu: 1 ♂, 1 ♀, alc., skulls, I-1900, ? Martienssen (paratype specimens of *Myonycteris relicta* Bergmans, 1980; ZMB 54936/37). Nguru Mountains: 1 ♀, 19-XI-1960, P. Martin (LACM 19517).
(Bagamoyo district, Kisarawe district, Pangani district, Rufiji district, eastern slopes Uzungwe Mountains.)
ZIMBABWE. 1 ♀, alc., skull, at the Haroni-Lusitu confluence, 8-XII-1973 (NHMBZ 62472).

*Diagnosis:* The largest member of the genus, inhabiting forests in East Africa, with a fal range of 65.9-75.1 and a gsl range of 35.5-39.2; with relatively strong, simple teeth, with reduced M$^2$ and M$_2$ and inner and outer ridges of P$_4$ fused anteriorly; no M$_3$; a palatal ridge pattern of 3 + 3 + 2 (possibly with as variant 3 + 4 + 2).

*Measurements:* Table 5. Some ratios are

| | | | |
|---|---|---|---|
| rl | ♂♂ | 35.7 - 36.7% of gsl (n = 2), | |
| | ♀♀ | 35.2 - 38.5% of gsl (n = 4); | |
| C$^1$-C$^1$ | ♂♂ | 18.9 - 19.4% of gsl (n = 2), | |
| | ♀♀ | 17.7 - 19.9% of gsl (n = 4); | |
| M$^2$-M$^2$ | ♂♂ | 28.3 - 28.7% of gsl (n = 2), | |
| | ♀♀ | 27.6 -≥28.4% of gsl (n = 2). | |

*Distribution:* Fig. 6.

*Related species:* Both *M. torquata* and *brachycephala* are smaller, with combined fal ranges of 54.9-67.1 and gsl ranges of 30.2-35.8, and possess small M$_3$. *Lissonycteris angolensis* averages larger, with a fal range of 67.8-88.0 and a gsl range of 36.4-46.4, has squarish P$^4$ and M$^1$, and possesses M$_3$ Superficially resembling sympatric *Rousettus egyptiacus* and *R. lanosus* are larger (fals above 85 and gsls above 38), have less specialized rostra and teeth, and possess M$_3$. Allopatric *Rousettus* may largely overlap in size but differ in the other characters.

### *Remarks*

Taxonomy: *M. relicta* was first discovered in the LACM collection, where in 1978 the present author re-identified a specimen from the Nguru Mountains stored since 1960 as *M. torquata* (LACM 19517). An initial proposal by the then assistant curator Dr. J. D. Smith to publish the novelty together ran aground because of an incompatibility of opinions. Most important, Dr. Smith advocated synonymization of *Myonycteris* and *Lissonycteris* with *Rousettus*, a concept the present author could not support, as has been substantiated in the present paper. In March 1979,

Table 5. Selected measurements of *Myonycteris relicta* Bergmans, 1980.

| | ♂ | ♂ | ♀ | ♀ | ♀ | ♀ |
|---|---|---|---|---|---|---|
| | RMNH | ZMB | ZMB | LACM | CMNH | NHMBZ |
| | 27909 | 54936 | 54937 | 19517 | 57685 | 62472 |
| | holotype | paratype | paratype | | | |
| | Shimba Hills | Usambara Mts. | Usambara Mts. | Nguru Mts. | Nguru Mts | Zimbabwe |
| fal | 69.3 | — | 75.1 | 69.4 | 65.9 | 69.4 |
| gsl | 36.4 | 36.5 | 39.2 | 35.5 | 35.9 | 36.9 |
| rl | 13.0 | 13.4 | 15.11 | 13.0 | 12.8 | 13.0 |
| iow | 7.1 | 7.3 | 8.1 | 6.7 | 7.0 | 6.9 |
| pow | 8.9 | 9.7 | 8.2 | 9.4 | 8.5 | 9.9 |
| zw | 21.4 | ≥22.5 | — | 20.6 | 21.1 | 21.5 |
| $C^1$-$C^1$ | 6.9 | 7.1 | 7.8 | 6.3 | 6.6 | 7.0 |
| $M^2$-$M^2$ | 10.3 | 10.5 | — | 9.8 | — | ≥10.5* |
| $C^1$-$M^2$ | 13.4 | 13.3 | 14.9 | 13.2 | 12.9 | ≥13.3* |
| $C_1$-$M_2$ | 13.6 | 13.4 | 14.5 | 13.1 | 13.2 | ≥13.1* |
| W | 48 | | | | | 56 |

* teeth heavily worn

the present author discovered two more specimens in the ZMB, collected in 1900 in Ambangulu in the southern foothills of the Usambara Mountains. In June 1979 the first Kenyan specimen, from Mukanda River in the Shimba Hills, was received by the RMNH and recognized by Dr. C. Smeenk, who kindly made it available. These three specimens served as type material for the description of *Myonycteris relicta.* Schlitter *et al.* (1981) reported on a CMNH specimen collected in 1960 in the Nguru Mountains. Dr. D. A. Schlitter (*in lit.*, 5-IV-1988) wrote that he collected further specimens in the Shimba Hills in 1985 and 1987. Of these, I have no details, except that Dr. M. E. Rutzmoser of the Museum of Comparative Zoology (*in lit.*, 18-XI-1988) drew my attention to a specimen collected in 1985 in the Mwele Forest in the Shimba Hills (MCZ 59868). Then, Mickleburgh *et al.* (1992) reported observations by Dr. K. M. Howell and Dr. D. Kock on the species' occurrence "in Pangani, Bagamoya [= Bagamoyo], Kisarawe and Rufiji districts south-westwards to the east slope of Uzungwe mountains" in Tanzania. These 'localities' have been introduced on the map (fig. 6), except 'Rufiji district' (Rufiji River runs from the Selous Game Reserve eastward through several map squares and reaches the Ocean at 8 S). Details on these specimens will be published by their reporters in a paper on Tanzanian forest bat diversity (Dr. D. Kock, *in lit.*, 6-II-1990). Finally, a specimen from eastern Zim-babwe identified as *Lissonycteris angolensis* by Smithers *et al.* (1979) together with other specimens of that species (examined for the present study and described above as *L. a. goliath* n. ssp.) also represents *Myonycteris relicta.*

Distribution and geographical variation: All localities known with some accuracy are in East African Zanzibar-Inhambane coastal mosaic: forest patches (type 16b in White, 1983), or in Undifferentiated Afromontane vegetation (type 19a in White, 1983) bordering on East African Zanzibar-Inhambane coastal mosaic (type 16a in White, 1983). The holotype specimen was caught over the Mukanda River, bordered by big thorn trees and fig trees, in the Shimba Hills, which are covered with a mosaic of open country and forest patches (personal observation). At the time of capture of the paratype specimens, in 1900, the Usambara Mountains will have been covered with forest more extensively than today. Schlitter *et al.* (1981) mentioned that their Nguru Mountains specimen was possibly captured in the Manyangu Forest (or in the east foothills, or the eastern Nguru Mountains), at 3000 feet elevation, by J. Williams on 17/20-IX-1960. The Nguru Mountains specimen in the LACM was collected by J. G. Williams and/or Purvis Martin, over a stream in a narrow belt of riverine forest (3000') in the foothills of the Nguru Mountains (eastern flank) 17 kms northwest of Turiani, approximately at 37 '35 E, 16 10 S, on 19-XI-1960. (The two Nguru Mountains specimens may actually have been taken together, in which case the date noted for the LACM specimen should be 19-IX-1960.) According to the map in Sayer *et al.* (1992) there are small patches of lowland rain forest left in all the districts mentioned by Mickleburgh *et al.* (1992). The collecting locality in Zimbabwe is a forest near the confluence of the rivers Haroni and Lusitu (now called Rusitu), at the southern end of the Chimanimani Mountains. Broadley (1974) gave a sketch map of the forest areas near this confluence. Closest, and the likely candidates, are the Haroni Forest at about 1 km north of it, between 300 and 450 m above sea level, and the slightly larger Lusitu Forest (195 ha) at 2.5 km to the west, between 300 to 600 m a.s.l. Robertson (1984) emphasized the importance of these small rain forests: The Haroni Forest, incorporated in the Chimanimani National Park, has become the last example of its type in Zimbabwe; a large portion of the Rusitu Forest (150 ha) has been protected as Botanical Reserve, and is the biologically most valuable of this category in the country, but severely threatened by illegal activities such as clearing and cattle grazing.

The distribution of the species in southeast Kenya and northeast Tanzania appears to be, or have been, continuous, but considering the nature of forest distribution in East Africa, distributional disjunctions are not unlikely. However, the numbers of reported specimens per locality are low and assessment of geographical variation must wait. Moreover, the species will certainly be discovered yet in some other areas in Tanzania, and possibly Mozambique.

### **Megaloglossus** Pagenstecher, 1885

*Megaloglossus* Pagenstecher, 1885a: 193 (type species: *Megaloglossus Woermanni* Pagenstecher, 1885a, 1885b: 126; Matschie, 1899: 101; Andersen, 1912: 738; Hood, 1989; Kirsch *et al.*, 1995; Springer *et al.*, 1995.

*Trygenycteris* Lydekker, 1891, *in:* Flower & Lydekker, 1891: 655 (type species: *Megaloglossus woermanni* Pagenstecher, 1885); Miller, 1907: 73; Andersen, 1912: 738.

The original description of *Megaloglossus* (Pagenstecher, 1885a, b) includes, next to comparative remarks referring to *Macroglossus minimus* (E. Geoffroy, 1810) and *Melonycteris melanops* Dobson, 1877 the following characters: dark brown fur (ventre: gray-brown) and membranes; wing membrane from 2nd and 3rd toe; short tail (two vertebrae); upper teeth 2.1.3.2, lower 2.1.3.3; surrounding rim of naral openings not protruding; vertical groove between nares; $C^1$ with anterior groove; $P^3$, and to a lesser extent $P^4$, anteriorly well developed and slightly recurved; lower incisors bifid; 5th and 6th palatal ridges divided; very long and relatively thick tongue. Pagenstecher's figures illustrate the whole animal, the seven palatal ridges, the naral region, the tongue and the wing insertion on the foot. Matschie (1899) added: snout very long and narrow; teeth all weak except canines; lower canines recurved; 3rd metacarpal about as long as 2nd digit (with claw). Miller (1907) added: skull less deflected if compared to *Macroglossus*, with alveolar line passing below middle of brain-case; short mandibular symphysis; perpendicular $I^1$; $P^1$ conspicuously smaller than $P^3$. Andersen (1912) used most of these data for his diagnosis and added or corrected the following: membranes inserted from base of first phalanx of 2nd or 3rd toe, or from in between these; adult ♂♂ with ruff of pale-coloured hair across foreneck; premaxillae subequal in breadth throughout and solidly united anteriorly; infraorbital canal short; cheek-teeth sublinear; forearm 40-43.5; 5th metacarpal much shorter than 3rd. Andersen illustrated several views of the skull.

The differential characters above were identified in comparison of *Megaloglossus* with other species ascribed to the Macroglossinae. The following characters, individually or in combination, serve to differentiate it from other Pteropodinae: narrow, tapering rostrum with width over $C^1$-$C^1$ hardly more than half the length over $C^1$-$M^2$; long and relatively thick tongue; very narrow cheek teeth with the distance between $P^3$-$P^3$ over 5 times the width of $P^3$; 5th metacarpal distinctly shorter than 3rd; membrane insertion at second or third toe, or in between.

## **Megaloglossus woermanni** Pagenstecher, 1885

*Megaloglossus woermanni* Pagenstecher, 1885a: 245 (type locality: Sibange farm), 1885b: 126; Andersen, 1912: 742; Cabrera, 1929: 17; Sanderson, 1940: 667; Krumbiegel, 1942: 340; Schouteden, 1944: 108; Rosevear, 1953: 83; Sanborn, 1953: 164; Hayman, 1954: 282; Eisentraut, 1956a: 514, 1956b, 1957: 624; Novick, 1960; Strinati, 1960; Eisentraut, 1963: 75; Hayman, 1963: 102; Eisentraut, 1964: 538; Rosevear, 1965: 123; Brosset, 1966b: 60, 1966c: 143; Hayman *et al.*, 1966: 25; Mumford, 1970; Hayman *et al.*, 1971; Jones, 1971: 130; Bergmans *et al.*, 1972; Eisentraut, 1973: 358; J.-P. Adam *et al.*, 1974: 150; Bergmans *et al.*, 1974: 41; Vielliard, 1974: 977; Czekala *et al.*, 1974; Jeffrey, 1975: 956; Coe, 1976: 546; Verschuren, 1977: 620; Addy *et al.*, 1978; Fain, 1978: 176; Happold *et al.*, 1978: 122; Bergmans, 1979: 181; Haiduk *et al.*, 1980; Kulzer *et al.*, 1980; Haiduk *et al.*, 1981; Kulzer, 1982; Honacki *et al.*, 1982: 117; Wolton *et al.*, 1982: 432; Anciaux de Faveaux, 1983: 32; Emmons *et al.*, 1983; Dobat *et al.*, 1985; Fedden *et al.*, 1986: 185; Happold, 1987: 48; Hickey *et al.*, 1987; Roth *et al.*, 1988: 184; Crawford-Cabral, 1989: 13; Koopman, 1989: 3; Dowsett *et al.*, 1991: 255; Mickleburgh *et al.*, 1992: 77.

*Trygenycteris woermanni*; Lydekker, *in:* Flower *et al.*, 1891: 655; Miller, 1907: 73.

*Trygenycteris*; Lydekker, 1901: 303, 317.

*Megaloglossus woermanni prigoginei* Hayman, 1966, *in:* Hayman *et al.*, 1966: 26 (type locality: Kiliza); Hayman *et al.*, 1971: 13; Bergmans *et al.*, 1972; Kingdon, 1974: 177.

*Megaloglossus woermanni woermanni*; De Vree *et al.*, 1969: 204, 1970: 43; De Vree, 1971: 41; De Vree *et al.*, 1971: 161; Hayman *et al.*, 1971: 13; Eisentraut, 1973a: 37.

### *Material examined*

ANGOLA. Canzele: 1 ♂, 1 ♀, 10-IV-1954, G. H. Heinrich (FMNH 81604/05); 1 ♀, 1 imm., alc., 1954, G. H. Heinrich (FMNH 81697/98). "Angola": 2 ♀♀, 1 imm., 1954, G. H. Heinrich (FMNH 81694/96).

(Dundo.)

CAMEROUN. 30 km W of Bertoua: 2 ♂♂, 2 ♀♀, 25-II/20-IV-1972, L. W. Robbins (AMNH 241025/28). Bipindihof nr Kribi: 1 skull, Käthke (ZMB 38958); 1 ♀, alc., skull, H. Zenker (ZMB 40162). Bitye: 1 ♀, 6-VIII-1912, G. L. Bates (MRAC RG 1479); 1 ♂, skin, 1 ♂, skull, 28-IV-1915, W. F. H. Rosenberg/G. L. Bates (ZMB 33340/41). Buea: 1 ♂, alc., 28-X-1973, J. Prévost (MNHN CG 1979-177). Eseka: 2 ♂♂, 20-VI-1973, L. W. Robbins (AMNH 236283/84). 7 km N of Eseka: 1 ♀, 3-XI-1972, L. W. Robbins (AMNH 236292). 6 km SE of Eseka: 1 ♂, 7-VI-1974, L. W. Robbins (AMNH 236291). 5 km SW of Eseka: 5 ♂♂, 5 ♀♀, 28-VI/6-VII-1974, L. W. Robbins (AMNH 236285/90; CMNH 40994/97). 8 km SW of Eseka: 1 ♀, 24-VI-1974, L. W. Robbins (AMNH 236293). Isobi: 1 ♂, 11-III-1958, M. Eisentraut (IRSN 13.101). Kribi: 2 ♂♂, 4 imm. ♂♂, 1 ♀, 1 imm. ♀, alc., 16/17-IV-1973, J. Prévost (MNHN CG 1979-168/75). Lolodorf: 1 imm. ♀, 1 specimen, 11/15-IV-1914, J. A. Reis (CMNH 3674, -80); 1 ♀, 15-VIII-1938, A. I. Good (CMNH 16062). 15 km SE of Mamfe: 1 ♀, 9-XII-1971, L. W. Robbins (AMNH 241030). Mbalmayo: 1 imm., 22/26-IX-1964, D. Thys van den Audenaerde (MRAC 33505). Above Mueli: 1 imm. ♀, 9-II-1958, M. Eisentraut (IRSN 13.102). Nkolbisson: 1 ♀, alc., 5-V-1973, J. Prévost (MNHN CG 1979-176). 7 km N of Ntui: 1 imm. ♂, 1 ♀, alc., 11-XI-1973, J. Prévost (MNHN CG 1979-166/67). Sangmelima: 1 imm. ♀, 14-V-1933, A. I. Good (CMNH 9507). Somalomo: 3 ♂♂, 1 ♀, alc., 10-II-1987, A. P. M. van der Zon (ZMA 23.521/24). Yaoundé: 1 ♂, alc., J. Prévost (MNHN CG 1979-178).

(Ambam, Assobam, 10 miles W of Bipindi, Dikume, Douala, Efulen, Ekona, Ekundu, Great Soppo, Korup Reserve, Kumba, Kupe, Lake Barombi, Lombe, Mangamba, Marienberg, Moliko, Mount Cameroun, Mpundu, Nyasoso, Obala, Sakbayeme, Tombel, Victoria.)

CENTRAL AFRICAN REPUBLIC. La Maboké: 3 ♀♀, alc., 10-V-1966 and without date, R. Pujol/P. Teocchi (MNHN).

CONGO. Dimonika: 3 ♀♀, 1 specimen, alc., 10-III-1972 (UBRA). Ile M'Bamou: 1 ♀, skull (UBRA 2-♀-23-03-71). Makaba: 1 ♀, formol, 12-III-1970 (UBRA). N'Gongo: 1 ♀, formol, 1-III-1970 (UBRA).

(Béna, Goumina, Koubotchi, Massif de Bangou.)

EQUATORIAL GUINEA.

(Aninzok, Engong, Evuenam, Mokula.)

FERNANDO POO.

(Moca, Musala, Refugium, San Carlos.)

GABON. Belinga: 3 ♂♂, 1 imm. ♂, alc., XII-1962, Mission Biologique au Gabon (= MBG) (HZM; ZMA 20.621/23); 2 ♂♂, 2 imm. ♂♂, 2 ♀♀, alc., XII-1962/II-1963, MBG (ZMA 20.627/33); 3 ♂♂, alc., I-1963, MBG (ZMA

20.624/26); 9 ♂♂, alc., 18/22-II-1963, ? 20-II-1963 and II/III-1963, MBG (MNHN); 2 ♂♂, 2 ♀♀, alc., II/VII-1963, MBG (ZMA 20.634/35, -41/42); 4 ♂♂, alc., 20-VI-1963, VI-1963, VI/VII-1963, MBG (MNHN), 1 skull, 1 imm. skull, VIII-1963, MBG (MNHN; ZMA 20.619); 1 ♀, alc., 22-XII-1963, P. J. H. van Bree (ZMA 7811); 5 ♂♂, alc., skulls, 1963, MBG (ZMA 20.636/40); 20 ♂♂, alc., XII-1963/II-1964, MBG (MNHN); 6 ♂♂, 1 ♀, 1 specimen, alc., 12-I/18-II-1964, P. J. H. van Bree (ZMA 7809/10, -12/17); 3 ♂♂, 1 imm. ♂, alc., skulls, II-1964, MBG (ZMA 20.643/46). Lastoursville: 2 ♂♂, 1 imm. ♀ (Muséum d'Histoire Naturelle, Genève). Makokou: 1 imm. ♀, alc., 5-XII-1963, MBG (ZMA 7818); 2 ♂♂, alc., 25-II-1964, MBG (ZMA 20.616/17); 1 imm. ♂, alc., 5-XII-1965, MBG (ZMA 20.618). Port Gentil and La Bamba, Bongolo Mission: 1 ♂, 1 ♀, 1 imm. ♀, alc., 10-IV/23-VII-1951, H. A. Beatty (FMNH 73818/20). Ssibange Farm: 1 ♀, mounted, skull, 21-I-1885, H. Soyaux (holotype specimen of *Megaloglossus woermanni* Pagenstecher, 1885; ZMB 54589).

(N'Doumbou.)

GHANA. Akoso Mbo: 2 ♀♀, 1 imm. ♀ (BMNH 68.365/67). Efeipo Krom: 1 ♂, 1 ♀, 14-VII-1968, J. C. Geest (USNM 424840/41). Ghiriso: 1 ♂, 3 ♀♀, 21/30-I-1968, J. C. Geest (USNM 414083/84, 414784/85). Legon: 1 ♂ (ROM 36578). Oda: 6 ♂♂, 1 ♀, 10/15-X-1968, J. W. LeDuc/H. W. Setzer/R. E. Vaden (USNM 439885/91). Odomi Jongo: 1 skin, 19-VI-1968, J. C. Geest (USNM 424839).

(Amum, Bibianaha, Boti Falls, Kade, Pampra-mase, Sefwi Asemparaye.)

IVORY COAST. Adiopodoumé: 1 ♀, 12-VIII-1971, L. W. Robbins (AMNH 239386). Adzope: 1 ♀, 8-III-1971, J. Vissault (ZMA 16.520). Banco Forest: 1 ♂, 29-V-1969, L. W. Robbins (USNM 467921). Bolo: 1 ♂, 1 imm. ♀, 31-I/1-II-1973, J. Vissault (ZMA 18.035/36). Lamto: 2 ♀♀, 2-VII-1970 and 8-III-1971, J. Vissault (MNHN; ZMA 16.521). "Ivory Coast": 2 specimens, 1970/73, J. Vissault (ZMA 18.037/38).

LIBERIA. Basse-Iti: 1 ♂, alc., 24-II-1966, Nimba Expedition (IRSN 16089). Mount Coffee: 1 ♀, 1 specimen, alc., skulls, 23-II/IV-1897, R. P. Currie (USNM 83803/04). Mount Nimba (West): 3 ♂♂, alc., 27-II/11-III-1966, Nimba Expedition (IRSN 16090/92). Schieffelinsville: 1 ♂ (RMNH 20402). Tars Town: 2 ♀♀, 2-VII-1971, D. A. Schlitter (USNM 481696/97). "Liberia": 2 ♂♂, VII-1965, J. Verschuren (IRSN 16758/59).

(Saniquellie, Sapo National Forest, Sino, Teaye.)

NIGERIA. 13 miles N of Calabar: 1 ♀, 10-III-1966, H. J. Herbert (USNM 377110). Ife: 2 ♂♂, alc., skulls, 15-VIII-1976, W. Bergmans (ZMA 18.606; NHMI). Igbo-Ora: 1 imm. ♂, 21-X-1966, H. W. Setzer (USNM 402579). Ikang: 2 ♂♂, 1 ♀, alc., 28-VII-1976, W. Bergmans (ZMA 18.603/05).

(Gambari Forest Reserve, Ibadan, Nikrowa, Oban, Sapoba Forest Reserve, Shasha Forest Reserve.)

TOGO. Edifou: 1 ♂, 11-XII-1968, A. De Roo/F. De Vree/W. N. Verheyen (LADA V 20.80). Fazao: 1 ♀, 23-VIII-1969, Deuxième Mission Zoologique Belge (LADA 16.05). Misahohe: 1 ♀, 8-VIII-1969, Deuxième Mission Zoologique Belge (LADA 14.48). Odjolo: 3 ♂♂, 5-II-1969, A. De Roo/F. De Vree/W. N. Verheyen (LADA 25.33, -.35, -.49); 1 ♀, 1969 (LADA 21.98).

UGANDA. Bundimusuba: 1 ♀, 10-VII-1967, A. L. Archer (LACM 51641). Bwamba area: 1 ♀, 18-III-1969, A. Williams (ROM 49296). Itama area: 1 ♀, 22-VI-1969, A. Williams (LACM 35508). Mongiro: 1 imm. ♂, 4-XI-1968, A. Williams (LACM 51654). Ntandi: 3 ♂♂, 2 imm. ♂♂, 1 ♀, 1/15-XI-1968 (LACM 51642/45, 51655/56).

(Bwamba, Bwamba Forest, Entebbe, nr Kampala, north of Kigezi, Mawokota, Zika.)

ZAIRE. Banana: 1 specimen, 1889 (SMF 2513). Beno: alc. material (BMNH). Bikoro: 1 ♀, 2-III-1921, H. Schouteden (MRAC 6548). Bokuma: 1 ♀, 14-XII-1952, P. P. Lootens (MRAC 22031). Ibembo: 1 ♀, J. Hutsebout (MRAC 19857). Ikela: 1 ♂, 1958, P. P. Lootens (MRAC 27017). Irangi: 1 ♂, 1 ♀, alc., 17-X-1990, W. Bergmans (ZMA 24.195/96). Kakanda: 1 ♀, alc., 29-VIII-1964 (MRAC 33065). Karambi: 1 imm. ♂, 1 imm. ♀, alc., 6-IV-1992, N. Masumbuko Kamitongo (ZMA 24.564/65). Kamituga: 1 ♂, 21-XII-1950, A. Prigogine (paratype specimen of *Megaloglo-ssus woermanni prigoginei* Hayman, 1966; MRAC 20429). Kiliza: 1 ♂, 25-V-1964, A. Prigogine (holotype specimen of *Megaloglossus woermanni prigoginei* Hayman, 1966; MRAC 32577); 4 ♀♀, 24/26-V-1964, A. Prigogine (paratype specimens of *Megaloglossus woermanni prigoginei* Hayman, 1966; MRAC 32578/79, -82/83). Kitongo: 2 ♀♀, 3/4-VI-1964, A. Prigogine (paratype of *Megaloglossus woermanni prigoginei* Hayman, 1966; MRAC 32580/81). Lukolela: 1 ♂, 12-VIII-1930, F. Edson (AMNH 86771l). Luluabourg: 1 specimen, alc., 26-IV-1964, De Roo (MRAC 33604); 2 ♂♂, 3 ♀♀, 5 specimens, partly: alc., 15-II/30-VI-1965, De Roo (MRAC 33341/46, 33370/71, 33553/54). Lundjulu: 1 ♀, 14-X-1952, M. Schepens (paratype specimen of *Megaloglossus woermanni prigoginei* Hayman, 1966; MRAC 21586). Malembe: 1 ♂, 20-IV-1992, N. Masumbuko Kamitongo (ZMA 24.566).

(Kinkole, Netonna.)

*Diagnosis:* The smallest of African fruit bats, with a fal of 38.6-49.4 and a gsl of 24.5-30.3, dark brown to grey brown fur, without facial markings, with a white ruff in adult ♂♂, a narrow, pointed snout and a long tongue, and very weak and narrow cheek teeth. Measurement ranges and ratios taken from all over the species' range:

| | | | |
|---|---|---|---|
| fal | ♂♂ | 38.6 - 49.4 | (n = 116), |
| | ♀♀ | 38.7 - 48.7 | (n = 64); |
| gsl | ♂♂ | 25.3 - 30.3 | (n = 48), |
| | ♀♀ | 24.5 - 29.2 | (n = 40); |

Table 6. Forearm length and greatest skull length ranges in *Megaloglossus woermanni* Pagenstecher, 1885 per country, arranged approximately in an order from west to east.

| | ♂♂ | | | | ♀♀ | | | |
|---|---|---|---|---|---|---|---|---|
| | | fal | | gsl | | fal | | gsl |
| country | n | min - max | n | min-max | n | min-max | n | min-max |
| Liberia | 6 | 40.4-44.1 | 1 | 27.9 | 2 | 41.7-42.2 | 3 | 25.6-27.2 |
| Ivory Coast | 4 | 40.0-43.4 | 1 | 26.5 | 4 | 40.0-43.4 | 4 | 25.7-26.6 |
| Ghana | 8 | 38.6-42.0 | 8 | 25.3-27.1 | 7 | 40.7-43.4 | 7 | 25.1-26.9 |
| Togo | 4 | 39.3-39.9 | 4 | 26.3-26.7 | 3 | 41.8-42.8 | 3 | 24.5-26.5 |
| Nigeria | 3 | 40.8-41.8 | 1 | 26.4 | 2 | 41.9-43.2 | 2 | 26.7-27.0 |
| Cameroun | 17 | 40.9-44.3 | 10 | 25.3-27.5 | 14 | 39.6-44.5 | 10 | 26.5-27.7 |
| C.A.R.[1] | | | | | 3 | 42.5-43.3[2] | | |
| Gabon | 60 | 39.8-45 | 6 | 14 26.2-29.2 | 6 | 42.6-45.3 | 1 | 28.1 |
| Congo | | | | | 3 | 43.7-45.0 | | |
| Angola | 1 | 44.3 | 1 | 28.1 | 1 | 48.6 | 1 | 28.9 |
| West Zaïre | | | | | 2 | 38.7-42.6 | | |
| Central Zaïre | 3 | 40.1-45.0 | | | 2 | 41.0-44.3 | 1 | 27.2 |
| East Zaïre | 4 | 43.2-49.4 | 2 | 29.9-30.3 | 9 | 44.1-48.7 | 2 | 27.7-28.5 |
| Uganda | 4 | 41.2-44.2 | 4 | 26.6-29.2 | 4 | 43.1-46.0 | 2 | 27.9-29.9 |

[1]) Central African Republic

[2]) Possibly immatures

| | | | |
|---|---|---|---|
| rl | ♂♂ | 10.1 - 12.7 | (n = 14), |
| | ♀♀ | 9.8 - 12.3 | (n = 20); |
| iow | ♂♂ | 3.7 - 4.5 | (n = 14), |
| | ♀♀ | 3.6 - 4.5 | (n = 22); |
| pow | ♂♂ | 6.3 - 7.7 | (n = 14), |
| | ♀♀ | 5.6 - 7.8 | (n = 21); |
| zw | ♂♂ | 13.3 - 14.7 | (n = 17), |
| | ♀♀ | 12.2 - 14.9 | (n = 19); |
| $C^1$-$C^1$ | ♂♂ | 4.3 - 5.6 | (n = 22), |
| | ♀♀ | 3.9 - 5.8 | (n = 22); |
| $M^2$-$M^2$ | ♂♂ | 5.7 - 7.2 | (n = 22), |
| | ♀♀ | 5.8 - 7.0 | (n = 21); |
| $C^1$-$M^2$ | ♂♂ | 8.2 - 9.7 | (n = 22), |
| | ♀♀ | 8.1 - 9.7 | (n = 22); |
| $C_1$-$M_3$ | ♂♂ | 9.0 - 10.9 | (n = 13), |
| | ♀♀ | 9.0 - 11.0 | (n = 22); |
| W | ♂♂ | 11 - 17 | (n = 21), |
| | ♀♀ | 12.6 - 20 | (n = 11); |
| rl | ♂♂ | 24.1 - 28.0 % gsl | (n = 14), |
| | ♀♀ | 23.2 - 28.7 % gsl | (n = 19); |
| $C^1$-$C^1$ | ♂♂ | 9.8 - 12.7 % gsl | (n = 21), |
| | ♀♀ | 9.3 - 12.1 % gsl | (n = 21); |
| $M^2$-$M^2$ | ♂♂ | 13.1 - 15.5 % gsl | (n = 22), |
| | ♀♀ | 12.9 - 15.3 % gsl | (n = 20). |

For a breakdown of measurements see table 6. There is some geographic variation, with larger specimens found in Liberia, Angola, and the Zaïre basin. See the Remarks below.

*Distribution:* Fig. 8.

*Related species:* The combination of the diagnostic characters mentioned above distinguish *Megaloglossus woermanni* from all other African Megachiroptera. According to the latest findings (see the Remarks below and the General remarks and conclusions), its nearest relative is *Lissonycteris angolensis*, which is much larger and more robust (fal 67.8-87.5, gsl 36.6-46.0), has a more dog-like snout, squarish cheek teeth, and a broad tongue, while the ruff in ♂♂ is never white. Another related genus then is *Myonycteris*, of which *M. torquata* is sympatric. This is also larger (fal 54.9-67.1, gsl 30.2-35.8), and lacks the narrow snout, the extreme reduction of cheek teeth dimensions, and the long tongue, while again the ruff in ♂♂ is never white.

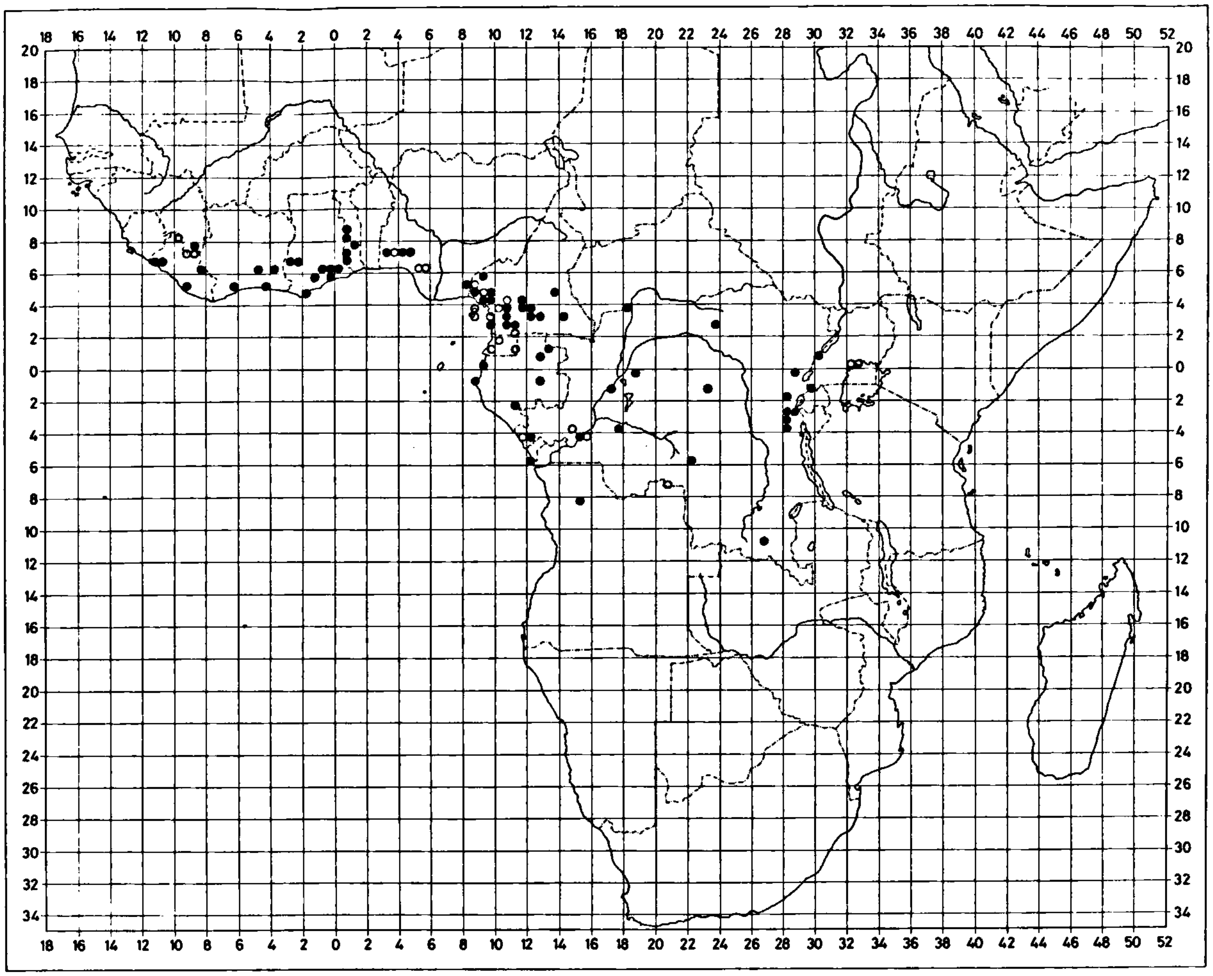

Fig. 8. Distribution of *Megaloglossus woermanni* Pagenstecher, 1885. Black dots: squares from which material has been identified by the author. Open circles: records from literature and correspondence.

*Remarks*

Taxonomy: As noted in the first part of this series (Bergmans, 1988: 78), the arrangement of supraspecific taxa would follow that in Hayman *et al.* (1971). This would have included the Subfamily Macroglossinae Gray, 1866, to accomodate *Megaloglossus woermanni* as its single African representative. Eisentraut (1963: 75; 1973a: 37) assigned family rank to it, as Macroglossidae, but he did not add any arguments and this idea needs no further consideration here. Since 1988, several authors have convincingly shown that this subfamily is not a natural assemblage (Hood, 1989; Colgan *et al.*, 1995; Kirsch *et al.*, 1995; Springer *et al.*, 1995) and that *M. woermanni* is not related to other macroglossine species, but associated with *Lissonycteris* (see Kirsch *et al.*, 1995). Their conclusions are followed here and *M. woermanni* is treated as a species of the Pteropodinae. In this repect it is of significance that during the present study *Megaloglossus* was found to share with *Lissonycteris* (and *Myonycteris*) the angular 'antitragal' lobe and distinctly, be it modestly, webbed toes.

The subfamily name Macroglossinae in mammalogy appears to be preoccupied in entomology. The Lepidoptera subfamily was diagnosed first as Macroglossiadae Harris, 1839, based on *Macroglossum* Scopoli, 1777 (or *Macroglossa* Boisduval, 1833 - Harris' paper is not available to the present author) and quoted first as Macroglossinae by Butler in 1877; Harris is considered the author (entomological data: courtesy of Mr. W.

Hogenes, *in lit.*, 28-XI-1988). In mammalogy, Gray (1866) published the name Macroglossina, based on *Macroglossus* Cuvier, 1824, which must be considered the type genus, and further including *Notopteris* Gray, 1859. The name Macroglossinae was first used by Trouessart in 1897. Blyth (1840) considered the genus name *Macroglossus* a junior homonym of *Macroglossum*, and proposed *Kiodotus* to replace it. (After him, several authors proposed other new names for it.) He was followed in this by Palmer (1898), who proposed that the name of the subfamily would become *Kiodotinae*, and both were followed by Miller, 1907. Andersen (1912: 746) did not agree that the two names are homonyms. Mayr (1969) and Mayr *et al.* (1991) emphasized that "even a single-letter difference prevents homonymy of generic names".

A similar problem has occurred concerning the name *Megaloglossus*. Lydekker (1891) proposed *Trygenycteris* to replace it because there was already a *Megaloglossa* Rondani, 1865, a genus of Diptera. He was followed by Miller (1907) but Matschie (1899) and Andersen (1912) rejected the homonymy of these names, and apparently all later students.

Bergmans *et al.* (1972), in their revision of the taxonomy of *Megaloglossus woermanni*, concluded from its description that the type specimen had been deposited in the Zoologisches Museum in Hamburg. As it could not be traced in that collection, they supposed it was probably lost during the Second World War. However, in 1980 the specimen, an adult ♀, mounted skin and skull, was located in the Zoologisches Museum in Berlin (as ZMB 54589; old number 9489). It was collected on 21-I-1885 by H. Soyaux at Ssibange Farm in Gabon.

Bergmans *et al.* (1972) further concluded from the description that fal and gsl of the type specimen fall within the variation ranges of the East Zaïrese populations described as *M. w. prigoginei* Hayman, 1966 on the basis of their large size, and that this subspecies should be considered a synonym of the typical form. The actual measurements of the type, fal 44.8 and gsl 28.1, although slightly smaller than those mentioned by Pagenstecher (undoubtedly partly due to dessication), do confirm that conclusion. The figures in Bergmans *et al.* (1972), plotting gsl and fal against longitude, suggest rather similar dimensions in West Africa from Liberia to Togo, a distributional gap in Nigeria, and a slight increase in dimensions from Mount Cameroun towards eastern Zaïre. New collecting since then, apart from bridging part of the Nigerian gap and further connecting the known distributions in West Central and East Central Africa, has generally confirmed this picture. Plotting gsl against fal (not figured here) produces an image of gradual, consistent but modest increase in size from west to east, with most of the East Zaïrese specimens being among the larger or largest specimens, two being separated from all the others by fals some 3 mm longer than the largest others. However, they are joined by a specimen from Canzele, Angola, where the species, represented by a small series of mostly immature specimens in the FMNH, apparently attains large dimensions as well. As for the third character used to distinguish *prigoginei* from the nominate subspecies, the heaviness of the rostrum, Bergmans *et al.* (1972) found an increase in $C^1$-$C^1$ and $M^2$-$M^2$ expressed as percentages of gsl from West to East, especially in $C^1$-$C^1$, but no apparent discontinuity between East Zaïrese and typical (Gabonese s.l.) populations. The type specimen, with $C^1$-$C^1$ 18.1% of gsl, fits in with this picture. The two Angolese specimens have even heavier rostra than any East Zaïrese or other specimen measured: $C^1$-$C^1$ in ♂ 19.5% and in ♀ 20.0% of gsl against a former maximum of 18.5% - but in absolute terms these differences are very minute.

If within *M. woermanni* subspecific divisions should be recognized, to which the present author remains opposed until more material is available from East Nigeria, Central Zaïre, and Angola, the populations from Liberia to Togo or Nigeria are possibly better candidates to be differentiated from the typical ones than are the East Zaïrese.

Distribution and geographical variation: *Megaloglossus woermanni* is a true lowland rain forest species. Of the 127 traceable localities 41 are in Wetter types of Guineo-Congolian lowland rain forest, 28 in Drier types of the same, 10 in a mosaic of the mentioned types, 3 in Swamp forest, 13 in a Mosaic of Guineo-Congolian rain forest and secondary grassland, 7 in (the lower strata of) Afromontane vegetation, and 6 in Mangrove (types 1a, 2, 3, 8, 11a, 19a and 77 in White, 1983). Of the remaining 19, 15 are on the border of one of the mentioned types with one of the others or with Transitional rain forest (1) and West African coastal mosaic (1), and only 4 are in woodlands: 1 in Wetter Zambezian miombo woodland dominated by *Brachystegia* and *Julbernardia* and 3 in Sudanian woodland with abundant *Isoberlinia* (types 25 and 27 in White, 1983).

## GENERAL REMARKS AND CONCLUSIONS

In this section, some remarks are made on the taxonomy of the higher taxa. A number of developments are shortly discussed, and a proposal is made for a modified classification of Megachiroptera down to genus level. Secondly, some recent papers are reviewed concerning the taxonomy of African Megachiroptera on species level. Finally, a first effort is made to analyse the distributional patterns found.

Suprageneric taxonomy: The debate on the suborders Megachiroptera and Microchiroptera being either monophyletic or diphyletic referred to earlier (Bergmans, 1988: 78) seems to have come to a temporary standstill. Monophyly appears to be supported by the majority of available molecular and morphological data (Simmons, 1994, 1995; Kirsch *et al.*, 1995). Some data appear to be conflicting, however, and the debate has not come to a final conclusion yet (e.g. Pettigrew, 1991; Nemec *et al.*, 1996).

On a lower taxonomic level, within the Megachiroptera between family and genus levels, another, quieter round of debates is going on. Although this study is primarily concerned with African taxa, it (and the author's work on certain Asian taxa) has equally led to views on fruit bat taxonomy at large. These views, and some recent publications by others, have prompted the writer to make some observations on the taxonomy of the whole suborder since the beginning of this century, which produced the important works by Miller (1907) and Andersen (1912).

Miller recognized only one family, Pteropidae Gray, 1821, which he divided into four subfamilies, with the following diagnostic characters:

1. Pteropinae Gray, 1821. Premaxillaries separate but usually in contact; bony palate narrowing gradually behind tooth rows; width of interpterygoid fossa, including hamulars, distinctly less than distance between posterior molars; canines parallel when jaws closed; cheek teeth well developed, without unusual development of cusps; tongue not specially elongated.
2. Kiodotinae Palmer, 1898. Premaxillaries at first separate, uniting later in life; bony palate narrowing gradually behind tooth rows; mandibular symphysis elongated, its upper surface parallel with alveolar line; tongue highly extensible; teeth (except canines) much reduced in size.
3. Nyctymeninae Miller, 1907. Premaxillaries broadly and solidly fused anteriorly, their boundaries completely lost in adults; bony palate not narrowing behind tooth rows; width of the interpterygoid fossa (including hamulars) slightly greater than distance between posterior molars; canines parallel when jaws closed; lower canines in contact with each other; no lower incisors; cheek teeth not usually cuspidate.
4. Harpyionycterinae Miller, 1907. Premaxillaries broadly and solidly fused anteriorly, their boundaries completely lost in adults; bony palate narrowing rapidly behind tooth rows; canines crossing each other at nearly right angles when jaws are closed; lower canines almost in contact with each other; lower incisors probably absent; cheek teeth cuspidate, each molar with five or six distinct sharply pointed cusps.

Meschinelli (1903) described the first known fossil fruit bat, *Archaeopteropus transiens*, from the Oligocene of Italy. Simpson (1945) made it the basis for a new subfamily, the Archaeopteropodinae. He did not give a diagnosis, presumably because of the elaborate original description of its type species. Habersetzer *et al.* (1987), who examined a surviving cast of the apparently lost type specimen of *A. transiens*, diagnosed it as Megachiroptera (because of considerable body size, broad plagiopatagium, high wing tip index, strong clawed thumb, strong second digit with claw, particular characters of the humerus, and long legs) and agreed that it should be placed in a subfamily of its own. They mentioned the following diagnostic characters:

5. Archaeopteropodinae. Third finger with three bony phalanges and long end phalanx; long tail (with ten caudal vertebrae, as in *Notopteris* Gray, 1859); teeth with pointed cusps (compare Dal Piaz, 1937, fig. 2); epitrochlea of humerus with relatively high and strong processus styloides; long, bony calcar at foot; relatively low measure of isometry of metacarpalia and basic phalanges of digits 3 to 5.

Andersen, in his revision of the Megachiroptera (1912), admitted to have changed some of his views during the years he worked at it, as is reflected in some places. In his treatment of plastic characters we can read (e.g. on pp. xlvi-xlvii) that the four natural sections (i.e. taxa on the level between subfamily and genus) of Megachiroptera are 1. the *Rousettus* section (including *Harpyionycteris),* 2. the *Epomophorus* section, and 3. the *Cynopterus* section (including *Nyctimene*), together forming the Pteropodinae; and 4. the Macroglossinae (or even Macroglossine section: see p. lii). However, in the taxonomic part the Harpyionycterinae are treated as a subfamily; he explained this as follows: "...the present genus ought to be classed in the subfamily *Pteropodinae,* immediately after *Dobsonia,* and it would have been so here, if not for the fact that the plan of this Catalogue (subdivision into subfamilies) had to be outlined before all the genera and species of Fruit-bats had been worked out in detail by the writer." (Andersen, 1912: 803-804). Another inconsistency is the division of the Macroglossinae into an *Eonycteris* section and a *Notopteris* section (p. lxiii) - which would enlarge the number of natural sections to five. Later these would appear subsections: In a final tree figure, showing the interrelations of subfamilies, sections and subsections (Fig. VI, p. lxv), Andersen named his sections Rousetti, Epomophori and Cynopteri, and his subsections Eonycterides and Notopterides. Andersen rejected subfamily status for Miller's Nyctimeninae and Harpyionycterinae, and had very serious doubts about the value of the Macroglossinae as a subfamily, truly distinct from the Pteropodinae (see p. 728). Therefore, his proposed division of the Megachiroptera into sections and subsections must stand as one of his most important contributions to the suprageneric taxonomy of Megachiroptera. The "section" as taxonomic category was used by some authors as one of the terms to name additional taxonomical subdivisions (cf. Mayr, 1969: 89-90). Andersen's most relevant diagnoses (somewhat abbreviated) are as follows:

1. Pteropodinae (p. xcii): Tongue simple: fixed to floor of mouth by posterior half, and without unfringed filiform papillae at tip.
    1.1. *Rousettus* section or Rousetti (of this, Andersen gave no diagnosis, but this can easily be drawn up from those of the subsections): Cranium simple or only slightly modified; rostrum not or slightly shortened; premaxillae simple or reduced in breadth; occiput either not elongated or subtubular; dental formula usually unmodified but loss of last molars in one species and of incisors in the dobsonian subsection; molar structure simple or specialized; tail present or absent; 3rd or 5th metacarpal longer than the others.
    1.1.1. Rousettine subsection (p.lii): Cranial characters simple, unmodified: rostrum never shortened; premaxillae not sublinear; occiput neither elongated nor subtubular; full megachiropteran dental formula (exceptions occasional); simple form of premolars and molars; tail present; 3rd metacarpal nearly always slightly but distinctly longer than 4th and 5th.
    1.1.2. Pteropine subsection (pp. lii-liii): Cranial characters rousettine except for the more subtubular occiput and relatively narrower palate; dental formula unmodified (exception: *Styloctenium*); molar structure sometimes simple but more often showing some degree of specialization; tail absent; 5th metacarpal nearly always slightly but distinctly longer than 3rd and 4th.
    1.1.3. Dobsonian subsection (including *Harpyionycteris*): Rostrum somewhat shortened; premaxillae reduced in breadth; lower canines situated close together at the extremity of the mandible; 1st upper

and lower incisors lost; molariform teeth with pronounced tendency to a high degree of specialization; tail present or absent; 3rd metacarpal nearly always distinctly the longest, 4th shortest, 5th intermediate.

1.2. *Epomophorus* section (p. lv) or Epomophori: Dentition on the whole weak; $P^1$, $M^2$ and $M_3$ lost except in *Plerotes*, which has retained $P^1$ and $M_3$ in rudimentary condition; molar structure simple, except for degeneration of surface structure in *Plerotes* and splitting of some ridges in *Hypsignathus*; 2 upper and 2 lower incisors; facial axis very little deflected against cranial axis (except *Plerotes*); brain-case distinctly flattened posteriorly (also found in the rousettine *Lissonycteris*); form of postdental palate highly variable; palate ridges more or less highly specialized (except *Plerotes*); tail rudimentary, not connected with interfemoral, or absent; often unusually highly developed secondary sexual characters.

1.2.1. *Epomops* subsection (p. lvi): Rostrum long; palate broad; postdental palate simple; at least some of the postdental palatal ridges unmodified (except in *Epomops dobsonii*).

1.2.2. *Nanonycteris* subsection (p. lvi): rostrum much shortened; postdental palate highly variable; postdental palatal ridges as in *Epomops* subsection.

1.2.3. *Epomophorus* subsection: rostrum varying in length; postdental palate depressed posteriorly; all palate-ridges modified.

1.3. *Cynopterus* section (p. lix) or Cynopteri (including *Nyctimene*): Rostrum conspicuously shortened; facial axis of skull only very slightly deflected (except *Myonycteris* and *Sphaerias*); 4 upper and 5 lower cheek-teeth (5 upper in *Balionycteris*, 5 upper and 6 lower in *Myonycteris*); prominent and crowded palate-ridges (except in *Myonycteris*); more numerous, large and crowded odontoid papillae than in other sections (exception: *Myonycteris*).

2. Macroglossinae (p. xcvii): Tongue more extensible, fixed to floor of mouth by its posterior third, its terminal fourth or fifth covered above with unfringed filiform papillae.

2.1. Eonycterine section (p. lxiii) or subsection Eonycterides (p. lxv): Infra-orbital canal short (as in Pteropodinae); premaxillae not or very little broader above than below; 3rd metacarpal longer than 4th and 5th or subequal; terminal phalanx of 3rd digit shorter than 3rd metacarpal.

2.2. Notopterine section (p. lxiii) or subsection Notopterides (p. lxv): infraorbital canal much less reduced; infraorbital foramen situated a considerable distance in front of orbit; praemaxillae about thrice or twice as broad above as below; long tail in one genus (*Notopteris*); 3rd metacarpal shorter than 5th; terminal phalanx of 3rd digit subequal to or longer than 3rd metacarpal.

Andersen critically analysed the description of *Archaeopteropus transiens*, and found it to have a genuine megachiropteran hand, perhaps a little more primitive than that of any living bat; from the published plate, he could not control the molar structure, and he did not refer the species to a subfamily. Simpson (1945) recognized the four subfamilies of Miller and proposed a fifth, Archaeopteropodinae, to accomodate *Archaeopteropus*. Lawrence *et al.* (1963) argued that the genera *Lissonycteris* and *Myonycteris* should be considered a section, apart from both the rousettine and cynopterine sections in which they had respectively been placed, and closer to the epomophorine section. Koopman *et al.* (1970), in a classification of all bats, proposed six tribes and five subtribes for the Megachiroptera, the majority of which is identical with Andersen's sections and subsections: The Pteropodinae were divided into the tribes Pteropini (= Andersen's *Rousettus* section), with subtribes Rousettina, Pteropodina and Dobsoniina; Harpyionycterini; Epomophorini (Andersen's *Epomophorus* section); and Cynopterini (with subtribes Cynopterina and Nyctimenina) (Andersen's *Cynopterus* section); the Macroglossinae were divided into the tribes Macroglossini (= Andersen's Eonycterine section) and Notopterini (Andersen's *Notopterus* section). Koopman *et al.* (1970) did not discuss the earlier literature nor did they include diagnoses of the (newly) proposed tribes and subtribes. Very short diagnoses were finally provided by Koopman (1994); apart from the inclusion of *Myonycteris* in the Rousettina, they contain no elements not also found in Andersen (1912). Hill *et al.* (1984) and Corbet *et al.* (1991; 1992) listed the four Recent subfamilies as in Miller (1907), and did not discuss suprageneric taxonomy. The latter authors listed the Archaeopteropodinae, and suggested that the second known fossil fruit bat, the Miocene *Propotto leakeyi* Simpson, 1967 should possibly be placed in a new subfamily. Hood (1989) showed that *Megaloglossus* is different from the other Macroglossinae in the morphology of the female reproductive tract. Colgan *et al.* (1995), who did not include *Megaloglossus*, found in their restriction fragment-length polymorphism study that the other macroglossine genera do not cluster together, and suggested polyphyly of the Macroglossinae. Kirsch *et al.* (1995) found as result of their DNA-hybridisation study, that the basic dichotomy among pteropodids appears to be between the nyctimenines and all other species, and confirmed that *Megaloglossus* is part of a discrete African assemblage. They recognized (at least) the subfamilies Pteropodinae (including the Macroglossinae) and the Nyctimeninae and a separation between *Pteropus*-like genera and *Rousettus*-like genera of the *Rousettus*-section. Springer *et al.* (1995) presented a list of morphological characters and character states for megachiropteran genera, gleaned from Andersen (1912) and Hood (1989). They leaned heavily on Andersen's interpretations and their cladistic analysis resulted in a phylogeny which is largely consistent with Andersen's. However, since Andersen wrote, some of the character states used have been explained in different ways. Also, new species have been described which have necessitated adaptations of the diagnoses of several genera (e.g. *Scotonycteris*, *Pteralopex*, *Rousettus*, *Myonycteris*), and several new genera, among which the peculiar *Neopteryx*, have been described. Moreover, some of the interpretations in Springer *et al.* are open to question. Some of the problems noted are shortly discussed below.

1. Length of the rostrum. A "medium or moderate length" (Springer *et al.*, 1995) is taken to be primitive. This is based on Andersen's valuation of the rousettine subsection of his *Rousettus* section, in which the "rostrum [is] never shortened" (Andersen, 1912: lii), and which for African *Rousettus* (except *R. obliviosus*, for which there are no data) and *Eidolon* species means that rostrum length equals 35-41% of the greatest skull length (Bergmans, 1990, 1994). Tomes (1860) emphasized that small species tend to retain juvenile traits in their adult stage to a larger extent than do larger species of the same higher taxon. Juvenile fruit bats have a smaller relative rostrum length than adults. Adults of small species have smaller relative rostrum length than adults of related large species. The Epomophorinae offers several examples: *Epomophorus*, *Scotonycteris*. If a medium or moderate rostrum length is primitive, is large overall size also primitive?
2. Deflection of facial axis relative to basicranial axis. "Little or no deflection" (Springer *et al.*, 1995; after Andersen, 1912: xvii) is regarded as primitive. However, within Recent genera of Andersen's *Rousettus* section and in the Macroglossinae (sensu Andersen, 1912), facial deflection is highly variable; it is generally greatest in genera and species with weak dentition (Andersen, 1912: xxiii; see on *Rousettus* also Bergmans, 1994: 81, and this paper), which itself is most probably derived (see under 4). Another aspect is that in juvenile fruit bats deflection is stronger than in adults and that smaller species may retain a stronger measure of this neotene deflection in adult life than larger species of the same genus (compare Tomes, 1860; Bergmans, 1977a).
3. Upper incisors. The presence of two incisors on each side is considered primitive. In *Rousettus bidens* (*Boneia* in Springer *et al.*, 1995), $I^1$ may be present on both sides, or one or both may be lost (Bergmans *et al.*, 1988). It can not just be listed as "lost" as in Springer *et al.* And if *Boneia* is synonymized with *Rousettus* (see Bergmans *et al.*, 1988; Corbet *et al.*, 1992; Bergmans, 1994, this paper), the problem presents itself what to do with obviously derived characters which have different states in species of the same genus. This problem is also met with in *Myonycteris*, where one species has lost $M_3$, and in *Eonycteris spelaea*, where $M_3$ is optional in one subspecies. These examples illustrate the general problem to identify actu-

al character states in supraspecific taxa of elements of the anatomy that are evidently subject to active processes of change. Should the character state be "in the process of losing $I^1$"?

4. Well-developed cheek teeth cusps. These are regarded by Springer *et al.* (1995) as derived features. This conclusion is based on the widespread occurrence among fruit bats of cheek-teeth without such cusps. However, in many species one can observe - if one studies series of specimens - that the dentition is actively degenerating; teeth become more simple and smaller, and especially first premolars and last molars may be lost or are in the process of disappearing (e.g. in *Myonycteris torquata*; see Bergmans, 1976). (The loss of incisors probably has several causes.) This process strongly suggests that in early Megachiroptera the original form of the molariform teeth must have been more complicated than what we see now in most species. The known details on the dentition of *Archeopteropus transiens* do support this (as do dentitions in Microchiroptera and Insectivora, which Springer *et al.* mentioned as their outgroups). Hill *et al.* (1978), studying the genus *Pteralopex* Thomas, 1888 and reviewing the literature on multicuspidate molariform teeth in Megachiroptera, concluded that it is perhaps more plausible to suggest that the smoother or laterally ridged crown represents a derived condition, instead of the multicuspidate condition.
5. Origin of membranes. *Rousettus* is classed as having its wings inserted high on dorsum, but *R. spinalatus* has them connected with the integument of the dorsum along the spinal line. This species is rather difficult to separate from *R. amplexicaudatus* by other differences, and their monophyly can hardly be questioned.

Springer *et al.* (1995) found Andersen's *Epomophorus* and *Cynopterus* sections both to be monophyletic (with the exclusion of *Plerotes* from the former and *Myonycteris* from the latter - the second conclusion being consistent with the results of Lawrence *et al.*, 1963), and his *Rousettus* section was found to be paraphyletic. Earlier in the present paper it has been argued that *Myonycteris* and *Lissonycteris* are closely related, synonymy being suggested but not yet claimed because of incomplete knowledge of some of the species involved. In a forthcoming paper by Juste B. *et al.*, a draft of which was kindly shown to the present author, evolutionary relationships between *Rousettus*, *Lissonycteris* and *Myonycteris* on the basis of electrophoretic analysis of 31 presumptive loci encoding 22 enzymatic systems are examined. Not all species of these genera could be considered, but *Lissonycteris* was found to differ from *Rousettus* and provisionally included, as a subgenus, in *Myonycteris*.

Based on the developments and considerations outlined above, and on the result of the present and other work by the author, the following tentative classification for Recent Megachiroptera (plus *Archaeopteropus*) is proposed. As explained above, this of course differs from that to be found for the African representatives in Bergmans (1988: 78). Subfamilies are arranged in chronological order of description, and for practical reasons authors of genera have been omitted. The genera wholly or partly treated in this series are marked with an *.

## SUBORDER MEGACHIROPTERA Dobson, 1875

Family Pteropodidae Gray, 1821
    Subfamily Pteropodinae Gray, 1821
        Tribe Pteropodini Gray, 1821
            Genera *Pteropus**, *Acerodon*, *Pteralopex*, *Styloctenium*, *Neopteryx*
        Tribe Macroglossini Gray, 1866
            Genera *Macroglossus* (type), *Syconycteris*
        Tribe Notopterini Andersen, 1912
            Genera *Notopteris* (type), *Melonycteris*, *Nesonycteris*
    Subfamily Nyctimeninae Miller, 1907
            Genera *Nyctimene* (type), *Paranyctimene*
    Subfamily Harpyionycterinae Miller, 1907
            Genus *Harpyionycteris*
    Subfamily Rousettinae Andersen, 1912
        Tribe Rousettini Andersen, 1912
            Genera *Rousettus** (type), *Eonycteris*, *Eidolon**
        Tribe Dobsoniini Andersen, 1912
            Genus *Dobsonia* (type), *Aproteles*
    Subfamily Epomophorinae Andersen, 1912
        Tribe Epomophorini Gray, 1866
            Genera *Epomophorus** (type), *Micropteropus**, *Hypsignathus**, *Epomops**, *Nanonycteris**
        Tribe Myonycterini Lawrence & Novick, 1963
            Genera *Myonycteris** (type), *Lissonycteris**, *Megaloglossus**
        Tribe Scotonycterini, new tribe
            Genera *Scotonycteris** (type), *Casinycteris**
        Tribe Plerotini, new tribe
            Genus *Plerotes** (type)
    Subfamily Cynopterinae Andersen, 1912
            Genera *Cynopterus* (type), *Ptenochirus*, *Megaerops*, *Dyacopterus*, *Balionycteris*, *Chironax*, *Thoopterus*, *Sphaerias*, *Aethalops*, *Penthetor*, *Latidens*, *Alionycteris*, *Otopteropus*, *Haplonycteris*
    Subfamily Archaeopteropodinae Simpson, 1945
            Genus *Archaeopteropus* (type)

In this classification, the Rousettinae, Epomophorinae and Cynopterinae, often recognized as distinct units, in particular by Andersen (1912), have been raised to subfamily rank. The Rousettinae is an apparently very old unit with a comparatively very large world distribution, matched only by the Pteropodinae, and the nearly unique habit among fruit bats of roosting in caves (only *Eidolon* roosts in trees, but see also the account of *E. dupreanum*, and the Epomophorine *Lissonycteris* also roosts in caves), which in the type genus *Rousettus* is connected with the development of an echolocation system. (The inclusion of *Eonycteris*, morphologically very similar to *Rousettus*, is tentative.) The Epomophorinae is a strictly African assemblage of 11 distinctive genera which have no apparent close relatives among other fruit bats. Their skull build, dental formula and palatal ridge patterns distinguish them, as does in many species the very outspoken sexual dimorphism. The Scotonycterini and Plerotini are both probably rather old and relatively aberrant units. The inclusion of the Plerotini in the Epomophorinae is tentative, pending a more complete knowledge of the single known species. The Cynopterinae is an Indomalayan assemblage of 14 distinctive genera which have no apparent close relatives among other fruit bats. Their stout skull build, short rostrum, dental formula, typical palatal ridges and odontoid papillae distinguish them.

Below, the diagnosis of the Pteropodinae is adapted because of the inclusion of most macroglossine genera and the exclusion of the rousettine and dobsonian subsections, and to differentiate it from the subfamily Archaeopteropodinae. Furthermore, the newly proposed tribes are diagnosed. (A systematic effort to diagnose all supra-generic taxa, in which *all* diagnostic characters used are examined in *all* taxa of the same rank and interpreted cladistically, is desirable but because of its much larger geographic extent falls outside the scope of this series. It will be the subject of a further study, as a logical follow-up of the present series.)

Subfamily Pteropodinae: Rostrum not shortened; premaxillae either in simple contact (or even narrowly spaced) or solidly united; palatum relatively narrow, narrowing behind tooth rows, with pterygoid fossa less than distance between posterior molars; cheek teeth usually well-developed, structure simple or more often with some degree of specialization; epitrochlea of humerus with relatively weak and low processus styloides; third finger with two bony phalanges; fifth metacarpal usually longer than, or subequal to, third; wing membrane from second, third, or fourth toe; calcar well developed or practically absent; tail rudimentary or absent, or, in *Notopteris*, exceptionally long.

Tribe Myonycterini (type genus *Myonycteris* Matschie, 1899): Rostrum shortened in the smaller species and little or not in the larger species; premaxillae in simple contact in some species, fused in front in others, and possibly sometimes fused in one species; postdental palate converging antero-posteriorly; dental formula normally 2/2, 1/1, 3/3, 2/3, but one $I_1$ lost in one species, $M^2$ and $M_2$ small to very small, and $M_3$ small to rudimentary and lost in one species; cheek teeth specialized, often short, roughly rectangular or squarish, with a tendency to wide spacing; palatal ridges from front to back: 3-4 undivided, 2-4 divided, and 1-2 serrate; 3rd metacarpal longer than or subequal in length to 5th; wings from 2nd toe; toes distinctly webbed; tail short to rudimentary; overall fur colour usually not light but rather dark; interfemoral furred; adult males with ventral collar of thick hairs.

Tribe Scotonycterini (type genus *Scotonycteris* Matschie, 1894): Skull and mandible solidly built; rostrum short and anteriorly narrow; praemaxillae well-developed, in simple contact; palate posteriorly not concave; postdental palatum either present, tapering backwards, or absent; canines relatively tall to very tall, curving backward, with or without an inner cusp; maxillary tooth rows diverging antero-posteriorly, teeth posterior in position, with large diastema $C^1$-$P^3$ and $M^1$ near ventral margin of orbital cavity; premolars and molars short, oval or subcircular; $M^1$ smaller than $P^4$ and $M_1$ smaller than $P_4$; palate with 3 to 7 thick and 6-16 thin and serrate ridges; overall fur colour a rather dark brown hue; white fur patches on dorsum of rostrum and behind eyes; white ear tufts either indistinct or absent; no shoulder tufts in adult males; wings from first toe; finger joints either same as or contrasting with dark wing membrane colour.

Tribe Plerotini (type genus *Plerotes* Andersen, 1910): Skull rather delicately built, and skull axis in the only species known distinctly deflected; rostrum low and broad, not shortened (39.3 % of gsl); praemaxillae relatively broad throughout, slanted forward, separated in front; palate broad, posteriorly not concave; teeth reduced in size; $P^1$, $M^2$, and $M_3$ may be present, in rudimentary form; surfaces of molars with traces of lateral ridges and median grooves only; 4 simple palate ridges and 4 divided and/or serrate ones; overall fur colour as in Epomophorini; white tufts at ear bases; wings from second toe.

Taxonomy of African species: The views of the present author on the taxonomy of African genera, species and subspecies have been dealt with in the species accounts in the successive parts of this series (Bergmans, 1988, 1989, 1990, 1994, this paper) and need not be repeated here. However, during these years, others have produced papers relevant to the subject. They are shortly reviewed and discussed in this section.

1. The most recent treatment of fruit bat taxonomy is to be found in Koopman (1994). That work was essentially completed in 1988, and few data were added since. The taxonomy of African species is largely consistent with Hayman *et al.* (1971). Notable exceptions are the lowering of *Pteropus aldabrensis* to subspecific rank under *P. seychellensis* (following Hill, 1971), the ranking of *Epomophorus anurus* as subspecies of *E. labiatus* (following Kock, 1969), and the recognition of *Rousettus madagascariensis* as a species, and not a subspecies of *R. lanosus* (following Bergmans, 1977). The first two of these and a number of other concepts regarding the species level in Koopman (1994) are not supported by the present author: *Epomophorus crypturus* and *E. pousarguesi* are considered subspecies of *E. gambianus*, *E. reii* as a synonym of that species, and *E. gambianus parvus* as a synonym of *E. gambianus crypturus*. *E. labiatus anurus* is considered a synonym of *E. labiatus*. The division of *E. wahlbergi* into two subspecies is not accepted. *Micropteropus grandis* is classified as *Epomophorus grandis*. The named subspecies of *Epomops franqueti*, *Scotonycteris zenkeri* and *Pteropus rufus* are not retained. *Eidolon helvum dupreanum* is considered a species, distinct from *E. helvum*. The subgenera *Rousettus* and *Stenonycteris* of the genus *Rousettus* are considered synonyms and the subgenus *Lissonycteris* is considered a genus, not closely related to *Rousettus*. The named subspecies of *Rousettus lanosus* are synonymized. The subgenera *Myonycteris* and *Phygetis* of *Myonycteris*, and the subspecies of *Myonycteris torquata*, i.e. *torquata*, *smithi* and *wroughtoni*, are not recognized. The subspecies of *Megaloglossus woermanni* are also not recognized.

2. After the review of the genus *Epomophorus* by the present author in 1988, Claessen *et al.* (1990) published theirs of some larger species of this genus. Their results essentially duplicate those in Bergmans (1988) but some of their interpretations differ. First, *E. gambianus crypturus* is considered a full species because there is no indication that it would represent the end of a (*gambianus*) cline, because of the large gap dividing typical *gambianus* and *crypturus* - while, according to these authors, the gap area would have been searched extensively for fruit bats -, and because of the advantage of not having to change a commonly used name. It is not the view of the present author that subspecies are necessarily parts of clines; with considerable variations, large gaps in African savanna species' distributions are numerous (e.g. giraffe, suni, Kirk's dikdik, steenbok, oribi, oryx, mountain reedbuck, rock hyrax, Kaokoveld ground squirrel, Cape hare, black-backed jackal, bat-eared fox, aardwolf and caracal, to mention some field guide examples). Balinsky (1962) introduced the idea of a "drought corridor", running roughly from Somalia to the Cape. This corridor was closed or narrowed by forests during cold and wet periods, enabling animals from the wet tropics to migrate from west to east and *vice versa*, and linking the arid southwest with the Somaliland arid area during hot and dry periods, thus accounting for the close links in the fauna of these areas. As Bigalke (1972) put it, the concept of a drought corridor offers a simple and satisfying way of unifying our ideas on discontinuous distribution and the historical events of which it is the result. Further, although not very relevant, it cannot be sustained that the gap in the area of *gambianus* - notably southeast Zaïre, northern Zambia and eastern, central and southern Tanzania - has been searched well for fruit bats: *Epomops dobsonii*, *Plerotes anchietae*, *Eidolon helvum*, *Rousettus lanosus*, and *Myonycteris relicta* are known from this area by one or a few specimens at most.

A second conclusion of Claessen *et al.* (1990) is the synonymization of *E. gambianus pousarguesi* with *E. g. gambianus*. According to Bergmans (1978), the only character distinguishing the two is the larger size of *pousarguesi*. In 1988 he synonymized them, but retained subspecific status for *pousarguesi* on the basis of its large measurements and because, on the basis of available evidence, he assumed it to represent a geographically isolated and ecologically different population. Claessen *et al.* did not examine *pousarguesi* material and did not find new distributional data. They found some typical *gambianus* with gsl ranges surpassing those given by Bergmans (1988: 87, and table 2) with 0.5 mm in ♂♂ and with 0.1 mm in ♀♀, and neglected the fact that the size ranges in *pousarguesi* are not known. They did not compare body measurements and did not add anything new on distribution or ecology. Therefore, their conclusion appears slightly precocious.

Finally, Claessen *et al.* found that the specimens from Sudan (an adult ♂ from Talanga and 2 immature ♀♀ from Gilo) listed under *gambianus* by Bergmans (1988), are in fact *wahlbergi* - the first for Sudan. As Claessen *et al.* had the skull of the adult extracted, their identification should be correct. In this connection it should be noted that whereas Kock (1969: 19) described the origin of two SMF specimens of *gambianus* labelled "Sennar" as uncertain, Claessen *et al.* mapped this locality for the species without comment.

3. In 1991, Claessen *et al.* published a revision of what they called, after Kingdon (1974), "the *Epomophorus anurus-labiatus-minor* complex". They synonymized *E. anurus* with *E. labiatus* which duplicates Bergmans (1988) and needs no further attention here. The results further include the description of a new species, *E. minimus*, based on Ethiopian, Somalian and Kenyan populations (with some localities just across the Kenyan borders with Uganda and Tanzania) of what had earlier been generally considered as *E. minor.* The new species differs from *E. labiatus* (including the remainder of *minor*, which is synonymized with *labiatus)* mainly in having smaller relative braincase width, smaller relative postdental palatal length, smaller relative $C^1$-$M^1$, and larger relative zygomatic width. *E. minimus* averages considerably smaller than *E. labiatus* in all measurements in localities were the species occur together (Claessen *et al.*, 1991). The general results of the principal component analysis of skull measurements by Claessen *et al.* (1991) look quite convincing. However, the dimensional variations in body and skull accepted for *labiatus* when including *minor*, i.e. of 37.3% in gsl (ranges 35.4-48.6 in ♂♂ and 33.5-46.0 in ♀♀) and 30.4-35.3% in fal (ranges 58.9-79.7 in ♂♂ and 58.3-76.0 in ♀♀; all ranges: Claessen *et al.*, 1991) are strikingly large for the relatively limited and continuous region under consideration, and would call for a further explanation. Claessen *et al.* (1991: 210) wrote that the results and conclusions presented by Bergmans *et al.* (1983), Baeten *et al.* (1984) and McLellan (1986) were on several points contradictory to their results. In short, Claessen *et al.* were often unable to allocate specimens from Tanzania to either *labiatus* or *minor* and could not detect a disjunction in their measurements; sexual dimorphism in body measurements in both small and large forms would not be reflected by the measurement ranges given by Bergmans (1988); they found the distributional gap between *labiatus* in Tanzania and Malawi to be "at least remarkable for such an intensively prospected area (...)"; they found specimens from Rwanda and Sudan identified as *minor* by Baeten *et al.* (1984) and McLellan (1986), respectively, to represent juvenile *labiatus*; they could not find differences between *labiatus* specimens from Rwanda and the more southern *labiatus* and *minor.* However, Bergmans (1988) extensively discussed the possible synonymy of the two taxa and concluded that (his) understanding of the relation between them was still unsatisfactory. The contention that the measurements given by Bergmans (1988) did not reflect sexual dimorphism in body size is simply not true. Nor can it be sustained, as observed above, that southeast Zaïre, northern Zambia and large parts of Tanzania have been prospected intensively for fruit bats. Although Claessen *et al.* (1991: 220-221) claimed to have studied the material from Malawi recorded as *labiatus* and *minor* by Bergmans *et al.* (1983) they never did, and they ignored the evidence that 'large' *labiatus* (reported as *anurus*) and small (but adult) *minor* had been found side by side in Malawi (Bergmans *et al.*, 1983). According to Claessen *et al.* "The maximum of gsl of ♀ *labiatus* in this region [the region of sympatry] is at most 40 mm, whereas the minimum of gsl of *crypturus* is 42.7 mm (...)." Incidentally, the latter measurement is also of a ♀. It is not explained why male measurements are left out. The present author measured a gsl range of 51.8-55.7 in *crypturus* ♂♂ (Claessen *et al.*: 51.2-56.0) and, in Malawi, a gsl of 47.1 in a ♂ of *labiatus* (further represented by a similar, subadult ♂) and a range of 35.4-39.3 in *minor* ♂♂ (both: sensu Bergmans, 1988). The situation in Malawi is particularly interesting, as the two intermediate specimens match the size of *labiatus* in the northeast of its range. Unless yet another new species is involved here, these specimens corrupt the concept of clinal variation in measurements (large specimens in the north, getting smaller going from west to east and from north to south) as postulated for *labiatus* by Claessen *et al.* (1991). Furthermore, Claessen *et al.* refrained from discussing reports on the occurrence of *labiatus* in Senegal (F. Adam *et al.*, 1972;

disputed by Bergmans, 1988), Ghana (Koopman, 1989; material so identified no longer to be found in the ROM collection: Dr. J. L. Eger, *in lit.*, 18-XII-1995), Congo (Bergmans, 1979), and Nigeria (Bergmans, 1988).

4. Gaucher (1992) recorded *Epomophorus labiatus* from the Arabian Peninsula, which is the first record of *Epomophorus* outside Africa.

5. Volpers *et al.* (1995) examined the ecological differences between *Epomophorus gambianus crypturus* and *E. wahlbergi* in Zimbabwe and found that there is not much distributional overlap. The first species is able to inhabit drier woodland with a long dry season, the second is restricted to river valleys and eastern mountain slopes with a good water supply for the arboreal vegetation and a relatively even climate. Their map shows that some earlier records of *wahlbergi* from central Zimbabwe were in fact based on misidentified *gambianus crypturus.*

6. Carroll *et al.* (1991) and Reason *et al.* (1994a, b) published new data on the occurrence and status of Megachiroptera of the Comoro Islands: *Pteropus livingstonii*, *P. seychellensis comorensis* and *Rousettus obliviosus.*

7. Peterson *et al.* (1995) published a book on the bats of Madagascar. This work had been left unfinished by the late Dr. R. L. Peterson, and was completed after his death by Dr. J. L. Eger and Dr. L. Mitchell. In this paper, *Pteropus rufus* (E. Geoffroy St.-Hilaire, 1803) is considered as probably monotypical, and *Eidolon dupreanum* (Pollen, 1867) as a species, different from *E. helvum* (Kerr, 1792). These conclusions support those by the present author (Bergmans, 1990) - who incidentally left out a reference to differences in baculum morphology between the two *Eidolon* species, as described by Didier (1965). In trying to place *Rousettus madagascariensis* Grandidier, 1929, Peterson *et al.* (1995) endeavoured a revision of all *Rousettus*, *Lissonycteris* and *Myonycteris* on the basis of multivariate analyses. Two of their conclusions are not acceptable to the present author: *Rousettus obliviosus*, of which they could not examine material, is considered a subspecies of *R. madagascariensis*; and *Myonycteris relicta* is considered to have no relations with other *Myonycteris* but to represent a species of *Rousettus.*

8. Cosson *et al.* (in press) recorded the occurrence of *Eidolon helvum* in Nouakchott, Mauretania, 240 km north of the most northern collecting locality for the species on the African west coast published so far. A record withheld in the account of this species by the present author (Bergmans, 1990) because he strongly doubted its reliability, but which now wins somewhat in credibility and at least deserves mentioning after all, is specimen ZMB 20528, according to its label caught on high sea near Las Palmas, Canary Islands on 8-IV-1915 by S. Kiekebusch and presented to the museum by the Zoologische Garten (probably of Berlin). Even if we assume that it has been caught south of Gran Canaria, this locality would be at least 1000 km north of Nouakchott.

9. Juste *et al.* (1993) described *Rousettus egyptiacus princeps* n. ssp. from the island of Principe and *R. e. tomensis* n. ssp. from the island of Sao Tomé. *R. e. princeps* has a small body, small and rounded ears, long fur, a small skull with posterior width not surpassing interorbital width, a narrow brain-case, robust zygomatic arches, and relatively strong mandibulum and teeth. *R. e. tomensis* is slightly larger than *R. e. unicolor*, has short and rounded ears, long and fluffy fur, a large skull with postorbital constriction elongated and usually not wider than interorbital width, a narrow brain-case, robust zygomatic arches, a massive mandibulum, and strong premolars and molars.

Distributional patterns: Megachiroptera are more or less specialized herbivores and in this series the species' distributions have been described in relation to the vegetation types as mapped by White (1983). For a general view, this has proven to be a very useful approach, explaining many details of the patterns found. On the other hand, it should always be kept in mind that White's map through its scale (1 : 5.000.000) necessarily leaves out many small elements, like small isolated forests and gallery forests, often crucial to fruit bat occurrence and dispersal.

From an ecological perspective, it may be useful to compare fruit bat distributions with those of fruit trees or plants with a proven essential value to them. This may yield further clues for distributional analyses and arguments for the important ecological roles of fruit bat species in forest and savanna conservation.

Many biogeographers tend to think of bats that "their mobility makes them of little zoogeographic interest" (e.g. Bigalke, 1972). The assumptions implicit in this statement, that bats may easily colonize islands, that mountain ridges or rivers cannot present serious barriers to them, etc., are of course only partly true. The capability to fly should not be confused with unlimited mobility. Geological and climatological events affect bats in similar ways as other species, and are reflected in their distribution and geographical variation (compare Kingdon, 1971; Bigalke, 1978). The greater mobility certainly adds an element to consider, with bats often being among the first colonizers of earlier abandoned or new and empty ground, but this does not apply to all bat species to the same degree, and complicates the task to explain the patterns found.

For a first appraisal of the collected distributional data on African fruit bats the species and subspecies, and in some cases populations, are grouped into four categories: island, forest, woodland, and generalist taxa. The following notes must be concise. Available details can be found in the species accounts in this series.

1. Island taxa

Exclusive island taxa belong to the genera *Pteropus* (8 species and 2 subspecies), *Rousettus* (2 species and 2 subspecies), *Eidolon* (1 species), and *Myonycteris* (1 species). *Eidolon* populations on Principe and Sao Tomé have not been distinguished from the mainland subspecies. Juste *et al.* (1994a) listed *Eidolon helvum* ssp? for Annobón. On Bioko, some slightly differentiated populations of the mainland species *Scotonycteris zenkeri* and *Lissonycteris angolensis angolensis* are found. In this survey, they are treated together with the mainland populations. All island taxa are essentially forest species, and all are thought to originate from the African mainland. Juste *et al.* (1994b) described the origins of bats on the islands in the Gulf of Guinea, which must all have come from the African mainland. Meirte (1984b) suggested that *Pteropus* has colonized the islands east of Africa from Asia. In Asia and the Pacific islands the genus has both its largest distribution and its largest differentiation into species. Northeast monsoon wind updraughts would have helped it to bridge the distance from Pakistan and India to the Comores, from where it would have colonized the other islands. That Recent *Pteropus* species can be strong flyers is shown by *P. seychellensis*, which must at one time have reached Mafia and the Seychelles from the Comores (according to Meirte the most probable centre of origin), or the other way around, and recently by an Australian *Pteropus* which flew to New Zealand, a distance of approximately 2000 km (Daniel, 1975). Although Meirte's hypothesis is attractive, it has some weak elements and does not consider another, more parsimonious solution. Meirte did not discuss the geological time scale of the supposed immigrations, nor all the necessary conditions. At present, not a single physical condition is in place except the wind. Andersen (1912) recognized 17 species groups within *Pteropus*. The eight Recent African species represent four of these groups: one endemic and three which would have their nearest living relatives not in Pakistan or India but much further away, in southeast Asia and the Pacific. Several of the African species are exceptional members of their respective groups. (A phylogenetic analysis of *Pteropus* is much needed, and the outcome may alter the picture for African species, although they will remain a highly diverse assemblage.) The only species presently found in Pakistan and India, *Pteropus giganteus* (Brünnich, 1782), does not belong to any of the *Pteropus* groups represented in the African islands. Unless we would accept flights from, e.g., the Indonesian archipelago (which the present author is not inclined to do), Meirte's hypothesis for an Asian origin of African *Pteropus* would necessitate the assumption of a formerly much more extended distribution of forests and *Pteropus* groups in Pakistan and India, and at least three or four different waves of immigration from there into the African western Indian Ocean region. But a true vicariance model may offer a more parsimonious solution to the problem than Meirte's dispersal model. Probably during the Early Miocene, some 20 (or 18) to 25 million years ago, there was still a more or less continuous rain forest connection between Asia and Africa, as argued, e.g., by Kortlandt (1972) to explain the African/Asian ape divergence. These forests, and possibly their accompanying woodlands, may then have been inhabited by several ancestral *Pteropus* species, representing precursors of Andersen's different groups. These assemblages, or parts thereof, may have occurred in (East) Africa and its continental islands as well, and may have been the source for the western Indian Ocean islands. As Hamilton (1992) resumes, there is considerable macrofossil and pollen evidence from East Africa showing a decline in the extent of forest over the last 20 million years. With time, *Pteropus* has survived only on the mentioned islands. The island specialisation of the present species has more than once been mentioned as one of the reasons why not one *Pteropus* species has colonized mainland Africa (e.g. Kingdon, 1974, 1990). However, in the vicariance model this specialization is a secondary adaptation.

To explain the occurrence of the *Rousettus* species on Madagascar and the Comores, Meirte (1984b) suggested a similar history as for *Pteropus*. His arguments were the monsoon wind mentioned earlier, the fact that tropical Asia is richer in *Rousettus* than Africa and therefore the likely centre of origin, and the resemblance of the Asian *R. leschenaultii* and the African *R. madagascariensis*, *obliviosus* and *lanosus*. However, although *Rousettus egyptiacus* is known to have colonized Sao Tomé at some 250 km off the mainland coast, the bats under consideration are much smaller than *Pteropus*, and much less likely to fly thousands of km. Moreover, Asia is not really much richer in *Rousettus*. There are presently only five species in the oriental regions, against four in Africa. Two of the Asian species, *amplexicaudatus* and *leschenaultii*, are differentiated into subspecies, which is to be expected in island regions like Indo-Malaya; two, *celebensis* and *bidens*, are endemic to the composite island of Sulawesi (*celebensis* is also found on some small off-lying islands), and monotypical; and one, *spinalatus*, from Sumatra and Borneo, is as yet poorly known. In Africa, the two mainland species, *egyptiacus* and *lanosus*, have also differentiated into various subspecies or discrete (groups of) populations. Sympatry of oriental species is very restricted, with only two species being sympatric on parts of the southeastern Asian mainland and on any given island, with the single exception of Sulawesi where three are found. This indicates that differentiation in the region has been very much a consequence of island isolations. Other genera of the tribe Rousettini are *Eidolon* (two species, two subspecies) in Africa and *Eonycteris* (two species, five subspecies) in Asia. On the level of the subfamily Rousettinae, differentiation in the Oriental Region (here including the New Guinea area) is larger than in Africa: Next to the Rousettini, the Rousettinae include the tribe Dobsoniini with its 2 genera and 12 species - restricted, however, to the wider New Guinean and East Indonesian regions. But even if the origin of the subfamily would be Oriental, to judge by its plesiomorph traits and large distribution the genus *Rousettus* itself is obviously a very old taxon, and the number of Recent species does not seem the best criterion to go by when trying to assess the origin of the genus. Mainland Asia, including India and southeast Pakistan, is inhabited by *Rousettus leschenaultii*. (The other Asian mainland species, *R. amplexicaudatus*, is found only from Southeast Burma further to the East, and does not concern us here.) In Pakistan, *leschenaultii* meets *R. egyptiacus arabicus*. The latter represents a species with a long African history and by its relict-like distribution in Southwest Asia (fig. 1 *in* Bergmans, 1994), it appears to support the concept of a 'green' connection between Asia and Africa, although probably more recent than, and - for *Rousettus* - not necessarily as humid as the one discussed above for *Pteropus*. This concept can easily embrace the Asian *R. leschenaulti* and the African *R. egyptiacus* or their ancestor(s). The cutting up of the green connection has progressively isolated the African assemblage from the Asian one (the Arabian Gulf may have remained passable for some time), and it is this assemblage which has developed into the present-day African *Rousettus* fauna. The migrations to Madagascar and the Comores may have occurred before or after the African isolation.

The origin of *Eidolon dupreanum* on Madagascar must be the opposite African mainland, as it is clearly a less evolved branche of the *Eidolon helvum* lineage. That these and other bats reached Madagascar from Africa is in itself proof that Asia need not have been the source of *Pteropus* and *Rousettus* on the western Indian Ocean islands.

The species of the African mainland are divided in woodland, forest, and generalist species. The latter are thought to be of forest origin but occur

Table 7. Distribution of selected African fruit bat species. Vegetation types according to White, 1983*. Little or too widely recorded species and forest/savanna transitions not included.

| | « | | Forests | | | » | « | | Savannas | | | » | « | | | Drier types | | | » |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1a | 2 | 3 | 4 | 8 | 9 | 25 | 26 | 27 | 28 | 29 | 30 | 31<br>35 | 38<br>44 | 45 | 51<br>54 | 58<br>61 | 63<br>64 | 71<br>74 |
| *Scotonycteris ophiodon* | * | * | * | | | | | | | | | | | | | | | | |
| *S. zenkeri* | * | * | * | * | | | | | | | | | | | | | | | |
| *Epomops buettikoferi* | * | * | * | | * | | | | | | | | | | | | | | |
| *Casinycteris argynnis* | * | * | * | * | * | | | | | | | | | | | | | | |
| *Epomops franqueti* | * | * | | | | | * | | * | | | | | | | | | | |
| *Megaloglossus woermanni* | * | * | * | * | * | | * | | * | | | | | | | | | | |
| *Myonycteris torquata* | * | * | * | * | | | * | | * | | * | | | | | | | | |
| *Hypsignathus monstrosus* | * | * | * | | * | * | * | | * | | * | | | | | | | | |
| *Nanonycteris veldkampi* | * | * | * | | * | | | | | | | * | | | | | | | |
| *Lissonycteris angolensis* | * | * | * | * | * | | * | | * | | * | | * | * | * | | | | |
| *Plerotes anchietae* | | | | | | | * | | | | | | | | | | | | |
| *Micropteropus pusillus* | | | | | | | * | | | | * | | | | | | | | |
| *Epomops dobsonii* | | | | | | | * | | | | | | | | * | | | | |
| *Epomophorus wahlbergi* | | | | | | | * | * | | * | * | | | * | * | * | | | |
| *E. labiatus* | | (*) | | | | | * | * | * | | * | | * | * | * | * | * | * | * |
| *E. angolensis* | | | | | | | * | | | * | * | | | | | * | | | * |
| *Epomophorus g. gambianus* | (*) | | | | | | | | * | | * | * | * | * | | | | | |
| *E. g. crypturus* | | | | | | | | | | | | | * | * | | | * | | |

* Abbreviated legenda vegetation types: 1a = wetter lowland rain forest; 2 = drier ditto; 3 = mosaic 1a/2; 4 = transitional rain forest; 8 = swamp forest; 9 = mosaic 1a/8; 25 = wetter Zambezian miombo woodland; 26 = drier ditto; 27 = Sudanian woodland; 28 = *Colophospermum mopane* woodland and scrub woodland; 29 = undifferentiated woodland; 30 = ditto with *Isoberlinia* islands; 31/35 = woodland mosaics, transitions; 38/44 = bushland, thicket; 45 = mosaic bushland/grassland; 51/54 = semi-desert; 58/61 = grassland; 63/64 = edaphic grassland mosaics; 71/74 = desert.

in both forest and woodland - and beyond. Table 7 lists a number of forest and woodland species and their distribution over various vegetation types. Because species for which there are too few records, species which occur in all vegetation types, and forest/savanna transitions obscure the picture, these have all been left out. Admittedly, the categories forest, woodland and drier types (than woodlands) are strongly symplifying reality, but the table nevertheless mirrors some important facts. Some forest species appear to be very restricted; about half the forest species have also been found in woodlands (the few occurrences of woodland species in true forest are questioned); and most woodland species have also been found in drier vegetation types. The great divide between forest and woodland species is distinct. As the only tribe, the Scotonycterini is clearly restricted to the Lowland rain forest and Swamp forest zones. Except *Epomops buettikoferi*, all other forest species included in the table have also been found in one or more woodland types. The woodland occurrence of two forest species, *Myonycteris torquata* and *Nanonycteris veldkampii*, can at least in part be attributed to their migrations in the rainy season from the forest to the Guinea Savanna in West Africa (D. W. Thomas, 1983). In the others, it may reflect similar but not yet described behaviour. The stated occurrence of *Lissonycteris angolensis* in drier habitats than woodlands would class the species as a generalist, but in fact it applies only to the excentric East African subspecies *petraea* and to some East African populations of *ruwenzorii.*

2. Woodland taxa. Three genera and one species of African Megachiroptera are essentially restricted to woodlands: *Epomophorus*, with 6 species and 3 subspecies; the closely related *Micropteropus*, with 2 species; *Plerotes*, with 1 species; and *Epomops dobsonii* (the generic placement of which is disputed - see Bergmans, 1989). All these belong to the African subfamily of the Epomo-phorinae (with one species extending into the southwestern Arabian peninsula), and are assumed to be of African origin. Only *Epomopho-rus gambianus* and *E. labiatus* have been reported once from forest localities but these records need confirmation. However, most woodland species do occur in woodland-forest mosaics.

Going from Senegal to Ethiopia and from there to the South, and south of the Central African Forest Block again to the West, several assemblages are met. In West and northern Central Africa, from Senegal to the Central Ethiopian Rift, *Epomophorus gambianus* and *Micropteropus pusillus* are found, the former species with a disjunction in eastern Central African Republic and Sudan. In Nigeria, Sudan and Ethiopia, *Epomophorus labiatus* overlaps, but West of Sudan *E. labiatus* is known from a few localities only, while East of the Central African Republic a slightly aberrant population of *E. gambianus* occupies a relatively small Ethiopian area only. Central and southern Ethiopia are occupied by *Epomophorus minimus* (the northern populations of what has been known as *E. minor*), which at its southern limit on the Tanzanian border is replaced by what the present author has called (the southern populations of) *E. minor* and what Claessen *et al.* (1991) proposed to synonymize with *E. labiatus*; this is found also in a small part of southeast Zaïre, in northeast Zambia and in and around Malawi. (In some localities in the latter region, two distinct size classes are found side by side, called *E. labiatus* and *E. minor* by the present author, but all assigned to *E. labiatus* by Claessen *et al.*, 1991.) Below 8 S, *E. gambianus crypturus* overlaps with *E. labiatus* and *E.* cf. *minor. E. g. crypturus* is found westward into eastern Angola but is separated from the West Angolan *E. angolensis*, and southward to eastern South Africa North of 34 S. *Micropteropus pusillus* is found West of the drought corridor from Ethiopia to the northeast coasts of Lake Victoria and further in several seemingly disjunct areas in eastern Zaïre, central South Zaïre, and West Angola. (In West Africa and in many areas in western Central Africa, e.g. South Cameroun, West Gabon and South Congo, this species is also found in savannah areas surrounded by forests.) In northern Kenya and adjoining Uganda, *Epomophorus wahlbergi* joins the woodland assemblage. This species roughly overlaps with *E. g. crypturus* and *E. angolensis* but is more widespread, connecting the areas of the two species mentioned, occupying a larger part of southern Zaïre and northern Angola, and joining *Micropteropus pusillus* in woodland areas in western Congo and Gabon. *Epomops dobsonii* has been found in Rwanda and East Tanzania, partly

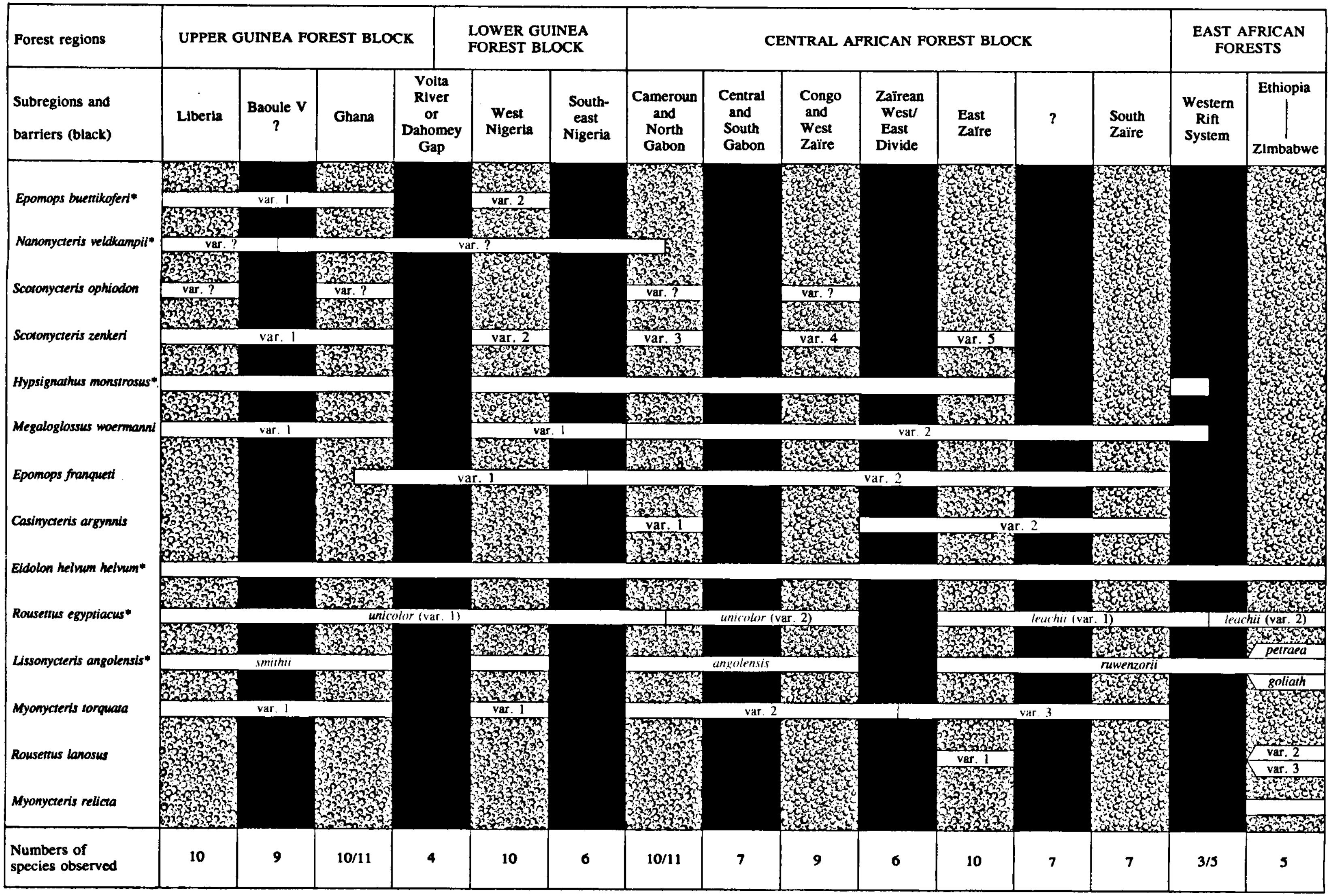

Fig. 9. Distribution of Megachiroptera over the various African forest regions, showing the important large barrier areas. Species marked with an * do occur west of Liberia. The supposed barriers "Baoule V?" and between East and South Zaïre may not hold. The abbreviation "var." indicates observed geographical variation below subspecific level.

overlapping wit *E. labiatus*, *E. minor* and *E. wahlbergi*, and like the latter species also connecting the distribution areas of *E. g. crypturus* and *E. angolensis* in Angola. *Plerotes anchietae* has been found in an area between Lake Upemba and the South tip of Lake Tanganyika, overlapping with *Epomophorus minor*, *E. g. crypturus*, *E. wahlbergi*, and *Epomops dobsonii*, and in an area in western Central Angola, overlapping with *Micropteropus pusillus*, *E. angolensis*, *E. wahlbergi*, and *E. dobsonii*. In fact, the two parts of its distribution coincide with the centres of the two large *dobsonii* regions. Finally, *Epomophorus grandis* and *Micropteropus intermedius* probably occupy a zone at either side of the northern Zaïrese/Angolese border, overlapping with *Epo-mophorus* cf. *labiatus* (in southwest Congo), *E. wahlbergi* and *Micropteropus pusillus*. For *E. gambianus*, *E. labiatus* and *Micropteropus pusillus* it is obvious that their distribution areas have been larger and are now disrupted. All other species have either continuous distributions (*Epomophorus minimus*, *E. minor*, *E. angolensis*, *E. wahlbergi*, *Epomops dobsonii*) or have insufficiently known distributions. The disruptions have given rise to subspecific and other variation only in *E. gambianus*, and can not be of very old age. The development of several closely related species (in the *E. gambianus* group, including *gambianus*, *labiatus*, *minor*, *minimus*) indicates other, earlier disruptions and subsequent vicariant speciation. The presence of various *Epomophorus* groups (*gambianus*, *wahlbergi* and *grandis*) and of the closely related genus *Micropteropus* finally indicates still earlier events of distributional fragmentation and separate developments; at this level, ecological separation is most evident (compare preferred vegetation types; see Volpers *et al.*, 1995). To judge from present patterns, important breaks in woodland fruit bat distributions, bringing about taxonomic variation on all levels below subfamily, have occurred in the regions: Southeast Tchad/East Central African Republic/West Sudan; northern half of Tanzania; and East Angola/adjoining Zaïre. It is remarkable that the Pleistocene West/East divide in the Lower Guinea Forest Block is reflected by a similar divide in the adjoining northern and southern woodland zones. The woodland fruit bat fauna of the region South of the Lower Guinea Forest Block, between about 4 and 15 S, is not well known. At the same time, it is the richest both in genera and species, and further collecting and study here may yield the best results for a better understanding of Africa's woodland fruit bats and their history.

3. Forest taxa

Many of the following remarks are illustrated in fig. 9. Within the Upper Guinea, Lower Guinea, and Central African forest blocks combined, between 7 and 11 forest fruit bat species are known from any given region. The poorest in species appears to be South Zaïre with 7 species, the richest are western Ghana and Cameroun/North Gabon, both believed to approximate to sites of forest refugia at the time of the last world glaciation, at 18,000 BP (Hamilton, 1992), with 10 to 11 species each. The areas identified here as gaps (the black bars in fig. 9) have yielded from 4 to 9 species each. Only 2 forest species (and 2 generalist species) continue into East Africa, while 1 species is exclusively East African; here, intraspecific differentiation is generally well developed.

On species level, 5 taxa are restricted to certain parts of the large forest blocks: *Epomops buettikoferi* is restricted to the Upper and Lower Guinea blocks; *Nanonycteris veldkampii* to the Upper and Lower blocks plus a part of Cameroun (and possibly further east); *Scotonycteris ophiodon* is restricted to the Guinea blocks plus the western Central block; *Casinycteris argynnis* is known from the Central block only. *Rousettus lanosus* is restricted to the eastern Central block (and East African forests). Nearly all species show intraspecific geographical variation. In fig. 9, the following areas are shown as important barriers:

1. The Volta River or the Dahomey Gap, separating mutually distinct populations of *Epomops buettikoferi* and *Scotonycteris zenkeri*; possibly acting as an eastern barrier to Upper Guinea *Scotonycteris ophiodon* and *Hypsignathus monstrosus* populations.

The existing forests in the Dahomey Gap have not been searched well for forest fruit bats. Of all the forest species here considered, only *Epomops franqueti* is known from Benin - and generalist *Eidolon helvum*. Robbins (1978) reevaluated the significance of the Gap as a barrier to high forest mammals, and concluded that it has not influenced mammal distributions or evolutionary changes. He found that these had been affected rather by the Volta and Niger Rivers. No records of *Epomops buettikoferi* or one of the *Scotonycteris* species from between the Volta and the Dahomey Gap exist, so Robbins' conclusion may hold for fruit bats as well.

2. Southeast Nigeria (either the Lower Niger or the Cross River, or the whole area in between and including these), separating mutually distinct populations of *Scotonycteris zenkeri*, *Megaloglossus woermanni* *Epomops franqueti* (for this species the Cross River is most likely), and *Myonycteris torquata*; separating or acting as transition area for two subspecies of *Lissonycteris angolensis*; and possibly posing a western barrier to Central African *Scotonycteris ophiodon* populations.

East Nigeria has not been searched well for forest fruit bats and it is not possible to rule out either the lower Niger or the Cross River as the actual barrier. The assemblage of Mount Cameroun is relatively well known and rich. Nigeria east of the Cross River possibly has a similar fruit bat fauna.

3. Central and South Gabon, separating mutually distinct populations of *Scotonycteris zenkeri* and possibly of *S. ophiodon*.

The nature of this divide is not clear but it may reflect the hypothesized fragmentation of the Cameroun/Gabon forest refugium into a northern and a southern part (Hamilton, 1992). Gabon as a whole has not been well searched for bats, but from available studies it is very likely that *S. ophiodon* is absent from the northeast of the country.

4. The great Zaïrean West-East divide. A wide band stretching from eastern Central African Republic and southeastern Sudan southwards through Central Zaïre in the direction of northeast Angola spacially separates mutually distinct populations of *Scotonycteris zenkeri* and possibly of *Myonycteris torquata* (this species may be continuous from West to East Zaïre) and subspecies of *Rousettus egyptiacus* and *Lissonycteris angolensis*. It possibly acts as the eastern barrier for *Scotonycteris ophiodon*.

This divide is in support of the glacial forest refugia hypothesis (e.g. Hamilton, 1992). It is remarkable that it appears to be continued both to the north and south into the savanna zones, where woodland fruit bat species seem to meet barriers as well.

5. The Zairean East/South divide. From a line roughly between the northern tip of Lake Tanganyika and 24 E, 8 S to the southeast, the lowland rain forest and its mosaics (types 2 and 11a in White, 1983) give way to Wetter Zambezian woodland and Edaphic and secondary grassland on Kalahari sand (types 25 and 60 in White, 1983), with a very broad stretch of rain forest intruding along the Lualaba River and most probably (not mapped by White, 1983) narrower galleries along other water courses. While *Epomops franqueti* and *Megaloglossus woermanni* have been found far south of the mentioned line in southwest Zaïre, *Scotonycteris zenkeri*, *Hypsignathus monstrosus* and *Casinycteris argynnis* have not.

The change in forest character and extent may pose a barrier to these species.

6. The Western Rift system, separating mutually distinct populations of *Rousettus egyptiacus* and *R. lanosus*, subspecies of *Lissonycteris angolensis*, and, largely, species of *Myonycteris*, namely *torquata* (which is found in Uganda, however) and *relicta*.

The Western Rift system is a very complicated and widely stretched geological system, and to explain its barrier effect calls for specific arguments for all the mentioned taxa. In the East Africa region itself, the forests are often mutually very far apart, both in the north-south and in the west-east directions, and several clear divides separate three subspecies of *Lissonycteris angolensis* and two morphologically distinct populations of *Rousettus lanosus*. Details are to be found in the accounts of the mentioned species.

4. Generalist taxa

The species *Rousettus egyptiacus* and *Eidolon helvum* have been put in this category to allow for some remarks not applying to the other species. The term "generalist" does not cover their distributional characteristics, but neither do others, like "opportunist" or "ecologically unspecialized" - although these terms all contain some truth. The species are both considered to originate from the forest, and most of their populations are still to be found there. *R. egyptiacus*, however, has two distinct subspecies, *egyptiacus* and *arabicus*, which do live entirely outside the true forest, in northeast Africa and adjoining Asia Minor. They must have developed from populations which have been separated from the others in tropical Africa and further south, by fragmentation of a formerly larger continuous distribution area, and have been able to adapt themselves to harsher conditions. They are still separated now by the Sudanese desert and the Arabian Gulf and surrounding deserts, respectively. The two other subspecies, *leachii* and *unicolor*, are also not exclusively forest dwellers. *Rousettus egyptiacus*' habit of roosting in caves and man-made cave-like structures enables it to explore and use many areas which themselves are not in the forest. It may fly considerable distances from its roost to its feeding areas and back. Both habits obviously allow the species to disperse more easily to other areas. At the same time, the need for caves is limiting both its occurrence and dispersal. Barrier areas have been discussed under the forest taxa. *Eidolon helvum* roosts gregariously in trees (not unlike *Pteropus*), which may be in the forest, in small groves, and in unnatural conditions such as trees in city centres. It is a strong flyer, and may fly considerable distances to its feeding grounds and back. Some populations are known to seasonally migrate over large distances. The species has been found in numerous localities far outside forest or even woodland. It has colonized several oceanic islands. Apart from the absence of food, e.g. under desert conditions, there are no apparent barrier areas for this species. And even in desert-like areas it has sometimes been found, leaving researchers at a loss on how it may survive.

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## REFERENCES

N.B. Only those references have been included which have not already been given in the first four parts of this series (Bergmans, 1988, 1989, 1990, 1994).

AGRAWAL, V. C. & Y. P. SINHA, 1973. Studies on the bacula of some Oriental bats. Anat. Anz., **133**: 180-192.

ANDERSEN, K., 1908. Preliminary description of two new species of *Myonycteris*. Ann. Mag. nat. Hist., (8) **2**: 450-451.

ANONYMOUS, 1987. Sao Tomé and Principe birds increase. World Birdwatch, **9** (4): 1-2.

BALINSKY, B. I., 1962. Patterns of animal distribution on the African continent. Ann. Cape Prov. Museums, II: 299-310.

BERGMANS, W., 1976. A revision of the African genus *Myonycteris* Matschie, 1899 (Mammalia, Megachiroptera). Beaufortia, **24** (317): 189-216.

—, 1980a. A new fruit bat of the genus *Myonycteris* Matschie, 1899, from eastern Kenya and Tanzania (Mammalia, Megachiroptera). Zool. Meded., **55** (14): 171-181.

—, 1980b. A new fruit bat from Shimba Hills. East Afr. nat. Hist. Soc. Bull., **1980** (6): 96.

—, 1988. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 1. General introduction; material and methods; results: the genus *Epomophorus* Bennett, 1836. Beaufortia, **38** (5): 75-146.

—, 1989. 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. Beaufortia, **39** (4): 89-153.

—, 1990. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 3. The genera *Scotonycteris* Matschie, 1894, *Casinycteris* Thomas, 1910, *Pteropus* Brisson, 1762, and *Eidolon* Rafinesque, 1815. Beaufortia, **40** (7): 111-177.

—, 1994. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 4. The genus *Rousettus* Gray, 1821. Beaufortia, **44** (4): 79-126.

— & P. J. H. VAN BREE, 1972. The taxonomy of the African bat *Megaloglossus woermanni* Pagenstecher, 1885 (Megachiroptera, Macroglossinae). Biol. gabonica, **3-4**: 291-299.

BHATNAGAR, K. P., 1967. Bacula of some Indian Megachiroptera. J. Mamm., **48** (3): 494-497.

BIGALKE, R. C., 1972. The contemporary mammal fauna of Africa: 141-194, *in:* A. Keast, F. C. Erk & B. Glass. Evolution, mammals and southern continents. State University of New York Press, Albany.

—, 1978. Present-day mammals of Africa: 1-16, *in:* V. J. Maglio & H. B. S. Cooke (eds.), Evolution of African mammals. Harvard University Press, Cambridge, London.

BLYTH, E., 1840. Mammalia, birds and reptiles. *In:* G. Cuvier, Animal Kingdom etc.: i-vii, 1-670. London. (Not seen by the author.)

BOCAGE, J. V. BARBOZA DU, 1889a. Chiroptères de l'Ile St. Thomé. Jorn. Sci. math. phys. nat., Ser. 2, **1** (3): 197-199.

—, 1892. Observations sur les espèces du genre *Cynonycteris* rencontrées en Angola par M. d'Anchieta. Jorn, Sci. math. phys. nat., Ser. 2, **7**: 173-178.

—, 1898. Sur une nouvelle espèce de *Cynonycteris* d'Angola. Jorn. Sci. math. phys. nat., Ser. 2, **5** (19): 133-139.

—, 1905. Contribution à la faune des quatre îles du Golfe de Guinée (suite). Jorn. Sci. math. phys. nat., Ser. 2, **7** (26): 65-96.

BROADLEY, D. G., 1974. The Lusitu Forest: a new protected area. Wild Rhodesia, **3**: 17.

BROSSET, A., 1984. Chiroptères d'altitude du Mont Nimba (Guinée). Description d'une espèce nouvelle, *Hipposideros lamottei*. Mammalia, **48** (4): 545-555.

CABRERA, A., 1920. Dos nuevos murciélagos frugívoros. Bol. R. Soc. esp. Hist. nat., **20**: 106-108.

CARROLL, J. B. & I. C. THORPE, 1991. The conservation of Livingstone's fruit bat *Pteropus livingstonii*, Gray 1866: a report on an expedition to the Comores in 1990. Dodo J. Jersey Wildl. Preserv. Trust, **27**: 26-40.

CLAESSEN, C. J. & F. DE VREE, 1990. Systematic and distributional notes on the larger species of the genus *Epomophorus* Bennett, 1836 (Chiroptera: Pteropodidae): 177-186. *In:* G. Peters & R. Hutterer (eds.), Vertebrates in the tropics. Museum Alexander Koenig, Bonn.

— & —, 1991. Systematic and taxonomic notes on the *Epomophorus anurus-labiatus-minor* complex with the description of a new species. Senckenbergiana biol., **71**

(4/6): 209-238.

COLGAN, D. J. & T. F. FLANNERY, 1995. A phylogeny of Indo-West Pacific Megachiroptera based on ribosomal DNA. Syst. Biol., **44** (2): 209-220.

COSSON, J.-F., M. TRANIER & F. COLAS. On the occurrence and possible migratory behaviour of the fruit bat *Eidolon helvum* in Mauretania, Africa. J. Afr. Zool. (in press).

COSSON, J.-F.. Captures of *Myonycteris torquata* (Chiroptera: Pteropodidae) in forest canopy in South Cameroon. Biotropica (in press).

CZEKALA, N. M. & K. BENIRSCKE, 1974. Observations on a twin pregnancy in the African long-tongued fruit bat (*Megaloglossus woermanni*). Bonn. zool. Beitr., **25** (4): 220-230.

DAL PIAZ, G., 1937. Mammiferi dell'-Oligocene Veneto. Mem. First Geol. Mineral. Univ. Padova **11** (6): 1-8.

DANIEL, M., 1975. First record of an Australian fruit bat (Megachiroptera: Pteropodidae) reaching New Zealand. New Zealand J. Zool., **2**: 227-231.

EISENTRAUT, M., 1956a. Der Langzungen-Flughund *Megaloglossus woermanni* ein Blütenbesucher. Z. Morph. Oek. Tiere, **45**: 107-112.

—, 1965. Der Rassenkreis *Rousettus angolensis* (Bocage). Bonn. zool. Beitr., **16** (1/2): 1-6.

— & H. KNORR, 1957. Les chauves-souris cavernicoles de la Guinée française. Mammalia, **21** (4): 321-335.

FLOWER, W. H. & R. LYDEKKER, 1891. An introduction to the study of mammals, living and extinct: i-xvi, 1-763. Adam and Charles Black, London.

GAUCHER, P., 1992. New record of an epauleted bat *Epomophorus labiatus* Temminck, 1837 (Mammalia: Chiroptera: Pteropodidae) in Saudi Arabia. Mammalia, 56 (4): 657-659.

HABERSETZER, J. & G. STORCH, 1987. Klassifikation und funktionelle Flügelmorphologie paläogener Fledermäuse (Mammalia, Chiroptera). Cour. Forsch.-Inst. Senckenberg, **91**: 117-150.

HAMILTON, A. C., 1992. History of forests and climate: 17-25, *in:* J. A. Sayer, C. S. Harcourt & N. M. Collins (eds.), The conservation atlas of tropical forests. Africa. Macmillan, United Kingdom.

HAYMAN, R. W., 1960. Notes on some small African mammals. Rev. Zool. Bot. afr., **62** (1-2): 59-65.

HELLER, K.-G., M. VOLLETH & D. KOCK, 1994. Notes on some vespertilionid bats from the Kivu region, Central Africa (Mammalia: Chiroptera). Senckenbergiana biol., **74** (1/2): 1-8.

HILL, J. E., 1983. Further records of bats from the Central African Republic (Mammalia: Chiroptera). Annls. Carnegie Mus., **52** (3): 55-58.

HILL, J. E. & W. N. BECKON, 1978. A new species of *Pteralopex* Thomas, 1888 (Chiroptera: Pteropodidae) from the Fiji Islands. Bull. Brit. Mus. nat. Hist. (Zool.), **34** (2): 65-82.

HILL, J. E. & J.D. SMITH, 1984. Bats. A natural history: (4), 1-243. British Museum (Natural History), London.

HOOD, C.S., 1989. Comparative morphology and evolution of the female reproductive tract in macroglossine bats (Mammalia, Chiroptera). J. Morphol., **199**: 207-221.

JUSTE, J. & C. IBANEZ, 1993. An asymmetric dental formula in a mammal, the Sao Tomé Island fruit bat *Myonycteris brachycephala* (Mammalia: Megachiroptera). Can. J. Zool., **71**: 221-224.

— & —, 1994a. Contribution to the knowledge of the bat fauna of Bioko Island, Equatorial Guinea (Central Africa). Z. Säugetierkunde, **59**: 274-281.

— & —, 1994b. Bats of the Gulf of Guinea islands: faunal composition and origins. Biodiversity and Conservation, **3** (9) (special issue): 837-850.

— & — & A. Machordom (in prep.). Evolutionary relationships among the West African rousette (*Rousettus egyptiacus*), the longhaired rousette (*R. angolensis*) and the collared fruit bats (*Myonycteris* spp.), (Chiroptera: Pteropodidae).

KINGDON, J., 1971. East African mammals. I. Academic Press, London, New York.

—, 1990. Island Africa. The evolution of Africa's rare animals and plants: 1-287. Collins, London etc.

KINGDON, J. & K. M. HOWELL, 1993. Mammals in the forests of eastern Africa: 229-241. *In:* J. C. Lovett & S. K. Wasser (eds.), Biogeography and ecology of the rain forests of eastern Africa. Cambridge University Press, Cambridge, New York, Melbourne.

KIRSCH, J. A. W., T. F. FLANNERY, M. S. SPRINGER & F.-J.

KITYO, M. R., 1993. Results of surveys of bats in Uganda. Bat Res. News, **34** (1): 24 (abstract).

KOOPMAN, K. F., 1989. Systematic notes on Liberian bats. Amer. Mus. Novit., **2946**: 1-11.

—, 1994. Chiroptera: Systematics: I-VII, 1-217. Handbook of Zoology 8, part 60. De Gruyter, Berlin, New York.

KOOPMAN, K. F. & J. K. JONES, 1970. Classification of bats: 22-28. *In:* B. H. Slaughter & D. W. Walton (eds.), About bats. A chiropteran symposium. Southern Methodist University Press, Dallas.

KORTLANDT, A., 1972. New perspectives on ape and human evolution: 1-100, 1 map. Stichting voor Psychobiologie, Amsterdam.

KRUTZSCH, P. H., 1959. Variation in the os penis of tropical fruit bats. J. Mammal., **40**: 387-392.

—, 1962. Additional data on the os penis of Megachiroptera. J. Mammal., **43**: 34-42.

KULZER, E., 1982. Nektar-lecken beim afrikanischen Langzungen-Flughund *Megaloglossus woermanni* Pagenstecher, 1885. Bonn. zool. Beitr., **33** (2-4): 151-

164.

— & R. STORF, 1980. Schlaf-Lethargie bei dem afrikanischen Langzungen-Flughund *Megaloglossus woermanni* Pagenstecher, 1885. Z. Säugetierkunde **45** (1): 23-29.

LAPOINTE, 1995. Phylogeny of the Pteropodidae (Mammalia: Chiroptera) based on DNA hybridisation, with evidence for bat monophyly. Aust. J. Zool., **43**: 395-428.

LYDEKKER, R., 1901. Die geographische Verbreitung und geologische Entwicklung der Säugetiere: i-xii, (1), 1-532, 1 map (authorized translation, second edition). Costenoble, Jena.

MARTIN, R. L., 1978. The baculum of some bats of Thailand with comments on taxonomic utility and adaptive value. Proc. fourth int. Bat Res. Conf., 199-204.

MAYR, E., 1969. Principles of systematic zoology: i-xiv, 1-428. McGraw-Hill, New York etc.

— & P. D. ASHLOCK, 1991. Principles of systematic zoology. Second edition: i-xx, 1-475. McGraww-Hill, New York etc.

MICKLEBURGH, S. P., A. M. HUTSON & P. A. RACEY (compilers), 1992. Old World fruit bats. An action plan for their conservation: i-viii, 1-252. IUCN, Gland.

MUMFORD, R. E., 1970. *Myonycteris torquata* and *Megalo glossus woermanni* from Uganda. J. Mammal., **51**: 169.

NADLER, T. & A. FEILER, 1993. Allgemeiner Bericht über eine zoologische Studienreise nach der Insel Sao Tomé (Golf von Guinea). Faun. Abh. staatl. Mus. Tierk. Dresden, **19** (1): 1-4.

NEMEC, P. & I. HORACEK, 1996. Chiropteran diphyly - definitely a past question? Bat Res. News, **37** (2 & 3): 83.

PAGENSTECHER, H. A., 1885a. *Megaloglossus Woermanni* nov. gen. et spec. Zool. Anz., **8** (193): 245.

—, 1885b. *Megaloglossus woermanni*, eine neue Form makroglosser Fledermäuse. Jb. wiss. Anst. Hamb., **2**: 123-130, 1 pl.

PETERSON, R. L., J. L. EGER & L. MITCHELL, 1995. Chiroptères. Faune de Madagascar, 84: 1-204. Muséum national d'Histoire naturelle, Paris.

PETTIGREW, j. d., 1991. A fruitful, wrong hypothesis? Response to Baker, Novacek and Simmons. Syst. Zool., **40** (2): 231-239.

QUAY, W. B., 1969. Structure and evolutionary implications of the musculi arrectores pilorum in Chiroptera. Anat. Rec., **163**: 587-594.

REASON, P. F. & W. J. TREWHELLA, 1994. The status of *Pteropus livingstonii* in the Comores. Oryx, **28**: 107-114.

- & —, J. G. DAVIES & S. WRAY, 1994. Some observations on the Comoro rousette *Rousettus obliviosus* on Anjouan (Comoro islands: Western Indian Ocean). Mammalia, **58** (3): 397-403.

ROBBINS, C. B., 1978. The Dahomey Gap - a reevaluation of its significance as a faunal barrier to West African High Forest mammals. Bull. Carnegie Mus. nat. Hist., **6**: 168-174.

ROBERTSON, F. 1986. A study of the conservation status of botanical reserves in Zimbabwe. The Zimbabwe Science News, **20** (7/8): 102-106.

SANBORN, C. C., 1953. Notes sur quelques mammifères de l'Afrique equatoriale française. Mammalia, **17**: 164-169.

SAYER, J. A., C. S. HARCOURT & N. M. COLLINS, 1992. The conservation atlas of tropical forests. Africa: i-viii, 9-288. Macmillan Publishers Ltd., United Kingdom.

SCHLITTER, D. A. & S. B. MCLAREN, 1981. An additional record of *Myonycteris relicta* Bergmans, 1980, from Tanzania (Mammalia: Chiroptera). Annls. Carnegie Mus., **50** (16): 385-389.

SIMMONS, N. B., 1994. The case for chiropteran monophyly. Amer. Mus. Novit., **3103**: 1-54.

—, 1995. Bat relationships and the origin of flight. Symp. zool. Soc. Lond., **67**: 27-43.

SPRINGER, M. S., L. J. HOLLAR & J. A. W. KIRSCH, 1995. Phylogeny, molecules versus morphology, and rates of character evolution among fruitbats (Chiroptera: Megachiroptera). Aust. J. Zool., **43**: 557-582.

THOMAS, O., 1908. On a new fruit-bat from Sierra Leone. Ann. Mag. nat. Hist., Ser. 8, **2**: 375-376.

TOMES, R. F., 1860. A monograph of the genus *Epomophorus*, with the description of a new species. Proc. zool Soc. Lond., **1860**: 42-58, pl. 75.

TREWHELLA, W. J., P. F. REASON, J. G. DAVIES & S. WRAY (in press). Observations on the timing of reproduction in the congeneric Comoro Island fruit bats, *Pteropus livingstonii* (Gray, 1866) and *P. seychellensis comorensis* (Nicoll, 1908). J. Zool. Lond.

TROUESSART, E.-L., 1897. Catalogus Mammaliam tam viventium quam fossilium: 1-664, pls i-iii. Friedländer & Sohn, Berlin.

VEIGA-FERREIRA, M. C., 1948. Notas acerca dos Megaquiropteros da Guiné Portuguesa. Anais. Jta Invest. colon., **3** (4): 57-73.

VOLPERS, T. & A. KUMIRAI, 1995. Ecological aspects of the distribution of *Epomophorus*-fruit bats (Mammal., Chiropt.) in Zimbabwe. Verhandl. Ges. f. Ökol., **24**: 89-92.

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# ANNEX: FIELD IDENTIFICATION KEY FOR AFRICAN MEGACHIROPTERA

African Megachiroptera comprise all African bats which combine the following characters: a continuous ear margin, a claw on the second finger, and a reduced tail membrane existing as a band along the inside of the tighs and the hinder end of the body. All other African bats are Microchiroptera.

This key is based on externally measurable and visible characters, including teeth, palatal ridges, and weights. All measurements are in mm, and weights in g. For easy use, known geographical ranges have been added. It should be added that the most recent key to all species, of Hayman et al. (1971), does not allow for the correct identification of *Micropteropus intermedius* and *Epomophorus grandis*, while *Rousettus obliviosus*, *Myonycteris relicta*, and *Epomophorus minimus* were described after its publication; apart from more detailed characters and some illustrations (not to scale and numbered 1-22, apart from the other figures in this paper), the many extensions of distributions and measurement ranges found in the course of the present work can now be included.

fal = *known* forearm length range
weight = *known* weight range
cheek teeth = teeth behind canines

**1** **a.** Facial fur with contrastingly white patches on nose and behind eyes, and/or at anterior and posterior ear bases; three upper and five lower cheek teeth (in one species four or five upper, and five to six lower cheek teeth) ....................**2**
**b.** No white facial fur patches or tufts at ear bases; five upper and six (in one species five) lower cheek teeth ............**18**

**2** **a.** White fur patches on nose and behind eyes; in one species, white fur tufts also at ear bases..........................................**3**
**b.** White fur tufts at ear bases only..........................................................................................................................**5**

**3** **a.** Cheeks and lips conspicuously white; ear tips rather rounded; fal ♂♂ 49-55, ♀♀ 54-64; weight ♂♂ 26, ♀♀ 28-34; finger joints contrastingly yellow; canines simple; forests of Cameroun and Zaïre..................................*Casinycteris argynnis*
**b.** Cheeks and lips not conspicuously white; ears tips either rounded or slightly pointed; finger joints dark and fal under 57, or finger joints contrastingly coloured and fal over 70; canines simple or with extra cusp ............................**4**

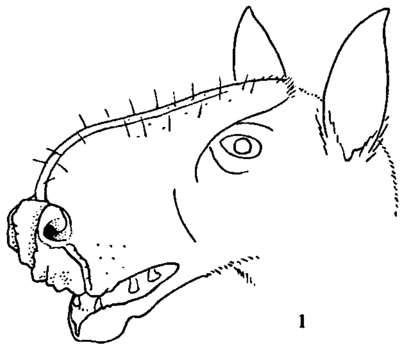
**4** **a.** Finger joints as dark as wing membranes; ear tips rounded; fal ♂♂ 45-55, ♀♀ 47-57; weight ♂♂ 16-24, ♀♀ 18-27; canines simple; forests of Liberia to East Zaïre (discontinuous)..........................................................*Scotonycteris zenkeri*
**b.** Finger joints whitish or yellowish; ears slightly pointed; fal ♂♂ 74-79, ♀♀ 75-88; weight ♂♂ 65-71, ♀♀ 65-95; canines with second, inner cusp; locally in forests of Liberia, Ghana, Cameroun and Congo.................*Scotonycteris ophiodon*

**5** **a.** White ear base tufts not very distinct; anterior end of muzzle truncated and with a fleshy plate (fig. 1); fal ♂♂ 120-139, ♀♀ 111-128; weight ♂♂ 290-420, ♀♀ 207-302; no white shoulder tufts; forests, sometimes woodlands, of Sierra Leone to Uganda, southwards to Angola..........................................................................................*Hypsignathus monstrosus*
**b.** White ear base tufts conspicuous; muzzle simple (fig. 2); fal under 105; adult males with retractable white shoulder tufts (not known for *Plerotes*) .......................................................................................................................**6**

**6** **a.** Interfemoral membrane extremely narrow; calcar absent; cheek teeth reduced in heighth and width and variable in number: four or five upper and five or six lower cheek teeth; woodlands of Angola, South Zaïre, North Zambia; fal 1 ♂ 50, 2 ♀♀ 50-52.5; weight not known ..........................................................................................*Plerotes anchietae*
**b.** Interfemoral membrane relatively well developed (fig. 3); calcar present; cheek teeth not much reduced; three upper and five lower cheek teeth (very incidentally rudimentary extra teeth); fal range variable ....................................**7**

**7** **a.** Thee thick palatal ridges in front, followed by five to eight thinner ridges (figs. 4-5); fal over 75....................................**8**
**b.** Five to nine thick ridges, followed by two to four thinner ridges; fal variable.................................................................**9**

**8** **a.** Third ridge normally whole; thin ridges rather narrowly divided medially (posterior ones whole) and finely serrate (fig. 4); fal ♂♂ 83-101, ♀♀ 76-97; weight ♂♂ 92-172, ♀♀ 61-130; Sierra Leone, eastern Ivory Coast to Uganda, southwards to Angola and Zambia ......................................................................................................*Epomops franqueti*
**b.** Third ridge normally divided medially; first four or five thin ridges clearly divided medially, irregularly serrate,



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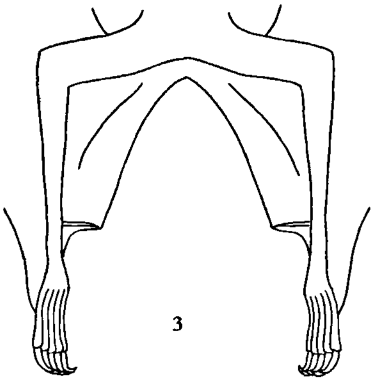

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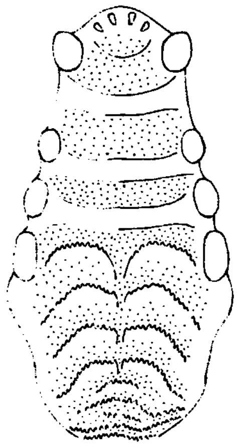

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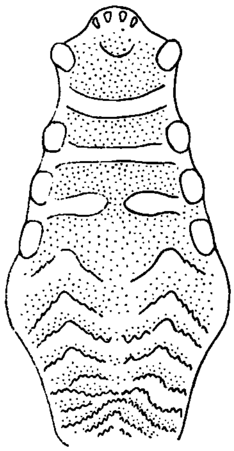

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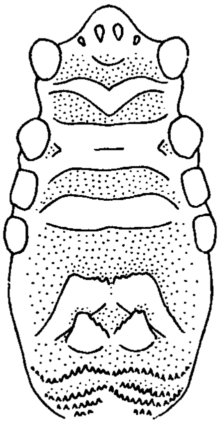

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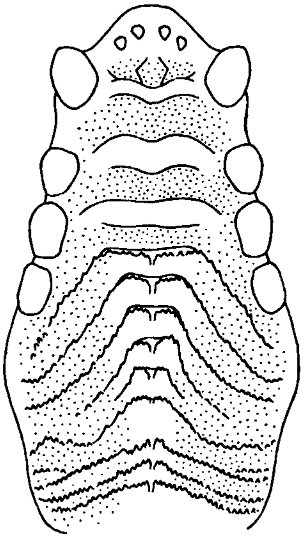

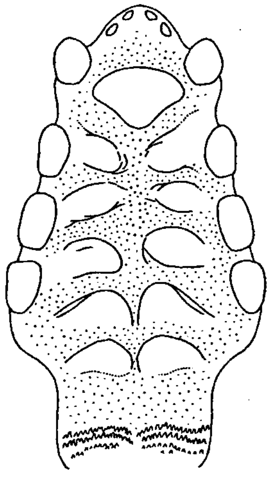

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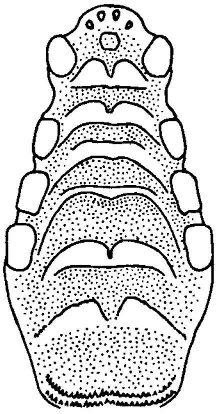

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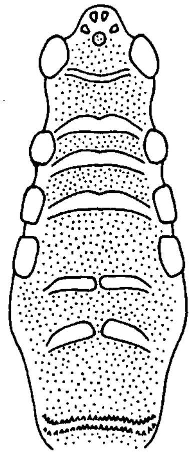

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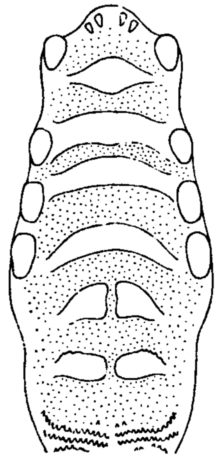

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each half generally with one large central projection pointing forward (5); posterior thin ridges undivided and more evenly serrated; fal ♂♂ 88-103, ♀♀ 82-95; weight ♂♂ 133-198, ♀♀ 94-132; Guinea to Ghana, locally in Nigeria ........................................................................................................................................................*Epomops buettikoferi*

**9** **a.** Five thick palatal ridges; second ridge wide and indistinctly bifurcate at its extremities; fourth and fifth postdental, each with two large projections, often triangular and pointing forward; three to four thin, serrated ridges (fig. 6); fal ♂♂ 84-94, ♀♀ 80-89; weight not known; woodlands of Central Angola, southeast Zaïre, Zambia, Malawi and eastern Tanzania and Rwanda........................................................................................................*Epomops dobsonii*
**b.** At least six thick palatal ridges; ridge pattern differ-ent. ........................................................................**10**

**10** **a.** Nine thick or partially thick ridges: three whole, the fourth narrowly divided in some specimens, the fifth to eighth or ninth medially notched with thick, prominent central portions and thin lateral parts; and three or four thin ridges (fig. 7); fal ♂♂ 44-50, ♀♀ 45-54; weight ♂♂ 19-21, ♀♀ 23-27; forests and woodlands from Guinea to Central African Republic ........................................................................................................................*Nanonycteris veldkampii*
**b.** At most six thick palatal ridges.......................................................................................................................**11**

**11** **a.** Six thick palatal ridges, one or two being postdental: first undivided, second to fourth either undivided or divided in the middle, fifth and sixth notched or narrowly divided; ridges never mutually fused..........................................**12**
**b.** Essentially six thick palatal ridges but fusions between second and third and sometimes others may obscure the picture; first ridge prominent and undivided, second and third either prominent or weak, fourth to sixth prominent; second to sixth palatal ridges divided by a deep, continuous median groove narrowing posteriorly.................................**17**

**12** **a.** Second to sixth ridges medially divided (fig. 8); fal 2 ♂♂ 62.3-62.8, 1 ♀ 65.8; weight not known; probably woodland, southern Congo, probably southern Zaïre, and northern Angola....................................................*Epomophorus grandis*
**b.** Second to fourth ridge undivided.......................................................................................................................**13**

**13** **a.** Five thick palatal ridges interdental and only one clearly postdental (fig. 9); fal ♂♂ 72.3-94.9, ♀♀ 67.7-87.5; weight ♂♂ 60-124, ♀♀ 54-125; woodlands of Angola, Congo, Gabon, Zaïre, Zambia, East Africa between 4 and 34 S ........................................................................................................................................................*Epomophorus wahlbergi*
**b.** Four thick palatal ridges interdental, fifth and sixth postdental (fifth exceptionally partly interdental) .......................**14**

**14** **a.** Fourth thick palatal ridge clearly nearer third than fifth (fig. 10); fal ♂♂ 85.2-93.9, ♀♀ 81.1-85.5; weight not known; woodlands West Angola and North Namibia..........................................................................*Epomophorus angolensis*
**b.** Fourth thick palatal ridge about halfway between third and fifth (fig. 11)..........................................................**15**

**15** **a.** Larger, on average; fal ♂♂ 80.0-100.0, ♀♀ 75.0-94.8; weight ♂♂ 91-155, ♀♀ 56-130; mainly woodlands, from Senegal to Central African Republic, in Ethiopia, and East Africa south of Lake Tanganyika..........*Epomophorus gambianus*
**b.** Smaller, on average; fal ♂♂ below 81, ♀♀ below 79; weight ♂♂ below 100, ♀♀ below 85 ......................................**16**

**16** **a.** Fal range in ♂♂ 66.7-80.3, in ♀♀ 64.8-78.3; weight ♂♂ 54-99, ♀♀ 51-81; mainly woodlands, northeast Nigeria, south Sudan to Erithrea and to northwest Tanzania; known from few localities in Congo, Malawi and southeast Kenya........................................................................................................................................*Epomophorus labiatus*
**b.** Fal range in ♂♂ 57.0-68.9, in ♀♀ 54.1-67.6; weight ♂♂ 32-58, ♀♀ 25-62; mainly woodlands East Sudan, Ethiopia, Somalia, lower parts of Kenya to South Malawi. ..........................................................................*Epomophorus minor*

N.B. This key follows the present series. Claessen *et al.* (1991) have separated populations in Ethiopia, Somalia, Uganda, Kenya and Tanzania from what is called *E. minor* here as *Epomophorus minimus*, and identified the remainder with *E. labiatus*. *E. minimus* has fal ranges of 53.7-66.7 in ♂♂ and 56.9-65.6 in ♀♀.

**17** **a.** All six thick palatal ridges prominent (fig. 12); second and third ridges may be fused, occasionally also third and fourth; fal ♂♂ 46-55, ♀♀ 49-56; weight ♂♂ 24-35, ♀♀ 20-34; woodlands Gambia to Ethiopia and West Kenyan border, southward to Central Angola and southeast Zaïre.......................................................................*Micropteropus pusillus*
**b.** Second and third palatal ridge weakly developed (apparently fused in part of the specimens) (fig. 13); fal 1 ♂ 58.1, 3 ♀♀ 57.2-63.6; weight not known; woodland and forest mosaic of western South Zaïre and adjoining Angola.................................................................................................................................................*Micropteropus intermedius*

**18 a.** Fal ♂♂ 38-50, ♀♀ 38-49; weight ♂♂ 11-20, ♀♀ 13-21; no tail; tongue highly extensible, with pointed, densely papillate tip; cheek teeth extremely reduced in height and width; males with ventral collar of thick, whitish hairs; forests Liberia and Guinea to Uganda, southwards to Angola and southeast Zaïre.......... *Megaloglossus woermanni*
**b.** Fal more than 55; tail present or absent; tongue not highly extensible, with rounded tip, not densely papillate; cheek teeth variable; males with or without collar but collar never whitish .......... **19**

**19 a.** Short but distinct external tail.......... **20**
**b.** No external tail.......... **29**

**20 a.** Toes partially webbed (fig. 14); fal range 54-90; length second digit 71-81% of fal; tibiae wholly or partly furred; ♂♂ with ruff of thick hairs; upper alveolar line with weak angle between third and fourth premolar (fig. 15); cheek teeth squarish or oblong (fig. 16); simplified palatal ridge pattern 7 + 2 (fig. 17).......... **21**
**b.** Toes not webbed; fal 66-107; length second digit 64-71% of fal; tibiae practically naked or, when furred, in combination with laterally depressed cheek teeth (fig. 18); ♂♂ without ruff of thick hairs; upper alveolar line practically straight (fig. 19); cheek teeth oblong, laterally depressed in one species; simplified palatal ridge pattern 7 + 1 (fig. 20) .......... **24**

**21 a.** Fal ♂♂ 68-88, ♀♀ 67-90; weight ♂♂ 60-97, ♀♀ 60-100; third metacarpal length 73-75% of fal; tibia length 42-46% of fal; tibia dorsally furred; $P^4$ and $M^1$ squarish in outline; two $I_1$ present; $M_3$ reduced but present; forests Guinea-Bissau to Central African Republic, southern Congo and northwestern Angola, and mountainous areas in eastern Central and East Africa from South Ethiopia to Zimbabwe and Mozambique .......... *Lissonycteris angolensis*
**b.** Fal 54-76; third metacarpal length 67-73% of fal; tibia length 36-43% of fal; distal quarter to third of tibia dorsally practically naked; $P^4$ and $M^1$ oblong in outline; two or one $I_1$ present; $M_3$ reduced or absent .......... **22**

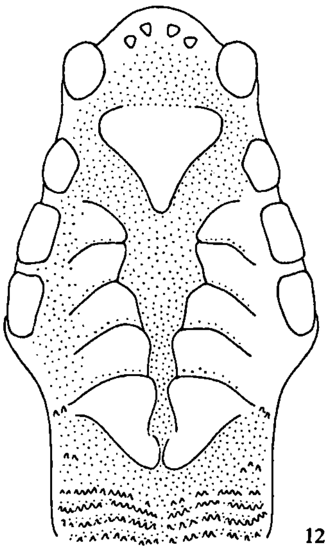
**22 a.** Fal 65-76; weight 1 ♂ 48, 1 ♀ 56; interfemoral membrane only furred near legs; simplified palatal ridge pattern 6 + 2 (possibly also 7 + 2); two $I_1$ present; $M_3$ absent; forests southeast Kenya, eastern Tanzania, East Zimbabwe.......... *Myonycteris relicta*
**b.** Fal 54-68; interfemoral membrane wholly furred; simplified palatal ridge pattern 7 + 2; either one or two $I_1$; $M_3$ reduced but normally present; West and Central Africa.......... **23**

**23 a.** Fal 54-68; weight ♂♂ 27-51, ♀♀ 31-60; two $I_1$; $C_1$ at least as high as $P_3$; $P_4$ with fused inner and outer ridges (fig. 21); forests from Guinea to northeast Zaïre, southwards to northwest Angola and North Zambia.......... *Myonycteris torquata*
**b.** Fal ≤62-65; weight not known; one lower incisor; $C_1$ lower than $P_3$; $P_4$ with inner and outer ridges widely and deeply separated (fig. 22); forests of Sao Tomé .......... *Myonycteris brachycephala*

**24 a.** Fal 66-107; weight ♂♂ below 180, ♀♀ below 165; back fur generally relatively dark brownish or reddish brown, never yellowish; back fur not sharply demarcated from wing membrane; tibiae practically naked or, if furred, in combination with reduced, laterally depressed cheek teeth; simplified palatal ridge pattern 7 + 1 (occasionally 8 + 1); wing inserted at first or second toe or in between.......... **25**
**b.** Fal 109-134; weight ♂♂ above 200, ♀♀ above 175; back fur grizzled straw-yellow and hair-brown, closely adpressed, sharply demarcated from wing membrane, or, in combination with a fal of over 120, greyish brown, more woolly, less adpressed and less sharply demarcated; cheek teeth never laterally depressed; simplified palatal ridge pattern 7 + 3; wing inserted at first toe.......... **28**

**25 a.** Fal 85-107; tibia furred or naked.......... **26**
**b.** Fal 66-77; tibia practically naked.......... **27**

**26 a.** Fal ♂♂ 85-94, ♀♀ 85-95; weight ♂♂ 102-140, ♀♀ 94-162; fur long, tibiae dorsally furred; wing insertion at second toe (occasionally between second and first); cheek teeth narrow, with widths of large premolars and molars half their lengths or slightly more; mostly above 1000 m in mountainous areas of southeast Ethiopia, South Sudan, East Zaïre, Uganda, Kenya,Tanzania, Malawi.......... *Rousettus lanosus*
**b.** Fal ♂♂ 85-107, ♀♀ 82-107 (southwest Asia: ♂♂ 85-95, ♀♀ 79-92); weight ♂♂ 111-168, ♀♀ 100-155 (Asia: ♂♂ 98-128, ♀♀ not known); fur short, tibiae dorsally practically naked; wing insertion at first toe (occasionally between first



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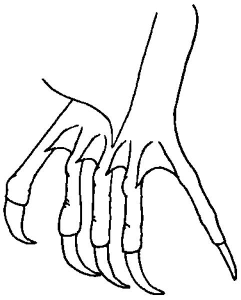

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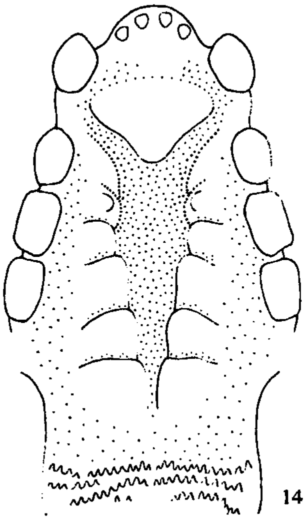

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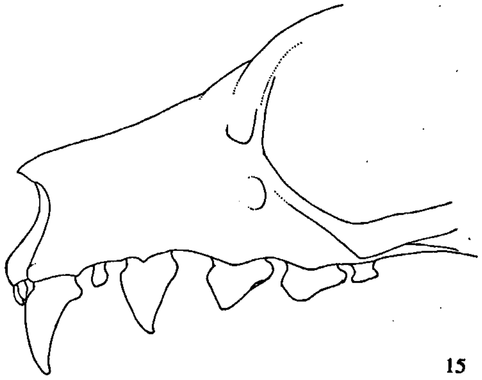

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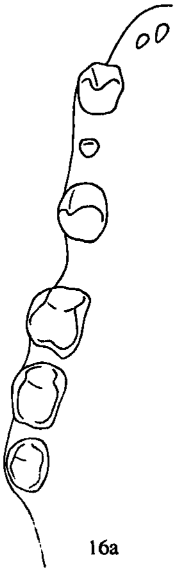

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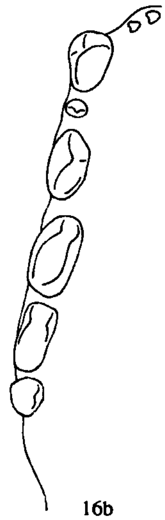

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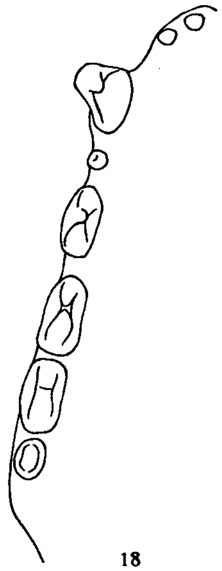

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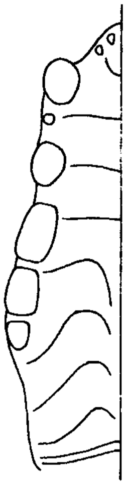

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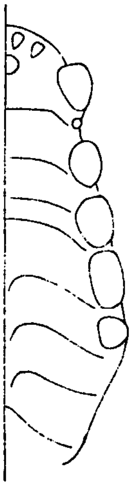

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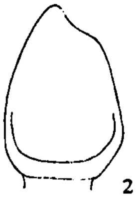

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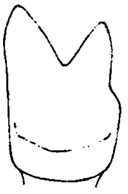

22

and second); widths of large premolars and molars clearly larger than half their lengths; predominantly lowland areas in Egypt to Turkey and Pakistan, from Gambia to Cameroun, southwards to northwest Angola, including Guinea Gulf islands, and from Ethiopia to South Africa, including continental islands.................................... *Rousettus egyptiacus*

**27 a.** Fal ♂♂ 71-77, ♀♀ 70-75; weight not known; wings inserted at base of second toe; widths of large premolars and molars clearly larger than half their lengths; the Comoros.................................... *Rousettus obliviosus*
**b.** Fal ♂♂ 67-76, ♀♀ 66-77; weight ♂♂ 60-83, ♀♀ 44-61; wings inserted between first and second toe; width of premolars and molars half their lengths or only slightly more; Madagascar.................................... *Rousettus madagascariensis*

**28 a.** Fal ♂♂ 129-134, ♀♀ 122-130; weight ♂♂ 245-340, ♀♀ 220-330; fur rather long and woolly, light greyish brown; back fur colour not sharply demarcated from wing membrane; tooth rows only weakly diverging backwards; premaxillae proclivous, with a distinct space between $I^2$ and $C^1$ when viewed from lateral; $P^4$ and $M^1$ with thick inner ridges and distinct median grooves; $M^2$ wider than long; lower incisors forming a semi-circle; $P_4$ with a rudimentary anterior and a distinct posterior inner cusp; $M_1$ with thick inner and outer ridges; Madagascar.......................... *Eidolon dupreanum*
**b.** Fal ♂♂ 109-131, ♀♀ 111-134; weight ♂♂ 212-311, ♀♀ 183-350; fur short, closely adpressed, grizzled straw-yellow and hair-brown; back fur colour sharply demarcated from wing membrane; tooth rows diverging backwards; hardly or no space between $I^2$ and $C^1$ when viewed from lateral; $P^4$ and $M^1$ with weak inner ridges and indistinct median grooves; $M^2$ longer than wide; lower incisors forming an almost straight row; $P_4$ without inner cusps; $M_1$ with thin inner and outer ridges; mainland Africa except deserts, and southwest Arabian Peninsula............................ *Eidolon helvum*

**29 a.** Fal below 110; ear length c. 12, ear nearly concealed in fur; tibia dorsally furred; Mauritius, Réunion (extinct) .................................... *Pteropus subniger*
**b.** Fal more than 110; ear length more than 20 .................................... **30**

**30 a.** Ear length usually 25 or more, ear subacutely pointed, well exposed; interfemoral membrane well-developed (up to about 15) in the middle.................................... **31**
**b.** Ear: either less than 25 long, pointed and largely concealed in the fur, or more than 25 long, rounded off and well-exposed; interfemoral membrane very narrow (some mm only) in the middle.................................... **34**

**31 a.** Larger: fal ♂♂ 168-171, ♀♀ 153-168; ear length 35-38; back fur dark brown, without admixed lighter hairs; Madagascar.................................... *Pteropus rufus*
**b.** Smaller: fal generally less than 164 in ♂♂ and than 159 in ♀♀; ear length variable; back fur colour variable but in larger specimens, with fal ≥ 145, blackish brown with admixed whitish and / or reddish brown hairs; not on Madagascar .................................... **32**

**32 a.** Smaller: fal ♂♂ 133-141; proximal part of dorsal side of tibia thickly furred, fur thinning out on distal part; weight ♂♂ 257-395, weight ♀♀ not known; Aldabra atol.................................... *Pteropus aldabrensis*
**b.** Larger: fal 145 or more; dorsal side of tibia at most partly thinly haired but essentially naked; weight ♂♂ 470-610, ♀♀ 430-600.................................... **33**

**33 a.** Fal ♂♂ 147-159, ♀♀ 151-155; ear length 29-37; fur of head golden yellowish or brownish yellow, fur of mantle golden yellowish or orange brown; weight ♂♂ 479-604, ♀♀ 450-508; Seychellen, Comoren, Mafia .......... *Pteropus seychellensis*
**b.** Fal ♂♂ 149-164, ♀♀ 145-159; ear length 26-28; fur of head mainly dark brown or reddish orange-brown, fur of mantle reddish in appearance; weight ♂♂ 470-610, ♀♀ 430-600; Pemba.................................... *Pteropus voeltzkowi*

**34 a.** Large: fal ♂♂ about 159-171, ♀♀ about 150-162; ear pointed, length c. 21, almost hidden in the long fur; back fur with a dark brown spinal track and buff on the sides; dorsal side of tibia furred; Mauritius, Réunion........ *Pteropus niger*
**b.** Either the same size or larger but with exposed, rounded ear and dorsal side of tibia essentially naked, or much smaller, with fal less than 140; back fur with out colour contrast.................................... **35**

**35 a.** Fal 161-172; ear semi-circular rounded off, exposed; ear length about 30; dorsal side of tibia essentially naked; Comoros.................................... *Pteropus livingstonii*
**b.** Fal ♂♂ 121-134, ♀♀ 123-129; ear pointed, almost hidden in the long fur; ear length about 22.5; dorsal side of tibia furred; weight ♂♂ 216-295, ♀♀ 204-306; Rodrigues, Round Island.................................... *Pteropus rodricensis*