BEAUFORTIA

A revision of the African genus *Myonycteris* Matschie, 1899 (Mammalia, Megachiroptera)

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ABSTRACT

The fruit bat genus *Myonycteris* Matschie, 1899, is considered to contain only two valid taxa: the species *M. torquata* (Dobson, 1878) inhabiting the forest blocks in West Africa and Central Africa, and *M. brachycephala* (Bocage, 1889) from the island of São Tomé. *M. wroughtoni* Andersen, 1908, and *M. leptodon* Andersen, 1908, are considered synonyms of *M. torquata*. The subgenus *Phygetis* Andersen, 1912, proposed for the species *brachycephala* only, is sunk into the synonymy of *Myonycteris*. A number of new (collecting) localities for *torquata* is recorded, among which the first one in Nigeria. Data are included on morphological variability, sexual dimorphism, ecology and biology. The possible type locality of *torquata*, and some evolutionary trends within the genus are discussed.

INTRODUCTION

In 1870 Gray described *Cynopterus collaris*. One of his two syntypes originated from "West Africa", the other from "Angola". According to Andersen (1912) "West Africa" stood for Lower Congo, presumably the Bas-Congo district in former Belgian Congo bordering the lower course of the river Congo west of 17° E, between 4° and 6° S (Schouteden, 1944). The Lower Congo specimen had been obtained by one Mr. Currer, in or before 1843. The specimen labelled "Angola" had been collected by the botanist F. M. Welwitsch, whose travels in Angola are described by Dolezal (1959; 1961). A study of Dolezal's work reveals (for reasons to be discussed later) as the most probable collecting "locality" of the Angola specimen a triangular area between Quizembro (3 miles north of Abriz) and the mouth of the river Cuanza at the coast, and Banza di Quisonde at about 250 miles from the coast. Welwitsch travelled this area from 10 September 1854 to 7 September 1857, and used the villages of Golungo Alto and Pungo Andongo as bases for his expeditions.

On account of its dental formula Dobson (1878) placed the species in *Cynonycteris* Peters, 1852, and because of prior use in 1852 of the combination *Cynonycteris collaris* by Peters, he changed the specific name in *torquata*. Dobson also mentioned the use of the combination *Cynopterus collaris* by Geoffroy prior to Gray — which reference I have not traced —, while Andersen (1912) cited the use of this combination by Kolenati in 1860. Dobson (*loc. cit.*) designated the Angola specimen as type of the species. In fact, this is the lectotype of the species, and the Lower Congo specimen the paralectotype.

A closely related species, *Cynonycteris brachycephala*, was described by Bocage, in 1889, from the island of São Tomé, where a single specimen had been collected by one Mr. Pires, in or before 1868.

Matschie (1899) referred both *torquata* and *brachycephala* to the genus *Xantharpyia* Gray, 1843 (=*Rousettus* Gray, 1821), the former as the type of a new subgenus, *Myonycteris*, and the latter as a member of the nominate race. Andersen (1907) raised *Myonycteris* to generic rank, which was accepted by all later students. He then regarded *brachycephala* as a synonym of *torquata*. In 1908 he described two new species, *Myonycteris wroughtoni* based on two specimens from "River Likandi" in north-east Zaïre, and *M. leptodon* based on one specimen from Sierra Leone (and including one from Liberia) — all specimens he still regarded as *torquata* a year before.

The most recent taxonomic treatment of the entire genus is still that by Andersen in 1912, who then knew only two specimens of *torquata*, *wroughtoni* and *leptodon* each, and but one of *brachycephala*, which he now, after having examined the type specimen, considered a distinct species. He even proposed a new subgenus, *Phygetis*, for this species, to establish its taxonomically more remote position from the three mainland species.

M. brachycephala is still only known from the type and it seems that after its description only Andersen and the present author studied this specimen. In his revision of 1912 Andersen confirmed its specific status, which to my knowledge has not been objected since by any other student. The relationships of the other three species, however, have been under discussion ever since more substantial material became available for study.

Allen, Lang & Chapin (1917) and Verschuren (1957; 1967) were content to assign their new north-east Zaïre specimens to the species *wroughtoni*. Eisentraut (1963), dealing with the variability in eight specimens from Mount Cameroon, identified by him as *torquata*, suggested that *wroughtoni* should be considered a subspecies of *torquata*, for which he received support from Brosset (1966a; 1966b), who wrote on *Myonycteris* from the People's Republic of Congo and from Gabon. Rosevear (1965) stated his doubt about the significance of the differences between *torquata* and *leptodon*. Kuhn (1965) argued that *leptodon* should be considered a subspecies of *torquata*. Hayman (1967) listed both *wroughtoni* and *leptodon* as subspecies of *torquata*, basing his view on the conclusions of Eisentraut (1963) and Kuhn (1965) and on the variability observed by him in a recently collected series of 22

specimens from Kumasi, Ghana. Jones (1971) agreed with this opinion, and so did Anciaux de Faveaux (1972) regarding *wroughtoni*, and De Vree, De Roo & Verheyen (1969), De Vree (1971), and De Vree & Van der Straeten (1971) regarding *leptodon*. Ansell (1967), Mumford (1970), and Bergmans, Bellier & Vissault (1974), reporting on specimens from Zambia, Uganda and Ivory Coast respectively, referred their specimens to *torquata*, but did not enter into the problems of subspecific classification.

Thus, the majority of authors reached a reasonable consensus on the conspecifity of *torquata, wroughtoni* and *leptodon*, but most of them at the same time felt the need to maintain the old divisions on a lower, i.e. subspecific level. In the old concept of three independant species it would not constitute a problem if eventually the three distribution areas would be found to overlap. The concept of one species divided into three subspecies not only leaves us with the problem of how to define these subspecies, but also introduces the need for a definition of their respective distribution areas. As for the subspecific characters, it has already been argued that those used by Andersen (1908; 1912) to distinguish the three species vary considerably, even locally, and are of doubtful diagnostic value in most cases (Eisentraut, 1963; Hayman, 1967; De Vree, 1971; Bergmans *et al.*, 1974). Concerning the distribution of *Myonycteris* and its possible species and subspecies, lack of sufficient material has so far prevented the involved authors from making overall accounts.

In the following notes alleged (sub)specific differences are reconsidered and aspects of the zoogeography, ecology and biology of *Myonycteris* will be discussed.

The used abbreviations indicate the following institutions and collections:

AIUF — Anatomical Institute of the University of Frankfurt, Frankfurt.

AMNH — American Museum of Natural History, New York.

BMNH — British Museum (Natural History), London.

IRSN — Institut Royal des Sciences Naturelles, Brussels.

LER — Laboratoire Emile Roubaud, Centre O.R.S.T.O.M., Brazzaville.

LPEE — Laboratoire de Primatologie et d'Écologie Équatoriale, Brunoy.

LMZ — Livingstone Museum, Livingstone.

MLZA — Museu e Laboratório Zoológico e Antropológico, Lisbon.

MNHN — Muséum National d'Histoire Naturelle, Paris.

MRAC — Musée Royal de l'Afrique Centrale, Tervuren.

NMB — National Museum, Bulawayo.

ORSTOM — Laboratoire d'Écologie des Mammifères et des Oiseaux, Centre O.R.S.T.O.M., Adiopodoumé.

PCMB — Powell Cotton Museum, Birchington.

REM — Collection R. E. Mumford, Lafayette.

RMNH — Rijksmuseum van Natuurlijke Historie, Leiden.

TUC   — Tulane University, Covington.
UBRA   — Laboratoire de Zoologie, Université de Brazzaville, Brazzaville.
UNM   — Museum of Southwestern Biology, University of New Mexico, Albuquerque.
USNM   — United States National Museum, Washington.
ZMA   — Zoölogisch Museum, Amsterdam.
ZMB   — Zoologisches Museum, Berlin.

MATERIAL EXAMINED

Sierra Leone: 1 ♂ (BMNH 91.2.13.1; type of *M. leptodon* Andersen).

Liberia: Schieffelinsville, 1 ♂ (RMNH 17359); Grand Gedeh Co (25 km N of Tchien = Zwedru), 1 ♂, 2 ♀♀ (AMNH 239350-239352); Mount Nimba, 8 ♂♂, 7 ♀♀ (BMNH 67.1436-67.1450).

Ivory Coast: Bolo, 4 ♂♂, 4 ♀♀, 3 of unknown sex (ORSTOM A9526, A9528-A9531, A9533, A9542, A9545-A9548); Lamto, 18 ♂♂, 14 ♀♀, 3 of unknown sex (ORSTOM, specified in Bergmans *et al.*, 1974); Saubre, 1 ♀ (USNM 467764); "Ivory Coast", 1 ♂, 5 of unknown sex (ORSTOM AXO733, AXO741, AXO745, AXO762, AXO766, AXO792).

Ghana: Kumasi, 5 ♂♂, 4 ♀♀ (BMNH 65.743, 66.620-66.627); 6 miles north of Kade, 5 ♂♂, 1 ♀ (USNM 414785-414789, 414791); 32 miles west of Prestea, 9 ♂♂, 18 ♀♀, (USNM 413755-413764, 413770-413774, 413780-413784, 413790-413794, 413803, 413804).

Nigeria: Ibadan, 1 ♂ (USNM 377094).

Fernando Poo: conform Musala, 1 ♀ (ZMB 58892; skin only).

Cameroon: 30 km west of Bertoua, 9 ♀♀ (AMNH 240998-241005); Bitye, 1 ♂, 1 ♀ (BMNH 13.9.12.2, 11.5.5.3); Ebolowa, 1 imm. (AMNH 54426); Kanyol Village, 1 ♂ (BMNH 33.8.4.19); Mey Joss Village, 1 of unknown sex (BMNH 33.8.4.20); Obala, 1 subadult, sex unknown (PCMB 514).

Central African Republic: La Maboké, 10 ♂♂, 30 ♀♀, 4 imm. (MNHN 1972.654-1972.697) and 1 of unknown sex (LER 294/196).

Gabon: Bélinga, 1 ♀ (ZMA 7802).

São Tomé: 1 ♀ (MLZA 449a; type of *Cynonycteris brachycephala* Bocage).

People's Republic of Congo: Brazzaville, 1 ♂ (MNHN); Dimonika, 7 ♀♀, 5 of unknown sex (UBRA 2,3-♀-70-03-08, 2,3-♀-70-03-09, 1,3-♀-70-06-14, 3-♀-70-06-10, and 5 without numbers); Makaba, 2 of unknown sex (UBRA); Odzala, 1 ♀ (MNHN); Pointe Noire, 1 ♂ (ZMA 15.423); Sibiti, 1 ♀ (MNHN); "Congo-Brazzaville", 1 of unknown sex (UBRA).

Zaïre: Congo Nil/Aka, 1 ♂ (MRAC 13525); Gangala-na-Bodio, 1 ♂ (MRAC 11657); Kinshasa, 1 of unknown sex (ZMA 11.163); "Lower Congo", 1 subadult of unknown sex (BMNH 43.9.27.2; paralectotype of *M. torquata* (Dobson)); Luluabourg, 2 ♂♂ (MRAC 33413, 33414); Medje, 1 ♂, 3 ♀♀ (AMNH 48752-48755); River Likati, 2 ♂♂ (BMNH 7.7.8.25 and 7.7.8.26; type and paratype of *M. wroughtoni* Andersen).

Angola: 1 ♂ (BMNH 66.1.20.4; lectotype of *M. torquata* (Dobson)).
Zambia: Salujinga, 2 ♂♂ (BMNH 65.534, 65.535).
Locality unknown: 1 ♂ (BMNH 50.8.29.1); 1 ♀ + young (ZMA 16.669).

Specimens cited from literature (where numbers are not in accordance with those in the cited papers, see also under "Material examined").
Liberia: Peloken, 1 specimen (? AIUF; Kuhn, 1965).
Ivory Coast: Adiopodoumé, 3 ♂♂, 5 ♀♀, 2 imm. (MRAC; De Vree, 1971).
Ghana: 6 miles north of Kade, 1 ♀ (USNM; Jones, 1971); Kumasi, 13 specimens (Hayman, 1967).
Togo: Ahoué-houé, 1 imm.; Edifou, 1 ♂; Ezimé, 1 ♂; Koutoukpa, 1 ♂ (De Vree, De Roo & Verheyen, 1969); Ebeva, 1 ♂, 1 ♀; Odjolo, 1 ♂ (De Vree & Van der Straeten, 1971).
Cameroon: Near Kumba, 2 specimens (Rosevear, 1965); Isobi and near Mueli, 2 ♂♂, 6 ♀♀ (Eisentraut, 1963).
Rio Muni: Ikunde, 5 ♂♂, 4 ♀♀ (TUC and UNM; Jones, 1971).
Gabon: Bélinga, 10 ♂♂, 16 ♀♀ (LPEE); Bélinga and Bengoué, 2 ♀♀, 2 imm., released after examination; Makokou, 1 ♂, 2 ♀♀, released after examination; locality not mentioned: 1 ♂, 1 ♀, in captivity (all in Brosset, 1966b).
Uganda: Bwamba Forest, 1 ♂ (REM 4062; Mumford, 1970).
Zambia: Salujinga, 2 ♂♂ (NMB 11556 and LMZ; Ansell, 1967).
Zaïre: Kamikoni, 1 ♀ (IRSN 1.694).

METHODS

In the past few years the present author could examine about two thirds of the more than 300 specimens of *Myonycteris* that are now known to exist in collections. The data regarding distribution, taxonomy and biology furnished by these specimens have been combined with those communicated in literature.

The distribution limits of the three subspecies of *Myonycteris torquata* as they are recognized by most authors, have been tentatively established, and their differential characters as originally stated by Andersen (1908, 1912) analyzed and evaluated. As sexual dimorphism in *Myonycteris* has been demonstrated (Bergmans *et al.,* 1974) the sexes have been treated separately.

All measurements are given in mm, and apply to obviously adult specimens, with the exception of cheek teeth lenghts which can be secured from all specimens with mature dentition.
Some measurements are explained in an earlier paper (Bergmans, 1975). Weights, taken from the collectors' labels, are given in grams.

RESULTS

Geographical distribution

All traced localities where specimens of *Myonycteris* have been captured are indicated on the map (fig. 1).
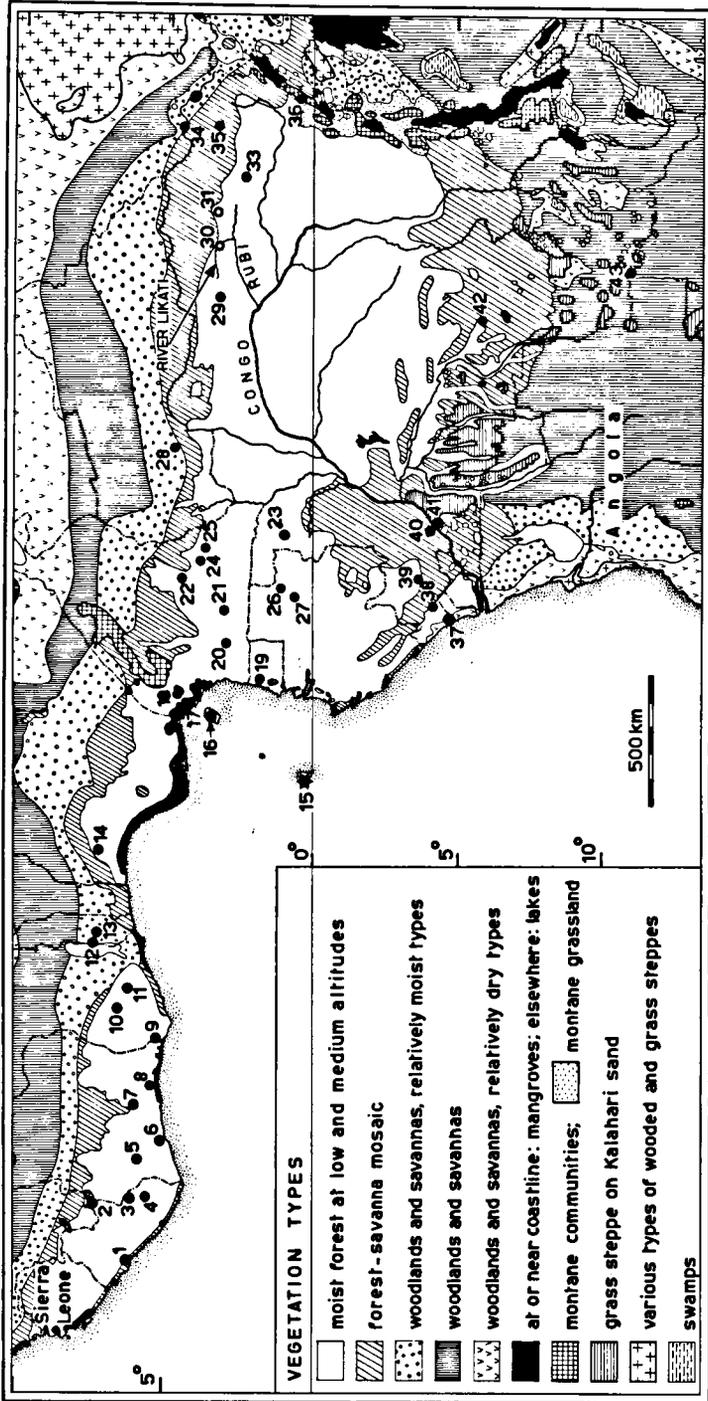
FIG. 1. Distribution of *Myonycteris torquata* (Dobson) (collecting localities: black dots; possible collecting localities: open circles) and of *Myonycteris brachycephala* (Bocage) (collecting locality: star). Vegetation types after Keay (1959).

1. Schieffelinsville
2. Mount Nimba
3. Grand Gedeh Co
4. Peloken
5. Saubre
7. Lamto
8. Adiopodoumé
9. 32 miles west of Prestea
10. Kumasi
11. 6 miles north of Kade
12. Ahoué-houé
13. Ebeva; Edifou; Ezimé; Koutoukpa; Odjolo
14. Ibadan
15. São Tomé
16. Fernando Poo
17. Isobi; Mueli
18. Near Kumba
19. Ikunde
20. Ebolowa
21. Bitye
22. 30 km west of Bertoua
23. Odzala
24. Kanyol Village; Mey Joss Village
25. Obala
26. Bélinga
27. Makokou
28. La Maboké
29. Kamikoni
30. Likati
31. Likandi
33. Medje
34. Congo Nil/Aka
35. Gangala-na-Bodio
36. Bwamba Forest
37. Pointe Noire
38. Dimonika; Makaba
39. Sibiti
40. Brazzaville
41. Kinshasa
42. Luluabourg
43. Salujinga

The types of *Myonycteris torquata* (Dobson) originate from "Angola" and from "Lower Congo". Other specimens that by their authors were considered conspecific and typical came from Fernando Poo (Krumbiegel, 1942) [1]); Isobi and Mueli (Eisentraut, 1963); near Kumba and South-eastern Cameroon — to judge from the present BMNH specimens probably Bitye, Kanyol Village and Mey Jos Village — (Rosevear, 1965); Brazzaville (Brosset, 1966a) [2]); Bélinga, Bengoué and Makokou (Brosset, 1966b). From the given measurements the specimens described by Jones (1971) from Ikunde appear typical (although no teeth measurements are given). A number of presently examined specimens from other localities that in my opinion are typical *torquata*, are from: Ebolowa; 30 km west of Bertoua; Obala; Odzala; La Maboké (mentioned but not commented by Vielliard, 1974); Pointe Noire; Dimonika; Makaba; Sibiti; and Kinshasa.

These examples cover an area from southern Cameroon, including Fernando Poo, and Central African Republic in the north, via Gabon and the People's Republic of Congo, to "Lower Congo" and "Angola" in the south.

[1]) Dr. I. Krumbiegel (*in lit.*, 16-VI-1975) informed me that this specimen had been identified by Dr. H. Pohle, at the time curator of mammals in the Zoologisches Museum at Berlin. The skull of the specimen could not be found (Dr. H. Hackethal, *in lit.*, 29-X-1975), but I have examined the skin (ZMB 58892) and am convinced that it is *Myonycteris*. I agree with Eisentraut (1964) that the occurrence of *M. torquata* on Fernando Poo is plausible, but in theory, of course, it could also be *M. brachycephala*.

[2]) The data with this specimen in the MNHN collection are: Sibiti, 28-XI-1963, and do not agree with Brosset's account.

The specimens from Salujinga and Luluabourg should probably be included here, but have preliminary been omitted because in theory they could be more related to the populations in north-east Zaïre (*wroughtoni*) as well. Hayman (1967) could not distinguish the Salujinga specimens from the typical form.

Andersen (1908) gives as the type locality of his *Myonycteris wroughtoni* River Likandi, but later (1912) spells it as River Likati. The positions of villages of both names as well as the River Likati are indicated on the map (fig. 1). The most probable type locality seems somewhere along or near the River Likati. Later several other specimens were identified as *wroughtoni* by their authors; they come from Medje (Allen *et al.,* 1917); Congo Nil/Aka and Gangala-na-Bodio (Verschuren, 1957); Kamikoni (Verschuren, 1966). Mumford records a specimen of *M. torquata* from Bwamba Forest, Toro, Uganda, which for obvious reasons is considered here together with the north-east Zaïre specimens rather than with those from the distant typical *torquata* populations. Brosset (1966a) reports on a large specimen from Sibiti, which he hesitatingly refers to *wroughtoni*. I examined this specimen and quite a few others from southern People's Republic of Congo (in fact the area, nearest to the type locality of *torquata*), and consider them all typical *torquata*. The known distribution of specimens, assigned to *wroughtoni*, is thus restricted to north-east Zaïre and adjacent Uganda.

The type locality of *Myonycteris leptodon* Andersen is Sierra Leone. Other specimens assigned to *leptodon* are from Schieffelinsville (Jentink, 1888; Andersen, 1908); Peloken (Kuhn, 1965); Kumasi (Rosevear, 1965); Ahoué-houé, Edifou, Ezimé and Koutoukpa (De Vree *et al.,* 1969); Adiopodoumé (De Vree, 1971); Ebeva and Odjolo (De Vree *et al,* 1971); 32 miles west of Prestea and 6 miles west of Kade (Jones, 1971). Other presently studied specimens that belong to the more western populations are from Mount Nimba; Grand Gedeh Co; Saubre; Bolo; Lamto; "Ivory Coast"; and Ibadan. The known distribution of *Myonycteris leptodon* would thus be from Sierra Leone to Ibadan.

Myonycteris brachycephala (Bocage) has not been collected ever since its description, and its known distribution area is therefore conform the type locality: São Tomé.

Taxonomy

Andersen (1908, 1912) used the following measurements to discriminate *Myonycteris torquata, M. wroughtoni,* and *M. leptodon:*
    total skull length
    rostrum length
    front width of rostrum (distance between inner bases of canines)
    lachrymal width
    length of combined orbital cavity and temporal fossa
    interorbital width
    P^4, M^1, M^2, P_4 and M_1 measurements

TABLE 1. Skull and teeth measurements of *Myonycteris* types as percentages of total skull length (t.s.l.) and palatilar length (p.l.), based on the data in Andersen (1908, 1912).

	leptodon		torquata			wroughtoni		
	mm	% p.l.	mm	% t.s.l.	% p.l.	mm	% t.s.l.	% p.l.
total skull length	16.3	100	31–31.8	100	209–212	34	100	206
palatilar length	10.2	63	14.8–15	48	100	16.5–16.8	49	100
rostrum length	3.3	20	9–9.2	29	61	10.7–10.5	31	63–65
front width of rostrum			3.7–4	12	25–26	3.7–4	11	22–24
lachrymal width			8.8–8.8	28	59	9.8–10	29	59–60
length orbital cavity + temporal fossa	9.8	60	9–9.8	29–31	34–35	10.7–11	31	36
interorbital width	5.8	36	5–5.2	16	6–6	6–6	18	36
P⁴ length	2.1	12.9	2.5–2.5	7.9–8.1	16.7–16.9	2.5–2.7	7.6	15.2–16.1
width	1.4	8.6	1.7–1.5	4.7–5.4	10.0–11.5	1.8–1.7	5.3	10.1–10.9
M¹ length	1.8	11.0	2.1–2.2	6.8–6.9	14.2–14.7	2.2–2.2	6.5	13.1–13.4
width	1.2	7.4	1.5–1.3	4.1–4.8	8.7–10.1	1.6–1.5	4.7	8.9–9.7
M² length	1.2	7.4	0.7–0.8	2.3–2.5	4.7–5.3	1.1–1.1	3.2	6.5–6.7
width	1	6.1	0.6–0.6	1.9	4.0–4.1	0.9–0.8	2.6	4.8–5.4
P₄ length	2.2	13.5	2.4–2.6	7.7–8.2	16.2–17.3	2.6–3	7.6	15.8–17.9
width	1.5	9.2	1.6–1.5	4.7–5.2	10.0–10.8	1.7–1.6	5.0	9.7–10.3
M₁ length	2	12.3	2.3–2.3	7.2–7.4	15.3–15.5	2.4–2.5	7.1	14.5–14.9
width	1.3	8.0	1.6–1.3	4.1–5.2	8.7–10.8	1.5–1.5	4.4	8.9–9.1

height of coronoid process
ear length
wing length
forearm length
length of third metacarpal
length of tibia
length of foot with claw
palatilar length ("palation to incisive foramina").

In table 1 the skull and cheek teeth measurements as given by Andersen (*loc. cit.*) are expressed as percentages of the total skull length and of the palatilar length. The latter relation is given because both total skull lengths of the *torquata* syntypes were estimated by Andersen, and that of his *leptodon* type could not be measured. The other discriminating characters cited by Andersen are body measurements which should be related to the overall size of the concerned specimens. As these types are dry skins and skulls, the total length could not be measured. Therefore the body measurements have been related to the forearm lengths (table 2).

From the figures in table 1 its is clear that even for the type specimens a

TABLE 2. Body measurements of *Myonycteris* types as percentages of forearm lengths, based on the data in Andersen (1912).

	leptodon		*torquata*		*wroughtoni*	
	mm	% f.a.l.	mm	% f.a.l.	mm	% f.a.l.
forearm length	61	100	56 —60.5	100	65 —67	100
ear length	14	23	14.5—15	25—26	16.5—17.5	25—26
length 3rd metacarpal	42	69	36 —39	64	44.5—45	67—68
tibia length	24.5	40	21.5—22	38	25.5—25	37—39
foot with claw	17.5	29	14.5	26	17 —18	25—28

number of differences, presented by Andersen as of diagnostic value, are not relative but absolute, being directly related to skull size, which is largest in the *wroughtoni* types, medium sized in the *leptodon* type, and smallest in the types of *torquata*. Such measurements are palatilar length, lachrymal width and combined length of orbital cavity and temporal fossa. The rostrum is very slightly shorter if related to the palatilar length in the types of *torquata* than in the others; they also have a relatively narrower interorbital width. The front width of the rostrum is smaller in the *leptodon* type than ·in the other types. Of the cheek teeth it seems sufficient to compare their lengths only, as their widths show a generally congruent variation. Then, P^4, M^1, P_4 and M_1 are longest in *torquata*, medium sized in *wroughtoni*, and shortest in *leptodon*, whereas M^2 is longest in *leptodon*, medium sized in *wroughtoni*, and shortest in *torquata*. The height of the coronoid process related to the mandible length, as measured by Andersen (1912) in the type specimens, is

40-41 % in *torquata*, 41-42% in *leptodon*, and 38-41% in *wroughtoni*, and cannot stand as a differential character.

The figures in table 2 show that the relative differences in tibia length are minimal and evidently without taxonomic value. The same applies to the relative foot length: the specific variation demonstrated in the two *wroughtoni* types indicates that the difference observed between the types of *torquata* and *leptodon* is of no apparent taxonomic significance. Further conclusions are that the *wroughtoni* types possess larger body measurements than those of *torquata* and *leptodon*, and that the *torquata* types are the smallest specimens. It is also suggested, that the ears of *leptodon* are slightly

TABLE 3. Measurements in mm and weights in grams of *Myonycteris* specimens from Sierra Leone, Liberia, Ivory Coast, Ghana, and Ibadan, Nigeria (*Myonycteris leptodon* Andersen).

	♂♂			♀♀		
	n	m	min-max	n	m	min-max
total length*	26	107.9	88—120	24	107.9	98—118
tail*	21	5.6	0—11	20	7.6	0—13
ear*	22	17.7	13—21	22	17	15—19
forearm length	37	61.2	57.3—65.1	36	61.5	56.0—67.1
third metacarpal	11	42.2	39.9—45.4	7	41.5	39.5—44.3
tibia*	10	26	24—28	4	25	22—27
foot*	16	17.2	14—21	19	18.3	14—21
greatest skull length	33	33.4	31.9—35.1	34	32.9	30.1—35.0
condylobasal length	25	32.0	30.5—34.3	30	31.6	28.7—34.0
rostrum length	33	11.9	11.2—12.7	33	11.6	10.6—12.7
palatal length	31	18.1	16.9—19.3	33	17.9	16.2—19.8
mandible length	34	25.6	23.9—27.4	33	25.3	23.0—27.3
cranium width	35	13.8	12.9—14.5	35	13.6	12.8—14.4
interorbital width	35	6.0	5.1—7.8	35	5.9	5.2—6.7
postorbital width	35	7.9	6.8—8.7	34	8.0	6.9—9.1
zygomatic width	26	19.7	18.8—20.6	32	19.1	16.4—21.3
C^1-C^1 interiorly	20	3.8	3.4—4.1	24	3.6	3.2—4.1
C^1-C^1 exteriorly	29	6.4	5.9—6.9	22	6.4	5.5—7.8
C^1-M^2	35	12.3	11.4—13.3	34	12.2	11.4—12.9
M^2-M^2	32	9.4	8.7—10.0	32	9.2	8.6—10.1
C_1-M_3	33	13.6	12.6—14.6	34	13.2	12.5—14.4
length P^1	34	0.57	0.4—0.8	30	0.58	0.4—0.7
length P^4	8	2.2	2.0—2.3	8	2.2	2.1—2.3
length M^x	33	2.0	1.8—2.2	38	2.0	1.85—2.3
length M^2	49	1.2	0.9—1.5	46	1.24	0.7—1.4
length P_4	8	2.4	2.2—2.7	8	2.35	2.25—2.5
length M_1	7	2.2	2.1—2.3	8	2.2	2.1—2.3
weight*	24	39.9	27—49	24	42.0	30—54

* collectors' measurements

TABLE 4. Measurements in mm and weights in grams of *Myonycteris* specimens from Cameroon, Central African Republic, Gabon, People's Republic of Congo, western Zaïre and Angola (*Myonycteris torquata* (Dobson)).

	♂♂			♀♀		
	n	m	min-max	n	m	min-max
total length*	2	93	86—100	8	103	90—114
tail*	3	8	8—8	8	7.3	0—11
ear*	4	16.3	14.5—18	8	18.3	18—21
forearm length	15	60.2	56—64.4	38	60.7	54.9—65.6
third metacarpal	1		41.2			
tibia*	3	22.7	21.5—24.7			
foot*	1		14.5	7	18.6	16—20
greatest skull length	11	32.4	30.9—33.2	25	31.7	30.2—33.5
condylobasal length	8	31.3	29.7—32.0	21	30.7	28.8—32.6
rostrum length	12	11.2	10.4—11.9	30	10.9	9.8—12.35
palatal length	5	16.9	16.5—17.5	28	17.0	15.3—18.65
mandible length	12	25.2	23.7—25.9	31	24.7	22.6—26.1
cranium width	12	13.5	13.0—14.0	29	13.3	12.8—13.9
interorbital width	12	5.5	4.9—5.8	31	5.4	4.8—6.2
postorbital width	12	7.6	6.7—8.6	31	7.7	6.1—8.3
zygomatic width	6	20.5	19.3—21.1	26	19.8	18.7—20.9
C^1-C^1 interiorly	9	3.6	3.4—3.9	14	3.3	2.9—3.3
C^1-C^1 exteriorly	12	6.4	5.9—6.7	21	6.5	5.8—7.6
C^1-M^2	12	12.0	11.4—12.7	28	11.9	11.0—12.7
M^2-M^2	12	8.6	8.1—9.0	26	8.5	7.7—9.3
C_1-M_3	12	13.3	12.7—13.8	29	13.2	12.2—14.0
length P^1	10	0.6	0.5—0.7	35	0.6	0.5—0.8
length P^4	1		2.25	9	2.3	2.1—2.5
length M^1	12	2.05	1.9—2.2	37	2.1	1.9—2.4
length M^2	12	0.9	0.8—1.1	36	0.9	0.3—1.2
length P_4	1		2.4	1		2.3
length M_1	1		2.2	1		2.2
weight				7	35.6	28—43

* collectors' measurements

shorter than those of the others, and that the *torquata* types have relatively shorter third metacarpals than the others.

In accordance with the distribution areas as defined above the studied specimens have been divided into three groups. The measurements of the specimens of each of these groups, specified per sex, are given in the tables 3, 4 and 5. Of some of these measurements the relative values, expressed as percentages of either forearm length (body measurements) or greatest skull length (skull and teeth measurements) are given in table 6.

From the data in these tables the following observations regarding the differential characters that remain to be analyzed can be made. The essence

TABLE 5. Measurements in mm of *Myonycteris* specimens from north-easthern Zaïre and adjacent Uganda (*Myonycteris wroughtoni* Andersen).

	♂♂			♀♀		
	n	m	min-max	n	m	min-max
total length*	2	116	102—130	2	113	112—114
tail*	2	7	4—10	2	9	6—12
ear*	2	18	18—18	2	19.5	19—20
forearm length	6	61.8	60.3—64.6	2	62.4	60.3—64.4
foot*	2	16.5	15—18	2	20	18—22
greatest skull length	3	33.3	33.2—33.5	2	32.9	32.5—33.3
condylobasal length	3	31.8	31.1—32.3	2	31.8	31.4—32.1
rostrum length	5	11.7	11.4—11.9	2	11.3	11.0—11.5
palatal length	3	18.2	18.0—18.4	2	17.7	17.2—18.1
mandible length	5	25.6	25.1—26.0	2	25.6	25.2—25.9
cranium width	4	13.6	13.2—14.1	2	12.7	12.6—12.8
interorbital width	5	5.7	5.3—5.9	2	5.6	5.5—5.6
postorbital width	3	7.6	7.0—8.1	2	7.6	7.3—7.9
zygomatic width	4	19.8	19.3—20.7	1		19.4
C^1-C^1 exteriorly	5	6.5	6.1—6.7	1		6.3
C^1-M^2	6	12.3	11.7—12.9	2	12.1	11.9—12.2
M^2-M^2	5	9.1	8.0—9.6			
C_1-M_3	5	13.7	13.3—13.9	2	13.3	13.2—13.4
length P^1	5	0.6	0.5—0.75	2	0.65	0.6—0.7
length M^1	3	2.25	2.2—2.35	2	2.25	2.2—2.3
length M^2	6	1.1	0.7—1.4	2	1.15	1.0—1.3

* collectors' measurements

of Andersen's diagnoses (tables 1 and 2) are here printed between brackets.

Absolute differences (tables 3, 4 and 5)

Greatest skull length — as a measure for absolute skull size (larger in *wroughtoni*, medium sized in *leptodon*, smaller in *torquata*). There is no apparent difference between *wroughtoni* and *leptodon*. The extreme and average values in *torquata* are lower, but the overlap of the *torquata* and *leptodon* ranges is great (in the female series even complete).

Forearm length — as a measure for absolute overall size (larger in *wroughtoni*, medium in *leptodon*, and smaller in *torquata*). The averages confirm Andersen's ideas, but the ranges overlap almost completely. The largest *torquata* male and female even match or surpass the largest *wroughtoni* male and female in forearm length.

Relative differences (table 6)

Relative rostrum length (smaller in *torquata* than in *wroughtoni* and *leptodon*). The measurements indicate that the relatively shortest rostrums

TABLE 6. Relative measurements of *Myonycteris* specimens; rounded percentages, except those for C¹-C¹ interiorly and for the teeth.

| | Sierra Leone, Liberia, Ivory Coast, Ghana, and Ibadan | | | | | | Cameroon, Central African Republic, Gabon, People's Republic of Congo, Kinshasa, and Angola | | | | | | North-eastern Zaire and adjacent Uganda | | | |
| | ♂♂ | | | ♀♀ | | | ♂♂ | | | ♀♀ | | | ♂♂ | | ♀♀ | |
	n	m	min-max	n	m	min-max	n	m	min-max	n	m	min-max	n	min-max	n	min-max
percentages of forearm length of:																
ear¹)	11	30	27 —31	15	28	23 —31	1		28.5	6	32	30 —35	2	29.5—30	2	31 —31.5
third metacarpal	10	70	68 —71	7	68	65 —70	1		66.5	2²)		64 —68	2	25 —29.5	2	30 —34
foot¹)																
percentages of greatest skull length of:																
rostrum length	10	35	35 —36.5	10	36	35 —37	9	35	33.5—36	17	34	32 —35	2	35 —36	2	34 —34.5
interorbital width	10	17.5	16 —23	10	18	17 —20	9	17	15 —18	17	17	15 —20	2	17 —17	2	17 —17
C¹-C¹ interiorly	20	11.3	10.1—12.3	23	11.2	10.2—12.5	9	11.1	10.4—12.4	11	10.6	9.4—11.8	2	18 —20	1	19
C¹-C¹ exteriorly	9	19	18 —21	10	20	18 —24	9	19.5	18 —22	11	20	19 —21				
length P⁴	6	6.7	6.1— 6.9	7	6.9	6.4— 7.5	1		6.9	4	7.2	6.7— 7.6				
length M¹	9	6.0	5.7— 6.6	11	6.2	5.7— 7.0	9	6.2	5.8— 7.1	14	6.7	6.1— 7.3			2	6.7— 7.1
length M²	9	3.8	3.5— 4.1	11	4.0	3.6— 4.5	9	2.9	2.6— 3.3	14	2.8	2.2— 3.2	2	2.1— 3.9	2	3.0— 4.0
length P₄	6	7.3	6.9— 7.9	7	7.3	6.9— 7.7	1		7.4							
length M₁	5	6.7	6.4— 7.0	7	6.8	6.4— 7.1	1		6.8							

¹) collectors' measurements (except forearm lengths)
²) subadult specimens

are found in *torquata*, but also that the differences between *torquata* and the others are minimal.

Relative frontal width of rostrum (smaller in *leptodon* than in *torquata* and *wroughtoni*). From the available data on the distance between the inner bases of the upper canines it does not follow that this distance is smaller in *leptodon* than in *torquata*. On the contrary it seems slightly smaller in *torquata* females than in *leptodon* females. Another measurement, exteriorly over the cingulae of the upper canines, shows a considerable variation in *leptodon*, where it is not really smaller than in *torquata* or *wroughtoni*.

Relative interorbital width (smaller in *torquata* than in *wroughtoni* and *leptodon*). Averaging slightly lower in *torquata* than in *leptodon*, although the ranges overlap almost completely. In the few examples of *wroughtoni* it is consistent with *torquata* and with the lower values in *leptodon*.

Relative lengths of P^4, M^1, P_4 and M_1 (small in *leptodon*, intermediate in *wroughtoni* and large in *torquata*). Data on fourth premolars in *wroughtoni* are lacking; the few *torquata* examples fall nearly within the known *leptodon* limits, indicating that the averages in *torquata* could be higher. The lenght of M^1 averages slightly lower in *leptodon* than in *torquata*; the sparse data on M^1 in *wroughtoni* suggest its conformity with *torquata*. Data on the length of M_1 in *wroughtoni* are lacking; the only example of *torquata* fits the range in *leptodon*.

Relative length of M^2 (large in *leptodon*, medium in *wroughtoni*, and small in *torquata*). In general Andersen's diagnosis seems right, although the picture is somewhat spoiled by the small relative M^2 length encountered in one of the *wroughtoni* males.

Relative ear length (small in *leptodon* and larger in the others). Andersen's statements are confirmed by the series of *torquata* and *leptodon* females, but not by any of the other categories.

Relative wing length (large in *wroughtoni*, medium in *torquata* and small in *leptodon*). Andersen does not support his diagnosis with numerical evidence, nor does he describe his method of measuring. The dry type skins do not allow any accurate wing length measuring. As this measurement was never taken by later collectors, I do not have any relevant information at hand.

Relative length of third metacarpal (smaller in *torquata*, larger in the others). The few available data hint that in *torquata* this measurement may average lower than in *leptodon*, but do not justify definite conclusions. On *wroughtoni* no data are available.

Accordingly, *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. The suggestion that other relative cheek teeth lengths average lower in *wroughtoni* than in *torquata* (table 1) is for M^1 contradicted by the examples in table 6; *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 third 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. (The two adult males from Salujinga that I examined had forearm lengths of 57.7 and 64.1 mm, greatest skull lengths of 32.2 and 32.4 mm, and M^2 lengths of 1.0 and 0.8 mm, and fit well into the range of the central populations. Two adult males from Luluabourg had forearm lengths of 59.8 and 62.2 mm, greatest skull lengths of 32.0 and 34.2 mm, and M^2 lengths of (both) 1.1 mm, and seem to link the central with the north-eastern populations.)

A recapitulation of the above statements learns that several of Andersen's observations regarding specific differences between *torquata*, *wroughtoni* and *leptodon* do not hold, while those that, to a certain degree, could be confirmed, in my opinion as differential characters are insufficient to warrant the recognition of subspecific divisions within *M. torquata*. I therefore propose to synonymize both *wroughtoni* and *leptodon* with *torquata*.

Status of *Myonycteris brachycephala*

While Bocage (1889) was not convinced that his *Myonycteris* specimen from São Tomé would hold as an independant species, Andersen (1912), who had the advantage of knowing the continental representatives of the genus, not only considered it as a valid species, but even proposed a new subgenus, *Phygetis*, to accomodate it. No other specimens than the single type having come to knowledge, we shall have to depend for our present studies mainly on Andersen's thorough account of this type specimen (1912), since, as appeared during my visit to the Museu Bocage in Lisbon (December 1975), the skull of the type specimen could not be found and apparently had been lost. Only the mounted skin, with stretched wings fixed on a small board, has remained. From this, I could check some of the wing measurements. The right forearm length is 64.2 mm, and the left 63.5 mm. This is rather in accordance with Andersen's report than with that of Bocage. The right third metacarpal measured 44.4 mm.

Apart from the somewhat longer fur, the important differences between *brachycephala* and *torquata* are to be found in the skull and the dentition, as described and figured by Andersen (1912), who wrote that the skull agrees mostly with those of his *wroughtoni* types. The following quotations are from Andersen's description (1912): "Skull in general aspect and even in size very similar to that of *M. wroughtoni*, but postdental palate distinctly narrower and with lateral margins more rapidly converging antero-posteriorly, interorbital 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 writes 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); that upper and lower cheek teeth are much larger and with considerably higher and sharper cusps; that outer and inner ridge of P^3 are obscurely separated (in stead of fused) and both raised as conical cusps; that the inner ridge in P^4 is similarly conical; and that the antero-internal base of P^4 is more prominent and ledge-like.

I have no doubt that *brachycephala* is taxonomically distinct from *torquata*, and I tentatively agree with Andersen that the differences are on a specific level. The character of the differences, as summed up by Andersen and quoted above, excludes the possibility of the one known *brachycephala* specimen being only an aberrant example of *torquata*; it points into a totally different direction, to be discussed later in this paper. It is nevertheless clear that *brachycephala* is closely related to *torquata*, and I cannot think of any reason to maintain a subgeneric division between the two, as proposed by Andersen. I propose therefore to sink *Phygetis* into the synonymy of *Myonycteris*.

My conclusions on the taxonomy of *Myonycteris* can be summarized as follows:

Genus *Myonycteris* Matschie, 1899 (synonym *Phygetis* Andersen, 1912)

    Species *M. torquata* (Dobson, 1878) (synonyms *M. wroughtoni* Andersen, 1908, and *M. leptodon* Andersen, 1908); African mainland.

        M. brachycephala (Bocage, 1889); São Tomé.

Notes on *Myonycteris torquata*

Variability

The forearm length in all known adult *M. torquata* specimens varies from 54.9 to 67.1 mm, the greatest skull length from 30.1 to 35.1 mm. According to Andersen (1912: xliv) the variation in the forearm length of a species should be at least 10%, and not more than 17% of the minimum measurement, provided that a sufficient series is at hand. When individual populations are considered, *M. torquata* shows a variation of 10 to 14%.

The fur colour and its variation have been described by Eisentraut (1963), Rosevear (1965) and Bergmans *et al.* (1974), while notes on the ruff colour in the males are also given by Brosset (1966b). Without exception, young specimens appear to be rather darkly coloured, a phenomenon that I also observed in juveniles of the epomophorine genera *Epomophorus* Bennett, 1836, *Epomops* Gray, 1870, *Micropteropus* Matschie, 1899 and *Nanonycteris* Matschie, 1899. It is thinkable that this dark colour in juveniles as an

invariable character has been favoured by their need for warmth and/or protection during the period when they are often left unattended by their foraging mothers. Among the many examined adult skins quite. a few featured rather light hair tips in the fur of the back, resulting in reddish brown, orange brown or even yellowish brown hues. There seems to be no apparent relation between a certain colouring and either sex, season, or geography.

The dentition in *M. torquata* is subjected to two evolutionary tendencies which are apparent in many, if not all, Megachiroptera (Eisentraut, 1959): reduction in teeth size and reduction in teeth number. In *Myonycteris* both processes are, so to speak, very active, but with regard to teeth size reduction different populations are not affected to the same extent, which, as discussed, has been interpreted as being of taxonomical significance (Andersen, 1908), while within a certain population individual specimens may show a fair differentiation in their degree of dental reduction. A subadult male from 6 miles north of Kade, USNM 414788, lacked both I^2. An adult male from La Maboké, MNHN 1972-689, and also a male from Ikunde (Jones, 1971), missed both P^1. An adult male from unknown locality, BMNH 50.8.29.1, had only one (reduced) M^2 and no M_3. A juvenile female from 32 miles west of Prestea, USNM 413794, had no M^2 (very small holes in the jaw suggest their former presence; the juvenile age of the specimen renders this unlikely) and only one extremely small M_3. An adult female from Adiopodoumé, MRAC 35002, had a reduced left M^2 and no (left?) M_3 (De Vree, 1971). Three adult females had only one M^2: MNHN 1972-674 and 1972-696 from La Maboké, and UBRA 2-♀-70-03-08 from Dimonika. That in 1972-696 was extremely small: 0.3 × 0.3 mm. A female from Lamto (ORSTOM 21.617) had no M_3, another female from Lamto (ORSTOM 21.632) had two reduced M_3. A male from Lamto (ORSTOM 1324) and another from Kumasi (BMNH 66.6221) had only one M_3. A male from Luluabourg (MRAC 33414) had only one, reduced, M_3.

Supernumerary teeth were also met. An adult male from Adiopodoumé, MRAC 34999, had one M^3 and two M_4 (De Vree, 1971). A male from Sierra Leone (BMNH 91.2.13.1; type of *M. leptodon* Andersen) had two M^3. A male from Ivory Coast (ORSTOM AX0745) and one from Ikunde (Jones, 1971) had both one M^3. One male from Lamto (ORSTOM 21.623) had two M_4. A female from 6 miles north of Kade (USNM 414789) and another from 32 miles west of Prestea (USNM 413803) had one M_4. Apart from these seemingly atavistic çases there were three specimens with aberrant supernumerary teeth. A subadult specimen from Ivory Coast (ORSTOM AX0733) had a very small extra tooth between the right M_2 and M_3. An adult female from Bitye (BMNH 11.5.5.3) had two small upper incisors in stead of the right I^2, and in front of these and also in front of the left I^2, an additional small tooth. A row of four additional small teeth in front of the four upper incisors was found in an adult male from Sibiti (MNHN; field number 556). The chance that, in the two last mentioned cases, the extra teeth were milk

teeth, is small, The specimens were clearly adult, and neither the position of the extra teeth in front of the mature teeth, nor their obtuse form reminded me of milk teeth. Andersen (1912: 577), in a footnote, remarks that in the type of *M. brachycephala* the entire space between I_2-I_2 was filled by one broad incisor.

Configuration and variations in the palatal ridge pattern of *Myonycteris torquata* are discussed by De Vree (1971), who also gives good photographs, and Bergmans *et al.* (1974), respectively. The palate could be studied in 76 specimens. Counting from the front, the third ridge was divided in one specimen, the fourth undivided in seven specimens (including the ones mentioned in Bergmans *et al., loc. cit.*), the sixth ridge reduced — mostly to their median parts — in four specimens, in one of which the ninth was also reduced. In two specimens there were only eight ridges: one ridge filling the space of the sixth and seventh; in one specimen the seventh ridge was only weakly curved and placed rather backward. One specimen had an extra ridge in between the seventh and eight ridges, two specimens had a normal pattern with some additional, irregular elements.

Sexual dimorphism

Whereas skull size averages slightly higher in males, females have longer forearm lengths and greater weights (tables 3, 4 and 5). But these characters cannot serve to determine the sex of individual specimens. Adult males are recogized by their ruff of aberrantly formed and coloured hairs, and lactating females by their enlarged nipples, but quite frequently one encounters specimens that are not distinctly juvenile and also lack one of the above mentioned characters. Too soon collectors are inclined to label such specimens as females, and not seldom experienced zoologists indulge in the same policy. Only a careful examination of the genital area can prevent mistakes. Verschuren (1957) bases his statement of male-like ruff hairs in a female of *Myonycteris* on what after re-examination for the present study appeared to be a male. As long as the involved specimens are preserved in alcohol, such a check is possible, but it is sometimes impossible to determine the sex of a dried skin, especially when the skin of the abdomen has been damaged by cutting.

In fact, there need not be any difficulty in ascertaining the sex of complete specimens, old or young, even without dissection. Misidentifications are mainly brought about by the fact that the males have a very short prepuce which, when somewhat flattened and pressed against the abdomen, may be taken for the female clitorideal pad. In normal position the rather broad, transverse clitorideal pad lies flat over the vulvar orifice, but sometimes it is folded along the median line, and stands off from the abdomen, and could possibly be taken for the male prepuce. The crucial difference is that the dark brown edge of the prepuce is circumferential, while the dark brown edge of the clitorideal pad is not. Frontal and lateral views of the male and female genital areas are given in the figures 2, 3, 4 and 5. Figure 6 gives a
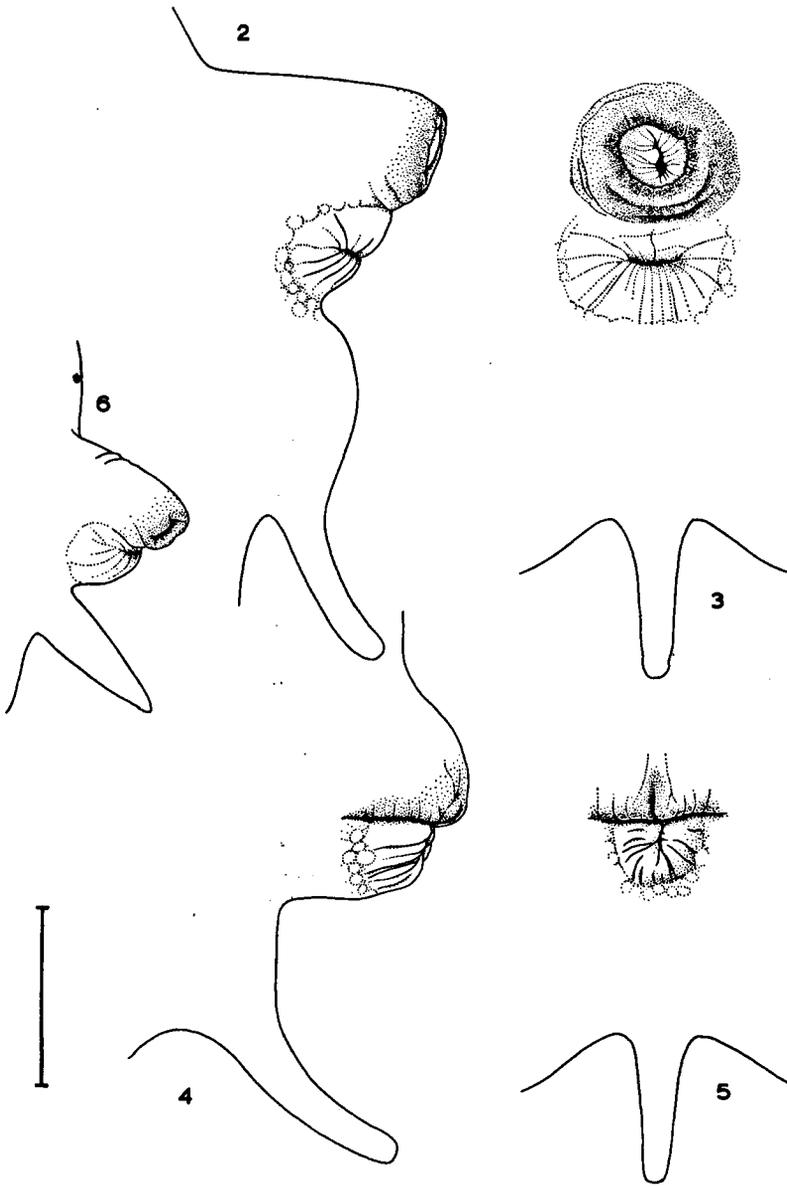
FIGS. 2-6. Genital areas in *Myonycteris torquata* (Dobson).
Figs. 2 and 3: lateral and frontal view of adult male (ZMA 15.423); figs. 4 and 5: lateral and frontal view of adult female (ORSTOM 21.784); fig. 6: lateral view of juvenile male (forearm length about 24 mm) (ZMA 16.669). Scale to all figures: 5 mm.

lateral view of the same area in a juvenile male (forearm length about 24 mm).

Ecology and biology

Most collecting localities of *M. torquata* (fig. 1; vegetation types after Keay, 1959) are in the "moist forest at low and medium altitudes" and in the surrounding "forest-savanne mosaic" and "woodlands and savannas,relatively moist types". Some are in the vicinity of montane areas: Mount Nimba, in Liberia, where *Myonycteris* was collected at an altitude of 500 m; Mount Cameroon; and Bwamba Forest, in Uganda, where it was captured at about 800 m. The specimen from Ibadan is stated to come from a "guinea savanna". Brosset (1966b) writes that *Myonycteris* is a seemingly solitary living forest species, with arboreal roosts, that does not avoid clearances and plantations. The specimens taken 6 miles north of Kade lived in "remnant high forest", those from 32 miles west of Prestea in "cutover high forest". Jones (1971) caught his Ikunde specimens in the village, between some trees and a house. In the "ville" (European quarter) of Pointe Noire I caught a specimen near mango trees in fruit, in a house garden, between 00.00 and 06.00 a.m. Nothing is known about the natural diet, but *Myonycteris* has been caught near mangos, guavas and bananas, and specimens in captivity took soft fruits, honey and butter (Brosset, 1966b). These captive specimens produced offspring twice a year, births occurring in June and in December/January. Unfortunately, no data concerning duration of pregnancy, size of newborn specimens, suckling period, growth rate of juveniles and age when sexual maturity is reached are given.

In north-east Gabon Brosset (*loc. cit.*) observed pregnancy or lactation in all 15 females caught from November to March and sexual inactivity in three females taken in June and July, and concluded that "natural" reproduction might be seasonal, while in captivity females might become polyestrous. Actual pregnancies were observed in females captured 1 February (Bolo, embryo length unknown), 13 May (Kumasi, embryo 3 mm), 14 July (Mount Nimba, embryo 16 mm), 31 July (Grand Gedeh Co, embryo length 24 mm), October (Ikunde, 3 embryos, lengths 13, 15 and 16 mm), 25 November (Sibiti, embryo 24 mm). Lactation has been observed in only two other females, one from La Maboké, captured 26 May, and one from Mount Cameroon, taken 16 February (Eisentraut, 1963). Testis measurements were conveyed by Jones (1971): three males taken at Ikunde in March had testes of 1 × 1, 3 × 3, and 5 × 4 mm, respectively; two males taken there in November had testes of 6 × 3, and 5 × 3 mm, respectively. A male I captured at Pointe Noire, 28 November, had testes of 5.1 × 3.8 mm, with the faintest trace of blood vessels on their outer surface.

The largest measured embryo (MNHN) had a greatest length, *in situ*, of 24 mm, and its head was about 15.5 mm long. The smallest juvenile (ZMA 16.669), when in foetal posture, had a greatest length of about 34 mm, a head length of about 20.5 mm, and a forearm length of 24 mm. At birth the

measurements will thus be somewhere between these two. Allen, Lang & Chapin (1917) report on a female taken with her young one (AMNH 48754 and 48753) in Medje on 6 September. This female had large nipples, suggesting lactation, while the juvenile, with a forearm length of 46.4 mm and a greatest skull length of 24.6 mm, almost had its complete mature dentition (a few milk teeth remained, pushed aside but not yet shed, and M^2 and M_3 on the point of emerging). Of course, more data are needed for a reconstruction of the possible reproduction cycle of *Myonycteris*, but I would not be surprised if the demi-annual periodicity observed in captive specimens (Brosset, 1966b) would also be found in the wild. In this context the possibility of slight differences between individual populations should be kept in mind.

<div align="center">DISCUSSION</div>

The type locality of *Myonycteris torquata*

As the Angola specimen collected by Welwitsch was selected as type of the species *torquata*, it is important to know whether its collecting locality and therewith the type locality can be restricted to a certain part of Angola. From the account of Welwitsch's travels in Angola (Dolezal, 1959, 1961) we learn that Welwitsch arrives in Angola at Luanda, his actual residence, on 30 September 1853. His first year there he examines the surroundings of Luanda and the coast from Quizembro (3 miles north of Abriz) to the mouth of the Cuanza river. On 10 September 1854 he starts on what he calls his first great expedition, from Luanda along the rivers Bengo and Cuanza eastward to Banza di Quisonde (about 250 miles from the coast), using the villages of Golungo Alto and Pungo Andongo as bases. On 27 September 1857 he returns at Luanda. In September 1858 he makes short trips in the Libongo district, north-east of Luanda. In June 1859 he sets out for his second great expedition to the highland of Huila. He refers to this as his "Benguella" expedition. On his way to Mossamedes, where he arrives by the end of June 1859, he makes a short trip at Benguela, where he studies the flora of the coastal area. From Mossamedes he travels along the coast southwards to Tiger Bay and back, to start his actual Huila expedition in Mossamedes in October 1859. The route is along the Maiombo river to Bumbo, at the slopes of the Serra da Chella, and from there to Lopollo, where he gets stuck through a local war. In June 1860 he is back at Mossamedes, from there he travels on to Luanda which he leaves by the beginning of December 1860 for Lisbon.

None of the places Welwitsch visited can be definitely excluded from the list of possible type localities of *Myonycteris torquata*. As he was a systematic botanist he must have appreciated the importance of collecting locality to be kept with each specimen, and therefore it is unlikely that Welwitsch himself is responsible for the incomplete label with the type, reading only "Angola" and not mentioning any date. On both his great expeditions Welwitsch collected some mammals (Gray, 1866, 1868; Peters, 1865). At least a
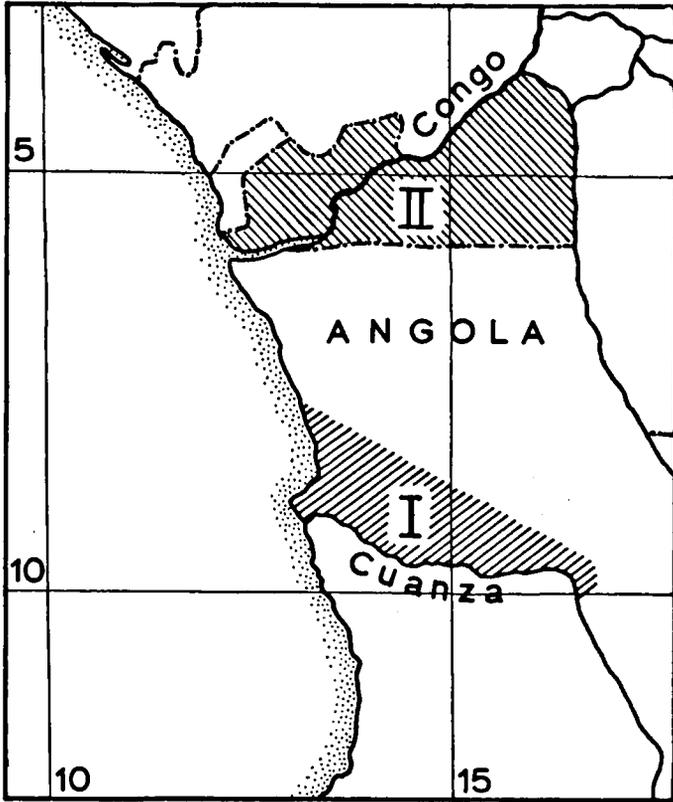
FIG. 7. Presumable collecting areas of the two types of *Myonycteris torquata* (Dobson). I = northern "Lower Cuanza Region", where F. M. Welwitsch possibly collected the lecto-type. II = "Lower Congo District", where Mr. Currer possibly obtained the paralectotype

number of these are from known localities, but some are just labelled "Angola".

A strong argument in favour of what I would like to call the northern "Lower Cuanza Region" (fig. 7) as type locality of *M. torquata* is provided by the analysis of the occurrences of West African and of East-South African mammals in Angola by Hill & Carter (1941). Although some East-South African mammals almost penetrate into the lower Cuanza region, no West African mammal has been recorded south of about Nova Lisboa. This is well in conformity with the division of the Angolan territory into two faunal subregions, the northern third belonging to the West African Subregion, the southern two-thirds to the East-South African Subregion. Hill & Carter (*loc. cit.*) tentatively record *M. torquata* under the West African mammals, in Angola.

Unfortunately, no other specimen than the type has ever been collected in Angola, and a definite restriction of the type locality can as yet not be established.

Evolutional perspectives

Because *Myonycteris brachycephala* and *M. torquata* are so evidently closely related, the assumption of a common ancestor, inhabiting the African main-land, is hardly speculative. Of this ancestral form a migration wave must once have reached the island of São Tomé, where it succeeded to maintain itself. Not very surprisingly the evolutionary tendency of teeth reduction — and inherent reduction of those skull elements supporting jaw muscles — slowed down in the insular offshoot as compared to the mainland popula-tions. As a result, *M. brachycephala* now differs chiefly from *M. torquata* by its generally heavier and more modified teeth and by a number of skull char-acters, partly related to this heavier dentition and partly of less apparent meaning (Andersen, 1912; quoted in the present results). As it is undoubtedly the more primitive of the two species, it should be credited much of our attention in discussions on extinct and living relatives of the genus. In this connexion it should be borne in mind that Lawrence & Novick (1963) considered that *M. brachycephala* was not as different from *Lissonycteris* Andersen, 1912, as *M. torquata*, especially because of certain dental char-acters.

In the results it has been concluded that differences in certain measure-ment ranges and averages, so slight as observed here between (groups of) mainland populations of *Myonycteris*, are of lower than subspecific value. The concept of a monotypical species is sustained by the presently known distribution pattern. Although certain regions have not yet yielded any *Myonycteris*, its continuous distribution can hardly be doubted. Of the here first published collecting localities Ibadan (also the first record for Nigeria), La Maboké, Odzala and Luluabourg are of special interest, in this respect. It cannot be denied, however, that certain differences are in the process of developing. As has been observed in the section on variability, teeth size reduction as an evolutionary tendency does not affect all populations to the same extent. The same applies to another possibly evolutionary process; an alteration in overall size. There is some slight evidence for the assump-tion that this is a process of diminution. The lowest size averages in *Myonyc-teris* are found in the more central populations (Mount Cameroon, La Maboké, north-east Gabon, Rio Muni, Peoples Republic of Congo), while the highest averages are met in certain peripheral populations (e.g. Mount Nimba: 6 males and 6 females with mean forearm lengths of 61.6 and 63.7 mm, respectively; north-east Zaïre and adjacent Uganda, table 5). This could be explained in terms of the theory that, in a given species, the central or subcentral populations are in the most favourable position to get adapted to certain environmental pressures (Mayr, 1970). Accordingly, in such populations, provided that the involved pressures exist equally through the whole distribution area, one may expect to find the most advanced examples of adaptation.

The data on dental reduction suggest that, in western and north-eastern populations, teeth size is possibly more affected than in central populations.

The suggested combination of a relatively small M^2 and relatively larger other cheek teeth in the central populations indicate that here a reduction in teeth number (by the eventual loss of M^2) may be at work.

It has been put forward by Lawrence & Novick (1963) that in evaluating generic relationships of *Myonycteris* the shape of the anterior teeth is far more important than the reduction in size and number of the last molars. It may be added that, because of its considerable variation within individual populations, it is equally undesirable to use the measure of such reductions in the taxonomy on (sub)specific level. This variation is obvious in the following example of four specimens of *Myonycteris* from Lamto (length x width of molars) which also suggests a positive correlation between the measure of reduction of the last molars and the measurements of the other molars in individual specimens.

Specimen	M^1	M^2	M_3	M_4
ORSTOM 21.623	2.0 × 1.3	1.3 × 0.9	normal	1.3 × 0.9
	2.0 × 1.3	1.3 × 0.9	normal	1.2 × 0.9
ORSTOM 21.632	1.9 × 1.2	1.0 × 0.9	very small	none
	1.9 × 1.2	1.0 × 0.9	very small	none
ORSTOM 1324	1.7 × 1.3	1.0 × 0.9	normal	none
	1.7 × 1.2	0.9 × 0.9	none	none
ORSTOM 21.617	1.8 × 1.2	1.0 × 0.8	none	none
	1.8 × 1.1	0.9 × 0.8	none	none

Since so little is known of the natural history of *Myonycteris*, one can but guess after the nature of the selective pressures which induces the presumed change in characters. Where quite a few fruit bat species with probably essentially identical food preferences coexist, the development of specific feeding habits is of course one of the evolutional answers likely to be successful. It is not at all unlikely that the process of changing to which *Myonycteris* seems subjected at present, would be related to this particular development.

RELIABILITY OF MEASUREMENTS

It is a well-known fact that bones may shrink by desiccation. The forearm lengths of 11 *Myonycteris* specimens that had been in alcohol for about six years and then were made into dry skins and skulls, shrunk with an average of 2.5% during the process of drying. This should not be forgotten when considering the absolute reliability of taxonomical conclusions based on measurements procured in part from dry specimens.

The body measurements (total length, tail, ear, tibia and foot) submitted in this paper were copied from labels and taken by six different collectors,

who possibly employed different methods. These measurements are therefore to be considered with some reservation.

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