

Systematic Palaeontology (Vertebrate Palaeontology)

The subfossil occurrence and paleoecological implications of *Macrotarsomys petteri* (Rodentia: Nesomyidae) in extreme southeastern Madagascar

Steven M. Goodman^{a,*}, Nathalie Vasey^b, David A. Burney^c

^aField Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA and WWF, BP 738, Antananarivo (101), Madagascar

^bDepartment of Anthropology, Portland State University, Portland, OR 97207-0751, USA

^cNational Tropical Botanical Garden, P.O. Box 1277, Kalaheo, HI 96741, USA

Received 5 May 2006; accepted after revision 8 September 2006

Available online 31 October 2006

Presented by Philippe Taquet

Abstract

Remains of a large-bodied species of endemic nesomyid rodent, *Macrotarsomys petteri* Goodman and Soarimalala, 2005, were identified from subfossil deposits recovered from Andrahomana Cave in extreme southeastern Madagascar. This recently described extant species was previously only known from a single specimen collected at a site about 450 km northwest of Andrahomana and with distinctly different forest habitat than currently found in the vicinity of the cave. Radiocarbon dating of remains of *M. petteri* from the cave site indicates that it persisted in the region subsequent to human settlement. Previous reports of a large member of *Macrotarsomys* from other Quaternary sites in southern Madagascar are almost certainly of *M. petteri*. It is proposed that this species once had a broad distribution across the southern portion of the island during a more mesic period and subsequent aridification of the region has led to its local extirpation across most of its former range. **To cite this article: S.M. Goodman et al., C. R. Palevol 5 (2006).**

© 2006 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Résumé

Présence subfossile de *Macrotarsomys petteri* (Rodentia : Nesomyidae) dans l'extrême Sud-Est de Madagascar et ses implications paléoécologiques. Des ossements d'une grande espèce d'un rongeur endémique des Nesomyidae, *Macrotarsomys petteri* Goodman & Soarimalala, 2005, ont été identifiés dans des dépôts subfossiles récupérés dans la grotte d'Andrahomana dans l'extrême Sud-Est de Madagascar. Cette espèce actuelle de rongeur, qui a été décrite récemment, n'était alors connue que par un seul spécimen, récolté dans une station sise à près de 450 km au nord-ouest d'Andrahomana, qui présente un habitat forestier nettement différent de celui actuellement rencontré aux alentours de la grotte. Une datation au radiocarbone des ossements de *M. petteri* ramassés dans la grotte indique que le rongeur avait survécu dans la région après la colonisation humaine. Les données antérieures se rapportant à un grand *Macrotarsomys* d'autres sites du Quaternaire du Sud de Madagascar sont presque certainement de *M. petteri*. Il est proposé de considérer une large distribution de cette espèce sur l'ensemble de la partie méridionale de l'île, au cours d'une période plus humide, qui se serait considérablement réduite lors d'une aridification ultérieure affectant cette région, en

* Corresponding author.

E-mail address: sgoodman@wwf.mg (S.M. Goodman).

se soldant par son extinction locale dans la plus grande partie de son aire de distribution ancienne. **Pour citer cet article:** S.M. Goodman et al., C. R. Palevol 5 (2006).

© 2006 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Keywords: Rodent; Nesomyidae; *Macrotarsomys*; Holocene; Madagascar

Mots clés : Rongeurs ; Nesomyidae ; *Macrotarsomys* ; Holocène ; Madagascar

Version française abrégée

Introduction

En se basant sur les éléments des dépôts subfossiles, il apparaît que les biomes de forêts sèches modernes de Madagascar, plus particulièrement ceux du quart méridional de l'île, ont subi des changements climatiques significatifs au cours du Quaternaire. Des données de dépôts palynologiques subfossiles montrent que cette région était particulièrement sèche il y a environ 3000 à 2000 ans [2], période qui coïncide avec l'extinction locale ou totale de plusieurs groupes distincts d'oiseaux et de mammifères [6,9,10,18]. Une part considérable du matériel subfossile de vertébrés utilisée dans cette étude provient de fouilles réalisées au cours d'anciennes explorations paléontologiques, alors que le contrôle stratigraphique n'était pas encore appliqué. Au cours des dernières années, des techniques de fouilles plus modernes ont été suivies dans un certain nombre de sites, qui nous permettent de présenter ici quelques-unes des nouvelles découvertes.

Les fouilles effectuées en 2003 au niveau de dépôts subfossiles de la grotte d'Andrahomana, dans l'extrême Sud-Est de Madagascar (Fig. 1), ont permis de disposer d'un matériel considérable se rapportant aux petits mammifères. La grotte, qui est située juste à l'ouest de la limite d'un écotone brusque entre un biome humide oriental et un biome sec occidental, contient des dépôts qui permettent de considérer la composition biotique locale qui régnait au Quaternaire. Parmi les ossements récupérés récemment dans la grotte, se trouvaient ceux d'un grand rongeur du genre endémique *Macrotarsomys*. Jusque récemment, ce genre n'était connu que de deux espèces avec *M. bastardi* (poids moyen adulte 24,5 g) à large distribution sur presque tout l'Ouest et le Sud, et *M. ingens* (poids moyen adulte 64,4 g), à distribution limitée à une petite région de forêt sèche caducifoliée du Centre-Ouest [4,14]. Une troisième espèce a été nommée récemment dans ce genre, *M. petteri*, qui n'est connue que par un seul spécimen récolté au nord de Toliara et qui pesait 105 g [11].

Comparaisons et conclusions

La comparaison des maxillaires et mandibules du matériel subfossile de la plus grande espèce avec ceux de deux espèces actuelles (*M. petteri* et *M. ingens*) indique que le taxon subfossile rentre dans la gamme de variation de *M. petteri*, aussi bien en ce qui concerne les caractères qualitatifs, que ceux quantitatifs (Tableau 1 ; Fig. 2), de sorte que nous attribuons le matériel subfossile à *M. petteri*. Des analyses au ^{14}C de deux spécimens de *M. petteri* récupérés dans les dépôts de la grotte indiquent des datations à 1760 ± 40 BP et 2480 ± 40 BP, qui correspondent à la période d'assèchement climatique du Sud de Madagascar [2].

Il existe une donnée ancienne rapportant une grande espèce de *Macrotarsomys* dans les dépôts subfossiles du Sud de Madagascar. Du matériel de membres de ce genre a été trouvé lors de fouilles d'un aven calcaire proche du lac Tsimanampetsotsa, dans l'extrême Sud-Ouest [23]. Trois gammes de taille avaient alors été rapportées, dont une série se rapportant à une espèce plus grande que *M. ingens* et considérée comme éteinte et nouvelle pour la science. Il existe une information se rapportant à la présence de *M. ingens* dans les dépôts subfossiles de la grotte d'Ankazoabo, au sud du lac Tsimanampetsotsa [5]. À partir d'une illustration publiée [23 (Fig. 4b)] et d'extrapolations d'ordre biogéographique, certains de ces spécimens se réfèrent à *M. petteri*. La découverte des ossements dans les dépôts de la grotte d'Andrahomana va dans le sens de cette conclusion.

Sur la base des éléments actuels, le matériel subfossile de *M. petteri* obtenu dans la grotte d'Andrahomana et d'autres sites de la partie méridionale de l'île se rapporte vraisemblablement à des populations éteintes datant de périodes géologiques récentes, lorsque le climat était plus humide et que la région présentait un biote assez différent.

Dans les dépôts d'Andrahomana, *M. petteri* est vraiment rare par rapport à l'espèce introduite par l'homme *Rattus rattus*. Il est possible que *M. petteri* ait pu être extrêmement vulnérable à un déplacement ou un

remplacement écologique par le rongeur introduit durant une période au cours de laquelle un assèchement climatique réduisait déjà son aire de distribution. Une relation a été proposée entre le déclin des rongeurs indigènes actuels et la pénétration de *R. rattus* dans les régions forestières les plus reculées de Madagascar [8]; les dépôts subfossiles d'Andrahomana documentent, pour la première fois, ce remplacement faunique dans un contexte géologique après colonisation par l'homme.

1. Introduction

On the basis of evidence from subfossil deposits, the modern Malagasy dry forest biomes, particularly those in the southern quadrant of the island, have undergone significant climatic change during the Quaternary. Evidence from subfossil pollen deposits, demonstrates that approximately 3,000–2,000 years ago the region underwent considerable desiccation [2], which included, for example, the drying-up of former freshwater lakes and the disappearance of a considerable portion of the associated bird fauna [10] and either local or complete extinction of several different groups of mammals [6, 9,18]. Most of the subfossil vertebrate material used in these studies came from excavations made during an earlier period of paleontological exploration of the island, largely prior to 1940, when stratigraphic control was not employed. Therefore, the sequence of events involving these extinctions and climatic vicissitudes are difficult to interpret. In recent years, more modern excavation techniques have been employed at a number of sites in southern Madagascar and herein we report on some new findings that provide a further window into understanding aspects of these climatic changes.

Excavations in 2003 of the subfossil deposits in Andrahomana Cave, located in extreme southeastern Madagascar (Fig. 1), have provided considerable new mammal material, including remains of small species. The cave, located just to the west of an extraordinarily abrupt ecotone between humid (east) and dry (west) biomes, contains deposits that provide an excellent faunistic barometer of the shifts in local biotic composition during periods of the Quaternary [13,28]. Amongst the recently recovered bone remains from the cave is a large species of rodent belonging to the genus *Macro-tarsomys*, which is part of an endemic radiation placed in the family Nesomyidae [17,19]. Until recently, the genus *Macro-tarsomys* was composed of two species, the diminutive kangaroo-rat-like *M. bastardi* (mean adult mass 24.5 g), which has a broad distribution

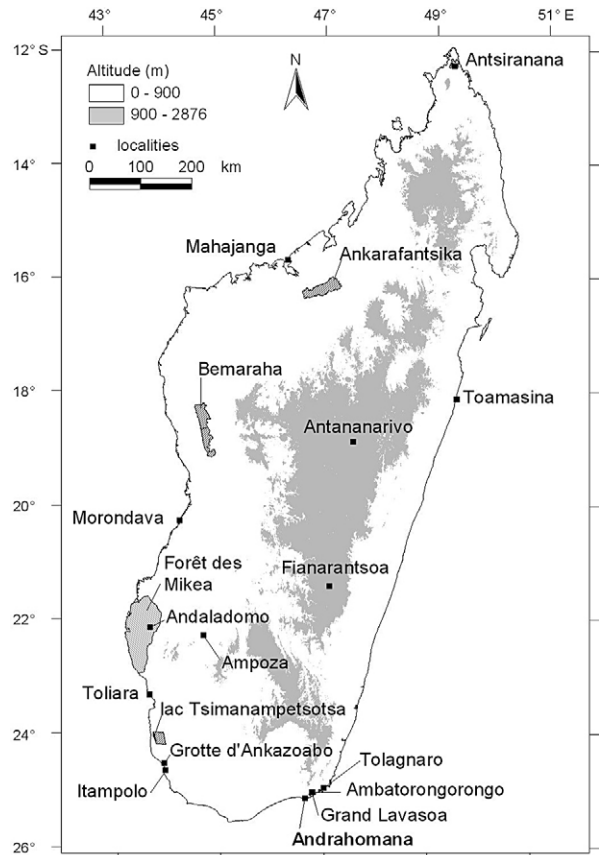


Fig. 1. Location of Andrahomana Cave and sites mentioned in the text.

Fig. 1. Localisation de la grotte d'Andrahomana et des sites mentionnés dans le texte.

across much of western and southern Madagascar, and the notably larger *M. ingens* (mean adult mass 64.4 g), which is believed to be limited to a small area of dry deciduous forest near Ankarafantsika in western central Madagascar [4,14] (Fig. 1). Recently, a third species was named for the genus, *M. petteri*, known from a single specimen collected in early 2003 in the Mikea Forest north of Toliara (Fig. 1) and that had a body mass of 105 g [11]. This latter species is distinguished from *M. ingens* by several external pelage and cranio-dental characteristics and measurements.

2. Materials and methods

2.1. Excavations

After surveying the Andrahomana Cave and digging a series of test pits to determine the locations of prior excavations, the group selected two undisturbed sites

for controlled excavation, AHA-I at the northernmost end of the main cave chamber, and AHA-F at the westernmost edge of the cave. AHA-F was situated beneath a raptor roost site, where a sinkhole in the cave ceiling resulted in the accumulation on the cave floor below of abundant small animal remains. At this site, we excavated a 2-m² area, using a soft brush, in measured increments to a depth of 50 cm. Between 20–50 cm, bone and shell density became quite low, though not entirely sterile. AHA-I was a much larger site containing both large and small vertebrate remains. At AHA-I, a grid system was laid over an area of 25 m², and 1-m² squares were excavated in layers, using a trowel and brush, and in sterile regions, a shovel. Beginning with our index square ‘A1’ located in the southwest corner of the site, squares were assigned numbers (2, 3, 4, etc.) to the north, and letters (B, C, D, etc.) to the east. Stratigraphy was recorded based on subtle changes in soil characteristics, which were then used to construct layers that were numbered from the surface downward. Sediment from both sites was dry-screened (1.5-mm mesh size), and bone, shell, seeds, and artifacts were bagged separately and labeled either by vertical depth in centimeters (AHA-F) or by square and layer (AHA-I). AHA-F appeared to be a relatively undisturbed deposit with intact stratigraphy. In contrast, there was no obvious vertical patterning to the deposits and AHA-I, and all sediments deeper than Layer 1 apparently belong to a single, vertically mixed deposit. Nonetheless, extinct taxa were recovered from AHA-I [7], and we therefore assume that AHA-I deposits accumulated over a significantly longer part of the Quaternary than at AHA-F. At both sites, bone preservation was very good and includes very fragile specimens.

2.2. Radiocarbon dating

Two bone samples from *Macrotarsomys petteri* from the AHA-I excavation were selected for ¹⁴C dating by Beta Analytic. Sample AHA-I-L6-CD1,2 was a mandible fragment from Layer 6, grid location near the corner formed by 1 m squares C1, D1, C2, and D2. Sample AHA-I-L1-CD3 was a mandible fragment from Layer 1, grid location along the edge of squares C3 and D3.

These samples (Lab numbers Beta-212738 and Beta-212739, respectively) were first crushed, then cold dilute HCl was repeatedly applied until the bone apatite fraction was eliminated. The collagen was then inspected for rootlets. None were present. The samples were pretreated with NaOH to ensure the absence of secondary organic acids. Graphite targets were made

from the collagen extract, and the carbon isotopes measured by Accelerator Mass Spectrometry. The results were corrected for isotopic fractionation to determine the conventional radiocarbon age, reported as mean ± 1σ yr BP (before present). These results were calibrated using the INTCAL 98 database [26] and reported as the 2σ calibrated range (cal yr AD or BC).

2.3. Morphometric analysis

In order to reach a conclusion about the specific identity of the bone remains of the large *Macrotarsomys* found amongst the Andrahomana subfossils, specimens of modern members of this genus housed in museum collections were examined. The acronyms of these institutions include: BMNH – The Natural History Museum [formerly British Museum (Natural History)] (London, UK), FMNH – Field Museum of Natural History (Chicago, USA) and UADBA – ‘Université d’Antananarivo, Département de biologie animale’ (Antananarivo, Madagascar).

Seven cranial and 10 dental measurements were taken using a digital caliper accurate to the nearest 0.1 mm, and for molar breadths to 0.01 mm. These measurements were chosen to maximize mensural comparisons that could be made between non-intact subfossil remains and modern specimens. Cranial and dental nomenclature follows Hershkovitz [16] and Voss [27]. Maxillary teeth are designated with an uppercase ‘M’ and superscript numbers and mandibular teeth with a lowercase ‘m’ and subscript numbers. Cranial measurements and their abbreviations (in parentheses) include: breadth of zygomatic plate (BZP) – the minimum distance from the anterior and posterior edges of the inferior zygomatic root; occlusal length of the maxillary molars (LMO) alveolar length of the maxillary molars (LMA) breadth of M¹ (BM¹) – measured across the widest portion of the protocone-paracone cusp pair on the first maxillary molar; breadth of M² (BM²) – measured across the widest portion of the protocone-paracone cusp pair on the second maxillary molar; breadth of M³ (BM³) – measured across the widest portion of the cusp on the third maxillary molar. Mandibular measurements and their abbreviations (in parentheses) include: symphysis-angular process (SAP) – measured from the alveolus of the incisor to posterior edge of angular process; symphysis-mandibular condyle (SMC) – measured from the alveolus of the incisor to posterior edge of mandibular condyle; incisor-mandibular condyle (IMC) – measured from the anterior edge of incisor to the posterior edge of the mandib-

ular condyle; constriction-molar (CONS) – the minimum distance from the constriction between the condyloid process and angular process to the leading edge of the first mandibular molar; symphysis-coronoid process (SCP) – measured from the alveolus of the incisor to posterior edge of coronoid process; incisor-coronoid process (ICP) – measured from the anterior edge of the incisor to posterior edge of coronoid process; occlusal length of the mandibular molars (LmO) alveolar length of the mandibular molars (LmA) breadth of m_1 (Bm_1) – measured across the widest portion of the hypocone-metacone cusp pair on the first mandibular molar; breadth of m_2 (Bm_2) – measured across the widest portion of the hypocone-metacone cusp pair on the second mandibular molar; breadth of m_3 (Bm_3) – measured across the widest portion of the cusp on the third mandibular molar. Only adults with the third molars fully erupted are used herein for comparative analyses.

3. Results

3.1. Provenance and dating

Material attributed to *Macrotarsomys petteri* was recovered in only one of the two excavated sites, AHA-I, the site with greater geological time depth. Remains of the introduced rodent, *Rattus rattus*, about the same body mass of *M. petteri*, were recovered at both sites, in addition to the diminutive commensal *Mus* and other native rodent taxa, including *Macrotarsomys bastardi* and *Eliurus myoxinus*. The relative proportions of *M. petteri* versus non-native human commensals (*Rattus* and *Mus*) are overwhelmingly in favor of the introduced species at every level (AHA-I).

Radiocarbon dating of the *Macrotarsomys petteri* samples from AHA-I shows the material was Late Holocene in age. The Layer-6 mandible (Beta-212738) was 1760 ± 40 yr BP (150–390 cal yr AD). The Layer 1 mandible (Beta-212739), from higher in the stratigraphy, was 2480 ± 40 yr BP (790–410 cal yr BC). These dates overlap a period of climatic desiccation in the region [2] and coincide with recent estimates for the earliest period of human activity on the island [3].

3.2. Morphometrics

As a caveat to the following morphometric comparisons, it is important to mention that only a single mod-

ern specimen of *M. petteri* is available and information on intraspecific variation in this taxon is lacking. Little variation was found in the quantitative and qualitative characters used herein for adult *M. ingens* ($n = 11$), and we presume that *M. petteri* shows a parallel pattern.

On the basis of osteological characters, a number of mensural and qualitative differences were found that clearly separate the large members of the genus *Macrotarsomys*, *M. petteri* and *M. ingens*, and these can also be recognized from the cranio-dental subfossil remains recovered from Andrahomana Cave. Qualitative adult characters in *M. petteri* that distinguish it from *M. ingens* include: mandible – the angular process terminates as a distinctly posteriorly curved and pointed structure, the capsular projection is prominent and forms a slightly pointed protuberance, the medial sulcus posterior to the capsular projection is distinctly less developed and does not extend as posterior along the ascending ramus, the inferior masseteric ridge is more prominent, and the mental foramen is centrally positioned on the ramus (as compared to dorsally) and more prominent; and cranial – the zygomatic plate is distinctly larger and the associated zygomatic notch open and rounded.

Several mensural characters show notable differences between *M. petteri* and *M. ingens*, with the former being larger (Table 1). Most notable in this regard are the symphysis-coronoid process (SCP) and incisor-coronoid process (ICP) lengths. Tooth-row lengths and molar breadths in the two species are notably similar to one another and in some cases overlap, with the exception of the third upper molar that is distinctly broader in *M. petteri*. In general, the configuration of the molar cusp structure is similar in the two species (Fig. 2).

Two different species of *Macrotarsomys* were recovered from the subfossil remains in Andrahomana Cave: the diminutive *M. bastardi*, which still occurs in the general region [4], and a much larger species. A comparison of the maxillary and mandibular subfossil material of the larger species to the two extant species (*M. petteri* and *M. ingens*) indicates that they fall within the range of variation of *M. petteri* for both the qualitative and quantitative characters (Table 1; Fig. 2), and we refer the subfossil specimens to *M. petteri*.

4. Discussion

Little is known about the natural history of *Macrotarsomys petteri*. The single specimen of an extant population was collected at Andaladomo within the Mikea Forest (Fig. 1). This region represents a zone

Table 1

Craniodontal measurements in millimeters of modern adult specimens of *Macrotarsomys petteri* ($N = 1$) and *M. ingens* (N as indicated) compared to subfossils referable to *Macrotarsomys* (n as indicated) from Andrahomana Cave

Tableau 1

Mesures craniodontaires en millimètres de spécimens adultes modernes de *Macrotarsomys petteri* ($n = 1$) et *M. ingens* (n comme indiqué), comparées à celles subfossiles référables à *Macrotarsomys* (n comme indiqué) de la grotte d'Andrahomana

Taxon	SAP	SMC	IMC	CONS	SCP	ICP	LmO	LmA	Bm ₁	Bm ₂	Bm ₃	BZP	LMO	LMA	BM ¹	BM ²	BM ³
<i>Macrotarsomys petteri</i>	21.7	23.9	27.5	11.7	19.0	22.2	5.3	5.4	1.44	1.56	1.19	4.1	5.2	5.5	1.51	1.42	1.31
<i>M. ingens</i>	19.0 ± 0.75	20.5 ± 0.48	24.0 ± 0.55	10.4 ± 0.50	15.6 ± 0.47	18.7 ± 0.44	4.9 ± 0.20	5.3 ± 0.21	1.29 ± 0.083	1.39 ± 0.055	1.13 ± 0.046	3.6 ± 0.29	4.5 ± 0.17	5.0 ± 0.28	1.47 ± 0.064	1.47 ± 0.081	1.08 ± 0.056
	18.0– 20.2	19.8– 21.2	23.2– 25.0	9.3– 11.0	14.7– 16.2	18.1– 19.5	4.7–5.2	5.0–5.6	1.08– 1.38	1.32– 1.49	1.05– 1.18	3.3– 4.1	4.3– 4.8	4.6– 5.4	1.32– 1.55	1.35– 1.61	0.98– 1.16
	$n = 11$	$n = 11$	$n = 10$	$n = 11$	$n = 11$	$n = 10$	$n = 11$	$n = 11$	$n = 11$	$n = 11$	$n = 11$	$n = 11$	$n = 10$	$n = 11$	$n = 11$	$n = 10$	$n = 10$
<i>Macrotarsomys large</i> subfossils		24.3 ± 1.05	27.3 ± 0.93	11.7 ± 0.44	19.6 ± 0.68	22.2 ± 0.40	5.5 ± 0.20	5.9 ± 0.29	1.40 ± 0.081	1.54 ± 0.038	1.24 ± 0.009	4.5 ± 0.34		5.8 ± 0.24	1.67 ± 0.083	1.56 ± 0.104	1.34 ± 0.052
	20.2– 21.5	22.1– 25.8	26.3– 28.8	10.9– 12.3	18.3– 20.1	21.6– 22.5	5.3–5.7	5.5–6.4	1.31– 1.54	1.50– 1.60	1.14– 1.41	4.1– 5.1	5.5	5.5– 6.3	1.53– 1.76	1.46– 1.68	1.28– 1.37
	$n = 2$	$n = 9$	$n = 6$	$n = 10$	$n = 6$	$n = 4$	$n = 3$	$n = 12$	$n = 6$	$n = 5$	$n = 8$	$n = 8$	$n = 1$	$n = 11$	$n = 8$	$n = 5$	$n = 6$



Fig. 2. **Top.** Left side of maxillary molar teeth (from left to right) of *Macrotarsomys petteri* (FMNH 176260, holotype) from the Mikea Forest, subfossil *M. petteri* (AHA-I, layer 4, cd 1,2) from Andrahomana Cave, and *M. ingens* (FMNH 156309) from the 'station forestière d'Ampijoroa'. **Mandible. Bottom.** Right side of mandibular molar teeth (from left to right) of *M. petteri* (FMNH 176260, holotype) from the Mikea Forest, subfossil *M. petteri* (AHA-I, layer 2, cd 3) from Andrahomana Cave, and *M. ingens* (FMNH 156309) from the 'station forestière d'Ampijoroa'. Fig. 2. **En haut.** Molaires maxillaires, côté gauche (de gauche à droite), de *Macrotarsomys petteri* (FMNH 176260, holotype) de la forêt de Mikea, subfossile *M. petteri* (AHA-I, étage 4, cd 1,2) de la grotte d'Andrahomana et *M. ingens* (FMNH 156309) de la station forestière d'Ampijoroa. **En bas.** Molaires mandibulaires, côté droit (de gauche à droite), de *M. petteri* (FMNH 176260, holotype) de la forêt de Mikea, subfossile *M. petteri* (AHA-I, étage 2, cd 3) de la grotte d'Andrahomana et *M. ingens* (FMNH 156309) de la station forestière d'Ampijoroa.

of transition between the spiny bush of the south and the dry deciduous forest of the central west. During the 2003 biological inventory of the Mikea Forest, six sites were visited and intensively surveyed, representing a range of different habitat types [22]. The forest of Andaladomo, which rests on red sandy soils, showed notable differences to the other five sites visited with regards to structural and floristic aspects – canopy reaching 20 m, relatively high densities of terrestrial (*Lissochilus*) and epiphytic (*Microcelia*) orchids, dense patches of grass, and a local vegetational community composed of mostly non-spiny plants.

There is previous evidence of a large species of *Macrotarsomys* in the subfossil record of southern Madagascar. Material of members of this genus was excavated from reputed Pliocene or Lower Pleistocene deposits in a cavity in karst limestone near Lake Tsimanampetsotsa in the extreme southwest [23]. Since no age measurements were performed however, the estimated age of this material was entirely conjectural. Three different size ranges of *Macrotarsomys* were reported: (1) *M. bastardi*, which is still extant in the region, (2) an unidentified species intermediate between *M. bastardi* and *M. ingens*, and (3) a species larger than

M. ingens that was considered extinct and new to science [23]. Further, there is a report of the occurrence of *M. ingens* in the subfossil deposits of the ‘grotte d’Ankazoabo’ [5]. Although we have not been able to examine the material collected at these sites referred to a large species of *Macrotarsomys*, based on the illustration in Sabatier & Legendre [23 (Fig. 4b)] and biogeographic inference, at least some of these specimens are almost certainly referable to *M. petteri*. The discovery of bone remains in the Andrahomana Cave deposits provides further support to this conclusion.

5. Deposition of material

On the basis of current knowledge, it is presumed that all three extant species of *Macrotarsomys* dig their terrestrial burrows into sandy ground [4] and except by chance would not venture into a cave. Diurnal birds of prey feed on *M. ingens* in the Ankarafantsika region [4] and these are presumed to be the Madagascar buzzard (*Buteo brachypterus*) or Madagascar harrier-hawk (*Polyboroides radiatus*). Both of these raptors can frequent rock outcrops and cave entrances; both are broadly distributed in southeastern Madagascar [13]. At roost sites, these predators dismantle prey, which can accidentally drop to the ground uneaten, and regurgitate ingested bone remains in the form of pellets. There is also evidence that the barn owl (*Tyto alba*) and Boidae snakes of the genera *Boa* and *Acrantophis* feed on *M. ingens* [21] – both of these groups of predators can frequent caves. Bone fragments of *M. ingens* have been found in the scats of the native Carnivora *Cryptoprocta ferox* and the introduced *Viverricula indica* [21]. Given the relatively intact state of the *Macrotarsomys* specimens recovered in the Andrahomana Cave deposits, we presumed that the majority of the remains, from both excavated sites, were left behind by raptors either in the form of dropped prey remains or regurgitated pellets. The stratigraphic reversal apparent in the dates presented confirms the excavators’ impression that material in this site has been stratigraphically mixed by some process, probably redeposition.

6. Does *Macrotarsomys petteri* still occur in the region?

During the course of the 2003 biological inventories of the Mikea Forest, where the holotype of *M. petteri* was captured, 3100 trap-nights (1 trap in place for 24 h = 1 trap-night) in total were accrued at six different

sites [24]. A single specimen of this taxon was captured at Andaladomo, a forest block with distinctly more mesic vegetation than the other five sites surveyed. Without more detailed and long-term inventories in the Mikea Forest, it cannot be discerned if this species occurs elsewhere in the region. What is apparent is that at Andaladomo, this species is uncommon or at least difficult to capture. Something on the order of 15 other sites have been surveyed for small mammals in southern dry forest or spiny bush forests, using the same field techniques as in the Mikea Forest, and no evidence of an extant large species of *Macrotarsomys* has been found. Our assumption is that *M. petteri* has a very restricted range within the Mikea Forest and continued habitat destruction in this region [1] has serious implications for the long-term viability of this species.

It is conceivable that *M. petteri* still occurs in the extreme South of Madagascar in pockets of forest with more mesic vegetation and with sandy or relatively soft substrates – based on the needed soil type for burrow construction. To the east of Andrahomana Cave there are the sites of Grand Lavasoa and Ambatorongorongo (also known as Ambatotsirongorongo) with remnant natural forests that show mixed humid, spiny and littoral forest floristic and faunistic composition [15,20]. These two sites were inventoried for small mammals in early 2005 by Zafimahery Rakotomalala and Vonjy Andrianjakarivelo and, based on collected specimens (in FMNH and UADBA), there is no evidence of *M. petteri* occurring locally. Virtually all of the native species they captured at these sites are typical of the southern spiny bush, although within their collections there is the Tenrecidae *Oryzorictes hova*, a species typical of mesic habitat.

Based on current evidence, the subfossil material of *M. petteri* recovered from Andrahomana Cave and other sites in the southern portion of the island represent extinct populations, dating from recent geological periods when the climate was more mesic and the region had a distinctly different biota. The absence of *M. petteri* from AHA-F at Andrahomana, a site with shallow time depth, provides further support that this animal may have been locally extinct for several hundred years, a point corroborated by our radiocarbon dates. Given the relative rarity of *M. petteri* at AHA-I compared with *Rattus rattus*, the possibility exists that *M. petteri* may have been particularly vulnerable to ecological displacement or replacement by this introduced rodent during a time period when climatic desiccation was also reducing its geographic range. Extreme disproportionate numbers of *Rattus rattus* versus native ende-

mic rodent taxa have been reported in extant forest rodent communities [12,14], and a connection has been suggested between the decline of the extant native animals and the penetration of *R. rattus* into even very remote forested regions of Madagascar [8]. The subfossil deposits from Andrahomana document, for the first time, this pattern of faunal turnover within a recent geological context following human settlement.

There are other parallels amongst extant Malagasy mammals to the marked range contraction found in *M. petteri* over the past few thousand years. The endemic rodent *Hypogeomys antimena*, which reaches an adult body mass of over 1 kg, once had a broad distribution in southwestern Madagascar [9]. The only extant population occurs in the Menabe region near Morondava and this species is threatened with extinction that appears to be in part associated with habitat destruction [25]. Subfossil material of this species from Ampoza (Fig. 1) was radiocarbon dated to 1350 ± 60 BP (Beta-72676) [9]. A second species, *H. australis* that was larger than *H. antimena*, has been recorded in Andrahomana Cave, but is now extinct across its former range [9]. Two radiocarbon dates are available for this taxon from the site: 4440 ± 60 BP (Beta-73370) and 1536 ± 35 BP (NZA-18996, R-28421/1) [3,9]. These data indicate that both taxa occurred in southern Madagascar until relatively recent times.

On the basis of these examples, different rodent species once occurred across the southern portion of the island, presumably in distinctly more mesic conditions than found today. As the region experienced aridification over the past few thousand years and local natural forest conditions changed, there was a notable contraction of their ranges. In some cases, remnant populations occur in western forests (*H. antimena* and *M. petteri*) and in at least one case a taxon is completely extirpated (*H. australis*). Certainly human modifications of the remaining forests in the core area of these species' ranges have added to their decline, and another important factor may have been the ecological success of introduced rodents. If the temporal scenarios postulated here are correct, the remnant populations of *M. petteri* and *H. antimena* are living relicts of a recent period when southern Madagascar had moister conditions.

Acknowledgements

For access to modern specimens of *Macrotarsomys* we are grateful to Prof. Daniel Rakotonirainy and Voahangy Randrianjafy (UADBA) and to Paula Jenkins (BMNH). Zafimahery Rakotomalala and Vonjy

Andrianjakarivelo made available small mammal collections from sites near Andrahomana Cave. For assistance with sorting the faunal remains from Andrahomana, we thank Heather Drought. Lucienne Wilmé prepared Fig. 1 and helped with the translation of text into French, and Rebecca Kramer prepared Fig. 2. The 2003 Andrahomana expedition was supported by NSF BCS-0129185 to DAB, Laurie Godfrey, and William Jungers, and a College of Liberal Arts and Sciences Research Stipend from Portland State University to NV. DAB and NV especially thank those who participated in their 2003 field work, including Laurie Godfrey, William Jungers, Ramilisonina, Mirya Ramarolahy, Leslie Seltzer, and Lydia Raharivony. This work was conducted under collaborative agreements with the 'Département de paléontologie et d'anthropologie biologique, université d'Antananarivo', and the 'Académie malgache'.

References

- [1] C. Blanc-Pamard, P. Milleville, M. Grouzis, F. Lasry, S. Razanaka, Une alliance de disciplines sur une question environnementale : la déforestation en forêt des Mikea (Sud-Ouest de Madagascar, Nat. Sci. Soc. 13 (2005) 7–20.
- [2] D.A. Burney, Late Holocene environmental changes in arid southwestern Madagascar, Quat. Res. 40 (1993) 98–106.
- [3] D.A. Burney, L.P. Burney, L.R. Godfrey, W.L. Jungers, S.M. Goodman, H.T. Wright, A.J.T. Jull, A chronology for late Prehistoric Madagascar, J. Hum. Evol. 47 (2004) 25–63.
- [4] M.D. Carleton, S.M. Goodman, *Macrotarsomys*, big-footed mice, in: S.M. Goodman, J.P. Benstead (Eds.), The natural history of Madagascar, The University of Chicago Press, Chicago, 2003, pp. 1386–1388.
- [5] C. Chanudet, Conditions géographiques et archéologiques de la disparition des subfossiles à Madagascar, mémoire de maîtrise, université de Bretagne occidentale, Brest, France, 1975.
- [6] L.R. Godfrey, W.L. Jungers, E.L. Simons, P.S. Chatrath, B. Rakotosamimanana, Past and present distributions of lemurs in Madagascar, in: B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn, S.M. Goodman (Eds.), New directions in lemur studies, Kluwer Academic, Plenum, New York, 1999, pp. 19–53.
- [7] L.R. Godfrey, W.L. Jungers, D.A. Burney, N. Vasey, W. Ramilisonina, P. Wheeler, L.J. Lemelin, G.T. Shapiro, S. Schwartz, J. King, M.F. Ramarolahy, L.L. Raharivony, G.F.N. Randria, New discoveries of skeletal elements of *Hadropithecus stenognathus* from Andrahomana Cave, southeastern Madagascar, J. Hum. Evol. 51 (2006) 395–410.
- [8] S.M. Goodman, *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna, Conserv. Biol. 9 (1995) 450–453.
- [9] S.M. Goodman, D. Rakotonirainy, The Holocene distribution of *Hypogeomys* (Rodentia: Muridae: Nesomyinae) on Madagascar, in: W.R. Lourenço (Ed.), Biogéographie de Madagascar, ORSTOM, Paris, 1996, pp. 283–293.
- [10] S.M. Goodman, L.M.A. Rakotozafy, Subfossil birds from coastal sites in western and southwestern Madagascar: A

- paleoenvironmental reconstruction, in: S.M. Goodman, B.D. Patterson (Eds.), *Natural change and human impact in Madagascar*, Smithsonian Institution Press, Washington, D.C., 1997, pp. 257–279.
- [11] S.M. Goodman, V. Soarimalala, A new species of *Macrotarsomys* (Rodentia: Muridae: Nesomyinae) from southwestern Madagascar, *Proc. Biol. Soc. Wash.* 118 (2005) 450–464.
- [12] S.M. Goodman, A. Andrainarimisa, L.E. Olson, V. Soarimalala, Patterns of elevational distribution of birds and small mammals in the humid forests of Montagne d’Ambre, Madagascar, *Eotropica* 2 (1996) 87–98.
- [13] S.M. Goodman, M. Pidgeon, A.F.A. Hawkins, T.S. Schulenberg, The birds of southeastern Madagascar, *Fieldiana: Zool. N. Ser.* 87 (1997) 1–132.
- [14] S.M. Goodman, J.U. Ganzhorn, D. Rakotondravony, Introduction to the mammals, in: S.M. Goodman, J.P. Benstead (Eds.), *The natural history of Madagascar*, University of Chicago Press, Chicago, 2003, pp. 1159–1190.
- [15] A. Hapke, J. Fietz, S.D. Nash, D. Rakotondravony, B. Rakotosamimanana, J.-B. Ramanamanjato, G.F.N. Randria, H. Zischler, Biogeography of dwarf lemurs: Genetic evidence for unexpected patterns in southeastern Madagascar, *Int. J. Primatol.* 26 (2005) 873–901.
- [16] P. Hershkovitz, Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group, *Fieldiana Zool.* 46 (1962) 1–524.
- [17] S.A. Jansa, M.D. Carleton, Systematics and phylogenetics of Madagascar’s native rodents, in: S.M. Goodman, J.P. Benstead (Eds.), *The natural history of Madagascar*, The University of Chicago Press, Chicago, IL, USA, 2003, pp. 1257–1267.
- [18] R.D.E. MacPhee, Morphology, adaptations, and relationships of *Plesiorcycteropus*, and a diagnosis of a new order of eutherian mammals, *Bull. Am. Mus. Nat. Hist.* 220 (1994) 1–214.
- [19] G.G. Musser, M.D. Carleton, Superfamily Muroidea, in: D.E. Wilson, D.M. Reeder (Eds.), *Mammal species of the World*, The Johns Hopkins University Press, Baltimore, 2005, pp. 894–1531.
- [20] J.-B. Ramanamanjato, P.B. McIntyre, R.A. Nussbaum, Reptile, amphibian, and lemur diversity of the Malahelo Forest, a biogeographical transition zone in southeastern Madagascar, *Biodivers. Conserv.* 11 (2002) 1791–1807.
- [21] R.V. Randrianjanfy, Contribution à l’étude de biologie de conservation de la communauté micromammalienne d’Ankarafantsika, thèse de 3^e cycle, université d’Antananarivo, Antananarivo, 2003.
- [22] A.P. Raselimanana, S.M. Goodman (Eds.), Inventaire floristique et faunistique de la forêt de Mikea : paysage écologique et diversité biologique d’une préoccupation majeure pour la conservation, Centre d’information et de documentation scientifique et technique, recherches pour le développement, *Ser. Sci. Biol.* 21 (2004) 1–105.
- [23] M. Sabatier, S. Legendre, Une faune à rongeurs et chiroptères plio-pléistocènes de Madagascar, Actes du 110^e Congrès national des sociétés savantes, Montpellier, section des sciences 6 (1985) 21–28.
- [24] V.R.L. Soarimalala, S.M. Goodman, Les Rodentia, Lipotyphla et Carnivora de la forêt de Mikea, A.P. Raselimanana, S.M. Goodman (Eds.), Inventaire floristique et faunistique de la forêt de Mikea : paysage écologique et diversité biologique d’une préoccupation majeure pour la conservation, Centre d’information et de documentation scientifique et technique, recherches pour le développement, *Ser. Sci. Biol.* 21 (2004) 69–80.
- [25] S. Sommer, A. Toto Volahy, U.S. Seal, A population and habitat viability assessment for the highly endangered giant jumping rat (*Hypogeomys antimena*), the largest extant endemic rodent of Madagascar, *Anim. Conserv.* 5 (2002) 263–273.
- [26] M. Stuiver, P.J. Reimer, E. Bard, J.W. Beck, G.S. Burr, K.A. Hughen, B. Kromer, F.G. McCormac, J. van der Plicht, M. Spurk, *INTCAL98 ¹⁴C, Radiocarbon* 40 (1998) 1041–1083.
- [27] R.S. Voss, Systematics and ecology of ichthyomyine rodents (Muroidea): Patterns of morphological evolution in a small adaptive radiation, *Bull. Am. Mus. Nat. Hist.* 188 (1988) 259–493.
- [28] A.C. Walker, Locomotor adaptation in Recent and fossil Madagascar lemurs, PhD thesis, University of London, 1967.