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The taxonomic status of *Chaerephon pumilus* from the western Seychelles: resurrection of the name *C. pusillus* for an endemic species

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We investigate the taxonomic status of a molossid bat from the western Seychelles that has been previously considered distinct and then subsequently synonomized with the widespread *Chaerephon pumilus*. We compare specimens available from the Seychelles (Aldabra and Amirantes), including the holotype and paratype of *C. pusillus*, to specimens assigned to *C. pumilus* from Kenya, the Comoros Archipelago (Mayotte, Mohéli, Anjouan, and Grande Comore), and from lowland areas of the northern half of Madagascar. Based on these comparisons, the animals from the Aldabra and Amirantes are distinctly smaller than these other regional island and mainland populations and we conclude that the name *C. pusillus* should be resurrected for this endemic Seychelles species.

Key words: *Chaerephon pusillus*, specific status, Aldabra, Amirantes

INTRODUCTION

The molossid species *Chaerephon pumilus* (Cretzschmar, 1830–1831) is broadly distributed across sub-Saharan Africa, southern portions of the Arabian Peninsula, and islands off the west and east coasts of Africa, including Bioko, São Tomé, Pemba, Zanzibar, the Comoros, Madagascar, and the Seychelles (Juste and Ibáñez, 1994; Bouchard, 1998; Simmons, 2005). This species is known to exhibit considerable phenotypic variation, particularly in pelage and wing coloration, which resulted in numerous taxonomic designations for populations across its range. Most bat taxonomists when confronted with the task of trying to sort out patterns of geographic variation in this species complex consolidate these different 'forms' under *C. pumilus* (e.g., Hayman and Hill, 1971; Simmons, 2005) or recognize numerous subspecies (e.g., Koopman, 1994). One study, using mitochondrial cytochrome *b,* found less than 0.9% divergence among African specimens from South Africa, Zambia, and Tanzania showing two distinct patterns in wing coloration (Jacobs *et al*., 2004), although many of these same individuals or at least populations show some differences in size and echolocation calls (Aspetsberger *et al*., 2003).

The eastern limit of *C. pumilus* is generally cited as the western Seychelles, specifically the Aldabra Atoll and the Amirantes

(Hutson, 2004). Miller (1902) described *Nyctinomus pusillus* from Aldabra Atoll based on two specimens. This species, subsequently placed in the genus *Tadarida* (e.g., Hayman and Hill, 1971) and more recently in the genus *Chaerephon* (Koopman, 1994), was characterized by Miller (1902) as being phenotypically similar to *C. pumilus*, but notably smaller in a variety of external, cranial, and dental characters. Hayman and Hill (1971: 64) noted, with regards to *Tadarida pusilla* Miller (1902), that "a specimen collected very recently seems identical with *pumila*" and they considered the name *pusilla* to be a junior synonym of *C. pumilus*. The basis for their conclusion is unclear, but one can infer that the recent specimen, presumably from the western Seychelles, fell within the range of typical *C. pumilus*. In that same year, Hill (1971) reviewed the known bat fauna of Aldabra Atoll and retained the name *pusilla* for the locally occurring molossid, but noted (p. 575) that "it is clearly related to *T. pumila* and with which it may prove conspecific". In Simmons's (2005) summary of bat species of the World, the *Chaerephon* occurring in the western Seychelles was referred to *C. pumilus*.

Recent chiropterological exploration of Madagascar and the Comoros Archipelago has resulted in new collections of *Chaerephon*, which, together with material from the African continent, provide the needed comparative collections to assess patterns of size variation in these populations, and place the molossid from the western Seychelles in a broader geographic context. The purpose of this paper is to assess the taxonomic status of *C.* '*pusillus*' from the Seychelles.

Materials and Methods

In order to understand patterns of morphological variation amongst animals referred to *Chaerephon* from the Seychelles and their specific designation, we have compared specimens available from this region (including the holotype and paratype of *C. pusillus*) to series of *C. pumilus* from Kenya, the four principal islands making up the Comoros Archipelago (Mayotte, Mohéli, Anjouan, and Grande Comore), and from lowland areas of the northern half of Madagascar. Comparisons are confined to adult specimens based on complete eruption of teeth and fused basisphenoid-basioccipital sutures. Specimens used in this paper are housed in The Natural History Museum, London (formerly British Museum of Natural History [=BMNH]), Field Museum of Natural History, Chicago (FMNH), and National Museum of Natural History (formerly United States National Museum [=USNM]). Seychelles specimens are listed in an appendix.

Members of the genus *Chaerephon* show sexual dimorphism in numerous morphological characters; however, in our different samples, the number of males and females are similar and this aspect was not taken into account in the analyses presented herein. This simplifies certain comparisons, but results in broader ranges and higher levels of variance in most measurements.

Five external measurements include: total length, tail length, hind foot length (excluding claws, at least for the Madagascar material), ear length, and forearm length. Body mass in grams was available from most specimens. For these variables, all of the values used from the Madagascar material were measured by FHR, those from the Comoros by SMG, and from Kenya by Bruce J. Hayward; FHR and SMG have very similar techniques for measuring specimens. In the case of the Seychelles specimens, several different field researchers were responsible for their collection, and it is presumed that there are differences in external measurement techniques.

Six cranial and three dental measurements were made using a digital caliper, accurate to the nearest 0.1 mm. The measurements and their definitions (derived largely from Freeman, 1981) are: anterior palatal width (C^1–C^1): taken across the outer alveolar borders of the canines; greatest skull length (GSKL): from posterior-most part of occipital to anterior-most point of premaxillary bone; greatest zygomatic breadth (ZYGO): width taken across zygomatic arches at the widest point; postorbital breadth (POB): dorsal width at most constricted part of skull; lacrimal width (LW): width across rostrum dorsally at lacrimal protuberances; mastoid breadth (MAST): maximum width of skull across mastoid processes; maxillary toothrow (C–M^3): length from anterior alveolar border of canine to posterior alveolar border of M^3; palatal length (PAL): from posterior border of hard palate to anterior edge of premaxillary bone; and

posterior palatal width (M^3–M^3): taken across the outer alveolar borders of the third molars. In order to better appreciate the relationships between different samples used herein, we conducted a principal component analysis using the program Statistica AX, version 7.0.

Results

For the external, cranial, and dental measurements, individuals of *C. pumilus* from northern Madagascar and Kenya show no noteworthy difference and the range of measurements is broadly overlapping (Tables 1 and 2). The only exception is hind foot length, but this is certainly related to measurement technique — in the Madagascar individuals, it was taken to the longest toe and for those from Kenya, presumably to the distal claw tip. Amongst the Kenyan material there are two distinct wing coloration patterns, dark or with extensive white areas, and less than 5% of the 50 individuals examined had intermediate coloration. In contrast, the two wing coloration extremes are present among the Madagascar specimens, but the variation tends to be continuous with lots of intermediate individuals. Comparison of cranial and dental morphology found no consistent difference between the Kenyan and Malagasy populations of *C. pumilus*.

In general, the specimens from the Comoros are on average smaller than those from Kenya and northern Madagascar. The specific status of the Comoros populations currently referred to *C. pumilus* will be the subject of a subsequent study, but these specimens are included here to show they are morphologically different from those from the western Seychelles. A specimen from Zanzibar (BMNH 92.11.22.1) cannot be separated based on cranial characters from other east African material referable to *C. pumilus*.

In contrast, the measurements of *Chaerephon* specimens from the western Seychelles are notably smaller than *C. pumilus*

Table 1. External measurements (in mm) and mass (in g) of *Chaerephon pumilus* from lowland portion of the northern half of Madagascar, Kenya, and the Comoros, and *C. pusillus* from the western Seychelles (Aldabra and Amirantes). Measurements presented as mean ± SD, minimum and maximum measurements, and number of specimens (in parentheses). Several of the *C. pusillus* external measurements were made by SMG from fluid preserved specimens and the balance were taken from museum specimen labels. The forearm length of the holotype (USNM 37852) is 37.6 mm

Region	Total length	Tail length	Hind foot length	Ear length	Forearm length	Body mass
C. pumilus						
Northern Madagascar	96.1 ± 2.18	33.3 ± 1.45	6.0 ± 0.21	16.7 ± 0.57	38.9 ± 1.08	12.1 ± 1.23
	92–101 (23)	29–36 (23)	6–7 (23)	16–18 (23)	37–41 (23)	10.0–14.5 (23)
Kenya	95.4 ± 4.01	33.0 ± 3.02	9.2 ± 0.73	16.9 ± 1.33	39.2 ± 1.75	9.7 ± 1.06
	87–104 (46)	28–41 (46)	8–11 (46)	13–19 (46)	36–42 (41)	8.0–12.0 (37)
Comoros	88.4 ± 1.93	30.7 ± 1.54	5.1 ± 0.37	17.2 ± 0.48	37.1 ± 0.75	8.1 ± 1.30
	84–93 (73)	27–36 (73)	4–6 (73)	16–18 (73)	36–38 (73)	5.9–11.5 (73)
C. pusillus						
Seychelles	79 (1)	30.1 ± 1.17	5.8 ± 0.40	15 (1)	37.9 ± 0.53	6.4 ± 0.10
		29–32 (6)	5–6 (6)		37.3–39.1 (9)	5.0–7.5 (5)

TABLE 2. Cranial and dental measurements (in mm) of *C. pumilus* from the lowland portion of the northern half of Madagascar, Kenya, and the Comoros, and *C. pusillus* from the western Seychelles (Aldabra and Amirantes). Measurements presented as mean ± SD, minimum and maximum measurements, and number of specimens (in parentheses)

Region	GSKL	ZYGO	POB	LW	MAST	PAL	$C–M^3$	$C^1–C^1$	$M^3–M^3$
C. pumilus									
Northern Madagascar	16.8 ± 0.26	10.6 ± 0.21	3.8 ± 0.10	6.0 ± 0.19	10.0 ± 0.21	6.7 ± 0.16	6.4 ± 0.12	4.7 ± 0.21	7.8 ± 0.15
	16.4–17.2 (24)	10.2–11.1 (24)	3.6–4.0 (24)	5.5–6.3 (24)	9.7–10.3 (24)	6.4–6.9 (24)	6.1–6.6 (24)	4.4–5.1 (24)	7.5–8.0 (24)
Kenya	17.1 ± 0.43	10.6 ± 0.32	3.9 ± 0.13	6.0 ± 0.25	9.9 ± 0.21	7.0 ± 0.25	6.4 ± 0.24	4.7 ± 0.26	7.6 ± 0.38
	16.2–17.9 (46)	9.9–11.2 (46)	3.5–4.1 (46)	5.5–6.6 (46)	9.5–10.4 (46)	6.6–7.7 (46)	5.9–6.9 (46)	4.1–5.3 (45)	7.0–8.2 (46)
Comoros	15.5 ± 0.27	9.6 ± 0.19	3.4 ± 0.10	5.5 ± 0.20	9.1 ± 0.18	6.3 ± 0.18	5.8 ± 0.13	4.2 ± 0.19	7.0 ± 0.16
	14.9–16.2 (73)	9.0–9.9 (73)	3.2–3.7 (73)	5.0–5.8 (73)	8.8–9.4 (73)	5.9–6.7 (73)	5.6–6.1 (73)	3.9–4.6 (73)	6.6–7.3 (73)
C. pusillus									
Seychelles	15.2 ± 0.40	9.0 ± 0.17	3.1 ± 0.04	5.0 ± 0.18	8.8 ± 0.17	6.3 ± 0.22	5.5 ± 0.14	3.8 ± 0.20	6.5 ± 0.20
	14.6–15.7 (6)	8.7–9.2 (7)	3.0–3.1 (7)	4.7–5.2 (7)	8.5–9.0 (6)	6.0–6.6 (6)	5.2–5.7 (8)	3.4–4.1 (8)	6.1–6.7 (7)
Holotype (USNM 37852)	–	9.1	3.1	5.1	8.9	6.4	5.4	3.9	6.7

from northern Madagascar and Kenya (Tables 1 and 2). In the former, external measurements tend to be either smaller than (total length) or close to the minimum measurements of *C. pumilus* specimens (hind foot length, ear length, forearm length), although there is broad overlap in one variable (tail length). The one measurement that shows a notable difference is body mass, which is significantly smaller in the Seychelles animals, as compared to *C. pumilus* (Seychelles, $\bar{x}$ = 6.4; combined Kenyan and Madagascar *C. pumilus* samples, $\bar{x}$ = 10.6; $t = 5.71$, $d.f. = 63$, $P < 0.001$).

Amongst the nine cranial and dental measurements, the animals from the western Seychelles are consistently smaller than *C. pumilus* from northern Madagascar and Kenya. In seven of these variables, there is no overlap between animals from Madagascar/Kenya and those from the Seychelles; the two exceptions are palatal length (PAL) and anterior palatal width ($C^1–C^1$). An examination of aspects of cranial morphology and tooth structure indicate that the animals from the Seychelles are very similar to those of *C. pumilus* from Madagascar, except for their diminutive size (Fig. 1). These conclusions are supported by a principal component analysis of cranio-dental variables in which the northern Madagascar and Kenya samples form a partially overlapping cluster, notably separated from the Comoros samples, which in turn are distinct from the Seychelles specimens (Fig. 2). The PC 1 factor loadings of eight variables (GSKL excluded because of reduced sample size) used in the analysis are negative with all values exceeding -0.850. This emphasizes that size is the major component explaining variation in these animals, with PC 1 accounting for 85.7% of the variation and separating the Madagascar-Kenyan group, animals from the Comoros, and from the western Seychelles. In turn, PC 2, which

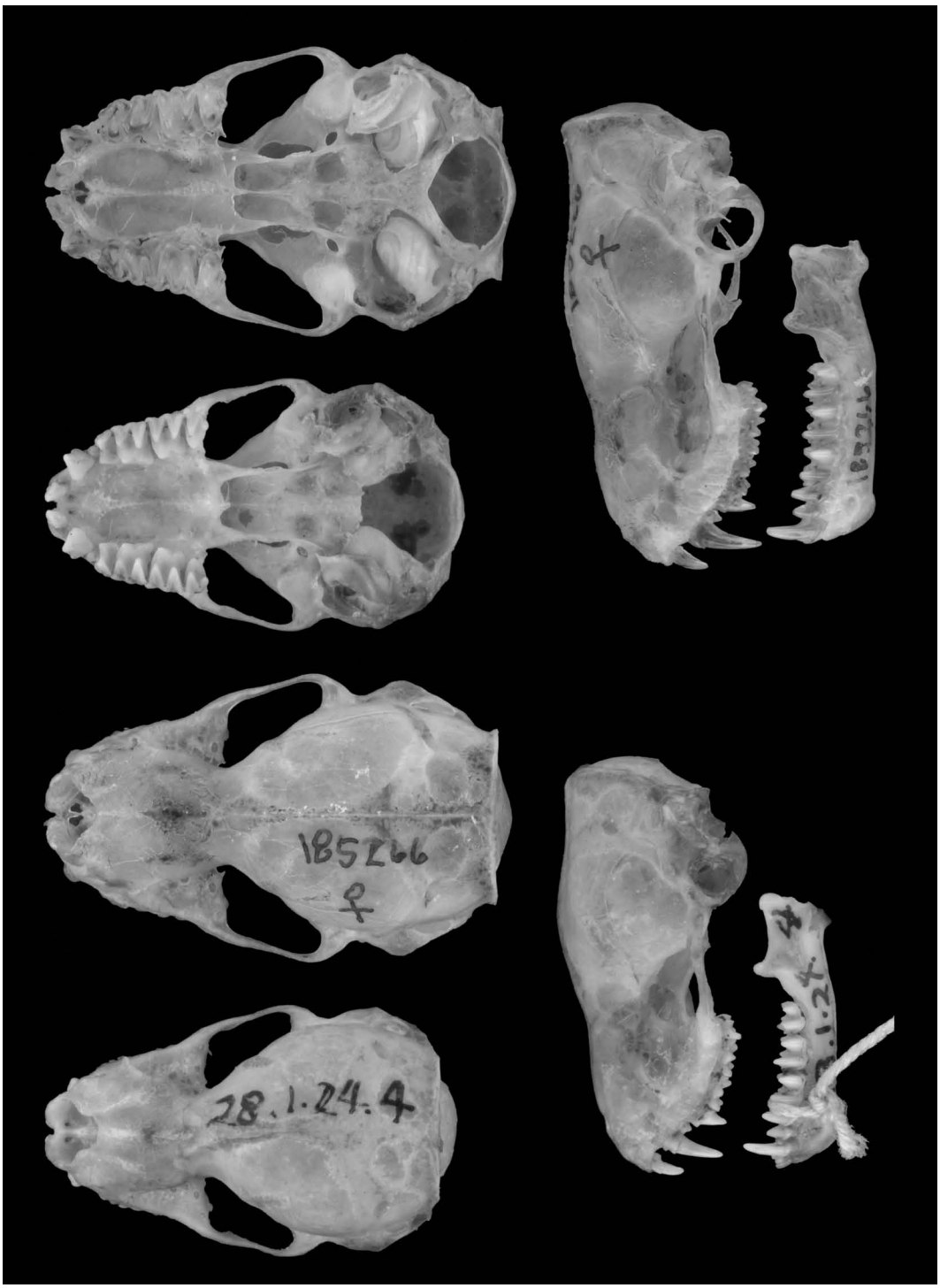

FIG. 1. Dorsal, ventral, and lateral views of adult crania and mandibles of *Chaerephon* spp.: left – *C. pusillus*, BMNH 28.1.24.4 (greatest skull length = 15.0 mm) from Amirantes, Seychelles; right – *C. pumilus*, FMNH 185266 (greatest skull length = 16.8 mm) taken at Farafangana, Madagascar. (Photograph taken by John Weinstein, FMNH image No. Z94449_09d.)

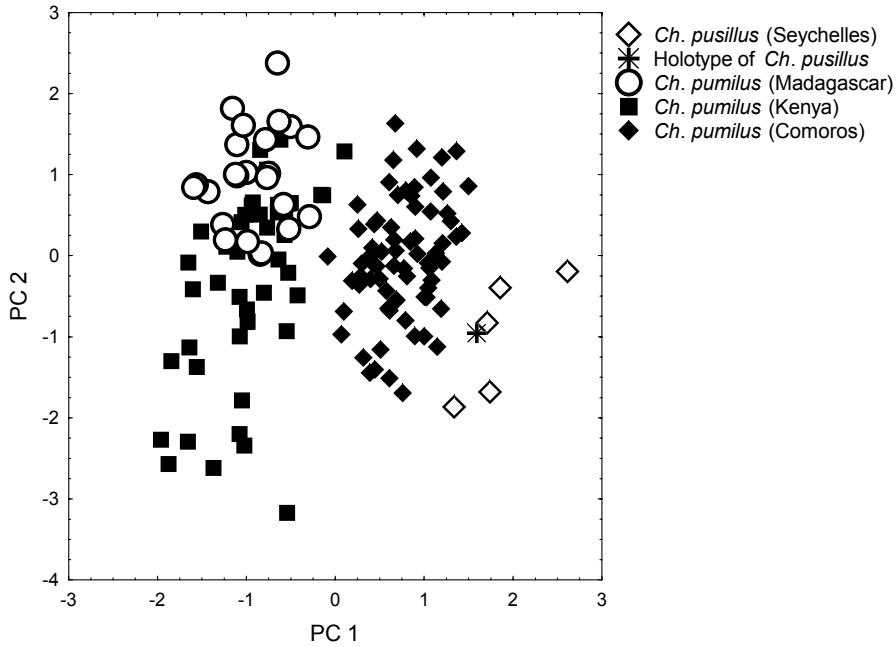

FIG. 2. Projections of PC 1 (*x*-axis) and PC 2 (*y*-axis) in the principal component analysis of select cranial-dental measurements

gives an indication of shape, accounts for 4.4% of the variation and separates specimens from Madagascar and western Seychelles. The highest factor loading for this component was for the variable PAL with a value of -0.421.

Notable differences were found in aspects of the external morphology of the head, rostrum, nostrils, and ear structure of the *Chaerephon* from the Seychelles (BMNH 69.784 and 69.785) and *C. pumilus* from east Africa (Fig. 3); for these characters Malagasy specimens are very similar to those from east Africa. As witnessed by skull measurements, the head of *C. pumilus* is notably larger than the western Seychelles *Chaerephon* (Table 2). The rostrum of *C. pumilus* is distinctly more elongated and rectangular, while that of the Seychelles animals is shorter and more pointed; the nostrils of *C. pumilus* are also larger and broader (Fig. 3). There is also a notable difference in the antitragus between these animals: in *C. pumilus* it is distinctly angular shaped and in the Seychelles *Chaerephon* more rounded, arch-shaped, and with a slight anterior elongation (Fig. 3).

There are some differences in pelage and skin coloration between the Seychelles *Chaerephon* and populations of *C. pumilus*. Comparisons were made between a series of recently collected specimens of *C. pumilus* from Madagascar preserved in alcohol and two animals from the Seychelles (BMNH 69.784 and 69.785) obtained in 1968 and preserved in alcohol. Dorsum — dark brown in *pumilus*, lighter in Seychelles animal; ventrum (chin to anus) — light brownish-gray in *pumilus* with often a well-developed white band of fur along the body edge, medium-brown in Seychelles animal without the white band; non-furred skin color of ears, face, wings, feet, and tail — dark brown, approaching black in *pumilus*, medium-brown in Seychelles animal. In general, the pelage coloration of the Kenyan series matches that of animals from Madagascar. While some of the differences in

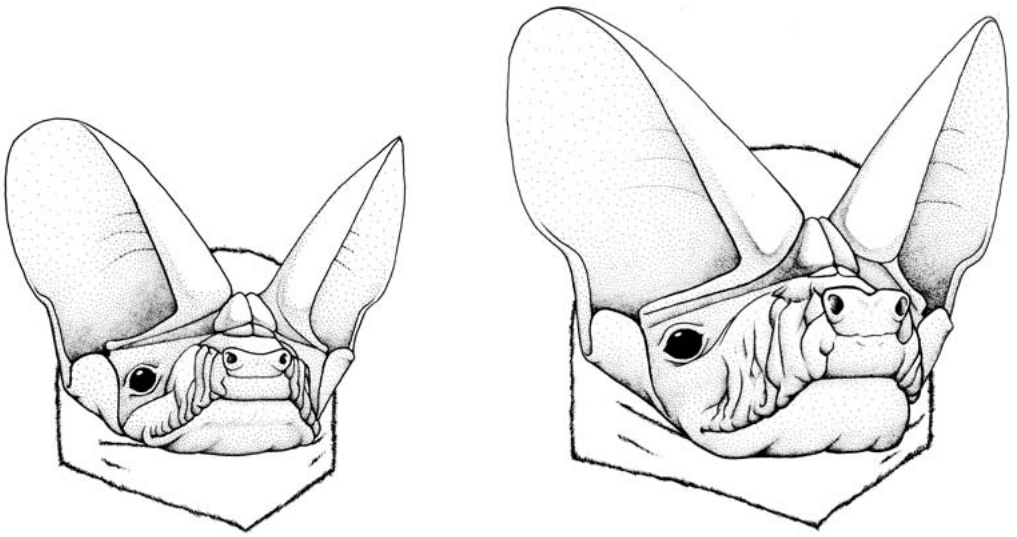

FIG. 3. Profiles of *Chaerephon* spp.: left — *C. pusillus*, BMNH 69.785 from Aldabra, Seychelles; right — *C. pumilus*, FMNH 137477 taken in Uganda. (Drawing by Rebecca Kramer)

pigmentation maybe associated with the discoloration of specimens stored in alcohol for nearly four decades, the darker ventrum and lack of the white underwing line in the Seychelles *Chaerephon* would indicate real pigmentation distinctions between these populations.

DISCUSSION

Based on the analyses presented here, it is evident that specimens of *Chaerephon pumilus* from northern Madagascar and Kenya show considerable mensural and morphological similarity, while those from the Comoros demonstrate some notable differences. The insular population on Madagascar does not display any reduction in size, with respect to specimens from east Africa. In contrast, the *Chaerephon* from the western Seychelles is substantially smaller than the northern Malagasy, Kenyan, and Comorian material.

An examination of measurements of *C. pumilus* from other portions of this species' range, particularly towards the distributional limits, such as the Arabian Peninsula (Harrison, 1964), shows that individuals from these zones fall within the range of continental African and Malagasy populations. Thus, there is a broad level of morphological similarity in this species across its range and across different bioclimatic regimes, with the exception of the Seychelles, and to a lesser extent the Comoros.

An endemic species of hemipteran ectoparasite of the family Polyctenidae, *Hypoctenes hutsoni*, was described from specimens referred to *Chaerephon* obtained on Aldabra Island (Maa, 1970). Although the genus *Hypoctenes* is broadly distributed in the Old World, this ectoparasite appears to be endemic to the small *Chaerephon* from Aldabra, lending further support that its host has been isolated from other populations of this bat genus for a considerable period.

The diminutive *Chaerephon* from Aldabra and the Amirantes in the western Seychelles has different morphological characters and is distinctly smaller than bats referable to *C. pumilus* from Africa and Madagascar. Based on these results, we

conclude that there has been significant differentiation of the Seychelles population and these animals should be considered as a distinct species. Hence, we propose that the name *C. pusillus* should be raised from junior synonymy under *C. pumilus* and be used for the small molossid known to occur on the Amirantes and Aldabra Atoll — Picard and South Islands (Appendix). The Amirantes Archipelago is made up of a series of islands, spanning a zone of over 250 km in length, and it is vague where BMNH 28.1.24.4, the only known specimen from this island complex, was collected. The measurements of this specimen fall within the range of individuals from Aldabra.

As the western most island complex in the Seychelles Archipelago, Aldabra Atoll is about 480 km to the northwest of the northern tip of Madagascar and 400 km from the eastern most portions of the Comoro Islands. These distances are approximately equivalent to those between the western coast of Madagascar and the eastern coast of Africa. Hence, the over water colonization of Aldabra by *Chaerephon*, based simply on a distance factor, could have been either from Madagascar or from the Comoros.

The Aldabra Atoll is about 680 km from the closest edge of the Amirantes and an arc of widely separate islands, where *C. pusillus* is not known to occur, links these two island groups. The Aldabra Atoll and the Amirantes Archipelago rise just slightly above modern sea-level heights and these landmasses would have been underwater during periods of the Quaternary. This would clearly imply that, within recent geological time, these populations have colonized or recolonized these islands.

There is a previous report of *C. pusillus* occurring on Mayotte in the Comoros Archipelago, as well as on Madagascar in the Toliara region (Peterson *et al*., 1995). We have evidence of a smaller former of '*C. pumilus*' on Madagascar, which is notably larger than *C. pusillus* from the Seychelles. Further, our recent material from Mayotte indicates that *Chaerephon* from this locality, as well as other islands in the Comoros Archipelago, are morphological different from *pumilus* from Madagascar and Kenya, as well as *C. pusillus* of the western Seychelles. Molecular studies of these animals are needed to understand their evolutionary history and phylogenetic relationships; however, to our knowledge fresh tissue samples of *C. pusillus* are not available.

Based on our current information, *C. pusillus* is a species endemic to the Seychelles and is currently only known from Aldabra Atoll and the Amirantes. What is known about the natural history of this species is summarized by Goodman and Gerlach (1997). *Chaerephon pusillus* is one of six species of Chiroptera recorded from the Seychelles Archipelago, which include *Pteropus aldabrensis* True, 1893 and *P. seychellensis* Milne Edwards, 1877 (Pteropodidae), *Coleura seychellensis* Peters, 1868 and *Taphozous mauritianus* E. Geoffroy, 1818 (Emballonuridae), and *Triaenops* sp. nov. (Hipposideridae — Goodman and Ranivo, In press). All of these different bats, with the exception of *Taphozous* and *P. seychellensis*, are endemic to the archipelago. Further, two of the six species (*P. aldabrensis* and *Triaenops* sp. nov.) are only known from Aldabra and *C. pusillus* is shared with the Amirantes, further emphasizing that this atoll holds a unique and largely endemic vertebrate biota.

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Appendix

Adult specimens referred to *Chaerephon pusillus* used in this study from the western Seychelles

Aldabra Island (coll. Dr. W. L. Abbot), ♀ (USNM 37852, holotype), unsexed (USNM 20990); Takamaka Grove, South Island, Aldabra Atoll, 12-14 February 1968 (coll. A. M. Hutson), ♂ (BMNH 68.938), ♀ (BMNH 68.939), ♀ (BMNH 68.940), ♀ (BMNH 68.941), ♀ (BMHH 68.942); Picard Island, Aldabra Research Station, 21 September 1975 (coll. J. Wilson), ♂ (BMNH 76.306); eastern shore of East Channel, South Island, Aldabra Atoll, 4 October 1965 (coll. Wright), ♂ (BMNH 66.5573); Picard Island, Aldabra Settlement, 7 June 1968 (coll. J. Frazier), ♂ (BMNH 69.18); Amirante Island (coll. Capt. K. Parcon), unsexed (BMNH 28.1.24.4).