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NEW FINDINGS AT ANDRAHOMANA CAVE, SOUTHEASTERN MADAGASCAR

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Abstract: A remote eolianite cave and sinkhole complex on the southeast coast of Madagascar has played a major role in the history of paleontology in Madagascar. Andrahomana Cave has yielded a rich fossil record of the extinct megafauna. Expeditions in 2000 and 2003 produced a wealth of new material and provided the first systematic information concerning the genesis, stratigraphy, and taphonomy of the site. Recovered bones of one of the most poorly understood extinct large lemurs, *Hadropithecus stenognathus*, include many skeletal elements previously unknown. Radiocarbon dates show that the site has sampled this disappeared fauna in the mid-to-late Holocene, but that bone-bearing layers are stratigraphically mixed, probably owing to the effects of reworking of the sediments by extreme marine events. The diverse biota recovered contains elements of both eastern rain forest and southwestern arid bushland, reflecting the cave's position in the zone of transition between wet and dry biomes. Bones of two unusual small mammals add to the previously long faunal list for the site: 1) the first fossil evidence for *Macrotarsomys petteri*, a large-bodied endemic nesomyid rodent previously known only from a single modern specimen; and 2) the type specimen and additional material of a newly described extinct shrew-tenrec (*Microgale macpheei*). Evidence for prehistoric and colonial-era humans includes artifacts, hearth deposits, and remains of human domesticates and other introduced species. Although previously protected by its extreme isolation, the unique site is vulnerable to exploitation. An incipient tourist industry is likely to bring more people to the cave, and there is currently no form of protection afforded to the site.

Introduction

Madagascar is noted for having many large and spectacular caves, and several of these have yielded troves of fossils of the extinct giant lemurs, huge elephant birds, pygmy hippos, and other elements of the island's lost Holocene subfossil biota (e.g., Simons et al., 1995; Burney et al., 1997, 2004). One of the richest of these, Andrahomana Cave on Madagascar's southeast coast, a remote collapsed-cave feature that has been visited by only a handful of outsiders, is both visually spectacular and scientifically important (see Appendix 1 for a chronological account of exploration).

The site is normally reached by climbing down gneissic cliffs to the east, then wading at low tide over exposed coral reefs. During the 2003 expedition, an alternative route was developed that was much faster and less dependent on the tides, consisting of direct approach to the northern, inland rim of the sinkhole, followed by a moderate rappel or cable-ladder descent down the vertical face. An approach along the rocky shoreline from the west was also used a few times, but proved to be too dangerous because the deep rills in the gneissic bedrock form deadly bore waves when the sea swell is very large.

The stony matrix from which the cave is sculpted is a roughly 100 m thick pile of eolianite, with at least three separate units of calcareous sandstones laid down by dune-forming winds. Current theory holds that these deposits are normally formed at the end of Pleistocene glacial cycles as sea level rises rapidly following deglaciation, grinding up coral reefs and other marine deposits (see Burney et al., 2001). These eolianite units lie exposed in a sheer south-facing cliff face cut by the rough seas that bring huge swells ashore from Antarctica. A gaping entrance near the base of this cliff leads into a double sinkhole, whose figure-eight-shaped footprint is partially roofed by a sweeping massive triple-arch shaped by multiple collapses. Beyond this complex natural bridge, with its large central pillar, is a small sunken rainforest thriving in the microhabitat provided inside the cave system. This moist refuge is surrounded above by a much drier landscape of spiny semiarid bushland.

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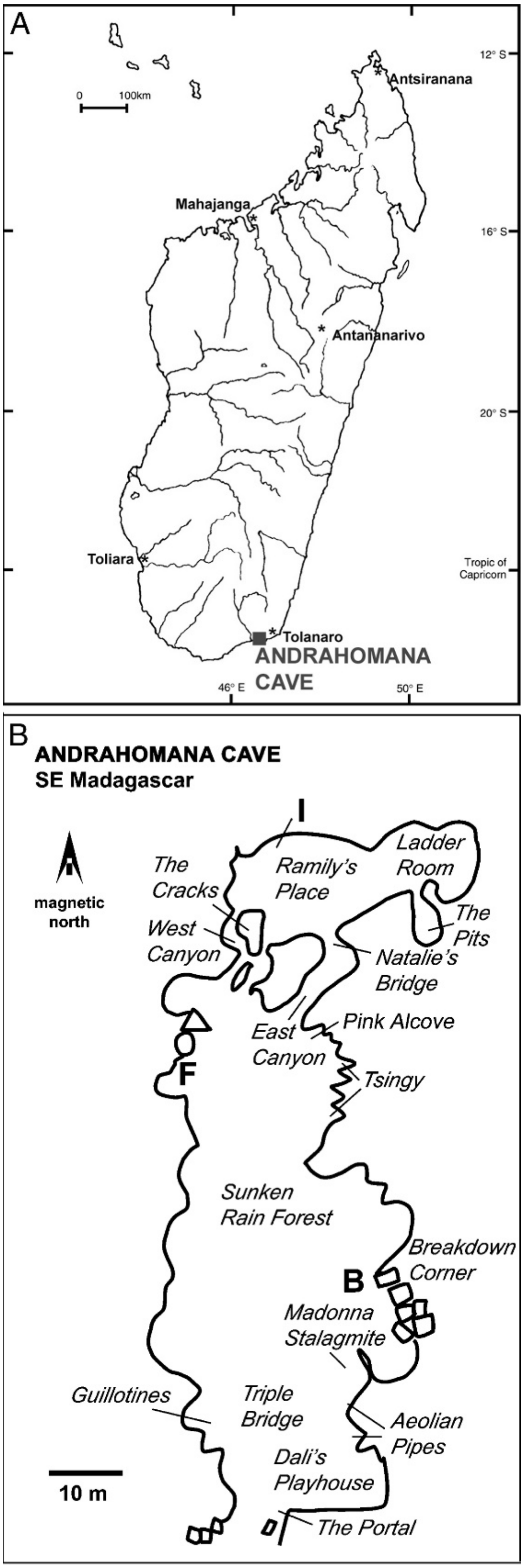

Figure 1. A. Location of Andrahomana Cave, on the southeast corner of Madagascar near Tolagnaro (formerly known as Ft. Dauphin). Entrance coordinates are S25°11′55″ E46°37′59″.

Around the edges of the collapsed areas, the remaining portions of the high vaulted ceiling are perforated by dozens of skylights and the walls are adorned with giant speleothems and unusual ruiniform features shaped like towers, fins, and buttresses. As interesting as these erosional and depositional features are, the great attraction for the sparse assemblage of paleontologists who have been coming here at long intervals since Franz Sikora's 1899 visit is the soft sandy sediments that mantle the floor, because these contain well-preserved bones of extinct megafauna, as well as a diverse collection of bones of smaller vertebrates and shells of large ornate land snails and other invertebrates. Remarkably, despite the proven potential of the site and the number of paleontologists who have visited, previous excavations have been largely undocumented and uncontrolled.

We report here the results of a brief survey in 2000 and a more extensive excavation program in 2003 that includes preliminary stratigraphic descriptions, faunal lists, radiometric dating, and paleoecological inferences. The goals of this work included not only recovering more complete material for rare taxa described previously from the site, but also the creation of a provisional chronostratigraphic context with which to interpret this material. These new details allow the first inferences regarding the paleoecology of the region, particularly the possible role of natural and human-induced changes in the history of the site.

SITE DESCRIPTION

Aside from the richness and preservation of its faunal remains, the site is also important because it is the only documented fossil vertebrate site from the entire southeastern portion of the island (S25°11′55″ E46°37′59″; Fig. 1A). Situated in an area of rapid transition from semiarid bushland to the west and humid rainforest to the east, the site potentially samples both types of environments.

The eolianite body here is complex and extensive, composed of three thick layers of calcareous sandstone that vary considerably in texture and color and in many places exhibit sharp zones of contact. The entire deposit lies unconformably on dense granitic and gneissic rocks that are exposed in the sea cliffs here and outcrop inland as a series of weathered hills, ridges, and inselbergs.

←

Figure 1. B. Survey map of the floor of Andrahomana Cave. Place names supplied by the authors. Capital letters B, F, and I indicate locations of excavations from the 2000 and 2003 expeditions. The cave roof is collapsed, except in the areas of Dali's Playhouse, the Triple Bridge, and Aeolian Pipes.

The overlying three-part eolianite in this area probably corresponds to, beginning at the bottom layer, Tatsimian, Karimbolian, and Aepyornian (Besairie, 1972). Although this material has not been dated, it is most likely mid- to late-Pleistocene in age; each unit probably reflects the depositional results of a post-glacial sea-level rise following a major ice-age cycle. These units are likely to have been deposited at least 100,000 years apart, reflecting the major component of glacial-interglacial cycles. Thus the cave's material would have been at least 200,000 years in the making, although it is not known whether these deposits are from the more recent, or earlier cycles.

In any case, these dune sands were consolidated through a process of recrystallization in which overlying acidic waters from the surface percolated through, dissolving highly soluble aragonitic calcium carbonate and replacing it, on drying, with harder and less soluble calcite. The addition of silica from overlying soils and atmospheric dust would have helped further harden this natural cement. This recrystallization phase was followed much later by dissolution, as ground water flowing between the porous eolianites and the relatively impervious basement rocks etched away the sandstone from below, producing a cavern. Further dissolution, probably aided by subsequent marine incursion, has led to the collapse of this cave in the central chamber. Considerable time, perhaps 100,000 years or more, passed before the cave collapsed, as the large inactive speleothems of up to 2 meters in diameter around the edge of the opening would have formed in the humid conditions of a more enclosed cave. Growth rates of similar-sized speleothems elsewhere in Madagascar and in similar climates in Africa have been measured by U-series techniques (Brook et al., 1990; Burney et al., 1994, 1997). These speleothems are likely to be at least as old if they formed at similar rates.

Since this collapse, Andrahomana has served as a natural trap for terrestrial sediments and biotic remains. Evidence in the lower parts of the cave shows that either high sea-stands or extreme marine events have brought the sea back into the cave on occasion, adding marine materials to these deposits as well.

Work from the 2000 and 2003 expeditions included mapping with compass, clinometer, and hip-chain, surface survey, sediment description from bucket-auger cores and test pits, and controlled excavation. Contrary to the claim of Alluaud (1900) that Sikora had excavated the entire place (*tout fouillé*) the year before, coupled with the digging efforts of subsequent visitors (see Appendix 1), a considerable amount of previously unexcavated sediments was located. Earlier excavations were easily recognized by the deranged nature of the sediment layers and lack of large bones in the old spoil piles. Fine-screening of this material rejected by earlier investigators, however, did provide a rich yield of smaller bones, teeth, and artifacts, and provided insight into the coarser methods of earlier investigators.

Controlled excavations were carried out at location B in 2000, and locations F and I in 2003 (Fig. 1B). Each showed a similar pattern: an upper unit, generally 10–20 cm thick, of brown humic silty sand, containing primarily bones of the present fauna, and a much thicker lower unit, of ca. 1 m to <3 m thickness, of coarser, lighter-colored sands, including a larger component of remains of extinct fauna. Artifacts of post-European colonization provenance, including glass and spent cartridges, occur near the top of the upper unit, with no definite evidence of humans deeper in the unit. Dates on bones from this unit are late Holocene, but are not in stratigraphic order (Table 1).

The lower unit lacks human artifacts and contains bones dating to the mid-Holocene that are not in consistent stratigraphic order. This suggests that late Holocene sediments here have been disturbed and perhaps largely eroded by extreme marine events, perhaps one or more tsunami or storm overwashes. Recent evidence for the Burckle Impact Crater, between southern Madagascar and Antarctica (Masse et al., 2006) suggests that at least one mega-tsunami of far greater magnitude than any recorded historically was generated in this area in the Holocene, as supported by the occurrence of chevron dune deposits in the coastal regions of extreme southern Madagascar.

Fauna

Table 2 provides a full list of taxa found in the subfossil deposits at Andrahomana in 2003 and additional occurrences in prior collections. Certain species are represented in both collections, but a few are represented in small numbers only in earlier collections, and many other species (especially non-mammals) are reported here for the first time.

Taxa typically confined to either dry or humid habitats are found in the collection, as might be expected given that Andrahomana is situated in an area of abrupt transition from semiarid spiny bushland to the west and humid rainforest to the east, a divide created in large part by the Anosyenne Mountains. Extant taxa typical of drier habitats include *Numida meleagris* among the birds, *Geogale aurita* and *Echinops telfairi* among the afrosoricidans, *Triaenops furculus* among the bats, *Lemur catta* among the primates, and *Macrotarsomys bastardi* among the rodents. These taxa are found in western dry deciduous forests and southern spiny bush areas of Madagascar (Carleton and Goodman, 2003; Eger and Mitchell, 2003; Goodman, 2003). *Lemur catta* regularly frequents the premises of the cave today and it is likely the other taxa do as well. In addition to these extant taxa, several extinct taxa recovered from Andrahomana also likely occupied drier habitats, including the primates *Megaladapis edwardsi* and *Hadropithecus stenognathus*, which are dominant elements of the subfossil fauna of the extreme south and southwest, but not elsewhere (see Godfrey and Jungers, 2002, for a review), and the rodent *Hypogeomys australis*, although the

Table 1. Acceleration mass spectrometer ^{14}C purified collagen dates from Andrahomana Cave.

Material/Method	Age B.P. ± 1σ	Calibrated 2σ Range[a]	Sample I.D. Provenance or Accession No.	Lab. Number	$\delta^{13}C$	Comments/Other
Hadropithecus stenognathus bone	6724 ± 54	B.P. 7660–7490	BJ-HS-1	AA-45963 T-16044A	−9.1	Humeral fragment
Hypogeomys australis bone	4440 ± 60	B.P. 5840–4420	Not Given	Beta-73370	…	In Goodman and Rakotondravony (2006)
Hypogeomys australis tooth	1536 ± 35	A.D. 428–618 B.P. 1522–1332	AHA-I-L1-CD1,2 AHA-03-1	NZA-18996 R-28421/1	−20.0	…
Macrotarsomys petteri bone	2480 ± 40	B.C. 790–410 B.P. 2740–2360	AHA-I-L1-CD3	Beta-212739	…	Demi-mandible; too small for ^{13}C
Macrotarsomys petteri bone	1760 ± 40	A.D. 150–390 B.P. 1800–1560	AHA-I-L6-CD1,2	Beta-212738	…	Demi-mandible; too small for ^{13}C
Megaladapis sp. bone	4566 ± 25	B.P. 5436–5059	AHA-03-7	NZA-18997 R-28421/7	−20.1	Infant femur

[a] Calibrations from Stuiver et al. (1998).

natural history and distribution of the latter species is still poorly known (Goodman and Rakotondravony, 1996).

Extant taxa confined to more humid habitats include *Microgale principula* among the afrosoricida, *Avahi laniger* among the primates, and *Nesomys rufus* among the rodents (Jenkins, 2003; Ryan, 2003; Thalmann, 2003). These species are found only in earlier collections; none were recovered from our excavations in 2003 despite deliberate effort not to bias our collection in favor of larger-bodied taxa. *Avahi laniger* and *Nesomys rufus* no longer live in the region and their occurrence in the subfossil deposits of Andrahomana has not been previously published. *Avahi laniger* is represented by a single skull apparently found by Sikora and currently housed in the British Museum (Natural History) (BMNH ZD.1960.2103), and a number of skulls collected by Sikora and housed in the BMNH were attributed to *Nesomys rufus*. The subfossil occurrence of another locally extinct species, *Macrotarsomys petteri*, further suggests at least slightly more humid climatic regimes in this region of Madagascar in recent millennia (Goodman et al., 2006). *Macrotarsomys petteri* was only recently described and named, known from a single specimen collected 450 km northwest of Andrahomana in the Mikea forest north of Toliara (Goodman and Soarimalala, 2005).

Among the vertebrates recovered at Andrahomana, the largest taxa are extinct, as are the largest species in several smaller-bodied orders. Elephant birds (*Aepyornis*, *Mullerornis*), giant lemurs (*Hadropithecus stenognathus*, *Archaeolemur majori*, *Megaladapis edwardsi*, and *Pachylemur insignis*), the carnivore, *Cryptoprocta spelea*, the pygmy hippo, *Hippopotamus lemerlei*, the giant jumping rat, *Hypogeomys australis*, and the giant land tortoise, *Geochelone grandidieri*, are gone, known only from fossils. Ostensibly smaller taxa fared better. Nevertheless, analyses underway on the minifauna of Andrahomana demonstrate that smaller taxa were not immune to anthropogenic and climatic changes occurring in recent millennia. In a recent publication, we describe a new subfossil shrew-tenrec from Andrahomana, *Microgale macpheei*, to date, the only known afrosoricidan that has gone extinct in recent millennia (Goodman et al., 2007). Furthermore, biostratigraphic analysis demonstrates the decline of endemic rodents in tandem with increases in the representation of the introduced rodents *Rattus* sp. and *Mus musculus* (Vasey and Burney, unpublished data).

Domestic dogs (*Canis lupus familiaris*), cattle (*Bos indicus*), and the possibly non-native soricomorphid, *Suncus madagascariensis*, are also present among the bones recovered in 2003, amply indicating the post-human settlement context of the more recently deposited sediments in the cave. We note, as did Walker (1967), the presence of burned bones on the surface. However, we are of the opinion that these are fully modern remains, probably left by local fishermen, who occasionally enter the cave to cook a meal. On the other hand, a skull of *Archaeolemur* from

Andrahomana once thought to bear signs of a fatal crushing blow from an axe, or similar tool (Walker, 1967), has recently been radiocarbon dated to the mid-Holocene (3975 ± 53 ^{14}C yr BP; Perez et al., 2005), making it entirely unlikely that humans directly caused the death of this animal. Presumably most of the larger taxa entered the cave by accidentally falling through one of many skylights, which today are frequently camouflaged at the surface by vegetation. Many of the smaller animals were likely deposited by raptors from roost sites in the form of discarded prey remains or regurgitated pellets.

An overview of the primates recovered bears mentioning because this is the most taxonomically rich order represented at Andrahomana and because the most significant find of the 2003 excavations draws from this order: the remains of *Hadropithecus stenognathus*. The faunal list includes eleven species of primates, consisting of six extinct species, and five extant species (*Lemur catta*, *Propithecus verreauxi*, *Microcebus* sp., *Cheirogaleus medius*, and *Avahi laniger*), one of which (*Avahi laniger*) no longer lives on this side of the Anosyenne Mountains divide as discussed above. Only two specimens of *Cheirogaleus* are present in the recent collection despite the reported coexistence in the general region of Tolagnaro today of *C. medius*, *C. crossleyi*, and *C. major* (Hapke et al., 2005). Presently, *Lemur catta* regularly frequents the cave, and *Propithecus verreauxi* and *Microcebus* sp. can be observed in nearby forests. The abundant *Microcebus* subfossils in the cave deposits appear to belong to a single species, most likely *M. griseorufus*, another denizen of dry forest.

Of the extinct primate species, four (*Hadropithecus stenognathus*, *Archaeolemur majori*, *Megaladapis edwardsi*, and *Pachylemur insignis*) are well represented in subfossil deposits from Andrahomana. Two (*Megaladapis madagascariensis* and *Archaeolemur* sp., cf. *edwardsi*) are poorly represented. *Megaladapis madagascariensis* is represented by a single specimen (distal radius) in the Sikora collection in the Vienna Naturhistorisches Museum (VNM 1934.V.56). Most of the *Archaeolemur* from Andrahomana fit comfortably within the size range of *A. majori*, but there are a few specimens in both the BMNH and VNM collections (representing both postcranial and cranial fragments) that are well outside this range of variation, and appear to represent *A. edwardsi* (Godfrey et al., 1999; LRG, unpubl. observations).

Numerous elements of a single subadult *Hadropithecus stenognathus* were recovered from location I (Godfrey et al., 2006a). In addition to isolated teeth and cranial fragments, these elements include the first associated fore- and hind-limb bones, and a number of previously unknown elements: the first scaphoid, hamate, metacarpals, scapular fragment, whole sacrum, vertebrae (including the first several caudal vertebrae), and ribs (Godfrey et al., 2006a; Lemelin et al., 2006, 2008). Alan Walker pointed out the possibility that the cranial fragments belonged to a skull that Sikora had found in 1899 at Andrahomana and that Lorenz von Liburnau (1902) described. Tim Ryan has now used CT scanning of the newly found orbits and Sikora's cranium in Vienna to confirm this association (Ryan et al., 2008).

These discoveries have led to a reassessment of prior hind-limb attributions for *Hadropithecus*, and a re-evaluation of its locomotor behavior. The newly discovered skeletal elements confirm the hind-limb allocations for *Hadropithecus* described by Godfrey et al. (1997) and refute earlier attributions by Lamberton (1938). They prove that *Hadropithecus*, like *Archaeolemur*, had a long tail, relatively short limbs, and a robust body build. Of particular interest are the new carpals and metacarpals that provide evidence for pronograde quadrupedalism and terrestriality (Godfrey et al., 2006a; Lemelin et al., 2006, 2008). An isolated upper molar of *Hadropithecus* from AHA-I was sectioned by Gary Schwartz, and from this specimen, data on enamel thickness, enamel prism characteristics, and the chronology of dental development in *Hadropithecus* were derived (Godfrey et al. 2005, 2006a,b). Research on the dental microstructure of that molar has demonstrated that molar crown formation time was prolonged in *Hadropithecus* and is more like that of extant hominoids (gorillas, chimpanzees, orangutans) than extant lemurs or even other extinct giant lemurs, whether larger or smaller in body size. The cuspal enamel of *H. stenognathus* is not as thick or heavily decussated as in *Archaeolemur*; these differences, along with differences in their stable isotope signatures, underscore variation in trophic adaptations within the Archaeolemuridae (Godfrey et al., 2005; Godfrey et al., 2008).

Terrestrial gastropods are well-represented in the Andrahomana fossil record. Some of the types present as fossils are still living in the area, including large species in the genera *Helicophanta*, *Tropidophora* and *Clavator*. Within the Pleistocene eolianites, shells of a *Clavator* species were fairly common. The general impression from the Holocene stratigraphy is that the prehuman snail fauna has generally survived to the present in the area, but detailed analysis, including identification to species, should be undertaken. The Andrahomana vicinity is rich in both fossil and living snails. Emberton (1997) has identified 80 extant land snail species in extreme southeastern Madagascar.

Discussion

Biogeography and Paleoecology

Located on the southeastern coast of Madagascar, Andrahomana is just west of the Anosyenne Mountains, and thus in dry habitat. Today, the high plateau of central Madagascar behaves as a formidable barrier separating the wet forests of the east and the dry forests of the west, and there are striking differences between the respective faunas as well as floras of these regions. The boundary between wet and dry biota is very sharp in places; the eastern and

Table 2. List of subfossil taxa recovered from deposits at Andrahomana by Burney *et al.* (this publication) and by previous collectors.

Class	Order	Family	Burney *et al.*	Previous Collectors
Aves	Aepyornithiformes	Aepyornithidae		*Aepyornis* sp.[a, b, c]
			Mullerornis	
	Anseriformes	Anatidae		*Centrornis* sp.[a]
	Procellariiformes	Procellariidae	*Puffinus* sp.	
	Falconiformes	Falconidae	*Falco newtoni*	
	Galliformes	Numidae	*Numida meleagris*	
	Gruiformes	Turnicidae	*Turnix nigricollis*	
		Rallidae	*Gallinula chloropus*	
	Columbiformes	Columbidae	*Streptopelia picturata*	
	Psittaciformes	Psittacidae	*Coracopsis vasa*	
	Cuculiformes	Cuculidae	*Coua cursor*	
			Coua cristata	
	Strigiformes	Tytonidae	*Tyto alba*	
		Strigidae	*Otus rutilis*	
	Apodiformes	Apodidae	*Apus* sp.	
	Coraciiformes	Upupidae	*Upupa marginata*	
	Passeriformes	Alaudidae	*Mirafra hova*	
		Sylviidae	*Nesillas* cf. *lantzii*	
			Thamnornis chloropetoides	
		Monarchidae	cf. *Tersiphone mutata*	
		Zosteropidae	*Zosterops maderaspatana*	
		Vangidae	*Vanga curvirostris*	
			Leptopterus viridis	
			Cyanolanius madagascarinus	
		Corvidae	*Corvus albus*	
		Ploceidae	*Ploceus sakalava*	
			Foudia madagascariensis	
Mammalia	Afrosoricida	Tenrecidae	*Geogale aurita*	"*Cryptogale australis*"[c]
			Microgale brevicaudata	
			Microgale longicaudata	
			Microgale nasoloi	
			Microgale pusilla	
			Microgale macpheei	
				"*Paramicrogale decaryi*"[c] (*Microgale principula*)
			Echinops telfairi	
			Setifer setosus	
			Tenrec ecaudatus	"*Centetes ecaudatus*"[b, c]
	Soricomorpha	Soricidae	*Suncus madagascariensis*	
	Chiroptera	Pteropodidae		"*Pteropus edwardsi*"[a, b] (*Pteropus rufus*)
			Eidolon dupreanum	
			Rousettus madagascariensis	"*Pelophilous madagascariensis*"[c]
		Hipposideridae	*Hipposideros commersoni*	
			Triaenops furculus	
		Vespertilionidae	*Miniopterus gleni*	
		Molossidae	*Mormopterus jugularis*	
			Mops leucostigma	

Table 2. Continued.

Class	Order	Family	Burney *et al.*	Previous Collectors
	Primates	Cheirogaleidae	*Microcebus* sp.	"*Cheirogaleus myoxinus*"[c]
			Cheirogaleus medius	"*Cheirogaleus samati*"[a]
		Lemuridae	*Lemur catta*	*Lemur catta*[c, d]
			Pachylemur insignis	"*Lemur insignis*"[a, b, c]
		Indriidae	*Propithecus verreauxi*	*Propithecus verreauxi*[a, b, c, d]
				Avahi laniger[d]
		Archaeolemuridae	*Archaeolemur majori*	*Archaeolemur majori*[a, c, d]
				Archaeolemur edwardsi[d]
			Hadropithecus stenognathus	*Hadropithecus stenognathus*[d]
		Megaladapidae	*Megaladapis edwardsi*	*Megaladapis edwardsi*[a, b, c, d, e]
				Megaladapis madagascariensis[d]
	Carnivora	Viverridae		"*Viverra fosa*" (var. nov. *alluaudi*, large size)[a, c]
		Eupleridae		*Cryptoprocta ferox* (var. nov. *spelea*, large size)[b, c]
		Canidae	*Canis lupus familiaris*	*Canis familiaris*
	Artiodactyla	Bovidae	*Bos indicus*	"*Bos madagascariensis*"[a, b, c]
		Hippopotamidae	*Hippopotamus lemerlei*	*Hippopotamus lemerlei*[a, d]
	Rodentia	Nesomyidae	*Eliurus myoxinus*	
			Eliurus sp. (larger species)	
			Hypogeomys australis	*Hypogeomys* nov. sp.[c]
			Macrotarsomys bastardi	
			Macrotarsomys petteri	*Nesomys rufus*[d]
		Muridae	*Mus musculus*	*Mus musculus*[b]
			Rattus sp.	"*Mus decumanus*"[a, b, c]
Reptilia	Testudines	Pelomedusidae	*Pelomedusa subrufa*	
		Testudinidae	*Dipsochelys* sp.	"*Geochelone* (*Testudo*) *grandidieri*"[a, b]
			Geochelone radiata	"*Geochelone* (*Testudo*) *radiata*"[b]
	Squamata	Chamaeleonidae	*Furcifer* cf. *verrucosus*	
		Gekkonidae	*Paroedura* sp.	
		Gerrhosauridae	*Zonosaurus* cf. *trilineatus*	
	Serpentes	Boidae	*Acrantophis* sp.	
		Colubridae	*Leioheterodon* sp.	
	Crocodylia	Crocodylidae	*Crocodylus niloticus*	
				Crocodilus robustus[a, b, c]
Amphibia	Anura	Mantellidae	*Laliostoma labrosa*	
		Ranidae	*Ptychadena mascareniensis*	
		Microhylidae	*Scaphiophryne* sp.	

Note: Further information concerning previous collections can be found in Appendix 1. The Alluaud, Gaubert and Grandidier Collections were all published in Grandidier (1902). Earlier nomenclature (i.e., synonyms) of various taxa from previous collections is retained in the previous collections column, listed in quotes and parentheses.
[a] Alluaud Collection
[b] Gaubert Collection
[c] Grandidier Collection
[d] Sikora Collection
[e] Walker Collection

western slopes of Andohahela in southeastern Madagascar provide a good example (Goodman, 2000). Yet in other places, the high plateau serves as a region of considerable exchange (see for example, Goodman et al., 2007). The sharp ecotonal boundaries that exist on the eastern and western slopes of mountains such as Andohahela may be recent effects of rapid orogeny (see de Wit, 2003). It is also clear that, in the past, the geographic boundaries of typically wet- and dry-adapted species were quite fluid; fingers of eastern forest once spread across the island.

Isolated forests with eastern elements occur in the west, e.g., the region of Zombitse-Sakaraha, east of Morondava, and the mist oasis of the Analavelona Massif, near Toliara (Du Puy et al., 1994; Langrand and Goodman, 1997; Carleton et al., 2001, Ganzhorn, 2006), and typical dry-loving species occur in some forests of the East (reviewed in Ganzhorn, 2006). A number of lemur species and other fauna are today, or were in the recent past, spread across the east-west divide. For example, it is now known that *Hapalemur simus*, restricted today to humid forests in the southeast (Irwin et al., 2005), once lived in the extreme north (Ankarana and Mt. des Français), central Madagascar (Ampasambazimba), the northwest (Anjohibe), and the extreme west (Bemaraha) (Godfrey et al., 2004). Paleoecological data confirm that the southwest was recently moister than it is today (Burney, 1993), and the Holocene distributions of rodents and birds prove the existence of a corridor south of $\sim 20^\circ$ latitude through which animals adapted to moist environments were able to spread westward (Goodman and Rakotondravony, 1996; Goodman and Rakotozafy, 1997).

There are several possible explanations for the observed mixture of wet- and dry-adapted fauna at Andrahomana. One is that these taxa were not actually synchronous but are a mixed assemblage of species that lived in the region at different times; their presence at Andrahomana would then reflect temporal fluctuation in the climate and vegetation of the area. Another is that the tolerance of certain species to variation in habitat was greater in the past than it is today. A third possibility is that the habitats themselves were richer, supporting a larger number of sympatric species with different resource requirements. Direct and indirect anthropogenic factors (hunting, deforestation, introduction of exotic species) may have contributed to changes and diminutions in the geographic ranges of endemic species. Regardless of whether past transitions between wet and dry biomes were gradual or abrupt in southern Madagascar (either temporally or spatially), the mixture of wet- and dry-adapted species at Andrahomana certainly reflects the position of the cave within the zone of transition.

Cave Genesis and Chronology

Although the eolianite units at Andrahomana are almost certainly too old for radiocarbon dating and even less conventional methods such as whole rock amino-acid racemization (see Hearty et al., 2000), some rough estimates can be made for Andrahomana's chronology of formation. For example, the cave has been formed by solution since the third eolianite unit was deposited (the topmost Aepyornian). That surely means that the cave was formed since the last interglacial depositional event, a minimum of approximately 130 kyr BP (isotope stage 5e).

Speleothems >1 m in diameter are found inside, and these were almost certainly deposited prior to cave collapse (the air is too dry in the cave today to permit significant dripstone formation). Similar formations in another cave in Madagascar required more than 40 kyr to reach a similar size (Burney et al. 1997). Combining these observations, the following scenario is plausible, but not proven by the data presented: 1) the limestone was laid down over the last quarter million years or more; 2) the cave was excavated by ground-water dissolution over the last ca. 100,000 years; 3) after perhaps 40,000 years of speleothem growth, the ceiling of the cave began to collapse, drying out the inside of the cave and permitting rapid sedimentation from terrestrial sources; 4) during the Holocene, sea level reached the bottom of the lowermost cave entrance; 5) extreme marine events, since mid-Holocene times, occasionally breached the interior of the cave, contributing to structural collapse and depositing marine sands and other material inside up to the highest parts of the floor, >8 m above present sea level.

If these linked scenarios are correct, mid-to-late Pleistocene fossils may be incorporated into the eolianite, the uppermost sediments are a mixture of Holocene terrestrial and marine materials, and deep down, below any excavation levels reached so far, and perhaps in fissure fills higher up, there could be mid-to-late Pleistocene cave breccias, perhaps containing bones and shells from times poorly sampled in fossil sites in Madagascar. Thus Andrahomana has some potential for filling the later portion of the large Cenozoic blind spot that has characterized paleontology in Madagascar (see Table 1 in Krause et al., 2006). For resolving the interesting questions regarding the timing of human arrival and the fate of the extinct subfossil fauna, however, the cave is not ideal. Because of the apparent disturbance, removal, and reworking of Holocene sediments, only limited stratigraphic resolution has been obtained in the excavated sediments.

It is abundantly clear from the detailed history of site exploration and development in Appendix 1 that, despite its extremely remote location, the site has attracted a great deal of attention from paleontologists. Ironically, however, none of these accomplished collectors provided any stratigraphic detail or information concerning the age or provenance of the many fossils collected. This is unfortunate, as much of the accessible deposits were removed or disturbed before the initiation of the present study. Confirming associations and finding previously undescribed elements of *Hadropithecus stenognathus* would alone justify continued efforts. The discovery of associated forelimb and hind-limb bones has indeed informed and improved reconstructions of the behavior of *Hadropithecus* (see reviews by Godfrey et al., 1997, 2006a). Far from completing the study of this interesting cave and exhausting its potential, our recent work at Andrahomana, which has yielded a site map, new insights on the stratigraphy and geochronology of the site, evidence for mega-tsunamis or other extreme marine events, and the collation of historical records for the site, merely underscores the need for more research. Two high priorities for future research would be larger-scale excavation and methodical searching for Pleistocene age breccias and fissure fills.

Until recently, the great isolation of the site has provided some protection from vandalism and looting of the natural treasures of the site. The ornate speleothems, abundant fossil bones and shells, and mineral deposits of the cave area are potentially vulnerable to the growing illegal trade in these materials (Krause et al., 2006). Local authorities, quite naturally, are anxious to see access to the site improved in anticipation of ecotourism revenues. Several local tour operators now offer visits to the site and more are planned according to local authorities. It is important, however, that any future development plans for the area include provision of some form of protection for the site.

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Appendix 1: History of the exploration of Andrahomana

1840	A map of the southern coast of Madagascar published by Leguével de Lacombe (later reproduced in A. Grandidier, 1885) shows a village at the Bay of Andrahomana labeled "Andrahoum."
1855	Marguin (cited by Grandidier, 1885) publishes a map of the site of the caverns ("Cap Andavaka" – in Malagasy, the "place of the caverns") and a detailed map of the "Baie d'Andrahomana." Neither of Marguin's maps is reproduced in Grandidier (1885).
1885	Alfred Grandidier (1885) briefly describes the existence of caverns on the southern coast of Madagascar in his "Histoire de la géographie." In 1892 this book was revised, reprinted and issued as the first volume of his monumental "Histoire Physique, Naturelle et Politique de Madagascar." Sometimes credited with having discovered the caves (e.g., see Decary, 1927), Alfred Grandidier actually learned of them from the Malagasy and through the experience of other westerners who had traveled to Madagascar in some cases well before Grandidier's first trip there (in 1865). Grandidier (1885) states that Cap Andavaka was known to 16th century European explorers of Madagascar.
1899	Austrian pipe-carver and naturalist, Franz (or François) Sikora, and a team of some twenty Malagasy workers, excavate Andrahomana Cave for a period of 18 days. Specimens of extinct lemurs and associated fauna collected during this expedition were sent to the Naturhistorisches Museum in Vienna and to the British Museum of Natural History in London. Sikora apparently left no written records documenting the exact location of his dig within the cave, nor did he make a log of stratigraphic associations. His most detailed treatment of his explorations, "Sept Ans à Madagascar," was published two years prior to his expedition to Andrahomana (Sikora, 1897). However, in terms of the sheer volume of specimens belonging to subfossil lemurs, Sikora's osteological collection from Andrahomana remains unsurpassed by those of subsequent explorers. Among Sikora's discoveries were the first complete skull and hemimandible, plus associated postcranial bones, of *Archaeolemur majori* (sent to the Natural History Museum, London) as well as a nearly complete skull and other skeletal elements of *Hadropithecus stenognathus* (sent to the Vienna Naturhistorisches Museum). Sikora's expedition to Andrahomana was briefly documented by Alluaud (1900). The specimens that Sikora collected there were studied initially by C.I. Forsyth Major (1899) and by Lorenz von Liburnau (1899, 1901, 1902, 1905), and later by Walker (1967), Tattersall (1973, 1982), Jungers (1976), and Godfrey (1977). Sikora also collected over 40 specimens of an extinct species of *Hypogeomys* (see below), now at the British Museum (Natural History).
1900	French entomologist Charles Alluaud conducts the first of a series of expeditions to Andrahomana and other localities in southern Madagascar. Only his first expedition (August 21–August 27, 1900) is well documented in the literature (Alluaud 1900, a letter dated August 30, 1900 and addressed to Guillaume Grandidier). On this expedition, Alluaud was accompanied by a French soldier, Lieutenant Gaubert. The two traveled together from the Poste de Manambaro to Ranopiso, and then to the rat-infested, recently constructed, Poste d'Andrahomana, located on a hill over the small peninsula bordering the Baie d'Andrahomana. Alluaud's (1900) letter to Grandidier describes the difficulty the two experienced in gaining access to the cave as well as various other frustrations. He complains that the cave had been completely excavated (*tout fouillé*) by his predecessor, Franz Sikora. It is noteworthy, however, that Alluaud and Gaubert spent only three days (August 23–25) actually excavating in or near the cave, and they had hired Malagasy helpers on only two of them. The team found relatively few subfossil specimens (although there were some giant tortoise and extinct lemur bones in the lot). Part of Alluaud's contribution was the construction of a path for easier access to the cave, and a botanical survey. The bounty of this first expedition was sent to the Muséum National d'Histoire Naturelle in Paris in 1900.
1901–02	On separate occasions, Charles Alluaud, Lieutenant Gaubert and Guillaume Grandidier (the son of Alfred) visit or revisit Andrahomana, to collect more specimens of extinct lemurs. These expeditions were apparently more successful than Alluaud and Gaubert's first one, but they are poorly described in the literature. Separate Alluaud, Gaubert, and G. Grandidier collections were sent to Paris in the spring of 1902 and were described by G. Grandidier (1902). No *Hadropithecus stenognathus* was listed as having been collected by any of these explorers. However, some *Hadropithecus* bones that may have come from Andrahomana are in the collections of the Paris museum (Godfrey et al., 2006a). Prize specimens of these missions were the types (MNHN MAD 1646 and MNHN MAD 1647) of a new species of extinct rodent, *Hypogeomys australis*, found by Alluaud and initially described by Grandidier (1903) (Goodman and Rakotondravony, 1996).
1902	Franz Sikora dies at the age of 39, fewer than three years after he had led his pioneering expedition to Andrahomana (Zapfe, 1971).

Appendix 1. Continued.

1906	French pharmacist and naturalist Martin François Geay collects bones of lemurs, rodents, and bats at the caverns of Andrahomana. Geay had studied natural history in France under the tutelage of Alphonse Milne-Edwards. He spent several years in Madagascar (1904–1907) collecting plants, wood, fossils, mollusks, fish, birds, reptiles, and rocks for the Paris natural history museum (Thevenin, 1907; Dorr, 1997). During that time, he sent 70 crates containing about 14,000 specimens to Paris. In his privately published book, Geay (1908, p. 99–100) briefly describes his trip to Andrahomana, stating only that he collected lemur, rodent, and bat bones there, and describing the terrestrial deposits into which the cave was cut. Geay also offers the following explanation for the name of the bay, Andrahomana (literally, "an" = at or where, "rano" = water, "homana" = eaten: "where the water is devoured"). At the end of Andrahomana Bay is a meandering brook that winds around tall, gloomy, and entirely denuded rocks bordering the ocean. The water of the brook disappears into (i.e., is eaten or consumed by) the sands of the beach.
1906?	Gaston-Jules Decorse (a French military doctor who collected plants, insects and fossils for the natural history museum in Paris) explores the region of Cap Andavaka (Decary, 1927, for the year 1926). Decorse was very interested in terrestrial mollusks and he collected specimens in the calcareous dunes near Andrahomana. Thevenin (1907) describes several explorers, including Grandidier and Decorse, collecting *Aepyornis* eggshell in the region.
1926	French military officer and naturalist Raymond Decary leads a scientific exploratory expedition to southern Madagascar (including Andrahomana) for the Museum National d'Histoire Naturelle (Paris). This mission began in June, 1926. Decary (1927) found little here in the way of giant subfossils, but he did find numerous bones of micromammals and other small vertebrates. He also published a survey of the plants and geology of the region (Decary, 1928).
1927	Decary sends some of the specimens that he collected at Andrahomana to Grandidier for study. Over the following 12 years, both Grandidier and Decary dispatch specimens from Andrahomana to the Museum of Comparative Zoology, Harvard University. These include some *Lemur catta*, *Microcebus* sp. (probably *M. griseorufus*), and some insectivores (now recognized as *Microgale principula* and *Geogale aurita*).
1928	Guillaume Grandidier (1928) names several new species of insectivores on the basis of specimens from Andrahomana Cave. He gave the name *Paramicrogale decaryi* to specimens with a relatively short and wide skull, and *Cryptogale australis* to others with a long and narrow skull. *Paramicrogale decaryi* was later synonymized with *Microgale* by Heim de Balsac (1972) and then with *M. principula* by MacPhee (1987). *Cryptogale australis* was later synonymized with *Geogale aurita* by Heim de Balsac (1972).
1964	René Battistini (1964) publishes his dissertation monograph on the geomorphology of southern Madagascar, with notes on the geology of Andrahomana.
1966	Bush pilot Ike Russell and his wife Jean accompany Alan Walker and Paul Martin on a flight from mainland Africa to Antananarivo (Walker, 2002; Paul Martin unpublished notes), and then to a number of subfossil sites, including Andrahomana. To reach Andrahomana, Russell landed his small aircraft on the dry bed of Lake Erombo, several miles from the cave. From there, Walker and Martin hiked to the cave while the Russells remained with their plane. Once in the cave, Walker and Martin found a piece of the scapula and a finger bone of *Megaladapis edwardsi*, as well as pieces of a smashed carapace and plastron of a giant tortoise that had fallen into the cave from above. They could only visit the cave for a short period before having to return first by foot to Erombo and then by plane to Fort Dauphin.
1971	Raymond Decary and André Kiener (1971) publish an inventory of caves of Madagascar.
1983	Ross MacPhee, Elwyn Simons, Prithijit Chatrath, Neil Wells, and Martine Vuillaume-Randriamanantena visit the cave August 18 for a few hours in connection with a Duke University Primate Center expedition to southern Madagascar. Although impressed with the beauty of the area, the group found only "very recent bones of *Microcebus*, *Propithecus*, *Rattus*, birds, and turtles. A few hand/foot bones of large size were discovered…they could be those of a giant lemur" (R. MacPhee, pers. comm., 2007).
2000	David Burney, Malagasy students, and local guides make a reconnaissance of the cave August 24–27, conducting a small controlled excavation at AHA-B and making surface collections and sediment borings.
2003	July 16 to August 8, Burney makes expedition to Andrahomana accompanied by the coauthors of this paper and local guides. Group undertakes mapping, and excavates sites AHA-F and AHA-I.
2006	Laurie Godfrey and colleagues revise postcranial attributions for *Hadropithecus stenognathus* on the basis of associated skeletal materials found at AHA-I in 2003 (Godfrey et al., 2006a). Collaborations with Steve Goodman lead to naming a subfossil species of shrew-tenrec (*Microgale macpheei*; Goodman, Vasey, and Burney, 2007) and publishing the first known fossil occurrence of the recently described nesomyid rodent *Macrotarsomys petteri* (Goodman et al., 2006).