Description of a new species of subfossil shrew tenrec (Afrosoricida: Tenrecidae: *Microgale*) from cave deposits in southeastern Madagascar

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Abstract.—A new species of shrew tenrec, *Microgale macpheei*, is described from subfossil deposits in Andrahomana Cave, extreme southeastern Madagascar. This species is distinguished from all named taxa of *Microgale* by a variety of osteological, dental, and mensural characters. It is presumed to be the sister taxon to the extant species *M. brevicaudata*, which is not known to occur in southeastern Madagascar. Although the genus contains well over 20 living species, *M. macpheei* is the first known extinct shrew tenrec in the Quaternary fauna of Madagascar.

Résumé.—Une nouvelle espèce de microgale, *Microgale macpheei*, trouvée dans les dépôts subfossiles de la grotte d'Andrahomana, dans l'extrême sud de Madagascar, est décrite. Cette espèce se distingue de tous les taxons nommés dans ce genre par divers caractères portant sur l'ostéologie, la dentition et les mesures. Elle semble montrer des affinités avec l'espèce actuelle *M. brevicaudata* qui n'est pas connue du sud-est de Madagascar. Bien que le genre soit représenté par bien plus de 20 espèces vivantes, la description de *M. macpheei* constitue la première évidence d'un microgale éteint dans la faune du Quaternaire de Madagascar.

Over the past 15 yr, numerous investigations have been conducted on lemur bones found at paleontological sites across the currently drier biomes of Madagascar. Research on these subfossil remains has provided a window into the magnitude of shifts in primate species richness and associated extinction levels (e.g., Godfrey et al. 1999), changes in community structure and potential ecological functioning (e.g., Godfrey & Jungers 2002), and the continuing debate over the role of human-induced versus natural changes in the origin of these ecological vicissitudes and extinction events (Burney et al. 2004). To a large extent, non-primate mammalian remains from Malagasy paleontological deposits have remained unstudied, although there are exceptions (Stuenes 1989, MacPhee 1994, Goodman & Rakotondravony 1996, Burney et al. 1997, Goodman et al. 2006). Coinciding with the renaissance of subfossil lemur work on Madagascar has been a revitalization of biological inventories examining the island's small mammals, which has provided new insight into the origin, species diversity and species limits, and distribution of this fauna (Goodman et al. 2003). These

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faunal surveys have resulted in the collection of new osteological material from a wide variety of small mammals that provides the necessary comparative foundation to advance studies of subfossils.

Among the small mammals of Madagascar, there is a remarkable adaptive radiation of Afrosoricida (sensu Bronner & Jenkins 2005), that were formerly placed in the Order Insectivora and more recently in the Order Lipotyphla (Olson & Goodman 2003); many of which resemble small insectivorous shrews. The most diverse genus of afrosoricidans on the island is *Microgale*, also known as the shrew tenrecs, for which 22 species, all endemic, are currently recognized (Jenkins 2003, Goodman & Soarimalala 2004, Olson et al. 2004, Goodman et al. 2006). Recent exploration of the dry forests of western and southern Madagascar revealed several previously undescribed taxa with rather limited geographical ranges (Jenkins & Goodman 1999, Goodman & Soarimalala 2004). Ongoing research using molecular and morphological data indicates that there are cryptic species of *Microgale* that need to be named or resurrected from synonymy. For example, *M. brevicaudata* G. Grandidier, 1899, a species found in the dry western biomes and a narrow band in the humid forest biome, is composed of a complex of at least two species that occur in allopatry (Olson & Goodman pers. obs.).

In 2000 and 2003, expeditions organized by DAB carried out excavations in Andrahomana Cave in extreme southeastern Madagascar (Fig. 1), where subfossil collections had previously been made by Sikora in 1899, Alluaud in 1900–1902, Geay in 1906, Decary in 1926, and Walker in 1966 (Walker 1967). Among the specimens recovered during the 2003 excavations are bones of small mammals, including a few cranial elements of *Microgale* that cannot be
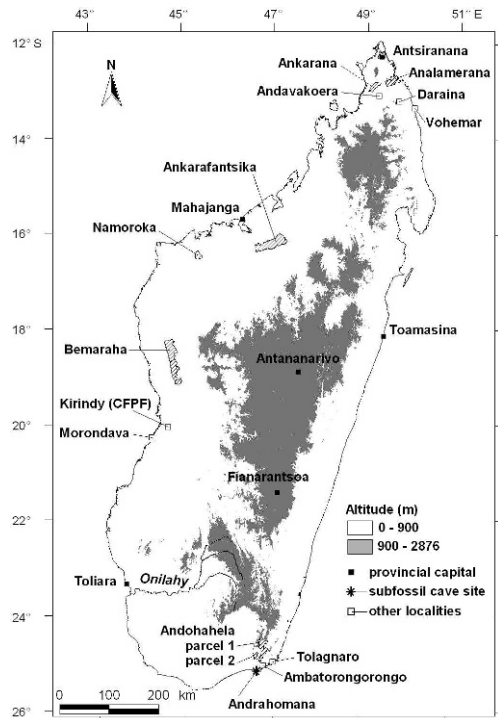

Fig. 1. Location of Andrahomana Cave and sites mentioned in the text.

assigned to any known taxon and that are described here as a new species.

Materials and Methods

Cave site and subfossil specimens.—In 2003, after surveying Andrahomana Cave (Fig. 1) and digging a series of test pits to determine the locations of prior excavations, the field team selected two undisturbed sites for controlled excavations, 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, where an opening in the cave ceiling resulted in the accumulation of abundant small animal remains on the cave floor below. At this site, a 2 m^2 area was excavated. AHA-I was a much larger site, containing both large and small vertebrate remains; a grid system was laid over an area of 25 m^2, and 1 m^2 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 define layers that were numbered from the surface downward. Sediment from both sites was dry-screened, and bone, shell, seeds, and artifacts were bagged separately and labeled either by vertical depth in cm (AHA-F) or by square and layer (AHA-I). There was no obvious vertical patterning to the deposits in 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 (Godfrey et al. 2006), and we, therefore, assume that AHA-I deposits accumulated over a significantly longer part of the Quaternary than at AHA-F, where no extinct taxa have been identified. At both sites, even fragile specimens are well preserved. The subfossil specimens of *Microgale* were found as isolated non-articulated bones and in no case were there clearly associated cranial and mandibular elements. A number of *Microgale* mandibular and postcranial elements were recovered from AHA-I, which cannot be confidently identified to species.

Specimens and measurements.—Extensive osteological collections of Malagasy small mammals at the Field Museum of Natural History (FMNH) were supplemented by specimens from the Museum of Comparative Zoology (MCZ), Harvard University, and the Muséum national d'Histoire naturelle (MNHN), Paris. The holotype (MCZ 45047) of *Paramicrogale occidentalis* Grandidier & Petit, 1931 [=*Microgale brevicaudata* (MacPhee, 1987)] from central western Madagascar was examined and associated drawings (MacPhee 1987, Fig. 5) were

compared with the Andrahomana Cave subfossils. The holotype of *M. brevicaudata* is from a humid forest zone south of Vohemar. Tooth abbreviations include: C = canine, P = premolar, and M = molar. Upper case tooth abbreviations with superscript are used for upper teeth and lower case abbreviations with subscript for lower teeth. Nomenclature of patterns of tooth eruption and cranial and dental morphology follow Hershkovitz (1977) and MacPhee (1987).

MacPhee's (1987) revision of the genus *Microgale* is important for clarifying morphological differences in the deciduous and permanent dentitions in species of shrew tenrecs, which had been confused by numerous taxonomists for nearly a century. We used MacPhee's ontogenetic stages 1 through 4 to determine the relative age of specimens of *Microgale*, in which the permanent molars erupt and are functional before the deciduous antemolar dentition begins to be replaced. *Microgale* specimens used in this study were all at stage 3 or 4 and those of *M. brevicaudata* are listed in Appendix 1. Most direct comparisons to the subfossils of *M. brevicauadata* included both sexes and were based on specimens collected in the southern portion of the species' range; the limited number does not allow for proper assessment of sexual dimorphism in this species.

The following measurements were made with dial calipers from both the subfossil and modern specimens (all in mm): width P^3 = greatest breadth across P^3 from the lateral-most surface of the ectostyle to the lingual-most portion of tooth, including the lingual ledge when present; width P^4 = greatest breadth across P^4 from the lateral-most surface of the ectostyle to the lingual-most portion of the lingual ledge; width M^2 = greatest breadth across M^2 from the lateral-most surface of the ectostyle to the lingual-most portion of the lingual ledge; width M^3 = greatest breadth across
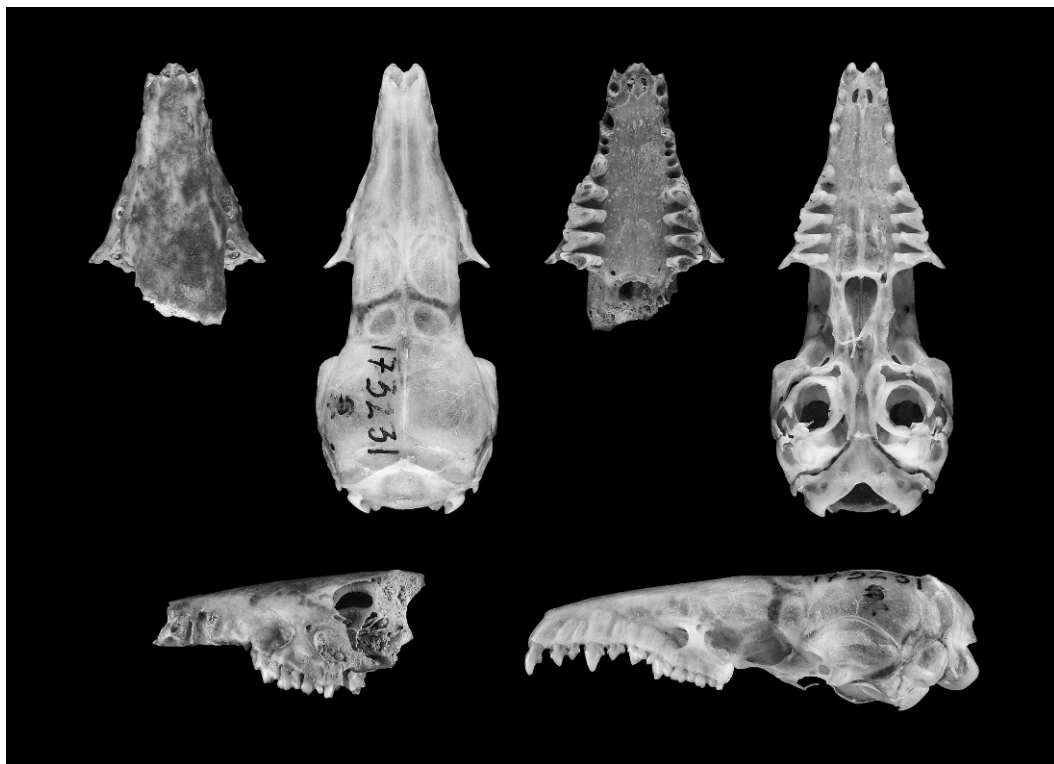
Fig. 2. Dorsal, ventral, and lateral views of adult crania of *Microgale* spp. Left, holotype of subfossil *M. macpheei* (FMNH 191249) from Andrahomana Cave (AHA-I, Layer 4, Square E3); right *M. brevicaudata* (FMNH 173231) from Sept Lacs, to the east of Toliara.

M^3 from the lateral-most surface of the ectostyle to the lingual-most portion of the lingual ledge; width M^4 = greatest breadth across M^4 from the lateral-most surface of the anterior ectostyle to the lingual-most portion of the lingual ledge; palatal length: the length from the posterior portion of the anterior palatine foramen to the posterior medial edge of the palatine; zygomatic breadth = greatest distance across the lateral-most portion of the zygomatic arches; upper molar toothrow = greatest length from the mesiostyle of M^2 to the distostyle of M^4.

Systematic Paleontology
Family Tenrecidae
Genus *Microgale* Thomas, 1882

The new species and *Microgale brevicaudata* differ from all other valid species of *Microgale* in having the rostrum differently shaped, shorter and blunt, and in the absence of a marked upper premolar diastema. In the post-P^3 dentition, the mesiostyle and distostyle in *M. brevicaudata* and *M. macpheei* are relatively small compared with most other species of *Microgale*.

Microgale macpheei, new species
Figs. 2–4, Table 1

Holotype.—FMNH 191249, partial cranium lacking the portion including and posterior to the parietal. Most of the rostrum is complete but lacks the incisors, canines, and the first premolars (P^2). P^3 and P^4 are present, the former only on the right side. There is no evidence of any ongoing tooth replacement and the specimen appears to have had all of its permanent teeth.
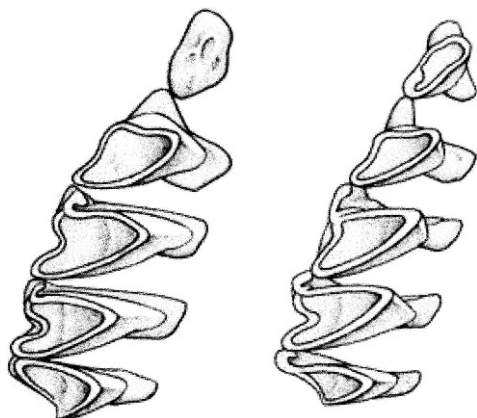
Fig. 3. Ventral view of right molariform tooth-rows in *Microgale* spp. Left, holotype of subfossil *M. macpheei* (FMNH 191249) from Andrahomana Cave (AHA-I, Layer 4, Square E3); right *M. brevicaudata* (FMNH 173231) from Sept Lacs, to the east of Toliara.

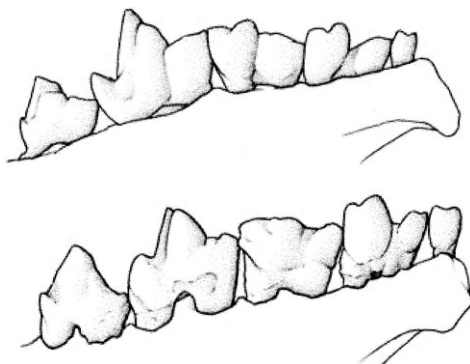Fig. 4. Labial view of right toothrow in *Microgale* spp. Top, holotype of subfossil *M. macpheei* (FMNH 191249) from Andrahomana Cave (AHA-I, Layer 4, Square E3); bottom *M. brevicaudata* (FMNH 173231) from Sept Lacs to the east of Toliara.

Measurements of holotype.—Width P^3 0.73 mm, width P^4 1.78 mm, width M^2 2.15 mm, width M^3 2.28 mm, width M^4 2.00 mm, palatal length 9.4 mm, zygomatic breadth 8.6 mm, and upper molar toothrow 3.0 mm.

Type locality.—Andrahomana Cave (25°11′55″S, 46°37′59″E), in extreme southeastern Madagascar.

Stratigraphic position and associated chronology.—The specimen was excavated on 2 July 2003 from site AHA-I, Layer 4, Square E3.

Paratype.—FMNH 191250, partial cranium lacking the portion including and posterior to the parietal. Most of the rostrum is complete but lacks the incisors, canines, and the first premolars (P^2). The left molar toothrow is broken away at the level of the palatine. There is no evidence of any ongoing tooth replacement and the specimen appears to have all of its permanent teeth. This specimen was recovered in Andrahomana Cave at site AHA-I, Layer 3, Squares CD 1,2.

Etymology.—Named after Ross D. E. MacPhee of the American Museum of Natural History, New York, for his

important contributions to understanding systematics and tooth eruption patterns and ontogeny in *Microgale*, as well to the Quaternary paleontology of Madagascar.

Diagnosis.—The rostrum in *Microgale macpheei* shows only a slight anterior mediolateral tapering to the level of the canine and terminates as a blunt-shaped muzzle (Fig. 2), whereas both sexes of *M. brevicaudata* display a notable anterior tapering of the muzzle, starting at the level of P^3 and ending as a slightly pointed and flat structure. The shape and size of the alveoli in the holotype of *M. macpheei* indicate that this species had a notably more robust dentition than *M. brevicaudata*, as emphasized by the last premolar (P^4) and molars, which are larger and heavier in general shape, and have broader occlusal surfaces and lingual ledges than in *M. brevicaudata* (Fig. 3). There is no notable diastema in *M. macpheei* between the premolars or their exposed roots.

Microgale macpheei is distinguished from *M. brevicaudata* by the shape and form of P^3, which in the latter possesses a distinct lingual extension of the protocone forming a reduced lingual ledge that is present in both adults (stages 3 and 4) and younger (stages 1 and 2) individuals.

Table 1.—Selected measurements (in mm) of *Microgale macpheei* and *M. brevicaudata* based on age classes following the system of MacPhee (1987). Sample statistics include the mean ± one standard deviation, the observed range of measurements, and sample size (n).

	Width P³	Width P⁴	Width M²	Width M³	Width M⁴	Palatal length	Zygomatic breadth	Upper molar toothrow
Subfossil								
M. macpheei								
Holotype (FMNH 191249)	0.73	1.78	2.15	2.28	2.00	9.4	8.6	3.0
Paratype (FMNH 191250)	0.75	1.73	2.02	2.14	1.91	9.7	—	3.0
Southern								
M. brevicaudata								
Age classes 3–4	0.62 ± 0.11 0.53–0.77 n = 4	1.48 ± 0.15 1.26–1.60 n = 4	1.76 ± 0.07 1.68–1.83 n = 4	1.89 ± 0.12 1.78–2.06 n = 4	1.74 ± 0.12 1.63–1.88 n = 4	8.1 ± 0.46 7.8–8.8 n = 4	7.8 ± 0.38 7.4–8.1 n = 3	2.7 ± 0.05 2.6–2.7 n = 4
Age classes 1–1	0.73 ± 0.07 0.64–0.82 n = 4	1.19 ± 0.04 1.14–1.24 n = 4	1.68 ± 0.02 1.66–1.71 n = 4	1.79 ± 0.10 1.64–1.89 n = 4	1.73 ± 0.09 1.64–1.82 n = 4	7.7 ± 0.44 7.2–8.2 n = 4	7.5 ± 0.30 7.2–7.9 n = 4	2.6 ± 0.24 2.3–2.8 n = 4
Western								
M. brevicaudata								
Age classes 3–4	0.68 ± 0.09 0.57–0.79 n = 4	1.29 ± 0.12 1.22–1.47 n = 4	1.56 ± 0.15 1.47–1.78 n = 4	1.68 ± 0.19 1.43–1.90 n = 4	1.83 ± 0.07 1.75–1.90 n = 4	7.6 ± 0.92 7.1–9.0 n = 4	7.9 ± 0.43 7.3–8.3 n = 4	2.6 ± 0.17 2.4–2.8 n = 4
Age classes 1–2	0.86 ± 0.05 0.80–0.93 n = 6	1.33 ± 0.11 1.20–1.46 n = 5	1.77 ± 0.06 1.72–1.86 n = 6	1.88 ± 0.07 1.80–1.96 n = 6	1.75 ± 0.06 1.68–1.82 n = 6	8.4 ± 0.29 8.0–8.7 n = 6	7.5 ± 0.13 7.4–7.7 n = 5	2.7 ± 0.14 2.5–2.9 n = 6

In *M. macpheei*, P³ lacks an elongated extension of the protocone and is distinctly peg-like in shape (Fig. 3). In *M. macpheei*, the lingual extension of the protocone in P⁴ to M³ is greatly reduced and oriented perpendicular to the main axis of the skull and the paracone is notably less prominent than in *M. brevicaudata*. The anterior portion of the P⁴ ectostyle in *M. macpheei* is notably more pronounced than in *M. brevicaudata* (Fig. 4) and is in close association with the anterior portion of the paracone, forming a distinct large cusp-like structure. P⁴ is a notably large and stocky tooth with an angular mesiostyle, well-developed anterior buccal cleft, and a rectangular lingual ledge. M¹ and M² in *M. macpheei* are relatively broad along the buccal edge with prominent ectostyles and distostyles, but with much reduced mesiostyles, and the lingual ledge is a rectangular structure. In *M. macpheei*, the anterior limit of the ectostyle of M³ occurs more medially than the distostyle of M², whereas in *M. brevicaudata* these two styles are nearly of equal length or the anterior limit of the ectostyle of M³ occurs more laterally than the distostyle of M².

Most of the measurements of *M. macpheei* fall outside the range of *M. brevicaudata* (Table 1). In seven of the eight variables, the holotype and paratype have measurements greater than the maximum measurements of *M. brevicaudata*. But because of the small sample sizes only four of the variables show statistical differences (*t*-tests) between the species: width M² ($t = 2.78$, $df = 4$, $P = 0.0009$), width M³ ($t = 2.78$, $df = 4$, $P = 0.03$), palatal length ($t = 2.78$, $df = 4$, $P = 0.02$), and upper molar toothrow ($t = 2.78$, $df = 4$, $P = 0.0009$).

Discussion

Three species of *Microgale* had been described previously from subfossil cave material, much of which was probably deposited as regurgitated pellets of raptors occupying the sites. *Microgale breviceps* Kaudern (1918) described on two mandibular rami from a cave near Mahajanga was subsequently synonymized with *M. brevicaudata* by MacPhee (1987). *Microgale decaryi* Grandidier (1928) described from a partially damaged skull with a few teeth recovered from the Andrahomana Cave by R. Decary in 1926 was synonymized by MacPhee (1987) with the living species, *M. principula* Thomas, 1926. *Cryptogale australis* Grandidier, 1928, described based on skulls from Andrahomana Cave was synonymized by Heim de Balsac (1972) with the extant *Geogale aurita* Milne-Edwards & Grandidier, 1872. This latter species is well represented in the bone remains recovered in the cave.

The *Microgale brevicaudata* group (sensu MacPhee 1987), including *M. macpheei*, has a broad distribution across portions of the island that encompasses several different biomes. *Microgale brevicaudata*, as it is currently defined, has been documented in the humid lowland forests of northeastern Madagascar (where the holotype is from), as far south as the Masoala Peninsula, to transitional forests of the Vohemar and Daraina regions, north to areas surrounding Antsiranana (e.g., Analamerana, Ankarana, and Andavakoera), and then south in the western lowlands through the deciduous forest (e.g., Namoroka, Bemaraha, and Kirindy (CFPF) (Goodman et al. 2003, Soarimalala & Goodman 2003, Andrianjakarivelo et al. 2005, S. M. Goodman pers. obs.; Fig. 1). The known southern limit of *M. brevicaudata* in southwestern Madagascar is the northern bank of the Onilahy River in riverine dry forest habitat (Emmett et al. 2003, S. M. Goodman pers. obs.). Several small mammal inventories have been conducted in spiny bush habitat in the extreme southern portion of Madagascar and no

evidence of this species has been found (e.g., Goodman et al. 1999). Thus, there is no known extant population of *M. brevicaudata* in the dry extreme southern portion of the island.

We do not have a radiocarbon date for specimens of *M. macpheei* but two dates are available for the rodent *Macrotarsomys petteri* Goodman & Soarimalala, 2005, from AHA-I (Goodman et al. 2006), from the same site in which the holotype (Layer 4) and paratype (Layer 3) of *Microgale macpheei* were collected. These include a mandible recovered in Layer 6 (Beta-212738) that yielded the date of 1760 ± 40 yr BP (150–390 cal yr AD) and another mandible from Layer 1 (Beta-212739) at 2480 ± 40 yr BP (790–410 cal yr BC). These dates overlap with a period of climatic desiccation in the region (Burney 1993) and coincide with recent estimates for the earliest period of human activity on the island (Burney et al. 2004).

Among the subfossil small mammals recorded in the Holocene deposits of Andrahomana Cave is an extinct rodent, *Hypogeomys australis* Grandidier, 1903, for which two radiocarbon dates are available (Goodman & Rakotondravony 1996, Burney et al. 2004): a bone fragment was dated to 4440 ± 60 BP (Beta-73370, CAMS-6394) and a tooth dated at 1536 ± 35 BP (NZA-18996, R-28421/1). Its extant congener, *H. antimena* Grandidier, 1869, formerly had a broad distribution during the Holocene across the southern portion of the island but is now restricted to the central western forests near Morondava, whereas *H. australis* is known only from this cave and a site in the Central Highlands near Antsirabe (Goodman & Rakotondravony 1996). Based on habitat extrapolations, it may be inferred that species of *Hypogeomys* formerly lived in more mesic conditions than currently available near the cave and the same is presumably the case for *Microgale macpheei*.

Andrahomana Cave is located at the western foot of the north-south aligned Anosyenne Mountains in a remarkably abrupt dry-wet ecotonal zone, and on the arid side of a dramatic rain shadow. The natural modern flora in the immediate vicinity of the cave is transitional spiny bush, although there are a few local pockets with more humid vegetation. On the eastern side of the mountain chain is a variety of humid forest formations and the biota on the two different slopes is notably different (Goodman et al. 1997). Thus, it is reasonable to assume that the fauna represented by the subfossil remains recovered in Andrahomana Cave included species inhabiting both wet and dry vegetational conditions, depending on the varying climatic conditions during the Quaternary.

There is no evidence that *M. macpheei* is still extant. Because *M. decaryi* and *M. breviceps* were synonymized with living taxa (MacPhee 1987), *M. macpheei* is so far the only species of Tenrecidae known to have become extinct in recent geological history. The rodent *Macrotarsomys petteri* was described from a single specimen trapped during an extensive inventory in 2003 of the Mikea Forest, north of Toliara (Goodman & Soarimalala 2005) but soon thereafter, its subfossil remains were identified from Andrahomana Cave (Goodman et al. 2006). In the case of *Microgale macpheei*, perhaps the opposite situation will occur so that after having been described from subfossils, an extant population will be found. The small parcel of remnant forest of Malahelo on Ambatorongorongo Mountain, situated not far from Andrahomana Cave, harbors plants and animals characteristic of distinctly more mesic sites on the eastern side of the Anosyenne Mountains (Ramanamanjato et al. 2002). It is conceivable that a remnant population of *M. macpheei* may occur there, and this area should be the focus of detailed small mammal inventories.

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Appendix 1

List of specimens of *Microgale brevicaudata* used in direct comparison with the subfossil of *M. macpheei*.

Province d'Antsiranana: RS d'Analamerana, Forêt d'Ankavanana, 15.8 km SE Anivorano-Nord, 25–28 Jan 2004, 12.795°S, 49.368°E, 200, m (FMNH 178781, 178855–178857); **Province de Mahajanga**: Station Forestière de l'Ankarafantsika, 5 km SSW Ampijoroa, 4–7 Feb 1997, 16.338°S, 46.793°E, 160 m (FMNH 161573, 161574); Parc National de Bemaraha, Forêt d'Andranogidro, 12 km SE Antsalova, 15 Feb 2001, 18.742°S, 44.745°E, 120 m (FMNH 169678); PN de Bemaraha, Ankidrodroa, 2.5 km NE Bemaraha, 22 Nov 2001, 19.132°S, 44.808°E, 100 m (FMNH 172702); PN de Bemaraha, 3.5 km E Bekopaka, 1 Dec 2001, 19.14°S, 44.828°E, 100 m (FMNH 172703-172706, 172736); **Province de Toliara**: Kirindy Forest (CFPF), 23 Jan 1997, 20.0833°S, 44.633°E, 45 m (FMNH 161572); Sept Lacs, 28 February–9 Mar 2002, 23.525°S, 44.159°E, 120–140 m (FMNH 173230–173233); Antafiky, 4–8 Feb 2002, 23.490°S, 44.062°E, 50 m (FMNH 173236–173238); Antafiky, 8 Feb 2002, 23.494°S, 44.077°E 250 m (FMNH 173239).