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## Systematic Studies of Madagascar's Endemic Rodents (Muroidea: Nesomyinae): Revision of the Genus *Eliurus*

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## ABSTRACT

Among Madagascar's seven genera of endemic rodents (Nesomyinae Major, 1897), members of the genus *Eliurus* are readily identified by their soft fur, broad hindfeet, and a long tail bearing a conspicuous terminal tuft. Based on examination of approximately 200 museum specimens representing 42 collecting localities, eight species, without subspecific divisions, are recognized: *E. myoxinus* Milne Edwards, *E. minor* Major, *E. majori* Thomas, *E. penicillatus* Thomas, *E. tanala* Major, *E. webbi* Ellerman, and two species described herein as new. Discrimination between species relies principally on size, chromatic and textural features of the pelage, development and color of the

tail tuft, proportional craniodental differentiation, and possession of certain qualitative cranial traits. Each species account summarizes the taxon's diagnostic traits, distributional information, and the limited data on ecology and reproduction. The greatest species diversity of *Eliurus* occurs within humid, evergreen forests in the east, where seven of the eight species are found. One species, *E. myoxinus*, is confined to dry deciduous forest and scrub formations in the west and south. External, cranial, dental, and skeletal features uniting the species of *Eliurus* are amplified as a basis for improved diagnosis of the genus and for future study of intergeneric relationships.

## INTRODUCTION

Compared to other groups of Muroidea, the rodents indigenous to Madagascar comprise a meager number of species, ten, which represent seven genera (Petter, 1972, 1975; Honacki et al., 1982; Corbet and Hill, 1991). The ten species are generally believed to have originated from a common ancestor that underwent a modest radiation during a long period of isolation, perhaps since the early Miocene, on the island-continent (Simpson, 1945; Lavocat, 1978). Consistent with the conventional interpretation (but see Ellerman, 1941), the several forms have been arranged as an endemic subfamily, Nesomyinae (Major, 1897), which is placed within either the Cricetidae, Muridae, or a broadly defined family Nesomyidae (see Carleton and Musser, 1984, for review of muroid classifications). The apparently unremarkable speciation of nesomyines has been accompanied by impressive morphological and ecological divergence between them—from gerbil-like (*Macrotarso-mys*) to volelike (*Brachyuromys*) to rabbitlike (*Hypogeomys*) forms—such that the seven genera recognized are well circumscribed and their specific members readily identifiable.

One of those morphologically distinctive genera is *Eliurus*, which embraces several broad-footed, long-tailed taxa known from

wet tropical forests in eastern Madagascar as well as dry forest associations in the west. Webb (1954) appropriately dubbed these rodents "tufted-tailed rats" in recognition of the usually dense penicillation of hairs toward the end of their tail, a development which constitutes the cardinal external trait of the genus. To date, six taxa of *Eliurus* have been named, five of them originally described as species, but recent classifications acknowledge only a large- and small-bodied species, *E. myoxinus* and *E. minor*, respectively (Petter, 1975; Honacki et al., 1982; Corbet and Hill, 1991).

In their review of museum collections of Nesomyinae, however, Carleton and Schmidt (1990) argued that the current definition of two species severely underestimates the biological variety within *Eliurus*. Indeed, further taxonomic study will probably reveal the genus as by far the most speciose of the seven genera of Nesomyinae. The central purpose of the present study is to begin to substantiate this contention. In doing so, I present the morphological basis for the identification of eight species, two of them newly described herein, summarize their geographic distributions, consolidate the limited data on their ecology and reproductive biology, and offer

a preliminary evaluation of interspecific relationships within *Eliurus*. This report is the second in a series (see Carleton and Schmidt, 1990) intended to document existing museum collections of Nesomyinae as a framework for pursuing higher-level phylogenetic investigations of the group.

#### TAXONOMIC HISTORY

In describing his new genus and species *Eliurus myoxinus*, Milne Edwards (1885) acknowledged its external resemblance, particularly as observed in its bushy tail, to dormice (family Myoxidae) and to *Platacanthomys* (formerly included with myoxids). The etymology of *Eliurus myoxinus* reflected this superficial impression, both for the generic (*Eliomys*, a European dormouse) and for the specific (Myoxides, an early family name of dormice) epithets adopted. Despite the affinity suggested by its scientific name, Milne Edwards recognized that the dentition of *Eliurus* aligned his new form with the Muridae (sensu lato) and, in particular, with the other genera of Malagasy rodents then known, namely *Nesomys*, *Brachytarsomys*, and *Hypogeomys*.

The zoological explorations of C. I. Forsyth Major in the middle 1890s contributed important additions to the systematic knowledge of *Eliurus* (Major, 1896b). Four new species were eventually described from these collections, two each by Oldfield Thomas and by Forsyth Major: *E. majori* Thomas, 1895 (type locality, Ambohimitambo); *E. minor* Major, 1896a (type locality, Ampitambe); *E. tanala* Major, 1896a (type locality, Vinanitelo); and *E. penicillatus* Thomas, 1908 (type locality, Ampitambe). In contrast to the west-coast provenance of *E. myoxinus*, all of these forms originated from the large humid forest block in eastern Madagascar. Diagnostic features of the several new species principally concerned differences in overall size, pilosity of the tail, and occurrence of a white tip on the tail.

The number of taxa within *Eliurus* remained stable for several decades after this brief episode of description. The Mission Zoologique Franco-Anglo-Américaine (= MZFAA) to Madagascar, conducted from April 1929 to May 1931 (Rand, 1936), yield-

ed no new rodent discoveries, and in his classification of Rodentia, Ellerman (1941) listed all five taxa of *Eliurus* as species as they were originally described. However, Ellerman did remark (p. 76) that "There seems no extreme difference between the named forms except that *minor* is constantly smaller than the others in the small series examined." Ellerman's impression in this regard foreshadowed his later taxonomic action that established the current view of species diversity within the genus.

In his 1949 addendum to *The Families and Genera of Living Rodents*, Ellerman reported on an important collection of Malagasy rodents gathered by Cecil S. Webb during the Second World War (see Webb, 1954). The fine series of many nesomyine taxa obtained by Webb enhanced Ellerman's appreciation of local and geographic variation within *Eliurus* and persuaded him (1949: 161) to rank all of the named forms, except *E. minor*, as subspecies of *E. myoxinus*: "... I am regarding all the above named forms [that is, *majori*, *tanala*, and *penicillatus*] as well-marked races of the first-named *E. myoxinus*." Ellerman obviously held reservations over this action, for he continued: "It is perhaps a rather extreme view, but the differences indicated and in material available to me do not seem to warrant full specific rank for any of them." Within this broad context of intraspecific variation, he (1949) described *E. myoxinus webbi* as another distinctive race, this one named from the coastal lowlands of southeast Madagascar (20 mi S Farafangana) but also occurring at higher elevations (about 1500 m) in mountains east of Ivohibe and in lowland rainforest far to the northeast around Antongil Bay.

Ellerman's (1949) arrangement of the highly differentiated races of *E. myoxinus* is better appreciated when considered within the decade of the 1940s, a period marked by the emerging biological species concept and the convention of using the subspecies category to somehow index patterns of intraspecific variation. His interpretation of species boundaries within *Eliurus*, consisting of a large-bodied polytypic *myoxinus* that frequently co-occurs with the smaller monotypic *minor*, was consistent with taxonomic practices engendered by the new species phi-

losophy, especially with respect to the treatment of morphologically similar, allopatric forms. Thus he observed (1949: 162) that "No two forms here regarded as races of *E. myoxinus* occur together, so far as I know."

Ellerman's interpretation has since remained the accepted species classification of *Eliurus* (Petter, 1972, 1975; Corbet and Hill, 1980, 1991; Honacki et al., 1982). Nevertheless, as I shall document below, this simple view misrepresents the biological diversity within *Eliurus*. The constancy of traits advanced for discriminating the various described forms is greater than appreciated by Ellerman, and new distributional records provide instances of sympatry or contiguous allopatry among them. The collective evidence recommends the elevation of all named forms of *E. myoxinus* to species and the recognition of yet other undescribed populations.

#### MATERIALS AND METHODS

**Specimens and Analytical Samples:** This revision is based on the examination of approximately 200 specimens of *Eliurus*, consisting principally of study skins with associated skulls, from 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 | Universitets Zoologisk Museum, Copenhagen           |

The specimens examined are generally listed according to the provenance supplied by the collector. The location of collecting sites, current geographic synonyms, and the determination of coordinates used for preparing

the distributional maps are discussed by Carleton and Schmidt (1990). Principal localities and their coordinates for specimens of *Eliurus* reported herein are provided in Appendix 1.

In view of the small sample sizes and inadequate geographic representation available for most nesomyine taxa, descriptive statistics and multivariate analyses were of necessity based on composite OTUs recognized as follows.

#### *Eliurus minor*

- OTU 1: N = 5, from vicinity of Hiaraka, Maroantsetra, and Andapa.  
 OTU 2: N = 9, from vicinity of Didy, Im-erimandrosa, and Perinet.  
 OTU 3: N = 2, from Ampitambe (type locality).  
 OTU 4: N = 13, from vicinity of Ambodiamontana and Andraina.  
 OTU 5: N = 7, from vicinity of Vondrozo.

#### *E. myoxinus myoxinus*

- OTU 6: N = 9, from vicinity of Bevilany.  
 OTU 7: N = 9, from vicinity of Analabe, Beroboka, Morondava, Tsilambana (type locality), and Tulear.

#### *E. m. majori*

- OTU 8: N = 5, from Mount D'Ambre, Ambohitambo (type locality), and Andringitra.

#### *E. m. penicillatus*

- OTU 9: N = 16, from Ampitambe (type locality).

#### *E. m. tanala*

- OTU 10: N = 18, from vicinity of Lohariandava and Perinet.  
 OTU 11: N = 18, from vicinity of Ambodiamontana, Andrambovato, and Vohiparara.  
 OTU 12: N = 3, from Vinanitelo (type locality).

#### *E. m. webbi*

- OTU 13: N = 5, from Mount d'Ambre.  
 OTU 14: N = 10, from vicinity of Andranofotsy, Ankovana, Antalaha, Antalavia, Hiaraka, Maroantsetra, and Rantabe.  
 OTU 15: N = 20, from vicinity of Andrambovato, Ifanadiana, and Kianjavato.



OTU 16: N = 6, from mountains east of Ivo-hibe.

OTU 17: N = 14, from vicinity of Farafan-gana (type locality) and Vondrozo.

*Eliurus* new species 1

OTU 18: N = 3, from vicinity of Fanovana (type locality), Perinet, and Rogez.

*Eliurus* new species 2

OTU 19: N = 2, from Hiaraka (type locality) and north of Rogez.

**AGE CRITERIA AND MEASUREMENTS:** Specimens were initially assigned to one of five broad age classes based on a combination of pelage condition and dental wear: juvenile, subadult, and young-, full-, and old-adult. However, sample sizes proved to be too small and good locality series too few to meaningfully assess either age or geographic variation, except in a qualitative fashion. Statistical analyses were thus limited to "adult" animals as recognized by the absence of the gray juvenile-subadult pelage and by the possession of fully erupted, though sometimes unworn, third molars.

A maximum of 7 external and 18 cranio-dental variables was recorded for each specimen examined. Total length (TOTL), lengths of tail (TL), hind foot (HFL), and ear (EL), all given in whole millimeters (mm), are those recorded by the collector on the skin label. Length of head-and-body (HBL) was obtained either as listed by the collector or by subtraction of TL from TOTL. Weight (WT) in grams was also transcribed from specimen labels, although this datum is generally unavailable for specimens preserved before the 1960s. Nor did early collectors always provide external dimensions, and where available, their measurement protocol is often unclear for certain variables (for example, EL from the crown or from the notch, and HFL with the claw or without). As an index of general body size, I therefore measured dry hind foot length (DHFL), including the claw, to the nearest 0.5 mm on museum skins whose metatarsal and phalangeal bones remained straightly aligned. Shrinkage of the hindfoot on a prepared *Eliurus* skin averages about 1–2 mm, as suggested by a comparison of DHFL with HFL for several species recently collected and standardly measured by the same

field crew—namely *minor* (OTU 4), *tanala* (OTU 11), and *webbi* (OTU 15). External measurements are provided for the purpose of general description and to aid field identification but were not employed for the multivariate comparisons of samples.

Sixteen cranial and two dental dimensions were measured to the nearest 0.1 mm using hand-held digital calipers accurate to 0.03 mm. These measurements, and their abbreviations as used herein, are defined and listed alphabetically below (see fig. 1).

|      |  |
|------|--|
| BBC  | breadth of the braincase: the distance measured across the hamular processes of the squamosals at the point where they are adnate to the mastoid bullae.   |
| BIF  | breadth of incisive foramina: the greatest transverse expanse across both incisive foramina, typically measured at the level of the premaxillary-maxillary suture.   |
| BM1s | breadth of bony palate across first upper molars: the transverse distance between the labial edges of the upper first molars, generally at their middle lamina.  |
| BOC  | breadth across the occipital condyles: the distance between the lateral edge of the dorsal lobes of the exoccipital condyles.  |
| BR   | breadth of rostrum: the distance between the lateralmost projection of the nasolacrimal capsules, located just anterior to the zygomatic plates.   |
| BZP  | breadth of zygomatic plate: the shortest distance between the anterior and posterior margins of the zygomatic plate, generally near its midsection.  |
| DAB  | depth of the auditory bulla: the distance between the dorsal rim of the auditory bullae, directly above the external auditory meatus, and its ventralmost curvature; the line of this dimension lies in the transverse plane of the skull and oblique to its sagittal plane. |
| IOB  | interorbital breadth: the minimum distance across the frontal bones between the orbital fossae, generally at the midpoint of the interorbital constriction.  |
| LBP  | length of bony palate: the shortest distance between the anterior margin of the mesopterygoid fossa and the posterior terminus of the left incisive foramen.   |
| LD   | length of diastema: the distance, on the same side, between the anterior edge of the first upper molar and the lesser curvature of the upper incisor, near its emergence from the incisive alveolus.   |

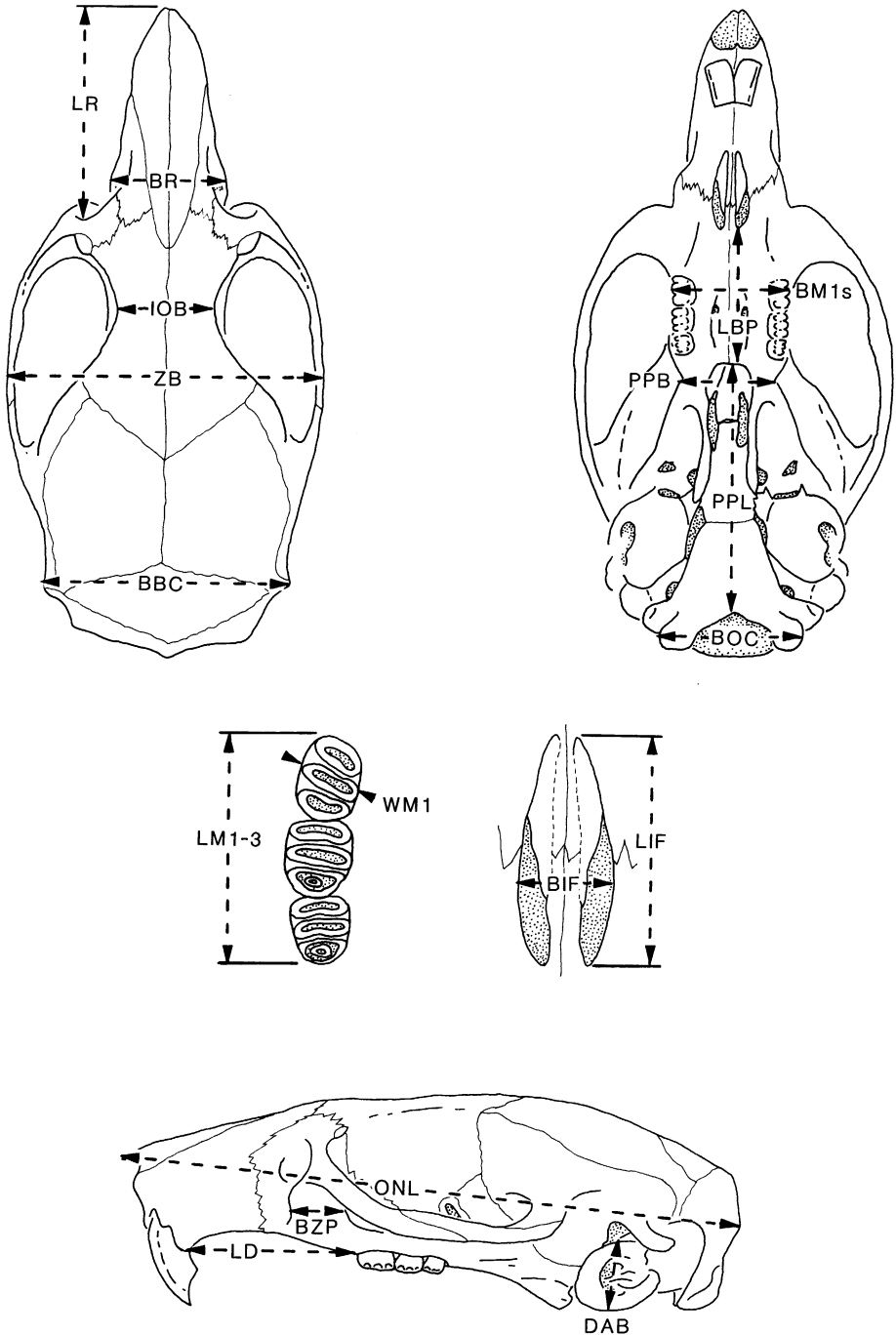


Fig. 1. Schematic views of the cranium (dorsal, ventral, lateral), right maxillary molar row, and incisive foramina of an adult *Eliurus myoxinus* showing the limits of the 18 craniocental measurements recorded for specimens of *Eliurus* (see Material and Methods for abbreviations and definitions of measurements).

- LIF length of incisive foramina: the greatest length of one incisive foramen.
- LM1-3 length of maxillary toothrow: a coronal length recorded from the anterior border of the first upper molar to the posterior margin of the third.
- LR length of rostrum: the distance, taken parallel to the longitudinal cranial axis, from the posterior border of the zygomatic notch to the tips of the nasal bones.
- ONL occipitonasal length: the distance between the tip of the nasals and the posteriormost edge of the occiput, just above the foramen magnum.
- PPB posterior breadth of bony palate: the least transverse span of the bony palate, recorded at the constriction of the maxillary bones behind the upper third molars and in front of the parapterygoid fossae.
- PPL postpalatal length: a distance measured along the basicranial midline, from the anterior margin of the mesopterygoid fossa to the midventral lip (basion) of the foramen magnum.
- WM1 width of first upper molar: the crown width of the upper first molar across its middle lamina.
- ZB zygomatic breadth: the maximum span between the lateral surfaces of the zygomatic arches, a point generally on the jugal bones and immediately in front of the jugal-squamosal suture.

**MORPHOMETRIC AND PHYLOGENETIC ANALYSES:** Standard descriptive statistics (mean, range, standard deviation) were computed for the OTUs. Principal components were extracted from the variance-covariance matrix and computed using the 18 craniodental variables, all of which were first transformed to natural logarithms. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components with the original external and cranial variables. All analytic procedures were carried out using Systat (Version 4.0, 1988), a series of statistical routines programmed for microcomputers.

Phylogenetic relationships were explored using PAUP Version 2.4.1 (Swofford, 1985) to find trees of minimal length (branch- and-bound option) by the criterion of Wagner parsimony. Characters were not weighted, and trees were rooted using a designated outgroup OTU. The congruent cladistic structure in

mutually parsimonious trees was summarized by the strict consensus method.

#### ACKNOWLEDGMENTS

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#### CHARACTERIZATION OF THE GENUS

Previous contributions have cursorily presented the distinctive external and cranial traits of *Eliurus*. Milne Edwards (1885) stressed only external appearance in his brief description of the genus, and Ellerman (1941, 1949) emphasized its laminate dentition in provisionally associating the taxon as the Group Eliuri within the subfamily Murinae. To avoid repetition of common traits in the species accounts, and as a basis for future phylogenetic study of nesomyines and improved diagnoses of the genera, I here amplify the external, skeletal, and dental features characterizing the genus *Eliurus* as viewed from the present understanding of its contents. Anatomical terminology generally follows Hershkovitz (1962), Carleton (1980), and Voss (1988).

#### EXTERNAL

Fur soft and fine, consisting of a thick coat of cover hairs interspersed with coarser guard hairs; dorsal pelage generally longer and denser than ventral. Guard hairs black throughout their length, occasionally silver-tipped, and protruding little above coat of cover hairs except on rump. Cover hairs

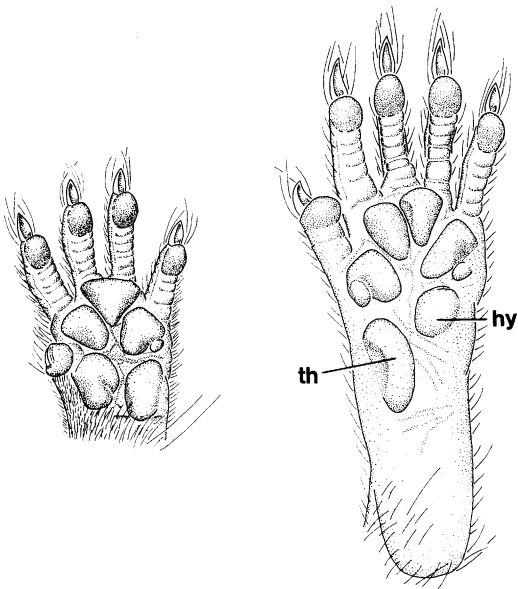


Fig. 2. Plantar views of left manus and left pes of *Eliurus majori* (AMNH 100854, Montagne d'Ambre; HFL = 31 mm). Abbreviations: hy, hypothenar pad; th, thenar pad.

chromatically banded, usually tricolored on dorsum and bicolored on venter; basal band long and colored some shade of gray; middle band of variable length and buffy to dull white; if present, terminal band always short and dark brown to black. Dorsal-ventral countershading apparent in most species, indistinct in two, but without pronounced lateral line. Dorsal effect usually some shade of brown to brownish gray, bright to somber in tone; underparts light to medium gray, variably creamy buff. Eyelids darkly pigmented, surrounded by blackish hairs giving a more or less defined impression of dark eye-rings; pre- or postauricular patches lacking.

Facial vibrissae include mystacial, submental, superciliary, genal, and interramal groups, the latter two consisting of just one or two vibrissae each. Pinnae typically darkly pigmented, appearing naked to unaided eye; clothed externally and internally with fine, usually dusky, hairs. Mammae six, distributed as one axillary, one abdominal, and one inguinal pair.

Tail relatively long, ranging from 110 to 135 percent of head and body length, and noticeably penicillate over distal half to one-quarter of its length. Caudal hairs light brown

to blackish to tip of vertebrae, or with a white terminal tuft in two species; hair and epidermis otherwise basically monocolored, or infrequently with pale midventral splotching toward base. Proximal section of tail appearing naked macroscopically, epidermal scales easily discernible; scales arranged as imbricating annuli with triad of hairs emerging from posterior margin of each scale (this pattern is progressively obscured as the hairs become longer toward the tail tip and mask its scutellation).

Forefoot with nail-bearing, stubby pollex, other four digits clawed. Dorsum of metacarpus and phalanges usually covered with white hairs; palmar surface naked with five prominent pads, consisting of three close-set interdigitals and the paired thenar and hypothenar (fig. 2).

Hindfoot comparatively short and broad, all digits with claws (fig. 2); clothed dorsally with white hairs, sometimes with a dusky metatarsal streak; unguis tufts of whitish hairs arch over full length of claws; plantar surface naked from phalanges to heel. Fifth digit relatively long, its claw reaching to base of claw of digit IV; claw of hallux extends to middle of first phalanx of digit II. Plantar pads six in number, large and fleshy; four interdigital pads clustered together at base of digits, the first and fourth occasionally bearing a smaller, incompletely delineated pad on their outer edge; hypothenar subequal in size to interdigitals and arranged close to them, thenar conspicuous and elongate.

#### CRANIAL AND POSTCRANIAL SKELETON

Rostrum moderately long, about 33 to 36 percent of occipitonasal length, gradually tapering anteriorly from bulge of nasolacrimal capsules (fig. 3); tips of nasals usually pointed, overhanging anterior nares; nasals terminate posteriorly even with or slightly beyond end of rostral processes of premaxillae. Zygomatic plate narrow, forming a distinct but shallow dorsal notch; anterior border of plate straight and oriented vertically, its forward edge not overlapping nasolacrimal capsule in lateral view; zygomatic arches parallel-sided to slightly bowed in midsection; jugal long and relatively stout, zygomatic processes of squamosal and maxillary well separated.

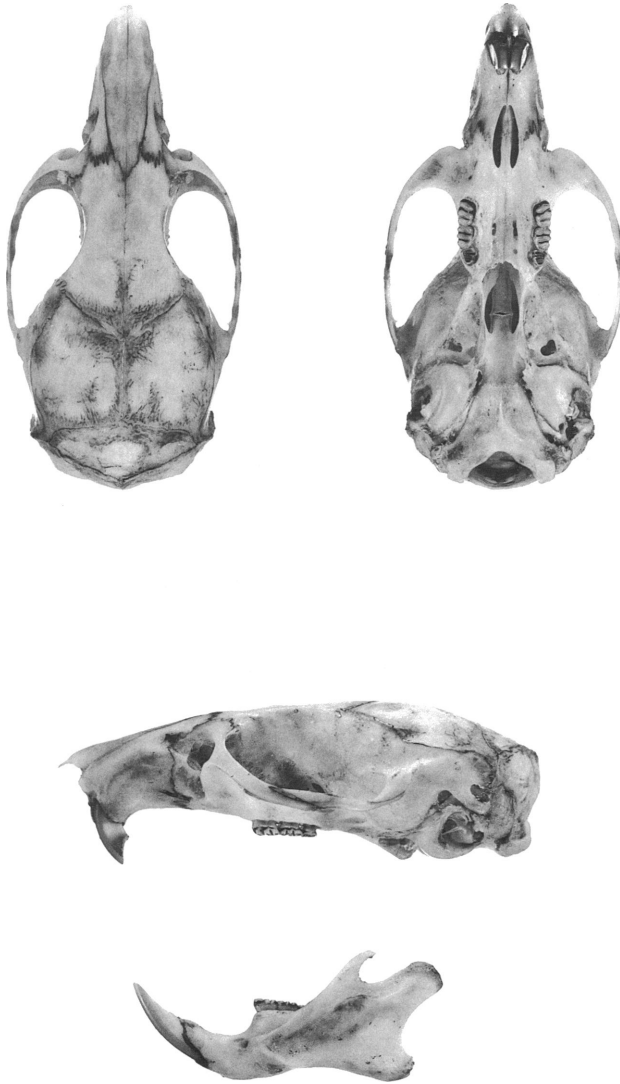


Fig. 3. General conformation ( $\times 1.75$ ) of the cranium and mandible of *Eliurus* as illustrated by an adult sample of the type species *E. myoxinus* (BMNH 47.1603, 5 mi E Bevilany; ONL = 36.7 mm).

Interorbital region hourglass-shaped, the supraorbital edges bluntly squared (not rounded over); supraorbital shelf or beading lacking. Braincase smooth and elongate in dorsal appearance, without temporal ridges; short lambdoidal ridges developed at exoccipital-squamosal junction but not continuous across supraoccipital; frontoparietal border formed at  $90^\circ$  angle; interparietal broad and conspicuous but lateral edges not contacting squamosals; dorsal profile of skull gently and evenly curved over calvarium, be-

coming almost straight over interorbit and rostrum.

Incisive foramina short (40–55% of diastemal length), narrow to moderate in width and terminating well anterior to molars; diastema appearing relatively long (fig. 3). Posterior border of bony palate set just anterior to or even with end of upper third molars, and lacking posterolateral palatal pits. Posterior palatine foramina situated at maxillopalatine suture near lingual root of second upper molars; variably expressed according

to species, small and ovate to large and elongate (in the latter condition, the palatine bones are pierced by secondary foramina behind the principal openings). Mesopterygoid fossa with anterior margin broadly horseshoe-shaped, lacking a medial spine, and with lateral borders (pterygoid processes) convergent posteriorly. Sphenopalatine vacuities large, exposing about equal lengths of the basisphenoid and presphenoid. Parapterygoid plates long and triangular, slightly recessed to form very shallow fossae; plates mostly bony with single opening (ventral aspect of foramen ovale) near their posterolateral corner.

Tympanic bullae small, with large posteromedial wedge of the petromastoid visible ventrally; passage of internal carotid artery marked by notch (carotid canal) just behind bony eustachian tubes; malleus of the parallel type, orbicular apophysis a distinct knob. Subsquamosal fenestra represented by a slight indentation to a moderate notch that defines a short hamular process of the squamosal; postglenoid foramen small, semicircular in form. Anterior flange of petromastoid (tegmen tympani) contacting and overlapping posteromedial edge of squamosal, thereby separating the postglenoid and middle lacerate foramina. Mastoid bullae small and bulbous, perforated by posterodorsal fontanelle.

Alisphenoid with dorsal segment extending above level of orbitosphenoid and forming a significant part of the rear wall of orbit. Masticatory-buccinator foramen separated from foramen ovale accessorius by alisphenoid strut (except in one species). Carotid circulatory pattern derived—stapedial and sphenofrontal foramina absent, squamosal-alisphenoid groove absent, and posterior opening of the alisphenoid canal occluded—supraorbital and infraorbital branches of the stapedial artery presumably lost.

Coronoid process of dentary falcate, arching dorsally to height of condylar process (fig. 3); sigmoid notch deep; angular notch broad and shallow; capsular projection of lower incisor variably expressed, indistinct to clearly defined.

Axial skeleton with 13 thoracic and 7 lumbar vertebrae; sacrum with 2 sacral and 2 pseudosacral vertebrae. First rib articulates only with first thoracic vertebra, not con-

tacting transverse process of seventh cervical. Neural spine of second thoracic vertebra conspicuously tall compared to neighboring thoracic spines. Entepicondylar foramen of humerus present.

#### DENTITION

Upper incisors asulcate and opisthodont, their enamel faces colored pale yellow to deep orange. Molars moderately hypsodont with planar occlusal surfaces and principal cusps undefined; molar crowns configured as three lamina oriented nearly transverse to the longitudinal axis of the tooth (fig. 4); individual lamina not connected by medial enamel connections (mures and murids) but uniting with wear at their labial and lingual edges. Upper and lower third molars two-thirds to subequal in size to second. Upper molars each anchored by three roots, lower molars by two.

#### ACCOUNTS OF SPECIES

Diagnostic traits of species within *Eliurus* involve variation around a discrete subset of characters or character complexes. Interspecific size differences, principally as reflected in the greatest dimensions of skin and skull, prove relatively constant, if subtle, in certain species comparisons. Other than size, the most useful diagnostic traits of the skin include the possession of a white or dark tail tuft, the relative pilosity of the tail, and degree of dorsal-ventral pelage contrast in color; fur texture and length of pelage are helpful when used in combination with other features.

Some specimens of dark-tufted species occasionally possess white hairs near the end of the tail, a condition which may be confused with a normal white pencil, as observed, for example, in *E. tanala*. In almost every such instance, however, the white hairs seem to have resulted from regenerative hair growth at the severed end of a tail injured in life. The tails of these specimens thus appear "bobbed" instead of gradually tapered, and their white terminal hairs issue as a dense whorl around the edge of the broken stump, instead of the graded elongation of hairs that occurs toward the tip of unbroken tails.

Major themes of craniodental differentiation, aside from size, concern the propor-

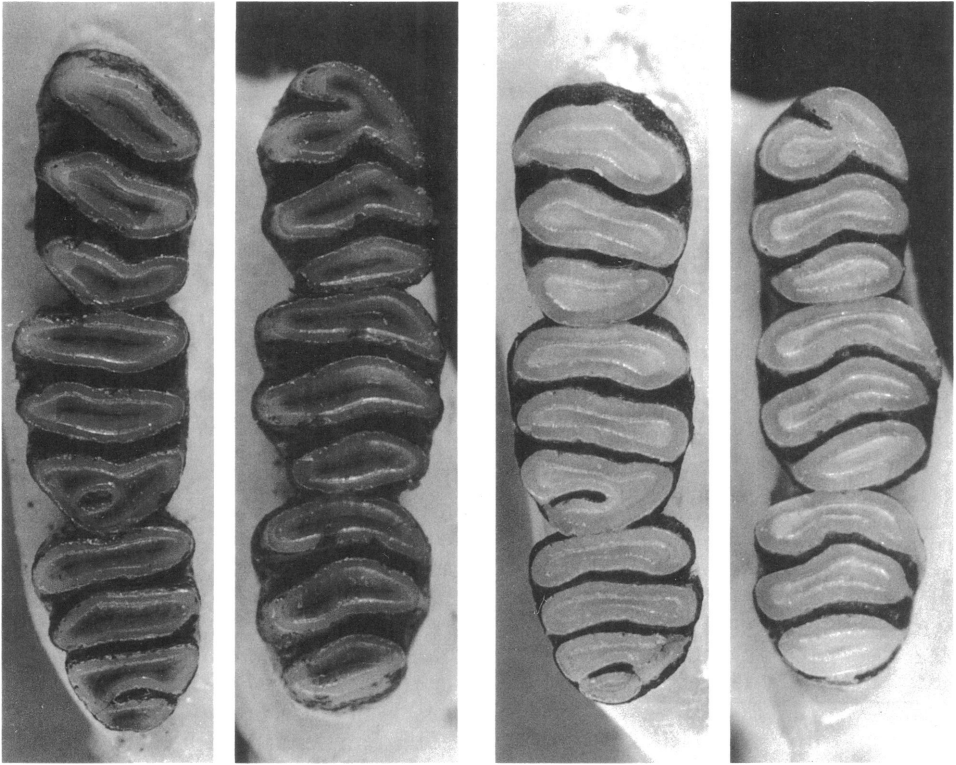


Fig. 4. Occlusal views ( $\times 15$ ) of the upper (left member in each pair) and lower (right member in each pair) right molars in representative species of *Eliurus*, illustrating their planar surface and trilaminar configuration. **Left pair**, *E. majori* (MCZ 45929, Ambohimitambo; LM1-3 = 6.26 mm); **right pair**, *E. webbi* (USNM 448994, 0.5 km N Kianjavato; LM1-3 = 5.43 mm).

tional development of the incisive foramina and the molar rows, as well as certain qualitative features—namely, the presence of supernumerary palatal foramina, the patency of the subsquamosal fenestra, and the conformation of the lower incisor alveolus. The small sample sizes and few localities available for most *Eliurus* species, however, compromise rigorous assessment of trait-frequency data and their utility in species discrimination.

The sexes of species of *Eliurus* apparently differ little in size and were not segregated for multivariate computations. One-way analyses of variance revealed inconsequential effects of sex on population variation in the largest population samples of *E. tanala* (OTU 11) and *E. webbi* (OTU 15) (table 1). Only one of 18 craniodental variables (LM1-3) in one sample (OTU 15) exhibited a significant F-value ( $P = 0.047$ ), a result which might be attributable to a Type I sampling error.

The general inadequacy of specimen samples also hinders meaningful treatment of geographic and age variation. The immatures of all species of *Eliurus* possess a distinctive juvenile pelt, light to medium gray and finer in texture than the adult pelage. The progress of the molt to the brown adult pelage is thus clearly marked. The occurrence of the postjuvenile molt seems to coincide with the eruption of the upper third molars and presumably the attainment of sexual maturity. Individuals in an intermediate stage of the postjuvenile molt typically exhibit fully erupted molar rows with little or no wear on the third molars.

Genus *Eliurus* Milne Edwards,  
1885

TYPE SPECIES: *Eliurus myoxinus* Milne Edwards, 1885, by monotypy.

CONTENTS: Six specific or subspecific forms

TABLE 1

## Results of One-Way Analyses of Variance

(For 18 cranial measurements of population samples of *Eliurus tanala* [OTU 11 = 10♂, 8♀] and *Eliurus webbi* [OTU 15 = 5♂, 13♀].)

| Variable | <i>E. tanala</i><br>F (sex) | <i>E. webbi</i><br>F (sex) |
|----------|-----------------------------|----------------------------|
| ONL      | 0.15                        | 1.02                       |
| ZB       | 1.60                        | 0.10                       |
| BBC      | 1.64                        | 0.02                       |
| IOB      | 2.66                        | 0.02                       |
| LR       | 0.02                        | 0.77                       |
| WR       | 2.27                        | 0.41                       |
| PPL      | 1.04                        | 0.01                       |
| LBP      | 0.21                        | 1.04                       |
| LIF      | 0.64                        | 0.16                       |
| LD       | 0.31                        | 0.55                       |
| LM1-3    | 0.30                        | 4.64*                      |
| WM1      | 1.06                        | 1.62                       |
| WIF      | 0.58                        | 0.02                       |
| BM1s     | 4.03                        | 0.16                       |
| PPB      | 0.25                        | 0.96                       |
| DAB      | 1.51                        | 0.01                       |
| WZP      | 0.01                        | 0.23                       |
| BOC      | 0.43                        | 0.41                       |

\* =  $P \leq .05$ .

of the genus have been described: *E. myoxinus* Milne Edwards, 1885; *E. major* Thomas, 1895; *E. minor* Major, 1896a; *E. tanala* Major 1896a; *E. penicillatus* Thomas, 1908; and *E. myoxinus webbi* Ellerman, 1949. The basis for regarding each as a valid species is discussed in the following species accounts, together with the description of two new forms.

*Eliurus myoxinus*  
Milne Edwards, 1885  
Figures 3, 6, 8B, 9B, 12

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

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

**HOLOTYPE:** MNHN 1886.1120; young adult female; mounted skin, skull, carcass in fluid with one fetus; collected by Alfred Grandidier, probably during his 1866 or 1869 voyage along the southwestern coast.

Milne Edwards did not designate a holotype for his new genus and species, a common omission for the period, or indicate the nature of the specimen upon which his descrip-

tion was based. The above specimen is that listed much later as the holotype by Rode (1945) in his catalog of MNHN rodent types and bears the museum's registration number (1886.1120), the number (330) corresponding to Rode's catalog enumeration, and a third digit (768) perhaps corresponding to a separate catalog for museum exhibits. In view of the 19th-century catalog date and the absence of any other *E. myoxinus* in the MNHN collected prior to the 1960s, I have no basis for doubting that this specimen is the one upon which Milne Edwards (1885) based his description, as previously concluded without explanatory comment by Rode (1945).

For its age and likely past use on exhibit, the full-mounted skin on pedestal remains in moderately good condition, with the pelage color slightly faded, the pinnae cracked but still attached, and the tail entire and fully furred; the DHFL, with phalanges slightly curled, measures 25.5 mm. The occipital region of the skull is damaged, but its condition is otherwise good with the teeth, bullae, and nasals intact. The type specimen is a young adult female, as indicated by the light tooth wear and the presence of a near-term fetus with the skinned carcass in fluid. The existence of the associated fluid-preserved material was mentioned by Rode (1945).

**TYPE LOCALITY:** Given only as "côte ouest de Madagascar" by Milne Edwards (1885). Rode (1945) indicated that the specific locality is "Forêts de Tsilambany," which Carleton and Schmidt (1990) equated with Grandidier's (1885) locale "Riv. Tsilambana" and placed it at approximately 65 km SSE Morondava, Toliara Province, 20°50'S, 44°00'E.

**EMENDED DIAGNOSIS:** A medium-size (ONL = 35–38 mm, DHFL = 25–28 mm) species of *Eliurus* differentiated by the relative shortness of its tail, generally 105 to 110 percent of head and body length, and by the possession of a conspicuous, long-haired pencil, which extends over the distal 60 to 70 percent of the tail length; dorsal coat a light sandy-brown color and fine-textured; rostrum strongly tapered with tips of nasals relatively attenuate; interorbit broad relative to zygomatic expanse; incisive foramina relatively narrow, their posterior ends only slightly more separated than the anterior ends.



**DISTRIBUTION:** Dry deciduous forest in southwestern Madagascar and xerophilous scrub in the south; from the latitude of the Tsiribihina River, south to the cape region, and east across the Mandrare River to the vicinity of Bevilany (fig. 5). The species is unknown above 245 m but few altitudes have been recorded.

Aside from the distinctive morphological features that mark *E. myoxinus*, its geographic and ecological distribution reduces the possibility of taxonomic confusion. The species, as presently documented in southwestern and southern Madagascar, is wholly allopatric to the several forms of the eastern forests (see figs. 10, 11). Its range may be expected to closely approach those of *E. minor* and *E. webbi* in southeastern Madagascar; nevertheless, even in this region the occurrence of strict ecological sympatry seems unlikely.

**DESCRIPTION:** Hairs of tail brush long (12–15 mm) and conspicuous over approximately 60–66 percent of tail length (fig. 12). Caudal hairs not arranged in distichous pattern, as remarked by Milne Edwards (1885), but distributed equally around circumference of tail in penicillate fashion. No terminal white tuft present, hairs monocolored plain brown to brownish-black. Scutellation apparent over basal third of tail length, fine basal hairs extend about two annuli in length.

Overall dorsal color a light or sandy brown, pelage texture soft and fine. Hairs of dorsum tricolored—basal portion long and plumbeous, middle band narrow and buffy, and terminal band short and pale brown. Terminal bands longer and darker on middorsum and interspersed with fine blackish guard hairs. Hairs on midrump 7 to 8 mm long. Underparts light gray to creamy gray from throat to groin. Ventral hairs bicolored with light gray bases and creamy to white tips. Whitish tips about equal in length to gray basal bands and impart a light appearance to the venter that contrasts sharply with the dorsum. Hindfoot relatively short and wide. Dorsal metatarsus and top of phalanges white, without dusky streak. Tops of forepaws whitish.

Skull stocky and squarish in appearance (figs. 6, 8B), as suggested by its relatively broad interorbit, parallel-sided zygomatic arches,

shorter rostrum, and elongate braincase. Rostrum, however, tapers abruptly to a comparatively delicate, attenuated tip. Posterodorsal borders of interorbit more square-edged than in other *Eliurus* but not forming a projecting ledge. Subsquamosal fenestra usually present but small, revealing the petrous portion of the periotic but little or none of the brain cavity; hamular process of squamosal stout. Tympanic bullae relatively most inflated in the genus (fig. 9B); hence, ventral exposed portion of periotic bone less expansive. Incisive foramina moderately long but narrow with acutely pointed anterior and posterior limits. Supernumerary posterior palatine foramina occasionally present but small. Mesopterygoid fossa extends slightly between the third molars, ending near the plane of their third lamina. Anterior face of upper incisors deep orange. Alveolus of lower incisor projects as slight bulge high on ramus, just below the anterior edge of sigmoid notch.

**COMPARISONS AND REMARKS:** The thickly haired, relatively short tail of *E. myoxinus*, combined with its generally lighter brown upperparts, immediately distinguishes this form from other *Eliurus*. Tail length in other species of *Eliurus* averages conspicuously longer than the head-and-body, typically on the order of 115 to 125 percent of HBL. In body size, *E. myoxinus* is smaller than any of the eastern species except *E. minor*, and its hind foot is relatively shorter and narrower as well (Appendix 2).

The skull of *E. myoxinus*, however, is comparatively robust, equaling in general size those of *E. majori* and *E. penicillatus* but differing from both species in the many proportional features detailed under their accounts. The relatively broad interorbit and short, strongly tapered rostrum of *E. myoxinus* contrast with the more elongate conformation of the crania of *E. tanala* and *E. webbi*, which are typically larger in most craniodental dimensions. The otic capsules of the species appear absolutely and relatively the largest in the genus, but the univariate measurement of the bullae (DAB) inadequately substantiates this visual impression.

The basis of Milne Edwards' (1885) report for the lengths of the head-and-body (155 mm) and tail (125 mm) of *E. myoxinus*, presumably measured on the type specimen, is

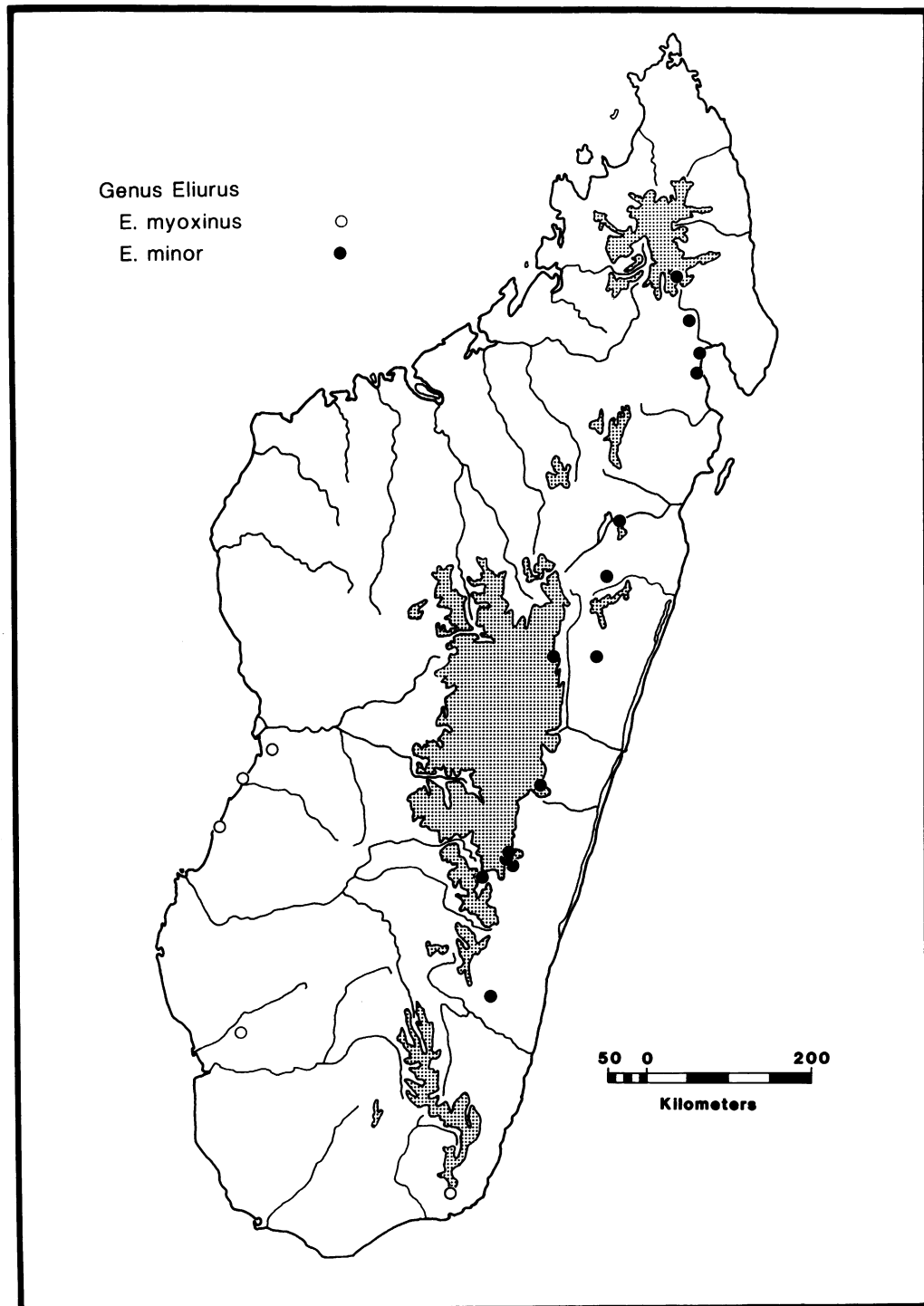


Fig. 5. Geographic occurrence of the species *Eliurus myoxinus* and *E. minor*. Shaded areas indicate highlands above 1000 m.

obscure. The caudal length of the specimen in MNHN is approximately the same as its head-and-body length, as can best be ascertained from a fully mounted figure, and no external data currently accompany the specimen. Milne Edwards' figures seemingly account for Ellerman's (1949) assertion that the tail of *myoxinus* is characteristically "shorter than head and body, which is an unusual character in the genus." Although the tail length of *E. myoxinus* is relatively the shortest in the genus, its caudal vertebrae do not average shorter than the length of head-and-body, nor do those of any other species of *Eliurus* known to date (Appendix 2).

Ellerman (1949) remarked on tail length variation among samples of typical *E. myoxinus* and implied that specimens from the region of Beroboka and Tulear possess relatively shorter tails, actually less than head-and-body length, compared to those from the vicinity of Bevilany in southeastern Madagascar. However, the tails of several individuals from the former area, including some tabulated by Ellerman, were clearly broken off or bobbed in natural life. Elimination of such specimens from statistical consideration reveals that proportional tail length in both samples is approximately the same and surpasses head-and-body length (Appendix 2).

The taxonomy and distribution of western *Eliurus* must be viewed as preliminary in light of the small samples and widely scattered localities available, a situation which typifies the scant museum-based documentation of Nesomyinae over vast areas of western Madagascar in general (see Carleton and Schmidt, 1990).

NOTES ON NATURAL HISTORY: All locality records associate this species with dry deciduous forest and xerophilous scrub formations in southwestern and southern Madagascar. Most museum specimens of *E. myoxinus* were obtained by C. S. Webb, whose interesting comments on skin tags and published recollections (1954) of his trapping experiences provide the best detail available on their habitat. Almost every specimen tag bears some indication that the animal was trapped on a tree branch. In light of these results, Webb concluded that "This *Eliurus* [= *myoxinus*] lives in holes in trees, no doubt owing to sandy nature of the floor of W. Coast forest [at Beroboka] and to the numerous snakes."

He further noted that *E. myoxinus* is "evidently plentiful in the S. W. [dry deciduous] forest but lacking or very scarce in the scrub forests." Their fundamentally arboreal nature clearly impressed Webb, for on another specimen tag, he observed: "they [western *Eliurus*] are more arboreal than those from the eastern forest and rarely descend to the ground."

Webb's perceptions in this regard must be given due attention, since he is one of the few biologists who has had firsthand experience with *Eliurus* of both western and eastern forests. In view of the abrupt transition between humid eastern and dry western plant communities in the southeast, the reserve at Andohahela may offer an ideal area to illuminate the key ecological requirements influencing the distribution of *E. myoxinus* and to contrast its habits with species of the eastern forest domain.

Specimens in juvenile pelage or in postjuvenile molt to adult pelage were collected during the months of July, August, and September. Three embryo counts—one, two, and three fetuses—are available for specimens sampled over the same period.

ETYMOLOGY: The species name recalls the family name of dormice, Myoxidae, a group characterized by a densely furred tail somewhat reminiscent of the strongly penicillate tail of this species.

SPECIMENS EXAMINED: 19 as follows: forêt d'Analabe, 60 km N Morondava (MNHN 1980.290, 1982.988); Beroboka, 40 mi N Morondava (BMNH 47.1608-9, 1987.50); 5 mi E Bevilany, Ambovombe-Fort Dauphin road, the hills, 800 ft (BMNH 47.1600-7, 66.2746); Morondava (MNHN 1973.516); Tsilambana (MNHN 1886.1120); 35 mi E Tulear (BMNH 47.1610-1, 47.1611a).

*Eliurus minor* Major, 1896a  
Figures 6, 8A, 9A, 12, 20B

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

HOLOTYPE: BMNH 97.9.1.153; young adult male; skin and skull; original number M494; collected 6 July 1895 by C. I. Forsyth Major.

TYPE LOCALITY: Given by Major (1896a) as "Ampitambé forest (N. E. Betsileo)." See



Fig. 6. Lateral view ( $\times 1.75$ ) of adult crania and mandibles of species of *Eliurus*: **top**, *E. myoxinus* (BMNH 47.1603, 5 mi E Bevilany; ONL = 36.7 mm); **bottom**, *E. minor* (USNM 448979, Ambohimontana; ONL = 29.3 mm).



Fig. 7. Lateral view ( $\times 1.75$ ) of adult crania and mandibles of species of *Eliurus*: **top**, *E. majori* (MCZ 45929, Ambohimantambo; ONL = 35.2 mm); **bottom**, *E. penicillatus* (USNM 49672, Ampitambe; ONL = 35.6 mm).

Carleton and Schmidt (1990) for the possible location of Ampitambe (= Ampitabe) as 45 km ESE Fandriana, ca. 900 m, Fianarantsoa Province, 20°22'S, 47°46'E.

**EMENDED DIAGNOSIS:** A species of *Eliurus* characterized by its small size (ONL = 29–31 mm, DHFL = 21–24 mm), generally bright brown hues of its dorsal fur, and a relatively well-developed, dark pencil that extends over the distal three-fifths to two-thirds of the tail length; skull relatively robust for its diminutive size and, as viewed in lateral profile, arch of cranial roof more pronounced.

**DISTRIBUTION:** Widely found in eastern rainforest from the eastern slopes of Tsara-

tanana and the vicinity of Antongil Bay south to the forested ridge west of Vondrozo (fig. 5); altitudinal occurrence broad, from sea level around Antongil Bay to 1800 m in mountains west of Andapa, near the western and upper limits of humid evergreen forest.

*Eliurus minor* ranges broadly in eastern Madagascar and has the greatest altitudinal limits thus far documented for a nesomyine rodent. Consistent with its broad geographic and altitudinal distribution, the species is known to co-occur with several other species of eastern *Eliurus*—including *E. penicillatus* (Ampitambe), *E. tanala* (Perinet and vicinity

of Ranomafana), and *E. webbi* (west of Maintimbato and west of Vondrozo)—and should be expected to occur with all others, except perhaps *E. myoxinus*. This distributional pattern influenced Ellerman (1949) to recognize only two species of *Eliurus* discriminated principally on size.

**DESCRIPTION:** Caudal pilosity well developed and covering distal 60 to 66 percent of tail length, densest over distal one-half (fig. 12). Scutellation moderately defined, evident over basal one-third of tail. Caudal hairs dark brown to blackish, generally monocolored throughout, and about 7–9 mm long near the terminal tuft. Ventral epidermis of basal tail segment marked with irregular light blotches in some individuals. Scale hairs near tail base extend over 1.5 to 2 caudal annuli in length.

Cover hairs of dorsal pelage basically tricolored, basal two-thirds plumbeous gray, with a bright buffy to ochraceous middle band and a short dark tip; fur 9 to 11 mm long on midrump. Overall tone of dorsum much brighter than venter, ranging from a light grayish brown to a rich cinnamon brown. A concentration of distinctly ochraceous-orange hairs accents the flanks and cheeks of some specimens. Guard hairs fairly numerous and black. Top of metatarsus generally dusky, wholly white in some individuals; dorsal surface of phalanges usually white. Pinnae relatively small, clothed externally and internally with fine blackish hairs.

Cover hairs of venter bicolored, basal two-thirds slate gray and distal portion light buff to dull white. General effect of underparts a dark gray with a buffy overwash or highlights; venter conspicuously demarcated from the brighter brown upperparts.

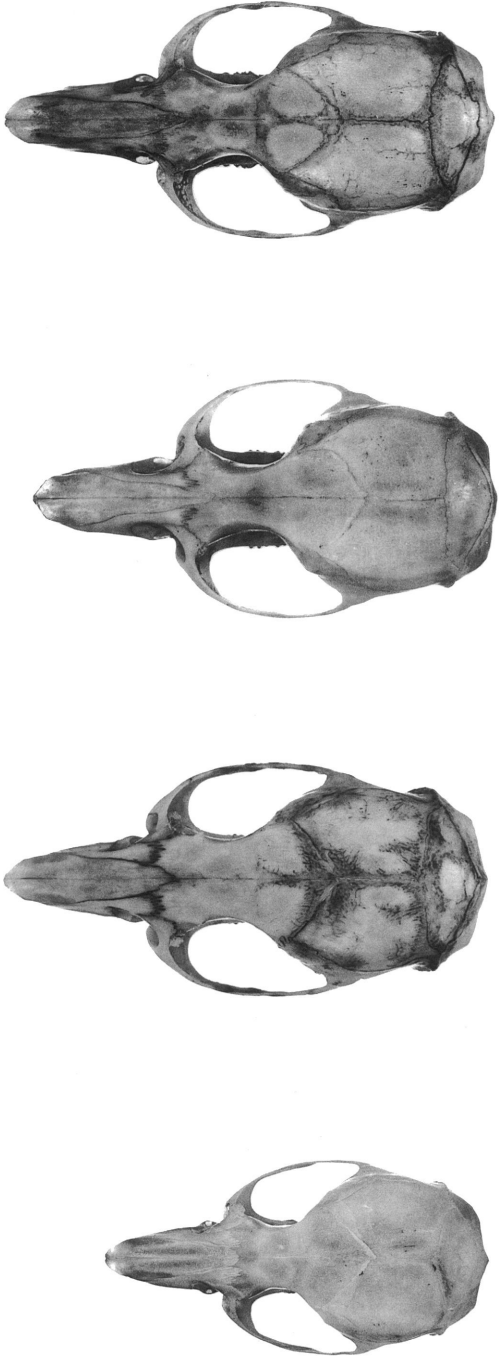
Despite small size, skull relatively stoutly constructed (figs. 8A, 9A). Dorsal profile of cranium conspicuously arched, sloping gradually toward the rostrum and sharply to the occiput from the point of strongest flexion above the postglenoid foramen (fig. 6). Incisive foramina extending little beyond anterior edge of zygomatic plates; foramina lunate in shape, their posterior ends more noticeably separated by the bridge of the maxillary bones. Tiny to moderate-size supernumerary palatal foramina usually present behind posterior palatine pair. Anterior margin of mesopterygoid fossa coaligned with

posterior ends of upper third molars. Subsquamosal fenestra typically present as a semicircular notch, defining a short hamular process but not generally exposing the brain cavity. Lower incisor alveolus extends to the level of the sigmoid notch and forms a moderately developed capsular projection with a weak sulcus (fig. 20B). Incisors relatively stout, their enameled surface dull orange.

**COMPARISONS AND REMARKS:** This species is immediately recognizable on the basis of its small bodily and cranial dimensions, the smallest recorded for the genus (Appendix 2). Nonetheless, the tail pencil in specimens of *E. minor* is well developed, being conspicuous over half of the tail length and surpassed only by that of *E. myoxinus* in its relative extent. Aside from its small size, the skull of *E. minor* is generally unremarkable in its features and proportions as compared to its larger congeners. One notable exception involves *E. minor*'s strongly flexed cranial vault, which contrasts with the flatter or gently curved profile in other species of *Eliurus*.

Further biological survey will likely disclose that the taxonomy of small-bodied *Eliurus*, here recognized as the one species *E. minor*, is more complicated. In particular, specimens from the lowlands around Antongil Bay (vicinity of Maroantsetra and west of Maintimbata) are notable for their slightly larger size and more russet-colored fur. However, the few specimens, some with incomplete skulls and known only by one per locality, prohibit definitive clarification of their biological status in relation to populations found at higher elevations. The type locality, Ampitambe, of Major's *minor* is thought to be situated around 900 m (Carleton and Schmidt, 1990), a place set within a highland zone that encompasses most known examples of the species.

**NOTES ON NATURAL HISTORY:** The fragmentary comments on the habitats of *E. minor* suggest a broader ecological tolerance than those of other *Eliurus*, although the fundamental association of the species with rainforest biotopes is clear. The wide altitudinal belt, sea level to 1800 m, documented for *E. minor* includes lowland and montane rainforest of various types. In primary lowland rainforest near Antongil Bay, Stephenson (1987) noted the usual occurrence of *E. mi-*



A B C D

Fig. 8. Dorsal view ( $\times 1.75$ ) of adult crania of same specimens and species of *Etilurus* shown in figures 6 and 7: A, *E. minor*; B, *E. myoxinus*; C, *E. majori*; and D, *E. penicillatus*.

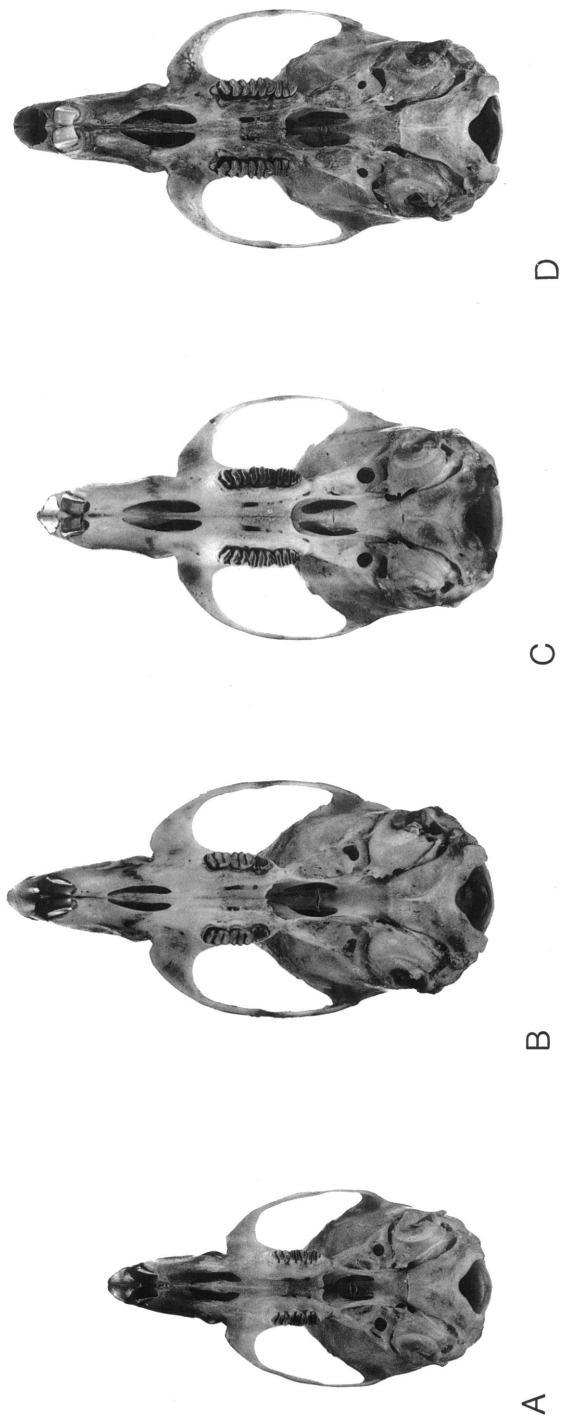


Fig. 9. Ventral view ( $\times 1.75$ ) of adult crania of same specimens and species of *Eliurus* shown in figures 6, 7, and 8: A, *E. minor*; B, *E. myoximus*; C, *E. majori*; and D, *E. penicillatus*.

*nor*, together with *E. webbi*, in areas with abundant lianas and a sparse understory. In middle elevation, lower-canopied rainforest around Perinet (= Andasibe), an area disturbed by ongoing logging, specimens were collected in denser herbaceous cover found along small streams and among fallen logs and boulders. Individuals of *E. minor* have also been obtained in a mixture of dense brush and bamboo bordering a stream (E Andraina) and in lush grass extending 1.5 m tall (N Didy). Placement of traps that caught *E. minor* include sites on the ground, on low tree branches, and on fallen trees of small trunk diameter.

Indication of reproductive habits is limited: a male with scrotal testes is recorded for May; a specimen in juvenile pelage for July; a embryo count of two for August; and a lactating female for August.

ETYMOLOGY: Name acknowledges the diminutive size of the species.

SPECIMENS EXAMINED: 50 as follows: Ambodiamontana, 7 km (by road) W Ranomafana, 950 m (USNM 448974-80, 448998, 449248-9); Ampitambe (BMNH 97.9.1.153; FMNH 5629); 1 day W Andapa (MNHN 1932.3513); 14 km E Andraina (USNM 328826); 9 km N Didy, Ambohijanahary (USNM 328827); Fianarantsoa, south of (MCZ 45936); Hiaraka, near Maroantsetra (MNHN 1981.870); 16 km E Imerimandroso, Lac Alaotra, 3500 ft (BMNH 47.1618-22); Mandraka, 45 mi E Tananarive, 4000 ft (BMNH 47.1613); 20 km SW Maroantsetra (AMNH 100719; BMNH 35.1.8.350); 40 km SW Maroantsetra, 10 km WSW Maintimbato (BMNH 1987.107); Perinet, near Moramanga, 3000 ft (AMNH 119712; BMNH 47.1615-7); Tamatave Road 68 (USNM 294535); 3 km (by road) NNW Vohiparara, 1225 m (USNM 449246-7); 20 km W Vondrozo (AMNH 100720-4; BMNH 35.1.8.343-9; MNHN 1932.3511-2, 1932.3514-6).

*Eliurus majori* Thomas, 1895

Figures 2, 4, 7, 8C, 9C

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

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

HOLOTYPE: BMNH 97.9.1.147; adult male;

skin, skull, and partial skeleton; original number M166; collected 24 January 1895 by C. I. Forsyth Major.

Thomas (1895) mentioned no number identifying the specimen on which his new species description was based. Major (1896a), in his recognition of *E. tanala*, incidentally supplied the field number (M166) of Thomas' type, which concurs with the original skin tag on the specimen in the BMNH, as do the particulars of the other field data and cranial measurements provided by Thomas (1895).

TYPE LOCALITY: Given by Thomas (1895) as "Ambolimitambo Forest, Central Madagascar. Alt. 4500 feet," the village name a misreading of Major's cursive script for Ambohimitambo (about 1200 m, Fianarantsoa Province, 20°43'S, 47°23'E).

Since Major did not generally record collecting elevations on his field tags, Thomas may have extracted the altitude from written information received with the first material Major shipped to BMNH from Madagascar. Regardless of Thomas' source, the figure of 4500 ft is consistent with Major's (1896b) later placement of Ambohimitambo at 1400 to 1500 m. The 1200-m figure is MacPhee's (1987) determination based on study of recent topographic maps.

EMENDED DIAGNOSIS: A medium-size (ONL = 35–37 mm, DHFL = 27–29 mm) species of *Eliurus* distinguished by a somber, dark-gray pelage that lacks marked contrast in dorsal-ventral coloration; tail brush relatively small, noticeable over terminal one-third of its length, dark completely to tip; toothrows comparatively robust, longest in the genus (LM1-3  $\geq$  6.1 mm); incisive foramina relatively wide and long.

DISTRIBUTION: Known only from widely separated localities in the northern (Montagne d'Ambre), central (Ambohimitambo), and southern highlands (Anjavidilava, Andringitra) (fig. 10); elevational records from 1000 and ca. 1200 m.

No other species of *Eliurus* is yet known to co-occur with *E. majori*, although sympatry with *E. minor* may be anticipated in view of the latter's wide elevational distribution. On Mt. d'Ambre, the two examples of *E. majori* were collected near the summit at 1000 m, but the elevation of collection of the series of *E. webbi*, taken at a later date,



at d'Ambre is unknown. Elsewhere in Madagascar, this species inhabits rainforest at low to middle elevations.

**DESCRIPTION:** Tail pencil appears relatively less developed, lacking the conspicuous distal expansion into a terminal tuft, an effect due to the more gradual increase in length and density of hairs toward the tip, where they measure 8 to 10 mm long. Tail dark all round to tip, epidermis blackish, hairs dark brown to black, pilosity principally evident over the distal third of the tail length. Scutellation near the base of tail finely textured.

General effect of dorsum a somber blackish gray, fur soft and thick, somewhat wooly in appearance, 10 to 12 mm long on rump. Basal two-thirds of dorsal cover hairs slate gray, followed by a short buffy band, and a dark terminal band; guard hairs relatively dense and long. Underparts predominantly dark gray, basal two-thirds of cover hairs dark gray and distal one-third dull white. Dorsal-ventral contrast inconspicuous, lacking sharp lateral line of demarcation. Top of metatarsus dark-furred, phalanges whitish. Pinnae very dark and relatively small. Dark eye-ring apparent in all of the few known specimens, extending between the eyes as a mask in one (MCZ 45929).

Molar rows robust, both relatively and absolutely the widest and longest in the genus (figs. 4, 9C). Height of molar crowns also appears greater than in other *Eliurus*. Upper third molars subequal in size to second molars. Face of upper incisors pigmented orange.

Cranium medium-size with relatively short rostrum and elongate braincase (figs. 7, 8C, 9C). Zygomatic arches strongly bowed laterally, in some individuals appearing broader across their anterior aspect. Incisive foramina wide and long, terminating anterior to M1s but appreciably beyond level of leading edge of zygomatic plates. Posterior palatine foramina generally a single pair, round to slightly oval in shape, usually lacking supernumerary palatal perforations. Anterior margin of the mesopterygoid fossa penetrates between M3s, to the level of the middle or front lamina of the tooth. The convergence of the long incisive foramina and mesopterygoid fossa imparts a more truncated appearance to the bony palate. Subsquamosal fenestra

always well defined, usually as an ovoid notch, exposing petrous portion of periotic and interior of braincase. Mandible stocky in form, deep and squared off in back, anterior edge of ascending ramus set more perpendicular to molar occlusal plane. Coronoid process rises above condyloid process, together enclosing a deep sigmoid notch. Lower incisor alveolus terminates below the anterior edge of the sigmoid notch, forming a slight bulge but not a raised capsular projection with medial sulcus.

**COMPARISONS AND REMARKS:** *Eliurus majori*, together with the morphologically similar species *E. penicillatus* (see following account), is a highly differentiated form within the genus. The dull coat color, lack of pronounced dorsal-ventral chromatic contrast, and weakly developed tail pencil separate the species on external features from its congeners. The general impression of its dorsal color superficially recalls that of *Gymnuromys roberti* or an immature *Rattus rattus*.

The cranial and dental proportions exhibited by *E. majori* (and *E. penicillatus*) even more convincingly underscore its uniqueness and collectively serve to identify the species with confidence. Although smaller in size compared to *E. webbi* or *E. tanala*, for example, the molars of *E. majori* are higher-crowned, wider, and longer (mean about 17% of occipitonasal length as compared to 14% in most other species). The upper third molars are relatively long, subequal to the M2s instead of one-half to two-thirds their size as observed in other species. The long, wide incisive foramina and short palate are also distinctive compared to the short incisive foramina and comparatively long palates of other *Eliurus*. The mesopterygoid fossa in specimens of *E. majori* extends farther forward to reach the plane of the middle or front lamina of M3, rather than the level of the third lamina (*minor* and *myoxinus*) or even with the posterior border of the tooth (*tanala* and *webbi*). The deep ascending ramus of the dentary in *E. majori* contrasts with the more elongate, low-slung mandibular conformation that characterizes other species.

The meager samples available for *E. majori* disallow assessment of variation either within or between localities. Aside from age-related size differences, the five known spec-

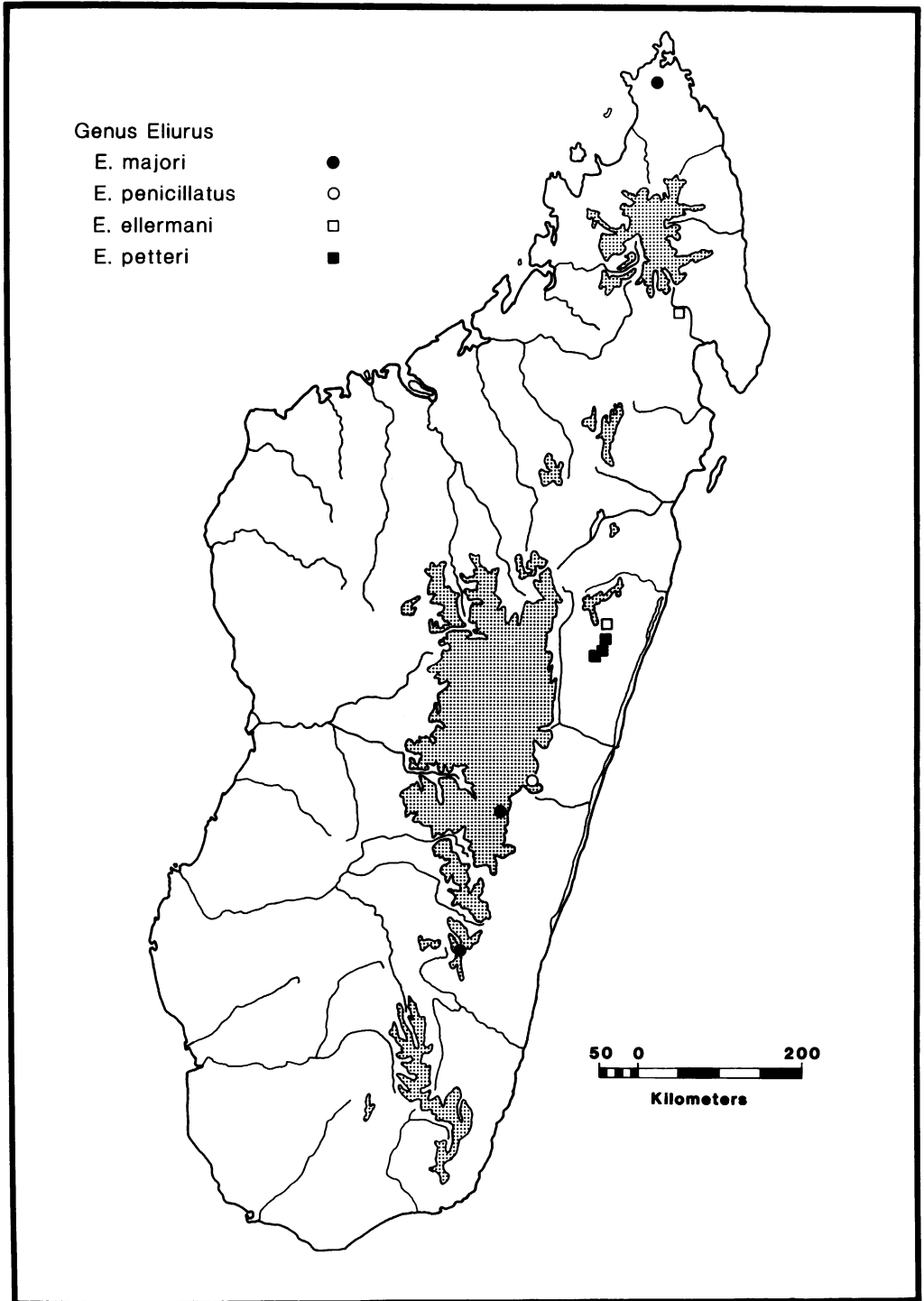


Fig. 10. Geographic occurrence of the species *Eliurus majori*, *E. penicillatus*, *E. petteri*, and *E. ellermani*. Shaded areas indicate highlands above 1000 m.

imens, representing three widely separated geographic regions, conform closely in morphology.

In his description of *E. tanala*, Major (1896a) compared his new species to Thomas' (1895) *E. majori*. Two of the specimens Major so identified by field number are actually examples of *E. penicillatus* (M430 = BMNH 1939.892 and M536 = MNHN 1909.191) that Thomas (1908) subsequently recognized as a distinct species. Although Thomas (1895) stated that he had only one specimen at hand for the description of *E. majori*, Major (1896a) subsequently listed two field numbers belonging to this species, the type and M159, the latter (MCZ 45929) acquired by Harvard University as part of the Grandidier collection. To date, this is the only other specimen of *E. majori* known to have been collected by Major at Ambohimitambo.

NOTES ON NATURAL HISTORY: Rand (1936: 192) characterized the forest on the summit of Montagne d'Ambre as a "damp, green, rainforest type containing many lianas and mosses." and where "In places . . . much herbaceous ground-cover occurred, though in other areas the forest floor was rather open." The specific character of the vegetation at Ambohimitambo or Anjavidilava where the other *E. majori* originated is unknown, but these localities are situated at nearly the same highland elevation or above. Nothing is known about the breeding biology of the species.

ETYMOLOGY: Described in recognition of the collector, C. I. Forsyth Major, based presumably on the first shipment of specimens received in BMNH prior to Major's own departure from Madagascar.

SPECIMENS EXAMINED: 5 as follows: Ambohimitambo (BMNH 97.9.1.147; MCZ 45929); Andringitra, Anjavidilava (MNHN 1972.602); Montagne d'Ambre, 1000 m (AMNH 100687, 100854).

*Eliurus penicillatus* Thomas, 1908  
Figures 7, 8D, 9D, 20A

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

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

HOLOTYPE: BMNH 97.9.1.149; adult fe-

male; skin and skull; original number M602; collected 20 July 1895 by C. I. Forsyth Major.

TYPE LOCALITY: Given by Thomas (1908) as "Ampitambe, N. E. Betsileo, Madagascar." See Carleton and Schmidt (1990) for the possible location of Ampitambe (= Ampitabe) as 45 km ESE Fandriana, ca. 900 m, Fianarantsoa Province, 20°22'S/47°46'E.

EMENDED DIAGNOSIS: Size, pelage coloration, and cranial proportions essentially as in *E. majori*, except tail tipped with white pencil and toothrow shorter (usually  $\leq 6.2$  mm).

DISTRIBUTION: Known only from the type locality where examples of *E. minor* were also obtained (fig. 10).

COMPARISONS AND REMARKS: The distinguishing features of *E. penicillatus* only require elaboration with respect to *E. majori*, which it otherwise recalls in pelage color and texture and in craniodental size and proportions (see figs. 7, 8D, 9D). The cardinal distinction between them rests with the white-tipped tail, which typically covers the terminal third of its length in specimens of *E. penicillatus*. The white marking involves the coloration of both the caudal hairs and the epidermis and contrasts with the dark hairs and epidermis of the proximal tail segment. The dorsum of *E. penicillatus* also appears more brownish gray compared to the slate gray of *E. majori*, but the reliability of such a subtle contrast in hue is difficult to assess on the basis of so few specimens of each form. Compared to *E. majori*, examples of *E. penicillatus* average smaller in most craniodental dimensions, particularly the size of the molars and incisive foramina, but their univariate ranges do overlap (Appendix 2). Again, the limited samples available disallow meaningful evaluation of the consistency of their apparent disparity in size, but the mean differences approach in degree that seen between other morphologically similar forms of *Eliurus* whose stature as species can be convincingly documented.

Among the eight species of *Eliurus* recognized herein, I regard the evidence for the formal separation of *penicillatus* from *majori* as the weakest. My decision to do so hinges partly on analogy to the situation concerning *E. tanala* and *E. webbi*, a pair of species which differ in the incidence of white-tail tipping, a chromatic distinction which further corre-

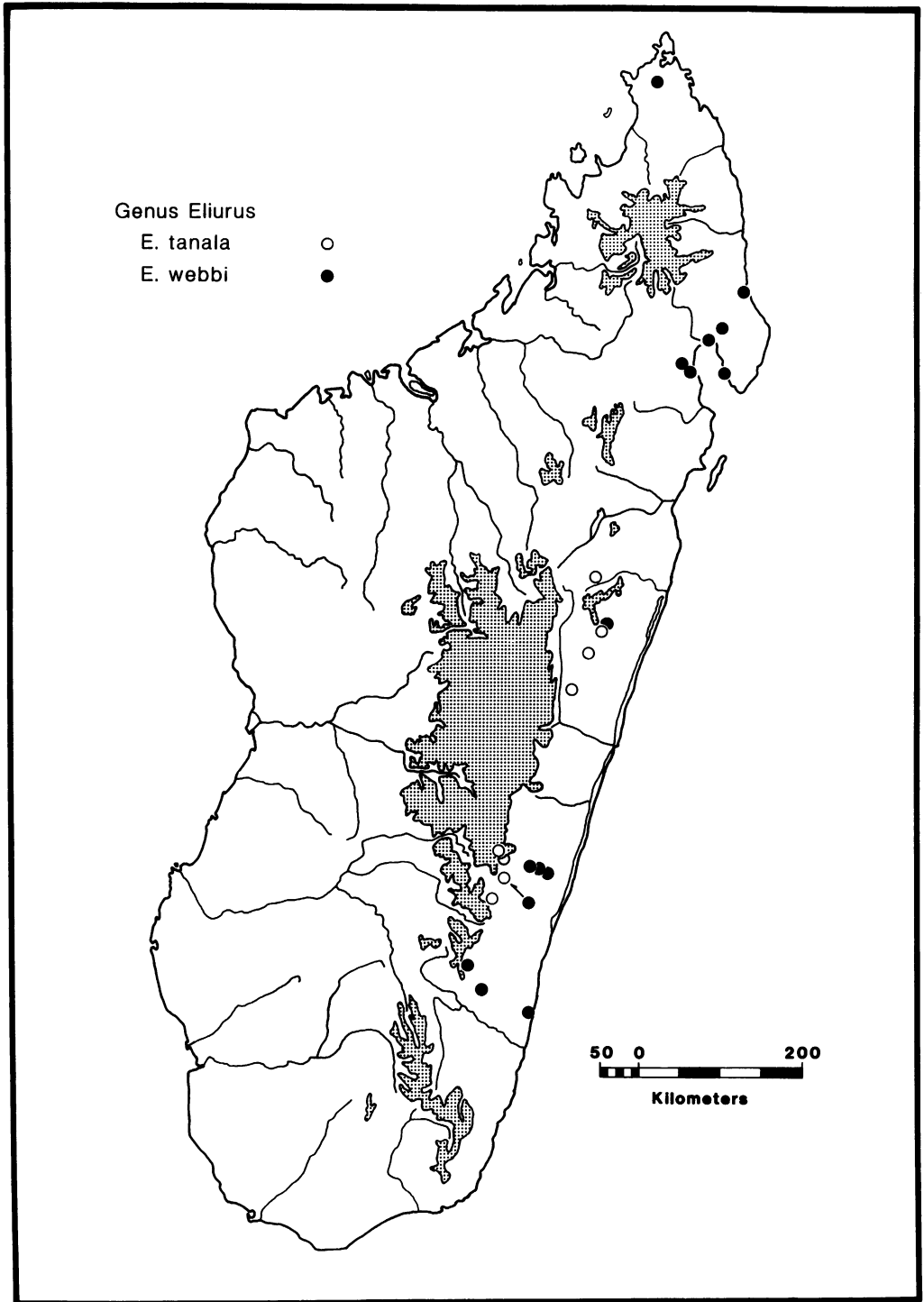


Fig. 11. Geographic occurrence of the species *Eliurus tanala* and *E. webbi*. Shaded areas indicate highlands above 1000 m.

lates with subtle but consistent craniodental contrasts of the two taxa. The possession of a terminal white segment on the tail presumably holds an important infraspecific communicative function, as demonstrated for the social behavior of other rodent species with contradistinctive tail tufts (for example, Eisenberg, 1967). In the case of *E. tanala* and *E. webbi*, however, the persistence of such differences can be demonstrated within and among larger sample sizes covering a broader geographic range, which evidence encourages their arrangement as separate biological species. Critical resolution of the level of relationship of *majori* and *penicillatus* must await the acquisition of better samples to assess variation and recourse to other kinds of taxonomic information, such as karyotypic and molecular data.

**NOTES ON NATURAL HISTORY:** Ecological and reproductive information are lacking for *E. penicillatus*. Major's field tags and expedition account (1896a) simply disclose that he collected in forest near Ampitambe. The presumed elevation of Ampitambe around 900 m would place the site within the zone of wet montane rainforest.

**ETYMOLOGY:** Epithet characterizes the relatively long and fine caudal hairs, which over the distal tail segment in this species are highlighted by their white color.

**SPECIMENS EXAMINED:** 17 as follows: Ampitambe (AMNH 31801; BMNH 97.9.1.148-50, 97.9.1.152, 1939.1892; FMNH 5630, 18822; LMCM A19.4.98.26; MCZ 12435, 45932; MNHN 1897.536, 1909.191; USNM 49672; UZMC 1219, 1224, 7941).

*Eliurus tanala* Major, 1896a

Figures 12, 13, 15C, 16C, 18, 19, 20C

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

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

**HOLOTYPE:** BMNH 97.9.1.154; adult female; skin and skull; original number M1358; collected 27 May 1896 by C. I. Forsyth Major.

**TYPE LOCALITY:** Given by Major (1896a) as "Forest of the Independent Tanala of Ikongo, neighbourhood of Vinanitelo, thirty

miles south of Fianarantsoa" (ca. 1300 m, Fianarantsoa Province, 21°43'S/47°16'E).

**EMENDED DIAGNOSIS:** A large species (ONL = 38–43 mm, DHFL = 30–36 mm) of *Eliurus* distinguished by a white terminal tuft on its tail; penicillate portion relatively short, confined to terminal one-third of tail length, and coarse scutellation exposed over proximal two-thirds; molars appearing relatively small for robustness of skull; subsquamosal fenestra little expressed, only posterior end of hamular process defined, if at all; supernumerary palatal foramina usually present behind posterior palatine pair.

**DISTRIBUTION:** Middle to upper elevation rainforest, from southeast of Lake Alaotra southward to Vinanitelo (fig. 11); recorded elevations range between 455 and 1300 m.

The species has been collected in sympatry with *E. minor* (Perinet and vicinity of Ranomafana) and *E. webbi* (NW of Andrambovato, 875 m). *Eliurus tanala* and *E. webbi* have also been recorded from closely approximate localities in the vicinity of Ranomafana and Lohariandava; in each such area, samples of *E. tanala* are associated with the localities of higher elevation.

**DESCRIPTION:** Penicillate portion of tail appears thin and limited to distal one-third of caudal vertebrae, the terminal section of which is tipped with bright white hairs 11 to 13 mm long (fig. 12). The white coloration includes the corresponding segment of the caudal epidermis. Terminal white portion of tuft approximately ranges from 30 to 60 mm in length, or an average 25 percent of tail length. Scutellation coarse and grossly apparent over proximal two-thirds to three-quarters of the tail. Basal tail segment appears naked to unaided eye, but covered with short scale hairs equal to or less than length of one annulation. Proximal section of caudal epidermis evenly dark all around or with irregular mottling on venter.

Cover hairs of dorsum bicolored or tricolored—basal three-quarters plumbeous gray and the distal one-quarter pale buffy, or sometimes tipped with a short black band. Guard hairs numerous, especially toward the middorsum and on rump, and notably longer than cover fur, which is 10 to 12 mm long on midrump. Overall appearance a dark grayish brown to brownish drab, the sides

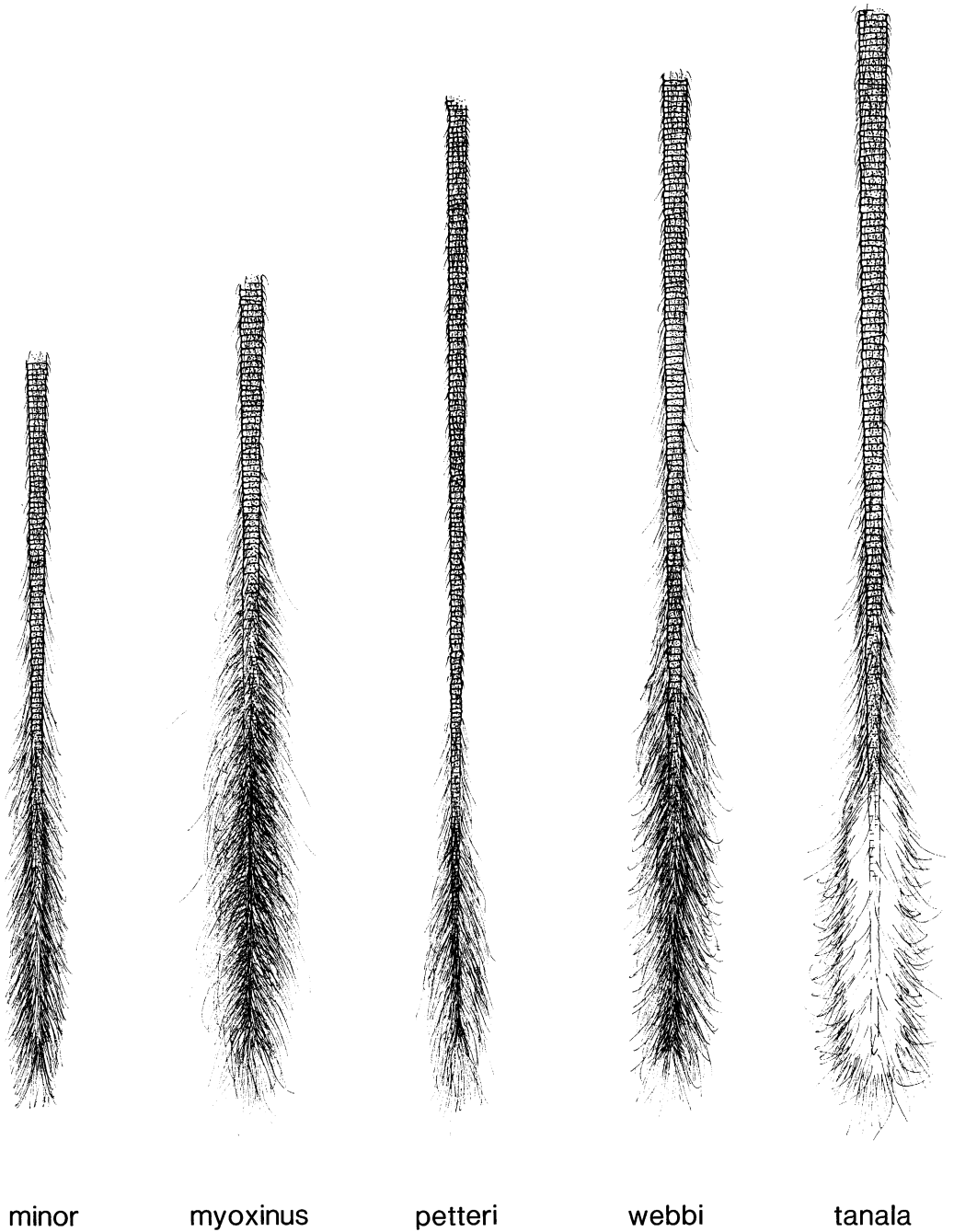


Fig. 12. Development of caudal pilosity in five species of *Eliurus*: *E. minor*; *E. myoxinus*; *E. petteri*; *E. webbi*; and *E. tanala*. Full lengths of caudal vertebrae are portrayed to same scale.



Fig. 13. Lateral view ( $\times 1.75$ ) of adult crania and mandibles of species of *Eliurus*: **top**, *E. tanala* (USNM 448983, Ambodiamontana; ONL = 42.1 mm); **bottom**, *E. webbi* (USNM 448993, 0.5 km N Kianjavato; ONL = 40.5 mm).

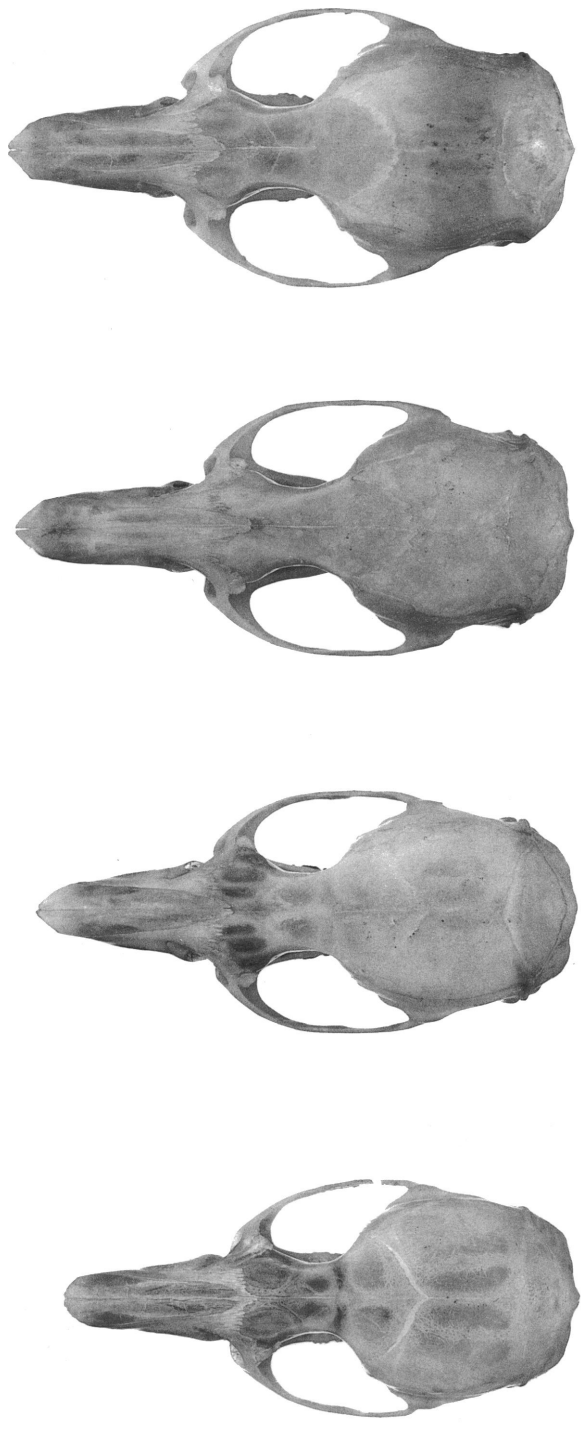
lighter in tone. In some individuals the center of the back is a noticeably darker gray, suggesting an indistinct, broad dorsal band. Hairs of ventral coat bicolored, their proximal half pale gray and distal half dull white. General ventral impression a light or buffy gray; some specimens with variably sized patches of hairs entirely white to base, imparting a creamy gray to nearly white appearance. Dorsum of metapodials and phalanges clothed with dull white hairs. Pinnae appear naked macro-



Fig. 14. Lateral view ( $\times 1.75$ ) of adult crania and mandibles of species of *Eliurus*: **top**, *E. petteri* (holotype, MNHN 1961.177, 8 km from Fanovana; ONL = 38.4 mm); **bottom**, *E. ellermani* (holotype, MNHN 1981.871, Hiaraka; ONL = 43.8 mm).

scopically but sparsely furred inside and outside with fine brown hairs.

Skull large for the genus, with the incisors, zygoma, rostrum, and mandible accordingly more heavily proportioned (figs. 13, 15C, 16C). Zygomatic arches gently bowed laterad in most specimens, nearly parallel-sided in some. Incisive foramina lunate, their anterior and posterior ends acutely pointed, and the posterior ends little divergent. Principal pair of posterior palatal foramina elongate and narrowly ovate to slitlike, not round-oval;



A B C D

Fig. 15. Dorsal view ( $\times 1.75$ ) of adult crania of same specimens and species of *Eliurus* shown in figures 13 and 14: **A**, *E. petteri*; **B**, *E. webbi*; **C**, *E. tanala*; and **D**, *E. ellermani*.





Fig. 16. Ventral view ( $\times 1.75$ ) of adult crania of same specimens and species of *Elurus* shown in figures 13, 14, and 15: A, *E. petteri*; B, *E. webbi*; C, *E. tanala*; and D, *E. ellermani*.

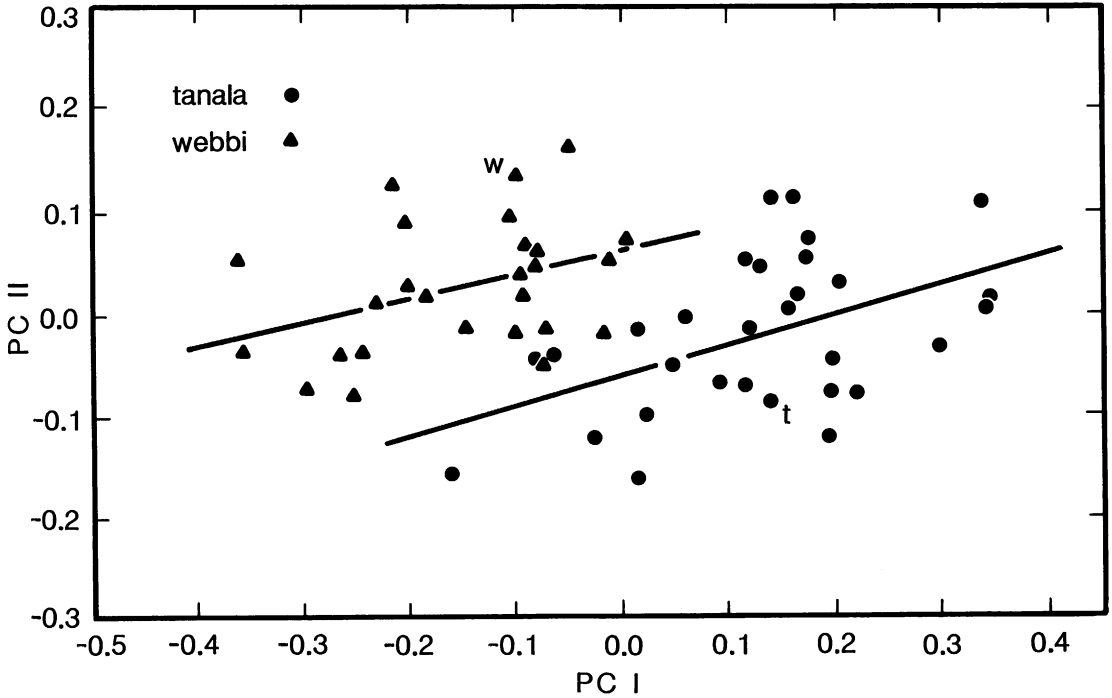


Fig. 17. Projection of individual specimen scores, based on the 18 log-transformed craniodental variables, onto the first two principal components extracted for selected OTUs of *Eliurus tanala* (OTUs 10, 11, 12; N = 30) and *E. webbi* (OTUs 15, 17; N = 26); see table 2. t corresponds to the holotype (BMNH 97.9.1.154) of *E. tanala* and w to that (BMNH 47.1576) of *E. webbi*. Regression lines of PC II on PC I differ significantly between species in their Y-intercepts ( $P < .001$ ) but not their slopes ( $P = .649$ ).

typically one pair of large supernumerary openings set behind posterior palatal foramina, these sometimes coalesced to form long palatal vacuities (fig. 16). Constriction of palate posterior to third molars relatively pronounced. Anterior border of mesopterygoid fossa set approximately even with the end of the third molars. Subsquamosal fenestra absent, or indistinctly defined as a shallow indentation above the mastoid bullae; in the latter condition, only the lateral surface of the periotic is exposed and a short, broad hamular process is incised. In adult specimens, lower incisor alveolus terminates as a pronounced capsular projection with a medial sulcus; the knobby projection ends beyond the base of the coronoid process and sets high on the ascending ramus, just below the ventral rim of the sigmoid notch (fig. 20C).

COMPARISONS AND REMARKS: The combination of large physical size and a tail bearing a white, gossamer tip serves to distinguish

specimens of *Eliurus tanala* from those of other *Eliurus*. In cranial robustness, *E. tanala* is only surpassed by the new species described below, which lacks a white-tipped tail. In craniodental proportions, *E. tanala* departs from *E. majori* and *E. penicillatus* in the same manner as do other species of *Eliurus*. Extended comparisons need only be reserved for the discrimination of *E. tanala* and *E. webbi* because the two are numerous in collections, are morphologically quite similar, and are broadly distributed in eastern forests where they may occur sympatrically.

The possession of a white tail tuft provides definitive separation of *E. tanala* and *E. webbi* (fig. 12). Curiously, Major (1896a) neglected to mention this characteristic in his diagnosis of *E. tanala*, but Ellerman (1949) emphasized the different terminal caudal colors in naming and comparing *E. myoxinus webbi*. The holotype of *E. tanala* (BMNH 97.9.1.154) clearly possesses a terminal white

section, at least 25 mm long (the fine tip seems to be missing), as does the other round skin (FMNH 5631) traceable to Major's type locality of Vinanitelo. In the larger series of *E. tanala* collected around Perinet and Ranomafana, the constancy of this chromatic distinction is underscored by its uniform presence on all specimens with the distal caudal vertebrae intact.

Aside from their obvious disparity in external dimensions (see Appendix 2), examination of series of *E. tanala* and *E. webbi*, side by side, discloses additional subtle differences in pelage color and tone. Although the dorsal ground color in both species is some shade of brown, examples of *tanala* typically exhibit a darker grayish cast, whereas those of *webbi* are browner and lighter in tone. The lighter pelage tone of *webbi* may result from the greater length of the subterminal buffy band in its dorsal cover hairs. The fur of *tanala* is slightly coarser in texture than that observed in *webbi*, with the guard hairs more densely distributed and distinctly black in color instead of brownish-black. The venter in specimens of *tanala* tends toward a light gray effect in contrast to the grizzled, drab gray seen in most *webbi*. Compared to *webbi*, the pinnae in *tanala* appear relatively shorter, and the scales near the base of its tail are larger. In addition, the finer scute hairs in samples of *tanala* are shorter, seldom overlapping more than one contiguous ring of scales. The tail pilosity of specimens of *tanala* thus appears generally less dense, a contrast perhaps heightened by the dark-haired terminal tuft of *webbi*. The contrasts related for each of these traits are best appreciated when comparing series of the two species; however, critical identification of single specimens should principally rely upon color of the tail tuft and cranial morphology.

The crania of specimens of *E. tanala* average slightly larger than those of *E. webbi* in most variables recorded (Appendix 2). Despite their fundamental cranial similarity and overlap in univariate ranges, separation of the two species in multivariate space is generally unambiguous. Dual clouds of points that correspond to specimens with (*tanala*) and without (*webbi*) white-tipped tails are consistently derived from principal component analyses of log-transformed cranioden-

TABLE 2  
Results of Principal Component Analysis and One-Way ANOVAs

(Performed on 18 cranial measurements of intact specimens of *Eliurus tanala* [N = 30] and *Eliurus webbi* [N = 26]; see text and fig. 17.)

| Variable   | PC I  | PC II | F (species) |
|------------|-------|-------|-------------|
| ONL        | 0.91  | 0.21  | 31.1        |
| ZB         | 0.88  | 0.00  | 33.4        |
| BBC        | 0.78  | -0.02 | 23.8        |
| IOB        | 0.33  | -0.28 | 6.4         |
| LR         | 0.83  | 0.23  | 31.7        |
| WR         | 0.70  | 0.03  | 10.3        |
| PPL        | 0.74  | 0.35  | 10.5        |
| LBP        | 0.79  | -0.03 | 40.5        |
| LIF        | 0.65  | 0.36  | 13.8        |
| LD         | 0.88  | 0.30  | 33.0        |
| LM1-3      | 0.74  | -0.52 | 135.7       |
| WM1        | 0.78  | -0.48 | 81.7        |
| WIF        | -0.16 | 0.33  | 4.0*        |
| BM1s       | 0.85  | -0.27 | 68.3        |
| PPB        | 0.35  | -0.52 | 8.0         |
| DAB        | 0.36  | 0.18  | 2.3*        |
| WZP        | 0.80  | 0.11  | 25.3        |
| BOC        | 0.81  | -0.04 | 48.4        |
| Eigenvalue | .033  | .006  |             |
| % Variance | 53.5  | 8.9   |             |

\* = NS; all other F values significant at  $P \leq .01$ .

tal data (fig. 17). Specimens of *tanala* generally score greater along the first principal component, which reflects their larger size and the uniformly high, positive correlations of most craniodental variables on that axis (table 2). Segregation of *tanala* and *webbi* along the second principal component primarily reflects differences in robustness of the molars (LM1-3, WM1), mensural traits which also account for the highest F values in analyses of variance (fig. 17; table 2). Age-related size increase undoubtedly explains much of the elliptical dispersion of individual scores within each species sample (for example, see Voss and Marcus, 1992). Relative age, as judged by tooth wear, must therefore be considered when attempting to identify unknowns, and greater attention should be given to dimensions of the tooththrows in rendering specific assignments.

Besides contrast in general size, the crania of *E. tanala* and *E. webbi* also differ in a

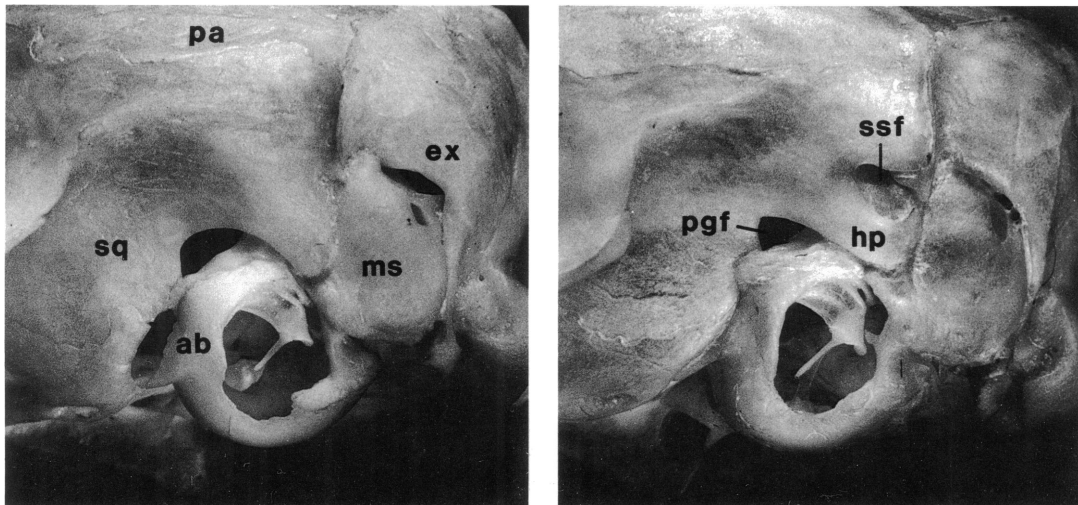


Fig. 18. Otic region (approximately  $\times 4.5$ ) and associated foramina in species of *Eliurus*: left, *E. tanala* (USNM 448983, Ambodiamontana); right, *E. webbi* (USNM 448993, 0.5 km N Kianjavato). Abbreviations: **ab**, auditory bulla; **ex**, exoccipital; **hp**, hamular process of squamosal; **ms**, mastoid; **pa**, parietal; **pgf**, postglenoid foramen; **sq**, squamosal; **ssf**, subsquamosal fenestra. Note presence of subsquamosal fenestra and corresponding development of the hamular process in *E. webbi* and their absence in *E. tanala*.

number of qualitative features. The subsquamosal fenestra is weakly expressed or absent in examples of *tanala*, which correspondingly have an indistinctly defined hamular process; in those of *webbi*, the fenestra is usually patent, revealing the lumen of the braincase and forming a short hamular process (fig. 18). Specimens of *webbi* typically lack the large supernumerary palatal foramina found in *tanala*; if present in *webbi*, these openings are notably smaller than the principal posterior palatal pair, not subequal to them as in *tanala* (fig. 19). The mandible in specimens of *tanala* bears a conspicuous capsular projection that sits high on the ascending ramus and terminates behind the anterior rim of the sigmoid notch; in *webbi*, the more delicate lower incisors produce a smaller capsular projection and their alveoli end anterior to the border of the sigmoid notch and lower on the ascending ramus (fig. 20). Since the posterior palatal constriction averages about the same width (5.1–5.2 mm) in both *tanala* and *webbi*, it thus appears more sharply indented, relative to the palatal breadth, in skulls of the former (fig. 16). In the absence of associated skins, the application of these qualitative criteria, together with dimensional data, should facilitate critical identification.

For his characterization of *E. tanala*, Major (1896a) had available at least three specimens from Vinanitelo, which he referenced by field number. One of these (M1358) corresponds to the type in the BMNH, another (M1510) to a specimen now in the FMNH. The provenance of the third specimen (MCZ 45690) here listed from Vinanitelo is questionable since it lacks original field tags. Its geographic source is indicated on secondary labels received with the Grandidier collection now at Harvard University. The whereabouts of Major's third specimen (M1515) thus remains unknown; it may still exist since a substantial portion of Major's original collection was exchanged or otherwise dispersed to other museums.

NOTES ON NATURAL HISTORY: Locality records of *E. tanala* place the species in evergreen rainforest, generally along a higher altitudinal belt (450–1300 m) than *E. webbi*. Description of the habitat of *E. tanala* is most detailed for forest near Perinet (900–1300 m), where Webb obtained a fine series (BMNH) in 1939–1940 and where K. Lange and J. Shaw subsequently collected a smaller number (USNM) in 1962–1963. Within primary rainforest, Lange (field journal, 1962) noted the diversity of microhabitats, including

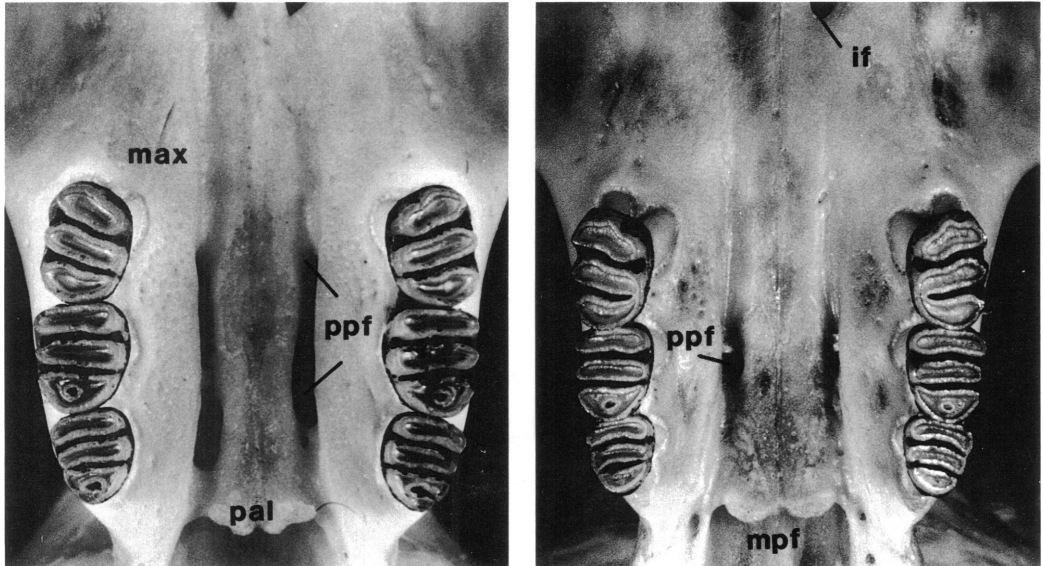


Fig. 19. Palatal region (approximately  $\times 7$ ) and associated foramina in species of *Eliurus*: left, *E. tanala* (USNM 448983, Ambodiamontana); right, *E. webbi* (USNM 448993, 0.5 km N Kianjavato). Abbreviations: **if**, incisive foramen; **max**, maxillary; **mpf**, mesopterygoid fossa; **pal**, palatine; **ppf**, posterior palatine foramen. Note elongate, slitlike posterior palatine foramina in *E. tanala* and their short, ovate shape in *E. webbi*.

grassy glades, lush herbaceous growth and viny entanglements along small streams, and stands of tree ferns and bamboo. He obtained several specimens from a dense concentration of ferns and other herbaceous plants growing beneath the undercut bank of a stream. Webb (1954) collected examples of *E. tanala* on low branches but also on ground sets.

Individuals in gray juvenile pelage or post-juvenile molt have been collected during October and November. A litter size of two is recorded for a specimen collected near Ranomafana in July. Males in breeding condition were noted during July and August in the same region.

**ETYMOLOGY:** A patronym identifying the people of the Tanala tribe who lived in the vicinity of Vinanitelo and assisted Major with his field collections.

**SPECIMENS EXAMINED:** 49 as follows: Ambodiamontana, 7 km (by road) W Ranomafana, 950 m (USNM 448981-90, 448997, 449250); Anosibe, km 55, route Anosibe (MNHN 1961.178); 1 km NW Andrambovato, 875 m (USNM 449256); 10 mi NW Lohariandava, 1500 ft (BMNH 47.1573); Per-

inet, near Moramanga, 3000 ft (BMNH 47.1557-72; MNHN 1961.176); 1 km E Perinet (USNM 341826); 2 km E Perinet (USNM 328828-30); 13 km E Perinet (USNM 341827); Sianaka Forest (BMNH 35.10.12.2, 36.11.2.1-2; MCZ 29249); 3 km (by road) NNW Vohiparara, 1225 m (USNM 449251-5); Vinanitelo, 30 mi S Fianarantsoa (BMNH 97.9.1.154; FMNH 5631; MCZ 45690).

*Eliurus webbi* Ellerman,  
1949, new rank  
Figures 4, 12, 13, 15B,  
16B, 18, 19, 20D

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

**HOLOTYPE:** BMNH 47.1576; adult male; skin and skull; original number FAR. 5; collected 14 August 1940 by Cecil S. Webb.

**TYPE LOCALITY:** Given by Ellerman (1949) as "20 miles south of Farafangana, south-east coast Madagascar." The skin tag of the holotype contains additional locality information: "4 mi from sea, 48°E  $\times$  23°S." Webb (1954) later acknowledged the village of Manombo (Fianarantsoa Province,

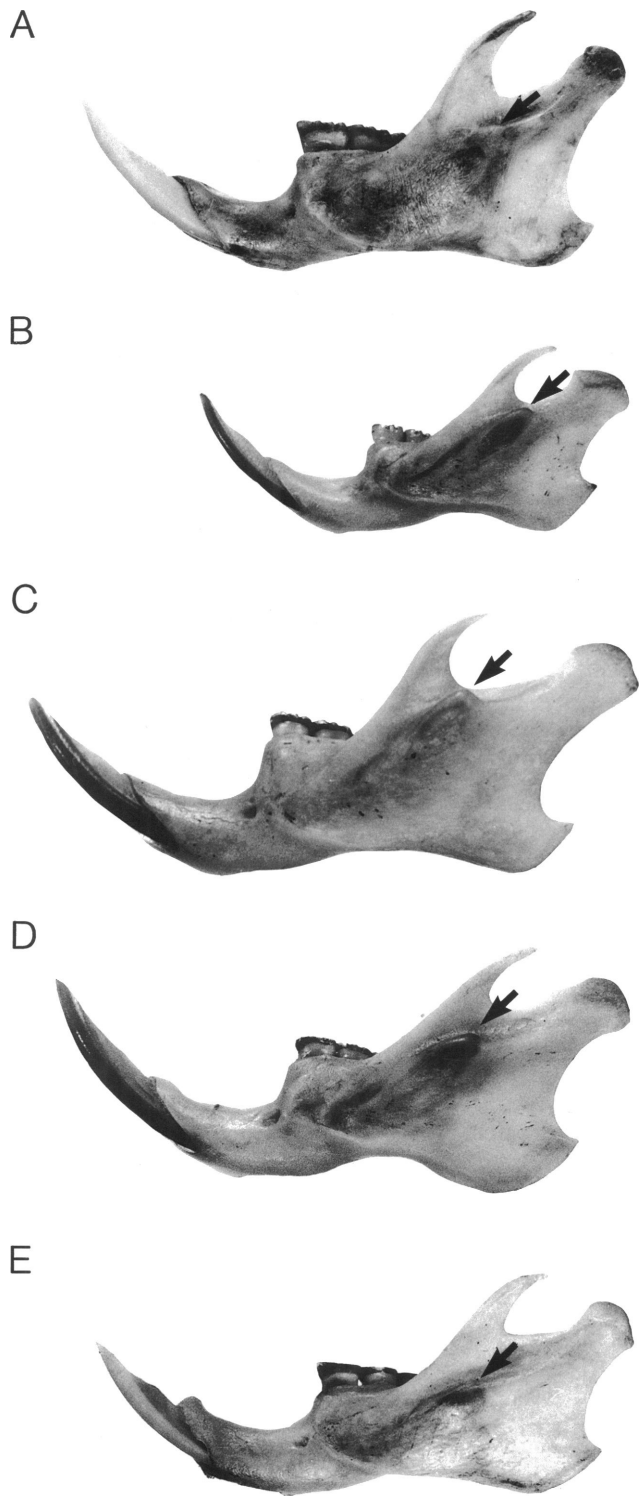


Fig. 20. Lateral view ( $\times 3$ ) of left mandibles of representative species of *Eliurus*: **A**, *E. penicillatus* (UZMC 7941, Ampitambe); **B**, *E. minor* (USNM 448979, Ambodiamontana); **C**, *E. tanala* (USNM 448983, Ambodiamontana); **D**, *E. webbi* (USNM 448993, 0.5 N Kianjavato); **E**, *E. petteri* (USNM 341825, 18 km E Perinet). Arrows point to the dorsalmost and posteriormost extension of the incisor alveolus.

23°02'S/47°44'E) as base camp for his field-work in the nearby forest.

**EMENDED DIAGNOSIS:** A moderately large (ONL = 36–41 mm, DHFL = 28–32 mm) species of *Eliurus* characterized by an entirely dark, well developed pencil extending over the distal two-fifths of the tail; skull suggests a lighter built, smaller version of *E. tanala* but subquamosal fenestra typically open, supernumerary palatal perforations absent or small, and taper of rostrum from nasolacrimal capsules more pronounced and nasal tips narrower.

**DISTRIBUTION:** An elongate belt of low to middle elevation rainforest, from Montagne d'Ambre in the north to the region of Farafangana in the south (fig. 11). Most geographic samples of *E. webbi* fall between sea level and 800 m, with the exception of their collection at 1500 m on the mountains east of Ivohibe.

Locality records document the sympatry of *E. webbi* with *E. minor* (west of Maintimbato and west of Vondrozo), *E. tanala* (NW of Andrambovato), and one of the new species described below (N of Rogez). Where *E. webbi* and *E. tanala* have been collected at nearby places (vicinity of Ranomafana and near Lohariandava), *E. webbi* is the form that originated from the localities of lower elevation.

**DESCRIPTION:** Penicillate section of tail typically conspicuous over distal two-fifths; caudal hairs light brown to blackish brown, monocolored to tip (fig. 12); tuft hairs 10–12 mm long. Scutellation near base of tail moderately defined. Fine caudal hairs of basal scutes extend over 1½ annulations.

Cover hairs of dorsum bicolored, proximal two-thirds plumbeous gray and distal one-third a bright buff, or tricolored with a faintly evident terminal band of black. Buffy band comparatively long and guard hairs more brownish, conveying a general buffy brown dorsal effect. Fur texture soft and fine compared to specimens of *E. tanala*. Dorsal (8–10 mm long on midrump) and ventral fur shorter than in examples of *E. tanala*. Metatarsals and phalanges covered with dull white hairs. Pinnae relatively large, approximately the same as *E. myoxinus* in absolute size; appear naked to unaided eye but lightly covered with fine reddish brown hairs. Cover hairs of underparts bicolored, medium gray

basally and cream to buff distally. Buff terminal band long relative to gray proximal segment, imparting a somewhat yellowish frosted, dingy gray appearance.

Skull generally smaller than that of *E. tanala* and lighter in construction (figs. 13, 15B, 16B; Appendix 2). Rostrum relatively as long as *E. tanala* but tips of nasals narrower. Zygomatic arches slightly bowed at midsection but less flaring than those of *E. tanala*. Subquamosal fenestra usually distinct and ovate, its forward extent exposing some of brain cavity as well as lateral surface of periotic; hamular process short but more completely formed than in specimens of *E. tanala* (fig. 18). Bony palate typically perforated with single pair of posterior palatal foramina (fig. 19); if present, supernumerary palatal openings appreciably smaller than primary pair. Anterior margin of mesopterygoid fossa approximately equal with end of third molars. Termination of lower incisor alveolus forms small capsular projection on dentary, with weak medial sulcus evident in older animals; posterior limit of capsular projection about even with the anterior margin of the sigmoid notch but positioned just below ventral rim of sigmoid notch (fig. 20D).

**COMPARISONS AND REMARKS:** The moderately robust size of *E. webbi* permits separation of this species from most other kinds of *Eliurus* (Appendix 2). Although *E. webbi* is larger in cranial size overall, its maxillary tooththrow is absolutely and relatively smaller than those of *E. majori* and *E. penicillatus*, which as a pair differ from it in other proportional features as enumerated in their respective accounts. Superficial inspection of examples of *E. webbi* may suggest only a smaller version of *E. tanala* with a darkly tufted tail; however, many qualitative traits of skin and skull distinguish the two, as detailed under the preceding discussion of *E. tanala*. The consistency of their morphological divergence, together with the distributional evidence, recommends the elevation of Ellerman's (1949) *webbi* to species status.

The several locality series that Ellerman (1949) assigned to *webbi* originate from disparate geographic regions collected over a wide altitudinal belt. The topotypes from Farafangana in the southeastern lowlands are paler dorsally and ventrally than those from

high (about 1500 m) on the flanks of Ivohibe Mountain or from the northeastern lowlands near Antongil Bay. The small series from Mt. d'Ambre (elevation unknown) exhibits the brightest pelage appearance among the geographic samples available. Creamy white hairs, monocolored to their bases, cover the venter of these specimens from the chin to groin; only one of five animals displays an appreciable expanse of the typical basally gray hairs over the midabdomen, which separates the white-colored fur of the groin and ventral forequarters. Still, size and proportions of the skin and skull, development and color of the tail pencil, and basic cranial resemblance suggest that all of these samples represent a single species.

It is remarkable that such a distinctive and relatively common species as *E. webbi*, with its wide distribution in rainforests along the eastern lowlands and coast, escaped notice by the early naturalists in Madagascar. The first examples of *E. webbi* were apparently collected in 1929 on a low forested ridge west of Vondrozo by the Mission Zoologique Franco-Anglo-Américaine. Regrettably, the mammalogical findings of the Mission Zoologique Franco-Anglo-Américaine were never synthesized and reported, especially for the few but highly interesting small mammals that their field teams obtained. Ellerman's (1949) formal discovery of *webbi*, two decades afterwards, was based on the more extensive series collected by Cecil Webb over a six-year period during World War II. In fact, the type locality of *webbi*, 20 mi S Farafangana, had been visited in 1929 by a team of the Mission Zoologique Franco-Anglo-Américaine, which obtained a single specimen of *Nesomys* but none of *Eliurus*. As exemplified by the belated recognition of *E. webbi* and elaborated by Carleton and Schmidt (1990), specimen-based documentation of Madagascar's endemic rodents is, as a rule, meager. The nature of the existing nesomyine material in museums advises the need for improved geographic representation and more careful census of individual localities.

NOTES ON NATURAL HISTORY: Except for the 1500-m site on mountains east of Ivohibe, most distributional records of *E. webbi* fall between sea level and 800 m. This altitudinal zone broadly coincides with the oc-

currence of high-canopy, lowland rainforest (Koechlin, 1972). The few habitat comments on specimen tags uniformly identify forest as the place of capture, and Rand (1932, 1936) characterized the localities—for example, W Vondrozo and S Farafangana—where series of *E. webbi* have been obtained as tall rainforest. In the only long-term ecological study of small mammals in lowland rainforest of Madagascar, Stephenson (1987) found *E. webbi*<sup>2</sup> to inhabit undisturbed primary forest with a sparse understory and herbaceous cover but abundant lianas. Although his live-trapping grid was laid on the ground, Stephenson observed that individuals of *E. webbi*, upon release, scampered toward trees and readily ascended lianas draped from a cliff. He characterized the species as scansorial. Webb also noted their capture on tree branches as well as on the ground.

Field studies should illuminate whether the distributions of *E. webbi* and *E. tanala* broadly correspond to the formation of lowland rainforest and lower montane rainforest (called medium-altitude dense rainforest by Koechlin, 1972), respectively. Around 800 m, the physiognomy and composition of the forest change; its canopy is lower, harboring a denser herbaceous understory and ground cover, a notable profusion of mosses on limbs and boulders, and greater abundance of lianas, epiphytes, and orchids. Although the two overlap in the range of 450–850 m, samples of *E. tanala* generally occupy a higher elevational belt than those of *E. webbi*, a relationship which may reflect the ecological transition between lowland and lower montane rainforest.

The record of *E. webbi* at 1500 m on Ivohibe Mountain is a conspicuous exception to this pattern. Webb's (1954: 263) later elaboration of the habitat at this site suggests a wet montane setting: "... the undergrowth of the forest was always dripping wet, and clouds often descended low to clothe every-

<sup>2</sup> Stephenson (1987) identified the larger of the two *Eliurus* encountered at his study site as *Eliurus* sp., the smaller one as *E. minor*. The single voucher (BMNH 1987.108) preserved of his unidentified form is referable to *E. webbi* and agrees with other examples of the species collected by Webb in the vicinity of Antongil Bay (for instance, near Rantabe).



thing in mist. Mosses and lichens festooned the trees and a wonderful variety of ferns issued from the crevices of rocks on the slopes of the steep ravines." Only specimens of *E. webbi* were obtained at this locality, but *E. tanala* may be expected to occur in the vicinity.

Juveniles of *E. webbi*, representing a variety of localities throughout the species' range, have been collected during the months of July through December. A count of three embryos was recorded for a specimen collected in August from south of Farafangana.

**ETYMOLOGY:** Described in honor of the collector, Cecil S. Webb, who had assembled the finest series of nesomyine rodents then known since the time of Forsyth Major.

**SPECIMENS EXAMINED:** 62 as follows: 2 km NE Andrambovato, 575 and 625 m (USNM 449266-8); 1 km NW Andrambovato, 875 m (USNM 449269); 3 mi E Andranofotsy, 12 km NE Maroantsetra, near sea level (BMNH 47.1585-8); Antalaha (MNHN 1961.179); Antalavia, E side Antongil Bay, near sea level (BMNH 47.1590); 20 mi S Farafangana, 4 mi from sea (AMNH 119706-7; BMNH 47.1574-84); 12 km E Ifanadiana (MNHN 1961.216-9); 6 mi E Ivohibe, 5000 ft (BMNH 47.1597-9; USNM 297483); 15 mi E Ivohibe, 5000 ft (BMNH 47.1594-6); 0.5 km N Kianjavato, 300 m (USNM 448991-5); 9 km ESE Kianjavato, 250–500 m (USNM 449257-65); 40 km SW Maroantsetra, 10 km WSW Maintimbato, 450–625 m (BMNH 1987.108); 40 km NE Maroantsetra, Ankovana, 900 ft (BMNH 47.1589); Mount d'Ambre (MNHN 1957.781, 1970.248-9, 1973.517-8); 8 mi W Rantabe, Antongil Bay, 500 ft (BMNH 47.1591-3); 13 mi N Rogez, near Lohariandava, 1300 ft (BMNH 47.1624); 20 km W Vondrozo (MNHN 1932.3517, 1957.782).

*Eliurus petteri*, new species

Figures 12, 14, 15A, 16A, 20E

**HOLOTYPE:** MNHN 1961.177; young adult male; skin and skull; original number 174; collected 6 October 1956 by Jean-Jaques Peter.

In a plastic bag attached to the skin are the intact, articulated elements of the left forelimb (scapula, humerus, and radius-ulna) and

the left hindlimb (femur and tibia-fibula); the left fore- and hindfeet remain on the skin. Also contained within the bag is the dried phallus in a capped vial. The condition of the skull is good with the exception of the incomplete right zygomatic arch.

Standard measurements (in mm) from the skin tag of the type include head-and-body length, 130; tail length, 205; hindfoot length, 33; and ear length, 22. Selected cranial dimensions recorded by me are: ONL, 38.4; ZB, 17.9; IOB, 5.2; PPL, 13.4; LBP, 8.4; LIF, 4.1; LM1-3, 5.05; and WM1, 1.38.

**TYPE LOCALITY:** 8 km from Fanovana.

**DIAGNOSIS:** A moderately large (ONL = 37–39 mm, DHFL = 31.5–33 mm) species of *Eliurus* characterized by bright white underparts sharply delimited from dark dorsum; tail length relatively longest in the genus, about 135 percent of head-and-body length, with small pencil confined to terminal one-fourth of tail; cranium appears delicate for its size, with a narrow rostrum and interorbit, the zygomatic arches weak and bowed little, and the incisive foramina short and narrow.

**PARATYPES:** MCZ 45928 from north of Rogez; adult, sex indeterminate; skin, skull, and partial skeleton; collected by M. Lavauden on 28 May 1929. USNM 341825 from 18 km E Perinet; old adult female; skin and skull; original number 576; collected 28 April 1963 by K. Lange.

**DISTRIBUTION:** The three known specimens were collected from closeby localities (Fanovana, Perinet, and Rogez), all situated about 18°50'S, 48°35'E in forest due east of Antananarivo (fig. 10) and from approximately 400 to 1000 m.

Sympatry with other *Eliurus* is currently undocumented but should be expected because specimens of *E. minor*, *E. tanala*, and *E. webbi* are recorded from nearby localities. For example, K. Lange, in 1963, obtained specimens of *E. tanala* in disturbed rainforest at distances 1, 2, and 13 km along the road east of Perinet (= Andasibe) and the single example of *E. petteri* from the place located 18 km east.

**DESCRIPTION:** Terminal tuft weakly developed, limited to distal 25 to 30 percent of tail length; hairs of tuft light brown to grayish brown, 8–10 mm long. Long proximal sec-

tion of tail appears naked macroscopically for approximately two-thirds to three-quarters of its length (fig. 12). Scutellation fine, scale hairs short (about one annulation long) and inconspicuous. Caudal epidermis dusky, either monocolored or with white splotches on proximal two-thirds of ventrum.

Cover hairs of dorsum tricolored—basal two-thirds light gray, middle band pale buff, and terminal band dark brown to blackish. Middorsum exhibits denser concentration of hairs with blackish tips and/or hairs with longer terminal bands. Tone muted, general color grayish brown but variation observable among three known specimens: type more charcoal-gray, especially middorsally where a broad but indistinct dark band is suggested; MCZ 45928 with more brownish tones, particularly on the head and flanks, darker on middle back; USNM 341825 an intermediate gray-brown. Dark eye-rings present in two of three specimens. Guard hairs dark but relatively inconspicuous, only slightly longer than cover fur. Pelage texture fine and soft, somewhat sleek in appearance, 8–10 mm long on midrump. Distinct narrow dusky streak extends over dorsum of tarsus and metatarsus; remainder of metatarsus and digits covered with white hairs. Tops of forefeet wholly white, dark dorsal pelage ending abruptly at carpus. Cover hairs of underparts monocolored white in all three specimens, giving the entire venter, including the inner surfaces of the fore- and hindlimbs, a bright white appearance from the chin to groin that contrasts sharply with the darkly colored dorsum. Mystacial vibrissae about 50–60 mm long, extending well past base of pinnae when appressed to skin. Pinnae pale dusky, in gross examination devoid of fur but clothed externally with short brown hairs and internally with fine white ones.

Skull only slightly smaller than that of *E. webbi* but conformation gracile (figs. 14, 15A, 16A), suggesting examples of *E. minor*. Zygomatic arches weakly developed, particularly over their middle span, little expanded laterally. Interorbital region hourglass-shaped, lacking any definition of suprorbital shelves and ridges, and braincase smooth and rounded, less elongate compared to other *Eliurus* except *E. minor*. Incisive foramina narrow and short, approximately the same size as in

*E. minor*. Posterior palatal foramina formed as a single pair of small openings. Anterior margin of mesopterygoid fossa about equal with the ends of the third molars. None of the three skulls possesses any trace of the bony strut of the alisphenoid that separates the masticatory-buccinator foramen and foramen ovale accessorius as seen in other species. Subsquamosal fenestra present in all three specimens, moderately large, about as in *E. webbi*, and revealing the inner braincase as well as the petrous portion of the petiotic; hamular process of squamosal thus well defined. Tympanic bullae appear relatively the smallest in the genus, only slightly larger in absolute dimensions than in specimens of *E. minor*.

Upper and lower incisors relatively thin in width and depth, hardly more robust than those of *E. minor*. Enamel face of upper incisors yellow to pale orange. Alveolus of lower incisors short, terminating at the level of the coronoid process and low on the ascending ramus (fig. 20E), without any capsular projection even in the oldest specimen. Molar rows as long relative to cranial size as in other *Eliurus* except *E. majori* and *E. penicillatus*.

COMPARISONS AND REMARKS: Examples of *E. petteri* recall a diminutive version of *E. webbi* at first inspection. Closer examination, however, reveals many features that contribute to the singular differentiation and straightforward identification of this form with respect to other members of the genus. Its white venter, whose purity and brightness are exaggerated by contrast to the somber-colored dorsum, is unmatched by any other species of *Eliurus*. Aside from the sharp dorsal-ventral contrast, the sleek texture of its dorsal pelage and the modest development of a monocolored tuft on a relatively long tail can alone serve to distinguish *E. petteri* from its similarly sized congeners, *E. tanala* and *E. webbi*.

The cranium of *E. petteri* is remarkable for its light and delicate appearance despite a size that approaches smaller individuals of *E. webbi* (figs. 15, 16). Characteristics that confer the impression of delicate proportions include the slender incisors, thin zygomatic arches, smoothly rounded braincase, and tiny auditory bullae. Specimens of *E. petteri* ap-

pear little larger than examples of *E. minor* in certain cranial dimensions, notably those of the incisive foramina, which are proportionately the smallest in the genus. The alveoli of the lower incisors in *E. petteri* are also extreme within *Eliurus* for their shortness and the lack of an incisive capsule on the lateral surface of the dentary (fig. 20E). If the absence of the alisphenoid strut holds true for larger samples of the new species, then this condition too would mark *E. petteri* as unique compared to other *Eliurus* in which the structure is consistently present.

The recorded length of 205 mm for the tail vertebrae of the holotype (MNHN 1961.177) seems inordinately long for its appearance relative to the head-and-body of the skin. Tail length on the dry specimen measures 185 mm, which is the value used for the calculation of its proportional length.

NOTES ON NATURAL HISTORY: Notations on skin tags indicate that the type specimen was obtained "en forêt vierge" and USNM 341825 in "Rainforest. In an area with large granite outcrops and tangled undergrowth. Hillside habitat." No additional natural history information is available.

ETYMOLOGY: The species name honors the substantial contributions of Dr. Francis Pether, Museum National d'Histoire Naturelle, to our systematic knowledge of Madagascar's endemic rodents. His research has uncovered the existence (1959, 1962) of new forms (*Macrotarsomys ingens* and *Brachytarsomys albicauda villosa*) and addressed the origin and relationships of Nesomyinae within the radiation of Muroidea (1961, 1972, 1990).

*Eliurus ellermani*, new species

Figures 14, 15D, 16D

HOLOTYPE: MNHN 1981.871; adult male; skin and skull; original number 15; collected January 1968 by R. Albignac.

Standard measurements (in mm) recorded on the skin tag of the type include head-and-body length, 152; tail length, 177; hindfoot length, 35; and ear length, 20. Selected cranial dimensions measured by me are: ONL, 43.8; ZB, 18.8; IOB, 6.3; PPL, 15.5; LBP, 9.2; LIF, 5.8; LM1-3, 5.82; and WM1, 1.61.

Skin with very tip of tail missing and patches of fur lost on the belly and left flank. Skull

in good condition except the left pterygoid process and rim of the left auditory bulla damaged. The collector's name appears only on a secondary tag that was clearly attached later, perhaps when cataloged in 1981, and is qualified by a question mark in parentheses.

TYPE LOCALITY: Hiaraka, near Maroantsetra, 850 m altitude. MacPhee (1987) located Hiaraka as 40 km NW Maroantsetra (Toamasina Province, about 15°10'S/49°30'E).

DIAGNOSIS: A large (ONL = 42–44 mm, DHFL = 33–34 mm) species of *Eliurus* that resembles a robust version of *E. tanala* except with the tail brush completely dark to the tip; skull stoutly constructed, especially as seen in its broader interorbit, braincase, and expanse of zygomatic arches.

PARATYPE: BMNH 47.1623 from 13 mi N Rogez, near Lohariandava, 1300 ft altitude; adult male; skin and skull (occiput broken); original number P.70; collected 10 December 1939 by Cecil S. Webb.

DISTRIBUTION: The two widely separated localities suggest that the species should be sought in low-to-intermediate elevation rainforest of northeastern Madagascar (fig. 10).

A specimen of *E. minor* is also recorded from the type locality, and the paratype was collected together with a much smaller *Eliurus* that I judge to be an example of *E. webbi*.

DESCRIPTION: Caudal pilosity moderately developed, extending about one-third of tail, tuft hairs 9–11 mm long. Hairs dark to tip of tail on the paratype and apparently so on the holotype, though its tip is missing; pencil hairs colored pale brown to dusky. Scutellation grossly apparent over basal two-thirds of tail and relatively coarsely defined; caudal epidermis darkly pigmented on dorsum and venter; hairs near base of tail about 1½ annulations long.

Dorsal pelage drab, coloration much as in examples of *E. webbi* but texture harsher. Cover hairs of dorsum mostly tricolored—proximal three-quarters plumbeous gray, and distal one-quarter pale buff, with or without a very short dark tip. Length of buffy band appears greater on sides and flanks, which are lighter than the middorsum. Guard hairs numerous and shiny black. Overall dorsal effect a dark grayish brown. Ventral cover hairs monocolored a dingy creamy buff from the

chin to groin on the holotype, but some basal gray banding evident on the paratype to give a darker tone. Dark eye-rings present, more conspicuously defined on the paratype.

Skull stout and heavy in build, suggesting a robust version of *E. tanala* in most features and proportions (figs. 14, 15D, 16D). Incisors wide and deep front to back, enamel pigment of uppers a strongly saturated orange. Both crania with supernumerary palatal perforations, those of the type small and those of the paratype about equal in size to the posterior palatal foramina themselves. Subsquamosal fenestra expressed on the type as a shallow indentation, not exposing any of the brain cavity, and on the paratype as a distinct notch, forming a short, broad hamular process. Termination of the lower incisors marked by a distinct capsular projection situated high on the ascending ramus, below the middle of the sigmoid notch.

COMPARISONS AND REMARKS: As observed in its large skull and hindfoot, this species is at the upper limits of size so far recorded for the genus. Only the very largest specimens of *E. tanala* match the two of *E. ellermani* in some cranial dimensions (Appendix 2; it should be remembered that the ONL of the paratype is some value greater than 42.6 mm since its occiput is broken). The skin of *E. ellermani*, on the other hand, more strongly resembles examples of *E. webbi* in dorsal and ventral pelage color and in the dark, monocolored tail tuft. One might suspect that the skull from a *tanala* and the skin of a *webbi* had been inadvertently associated were it not for the combination of these cranial and pelage traits in two specimens, obtained by different collectors from distant localities at separate times. The correspondence of features exhibited by both of these examples seems too compelling for me to twice dismiss their uniqueness to an error of specimen processing. Further material is needed to ascertain the typical morphological condition for certain cranial foramina that differ slightly in the two available specimens.

NOTES ON NATURAL HISTORY: No ecological or reproductive information is associated with either of the known specimens.

ETYMOLOGY: The species is named in recognition of Sir John Reeves Ellerman, one-time shipping magnate and research associate

with the British Museum (Natural History), London. Among his many systematic compendia of mammals, Ellerman's scientific reputation is linked principally to his three-volume treatise on The Families and Genera of Living Rodents (1940, 1941, 1949). His contributions to our understanding of nesomyine rodents remain little appreciated; however, the last published and least cited third volume of Families and Genera contains an appendix on the material collected by Cecil Webb, together with a summary of the known nesomyine taxa and description of the distinctive form *Eliurus myoxinus webbi*. His chapter was the most valuable synopsis of the group published to that date and established the species-level taxonomy recognized today. Moreover, Ellerman (1940, 1941) promulgated the most radical classificatory treatment yet of Madagascar's rodents, in disputing their common ancestry and instead allocating the seven genera among five subfamilies of a broadly defined Family Muridae. His arguments for departing from the traditional classification have yet to be seriously addressed and convincingly refuted.

#### INTERSPECIFIC RELATIONSHIPS

Interpretation of phylogenetic affinities among the species of *Eliurus* must be considered preliminary at this stage, as it is limited to morphological data derived from the skin and skull as summarized by morphometric analyses and by resemblances in a few discrete traits.

Little sense of specific relationships can be gleaned from the early descriptive literature, which contains scant comparative evaluations. Ellerman (1941), however, first stressed general size as a fundamental criterion of kinship within the genus by noting the markedly smaller dimensions of *E. minor* in contrast to all other species then known (*majori*, *myoxinus*, *penicillatus*, and *tanala*). In 1949, he formalized this viewpoint and relegated the larger-bodied taxa (*majori*, *penicillatus*, *tanala*, and *webbi*) to subspecies of a polytypic *E. myoxinus*, which as a result constituted the lone congener to the monotypic *E. minor*. His formal classification of *Eliurus* thus conveys, ignoring differences in assign-

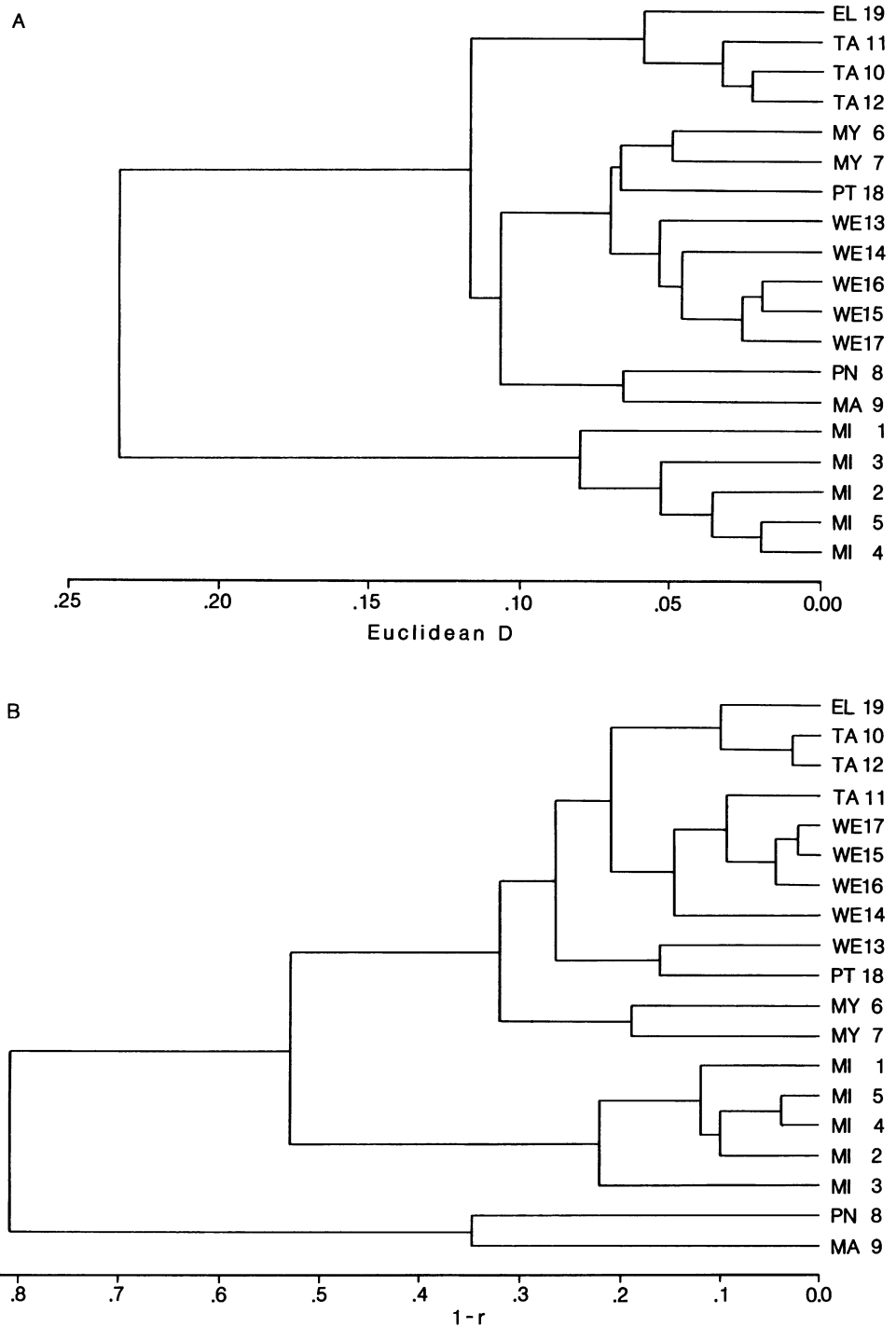


Fig. 21. UPGMA clustering of log-transformed sample means for the 19 OTUs of *Eliurus* identified in the Materials and Methods, using both a Euclidean distance coefficient (A) and the Pearson correlation coefficient (B). Species abbreviations: EL, *E. ellermani*; MA, *E. majori*; MI, *E. minor*; MY, *E. myoxinus*; PN, *E. penicillatus*; PT, *E. petteri*; TA, *E. tanala*; WE, *E. webbi*.

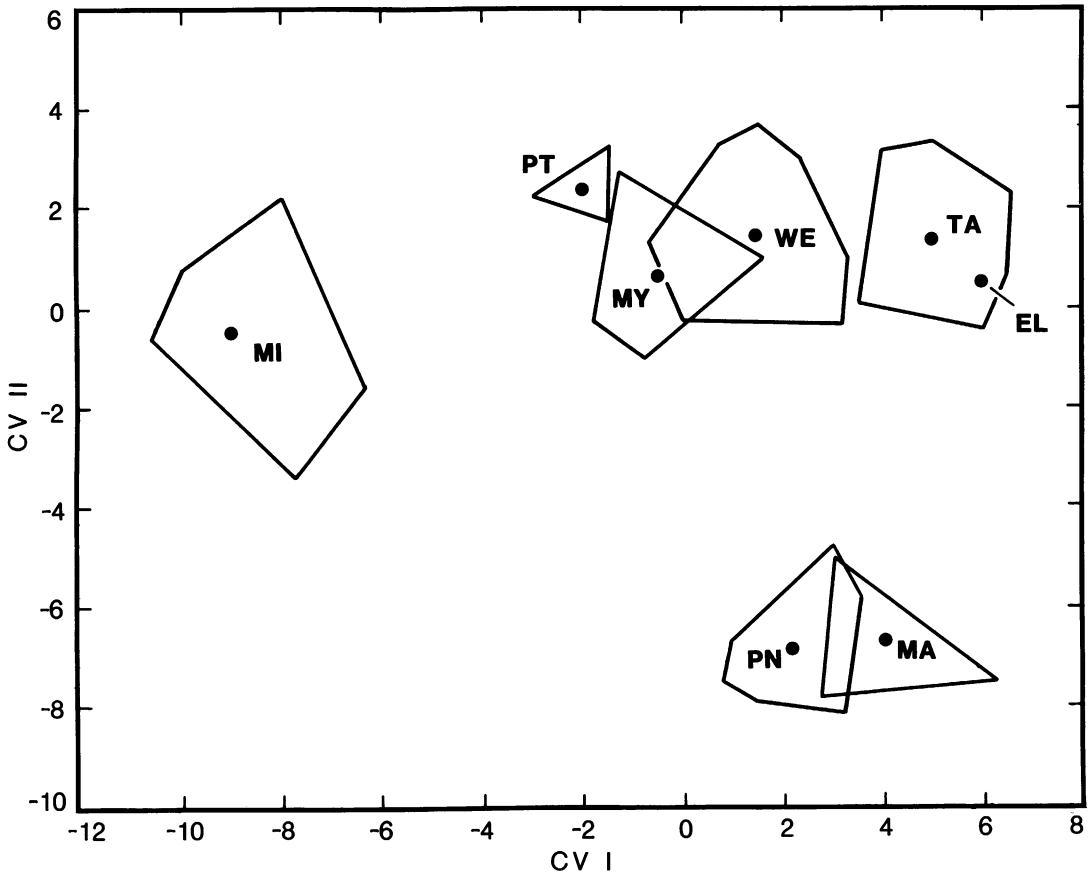


Fig. 22. Plots of first two canonical variates extracted from discriminant function analysis performed on eight species of *Eliurus* and using all specimens with intact skulls ( $N = 128$ ). Polygons enclose maximal dispersion of individual specimen scores around group-centroids for each of eight species (see tables 3 and 4). Species abbreviations and sample sizes: EL, *E. ellermani* ( $N = 1$ ); MA, *E. majori* ( $N = 4$ ); MI, *E. minor* ( $N = 28$ ); MY, *E. myoxinus* ( $N = 9$ ); PN, *E. penicillatus* ( $N = 12$ ); PT, *E. petteri* ( $N = 3$ ); TA, *E. tanala* ( $N = 31$ ); WE, *E. webbi* ( $N = 40$ ).

ment of taxonomic rank, only a simple dichotomy determined principally by size.

#### MORPHOMETRIC COMPARISONS

Results of the multivariate analyses do not fully sustain Ellerman's appraisal of morphological divergence among the described forms and instead offer alternative estimates of their interrelationship. Pair-wise association of OTUs based on a distance coefficient corresponds to the specific groupings advanced herein, and the first bifurcation does impart a simple division of small versus large forms (fig. 21A) in general accordance with Ellerman's (1941, 1949) taxonomy. In con-

trast, use of a correlation measure, more sensitive to proportional similarities (for example, see Minkoff, 1965), reveals the strong separation of *E. majori* and *E. penicillatus* from other *Eliurus* (fig. 21B). Using a correlation coefficient, the cluster of *E. minor* OTUs still remains well defined, as does that of *E. myoxinus*, but examples of *E. webbi*, *E. tanala*, and *E. ellermani* are somewhat interspersed, reflecting their fundamental resemblance in craniodental proportions. As noted in the appropriate species accounts, justification for the specific status of these three forms draws from qualitative character differences as well as distributional information.

TABLE 3

**Results of Discriminant Function Analysis**  
(Performed on 18 cranial measurements of intact specimens of *Eliurus* [N = 128]; see fig. 22.)

| Variable | Correlations |       | F (group)* |
|----------|--------------|-------|------------|
|          | CV I         | CV II |            |
| ONL      | 0.93         | 0.27  | 156.1      |
| ZB       | 0.89         | 0.89  | 65.2       |
| BBC      | 0.90         | 0.22  | 89.7       |
| IOB      | 0.77         | 0.41  | 48.7       |
| LR       | 0.90         | 0.29  | 118.3      |
| WR       | 0.83         | 0.07  | 36.0       |
| PPL      | 0.87         | 0.26  | 70.9       |
| LBP      | 0.84         | 0.47  | 120.5      |
| LIF      | 0.84         | -0.17 | 48.9       |
| LD       | 0.87         | 0.38  | 109.9      |
| LM1-3    | 0.93         | -0.31 | 228.8      |
| WM1      | 0.91         | -0.24 | 102.2      |
| WIF      | 0.56         | -0.39 | 20.0       |
| BM1s     | 0.95         | 0.04  | 133.9      |
| PPB      | 0.83         | -0.17 | 47.3       |
| DAB      | 0.83         | -0.03 | 73.0       |
| WZP      | 0.82         | 0.40  | 67.3       |
| BOC      | 0.93         | 0.17  | 109.0      |

\* = All univariate F tests significant at  $P \leq .001$ .

In like manner, three phenetic clusters are readily apparent in discriminant function analysis. One is composed of examples of *E. minor* and another of larger species (*E. ellermani*, *E. myoxinus*, *E. petteri*, *E. tanala*, and *E. webbi*), a separation consistent with Ellerman's (1949) revision. The third group also represents larger-bodied taxa (*E. majori* and *E. penicillatus*) that are as differentiated in character space from the set of other large species as is *E. minor* (fig. 22). The hiatus delimiting specimens of *E. majori* and *E. penicillatus* issues from proportional contrasts such as their relatively robust molar rows, long and wide incisive foramina, a short bony palate, and narrow interorbital region (table 3). Average Mahalanobis distances derived among the 8 species samples of *Eliurus* (table 4) fall well within the range or exceed those recorded for other congeneric species of muroid rodents (Voss and Marcus, 1992).

#### PHYLETIC INFERENCES

Any attempt to marshal cladistic analyses of relationship among species of *Eliurus* is hindered by the same two factors which gen-

TABLE 4

**Matrix of Mahalanobis Distances Between Centroids of Species Samples of *Eliurus* (see fig. 22)**

Species abbreviations: MA = *E. majori*; PN = *E. penicillatus*; MY = *E. myoxinus*; MI = *E. minor*; PT = *E. petteri*; WE = *E. webbi*; TA = *E. tanala*; EL = *E. ellermani*.

|    | Species |      |      |      |      |      |      |
|----|---------|------|------|------|------|------|------|
|    | PN      | MY   | MI   | PT   | WE   | TA   | EL   |
| MA | 7.6     | 11.8 | 15.6 | 14.1 | 10.7 | 9.7  | 9.1  |
| PN | —       | 9.6  | 13.9 | 11.9 | 9.2  | 9.8  | 10.3 |
| MY |         | —    | 10.5 | 7.8  | 6.2  | 8.3  | 10.1 |
| MI |         |      | —    | 10.4 | 11.5 | 14.7 | 15.8 |
| PT |         |      |      | —    | 7.7  | 10.2 | 11.2 |
| WE |         |      |      |      | —    | 5.9  | 7.5  |
| TA |         |      |      |      |      | —    | 5.0  |

erally plague an enhanced phylogenetic understanding of muroid rodents at the species level. These are: 1) the paucity of phenotypic variation that is expressed as discrete alternatives and that lends itself to clear character-state definitions; and 2) the lack of strongly corroborated, higher-level phylogenies within Muroidea sufficient to allow confident identification of sister taxa and thereby to illuminate polarity interpretations among what few qualitative characters can be meaningfully considered.

Consideration of the second factor pointedly illustrates our lack of knowledge with regard to the genus under current study. Winge (1941), for example, arranged *Gymnuromys* as the nearest living relative of *Eliurus*, both classified within the group Rhizomyes, in which he included the other Malagasy rodents, African mole rats (*Tachyoryctes*), and Asian bamboo rats (*Rhizomys*). Ellerman (1940, 1941), on the other hand, placed *Eliurus* as the lone genus of the group Eliuri within the subfamily Murinae and dispersed the other Malagasy genera among the Cricetinae, Gymnuromyinae, Microtinae, and Tachyoryctinae. Both authors advocated a broadly inclusive definition of the Family Muridae. Their dramatically contrasting viewpoints underscore the more fundamental and still unsettled phylogenetic issue of the monophyly of the subfamily Nesomyinae (see Carleton and Musser, 1984, and Petter, 1990, for reviews), resolution of which is far beyond the scope of this study. Notwith-

TABLE 5

**Matrix of Character States Among Eight Species of *Eliurus* (see text and fig. 23)**

Species abbreviations: MA = *E. majori*; PN = *E. penicillatus*; MY = *E. myoxinus*; MI = *E. minor*; PT = *E. petteri*; WE = *E. webbi*; TA = *E. tanala*; EL = *E. ellermani*; OG = composite outgroup.

| Character                 | Species |    |    |    |    |    |    |    |    |
|---------------------------|---------|----|----|----|----|----|----|----|----|
|                           | MA      | PN | MY | MI | PT | WE | TA | EL | OG |
| 1. Pelage contrast        | c       | c  | a  | a  | b  | a  | a  | a  | ?  |
| 2. Fur texture            | b       | b  | a  | a  | a  | a  | a  | a  | ?  |
| 3. Tail penicillation     | a       | a  | c  | b  | b  | b  | b  | b  | a  |
| 4. Tail color             | a       | b  | a  | a  | a  | a  | b  | a  | a  |
| 5. Zygomatic notch        | a       | a  | b  | b  | b  | b  | b  | b  | a  |
| 6. Incisive foramina      | c       | c  | b  | b  | a  | b  | b  | b  | ?  |
| 7. Palatal foramina       | a       | a  | a  | b  | a  | a  | b  | b  | a  |
| 8. Mesopterygoid fossa    | a       | a  | b  | b  | b  | b  | b  | b  | a  |
| 9. Molar rows             | a       | a  | b  | b  | b  | b  | b  | b  | a  |
| 10. Third molars          | a       | a  | b  | b  | b  | b  | b  | b  | a  |
| 11. Subsquamosal foramina | a       | a  | a  | a  | a  | a  | b  | b  | a  |
| 12. Alisphenoid strut     | a       | a  | a  | a  | b  | a  | a  | a  | a  |
| 13. Basicranial flexion   | a       | a  | a  | b  | a  | a  | a  | a  | a  |
| 14. Lower incisor         | b       | b  | b  | b  | a  | b  | c  | c  | ?  |
| 15. Mandibular shape      | b       | b  | a  | a  | a  | a  | a  | a  | a  |

? = Character state coded as unknown.

standing the evolutionary uncertainties expressed at the ranks of tribe and subfamily, the numerous and distinctive craniodental and external features shared by the eight known species of *Eliurus*, whether contrasted to other nesomyines or to any other muroid, convince me that the monophyly of the genus is a reasonable hypothesis at this stage of inquiry.

Without a firm phylogenetic framework, some guidance on transformation polarities may be gleaned from character data used in investigations of other radiations of Muroidea (for example, Carleton, 1980; Hershkovitz, 1962; Musser and Newcomb, 1983; Voss, 1988), and this is the course adopted here. The outgroup traits thus identified (table 5) and used to root the cladograms produced in the PAUP analyses are a composite of the character polarity arguments contained in the aforementioned studies of Muroidea. Decisions on the ancestral-derived condition of character attributes, however, depend much upon the taxonomic level of one's analysis; therefore, polarity hypotheses drawn from the perspective of the superfamily may obscure local instances of character-state reversals, for example at the generic and specific levels. The weakness of my approach is here accepted as an exploratory exercise to spur more

rigorous evaluations of kinship among species of *Eliurus*.

**Characters:** A total of 15 qualitative characters, as described below and listed in table 5, was distilled from the foregoing morphological comparisons. The alphabetic order of states within most characters represents the hypothesized sequence of primitive-derived changes, in which all transformations are linear (from a to b, or from a to b to c); the ancestral state of a few was treated as unknown. This character set predicts a minimum-length network or tree of 19 steps. Several of the character states are simple verbalizations of the shape differences uncovered in multivariate analyses; others involve discrete trait variation that is not easily described by conventional landmark measurements.

**Character 1. Dorsal-ventral pelage contrast:** (a) moderate—venter grayish, dorsum dark brown to blackish; (b) strong—venter white and dorsum dark, lateral demarcation sharply defined; (c) weak—venter colored about as dark as dorsum, little lateral demarcation.

**Remarks:** Moderately pronounced countershading, with a lighter gray to grayish-white venter, is commonplace among species of Muroidea and may be plausibly assumed as



the ancestral state. Voss (1988), however, interpreted a darkly colored venter as primitive within ichthyomyine rodents (Sigmodontinae). Consideration of either state as ancestral does not undermine the fundamental relationships predicted below, but in view of the uncertainty, the character was treated as unknown in the outgroup.

**Character 2. Fur texture:** (a) normal, harsher; (b) wooly and fine.

**Character 3. Development of tail penicillation:** (a) little pronounced; (b) moderate; (c) conspicuously long and bushy.

Remarks: See discussion under next character.

**Character 4. Color of tail tuft:** (a) dark to tip; (b) white tip.

Remarks: Tails with contradistinctively colored tips, usually bright white, and with distally elongated hairs have evolved in a number of rodent groups, most notably the stylized "banner" tails found in many Old World jerboas (Dipodidae) and New World kangaroo rats (Heteromyidae). The occurrence of white-tipped, conspicuously penicillate tails is seemingly rarer within Muridae, although they are known in other genera of broad-footed, arboreal murids like *Chiropodomys* and *Margaretamys* (Musser, 1979, 1981). The choice of the derived state seems clear as does the probable independent acquisition of white caudal tips within Muridae. Even within *Eliurus*, strong evidence supports convergent evolution of the plumed white tips exhibited by *E. penicillatus* and *E. tanala* (see below).

**Character 5. Relative depth of zygomatic notch:** (a) shallow, zygomatic plate narrow; (b) moderate, zygomatic plate relatively broader.

Remarks: The distinction between *E. majori-penicillatus* and other *Eliurus* in expression of a zygomatic notch is slight compared to the conspicuously deep notches and broad plates developed in some muroids (for example, Gerbillinae). The direction of change, however, is consistent with previous interpretations of variation in this character in other muroids (Carleton, 1980; Carleton and Musser, 1989; Musser and Heaney, 1992).

**Character 6. Relative length of incisive foramina:** (a) short; (b) moderate; (c) long.

Remarks: The above descriptions of foramina length are meaningful only within

*Eliurus*, since the incisive foramina in the genus are short compared to those of many species of Muroidea. Assignment of a plesiomorphic state is problematic in view of the common occurrence of species with short or long foramina within the superfamily. Wahlert (1985) viewed the elongate foramina of muroids, whose aperture traverses equal lengths of the premaxillary and maxillary bones, as derived within Rodentia, and Musser and Newcomb (1983) scored longer incisive foramina as derived within Malaysian murines. Quay (1954), however, provided persuasive evidence for reduction in size of the incisive foramina in certain Arvicolinae. The outgroup condition was coded as indeterminate.

**Character 7. Posterior palatal foramina:** (a) single pair of foramina; (b) supernumerary foramina present, posterior to principal pair and sometimes conjoined to form elongate vacuities.

Remarks: The condition observed in most *Eliurus* is typical of muroids in general, and the postulated evolutionary sequence follows Carleton (1980), who encountered unusually long posterior palatal foramina only among Gerbillinae. Samples of *E. minor* are polymorphic for this character, but the derived state characterizes most individuals examined.

**Character 8. Forward extent of mesopterygoid fossa:** (a) penetrates slightly between upper third molars; (b) terminates level with posterior border of third molars.

Remarks: The contrast between species of *Eliurus* does not match that typical of the short and long bony palates noted by Hershkovitz (1962) for various groups of South American sigmodontines. The difference is nonetheless consistent, and the direction of change agrees with the interpretations presented in other phylogenetic studies of muroids (Carleton, 1980; Hershkovitz, 1962; Musser and Newcomb, 1983).

**Character 9. Relative length of molar rows:** (a) long (about 16–17% of ONL); (b) short (about 13–14% of ONL).

Remarks: The relatively and absolutely longer toothrows observed in *E. majori* and *E. penicillatus* are hypothesized to be the plesiomorphic state.

**Character 10. Relative length of upper third**

**molars:** (a) subequal to M2; (b) smaller than M2.

Remarks: Reduction in size of the M3 concurs with the polarity conclusions of other studies but is a trend that has obviously evolved in parallel within several lines of Muroidea (Carleton, 1980; Musser and Newcomb, 1983; Voss, 1988). Characters 8, 9, and 10 could plausibly be viewed as redundant descriptions of a single anatomical complex; that is, reduction in size of the third molars achieves a relatively shorter molar row overall and imparts a correspondingly longer appearance to the bony palate.

**Character 11. Development of subsquamosal fenestra:** (a) present, usually revealing brain cavity; (b) absent, or small forming a shallow notch and not revealing the interior of the braincase in lateral view.

Remarks: While noting that subsquamosal fenestrae are present in most representatives of the Gerbillinae, Microtinae, Old World cricetines, South American cricetines, and neotomine-peromyscines, I earlier (1980: 44) persuaded myself that their absence represented the ancestral state. Voss (1988) questioned this polarity decision and reopened the larger issue of the presumed homology of this opening with the squamosomastoid foramen found in other rodents (see Voss, 1988: 295, and Wahlert, 1985, for discussions). In light of this uncertainty, my character-state transition straightforwardly recognizes the wider taxonomic distribution of an open fenestra as indicative of primitiveness.

**Character 12. Occurrence of alisphenoid strut:** (a) present; (b) absent.

Remarks: Loss of the alisphenoid strut has occurred in several murid groups (Carleton, 1980; Musser and Newcomb, 1983). The derived state was recorded only for the three examples of *E. petteri*, and the character was omitted from the phylogenetic analyses.

**Character 13. Degree of basicranial flexion:** (a) weakly pronounced, foramen magnum oriented mostly caudad; (b) strongly pronounced, foramen magnum oriented posteroventrally.

Remarks: The strongly arched cranial vault of *E. minor* resembles the contrast noted by Carleton and Musser (1989) between certain oryzomyines and that they coded as apomorphic. Recorded for only one species of

*Eliurus*, this character too was eliminated from construction of evolutionary trees.

**Character 14. Development of lower incisor:** (a) alveolus short, ending anterior to sigmoid notch, without lateral capsular projection; (b) alveolus moderate in length, ending below the coronoid process and forming a slight capsular projection; (c) alveolus long, ending below the rim of the sigmoid notch and forming a distinct capsular projection.

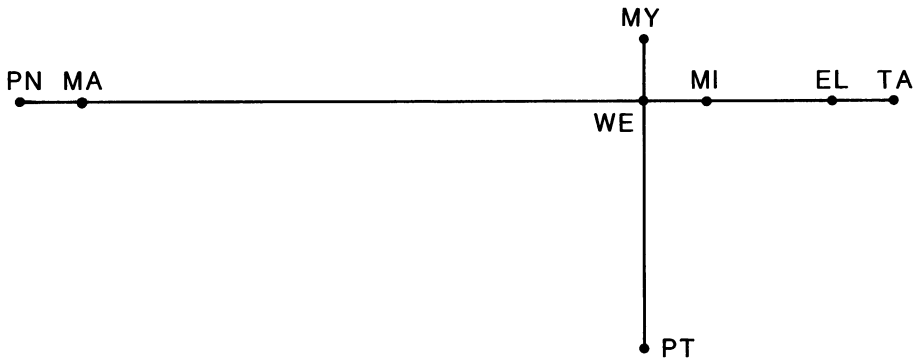
Remarks: The morphology described under (b) corresponds to the common condition observed within Muroidea; however, the formation of a distinct capsular projection or knob (c) occurs frequently as well and within many subfamilies, whereas that identified as (a), here noted for only *E. petteri*, is rarer. I cannot offer any compelling rationale for the polarity of this character, and it was entered as an unknown in the hypothetical outgroup (table 5).

**Character 15. Mandibular conformation:** (a) slender appearance, ramus low slung; (b) stocky appearance, high ascending ramus and arching coronoid process.

Remarks: The state tentatively recognized as derived suggests the remodeling of the mandible described in the evolution of the Arvicolinae from generalized cricetids (Repenning, 1968), although none of the associated dental specializations of arvicolines pertains to species of *Eliurus*.

Results using PAUP: Treatment of all 15 characters as unordered produced a rootless network of 20 steps (fig. 23A). The large hiatus separating *E. majori* and *E. penicillatus* from other *Eliurus* derives from the many proportional differences of their crania (character states 5a, 6c, 8a, 15b) and dentition (9a, 10a), as well as their distinctive pelage (1c, 2b, 3a). The next greatest distance generated over all characters along the network reflects the several unique traits (1b, 6a, 12b, 14a) observed in the new species *E. petteri*. Possession of a white terminal pencil (4b) by *E. tanala* accounts for the single-step difference between it and *E. ellermani*, both of which otherwise share similarities in their palatal morphology (7b), patency of the subsquamosal fenestra (11b), and development of the lower incisor (14c). The divergence of *E. minor* from large-bodied forms like *E. myoxinus* and *E. webbi*, considered on the basis of

A



B

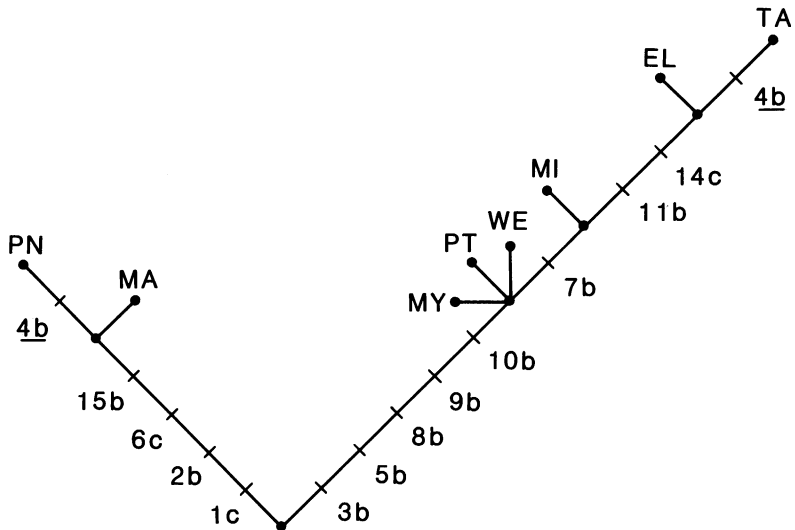


Fig. 23. Affinity among species of *Eliurus* based on 15 qualitative characters (see text and table 5): **A**, minimum-length network ( $L = 20$ ) with all multistate characters treated as unordered; **B**, strict consensus summary of phylogenetic relationships based on 15 most parsimonious trees ( $L = 18$ ,  $ci = 0.94$ ). Character state changes depicted are common to all 15 most parsimonious trees; single homoplasious transition (4b) is underlined; autapomorphies are not indicated for *E. myoxinus* (3c) and *E. petteri* (1b, 6a, 14a). Species abbreviations: **EL**, *E. ellermani*; **MA**, *E. majori*; **MI**, *E. minor*; **MY**, *E. myoxinus*; **PN**, *E. penicillatus*; **PT**, *E. petteri*; **TA**, *E. tanala*; **WE**, *E. webbi*.

qualitative features unrelated (presumably) to size, is unremarkable in contrast to the results disclosed in the various multivariate analyses of craniodental data.

Generation of evolutionary trees using the 13 cladistically informative characters (nos. 12 and 13 were omitted) produced 15 equally

parsimonious trees (fig. 23B;  $L = 18$ ,  $ci = 0.94$ ). The variation in the 15 trees involved the branching patterns predicted around the node subtending *E. myoxinus*, *E. petteri*, *E. webbi*, and the *E. minor-ellermani-tanala* clade. Moreover, these variations all involved zero-length branches that portrayed

the theoretical cladistic possibilities around that node, and no distance separated the hypothesized outgroup from the basal node. A strict consensus tree was computed to summarize the branching topography and character state transitions common to the 15 most parsimonious trees (fig. 23B).

The cladistic information contained in the discrete character data is insufficient for wholly resolving relationships among the eight species of *Eliurus*, but certain patterns of descent do emerge. *Eliurus majori* and *E. penicillatus* are predicted to share a common ancestor that differentiated early relative to the radiation of other species of *Eliurus*. These two species possess several characters that can be credibly posited as plesiomorphic—such as the narrow zygomatic plate and indistinct notch (5a), shorter bony palate (8a), robust third molars (10a)—and two others that could be so interpreted appropos of certain polarity arguments—like the indistinct dorsal-ventral countershading (1c) and wider and longer incisive foramina (6c). The phylogenetic analysis nonetheless treated the latter traits as derived for the *majori-penicillatus* clade, given the assignment of unknown states to the outgroup and application of parsimony criteria.

The remaining *Eliurus* species, including *E. minor*, display apomorphic features for many of these same characters (3b, 5b, 8b, 9b, 10b) and form a well-supported monophyletic group. Relationships within this complex are less clear, particularly with regard to *E. myoxinus*, *E. petteri*, and *E. webbi*. In surprising contrast to Ellerman's (1949) classification and some of the morphometric evaluations, *E. minor* is represented as more closely related to the largest species, *E. tanala* and *E. ellermani*, based on its typical possession of supernumerary palatine foramina and a more fenestrated palate (7b). My own preconception of kinship patterns had favored a sister-group relationship of *E. webbi* to *E. tanala-ellermani*, a conjecture shaped by the phenetic analyses but not borne out by the cladistic evaluation of the discrete characters. Recourse to other kinds of systematic data is clearly required to test and refine the preliminary patterns of phenetic divergence and phylogenetic relationship developed herein.

## NATURAL HISTORY INFORMATION

In a 1985 IUCN survey of African rodents that may warrant conservation concern, Schlitter then characterized our systematic and biological understanding of most nesomyine species, including *Eliurus myoxinus* (sensu Ellerman, 1949) and *E. minor*, as "Insufficiently Known." Knowledge of the ecology, diet, and reproduction of *Eliurus* has improved little and remains fragmentary at best. Available information derives mostly from anecdotal sources such as specimen tags and fieldnotes, not from explicitly designed field investigations. What is known, or plausibly suspected, may be summarized as follows.

Species of *Eliurus* are uniformly associated with arborescent habitats, most species in humid evergreen forests along the eastern lowlands and contiguous escarpment, but one (*E. myoxinus*) in dry deciduous forest and scrub formations in the west and southwest. The fidelity of species to given floristic formations and nature of preferred microhabitats are largely unknown. Stephenson (1987) demonstrated the importance of dense viny growth and a sparse understory in predicting the presence of *E. minor* and *E. webbi* in lowland rainforest. In eastern forest, limited distributional evidence, notably for *E. tanala* and *E. webbi*, suggests altitudinal stratification approximately coincident with the ecotone from lowland to montane rainforest. *Eliurus minor*, on the other hand, ranges widely in altitude and occupies both types of forest, but the consanguinity of populations allocated to this nominal species needs verification.

Notes on trap placement substantiate highly developed scansorial abilities, which conform predictably to the broad-footed, long-tailed physiognomy characteristic of the genus. Whether the tufted-tailed rats of Madagascar utilize upper portions of the forest canopy has yet to be explored. "Arboreal" sampling using conventional trapping methods, which undoubtedly accounts for most nesomyines in museum collections, is limited to reachable branches and vines, usually 2 m or less in height. In lowland tropical rainforest in Brazil, for example, Malcolm (1990) revealed greater activity levels and population densities for certain muroid rodents

(*Oecomys* and *Rhipidomys*) in upper canopy (15 m) than on the ground where they are sometimes captured. The bodily conformation of these sigmodontine genera recalls, in a general way, that of *Eliurus*.

The trophic niche of *Eliurus* similarly lacks detailed substantiation. Stephenson (1987) noted that in captivity both *E. webbi* and *E. minor* relished coconut, but whether their predilection under this circumstance conveys much about their regular diet needs documentation. Dietary studies would be highly interesting in light of the moderately developed hypsodonty and laminate dentition that characterize the genus. Such dental adaptations contrast with the low-crowned, cuspidate molars found in other scansorial or arboreal muroids with a bodily form like that of *Eliurus*, for example, the Neotropical genera *Oecomys* and *Rhipidomys*. Crown height in *Eliurus* instead resembles the condition observed in species of *Holochilus*, some *Phyllotis*, or some *Otomys*, all of which are terrestrial forms inhabiting savanna-grassland biomes and whose herbivory is better established. The laminate occlusal topography found in *Eliurus* is reminiscent of molar structure in the Philippine murid *Phloeomys*, a much larger rodent believed to be an arboreal folivore (Eisenberg, 1978).

The range of incisor development within the genus also invites investigation. In particular, the weak incisors and short incisive

alveoli of *E. petteri* raise questions about its diet compared to foodstuffs ingested by other *Eliurus*. The length of the lower incisor alveolus and size of the capsular projection presumably reflect the degree of wear on the incisor tips and may correspond to the relatively indurate nature of seeds or insects consumed. These incisor and mandibular differences are not simply due to size-allometry factors, for relative length of the lower incisor and corresponding protrusion of the capsular process are well expressed in the smaller-bodied *E. minor*.

Anecdotal observations by collectors suggest that some species, notably *E. myoxinus*, nest in tree-holes, but the generality of this habit for the genus needs careful substantiation in the field. Litter size in *Eliurus*, based only on six records, is apparently small, ranging from one to three young. These records and other kinds of evidence (testes descended, lactation, juveniles present) document some breeding activity at least over the latter half of the year (July–December). Most field surveys, however, have been conducted during this same period, which encompasses about 75 percent of nesomyine specimens with known collecting dates. The bias and insufficiency of these data are plainly evident and underscore the conclusion that the reproductive phenology of no species population of *Eliurus* is understood.

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## APPENDIX 1

Gazetteer of *Eliurus*  
Collecting Localities

The specimens of *Eliurus* reported in the preceding species accounts represent 42 principal collecting sites, which are listed below together with the coordinates used to map distributions. The localities are grouped under current provincial divisions and arranged by consecutive number from north to south along the eastern versant of Madagascar and from south to north along the western (see fig. 24). Nearby localities whose coordinates are virtually the same are indicated in parentheses, and current synonyms of older geographic names are provided in brackets [=]. Latitude and longitude figures correspond to that portion of the locality designation printed in boldface. Additional locality information and rationale for use of these geographic coordinates are discussed by Carleton and Schmidt (1990).

## Antsiranana Province

1. **Montagne d'Ambre** [= Ambohitra], 1000 m, 12°30'S/49°10'E.
2. **One day W Andapa**, 1800 m, ca. 14°39'S/49°22'E.
3. **Antalaha**, near sea level, 14°53'S/50°17'E.

## Toamasina Province

4. **Ankovana** [= Ankovona], 40 km NE Maroantsetra, 275 m, 15°18'S/49°59'E.
5. **3 km E Andranofotsy**, 12 km NE Maroantsetra, near sea level, ca. 15°25'S/49°49'E.
6. **Antalavia**, eastern side Antongil Bay, near sea level, 15°47'S/50°01'E.
7. **Hiaraka**, near Maroantsetra, 850 m, ca. 15°10'S/49°30'E.
8. **20 km SW Maroantsetra**, near sea level, 15°31'S/49°38'E.
9. **8 mi W Rantabe**, Antongil Bay, 150 m, ca. 15°42'S/49°30'E.
10. **10 km WSW Maintimbata**, 40 km SW Maroantsetra, 450–625 m, 15°46'S/49°36'E.
11. **16 mi E Imerimandroso**, Lac Alaotra, 1065 m, 17°24'S/48°42'E.
12. **9 km N Didy**, 1000 m, ca. 18°02'S/48°32'E.
13. **Sihanaka Forest**, ca. 18°05'S/48°30'E.
14. **10 mi NW Lohariandava** (including 12 mi NW), 455 m, 18°42'S/48°35'E.
15. **Rogez** [= Andekaleka], 18°48'S/48°37'E.
16. **13 mi N Rogez** [= Andekaleka], 395 m, 18°38'S/48°37'E.

17. **Fanovana**, 500 m (including 8 km from Fanovana), 18°55'S/48°34'E.
18. **18 km E Perinet** [= Andasibe], ca. 18°56'/48°31'E.
19. **Perinet** [= Andasibe], 915 m (including 1, 2, and 13 km E), 18°56'S/48°25'E.
20. **55 km along route to Anosibe**, ca. 19°20'S/48°14'E.

## Antananarivo Province

21. **Mandraka**, 1220 m, 18°55'S/47°56'E.

## Fianarantsoa Province

22. **Ampitambe** [= Ampitabe], 900 m, ca. 20°22'S/47°46'E.
23. **Ambohimitambo**, 1200 m, 20°43'S/47°23'E.
24. **12 km E Andraina** [= Manandroy] (including 14 km E), 1500 m, ca. 21°09'S/47°23'E.
25. **3 km by road NNW Vohiparara**, 1225 m, 21°13'S/47°22'E.
26. **Ambodiamontana**, 7 km by road W Ranomafana, 950 m, 21°16'S/47°26'E.
27. **2 km NE Andrambovato**, 575 and 625 m, 21°30'S/47°27'E.
28. **1 km NW Andrambovato**, 875 m, 21°30'S/47°25'E.
29. **12 km E Ifanadiana**, ca. 21°22'S/47°47'E.
30. **0.5 km N Kianjavato**, 300 m, 21°23'S/47°52'E.
31. **9 km ESE Kianjavato**, 250–500 m, 21°24'S/47°57'E.
32. **Fianarantsoa**, south of, 21°26'S/47°05'E.
33. **Vinanitelo**, 1300 m, 21°43'S/47°16'E.
34. **Andringitra**, 22°20'S/46°55'E.
35. **6 mi E Ivohibe** (including 15 mi E), 1525 m, 22°30'S/47°00'E.
36. **20 km by road W Vondrozo**, 500 m, ca. 22°48'S/47°10'E.
37. **20 mi S Farafangana**, 4 mi from sea, 23°02'S/47°44'E.

## Toliara Province

38. **5 mi E Bevilany**, 245 m, ca. 25°00'S/46°40'E.
39. **35 mi E Tulear** [= Toliara], 23°12'S/44°12'E.
40. **Tsilambana**, ca. 20°50'S/44°00'E.
41. **Morondava**, 20°17'S/44°17'E.
42. **Beroboka**, 7 km from sea (including Analabe), 19°58'S/44°36'E.



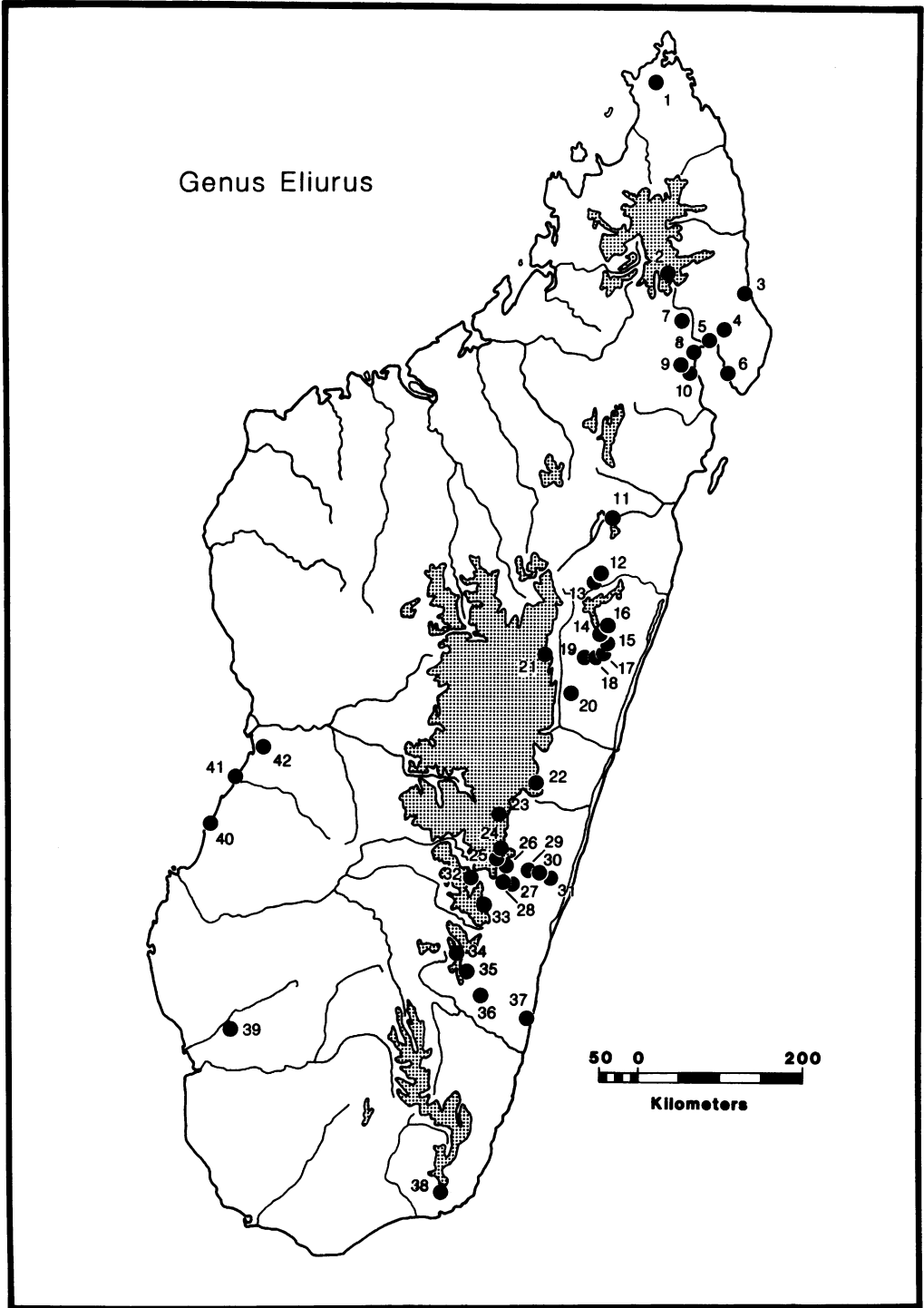


Fig. 24. Principal collecting localities of specimens of *Eliurus* reported in this study. Numbered localities correspond to those listed in the gazetteer (Appendix 1). Shaded areas indicate highlands above 1000 m.

## APPENDIX 2

Descriptive Statistics for Selected Cranial and External Variables and OTUs of *Eliurus*

| Species and OTU                   | N  | Mean | Range      | SD  |
|-----------------------------------|----|------|------------|-----|
| <b>Occipitonasal Length</b>       |    |      |            |     |
| <i>minor</i> OTU 2                | 9  | 29.7 | 28.8–30.9  | 0.8 |
| <i>minor</i> OTU 4                | 12 | 30.1 | 28.7–31.3  | 0.9 |
| <i>myoxinus</i> OTU 6             | 6  | 36.1 | 35.0–36.9  | 0.7 |
| <i>myoxinus</i> OTU 7             | 4  | 36.9 | 34.9–38.1  | 1.4 |
| <i>majori</i> OTU 8               | 5  | 36.3 | 35.2–37.5  | 0.9 |
| <i>penicillatus</i> OTU 9         | 14 | 36.0 | 32.9–37.4  | 1.4 |
| <i>tanala</i> OTU 10              | 11 | 40.8 | 38.2–44.1  | 1.9 |
| <i>tanala</i> OTU 11              | 18 | 41.1 | 38.5–43.8  | 1.5 |
| <i>webbi</i> OTU 15               | 20 | 38.8 | 34.4–41.0  | 1.6 |
| <i>webbi</i> OTU 17               | 11 | 39.0 | 36.1–41.8  | 1.5 |
| <i>petteri</i> OTU 18             | 3  | 38.3 | 37.6–38.8  | 0.6 |
| <i>ellermani</i> OTU 19           | 2  | 43.2 | 42.6, 43.8 | —   |
| <b>Length of Rostrum</b>          |    |      |            |     |
| <i>minor</i> OTU 2                | 9  | 9.9  | 9.1–10.7   | 0.5 |
| <i>minor</i> OTU 4                | 13 | 10.1 | 9.2–10.8   | 0.5 |
| <i>myoxinus</i> OTU 6             | 6  | 12.3 | 12.0–12.5  | 0.2 |
| <i>myoxinus</i> OTU 7             | 6  | 12.1 | 11.4–12.7  | 0.5 |
| <i>majori</i> OTU 8               | 5  | 12.5 | 12.0–13.1  | 0.5 |
| <i>penicillatus</i> OTU 9         | 14 | 12.3 | 10.8–13.2  | 0.7 |
| <i>tanala</i> OTU 10              | 15 | 14.4 | 13.3–16.4  | 0.9 |
| <i>tanala</i> OTU 11              | 18 | 14.8 | 13.3–15.9  | 0.7 |
| <i>webbi</i> OTU 15               | 20 | 13.7 | 11.8–14.8  | 0.8 |
| <i>webbi</i> OTU 17               | 11 | 13.6 | 12.4–14.6  | 0.8 |
| <i>petteri</i> OTU 18             | 3  | 13.5 | 13.0–13.9  | 0.5 |
| <i>ellermani</i> OTU 19           | 2  | 15.6 | 15.1, 16.1 | —   |
| <b>Greatest Zygomatic Breadth</b> |    |      |            |     |
| <i>minor</i> OTU 2                | 7  | 14.4 | 13.9–15.2  | 0.4 |
| <i>minor</i> OTU 4                | 13 | 15.0 | 14.4–15.7  | 0.4 |
| <i>myoxinus</i> OTU 6             | 5  | 17.4 | 17.0–17.8  | 0.4 |
| <i>myoxinus</i> OTU 7             | 5  | 18.2 | 17.5–19.1  | 0.7 |
| <i>majori</i> OTU 8               | 5  | 18.8 | 18.3–19.3  | 0.5 |
| <i>penicillatus</i> OTU 9         | 14 | 17.9 | 15.9–19.2  | 0.9 |
| <i>tanala</i> OTU 10              | 16 | 19.5 | 17.1–21.2  | 1.3 |
| <i>tanala</i> OTU 11              | 18 | 19.3 | 18.3–20.6  | 0.7 |
| <i>webbi</i> OTU 15               | 20 | 18.2 | 15.7–19.2  | 0.9 |
| <i>webbi</i> OTU 17               | 9  | 18.0 | 16.2–19.0  | 0.8 |
| <i>petteri</i> OTU 18             | 3  | 17.2 | 16.6–17.9  | 0.7 |
| <i>ellermani</i> OTU 19           | 2  | 21.1 | 20.6, 21.7 | —   |
| <b>Interorbital Breadth</b>       |    |      |            |     |
| <i>minor</i> OTU 2                | 9  | 4.9  | 4.7–5.2    | 0.2 |
| <i>minor</i> OTU 4                | 13 | 4.9  | 4.7–5.2    | 0.1 |
| <i>myoxinus</i> OTU 6             | 6  | 5.7  | 5.5–6.0    | 0.2 |
| <i>myoxinus</i> OTU 7             | 6  | 5.4  | 5.1–5.8    | 0.2 |
| <i>majori</i> OTU 8               | 5  | 5.2  | 5.0–5.5    | 0.2 |
| <i>penicillatus</i> OTU 9         | 14 | 5.3  | 5.1–5.6    | 0.2 |
| <i>tanala</i> OTU 10              | 16 | 6.0  | 5.6–6.4    | 0.2 |
| <i>tanala</i> OTU 11              | 18 | 5.9  | 5.6–6.8    | 0.3 |
| <i>webbi</i> OTU 15               | 20 | 5.8  | 5.1–6.2    | 0.3 |
| <i>webbi</i> OTU 17               | 11 | 5.7  | 5.3–6.0    | 0.2 |
| <i>petteri</i> OTU 18             | 3  | 5.4  | 5.2–5.6    | 0.2 |

## APPENDIX 2—(Continued)

| Species and OTU                          | N  | Mean | Range     | SD   |
|--|----|------|-----------|------|
| <i>ellermani</i> OTU 19                  | 2  | 6.3  | 6.3–6.3   | —    |
| <b>Postpalatal Length</b>                |    |      |           |      |
| <i>minor</i> OTU 2                       | 7  | 10.2 | 9.6–11.0  | 0.5  |
| <i>minor</i> OTU 4                       | 12 | 10.7 | 10.0–11.2 | 0.4  |
| <i>myoxinus</i> OTU 6                    | 5  | 13.0 | 12.7–13.4 | 0.3  |
| <i>myoxinus</i> OTU 7                    | 4  | 14.1 | 13.0–14.7 | 0.8  |
| <i>majori</i> OTU 8                      | 5  | 12.7 | 11.9–13.2 | 0.6  |
| <i>penicillatus</i> OTU 9                | 14 | 12.8 | 11.5–13.8 | 0.7  |
| <i>tanala</i> OTU 10                     | 16 | 14.4 | 12.9–15.7 | 0.9  |
| <i>tanala</i> OTU 11                     | 18 | 14.4 | 13.9–15.5 | 0.3  |
| <i>webbi</i> OTU 15                      | 19 | 13.7 | 11.8–14.8 | 0.8  |
| <i>webbi</i> OTU 17                      | 9  | 13.9 | 12.5–14.8 | 0.6  |
| <i>petteri</i> OTU 18                    | 3  | 13.5 | 13.1–13.9 | 0.4  |
| <i>ellermani</i> OTU 19                  | 1  | 15.5 | —         | —    |
| <b>Length of Bony Palate</b>             |    |      |           |      |
| <i>minor</i> OTU 2                       | 9  | 5.8  | 5.1–6.3   | 0.4  |
| <i>minor</i> OTU 4                       | 12 | 6.2  | 5.4–6.6   | 0.3  |
| <i>myoxinus</i> OTU 6                    | 5  | 7.7  | 7.4–7.9   | 0.2  |
| <i>myoxinus</i> OTU 7                    | 6  | 7.4  | 7.1–7.9   | 0.3  |
| <i>majori</i> OTU 8                      | 5  | 7.3  | 6.9–7.7   | 0.3  |
| <i>penicillatus</i> OTU 9                | 14 | 6.7  | 6.3–7.4   | 0.3  |
| <i>tanala</i> OTU 10                     | 15 | 9.4  | 8.2–11.0  | 0.7  |
| <i>tanala</i> OTU 11                     | 18 | 9.2  | 8.2–10.1  | 0.4  |
| <i>webbi</i> OTU 15                      | 19 | 8.5  | 7.3–9.0   | 0.4  |
| <i>webbi</i> OTU 17                      | 11 | 8.4  | 7.7–9.2   | 0.5  |
| <i>petteri</i> OTU 18                    | 3  | 8.1  | 7.6–8.4   | 0.5  |
| <i>ellermani</i> OTU 19                  | 2  | 9.9  | 9.2, 10.7 | —    |
| <b>Length of Incisive Foramen</b>        |    |      |           |      |
| <i>minor</i> OTU 2                       | 9  | 4.2  | 4.0–4.4   | 0.12 |
| <i>minor</i> OTU 4                       | 13 | 3.9  | 3.5–4.3   | 0.14 |
| <i>myoxinus</i> OTU 6                    | 6  | 4.6  | 4.4–4.9   | 0.20 |
| <i>myoxinus</i> OTU 7                    | 6  | 5.0  | 4.6–5.4   | 0.31 |
| <i>majori</i> OTU 8                      | 5  | 5.9  | 5.5–6.1   | 0.25 |
| <i>penicillatus</i> OTU 9                | 14 | 5.4  | 5.0–5.9   | 0.31 |
| <i>tanala</i> OTU 10                     | 16 | 5.4  | 4.1–6.4   | 0.57 |
| <i>tanala</i> OTU 11                     | 18 | 5.5  | 4.9–6.1   | 0.37 |
| <i>webbi</i> OTU 15                      | 20 | 5.0  | 4.0–5.5   | 0.38 |
| <i>webbi</i> OTU 17                      | 11 | 5.2  | 4.8–6.2   | 0.42 |
| <i>petteri</i> OTU 18                    | 3  | 4.0  | 3.7–4.1   | 0.23 |
| <i>ellermani</i> OTU 19                  | 2  | 5.6  | 5.4, 5.8  | —    |
| <b>Breadth of Bony Palate across M1s</b> |    |      |           |      |
| <i>minor</i> OTU 2                       | 9  | 5.8  | 5.6–6.0   | 0.14 |
| <i>minor</i> OTU 4                       | 13 | 6.0  | 5.8–6.2   | 0.14 |
| <i>myoxinus</i> OTU 6                    | 6  | 7.0  | 6.5–7.3   | 0.31 |
| <i>myoxinus</i> OTU 7                    | 6  | 6.9  | 6.6–7.4   | 0.29 |
| <i>majori</i> OTU 8                      | 5  | 7.7  | 7.1–8.3   | 0.50 |
| <i>penicillatus</i> OTU 9                | 14 | 7.3  | 6.8–7.9   | 0.33 |
| <i>tanala</i> OTU 10                     | 16 | 8.1  | 7.6–8.6   | 0.33 |
| <i>tanala</i> OTU 11                     | 18 | 7.9  | 7.6–8.6   | 0.23 |
| <i>webbi</i> OTU 15                      | 20 | 7.3  | 6.8–7.8   | 0.28 |
| <i>webbi</i> OTU 17                      | 11 | 7.5  | 7.1–7.7   | 0.21 |
| <i>petteri</i> OTU 18                    | 3  | 6.9  | 6.6–7.1   | 0.25 |

## APPENDIX 2—(Continued)

| Species and OTU                     | N  | Mean | Range      | SD   |
|-------------------------------------|----|------|------------|------|
| <i>ellermani</i> OTU 19             | 2  | 8.1  | 7.9–8.4    | —    |
| <b>Length of Maxillary Toothrow</b> |    |      |            |      |
| <i>minor</i> OTU 2                  | 10 | 4.1  | 3.9–4.3    | 0.12 |
| <i>minor</i> OTU 4                  | 13 | 4.2  | 4.0–4.3    | 0.08 |
| <i>myoxinus</i> OTU 6               | 9  | 5.1  | 4.8–5.5    | 0.24 |
| <i>myoxinus</i> OTU 7               | 9  | 4.9  | 4.8–5.0    | 0.10 |
| <i>majori</i> OTU 8                 | 5  | 6.4  | 6.1–6.8    | 0.26 |
| <i>penicillatus</i> OTU 9           | 14 | 6.0  | 5.7–6.3    | 0.15 |
| <i>tanala</i> OTU 10                | 18 | 5.8  | 5.4–6.2    | 0.20 |
| <i>tanala</i> OTU 11                | 18 | 5.7  | 5.5–6.0    | 0.14 |
| <i>webbi</i> OTU 15                 | 20 | 5.2  | 4.7–5.4    | 0.18 |
| <i>webbi</i> OTU 17                 | 14 | 5.3  | 5.0–5.7    | 0.20 |
| <i>petteri</i> OTU 18               | 3  | 5.0  | 4.9–5.1    | 0.10 |
| <i>ellermani</i> OTU 19             | 2  | 5.7  | 5.6, 5.8   | —    |
| <b>Width of First Upper Molar</b>   |    |      |            |      |
| <i>minor</i> OTU 2                  | 10 | 1.10 | 1.06–1.13  | 0.03 |
| <i>minor</i> OTU 4                  | 13 | 1.14 | 1.02–1.19  | 0.05 |
| <i>myoxinus</i> OTU 6               | 9  | 1.37 | 1.25–1.48  | 0.08 |
| <i>myoxinus</i> OTU 7               | 9  | 1.31 | 1.27–1.40  | 0.04 |
| <i>majori</i> OTU 8                 | 5  | 1.67 | 1.17–1.78  | 0.12 |
| <i>penicillatus</i> OTU 9           | 14 | 1.57 | 1.49–1.63  | 0.04 |
| <i>tanala</i> OTU 10                | 18 | 1.61 | 1.43–1.79  | 0.09 |
| <i>tanala</i> OTU 11                | 18 | 1.53 | 1.42–1.68  | 0.05 |
| <i>webbi</i> OTU 15                 | 20 | 1.38 | 1.23–1.53  | 0.07 |
| <i>webbi</i> OTU 17                 | 14 | 1.42 | 1.35–1.57  | 0.06 |
| <i>petteri</i> OTU 18               | 3  | 1.40 | 1.35–1.47  | 0.06 |
| <i>ellermani</i> OTU 19             | 2  | 1.62 | 1.61, 1.63 | —    |
| <b>Head-and-Body Length</b>         |    |      |            |      |
| <i>minor</i> OTU 2                  | 10 | 101  | 90–116     | 7.9  |
| <i>minor</i> OTU 4                  | 11 | 106  | 95–116     | 6.5  |
| <i>myoxinus</i> OTU 6               | 9  | 128  | 114–136    | 7.5  |
| <i>myoxinus</i> OTU 7               | 7  | 135  | 115–145    | 9.9  |
| <i>majori</i> OTU 8                 | 2  | 152  | 145–159    | —    |
| <i>tanala</i> OTU 10                | 16 | 154  | 124–176    | 16.0 |

## APPENDIX 2—(Continued)

| Species and OTU             | N  | Mean | Range      | SD   |
|-----------------------------|----|------|------------|------|
| <i>tanala</i> OTU 11        | 17 | 156  | 144–175    | 9.8  |
| <i>webbi</i> OTU 15         | 18 | 147  | 135–159    | 7.6  |
| <i>webbi</i> OTU 17         | 12 | 137  | 120–149    | 6.7  |
| <i>petteri</i> OTU 18       | 2  | 133  | 130, 136   | —    |
| <i>ellermani</i> OTU 19     | 1  | 152  | —          | —    |
| <b>Tail Length</b>          |    |      |            |      |
| <i>minor</i> OTU 2          | 10 | 119  | 109–126    | 5.3  |
| <i>minor</i> OTU 4          | 10 | 125  | 110–141    | 8.8  |
| <i>myoxinus</i> OTU 6       | 9  | 141  | 125–149    | 7.3  |
| <i>myoxinus</i> OTU 7       | 5  | 142  | 133–160    | 10.7 |
| <i>majori</i> OTU 8         | 2  | 177  | 170–183    | —    |
| <i>tanala</i> OTU 10        | 12 | 183  | 166–204    | 11.8 |
| <i>tanala</i> OTU 11        | 14 | 185  | 163–210    | 12.5 |
| <i>webbi</i> OTU 15         | 15 | 179  | 165–195    | 8.2  |
| <i>webbi</i> OTU 17         | 12 | 175  | 155–195    | 10.8 |
| <i>petteri</i> OTU 18       | 2  | 191  | 178, 205   | —    |
| <i>ellermani</i> OTU 19     | 1  | 177  | —          | —    |
| <b>Dry Hind Foot Length</b> |    |      |            |      |
| <i>minor</i> OTU 4          | 11 | 22.6 | 22.0–23.5  | 0.5  |
| <i>myoxinus</i> OTU 6       | 9  | 26.3 | 25.0–28.5  | 1.1  |
| <i>myoxinus</i> OTU 7       | 7  | 26.5 | 25.5–28.0  | 1.1  |
| <i>majori</i> OTU 8         | 4  | 28.5 | 27.0–29.5  | 1.1  |
| <i>penicillatus</i> OTU 9   | 8  | 28.7 | 27.5–30.0  | 0.9  |
| <i>tanala</i> OTU 10        | 15 | 33.3 | 30.0–36.5  | 1.8  |
| <i>tanala</i> OTU 11        | 15 | 32.9 | 31.5–34.5  | 0.9  |
| <i>webbi</i> OTU 15         | 17 | 30.6 | 29.0–32.0  | 0.8  |
| <i>webbi</i> OTU 17         | 12 | 30.7 | 29.5–32.0  | 0.7  |
| <i>petteri</i> OTU 18       | 2  | 32.3 | 31.5, 33.0 | —    |
| <i>ellermani</i> OTU 19     | 2  | 33.5 | 33.0, 34.0 | —    |
| <b>Weight</b>               |    |      |            |      |
| <i>minor</i> OTU 4          | 11 | 34   | 25–39      | 4.6  |
| <i>tanala</i> OTU 11        | 17 | 90   | 66–115     | 12.5 |
| <i>webbi</i> OTU 15         | 14 | 78   | 64–93      | 10.1 |
| <i>petteri</i> OTU 18       | 1  | 74   | —          | —    |

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