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Systematic Revision of Sub-Saharan African Dormice (Rodentia: Myoxidae: *Graphiurus*) Part 1: An Introduction to the Generic Revision, and a Revision of *Graphiurus Surdus*¹

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ABSTRACT

African dormice, genus *Graphiurus* (Rodentia: Myoxidae), occur from the Cape of Good Hope to Senegal. The genus has never been adequately revised, and thus the species diversity within the genus, interspecific relationships, and biogeography have not been documented. This report constitutes the first of seven papers whose collective purpose is to provide a morphological revision of the genus, explore the phylogenetic relationships of species or species groups within the genus, and document biogeographic patterns inferred from species distributions and relationships. Over 2700 museum specimens of African dormice have been examined and measured from institutions in the United States, Europe, and Africa for this study.

This introductory paper, that includes a revision

of *Graphiurus surdus*, represents the first distillation of the large amount of data that has been collected. The completed revision of the genus will form one of the few comprehensive taxonomic revisions for any group of African rodents in which the intent is to present a reliable estimate of species diversity and document patterns of geographical distributions. It will provide a framework for the future tasks of testing hypotheses of species limits and interspecific relationships within *Graphiurus* using molecular and perhaps other anatomical data, and determining the significance of the documented geographic distributional patterns relative to distributions of other African mammals and environmental associations.

This first report contains an introduction to the

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entire revision, including an overview of the intended scope and organization, and a review of historic taxonomic treatments of species of *Graphiurus*. A species account of *Graphiurus surdus*, and a comparison of that species with *G. christyi* and *G. lorrainus*, follows. *Graphiurus surdus* was previously known only from southern Cameroon; its range is shown to extend at least to northeast and central Zaire. *Graphiurus schwabi*, previously thought to be a synonym of *G. lorrainus*, is allocated as a junior synonym of *G. surdus*. *Graphiurus surdus* has alternately been recognized as a valid species, included in the problematic species complex *G. murinus*, or obscured along with *G. lorrainus* under *G. murinus lorrainus*.

Comparisons with *G. christyi*, a member of the *G. murinus* complex from the same geographic area, show that there are significant shape differ-

ences between the two similarly sized species. Although the geographic range of both extends from southern Cameroon to northeast and south-central Zaire, the two have never been taken at the same collecting locality, and may have different microhabitat requirements.

Comparisons are also made between *G. surdus* and *G. lorrainus*, as *G. surdus* has previously been synonymized with *G. lorrainus* as a subspecies of *G. murinus*. *Graphiurus lorrainus* is not allied with the *G. murinus* complex, and is sympatric with representatives of that assemblage throughout its range, including *G. christyi*. Sympatry of *G. lorrainus* with *G. surdus* in southern Cameroon and central Zaire is documented. Comparisons between the two species show that they are easily separated by significant size and shape differences.

RESUMÉ

Les loirs africains du genre *Graphiurus* (Rodentia: Myoxidae) ont une distribution géographique allant du Cap au Sénégal. Ce genre n'a jamais été révisé de façon adéquate. Par conséquent, ni la diversité spécifique intragénérique, ni les relations interspécifiques non plus que la biogéographie ne sont bien documentées. Ce rapport est la premier d'une série de sept publications décrivant la morphologie du genre *Graphiurus*, les relations phylogénétiques entre espèces ou groupes d'espèces, ainsi que les modèles biogéographiques qui découlent des distributions spécifiques et des relations phylogénétiques.

Pour réaliser cette étude, plus que 2700 spécimens conservés dans des institutions scientifiques américaines, européennes, et africaines ont été examinés et mesurés.

Cette introduction, qui comprend une révision de *Graphiurus surdus*, doit être considérée comme le premier "distillat" de la masse de données dont nous disposons. La révision complète du genre formera une des rares études taxonomiques exhaustives d'un groupe de rongeurs africains dans le but d'en présenter une évaluation fidèle de sa diversité spécifique et de formuler des schémas de distribution géographique. Elle fournira le cadre approprié pour tester les hypothèses futures concernant les limites spécifiques et les relations interspécifiques dans le genre *Graphiurus* à l'aide de données moléculaires et, peut-être d'autres données anatomiques, ainsi que pour évaluer la valeur des modèles biogéographiques par rapport à ceux d'autres Mammifères africains et les associations avec l'environnement.

Ce premier texte comprend outre une introduction à la révision globale, un résumé du plan de

travail et une récapitulation historique de la position taxonomique des espèces de *Graphiurus*. Suit une redéfinition spécifique de *G. surdus*, et une comparaison de cette espèce avec *G. christyi* et *G. lorrainus*.

Jusqu'alors, *G. surdus* était connu uniquement au Sud du Cameroun mais nous avons démontré que son aire de distribution s'étend au moins jusqu'aux régions centrales et du Nord-Est du Zaïre. *Graphiurus surdus* a été successivement retenu comme espèce valide, inclu dans le complexe spécifique douteux de *G. murinus*, ou regroupé comme sous-espèce avec *G. lorrainus*. *Graphiurus schwabi* doit être mis en synonymie avec *G. surdus*.

Des comparaisons avec *G. christyi*, un membre du complexe spécifique de *G. murinus*, habitant le même région géographique et de même taille, ont montré qu'il y a des différences morphologiques importantes. Bien que la distribution géographique de ces deux espèces couvre une région allant du Sud du Cameroun au Nord-Est du Zaïre, elles n'ont jamais été récoltées dans la même localité mais pourraient exiger des microhabitats différents.

Des comparaisons de *G. surdus* et de *G. lorrainus*, s'imposaient aussi parce que le premier a été mis en synonymie et regroupé avec le second sous le nom de *G. murinus lorrainus*. Toutefois, *G. lorrainus* ne peut être inclu dans le complexe *G. murinus*. Il est sympatrique, sur toute son aire de distribution, des représentants de ce groupe d'espèces, y compris *G. christyi*. La sympatrie de *G. lorrainus* et de *G. surdus* au Sud du Cameroun et au Zaïre central a été démontrée. Ces deux espèces peuvent être distinguées aisément par des différences de taille et de forme.

INTRODUCTION

Recent quality systematic revisions of inadequately studied groups often result in the recognition of a greater diversity of species in those groups than was previously acknowledged. For some smaller and relatively well-known groups, such as mammals, species diversity estimates might produce higher numbers and be made more accurate by focusing more attention on recent systematic revisions in addition to the relatively few descriptions of new taxa that are published each year. These estimates may then provide finer documentation of biogeographic patterns, and aid in assessing conservation priorities.

Objections might be made that estimates of species diversity depend on the particular species concepts used by the authors of systematic revisions. The same arguments apply to descriptions of new species; one worker might reason that a "new species" is simply a diagnosable population that should not be recognized as a separate species, whereas others may feel that the population should be recognized as a species precisely because it is diagnosable. Species concepts obviously affect the numbers of species recognized by a given author, and if the concept followed is at either end of the theoretical spectrum (see Endler, 1989; Frost and Hillis, 1990; O'Hara, 1994; and Templeton, 1989, for reviews), the differences in numbers of species recognized can be dramatic (see discussions in Cracraft, 1989; O'Hara, 1994; and Patton and Smith, 1994). A perusal of mammalian systematic literature reveals that most authors explicitly or implicitly use the reproductive isolation species concept *sensu* Mayr (1942, 1969), providing either genetic proof or evidence (sympatry or morphological divergence) of reproductive isolation. The theoretical (but not necessarily operational) species concept followed by most modern mammalian systematists is therefore somewhat pervasive. The relative strengths and weaknesses of the isolation and other process-based species concepts versus phylogenetic concepts have been extensively discussed (e.g., Baum, 1992; de Queiroz and Donoghue, 1988, 1990a, 1990b; Nixon and Wheeler, 1990; O'Hara, 1994). Although I do not support universal usage of a particular species concept, my rea-

sons for following the conceptual approach taken in this revision are detailed below under Materials and Methods.

Workers who adopt the same theoretical species concept may obtain different estimates of species diversity for a given group, because there are often several subjective estimates of diversity that can be justified by differing operational practices consistent with the same theoretical concept. Therefore, the operational concept followed in a given work should be clearly stated. In addition, it is essential that adequate data are presented for reasonable geographic samples (populations) of each alleged species, if such samples are available. Researchers who adopt different operational or theoretical species concepts may then make use of data contained in such revisions and possibly build upon them, even if they reject the overall estimate of species diversity, or species diagnoses.

New species of small African mammals are described each year (for example, look at species accounts of African shrews in Hutterer, 1993, and African muroid rodents in Musser and Carleton, 1993), and new species of large African mammals are even occasionally discovered (*Cercopithecus solatus* from Gabon, for example; see Groves, 1993) or rediscovered (*Phacochoerus africanus*, the other species of warthog; see Grubb, 1993). However, many groups of small and some larger African mammals require taxonomic revisions that address questions regarding diversity of genera and species, as well as biogeographic patterns.

In the absence of sound revisions describing species limits, ecological studies are often compromised, if not rendered useless, if the taxonomy followed is incomplete or incorrect. For example, the very few ecological studies that include African dormice are often only informative at the generic level. The assignment of the specimens to problematic species or species complexes without comment obscures the true identities of the species reported upon. Voucher specimens are frequently not collected, and detailed descriptions of the animals caught are often lacking. Well-documented revisions of problematic groups would help alleviate such

weakened efforts by providing accessible references upon which ecologists may rely.

These systematic revisions would ideally be based on a combination of morphological and molecular data; however, for most small African mammal taxa, potential morphological samples (in the form of museum specimens) abound, whereas molecular samples are few, if they exist at all. For this reason morphological systematic studies are often essential before any sense can be made of the often incidental molecular data. Morphological studies also give critical information, such as locations of potential hybrid or contact zones, that could help make molecular sampling over this vast continent more efficient.

One group of small African mammals that has not yet received rigorous review is the genus *Graphiurus* (Myoxidae: Rodentia), a group of dormice occurring throughout most of the habitats found in Africa south of the Sahara. Estimates of the number of species in *Graphiurus* have been made in several checklists (e.g., Allen, 1939; Ellerman, 1940; Holden, 1993), and an identification manual (Misonne, 1974), and were the foci of both a generic revision (Genest-Villard, 1978) and regional taxonomic revisions (e.g., Robbins and Schlitter, 1981; Schlitter et al., 1985; Ansell, 1974; Ansell and Dowsett, 1988). However, no comprehensive systematic revision of the genus is available that documents the number of species in the group, their unambiguous morphological and distributional limits, their phylogenetic relationships, and their contribution to understanding African biogeography.

I intend to provide a new estimate of the number of species in *Graphiurus* that will derive from a comprehensive, substantially documented systematic revision of the genus, based on detailed examination of more than 2700 specimens. A revision of *G. surdus* is included in this first of an intended series of reports. Each subsequent paper will include accounts of one or more additional species. Each species account will contain history of taxonomic treatment, synonyms (if any), morphological description, geographic distribution, morphometric comparisons with other taxa, and discussion of significant geographic variation. Any karyological, molecular, or ecological information (though often minimal) will be included. In the final report

I will review the number of species detected and their diagnostic morphological features in the context of characterizing the genus *Graphiurus*, attempt to reconstruct possible phylogenetic relationships among the species or species groups, explore biogeographic patterns found within the genus, and summarize any concordance between geographic distributions of dormice species with ranges of other African vertebrate groups. Finally, the significance of the evolutionary interspecific alliances, and the geographic and ecological distribution of each species, in understanding present biogeographic patterns in Africa will be explored.

MATERIALS AND METHODS

INSTITUTIONS: Specimens I examined for this report (Part 1) of the *Graphiurus* revision are housed in collections of the following institutions (identified throughout the report by the appropriate acronym):

AMNH	American Museum of Natural History, New York
BM(NH)	The Natural History Museum, formerly the British Museum (Natural History), London
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
KM	Kaffrarian Museum, King William's Town
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MHNG	Muséum d'Histoire Naturelle de Genève, Genève
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAC	Musée Royal de l'Afrique Centrale, Tervuren
RUCA	Universiteit d'Anvers, Rijksuniversitair Centrum Antwerpen, Antwerpen
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main
TM	Transvaal Museum, Pretoria
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMB	Zoologisches Museum und Institut für Spezielle Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin

CHOICE OF MEASUREMENTS: Genest-Villard (1978) explained why she found certain measurements of the skull and dentition to be important in dormice systematics. The 24 cranial and dental measurements I employed for this study were chosen because: 1) based on a preliminary survey I thought them to be potentially informative of species-level differences (they varied among species); 2) they sample a variety of cranial and dental features; 3) I could compare them directly with data presented in the only previous taxonomic revision (Genest-Villard, 1978), and regional studies (e.g., Robbins and Schlitter, 1981; Schlitter et al., 1985), even if I had to take redundant measurements, such as crown length of M1-M3 (preferred by me), and crown length of P4-M3 (published in the literature), and breadth of M1 (preferred by me) versus breadth of M2 (found in the published literature); 4) some regions of preserved crania are commonly damaged, and I sometimes took alternative measurements that estimated a similar dimension, because it was impossible to predict which measurement would yield a larger sample. (For example, I preferred condyloincisive length for estimating cranial length, but many examples of some species have missing or broken incisors and damaged incisor alveoli; greatest length of skull was also taken so that I would potentially have larger samples with an estimate of skull length of those species to include in morphometric analyses.) In selecting craniodental measurements with the above considerations in mind, I was sensitive to the discussion by Voss (1988: 361), in which ideal measurement protocols were weighed against practical limitations.

I did not restrict my suite of measurements to include only those that were obtainable from most crania, which could be included in multivariate analyses, for descriptive statistics could still be calculated for those potentially informative measurements. For the multivariate analyses I simply extracted the sample of specimens that had complete measurement sets for an informative subset of the 24 dimensions measured.

MEASUREMENTS: Values for external, cranial, and dental measurements are given in millimeters. Length of head and body (LHB), length of tail (LT), length of hind foot (LHF), and length of ear (LE) were the only external

measurements used in statistical analyses. Most values for the latter three were taken from labels attached to study skins; I measured lengths of hind foot (including claws) and ear on a few dry skins and fluid-preserved specimens. Total length was also recorded on most labels, and I obtained length of head and body by subtracting tail length from the total length. Weights (WT), in grams, were sometimes recorded by collectors and these were included in some summary statistics.

External measurements reflect not only the variation due to age, sex, and individual expression inherent in any sample, but to measuring techniques and competence of the variety of collectors who are represented in these samples. In particular, two techniques of measurement of hind foot length (inclusive and exclusive of claws) were represented in samples of all species. I used the hind foot length and the other external measurement values in my analyses as a general guide to differences and similarities in size and proportions but excluded them from multivariate analyses. Despite differences in measurement techniques and accuracy, the size and proportional differences between the species summarized in the ratio diagrams and summary statistics mirror those observed upon first-hand examination of specimens. Genest-Villard (1978), who has provided the only published revision of *Graphiurus*, used some of these same external measurements and presents her interpretation of their strengths and weaknesses in diagnosing species.

Cranial and dental measurements were taken with dial calipers graduated to tenths of millimeters. The limits of each measurement are illustrated in figure 1. These measurements are abbreviated in text, tables, and figures as follows:

GLS	greatest length of skull
CIL	condyloincisive length
ZB	zygomatic breadth
IB	interorbital breadth
BBC	breadth of braincase
HBC	height of braincase
BR	breadth of rostrum
LHR	least height of rostrum
LN	length of nasals
LD	length of diastema
PL	palatal length
LBP	length of bony palate

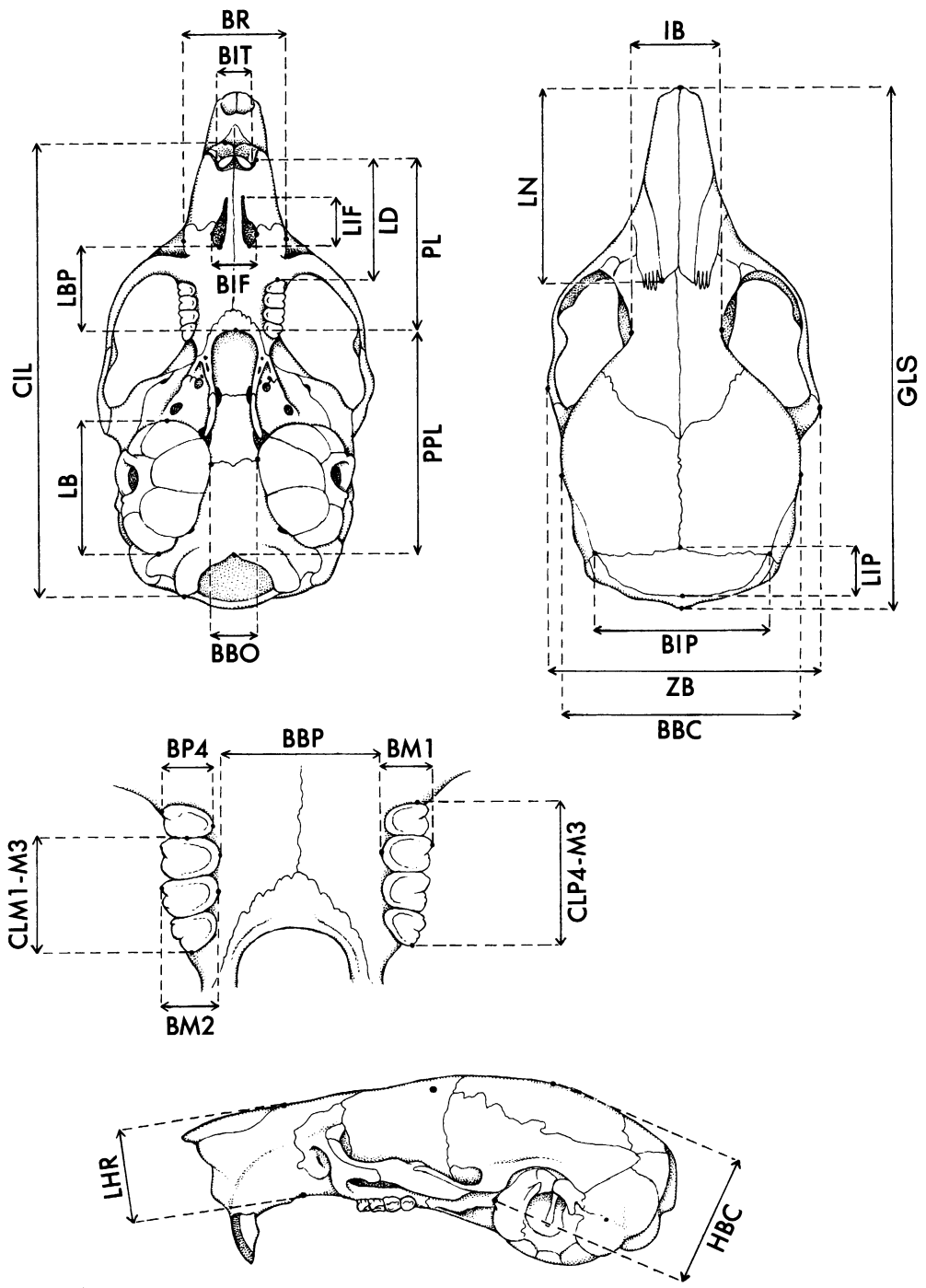


Fig. 1. Diagrammatic views of cranium and toothrows of an adult *Graphiurus christyi* illustrating limits of cranial and dental measurements.

LIF	length of incisive foramina
BIF	breadth of incisive foramina
BBP	breadth across bony palate at M1
CLP4-M3	crown length of maxillary toothrow
CLM1-M3	crown length of maxillary molar row
BP4	breadth of fourth upper permanent premolar
BM1	breadth of first upper molar
BM2	breadth of second upper molar
BIT	breadth of upper incisor tips
PPL	postpalatal length
LB	length of auditory bulla
BBO	breadth of basioccipital

MANDIBLE AND DENTITION: The *Graphiurus* dentary was illustrated by Wahlert et al. (1993: 15); that conformation typifies all the species. I neither measured the mandibles of *Graphiurus* nor used their traits to help distinguish among taxa. I surveyed the dentaries in all my samples and, except for differences in size, could not detect qualitative traits that increased my ability to distinguish among taxa over what was present in the crania.

My study of dentition is limited to morphometric comparisons among taxa. I did not survey occlusal patterns to determine whether the variation seen enabled discrimination among species, or provided characters useful in resolving phylogenetic relationships. The premolars and molars of all species of *Graphiurus* are simple and basined, their occlusal surfaces vaguely sculptured by low ridges and shallow valleys in patterns illustrated by Wahlert et al. (1993: 18) for *G. lorrainensis* and in figure 5 for *G. surdus*. These indistinct patterns are typical of those found in most species of *Graphiurus*, with the notable exceptions of *G. crassicaudatus* and *G. huetti*. They exhibit high variability and I found them extremely difficult to examine critically without electron microscopy. Determining the significance of variation in occlusal patterns within and between species would be an arduous study by itself. Results of such an inquiry could be used to test hypotheses formulated in my revision, which is based on other characters.

The occlusal patterns of most species of *Graphiurus* have never been documented, and if adequate specimens are available, a scanning electron micrograph of the occlusal surface of one example of each species diagnosed will be included. Such a coarse survey of oc-

clusal patterns present in African dormice may reveal whether the patterns exhibit interesting interspecific variation for phylogenetic studies, and may aid in diagnoses of extant and extinct species.

AGE CRITERIA AND SAMPLES: Specimens were assigned to one of four age classes based primarily on stage of tooth eruption and wear, but degree of fusion of cranial sutures as well as pelage characteristics were also evaluated. The range from young adults through old adults provided the data for morphometric analyses and computation of summary statistics and ratio diagrams. Combining this broad range of adult stages was necessary to obtain adequate samples for analysis; series of African dormice are, with a few exceptions, characteristically small and from scattered localities.

The age classes recognized are:

Juvenile: Deciduous upper fourth premolar (DP4) present, or occlusal surface of fourth premolar (P4) not yet even with chewing surface of molar row.

Young Adult: Occlusal surface of P4 level with top of molar row, but exhibits little or no wear, molars unworn or only slightly so.

Adult: All teeth moderately worn (lingual and labial facets worn, transverse ridges worn but not obliterated).

Old Adult: Premolars and molars very worn and sometimes sharply beveled or eroded on their labial surfaces, many or all transverse ridges obliterated or distorted, occlusal surfaces often worn flat to the roots.

SEXUAL DIMORPHISM AND SAMPLES: Females and males of the species of *Graphiurus* included in this first report are approximately equal in body size and very similar in morphological characters not associated with sexual traits. No adequate sample (at least 10 females and 10 males, young adults to old adults with complete crania, from the same locality) exists from which to derive univariate statistics of each sex in the samples of either *G. surdus* or *G. christyi*. There is such a series available for *G. lorrainensis*, but it is from Ndola, Zambia, which is outside the geographic region that is encompassed by this report on *G. surdus*. Nevertheless, this sample illustrates the nature of intergender

TABLE 1

Summary Statistics for Cranial and Dental Measurements (mm) of Female and Male *Graphiurus lorrainaeus* from Ndola, Zambia

(Mean, \pm 1 SD, observed range [in parentheses], and number of specimens in sample are listed for each measurement. An ontogenetic range from young to old adults is represented in the total sample of each gender. No statistically significant differences [at the $\alpha = 0.05$ level] exist between sample means of males and females for any of the measurements listed below.)

	Females ^a	Males ^b
CIL	21.1 \pm 0.44 (20.2–21.8) 14	21.2 \pm 0.33 (20.5–21.9) 14
ZB	13.8 \pm 0.41 (13.0–14.4) 14	14.1 \pm 0.30 (13.5–14.5) 14
IB	3.9 \pm 0.15 (3.6–4.2) 14	4.0 \pm 0.13 (3.8–4.2) 14
BBC	11.8 \pm 0.34 (10.9–12.2) 14	11.9 \pm 0.27 (11.4–12.3) 14
HBC	7.1 \pm 0.25 (6.6–7.5) 14	7.3 \pm 0.21 (7.0–7.6) 14
BIT	1.4 \pm 0.12 (1.3–1.6) 14	1.5 \pm 0.12 (1.2–1.7) 14
LHR	4.3 \pm 0.18 (4.0–4.5) 14	4.4 \pm 0.12 (4.3–4.7) 13
LN	8.1 \pm 0.24 (7.8–8.6) 14	8.2 \pm 0.19 (8.0–8.5) 13
LD	4.7 \pm 0.16 (4.5–5.0) 14	4.7 \pm 0.12 (4.5–4.9) 14
PL	7.6 \pm 0.23 (7.2–7.9) 13	7.7 \pm 0.13 (7.4–7.9) 14
PPL	10.3 \pm 0.35 (9.6–10.9) 13	10.3 \pm 0.26 (9.8–10.6) 14
LIF	2.8 \pm 0.21 (2.4–3.0) 14	2.7 \pm 0.20 (2.4–3.2) 14
BIF	1.7 \pm 0.08 (1.5–1.8) 14	1.7 \pm 0.11 (1.5–1.8) 14
BBP	2.7 \pm 0.18 (2.4–3.1) 14	2.7 \pm 0.16 (2.3–2.9) 14
CLP4-M3	3.1 \pm 0.12 (2.9–3.3) 14	3.1 \pm 0.10 (3.0–3.3) 14
CLM1-3	2.5 \pm 0.11 (2.3–2.7) 14	2.5 \pm 0.08 (2.4–2.7) 14
BM1	1.1 \pm 0.05 (1.0–1.1) 14	1.1 \pm 0.05 (1.0–1.1) 14
BM2	1.2 \pm 0.05 (1.1–1.2) 14	1.1 \pm 0.07 (1.0–1.2) 14
BP4	0.9 \pm 0.06 (0.8–1.0) 14	0.9 \pm 0.07 (0.8–1.0) 14
LB	7.3 \pm 0.18 (7.0–7.6) 14	7.3 \pm 0.16 (6.9–7.4) 14
LBP	3.9 \pm 0.18 (3.6–4.1) 13	4.0 \pm 0.16 (3.8–4.3) 14
BBO	1.9 \pm 0.17 (1.5–2.3) 14	2.1 \pm 0.11 (1.9–2.3) 14
BR	4.9 \pm 0.30 (4.4–5.5) 14	4.9 \pm 0.26 (4.5–5.4) 14

^a BM(NH) 20.11.3.106–20.11.3.108, 20.11.3.110–20.11.3.114; KM 3765; TM 2570, 2576, 2587, 2589, 2593.

^b BM(NH) 20.11.3.96, 20.11.3.101–20.11.3.105; KM 3766; TM 2571, 2573, 2577, 2580, 2582, 2583, 2585.

sexual variation also encountered within samples of *G. surdus* and *G. christyi*, and it is the one for which meaningful summary univariate statistics could be calculated separately for females and males. Comparisons between the sexes of *G. lorrainaeus* are presented in table 1. There are no statistically significant differences (at the $\alpha = 0.05$ level) between sample means of females and males for any of the cranial and dental measurements listed. All other univariate and multivariate statistical analyses were performed on samples that included whatever combination of genders were present in a collection from a particular locality (or pooled localities): either all females, all males, or a mixture of both.

MULTIVARIATE ANALYSES: Morphometric comparisons among species samples of *Graphiurus* were analyzed by factors representing

general size (growth) and growth-invariant divergence (Voss et al., 1990; Voss and Marcus, 1992). All analyses were based on measurements transformed to their natural logarithms. The factor coefficients of general size (which includes allometry) were estimated as the elements of the first eigenvector of the pooled-within covariance matrix. Specimen scores on general size are age-correlated within species, specimens with unworn teeth generally having smaller size scores than conspecifics with well-worn teeth. The normalized coefficients of size-invariant species divergence were calculated from mean differences estimated in variable-by-variable analyses of covariance (ANCOVAs) with general size as the covariate; the requisite assumption of equal slopes was evaluated by eye. In view of the motley composition of species samples (which contain, in some cases,

conspecifics from widely scattered populations), and the general lack of information to evaluate sampling assumptions, tests for statistical significance of species differences are best avoided. Instead, I emphasize the relative magnitude of size-adjusted difference coefficients and the congruence of multivariate results with visually obvious contrasts in arguing the biological significance of morphometric comparisons.

SPECIES CONCEPT: The theoretical concept followed in this report is the cohesion species concept (Templeton, 1989). Beurton (1995) recently proposed that gene circulation, which he usefully differentiated from gene flow, is the fundamental cohesion mechanism. As he pointed out, the concept of "gene flow" used by Mayr (1942, 1963, and other references to Mayr listed by Beurton, 1995: 195), Templeton (1989), and others implicitly includes gene circulation. However, Beurton does not demonstrate that gene flow, in the strict sense defined by him, is not an important cohesion mechanism in some cases. Rather than viewing Templeton's broad cohesion species concept and the relatively limited "Heraclitean" species concept of Beurton, that espouses gene circulation as the fundamental cohesion mechanism, as alternative concepts, it seems better to add gene circulation (or separate it from the broader category of gene flow) to Templeton's classification of cohesion mechanisms (Templeton, 1989: 13).

A species concept "... that is consistent with recovered phylogenetic history" (Frost and Hillis, 1990) is intellectually appealing, and it is recognized that "... the potential for gene exchange is only loosely coupled to historical relatedness—the central consideration of systematics" (Baum, 1992). However, monophyly of species may be the exception rather than the rule (Patton and Smith, 1994), and in many cases the application of phylogenetic concepts is fraught with at least as many difficulties as process-based species concepts (Baum, 1992; O'Hara, 1994; Patton and Smith, 1994).

One phylogenetic species concept requires that a group of organisms possess at least one "diagnostic character," either primitive or derived (Cracraft, 1983, 1987, 1989; Wheeler and Nixon, 1990; Nixon and Wheeler, 1990), and furthermore that the character must be

inferred to have a genetic basis, be fixed within the species (present in all individuals), and absent from closely related species (Baum, 1992; Cracraft, 1983, 1987, 1989; Davis and Manos, 1991). Groups of African dormice that are obviously "species" (in some cases sympatric) can sometimes only be diagnosed by a combination of characters, because some characters are either not present or hard to distinguish in some individuals (particularly juveniles), and in those cases other distinguishing characters (that also may not be exhibited in 100 percent of the specimens) need to be considered. Even if the requirement of 100 percent diagnosability were met, some of the distinguishing characters are not always absent from "close relatives." The interspecific relationships of African dormice have yet to be explored, so that all (except for a few obviously morphologically divergent species) hypothesized species of *Graphiurus* are at present considered close relatives.

The alternative phylogenetic species concept emphasizes the criterion of monophyly, with the intention of circumventing problems with the diagnosability standard (Baum, 1992; de Quieroz and Donoghue, 1988, 1990; Donoghue, 1985; Mishler and Brandon, 1987; Ridley, 1989; Rosen, 1979). Applying the criterion of monophyly to species, however, is problematic (Wheeler and Nixon, 1990; Nixon and Wheeler, 1990), and summarized by Baum (1992):

Thus, species monophyly is a difficult criterion to apply using currently available cladistic methodologies, and even if monophyly could be accurately assessed this would still leave the problem of establishing exclusivity of descent. It remains to be seen whether protocols can be developed for studying species monophyly and exclusivity ... and whether these will be sufficiently practical to gain acceptance in the systematic community.

As no practical protocol for studying species monophyly and exclusivity has been generated, for this study it seems reasonable to focus on subjective estimates of genetic or ecological cohesion, based on shared distinctive, diagnosable morphologies (of sometimes unknown polarity, and sometimes only diagnosable by a combination of characters) over geography, and ecological data. It is pos-

sible that species diversity may be underestimated if morphological divergence has not accompanied speciation, but data to discern such situations are unavailable at present. Additionally, molecular data might provide evidence for recognizing a greater (or lesser) diversity of species of *Graphiurus* than hypothesized by this revision, but at present no molecular samples exist for most species of African dormice, and no species has been adequately sampled across its geographic range.

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HISTORICAL TAXONOMIC TREATMENTS OF TAXA

Members of *Graphiurus* occur throughout sub-Saharan Africa, from the Cape of Good Hope north to Senegal in the northwest and Somalia in the northeast. Significant variation in morphology and ecology would be expected in small-bodied rodents found over such a vast continental region. Such variation is typical of *Graphiurus* as is evident by the four generic and 76 specific and subspecific scientific names proposed by taxonomists to represent the impressive morphological diversity detected within the genus.

Taxonomic information about subsaharan dormice has been summarized in eight primary reports published between the late 1800s and the present. Highlights of each are listed below. These references cover the spectrum of species and are not regionally focused. Other taxonomic reports and checklists of species present taxonomic information for particular geographic regions: southern Africa (Shortridge, 1934; Roberts, 1951; Ellerman et al., 1953; de Graaff, 1981; Meester et al., 1986; Skinner and Smithers, 1990); Botswana (Smithers, 1971); Zimbabwe (Smithers and Wilson, 1979); Zambia (Ansell, 1974, 1978); Malawi (Ansell and Dowsett, 1988); Mozambique (Smithers and Tello, 1976); Tanzania (Swynnerton and Hayman, 1951);

Angola (Hill and Carter, 1941); Zaire (Hatt, 1940); Kenya (Hollister, 1919); Uganda (Delany, 1975); Ethiopia (Yalden et al., 1976), and West Africa (Rosevear, 1969; Robbins and Schlitter, 1981; Schlitter et al., 1985). A survey of the treatments of dormice taxa found in those publications is not included here. That information will be evaluated in appropriate accounts of species in forthcoming sections of my revision of *Graphiurus*.

I include this historical perspective on species diversity within *Graphiurus* here for two reasons. It summarizes various taxonomic treatments and philosophies of researchers who have worked with the group and provided differing hypotheses of species numbers and definitions, and it will be useful for my subsequent reports. The different treatments also provide the past taxonomic context in which *surdus*, the taxon I discuss in this first paper, has been viewed by other workers.

Four generic names, all published between 1832 and 1936, have been proposed for grouping the morphological variation observed in sub-Saharan African dormice. The validity of the species clusters designated by these generic titles will be addressed in the final section of my systematic revision. Until then I will use *Graphiurus* for all the species of sub-Saharan dormice treated in my revision. *Graphiurus* is the oldest valid name for the genus and was proposed by Smuts (1832) for *capensis*, which is a synonym of the South African *ocularis*, one of the most distinctive species in the genus. The three other generic names used for sub-Saharan species are introduced below.

More than 50 years after *Graphiurus* was proposed, Jentink (1888) described a new species, the small-bodied *crassicaudatus* from Liberia. He thought its tail to be so unusual that he placed the species in a new genus, *Claviglis* ("characterized by a club-shaped, not distichous tail," Jentink, 1888: 42).

Jentink's genus was recognized by Thomas and Hinton in 1925 (p. 232) when they reported on material collected in "South-West Africa" (Namibia). They described a new species and subspecies of dormouse and noted that "... in determining these specimens we have made an examination of all the African Dormice commonly referred to the ge-

nus *Graphiurus*. It has long been obvious to us that the Cape Dormouse (*Graphiurus ocularis*) as not properly congeneric with the other African species and we may take this opportunity to reclassify the group." Thomas and Hinton proposed the genus *Gliriscus* for rock dormice, with *G. platyops* as the type species, and provided key characteristics by which it, *Graphiurus* (containing only the Cape dormouse), and *Claviglis* (all the forest dormice) could be distinguished from one another.

Finally, Allen (1936) proposed *Aethoglis*, with "genotype *Graphiurus nagtglasii* Jentink" for *hueti*, an older name for the same species represented by *nagtglasii*. The large body size of *hueti*, along with a variety of pelage, cranial, and dental traits, were used by Allen to diagnose the new genus.

In his "Checklist of African Mammals," Allen (1939) recognized all four genera. Lists and revisions published after Allen's compilation, however, admitted only the genus *Graphiurus*, but taxonomic arrangements below this level were characterized by disagreement. Some easily distinguished species, such as *G. crassicaudatus*, *G. hueti*, and *G. ocularis*, retained their integrity in most checklists and revisions, and rarely were the subjects of taxonomic confusion (*crassicaudatus* as treated by Misonne, 1974, is an exception). Others, such as *G. parvus*, *G. surdus*, and *G. lorrainensis* have been alternately lumped into one widely distributed, morphologically variable species, usually identified as *G. murinus*, or separated into geographically restricted species without substantive documentation of their species limits. These disparate treatments of the species are summarized below.

1. **Reuvs (1890a):** "Die Myoxidae Oder Schlaefer," Reuvs's privately published "Inaugural-Dissertation" that was the first comprehensive treatise on the osteology and systematics of dormice. Extracts of the Dissertation were published the same year in Notes from the Leyden Museum (Reuvs, 1890b). The sub-Saharan species recognized by Reuvs were placed in three subgenera of the genus *Myoxus*.

FAMILY MYOXIDAE

Genus *Myoxus*

Subgenus *Eliomys*

"*E. nagtglasii*"
 "*E. kelleni*"
 "*E. crassicaudatus*"
 "*E. murinus*"
 "*E. orobinus*"

Subgenus *Graphiurus*

"*G. capensis*"
 "*G. hueti*"

Subgenus *Myoxus*

M. elegans

2. **Trouessart (1897):** "Catalogus mammalium tam viventium quam fossilium" and an appendix of "addenda et corrigenda." This, the first real catalog or checklist that included sub-Saharan dormice taxa, was a prominent reference in its time and the list to which subsequent authors—Allen (1939), for example—compared their contributions. Notice that during Trouessart's time, many sub-Saharan species were allocated to the genus *Eliomys*, a group we now realize contains only North African, Middle Eastern, and European forms, and one that is phylogenetically not closely related to sub-Saharan *Graphiurus* (Wahlert et al., 1993).

FAMILY MYOXIDAE

Genus *Eliomys* (synonym: *Claviglis*)

E. natglasii (sic)
E. kelleni
E. smithii
E. parvus
E. nanus
E. crassicaudatus
E. murinus (synonyms: *coupei*, *lalandianus*, *erythrobronchus*, *cineraceus*, *microtis*)
E. orobinus

Genus *Graphiurus*

G. capensis (synonyms: *ocularis*, *cattoiri*, *typicus*, *elegans*)
G. hueti

In an appendix of "addenda et corrigenda" Trouessart (1899) made these changes and additions:

Genus *Graphiurus*

G. hueti (synonym: *natglasii* [sic])
G. johnstoni
G. angolensis

3. **Trouessart (1904):** "Catalogus mammalium tam viventium quam fossilium," the "quinquennale supplementum." In this last and most complete revision of his catalog, Trouessart transferred to *Graphiurus* the sub-

Saharan species he had formerly listed under *Eliomys* and made minor adjustments in synonymies.

FAMILY MYOXIDAE

Genus *Graphiurus*

G. hueti (synonym: *natglasii*)
G. crassicaudatus
G. kelleni
G. angolensis
G. smithi
G. johnstoni
G. parvus
G. nanus
G. murinus
G. platyops
G. ocularis (synonym: *capensis*)
G. orobinus

4. **Allen (1939):** "A Checklist of African Mammals," an influential reference of its time. Explaining the reason behind the checklist's creation, Allen noted "that the mammalian fauna of Africa is fairly well ascertained, and that the likelihood of many more really new genera or species being found is small. Nevertheless much revisionary work is yet to be done as adequate collections accumulate in the larger museums. As a first necessity in indicating what has been done and where further study is urgent, a complete checklist of the names applied to African mammals is here presented, intended to include all those currently regarded as valid as well as all synonyms through July 1938, so far as possible" (p. 3). Allen recognized all four genera, one of which he had described, and listed 37 species.

FAMILY MUSCARDINIDAE

Genus *Aethoglis*

A. hueti (valid subspecies: *hueti*, *argenteus*, *monardi*, *nagtglasii*)

Genus *Claviglis*

C. alticola
C. ansorgei
C. cuanzensis
C. brockmani (valid subspecies: *brockmani*, *internus*)
C. butleri
C. christyi
C. coupeii
C. crassicaudatus (valid subspecies: *crassicaudatus*, *dorotheae*)
C. foxi

- C. griselda*
- C. haedulus*
- C. schwabi*
- C. kelleni*
- C. littoralis*
- C. lorrainensis*
- C. murinus* (synonyms: *lalandianus*, *erythrobronchus*, *cineraceus*, *cinerascens*, *microtis*; valid subspecies: *griseus* [synonym: *johnstoni*], *isolatus*, *pretoriae*, *raptor*, *saturatus*, *selindensis*, *tzaneenensis*)
- C. nanus*
- C. olga*
- C. orobinus*
- C. parvulus*
- C. parvus* (valid subspecies: *parvus*, *dollmani*)
- C. personatus*
- C. smithii*
- C. soleatus* (valid subspecies: *soleatus*, *collaris*)
- C. spurrelli*
- C. streeteri*
- C. surdus*
- C. tasmani*
- C. vandami*
- C. vulcanicus*
- C. woosnami*
- C. zuluensis*
- Genus *Gliriscus*
 - G. angolensis* (valid subspecies: *angolensis*, *jordani*)
 - G. platyops*
 - G. rupicola* (valid subspecies: *rupicola*, *montosus*)
- Genus *Graphiurus*
 - G. eastwoodae*
 - G. ocularis* (synonyms: *typicus*, *capensis*, *elegans*)

5. Ellerman (1940): "The Families and Genera of Living Rodents. Volume I. Rodents Other than Muridae." Following Allen's list by only a year, Ellerman's work recognized only one African dormouse genus, *Graphiurus*, but did group the 40 species listed into three subgenera. He noted (p. 607) that *Graphiurus*,

... which is in much need of revision, is extremely difficult to arrange in any natural order. Apart from the subgenera, *Graphiurus*, for *ocularis*, and *Gliriscus* for *platyops* group, there remains a large assemblage of more normal African Dormice. Both Mr. Hayman and myself have tried to arrange these into groups, but without much success. Mr. Hayman reports: "Subgenus *Claviglis*, this contains the remainder and by far the largest number of African dormice. Attempts have been made to divide them into

groups of related forms, but apart from perhaps four easily distinguished forms the remainder do not appear separable into definite groups. Variation in size is considerable in some forms, so that overlapping invalidates any arrangement based on size, while although extremes of colour in the subgenus are wide (from pale grey to brown), division into groups based on colour breaks down when it is seen that in a very large series from northern Rhodesia nearly all the colour shades found in forms from elsewhere in the range of the genus are represented."

Ellerman could easily distinguish four species and noted that "certainly *monardi* and *crassicaudatus* and, I think, probably *woosnami* and *surdus* are sufficiently distinct to be regarded as types of specific groups. The remainder will have to be referred to a single group, in which it appears that there are far too many outstanding 'distinct species' at the present day" (p. 607).

FAMILY MUSCARDINIDAE

Genus *Graphiurus*

Subgenus *Graphiurus*

G. ocularis (synonyms: *capensis*, *typicus*, *elegans*, *cattoiri*)

Subgenus *Gliriscus*

G. platyops

G. eastwoodae

G. rupicola (valid subspecies: *rupicola*, *montosus*)

Subgenus *Claviglis* (synonym: *Aethoglis*)

hueti group

G. hueti (valid subspecies: *hueti*, *argenteus*, *nagtglasi* [sic])

crassicaudatus group

G. crassicaudatus (valid subspecies: *crassicaudatus*, *dorotheae*)

surdus group

G. surdus

woosnami group

G. woosnami

monardi group

G. monardi

murinus group

G. olga

G. orobinus

G. butleri

G. brockmani (valid subspecies: *brockmani*, *internus*)

G. foxi

G. parvus (valid subspecies: *parvus*, *dollmani*)

G. soleatus (valid subspecies: *soleatus*, *collaris*)

G. personatus
G. murinus (synonyms: *coupei*, *erythrobronchus*, *cineraceus*, *lalandianus*; valid subspecies: *murinus*, *tzaneenensis*, *isolatus*, *griseus* [synonym: *johnstoni*], *saturatus*, *raptor*)
G. microtis
G. smithi (sic) (synonym: *subrufus*)
G. ansorgei
G. lorraineus
G. spurrelli
G. haedulus
G. christyi
G. angolensis (valid subspecies: *angolensis*, *jordani*)
G. griselda (valid subspecies: *griselda*, *pretoriae*)
G. kelleni
G. nanus
G. johnstoni

Representatives of nine forms were not seen by Ellerman and "not allocated to group:"

G. alticola
G. littoralis
G. streeteri
G. tasmani
G. vandami
G. zuluensis
G. schwabi
G. parvulus
G. vulcanicus

6. Misonne (1974): "Order Rodentia" in "The Mammals of Africa, an Identification Manual." One genus, two subgenera, and five species were recognized by Misonne, and not all synonyms were listed.

FAMILY GLIRIDAE

Genus *Graphiurus*

Subgenus *Graphiurus*

G. ocularis

subgenus *Claviglis*

G. monardi

G. hueti ("includes" *argenteus*, *nachtglasii*)

G. platyops ("includes" *angolensis*, *australis*, *eastwoodae*, *jordani*, *kaokensis* [sic], *montosus*, *parvulus*, *rupicola*)

G. murinus ("includes" *alticola*, *ansorgei*, *brockmani*, *butleri*, *christyi*, *collaris*, *cuanzensis*, *coupei*, *dasilvai*, *dollmani*, *etoshae*, *foxi*, *griselda*, *griseus*, *haedulus*, *internus*, *isolatus*, *johnstoni*, *kelleni*, *littoralis*, *lorraineus*, *marrensis*, *microtis*, *nanus*, *olga*, *orobinus*, *personatus*, *pre-*

toriae, *raptor*, *saturatus*, *schneideri*, *selindensis*, *smithi* [sic], *soleatus*, *spurelli* [sic], *streeteri*, *sudanensis*, *surdus*, *tasmani*, *tzaneenensis*, *vandami*, *vulcanicus*, *woosnami*, *zuluensis*; "perhaps not readily separable from *murinus*:" *crassicaudatus*, *dorotheae* [sic])

7. Genest-Villard (1978): "Révision systématique du genre *Graphiurus* (Rongeurs, Gliridae)." Genest-Villard did not recognize subgenera, retained only six species, but noted that certain subspecies might turn out to be valid species. Although preceded by checklists and faunal accounts dealing with taxonomy of sub-Saharan dormice, her contribution was the only attempt to understand the array of morphological and ecological diversity represented by samples and present hypotheses of species limits within the context of a systematic revision of the entire genus. Her results would eventually be tested and some conclusions not accepted (for example, Ansell, 1978, 1989; Robbins and Schlitter, 1981; Schlitter et al., 1985), and Holden (1993: 763) commented that "the revision by Genest-Villard (1978), based mostly on size grades, underestimated species diversity, particularly in the *murinus* group."

FAMILY GLIRIDAE

Genus *Graphiurus*

G. parvus ("Formes mises en synonymie:" *brockmani* [valid as a subspecies], *dollmani*, *foxi*, *internus*, *nanus*, *olga*, *personatus*, *tasmani*; "Formes douteuses:" *kelleni*, *Claviglis ansorgei cuanzensis*)

G. murinus ("Liste par ordre alphabétique des formes décrites réféables à *G. murinus*:" *alticola*, *angolensis*, *ansorgei*, *butleri*, *christyi*, *cineraceus*, *collaris*, *coupei*, *erythrobronchus*, *griselda* [valid as a subspecies], *griseus*, *haedulus*, *isolatus*, *johnstoni*, *jordani*, *lalandianus*, *littoralis*, *lorraineus* [valid as a subspecies], *marrensis*, *microtis* [valid as a subspecies], *murinus* [valid as a subspecies], *orobinus* [valid as a subspecies], *parvulus*, *pretoriae*, *raptor* [valid as a subspecies], *saturatus*, *schwabi*, *selindensis*, *smithii*, *soleatus*, *spurelli* [sic] [valid as a subspecies], *surdus*, *tzaneenensis*, *vandami*, *vulcanicus*, *woosnami*, *zuluensis*)

G. crassicaudatus ("Forme mise en synonymie:" *dorotheae*)

G. platyops ("Formes mises en synonymie:"

australis, *eastwoodae*, *montosus*, *rupicola* [valid as a subspecies], *schoutedeni*)

G. hueti ("Formes mises en synonymie:" *argenteus* [valid as a subspecies], *monardi* [valid as a subspecies], *nachtglasi* [sic])

G. ocularis ("Formes mises en synonymie d'après Ellerman:" *capensis*, *typicus*, *elegans*, *cattoiri*)

8. Holden (1993): "Family Myoxidae" a chapter in "Mammal Species of the World, a taxonomic and geographic reference." I did not recognize subgenera and listed 14 species, commenting that a "systematic revision of *Graphiurus* is in progress and the species recognized below reflect information in the literature as well as examination of museum specimens; results are provisional and assignment of synonyms incomplete" (p. 763). The list reflected my unpublished research based on museum specimens as well as the conclusions in certain reports defining limits of species in particular African regions (for example, Ansell and Dowsett, 1988; Robbins and Schlitter, 1981; Schlitter et al., 1985).

FAMILY MYOXIDAE

Genus *Graphiurus*

G. christyi

G. crassicaudatus (synonym: *dorotheae*)

G. hueti (synonyms: *argenteus*, *nachtglasii*)

G. kelleni (synonyms: *ansorgei*, *johnstoni*, *nanus*)

G. lorraineus (synonyms: *collaris*, *haedulus*, *spurrelli*)

G. microtis

G. monardi (synonym: *schoutedeni*)

G. murinus (synonyms: *alticola*, *butleri*, *cineraceus*, *cinerascens*, *dasilvai*, *erythrobronchus*, *etoschae*, *griselda*, *isolatus*, *landianus*, *littoralis*, *marrensis*, *pretoriae*, *raptor*, *saturatus*, *schneideri*, *selindensis*, *soleatus*, *streeteri*, *sudanensis*, *tzaneenensis*, *vandami*, *vulcanicus*, *woosnami*, *zuluensis*; "the synonyms . . . almost certainly contain names which are actually synonyms of *G. microtis* and other species," p. 764)

G. ocularis (synonyms: *capensis*, *elegans*, *typicus*)

G. olga

G. parvus (synonyms: *brockmani*, *dollmani*, *foxi*, *internus*, *personatus*)

G. platyops (synonyms: *angolensis*, *eastwoodae*, *jordani*, *parvulus*)

G. rupicola (synonyms: *australis*, *kaokoensis*, *montosus*)

G. surdus (synonym: *schwabi*)

SPECIES LIMITS OF *GRAPHIURUS SURDUS*

"A small-eared species allied to *murinus*," was Dollman's (1912: 314) introduction to the new species he named and described as *Graphiurus surdus*. He drew attention to the ears, "... remarkably small, about 5 mm shorter than those of the South-African species," and was impressed by the cranium, so "... markedly different from that of any other known form, the occipital part of the braincase broad and almost rectangular in shape, giving the skull a very unusual appearance." Dollman was convinced that "The small ears, large hind feet, and unusual shape of the occipital region immediately distinguish this dormouse from all the other allied forms."

Graphiurus surdus maintained its identity in relevant checklists for at least six decades. Allen (1939), for example, in his checklist of African mammals, listed *surdus* as a species, and Ellerman (1940), in his monograph on families and genera of living rodents, characterized *G. surdus* as being easily distinguishable from other species of *Graphiurus*. Morphology of *G. surdus* seemed so distinctive to Ellerman that he made the species a member of a separate group (see the historical outline above).

The species that seemed so distinctive to Dollman and Ellerman lost its species status in the 1970s. In his chapter on rodents for an African mammal identification manual, Misonne (1974) relegated *surdus*, without comment, to *G. murinus*. A similar action was taken by Genest-Villard (1978) in the only taxonomic revision of *Graphiurus* prior to my present report; she referred *surdus* to *G. murinus lorraineus*.

A few years later, Robbins and Schlitter (1981) reported on their collection of Cameroon dormice and reinstated *surdus* as a species representing a distinctive element of the Cameroon fauna. They were able to provide key morphological characters that would distinguish specimens of *G. surdus* from samples of the other four kinds of dormice they identified from Cameroon: *G. hueti*, *G. crassicaudatus*, *G. lorraineus*, and *G. christyi*. Based on my study of those same Cameroon specimens, as well the type series of *surdus*, I too could not accept the arrangements defended

by either Misonne (1974) or Genest-Villard (1978), but could agree with Ellerman (1940) and Robbins and Schlitter (1981), and recognized *surdus* as a species in the myoxid chapter of the taxonomic and geographic reference to mammal species of the world (Holden, 1993).

Redescribing *G. surdus* is the subject of this first section of my systematic revision of the genus. Previous workers had access to only a few examples of the species collected in southern Cameroon and Rio Muni. I have been able to locate 22 specimens in institutional collections. Some of these, the type series and those reported on by Robbins and Schlitter (1981), for example, had already been identified as *G. surdus*. Others were hidden in collections under misidentifications or simply identified as "*Graphiurus* sp.," and a few have been recently collected and generously loaned to me for study by their holding institutions.

Although 22 specimens constitute a small sample, it is large enough to provide morphological data by which I am able to affirm Dollman's view that *G. surdus* is one of the more morphologically distinctive species of *Graphiurus*. The evidence is presented below in the context of description, diagnosis, and comparisons with morphologically similar species. Because I have studied more specimens of *G. surdus*, obtained from localities covering a larger geographic region than were available to previous researchers, I am able to sketch a more revealing depiction of its geographic distribution.

Graphiurus surdus Dollman, 1912

Graphiurus surdus Dollman, 1912: 314.

Graphiurus schwabi G. M. Allen, 1912: 441.

HOLOTYPE AND TYPE LOCALITY: BM(NH) 0.2.5.55, an adult female collected by G. L. Bates along the Benito River, "French Congo" (actually Rio Muni in Equatorial Guinea) in July, 1899. The specimen consists of a stuffed skin (originally preserved in fluid), cranium, and mandible. The skin and skull (fig. 4) are intact and undamaged. Measurements of the holotype are listed in table 2.

ETYMOLOGY: The Latin *surdus* means

"deaf, silent, mute, faint" (Brown, 1956). Presumably Dollman (1912) chose this name to dramatize the pinnae of the specimen he had selected as the holotype. He thought its ears were very small (table 2), and were unique to and diagnostic of the species.

DISTRIBUTION: The actual geographic range of *G. surdus* is unknown. Specimens have been collected from eight localities in southern Cameroon, one in Equatorial Guinea (Rio Muni), one in northeastern Gabon, and two in Zaire, one in the northeast and the other in the south-central part of the country (see fig. 2 and gazetteer below). All sites are below 1000 m in the central African portion of the "Guineo-Congolian regional centre of endemism," the floristic region described by White (1983), in the memoir accompanying the Unesco/AETFAT/UNSO vegetation map of Africa. Within that regional center are subdivisions described by White and delimited on the map.

Localities 1–7 in Cameroon, locality 10 in Gabon, and locality 12 in Zaire fall in "Wetter Guineo-Congolian rain forest," locality 11 in Zaire is in "Drier Guineo-Congolian rain forest," and localities 8 in Cameroon and 9 in Rio Muni are congruent with a mapping unit reflecting a forest mosaic of "wetter" and "drier" Guineo-Congolian rain forest. Locality 11 is the only locality from the region that is not at least partially characterized as being wetter Guineo-Congolian rain forest on the vegetation map. Each general delimited region on the map is described in terms of the dominant vegetation types found therein. Locality 11 is "Inkongo, Sankuru river" (Inkongo is situated on the left bank of the Sankuru river), and it is plausible that the specimen was taken from a wetter forest than is the dominant forest type of that region. The Masako specimen was taken from the Masako Forest Reserve (locality 12), which is situated in a loop of the Tshopo river (Hutterer and Dudu, 1990); this locality is discussed further under Natural History below. It is possible that *G. surdus* will be found to be associated with wetter Guineo-Congolian rain forest.

The general geographic distribution of *G. surdus* may coincide with what Carleton and Robbins (1985: 987) called the "evergreen

TABLE 2
Comparisons of Measurements (mm) Among Ho-
lotypes Representing Three Species of *Graphiurus*
from Equatorial Africa

	<i>G. surdus</i>		<i>G. lorrai-</i>	<i>G. christyi</i>
	<i>schwabi</i>	<i>surdus</i>	<i>neus</i>	
	MCZ	BMNH	BMNH	BMNH
	8607 ^a	0.2.5.55 ^b	7.7.8.115 ^c	14.2.1.1.8 ^d
Age	juv	adult	adult	adult
Sex	?	female	female	male
LHB	74	87 ^e	95	105
LT	64	67 ^e	62	95
LHF	18.5	20 ^f	16	18
LE	7	9 ^e	12	12
GLS	26.2	27.5	—	—
CIL	22.5	25.9	—	—
ZB	13.1	14.1	14.3	15.2
IB	4.3	4.5	5.0	4.8
BBC	12.5	12.8	12.3	12.3
HBC	8.3	7.7	—	—
BR	5.0	5.6	5.3	5.9
LHR	4.4	4.8	5.0	5.5
LN	10.3	10.7	9.4	10.2
LD	6.2	6.4	5.1	5.7
PL	9.0	9.4	8.0	8.3
LBP	5.1	5.2	4.5	4.8
LIF	2.5	2.8	2.7	2.4
BIF	1.6	1.7	1.8	2.0
BBP	3.6	3.3	3.1	3.7
CLP4-M3	3.2	3.3	3.3	—
CLM1-3	2.5	2.7	2.7	—
BP4	—	0.9	0.9	—
BM1	0.9	1.1	1.1	1.1
BM2	1.0	1.1	1.1	1.2
BIT	1.7	1.9	1.6	1.9
PPL	10.7	11.7	—	—
LB	7.0	7.2	7.1	7.2
BBO	2.5	2.7	2.3	—

^a Cameroon; skin and skull; fourth premolar erupted halfway between alveolus and occlusal surfaces of molars.
^b Equatorial Guinea; skin and skull, originally preserved in fluid; maxillary teeth slightly to moderately worn.
^c Zaire; skin and skull; maxillary teeth slightly to moderately worn.
^d Zaire; skin and skull; maxillary teeth slightly to moderately worn, occlusal surface obscured by glue.
^e Recorded by Dollman (1912: 314), who indicated the dimensions were “measured from spirit-specimen.” I could not obtain accurate measurements for length of head and body and length of tail. I measured the dry ear and obtained 8 mm for its length; presumably shrinkage accounts for the difference between my value and that

rainforests of Central Africa,” or the “Central African Forest” (p. 984), which is “. . . approximately equivalent to the Congo Forest Block of Booth [1958] or the Lower Guinea Forest of Moreau [1966, 1969].” Although from widely scattered localities, the examples of *G. surdus* have come only from the Zaire basin and the southern Cameroon–northern Gabon region—the “Central African Forest”—and not from the West African portion of the Guineo-Congolian rain forest that extends west of the Cross and Niger rivers.

Only two specimens of *G. surdus* have been taken in Zaire; one at Inkongo in 1912, and the other at Masako in 1986, despite extensive collecting expeditions to various parts of that country. It is conceivable that future small mammal surveys may extend the distributional limits of *G. surdus* further to the north and west.

GAZETTEER AND SPECIMENS: 22 specimens of *Graphiurus surdus* from 12 localities comprise all the known examples of the species preserved in institutional collections. The numbers preceding these localities match the numbered dots on the distribution map of *G. surdus* (fig. 2).

CAMEROON

1. **Ayina (Aïna) River** (1.48N, 13.10E): MRAC 1093.
2. **Bitye** (3.10N, 12.20E): BM(NH) 14.7.23.15.
3. **Edea** (3.47N, 10.13E): ZMB 71341.
4. **Eseka** (3.38N, 10.47E): CM 42202, 42205, 42208, 42209, 42210; AMNH 236482.
5. **Kribi** (2.56N, 9.54E): MCZ 8607 (holotype of *Graphiurus schwabi*).
6. **Efulan (Efulen)** (2.40N, 10.45E): AMNH 90067.
7. **Metet** (3.23N, 11.43E): MCZ 14669, 17605, 17606.
8. **Sangmelima** (2.56N, 11.58E): CM 10331.

←

reported by Dollman (1912: 314), although we may not have measured the ear the same way.

^f Obtained by me from the dry hind foot (includes claws). Dollman (1912: 314) gave 19 mm, obtained presumably when the specimen was wet.

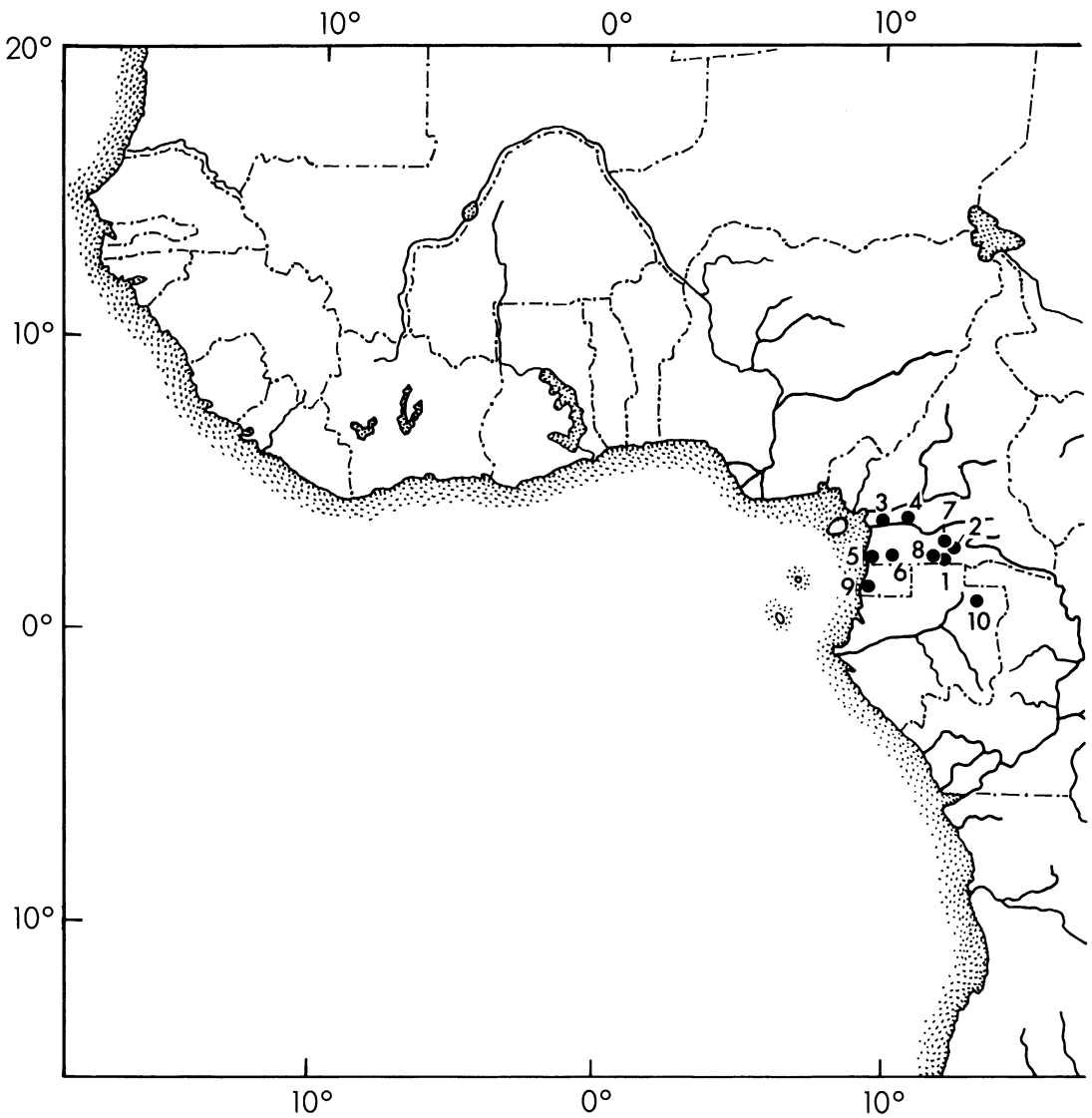


Fig. 2. Geographic distribution of *Graphiurus surdus* as indicated by specimens I identified. Each numbered locality corresponds to the numbered place name in the gazetteer of collection sites and specimens for *G. surdus*.

EQUATORIAL GUINEA

9. **Rio Muni, Benito River:** BM(NH) 0.2.5.53, 0.2.5.54, 0.2.5.55 (holotype of *Graphiurus surdus*), 0.2.5.56.

GABON

10. **Belinga** (1.09N, 13.12E): MNHN 1983-186.

ZAIRE

11. **Inkongo, Sankuru River** (4.55S, 23.15E): BM(NH) 13.4.7.2.
12. **Masako** (0.36N, 25.13E), 500 m: RUCA D1655.

SYMPATRY: The geographic ranges of four species of *Graphiurus* overlap the known distribution of *G. surdus*, but records of sym-

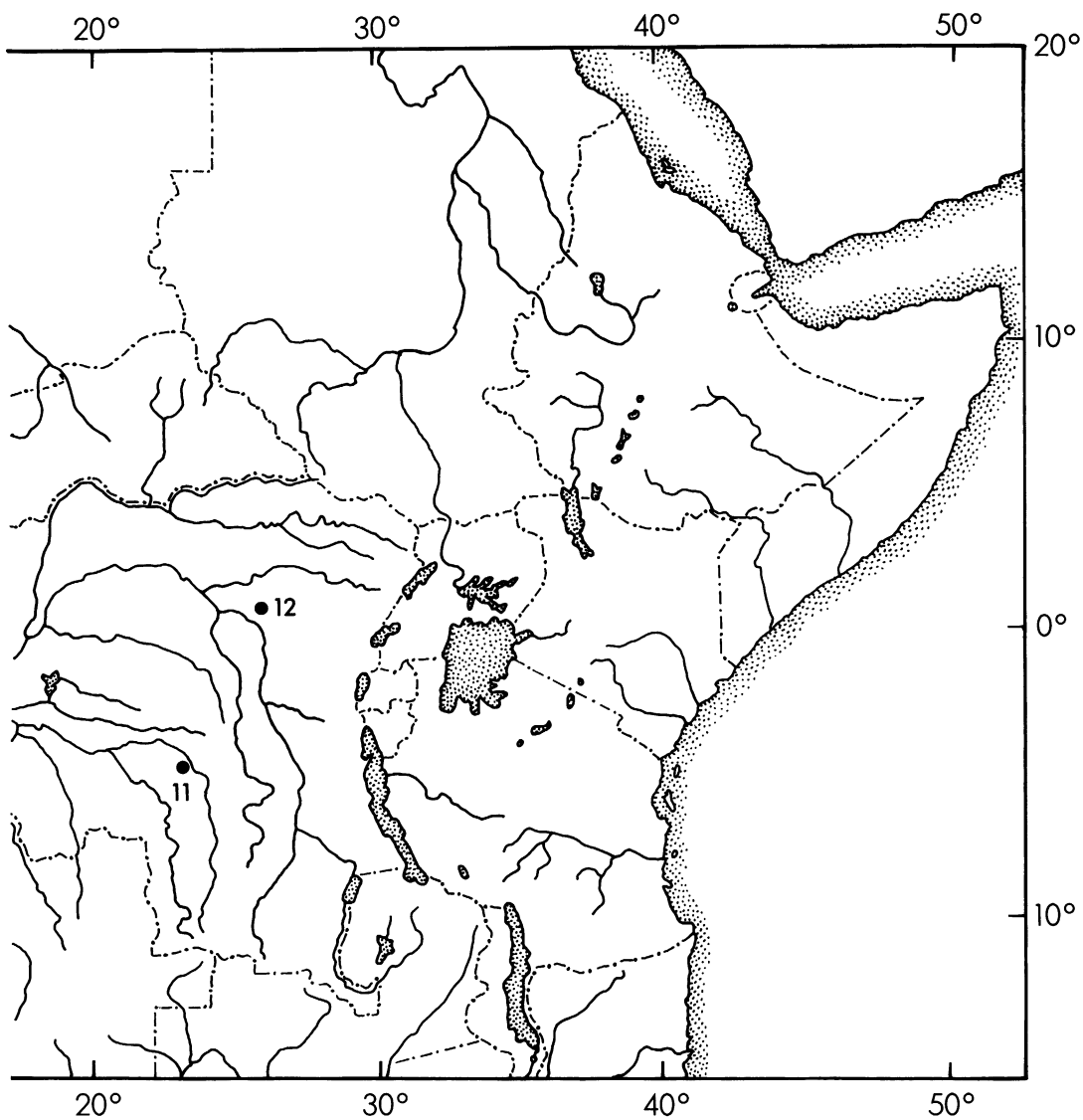


Fig. 2. Extended.

patry, based on specimens I identified, exist only between *G. surdus* and *G. lorrainus* (Cameroon, Equatorial Guinea, and Zaire), *G. crassicaudatus* (Cameroon), and *G. hueti* (Cameroon); table 3. Most records of the fourth species, *G. christyi*, are from north-eastern and northern Zaire (see the map in Schlitter et al., 1985, for example), but a series was collected at Lolodorf in southern Cameroon (see gazetteer of *G. christyi* below), a place not far from Efulan from which a

specimen of *G. surdus* was obtained (see the map of Cameroon localities in Robbins and Schlitter, 1981).

EMENDED DIAGNOSIS: When compared with *G. christyi* and *G. lorrainus*, the only species of *Graphiurus* with which it is likely to be confused, *G. surdus* exhibits 1) small ears relative to size of head and body, 2) silky fur, 3) inconspicuous eye mask, 4) relatively straight conformation of the zygomatic arch in lateral view, 5) long palatal region relative

TABLE 3

Records of *Graphiurus lorrainaeus*, *G. crassicaudatus*, and *G. hueti* (referenced by museum acronym and catalog number) taken together with *G. surdus* at localities in Cameroon, Equatorial Guinea, and Zaire (Numbers in parentheses refer to localities in gazetteer and symbols on map in fig. 2. Specimens of *G. surdus* from each place are listed in the gazetteer.)

Locality	<i>G. lorrainaeus</i>	<i>G. crassicaudatus</i>	<i>G. hueti</i>
CAMEROON			
(2) Bitye	BM(NH) 13.2.8.6, 13.9.12.8, 23.1.22.53 MRAC 10939	BM(NH) 23.1.22.52	—
(4) Eseka	—	AMNH 236483; CM 42204	—
(5) Kribi	MCZ 8678	—	—
(6) Efulan	—	—	BM(NH) 1.11.21.13, 96.3.20.12, USNM 125434
(7) Metet	CM 4645, 4646, 4674 FMNH 48926	—	MCZ 17607
(8) Sangmelima	CM 42720, 9529, 9530, 10336	—	CM 9525, 9527, 10332–10335, 10337, 10338
EQUATORIAL GUINEA			
(9) Benito River	BM(NH) 58.336	—	—
ZAIRE			
(11) Inkongo	BM(NH) 13.4.7.3, MRAC 7220, 12190	—	—

to skull length, 6) relatively short and narrow incisive foramina, 7) relatively narrow P4, and 8) low rostrum relative to its breadth.

DESCRIPTION: A compact body and relatively short tail characterize the body form of *G. surdus* (fig. 3; table 4), a configuration common to most species of subsaharan African dormice. The grayish brown, silky dorsal pelage is composed of overhairs, short and fine guard hairs that barely extend beyond the overfur, but no intermixed layer of underhairs. The short and silky ventral coat is dark gray washed with whitish buff: the hairs are dark gray for most of their lengths and tipped with either white or pale buff. The intermixing of long brown and unpigmented hairs, and brown hairs with unpigmented tips, along the caudal vertebrae provide *G. surdus* with its characteristic frosted brown tail. The small pinnae are dark gray, their inner and outer surfaces clothed with short, fine hairs. Facial mask and eye rings are indistinct. Dorsal surfaces of metacarpal and metatarsal regions are brown, tops of digits are covered with silvery hairs. As in all other species of *Graphiurus*, *G. surdus* females have four pairs of mammae (one pectoral, one postaxillary,

and two inguinal), and both sexes have short, wide arboreal feet with six plantar pads.

The skull of *G. surdus* is exemplified by the holotype in figure 4 and specimens from Cameroon and Zaire in figures 6–10. Its general conformation, relationships of cranial bones to one another, and position and number of cranial foramina are very similar to those in the skull drawings of *Graphiurus* presented by Wahlert et al. (1993: 11–14), in which the bony elements and foramina are also labeled. The rostrum is wide and moderately long, the interorbit shaped like an hourglass in dorsal perspective, the braincase rounded, and the zygomatic arches flair slightly outward. The palatal region is relatively long and the auditory bullae are not enlarged. Each zygomatic arch meets the rostrum in a smooth, concave wide angle, and not sharply at a right angle. The dorsal maxillary root of each zygomatic arch lies anterior to the ventral maxillary root. Structural details will be elaborated in the following section where I compare the cranium of *G. surdus* with that of other species.

The dentary of *G. surdus* is shaped very much like the labeled drawing of a *Graphiu-*

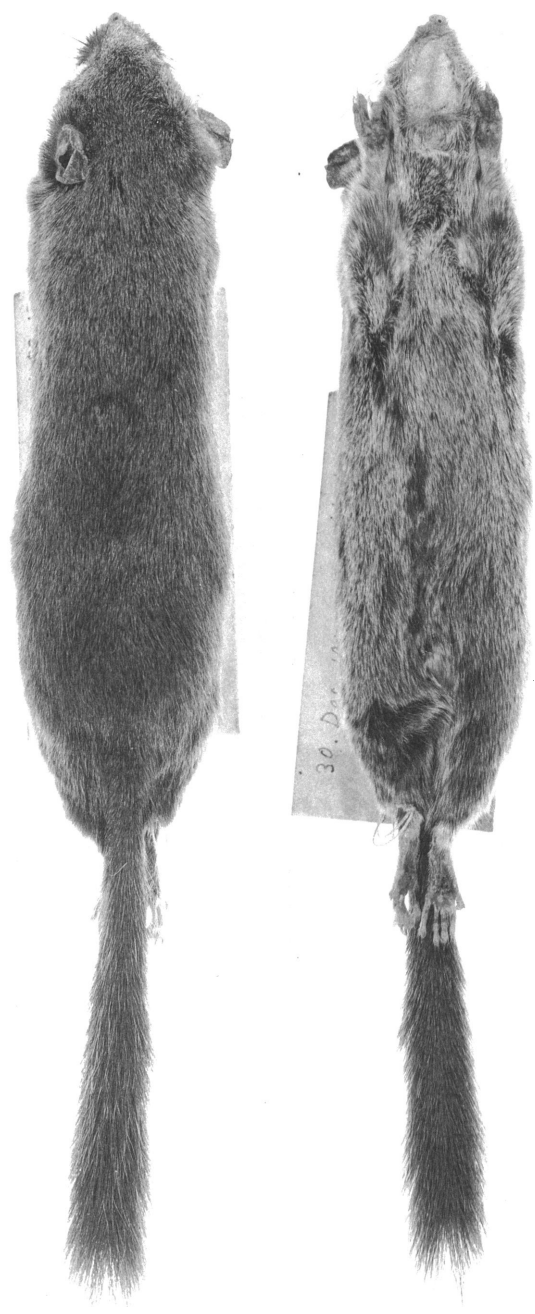


Fig. 3. Stuffed skin of an adult *Graphiurus surdus*, BM(NH) 14.7.23.15, from Cameroon. Measurements (mm): LHB = 95; LT = 65; LHF = 18; LE = 13. The tail tip appears to be slightly damaged, and the accuracy of length of tail in this specimen is questionable.

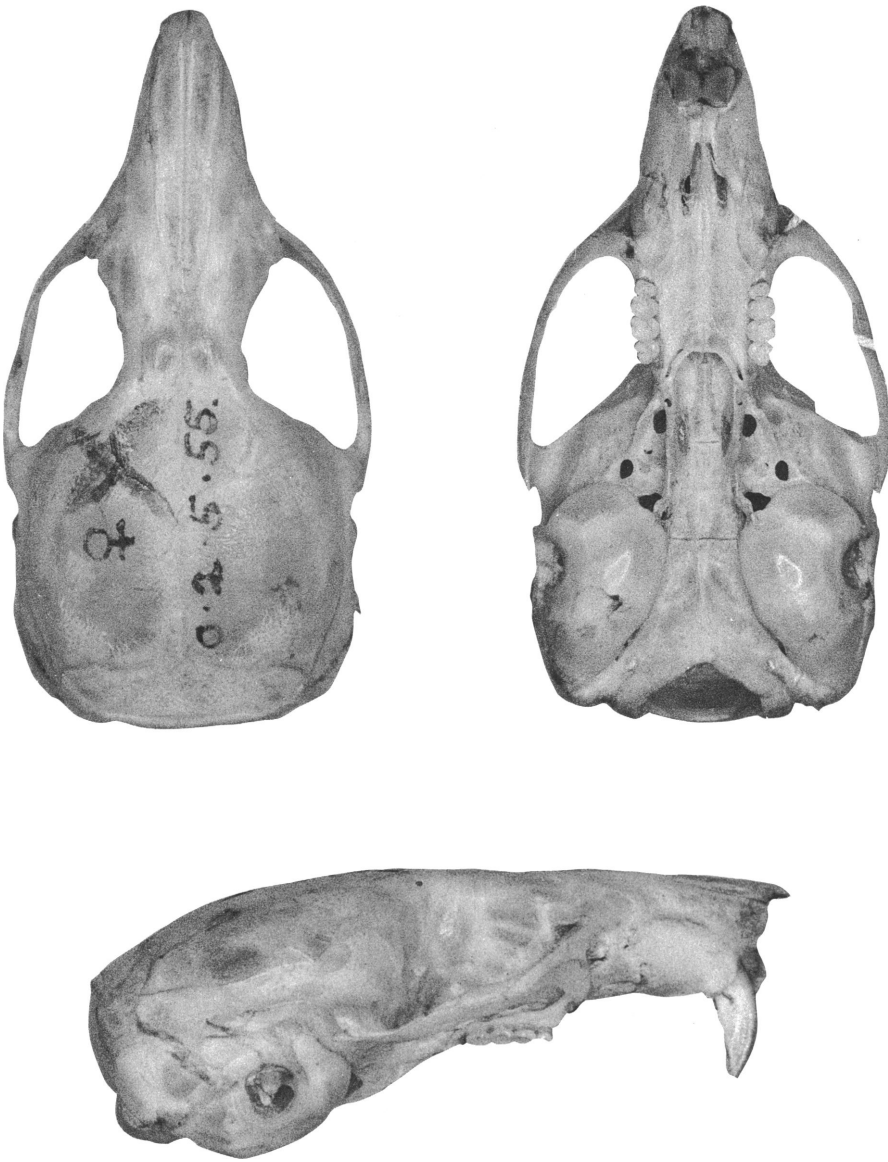


Fig. 4. Cranial views ($\times 3.5$) of the holotype of *Graphiurus surdus*: BM(NH) 0.2.5.55, an adult female from the Benito River, Rio Muni, Equatorial Guinea. Measurements are listed in table 2.

rus dentary illustrated in Wahlert et al. (1993: 15). I did not study the mandible in any comparative detail for the reasons listed above under Materials and Methods.

An example of the dentition of *G. surdus* in occlusal perspective is provided in figure 5. See the section on Mandible and Dentition under Materials and Methods above for additional discussion.

KARYOTYPIC AND MOLECULAR DATA: No sample of *G. surdus* has been analyzed for chromosomal or biochemical information. Molecular data may only be retrieved from museum skins, or carcasses preserved in alcohol; no specially preserved tissue samples have been obtained.

GEOGRAPHIC VARIATION: The geographically biased sampling, combined with the

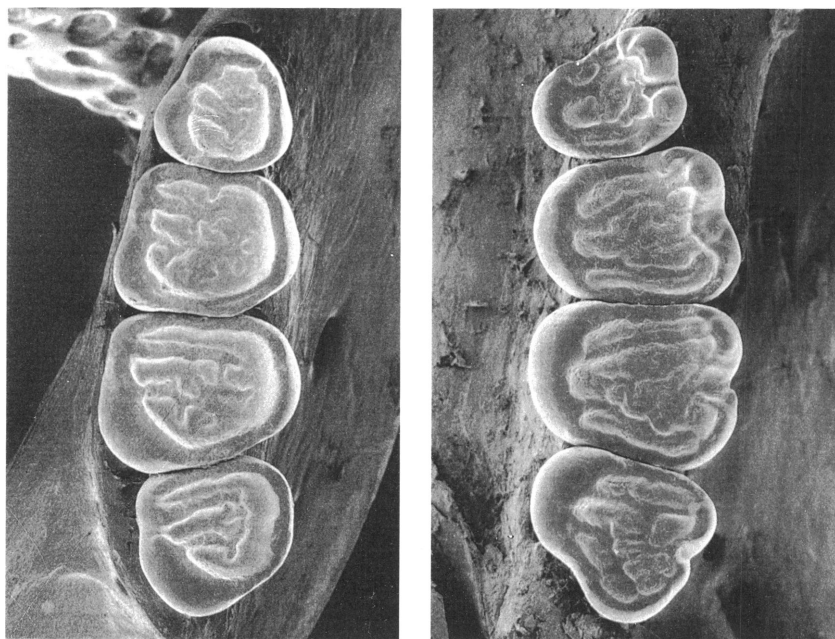


Fig. 5. Scanning electron micrographs of the left lower (on the left; clp4-m3 = 3.2 mm) and upper right (on the right; CLP4-M3 = 3.3 mm) tooththrows (fourth premolar to third molar) of a young adult *Graphiurus surdus* (AMNH 90067) from Efulan, Cameroon.

small sample size from each locality, prevents any useful analysis of geographic variation. The known geographic range of the species is represented mostly by collecting localities in southern Cameroon, one in near-by Rio Muni and one in Gabon, and two scattered far to the east in Zaire. The collecting localities therefore do not provide adequate geographic samples to discern any significant patterns of variation. The total number of specimens is only 22, and each geographic sample is too small to provide information regarding variation within and between populations. Out of the 12 localities, nine are represented by only one specimen, and the other three by 4–6 animals. Without large samples containing a range in age so series of comparable stages can be compared, and without samples that cover most of the geographic range, no rigorous inquiry into how morphology or other traits may vary geographically is possible.

Nearly all values obtained from the two specimens from Zaire fall within the observed ranges of respective measurements in the pooled sample from Cameroon, Equatorial

Guinea, and Gabon (table 4). The only exception is the incisor tips of the animal from Masako, which are wider than any of the other specimens measured.

DISCUSSION OF SYNONYM: *Graphiurus schwabi*, based on one specimen from Kribi, Cameroon, was described by G. M. Allen in April, 1912, just one month after Dollman named *G. surdus*. Allen (1912: 441) characterized *G. schwabi* as "A small dark gray species, with the orbital rings scarcely distinguishable from the general dark slaty color of the head. Feet except the distal portion of the toes entirely dusky. Tail white bordered, ears small."

Allen apparently revised his opinion about *schwabi*, for in 1939 he placed the name in the synonymy of *G. haedulus* (a taxon I include at present in *G. lorrainus*; Holden, 1993). Subsequent workers did not always agree, and during the next 50 years, *schwabi* was treated again as a species, relegated to the synonymy of *G. surdus*, omitted from a checklist, referred to *G. murinus*, combined with *haedulus* again to be placed in the synonymy of *G. lorrainus*, and finally returned

TABLE 4
Comparisons of Measurements (mm) and Weight (g) Between Geographic Samples of *Graphiurus surdus*

(Mean \pm 1 SD, range [in parentheses], and number of specimens are listed for the large sample containing more than one specimen. Only individuals in the age range young to old adults were measured.)

	Eq. Guinea (Benito River), Cameroon (Kribi, Metet, Bitye, Eseka, Sangmelima), Gabon (Belinga) ^a	Zaire	
		Inkongo ^b	Masako ^c
LHB	99.0 \pm 7.93 (87–110) 8	95	98
LT	72.3 \pm 6.19 (65–82) 6	70	70
LHF	20.8 \pm 1.29 (18–22) 12	18	19
LE	12.3 \pm 1.62 (9–14) 11	11	14
WT	24.8 \pm 5.31 (18–34) 6	—	26
GLS	27.6 \pm 0.98 (26.5–29.4) 10	—	28.6
CIL	24.9 \pm 1.03 (23.5–26.3) 11	—	25.4
ZB	14.6 \pm 0.61 (13.4–15.7) 11	—	15.2
IB	4.5 \pm 0.19 (4.1–4.8) 14	4.5	4.6
BBC	12.6 \pm 0.41 (11.7–12.8) 11	—	12.1
HBC	8.1 \pm 0.27 (7.7–8.5) 10	—	8.1
BR	5.7 \pm 0.33 (5.2–6.4) 16	—	5.9
LHR	4.8 \pm 0.39 (4.0–5.5) 13	4.8	4.9
LN	10.4 \pm 0.53 (9.8–11.3) 13	10.6	11.6
LD	6.5 \pm 0.36 (5.9–7.0) 16	6.6	6.5
PL	9.3 \pm 0.43 (8.6–10.3) 16	—	9.7
LBP	5.2 \pm 0.29 (4.8–5.8) 16	—	5.6
LIF	2.8 \pm 0.20 (2.5–3.2) 16	3.0	2.9
BIF	1.8 \pm 0.12 (1.6–2.0) 16	—	1.8
BBP	3.4 \pm 0.16 (3.1–3.6) 15	—	3.4

TABLE 4—(Continued)

	Eq. Guinea (Benito River), Cameroon (Kribi, Metet, Bitye, Eseka, Sangmelima), Gabon (Belinga) ^a	Zaire	
		Inkongo ^b	Masako ^c
CLP4-M3	3.2 \pm 0.16 (2.9–3.5) 16	3.2	3.1
CLM1-3	2.6 \pm 0.13 (2.4–2.8) 16	2.6	2.5
BP4	0.8 \pm 0.07 (0.7–0.9) 14	0.9	0.8
BM1	1.0 \pm 0.08 (0.9–1.1) 14	1.0	1.0
BM2	1.1 \pm 0.06 (1.0–1.2) 14	1.0	1.0
BIT	1.9 \pm 0.16 (1.7–2.2) 15	—	2.6
PPL	11.8 \pm 0.62 (11.0–12.9) 11	—	12.1
LB	7.3 \pm 0.20 (6.9–7.7) 14	—	7.7
BBO	2.7 \pm 0.13 (2.4–2.8) 13	—	2.5

^a AMNH 90067, 236482; BMNH 0.2.5.55 (holotype), 0.2.5.53–0.2.5.56, 14.7.23.15; CM 10331, 42202, 42205, 42208–42210; MCZ 17605, 17606; MNHN 1983-186.

^b BMNH 13.4.7.2.

^c RUCA D1655.

to *G. surdus*, as outlined below. Ellerman (1940) was the only one who recognized *schwabi* as a species, but because he had not examined the holotype, listed the taxon under the heading “not seen and not allocated to group.” Perret and Aellen (1956) also did not examine the holotype of *G. schwabi*, but they proposed, based on Allen’s (1912) original description, that *schwabi* was probably a synonym of *G. surdus*, not *G. haedulus*. Their knowledge of *G. surdus* was limited to Dollman’s (1912) description; they had also not studied that holotype. In his checklist, Misonne (1974) did not include *schwabi*. Genest-Villard (1978: 409) placed both *schwabi* and *surdus* as synonyms of *G. murinus lorraineus*.

Robbins and Schlitter (1981) maintained that *schwabi* and *haedulus* were synonyms of *G. lorraineus*. However, they provided no reason for their allocation of *schwabi* to *G. lorraineus*. Their only discussion of *schwabi* is in the account of *G. surdus* where they

TABLE 5

Comparisons of Selected Measurements (mm) Among Three Species of *Graphiurus* from Equatorial Africa

(Mean \pm 1 SD, range [in parentheses], and number of specimens are listed for each measurement. The range in age from young to old adults is contained within each sample.)

	<i>G. crassicaudatus</i> ^a Cameroon	<i>G. surdus</i> ^b Eq. Guinea, Cameroon, Gabon	<i>G. hueti</i> ^c Cameroon
LHB	92.6 \pm 4.0 (83–98) 11	99.0 \pm 7.93 (87–110) 8	145.9 \pm 5.54 (134–152) 11
LT	59.4 \pm 4.42 (55–70) 9	72.3 \pm 6.19 (65–82) 6	131.1 \pm 11.31 (114–149) 8
LHF	17.7 \pm 0.89 (16–19) 12	20.8 \pm 1.29 (18–22) 12	31.5 \pm 0.82 (30–32) 11
LE	13.0 \pm 1.12 (11–14) 9	12.3 \pm 1.62 (9–14) 11	22.3 \pm 3.69 (20–31) 8
GLS	26.6 \pm 0.79 (25.2–27.8) 8	27.6 \pm 0.98 (26.5–29.4) 10	38.1 \pm 0.98 (36.3–39.5) 15
ZB	16.1 \pm 0.35 (15.7–16.6) 6	14.6 \pm 0.61 (13.4–15.7) 11	—
IB	4.9 \pm 0.17 (4.7–5.2) 14	4.5 \pm 0.19 (4.1–4.8) 14	6.2 \pm 0.23 (5.7–6.5) 20
LN	8.9 \pm 0.53 (8.1–9.9) 12	10.4 \pm 0.53 (9.8–11.3) 13	—
CLP4-M3	3.8 \pm 0.21 (3.4–4.2) 14	3.2 \pm 0.16 (2.9–3.5) 16	5.2 \pm 0.15 (5.0–5.6) 17
CLM1-3	3.0 \pm 0.12 (2.8–3.2) 14	2.6 \pm 0.13 (2.4–2.8) 16	4.2 \pm 0.17 (3.8–4.6) 18
BP4	1.1 \pm 0.07 (0.9–1.1) 12	0.8 \pm 0.07 (0.7–0.9) 14	—
BM1	1.3 \pm 0.05 (1.2–1.3) 12	1.0 \pm 0.08 (0.9–1.1) 14	1.8 \pm 0.05 (1.7–1.8) 16
BM2	1.3 \pm 0.06 (1.2–1.4) 13	1.1 \pm 0.06 (1.0–1.2) 14	—
BIT	1.5 \pm 0.11 (1.3–1.7) 13	1.9 \pm 0.16 (1.7–2.2) 15	—
LB	6.7 \pm 0.12 (6.5–6.9) 11	7.3 \pm 0.20 (6.9–7.7) 14	—

^a AMNH 89582, 89583, 236483; BM(NH) 23.1.22.52; CM 2973, 42203, 42204, 42206, 42207, 42211, 42715, 42718, 59453; ZMB 71312.

^b Data derived from specimens listed in table 4.

^c BM(NH) 1.11.21.13, 36.10.28.26, 36.10.28.27, 96.3.20.12; CM 2888, 3676, 6123, 6124, 9525, 10332–10335, 10337, 42200, 42201, 16134; MCZ 17607, 17920; USNM 125434.

outlined the treatment of *schwabi* by Allen (1939), and Perret and Aellen (1956), and noted that the original descriptions of both *G. surdus* and *G. schwabi* included reference to their small ears (“9 and 7 mm, respectively”), and continued, “However, external measurements of *G. surdus* were taken from fluid preserved specimens, whereas those of *G. schwabi* were from a dried skin originally preserved in formalin. The ears of our specimens measured 12 to 14 mm” (p. 286). Why

ear length has any relevance here is mystifying. Absolute length does not distinguish samples of *G. surdus* from *G. lorraineus*, as is apparent with their data (p. 274) and mine (table 6). They finally asserted that “Examination of specimens from Rio Muni and southern Cameroon indicates that *G. surdus* is a species distinct from *G. haedulus* and *G. schwabi*; the latter two taxa are synonyms of *G. lorraineus*.”

After examining all existing holotypes, as



Fig. 6. Comparisons among adult crania of *Graphiurus* from a dorsal perspective. **Left:** *G. crassicaudatus*, BM(NH) 12.1.12.1 (holotype of *G. c. dorotheae*), Nigeria. **Middle:** *G. surdus*, BM(NH) 14.7.23.15, Cameroon. **Right:** *G. hueti*, CM 42201, Cameroon. $\times 2.5$. Note that the anterolateral margin of the dorsal maxillary process of each zygomatic arch joins the rostrum at a right angle in *G. crassicaudatus* and *G. hueti*, but at an obtuse angle in *G. surdus*. That species is obviously smaller than *G. hueti* and contrasts with *G. crassicaudatus*, which is similar in size, by its longer nasals and a narrower interorbit (see table 5) that is not defined by supraorbital shelves (also see discussion in text).

well as most museum specimens of *Graphiurus*, I do not hesitate to arrange the name *schwabi* as a junior synonym of *G. surdus*. The holotype of *G. schwabi* is a juvenile, with permanent premolars just beginning to erupt. The small size of this young specimen may account for its erroneous association with *haedulus* and placement in the synonymy of *G. lorraineus*. Almost all specimens of *G. surdus* that I examined have the characteristic relatively horizontal and straight and robust zygomatic arch that distinguishes this species from *G. lorraineus*; the holotype of *G. schwabi* shares this zygomatic conformation. *Graphiurus surdus* also has very short and narrow incisive foramina, another trait that is conspicuous in the holotype of *G. schwabi*. And even allowing for some shrinkage (in his description of *schwabi*, Allen (1912: 442) noted that “The ears seem unusually small, but may

have shrunken unduly”), the pinnae of *G. schwabi* are actually very small, even for a young dormouse.

Comparisons with Other Species of *Graphiurus*

Four other species of *Graphiurus* occur in the general forested region where *G. surdus* is found. Two of these have very different morphologies and have rarely been confused with *G. surdus*. Set apart from all the other West African forest species of *Graphiurus* by its large body and skull dimensions, *G. hueti* has always been recognized as a distinctive species easily separated not only by size but by morphology (table 5; figs. 6, 7; also see the key to Cameroon forest species in Robbins and Schlitter, 1981); *hueti* has never been associated with *surdus* in synonymy or group-



Fig. 7. Ventral views ($\times 2.5$) of the same crania of *Graphiurus* shown in figure 6. **Left:** *G. crassicaudatus*. **Middle:** *G. surdus*. **Right:** *G. hueti*. $\times 2.5$. Compared with *G. crassicaudatus*, *G. surdus* has a narrower cranium, larger auditory bullae, wider incisors, shorter tooththrows and narrower maxillary teeth (see table 5, and discussion in text).

ings in any published checklist or faunal account.

The other, *G. crassicaudatus*, although similar in body and skull size to *G. surdus* (table 5), is at once separable by its shorter nasal bones, wide interorbit defined by prominent supraorbital shelves, smaller auditory bullae, narrower incisors, and much larger teeth (table 5; figs. 6, 7; Robbins and Schlitter, 1981). Also, in both *G. crassicaudatus* and *G. hueti*, the anterolateral margin of the dorsal maxillary root of each zygomatic arch contacts the rostrum at a right angle, not the wide angle forming a concave outline between arch and end of rostrum that is characteristic of *G. surdus* and most other species of *Graphiurus*. Except for Misonne (1974), who included *crassicaudatus* ("perhaps not readily separable from *murinus*"), along with *surdus*, in *G. murinus*, everyone who has published checklists and relevant faunal reports concerning subsaharan dormice has accepted

the infrequently collected *G. crassicaudatus* as a distinct species.

I will present my taxonomic revisions of *G. crassicaudatus* and *G. hueti* in future reports; further comparison, other than the morphometric contrasts mentioned above, indicated in table 5, shown in figures 6 and 7, and outlined by Robbins and Schlitter (1981), are not needed here to clarify the morphological identity of *G. surdus*.

Samples of two other species do require careful comparison with material representing *G. surdus*. Individuals of *G. christyi* and *G. lorraineus* are superficially similar in morphology to specimens of *G. surdus*, found in the same forest region, and these two species have been misidentified as *G. surdus* in the published literature and collections of museums; comparisons among the three are critical to the definition of *G. surdus*.

Dollman (1914: 80) described *G. christyi*, stating that it was "related to *Graphiurus*

spurrelli Dollm., similar in colour and size but differing in the general form of the skull." The name was accepted to indicate a species of *Graphiurus* in the checklists provided by Allen (1939) and Ellerman (1940), but was included in *G. murinus* by Misonne (1974) and in *G. murinus lorraineus* by Genest-Villard (1978); those two authors also immersed *surdus* within their vague definitions of *G. murinus*. Robbins and Schlitter (1981) extracted *christyi* as a diagnosable species within the context of documenting the identification of samples from Cameroon, and Schlitter et al. (1985) reasserted its integrity and outlined its geographic distribution in southern Cameroon and northern Zaire.

I agreed with the observations made by Schlitter and his colleagues (Holden, 1993). Morphological traits of all the specimens I have seen from southern Cameroon and northern Zaire are like those characterizing the holotype of *christyi* and other specimens Dollman described, and separate them from any of the other species of dormouse recorded from the same region.

Graphiurus lorraineus was also named by Dollman (1910: 285) who noted that the "species is easily distinguished from the other members of the genus by the brilliant buff coloration of the upper parts of the body, the comparatively small ears, and short and rather stoutly built skull." Through the years, the treatment of this species in the literature paralleled that of *christyi*: recognized as a species by Allen (1939) and Ellerman (1940); merged with *G. murinus*, along with *christyi* and *surdus*, by Misonne (1974) and Genest-Villard (1978); reestablished as morphologically distinctive by Robbins and Schlitter (1981), who documented samples of it and *G. christyi* from southern Cameroon (Lolodorf); reported upon again by Schlitter et al. (1985), who noted that *G. lorraineus* "is widely distributed and frequently common in forested and second growth situations in West and Equatorial Africa"; and recognized as a species by me (Holden, 1993). Based on specimens studied, my estimate of the geographic distribution of *G. lorraineus* is much broader than indicated in the literature; its geographic distribution will be fully documented in the forthcoming systematic revision of that species.

Although both *christyi* and *lorraineus* were

once relegated to the synonymy of *G. murinus*, each is morphologically diagnosable, particularly in those regions where their geographic ranges overlap. Furthermore, they have been caught at the same localities [records documented below in the gazetteers, and also noted by Hatt (1940)] in Cameroon (Lolodorf) and Zaire (Niangara, Medje, Ya-losemba). Based on my observations, *Graphiurus lorraineus* is not morphologically similar to any member of the *G. murinus* complex. *Graphiurus christyi*, however, is allied with the *G. murinus* group, but its interspecific relationships within that complex are unclear, and it is possible that detailed study may place it as a junior synonym of another species now contained within the *G. murinus* complex.

Systematic revisions of *G. christyi* and *G. lorraineus* will be the subjects of future sections of my overall revision of *Graphiurus*, and maps showing their known geographic ranges as documented by specimens will be included in each of those respective accounts. What I intend to present here are the contrasts between those two species and *G. surdus*. To accomplish this, I brought together 35 adults of *G. christyi* and 112 of *G. lorraineus*. The examples that I studied and the localities at which they were collected are listed in the following gazetteers. These are only a small portion of the known museum specimens of the two species that I examined. I used these smaller samples obtained from southern Cameroon and northeastern and central Zaire, to compare with the sample of *G. surdus*, whose known geographic distribution is in the same general region.

Graphiurus christyi

CAMEROON

1. **Lolodorf** (3.14N, 10.48E): CM 2912, 2953, 2972, 4606.

ZAIRE

2. **Avakubi** (1.18N, 27.35E): AMNH 49890.
3. **Niangara** (3.45N, 27.54E): AMNH 49882.
4. **Mambaka** (0.51N, 27.33E): BM(NH) 14.2.11.8, 14.2.11.9.
5. **Medje** (2.25N, 27.18E): AMNH 49891, 49894, 49895, 49897, 49900–49902, 49905, 49912–49917, 49919, 49920, 51297; BM(NH) 19.5.8.66; USNM 259140.

6. **Yalosemba** (2.35N, 21.47E): CM 86748–86754, 86756.

Graphiurus lorraineus

CAMEROON

1. **7 km NW Ambam** (Ambam = 2.23N, 11.16E), **Meyo/Ambam**: MHNG 912/65.
2. **Assobam** (3.15N, 14.02E): BM(NH) 9.10.2.21.
3. **Bafia** (4.40N, 11.05E): CM 9528.
4. **Bitye** (3.10N, 12.20E): BM(NH) 13.2.8.6, 13.9.12.8, 23.1.22.53; MRAC 10939.
5. **Ebolowa** (2.56N, 11.11E): CM 16135.
6. **Kribi** (2.56N, 9.54E): MCZ 8678.
7. **Lolodorf** (3.14N, 10.48E): CM 2879, 2915, 2969, 2971, 2999, 3685, 3914, 3915, 4560, 4561, 4867, 4868, 5638, 5641, 5679, 5686, 5699, 5704, 5733, 5737, 6120–6122, 13252, 14927, 16136, 16142–16144; MCZ 8676, 17921, 17922.
8. **Metet** (3.23N, 11.43E): CM 4645, 4646, 4673, 4674; FMNH 48926.
9. **Sangmelima** (2.56N, 11.58E): CM 42720, 9529, 9530, 10336.
10. **Yaoundé** (3.51N, 11.31E): CM 42721.
11. **Yokadouma** (3.25N, 15.08E): CM 42719.

EQUATORIAL GUINEA

12. **Rio Muni, Benito River**: BM(NH) 0.2.5.57.

GABON

13. **Mitzié** (0.48N, 11.30E): BM(NH) 58.336.

ZAIRE

14. **Bafwabaka** (2.10N, 27.39E): AMNH 49888, 49889.
15. **Barumbu** (1.15N, 23.29E): MRAC 9209.
16. **Faradje** (3.45N, 29.43E): AMNH 49886.
17. **Inkongo** (4.55S, 23.15E): BM(NH) 13.4.7.3, 7220; MRAC 12190.
18. **Kananga** (5.53S, 22.26E): AMNH 86311, 86316, 86318; BM(NH) 26.7.6.192; MRAC 7144, 7491; TM 9767, 9768.
19. **Kinshasa, Pool Malebo (Stanley Pool)** (4.15S, 15.25E): SMF 6299.
20. **Equateur Province, Lukolela** (1.10S, 17.11E): AMNH 86893, 86894, 86896.
21. **Medje** (2.25N, 27.18E): AMNH 49904, 49906.
22. **Niangara** (3.45N, 27.54E): AMNH 49878; USNM 259142; MRAC 12993.
23. **Nzoro (Vankerckhovenville)** (3.21N, 29.32E): AMNH 49885.
24. **Poko** (3.08N, 26.52E): BM(NH) 19.5.8.67.
25. **Yalosemba** (2.35N, 21.47E): CM 86755, 86758–86761.

GRAPHIURUS SURDUS COMPARED WITH *G. CHRISTYI*: *Graphiurus christyi*, out of all the dormice species found in the central African forest region, is the most similar to *G. surdus* in body size, fur coloration, and cranial morphology. Adults of both species have about the same body size (judged by length of head and body), but *G. surdus* has, on the average, absolutely shorter tail and ears, and longer hind feet (table 6). Proportional differences, diagrammed in figure 13, reflect these contrasts in absolute values listed in table 6: Relative to length of head and body, *G. surdus* has significantly shorter tail and ears but longer hind feet, compared to the sample of *G. christyi*. In this set of comparisons, short ears, as Dollman (1912) noted, are diagnostic of *G. surdus*, and the difference is evident when examples of each species are compared side-by-side. The differences in lengths of tail and hind feet are not always apparent by examination of specimens, but become evident when means of samples are compared.

The two species differ in texture and color of pelage. The dorsal coat of *G. surdus* is very soft and silky to the touch, whereas that of *G. christyi* is velvety. This contrast may be produced by differences in hair morphology, by a denser distribution of hairs in the coat of *G. surdus*, by the slightly greater length of the dorsal fur and guard hairs in *G. surdus*, or some combination thereof. The rump hairs measure between 5 and 7 mm (dorsal guard hairs 9 to 11 mm) in specimens of *G. surdus*, and rump hairs range from 4 to 6 mm (dorsal guard hairs 7 to 11 mm) in examples of *G. christyi*.

Dark grayish brown upperparts characterize specimens of *G. surdus*; the range from brownish gray to dark brownish buff or even reddish brown is typical of *G. christyi*. The overall color of grayish brown of *G. surdus* is flat, but the silky hairs of specimens in good condition have a sheen, so that the dorsal coat of these specimens gleams when held near a light source, not unlike the fur of some amphibious mammals. I do not believe that this is due to so many of the skins having been prepared from fluid specimens, as some examples of *G. christyi* were also prepared from specimens preserved in alcohol, and do not have this characteristic sheen, and some specimens of *G. surdus* that exhibit this trait

TABLE 6

Comparisons of Measurements (mm) and Weight (g) Among Three Species of *Graphiurus* from Equatorial Africa

(Mean \pm 1 SD, range [in parentheses], and number of specimens are listed for each measurement. The range in age from young to old adults is contained within each sample.)

	<i>G. surdus</i> ^a Cameroon, Gabon, Zaire, Eq. Guinea	<i>G. christyi</i> ^b Cameroon, Zaire	<i>G. lorraineus</i> ^c Cameroon, Gabon, Zaire, Eq. Guinea
LHB	98.5 \pm 7.11 (87–110) 10	96.9 \pm 5.52 (86–170) 30	80.5 \pm 5.28 (70–93) 57
LT	71.8 \pm 5.34 (65–82) 8	80.2 \pm 5.39 (73–95) 27	66.8 \pm 6.13 (45–77) 50
LHF	20.4 \pm 1.45 (18–22) 14	18.1 \pm 1.22 (16–20) 31	16.5 \pm 1.55 (12.7–19.1) 57
LE	12.5 \pm 1.66 (9–15) 13	14.2 \pm 1.09 (12–17) 27	12.4 \pm 1.49 (9–15) 27
WT	25.0 \pm 4.86 (18–34) 7	29.0 \pm 3.22 (25–33) 6	16.8 \pm 4.15 (12–24) 5
GLS	27.7 \pm 0.98 (26.5–29.4) 11	28.0 \pm 1.00 (26.7–29.7) 25	24.5 \pm 0.74 (22.7–26.2) 47
CIL	25.0 \pm 0.99 (23.5–26.3) 12	24.1 \pm 1.03 (22.5–26.0) 26	21.3 \pm 0.71 (19.6–22.8) 52
ZB	14.6 \pm 0.61 (23.4–15.7) 12	15.1 \pm 0.76 (13.3–16.7) 23	13.8 \pm 0.48 (13.0–14.9) 41
IB	4.5 \pm 0.18 (4.1–4.8) 16	4.7 \pm 0.17 (4.3–5.2) 34	4.2 \pm 0.18 (3.7–4.7) 82
BBC	12.5 \pm 0.41 (11.7–11.9) 12	12.6 \pm 0.42 (12.1–13.7) 27	11.7 \pm 0.38 (10.8–12.4) 51
HBC	8.1 \pm 0.25 (7.7–8.5) 11	8.1 \pm 0.28 (7.5–8.7) 27	7.4 \pm 0.33 (6.4–8.2) 43
BR	5.7 \pm 0.33 (5.2–6.4) 17	5.8 \pm 0.26 (5.4–6.2) 21	5.1 \pm 0.28 (4.5–5.7) 66
LHR	4.8 \pm 0.36 (4.0–5.5) 15	5.3 \pm 0.39 (4.4–6.1) 31	4.5 \pm 0.25 (3.9–5.0) 75
LN	10.5 \pm 0.57 (9.8–11.6) 15	10.5 \pm 0.54 (8.7–11.3) 32	9.1 \pm 0.44 (7.5–10.0) 96
LD	6.5 \pm 0.34 (5.9–7.0) 18	6.1 \pm 0.39 (5.2–6.9) 34	5.1 \pm 0.29 (4.2–6.0) 81
PL	9.3 \pm 0.43 (8.6–10.3) 17	8.6 \pm 0.39 (7.7–9.1) 29	7.8 \pm 0.32 (6.9–8.4) 70
LBP	5.2 \pm 0.29 (4.8–5.8) 17	4.7 \pm 0.25 (4.2–5.0) 30	4.2 \pm 0.26 (3.6–4.8) 66
LIF	2.8 \pm 0.19 (2.5–3.2) 18	3.0 \pm 0.25 (2.4–3.3) 32	2.7 \pm 0.22 (2.0–3.2) 77
BIF	1.8 \pm 0.11 (1.6–2.0) 17	2.2 \pm 0.13 (2.0–2.4) 32	1.7 \pm 0.13 (1.2–2.0) 76
BBP	3.4 \pm 0.15 (3.1–3.6) 16	3.5 \pm 0.15 (3.3–3.9) 32	3.1 \pm 0.16 (2.7–3.5) 77
CLP4-M3	3.2 \pm 0.15 (2.9–3.5) 18	3.2 \pm 0.09 (2.9–3.5) 33	3.1 \pm 0.15 (2.8–3.4) 79
CLM1-3	2.6 \pm 0.14 (2.4–2.8) 18	2.5 \pm 0.09 (2.4–2.8) 33	2.5 \pm 0.13 (2.1–2.7) 80
BP4	0.8 \pm 0.07 (0.7–0.9) 16	0.9 \pm 0.05 (0.8–0.9) 20	0.8 \pm 0.07 (0.7–1.1) 70
BM1	1.0 \pm 0.07 (0.9–1.1) 16	1.0 \pm 0.03 (1.0–1.1) 24	1.0 \pm 0.06 (0.8–1.1) 75

TABLE 6—(Continued)

	<i>G. surdus</i> ^a Cameroon, Gabon, Zaire, Eq. Guinea	<i>G. christyi</i> ^b Cameroon, Zaire	<i>G. lorrainaeus</i> ^c Cameroon, Gabon, Zaire, Eq. Guinea
BM2	1.1 ± 0.07 (1.0–1.2) 16	1.1 ± 0.05 (1.0–1.2) 26	1.1 ± 0.07 (0.9–1.2) 76
BIT	1.9 ± 0.15 (1.7–2.2) 16	1.9 ± 0.13 (1.7–2.2) 33	1.6 ± 0.12 (1.3–1.9) 74
PPL	11.8 ± 0.60 (11.0–12.9) 12	12.2 ± 0.65 (11.3–13.3) 21	10.5 ± 0.55 (9.5–11.7) 41
LB	7.3 ± 0.22 (6.9–7.7) 15	7.4 ± 0.37 (6.6–7.9) 31	7.0 ± 0.31 (6.4–7.8) 76
BBO	2.7 ± 0.13 (2.4–2.8) 14	2.5 ± 0.24 (2.1–3.0) 23	2.1 ± 0.16 (1.8–2.5) 63

^a Data derived from specimens listed in table 4.

^b AMNH 49884, 49890, 49891, 49894, 49895, 49897, 49900–49902, 49905, 49912–49917, 49919, 49920, 51297; BM(NH) 14.2.11.8, 14.2.11.9, 19.5.8.66; CM 2953, 2912, 2972, 4606, 86748–86754; USNM 259140.

^c BM(NH) 9.10.2.21, 13.2.8.6, 13.9.12.8, 23.1.22.53; CM 2869, 2879, 2915, 2971, 2999, 3685, 3914, 3915, 4560, 4561, 4645, 4646, 4673, 4674, 4867, 4868, 5704, 5638, 5641, 5679, 5686, 5699, 5733, 5737, 6120–6122, 9528, 10336, 13252, 14927, 16135, 16142–16144, 16186, 46720; FMNH 48926; MCZ 8676, 8678, 17921.

were never immersed in spirit. The brownish buff of the dorsal coat of *G. christyi* is rich and lustrous, but lacks the shininess seen in examples of *G. surdus*.

Portions of the long hairs that make up the dark gray and bushy tail of *G. surdus* are unpigmented at their tips, and some hairs are unpigmented from base to tip; this results in the tail appearing frosted. The pattern is characteristic of almost all examples examined of *G. surdus*; it is conspicuous in some (particularly younger) samples, and while less prominent in other specimens, it is almost always evident upon careful inspection. This frosting pattern on the tail was not detected in some skins preserved in alcohol, and because those specimens are discolored (by being either overly darkened or foxed), the pattern, if present, is obscured. Robbins and Schlitter (1981) considered this trait to be diagnostic of the species. Hairs in the tail of *G. christyi* are pigmented to their tips so the tails are the same color as the dorsum and not frosted. This pattern holds for most of the adult *G. christyi* I studied; a few individuals had slight frosting on parts of the tail, but never over the entire tail.

Examples of *G. surdus* have a very faint eye mask extending from the nose or base of the whiskers, circumscribing the eyes, and ending anterior to the base of the ear pinnae.

Specimens of *G. christyi* in general have a more clearly delineated eye mask, and a distinct eye mask is commonly exhibited by members of the *G. murinus* complex, based on my examination of hundreds of specimens. This difference in prominence of the eye mask is another trait used by Robbins and Schlitter (1981) to help distinguish the two species (however, they described it as absent in *G. surdus*, but present in *G. christyi*), and one that I could verify.

Skulls of the two species appear alike in size and shape (figs. 8–10), but the similarity is superficial. Significant absolute and proportional differences exist. Robbins and Schlitter (1981: 286) remarked that *G. surdus* “has a long and narrow skull with a short maxillary toothrow and short depth of rostrum.” The accuracy of this statement depends on the species being compared to *G. surdus*. Absolute length and width of skull and length of toothrow are not useful for separating specimens of *G. surdus* from those of *G. christyi*. Means of greatest length of skull and condyloincisive length (estimating skull length), zygomatic breadth and breadth of braincase (indices of skull width), and length of toothrow (that includes premolars and molars or only molars) in my two samples are not significantly different (table 6). Furthermore, none of these measurements influence



Fig. 8. Comparisons among adult crania of *Graphiurus* from a dorsal perspective. From left to right: *G. christyi*, AMNH 49919, Medje, Zaire; *G. surdus*, RUCAD1655, Masako, Zaire; *G. surdus*, BM(NH) 14.7.23.15, Bitye, Cameroon; *G. lorrainus*, MCZ 17921, Lolodorf, Cameroon. $\times 3.5$. The two examples of *G. surdus* represent samples from opposite areas of its geographic range.

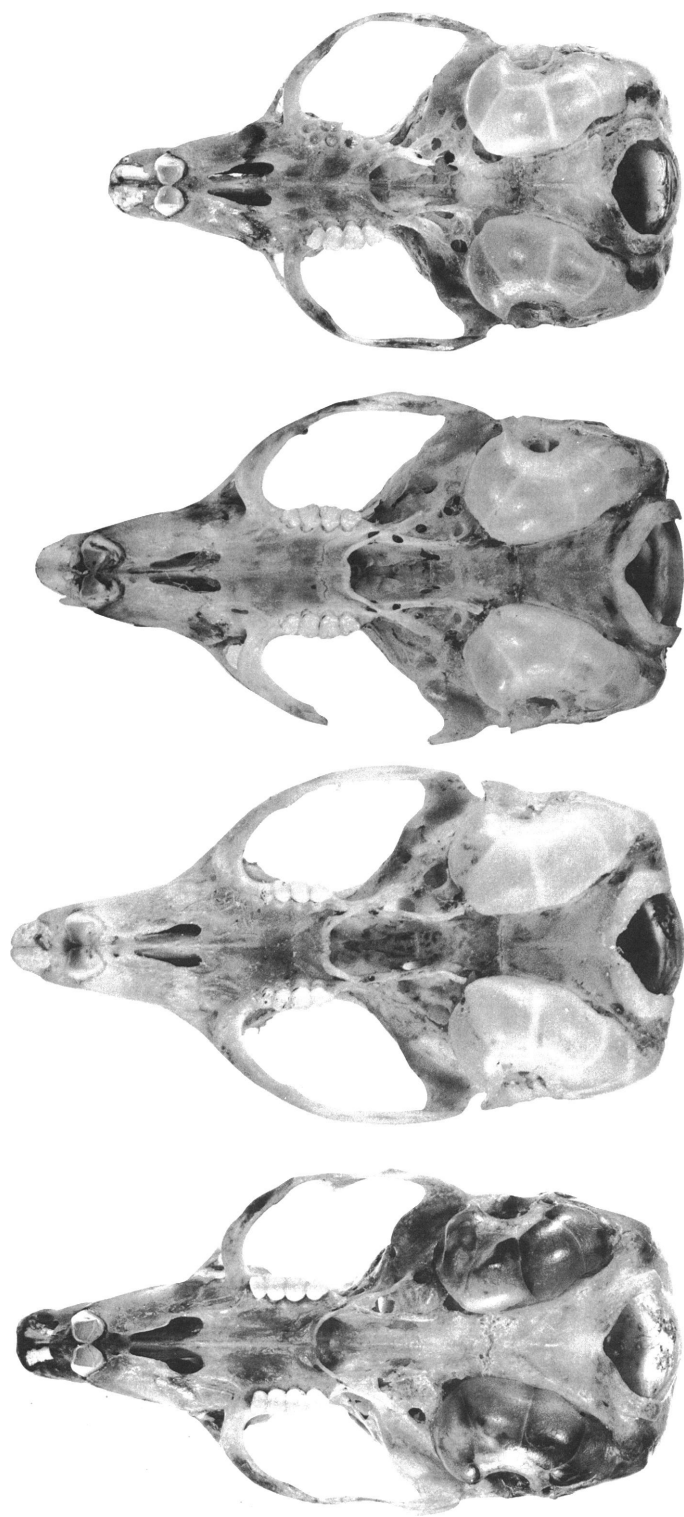


Fig. 9. Ventral views ($\times 3.5$) of the crania illustrated in figure 8. From left to right: *G. christyi*, Zaire; *G. surdus*, Zaire; *G. surdus*, Cameroon; *G. lorrainensis*, Cameroon.

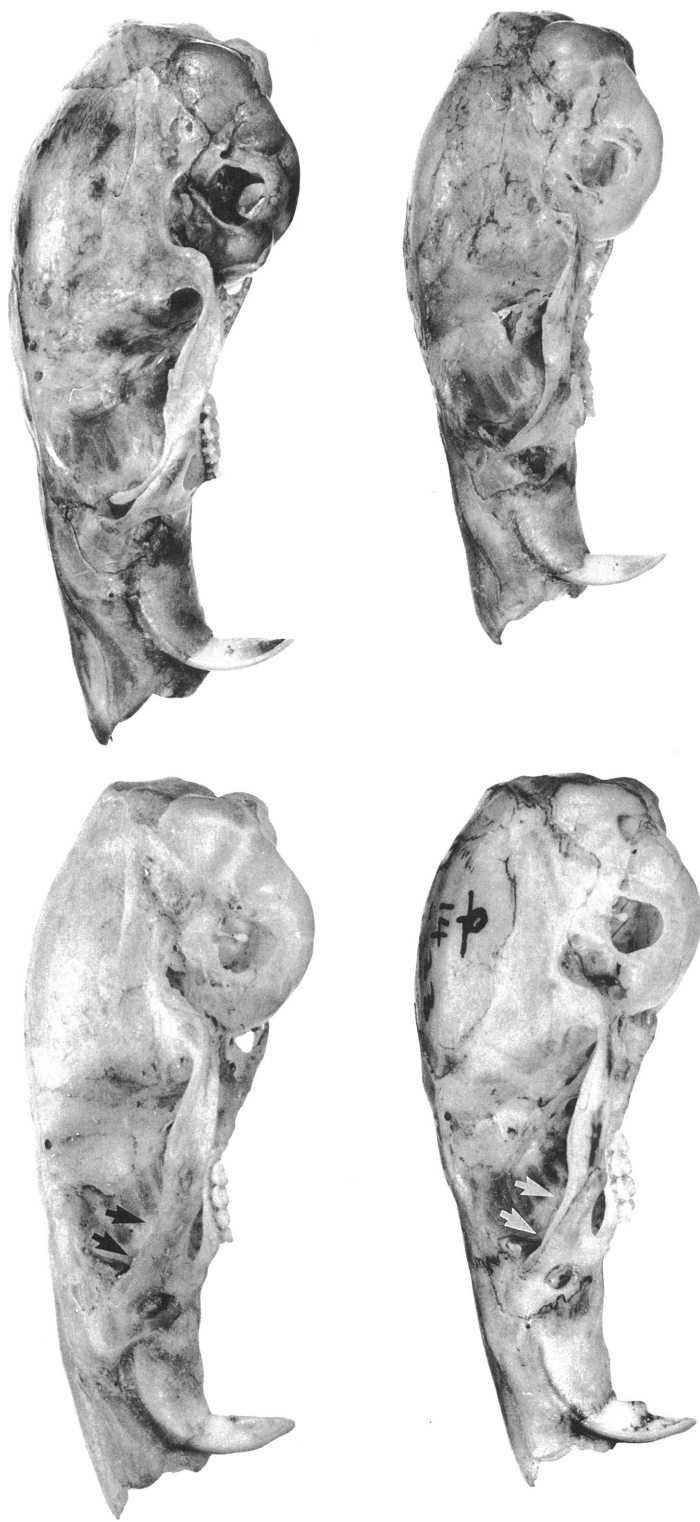


Fig. 10. Lateral views ($\times 3.5$) of the crania of *Graphiurus* portrayed in figure 8. Top left: *G. surdus*, Zaire. Top right: *G. christyi*, Zaire. Bottom left: *G. surdus*, Cameroon. Bottom right: *G. lorrainus*, Cameroon. Note the relatively straight dorsal margin of the anterior portion of the zygomatic arch in *G. surdus* (indicated by arrows); the dorsal surface is strongly arcuate in other species of *Graphiurus*, such as *G. christyi* and *G. lorrainus*.

TABLE 7

Factor Coefficients for General Size and Species Differences (adjusted for general size) Estimated from Log-Transformed Values of 14 Cranial and 1 Dental Measurements of *G. christyi* and *G. surdus*

(Sample of *G. christyi* is from Cameroon and Zaire; that of *G. surdus* comes from Cameroon, Gabon, Equatorial Guinea, and Zaire. Specimen scores are plotted in fig. 11.)

	General size (factor 1)	Species differences (factor 2)
GLS	.259	-.035
IB	.058	.115
BBC	.115	.005
BIT	.436	-.136
LHR	.334	.281
LN	.280	-.057
LD	.372	-.280
PL	.240	-.322
LIF	.342	.122
BIF	.290	.679
BBP	.173	.100
CLP4-M3	.021	.041
CLM1-3	.037	-.008
LB	.217	.053
LBP	.224	-.461

the spread of scores on factors representing general size versus size-adjusted differences between the two species (table 7; fig. 11).

Robbins and Schlitter (1981) were correct about depth of rostrum; *G. surdus* is characterized by a significantly shallower rostrum, not only in absolute mean value (table 6), but also relative to breadth of rostrum when compared with *G. christyi* (fig. 13). Least height of rostrum is also one of the size-adjusted differences influencing morphometric separation of the two species in multivariate space (table 7; fig. 11).

Skulls of *G. surdus* are characteristically elongate, but in the palatal region, not in overall length. Palatal length, length of bony palate, and length of diastema strongly influence separation of the samples of *G. surdus* and *G. christyi* in the principal components analysis (table 7; fig. 11). Absolute values of means of these measurements are also dissimilar between the two species (table 6), as are proportional relationships illustrated in the ratio diagram (fig. 13). There the profiles

TABLE 8

Factor Coefficients for General Size and Species Differences (adjusted for general size) Estimated from Log-Transformed Values of 14 Cranial and 3 Dental Measurements of *G. lorrainaeus* and *G. surdus*

(Samples of *G. surdus* are from Cameroon, Equatorial Guinea [Rio Muni], and Zaire; those of *G. lorrainaeus* were obtained in Cameroon, Equatorial Guinea [Rio Muni], Gabon, and Zaire. Specimen scores are plotted in fig. 12.)

	General size (factor 1)	Species differences ^a (factor 2)
GLS	.180	.154
IB	.052	.129
BBC	.157	.024
BIT	.381	.232
LHR	.225	-.063
LN	.313	.113
LD	.206	.423
PL	.191	.308
LIF	.258	-.173
BIF	.292	-.166
BBP	.110	.122
CLM1-3	.234	-.087
BM1	.288	-.188
BP4	.406	-.520
LB	.153	-.005
LBP	.107	.470
BR	.258	.087

^a Signs of coefficients changed following convention in Voss and Marcus (1992: 1923).

indicate that relative to greatest length of skull, the palatal region (indexed by the significantly greater palatal length, and lengths of diastema and bony palate) is significantly longer than in *G. christyi*; postpalatal length, however, is relatively shorter in *G. surdus*, an expected configuration given that overall skull length is nearly the same in the two species.

Breadth of incisive foramina also helps separate the two species (table 7; fig. 11). It is absolutely narrower in *G. surdus* than in *G. christyi* (table 6), and significantly narrower relative to breadth of rostrum (fig. 13).

Other morphometric distinctions between the two samples exist in absolute mean values (table 6) but are not significant. However, there are additional significant proportional distinctions. For example, compared with *G.*

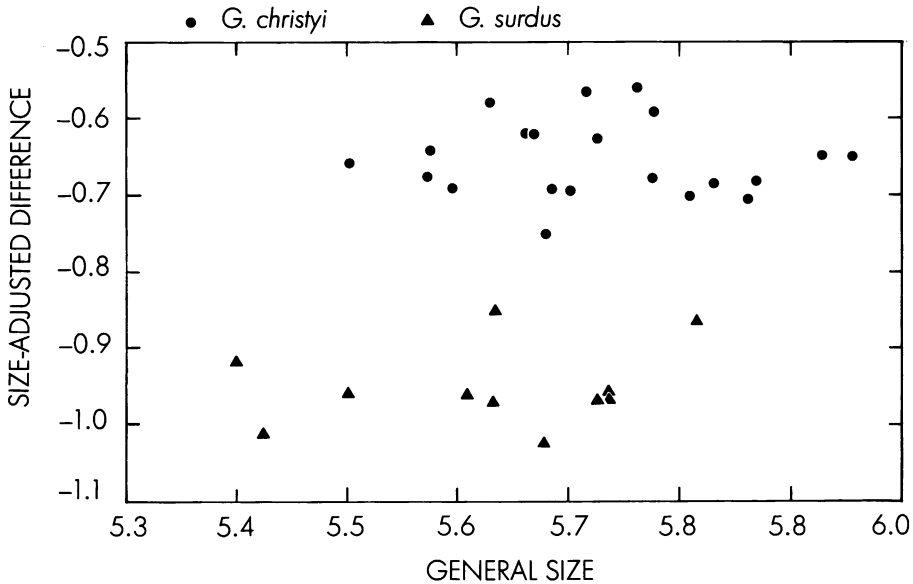


Fig. 11. Discrimination between samples of *Graphiurus surdus* from Cameroon, Gabon, Equatorial Guinea, and Zaire (N = 11) and *G. christyi* from Cameroon and Zaire (N = 21) as indicated by individual specimen scores plotted on factors representing general size and size-adjusted species differences. The separation along the size-adjusted axis is predominantly influenced by differences in breadth of incisive foramina and length of bony palate, and to a lesser extent by palatal length, least height of rostrum, and length of the diastema (table 7).

christyi, the sample of *G. surdus* has shorter incisive foramina relative to length of diastema, narrower bony palate relative to its length, narrower fourth upper premolar relative to the first upper molar, and wider basioccipital relative to bullar length (reflecting the absolute smaller bullae of *G. surdus*; fig. 13).

One qualitative cranial character found in most specimens examined is unique to *G. surdus*. In lateral view, the side of each zygomatic arch (primarily the jugal and squamosal process) has relatively straight dorsal and ventral surfaces; the dorsal surface is strongly arcuate and ventral margin shallowly concave in other species of *Graphiurus*, such as *G. christyi* and *G. lorraineus*. The extremes in variation of this character, and comparisons with *G. christyi* and *G. lorraineus* can be seen in figure 10. The *G. surdus* specimen from Masako, Zaire (top left) strongly exhibits this trait, whereas it is much less evident in the specimen from Bitye, Cameroon (bottom left). This character is also

clearly exhibited by the holotype of *G. surdus* (fig. 4).

G. SURDUS COMPARED WITH G. LORRAINEUS: The primary reasons for contrasting samples of *G. surdus* and *G. lorraineus* is simply that *surdus*, along with *lorraineus*, was either referred to another species, *G. murinus*, (Misonne, 1974), or allocated as a synonym of *G. murinus lorraineus* (Genest-Villard, 1978), despite evidence for sympatry and apparent dissimilar morphologies of *surdus* and *lorraineus*.

Within the geographic region where both *G. surdus* and *G. lorraineus* occur, examples of *G. surdus* are conspicuously larger, a contrast reflected in mean differences of most measurements (table 6). Among the external measurements, mean ear length is about the same in the two species, but relative to length of head and body, ear length is significantly shorter in *G. surdus* than in *G. lorraineus* (fig. 14). The tail is absolutely longer in *G. surdus*, but significantly shorter relative to length of head and body compared with *G. lorraineus*

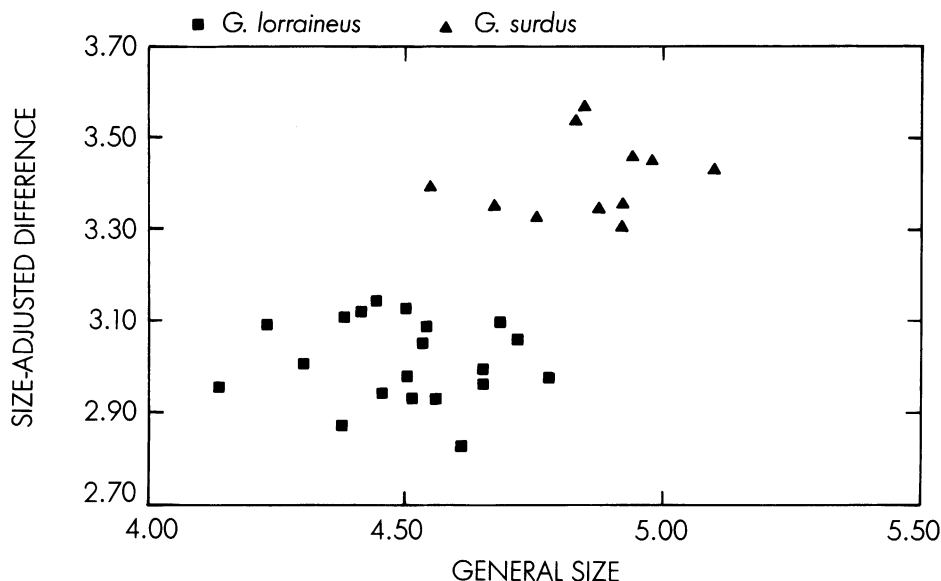


Fig. 12. Discrimination between samples of *Graphiurus surdus* from Cameroon, Equatorial Guinea, and Zaire (N = 11) and *G. lorrainus* from Cameroon, Equatorial Guinea, Gabon, and Zaire (N = 20) as reflected by specimen scores plotted on factors representing general size and size-adjusted species differences. Spread along the size-adjusted axis is most strongly influenced by differences between samples of the two species in breadth of the fourth upper premolar, length of bony palate, length of the diastema, and to some extent by differences in palatal length and breadth of incisor tips (table 8).

(fig. 14). Relatively shorter tail and ear also distinguished *G. surdus* from *G. christyi*. Length of hind foot, although absolutely longer in *G. surdus*, does not differ significantly relative to length of head and body when compared with *G. lorrainus* (fig. 14).

Contrasts between *G. surdus* and *G. lorrainus* in texture and color of fur parallel those observable between *G. surdus* and *G. christyi*. Compared with the silky, grayish brown dorsal coat of *G. surdus*, that of *G. lorrainus* is velvety and coppery brown; *G. surdus* has inconspicuous eye rings, *G. lorrainus* has conspicuous dark rings; the tail of *G. surdus* is frosted, that of *G. lorrainus* is usually monocolored (although it should be noted that some juvenile specimens of *G. lorrainus* have some unpigmented hairs mixed in their otherwise brown tails).

In addition to the greater mean values of most cranial measurements of *G. surdus* compared with *G. lorrainus* (table 6), there are significant proportional differences illustrated in the ratio diagram (fig. 14). For ex-

ample, certain dimensions reflecting cranial lengths in *G. surdus* (condyloincisive and palatal lengths, lengths of nasals, diastema, and bony palate) are significantly longer relative to particular breadth dimensions (zygomatic and interorbital breadths, breadths of braincase, rostrum, and incisive foramina), compared with *G. lorrainus*. Thus, when compared with *G. lorrainus* (but not with *G. christyi*, see discussion above), *G. surdus* does not have a long, narrow skull as described by Robbins and Schlitter (1981: 286). In *G. surdus*, the rostrum is lower (least height of rostrum) relative to rostral breadth (also noted by Robbins and Schlitter, 1981), and the incisors are significantly broader relative to rostrum and other breadth dimensions compared with *G. lorrainus*. The auditory bullae of *G. surdus* are smaller relative to condyloincisive length than those of *G. lorrainus*; this is reflected in the broad basioccipital of *G. surdus*, which is wider relative to most of the other breadth dimensions, as well as length of the bullae (fig. 14).

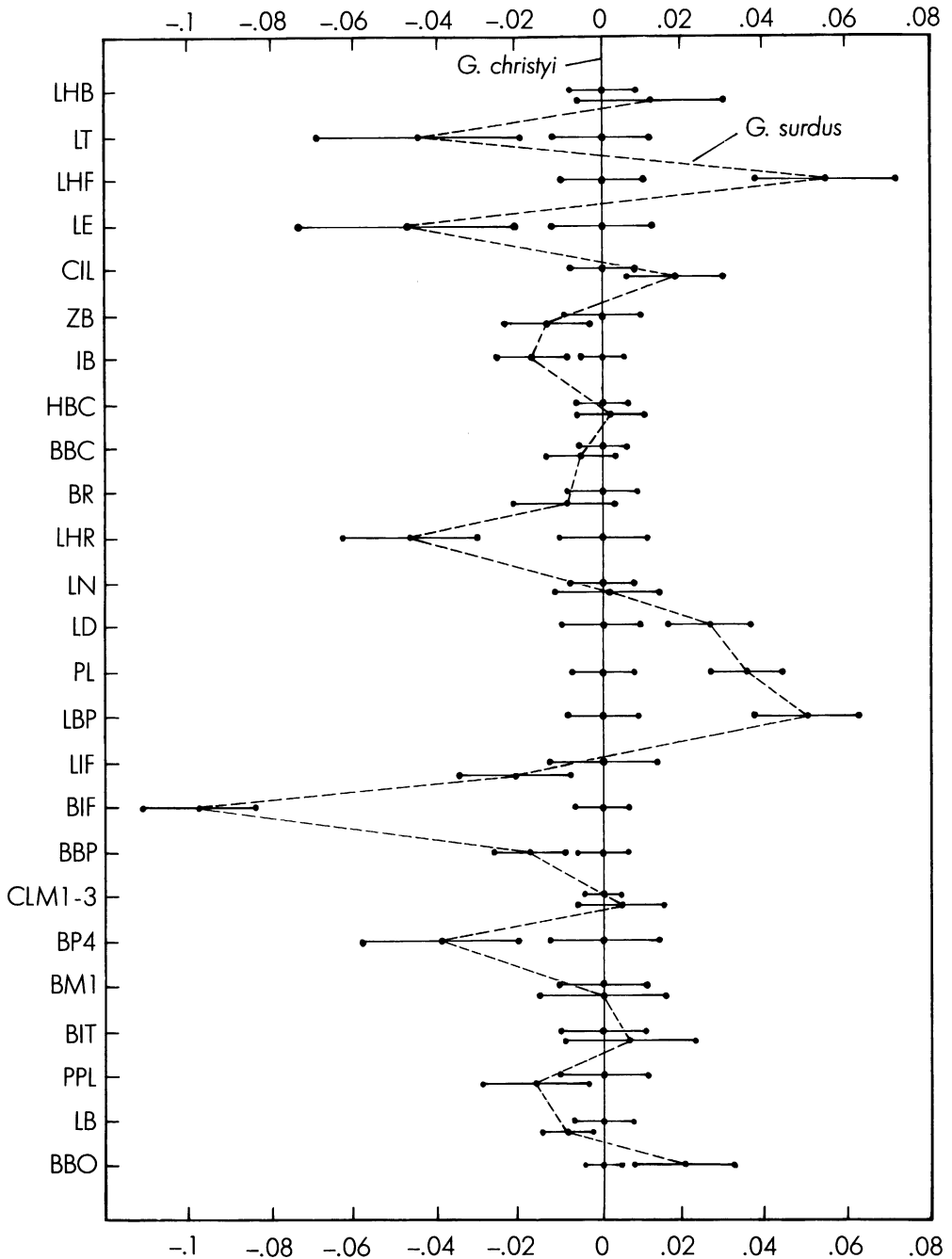


Fig. 13. Ratio diagram indicating some proportional relationships between samples of *Graphiurus*. Dimensions are compared between samples of *Graphiurus christyi* (the standard) from Cameroon and Zaire and *G. surdus* from Cameroon, Zaire, Gabon, and Equatorial Guinea (see discussion in text). For each measurement, the absolute value of the mean, and plus and minus two standard errors of the mean, were converted to logarithms. For each dimension, the logarithm of the mean of the standard (*G. christyi*) was subtracted from the logarithm of the mean of the series of *G. surdus*, and the logarithms of plus and minus two standard errors of the mean of the standard were subtracted from the logarithms of plus

Portions of the palatal region of *G. surdus* are relatively long. Compared with *G. lorrainus*, the diastema is significantly longer relative to condyloincisive length in *G. surdus* (influenced in part by the relatively shorter tooththrow of *G. surdus*), and the incisive foramina are significantly shorter relative to diastemal length (fig. 14). Similar proportional differences in the diastemal region were found between *G. surdus* and *G. christyi* (fig. 13). The palatal length of *G. surdus* is only slightly longer than that of *G. lorrainus* relative to condyloincisive length (fig. 14), although this small difference does aid in discrimination between the species in multivariate space (fig. 12, table 8).

Mean values of the various dental measurements do not differ significantly between the two species; basically, the upper premolars and molars of *G. surdus* are the same absolute size as those of *G. lorrainus*, but set in a larger skull (table 6). So although these dimensions do not differ in absolute terms, they are relatively dissimilar. Compared with *G. lorrainus*, length of molar row, for example, is significantly shorter relative to length of bony palate in *G. surdus*, and the fourth upper premolar is significantly narrower relative to the first upper molar (fig. 14).

Separation along the size-adjusted axis in multivariate space of samples of the two species is most strongly influenced by differences in breadth of the fourth upper premolar, and lengths of diastema and bony palate (table 8; fig. 12).

Finally, the qualitative trait that often separates *G. surdus* from *G. christyi* also discriminates between the former species and *G. lorrainus*. The configuration of the zygomatic arch in *G. lorrainus* in lateral view

resembles the shape characteristic of *G. christyi*, and differs from the horizontal configuration with its nearly straight top and bottom that is diagnostic of most specimens of *G. surdus* (fig. 10, top left) (see discussion of variation of this character under comparison with *G. christyi*).

NATURAL HISTORY

Very little information is available regarding the ecology of *G. surdus*. The only data I have located comes from collectors. A specimen collected in Bitye, Cameroon, by G. L. Bates was "smoked out of a hollow tree" (written on skin tag, BM(NH) 14.7.23.15). This suggests that like *G. crassicaudatus*, *G. huetti*, and *G. lorrainus*, and possibly some other species of *Graphiurus*, *G. surdus* may often nest in hollow trees.

However, *G. surdus* may also have the capacity to build nests in other suitable cavities or locations. Robbins and Schlitter (1981: 286), for example, wrote that "the specimens [of *G. surdus*] from Eseka were taken in the same trapline as *G. crassicaudatus*." They described the trapline in their discussion of that species (p. 284):

Specimens [of *G. crassicaudatus*] from the vicinity of Eseka were trapped in Sherman non-folding aluminum live-traps set on vines and horizontal branches in secondary high forest. No hollow trees were seen in the immediate area. All traps were baited with the nut of the oil palm (*Elaeis*). Traps were in position for two or more weeks before dormice entered.

Notes written on the skin tag of the specimen from Inkongo, Zaire (BM(NH) 13.4.7.2), recorded only that the animal was "killed in forest. This or a similar species [is] often found in thatched roofs of houses. Na-

←

and minus two standard errors of the mean of *G. surdus*. Measurements larger than the standard are represented by positive values, those smaller by negative values. In each sample, the solid or dashed lines connect the means of measurements, the horizontal bars represent plus or minus two standard errors of the mean. A sample with the same proportions as the standard will be represented by mean values on a line parallel to that of the standard regardless of absolute size. Also, if values for the samples being compared with the standard are similar in absolute size, they will be close together on the diagram. If proportions between any of the measured dimensions are similar, the positions of their points relative to each other on the horizontal scale will be similar. The diagram was constructed from values for mean, standard deviation, and sample size of variates listed in table 6.

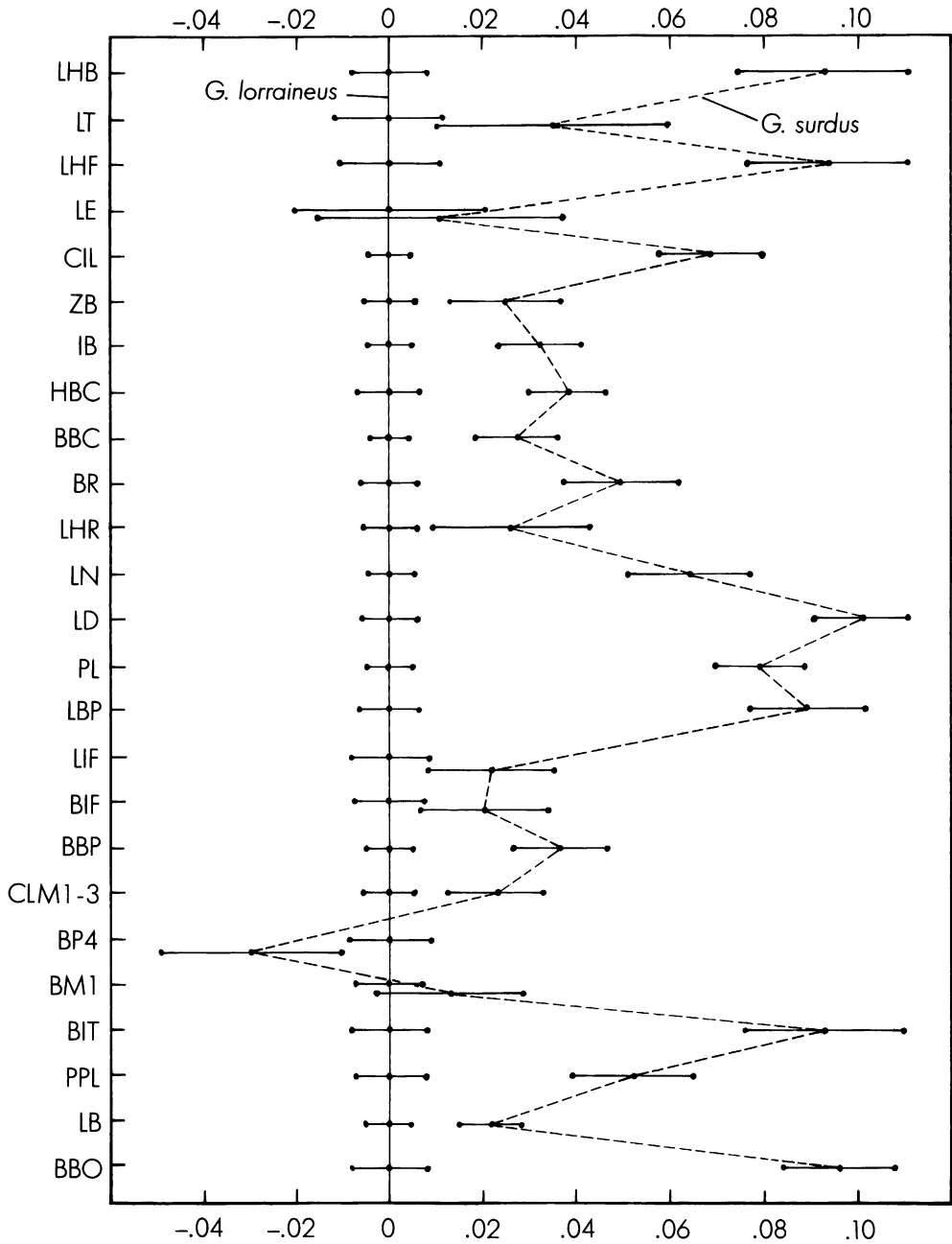


Fig. 14. Ratio diagram indicating some proportional relationships between species of *Graphiurus*. Dimensions are compared between samples of *G. lorraineus* (the standard) and *G. surdus* from Cameroon, Gabon, Zaire, and Equatorial Guinea (see discussion in text). Basic properties of the ratio diagram are explained in the legend to figure 13. This visual proportional representation was derived from the values for mean, standard deviation, and sample size of the variates listed in table 6.

tive name Kankyesa.” It is doubtful that *G. surdus* was the species commonly found in thatched roofs of houses at Inkongo. Specimens of *G. lorraineus* are often recorded as having been taken from either thatched roofs or simply from houses, and this species was also collected in greater numbers at Inkongo (table 3).

The animal collected at Masako (from the Masako Forest Reserve) was captured in a Victor snaptrap baited with fruit of oil palm (*Elaeis guineensis*). The trap was set on the ground in secondary forest (W. Verheyen, personal commun.). The Reserve, according to Hutterer and Dudu (1990: 305) “. . . is situated 14 km northeast of Kisangani (Haut-

Zaire), in a loop of the river Tshopo. Of the 2105 ha of the reserve, one-third is covered by primary forest with *Gilbertiodendron deweyrei* as the dominant tree, and two-thirds by secondary forest grown upon primary forest logged between 1948 and 1955.”

Much remains to be learned about the ecology of *G. surdus*. Its diet, reproductive biology, behavior, kinds of nest sites, and nest construction are unknown. Specimens have been trapped in forests, but we are ignorant of the animal's microhabitat. How *G. surdus* and the other three (possibly four) species of dormice with which it is sympatric coexist and partition resources is an intriguing question that needs to be explored.

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