Taxonomic review of *Miniopterus minor* Peters, 1867 (Mammalia: Chiroptera) from western central Africa

J. Juste & C. Ibáñez

Abstract. Western populations of *M. minor* from São Tomé Island, Zaire and the Republic of Congo are compared to one another and with the known eastern subspecies, using either quantitative and qualitative parameters. The analyses confirm the subspecific character of both the São Tomé population (described as *M. newtoni* Bocage, 1893) and the western continental population, distinguished by cranial relationships and qualitative characters from the other known populations and hereby described as a new subspecies. In addition, a neotype for *newtoni* is designated.


Introduction

The genus *Miniopterus* is characterized by a remarkable morphological uniformity among species (Dobson 1878) throughout its wide distribution in the Old World. This made a classification of all the different forms difficult. Unlike the Asian *Miniopterus*, which were recently reviewed (Peterson 1981, Maeda 1982), the African species lack a thorough re-examination through comparative analysis with modern quantitative techniques, probably due to the scarce material available in collections.

Currently, out of the twelve species referred to by Allen (1939) for Africa, just four are considered to be valid (Hayman & Hill 1971). Two of them are of big size, *M. schreibersi* Kuhl, 1819 and *M. inflatus* Thomas, 1903. The former occurs throughout the continent except for the Saharian Belt (Koopman 1975); the latter is more restricted to Equatorial Africa. The two others, *M. fraterculus* Thomas & Schwann, 1906 and *M. minor* Peters, 1867 are smaller, and some authors have considered them as conspecific (Aellen & Brosset 1968), even though they were later set apart due to differences in cranial proportions. *M. fraterculus* occupies a strip on the southeast side of the continent, from Transvaal to southern Malawi (Hayman & Hill 1971, Happold et al. 1987).

In terms of its smaller size, *Miniopterus minor* was described in comparison to *M. schreibersi*; the type specimen came from the coast opposite to Zanzibar (Tanzania). The species shows an unclear distribution in two areas, one on the east side of the continent and one on the west, both separated by a remarkable distance (Fig. 1). There are three known populations in Eastern Africa, one in the south of Kenya and Tanzania (Aggundey & Schlitter 1984), another in Madagascar, and the last in the Archipelago of Comoro. The taxonomic status of these populations was reviewed by Harrison (1959), who differentiated, apart from the nominal continental subspecies, the endemic *M. m. manavi* Thomas, 1906 in Madagascar, and described a new subspecies, *M. m. griveaudi*, for Grande Comore Island.
In West Africa, two populations attributed to this species are known. The first one cited was from São Tomé Island, which Bocage (1889, 1903) described as *M. newtoni*, separating it from eastern forms on the basis of bibliographic descriptions, according to the different distribution of fur on the uropatagium. In 1979 all specimens examined by Bocage, including the type, were lost in a fire at the Lisbon Museum.

The other western population is found on the lower course of the Zaire River, from where Hayman (1954) mentioned three specimens and attributed them to the eastern coast’s nominal form. More recently, Aellen & Brosset (1968) provided measurements of new specimens from several caves in the south of the Congo Republic. These authors considered the population from the western coast as part of *newtoni*, which they included in *minor* because of the similarities between external measurements of these specimens and those referred to by Bocage from São Tomé.

As new material has been obtained on São Tomé Island, the aim of this paper is to review the taxonomic status of the western populations of *M. minor*. New data are provided, based on the first comparative study of western and eastern subspecies, combining multivariate and univariate statistical analyses with a traditional study of the morphological characteristics.

**Material and Methods**

A total of 125 *M. minor* specimens from the following institutions were examined. Estación Biológica de Doñana, Sevilla, Spain (EBD); British Museum of Natural History, London, England (BMNH); Harrison Zoological Museum, Sevenoaks, England (HZN); Museum d’Histoire Naturelle, Geneve, Switzerland (MHNG) and Musee Royal de l’Afrique Centrale, Tervuren, Belgium (MRAC). All specimens were considered adults according to morphological features.

**Quantitative analysis:**

Variables measured and their abbreviations are as follows: body weight (W), total length (TL), tail length (TAL), forearm (FA), third digit metacarpal (IIMC), first phalanx (IIIF1), second phalanx (IIIF2), fourth metacarpal (IVMC), first phalanx (IVF1), second phalanx (IVF2), fifth metacarpal (VMC), first phalanx (VF1), second phalanx (VF2), greatest skull length (GSL), condyle-incisive length (CBL), condyle-canine length (CCL), palatal length (PL), mastoid breadth (MB), braincase breadth (BCB), zygomatic breadth (ZB), interorbital breadth (IOB), rostrum breadth (RB), length of toothrow (I1-M2), length of toothrow (C1-M3), length of chewing toothrow (P4-M3), breadth across upper canines (C1-C1), breadth across molars (M2-M3), mandible toothrow length (I-Ma).

The cranial variables were measured according to Maeda (1982), adding RB according to Peterson (1981), and PL as the minimum distance between the rear and the fore edges of palate. Every measurement was taken by the senior author using a magnifying glass and through digital caliper (Brown and Shape no 599-571-3) connected to a personal computer, with 0.1 mm precision.

The normality of the variables’ values distribution for each sex was tested through Kolgomorov’s test in representative populations. For the following statistical analysis the pack BMPD (Dixon 1987) was used. ANOVAS carried out for each external variable among sufficiently represented populations (São Tomé and Madagascar) pointed out the absence of significant differences between sexes for any variable. Nevertheless, in cranial (carried out only on the São Tomé population) differences between sexes for C1-C1 (p < 0.001) and GSL, CCL and C-M3 variables (all of them p < 0.05) were shown to be significant, a similar result to that obtained through other studies on *Miniopterus* (Maeda 1982, 1983, 1984).

Once these variables were eliminated, MANOVAS (Hotelling’s T-square) confirmed at a multivariate level the absence of significant differences between sexes (F = 0.96; DF = 12;
P = 0.512) due to possible interactions between the other cranial variables (Willig et al. 1986, Willig & Owen 1987). Thus, the absence of perceptible sexual dimorphism within the species for the variables considered was accepted, sexes being grouped together for each population.

In multivariate analysis, from each of the variables set (external and cranial), those offering most precise measurements were selected, trying to minimize any possible correlation between them and maximizing the size of samples (Wilson et al. 1991). From the external ones only wing variables were used, except from I1F2; and from cranials, CBL, MTB, IOB, I-M^3, P^4-M^3, M^3-M^3, and I-M_2 were used.

Once the consistency of grouping together the different geographic populations (Congo and Zaire on one side, Kenya and Tanzania on the other) was confirmed through the axis of prin-
principal components analysis, comparative groups included the four sub-species currently accepted (considering as *newtoni* only the population from São Tomé) and the populations from Congo and Zaire.

Through canonic discriminant analysis (CDA), differences among groups within the area determined through canonic variables were analyzed, and through discriminant function analysis (DFA), the lineal combination of original variables with the highest discriminating capability were determined. The percentage of correct categorizing has been calculated and the consistency of analysis was tested (jack-knife method) (Williams 1983, Williams & Titus 1988).

Concerning univariate analysis, the significance of differences in selected variables and relations between cranial variables with a systematic use within the group (Harrison 1953, Aellen 1957, Peterson 1981, Maeda 1982) was tested through ANOVAS. Significance between groups was analyzed through Tukey's range test.

**Qualitative analysis:**
Comparisons on the colour of specimens' fur (including holotypes) from different populations were carried out. The presence and distribution of fur on the uropatagium was also studied and compared, characteristics which have traditionally been used in order to differentiate the various subspecies, as well as possible variations in general cranial morphology.

**Results**

**Quantitative analysis:**
For the eight wing variables, the DFA carried out geographically grouping together the populations results in a correct classification of just 63.3 % of cases, populations overlapping in CDA representation. Concerning cranial variables, the DFA correctly classifies 90.3 % of cases; this percentage is maintained, slightly lower, after the jack-knife procedure (84.7 %). The group of individuals from Congo and Zaire stands out, since it is correctly classified in 100 % of cases (Table 1). CDA separates, within the area determined by the two former canonic variables, the populations from Madagascar and Comoro on the one hand and *minor* and *newtoni* on the other. The western continental one remains between the latter ones (Fig. 2).

Eliminating the populations from Madagascar and Comoro, not fairly represented, and considering as to the analysis only *minor*, *newtoni* and the western continental population, the percentage of DFA global classification increases to 92.2 %

**Table 1:** Classifications in the percentage of specimens to subspecies according to discriminant functions (FDAs), considering all the subspecies (above), and only three of them (bottom). Within parentheses, the same percentage after jack-knife procedure and within brackets the number of individuals considered in the analyses.

<table>
<thead>
<tr>
<th></th>
<th>newtoni</th>
<th>occidentalis</th>
<th>minor</th>
<th>manavi</th>
<th>griveaudi</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. m. newtoni</em></td>
<td>93.0 (90.7)</td>
<td>7.0 (7.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (2.3)</td>
</tr>
<tr>
<td><em>M. m. occidentalis</em></td>
<td>0.0 (0.0)</td>
<td>100 (90.0)</td>
<td>0.0 (10.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td><em>M. m. minor</em></td>
<td>9.1 (9.1)</td>
<td>9.1 (9.1)</td>
<td>81.8 (81.8)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td><em>M. m. manavi</em></td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>80.0 (80.0)</td>
<td>20.0 (20.0)</td>
</tr>
<tr>
<td><em>M. m. griveaudi</em></td>
<td>0.0 (66.7)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>33.3 (33.3)</td>
<td>67.7 (0.0)</td>
</tr>
</tbody>
</table>

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Fig. 2: Plots of the canonic discriminant analysis among *Miniopterus minor* populations. Considering all the subspecies (left) and considering São Tomé and continental ones only (right). Inverted triangles, *M. m. minor*; circles, *M. m. occidentalis*; crosses, *M. m. newtoni*; triangles, *M. m. griveaudi*; stars, *M. m. manavi*.

(87.5 % after the jack-knife procedure), the western continental population still being identified in 100 % of cases (Table 1). CDA representation clearly separates *minor, newtoni* and Zaire and Congo population individuals.

At the univariate level concerning wing variables, *minor* population is markedly larger than the others, while *newtoni* and the western continental population are not significantly different, even though the former shows higher values. At the cranial level, *minor* keeps showing higher values than the other populations, while the western continental population is significantly distinguished from *newtoni* on the basis of higher values for BCB and, nevertheless, lower values for M$^3$-M$^3$ and ML, with significant BCB/CBL variations in cranial relations as well (Table 2).

**Qualitative analysis:**

Differences in the various forms are perceived regarding the monocolour dorsal and biocolour ventral colouration, as they remain reasonably homogeneous within each population. There are two different phases in both *newtoni* and *manavi*, not related to sex and not found in the other populations, although they have also been described for *minor* (McWilliam 1988). Specimens from Congo and Zaire cannot be discerned from one another, and their deep brown colour, much lighter than in *newtoni*, differentiates them. Through the different comparisons, specimens from São Tomé have always been remarkable due to their darker and deeper colour in both phases, compared to the other populations. The nominal form shows a distinctive grayish shade which differs from the reddish-brown *manavi* and *griveaudi* (holotypes BMNH 97.9.37, and BMNH 67.12.31, respectively).

The distribution of fur on the wing uropatagium is variable and scarcely definite in the several populations, whereas the permanent existence of a thin hairy covering on the uropatagium is remarkable for Madagascar and western continental populations, including specimens from Zaire as well as from Congo (e. g. MRAC 18016 and MHNG 1074.13). This fur spreads throughout the interfemoral area of the uro-
Table 2: Means and standard deviations for selected external and cranial measurements, and cranial ratios of *Miniopterus minor* from the five subspecies studied. Values in the same row with the same superscript letter are not significantly different (ANOVA, Tukey multiple range test, $p < 0.05$).

<table>
<thead>
<tr>
<th></th>
<th><em>M. m. newtoni</em></th>
<th><em>M. m. occidentalis</em></th>
<th><em>M. m. minor</em></th>
<th><em>M. m. griveaudi</em></th>
<th><em>M. m. manavi</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>External</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FA</td>
<td>$39.0\pm0.66^b$</td>
<td>$38.2\pm0.74^b$</td>
<td>$39.8\pm0.65^c$</td>
<td>$35.9\pm1.80^a$</td>
<td>$37.0\pm1.03^a$</td>
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<tr>
<td>IIHM</td>
<td>$34.4\pm0.71^b$</td>
<td>$33.7\pm0.74^ab$</td>
<td>$35.4\pm0.84^c$</td>
<td>$32.9\pm2.02^a$</td>
<td>$33.3\pm0.74^a$</td>
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<td>IIIF</td>
<td>$9.2\pm0.41^a$</td>
<td>$9.2\pm0.37^a$</td>
<td>$9.4\pm0.98^a$</td>
<td>$9.3\pm0.20^a$</td>
<td>$9.2\pm0.66^a$</td>
</tr>
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<td>IVMC</td>
<td>$33.1\pm0.74^a$</td>
<td>$32.5\pm0.76^a$</td>
<td>$34.4\pm0.89^b$</td>
<td>$31.8\pm1.95^b$</td>
<td>$32.3\pm0.82^a$</td>
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<tr>
<td>IVF1</td>
<td>$7.2\pm0.33^a$</td>
<td>$7.2\pm0.27^a$</td>
<td>$7.2\pm0.36^a$</td>
<td>$6.9\pm0.36^a$</td>
<td>$7.1\pm0.75^a$</td>
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<tr>
<td>IVF2</td>
<td>$14.1\pm0.64^a$</td>
<td>$14.5\pm0.68^ab$</td>
<td>$15.1\pm0.69^b$</td>
<td>$13.7\pm0.51^a$</td>
<td>$13.9\pm1.15^a$</td>
</tr>
<tr>
<td>VMC</td>
<td>$30.2\pm0.63^a$</td>
<td>$30.1\pm0.67^a$</td>
<td>$31.4\pm0.76^b$</td>
<td>$29.3\pm1.97^a$</td>
<td>$29.9\pm0.85^a$</td>
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<tr>
<td>VF1</td>
<td>$7.5\pm0.27^ac$</td>
<td>$7.6\pm0.23^ac$</td>
<td>$7.7\pm0.42^c$</td>
<td>$7.0\pm0.26^a$</td>
<td>$7.0\pm0.55^ab$</td>
</tr>
<tr>
<td>VF2</td>
<td>$7.2\pm0.67^c$</td>
<td>$6.6\pm0.64^ab$</td>
<td>$6.8\pm0.37^b$</td>
<td>$5.8\pm0.92^a$</td>
<td>$6.6\pm0.40^ab$</td>
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<tr>
<td>Cranial</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CBL</td>
<td>$13.3\pm0.25^a$</td>
<td>$13.1\pm0.16^a$</td>
<td>$13.6\pm0.22^b$</td>
<td>$13.2\pm0.35^a$</td>
<td>$13.2\pm0.20^a$</td>
</tr>
<tr>
<td>PL</td>
<td>$5.0\pm0.15^a$</td>
<td>$5.2\pm0.16^bc$</td>
<td>$5.4\pm0.17^c$</td>
<td>$5.5\pm0.20^c$</td>
<td>$5.2\pm0.10^ab$</td>
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<tr>
<td>MB</td>
<td>$7.5\pm0.14^a$</td>
<td>$7.5\pm0.12^a$</td>
<td>$7.8\pm0.14^c$</td>
<td>$7.1\pm0.21^a$</td>
<td>$7.2\pm0.09^a$</td>
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<td>BCB</td>
<td>$7.0\pm0.13^b$</td>
<td>$7.1\pm0.06^c$</td>
<td>$7.3\pm0.12^d$</td>
<td>$6.6\pm0.14^a$</td>
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<td>ZB</td>
<td>$7.5\pm0.12^b$</td>
<td>$7.5\pm0.14^bc$</td>
<td>$7.7\pm0.14^c$</td>
<td>$6.9\pm0.07^a$</td>
<td>$7.2\pm0.12^a$</td>
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<td>IOB</td>
<td>$3.5\pm0.09^c$</td>
<td>$3.5\pm0.08^c$</td>
<td>$3.5\pm0.09^c$</td>
<td>$3.3\pm0.21^b$</td>
<td>$3.2\pm0.09^a$</td>
</tr>
<tr>
<td>RB</td>
<td>$4.5\pm0.21^b$</td>
<td>$4.5\pm0.17^a$</td>
<td>$4.0\pm0.43^a$</td>
<td>$4.4\pm0.10^b$</td>
<td>$4.4\pm0.14^b$</td>
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<tr>
<td>1-M^3</td>
<td>$6.3\pm0.09^a$</td>
<td>$6.2\pm0.13^a$</td>
<td>$6.4\pm0.08^b$</td>
<td>$6.3\pm0.26^ab$</td>
<td>$6.2\pm0.09^a$</td>
</tr>
<tr>
<td>P^4-M^3</td>
<td>$3.8\pm0.11^a$</td>
<td>$3.7\pm0.13^a$</td>
<td>$3.9\pm0.14^b$</td>
<td>$3.6\pm0.20^a$</td>
<td>$3.8\pm0.11^a$</td>
</tr>
<tr>
<td>M^3-M^3</td>
<td>$5.7\pm0.13^c$</td>
<td>$5.5\pm0.14^b$</td>
<td>$5.7\pm0.12^c$</td>
<td>$5.3\pm0.10^ab$</td>
<td>$5.3\pm0.17^a$</td>
</tr>
<tr>
<td>ML</td>
<td>$10.0\pm0.28^b$</td>
<td>$9.7\pm0.22^a$</td>
<td>$10.3\pm0.28^b$</td>
<td>$10.2\pm0.42^bc$</td>
<td>$10.1\pm0.17^bc$</td>
</tr>
<tr>
<td>I-M^3</td>
<td>$6.5\pm0.13^a$</td>
<td>$6.5\pm0.11^a$</td>
<td>$6.7\pm0.09^b$</td>
<td>$6.4\pm0.21^a$</td>
<td>$6.5\pm0.16^a$</td>
</tr>
</tbody>
</table>

| Cranial Ratios |               |                      |               |                  |               |
|----------------|----------------|----------------------|---------------|                  |               |
| BCB/RB         | $1.56\pm0.070^a$ | $1.58\pm0.058^a$   | $1.85\pm0.186^b$ | $1.48\pm0.008^a$ | $1.57\pm0.048^a$ |
| M^3-M^3/LCB    | $0.43\pm0.007^d$ | $0.42\pm0.010^cd$  | $0.42\pm0.010^bc$ | $0.40\pm0.015^ab$ | $0.40\pm0.014^a$ |
| BCB/LCB        | $0.52\pm0.009^b$ | $0.54\pm0.007^c$   | $0.54\pm0.013^c$ | $0.50\pm0.018^a$ | $0.51\pm0.007^a$ |

* Reported as a range in cases where data are missing for some values.

patagium dorsal surface and along the first two vertebrae as an elongation of dorsal fur, and lacks in the other populations.

With regard to cranial morphology, the Madagascar and Comoro populations are differentiated from the other forms in the skull's general appearance, which is narrower. Concerning the dental morphology no differences can be perceived.

**Discussion**

At the level of external characters, these analyses do not show differences between the various populations. The whole genus has repeatedly shown this poor morphological variation at this level (Dobson 1878, Hayman & Hill 1971, Maeda 1982).
At the cranial level, DFAs represent the different populations in a way consistent with their geographic distribution. Particularly in the eastern insular populations which are more clearly differentiated there is hardly any overlap in CDA representation.

At the univariate level, differences are very subtle and measurement ranks on the various populations do overlap. As in many oriental species of the genus (Maeda 1982), proportions and relations between them define the differences and, for this particular case, are identified through discriminant analysis. In fact, with regard to cranial relations, M. minor tends to show a significantly lower interorbital breadth compared to newtoni and to the western continental population, whereas the latter as well as minor show proportionally a wider cranium as compared with newtoni (Table 2).

The clinal variation of colour in some widely distributed African Miniopterus may cause some confusion as far as the taxonomic use of this feature is concerned (Etemad 1967). Nevertheless in the case of M. minor it seems to be useful in order to characterize the various populations, as they are non-continuous and relatively homogeneous.

The existence of a hairy covering on uropatagium, a feature Harrison (1959) pointed out in order to distinguish manavi from griveaudi, is also useful to characterize Zaire and Congo populations with regard to newtoni, as the latter's uropatagium remains bold in all observed individuals. The spreading down throughout the wing membrane, a feature used to diagnose minor (Dobson 1878) and newtoni (Bocage 1889), has nevertheless been of little utility.

Combining quantitative and qualitative characteristics allows us to differentiate, within the M. minor western populations, the insular population described by Bocage from São Tomé (currently without a type), from those of Zaire and Congo, and both on a subspecific level from the nominal form. Thus, the following taxonomic classification is proposed:

**Miniopterus minor newtoni** Bocage, 1889


**Neotype**: EBD 17. 350 adult male (in alcohol, with skull extracted). Collected 4 April 1988 by Javier Juste and Carlos Ibáñez, from Santa Catarina, São Tomé Island (0° 16' N, 6° 29' E), Republic of São Tomé and Príncipe, in a cave near the seashore.

**Diagnosis**: Bright dark blackish brown or deep reddish brown fur. Hairless uropatagium and skull with the braincase proportionally narrow.

**Distribution**: Known only in São Tomé Island where it has been found to be common at sea level (Agua y Zé and Santa Catarina) as well as in locations above 1300 m (Morro Palmira) and in non-altered forest as well as in anthropic environments (cocoa plantations).

**Neotype measurements** (mm and g): Body measurements: W: 5; FA: 39.0; TL: 96.0; TAL: 45.0; IIIMC: 34.6; IIIF1: 9.7; IIIF2: 31.7; IVMC: 33.1; IVF1: 7.4; IVF2: 14.1; VMC: 31.0; VFI: 7.4; VF2: 7.7. GSL: 14.2; CBL: 13.4; CCL: 12.7; PL: 5.1; MB: 7.6; BCB: 7.1; IOB 3.6; RB: 4.4; P4-M3: 3.8; C-M3: 5.3; MP: 6.3; C1-C': 3.9; M3-M4: 5.7; ML: 10.4; C-Ms: 5.5; I-Ms: 6.4.

**Remarks**: To the original description of Bocage (1889) we must add that M. m. newtoni presents a general skull shape similar to that of the nominal subspecies but somewhat smaller and with the braincase proportionally narrower. It shows no sign of sagittal crest, but the lambdoid crests are relatively well marked.
**Miniopterus minor occidentalis** ssp. n.


**Diagnosis**: Deep brown fur. Uropatagium covered with thin fur on the proximal half of the dorsal side. Skull smaller than that of the nominal subspecies, with a proportionally wide braincase.

**Description**: The body is deep brown on the back and with a similar but more grayish colour on the abdomen which is, due to the light shade of ventral down ends, bicoloured. The uropatagium, deep brown, is covered on its proximal half with a down layer, an elongation of the dorsal down. The skull is clearly smaller than those of the nominal subspecies and slightly smaller than in *M. m. newtoni*, but with regard to this, it presents a wider and bulkier braincase.

**Distribution**: It is spread throughout a restricted area from the south of Congo to Zaire along both sides of lower course of Zaire River, apparently not reaching the coast.

**Holotype measurements** (mm): FA: 38.2; IIIMC: 34.0; IIIF1: 8.5; IIIF2: 30.1; IVMC: 32.3; IVF1: 6.8; IVF2: 14.4; VMC: 30.0; VFI: 7.4; VF2: 7.1. GSL: 13.8; CBL: 13.1; CCL: 12.4; PL: 5.2; MB: 7.5; BCB: 7.1; ZB: 7.5; IOB: 3.5; RB: 4.5; P^4-M^3: 3.7; C-M^3: 5.2; I-M^3: 6.2; C^1-C^3: 3.7; M^3-M^5: 5.5; ML: 9.6; C-Ms: 5.6; I-Ms: 6.5.

**Remarks**: *M. minor occidentalis* clearly shows the greatest affinity with the closest western subspecies *M. m. newtoni*, linking this with the other continental subspecies, *minor*. Further, both eastern insular forms (*manavi* and *griveaudi*) form a group neatly differentiated regarding their smaller size and their different cranial morphology, very close to one another; but the lack of more extensive representative material does not permit a conclusive comparative study at a quantitative level. Accepting in *Miniopterus* the general tendency to develop and widen the braincase (Peterson 1981), the eastern insular forms would constitute the most primitive forms, while the *minor* nominal would have drifted more than any other in this direction.

**Biogeographical considerations**: For African equatorial bats, apart from a sole attempt (Kingdon 1978), no global biogeographic analysis has been carried out, as has been done on birds (Moreau 1966, Diamond & Hamilton 1980, Pomeroy & Ssekabira 1990) or other groups of mammals (Grubb 1978, 1982, Colyn et al. 1991) and to which the current distribution of *Miniopterus minor* could be compared.

Differences between the various populations of this species, even though subtle due to the conservative morphology of *Miniopterus* indicate a genetic isolation between them, as does the disjunct distribution actually shown (Fig. 1). This kind of distribution would be due to ecological reasons related to a long-distance colonization or, alternatively, to historical reasons, particularly probable when the distribution of the species is consistent with the habitat it occupies (Diamond & Hamilton 1980). Not much is known about the optimal environment for *M. minor*. The insular forms *manavi* and *newtoni* seem to occupy different habitats in Madagascar (Dorst 1947) and São Tomé along altitudinal gradients. With regard to continental forms, all sites actually known for *occidentalis* are located in wooded savannas (Bergmans 1979) while *minor* occupies coastal savannas. Both vegetation types, included within moist savanna (Kingdon 1990), are located on the lower border of the equatorial wet rain forest and their distribution, currently non-continuous, must have changed particularly during the climatic fluctuations in the late Pleistocene (Bonnefille et al.
1990). The spread of this vegetation type might have favoured the expansion of this and other species (*Triaenops* sp., *Rinolophus* sp.), which are considered to be characteristically oriental (Allen & Brosset 1968). During this expanding period, *Miniopterus minor* may well have reached São Tomé Island. The distance to the mainland and the size of the island changed remarkably during climatic pulsations (Juste & Ibáñez, in press), and its colonisation would have been possible without human aid, as has been suggested (Feiler 1988). A later withdrawal and fragmentation of this vegetation formation may have isolated the different populations.

The thinly haired uropatagium shown in Madagascar and the Zaire River populations may suggest a vicariant origin of the present distribution of *Miniopterus minor*. Nevertheless, a deeper knowledge of the biology and distribution of this species is needed in order to attempt the reconstruction of its past.


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**Zusammenfassung**


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