Rock matrix surrounding subfossil lemur skull yields diverse collection of mammalian subfossils: Implications for reconstructing Madagascar's paleoenvironments

Karen E. Samonds[1], Sara N. Parent[2], Kathleen M. Muldoon[3], Brooke E. Crowley[4] & Laurie R. Godfrey[5]

[1]Redpath Museum, McGill University, 859 Sherbrooke St. W., Montreal, Quebec, Canada H3A 2K6
Email: karen.samonds@mcgill.ca

[2]Department of Anatomical Sciences, School of Medicine, Health Sciences Center, Stony Brook University, Stony Brook, New York 11794, USA
Email: sparent@ic.sunysb.edu

[3]Department of Anatomy, Dartmouth Medical School, and Department of Anthropology, Dartmouth College, Hanover, New Hampshire 03755, USA
Email: kathleen.m.muldoon@dartmouth.edu

[4]Department of Anthropology, 19 Russell Street, University of Toronto, Toronto, Ontario, Canada M5S 2S2
Email: brooke.crowley@utoronto.ca

[5]Department of Anthropology, 240 Hicks Way, University of Massachusetts, Amherst, Massachusetts 01003, USA
Email: lgodfrey@anthro.umass.edu

Abstract

Due to the near lack of a Cenozoic fossil record, little is known about the origin and evolution of Madagascar's extant fauna. Madagascar's subfossil record (Late Pleistocene and Holocene) has been important for filling in the most recent part of this informational gap, contributing details on diversity and distribution changes in the recent past, but most research has focused on larger animals. Less attention has been given to the subfossil record of small mammals, despite the fact that these groups represent a substantial portion of the extant mammalian diversity. To evaluate the potential presence of subfossil microfaunal remains in cave breccias (calcite sediment), we used acetic acid to dissolve the matrix surrounding a nearly complete skull and mandible of *Archaeolemur* sp. cf. *A. edwardsi* from Anjohibe Cave, northwestern Madagascar. The resulting residue included fossil remains of all five orders represented by Madagascar's extant mammals (Afrosoricida, Carnivora, Chiroptera, Rodentia, and Primates), and one order, Artiodactyla, currently extinct in Madagascar, except for introduced forms. Species identified include *Microgale* sp. (Afrosoricida: Tenrecidae), *Eliurus myoxinus* (Rodentia: Nesomyidae), *Hipposideros* sp. cf. *H. besaoka* and *Triaenops* sp. (Chiroptera: Hipposideridae), *Galidia elegans* (Carnivora: Eupleridae), *Cheirogaleus medius* and *Microcebus murinus* (Primates: Cheirogaleidae), and *Hippopotamus lemerlei* (Artiodactyla: Hippopotamidae). Radiocarbon dating shows that non-associated surface finds of small mammals tend to be younger than extinct larger mammals at Anjohibe, underscoring the importance of using other methods to establish temporal associations of small and large mammals. This research demonstrates the potential for recovering subfossils from matrix that are typically discarded during the preparation of larger fossils, and highlights the potentially significant loss of information if such sediments are ignored.

Keywords: Small mammals, paleontology, acetic acid preparation, subfossils, Madagascar

Résumé détaillé

En raison de l'absence presque complète d'un registre fossile Cénozoïque à Madagascar, nous ne connaissons presque rien des origines et de l'évolution de sa faune actuelle. La plupart des fossiles décrits de la Cénozoïque sont des « subfossiles », c'est-à-dire seulement quelques milliers d'années d'âge. Ces subfossiles ont été très importants pour augmenter nos connaissances des faunes récentes, y compris les distributions passées des espèces (actuelles et disparues), et en précisant les dates d'arrivées récentes. Toutefois, la plupart de ces recherches était sur les animaux assez grands ; ces animaux donc constituent la plupart des espèces décrites du registre subfossile. Actuellement, moins est connu sur le registre subfossile des animaux plus petits, malgré leur dominance numérique parmi les faunes actuelles. En d'autres pays, les petits mammifères ont été très utiles pour mieux comprendre les changements climatiques, le paléo-environnement et l'écologie des espèces et des écosystèmes disparus.

Nous avons évalué la présence des os subfossiles des petits mammifères dans les sédiments calcaires

Samonds, K. E., Parent, S. N., Muldoon, K. M., Crowley, B. E. & Godfrey, L. R. 2010. Rock matrix surrounding subfossil lemur skull yields diverse collection of mammalian subfossils: Implications for reconstructing Madagascar's paleoenvironments. *Malagasy Nature*, 4: 1-16.

consolidés de la grotte d'Anjohibe, au Nord-ouest de Madagascar. Cette grotte a déjà produit des subfossiles de plusieurs animaux disparus, dont les lémuriens, hippopotames et crocodiles. Nous avons utilisé l'acide acétique pour faire fondre une brèche entourant un crâne et une mandibule presque complète d'*Archaeolemur* sp. cf. *A. edwardsi*. Le résidu résultant a inclus des os subfossiles attribuable à chaque ordre des mammifères actuels de Madagascar (Afrosoricida, Carnivora, Chiroptera, Rodentia et Primates), et un ordre qui était présent, mais est actuellement disparu à Madagascar (Artiodactyla ; les hippopotames sont disparus, les espèces restantes sont introduites). Les espèces identifiées incluent *Microgale* sp. (Afrosoricida: Tenrecidae), *Eliurus myoxinus* (Rodentia: Nesomyidae), *Hipposideros* sp. cf. *H. besaoka* et *Triaenops* sp. (Chiroptera: Hipposideridae), *Galidia elegans* (Carnivora: Eupleridae), *Cheirogaleus medius* et *Microcebus murinus* (Primates: Cheirogaleidae) et *Hippopotamus lemerlei* (Artiodactyla: Hippopotamidae). La présence de *Galidia*, un carnivore spécifique aux milieux forestiers, représente la première récolte de ce genre d'Anjohibe, et sa présence corrobore la reconstruction d'un écosystème forestier (en accord avec la présence des grands lémuriens adaptés à la locomotion arboréale). Deux espèces disparues ont été récoltées (*Hipposideros besaoka* et *Hippopotamus lemerlei*), ce qui nous donne une reconstruction plus complète de la biodiversité des siècles et millénaires passés dans ce site. Nous avons aussi utilisées la datation par le carbone-14 pour montrer que les fossiles des mammifères actuels d'Anjohibe ne sont pas de même âge que les fossiles des espèces disparus ; l'association des spécimens est alors très importante pour les interprétations paléo-écologiques.

Cette recherche nous donne un exemple de la présence des petits subfossiles dans les sédiments des sites subfossiles, et le potentiel pour dévoiler l'écologie et l'évolution des espèces passées et leurs environnements. Malheureusement, ces sédiments sont souvent perdus (peut-être avec des petits fossiles dedans) ou détruits lors de la préparation des grands fossiles. Actuellement, les méthodes paléontologiques, sur le terrain et au laboratoire, peuvent contribuer à la disparition des petits subfossiles. Les petites dents et les petits os sont généralement plus fragiles et plus susceptibles d'être détruits par des processus taphonomiques. En plus, leur taille les rendent plus difficile à trouver par des paléontologues sur terrain, et les méthodes de collecte (techniques de reconnaissance, la taille des fossiles récupérés par les tamis, priorités de récolte et choix des sites) peuvent affecter la taille moyenne des fossiles collectionnés. Par ailleurs, les petits fossiles peuvent être perdus ou détruits en train de préparation des fossiles et sédiments. Cette préparation peut inclure la préparation d'acide pour les sédiments calcaires (qui, généralement, préservent les petits fossiles), ou l'enlèvement manuel du sédiment entourant un fossile intéressant (qui, généralement, détruit les petits fossiles ou les laisse enchâssés dans le sédiment).

Nous suggérons que les paléontologues doivent considérer les effets de leurs méthodes de reconnaissance, de collecte, et de préparation sur leur réussite en récupération des petits fossiles. Actuellement, il parait qu'il y a une balance entre la récupération rapide des plus grands fossiles et la récupération d'une faune plus complète, qui peut prendre plus de nos efforts et de notre temps. Néanmoins, si nous augmenterons la représentation des petits fossiles aux études paléontologiques à Madagascar, ils nous donneront une reconstruction plus complète de l'histoire de la faune malgache, dont la diversité des communautés passées, et l'évolution des distributions des espèces et écosystèmes. Ces efforts nous donneront une meilleure compréhension de la chronologie de cette histoire, et peuvent aussi nous donner un cadre pour évaluer les hypothèses sur les causes de ces changements ; alors, on peut mieux comprendre l'histoire environnementale de la faune malgache en même temps qu'évaluer les effets des changements écologiques présents et futurs.

Mots clés: Petits mammifères, paléontologie, préparation en acide acétique, subfossiles, Madagascar

Introduction

Madagascar's modern fauna is unique and exhibits one of the highest levels of endemism on the planet (Goodman & Benstead, 2005). Exploring how, when, and from where the island's animals arrived has been called "*one of the greatest unsolved mysteries of natural history*" (Krause *et al.*, 1997). The evolutionary and biogeographic history of many of the island's groups remains poorly known due to the near-lack of a Cenozoic fossil record (see Krause *et al.*, 2006 for discussion).

Our only direct window into the evolutionary history of modern Malagasy mammals is based on very recent subfossil remains, with the deepest glimpse at a mere ~80,000 years before present (BP) (Samonds,

2007). A diverse subfossil fauna has been described including lemurs, bats, carnivorans, rodents, pygmy hippos, afrosoricids, the aardvark-like *Plesiorycteropus* (Order Bibymalagasia), crocodyliforms, tortoises, and elephant birds (Godfrey *et al.*, 1990; Goodman, 1994; MacPhee, 1994; Burney *et al.*, 1997; Godfrey *et al.*, 1999; Burney *et al.*, 2004; Muldoon & Simons, 2007; Samonds, 2007; Muldoon *et al.*, 2009). Explorers at subfossil sites in Madagascar during the end of the 19th and the first third of the 20th century (Forsyth-Major, 1894; Filhol, 1895; Grandidier, 1899; Lorenz von Liburnau, 1900; Grandidier, 1905; Standing, 1905, 1908; Lamberton, 1934a, 1934b) collected mainly larger fossils including giant lemurs, hippos, carnivorans, and elephant birds. Indeed, interest in Anjohibe Cave (our study site) as a subfossil locality was sparked by Raymond Decary's (1934, 1938) announcement of large extinct species there (a hippo, giant tortoise, and two giant lemur species). Consequently, large species comprise the vast majority of identified and catalogued subfossil material from Madagascar. Given that large-bodied mammals make up only a small portion of Madagascar's extant mammal diversity, knowledge of smaller-bodied fauna is critical for an accurate assessment of mammalian diversity in the recent past (late Pleistocene and Holocene), as well as for accurate reconstructions of past environments and environmental change.

Nonetheless, research on Malagasy subfossils has produced valuable details of an island-wide Holocene extinction that exterminated nearly all of Madagascar's large native animals (Burney *et al.*, 2004). Radiocarbon dates demonstrate that these extinctions postdated the arrival of humans, some 2000 years ago, who no doubt played a role in their demise (Simons *et al.*, 1995; Burney *et al.*, 1997, 2003; Burney, 1999, 2003; Godfrey & Irwin, 2007; Crowley, 2010). These megafaunal extinctions were likely aided by a complex interaction with Late Pleistocene and Holocene climate change (particularly in the south and southwest, but also in other regions; Burney, 1993, 1999; Burney *et al.*, 1997, 2003, 2004; Gasse & Van Campo, 1998; Burney & Flannery, 2005; Virah-Sawmy *et al.*, 2010). Although populations were decimated during the Holocene, some evidence suggests that several of these large animals persisted to as recently as the end of the 19th century or even later (Godfrey, 1986; Burney & Ramilisonina, 1999). In contrast to the well-documented extinction of Madagascar's megafauna, the degree to which small mammals experienced extinction or range contraction has only begun to be explored.

Several studies illustrate the importance of studying small mammals at Malagasy subfossil sites. Recent studies have produced evidence of both range contraction (Goodman & Rakotondravony, 1996; Godfrey *et al.*, 1999; Goodman *et al.*, 2005, 2006a; Burney *et al.*, 2008; Muldoon *et al.*, 2009) and extinction (Goodman *et al.*, 2006a, 2007; Samonds, 2007; Burney *et al.*, 2008). It has also been demonstrated that extant small mammal communities in Madagascar are correlated with the island's major habitat types (Muldoon & Goodman, 2010), and as such are useful for paleoenvironmental reconstruction of subfossil localities (Muldoon, 2010). However, the majority of small mammal subfossils have been surface collected at open-air paleontological localities (as smaller subfossils are most easily collected on or near the surface) and "assemblages" may therefore span a large temporal and/or geographic range, possibly mixing faunas from different environments. It is also possible that some surface finds, although "subfossilized" (partially remineralized), will be very recent and not contemporaneous with extinct species. Pit caves, on the other hand, are natural traps for animals, and may provide a better taxonomic representation of past communities, albeit sometimes for only brief time intervals (Muldoon *et al.*, 2009). At cave sites, just as at open sites, small mammal remains may be found on the surface, with uncertain temporal associations. However, when temporal and spatial association with extinct megafauna can be documented, subfossil micromammal remains may yield finer-scale evidence of changes in diversity and distribution of communities through time.

Our study, which uses subfossils from Anjohibe Cave to investigate the utility of small mammal remains in reconstructing paleoenvironments, has two goals. First, we seek to evaluate whether small mammal subfossils are present in consolidated sediments encasing large-bodied subfossil vertebrates, with attention to whether analysis of such matrix material can improve our knowledge of mammal associations and indeed the presence of particular species at subfossil locations. Second, because many sites accumulate fossils over large spans of time, we also test whether surface-collected subfossils of still-extant mammals at Anjohibe are coeval with subfossil remains from extinct large mammals from the same site. We use radiocarbon dating to establish the period during which the remains of *Archaeolemur* sp. cf. *A. edwardsi* and other megafauna (*Hippopotamus lemerlei*) accumulated at Anjohibe, and date an assortment of surface collected small-bodied extant

mammals that were not found in association with *Archaeolemur* and *H. lemerlei*. A lack of evidence of temporal association cannot prove that these extant species were not contemporaneous with these species at Anjohibe, but it would caution against using such specimens in drawing inferences about extinct species, and would underscore the importance of recovering small mammals in temporal association with megafauna.

Materials and methods

Study site

Anjohibe Cave (15°32.55'S, 46°53.17'E) is located in the southern part of the current dry savannah of the Mahavo plains in northwestern Madagascar, northeast of Mahajanga (Decary, 1934). This region has undergone extensive human modification, and subfossils of arboreal animals (e.g., sloth lemurs) suggest that this region was at least partially forested in the recent past (Burney *et al.*, 1997). Within the cave interior is a variety of depositional environments suggesting that deposition was episodic. Fossils are 1) concentrated into bone breccias (bone fragments and sediment cemented together with mineral deposits formed within the cave system over time); 2) embedded in the consolidated sediment on the cave floor, which covers the flowstone; 3) buried in loose sediment; and/or 4) accumulated near entrances, beneath skylights, or in around sunken forests where the cave ceiling has collapsed because of bird or carnivoran predation.

Within the cave there are places with deep unconsolidated fossil-rich reddish-brown clay or silt deposits overlying both finer and coarser sediments of different coloration, and dating of sediment cores has yielded basal dates of around 8,000 years before present (Burney *et al.*, 1997). Burney *et al*. (1997) interpreted a sharp rise in microscopic charcoal particles in a sediment core to signal the arrival of humans into the area between 1000 and 2000 years ago. The most fossil rich sites were in chambers that once held standing water. One such site included at least eight partially articulated skeletons of *Hippopotamus lemerlei* in unstratified reddish-brown silty clay. Beneath the clay layer were rounded limestone concretions one of which contained an infant *Megaladapis* skull. The hippos appear to have belonged to a single herd that was trapped within the cave, either by falling through a skylight or by washing in during a flash flood (Burney *et al.*, 1997). Clearly, the fossils in the concretions were secondarily deposited there and are of considerably older age.

Also of interest are pollen-rich speleothems, which preserve a record of vegetation and climate change through time. Brook *et al*. (1999) demonstrated that these speleothems comprise annual layers that form like tree rings and preserve evidence of seasonal changes in rainfall. Two active speleothems yielded detailed records of climate from modern time backwards (Brook *et al.*, 1999). Uranium series dates demonstrated that one speleotherm began forming 7000 years ago and the other 3500 years ago.

Calcareous breccias in Anjohibe themselves demonstrate a large range of depositional processes; some fossils buried in breccias are pristine while others show signs of having been transported considerable distances by subterranean streams before being deposited (Burney *et al.*, 1997). The cave matrix breccias used in this current study were collected from Anjohibe Cave, chiseled from the cave floor directly northeast of Entrance P (Figure 1). A thick layer of consolidated sediment, which surrounded the skull and mandible of an *Archaeolemur* sp. cf. *A. edwardsi*, was removed as a block and prepared in the laboratory.

Fossil preparation and identification

Approximately 1 kg of calcareous breccia surrounding a skull and mandible of *Archaeolemur* sp. cf. *A. edwardsi* (Figure 2) was prepared using standard acetic acid preparation techniques (Toombs & Rixon, 1959; Grant, 1989; Leiggi & May, 1994; Lindsay, 1995). Recovered bone material was sorted under a microscope and identifiable bone or tooth matter was collected and catalogued. A large comparative sample of epoxy dental casts, photographs, and measurements of modern Malagasy species was used to facilitate identification. Measurements were made with 500-172 Mitutoyo digital calipers to 0.01 mm, or with an MA285 Meiji Techno optical reticule X, 1/100 (0.01 mm).

Radiocarbon dating

Radiocarbon dates were obtained for *Archaeolemur* sp. cf. *A. edwardsi* (n = 3), *Hippopotamus lemerlei* (n = 7), an assortment of remains of extant endemic species (n = 13), and introduced *Rattus rattus* (n = 2) collected from the floor of Anjohibe Cave (Table 1). These dates supplement previously published radiocarbon dates for four specimens from the same cave (one *Archaeolemur*, one bat, and two *Hippopotamus*; Burney *et al*., 1997). Unfortunately, most specimens recovered from the breccia were too small to date (often single teeth), though an attempt to

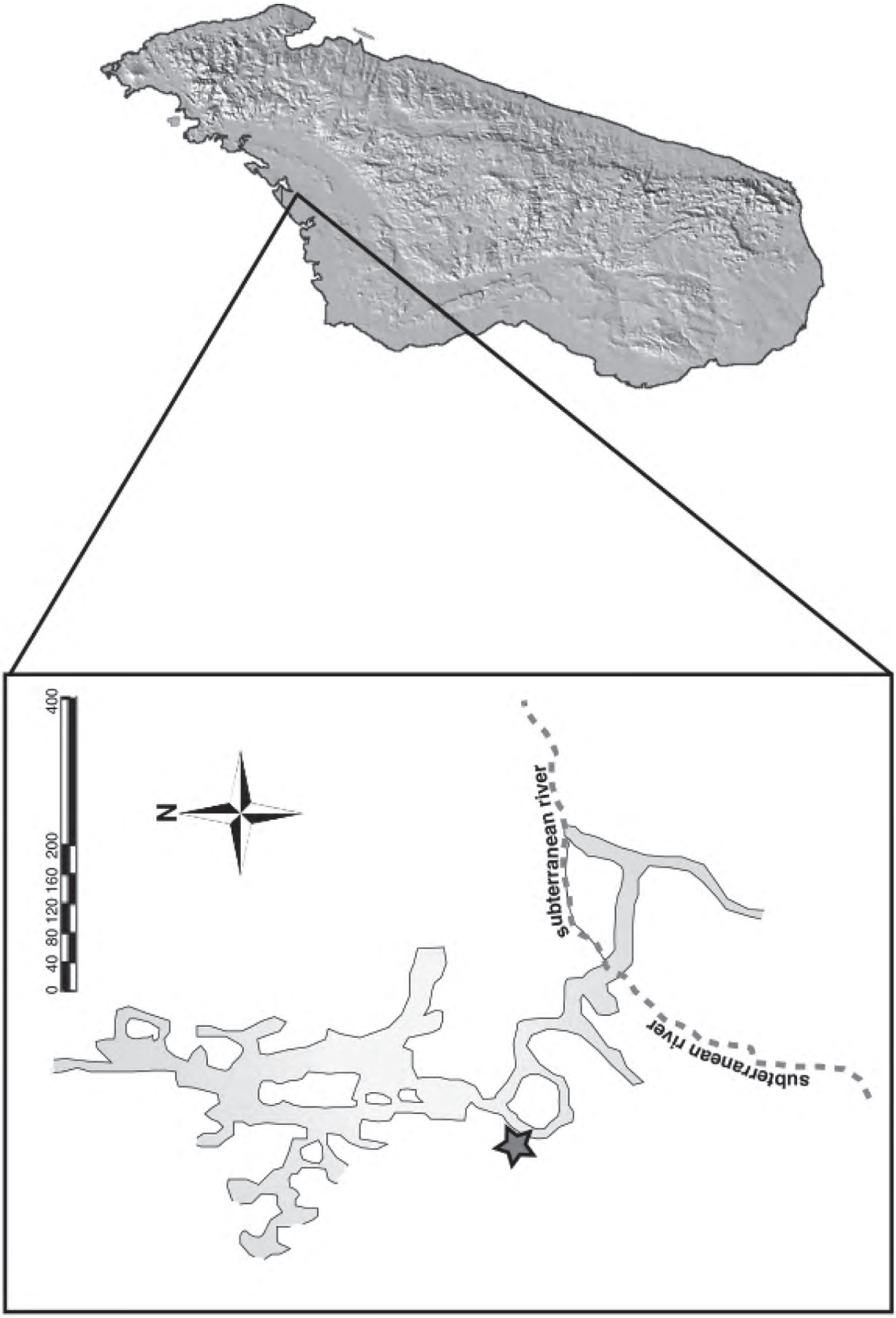

Figure 1. Anjohibe Cave, northwestern Madagascar. Adapted from de Saint-Ours & Paulian (1953) and Burney *et al.* (1997). Star marks Entrance P. Map scale in meters.

Figure 2. Skull and mandible of *Archaeolemur* sp. cf. *A. edwardsi* with associated matrix (left), and matrix removed (right) to show the approximate amount of material prepared in our sample. The skull and mandible are shown in the position in which they occurred in the matrix.

date the largest bone fragment (*Hippopotamus* orbit UA 9570) was successful (see Results).

Approximately 200 mg of bone were collected from fragmented specimens. Samples were decalcified in 0.5 M EDTA for 10 days at 10°C, and 12 days at room temperature, rinsed 10 times in ultra pure water, and gelatinized in 0.01 N HCl at 57°C. Collagenous residues were then filtered using a 1.5 micrometer glass-fiber filter and dried under vacuum. Collagen integrity was determined by analyzing samples on a ThermoElectron (Finnigan) Delta+XP continuous flow system connected to an Elemental Analyzer at the University of California, Santa Cruz Stable Isotope Lab, and verifying acceptable atomic C:N ratios, stable isotope values, and collagen yield (Ambrose, 1991). Radiocarbon dates were obtained at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. Conventional radiocarbon dates (^{14}C BP) were calibrated to 2σ calendar years before present (Cal BP) using a 20-year moving average on Calib 5.01 (Stuiver & Reimer, 1993) and the Southern Hemisphere calibration curve SHCal04 (McCormac *et al.*, 2004). We rounded 2σ calibrated dates to the nearest decade, and then calculated the mean calibrated date ± 1σ.

Results

The subfossil specimens recovered (Table 2, Figure 3) from the 1 kg of matrix that encrusted a single skull and mandible of *Archaeolemur* sp. cf. *A. edwardsi* include eight species within all five extant Malagasy mammalian orders: Afrosoricida (Tenrecidae), Carnivora (Eupleridae), Chiroptera (Hipposideridae), Rodentia (Nesomyidae), and Primates (Cheirogaleidae). Of the seven small-bodied species represented in this sample, one is extinct and another is locally extirpated. In addition, material from the order Artiodactyla (Hippopotamidae), a family now extinct in Madagascar except for introduced forms, was recovered.

Radiocarbon dates of specimens of *Archaeolemur* sp. cf. *A. edwardsi* and *Hippopotamus lemerlei* from Anjohibe span approximately 6000 years beginning ca 8500 Cal BP (Table 1), which corresponds to the time that basal sediments were deposited at core location AM-2 within the cave (Burney *et al.*, 1997). The most recent dates that we obtained for *Archaeolemur* and *Hippopotamus* subfossils are 1700 ± 35 ^{14}C BP and 2635 ± 40 ^{14}C BP, respectively (1555 ± 135 and 2635 ± 145 Cal BP, respectively; Table 1). If fecal samples from a nearby cave, Anjohikely, do indeed belong to *Archaeolemur* (Burney *et al.*, 2004), then the temporal range for *Archaeolemur* in this region

Table 1. Radiocarbon dates for faunal remains from Anjohibe. ^{14}C and calibrated calendar ages are years before present (BP). Due to changes in atmospheric ^{14}C concentrations after atomic bomb testing, any date less than 50 years old is considered modern. **UA**, Université d'Antananarivo, Madagascar; **UM**, University of Antananarivo, Madagascar; **UMASS**, University of Massachusetts, Amherst. Field numbers are included when available for uncataloged specimens.

Specimen	^{14}C Age ± 1σ	Calibrated Age ± 1σ	Specimen number	AMS Lab number	Source[a]
ENDEMIC					
Archaeolemur sp. cf. *A. edwardsi*	7790 ± 70	8530 ± 150	Uncataloged (UA; HFJ-93-1-A)	β−64960 CAMS 8647	1
A. sp. cf. *A. edwardsi*	1700 ± 35	1555 ± 135	UA 8701	CAMS 143118	2
A. sp. cf. *A. edwardsi*	4500 ± 130	5090 ± 380	Uncataloged (UMASS; TW6 A)[b]	CAMS 143260	2
A. sp. cf. *A. edwardsi*	2820 ± 35	2860 ± 90	UA 8697	CAMS 143127	2
Eidolon dupreanum	330 ± 70	325 ± 175	Uncataloged (UA)	β−56770 CAMS 4255	1
Eulemur fulvus	285 ± 25	300 ± 140	UA 8670	CAMS 142608	2
E. fulvus	280 ± 25	295 ± 145	UA 8693	CAMS 142560	2
E. fulvus	2320 ± 30	2250 ± 90	Uncataloged (UMASS; A29.2 N2 Extn. L. Branch)	CAMS 143192	2
Hippopotamus lemerlei	5300 ± 60	6050 ± 150	Uncataloged (UA; HFJ-93-2-B)	β−64961 CAMS 8648	1
H. lemerlei	3730 ± 70	4035 ± 205	Uncataloged (UA; HFJ-92-11)	β−55093 CAMS 3562	1
H. lemerlei	2890 ± 40	2940 ± 140	UA 3558	CAMS 143068	2
H. lemerlei	6310 ± 60	7150 ± 160	UA 4917	CAMS 142559	2
H. lemerlei	4055 ± 40	4540 ± 240	UA 3591	CAMS 143194	2
H. lemerlei	3455 ± 25	3685 ± 125	UA 3560	CAMS 143195	2
H. lemerlei	2635 ± 40	2635 ± 145	Uncataloged (UA)	CAMS 143193	2
H. lemerlei	3095 ± 30	3250 ± 110	Uncataloged (UA; 1992-M-395)	CAMS 143120	2
H. lemerlei	4815 ± 40	5660 ± 330	UA 9570	CAMS 144110	2
Lepilemur edwardsi	230 ± 25	225 ± 75	UA 2776	CAMS 142558	2
Propithecus coquereli	235 ± 25	225 ± 75	UA 8994	CAMS 142621	2
P. coquereli	195 ± 25	145 ± 145	UA 9002	CAMS 143119	2
P. coquereli	245 ± 25	230 ± 80	UA 8967	CAMS 142561	2
P. coquereli	360 ± 25	385 ± 75	UA 8968	CAMS 142730	2
P. coquereli	260 ± 30	235 ± 85	UA 8999	CAMS 142913	2
P. coquereli	255 ± 30	235 ± 85	UA 8976	CAMS 142899	2
Tenrec ecaudatus	250 ± 25	230 ± 80	Uncataloged (UA; UM 5085)	CAMS 143199	2
T. ecaudatus	320 ± 25	375 ± 75	Uncataloged (UA; UM 5089)	CAMS 143197	2
INTRODUCED					
Rattus rattus	Modern	Modern	Uncataloged (UMASS)	CAMS 143121	2
R. rattus	Modern	Modern	Uncataloged (UMASS)	CAMS 143122	2

[a]Sources: (1) Burney *et al*. (1997), and (2) this paper.

[b]Recent research on *Archaeolemur* sp. cf. *A. edwardsi* specimen UMASS TW6A, suggests that these postcranial bones and the skull and mandible whose matrix we analyzed belong to the same individual. If this is the case, the date for this individual is slightly younger than the hippo orbit found buried under the skull, as we originally predicted.

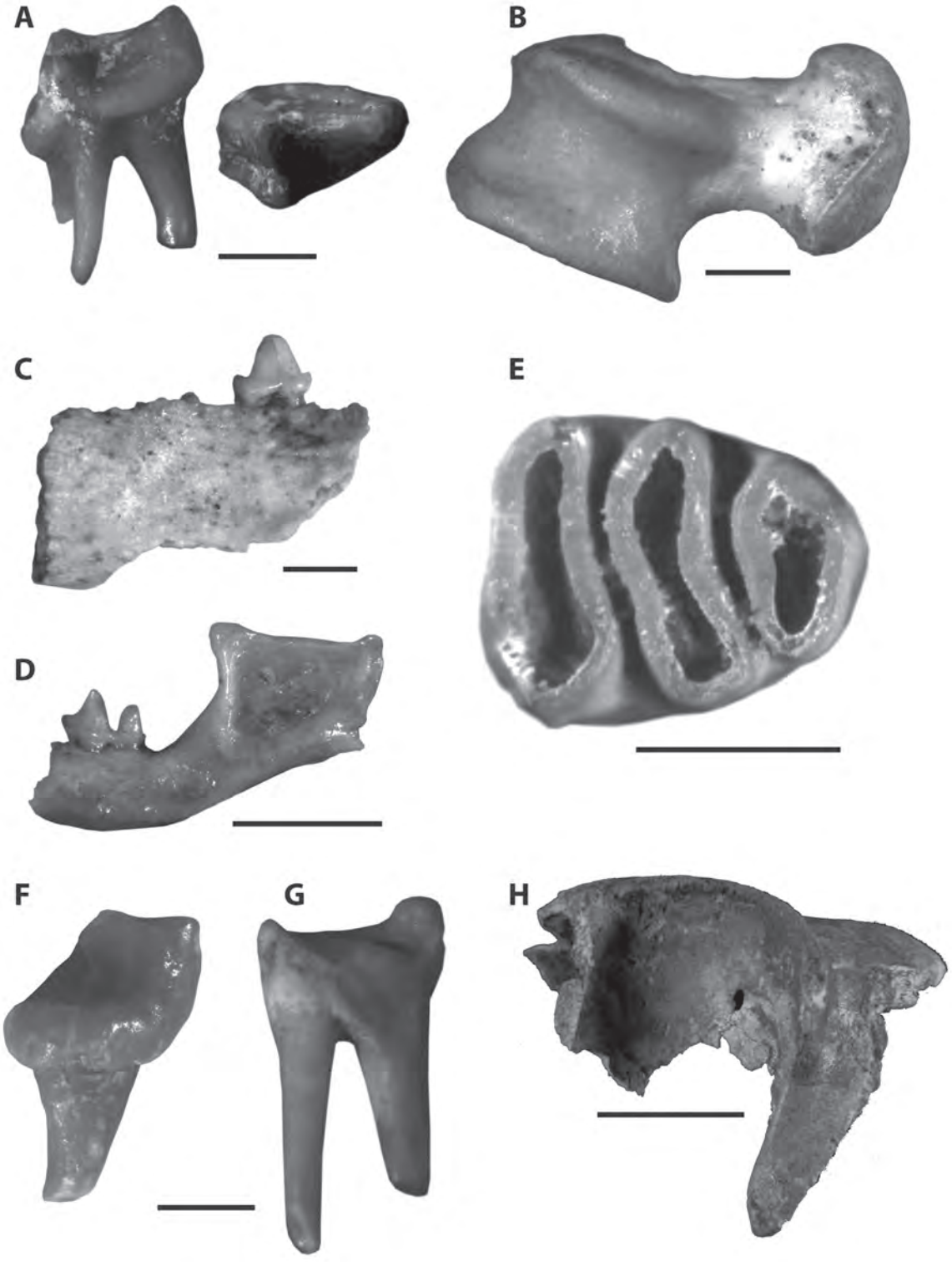

Figure 3. A, Left dp3 of *Microgale* sp. (UA 9569) lateral view on the right, occlusal view on the left, scale bar = 1 mm; B, left astragalus of *Galidia elegans* (UA 9554), scale bar = 2 mm; C, lingual view of left *Hipposideros* sp. cf. *H. besaoka* (UA 9582) mandible with P4, anterior at right,scale bar = 2 mm; D, labial view of partial left dentary of *Triaenops* sp. with M3 (UA 9581), scale bar = 2 mm; E, occlusal view of *Eliurus myoxinus* molar, right M3 (UA 9556), scale bar = 1 mm; F, partial left P2 of *Cheirogaleus medius* (UA 9572), scale bar = 1 mm; G, worn left M3 of *Microcebus murinus* (UA 9571), scale bar = 1 mm; H, *Hippopotamus lemerlei* fragmentary left orbit (UA 9570), scale bar = 2 cm.

Table 2. Taxa and specimens recovered from calcareous breccia surrounding *Archaeolemur* sp. cf. *A. edwardsi* specimen. UA, Département de Paléontologie et Anthropologie Biologique, Université d'Antananarivo, Madagascar.

Order	Family	Genus	Species	Referred Specimens
Afrosoricida	Tenrecidae	*Microgale*	sp.	Upper left dP3 (UA 9569)
Carnivora	Eupleridae	*Galidia*	*elegans*	One right and one left astragalus (UA 9553, UA 9554)
Chiroptera	Hipposideridae	*Hipposideros*	sp. cf. *besaoka*	Partial edentulous skull (UA 9586); right maxilla with M^{1-2}; right maxilla with P^4-M^2 (UA 9587); RC^1(UA 9576); RP^4 (UA 9580 [lot of 2]); and RM^1 (UA 9575); LP^4 (UA 9589); LM^2 (UA 9574 [lot of 2]); right mandible with M_{1-2} (UA 9585); RP_2 (UA 9591 [lot of 3]); RP_4 (UA9578); RM_1 (UA 9573); left mandible with P_4 (UA 9582); left mandible with M_2 (UA 9588); LC_1 (UA 9577 [lot of 2]; lower incisor (UA 9590)
		Triaenops	sp.	Two partial lower jaws, one left dentary with M3 (UA 9581) and left dentary with M2 (UA 9592)
Rodentia	Nesomyidae	*Eliurus*	*myoxinus*	Five isolated molars (UA 9555–9559); two right M^2, one right M_3 (Figure 3), left M^1 and M^3
Primates	Cheirogaleidae	*Microcebus*	*murinus*	Worn left M_3 (UA 9571)
		Cheirogaleus	*medius*	Broken left P_2 fragment with lingual portion intact (UA 9572)
Artiodactyla	Hippopotamidae	*Hippopotamus*	*lemerlei*	Fragmentary left orbit (UA 9570)

extends to at least 1000 Cal BP. With the exception of one record (*Eulemur fulvus* CAMS 143192), all dates for extant animals are modern or historical, including one species that was introduced to the island (*Rattus rattus*) (Table 1). Thus, even though the specimens we dated were all collected on the surface within the single cave system, the larger-bodied extinct species yielded older dates while smaller-bodied extant species yielded much younger dates.

One specimen from the matrix surrounding the *Archaeolemur* skull was sufficiently large for dating; this was a partial orbit of a young *Hippopotamus lemerlei* (UA 9570). This specimen was fully embedded in matrix and located just beneath the *Archaeolemur* skull. Radiocarbon dating produced a date of 4815 ± 40 ^{14}C BP (5660 ± 330 Cal BP).

Discussion

There are 22 living species of *Microgale*, making this genus the most speciose of the terrestrial mammals on the island today (Goodman *et al.*, 2006a, 2007; Olson *et al.*, 2009). *Microgale brevicaudata* is the only extant species currently recorded from the Anjohibe Cave region, although *M. grandidieri* was recently named from the Tsingy de Namoroka Strict Nature Reserve (Olson *et al*., 2009). Subfossil *Microgale,* and specifically *M. brevicaudata*, are described from a number of cave and surface sites widely distributed on the island (MacPhee *et al.*, 1985; MacPhee, 1987; Burney *et al.*, 1997; Muldoon *et al.*, 2009). An extinct species, *M. macpheei*, was named from Andrahomana Cave, southeastern Madagascar (Goodman *et al.*, 2007). The specimen from Anjohibe likely represents either *M. brevicaudata* or *M. grandidieri* (see Olson *et al.*, 2009). We refer UA 9569 to *Microgale* sp. until more diagnosable material is recovered (Figure 3).

The subfossil *Galidia elegans* reported here (Figure 3) is the second subfossil occurrence for this species across the island; it is also described from Ankilitelo, in the southwest (Muldoon *et al.*, 2009), more than 1,000 km away from Anjohibe Cave. This endemic genus is currently restricted to the eastern rainforest, the northwest in the forests of Montagne d'Ambre and the Sambirano, and isolated populations extending from the northwest south to Bemaraha (Bennett *et al.*, 2009). *Galidia* is considered a forest-dwelling animal (Goodman, 2003); thus, this record provides evidence that the Anjohibe region (now largely grassland) was more densely forested in the past.

Hipposideros is a widely distributed Old World tropical bat genus, and *H. commersoni* inhabits Anjohibe Cave today (S. M. Goodman, pers. comm.). Subfossil *H. commersoni* have been reported from Anjohibe Cave (Burney *et al.*, 1997; Samonds,

2007) and from the Lake Tsimanampetsotsa region in the southwest (Sabatier & Legendre, 1985; MacPhee, 1986). A subfossil Malagasy species (*H. besaoka*) with larger and more robust teeth than seen in modern Malagasy *H. commersoni* was described from Anjohibe Cave (Samonds, 2007). The specimens considered here (Figure 3) are referable to *Hipposideros* based on the dental formula and tooth morphology (see Samonds, 2007). The molar measurements of the *Hipposideros* fossils recovered from the breccia are intermediate between the two species reported from the cave, although they are most similar to *H. besaoka*; our material is tentatively referred to *Hipposideros* sp. cf. *H. besaoka*.

The bat genus *Triaenops* is widespread throughout eastern Africa, Madagascar, the coast of the Arabian Peninsula, and Aldabra Island. Extant populations of *T. menamena* and *T. furculus* are described from Anjohibe Cave. Subfossil specimens of an extinct species, *T. goodmani* (Samonds, 2007) have been named from Anjohibe Cave. Subfossils reported here (Figure 3) are clearly referable to *Triaenops*, but diagnosis to the species level was not possible.

The endemic rodent genus *Eliurus* includes 12 species (Musser & Carleton, 2005; Carleton & Goodman, 2007; Goodman *et al.*, 2009). Subfossil materials of *Eliurus myoxinus* and *Eliurus* sp. are reported from the Anjohibe Cave region (Burney *et al.*, 1997). The three species known from western central Madagascar are *E. myoxinus*, *E. antsingy*, and *E. minor* (Rakotondravony *et al*., 2002; Carleton, 2003). Although *E. myoxinus* shows considerable morphological variation over its large geographic range, the subfossil specimens reported here fit the size range of the larger of the two morphs that are currently included in *Eliurus myoxinus*, and are referred to this species (Figure 3).

Within Primates, the genus *Microcebus* has 19 recognized species, 15 of which have been described within the last 10 years (Mittermeier *et al.*, 2008; Radespiel *et al.*, 2008). The species living closest to Anjohibe are *M. murinus* and *M. ravelobensis* (Olivieri *et al.*, 2007); based on the size and morphology of UA 9571, this specimen is referred to *M. murinus* (Figure 3).

Cheirogaleus has been reported to include as many as seven different species (Groves, 2000) but recent morphological and genetic work suggests the presence of only four (Groeneveld, 2008; Blanco *et al*., 2009). *Cheirogaleus medius* and *C. crossleyi* are known from the nearby Ankarafantsika forest (Groves, 2000; Groeneveld *et al.*, 2009), and the specimen reported here is referred to *C. medius* based on its morphology and smaller size (Figure 3).

Across the world, the genus *Hippopotamus* contains 27 taxa (some authors divide these among two genera), with three diminutive extinct species described as subfossils from Madagascar (*H. lemerlei*, *H. madagascariensis*, and *H. laloumena*; Stuenes, 1989; Faure & Guerin, 1990). The partial orbit (UA 9570) extracted from the carbonate matrix surrounding our focal *Archaeolemur* skull most closely matches the morphology of *H. lemerlei* (Figure 3); this species has been previously reported from Anjohibe Cave (Burney *et al.*, 1997). Although the most recent date for Anjohibe *Hippopotamus* is ca. 2635 Cal BP, Malagasy pygmy hippos are considered recent extinctions, as there is compelling evidence that some survived into the historical period (Burney & Ramilisonina, 1999; Burney *et al.*, 2004).

Significance and broader implications

With the near-lack of an older Cenozoic terrestrial fossil record, subfossils (oldest ~80,000 years; Samonds, 2007) are our best direct tool for elucidating important details of the evolutionary history of Madagascar's vertebrate fauna. While the Quaternary fauna of Madagascar is not ancient enough to provide details of how, when, and from where most groups arrived (the youngest arrival date for mammals native to Madagascar is 19 million years ago; Poux *et al.*, 2005), this record can contribute important information for understanding recent extinctions, and ecological and biogeographic change.

First, subfossils can elucidate past geographic ranges of still-extant species (Godfrey & Vuillaume-Randriamanantena, 1986; Goodman *et al.*, 2006b; Burney *et al.*, 2008; Muldoon *et al.*, 2009), which may have been significantly larger than those of modern populations, and may have included regions that no longer provide suitable habitat (see Burney *et al.*, 1997; Muldoon, 2010). For example, we recovered *Galidia elegans* from the Anjohibe breccia matrix. Although *G. elegans* is currently found to the north and the south of the cave, Anjohibe is situated within a gap in this species' modern range, suggesting that this region was more forested in the past. This is consistent with the past presence of arboreally-adapted lemurs such as the extinct "sloth" lemurs *Palaeopropithecus* and *Babakotia* (Burney *et al.*, 1997). Additionally, one of the most common subfossil lemur species in surface deposits at Anjohibe is the still-extant *Prolemur* (*Hapalemur*) *simus*, currently restricted to the eastern rainforest of Madagascar. This species has a

specialized diet and occurs in habitats very different from those found in the Anjohibe region today.

Second, these sub-fossil assemblages can help establish the timing of extinctions relative to human arrival, which is useful in testing hypotheses about their causes (Godfrey & Jungers, 2003; Burney *et al.*, 2004; Goodman *et al.*, 2004, 2006b). Dating of subfossil pygmy hippos, elephant birds, giant tortoises, and lemurs demonstrates that most, if not all, of these large-bodied extinct taxa were present on the island when humans arrived ca. 2000 years ago (Burney *et al.*, 2004). The radiocarbon dates we present here include the most recent direct records reported for *Archaeolemur* sp. cf. *A. edwardsi* and *Hippopotamus lemerlei* at Anjohibe (the coprolite from the nearby cave Anjohikely was dated to 830 ^{14}C BP, Burney *et al*., 1997), and our most recent date for *Archaeolemur* at this site falls within the human period. Nevertheless, the absence of specimens < 1000 Cal BP (with the exception of the coprolite) bears testimony to the decline or local extirpation of these species following the arrival of humans.

Finally, subfossils can also help pinpoint the timing of recent arrivals, especially with regards to invasive species (Hingston *et al.*, 2005). This is particularly important for understanding population dynamics as research indicates that invasive species replace endemics (Goodman, 1995). We recovered no invasive species within the subfossil matrix surrounding the *Archaeolemur* skull, which suggests that introduced animals are a relatively recent addition to the Anjohibe fauna, most likely with the arrival of humans. In agreement with this assumption, two modern *Rattus rattus* individuals comprise the only dated introduced species from Anjohibe.

While the valuable information contained in subfossils is clear, the question remains as to why go to the trouble of looking for small mammals in breccias when they may be more abundantly and easily found elsewhere? Even when breccias do not contain abundant bone, as in the case of the cave matrix treated here, they may contain small specimens that provide valuable contextual information. While it is possible that redeposition occurs during their formation, breccias may have a better chance of representing short time periods than open-air surface-collected fossils (Conroy, 1996). As we have seen, most of the surface collected specimens of small-bodied extant animals yielded dates that do not overlap with the known temporal range for *Archaeolemur* and *H. lemerlei* at Anjohibe. This is not because small animal bones are not preserved well in caves; indeed the oldest Quaternary fossils from Madagascar are bats in a bone breccia demonstrated to have formed some time between 69,600 and 86,800 BP (Samonds, 2007). Instead, it appears to be because small mammals have not always been targeted during excavations or dating.

The date from the hippo orbit (5660 ± 330 Cal BP) gives us the likely period for the taxa remains found in the breccia. While we cannot rule out taphonomic processes having mixed some temporally non-overlapping taxa within the breccia, based on this date, we surmise that these breccias formed prior to human arrival. The overlying matrix may have accumulated shortly following the deaths of the *Archaeolemur* and the *Hippopotamus* lying directly below the *Archaeolemur* skull. The implied contemporaneity of *Archaeolemur* and *Hippopotamus* at this site is unsurprising and is supported by radiocarbon dates for other specimens from the cave; their likely association with *Galidia elegans* and the other small mammals described here is a more novel contribution to the paleoecology of this site.

In recent decades, small mammal fossils have been increasingly recognized as an important component of paleontological studies, and several newly named subfossil species have been described from Madagascar (Goodman *et al.*, 2006, 2007; Samonds, 2007). Small mammals in particular are important indicators of climate change (Wesselman, 1985; Blois & Hadly, 2009), and can contribute to our understanding of paleoenvironment and paleodiet (Hopley *et al.*, 2006; Garcia-Alix *et al.*, 2008; Muldoon, 2010; Muldoon and Goodman, 2010). In light of the information that can be gained from subfossil small mammals, it is important to ask whether current paleontological research techniques are effective at recovering these remains. First, small fossils are generally more delicate and may be more susceptible to destructive taphonomic processes (Andrews, 1990; Cooper *et al.*, 2006; Grady & Olson, 2006), thus a bias may exist even before collection. Second, small fossils are also more easily overlooked by field collectors (Valentine *et al.*, 2006), and method of collection (e.g., prospecting techniques, sieve size, collection priorities, and site choice) affects which fossils are recovered (Kowalewski & Hoffmeister, 2003; Jeppsson, 2005).

Small fossils can also be lost or destroyed during most forms of fossil preparation. Many fossils are collected encased in matrix, which is removed in order to reveal the larger fossils of interest. Matrix removal is usually accomplished by acid preparation for

limestone sediments (which typically preserves small fossils), or physical removal using hand tools (which is more likely to destroy small fossils, or leave them embedded in pieces of matrix). Fossil preparators are often paid by the project or hour, and are typically not expected to systematically examine pieces of matrix to see if they contain small fossils.

The presence of a collection bias is well-known in paleontological studies, but less attention has been paid to "preparation bias", meaning that the type of preparation technique used has an important (and largely irreversible) effect on the size and type of material recovered. The results presented here suggest that when making choices about collection and preparation techniques, paleontologists should consider this trade-off between getting fossils prepared quickly and efficiently and preserving as much information as possible.

The discovery of smaller-bodied extinct species in cave deposits is increased if fragmentary remains are retrieved from breccias (Samonds, 2007). Currently, most described subfossil species are megafauna; recovery of extinct small mammals will allow a more complete reconstruction of morphological and ecological diversity at the species and community level (e.g., Muldoon, 2010).

Conclusion

This study demonstrates the potential of sediments that might otherwise be discarded to yield valuable information on subfossil cave deposits. As larger-bodied animals are frequently prioritized in both collection and preparation, the practice of discarding matrix around a specimen of interest may eliminate the possibility of recovering identifiable small mammal remains.

In the case examined here, in only 1 kg of cave matrix, we have demonstrated the existence of eight species, two of which are extinct (*Hipposideros* sp. cf. *H. besaoka* and *Hippopotamus lemerlei*). Furthermore, the presence of *Galidia elegans*, a forest-dwelling carnivoran, represents the first subfossil occurrence of this genus at Anjohibe Cave, and corroborates other evidence, such as the past presence of arboreal sloth lemurs and greater bamboo lemurs, that the vegetation of this region was more densely forested in the recent past. Future research should seek to address whether typical collection and preparation techniques are adequately recovering small fossils from Malagasy subfossil sites. Researchers should seek to improve collections of small fossils, as well as identifying and describing specimens in existing collections. In addition, because of complicating factors such as ecogeographic size variation, biological inventories of living species at or near subfossil sites will help researchers better interpret what is documented in the subfossil record (Muldoon & Simons, 2007; Ranivo & Goodman, 2007a, 2007b; Samonds, 2007).

More than 70 subfossil localities, many of which are caves, are recognized on the island (Godfrey *et al.*, 1999; Burney *et al.*, 2004). Greater attention to small taxa in studies of Malagasy subfossil assemblages, particularly their spatial and temporal variability, will reveal a more complete picture of how species richness, diversity, and the geographic distributions of particular animals changed through time. This will increase our understanding of the history of Madagascar's fauna, while also allowing for more accurate tests of hypotheses regarding the effects of ecological change through time.

Acknowledgements

We wish to thank the Government of Madagascar for permission to conduct research in Madagascar, which was in collaboration with the Département de Paléontologie et Anthropologie Biologique, Université d'Antananarivo, Antananarivo. We are grateful to the museums and curators that helped to facilitate this research, including B. Stanley (FMNH), J. Chupasko (MCZ), N. Simmons, B. Randall, and J. Spence (AMNH), L. Gordon and H. James (USNM), and A. Rasoamiaramanana and the late G. Randria (UA). For assistance at various stages of this study, we thank D. Boyer, L. Chapman, S. Goodman, J. Groenke, V. Heisey, L. Horn, M. Irwin, D. Krause, M. O'Leary, L. Piche, S. Rachootin, J. Ratsimbazafy, T. Worthy, and P. Zermeno. We thank the research team that collected the Anjohibe Cave breccia, including D. Burney, M. Burney, M. Egan, L. Godfrey, H. James, W. Jungers, T. Olson, and T. Worthy. We are grateful to F. Grady (USNM) for his instruction in acetic acid preparation techniques. Thanks to M. Blanco for her photograph for Figure 2. Grant support was provided by the American Philosophical Society to K. Samonds, a UCOP Lab Fees Grant to N. Dominy, and NSF grant BCS-0129185 to D. Burney, W. Jungers, and L. Godfrey.

References

Ambrose, S. H. 1991. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. *Journal of Archaeological Science*, 18: 293-317.

Andrews, P. 1990. *Owls, caves, and fossils: Predation, preservation, and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset, UK*. The University of Chicago Press, Chicago.

Bennett, C. E., Pastorini, J., Dollar, L. & Hahn, W. J. 2009. Phylogeography of the Malagasy ring-tailed mongoose, *Galidia elegans*, from mtDNA sequence analysis. *Mitochondrial DNA*, 20: 7-14.

Blanco, M. B., Godfrey, L. R., Rakotondratsima, M., Samonds, K. E., Raharison, J.–L. & Irwin, M. T. 2009. Discovery of sympatric dwarf lemur species in the high-altitude rainforest of Tsinjoarivo, eastern Madagascar: Implications for biogeography and conservation. *Folia Primatologica*, 80: 1-17.

Blois, J. L. & Hadly, E. A. 2009. Mammal response to Cenozoic climate change. *Annual Review of Earth and Planetary Sciences*, 37: 181-208.

Brook, G. A., Rafter, M. A., Railsback, L. B., Sheen, S.-W. & Lundberg, J. 1999. A high-resolution proxy record of rainfall and ENSO since AD 1550 from layering in stalagmites from Anjohibe Cave, Madagascar. *The Holocene*, 9: 695-705.

Burney, D. A. 1993. Late Holocene environmental changes in arid southwestern Madagascar. *Quaternary Research*, 40: 98-106.

Burney, D. A. 1999. Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In *Extinctions in near time*, ed. R. MacPhee, pp. 145-164. Kluwer Academic/Plenum Publishers, New York.

Burney, D. A. 2003. Madagascar's prehistoric ecosystems. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 47-51. The University of Chicago Press, Chicago.

Burney, D. A. & Flannery, T. F. 2005. Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology & Evolution*, 20: 395-401.

Burney, D. A. & Ramilisonina. 1999. The kilopilopitsofy, kidoky, and bokyboky: Accounts of strange animals from Belo-sur-mer, Madagascar, and the megafaunal "extinction window". *American Anthropologist*, 100: 957-966.

Burney, D. A., James, H. F., Grady, F. V., Jean-Gervais Rafamantanantsoa, R., Wright, H. T. & Cowart, E. J. B. 1997. Environmental change, extinction and human activity: Evidence from caves in NW Madagascar. *Journal of Biogeography*, 24: 755-767.

Burney, D. A., Robinson, G. S. & Burney, L. P. 2003. *Sporormiella* and the late Holocene extinctions in Madagascar. *Proceedings of the National Academy of Sciences, USA*, 100: 10800-10805.

Burney, D. A., Burney, L. P., Godfrey, L. R., Jungers, W. L., Goodman, S. M., Wright, H. T. & Jull, A. J. T. 2004. A chronology for late prehistoric Madagascar. *Journal of Human Evolution*, 47: 25-63.

Burney, D. A., Vasey, N., Godfrey, L. R., Ramilisonina, Jungers, W. L., Ramarolahy, M. & Raharivony, L. 2008. New findings at Andrahomana Cave, southeastern Madagascar. *Journal of Cave and Karst Studies*, 70: 13-24.

Carleton, M. D. 2003. *Eliurus*, tufted-tailed rats. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 1373-1380. The University of Chicago Press, Chicago.

Carleton, M. D. & Goodman, S. M. 2007. A new species of the *Eliurus majori* complex (Rodentia: Muroidea: Nesomyidae) from south-central Madagascar, with remarks on emergent species groupings in the genus *Eliurus*. *American Museum Novitates*, 3547: 1-21.

Conroy, G. C. 1996. The cave breccias of Berg Aukas, Namibia: A clustering approach to mine dump paleontology. *Journal of Human Evolution*, 30: 349-355.

Cooper, R. A., Maxwell, P. A., Crampton, J. S., Beu, A. G., Jones, C. M. & Marshall, B. A. 2006. Completeness of the fossil record: Estimating losses due to small body size. *Geology*, 34: 241-244.

Crowley, B.E. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Journal of Quaternary Science*, 29: 2591-2603.

Decary, R. 1934. Les grottes d'Anjohibe. *La Revue de Madagascar*, 8: 81-85.

Decary, R. 1938. Les grottes d'Andranoboka. *La Revue de Madagascar*, 1938: 7-48.

Faure, M. & Guerin, C. 1990. *Hippopotamus laloumena* nov. sp., la troisième espèce d'hippopotame Holocène de Madagascar. *Comptes Rendus de l'Académie des Sciences,* série 11, 310: 1299-1305.

Filhol, M. H. 1895. Observations concernant les mammifères contemporains des *Aepyornis* à Madagascar. *Bulletin de Muséum national d'Histoire naturelle*, 1: 12-14.

Forsyth-Major, C. I. 1894. On *Megaladapis madagascariensis*, an extinct gigantic lemuroid from Madagascar, with remarks on the associated fauna, and on its geologic age. *Philosophical Transactions of the Royal Society of London,* series B, 185: 15-38.

Garcia-Alix, A., Minwer-Barakat, R., Suarez, E. M., Freudenthal, M. & Martin, J. M. 2008. Late Miocene-Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography Palaeoclimatology Palaeoecology*, 265: 214-225.

Gasse, F. & Van Campo, E. 1998. A 40,000-yr pollen and diatom record from Lake Tritrivakely, Madagascar, in the southern tropics. *Quaternary Research*, 49: 299-311.

Godfrey, L. R. 1986. The tale of the tsy-aomby-aomby. *The Sciences*, Jan/Feb: 48-51.

Godfrey, L. R. & Irwin, M. T. 2007. The evolution of extinction risk: Past and present anthropogenic impacts on the primate communities of Madagascar. *Folia Primatologica,* 78: 405-419.

Godfrey, L. R. & Jungers, W. L. 2003. The extinct sloth lemurs. *Evolutionary Anthropology*, 12: 252-263.

Godfrey, L. R. & Vuillaume-Randriamanantena, M. 1986. *Hapalemur simus*: Endangered lemur once widespread. *Primate Conservation*, 7: 92-96.

Godfrey, L. R., Simons, E. L., Chatrath, P. J. & Rakotosamimanana, B. 1990. A new fossil lemur (*Babakotia,* Primates) from northern Madagascar. *Comptes rendus de l'Académie des sciences Paris*, 310: 81-87.

Godfrey, L. R., Jungers, W. L., Simons, E. L., Chatrath, P. S. & Rakotosamimanana, B. 1999. Past and present distributions of lemurs in Madagascar. In *New directions in lemur studies*, eds. B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn & S. M. Goodman, pp. 19-53. Plenum Publishers, New York.

Goodman, S. M. 1994. The enigma of antipredator behavior in lemurs: Evidence of a large extinct eagle on Madagascar. *International Journal of Primatology*, 15: 129-134.

Goodman, S. M. 1995. *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. *Conservation Biology*, 9: 450-453.

Goodman, S. M. 2003. *Galidia elegans*, ring-tailed mongoose, *vontsira mena*. In *The natural history of Madagascar*, eds. S. M. Goodman & J. P. Benstead, pp. 1351-1354. The University of Chicago Press, Chicago.

Goodman, S. M. & Benstead, J. P. 2005. Updates estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39: 73-77.

Goodman, S. M. & Rakotondravony, D. 1996. The Holocene distribution of *Hypogeomys* (Rodentia: Muridae: Nesomyinae) on Madagascar. In *Biogéographie de Madagascar*, ed. W. Lourenço, pp. 283-293. ORSTOM, Paris.

Goodman, S. M., Rasoloarison, R. M. & Ganzhorn, J. U. 2004. On the specific identification of subfossil *Cryptoprocta* (Mammalia, Carnivora) from Madagascar. *Zoosystema*, 26: 129-143.

Goodman, S. M., Andriafidison, D., Andrianaivoarivelo, R., Cardiff, S. G., Ifticene, E., Jenkins, R. K. B., Kofoky, A., Mbohoahy, T., Rakontrondravony, D., Ranivo, J., Ratrimomanarivo, F., Razafimanahaka, J. & Racey, P. A. 2005. The distribution and conservation of bats in the dry regions of Madagascar. *Animal Conservation*, 8: 1-13.

Goodman, S. M., Raxworthy, C. J., Maminirina, C. P. & Olson, L. E. 2006a. A new species of shrew tenrec (*Microgale jobihely*) from northern Madagascar. *Journal of Zoology*, 270: 384-398.

Goodman, S. M., Vasey, N. & Burney, D. A. 2006b. The subfossil occurrence and paleoecological implications of *Macrotarsomys petteri* (Rodentia: Nesomyidae) in extreme southeastern Madagascar. *Comptes Rendus Palevol*, 5: 953-962.

Goodman, S. M., Vasey, N. & Burney, D. A. 2007. Description of a new species of subfossil shrew tenrec (Afrosoricida: Tenrecidae: *Microgale*) from cave deposits in southeastern Madagascar. *Proceedings of the Biological Society of Washington*, 120: 367-376.

Goodman, S. M., Raheriarisena, M. & Jansa, S. A. 2009. A new species of *Eliurus* Milne Edwards, 1885 (Rodentia: Nesomyinae) from the Réserve Spéciale d'Ankarana, northern Madagascar. *Bonner zoologische Beiträge*, 56: 133-149.

Grady, F. V. & Olson, S. L. 2006. Fossil bats from Quaternary deposits on Bermuda (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, 87: 148-152.

Grandidier, G. 1905. Recherches sur les lémuriens disparus et en particulier sur ceux qui vivaient à Madagascar. *Nouvelles Archives du Muséum national d'Histoire naturelle, Paris*, 7: 1-142.

Grandidier, M. 1899. Description d'ossements de lémuriens disparus. *Bulletin du Muséum national d'Histoire naturelle*, 5: 344-349.

Grant, R. E. 1989. Extraction of fossils from carbonates by acid. In *Paleotechniques*, eds. R. M. Feldmann, R. E. Chapman & J. T. Hannibal, pp. 237-243. The Paleontological Society Special Publication, Knoxville.

Groeneveld, L. F. 2008. Species delimitation, phylogeography, and population genetics of the endemic Malagasy dwarf lemurs (genus *Cheirogaleus*). Ph.D. dissertation, University of Göttingen, Göttingen.

Groeneveld, L. F., Weisrock, D. W., Rasoloarison, R. M., Yoder, A. D. & Kappeler, P. M. 2009. Species delimitation in lemurs: Multiple genetic loci reveal low levels of species diversity in the genus *Cheirogaleus*. *BMC Evolutionary Biology*, 9: 30.

Groves, C. P. 2000. The genus *Cheirogaleus*: Unrecognized biodiversity in dwarf lemurs. *International Journal of Primatology*, 21: 943-962.

Hingston, M., Goodman, S. M., Ganzhorn, J. U. & Sommer, S. 2005. Reconstruction of the colonization of southern Madagascar by introduced *Rattus rattus*. *Journal of Biogeography*, 32: 1549-1559.

Hopley, P. J., Latham, A. G. & Marshall, J. D. 2006. Palaeoenvironments and palaeodiets of mid-Pliocene micromammals from Makapansgat Limeworks, South Africa: A stable isotope and dental microwear approach. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 233: 235-251.

Jeppsson, L. 2005. Biases in the recovery and interpretation of micropalaeontological data. In *Conodont biology and phylogeny - interpreting the fossil record, Special Papers in Palaeontology*, eds. M. Purnell & P. Donoghue, 73, 57-71. The Paleontological Association.

Kowalewski, M. & Hoffmeister, A. P. 2003. Sieves and fossils: Effects of mesh size on paleontological patterns. *Palaios*, 18: 460-469.

Krause, D. W., Hartman, J. H. & Wells, N. A. 1997. Late Cretaceous vertebrates from Madagascar: Implications for biotic change in deep time. In *Natural change and human impact in Madagascar*, eds. S. M. Goodman & B. D. Patterson, pp. 3-43. Smithsonian Institution Press, Washington, D. C.

Krause, D. W., O'Connor, P. M., Rogers, K. C., Sampson, S. D., Buckley, G. A. & Rogers, R. R. 2006. Late Cretaceous terrestrial vertebrates from Madagascar: Implications for Latin American biogeography. *Annals of the Missouri Botanical Garden,* 93: 178-208

Lamberton, C. 1934a. Contribution à la connaissance de la faune subfossile *Archaeoindris fontoynonti* de Madagascar. Lémuriens et Ratites. *Mémoires de l'Académie Malgache*, 17: 9-39.

Lamberton, C. 1934b. Contribution à la connaissance de la faune subfossile de Madagascar. Lémuriens et Ratites. *Chiromys robustus* sp. nov. Lamb. *Mémoires de l'Académie Malgache*, 17: 40-46.

Leiggi, P. & May, P. 1994. Organic acid extraction of fossils from carbonate matrices: Direct immersion or modified transfer methods. In *Vertebrate paleontological techniques*, eds. P. Leiggi & P. May, pp. 156-179. Cambridge University Press, Cambridge.

Lindsay, W. 1995. A review of the acid technique. In *The care and conservation of palaeontological materials*, ed. C. Collins, pp. 95-101 Butterworth-Heinemann Ltd., Oxford.

Lorenz von Liburnau, L. 1900. Über einen Reste ausgestorbener Primaten von Madagaskar. *Denkschriften der kaiselichen Akademie der Wissenschaften in Wien*, 70: 1-15.

MacPhee, R. D. E. 1986. Environment, extinction, and Holocene vertebrate localities in southern Madagascar. *National Geographic Research*, 2: 441-455.

MacPhee, R. D. E. 1987. The shrew tenrecs of Madagascar: Systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). *American Museum Novitates*, 2889: 1-45.

MacPhee, R. D. E. 1994. Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of eutherian mammals. *Bulletin of the American Museum of Natural History*, 220: 1-214.

MacPhee, R. D. E., Burney, D. A. & Wells, N. A. 1985. Early Holocene chronology and environment of Ampasambazimba, a Malagasy subfossil lemur site. *International Journal of Primatology*, 6: 463-489.

McCormac, F. G., Hogg, A. G., Blackwell, P. G., Buck, C. E., Higham, T. F. G. & Reimer, P. J. 2004. SHCal04 Southern Hemisphere Calibration 0 - 1000 cal BP. *Radiocarbon*, 46: 1087-1092.

Mittermeier, R., Ganzhorn, J., Konstant, W., Glander, K., Tattersall, I., Groves, C., Rylands, A., Hapke, A., Ratsimbazafy, J., Mayor, M., Louis, E. E., Rumpler, Y., Schwitzer, C. & Rasoloarison, R. 2008. Lemur diversity in Madagascar. *International Journal of Primatology*, 29: 1607-1656.

Muldoon, K. M. 2010. Paleoenvironment of Ankilitelo Cave (late Holocene, southwestern Madagascar): Implications for the extinction of giant lemurs. *Journal of Human Evolution*, 58: 338-352.

Muldoon, K. M. & Goodman, S. M. 2010. Ecological biogeography of Malagasy non-volant mammals: community structure is correlated with habitat. *Journal of Biogeography*, 37: 1144-1159.

Muldoon, K. M. & Simons, E. L. 2007. Ecogeographic size variation in small-bodied subfossil primates from Ankilitelo, southwestern Madagascar. *American Journal of Physical Anthropology*, 134: 152-161.

Muldoon, K. M., DeBlieux, D. D., Simons, E. L. & Chatrath, P. S. 2009. The subfossil occurrence and paleoecological significance of small mammals at Ankilitelo Cave, southwestern Madagascar. *Journal of Mammalogy*, 90: 1111-1131.

Musser, G. G. & Carleton, M. D. 2005. Superfamily Muroidea. In *Mammal species of the World: A taxonomic and geographic reference*, eds. D. Wilson & D. Reeder, pp. 894-1531. Johns Hopkins University Press, Baltimore.

Olivieri, G., Zimmermann, E., Randrianambinina, B., Rasoloharijaona, S., Rakotondravony, D., Guschanski, K. & Radespiel, U. 2007. The ever-increasing diversity in mouse lemurs: Three new species in north and northwestern Madagascar. *Molecular Phylogenetics and Evolution*, 43: 309-327.

Olson, L. E., Rakotomalala, Z., Hildebrandt, K. B. P., Lanier, H. C., Raxworthy, C. J. & Goodman, S. M. 2009. Phylogeography of *Microgale brevicaudata* (Tenrecidae) and description of a new species from western Madagascar. *Journal of Mammalogy*, 90: 1-25.

Poux, C., Madsen, O., Marquard, E., Vieites, D. R., de Jong, W. W. & Vences, M. 2005. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. *Systematic Biology*, 54: 719-730.

Radespiel, U., Olivieri, G., Rasolofoson, D. W., Rakotondratsimba, G., Rakotonirainy, O., Rasoloharijaona, S., Randrianambinina, B., Ratsimbazafy, J. H., Ratelolahy, F., Randriamboavonjy, T., Rasolofoharivelo, T., Craul, M., Rakotozafy, L. & Randrianarison, R. M. 2008. Exceptional diversity of mouse lemurs (*Microcebus* spp.) in the Makira region with the description of one new species. *American Journal of Primatology*, 70: 1033-1046.

Rakotondravony D., Randrianjafy V. & Goodman S. M. 2002. Evaluation rapide de la diversité biologique des micromammifères de la Réserve Naturelle Intégrale d'Ankarafantsika. In *Une Evaluation biologique de la Réserve Naturelle Intégrale d'Ankarafantsika*, eds. L. E. Alonso, T. S. Schulenberg, S. Radilofe & O. Missa. *RAP Bulletin of Biological Assessment*, 23: 83–87.

Ranivo, J. & Goodman, S. M. 2007a. Patterns of ecomorphological variation in the bats of western Madagascar: Comparisons among and between communities along a latitudinal gradient. *Mammalian Biology*, 72: 1-13.

Ranivo, J. & Goodman, S. M. 2007b. Variation géographique de *Hipposideros commersoni* de la zone sèche de Madagascar (Mammalia, Chiroptera, Hipposideridae). *Verhandlungen des*

Naturwissenschaftlichen Vereins in Hamburg, 43: 33-56.

Sabatier, M., & Legendre, S. 1985. Une faune á rongeurs et chiroptères Plio-Pléistocenes de Madagascar. *Actes du 110e Congrès National des Sociétés Savantes*, 6: 21-28.

Samonds, K. E. 2007. Late Pleistocene bat fossils from Anjohibe Cave, northwestern Madagascar. *Acta Chiropterologica*, 9: 39-65.

Simons, E. L., Burney, D. A., Godfrey, L. R., Jungers, W. L. & Rakotosamimanana, B. 1995. AMS ^{14}C dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quarternary Research*, 43: 249-254.

Standing, H. F. 1905. Rapport sur des ossements subfossiles provenant d'Ampasambazimba. *Bulletin de l'Académie Malgache*, 4: 95-100.

Standing, H. F. 1908. On recently discovered subfossil primates from Madagascar. *Transactions of the Zoological Society of London*, 18: 69-162.

Stuenes, S. 1989. Taxonomy, habits and relationships of the sub-fossil Madagascan hippopotamuses, *Hippopotamus lemerlei* and *H. madagascariensis*. *Journal of Vertebrate Paleontology*, 9: 241-268.

Stuiver, M. & Reimer, P. J. 1993. Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon*, 35: 215-230.

Toombs, H. A. & Rixon, A. E. 1959. The use of acids in the preparation of vertebrate fossils. *Curator*, 11: 304-312.

Valentine, J. W., Jablonski, D., Kidwell, S. & Roy, K. 2006. Assessing the fidelity of the fossil record by using marine bivalves. *Proceedings of the National Academy of Sciences of the United States of America*, 103: 6599-6604.

Virah-Sawmy, M., Willis, K. J. & Gillson, L. 2010. Evidence for drought and forest declines during the recent megafaunal extinctions in Madagascar. *Journal of Biogeography*, 37: 506-519.

Wesselman, H. B. 1985. Fossil micromammals as indicators of climatic change about 2.4 Myr ago in the Omo Valley, Ethiopia. *South African Journal of Science*, 81: 260-261.