

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024

Number 2987, 36 pp., 8 figs., 2 tables

October 25, 1990

Systematic Studies of Madagascar's Endemic Rodents (Muroidea: Nesomyinae): an Annotated Gazetteer of Collecting Localities of Known Forms

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ABSTRACT

The native muroid rodents inhabiting Madagascar are arranged as an endemic subfamily, the Nesomyinae, that contains only 10 species and 7 genera according to recent authorities. This contribution summarizes the geographic distribution of named forms based on examination of approximately 750 specimens representing 73 principal collecting localities. Each locality account includes its geographic coordinates, the taxa collected, and miscellaneous remarks on habitat, collectors, and other relevant data. Abbreviated synonymies are provided for the described forms, listed according

to current classifications, as well as information on the location of type localities. The apparent sympatry or contiguous allopatry of certain taxa of *Eliurus* and *Nesomys* now viewed as subspecies suggests that the group is more speciose than presently recognized. The notion of nesomyines as an impoverished fauna is discussed from the perspective of rodent species diversity on other islands within tropical latitudes and in light of the poor specimen-based documentation that exists for understanding nesomyine taxonomy and distribution.

INTRODUCTION

As with so many other aspects of Madagascar's biota, the mammalian radiations unique to the island-continent have com-

manded the attention of a wide array of biologists, including systematists, ecologists, and conservationists. Among the endemic

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mammals, however, interest has overwhelmingly concentrated on lemuriform primates, which have been the subject of major revisions, syntheses, and symposia (Schwarz, 1931; Jolly, 1966; Jolly et al., 1984; Petter et al., 1977; Tattersall, 1982; Tattersall and Sussman, 1984). The collective research efforts on lemurs (*sensu lato*) are particularly impressive for the variety of methods being applied to the understanding of their biology and evolutionary history, involving paleontological work, karyological surveys, and intensive field studies (see, for example, Petter et al., 1977, and Tattersall and Sussman, 1984). Tenrecid insectivores and viverrid carnivores have also been the focus of recent behavioral, ecological, and taxonomic investigations (Albignac, 1973; Eisenberg and Gould, 1970, 1984; MacPhee, 1987; Wozencraft, 1986).

Another of Madagascar's singular mammalian radiations has thus far escaped such multifaceted scrutiny of its systematic biology. This is the Nesomyinae, a modest complex of murid rodents which numbers only 10 living species and 7 genera according to current authorities (Petter, 1972, 1975; Honacki et al., 1982; Corbet and Hill, 1986). The oversight is unfortunate because the nesomyines constitute a more speciose assemblage than presently recognized and because enhanced comprehension of their origin and diversification bears on broader biogeographic and phylogenetic issues (see review in Carleton and Musser, 1984). Our appalling lack of fundamental systematic and biological knowledge of the Nesomyinae is underscored by the recent IUCN report on conservation priorities for Madagascar's endemic species, in which the scant chapter on rodents contains almost as much ecological and distributional information about introduced *Rattus* as about the 7 endemic genera combined (Rakotondravony, 1987).

The information reported herein initiates a series of studies aimed at filling this void. The purposes of the present study are (1) to document the collecting localities and existing collections of nesomyine rodents based on examination of museum specimens, and (2) to summarize the geographic distributions of described forms based on this material. Synthesis of the geographic data marks the

first step toward subsequent species-level revisions, especially required for *Eliurus* and *Nesomys*, which in turn will provide an improved framework for addressing questions of nesomyine intergeneric relationships, the monophyly of the subfamily, and the phylogenetic relationship of nesomyine rodents with regard to the radiation of other murid assemblages.

MATERIALS AND METHODS

The taxonomic distributions presented here are based on the examination of approximately 750 specimens of Nesomyinae by Carleton. The specimens consist principally of study skins with associated skulls contained in the following collections, each preceded by the museum acronym adopted throughout the paper.

- AMNH American Museum of Natural History, New York City
- BMNH British Museum (Natural History), London
- FMNH Field Museum of Natural History, Chicago
- LMCM Merseyside County Museums, Liverpool
- MCZ Museum of Comparative Zoology, Harvard University
- MNHN Museum National d'Histoire Naturelle, Paris
- RMNH Rijksmuseum van Natuurlijke Historie, Leiden
- USNM National Museum of Natural History, Washington D.C.
- UZMC Universitet Zoologisk Museum, Copenhagen

A variety of cartographic sources were used to locate and verify collecting localities of nesomyine rodents. Our principal references included: a collection of 1:500,000 maps published by the Geographical Section, British War Office (= BWO), dated 1941–1943; the topographic series (1:100,000, 1970–1977; and 1:500,000, 1979–1985) published by Foiben-Taosarintanin'i Madagasikara, Antananarivo (= FTM); and the Gazetteer of Madagascar (Washington D.C., Defense Mapping Agency, 1989), with names approved by the U.S. Board of Geographic Names (= BGN). In addition, we consulted

historical maps of Madagascar available in the Library of Congress, the most informative of which proved to be the 1895 edition of *Carte de Madagascar* (1:1,000,000) by E. Laillet and L. Suberbie (Paris: A. Challamel, ed.) and the 1902 edition of *Atlas des Colonies Françaises* (1:1,000,000) by P. Pelet (Paris: Librairie Armand Colin). Certain expeditionary accounts and memoirs, many containing detailed maps, have also been invaluable, such as those of A. Grandidier (1867, 1871, 1885, 1893), Cowan (1882), Forsyth Major (1896c), Rand (1932, 1936), and Webb (1954). Nesomyine collecting sites were further checked against the interpretations of other recently published catalogs and revisions of Malagasy mammals, particularly those of Buettner-Janusch and Tattersall (1985), Tattersall (1986), Jenkins (1987), MacPhee (1987), and Yoder (in prep.).

The 750 nesomyine rodents examined represent 73 principal collecting localities, which were assigned consecutive numbers for identification on the accompanying maps (figs. 1–6). The localities are grouped under current provincial divisions and arranged from north to south along the eastern versant of Madagascar and from south to north along the western. Each locality account contains four subheadings of information: the numbered locality designation itself, which corresponds to the numeric codes in figure 1; latitudinal and longitudinal coordinates; the taxa collected at the locality; and remarks.

Geographic names are presented as used by the collector, although spelling variations and early phonetically rendered facsimiles have been standardized following the BGN. One exception to this protocol has been the dropping of “forest” or “forêt de” from the specific locality (for example, Ampitambe forest), a naming convention which generally connotes “forest in the vicinity of,” not (usually) a proper name. The collector's original wording and typically encountered variations may be found under Remarks. Nearby localities whose coordinates are virtually the same are indicated in parentheses, and current synonyms of older geographic names are provided in brackets [=]. Altitudes of the localities were converted to meters, but such cases are identified by giving the collector's original English-system value in brackets.

Sources for altitudes not indicated on specimen tags, for instance field catalogs and publications, are provided under Remarks.

Latitude and longitude figures correspond to that portion of the locality designation printed in boldface. The authority for the coordinates listed are flagged by an accompanying initial to signify either the collector (c), the BGN gazetteer (g), or another publication (p). Coordinates estimated from a map (m) are preceded by “ca.” and the map used is also indicated (for example, *m* = FTM). Differences between the collector's own coordinates and those employed for mapping the locality are explained in the Remarks section.

The scientific names enumerated under Taxa conform to current specific and sub-specific arrangements (Ellerman, 1949; Petter, 1972, 1975; Honacki et al., 1982). In accordance with these, certain forms of *Eliurus* and *Nesomys* initially described as species are herein treated as races. Although our taxonomic assignments are based on recent review of most museum collections and holotypes, we stress that they are tentative pending the completion of much needed revisions. Because Carleton was unable to complete critical examination of *Macrotarsomys*, the assignment of localities to subspecies of *bastardi* basically follows the ranges outlined by Ellerman (1949). Descriptions of ecology and microhabitat, particularly impressions of the collector, are related under Remarks.

ACKNOWLEDGMENTS

We thank the various curators and museum staff who made specimens available for study, either through loans or use of their collections, especially: Dr. Guy G. Musser (AMNH); Dr. Ian Bishop, Ms. Paula Jenkins, and Ms. Jean Ingles (BMNH); Dr. Bruce Patterson (FMNH); Dr. Malcolm Lagen (LMCM); Ms. Maria Rutzmoser (MCZ); Drs. Francis Petter and Michel Tranier (MNH); Dr. Chris Smeenk (RMNH); and Dr. Hans Baagøe and Mr. Mogen Andersen (UZMC). The senior author especially appreciates the many courtesies extended him by Jean Ingles, Chris Smeenk, Michel Tranier, and Francis Petter during his visit to their incomparable museums and invaluable collections. Ms. Anne Yoder (Duke University) generously

allowed access to her unpublished compilation of lemurs contained in MNHN, and Mr. Peter J. Stephens (University of London) provided a copy of his report on small mammals of a lowland rain forest near Antongil Bay. We appreciate the cooperation of Dr. Louis L. Jacobs (Southern Methodist University), who made available for loan a cast of the Miocene fossil *Protaromys*. All or parts of the manuscript were reviewed by the following individuals: G. Ken Creighton, Lawrence R. Heaney, Guy G. Musser, Ross D. MacPhee, James M. Ryan, and Anne D. Yoder. We are grateful for the thoughtful comments each contributed to improve the final contents of this paper.

EARLY COLLECTORS AND COLLECTIONS

This brief review highlights those collectors and expeditions responsible for accruing the foremost museum collections of nesomyine rodents. The many explorers and naturalists who contributed to the natural history foundation of other Malagasy mammals, and vertebrates in general, have been summarized by other authors (Rand, 1936; Tattersall, 1982). Our account inevitably overlaps such previous summaries in view of the broad biological interests of Madagascar's first European naturalists.

Reflective of the essentialistic species concept of the period, our initial systematic understanding of Nesomyinae was founded on few specimens with vague or unknown provenience. Like so many other aspects of Madagascar's geography and natural history, Alfred Grandidier's explorations in the middle 1800s also yielded significant discoveries of the island's endemic rodents. Grandidier's navigations along the western coast in his bark *Infatigable* recovered the first specimens of the spectacular giant rat *Hypogeomys antimena* (Grandidier, 1869) and of *Eliurus myoxinus* (Milne Edwards, 1885). Other taxonomic contributions during this period of discovery emerged incidentally from the activities of various naturalists, missionaries, and explorers. Notable among them are A. Crossley (who collected the types of *Brachytarsomys albicauda* Gunther, 1875, and perhaps *Nesomys rufus* Peters, 1870), J. Aude-

bert (the type of *Hallomys audeberti* Jentink, 1879), Thomas Waters (the type of *Nesomys betsileoensis* Bartlett, 1879), and E. Bastard (the type of *Macrotarsomys bastardi* Milne Edwards and G. Grandidier, 1898). The 1928 description of *Nesomys lambertoni* (collector unknown) by G. Grandidier may be taken to conclude the early descriptive phase of nesomyine taxonomy.

Our current knowledge of nesomyine biological diversity issues largely from three field collections, which still are preeminent in terms of the number of specimens and taxa obtained and the breadth of the geographic sampling. They are the mid-1890s expedition of C. I. Forsyth Major, the joint Mission Zoologique Franco-Anglo-Américaine (MZFAA) conducted from April 1929 to May 1931, and the 1939–1945 survey of Cecil S. Webb. The latter two expeditions transpired concurrent with the inception of what has become standard protocol for field systematics; the field methods and specimen tags of MZFAA and Webb evince an appreciation of clear locality documentation and the value of population samples. The collection of Major generally met these same criteria, a quality which, for the time period, marks it as all the more remarkable.

Indeed, the late 19th century expedition of C. I. Forsyth Major may be justifiably argued as having produced the single most important collection of nesomyine rodents. Compared to the material accumulated prior to his work, Major's field methods were exemplary for consistently providing provenance, for acquiring series of a species from a single locality, and for preserving specimens as complete skeletons or fluids, in addition to conventional round skins and skulls. Major (1896c) published a summary of his itinerary and taxonomic results soon after he returned from Madagascar. The details of his travels, however, are incompletely or vaguely related in this account, which in several passages reveals the frustrations and personal hazards he faced in attempting fieldwork at the time of the French annexation of Madagascar.

Major (1896c) himself estimated that his two years of collecting had yielded about 100 native rodents, which nevertheless represent a small fraction of the nearly 1600 mammals obtained. Our museum researches have un-

TABLE 1
Summary of C. I. Forsyth Major's 1894-1896 Expedition
(based on rodents collected)

Locality	Minimum period of stay	Field nos. and totals	Taxa collected
Ambohimitombo	12 Jan-24 Jan 1895	120-166 N = 9	<i>Eliurus majori</i> <i>Nesomys rufus</i>
Ampitambe (1st visit)	23 Jun-11 Aug 1895	429-773 N = 57	<i>Brachyuromys betsileoensis</i> <i>B. ramirohitra</i> <i>Eliurus minor</i> <i>E. penicillatus</i> <i>Gymnuromys roberti</i> <i>Nesomys rufus</i>
Ampitambe (2nd visit)	8 Mar-19 Mar 1896	815-1049 N = 51	<i>Brachyuromys betsileoensis</i> <i>B. ramirohitra</i> <i>Eliurus penicillatus</i> <i>Gymnuromys roberti</i> <i>Nesomys rufus</i>
Vinanitelo	25 May-4 Jun 1896	1315-1510 N = 9	<i>Brachytarsomys albicauda</i> <i>Brachyuromys betsileoensis</i> <i>Eliurus tanala</i>
Ambohimanana	25 May-30 May 1896	1325-1446 N = 12	<i>Brachyuromys betsileoensis</i>
Amboasary	4 Jun-6 Jun 1896	1509, 1511 N = 2	<i>Brachyuromys ramirohitra</i> <i>Gymnuromys roberti</i>

covered 140 nesomyine specimens (table 1) that are definitely traceable, usually by means of their original field tags, to Major's 1894-1896 collections. The majority are housed in the BMNH (about 80), but his locality series were unfortunately broken up in the early 1900s and traded or otherwise dispersed to other public and private collections. Consequently, another 60 specimens, ranging from one to as many as 14, are distributed among the eight other museums listed above. Additional portions of Major's collection may exist in other institutions.

The precise location of Major's collecting sites, notably Ampitambe, has since assumed critical importance in view of the number of nesomyine taxa described from them. Only five localities are represented among the 140 rodents examined, yet they served as the basis for two new generic (*Brachyuromys* and *Gymnuromys*) and six new specific diagnoses. The species include: from Ambohimitambo, *Eliurus majori* Thomas (1895); from Vinanitelo, *Eliurus tanala* Major (1896b); and from Ampitambe, *Brachyuromys ramirohitra* Ma-

jor (1896a), *Gymnuromys roberti* Major (1896a), *Eliurus minor* Major (1896b), and *E. penicillatus* Thomas (1908). Some of these taxa have never been collected again (*Eliurus penicillatus*) or never again in the same abundance (*Brachyuromys ramirohitra* and *Gymnuromys*). The composition and proportion of species recovered intimate that Major's field assistants were more successful in catching terrestrial and/or diurnal rodents (such as *Brachyuromys*, *Gymnuromys*, and *Nesomys*), than arboreal and nocturnal forms (such as *Brachytarsomys* and *Eliurus*).

The collation of dates, field numbers, and collecting sites (table 1) agrees with the general itinerary sketched by Major (1896c). The proximity of the collection dates further suggests that certain localities—namely, Vinanitelo, Ambohimanana, and Amboasary—were practically contiguous to one another, a point that bears on the interpretation of their geographic placement (see remarks on Major localities under following Gazetteer).

Austin L. Rand participated in almost every phase of the MZFAA project, and most

specimen tags bear his name as collector, with some attributable to J. Delacour, W. R. Lowe, and R. Archbold. Rand (1932, 1935, 1936) thoroughly summarized the MZFAA itinerary, location of collecting sites, and descriptions of habitats. His 1932 and 1936 publications are especially helpful in providing village names and altitudes not recorded on the original MZFAA skin tags. Although his separate expedition accounts largely overlap one another, the 1932 publication contains more notations about the mammals observed and collected. Regrettably for the rodent specialist, the MZFAA field teams clearly focused on the avifauna and, among mammals, on the lemurs. For example, recent compendia of lemuriform primates in AMNH, BMNH, and MNHN enumerated some 470 specimens that stem from the field operations of the MZFAA (Buettner-Janusch and Tattersall, 1985; Jenkins, 1987; Yoder, in prep.). In contrast, approximately 70 nesomyine specimens, equivalently divided among the museums involved (AMNH, BMNH, and MNHN), can be confidently associated with the MZFAA. Although no new nesomyine taxa have emerged from these collections, most series obtained then represented new distributional limits and some still do, notably for examples of *Eliurus* and *Nesomys*.

Cecil S. Webb's sojourns throughout Madagascar were sometimes unpleasant ordeals for him, but they proved a boon for systematic mammalogy in generating an outstanding collection of Nesomyinae. On assignment from the BMNH to rediscover the giant rat (*Hypogeomys*) and Madagascar gerbil (*Macrotarsomys*), Webb arrived in Madagascar in 1939, just before the advent of World War II (Webb, 1954). Stranded away from his homeland until 1945, during the Vichy governance of Madagascar, he seemed to welcome opportunities to retreat to the field, where his efforts produced the largest and most geographically widespread series of nesomyine rodents assembled to that date or thereafter. Most notably, Webb's collections of rodents from the dry biomes in southwestern and southern Madagascar remain the best ever assembled.

We identified almost 180 specimens, most contained in BMNH, that resulted from

Webb's field activities. This figure closely matches Ellerman's (1949) tabulation of material received at the British Museum. Webb carefully documented his field sites and was the first to supplement his locality designations with geographical coordinates. This practice, together with his popular essay (1954) about his travels and trapping experiences, removes uncertainty from the mapping of his localities. In addition, Webb faithfully noted habitat information on skin tags and even indicated general trap placement for some specimens. Ellerman's (1949) report on the Webb collection included the description of two new taxa, *Eliurus myoxinus webbi* and *Macrotarsomys bastardi occidentalis*, and a valuable synopsis of the Nesomyinae that established the alpha-taxonomic rankings that systematists recognize today.

The modern phase of nesomyine taxonomy has benefitted primarily from the research of Francis Petter of the MNHN. Although Petter's contributions have emphasized higher-level systematic questions involving Nesomyinae (for example, 1961, 1972), he has nonetheless described (1959, 1962) two new forms, *Macrotarsomys ingens* and *Brachytarsomys albicauda villosa*, both highly distinctive taxa which represent the latest nesomyines to be described.

GAZETTEER OF NESOMYINE COLLECTING LOCALITIES Antsiranana Province

1. **Montagne d'Ambre** [= Ambohitra], 1000 m.

Coordinates: 12°30'S/49°10'E g.

Taxa: *Eliurus myoxinus majori*, *Eliurus m. webbi*.

Remarks: The 1000 m altitude was supplied by Rand (1936: 192) and marked the site of a forestry station situated in "damp, green rain forest . . . containing many lianas and mosses." He contrasted this habitat with the dryer forest found on the lower slopes of Mt. d'Ambre. The specimens of *Eliurus myoxinus majori* were collected by MZFAA and originated from this 1000 m locality. The altitude of the series of *E. m. webbi*, collected in 1965 by J.-J. Petter, is not indicated on their field tags.

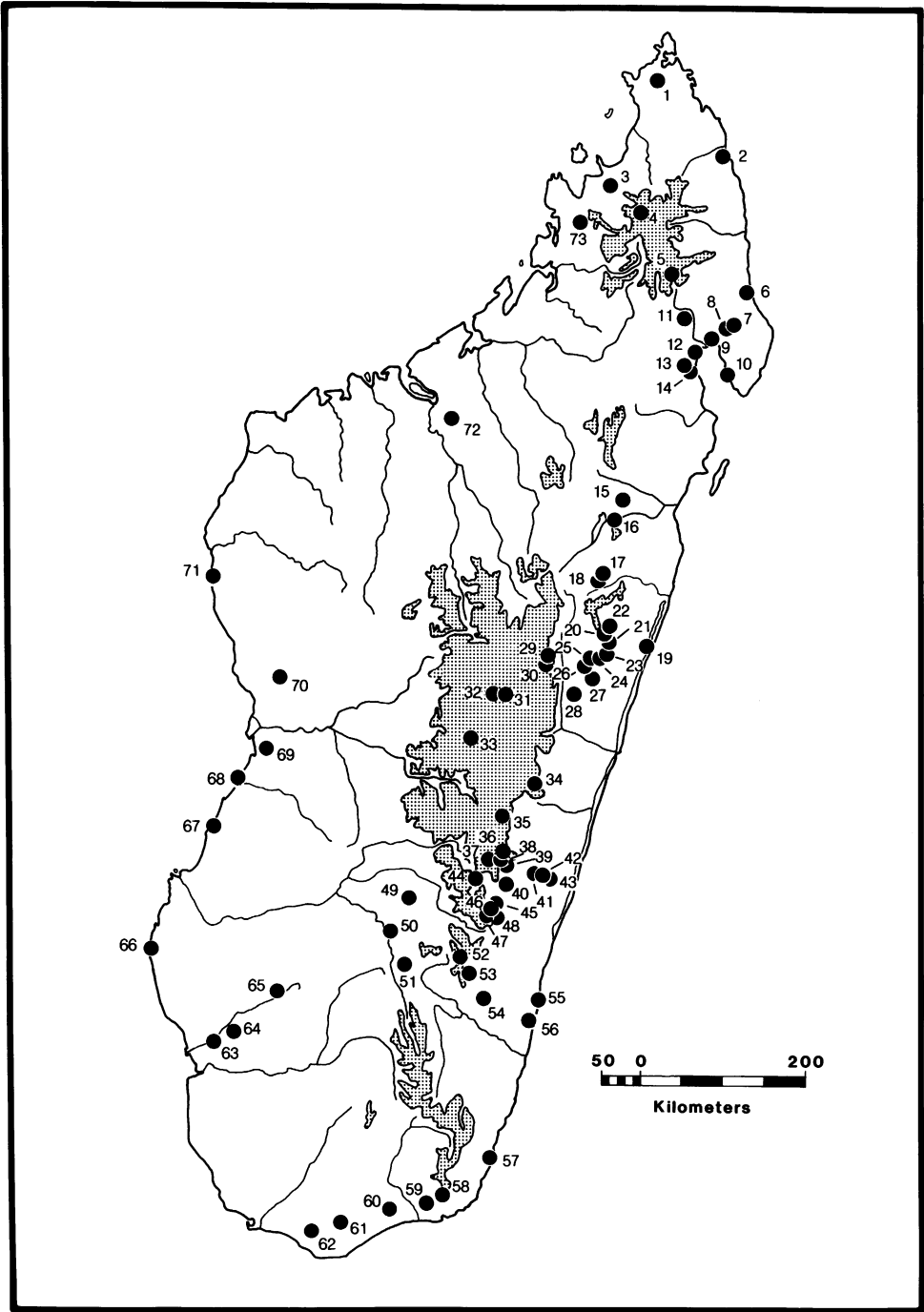


Fig. 1. Geographic distribution of the principal collecting localities of nesomyine rodents. Numbered localities correspond to those listed in the gazetteer. Shaded areas indicate highlands above 1000 m.

2. **Vohima** [= Iharana].

Coordinates: 13°21'S/50°00'E g.

Taxa: *Nesomys rufus rufus*.

Remarks: Type locality of Peters' (1870) *Nesomys rufus*; also as Vohemar and Vohimarina.

3. **One day S Anaborano**.

Coordinates: 13°40'S/48°39'E g.

Taxa: *Nesomys rufus rufus*.

Remarks: Rand (1932, 1936) located this MZFAA locality as near the divide between the Ifasy and the Sambirano rivers and characterized the habitat of the region as "humid evergreen forest and brush." Rand (1932) indicated that the field team had camped near the village of "Ansahabé" on a ridge of low hills between the two drainage basins. We located an Antsahabé about 20 km SW of Anaborano (ca. 200–400 m), a setting which concurs with Rand's descriptions, and used its coordinates for the locality.

4. **Tsaratanana Massif**, 2300 m.

Coordinates: 14°00'S/49°00'E g.

Taxa: *Nesomys rufus rufus*.

Remarks: The coordinates are for the central massif; an exact locality was not given.

5. **One day W Andapa**, 1800 m.

Coordinates: ca. 14°39'S/49°22'E p.

Taxa: *Eliurus minor*, *Nesomys rufus rufus*.

Remarks: The altitude was later provided by Rand (1932, 1936) whose 1930 field camp was situated in hilly country on the upper edge of forest that receded to an open plateau. The floristic composition was mixed, including "low moss and lichen-draped trees," "forest of taller trees," "swamps with grass or reeds," and "ridges covered with low brush, bracken, and grass." Rand (1932) had earlier placed the site as near the village of "Antanombo Manandriana," a compound name which we could not locate as such. The coordinates, which plot a site 30 km due west of Andapa, are those estimated by Jenkins (1987) and apparently reflect Rand's (1936) statement that MZFAA teams averaged about 30 km of trail per day.

6. **Antalaha**, near sea level.

Coordinates: 14°53'S/50°17'E g.

Taxa: *Eliurus myoxinus webbi*.

7. **Two days NE Maroantsetra**, 1000 m.

Coordinates: 15°16'S/50°03'E g.

Taxa: *Nesomys rufus audeberti*.

Remarks: Rand (1936) subsequently gave the altitude and specified the locality as Ambohimarahavavy [= Ambohimirahavavy], a small village which corresponds to the coordinates listed above. The country here was portrayed as mountainous with steep slopes, rapid streams, and heavy forest shrouding an entangled ground cover.

Toamasina Province

8. **Ankovana** [= Ankovona], 40 km NE Maroantsetra, 275 m [900 ft].

Coordinates: 15°18'S/49°59'E g.

Taxa: *Eliurus myoxinus webbi*.

Remarks: The coordinates were given by the collector C. S. Webb as 15.2°S/49.9°E.

9. **3 km E Andranofotsy**, 12 km NE Maroantsetra, near sea level.

Coordinates: ca. 15°25'S/49°49'E m = FTM.

Taxa: *Eliurus myoxinus webbi*.

Remarks: The collector C. S. Webb recorded his approximate coordinates as 15.5°S/49.8°E.

10. **Antalavia**, eastern side Antongil Bay, near sea level.

Coordinates: 15°47'S/50°01'E g.

Taxa: *Eliurus myoxinus webbi*.

Remarks: The coordinates given by the collector C. S. Webb are 15.8°S/50.0°E.

11. **Hiaraka**, near Maroantsetra, 400 and 850 m.

Coordinates: ca. 15°10'S/49°30'E m = FTM.

Taxa: *Eliurus minor*, *Eliurus myoxinus webbi*, *Nesomys rufus audeberti*.

Remarks: MacPhee (1987) located Hiaraka as 40 km NW Maroantsetra. The *Eliurus* were collected at 850 m and the *Nesomys* at 400 m.

12. **20 km SW Maroantsetra**, near sea level.

Coordinates: 15°31'S/49°38'E g.

Taxa: *Eliurus minor*.

Remarks: Rand (1936) fixed the specific locality as Manombia [= Manambia], a place in flat country near the northwestern shore of Antongil Bay. The coordinates are for the village. Here the forest consisted of both unflooded and flooded sectors—the former with tall trees, an abundance of palms, and a sparse

understory and ground cover—the latter with a lower canopy and a densely moss-paved floor or inundated marshy areas.

13. **8 mi W Rantabe**, Antongil Bay, 150 m [500 ft].

Coordinates: ca. 15°42'S/49°30'E *m* = FTM.

Taxa: *Eliurus myoxinus webbi*.

Remarks: C. S. Webb's original longitudinal designation (49.7°E) places this site to the east of Rantabe in Antongil Bay.

14. **10 km WSW Maintimbata**, 40 km SW Maroantsetra, 450–625 m.

Coordinates: 15°46'S/49°36'E *c*.

Taxa: *Eliurus minor*, *E. myoxinus webbi*.

Remarks: The collector (Stephenson, 1987) identified the specific area as Forêt d'Anandrivola, a tract of lowland rain forest. Both species of *Eliurus* were found to occur deep within primary forest where the herbaceous understory is sparse but abundant lianas trail from the canopy.

15. **30 mi NE Imerimandroso**, Lac Alaotra, 760 m [2500 ft].

Coordinates: 17°12'S/48°48'E *c*.

Taxa: *Brachytarsomys albicauda*.

16. **16 mi E Imerimandroso**, Lac Alaotra, 1065 m [3500 ft].

Coordinates: 17°24'S/48°42'E *c*.

Taxa: *Eliurus minor*.

17. **9 km N Didy**, 1000 m.

Coordinates: ca. 18°02'S/48°32'E *m* = FTM.

Taxa: *Brachyuromys betsileoensis*, *Eliurus minor*.

Remarks: The field tags and notes of both collectors (K. Lange and J. Shaw, 1962) list Ambohijanahary in parentheses following Didy, suggesting either their synonymy or a local place-name; we could not verify such a locale in the vicinity indicated. The elevation was extracted from the collector's fieldnotes. The habitat where the nesomyines were collected was described as an extensive meadow of dense grass, 2–4 ft tall, intermixed with sedges, clubmosses, and bracken (K. Lange field journal).

18. **Sihanaka Forest**.

Coordinates: ca. 18°05'S/48°30'E *p*.

Taxa: *Brachytarsomys albicauda*, *Eliurus myoxinus tanala*.

Remarks: Sihanaka Forest (also as Sianaka

or Antsihanaka) is a commonly encountered designation of uncertain provenance found on many birds and mammals collected in the 19th century. Rand (1932, 1936) placed this locale as the forest around Didy and Fito, situated to the southeast of Lake Alaotra, particularly for those specimens purchased from a local collector, Herschell Chauvin. Consistent with Rand's interpretation, Jenkins (1987) estimated the coordinates of Sihanaka Forest as 18°05'S/48°30'E, which places it to the north of Didy and near the locality visited by Shaw and Lange (see locality 17). The above coordinates correspond to Jenkins' estimation and are intended only for those nesomyine specimens that bear documentation as purchased from Chauvin.

Buettner-Janusch and Tattersall (1985), however, suggested that Sihanaka was an indeterminate region of forest to the north or west of Lake Alaotra. The place-name may plausibly apply to specimens obtained from either area. The routes of early explorers who crossed the region (see Grandidier, 1885) would have regularly encountered members of the Sihanaka tribe, who lived along the eastern perimeter of Lake Alaotra and its forest fringes over a wide north-south expanse. Grandidier (1893), for example, illustrated the first line of Sihanaka villages encountered in the forest just northeast of Lake Alaotra. Other maps produced in the late 19th and early 20th centuries variously identify a Sihanaka or Antsihanaka region that surrounds Lake Alaotra and usually includes the forested ridges to the east.

Wozencraft (1986) and Jenkins (1987) also cited a Sihanaka Forest at 21°46'S/48°08'E (listed in BGN), but we cannot reliably associate any nesomyine specimens with this place on the southeastern coastal plain.

19. **Brickaville** [= Ampasimanolotra].

Coordinates: 18°49'S/49°04'E *g*.

Taxa: *Brachytarsomys albicauda*.

Remarks: This locality, Lohariandava, Rogez, Fanovana, and Perinet are, or were, railroad stations and associated villages distributed along the line between Tamatave [= Toamasina] and Antananarivo, a route which provided a convenient transect through the Great Forest of the East. At Brickaville, the railway turned west and ascended the eastern

escarpment and its forests and ridges. In some cases, it is ambiguous whether the place-name signifies a specimen's point of embarkation or its actual site of collection.

20. **10 mi NW Lohariandava** (including 12 mi NW), 455 m [1500 ft].

Coordinates: 18°42'S/48°35'E *m* = FTM.

Taxa: *Brachytarsomys albicauda*, *Eliurus myoxinus tanala*, *Nesomys rufus audeberti*.

Remarks: These localities and those north of Rogez are apparently situated in nearly the same forested hills. On his field tags, C. S. Webb provided identical coordinates (18.8°S/48.6°E) for specimens from both places but used different locality designations and altitudes.

21. **Rogez** [= Andekaleka].

Coordinates: 18°48'S/48°37'E *g*.

Taxa: *Eliurus myoxinus tanala*, *Nesomys rufus audeberti*.

Remarks: The two specimens bearing this provenance may have originated from the forest to the north of Rogez.

22. **13 mi N Rogez** [= Andekaleka], 395 m [1300 ft] (including 15 mi N, 610 m [2000 ft]).

Coordinates: 18°38'S/48°37'E *m* = FTM.

Taxa: *Brachytarsomys albicauda*, *Nesomys rufus audeberti*, *Eliurus myoxinus webbi*.

Remarks: See comments under Loharian-dava (Locality No. 18). The *Eliurus* and *Nesomys* were obtained at the lower elevation and the *Brachytarsomys* at the upper.

23. **Fanovana**, 500 m (including 8 km from Fanovana).

Coordinates: 18°55'S/48°34'E *g*.

Taxa: *Eliurus myoxinus tanala*, *Nesomys rufus audeberti*.

Remarks: MacPhee (1987) provided the altitude. For the 8-km site, the direction from Fanovana was not indicated by the collector. Lange (1963 field journal) approximated Fanovana as 25 km by road E Perinet.

24. **18 km E Perinet** [= Andasibe].

Coordinates: ca. 18°56'S/48°31'E *m* = FTM.

Taxa: *Eliurus myoxinus tanala*.

Remarks: In his field journal (1963), K. Lange only noted that his transect was set in rain forest.

25. **Perinet** [= Andasibe], 915 m [3000 ft] (including 1, 2, and 13 km E).

Coordinates: 18°56'S/48°25'E *g*.

Taxa: *Brachytarsomys albicauda*, *Eliurus minor*, *Eliurus myoxinus tanala*, *Gymnuro-mys roberti*, *Nesomys rufus audeberti*.

Remarks: C. S. Webb, who visited the site in 1939, gave 19.0°S/48.5°E for his coordinates at Perinet.

K. Lange and J. Shaw collected at the sites east of Perinet in 1962 and Lange returned to them in 1963. Lange (field journal, 1962) listed the altitude for the 2-mi-E location as 1300 m. He characterized the region as tropical rain forest with logging ongoing and some introduced groves of eucalyptus and pine. The primary rain forest harbored a rich variety of microhabitats, including grassy glades, dense herbaceous growth along small streams and ponds, and stands of tree ferns and bamboo. Eisenberg and Gould (1970) provided additional description of the Perinet area.

26. **Ambodiriana**.

Coordinates: 19°02'S/48°21'E *g*.

Taxa: *Nesomys rufus rufus*.

Remarks: The original tag gives the site as "Forêt d'Amboudiriana," a variant spelling of the village about 14 km SW Perinet.

27. **Lakato**.

Coordinates: 19°11'S/48°26'E *g*.

Taxa: *Brachytarsomys albicauda*.

Remarks: Skin-tag designation as "Forêt de Lakato."

28. **55 km along route to Anosibe**.

Coordinates: ca. 19°20'S/48°14'E *m* = FTM.

Taxa: *Eliurus myoxinus tanala*.

Remarks: Which Anosibe was deduced from other localities visited by the collector, J.-J. Petter, who noted the habitat as forest at the border of rice fields.

Antananarivo Province

29. **Mandraka**, 1220 m [4000 ft].

Coordinates: 18°55'S/47°56'E *g*.

Taxa: *Eliurus minor*.

Remarks: C. S. Webb's field tags read "La Mandraka, 45 mi E Antananarivo" with coordinates designated as 18.9°S/47.9°E. A Mandraka exists at this approximate location, but Webb's recorded distance east of Antananarivo presumably reflects a by-road calculation. He later (1954) placed this locality as a small patch of forest about 30 mi east of Antananarivo.

30. **Andrangoloka** [= Andrangolaoka], 950 m.

Coordinates: 19°02'S/47°55'E g.

Taxa: *Brachyuromys betsileoensis*.

Remarks: MacPhee (1987) listed Andrangolaoka as a mission about 70 km E Antananarivo and 25 km SW Moramanga.

31. **Manjakatampo**, 1705 and 1980 m [5600 and 6500 ft].

Coordinates: 19°20'S/47°26'E g.

Taxa: *Brachyuromys betsileoensis*.

Remarks: MZFAA skin tags and Rand (1936) recorded the spelling as "Monjakatampo," a place just below forest on the middle slopes of Mt. Ankaratra.

32. **20 km NW Ambatolampy**, Lac Froid, 1750 m.

Coordinates: ca. 19°20'S/47°17'E m = FTM.

Taxa: *Brachyuromys betsileoensis*.

Remarks: The coordinates approximate the distance northwest of Ambatolampy, not the specific locality Lac Froid, a small impoundment for rice cultivation whose precise location we could not verify. The altitude was secured from the fieldnotes of K. Lange, who obtained the *Brachyuromys* in a dense grassy meadow bordering a creek. Remnant patches of rain forest occurred on hillsides otherwise dominated by introduced pine.

33. **Antsirabe**, 1500 m.

Coordinates: 19°51'S/47°02'E g.

Taxa: *Brachyuromys betsileoensis*.

Remarks: The altitude was indicated by MacPhee (1987). "Tsirabe" and "Sirabe" are common spelling variants.

Fianarantsoa Province

34. **Ampitambe** [= Ampitabe].

Coordinates: ca. 20°22'S/47°46'E m = FTM.

Taxa: *Brachyuromys betsileoensis*, *B. ramirohitra*, *Eliurus minor*, *E. myoxinus penicillatus*, *Gymnuromys roberti*, *Nesomys rufus rufus*.

Remarks: Ampitambe is an important Forsyth Major collecting site that constitutes the type locality for *Brachyuromys ramirohitra* Major (1896a), *Eliurus minor* Major (1896b), *E. penicillatus* Thomas (1908), and *Gymnuromys roberti* Major (1896a), as well as other small mammals, chiefly *Microgale*. Despite its bearing on the taxonomy of so many

forms, the present-day location of Ampitambe has been subject to diverse interpretations. In his descriptions, Major (1896a, 1896b) referred to the locale in various ways, for example "Ampitambé forest (N.E. Betsileo)," or "from the neighbourhood of Ampitambé," or in the most expansive version, "Ampitambé forest, Betsimisaraka country (on the border of N.E. Betsileo), 6 hours S.E. Fandriana." This last citation would seemingly restrict the search-radius for an Ampitambe (or Ampitabe), but an eminent candidate within the probable area has escaped detection. Morrison-Scott (1948) listed, without explanation, the coordinates as 20°20'S/47°30'E, a point located about 20 km SE Fandriana, but no appropriately named village occurs nearby. His coordinates may represent an estimation based on the likely distance covered on foot in 6 hours.

Tattersall (1986), followed by Jenkins (1987), identified the Ampitambe found in the coastal lowlands (ca. 300–400 m) north of the Mangoro River as Major's collecting site. His interpretation apparently reflected Major's (1896c: 972) exasperated comment: "Finally, losing patience, I left Sirabé, crossed over the whole central plateau to the east, and settled in the forest at Ampitambé, on the border of the Betsimisaraka country . . ." However, this statement does not necessarily imply that he had descended the eastern escarpment, and MacPhee (1987) remarked that the great distance and contrary direction from Fandriana (125 km NE) rendered this placement improbable. Nor is such a lowland site consistent with Major's report of working with members of both the Betsimisaraka and Betsileo tribes, the latter living on the southcentral plateau and its eastern margins. Actually, Major (1896b, 1899) viewed the Taiva Tanala, who inhabited the rugged middle to upper-elevation forests immediately to the east of the Betsileo (see Grandidier and Grandidier, 1908), as part of the Betsimisaraka tribe. Therefore, his repeated reference to operating at the border of northeast Betsileo and Betsimisaraka country may be taken, with equal plausibility, to indicate a highland forest, not necessarily a lowland one wholly within the domain of the coastal peoples typically known as Betsimisaraka.

The composition of the rodent fauna from

Ampitambe more critically negates the hypothesized lowland setting. The forms of *Nesomys* (*rufus*) and *Eliurus* (*penicillatus*) present at Major's Ampitambe are different than those that would be expected to dwell in a lowland rain forest, namely *Nesomys* *r. audeberti* and *Eliurus* *m. webbi*. Furthermore, *Brachyuromys*, both species of which were common at Major's Ampitambe, is a genus whose distribution is limited to the central plateau and its fringes and whose lowest known altitudinal occurrence is about 900 m (see distributional summaries below).

MacPhee (1987) left the matter of Ampitambe's location as undecided. As a possible candidate, he mentioned an Ampitabe (600 m), situated about 70 km SE Fandriana, but simultaneously noted that its distance is probably too far for a 6-hour journey. The low elevation also casts doubt on the site from the standpoint of the expected rodent fauna. Major's (1899) later comments on the distribution of *Lemur rubriventer* emphasize a highland setting, for he cited four localities where he had taken the species—Ampitambe, Ambohimitambo, Ivohimanitra, and Vinanitelo—and placed all within an altitudinal range of 900 to 1300 m, with Ivohimanitra being the lowest site. The overall evidence instead portrays an upland area at the eastern reaches of the central plateau where native grasses and marshlands intermingle with humid forest.

The locality that we provisionally advance as Major's Ampitambe is found about 45 km ESE Fandriana. There, we located an "Ampitambe" on the 1942 BWO map (sheets 17-18) and an "Ampitabe" on the 1971 FTM map (section Q50), though the coordinates of neither orthography could be precisely matched to a BGN entry. The village is situated in forest around 900 m, set at the headwaters of a small tributary of the Nosivolo, and reachable by trail from Fandriana. Such a setting would conform to Major's regional characterizations as "N. E. Betsileo" and "on the border of Betsimisaraka country." Furthermore, Major would have, from Antsirabe, "crossed over the whole central plateau to the east" in order to reach the area. The altitudinal estimate is consistent with the mixture of rodent species Major obtained.

Corroborative evidence that Major was in

this highland region around this period is adduced from the type specimen of *Limnogale mergulus*. Major (1896a) described this aquatic tenrec from "Imasindrary, N.E. Betsileo" based on a specimen (original number M1024) collected 18 March 1896. Its field number and date place this site within the vicinity of Ampitambe (see table 1). A Masindrary [= Masindray, 20°17'S/47°31'E g] is found on the 1942 BWO map about 15 km ESE Fandriana, at the border of forest and on the same trail leading to Ampitambe.

The straight-line distance of 45 km from Fandriana, undoubtedly farther on a winding footpath, still seems overly long to travel in 6 hours. Nevertheless, Rand (1936) reckoned that his field crews averaged 5–6 km per hour, or 30–40 km per day, which suggests that 6 hours is a minimum time on the trail when allowing for the breaking and pitching of camp and rest stops. On occasion, he covered 50 km. Lloyd (1851) presented similar journey times and distances, including the ascent from Beforona to Moramanga, a minimum distance of 40 km, as a possible one-day passage. And Major (1896b) equated the 48 km distance between Fianarantsoa and Vinanitelo as a "one day's journey south." Although they approach the upper extreme, the time and distance of this Ampitambe from Fandriana are not wholly unbelievable. Moreover, the fact that Major was collecting material from Masindrary during the same period indicates that his assistants operated over a wide area and that his field camp may have been based in forest to the northwest of Ampitambe, lessening the actual distance from Fandriana. Finally, Major's recollection of the precise chronology must be accorded some allowance for error. His (1896c) expedition commentary intimates that the events leading up to both trips to Ampitambe were traumatic ones for him and his French assistant, Alphonse Robert. Under such circumstances, a memory lapse of a few hours is understandable.

As an addendum, we note that the position of Ampitambe in highland forest southeast of Fandriana would remove the enigmatic distribution of subspecies of *Propithecus diademata* mapped by Tattersall (1986). Tattersall acknowledged that his location of Ampitambe north of the Mangoro River disputed

the traditional subspecific boundary by extending the largely black subspecies *edwardsi* northward within the range of the multicolored nominate subspecies. If correct, our coordinates for Ampitambe place these examples of *edwardsi* far south of the Mangoro River, close to other documented localities of the subspecies at Ambohimitambo and Ivohimanitra (Tattersall, 1986). The Mangoro River may continue to approximate the range limits of the two races of *Propithecus diadema*.

35. Ambohimitambo, 1200 m.

Coordinates: 20°43'S/47°23'E g.

Taxa: *Eliurus myoxinus majori*, *Nesomys rufus rufus*.

Remarks: Ambohimitambo is the type locality of *Eliurus majori* described by Thomas (1895), who interpreted the script on Forsyth Major's field tag as "Ambolimitambo." The altitude is listed according to MacPhee (1987), but Major's (1896c) own recollections placed it closer to 1400–1500 m.

36. 12 km E Andraina [= Manandroy] (including 14 km E), 1500 m.

Coordinates: ca. 21°09'S/47°23'E m = FTM.

Taxa: *Brachyuromys betsileoensis*, *Eliurus minor*.

Remarks: The collector K. Lange recorded (field journal, 1962) the altitude as about 1500 m, but MacPhee (1987) placed it as 1000 m. Lange described the habitat as degraded forest interspersed with grassy meadows and sedge marshes. The *Brachyuromys* originated from a lush meadow and the *Eliurus* from a brush-covered stream bank.

37. Ankafana [= Ankafina], 1600 m.

Coordinates: 21°12'S/47°12'E g.

Taxa: *Nesomys rufus rufus*.

Remarks: The single specimen of *Nesomys* was collected by W. Deans Cowan, a missionary who made natural history observations and collections during his travels through Betsileo country, including Ankafana forest (Cowan, 1882). Thomas (1906) later acknowledged the accessioning of 32 specimens obtained by Cowan from the "Ankafina Forest, Eastern Betsileo." Tattersall (1986) and MacPhee (1987) equated the two place-names as a regional designation for the forested hill just west of Tsarafidy. The altitude is listed fide MacPhee (1987).

38. 3 km by road NNW Vohiparara, 1225 m.

Coordinates: 21°13'S/47°22'E c.

Taxa: *Brachyuromys betsileoensis*, *Eliurus minor*, *E. myoxinus tanala*, *Nesomys rufus rufus*.

39. Ambodiamontana, 7 km by road W Ranomafana, 950 m.

Coordinates: 21°16'S/47°26'E c.

Taxa: *Brachytarsomys albicauda*, *Eliurus minor*, *E. myoxinus tanala*, *Gymnuromys roberti*, *Nesomys rufus rufus*, *N. r. audeberti*.

40. 2 km NE Andrambovato, 575 and 625 m (including 1 km NW, 875 m).

Coordinates: 21°30'S/47°27'E c.

Taxa: *Eliurus myoxinus tanala*, *E. m. webbi*.

Remarks: The coordinates for 1 km NW are 21°30'S/47°25'E.

41. 12 km E Ifanadiana.

Coordinates: ca. 21°22'S/47°47'E m = FTM.

Taxa: *Eliurus myoxinus webbi*.

Remarks: Skin-label spelling as "Ifanadiane."

42. 0.5 km N Kianjavato, 300 m.

Coordinates: 21°23'S/47°52'E c.

Taxa: *Eliurus myoxinus webbi*.

43. 9 km ESE Kianjavato, 250–500 m.

Coordinates: 21°24'S/47°57'E c.

Taxa: *Eliurus myoxinus webbi*.

44. Fianarantsoa, south of.

Coordinates: 21°26'S/47°05'E g.

Taxa: *Eliurus minor*.

Remarks: The "south of" locality modifier may indicate that this specimen, part of the G. Grandidier collection acquired by MCZ, originated from Vinanitelo, 30 mi south of Fianarantsoa.

45. Vinanitelo, 1300 m.

Coordinates: 21°43'S/47°16'E g.

Taxa: *Brachytarsomys albicauda*, *Brachyuromys betsileoensis*, *Eliurus myoxinus tanala*.

Remarks: Major's field tags read only "Vinanitelo" and lack altitudes. Later, in his description of *Eliurus tanala*, he (1896b: 463) refined the locality as "Forest of the Independent Tanala of Ikongo, in the neighbourhood of Vinanitelo, thirty miles south of Fianarantsoa." In the same paper, Major approximated this distance as "one day's journey south." MacPhee (1987) reported the elevation as 1300 m.

46. *Ambohimanana*.

Coordinates: ca. 21°44'S/47°15'E *m* = 1895.

Taxa: *Brachyuromys betsileoensis*.

Remarks: MacPhee (1987) interpreted this Forsyth Major site as "9 km WSW Ambohimitambo." However, the skin tag data of the *Brachyuromys* rule this placement of Major's Ambohimanana as unlikely. Instead their field numbers indicate that they were obtained in the neighborhood of Vinanitelo. Some specimens from Ambohimanana and Vinanitelo even bear the same date of collection in May 1896 (see table 1), about 6 weeks before Major departed the island. Furthermore, his (1896c) expedition summary provides no evidence that he later returned to the vicinity of Ambohimitambo, a site visited in January 1895.

A better candidate may be found approximately 2 km SW Vinanitelo, where we located an Ambohimanana on the 1895 Laillet and Suberbie map and so interpolated the coordinates given. We could not verify an Ambohimanana at this position using more recent maps or the BGN gazetteer. Perhaps its identity has been subsumed by the growth of Vinanitelo. The geographic location of Ambohimanana warrants future clarification as it is the type locality of Elliot's (1905) *Microgale cowani nigrescens*.

47. *Amboasary*.

Coordinates: 21°51'S/47°14'E *g*.

Taxa: *Brachyuromys ramirohitra*, *Gymnuromys roberti*.

Remarks: Two of Major's specimens possess a barely legible locality name that is most plausibly decipherable as "Amboasari." The specimen numbers and dates of collection suggest that they were captured during the last part of his stay around Vinanitelo (see table 1). Amboasary is a common place-name throughout the eastern forest, but the one provisionally accepted as Major's site is situated about 15 km SW Vinanitelo and appears on the historical maps of Cowan (1882) and Grandidier (1893) and on the 1942 BWO map (sheet 20-21).

48. *Forêt d'Ikongo*.

Coordinates: 21°53'S/47°20'E *g*.

Taxa: *Brachyuromys betsileoensis*.

Remarks: An unverified name for the forest west of Ikongo (21°53'S/47°26'E). Wheth-

er the collector (G. Grandidier in 1901) visited this particular area or some other part of the forest around Ikongo is uncertain.

49. *Ravori*.

Coordinates: ca. 21°38'S/46°18'E *m* = FTM.

Taxa: *Macrotarsomys bastardi bastardi*.

Remarks: This village is the type locality of *Macrotarsomys bastardi* Milne Edwards and G. Grandidier (1898). The describers acknowledged an E. Bastard as the discoverer of the single specimen of their new genus and species and approximated its origin as "sud du Mangoky, entre Midongy et Thosy." In a footnote, they elaborated the geographic location as near the village Ravori, situated to the east of the river Thosy [= Ihosy] and about 3-days' journey to the south of the upper Mangoky River. The French explorer Bastard confined his earlier travels to the valley of the lower Mangoky and Fiherenana rivers (1898), but on 13 August 1897, he departed from Saint Augustin Bay [= Anantsona] and traversed the interior from the southwest to the northeast, arriving in Antananarivo on 13 February 1898. The holotype of *Macrotarsomys bastardi* was collected during this last leg of his journeys.

Pelet (Atlas des Colonies Françaises, 1902) illustrated Bastard's route between Ihosy and Midongy and figured the village Ravori east of the upper Vorondreo [= Ivorondreo] River, a small northern tributary of the Zomandao. According to Pelet's scale, Ravori is situated about 70 km NNE of Ihosy; however, a 70-km distance places the site in the Zomandao River on recent maps. To judge from the position of Ravori with respect to the Ivorondreo River, and using the FTM topographic series, the type locality appears closer to 85 km NNE Ihosy, which represents the point of our estimated coordinates. We have not located a Ravori or an unequivocal phonetic counterpart in the appropriate region on later maps or in the BGN, but the modern village of Mandroarea (ca. 800 m) occurs in the probable vicinity of Bastard's locality. In 1899, Bastard apparently published an account of his sojourn through Bara country in the French geographic periodical "Notes, Reconnaissances, and Explorations," which was referenced by Pelet but has not been seen by us.

Based on information received from Bastard, Milne Edwards and Grandidier (1898) reported the habitat as a treeless region with rocky outcrops.

50. **35 mi N Ihosy** (also 20, 25, and 30 mi N), 915 m [3000 ft].

Coordinates: 22°02'S/46°06'E *g*.

Taxa: *Macrotarsomys bastardi bastardi*.

Remarks: On assignment for the BMNH to rediscover the Madagascar gerbil, Webb (1954) retraced Bastard's probable route between Midongy de l'Ouest [= Midongy Nord] and Ihosy, starting from both the northern and southern places. He found *Macrotarsomys* only on his trek north from Ihosy. Webb indicated the same altitude and coordinates (22.0°S/46.1°E) for all sites; the one plotted is closest to 35 mi N, where most of the *Macrotarsomys* specimens were obtained. Webb (1954) later identified the 25-km-N site as near Ambararatra [= Ambararata, 22°19'S/46°14'E *g*] and the 35-mi-N site as east of the Bara village of Atáratra [= Antaratra], which corresponds to the coordinates listed. At the latter place, he found *Macrotarsomys* dwelling on sparsely vegetated sandy plains dominated by low lateritic hills.

51. **5 km E Route Nationale 7 on road to Ivohibe**, 750 m.

Coordinates: ca. 22°26'S/46°14'E *m* = FTM.

Taxa: *Macrotarsomys bastardi bastardi*.

Remarks: The elevation was extracted from the field journal (1962) of the collector K. Lange, who described the vegetation as dry, open grassland with scattered trees and bushes and noted that *Macrotarsomys* seemed to avoid areas of dense cover. The site is 5 km E of the junction between the Ivohibe road and national route 7, approximately 11 km ESE Ihosy.

52. **Andringitra**.

Coordinates: 22°20'S/46°55'E *g*.

Taxa: *Brachyuromys betsileoensis*, *B. ramirohitra*, *Eliurus myoxinus majori*.

Remarks: The collector A. Peyrieras used Andringitra as a general designation for a number of specific localities, namely Andohariana Plateau, Anjavidilava, *Aguaria* forest, Cuvette Boby, Varavarana, Ivangomena, and Gui de la Riambavy. Few of these places are identified in the BGN, but Perrier de la Bathie (1927) illustrated several of them in

his map of the Andringitra Massif. Apparently all are highland sites around 2000 m or above.

53. **6 mi E Ivohibe** (including 15 mi E), 1525 m [5000 ft].

Coordinates: 22°30'S/47°00'E *c*.

Taxa: *Eliurus myoxinus webbi*.

Remarks: C. S. Webb listed the same coordinates (22.5°S/47.0°E) for both distances and elevations. Notes on his skin tags indicate that the specimens were trapped in "high rain forest." Webb (1954) later recorded his impressions of the very moist character, lush herbaceous undercover, and torrential streams of these forests situated on the western and southern flanks of Ivohibe Mountain.

54. **20 km by road W Vondrozo**, 500 m.

Coordinates: ca. 22°48'S/47°10'E *m* = FTM.

Taxa: *Eliurus minor*, *Eliurus myoxinus webbi*, *Gymnuromys roberti*, *Nesomys rufus audeberti*.

Remarks: Rand (1936) afterwards placed the altitude at about 500 meters and characterized the vegetation as tall rain forest with many buttressed trees, trailing lianas, and abundant bamboo. Jenkins (1987) gave the coordinates as 22°45'S/47°15'E.

55. **Farafangana**.

Coordinates: 22°49'S/47°50'E *g*.

Taxa: *Nesomys rufus audeberti*.

Remarks: Given the locality designation as "region de Farafangana," the single specimen may have originated from forest south of the city.

56. **20 mi S Farafangana**, 4 mi from sea (including Manombo).

Coordinates: 23°02'S/47°44'E *g*.

Taxa: *Eliurus myoxinus webbi*, *Nesomys rufus audeberti*.

Remarks: The 20-mi-S designation reflects the provenance on Webb's skin labels and corresponds to the type locality used by Ellerman (1949) for his description of the *Eliurus* series collected by Webb in 1940. Manombo, visited in 1929 by an MZFAA team who secured the single *Nesomys*, effectively plots as the same locality, and in his reminiscences, Webb (1954) cited the village as his base camp for working in the nearby forest. Located on the eastern coastal plain, Rand (1936) found marshes and meandering streams in low-lying areas and degraded high

forest with scant ground cover on better-drained volcanic soils. The coordinates listed are for the village since Webb's own figures, 23.0°S/48.0°E, define a point that falls in the Indian Ocean.

Toliara Province

57. **Bemangily**, Poste Manantenina.

Coordinates: 24°33'S/47°13'E *g*.

Taxa: *Nesomys rufus audeberti*.

Remarks: The original locality designation was given as "Bemangidy," which the collector H. Hoogstraal placed (field catalog, 1948) at 72 km N Ft. Dauphin [= Tôlanaro]. We located a "Bemangily" in the hills just west of the Dauphin–Manantenina road and about 30 km SSW Manantenina. This place lies at the appropriate distance from Ft. Dauphin, which further suggests its synonymy with Hoogstraal's Bemangidy. The specimen of *Nesomys* was "shot on the ground in late afternoon in original forest."

58. **5 mi E Bevilany**, 245 m [800 ft] (including Bevilany, 90 m [300 ft]).

Coordinates: ca. 25°00'S/46°40'E *m* = FTM.

Taxa: *Eliurus myoxinus myoxinus*, *Macrotarsomys bastardi occidentalis*.

Remarks: The coordinates on Webb's skin tags read 25°S/46.6°E, which corresponds to those of Bevilany itself (*g*). The figures given above approximate the low hills to the east, just north of the Ambovombe–Fort Dauphin road, where Webb obtained most of his *Macrotarsomys* and all of the *Eliurus*. Notes on his skin tags describe the habitat as an abrupt "transition between dry scrub and evergreen forest."

59. **7 mi NE Lake Anongy** [= Farihy Anony].

Coordinates: 25°06'S/46°30'E *c*.

Taxa: *Macrotarsomys bastardi occidentalis*.

Remarks: According to his later comments (1954), Webb encamped at the village of Antsovelo on the northwestern shore of Lake Anongy. He located the *Macrotarsomys* about 7 mi to the northeast in gallery forest along dry stream beds, not in the nearby *Didierea-Euphorbia* scrub.

60. **Ambovombe**.

Coordinates: 25°10'S/46°05'E *g*.

Taxa: *Macrotarsomys bastardi occidentalis*.

61. **Tsihombe** [= Tsiombe].

Coordinates: 25°18'S/45°29'E *g*.

Taxa: *Macrotarsomys bastardi occidentalis*.

Remarks: Webb, in 1944, listed the coordinates as 25.3°S/45.5°E and found the area to be very arid with "low scrub, bushes 3–4 feet high, soil almost barren." In 1962, K. Lange (field journal) similarly categorized the region as arid scrub with many euphorbs and patches of *Didierea* forest, scattered baobab trees, and rocky outcrops.

62. **20 km N Cap Sainte Marie** [= Tanjona Vohimena].

Coordinates: ca. 25°25'S/45°07'E *m* = FTM.

Taxa: *Macrotarsomys bastardi occidentalis*.

63. **26 mi E Tulear** [= Toliara].

Coordinates: 23°17'S/43°59'E *g*.

Taxa: *Macrotarsomys bastardi occidentalis*.

Remarks: The coordinates given by C. S. Webb are 23.2°S/44.1°E, but he (1954) apparently conducted his fieldwork around the village of Andranohilany [= Andranohinaly], situated just south of the Tulear–Ihosy road, which corresponds to the point we mapped. Field-tag notes capture the nature of the habitat: "Scrub forest, dry and mainly stony. A mixture of small trees, 10–20 feet high, and dense scrub." Webb (1954) afterwards identified the vegetation as transition between subdesert scrub and deciduous forest.

64. **35 mi E Tulear** [= Toliara].

Coordinates: 23°12'S/44°12'E *c*.

Taxa: *Eliurus myoxinus myoxinus*, *Macrotarsomys bastardi occidentalis*.

Remarks: In contrast to the preceding site, Webb's skin labels mark the habitat as deciduous forest.

65. **Lambomakandro**, Forêt de Sakaraha.

Coordinates: 22°42'S/44°42'E *g*.

Taxa: *Eliurus myoxinus myoxinus*, *Macrotarsomys bastardi occidentalis*.

Remarks: The original tags give the spelling as "Lamboromakandro," which we interpret as the village situated in dry forest about 30 km NE Sakaraha.

66. **Lamboharana**.

Coordinates: 22°12'S/43°14'E *g*.

Taxa: *Macrotarsomys bastardi occidentalis*.

67. Tsilambana.

Coordinates: ca. 20°50'S/44°00'E *m* = FTM.

Taxa: *Eliurus myoxinus myoxinus*.

Remarks: Milne Edwards (1885) vaguely attributed the collecting locality of his new genus and species *Eliurus myoxinus* as the west coast of Madagascar, based on a single specimen received from A. Grandidier. This regional designation has generally been repeated in subsequent taxonomic compendia (Ellerman, 1941, 1949; Honacki et al., 1982). In his catalog of mammalian types in MNHN, however, Rode (1945) identified "Forêts de Tsilambany" as the specific locality.

Alfred Grandidier (1885: 115) had mentioned a "Riv. Tsilambana," an intermittent stream which emptied into an inlet of the sea at Antanimanimbo, and cited himself as first employing this name in 1867. Grandidier (1893) later figured both place-names on the southwestern coast, about 70 km SSE of Morondava, and we located a Tsilambana (as a small village) at the same location on the BWO map (sheet 16). In view of Grandidier's voyages along Madagascar's western coast, particularly in 1866 and 1869, a stopover for natural history reconnaissance in this area is plausible. Moreover, Milne Edward's holotype compares closely with other *myoxinus* obtained in the region, for example those north of Morondava and east of Tulear. Until other evidence advises otherwise, we view the above coordinates as the approximate site of Grandidier's Riv. Tsilambana and accept its equivalence to the type locality of Milne Edward's *Eliurus myoxinus*.

68. Morondava.

Coordinates: 20°17'S/44°17'E *g*.

Taxa: *Eliurus myoxinus myoxinus*, *Hypogeomys antimenae*, *Macrotarsomys bastardi occidentalis*.

Remarks: We are uncertain whether these taxa, particularly *Hypogeomys*, were actually obtained from Morondava and its vicinity or from the places north of the city.

69. Beroboka, 40 km N Morondava, 7 km from sea (including Analabe).

Coordinates: 19°58'S/44°36'E *g*.

Taxa: *Eliurus myoxinus myoxinus*, *Hypogeomys antimenae*, *Macrotarsomys bastardi occidentalis*.

Remarks: C. S. Webb had obtained a small

series of *Macrotarsomys* in flat coastal forest around Beroboka, which became the type locality of Ellerman's (1949) *M. bastardi occidentalis*. Analabe is the name of a private natural reserve that Petter et al. (1971) identified as approximately 60 km north of Morondava (near Lake Andranovala, an expansion of the Kirindy River) and which they equated with Beroboka. The authors described the vegetation of the reserve as dry deciduous forest, including numerous baobabs, with a canopy about 10 to 15 m high and a dense bushy understory.

70. Bekopaka, Antsingy Forest.

Coordinates: 19°09'S/44°48'E *g*.

Taxa: *Eliurus myoxinus myoxinus*.

71. Maintirano, vicinity of.

Coordinates: 18°04'S/44°01'E *g*.

Taxa: *Nesomys rufus lambertoni*.

Remarks: Petter (1962) recognized that this site is the type locality of *Nesomys lambertoni*, whose geographic origin G. Grandidier (1928) had omitted from his species description.

Mahajanga Province

72. Ampijoroa, 40 km S Marovoay, Ankarafantsika Reserve.

Coordinates: 16°18'S/46°49'E *g*.

Taxa: *Macrotarsomys bastardi occidentalis*, *M. ingens*.

Remarks: Type locality of *Macrotarsomys ingens* Petter (1959). The general vegetation of the reserve is dry deciduous forest, but information on the microhabitat requirements of *bastardi* (collected by K. Lange, 1963) and *ingens* is wanting.

73. One day E Maromandia.

Coordinates: 14°06'S/48°17'E *g*.

Taxa: *Nesomys rufus rufus*.

Remarks: In his account of the MZFAA itinerary, Rand (1936) identified this camp as on the lower edge of forest near Andampy, a village about 22 km NE Maromandia which corresponds to the coordinates given. Collections were apparently made in tall, relatively wet forest on steeply rising slopes just to the east of Andampy. The village itself is situated around 100 m, but depending on the distances worked to the east, specimens may have originated from forests at 200 to 500 m.

Indeterminate Localities

1. Maisine and Savary, N.E. Madagascar.

Taxa: *Nesomys rufus audeberti*.

Remarks: J. Audebert, a German naturalist, made significant collections of birds and mammals for RMNH along Madagascar's eastern coast from 1876 to 1880. Audebert's orthographic renditions of Malagasy place-names, however, have challenged attempts to associate them with conventional geographic spellings and created considerable uncertainty about the distribution of the taxa he collected (see Vuillaume-Randriamanantena et al., 1985; Tattersall, 1986). Fortunately for the rodent systematist, Audebert mostly collected lemurs; unfortunately, the three rodent specimens that he did obtain comprise the syntypes for Jentink's (1879) description of *Hallomys* (= *Nesomys*) *audeberti*.

The three specimens of *Nesomys audeberti* were collected in February and March 1878 from two localities, Maisine and Savary. The systematic catalogs of RMNH holdings compiled by Jentink (1887, 1888, 1892) reveal that Audebert had remained around these sites from late 1877 through 1878. Certain taxa recorded from Maisine and Savary bear the same or successive collecting dates, suggesting that the two places are in close proximity. In his description of *audeberti* and in his catalogs, Jentink placed the localities in "N. E. Madagascar," but we are uncertain whether this attribution was drawn from original tags, based on information received in litt., or represented his own interpretation. Other localities whose dates refer them to the same region as Maisine and Savary include Malewo, Marovato, Mamtibatato, and "Pays Andalusana, Betsileo." The last place has been discussed by Tattersall (1986), who suggested its correspondence to Nandihizana, an isolated patch of forest on the eastern rim of the central plateau which was visited by many early European naturalists and explorers. Whether or not these spelling variations signify the same specific locality, the whereabouts of Betsileo can hardly be misconstrued for some other geographic area.

Audebert apparently spent the year 1876 visiting sites along the northeast coast from the vicinity of Antongil Bay to Toamasina. Locality designations from this year can be plausibly linked to places along this coastal

section, including Maranzettra [= Maroan-tsetra], Mananare [= Mananara], Passumbe [= Ampasimbe], Mahambo, Foulpointe [= Mahavelona], and Vidoutra [= Vohidrotra] (also see Vuillaume-Randriamanantena et al., 1985). Following this collecting period, an interlude of 10 months transpired until November 1877 through the following year, when Maisine, Savary, and other place-names are encountered. After a lapse of one month, a different set of localities appears on Audebert's specimens collected during 1879–1880, including Antsompirina, Antsondrizima, Ambasimbato, Andranofohiz, and Manakava. Both Grandidier (1885) and Connorton (1896) indicated that Audebert had settled in the region of Farafangana at this time and journeyed inland from there (see also Tattersall, 1986).

Future attempts to illuminate Audebert's travels should therefore consider the possibility that he worked extensively along the southeastern coast as well. The region of Mananjary and inland routes to Fianarantsoa warrant attention in this regard. Perhaps most of the ambiguity surrounding his localities can be removed, but the combination of archival and taxonomic research required is beyond the scope of this report.

2. Tamatave Road 68.

Taxa: *Eliurus minor*.

Remarks: A single specimen collected 29 February 1952 by V. J. Tipton.

3. Yandbrazza.

Taxa: *Nesomys rufus audeberti*.

Remarks: A single specimen, date unknown, collected by J. Delacour.

TAXONOMIC AND DISTRIBUTIONAL SUMMARY

We here briefly summarize the nomenclatural foundation and known distributional data for the 18 described forms of *Nesomyinae* (figs. 2 to 6). Abbreviated synonymies trace the original authorship of a species-group name and the revisionary source for currently recognized name combinations. Type locality designations are presented both as worded by the original describer and as located in the foregoing gazetteer (the latter stated in brackets to distinguish it as an updated refinement).

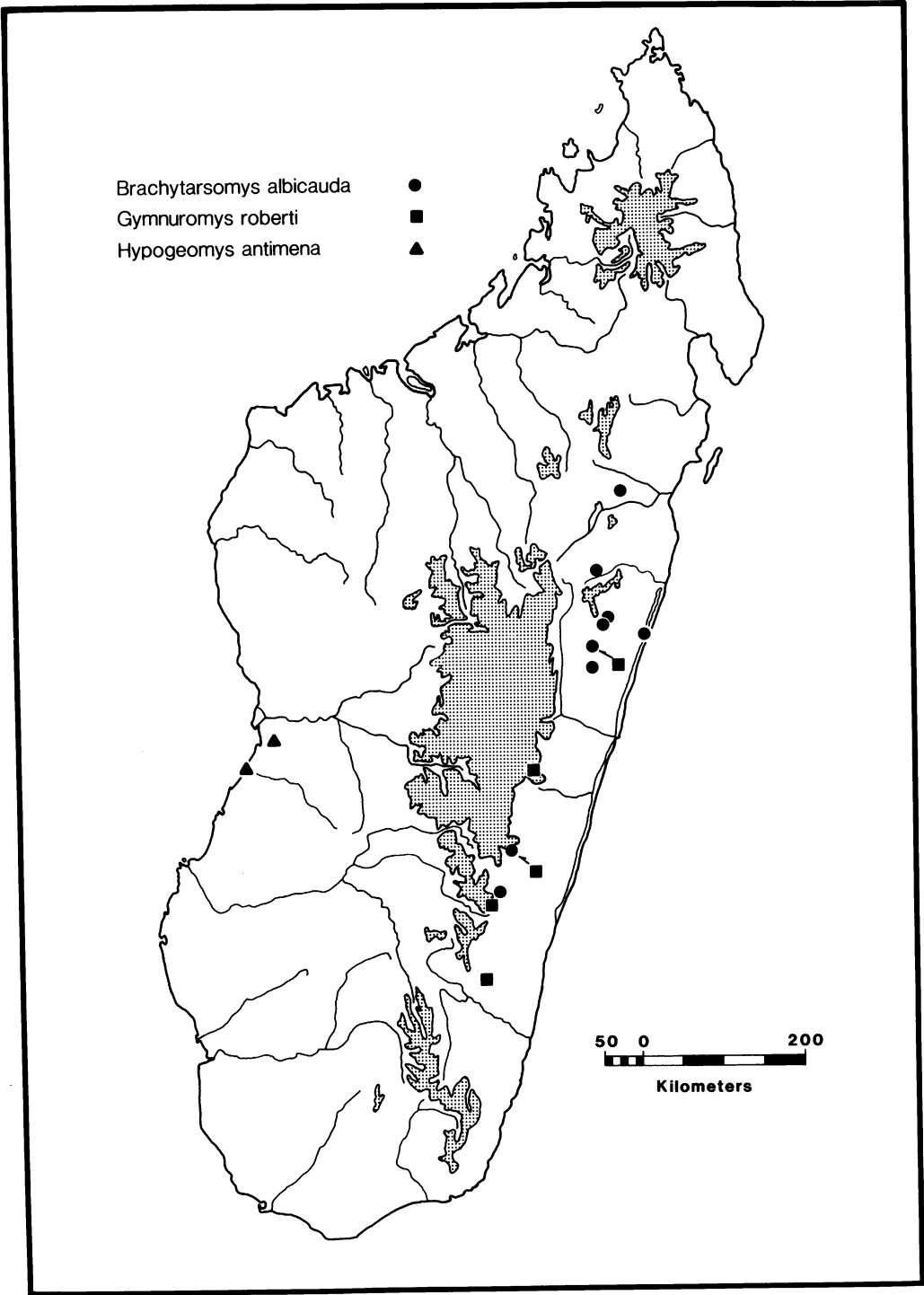


Fig. 2. Geographic distribution of species of *Brachytarsomys*, *Gymnuromys*, and *Hypogeomys*.

Brachytarsomys Gunther, 1875

Brachytarsomys albicauda Gunther, 1875: 80. Allen, 1939: 316. Ellerman, 1941: 556; 1949: 166. *B. a[lbicauda] albicauda*, Petter, 1975: 2.

TYPE LOCALITY: In his report, Gunther acknowledged the receipt of a collection of specimens from Crossley "made on his way from Tamantave to Murundava." Consequently, "between Tamatave and Morondava" has remained the usual locality referenced for the source of Gunther's *Brachytarsomys albicauda* (Allen, 1939; Ellerman, 1941, 1949; Honacki et al., 1982).

Since *Brachytarsomys albicauda* is indigenous to the eastern rain forest, its type locality can perhaps be restricted more precisely. Sihanaka Forest is a reasonable candidate in view of Crossley's westerly excursions from points on the east coast, including Tamatave [= Toamasina], toward Lake Alaotra and the villages of the Sihanaka (Grandidier, 1885). Grandidier (1870), for example, based his description of *Cheirogaleus crossleyi* on a specimen received from Crossley, which he had apparently collected in forests east of the "Antsianak." Further research on the dates and routes of Crossley's travels and the receipt of material at the BMNH may clarify this suggestion.

DISTRIBUTION: Eastern rain forest at middle elevations (450–1300 m), from northeast of Lake Alaotra to Vinanitelo, south of Fianarantsoa (fig. 2). Only 29 of the 51 specimens of *B. albicauda* examined possess trustworthy locality data. The distributional picture resulting from the widely scattered localities emphasizes the need for further refinement of its range.

Brachytarsomys albicauda villosa Petter, 1962: 570; 1975: 2.

TYPE LOCALITY AND DISTRIBUTION: This highly distinctive form is unquestionably specifically distinct from *albicauda*. Petter had discovered the sole specimen, eventually to become the holotype of *villosa*, preserved in alcohol after it had been maintained in captivity at the Vivarium de Parc Tsimbazaza. The rediscovery of this species in the wild and investigation of its geographic distribution and ecology are urgently needed. Petter (1962) conjectured that it may have originated from somewhere in the west, but the

arboreal physiognomy of *Brachytarsomys* seems more typical of a rainforest denizen. Vast areas of lowland forest around Antongil Bay or the forested slopes of Tsaratanana have yet to be thoroughly sampled.

Brachyuromys Major, 1896a

Nesomys betsileoensis Bartlett, 1879: 770. Grandidier, 1928: 95.

Brachyuromys betsileoensis, Major, 1896a: 322. Allen, 1939: 316. Ellerman, 1941: 492; 1949: 166. Petter, 1975: 2.

TYPE LOCALITY: Given by Bartlett as "S. E. Betsileo."

DISTRIBUTION: The eastern part of the central highlands and along its eastern fringes, from southeast of Lake Alaotra to the Andringitra massif (fig. 3). Known altitudinal range from about 900 to 2000 m. Where noted by the collector, individuals of *Brachyuromys* seem to inhabit lush native meadows and wetlands.

Brachyuromys ramirohitra Major, 1896a: 323. Allen, 1939: 316. Ellerman, 1941: 492; 1949: 166. Petter, 1975: 2.

TYPE LOCALITY: Given by Major as "Ampitambe forest, Betsimisaraka country (on the border of N. E. Betsileo), 6 hours S. E. of Fandriana." See Remarks under locality 34 for possible location of Ampitambe as [45 km ESE Fandriana, ca. 900 m, Fianarantsoa Prov., ca. 20°22'S/47°46'E].

DISTRIBUTION: Known only from Ampitambe and Amboasary, both Forsyth Major collecting localities, and by a single specimen from *Agauria* forest, Andringitra. These meagre records suggest an altitudinal belt complementary to that of *B. betsileoensis*, obtained sympatrically with *ramirohitra* at Ampitambe and on Andringitra, but having a more restricted distribution in southern highlands (fig. 3). The limits of its range, however, remain essentially unknown.

Eliurus Milne Edwards, 1885

Eliurus myoxinus Milne Edwards, 1885: 1. Allen, 1939: 317. Ellerman, 1941: 76.

E. m[yo]xinus *myoxinus*, Ellerman, 1949: 166. Petter, 1975: 3.

TYPE LOCALITY: Milne Edwards referenced the origin of the single specimen obtained by A. Grandidier as "côte ouest de Madagas-

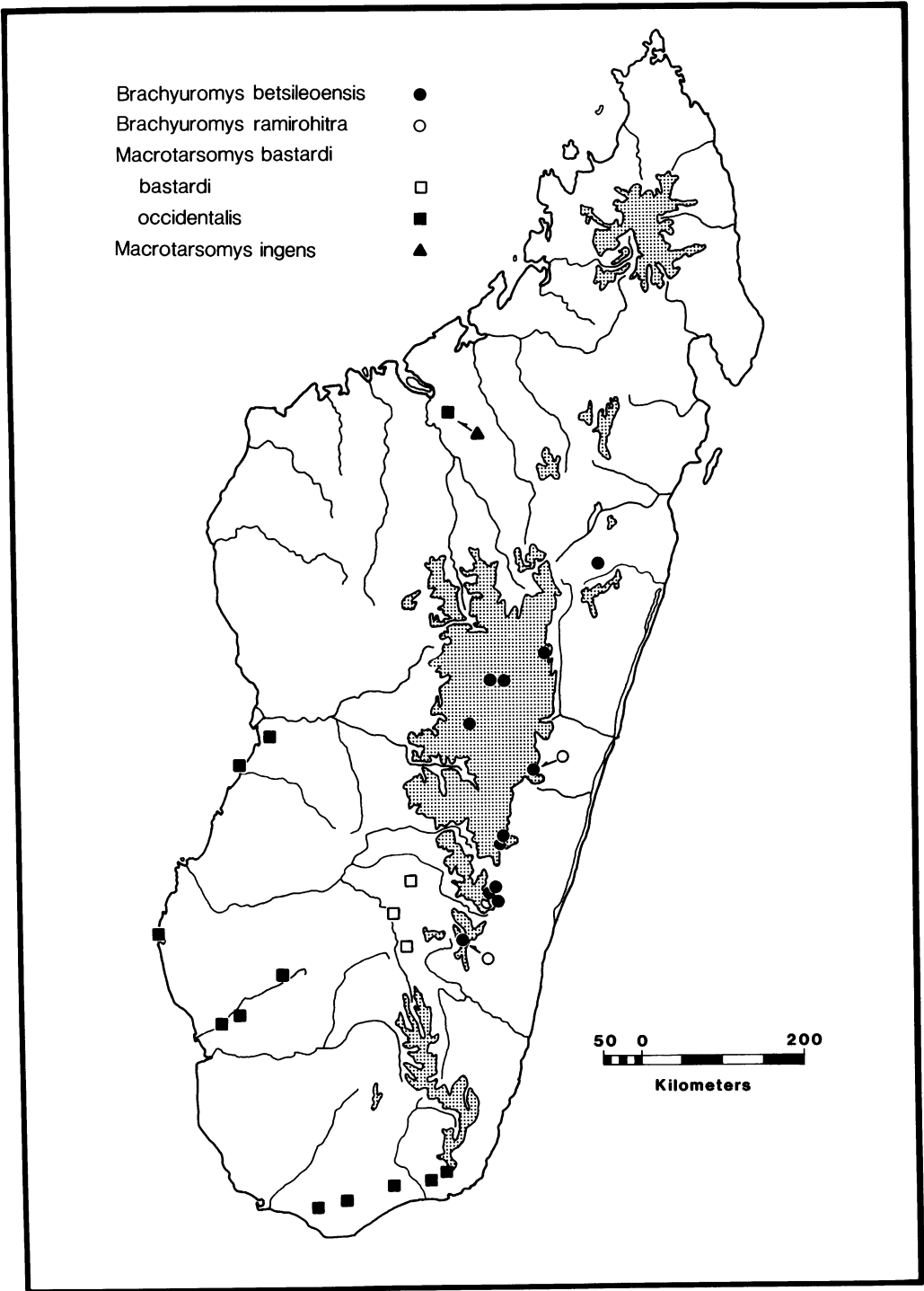


Fig. 3. Geographic distribution of species and subspecies of *Brachyuromys* and *Macrotarsomys*.

car." As argued above, we believe that the animal originated from Tsilambana, a place on Madagascar's southwestern coast cited and mapped by Grandidier (1885, 1893) but not found on recent maps or in the BGN (see Remarks under locality 67). [Tsilambana, ca. 65 km SSE Morondava, Toliara Prov., ca. 20°50'S/44°00'E]

DISTRIBUTION: Dry deciduous forest in southwestern Madagascar and xerophilous scrub in the south, from Antsingy Forest at the latitude of the Manambolo River, south to the cape region, and east across the Mandrare River to the vicinity of Bevilany (fig. 4). *Eliurus myoxinus* proper is unknown above 245 m but few altitudes have been recorded.

Eliurus majori Thomas, 1895: 164. Allen, 1939: 317. Ellerman, 1941: 76.

Eliurus myoxinus majori, Ellerman, 1949: 166. Petter, 1975: 3.

TYPE LOCALITY: Given by Thomas as "Ambolimitambo Forest, Central Madagascar. Alt. 4500 feet," the village name a misreading of Ambohimitambo [ca. 1200 m, Fianarantsoa Prov., 20°43'S/47°23'E].

DISTRIBUTION: Known by only five specimens from three widely separated localities in the northern (Montagne d'Ambre), central (Ambohimitambo), and southern highlands (Anjavidilava, Andringitra) (fig. 4). Elevational records from 1000 and ca. 1200 m. If Rand's (1936) description of the habitat near the summit of Montagne d'Ambre is typical of its occurrence, *majori*, and perhaps its close relative *penicillatus*, may be restricted to montane woodlands characterized as "mossy forest," a formation which has greatly declined in extent (Koechlin, 1972).

Eliurus tanala Major, 1896b: 462. Allen, 1939: 317. Ellerman, 1941: 76.

Eliurus myoxinus tanala, Ellerman, 1949: 166. Petter, 1975: 3.

TYPE LOCALITY: Given by Major as "Forest of the Independent Tanala of Ikongo, in the neighbourhood of Vinanitelo, thirty miles south of Fianarantsoa." [Vinanitelo, ca. 1300 m, Fianarantsoa Prov., 21°43'S/47°16'E]

DISTRIBUTION: Middle to upper elevation eastern rain forest, from southeast of Lake Alaotra south to Vinanitelo (fig. 5). Recorded elevations range between 455 and 1300 m.

The distribution of *E. tanala* appears largely congruent with that of *Brachytarsomys albicauda*.

Eliurus penicillatus Thomas, 1908: 453. Ellerman, 1941: 76.

Eliurus myoxinus penicillatus, Ellerman, 1949: 166. Petter, 1975: 3.

TYPE LOCALITY: Given by Thomas as "Ampitambé, N. E. Betsileo." See Remarks under locality 34 for the possible location of Ampitambe as [45 km ESE Fandriana, ca. 900 m, Fianarantsoa Prov., ca. 20°22'S/47°46'E].

DISTRIBUTION: Known only from the type locality (fig. 5).

Eliurus myoxinus webbi Ellerman, 1949: 163. Petter, 1975: 3.

TYPE LOCALITY: Given by Ellerman as "20 miles south of Farafangana, south-east coast Madagascar, 48°E. 23°S." [20 mi S Farafangana, 4 mi from sea, Fianarantsoa Prov., ca. 23°02'S/47°44'E]

DISTRIBUTION: An elongate belt of low to middle elevation eastern rain forest, from Montagne d'Ambre in the north to the region of Farafangana in the south (fig. 5). Almost all collecting localities of *webbi* fall between sea level and 800 m, but their occurrence in the mountains east of Ivohibe seems atypical for the altitude (1525 m) and habitat (see locality 53).

Eliurus minor Major, 1896b: 462. Allen, 1939: 317. Ellerman, 1941: 76; 1949: 166. Petter, 1975: 3.

TYPE LOCALITY: Given by Major as "Ampitambé forest (N. E. Betsileo)." See Remarks under locality 34 for the possible location of Ampitambe as [45 km ESE Fandriana, ca. 900 m, Fianarantsoa Prov., ca. 20°22'S/47°46'E].

DISTRIBUTION: Widely found in eastern rain forest from the eastern slopes of Tsaratanana and the vicinity of Antongil Bay south to the forested ridge west of Vondrozo (fig. 4). Its altitudinal occurrence is broad also, from near sea level around Antongil Bay to 1500 m near the western and upper limits of humid evergreen forest. *Eliurus minor* is known to occur sympatrically with all other forms of *Eliurus* except *majori*, which may only indicate inadequate sampling in view of *minor*'s broad elevational range.

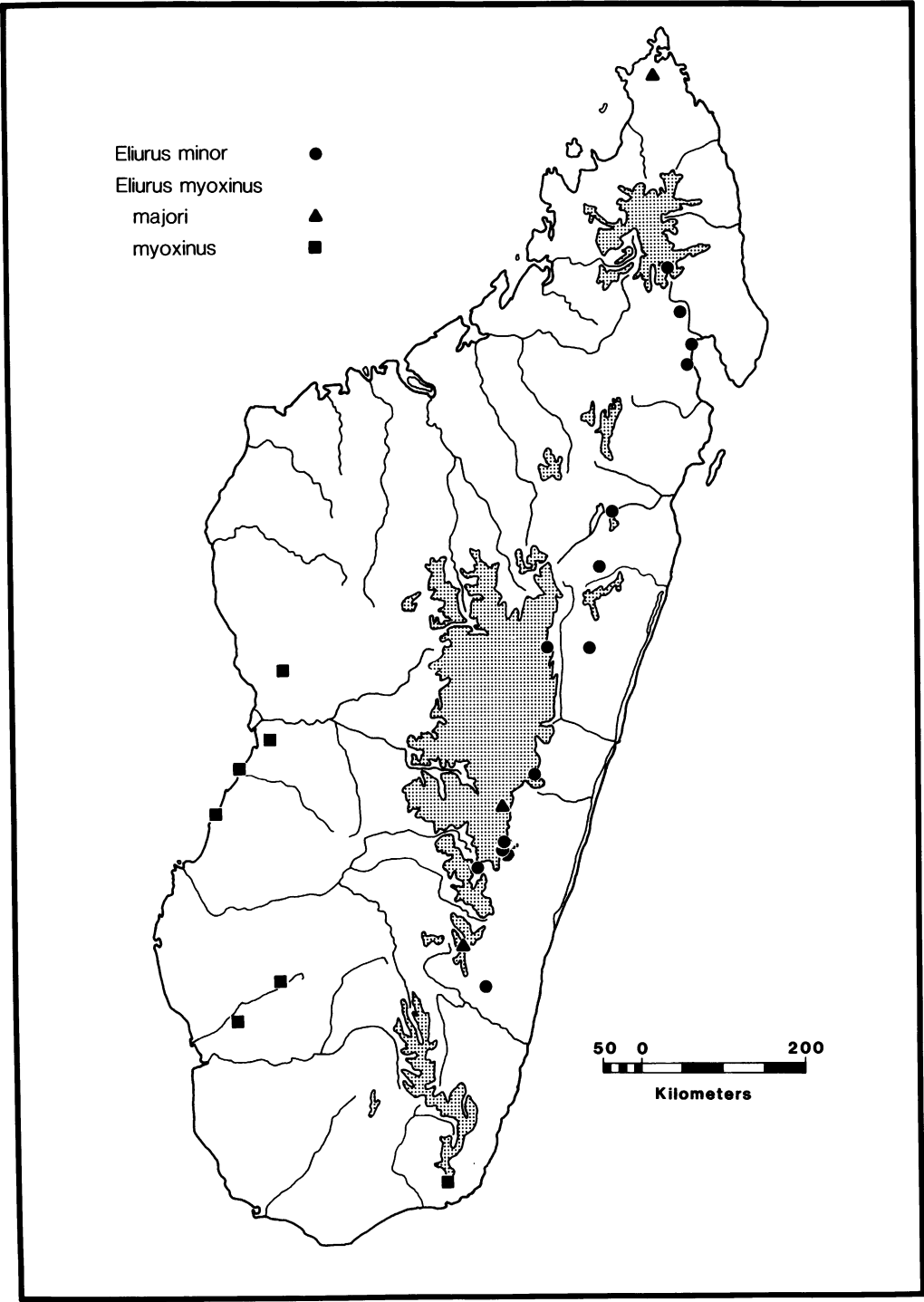


Fig. 4. Geographic distribution of *Eliurus minor* and certain subspecies of *Eliurus myoxinus*.

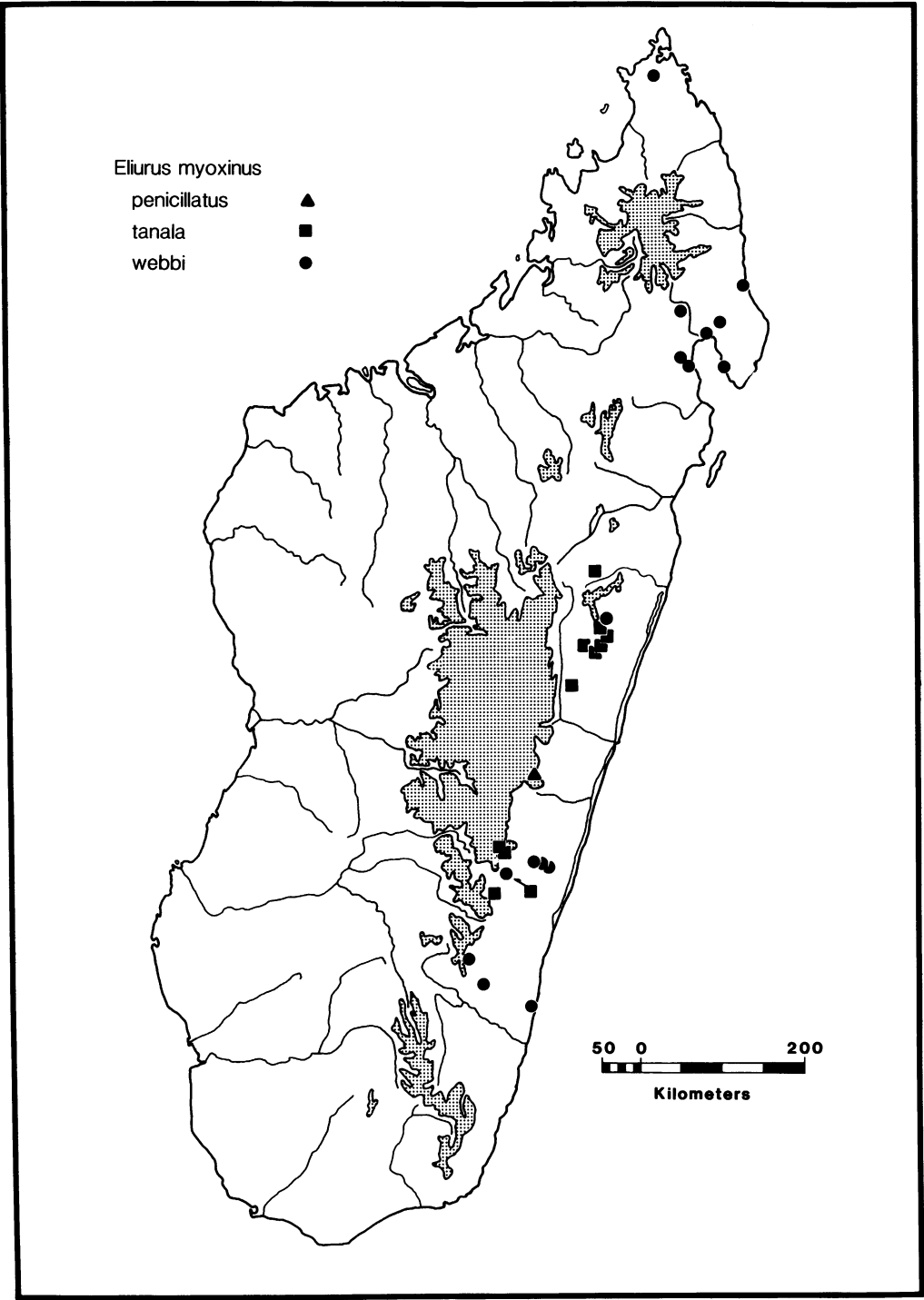


Fig. 5. Geographic distribution of certain subspecies of *Eliurus myoxinus*.

Gymnuromys Major, 1896a

Gymnuromys roberti Major 1896a: 324. Allen, 1939: 317. Ellerman, 1941: 489; 1949: 166. Petter, 1975: 2.

TYPE LOCALITY: Given by Major as "Ampitambé forest." See Remarks under locality 34 for the possible location of Ampitambe as [45 km ESE Fandriana, ca. 900 m, Fianarantsoa Prov., ca. 20°22'S/47°46'E].

DISTRIBUTION: Eastern rain forest from the vicinity of Perinet [= Andasibe] south to the forest west of Vondrozo (fig. 2). The locality of one BMNH specimen, apparently not acquired from Chauvin, is given as Sihanaka Forest, which, if correct, would plausibly extend the northern limits to include the forested ridges east of Lake Alaotra. The known altitudinal range of *Gymnuromys* is narrow, 500 to 950 m, but the fragmentary picture of its distribution warrants enhancement.

Hypogeomys A. Grandidier, 1869

Hypogeomys antimenae A. Grandidier, 1869: 339. Allen, 1939: 318. Ellerman, 1941: 481; 1949: 166. Petter, 1975: 2.

TYPE LOCALITY: Stated by Grandidier as "sur les rives du Tsidsibon et de l'Andranoumène, deux rivières du Menabé indépendant." Grandidier's accounts (1867, 1871) of his voyages along the southwestern coast clearly reveal that he used Tsidsibon to identify the river now known as Tsiribihina. The mouth of the smaller Andranomena lies some 40 km south of the delta of the Tsiribihina and 10 km north of Morondava. The geographic source of Grandidier's specimens, however, may be localized more precisely within this broad range, for his excursion up the Tsiribihina in 1869, when *Hypogeomys* was discovered, was no more than 20 mi (Grandidier, 1871: 94).

DISTRIBUTION: Apparently restricted to a narrow coastal zone of dry deciduous forest with a sandy floor, extending south of the Tsiribihina River and north of Morondava (fig. 2).

Macrotarsomys Milne Edwards and G. Grandidier, 1898

Macrotarsomys bastardi Milne Edwards and G. Grandidier, 1898: 179. Allen, 1939: 318. Ellerman, 1941: 485.

Macrotarsomys bastardi bastardi, Ellerman, 1949: 158. Petter, 1975: 3.

TYPE LOCALITY: Given by Milne Edwards and G. Grandidier as between Midongy and Ihosy, near the village of Ravori, east of the Ihosy River, a 3 days' journey south of the upper Mangoky. The authors erroneously reported the date of collection as 3 October 1857, evidently a misprint for 1897, the year the naturalist Bastard undertook his expedition across the interior where he discovered the specimen that bears his name. See Remarks under locality 49 on the possible location of Ravori as [85 km NNE Ihosy, ca. 800 m, Fianarantsoa Prov., ca. 21°38'S/46°18'E].

DISTRIBUTION: The three localities known are restricted to dry open savannah and sandy plains in the environs of Ihosy, southcentral Madagascar (fig. 3). Altitudinal records range between 750 and 915 m. Although the samples are limited, their vegetational and altitudinal character contrasts with that known for the more broadly distributed subspecies *occidentalis*.

Macrotarsomys bastardi occidentalis Ellerman, 1949: 157. Petter, 1975: 3.

TYPE LOCALITY: Given by Ellerman as "Beroboka, 40 mi north of Morondava, West Madagascar, 44.5°E. 22°S." [Beroboka, 40 mi N Morondava, 7 mi from sea, Toliara Prov., 19°58'S/44°36'E]

DISTRIBUTION: Dry deciduous forests and arid bush and thicket formations in southwestern and southern coastal regions, from south of the Tsiribihina River to the hills east of the Mandrare River (fig. 3). The form is recorded from sea level to 245 m. We provisionally assign the *Macrotarsomys bastardi* from Ampijoroa, Mahajanga Province, to this subspecies, but this allocation will require careful assessment. Aside from this extralimital occurrence, the distribution of *M. b. occidentalis* broadly overlaps that of *Eliurus m. myoxinus*.

Macrotarsomys ingens Petter, 1959: 140; 1975: 3.

TYPE LOCALITY: Given by Petter as 200 meters from Ampijoroa, a village about 100 km from Majunga and next to the Ankafantsika Reserve. [Ampijoroa, Ankafantsika Reserve, Mahajanga Prov., 16°18'S/46°49'E]

DISTRIBUTION: Known only by three specimens from the type locality (fig. 3).

Nesomys Peters 1870

Nesomys rufus Peters, 1870: 55. Allen, 1939: 318. Ellerman, 1941: 376; 1949: 166.
N. rufus rufus, Petter, 1962: 571; 1975: 3.

TYPE LOCALITY: Given by Peters as "Vohima." [Vohima, Antsiranana Prov., 13°21'S/50°00'E]

DISTRIBUTION: Broadly distributed in northern and eastern humid forest, from the western and eastern slopes of the Tsaratanana Massif, south along the eastern escarpment to the vicinity of the upper Namorona drainage system (fig. 6). The distribution of this smaller, reddish-bellied morph of *Nesomys* conceivably extends farther to the south. In the eastern forest block, the form occurs at middle to upper altitudes, presumably into montane forest (known from 900 to 2300 m). The allocation of localities from the lower western slopes of the Tsaratanana Massif (those near Maromandia and Anaborano) is considered tentative, as is the attribution of the name *rufus* to this morphology.

Hallomys audeberti Jentink, 1879: 107. Allen, 1939: 317.

Nesomys audeberti, Ellerman, 1941: 376; 1949: 175.

Nesomys rufus audeberti, Petter, 1975: 3.

TYPE LOCALITY: Jentink (1879) based his new genus and species on three specimens in J. Audebert's series from "Maisine and Savary.—N. E. Madagascar," apparently the only rodents that Audebert had collected. Jentink (1879) did not designate a holotype or mention specimen numbers, and in his systematic catalogs (1887, 1892), he referred to each as one of the types of the species. The young adult male from Savary (RMNH 26527), preserved as a mounted skin with skull and skeleton, seems overall to fit the measurements and figures Jentink presented in his description (1879) and osteological catalog (1887), respectively, and may one day qualify for designation as a lectotype. The other two specimens originated from Maisine—an adult male (RMNH 26528) preserved as a mounted skin with skull, and an adult female (RMNH "c") preserved whole in fluid with three fetuses.

As reviewed above, the geographic placement of Audebert's localities Maisine and Savary, among others, remains enigmatic. The three specimens, however, conform closely to the larger, whitish-bellied *Nesomys* that inhabits low to middle elevation rain forest along the eastern coast. The association of this name and morphology must be considered tentative pending completion of the generic revision.

DISTRIBUTION: Broadly distributed throughout eastern rain forest, from localities around Antongil Bay south to the region of Manantenina (fig. 6); from sea level to 1000 m.

Nesomys lambertoni G. Grandidier, 1928: 95. Ellerman, 1941: 376; 1949: 175.

N. rufus lambertoni, Petter: 1962: 571; 1975: 3.

TYPE LOCALITY: In his description, Grandidier failed to provide a specific locality or even the region from which the three specimens of his new species originated. Ellerman (1941, 1949) erroneously interpreted Grandidier's (1928: 99) remarks to indicate their source from "Rogez, near Brickaville, East Madagascar," but in context, Grandidier was clearly referring to an example of what he recognized as the eastern species *Nesomys rufus* (probably a specimen of *audeberti*). Based on the single skin in MNHN, Petter (1962: 571) later supplied the correct locality, "région de Maintirano, sur la côte occidentale," which agrees with the provenance of the two topotypes in MCZ. [vicinity of Maintirano, Toliara Prov., 18°04'S/44°01'E]

DISTRIBUTION: Known only from the type locality (fig. 6).

DISCUSSION AND RESEARCH NEEDS

Paulian (1984: 153) characterized the endemic rodents of Madagascar as an "exceptionally poor fauna with little speciation." Earlier, Darlington (1957: 522) had assessed the paucity of species as "a discordant detail [that] may be due to chance." Their statements echo the prevailing view that the nesomyine rodents of Madagascar represent an unusually impoverished fauna (see also Brygoo, 1972; Woods and Eisenberg, 1989). The existence of only 10 species representing 7 genera does seem anomalous when viewed

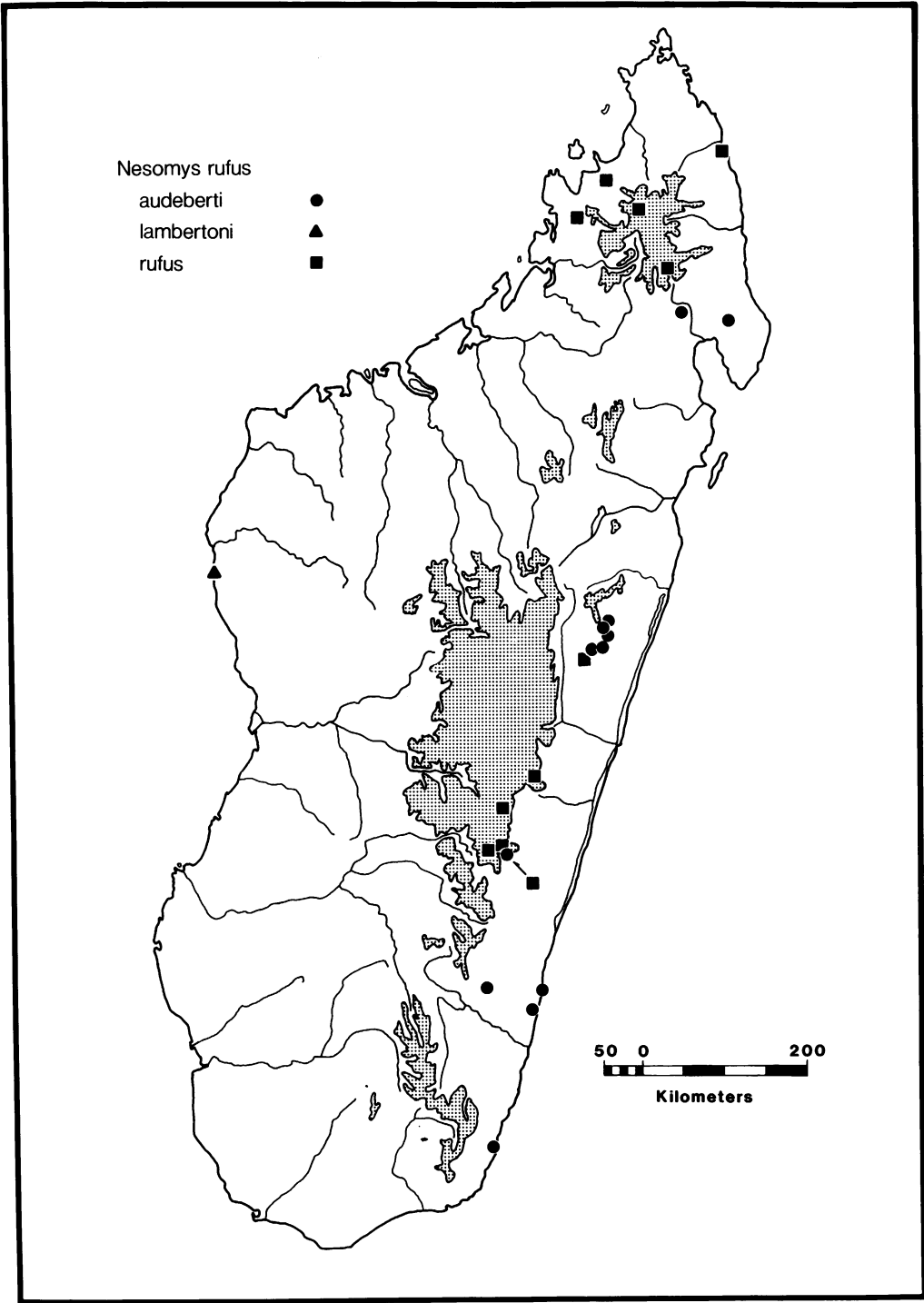


Fig. 6. Geographic distribution of subspecies of *Nesomys rufus*.

TABLE 2

Comparison of Number of Native Rodent and Primate Species On Large Islands that Support Diverse Tropical Floras

Island (type)*	Area (km ²)	Elev. (m)	Rodentia (muroids/others)	Primates	Source
New Guinea (C)	792,500	5209	60 (60/0)	0	1
Borneo (C)	743,244	4101	57 (19/38)	13	2
Madagascar (O)	587,041	2876	10 (10/0)	24-30	3
Sumatra (C)	473,244	3805	46 (21/25)	11	4
Sulawesi (O)	178,700	3455	42 (36/6)	6	1
Java (C)	125,628	3428	24 (12/12)	5	4
Luzon (O)	108,171	2930	23 (23/0)	1	4
Mindinao (O)	99,078	2954	17 (14/3)	2	4
Palawan (C)	11,785	2084	10 (3/7)	1	4
Mindoro (O)	9,735	2585	6 (6/0)	1	4

* = continental shelf island (C) or oceanic island (O).

1 = Musser, 1987. 2 = Medway, 1977; Musser, 1981. 3 = Petter, 1975; Petter et al., 1977; Tattersall, 1982; Meier et al., 1987; Simons, 1988. 4 = Heaney, 1986.

against the size of Madagascar (587,041 km² in area), the diversity of its climate, topography and flora, and the differentiation that has marked other mammal groups isolated there.

Notably, the species diversity of primates and their abundance relative to the rodents (table 2) constitute a unique situation as judged against the relative diversification of these groups on other archipelagos and oceanic islands (see, for example, Heaney, 1986; Musser, 1987; Woods and Eisenberg, 1989). Woods and Eisenberg (1989) attributed this difference to the later arrival of nesomyines to Madagascar, where many ecological niches typically filled by rodents were already populated by an earlier Tertiary diversification of tenrecs and lemurs. The seemingly disproportionate number of strepsirhine primates is even greater if one includes the lemurs known as subfossils (another 13 species and 6 genera), which persisted until shortly after the appearance of humans on Madagascar, approximately 1500 to 2000 years ago (Tattersall, 1982). If this unbalanced faunal composition is real, the meagre number of Malagasy rodents, in and of itself, poses interesting ecological and evolutionary questions.

The timing of the emigration of the first nesomyine or nesomyines into Madagascar remains inferential given the lack of critical Tertiary strata on the island and the rarity of

appropriately aged fossil muroids from sites in eastern Africa. Lavocat (1978) postulated their entrance by overwater dispersal in the lower Miocene, in part because this epoch marks the first appearance of archaic cricetodontids in Africa. A period later than the lower to middle Miocene would prove difficult to reconcile with Madagascar's lack of murines, which appear in the late Miocene of Africa and become commonplace in Pliocene beds. A more pivotal consideration, however, is the afrocricetodontine *Protarsomys macinnesi*, which Lavocat (1973) described from the Rusinga formation, lower Miocene of Kenya, and which he (1978) viewed as close to the ancestry of the Malagasy Nesomyinae.

Chaline et al. (1977) formalized this interpretation by synonymizing *Protarsomys* under *Macrotarsomys*. Inspection of a cast of the holotype of *Protarsomys* (National Museum of Kenya 2350) leads us to question this level of relationship. *Protarsomys* and *Macrotarsomys* do share certain dental features, for instance, a brachyodont cuspidation and an incipient anterocone(id), but these primitive features do not necessarily support their synonymy. *Protarsomys* contrasts strikingly with *Macrotarsomys* in the architecture of its infraorbital canal and rudimentary zygomatic plate. In these traits, *Macrotarsomys* approaches the typical murid condition as

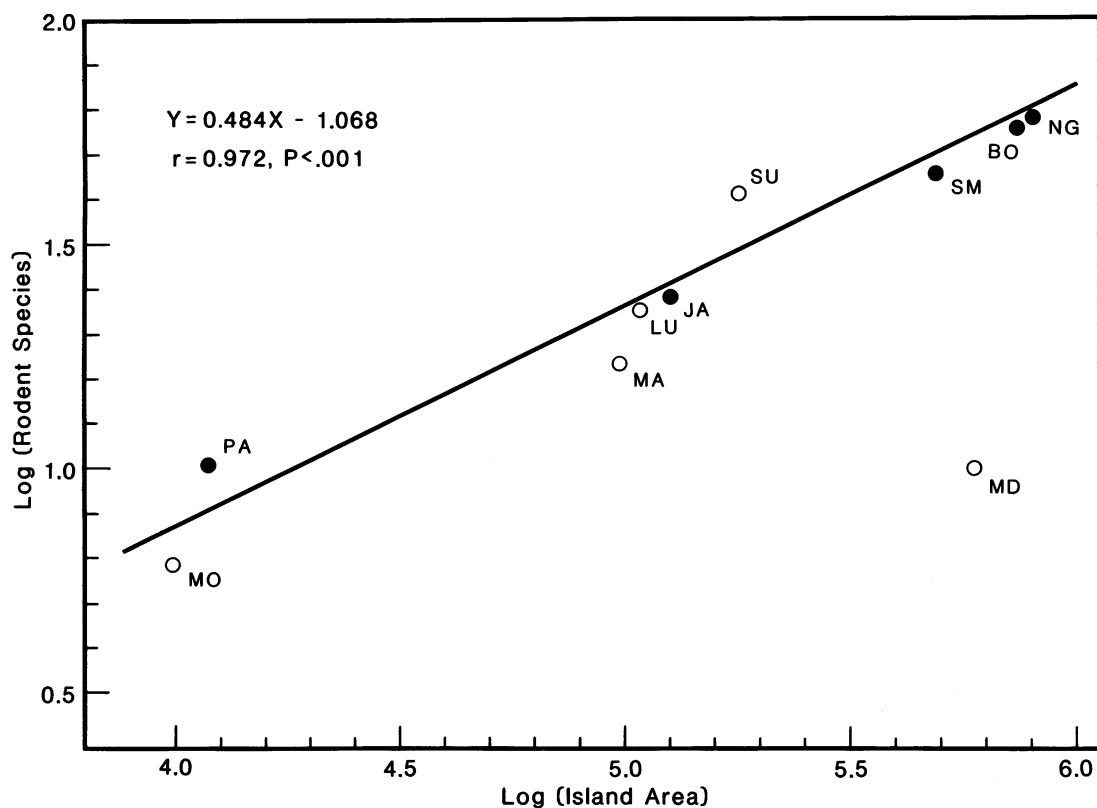


Fig. 7. Relationship between log of island area and log of number of endemic rodent species for large islands with diverse tropical floras (BO, Borneo; JA, Java; LU, Luzon; MA, Mindinao; MD, Madagascar; MO, Mindoro; NG, New Guinea; PA, Palawan; SM, Sumatra; SU, Sulawesi). Solid circles denote continental-shelf islands and open circles oceanic islands. Madagascar was not included in the calculation of the regression statistics ($N = 9$); see table 2.

observed in other nesomyines, whereas *Protarsomys* exhibits a round infraorbital canal and a small, almost horizontal zygomatic plate as found in other Miocene afrocricetodontines (Lavocat, 1978). These differences do not substantiate the union of the fossil species *macinnesi* with those of *Macrotarsomys*. Like other early muroids, *Protarsomys* displays a somewhat generalized morphology, but whether it is phylogenetically associated with nesomyines or another African group is a matter for further study.

A comparison of nesomyine species diversity with rodent assemblages found on other large islands underscores the notion of impoverishment. For a variety of islands occurring within tropical latitudes, there exists a strong positive correlation ($r^2 = .945$) be-

tween island area and the number of indigenous rodent species (fig. 7), a relationship which generally agrees with more robust studies using larger suites of nonvolant mammals (for example, Heaney, 1986; Lawlor, 1986). Madagascar, with its depauperate rodent fauna, is a conspicuous outlier from this regression. Its position in this regard even contrasts with that of other large, geologically old oceanic islands with long histories of isolation, for instance Sulawesi and Luzon. Such a picture of low species diversity is difficult to reconcile with the proven colonizing ability and cladogenetic vigor of rodents, particularly Muroidea, whether demonstrated on a continental scale, such as Australia and South America, or on an insular one, such as New Guinea and Sulawesi.

One must ask, however, to what extent Madagascar's departure from the species-area curve is an artifact of insufficient biological survey and basic taxonomic study. Our examination of rodent material in nine large museums uncovered approximately 750 specimens, which constitute the empirical basis for our knowledge of nesomyine taxonomic diversity and geographic distributions. By way of contrast, the lemur holdings in just the AMNH, BMNH, and MNHN total about 2800 specimens (Buettner-Janusch and Tattersall, 1985; Jenkins, 1987; Yoder, in prep.). These collections, together with significant holdings in other museums such as RMNH and MCZ, establish a much firmer systematic foundation for the 24 to 30 recognized lemur species (Petter et al., 1977; Tattersall, 1982). The disparity between rodents and lemurs in specimen-based reference collections is especially apparent in the superior geographic coverage and more extensive locality series that exist to document our taxonomic understanding of Madagascar's primates. Even so, discoveries of new species of lemurs and viverrid carnivores are still occurring (Meir et al., 1987; Simons, 1988; Wozencraft, 1986). What then is the likelihood that smaller, reclusive species such as nesomyine rodents and shrew tenrecs have escaped detection, either in the field or in museum cases?

The portrayal of Madagascar's endemic rodents as an "impoverished fauna," in the sense of Paulian (1984), must await critical substantiation. Certainly, it is an unbalanced one in comparison to the African mainland, the hypothesized source area for many of the island's terrestrial mammals (though, this conventional interpretation is not without its weaknesses—see Gingerich, 1975). Conspicuous by their absence from Madagascar are the sciurids, hystricognaths, and the many subfamilies of murids that dominate Africa's small mammal communities. Nevertheless, the inadequacy of small mammal inventory on Madagascar leaves open the possibility that the species richness of nesomyines will be found to approach the rodent assemblages that have populated other large islands with diverse tropical floras.

In our opinion, the described forms of Nesomyinae, with the possible exception of Ell-

erman's (1949) *Macrotarsomys bastardi occidentalis*, represent valid biological species. The sympatric or parapatric distributions observed for certain forms—such as *Eliurus tanala* and *E. webbi* or *Nesomys rufus* and *N. audeberti*—intimate their genetic isolation. Documentation of this perception, based on available museum series, forms the object of alpha-level revisionary studies now in progress. In addition to syntheses of existing collections, three other areas of research deserve attention in order to enhance our comprehension of nesomyine systematics and evolution.

1. Archival research on early museum collections and early collectors. — We have the impression that the indeterminate or obscure provenance associated with many specimens acquired in the late 1800s can be recovered, or at least their collecting locations can be restricted with greater assurance than exists now. Since many such older specimens serve as types or as members of type series, refinement of their geographic origin holds obvious relevance for taxonomic and biogeographic studies. The research needed will blend the sleuthing talents of the biographer, the systematist, and the orthographer.

With regard to the Nesomyinae, the expeditions of J. Audebert (1876–1880) and Forsyth Major (1894–1896) especially require illumination, but the results of such archival research would benefit the systematic understanding of Malagasy mammals in general. For example, the sorting of dates, original field numbers, taxa, and localities of the series obtained by Forsyth Major (table 1) helped us to clarify segments of his itinerary that were vaguely related in his own account (1896c). The rodents, however, form a small portion of Major's total collection, and their collation still leaves considerable gaps in our summary of his field movements. Many other mammals were procured by Major and constitute the basis of new taxa described by him and by other systematists who have used his collections. Collaborative effort from several specialists is required to supply rigorous identifications in order to delimit with greater certainty the locations he visited, the placement of type localities, and the distributions of the taxa he collected. Such museum-based research will also distill the

known distributional data as a framework for designing field surveys and resolving specific taxonomic problems.

2. Field inventory of nesomyine distribution and taxonomic diversity. — As argued above, the empirical basis underlying our comprehension of nesomyine biological diversity is poor. Basic biological surveys of many areas of the island are needed to redress this weakness. Perhaps only middle-elevation rain forest has been adequately sampled for rodents, yet even within this extensive and complex biome, only two areas, namely around Andasibe and Ranomafana, possess satisfactory documentation. Poorly known regions abound, the most conspicuous being western deciduous woodlands, in particular the broad swath stretching from the Tsiribihina River in the midwest to the Ampasindava Peninsula in the northwest (see fig. 1). Other areas warranting critical attention are lowland forest around Antongil Bay, montane and subalpine communities of the principal massifs, and the ecotone between xerophilous bush and evergreen forest in the southeast.

With the exception of the expeditions of Major and Webb, most nesomyine museum specimens collected prior to the 1980s seem to have resulted from an opportunistic or sporadic sampling approach. As a result, specimen-based documentation of the community of rodents to be expected within a given plant association is generally meagre. This shortcoming advises that field surveys emphasize longer-term, intensive site visits. Elevational transects from montane to lowland communities would be informative in view of the apparent altitudinal stratification of rodents along the island's eastern escarpment (see fig. 8). Unfortunately, the extensive loss of primary habitats renders a census through intergrading vegetation types difficult if not impossible to undertake. The eastern slopes of Tsaratanana or Andringitra may offer the best possibilities. Finally, effort should be made to return to type localities, or whatever remnants of original vegetation persist in their vicinity, in order to preserve new material using a variety of methods that will broadly serve systematic investigations.

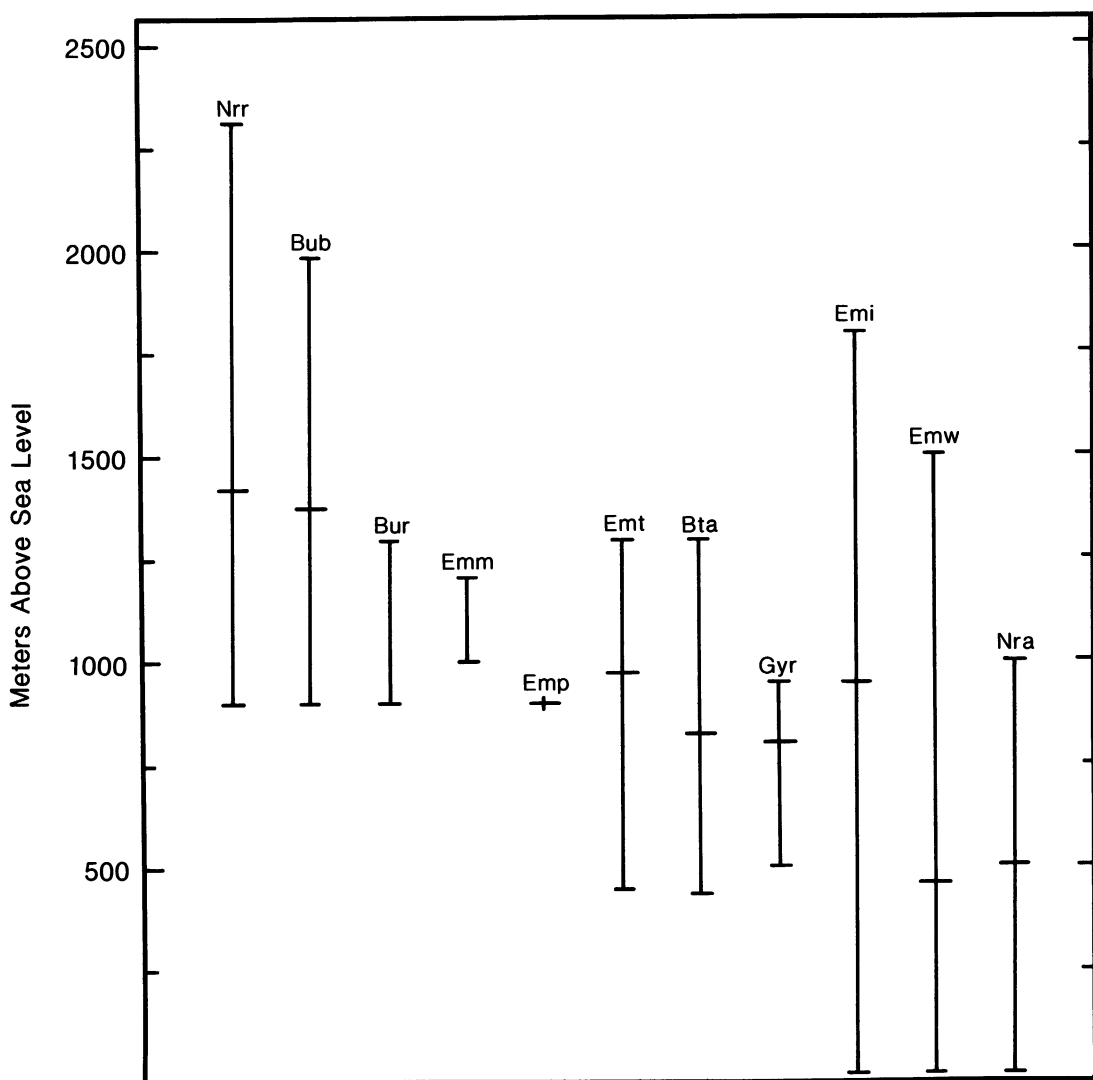
3. Studies of nesomyine ecology, reproductive biology, and life history. — Aside

from Letellier and Petter's (1962) observations on captive *Macrotarsomys bastardi*, appreciation of these facets of nesomyine biology issues almost entirely from anecdotal comments in field catalogs and scattered notes on skin labels. Comprehensive, long-term laboratory and field studies are therefore warranted for all areas of their natural history and sociobiology.

Ecological investigations should regularly preserve voucher specimens to verify species identifications. The probable sympatric occurrence of forms currently arranged as subspecies, for example those of *Nesomys rufus* and *Eliurus myoxinus*, and the likelihood of encountering undescribed species necessitate this elementary precaution. Although generally discussed at supraspecific levels, a firm genealogical framework is considered by many to be integral to the evolutionary interpretation of characteristics—morphological, behavioral, ecological, etc.—observed among and within species (for example, Coddington, 1988; Dobson, 1985). In analogous fashion, the context of population studies on ecology and behavior presupposes a concrete species taxonomy. This classificatory foundation is demonstrably inadequate for several genera of the Nesomyinae.

A related focus of ecological investigations of nesomyine rodents should concern the nature of their association with the introduced commensals, *Rattus rattus*, *R. norvegicus*, and *Mus musculus*. The notion that these transplanted murines have invaded native habitats and are depressing nesomyine populations seems generally accepted but scantily researched (see Brygoo, 1972; Rakotondravy, 1987). In particular, *Gymnuromys roberti* has been mentioned as threatened by the presence of *Rattus rattus* (Nicoll et al., unpub.—cited in Stephenson, 1987). In light of this conjecture, it is interesting that the ratlike *Gymnuromys roberti* was as abundant as were species of *Nesomys* and *Brachyuromys* in Major's 1895–1896 collections from Ampitambe.

If true, this encroachment would prove an exception to the general pattern of interaction between introduced species and native rodent faunas in other parts of the world. Musser (1977, 1987), for instance, has identified a cohort of five *Rattus* species and *Mus mus-*



Nesomyines of the Eastern Forest and Central Plateau

Fig. 8. Means and ranges of altitudinal distribution for nesomyine rodents from the eastern forest and central plateau. **Bta**, *Brachytarsomys albicauda* (N = 6 localities); **Bub**, *Brachyuromys betsileoensis* (N = 10); **Bur**, *B. ramirohitra* (N = 2); **Emi**, *Eliurus minor* (N = 13); **Emm**, *E. myoxinus majori* (N = 2); **Emp**, *E. m. penicillatus* (N = 1); **Emt**, *E. m. tanala* (N = 8); **Emw**, *E. m. webbi* (N = 14); **Gyr**, *Gymnuromys roberti* (N = 4); **Nra**, *Nesomys rufus audeberti* (N = 10); **Nrr**, *N. r. rufus* (N = 7).

culus that have been broadly introduced throughout Southeast Asia, the Philippines, and the Indomalaysian region, accompanying the migrations and activities of humans. One or more of these murines usually occurs in habitats modified by humans, but where

the forest remains untouched, one discovers the indigenous rats and mice.

Comments of earlier collectors in Madagascar inevitably link the capture of commensal rodents with habitats degraded to one degree or another, even lush second-genera-

tion rain forest (Kaudern, 1915; Rand, 1932; Webb, 1954), or give no clue to the history of habitat use. The survey of J. Shaw and K. Lange in the early 1960s produced many examples of *Rattus rattus*, yet their field journals generally indicate the near presence of people and some habitat alteration for every such locality. Stephenson (1987), on the other hand, found that *Rattus rattus* did not penetrate undisturbed vegetation within his lowland rainforest site. Thus, whether *Rattus* species and other commensals pose a competitive threat will require clearer substantiation in the context of well-designed field investigations. At present, the available but mostly circumstantial evidence suggests that habitat modification remains the principal menace to native rodent populations and that the presence of the commensals gives secondary testimony to this degradation.

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