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Authors: Carleton, Michael D., and Goodman, Steven M.

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A New Species of the *Eliurus majori* Complex (Rodentia: Muroidea: Nesomyidae) from South-central Madagascar, with Remarks on Emergent Species Groupings in the Genus *Eliurus*

MICHAEL D. CARLETON[1] AND STEVEN M. GOODMAN[2]

ABSTRACT

A new species of *Eliurus*, *E. danieli* (Nesomyidae: Nesomyinae), is described from the Parc National de l'Isalo in south-central Madagascar. Although geographically intermediate to eastern and western forms, diagnostic traits convincingly relate the new species to *E. majori* and *E. penicillatus*, forms distributed primarily in eastern humid forest; it is morphometrically most similar to *E. penicillatus*. In view of the increase in number of *Eliurus* species (11 now described), discussion is devoted to emerging species associations (5 are identified) and to taxonomic and distributional problems introduced by the accumulation of larger series and new localities over the past decade.

RÉSUMÉ

Une nouvelle espèce d'*Eliurus*, *E. danieli* (Nesomyidae: Nesomyinae), provenant du Parc National de l'Isalo, situé au centre-sud de Madagascar est décrite ci-dessous. Géographiquement, c'est un taxon intermédiaire entre l'Est et l'Ouest. Les caractères déterminants de cette nouvelle espèce sont similaires à ceux de *E. majori* et *E. penicillatus* dont la distribution primaire se situe dans la forêt humide de l'Est. Morphometriquement elle se rapproche plus de *E. penicillatus* que de

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[1] Research Associate, Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History; and Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0111 (carleton@si.edu).

[2] Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, and World Wide Fund for Nature, BP 738, Antananarivo (101), Madagascar (sgoodman@fmnh.org, sgoodman@wwf.mg).

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E. majori. En vue du nombre croissant des espèces d'*Eliurus* (11 actuellement décrites), une discussion est consacrée à l'association des espèces émergeant (5 sont identifiées) et aussi sur les problèmes de distribution et taxonomiques engendrés par l'accumulation des grandes séries de nouvelles localités durant cette dernière décade.

INTRODUCTION

Most species of Madagascar's tufted-tailed rats, genus *Eliurus* (Nesomyidae: Nesomyinae sensu Musser and Carleton, 2005), are known to inhabit the eastern humid forest biome (Carleton, 1994, 2003; Carleton and Goodman, 1998). However, diversity of *Eliurus* in the island's central and western landscapes has been historically underappreciated, as evidenced by the recent description of *E. antsingy* and discovery of extralimital forms that demonstrate affinity to eastern species (Jansa et al., 1999; Carleton et al., 2001). The taxonomic status and relationships of one of those outlying forms, from the Parc National de l'Isalo in south-central Madagascar, are treated herein. First known from a specimen collected in April 1995 by an inventory team led by A. F. A. Hawkins (Hawkins, 1995), Carleton sketched (26 July 1996) his impressions as "An *Eliurus* to be sure but probably new …. In its robust molars, overall shape and mandibular conformation, skull suggestive of the *majori-penicillatus* complex." Tissues of the specimen had been preserved, and molecular data closely affiliated the individual (called "sp. A") with *E. majori* Thomas (1895) among the eight *Eliurus* species studied (Jansa et al., 1999). In December 2002, Goodman returned to the area and obtained two additional specimens. These exhibit the same unique combination of morphological traits and sustain description of the Isalo specimens as a new species. In addition, we provisionally arrange the 11 currently recognized species of *Eliurus* into five species groups, present new range records for certain species (*E. antsingy* Carleton, Goodman, and Rakotondravony, 2001; *E. myoxinus* Milne Edwards, 1885; *E. petteri* Carleton, 1994; *E. penicillatus* Thomas, 1908), and highlight taxonomic problems that have emerged coincidentally as sample sizes and geographic inventory of nesomyine rodents have markedly improved over the past decade.

MATERIALS AND METHODS

Specimens reported herein consist principally of study skins and skulls from the following museum collections: the American Museum of Natural History, New York City (AMNH); the Natural History Museum, London (BMNH, formerly British Museum of Natural History); Field Museum of Natural History, Chicago (FMNH); Merseyside County Museums, Liverpool (LMCM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Département de Biologie Animale, Université d'Antananarivo, Antananarivo (UADBA); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM, formerly U.S. National Museum); Universitets Zoologisk Museum, Copenhagen (UZMC); and Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Coordinates used to compose the range map are those given by collectors for recent collections (see appendix 1) or those estimated by Carleton and Schmidt (1990) for older ones.

Six external and 18 craniodental variables were recorded in millimeters (mm) for each specimen examined. The external variables, as extracted from collectors' skin tags or field catalogs, include: total length of body and tail (TOTL); head and body length (HBL); length of tail vertebrae (TL); hind-foot length (HFL, usually without claw for recent collections); ear (pinna) length (EL); and weight in grams (WT). The 16 cranial and two dental variables (all measured by Carleton) were recorded to 0.01 mm using handheld digital calipers and while viewing the skull under a microscope. According to the anatomical landmarks defined and illustrated in Carleton (1994), these include: breadth of the braincase (BBC); breadth across both incisive foramina (BIF); breadth of the bony palate across the first upper molars (BM1s); breadth across the occipital condyles (BOC); breadth of the rostrum (BR); breadth of the zygomatic plate (BZP); depth of the auditory bullae (DAB); interorbital breadth (IOB); length of bony palate (LBP); length of diastema (LD); length of incisive foramen (LIF); coronal length of maxillary toothrow (LM1-3); length of rostrum (LR); occipitonasal length (ONL); posterior breadth of the bony palate (PPB); postpalatal length (PPL); width of the first upper molar (WM1); and zygomatic breadth (ZB). Morphological description of the muroid skull generally follows the terms defined and/or illustrated in Hershkovitz (1962), Carleton (1980), and Voss (1988).

The new species to be described requires closest comparison with *E. antsingy* and species of the *E. majori* complex (*E. majori*, *E. penicillatus*). The degree of its morphometric differentiation was broadly assessed against samples of these three species as grouped into the operational taxonomic units (OTUs) identified below. Catalog numbers, full locality data, and museum sources of all specimens analyzed are provided in appendix 1. We use the following abbreviations for the different types of Malagasy protected areas: PN, Parc National; RNI, Réserve Naturelle Intégrale; RS, Réserve Spéciale.

Eliurus antsingy: (1) PN de Bemaraha, *N* = 3; (2) PN (formerly RNI) de Namoroka, *N* = 10; (3) RS d'Ankarana, *N* = 9; (4) Daraina, *N* = 4.
Eliurus majori: (5) PN de la Montagne d'Ambre, *N* = 27; (6) RS de Manongarivo, *N* = 5; (7) RS d'Anjanaharibe-Sud, *N* = 16; (8) PN de Marojejy, *N* = 17; (9) RS du Pic d'Ivohibe, *N* = 4; (10) PN (formerly RNI) d'Andringitra, *N* = 17; (11) PN (formerly RNI) d'Andohahela, *N* = 4.
Eliurus, new species: (12) PN de l'Isalo, *N* = 4.
Eliurus penicillatus: (13) Ampitambe, N = 17.

Univariate descriptive statistics (mean, range, and standard deviation) and multivariate analyses were derived for specimens of adult age classes (young, full, and old) defined on grades of dental wear. Juveniles and subadults, identified by their complete or partial gray coats and newly erupted or little worn third molars, were excluded. Sample statistics for external dimensions are reported in tabular comparisons as a general index of size differences among species, but these variables were not employed in multivariate analyses. Computation of canonical variates and principal components was based on the 18 craniodental measurements, all of which had been first transformed to natural logarithms. Loadings are expressed as Pearson correlation coefficients of the extracted factors with logs of the original skull variables. All analytical results were obtained using Systat for Windows (2002, version 10.2).

***Eliurus danieli*, new species**
figures 1–3; table 1

HOLOTYPE: Field Museum of Natural History number 175934, an adult male prepared as skin, skull, and partial skeleton, collected 10 December 2002 by Steven M. Goodman (original number SMG 13,425).

The round skin and skull are in fine condition. External data recorded on the skin tag include: TOTL, 335 mm; HBL, 150 mm; TL, 179 mm; HFL, 30 mm; EL, 26 mm; and WT, 91 gm. The animal was noted as having scrotal testes (12 × 5 mm) with convoluted epididymides; tissues were preserved in EDTA (ethylene diamine tetraacetic acid).

TYPE LOCALITY: Madagascar, Fianarantsoa Province, Parc National de l'Isalo, 28 km SE Berenty-Betsileo, along Sahanafa River near foot of Bevato Mountain, 650 m; geographic coordinates: 22°19.0′S, 45°17.6′E.

DIAGNOSIS: A species of *Eliurus* characterized in combination by a gray dorsal pelage, contrasting grayish-white venter, and a distinctive bright-white tail tuft (fig. 1). Cranial size moderately large (ONL ca. 37–41 mm; figs. 2, 3), molar rows absolutely and relatively long (LM1–3 ca. 6.0–6.5 mm), incisive foramina relatively long and wide (LIF/LD ca. 56%), and ectotympanic bullae large for the genus. Alveolus of lower incisor short, not forming a capsular process.

REFERRED SPECIMENS: Three additional specimens are known, all from the PN de l'Isalo: FMNH 175933, a young adult male also collected by Goodman (SMG 13,387) in the same month (5 Dec) from 24 km W Ranohira bas, Andranohavo (Canyon des Rats), 700 m, 22°28.9′S, 45°22.9′E; UADBA 10483, a young adult female obtained 2 April 1995, A. F. A. Hawkins (FH 3), from a site within 300 m of where the holotype was obtained (Georges Rabeony, personal commun.); and UADBA 46805 obtained between

Fig. 1. Photograph of live *Eliurus danieli* (FMNH 175933), a young adult male from Andranohavo (Canyon des Rats) in the PN de l'Isalo. The new species is characterized by a bright white caudal tuft that is accentuated by the concentration of intensely black hairs along the middle portion of the tail. Photograph taken by Harald Schütz.

2 and 9 February 1995 (Hawkins, 1995), by A. F. A. Hawkins (FH 23) in the Canyon des Rats.

DISTRIBUTION: To date known only from the PN de l'Isalo, south-central Madagascar.

DESCRIPTION: Fur texture soft and fine. Cover hairs 9–10 mm in length over middle rump. Basal four-fifths of dorsal cover hairs bright plumbeous gray, distal one-fifth medium buff, some hairs tipped with a third band of faint dusky brown. Guard hairs dark brown to blackish, only slightly longer than the cover hairs except over the rump. General effect of upperparts a pale brownish gray; forehead, face, and lower legs a purer medium gray. Boundary of dorsal and ventral pelage clearly demarcated along sides. Ventrum variable in coverage of white hairs: entirely bright buff white (UADBA 10483); or dull buff white over the chin, throat, and chest with some basal gray thinly showing over the lower abdomen and inguinum (FMNH 175934); or wholly white hairs confined to the chin and throat, cover hairs over the chest and abdomen bicolored (basal half gray, distal half white), and the underparts overall light grayish white (FMNH 175933). Medial dusky brown band extends over the tarsus and proximal metatarsus; remainder of metatarsus and toes, as well as tops of forefeet, covered with bright white hairs; ungual tufts at base of claws well developed.

Caudal tuft prominent over distal half of tail length, tuft hairs becoming gradually longer toward the tip and measuring about 12–15 mm long over the terminal portion (fig. 1). Terminal one-third of tail length covered with pure white hairs, forming a brilliant white tuft accentuated by the intensely black hairs of the proximal tuft (distal white segment = 35 mm in UADBA 10483, 45 mm in FMNH 175934, and 75 mm in FMNH

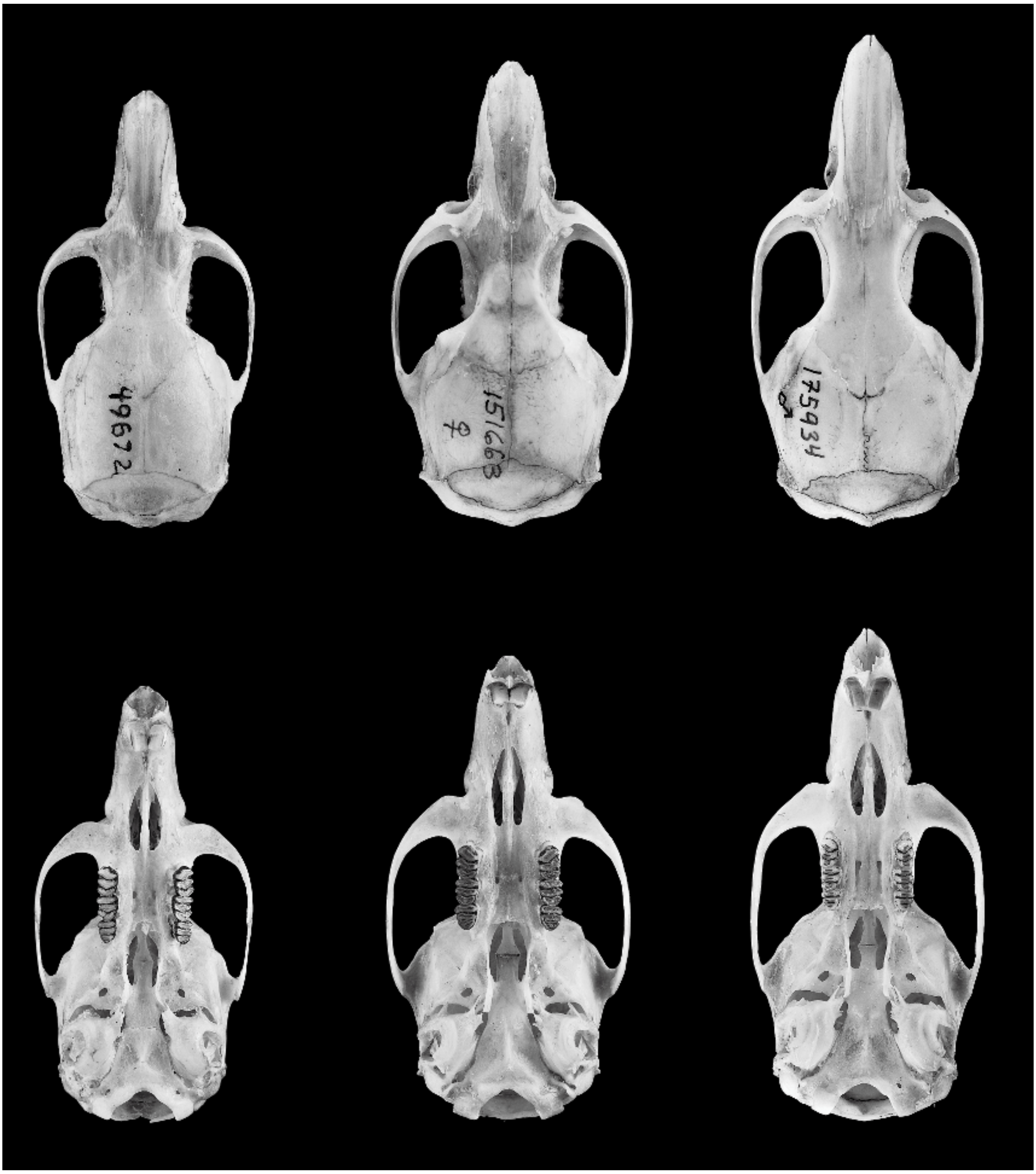

Fig. 2. Dorsal (upper row) and ventral (lower row) views (ca. 1.75×) of adult crania of species composing the *Eliurus majori* species group as recognized herein (see Discussion): **left pair**, *E. penicillatus* Thomas (USNM 49672; Fianarantsoa Province, Ampitambe, ca. 900 m; ONL = 35.6 mm); **middle pair**, *E. majori* Thomas (FMNH 151663; Fianarantsoa Province, PN d'Andringitra, 40 km S Ambalavao, along Volotsangana River, 1210 m; ONL = 38.1 mm); and **right pair**, *E. danieli* new species (FMNH 175934, type specimen; Fianarantsoa Province, Parc National de l'Isalo, 28 km SE Berenty-Betsileo, along Sahanafa River near foot of Bevato Mountain, 650 m; ONL = 40.6 mm).

Fig. 3. Lateral view (ca. 1.75×) of adult crania of species composing the *Eliurus majori* species group as recognized herein (same specimens as depicted in fig. 2): **top**, *E. danieli* new species; **middle**, *E. majori*; and **bottom**, *E. penicillatus*.

175933). Proximal half of tail clothed with short black hairs that do not mask the caudal scales; scalation moderately textured; epidermis pale gray to whitish toward the base of the tail, lighter underneath, but paleness visually obscured by the black hairs.

Hind feet short and broad. Six plantar pads arranged as characteristic of the genus; pads not so bulbous and crowded as in *E. antsingy*. Pinnae medium-sized, more rounded, not so elongate as *E. tanala* Major (1896); color pale dusky brown externally, somewhat lighter internally, and sparsely clothed with fine brown hairs inside and outside.

Cranium moderately large (ONL = 37–41 mm; figs. 2, 3), agreeing with largest geographic examples of *E. majori* (e.g., from PN de Marojejy), smaller than *E. antsingy* and large-bodied *E. tanala* (e.g., from RS d'Anjanaharibe-Sud). Dorsal profile of skull arched (fig. 3), sloping gradually toward the rostrum and more steeply toward the occiput, not so flat as in *E. tanala* of similar size. Rostrum proportionally long (LR/ONL = 36.2%) for the genus, comparable to relative length in the *E. tanala* complex but longer than *E. myoxinus* or *E. majori*. Braincase rounded and smoothly contoured; subsquamosal fenestra patent and medium-sized, exposing the interior braincase and dorsal periotic; hamular process of the squamosal stout but well delineated. Zygomatic arches almost parallel-sided in the three specimens; zygomatic plate medium in width for the genus, forming a shallow but distinct dorsal notch, more incised than in *E. penicillatus* and *E. majori*. Incisive foramina bluntly pointed on their posterior ends, more acute at the anterior; wide and relatively long (LIF/LD = 56%) for the genus, in proportion resembling *E. antsingy* and the *E. majori* complex (fig. 2). Posterior palatine foramina oval, situated within the maxillary-palatine suture at the level of the M1-M2; supernumerary palatal foramina occurring in the palatine bones, but minute in size and irregularly formed; slitlike palatal vacuities absent. Posterior margin of the bony palate terminates just short of the ends of the third molars; anterior expanse of mesopterygoid fossa broad and horseshoe-shaped, its sides gently incurved. Alisphenoid strut present on both sides in all three individuals examined. Auditory bullae relatively large for the genus, the ectotympanic covering nearly all of the periotic in ventral view, even more so than in *E. antsingy* and *E. myoxinus*. Mandible stocky in form, ascending ramus deep.

Enamel face of upper and lower incisors dull yellowish-orange in color. Alveolus of lower incisor relatively short, terminating posteriorly at the level of the coronoid process and well below the sigmoid notch; tip of incisor root indicated by slight mound on mandibular ramus but not forming a projecting capsular process. Toothrows long (LM1-3 = 6.0–6.5 mm) relative to cranial size, in proportion like those of *E. majori* and *E. penicillatus*; molars robust with laminate occlusal configuration as per the genus, higher crowned than most *Eliurus* but again approximating *E. majori* and *E. penicillatus* in this detail; upper and lower third molars about equal in length to second molars or only slightly shorter.

Other external, cranial, and dental features as described for the genus (Carleton, 1994; Carleton and Goodman, 1998).

MORPHOLOGICAL AND MORPHOMETRIC COMPARISONS: The cardinal traits of *E. danieli* implicate the eastern species *E. majori* and *E. penicillatus* or western *E. antsingy* as its closest relatives. All four are relatively large species of *Eliurus* and possess long incisive foramina that span over half the diastema (fig. 2) and short lower incisors that lack a prominent capsular process. In combination, these qualitative features serve to distinguish the four from all other species of *Eliurus* (see Carleton, 1994, Carleton and Goodman, 1998, and Carleton et al., 2001, for discussion of interspecific variation in these characters).

Other character differences associate *E. danieli* more closely to *E. majori* and *E. penicillatus* instead of *E. antsingy*. Foremost, specimens of *E. danieli* have long, robust molar rows in proportion to cranial size (LM1-3 ca. 16–17% of ONL), a configuration that agrees with *E. majori* and *E. penicillatus* (Carleton, 1994). In contrast, examples of *E. antsingy* have shorter toothrows in relation to cranial size (LM1-3 ca. 13–14% of ONL), resembling in this regard all other species of *Eliurus* (Carleton et al., 2001). A simple bivariate plot underscores the segregation of the two groups by dental proportion (fig. 4); only one stray individual (an *E. danieli*) overlaps the otherwise clearly delineated data-point constellations. The morphogenetic determination of these dental shape contrasts is such that molar variables (LM1-3, WM1) always contribute most heavily to group separation on the first factor extracted in all ordinations of our cranial measurements, whether principal component (not illustrated) or canonical variate (fig. 5, table 2). *Eliurus danieli*, together with *E. majori* and *E. penicillatus*, also differ from *E. antsingy* in fur texture (not so fine and soft), plantar pads (not as large, bulbous, and close-set), size of upper and lower third molars (not smaller than second molars), and molar hypsodonty (not as low-crowned). These impressionistic differences are not so easily quantifiable as is the disparity in toothrow proportions.

Eliurus danieli can be distinguished from *E. majori* and *E. penicillatus* by means of the following traits. Although similar in size to *E. majori*, specimens of *E. danieli* possess a conspicuous white caudal tuft. This trait is unknown in nearly all geographic samples of *E. majori*, in which the tuft is wholly dark brown or black to the tip (Carleton, 1994; Goodman and Carleton, 1996). In the PN de Marojejy, however, Carleton and Goodman (2000) reported that nine of the 20 *E. majori* specimens collected possess a white caudal tip of variable extent. The white tail tip in those particular *E. majori*, however, is not accentuated by a contiguous band of dense black hairs as found in *E. danieli*. Furthermore, in other features and in morphometric analyses, the Marojejy sample unambiguously accords with typical *E. majori* (Carleton and Goodman, 2000; also see next), not *E. danieli*. Although possessing a white caudal tuft as diagnostic of *E. penicillatus*, specimens of *E. danieli* are conspicuously larger in nearly all variables

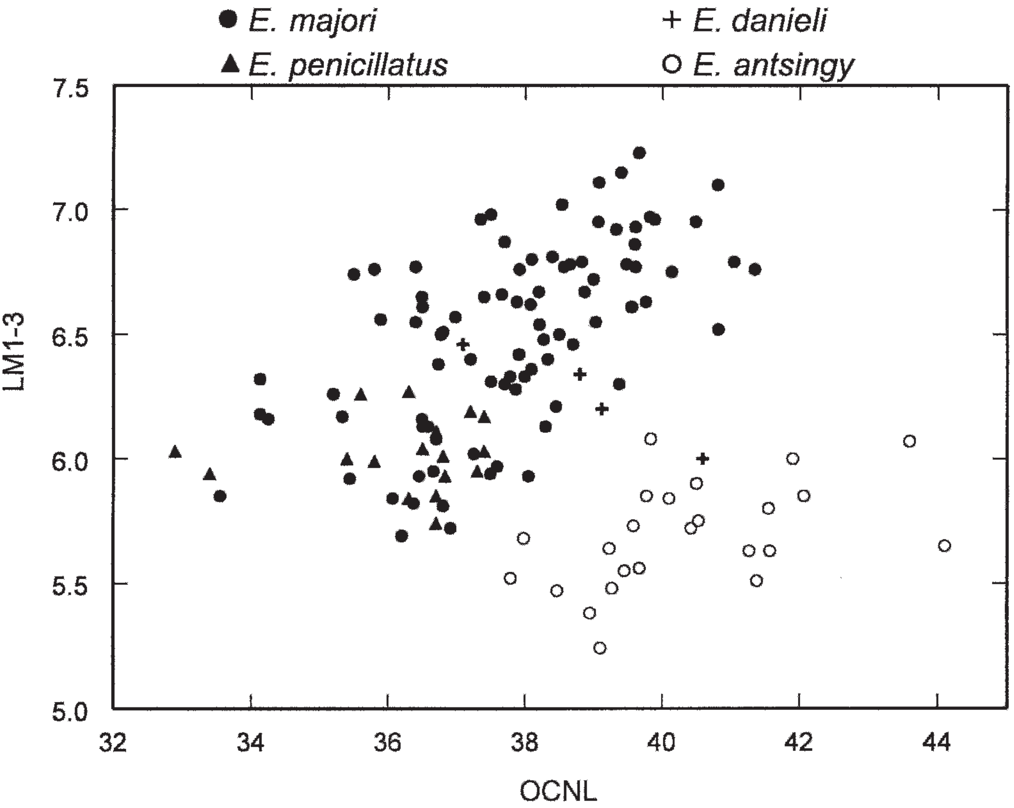

Fig. 4. Scatter plot of length of the upper molar row (LM1-3) versus greatest length of skull (ONL) for intact specimens of *E. antsingy*, *E. danieli*, *E. majori*, and *E. penicillatus*. Note that examples of the latter three species possess longer toothrows in relation to cranial size compared with those of *E. antsingy*.

measured (figs. 2, 3; table 1); in view of that great size disparity, the two species are strongly circumscribed in morphometric space (fig. 5). Finally, in contrast to *E. majori* and *E. penicillatus*, *E. danieli* has gray dorsal pelage, bright in tone (in both eastern species, dorsum blackish gray to blackish brown and somber colored); its venter is bright buff white or grayish white and clearly delineated from the dorsum (in both eastern species, venter paler but similarly colored to the dorsum and dorsal-ventral pelage contrast less well marked); its ectotympanic bulla is absolutely larger (table 1), obscuring nearly all of the periotic in ventral view (in both eastern species, ectotympanic less inflated, exposing posteromedial wedge of the periotic); and its zygomatic plate projects forward to form a distinct dorsal notch (in both eastern species, zygomatic plate narrower and dorsal notch weakly incised).

In projections of the first three canonical variates (cumulative variation explained = 85.5%) extracted from 13-group discriminant function analysis, the three specimens from PN de l'Isalo are wholly isolated in morphometric space from all other OTUs and species (fig. 5). As commented above, the two molar variables (LM1-3, WM1) most strongly influence separation of groups along the first canonical variate (table 2). Other dimensions that load moderately along this factor include those that reflect palatal breadth (BM1s, PPW) and interorbital width (IOB); compared with *E. antsingy*, the palate is relatively broader and interorbit narrower in *E. danieli*, *E. majori*, and *E. penicillatus* (table 1). Size as a general factor is expressed along the second canonical variate, as indicated by the positive and moderately strong correlations (Pearson's R = 0.6–0.8, $P \leq .001$) of most variables with this factor (table 2). In general size, specimens

TABLE 1

Selected External and Craniodental Measurements for the Type Series of *E. danieli* and Samples of *E. majori*, *E. penicillatus*, and *E. antsingy*

(Sample statistics include the mean, ± 1 SD, and the observed range)

Variable	*E. danieli* Isalo (*N* = 4)	*E. majori* Andringitra (*N* = 17)	*E. penicillatus* Ampitambe (*N* = 17)	*E. antsingy* Ankarana (*N* = 9)
HBL	150, 152	158.3 ± 7.2 145–171	—	141 ± 9.1 133–153
TL	179, 195	189 ± 11.1 170–207	—	166 ± 12.2 145–183
HFL	30, 32	28.8 ± 1.3 27–31	—	28.3 ± 1.4 25–30
EL	26, 28	19.6 ± 0.7 18–21	—	23.7 ± 1.1 22–25
WT	91, 100	101.0 ± 12.9 77–122	—	86.4 ± 9.9 72–99
ONL	38.9 ± 1.4 37.1–40.6	37.6 ± 1.0 35.5–39.4	36.2 ± 0.9 32.9–37.4	39.3 ± 1.0 37.8–40.5
ZB	18.5 ± 0.9 17.4–19.2	19.1 ± 0.5 18.1–19.8	18.0 ± 0.9 15.9–19.4	19.0 ± 0.7 18.2–20.1
BBC	14.9 ± 0.2 14.6–15.1	14.3 ± 0.4 13.4–14.8	13.6 ± 0.4 12.7–14.3	14.7 ± 0.5 13.9–15.4
IOB	5.4 ± 0.2 5.3–5.7	5.3 ± .02 4.9–5.7	5.1 ± 0.2 5.1–5.8	5.7 ± 0.2 5.3–6.0
LR	14.1 ± 0.8 13.0–14.9	13.1 ± 0.5 11.6–14.0	12.4 ± 0.6 10.8–13.2	13.3 ± 0.4 12.7–13.9
BR	7.1 ± 0.3 6.6–7.5	7.1 ± 0.2 6.8–7.6	6.9 ± 0.4 6.1–7.4	6.9 ± 0.4 6.2–7.4
PPL	13.7 ± 0.9 12.7–14.2	13.4 ± 0.5 12.4–14.6	12.9 ± 0.7 11.5–14.2	14.2 ± 0.5 13.4–15.0
LBP	7.5 ± 0.2 7.3–7.7	7.5 ± 0.4 6.9–8.6	6.8 ± 0.3 6.3–7.4	7.6 ± 0.3 7.1–8.0
LIF	5.8 ± 0.4 5.4–6.1	6.3 ± 0.3 5.6–6.7	5.5 ± 0.3 5.0–5.9	5.7 ± 0.3 5.3–6.2
BIF	2.7 ± 0.3 2.4–2.9	2.7 ± 0.2 2.4–3.1	2.7 ± 0.2 2.4–2.9	2.6 ± 0.2 2.4–2.9
LD	10.2 ± 0.6 9.6–10.9	10.8 ± 0.4 10.0–11.8	9.9 ± 0.6 8.5–10.7	11.0 ± 0.5 10.2–11.7
BM1s	7.6 ± 0.1 7.5–7.7	8.1 ± 0.3 7.1–8.6	7.3 ± 0.3 6.8–7.9	7.4 ± 0.4 6.9–8.0
DAB	5.7 ± 0.1 5.6–5.9	5.2 ± 0.1 5.1–5.5	5.4 ± 0.2 5.0–5.6	5.3 ± 0.2 5.1–5.6
BZP	3.6 ± 0.5 2.9–3.8	3.5 ± 0.2 2.9–3.9	2.9 ± 0.3 2.5–3.4	3.5 ± 0.3 3.1–4.1
BOC	8.3 ± 0.3 7.9–8.6	8.5 ± 0.3 8.0–9.0	8.0 ± 0.3 7.4–8.4	8.8 ± 0.3 8.2–9.2
LM1–3	6.25 ± 0.20 6.00–6.46	6.65 ± 0.24 6.13–7.15	6.02 ± 0.15 5.74–6.27	5.61 ± 0.20 5.24–5.90
WM1	1.66 ± 0.12 1.48–1.74	1.76 ± 0.07 1.66–1.88	1.58 ± 0.05 1.49–1.68	1.53 ± 0.09 1.41–1.65

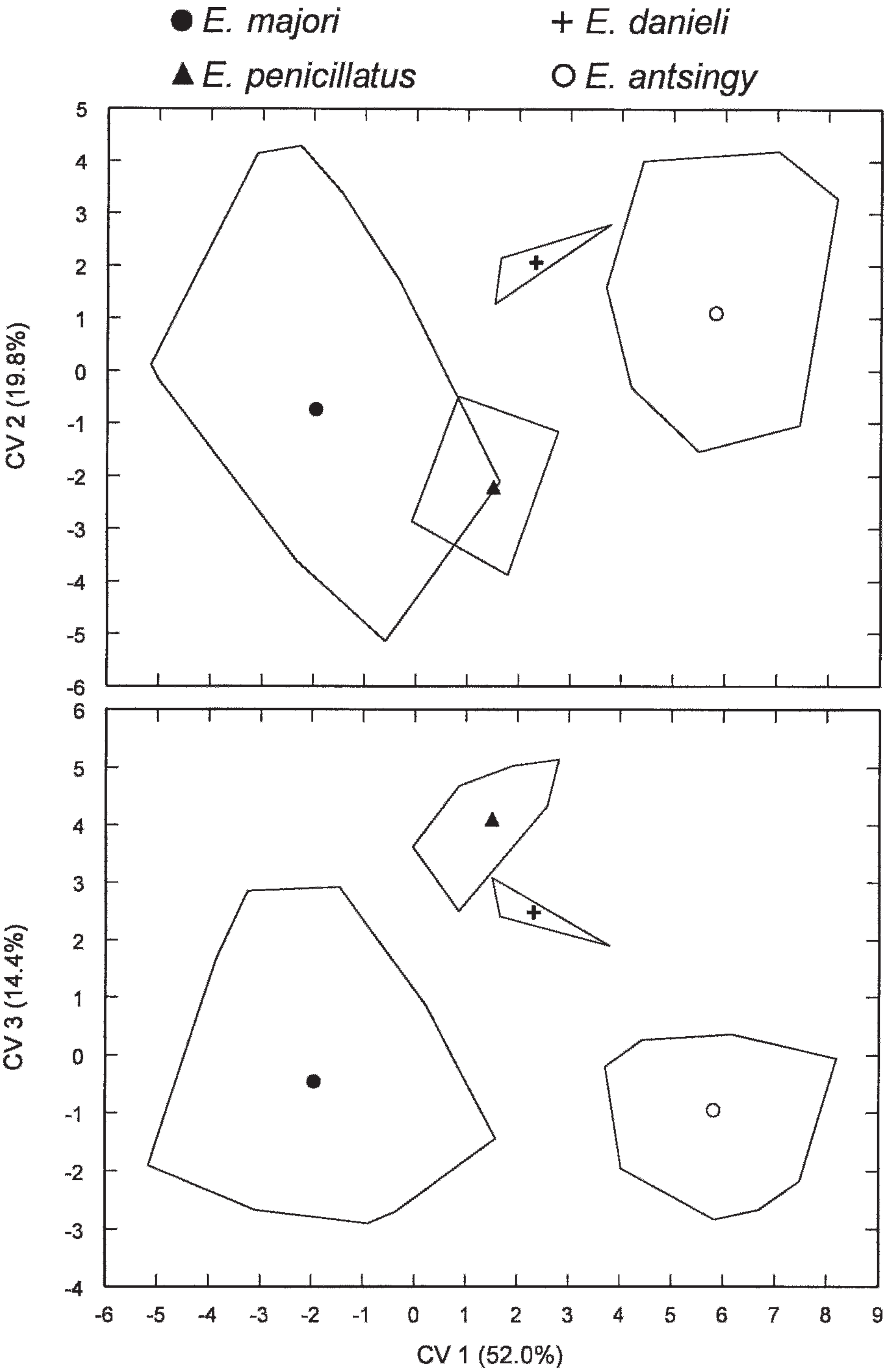

Fig. 5. Results of discriminant function analysis performed on 18 log-transformed craniodental variables, as measured on 130 specimens representing 13 OTUs of *Eliurus* (see Materials and Methods). **Top**, projection of individual scores onto the first and second canonical variates extracted. **Bottom**, projection of

TABLE 2

Results of 13-group Discriminant Function Analysis

(OTUs represented include four of *E. antsingy, N* = 24; one of *E. danieli, N* = 3; seven of *E. majori, N* = 90; and one of *E. penicillatus, N* = 13. See Materials and Methods and fig. 4)

Variable	Correlations CV 1	CV 2	CV 3
ONL	0.37	0.75	−0.20
ZB	−0.05	0.72	−0.23
BBC	0.27	0.73	−0.30
IOB	0.58	0.43	−0.01
LR	0.18	0.69	−0.13
BR	−0.23	0.48	0.01
PPL	0.41	0.66	−0.14
LBP	−0.12	0.53	−0.39
LIF	−0.08	0.71	−0.09
BIF	0.24	0.46	0.43
LD	0.15	0.55	−0.39
BM1s	−0.48	0.59	0.01
PPB	−0.49	0.60	−0.17
DAB	0.36	0.68	0.38
BZP	0.07	0.66	−0.42
BOC	0.46	0.45	−0.41
LM1–3	−0.82	0.46	0.15
WM1	−0.71	0.44	0.08
Canonical correlations	0.96	0.90	0.87
Eigenvalue	10.9	4.4	3.0
% Variance	51.1	20.3	14.1

of *E. danieli* match the larger samples of *E. majori* and *E. antsingy* and conspicuously exceed the diminutive *E. penicillatus* in most dimensions quantified (table 1). Between-group variation summarized by the third canonical variate conveys the morphometric association of *E. danieli* and *E. penicillatus* (fig. 5). The few cranial variables (BIF, LD, LBP, DAB, BZP) that account for this association constitute proportional subtleties that are not readily apparent in side-by-side skull comparisons of the two species due to their gross size disparity; notable among these are the relatively spacious incisive foramina (BIF) and short diastema (LD). Although visually unimpressive, such proportional features nevertheless influence the phenetic pairing of the *E. danieli* and *E. penicillatus* samples among all OTUs represented, as indexed by Mahalanobis distances between group centroids (fig. 6). The multivariate level of divergence between the two (Mahalanobis D^2 = 52.3) surpasses that derived for the most strongly differentiated samples within either *E. majori* or *E. antsingy*.

ECOLOGICAL NOTES: The PN de l'Isalo is located on the Isalo Massif, a vast area of badlands composed of ruiniform Jurassic sandstone. Much of the park includes rocky habitat with sparse short scrub or completely lacking any plants. Many deep canyons found within this formation contain permanent rivers that are in part responsible for the steeply cut valley sides, and the precipitous facies have a unique rupicolous plant community. Gallery forest can be found along river margins at the base of these canyons and at their mouths. An evergreen sclerophyllous forest formation dominated by the genus *Uapaca* (Euphorbiaceae) covers more gently sloping hillsides. Although the region receives around 850 mm of rain per year and has a pronounced dry season (Nicoll and Langrand, 1989), the water-fed canyons retain moist conditions and support vegetation whose floral affinity is transitional between humid and deciduous formations (Gautier and Goodman, 2003). Within these moist canyons occur numerous animals that represent taxa or species groups otherwise known from the eastern humid forests.

Microhabitats where specimens of *E. danieli* were captured are noted on skin tags or in original specimen catalogs as follows: "On rocky cliff about one-half way up Bevato Mt. in zone with little woody vegetation. Trapped on ground in small hole leading into rock fall" (FMNH 175934, holotype); "on the rocky mountain of Sahanafa" [translated from the

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←

individual scores onto the first and third canonical variates extracted. The maximally inclusive polygons enclose specimen scores around an OTU's centroid; in view of extensive overlap and visual confusion, the sample polygons for *E. antsingy* (4 OTUs) and *E. majori* (7 OTUs) were collapsed to enclose maximal dispersion around the species' grand centroid. See table 2 for variable correlations and percent variance explained.

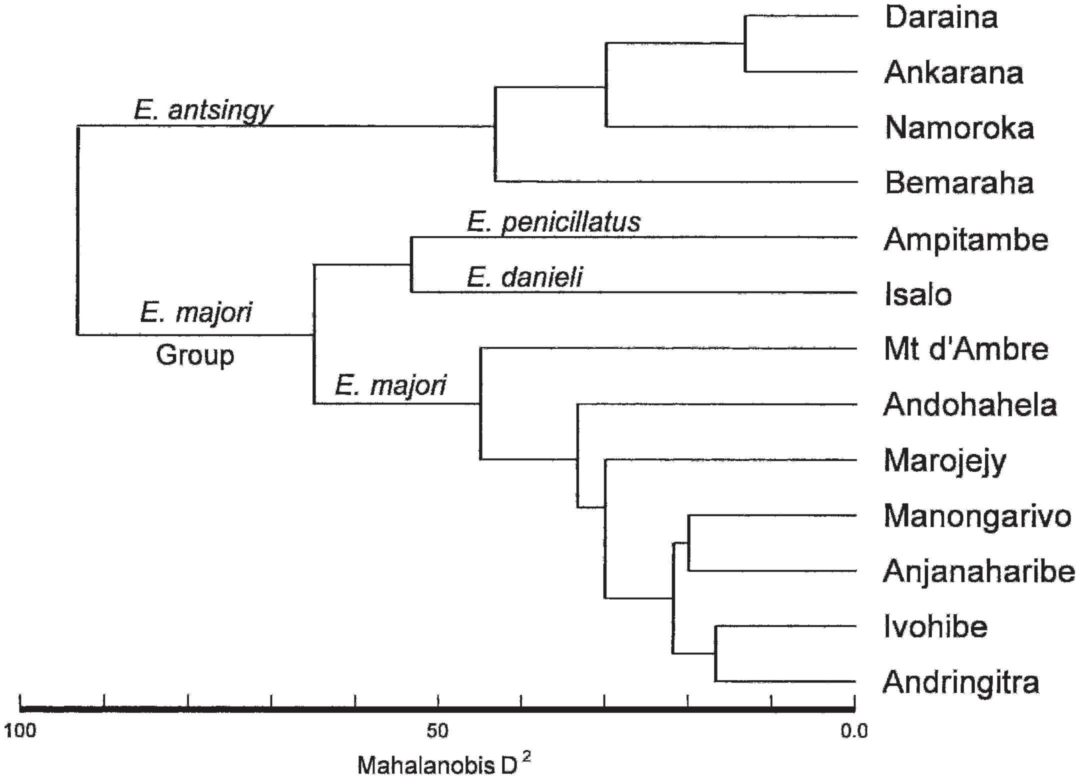


Fig. 6. Phenogram produced from clustering (UPGMA) of Mahalanobis' distances derived from discriminant function analysis of 13 OTUs representing four species of *Eliurus* (see fig. 5).

French] (UADBA 10483); "In canyon with vegetation at base of rock face and along river banks—sandy soil. Trap on ground under opening of large boulder at river edge and surrounded by ferns and dense rupicolous vegetation" (FMNH 175933); and "in the interior of the Canyon des Rats, a site of exposed rock and at a level more than 30 m above the water [= river] level" [translated from the French] (UADBA 46805). This information suggests that the species is at least in part terrestrial and lives outside forest formations.

On the basis of considerable field experience with members of *Eliurus*, Goodman has never captured an individual in an ecological setting similar to that of the *E. danieli* holotype. The site at the foot of Mt. Bevato is a broad expanse of exposed pseudosteppe, on a steep rocky slope, and approximately 500 m from the nearest forest. According to M. George Rabeony, an employee of the park service who has accompanied numerous researchers in the PN de l'Isalo, this is also the locale where UADBA 10483 was trapped in April 1995. In late December 2002, Goodman returned to this site and placed thirty traps (10 Nationals and 20 Shermans) on the ground under large rock outcrops between the forest edge and the middle portion of Mt. Bevato. The individual (FMNH 175934) was captured in one of the highest-elevation traps set along the Bevato cliff face. Other mammals captured in this trap line include the introduced *Rattus rattus* and the large tenrecid *Tenrec ecaudatus*. A few individuals of *E. myoxinus* were trapped within the Sahanafa Forest, about 1.5 km from where the holotype of *E. danieli* was obtained. In the Andranohavo Forest (Canyon des Rats), *E. myoxinus* and *R. rattus* were common and captured within a short distance of *E. danieli*.

TAXONOMIC AND BIOGEOGRAPHIC REMARKS: The phenetic union of *E. danieli* and *E. penicillatus* and their joint possession of a white tail tuft, largely to the exclusion of *E. majori*, offer a provisional hypothesis of sister-group relationship. Nonetheless, we are not persuaded that this cognate relationship will be necessarily sustained by other data sources, such as gene-sequence studies. First, with only four specimens at hand, the sample size of *E. danieli* is too small to adequately represent variational bounds in the species population. Second, as enumerated above, *E. majori* and *E. penicillatus* do share a number of morphological similarities not found in *E. danieli*. In view of their distribution in eastern humid forest, the possibility that *E. majori* and *E. penicillatus* form a clade vicariantly related to *E. danieli* in west-central Madagascar remains as viable an interpretation (and see below).

Compared with other *Eliurus* that have a white caudal tuft (*E. grandidieri*, *E. penicillatus*, *E. tanala*), that possessed by *E. danieli* is the most visually striking. As we currently understand interspecific affinities (see Discussion) and assuming that an all-dark tuft represents the primitive state, a terminal white tuft has evolved at least three times within the genus. The significance of these contradistinctive caudal flags to social behavior of the species or in interspecific encounters deserves investigation.

Although the Isalo Massif today receives only moderate amounts of rainfall per year and experiences a pronounced dry season, organisms identified from regional paleontological sites supply ample biotic evidence that local climatic conditions were distinctly more mesic during the Late Pleistocene and Holocene (Burney, 1997; Goodman and Rakotozafy, 1997; Godfrey et al., 1999). Relicts from this more mesic phase of late Quaternary climate persist in the modern flora of the Isalo area, most notably in the deep canyons where many plants show phytogeographic affinities to the eastern humid forests. The same relictual biogeographic pattern has also emerged from the study of certain birds, reptiles, and amphibians that inhabit the Isalo Massif (e.g., Raxworthy and Nussbaum, 1996, 1997; Fjeldsa et al., 2000). Two kinds of taxonomic evidence have been identified among those vertebrate groups: (1) the same species is found in common between Isalo and sites in the eastern humid forests; or (2) closely related taxa occur in these two areas and are presumed to have originated through east-west vicariance. The presence of *E. danieli* in the Isalo region and its proposed sister-group relationship to *E. majori* and/or *E. penicillatus* exemplify the second line of evidence for a former east-west continuity of humid forest.

ETYMOLOGY: We name this new species to honor Professor Daniel Rakotondravony, Département de Biologie Animale, Université d'Antananarivo, especially for his contributions to our knowledge on Malagasy rodents and for helping to foster zoological research on Madagascar for numerous national and foreign scientists.

DISCUSSION

Carleton based his 1994 revision of *Eliurus* on approximately 200 specimens that were then available in the world's museum holdings. With the resurgence of intensive systematic fieldwork over the past decade (see Andriamialisoa and Langrand, 2003), that number has climbed to nearly 900 specimens, a vastly improved empirical base that boasts both larger locality series and denser geographic inventory. The new specimens have provided a fresh and more rigorous understanding of nongeographic and geographic variation within *Eliurus* species, as well as the discovery of new forms (Carleton and Goodman, 1998; Carleton et al., 2001; this paper). Coincidentally, or perhaps inevitably, the greater sample sizes and proliferation of intermediate localities have also disclosed problematic variants that raise questions about definitions of species limits, distributions, and interspecific relationships. We here review the 11 *Eliurus* species currently recognized, highlight populations and geographic areas of taxonomic uncertainty, and arrange those discussions around five emergent species assemblages. These species groups are principally based on morphological similarity—notably as judged by size, cranial and dental conformation, morphometric cohesion, and pelage traits. Soft anatomical systems, such as the character-rich reproductive tract, have yet to be comprehensively surveyed. Gene-sequence evidence (cytochrome *b*) supplies phylogenetic perspective that supports the monophyly of certain of these groups (Jansa et al., 1999), but not all species nor the problematic populations discussed below have yet to be evaluated using such molecular information.

Eliurus majori Group (*E. majori* Thomas, 1895; *E. penicillatus* Thomas, 1908; *E. danieli* Carleton and Goodman, 2006): As reviewed above, these three species constitute a strongly circumscribed morphologic subset within the genus. They are moderately large in size and the hind feet comparatively short. The tail is well furred, but the caudal hairs gradually lengthen toward the tip rather than abruptly elongate as an expansive terminal tuft. Two of the three species bear a white caudal tip (*E. danieli*, *E. penicillatus*), but certain northern populations of the third (*E. majori*) vary in the incidence of white tipping (PN de Marojejy–Carleton and Goodman, 2000). Their molar rows are exceptionally robust with the third molars subequal to the second, the incisive foramina are wide and long (> 50% of diastemal length), and the lower incisor is short and does not form a protruding capsular process (see Carleton, 1994: fig. 20). Carleton (1994) thought that *E. majori* and *E. penicillatus* retained several plesiomorphic traits and his cladistic interpretation represented the two as a basal clade within *Eliurus*; however, the molecular results of Jansa et al. (1999) indicate that, although *E. majori* (and *E. danieli*, reported as "sp. A") subtended the *E. tanala* and *E. myoxinus* groups, *E. grandidieri*-*Voalavo* composed the most basal cladistic position among eliurine Nesomyinae.

The species complex is principally confined to montane and sclerophyllous montane forest settings in the eastern humid forest (Carleton, 2003). Size within *E. majori* is fairly uniform over much of its geographic range, from the southern Anosyenne Mountains in the south to the Northern Highlands, but the northernmost population on the isolated peak Montagne d'Ambre is diminutive. With skulls arrayed side-by-side, the Montagne d'Ambre animals "look" like a separate species, but shape features and genetic data clearly affiliate this montane outlier with *E. majori* proper (Carleton and Goodman, 1998; Jansa et al., 1999). Extralimital populations have been also uncovered in remnant montane forests of the Central High Plateau (Jansa et al., 1999; Carleton et al., 2001). That from the PN de l'Isalo is herein diagnosed as a new species based on recently collected material. Still other western populations of uncertain status possess *majori*-like features, namely those from the RS d'Ambohijanahary and RS d'Ambohitantely (appendix 1); these specimens have an all-dark tail tuft and approximate the Montagne d'Ambre sample of *E. majori* in their smaller size.

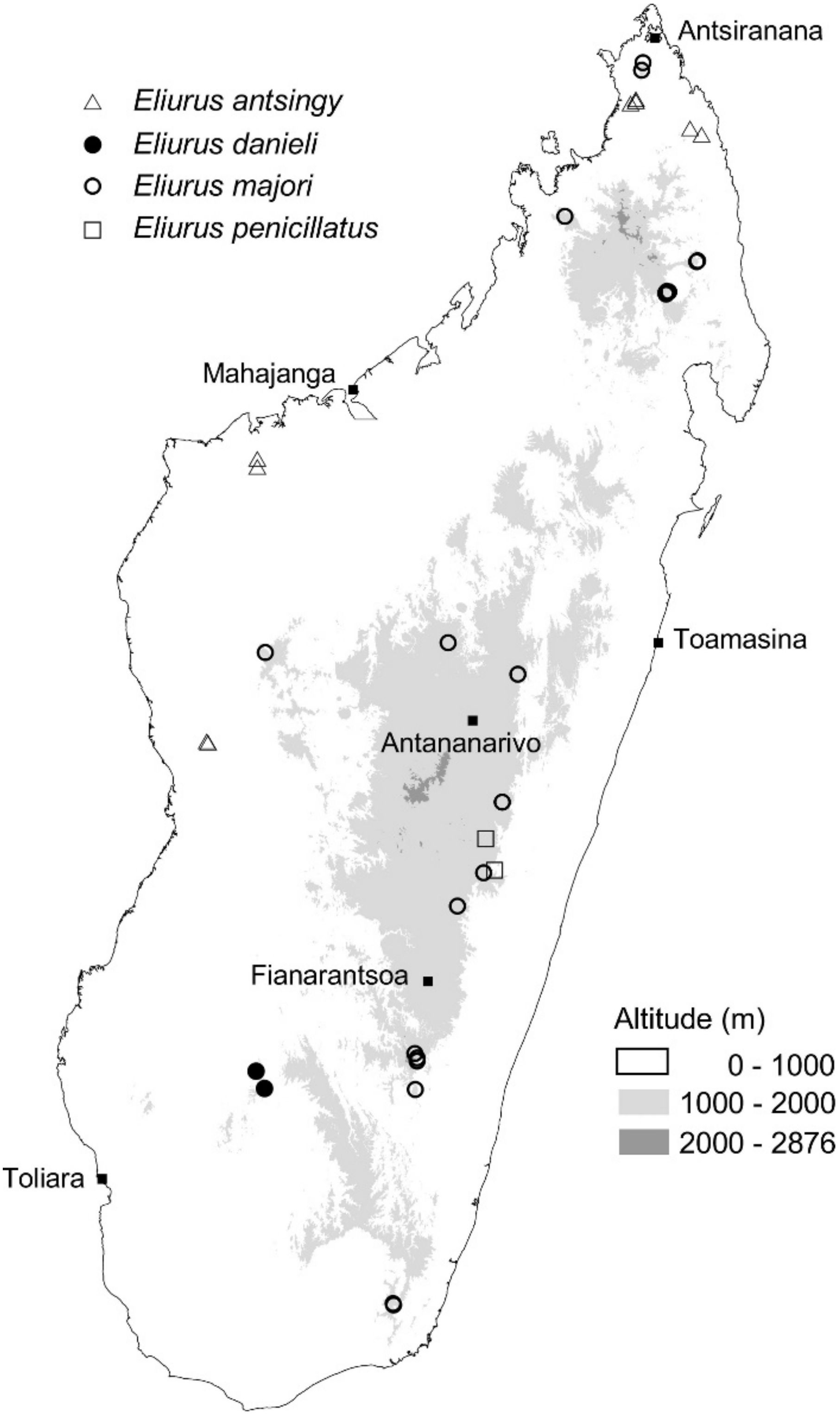
Carleton (1994) doubtfully retained *E. penicillatus* as distinct from *E. majori*, but the accumulation of larger samples of the latter species, now available over a broad north-south geographic swath, continues to underscore the clear-cut morphometric separation of the two (Carleton and Goodman, 2000; this study). Jansa et al.'s (1999) cytochrome-*b* genetic evidence divulged close relationship of the Isalo species, *E. danieli* (called "sp. A"), and *E. majori*, whereas our morphometric evaluation identified *E. penicillatus* as an alternative possibility of cognate affinity. Jansa et al. (1999) lacked tissues for *E. penicillatus*, which until recently has been known only from the type locality, Ampitambe, and all specimens collected by Forsyth Major in 1895–1896 (see Jenkins and Carleton, 2005). A lone specimen (UADBA 16209) collected in 2000 from Ankerana, about 35 km NE of Fandriana, represents only the second locality that we consider definitely referable to *E. penicillatus*, but it supplies evidence that the species still survives. Ampitambe is about 45 km SE Fandriana (see Carleton and Schmidt, 1990, for discussion). Perhaps the distribution of *E. penicillatus*, like *E. petteri*, is notably localized along the eastern flank of the Central High Plateau. Renewed search for the species and preservation of fresh material to investigate its status and relationship with regard to *E. majori* and *E. danieli* are warranted.

Eliurus antsingy Group (*E. antsingy* Carleton, Goodman, and Rakotondravony, 2001): *Eliurus antsingy* is the most recent of the morphological themes within *Eliurus* to be formally recognized. A large species with a dark tail tuft and extremely bulbous plantar pads, *E. antsingy* possesses some characteristics that intimate relationship with the *E. majori* group: namely, small and rounded pinnae; a short lower incisor that terminates in an indistinct incisive capsule; and long and wide incisive foramina. However, unlike species of the *E. majori* group, its molars are decidedly less robust in relation to cranial size (fig. 4), and the upper and lower third molars are smaller than the second; according to these features, *E. antsingy* resembles other species of *Eliurus*. Until evaluated with other data sources, we isolate *E. antsingy* in its own group.

The distribution of *E. antsingy* is highly disjunct, so far known from three widely separate regions (fig. 7). As conveyed by the specific epithet, the first examples identified, from the PN de Bemaraha and PN de Namoroka, appeared to be restricted to limestone *tsingy* physiography and associated forest habitat. Recent collecting has extended the range northward, including other sites in *tsingy* in the RS d'Ankarana but also near massive metamorphic rock outcrops at the edge of transitional dry-humid forest in the Forêt d'Ambilondambo, near Daraina (see appendix 1 for detailed localities). Collecting sites with known elevation are all relatively low, 50–550 m. The animals from the PN de Namoroka, as noted by Carleton et al. (2001), are slightly smaller and possess all-white venters compared with those from the PN de Bemaraha. In ventral pelage color, those from Ankarana and Daraina recall the series from PN de Namoroka but are again smaller by an increment comparable to that between the Bemaraha and Namoroka series. The overall amount of craniodental differentiation among the three regions approximates that derived among samples of the broadly distributed *E. majori* (fig. 6), as the latter is currently understood, and they marginally overlap in morphometric space (not illustrated). We continue to recognize these regional samples as the one species *E. antsingy*, but stress the need for collections from intermediate localities, wherever potential habitat exists, and for the application of genetic data to assess levels of divergence and phylogeographic structure.

ELIURUS MYOXINUS GROUP (*E. MYOXINUS* MILNE EDWARDS, 1885; *E. MINOR* MAJOR, 1896): Affiliation of these two species in a single species group at first seems incongruous given that each was conventionally accepted as one of the only two valid species of *Eliurus* (Ellerman, 1949; Petter 1972, 1975; Honacki et al., 1982; Corbet and Hill, 1991). In light of current research, the polytypic construct of *E. myoxinus* that so long masked the distinctive morphologies and genetic divergence of forms such as *E. majori* and *E. tanala* almost defies comprehension. Unencumbered by identification with these species and others, the morphological similarity of *E. myoxinus* and *E. minor* is more readily appreciable: size small (*E. minor*) to medium (*E. myoxinus*); skull stockily built with a relatively broad interorbit, short rostrum, and incisive foramina medium in length; dorsal pelage color dominated by brown tones; caudal pilosity dense and tuft long, covering one-half to two-thirds of the tail length. Although no special affinity was appreciated by Carleton (1994), Jansa et al. (1999) presented molecular data that lend confidence in the sister-group relationship of *E. myoxinus* and *E. minor*.

Morphological resemblance of the two species is more convergent among their northernmost populations. Carleton (1994) drew attention to the large size of *E. minor* that inhabit lowlands around Antongil Bay; robust proportions also characterize those obtained from the RS de Manongarivo. Size variation within *E. myoxinus*, on the other hand, trends from larger in the south (Petriky Forest) to smaller in the northwest (PN de l'Ankarafantsika), as the species range was then known to Carleton et al. (2001). Recent surveys have now documented *E. myoxinus* even farther to the north, from the RS de Manongarivo, Daraina Forest, and the northwestern sector of the PN de Marojejy in Antsiranana Province (Goodman and Soarimalala, 2002; Soarimalala and Goodman, 2003; appendix 1). These northern samples continue the pattern of size decline, representing the smallest specimens of the species we have so far examined, but they generally


△ Eliurus antsingy
● Eliurus danieli
○ Eliurus majori
□ Eliurus penicillatus
Antsiranana
Mahajanga
Toamasina
Antananarivo
Fianarantsoa
Toliara
Altitude (m)
0 - 1000
1000 - 2000
2000 - 2876

conform to the cranial proportions and external morphology that typify *E. myoxinus* populations to the south (unpublished data and analyses). Sample sizes and geographic representation of both forms have vastly improved since Carleton's (1994) revision and should enable a critical and much-needed evaluation of the complex. Careful scrutiny should be devoted to northern Madagascar where the ranges of *E. myoxinus* and *E. minor* appear to interdigitate in a complex manner, unlike the southern facies of their distributions where biotic transition is dramatically abrupt and their morphological differentiation is just as sharply marked (Goodman et al., 1999).

Eliurus petteri Group (*E. petteri* Carleton, 1994; *E. grandidieri* Carleton and Goodman, 1998): These two species are medium in size, possess soft-textured and short pelage, and have small auditory bullae, delicately built upper and lower incisors, and an extremely short lower incisor without a capsular projection. Their tails are relatively long and the tail tuft very short and weakly developed in both (ca. distal one-fourth of tail length), one with a white-tip (*E. grandidieri*) and the other dark (*E. petteri*). Some of these conditions are the extreme expression of the character as so far observed within the genus (see Carleton and Goodman, 1998: 173). Genetic investigation to date is limited to *E. grandidieri*, which surprisingly is revealed as most closely allied to *Voalavo gymnocaudus* according to these data (Jansa et al., 1999). These results puzzle us in view of the morphological traits that characterize *Voalavo* and unambiguously distinguish it from all species of *Eliurus* (Carleton and Goodman, 1998: 189–194). Further, *Voalavo* possesses a relatively large midventral gland, unknown in any species of *Eliurus*, that produces a distinctly musky odor. Although the two genus-group taxa are undoubtedly close kin (Carleton and Goodman, 1998; Jansa and Weksler, 2004), the possible paraphyly of *Eliurus* as indicated earlier by Jansa et al. (1999) requires further corroboration and its generic diagnosis and contents amended if appropriate. Inclusion of tissues from *E. petteri*, along with additional geographic samples of *E. grandidieri*, may provide a fresh taxonomic scope to do so.

The range of *E. grandidieri* is more extensive than that of *E. petteri*, the former known in the Northern Highlands and northern Central High Plateau, within montane and upper montane forest (ca. 1200–1900 m), and the latter restricted to a small area in east-central Madagascar, at intermediate elevations (ca. 400–1100 m) within Toamasina Province (Carleton, 2003). Recent recoveries of *E. petteri*—from Andriantantely, Saharay, and Sandranantitra (appendix 1)—originated from the same localized area and reaffirm the species' distinctive morphology.

Eliurus tanala Group (*E. tanala* Major, 1896; *E. webbi* Ellerman, 1949; *E. ellermani* Carleton, 1994): These are large species, *E. ellermani* and some northern samples of *E. tanala* being fully as robust as *E. antsingy*, but in cranial and dental proportions, the three differ strikingly from that species and from those of the *E. majori* group. The molars are shorter and narrower relative to cranial size, with the third molars smaller than the second; upper and lower incisors are stout, and the lower is long and terminates as a moderately (*E. webbi*) to strongly (*E. tanala*, *E. ellermani*) pronounced capsular process on the upper mandibular ramus. The lunate incisive foramina are medium in length for the genus, supernumerary palatal foramina are commonplace, often coalesced as elongate vacuities, and the subsquamosal fenestra is small (most *E. webbi*) or absent (*E. tanala*, *E. ellermani*). The pinnae are pliant and elongate, averaging the longest in the genus, and the caudal tuft is well developed but confined to the terminal 30–40% of tail length. Carleton (1994) speculated that *E. webbi* is sister species to the clade *E. tanala*–*E. ellermani*, an expectation not sustained by the few cladistic characters he mustered. Jansa et al. (1999), using cytochrome *b* sequences,

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Fig. 7. Geographic occurrence of the new species *E. danieli*, known only from PN de l'Isalo, and its eastern relatives *E. majori* and *E. penicillatus*. Also illustrated is the currently documented range of *E. antsingy* based on new records reported herein.

demonstrated phylogenetic pairing of *E. webbi* and *E. tanala* among the eight species studied.

The *E. tanala* group presents many taxonomic problems that require attention. For one, the status of *E. ellermani* as a species distinct from *E. tanala* merits reexamination. Application of molecular techniques to fresh material from the amended type locality of *E. ellermani* (Carleton and Goodman, 1998), along with examples of the large, creamy white–bellied *E. tanala* from the Northern Highlands, should provide the pivotal evidence.

As in the *E. majori* group, western outliers of the *E. tanala* assemblage have been recently documented (Carleton et al., 2001; appendix 1). Compared with eastern *E. tanala* proper, those from the PN de Bemaraha have a distinctive color pattern—notably the pale brown dorsum, entirely creamy-white underparts, and the alternately banded tail tuft—but in cranial shape and their robust size, they suggest *E. ellermani* and northern *E. tanala*. That from the RS de Maningoza is similar in size and body color but possesses a monocolored tail tuft. Such chromatic contrasts, coupled with the wide geographic hiatus between the western *tanala*-like populations and the eastern range of *E. tanala* proper, cast doubt on their conspecific stature. The taxonomic status and distributional extent of the western morphs invite critical review.

Morphological variability within both *E. tanala* and *E. webbi* increases in the northern segments of their ranges and complicates their identification (Carleton and Goodman, 1998, 2000). Variability is particularly evident in the invasiveness of all creamy-white hairs on the ventrum, the constancy of tail tuft coloration, closure of the subsquamosal fenestra, and overall size. Across the central and southern parts of their distributions, such features appear more stable in their population expression and meaningfully contribute to specific discrimination (Carleton, 1994). The mixture of traits exhibited by certain northern samples, such as those from the Daraina region (appendix 1) and perhaps the RS de Manongarivo (Goodman and Soarimalala, 2002—listed as *E. webbi*), is so atypical that specific allocation is uncertain. These specimens may constitute a different species altogether or represent exceptional morphological convergence of *E. webbi* toward the *E. tanala* morphotype. Teasing apart these hypotheses will require denser transects within the troublesome geographic region in question, broad distributional sampling of typical *E. tanala* and *E. webbi* against which to gauge the differentiation of the northern samples, and application of multiple information sources.

In summary, we can be confident that *Eliurus* comprises many more than the two species so long recognized as valid by Ellerman (1949) and others. Nevertheless, the genus obviously requires further field, museum, and laboratory investigation to improve its alpha-level systematics. Some of the research challenges outlined above will undoubtedly reveal new species, but of greater systematic interest, the next phase of *Eliurus* investigation should aim to refine relationships among species and to explore patterns of their biogeographic origination.

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APPENDIX 1

SPECIMENS EXAMINED OF *ELIURUS*

Listed below are specimens that formed the basis for the study's morphological comparisons, sample statistics, morphometric analyses, mapped distributions, and range extensions. Abbreviations for protected areas in Madagascar are: PN, Parc National; RNI, Réserve Naturelle Intégrale; RS, Réserve Spéciale.

ELIURUS AFF. *E. MAJORI* GROUP: Mahajanga Province: RS d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 1150 m, 18°15.7′S, 45°25.2′E (FMNH 167546, 167555). Antananarivo Province: RS d'Ambohitantely, 24 km NE Ankazobe, Jardin Botanique, 1450 m, 18°10.1′, S, 47°16.6′E (FMNH 165505, 176019–176022).

ELIURUS AFF. *E. TANALA* GROUP: Antsiranana Province: Forêt de Binara, 7.5 km SW Daraina, near Analamazava River, 325–550 m, 13°15.3′S, 49°37.0′E (FMNH 172665–172675). Mahajanga Province: RS de Maningoza (FMNH 167562). Mahajanga Province: Bekopaka (MNHN 1966.221); PN de Bemaraha, 2.5 km NE Bekopaka, Ankidrodroa, 100 m, 19°07.9′S, 44°48.5′E (FMNH 172722); PN de Bemaraha, 3.5 km E Bekopaka, near Tombeau Vazimba, 100 m, 19°08.4′S, 44°49.7′E (FMNH 172723–172725).

Eliurus antsingy: Antsiranana Province: Forêt d'Ambilondambo, 5 km N Daraina, Andrafia, 300–550 m, 13°09.9′S, 49°38.9′E (UADBA 46062, 46072, 46073); Forêt de Bobankora, 11 km ESE Daraina, Beantely, 350–550 m, 13°13.4′S, 49°45.6′E (UADBA 46101); RS d'Ankarana, 2.6 km E Andrafiabe, forest near Andrafiabe Cave, 50 m, 12°55.9′S, 49°03.4′E (FMNH 169718–169720); RS d'Ankarana, 7.5 km NW Mahamasina, Anilotra, 125 m, 12°54.5′S, 49°06.6′E (FMNH 173104–173106, 173109); RS d'Ankarana, 10 km NW Mahamasina, 100 m, 12°53.2′S, 49°06.6′E (FMNH 173107, 173108). Mahajanga Province: RNI [now PN] de Namoroka (FMNH 167563–167566; UADBA 16169); RNI [now PN] de Namoroka, 26 km NW Andranomavo, Forêt d'Ambovonomby, 200 m, 16°28.2′S, 45°20.9′E (FMNH 175909–175911); RNI [now PN] de Namoroka, 31 km NW Andranomavo, Forêt de Mahabo, 100 m, 16°23.4′S, 45°20.9′E (FMNH 175912, 175913). Mahajanga Province: Antsingy forest near Bekopaka, ca. 19°07.5′S, 44°49.0′E (MNHN 1966.2220, 1966.2222); PN de Bemaraha, 3.5 km E Bekopaka, near Tombeau Vazimba, 100 m, 19°08.4′S, 44°49.7′E (FMNH 172721).

Eliurus majori: Antsiranana Province: Montagne d'Ambre, 1000 m (AMNH 100687, 100854); PN de Montagne d'Ambre, 12 km SW Joffreville, Grand Lac, 1325 m, 12°35.8′S, 49°09.6′E (FMNH 154345); PN de Montagne d'Ambre, 5.5 km SW Joffreville, 1000 m, 12°31.6′S, 49°10.3′E (FMNH 154536–154539, 154603–154616); RS de Manongarivo, 17.3 km SW Antanambao, 1600 m, 14°01.3′S, 48°25.1′E (FMNH 166211–166213); PN de Marojejy, 11 km NW Manantenina, 1325 m, 14°26.2′S, 49°44.5′E (FMNH 159624, 159709); PN de Marojejy, 10.5 km NW Manantenina, Antranohofa, 1625 m, 14°26.4′S, 49°44.5′E (FMNH 159625–159637, 159710–159715, UA-SMG 8463); PN de Marojejy, 11 km NW Manantenina, 1875 m, 14°26.8′S, 49°44.1′E (FMNH 159638); RS d'Anjanaharibe-Sud, 9.2 km WSW Befingotra, 1260 m, 14°44.7′S, 49°27.7′E (FMNH 154052, 154241–154243, 154258, 154266, UA-SMG 6981, 6998); RS d'Anjanaharibe-Sud, 11 km WSW Befingotra, 1550 m, 14°44.5′S, 49°26.0′E (FMNH 154053, 154244); RS d'Anjanaharibe-Sud, 12.2 km WSW Befingotra, 1950 m, 14°44.8′S, 49°26.0′E (FMNH 154054, 154245, 154298; UA-SMG 7090). Mahajanga Province: Western slope Anjanaharibe-Sud, 13 km SW Befingotra, 1600 m, 14°45.9′S, 49°25.9′E (FMNH 167452–167457). Antananarivo Province: 16.2 km SE Tsinjoarivo, Andrindizimbolo River, Forêt d'Ankilahila, 1400 m, 19°42.4′S, 47°50.1′E (FMNH 166162, 166613). Fianarantsoa Province: Ambohimitombo (BMNH 97.9.1.147; MCZ 45929); RNI [now PN] d'Andringitra, 38 km S Ambalavao, ridge east of Volotsangana River, 1625 m, 22°11′39″S, 46°58′16″E (FMNH 151666, 151667, 151732, 151752, 151851–151858); RNI [now PN] d'Andringitra, 40 km S Ambalavao, along Volotsangana River, 1210 m, 22°13′22″S, 46°58′18″E (FMNH 151661–151665, 151730, 151731, 151847–151849); Andringitra Massif, Anjavidilava, 2030 m (MNHN 1972.602); RS du Pic d'Ivohibe, 1575 m (FMNH 161891, 162073–162075). Toliara Province: RNI [now PN] d'Andohahela, Parcel 1, 13.5 km NW Eminiminy, 1200 m, 24°35.0′S, 46°44.1′E (FMNH 156503, 156615); RNI [now PN] d'Andohahela, Parcel 1, 15.0 km NW Eminiminy, 1500 m, 24°34.2′S, 46°43.9′E (FMNH 156616, 156617, 156658).

Eliurus myoxinus: Antsiranana Province: Forêt de Binara, 7.5 km SW Daraina, near Analamazava River, 325–550 m, 13°15.3′S, 49°37.0′E (FMNH 172655–172664); RS de Manongarivo, 12.8 km SW Antanambao, 785 m, 13°58.6′S, 48°25.4′E (FMNH 166252); RS de Manongarivo, 14.5 km SW Antanambao, 1240 m, 14°00.0′S, 48°25.7′E (FMNH 166253); PN de Marojejy, along Bemanavy River, 11.5 km SE Doany, 810 m, 14°25.6′S, 49°36.5′E (FMNH 172606–172614, 173207, 173209–173214, 173216, 173220–173224).

Eliurus penicillatus: Fianarantsoa Province: Ampitambe (BMNH 97.9.1.148–97.9.1.150, 97.9.1.152, 1939.1892; FMNH 18822; LMCM A19.4.98.26; MCZ 12435, 45932; MNHN 1897.536, 1909.191; USNM 49672; UZMC 1219, 1224, 7941; ZFMK 82.217, 83.56); Prefecture de Fandriana, Ankerana, 1670 m, 20°03′49″S, 47°40′18″E (UADBA 16209).

Eliurus petteri: Toamasina Province: Andriantantely, 530 m (FMNH 166062, 166063); Saharay, 1000–1145 m, 18°41.7′S, 48°35.24′E (UADBA 19139); Sandranantitra, 450 m (FMNH 16604).

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