

Environmental change, extinction and human activity: evidence from caves in NW Madagascar

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Abstract. In the last 2000 years, changes on the island of Madagascar have resulted in the modification of key environments and the extinction of nearly all large native animals. Humans have long been suspected as the primary cause of this ecological catastrophe, but the exact mechanisms of the island's rapid transformation and the role of natural factors such as climate change remain uncertain. Caves in northwestern Madagascar are helping researchers to disentangle these factors, by providing many types of datable information concerning the past in close physical proximity. *U*-series dated pollen spectra from the caverns of Anjohibe provide a 40,000-year record of vegetation

in the vicinity. Bone deposits from caves in the region provide new site records for extinct taxa, including *Babakotia radofilai* Godfrey *et al.* 1990, *Plesiorycteropus madagascariensis* Filhol 1895, and *Mullerornis* sp. Several extant taxa that were present in the region in the late Holocene are now locally extinct. Archaeological evidence from the caves suggests little or no human activity in the vicinity or interaction with the fauna at these sites until recent centuries.

Key words. Madagascar, extinctions, human impacts, caves, paleobiogeography.

Résumé. Dans les dernier deux mille ans, les changements à l'île de Madagascar ont abouti à la modification des environnements premiers et l'extinction de près tout les grandes animaux indigènes. Les humains ont été soupçonnés depuis longtemps comme la raison première de cette catastrophe écologique, mais la mode exacte de la transformation rapide de l'île et le rôle des agents naturel tel que les changements climatique restent irrésolu. Les grottes au nord-ouest de Madagascar aident les chercheurs démêler ces agents, par pourvoir de nombreux types des informations datable a l'égard du passé en proximité physique. Les spectres polliniques avec datation *U*-series des grottes d'Anjohibe pourvoient un archive de la

végétation dans le voisinage à 40,000 ans. Les dépôts des ossements dans la région pourvoient les nouveaux records d'emplacement pour les taxons étients, y compris *Babakotia radofilai* Godfrey *et al.*, 1990, *Plesiorycteropus madagascariensis* Filhol, 1895, et *Mullerornis* sp. Plusieurs taxons survivant qui existent avant dans la région pendant l'Holocène tard sont actuellement éteints localement. L'évidence archéologique des grottes indique peu ou point de l'activité humaine dans le voisinage ni impact sur la faune à ces sites jusqu'aux les siècles récents.

Mots clés. Madagascar, les disparitions, les impactes humains, les grottes, paléobiogéographie.

INTRODUCTION

Although Madagascar is renowned for its high proportion of unique species, its modern ecosystems are depauperate compared with those of only a few thousand years ago. At that time, the vertebrate fauna was enriched by pygmy hippos, giant tortoises, elephantbirds and giant lemurs up to gorilla size. The crocodile is the only survivor, among the megafauna, of an island-wide extinction event that also claimed at least eight vertebrates of more modest size.

Most discussions of probable causes of these extinctions

have invoked human actions (reviewed in MacPhee, Burney & Wells, 1985), such as over-hunting (Walker, 1967), introduction of competitors (Dewar, 1984), burning of forests (Humbert, 1927), or a synergistic combination of these factors (Burney & MacPhee, 1988). Radiocarbon dating has shown that many (perhaps all) of these extinctions postdate the arrival of humans about 2000 years ago (MacPhee & Burney, 1991).

Although many authors have favoured some version of the human-agency hypothesis, others have stressed that climatic change may have played a role as well.

Paleontologists working in the arid southern part of the island have often pointed out that late Holocene desiccation may have made this region less suitable for some of the now-extinct animals (Battistini, 1971; Mahe & Sourdat, 1972; MacPhee, 1986), and major vegetation changes probably associated with drier conditions have been demonstrated by pollen analysis from a site in the southwest (Burney, 1993).

In the early twentieth century, French botanists working in Madagascar promoted the idea, which seemed reasonable at the time, that the entire island was covered by 'climax' forest prior to human arrival (Perrier de la Bâthie, 1921; Humbert, 1927). Their belief that fire was 'introduced' to these environments by arriving humans, with the result that this forest was rapidly replaced by depauperate grasslands, was shown to be an oversimplification by subsequent research. Pollen and charcoal analysis of sediment cores from the mountainous central and northern regions of the island (MacPhee *et al.*, 1985; Burney, 1987a,b,c), the arid southwest (Burney, 1993) and the intensely seasonal northwest (Matsumoto & Burney, 1994) indicates that some grasslands and wooded savannas existed thousands of years before the presumed time of human arrival. Natural fires were a part of seasonal environments in Madagascar at times when only lightning, volcanoes or other non-human sources could have started them. Nevertheless, human impacts on the vegetation are discernible in the pollen record of the southwest beginning perhaps two millennia ago, and 500–1200 yr BP at various sites in the centre and northwest of the island.

Considerable differences in climate and geology from one region of Madagascar to another underlie the development of distinctive phytogeographical regions, including rain forest on the eastern escarpment; woodland, grassland, and montane vegetation in the highlands; dry forest and wooded grassland in the west; and arid bushland in the south and southwest. We might expect each region to have a somewhat independent history in terms of human, plant and animal interactions. To arrive at a better understanding of extinctions, regional records of human and ecological history need to be developed. This can be achieved through multi-disciplinary studies that, in the same or adjacent sites, can develop well-dated chronologies for as many types of relevant data as possible, including analyses by paleontologists, archaeologists and paleoecologists. The fundamental problem is that suitable sites are relatively rare, and the methods for extracting and coordinating these several lines of evidence are still under development. Good preliminary results of this type have been obtained in the southwest (Burney, 1993) and central region (MacPhee *et al.*, 1985) of Madagascar, but in open sites where the evidence is scattered over a wide area (requiring large-scale excavation), with less-than-ideal stratigraphic resolution. Where they are available, caves may provide superior sources of data, by preserving and concentrating the bones of extinct animals, human artefacts and sedimentary microfossils in a relatively small area. During the 1992 field season, we explored the possibilities for using caves in this way in northwestern Madagascar.

STUDY SITES

The Eocene limestone plateau NE of Mahajanga, Madagascar, consists of an uplifted plain with elevations of ca. 50–200 m (Fig. 1a). The surface is primarily rolling grassy hills of very moderate relief, covered sparsely in many areas with endemic satra palms (*Medemia nobilis* Gallierand) and other trees adapted to a long dry season and periodic fires. Dry mesic woodlands and forest patches occur in areas of higher soil moisture. Most of the known caves in the area are very shallow, with numerous dolines (large sinkholes) and skylights (openings in the ceiling). The best-known of the caves in this area is Anjohibe ('big cave' in Malagasy). Older accounts (e.g. Decary, 1938; de Saint-Ours & Paulian, 1953) use the name 'Andranoboka', especially in reference to the entire system of caves in the area. Anjohibe has 5.3 km of passages and more than two dozen entrances (Fig. 1b,c). This cave has previously yielded fossils of extinct animals (Decary, 1938; MacPhee *et al.*, 1984; Ravoavy, 1986; Goodman & Ravoavy, 1993).

About 2 km south of Anjohibe are the less well-known caves known collectively as Anjohikely ('little cave' in Malagasy) (Fig. 1b,d). Recent exploration and mapping by a group of German cavers (Laumanns, Burgsmüller & Geucke, 1991) has shown that two of the three caves in this group are linked by subterranean passages, and the third is probably linked by an unexplored passage, giving the 'little cave' a length of more than 2.5 km. Both Anjohibe and Anjohikely were formed by solution of limestone near the top of the saturated zone when the water table was higher. Although most passages in Anjohikely are relatively small in diameter, with somewhat limited development of speleothems (stalactites, stalagmites, and other dripstone formations), Anjohibe has rooms and passages with diameters of >20 m, and dripstone columns and curtains of >3 m diameter.

Limestone outcrops in the area also contain many small fissure caves, unexplored openings and rock shelters. We excavated in one rock shelter (Fig. 1b), which we named Lavakasaka, meaning 'cave of the cat' (in reference to its small size).

METHODS

At the beginning of the study, we mapped the locations of all promising surface deposits, including bone accumulations, owl pellet deposits and archaeological materials. In order to assess the character and thickness of soft sediment deposits, a bucket auger was used to make sediment transects, which can yield a three-dimensional impression of subsurface sedimentology (e.g. Bliley & Burney, 1988). Over 100 small-diameter holes were bored throughout Anjohibe; sediments were sampled less systematically in Anjohikely. All holes were covered afterward for aesthetic and safety reasons. Augering also enhanced our search for subsurface bone deposits.

Speleothems were sampled and processed for uranium-series ($^{230}\text{Th}/^{234}\text{U}$) dating and pollen analysis, as in our related studies in Africa (e.g. Brook, Burney & Cowart, 1990; Burney, Brook & Cowart, 1994). In the surface environs of

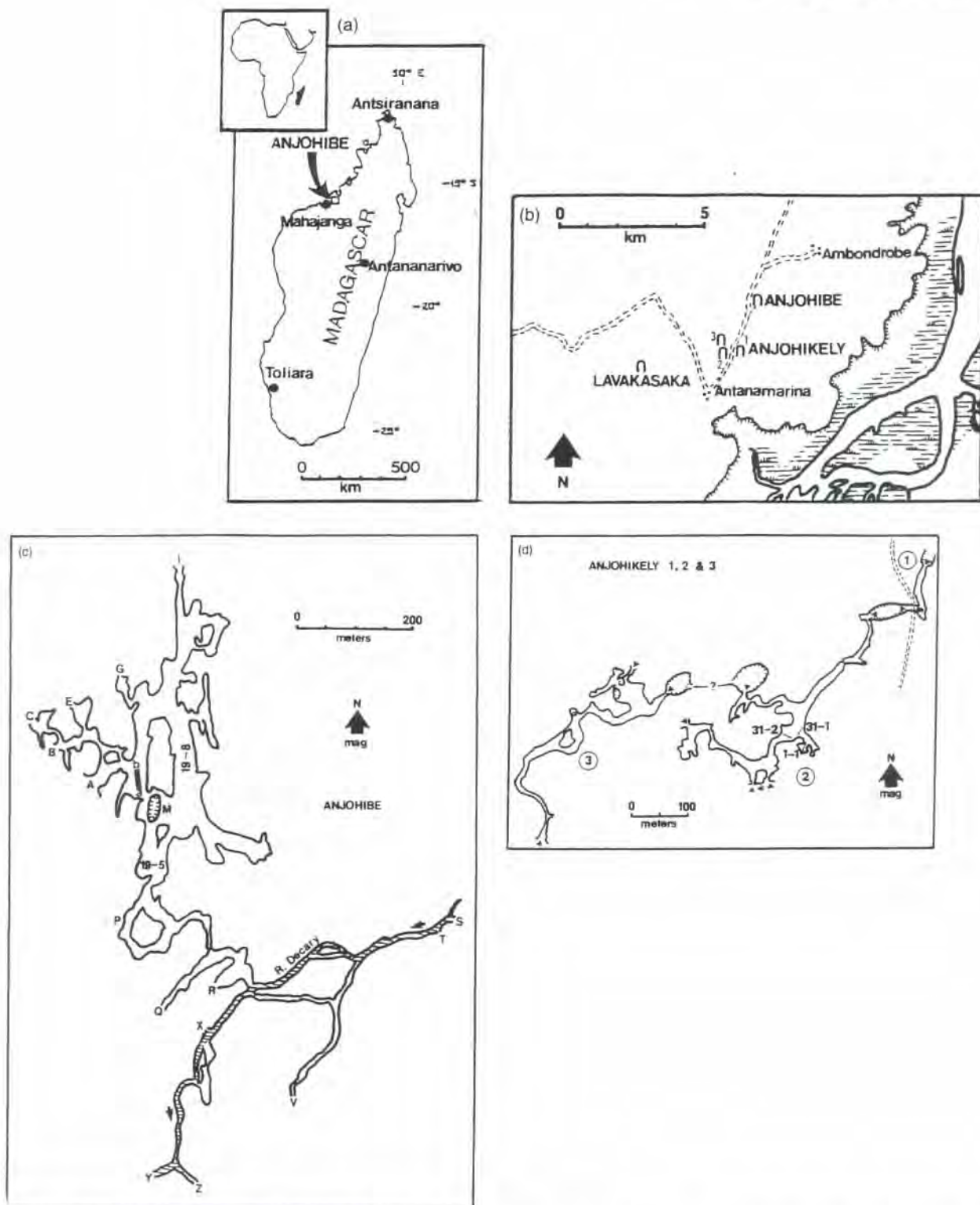


FIG. 1. (a) Location of the Anjohibe area in NW Madagascar, $S15^{\circ}32.55'$ $E46^{\circ}53.17'$, approximate elevation 100 m. (b) Location of Anjohibe, the three Anjohikely caves and the Lavakasaka Rockshelter. (c) Map of the cavern of Anjohibe, redrawn from Laumanns *et al.* (1991), and showing primary entrances in capital letters and place names as designated in de Saint-Ours & Paulian (1953). Numbers indicate sampling sites discussed in the text. Line a-b denotes coring transect pictured in Fig. 2 and diagrammed in Fig. 3. (d) Map of the three Anjohikely caves, redrawn from Laumanns *et al.* (1991). Numbers denote sites discussed in the text. Known entrances marked by small black triangles. Question mark in central region denotes unexplored passages that may connect Anjohikely 2 and 3.

the caves, large trees were bored for a preliminary assessment of the possibilities for tree-ring analysis. Rings that probably represent annual increments were derived from several species. Preliminary results from the tree ring investigations appear elsewhere (Burney *et al.*, 1993). We also cored a small pond on the surface nearby, but it yielded only *ca.* 1 m of sediment above a hard surface that probably indicates complete drying some time in recent millennia.

Our paleontological investigations had four principal goals: (1) to determine the composition of the local fauna before the extinctions, (2) to develop a better chronology for the extinctions, (3) to study paleoecological conditions surrounding the extinction event, and (4) to search for evidence of past human-animal interactions. Accelerator mass spectrometer (AMS) radiocarbon dating was used to obtain dates from bone collagen of extinct animals, or from associated organic remains. For paleoecological studies, we made a special effort to collect bones of smaller vertebrates in a stratigraphic context. To understand better the factors affecting fossil preservation in the cave, we documented the distribution of bones in various types of surface and subsurface deposits. For comparison with the fossil assemblages, we sampled modern predator accumulations, mostly barn owl (*Tyto alba* Scopoli 1769) roosts, as well as bat roosts and remains of animals that died recently in the cave.

A number of promising paleontological and archaeological sites were selected for subsurface sampling using stratigraphic excavation techniques and fine-sieving of sediment as in previous studies (e.g. James *et al.*, 1987; Kirch *et al.*, 1992). After sieving, most of the concentrated sediment was shipped to the National Museum of Natural History, Smithsonian Institution, where very small bones and shells could be extracted in the laboratory.

Surface collections and small excavations were made in a wide range of archaeological site types distributed throughout the caves, to assess the sites' full potential for future excavations on a larger scale. Archaeological information derived from our collections concerning past human use of the caves was augmented by interviews with elderly people living in the vicinity who could share their knowledge concerning oral traditions associated with the caves.

RESULTS

Cave sediments

The floors of some parts of Anjohibe contain deep soft sediment deposits. In most areas sampled, these consisted of brown to reddish-brown silt or clay from the surface down to depths of 0.4–1 m. Below this brown material, the deeper sites showed a thin layer of very fine red clay. In the deepest sites, this was underlain by various deposits ranging from grey clays to yellow sands. The chamber of the cave with the deepest sediments detected was the large, ornately speleothem-draped room directly between entrance A and the large doline designated M. This site (pictured in Fig. 2) was selected for more detailed stratigraphic analysis, with systematic augering along transects throughout the

chamber. A representative transect (a–b in the central portion of Fig. 1c) was used to trace the key sedimentary units laterally through the long axis of the room (Fig. 3) using a cave-adapted version of the methods developed for bogs and lakes (Digerfelt, 1975; Bliley & Burney, 1988).

Radiocarbon dates have been obtained from one of the cores (ANJ-AM-2) using the accelerator mass spectrometer method. Small samples of unmixed sediments were pretreated with HCl to remove carbonates before dating. The no. 2 core was processed for pollen and charcoal analysis using established methods (Swain, 1973; Burney, 1987c). Pollen preservation was poor in the lower units, but charcoal was well-preserved throughout.

At a level dated 7080 ± 80 ^{14}C yr BP, fine grey clay began accumulating on a bed of limestone nodules and blackened bone fragments. Some of the bone fragments are quite large and were probably derived from the extinct megafauna, but they appear to have been rolled and heavily abraded by water. In the lowest portion of the room, a bed of yellow sand, perhaps indicating a flood deposit, caps the grey clay. On top of the water-borne clays and sand is a thin bed of very fine red clay, probably representing aeolian (wind) deposition. This is very likely to be the same red clay layer that can be traced throughout the cave in deep sediment deposits. Above the red clay, a brown silt or silty clay occurs throughout the room and in many other areas of the cave. This deposit contains many bones, particularly of small animals.

A radiocarbon date of 7040 ± 70 yr BP from the lower part of this unit suggests that the lower clay unit, the sand lens and the aeolian red clay may have all been deposited in a few decades or less around 7000 radiocarbon years ago (c. 8000 calendar years; Stuiver & Reimer, 1986), since this date and the date from the bottom of the sequence are statistically indistinguishable. The uppermost unit, the brown silts and silty clays, shows a steep rise in charcoal content (Fig. 4) after this time, and it is likely that this unit represents slow or intermittent sedimentation up to the present, with some sediment mixing. Despite the episodic nature of sedimentation at this site, the patterns shown by the microscopic charcoal particles in this sediment core are consistent with those obtained from other late Holocene sites in Madagascar (Burney, 1987a,b,c, 1993; Wright *et al.*, 1997). These records all show low to medium background levels of charcoal in the part of the late Holocene prior to the presumed time of human arrival in the area (1000–2000 yr BP in various regions of the island), followed by a drastic increase in the human period. In the case of the Anjohibe core, most of the charcoal in all but the uppermost levels was derived from non-graminoid sources (probably trees and shrubs). This trend is followed by a large increase in graminoid (grass-derived) charcoal at a depth of 20 cm. This suggests that the late Holocene vegetation pattern may have been one of declining forests and expanding grasslands, a trend documented from the nearest dated lake-coring site c. 125 km SW of Anjohibe (Matsumoto & Burney, 1994).

Speleothem dating and pollen analysis

Table 1 shows the uranium-series ages of Anjohibe speleothems sampled for dating and pollen analysis.



FIG. 2. Photograph of the site in Anjohibe used for the sediment coring transect denoted a–b in Fig. 1c, and diagrammed in Fig. 3. This area is typical of many parts of the cave, with large speleothems and a floor of soft clastic sediments (photograph by David Burney.).

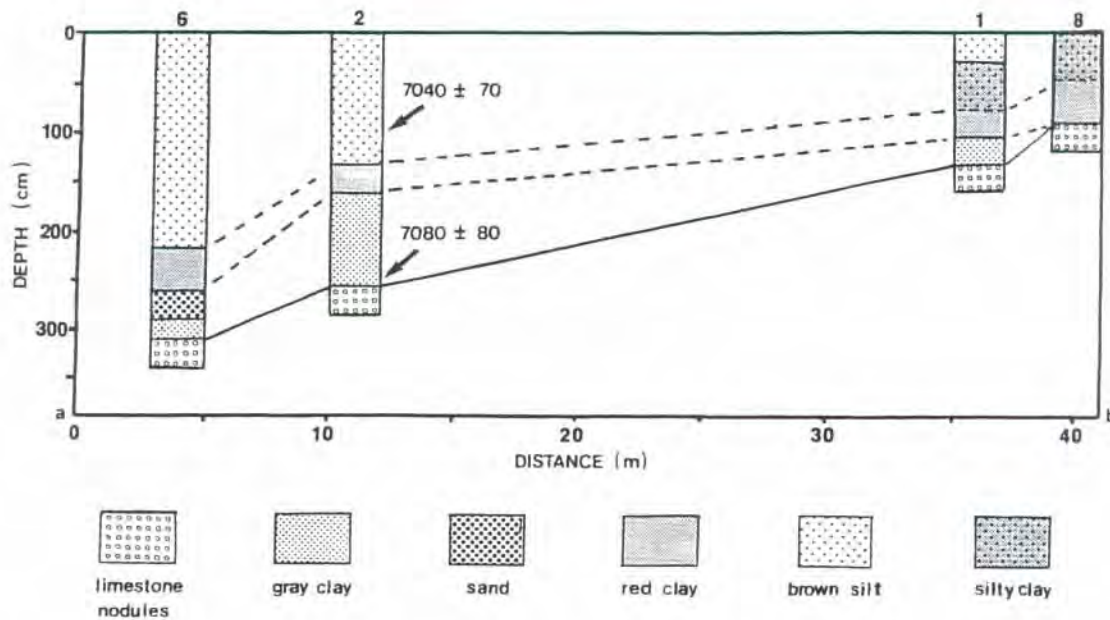


FIG. 3. Stratigraphic correlation of sediment units discerned in cores collected from the transect a–b shown in Fig. 1c. Water-borne silts and clays enter from entrance A and are deposited in the transect area from the NW end of the large chamber between A and the large doline at M. Dashed lines trace a fine red clay layer, probably windblown dust, across the chamber. Solid line delineates the limestone floor beneath the soft sediments.

Replicate samples of *c.* 10–60 g each were used for dating and pollen analysis.

Samples are arrayed in inferred chronological order in Fig. 5. The order is based on the *U*-series dates, but samples ANJ-92-2:25 cm and 50 cm were not dated but are inferred to be intermediate in age between ANJ-92-2:0 cm and 100 cm because they are at intermediate positions between the 0 and 100 cm samples, which are from the edge and the center of a large fallen column, respectively. Pollen preservation in all samples was moderately good for speleothems, with

crumpled indeterminate grains making up <25% of the raw sum at all levels.

The pollen spectra presented may be thought of as six 'snapshots' of the inferred paleovegetation spanning the last *c.* 40 kyr BP. The topmost sample, from the surficial layers of a presently-accreting stalagmite near entrance H (*U*-series dating confirms that it is <4 kyr in age, but the method is not generally suitable for dating material from the last four millennia; Brook *et al.*, 1990) shows a pollen spectrum comparable to those from the late Holocene at Lake

ANJOHIBE, NW MADAGASCAR
CORE ANJ-AM-2
CHARCOAL ANALYSIS

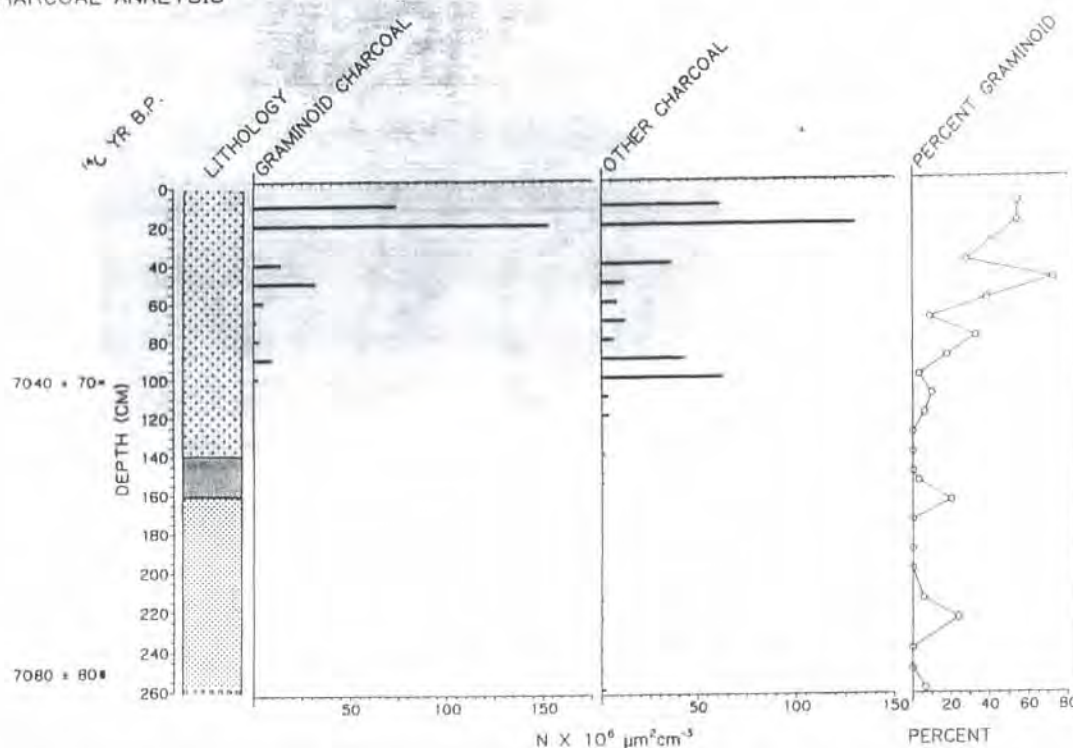


FIG. 4. Charcoal diagram providing a Holocene fire history of Anjohibe. Stratigraphy is from core ANJ-AM-2, shown as '2' in the coring transect in Fig. 3. Charcoal quantity per cm^{-3} is expressed in units of projected area in pollen slides.

TABLE 1. Uranium-series ages for Anjohibe speleothems.

Sample	Inferred $^{230}\text{Th}/^{234}\text{U}$ Age ^a	$^{232}\text{Th}/^{230}\text{Th}$ Ratio	Remarks
ANJ-92-2			
0–2 cm	6.52 ± 2.64 kyr BP	0.15 ^b	Outermost layers of large collapsed column at M, weathering rind removed
50 cm	not datable ^c	—	Ca. midway to centre of collapsed column
100 cm	40.11 ± 7.21 kyr BP	0.05	Near centre of the collapsed column
ANJ-92-3			
0–3 cm	<4.0 kyr BP	—	Finely-laminated active stalagmite near H, outermost portion
ANJ-92-4			
0–2 cm	22.88 ± 4.48 kyr BP	0.0	Tip of large fallen speleothem lying on bone-filled sediment deposits of site 19-8 (the 'Bat Site')
ANJ-92-5	37.55 ± 4.67 kyr BP ^d	0.26	Same as ANJ-92-2, 02 cm, except weathering rind not removed

^a Ages in thousands of years, from α -counting technique. Error represents $\pm 1\sigma$.

^b Based on low number of counts.

^c ^{230}Th below detection limits (low yield from sample).

^d Date rejected, due to high $^{232}\text{Th}/^{230}\text{Th}$ ratio, indicating likely contamination of sample from cave exterior.

Mitsinjo (Matsumoto & Burney, 1994) c. 125 km SW. The moderate value for the endemic palm *Medemia nobilis* and high value for grass pollen (Gramineae), with only traces of other types, reflects the modern vegetation of the site, a palm savanna. The outermost portion of a big broken

column at M (ANJ-92-2, 0 cm, abbreviated as 2:0 in Fig. 4), which dates to 6.52 ± 2.64 kyr BP, shows a similar spectrum, but with more *Medemia* pollen and less grass pollen. The 25 cm and 50 cm samples from this speleothem show similar spectra, except with lower overall pollen

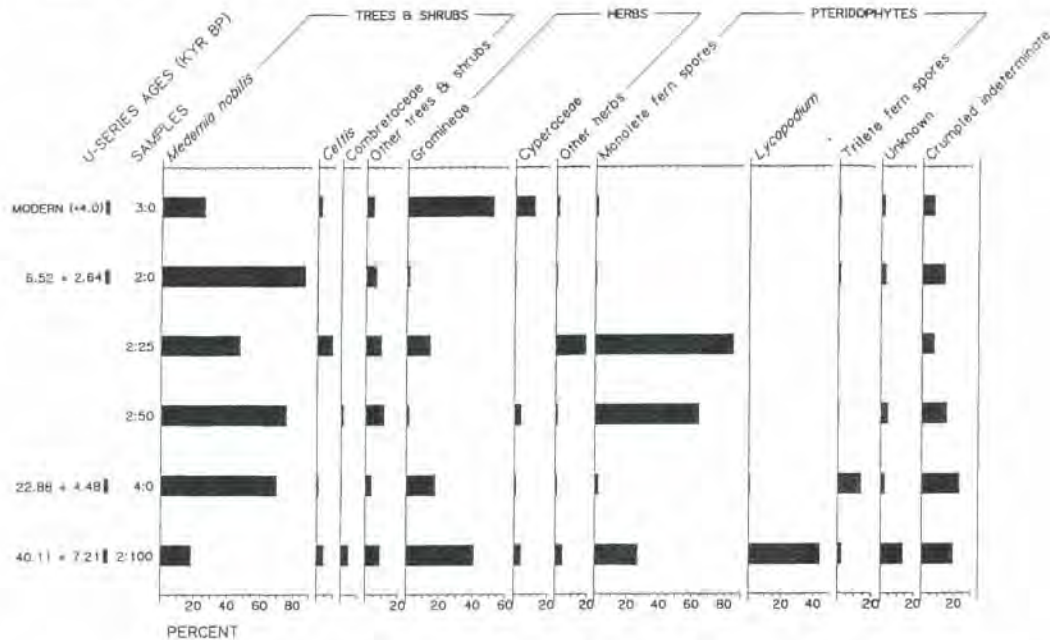
ANJOHIBE, NW MADAGASCAR
 SPELEOTHEM POLLEN SPECTRA


FIG. 5. Pollen spectra from U-series dated speleothems from Anjohibe. Pollen sum is based on all pollen types. Spore and crumpled indeterminate percentages calculated from raw sum (pollen + spores + indeterminates).

concentrations, slightly higher percentages of some trees of open country and forest edges, and very high values for monolete fern spores. Such ferns are common denizens of the twilight regions of caves.

A sample (ANJ-92-4:0 cm) from the tip of the large fallen speleothem at site 19-8 (Fig. 1c), denoted 4:0 in Fig. 5, shows a very similar spectrum to these, but has a low percentage of monolete fern spores and moderate amounts of trilete fern spores. This sample dates to the full glacial times of the late Pleistocene at 22.88 ± 4.48 kyr BP.

The sample from near the centre of the big column at M (ANJ-92-2, 100 cm) dates to 40.11 ± 7.21 kyr BP, the mid-Wisconsinan portion of the late Pleistocene. The spectrum is remarkably similar to that of the modern sample, with moderate values for *Medemia*, high Gramineae, and traces of various savanna and woodland tree pollen types. Unlike any other spectrum, however, there is a high percentage of pollen of club mosses (*Lycopodium*) a common denizen of cool moist environments.

Paleontology

A faunal list of higher vertebrates from Anjohibe and nearby caves is given in Appendix 1. Although we have not yet made final species determinations for some of the mammals we collected, we can say that c. sixty-six species of higher vertebrates are represented in our collections and those of the previous paleontological expeditions to these caves (Decary, 1938; MacPhee *et al.*, 1984; Ravoavy, 1986; Goodman & Ravoavy, 1993). Eight to eleven of these species are now extinct, and three of the extant species no longer occur near Anjohibe.

We originally expected that the many high skylights in Anjohibe would serve as natural traps for larger vertebrates that chanced to fall in, but we failed to find rich fossil accumulations under these openings, perhaps because the bones have been washed out during floods. The two excavations that were most productive of fossils were near but not directly under skylights, in areas that had once held standing water. The first of these is the Hippo Site (19-5, Fig. 1c), located in a low alcove of Salle R. de Joly, an area once occupied by a shallow pond that left behind distinctive horizontal water marks on the wall from precipitation of cave minerals and iron oxide staining.

Two skulls of the extinct pygmy hippopotamus (*Hippopotamus cf. lemerlei* A. Grandidier 1868) protruding slightly through the sediment were our clue to the presence of subsurface fossils here. Our excavation of a 2 m² area of the site produced partial skeletons of at least eight individual hippopotamuses in an excellent state of preservation, including five adults and three immatures of different age, one possibly fetal or neonatal. The hippopotamus skeletons were partly articulated and closely packed together, so that bones from different individuals were nestled like puzzle pieces and in some places had no sediment between them. Bones were abundant throughout the sediment, which consisted of 18–26 cm of unstratified reddish-brown silty clay. There was some stratification of bones in the deposit, with larger bones (e.g. skulls, mandibles, pelvis, and long bones) generally overlying smaller ones (e.g. ribs, metapodials, and phalanges).

The floor of the cave underneath the deposit was covered with fist-sized limestone concretions typical of those we saw under standing water in other parts of the cave. An

undetermined number of additional hippopotamus individuals are present in unexcavated portions of the site, which bucket-augering revealed to be limited to this small alcove.

From the presence of partly articulated skeletons with many largely undamaged bones of different individuals piled together, we infer that these animals died contemporaneously at the site. Some of the isolated teeth and bone fragments are water-worn, indicating that there was water movement through the site at one time. We found no evidence to implicate humans in the animals' death. Apparently, a herd of hippopotamuses became trapped in the cave and died together in the shallow pond that may have existed at that time. The hippos could have fallen through a skylight or washed into the cave in a flood. Another possibility is that they walked into Entrance I and followed the skylights of the Grande Avenue until they arrived at their final resting place in Salle R. de Joly. The animals' milling about may have knocked over a number of small speleothems (fifteen pieces; length \times diameter, 10×3 to 20×10 cm) that were interred along with the bones. A radiocarbon date of 3730 ± 70 yr BP on hippopotamus bone collagen places the hippopotamuses' catastrophe well before the inferred time of human arrival in Madagascar.

Our most successful excavation in terms of variety of species recovered was the Bat Site (19-8, Fig. 1c), located in the Grande Avenue, a long high room decorated with massive speleothems and many skylights that allow shafts of sunlight through to produce a cathedral-like aspect. The bones were preserved in a large rimstone dam, a cave formation that grows by accretion of recrystallized limestone around the edges of a pool of water. The pool was no longer present when we excavated, although the lower part of Layer 2 was saturated with water. At some time in the past, an enormous speleothem (ANJ-92-4, the outermost layer U-series dated to 22.88 ± 4.48 kyr BP) fell across the rimstone dam, capping it with a low ceiling that may have sheltered the fossils, but also made the excavator's job a very awkward one.

Our attention was first drawn to the area when we noticed many bones of an extant fruit bat *Eidolon dupreanum* (Schlegel 1867) on the surface, mixed with occasional bones of other animals, including a femur of the extinct baboon-sized lemur *Archaeolemur* cf. *edwardsi* (Filhol 1895). From our surface collections and excavations here we recovered abundant bat bones, a few bones each of *Archaeolemur* and an immature hippopotamus, and partial skeletons of various other mammals and birds. Notable among the bones from the site are a cranium, tibiofibula, radius and two foot bones of the rarely collected, extinct aardvark-like mammal *Plesiorycteropus madagascariensis* Filhol 1895. A partial mandible of the large extinct lemur *Babakotia radofilai* Godfrey et al., 1990 from this site provides a second location for this recently described new genus and species (Godfrey et al., 1990). We also found bones of the broad-nosed gentle lemur (*Hapalemur simus* Gray 1870), which no longer occurs in the region (Godfrey & Vuillaume-Randriamanantena, 1986), and a series of rodent bones including one from a fairly large undescribed species (genus *Nesomys*, fide M. Carleton) that had not been recorded in the region and may

be extinct. The birds from the site include four species that no longer occur near Anjohibe: three large cuckoos [*Coua gigas* (Boddaert, 1783), *C. primavea* Milne-Edwards & Grandidier, 1895, and *C. berthae* Goodman & Ravoavy, 1993] and the white-browed owl [*Ninox superciliosus* (Vieillot, 1817)]. *Coua primavea* and *C. berthae* are extinct (Goodman & Ravoavy, 1993).

The site stratigraphy consists of humic black silt (Layer 1) overlying a very wet, partly indurated orange-yellow silty clay (Layer 2, depth 11–18 cm). The upper 3 cm of Layer 2 was so indurated that a rock hammer was required to gain access to the softer clay below, which was itself indurated in pockets. Bones were abundant throughout the deposit, including the indurated parts of Layer 2.

The first ^{14}C date we obtained from the Bat Site was a surprisingly recent date of 330 ± 70 yr BP from the collagen fraction of bones of the extant fruit bat, collected in the lower part of Layer 2 (Table 2). Calibration of this date to the tree ring record (Stuiver & Pearson, 1986) indicates a 95% probability that the true age of the sample falls between 510 yr BP and the present. This date raised the intriguing possibility that the extinct animals whose remains were found on the surface (*Hippopotamus*, *Archaeolemur*, *Plesiorycteropus*, *Nesomys* and *Coua*) survived until AD 1440 or later. However, we also found evidence that bones at the Bat Site are stratigraphically mixed. We noted, in the case of a few rare animals, that bones probably belonging to the same individual could be traced from the surface down to Layer 2.

Two additional dates obtained on bones of extinct animals from the site surface confirm that these extinct animals died thousands of years earlier than the fruit bats in the lower layers. Dates of 7790 ± 70 yr BP on *Archaeolemur* and 5300 ± 60 yr BP on *Hippopotamus* indicate that the Bat Site is a polychronic mixture of bones spanning most of the Holocene.

Bucket augering throughout Anjohibe showed that most of the cave sediments contain only a low density of bones. We selected one auspicious spot in the Grande Avenue, 5 m north of the talus cone at entrance J, for systematic excavation (Site 21-4, Fig. 1c). The excavation was placed to encompass an archaeological surface deposit of charcoal and ceramics mixed with faunal remains. However, as with our archaeological test pits in other areas of the cave (see section on archaeology to follow), the human artefacts were concentrated in a thin surficial layer. Below this archaeological layer, we obtained a stratigraphic sample of small vertebrates that we hope will span the period of the extinctions. The collection is still being processed in the laboratory.

By collecting bones exposed on the surface in various rimstone dams in Anjohibe, we obtained the first fossil record of the endemic avian family Mesitornithidae (the mesites, a peculiar rail-like group of birds of uncertain affinity to other bird groups). The fossil mesite bones are referable to the genus *Monias*, which now occurs only in the southwestern part of the island.

We also made a representative surface collection of wild animals from archaeological contexts. However, the only

TABLE 2. New radiocarbon dates from Anjohibe and vicinity.

Location/site no.	Lab no.	¹⁴ C Age ^a	Calibrated age range ^b	Material dated
Anjohibe/19-8	β-64960 CAMS-8647	7790 ± 70	8729-8389 BP 6780-6440 BC	Partial pelvis of <i>Archaeolemur</i> cf. <i>edwardsi</i>
Anjohibe/AM-2	β-58395 CAMS-4628	7080 ± 80	8039-7679 BP 6090-5730 BC	Basal sediments from depths of 248–252 cm in core ANJ-AM-2
Anjohibe/AM-2	β-60947 CAMS-5645	7040 ± 70	8024-7617 BP 6075-5668 BC	Sediments from a depth of 100 cm in core ANJ-AM-2
Anjohibe/19-8	β-64961 CAMS-8648	5300 ± 60	6262-5929 BP 4313-3980 BC	Mandible of immature <i>Hippopotamus</i> cf. <i>lemerlei</i>
Anjohibe/19-5	β-55093 CAMS-3562	3730 ± 70	4269-3849 BP 2320-1900 BC	Rib bone of <i>Hippopotamus</i> cf. <i>lemerlei</i>
Lavakasaka/Layer I	β-55094 CAMS-3547	2380 ± 70	2712-2200 BP 763-251 BC	Eggshell, cf. <i>Mullerornis</i>
Anjohikely/31-1	β-55095 CAMS-3709	2060 ± 70	2281-1840 BP 332 BC–110 AD	Fragments of long bones of <i>Archaeolemur</i> cf. <i>edwardsi</i>
Anjohikely/1-1	β-55060 CAMS-3543	830 ± 60	903-670 BP 1047–1280 AD	Faecal pellet, probably from <i>Archaeolemur</i>
Anjohibe/19-8	β-56770 CAMS-4255	330 ± 70	510 BP-modern 1440 AD-modern	Postcranial bones of large bat. <i>Eidolon dupreanum</i>

^a Determinations made by Accelerator Mass Spectrometry (AMS), corrected for isotopic fractionation, and expressed as radiocarbon years $\pm 1\sigma$.

^b Calibrated after subtracting 30 yr from radiocarbon age (Southern Hemisphere correction; Stuiver & Pearson, 1986). Calibrated on the 20 yr atmospheric curves (Stuiver & Reimer, 1986). Ranges given at 2σ (95% confidence interval).

extinct animals that we found in clearly cultural contexts were large tortoises.

In the nearby cave called Anjohikely 2 (Fig. 1b), we collected surface bones and dry cave sediment for sieving from small rimstone dams in adjacent rooms near two small skylights (Fig. 1d). These sites were very productive of small reptiles and bats, and also contained remains of larger animals, including at least five individuals of *Archaeolemur*. The latter were collected from three sites on steep limestone slopes at the side of the two rooms (sites 31-1, 31-2 and 1-1, Fig. 1d), where the animals had presumably crawled up to die after entering through the skylights. One skeleton was particularly well-preserved, with skull, mandible, and many postcranial bones present. A date of 2060 ± 70 ¹⁴C yr BP on bone fragments from this individual places its death marginally within the projected period of human activity on Madagascar.

At Site 1-1, our excavation of a small rimstone dam filled with moist sand yielded an immature *Archaeolemur* along with about thirty elliptical faecal pellets (1.5 cm diameter, 2–4 cm length). It is possible that these are dung or colon contents from the *Archaeolemur*. Bones of a small, extant lemur (*Eulemur* cf. *fulvus* E. Geoffroy 1796) were also found at the site, but this animal produces dung of a very different sort (A. Jolly, pers. comm.).

Another possibility that we considered is that the faecal pellets were left by an animal that did not happen to die at the site, such as one of the endemic viverrid (mongoose family) carnivores. However, we examined faeces obtained from an African viverrid (*Suricata suricatta* Schreber 1776), housed at the Bronx Zoo and fed mice on the day prior to collection. These scats were not at all similar, showing a more cylindrical shape, highly variable length, and bone fragments in the much larger pieces characteristic of a

carnivore that tears and bolts its food rather than masticating as one would expect an omnivorous primate to do. The contents of the subfossil faecal pellets, on the other hand, showed evidence of an omnivorous diet, thoroughly chewed to fine consistency. Contents included finely masticated fragments of bones [including some recognizable as belonging to the cave-roosting bat *Hipposideros commersoni* (E. Geoffroy, 1813)], pollen of savanna plants, plant fibres, and tiny seeds. A radiocarbon date from one of these pellets yielded an age of 830 ± 60 yr BP. If these are indeed *Archaeolemur* scats, the date is a very late occurrence (1041–1280 cal yr AD, 95% confidence) for a large extinct lemur.

The only remains of elephantbirds that we found were eggshell fragments from our excavation of the small rock shelter of Lavakasaka. Because the shells are not particularly thick we have referred them to the relatively small elephantbirds, genus *Mullerornis*. A date on their protein fraction yielded an age of 2380 ± 70 ¹⁴C yr BP, confirming that this large terrestrial bird survived in the area until at least a few centuries before human arrival on Madagascar. Controlled experiments with bird eggshell dating (Long, Hendershott & Martin, 1983) have shown the protein fraction to be highly reliable for ¹⁴C determinations.

Archaeology and ethnography

A wide variety of human artefacts were noted on the floor of Anjohibe, especially in the northern and western chambers. Between entrance I and the doline at M, several of the areas most spectacularly decorated with dripstone formations show evidence of past use that appears to be of a ritual nature. At one site a multi-coloured bead necklace, found partly encrusted in calcium carbonate, appeared to

have been placed in a nook below a speleothem curtain as an offering. In another spot we found a ceramic incense burner. Ceramic vessels, many appearing to have been broken in place (a common ritual practice) are found throughout the cave. Concentrations of cow, goat and fish bones, wild plant and animal remains, and charcoal from fires and torches suggest domestic or ritual use. The beads, pottery and wooden artefacts found in the cave were for the most part, non-diagnostic in terms of cultural periods. The glass beads found, for instance, were of types that have been used continuously in Madagascar for a millennium or more. Ceramics were mostly of types that have been used over the last four centuries. None of the types of Asian imported wares characteristic of 11th–14th century sites in Madagascar (Vérin, 1986; Wright *et al.*, 1997) were found. These types of cultural evidence, as well as the surficial character of the human-derived deposits in the paleontological excavation at 21-4 described above, suggest that human use of the cave may go back only a few centuries.

To test this notion, two small archaeological excavations were made in areas of concentrated surface artefacts. Site 20-1 showed the same pattern as the nearby site 21-4, with artefacts near the surface and, well below the human levels, the bones of extinct animals (including a toe bone and tooth probably from *Archaeolemur*). This site did, however, confirm that humans have used the cave at some time in the past for another purpose. Two post-holes were excavated. These originate in the upper (human) layers, but protrude into lower layers.

The other archaeological excavation, site 22-5, was made in the large ornate chamber inside entrance E (Fig. 1c). This entrance has the largest and most well-preserved of the stone walls that have been constructed across a few of the entrances. Well-fitted local stones have been in place in the wall long enough to support a thick growth of colonizing lichens and mosses, and even a very large *Ficus* tree that has encased part of the wall with massive roots.

The test pit was made along the back wall of the room in the vicinity of a large wooden spoon and some surficial pottery. Like the other sites, the stratigraphy suggested human domestic and perhaps ritual use, probably in recent centuries but not before.

More recent human visitors have left artefactual evidence throughout the cave in the form of broken glass, metal cans, and other refuse of various decades of the twentieth century. These materials confirm oral history accounts of cave use by French colonial soldiers and tourists.

As with most large caves in Madagascar, local legends of strange apparitions abound. These superstitions, in addition to adding local charm, may have functioned to give some measure of protection to the cave's vulnerable features.

DISCUSSION

The many types of data we have gleaned from our first field season at Anjohibe have helped clarify some aspects of the region's past. *U*-series dating of speleothems confirms that the large passages and giant speleothems represent at least 40,000 years of erosion and accretion. Our dates are not from the very largest speleothems, however, which may

represent, by analogy to our work on similar caves in Africa (Brook *et al.*, 1990), >100,000 years of growth. We do not know when the cave opened to the outside world, and therefore began to collect fossils, but the deepest and presumably oldest soft sediments and the oldest bones we have dated are roughly 8000 years old. It is likely that the cave had only a few small openings to the surface during the Pleistocene, so that few bones of this period were deposited inside.

The speleothem-derived pollen spectra provide a sketchy view of late Pleistocene conditions in the vicinity. The same pollen types, and in similar proportions, characterize the 40 kyr BP sample as the recent sample, suggesting that a wooded grassland with satra palms (*Medemia nobilis*) was typical then as now. The sample from c. 23 kyr BP is similar, but with more of the palm pollen and less grass pollen. The higher proportion of club moss and fern spores in the Pleistocene may point to cooler, moister conditions on the savanna, but they could also be a reflection of more humid conditions in the immediate cave vicinity. An experimental study (Burney & Burney, 1993) suggests that most pollen and spores reach speleothems from the air that circulates from nearby openings. The charred grass cuticles in the Pleistocene and pre-human Holocene samples confirm that, long before humans were present to set them, fires were occurring on the surface nearby (the satra palm is notably fire-tolerant).

During the Holocene, surface erosion and solution of the limestone roof of the cave have probably created many additional openings. Giant dolines such as M, with its 'sunken forest', may have begun as skylights such as the ones all through the Grande Avenue in the vicinity of the Bat Site (19-8, Fig. 1c). This would account for the many collapsed columns and stalactites near the openings, and also the apparent preponderance of mid-to-late Holocene fossils, since more natural traps and openings for surface animals to enter have appeared with the passage of time. The sudden influx of soft sediments in the AM passage, and the toppling of the ANJ-92-2 speleothem nearby, both events apparently dating to about 7–8 kyr BP (the same approximate age as the oldest bone dated), suggest that major changes in the cave environment may have occurred then. The pollen spectrum from this time shows the highest values for the satra palm, suggesting that the savanna may have been more densely wooded than in the late Pleistocene, although the diversity of tree species represented is not very high.

In the Holocene, the cave provided a final resting place for a wide array of large animals, but also many smaller animals, some of which were probably often brought in by roosting owls and other carnivores. Anjohibe and nearby caves have yielded remains of eight to eleven extinct species of higher vertebrates, from large animals such as hippopotamuses to medium-sized forms such as *Archaeolemur* and the peculiar *Plesiorycteropus*, once thought to be an armadillo relative but recently proposed as a separate order (MacPhee, 1994).

The occurrence of the large extinct lemur *Babakotia radofilai* at the site poses a paleobiogeographical conundrum. This arboreally adapted taxon was known

previously only from two caves in the Ankarana Massif of extreme northern Madagascar. A date of 4400 ± 60 yr BP on one of the Ankarana specimens (Simons *et al.*, 1995) confirms its contemporaneity with the other members of the Holocene megafauna, yet it is unknown from the large number of subfossil sites in central, western and southern Madagascar. Thus, unlike most of the subfossil megafauna, *Babakotia* appears to have had a relatively small range in Holocene Madagascar. Whether this reflects habitat specificity, competitive exclusion, or some other limiting factor is unknown.

Although investigators have emphasized that most of the extinct 'subfossil megafauna' were relatively large, some of the smaller animals found in the caves also became extinct, including two large cuckoos (*Coua*) and probably a rodent (*Nesomys*). Another small animal that may be extinct is the mesite, genus *Monias*. The bones of this bird from Anjohibe belong either to an undescribed species or to the only extant species in this genus, which now occurs far to the south of the cave in dry thorn-scrub. The broad-nosed gentle lemur (*Hapalemur simus*) is now found only in the eastern forests of Madagascar, but occurs as a fossil in a few sites outside the eastern region besides Anjohibe (Godfrey & Vuillaume-Randriamanantena, 1986). Our finds also extend the range of some other species.

Our dating of the extinct fauna shows that some of these creatures were still around the caves when humans are thought to have arrived in Madagascar. It also appears that some extinct animals (tortoises, perhaps *Archaeolemur*, and perhaps others) may have persisted here for a millennium or more after human arrival on the island. This would not be surprising if, as the archaeological data suggest, there was very little human activity in the immediate vicinity until just a few centuries ago. Archaeological evidence from the NW coast (Wright *et al.*, 1997) and paleoecological results from a lake about 125 km SW (Matsumoto & Burney, 1994) suggest relatively low human density along this part of the NW coast until about 500 years ago, when migration and perhaps population growth associated with an intensification of agriculture led to an escalation of human impacts on the landscape. If Anjohibe was a remote hinterland then, as it is even today, it would not be surprising that extinct fauna survived here well into the human period. However, the caves in the area have not shown definite evidence for direct interaction between humans and extinct species other than tortoises.

Although the mysteries surrounding the disappearance of these animals and the controversies regarding the roles of various human activities and natural changes in their demise are still far from being dispelled, we have added some useful details regarding the past of a little-known region of the island. Caves have been under-utilized for combined paleontological, archaeological and paleoecological research on the extinctions and environmental changes in Madagascar, and work of this type deserves a higher priority. These deposits are valuable, but they are also extremely vulnerable resources that need protection from vandalism, commercial exploitation and careless digging. As in many parts of the world, Madagascar's caves have been insufficiently appreciated as important

repositories of scientific information and precious natural and cultural resources.

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REFERENCES

- Battistini, R. (1971) Conditions de gisements des sites littoraux de subfossiles et causes de la disparition de la faune des grands animaux dans le Sud-Ouest et l'Extrême Sud de Madagascar. *Taloha*, **4**, 7–18.
- Bliley, D.J. & Burney, D.A. (1988) Late Pleistocene climatic factors in the genesis of a Carolina bay. *Southeastern Geol.* **29**, 83–101.
- Brook, G.A., Burney, D.A. & Cowart, J.B. (1990) Desert paleoenvironmental data from cave speleothems with examples from the Chihuahuan, Somali-Chalbi, and Kalahari deserts. *Palaeoogeogr. Palaeooclimatol. Palaeoecol.* **76**, 311–329.
- Burney, D.A. (1987a) Late Holocene vegetational change in central Madagascar. *Quat. Res.* **28**, 130–143.
- Burney, D.A. (1987b) Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. *Palaeoecol. Afr.* **18**, 357–381.
- Burney, D.A. (1987c) Late Quaternary stratigraphic charcoal records from Madagascar. *Quat. Res.* **28**, 274–280.
- Burney, D.A. (1988) Modern pollen spectra from Madagascar. *Palaeoogeogr. Palaeooclimatol. Palaeoecol.* **66**, 63–75.
- Burney, D.A. (1993) Late Holocene environmental changes in arid southwestern Madagascar. *Quat. Res.* **40**, 98–106.
- Burney, D.A. & MacPhee, R.D.E. (1988) Mysterious island: what killed Madagascar's large native animals? *Nat. Hist.* **97**, 46–55.
- Burney, D.A. & Burney, L.P. (1993) Modern pollen deposition in

- cave sites: experimental results from New York State. *New Phytol* **124**, 829–835.
- Burney, D.A., Burney, L.P., Rafamantanantsoa, J.-G., D'Arrigo, R.D. & Jacoby, G.C. (1993) Laminated sediment cores, tree ring records, and laminated speleothems from Madagascar. *Eos* **4/20**, 93.
- Burney, D.A., Brook, G.A. & Cowart, J.B. (1994) A Holocene pollen record for the Kalahari Desert of Botswana from a U-series dated speleothem. *Holocene*, **4**, 225–232.
- Decary, R. (1938) Les grottes d'Andranoboka. *Bull. Acad. Malgache* (new series), **21**, 71–80.
- de Saint-Ours & Paulian, R. (1953) *Les grottes d'Andranoboka*. l'Institut de Recherche Scientifique, Antananarivo.
- Dewar, R.E. (1984) Recent extinctions in Madagascar: the loss of the subfossil fauna. *Quaternary extinctions: a prehistoric revolution* (ed. by P.S. Martin and R.G. Klein), pp. 574–593. University of Arizona Press, Tucson.
- Digerfelt, G. (1975) Post-glacial water level changes in Lake Lyngsö, central Halland. *Geologiska Föreningens i Stockholm Förhandlingar*, **98**, 329–336.
- Godfrey, L.R. & Vuillaume-Randriamanantena, M. (1986) *Hapalemur simus*: endangered lemur once widespread. *Primate Conserv.* **7**, 92–96.
- Godfrey, L.R., Simons, E.L., Chatrath, P. & Rakotosamimanana, B. (1990) A new fossil lemur (*Babakotia*, Primates) from northern Madagascar. *C.R. Acad. Sci. Paris*, **310**, 81–87.
- Goodman, S.M. & Ravoavy, F. (1993) Identification of bird subfossils from cave surface deposits at Anjohibe, Madagascar, with a description of a new giant *Coua* (Cuculidae: Couinae). *Proc. Biol. Soc. Wash.* **106**, 24–33.
- Humbert, H. (1927) Destruction d'une flore insulaire par le feu: principaux aspects de la végétation à Madagascar. *Mém. Acad. Malgache*, **5**, 1–80.
- James, H.F., Stafford Jr, T.W., Steadman, D.W., Olson, S.L., Martin, P.S., Jull, A.J.T. & McCoy, P.C. (1987) Radiocarbon dates on bones of extinct birds from Hawaii. *Proc. Natl. Acad. Sci. USA*, **84**, 2350–2354.
- Kirch, P.V., Flenley, J.R., Steadman, D.W., Lamont, F. & Dawson, S. (1992) Ancient environmental degradation. *Nat. Geogr. Res. Expl.* **8**, 166–179.
- Laumanns, M., Burgsmüller, J. & Geucke, W. (1991) Höhlenkundliche Aktivitäten der HuK Nordrhein nordöstlich Majunga und südlich Antsirabe. *Mitteilungen des Verbandes der deutschen Höhlen- und Karstforscher*, **37**, 68–73.
- Long, A., Hendershott, R.B. & Martin, P.S. (1983) Radiocarbon dating of fossil eggshell. *Radiocarbon*, **25**, 533–539.
- MacPhee, R.D.E. (1986) Environment, extinction, and Holocene vertebrate localities in southern Madagascar. *Nat. Geogr. Res.* **2**, 441–455.
- MacPhee, R.D.E. (1994) Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of eutherian mammals. *Bull. Am. Mus. Nat. Hist.* **220**, 1–214.
- MacPhee, R.D.E. & Burney, D.A. (1991) Dating of modified femora of extinct dwarf *Hippopotamus* from southern Madagascar: implications for constraining human colonization and vertebrate extinction events. *J. Archaeol. Sci.* **18**, 695–706.
- MacPhee, R.D.E., Simons, E.L., Wells, N.A. & Vuillaume-Randriamanantena, M. (1984) Team finds giant lemur skeleton. *Geotimes*, **29**, 10–11.
- MacPhee, R.D.E., Burney, D.A. & Wells, N.A. (1985) Early Holocene chronology and environment of Ampasambazimba, a Malagasy subfossil lemur site. *Int. J. Primatol.* **6**, 461–487.
- Mahé, J. & Sourdau, M. (1972) Sur l'extinction des vertébrés subfossiles et l'aridification du climat dans le sud-ouest de Madagascar. *Bull. Soc. Géol. Fr.* **14**, 295–309.
- Matsumoto, K. & Burney, D.A. (1994) Late Holocene environmental changes at Lake Mitsinjo, northwestern Madagascar. *Holocene*, **4**, 16–24.
- Perrier de la Bâthie, H. (1921) La végétation malgache. *Ann. Musée Colon. Marseille*, **9**, 1–266.
- Ravoavy, F. (1986) Identification et mise en catalogue des vertébrés non-primates subfossiles et actuels des grottes d'Anjohibe (Majunga). Fouille 1986. Thèse DEA, Université d'Antananarivo, Madagascar.
- Simons, E.L., Burney, D.A., Chatrath, P.S., Godfrey, L.R., Jungers, W.L. & Rakotosamimanana, B. (1995) AMS ¹⁴C dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quat. Res.* **43**, 249–254.
- Stuiver, M. & Pearson, G.W. (1986) High-precision calibration of the radiocarbon time scale, AD 1950–500 BC. *Radiocarbon*, **28**, 805–838.
- Stuiver, M. & Reimer, P.J. (1986) A computer program for radiocarbon age calibration. *Radiocarbon*, **28**, 1022–1030.
- Swain, A.M. (1973) A history of fire and vegetation in north-eastern Minnesota, as recorded in lake sediments. *Quat. Rev.* **3**, 383–396.
- Vérin, P. (1986) *The history of civilization in north Madagascar*. Balkema, Rotterdam.
- Walker, A. (1967) Patterns of extinction among the subfossil Madagascar lemuroids. *Pleistocene extinctions: the search for cause* (ed. by P.S. Martin and H.E. Wright Jr.), pp. 407–424. Yale University Press, New Haven.
- Wright, H.T., Vérin, P., Ramilisonina, Burney, D., Burney, L.P. & Matsumoto, K. (1997) The evolution of settlement systems in the Bay of Boeny and the Mahavavy River Valley north-western Madagascar. *Azania*, **31**, 37–73.

APPENDIX 1. List of the higher vertebrates identified from bones in Anjohibe and nearby caves.

Aves

- Aepyornithiformes
 Aepyornithidae, elephant birds
 †*Mullerornis* sp.
- Ciconiiformes
 Ardeidae, herons
Bulbulcus ibis (Linnaeus, 1758)
 Ciconiidae, storks
Anastomus lamelligerus Temminck, 1823
 Plataleidae, ibises
Lophotibis cristata (Boddaert, 1793)
 Phoenicopteridae, flamingos
Phoeniconaias minor (Geoffroy, 1798)
- Falconiformes
 Accipitridae, hawks and kites
Milvus migrans (Boddaert, 1783)
Buteo brachypterus Hartlaub, 1860
 Falconidae, falcons
Falco newtoni (Gurney, 1863)
- Galliformes
 Phasianidae, pheasants and quails
Coturnix sp.¹
 Numididae, guineafowl
Numida meleagris Linnaeus, 1766
- Gruiformes
 Mesitornithidae, mesites
 †? *Montias* sp.

- Gruiformes *continued*
 Turnicidae, buttonquails
Turnix nigricollis (Gmelin, 1789)
- Columbiformes
 Columbidae, pigeons and doves
Streptopelia picturata (Temminck, 1813)
- Psittaciformes
 Psittacidae, parrots
Coracopsis vasa (Shaw, 1812)
Agapornis vana Gmelin, 1788)
- Cuculiformes
 Cuculidae, cuckoos
 †*Coua berthae* Goodman & Ravoavy, 1993
 †*Coua primavea* Milne-Edwards & Grandidier, 1895
Coua gigas (Boddaert, 1783)
Coua, medium-sized species
Coua, small species
Cuculus rochii Hartlaub, 1862
Centropus toulou (Müller, 1776)
- Strigiformes
 Tytonidae, barn owls
Tyto alba (Scopoli, 1769)
 Strigidae, Typical owls
Otus rutilus (Pucheran, 1849)
Ninox superciliosus (Vieillot, 1817)
Asio madagascariensis (A. Smith, 1834)
- Apodiformes
 Apodidae, swifts
Apus barbatus (P.L. Sclater, 1865)
- Coraciiformes
 Alcedinidae, kingfishers
Alcedo vintsioides Eydoux & Gervais, 1836
- Meropidae, bee eaters
Merops superciliosus Linnaeus, 1766¹
- Leptosomatidae, cuckoo rollers
Leptosomus discolor (Hermann, 1783)
- Passeriformes
 Alaudidae, larks
Mirafra hova Hartlaub, 1860
- Hirundinidae, swallows
Phedina borbonica Gmelin, 1789
- Pycnonotidae, bulbuls
Hypsipetes madagascariensis (Müller, 1776)¹
- Sylviidae, Old World warblers
Newtonia brunneicauda (A. Newton, 1863)
- Ploceidae, weaver finches
Foudia madagascariensis (Linnaeus, 1766)
- Mammalia*
 Insectivora
 Tenrecidae, tenrecs
 cf. *Microgale* sp.
Tenrec ecaudatus (Schreber, 1777)
- Soricidae, shrews
Suncus sp.
- Chiroptera
 Pteropodidae, flying foxes
Eidolon dupreanum (Schlegel, 1867)
Rousettus madagascariensis G. Grandidier, 1928
- Rhinolophidae, horseshoe bats
Hipposideros commersoni (E. Geoffroy, 1813)
Triaenops cf. *furcatus* Trouessart, 1906
 (ca. 4 undetermined species of microchiropterans)
- Primates
 Cheirogaleidae, dwarf and mouse lemurs
Cheirogaleus medius E. Geoffroy, 1812
Microcebus murinus (J. F. Miller, 1777)
- Lemuridae, 'true' lemurs and gentle lemurs
Eulemur cf. *fulvus* (E. Geoffroy, 1796)
Haplemur cf. *griseus* (Link, 1795)
Haplemur simus Gray, 1870
- Megaladapidae, sportive lemurs and relatives
Lepilemur sp.
- Indridae, sifakas and relatives
 †*Babakotia radofilai* Godfrey *et al.*, 1990
Propithecus verreauxi A. Grandidier, 1867
 †*Archaeolemur* cf. *edwardsi* (Filhol, 1895)
 †*Palaeopropithecus ingens* G. Grandidier, 1899²
- Carnivora
 Viverridae, mongooses
Cryptoprocta ferox Bennett, 1833¹
 †? *Cryptoprocta spelea* Lamberton, 1939²
 cf. *Fossa fossana* (Müller, 1776)
- Bibymalagasia
 Plesiorycteropidae, aardvark-like endemic mammals
 †*Plesiorycteropus madagascariensis* Filhol, 1895
- Artiodactyla
 Suidae, pigs
Potamochoerus larvatus (F. Cuvier, 1822)
- Hippopotamidae, hippopotamuses
 †*Hippopotamus* cf. *lemerlei* A. Grandidier, 1868
- Rodentia
 Muridae, murid rodents
Eliurus myoxinus Milne-Edwards, 1855
Eliurus sp.
 †? *Nesomys*, new species
Rattus rattus (Linnaeus, 1758)
 (a few other species of rodents)

Identifications are based on comparisons with the osteological reference collections of the United States National Museum, Field Museum of Natural History, and American Museum of Natural History. Numerical footnotes indicate species that were not found in our collections from Anjohibe but were reported by previous investigators, as follows: ¹Goodman & Ravoavy (1993), ²MacPhee *et al.* (1984), ³Ravoavy (1986).
 †Extinct species; †?probable extinct species; **Cryptoprocta spelea* is a doubtfully valid taxon, often listed in synonymy with *C. ferox*.