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# Taxonomy of nesomyine rodents (Muroidea: Nesomyidae: Nesomyinae): Designation of lectotypes and restriction of type localities for species-group taxa in the genus *Nesomys* Peters

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*Abstract*.—Key foundational elements of taxonomic description were omitted in the original naming of species-group taxa now recognized in the Malagasy genus *Nesomys*: *N. rufus* Peters, 1870, *N. audeberti* (Jentink, 1879), and *N. lambertoni* G. Grandidier, 1928. Based on our review of the material available to the authors, we identified the holotype by monotypy of *N. rufus*, designated lectotypes of *N. audeberti* and *N. lambertoni*, restricted the type localities of *N. audeberti* and *N. lambertoni*, and localized the probable geographic source of the holotype of *N. rufus*. Refinement of the geographic source of *N. lambertoni* and *N. rufus* illuminates the incorrect placement of their type localities as currently interpreted and brings them within the presently understood distributions of those species. Extensive discussion is devoted to the travels of J. Audebert and A. Crossley, collectors not only of the types of *N. audeberti* and *N. rufus*, respectively, but also of important series of lemurs that remain relevant to understanding the taxonomy and distribution of these endangered mammals.

**Keywords**: J. Audebert, A. Crossley, Madagascar, *Nesomys audeberti*, *Nesomys lambertoni*, *Nesomys rufus*, nomenclature

The genus *Nesomys* Peters, 1870, includes three living species of muroid rodents (Nesomyidae: Nesomyinae) that are endemic to Madagascar (Ryan 2003): *N. rufus* Peters, 1870; *N. audeberti* (Jentink, 1879); and *N. lambertoni* G. Grandidier, 1928. Although these species-group taxa were once viewed as subspecies of the first-named *N. rufus* (Petter 1972, 1975), each is today understood to represent a valid biological species (Musser & Carleton 2005, Soarimalala & Goodman 2011).

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For the era of biological discovery, the original descriptions of the three species-group taxa of *Nesomys* were understandably incomplete and uneven compared with modern standards of taxonomic validation. No holotype or unique registration number was explicitly identified as a name-bearing specimen for any of the new names. The description of *N. lambertoni* omitted a type locality, and geographic origin of the other two species was ambiguous or obscure; in fact, the type locality as conventionally interpreted for two species, *N. lambertoni* and *N. rufus*, is extralimital to their specific distributions

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as presently defined based on recently collected specimens. No collector, collection date, or illustration of type material accompanied the description of *N. rufus* (Peters, 1870); no date of collection or illustration of type material was provided for *N. audeberti* (Jentink, 1879); no collector or date of collection was provided for *N. lambertoni* (G. Grandidier, 1928). For the two species that inhabit the island's humid forests, *N. audeberti* and *N. rufus*, such omissions have led past authors to caution that application of these names to the species morphologies as conventionally accepted nowadays may be incorrect (Carleton & Schmidt 1990, Goodman & Carleton 1996).

The aim of this paper is to secure the applicability of species-group epithets within *Nesomys* for future systematic research. Namely, we have relocated and here document by museum catalog number the specimens that Peters (1870), Jentink (1879), and Grandidier (1928) had at hand when they described their new species; identify the holotype of *N. rufus* and designate lectotypes for *N. audeberti* and *N. lambertoni*; fix the type localities of *N. audeberti* and *N. lambertoni* and clarify the geographic origin of *N. rufus*; and summarize this information within updated synonymies of these taxa. In view of the increasing application of gene-sequencing methodology to the systematics of Malagasy small mammals and the attending emergence of unsuspected biodiversity (e.g., Goodman et al. 2009, Olson et al. 2009), we consider it important to resolve these crucial foundational elements of taxonomic description, as recommended by the International Code of Zoological Nomenclature (1999, 4th edition).

## Materials and Methods

Nomenclatural conclusions presented herein are based on examination of specimens, consisting principally of study skins with associated skulls, maintained in the following collections, listed alphabetically by the museum abbreviation adopted throughout the paper.

| | |
|---|---|
| BMNH | The Natural History Museum, London (formerly British Museum [Natural History]) |
| FMNH | Field Museum of Natural History, Chicago, Illinois |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| PBZT | Parc Botanique et Zoologique de Tsimbazaza, Antananarivo |
| RMNH | Naturalis Biodiversity Center, Leiden (formerly Rijksmuseum van Natuurlijke Historie) |
| USNM | National Museum of Natural History, Smithsonian Institution, Washington, D.C. (formerly U.S. National Museum) |
| ZMB | Museum für Naturkunde (MfN), Berlin; zoological collections (formerly Zoologisches Museum Berlin) |

In addition to study of original type material (MCZ, MNHN, RMNH, ZMB) and miscellaneous older specimens collected in the 1870s (BMNH, MNHN), we also examined recently collected specimens housed in the FMNH and USNM as a basis for comparing pelage color and morphologies and for quantifying variation in body and cranial size. Of particular importance are series of *N. audeberti* and *N. rufus* collected sympatrically in the Parc National de Ranomafana (see Appendix 1 for exact locality data and catalog numbers).

Seven external and 18 craniodental variables were recorded depending upon the condition of the specimen. Total length (TOTL), lengths of tail (TL), hind foot (HFL), and ear (EL), all given in whole millimeters (mm), are those recorded by

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Table 1.—External dimensions based on adult samples of three extant species of *Nesomys*. (Variable abbreviations are defined in Materials and Methods; sample statistics include the mean, ± 1 standard deviation, observed range, and sample size in parentheses. See Appendix 1 for localities and specimen numbers.)

| Variable | *N. rufus* | *N. audeberti* | *N. lambertoni* |
|---|---|---|---|
| TOTL | 345.8 ± 13.0 | 380.8 ± 16.7 | 387.0 ± 4.0 |
| | 322–365 (22) | 345–410 (15) | 383–391 (3) |
| HBL | 182.3 ± 9.4 | 197.4 ± 8.4 | 203.7 ± 20.5 |
| | 163–198 (22) | 178–213 (15) | 189–227 (3) |
| TL | 162.9 ± 9.3 | 181.7 ± 14.0 | 178.0 ± 16.1 |
| | 139–180 (22) | 167–210 (15) | 160–191 (3) |
| HFL* | 48.4 ± 2.2 | 54.6 ± 2.1 | 48.7 ± 3.2 |
| | 43.0–52.0 (26) | 51.0–58.0 (11) | 45.0–51.0 (3) |
| DHFL | 47.3 ± 1.6 | 53.6 ± 1.1 | 52.3 ± 1.1 |
| | 43.0–50.0 (20) | 51.8–55.5 (10) | 51.0–53.0 (3) |
| EAR | 26.7 ± 1.1 | 26.6 ± 1.4 | 30.0, 31.0 |
| | 25.0–29.0 (26) | 24.0–28.0 (12) | |
| WT | 163.7 ± 20.7 | 201.7 ± 26.4 | 225.0, 243.0 |
| | 122–205 (23) | 155–235 (11) | |

* Measured with the middle claw for most specimens of *N. audeberti* and *N. rufus*, but without claw for those of *N. lambertoni*. For proportional size of the hind foot, DHFL, with claw, was more uniformly measured across species.

the collector on the skin label. Length of head-and-body (HBL) was obtained either as listed by the collector or by subtraction of TL from TOTL. Weight (WT) in grams (g) was also transcribed from specimen labels, although this datum is generally unavailable for specimens preserved before the 1960s. Nor did early collectors always provide external dimensions, and where available, their measurement protocol is often unknown for certain variables (for example, EL from the crown or from the notch, and HFL with the claw or without). Early collectors seldom provided external dimensions. As an index of general body size, Carleton measured dry hind foot length (DHFL), including the claw, to the nearest 0.5 mm on museum skins whose metatarsal and phalangeal bones remained more or less straightly aligned after preparation in the field. Shrinkage of the hindfoot on a prepared *Nesomys* skin averages about 1 mm, as suggested by a comparison of DHFL with HFL for recently collected samples as uniformly measured by the same field personnel (Table 1).

Sixteen cranial and two dental dimensions were measured to the nearest 0.1 mm using hand-held digital calipers accurate to 0.02 mm, while viewing skulls under a dissecting scope for smaller dimensions. Landmarks for defining variables follow Carleton (1994:5–6). Variable abbreviations as used in the text and tables are: BBC, breadth of the braincase; BIF, breadth of incisive foramina; BM1s, breadth of bony palate across first upper molars; BOC, breadth across the occipital condyles; BR, breadth of rostrum; BZP, breadth of zygomatic plate; DAB, depth of the auditory bulla; IOB, least interorbital breadth; LBP, length of bony palate; LD, length of diastema; LIF, length of incisive foramina; LM1-3, length of maxillary toothrow; LR, length of rostrum; ONL, occipitonasal length; PPB, postpalatal breadth; PPL, postpalatal length; WM1, width of first upper molar; ZB, zygomatic breadth. All measurements were taken by Carleton, except for the type of *N. rufus*, which was examined and measured by Robert S. Voss of the American Museum of Natural History.

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Standard descriptive statistics (mean, range, and standard deviation) were derived for adult specimens as recognized by their fully erupted, though sometimes little worn, third molars. Analytical procedures were implemented using statistical packages contained in SYSTAT (Version 11.0, 2004).

## Results and Discussion

We consider the various nomenclatural issues that concern each species of *Nesomys* as separate essays, addressed in reverse order of their description. Within each account, we first identify the name-bearing specimens used by the authors as the basis of their descriptions and secondly consider their geographic origins.

### *Nesomys lambertoni* G. Grandidier, 1928

*Type material and lectotype selection.*—In 1928, Guillaume Grandidier described a large species of *Nesomys* based on three specimens deposited in the Académie Malgache, Antananarivo. Although written in a relatively modern era of taxonomic description, the author failed to designate a type specimen, to provide a type locality, to indicate any museum or field catalog numbers, or to identify dates of collection. Notwithstanding the omission of such critical elements of a new species description, Grandidier's illustrations and morphological comparisons are exceptional in their detail, which removes any doubt about the species to which his epithet *lambertoni* applies or the specimens on which it was based.

All three specimens that comprise Grandidier's original type series received at the Académie Malgache are now housed in other museum collections and bear registration numbers that were applied years later. He (1928:95) noted that two of the three specimens were in extremely poor condition and serviceable only for general size and color comparisons. These two specimens, now stored in the MCZ (MCZ 45933, 45934), consist of unprepared skins, contorted in shape presumably as hastily dried in the field or under the blazing sun, with the anterior portions of the skull and lower limb bones still preserved inside; both skins are unevenly perforated with tiny pellet holes, suggesting their collection by a shotgun with relatively small shot. Field workers occasionally resorted to roughed-out preparations like these as a temporary expedient when time prohibited assembly of conventional round skins or when the intent was to later fashion taxidermic mounts. Grandidier identified his third specimen as well preserved with a complete, articulated skeleton. The round skin of this specimen now resides in the MNHN (MNHN 1961.106), but its companion skull and post-cranial skeleton (minus the podials) are housed in the MCZ (MCZ 45941), together with the two mummified, unprepared skins. This last specimen (MCZ 45941/MNHN 1961.106) undoubtedly served as the principal basis for Grandidier's morphological description, measurement tables, and his accompanying illustrations.

The MNHN round skin is well prepared, in excellent condition except for a patch of hairs missing just below the tail tip, and its color still bright and unfaded. No original tags were associated with it when examined by Carleton in 1987 and Goodman in 2002, but a relatively new tag indicates "Peau du type décrit par G. Grandidier en 1928–29. Environs de Maintirano." The year (1961) when the specimen was cataloged into the MNHN collection implies that the specimen's importance was not appreciated until many years after Grandidier's (1928) description; Rode (1945:28) did not list it in his type catalog of rodents maintained in the MNHN. Its significance was apparently discovered by the late Francis Petter during the course of his important studies on Nesomyinae, for it was he (1962:571) who much later supplied the type locality

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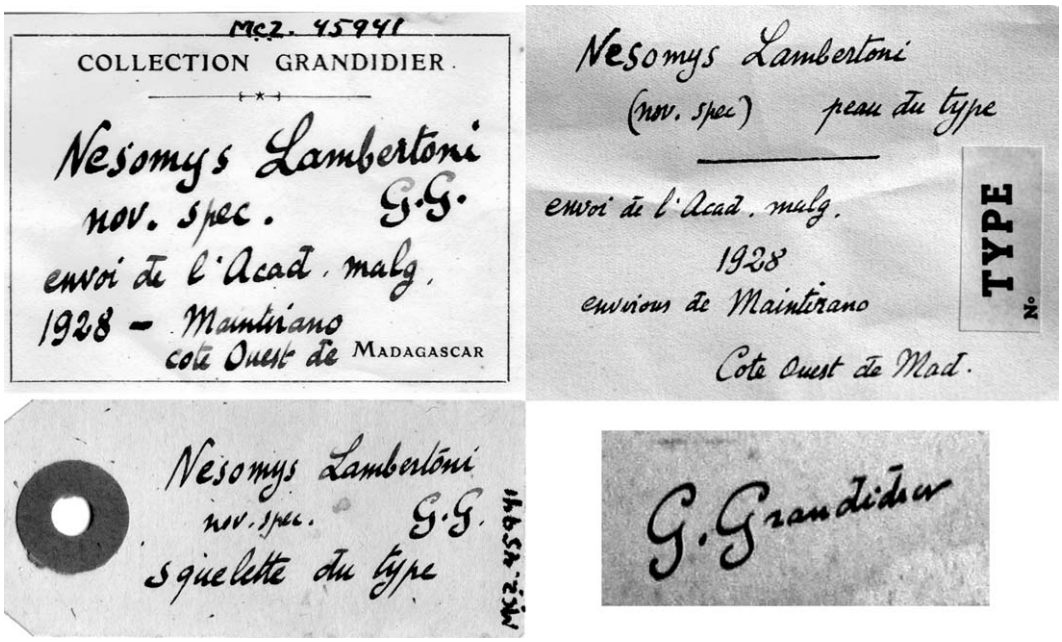



Fig. 1. Museum labels associated with the type material of *Nesomys lambertoni*, herein designated as lectotype (MCZ 45941/MNHN 1961.106): left pair, labels found with the skull and companion postcranial skeleton (MCZ 45941) housed in the Museum of Comparative Zoology, Harvard (reproduction permitted by the Mammalogy Department, MCZ); upper right, label associated with the round skin (MNHN 1961.106) maintained in the Muséum National d'Histoire Naturelle, Paris (reproduction permitted by the MNHN, copyright C. Callou); lower right, example of Guillaume Grandidier's signature as found on archives preserved in the Académie Malgache, Antananarivo. Grandidier's signature, especially the unmistakable double "G. G."s, confirms that these labels were written in his hand.

"région de Maintirano, sur la côte occidentale" based on an original label that accompanied the *N. lambertoni* skin. Dr. Cécile Callou of the MNHN kindly located the original label mentioned by Petter and supplied us with a digital copy (Fig. 1), which information authenticates this skin as part of the type series reported by Grandidier (1928). The skin of MNHN 1961.106 exhibits the two most distinctive external traits accurately captured by Grandidier's frontispiece (Fig. 2) to his description of *N. lambertoni*: the large pinnae and the exceptionally hairy tail. Both features are characteristic of *N. lambertoni*, and Grandidier (1928:99) emphasized both in justifying his description of *lambertoni* as a new species. The longer ears are borne out by measurements of recently collected, uniformly measured specimens compared with those of *N. audeberti* (Jentink, 1879) and *N. rufus* Peters, 1870 (Table 1). The densely pilose tail of *N. lambertoni* is visually striking at first glance (Fig. 2), the caudal hairs measuring ~15–17 mm long over the middle tail and entirely obscuring the caudal scales; in examples of *N. audeberti* and *N. rufus*, caudal hairs are much shorter, ~3–4 mm over the middle tail, and expose the epidermal scales for most of its length (Fig. 3; also see Figs. 73–75 in Soarimalala & Goodman [2011] for interspecific differences in caudal hairiness).

Petter (1962) reported that he could not locate the associated skull when he documented the existence of MNHN 1961.106 as a skin of *N. lambertoni* related to

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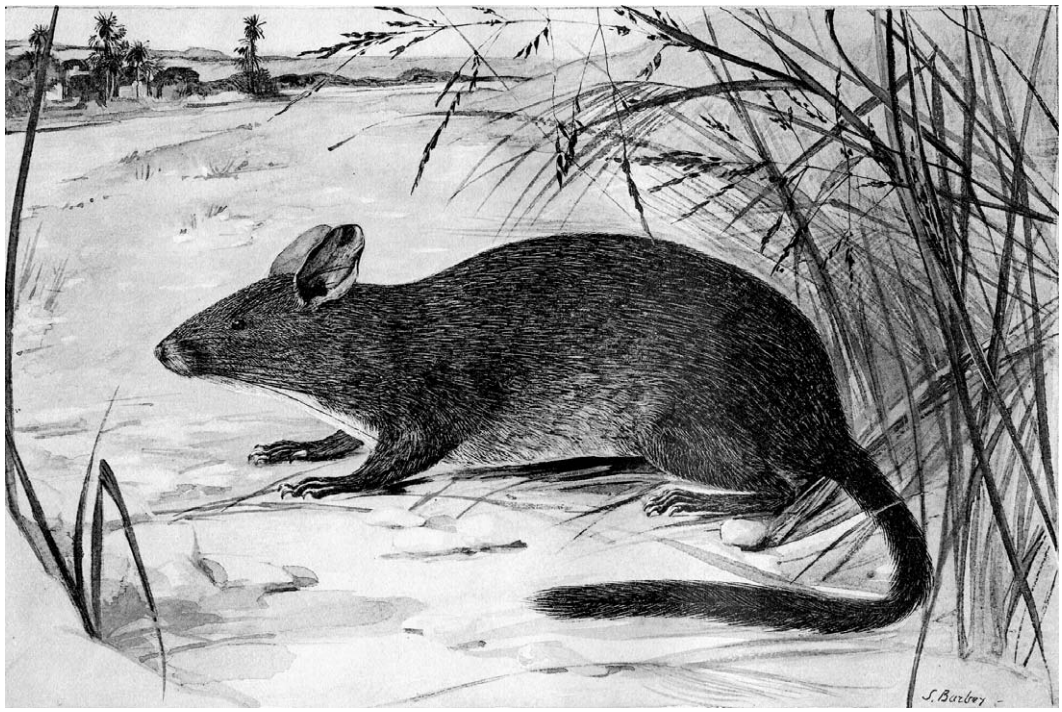



Fig. 2. Frontispiece of *Nesomys lambertoni* from Grandidier's description of the species (1928:facing p. 95), illustrating artist's rendition of the living animal as visualized based on one (now = MNHN 1961.106) of three skins received at the Académie Malgache. Among living species of *Nesomys*, the drawing captures two external traits characteristic of *N. lambertoni*, its elongate pinnae and densely pilose tail (compare with Fig. 3).

Grandidier's original description. In his first visit to the MCZ (Aug 1983), therefore, Carleton was delighted to discover a skull with partial skeleton (MCZ 45941) that seemed to fit Grandidier's description and figures, as later substantiated by Goodman & Schütz (2003). As recounted by Helgen (2002), G. Grandidier's personal collection of some 1100 mammal specimens was purchased by Robert Barbour in 1947 for accession by the MCZ Mammal Department and in memory of his older brother Thomas Barbour (1884–1946), long-time Director of the Harvard Museum. It was commonplace for naturalists and gentleman-collectors of the late nineteenth and early twentieth centuries to maintain a private cabinet of natural history curiosities (e.g., Morris 2010), and that assembled by G. Grandidier was substantial. The box label and specimen tag associated with this skull and skeleton are penned in cursive French that matches the hand-writing on the old label of the MNHN skin; in addition, the MCZ tags bear the distinctive initials "G. G.," which represent Grandidier's own script as found on other museum labels and archival material directly attributable to him (Fig. 1). The MCZ and MNHN labels substantiate that this was one of the specimens that Grandidier had at hand when he named *N. lambertoni*.

The skull of MCZ 45941 evidences the telltale damage of an animal that had been dispatched with a shotgun blast (Fig. 4): the left zygomatic arch is missing and the right is incomplete; the zygomatic plates and nasolachrymal capsules are fractured and incomplete on both sides; and small to

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Fig. 3. Unnumbered figure, entitled *Nesomys rufus* Peters, from Grandidier's description of *N. lambertoni* (1928:facing p. 99). The skin used to model this interpretation of the living animal may represent the specimen from Rogez, near Brickaville, mentioned by Grandidier (1928:96) and used as an example of the eastern species.

large holes perforate the right auditory bulla, supraorbital, and orbital walls. Cranial dimensions as measured by us jibe closely with those reported by Grandidier for comparable variables (1928:98; and see Table 2). The general shape of the cranium of MCZ 45941 reasonably resembles the skull portrayed in his description (Fig. 5), enhanced liberally by artistic reconstruction. The heavy line-shading and cross-hatching technique employed by the artist obscures much detail, but the small size of the auditory bullae and relatively long incisive foramina, acutely pointed at both ends, are apparent; these variables, along with larger size, help to mensurally differentiate the skull of *N. lambertoni* from those of *N. audeberti* and especially *N. rufus* (see Tables 2, 3, 5). The molar drawings included in Grandidier's cranial

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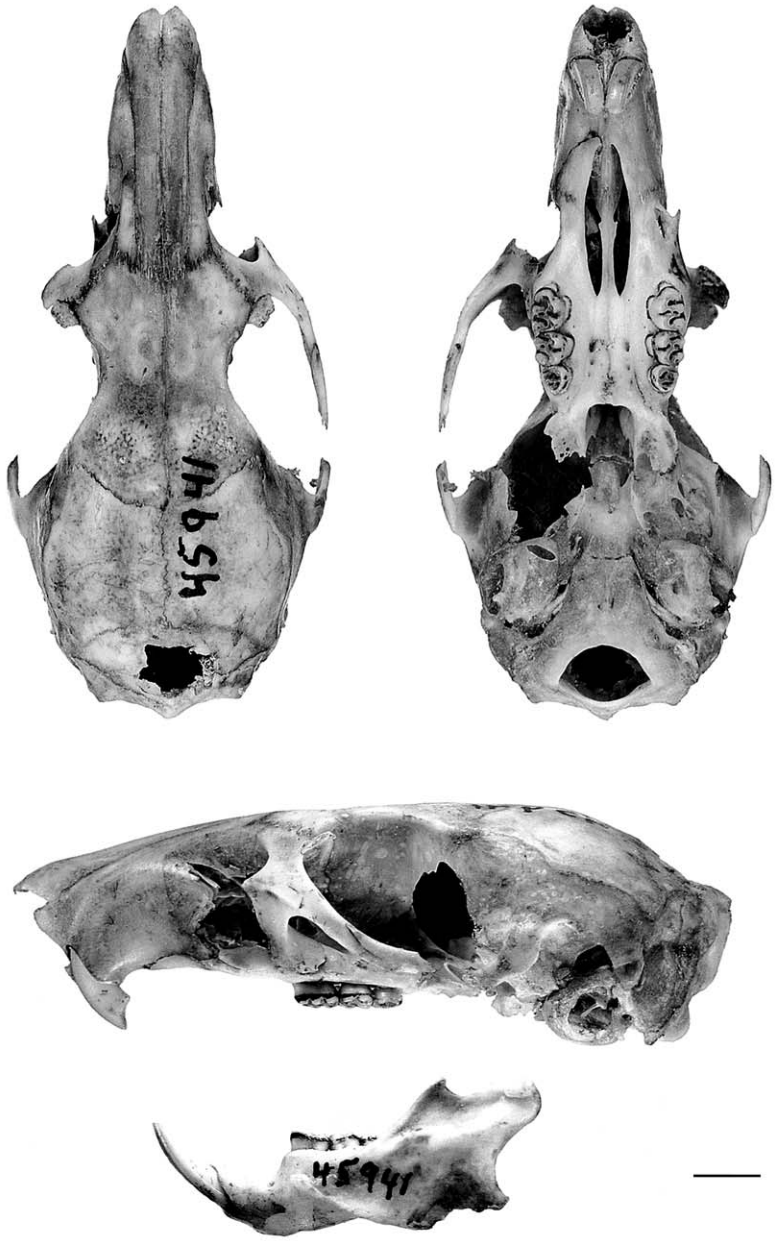



Fig. 4. Dorsal, ventral, and lateral views of the skull (MCZ 45941) here designated as part of the lectotype of *Nesomys lambertoni* G. Grandidier, 1928 (ca. ×2, ONL = 53.8 mm). Scale bar in lower right = 5 mm. Compare with cranial drawings of the same specimen as depicted in Grandidier's description (Fig. 5).

plate are remarkable for their detail and accuracy. In particular, they portray the enamel-dentin bridge (medial mure) that connects the protocone and paracone (Fig. 5), a distinctive crown pattern of the M1 and M2 possessed by *N. lambertoni*. Such an enamel-dentin bridge is usually absent in *N. audeberti* and *N. rufus*, a loss that produces a deep reentrant valley that obliquely crosses those anterior molars.

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Table 2.—Sex, age, and measurements of the designated lectotype of *Nesomys lambertoni* G. Grandidier (1928) and two recently collected specimens from the Parc National de Bemaraha. (M and F = male and female, respectively; A = full adult class. Variable abbreviations are defined in Materials and Methods.)

| Variable | MCZ 45941/MNHN 1961.106 Lectotype | FMNH 172726 | FMNH 172727 |
|---|---|---|---|
| Sex | M | F | F |
| Age | A | A | A |
| TOTL | 387* | 383 | 391 |
| HBL | 227* | 195 | 189 |
| TL | 160* | 183 | 191 |
| DHFL | 53.0 | 51.0 | 53.0 |
| EAR | 29* | 31 | 30 |
| WT | – | 243 | 225 |
| ONL | 53.8 (55*) | 51.0 | 49.7 |
| ZB | 25.1 (25*) | 26.0 | 26.0 |
| BBC | 18.3 | 18.1 | 17.9 |
| BOC | 11.2 | 10.7 | 11.3 |
| IOB | 9.4 (10*) | 8.9 | 8.9 |
| LR | 20.5 | 20.3 | 19.5 |
| BR | – | 9.3 | 9.1 |
| PPL | 18.0 | 16.8 | 16.8 |
| LBP | 8.1 | 8.2 | 8.6 |
| BM1s | 11.3 | 10.5 | 10.3 |
| PPB | 8.5 | 7.3 | 7.7 |
| LD | 13.9 | 13.9 | 13.5 |
| LIF | 11.1 | 10.1 | 9.9 |
| BIF | 3.4 | 3.5 | 3.4 |
| BZP | – | 5.3 | 5.0 |
| DAB | 7.1 | 6.3 | 6.5 |
| LM1–3 | 7.79 (8*) | 7.32 | 7.25 |
| WM1 | 2.38 | 2.40 | 2.28 |

* External and cranial measurements as originally given by G. Grandidier (1928:98); his cranial dimensions, listed in parentheses, were given in meters and are here converted to mm.

Petter (1962:571) considered the MNHN skin (1961.106) as "le type" of *N. lambertoni*, and this notion was repeated by Goodman & Schütz (2003), who called it the holotype. Similarly, Helgen & McFadden (2001) and Helgen (2002) referenced MCZ 45941 as the holotype of Grandidier's taxon. Regrettably, Carleton had misinformed Helgen when he called the MCZ skull the "holotype" of *N. lambertoni* while conveying that it is the missing companion to the skin stored in the MNHN (e-mail of 6 Aug 1999). Grandidier (1928), however, neglected to identify a type specimen in the original description, nor did he employ the word "type" in any of its compound formulations. He did specify the number of specimens, three, that formed the basis for his new species, and these three—MCZ 45933, MCZ 45934, MCZ 45941/MNHN 1961.106—de facto compose the type series or syntypes of *N. lambertoni* (ICZN 1999: Articles 72.1.1, 72.4.1, 73.2). Of the three, MCZ 45941/MNHN 1961.106 is in far superior condition to the other two, was certainly the one used by Grandidier as the basis for his illustrations and cranial measurements, and was the one viewed by Grandidier himself as the "squelette du type," as documented posthumously (Fig. 1). We here designate MCZ 45941/MNHN 1961.106 as the lectotype of *Nesomys lambertoni* Grandidier, 1928 (ICZN 1999: Article 74.1, 74.7). One could argue that the lectotype should be restricted to the skull and partial skeleton preserved in the MCZ because it retains original labels that bear Grandidier's initials, but we believe that it is taxonomically important to stress the unity of the MCZ and MNHN preparations, formerly available as the well-preserved specimen that was the centerpiece of Grandidier's species description and interspecific comparisons. Petter's (1962) reference to the MNHN skin as "le type" does not qualify as fixation of a lectotype by inference because the author did not demonstrate any awareness that a type series existed and that he was selecting one specimen amongst them (ICZN 1999: Articles 74.5, 74.6); in fact, Petter (1972:664) later affirmed that the taxon *N. r. lambertoni* was known by "a solitary specimen," undoubtedly referring to the skin that he had earlier reported. After 1999, designation of a lectotype must deliberately employ the term "lectotype," thereby invalidating later references to the MCZ and MNHN material as holotype by Helgen & McFadden (2001) and Goodman & Schütz (2003) (ICZN 1999: Article

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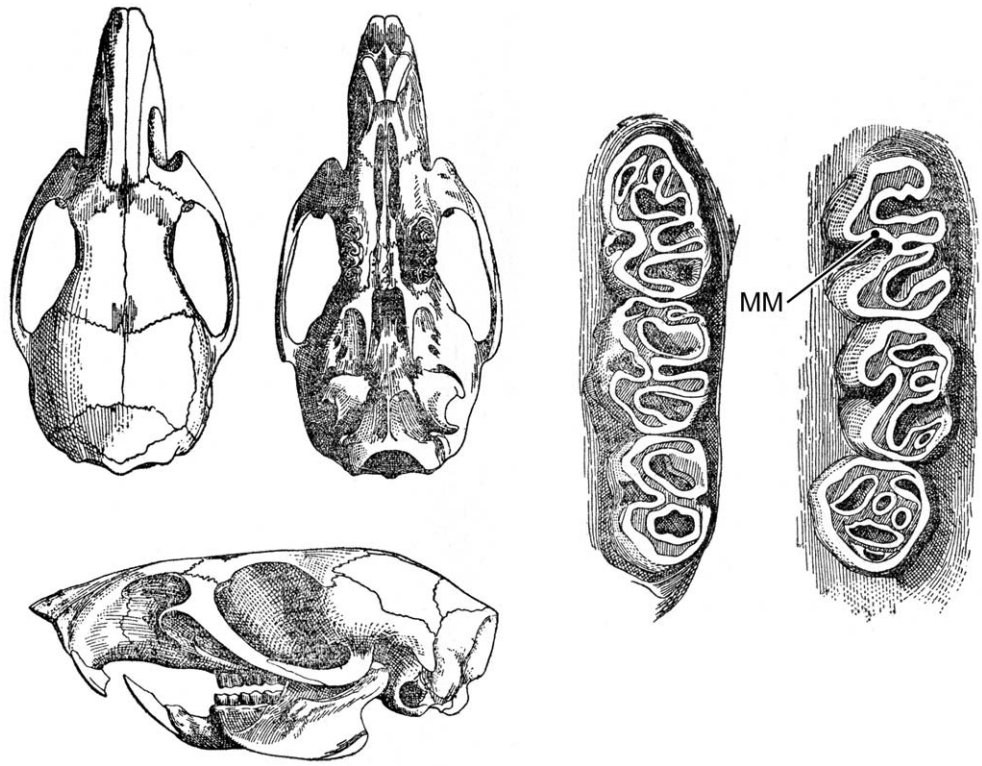



Fig. 5. Unnumbered figure, entitled *Nesomys lambertoni*, from Grandidier's description of the species (1928:96), illustrating: left set) dorsal, ventral, and lateral views of cranium and lateral view of mandible (original skull views given as ×1.5, here reproduced about ×1.1); right set) occlusal views of left lower and left upper molar rows (original dental views given as ×8, here reproduced about ×7). The label and arrow were here added to the original dental view to indicate enamel connection (MM, medial mure) characteristic of the upper first and second molars of *N. lambertoni*, a structure typically absent in examples of both *N. audeberti* and *N. rufus*. See Figure 4 for photograph of skull (now = MCZ 45941) used by Grandidier in his cranial plate of *N. lambertoni*.

74.7). As part of the original type series, MCZ 45933 and 45934 are perforce recognized as paralectotypes (ICZN 1999: Article 74.1.3). In an envelope attached to MCZ 45934 is a short note, again written by Grandidier, that identifies it as one of the "2 peaux de *Nesomys lambertoni* (nov. spec.) cotypes." Although the latter term is no longer used (ICZN 1999: Recommendation 73E), it underscores in Grandidier's own words that these two skins formed part of his original type series.

Grandidier (1928) misunderstood both the generic boundaries of *Nesomys* and the species limits of *N. rufus* at the time he described *N. lambertoni*. He accepted *Nesomys betsileoensis* Bartlett, 1879, as one of the two eastern species of *Nesomys*, along with *N. rufus*, but dismissed it in his ensuing comparisons because its bodily form departed so strikingly from that of *N. lambertoni*. He even speculated that *betsileoensis* may represent a separate genus, unaware that Major (1896a) had earlier resolved this problem when he named *Brachyuromys*, designated the newly named *B. ramirohitra* as type species, and reallocated *Nesomys betsileoensis* Bartlett, 1879, as a second species of his new genus. Similarly, Grandidier had overlooked Jen-

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tink's (1879) description of *Hallomys audeberti* and Major's (1897) subsequent referral of Jentink's species to *Nesomys*. Among Grandidier's study sample of *N.* "*rufus*" are specimens of *N. audeberti* along with true *N. rufus*. His cranial illustration of *N. rufus* (1928:97, un-numbered figure) does represent an example of that species, but his rendition of the living animal (1928: facing page 99, un-numbered figure) appears to be based on *N. audeberti* (see Fig. 3). The model for his drawing may be the specimen from Rogez (= Andekaleka), near Brickaville (= Ampasimanolotra), that impressed Grandidier (1928:96) for its broad expanse of white on the venter. To date, the only specimen that we can locate from this locality is MCZ 45940, a skin with skull that was also included in the Grandidier Collection purchased by Robert Barbour and an example of *N. audeberti*. In spite of these taxonomic confusions, the traits of *N. lambertoni* emphasized by Grandidier are sufficiently distinctive and unambiguous for recognizing it as a member of *Nesomys* and for distinguishing it from the two eastern species, *N. audeberti* and *N. rufus*.

*Restriction of the type locality*.—Although Grandidier (1928) omitted any mention of a collecting locality in his description, he pointedly contrasted *Nesomys lambertoni* to its congeners that inhabit the eastern forests of Madagascar. By default perhaps, such remarks imply an east-west geographic axis, presumably a western habitat for his new species; however, he nowhere stated this in the 1928 description nor in his treatise of the *Zoologie de Madagascar*, in which the generic distribution of *Nesomys* is summarized only as the eastern region ("Région orientale"—Grandidier & Petit 1931:101). Ellerman (1941, 1949) unnecessarily beclouded matters when he misconstrued Grandidier's (1928:96) remarks to indicate the origin of *N. lambertoni* from "Rogez, near Brickaville, East Madagascar." In context, however, Grandidier was referring to an example of what he thought to be *N. rufus*, possibly the one used as a model for his life-like illustration of the eastern species (see Fig. 3), which served as the standard for his pelage contrasts between *N. lambertoni* and *N. rufus*. Finally, Petter (1962) corrected the geographic source of *N. lambertoni* when he reported the rediscovered skin (MNHN 1961.106) and supplied the type locality as the "région de Maintirano, sur la côte occidentale." This geographic information concurs with that written on the MCZ and MNHN original labels in Grandidier's script (Fig. 1).

In our view, "région de Maintirano" should be accorded a geographically loose interpretation, not restricted to the modern city or its immediate vicinity on Madagascar's west-central coast (Fig. 6). Fortunately, the rediscovery of the species, based on specimens collected 70 years after Grandidier's (1928) description, provides ecological evidence for reinterpreting the source of his type series. In late 2001, Goodman secured two specimens of *N. lambertoni* from the Parc National de Bemaraha, east of Bekopaka, in dry deciduous forest associated with limestone karst outcroppings (*tsingy*), formations patchily distributed in western and northern Madagascar. Small mammals whose distributions are restricted to *tsingy* formations and their associated habitats continue to emerge and include certain bats, tenrecs, and other nesomyine rodents (Carleton et al. 2001, Goodman et al. 2009, 2011; Olson et al. 2009, Ramasindrazana & Goodman 2011). *Nesomys lambertoni*, as documented by Goodman & Schütz (2003), appears to be another member of this stenotopic assemblage.

The *tsingy* forest formation closest to Maintirano is the Beanka Forest (Fig. 6), which overlies a north-south aligned limestone massif of low relief, about 200–450 m above sea level and 50 km due east of the city. Goodman & Schütz (2003) had supposed that Grandidier's specimens were obtained from this limestone tract.

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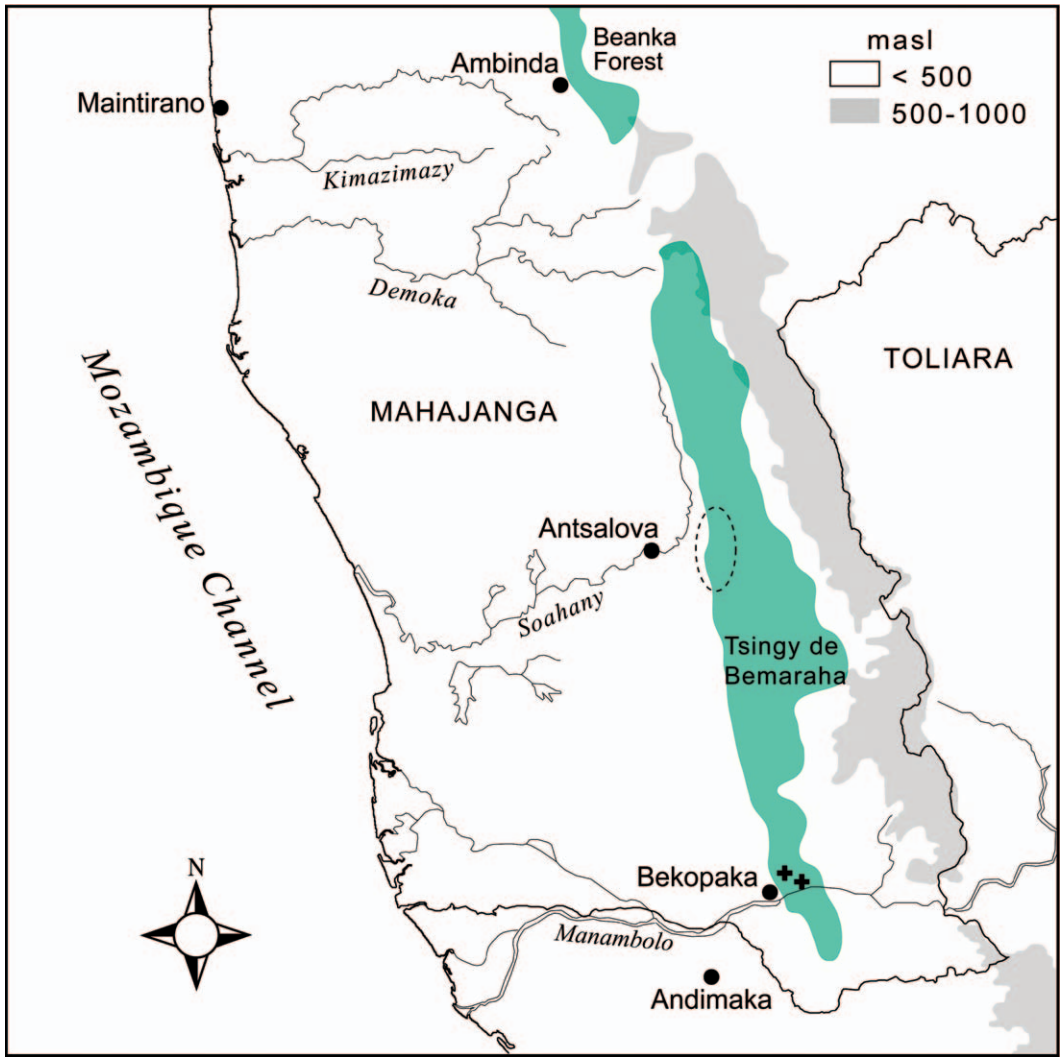



Fig. 6. Map of west-central Madagascar (ca. 17°58′ to 19°23′S) illustrating place names (filled circles) mentioned in the text. The sea port of Maintirano (18°04′S, 44°01′E) has been mistakenly accepted as the type locality of *Nesomys lambertoni* Grandidier, 1928, but we restrict the origin of Grandidier's three specimens to an area (indicated by oval dashed line) east of the village of Antsalova (18°41′S, 44°37′E), at the western margin of *tsingy* forest found along the lower western slopes of the Bemaraha Massif. Crosses = localities in the Tsingy de Bemaraha where recent specimens of *N. lambertoni* have been documented.

Recent biotic inventory of the Beanka Forest has involved multiple trips and several months of trapping in different parts of its southern section, accessible from the nearby village of Ambinda, and has yet to yield any specimens of *N. lambertoni* (Zafindranoro 2012). These surveys included many hours spent walking in the Beanka Forest during crepuscular periods, when *N. lambertoni* are active like their eastern congeners (Ryan et al. 1993), but no example of *Nesomys* was observed (Goodman pers. obv.). In contrast, *N. lambertoni* was regularly witnessed in the Bemaraha *tsingy* region "where two or three individuals could often be observed during a late afternoon walk" (Goodman & Schütz 2003:447).

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Furthermore, personal interviews elicited no positive recognition of a large diurnal rodent by people who live in the vicinity of the Beanka Forest and who are familiar with the local forest-dwelling vertebrates. The only informant who recognized this species by its vernacular name *kibojenjy*, per the Sakalava dialect of Malagasy, responded that it could be found further south in the *tsingy* of Bemaraha. Hence, we doubt that *N. lambertoni* occurs in dry forest associated with the Beanka Massif, at least in its southern section.

Instead, we believe that Grandidier's original series was procured in *tsingy* forest habitat that occurs along the lower western slopes of the Bemaraha Massif (Fig. 6), not so far from where it has been recently documented (Goodman & Schütz 2003), drawing upon the following lines of argument. The southern end of the Beanka formation is separated from the northern extension of the Bemaraha Massif by a 40-km gap of non-*tsingy* habitat. Grandidier (1928:95) recorded that the three rodent specimens had been received from a hunter retained by the Académie Malgache ("d'un de ses chasseurs"), which is certainly consistent with the dilapidated condition of the MCZ skins and damaged skull in his type series (Fig. 4). In the Parc Botanique et Zoologique de Tsimbazaza (PBZT), there is a series of bird specimens collected during the first week of January, 1928, at "Maintirano," and lacking any indication of collector. These bear Académie Malgache labels, and on past occasions, the Académie transferred portions of its holdings to what is now the PBZT. Just prior to Grandidier's publication on *N. lambertoni*, he & Berlioz (1928:83) had described a new species of rail, *Porzana* (now = *Amaurornis*) *olivieri*, from "Antsalova, province de Maintirano." Their description appeared in the same volume (No. 11) of the *Bulletin de l'Académie Malgache* as did the article on *N. lambertoni* but preceded it by a few pages (pp. 83–84 versus 95–99). Although the village of Antsalova (18°41′S, 44°37′E) is about 93 km SE Maintirano (18°04′S, 44°01′E), we underscore that Grandidier & Berlioz situated it within the "province de Maintirano"; during the early 1900s, Maintirano was one of 25 first-order administrative regions delineated by the French after their annexation of Madagascar in the 1890s (e.g., Grandidier & Grandidier 1908: map facing p. 357). Therefore, references to the type locality as the "région" or "environs" of Maintirano, as stated by Petter (1962) or as found on the older skin label associated with MNHN 1961.106, may broadly correspond to an older provincial boundary, not intentionally the city of the same name. As an historical anecdote, the rail described by Grandidier & Berlioz (1928) from Antsalova has been found recently in a marsh just south of the Bemaraha Massif, near Andimaka (19°15′S, 44°43′E; Willard & Goodman 2002), on the same fieldtrip when *Nesomys lambertoni* was rediscovered. Forest typical of the Bemaraha *tsingy* occurs just 8–10 km to the east of Antsalova, a distance well within the searching radius of a hunter who used the village as his base camp. We conjecture that the anonymous hunter shot the three individuals of *N. lambertoni* in *tsingy* habitat of the Bemaraha Massif (Fig. 6), presumably within the present boundaries of the protected area that encompasses most of the local occurrence of this habitat type.

Taken individually, none of the foregoing lines of evidence is conclusive. Collectively, they plausibly reinforce one another and persuade us that the type locality of *Nesomys lambertoni* Grandidier, 1928, should be restricted to Madagascar, Mahajanga Province (former), Melaky Région, Antsalova District, *tsingy* habitat at the western margin of the Bemaraha Massif and east of Antsalova. As so restricted, the known distributional records, including credible photographic documentation of the species (see Goodman & Schütz 2003), indicate that *N.*

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*lambertoni* occurs in the southern half of the Bemaraha Massif, from the latitude of Antsalova south to the Manambolo River (Fig. 6). With so small a known range and the apparent ecological dependence of the species on patchy subhumid settings within it, the conservation status of *N. lambertoni* is appropriately regarded as Endangered (IUCN Red List 2008).

At the inception of our nomenclatural sleuthing, we suspected that Grandidier had selected *lambertoni* as the specific epithet because the specimens had been collected by Charles Lamberton, or by one of his field party's hunters, in the course of his paleontological prospecting for subfossil lemurs in western Madagascar. However, combing through the paleontological literature and through museum records of recent birds and mammals collected by Lamberton uncovered no reliable association of his excavation sites with Maintirano, Antsalova, or other places in or near the Bemaraha Massif. Grandidier's choice of *lambertoni* was solely an honorary gesture, saluting a scientific contemporary also interested in the island's endemic fauna and a fellow member of the Académie Malgache (In 1929, G. Grandidier was an honorary member and Lamberton the Académie's Secretary). Appropriately, the scientific legacy and reputation of both young Frenchmen would be forever linked to their years lived on la Grande Île.

*Nesomys audeberti* (Jentink, 1879)

*Type material and lectotype selection.*—In the inaugural volume (1879) of the *Notes from the Royal Zoological Museum of the Netherlands at Leyden* (later renamed *Notes from the Leyden Museum*), Fredericus Anna Jentink (1844–1913), Curator of Mammals and later Director of the Museum, described a new genus and species of Malagasy rodent, *Hallomys Audeberti*. The description was based on three specimens of a large mouse-like rodent (by general indication called "Mus") included among the Malagasy collections received from Joseph Peter Audebert (1848–1933), a German naturalist and collector whom Jentink honored in creating the patronym. Jentink's original description lacked designation of a holotype, any mention of catalog numbers, or type illustration, common omissions for the era of taxonomic discovery. Among the three specimens, however, Jentink (1879:109) did give select external and cranial measurements (in mm) for a single specimen, an adult male, as quoted below.

| | |
|---|---|
| Head and body | 230 |
| Tail | 190 |
| Ear | 23 |
| Hind foot with claws | 57 |
| Length skull | 51 |
| Width skull | 26 |
| Length upper molar series | 8 |
| Distance between incisor and first upper molar | 13.5 |
| Distance between incisor and first lower molar | 7 |

Jentink subsequently amplified individual specimen data of *Hallomys audeberti* in his *Catalogue ostéologique* (1887) and the first volume of his *Catalogue systématique* (1888) of mammalian holdings deposited in the Leiden Museum. The 1887 osteological catalog contains the skulls and skeletons, and the 1888 (and its 1892 sequel) "systematic catalog" covers the skins. In both catalogs, he referred to each of the three specimens as one of the types of the species ("un des types de l'espèce") and, as was his custom, serially arranged them by letters as a, b, and c. Confusingly, Jentink employed different letters for the complementary parts of the individual specimens in the osteological and systematic catalogs. Thus, the skull with mounted skin and the skull-and-skeleton (preserved in alcohol) with mounted skin are listed as "a" and "b," respectively, in the osteological catalog (1887:216–217), whereas the associated mounted skin preparations

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themselves are identified as "b" and "a" in the systematic catalog (1888:74). Fortunately, Jentink did cross-reference the alphabetic assignments used in the earlier osteological catalog to those adopted in the later systematic catalog in order to associate the component parts of the individual specimens. Both specimens have now been recataloged: the mounted skin "a" with its skeleton "b" (and viscera) preserved in alcohol as RMNH 26527; mounted skin "b" with its skull "a" as RMNH 26528. Jentink's third specimen consists of a whole carcass preserved in alcohol, an adult female (on the old label erroneously given as "♂") with three near-term fetuses; it was listed in the systematic catalog (1888:74) as specimen "c," in agreement with the old jar label, and later recataloged as RMNH 39356. These three correspond to Jentink's original type series and are appropriately considered syntypes sensu the ICZN (1999: Article 73.2).

Older labels of the stands of both mounted skins (RMNH 26527 and 26528) and of the two jars with alcoholic preparations indicate "type," but newer labels added when the specimens were numerically cataloged correctly identify each as "syntype." Both mounted skins are in adequate condition with complete tails, but the pelage appears somewhat faded and their pinnae are tattered and torn (Fig. 7), deterioration presumably due to decades of exhibit and handling in the Museum's galleries. Caudal hairs are short and reveal the caudal scales over most of the tail length, unlike the bushy tail characteristic of *N. lambertoni*; the tails of both specimens are tipped with white hairs (now soiled and partly abraded) that invest the entire circumference, the terminal white section measuring 12 mm (RMNH 26527, Fig. 7) or 35 mm (RMNH 26528) long. Although slightly faded, the dorsal pelage does not exhibit the strong suffusion of rufous along the flanks as observed in most examples of *N. rufus*. The ventral pelage is colored a dingy yellow-white from the chin to the inguinal region, the dorsal pelage color slightly converging but not contacting mid-ventrally along the middle abdomen. Although no longer bright white as seen in recently collected specimens of *N. audeberti*, such a former ventral color is suggested by the mounted skins, and though diminished with time, still departs from the predominantly rufous coloration and lack of a pronounced dorsal-ventral contrast that typify most *N. rufus*. A clear orange-rufous band borders the white ventrum from the cheeks to the inguinal region, sharply demarcated from the white underside but gradually merging with the brown cheeks, breast and flanks; this lateral coloration is most clearly visible in RMNH 26527. We emphasize that the two skins were prepared differently. The pedestal of RMNH 26527 reads "tiré de l'alcohol" ("removed from alcohol"), suggesting that it was in fluid for as long as a year, having been collected in Feb 1878 and described in Mar 1879. Specimen RMNH 26528, however, was almost certainly prepared from a fresh skin. When still in clean condition, Jentink (1879:108) had characterized the underparts of his new species as "Chin, lower parts of cheeks, throat, chest, and middle of belly and abdomen pure white." His description still applies to RMNH 26528 (though now looking somewhat dirty), but in RMNH 26527, the ventral color is notably yellowish, probably due largely to discoloration in alcohol.

Of the crania associated with the two mounted specimens, RMNH 26527 (from "Savary") is a young adult male, and RMNH 26528 (from "Maisine"; see below for further discussion of these two localities) is a fully adult male according to our tooth-wear criteria. The skulls of both specimens bear evidence of collection using a fowling piece, perforated with tiny to small holes that appear to result from birdshot pellets. That of RMNH 26527 is nearly intact, lacking its left auditory bulla, the right bulla broken but still

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Fig. 7. Mounted skin here selected as lectotype (RMNH 26527) of *Hallomys audeberti* Jentink, 1879; listed as skin "a" in Jentink's (1888:74) *Catalogue systématique* and companion to specimen "b," the skull listed in Jentink's (1887:217) *Catalogue ostéologique* (see Fig. 10). The old label tacked to the wooden base dates from Jentink's period and displays essential data on the restricted type locality (Savary, N. E. Madagascar), collection date (February 1878), and collector (expedition of J. Audebert). Jentink (1879) gave the external measurements (in mm) as head and body length, 230; length of tail, 190; hindfoot length, with claw, 57; ear length, 23. Figured about 42% natural size; photograph courtesy of Naturalis Biodversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden.

attached, and tips of the pterygoid processes missing; the posterior part of the left mandible is broken off just behind the toothrow and missing. RMNH 26528 is more severely damaged: its posterior braincase is fractured, the fused occipital shield and basioccipital are separated but present, both auditory bullae are missing, and the right mandible is fractured and lacking the m1.

Examples of *N. audeberti* are generally larger than those of *N. rufus* (Fig. 8), and this size difference is most accentuated by certain external and cranial dimensions, such as those of the hind foot, interorbital constriction, and rostrum (Ryan et al. 1993, Goodman & Carleton 1996). In this regard, cranial measurements of the two RMNH syntypes fall within the range of variation recorded for the large series of *N. audeberti* collected in the Parc National de Ranomafana (Table 3, Fig. 9). Unless breakage of RMNH 26528 occurred sometime in the century between Jentink's description (Mar 1879) and Carleton's examination (Aug 1987), we presume that Jentink would have logically selected an intact individual (RMNH 26527) for measurement. Without knowing Jentink's exact measurement protocol, the values obtained by Carleton (Table 3) for seemingly comparable dimensions of the skull (ONL, ZB, LD, LM1-3) and hindfoot (DHFL) do not permit indisputable association of either specimen with the single individual whose measurements Jentink provided (see above) in his original description of *Hallomys audeberti*. However, Jentink (1879:109) also presented vertebral counts of his new form, and the prepara-

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Fig. 8. Dorsal cranial view (ca. ×2) of two *Nesomys* species collected in the Parc National de Ranomafana, both from Ambodiamontana, 7 km W Ranomafana, 950 m: left, *N. audeberti* (USNM 448969; ONL = 50.7 mm) an adult, gender indeterminate; right, *N. rufus* (USNM 448958; ONL = 46.5 mm), an adult male. In addition to the generally robust cranial proportions of *N. audeberti* compared with the smaller *N. rufus*, its interorbital region is relatively broad and obscures the floor of the orbit in dorsal view. Scale bar in middle bottom = 3 mm.

tion of RMNH 26527 includes a partial postcranial skeleton, as he later documented for specimen "b" in the osteological catalog (1887:217). Most significantly, Jentink provided an excellent illustration, drawn and lithographed in natural size by Hendrik Verlint (1846–1918), of the cranium of specimen "b" in the cranial plates supplemental to the osteological catalog (Plate VII: Figs. 1–4; here reproduced in Fig. 10). Cranial characters, the location of cranial breakage, and the position of pellet holes that Jentink figured for specimen "b" precisely correspond to the condition we observed for the skull of RMNH 26527.

We are confident that RMNH 26527 represents the specimen for which Jentink published select measurements in his original description (1879) and whose cranium and mandible he subsequently illustrated in the osteological catalog (1887). For that reason and in view of the skull's largely

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intact condition, we designate RMNH 26527 as lectotype of *Hallomys audeberti* Jentink, 1879. The specimen was collected in February 1878, presumably by Audebert himself. Prior museum identifiers associated with the lectotype include specimen "b," as listed for the skull and partial skeleton in the osteological catalog of the Leiden Museum (Jentink 1887:217); specimen "a," as listed for the taxidermy mount of the skin in the systematic catalog (Jentink 1888:74); and "1879" (with an "a" added in pencil), as found on the old label of the mounted skin and indicating the year of acquisition by the Leiden Museum coupled with Jentink's catalog letter. Per stipulations of the ICZN (1999: Articles 73.2.2, 74.1.3), RMNH 26528—a whole-mounted skin and skull collected 16 March 1878—and RMNH 39356—a whole carcass and its three fetuses preserved in fluid and collected 6 March 1878—become paralectotypes of Jentink's taxon. Other museum identifiers historically associated with paralectotype RMNH 26528 include specimen "a," as listed for its cranium in the osteological catalog (1887:216); specimen "b," as given for the full-mounted skin in the systematic catalog (1888:74); and "1879" (with "b" added in pencil), as found on the old label of the mounted skin and indicating the year of acquisition by the Leiden Museum coupled with Jentink's catalog letter. The paralectotype preserved in alcohol, RMNH 39356, was earlier referenced as specimen "c" in Jentink's systematic catalog (1888:74).

Jentink (1879:107) appreciated that his new genus and species *Hallomys audeberti* was a native form, like *Hypogeomys antimena* A. Grandidier, 1869, which he mentioned as "peculiar to Madagascar," and unlike the murids *Mus musculus* and *Mus* (= *Rattus*) *rattus*, which he supposed were "probably introduced by vessels." In addition to the commensal murids, Jentink contrasted the pelage color and texture of his new form to certain native murids of continental Africa (*Pelomys*, and a few species of "*Mus*" now classified in *Arvicanthis*). Within such a broad taxonomic framework, compared with such dissimilar and distantly related muroids, Jentink's differential diagnosis of *Hallomys* was straightforward. Nevertheless, Jentink was unaware of other taxa indigenous to the island and already known before 1879—namely *Nesomys rufus* Peters, 1870, and *Brachytarsomys albicauda* Günther, 1875—nesomyines that are morphologically more similar and whose consideration would have complicated his definition of *Hallomys*. Major (1897) would later correct this oversight and place *Hallomys* Jentink, 1879, as a junior synonym of *Nesomys* Peters, 1870. Notwithstanding its uncritical treatment as a subspecies or full synonym of *N. rufus* in the latter 1900s (Petter 1972, 1975; Honacki et al. 1982, Musser & Carleton 1993), the distributional, morphological, and genetic evidence subsequently marshaled to support *audeberti* as a valid species is incontrovertible (Carleton & Schmidt 1990, Ryan et al. 1993, Goodman & Carleton 1996, Jansa et al. 1999, Ryan 2003, Musser & Carleton 2005, Soarimalala & Goodman 2011).

Jentink (1879) interpreted the hind foot morphology of *audeberti*—its relatively large size and elongation of the central three digits—to indicate "its leaping habit," which inspired his comparisons to bipedal rodents, namely *Pedetes* (Anomaluromorpha: Pedetidae) and *Scirtetes*, now a junior synonym of *Allactaga* (Myomorpha: Dipodidae). The supposed locomotory habit of leaping was captured in Jentink's generic construction *Hallomys*, joining the Greek words that mean "to leap" and "mouse" (Palmer 1904). Individual *Nesomys* are ambulatory or cursorial, progressing by a bounding quadrupedal gait when moving swiftly over short distances; however, they are not bipedal ricochets as Jentink implied by his generic comparisons.

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Table 3.—Sex, age, and measurements of the type series of *Nesomys audeberti* (Jentink, 1879) compared with a recently collected population sample from the Parc National (PN) de Ranomafana. (M and F = male and female, respectively; Y and A = young and full adult class, respectively. Variable abbreviations are defined in Materials and Methods; sample statistics include the mean, ± 1 standard deviation, observed range, and sample size in parentheses. See Appendix 1 for specimen numbers.)

| Variable | RMNH 26527 lectotype "Savary" | RMNH 26528 paralectotype "Maisine" | RMNH 39356 paralectotype "Maisine" | PN de Ranomafana |
|---|---|---|---|---|
| Sex | M | M | F | |
| Age | Y | A | A | |
| DHFL | 54 | 52.5 | 55* | 53.6 ± 1.1<br>51.8–55.5 (10) |
| ONL | 48.5 | – | – | 49.1 ± 1.2<br>46.5–51.2 (19) |
| ZB | 24.4 | 25.4 | – | 25.5 ± 1.3<br>23.3–28.5 (18) |
| BBC | 16.9 | – | – | 17.3 ± 0.5<br>16.5–18.2 (19) |
| BOC | 11.4 | 11.0 | – | 10.6 ± 0.4<br>9.9–11.3 (19) |
| IOB | 8.7 | 10.0 | – | 9.4 ± 0.6<br>8.3–10.3 (19) |
| LR | 18.4 | 19.4 | – | 18.6 ± 0.7<br>17.3–19.9 (19) |
| BR | 8.5 | 9.4 | – | 9.5 ± 0.5<br>8.6–10.5 (19) |
| PPL | 16.3 | – | – | 16.2 ± 0.4<br>15.4–17.2 (19) |
| LBP | 8.7 | 9.3 | – | 8.8 ± 0.3<br>8.0–9.3 (19) |
| BM1s | 9.6 | 10.4 | – | 10.1 ± 0.5<br>9.2–11.1 (19) |
| PPB | 6.8 | 7.3 | – | 6.9 ± 0.3<br>6.3–7.4 (19) |
| LD | 13.2 | 14.0 | – | 13.4 ± 0.5<br>12.1–14.3 (19) |
| LIF | 9.4 | 9.8 | – | 9.4 ± 0.4<br>8.7–10.0 (19) |
| BIF | 3.4 | 4.0 | – | 3.6 ± 0.2<br>3.1–4.0 (19) |
| BZP | 4.4 | 4.3 | – | 4.9 ± 0.3<br>4.5–5.7 (19) |
| DAB | – | – | – | 7.3 ± 0.3<br>6.9–7.8 (19) |
| LM1–3 | 7.15 | 7.60 | – | 7.27 ± 0.25<br>6.88–7.89 (19) |
| WM1 | 2.09 | 2.28 | – | 2.25 ± 0.11<br>2.10–2.45 (19) |

* A "wet" hindfoot length was obtained from the fluid specimen (RMNH 39356).

*Restriction of the type locality*.—In his provision of the taxon's "Hab[itat]," Jentink (1879:109) mentioned two localities, "Maisine and Savary.—N. E. Madagascar," a compound designation that encompasses the type locality of all three syntypes. Selection of RMNH 26527 as lectotype correspondingly fixes the type locality as Savary (ICZN, 1999: Articles 73.2.3, 76.2). Restriction of the type locality to "Savary" is straightforward, following stipulations of the ICZN, but

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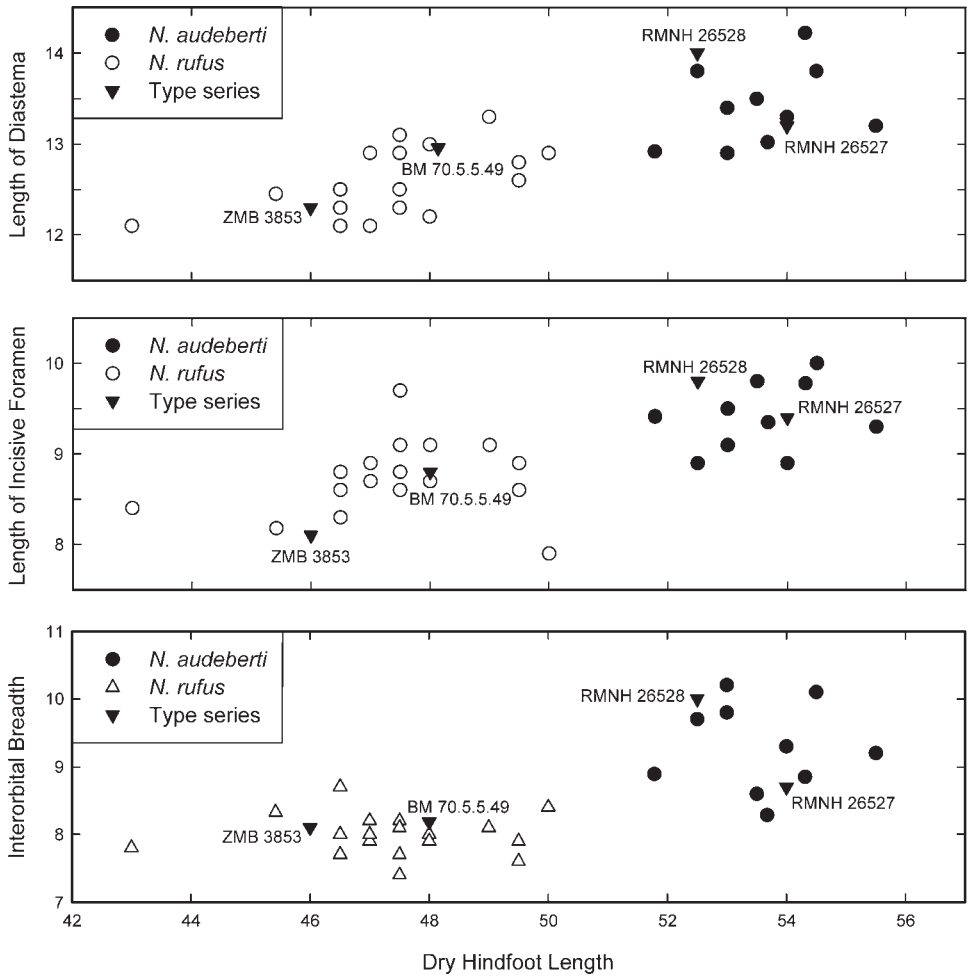



Fig. 9. Scatterplots (in mm) of dry hindfoot length versus select cranial dimensions for samples of *Nesomys audeberti* and *N. rufus* from the Parc National de Ranomafana, including relevant specimens from the original type series in the RMNH and ZMB, respectively, along with a comparably old specimen of *N. rufus* housed in the BMNH (see text for discussion). Notable are the specific associations of RMNH 26527, herein designated as lectotype of *Hallomys audeberti* Jentink, 1879, and ZMB-MAM 3853, the holotype by monotypy of *Nesomys rufus* Peters, 1870.

the modern-day location of Audebert's collecting locality Savary is problematic.

Audebert's orthographic renditions of Malagasy place-names have challenged attempts to equate them to modern geographic spellings and generated uncertainty about the distributions of many animals he collected (see discussions of Audebert's localities in Tattersall [1982:15], Vuillaume-Randriamanantena et al. [1985:111], and Carleton & Schmidt [1990:18]). This uncertainty is especially problematic for the significant series of lemurs he obtained (Schwarz 1931, Vuillaume-Randriamanantena et al. 1985, Tattersall 1982, 1986; Vasey & Tattersall 2002). Such also is the case with the three rodents he collected at Maisine and Savary, which verbatim spellings do not correspond to any geographic listings in the Gazetteer of Madagascar (U.S. Board of Geographic Names 1989) or in the online GeoNames server for the

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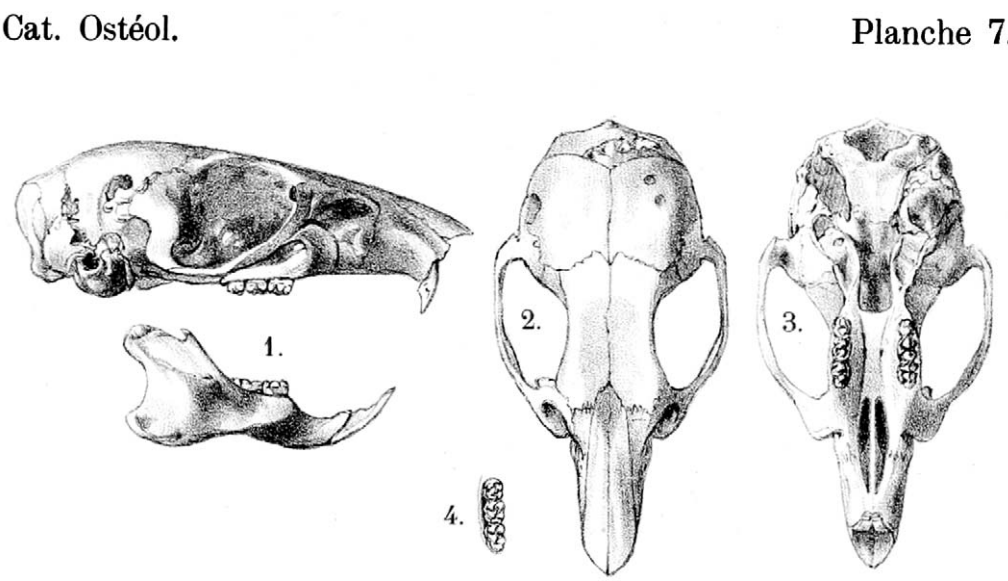



Fig. 10. Illustration of *Hallomys audeberti* as provided by Jentink in his *Catalogue ostéologique* of Leiden's mammal collections (1887:Plate 7), a work published eight years after his description of the species (1879). This illustrated individual, specimen "b" as then identified, is herein designated as the lectotype (RMNH 26527) of *Hallomys audeberti* Jentink, 1879. Jentink figured lateral views of the cranium and mandible (1), dorsal view of the cranium (2), ventral view of the cranium (3), and occlusal view of the right lower molars (4) (here reproduced ca. ×1.1; ONL = 48.5 mm). Certain details of cranial damage, especially apparent in the dorsal and ventral views, match the condition observed in RMNH 26527 and persuade us that this is the individual illustrated by Jentink in 1887, which correspondence heightens its utility as lectotype.

National Geospatial-Intelligence Agency (http://geonames.nga.mil/ggmagaz/; last accessed July 2013).

We integrated three information sources to improve understanding of Audebert's fieldwork in northeastern Madagascar: excerpts from his field diaries; correspondence preserved in the RMNH archives; and dates and localities recorded from RMNH specimen labels on non-passerine birds (ca. 400 specimens) and all orders of mammals (210 specimens). The whereabouts of Audebert's original field diaries are unknown and they may have become lost. However, some extracts from them remain in private possession, and these were located and kindly made available to us by Rudolf Herz from München, Germany. Unfortunately, these were transcribed in abstract form, not verbatim, seem inaccurate in places, and the typing is bad. We relied on these secondary extracts only where they elucidated information contained in the correspondence and on specimen labels. In the archives of the Leiden Museum are 14 letters sent by Audebert from Madagascar and addressed to Hermann Schlegel (1804–1884), then Director of the Leiden Museum, or to François P. L. Pollen (1842–1886), a Dutch merchant and naturalist. On Schlegel's instigation, Pollen and his assistant D. C. van Dam had earlier collected (1864–1866) in northwestern Madagascar for the Leiden Museum (e.g., Pollen 1868), and, being independently wealthy, Pollen had contracted Audebert to continue those activities in eastern parts of the island. The letters substantiate Audebert's travels along the northeastern coast during the years 1875–1879. Communications were sent from Tamatave (9 and 18 [two letters]

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July 1876, 12 January 1877), Antongil Bay (Sep 1876 [two letters]), Savary (4 March 1878 [two letters, discussed below]), Maranzettra (October 1878), Ngontzy Hill (illegibly dated; "1878" added in pencil in another hand), and Sambava (January "1878"—clearly a lapsus for 1879); one letterhead only reads Madagascar and two lack any locality of posting. Audebert prepared field tags with collecting localities and dates of collection, a progressive innovation for the era of natural history discovery. Unfortunately, his original notes have not been preserved, but the information was copied onto specimen labels written in Leiden, and conveniently for our purposes here, Jentink (1887, 1888, 1892) specified individual specimen localities and collection dates in his osteological and systematic catalogs of the Leiden Museum. Collation and reconciliation of these data sources reveal that many mistakes in labeling had occurred, probably during processing in the Leiden Museum, because several places and dates appear incongruous with a single itinerary, unless one assumes that he occasionally received specimens collected by others during the same period. Although Audebert did occasionally engage local hunters to procure specimens for him while collecting in a given area, as substantiated by his letters, we uncovered no evidence that he continued to receive specimens from these places after his departure.

Notwithstanding such inconsistencies, the specimen data, letters, and journal extracts allow a rough approximation of Audebert's travels in northeastern Madagascar (place-names are here spelled as they appear in his letters and on tags—see Table 4 for probable equivalents and collecting periods). Having received training and instructions from Pollen and Schlegel in the Leiden Museum, Audebert departed for Madagascar in 1875 (Holthuis 1997:280–281). After a four-week stopover in Mauritius, where he collected birds, Audebert probably arrived at Tamatave in September 1875. He proceeded northwards (Fig. 11), following the coastal trail that would become route nationale 5, to Vidoutra (also spelled Vouhidoutra), Foulpoint, Mahambo, and Fenerivo, places where he collected from October 1875 to July 1876; his main collecting stations were Vidoutra (October 1875), Foulpoint (November–December 1875) and Mahambo (February–June 1876). In July 1876, he returned to Tamatave, the port of shipment of his first collection to Leiden, via Hamburg as arranged through a German agent. Audebert traveled north again (on foot), reaching the southwest shore of Antongil Bay after a laborious march of seven days and collecting extensively around Mananare over August–December1876. From Mananare, he dispatched two more collections in September to a French agent at Tamatave, for eventual transport to Leiden via Marseille. In January 1877, he had settled again in Tamatave, the origin of another shipment of specimens. From this point, there is a 10-month hiatus in Audebert's letters and collecting dates; he apparently began a journey to Antananarivo, a trip not completed probably due to severe illness as he alluded in his letter of 4 March 1878 to Pollen. Audebert had resumed his field activities in November 1877 at Savary (Table 4), and he worked intermittently in this area until June 1878, along with other places such as Maisine and Mamtinbato; most material was collected at Savary and Maisine. Savary conceivably served as his headquarters because he apparently received mail here and some letters bear this locality in the letterhead (see below). Later in 1878, he revisited Mananare (June or July), Malewo (July–August), and Maranzettra (October), Mananare and Maranzettra being ports from which additional collections were shipped to Tamatave and thence onwards to Leiden. In January 1879, he was at Sambava and from there planned to go farther north, but his travels in this region

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are only summarily known from the diary excerpts, and Jentink (1887, 1888, 1892) recorded no mammals or birds collected from Sambava. Subsequently in 1879, other localities appear on mammal labels—Antsondrizima (February–March), Antsompirina (February–April), Ambasimbato (March), Andranafohiz (September)—but we haven't attempted to locate them. We surmise that Audebert journeyed back to Tamatave by ship. With his financial support from Pollen exhausted and having sought a new benefactor, he departed in 1880 for southeastern Madagascar, to the region of Farafangana and its hinterland, as documented in his own published travel accounts (Audebert 1882, 1883) as well as in period literature (Grandidier 1892, Connorton 1896).

In a letter to Schlegel (in German), dated 4 March 1878, Audebert approximated the location of Savary, addressing his letterhead as "Savary 4 Marz [sic] 1878 – Antongil Bai – westl[ich] v[on] Mananare, Grenze von Ancai, 7 Tagereisen im Innern" (= Savary 4 March 1878 – Antongil Bay – west of Mananare, border of Ancai, 7 days' journey into the interior). The date of Audebert's letter is chronologically consistent with the month of collection recorded for the lectotype RMNH 26527 (February 1878) and with Jentink's (1879) general placement of the locality in "N. E. Madagascar." The paralectotypes from Maisine, RMNH 26528 and 39356, are dated 16 and 6 March 1878, respectively. The timeframe of these collecting dates closely corresponds to the two missives Audebert wrote from Savary (4 March 1878), to Schlegel and Pollen, and dates for specimens collected at Maisine and Savary overlap in early 1878 (January–March; Table 4). These localities must lie in close proximity to one another, reachable by foot within the same local region.

"Mananare" as used by Audebert surely indicates the village Mananara at the mouth of Antongil Bay around which he collected in 1876 (Table 4, footnote 2), but it also references a provincial designation in the 1800s. At the height of its political and military domination, the Merina Kingdom had established a system of provinces, quasi-administrative units with loosely defined boundaries (Oliver 1886, Grandidier & Grandidier 1908); redistricting of provincial boundaries was instituted by the French in the late 1890s. At the time of Audebert's survey, the small Imerina province of Mananara[1] occupied the region to the west of Mananara village and Antongil Bay (e.g., Grandidier & Grandidier 1908: map facing p. 348). Mananara Province during the Imerina sovereignty is approximately congruent with the Mananara Avaratra Fivondronana, or District, according to present-day administrative subdivisions within Madagascar (see Fig. 11). Audebert's "Ancai," on the other hand, plausibly relates to the Ancai people (also spelled variously as Ancay, Ankay, Tankay, or Antankay in the early litera-

[1] Boundaries of the Imerina provinces were indefinite, their northern and southern borders along the eastern coast being roughly defined by east-west trending rivers. Oliver (1886:263) stated that Mananara Province was delimited by the Manambolosy River (mouth at 16°03′S) on the north and the Manompana River (mouth at 16°42′S) on the south, just opposite the northern tip of Ile Sainte Marie; to the west, "there is no definite line of frontier limiting the western boundaries, which extend into the forests which cover the eastern slopes of the lower and outer mountain ranges, extending parallel to the shore at a distance from the sea of from thirty to forty miles" (48–64 km). The distance Oliver gave for the western limit of Mananara approximately aligns with the present-day provincial boundary between Mahajanga and Toamasina. Grandidier & Grandidier (1908:349) instead interpreted the northern and southern borders of Mananara Province as the Fananehana River (mouth at 15°54′S) and Anove River (mouth at 16°37′S), respectively. The areal extent of Mananara as given by Grandidier & Grandidier is displaced slightly northward of that delimited by Oliver and is more or less congruent with the current borders of Fivondronana Mananara Avaratra (Fig. 11). A Sahavary and Sahafary lie just within the southern limits of either provincial definition.

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ture), an ethnographic group properly known as the Bezanozano. The Ankay or Bezanozano principally live within the Valley (or Plain) of Ankay, an open region on an intermediate plateau (700–950 m), bounded to the north by Lac Alaotra and to the south by Moramanga and enclosed along the east and west by forested uplands (Fig. 11). An Ancai border, found to the west of Mananara per Audebert's diary and his 1878 letter, may seem improbable because the physiographic limits of the Valley of Ankay and the ethnological distribution of the Ankay as understood today do not concord with his description. However, contemporary ethnographic maps, presumably available to Audebert, indicate an extension of the "Tankay" directly west of Antongil Bay (Sibree 1880, Oliver 1886); furthermore, Oliver (1886: map, facing p. 177) depicts the Plain of Ankay as extending far to the north of Lac Alaotra, to a latitude of about 16°30′S. Such period documents offer support to Audebert's 1878 interpretation of an Ancai border positioned to the west of Mananara and in proximity to Antongil Bay. We underscore that triangulation-mapping of Madagascar's geographic features and recognition of the island's indigenous peoples were being actively investigated in the late 1800s and were as yet poorly understood. Lastly, we should acknowledge the possibility that Audebert employed "Ancai" according to its strict Malagasy definition. Sibree (1880:129), for example, explained that "This open space is known as Ankày (from *hày*, a clearing), and the inhabitants are variously known as Tankày (or Takày)." In this context, Audebert may only have been describing open country at the border of forest or, generically, the people living in such open areas, which he encountered upon emerging from forest following his journey of seven days.

We agree with Vasey & Tattersall (2002) that Audebert's "Savary" is a plausible phonetic rendering, to a western European ear, of Sahavary or Sahafary, given the nearly silent emphasis of "h" in the antepenultimate syllable in Malagasy speech. These authors mapped (2002:Fig. 3) a Sahavary (15°19′S, 49°50′E) about 16 km NE Maroantsetra along the eastern bank of the Andranofotsy River (see our Fig. 11; National Geospatial-Intelligence Agency does not list a Sahavary in this region). Their regional interpretation of Audebert's Savary,[2] however, does not jibe with his placement of the locality to the west of Antongil Bay (letter of 4 March 1878 to Schlegel). Furthermore, the diary excerpts relate the treacherous crossing of the Mananara River during his westward trek to reach Savary, and in the companion letter of 4 March 1878 (in French) to Pollen, Audebert mentioned that he was planning to later descend (logically via the Mananara River) to Mananare on the coast to dispatch his collection ("Je voir descendre en quelque temps à Mananare à la côte pour vous expédier la collection ….."). Had Audebert descended (via the Andranofotsy River) from the Sahavary located to the north of Antongil Bay, as mapped by Vasey and Tattersall (2002), Maroantsetra would have been the logical destination for shipping his specimens. The

[2] The precise geographic location of "Savary," and other Audebert localities, is obviously critical to Vasey & Tattersall's (2002) study of ruffed lemurs, genus *Varecia*, and bears on their recognition of *V. variegata* and *V. rubra* as distinct species and interpretation of a hybrid zone between them. The authors (2002:Figs. 2–3, Table 2), citing Jentink (1892), reported examples of *V. variegata* and-or *V. rubra* at three Audebert localities: Maranzettra (both forms), Savary (*V. variegata*), and Malewo (*V. rubra*, plus one purported hybrid), and mapped these places to the north of Antongil Bay. If Audebert's Savary was instead to the west of the bay, as specified in his letter of 4 March 1878 and his diary extracts, then it would lie well within the distribution area of *V. variegata* as mapped by Vasey & Tatersall (2002:Fig. 2). Of course, in view of the immense technological strides in recovering DNA from old museum skins, actual genetic data would be preferred to infer hybridization rather than the apparent intermediacy of pelage chromatic patterns.

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Table 4.—Summary of localities listed in Jentink's catalogs (1887, 1888, 1892) for mammal specimens collected by J. P. Audebert, 1875–1878, in northeastern Madagascar (see Fig. 11), interspersed with dates of correspondence preserved in the Leiden Museum. Coordinates are indicated only to degrees and minutes (per NGA); collection dates indicated only for month and year (with plausible corrections bracketed where contradicted by correspondence and Audebert's diary excerpts).

| Audebert's orthography | Probable modern locality | Coordinates | Month and year |
|---|---|---|---|
| Vidoutra | Vohidrotra | 18°04′S, 49°24′E | October 1876 [lapsus for 1875[1]] |
| Maranzettra | Maroantsetra | 15°26′S, 49°45′E | August 1876 [1878], January 1876 [1879] |
| Mahambo | Mahambo | 17°29′S, 49°27′E | February–June 1876 |
| Tamatave | Toamasina | 18°09′S, 49°25′E | 3 letters, 9 & 18 July (2) 1876 |
| Foulpoint | Foulpointe | 17°41′S, 49°31′E | August 1876 |
| Mananare[2] | Mananara | 16°10′S, 49°46′E | August–December 1876 |
| Antongil Bay | [Mananara?] | | 2 letters, September 1876 |
| Passumbée[3] | [Ampasimbe?] | 17°05′S, 49°29′E | Sep 1876, November–December 1876 |
| Tamatave | Toamasina | 18°09′S, 49°25′E | Letter, 12 January 1877 |
| [No specimen records] | | | January–October 1877 |
| Savary[4] | Sahavary? | 16°32′S, 49°26′E | November–December 1877, January–June 1878 |
| Savary | Sahavary? | ? | 2 letters, 4 March 1878 |
| Maisine[5] | ? | ? | November–December 1878 [1877], January–May 1878 |
| Mamtinbato | [Maintimbato?] | ? | March–May 1878 |
| Mananare | Mananara | 16°10′S, 49°46′E | July 1878 |
| Malewo[6] | [Mahalevona?] | 15°24′S, 49°55′E | July–August 1878, January 1878 [1879] |
| Antongil Bay | [Maroantsetra?] | ? | Letter, September 1878 |
| Maranzettra | Maroantsetra | 15°26′S, 49°45′E | Letter, October 1878 |
| Marovato[7] | Marovato | ? | October 1878 |
| Sambava | Sambava | 14°16′S, 50°10′E | Letter, January 1878 [lapsus for 1879[8]] |

[1] Jentink (1887) gave the date for the lone mammal specimen collected as 20 October 1876, but a larger series of non-passerine birds were collected here, as "Vouhidoutra," from 8–21 October 1875. We suspect a transcription mistake.

[2] Mananare sensu Audebert is clearly the village Mananara, or Mananara Avaratra, located at the southwestern lip of Antongil Bay. Schlegel (1879:99) referenced "Mananare a place on the South-Western shore of the bay of Antongil" in his description of a new cuckoo species based on an Audebert specimen, collected 10 June 1878 at Ambodikilo near Mananare, and apparently paraphrasing data received from him (not preserved in the RMNH archives).

[3] Vuillaume-Randriamanantena et al.'s (1985) nomination of Ampasimbe is a plausible transliteration of Audebert's Passumbée, possibly the one they mapped near the coast and to the north of Mahambo (see Fig. 11) among the several villages of the same name in former Toamasina Province. However, collecting dates for Audebert's Passumbée are intermixed with those of Mananare and suggest closer proximity than the Ampasimbe proposed by Vuillaume-Randriamanantena et al. (1985). We cannot locate another Ampasimbe or its phonetic facsimile within the vicinity of Mananara.

[4] Vasey & Tattersall's (2002) phonetic interpretation of Audebert's Savary as Sahavary or Sahafary seems reasonable. They (2002:Fig. 3) located a Sahavary along the Andranofotsy River to the northeast of Maroantsetra. Other possibilities within the former Toamasina Province are situated to the southwest of Antongil Bay, which placement is consistent with Audebert's letters of 4 Mar 1878 (see Fig. 11 and text for discussion).

[5] Schwarz (1931) questionably listed "Fenerive" (= Fenoarivo Atsinanana) as the modern-day equivalent to Audebert's Maisine, but the phonemic elements of the two place names seem too dissimilar phonically to be the same collecting locality. Audebert mentioned (letter of 9 July 1876) Fenerivo as the coastal village where he had consigned a shipment to Tamatave, clearly distinguishing the two places; he also collected birds here, correctly labeled "Fenerivo"; his diary excerpts located Maisine to the west of Mananare and near Savary. The location of Maisine and its proper orthography remain obscure.

[6] Vasey & Tattersall (2002) equated Malewo to Mahalevona, in particular the village (15°24′S, 49°55′E) at the head of Antongil Bay to the east of Maroantsetra. We remain uncertain about the phonetic equivalence of these place-names, but Vasey & Tattersall's interpretation concords with Audebert's later letters posted from

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gazetted place-names Sahavary, a stream (16°30′S, 49°23′E), and Sahafary, a village (16°32′S, 49°26′E), do occur in close proximity near the boundary of Mananara Province as known in the 1870s (Fig. 11), to the southwest of Antongil Bay and just north of the Anove River (about a 50–55 km straight-line distance SW Mananara). At this point, we cannot conclude which of these places, if either, is the locality visited long ago by Audebert. We suspect that he would have preferred a settlement that could serve as a base and where mail could be received and dispatched via Mananara. Either geographic interpretation of Savary, whether to the north or to the west of Antongil Bay, falls within the broad distribution of the larger, white-bellied *Nesomys*, *N. audeberti*, as now documented in eastern rainforest from sea level to 1000 m (Carleton & Schmidt 1990, Ryan 2003, Soarimalala & Goodman 2011, Carleton & Goodman pers. obs.).

Although the geographic circumscription of Savary as summarized above is plausible, it ostensibly conflicts with Audebert's statement that Savary was reached upon a seven-day journey into the interior. Some early explorers, missionaries, and naturalists left meticulous records of hours and distances traveled overland in Madagascar along the then rudimentary trail system, typically following alongside waterways (Lloyd 1851, Pearse & Aitken 1875, Oliver 1886, Rand 1936). Distances of 30–40 km (18–25 mi) per day were commonly achieved on the trail, allowing for wide variation according to weather, trail condition, and topography. Audebert's locality modifiers for Savary, "Antongil Bay – west of Mananare," and the diary excerpts place the starting point of his trek at Mananara village. Even accepting the lower estimate of 30 km traveled per day, he would have penetrated deeply into the modern Mahajanga Province by the end of 7 days, journeying far to the west of eastern humid forest and the documented distribution of *N. audeberti*. However, Audebert complained to Pollen (letter of 4 March 1878) that the journey into the interior was extremely arduous, and the diary extracts relate his difficulties in bridging deep rivers and trailblazing the narrow, overgrown paths. Surmounting such hurdles would substantially diminish the number of kilometers a field team could cover per day. The diary extracts, like Audebert's letterhead, also confirm that the journey took seven days, with the added remark that it might have taken others even longer. Per the diary extracts, the expedition to Savary traversed countryside inhabited by the Betsimisaraka, a people who occupy coastal areas and lower woodlands of eastern Madagascar (approximately from Toamasina to Antalaha), not the Sihanaka or Sakalava who dwell in more interior regions westwards of Mananara. This ethnic evidence too, assuming that Audebert correctly characterized the local peoples, indicates that he had not penetrated so deeply into the interior as a typical 7-day trek would suggest.

←
Maroantsetra, with the plausible relocaton of his field activity to the north of the Bay before he set off northeastwards for Sambava, and with the known range of the red ruffed lemur (*Varecia rubra*) based on specimens collected at that site.

[7] The common occurrence of this village name within the former Toamasina Province disallows confident location of Audebert's Marovato. The dates for this locality based on mammal and non-passerine bird specimens are 17 October and 7 November 1878, a time frame which indicates its general location in the area of Maroantsetra.

[8] In his letter of October 1878 to Schlegel, Audebert related that his next destination would be Sambava ("Bin auf der Reise nach Sambava"). January "1878" must have been a New Year's lapsus for 1879.

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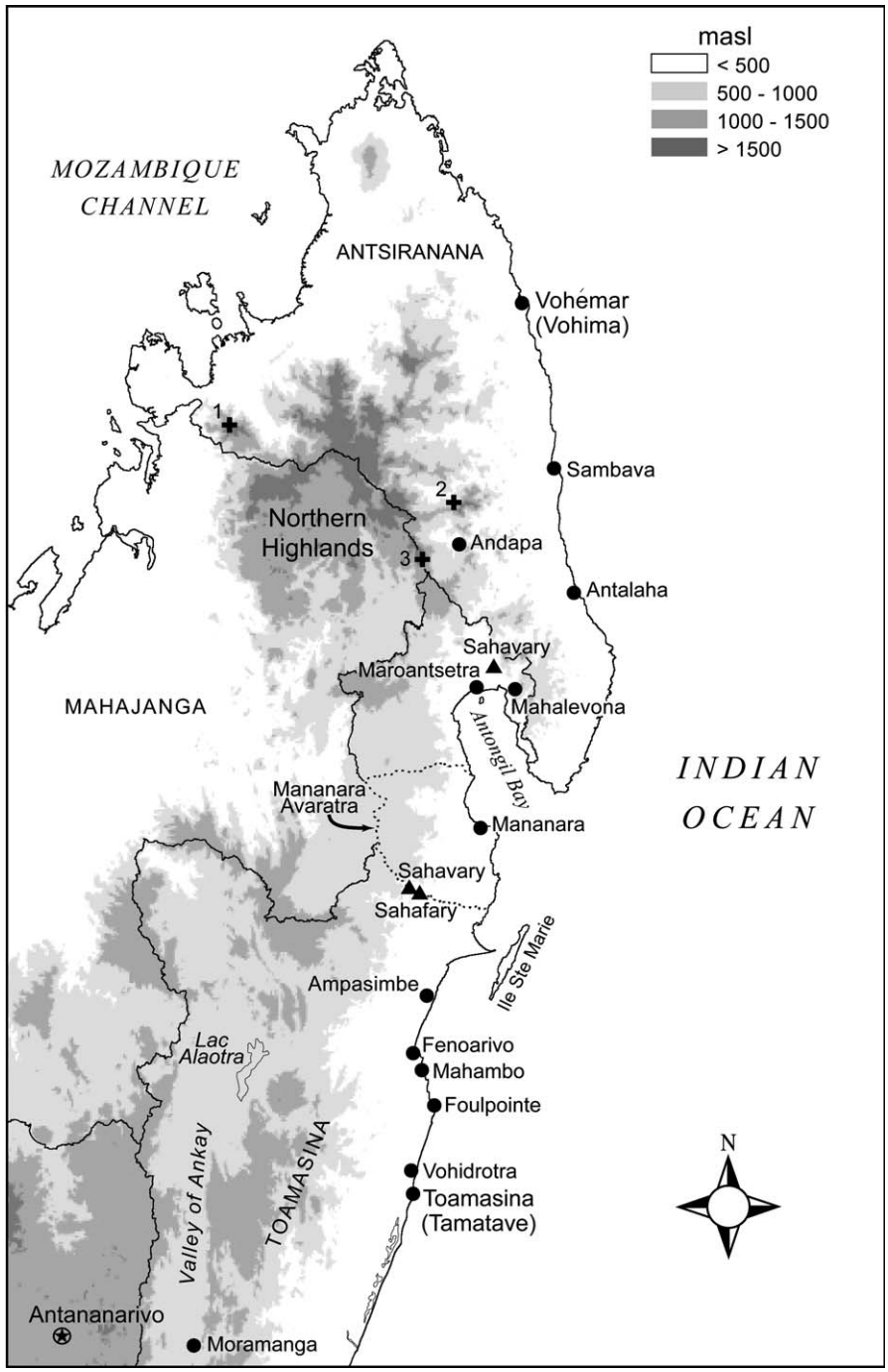



Fig. 11. Map of northeastern Madagascar illustrating provincial boundaries, place names, and geographic features mentioned in the text. Symbols: filled circles = towns and villages; filled triangles = localities possibly corresponding to "Savary," the restricted type locality of *Nesomys audeberti* (Jentink, 1879); crosses = localities in the Northern Highlands where recent specimens of *Nesomys rufus* have been documented (1, Réserve Spéciale de Manongarivo; 2, Parc National de Marojejy; 3, Réserve Spéciale d'Anjanaharibe-Sud). The dotted line indicates the current boundaries of Fivondranana Mananara Avaratra, which approximately

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Based on the evidence reviewed above, we emend the type locality of *Hallomys audeberti* Jentink as Madagascar, Toamasina Province (former), Analanjirofo Région, west of Antongil Bay toward the western frontier of Fivondronana Mananara Avaratra, "Savary."

*Nesomys rufus* Peters, 1870

*Type material and identification of the holotype.—Nesomys rufus* was described by Wilhelm Karl Hartwich Peters (1815–1883), German naturalist, explorer, and a longtime Curator and Director in the Zoological Museum of Berlin. At the time, Peters's (1870) new genus and species represented only the second endemic rodent known from Madagascar, named a year after A. Grandidier (1869) announced his discovery of the Giant Jumping Rat *Hypogeomys antimena*. Although Peters's description lacked mention of a holotype, unique catalog number, or illustration, the final line in his article (1870:55) conveyed that his new form was based on a dried male specimen from Vohima ("Ein getrocknetes männliches Exemplar aus Vohima"). This last bit of information enables certain identification of the type specimen of *N. rufus*.

Preserved in the archives of the Museum für Naturkunde, Berlin, is correspondence from Edward Gerrard Jr. addressed to Peters (see Appendix 2). One letter, dated 11 May 1870, proposed a transaction: "I beg to offer you the following skins from Vohima, Madagascar …," a listing that included one "Mus. About the size of a rat, chestnut colour with white under part" ("Mus" here connotes only a mouse-like rodent, not, necessarily, a species of the genus *Mus* Linnaeus). A subsequent letter from Gerrard, dated 18 May 1870, confirmed the purchase: "I have this day sent off a box containing several skins …," a shipment that contained the one "Mus" along with several tenrecs and lemurs (Edward Gerrard Jr. represented E. Gerrard & Sons, a business based in London that specialized in taxidermy; we shall expand on the Gerrard family in the next section). The acquisition and shipment of the "Mus" from Vohima predate Peters's description of *Nesomys rufus*, published 18 October 1870. The specimen received from Gerrard was undoubtedly the one that Peters cataloged in the Museum's Acquisition Catalogue of the Mammal Collection as "A1240 Mus Madagascar Gerrard." This same specimen later received its unique registration number and name in the General Catalogue of the Mammal Collection—"3853 | Nesomys rufus Ptrs. [= Peters] | Vohima, Madagaskar | mas. [= masculinus, male] | gek. [= gekauft, purchased from] Gerrard"—information that was all entered in Peters's handwriting (see Fig. 12) except "mas.," which was added by Angermann in 1991. Peters had initiated the Museum's continuous-numbering catalog system in 1857 (Angermann 1989), and he usually annotated specimens that he believed or knew to represent types with an asterisk, a mark applied next to ZMB 3853 (Fig. 12).

The evidence is persuasive that ZMB-MAM 3853 ("MAM" was latter added to indicate a mammal specimen) represents the sole example then available to Peters when he named his new taxon. Peters (1870) mentioned only a single specimen in his description of *N. rufus*; the particulars of its purchase indicate that only one "Mus" specimen from Vohima was re-

←
corresponds to the limits of the Imerina province of Mananara circa the late 1800s. The conventional interpretation of Vohima (= Vohémar or Iharana), a seaport on the northeast coast, as the type locality of *Nesomys rufus* Peters, 1870, is far removed from the known distribution of the species in upper lowland and montane forest (700–2300 m, fide Soarimalala & Goodman 2011).

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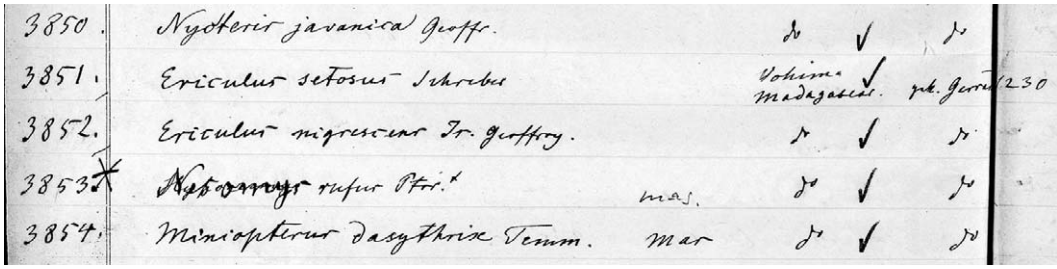



Fig. 12. Page from the General Catalog of the ZMB mammal collection that includes the entry for the specimen of *Nesomys rufus* (ZMB-MAM 3853), here identified as the holotype by monotypy of Peters's (1870) species. Although the original description contained no catalog number, Peters later applied an asterisk to specimens that he believed or knew to represent types.

ceived in 1870; no other specimens of *Nesomys* were cataloged along with ZMB-MAM 3853. Under these circumstances, ZMB-MAM 3853 is rightly considered the holotype, as fixed by monotypy, of *Nesomys rufus* Peters, 1870 (ICZN 1999: Article 73.1.2). Similarly, *Nesomys rufus* Peters, 1870, stands as type species of the genus by reason of monotypy (ICZN 1999: Article 68.3).

The holotype is in poor condition, the skin partially bald and the skull heavily damaged. Only secondary labels are attached, in the handwriting of Inge Johnke, technician of Hermann Pohle (1892–1977), former Curator of Mammals in the ZMB; the skin was probably converted from a whole mount to study skin and the skull repaired during his curatorship (1926–1951; Angermann 1989). Robert S. Voss, American Museum of Natural History, elaborated on the condition of the holotype during a visit to the Museum für Naturkunde, in a letter (November 1996) sent to Carleton and quoted verbatim below.

> "ZMB 3853. Vohima, Madagascar, Gerrard V. [information penned on skin tag]
>
> The skin, probably remade from a live-mount, and possibly originally preserved in fluid (the exposed skin where the fur has slipped off has that appearance) [originally a dry specimen according to Gerrard's invoice], is missing large patches of fur, esp. on the left side of head and neck, the entire rump, and (alas!) most of the ventral surface.
>
> Dorsally, the animal appears to have been a shaggy uniformly red-brown rat. Ventrally, there is pale fur that may have once been white (the specimen is now extremely dirty) or cream; some of the fur on the throat might have been pale to the roots, but the pale hair on the chest appears to be gray based (or it could be dirty); certainly, however, the venter was not uniformly red like the dorsal surface. Fur is missing midventrally over the abdomen and groin, but some lateral abdominal fur remains and that is red-brown over gray. The right HF [hind foot] is measurable and is about 46 mm from heel to claw of longest digit.
>
> The skull is broken, with a braincase once repaired by fabric and glue but now falling apart again. There are only bits and pieces of the mandible. However most of the anterior part of the skull is intact and measurable: [See Table 5].
>
> The animal is an adult with fully erupted and moderately worn M3s."

Peters's (1870) specific description, rendered when his single specimen was in much better condition, is sufficiently detailed to remove any doubt about the morphological identity of the new species *N. rufus*, particularly as it can be distinguished from Jentink's (1879) *N. audeberti*. Peters viewed *rufus* to be as large as *Mus decumanus* (= *Rattus norvegicus*), a reasonable size approximation for all living species of *Nesomys* known today (Table 1), but uninformative for specific discrimination. He described the dorsal pelage as russet-brown, intermixed with buff and accented by brighter rusty-red along the cheeks, flanks, and upper fore and hind limbs. The reddish intensity along the sides is typical of examples of *N. rufus*, less

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pronounced in those of *N. audeberti*. He described the ventral pelage—lips, chin, throat, chest, and middle abdomen—as white, but significantly remarked that the ventral hairs are slate-colored at their base. In examples of *N. audeberti*, the white coloration of the underparts typically includes the base of hairs (ventral hairs self-colored white). Peters also noted that the tail tip is covered with short white hairs, contrasting with the dusky hairs that envelope most of the tail, but this trait variably occurs in both eastern species (notably, the two mounted skins in the type series of *N. audeberti* also possess white tips; see above). Measurements of the hindfoot of ZMB-MAM 3853—46 mm, with claw, per Voss and 48 mm per Peters (method unknown)—fall within the range recorded for population samples identified as *N. rufus* (Table 5). Difference in length of the hind foot is a useful feature for separating examples of *N. rufus* from those of *N. audeberti*, the former averaging smaller than the latter with minimal overlap in their ranges (Ryan et al. 1993, Goodman & Carleton 1996; and see Tables 1, 3, and 5). Lastly, those cranial variables that could be recorded from the broken skull of ZMB-MAM 3853 unambiguously associate it with the smaller species of *Nesomys* known to inhabit humid forests (Fig. 9, Table 5).

Two other specimens, MNHN 1872.321 and BMNH 70.5.5.49, deserve mention for their antiquity. MNHN 1872.321 consists of a skin mounted in a lifelike pose upon a wooden pedestal. It is labeled as a "type" of *Nesomys rufus* and bears a supplementary red type-tag numbered 328, the sequential number assigned in Rode's (1945:28) type catalog of MNHN Rodentia. The provenience is given only as Madagascar. The skin's condition is poor, the pelage badly faded with patches of fur missing, the tip of its tail and pinnae broken off and missing. Although obviously faded, presumably after decades on exhibit and exposure to light, the dorsal color agrees reasonably with the reddish form typical of *N. rufus*; the ventral fur is paler, especially on the chin, throat, and chest, but becomes darker over the abdomen and inguinal region where it is only slightly paler than the dorsum. In spite of the general bleaching, the dorsal-ventral pelage transition, even on the forequarters, does not suggest the sharp contrast of bright white underparts as commonly observed in specimens of *N. audeberti*. The plantar surface of the hind foot is positioned nearly prone on the pedestal; the DHFL of MNHN 1872.321 measures 47 mm, decidedly within the range documented for samples of *N. rufus* (Table 5). Rode (1945) reported that the skull had been removed and lost, and Carleton located no skull when he examined the specimen in 1987. Rode formally reported MNHN 1872.321 as a paratype of *N. rufus*, obtained from W. Peters of the ZMB (a transaction also substantiated on the bottom of the wooden base—"Acquis par exchange à Mr. Peters"). The ZMB Acquisition Catalogue does document a "*Nesomys* Madagaskar Gerrard," number A1287, penciled by Peters as exchanged to Paris ("vertauscht nach Paris für *Cryptoprocta*"). As explained above, ZMB-MAM 3853 is the holotype by monotypy of *N. rufus*, and no other specimen can be demonstrably associated with Peters's original description. MNHN 1872.321 is not a paratype of Peters's (1870) taxon and lacks any name-bearing significance. The MNHN skin may be viewed as an old specimen of *N. rufus*, collected very early in the discovery of Madagascar's indigenous rodents, but without archival research to illuminate its geographic origin, its possible stature as an original topotype is doubtful (and see discussion below).

BMNH 70.5.5.49 consists of a round skin with imperfect skull. The occipital region is missing, a condition suggesting that the specimen was originally prepared like a bird skin, with the brain removed and the skull extracted later for cleaning.

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The pelage color and pattern, including a white tail-tip (10 mm long), size of hind foot (DHFL = 48 mm), and measurable cranial dimensions collectively confirm the specimen's identification as *N. rufus* (Fig. 9, Table 5). The skin label is old, although apparently not an original field tag, and indicates "Vohima, Madagascar" as the locality, purchased from a Mr. Cutter as part of the Crossley accession. Thomas (1906) acknowledged a collection of 133 mammals from Madagascar received in 1870 from Alfred Crossley, which included the specimen eventually cataloged as BMNH 70.5.5.49 (also confirmed by Paula Jenkins, BMNH, pers. com.). It was initially identified only as "*Mus*" in the museum register but later corrected to "*Nesomys rufus* Ptrs." The museum number indicates that it was the 49th specimen cataloged on 5 May 1870, the same month and year when Gerrard offered the "Mus" from Vohima to Peters and the ZMB. BMNH 70.5.5.49, like MNHN 1872.321, has no name-bearing value, but circumstantial evidence suggests that it is an original topotype, acquired by the same collector (Crossley) who obtained the holotype ZMB-MAM 3853 (as elaborated below).

The generic name *Nesomys* combines the Greek words for island and mouse (Palmer 1904:458), perhaps conveying Peters's (1870) appreciation of the unique characters possessed by this rodent dwelling on the faraway island of Madagascar. In the ZMB catalog, Peters's new genus *Nesomys* is written over and partially obscures another genus (see Fig. 12), which we believe to be *Hypogeomys*, the first-known nesomyine described a year earlier by A. Grandidier (1869). Peters would have been familiar with Grandidier's new taxon and may have initially considered naming *rufus* as a second species of *Hypogeomys*. Instead, he (1870) ultimately emphasized the complex molar enamel patterns in his generic diagnosis of *Nesomys* and drew attention to its dental resemblance to *Hesperomys* (= *Peromyscus*) of the Western Hemisphere, not to the gerbilline and murine rodents that inhabit nearby continental Africa. Peters was familiar with the comparatively simple molars of these rodent groups as a result of his extensive natural history collecting in southern Africa, in contrast to the complex molars of *Hesperomys* (*Peromyscus*) that he could observe using exchange material maintained in ZMB at the time (e.g., ZMB-MAM 1681–1701).

*Localization of a type locality*.—Peters (1870) identified the single specimen of *Nesomys rufus* as a male from Vohima. "Vohima" was thereafter repeated as the type locality of Peters's taxon, without comment on its geographic location or possible correspondence to modern placenames (Trouessart 1904, Allen 1939, Ellerman 1941, Honacki et al. 1982). In his taxonomic study of the island's iconic lemurs, however, Schwarz (1931) cited older specimens collected by Crossley at Vohima as from "Vohémar, N. E. coast," clearly intending the seaport village on Madagascar's northeastern coast, former Antsiranana Province (Fig. 11); the equivalence of Vohima to Vohémar was offhandedly accepted in later gazetteers published for various Malagasy groups (Jenkins 1987, Carleton & Schmidt 1990). Ivohimarina, Vohimarina, Vohima, Vohémar, and Vohémaro were used interchangeably on period maps and geographic literature in the latter 1800s for the coastal village now called Iharana (13°21′S, 50°00′E); for example, A. Grandidier (1892:216 bis) mapped the start of Crossley's 1869 expedition as Vohimarina, but listed his itinerary in the accompanying table as originating from Vohémar (1892:216). Acceptance of this Vohima (Vohémar) as Peters's type locality presents an enigma. As currently documented, populations of *N. rufus* inhabit upper lowland to montane forests, 800–2300 m; the species has not been obtained in more lowland settings along the eastern portion

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Table 5.—Sex, age, and measurements of the holotype of *Nesomys rufus* Peters, 1870, two old specimens perhaps also collected by Crossley in the early 1870s, and a recently collected population sample from the Parc National (PN) de Ranomafana. (M = male; A = full adult class. Variable abbreviations are defined in Materials and Methods; sample statistics include the mean, ± 1 standard deviation, observed range, and sample size in parentheses. See Appendix for specimen numbers.)

| Variable | ZMB-MAM 3853* holotype | BMNH 70.5.5.49 topotype? | MNHN 1872.321 topotype? | PN de Ranomafana |
|---|---|---|---|---|
| Sex | M | ? | ? | |
| Age | A | A | A | |
| DHFL | 46.0 | 48.0 | 47.0 | 47.3 ± 1.6<br>43.0–50.0 (20) |
| ONL | – | – | – | 45.5 ± 0.9<br>43.8–47.5 (29) |
| ZB | – | 22.6 | – | 23.7 ± 0.6<br>22.6–24.7 (29) |
| BBC | – | – | – | 16.6 ± 0.4<br>16.0–17.3 (30) |
| BOC | – | – | – | 9.8 ± 0.3<br>9.1–10.3 (29) |
| IOB | 8.1 | 8.1 | – | 7.9 ± 0.3<br>7.4–8.7 (30) |
| LR | – | 17.5 | – | 16.8 ± 0.6<br>15.8–17.9 (29) |
| BR | 8.6 | 8.4 | – | 8.6 ± 0.3<br>7.9–9.2 (29) |
| PPL | – | – | – | 15.2 ± 0.4<br>14.3–15.9 (30) |
| LBP | – | 8.5 | – | 8.4 ± 0.5<br>7.6–9.6 (30) |
| BM1s | 9.7 | 9.7 | – | 9.8 ± 0.3<br>9.1–10.4 (30) |
| PPB | – | – | – | 6.5 ± 0.3<br>6.0–7.1 (30) |
| LD | 12.3 | 13.0 | – | 12.5 ± 0.4<br>11.7–13.3 (29) |
| LIF | 8.1 | 8.8 | – | 8.7 ± 0.4<br>7.8–9.7 (29) |
| BIF | 3.0 | 3.3 | – | 3.4 ± 0.2<br>3.1–3.7 (30) |
| BZP | 3.9 | 4.2 | – | 4.3 ± 0.2<br>3.9–4.8 (30) |
| DAB | – | – | – | 6.7 ± 0.2<br>6.3–7.2 (27) |
| LM1–3 | 6.80 | 6.94 | – | 7.04 ± 0.17<br>6.71–7.43 (30) |
| WM1 | 2.10 | 2.01 | – | 2.21 ± 0.09<br>2.02–2.46 (30) |

* Measurements kindly recorded by R. S. Voss (AMNH).

of the island, places where the larger *N. audeberti* is known to occur (Carleton & Schmidt 1990, Ryan 2003, Soarimalala & Goodman 2011). The sites nearest to Vohima where examples of *N. rufus* have been obtained lie in the Northern Highlands (Fig. 11), e.g., in the protected areas of Anjanaharibe Sud and Marojejy (Goodman & Carleton 1998, Carleton & Goodman 2000).

As documented by archival letters in the Museum für Naturkunde (Appendix 2),

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the specimen from Vohima that was to become Peters's type was purchased from one Edward Gerrard Jr. Edward Gerrard Jr. (1832–1927), or the second, was the eldest son of the E. Gerrard (1810–1910) who long worked for the BMNH during its formative era, notably as Curator of the skeletal collections and Keeper of the museum's registers (Sharpe 1906, Morris 2004). Although the senior Gerrard remained a lifelong museum employee, he also established a commercial firm, E. Gerrard & Sons, which featured taxidermy and related business ventures and remained a family enterprise until the 1960s (Frost 1987, Morris 2004, 2010). Early business pamphlets and company letterheads of E. Gerrard & Sons advertised their services not only as "Naturalists and Taxidermists" but also as supplier of natural history material to museums; in his history of the BMNH bird collections, Sharpe (1906) identified E. Gerrard Jr. as an important purchasing agent for the British Museum during the years 1870–1905. Trade in natural history specimens thrived in the late 1800s, supporting a cadre of dealers and purchasing agents, middle men who directly procured specimens from explorers and naturalists and widely dispensed them to European museums, often without transmitting critical data about the collector or geographic source. Schwarz (1931:399) encountered this problem in his revision of Lemuridae: "Among the older collections, two are most conspicuous, those of A. Crossley and J. Audebert; both of them have passed through the hands of dealers—Cutter and Gerrard have sold Crossley's, and G. Schneider [has sold] Audebert's collections." Similarly, labels on older nesomyine specimens may bear the name of Boucard, Cutter, Gerrard, or Rosenberg, but their significance, whether as original collector or natural history dealer, is sometimes obscure.

Knowledge that the ZMB acquired the specimen of *N. rufus* from E. Gerrard Jr. persuasively identifies its collector and plausibly narrows the geographic possibilities of its origin. Thomas (1906), for mammals, and Sharpe (1906), for birds, reported several important vertebrate accessions acquired from Madagascar over the years 1870–1875; these originated from the expeditions of Alfred Crossley and were purchased for the BMNH through the agencies of William D. Cutter or E. Gerrard Jr. The oldest BMNH specimen of *N. rufus* (70.5.5.49) is from Vohima, was acquired by Cutter as part of the Crossley collection, and was cataloged in the same month that Gerrard had confirmed the sale of the "Mus" from Vohima to the ZMB. Alfred Grandidier (1892) identified several itineraries of Crossley in 1869, one from Vohémar (or Vohimarina per the map) to Antalaha along the northeastern coast and others from the eastern coast (Mahambo, Tamatave) inland to the region of the "Antsihanaka" (We have not, at this stage, authenticated Grandidier's map and dates—whether his primary sources were based on common knowledge shared by early European explorers, correspondence with those individuals, or unpublished travel logs—all of which, while ultimately necessary, is a daunting research project by itself).

Richard Bowdler Sharpe (1847–1909), renowned ornithologist and Assistant Keeper in the BMNH, promptly published upon several Crossley accessions in a series of articles in the *Proceedings of the Zoological Society of London* (Sharpe 1870, 1871, 1872, 1875). In the first of these reports, Sharpe acknowledged the receipt and geographic origin of the birds as follows (1870:384–385; read to the Zoological Society on 9 June).

> "I have recently been favoured by Mr. Cutter, Natural History Agent, of 35 Great Russell Street, Bloomsbury [neighborhood of London], with the inspection of birds formed by Mr. A. Crossley in the northern portion of Madagascar. Ornithologists are greatly indebted to Mr. C.

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> Ward of Halifax, who, at his own expense, equipped Mr. Crossley for this expedition." ….
>
> "Mr. Cutter informs me that Mr. Crossley first made a trip into the province of Vohima, in the northern corner of the island; but on this excursion he does not seem to have collected many birds. Afterwards returning to Tamatave, he proceeded inland to Antananarivo and thence northwards to Nossi Vola, which he informs me, is to the southeast of Lake Alout. Here, and at Saralalan, a place about seven or eight miles to the eastward of Nossi Vola, most of the birds were collected."

Sharpe's remarks are revelatory in several regards. First, the knowledge that Crossley traveled "into the province of Vohima" indicates that the collecting designation Vohima was meant as a region, not strictly the village of the same name on the northeast coast. In the late 1800s, a Vohémar or Iharana province or district of indeterminate boundaries occupied what is now the eastcentral portion of the former Antsiranana Province (Oliver 1886, Grandidier & Grandidier 1908). Such an older provincial designation would have included eastern ranges of the Northern Highlands and introduces many possible landscapes where examples of *N. rufus* could have been obtained. If Crossley had followed the 1869 coastal itinerary mapped by Grandidier (1892), from Vohémar to Antalaha, a side excursion from Sambava to Andapa would have placed him amidst mountains and surrounded by appropriate montane forest inhabited by populations of *N. rufus* (Fig. 11). Indeed, the Mission Zoologique Franco-Anglo-Américaine would follow the trail between Andapa and Sambava a half-century later and collect *N. rufus* in the mountains to the west of Andapa (Rand 1936, Carleton & Schmidt 1990). Second, Crossley apparently curtailed his collecting along his Vohémar-Antalaha route, due to unproductive results, and next focused his field activities in the eastcentral region. Here, Grandidier (1892) depicted several itineraries of Crossley in 1869: e.g., from the coastal village of Mahambo inland to the Antsihanaka region, eastwards of Lac Alaotra; and from Tamatave to Ambatondrazaka (17°50′S, 48°26′E), a village directly south of Lac Alaotra. Such treks would have crossed highlands and their montane forests to the east of the Valley of Ankay, passing through mountains where examples of *N. rufus* have been more recently vouchered (Carleton & Schmidt 1990, Carleton & Goodman pers. obs.). Curiously, Sharpe (1870, 1871, 1872, 1875) never mentioned Vohima as a collecting site in any of his four reports on Malagasy birds obtained by Crossley; instead, most specimens are documented from Nossi Vola (17°43′S, 48°39′E, as Nosivola) and Saralalan (not located), including the discovery of *Mystacornis crossleyi* new genus and species, with dates of collection given for Nov 1869. Nonetheless, some mammals survive that bear Vohima as their collecting locality, including specimens of *N. rufus* (BMNH 70.5.5.49, ZMB-MAM 3853) and certain primates (Schwarz 1931, Jenkins 1987); we broadly interpret this geographic source to indicate the older "province Vohima," not the coastal village. Third, Sharpe's remarks, as quoted above and as found in his other papers, reveal that some correspondence may yet exist, between Sharpe, Crossley, and-or Cutter, that would shed light on Crossley's travels and collecting localities. In the last of his taxonomic reports, Sharpe (1875:70) referred to Crossley as "my old correspondent."

In summary, we accept that the holotype of *Nesomys rufus* (ZMB-MAM 3853) originated from one of Alfred Crossley's expeditions conducted in 1869 and that it was acquired from him by Edward Gerrard Jr., a London natural history dealer who sold it to the Berlin Museum in May 1870. Furthermore, we are confident that the type specimen did not issue from the coastal village and port of Vohima (Vohémar), as conventionally understood (e.g., Carleton & Schmidt 1990). Accepting

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that specimen data can be interpreted broadly to mean the late-1800s province of Vohima, sensu Sharpe (1870), then "former Province of Vohima, Northern Highlands, mountains surrounding Andapa" is a reasonable, albeit nonspecific, reformulation of the type locality. Without additional archival research, however, we cannot exclude the possibility that the holotype was obtained in forested ridges to the east of Lac Alaotra, collected during one of Crossley's later expeditions that originated from the east-central coast, and all subsequently conflated by indiscriminate natural history dealers as from "Vohima."

## Postscript and Taxonomic Summary

A note on the tag attached to a round skin of *Nesomys audeberti* (USNM 360852), obtained 23 December 1948 by Harry Hoogstraal, tersely records the circumstances of the specimen's collection: "Shot in late afternoon on ground in original forest. Skull shattered." Hoogstraal's encounter probably typifies the happenstance manner by which all original specimens that comprise the type or type series of the three species of *Nesomys* were procured: dispatched by shotgun, using small shot intended for killing birds, by hunters who opportunistically crossed paths with large rodents active in the early morning or late afternoon, a time frame consistent with the biphasic diurnal habits of the three species (Ryan et al. 1993, Goodman & Schütz 2003). Certainly, the damage sustained by Hoogstraal's specimen resembles, to a greater or lesser degree, that which we observed among the name-bearing holdings of *Nesomys*. Not until C. I. Forsyth Major's expedition of 1894–1896 did Madagascar's small mammals become the focus of directed biological survey, collected in series and using field methods that (usually) preserved intact the animal's cranium and skin (Major 1896b, Jenkins & Carleton 2005).

Too little attention has been devoted to pinpointing the collecting localities of Audebert and Crossley and recovering their itineraries, conducted at a time when Madagascar's forested landscapes were notably more pristine than today and native mammal populations were still hale and unfragmented. As attested by numerous authors in various contexts (e.g., Schwarz 1931, Vuillaume-Randriamanantena et al. 1985, Tattersall 1982, 1986; Vasey & Tattersall 2002; also see our footnote 2), the irreplaceable collections of lemurs obtained by Audebert and Crossley remain relevant to understanding their taxonomy and distributions and alone justify such a research investment. As covered herein, taxonomy of Madagascar's indigenous small mammals too would profit from such an investigatory undertaking.

Of the two explorer-naturalists, the itinerary of Audebert is the more tractable reclamation project. Nevertheless, it will require a multifaceted collaboration that blends the talents of a multilingual expert, a geographer conversant with older Madagascan place-names and their transliteration into French or English, search for more material in Leiden and other museums, and knowledgeable systematists to critically reidentify Audebert's specimens, especially the birds and lemurs, according to the best taxonomic standards. The existence of some of Audebert's original correspondence to Pollen or Schlegel, preserved in the Leiden Museum, has proved to be a promising start. Collation of localities and dates, as given on specimen labels and, for mammals, in Jentink's (1887, 1888, 1892) catalogs, has helped us to sketch Audebert's travels, identifying some hitherto indeterminate place-names or at least restricting the areas where these places must have occurred. Nonetheless, we encountered several discrepancies between dates and localities,

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probably, or in some cases clearly, stemming from errors in transcription of Audebert's original data. Regrettably, his original labels were not preserved, and many specimens bear incomplete data that cannot be reconstructed for want of the original tags and field journals. Many of Audebert's specimens, regarded as "duplicates" by the Leiden Museum, were sold to dealers (G. A. Frank Jr. of Amsterdam and Gustav Schneider in Basel) or exchanged with other museums, as commonly practiced in that period. Location and inclusion of such material should further refine Audebert's expedition that we developed here. According to Audebert's letters, the totals of bird specimens being shipped to Leiden substantially outnumbered those of the mammals he collected (principally lemurs); consequently, distillation of all the ornithological data may prove more informative (Audebert also mentioned collections of other animal groups that were returned). Together, the geographic intersection of birds and mammals with restricted distributions will greatly narrow the possible search limits for Audebert's indeterminate localities.

Astonishingly little is known about the specific routes traveled and localities visited by Alfred Crossley (1829–1877), British collector who worked in Madagascar principally over the years 1869–1875. His field efforts contributed significantly not only to the early documentation of lemur taxonomy (Schwarz 1931, Tattersall 1982), but also generated important series of small mammals, birds, insects, and plants (Thomas 1906, Sharpe 1906, Dorr 1997). Crossley's collections were dispersed to multiple museums by commercial dealers, especially Cutter and Gerrard, and original locality information, if it existed, has been lost for many specimens that bear his name as collector. Still, we are encouraged by Sharpe's (1870) remarks, suggesting that some correspondence, between him, Crossley, and-or the dealers Cutter and Gerrard, may yet reside in museum archives. Our fragmentary knowledge of Crossley's collecting sites would be considerably improved by efforts to locate such correspondence and to consolidate whatever data can be retrieved for probable Crossley specimens housed in various museums. For one example, Powzyk & Thalmann (2003) puzzled over *Lichanotus mitratus* Peters (1872), a synonym of *Indri indri*, and Schwarz's (1931) opinion that the holotype originated from the Masoala Peninsula, east of Antongil Bay. Indri are not currently known to occur in this region. However, the sources of *Lichanotus* mentioned by Peters, Nossi Vola and Saralalana, recall the correspondence between Cutter and Sharpe (as paraphrased in Sharpe 1870:384–385; see above), which places these localities to the southeast of Lac Alaotra, situated in upland forest well within the documented distribution of *Indri indri*.

Happily, our three nomenclatural essays on *Nesomys* have disclosed no contradictions between original descriptions and the current systematic understanding of specific identifications and distributions. In particular, and notwithstanding the reservations of some (Carleton & Schmidt 1990, Goodman & Carleton 1996), observations and measurements recorded for the primary name-bearing specimens of *N. rufus* and *N. audeberti* vindicate the application of those names to the species morphologies and genetic entities as now understood for populations in eastern Madagascar (Fig. 8). In summary, we present full synonymies for the living species of *Nesomys* that incorporate the amended elements of their taxonomic foundation as here proposed.

## *Nesomys* Peters, 1870

*Nesomys* Peters, 1870:54.
*Hallomys* Jentink, 1879:107.

*Type Species*.—*Nesomys rufus* Peters, 1870, by monotypy.

*Contents*.—*Nesomys rufus* Peters, 1870; *N. audeberti* (Jentink, 1879); *N. lambertoni*

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G. Grandidier, 1928; †*N. narindaensis* Mein, Sénégas, Gommery, Ramanivosoa, Randrianantenaina, & Kerloc'h, 2010.

*Nesomys rufus* Peters, 1870

*Nesomys rufus* Peters, 1870:55.—Trouessart, 1897:510, 1904:396 (systematic checklists).—Grandidier & Petit, 1932:100 (taxonomic summary).—Allen, 1939:318 (systematic checklist).—Ellerman, 1941:376, 1949:174 (classifications).—Rode, 1945:28 (type catalog).—Petter, 1972:664 (taxonomic synopsis).—Honacki et al., 1982:432 (systematic checklist).—Corbet & Hill, 1980:158, 1986:177, 1991:166 (systematic checklists).—Carleton & Schmidt, 1990:26 (gazetteer, distributional summary).—Ryan et al., 1993:101 (natural history summary).—Musser & Carleton, 1993:679 (systematic checklist).—Goodman & Carleton, 1996:273 (faunal report, morphological identification), 1998:210 (faunal report).—Goodman et al., 1999:232 (faunal report).—Jansa et al., 1999:255 (phylogenetic relationship).—Carleton & Goodman, 2000:250 (faunal report).—Goodman & Soarimalala, 2002:387 (faunal report).—Ryan, 2003:1388 (natural history summary).—Musser & Carleton, 2005:952 (systematic checklist).—Marquart & Harisoa, 2006:197 (ecology).—Soarimalala & Goodman, 2011:121 (field guide, distribution, morphological recognition).

*Nesomys r*[*ufus*] *rufus*: Petter, 1962:571 (new rank, retained as valid subspecies); 1975:3 (identification manual).

*Holotype*.—ZMB-MAM 3853, as fixed by monotypy, skull with skin, an adult male probably collected by A. Crossley in 1869.

*Type locality*.—"Vohima" as given by Peters (1870:55). Not here restricted, but see above discussion for possible interpretation as "former Province of Vohima, Northern Highlands, mountains surrounding Andapa."

*Nesomys audeberti* (Jentink, 1879)

*Hallomys audeberti* Jentink, 1879:107.—Jentink, 1887:216, 1888:74 (museum catalogs).—Trouessart 1897:510, 1904:396 (systematic checklists).—G. Grandidier & Petit, 1932:102 (taxonomic summary).—Allen, 1939:317 (systematic checklist).

*Nesomys audeberti*: Major, 1897:712 (name combination, generic reassignment).—Ellerman, 1941:376, 1949:175 (classifications).—Carleton & Schmidt, 1990:26 (gazetteer, distributional summary).—Ryan et al., 1993:101 (natural history, morphological identification).—Goodman & Carleton, 1996:273 (faunal report, morphological identification).—Jansa et al., 1999:255 (phylogenetic relationship).—Ryan, 2003:1388 (natural history summary).—Musser & Carleton, 2005:952 (systematic checklist).—Soarimalala & Goodman, 2011:119 (field guide, distribution, morphological recognition).

*Nesomys r*[*ufus*] *audeberti*: Petter, 1975:3 (identification manual; new rank, reallocated as valid subspecies).

*Nesomys rufus* [*audeberti*]: Honacki et al., 1982:432 (systematic checklist, listed as synonym without indication of rank).—Musser & Carleton, 1993:679 (systematic checklist, listed as synonym without indication of rank).

*Lectotype*.—RMNH 26527, as herein designated, a skull and partial skeleton with mounted skin, young adult male collected February 1878 by J. P. Audebert.

*Type locality*.—Madagascar, Toamasina Province (former), Analanjirofo Région, west of Antongil Bay toward the western frontier of Fivondronana Mananara Avaratra, "Savary," as herein restricted.

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*Paralectotypes*.—RMNH 26528, skull with whole-mounted skin, an adult male collected 16 March 1878 by J. P. Audebert; RMNH 39356, whole carcass preserved in fluid, an adult female (with three fetuses) collected 6 March 1878. Both paralectotypes were obtained at "Maisine." See above discussion for the probable location of Maisine in close vicinity to Savary; that is, Toamasina Province (former), Analanjirofo Région, west of Antongil Bay toward the western frontier of Fivondronana Mananara Avaratra, "Maisine."

*Nesomys lambertoni* G. Grandidier, 1928

*Nesomys lambertoni* G. Grandidier, 1928:95.—Grandidier & Petit, 1932:100 (taxonomic summary).—Ellerman, 1941:376, 1949:175 (classifications).—Carleton & Schmidt, 1990:26 (gazetteer, distributional summary).—Helgen & McFadden, 2001:120 (type catalog).—Goodman & Schütz, 2003:446 (distributional report, ecology, morphological identification).—Ryan, 2003:1388 (natural history summary).—Musser & Carleton, 2005:952 (systematic checklist).—Soarimalala & Goodman, 2011:120 (field guide, distribution, morphological recognition).

*Nesomys r*[*ufus*] *lambertoni*: Petter, 1962:571 (new rank, retained as valid subspecies), 1972:664 (taxonomic synopsis), 1975:3 (identification manual).

*Nesomys rufus* [*lambertoni*]: Honacki et al., 1982:432 (systematic checklist, listed as synonym without indication of rank).—Musser & Carleton, 1993:679 (systematic checklist, listed as synonym without indication of rank).

*Lectotype*.—MCZ 45941/MNHN 1961.106, as herein designated, skull with partial skeleton (MCZ 45941) and round skin (MNHN 1961.106), adult male collected by an anonymous hunter (possibly in January 1928).

*Type locality*.—Madagascar, Mahajanga Province (former), Melaky Région, Antsalova District, *tsingy* habitat at the western margin of the Bemaraha Massif and east of Antsalova, as herein restricted.

*Paralectotypes*.—MCZ 45933, unprepared skin with partial skull and lower limb bones preserved inside, adult male; MCZ 45934, unprepared skin with partial skull and lower limb bones preserved inside, adult male. Both paralectotypes originated from the same locality where the lectotype was collected, presumably by the same anonymous hunter at the same time.

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## Appendix 1

Listed below are recently collected specimens of *Nesomys* used to conduct morphological comparisons and to derive sample statistics (Tables 1–3, 5).

*Nesomys audeberti*.—FIANARANTSOA PROVINCE, Parc National de Ranomafana: Ambodiamontana, 7 km (by road) W Ranomafana, 950 m (USNM 448892–448895, 448944–448951, 448959, 448968, 448969, 448971, 448973, 449231, 449232, 449353); Vatoharana, 4 km SW Ranomafana, 1025 m (FMNH 170845–170848).

*Nesomys lambertoni*.—MAHAJANGA PROVINCE, Parc National de Bemaraha: 2.5 km NE Bekopaka, 100 m (FMNH 172726); 3.5 km NE Bekopaka, 100 m (FMNH 172727).

*Nesomys rufus*.—FIANARANTSOA PROVINCE, Parc National de Ranomafana: Ambodiamontana, 7 km (by road) W Ranomafana, 950 m (USNM 448896–448899, 448952–448958, 448960–448967, 448970, 448972, 449233); Vatoharana, 4 km SW Ranomafana, 1025 m (FMNH 170849–170852); 3 km (by road) NNW Vohiparara, 1225 m (USNM 449234–449245, 449354–449357).

## Appendix 2

The letters from Gerrard Jr. to Peters that we quoted in the account of *Nesomys rufus* are maintained in the Historische Bild- und Schriftgutsammlungen of the Museum für Naturkunde, Berlin. Archival materials relating to the zoological collections (Bestand: Zoologisches Museum) are filed by their catalog designation (Signatur) and prefixed by S II (Schriftgut II) for the archival letters we consulted; page (Blatt) numbers distinguish separate documents within the same Signatur. The two letters with their full abbreviation (MfN, HBSB, ZM, S II) are:

Letter addressed to W. Peters dated 11 May 1870 (MfN, HBSB, ZM, S II, Gerrard, Edward jun., Schriftwechsel, Blatt 73).

Letter addressed to W. Peters dated 18 May 1870 (MfN, HBSB, ZM, S II, Gerrard, Edward jun., Schriftwechsel, Blatt 88).

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