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THE HOLOCENE DISTRIBUTION OF *HYPOGEOMYS* (RODENTIA: MURIDAE: NESOMYINAE) ON MADAGASCAR

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ABSTRACT. - Subfossils from Holocene deposits on Madagascar contain remains of two endemic rodents, *Hypogeomys antimena* and *H. australis*. *H. antimena* is currently restricted to a limited area of forest north of Morondava and the subfossil remains indicate that over the past 1,400 years its range extended at least 475 km further south. *H. australis* was still extant 4400 years ago, and it once occurred from southeastern Madagascar north to at least the Antsirabe region.

KEY-WORDS.- *Hypogeomys*, Nesomyinae, Range contraction, Extinction, Madagascar

RESUME.- Des dépôts de l'Holocène contiennent des restes subfossiles de deux rongeurs endémiques malgaches: *Hypogeomys antimena* et *H. australis*. Actuellement, la distribution géographique d'*H. antimena* est limitée à une zone forestière restreinte au nord de Morondava. Des restes subfossiles indiquent cependant qu'il y a 1400 ans environ, son aire de répartition s'étendait d'au moins 475 km vers le sud de Madagascar. *H. australis* s'est éteint il y a 4400 ans, mais à un moment donné, l'espèce était présente depuis l'extrême sud-est de Madagascar jusqu'au moins la région d'Antsirabe vers le nord.

MOTS-CLES. - *Hypogeomys*, Nesomyinae, Distribution réduite, Extinction, Madagascar

INTRODUCTION

Over the past few millennia the fauna of Madagascar has undergone dramatic changes. Paleontologists are still trying to understand the extent, impact, and causes of these changes, but it is clear that numerous vertebrates have gone extinct and the distributions of others have greatly contracted. Few extant mammals on Madagascar have a more geographically limited range than the Malagasy Giant Jumping Rat *Hypogeomys antimena*. Paleontological evidence indicates that during the Quaternary this genus had a much broader distribution on the island. The purpose of this paper is to review the taxonomy and history of subfossil *Hypogeomys* and to present some ideas on why members of this genus may have disappeared from portions of their former ranges.

Hypogeomys belongs to the subfamily Nesomyinae (Family Muridae), an endemic group of Malagasy rodents (MUSSER & CARLETON, 1993). All of the native rodents of the island are placed in the Nesomyinae, although it is unknown if this subfamily is monophyletic. The modern distribution of *H. antimena*, the only living species within the

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genus, is restricted to a narrow coastal zone of dry deciduous forest north of Morondava (Fig. 1). *H. antimena* has several unusual morphological and behavioral adaptations. It has unusual social behavior, is herbivorous, and digs deep extensive subterranean burrows in sandy soil (COOK *et al.*, 1991; VEAL, 1992; SOMMER, 1994).

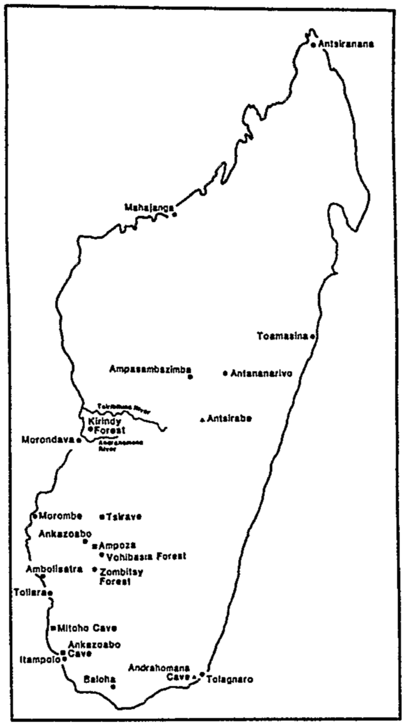

Fig. 1. Map of the Holocene and current distribution of *Hypogeomys* spp. on Madagascar. Circles = general localities mentioned in text, squares = subfossil sites of *Hypogeomys antimena*, and triangles = subfossil sites of *H. australis*.

In 1869, A. GRANDIDIER (p. 339) described *Hypogeomys antimena* from the region « sur les rives du Tsidsibon [=Tsiribihina] et de l'Andranoumène [=Andranomena], deux rivières du Ménabé indépendant » (portions in brackets after CARLETON & SCHMIDT [1990, p. 25]). Subfossils of *H. antimena* have been previously reported from two localities on the Mahafaly Plateau, southwestern Madagascar, both outside of this species' known modern range. In 1937 LAMBERTON (p. 18) described remains of *H. antimena* from Ankazoabo Cave (24°34'S, 43°55'E), about 15 km N of Itampolo, and 475 km S of Morondava. Further, MACPHEE (1986) recovered material of *H. antimena* in Mitoho Cave (24°03'S, 43°45'E), Lake Tsimanampetsotsa, which is about 70 km N of Itampolo. No radiocarbon date is available for these *Hypogeomys* subfossils, but based on C^{14}-dates of similar types of subfossils, all are of Quaternary age, presumably Holocene. The basis for the record reported by CHANUDET (1975 : 235) of *H. antimena* from Ampasambazimba (18°39'S, 46°01'E) on the central high plateau, about 100 km W of Antananarivo, is unknown.

In 1903 G. GRANDIDIER described a subfossil species, *Hypogeomys australis*, based on material found by Alluaud in Andrahomana Cave (25°50'S, 46°40'E), 40 km W of Tolagnaro, and now housed in the Muséum National d'Histoire Naturelle, Paris (MNHN). The type specimens illustrated by Grandidier (1903) of *H. australis* are a right mandible (MNHN MAD 1646) and right maxilla (MNHN MAD 1647), both specimens have complete molar dentition. The teeth of the latter specimen are distinctly more worn than the former, and they presumably represent two individuals (Fig. 2a & b). The excavations of Alluaud in the Andrahomana Cave were continued by Sikora (GRANDIDIER, 1902; CHANUDET, 1975) and a collection of over 40 *Hypogeomys* bones were obtained which are now held in the Natural History Museum, London (BMNH). Only one other record of *H. australis* has been traced. LAMBERTON (1946, plate IIIf) published a photograph of a rodent bone labelled, « fémur de l'*Hypogeomys australis.* » The bone is inscribed with the locality « Beloha » (25°10'S, 45°03'E), which is a subfossil site in extreme southern Madagascar that Lamberton worked in 1932. This specimen has not been located.

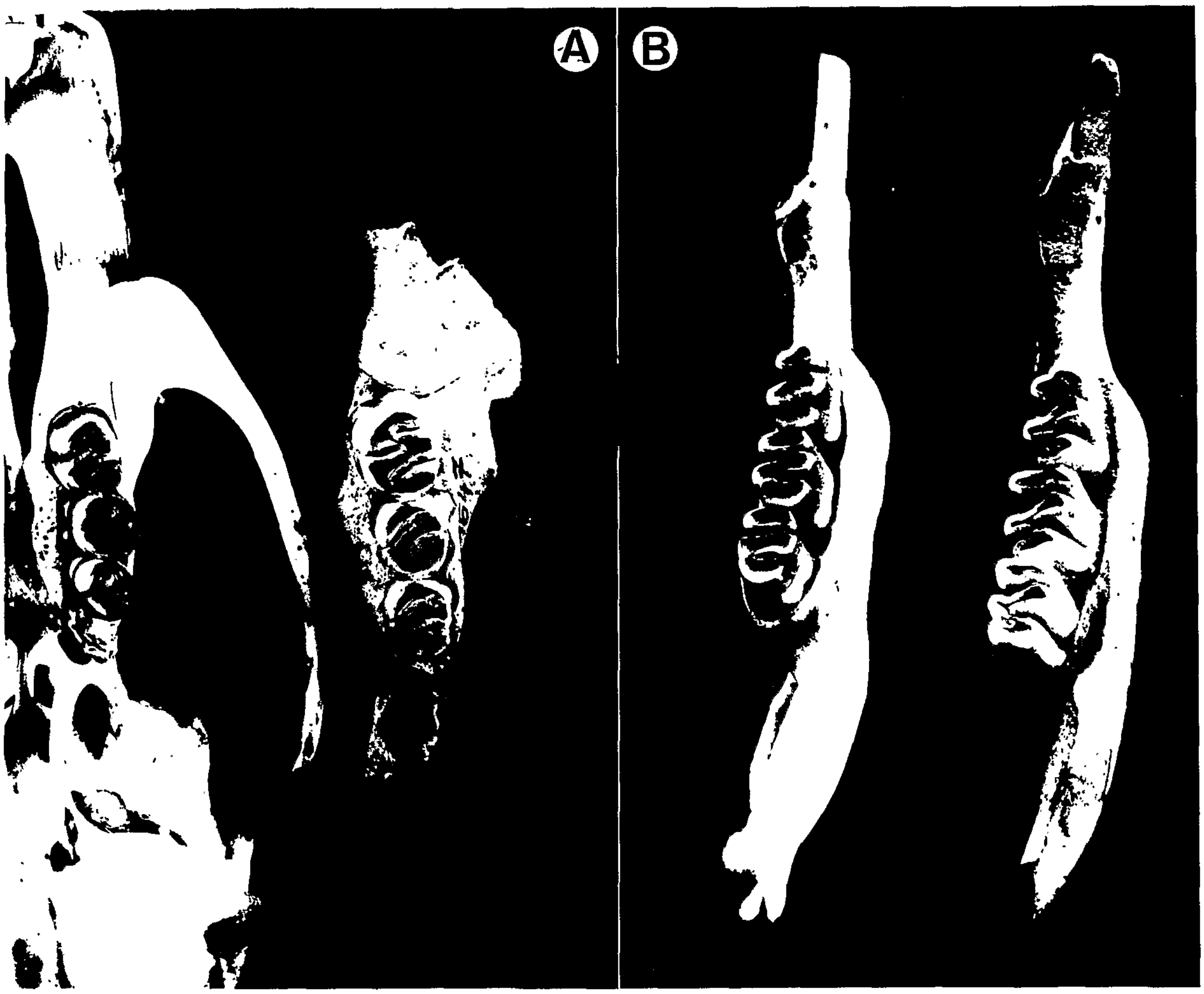

Fig. 2. a) View of maxillary tooth rows of recent *Hypogeomys antimena* (left) collected in the Kirindy Forest, Morondava (Field Museum of Natural History [FMNH] 151995) and the type of *Hypogeomys australis* (right) excavated from Andrahomana Cave (MNHN MAD 1647) and b) view of mandibles of *antimena* (left) from Kirindy (FMNH 151995) and type of *australis* (right) from Andrahomana (MNHN MAD 1648). Photograph by Diane White.

G. GRANDIDIER (1912) described a second subfossil species, *Hypogeomys boulei*, from remains recovered at Ampasambazimba. When this material was reviewed by LAMBERTON (1946, p. 40), it was determined to be of an extinct « aardvark, » *Plesiorycteropus madagascariensis*, a genus which has been recently revised and allocated to a new order of mammals (MACPHEE, 1994).

In the MNHN there are other specimens referable to *Hypogeomys*. These include a tibia (MAD 355) from Tsirave (21°50'S, 45°07'E), located near the Mangoky River and about 165 km inland from Morombe; a proximal half of a tibia (1931.6) from Ampoza, (22°20'S, 44°44'E), east of Ankazoabo and about 125 km southeast of Morombe; and three tibia (MAD 356-358) obtained near Antsirabe (19°51'S, 47°02'E), on the central high plateau.

DISCUSSION

IS *HYPOGEOMYS AUSTRALIS* A DISTINCT SPECIES?

Sufficient material of modern *Hypogeomys antimena* from the Morondava region and subfossil *H. australis* from the Andrahomana Cave is available for morphometric comparison (Table I). Within the modern *antimena* sample there is no evidence of sexual dimorphism and in all subsequent analyses males, females, and unsexed specimens have been combined. In virtually all cases, there is little to no overlap in the bone measurements of the Morondava and Andrahomana samples and they are statistically different from one another. *Australis* was a distinctly larger animal than *antimena*, although the two were similar in tooth and cusp structure.

SPECIFIC ALLOCATION OF *HYPOGEOMYS* SUBFOSSILS FROM CENTRAL MADAGASCAR

The material recovered from near Antsirabe consists of two completely ossified tibia and one partially ossified tibia. The total length of the two ossified bones (MNHN MAD 358 and 356) exceeds the known range of *antimena* from Morondava and falls within the range of *australis* from Andrahomana Cave (Fig. 3, Table I). The proximal tibia of one of the two ossified specimens is partially broken while the proximal width of the second tibia (MAD 358) falls within the range of *australis*. There is no significant difference in the distal tibia width between the two species (Table I). The proximal portion of a tibia from Ampoza falls within the size range of *antimena*. The specimen from Tsirave is unossified, but in general size and shape appears to be assignable to *antimena* (Fig. 4). On the basis of the available material, it appears that *Hypogeomys australis* once occurred at sites near Tolagnaro in the southeast and north to at least the Antsirabe region, while the distribution of *antimena* once extended much further south than the current limited range near Morondava (Fig. 1).

RADIOCARBON DATING

Two AMS radiocarbon dates are available for material of *Hypogeomys*. A small fragment from the Ampoza (MNHN 1931.6) tibia assigned to *antimena*, produced a date of 1350 ± 60 BP (Beta-72676 CAMS-13677) and a piece of *australis* bone from Andrahomana Cave (BMNH M.7395) yielded a date of 4440 ± 60 BP (Beta-73370, CAMS-14053).

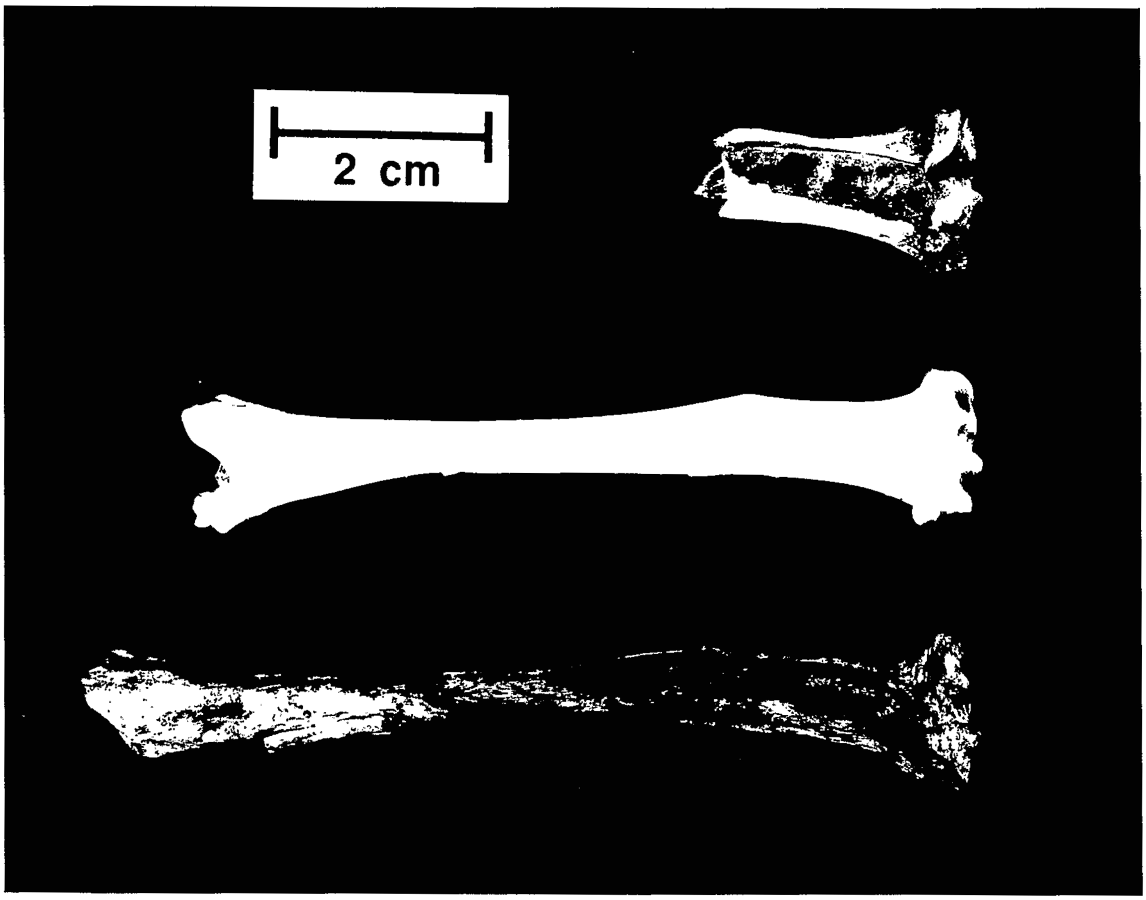

Fig. 3. Tibia (from left to right) of *Hypogeomys antimena* collected from the subfossil site of Ampoza (MNHN 1931.6), modern *antimena* from the Kirindy Forest (FMNH 151995), and *Hypogeomys australis* obtained from a subfossil site near Antsirabe (MNHN MAD 356). Photograph by Diane White.

WHAT FACTORS LED TO THE DRAMATIC CHANGE IN THE DISTRIBUTION OF *HYPOGEOMYS* SPP.?

Since nothing is known about the natural history of *Hypogeomys australis* it is difficult to extrapolate clues to understand its disappearance. However, like *antimena*, *australis* is presumed to have lived in excavated burrows in areas with friable or sandy soils. In modern times *H. antimena* is restricted to a limited region and specific habitat -

coastal deciduous dry forest mixed with baobabs on sandy or lateritic soils (Cook *et al.*, 1991). Further, they tend to occur in forests where the floor is largely covered with leaf litter. The average annual rainfall near Morondava is 800 mm (Donque, 1975). This is in contrast to the Mahafaly Plateau, where the flora is composed of sub-arid thorn scrub, dominated by a highly specialized xerophytic flora, with virtually no leaf litter, and an annual average rainfall of less than 350 mm (Donque, 1975; Koechlin *et al.*, 1974; MacPhee, 1986). Although both of these forest types belong to the Western Region, they show many floristic differences (Humbert, 1954; White, 1983).

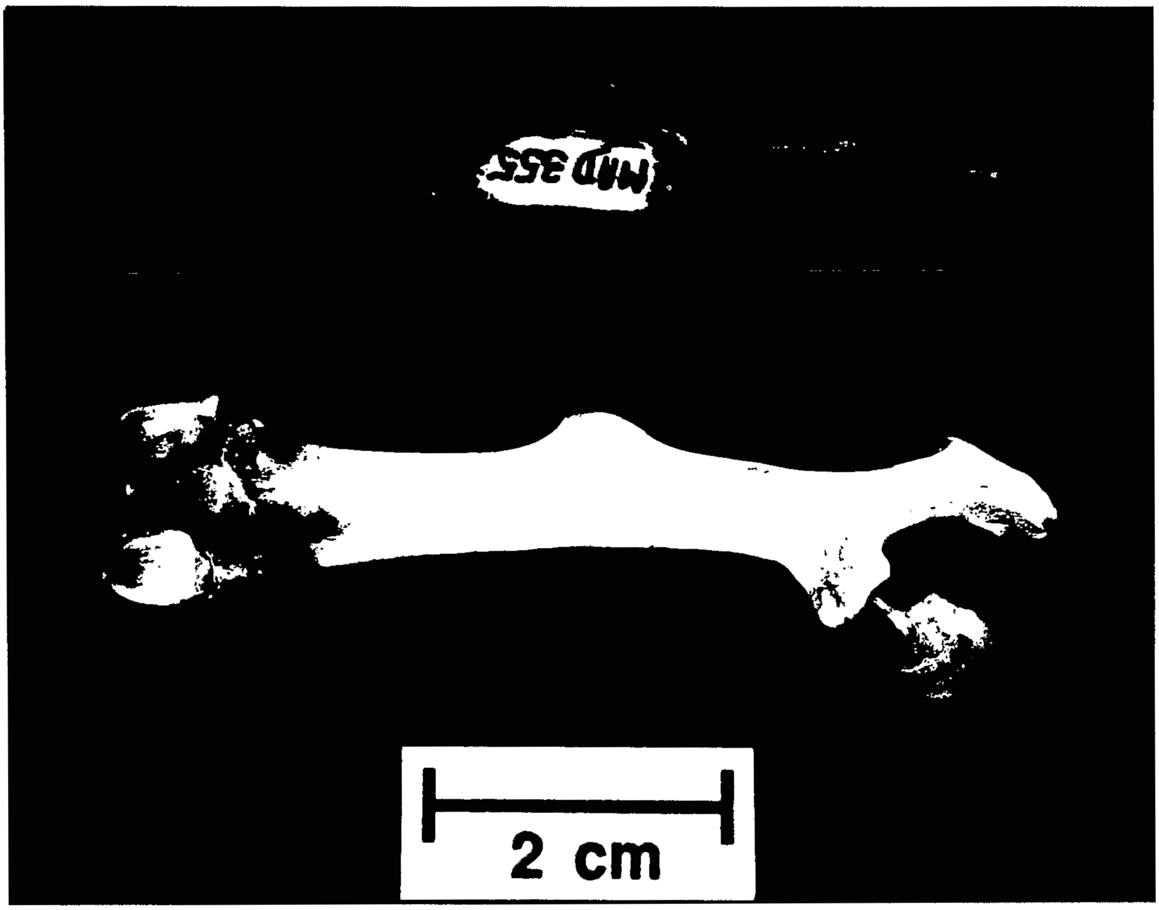

Fig. 4. Femurs of (left to right) of a subfossil, subadult *Hypogeomys antimena* from Tsirave (MNHN MAD 355) and modern *H. antimena* from the Kirindy Forest (FMNH 151995). Photograph by Diane White.

One of the problems in trying to interpret the habitat formerly occupied by *Hypogeomys antimena* in the Mahafaly Plateau region, is to understand exactly where it occurred. The plateau is a broad expanse of exposed and extremely rugged limestone with relatively pristine sub-arid thorn scrub. The western escarpment is covered with limestone debris, and then abruptly drops about 100 m in elevation to the Lake Tsimanampetsotsa plain and to an area of pulverized chalk grading into coastal sand dunes (see diagram in Perrier de la Bathie, 1934, p. 165). Mitoho Cave, the site at which MACPHEE recovered material of *H. antimena*, is located near the base of the escarpment and within a kilometer of the lake edge. Ankazoabo Cave is also on the edge of the Mahafaly Plateau escarpment (LAMBERTON, 1937, p. 13). Since extant *H. antimena* dig deep subterranean burrows in friable soils, it is presumed that the animals formerly occurring in the Mahafaly Plateau region inhabited the sandy coastal plain to the west of the escarpment (DURANTON, 1975), rather than the jagged rocky plateau, and either visited the caves in search of freshwater or were deposited there as remains of predators' meals. Bones of large carnivores (*Cryptoprocta*) and a large extinct eagle (*Aquila*) have been identified from Mitoho and Ankazoabo caves (LAMBERTON, 1937; MACPHEE, 1986, GOODMAN; 1994). The soils near Ampoza, further inland, are made up of friable sandy ground, which would meet the habitat requirements of *H. antimena*.

An intriguing question is what caused the dramatic change in the distribution of *H. antimena* over a relatively short period of time? This species experienced a range reduction of hundred of kilometers in less than 1400 years. Three possibilities can be offered: natural ecological change, specifically aridification; human-induced habitat modification; or local extinction caused by human hunters (DEWAR, 1984):

1) Ecological change - There is good evidence that in the past few millennia southwestern Madagascar has become distinctly drier. The dramatic effects of this aridification are supported by the extinction or local disappearance of several vertebrates that required more mesic conditions than currently available in the region (MACPHEE, 1986; GOODMAN & RAKOTOZAFY, in review). BURNEY (1993) analyzed a pollen core, representing a 5,000 year sequence, taken from a coastal area near Ambolisatra, about 35 km N of Toliara. His analysis shows that this region until about 3,000 years ago was distinctly more mesic, and over the course of the following 1,000 years there is evidence of aridification. At a point in the stratigraphic column C^{14}-dated to about 1900 B.P., he found a dramatic increase in grass pollen and a decrease in woody plant pollen. BURNEY'S research demonstrates that even before evidence of extensive human habitat modification, the coastal region of southwestern Madagascar underwent a dramatic transformation. Thus, it is plausible that the local extinction of *H. antimena* from the region was a direct result of Holocene aridification and floral shifts in southwestern Madagascar. For example, critical elements in the diet of this animal may have disappeared.

2) Human-induced habitat change - The assumption here is that human disturbance, either through cutting or burning of natural vegetation, caused the degradation or total destruction of critical habitat required for *H. antimena*. The sandy plain to the west of the Mahafaly Plateau has been extensively modified by humans and is currently used by pastoralists to graze their cattle herds, and portions are regularly burned to stimulate herb growth. Although much of the area has been cleared of its former original vegetation, there are several relatively intact coastal forests resting on sandy soils, such as Hatokaliotsy (~22,000 ha), composed of sub-arid thorn scrub (NICOLL & LANGRAND, 1989). It is possible that human fragmentation of forest habitat led to the local extirpation of populations of *Hypogeomys antimena*. However, this seems unlikely in itself since a population of *antimena* remains north of Morondava in the relatively small and degraded Réserve Spéciale d'Andranomena (6,400 ha), while larger areas of forest occur to the west of the Mahafaly Plateau, such as Hatokaliotsy, and further inland the forests of Vohibasia (~19,000 ha) and Zombitsy (21,500 ha) near Ampoza lack this species (GOODMAN & GANZHORN, 1994). Given the distribution of sandy soils on the island, populations of *Hypogeomys* spp. would have had naturally fragmented distributions.

3) Human hunting pressure - given the lack of midden remains or information on the sequence of early human colonization in southwestern Madagascar (DEWAR & WRIGHT, 1994), the potential effect of hunting pressure on *Hypogeomys* is impossible to assess. However, amongst all of the local tribes inhabiting this region the consumption of rodent meat is strictly taboo. In January 1994 older inhabitants of the Vezo village Efoetse, not far from Mitoho Cave, were asked if they knew anything about a large rodent inhabiting the region - their unanimous response was negative. Further, Barra tribesmen living near the forests close to Ampoza were unfamiliar with large forest rodents. Thus, any memory of *Hypogeomys* occurring in these areas no longer lingers in local oral history.

CONCLUSIONS

On the basis of subfossil remains *Hypogeomys antimena* formerly occurred in the sandy plain to the west of the Mahafaly Plateau and inland areas of southwestern Madagascar, close to 500 kilometers south of its modern range. There is evidence that over the past few millennia this region has under gone natural aridification, and subsequently there was human modification of the environment. Natural and perhaps « finally human-induced factors » can account for the disappearance of this species from southwestern Madagascar. An extinct species, *H. australis*, once lived in the Tolagnaro area north to at least Antsirabe. There is no evidence that these two species lived in sympatry.

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Table I. Cranial and post-cranial measurements of adult *Hypogeomys antimena* from the Morondava region and *H. australis* from Andrahomana, and other *Hypogeomys* subfossils.

	IOB	LM 1-3	LM1	LM2	LM3	Lm 1-3	Lm1	Lm2	Lm3
antimena-type MNHN 1888.6	11.5	13.5	4.8	4.5	4.0	14.8	4.3	4.7	4.8
antimena modern	10.5 ± 0.65 9.0-11.5, 26	13.2 ± 0.48 12.0-14.1, 26	4.7 ± 0.33 3.8-5.1, 25	4.1 ± 0.32 3.2-4.6, 25	3.6 ± 0.05 3.2-4.0, 24	14.2 ± 0.49 13.4-15.3, 24	4.8 ± 0.41 3.9-5.5, 24	4.4 ± 0.27 3.8-4.8, 25	4.3 ± 0.34 3.6-4.9, 24
australis-types MNHN 1647		15.3	5.8	4.5	4.8				
MNHN 1646						17.7	5.2	4.7	4.7
australis	10.4	15.3	5.6 ± 0.17 5.4-5.8, 4	4.8 ± 0.25 4.5-5.1, 4	4.5 ± 0.36 4.1-4.8, 3	17.6, 17.7	5.7 ± 0.42 5.2-6.4, 10	4.9 ± 0.29 4.6-5.5, 8	5.2 ± 0.52 4.6-5.9, 7
T-statistic	-	-	**	**	**		**	**	**

	FEM-TL	FEM-WP	FEM-WD	TIB-TL	TIB-WP	TIB-WD	HUM-TL
antimena	63.8 ± 2.9 59.7-69.9, 9	17.5 ± 0.65 16.8-18.5, 9	14.1 ± 0.63 13.4-15.5, 9	72.7 ± 1.41 71.2-75.0, 8	14.5 ± 0.77 13.0-15.4, 8	12.0 ± 1.51 9.8-13.5, 8	43.7 ± 1.60 41.7-46.2, 8
australis	72.1 ± 1.66 69.9-75.1, 10	19.9 ± 0.92 18.6-21.5, 13	16.5 ± 0.67 15.6-17.5, 9	82.3 ± 2.71 80.3-86.9, 5	17.1 ± 0.24 16.9-17.4, 4	11.7 ± 1.49 10.0-13.4, 10	50.8 ± 1.67 48.1-52.7, 6
T-statistic	**	**	**	**	*	n.s.	**
Other material Antsirabe				81.1, 82.8 [75.8]	16.8, [14.3] [13.3]	10.3, 10.5 [9.5]	
Ampoza					15.4		

Key to cranial measurements: IOB=interorbital breadth, LM 1-3=length of maxillary tooth row, LM1=length of first upper molar, LM2=length of second upper molar, LM3=length of third upper molar, Lm 1-3=length of mandible tooth row, Lm1=length of first lower molar, Lm2=length of second lower molar, Lm3=length of third lower molar.

Key to post-cranial measurements: FEM=femur, TIB=tibia, HUM=humerus, TL=total length, WP=width proximal, WD=width distal. Measurements in brackets are approximate.

Key to T-statistics: - = no statistics calculated, n.s. = not significant, * = $p > 0.05$, ** = $p > 0.001$