Chapter 9

Systematic Revision of Sub-Saharan African Dormice (Rodentia: Gliridae: *Graphiurus*)
Part II: Description of a New Species of *Graphiurus* from the Central Congo Basin, Including Morphological and Ecological Niche Comparisons with *G. crassicaudatus* and *G. lorraineus*[1]

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ABSTRACT

A new species of *Graphiurus*, *G. walterverheyeni*, is described. It is represented by two young adults, a female (holotype) and male (paratype), obtained from two sites in the central Congo Basin, Democratic Republic of the Congo. The new species is the possible morphological and phylogenetic counterpart of *G. crassicaudatus*, endemic to West Africa. Although the new species resembles *G. crassicaudatus* in texture and coloration of pelage, along with certain derived cranial features, *G. walterverheyeni*, n. sp., is separated not only by its much smaller body size as evidenced by the significant contrasts in external, cranial, and dental metrics between the two species, but also by proportional differences.

The South Central faunal region of equatorial Africa (Grubb, 1978, 1982, 2001; Colyn, 1991; Colyn and Van Rompaey, 1994; Happold, 1996), and the Salonga-Lukenie-Sankuru landscape (Congo Basin Forest Partnership, 2006), identify the biogeographic landscape of *G. walterverheyeni*, n. sp. Scant habitat information associated with the specimens suggests that this Congo Basin endemic occurs in seasonally flooded tropical lowland forest formations. Two other species of *Graphiurus*, *G. lorraineus* and *G. surdus*, are broadly sympatric with the new species, but neither has been recorded from the two collection localities.

Determining species diversity of sub-Saharan dormice embraces epidemiological concerns in addition to strictly taxonomic and biogeographic inquiries. The first documented outbreak of human monkeypox outside Africa occurred in the midwestern United States in 2003 and was associated with a shipment of captive mammals (*Funisciurus* sp., *Heliosciurus* sp., *Cricetomys* sp., *Atherurus* sp., *Hybomys* sp., and *Graphiurus* sp.) from Ghana (Guarner et. al., 2004). Following this outbreak, certain species of African dormice occurring in West and Central Africa are currently being scrutinized as possible hosts of monkeypox virus (*Orthopoxviridae*), which can produce a severe illness in humans resembling smallpox (Hutson et al., 2007; Levine et al., 2007). Understanding the ecology and epidemiology of this virus requires correct identification of mammalian host species so that accurate, relevant geographic and ecological data can be analyzed.

INTRODUCTION

Lying south of the great bend of the Congo River, and embraced in the west by the mighty western arm of the Congo and in the east by its grand tributary, the Lualaba River, is a vast expanse of tropical lowland evergreen rainforest punctuated by lakes, marshes, and swamps recognized as the south-central forest region (Grubb, 1978, 1982, Grubb 2001, and authors cited therein; Colyn, 1991; Colyn and Van Rompaey, 1994; Happold, 1996; White, 2001). One elephant shrew (Macroscelidae), 18 kinds of primates (in the families Galagidae, Cercopithecidae, and Hominidae), one mongoose (Herpestidae), and two rodents (Muridae) occur here and nowhere else in sub-Saharan Africa. To this unique mammalian assemblage can now be added a species of dormouse (*Graphiurus*), which we name and describe here as a contribution toward a systematic revision of the genus (Holden, 1993, 1996, 2005, in press).

Two specimens document the new species of *Graphiurus*, one collected in 1917 and stored in the Natural History Museum in London, the other obtained in 1987 and housed at the Royal Museum for Central Africa in Tervuren. The species is sympatric with two other equatorial *Graphiurus*, the larger-bodied *G. surdus*, and *G. lorraineus* which is similar in body size to the new form. Aspects of its cranial morphology suggest that the new *Graphiurus* is not closely related to either of these two sympatric forms, but rather to *G. crassicaudatus*, endemic to West Africa.

The description of this new species of *Graphiurus*, apparently endemic to the south-central forest region, spotlights the critical role of museums and other kinds of research institutions in maintaining collections of mammals and making them available to researchers. These specimens are primary data sources. In the case of the new *Graphiurus*, one skin and skull resided in a collection for 91 years before it was identified as an example of an undescribed species; a carcass in fluid and extracted skull sat misidentified for 22 years. With their new identity documented here comes fresh infor-

mation regarding the diversity of species within sub-Saharan dormice, an additional datum supporting the integrity of the region south of the great bend of the Congo River as an endemic mammalian faunal area. Additionally, it presents opportunities to discuss the zoogeographical significance of dormice distributions in equatorial Africa and test hypotheses of phylogenetic relationships among species of sub-Saharan African dormice, which range from Senegal to the Cape of Good Hope.

MATERIALS AND METHODS

INSTITUTIONS AND SPECIMENS: Specimens cited by institutional abbreviations and catalog numbers are stored in the collections of the Amathole Museum (formerly the Kaffrarian Museum), King William's Town (AM); American Museum of Natural History, New York (AMNH); Natural History Museum, London (BMNH); Carnegie Museum of Natural History, Pittsburgh (CMNH); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Michigan State University, East Lansing (MSU); the Natural History Museum, Bulawayo, Zimbabwe (NHMZ); Royal Belgian Institute of Natural Sciences, Brussels (RBINS); Royal Museum for Central Africa, Tervuren (MRAC); National Natuurhistorisch Museum, Leiden (RMNH); Université d'Anvers, Rijksuniversitair Centrum Antwerpen, Antwerpen (RUCA); Transvaal Museum, Pretoria (TM); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Staatliches Museum für Naturkunde Stuttgart, Stuttgart (SMNS); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK); and Zoologisches Museum und Institut für Spezielle Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin (ZMB). The abbreviations preface catalog numbers referring to specimens listed in the gazetteer, tables, text, and figure legends. Most of the material consists of standard museum preparations (a stuffed

skin accompanied by a cranium and mandible); a few specimens are preserved in fluid.

MEASUREMENTS: Values (in millimeters) for total length and length of tail are those recorded by collectors on labels attached to skins; subtracting length of tail (LT) from total length produced a value for length of head and body (LHB). Proportion of tail length relative to length of head and body is expressed in percent derived from LT/LHB. Values for length of hind foot (LHF), which includes claws, were obtained either from skin labels or from Holden's measurements of dry study skins and specimens preserved in fluid; those for length of ear (LE) come from collector's measurements notated on skin labels (presumably they represent greatest length, from the notch to the distal margin of the pinnae). Weights in grams (WT) were sometimes recorded by collectors and these are included in some descriptive statistics.

With the aid of a dissecting microscope, Holden used handheld digital calipers to measure (values were recorded to the nearest 0.1 mm) the following cranial and dental dimensions listed in the sequence they appear in tables:

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
LIF	length of incisive foramina
BIF	breadth of incisive foramina
BBP	breadth across bony palate at M1
CLP4-M3	crown length of maxillary tooth row
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 across upper incisor tips
PPL	postpalatal length
LB	length of bulla
BBO	breadth of basioccipital

Limits of these measurements are illustrated in figure 1 and reasons behind their selection are elaborated by Holden (1996; one dimension shown in the figure, LIP, length of interparietal, was not measured). Only the cranial and dental measurement values were incorporated in multivariate analyses; values from external measurements portray general body size and lengths of appendages.

AGE AND SEXUAL DIMORPHISM: Data used in the tables of descriptive univariate statistics and multivariate statistical analyses were derived from "adults" only, which includes the following three age classes.

Young adult: Occlusal surface of fourth premolar is level with surfaces of the molars. The premolar and molars show slight or no wear.

Adult: Occlusal surfaces of all teeth are moderately worn (lingual and buccal facets are worn, transverse ridges are worn but not obliterated).

Old adult: Chewing surfaces of all teeth are very worn. The labial margins are often sharply beveled or eroded, many or all of the transverse ridges are obliterated or distorted, and the teeth appear flattened, worn nearly to tops of their roots.

Although stage of tooth eruption and wear were the primary criteria for assigning specimens to the age classes, we also evaluated degree of fusion of cranial sutures along with pelage characteristics. All specimens identified as "adults", for example, have shed the juvenile coat and are clothed in full adult pelage. Uniting such a broad range of adult stages was the only way to obtain adequate samples for analysis; "series of African dormice are, with a few exceptions, characteristically small and from scattered localities" (Holden, 1996: 7).

The multivariate statistical analyses and tables of descriptive statistics are derived from samples containing both sexes combined. Males and females of most species of *Graphiurus* are about equal in body size and closely similar in morphological features not associated with sexual traits. Our data
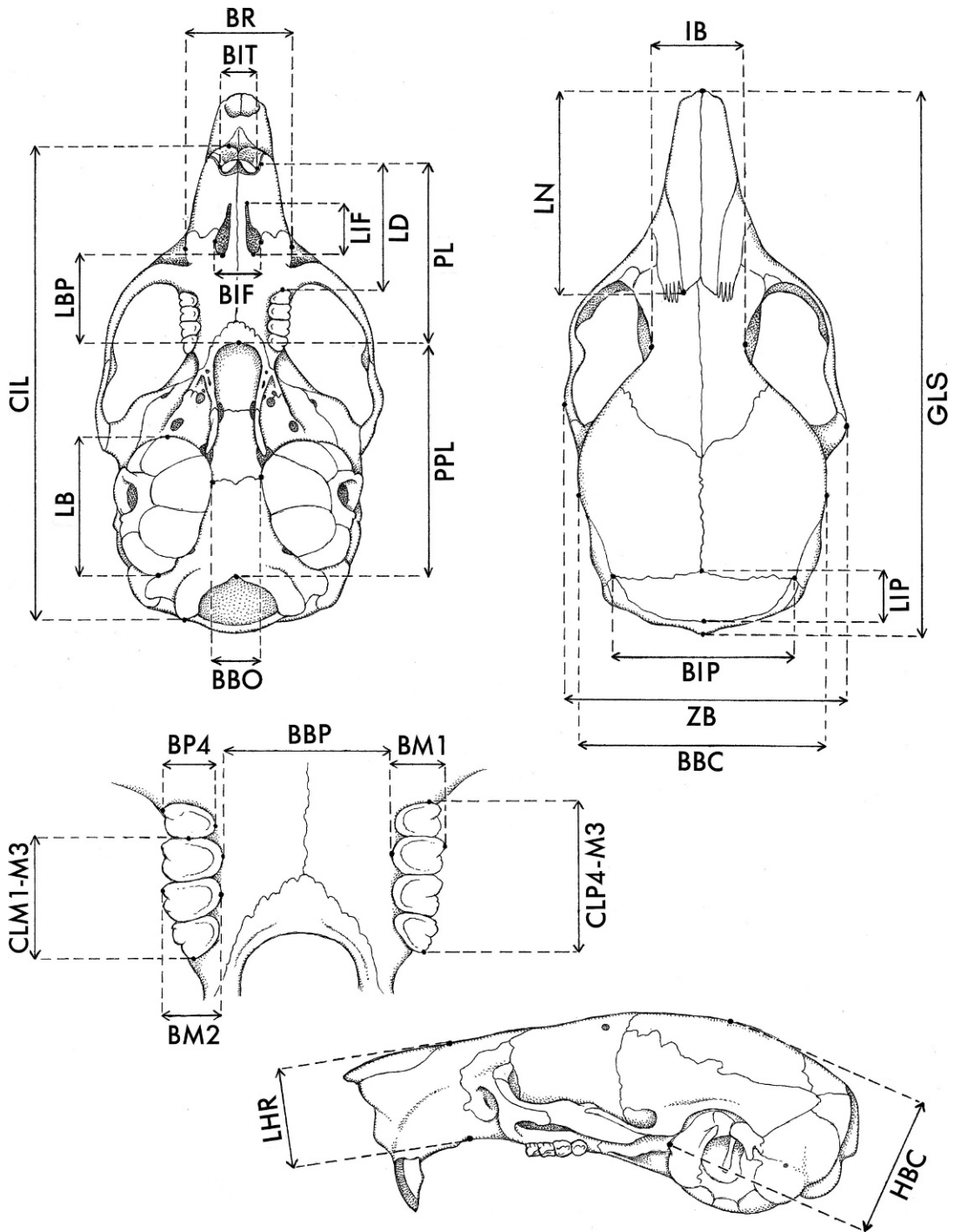
Fig. 1.　Limits of cranial and dental measurements imposed upon the outline of an adult *Graphiurus christyi*. Abbreviations are explained in the text.

demonstrate no consistent patterns of sexual size dimorphism within available samples of the species of *Graphiurus* discussed here (see Holden, 1996, for a broader discussion covering the nature of intergender sexual variation within samples of *Graphiurus*).

STATISTICAL ANALYSES: We calculated standard univariate descriptive statistics (mean, standard deviation, and observed range). Values are listed in table 4 for the sample of *G. walterverheyeni*, n. sp., and samples of *G. crassicaudatus*, *G. lorraineus*, and *G. surdus* to which the new species is compared.

Multivariate statistical results take the form of principal components analyses employing values from 11 (fig. 11), 13 (fig. 12), or 15 (fig. 13) of the 24 cranial and dental measurements taken from adults. The reduction from 24 was necessary because the incidence of broken skulls is high and complete sets of measurements for the samples were available only for those subsets of variables; also a very few measurements were excluded from the analyses because they revealed no discriminatory resolution (usually highly correlated with other measurements). All measurement values were transformed to natural logarithms, and principal components were extracted from a covariance matrix. Plots of specimen scores in cluster analyses provided visual patterns that reflect similarity or contrast in the combined cranial and dental dimensions surveyed among samples of different species, each composed of specimens from more than one collection locality. SYSTAT® software for Windows® (version 11.00.01, 2004) was used for processing all morphometric analyses.

RATIO DIAGRAM: Proportional craniometric relationships among three species of *Graphiurus* are illustrated using the ratio diagram in figure 10. 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. crassicaudatus* from Cameroon, Nigeria, Togo, Ghana, Côte d'Ivoire, Liberia, and Equatorial Guinea; $N = 36$) was subtracted from the logarithm of the mean of *G. lorraineus* (from Cameroon, Gabon, D.R.

Congo, and Equatorial Guinea; $N = 96$) and the new species (from the central Congo Basin; $N = 2$; the holotype and paratype). The logarithms of plus and minus two standard errors of the mean of the standard were subtracted from the logarithms of plus and minus two standard errors of the mean of the two comparative species. A species 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. If values for the species being compared with the standard are similar in absolute size, they will be close together on the diagram. Proportional differences will be indicated by deviation from a comparative species' hypothetical parallel line along the horizontal scale. Data are derived from values for mean, standard deviation, and sample size of variables listed in table 4.

ANATOMICAL DEFINITIONS: Most anatomical terms for cranial foramina and osseous elements are illustrated and described for dormice by Wahlert et al. (1993). Other features (sphenopterygoid vacuities, mesopterygoid and pterygoid fossae) are depicted in Musser and Holden (1991: 346).

ECOLOGICAL NICHE MODELING: Sources of data and algorithms used to generate the predicted distribution maps in figures 14–16 and pertinent discussion are described below.

Provenances for the specimens of *Graphiurus*: Collection localities for *G. crassicaudatus*, *G. walterverheyeni*, n. sp., "true" *G. lorraineus* (samples from west-central, south-central, and east-central forest regions), and the *G. lorraineus* complex were compiled through Holden's comprehensive examination of preserved specimens (skins, skulls, and fluid-preserved material) in the 18 museums listed in the Institutions and Specimens section. Limits of species are derived from qualitative anatomical data combined with morphometric information. Decimal longitude and latitude coordinates, accurate to at least one minute, of all collection localities were determined utilizing one or more of the following sources for each specimen: localities and coordinates recorded on specimen tags by collectors; collectors' field notes; personal communication with collectors, and scientific publications provid-

TABLE 1
Annual Values for Environmental Variables at Geo-referenced Collection Localities (Occurrence Points) for *Graphiurus crassicaudatus*[a] (29 locations), *G. walterverheyeni*[a] (2 locations), and *G. lorraineus*[b] (26 locations) in Equatorial Africa
(Data are summarized by mean, followed by median in parentheses, and range.)

Environmental Variable	G. crassicaudatus	G. walterverheyeni	G. lorraineus
Mean temperature (°C)	25.7 (26) 26.1–27.2	25 (25) 24.8–25.1	24.3 (24.1) 23.3–26.6
Maximum temperature (°C)	30.1 (30.4) 27.9–31.9	30.1 (30.1) 29.9–30.2	29.3 (29.4) 27.8–30.8
Minimum temperature (°C)	21.3 (21.6) 19.2–23.1	19.9 (19.9) 19.5–20.3	19.3 (19.4) 17.3–22.7
Diurnal temperature range (°C)	8.8 (8.7) 7.7–10.7	10.1 (10.1) 9.6–10.6	9.9 (10.2) 7.9–12.7
Precipitation (mm/day/month)	55.3 (58) 33–77	49 (49) 47–51	47.8 (47) 39–62
Wet days (days/month)	13.1 (13.3) 8.5–16.5	11 (11) 10.8–11.1	12.2 (12) 9–15
Days of ground frost (days/month)	0.56 (0) 0–3	0 (0) 0–0	0.36 (0) 0–2
Altitude (m)	286.8 (181) 69–1183	414.5 (181) 398–431	521.3 (543) 18–804

[a] Collection localities and specimens are identified in the Gazetteer.

[b] Samples are from southern Cameroon, Equatorial Africa (Bioko), Gabon, and Democratic Republic of the Congo, which represent "true" *G. lorraineus* (see collection localities and specimens listed in the gazetteer and discussion in text).

ing coordinate data and maps of *Graphiurus* collecting localities (referenced in Holden, 2005, in press). Coordinate data were corroborated when possible by utilizing the Alexandria Digital Library Gazetteer (1999–) and other reference sources. Collection localities were considered only once with no weighting to account for multiple collections of the same species at a single place, as our goal in performing ecological niche modeling (ENM) was to identify only the species (or species complex) distribution and not its abundance within any zones of favorable habitat. The final set of data derived from collection localities contained a total of 29 (fig. 14), 2, 26 (fig. 15), and 106 (fig. 16) verified and unique points (each referring to a georeferenced collection site) for *G. crassicaudatus*, *G. walterverheyeni*, true *G. lorraineus*, and the *G. lorraineus* complex, respectively. These localities are listed in the gazetteer for *G. crassicaudatus*, *G. walterverheyeni*, true *G. lorraineus*, and the *G. lorraineus* complex.

Geographic and environmental data: Thirteen environmental data parameters were selected as ecological input layers in ASCII raster grid format for ENM using Genetic Algorithm for Rule-set Production (GARP) software (Version 1.1.3, 2003). All data layers were resolved (pixel size) to ~10 × ~10 km (0.1 × 0.1°) for analysis. Of these 13 parameters, seven were annual climatic data

layers averaged over the period 1961–1990 and obtained from the Intergovernmental Panel on Climate Change (IPCC; native resolution ~50 × ~50 km; http://ipcc-ddc/cru.uea.ac.uk/): mean temperature, mean maximum temperature, mean minimum temperature, diurnal temperature range, mean precipitation, wet days, and ground frost days (see table 1). Five land-surface data layers were obtained from the U.S. Geological Survey's Hydro-1K data set (native resolution 1 × 1 km; http://edc.usgs.gov/products/elevation/gtopo30/hydro/): elevation, flow direction, flow accumulation (number of pixels in watershed), topographic aspect (direction of pixel slope), and compound topographic index (a measure of the tendency of water to pool). The remaining data layer was obtained from the University of Maryland Global Land Cover Facility (http://glcf.umiacs.umd.edu/index.shtml): land use/land cover.

Modeling method: We applied a machine-learning algorithm to model the ecological niches occupied by two of the three dormouse species of interest, *G. crassicaudatus* and *G. lorraineus* (both true *G. lorraineus* and the *G. lorraineus* complex; see discussion below), and predict their geographic distributions based on the spatial locations of this niche, where the ecological niche is defined as set of environmental conditions within which the species is able to maintain populations without immigration (Grinnell, 1917; Holt
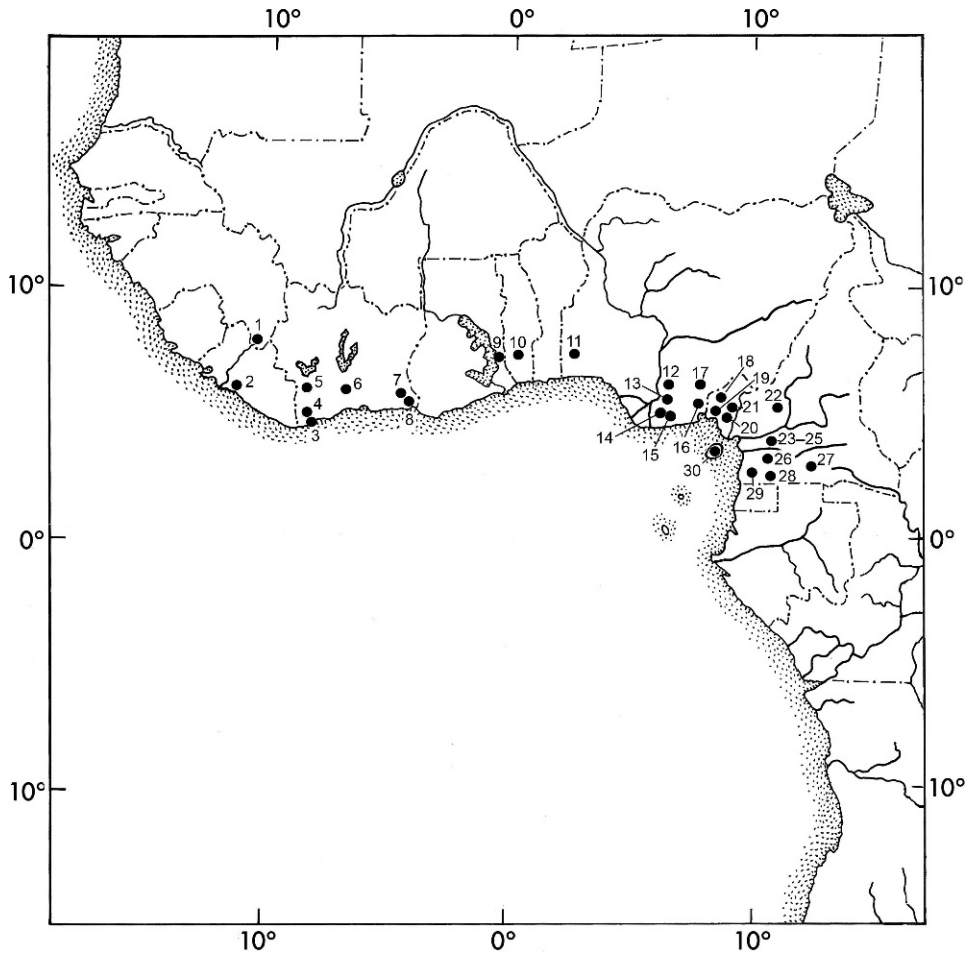
Fig. 2. Collection localities for *Graphiurus crassicaudatus* (localities 1–30) and *G. walterverheyeni* (localities 31 and 32). Numerals refer to numbered localities in the gazetteer where locality information is provided and specimens are identified by museum abbreviations and catalog numbers.

and Gaines, 1992). Ecological niche modeling of the third species, *G. walterverheyeni*, n. sp., was not attempted due to small sample size (only two known occurrences). Ecological niche models were created using Genetic Algorithm for Rule-set Production (GARP) software (Version 1.1.3, 2003), an algorithm specifically designed for predicting and modeling the ecological niches of species (Stockwell and Peters, 1999), and publicly available for download as a desktop application (http://www.nhm.ku.edu/desktopgarp/).

GARP models ecologic niches of species by relating the previously described point-occurrence data to the environmental data grids and produces a diverse set of logical,

range, and logistic rules that describe the potential distribution of species in ecological dimensions (Stockwell and Peters, 1999). As a genetic algorithm, it is designed for problem solving based on "natural selection," and therefore the rules describing the species niche are automatically evolved using simulated processes of mutation, recombination, and selection, thereby creating an optimized set of distribution rules which subsequently predict the potential distribution of the species in geographic space (Peterson et al., 2002). GARP models have been shown to have predictive value that is statistically significant by both rigorous intrinsic tests, performed on a subset of the
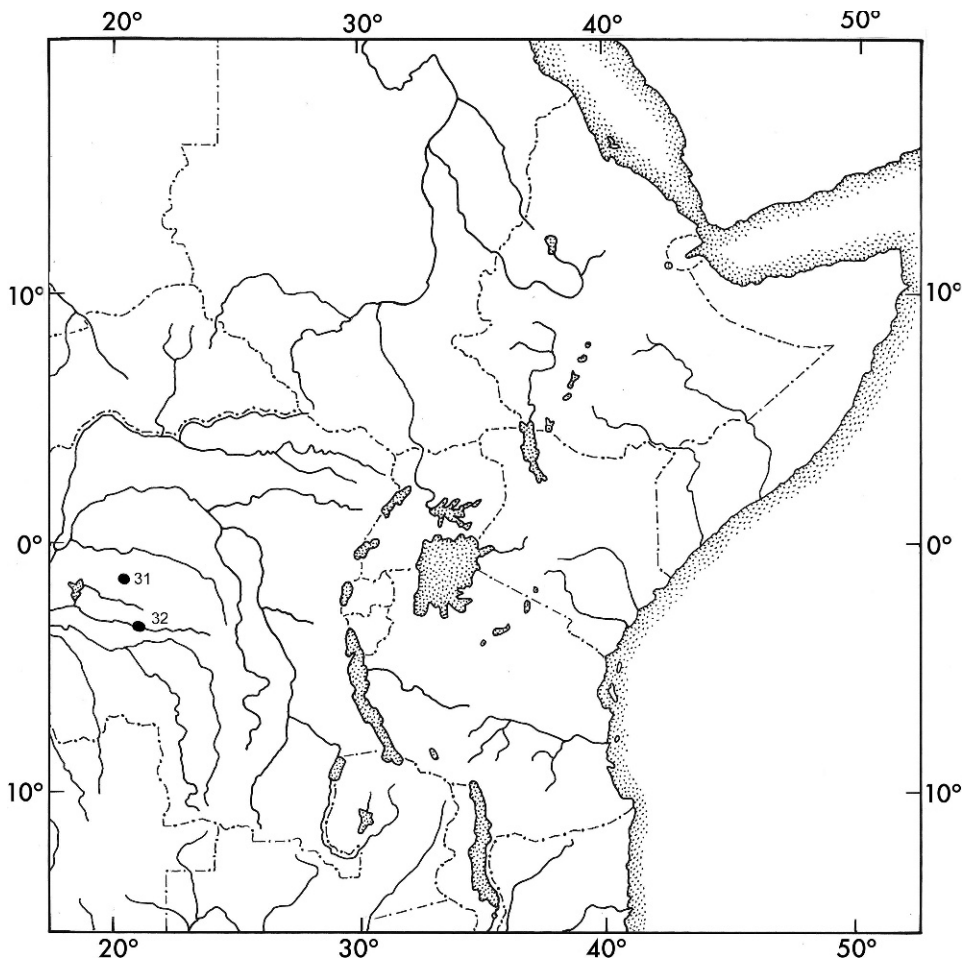
Fig. 2. *(Continued.)*

data during model development, and extrinsic tests, performed using data not included in model development (Peterson, 2001: Levine et al., 2004a, 2004b, 2007; Benedict et al., 2007).

We created 10 GARP models for each of the two dormouse species and summed them using ArcView GIS 3.3 (http://www.esri.com/) to create each of the final prediction maps. Therefore, individual pixels of all maps were assigned values of 0–10 representing the number of models that predicted ecological suitability in that pixel, which are represented by color gradations. Darker shades of color indicate the increasing proportion of times out of 10 that specific areas (pixels) were included in the predicted distribution. All models were created using a maximum of 100,000 iterations

and a convergence criterion (degree of change between each model during the development process) of 0.0001.

GAZETTEER AND SPECIMENS

Holden examined 41 specimens of *Graphiurus crassicaudatus*, two examples of *G. walterverheyeni*, n. sp., 22 specimens of *G. surdus*, 86 of true *G. lorraineus*, and 305 specimens representing the *G. lorraineus* complex. The specimens (identified by institutional abbreviation and catalog number) and localities from which they were collected are listed below. Coordinates are given first in the traditional format of degrees and minutes latitude and longitude, followed by decimal degrees longitude and latitude in parentheses.

For *G. crassicaudatus* and *G. walterverheyeni*, n. sp., the number preceding each gazetteer entry corresponds to the same numbered locality on the distribution map in figure 2.

Graphiurus crassicaudatus

GUINEA

1. **Mount Nimba, Ziéla**, 07°42′N, 08°21′W (−8.35, 7.71): This record is based upon a specimen identified by Heim de Balsac and Lamotte (1958: 340). Holden was unable to locate the specimen, but their detailed description indicates that it is correctly identified.

LIBERIA

2. **Du Queah River, Hill Town**, approximately 06°37′N, 10°47′W (−10.78, 6.67): RMNH 26639 (holotype of *G. crassicaudatus*).

CÔTE D'IVOIRE

3. **Tabon (Tabou)**, 04°28′N, 07°20′W (−7.33, 4.46): ZMB 71325.
4. **Grabo**, 04°57′N, 07°30′W (−7.5, 4.95): MNHN 1980-79.
5. **Tai**, 05°50′N, 07°30′W (−7.5, 5.83): MNHN 1980-80.
6. **15 km N Lakota**, 06°00′N, 05°43′W (−5.71, 6.0): CMNH 69339.
7. **Bouroukrou**, 05°51′N, 04°11′W (−4.18, 5.85): MNHN 1956-644.
8. **Idert**, 05°20′N, 04°07′W (−4.12, 5.33): RUCA 5313.

GHANA

9. **Okajakrom Forest Reserve, Jasikan**, 07°28′N, 00°33′E (0.55, 7.47): BMNH 65.778.

TOGO

10. **EZIME**, 07°29′N, 00°56′E (0.93, 7.48): USNM 429506.

NIGERIA

11. **Ilobi**, 06°45′N, 03°02′E (3.03, 6.75): BMNH 67.2165, 67.2166.
12. **40 km W of Enugu, Mamu River Forest Reserve**, 06°26′N, 06°59′E (6.98, 6.43): BMNH 76.1497.
13. **Awka District**, 06°12′N, 07°35′E (7.58, 6.2): BMNH 12.2.29.5.

14. **Owerri**, 05°29′N, 07°02′E (7.03, 5.48): BMNH 50.839.
15. **Umuahia**, 121 m 05°13′N, 07°26′E (7.43, 5.22): BMNH 46.295, 46.295.
16. **Oban District**, 05°17′N, 08°33′E (8.55, 5.28): BMNH 12.1.12.1 (holotype of *G. c. dorotheae*), 12.10.28.12.
17. **Ekuri Beach**, 05°56′N, 08°06′E (8.1, 5.93): BMNH 48.900.

UNVERIFIED LOCALITIES IN NIGERIA (NOT PLOTTED): **Gambari Forest Reserve**, 07°08′N, 03°50′E (3.83, 7.13) **and Lokoja, Shinkako House**, 07°48′N, 06°44′E (6.73, 7.8): Five fluid-preserved specimens from southern Nigeria are held in the FMNH (98863–67) and are identified as *G. crassicaudatus*; Holden has not examined this series and cannot verify the identifications.

CAMEROON

18. **Mamfe, Bashauo**, 212 m 06°08′N, 09°25′E (9.42, 6.13): BMNH 48.898, 48.899.
19. **Ikassa, N'Dian Estate**, 04°56′N, 08°50′E (8.83, 4.93): BMNH 61.1299. **Ikassa, N'Dian Estate, "field"**: BMNH 61.459, 62.2081.
20. **Mundame**, 04°35′N, 09°31′E (9.52, 4.58): ZMB 71338.
21. **Rumpi Hills**, 04°50′N, 09°05′E (9.08, 4.83): ZFMK 72.59.
22. **Bafia**, 04°40′N, 11°05′E (11.08, 4.67): CMNH 42718.
23. **Eseka**, 03°38′N, 10°47′E (10.78, 3.63): AMNH 236483; CMNH 42202, 42204, 42206, 42207.
24. **4 km S, 2 km E Eseka**, 03°36′N, 10°48′E (10.8, 3.6): CMNH 59453.
25. **8 km SW Eseka**, 03°35′N, 10°44′E (10.73, 3.58): CMNH 42211.
26. **Lolodorf**, 03°14′N, 10°48′E (10.8, 3.23): CMNH 2973, 5131.
27. **Bitye** 606 m, 03°10′N, 12°20′E (12.33, 3.17): BMNH 23.1.22.52.
28. **Ebolowa**, 02°56′N, 11°11′E (11.18, 2.93): CMNH 42715.
29. **Bipindi**, 03°06′N, 10°30′E (10.5, 3.1): AMNH 89582, 89583; ZMB 71312.

EQUATORIAL GUINEA

30. **Bioko (Fernando Po)**, 03°30′N, 08°41′E (8.68, 3.5): BMNH 62.12.2.11. (See

discussion regarding the validity of this locality below.)

Graphiurus walterverheyeni, n. sp.

DEMOCRATIC REPUBLIC OF THE CONGO

31. **Wafanya (Wafania)**, 01°21′S, 20°20′E (20.33, −1.35): MRAC 88-005-M12 (paratype).
32. **Lukenie River**, 500 m 03°30′S, 22°30′E (22.5, −3.50): BMNH 27.3.1.35 (holotype).

Graphiurus surdus

Below are listed the 22 specimens of *G. surdus* from 12 collection localities that we compared with the two examples of *G. walterverheyeni*. The descriptive statistics listed for *G. surdus* in table 3 were derived from measurements of these specimens.

CAMEROON

1. **Ayina (Aïna) River**, 01°48′N, 13°10′E (13.17, 1.80): MRAC 1093.
2. **Bitye**, 03°10′N, 12°20′E (12.33, 3.17): BMNH 14.7.23.15.
3. **Edea**, 03°47′N, 10°13′E (10.22, 3.78): ZMB 71341.
4. **Eseka**, 03°38′N, 10°47′E (10.78, 3.63): AMNH 236482; CMNH 42202, 42205, 42208–42210.
5. **Kribi**, 02°56′N, 09°54′E (9.9, 2.93): MCZ 8607 (holotype of *G. schwabi*).
6. **Efulan**, 02°40′N, 10°45′E (10.75, 2.67): AMNH 90067.
7. **Metet**, 03°23′N, 11°43′E (11.72, 3.38): MCZ 14669, 17605, 17606.
8. **Sangmelima**, 02°56′N, 11°58′E (11.97, 2.93): CMNH 10331.

EQUATORIAL GUINEA

9. **Rio Muni, Benito River**, approximately 01°35′N, 09°37′E (9.62, 1.58): BMNH 0.2.5.53, 0.2.5.54, 0.2.5.55 (holotype of *G. surdus*), 0.2.5.56.

GABON

10. **Belinga**, 01°09′N, 13°12′E (13.2, 1.15): MNHN 1983-186.

DEMOCRATIC REPUBLIC OF THE CONGO

11. **Inkongo, Sankuru River**, 04°55′S, 23°15′E (23.25, −4.92): BMNH 13.4.7.2.

12. **Masako**, 00°36′N, 25°13′E (25.27, 0.6): RUCA D1655 (this is one of the two specimens reported by Mukinzi et al., 2005).

True *Graphiurus lorraineus*

We studied 86 specimens of *G. lorraineus* from the 26 collection localities listed below in the West Central, South Central, and East Central faunal regions (Cameroon, Democratic Republic of the Congo, Equatorial Guinea, and Gabon), the documented geographic range of what we here consider to be true *G. lorraineus*. The specimens were utilized for comparisons with the sample of *G. walterverheyeni* in the form of side-by-side qualitative observation, descriptive univariate statistics (table 4), and principal components analysis (fig. 12, table 6). These localities are the actual collection sites shown in figure 15, which illustrates the predicted geographic distribution of true *G. lorraineus* derived from ecological niche modeling.

CAMEROON

1. **7 km NW Ambam, Meyo/Ambam**, 02°23′N, 11°16′E (11.26, 2.38): MHNG 912/65.
2. **Assobam**, 03°15′N, 14°02′E (14.03, 3.25): BMNH 9.10.2.21 (holotype of *G. haedulus*).
3. **Bafia**, 04°40′N, 11°05′E (11.08, 4.67): CMNH 9528.
4. **Bitye**, 03°10′N, 12°20′E (12.33, 3.17): BMNH 13.2.8.6, 13.9.12.8, 23.1.22.53; MRAC 10939.
5. **Ebolowa**, 02°56′N, 11°11′E (11.18, 2.93): CMNH 16135.
6. **Kribi**, 02°56′N, 09°54′E (9.9, 2.93): MCZ 8678.
7. **Lolodorf**, 03°14′N, 10°48′E (10.8, 3.23): CMNH 2879, 2915, 2969, 2971, 2999, 3685, 3914, 3915, 4560, 4561, 4867, 4868, 5638, 5641, 5679, 5686, 5699, 5704, 5733, 5737, 6120, 6121, 6122, 13252, 14927, 16136, 16142, 16143, 16144; MCZ 8876, 17921, 17922.
8. **Metet**, 03°23′N, 11°43′E (11.72, 3.38): CMNH 4645, 4646, 4673, 4674; FMNH 48926.
9. **Sangmelima**, 02°56′N, 11°58′E (11.97, 2.93): CMNH 9529, 9530, 10336. 42720.
10. **Yaoundé**, 03°51′N, 11°31′E (11.52, 3.85): CMNH 42721.

11. **Yokadouma**, 03°25′N, 15°08′E (15.13, 3.42): CMNH 42719.

EQUATORIAL GUINEA

12. **Rio Muni, Benito River**, approximately 01°35′N, 09°37′E (9.62, 1.58): BMNH 0.2.5.57.

GABON

13. **Mitzic**, 00°48′N, 11°30′E (11.5, 0.8): BMNH 58.336.

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14. **Bafwabaka**, 02°10′N, 27°39′E (27.65, 2.17): AMNH 49888, 49889.
15. **Barumbu**, 01°15′N, 23°29′E (23.48, 1.25): MRAC 9209.
16. **Faradje**, 03°45′N, 29°43′E (29.72, 3.75): AMNH 49886.
17. **Inkongo**, 04°55′S, 23°15′E (23.25, −4.92): BMNH 13.4.7.3; MRAC 12190, 7220.
18. **Kananga**, 05°53′S, 22°26′E (22.43, −5.88): AMNH 86311, 86316, 86318; BMNH 26.7.6.192; MRAC 7144, 7491; TM 9767, 9768.
19. **Kinshasa, Pool Malebo (Stanley Pool)**, 04°15′S, 15°25′E (15.42, −4.25): SMF 6299.
20. **Lukolela**, 01°10′S, 17°11′E (17.18, −1.17): AMNH 86893, 86894, 86896.
21. **Medje**, 02°25′N, 27°18′E (27.3, 2.42): AMNH 49904, 49906.
22. **Molegbwe**, 04°14′N, 20°52′E (20.87, 4.23) BMNH 7.7.8.115 (holotype of *G. lorraineus*).
23. **Niangara**, 03°45′N, 27°45′E (27.75, 3.75): AMNH 49878; MRAC 12993; USNM 259142.
24. **Nzoro (Vankerckhovenville)**, 03°21′N, 29°32′E (29.53, 3.35): AMNH 49885.
25. **Poko**, 03°08′N, 26°52′E (26.87, 3.13): BMNH 19.5.8.67.
26. **Yalosemba**, 02°35′N, 21°47′E (21.78, 2.58): CMNH 86755, 86758–86761.

The *Graphiurus lorraineus* Complex

The 78 localities and 305 specimens listed below combined with the 26 localities and 86 specimens enumerated above are the actual collection sites illustrated in figure 16, which presents the predicted geographic distribution of the *G. lorraineus* complex derived from ecological niche modeling.

GUINEA

1. **Dubreka, Kourid**, 10°06′N, 13°45′W (−13.75, 10.1): RBINS 15918.
2. **Mount Nimba**, 07°39′N, 08°30′W (−8.5, 7.65): MNHN 1986-104.
3. **Mount Nimba, Nzo**, 07°40′N, 08°19′W (−8.32, 7.67): MNHN 1987-137, 1987-138.
4. **Seredou**, 08°23′N, 09°39′W (−9.65, 8.38): MNHN 1950-730, 1959-735, 1960-672, 1961-473, 1961-474, 1961-475, 1961-676, 1970-534, 1970-542, 1970-543.

UNVERIFIED LOCALITIES IN GUINEA (NOT PLOTTED): **Boola**, 08°22′N, 08°43′W (−08.72, 08.37), **Gouécké**, 8°02′N, 8°43′W (−08.72, 08.03), **Mount Nimba, Nion**. 07°37′N, 08°29′W (−8.48, 7.61), **Mount Nimba, Véblo**, 07°41′N, 08°19′W (−8.31, 7.68), **Mount Nimba, Yalé**, 07°39′N, 08°30′W (−8.5, 7.65), and **Mount Nimba, Ziéla**, 07°42′N, 08°21′W (−8.35, 7.71): these records are reported and described in Heim de Balsac and Lamotte (1958: 340). Holden was unable to locate the specimens and verify the identifications.

SIERRA LEONE

5. **Kamakwie**, 09°30′N, 12°14′W (−12.23, 9.5): USNM 538792.
6. **Konia**, 08°07′N, 11°10′W (−11.17, 8.12): USNM 539578.
7. **Magburaka**, 08°43′N, 11°57′W (−11.95, 8.72): BMNH 50.1990.
8. **Makeni**, 61 m, 08°53′N, 12°03′W (−12.05, 8.88): BMNH 38.6.10.21, 38.6.10.22.
9. **Musaia**, 09°27′N, 11°26′W (−11.34, 9.45): BMNH 54.940.
10. **Niahun (Mano-Kotuhun)**, 08°01′N, 11°02′W (−11.03, 8.02): USNM 540553.
11. **Niawama**, 08°05′N, 12°05′W (−12.08, 8.08): BMNH 16.1.27.7.
12. **Njala**, 08°07′N, 12°05′W (−12.08, 8.12): BMNH 50.1988, 50.1989, 56.67–56.69, 61.38.
13. **Sandaru**, 396 m, 08°24′N, 10°42′W (−10.7, 8.4): BMNH 30.12.23.16.

LIBERIA

14. **Bobei (Bobe) Mountains**, 07°22′N, 08°36′W (−8.61, 7.37): AMNH 167549.
15. **Ganta**, 07°18′N, 08°32′W (−8.53, 7.30): AMNH 167546–167548, 167551.

16. **Grassfield Yekepa**, 07°35′N, 08°32′W (−8.54, 7.58): RBINS 16413.
17. **Mount Nimba**, 07°37′N, 08°30′W (−8.5, 7.61): BMNH 67.1466–67.1469.
18. **Mount Nimba, New Camp**, 07°29′N, 08°35′W (−8.58, 7.48): RBINS 16410–16412.
19. **Peahtah (= Piatah)**, 07°15′N, 09°50′W (−9.83, 7.25): MCZ 24043.

CÔTE D'IVOIRE

20. **Abengourou**, 06°44′N, 03°29′W (−3.48, 6.73): RUCA 8584.
21. **Adiopodoume**, 05°19′N, 04°08′W (−4.13, 5.32): RUCA 511, 2536, 6147, 6158, 6184, 6185, A610, A611, A614, A616, A254, A310, A313, A811, A879, A6564, A8285, A8286, A8289, A8294, 17.819.
22. **Dabou**, 05°21′N, 04°26′W (−4.43, 5.35): RUCA 2592, 7062.
23. **Divo**, 05°53′N, 05°14′W (−5.23, 5.88): RUCA 8058, 8165, 8757, 8912.
24. **Elfenbeinkuste, Azagny National Park**, 05°13′N, 04°53′W (−4.88, 5.22): ZFMK 84.384.
25. **Gopopleu**, 07°26′N, 08°17′W (−8.28, 7.43): RUCA A2866.
26. **Idert**, 05°20′N, 04°07′W (−4.12, 5.33): RUCA 511, 2357, 2534, 4006, 4434, 6147, 6158, 6159, 6184.
27. **Jaqueville**, 05°12′N, 04°25′W (−4.42, 5.2): RUCA A2533; USNM 520470.
28. **Kahin**, 06°55′N, 07°37′W (−7.62, 6.92): USNM 467523–467525.
29. **15 km N Lakota**, 05°54′N, 05°43′W (−5.72, 5.90): CMNH 59465, 69337–69340.
30. **Lamto Research Station**, 06°12′N, 04°59′W (−4.97, 6.2): RUCA 1458, 1456, 1509, 1543, 1544, 1701, 1727, 1851, 1895, 1938, 11006, 11165, 11166, 11387, 11388, 11444, 11497, 11742, 11977, 21113, 21155, 21169, 21459, 21481, 21483.
31. **Matonguine**, 07°18′N, 08°04′W (−8.07, 7.3): RUCA A2758.
32. **Mopoyemé (Mopoyem)**, 05°19′N, 04°28′W (−4.47, 5.32): RUCA 728, 4376, 7272, A4618, A4682.
33. **Tule**, 07°56′N, 06°08′W (−6.13, 7.93): USNM 465665–465667.

GHANA

34. **Akim Oda (Oda)**, 05°55′N, 00°56′W (−0.93, 5.92): MSU 16580.

35. **Bibianaha (Bibiani)**, 213 m, 06°28′N, 02°20′W (−2.33, 6.47): BMNH 10.4.13.2 (holotype of *G. spurrelli*), 11.1.22.12, 11.1.22.13, 11.6.2.35, 11.6.2.36, 12.4.10.1, 12.6.20.9–12.6.20.11.
36. **Bobiri Forest Reserve**, 06°38′N, 01°17′W (−1.28, 6.63): BMNH 65.771, 65.772.
37. **Brong-Ahafo, Wenchi**, 07°44′N, 02°06′W (−2.1, 7.73): BMNH 64.1273, 65.773.
38. **Dwinase Hill**, 06°13′N, 02°29′W (−2.48, 6.22): BMNH 76.1769–76.1771.
39. **Goaso (Gawso)**, 06°48′N, 02°31′W (−2.52, 6.8): BMNH 35.10.22.109.
40. **6 km N Kade**, 06°06′N, 00°51′W (−0.85, 6.1): USNM 413459, 420996.
41. **Keta**, 5°33′N, 0°35′E (0.59, 5.55): BMNH 75.385.
42. **Korle Bu**, 05°33′N, 00°13′W (−0.21, 5.55): BMNH 32.8.17.10.
43. **Kumasi (Coomassie), Kuwari**, 274 m, 06°42′N, 01°37′W (−1.62, 6.7): BMNH 25.10.24.23, 25.10.24.24, 29.5.29.17–29.5.29.20, 60.1851, 65.774.
44. **Kumasi (Coomassie), Kwadaso**, 06°42′N, 01°39′W (−1.65, 6.7): BMNH 75.1386.
45. **Mampong**, 07°04′N, 01°24′W (−1.4, 7.07): BMNH 37.8.12.13.
46. **Okajakrom Forest Reserve, Jasikan**, 07°24′N, 00°28′E (0.47, 7.4): BMNH 65.779.
47. **Pampramase, Gliksten's Area 12**, 06°40′N, 02°55′W (−2.92, 6.67): BMNH 76.1763–76.1765.
48. **Sefwi Asemparaye (Asampaniye)**, 06°30′N, 02°54′W (−2.9, 6.5): BMNH 76.1768.
49. **Sefwi Wawjo (Sefwi Anwiawso)**, 06°20′N, 02°16′W (−2.27, 6.33): BMNH 76.1767.

UNVERIFIED LOCALITIES IN GHANA (NOT PLOTTED): **Kpong**, 06°09′N, 00°04′E (0.07, 6.15), and **Shai Hills**, 05°54′N, 00°04′E (0.07, 5.9): One specimen from each locality, identified as *G. lorraineus* by S. McLaren, is represented in the CMNH collection; Holden has not examined these specimens.

NIGERIA

50. **Owerri**, 05°29′N, 07°02′E (7.03, 5.48): BMNH 50.840.

CAMEROON

51. **Akum, 7 km S Bamenda**, 05°55′N, 10°10′E (10.17, 5.92): CMNH 59460.

52. **Babadjou**, 1524 m, 05°45′N, 10°12′E (10.2, 5.75): CMNH 16137–16141.
53. **Bambuluwe (Bambului), Mount Lefu**, 05°50′N, 10°20′E (10.33, 5.83): ZFMK 74.338–74.343.
54. **11 km S, 1 km E Bamenda**, 05°55′N, 10°11′E (10.18, 5.92): CMNH 59461–59465.
55. **Bebai (vicinity of Campo)**, 02°22′N, 09°49′E (9.82, 2.37): ZMB 71339.
56. **Near Lake Oku (Mauwes See), Lager IV**, 2100 m, 06°10′N, 10°25′E (10.42, 6.17): MNHN 1981-852; ZFMK 69.263–69.283, 91.272.
57. **Musake Hütte, Mount Cameroon**, 1850 m, 4°12′N, 9°11′E (9.18, 4.2): SMNS 6555, 6556.
58. **Sakbayeme**, 04°02′N, 10°34′E (10.57, 4.03): MCZ 20564.
59. **Yoko**, 05°29′N, 12°19′E (12.32, 5.48): CMNH 42716, 42717.

UNVERIFIED LOCALITY IN CAMEROON (NOT PLOTTED): **Ikenge Research Station, Korup National Park**, 05°16′N, 09°08′E (9.13, 5.27): One specimen identified by S. McLaren as *G. lorraineus* cf. *haedulus* is represented in the CMNH collection; it has not been examined by Holden.

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60. **Bangui**, 04°21′N, 18°37′E (18.62, 4.35): MNHN 1961-887, 1963-1129, 1963-1311.
61. **Boukoko**, 3°54′N, 17°55′E (17.93, 3.9): MNHN 1965-300, 1980-276.
62. **La Maboke (Mbaiki)**, 3°52′N, 18°00′E (18.0, 3.88): MNHN 1971-716–1971-724, 1971-760, 1971-761, 1972-542–1972-544, 1979-125, 1979-126, 1982-484, 1982-534, 1983-845, 1983-846, one uncataloged specimen.

UNVERIFIED LOCALITIES IN C.A.R. (NOT PLOTTED): **Dzanga-Sangha Reserve, near Ouonga Camp**, 02°55′N, 16°21′E (16.35, 2.91). Four specimens housed at the USNM are identified as *G. lorraineus*, but have not been examined by Holden: USNM 580167, 580344–580346.

EQUATORIAL GUINEA

63. **Bioko, Refugium, on north slope of Pico Basile** (Mount Santa Isabel), 2000 m, 3°35′N, 8°46′E (8.77, 3.58): ZFMK 64.488.

GABON

64. **Makokou**, 00°34′N, 12°52′E (12.87, 0.57): MNHN 1983-187.
65. **Ngomo, on the Ogoue (Ogooue) River**, 00°49′S, 09°57′E (9.95, −0.82): MNHN 1911-799.

REPUBLIC OF THE CONGO

66. **Brazzaville**, 04°14′S, 15°14′E (15.23, −4.23): MNHN 1961-886, 1965-76.

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67. **Lubumbashi, Kiswishi River**, 11°40′S, 27°28′E (27.47, −11.67): BMNH 23981, 23979; MRAC 23979–23981.
68. **Parc National l'Upemba, Kabwe sur la Muye**, 1320 m, 09°00′S, 26°43′E (26.72, −9): RBINS 11376.
69. **Parc National l'Upemba, Mukana**, 1810 m, 09°15′S, 27°12′E (27.2, −9.25): RBINS 11375.
70. **Tandala**, 02°57′N, 19°21′E (19.35, 2.97): CMNH 86762, 86763.

ANGOLA

71. **Northeast, near Democratic Republic of the Congo border**, 7°33′S, 20°50′E (20.83, −7.55): BMNH 67.1250.

ZAMBIA

72. **Chambeshi River, E of Bangweulu**, 11°30′S, 30°15′E (30.25, −11.5): BMNH 9.12.4.32.
73. **Kabompo Boma**, 13°35′S, 24°12′E (24.2, −13.58): NHMZ 9088.
74. **Mundwiji Plain**, 11°44′S, 24°43′E (24.72, −11.73): BMNH 73.1792; NHMZ 3705.
75. **N'dola**, 1286 m, 12°58′S, 28°38′E (28.63, −12.97): AM 3765, 3766; BMNH 2.3.28.3, 22.3.28.4, 20.11.3.95–20.11.3.115; TM 2570, 2571, 2573, 2574, 2576, 2577, 2579, 2580, 2582, 2583, 2585, 2587, 2589, 2590, 2593, 2594.
76. **Sakeji Stream**, 11°15′S, 24°45′E (24.75, −11.25): BMNH 61.951; NHMZ 3706.
77. **Salujinga, Kanyale Stream**, 10°58′S, 24°07′E (24.12, −10.97): CMNH 86995; NHMZ 3704, 3707, 3708; PDHA 277 (see Ansell, 1974: table VII).
78. **Zambezi Source**, 11°22′S, 24°18′E (24.3, −11.37): NHMZ 3709.

DESCRIPTION OF THE NEW *GRAPHIURUS* AND RELEVANT COMPARISONS WITH OTHER SPECIES

The new species described here is one of six occurring in equatorial African forests. Three of these—*G. surdus*, *G. christyi*, and *G. nagtglasii*—do not require such detailed contrasts with the new species as do two others, *G. crassicaudatus* and *G. lorraineus*. Of the first three, *G. surdus* ranges from southern Cameroon south to Equatorial Guinea and Gabon and eastward to northeastern and south-central portions of Democratic Republic of the Congo (Holden, 1996, 2005, in press)—a distribution covering the West Central, South Central, and East Central faunal regions (see maps in Colyn and Van Rompaey, 1994: 480; Happold, 1996: 250), and is the only one of these three species with a distribution overlapping that of *G. walterverheyeni*, n. sp. It is much larger in body size (table 4), and strongly differs, among other traits, by pelage coloration, having a longer rostrum and nasals, narrower interorbital and postorbital regions without dorsolateral ridging, different configuration of the anterolateral margin of the dorsal maxillary root of each zygomatic arch (contacting the rostrum at a shallow angle, not a right angle), and shorter bullae and tooth rows relative to length of skull (compare figs. 8–10 in Holden, 1996, with figs. 4–5 here). The 22 specimens of *G. surdus* we compared with the new species are listed in the gazetteer.

Records of *G. christyi* portray a spotty distribution. The western limit, a locality in southern Cameroon (West Central faunal region), is separated by a wide gap from the bulk of specimens, which come from northeastern Democratic Republic of the Congo in the watershed on the right side of the Congo-Lualaba rivers, the East Central faunal region (Holden, 2005, in press). No specimens are known from the left side of the Congo-Lualaba rivers, rendering the geographic range of *G. christyi* allopatric to that of the new species. Anatomical characteristics, including body size, of *G. christyi* are similar to those of *G. surdus* (see the comparisons, illustrations, and tables in Holden, 1996), and morphological differenc-es between *G. christyi* and *G. walterverheyeni*, n. sp., recall those summarized above between the latter and *G. surdus*.

A West African endemic, *G. nagtglasii* ranges from Sierra Leone to Togo, is interrupted at nearby Benin where the species is unrecorded, and continues through southern Nigeria, Cameroon, and Central African Republic to Gabon (Holden, 2005, in press). This is one of the largest sub-Saharan dormice and is twice the body size of the new species (for example, mean and range for length of head and body in 11 *G. nagtglasii* is 145.9 m, 134–152 m, respectively; compare these values and other measurements tabulated by Holden, 1996: 25, with those of *G. walterverheyeni*, n. sp., listed in table 2).

Two equatorial forest species do require close scrutiny within the context of contrasting them with *G. walterverheyeni*, n. sp. The distribution of *G. crassicaudatus* is allopatric to the range of the new species, and it may be its closest morphological ally. The geographic range of *G. lorraineus* overlaps the two collection sites of *G. walterverheyeni*, n. sp., and bears a superficial similarity to it in body size and other characteristics. We introduce both by providing summaries of their distinctive morphological attributes and geographic ranges. These synopses are followed by the description of the new species and its contrasts with *G. crassicaudatus* and *G. lorraineus*.

***Graphiurus crassicaudatus*:** *Graphiurus crassicaudatus* was named and described by Jentink (1888) as a new genus and species *Claviglis crassicaudatus*, based on an adult female (RMNH 26639) collected at Hill Town along the Du Queah River in Liberia (see gazetteer and table 2). Although the genus name *Claviglis* has most commonly been treated either as a synonym or subgenus of *Graphiurus* (Holden, 1996, 2005, in press), the taxon *crassicaudatus* has historically been recognized as a distinctive species. Certain morphological similarities, primarily cranial features, which are shared by *G. crassicaudatus* and *G. nagtglasii*, have prompted researchers to view the two species as phylogenetically more closely related to each other than to any other species of *Graphiurus* (Dollman, 1912; Rosevear, 1969; Holden, 1996). An opposing position, however, was supported by results of Pavlinov and Pota-
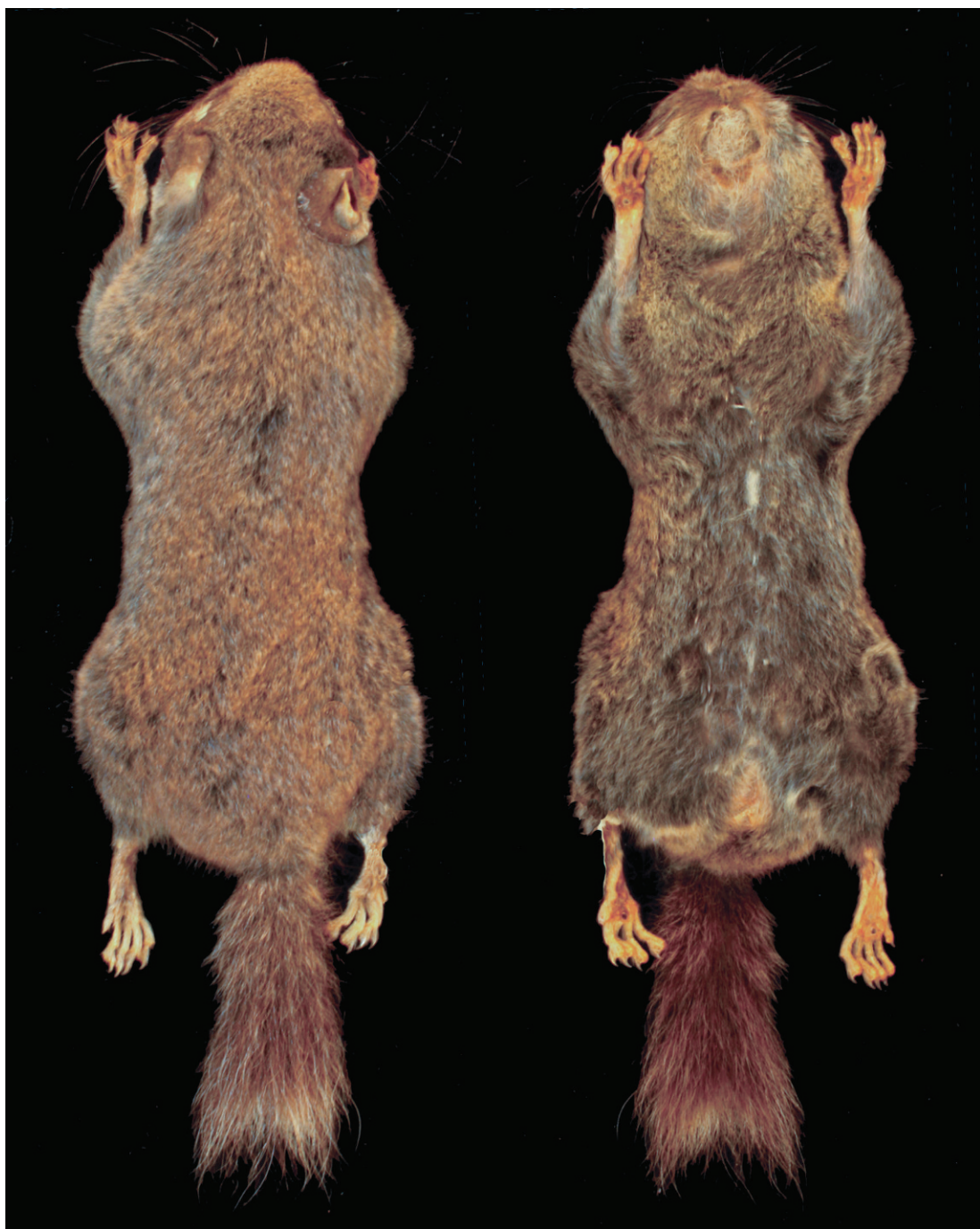
Fig. 3.   Stuffed skin of the holotype of *Graphiurus walterverheyeni* (BMNH 27.3.1.35), a young adult female captured near the Lukenie River, south of the great bend of the Congo River in the Democratic Republic of the Congo. Values for external measurements are listed in table 2.

Fig. 4. Cranial views of the holotype of *Graphiurus walterverheyeni* (BMNH 27.3.1.35) captured near the Lukenie River, Democratic Republic of the Congo. Values for cranial and dental measurements are listed in table 2. ×3.5.

pova's (2003) cladistic analysis of species of *Graphiurus* based on anatomy of the skull and middle ear, which indicated that characters shared by *G. crassicaudatus* and *G. nagtglasii* are probably primitive for the genus, and that

G. crassicaudatus shares several derived traits with other species of *Graphiurus* rather than with *G. nagtglasii*. Their analysis also revealed a cluster of autapomorphies describing each of the two species. Results of analyses derived
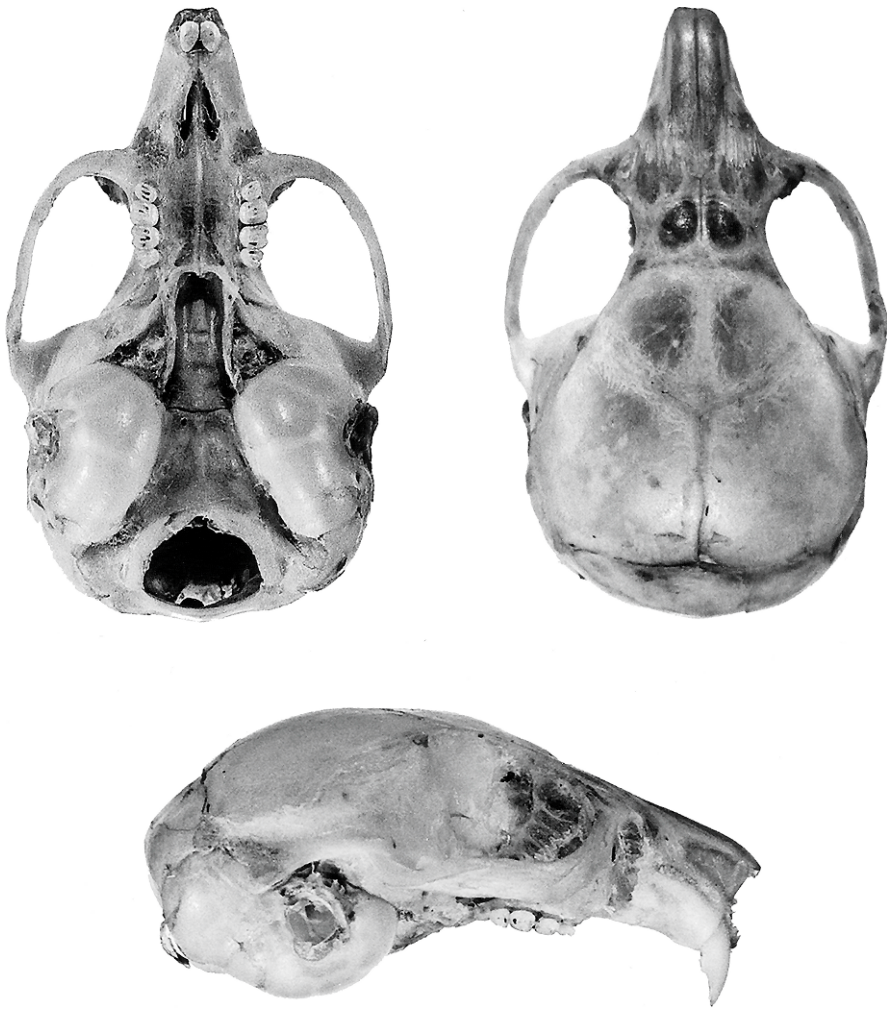
Fig. 5.   Cranial views of the paratype of *Graphiurus walterverheyeni* (MRAC 88-005-M12), a subadult male from Wafanya, Democratic Republic of the Congo. Values for cranial and dental measurements are listed in table 2. ×3.5.

from molecular sources would be a welcome test of these two conflicting views.

Occurring in or near primary and secondary rainforest formations, *G. crassicaudatus* is a West African endemic, documented by specimen collection localities ranging from Liberia and Guinea east through Côte d'Ivoire, Ghana, Togo, southern Nigeria, and southern Cameroon (excluding Benin) to Gabon and Bioko Island in Equatorial Guinea (see gazetteer, map in fig. 2, and distributional summaries in Holden [2005, in press]). It must be noted that there is some doubt about the historical (or current) occur-

rence of *G. crassicaudatus* on Bioko Island; Rosevear (1969) remarks that the Bioko specimen was part of a rather jumbled collection purchased from Lady Burton. There were some excursions to the mainland by the collectors as far away as Mount Cameroon, and the collection was disorderly enough that Cabrera (1929) discounted the occurrence of *G. crassicaudatus* on Bioko. We have kept the locality as given by Lady Burton, with some reservation, in absence of any additional information regarding the specimen. Only one other specimen of *Graphiurus* has been collected from Bioko (Eisen-

TABLE 2
External, Cranial, and Dental Measurements (mm) for *Graphiurus walterverheyeni* from the Democratic Republic of the Congo

Variable	Holotype BMNH 27.3.1.35	Paratype RMCA 88-005-M12[b]
Age	Young adult	Young adult
Sex	Female	Male
LHB	72	—
LT[a]	[25]	64
LHF	14	15
LE	11	11
GLS	22.9	22.5
CIL	20.3	20.2
ZB	14.5	14.2
IB	4.5	4.6
BBC	11.8	12.3
HBC	8.1	8.1
BR	4.8	4.9
LHR	4.8	4.2
LN	7.0	6.9
LD	4.7	4.7
PL	7.9	7.9
LBP	4.7	4.8
LIF	1.8	2.3
BIF	1.4	1.3
BBP	2.8	2.9
CLP4-M3	2.8	3.1
CLM1-M3	2.5	2.5
BP4	0.8	0.8
BM1	1.1	1.0
BM2	1.1	1.1
BIT	1.1	1.0
PPL	9.4	9.0
LB	6.7	6.6
BBO	2.1	2.3

[a] Value in brackets for the holotype is from damaged tail (undamaged total length unknown).

[b] Lengths of tail, hind foot, and ear were obtained by Holden from the fluid-preserved carcass; length of head and body could not be measured.

traut, 1973); this specimen is for now identified as representing the *G. lorraineus* complex, although it may be allied with montane Cameroon populations (discussed below under *G. lorraineus*) that may in the future be shown to represent a distinct species. All but one of the five specimens listed by Rosevear from Liberia (the type specimen from Du Queah River, Hill Town) under *G. crassicaudatus* have been examined and identified by Holden to represent the *G. lorraineus* complex and are listed in the gazetteer.

Intermediate in body size among species of *Graphiurus* (tables 3, 4), *G. crassicaudatus* has a stubby snout, large eyes, short and rounded brown ears, and a proportionally short tail. Some individuals exhibit a conspicuous dark, narrow stripe (eye mask) that extends from the snout to the bases of the ears; some specimens exhibit only a thin dark line (eye ring) encircling the eyes. Dorsal and lateral surfaces of head and body are covered by soft and short fur (rump hairs are 4–5 mm long, guard hairs extend to 10 mm) that is uniformly reddish brown without patterning such as contrasting postauricular patches, the underparts are usually clearly delineated by gray pelage, washed with ochre, cream, or white in some specimens. Dorsal surfaces of the short and wide hind feet are white in some specimens, white with a dark metatarsal streak in others. The tail is conspicuously shorter than length of head and body (table 2) and hairy, the short hairs near the base (3–4 mm long) giving way to increasingly longer hairs along the length of the tail (tail tip hairs up to 27 mm long). The tail color matches that of the dorsal pelage; a few white hairs are intermixed with the reddish-brown tail hairs, but the tail tip is not conspicuously white, a trait exhibited by some other species of *Graphiurus*. Four pairs of mammae (one pectoral, one brachial, and two inguinal) characterize *G. crassicaudatus* and all other species of *Graphiurus*.

A broad skull, vaulted braincase, and wide interorbital and postorbital regions bordered by shelf-like ridges form the diagnostic cranial outline of *G. crassicaudatus* (figs. 6–8). The rostrum is short and narrow and with correspondingly short nasal bones. Robust zygomatic arches jut out at a 90° angle from the rostrum. The incisive foramina are short and very narrow relative to skull length; the bony palate and upper tooth row are proportionally long. The anterior chamber of each auditory bulla is usually markedly less inflated than the posterior chambers, and the bullae themselves are short and uninflated relative to skull size.

Careful documentation of morphological variation exhibited by samples of *G. crassicaudatus* is unavailable. Only approximately 50 museum specimens represent this species, and the samples from each locality are

TABLE 3
**External, Cranial, and Dental Measurements (mm) for Holotypes of *Graphiurus*
Associated with *G. crassicaudatus* and *G. lorraineus***

Variable	*G. crassicaudatus* NNM 26639 Liberia	*G. c. dorotheae* BMNH 12.1.12.1 S Nigeria	*G. lorraineus* BMNH 7.7.8.115 D.R. Congo	*G. l. haedulus* BMNH 9.10.2.21 S Cameroon	*G. l. spurrelli* BMNH 10.4.13.2[b] Ghana
Age	adult	adult	adult	adult	adult
Sex	female	female	female	male	female
LHB	100	89	95	88	100
LT[a]	[50]	[45]	62	70	75
LHF	15	15	16	18	18
LE	7	12	12	14	14
GLS	26.1	26.9	—	24.6	—
CIL	23.7	24.6	—	22.1	23.7
ZB	15.7	15.7	14.3	—	—
IB	5.1	5.2	5.0	4.3	4.7
BBC	12.6	12.6	12.3	—	12.5
HBC	7.9	7.8	—	7.7	7.7
BR	5.3	5.7	5.3	5.7	5.7
LHR	4.8	5.1	5.0	4.7	—
LN	9.2	8.9	9.4	9.5	—
LD	6.2	5.9	5.1	5.5	5.4
PL	—	10.0	8.0	8.2	8.2
LBP	—	5.8	4.5	4.6	4.8
LIF	2.7	2.6	2.7	2.8	2.4
BIF	1.4	1.7	1.8	1.6	1.8
BBP	3.2	3.3	3.1	3.1	3.7
CLP4-M3	4.1	3.8	3.3	3.1	2.9
CLM1-M3	3.3	3.1	2.7	2.5	2.4
BP4	1.2	1.1	0.9	1.0	0.9
BM1	1.3	1.2	1.1	1.1	1.0
BM2	1.4	1.3	1.1	1.1	1.0
BIT	1.4	1.5	1.6	—	1.7
PPL	—	10.9	—	10.5	11.8
LB	6.5	6.9	7.1	7.0	7.7
BBO	3.1	2.7	2.3	2.2	2.7

[a] Values in brackets are from damaged tails (total length unknown for undamaged tails).

[b] Values for lengths of head and body, tail, hind foot, and ear are from Dollman's (1912) original description; he obtained head and body length and tail length from the dry skin.

disappointingly small and usually consist of a single individual. The largest sample size, obtained from Eseka, Cameroon, consists of five individuals (four males and one female). Samples are also geographically biased: Individuals obtained from Cameroon and Nigeria comprise roughly 50% and 25%, respectively, of all known specimens. The remaining 25% consists of six specimens from Côte d'Ivoire, and single individuals from Liberia, Guinea, Ghana, Togo, and Equatorial Guinea. Judged by our inspections of specimens, samples of *G. crassicaudatus*, no matter their provenances, appear similar in external mor-

phology, coat color, cranial anatomy, and body size. These observations are generally reinforced by results of principle components analysis of cranial and dental measurements that are derived from samples at hand (fig. 11). The scatter of specimen scores within an ordination bounded by first and second principle components, for example, does not condense into clusters with geographic significance—namely, West Africa versus West Central faunal regions. Two scores for Côte d'Ivoire and one for Ghana are at the margin of the main cluster of points, but two other scores for Côte d'Ivoire are

nested within the larger cloud representing specimens from Bioko, southern Nigeria, and Cameroon. Larger series from more localities will be required to better understand geographic variation of morphological traits in the species.

An adult female (table 2) from the Oban District of southern Nigeria is the basis for Dollman's (1912) description of *G. c. dorotheae*, which is the only other scientific name associated with *G. crassicaudatus*. Within the context of the morphometric traits seen in samples of *G. crassicaudatus* presently available, no basis exists for recognizing *dorotheae* as a distinct taxon. In our principle component analyses of cranial and dental variables derived from geographic samples of *G. crassicaudatus*, the score for the holotype of *dorotheae* nests inside the main cluster of scores representing other specimens from Nigeria along with those from Bioko, Cameroon, and Côte d'Ivoire (fig. 11). Pelage coloration and other external traits of the holotype also fall well within the range of variation exhibited by other samples from these regions.

***Graphiurus lorraineus*:** An adult female (table 2) collected at Molegbwe, near the Welle (Uele) River south of the Setema Rapids, in northern Democratic Republic of the Congo (see gazetteer), is the basis for Dollman's (1910) description of *G. lorraineus*. Dollman regarded *lorraineus* as a species separate from other *Graphiurus*, and while we certainly endorse that view, the taxon has in the past also been treated as a subspecies or synonym of *G. murinus* (see reviews and references in Holden, 1993, 1996, 2005, in press).

Dollman's *lorraineus*, treated as true *G. lorraineus* here, is not at this time considered to be aligned with *G. murinus* (see Holden 1996: 28), but geographic variation in morphological traits in samples now identified as "true *G. lorraineus*" and the "*G. lorraineus* complex" (discussed below) have yet to be thoroughly analyzed. Unpublished preliminary analyses performed by Holden indicate that there is considerable variation in morphometric attributes and pelage coloration among certain geographic clusters of samples, and future research will likely reveal that more than one species is contained in what is now recognized as a single species. For this reason, we refer to samples from southern Cameroon, Equatorial Guinea, Gabon, and Democratic Republic of the Congo as "true *G. lorraineus*," because from preliminary analyses these populations seem to form a somewhat cohesive entity, although it is possible that there is hidden species diversity even within this constituent. When discussing samples of "true *G. lorraineus*" combined with *G. lorraineus*-like material from other localities from Guinea and Sierra Leone to northern Zambia, we refer to the combined samples as the "*G. lorraineus* complex" to highlight our view that several species are contained therein. We compared the new species with holotypes bearing the scientific names currently associated with true *G. lorraineus* (table 2), and with the specimens defining the entire range of the *G. lorraineus* complex (entered in the gazetteer). Comparative studies of museum specimens representing all species of *Graphiurus*, comparisons with *G. christyi* and *G. surdus* (Holden, 1996), and preliminary multivariate analyses of cranial and dental dimensions (M.E. Holden, unpubl.), indicate that the entire *G. lorraineus* complex is distinguishable from other species of *Graphiurus*, and that certain populations of the complex appears to be morphologically most closely related to *G. johnstoni* from southern Malawi (Holden, 2005).

Based on collectors' notes and locality data, individuals have been captured in gallery forests, forest margins, woodland savanna, and disturbed areas (including farms and buildings) throughout West and Central Africa, and apparently do not inhabit primary forest formations. Specimens in collections of museums portray a split geographic range, one segment in the West Africa forest block, the other in the Central Africa forest block. Holden (2005, in press) listed the western limit of the *G. lorraineus* complex as Sierra Leone, but later discovered the existence of specimens from western Guinea (Kouratongo, Dubreka, listed in the gazetteer). The West Africa distribution extends from Guinea and Sierra Leone eastward through, Liberia, Côte d'Ivoire, and Ghana. No records of the species exist in adjacent Togo, Benin, and Nigeria west of the Niger River. The Central Africa segment

TABLE 4
Descriptive Statistics for Cranial and Dental Measurements (mm) and Weight (g)
for Samples of Four Species of *Graphiurus* from Equatorial Africa
(Mean plus or minus one SD, observed range in parentheses, and number of specimens are listed for each variable. The range in age from young to old adults is contained within each sample. LHB/LT is computed from mean values for those dimensions. Specimens measured are identified in footnotes.)

Variable	*G. walterverheyeni*[a] D.R. Congo	*G. crassicaudatus*[b] Cameroon, Nigeria, Togo, Ghana, Ivory Coast, Liberia, Eq. Guinea	*G. lorraineus*[c] Cameroon, Gabon, D.R. Congo, Eq. Guinea	*G. surdus*[c] Cameroon, Gabon, D.R. Congo, Eq. Guinea
LHB	72.0 ± 0.00 1	88.9 ± 6.70 (77–100) 26	80.5 ± 5.28 (70–93) 57	98.5 ± 7.11 (87–110) 10
LT	64.0 ± 0.00 1	58.4 ± 4.17 (53–70) 15	66.8 ± 6.13 (45–77) 50	71.8 ± 5.34 (65–82) 8
LHB/LT (%)	89	66	83	73
LHF	14.5 ± 0.71 (14–15) 2	16.4 ± 1.58 (13–19) 26	16.5 ± 1.55 (13–19) 57	20.4 ± 1.45 (18–22) 14
LE	11.3 ± 0.35 (11–11.5)	12.0 ± 2.00 (7–15) 24	12.4 ± 1.49 (9–15) 27	12.5 ± 1.66 (9–15) 13
WT	—	23.6 ± 3.50 (19–29) 8	16.8 ± 4.15 (12–24) 5	25.0 ± 4.86 (18–34) 7
GLS	22.7 ± 0.28 (22.5–22.9) 2	25.6 ± 0.95 (24.1–27.8) 29	24.5 ± 0.74 (22.7–26.2) 47	27.7 ± 0.98 (26.5–29.4) 11
CIL	20.3 ± 0.07 (20.2–20.3) 2	23.0 ± 0.80 (21.4–24.9) 33	21.3 ± 0.71 (19.6–22.8) 52	25.0 ± 0.99 (23.5–26.3) 12
ZB	14.4 ± 0.21 (14.2–14.5) 2	15.5 ± 0.51 (14.5–16.6) 25	13.8 ± 0.48 (13.0–14.9) 41	14.6 ± 0.61 (23.4–15.7) 12
IB	4.5 ± 0.07 (4.5–4.6) 2	4.9 ± 0.23 (4.4–5.5) 36	4.2 ± 0.18 (3.7–4.7) 82	4.5 ± 0.18 (4.1–4.8) 16
BBC	12.1 ± 0.35 (11.8–12.3) 2	12.5 ± 0.37 (11.6–13.1) 31	11.7 ± 0.38 (10.8–12.4) 51	12.5 ± 0.41 (11.7–11.9) 12
HBC	8.1 ± 0.00 2	7.7 ± 0.29 (7.2–8.5) 29	7.4 ± 0.33 (6.4–8.2) 43	8.1 ± 0.25 (7.7–8.5) 11
BR	4.9 ± 0.07 (4.8–4.9) 2	5.4 ± 0.32 (4.7–6.3) 32	5.1 ± 0.28 (4.5–5.7) 66	5.7 ± 0.33 (5.2–6.4) 17
LHR	4.5 ± 0.42 (4.2–4.8) 2	4.9 ± 0.18 (4.5–5.2) 33	4.5 ± 0.25 (3.9–5.0) 75	4.8 ± 0.36 (4.0–5.5) 15
LN	7.0 ± 0.07 (6.9–7.0) 2	8.8 ± 0.43 (8.0–9.9) 30	9.1 ± 0.44 (7.5–10.0) 96	10.5 ± 0.57 (9.8–11.6) 15
LD	4.7 ± 0.00 2	5.6 ± 0.34 (4.8–6.4) 35	5.1 ± 0.29 (4.2–6.0) 81	6.5 ± 0.34 (5.9–7.0) 18
PL	7.9 ± 0.00 2	9.3 ± 0.48 (8.3–10.6) 33	7.8 ± 0.32 (6.9–8.4) 70	9.3 ± 0.43 (8.6–10.3) 17
LBP	4.8 ± 0.07 (4.7–4.8) 2	5.6 ± 0.34 (4.9–6.4) 32	4.2 ± 0.26 (3.6–4.8) 66	5.2 ± 0.29 (4.8–5.8) 17
LIF	2.1 ± 0.35 (1.8–2.3) 2	2.5 ± 0.19 (2.1–2.9) 35	2.7 ± 0.22 (2.0–3.2) 77	2.8 ± 0.19 (2.5–3.2) 18
BIF	1.4 ± 0.07 (1.3–1.4) 2	1.6 ± 0.19 (1.1–2.0) 35	1.7 ± 0.13 (1.2–2.0) 76	1.8 ± 0.11 (1.6–2.0) 17
BBP	2.9 ± 0.07 (2.8–2.9) 2	3.2 ± 0.29 (2.3–3.8) 35	3.1 ± 0.16 (2.7–3.5) 77	3.4 ± 0.15 (3.1–3.6) 16
CLP4-M3	3.0 ± 0.21 (2.8–3.1) 2	3.7 ± 0.21 (3.4–4.3) 36	3.1 ± 0.15 (2.8–3.4) 79	3.2 ± 0.15 (2.9–3.5) 18
CLM1-M3	2.5 ± 0.00 2	3.0 ± 0.17 (2.7–3.5) 36	2.5 ± 0.13 (2.1–2.7) 80	2.6 ± 0.14 (2.4–2.8) 18
BP4	0.8 ± 0.00 2	1.1 ± 0.07 (0.9–1.2) 34	0.8 ± 0.07 (0.7–1.1) 70	0.8 ± 0.07 (0.7–0.9) 16

TABLE 4
(Continued)

Variable	*G. walterverheyeni*[a] D.R. Congo	*G. crassicaudatus*[b] Cameroon, Nigeria, Togo, Ghana, Ivory Coast, Liberia, Eq. Guinea	*G. lorraineus*[c] Cameroon, Gabon, D.R. Congo, Eq. Guinea	*G. surdus*[c] Cameroon, Gabon, D.R. Congo, Eq. Guinea
BM1	1.1 ± 0.07 (1.0–1.1) 2	1.2 ± 0.07 (1.1–1.4) 35	1.0 ± 0.06 (0.8–1.1) 75	1.0 ± 0.07 (0.9–1.1) 16
BM2	1.1 ± 0.00 2	1.3 ± 0.07 (1.2–1.5) 35	1.1 ± 0.07 (0.9–1.2) 76	1.1 ± 0.07 (1.0–1.2) 16
BIT	1.1 ± 0.07 (1.0–1.1) 2	1.5 ± 0.13 (1.2–1.8) 34	1.6 ± 0.12 (1.3–1.9) 74	1.9 ± 0.15 (1.7–2.2) 16
PPL	9.2 ± 0.28 (9.0–9.4) 2	10.4 ± 0.56 (9.2–11.4) 27	10.5 ± 0.55 (9.5–11.7) 41	11.8 ± 0.60 (11.0–12.9) 12
LB	6.7 ± 0.07 (6.6–6.7) 2	6.6 ± 0.21 (6.0–6.9) 33	7.0 ± 0.31 (6.4–7.8) 76	7.3 ± 0.22 (6.9–7.7) 15
BBO	2.2 ± 0.14 (2.1–2.3) 2	2.8 ± 0.29 (2.4–3.6) 24	2.1 ± 0.16 (1.8–2.5) 63	2.7 ± 0.13 (2.4–2.8) 14

[a] BMNH 27.3.1.35 (holotype); MRAC 88-005-M12 (paratype). Measurements for each specimen are listed in table 2; we list univariate means here for ready comparison with the other three species, realizing that a sample size of $n = 2$ is inadequate for statistical purposes.

[b] AMNH 89582, 89583, 236483; BMNH 23.1.22.52, 48.899, 61.1299, 61.459, 62.12.2.11, 12.1.12.1 (holotype of *G. c. dorotheae*), 12.10.28.12, 12.2.29.5, 46.296, 48.900, 50.839, 67.2165, 67.2166, 76.1497, 65.778; CMNH 2973, 42203, 42204, 42206, 42207, 42211, 42715, 42718, 59453, 69339; MNHN 1956-644, 1980-79, 1980-80; NNM 26639 (holotype of *G. crassicaudatus*); RUCA 5313; USNM 429506; ZFMK 77.59; ZMB 71325.

[c] Specimens measured are listed in the gazetteer.

reaches from Nigeria east of the Niger River through southern Cameroon, Central African Republic, Gabon, Republic of Congo, Bioko Island, northern Angola, Democratic Republic of the Congo, and into northern Zambia (see the documented reviews by Holden [2005, in press] and fig. 16).

The geographic range of the *G. lorraineus* complex is sympatric with that of *G. crassicaudatus* in West Africa; both species have been collected at the same or nearby sites in Guinea, Côte d'Ivoire, Ghana, Nigeria, southwestern Cameroon, and Bioko (if *G. crassicaudatus* truly occurs in Bioko; see discussion under *G. crassicaudatus*). Among the small-bodied species of *Graphiurus*, *G. lorraineus* resembles *G. crassicaudatus* in pelage coloration, thickness, and texture, but is physically smaller and has a longer tail relative to length of head and body (table 4). Upperparts are usually reddish brown, sandy or golden brown in some individuals; underparts are most often dark gray washed with cream or ochre. Dorsal and ventral pelage colors are often not clearly delineated. Some individuals exhibit a con-

spicuous narrow eye mask that extends from the snout to the bases of the ears; others exhibit only a thin dark eye ring encircling the eyes. Ears are brown, short, and rounded; and cheeks are dark grey washed with cream or ochre. Most samples express a uniform brownish dorsum from head to rump, but some individuals (especially samples from southern Cameroon) exhibit white postauricular patches. The hind feet are usually white marked by a dark dorsal metatarsal streak. The tail is moderately long but shorter than length of head and body (table 3). Tail hairs match that of the dorsal pelage in coloration; hairs are shorter at the base of the tail (2–3 mm) but longer at the tip (up to 21 mm), and tails often appear splayed because in some specimens the hairs project laterally. Number of teats (four pairs) and their positions on the body (one pectoral, one brachial, and two inguinal) match the pattern exhibited by all other species of *Graphiurus*.

The skull of *G. lorraineus* is short, broad, and moderately vaulted, conspicuously shorter and narrower than that of *G. crassicaudatus* and with absolutely and proportionally

Fig. 6. Dorsal views comparing adult crania from three species of *Graphiurus*. Top left: *G. crassicaudatus* (holotype of *G. c. dorotheae*, BMNH 12.1.12.1, southern Nigeria). Top right: *G. walterverheyeni* (paratype, MRAC 88-005-M12, Wafania D. R. Congo). Bottom left: *G. lorraineus* (holotype, BMNH 7.7.8.115, D.R. Congo). Bottom right: *G. lorraineus* (cf. *haedulus*, CMNH 17921, southern Cameroon). ×3.

Fig. 7. Ventral views of the same crania from *Graphiurus* illustrated in figure 6. Top left: *G. crassicaudatus dorotheae*. Top right: *G. walterverheyeni*. Bottom left: *G. lorraineus*. Bottom right; *G. lorraineus* cf. *haedulus*. All ×3.
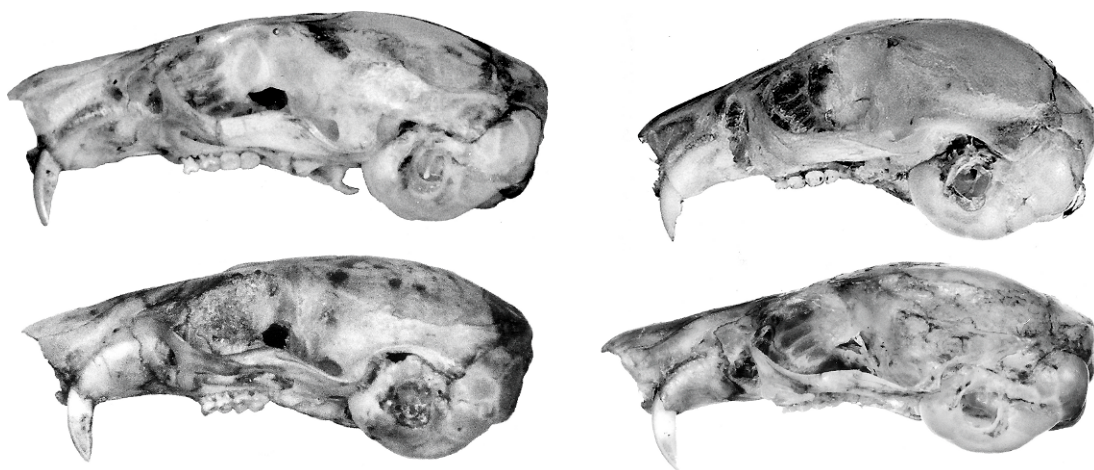
Fig. 8. Lateral views of the same crania from *Graphiurus* portrayed in figures 6 and 7. Top left: *G. crassicaudatus dorotheae*. Top right: *G. walterverheyeni*. Bottom left: *G. lorraineus*. Bottom right; *G. lorraineus* cf. *haedulus*. ×2.7.

narrower interorbital and postorbital regions unbordered by ridges (figs. 6–8; table 4). The rostrum and nasals are short relative to skull length, the incisive foramina are narrow (but wider relative to breadth of rostrum than in *G. crassicaudatus*), the bony palate and upper tooth rows are moderately long (but shorter than in *G. crassicaudatus*, as are most cranial
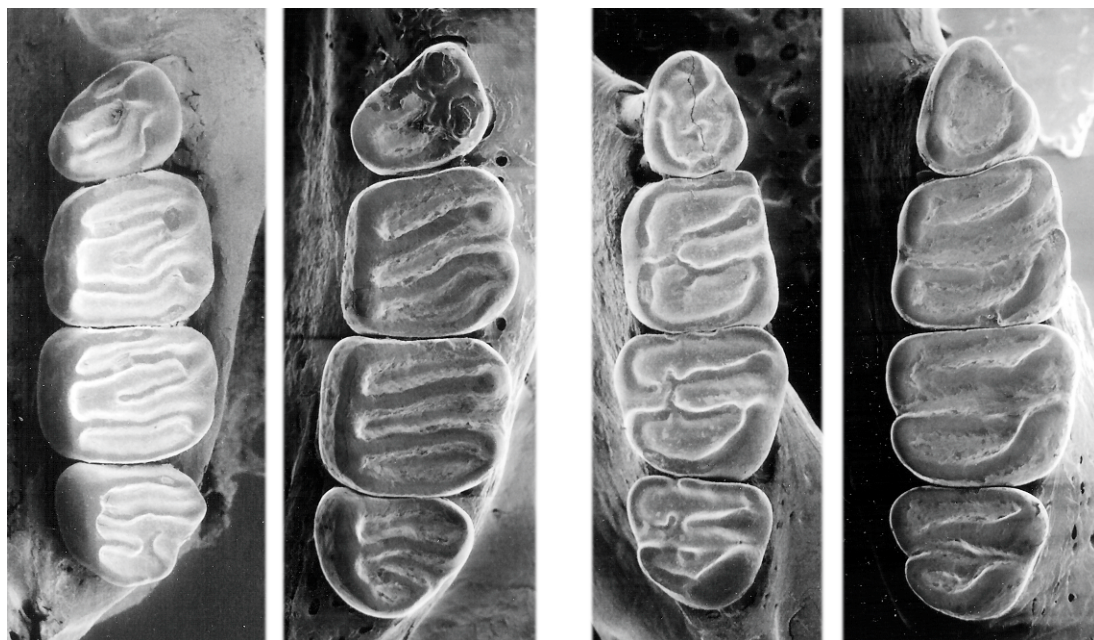
Fig. 9. Scanning electron micrographs of left maxillary (left pair) and right mandibular (right pair) tooth rows from adult *Graphiurus*. Left row in each pair is *G. lorraineus* (CMNH 42203, southern Cameroon); the right row of each pair is *G. crassicaudatus* (ZMB 71325, Côte d'Ivoire). Approximately ×21. Occlusal patterns of the teeth in *G. crassicaudatus* resemble those of *G. walterverheyeni*.
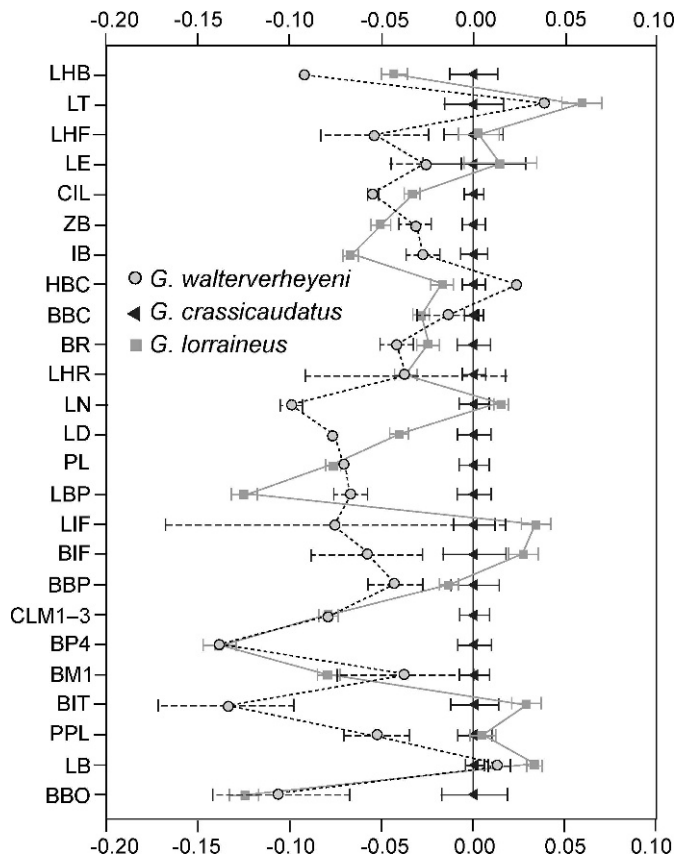
Fig. 10. Ratio diagram illustrating proportional relationships in cranial and dental dimensions among samples of adult *Graphiurus*. The standard is *G. crassicaudatus* from Cameroon, Nigeria, Togo, Ghana, Côte d'Ivoire, Liberia, and Equatorial Guinea ($N = 36$) contrasted with samples of *G. walterverheyeni* from the Central Congo Basin ($N = 2$, the holotype and paratype) and *G. lorraineus* from Cameroon, Gabon, D.R. Congo, and Equatorial Guinea ($N = 96$).

and dental dimensions in *G. lorraineus*), and the auditory bullae are somewhat long relative to length of skull (proportionally significantly longer than in *G. crassicaudatus*). The anterior chamber of each bulla is noticeably less inflated than the posterior chambers in some individuals (particularly some individuals from D.R. Congo), but this discrepancy of relative inflation is usually not as drastic as that observed in *G. crassicaudatus*, and this trait varies within the *G. lorraineus* complex. In addition to the absolute differences in cranial and dental dimensions between *G. lorraineus* and *G. crassicaudatus* (table 4), there are marked proportional distinctions that are portrayed in the ratio diagram in figure 10.

With such a broad geographic range, extending from Guinea and Sierra Leone in West Africa to northern Zambia in the south-central part of the continent, geographic variation in external, cranial, and dental traits among samples of the *G. lorraineus* complex should not be unexpected and in fact has been recognized as is signaled by two other scientific names associated with the species, as well as preliminary multivariate analyses of morphometric traits. In 1912, Dollman named and described *G. spurrelli*, based on an adult female from Ghana (table 2) as a species "distinguished from the allied form *lorraineus* by its larger size, paler colour, and smaller teeth" (Dollman, 1912: 316). The same report also contained a
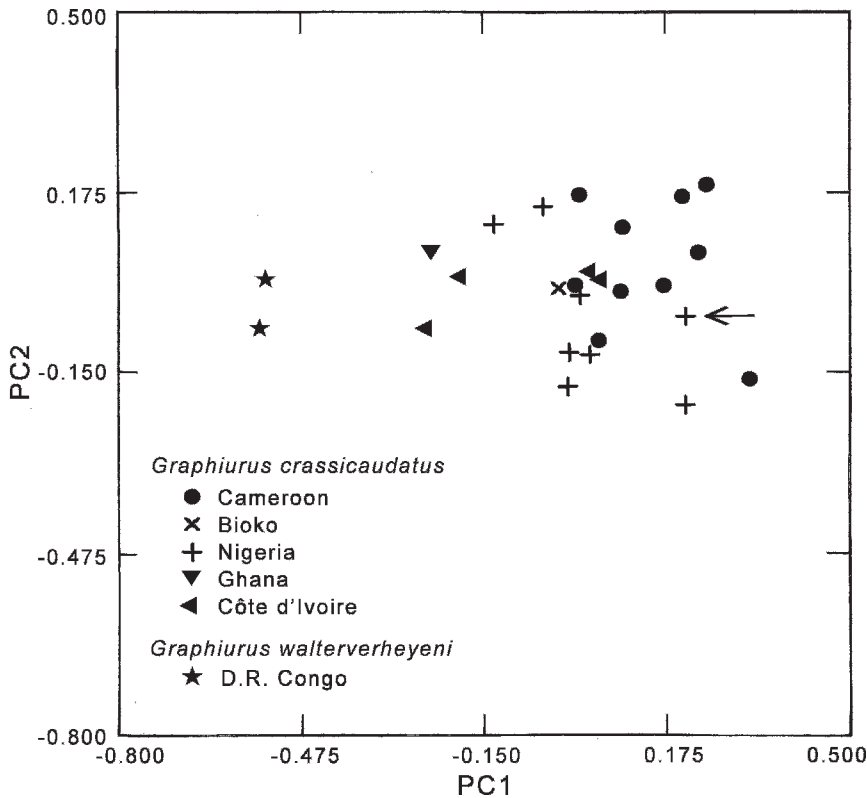
Fig. 11. Principal components analysis (performed on cranial and dental variables) showing dispersion of specimen scores representing *Graphiurus crassicaudatus* and *G. walterverheyeni* along the first two principal components. Arrow identifies score for the holotype of *G. c. dorotheae*. See discussion in text and table 5.

description of *G. haedulus*, derived from an adult male collected in southern Cameroon, a species in which Dollman (1912: 317) noted its coloration to be "so unlike that of all the other West African forms that it is readily distinguished from its near allies."

Preliminary multivariate analyses of cranial and dental measurements by Holden (unpubl.) indicates that animals in populations living in southern Cameroon (*haedulus*) and eastern Democratic Republic of the Congo (*lorraineus*) average smaller than those populations in Ghana (*spurrelli*), a difference possibly concordant with the geographic range that is divided into West Africa and Central Africa segments. As a further complication, there are populations living in the high mountains of Cameroon (and a single individual from Bioko) that, while generally resembling *G. lorraineus*, exhibit notable morphological and ecological

differences compared with lowland samples and will likely prove to be a different species (Eisentraut, 1963; Holden, in press).

Geographic variation within what is now recognized as *G. lorraineus* clearly requires resolution. While we are uncertain whether the *G. lorraineus* complex as discussed here is a single entity or a complex of species, we can confidently report that none of the *lorraineus* material we examined matches the two specimens of the new species. Our comparisons focused on the samples of true *G. lorraineus* from Cameroon, Equatorial Guinea, Gabon, and Democratic Republic of the Congo listed in the gazetteer, but we also compared the new species with holotypes bearing the scientific names currently associated with *G. lorraineus* (table 2), and with the specimens defining the entire range of *G. lorraineus*-like material collected from Guinea and Sierra Leone to northern Zambia (*G.*
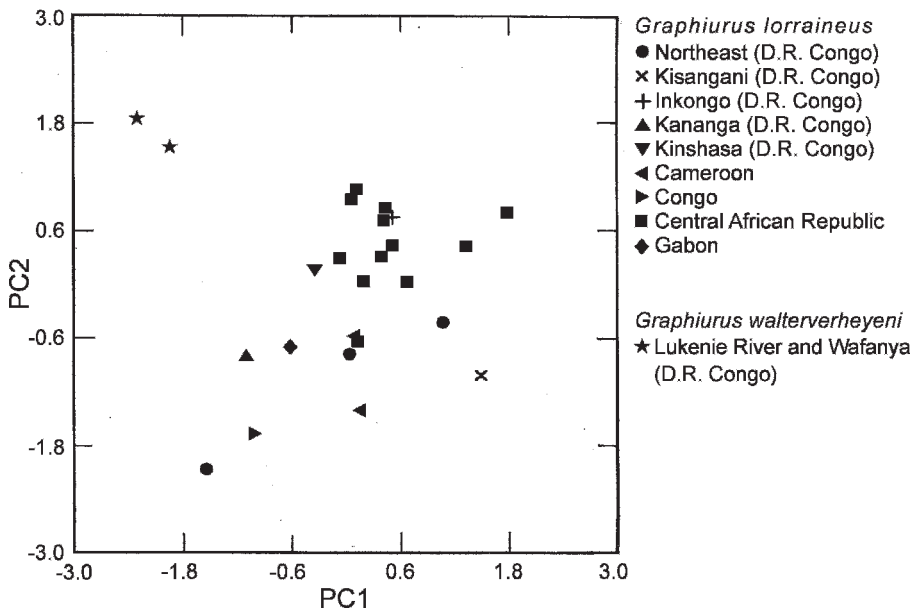
Fig. 12.   Principal components analysis (performed on cranial and dental variables) showing dispersion of specimen scores representing *Graphiurus lorraineus* and *G. walterverheyeni* along the first two principal components. See discussion in text and table 6.

lorraineus complex), also entered in the gazetteer.

The species we describe below averages smaller in most external and cranial dimensions compared to either *G. lorraineus* or *G. crassicaudatus*, and its geographic range is sympatric with that of the former species but allopatric to the distribution of the latter.

Graphiurus walterverheyeni, new species

HOLOTYPE AND TYPE LOCALITY: The holotype (BMNH 27.3.1.35) is a young adult female collected by Douglas C. Fraser (original number 46) on 21 October 1926. The specimen preparation consists of a stuffed skin, cranium, and mandible. The skull and mandible are in good condition (fig. 4) as is the skin, although the limbs are slightly contorted and the pinnae are flattened (fig. 3). The tail is unnaturally short or "bobbed" due to an injury sustained during the animal's life; that the terminal tail hairs had time to cover this region and undergo a change in pigmentation (the end of the bobbed tail is tipped with white hairs) indicates that the injury did not occur immediately prior to or during this animal's

capture. Holden's personal experience derived from studying hundreds of specimens of *Graphiurus* confirms that tail injuries are often accompanied by a bushy, white-tipped growth of hair over the truncated tail tip. This condition has also been recorded for *Eliomys* by Miller (1912) and for *Muscardinus* by Juškaitis (2006). External, cranial, and dental measurements of the holotype are listed in table 2.

The type locality, noted on the specimen tag by Fraser, is "River Lukenie (Meridian 22.30E), 500 meters," with the additional annotation that the dormouse was "caught close to the river." No village name was given for a point of reference; the coordinates are approximated to be 03°30′S, 22°30′E (fig. 2). The Lukenie River flows westward to its confluence with the waters draining Lac Mai-Ndombe; after this junction the river is known as the Fimi, which later joins the Kasai River; together these form the westward flowing Kwa River, one of the large tributaries of the Congo River.

REFERRED SPECIMEN: Only one other specimen of *G. walterverheyeni* is known to exist (MRAC 88–005–M12), a young adult
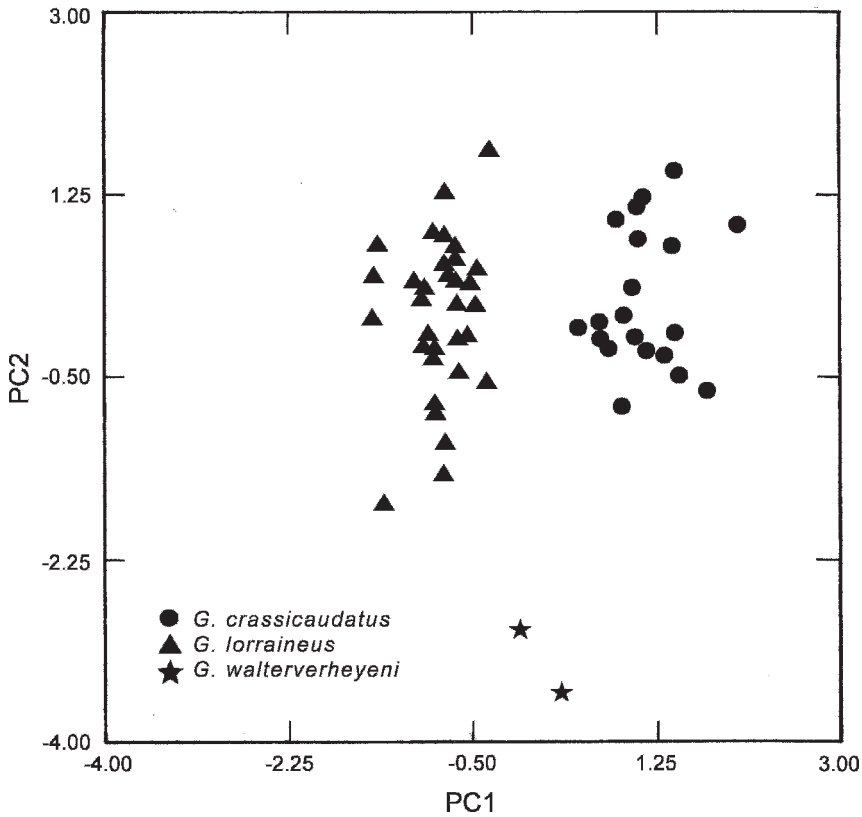
Fig. 13.   Principal components analysis (performed on cranial and dental variables) showing dispersion of specimen scores representing *Graphiurus crassicaudatus*, *G. lorraineus*, and *G. walterverheyeni* along the first two principal components. See discussion in text and table 7.

male, captured at "Wafanya" (Wafania), 01°21′S, 20°20′E, Democratic Republic of the Congo, on 4 December 1987 by E.P.P. Lootens (original number 2110). Wafania is located near the left bank of the Luilaka River, an eastern tributary of the Ruki River that flows westward into the Congo River. The specimen consists of a skull (fig. 5), mandible, and carcass in alcohol.

DIAGNOSIS: *Graphiurus walterverheyeni* shares several morphological similarities with *Graphiurus crassicaudatus* (for example, a stubby snout, short rostrum and nasals, broad skull, vaulted braincase, and wide interorbital and postorbital regions with their dorsolateral margins delimited by ridges), but is most easily distinguished from that species by its overall smaller size, which is reflected in the often markedly absolutely smaller

external, cranial, and dental dimensions (tables 2–4, figs. 6–8), and proportional differences (fig. 10).

GEOGRAPHIC DISTRIBUTION: *G. walterverheyeni* is known only from the two localities described above, one along the Lukenie River, the other near the Luilaka River, both places within an area circumscribed by the western arm of the Congo River and by its large eastern tributary, the Lomami River. The species may be endemic to that vast equatorial tropical rainforest stretching south from the great bend of the Congo River between its western arm and the Congo-Lualaba River to the east within the Central Congo Basin, an area known as the south-central forest region (Grubb 1978, 1982, Grubb, 2001, and references therein; Colyn, 1991; Colyn and Van Rompaey, 1994;

Happold 1996; White, 2001) and the Salonga-Lukenie-Sankuru landscape (Congo Basin Forest Partnership, 2006).

ETYMOLOGY: The patronym honors the late Dr. Walter Verheyen, whose extensive field, laboratory, and museum research on African mammals, particularly rodents, resulted in many significant and influential publications in the fields of ecology and systematics. Verheyen generously provided Holden access to specimens and data during her research on *Graphiurus* systematics.

DESCRIPTION AND COMPARISONS: The description is presented in the context of comparisons among *G. walterverheyeni*, *G. crassicaudatus* (its closest morphological and possible phylogenetic relative), and the sympatric true *G. lorraineus*, which it resembles in body size. In its external features, *G. walterverheyeni* superficially resembles both *G. crassicaudatus* and *G. lorraineus*. It has a much shorter head and body than *G. crassicaudatus*, and averages slightly smaller than *G. lorraineus*, and the hind feet are shorter relative to length of head and body than is typical of either *G. crassicaudatus* or *G. lorraineus* (fig. 10, table 4). The dorsal pelage is uniformly dull rufous brown, soft, and short; it is composed of soft overhairs (4 mm long over the body) and short, fine guard hairs (6–7 mm long near the rump) inconspicuously projecting beyond the overhair layer. Overhairs are steel gray for most of their length, and tipped with a rusty-yellow band, which darkens to a darker brown tip on some hairs; guard hairs are dark brown. The skin, while in good condition, was perhaps molting at the time of capture, so that many gray bases of the overhairs are visible; it is likely that color of the dorsal pelage is similar to the richer rufous brown of *G. crassicaudatus*. The short, soft ventral coat is dark gray washed with buff. Dorsal and ventral pelage colors are not clearly delineated, a character shared with most specimens of true *G. lorraineus*; most specimens of *G. crassicaudatus* exhibit clear delineation of the dorsal and pelage colors. Head coloration is similar to that of the dorsal pelage, and each eye is encircled by an inconspicuous, narrow eye ring. Coloration of the tail generally matches that of the dorsal pelage, although white hairs are scattered conspicuously throughout the

tail, and on the holotype (which has a bobbed tail –see discussion under Holotype and Type Locality) the tail is conspicuously tipped in white due to prior injury. The external pinnae are short and ovate, clothed in fine, dark brown hairs, and the pelage color behind the ears matches that of the dorsal pelage (postauricular patches are not present; they are exhibited in some samples of *G. lorraineus* and other species of *Graphiurus*). Dorsal surfaces of the hind feet are white with a dark metatarsal streak. No mammae count is available from the single female specimen, but it is presumed to be concordant with that of all other species of *Graphiurus* as well as other glirids: females usually have four pairs of nipples (one pectoral, one brachial, and two inguinal), although some variation has been documented in the non-African *Glis* (Kryštufek, 2004).

COMPARISON WITH *G. CRASSICAUDATUS*: The skull of *G. walterverheyeni* superficially connotes a miniature of *G. crassicaudatus*, but exhibits contrasts related to proportions of certain cranial and dental dimensions (figs. 3, 4). Although *G. walterverheyeni* is smaller than *G. crassicaudatus* in nearly all cranial and dental dimensions (table 4), the two species share: a short and narrow rostrum; vaulted braincase; dorsal maxillary roots of the zygoma that flare out at almost a 90° angle from the rostrum with ventral zygomatic roots originating anterior to the dorsal roots; pronouncedly wide interorbital and postorbital regions, with their dorsolateral salients defined by ridges transforming to beading along dorsolateral margins of the braincase and fading out above squamosal roots of the zygomatic arch; a conspicuous lacrimal; an anterior bullar chamber that is notably less inflated than the posterior chambers; and incisor tips that usually form a straight cutting surface (rather than V-shaped). Occlusal patterns of ridges and valleys on premolar and molars were not closely studied, but seem similar to those characteristic of *G. crassicaudatus* (fig. 9).

Proportional differences (in addition to overall smaller size) contrast the skulls of *G. walterverheyeni* and *G. crassicaudatus* (fig. 10). Compared with that West African endemic, *G. walterverheyeni* has a markedly significantly shorter and wider rostrum (in-

dexed by length of nasals) relative to length of skull (using condyloincisive length as the measure for skull length), which is also reflected in its absolutely shorter incisive foramina; the zygomatic breadth is broader relative to length of skull; the interorbital region is wider relative to length of skull (but the dorsolateral ridges are not as pronounced); the braincase is deeper relative to its breadth (*G. walterverheyeni* also exhibits greater cranial flexion, perhaps correlated with the deeper braincase); the entire skull behind the rostrum is smaller relative to overall skull length (relatively shorter diastema, bony palate, and molar row; and shorter palatal length); wider bony palate relative to its length; broader first molar relative to length of the molar row; markedly narrower incisors and smaller fourth premolar relative to nearly all other cranial and dental dimensions; and much larger auditory bullae relative to size of skull, with a correlated decrease in breadth of the basioccipital between the bullar capsules. The two examples of *G. walterverheyeni* are young adults, but the distinctions between that species and *G. crassicaudatus* do not reflect those associated with age as the same contrasts can be demonstrated comparing young adults of each species.

The size discrepancy that distinguishes *G. walterverheyeni* and *G. crassicaudatus* can be appreciated by viewing results of the principle components analysis (complete sets of measurements were available only for 15 of the 24 variables measured) in figure 11 where the distribution of specimen scores form two discrete clusters along the first axis; size predominantly affects the spread of scores. The isolation of the two points representing *G. walterverheyeni* from those scores for *G. crassicaudatus* results from size differences in nearly all included variables, but particularly breadth across the incisor tips, breadth of incisive foramina, and lengths of nasals, diastema, bony palate, and tooth row (table 5). Length of bulla (and breadth of basioccipital, which is not shown) is negligible in its effect on dispersion of scores. An ordination employing second and third principle components (not illustrated) also yields two separate clusters, each representing one of the two species. Here the divergence of scores is along the third axis, where the

TABLE 5
Results of Principal Components Analysis of Adult *Graphiurus walterverheyeni* ($N = 2$) and *G. crassicaudatus* ($N = 24$)
(Principal components are extracted from a covariance matrix of 15 log-transformed cranial and dental variables; see table 4, fig. 11.)

Variable	PC1	PC2	PC3
CIL	0.048	0.003	0.002
IB	0.035	0.014	−0.032
BIT	0.116	0.035	−0.009
LHR	0.028	0.008	−0.013
LN	0.075	0.002	0.009
LD	0.071	0.009	0.006
PL	0.054	0.010	0.028
PPL	0.058	−0.000	−0.020
LIF	0.048	−0.044	0.072
BIF	0.072	−0.092	−0.037
BBP	0.043	0.005	−0.042
CLP4-M3	0.064	0.010	0.023
BM1	0.045	0.011	0.006
LB	0.002	−0.004	−0.006
LBP	0.061	0.020	0.005
Eigenvalue	0.054	0.013	0.011
% variance	56.791	13.523	12.105

dispersion of scores is influenced primarily by interorbital breadth (proportionally wider in the new species than in *G. crassicaudatus*), palatal length (proportionally shorter), length and breadth of the incisive foramina (breadth is wider relative to the proportionally shorter length), and breadth of the bony palate (relatively wider relative to palate length) (table 5).

Side-by side comparisons of skulls (figs. 6–8), combined with results from morphometric analyses that incorporate univariate statistics (table 4), a ratio diagram (fig. 10), and a principle components analysis (fig. 11; table 5) document the primary distinctions between the two species of dormice. Not only is *G. walterverheyeni* markedly physically smaller than *G. crassicaudatus*, but regions of the skull are proportionally different, as is highlighted by the relatively stubbier rostrum of *G. walterverheyeni*, its relatively shorter skull anterior to the braincase, wider interorbital region, higher braincase, and relatively much larger auditory bullae.

The mandible of *G. walterverheyeni* was not studied in detail, but generally resembles that of *G. crassicaudatus*.

COMPARISON WITH *G. LORRAINEUS*: The sympatric true *G. lorraineus* is physically smaller than *G. crassicaudatus* and closer in body size to *G. walterverheyeni*, but the latter has a shorter head and body, hind feet, and ears compared with true *G. lorraineus* (table 4). Many cranial and dental dimensions are either similar or only slightly different in the two species; however, *G. walterverheyeni* has a greater zygomatic breadth, wider interorbit and braincase, higher braincase (reflecting markedly greater cranial flexion), and longer bony palate (table 4). Coordinated with the longer palate, the incisive foramina are strikingly shorter (and narrower) in *G. walterverheyeni* and the postpalatal dimension less. The new species also exhibits appreciably narrower incisors and shorter nasals. These similarities and distinctions between the two species portray *G. walterverheyeni* as closer in body size to *G. lorraineus* than to *G. crassicaudatus*, but differing rather spectacularly from *G. lorraineus* by its attenuated, stubby rostrum; wider interorbital region with the dorsolateral margins marked by ridging, which is generally absent in *G. lorraineus*; vaulted braincase as part of greater cranial flexion; narrower incisor tips; and longer bony palate with attendant lesser values associated with length of incisive foramina and the postpalatal region. The contrasts in conformation of rostrum, interorbital region, and braincase are easily observed in illustrations of skulls in figures 6–8.

These dimensional dissimilarities between the two species that are reflected in absolute values are also evident in proportional context and can be visualized in the ratio diagram (fig. 10). For example, relative to size of skull, *G. lorraineus* has a significantly much longer rostrum than does *G. walterverheyeni*; a narrower interorbital region and breadth across the zygomatic arches, lower braincase, a markedly shorter and wider bony palate, larger incisive foramina, longer postpalatal region, and wider incisor tips. Proportions of the teeth (breadths of fourth premolar and first molar, length of molar row) seen in *G. lorraineus* match those for *G. walterverheyeni*, but size of the braincase, breadth of rostrum, and length of diastema relative to length of skull in *G. lorraineus* fits with the proportions in *G. crassicaudatus* and not *G. walterverheyeni*.

The ordination of specimen scores in multivariate space rendered by principal components analysis shows two discrete clusters, one representing the two examples of *G. walterverheyeni*, the other depicting samples of true *G. lorraineus* from Cameroon, Gabon, Congo, Central African Republic, and Democratic Republic of Congo (fig. 12). Size, as usual, is primarily responsible for separating the two groups of scores along the first axis. Nearly all variables contribute to the dispersion of scores, but condyloincisive and postpalatal lengths, length of nasals, breadth of incisive foramina, and breadth of bony palate are most influential (table 6). The low value for interorbital breadth (0.001) indicates the wider interorbital region in *G. walterverheyeni*, and its relatively higher braincase evidenced by the negative value for that variable. Separation of the two species-clusters along the second axis is of lesser magnitude. Here zygomatic breadth and breadth of incisive foramina weigh heavily in the scatter of scores, but most of the other variables also contribute to some extent. The relatively shorter rostrum of *G. walterverheyeni*, and its relatively narrower incisive foramina and bony palate is reflected in the negative values. The ordination of first and third, and second and third components also demonstrated two constellations of scores (not illustrated here), each representing the two species. Breadth of incisive foramina and length of nasals are basically responsible for the separation of clusters (table 6).

Graphiurus walterverheyeni and *G. lorraineus* share small body size and general pelage coloration along with certain cranial and dental dimensions, but configurations of the rostrum, interorbital region, and braincase easily distinguish the two. Additionally, the incisor tips of specimens of *G. lorraineus* (both true *G. lorraineus* and the complex) form a V-shaped cutting edge, a trait exhibited by most species of *Graphiurus*; the incisor tips of almost all individuals of *G. crassicaudatus* and both specimens of *G. walterverheyeni* form a straight cutting surface.

COMPARISON SUMMARY: In summary, the three discrete clusters of specimen scores,

TABLE 6
Results of Principal Components Analysis of Adult
Graphiurus walterverheyeni ($N = 2$)
and *G. lorraineus* ($N = 22$)
(Principal components are extracted from a
covariance matrix of 13 log-transformed cranial and
dental variables; fig. 12.)

Variable	PC 1	PC 2	PC 3
CIL	0.041	0.022	−0.006
ZB	0.026	0.038	0.007
IB	0.001	0.017	0.006
BBC	0.019	0.019	0.006
HBC	−0.011	0.020	0.014
LN	0.062	−0.018	−0.041
LD	0.051	0.014	0.008
PL	0.016	0.025	0.000
PPL	0.063	0.017	−0.015
BIF	0.104	−0.032	0.035
BBP	0.048	−0.004	−0.003
CLM1-M3	0.007	0.010	−0.005
LB	0.032	0.011	−0.008
Eigenvalue	0.028	0.006	0.004
% variance	62.927	13.033	8.510

TABLE 7
Results of Principal Components Analysis of Adult
Graphiurus walterverheyeni ($N = 2$),
G. crassicaudatus ($N = 22$), **and** *G. lorraineus* ($N = 32$)
(Principal components are extracted from a
covariance matrix of 11 log-transformed cranial and
dental variables; fig. 13.)

Variable	PC1	PC2	PC3
CIL	0.037	0.034	0.001
IB	0.067	0.012	0.013
HBC	0.017	0.004	0.014
LN	−0.001	0.048	−0.015
LD	0.055	0.045	0.005
PL	0.101	0.018	0.006
PPL	−0.004	0.051	−0.002
BIT	−0.051	0.105	−0.053
BIF	−0.062	0.083	0.072
CLP4-M3	0.092	0.022	−0.009
LBP	0.152	0.015	0.003
Eigenvalue	0.058	0.027	0.009
% variance	55.737	26.331	8.423

derived from all samples, in the ordination of first and second principle components summarized in figure 13 acknowledges three entities defined by morphometric traits. These groups translate to the reality of *G. crassicaudatus*, true *G. lorraineus*, and *G. walterverheyeni*, and supports the hypothesis that the two small-bodied specimens from south of the great bend of the Congo River, although similar to *G. crassicaudatus* in particular cranial features, do not mark merely a population of *G. crassicaudatus* occurring in the Congo basin, but instead represent a species as distinct from *G. crassicaudatus* as that species is from *G. lorraineus*. Condyloincisive and palatal lengths, lengths of bony palate and tooth row, and interorbital breadth partly influence the scatter of specimen scores along the first principle component (table 7); all these dimensions are markedly greater in *G. crassicaudatus* than in either of the other two species, differences readily apparent in the table of descriptive statistics (table 4). The large negative values associated with breadth across the incisor tips and breadth of incisive foramina reflect their smaller size in *G. walterverheyeni* compared to either *G. crassicaudatus* or *G. lorraineus* (table 4). Specimen

scores for the two *G. walterverheyeni* that are isolated from the other clusters along the second axis is mostly influenced by condyloincisive and postpalatal lengths, lengths of nasals and diastema, and breadths of incisor tips and incisive foramina, all dimensions that are relatively less than in *G. crassicaudatus* and *G. lorraineus*. An ordination pitting the second principle component against the third left the two specimen scores for *G. walterverheyeni* isolated, but scores for the other two species melded together into a single cluster; no informative structure emerged by plotting first versus third components (these diagrams are not illustrated here).

KARYOTYPE AND MOLECULAR DATA: No data are available. The holotype and paratype do not have karyotype, tissue, or molecular preparations associated with them.

ECOLOGY: The two collecting localities are within the South Central faunal region (Grubb, 1978, 1982, 2001; Colyn, 1991; Colyn and Van Rompaey, 1994; Happold, 1996; White, 2001), and the Salonga-Lukenie-Sankuru landscape (Congo Basin Forest Partnership, 2006) of equatorial Africa. Aside from the scant habitat information written on the specimen tag of the type specimen, and from general habitat descriptions derived from Fraser (1927), no direct,

detailed habitat information is available; however, utilizing vegetation maps as well as habitat information reported for sympatric species (Colyn, 1991; Colyn and Van Rompaey, 1994; Happold, 1996; Gauthier-Hion et al., 1999), conservation efforts (Congo Basin Forest Partnership, 2006), and other sources (e.g., Inogwabini, 2005; Seyler et al., 2005), the new species habitat can be generally characterized. Most of the region (94%) is covered by dense, intact, diverse tropical forest formations (on poorly drained, hydromorphic soil) that sustain major seasonal flooding: Swamp or floodplain forests comprise 23.6%, and terra firma forests account for 70.8% of the forest formations (Bailey, 1986; White, 2001; Congo Basin Forest Partnership, 2006). As much as one-half of the forest may be inundated during the rainy seasons, particularly during the September–December interval, with the flood plain extending up to 2.5 km from the river bank in certain areas (Bailey, 1986; Gauthier-Hion et al., 1999; Inogwabini, 2005). Vegetation is described by Evrard (1968), Gauthier-Hion et al. (1999), White (2001), Inogwabini (2005), and the Congo Basin Forest Partnership (2006).

SYMPATRIC ASSOCIATIONS WITH OTHER *GRAPHIURUS*: Of the five equatorial species of *Graphiurus*, the ranges of only two overlap the geographic distribution of *G. walterverheyeni*, but examples of those two have not been collected at either of the sites yielding *G. walterverheyeni*. Twenty of the known 23 specimens in museum collections identified as *G. surdus* are from the western portion of the Central Forest Block in southern Cameroon, Equatorial Guinea, and Gabon (see map in Holden, 1996). Three others are from farther east in the Democratic Republic of the Congo. One was collected along the Sankuru River at Inkongo, in the watershed south of the great bend of the Congo River, and approximately 175 air km east-southeast of the site along the Lukenie River where the holotype of *G. walterverheyeni* was obtained, and about 500 air km southeast of Wafania, the provenance of the paratype. The other D.R. Congo specimen of *G. surdus* examined by Holden was collected at Masako Forest Reserve northeast of Kisangani in a loop of the Tshopo River (Hutterer and Dudu, 1990) (only one of two specimens collected at

Masako reported by Mukinzi et al., 2005, was available for study). Masako is approximately 550 air km northeast of the type locality (Lukenie River), and about 580 air km east-northeast of paratype collection site (Wafania). Holden (1996: 39) compiled what meager ecological information is tied to specimens of *G. surdus*.

With a documented range extending from Guinea and Sierra Leone to northern Zambia (Holden, 2005, in press; fig. 16), the *G. lorraineus* complex has an appreciably more expansive geographic distribution than does *G. surdus*. Besides *G. walterverheyeni* and *G. surdus*, it is the only other species of dormouse documented from the Congo basin south of the great bend of the Congo River. The new species and *G. lorraineus* have not been collected at the same locality, and it is possible that their habitat requirements are distinct; *G. lorraineus* seems to be associated with secondary forest and anthropogenic habitats (see discussion under Kinship and Zoogeography below).

ENDEMICITY: While two localities do not provide the strongest data bolstering the hypothesis that a distinctive faunal region exists, the known distribution of *Graphiurus walterverheyeni* is concordant with ranges of a small suite of equatorial nonvolant rainforest mammals that are unknown outside the South Central faunal region: one species of elephant shrew, seven or more primates, one mongoose, and several species of murid rodents.

The taxon, *tordayi*, marks a very morphologically distinctive population of the four-toed elephant shrew, *Petrodromus tetradactylus*, that is endemic to this region (see maps in Kingdon, 1974a: 66, 1974b: 55). Among populations of *P. tetradactylus*, which ranges beyond the Congo and Lualaba rivers to East Africa, *tordayi* is the only shrew that occurs in tropical evergreen rainforest, and although now treated as a subspecies of *P. tetradactylus*, is likely a separate species (Kingdon, 1974a, 1974b, 1997; Schlitter, 2005).

Eighteen taxa representing species and distinctive subspecies of primates are endemic to the south-central region: the galago *Galago demidoff phasma* (after taxonomic revision of the "*demidoff* species group," *phasma* may prove to be a separate species endemic to the Congo basin south of the

great bend of the Congo River [Groves, 2001; *phasma*'s range is rendered in blue on Kingdon's map, 1997: 109]); the cercopithecines *Allenopithecus nigroviridis*, *Cercocebus chrysogaster*, *Cercopithecus ascanius* (the subspecies *ascanius*, *atrinasus*, *katangae*, and *whitesidei*), *Cercopithecus dryas*, *Cercopithecus mitis heymansi*, *Cercopithecus wolfi* (the subspecies *elegans*, *pyrogaster*, and *wolfi*), *Lophocebus aterrimus*, and *Lophocebus opdenboschi*; the colobines, *Colobus angolensis angolensis*, *Piliocolobus foai parmentierorum*, and *Piliocolobus thollon*; and the hominid, *Pan paniscus* (Colyn et al., 1991; Groves, 2001, 2005; Kingdon, 1997, provides informative figures depicting ranges of some of these primates).

The only carnivore apparently endemic to the South Central faunal region of the Congo basin is the herpestid, *Crossarchus ansorgei nigricolor* (Colyn and Van Rompaey, 1994; Kingdon, 1997: 249).

Two murid rodents have been recorded in rainforests south of the great bend of the Congo River and nowhere else. One is the deomyine, *Lophuromys huttereri*, a sister species to *L. nudicaudus*, which occurs on the right side of the Congo River and ranges from there to the western coast in lowland tropical evergreen rainforest (Musser and Carleton, 2005; Verheyen et al., 1996). The other is *Praomys minor*, a murine still known only by three specimens collected at Lukolela, on the left bank of the Congo River in the South Central faunal region (Nicolas et al., 2005; Musser and Carleton, 2005: 1448).

Future studies may alter the endemic status of the mammals listed above based on right-bank versus left-bank localities, which, for example, has already been realized for the murines *Praomys lukolelae* and *P. muttoni*. The former was known only by the type series collected at Lukolela on the left bank of the Congo River, within the South Central faunal region, but a large series has been obtained in the Kisangani region on the right bank of the Congo River, within the East Central faunal region (Musser and Carleton, 2005: 1447). *Praomys muttoni* was first collected in the Masako Forest Reserve on the right side of the Congo River (East Central faunal region), and has now been found in the Kisangani region on the left bank of the river (South Central faunal region) (Mukinzi et al., 2005; Nicolas et al., 2005).

How *Graphiurus walterverheyeni*'s membership in the mammalian guild endemic to the South Central faunal region may be altered, or not, will depend upon results of future surveys concentrating on diversity of small mammals south of the Congo River. One long-term inventory already reinforces the distribution of *G. walterverheyeni* as restricted to the South Central faunal region. Results from a survey of small mammals (mostly rodents and shrews) around Kisangani in various kinds of forests as well as anthropogenic habitats undertaken from 1979 to 2003 has yielded only small samples of *G. surdus* and *G. lorraineus* (Mukinzi et al., 2005). The absence of *G. walterverheyeni* in historic samples consisting of hundreds of specimens of *Graphiurus* collected in West Africa and the West Central faunal region in particular, especially in southern Nigeria and southern Cameroon, suggests that the distribution of the new species does not extend into these regions. It must be noted, however, that certain species of African dormice (e.g., *G. crassicaudatus* and *G. surdus*) are uncommon at best, and the hypothesized distribution of *G. walterverheyeni* may well be an artifact of inadequate sampling.

KINSHIP AND ZOOGEOGRAPHY: These are subjects for future reports. Through our simple inspection of skulls, particular cranial conformations suggest a closer morphological link between *G. walterverheyeni* and *G. crassicaudatus* than between *G. lorraineus* or any other equatorial forest species of dormouse. Both *G. walterverheyeni* and *G. crassicaudatus*, to the exclusion of *G. lorraineus*, share a short rostrum relative to length of skull, relatively wide interorbital and postorbital regions bordered by some expression of ridging, and a vaulted braincase. On the other hand, proportional relationships involving dimensions of individual molars, complete molar row, and auditory bulla recall *G. lorraineus*. Recovering the phylogenetic affinities of *G. walterverheyeni* will entail a cladistic inquiry using a variety of anatomical traits and molecular data obtained from samples of many species of *Graphiurus*, both those occurring in equato-

rial forests and species found primarily in bordering savanna woodlands. That tropical lowland forest species such as *G. crassicaudatus*, *G. walterverheyeni*, and *G. lorraineus* may be closer relatives of one another to the exclusion of savanna species seems intuitively sensible but may not reflect phylogenetic reality. Possibly a forest dweller is closer kin to a savanna inhabitant than to another equatorial forest species. While the core of its geographic range is in the belt of equatorial lowland tropical forest, *G. lorraineus* has apparently never been trapped in primary forest but instead inhabits gallery forests, forest margins, woodland savanna, and disturbed areas, especially those formed by anthropogenic activities resulting in plantations of banana, cocoa, palmyra, and pawpaw, as well as in occupied and abandoned buildings (Holden, in press). Such habitats are structurally similar to woodland savanna.

If *G. walterverheyeni* is the closest relative of *G. crassicaudatus* among equatorial species of *Graphiurus*, the phylogeographic pattern (*G. crassicaudatus* in western Africa, *G. walterverheyeni* in the Congo basin) formed would be similar to those of a host of other equatorial rainforest mammals, among them species of murid rodents (Carleton and Robbins, 1985: Musser and Carleton, 2005), primates and artiodactyls (see review by Happold, 1996; Groves, 2001), and carnivores (for example, Colyn and Van Rompaey, 1994). These distributions overlaid with patterns of phylogeographic relationships among species of equatorial *Graphiurus* should add substantial information to the evolutionary history of Africa's tropical forest endemics.

ECOLOGICAL NICHE MODELING: Incorporating ecological niche modeling in the present report allowed us to compare the known geographical range versus predicted geographical range for two of the three species discussed in this report. We have examined most, and in one case all, existing museum specimens of the three *Graphiurus* species discussed in this paper. The collection localities associated with those specimens provide a general idea or hypothesis of the geographic range for each species. For species that are fairly commonly captured in faunal studies, the known geographic range based on

specimen collecting localities may closely approximate the actual geographic range. For species that are uncommonly (*G. crassicaudatus*) or rarely (*G. walterverheyeni*) encountered, it is likely that the actual geographic distribution exceeds the known geographic range based on specimen data. It is of benefit to model the possible distribution of such species, as ecological niche models provide ''first-pass hypotheses [of areas of occurrence] that may be the only usable information for many rare and poorly known taxa'' (Peterson, 2001). This first pass allows researchers to identify potentially critical sampling sites for certain species, and when many species' predicted distributions are overlaid, it provides a cogent prediction of community composition for any analyzed site. Such cross-species prediction of community composition aids in pinpointing areas as conservation priorities (Peterson et al., 2000; Peterson, 2001). Distributional modeling also provides clues regarding the ecology of poorly known species.

Predicting species distributions has obvious applications in epidemiology. Certain African dormouse species, including *G. lorraineus*, *G. crassicaudatus*, and *G. kelleni*, are considered as possible hosts of monkeypox virus (Orthopoxviridae). Accurate or at least reasonable predictions of host distributions and ecology allow for enhanced understanding and analyses of virus ecology and epidemiology. If one or more species of *Graphiurus* is the primary host (or one of several hosts) of monkeypox virus, accurately predicting the distributions of these dormouse species would help predict where outbreaks of monkeypox may likely occur.

The predicted distribution of *G. crassicaudatus* (fig. 14) is somewhat surprising. All historical collection localities are in West Africa (western and west-central forest regions), but the model indicates strong ecological suitability (indicated by darker-shaded pixels) in the south-central region. This is interesting because (1) it may be that suitable habitat exists, but for a variety of other reasons, such as chance, geographic barriers, population extinction, climate change leading to isolation of populations (Colyn et al., 1991), the species does not currently occur there; (2) the species may actually occur
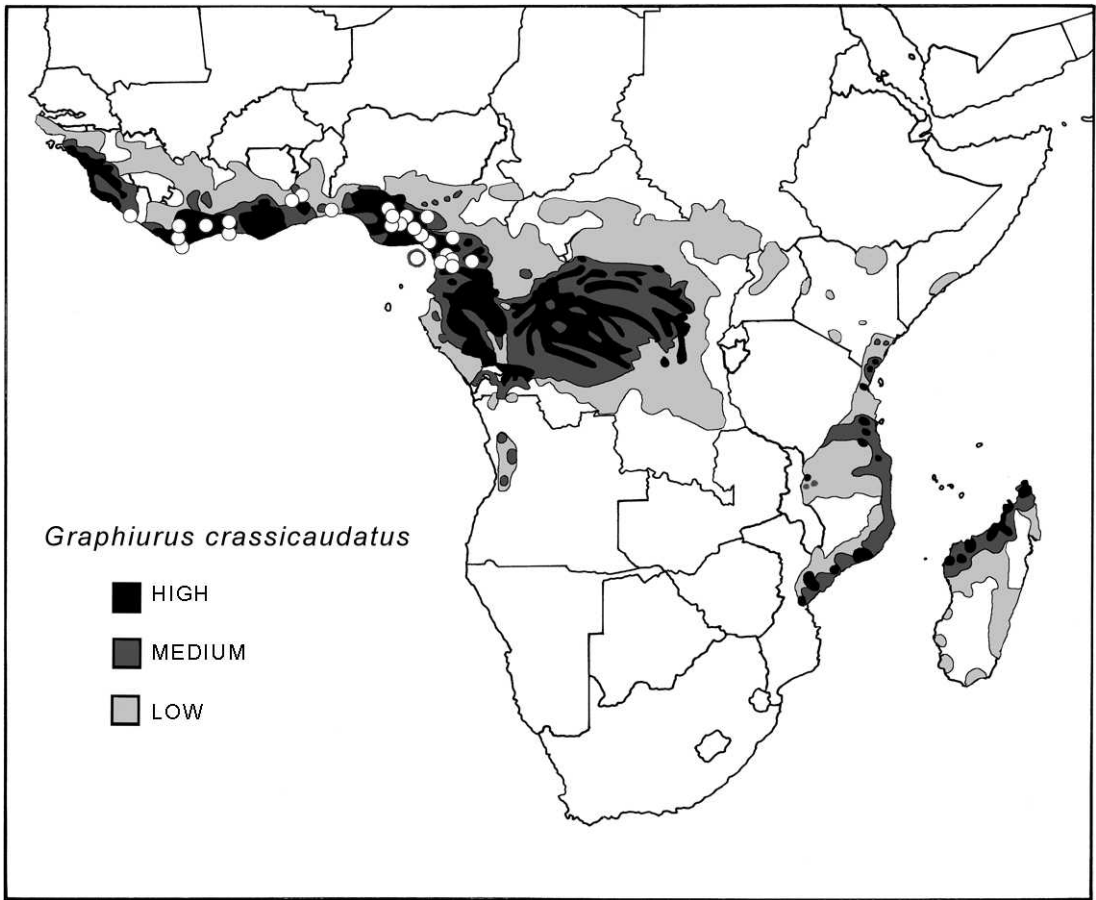
Fig. 14.   The predicted geographic distribution of *Graphiurus crassicaudatus* derived from ecological niche modeling. Darker shades signify the most hospitable regions for the species as predicted by the model. White circles identify actual collection localities (which are listed in the gazetteer, along with the specimens collected from each place).

there, but has not been captured due to low population density, trapping technique, fewer comprehensive faunal studies, and/or chance (if so, it would be sympatric with *G. walterverheyeni*); and (3) the new species, *G. walterverheyeni*, which we hypothesize to be closely relate to *G. crassicaudatus*, may occupy a similar ecological niche—its distribution falls within the more likely predicted range of *G. crassicaudatus* in the south-central region. Niche modeling unfortunately could not be performed to predict the distribution of *G. walterverheyeni* due to too few occurrence points (only two collecting localities).

We produced two models for the *G. lorraineus* complex: one incorporating only true *G. lorraineus* (see gazetteer; fig. 15), and the other including all samples of the *G. lorraineus* complex from Guinea and Sierra Leone to northern Zambia (see gazetteer; fig. 16). Figure 15 bolsters the idea that what we refer to here as true *G. lorraineus* is in fact a distinct species from the other samples included in the *G. lorraineus* complex. Based on actual collection localities and the ecological parameters shared by those localities, the known geographic distribution for true *G. lorraineus* is within the West Central, South Central, and East Central faunal regions (historical collection locality points are plotted in fig. 15). Interestingly, ecological niche modeling for true *G. lorraineus* predicts few areas (indicated by dark shading of pixels) of
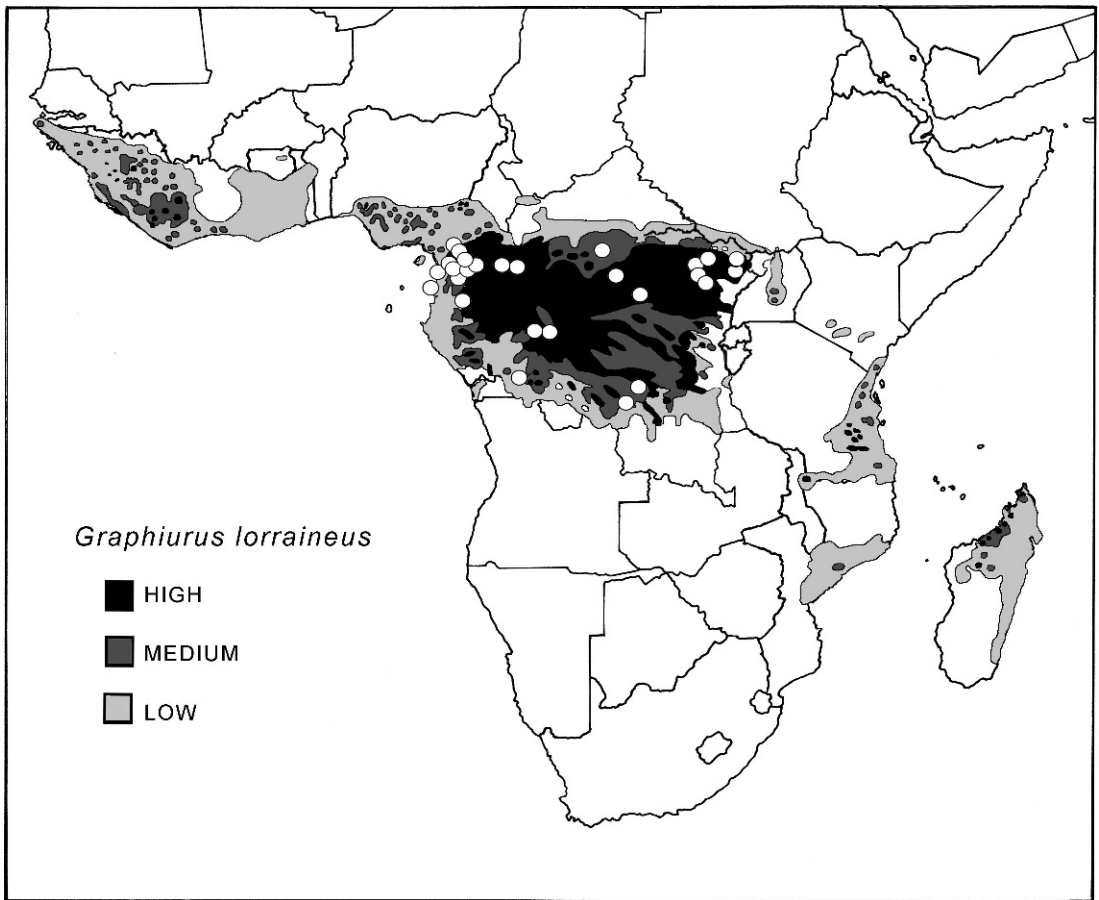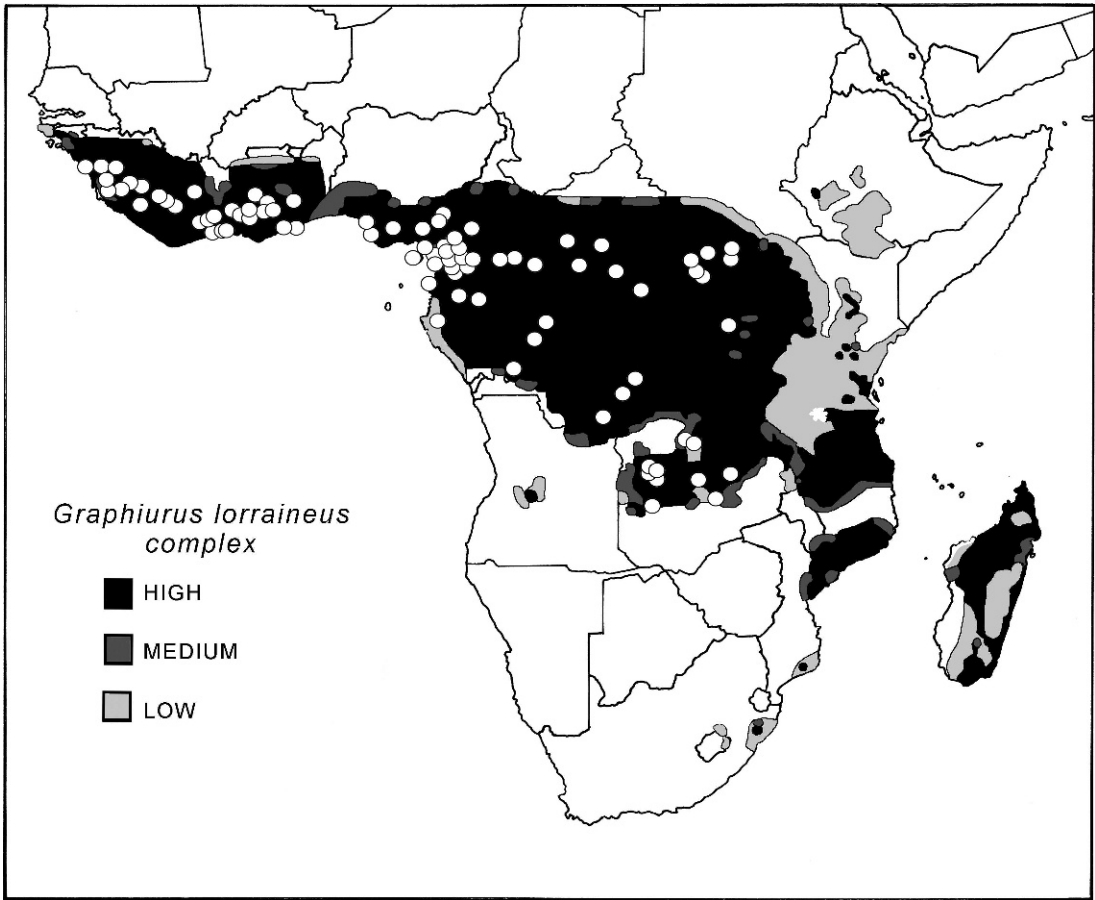
Fig. 15. The geographic distribution of true *Graphiurus lorraineus* (includes *haedulus* from southern Cameroon but excludes *spurrelli* from West Africa) as predicted from ecological niche modeling. Darker shades signify the most hospitable regions for the species as predicted by the model. White circles identify actual collection localities yielding specimens (places and specimens are listed in the gazetteer).

strong ecological suitability outside its known range, indicating that the suite of ecological requirements for that species is uniquely found in the three forest regions in which it has been documented to occur. There are areas within the known range where occurrence is most likely based on strong ecological suitability, especially in eastern Gabon, northern Congo, and northwestern D.R. Congo (fig. 15), and these areas should be considered when identifying possible study sites for this species.

When all specimens referred to the *G. lorraineus* complex (a complex that we believe contains several separate species) are included in the analysis, the distributional model predicts strong ecological suitability over large areas far outside the known geographic range of the complex (even much of Madagascar). If we are correct that several distinct species have been modeled together under the umbrella of the *G. lorraineus* complex, then it makes sense that the usefulness of the model breaks down. In this case, the dominant ecological requirement of the entire complex would be tropical rainforest or deciduous tropical forest, and would not aid in identifying important survey or conservation efforts, or in epidemiological studies. This illustrates some of the limitations of distributional modeling. For genera that have not been adequately systematically revised, where

Fig. 16.   The geographic distribution of the *Graphiurus lorraineus* complex (includes *haedulus* from southern Cameroon and *spurrelli* from West Africa) derived from ecological niche modeling. Darker shades signify the most hospitable regions for the species as predicted by the model. White circles identify actual collection localities, which are listed in the gazetteer, along with the specimens collected from each place.

several species are in fact grouped together in the same taxon, ecological niche modeling will probably not yield informative results. For those taxa that have been revised or at least sorted into more refined units, the application of ecological niche modeling provides potentially useful predictions of geographical distributions (providing enough historical collection localities exist), and overlain with other species' models, aids in prioritization of conservation sites.

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