

# Subfossil lemur discoveries from the Beanka Protected Area in western Madagascar

David A. Burney<sup>a\*</sup>, Haingoson Andriamialison<sup>b</sup>, Radosoa A. Andrianaivoarivelo<sup>c</sup>, Steven Bourne<sup>d</sup>, Brooke E. Crowley<sup>e</sup>, Erik J. de Boer<sup>f</sup>, Laurie R. Godfrey<sup>g</sup>, Steven M. Goodman<sup>h,i</sup>, Christine Griffiths<sup>c</sup>, Owen Griffiths<sup>c,i</sup>, Julian P. Hume<sup>j</sup>, Walter G. Joyce<sup>k</sup>, William L. Jungers<sup>l</sup>, Stephanie Marciniak<sup>m</sup>, Gregory J. Middleton<sup>n</sup>, Kathleen M. Muldoon<sup>o</sup>, Eliette Noromalala<sup>b</sup>, Ventura R. Pérez<sup>g</sup>, George H. Perry<sup>m</sup>, Roger Randalana<sup>c</sup>, Henry T. Wright<sup>p</sup>

<sup>a</sup>National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, Hawaii 96741, USA

<sup>b</sup>Mention Anthropobiologie et Développement Durable, Domaine Sciences et Technologie, Université de Antananarivo, B.P. 906, Antananarivo 101, Madagascar

<sup>c</sup>Biodiversity Conservation Madagascar, B.P. 11028, Antananarivo 101, Madagascar

<sup>d</sup>Naracoorte Lucindale Council, P.O. Box 2153, Naracoorte, Australia

<sup>e</sup>Departments of Geology and Anthropology, University of Cincinnati, Cincinnati, Ohio 45221, USA

<sup>f</sup>Institute of Earth Sciences Jaume Almera (ICTJA-CSIC), Lluís Solé i Sabaris s/n, 08028 Barcelona, Spain

<sup>g</sup>Department of Anthropology, University of Massachusetts–Amherst, 240 Hicks Way, Amherst, Massachusetts 01003, USA

<sup>h</sup>Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA

<sup>i</sup>Australian Museum, 1 William St., Sydney, New South Wales 2010, Australia

<sup>j</sup>Bird Group, Department of Life Sciences, Natural History Museum, Akeman Street, Tring HP23 6AP, United Kingdom

<sup>k</sup>Department of Geosciences, University of Fribourg, 1700 Fribourg, Switzerland

<sup>l</sup>Association Vahatra, BP 3972, Antananarivo 101, Madagascar

<sup>m</sup>Department of Anthropology, Pennsylvania State University, Old Main, State College, Pennsylvania 16801, USA

<sup>n</sup>Sydney Speleological Society, Box 269, Sandy Bay, Tasmania 7006, Australia

<sup>o</sup>Department of Anatomy, College of Graduate Studies, Midwestern University, Glendale, Arizona 85308, USA

<sup>p</sup>Museum of Anthropological Archaeology, University of Michigan, Ann Arbor, Michigan 48109, and Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA

\*Corresponding author at: P.O. Box 36, Gloucester, North Carolina 28528, USA. E-mail address: [dburney999@gmail.com](mailto:dburney999@gmail.com) (D.A. Burney).

(RECEIVED March 5, 2019; ACCEPTED July 27, 2019)

## Abstract

A new fossil site in a previously unexplored part of western Madagascar (the Beanka Protected Area) has yielded remains of many recently extinct vertebrates, including giant lemurs (*Babakotia radofilai*, *Palaeopropithecus kelyus*, *Pachylemur* sp., and *Archaeolemur edwardsi*), carnivores (*Cryptoprocta spelea*), the aardvark-like *Plesiorycteropus* sp., and giant ground cuckoos (*Coua*). Many of these represent considerable range extensions. Extant species that were extirpated from the region (e.g., *Prolemur simus*) are also present. Calibrated radiocarbon ages for 10 bones from extinct primates span the last three millennia. The largely undisturbed taphonomy of bone deposits supports the interpretation that many specimens fell in from a rock ledge above the entrance. Some primates and other mammals may have been prey items of avian predators, but human predation is also evident. Strontium isotope ratios ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) suggest that fossils were local to the area. Pottery sherds and bones of extinct and extant vertebrates with cut and chop marks indicate human activity in previous centuries. Scarcity of charcoal and human artifacts suggests only occasional visitation to the site by humans. The fossil assemblage from this site is unusual in that, while it contains many sloth lemurs, it lacks ratites, hippopotami, and crocodiles typical of nearly all other Holocene subfossil sites on Madagascar.

**Keywords:** *Babakotia*; Lemur extinction;  $^{14}\text{C}$  dating;  $\delta^{13}\text{C}$ ;  $\delta^{15}\text{N}$ ;  $^{87}\text{Sr}/^{86}\text{Sr}$ ; Biogeography

## INTRODUCTION

The Beanka Protected Area of central western Madagascar, a remote area of dry forest on rugged limestone, offers an

opportunity to study newly discovered “subfossil” sites (i.e., sites containing unfossilized remains from recent millennia). These were previously unknown to the scientific world and largely undisturbed by local people or other human visitors. Precious finds of this sort provide special opportunities to study paleodistributions, extinction patterns, and paleoecological characteristics of extinct species as well as the living fauna.

**Cite this article:** Burney, D. A. *et al* 2019. Subfossil lemur discoveries from the Beanka Protected Area in western Madagascar. *Quaternary Research* 1–17. <https://doi.org/10.1017/qua.2019.54>

Beanka offers a wealth of untouched bone material lying on sheltered cave surfaces, as well as in situ stratigraphic contexts not excavated previously or otherwise disturbed by recent human activity. This in itself is important, because the rarest type of subfossil site on Madagascar is one that has not been previously disturbed by large-scale collection. Notable exceptions, such as parts of the Ankarana Massif in northern Madagascar (Simons et al., 1995) and Anjohikely in northwestern Madagascar (Burney et al., 1997), have offered possibilities for geochronological, taphonomic, and paleoecological analyses otherwise hampered in the majority of sites by the rapid and careless excavation and collection techniques typical of earlier centuries and decades.

The location of Beanka provides the opportunity to fill in gaps concerning the inferred ranges of extinct species in a large region previously understudied for extinct fauna characteristic of the late Holocene. Beanka is situated well north of the many subfossil sites of semiarid southwestern Madagascar and south of the mesic subfossil sites in the northwest. Only a few subfossils have been described from the nearby Bemaraha karst formation (Godfrey et al., 2004). With the new material from Beanka, it is now feasible to see whether the fauna of this previously unknown region is more similar to the mesic fossil sites of the northwest or the arid southwestern sites or whether it represents a combination of the two or a unique assemblage.

In addition, the extremely rugged and isolated nature of the Beanka region raises the possibility that some taxa that are believed to have gone extinct earlier (Burney et al., 2004; Crowley, 2010) might have survived significantly later in such a remote and virtually impenetrable landscape. Some extinction hypotheses for the demise of the island's megafauna would predict a mosaic-like pattern of extinction that would include pockets of late survival in habitat that was resistant to anthropogenic change—an example of “synergy” (Burney, 1999; Burney et al., 2003) or “subsistence shift” (Godfrey et al., 2019). In contrast, two hypotheses proposed for late prehistoric extinctions following human arrival, “blitzkrieg” (Martin, 1984) and “hypervirulent disease” (MacPhee and Marx, 1997), predict that extinction on a landmass following human arrival would proceed as a wave in the former case or break out everywhere simultaneously (in geologic time) in the latter (Burney et al., 2004). Hypotheses that invoke climate change as a major factor, such as Virah-Sawmy et al. (2010), do not make an explicit prediction regarding patterns of extinction over the landscape, but it would be reasonable to expect that areas with late survival would be somehow buffered against drought conditions.

In the last few years, protected area staff and scientific collaborators have systematically explored Beanka, discovering many caves and rock shelters containing promising materials for paleontological and archaeological studies. Here we report the first results from a richly fossiliferous cave, named by the discovery group as “Anjohingidrobe” (Giant Lemur Cave; hereafter AGB), and a small fissure or slot cave nearby that the group named “Anjohimaletsy” (Narrow Cave; hereafter AMT). By providing a description of the

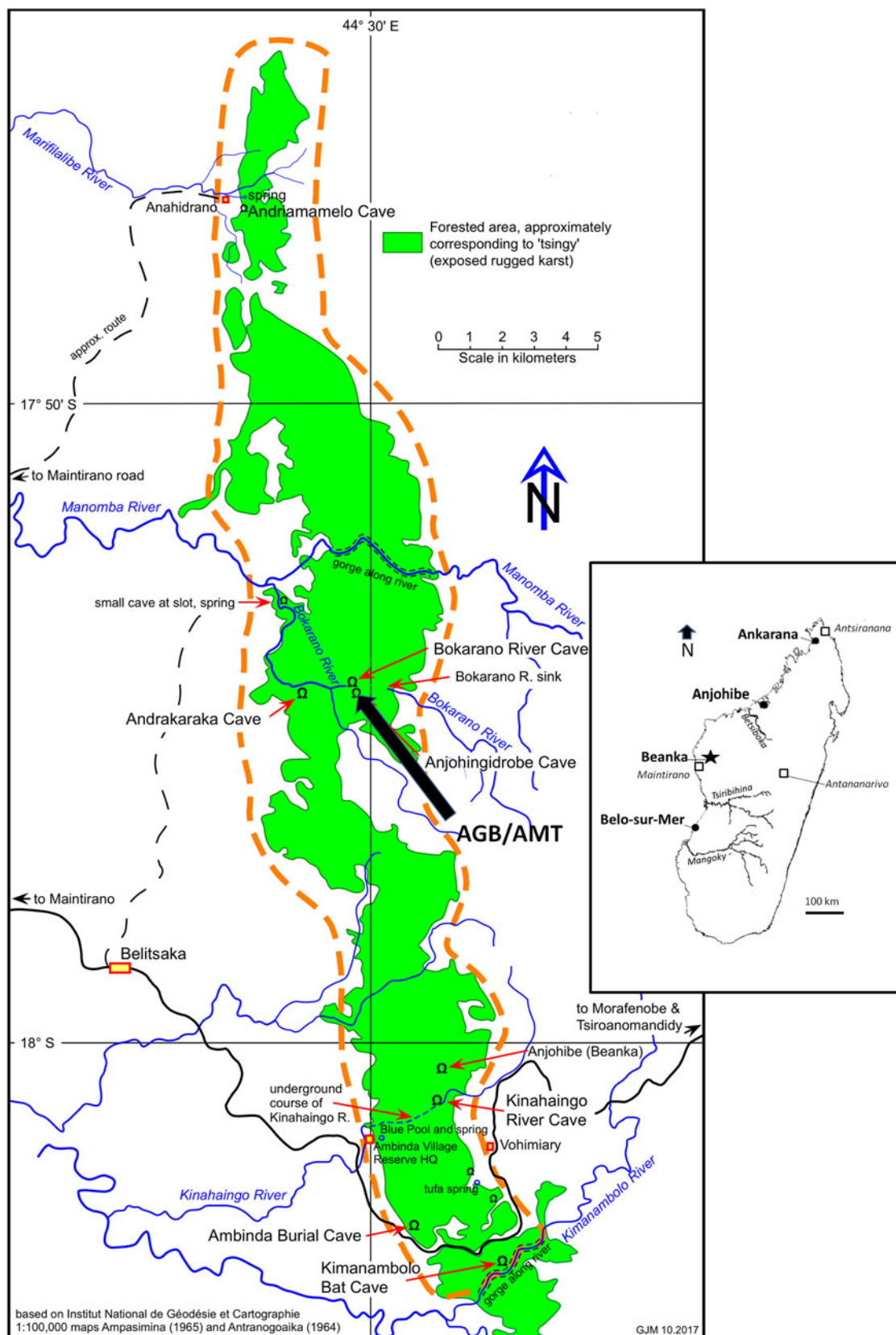
deposits, including positional and stratigraphic information, a preliminary radiocarbon chronology, and evaluation of preservation and paleoecological potential, we hope to provide some insight concerning environmental change and extinction dynamics as a backdrop to the late Holocene biodiversity crisis that is continuing and perhaps accelerating in Madagascar today. We also wish to set the stage for studies in progress, focusing on the details of chronology, biogeochemistry, systematics, and biogeography of an extensive area of Madagascar whose past was until now essentially unknown.

## LOCATION AND METHODS

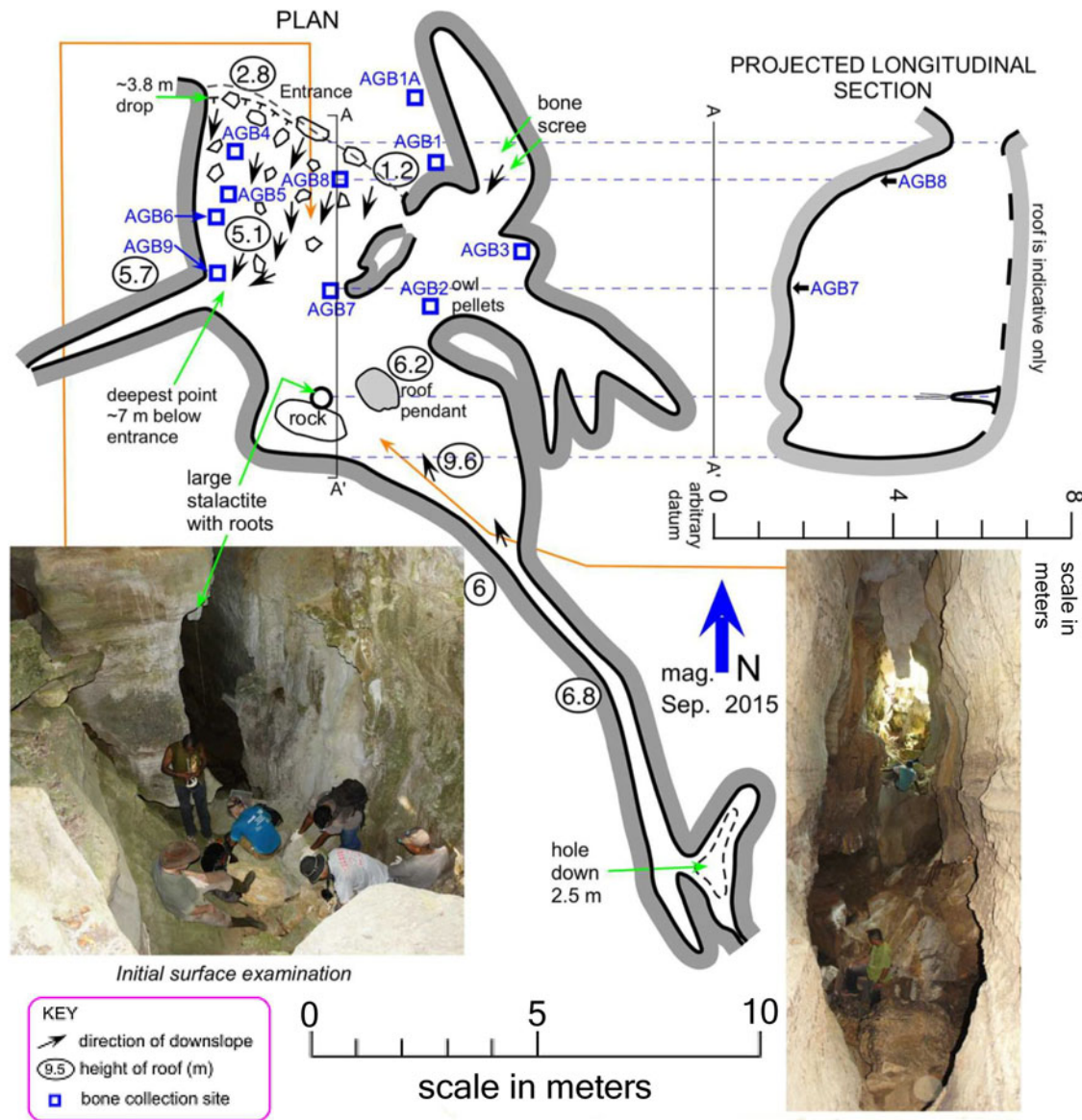
The Paysage Harmonieux Protégé de Beanka, a 17,100-ha protected area that was officially recognized on April 22, 2015, by a Malagasy government decree and is managed by Biodiversity Conservation Madagascar (BCM), is located ca. 350 km northwest of Antananarivo and 55 km east of Maintirano (Fig. 1). It is part of an extensive karst region (*tsingy* in Malagasy) that includes the Parc National de Bemaraha to the south, which is a UNESCO World Heritage site, and the remote Antsingimavo karst area to the north. The primary rock formation at Beanka is a Middle Jurassic limestone (Roig et al., 2012; Crowley and Sparks, 2018). Outcrops of Jurassic sandstone and shale are found along its eastern edge, and mid-Cretaceous sandstone, conglomerate, and shale flank its western edge. Within the limestone, rugged karst surface features, caves, narrow canyons, and subterranean rivers are covered in dense dry deciduous forest, thick with lianas, and more open woodlands. The nearly impenetrable nature of this landscape, combined with modern low human population densities, has resulted in limited anthropogenic pressure in this vast area, preserving natural habitats and endemic species and offering good potential for the discovery of caves containing previously untouched evidence for past life.

The Beanka area was briefly visited by speleologists in 1996, and the group returned in 2006 for a more detailed survey that revealed several interesting caves (Middleton, 2013). As in the adjacent karst areas, many caves are *grikes*, limestone features thought to have been formed by the solution of joints in the rock below the water table that subsequently opened to the surface (Veress et al., 2008).

Deep in the central part of the protected area is the Bokarano River, which itself flows underground through a winding cave passage for more than 1.6 km. Near the river, but higher up the hillside, is a small nearly vertical cave (AGB) that is ideally configured to collect and preserve animal remains (Fig. 2). In 2009, BCM project manager Roger Randalana discovered the small opening and noted that many bones, some visibly larger than any of the living lemurs of the area, littered the surfaces inside. In subsequent years, AGB and a smaller fissure cave nearby (AMT) were inspected by several collaborating scientists, and plans were made, including procurement of the necessary permits, to mount an expedition primarily for the purpose of making surface bone



**Figure 1.** (color online) Large arrow indicates location of Anjohingidrobe Cave (AGB) near the center of the Beanka Protected Area in western Madagascar, at 17°54.35'S, 44°29.40'E (WGS 84) and 218 m above sea level. Anjohimaletsy (AMT) is a small fissure cave 80 m east of AGB.



**Figure 2.** (color online) Plan map, vertical profile, and photographs of Anjohingidrobe Cave in the Beanka Protected Area. Surveyed by GJM with compass, inclinometer, and laser distance measure, September 21, 2013, and September 5, 2015.

collections, excavating test pits, and mapping the cave deposits. This work was conducted from September 5 to September 7 in 2015.

### Description of caves

AGB has a single opening, facing northeast, about 5 m wide and varying from 1 to 3 m high, at  $17^{\circ}54.35'S$ ,  $44^{\circ}29.40'E$  (WGS 84) and 218 m above sea level. Directly above the opening on the outside, there is a large rock ledge, 9.4 m above the top of the cave opening and greater than  $1\text{ m}^2$  in area. Immediately inside the cave opening (Fig. 2), the floor drops 3.8 m; large boulders form pockets inside at succeeding depths toward the back of the main chamber, where the ceiling is generally 6 to 9 m high and stalactites extend ca. 1 m from the ceiling. Rock shelves and scree slopes typify the east wall, and two small chambers end in soft clay sediment

deposits. On the west wall, the boulder slope continues into the deepest point of the cave, 7 m below the entrance. A narrow passage at the rear (south) end of the cave continues upward to end at a small hole in the floor lacking sediment. On the outside, 3 m east of the entrance, a small indentation in the rock forms a dead-end passage containing clay sediments, and similar material continues back along the cave wall westward to the cave entrance.

### Sublocations within AGB

Because the cave is predominantly vertical, with no large areas of horizontal or near-horizontal floor, it was necessary to distinguish bone accumulations in and near the cave by separate sublocation numbers, rather than a grid reference. These are noted in Figure 2, and Table 1 summarizes the characteristics of each sublocation. AGB-1 is the sediment layer

**Table 1.** Characteristics of sublocations.

Label	Location	Description
AGB-1	Outside cave entrance, east side	Mixture of limestone chips, boulders, and fine sediment
AGB-1A	3 m east of ABG-1	Fine to coarse sediments in small dead-end chamber
AGB-2	East wall inside cave	Sloping ledge with owl pellet deposits
AGB-3	Below east wall inside cave	Small dead-end chamber with fine sediment and bones
AGB-4	Below entrance drop-off	Surficial bone scatter in pocket between boulders
AGB-5	Downslope from AGB-4	Surficial bone scatter in pocket between boulders
AGB-6	Downslope from AGB-5	Surficial bone scatter in pocket between boulders
AGB-7	Farther inside near AGB-6	Nearly level area with several small bone pockets A–E
AGB-8	Below floor at drop-off	Small chamber below main floor level with sediments
ABG-9	Downslope from AGB-6	Deepest point of cave, with soft bone breccias
AMT	80 m E of AGB entrance	Small slot cave with soft sediment and breccias.

immediately east of the cave entrance. Where this rock wall enfolds to produce a small alcove, surface material and sediments were sublocated as AGB-1A. Proceeding into the main cave, a small ledge on the east wall inside is covered with a slope of fine debris (ABG-2). Directly below on the cave floor, a dead-end chamber descends farther under the east wall and is partially filled with soft clay sediment (AGB-3). Returning to the entrance, small pockets of bone-rich debris and sediment have accumulated at the base of the 3.8 m entrance drop, in a series of steps downward (AGB-4, AGB-5, and AGB-6). Immediately below AGB-5 and AGB-6 on the southward slope going back into the cave is a larger area of uneven topography, composed of large stones interspersed with bone-rich debris and sediment. This is the very productive sublocation AGB-7. Beneath the uneven floor of the cave near the entrance, there is a small chamber containing sediments with bones (AGB-8). On the opposite (west) wall of the cave, the cave floor descends to its lowest depth below the entrance at  $-7$  m. There is a lag concentrate of darkly stained bones and fine limestone chips in this deepest pocket, in places lightly cemented into a breccia (AGB-9).

AMT, at  $17^{\circ}54.35'S$ ,  $44^{\circ}29.41'E$ , is a small fissure cave, or slot cave, about 80 m east of AGB, at approximately the same elevation. The entire floor comprises only about  $1\text{ m}^2$  of sediment. At the back of the small cave is a narrow solution pit that descends another ca. 5 m.

### Bone extraction

At each sublocation inside AGB, the bone surface scatter was described and photographed with orientation and scale, and larger bones were then picked up individually and packed in labeled plastic bags or boxes. The smaller bones were placed in labeled containers along with all associated sediment and detritus and were removed from the cave for sifting. After removal of a layer of large bones and the associated fines down to ca. 10 cm, the sublocation was rephotographed and all the remaining material taken out down to another 10 cm if that much was available. Most of these bone pockets, however, were very shallow, ending at bare rock in 10 cm or less.

### Excavation

Two sublocations (AGB-3 and AGB-8) contained deeper sediments. AGB-3 was excavated in 10 cm levels down to rock at 50 cm in a ca.  $1.0\text{ m}^2$  floor surface, and excavated sediment was carried outside for sifting. Excavation was undertaken with bare hands and small plastic tools, taking care to avoid contact that might damage the bones. AGB-8 was left intact for future research options. Only the visible remains on or within 10 cm of the surface were collected.

Outside the cave along the wall east of the entrance (AGB-1) and in the adjacent small chamber (AGB-1A), a mixture of boulders, limestone breakdown, and clay was excavated down to rock base. Sediments were removed in approximately 10-cm levels, large bones were packed and labeled, and all fines were sifted. Small metal tools were used in the hard stony material.

At AMT, surface bones were collected and loose breccia was excavated to 50 cm depth from the narrow floor (with some careful use of metal tools to dislodge crusts). This material was disaggregated and sifted.

### Sifting and cataloging

Fine material collected from the surface or excavated from deeper layers was dry-screened through mesh down to 3 mm, and all biological materials were picked, sorted, and labeled. Each accessioned specimen container was labeled with sublocation and depth in sediment (0 cm or 0–10 cm for materials on bare surface or embedded in surface material, respectively). In sublocation AGB-7, because of its uniformity and larger size compared with other sublocations, labels for individual pockets of bone received a letter subscript (A through E). The fossils were divided, accessioned, and cataloged by the Université d'Antananarivo (UA) and the Field Museum of Natural History (FMNH) in Chicago.

### Fossil analyses

Sediment samples from AGB-1 and AGB-3 were processed for pollen and microscopic charcoal analysis at the University

of Amsterdam following methods described in De Boer et al. (2013), including a heavy liquid separation using a bromoform-ethanol mixture. Microfossil slides were examined for pollen, spores, and charcoal at 400× and 1000× oil immersion under a light microscope. Bones collected were identified by direct comparison to reference materials housed primarily in the collections of UA and FMNH, with reference in some cases to other extensive collections (listed in the “Acknowledgments”).

### Isotopic analysis and radiocarbon dating

Approximately 200 mg of bone fragments were removed from each of 25 specimens chosen for dating, using tin snips. Specimens were included from all sublocations. Roughly 200 mg of each specimen was processed for radiocarbon and stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis. Collagen was isolated following methods modified from Fox-Dobbs et al. (2008) and Sparks and Crowley (2018). Samples were demineralized in 0.5 N hydrochloric acid at 4°C and rinsed five times with ultrapure water. They were then soaked in 0.01 N sodium hydroxide for 2 hours to remove humic acids, rinsed five times with ultrapure water, and lyophilized. Samples were gelatinized in 0.01 N hydrochloric acid at 80°C for 15–17 hours. To maintain acidity, 100  $\mu\text{l}$  of 0.1 N HCl were added after several hours (Ambrose 1990). Samples were then filtered through 1.5  $\mu\text{m}$  glass-fiber filters and lyophilized.

Approximately 0.3 mg of dried collagenous residue from each sample were weighed into tin boats. Stable isotope and elemental concentration data were analyzed on a Costech Elemental Analyzer connected to a ThermoFisher Delta V Isotope Ratio Mass Spectrometer via a ConFlo IV in the Stable Isotope Biogeochemistry Laboratory at the University of Cincinnati. Isotope data were normalized for size (linearity), drift, and scale (Coplen et al., 2006; Skrypzek 2013). We used an internal reference material (caffeine) for linearity and drift, and we used caffeine and USGS 41 L-glutamic acid for scale. Analytical precision, which was calculated using caffeine, USGS 41, and two independent internal reference materials (glycine and gelatin), was  $\pm 0.15\%$  and  $\pm 0.09\%$  for carbon and nitrogen, respectively. Sample preservation was assessed using visual observation (including bone strength and coloration), collagen yield, and atomic C:N ratios. Only eight samples yielded C:N ratios between 2.9 and 3.6. These were deemed sufficiently robust and were selected for radiocarbon dating (Ambrose, 1990).

Samples were dated in the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry (AMS) Laboratory at the University of California, Irvine, and the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory. Conventional radiocarbon age estimates were based on a 5568 yr half-life,  $^{13}\text{C}$  corrected, and include a background subtraction based on simultaneously prepared modern and  $^{14}\text{C}$ -free bone standards.

Two additional AMS radiocarbon dates obtained from Beta Analytic were supplied by Steven Goodman from

sublocation AGB-1. This lab’s methods differ slightly from those outlined earlier (Hood, D., personal communication). The bone samples were washed with deionized water, the outermost layers of their surfaces were scraped free, and then the samples were gently crushed. Dilute, cold HCl was repeatedly applied and replenished until the mineral fraction was eliminated. The demineralized bone was then dissected and inspected for rootlets. Any rootlets present were also removed when replenishing the acid solutions. Collagen residue was then pretreated with NaOH to ensure the absence of secondary organic acids.

Radiocarbon dates were converted to calendar years (cal yr BP) using Calib 7.1 and the ShCal13 calibration curve (Stuiver and Reimer, 1993; Hogg et al., 2013). Resulting  $2\sigma$ -calibrated age ranges were rounded to the nearest 5-yr interval.

Seven of the dated samples were also processed for strontium isotope ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) analysis. Roughly 20 mg were pulverized using an agate mortar and pestle and chemically pretreated following Crowley and Wheatley (2014). Samples were soaked in 30%  $\text{H}_2\text{O}_2$  at room temperature for 72 hours (liquid was refreshed after 24–48 h) and rinsed five times with ultrapure water. They were then soaked in 1 M acetic acid buffered with calcium acetate at 4°C for 24 hours, rinsed five times with ultrapure water, and lyophilized. Samples were analyzed in the Multicollector ICPMS Laboratory in the Department of Geology at the University of Illinois, Urbana–Champaign. Strontium was isolated by dissolving 3–5 mg of each sample in 0.5 ml of 3 N  $\text{H}_2\text{NO}_3$  and filtering the dissolved sample through 0.2 ml of Eichrom strontium-specific resin in Teflon cation-exchange columns. Samples were then eluted with 0.05 N  $\text{H}_2\text{NO}_3$  into 4 ml autosampler vials and analyzed on a Nu Plasma HR Multi-collector inductively coupled plasma mass spectrometer. Data were corrected for mass bias fractionation using an internal normalization ( $^{86}\text{Sr}/^{88}\text{Sr} = 0.1194$ ) and normalized using international standard NBS 987 and two internal laboratory standards (“E & A” and South China Sea Coral). Precision for all analyses was  $\pm 0.0005$ .

## RESULTS

The sediments that have accumulated on the east side of the cave entrance at sublocation AGB-1 are a mixture of cobbles, angular limestone fragments spalled off the cave wall, and well-preserved bones. Pollen, spores, and charcoal are preserved in the finer component of the sediments. However, large pieces of rock that have fallen off the wall above have disturbed the stratigraphy here. Sediments are also penetrated by roots and bioturbated by soil invertebrates and rodents. From 0 to 50 cm, a 0.5 m<sup>2</sup> test pit revealed pale brown silty clay (Munsell color 10YR 6/3) with stones of gravel to cobble size and one small boulder. At 50 cm, we found two small light gray sherds of thin, burnished pottery with triangles around the rim, probably part of a hole-mouth jar. They have a relatively fine clay body with sandy inclusions, fired in a reducing atmosphere. Around the rim are large impressed

triangles alternating in a false-chevron design. This is a well-known and well-dated early west coast pottery type of the Kingany phase, found in village sites on the central west coast of Madagascar and dated between AD 1350 and AD 1550 (Wright et al., 1996; also see figs. 103 and 104 in Vérin, 1975). The sherds were collected with some small charcoal fragments in apparent association.

Excavation was stopped at this level, as only friable limestone was detected below. One large stone was removed, with a small amount of sediment underneath, including two oval objects 20 mm × 15 mm, made of very fine organic material. These are likely to be coprolites of a large primate. They are similar to *Archaeolemur* coprolites described from caves in northwest Madagascar (Burney et al., 1997; Vasey et al., 2013) but differ in being finer textured and lacking any macroscopic animal or plant remains.

About 2 m north of AGB-1, a second 0.5 m<sup>2</sup> test pit, AGB-1A, was excavated in the floor of a small overhang. From 0 to 30 cm, the matrix was light reddish-brown (5YR 6/4) silty clay containing bones, land-snail shell fragments, and one pottery sherd of a local type of unknown age. At 30 cm there is a discontinuous 2-cm band of dark brown (7.5 YR 3/4) humic silt. Below this level, from 32 to 45 cm is reddish-brown (7.5YR 4/4) silty clay, resting on limestone.

Inside the cave entrance, surface bone scatters extend from AGB-4 just below a steep drop-off to successively lower levels at AGB-5, AGB-6, AGB-7, and AGB-9. The distributions of animal long bones show no strong patterns, instead following the contours of the spaces between other bones and the enclosing rocks. No articulated bones were observed. Smaller bones were mixed with sediment and plant detritus. Tan-colored crusts, generally <1 cm thick and 2–5 cm across, were scattered among these bones. They are currently under study as possible raptor coprolites, as they are similar to deposits often observed beneath raptor nests. No pottery or other human evidence was recovered from these surface scatters, although some bones from different parts of the cave are under study for evidence of butchery. Tooth marks are not abundant on this material, but where present appear to be postmortem rodent chewing. Evidence for scavenging by snails was also noted, in the form of shallow sinuous channels on some bone surfaces.

Beneath the floor of the uppermost bone scatters, there is a small chamber (AGB-8) with access from the east side. It contains sediment similar to that of the excavated sites, but was left intact for future research.

Inside the cave, on a sloping shelf along the east wall (AGB-2), a bone deposit was collected from the surface that appears to be, at least in part, a debris cone made up of dissociated owl pellets, based on the occurrence of bones of many small prey items and a lack of tooth marks. Approximately 5 m below this shelf at the base of the wall, an excavation was conducted in soft sediment inside a small lateral passage (AGB-3). A 1-m<sup>2</sup> pit was excavated down to the limestone floor at 50 cm, following the contour of natural layers. Sediments were a uniform light reddish-brown (7.5YR 6/4) silty clay, with well-preserved bones scattered throughout.

Pollen preservation in these sediments is poor, although microscopic charcoal particles are abundant and fungus spores are present.

The test pit from AMT yielded sediment that was a partly consolidated light reddish-brown (7.5YR 6/4) silty-clay breccia. A few bones of all sizes occurred from the surface down to the limestone floor at ca. 50 cm depth.

## Faunal remains

Six species of extinct large mammals and one extinct bird have been identified to date in the bone assemblages from AGB and AMT (Table 2), including four species of large-bodied extinct lemurs. These deposits are dominated by specimens of *Babakotia radofilai* (Fig. 3), and represent a considerable southwesterly range extension for this medium-sized sloth lemur. Remains of *Palaeopropithecus kelyus* also indicate significant range extensions for this highly suspensory large lemur. Both *B. radofilai* and *P. kelyus* were previously known from clusters of cave sites in the western dry forests near Mahajanga; *Babakotia* is also known from caves in the extreme north (the Ankarana Massif), just south of Antsirana (Fig. 4, Table 3).

*Archaeolemur edwardsi* (Fig. 5) was previously known from a broad array of sites and habitats (Table 3), ranging from the extreme north to the Central Highlands and dry west, but there are no prior records of *Archaeolemur* in the Beanka or Bemaraha regions. *Pachylemur* is difficult to assess, because species allocations of this broadly distributed genus need reevaluation (Godfrey and Jungers, 2002; Godfrey et al., 2010). Populations are known from a wide range of habitats, including dry spiny forest, succulent woodland, central mosaic, and western dry forest; again, there are no prior records from the Beanka region or nearby (Fig. 4, Table 3).

Two other extinct mammals identified among the recovered fossils were the large carnivoran *Cryptoprocta spelea* (family Eupleridae) and the aardvark-like *Plesiorycteropus* sp. (tentatively placed in the order Afrosoricida). These findings represent yet another significant range expansion, as *C. spelea* was previously known primarily from sites in the dry spiny thicket, the succulent woodlands, and the southern part of the western dry forest. It was rare in the Central Highlands (Fig. 4, Table 3). *Plesiorycteropus* was previously known from a wide variety of habitats, including dry spiny forest, central mosaic, and western dry forest in the northwest (near Mahajanga) as well as the central west (Belo-sur-Mer), but it was not previously recorded at sites close to Beanka (Fig. 4). Finally, we have recovered remains of a large extinct terrestrial bird, referable to the genus *Coua* (family Cuculidae).

Two extant species that are regionally extirpated were discovered in the faunal remains: the critically endangered greater bamboo lemur *Prolemur* (= *Hapalemur*) *simus* and *Eulemur mongoz*. Beanka falls well outside *P. simus*'s modern range in eastern rain forests (Wright et al., 2008) but within the geographic envelope of other fossil sites that

**Table 2.** Vertebrates identified from bones found in Anjohingidrobe and Anjohimaletsy.<sup>a</sup>

Mammalia		
<u>Primates</u>		
Archaeolemuridae	† <i>Archaeolemur edwardsi</i>	Monkey lemur
Palaeopropithecidae	† <i>Babakotia radofilai</i> † <i>Palaeopropithecus kelyus</i>	Radofilao's sloth lemur Medium-sized sloth lemur
Cheirogaleidae	<i>Cheirogaleus medius</i> cf. <i>Cheirogaleus medius</i> <i>Microcebus</i> cf. <i>myoxinus</i>	Fat-tailed dwarf lemur Pygmy mouse lemur
Lemuridae	<i>Eulemur rufus</i> <i>Eulemur mongoz</i> <i>Hapalemur</i> cf. <i>griseus</i> † <i>Pachylemur</i> sp. ‡ <i>Prolemur simus</i>	Rufus brown lemur Mongoose lemur Lesser bamboo lemur Giant ruffed lemur Greater bamboo lemur
Indriidae	<i>Avahi</i> cf. <i>cleesei</i> <i>Propithecus deckenii</i>	Woolly lemur Von der Decken's sifaka
Lepilemuridae	<i>Lepilemur</i> cf. <i>randrianasoloi</i>	Randrianasolo's sportive lemur
<u>Chiroptera</u>		
Molossidae	<i>Chaerephon leucogaster</i> <i>Mormopterus jugularis</i> cf. <i>Otomops madagascariensis</i>	Grandidier's free-tailed bat Peter's wrinkle-lipped bat Madagascar free-tailed bat
Hipposideridae	<i>Macronycteris commersoni</i> cf. <i>Macronycteris</i>	Commerson's leaf-nosed bat
Rhinonycteridae	<i>Triaenops menamena</i>	Madagascar trident bat
Miniopteridae	cf. <i>Miniopterus</i> (small species) <i>Miniopterus</i> (medium species)	Long-fingered bats
<u>Artiodactyla</u>		
Bovidae	* <i>Capra aegagrus hircus</i>	Goat
Suidae	* <i>Potamochoerus larvatus</i>	Bushpig
<u>Carnivora</u>		
Eupleridae	<i>Cryptoprocta ferox</i> † <i>Cryptoprocta spelea</i> <i>Galidia elegans</i>	Fosa Giant fosa Ring-tailed mongoose
Felidae	* <i>Felis lybica</i>	African wildcat
<u>Viverridae</u>	* <i>Viverricula indica</i>	Small Indian civet
<u>Rodentia</u>		
Nesomyidae	<i>Eliurus myoxinus</i> <i>Eliurus</i> sp. nov.	Dormouse tufted-tailed rat
Muridae	* <i>Rattus rattus</i> * <i>Mus musculus</i>	Black rat Mouse
<u>Afrosericida</u>		
Tenrecidae	<i>Microgale</i> cf. <i>brevicaudata</i> ‡ <i>Microgale talazaci</i>	Short-tailed shrew tenrec Talazac's shrew tenrec



	<i>Setifer setosus</i>	Greater hedgehog tenrec
	<i>Tenrec ecaudatus</i>	Tailless tenrec
Plesiorcycteropodidae	† <i>Plesiorcycteropus</i> sp.	Bibymalagasy or Madagascar aardvark
Aves		
<u>Accipitriformes</u>		
Accipitridae	cf. <i>Buteo</i>	Common buzzard
	cf. <i>Accipiter madagascariensis</i>	Madagascar sparrowhawk
<u>Cuculiformes</u>		
Cuculidae	<i>Coua gigas</i>	Giant coua
	<i>Coua cristata</i>	Crested coua
	† <i>Coua</i> sp.	Giant extinct coua
<u>Pelecaniformes</u>		
Threskiornithidae	cf. <i>Lophotibis cristata</i>	Madagascar ibis
<u>Galliformes</u>		
Numididae	* <i>Numida meleagris</i>	Helmeted guineafowl
Phasianidae	<i>Margaroperdix madagascariensis</i>	Madagascar partridge
<u>Gruiformes</u>		
Rallidae	<i>Dryolimnas cuvieri</i>	White-throated rail
	<i>Porphyrio madagascariensis</i>	African swampphen
<u>Coraciiformes</u>		
Coraciidae	<i>Eurystomus glaucurus</i>	Broad-billed roller
<u>Leptosomiformes</u>		
Leptosomidae	<i>Leptosomus discolor</i>	Cuckoo roller
<u>Passeriformes</u>		
	cf. <i>Motacilla flaviventris</i>	Madagascar wagtail
<u>Psittaciformes</u>		
Psittichasidae	<i>Coracopsis nigra</i>	Lesser vasa parrot
Reptilia		
<u>Testudines</u>		
Podocnemididae	<i>Erymnochelys madagascariensis</i>	Madagascar big-headed turtle
Testudinidae	<i>Pyxis</i> sp.	Spider tortoise
<u>Squamata</u>		
Gekkonidae	<i>Geckolepis</i> sp.	Fish scale gecko
AMPHIBIA	cf. Boophinae (Anura, Mantellidae)	Unidentified frog

<sup>a</sup> Symbols: \*, Introduced to Madagascar; †, extinct; ‡, believed extinct in western Madagascar.

have yielded remains from this species (Muldoon et al., 2017). This species has been previously recorded in subfossil deposits of the Bemaraha Massif, just south of the Beanka Protected Area (Godfrey et al., 2004). *Prolemur simus* appears to have had a past distribution similar to that of *A. edwardsi*, through the Central Highlands and the western dry forests of the extreme north and northwest. *Eulemur mongoz* no longer lives at Beanka, although it occurs today at Anjamena near the Betsiboka River (Dammhahn et al.,

2013), where it is sympatric with *Eulemur rufus*, and also east of the Betsiboka.

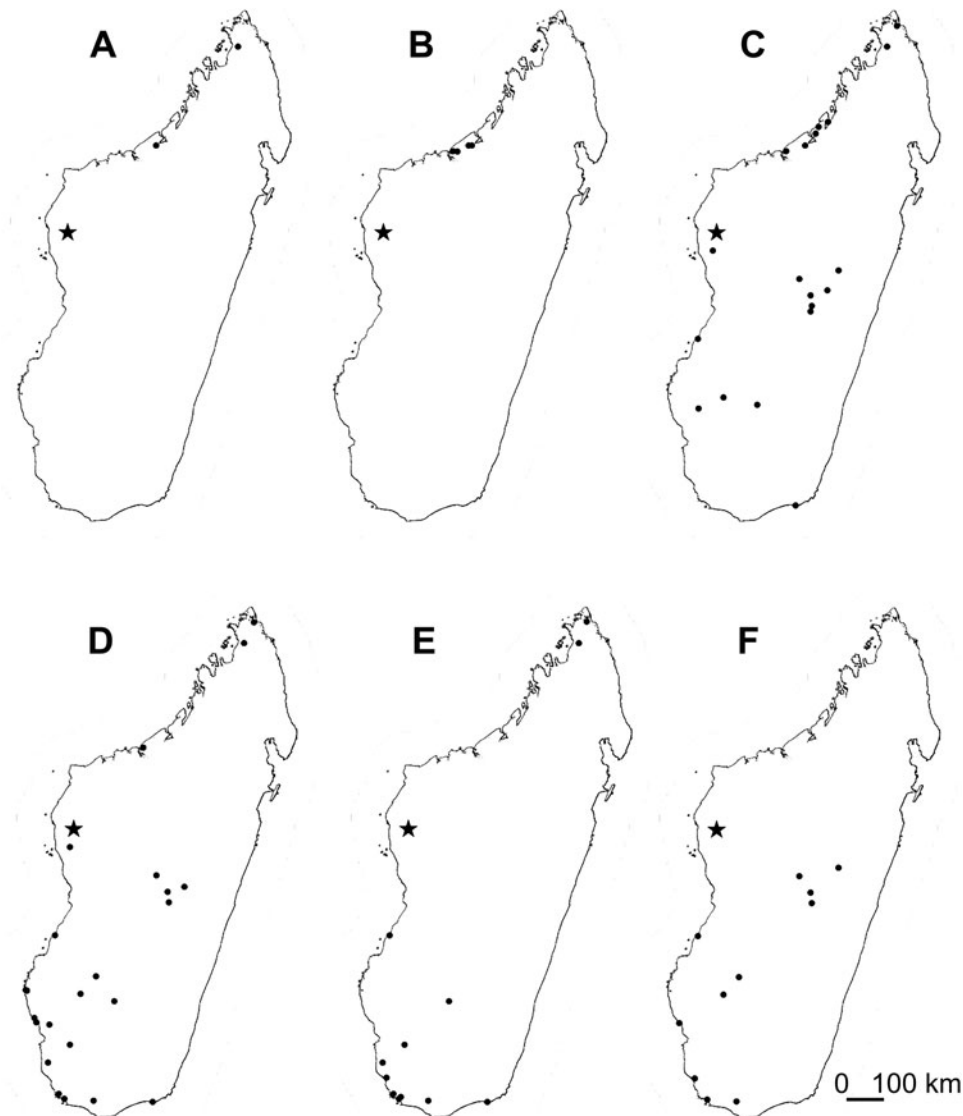
Bones of eight additional primate taxa were identified, almost all of which are still extant in the Beanka forests (Dammhahn et al., 2013). These include some widespread taxa, such as the “eastern” lesser bamboo lemur *Haplemur* cf. *griseus*, the fat-tailed dwarf lemur *Cheirogaleus medius*, and an undescribed species of *Cheirogaleus* with a wide geographic distribution in western Madagascar (Dammhahn et al., 2013).



**Figure 3.** (color online) Left maxilla of *Babakotia radofilai* from Anjohingidrobe Cave, site AGB-1 (outside the cave entrance on the east side), FMNH PM 70197, showing full adult postcanine dentition (two premolars and three molars) in occlusal view.

There are also some rare taxa, including some species endemic only to the zone between the Tsiribihina and Betsiboka Rivers (e.g., *Avahi cf. cleesei*, *Propithecus deckenii*, and *Lepilemur cf. randrianasoloi*).

Unlike most subfossil sites elsewhere in Madagascar (Goodman and Jungers, 2014), this site produced no remains of ratites or hippopotami. Crocodiles are present today just a few hundred meters downslope from the caves in the adjacent Bokarano River, but thus far we have not identified any crocodile remains. The subfossil cave sites are situated in sharp limestone tsingy and a tangle of huge vines high above the river. Given the location of the site on an upland forest slope, we did not expect to find crocodile bones, although we did recover bones of a freshwater turtle, the Madagascar big-headed turtle (*Erymnochelys madagascariensis*). It is critically endangered; whereas it occurs in the region today,



**Figure 4.** Previously known fossil occurrences of extinct species on Madagascar (dots) in relation to the Beanka Protected Area (star). (A) *Babakotia radofilai*; (B) *Palaeopropithecus kelyus*; (C) *Archaeolemur edwardsi*; (D) *Pachylemur* sp.; (E) *Cryptoprocta spelea*; (F) *Plesiorcyteropus* spp. See Table 3 for details.

**Table 3.** Previously known distribution of extinct vertebrate species from Beanka.<sup>a</sup>

Genus and species	Subfossil sites in addition to Beanka
<i>Babakotia radofilai</i>	Previously known only from lowland sites (Ankarana in the extreme north and the Grottes d'Andranoboka in the Mahajanga region). Habitat: western dry forest
<i>Palaeopropithecus kelyus</i>	Previously known only from lowland sites in the Mahajanga region (Ambongonambakoa, Amparihingidro, Belobaka, and the Grottes d'Andranoboka). Habitat: western dry forest
<i>Archaeolemur edwardsi</i>	Previously known from sites of varying elevation in the extreme north, northwest, central highlands, and west: Ambararatra–Mahabo, Amparihingidro, Ampasambazimba, Ampoza–Ankazoabo, Ankarana, Ankomaka, Antsingiavo A and B, Antsirabe, Belo-sur-mer, Bungo Tsimanindroa, Christmas River, Grottes d'Andranoboka, Masinandraina, Montagne des Français, Morarano-Betafo, Narinda, Sambaina, and Vakinanakaratra. Also rare (but present) in the southeast (Andrahomana). Habitat: western dry forest, central mosaic
<i>Pachylemur</i> sp.	<i>Pachylemur</i> tends to be rare (but present) in the north and northwest (Ankarana, Montagne d'Ambre, and Montagne des Français), and very common at certain sites in the southwest (Taolambiby, Tsimanampesotse) and south-central Madagascar (Tsirave). Ambararatra–Mahabo, Ambolisatra, Amparihingidro, Ampasambazimba, Ampoza–Ankazoabo, Andrahomana, Ankilitelo, Antsirabe, Beloha Anavoaha, Belo-sur-mer, Bemafandry, Christmas River, Itampolobe, Lamboharana, Manombo–Toliara, Masinandraina, Morarano–Betafo, Taolambiby, Tsiandroina, Tsimanampesotse, and Tsirave. Wide range of habitats, including dry spiny forest, central mosaic, succulent woodland, and western dry forest
<i>Cryptoprocta spelea</i>	<i>Cryptoprocta spelea</i> is previously known primarily from the south and southwest, and sporadically from the extreme north. Andrahomana, Ankarana, Grotte d'Ankazoabo, Beavoaha, Beloha Anavoaha, Belo-sur-mer, Bemafandry, Christmas River, Lakaton'ny akanga, Taolambiby, Tsiandroina, and Tsimanampesotse (Mitoho, Malazamanga, and Vintany). Rare or absent in the Central Highlands. Habitat: dry spiny forest, succulent woodland, western dry forest
<i>Plesiorycteropus</i> spp.	Two species have been described, previously known from sites of varying elevation in southern, central, western, and northwestern Madagascar (the latter in the region of Mahajanga): Ambolisatra, Ampasambazimba, Ampoza, Anavoaha, Anjohibe, Ankevo, Antsirabe, Belo-sur-mer, Bemafandry, Masinandraina, Sambaina, and Tsirave. Not previously recorded in the region of Bemaraha. Wide range of habitats, including dry spiny forest, central mosaic, and western dry forest

<sup>a</sup>See Godfrey and Jungers (2002), Goodman and Jungers (2014), and Meador et al. (2019) for biogeographic references. See Fig. 4 for mapped occurrences.

it is rare because it is exploited by humans. Bones of a small tortoise, the spider tortoise (*Pyxis* sp.), were also found, well outside the modern range in southwestern Madagascar. As



**Figure 5.** (color online) Left maxilla of *Archaeolemur edwardsi* from Anjohingidrobe Cave, site AGB-8 (below the floor at a drop-off), FMNH PM 70196, showing full adult dentition (two incisors, canine, three premolars, and three molars) in lateral view.

turtles and tortoises are unlikely to negotiate such rugged terrain, they were probably transported to the site by humans or other predators. We also found skeletal material belonging to an unidentified frog and a fish scale gecko (*Geckolepis* sp.).

Extant species in the subfossil deposits include, in addition to the four herpetofaunal species mentioned earlier, a total of 12 birds, 4 rodents (*Eliurus* spp.), 4 tenrecs, 8 bats, and 4 carnivorans. The extant birds include two predatory species [probably Madagascar buzzard (cf. *Buteo*) and Madagascar sparrowhawk (cf. *Accipiter madagascariensis*)] and two extant couas. The tenrecs include a species, *Microgale talazaci* (Talazac's shrew tenrec), that lives today in the eastern rainforest and was previously entirely unknown in dry western forest habitats. Work on these assemblages indicates that within AGB, AGB-2 (inferred to contain dissociated owl pellets) was especially rich and diverse in microfauna. The small slot cave (AMT) sampled faunal elements at lower rates than the larger AGB, although the species lists for AGB and AMT were similar.

### Temporal trends

We successfully obtained radiocarbon dates for 10 specimens: seven from *Babakotia* and three from *Archaeolemur*

**Table 4.** Radiocarbon dates and isotopic data for extinct lemur bones from Anjohingidrobe and Anjohimaletsy.

Taxon	Element	Provenance	<sup>14</sup> C lab no.	Conventional <sup>14</sup> C age ± 1σ	2σ cal yr BP range <sup>a</sup>	δ <sup>13</sup> C (‰)	δ <sup>15</sup> N (‰)	<sup>87</sup> Sr/ <sup>86</sup> Sr
<i>Babakotia</i>								
<i>B. radofilai</i>	Proximal phalanx	AGB-3: 10-20	UCI-184462	1180 ± 15	980–1065	−20.1	5.3	0.70801 <sup>c</sup>
<i>B. radofilai</i>	Proximal phalanx	AGB-3: 20-30	UCI-184464	1210 ± 15	985–1175	−20.5	6.8	0.70782
<i>B. radofilai</i>	Proximal phalanx	AGB-2: 10	UCI-184463	1180 ± 15	980–1065	−20.5	10.4	
<i>B. radofilai</i>	Proximal phalanx	AGB-1(3)	UCI-184459	2070 ± 15	1930–2015	−21.7	6.4	0.70778
<i>B. radofilai</i>	Proximal phalanx	AGB-1: 20-30 (3)	UCI-185121	1150 ± 15	960–1055	−20.3	6.4	0.70795
<i>B. radofilai</i>	Proximal phalanx	AGB-7D	CAMS-178787	1270 ± 30	1065–1265	−20.6	7.1	0.70891
<i>B. radofilai</i>	Cranial fragment	AGB-1	Beta-354603	1160 ± 30 <sup>b</sup>	960–1070	−20.8 <sup>b</sup>	—	
<i>Archaeolemur</i>								
<i>A. edwardsi</i>	Right distal ulna	AGB-1(2)	UCI-184461	2300 ± 20	2175–2345	−22.0	6.4	0.70786
<i>A. edwardsi</i>	Right lower lateral incisor	AMT-2	UCI-184460	1485 ± 15	1305–1360	−20.4	6.7	0.70795
<i>A. edwardsi</i>	Long bone shaft	AGB-1	Beta-354602	2730 ± 30 <sup>b</sup>	2750–2855	−21.0 <sup>b</sup>	—	

<sup>a</sup>Calibrated using 2σ ranges in Calib 7.1 (Stuiver and Reimer 1993; Hogg et al. 2013). Age ranges rounded to nearest 5 yr.

<sup>b</sup>Beta Analytic δ<sup>13</sup>C determinations were excluded from regression analysis in Fig. 6, as the methods differed in some particulars (see “Location and Methods”).

<sup>c</sup>Analytical error was ± 0.00005 for all specimens.

(Table 4). Extreme care was taken, through attention to provenance by sublocation and recording the skeletal element used, to avoid sampling the same individual twice. Combined calibrated radiocarbon dates (2σ) ranged from ca. 1305–2855 cal yr BP for *Archaeolemur* and ca. 960–2015 cal yr BP for *Babakotia*. Five of the *Babakotia* have ages that are ca. 1000 cal yr BP. These are among the most recent ages reported for extinct megafauna on the island (Simons et al., 1995; Simons, 1997; Burney et al., 1997, 2004; Crowley, 2010; Crowley et al., 2017).

### Isotopic trends

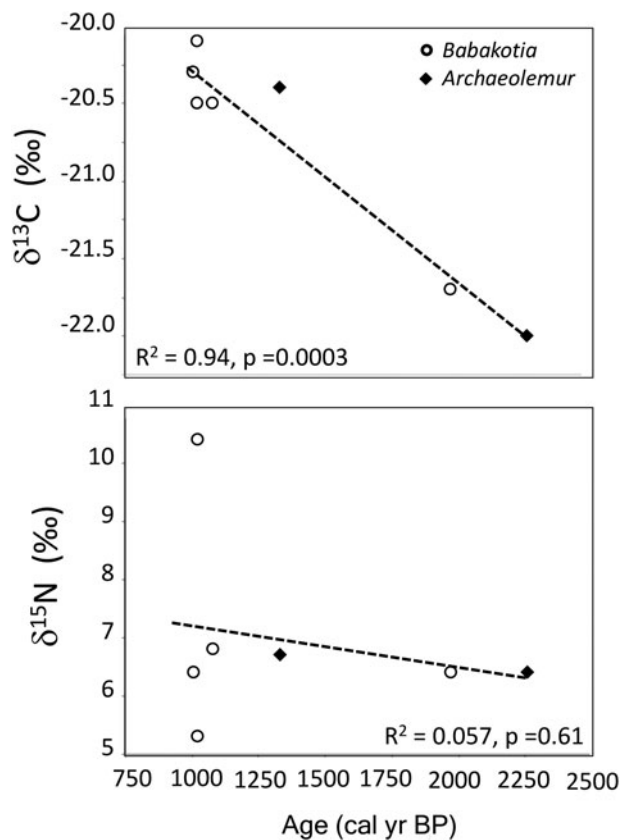
Carbon isotope data are similar for *Babakotia* and *Archaeolemur*, and range less than 2‰ for both taxa (Table 4). Assuming a collagen-diet offset of 5‰ (Koch, 1998), and correcting for isotopic shifts in atmospheric CO<sub>2</sub> over time (ca. −1.2‰ in the Southern Hemisphere; Keeling et al., 2010; Crowley et al., 2012), carbon isotope data suggest that both taxa consumed C<sub>3</sub> vegetation and inhabited a relatively arid habitat similar to modern dry forest and scrub in western Madagascar (Crowley et al., 2011). There is a strong correlation ( $R^2 = 0.93$ ,  $P < .001$ ,  $n = 8$ ) between δ<sup>13</sup>C values and time (Fig. 6). This isotopic trend may reflect late Holocene habitat changes, for instance, from precipitation changes or a slight opening of the habitat between 2000 and 1000 yrs ago. However, if this were the case, we would also expect a temporal shift in δ<sup>15</sup>N values, which we do not observe (see following paragraph). High-resolution δ<sup>18</sup>O records from speleothems in Anjohibe Cave north of Beanka also show relatively little climate change during this period and no simple unidirectional trend (Scroton et al., 2017; Wang et al., 2019). Another possible explanation for the observed isotopic trend is that it reflects a gradual behavioral change, such as animals feeding higher in the canopy over time. Such a

behavioral shift might be expected if these lemurs were increasingly threatened by ground predators, such as humans, or adjusting to some change in forest structure.

Nitrogen isotope (δ<sup>15</sup>N) data are considerably more variable. Whereas the two *Archaeolemur* individuals have δ<sup>15</sup>N values between 6.4‰ and 6.7‰, values for *Babakotia* range from 5.3‰ to 10.4‰ (Table 4). Unlike carbon isotope data, nitrogen isotope values show no clear chronological trend (Fig. 6). Both *Archaeolemur* individuals and the oldest *Babakotia* individual have δ<sup>15</sup>N values between 6‰ and 7‰; the large range in δ<sup>15</sup>N values is only observed in the five *Babakotia* measured for δ<sup>15</sup>N that are younger than 1200 cal yr BP. This could indicate differences in dietary breadth among individuals, differing habitats, or differing locations. With the exception of a single sample from AGB-7D, strontium isotope ratios vary little (Table 4), suggesting that most individuals lived on the same geological substrate.

### DISCUSSION

Radiocarbon dates obtained for Beanka subfossil material so far suggest that elements of the local fauna, notably large extinct lemurs, were deposited into the pit below the cave entrance over approximately the last three millennia. *Babakotia* was still present a millennium ago, well after humans began colonizing the island. Based on just ten <sup>14</sup>C determinations, it is too early to specify the entire time range that this site has been sampling the local fauna or when *Babakotia* became locally extinct. However, on the basis of collagen preservation, we can speculate that the bone deposits may span considerably more than 3000 yrs. Of 27 bones tested, only 10 yielded collagen deemed suitable for dating. The deepest sublocation, AGB-9, contained bones that were heavily mineral stained and in some cases encrusted in weakly cemented breccias. The two bones from this unit



**Figure 6.** Linear regression plots of  $\delta^{13}\text{C}$  vs. age and  $\delta^{15}\text{N}$  vs. age for bones of extinct large lemurs from Beanka caves.

that were tested lacked collagen, as did some bones from other sublocations such as AGB-7 directly above. It is possible that these are significantly older bones, or merely that collagen preservation conditions are not as good in the deeper and more alkaline parts of the cave.

AGB appears to be an active bone accumulation site today, and the faunal list (Table 2) contains undated bones of many smaller species found in good condition in surface deposits inside the cave. Six species were identified that are believed to have been introduced by humans (*Numida meleagris*, *Potamochoerus larvatus*, *Felis lybica*, *Viverricula indica*, *Mus musculus*, and *Rattus rattus*), but the dates of these introductions to Beanka are not constrained. There is also some fragmentary material that may be goat (*Capra aegagrus hircus*). Only further dating of specimens believed to be relatively recent on the basis of stratigraphic position and preservation will confirm whether the large extinct lemurs, such as *Babakotia*, indeed declined locally sometime around 1000 yrs ago, or more recently. In any case, the dates from Beanka are far more recent than the single mid-Holocene date obtained for this taxon previously from Ankarana (Simons et al., 1995) and add to late dates previously obtained for *Archaeolemur*, *Daubentonia robusta*, *Pachylemur*, *Megaladapis*, and *Palaeopropithecus* (Simons, 1997; Burney et al., 2004; Crowley, 2010; Crowley et al., 2017). The scarcity of pottery and other human evidence in the cave vicinity suggests only occasional human presence over the centuries.

Cuts and chop marks on some bones recovered are under study, but none of the sublocations described contained a concentration of bones, pottery, or charcoal that could be attributed exclusively to human activity.

The late occurrence of *Babakotia* at this site is consistent with extinction hypotheses such as synergy (Burney, 1999; Burney et al., 2003) and subsistence shift (Godfrey et al., 2019) that predict local extinctions may lag behind the more general trend in isolated pockets where human impacts are delayed by local conditions. Likewise, these results showing late survival contradict any hypothesis that predicts rapid island-wide extinction, such as blitzkrieg (Martin, 1984) and hypervirulent disease (MacPhee and Marx, 1997). The date of human arrival to Madagascar has been regarded in recent decades to have been ca. 2.5 ka BP (Burney et al., 2004; Crowley, 2010), but more recent estimates have ranged from as early as ca. 11 ka BP (Hansford et al., 2018) to as late as AD 700 (Anderson et al., 2018). Regardless of the chosen scenario, however, the Beanka sites support the notion that some large lemurs survived for at least a few centuries or more after human arrival.

There is no current or recent evidence for the use of the site as a large mammalian carnivore lair. Owls continue to use the ledges inside and outside the cave, but no fresh mammalian scat was found in the surface material and sifted sediment, and only a few bones showed tooth marks. The only definite subfossil coprolites were two that appear to be fine-textured dung from a large lemur. Ancient DNA testing is inconclusive so far as to whether these are, as we hypothesize, from *Babakotia*. Ancient DNA testing has also been inconclusive thus far regarding the material collected as possible subfossil scatological evidence for eagles or other large raptors.

### Paleoecological and biogeographic inferences

The major factors affecting vertebrate species distributions in Madagascar continue to be debated (e.g., Vences et al., 2009; Ganzhorn et al., 2014). Robert Martin (1972) suggested that large perennial rivers are primary among them. Other important factors include ecogeographic constraints such as variation in rainfall, temperature, and habitat (e.g., Albrecht et al., 1990; Yoder and Heckman, 2006) and watershed boundaries (Wilmé et al., 2006). On the basis of their review of the geographic distributions of extant species, Wilmé et al. (2006) identified Melaky (the biogeographic region in which Beanka falls) as one of several centers of exceptional microendemism in Madagascar today. They suggested that such “centers of high microendemism” owe their existence to climatic fluctuations, which affect riverine forests differently, depending on whether the river sources are at lower or higher elevations. Watersheds with river sources at lower elevations are more easily isolated during periods of high aridity, and these therefore become centers of unusual microendemism. Subfossil deposits may hold the key to a better understanding of this and other isolating mechanisms. They can reveal past corridors of dispersal for species on Madagascar, how climate fluctuations relate to the expansion and contraction of forests

and other types of habitat, and how these in turn help to explain the current distribution of species (Burney et al., 1997; Muldoon et al., 2009).

The Beanka Protected Area lies within the low-elevation center of microendemism bordered by the Tsiribihina River to the south and the Betsiboka River to the north and east. Some extant vertebrates in this region, including some primates, have been shown to conform to the expectations of the centers-of-endemism hypothesis (Wilmé et al., 2006), but the pattern is by no means universal (see Dammhahn et al., 2013). Similarly, our review of subfossils at Beanka supports the notion that the isolation of the low-elevation watersheds due to fluctuations in climate may not have been the dominant force shaping faunal compositions in this region in the past. Most of the taxa that we documented are western in character, but many are not limited in geographic range to the center of microendemism bounded by the Tsiribihina River to the south and the Betsiboka River to the north. Some were distributed broadly across the dry deciduous (“western”) forests, some from the northernmost tip of Madagascar to the Mangoky River, and some even south of the Mangoky, into the dry spiny bush. Some ranged into the mosaic habitats of the Central Highlands, suggesting greater tolerance of high elevation and perhaps cold temperatures. Some likely depended on particular resources (e.g., species of bamboo) that were undoubtedly far more abundant across northern, central, and western Madagascar in the past than they are now. Finally, it is possible that moist forested corridors once crossed the Central Highlands, at least intermittently, and connected the forests of the east and the forests of the Tsiribihina–Betsiboka interriver zone in the west (Godfrey et al., 1999).

Based on the faunal composition of the AGB and AMT localities, it is likely that the late Holocene environment of Beanka was very similar to the environment of today in terms of floristic composition and climate. The paleohabitat at Beanka supported extinct lemurs that probably spent most of their time in trees, such as sloth lemurs. *Archaeolemur* has been identified as the most likely of the extinct large lemurs to have been comfortable in a wide variety of habitats, spending considerable time on the ground. It has been considered a habitat generalist based on bone morphology, teeth, and coprolites (Burney et al., 1997; Godfrey et al., 2005; Vasey et al., 2013). *Pachylemur* was likely as comfortable on the tsingy as are extant lemurids today. *Plesiorycteropus*, as suggested by MacPhee (1994), may have been a more adept climber than the more familiar African aardvark or many other large insectivorous mammals (assuming it was able to negotiate the adjacent tsingy, and not transported there by a predator). Two species of *Cryptoprocta* (*C. ferox* and *C. spelea*) are present in the subfossils at Beanka. While *C. spelea* is now extinct, *C. ferox* persists in the region. The absence of evidence for large-carnivore gnawing or other mammalian processing (other than rodents) on the Beanka bone specimens makes it doubtful that the primary mode of bone transport to these caves was via *Cryptoprocta*.

At least three (and perhaps all four) of the extinct large lemurs (i.e., *B. radofilai*, *P. kelyus*, and *A. edwardsi*), as

well as some of the locally extirpated species that have been recovered, are taxa with affinities to the western dry forests of the island, rather than the spiny bush of the southwest, although *A. edwardsi* was also abundant in the subhumid forests of the Central Highlands (Goodman and Jungers, 2014). The biogeographic implications of the presence at Beanka of the fourth extinct lemur, *Pachylemur*, are more difficult to assess. This genus was widespread throughout Madagascar, though its concentration was highest in the spiny bush of the southwest and in the Central Highlands. Populations of *Pachylemur* from these two regions have been attributed to different species (*P. insignis* and *P. jullyi*), but these attributions have been questioned (Godfrey and Jungers, 2002; Godfrey et al., 2010). The identity of specimens from the dry forests of the north, due to the dearth of specimens, has not yet been determined. Furthermore, only a few specimens of *Pachylemur* have been found at Beanka thus far, and they will require further evaluation. If there were indeed two species of *Pachylemur* on Madagascar, as has been claimed, and if the *Pachylemur* at Beanka belonged to the species that occupied the Central Highlands, then this species may have had a geographic range similar to that of *A. edwardsi*, including the dry forests of the north and northwest. Alternatively, if the Beanka population was conspecific with the *Pachylemur* population from the southwest, it would represent a range distribution very different from those of all other giant lemurs at Beanka.

Several extant species have disjunct distributions today in the humid eastern forests and the Beanka region in the west. This includes the eastern lesser bamboo lemur *H. griseus* and the euplerid *Galidia elegans* (the ring-tailed vontsira). The western population of the “eastern” lesser bamboo lemur may have diverged sufficiently long ago to be genetically distinct; it is therefore referred to here as *H. cf. griseus*. It is also genetically distinct from *H. occidentalis* (which lives in the northeast and the more mesic forests of the north and northwest). Eastern and western populations of the vontsira or ring-tailed mongoose, *G. elegans*, may similarly be genetically distinct (Bennett et al., 2009). There is today a population in the dry forests of the extreme north that is genetically closer to the eastern population than are populations in the northwest (Bennett et al., 2009). Interestingly, Muldoon et al. (2009) reported *G. elegans* in the subfossil fauna of Ankilitelo Cave in the southwest; this is its first documented occurrence in the spiny bush ecoregion. Two additional extant species present in the Beanka subfossil deposits are now limited to the eastern rainforest. These are *P. simus* and *M. talazaci*. As stated earlier, subfossil *Prolemur* is also known from the adjacent Bemaraha and other subfossil sites in the extreme north, northwest, and central regions of Madagascar.

The Beanka site is remarkable for the apparent absence of the “typical” subfossil megafauna of many other Madagascar sites (see Goodman and Jungers, 2014). With its lack of hippopotami and ratites, Beanka resembles the tsingy of Ankarana (Simons et al., 1995). Ankarana, however, did have *Megaladapis* and other large lemur taxa (e.g.,

*Mesopropithecus dolichobrachion*) lacking at Beanka. Limestone areas less rugged or extensive, on the other hand, such as Anjohibe (Burney et al., 1997) and Andrahomana (Burney et al., 2008), generally sample most of these taxa.

It is possible that some of the subfossil bones at Beanka were transported there from other localities. However,  $^{87}\text{Sr}/^{86}\text{Sr}$  for the subset of *Babakotia* and *Archaeolemur* specimens that we analyzed are, with one possible exception, consistent with what we would expect for individuals that foraged on the local Jurassic limestone (McArthur et al., 2001). This substantially decreases the likelihood that the individuals were gathered from a broad geographic area, but is consistent with the possibility that animals lived in a variety of habitats within Beanka. Variability in  $\delta^{15}\text{N}$  values among the more recent *Babakotia* specimens could also reflect different habitats at Beanka, which even today is heterogeneous in terms of vegetation structure and floristic diversity (Gautier et al., 2013; Rakotozafy et al., 2013). Perhaps they were gathered to this location by a predator, such as the extinct primate-eating eagle *Stephanoaetus mahery*, discussed in Goodman and Jungers (2014). Its living African congener, the crowned eagle (*S. coronatus*) feeds primarily on monkeys (Williams and Arlott, 1980), including large specimens in the estimated size range of *Babakotia* (Jungers et al., 2008). *Cryptoprocta spelea* could be expected to take prey in this size range as well (Meador et al., 2019). People were butchering and eating animals at Beanka at some point in time, so their impact on the distribution of faunal remains cannot be discounted.

## CONCLUSIONS

Evidence presented here demonstrates that the extinct large sloth lemur *B. radofilai* and other extinct taxa persisted in the remote Beanka region many centuries and perhaps millennia after human arrival to the island, contrary to the expectations of any extinction hypothesis predicting a rapid, island-wide extinction pattern. More work in largely undisturbed paleontological sites, such as these in Beanka, focusing on dating of shallow deposits as those most likely to contain late-occurring specimens, will help clarify the timing and causes of disappearance of Madagascar's unique fauna of large lemurs and other extinct species. In addition, the assemblage described shows that taxa present here include elements of both wetter- and drier-adapted faunas described elsewhere and show no strong pattern of microendemism for the species sampled by the fossil record. The late survival of extinct taxa at Beanka, as well as the high diversity that persists in this region today, points to the value of this new protected area and others like it for preservation of what remains of Madagascar's threatened natural heritage.

## ACKNOWLEDGMENTS

Research at Beanka was supported by the National Geographic Society via Waitt Foundation grants W263-13 and W388-15 to DAB, and by the site-managing organization, Biodiversity Conservation

Madagascar (BCM). EJdB was supported by a travel grant from the Society for Advancement of Research in the Tropics (Treib Maatschappij). The scientific study authorization was provided by the Bureau du Cadastre Minier de Madagascar with the reference 024/2015. Many thanks to faculty of the Université d'Antananarivo and staff of BCM and Association Vahatra for assistance with permits and logistics. To the staff of BCM and the people of the village of Ambinda, we extend special thanks for hospitality and assistance with fieldwork and information regarding sites and access. Bone specimens were identified from studies of comparative materials at the Field Museum of Natural History, the Université d'Antananarivo, Association Vahatra, Duke Lemur Center, Muséum national d'Histoire naturelle (Paris), the Natural History Museum (London), the Smithsonian Institution, the American Museum of Natural History, and the University of Massachusetts, Amherst. Species identifications were supported in part by NSF BCS-1750598 (to LRG). Isotopic and radiocarbon analyses were supported in part by NSF BCS-1749676 (to BEC). Thanks to T. Johnson, G. Bartov, T. Guilderson, and J. Southon for analytical assistance.

## REFERENCES

- Albrecht, G.H., Jenkins, P.D., Godfrey, L.R., 1990. Ecogeographic size variation among the living and subfossil prosimians of Madagascar. *American Journal of Primatology* 22, 1–50.
- Ambrose, S.H., 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. *Journal of Archaeological Science* 17, 431–451.
- Anderson, A., Clark, G., Haberle, S., Higham, T., Nowak-Kemp, M., Prendergast, A., Radimilahy, C., et al., 2018. New evidence of megafaunal bone damage indicates late colonization of Madagascar. *PLoS ONE* 13, e0204368.
- 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.
- Burney, D.A., 1999. Rates, patterns, and processes of landscape transformation and extinction in Madagascar. In: MacPhee, R.D.E. (Ed.), *Extinctions in Near Time: Causes, Contexts, and Consequences*. Plenum, New York, pp. 145–164.
- 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., James, H.F., Grady, F.V., Rafamantanantsoa, J.-G., Ramilisonina, Wright, H.T., Cowart, 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., Vasey, N., Godfrey, L.R., Ramilisonina, Jungers, W.L., Ramarolahy, M., Raharivony, L., 2008. New findings from Andrahomana Cave, southeastern Madagascar. *Journal of Cave and Karst Studies* 70, 13–24.
- Coplen, T.B., Brand, W.A., Gehre, M., Gröning, M., Meijer, H.A.J., Toman, B., Verkouteren, R.M., 2006. New guidelines for  $\delta^{13}\text{C}$  measurements. *Analytical Chemistry* 78, 2439–2441.
- Crowley, B.E., 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quaternary Science Reviews* 29, 2591–2603.

- Crowley, B.E., Godfrey, L.R., Bankoff, R.J., Perry, G.H., Culleton, B.J., Kennett, D.J., Sutherland, M.R., Samonds, K.E., Burney, D.A., 2017. Island-wide aridity did not trigger recent megafaunal extinctions in Madagascar. *Ecography* 40, 901–912.
- Crowley, B.E., Godfrey, L.R., Guilderson, T.P., Zerméño, P., Koch, P.L., Dominy, N.J., 2012. Extinction and ecological retreat in a community of primates. *Proceedings of the Royal Society of London B* 279, 3597–3605.
- Crowley, B.E., Sparks, J., 2018. Site 81: Beanka, Géologie/Geology. In: Goodman, S.M., Raheirilalao, M.J., Wohlhauser, S. (Eds.), *Les Aires Protégées Terrestres de Madagascar: Leur Histoire, Descriptions et Biotes/The Terrestrial Protected Areas of Madagascar: Their History, Descriptions and Biota*. Association Vahatra, Antananarivo, pp. 1445–1446.
- Crowley, B.E., Thorén, S., Rasoazanabary, E., Vogel, E.R., Barrett, M.A., Zohdy, S., Blanco, M.B., et al., 2011. Explaining geographical variation in the isotope composition of mouse lemurs (*Microcebus*). *Journal of Biogeography* 38, 2106–2121.
- Crowley, B.E., Wheatley, P.V., 2014. To bleach or not to bleach? Comparing treatment methods for isolating biogenic carbonate. *Chemical Geology* 381:234–242.
- Dammhahn, M., Markolf, M., Lührs, M.-L., Thalmann, U., Kappeler, P.M., 2013. Lemurs of the Beanka Forest, Melaky Region, western Madagascar. In: Goodman, S.M., Gautier, L., Raheirilalao, M.J. (Eds.), *The Beanka Forest, Melaky Region, Western Madagascar. Malagasy Nature* 7, 259–270.
- De Boer, E.J., Hooghiemstra, H., Florens, F.B.V., Baider, C., Engels, S., Dakos, V., Blaauw, M., Bennett, K.D., 2013. Rapid succession of plant associations on the small ocean island of Mauritius at the onset of the Holocene. *Quaternary Science Reviews* 68, 114–125.
- Fox-Dobbs, K., Leonard, J.A., Koch, P.L., 2008. Pleistocene megafauna from eastern Beringia: paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 261, 30–46.
- Ganzhorn, J.U., Wilmé, L., Mercier, J.-L., 2014. Explaining Madagascar's biodiversity. In: Scales, I.R. (Ed.), *Conservation and Environmental Management in Madagascar*. Routledge, New York, pp. 17–43.
- Gautier, L., Bolliger, R., Callmander, M., Hanitrarivo, M.R., Luino, I., Nusbaumer, L., Phillipson, P., et al., 2013. Inventaire des plantes vasculaires de la région de Beanka, Région Melaky, Ouest de Madagascar. In: Goodman, S.M., Gautier, L., Raheirilalao, M.J. (Eds.), *The Beanka Forest, Melaky Region, Western Madagascar. Malagasy Nature* 7, 127–160.
- Godfrey, L.G., Jungers, W.L., Burney, D.A., 2010. Subfossil lemurs of Madagascar. In: Werdelin, L., Sanders, W. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 351–367.
- Godfrey, L.G., Scroxton, N., Crowley, B.E., Burns, S.J., Sutherland, M.R., Pérez, V.R., Faina, P., McGee, D., Ranivoharimanana, L., 2019. A new interpretation of Madagascar's megafaunal decline: the "Subsistence Shift Hypothesis." *Journal of Human Evolution* 130, 126–140.
- Godfrey, L.R., Jungers, W.L., 2002. Quaternary fossil lemurs. In: W. Hartwig (Ed.), *The Primate Fossil Record*. Cambridge University Press, New York, pp. 97–121.
- Godfrey, L.R., Jungers, W.L., Simons, E.L., Chatrath, P.S., Rakotosamimanana, B., 1999. Past and present distributions of lemurs in Madagascar. In: Rakotosamimanana, B., Rasamimanana, H., Ganzhorn, J.U., Goodman, S.M. (Eds.), *New Directions in Lemur Studies*. Plenum Press, New York, pp. 19–53.
- Godfrey, L.R., Semperebon, G.M., Schwartz, G.T., Burney, D.A., Jungers, W.L., Flanagan, E.K., Cuzzo, F.P., King, S.J., 2005. New insights into old lemurs: the trophic adaptations of the Archaeolemuridae. *International Journal of Primatology* 26, 825–854.
- Godfrey, L.R., Simons, E.L., Jungers, W.L., DeBlieux, D.D., Chatrath, P.S., 2004. New discovery of subfossil *Hapalemur simus*, the greater bamboo lemur, in western Madagascar. *Lemur News* 9, 9–11.
- Goodman, S.M., Jungers, W.L., 2014. *Extinct Madagascar: Picturing the Island's Past*. University of Chicago Press, Chicago.
- Hansford, J., Wright, P.C., Rasoamiamanana, A., Pérez, V.R., Godfrey, L.R., Erickson, D., Thompson, T., Turvey, S.T., 2018. Early Holocene human presence in Madagascar evidenced by exploitation of avian megafauna. *Science Advances* 4, eaat6925.
- Hogg, A.G., Hu, Q., Blackwell, P.G., Niu, M., Buck, C., Guilderson, T.P., Palmer, J.G., et al., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. *Radiocarbon* 55, 1889–1903.
- Jungers, W.L., Demes, B., Godfrey, L.R. 2008. How big were the "giant" extinct lemurs of Madagascar? In: Fleagle, J.G., Gilbert, C.C. (Eds.), *Elwyn Simons: A Search for Origins*. Springer, New York, pp. 343–360.
- Keeling, R.F., Piper, S.C., Bollenbacher, A.F., Walker, S.J., 2010. Monthly atmospheric  $^{13}\text{C}/^{12}\text{C}$  isotopic ratios for 11 SIO stations. In: *Trends: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, TN.
- Koch, P.L., 1998. Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences* 26, 573–613.
- MacPhee, R.D.E., 1994. Morphology, adaptations, and relationships of *Plesiorcycteropus*, 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., Marx, P.A., 1997. The 40,000-year plague: humans, hypervirulent diseases, and first-contact extinctions. In: Goodman, S.M., Patterson, B.D. (Eds.), *Natural Change and Human Impacts in Madagascar*. Smithsonian Institution Press, Washington, DC, pp. 169–217.
- Martin, P.S., 1984. Prehistoric overkill: the global model. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 354–403.
- Martin, R.D., 1972. Adaptive radiation and behaviour of the Malagasy lemurs. *Philosophical Transactions of the Royal Society of London B* 264, 295–352.
- McArthur, J.M., Howarth, R.J., Bailey, T.R., 2001. Strontium isotope stratigraphy: LOWESS Version 3: best fit to the marine Sr-isotope curve for 0–509 Ma and accompanying look-up table for deriving numerical age. *Geology* 109, 155–170.
- Meador, L.R., Godfrey, L.R., Rakotondramavo, J.C., Ranivoharimanana, L., Zamora, A., Sutherland, M.R., Irwin, M.T., 2019. *Cryptoprocta spelea* (Carnivora: Eupleridae): what did it eat and how do we know? *Journal of Mammalian Evolution* 26, 237–251.
- Middleton, G.J., 2013. Caves of the Beanka karst, Melaky Region, western Madagascar. In: Goodman, S.M., Gautier, L., Raheirilalao, M.J. (Eds.), *The Beanka Forest, Melaky Region, Western Madagascar. Malagasy Nature* 7, 27–47.



- Muldoon, K.M., Crowley, B.E., Godfrey, L.R., Simons, E.L., 2017. Predation on subfossil *Prolemur simus* by multiple predator species at Ankarana Massif, northern Madagascar. *International Journal of Primatology* 38, 58–79.
- Muldoon, K.M., de Bliieux, D.D., Simons, E.L., Chatrath, P.S. 2009. The subfossil occurrence and paleoecological significance of small mammals at Ankiliteho Cave, Southwestern Madagascar. *Journal of Mammalogy* 90, 1111–1131.
- Rakotozafy, B.F.L., Hanitrarivo, R.M., Ranirison, P., Tahinarivony, J.A., Edmond, R., Gautier, L., 2013. Structure et composition floristique de la forêt sur faciès karstique de Beanka, Région Melaky, Ouest de Madagascar. In: Goodman, S.M., Gautier, L., Raherilalao, M.J. (Eds.), *The Beanka Forest, Melaky Region, Western Madagascar*. *Malagasy Nature* 7, 105–125.
- Roig, J.Y., Tucker, R.D., Delor, C., Peters, S.G., Théveniaut, H., 2012. *Carte Géologique de la République de Madagascar à 1/1,000,000*. Ministère des Mines, Programme de Gouvernance des Ressources Minérales, Antananarivo, République de Madagascar.
- Scroxton, N., Burns, S.J., McGee, D., Hardt, B., Godfrey, L.R., Ranivoharimanana, L., Faina, P., 2017. Hemispherically in-phase precipitation variability over the last 1700 years in a Madagascar speleothem record. *Quaternary Science Reviews* 164, 25–36.
- Simons, E.L., 1997. Lemurs: old and new. In: Goodman, S.M., Patterson, B.D. (Eds.), *Natural Change and Human Impacts in Madagascar*. Smithsonian Institution Press, Washington, DC, pp. 142–168.
- Simons, E.L., Burney, D.A., Chatrath, P.S., Godfrey, L.R., Rakotosamimanana, B., 1995. AMS 14C dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quaternary Research* 43, 249–254.
- Skryzpek, G., 2013. Normalization procedures and reference material selection in stable HCNOS isotope analyses: an overview. *Analytical and Bioanalytical Chemistry* 405, 2815–2823.
- Sparks, J.M., Crowley, B.E., 2018. Where did people forage in prehistoric Trinidad? Testing the utility of a multi-isotope approach for tracking the origins of terrestrial prey. *Journal of Archaeological Science Reports* 19, 968–978.
- Stuiver, M., Reimer, P.J., 1993. Extended 14C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35, 215–230.
- Vasey, N., Burney, D.A., Godfrey, L.R., 2013. Coprolites associated with *Archaeolemur* remains in north-western Madagascar suggest dietary diversity and cave use in a subfossil prosimian. In: Masters, J., Gamba, M., Génin, F. (Eds.), *Leaping Ahead: Advances in Prosimian Biology*. Springer, Dordrecht, Netherlands, pp. 149–157.
- Vences, M., Wollenberg, K.C., Vietes, D.R., Lees, D.C., 2009. Madagascar as a model region of species diversification. *Trends in Ecology and Evolution* 24, 456–465.
- Veress, M., Lóczy, D., Zental, Z., Toth, G., Schläffer, R., 2008. The origin of the Bemaraha tsingy (Madagascar). *International Journal of Speleology* 37, 131–142.
- Vérin, P., 1975. Les échelles anciennes du commerce sur les côtes nord de Madagascar. Department of Reproduction of the Doctoral Theses of the University of Lille, Lille.
- Virah-Sawmy, M., Willis, K.T., Gillson, L., 2010. Evidence for drought and forest decline during the recent megafaunal extinctions in Madagascar. *Journal of Biogeography* 37, 506–519.
- Wang, L., Brook, G.A., Burney, D.A., Voarintsoa, N.R., Liang, F., Cheng, H., Edwards, R.L., 2019. The African Humid Period, rapid climate change events, the timing of human colonization, and megafaunal extinctions in Madagascar during the Holocene: evidence from a 2m Anjohibe Cave stalagmite. *Quaternary Science Reviews* 210, 136–153.
- Williams, J.G., Arlott, N., 1980. *A Field Guide to the Birds of East Africa*. Collins, London.
- Wilmé, L., Goodman, S.M., Ganzhorn, J.U. 2006. Biogeographic evolution of Madagascar's microendemic biota. *Science* 312, 1063–1065.
- Wright, H.T., Vérin, P., Ramilisonina, Burney, D.A., Burney, L.P., Matsumoto, K., 1996. The evolution of settlement systems in the Bay of Boeny and the Mahavavy River Valley, north-western Madagascar. *Azania* 31, 37–73.
- Wright, P.C., Johnson, S.E., Irwin, M.T., Jacobs, R., Schlichting, P., Lehman, S., Louis, E.E., et al., 2008. The crisis of the critically endangered greater bamboo lemur (*Prolemur simus*). *Primate Conservation* 23, 5–17.
- Yoder, A.D., Heckman, K., 2006. Mouse lemur phylogeography revises a model of ecogeographic constraint in Madagascar. In: Lehman, S.M., Fleagle, J. (Eds.), *Primate Biogeography: Progress and Prospects*. Kluwer, New York, pp. 255–268.