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A NEW FRUIT BAT OF THE GENUS *MYONYCTERIS* MATSCHIE, 1899, FROM EASTERN KENYA AND TANZANIA (MAMMALIA, MEGACHIROPTERA)

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With 4 text-figures

Abstract

Myonycteris relicta n. sp. is described from the Shimba Hills in southeast Kenya and from the Usambara Mountains in northeast Tanzania. The species is larger than the only other known African mainland species of the genus, *Myonycteris torquata* (Dobson, 1878), from the Central and West African rain forests and, if compared to *M. torquata* and the only other species in the genus, *M. brachycephala* (Bocage, 1889) from São Tomé, has a relatively longer rostrum, a more deflected cranial axis, and further differs in number, shape and position of its teeth. The new species provides new arguments for the relationship between the genera *Myonycteris* Matschie, 1899, and *Lissonycteris* Andersen, 1912. It is believed that *Myonycteris relicta* may be a forest species and as such restricted to isolated East African forests.

Introduction

During a visit to the Zoologisches Museum in Berlin (ZMB), in April 1979, the author found two fruit bat specimens from the Tanzanian Usambara Mountains, which proved to represent an undescribed taxon. Later, in June 1979, Dr C. Smeenk of the Rijksmuseum van Natuurlijke Historie at Leiden (RMNH) recognized a third specimen of this taxon in newly acquired material from the Shimba Hills in southeast Kenya.

The bats differ on specific level from all other known fruit bats, and are described in the present paper. The new species is of particular interest, because it probably is an East African endemic, with its nearest relative in Central and West Africa. As such, it would offer support to the theory of former forest connections between eastern Central Africa and the East African coastal regions.

Supraspecific taxonomy

Andersen (1912) divided the Pteropodinae into three sections: the *Rousettus* section, the *Epomophorus* section, and the *Cynopterus* section, all three with representatives in Africa. The *Rousettus* section contained, among others, the genus *Rousettus* Gray, 1821. Andersen listed 14 species of *Rousettus*, six of which were African. Two African species were united in a new subgenus, *Lissonycteris* Andersen, 1912: *R.* (*L.*) *angolensis* (Bocage, 1889) and *R.* (*L.*) *smithi* Thomas, 1908 (now considered a subspecies of *angolensis*). Of *R.* (*Lissonycteris*) *angolensis*, Andersen wrote that it "is the most aberrant species of *Rousettus*" with in its skull shape "distinct leanings towards the genus *Epomophorus*" Bennet, 1836. On page xlix of the same work Andersen claims resemblance of the skull of *Lissonycteris* to that of another epomophorine genus, *Epomops* Gray, 1870.

The *Cynopterus* section contained ten Asian and Australasian genera, and only one African: *Myonycteris* Matschie, 1899. Concerning this, Andersen wrote that it is "intermediate between the Rousettine and Cynopterine sections" and he classed it as the first (most "primitive") genus of the Cynopterine section, because he thought it to be nearer to *Cynopterus* than to *Rousettus*, "though it might with equal right be considered a specialized offshoot of the Rousettine branch showing modifications similar to or approaching those of *Cynopterus*".

Novick (1958) treats *Lissonycteris* as an independent genus on the basis of differences in limb use and roosting posture between *Lissonycteris* and *Rousettus* sensu stricto. These arguments were elaborated by Lawrence & Novick (1963) (and not 1958 as suggested by Novick in that year), who moreover provided an array of morphological characters separating both genera, and emphasized the lack in *Lissonycteris* of the highly developed sonar system present in typical *Rousettus*, as further evidence for its distinctness. In their view, *Lissonycteris* is most closely related to *Myonycteris* (the close cynopterine affinities of which are likewise discussed and rejected). Consequently, Lawrence & Novick suggest that *Lissonycteris* and *Myonycteris* be removed from Andersen's rousettine and cynopterine sections, respectively, and that these genera form "a natural group probably intermediate between the rousettine and epomophorine groups, and one whose resemblances to the cynopterines are more apparent than real".

By a number of external characters, such as wing size and wing insertion, fur colours, and the ruff of coarse hair in adult males, the new species is readily recognized as belonging in the myonycterine section sensu Lawrence & Novick. Skull and dentition tend to confirm this conclusion. Its facial axis is notably deflected, which indicates that within this section it is possibly the

most "primitive" species, i.e. standing closest to the supposedly rousettine ancestor. At the same time it combines some of the characters of *Myonycteris* and *Lissonycteris*, and provides further evidence for the close relationship between these two genera. In this respect it offers an interesting parallel to *Myonycteris brachycephala* (Bocage, 1889) from São Tomé, which in view of the greater differentiation of its teeth is more related to *Lissonycteris* than is *M. torquata* (see Lawrence & Novick, 1963; Bergmans, 1976).

The new species is definitely larger than *Myonycteris torquata* (see for measurements of the latter Bergmans, 1976) and most probably also larger than *M. brachycephala* (only known from the holotype, which specimen suggests, however, a size range not much different from that of *torquata* — see Andersen, 1912). It is smaller than East African representatives of *Lissonycteris angolensis* (Bocage, 1898) — the only species of its genus —, although in some measurements, e.g. forearm length, there is some overlap (Eisentraut, 1965; Bergmans, unpublished notes). Skull proportions in the new species are rather as *Myonycteris*; its rostrum, however, is not shortened as in *M. torquata* and *M. brachycephala*, but long as in *Lissonycteris*, though with a quite different profile. Its zygomatic arches are slender and curve down about as low as the alveolar line when viewed from the side, as in *Myonycteris* (in *Lissonycteris* they stay clearly above this line). Its cheek teeth are relatively longer than in both *Myonycteris* species, but essentially of the same shape and not broadened nor as differentiated as in *Lissonycteris*. Other characters placing the new species rather nearer to *Myonycteris* than to *Lissonycteris* are its relatively low P^3, M^1, M^2, M_1 and M_2, the notable reduction of M^2, and the loss of M_3 (almost rudimentary in *Myonycteris torquata* and *M. brachycephala*, but much less reduced in *Lissonycteris*). The species seems essentially closer to the known species of *Myonycteris* than to *Lissonycteris* and is therefore assigned to the former genus.

In the following description colour names with capital first letters are Ridgway names found through comparison with Ostwald's colour plates (1939) and the tables of Zimmerman (1952). The designation of teeth is after Andersen (1912).

Myonycteris relicta n. sp. (figs. 1-4)

Holotype: adult male, skin and skull, collected 30-VII-1978 by Mr. Robert N. Kyongo (field number RK 594), in the Shimba Hills, southeast Kenya (RMNH 27909). "Caught over water, about 1.20 m high, at about 10 p.m. local time, Mukanda River, Lukore area, Shimba Hills; along the river: big thorn trees and fig trees" (R. N. Kyongo in litt.).

Paratypes: adult male and adult female, in alcohol, skulls separate (and damaged to some extent), collected in January 1900 (collector unknown) at Ambangulu (5°5′ S, 38°26′ E), Usambara Mountains, northeast Tanzania (ZMB 54936 and 54937, respectively).

TABLE I

Measurements in mm of holotype and paratypes of *Myonycteris relicta* n. sp.

Collection and reg.no.	Holotype RMNH 27909	Paratype ZMB 54936	Paratype ZMB 54937
Preservation	dry	alcohol and skull	alcohol and skull
Sex/age	♂ adult	♂ adult	♀ adult
Locality	Shimba Hills	Ambangulu	Ambangulu
Date	30 July 1978	January 1900	January 1900
Collector	R. Kyongo	Unknown	Unknown
Total length	124 "')	---	
Tail length	9 "')	---	8.3
Ear length	22 "')	20.5	20.0
Hindfooth length	19 "')	---	19.9
Tibia length	26.7	---	29.3
Forearm length	69.3	---	75.1
1st digit metacarpal length	9.9	10.8	12.0
1st phalanx length')	19.9	20.8	22.0
2nd digit metacarpal length	35.3	---	37.9
1st phalanx length	7.2	8.0	8.5
2nd phalanx length	9.2	9.0	9.3
3rd digit metacarpal length	49.5	48.9	53.3
1st phalanx length	32.4	33.8	35.8
2nd phalanx length	43.7	---	49.0
4th digit metacarpal length	46.4	46.4	50.8
1st phalanx length	24.7	---	26.5
2nd phalanx length	27.5	---	31.0
5th digit metacarpal length	46.0	46.6	51.7
1st phalanx length	21.9	---	24.3
2nd phalanx length	25.0	---	28.6
Greatest skull length	36.4	36.5	39.2
Condylobasal length	35.0	34.8	38.9
Rostrum length")	13.0	13.4	15.1
Palatal length	19.6	19.0	21.1
Cranium width	14.7	15.9	14.9
Interorbital width	7.1	7.3	8.1
Postorbital width	8.9	9.7	8.2
Zygomatic width	21.4	---	---
Mandible length	27.9	28.2	30.4
C^1-C^1 width exteriorly over cingula	6.9	7.1	7.8
C^1-M^2 length over cingula	13.4	13.3	14.9
M^2-M^2 width over cingula	10.3	10.5	---
C_1-M_2 length over cingula	13.6	13.4	14.5
Length x width of			
P^3	2.6 x 1.4	2.4 x 1.5	2.5 x 1.6
P^4	2.9 x 1.6	2.9 x 1.65	3.1 x 1.65
M^1	2.6 x 1.3	2.3 x 1.4	2.5 x 1.35
M^2	1.45 x 1.15	1.3 x 0.9	1.5 x 1.1
P_3	2.0 x 1.3	2.0 x 1.3	2.15 x 1.4
P_4	2.85 x 1.6	2.8 x 1.6	3.25 x 1.65
M_1	2.95 x 1.4	2.9 x 1.3	2.9 x 1.4
M_2	2.1 x 1.3	1.8 x 1.25	2.0 x 1.25

') Claw included
") From front of orbit to tip of premaxilla
"') Collector's measurement

Diagnosis. — *Myonycteris relicta* is a large member of its genus (forearm lengths 69.3-75.1 mm and greatest skull lengths 36.4-39.2 mm in the three specimens known), with deflected facial axis, relatively slender rostrum, dental formula $\frac{2.1.3.2}{2.1.3.2}$, elongate teeth, and reduced M^2.

Description of holotype (notes concerning soft parts checked on paratypes). — Snout relatively long, with linear dorsal profile. Posterior part of head rather domed. Nose skin brown, nostrils pointed forward and outward, separated by a shallow but distinct groove. Chin pad narrow, notched at its proximal end in the median plane, with small and narrow offshoots along lower lips. Upper and lower lips quite thick, upper with a row of small pointed papillae on inner margin, extending backward from close behind the nose, lower with same from about halfway. Tongue with long and narrow field of toothed papillae on anterior part. Ears moderately long, anterior margin thickened, posterior margin convex with slight emargination just below tip; tip rather distinctly pointed; conchs darkish brown, with about ten transverse folds; antitragal lobe moderate, angular. Top and sides of head furred with soft woolly hair, very short and sparse near nose and somewhat longer and very dense backward from in between and under eyes, near Ecru-Drab, tipped with near Verona Brown on snout, forehead and cheeks, and with orange-brown on top of head. Same light short hair in zone along lower lip (centre of chin furred like ventral body side; see below). Sides of rostrum, a narrow zone around eyes, and lower lips furnished with additional, mostly dark brown, tactile hairs: many shorter ones, a few longer ones.

Dorsally, body densely furred with bicoloured hair (6-10 mm long), Light Cinnamon-Drab with Brüssels Brown to Tawny tips, the tips dominating the overall — light reddish brown — colour impression. Hair of same colours extending on arm, down to (and much shorter on) first half of forearm, on small areas of patagium in axillar region and below elbow, on hind legs almost down to ankles, and on adjoining parts of uropatagium, surpassing its caudal margin at either side of tail.

Ventrally, body covered with dense, short hair (length 3.5-5 mm), Fawn Colour with slightly darker bases; also on upper arm and proximal half of forearm, along upper legs to slightly below knee, and on proximal part of uropatagium. Holotype (and male paratype) with throat ruff of relatively coarse hair; foremost point of ruff on chin between mouth corners; ruff gradually widening to greatest width at throat level, with 'crowns' on shoulders, and ending on breast, about on level with antebrachial membrane insertion; ruff hairs with short thin bases and thick shafts, wavy and growing

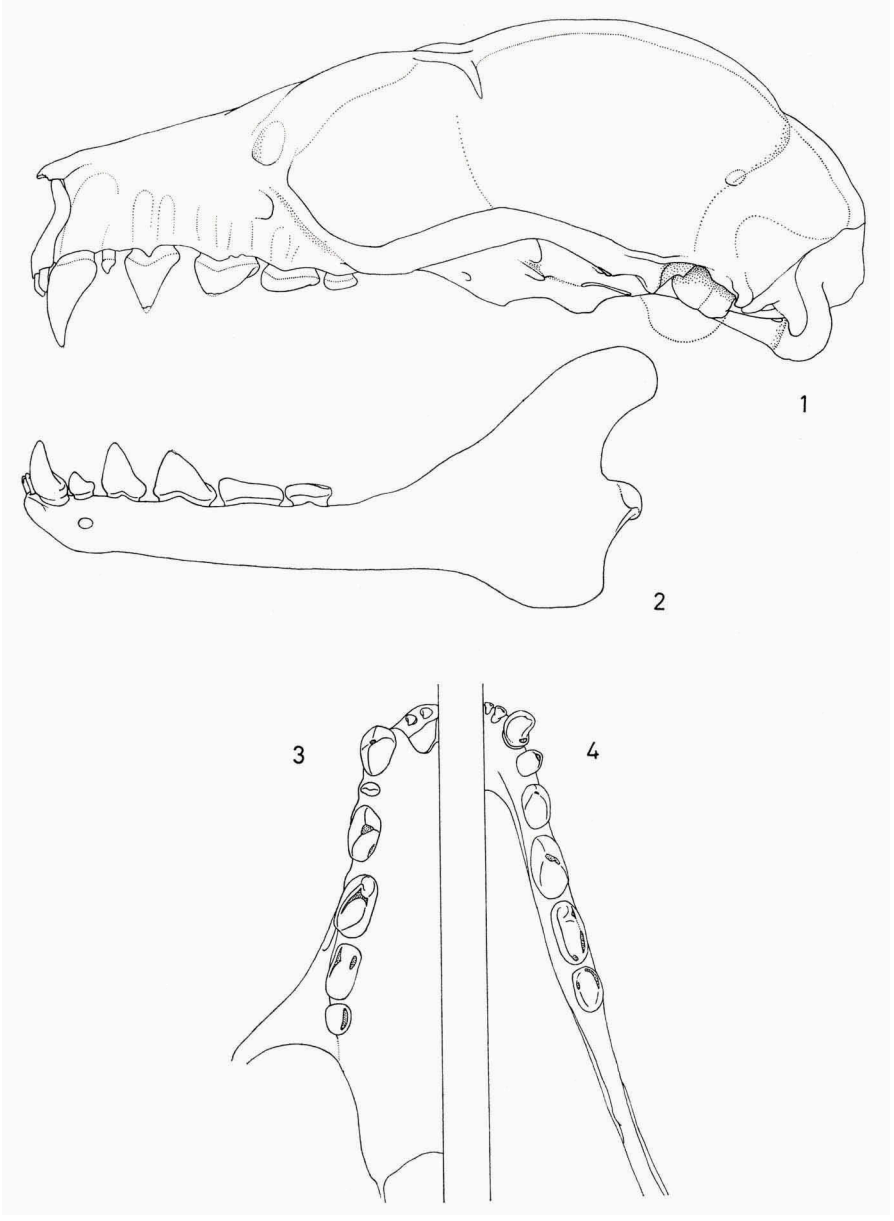
in clusters of about 12 in centre of ruff, but less coarse, less wavy and less obviously clustered towards ruff margins; ruff hairs in holotype from about Light Ochraceous Buff to Tawny Olive, with darkest hairs on chin. (Ruff colour in paratype ZMB 54936 very light, but possibly somewhat bleached.) Female paratype without ruff. Propatagium near furred part of arm, and endopatagium between furred part of arm and body, thinly covered with Fawn Coloured or in places weakly reddish brown hairs.

Wings rather large (see table 1 for proportions), darkish brown. Endopatagium attached near middle of first phalanx of second toe. Toes 'webbed' to middle of first phalanges. Calcar length about 7 mm. Caudal margin of stretched uropatagium almost linear between end of calcar and a point on the dorsal side of the tail at about 3 mm from its external base. Soft palatum not preserved in the studied specimens.

Skull (figs. 1-4) lightly built. Facial axis deflected. Alveolar line, if projected backward, passing slightly above upper edge of occipital condyle. Premaxillae slender, fused anteriorly (only clearly co-ossified in specimen ZMB 54937). Rostrum relatively long, with nearly linear dorsal profile. Lateral pair of frontal sinuses quite strongly inflated, medial pair somewhat less. Behind these, a third pair of externally slightly inflated interorbital sinuses, roundish in outline, in between postorbital foramina and not extending beyond postorbital constriction, well visible in holotype and male paratype, indistinct in female paratype. Postorbital processes well developed, slender. Postorbital foramina small, distinct. Braincase rather domed, inflated behind interorbital sinuses, somewhat constricted at level of posterior zygomatic arch insertions, elongated posteriorly. Temporal ridges distinct but weak, not fusing into a sagittal crest. Supraoccipital crest low. Zygomatic arches slender, curving down about as low as the alveolar line when viewed from the side. Orbit large. Tympanic bullae of moderate size (greatest length in specimen ZMB 54936 4.6 mm). Bony palate concave, with greatest depth at level of M^1; postdental margins rather straight and weakly converging backward.

Mandible delicate, with narrow rami and low coronoid processes; angle between alveolar line and anterior margin of coronoid process about 145°.

Upper incisors minute, with tips curved backward, crowded (distance I^1-I^1 slightly smaller than I^1-I^2); I^2 at about 1 mm from canine. Upper canine short (reconstructed height from cingulum in specimen RMNH 27909 3.5 mm), with only weakly recurved tips; basal outline rectangularly ovate; anterointernal face flat or slightly concave, without longitudinal groove; anterior keel distinct, not sharp; labial face quite evenly rounded; posterior face sharply defined, narrow, concave; lingual face concave except in the middle,



Figs. 1-2. Skull of holotype of *Myonycteris relicta* n. sp. (RMNH 27909). Fig. 1: Left aspect of skull; size of tympanic bulla indicated, as derived from paratype (ZMB 54936). Fig. 2: Left aspect of mandible. Figs. 3-4. Teeth and outline of bony palate of holotype of *Myonycteris relicta* n. sp. (RMNH 27909). Fig. 3: right row of upper teeth from below, and outline of right half of bony palate. Fig. 4: right row of lower teeth from above. In figs. 3 and 4 worn areas on the teeth have been stippled.

its orientation inward and backward, with trace of horizontal shelf at its base. Anterior upper premolar (P^1) small, about 2 to 3 times the bulk of an upper incisor, wider than long, with rounded anterior and flattish posterior face and an obtuse cusp. Second upper premolar (P^3) oblong, basal outline more or less triangular, with a pointed (outer) cusp just before the middle; lateral (outer) profile sub-triangular; with very weakly rounded labial face, obtuse anterior keel, rather flat antero-internal face and well-defined, slightly concave lingual (postero-internal) face; greatest width at level of keel separating antero-internal and postero-internal face; orientation of latter face either parallel with, or converging backward toward, labial face (thence the variable tooth outline). Third upper molar (P^4) oblong, subrectangular, with a pointed (outer) cusp before the middle; rather obtuse anterior (outer) and posterior outer ridges from cusp tip to cingulum; a weak commissure from tip to lingual side; antero-internal and postero-internal faces concave. First upper molar (M^1) essentially as P^4, but smaller and lower, with less rounded anterior side and strongly reduced cusp. Second upper molar (M^2) small, ovate to triangularly ovate in outline, greatest width in front, even less differentiated than M^1, at some distance from posterior margin of anterior zygomatic arch insertion.

Lower incisors small, outer ones (I_2) slightly larger than inner ones (I_1); tips bicuspid, inner cusp the larger in both I_1 and I_2; distances I_1-I_1 and I_1-I_2 minimal, distance from I_2 to lower canine same or slightly larger. Lower canine short (height from cingulum in holotype specimen 1.8 mm); basal outline broadly ovate, with rather straight posterior side; tip hardly recurved, pointing outward; no distinct keels; antero-internal and labial faces rounded, lingual (postero-internal) face straight or concave, with a narrow shelf at its base. First lower premolar (P_1) relatively large; outline squarish or more rounded; cusp rather obtuse, separating rounded vertical antero-external face from sloping postero-internal face; latter ending almost horizontally. Second lower premolar (P_3) somewhat shorter than lower canine, with pointed cusp well in front of the middle; basal outline ovate (with truncated posterior side in holotype); labial face rather straight or weakly rounded; no anterior keel; antero-internal face rounded; posterior face somewhat concave, sloping, ending almost horizontally; postero-external longitudinal ridge distinct, obtuse. Third lower premolar (P_4) largest of all teeth; basal outline oblong, with about parallel labial and lingual sides and rounded anterior and posterior sides; the single cusp well in front of the middle, with ill-defined anterior keel and blunt postero-external ridge running from it; both labial and lingual faces weakly rounded and gradually passing into essentially round and sloping anterior face; postero-internal face an even,

weakly concave slope without a clear horizontal posterior basal part. First lower molar (M_1) long, narrow, low; labial and lingual faces parallel; anterior and posterior faces somewhat truncated; outer longitudinal ridge higher than inner one (and with traces of antero-median cusp and commissure from cusp to lingual ridge in holotype); upper surface concave. Second lower molar (M_2) rectangularly ovate in outline, reduced, low, undifferentiated; surface flat or weakly concave.

Salient aspects of upper tooth rows when viewed from below (fig. 3) are the relatively heavy third premolars (P^4) and the more or less coulisse-like arrangement of second and third premolars and first molar, with longitudinal axes pointing forward — in the line of the row — but also somewhat inward; and of lower tooth rows when viewed from above (fig. 4) the large third premolars (P_4) and the absence of M_3.

Measurements: table 1. The only known weight is that of the adult male holotype: 48 g.

Discussion

The assumed relict character of *Myonycteris relicta* is suggested by a number of both taxonomical and zoogeographical facts.

In the section on supraspecific taxonomy the concept of a myonycterine fruit bat section sensu Lawrence & Novick (1963), including the genera *Myonycteris* and *Lissonycteris*, has been adopted. Some of the arguments listed by Lawrence & Novick are less convincing than others, and it is unfortunate that the authors did not list the material they examined, nor the measurements they took. In their discussion of wing proportions, for example, it is not stated how many specimens of which species of *Rousettus* were at their disposal. But nevertheless they made it very clear that the myonycterines are much stronger related mutually than to species of the rousettine section, not to mention the cynopterine section. It is of interest to note here that also in 1963 Eisentraut independently concluded that *Myonycteris* is not related to the cynopterines but to the rousettines, and especially to *Rousettus angolensis* — at present referred to as *Lissonycteris angolensis*. And following Novick (1958) and Lawrence & Novick (1963), many authors considered *Lissonycteris* as a valid genus (Rosevear, 1965; Brosset, 1966; Aellen & Brosset, 1968; De Vree, 1971; Anciaux de Faveaux, 1972; Bergmans, Bellier & Vissault, 1974; Kingdon, 1974; Bergmans, 1979). New arguments for the unision of *Myonycteris* and *Lissonycteris* in a myonycterine section, produced by the present study, are the narrowing of the anterior palate (so that the upper tooth rows do not form straight, but inward-bent lines), and the relative heaviness of P_4. Other arguments may come forth

from a examination of the hair structure and of the morphology of the baculum (Bergmans, in preparation).

Both its relationships and its known distribution lead me to believe that *Myonycteris relicta* is most probably a species of the lowland forest. *M. torquata* and *Lissonycteris angolensis* are essentially lowland forest species, although the latter has been collected up to an altitude of 1640 m on Mount Ruwenzori (Eisentraut, 1965). The two known collecting sites of *M. relicta* are in areas at least partly covered with forest (Keay, 1959; Moreau, 1966). The altitude of Ambangulu is not known to me, but the occurrence of *M. relicta* in the virtual lowland of the Shimba Hills labels it as a lowland species. It has never been collected in savannas in East Africa, despite considerable fruit bat collecting activities in these regions (Kingdon, 1974; Bergmans, unpublished notes), which also indicates forest as its likely habitat. If this holds true, its present occurrence will be determined by the very restricted and patchy distribution of East African lowland forest and its status may be equally threatened (Anon., 1979). These forests are completely isolated from the Central African lowland forest block but house, for instance, several species of butterflies, birds and mammals with counterparts (conspecific or differing on subspecies or species level) in the Central (and West) African lowland forest block (Moreau, 1966; Andrews, Groves & Horne, 1975). To explain this vicariance the former existence of forest corridors from eastern Zaire to coastal East Africa has been postulated. The differentiation on various taxonomic levels indicates, in this concept, the existence of more than one functional bridge during geological times. The difficulties of envisaging such connections are pointed out by Moreau (1966: 168-169). The known distribution of myonycterine fruit bats might be interpreted as support for this bridge theory.

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