

## **BIOGEOGRAPHY OF THE BATS OF MADAGASCAR**

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**ABSTRACT.**- Seven of the 17 families of bats are represented on Madagascar, one of which, the Myzopodidae, is endemic to the island. Three genera, *Pteropus*, *Emballonura* and *Mormopterus*, occur in Madagascar and Asia but not in Africa. Two other genera found in Madagascar, *Eidolon* and *Triaenops*, do not occur in Asia but are found in Africa. Of the 28 species of Madagascar bats for which specimen records exist, 18 species are endemic. Based on distribution records and phenetic analyses, we found that ten of the endemic species have African affinities, six have obvious Asian affinities while two species lack sufficient data for classification. Of the non-endemic species, nine are African in origin, and one needs further study.

**KEY-WORDS.**- Systematics, Biogeography, Bats, Endemic species, Madagascar

**RESUME.**- Sept des 17 familles de chauve-souris sont représentées sur l'île de Madagascar, dont une, est endémique, le Myzopodidae. Trois genres, *Pteropus*, *Emballonura* et *Mormopterus*, sont présents à Madagascar et en Asie mais pas en Afrique. Deux autres genres, *Eidolon* et *Triaenops*, existent à Madagascar et en Afrique, mais sont absents en Asie. Parmi les 28 espèces des chauve-souris malgaches, dont il existe des spécimens, 18 sont endémiques. Sur la base de leur distribution et des analyses phénétiques, dix espèces endémiques à affinités africaines et six à affinités asiatiques évidentes sont retenues alors que les données sur deux de ces espèces endémiques sont insuffisantes pour leur classification. Parmi les espèces non endémiques, neuf sont d'origine africaine; et une demande des études plus approfondies.

**MOTS-CLES.**- Systématique, Biogéographie, Chauve-Souris, Espèces endémiques, Madagascar

### **INTRODUCTION**

While descriptive studies began early in the nineteenth century, the systematics and detailed biogeography of Madagascar bats have been relatively little-studied. However, it has long been believed that Madagascar bats have affinities to both Asian and African species. This paper summarizes the results of a study by PETERSON *et al.* (1995), of the systematics and zoogeographic affinities of Madagascar bats.

### **MATERIALS & METHODS**

Systematic relationships among extant species and genera were evaluated using phenetic (multivariate statistical) analyses of 26 to 35 morphological characters,

primarily skeletal (PETERSON *et al.*, 1995). Current species distribution data, and fossil and geological information (BESSE & COURTILOT, 1988), were applied in evaluating the results of the systematic analyses.

## RESULTS

Phenetic analyses of Madagascar bat species confirm the presence of at least 28 species in 17 genera, seven families and two sub-orders. Eighteen of the species are endemic. This is a high degree of endemism for chiroptera in an area as small as Madagascar, but consistent with Madagascar's relative isolation and, possibly, with the opportunities for speciation offered by Madagascar's ecological diversity.

Madagascar's location between Africa and Asia, as well as its isolation, is reflected in the apparent geographic origins of its bat fauna. The systematic relationships between Madagascar bats and Asian/African bats, as determined by the study, are summarized in table I.

Among the Madagascar bat species there are three endemic species which are members of genera found in Asia but not Africa. These genera are *Pteropus*, *Emballonura*, and *Mormopterus* (see Fig. 1). Eleven endemic species are members of genera found in both Asia and Africa, *Rousettus*, *Nycteris*, *Myotis*, *Eptesicus*, *Tadarida* and *Otomops*, each with one endemic species, *Scotophilus* with two endemic species, and *Miniopterus* with three endemics (see Fig. 2 bottom, Fig. 3, and Fig. 4 top). *Eidolon*, an African-only genus, is represented on Madagascar by one endemic species (see Fig. 2 top). One endemic family, the Myzopodidae, exists and on the basis of recent fossil evidence is believed to have been present in East Africa during the Pleistocene (BUTLER, 1978). Two endemic species and one non-endemic species are members of an African-Middle Eastern genus, *Triaenops* (see Fig. 2 middle). Eight other non-endemic species belonging to Asian and African genera, are represented on the east and/or south African mainland only. Finally, there are at least two *Pipistrellus* species of uncertain taxonomic status.

## DISCUSSION

Although once part of the large Gondwana landmass, by 65 million years ago, Madagascar had separated from Africa and Asia (BESSE & COURTILOT, 1988). The oldest known bat fossil, *Icaronycteris index*, is some 50 million years old, and by the late Eocene, at least five modern families of bats had evolved. Therefore it seems impossible that bats colonized Madagascar via a land connection and must have arrived by a sweepstakes method. Madagascar is approximately 400 kilometres from the closest point on the African mainland, 2800 kilometres from Saudi Arabia (the closest point in Asia), 3800 kilometres from the southern tip of India and 6900 kilometres from western Australia.

Given the relative distances to the surrounding continents, it seems most likely that non-endemic species of Madagascar bats would have arrived from Africa, with Asia and Australia being much less likely points of origin. This is confirmed by the geographic

distribution of the non-endemic species which are, without exception, present in the eastern and southern areas of mainland Africa, closest to Madagascar.

Table I. Species of Madagascar bats

Species (bold=endemic)	Asia- only genus	Africa- only genus	Africa- Middle East genus	Africa/ Asia genus	Ende- mic family	Austral/ Asia/ America genus	Africa/ Austral/ Asia genus	World- wide genus
<i>Pteropus rufus</i>	•							
<i>Eidolon dupreanum</i>		•						
<i>Rousettus madagascariensis</i>				•				
<i>Emballonura atrata</i>	•							
<i>Taphozous mauritanus</i>							•	
<i>Nycteris madagascariensis</i>				•				
<i>Hipposideros commersoni</i>				•				
<i>Triaenops furculus</i>			•					
<i>Triaenops auritus</i>			•					
<i>Triaenops rufus</i> =( <i>T.persicus</i> )			•					
<i>Myotis goudoti</i>								•
<i>Pipistrellus sp.</i>								•
<i>Eptesicus matroka</i>								•
<i>Eptesicus somalicus</i>								•
<i>Scotophilus robustus</i>				•				
<i>Scotophilus borbonicus</i>				•				
<i>Miniopterus manavi</i>							•	
<i>Miniopterus fraterculus</i>							•	
<i>Miniopterus majori</i>							•	
<i>Miniopterus gleni</i>							•	
<b><i>Myzopoda aurita</i></b>					•			
<i>Mormopterus jugularis</i>						•		
<i>Tadarida fulminans</i>							•	
<i>Tadarida pumila</i>							•	
<i>Tadarida leucogaster</i>							•	
<i>Tadarida leucostigma</i>							•	
<i>Tadarida midas</i>							•	
<i>Otomops madagascariensis</i>				•				

Similarly, endemic species are more likely to have evolved from African migrants than from Asian or Australian migrants. In seeming confirmation of this, the endemic species, other than *Myzopoda*, belong to 13 genera; of these, ten genera are present in Africa and only three are present in Asia but not Africa. The above suggests that, of the 28 species of Madagascar bats with relationships at the genus or species level to bats elsewhere, 25 might be assumed to have originated in Africa.

However, there are several possible exceptions to an « African origin » explanation of Madagascar bat species. Three species belong to genera not known to be present,

other than accidentally, on the African mainland. Of these genera, *Emballonura* and *Mormopterus* are found today no closer to Madagascar than Sumatra. Furthermore, *Rousettus madagascariensis*, *Scotophilus robustus* and *Otomops madagascariensis*, while all members of genera present in Africa, appear to be more closely related to Asian species of the same genus, on the basis of phenetic evidence. These six species offer evidence that at least some Madagascar bats arrived from Asia. Only *Pteropus rufus*, *Emballonura atrata*, *Mormopterus jugularis* and the endemic *Myzopoda* have no known systematic relationship with extant African genera or species.

A clue to the origins of the endemic Myzopodidae may be found in a fossil humerus from northern Kenya identified as *Myzopoda* (BUTLER, 1978); this suggests an African origin for this family, with mainland representatives since having become extinct.

Other extinctions might conceal the former presence, on the African mainland, of species of *Pteropus*, *Emballonura* or *Mormopterus*, and the possibility of an African origin for the Madagascar species of these genera may not be entirely dismissed. However, it appears more likely that the oceanic ridges known to have connected India, the Maldives, the Seychelles, the Mascarenes and Madagascar during periods of Pleistocene glaciation facilitated the colonization of Indian Ocean islands, including Madagascar, from areas now widely separated by water. A likely example is evident in the current widespread distribution of *Pteropus* species in the western Indian Ocean.

## CONCLUSIONS

Based on their systematic relationships with extant genera and species elsewhere, we conclude that most of the Madagascar bat species had origins on the African mainland. Six species appear most likely to have originated in Asia, despite the large distances now separating Madagascar from Asia. However, the possibility of an African origin for these species, with subsequent extinction of the ancestral populations on the African mainland, may not be entirely ruled out. The endemic *Myzopoda* family appears, on the basis of fossil evidence, to be African in origin.

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## REFERENCES

- BESSE, J. & V. COURTILOT, 1988. Paleogeographic maps of the continents bordering the Indian Ocean since the early Jurassic. *J. Geographical Research*, 93: 11791-11808.

BUTLER, D.M., 1978. Insectivora and Chiroptera. *In*: V.J. Maglio & H.B.S. Cook (eds.), *Evolution of African mammals*. pp. 56-68. Harvard University Press, Cambridge.

PETERSON, R.L., J.L. EGER & L. MITCHELL, 1995. *Chiroptères. Faune de Madagascar*. No. 84. Paris: Muséum national d'Histoire naturelle, 204 pp.

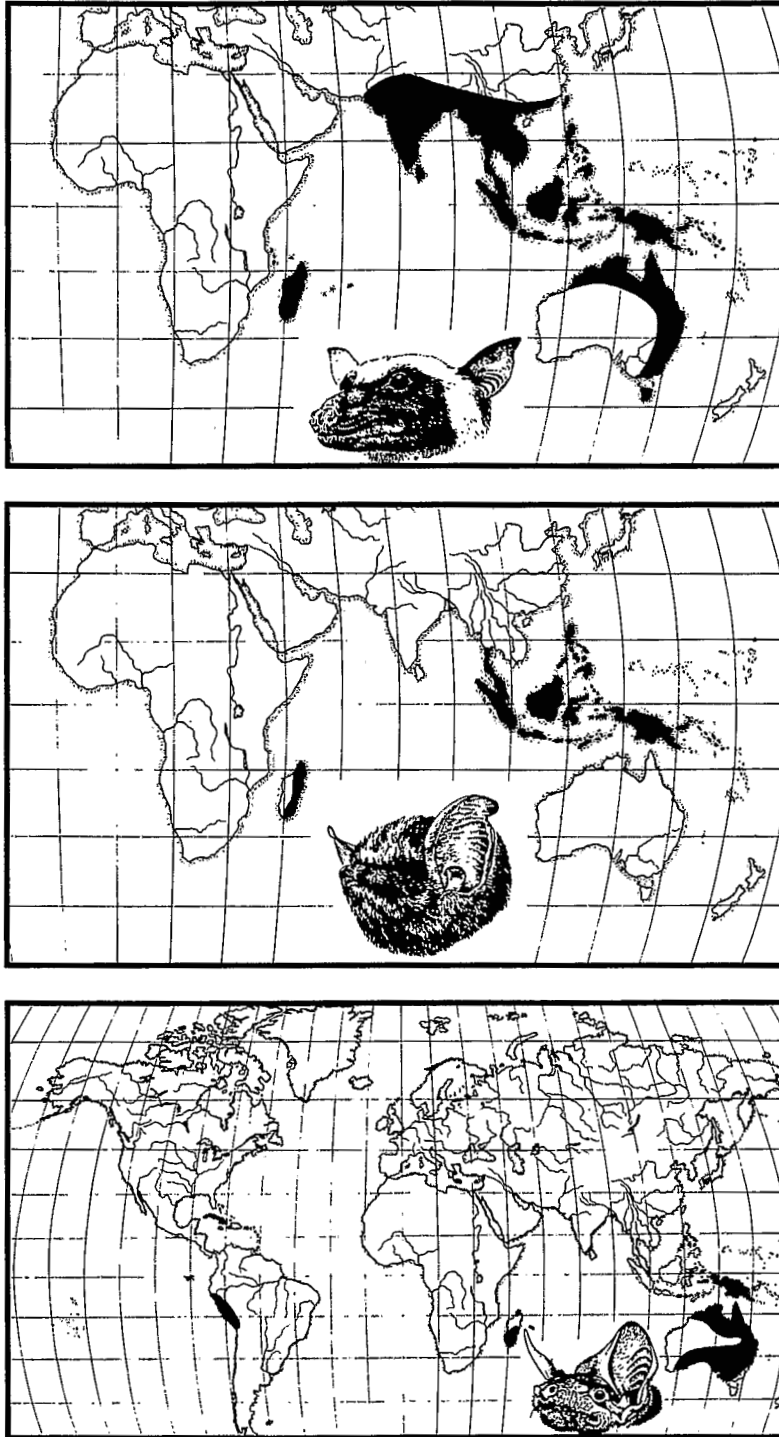


Fig. 1. Distribution of *Pteropus* (top), *Emballonura* (middle), and *Mormopterus* (bottom).

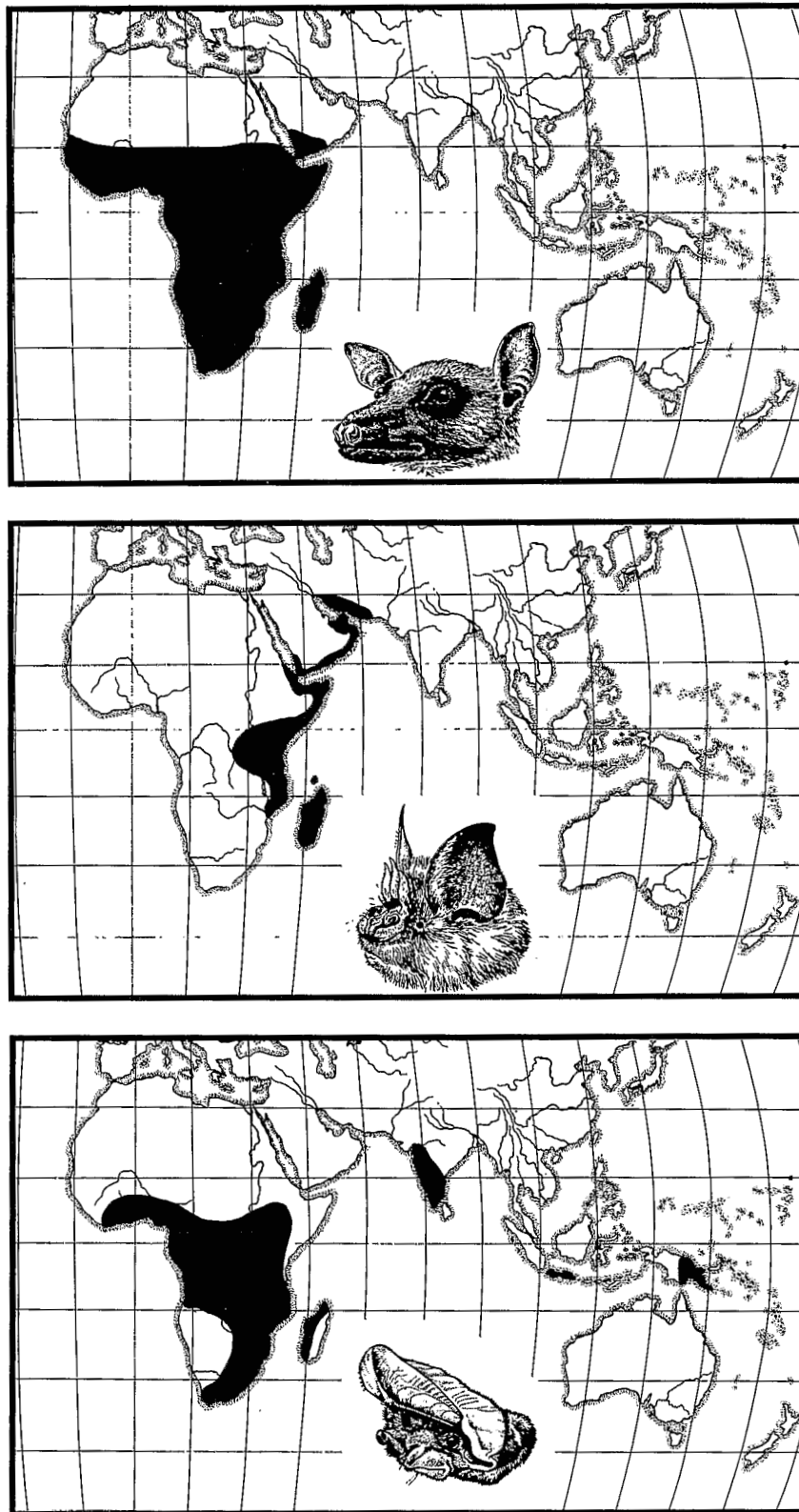


Fig. 2. Distribution of *Eidolon* (top), *Triaenops* (middle), and *Otomops* (bottom).

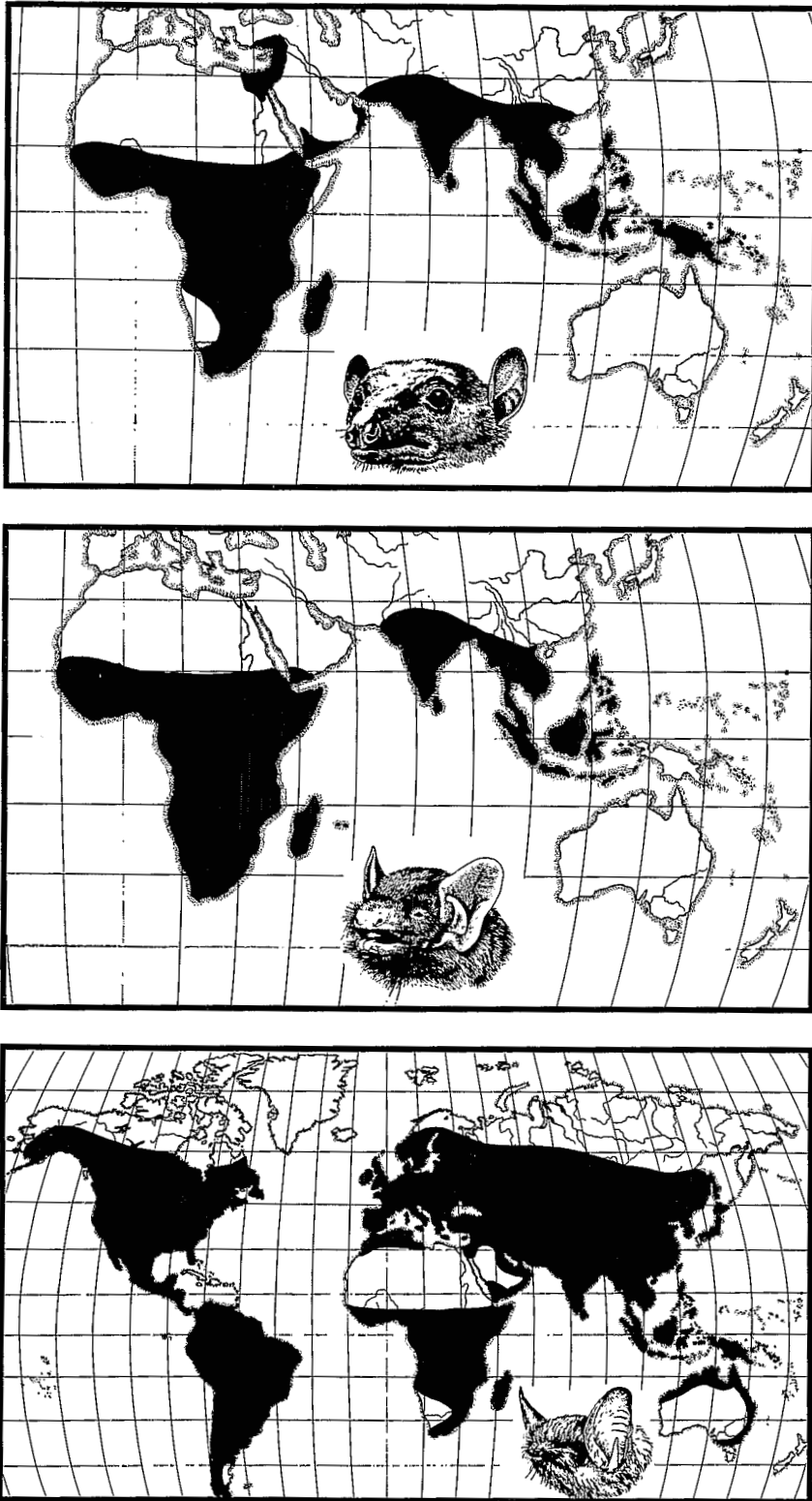


Fig. 3. Distribution of *Rousettus* (top), *Scotophilus* (middle), and *Myotis* (bottom).

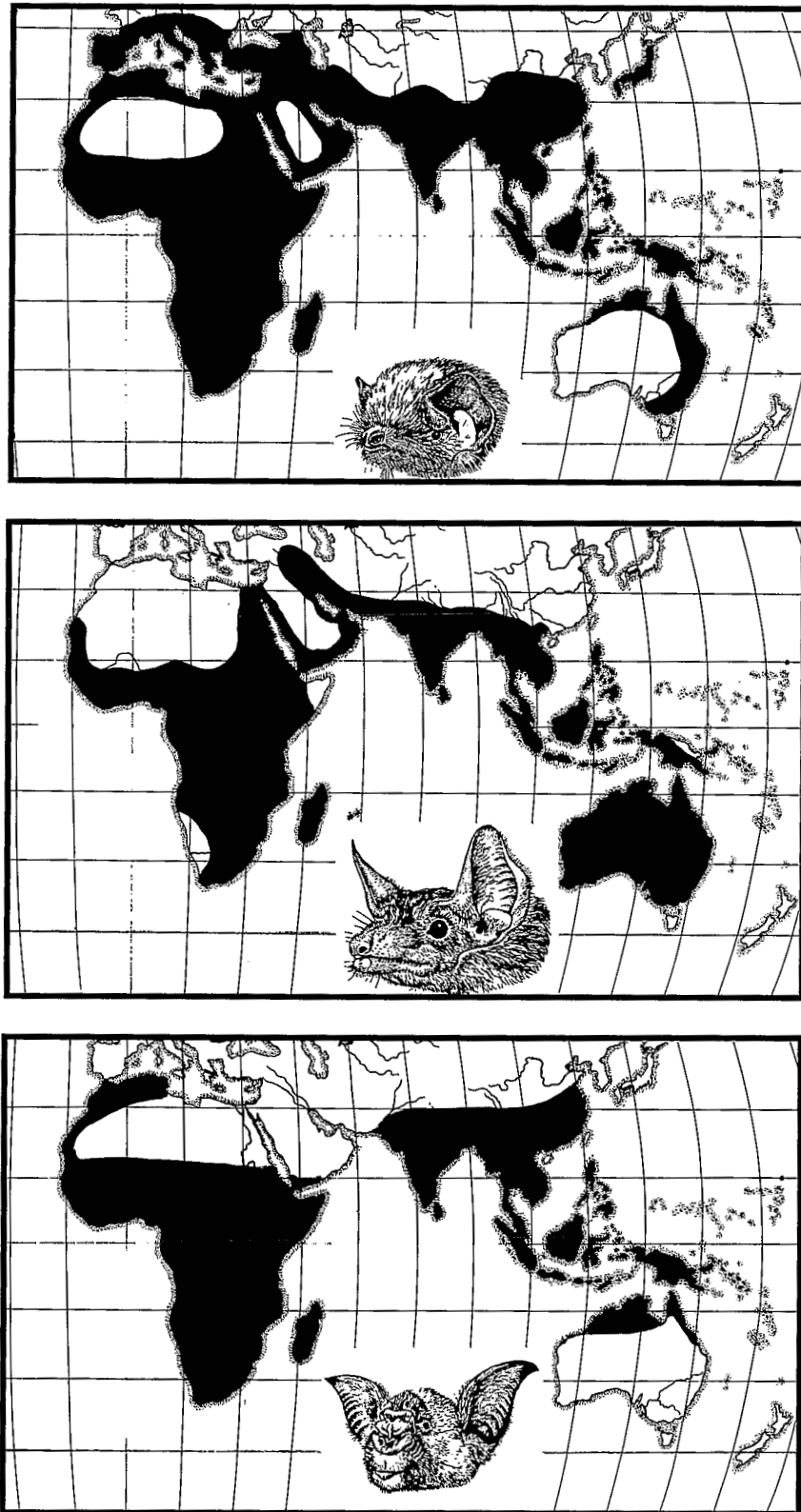


Fig. 4. Distribution of *Miniopterus* (top), *Taphozous* (middle), and *Hipposideros* (bottom).