Late Pleistocene bat fossils from Anjohibe Cave, northwestern Madagascar

KAREN E. SAMONDS

Redpath Museum, McGill University, 859 Sherbrooke St. W., Montréal, Québec H3A 2K6, Canada
E-mail: karen.samonds@mcgill.ca

In spite of decades of research on Madagascar's unique and endemic modern fauna, the evolutionary history of the island's bat fauna remains largely unknown. Their origin and evolution is largely unknown because of the nature of the fossil record; the deepest well-dated glimpse of Madagascar's mammal groups comes from only 26,000 years ago. Bat remains have frequently been recovered from paleontological sites, but have been rarely identified or described. It therefore remains unknown whether bats underwent a reduction in species diversity similar to that seen in many of Madagascar's vertebrate clades. Herein I describe a collection of newly discovered subfossil bats from Anjohibe Cave, northwestern Madagascar, some estimated to have been deposited about 80,000 years ago. Five bat genera are represented as subfossil (*Rousettus*, *Eidolon*, *Hipposideros*, *Triaenops*, and *Myotis*) with four of these genera present in Anjohibe Cave today. The subfossil material has yielded two new species, indicating that Malagasy bats experienced recent species turnover, paralleling what is seen in much of the island's terrestrial vertebrate fauna.

Key words: Madagascar, subfossil, Chiroptera, Anjohibe Cave, Late Pleistocene

INTRODUCTION

Madagascar's extant fauna is one of the most unique and endemic on the planet (Goodman and Benstead, 2005), and exploring the circumstances leading to the modern distribution of its animals has been the focus of decades of scientific research. However, in spite of these efforts, the evolutionary history of the island's bats, perhaps the least-studied of Madagascar's extant mammals, has remained poorly known.

Present knowledge regarding the evolutionary history of modern Malagasy mammals is based on subfossils (referring to their geologically shallow age), with our first glimpse at a mere ≈ 26,000 years BP

(Simons *et al*., 1995). A diverse subfossil fauna has been described from Holocene deposits, including crocodyliforms, turtles, giant lemurs, bats, carnivorans, pigs, rodents, pygmy hippos, the aardvark-like *Plesiorycteropus*, and birds (e.g., Godfrey *et al*., 1990; Burney *et al*., 1997; Gommery *et al*., 2003; Goodman *et al*., 2004). More than 30 subfossil localities are presently recognized on Madagascar, and are largely distributed in the western and southern portions of the island, with a few in the north and on the Central High Plateau (Godfrey *et al*., 1999; Burney *et al*., 2004). During the end of the 19th and first third of the 20th century, an emphasis was placed on the collection of larger fossils such as primates,

hippos, carnivorans, and elephant birds; while bat remains have been recovered from subfossil sites, they have seldom been identified or described (Sabatier and Legendre, 1985; Ravoavy, 1986; Burney et al., 1997).

As of May 2007, 37 species of extant bats are presently recognized in Madagascar, ≈ 60% of which are endemic (Eger and Mitchell, 2003; Goodman and Cardiff, 2004; Goodman et al., 2005a, 2005b, 2006a, 2006b, In press; Bates et al., 2006). As more concentrated collecting efforts are made, new species of Malagasy bats are still being discovered at a high rate (e.g., Goodman and Cardiff, 2004; Goodman et al., 2005a, 2006a, 2006b, In press).

Madagascar's present assemblage of vertebrate species, while exceptionally unique, represents only a subset of the diversity known from the island's recent geological past. Multiple extinction events during the Holocene exterminated nearly all of Madagascar's large-bodied native animals (MacPhee, 1986; MacPhee and Marx, 1997; Burney, 1999). Radiocarbon dates suggest that these extinctions, occurring approximately 2,000 to 500 years BP, likely postdated the arrival of humans (Burney, 1999, 2003; Burney et al., 1997, 2003, 2004), estimated at approximately 2,300 years BP (Burney et al., 2004; Perez et al., 2005).

Herein I report on a diverse assemblage of newly discovered bat fossils from Anjohibe Cave, northwestern Madagascar; some of this material is estimated to have been deposited approximately 80,000 years ago. This is more than three times the age of the oldest described Cenozoic vertebrate subfossils, providing a deeper glimpse into this gap and the evolutionary history of Malagasy bats.

MATERIALS AND METHODS

Study Site

Anjohibe Cave, also known in the literature as Tsinjomitondraka or Grottes d'Andranoboka, is located in the southern part of the current dry savannah of the Mahavo plains in northwestern Madagascar, northeast of Mahajanga (Decary, 1934; Burney et al.,
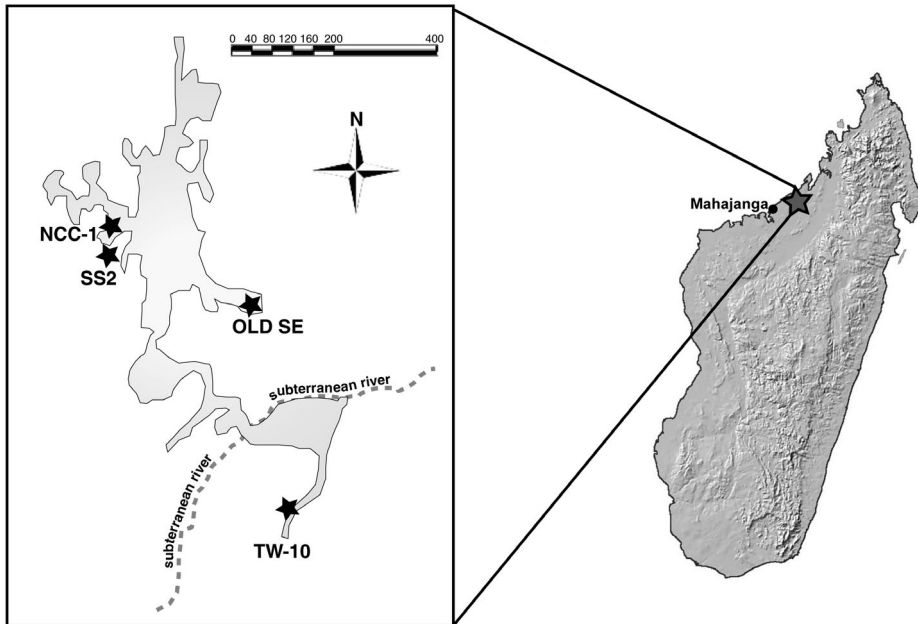

FIG. 1. Anjohibe Cave, northwestern Madagascar. Breccia localities are shown in small black stars on the Anjohibe Cave detail map. Adapted from de Saint-Ours and Paulian (1953) and Burney et al. (1997). Map scale in meters

1997 — Fig. 1). The caves at Anjohibe are part of a karst cave system formed within the Eocene limestone plateau (Besairie, 1956). Anjohibe ('big cave' in Malagasy) consists of a large cave system with an underground river running in the southeastern portion (de Saint-Ours and Paulian, 1953; Burney *et al.*, 1997), and several extant animals inhabiting the cave, including bats. The region has undergone extensive human modification, and subfossil representation of arboreally adapted groups (e.g., sloth lemurs) suggests that this region was considerably more forested in the past.

Fossils frequently occur in accumulations beneath dolines (large sinkholes) or skylights (openings in the ceiling), as animals fall through these from the surface. Within the cave interior, some fossils are also concentrated into bone breccias, collections of bone fragments and sediment cemented together with mineral deposits. Breccias demonstrate a large range of depositional processes; some fossils appear to have been slowly trapped within forming speleothems, while others appear to have been transported large distances by subterranean streams, and subsequently deposited and consolidated. The breccia samples used in this study were collected from four localities in Anjohibe Cave (Fig. 1 and Table 1). In some cases, these samples contained high concentrations of bat bones (Fig. 2).

Uranium-Series Dating

Breccia samples were dated at Florida State University using Uranium-series (^{230}Th/^{234}U) techniques on the flowstone intercalated with the bone breccia layers. Speleothems were sampled and analyzed according to standard dating techniques (e.g., Brook *et al.*, 1990; Burney *et al.*, 1994, 2004).

Fossil Preparation

The breccias containing these fossils were collected in 1996 by the team of Dr. David Burney, and accessed into the collections of the Département de Paléontologie et Anthropologie Biologique, Université d'Antananarivo, Madagascar (UA). Fossils were extracted from breccia matrix using standard acetic acid preparation techniques (Toombs and Rixon, 1959; Grant, 1989; Leiggi and May, 1994; Lindsay, 1995).

Species Identification

The osteological terminology and measurements used herein follow Hershkovitz (1971), Sigé *et al.*

TABLE 1. Age determinations based on U-series analysis for breccia samples collected from Anjohibe Cave

Provenance	Material	Dating method	Age estimate	Lat/Long /Elevation	Comments	Source
NCC-1 #3	Speleothem	U-series	69.6 ± 7.3 kyr BP	15°32.55'S 46°53.17'E 100 m	Directly below bone breccia in collapsed-cave deposit	Burney *et al.* (2004)
NCC-1 #4	Speleothem	U-series	86.8 ± 7.8 kyr BP	15°32.55'S 46°53.17'E 100 m	Laminated stalagmite on floor of collapsed-cave feature	Burney *et al.* (2004)
OLD SE	Speleothem	U-series[1]	≤ 10,000 kyr BP	–	Collapsed cave region	D. A. Burney, pers. comm., 2001
TW-10	Speleothem	U-series[1]	≤ 10,000 kyr BP	–	Collapsed cave region	D. A. Burney, pers. comm., 2001
SS2	Surface block	U-series[2]	> ? kyr	15°32.39'S 46°53.09'E 222 m	Collected near cave entrance	D. A. Burney, pers. comm., 2001

(1982), Hand (1993, 1998), Freeman (1998), and Samonds (2006). A large comparative sample of photographs, epoxy dental casts, and measurements of modern Malagasy bats was collected to facilitate identification, focusing when possible on specimens collected from Anjohibe Cave (Samonds, 2006). In addition, collections of non-Malagasy bats were photographed and measured to aid in interpreting material that did not match modern taxa known from the island. Measurements were made with 500-172 Mitutoyo digital calipers to 0.01 mm, or with an MA285 Meihi Techno optical reticule X, 1/100 (0.01 mm).

Quantitative Methods

When sample sizes were adequate, discriminant function analysis was used to examine potential group differences and degrees of group overlap. This analysis (SPSS 11.0) includes a multivariate analysis of variance to test for significant differences among designated groups (e.g., Wilks' lambda for the overall analysis as well as subsets of the discriminant axes). The percentage variance explained by each axis is reported, and classification results pinpoint any individual 'misclassified' to another group. When sample

sizes were judged too small, including cases where there was only one specimen in a group, one-sample t-tests were enlisted to evaluate 'group' differences, or whether or not the sample value belonged to the larger, given 'population'.

Anjohibe Cave Breccia Localities

OLD SE Locality

The OLD SE samples were collected 13 August 1996 from a collapsed area that blocked a long, dead-end passage extending southeastward from one of the cave's largest caverns (Fig. 1). Dating indicates that the four samples collected were approximately 10,000 years old or younger (D. A. Burney, pers. comm., 2003; see Table 1).

TW-10 Locality

Breccia samples were recovered from the TW-10 locality, approximately 60 m north of Entrance V1 (de Saint-Ours and Paulian, 1953), and located on the southeast side of the subterranean river (Fig. 1). Dating indicates that these samples were approximately 10,000 years old or younger (D. A. Burney, pers. comm., 2003; see Table 1).
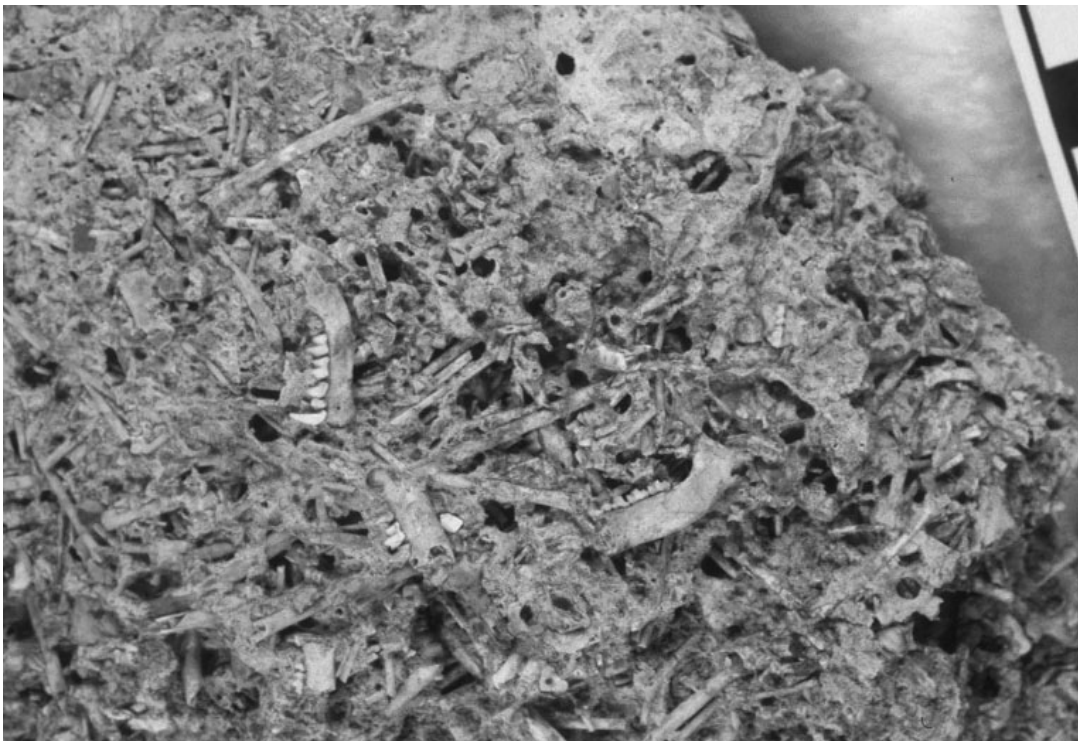

FIG. 2. Anjohibe Cave breccia sample TW-10, illustrating density of bones and teeth

NCC-1 Locality

The breccia samples from NCC-1 were collected from deep within Anjohibe Cave in an open-air fissure (Fig. 1). Dating indicates that NCC-1 is the oldest of the dated bone breccias estimated as 69,600 to 86,800 years old (Burney *et al.*, 2004; Table 1).

SS2 Locality

Unlike the other three samples, which were excavated from the cave interior, the SS2 sample was collected from the surface, near the main cave entrance (Fig. 1). Dating attempts revealed that this sample was contaminated by detrital thorium, not meeting the 'closed system' required for successful U-series dating (Table 1).

Abbreviations Used in Text

Institutions

AMNH — American Museum of Natural History, New York; FMNH — Field Museum of Natural History, Chicago; MCZ — Museum of Comparative Zoology, Harvard University, Cambridge; MNHN — Muséum National d'Histoire Naturelle, Paris; ROM — Royal Ontario Museum, Toronto; UA — Département de Paléontologie et Anthropologie Biologique, Université d'Antananarivo, Antananarivo; USNM — Smithsonian Institution, National Museum of Natural History, Washington, D.C.

Morphometrics

MD = mesiodistal; BL = buccolingual; HT = height.

SYSTEMATIC PALEONTOLOGY

Locality: OLD SE

Order Chiroptera Blumenbach 1779
Family Pteropodidae Gray 1821
Genus *Eidolon* Rafinesque 1815

Included Species and Distribution

The genus *Eidolon* contains two recognized species: *E. helvum* Kerr, 1792 and *E. dupreanum* Pollen, 1866. *Eidolon helvum* is presently distributed from Senegal to Ethiopia and to South Africa, southwestern Arabia and Oman, and islands in the Gulf of Guinea and off east Africa (Simmons, 2005). The species *E. dupreanum* is endemic to Madagascar (Peterson *et al.*, 1995).

Eidolon dupreanum (Schlegel 1867)

Referred Specimens

Two left distal humeri (UA 8995, 8996), two right proximal radii (UA 8997, 8998), sub-adult left maxilla with C^1 and P^3 in crypts (UA 8999), isolated left P^4, upper incisor, and P_3, and right C_1, P_2, and P^4 (UA 9000–9005), partial posterior braincase (UA 9006), right scaphocentralolunate (UA 9007), left partial scapula (UA 9008).

Description

Both left distal humeri (UA 8995, 8996) possess a short trochlea, a capitulum with a relatively low and domed central surface and a short, squared off lateral surface, and a broad but low epitrochlea with a superior surface not exceeding the height of the trochlea. Both right proximal radii (UA 8997–8998) possess broad expanded tips with shallow excavations for articulation with the humerus. The lateral edges contain deep lips that wrap a short distance anteriorly and posteriorly, and the medial edges possess thin shelves.

The immature jaw (UA 8999) consists of the anterior portion of a left maxilla with alveoli for C^1, P^2, P^3 and P^4. The upper canine remains within the crypt and is partially erupted, P^2 is missing, the crown of P^3 can be seen partially formed within the crypt but has not yet passed the alveolar surface, and P^4 is missing, with the posterior edge of the crypt broken.

A number of other possibly associated teeth of this skull were also recovered, including a left P^4, upper incisor, and P_3, and a right C_1, P_2, and P^4 (UA 9000–9005). P^4 (UA 9000, UA 9005) has a medial and lateral ridge, with a shallow excavation between. The anterior aspect of the cusp has a slight elaboration of the protocone, and

a lower but well-formed paracone. There is a thin ridge connecting the two cusps mediolaterally, and the posterior aspect of the crown is open between the medial and lateral ridges. The left upper incisor (UA 9001) contains a single cusp terminating at a blunt point. P_3 (UA 9004) has a tall, blunt cusp anteriorly, with a small posterior shelf, and a strong excavation on the posterior aspect of the cusp. C_1 (UA 9002) is tall with a wide base, and possesses a thin groove on its anterior surface. P_2 (UA 9003) has a short, wide crown with a single cusp on the anterolateral aspect. Only UA 9001 and 9002 have any root formation; the remaining teeth possess crowns with no roots.

The partial posterior braincase (UA 9006) consists of the parietal and occipital regions. UA 9006 has a poorly defined sagittal crest and relatively well-developed lambdoidal crest with posteriorly deflected and thin paraoccipital processes. The braincase is superior-inferiorly compressed, and the foramen magnum is ovoid with elongated and well-developed occipital condyles.

The right scaphocentralolunate (UA 9007) is large, with a broad and flat proximal articular surface for its articulation with the radius. The lateral distal surface contains a large fossa for the trapezium, and the medial aspect tapers to a narrow point. The partial left scapula (UA 9008) contains a narrow, shallow glenoid fossa, a short, robust acromial process, and a relatively longer and more slender coracoid process.

Comparison

The three pteropodid bats presently inhabiting Madagascar are of dramatically different body size; from largest to smallest these are: *Pteropus rufus* (500–750 g), *E. dupreanum* (235–346 g), and *Rousettus madagascariensis* (35–84 g) (Peterson *et al*., 1995; Russ *et al*., 2001). The distal humeral widths of UA 8995 and 8996 (13.70 and 13.47 mm, respectively) place them near but outside the observed values of the modern Malagasy *E. dupreanum* ($n = 4$, $\bar{x} = 12.73$ mm, SD = 0.36). One-sample *t*-tests suggest that both of these measurements are significantly larger than in modern populations ($P = 0.012$ and 0.025, respectively). However, extant male *E. dupreanum* are about 10% larger than females (MacKinnon *et al*., 2003) and, given that none of the measured museum specimens were of known sex determination, the possibility exists that this discrepancy in size between fossil and modern specimens reflects differences in size dimorphism. Based on this information, and the morphology of these elements, both are referred to *E. dupreanum*.

The proximal radii UA 8997 and 8998 are also referable to the family Pteropodidae based on their large size. The maximum proximal radius width of UA 8997 and 8998 (7.73 mm and 7.80 mm, respectively) places them within observed values of modern Malagasy *E. dupreanum* ($n = 4$, $\bar{x} = 7.86$ mm, SD = 0.378). One-sample *t*-tests suggest that neither of these specimens are significantly different from modern populations ($P = 0.54$ and 0.77, respectively).

UA 8999 is referred to Pteropodidae based on the simple morphology and size of the teeth, as pteropodid teeth are highly modified for frugivory and nectarivory (Bergmans, 1990), and frequently peg-shaped with little or no elaboration of the crown. As the isolated teeth (UA 9000–9005) are unworn, their size and morphology can be closely matched to those of modern Malagasy *E. dupreanum*. The presence of this subadult in the deposits could indicate that the cave was used as a nursery colony for this taxon. Detailed comparisons of maximum neurocranial breadth and height are impossible due to the fragmentary nature of specimen UA

9006, but the broad shape and relatively large size of the partial braincase allows for identification of UA 9006 as *E. dupreanum*.

While the morphology and articular relationships of the scaphocentralolunate are similar in all bats (Stafford and Thorington, 1998), UA 9007 is identified as pteropodid based on its extremely large size. Detailed statistical comparisons were not possible due to the lack of comparative museum specimens, as bat postcrania (specifically isolated wrist and ankle bones) are extremely rare. However, the length of this element (10.45 mm) appears to fall most appropriately within the size range of the medium-sized Malagasy fruitbat *E. dupreanum*, because *P. rufus* has a substantially larger scaphocentralolunate (14.25 mm, *n* = 2) and *R. madagascariensis* has a much smaller body size.

The relatively simple morphology and large size of the scapula UA 9008, in addition to the glenoid size (height = 7.29 mm, breadth 4.40 mm) places it within the observed values of *E. dupreanum* (mean height = 7.11 mm, SD = 0.36; mean breadth = 4.25 mm, SD = 0.32, in both cases *n* = 4). One-sample *t*-tests suggest that both of these measurements are not significant from modern populations (P = 0.40 and 0.43, respectively).

Family Hipposideridae Lydekker 1891

Genus *Hipposideros* Gray 1831

Included Species and Distribution

Hipposideros is a widely distributed genus that occurs throughout the Old World tropics. The species *H. commersoni* is endemic to Madagascar (Simmons, 2005). Subfossil *H. commersoni* have previously been reported from the younger deposits of Anjohibe Cave (Burney *et al*., 1997) and from the Lake Tsimanampetsotsa region in the southwest (Sabatier and Legendre, 1985; MacPhee, 1986).

Hipposideros sp. cf. *H. commersoni*

Referred Specimens
Left P^4.

Description

UA 9009 consists of a left P^4 possessing one main cusp anteriorly and a smaller posterior shelf. There is no anterolingual cusp present, as in the case of several species of *Hipposideros*. The hypoconal basin is shallow. There is a low but distinct cingular heel and a basal cingulum surrounds the majority of the crown. The anterior aspect of the main cusp is convex anteriorly.

Comparison

The morphology of UA 9009 most closely resembles that of members of the family Hipposideridae, which possess a P^4 that is generally tall with a well-developed principal cusp, well-formed posterior shelf, and shallow hypoconal basin. Within the two genera of Hipposideridae presently on Madagascar, this tooth most closely matches those of *Hipposideros*; representatives of the other genus, *Triaenops*, are significantly smaller. Further support for this designation is the fact that *H. commersoni* is the only extant Malagasy non-pteropodid bat species comparable in size. The only other bat on Madagascar approaching the large size of *H. commersoni* is *Mops midas* (45 g — Fenton and Rautenbach, 1986), but this molossid species has a P^4 with a more flattened anterior face, stronger lingual cingulum, and taller main anterior cusp.

Although similar in overall tooth morphology, a one-sample *t*-test suggests that UA 9009 is significantly different from modern *H. commersoni*, exhibiting larger dimensions for mesiodistal length, buccolingual breadth, and height, and

subfossil *H. besaoka* sp. nov. (Table 2; see Locality: *TW-10, below*). Its P^4 also lacks an anterolingual cusp (present in both extant *H. commersoni* and *H. besaoka*). Based on the data presented here, UA 9009 is referred to *Hipposideros* sp. cf. *H. commersoni*, and considered distinct from both taxa.

Genus *Triaenops* Dobson 1871

Included Species and Distribution

Species of *Triaenops* are widespread throughout eastern Africa, Madagascar, the coast of the Arabian Peninsula, and Aldabra Island. This genus is presently divided into five species, with three of them endemic to Madagascar (*T. auritus*, *T. furculus*, and *T. rufus*), one endemic to the Aldabra Island (*Triaenops* nov. sp.), and one known only from Africa and parts of the Middle East (*T. persicus* — Simmons, 2005; Ranivo and Goodman, 2006; Goodman and Ranivo, In press).

Triaenops goodmani sp. nov.
(Fig. 3A–D)

Etymology

Specific name for Dr Steven M. Goodman, in recognition of his significant contributions to the field of modern Malagasy bat research.

Type Specimen

Partial left dentary with P_4M_{1-2} (UA 9010; Fig. 3A–B).

Referred Specimens

Partial left dentary with M_{2-3} (UA 9011; Fig. 3C); partial right dentary with M_{2-3} (UA 9012; Fig. 3D).

Diagnosis

Larger than any known species of *Triaenops*. Molar crowns narrow, with protoconid and hypoconid more rounded labially than seen in modern *Triaenops* species. M_2 molar dimensions significantly longer than in *T. auritus*, *T. rufus*, and *T. furculus* ($P < 0.001$). Protoconid only slightly taller than hypoconid; in *T. auritus*, *T. rufus*, and *T. furculus*, the protoconid is noticeably taller than the hypoconid. Relative height of paraconid, entoconid, and metaconid all shorter than in *T. auritus*, but similar to condition in *T. rufus* and *T. furculus*. Molars lacking well developed preentocristid between metaconid and entoconid. Talonid noticeably wider than talonid. Molars containing small, labially expanded anterior and posterior cingula, and M_2 containing small lingually expanded shelf between protoconid and hypoconid.

Description

UA 9010 (Fig. 3A, B) is a partial left dentary containing P_4M_{1-2}. It is relatively complete anteriorly, with alveoli for P_2 and the lateral incisor, but is broken posteriorly. P_4 is approximately the height of the tallest cusp (paracone) of M_1, or only slightly higher. The morphology is caniniform with one very tall median cusp lacking a mesial and buccal shelf. M_1 is unworn, and has

TABLE 2. One-sample *t*-test results (2-tailed) for single *Hipposideros* P^4 from OLD SE (UA 9009), compared to extant *H. commersoni* and subfossil *H. besaoka* from Anjohibe Cave (TW-10). Probability level: *** — $P < 0.001$

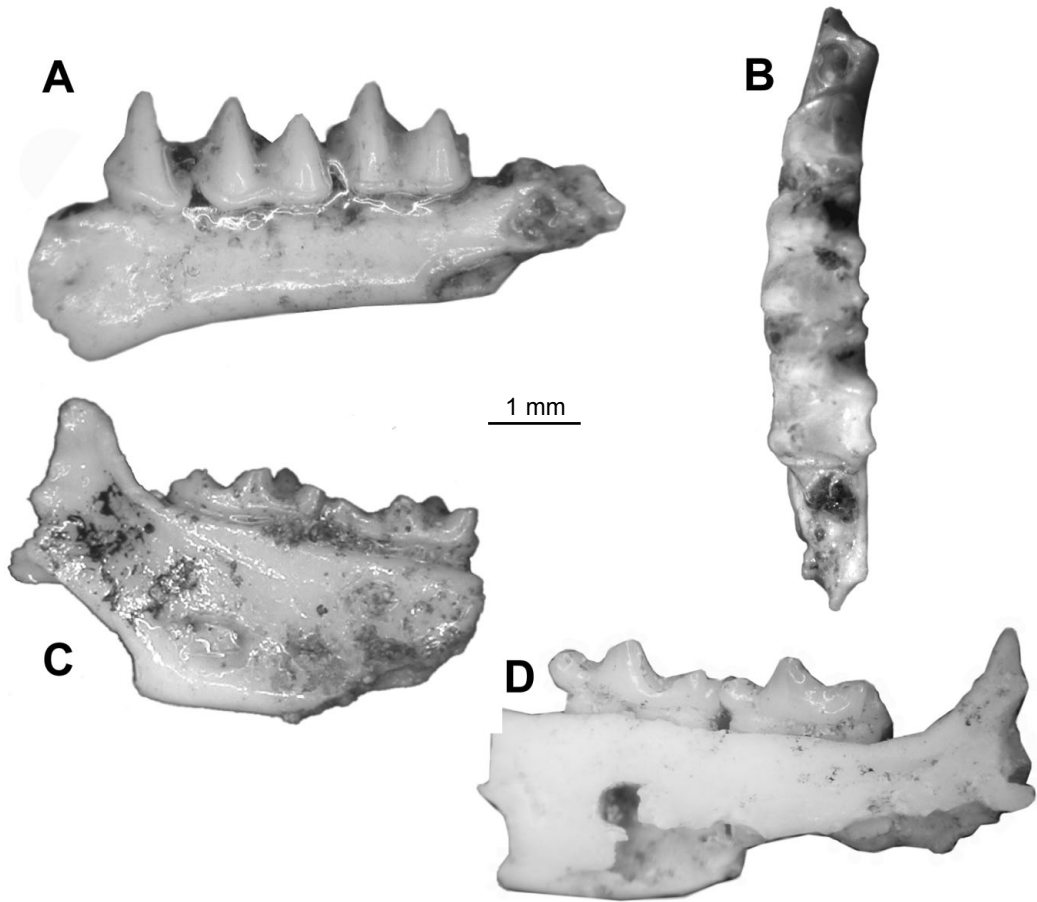| Character	UA 9009	vs. *H. commersoni*				vs. *H. besaoka*			
		n	$\bar{x}$	SD	*t*-test	*n*	$\bar{x}$	SD	*t*-test
MD length of P^4	2.12	40	1.99	0.145	-5.31***	31	2.13	0.104	0.57
BL length of P^4	2.40	40	2.14	0.132	-12.33***	31	2.52	0.168	3.97***
HT P^4	2.35	37	2.15	0.137	-8.79***	27	2.18	0.152	-5.73***

FIG. 3. Specimens of *T. goodmani* sp. nov. from OLD SE. A — UA 9010, labial view of type specimen of *T. goodmani* sp. nov. partial left dentary with P_4M_{1-2}; B — UA 9010, occlusal view; C — UA 9011, lingual view of *T. goodmani* sp. nov. partial left dentary with $M_{2,3}$; D — UA 9012, lingual view of *T. goodmani* sp. nov. partial right dentary with $M_{2,3}$

a tall trigonid and only slightly lower talonid. The protoconid is the tallest cusp, and there is a well-developed but only slightly shorter hypoconid. The paraconid and entoconid are shorter than the hypoconid, but approximate each other in height, while the metaconid is slightly lower. The hypoconulid is the lowest cusp; it is noticeable but small. There is a distinct gap between the entoconid and hypoconulid, and no distinct ridge uniting the metaconid and entoconid. M_1 possesses a talonid wider than the trigonid. M_2 is comparable in morphology and size to M_1, but contains a talonid only slightly wider than the trigonid.

UA 9011 is a partial left dentary (Fig. 3C) broken anterior to M_2, but containing both M_2 and M_3, both of which are relatively worn. UA 9011 has a complete ascending ramus and a relatively deep mandibular corpus. The morphology of M_2 is the same as that seen in UA 9010. M_3 also mirrors the overall morphology of the other molars, but is slightly smaller, and has no space between the entoconid and hypoconulid. There is a weak ridge between the metaconid and entoconid, which is deflected slightly labially; in both M_1 and M_2 this angle is more parallel to the toothrow. M_3 possesses a trigonid and talonid of equal width.

UA 9012 is a partial right dentary containing M_2 and M_3 (Fig. 3D), and consists of a partial ascending ramus with a relatively shallow mandibular corpus. M_2 and M_3 are worn, but share the morphology described for UA 9011 and UA 9010.

Comparison

All three lower jaws (UA 9010–9012) share the specialized insectivorous bat molar morphology of high cusped teeth and relatively robust mandibles (Freeman, 1998). The size and molar morphology of UA 9010–9012 most closely match those of *Triaenops* species. *Triaenops* is characterized by having a P_4 with a single main cusp anteriorly with its mesial aspect in line with the mesial edge of the tooth. M_1 and M_2 possess a trigonid with tall and well-developed protoconid, paraconid, and metaconid, and a lower talonid posteriorly with a well-developed hypoconid buccally and a small entoconid and hypoconulid lingually with a distinct gap between. M_3 is shorter in length and possessing a short ridge between the metaconid and entoconid, deflected slightly labially.

Discriminant function analyses of cranial and dental measurements of modern *Triaenops* species suggest suggests that dental measurements provide the best separation between extant members of this genus (Samonds, 2006). When M_2 (the common tooth to UA 9010–9012) was compared to each of the modern species using one-sample *t*-tests, in all cases, subfossil *T. goodmani* were significantly larger in mesiodistal dimensions than the three extant species (Table 3). UA 9010 and 9011 were significantly different in buccolingual width from both *T. auritus* and *T. rufus*, but not from *T. furculus*, although UA 9012 was ($P = 0.001$). In a bivariate plot of M_2 measurements, *T. goodmani* cluster in the upper portion of the range of *T. furculus* and *T. rufus*, with slightly longer molar dimensions (Fig. 4); *T. furculus* and *T. rufus* use Anjohibe Cave region today as a day roost site (Goodman *et al*., 2005*b*). However, while subfossil *Triaenops* specimens fall outside the modern range for mesiodistal M_2 dimensions, all three fall within the modern range of measurements for buccolingual dimensions (Fig. 4).

Previous analyses have suggested that *T. rufus* is closely allied with *T. persicus*, and that *T. auritus* and *T. furculus* are distinct from each other but closely related (Peterson *et al*., 1995; Ranivo and Goodman, 2006). Recent genetic analyses also support these conclusions (Russell *et al*., 2007).

TABLE 3. One-sample *t*-test results for three specimens of *T. goodmani* from OLD SE (MD length and BL length of M_2, respectively) compared to extant Malagasy species of *Triaenops*. Mean ± SD, and sample size (*n*) are also shown. Probability level: * — $P < 0.05$, *** — $P < 0.001$

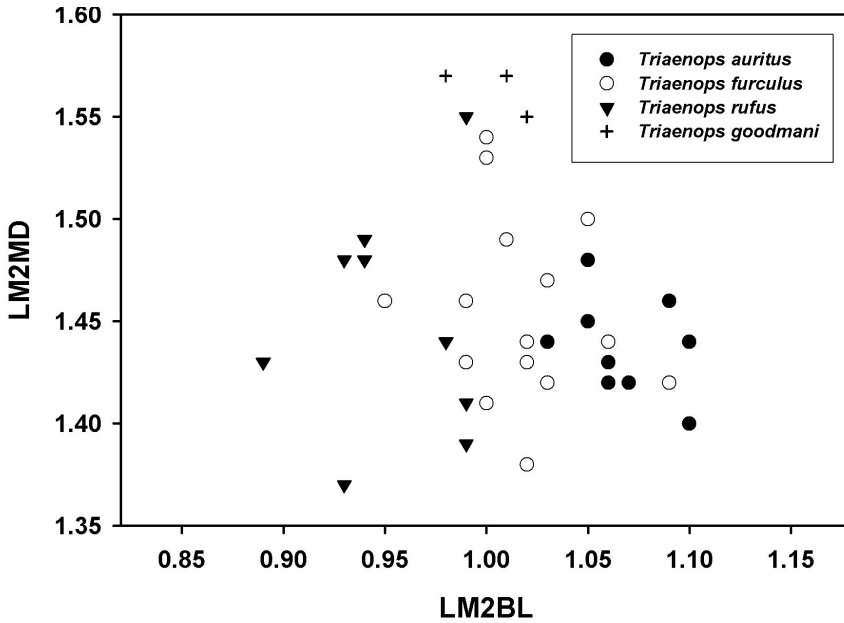| *T. goodmani*	*T. auritus*	*T. furculus*	*T. rufus*
	MD length of M_2		
	1.99 ± 0.145 (40)	2.13 ± 0.104 (31)	1.45 ± 0.055 (10)
UA 9011: 1.57	16.62***	9.96***	-6.75***
UA 9010: 1.55	14.11***	8.23***	-5.60***
UA 9012: 1.57	16.62***	9.96***	-6.75***
	BL length of M_2		
	2.14 ± 0.132 (40)	2.52 ± 0.168 (31)	0.95 ± 0.034 (10)
UA 9011: 1.01	7.11***	0.85	-5.41***
UA 9010: 1.02	5.88***	0.31	-6.34***
UA 9012: 0.98	10.81***	4.35***	-2.61*

FIG. 4. Bivariate plot for mesiodistal and buccolingual dimensions of M_2 for three extant Malagasy species of *Triaenops* (*T. auritus*, *T. furculus*, and *T. rufus*) and subfossil *T. goodmani* sp. nov. from OLD SE

Triaenops sp.

Referred Specimens

Left distal humerus (UA 9200).

Description

UA 9200 is the distal half of a left humerus possessing a well-developed trochlea and short broad epitrochlea. The central surface of the capitulum is displayed laterally with the lateral surface of the capitulum approximately the same size as the central portion, with a slight rounded expansion of its inferior aspect.

Comparison

The distal humeral width (3.58 mm) falls within the range of that observed for the genus *Triaenops*. While the detailed morphology of the distal aspect of UA 9200 most closely matches that of *T. rufus*, the size difference between *T. rufus* and *T. goodmani* is small, and this specimen could represent either species.

Locality: TW-10

Family Hipposideridae Lydekker 1891
Genus *Hipposideros* Gray 1831

Hipposideros besaoka sp. nov.
(Figs. 5A–C, 6A–D)

Etymology

The word *besaoka* (bay-SOH-ka) is derived from the Malagasy and means 'big chin'.

Type Specimen

Right maxilla with $CP^{2,4}M^{1-3}$ (UA 9478; Fig. 5A).

Diagnosis

Larger and more robust than *Hipposideros commersoni*; similar to *H. commersoni* in possessing a great range of mandibular corpus depths and thickness (Figs. 5B and 6C–D). Upper molars significantly broader, relative to length, than *H. commersoni* (Figs. 5A and 6B).
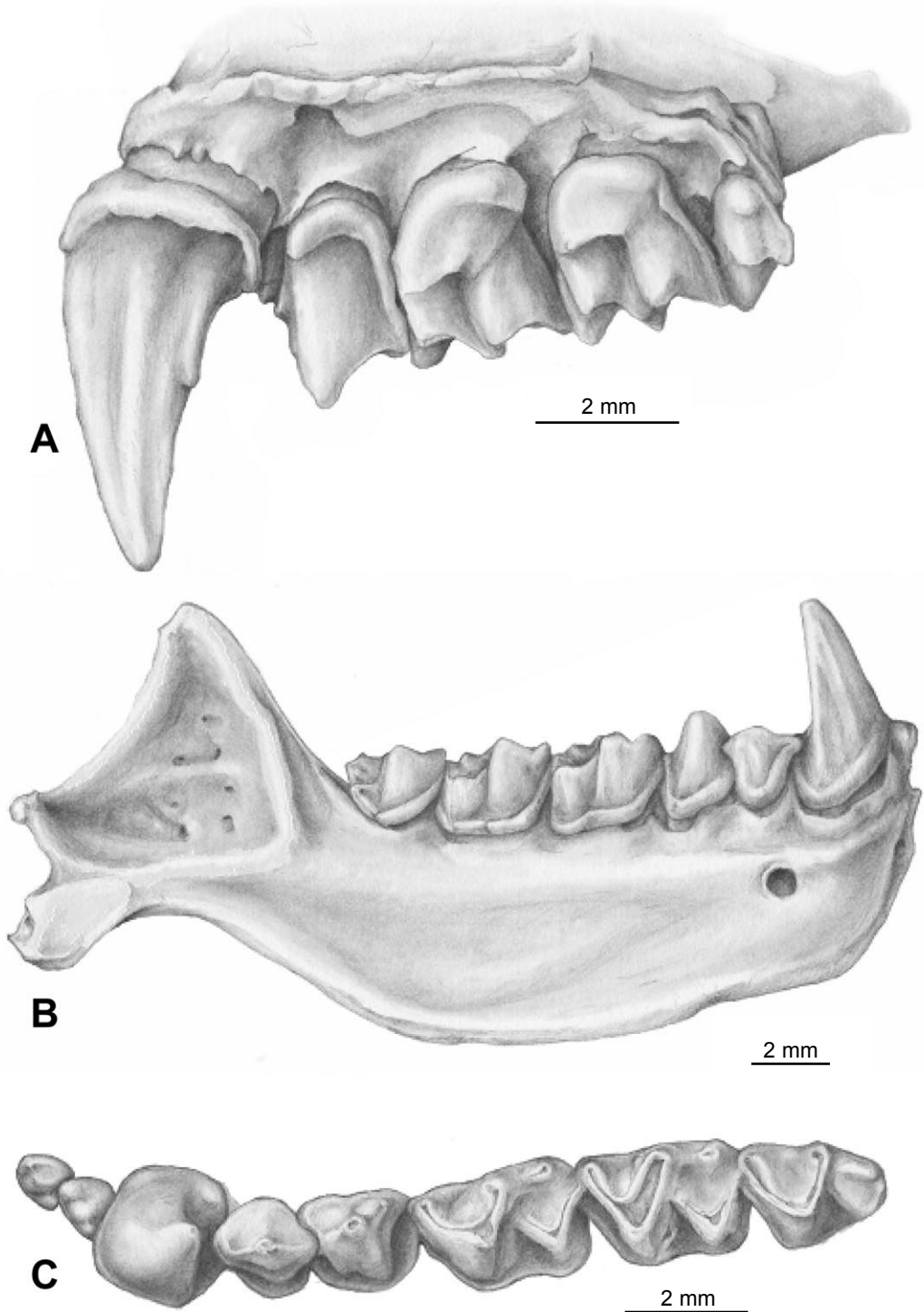
K. E. Samonds

FIG. 5. *Hipposideros besaoka* sp. nov. from TW-10, Anjohibe Cave, Madagascar. A — UA 9478, lingual view of type specimen, right maxilla with $CP^{2,4}M^{1-3}$ (P^2 out of view); B — UA 9320, labial view of right dentary with $I_{1-2}CP_{2,4}M_{1-3}$; C — UA 9552, occlusal view of left dentary with $I_{1-2}CP_{2,4}M_{1-3}$

Referred Specimens

Twenty-six upper right maxillae (UA 9284–9301, 9478, 9504–9511; Fig. 5A), 27 upper left maxillae (UA 9269–9283, 9512–9523; Fig. 6A–B), 78 left dentaries (UA 9232–9268, 9302–9319, 9330–9345, 9497–9503, 9552; Fig. 6C–D), 40 right dentaries (UA 9218–9231, 9320–9329, 9481–9496; Fig. 5B), 42 left and right premaxillae (UA 9346–9387), 26 isolated upper incisors (UA 9525, 9480 [lot of 25]), 118 isolated lower incisors (UA 9526, 9479 [lot of 117]), 41 upper left canines (UA 9398–9404, 9437–9470), 43 upper right canines (UA 9527, 9388–9397, 9405–9436), 26 lower left canines (UA 9528 [lot of 26]), 25 lower right canines (UA 9530, 9529 [lot of 24]), 22 left P_2 (UA 9531, 9472 [lot of 17], 9550 [lot of 4]), 26 right P_2 (UA 9551, 9471 [lot of 25]), 2 right P^4 (UA 9532, 9548), 4 left P^4 (UA 9537, 9473, 9547 [lot of 2]), 1 right P_4 (UA 9539), 3 left P_4 (UA 9538, 9549 [lot of 2]), 7 right M^1 (UA 9543 [lot of 7]), 7 left M^1 (UA 9474, 9545 [lot of 6]), 8 right M^2 (UA 9476, 9477, 9544 [lot of 6]), 7 left M^2 (UA 9475, 9546 [lot of 6]), 1 right M^3 (UA 9533), 3 left M^3 (UA 9534 [lot of 3]), 18 right M_{1-2} (UA 9541 [lot of 18]); 13 left M_{1-2} (UA 9536 [lot of 4], 9542 [lot of 9]), 8 right M_3 (UA 9540 [lot of 8]), 6 left M_3 (UA 9535 [lot of 6]).

Description

The premaxillae rami were frequently fused at the midline; these elements were never found in association with skulls. The posterior margin of the premaxilla is narrowed to a thin point and flares gently anteriorly. The anterior margin tapers to a V-shape posteriorly between the incisors, which are located at the anteriormost edge near the tip of each anterolateral projection. The ventral surface is concave longitudinally. Each premaxilla has a large anterior palatal foramen. The line of contact between premaxillae is thin with no crest on the dorsal surface. Each premaxilla houses a single incisor, which is directed anteroventrally. Upper incisors are reduced and weakly bilobed, with small flat crowns and thin roots that project minimally above the alveolar line.

The maxillae (Figs. 5A and 6A–B) are frequently well preserved, although many contain worn teeth. Maxillae possess upper canines with one long principal cusp and a small posterior shelf approximately halfway up the posterior aspect of the tooth, extremely reduced anterior upper premolar (P^2) wedged between the upper canine and P^4, and a wide P^4 with a tall anterior cusp, lower posterior shelf, and a well-defined anterolingual cusp. M^1 has a closed protofossa with weak dihedral crest and a posteriorly deflected but low cingular heel. M^2 is comparable to M^1 but is squarer and slightly smaller, with a less developed and posteriorly deflected heel. M^3 has an extremely reduced W-pattern, where the premetacrista is less than 1/3 the length of the preparacrista, and is significantly smaller (about $^1/_2$) than in both M^1 and M^2.

Lower jaws (Figs. 5B and 6C–D) show a large range of corpus depth and thickness, with some extremely thin and shallow (UA 9244; Fig. 6C), and others robust and deep (UA 9338; Fig. 6D). The dentary contains two small, anteroposteriorly compressed lower tricuspid incisors of approximately the same size. The lower canine has a single tall and narrow cusp. P_2 is large and moderately wide with a large main cusp connected by steep crests to the anterior and posterior edges of the crown, and a smaller cusp posterior to the main cusp within the posterior crest. P_4 has two distinct roots, one tall median cusp, a tiny anterolingual cusp, and a small but well-developed posterolingual cusp. The posterior ridge descending from the main cusp consists of two parts; the first descending

weakly and the second turning more sharply inferiorly towards the posterolingual cusp.

M_1 is large, with a high trigonid and relatively low talonid basin (Fig. 5C). The protoconid is very tall and well-developed, the metaconid is slightly lower, and the paraconid approximates the height of the metaconid or surpasses it slightly. The
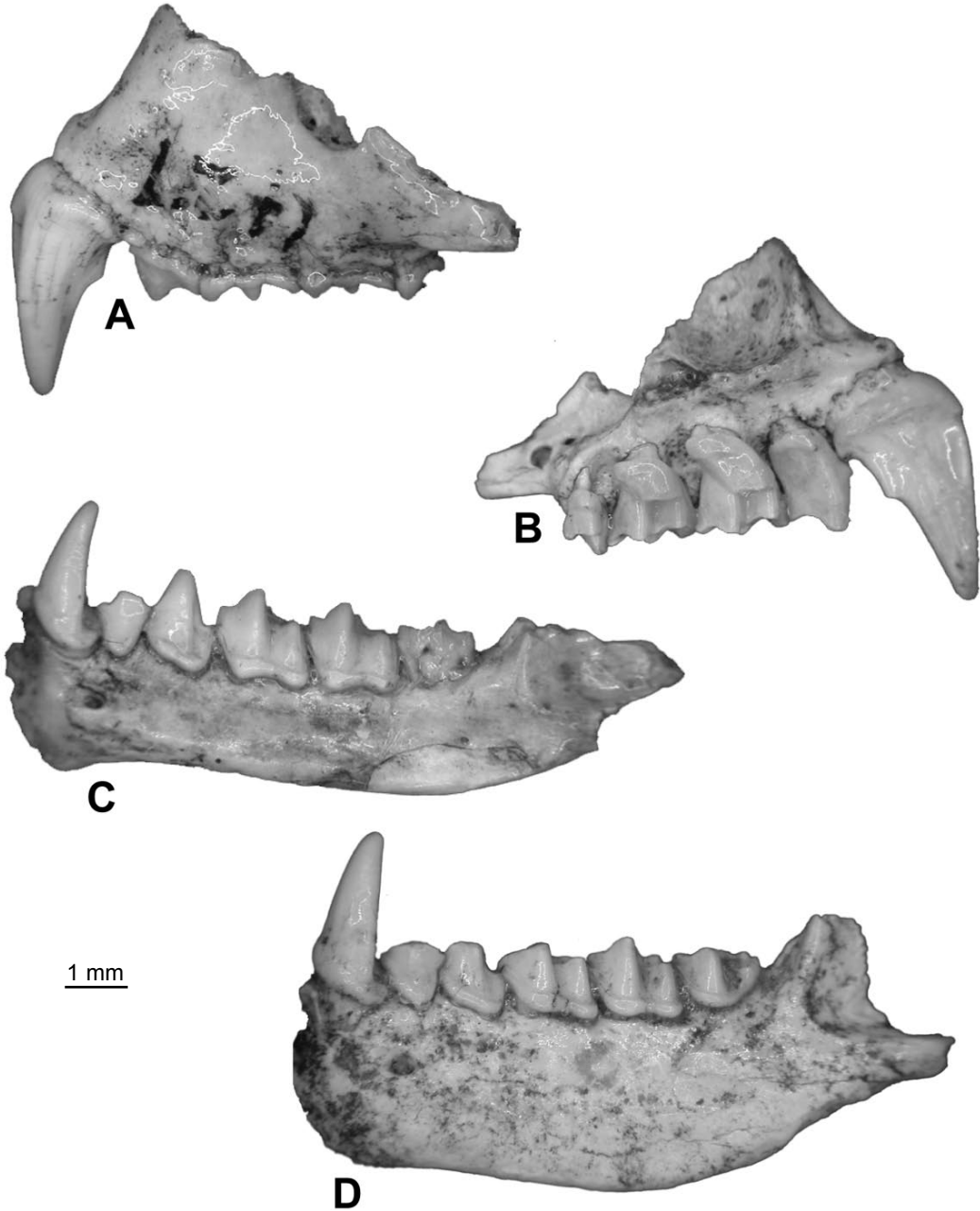

FIG. 6. Specimens of *H. besaoka* sp. nov. from TW-10, Anjohibe Cave, Madagascar. A — UA 9272, labial view of left maxilla with $CP^{2,4}M^{1-3}$; B — UA 9272, lingual view of left maxilla with $CP^{2,4}M^{1-3}$; C — UA 9244, labial view of left dentary with $CP_{2,4}M_{1-2}$ and partial M_3; D — UA 9338, labial view of left dentary with $CP_{2,4}M_{1-3}$ illustrating depth of mandibular corpus

hypoconid is quite low. Both the anterior and posterior cingula are weak, and the protoconid and hypoconid are at approximately the same distance from the midline of the tooth. The morphology of M_2 mirrors that of M_1, and the size is comparable, or only slightly smaller. The angle made by the pre- and postprotocristid is conspicuously narrower in M_2 and M^3 than in M_1. M_3 is much shorter than M_1 and M_2 in mesiodistal length, and has a greatly reduced talonid. The ridge between the metaconid and entoconid is well developed but its posterior margin is flexed laterally; the hypocristid is completely absent.

Comparison

For complete dentitions, the specimens considered here are immediately referable to *Hipposideros* based in part on the dental formula 1/2 1/1 2/2 3/3, the small upper premolar shifted laterally relative to the rest of the toothrow (such that the canine and second upper premolar are in contact or nearly so), and the distinctive morphology of P_2, being large and possessing a steeply sloped and broad buccal surface (Hand and Kirsch, 1998, 2003). A Discriminant Function Analysis of the *Hipposideros* fossils from TW-10 indicates that the subfossil sample is significantly different than modern *H. commersoni* (Fig. 7); *H. besaoka* upper molars are significantly broader (e.g., buccolingual dimensions) than seen in modern *H. commersoni* (Fig. 8).

Subfossil *Hipposideros* mandibles also show a large range of mandibular corpus depth and thickness sizes significantly different from modern samples (Fig. 9). Overall, subfossil *Hipposideros* mandibles have a thicker and more robust mandibular corpus for their depth than modern *H. commersoni*, a morphology that, in molossid bats, has been correlated with specializations for hard-object feeding (Freeman, 1981).

To compare subfossil *Hipposideros* specimens from Anjohibe to modern populations on the island, it was important to address the issue of latitudinal clines. *Hipposideros commersoni* is broadly distributed throughout Madagascar, encompassing a wide range of habitats and temperature gradients. If modern groups display predictable relationships between size and latitude, the larger size of subfossil *Hipposideros* might, at least in part, be attributable to changes in climate, as has been previously demonstrated for bats elsewhere in the Old World tropics (Storz *et al.*, 2001).

Modern populations of *H. commersoni* from four distant regions of the island were compared to each other in an attempt to address this issue. These four regions were divided into operational taxonomic units (OTU's) based on geography including Analamerana, the northwest of the island (including Anjohibe Cave, Mampikony, and Ankarafantsika), Bemaraha, and Isalo (Fig. 10). Subpopulations of *H. commersoni* do demonstrate significant differences between sites, with the most northern (Analamerana) and the most southern (Isalo) showing the closest relationship, and the other two sites clustering discretely (Fig. 10).

Nevertheless, when six upper molar measurements available for the subfossil sample are examined, and other extralimital species of *Hipposideros* that were formerly considered subspecies of *H. commersoni* are included, *H. commersoni* specimens group closely together, with the subfossils and extralimital species grouping farther away (Fig. 11). This suggests that the morphological differences between the fossil specimens and extant Malagasy *H. commersoni* exceed the differences observed among the various extant *H. commersoni* populations within Madagascar.

Locality: NCC-1

Hipposideros commersoni
E. Geoffroy 1813

Referred Specimens

Isolated lower incisor (UA 9201), right M_3 (UA 9202).

Description

UA 9201 has a well-defined crown that is trilobed and anteroposteriorly compressed. The central lobe is the largest, with the mesial lobe slightly smaller and the distal lobe smallest. It contains a single root with a slight flare at its tip. UA 9202 is a M_3 consisting of a complete crown with no roots preserved. The protoconid is tall and well-developed, while the paraconid and metaconid are relatively low. There is a well-developed crest (preentocristid) linking the metaconid to the entoconid, which is roughly parallel to the protocristid. The trigonid is relatively wide. The talonid is extremely reduced to a small shelf containing a small hypoconid.
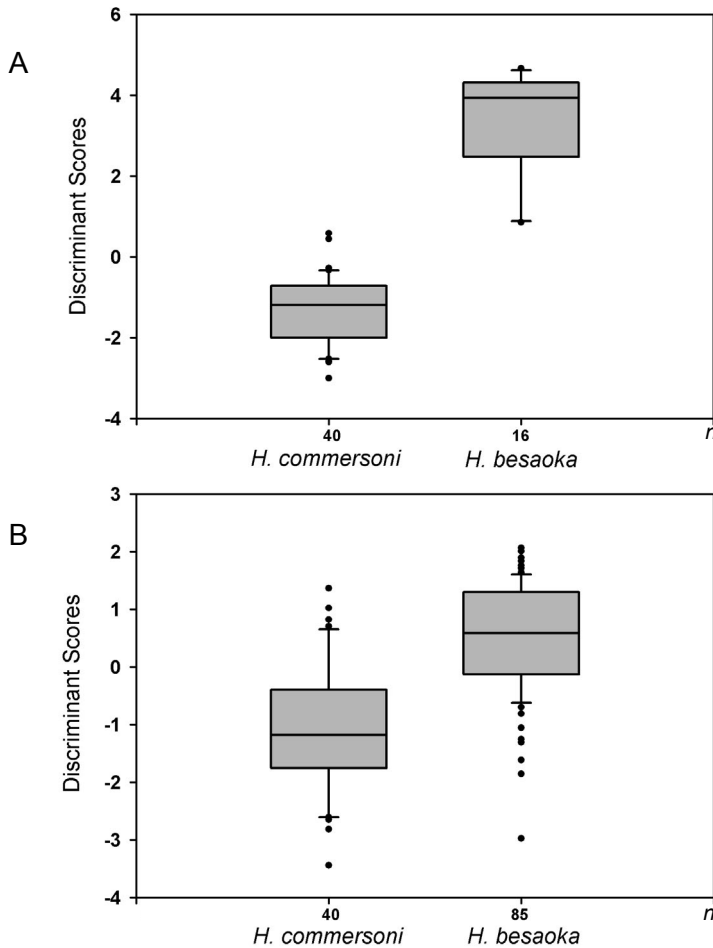
FIG. 7. Canonical discriminant function coefficients for *Hipposideros* from TW-10 and *H. commersoni*. A — upper molar measurements (M^1MD, M^1BL, M^2MD, M^2BL, M^3MD, M^3BL), Wilks' lamba = 0.18, Chi-square = 88.25, $P < 0.001$; B — lower molar measurements (M_1MD, M_1BL, M_2MD, M_2BL, M_3MD, M_3BL); Wilks' lamba = 0.64, Chi-square = 54.07, $P < 0.001$. Line represents median, all outliers included
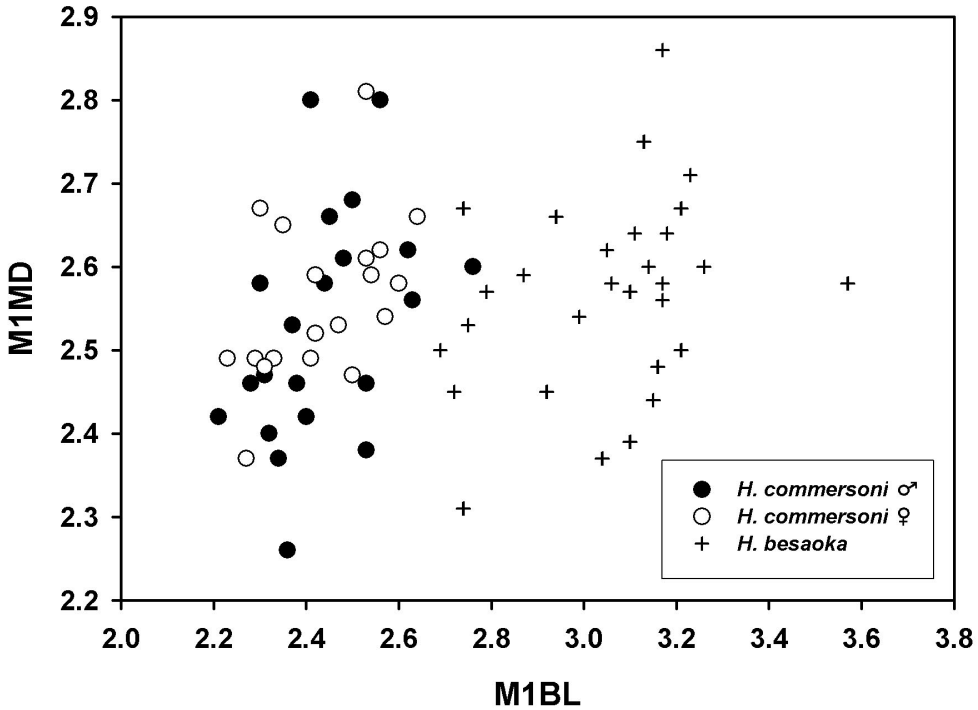
FIG. 8. Bivariate plot for mesiodistal and buccolingual M^1 molar dimensions for *Hipposideros commersoni* males and females, and subfossil *H. besaoka* from TW-10

Comparison

The morphology and size of UA 9201 matches that seen in the modern form of *Hipposideros commersoni*. UA 9202 shows the distinctive M_3 morphology associated with typical insectivorous bats, and is within the general size range of both the Malagasy *Hipposideros* and *Mops midas miarensis*. However, *M. m. miarensis* has a slightly different M_3 morphology, with a more anteroposteriorly compressed trigonid, and a preentocristid that does not parallel the protocristid, but rather forms a greater angle at its junction with the metaconid.

An analysis of UA 9202 indicates that it is not statistically distinct from modern *H. commersoni*, but is different from the referred material of *H. besaoka* described from locality TW-10 (Table 4). UA 9202 is therefore referred here to *H. commersoni*.

Triaenops sp.

Referred Specimens

Two left dentaries, one with P_4M_1 (UA 9203), and one with M_{1-2} and part of a broken M_3 (UA 9204).

Description

UA 9203 is a well-preserved left dentary with P_4M_1 intact. There is a small alveolus for P_2, but the jaw is broken anteriorly. The posterior portion of the jaw is broken, and the mandibular corpus depth is relatively shallow. A relatively large mental foramen is present in line with the anterior aspect of P_4. P_4 has a single tall median cusp, and is approximately the same height as the tallest cusp of M_1 (paracone). M_1 is unworn, and possesses a relatively tall trigonid. The paraconid, entoconid, and metaconid are approximately the same height. The hypoconulid is small, and there is a distinct gap
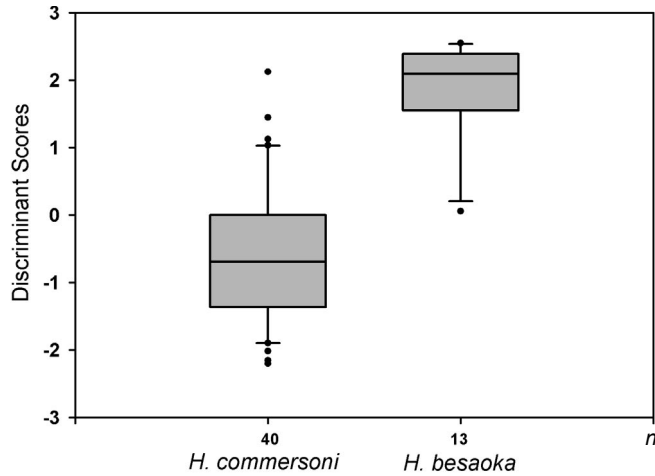
FIG. 9. Canonical discriminant function coefficients for *Hipposideros* from TW-10, measurements include corpus depth, corpus thickness, and ascending ramus height; Wilks' lamba = 0.62, Chi-square = 74.77, *P* < 0.001. Line represents median, all outliers included

between the entoconid and hypoconulid. M_1 also has a ridge between the metaconid and entoconid. UA 9204 is a left dentary with M_{1-2}, a broken M_3, and a shallow thin mandibular corpus. The M_1 morphology is identical to that described for UA 9203, and the morphology of M_2 mirrors that of M_1. M_3 is similar in morphology to the other molars, but is slightly smaller, and has no space between the entoconid and
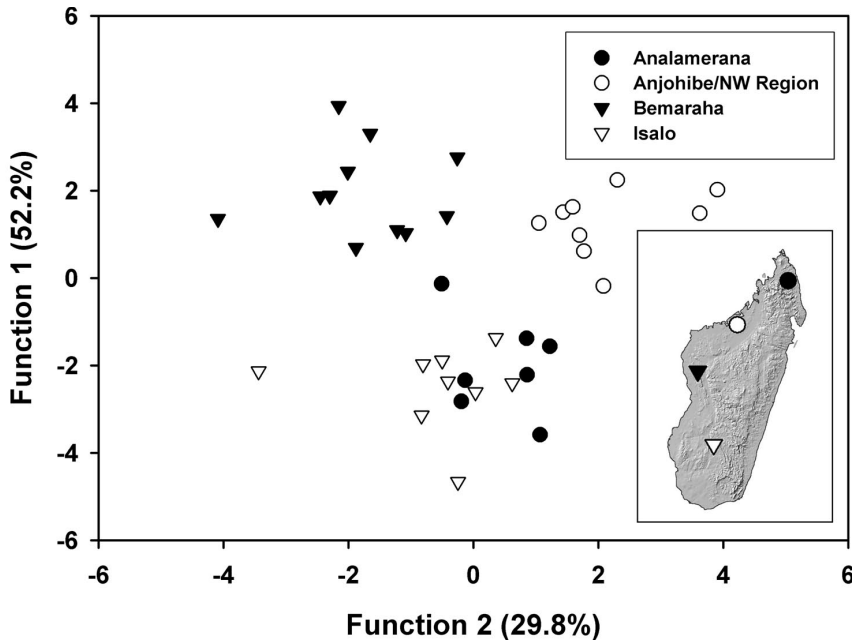
FIG. 10. Canonical discriminant function coefficients based on dental and mandibular measurements for four populations of Malagasy *H. commersoni* by site; % variance explained presented in parentheses. Measurements include mandible length, corpus depth, corpus thickness, ascending ramus height, P^4MD, P^4BL, M^1MD, M^1BL, M^2MD, M^2BL, M^3MD, M^3BL, P_4MD, P_4BL, M_1MD, M_1BL, M_2MD, M_2BL, M_3MD, M_3BL, and M_3HT
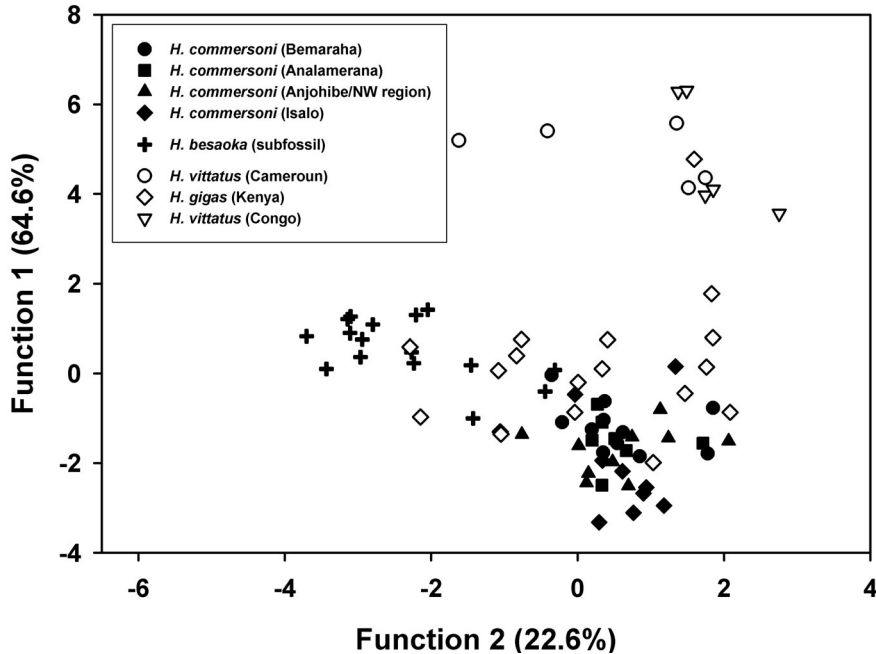
FIG. 11. Canonical discriminant function coefficients for seven extant species previously recognized as subspecies of *H. commersoni*, and one extinct species (*H. besaoka*), based on mesiodistal and buccolingual molar dimensions (M^{1}MD, M^{1}BL, M^{2}MD, M^{2}BL, M^{3}MD, M^{3}BL). Closed solid symbols indicate *H. commersoni* organized by locality, subfossil *H. besaoka* indicated by (+), open symbols indicate non-Malagasy species previously within this species complex; % variance explained shown in parentheses

hypoconulid. There is a small ridge between the metaconid and entoconid, which is oriented slightly bucally; in both M$_1$ and M$_2$ this ridge is more parallel to the toothrow.

Comparison

UA 9203 and 9204 most closely match those of *Triaenops* species in size and overall morphology. When the mesiodistal and buccolingual dimensions of M$_1$ (the tooth common to UA 9203 and 9204) were compared to those of each of the modern species of *Triaenops* using one-sample *t*-tests, the subfossil M$_1$ were generally longer in mesiodistal length and smaller in buccolingual width than the four extant species of *Triaenops* for which post-cranial specimens are available (Table 5). Due to a lack of comparable specimens of *T. goodmani* (only UA 9010 has an intact M$_1$), it was not possible to perform an adequate comparative

analysis. However, in an analysis of M1 dimensions relative to the modern species (Fig. 12A–B), it appears that UA 9203 and 9204 are not immediately referable to *T. goodmani* since they cluster far from this species in both mesiodistal and buccolingual dimensions. UA 9203 and 9204 also possess a relatively strong ridge between the metaconid and entoconid; a character lacking in *T. goodmani*. Due to small sample sizes, these two jaws are referred simply to the genus *Triaenops*.

Genus *Rousettus*

Included Species and Distribution

The genus *Rousettus* is distributed in Africa, Europe, Asia, Comoros, and Madagascar (Simmons, 2005); *R. madagascariensis* is endemic to Madagascar, and is the sole species of this genus present on the

TABLE 4. One-sample *t*-test (2-tailed) results for *Hipposideros* sp. from NCC-1 compared to extant *H. commersoni* and subfossil *H. besaoka* from Anjohibe Cave (TW-10). Mean, SD, and sample size (*n*) are also shown. Probability level: *** — $P < 0.001$

Character	UA 9015	vs. *H. commersoni*				vs. *H. besaoka*			
		n	$\overline{x}$	SD	*t*-test	*n*	$\overline{x}$	SD	*t*-test
MD length of M_3	2.23	40	2.22	0.127	-0.55	100	2.37	0.098	14.06***
BL length of M_3	1.65	40	1.69	0.132	1.82	100	1.76	0.087	13.19***

island. It is presently distributed throughout the eastern rainforest, the deciduous forests of the west, southwest and north, and the Central High Plateau (MacKinnon *et al*., 2005).

Rousettus sp. cf. *R. madagascariensis*

Referred Specimens
Right M_3 (UA 9206).

Description
UA 9206 consists of a partial tooth with part of its crown missing. The two roots are partially intact. The base of the crown is very shallow and relatively broad. The anterobuccal aspect of the crown is complete, and preserves a distinct ridge.

Comparison
Based on the small size and overall shape of the crown base and roots, UA 9206 is assigned to the genus *Rousettus*, species of which possess teeth that are typically simple and 'rousettine', but are also considerably narrow (Bergmans, 1977, 1994). UA 9206 appears to best match the morphology of M_3, as this tooth lacks well-developed cusps, has a narrow width, and is short in length.

Locality: SS2

Hipposideros sp. cf. *H. commersoni*

Referred Specimens
Two isolated left M_3 (UA 9207, 9208), isolated left M^1 (UA 9209), partial right maxilla (UA 9210), right dentary with P_4 (UA 9211), left dentary with isolated M_1 (UA 9214), right P^4 (UA 9213).

Description
UA 9207 and 9208 are both left M_3 consisting of complete crowns with partial roots intact. In both, the trigonid is relatively wide and the protoconid and metaconid are similar in height. The protoconid is

TABLE 5. One-sample *t*-test results for MD and BL lengths of M_1 for *Triaenops* sp. from NCC-1. Malagasy species include *T. auritus*, *T. furculus* and *T. rufus*; *T. persicus* is distributed in Africa and the Middle East. Mean ± SD, and sample size (*n*) are also shown. Probability level: * — $P < 0.05$, ** — $P < 0.01$, *** — $P < 0.001$

Triaenops sp.	*T. auritus*	*T. furculus*	*T. rufus*	*T. persicus*
		MD length of M1		
	1.48 ± 0.046 (9)	1.46 ± 0.041 (15)	1.59 ± 0.057 (10)	1.56 ± 0.066 (6)
UA 9016: 1.69	-13.64***	-22.00***	-5.33***	-4.80**
UA 9017: 1.55	-4.50**	-8.65***	2.44*	0.44
		BL length of M1		
	1.02 ± 0.039 (9)	0.99 ± 0.054 (15)	0.90 ± 0.048 (10)	0.94 ± 0.056 (6)
UA 9016: 0.82	15.49***	12.11***	5.46***	5.13**
UA 9017: 0.85	13.21***	9.95***	3.49**	3.81*

well-developed, and the talonid basin is extremely reduced with a small hypoconid. The preentocristid is more or less parallel to the protocristid. UA 9209 consists of a left M^1 crown with partial roots, but the hypoconal basin is broken. The protofossa is closed, and the large cingular heel is deflected posteriorly.

The partial right maxilla, UA 9210, contains $P^{2,4}M^{1-3}$. A large infraorbital foramen lies superior to M^1. P^2 is vestigial and extremely reduced. It is displaced laterally
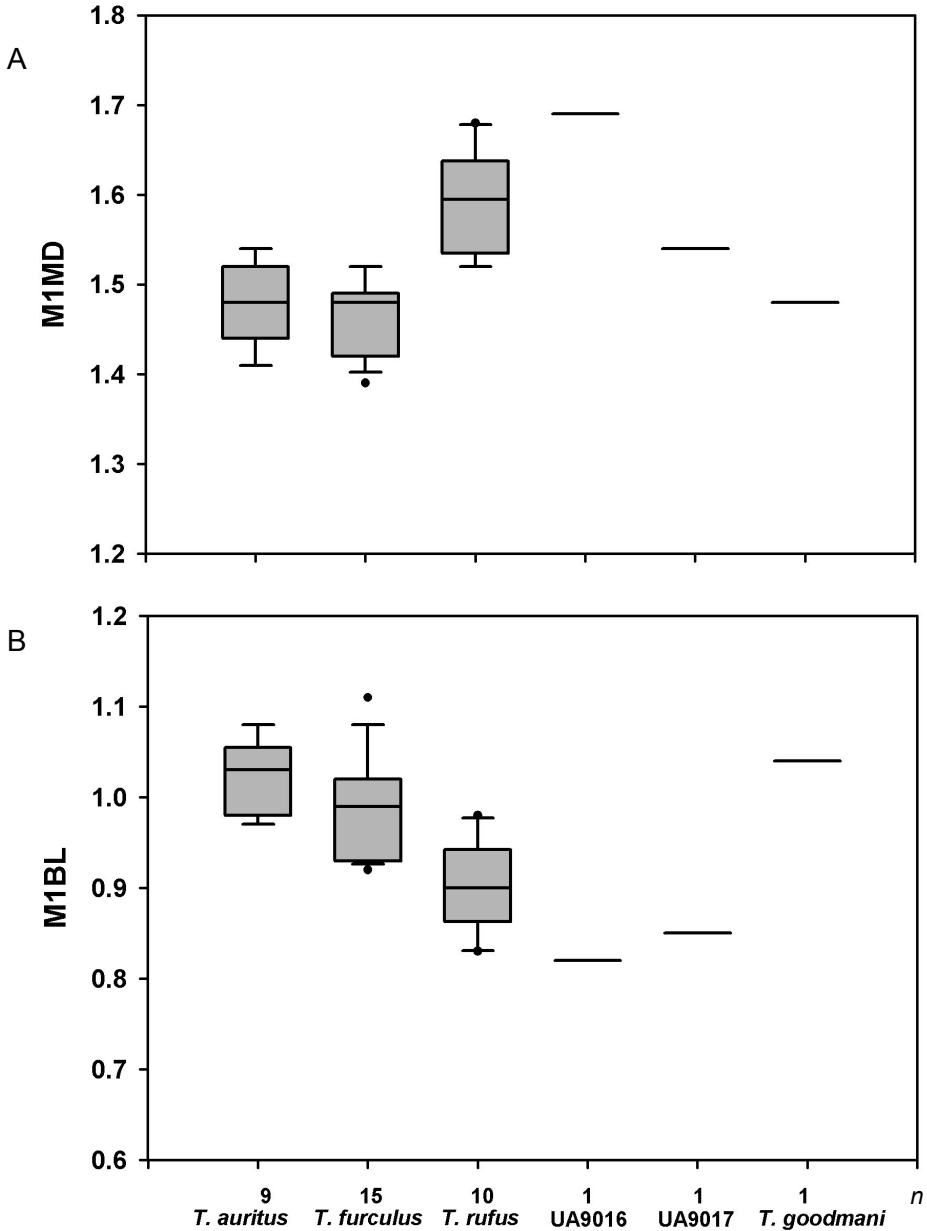
FIG. 12. Boxplots of mesiodistal and buccolingual dimensions of M_1 for three extant Malagasy species of *Triaenops* (*T. auritus*, *T. furculus*, and *T. rufus*), subfossil *Trianeops* from NCC-1, and subfossil *T. goodmani* sp. nov. from OLD SE; A — mesiodistal dimensions; B — buccolingual

such that it is situated lateral to the anterobuccal corner of P^4. P^4 has a tall, well-developed principal cusp, a relatively tall posterior cusp, a tiny cingular cusp, and a shallow hypoconal basin. The lingual aspect of the crown has a relatively well-developed cingulum. M^1 has a well-developed but low cingular heel. The paracone and metacone are the tallest cusps, followed by the parastyle, mesostyle, and metastyle respectively; the protocone is low. The paracrista and premetacrista are approximately equal in length and parallel to each other, as are the postparacrista and metacrista. The hypoconal basin is well-developed and the heel is posteriorly deflected. M^2 is similar to M^1, although it has a smaller hypoconal basin and less posteriorly deflected heel. M^3 is substantially reduced in size, and has complete loss of the talonid, a medially displaced metaconid, and only the remnant of a heel.

UA 9211 is a right dentary with P$_4$, which has a tall median cusp and a shorter posterior cusp. The corpus is relatively deep and robust, and there are alveoli present for P$_2$, C and the lateral lower incisor. UA 9214 consists of a left dentary with M$_1$. The ramus is broken and is relatively deep. M$_1$ has a tall protoconid, slightly shorter hypoconid, and lower but approximately equal paraconid and entoconid; the lowest cusp is the hypoconulid. The trigonid is high while the talonid is low but complete.

UA 9213 is a right P^4 with a large main cusp, a small posterior shelf, and a vestigial anterolingual cusp. There is a low cingular heel and the crown is surrounded by a basal cingulum. The hypoconal basin is shallow.

Comparison

All of these specimens are referable to *Hipposideros*. However, the fact that UA 9207 and 9208 appear significantly different from both *H. commersoni* and

H. besaoka (Table 6), and combined with the small sample size, this makes assignment to species uncertain.

Rousettus madagascariensis

Referred Specimen

Distal right humerus (UA 9216).

Description

UA 9216 is the distal end of a relatively large right humerus, with a relatively well-developed trochlea, and a flat broad capitulum. The shaft is extremely thin and the epitrochlea is flat and broad. The trochlea is low and steeply angled towards the junction with the epitrochlea, and the lateral surface of the capitulum has a round excavation on its lateral surface.

Comparison

Pteropodid humeri are typically relatively simple and primitive, with less elaboration of the distal aspect than seen in other bats. Based on the size and specific morphology of this specimen, UA 9216 is referred to *R. madagascariensis*.

Family Vespertilionidae Gray 1821
Subfamily Vespertilioninae Gray 1821
Genus *Myotis* Kaup 1829

Included Species and Distribution

Myotis is a very speciose and widespread genus, with 100 species presently recognized (Simmons, 2005). Two subspecies of *M. goudoti* were previously recognized: *M. g. anjouanensis* Dorst, 1960, restricted to Anjouan Island in the Comoros and *M. g. goudoti* Dorst, 1960, endemic to Madagascar; both of these are now recognized as distinct species (Simmons, 2005). *Myotis goudoti* inhabits most habitat types in Madagascar (Eger and Mitchell, 2003).

TABLE 6. One-sample *t*-test results for *Hipposideros* from SS2 (M$_3$) compared to extant *H. commersoni* and subfossil *H. besaoka* from Anjohibe Cave (TW-10). Mean ± SD, and sample size (*n*) are also shown. Probability level: * — *P* < 0.05, *** — *P* < 0.001

Hipposideros sp.	*H. commersoni*	*H. besaoka* (TW-10)
	MD length of M$_3$	
	2.22 ± 0.127 (40)	2.37 ± 0.098 (100)
UA 9020: 2.32	-5.03***	4.87***
UA 9021: 2.27	-2.54*	9.97***
	BL length of M$_3$	
UA 9020: 1.63	2.77**	15.49***
UA 9021: 1.70	-0.57	7.44***

Myotis goudoti

Referred Specimen

Lower right canine (UA 9217).

Description

UA 9217 is a very small isolated right canine with a single tall pointed main cusp. The lingual surface is spade-shaped and slightly concave.

Comparison

UA 9217 matches the morphology and size of *M. goudoti*. This species has unique small pointed canines with a single main cusp, and the unique lingual spade-shaped surface, which is broad inferiorly. This isolated canine (1.47 mm) fits within the modern size range seen in this species ($\bar{x}$ = 1.33, *n* = 3, SD = 0.076, one-sample *t*-test, *P* = 0.083).

DISCUSSION

Subfossil versus Modern Assemblages

Of the subfossil bat specimens described in these breccia samples, all are attributable to genera represented on the island today. Nine species of extant bats are known to use the Anjohibe Cave system as a day roost based on a recent census (*Pteropus rufus*, *R. madagascariensis*, *H. commersoni*, *T. furculus*, *T. rufus*, *Miniopterus manavi*, *M. gleni*, *Myotis goudoti*, and *Otomops madagascariensis* — Goodman *et al*., 2005; S. M. Goodman, pers. comm.). The subfossils recovered from Anjohibe Cave indicate the presence of five genera, one of which (*Eidolon*) no longer inhabits this cave system. Of the subfossil taxa identified and described here, only four extant species (*E. dupreanum*, *R. madagascariensis*, *H. commersoni*, and *Triaenops* sp. cf. *T. furculus*) were previously recorded from the younger sediments of Anjohibe Cave (Burney *et al*., 1997); one is new for the site (*M. goudoti*). Furthermore, two of the taxa identified are new and described here (*T. goodmani* and *H. besaoka*).

The large sample of subfossils referable to *Hipposideros*, its presence in all breccia samples, and the fact that species are also commonly found in the younger sediments of the cave indicates that the genus was well represented in the overall cave fauna in the recent geological past. The only other record of *Hipposideros* from a subfossil deposit on the island is from Lake Tsimanampetsotsa, southwestern Madagascar (Sabatier and Legendre, 1985).

The evidence of a distinctly larger species of *Hipposideros* (*H. besaoka*) from TW-10 is especially significant, because the extant species *H. commersoni* is the largest insectivorous bat known from the island (Russ *et al*., 2001). This new species has significantly wider molars than seen in modern populations of *H. commersoni*, with a more robust and deeper mandibular corpus.

Although common as a breccia subfossil, and extremely numerous within the more recent Holocene deposits, *Eidolon dupreanum* is currently locally extinct in the Anjohibe Cave system. This species has been recorded from many regions of Madagascar, but may be susceptible to human

pressures (Racey *et al*., 2002; MacKinnon *et al*., 2003). Roost sites appear to be especially at risk; recent ecological studies suggest that nearly half of the *Eidolon* roosts surveyed were deserted at least in part due to human hunting (Racey *et al*., 2002). In many regions *Eidolon* is able to persist in deforested areas (MacKinnon *et al*., 2003).

The extinction of *Eidolon* at Anjohibe appears to have occurred in the past few decades. Interviews with local villagers suggest that older adults recognize the bones of *Eidolon* as a 'fanihy' (fruit bat) that no longer occurs in the cave, but one that lived previously in the cave system during their childhood (S. M. Goodman, pers. comm.). The large quantity of *Eidolon* bones on the surface of the cave floor also supports a recent extinction event.

It is interesting to note that not all species presently inhabiting the cave were detected as subfossils (e.g., *Otomops*, *Miniopterus*). This may indicate that these genera colonized the cave more recently. However, it is equally possible that they were not represented in this sample due to chance or taphonomic factors.

CONCLUSIONS

Caves are among the most delicate and vulnerable ecosystems (Watson *et al*., 1997; van Beynen and Townsend, 2005), and are particularly susceptible to human pressures. Previous research has demonstrated a major loss of biodiversity in many of Madagascar's species during the Holocene (Godfrey *et al*., 1990; Goodman, 1994; Burney *et al*., 1997; Gommery *et al*., 2003), yet whether Malagasy bats experienced similar extinctions has never been addressed. This paper marks the first systematic study of subfossil Malagasy bats.

On the basis of subfossil remains recovered within Anjohibe Cave, it is clear that bats on the island experienced local

extirpation (as seen in *Eidolon*) and island-wide extinction as seen by *T. goodmani* and the largest known insectivorous bat on the island, *H. besaoka*. It is also interesting to note that the subfossil forms tend to be larger than their extant relatives, although the difference is less than in other groups (e.g., *Cryptoprocta* — Goodman *et al*., 2004; various lemur groups including *Daubentonia* — Godfrey and Jungers, 2002).

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