

THE MAMMALS OF
PARACOU, FRENCH GUIANA:
A NEOTROPICAL LOWLAND
RAINFOREST FAUNA
PART 1. BATS

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 237, 219 pages, 77 figures, 80 tables, 2 appendices

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ABSTRACT

This report describes the results of bat inventory fieldwork at Paracou, a lowland rainforest locality in northern French Guiana. Working within a 3-km radius over the course of 168 sampling days from 1991 to 1994, we captured 3126 bats, of which about 78% were taken in ground-level mistnets, 10% in mistnets suspended above ground level, and 12% at roosts. We identified a total of 78 species, including 10 emballonurids, 2 noctilionids, 1 mormoopid, 49 phyllostomids, 1 furipterid, 1 thyropterid, 5 vespertilionids, and 9 molossids.

Among our taxonomic results, we describe a new species of *Micronycteris* (sensu stricto) to honor André Brosset, pioneering monographer of rainforest bat faunas in India, Africa, and South America. In addition, we report the first records of eight other species from French Guiana: *Centronycteris maximiliani*, *Peropteryx kappleri*, *Sacopteryx gymnura*, *Micronycteris homezi*, *Micronycteris schmidtorum*, *Molossops pararus*, *Molossus sinaloae*, and *Promops centralis*. Most of these were previously known from Surinam, but the range extensions are significant for *Sacopteryx gymnura* (ca. 900 km), *Micronycteris homezi* (2200 km), and *M. schmidtorum* (1500 km). Altogether, the known bat fauna of French Guiana now consists of 102 species.

The following significant taxonomic results are also reported herein. (1) Comparison of Paracou specimens referable to *Peropteryx macrotis* (Wagner) with the holotype of *P. trinitatis* Miller supports the conclusions of recent investigators that these taxa are separate species. (2) Morphological variation among specimens of small *Choeroniscus* from Paracou, together with examination of type material and a critical review of the literature, suggest that *C. minor* (Peters), *C. intermedius* (Allen and Chapman), and *C. inca* Thomas are conspecific; the oldest available name for the species is Peters'. (3) *Glyphonycteris* Thomas (including *Barticonycteris* Hill as a synonym), *Micronycteris* Gray (including *Xenotenes* Miller as a synonym), and *Trinycteris* Sanborn are rediagnosed as distinct genera; *Lampronnycteris* Sanborn and *Neonycteris* Sanborn, two other erstwhile subgenera of *Micronycteris* (sensu lato), should also be treated as full genera. (4) *Micronycteris homezi* Pirlot, based on a lost holotype and previously considered a nomen dubium, is redescribed and rediagnosed as a valid species. (5) *Micronycteris megalotis* (Gray) and *M. microtis* Miller are distinct species represented by sympatric collections from Paracou and other material similarly interpreted by recent investigators. (6) *Mimon bennettii* (Gray) and *M. cozumelae* Goldman are diag-

nosable as distinct species by consistent external and craniodontal character differences. (7) *Ectophylla* H. Allen is rediagnosed to include *Mesophylla* Thomas in recognition of the sister-group relationship between *E. alba* H. Allen and *E. macconnelli* (Thomas). (8) The recent hypothesis that *Sturnira lilium* (E. Geoffroy) and *S. luisi* Davis are conspecific is rejected as implausible because of trenchant cranial character differences. (9) The Venezuelan and French Guianan specimens recently identified in the literature as *Eptesicus andinus* J. A. Allen are not conspecific with the holotype of that species; instead, examination of type specimens, other comparative material, and the primary literature suggests that this material is referable to *E. chiriquinus* Thomas. (10) All currently accepted synonymies for taxa included within Davis's (1966) *andinus* group of *Eptesicus* are apparently incorrect; in our view, *E. andinus* is a senior synonym of *E. montosus* Thomas and *E. chiralensis* Anthony, whereas *E. chiriquinus* is a senior synonym of *E. inca* Thomas. (11) We review the contents of *Cynomops* Thomas, currently ranked as a subgenus of *Molossops* Peters, and tabulate diagnostic characters for the four species we regard as valid: *M. abrasus* (Temminck), *M. greenhalli* (Goodwin), *M. pararus* (Thomas), and *M. planirostris* (Peters). (12) *Molossus barnesi* Thomas is a valid species readily distinguishable from both *M. molossus* (Pallas) and *M. coibensis* J. A. Allen.

Analyses of our sampling results indicate that (1) distinct sets of species are effectively sampled by different capture methods; (2) distinct sets of species inhabit different local habitats; and (3) increased sampling effort with any method generally results in more species, although the rate of accumulation declines with sample size (number of captures). Based on nonparametric statistical extrapolations, we estimate that the Paracou bat fauna probably consists of somewhere between 85 and 95 species; the more conservative richness estimator suggests that our inventory is perhaps about 90% complete. Judging from the known or inferred behaviors of the rare taxa (singletons and doubletons) in our data, most of the local species missing from this inventory are probably aerial insectivores, gleaning insectivores, or nectarivores.

In terms of higher taxonomic composition, the bat fauna at Paracou is typical of those found throughout the humid Neotropical lowlands. A quantitative analysis of faunal similarity at the species level among 14 rainforest localities chosen as exemplars clusters the Paracou list with others previously reported from the Guiana sub-

region of Amazonia, next with lists from elsewhere in Amazonia, and lastly with Central American lists. Not surprisingly, pairwise similarity values show a positive correlation between faunal resemblance and geographic proximity within the Neotropical rainforest biome. Many (47%) of the bat species in the Paracou fauna are essentially pan-Neotropical in distribution and most of these are also known from habitats other than rainforest. The remaining species exhibit more restricted geographic distribution patterns, but true Amazonian endemics constitute only a minor fraction of the Paracou bat fauna.

Species richness comparisons among inventory sites are complicated by problems of inconsistent methodology, habitat representation, and sampling effort. For example, the apparently exceptional diversity of emballonurids, phyllostomines, and molossids in the Paracou fauna is plausibly explained by our intensive use of elevated netting and roost surveys, and by prolonged effort, all of which factors act to reduce the well-known capture bias of ground-level mistnets (which consistently undersample these taxa in the short term). However, the low richness of carollines and steno-dermatines at Paracou by comparison with most other Amazonian (especially western Amazonian) localities is apparently real. The only approximately valid statistical comparison of species richness that we can make between sites based on published capture-frequency data suggests an increase of approximately 50% in understory bats

from eastern Central America to Amazonia, but the real or artifactual nature of this estimated difference remains to be evaluated.

A trophic classification of Paracou bats indicates that aerial insectivores are the most speciose feeding guild in the local fauna, followed by gleaning animalivores, frugivores, and nectarivores; omnivores, sanguivores, and piscivores are minor components. Patterns of differential habitat use among species within some feeding guilds can be inferred from our capture-frequency data, notably for aerial insectivores and frugivores. By contrast, gleaning animalivores appear to be largely restricted to primary forest, a puzzling phenomenon previously reported from other Neotropical rainforest localities.

To facilitate future inventory fieldwork we provide (1) detailed descriptions of survey and capture methods, (2) illustrations of most local habitats recognized as distinct, (3) complete breakdowns of capture frequencies by method and habitat for each species, (4) photographs of numerous roosts at which bats were captured, and (5) descriptions and/or illustrations of useful characters for identifying species hitherto frequently confused in the field. Finally, we make recommendations for improving bat inventory efficiency, suggest minimal standards for reporting inventory data, urge the adoption of quantitative methods for intersite diversity comparisons, and comment on the prospects for rapid diversity assessment of rainforest bat faunas.

RÉSUMÉ

Dans ce rapport nous décrivons les résultats de l'inventaire du peuplement de chauves-souris effectué sur le terrain à Paracou, un site de forêt hygrophile de basse altitude en Guyane française. Dans un rayon de 3 km étudié pendant 168 jours d'échantillonnage de terrain de 1991 à 1994, nous avons capturé 3126 chauves-souris, soit 78% dans des filets près du sol, 10% dans des filets élevés suspendus au-dessus du sol, et 12% à des dortoirs. Nous avons identifié 78 espèces au total, dont 10 emballonuridés, 2 noctilionidés, 1 mormoopidé, 49 phyllostomidés, 1 furipteridé, 1 thyropteridé, 5 vespertilionidés et 9 molossidés.

Parmi nos résultats taxonomiques nous décrivons une espèce nouvelle de *Micronycteris* (sensu stricto) en l'honneur d'André Brosset, auteur de monographies innovatrices sur les faunes de chauves-souris des forêts hygrophiles de l'Inde, de l'Afrique et de l'Amérique du Sud. De plus, nous présentons les premières données concernant la présence de huit autres espèces en Guyane française: *Centronycteris maximiliani*, *Peropteryx*

kappleri, *Saccopteryx gymnura*, *Micronycteris homezi*, *Micronycteris schmidtorum*, *Molossops paranus*, *Molossus sinaloae* et *Promops centralis*. La plupart de ces espèces étaient déjà connues du Suriname, mais les extensions des aires de répartition sont substantielles pour *Saccopteryx gymnura* (près de 900 km), *Micronycteris homezi* (2200 km) et *M. schmidtorum* (1500 km).

Dans ce travail, nous rapportons également les importants résultats taxonomiques suivants. (1) La comparaison d'exemplaires de Paracou se rapportant à *Peropteryx macrotis* (Wagner) avec l'holotype de *P. trinitatis* Miller, confirme la conclusion d'auteurs récents, que ces taxons appartiennent à des espèces différentes. (2) La variabilité morphologique décelable parmi les exemplaires de petits *Choeroniscus* de Paracou, conjointement avec l'étude des types et avec une révision critique de la littérature, suggèrent que *C. minor* (Peters), *C. intermedius* (Allen et Chapman) et *C. inca* Thomas sont conspécifiques; le plus ancien nom disponible pour l'espèce est celui

de Peters. (3) De nouvelles diagnoses sont données pour *Glyphoncteris* Thomas (qui inclut *Barticoncteris* Hill comme synonyme), et pour *Trinycteris* Sanborn; *Lamproncteris* Sanborn et *Neonycteris* Sanborn, deux anciens sous-genres de *Micronycteris* (sensu lato) devraient également être considérés comme des genres. (4) *Micronycteris homezi* Pirlot, fondé sur un holotype perdu et considéré précédemment comme un nomen nudum, est redécrit et diagnostiqué à nouveau comme une espèce valable. (5) *Micronycteris megalotis* (Gray) et *M. microtis* Miller sont des espèces distinctes représentées par des exemplaires récoltés en sympatrie à Paracou et par d'autre matériel, ce qui est interprété de façon similaire par des chercheurs récents. (6) *Mimon bennettii* (Gray) et *M. cozumelae* Goldman peuvent être diagnostiquées comme deux espèces distinctes grâce à des différences de caractères externes et craniodentaires. (7) Le genre *Ectophylla* H. Allen est diagnostiqué à nouveau pour y inclure *Mesophylla* Thomas, ce qui reconnaît ainsi les rapports d'espèces-soeurs entre *E. alba* H. Allen et *E. macconnelli* (Thomas), cette dernière appelée auparavant *Mesophylla*. (8) L'hypothèse, récemment émise, que *Sturnira lilium* (E. Geoffroy) et *S. luisi* Davis sont conspécifiques est rejetée comme étant peu plausible à cause de différences marquées des caractères craniaux. (9) Les exemplaires du Vénézuéla et de Guyane française récemment déterminés dans la littérature comme appartenant à *Eptesicus andinus* J. A. Allen ne sont pas conspécifiques avec l'holotype de cette espèce; en revanche, l'étude des exemplaires types, de matériel comparatif additionnel, et de la littérature originale, suggèrent que ce matériel peut être rapporté à *E. chiriquinus* Thomas. (10) Toutes les synonymies acceptées à l'heure actuelle pour les taxons inclus au sein du groupe d'*Eptesicus* appelé groupe *andinus* par Davis (1966) semblent être incorrectes; d'après nous, *E. andinus* est un synonyme plus ancien d'*E. montosus* Thomas et de *E. chiralensis* Anthony, tandis que *E. chiriquinus* est un synonyme plus ancien d'*E. inca* Thomas. (11) Nous révisons la teneur de *Cynomops* Thomas, actuellement classé comme un sous-genre de *Molossops* Peters, et présentons sous forme tabulaire les caractères diagnostiques des quatre espèces que nous considérons comme valables: *M. abrasus* (Temminck), *M. greenhalli* (Goodwin), *M. paranus* (Thomas), et *M. planirostris* (Peters). (12) *Molossus barnesi* (Thomas) est une espèce valable, aisément différenciable à la fois de *M. molossus* (Pallas) et de *M. coibensis* J. A. Allen.

L'analyse de notre échantillonnage indique que: (1) des assemblages d'espèces distincts sont effectivement échantillonnés par différentes méthodes de capture; (2) des assemblages d'espèces dis-

tinctes occupent des biotopes différents au sein de notre zone d'étude; et (3) un effort accru d'échantillonnage, quelle que soit la méthode, produit en général davantage d'espèces, bien que le taux d'accumulation baisse avec une augmentation de la taille de l'échantillon (nombre de captures). Sur la base d'extrapolations statistiques non-paramétriques, nous estimons que le peuplement de chauves-souris de Paracou contient entre 85 et 95 espèces; l'estimation conservatrice de cette richesse suggère que notre inventaire est peut-être à 90% complet. Si nous nous basons sur les comportements, connus ou inférés, des taxons rares (représentés dans notre échantillonnage par des exemplaires uniques ou des doublets), la plupart des espèces qui manquent encore à cet inventaire sont probablement des insectivores aériens, des insectivores glaneurs ou des nectarivores.

En ce qui concerne sa composition taxonomique supragénérique, la faune de chauves-souris de Paracou est typique de celles que l'on trouve dans l'ensemble des régions humides néotropicales de basse altitude. Une analyse quantitative de la ressemblance faunistique au niveau spécifique parmi 14 sites choisis comme exemples de forêt hygrophile, place la liste de Paracou, d'abord parmi d'autres mentionnées auparavant de la subrégion guyanaise de l'Amazonie, ensuite parmi des listes provenant d'autres régions de l'Amazonie, et enfin parmi des sites d'Amérique centrale. Les valeurs des indices de similarité, comparées deux à deux, montrent une corrélation positive entre la ressemblance faunistique et la proximité géographique des sites au sein du biome forêt hygrophile néotropical. De nombreuses espèces de chauves-souris du peuplement de Paracou (47% du total) ont une répartition essentiellement pan-néotropical, et la plupart d'entre elles sont connues d'habitats autres que la forêt hygrophile. Les autres espèces montrent des schémas de distribution géographiquement plus restreints, mais les vrais endémiques amazoniens ne constituent qu'une fraction mineure du peuplement de chauves-souris de Paracou.

Les comparaisons de richesse spécifique parmi les sites inventoriés précédemment sont rendues compliquées par des problèmes de méthodologie inégale, de représentation d'habitats et d'effort d'échantillonnage. Par exemple, l'explication de la diversité, à première vue exceptionnelle, des emballonuridés, phyllostomins et molossidés dans la faune de Paracou, est rendue plausible par notre emploi intensif de filets élevés et par notre étude de dortoirs, ainsi que par un effort prolongé, méthodes d'échantillonnage qui toutes réduisent la tendance bien connue de surcapturer lorsque les filets sont posés près du sol, ce qui donne, dans

le court terme, un sous-échantillonnage de ces taxons. Toutefois, la faible richesse des carollinés et des sternoderminés à Paracou, comparée à celle de la plupart des autres localités amazoniennes (spécialement d'Amazonie occidentale), ne paraît pas artefactuelle. La seule comparaison statistique à peu près valable que nous pouvons faire de richesse spécifique entre sites, basée sur des données de fréquences de captures dans la littérature, suggère que la proportion de chauves-souris du sous-bois augmente d'environ 50% entre l'Amérique centrale orientale et l'Amazonie, mais la nature réelle ou artificielle de cette différence estimée reste à être évaluée.

Une classification trophique des chauves-souris de Paracou indique que les insectivores aériens sont la guilda du peuplement local contenant le plus d'espèces, suivie par les animalivores glaneurs, les frugivores et les nectarivores; les omnivores, sanguivores et piscivores ne représentent que des fractions mineures. Les patrons d'utilisation différentielle des habitats au sein de certaines guildes alimentaires peuvent être déduits à partir de nos données de fréquences de captures, notamment pour les insectivores aériens et les frugivores. Par contre, les animalivores glaneurs

semblent être largement limités à la forêt primaire, un phénomène déconcertant, déjà mentionné auparavant pour d'autres localités de la forêt hygrophile néotropicale.

Dans le but de faciliter de futurs inventaires de terrain: (1) nous donnons des descriptions détaillées de nos méthodes d'étude et de capture, (2) nous illustrons la plupart des habitats locaux reconnus comme distincts, (3) nous indiquons, pour chaque espèce, la répartition complète des fréquences de capture par méthode et par habitat, (4) nous présentons des photographies des nombreux dortoirs où nous avons capturé des chauves-souris, et (5) nous décrivons et/ou illustrons des caractères utiles pour la détermination d'espèces qui ont été fréquemment confondues jusqu'à présent sur le terrain. Finalement, nous faisons des recommandations visant à améliorer l'efficacité des inventaires de chauves-souris, nous suggérons des niveaux minimaux pour les rapports de données d'inventaires, nous conseillons vivement l'adoption de méthodes quantitatives pour des comparaisons de diversité inter-sites, et nous faisons des remarques au sujet de l'évaluation rapide de la diversité des faunes de chauves-souris en forêt hygrophile.

INTRODUCTION

The most species-rich mammalian faunas in the world are probably those that inhabit the lowland rainforests of certain parts of Central and South America, but compelling evidence to support this conjecture is sparse. Much of what we know about Neotropical rainforest mammal diversity comes from just a handful of sites where large species lists were built up over many years as byproducts of field research on behavior, community ecology, demography, and other natural history topics (e.g., Anthony, 1921; Enders, 1935; Glanz, 1982; Janson and Emmons, 1990; Handley et al., 1991; Timm, 1994; Hutterer et al., 1995). Such haphazardly collected data are difficult to analyze for completeness, and estimating species richness at most sites is therefore a matter of more-or-less educated guesswork (Voss and Emmons, 1996).

For both research and conservation purposes it would be useful to know how much time and effort and what combination of inventory methods are necessary to obtain reasonably complete species lists of mammals

at rainforested Neotropical localities. Unfortunately, the current literature does not provide an adequate basis for making such estimates. Among other problems, few inventory reports have included sufficient methodological information to know exactly what was done, the local habitats actually sampled for mammals are seldom identified explicitly, relevant measures of sampling effort are rarely provided, and the frequency data necessary to judge inventory completeness are almost never published.

Species identifications are another major impediment to interpreting inventory results. Most genera of Neotropical rainforest mammals have never been revised, or were revised long ago from sparse and geographically scattered material. Much of the secondary literature commonly consulted for specimen identification (e.g., keys, checklists, and field guides) therefore reflects taxonomic conventions that have not been tested by recent analyses of character data. For many genera, reliable identifications can only be obtained by consulting the primary literature

and by directly comparing voucher specimens with types. Unfortunately, published species lists from rainforest mammal inventory projects are seldom accompanied by sufficient documentation to judge the reliability of the identifications they contain.

To provide a baseline for more effective research on Neotropical rainforest mammal diversity, we looked for a study site where we could return year after year to obtain results from sustained sampling effort using the full range of methods required for taxonomically comprehensive surveys (Voss and Emmons, 1996). We were attracted to French Guiana because of its unique combination of extensive primary rainforest in close proximity to modern transportation and communication networks. At Paracou—a research area with primitive but adequate living quarters in the midst of a large tract of forest only a few kilometers by excellent roads from post offices, telephones, fax machines, markets, and hospitals—we found an ideal location for our project.

This is the first of two monographs based on our fieldwork at Paracou, which began in 1991 and continued to 1994. Herein we describe the research area, explain the methods used to sample the bat fauna, and report our bat-sampling results. We document all taxonomic identifications by reviewing the relevant literature, by providing tables of external and craniodental measurements of voucher specimens, and by detailed comparisons with types and other relevant material in cases where we encountered significant problems. We summarize field observations for each species by capture method and habitat, and we remark noteworthy ecological differences between congeners or other closely related taxa. We analyze our sampling results to assess methodological bias, habitat differences, temporal variation, and completeness. We select 13 other Neotropical rainforest bat inventories as comparative exemplars, and we discuss these together with the Paracou fauna in terms of taxonomic composition, biogeography, species richness, and trophic structure. Finally, we offer suggestions for future work based on the outcome of our field and museum research with Paracou bats.

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Special thanks are due to P. Petronelli, a gifted amateur naturalist and long-time resident at Paracou, who generously shared his special knowledge of the forest besides repairing almost everything that broke or malfunctioned around camp. Without his help it would have taken us much longer to learn the trail system, identify plants, find bat roosts, and generally use our time efficiently in the field. Whatever measure of success we achieved at Paracou is in large part owed to him.

For their assistance with bat inventory fieldwork we thank Darrin Lunde, who was always there to help from 1991 to 1993; to Suzanne Smith, who competently bore the brunt of the mistnetting effort in 1993; to Roland Kays, who climbed trees and assisted in many other ways in 1993; to Andrea Peffley, who did almost everything almost every day in 1994; and to Nancy Voss, whose stalwart assistance helped make our last field season the most productive ever. Amy Berkov and Louise Emmons also helped us net bats in 1993 and 1994, respectively.

Back at the museum we were grateful for the assistance of Eleanor Sterling who first set up the Paracou database, to Darrin Lunde and Burton Barnett who completed and proofed it, and to Tenley Conway who patiently made numerous revisions and printouts as our species identifications were refined. Darrin Lunde, Eleanor Sterling, and Andrea Peffley cataloged specimens, pulled skulls, and curated the collections. Pat Brunnauer resourcefully tracked down dozens of references in the AMNH library, and Don Clyde always found the rest somewhere else. Peter Goldberg skillfully print-

ed all of the photographs we took in the field, and Pat Wynne did all of the splendid artwork.

For the loan of specimens or for their hospitality while we visited their respective institutions (abbreviated as below), we thank P. D. Jenkins (BMNH); D. A. Schlitter and S. B. McLaren (CM); L. R. Heaney and B. D. Patterson (FMNH); L. Granjon and M. Tranter (MNH); V. Pacheco (MUSM); M. D. Engstrom (ROM); and M. D. Carleton, L. K. Gordon, and C. O. Handley, Jr. (USNM).

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We dedicate this report to our late friend and colleague, Karl F. Koopman, whose patience, help, and encouragement were essential at many points in our museum research. The systematic accounts would not have been the same without him, and we are saddened that he did not live to see them completed.

SITE DESCRIPTION

TOPOGRAPHY, SOILS, AND VEGETATION

The collections and observations reported below were obtained within the Domaine Experimental Paracou (hereafter, Paracou), a large tract of land administered as a research concession by the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD). From a field camp at 5°16'31"N, 52°55'25"W (approximately 12 km SSE of Sinnamary and 33 km WNW of Kourou; figs. 1, 2), we worked in a roughly circular area with a radius of about 3 km.¹ The local terrain consists of low, densely forested hills drained by the headwaters of four streams: Crique Mogestern and Crique Verlot (both tributaries of the lower Sinnamary River), and Crique Parakou and Crique Malmanoury (which flow separately into the Atlantic Ocean). The minimum elevation above sea level within our study area is about 4 m, the maximum about 45 m (IGN, 1991).

¹ We estimated the coordinates of our camp as the mean of four readings obtained in 1994 with a Panasonic KX-G5500 GPS receiver using the WGS84 (standard) map datum. A few bats collected under old highway bridges crossing Crique Renner (ca. 7.2 km to the NE) and Crique Paracou (ca. 7.1 km N) are reported among our voucher material, but all of these belong to species found within our 3-km sampling radius.

Local soils are the result of in situ weathering from quartzites and schists of the Bonidoro series (Bariteau, 1993; Durrieu de Madron, 1993). Over most of our study area, the substrate is an acidic brownish or reddish sandy clay (mixed with ironstone concretions on some ridgetops and hillsides), but a few patches of almost pure white sand also occur (Barthes, 1991). Although heavily weathered quartzite boulders are occasionally exposed in streams, there are no large rocky outcrops or caves in the region. Local watercourses are all small (mostly 5 m or less in width), shallow (usually 1 m or less in depth), and heavily shaded, with transparent, tea-colored ("black") water flowing slowly over predominantly sandy beds.

Most of this landscape is covered with primary rainforest² (fig. 3), but the new asphalt highway from Kourou to Sinnamary cuts

² No macroscopic soil charcoal was observed when D. P. Lunde and R. W. Kays dug 55 pits, each about 40 cm deep and 30 cm in diameter, to install pitfall traps in 1993 (Voss et al., in prep.). We likewise saw no charcoal in the spoil from numerous soil sample cores made in a 25-ha plot (Parcel 16) by a forestry research class in 1994. Soil charcoal has been interpreted as evidence of prehistoric agriculture at other Neotropical rainforest localities (e.g., by Lovejoy and Bierregaard, 1990; McDade and Hartshorn, 1994), and its absence suggests that the mature forest at Paracou has not been cleared for centuries.

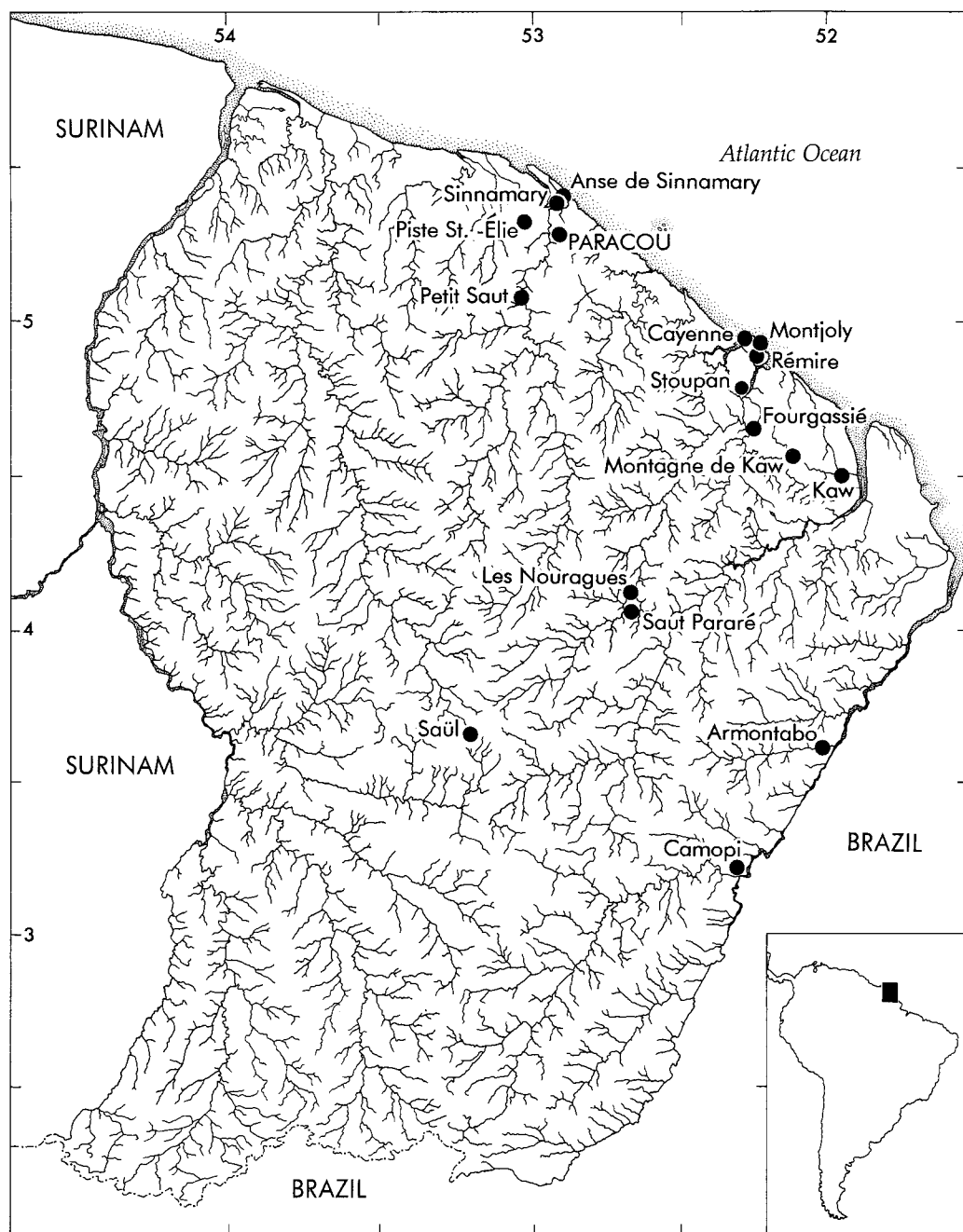


Fig. 1. Map of French Guiana showing the location of our study site at Paracou in relation to other localities mentioned in the text. One degree of latitude or longitude is approximately equal to 110 km.



Fig. 2. Our camp at Paracou with primary forest in the background. Ground-level mistnets that we erected in this small clearing on 20 nights from 1991 to 1994 caught 21 species of bats, of which the most frequently captured were *Carollia perspicillata*, *Sturnira lilium*, *Glossophaga soricina*, *Sturnira tildae*, and *Artibeus cinereus*. All of these species are locally common in manmade clearings because they feed on the fruits of early-successional plants that grow in dense thickets at the forest edge. However, small clearings are also visited by rarer bats, among them *Saccopteryx gymnura* and *Vampyrus spectrum*, both of which were netted here.

across our study area, as do several narrow dirt roads that provide access from the highway to a small village of forestry workers and to numerous small experimental plantations (e.g., of cacao, bananas, coconuts, oil palms). Altogether, roads, plantations, clearings around the worker village, a few small patches of savanna, and tracts of closed-canopy secondary growth (from selective logging several decades ago) probably amount to less than 20% of the area within our sampling radius. Just beyond our study area to the north and east is a flat littoral zone of savannas and mangrove swamps, but in all directions from the WSW to the ESE primary rainforest extends without significant interruption for hundreds of kilometers.

The natural vegetation at Paracou resem-

bles that described at topographically similar sites in Surinam and French Guiana by many authors, whose accounts should be consulted for detailed descriptions of forest physiognomy and floristics (e.g., Lindeman and Moolenaar, 1959; Mori and Boom, 1987; de Granville, 1993). Two major subtypes of rainforest occupy almost all of the undisturbed land in our study area. *Well-drained forest* ("high dryland forest" of Lindeman and Moolenaar, 1959; "forêt sur sols drainés" of de Granville, 1993) has a high canopy (ca. 30–40 m, with occasional canopy emergents >45 m) and an open understory; as its name implies, this formation occurs on ridgetops, hillsides, and other sites where standing water does not accumulate, even after heavy rains. *Swampy forest* (the *Sym-*



Fig. 3. Primary rainforest at Paracou. Very large trees like this canopy emergent are generally restricted to well-drained sites. Folds and cavities in these buttresses sheltered several species of bats: a vertical chimney formed by two fused buttresses (not visible in this view) was occupied by a roosting group of *Saccopteryx bilineata*, and a rotted chamber at the base of another buttress (detail shown in fig. 33) was occupied by roosting groups of *Micronycteris microtis* and *Carollia perspicillata*.

phonia-Virola “swamp forest” association of Lindeman and Moolenaar, 1959; “forêt marécageuse” of de Granville, 1993) has a lower canopy (ca. 15–25 m) and generally denser undergrowth; this formation occurs in low-lying valley bottoms where soils are seasonally or permanently waterlogged. In addition, we use the term “creekside forest” for riparian vegetation that seemed to us intermediate in character between well-drained and swampy formations.

Some conspicuous physiognomic differences between well-drained and swampy forest are relevant for recognizing mammalian habitats at Paracou. Palms are common in the undergrowth and subcanopy of well-drained forest, but they are usually more abundant in swampy forest where some species, especially *Euterpe oleracea* at very wet sites, are

canopy emergents.³ Whereas the undergrowth of well-drained forest consists predominantly of young trees (fig. 4), large herbaceous monocots (especially Araceae, Marantaceae, and Rapateaceae) are often conspicuous in the undergrowth of swampy forest. *Phenakospermum guyannense* (Strelitziaceae), the giant leaves of which provide important daytime refugia for some foliage-roosting bats, occurs in wet openings in swampy forest, in secondary growth, and along savanna margins, but not in well-drained primary forest. Lianas often attain great size in well-drained forest, but seldom

³ The large and distinctive swamp palm *Mauritia flexuosa*, common in nearby savannas and along the Sinnamary River, was not observed within the limits of our study area.



Fig. 4. Typical ground-level view of well-drained primary forest at Paracou. The understory vegetation of mature forest on hillsides, ridgetops, and other well-drained sites is always dominated by woody plants, mostly seedlings and saplings of dicotyledonous trees.

form the extensive tangles in the subcanopy and understory that are characteristic of some swampy forest sites (fig. 5).

According to Bariteau (1993), primary rainforest at Paracou has an average density of 607 trees (≥ 10 cm in diameter) per hectare (ha) and an average total basal area of 31 m²/ha, both of which measurements fall well within the range of values obtained at other Amazonian rainforest localities (Mori and Boom, 1987: table II-III). Although no local floristic inventory has yet been carried out, the forest at Paracou is probably similar in overall composition to that at Piste St.-Élie (only ca. 14 km to the WNW) where the five dominant families of trees (in decreasing order of importance) are Lecythidaceae, Caesalpiniaceae, Chrysobalanaceae, Annonaceae, and Sapotaceae (Sabatier, 1993).

To a zoologist with prior experience in Central America and western Amazonia, the Paracou rainforest appears unusual in several respects. Epiphytic orchids and bromeliads

are uncommon in the understory and occur sparsely even in the canopy; instead, the most conspicuous vascular epiphytes are aroids, a floristic peculiarity shared by physiognomically similar forests near Saül (ca. 180 km to the SSW) and attributed by Mori and Boom (1987) to a short but severe dry season (see below). We saw no bamboo, and the few tree ferns we encountered were restricted to wet valley bottoms. Likewise, gingers (Zingiberaceae) and heliconias (Heliconiaceae) seem to be rare at Paracou by comparison with the numbers of these plants commonly seen in some Central American and western Amazonian forests. In fact, the relative scarcity of flowering and fruiting plants in the primary forest understory is conspicuous, a phenomenon that Gentry and Emmons (1987) associate with a strong dry season and/or very poor soils. By contrast, the early-successional vegetation bordering roadways and other manmade clearings at Paracou includes many plants that bear abun-



Fig. 5. Tangled lianas in the understory of swampy forest, characteristic of many sites with waterlogged soil at Paracou. Such tangles may indicate the location of old treefalls, with the living stems of the climbers remaining after the tree itself has rotted away; their frequency in swampy forest suggests a high rate of treefalls in this habitat, an inference consistent with the generally lower and irregular canopy here.

dant fruit near ground level, notably species of *Piper* (Piperaceae), *Solanum* (Solanaceae), and *Vismia* (Clusiaceae).

CLIMATE AND PHENOLOGY

The local climate is uniformly hot with only trivial seasonal variation in temperature. According to Snow's (1976) meteorological synopsis of French Guiana, the mean annual temperature 15 km inland from the coast (the approximate location of Paracou) is 25.5°C, and the average temperature difference between the hottest and coldest months is less than 2°. As elsewhere in the tropics, the diurnal temperature range is greater than the seasonal range. Two shaded thermometers that we installed 1.3 m above the ground in primary forest near our camp from 17 July to 28 August 1991 recorded a 24-hour average maximum temperature of 27.3°C and an average minimum of 22.5°C.

Weather records from 1979–1985 document an average annual rainfall of 3159 mm at Paracou, and slightly more extensive data (from 1978–1986) document a similar annual average (3209 mm) at nearby Piste St.-Élie; both of these inland sites are substantially wetter than adjacent localities in the coastal savanna zone (see Bariteau, 1993: table 2). The seasonal distribution of rainfall (fig. 6) is likewise similar at Paracou and at Piste St.-Élie. Whereas heavy rains that usually begin in mid-December and extend through early July account for over three-quarters of the total annual precipitation, rainfall in the two driest months (September and October) accounts for less than 5%.

Forest-wide patterns of flowering, fruiting, and leaf-fall are conspicuously correlated with the seasonal distribution of local rainfall. Most tree species, and most individual trees, flower in the dry season and bear ripe fruit in

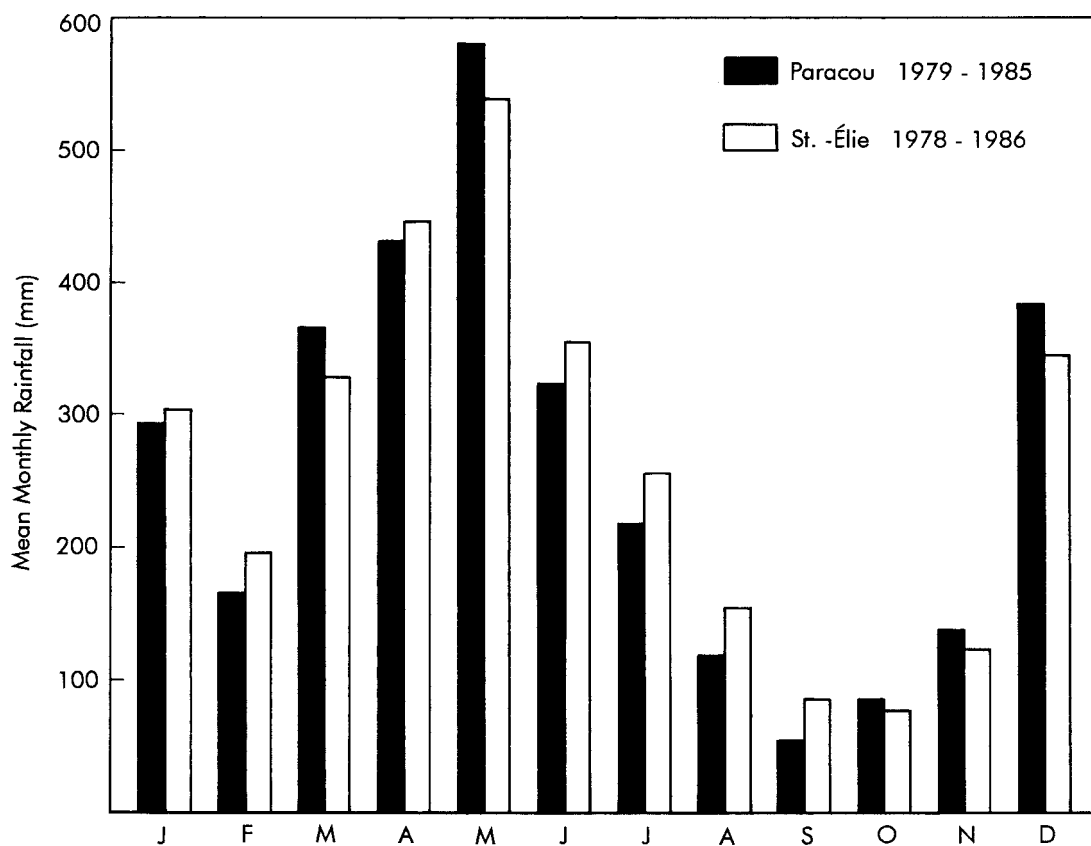


Fig. 6. Seasonal distribution of rainfall at Paracou and nearby Piste St.-Élie (from weather records tabulated by Bariteau, 1993).

the rainy season (Sabatier, 1985; Henry, 1994). Forest phenology at Paracou is not subtle. Mast and ripe fruit are abundantly scattered over the forest floor in the rainy season, but in the middle to late dry season only unripe fruits (partially chewed and discarded by canopy-foraging animals: kinkajous, monkeys, and parrots) and decomposing seeds are usually seen on the ground. The forest floor in the dry season is instead thickly littered with dead leaves and wilted flowers, and the

soft pattering of falling flower parts can be heard throughout the forest on still, dry nights. Many streams in our study area are dry by late October or early November, and after long periods without rain much of the understory vegetation has a distinctly wilted appearance. Despite the strongly seasonal pattern of leaf-fall, however, only a few trees are without foliage at any time, and the canopy as a whole is always green and densely leafy.

BAT INVENTORY METHODS

Because the purpose of our fieldwork at Paracou was to exhaustively inventory the local fauna, we used a variety of equipment, methods, and strategies to maximize the number of species found. It was not our in-

tention to standardize capture methods for comparisons of results across years or seasons, or to imitate the methods used by previous researchers for geographic comparisons of relative or absolute abundances.

Therefore, we freely changed our equipment and modified our procedures from season to season (sometimes from day to day) as suggested by our own accumulating results, prompted by recommendations from our colleagues, or demanded by changing climatic and phenological circumstances in the field.

MISTNETTING

At the beginning of our survey (in 1991) we used standard-weight 70-denier (70 d) mist nets to catch bats. We later (1992) switched to light-weight 30- and 50-denier (30 d and 50 d) nets and used them almost exclusively thereafter. The nets we used at Paracou were 2.6 m high and came in 6-, 13-, and 18-m lengths; the size of the nylon mesh was 36 mm.

GROUND-LEVEL NETTING: To catch bats at ground level, 0–3 m by our convention, we mounted nets on poles (usually made from saplings cut and trimmed in situ) thrust into the soil and braced by guys of braided nylon cord (fig. 7). To minimize disturbance of the understory vegetation that might alarm bats patrolling familiar territory, we usually tried to set nets along preexisting trails. Even so, some clearing was usually necessary to avoid entangling nets in trailside vegetation, and to leave enough space for people to work on each side. Lightweight (30 d) nets are so fragile and hard to clean of entangled litter that it is generally also necessary to sweep the ground clean of leaves and twigs under each net.

As a general rule, nets must be moved every night because bats quickly learn to avoid them. Netting effectively on a nightly schedule therefore required at least two persons: one to stay in camp and process the last night's catch, and the other to survey the forest for new net locations, clear new net lanes, and set up for the next night's work. We chose net locations to sample as many forest microhabitats as possible: well-drained sites, palm swamps, streambeds, unusual plant associations, etc.

We often opened nets shortly before dusk (when it was still light enough to read easily) because some bats emerge from their roosts in the late afternoon. Once the nets were opened we stayed with them constantly be-

cause large bats chew holes in nets unless they are promptly removed, and because small bats often escape from nets unless they are immediately seized. We regularly kept nets open from dusk to dawn in 1991 and 1992, but netting after 22:00 hours was seldom productive, so we usually closed our nets before midnight in subsequent years.

In addition to passively waiting for bats to fly into our nets, we used the Audubon Bird Call (fig. 8) to attract them. This simple device produces high-pitched (but not ultrasonic) squeaks resembling (among other things) the distress calls of stenodermatines, which sometimes flock to the sound in large numbers (Handley et al., 1991). Of greater interest for inventory work, some phyllostomines that are otherwise hard to capture (e.g., *Chrotopterus auritus*, *Glyphoncteris daviesi*, *Tonatia schulzi*, *Vampyrum spectrum*) are likewise attracted, perhaps because they are interested in distressed bats, singing orthopterans (Tuttle et al., 1985), or other small animals with high-pitched vocalizations as prey. We first used Audubon Bird Calls sparingly in 1992, but in later years we frequently used them when bored by the absence of bat activity around our nets.

Bats were removed from nets as soon as possible after capture and placed in cloth bags closed by drawstrings. When too many bats were captured to place each in its own bag, we often put two or more conspecifics together, but we never knowingly mixed species in bags. In general, we bagged all captured bats whether or not they were required as specimens in order to prevent recaptures on the same night; after the nets were closed, unwanted bats were checked for correct identification and sex, and then released. Bags containing captured bats were always suspended from cords tied horizontally between nearby trees to keep them away from prowling opossums.

ELEVATED NETTING: To catch bats in the subcanopy (fig. 9) and in the canopy itself (fig. 10), we mounted our nets on slender poles, the sawn-off top and bottom ends of which were wrapped with duct tape (to prevent splitting) and fitted with small eyebolts. Swivel-snaps were used to attach the poles to a length of $\frac{1}{8}$ -inch (ca. 3 mm) braided nylon line that formed a continuous running



Fig. 7. Ground-level mistnets (furlled in this daytime photograph) in swampy primary forest; portions of three nets (arrows) supported by guyed poles are shown. We caught 30 species of bats in 11 nights of ground-level netting at this site from 1991 to 1994, including our only examples of *Glyphonyscteris daviesi*. The most commonly captured species here were *Carollia perspicillata*, *Artibeus jamaicensis*, *A. obscurus*, *Phyllostomus elongatus*, *Rhinophylla pumilio*, *Tonatia saurophila*, and *Trachops cirrhosus*.



Fig. 8. The Audubon Bird Call (available from R. W. Eddy, Box 0172, Newington CT 06131) consists of a pewter key in a hollow wooden cylinder; twisting the key produces high-pitched squeaks that can be used to attract bats to nets. Handley et al. (1991: fig. 12-1) provided a spectrographic analysis of the sounds produced by this useful device, all of which are in the audible range.

loop by means of which the net could be raised or lowered (flagpole fashion) at each end. The running loops were threaded through overhead supports (eyebolts or brass rings), the positions of which determined the height to which nets could be raised.

When trees on either side of a suitable canopy gap or flyway were close together (without enough room between their crowns to suspend a net) and not too large (≤ 35 cm diameter), we climbed them using French tree-climbing spikes (Model 502, available from ETS Lacoste, 24160 Excideuil, France; see Mori, 1987: fig. I-3A) and screwed large eyebolts directly into the trunks. To fix supports across larger gaps, we used the giant slingshot designed by Munn (1991) to shoot lead fishing weights tied to heavy monofilament line (on a spin-casting reel) into or over the crowns of trees on either side.⁴ Brass rings (through which the running loops were first threaded) were then drawn up on braided line; our simplest net rigs used a single top-line to hold the rings in place.

In addition to having suitable overhead supports on each side of a canopy gap, elevated net sites must be clear enough at

ground level that nets can be raised and lowered without obstruction. Unfortunately, most natural gaps in the canopy are treefalls, which are always littered with prostrate trunks and limbs. Roads and clearings provide canopy gaps that are generally free of such obstacles (fig. 11), but manmade openings in the forest are often bordered by young trees that are not tall enough to support high nets. These constraints, together with the labor required to rig elevated nets, precluded frequent site changes in sampling the canopy bat fauna at Paracou.

We measured the approximate height of elevated nets by attaching a tape measure to the bottom of one of the net poles; capture height was then recorded as the 3-m interval from the bottom to the top of the net (i.e., 10–13 m for bats caught in a net with lowermost pole ends 10 m above the ground). However, we found it essential to keep a sharp eye on elevated nets as they were lowered to remove entangled bats because low-flying species were often captured in the process; capture height data from carelessly monitored nets could therefore overestimate the vertical activity range of understory species.

SEARCHING FOR ROOSTS

Many rainforest bats that are hard to catch in mistnets can easily be collected or observed at their diurnal roosts. We found some roosts by chance, when bats flew up suddenly as we passed an unsuspected retreat in the forest understory. In such cases, we stepped a few meters away and stood quietly until the animals returned (usually in just a few minutes). Most roosts, however, were discovered by deliberate searching along trails. Among other potential roost sites in primary and secondary forest, we searched beneath undercut streambanks, under the buttresses of fallen trees, inside hollow logs, inside hollow standing trees, under loose bark on standing trees, and in foliage (especially among the leaves of large monocots such as palms, *Heliconia* spp., *Phenakospermum guyannense*, *Philodendron* spp.). Although we sometimes made special efforts to find particular roost types (e.g., leaf tents or hollow trees), we never ignored other kinds of roosts encoun-

⁴ D. P. Lunde and R. W. Kays constructed and tested our line-shooting equipment and helped install the first canopy nets at Paracou.



Fig. 9. Subcanopy of well-drained primary forest at Paracou, here viewed from about 20 m above the ground (photograph by R. W. Kays). The subcanopy is much less cluttered by leafy vegetation than the undergrowth, which may explain the higher capture rates of aerial insectivores like *Cormura brevirostris*, *Peropteryx kappleri*, *Saccopteryx bilineata*, and *S. leptura* at this level. At least 16 species of phyllostomids are probably also active in this habitat, although most of our elevated net captures of them were over roads, not inside the forest.

tered as we searched. In addition to looking for natural roosts, we investigated reports of bats roosting in houses and storage sheds, and we searched every culvert under roads within our sampling radius.

Most bats were located visually in their diurnal retreats, and some with distinctive posture, coloration, or other external characters could be reliably identified without capture. Likely patches of subcanopy foliage were scanned with binoculars, which were also useful for examining well-lit roosts in the forest understory that could not be closely approached without frightening the inhabitants. Roosts under fallen trees, inside hollow logs, and other dark refugia were examined with a headlight (which leaves the hands free to push aside obstructing vegetation, wield a net, aim a gun, or take notes). Short-handled butterfly nets were sometimes useful for capturing roosting bats, but in many situations shooting

(with number 12 shot in .22 caliber or .410 loads) was the only option.

Occasionally, roosting bats could be heard fluttering inside tree holes, hollow logs, or other places where they could not be seen or reached. In such situations, we plugged all but one entrance, around which we built a mistnet enclosure to catch the animals as they emerged at dusk. We used short (6 m) 70-d mistnets wrapped around upright poles to enclose the roost opening on all sides, and then thatched the enclosure with palm fronds to prevent emerging bats from escaping upward. Such enclosures usually captured every emerging bat.

To obtain data on roost occupancy in successive years, we assigned every roost a unique number; durable roosts (those that could be expected to last for more than a few months, e.g., hollow logs, tree cavities) were identified by nailed aluminum tags. We tried



Fig. 10. View over the forest canopy from the crown of an emergent tree, about 45 m above the ground (photograph by R. W. Kays). The unobstructed airspace above the trees is probably used mostly by species of *Diclidurus*, *Eptesicus*, *Lasiurus*, and molossids, although most of our captures of these taxa were made closer to the ground in nets suspended across a road through the forest or over roadside puddles. Many phyllostomids are probably active in the canopy itself, although we captured only *Phyllostomus hastatus*, *Ametrida centurio*, and *Chiroderma villosum* in our highest nets.

to revisit each durable roost every subsequent field season and record the species and numbers of bats in residence, but some roosts were destroyed when new land was cleared for agricultural experiments and others could not be found again. Some foliage roosts were revisited several times per field season following removal of the original occupants to determine whether leaf-tents used by one species are ever subsequently colonized by another.

To explore the effects of observer bias in searching for roosts, and to obtain data on roost density, we systematically surveyed a 25-ha plot of primary forest (Parcel 16 of CIRAD's forestry research program), which was conveniently divided by a square grid of surveyed trails into 1-ha quadrats (fig. 12). Four searchers with widely varying prior experience were assigned quadrats by lottery in 1994. Each 1-ha quadrat was then surveyed for roosts by one searcher who first walked the perimeter trails (totaling 400 m) and then

the trailless interior; the interior was searched in four parallel transects spaced 20 m apart. Thus, no point within any quadrat was more than 10 m from a searched path or transect. Searchers were instructed to investigate all likely roosting sites and to flag all discovered roosts so that they could be subsequently revisited and confirmed by the most experienced searcher. Because Parcel 16 was set aside for nondestructive research, it was not possible to determine the identification of all roosting bats found in this survey.

SPECIMEN COLLECTION AND PRESERVATION

We preserved voucher specimens using standard procedures described and illustrated by Handley (1988). In collecting specimens, our objective was to preserve enough examples of each species to assess the taxonomic status of the Paracou population with



Fig. 11. A narrow dirt road across which we raised nets to catch high-flying bats. The road is bordered by young secondary growth and selectively logged forest, but primary forest occurs within about 50–100 m on either side.

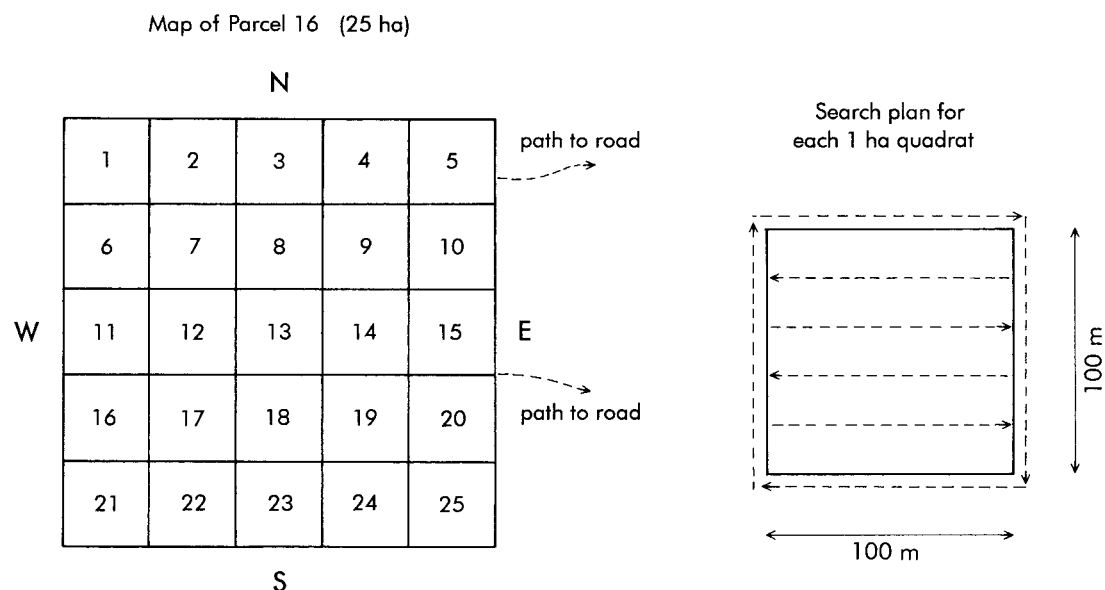


Fig. 12. Map of a 25-ha plot of primary forest (Parcel 16) divided by a grid of surveyed trails into 1-ha quadrats (left) and the plan used to search each 1-ha quadrat for bat roosts (right). Two trails on the east side provided access from a dirt road ca. 0.5 km away. Most of the surveyed habitat was well-drained forest, but quadrats 5, 11, 12, 16, 17, 21, 22, and 25 also contained swampy forest. The standard search procedure for each quadrat is explained in the text.

respect to populations sampled at other localities. Usually, we limited our removal to about 20 individuals (10 males and 10 females) per species, enough to obtain meaningful estimates of the range of variation and central tendency in each sex for characters of taxonomic interest. For open populations of most rainforest bats, destructive sampling on this scale is probably trivial by comparison with natural demographic processes.⁵

⁵ Leigh and Handley (1991) estimated a population density of about 200 *Artibeus jamaicensis* per square kilometer of lowland forest in central Panama. Because their study site was rich in fig trees, the primary food resource of *A. jamaicensis*, this estimate is perhaps on the high side for the species. However, *A. jamaicensis* is larger (45 g) than most Neotropical rainforest bats, whose caloric requirements can probably be obtained in smaller home ranges. On the assumption that 100 individuals/km² is a conservative average value for many stenodermatines, we could expect about 2800 individuals of each species within our study area (ca. 28 km²). An annual survivorship of 64% (the highest figure suggested by Leigh and Handley for *A. jamaicensis*) would then imply about 1000 natural deaths per species per year at Paracou. Presumably, such mortality is annually compensated by recruitment in all species that maintain stable local populations.

ACOUSTIC SURVEY

In the last year of our work at Paracou (1994), we used a custom-made electronic bat detector borrowed from Elisabeth K. V. Kalko (University of Tuebingen, Germany, and Smithsonian Tropical Research Institute, Panama) to record the echolocation calls of bats foraging along roads and in manmade and natural clearings. The signals were amplified, fed into a transient recorder, and read out at $\frac{1}{15}$ reduced speed on a Sony Walkman Professional cassette tape recorder. We made 198 recordings over the course of 10 nights between 9 October and 30 October 1994. Analyses of these recordings are currently in progress, and the results will be presented elsewhere.

SCHEDULING AND PERSONNEL

We worked at Paracou from 1991 to 1994, with the dates, personnel, and methods listed below. Although all personnel helped to some extent with the bat inventory, some were primarily engaged in other activities; only those chiefly responsible for the listed

methods are identified parenthetically. Italics indicate the authors of fieldnotes (deposited in the AMNH Department of Mammalogy archives) that should be consulted for detailed information about relevant methods.

1991: 26 June–27 August; Darrin P. Lunde, Nancy B. Simmons, and Robert S. Voss; ground-level netting (*Simmons*) and searching for roosts (*Voss*).

1992: 20 October–18 November; Darrin P. Lunde, Nancy B. Simmons, and Robert S. Voss; ground-level netting (*Simmons*, *Voss*) and searching for roosts (*Voss*).

1993: 20 July–15 September; Roland W. Kays, Darrin P. Lunde, Suzanne E. Smith, and Robert S. Voss; ground-level and elevated netting (*Smith*, *Voss*) and searching for roosts (*Voss*).

1994: 19 September–13 November; Louise H. Emmons, Andrea L. Peffley, Nancy B. Simmons, Nancy A. Voss, and Robert S. Voss; ground-level and elevated netting (*Peffley*, *Simmons*, *N. A. Voss*, *R. S. Voss*), searching for roosts (*Peffley*, *Simmons*, *N. A. Voss*, *R. S. Voss*), and ultrasonic census (*Peffley*, *Simmons*).

SYSTEMATIC ACCOUNTS

The following accounts are arranged systematically by family (and by subfamily within Phyllostomidae), and then alphabetically by genus and species. Unless noted otherwise, the nomenclature and taxonomic sequence used herein follows Koopman (1993). The organization of most accounts employs several standard subheadings.

VOUCHER MATERIAL: This section summarizes information about specimens collected, which are listed by sex and museum catalog number. Individuals measured for tables are indicated with asterisks.

IDENTIFICATION: In the field, we made extensive use of Emmons' (1990) generally excellent descriptions of external characters to make preliminary identifications. Although subsequent museum study of voucher specimens confirmed most of our field determinations, we also encountered numerous taxonomic problems that had to be resolved to justify the nomenclature adopted below.

In cases where identification was relatively straightforward, we simply list the technical references we consulted at the beginning of each account and remark any noteworthy points in which our material differs from published descriptions. Species identifications involving significant taxonomic problems are treated at length, with reviews of the relevant literature and analyses of character variation in the specimens examined. We also discuss currently recognized subspecies in this section, although we do not use trinomial headings below.

Measurements of voucher specimens and

comparative material are provided in tables accompanying each species account. These morphometric summaries include only measurements of adults with closed epiphyses. Linear measurements of external and craniodental dimensions are reported in millimeters (mm); weights are reported in grams (g). The following measurements were taken for all or some of the species treated below.

Total length: Distance from the tip of the snout to the tip of the last caudal vertebra.

Tail length: Measured from the point of dorsal flexure of the tail with the sacrum to the tip of the last caudal vertebra.

Hindfoot length: From the anterior edge of the base of the calcar to the tip of the claw of the longest toe.

Ear length: From the notch to the fleshy tip of the pinna.

Forearm length: From the elbow (tip of the olecranon process) to the wrist (including the carpal). This measurement is made with the wing at least partially folded.

Tibia length: From the proximal end of the tibia to the posterior base of the calcar.

Thumb length: From the metacarpal-phalangeal joint to the tip of the claw.

Greatest length of skull: From the posteriormost point on the occiput to the anteriormost point on the premaxillae (excluding the incisors).

Condylolincisive length: From the posteriormost point on the occipital condyles to the anteriormost point on the upper incisors.

Condyllocanine length: From the posteriormost point on the occipital condyles to the anteriormost point on the upper canines.

Lacrima breadth: Greatest breadth across the lac-

rimal (= anteorbital) ridges, when present and well defined.

Postorbital breadth: Least breadth across the frontals posterior to the postorbital processes or bulges.

Zygomatic breadth: Greatest breadth across the zygomatic arches.

Braincase breadth: Greatest breadth of the globular part of the braincase.

Mastoid breadth: Greatest cranial breadth across the mastoid region.

Maxillary toothrow length: From the anteriormost edge of the canine crown to the posteriormost edge of the crown of M3.

Breadth across molars: Greatest breadth across the outer edges of the crowns of the upper molars.

Breadth across canines: Greatest breadth across the outer edges of the crowns of the upper canines.

To confirm identifications of problematic species, we compared our voucher material to museum specimens from other localities, and we often consulted literature descriptions of types that we did not personally examine. We identify the museums in which vouchers and other specimens are preserved by the following abbreviations: AMNH, American Museum of Natural History (New York); BMNH, British Museum of Natural History (London); CM, Carnegie Museum of Natural History (Pittsburgh); FMNH, Field Museum of Natural History (Chicago); MNHN, Muséum National d'Histoire Naturelle (Paris); MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima); RMNH, Rijksmuseum van Natuurlijke Historie (Leiden); SMN, Staatliches Museum für Naturkunde (Stuttgart); USNM, National Museum of Natural History (Washington, D.C.); ZMH, Zoologisches Museum Hamburg (Hamburg).

FIELD OBSERVATIONS: This section summarizes our capture records and roost observations, and includes discussion of habitats, behavior, and other natural history topics. In reporting our observations for each species, we first list capture frequencies by inventory method, and then provide a breakdown of capture frequencies by habitat for each method. If every recorded capture is known to represent a unique individual, we state the number of individuals captured. Although we did not mark released bats, the number of

individuals known to have been captured is occasionally larger than the number of vouchers we preserved because only one individual of each sex was released for some species. If more than one individual of either sex were released, we state the number of captures recorded and note that these "possibly" or "probably" (a subjective judgment) include some recaptures. For each species caught in elevated nets, we summarize capture height records as the interval from the bottom of the lowest elevated net in which the species was taken to the top of the highest net (e.g., 10–21 m for a species taken once in a net suspended 10–13 m above the ground and again in a net 18–21 m above the ground). We also note any conspicuous differences in mistnet capture-habitat or capture-height frequencies between congeners or other closely related species. We next provide information about roosting habits, especially roost type (hollow log, tree cavity, leaf-tent, etc.), roosting habitat, numbers of individuals in roosting groups observed, and the age and sex of captured roosting-group members.

In reporting habitat data for each species, we use the following categories: (1) well-drained primary forest, (2) swampy primary forest, (3) creekside primary forest, (4) tree-fall openings in primary forest, (5) manmade clearings (roadways, gardens, plantations, etc.), (6) closed-canopy secondary growth (including selectively logged forest), and (7) roadside puddles. The term "primary forest" (without modifiers) includes categories 1–4, whereas categories 5–7 are often referred to collectively as "modified habitats."

EMBALLONURIDAE

We captured 10 emballonurid species at Paracou, three of which are here reported for the first time from French Guiana. The species we identified from morphological voucher material represent the genera *Centronycteris*, *Cormura*, *Diclidurus*, *Peropteryx* (including *Peronymus*), *Rhynchonycteris*, and *Saccopteryx*. Published records from elsewhere in French Guiana and Surinam include another four emballonurid species that might also occur in our study area (appendix 1).

Centronycteris maximiliani (Fischer)

Figure 13

VOUCHER MATERIAL: 1 male (AMNH 267397); see table 1 for measurements.

IDENTIFICATION: Previously regarded as monotypic (e.g., by Koopman, 1993), the genus *Centronycteris* was recently shown to contain at least two species by Simmons and Handley (1998). According to these authors, the known range of *Centronycteris maximiliani* includes southern Venezuela, the Guianas, and northern, eastern, and southeastern Brazil, whereas *C. centralis* Thomas (1912b) occurs in Central America, Colombia, Peru, and on both sides of the Andes in Ecuador. Both species are known from only a few specimens, however, and their true geographic ranges may be considerably larger. In fact, because no known biogeographic barriers separate the ranges of *C. maximiliani* and *C. centralis*, these bats might occur sympatrically almost anywhere in Amazonia. Our Paracou voucher is the first known specimen of *C. maximiliani* from French Guiana.

Measurements and descriptions of *Centronycteris maximiliani* from the Guianas and elsewhere were provided by Thomas (1913), Husson (1962, 1978), Williams et al. (1983), and Simmons and Handley (1998). The latter authors summarized craniodental characters and measurements that distinguish *C. maximiliani* from *C. centralis*. Our Paracou voucher formed much of the basis of their description of *C. maximiliani*.

FIELD OBSERVATIONS: Our single individual of this species was shot in the late afternoon (about 16:00 hours) as it perched about 3 m above the ground on the underside of a large (ca. 20 × 30 cm) unmodified leaf of a small melastomataceous tree beside a trail in well-drained primary forest.

Cormura brevirostris (Wagner)

VOUCHER MATERIAL: 17 females (AMNH *266009, *267070, 267076, *267078, *267389, *267391, *267823, *267824, *267825, *267826, *267828; MNHN *1995.823, *1995.824, *1995.825, *1995.826, *1995.833, *1995.834) and 18 males (AMNH *265994, *266002, *266003, *267069, *267071, *267074, *267075, 267079, *267390, *267394, *267822,

*267827; MNHN *1995.827, *1995.828, 1995.829, *1995.830, *1995.831, *1995.832); see table 1 for measurements.

IDENTIFICATION: *Cormura brevirostris* can be distinguished easily from other emballonurids by the unique location of the antebrachial wing sac (Sanborn, 1937: fig. 37; Jones and Hood, 1993: fig. 1). Craniodental characters and measurements of *C. brevirostris* from the Guianas and other parts of South America were discussed by Sanborn (1937), Husson (1962, 1978), Brosset and Charles-Dominique (1990), and Jones and Hood (1993). Husson (1962) provided a revised description of *Cormura* and a detailed discussion of *Myopteryx pullus*, which he and all subsequent authors have considered to be a junior synonym of *C. brevirostris*. No subspecies are currently recognized (Jones and Hood, 1993; Koopman, 1994).

Our specimens from Paracou conform to previous descriptions of *Cormura brevirostris* and fall within the range of size variation previously documented in Surinam and French Guiana.

FIELD OBSERVATIONS: We recorded 42 captures (possibly including some recaptures) of *Cormura brevirostris* at Paracou: 7 in ground-level mistnets, 12 in elevated mistnets, and 23 at roosts. Of the seven ground-level mistnet captures, one was in well-drained primary forest, three were in creek-side primary forest, two were in a treefall opening in creek-side primary forest, and one was in a manmade clearing. Eight elevated-net captures were between 10 and 21 m above a narrow dirt road, and four were made between 10 and 38 m over a treefall gap in well-drained primary forest.

We encountered 10 different roosting groups of *Cormura brevirostris* at eight unique roost sites (one site was revisited twice). Five roost sites were on the dark undersides of fallen trees (e.g., fig. 14), but one roosting group was found clinging to an unmodified leaf of *Phenakospermum guyanensis* (fig. 15), another occupied a shallow cavity in the base of a living tree suspended by its roots over a stream, and another was found under a concrete bridge. In addition to the bridge roost, two natural roosts (both in primary forest) were over small streams, but

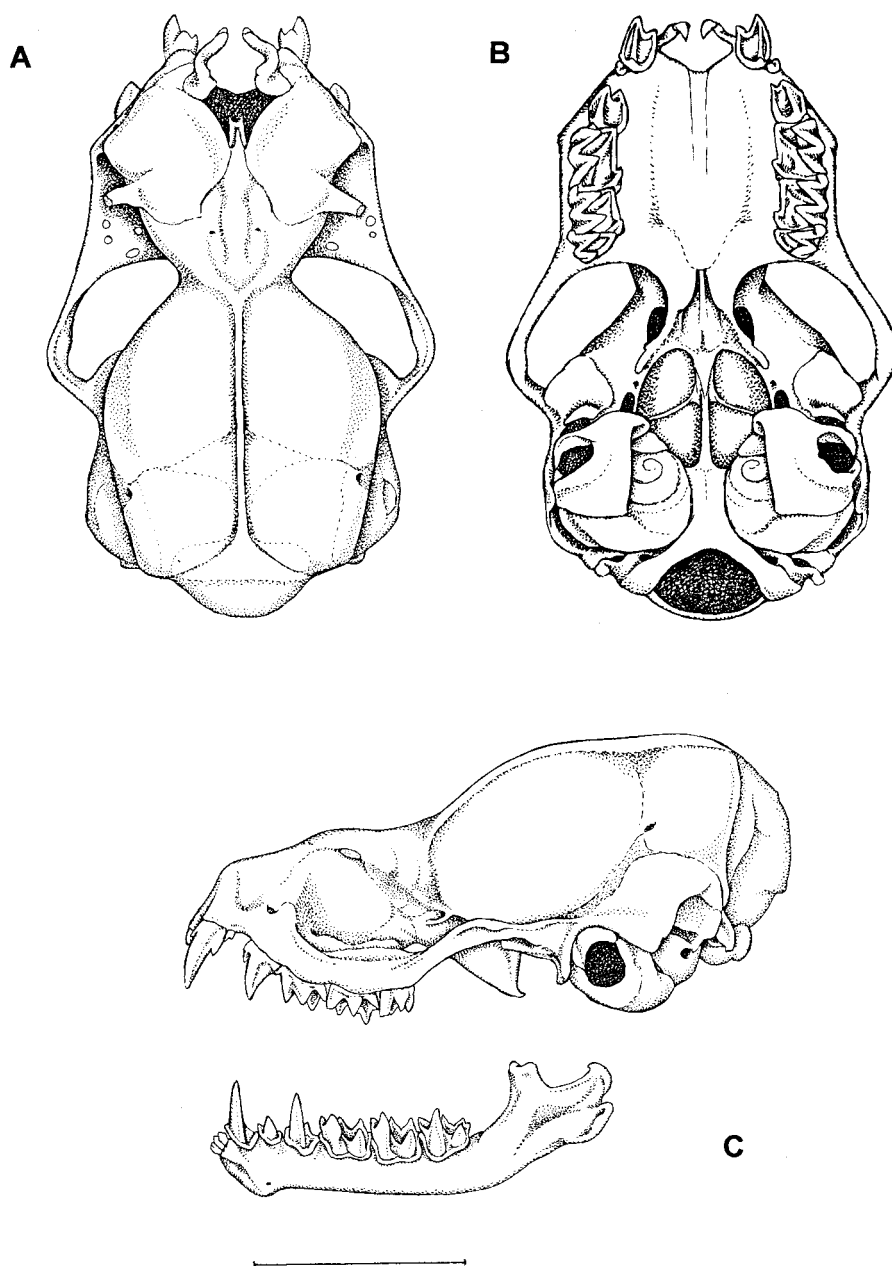


Fig. 13. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Centronycteris maximiliani* (AMNH 267397; male) from Paracou. Note the small anterior upper premolar and the large basisphenoid pits extending between the hamular processes of the pterygoids. *C. centralis* (not known from the Guianas) has a larger anterior upper premolar and smaller basisphenoid pits that do not extend between the hamular processes. Scale bar = 5 mm.



Fig. 14. Roost of *Cormura brevirostris* beneath a fallen tree in primary forest at Paracou. Five bats were found roosting on the dark underside of the trunk (arrow), about 1 m above the water when this dry-season photograph was taken. Nets set across this stream captured our only examples of *Noctilio leporinus*.

TABLE 1
Measurements^a of *Centronycteris* and *Cormura* Collected at Paracou

	<i>Centronycteris</i> <i>maximiliani</i>	<i>Cormura</i> <i>brevirostris</i>
Number/Sex	1 male	16 females 16 males
Weight	4.5	8.9 (6.8–11.0) 16 8.1 (7.3–9.0) 16
Total length	67.0	69.1 (58.0–72.0) 16 66.3 (58.0–71.0) 16
Tail length	26.0	14.1 (9.0–17.0) 16 13.0 (9.0–16.0) 16
Hind foot length	7.0	7.8 (6.0–9.0) 16 7.9 (7.0–9.0) 16
Ear length	17.0	14.7 (13.0–16.0) 16 14.5 (13.0–16.0) 16
Forearm length	41.5	47.2 (45.0–49.0) 16 46.3 (44.5–48.0) 15
Condylacanine length	13.38	14.23 (13.67–14.73) 6 14.42 (13.92–14.88) 6
Zygomatic breadth	8.93	10.02 (9.64–10.36) 5 10.03 (9.85–10.16) 6
Maxillary toothrow length	5.67	6.17 (6.01–6.35) 6 6.18 (5.91–6.50) 6
Breadth across molars	6.73	7.27 (6.98–7.55) 6 7.39 (7.23–7.55) 6

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.



Fig. 15. Roost of *Cormura brevirostris* in young secondary growth at Paracou. Three bats were found hanging in a cluster from a torn lateral vein (arrow) on the underside of this leaf of *Phenakospermum guyannense* (Strelitziaceae). This is the only known instance of *Cormura brevirostris* roosting in foliage, probably not a characteristic behavior of the species.

five others (four in primary forest and one in secondary forest) were far from water.

The 10 roosting groups of *Cormura brevirostris* we found at Paracou (table 2) consisted of two to five individuals, with a modal group size of three. Whereas three roosts each contained two adult males, we never found more than one adult female per roost. In all eight roosting groups that we were able to observe closely before the bats were disturbed, the animals were clustered together in a compact mass; in four groups we were able to see that the individuals were actually touching one another back-to-belly. Although three species of *Peropteryx* (*P. kappleri*, *P. leucoptera*, and *P. macrotis*) previously or subsequently occupied some of the same roosts where we captured *C. brevirostris*, we never found more than one of these (or any other emballonurid species) sharing the same roost simultaneously.

Diclidurus scutatus Peters

VOUCHER MATERIAL: 1 female (AMNH 267832); see table 3 for measurements.

IDENTIFICATION: Ceballos and Medellín (1988) provided a key to species based on external and dental measurements, and Jones and Hood (1993) modified this key by addition of characters of the palate. However, we found an often-overlooked paper by Ojasti and Linares (1971) to be more useful than any other single reference: they noted features of the premolars and basicranium distinguishing the subgenera and species of *Diclidurus*, and they provided comparative descriptions of each species.

Husson (1962, 1978) described *Diclidurus scutatus* in detail and figured the glandular pouches of the uropatagium, which may have a unique structure in this species. Measurements of other referred specimens were provided by Ojasti and Linares (1971), Jones and Hood (1993), and Brosset and Charles-Dominique (1990). Subspecies of *D. scutatus* are not currently recognized (Koopman, 1994).

Our specimen conforms externally in all respects to previous descriptions of this species. Because the identification seemed unambiguous, we did not extract the skull in

order to preserve the soft tissues of the head for future study.

FIELD OBSERVATIONS: Our single example of this widespread but seldom collected bat was captured at 19:30 hours in a mistnet suspended 17–20 m above a narrow dirt road through well-drained primary forest.

Peropteryx

Peropteryx and *Peronymus* have been traditionally recognized as distinct genera (e.g., Miller, 1907; Sanborn, 1937; Husson, 1962, 1978), and many recent authors have continued to treat them as such (e.g., Brosset and Charles-Dominique, 1990). However, *Peronymus* and *Peropteryx* share a unique morphology of the antebrachial wing sac (Sanborn, 1937; Jones and Hood, 1993), and phylogenetic studies have shown that these taxa form a monophyletic group (Griffiths and Smith, 1991). Indeed, the principal distinguishing character of *Peronymus leucopterus* (the only species referred to the genus) is its white wing membranes, which are clearly autapomorphic. Accordingly, we follow Cabrera (1958), Jones and Hood (1993), and Koopman (1993, 1994) in regarding *Peronymus* as a junior synonym of *Peropteryx*. A useful key to the species of *Peropteryx* so defined was provided by Jones and Hood (1993).

Peropteryx kappleri Peters

VOUCHER MATERIAL: 15 females (AMNH *265991, *265992, *265996, *265998, *265999, *267081, *268082, 267083, *267833, *267834; MNHN *1995.835, *1995.836, *1995.837, 1995.838, *1995.839) and 10 males (AMNH *265989, *265995, *267084, *267085, *267291, 267393, *267836; MNHN *1995.840, *1995.841, *1995.842); see table 4 for measurements.

IDENTIFICATION: Descriptions and measurements of *Peropteryx kappleri* were provided by Sanborn (1937), Goodwin and Greenhall (1961), Husson (1962, 1978), and Jones and Hood (1993). In the field, *P. kappleri* is easily confused with *Cormura brevirostris*, which is approximately the same size and color. However, these species can be distinguished unambiguously based on morphology of the antebrachial wing sac (illustrated

TABLE 2
Roosting Groups of *Cormura brevirostris* Observed at Paracou

Date	Roost site	Group size	Entire group captured?	Age and sex of captured group members
12 Aug 1991	leaf	3	no	1 ad. female
17 Aug 1991	fallen tree	2	no	1 ad. male
20 Aug 1991	fallen tree	4	no	1 ad. male, 1 ad. female
21 Aug 1991	bridge	4	no	1 ad. male, 1 ad. female
20 Oct 1992	fallen tree	3	no	1 ad. male, 1 ad. female
4 Nov 1992	fallen tree	3	yes	1 ad. male, 1 ad. female, 1 subad. male
7 Nov 1992	tree cavity	3	yes	2 ad. males, 1 subad. female
7 Nov 1992	fallen tree	5	no	1 ad. male, 1 ad. female, 1 juv.
14 Sep 1994	fallen tree	3	yes	2 ad. males, 1 ad. female
4 Nov 1994	fallen tree	3	yes	2 ad. males, 1 ad. female

by Sanborn [1937: fig. 37] and Jones and Hood [1993: fig. 1]). Two subspecies are currently recognized, of which the nominate form, *P. k. kappleri*, occurs throughout northern South America, including the Guianas (Koopman, 1994).

Our specimens, the first to be reported from French Guiana, conform to previous descriptions of *Peropteryx kappleri* and fall within the range of variation previously reported from northern South America by the authors cited above.

FIELD OBSERVATIONS: We captured 26 individuals of *Peropteryx kappleri*, which would appear to be a moderately common bat at Paracou despite the absence of any previous country records: 4 were taken in ground-level mistnets (3 in swampy primary

forest and 1 in creekside primary forest), 5 others were taken in mistnets suspended 13–21 m above a narrow dirt road, and the remaining 17 were captured at roosts.

We found 11 roosting groups at seven unique roost sites (three roosts were each revisited once). Most (five) roost sites were dark horizontal concavities on the undersides of fallen trees (fig. 16), but two roosts were in large hollow logs (≥ 60 cm in inside diameter). All roost sites were in well-drained primary forest and none was near water.

The roosting groups we observed (table 5) consisted of one to four individuals, with a mode of two; whereas two roosting groups each contained multiple adult females, no more than one adult male was captured per roost. In three undisturbed roosting groups that we were able to observe closely, the bats were perched well separated from one another (four bats in one group were perched side-by-side in line but not touching). We did not observe this species to share its roosts simultaneously with other bats, although *Furipterus horrens* was once found roosting in a separate chamber between buttresses on the opposite side of the same fallen tree, and other emballonurid species (*Cormura brevirostris* and *Peropteryx macrotis*) previously or subsequently occupied some of the same sites where we collected *Peropteryx kappleri*.

TABLE 3
Measurements^a of *Diclidurus scutatus*
Collected at Paracou

Number/Sex	1 female
Weight	12.0
Total length	88.0
Tail length	22.0
Hind foot length	9.5
Ear length	13.0
Forearm length	57.0

^a Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods. Craniodental measurements are not reported for this taxon because the skull was not been removed from the only specimen collected.

Peropteryx leucoptera Peters

VOUCHER MATERIAL: 7 females (AMNH *266010, *266011, *267837, *267839;

TABLE 4
Measurements^a of *Peropteryx* Collected at Paracou

	<i>Peropteryx kappleri</i>		<i>Peropteryx macrotis</i>	
Number/Sex	13 females	9 males	2 females	3 males
Weight	8.8 (7.1–11.6) 13	7.7 (6.7–8.5) 9	5.3 (5.3–5.4) 2	4.2 (3.8–4.6) 3
Total length	73.5 (69.0–78.0) 13	69.9 (65.0–74.0) 9	62.0 (60.0–64.0) 2	56.7 (53.0–58.0) 3
Tail length	13.8 (10.0–17.0) 13	12.7 (9.0–15.0) 9	12.5 (12.0–13.0) 2	11.7 (11.0–12.0) 3
Hind foot length	11.2 (9.0–13.0) 13	10.6 (9.0–12.0) 9	8.0 (8.0–8.0) 2	7.7 (7.0–8.0) 3
Ear length	18.2 (17.0–19.0) 13	18.2 (17.0–20.0) 9	14.5 (14.0–15.0) 2	14.0 (14.0–14.0) 3
Forearm length	51.1 (50.0–52.5) 10	48.6 (47.0–50.0) 9	45.0 (45.0) 1	40.7 (39.7–42.2) 3
Condylacanine length	15.85 (15.63–16.17) 4	15.69 (15.69) 1	12.69 (12.69) 1	12.50 (12.50) 1
Zygomatic breadth	10.26 (9.90–10.40) 4	10.63 (10.63) 1	8.36 (8.30–8.41) 2	8.27 (8.27) 1
Maxillary tooththrow length	7.18 (7.14–7.25) 4	7.26 (7.26) 1	5.52 (5.42–5.63) 2	5.32 (5.24–5.41) 3
Breadth across molars	7.94 (7.84–8.04) 4	7.99 (7.99) 1	6.16 (6.15–6.16) 2	5.84 (5.73–5.95) 2
	<i>Peropteryx leucoptera</i>			
Number/Sex	6 females	4 males		
Weight	6.5 (5.5–7.8) 6	6.2 (6.0–6.4) 4		
Total length	64.0 (61.0–66.0) 6	65.0 (63.0–69.0) 4		
Tail length	14.0 (12.0–17.0) 6	13.9 (13.0–15.0) 4		
Hind foot length	8.9 (8.0–10.0) 6	8.5 (8.0–9.0) 4		
Ear length	16.7 (15.0–18.5) 6	15.9 (15.0–16.5) 4		
Forearm length	43.8 (42.0–45.0) 6	42.3 (41.0–43.0) 4		
Condylacanine length	13.51 (13.23–13.79) 2	—		
Zygomatic breadth	9.45 (9.36–9.53) 2	—		
Maxillary tooththrow length	5.82 (5.58–6.06) 2	—		
Breadth across molars	6.82 (6.72–6.91) 2	—		

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

MNHN *1995.820, 1995.821, *1995.822), and 4 males (AMNH *267088, *267280, *267838, MNHN *1995.819); see table 4 for measurements.

IDENTIFICATION: Descriptions and comparative measurements of *Peropteryx leucoptera* from the Guianas and elsewhere were provided by Sanborn (1937), Husson (1962, 1978), Ochoa (1984), Brosset and Charles-Dominique (1990), and Jones and Hood (1993). Two subspecies are currently recognized: *P. l. leucoptera* (southeastern Colombia to the Guianas and northeastern Brazil) and *P. l. cyclopes* (eastern Peru) (Koopman, 1994).

Our voucher material conforms in all respects to previous descriptions of *Peropteryx leucoptera*, and measurements of our material fall within the range of size variation previously documented in the Guianas.

FIELD OBSERVATIONS: We captured 14 individuals of *Peropteryx leucoptera* at Paracou, of which 1 was taken in a ground-level mistnet (in a treefall gap in well-drained primary forest) and the other 13 at roosts. The six roosting groups we found (table 6) occupied four unique roost sites (one roost was revisited twice); all were dark horizontal chambers between buttresses on the undersides of fallen trees (figs. 17, 18) in well-drained primary or selectively logged forest. These roosting groups consisted of two to seven or eight individuals, which were consistently found perching apart from one another (never in a cohesive cluster). Three groups contained at least two adult females each, but we did not capture more than one adult male in any roost. One roost inhabited by a group of *P. leucoptera* that we collected in 1991 was subsequently occupied by *Cor-*



Fig. 16. Roost successively occupied by three species of emballonurids in well-drained primary forest at Paracou. The dark concave underside of this broken trunk (arrow) sheltered roosting groups of three *Peropteryx macrotis* in 1991, four *P. kappleri* in 1992, and three *Cormura brevirostris* in 1994; the roost was found vacant in 1993.

TABLE 5
Roosting Groups of *Peropteryx kappleri* Observed at Paracou

Date	Roost site	Group size	Entire group captured?	Age and sex of captured group members
14 Aug 1991	fallen tree	?	?	1 ad. male, 1 ad. female
18 Aug 1991	hollow log	2	yes	1 ad. male, 1 ad. female
18 Aug 1991	fallen tree	4	yes	1 ad. male, 2 ad. females, 1 subad. female
20 Oct 1992	fallen tree	4	yes	3 ad. females, 1 subad. female
21 Oct 1992	fallen tree	1	yes	1 ad. male ^a
21 Oct 1992	fallen tree	1	yes	1 ad. male ^a
27 Oct 1992	fallen tree	2	no	1 ad. female
1 Aug 1993	fallen tree	2	no	1 ad. male
21 Aug 1993	hollow log	2	no	none captured
31 Aug 1993	fallen tree	3	no	1 ad., released, sex unrecorded
9 Nov 1994	fallen tree	3–4	no	none captured

^a Roosting alone in widely separated cavities between buttresses on opposite sides of the same tree.



Fig. 17. Roost of *Peropteryx leucoptera* and *Furipterus horrens* in well-drained primary forest at Paracou (some understory vegetation was selectively removed for photography). Two individuals of *P. leucoptera* were found roosting in a horizontal chamber (arrow) between two buttresses of this fallen tree in 1992, and one *F. horrens* occupied a similar chamber on the other side at the same time. This roost was vacant in 1993 and was destroyed by a treefall in 1994. Deep recesses between the buttresses of fallen trees like this provide roosts for several bat species besides the two found here, including *Peropteryx kappleri*, *Choeroniscus minor*, and *Lonchophylla thomasi*. However, whereas emballonurids usually occupy dimly lighted sites between lateral buttresses, glossophagine roosts are always on the darker underside (where they can be seen only by crawling underneath such trees with a headlight).

TABLE 6
Roosting Groups of *Peropteryx leucoptera* Observed at Paracou

Date	Roost site	Group size	Entire group captured?	Age and sex of captured group members
23 Aug 1991	fallen tree	4	yes	1 ad. male, 2 ad. females, 1 subad. female
23 Oct 1992	fallen tree	2	no	1 ad. male
23 Oct 1992	fallen tree	3?	no	1 ad. male, 1 ad. female
11 Aug 1993	fallen tree	5	no	2 ad. females, 1 unsexed ad.
25 Sep 1994	fallen tree	4	no	none captured
13 Nov 1994	fallen tree	7-8	no	1 ad. male, 2 ad. females



Fig. 18. Roost of *Peropteryx leucoptera* at the margin of an experimental plot in well-drained forest at Paracou. Felled by cuts through the buttresses about 1 m above the ground, this tree was the only roost of *P. leucoptera* that we found unobstructed by dense understory vegetation. Seven or eight bats were observed roosting in the cave-like recess (arrow) formed by the standing base and the fallen trunk.

mura brevirostris in 1992, and we once found *Furipterus horrens* simultaneously roosting beneath the same fallen tree as *P. leucoptera*, but in a different chamber separated by large buttresses. Otherwise, this species was not observed to share roost sites with other bats.

On several occasions we saw bats with white wings, almost certainly *Peropteryx leucoptera*, flying regular beats 1–2 m above the ground at dusk in our camp clearing.

Peropteryx macrotis (Wagner)

Figures 19, 20

VOUCHER MATERIAL: 2 females (AMNH *266006, *267396) and 3 males (AMNH *266005, *266007; MNHN *1995.843); see table 4 for measurements.

IDENTIFICATION: Brosset and Charles-Dominique (1990) recognized two small *Peropteryx* species in French Guiana that they identified as *P. macrotis* (originally de-

scribed by Wagner [1843] based on a Brazilian specimen from Mato Grosso) and *P. trinitatis* (described by Miller [1899] based on four specimens from Trinidad). Previously, Sanborn (1937) and Goodwin and Greenhall (1961) had concluded that *trinitatis* was no more than subspecifically distinct from *macrotis* because specimens referable to these taxa are similar and were not then known from sympatry. Although Handley (1976) subsequently reported that *P. macrotis* and *P. trinitatis* occur sympatrically in Venezuela, he provided no discussion of diagnostic characters. In consequence, most recent authors (e.g., Jones and Hood, 1993; Koopman, 1993, 1994) have continued to recognize *trinitatis* as a subspecies of *P. macrotis*.

According to Brosset and Charles-Dominique (1990), *Peropteryx macrotis* and *P. trinitatis* can be distinguished in French Guiana based on size (e.g., forearm length 43.0–

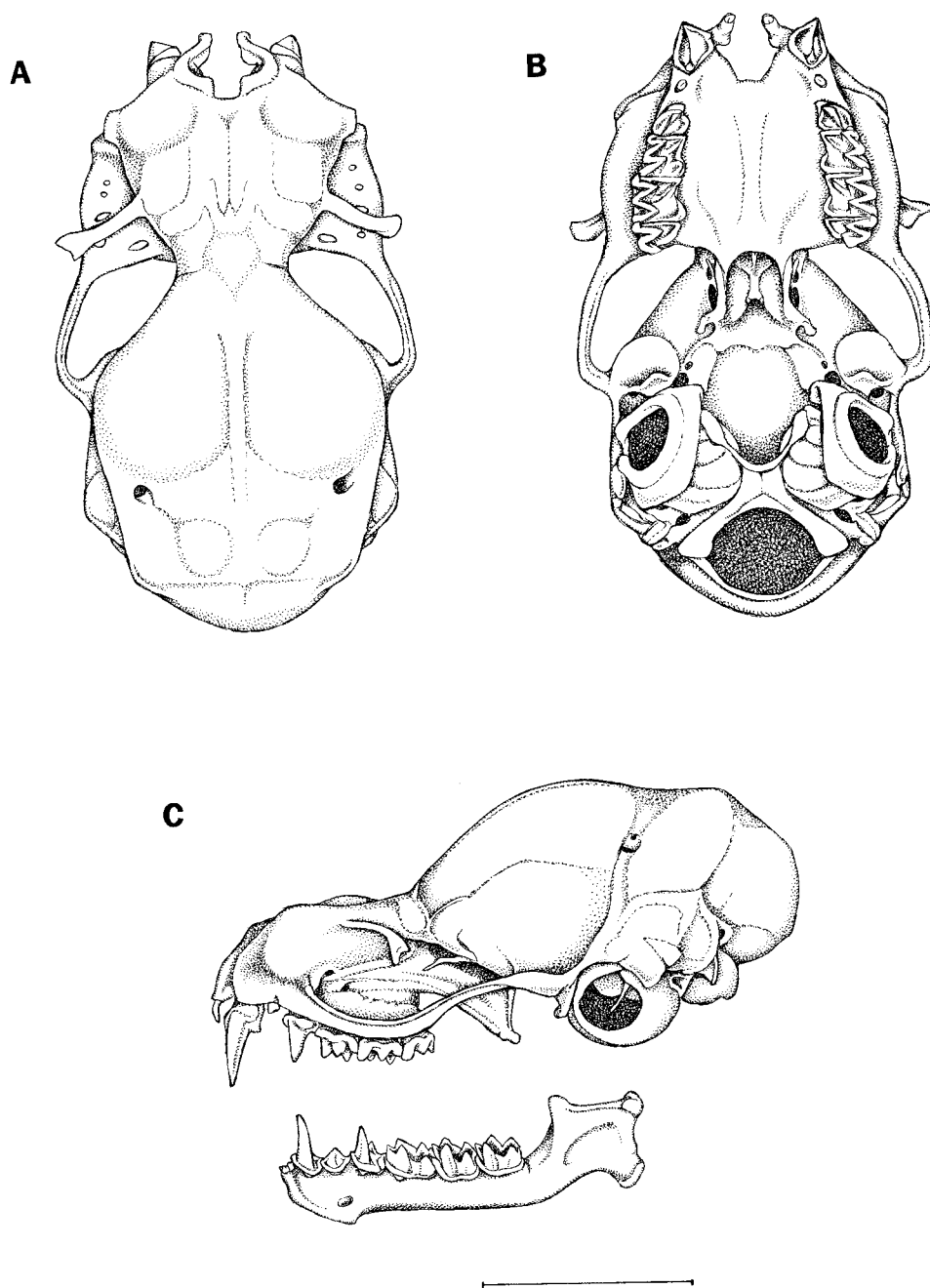


Fig. 19. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Peropteryx macrotis* (AMNH 266005; male) from Paracou. Scale bar = 5 mm.

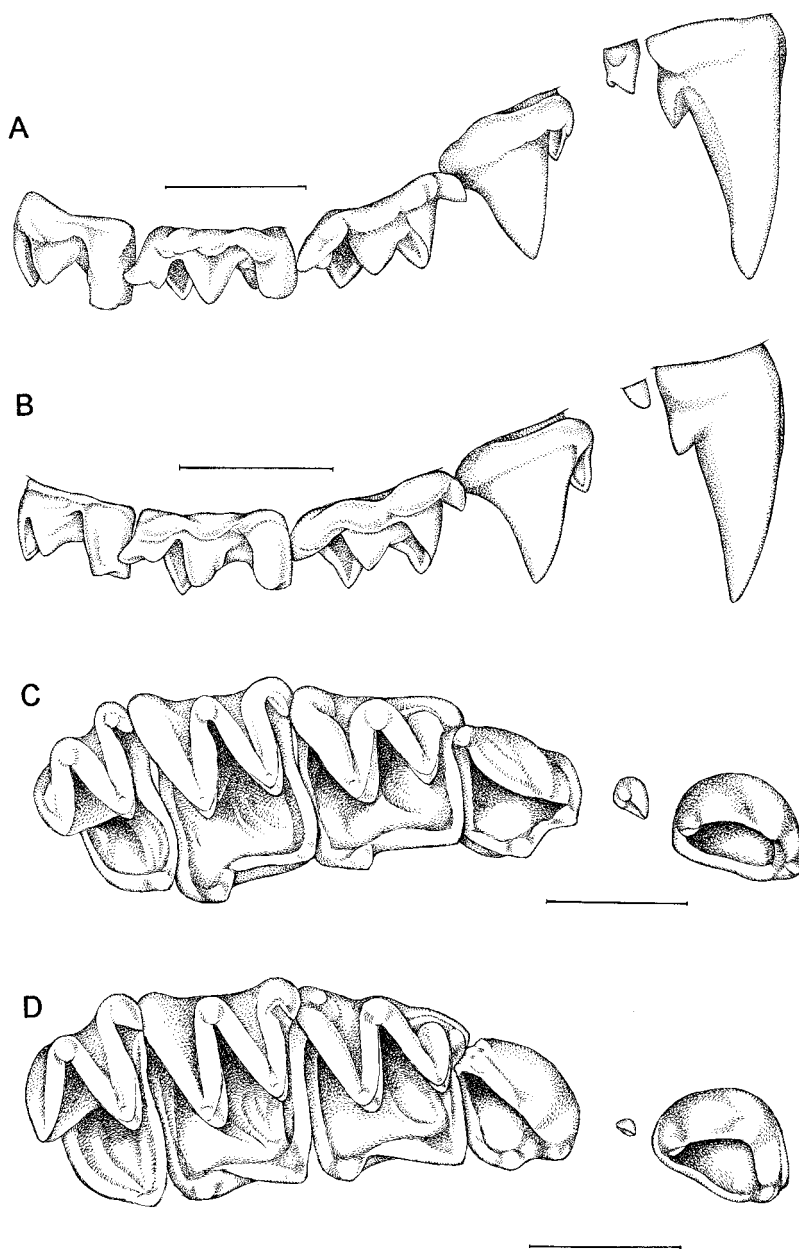


Fig. 20. Close-up lateral views of the upper right dentition of (A) *Peropteryx macrotis* (AMNH 267396; female) from Paracou and (B) the holotype of *P. trinitatis* (AMNH 7496; female) from Trinidad. Occlusal views of the upper right dentition (C) *P. macrotis* (AMNH 267396; female) and (D) the holotype of *P. trinitatis* (AMNH 7496; female) are shown below. Note the species difference in morphology of the anterior upper premolar. Scale bars = 5 mm.

47.0 mm, maxillary tooththrow length 5.3–6.0 mm in *P. macrotis*, forearm 39.5–40.4 mm, maxillary tooththrow 4.7–4.8 in *P. trinitatis*, skull shape (shorter, more rounded in *P. trinitatis*), and ear and tragus shape (both narrower in *P. trinitatis*). They also observed differences in sexual dimorphism (females larger than males in *P. macrotis* but not in *P. trinitatis*) and social behavior (social groups of 1–4 individuals in *P. macrotis*, much larger [> 100] in *P. trinitatis*). Unfortunately, all of their observations concerning *P. trinitatis* were based on a single colony from which only two specimens (one male and one female) were collected (Brosset and Charles-Dominique, 1990).

Our voucher material from Paracou appears to represent the same species that Brosset and Charles-Dominique identified as *Peropteryx macrotis* despite some discrepancies in measurements. Whereas all measurements of the two females in our sample (table 4) fall within the range of variation they reported for female *P. macrotis* (op. cit.), the forearm measurements of our three males (39.7, 40.1, and 42.2 mm) correspond more closely to values they reported for *P. trinitatis*. Examination of skull shape and ear morphology, however, suggest that all of our specimens represent *P. macrotis* sensu Brosset and Charles-Dominique. Therefore, if there are two diagnosable taxa of small *Peropteryx* in French Guiana, it appears that males cannot be distinguished on the basis of forearm measurements alone.

To test our identification of the Paracou specimens, we compared our series with the adult female holotype (AMNH 7496) of *Peropteryx trinitatis*. The forearm of the holotype measures 41.9 mm, much smaller than those of either of our Paracou females. Although the skull of the holotype is badly damaged, the rostrum and tooththrows remain largely intact (fig. 20). The maxillary tooththrow length of AMNH 7496 is 5.21 mm, and the breadth across the upper molars is 5.74 mm, values that likewise fall well below those of our female Paracou vouchers (table 4) and of the female specimen identified as *P. macrotis* by Brosset and Charles-Dominique (1990). We also noted one qualitative difference between the holotype of *trinitatis* and our voucher material: the anterior upper pre-

molar is peglike and lacks well-defined anterior and posterior cusps in *trinitatis*, but this tooth is larger and has a distinct posterior cusp in the Paracou specimens. Paratypes (AMNH 7493, 7494, 7495) and topotypes (AMNH 175556, 175558, 175559) of *trinitatis* resemble the holotype in size and also have tiny, peglike anterior upper premolars.

According to Carter and Dolan (1978), the holotype of *Peropteryx macrotis* is an uncatalogued adult female preserved in alcohol at the Naturhistorisches Museum Wien. Unfortunately, the skull is missing and presumed lost. However, the forearm measurement of the holotype reported by Carter and Dolan, 45.8 mm, corresponds closely with that of our female specimen from Paracou (45.0 mm) and with those identified as *P. macrotis* by Brosset and Charles-Dominique (43.9–47.0 mm). These measurements are larger than, and do not overlap with, measurements previously reported for females of *P. trinitatis* (e.g., by Goodwin and Greenhall, 1961). We therefore follow Brosset and Charles-Dominique in referring the larger of the two small *Peropteryx* from French Guiana to *P. macrotis*.

FIELD OBSERVATIONS: We captured only five individuals of *Peropteryx macrotis*, all of them at roosts. One roosting group of three bats (two adult males and one adult female) was found beneath the broken trunk of a fallen tree cantilevered about 1.5 m above the ground in well-drained primary forest (fig. 16). Another group of three individuals (of which only one adult male and one subadult female were captured) was found in a large hollow log (ca. 60 cm in inside diameter), also in well-drained primary forest.

Rhynchonycteris naso (Wied)

VOUCHER MATERIAL: 4 females (AMNH *265985, *265988, *267373; MNHN *1995.844) and 6 males (AMNH *265981, *265986, *265987, *267372; MNHN *1995.845, *1995.846); see table 7 for measurements.

IDENTIFICATION: Sanborn (1937) and Jones and Hood (1993) discussed cranial and dental characters of *Rhynchonycteris naso*, and Husson (1962, 1978) provided a detailed description and comparative measurements.

TABLE 7
Measurements^a of *Rhynchonycteris naso* Collected at Paracou

Number/Sex	4 females	6 males
Weight	4.1 (3.5–4.6) 4	3.8 (3.5–4.0) 6
Total length	56.8 (53.0–60.0) 4	53.9 (50.0–56.5) 6
Tail length	12.5 (11.0–14.0) 4	12.2 (12.0–13.0) 6
Hind foot length	7.5 (7.0–8.0) 4	7.2 (7.0–8.0) 6
Ear length	12.8 (12.0–14.0) 4	12.8 (12.0–13.0) 6
Forearm length	37.6 (35.0–40.0) 4	37.1 (35.0–38.0) 5
Condyllocanine length	10.59 (10.56–10.61) 2	10.46 (10.21–10.72) 3
Zygomatic breadth	6.88 (6.86–6.89) 2	6.98 (6.67–7.28) 3
Maxillary tooththrow length	4.39 (4.24–4.54) 2	4.33 (4.25–4.44) 3
Breadth across molars	4.56 (4.52–4.60) 2	4.57 (4.50–4.58) 3

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

Measurements of specimens previously collected in French Guiana were reported by Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Koopman, 1994).

Our voucher specimens conform to previous qualitative descriptions of *Rhynchonycteris naso* and measurements fall within the range of size variation previously reported for the species. However, our morphometric data (table 7) somewhat exceed the range of size variation known from the Guianas, representing specimens both slightly smaller and slightly larger than those reported by Husson (1962, 1978) and Brosset and Charles-Dominique (1990).

FIELD OBSERVATIONS: We captured 10 individuals of *Rhynchonycteris naso*, all of which were found roosting over water in large (3–4 m in diameter) metal culverts or under concrete bridges. The five roosting groups we observed ranged in size from three to about nine individuals. One group of three bats consisted of two adult males and one adult female, and one group of about nine contained at least two adult males, but our information about the age and sex composition of the other groups is too incomplete to be informative.

Saccopteryx

References useful for identifying species of *Saccopteryx* include Sanborn (1937) and Jones and Hood (1993); both papers provide

keys based on external and craniodental morphology. Although three size-graded species (from large to small, *S. bilineata*, *S. leptura*, and *S. canescens*) are commonly collected sympatrically in Amazonia, the small species at Paracou is *S. gymnura*, previously unknown from the Guianas.

Saccopteryx bilineata (Temminck)

VOUCHER MATERIAL: 11 females (AMNH *265963, *265965, *267058, *267060, *267377, *267379, *267842; MNHN *1995.847, *1995.848, *1995.849, *1995.850) and 11 males (AMNH *265962, 265964, *265966, *267057, *267064, *267374, *267378, *267840; MNHN *1995.851, *1995.852, *1995.853); see table 8 for measurements. One individual of unknown sex (AMNH 266977) was recovered from the crop of a bat falcon.

IDENTIFICATION: Descriptions and measurements of *Saccopteryx bilineata* from the Guianas and elsewhere were provided by Thomas (1904), Sanborn (1937), Goodwin and Greenhall (1961), Husson (1962, 1978), and Brosset and Charles-Dominique (1990). There is considerable disagreement concerning trinomial nomenclature. Thomas (1904) explicitly recognized only two subspecies, *S. b. bilineata* in northern South America (including Trinidad), and *S. b. centralis* in Central America. Subsequently, Sanborn (1937) argued that size variation in this species was continuously distributed and precluded delin-

TABLE 8
Measurements^a of *Saccopteryx* Collected at Paracou

	<i>Saccopteryx</i> <i>bilineata</i>		<i>Saccopteryx</i> <i>gymnura</i>
Number/Sex	11 females	10 males	2 males
Weight	9.5 (7.8–13.2) 11	8.3 (6.7–9.9) 10	3.4 (3.3–3.5) 2
Total length	79.7 (76.0–86.0) 11	74.8 (72.0–78.0) 10	53.0 (52.0–54.0) 2
Tail length	20.3 (18.0–24.0) 11	18.5 (15.0–22.0) 10	13.5 (13.0–14.0) 2
Hind foot length	11.9 (11.0–13.0) 11	11.6 (11.0–13.0) 10	5.8 (5.5–6.0) 2
Ear length	16.1 (14.0–17.0) 11	16.4 (15.0–17.0) 10	12.3 (11.5–13.0) 2
Forearm length	49.4 (48.0–51.0) 11	47.0 (45.0–48.0) 10	34.6 (34.0–35.3) 2
Condylacanine length	15.69 (15.41–15.99) 5	15.61 (15.39–15.82) 6	11.35 (11.35) 1
Zygomatic breadth	11.06 (10.79–11.33) 5	10.91 (10.54–11.18) 6	7.79 (7.79) 1
Maxillary tooththrow length	7.20 (7.04–7.37) 5	7.16 (7.02–7.26) 6	4.61 (4.61) 1
Breadth across molars	7.55 (7.42–7.69) 5	7.40 (7.15–7.65) 6	5.11 (5.11) 1
	<i>Saccopteryx</i> <i>leptura</i>		
Number/Sex	12 females	12 males	
Weight	5.1 (4.2–6.4) 12	4.2 (3.8–4.6) 12	
Total length	62.8 (54–69) 12	57.3 (52.0–52.0) 12	
Tail length	13.6 (8.0–17.0) 12	13.7 (10.0–17.0) 12	
Hind foot length	8.5 (7.0–9.0) 12	8.6 (8.0–10.0) 12	
Ear length	13.3 (12.0–16.0) 12	13.0 (12.0–15.0) 12	
Forearm length	40.1 (39.0–42.0) 12	38.4 (36.0–40.0) 12	
Condylacanine length	12.49 (12.24–12.56) 4	12.31 (11.93–12.23) 3	
Zygomatic breadth	8.86 (8.72–8.95) 4	8.56 (8.55–8.80) 3	
Maxillary tooththrow length	5.21 (5.10–5.29) 4	5.22 (5.09–5.32) 3	
Breadth across molars	6.08 (5.94–6.25) 4	5.89 (5.87–5.89) 3	

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

ation of subspecies in the absence of other significant characters; in his revision, the names *insignis*, *perspicillifer*, and *centralis* were therefore regarded as strict synonyms of *S. bilineata*.

Although many authors have followed Sanborn's (1937) opinion (e.g., Husson, 1962, 1978), others have not. Cabrera (1958), for example, recognized *S. perspicillifer* (from Trinidad) as a distinct species, and Goodwin and Greenhall (1961) later treated *perspicillifer* as a valid subspecies of *S. bilineata*. Most recently, Koopman (1994) recognized *S. b. bilineata* as ranging from tropical Mexico throughout Central America and tropical South America except northern Venezuela, Trinidad, and Tobago, and *S. b. perspicillifer* as occurring in northern Venezuela, Trinidad, and Tobago).

Recognition of *perspicillifer* as a taxon

distinct from *bilineata* is apparently based entirely on size, with specimens from northern Venezuela, Trinidad (the type locality), and Tobago supposedly being larger and more robust than specimens from elsewhere in the Neotropics (Miller, 1899; Goodwin and Greenhall, 1961). However, this putative geographic pattern is not supported by available data. Instead, our personal observations and data reported by Thomas (1904), Sanborn (1937), Husson (1962, 1978), and Brosset and Charles-Dominique (1990) indicate that specimens from eastern Ecuador, Guyana, Surinam, French Guiana, Brazil, and Bolivia exhibit similar forearm, skull, and dental measurements as specimens from northern Venezuela, Trinidad, and Tobago. Thus, although significant geographic variation may exist among some populations of *Saccopteryx bilineata*, none of the subspecies



Fig. 21. Roost of *Saccopteryx bilineata* and *Micronycteris hirsuta* in creekside primary forest at Paracou. Small roosting groups of *S. bilineata* occupied the half-open basal part of the central cavity (large arrow) where they were just visible without artificial illumination in 1992 and 1994. A roosting group of *M. hirsuta* occupied the completely enclosed dark interior (small arrow) several meters above the colony of *S. bilineata* in 1992. In 1993 this roost was occupied only by *Carollia perspicillata*.

traditionally recognized by authors appear to be justified by the evidence at hand.

Our voucher material from Paracou conforms with previous descriptions of the species, and measurements fall within the range of size variation previously documented from the Guianas.

FIELD OBSERVATIONS: We recorded 34 captures (possibly including some recaptures) of *Saccopteryx bilineata*: 14 in ground-level mistnets, 11 in elevated mistnets, and 9 at roosts; additionally, 1 specimen was recovered from the crop of a road-killed *Falco rufigularis* (which had also eaten a specimen of *S. leptura*). Of the 14 ground-level mistnet captures, 4 were made in well-drained primary forest, 2 in swampy primary forest, 3 in creekside primary forest, and 5 in man-made clearings. Six *S. bilineata* were taken in nets suspended 10–21 m over a narrow dirt road, two were netted 10–13 m over a treefall gap in creekside primary forest, and three were netted 7–10 m above the ground in the subcanopy of swampy primary forest. Six of our mistnet captures were made before dark, between 18:00 and 18:35 hours.

We found five roosting groups of *Saccopteryx bilineata* at Paracou. All of these occupied more-or-less vertical cavities (by contrast with the essentially horizontal chambers typically used by *Cormura brevirostris* and *Peropteryx* spp.) with not-quite-completely dark interiors (the roosting bats were usually just visible without illumination), but other roost characteristics differed. One roost was in a 2-m-high chimney, open above and below, formed by the fused buttresses of a large tree (fig. 3); another was in the semicylindrical basal opening of a central cavity that extended far up into the trunk of a much smaller tree (fig. 21); two were in the open bases of hollow trees big enough for a grown man to stand inside; and the fifth was an open cleft, 12 m above the ground at its lowest point, in the trunk of another big tree (accessed by climbing a rope). Roosting groups that we were able to count varied from one to five individuals. Two individuals that we found roosting alone were both adult males. One group of five that we captured in its entirety consisted of two adult males, two adult females, and one juvenile.

Saccopteryx gymnura Thomas

Figure 22

VOUCHER MATERIAL: 2 males (AMNH *267843; MNHN *1995.862); see table 8 for measurements.

IDENTIFICATION: Characters and measurements of *Saccopteryx gymnura* were discussed by Thomas (1901b) and Sanborn (1937). No subspecies are current recognized (Koopman, 1994).

Our material of *Saccopteryx gymnura* from Paracou represents a range extension of approximately 900 km for this species, which was previously known only from a few localities along the lower Amazon in Brazil (Koopman, 1994). Despite this considerable geographic hiatus, the Paracou specimens conform closely with published descriptions of the holotype (Thomas, 1901b; Sanborn, 1937) and are indistinguishable from other Brazilian material referable to *S. gymnura* (AMNH 93519, 93520; USNM 392995, 460080).

The only species that might be confused with *Saccopteryx gymnura* is *S. canescens*. Although similar in size, these tiny bats can be distinguished unambiguously by (1) dorsal fur color (dark brown in *gymnura*, brown with strong grayish or yellowish frosting in *canescens*), (2) dorsal fur markings (stripes absent or very faint in *gymnura*, a pair of white stripes always visible and often bright in *canescens*), (3) ventral fur banding (unicolored dark brown in *gymnura*, bicolored black or dark brown with tan tips in *canescens*), (4) origin of the posterior part of the wing membrane (from the metatarsals in *gymnura*, from the tibia in *canescens*), and (5) length of the forearm (33.5–35.3 mm in *gymnura*, 35.8–40.8 mm in *canescens*). Although there is some species overlap in length of the maxillary tooththrow, our specimens of *gymnura* have shorter tooththrows (4.6 mm) than those previously reported for specimens of *canescens* (4.9–5.0 mm) from French Guiana (Brosset and Charles-Dominique, 1990).

FIELD OBSERVATIONS: Both of our specimens of *Saccopteryx gymnura* were captured in ground-level mistnets, one in a small clearing bordered by well-drained primary forest (fig. 2), the other over a narrow dirt

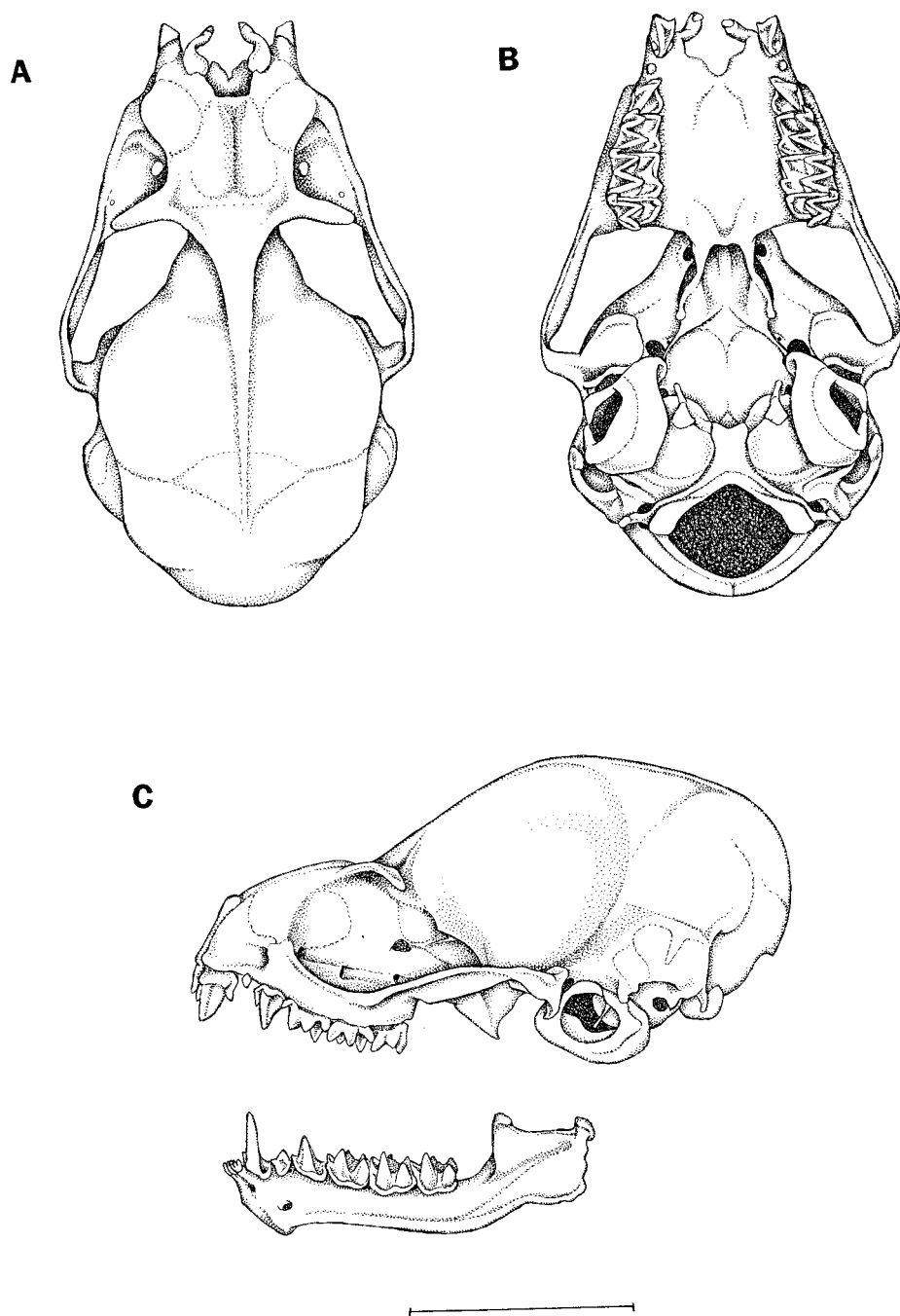


Fig. 22. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Saccopteryx gymnura* (MNHN 1995.862; male) from Paracou. Scale bar = 5 mm.

road bordered by secondary growth but with well-drained primary forest nearby (fig. 11). Both captures were made shortly after dark (18:55–19:15 hours).

Saccopteryx leptura (Schreber)

VOUCHER MATERIAL: 12 females (AMNH *265968, *265972, *267067, *267383, *267388, *267845, *267848, *267849; MNHN *1995-854, *1995-855, *1995-856, *1995-857) and 13 males (AMNH *265969, *265971, *267065, *267066, *267068, *267387, *267844, *267846, *267847; MNHN 1995-858, *1995-859, *1995-860, *1995-861); see table 8 for measurements. One individual of unknown sex (AMNH 266978) was recovered from the crop of a bat falcon (see Field Observations).

IDENTIFICATION: Descriptions and comparative measurements of *Saccopteryx leptura* from the Guianas and other regions of northern South American were provided by Sanborn (1937), Husson (1962, 1978), Brosset and Charles-Dominique (1990), and Jones and Hood (1993). No subspecies are currently recognized (Koopman, 1994).

Our specimens conform in all respects to previous descriptions of *Saccopteryx leptura*.

FIELD OBSERVATIONS: Of the 25 individuals of *Saccopteryx leptura* we captured at Paracou, 10 were taken in ground-level mistnets, 6 in elevated mistnets, and 9 at roosts; in addition, 1 specimen was found in the crop of a road-killed *Falco rufigularis* (which had also eaten a specimen of *Saccopteryx bilineata*). Of the 10 bats captured in ground-level mistnets, 1 was taken in well-drained primary forest, 1 in creekside primary forest, and the remaining 8 in manmade clearings. Of the six specimens captured in elevated nets, two were taken between 10 and 21 m above a narrow dirt road, two at 35–38 m in a treefall gap in well-drained primary forest, and two at 7–10 m in the subcanopy of swampy primary forest. Five mistnet captures were made before dark, between 18:00 and 18:40 hours.

We observed five roosting groups of *Saccopteryx leptura*, each at a different site. As for *S. bilineata*, roosts of this species are vertically oriented spaces, but we found *S. leptura* roosting in more exposed sites that were

not as dark as those used by *S. bilineata*. One roost was in the half-hollow trunk of a dead tree in secondary vegetation (fig. 23), three were in shallow recesses between the buttresses of living trees (in both swampy and well-drained primary forest), and the fifth was inside the semicylindrical basal sheath of a dead palm frond dangling about 20 m above the ground in the subcanopy of swampy primary forest. The roosting groups we found at Paracou consisted of one to four individuals. Three groups collected in their entirety consisted of (1) a solitary adult male, (2) an adult male-female pair, and (3) two adult males, one adult female, and one juvenile.

NOCTILIONIDAE

We captured both of the two known species of *Noctilio* at Paracou.

Noctilio albiventris Desmarest

MATERIAL: 1 male (AMNH *267089); see table 9 for measurements.

IDENTIFICATION: Husson (1962, 1978), Davis (1976b), and Brosset and Charles-Dominique (1990) provided descriptions and measurements of *Noctilio albiventris*. Davis (1976b) recognized four subspecies in his revision: *N. a. minor* (southern Mexico to northwestern Venezuela), *N. a. affinis* (western Amazonia, northern Venezuela and the coastal Guianas), *N. a. albiventris* (southeastern Venezuela and southern Guyana to eastern Brazil), and *N. albiventris cabrerai* (southwestern Brazil, Paraguay, and northern Argentina).

According to Davis (1976b), the coastal Guianan form, *N. a. affinis*, is substantially larger than the nominate subspecies. Although some overlap in size was reported in length of the maxillary tooththrow in both sexes and in forearm length of females (op. cit.), nonoverlapping measurements were given for forearm length in males (56.3–60.3 mm in *N. a. albiventris*, 61.5–70.0 mm in *N. a. affinis*). Unfortunately, the geographic samples closest to Paracou that Davis personally examined were from coastal Guyana (representing *affinis*) and near the mouth of the Amazon (representing *albiventris*), leaving a wide hiatus with no representative specimens



Fig. 23. Roost of *Saccopteryx leptura* in closed-canopy secondary growth at Paracou. Four individuals were found roosting together about 2 m above the ground in the semicylindrical interior of this broken trunk (arrow). Other roosts of this species were found in equally well-lighted spaces between the buttresses of living trees.

TABLE 9
Measurements^a of *Noctilio* Collected at Paracou

	<i>Noctilio albiventris</i>	<i>Noctilio leporinus</i>
Number/Sex	1 male	3 females
Weight	25.8	49.0 (44.5–52.0) 3
Total length	89.0	118.3 (112.0–123.0) 3
Tail length	20.0	24.3 (22.0–26.0) 3
Hind foot length	18.0	29.0 (29.0–29.0) 3
Ear length	23.0	28.0 (27.0–29.0) 3
Forearm length	61.0	79.3 (78.0–81.0) 3
Greatest length of skull	20.44	25.16 (25.16) 1
Condylolincisive length	19.03	23.65 (23.65) 1
Zygomatic breadth	14.86	18.78 (18.78) 1
Maxillary tooththrow length	7.66	9.61 (9.61) 1
Breadth across molars	9.97	12.29 (12.29) 1

^a Summary statistics (mean, observed range, and sample size) of measurements for each species. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

examined (i.e., Surinam, French Guiana, and the Brazilian State of Amapá). Based on the measurements of a Surinamese specimen reported by Husson (1962), however, Davis extended the presumed range of *affinis* to include the entire coastal region of the Guianas. Based on Davis' (1976b) map (reproduced by Hood and Pitocchelli [1983] without the dots indicating collecting localities), specimens from French Guiana would presumably represent *N. a. affinis*.

Contrary to that expectation, our specimen from Paracou and another reported from nearby Sinnamary (Brosset and Charles-Dominique, 1990) are morphologically intermediate to *affinis* and *albiventris* as those taxa were described by Davis (1976b). Maxillary tooththrow lengths of both French Guianan specimens fall in the zone of overlap between the low end of the range of variation reported for *N. a. affinis* and the high end of the range of variation reported for *N. a. albiventris*. The forearm measurement of the female reported by Brosset and Charles-Dominique (1990) similarly falls in the zone of subspecific overlap, while the forearm measurement of our male (table 9) fits within the gap that Davis reported between the ranges of variation of *affinis* and *albiventris* males.

Although Davis (1976b: fig. 5) mapped a discontinuity between the geographic distributions of *N. a. affinis* and *N. a. albiventris* extending across the Brazilian state of Amapá, there is no reason to believe that this is anything but an artifact of inadequate collecting. Rainforest habitats are distributed more-or-less continuously across the eastern Guianas to the Amazon, and we suspect that *Noctilio albiventris* is present throughout the area. Based on the morphologically intermediate material now available from French Guiana and on the likelihood that other intergrades will be found with future collecting in Amapá, we see no merit in continuing to recognize a subspecific distinction between the coastal Guianan and interior Amazonian populations of this species.

FIELD OBSERVATIONS: Our single specimen of *Noctilio albiventris* was mistnetted 1 m above the surface of a roadside puddle adjacent to well-drained primary forest.

Noctilio leporinus (Linnaeus)

VOUCHER MATERIAL: 3 females (AMNH *265974, *267398; MNHN *1995.863); see table 9 for measurements.

IDENTIFICATION: Descriptions and comparative measurements of *Noctilio leporinus* can be found in Husson (1962, 1978) and Davis (1973). Davis recognized three subspecies in his revision: *N. l. mastivus* (Mexico and the southernmost Bahamas south to western Ecuador and Venezuela), *N. l. leporinus* (Guianas and eastern Ecuador to eastern Brazil), and *N. l. rufescens* (Bolivia and southern Brazil to northern Argentina).

Our Paracou vouchers conform with Davis' (1973) description of the nominate subspecies and are similar in size to specimens previously reported from Surinam. These Guianan specimens are among the smallest known representatives of the species (Davis, 1973), one of our vouchers (MNHN 1995.863) having the smallest body weight (44.5 g) yet recorded for an adult *Noctilio leporinus*.

FIELD OBSERVATIONS: All three specimens that we captured at Paracou were taken in ground-level mistnets set across a small stream (fig. 14) in primary forest.

TABLE 10
Measurements^a of *Pteronotus parnellii* Collected at Paracou

Number/Sex	6 females	13 males
Weight	23.7 (19.6–27.2) 6	23.5 (19.8–27.1) 12
Total length	103.0 (99.0–106.0) 6	102.2 (94.0–109.0) 12
Tail length	26.3 (24.0–28.0) 6	25.9 (21.0–30.0) 12
Hind foot length	16.3 (15.0–18.0) 6	16.8 (15.0–19.0) 12
Ear length	22.5 (19.0–25.0) 6	23.8 (20.0–26.0) 12
Forearm length	63.8 (62.0–65.0) 6	63.3 (59.0–66.0) 12
Greatest length of skull	22.23 (21.96–22.72) 3	22.80 (21.60–23.19) 6
Condylolincisive length	21.63 (21.23–22.19) 3	22.59 (21.46–23.06) 6
Zygomatic breadth	12.93 (12.52–13.39) 3	13.45 (12.88–13.52) 6
Maxillary tooththrow length	9.75 (9.59–10.01) 3	10.13 (9.68–10.49) 6
Breadth across molars	8.46 (8.14–8.84) 3	8.90 (8.50–9.13) 6

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

MORMOOPIDAE

Although we collected only one mormoopid species at Paracou, another two could plausibly be expected to occur in the area (appendix 1). Smith's (1972) revision of the family is still the standard reference for identifying species of *Pteronotus*, the only mormoopid genus widespread in South American rainforests.

Pteronotus parnellii (Gray)

VOUCHER MATERIAL: 6 females (AMNH *267283, *267401, *267406, *267851; MNHN *1995.865, *1995.866) and 13 males (AMNH *267282, *267284, *267285, *267286, *267288, *267289, *267399, *267400, *267405, *269115; MNHN *1995.867, *1995.868, *1995.869); see table 10 for measurements. One individual of unknown sex (MNHN 1995.864) was found dead.

IDENTIFICATION: Descriptions and measurements of *Pteronotus parnelli* from the Guianas and elsewhere were provided by Husson (1962, 1978), Smith (1972), and Brosset and Charles-Dominique (1990). Smith (1972) recognized two subspecies on the South American mainland: *P. p. fuscus* (northeastern Colombia and northern Venezuela) and *P. p. rubiginosus* (southern Central America, Trinidad, and throughout Amazonia). Guianan specimens referred to *P. p. rubiginosus* are characterized by relatively large size

(forearm length 58.3–67.0 mm, maxillary tooththrow length 9.0–9.9 mm) and dark pelage (Husson, 1962, 1978; Smith, 1972; Brosset and Charles-Dominique, 1990).

Our voucher material conforms to Smith's (1972) description of *Pteronotus parnellii rubiginosus*, although many of the Paracou specimens are slightly larger than those previously reported from the Guianas.

FIELD OBSERVATIONS: All of the 18 individuals of *Pteronotus parnellii* that we captured at Paracou were taken in ground-level mistnets; additionally, two specimens were found dead under a concrete bridge. Seven individuals were netted in well-drained primary forest, five in swampy primary forest, three in creekside primary forest, two in manmade clearings, and one over a roadside puddle.

PHYLLOSTOMIDAE

The generic and higher level classification of phyllostomids used herein follows Peffley et al. (MS). Notable changes from current usage (Koopman, 1993) include our use of Glossophaginae to include lonchophyllines, our recognition of *Glyphoncyteris* and *Trinycteris* (formerly included in *Micronycteris*) as full genera, and our use of *Ectophylla* to include *Mesophylla*. Emended diagnoses of *Glyphoncyteris*, *Micronycteris*, *Trinycteris*, and *Ectophylla* are provided to justify these new usages.

TABLE 11
Measurements^a of Desmodontines Collected at Paracou

Number/Sex	<i>Desmodus rotundus</i>		<i>Diaemus youngi</i>	
	3 females	2 males	1 female	2 males
Weight	29.7 (28.8–30.6) 3	27.7 (25.8–29.6) 2	27.8	27.8 (26.6–29.0) 2
Total length	79.3 (76.0–82.0) 3	79.5 (75.0–84.0) 2	76.0	79.5 (74.0–85.0) 2
Tail length	0 (0–0) 3	0 (0–0) 2	0	0 (0–0) 2
Hind foot length	19.3 (18.0–21.0) 3	19.0 (18.0–20.0) 2	15.5	19.0 (18.0–20.0) 2
Ear length	19.0 (18.0–20.0) 3	18.5 (18.0–19.0) 2	17.0	17.0 (17.0) 1
Forearm length	60.8 (59.5–62.0) 3	55.5 (54.0–57.0) 2	48.6	49.0 (46.9–51.0) 2
Greatest length of skull	23.77 (23.71–23.82) 2	23.33 (23.33) 1	—	23.67 (23.67) 1
Condylolincisive length	22.00 (21.47–22.53) 2	21.31 (21.31) 1	—	21.22 (21.22) 1
Postorbital breadth	5.28 (5.22–5.34) 2	5.23 (5.23) 1	—	6.42 (6.42) 1
Braincase breadth	12.16 (12.15–12.17) 2	11.86 (11.86) 1	—	12.81 (12.81) 1
Mastoid breadth	12.16 (12.12–12.19) 2	11.99 (11.99) 1	—	12.55 (12.55) 1
Zygomatic breadth	11.91 (11.77–12.04) 2	11.86 (11.86) 1	—	12.80 (12.80) 1
Maxillary toothrow length	1.40 (1.37–1.42) 2	1.50 (1.50) 1	—	1.21 (1.21) 1
Breadth across molars	6.70 (6.43–6.97) 2	6.25 (6.25) 1	—	6.09 (6.09) 1

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

In the course of our fieldwork at Paracou we captured 49 phyllostomid species belonging to the subfamilies Desmodontinae (2 species), Glossophaginae (5 species), Phyllostominae (25 species), Carollinae (2 species), and Stenodermatinae (15 species). An additional 15 species (3 glossophagines, 4 phyllostomines, 1 carolline, and 7 stenodermatines) are known from other collecting localities in French Guiana and Surinam (appendix 1), and some of these could also be expected to occur in our study area. One of the phyllostomid species reported below is described as a new species, and two others were previously unknown from French Guiana.

DESMODONTINAE

We captured both of the two vampire species known to occur in the Guianas at Paracou. External characters (summarized by Emmons, 1990, 1997) are sufficient for field identifications of species in this subfamily, and Koopman's (1988) key includes useful craniodental characters as well.

Desmodus rotundus (E. Geoffroy)

VOUCHER MATERIAL: 3 females (AMNH *267211, *267504; MNHN *1995.985) and

2 males (AMNH *267503, *267505); see table 11 for measurements.

IDENTIFICATION: Numerous authors have provided descriptions and measurements of *Desmodus rotundus*, including Husson (1962, 1978), Swanepoel and Genoways (1979), Hall (1981), Koopman (1988), and Greenhall et al. (1983). Two subspecies are recognized by some authors (e.g., Hall, 1981; Jones and Carter, 1976; Greenhall et al., 1983): *D. r. rotundus* Geoffroy (1810) and *D. r. murinus* Wagner (1840). Whereas Cabrera (1958) and Husson (1962, 1978) referred all South American specimens to *D. r. rotundus*, Jones and Carter (1976) and Greenhall et al. (1983) gave the range of *D. r. murinus* as extending from Mexico southward throughout northern South America to Amazonia. Unfortunately, no data were presented to support either the differentiation of these two forms or their geographic distribution. Although we are aware of some potentially significant geographic variation within *D. rotundus*, it is not currently possible to distinguish subspecies in the absence of a comprehensive revision.

Our material of *Desmodus rotundus* corresponds closely to that described from Surinam by Husson (1962, 1978) and from

French Guiana by Brosset and Charles-Dominique (1990).

FIELD OBSERVATIONS: All of the five *Desmodus rotundus* we captured at Paracou were taken in ground-level mistnets. Two individuals were taken in well-drained primary forest, two in swampy primary forest, and one in a manmade clearing.

Diaemus youngi (Jentink)

VOUCHER MATERIAL: 1 female (AMNH *268571) and 2 males (AMNH *266347; MNHN *1995.984); see table 11 for measurements.

IDENTIFICATION: Descriptions and measurements of *Diaemus youngi* appear in Husson (1962, 1978), Swanepoel and Genoways (1979), Hall (1981), Koopman (1988), and Greenhall and Schutt (1996). Some authors place *D. youngi* in the genus *Desmodus* (e.g., Handley, 1976; Emmons, 1990), but we retain *Diaemus* as a distinct genus following Cabrera (1958), Husson (1962, 1978), Jones and Carter (1976), Hall (1981), Koopman (1993, 1994), and Greenhall and Schutt (1996). Although Thomas (1928c) named *D. y. cypselinus* based on material from Peru, Husson (1962: 198) noted that *cypselinus* was probably "not subspecifically different from the typical form." Subspecies of *Diaemus youngi* have not been recognized by most authors (e.g., Cabrera, 1958; Koopman, 1993, 1994; Greenhall and Schutt, 1996).

Our material of *Diaemus youngi* from Paracou conforms closely with previous qualitative descriptions of the species. Although forearm and cranial dimensions of our specimens are considerably smaller than those reported for specimens from Mexico, Costa Rica, Peru, Venezuela, and Trinidad, they are only slightly smaller than those previously reported from the Guianas (Thomas, 1928b; Goodwin and Greenhall, 1961; Husson, 1962; Hall, 1981; Brosset and Charles-Dominique, 1990; Greenhall and Schutt, 1996). The significance of this variation is not clear, but we note that the Guyanese holotype of *D. youngi* (RNH 12088) is one of the smallest specimens hitherto reported in the literature (Husson, 1962; Carter and Dolan, 1978). Thus, if subspecies are recognized in some future revisionary study, our material would

TABLE 12
Measurements^a of *Anoura caudifera*
Collected at Paracou

Number/Sex	1 male
Weight	8.9
Total length	60.0
Tail length	0.0
Hind foot length	11.0
Ear length	13.0
Forearm length	33.6
Greatest length of skull	21.61
Condylolincisive length	20.74
Postorbital breadth	4.64
Braincase breadth	8.68
Mastoid breadth	9.02
Zygomatic breadth	9.60
Maxillary tooththrow length	7.85
Breadth across molars	5.68

^a Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

presumably be referred to the nominate form.

FIELD OBSERVATIONS: Two of the three *Diaemus youngi* we captured at Paracou were taken in ground-level mistnets, one in well-drained primary forest, and the other in a manmade clearing. The third specimen was captured in a mistnet suspended 17–20 m above a narrow dirt road.

GLOSSOPHAGINAE

We captured five glossophagine species at Paracou, but one or two additional species might also be expected in our study area (appendix 1). Great care must be exercised in identifying glossophagines in the field, as even some genera can be hard to distinguish externally until familiarity is gained with the nuances of character expression in this group.

Anoura caudifera (E. Geoffroy)

VOUCHER MATERIAL: 1 male (AMNH *267290); see table 12 for measurements.

IDENTIFICATION: Keys to the species of *Anoura* were provided by Tamsitt and Nagorsen (1982) and Handley (1984), but new species have been described subsequently (Molinari, 1994) and additional taxa still await description (Emmons, 1997). Handley (1984) and

Molinari (1994) are especially useful references because they tabulated measurement data and provided detailed morphological comparisons among species that could easily be confused. Other useful references containing descriptions and measurements of *A. caudifera*⁶ are Husson (1962, 1978), Tamsitt and Valdivieso (1966), Taddei (1975b), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Webster and Jones (1984), and Brosset and Charles-Dominique (1990). No subspecies of *A. caudifera* are currently recognized (Koopman, 1994; Molinari, 1994).

Although our single specimen agrees in most respects with previous descriptions of *Anoura caudifera*, several of its measurements fall in the zone of morphometric overlap between *A. caudifera* and a smaller species recently described by Molinari (1994), *A. luismanueli*. Like two individuals of *caudifera* reported from Surinam by Williams and Genoways (1980a), the Paracou specimen lacks a distinct tail enclosed within the uropatagium, and thus total body length is reduced. Forearm length of the Paracou specimen likewise falls at the bottom end of the range of variation previously reported for *A. caudifera* (e.g., by Tamsitt and Valdivieso, 1966). Molinari (1994) suggested that Tamsitt and Valdivieso may have included specimens of *luismanueli* or another small undescribed *Anoura* in their samples, but Molinari's estimate of the range of forearm length in *caudifera* differs little from those of previous authors. Our specimen has a forearm slightly smaller than Molinari reported for true *caudifera* (33.6 mm as compared with 34.6), a difference that we do not regard as significant given the range of variation commonly seen within other phyllostomid species. The Paracou specimen also has a shorter maxillary tooththrow than do specimens of *caudifera* previously reported from French Guiana and Venezuela, but in this respect it resembles Surinamese material measured by Husson (1962, 1978), Williams and Genoways (1980a), and Molinari (1994).

Comparisons of our voucher to Molinari's

(1994) descriptions of *Anoura luismanueli* and *A. caudifera* are otherwise consistent with its identification as a small example of *caudifera*. The Paracou specimen has a longer calcar and broader uropatagium than seen in *luismanueli*, and it lacks a continuous, dense fringe of hairs along the uropatagial edge. Instead, the free margin of the uropatagium is lightly furred near the midline but is naked laterally, a trait diagnostic of *caudifera* (Molinari, 1994). Other aspects of the pelage of the Paracou specimen agree with Molinari's description of *caudifera* with the exception of the color of the bases of the hairs in our specimen, which are grayish-white rather than yellowish- or creamy-white as he described. Given the range of variation in basal fur color that we have observed in other species, we interpret this as within-species variation.

FIELD OBSERVATIONS: Our single example of *Anoura caudifera* was taken in a ground-level mistnet in creekside primary forest.

Choeroniscus minor (Peters)

Figure 24

VOUCHER MATERIAL: 8 females (AMNH *266120, *266121, *266123, *266377, *267153; MNHN *1998.668, 1998.669, *1998.670) and 5 males (AMNH *266124, *267946, *267947, *267948; MNHN 1998.671); see tables 13 and 14 for measurements.

IDENTIFICATION: The complex taxonomic history of *Choeroniscus*, particularly of the smaller species originally placed in the genus *Choeronycteris*, is unfortunately relevant for understanding the correct identification of our Paracou vouchers.

Choeronycteris minor was first described by Peters (1868) based on a specimen from Surinam. Although Goodwin and Greenhall (1961) stated that the type was destroyed in World War II, Husson (1962) reported that Peter's original specimen was, in fact, still intact at the Stuttgart museum. Husson (1962) published measurements and a photograph of the holotype (SMN 441), and also provided a detailed description. A second small species, *Choeronycteris intermedia*, was described by Allen and Chapman (1893) based on specimens from Trinidad, and Tho-

⁶ We follow Handley's (1984) spelling of the specific epithet, which Koopman (1993) and most other authors have incorrectly spelled "*caudifer*."

mas (1912a) named a third, *Choeronycteris inca*, based on a specimen from Peru. Thomas (1928a) subsequently subdivided *Choeronycteris*, placing *minor*, *intermedia*, and *inca* in his new genus *Choeroniscus*.

Considerable confusion has surrounded the use of these three specific epithets (Thomas, 1912a; Sanborn, 1954; Goodwin and Greenhall, 1961; Husson, 1962; Koopman, 1978; and Williams and Genoways, 1980a), much of it the result of small available sample sizes and marked sexual dimorphism (Genoways et al., 1973; Koopman, 1978). The latter factor is crucial because the holotypes of *minor* and *inca* are males, while that of *intermedius* is a female. Conflicting reports concerning the morphology and sex of the supposedly lost holotype of *minor* only served to compound the real biological problem, whether these names really represent three or fewer species.

There is general agreement that Allen and Chapman (1893) named their Tinidadian material as a new species in part because several measurements of *minor* were incorrectly reported by Peters (1868). Thomas (1912a: 404) observed that

The Trinidad bat described by Allen and Chapman as *Ch. intermedia* is very probably the same as *Ch. minor*, as those authors were deceived by Peter's impossible measurement of 11 mm. for the calcar, an organ drawn as about 5 mm. long in the more recently published plate of the latter species . . .

Thomas (1912a) then described *inca* based on dental proportions (length and width of the premolars and molars) in which it supposedly differed from *minor*. He also noted that the skull of *inca* was larger and broader than that of *minor*, but this comparison was apparently based on a specimen of *minor* other than the holotype, as measurements of the latter do not confirm his observation (table 13).

Most recent authors have followed Koopman (1978) in regarding *inca* as a junior synonym of *minor*, and *intermedius* as a potentially distinct species. Koopman's (1978: 8) conclusion that two species could be recognized was based on observations concerning dental variation and length of the rostrum:

Study of a number of skulls of *Choeroniscus* from Trinidad, British Guiana, Brazil, Peru, and Ecuador [has] convinced me that two species can be distin-

guished . . . by rostral length, which is reflected in maxillary tooth row length. Thomas (1912[a]) distinguished *inca* from *minor* solely by the relative sizes of the premolars and molars. On the basis of these skulls, I can see considerable variation in this character, but no clearcut distinction between two forms. The species with the longer rostrum would then be called *C. minor* (*inca* a synonym) and the species with the shorter rostrum would stand as *C. intermedia* [sic].

Koopman (1994) gave the range of *minor* as extending from coastal Ecuador to the mouth of the Amazon, northward to eastern Venezuela, and southward to northwestern Bolivia. Although most specimens of small *Choeroniscus* recently collected in the Guianas have been identified as *intermedius* (e.g., by Brosset and Charles-Dominique, 1990), a long-muzzled female from Guyana (AMNH 140471) was referred to *minor* by Williams and Genoways (1980a).

In attempting to identify our material from Paracou, we examined the holotype of *intermedius*; Husson's (1962) measurements, photographs, and description of the holotype of *minor*; Thomas's (1912a) description of the holotype of *inca*; specimens referred to *intermedius* and *minor* in the AMNH; and measurements of additional specimens referred to *intermedius* and *minor* by Genoways et al. (1973), Genoways and Williams (1980a), Ochoa and Fernández (1982), Brosset and Charles-Dominique (1990), and Anderson (1997). Although we kept males and females separate, and investigated variation in size, skull shape, and dental morphology, we found no consistent differences among named forms of small *Choeroniscus*. For example, dental morphology in our series of 13 specimens from Paracou is highly variable, with some individuals having much shorter or longer teeth than others, others having narrower or broader teeth, etc. These differences form no consistent pattern and do not appear to be correlated with body size or with rostral proportions. Because our sample includes individuals with both "*minor*-type" and "*inca*-type" teeth (sensu Thomas, 1912a), as well as others with intermediate conditions, we follow Koopman (1978, 1993, 1994) in concluding that *minor* and *inca* are conspecific.

Dental morphology has never been used to separate *minor* (or *inca*) from *intermedius*.

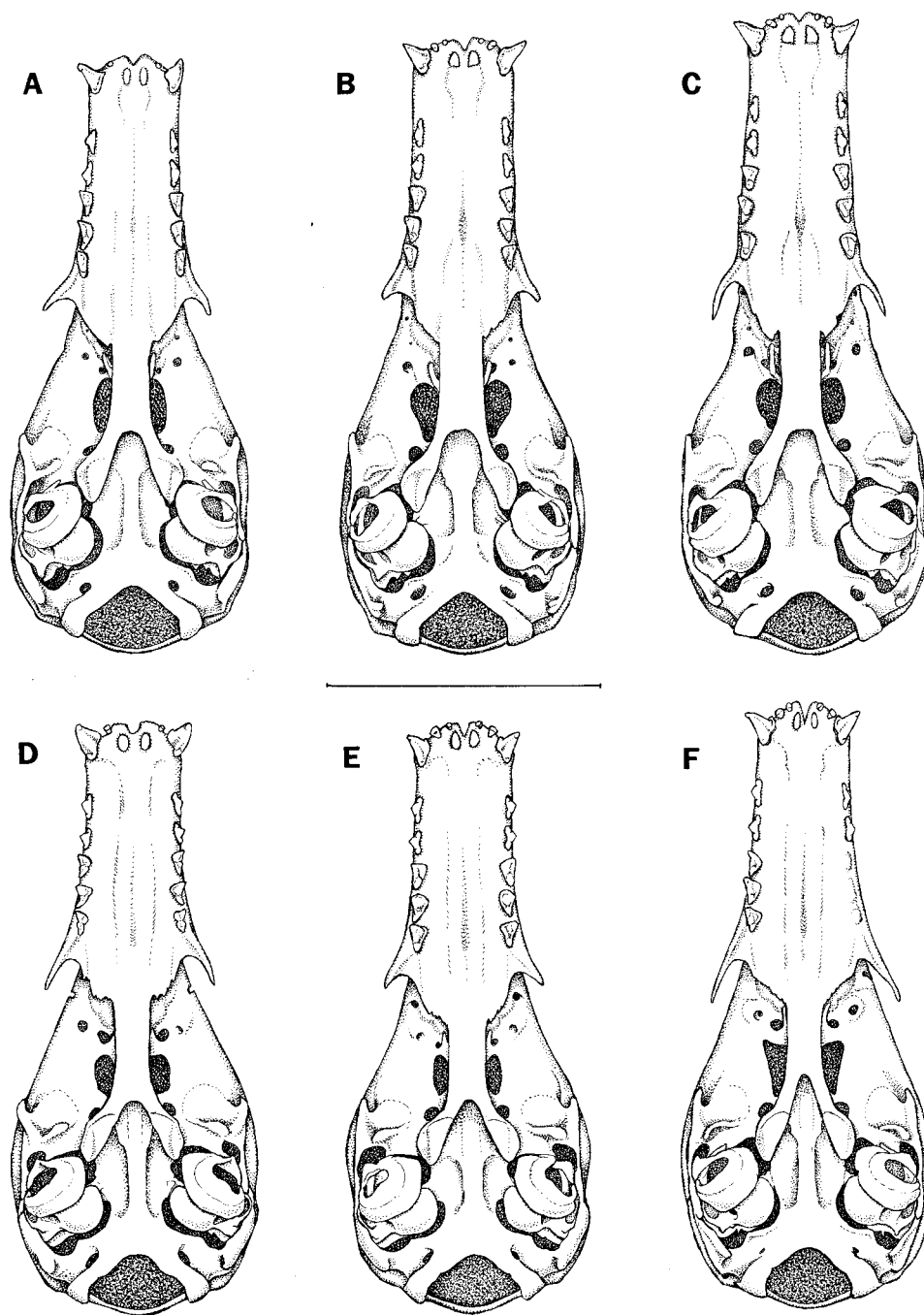


Fig. 24. Ventral views of the skull of six individuals of *Choeroniscus minor* from Paracou showing intraspecific variation in craniodental morphology. (A) AMNH 266377 (female); (B) MNHN 1995.1271 (female); (C) AMNH 266123 (female); (D) AMNH 267948 (male); (E) AMNH 267946 (male); (F) AMNH 267947 (male). Note variation in relative size of the premolars and molars, skull length and breadth, rostral proportions, and form of the palate. This series includes individuals with “*minor*-type”

TABLE 13
Measurements^a of Male *Choeroniscus minor*

	<i>Choeroniscus minor</i> from Paracou	<i>Choeroniscus</i> "intermedius" from Trinidad ^b (= <i>C. minor</i>)	Holotype of <i>Choeroniscus minor</i> from Suriname ^c (SMN 441)	Holotype of <i>Choeroniscus inca</i> from Peru ^d (BMNH 12.9.5.2)
Number/Sex	4 males	10 males	1 male	1 male
Weight	8.0 (7.0–8.8) 4	—	—	—
Total length	63.8 (61.0–68.0) 4	63.1 (61.0–66.0) 10	—	62.0
Tail length	8.0 (7.0–9.0) 4	7.8 (6.0–9.0) 10	—	8.0
Hind foot length	9.1 (8.5–10.0) 4	8.5 (7.5–9.0) 10	—	—
Ear length	12.3 (12.0–12.5) 4	12.8 (11.0–14.0) 10	—	—
Forearm length	34.3 (33.0–35.0) 4	34.1 (32.5–35.7) 10	34.8	33.0
Greatest length of skull	22.19 (21.76–22.36) 4	21.8 (21.2–22.9) 10	21.9	—
Condylolincisive length ^e	21.76 (21.16–21.85) 4	21.2 (20.5–22.0) 10	21.6	—
Braincase breadth	8.65 (8.50–8.87) 4	8.3 (8.1–8.8) 10	8.8	8.5
Mastoid breadth	8.40 (8.22–8.62) 4	8.3 (8.0–8.6) 10	8.6	—
Zygomatic breadth	8.29 (8.23–8.36) 3	—	8.5	—
Maxillary tooththrow length	7.74 (7.50–7.99) 4	7.5 (7.0–7.9) 10	7.7	7.8
Breadth across molars	4.08 (3.98–4.25) 3	4.3 (4.0–4.7)	4.6	—
Breadth across canines	3.92 (3.75–4.00) 4	—	—	—

^a Summary statistics (mean, observed range, and sample size) of measurements for each sample. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

^b Data from Genoways et al. (1973); they identified these bats as *Choeroniscus intermedius*.

^c Data from Husson (1962).

^d Data from Thomas (1912a).

^e Because the incisors are tiny teeth that are often missing in *Choeroniscus*, this measurement was made to the anteriormost end of the premaxilla, which forms a flat projection beyond the canines. This measurement, which we list as "condylolincisive length" for convenience, is equivalent to that termed "condylobasal length" by most authors, but is not strictly homologous to either measurement as applied to other taxa with larger incisors.

Instead, measurements of the skull, rostrum, and maxillary tooththrow appear to be the only characters so employed in recent years (Koopman, 1978; Williams and Genoways, 1980a). Rather than confirming that *minor* and *intermedius* are distinct species, our comparisons of measurement data show the opposite. Whereas measurements of our female specimens from Paracou broadly overlap those of the female holotype of *intermedius*, measurements of our males overlap those of the male holotypes of *minor* and *inca* (tables 13, 14). For both sexes, mea-

surements of our sample correspond closely to those reported for a large series (10 males and 26 females) of toptotypical *intermedius* from Trinidad (Genoways et al., 1973). Measurements of other specimens from Venezuela and the Guianas (reported by Genoways and Williams [1980a], Ochoa and Fernández [1982], and Brosset and Charles-Dominique [1990]) and Bolivia (Anderson, 1997) further fill the morphometric gap that Koopman (1978) observed between his small series of *minor* and *intermedius*. Considering the possibility that our largest voucher specimens

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dentitions (short premolars and long molars; e.g., **E**), others with "inca-type" teeth (premolars and molars subequal in length; e.g., **D**), and dental intermediates (e.g., **A**). It also includes large individuals with a relatively long ("minor-type") rostrum (e.g., **C**), smaller specimens with a shorter ("intermedius-type") rostrum (e.g., **A**), and intermediates (e.g., **B**). Scale bar = 10 mm.

TABLE 14
Measurements^a of Female *Choeroniscus minor*

	<i>Choeroniscus minor</i> from Paracou	<i>Choeroniscus</i> "intermedius" from Trinidad ^b (= <i>C. minor</i>)	Holotype of <i>Choeroniscus intermedius</i> from Trinidad (AMNH 6072/4791)	<i>Choeroniscus minor</i> from Kamakusa, Guyana ^c (AMNH 140471)
Number/Sex	7 females	26 females	1 female	1 female
Weight	9.8 (8.0–12.0) 7	—	—	—
Total length	68.1 (65.0–70.0) 7	63.4 (56.0–71.0) 26	—	—
Tail length	7.8 (6.0–9.0) 7	7.6 (4.0–11.0) 26	—	—
Hind foot length	9.0 (9.0–9.0) 7	8.8 (7.0–11.0) 26	—	—
Ear length	12.3 (11.0–13.0) 7	12.1 (10.0–14.0) 26	—	—
Forearm length	34.3 (33.0–36.0) 6	34.7 (26.5–38.4) 26	34.5	37.1
Greatest length of skull	23.36 (22.62–23.99) 7	23.1 (22.3–24.1) 26	22.58	24.44
Condylolincisive length ^d	22.75 (21.75–23.55) 7	22.5 (21.6–23.4) 26	21.90	23.90
Braincase breadth	8.59 (8.41–8.94) 7	8.5 (8.1–8.9) 26	8.43	8.72
Mastoid breadth	8.59 (8.44–9.07) 7	8.6 (8.4–9.0) 26	8.41	8.93
Zygomatic breadth	8.42 (8.09–8.90) 5	—	—	8.81
Maxillary toothrow length	8.08 (7.87–8.46) 7	8.1 (7.5–8.7) 26	7.75	8.33
Breadth across molars	4.25 (3.96–4.39) 7	4.3 (4.2–4.7) 26	4.37	4.67
Breadth across canines	4.14 (3.74–4.40) 6	—	3.85	4.39

^a Summary statistics (mean, observed range, and sample size) of measurements for each sample. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

^b Data from Genoways et al. (1973); they identified these bats as *Choeroniscus intermedius*.

^c This specimen, measured by us, was identified as *Choeroniscus minor* by Karl Koopman based on size and length of the rostrum. Some measurements of this specimen were reported by Genoways and Williams (1980a), who cited it as a possible example of *minor* for comparison with slightly smaller specimens that they referred to *intermedius*.

^d Because the incisors are tiny teeth that are often missing in *Choeroniscus*, this measurement was made to the anteriormost end of the premaxilla, which forms a flat projection beyond the canines. This measurement, which we list as "condylolincisive length" for convenience, is equivalent to that termed "condylobasal length" by most authors, but is not strictly homologous to either measurement as applied to other taxa with larger incisors.

might represent *minor* and the smallest *intermedius*, we carefully examined variation in external and craniodental morphology within our series, but ultimately found no evidence that the Paracou material represents more than one species. In our view, specimens identified as *intermedius* in the literature simply represent the lower end of a normal range of within-species size variation, while those identified as *minor* and *inca* represent the upper end of this range. We therefore conclude that these epithets represent a single species for which the oldest available name is *Choeroniscus minor* (Peters, 1868). Recognition of subspecies appears to be unjustified based on the data currently at hand.

FIELD OBSERVATIONS: We captured 13 individuals of *Choeroniscus minor* at Paracou, of which 7 were taken in ground-level mist-

nets and 6 at roosts. Three individuals were netted in swampy primary forest, three in creekside primary forest, and one in a man-made clearing. One roosting group of six bats was found on the dark underside of a fallen tree with large buttresses (similar to that shown in fig. 17) in well-drained primary forest; of this group, one adult male and four adult females were captured, and one bat escaped. Another roosting bat, a solitary adult male, was found hanging beneath the undercut bank of a dry streambed in well-drained primary forest.

Glossophaga soricina (Pallas)

VOUCHER MATERIAL: 10 females (AMNH *267134, *267137, *267138, *267448, *267449, *267953, *267956, 267958; MNHN

TABLE 15
Measurements^a of *Glossophaga* and *Lichonycteris* Collected at Paracou

Number/Sex	<i>Glossophaga soricina</i>		<i>Lichonycteris obscura</i>
	9 females	22 males	1 female
Weight	9.1 (8.3–10.5) 9	8.9 (7.4–10.0) 22	10.4
Total length	61.4 (57.0–66.0) 9	61.8 (56.0–69.0) 22	53.0
Tail length	8.4 (5.0–11.0) 9	8.0 (5.0–9.0) 22	7.0
Hind foot length	10.8 (9.5–11.0) 9	10.6 (9.0–11.0) 22	10.0
Ear length	13.6 (13.0–14.0) 8	13.1 (12.0–14.0) 22	12.0
Forearm length	35.1 (34.0–36.5) 9	34.6 (33.0–36.0) 21	35.0
Greatest length of skull	20.31 (20.12–20.50) 2	20.23 (19.68–20.71) 7	—
Condylolincisive length	19.21 (18.97–19.45) 2	19.16 (18.70–19.67) 7	—
Postorbital breadth	4.78 (4.72–4.84) 2	4.64 (4.54–4.74) 5	—
Braincase breadth	8.57 (8.52–8.62) 2	8.66 (8.37–8.95) 7	—
Mastoid breadth	8.82 (8.71–8.92) 2	8.85 (8.71–9.14) 7	—
Zygomatic breadth	9.21 (9.11–9.30) 2	9.17 (8.83–9.77) 7	—
Maxillary toothrow length	6.91 (6.71–7.10) 2	6.80 (6.66–7.00) 7	—
Breadth across molars	5.37 (5.32–5.42) 2	5.23 (5.12–5.39) 7	—

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

*1995.1040, *1995.1041) and 25 males (AMNH *266090, *266091, *266092, *266093, *266094, *266095, 266099, *267139, *267140, *267949, *267950, *267951, 267954, *267955, 267957, *267959; MNHN *1995.1042, *1995.1043, *1995.1044, *1995.1045, *1995.1046, *1995.1047, 1995.1048, *1995.1049, *1995.1050); see table 15 for measurements.

IDENTIFICATION: The most useful reference for identifying species of *Glossophaga* is Webster's (1993) revision, which includes a key as well as detailed descriptions and comparative measurements. Alvarez et al. (1991) provided a good description of *G. soricina*, but the principal reference for the species is also Webster's revision. Five subspecies of *G. soricina* are currently recognized, of which three occur in South America: *G. s. handleyi* (Mexico throughout Central America to northern and western Colombia), *G. s. soricina* (South America east of the Andes from Colombia and Venezuela in the north to Paraguay and northern Argentina), and *G. s. valens* (drier areas of western Ecuador and Peru) (Alvarez et al., 1991; Webster, 1993; Koopman, 1994). Measurements of specimens taken in the Guianas were reported by

Husson (1962, 1978), Brosset and Charles-Dominique (1990), and Webster (1993).

Our Paracou material conforms in all respects with Webster's (1993) description of *Glossophaga soricina soricina*, and their measurements (table 15) fall within the range of variation previously reported for *G. soricina* in Brazil and the Guianas (Husson, 1962, 1978; Taddei, 1975b; Brosset and Charles-Dominique, 1990; Webster, 1993).

FIELD OBSERVATIONS: We recorded 56 captures (possibly including some recaptures) of *Glossophaga soricina* at Paracou, of which 45 were in ground-level mistnets and 11 were at roosts. Seven of the mistnet captures were in well-drained primary forest, 11 were in swampy primary forest, 3 were in creek-side primary forest, and 24 were in manmade clearings. The proportional difference in capture-habitat frequencies between this species and *Lonchophylla thomasi*, the only other common glossophagine at Paracou (see below), is noteworthy: *G. soricina* was more commonly netted in modified habitats and *L. thomasi* in primary habitats than would be expected if these sympatric nectarivores did not differ in habitat use (table 16). Although this result is consistent with Brosset and

TABLE 16
Comparison of Capture-Habitat Frequencies
Between *Glossophaga soricina* and
Lonchophylla thomasi Taken in
Ground-Level Mistnets at Paracou^a

	Capture habitats		Totals
	Primary	Modified	
<i>G. soricina</i>	21	24	45
<i>L. thomasi</i>	28	8	36
Totals	49	32	81

$\chi^2 = 8.1$, $df = 1$, $p < 0.01$

^a Table entries are numbers of captures (possibly including some recaptures). The chi-square value calculated from these data tests the null hypothesis of no interspecific difference in proportions of captures by habitat.

Charles-Dominique's (1990) characterization of *G. soricina* as a species of modified biotopes, we note that specimens are in fact known from ecologically pristine localities in French Guiana (e.g., USNM 548471, 548472, collected by L. H. Emmons at Saut Pararé in 1984).

Of the three roosts of *Glossophaga soricina* we found at Paracou, two were in tree cavities (figs. 25, 26) and one was under under a concrete bridge. The bridge roost contained many *G. soricina*, perhaps hundreds (of which seven males and one female were collected as vouchers), as well as roosting groups of *Rhynchonycteris naso* and *Carollia perspicillata*. One tree cavity roost occupied by an adult male-female pair of *G. soricina* (fig. 26) was also shared with *C. perspicillata*; the other tree cavity roost was occupied a solitary adult male.

Lichonycteris obscura Thomas

VOUCHER MATERIAL: 1 female (AMNH *267960); see table 15 for measurements.

IDENTIFICATION: Two color morphs occur among specimens of *Lichonycteris*, a dark brown form that agrees with Thomas' (1895) original description of *L. obscura*, and a pale brown form that is often identified as *L. degener* Miller (1931). However, the taxonomic status of the latter is problematic due to confusion regarding patterns of variation in both craniodental and pelage characters (Gardner,

1976; Hill, 1985; Ochoa et al., 1993). Pending a revision of the genus, we follow Gardner (1976), Hill (1985), Ochoa et al. (1993), and Koopman (1993, 1994) in regarding *degener* as a junior synonym of *obscura*. Descriptions and comparative measurements of *L. obscura* so defined can be found in Husson (1962, 1978), Gardner (1976), Swanepoel and Genoways (1979), Hill (1985), Brosset and Charles-Dominique (1990), and Ochoa et al. (1993).

Our chocolate-brown specimen agrees closely with previous descriptions of *Lichonycteris obscura*, and falls within the range of variation in measurements previously reported in the literature.

FIELD OBSERVATIONS: Our specimen was captured in a ground-level mistnet in well-drained primary forest.

Lonchophylla thomasi J. A. Allen

VOUCHER MATERIAL: 15 females (AMNH *266100, *266107, *266108, *266109, *267147, *267148, *267149, *267451, *267452, *267939; MNHN *1995.1096, *1995.1097, *1995.1098, *1995.1099, *1995.1100) and 23 males (AMNH *266101, *266102, *266103, *266104, *266105, *266106, *266110, *266113, *266114, *266116, *266117, *267150, *267940, *267941, *267942, *267943; MNHN *1995.1101, *1995.1102, *1995.1103, *1995.1104, *1995.1105, *1995.1106, *1995.1107); see table 17 for measurements.

IDENTIFICATION: The most useful reference for identifying species of *Lonchophylla* is Taddei et al. (1983), who provided a key and discussed variation. We consulted descriptions and comparative measurements of *Lonchophylla thomasi* in Husson (1962, 1978), Hill (1964, 1980), Gardner (1976), Taddei et al. (1978, 1983), Swanepoel and Genoways (1979), and Brosset and Charles-Dominique (1990). No subspecies of *L. thomasi* are currently recognized (Taddei et al., 1983; Koopman, 1994).

Our voucher material, one of the largest series available from a single locality, conforms in all respects to previous descriptions of *Lonchophylla thomasi*.

FIELD OBSERVATIONS: We recorded 55 captures (possibly including some recaptures) of



Fig. 25. A large kimboto, *Pradosia cochlearia* (Sapotaceae), a common canopy emergent in well-drained primary forest at Paracou that often has rotted cavities sheltering bats and other mammals. In 1991 the cavernous lower chamber of this tree (arrow) contained a solitary *Glossophaga soricina*, but in 1992 we found a roosting group of four *Micronycteris megalotis* and another consisting of one *Carollia perspicillata* in the same space; in 1993 and 1994 this roost was occupied by small groups of *C. perspicillata* only.



Fig. 26. Roost of *Glossophaga soricina*, *Phyllostomus elongatus*, and *Carollia perspicillata* in well-drained primary forest at Paracou. This tree cavity, about 60–70 cm in diameter and several meters high, contained about 20 *C. perspicillata* (two of which, both adult females, were collected as vouchers) and one adult male *P. elongatus* in 1992. In 1993 the same space contained about 10 *C. perspicillata* and 2 *G. soricina* (an adult male-female pair). It is possible that this roost was used by *Vampyrum spectrum* in 1991, when RSV observed two huge bats vocalizing loudly and flying around the opening at night; however, the roost was vacant when we climbed the tree to investigate two days later.

TABLE 17
Measurements^a of *Lonchophylla thomasi* Collected at Paracou

Number/Sex	14 females	21 males
Weight	7.9 (6.5–9.9) 14	6.7 (5.5–8.6) 21
Total length	59.8 (53.0–67.0) 14	59.4 (56.0–64.0) 21
Tail length	8.5 (7.0–10.0) 14	9.0 (7.0–11.0) 21
Hind foot length	9.6 (8.0–10.0) 14	9.5 (7.5–10.0) 21
Ear length	14.4 (13.0–18.0) 14	14.2 (13.0–17.0) 20
Forearm length	33.0 (32.0–34.0) 12	32.6 (31.0–34.0) 19
Greatest length of skull	20.24 (19.98–20.57) 3	20.53 (20.13–20.80) 5
Condylolincisive length	19.44 (19.27–19.58) 3	19.87 (19.52–20.30) 5
Postorbital breadth	4.24 (4.18–4.29) 3	4.06 (3.84–4.30) 5
Braincase breadth	8.32 (8.14–8.65) 3	8.51 (8.38–8.69) 5
Mastoid breadth	8.56 (8.48–8.67) 3	8.91 (8.83–9.01) 5
Zygomatic breadth	8.82 (8.75–8.86) 3	9.11 (8.90–9.20) 5
Maxillary toothrow length	6.44 (6.20–6.65) 3	6.61 (6.56–6.68) 5
Breadth across molars	5.22 (5.12–5.25) 3	5.13 (4.98–5.30) 5

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

Lonchophylla thomasi at Paracou, of which 36 were in ground-level mistnets, 1 was in an elevated net, and 18 were at roosts. Of the 36 ground-level mistnet captures, 12 were in well-drained primary forest, 15 were in swampy primary forest, 1 was in creekside primary forest, and 8 were in manmade clearings. Our single capture in an elevated net was made at 18–21 m over a narrow dirt road.⁷

We observed eight roosting groups of *Lonchophylla thomasi* at seven unique roost sites (one site was revisited once). Five roost sites were inside hollow logs (e.g., fig. 27) and two were under fallen trees (like that shown in fig. 17). Three roost sites were in well-drained primary forest, three were in disturbed forest, and one was in secondary growth. Entire roosting groups were difficult to capture, but at least one contained multiple adult males (table 18).

PHYLLOSTOMINAE

The Paracou fauna is rich in phyllostomines, of which we captured 25 species rep-

resenting the genera *Chrotopterus*, *Glyphon-ycteris*, *Macrophyllum*, *Micronycteris* (sensu stricto), *Mimon*, *Phylloderma*, *Phyllostomus*, *Tonatia*, *Trachops*, *Trinycteris*, and *Vampyrum*. Only four additional phyllostomine species have been reported from other collecting localities in French Guiana or Surinam (appendix 1). One phyllostomine species is described herein as new, and two others were previously unknown from the Guianas. The sympatric diversity we report for bats of the genus *Micronycteris* sensu stricto (seven species) and *Tonatia* (five species) has, to the best of our knowledge, not been equalled at any other inventory site.

Chrotopterus auritus (Peters)

VOUCHER MATERIAL: 3 females (AMNH *267131, *267852; MNHN *1995.986) and 2 males (AMNH *267130, *267444); see table 19 for measurements.

IDENTIFICATION: Descriptions and measurements of *Chrotopterus auritus* can be found in Thomas (1905b), Taddei (1975a), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Hall (1981), and Medellín (1989). Three subspecies were recognized by Thomas (1905b), Cabrera (1958), and Jones and Carter (1976): *C. a. auritus* (Mexico south to Panama and adjacent parts of northern South America), *C. a. australis*

⁷ Unfortunately, this unique capture of *Lonchophylla thomasi* in an elevated net is unvouchered. It is possible that the animal in question was really *Lionycteris spur-relli*, which somewhat resembles *Lonchophylla thomasi*, is known to fly in the subcanopy, and has been collected at nearby Piste St.-Élie (Brosset and Charles-Dominique, 1990).



Fig. 27. Roost of *Lonchophylla thomasi* in well-drained primary forest at Paracou. At least five *L. thomasi* occupied the dark interior of this hollow log several meters to the right of the opening indicated by the arrow, and a group of unidentified emballonurids was simultaneously roosting near a second opening to the far right (not shown in this view).

(southern Brazil, Paraguay, northern Argentina), and *C. a. guianae* (Venezuela, the Guianas, northern Brazil). However, Handley (1966) expressed doubt that these taxa could be distinguished and Koopman (1994) did not use trinomial nomenclature for *Chrotop-*

terus. Although Williams and Genoways (1980a) identified their Surinamese material as *C. a. guianae*, they did not comment on the implied validity of a subspecific classification.

Thomas (1905b) distinguished *Chrotop-*

TABLE 18
Roosting Groups of *Lonchophylla thomasi* Observed at Paracou

Date	Roost site	Group size	Entire group captured?	Age and sex of captured group members
17 Aug 1991	hollow log	4	yes	2 ad. males, 2 ad. females
20 Aug 1991	fallen tree	3	no	1 ad. male, 1 ad. female
21 Aug 1991	hollow log	1	yes	1 ad. male
23 Aug 1991	fallen tree	?	?	1 ad. male, 1 ad. female
21 Oct 1992	hollow log	2	no	1 ad. female
9 Nov 1992	hollow log	?	?	1 ad. male, 2 ad. females, 2 juv.
11 Aug 1993	hollow log	3?	no	1 ad. male, 1 ad. female
12 Sep 1993	hollow log	2	no	1 ad. female

TABLE 19
Measurements^a of *Chrotopterus auritus* Collected at Paracou

Number/Sex	3 females	2 males
Weight	68.8 (66.0–73.0) 3	65.6 (59.0–72.5) 2
Total length	119.0 (116.0–122.0) 3	107.5 (106.0–109.0) 2
Tail length	15.0 (14.0–16.0) 3	6.0 (6.0–6.0) 2
Hind foot length	25.0 (24.0–27.0) 3	24.0 (23.0–25.0) 2
Ear length	46.3 (46.0–47.0) 3	46.0 (44.0–48.0) 2
Forearm length	79.0 (78.0–80.0) 3	78.5 (77.0–80.0) 2
Greatest length of skull	34.69 (34.44–34.93) 2	33.14 (33.14) 1
Condylolincisive length	31.16 (30.92–31.39) 2	28.99 (28.99) 1
Postorbital breadth	6.27 (6.22–6.32) 2	6.06 (6.06) 1
Braincase breadth	13.20 (12.93–13.47) 2	13.05 (13.05) 1
Mastoid breadth	16.78 (16.67–16.88) 2	16.21 (16.21) 1
Zygomatic breadth	18.98 (18.79–19.17) 2	17.83 (17.83) 1
Maxillary toothrow length	12.98 (12.80–13.15) 2	12.36 (12.36) 1
Breadth across molars	12.26 (12.25–12.27) 2	11.74 (11.74) 1

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

rus auritus auritus, *C. a. australis*, and *C. a. guianae* on the basis of skin and pelage characters alone; no craniodental or measurement differences were noted. Characters remarked by Thomas included: (1) color of the wingtip (dark in *auritus*, small white tip in *australis*, broad white tip in *guianae*); (2) color of the distal phalanges of digit III of wing (dark in *australis*, distalmost phalanx white in *australis*, two distal phalanges white in *guianae*); (3) color of the membranous edge between wing digits IV and V (dark in *auritus* and *australis*, trace of white along edge in *guianae*); (4) distinct metacarpal patch of woolly fur at the base of the thumb (present in *australis*, absent in *guianae*, not mentioned for *auritus*); and (5) extension of body fur onto the flight membranes (fur extending onto the ventral surface of the wing membrane behind the elbow and onto the dorsal surface of the interfemoral membrane in *australis*, no fur extending onto membranes in *guianae*, not mentioned for *auritus*).

Our Paracou specimens of *Chrotopterus auritus* correspond to previous qualitative and morphometric descriptions of the species. However, our material exhibits external character variation that does not conform with any of Thomas' (1905b) subspecific diagnoses. For example, the Paracou specimens have a small white wingtip (supposedly characteristic of *C. a. australis*), the two dis-

tal phalanges of wing digit III are white (supposedly characteristic of *C. a. guianae*), the edge of the wing membrane between the fourth and fifth digits is dark in one specimen (supposedly characteristic of *C. a. auritus* and *C. a. australis*) and white (supposedly characteristic of *C. a. guianae*) in others; there is a distinct metacarpal patch of woolly fur at the base of the thumb (supposedly characteristic of *C. a. australis*), the body fur extends onto the ventral surface of the wing membrane behind the elbow (supposedly characteristic of *C. a. australis*), but the body fur does not extend onto the dorsal surface of the interfemoral membrane (supposedly characteristic of *C. a. guianae*). We therefore agree with Handley (1966) and Koopman (1994) that a subspecific classification of *C. auritus* is not currently useful.

FIELD OBSERVATIONS: All five of the *Chrotopterus auritus* we collected at Paracou were taken in ground-level mistnets; four were captured in well-drained primary forest and one in creekside primary forest. Three individuals were captured singly (on different nights), but an adult male and an adult female, presumably travelling together, were captured in the same net within seconds of one another on 22 July 1993.

Glyphonycteris

With few exceptions, *Glyphonycteris* has been regarded as a subgenus of *Micronycter-*

is since Sanborn's (1949) influential revision of the latter taxon. However, Peffley et al. (MS) have recently shown that *Micronycteris* (sensu Sanborn) is not monophyletic, and suggested that *Glyphonycteris* and several other erstwhile subgenera (*Lampronnycteris*, *Neonycteris*, and *Trinycteris*) be restored to generic rank.

The type species of *Glyphonycteris*, as originally described and designated by Thomas (1896), is *G. sylvestris*. Hill (1964) subsequently described another new genus, *Barticonycteris*, to contain the single species *B. daviesi*. Many workers have recognized a close relationship between *G. sylvestris* and *B. daviesi* (e.g., Hill, 1964; Koopman, 1978, 1994; Arnold et al., 1983; Genoways and Williams, 1986), and a recent phylogenetic analysis (Simmons, 1996b) confirmed that these species are sister taxa. We therefore follow Handley (1976), Genoways and Williams (1986), and Simmons (1996b) in referring *daviesi* to the genus *Glyphonycteris*. Because previous authors have not explicitly diagnosed *Glyphonycteris* as so defined (*Barticonycteris* a synonym), we provide an emended diagnosis below.

EMENDED DIAGNOSIS OF *GLYPHONYCTERIS*: Dorsal fur unicolored or tricolored, not bicolored; ventral fur dark brown or gray; fur on external surface of leading edge of pinna short (≤ 4 mm); pinna pointed, with concavity on posterior border near tip; interauricular band absent; ventral margin of narial horseshoe grades gradually into upper lip (without any thick ridge or free flap of skin marking boundary); chin with pair of dermal pads arranged in a "V" with no central papilla; fourth metacarpal shortest, fifth longest; second phalanges of wing digits III and IV longer than first phalanges; calcar markedly shorter than hindfoot; rostrum and anterior orbital region of skull inflated, dorsum of rostrum flat or convex; basisphenoid pits deep; mastoid breadth less than zygomatic breadth; P3 and P4 subequal in crown height; P3 molariform with well-developed lingual cingulum and cusp; P4 with lingual cingulum convex in outline, edge not raised, lingual cusp well developed; upper canine much less than twice the height of the inner upper incisor; outer upper incisor either absent or moved dorsally and excluded from occlusion

by close apposition of inner incisor and canine; lower incisors trifid; lower premolars aligned in row on mandible, none excluded from toothrow; coronoid process low, with little slope along dorsal margin.

Glyphonycteris daviesi (Hill)

VOUCHER MATERIAL: 1 female (MNHN *1995.1029) and 1 male (AMNH *267856); see table 20 for measurements.

IDENTIFICATION: Hill's (1964) detailed original description was based on only a single specimen. Comparative measurements of additional material were subsequently reported by Swanepoel and Genoways (1979), Genoways and Williams (1986), Brosset and Charles-Dominique (1990), and McCarthy and Ochoa (1991). Pine et al. (1996) provided a comprehensive review of *Glyphonycteris daviesi* with measurements of specimens from throughout its known range. No subspecies are currently recognized (Koopman, 1994; Pine et al., 1996).

Our specimens of *Glyphonycteris daviesi* conform closely to previous descriptions of the species, although our male (AMNH 267856) has a slightly shorter forearm than previously reported.

FIELD OBSERVATIONS: Our two specimens of *Glyphonycteris daviesi*, an adult male and an adult female, were captured in the same ground-level mistnet on the same night in swampy primary forest.

Glyphonycteris sylvestris Thomas

VOUCHER MATERIAL: 1 male (AMNH *267897); see table 20 for measurements.

IDENTIFICATION: Useful descriptions and measurements of *Glyphonycteris sylvestris* were provided by Andersen (1906), Sanborn (1949), Goodwin and Greenhall (1961), Swanepoel and Genoways (1979), and Genoways and Williams (1986). No subspecies are currently recognized (Koopman, 1994).

As mentioned above, most previous workers have placed *Glyphonycteris sylvestris* in the genus *Micronycteris* and have discussed differences between *sylvestris* and other species in that context. We find it more useful to compare *G. sylvestris* with its congener *G. daviesi*, noting that these taxa can be easily distinguished based on the following: (1) size

TABLE 20
Measurements^a of *Glyphonycteris*
Collected at Paracou

	<i>Glyphonycteris daviesi</i>		<i>Glyphonycteris sylvestris</i>
Number/Sex	1 female	1 male	1 male
Weight	20.0	17.4	7.7
Total length	83.0	80.0	57.0
Tail length	10.0	10.0	9.0
Hind foot length	17.0	17.0	12.0
Ear length	28.0	27.0	22.0
Forearm length	57.0	52.5	38.7
Tibia length	24.7	21.6	14.6
Thumb length	13.8	13.1	9.5
Greatest length of skull	24.56	—	—
Condylolincisive length	24.58	—	—
Postorbital breadth	5.97	—	—
Braincase breadth	10.27	—	—
Mastoid breadth	10.87	—	—
Zygomatic breadth	12.68	—	—
Maxillary toothrow length	10.27	—	—
Breadth across molars	8.98	—	—

^a Summary measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

large (*daviesi*; see table 20) versus small (*sylvestris*), (2) dorsal fur unicolored brown or gray (*daviesi*) or tricolored (*sylvestris*), (3) upper outer incisor absent (*daviesi*) or moved dorsally and excluded from occlusion by close apposition of inner incisor and canine (*sylvestris*), and (4) lower incisors with crown height approximately twice crown width in anterior view (*daviesi*) or with crown height approximately equal to crown width (*sylvestris*).

Besides *sylvestris* and *daviesi*, the only other named form referable to *Glyphonycteris* is *Schizostoma behnii* Peters (1865a). About this form, Simmons (1996b: 4) wrote:

M[icronycteris]. behnii may be a senior synonym of *M. sylvestris*, but this has yet to be resolved. The two species are currently distinguished on the basis of size (forearm 37–44 mm in *sylvestris*, 45–47 mm in *behnii*) and the degree of grooving on the upper incisors (prominent in *sylvestris*, somewhat less prominent in *behnii*; Andersen, 1906; Koopman, 1994). Only three specimens have been referred to *behnii*: the holotype (ZMB 5154), and two specimens in the British Museum (BMNH 69.5.13.3, 69.5.13.4) that Andersen referred to *behnii* in his 1906 revision. I examined the

latter specimens (both in alcohol, one with skull cleaned), and found that they fall within the range of variation of *sylvestris* in all measurable dimensions. The forearms of both specimens are broken; Andersen (1906) reconstructed their length as 45 mm, but I estimate the actual length to be closer to 40–42 mm. The degree of grooving of the upper incisors also falls within the range I have observed in *sylvestris*. Unfortunately, I have not yet seen the holotype of *behnii*, which Peters (1865[b]) described as having a forearm length of 47 mm.

We have encountered several museum specimens labeled “*Micronycteris behnii*,” but examination of all has shown that they represent either *Glyphonycteris sylvestris* as currently recognized or are misidentified specimens of other taxa (e.g., *Trinycteris nicefori*). The observed range of forearm length in *G. sylvestris* is 37.0–41.8 for males and 39.2–43.8 for females (Andersen, 1906; Sanborn, 1949; Linares, 1969; Swanepoel and Genoways, 1979; Genoways and Williams, 1986; personal obs.), and additional variation seems likely given the relatively small number of available specimens. Although we expect that *behnii* will eventually prove to be a senior synonym of *sylvestris*, we have not yet seen Peter’s type in the Berlin museum; therefore, we continue to use *sylvestris* for the smaller of the two *Glyphonycteris* species examined to date.

The single specimen of *Glyphonycteris sylvestris* that we collected at Paracou agrees in all respects with previous descriptions of the species.

FIELD OBSERVATIONS: The single individual we captured at Paracou was taken shortly before dark (at 18:20 hours) in a ground-level mistnet in swampy primary forest dominated by the palm *Euterpe oleracea*.

Macrophyllum macrophyllum (Schinz)

VOUCHER MATERIAL: 3 females (AMNH *266039, 266040; MNHN 1995.987); see table 21 for measurements.

IDENTIFICATION: Descriptions and measurements of *Macrophyllum macrophyllum* from the Guianas and elsewhere were provided by Hill (1964), Harrison and Pendleton (1974), Harrison (1975), Husson (1978), Williams and Genoways (1980a), Swanepoel and Genoways (1979), and Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Koopman, 1994).

TABLE 21
Measurements^a of *Macrophyllum macrophyllum*
Collected at Paracou

Sex	1 female
Weight	7.5
Total length	93.0
Tail length	45.0
Hind foot length	15.0
Ear length	19.0
Forearm length	35.5
Greatest length of skull	16.57
Condylolincisive length	14.85
Postorbital breadth	3.19
Braincase breadth	8.08
Mastoid breadth	9.13
Zygomatic breadth	9.38
Maxillary tooththrow length	5.64
Breadth across molars	6.56

^a Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

Our specimens of *Macrophyllum macrophyllum* conform in all respects to previous descriptions of the species, and measurements fall within the range of variation reported for specimens from French Guiana and Surinam by the authors cited above.

FIELD OBSERVATIONS: Our three specimens of *Macrophyllum macrophyllum* from Paracou were found roosting together in a large culvert (2.5 m in diameter) through which a small stream passed beneath a dirt road through secondary forest. Other bats found in the same culvert were *Trachops cirrhosus* and *Carollia perspicillata*.

Micronycteris

As discussed previously under the account for *Glyphonnycteris*, the genus *Micronycteris* as traditionally defined by Sanborn (1949) and by most subsequent authors is not monophyletic. Peffley et al. (MS) consequently recommended that the subgenera of *Micronycteris* recognized by Simmons (1996b) be elevated to generic rank to achieve a monophyletic classification. This change results in recognizing four genera in addition to *Micronycteris* sensu stricto: *Glyphonnycteris* (including *behnii*, *daviesi*, and *sylvestris*), *Lampronnycteris* (for *brachyotis*), *Neonycteris* (for

pusilla), and *Trinycteris* (for *nicefori*). None of these generic names are new or even recent. *Glyphonnycteris* was proposed by Thomas (1896), and the latter three taxa were proposed as subgenera by Sanborn (1949).

So restricted, *Micronycteris* is the monophyletic group that Simmons (1996a, 1996b) defined as including *M. hirsuta*, *M. megalotis*, *M. microtis*, *M. minuta*, *M. sanborni*, and *M. schmidtorum*. Below we describe two additional species (one new and one previously considered a nomen dubium) belonging to this clade. Because Simmons (1996b) did not explicitly diagnose *Micronycteris* sensu stricto, we do so below.

EMENDED DIAGNOSIS OF *MICRONYCTERIS*: Dorsal fur bicolored (the hairs brown with white bases); pinnae large, rounded distally, connected by notched band of skin (interauricular band) across crown of head; ventral edge of narial horseshoe defined by thick ridge; chin with pair of dermal pads arranged in a "V" with no central papilla; third metacarpal shortest, fifth longest; first and second phalanges of wing digit III subequal in length; first and second phalanges of wing digit IV either subequal or second phalanx shorter than first; rostrum and anterior orbital region not inflated; basisphenoid pits shallow; dental formula I 2/2, C 1/1, P 2/3, M 3/3 \times 2 = 34; height of upper canine greater than or equal to twice height of inner upper incisor; outer upper incisor in normal position between inner incisor and canine, not excluded from occlusion with lower incisors; P3 not molariform, lingual cingulum and cusp absent; lingual cingulum of P4 with concave outline and raised edge, lingual cusp small or absent; lower incisors bifid; lower premolars aligned in row on mandible, none excluded from tooththrow.

Micronycteris brosetti, new species

Figure 28

TYPE MATERIAL: The holotype (MNHN 1995.1030), an adult male preserved in alcohol with the skull removed and cleaned, was collected at Paracou by N. B. Simmons and R. S. Voss (original number: NBS 372) on 20 August 1991. Paratypes include 3 females (AMNH *266033, *266038; MNHN *1995.1031) and 4 males (AMNH *266032,

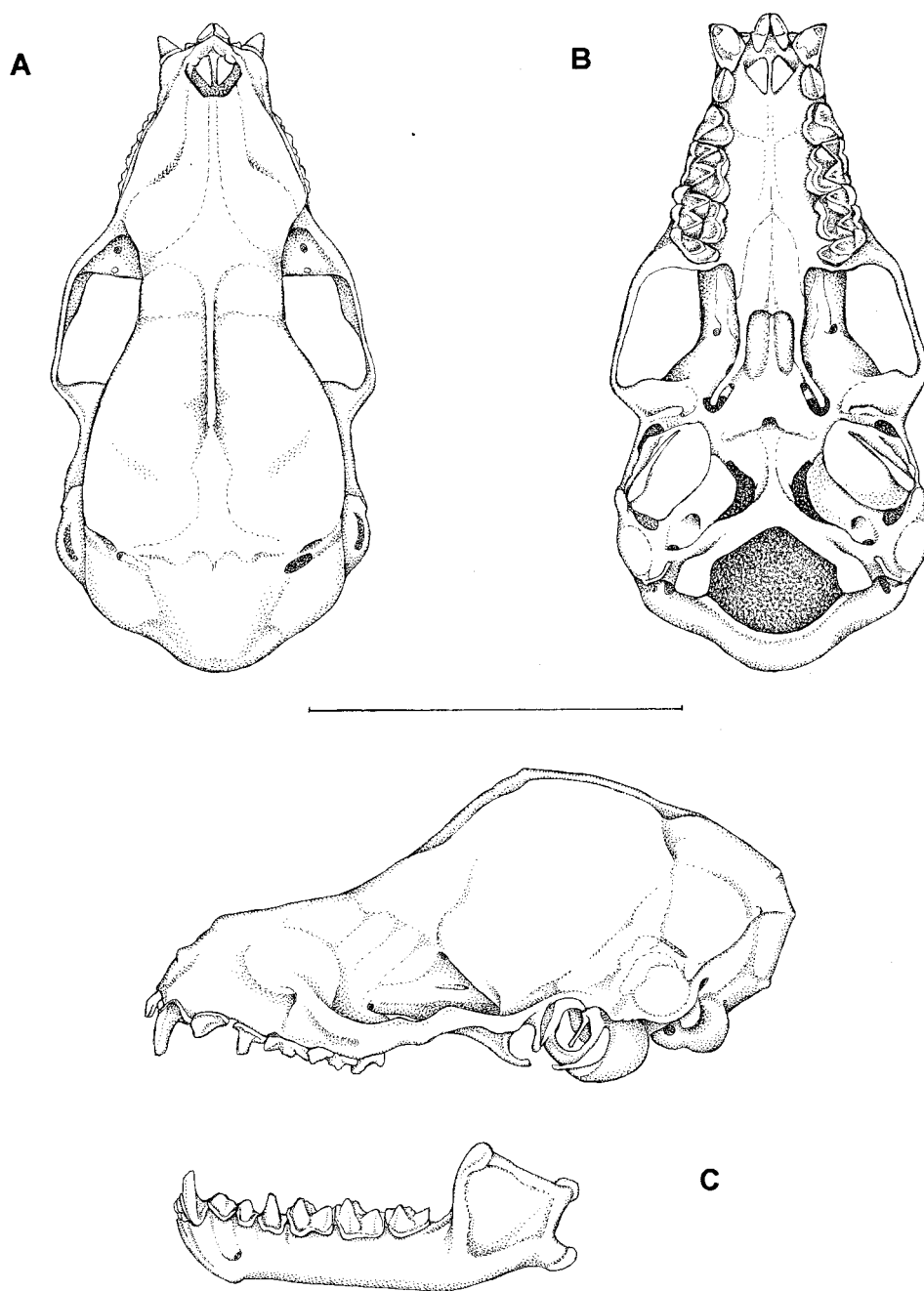


Fig. 28. Dorsal (A), ventral (B), and lateral (C) views of the skull of the holotype of *Micronycteris brosetti* (MNHN 1995.1030; male). Scale bar = 10 mm.

TABLE 22
Measurements^a of the Type Series of *Micronycteris brosetti*, new species

	Holotype MNHN 1995.1030	Paratype AMNH 266032	Paratype AMNH 266034	Paratype AMNH 266035	Paratype AMNH 267419	Paratype MNHN 1995.821	Paratype AMNH 266033	Paratype AMNH 266038
Sex	male	male	male	male	male	female	female	female
Weight	5.0	5.0	4.3	5.0	4.8	4.5	5.0	5.0
Total length	60.0	55.0	52.0	58.0	61.0	55.0	60.0	57.0
Tail length	14.0	13.0	10.0	13.0	11.0	12.0	13.0	13.0
Hind foot length	11.0	11.0	11.0	10.0	10.0	10.0	11.0	10.0
Ear length	20.0	20.0	19.0	20.0	19.0	19.0	19.0	19.0
Forearm length	34.0	32.5	31.5	33.0	34.0	31.5	34.0	33.0
Tibia length	14.2	14.0	13.2	13.7	13.2	12.8	13.7	—
Thumb length	8.1	7.5	7.9	7.9	8.0	—	7.9	—
Greatest length of skull	17.36	17.22	16.97	17.50	—	16.60	16.91	17.63
Condylolincisive length	15.77	15.72	15.30	15.89	—	15.31	15.38	15.71
Postorbital breadth	3.90	3.94	4.00	3.99	—	3.89	3.80	3.98
Braincase breadth	7.23	7.36	7.35	7.51	—	7.24	7.25	7.28
Mastoid breadth	8.18	7.91	7.88	8.17	—	7.91	8.03	8.24
Zygomatic breadth	8.61	8.52	8.22	8.61	—	8.28	8.43	8.47
Maxillary tooththrow length	6.42	6.59	6.47	6.54	—	6.29	6.24	6.62
Breadth across molars	5.66	5.74	5.61	5.71	—	5.49	5.45	5.55

^a Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

*266034, *266035, *267419), all of which were likewise collected at Paracou. See tables 22 and 23 for measurements.

REFERRED MATERIAL: In addition to the

type series from Paracou, we also refer nine specimens to *Micronycteris brosetti* from four other South American localities as follows: PERU, Loreto, Puerto Indiana, Río

TABLE 23
Summary of Available Measurements^a of All Specimens Referred to *Micronycteris brosetti*, new species

Number/Sex	9 males	8 females
Weight	4.9 (4.3–5.0) 6	4.8 (4.5–5.0) 3
Total length	57.3 (52.0–61.0) 8	57.5 (55.0–60.0) 4
Tail length	11.8 (10.0–14.0) 8	12.0 (10.0–13.0) 4
Hind foot length	10.4 (10.0–11.0) 7	10.4 (10.0–11.0) 5
Ear length	19.3 (18.0–20.0) 8	18.9 (18.5–19.0) 5
Forearm length	33.0 (31.5–34.0) 8	33.1 (31.5–34.0) 5
Tibia length	13.7 (13.2–14.2) 5	13.3 (12.8–13.7) 2
Thumb length	8.0 (7.5–8.7) 6	8.3 (7.9–8.5) 4
Greatest length of skull	17.31 (16.87–17.60) 5	17.24 (16.60–17.63) 6
Condylolincisive length	15.72 (15.30–15.98) 7	15.65 (15.31–15.85) 7
Postorbital breadth	3.94 (3.89–4.00) 8	3.89 (3.80–3.98) 7
Braincase breadth	7.34 (7.27–7.51) 7	7.35 (7.23–7.59) 7
Mastoid breadth	8.07 (7.88–8.23) 5	8.16 (7.91–8.39) 6
Zygomatic breadth	8.56 (8.22–8.68) 8	8.48 (8.28–8.62) 5
Maxillary tooththrow length	6.52 (6.42–6.64) 8	6.47 (6.24–6.62) 7
Breadth across molars	5.71 (5.61–5.85) 5	5.58 (5.45–5.76) 6

^a Includes Paracou sample plus specimens from other localities; see text for specimen numbers. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

Amazonas near mouth of Río Napo (AMNH 73495, 73496, 73498, 73499); Peru, *Loreto*, Jenaro Herrera (MUSM 5528); Peru, *Loreto*, Río Yavarí Mirím, Quebrada Esperanza (FMNH 89100, 89101, 89102); BRAZIL, *São Paulo*, Rio Juquiá, Barra (FMNH 92997). One of these specimens (MUSM 5528) was previously identified as *M. schmidtorum* by Ascorra et al. (1991a).

DISTRIBUTION: Although specimens of *Micronycteris brosetti* are currently known only from eastern Peru, French Guiana, and south-eastern Brazil, the species could reasonably be expected to occur throughout Amazonia and the Brazilian Atlantic forest.

ETYMOLOGY: We name this species to honor André Brosset in recognition of his many important contributions to knowledge of tropical bat faunas in India, Africa, and South America. In particular, Brosset and Charles-Dominique (1990) provided an indispensable guide to the bat fauna of French Guiana, as the tattered covers, creased pages, and annotated margins of our well-thumbed field copy eloquently attest.

DIAGNOSIS: A small *Micronycteris* with dark brown dorsal fur and pale (gray or buff) ventral fur; dorsal hairs bicolored, 7–8 mm long in shoulder region, with white base comprising $\frac{1}{3}$ – $\frac{1}{2}$ of each hair; fur on outside of medial third of pinna short (≤ 3 mm) and dense; pinnae large with rounded tips, connected across crown of head by low interauricular band with shallow midline notch; thumb small; second phalanx of wing digit IV shorter than first; calcar longer than foot; mastoid breadth less than zygomatic breadth; crown height of upper incisors not reduced; no gap present between outer upper incisor and canine; P3 and P4 subequal in anteroposterior length, height of P3 slightly less than that of P4; P4 with small lingual heel and poorly developed lingual cusp; M1 narrower than M2; no noticeable gap between posterior edge of cingulum of M2 and anterolingual edge of M3 when toothrow seen in occlusal view; lower incisors small and bilobed; p2 and p4 subequal in anteroposterior length and height, p3 smaller in both dimensions; coronoid process high, upper margin of ascending process with steep slope (25–30°).

Of the characters listed above, four are particularly useful for field identification of *M. brosetti*: color of the ventral fur (pale gray or buff), length of the fur on the leading edge of the pinna (short, ≤ 3 mm), relative length of the first and second phalanges of wing digit IV (second shorter than first), and the calcar (longer than foot). Within the genus *Micronycteris*, this combination of traits is unique to *M. brosetti*.

MEASUREMENTS: A summary of measurements of *Micronycteris brosetti*, including those of the type series and of all other referred specimens, is provided in table 23.

DESCRIPTION AND COMPARISONS: *Micronycteris brosetti* requires close comparison with six other like-size congeners with which it might be confused, namely *M. homezi*, *M. megalotis*, *M. microtis*, *M. minuta*, *M. sanborni*, and *M. schmidtorum*. By contrast, *M. hirsuta* stands out from all other members of the genus by its larger size and unique lower incisor morphology (see table 24 and species account for *hirsuta* below). The following paragraphs therefore omit *hirsuta* from further consideration and focus only on the remaining seven species.

Micronycteris brosetti is one of the smallest members of the genus, with mean values for most of its measurements falling well below those of other species found at Paracou (tables 23–25). Despite some morphometric overlap between larger individuals of *brosetti* and a few smaller specimens in the congeneric series measured by Simmons (1996b: table 2), measurements are clearly useful for distinguishing *brosetti* from most other *Micronycteris* species where they occur sympatrically. At Paracou, the only species from which *brosetti* is indistinguishable in univariate morphometric comparisons (tables 23–25) is *microtis*.

At Paracou, *brosetti* is consistently smaller than *megalotis* in body weight (females only), ear length, thumb length, greatest length of skull (males only), braincase breadth (females only), mastoid breadth, zygomatic breadth (females only), maxillary toothrow length, and breadth across molars (males only). Similarly, *brosetti* is smaller than *homezi* (known only from one male; see species account below) in body weight, ear length, forearm length, tibia length, and in

TABLE 24
Summary of Measurements^a of Dark-Bellied Species of *Micronycteris* Collected at Paracou

	<i>Micronycteris microtis</i>		<i>Micronycteris megalotis</i>	
	8 females	8 males	4 females	5 males
Number/Sex				
Weight	5.7 (5.1–6.5) 8	5.6 (5.0–6.5) 8	5.6 (5.2–6.3) 4	5.4 (5.0–6.0) 5
Total length	58.9 (55.0–62.0) 8	59.4 (56.0–63.0) 8	61.3 (59.0–63.0) 4	59.2 (57.0–62.0) 5
Tail length	12.8 (11.0–14.0) 8	13.9 (11.0–17.0) 8	14.0 (12.0–15.0) 4	14.4 (13.0–16.0) 5
Hind foot length	10.8 (10.0–11.0) 8	10.6 (10.0–12.0) 8	9.5 (9.0–10.0) 4	9.6 (9.0–10.0) 5
Ear length	20.3 (19.0–21.0) 8	20.2 (19.0–21.0) 8	22.5 (22.0–23.0) 4	22.8 (22.0–23.0) 5
Forearm length	34.3 (33.5–35.0) 8	33.8 (32.5–35.5) 8	34.3 (34.0–35.0) 4	34.3 (32.5–35.0) 5
Tibia length	13.7 (12.8–14.5) 8	13.6 (12.7–14.3) 7	13.9 (13.3–14.6) 4	13.5 (12.8–14.4) 5
Thumb length	8.5 (8.1–9.0) 7	8.4 (7.8–8.9) 7	8.8 (8.4–9.4) 3	8.8 (8.6–9.4) 5
Greatest length of skull	17.66 (17.09–18.06) 8	17.81 (17.23–18.44) 8	17.97 (17.50–18.55) 4	18.19 (17.86–18.46) 4
Condylolincisive length	15.81 (15.40–16.13) 8	15.88 (15.55–16.17) 8	16.14 (15.61–16.94) 4	16.12 (15.87–16.38) 3
Postorbital breadth	4.09 (3.94–4.18) 8	4.02 (3.90–4.09) 8	3.85 (3.69–3.95) 4	3.93 (3.87–3.98) 2
Braincase breadth	7.39 (7.14–7.51) 8	7.47 (7.19–7.63) 8	7.43 (7.32–7.61) 4	7.58 (7.33–7.78) 4
Mastoid breadth	8.32 (8.19–8.46) 7	8.30 (8.02–8.50) 8	8.33 (8.08–8.54) 3	8.24 (8.13–8.46) 4
Zygomatic breadth	8.69 (8.34–9.19) 8	8.66 (8.56–8.82) 8	8.73 (8.59–8.94) 3	8.54 (8.51–8.57) 3
Maxillary tooththrow length	6.59 (6.33–6.71) 8	6.62 (6.45–6.75) 8	6.83 (6.63–7.10) 4	7.00 (6.90–7.15) 4
Breadth across molars	5.73 (5.52–5.86) 8	5.79 (5.64–5.96) 8	5.74 (5.39–5.87) 4	5.78 (5.75–5.80) 3
<i>Micronycteris hirsuta</i>				
	3 females	6 males		
Number/Sex				
Weight	12.6 (12.0–13.1) 3	12.0 (11.0–12.6) 6		
Total length	76.3 (75.0–78.0) 3	76.2 (72.0–79.0) 6		
Tail length	13.7 (12.0–15.0) 3	14.7 (13.0–17.0) 6		
Hind foot length	13.3 (13.0–14.0) 3	12.7 (12.0–14.0) 6		
Ear length	25.0 (25.0–25.0) 3	24.3 (24.0–25.0) 6		
Forearm length	43.8 (42.0–45.0) 3	42.6 (41.0–43.0) 6		
Tibia length	19.5 (19.3–19.8) 3	19.3 (18.7–20.0) 6		
Thumb length	12.1 (11.7–12.7) 3	11.7 (11.2–12.3) 6		
Greatest length of skull	23.28 (23.28) 1	23.02 (22.75–23.40) 3		
Condylolincisive length	20.19 (20.19) 1	20.41 (19.89–20.76) 3		
Postorbital breadth	5.09 (5.09) 1	5.07 (4.98–5.16) 3		
Braincase breadth	8.87 (8.87) 1	8.78 (8.59–8.91) 3		
Mastoid breadth	10.49 (10.49) 1	10.29 (10.07–10.64) 3		
Zygomatic breadth	11.69 (11.69) 1	11.69 (11.42–12.00) 3		
Maxillary tooththrow length	9.05 (9.05) 1	9.10 (9.04–9.16) 3		
Breadth across molars	7.28 (7.28) 1	7.35 (7.27–7.45) 3		

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

all craniodental measurements. In comparison with *minuta*, *brosseti* is consistently smaller in body weight, ear length, greatest length of skull (females only), condylolincisive length (females only), postorbital breadth, braincase breadth (females only), mastoid breadth, maxillary tooththrow length (females only), and breadth across molars (females only). Likewise, *brosseti* is smaller

than *schmidtorum* in many measurements, including body weight, ear length, tibia length, thumb length, and all craniodental measurements.

The entire dorsal pelage of *brosseti* is composed of bicolored hairs with white bases and brown tips. In the upper back region, the white bases comprises approximately one-third to one-half of the length of each

TABLE 25
Summary of Measurements^a of Pale-Bellied Species of *Micronycteris* Collected at Paracou

	<i>Micronycteris brosseti</i> , n. sp.		<i>Micronycteris schmidtorum</i>
Number/Sex	3 females	5 males	2 males
Weight	4.8 (4.5–5.0) 3	4.8 (4.3–5.0) 5	5.8 (5.5–6.0) 2
Total length	57.3 (55.0–60.0) 3	57.2 (52.0–61.0) 5	56.5 (56.0–57.0) 2
Tail length	12.7 (12.0–13.0) 3	12.2 (10.0–14.0) 5	11.0 (11.0–11.0) 2
Hind foot length	10.3 (10.0–11.0) 3	10.6 (10.0–11.0) 5	9.5 (9.0–10.0) 2
Ear length	19.0 (19.0–19.0) 3	19.6 (19.0–20.0) 5	19.0 (19.0–19.0) 2
Forearm length	32.8 (31.5–34.0) 3	33.0 (31.5–34.0) 5	33.5 (33.0–34.0) 2
Tibia length	13.3 (12.8–13.7) 2	13.7 (13.2–14.2) 5	15.6 (15.3–15.8) 2
Thumb length	7.9 (7.9) 1	7.9 (7.5–8.1) 5	9.6 (9.3–9.8) 2
Greatest length of skull	17.05 (16.60–17.63) 3	17.24 (16.87–17.50) 4	18.56 (18.48–18.64) 2
Condylolincisive length	15.47 (15.31–15.71) 3	15.67 (15.30–15.89) 4	16.59 (16.34–16.83) 2
Postorbital breadth	3.89 (3.80–3.98) 3	3.96 (3.90–4.00) 4	4.10 (4.06–4.13) 2
Braincase breadth	7.26 (7.24–7.28) 3	7.36 (7.23–7.51) 4	7.77 (7.71–7.83) 2
Mastoid breadth	8.06 (7.91–8.24) 3	8.04 (7.88–8.18) 4	8.55 (8.45–8.64) 2
Zygomatic breadth	8.39 (8.28–8.47) 3	8.49 (8.22–8.61) 4	8.73 (8.72–8.74) 2
Maxillary tooththrow length	6.38 (6.24–6.62) 3	6.51 (6.42–6.59) 4	7.14 (7.11–7.17) 2
Breadth across molars	5.50 (5.45–5.55) 3	5.68 (5.61–5.74) 4	5.97 (5.97–5.97) 2
	<i>Micronycteris homezi</i>	<i>Micronycteris minuta</i>	
Number/Sex	1 male	3 males	3 females
Weight	6.8	5.8 (5.3–6.4) 3	6.2 (5.9–6.5) 3
Total length	59.0	58.7 (56.0–62.0) 3	57.3 (56.0–58.0) 3
Tail length	11.0	11.7 (11.0–12.0) 3	12.3 (11.0–14.0) 3
Hind foot length	11.0	11.3 (10.0–13.0) 3	12.0 (11.0–13.0) 3
Ear length	23.0	21.7 (21.0–23.0) 3	22.2 (21.5–23.0) 3
Forearm length	36.5	34.3 (33.0–35.0) 3	35.0 (34.0–36.0) 3
Tibia length	15.5	14.3 (14.1–14.5) 3	14.2 (14.1–14.3) 2
Thumb length	8.1	7.9 (7.8–8.0) 3	8.7 (8.4–8.9) 2
Greatest length of skull	18.82	17.39 (17.39) 1	18.28 (18.22–18.34) 2
Condylolincisive length	16.79	15.16 (15.16) 1	16.50 (16.33–16.67) 2
Postorbital breadth	4.52	4.14 (4.14) 1	4.11 (4.09–4.13) 2
Braincase breadth	7.88	7.37 (7.37) 1	7.56 (7.48–7.64) 2
Mastoid breadth	8.99	8.21 (8.21) 1	8.86 (8.74–8.97) 2
Zygomatic breadth	8.64	8.20 (8.20) 1	8.34 (8.23–8.44) 2
Maxillary tooththrow length	6.89	6.20 (6.20) 1	6.71 (6.69–6.72) 2
Breadth across molars	5.79	5.59 (5.59) 1	5.71 (5.71–5.71) 2

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

hair. This is comparable to the pattern seen in *microtis*, *megalotis*, *schmidtorum*, and *homezi*, in which the white bases comprise one-fourth to one-half of each hair on the upper back. In contrast, the white bases are much more extensive in *minuta* (one-half to two-thirds of each hair) and *sanborni* (two-thirds to three-fourths of each hair).

The length of the dorsal fur over the upper

back in *brosseti* is approximately 7–8 mm, comparable to that of *microtis* and *homezi*. In contrast, *minuta* and *sanborni* have shorter fur over the shoulders (5–7 mm), while *megalotis* and *schmidtorum* have longer fur (8–11 mm).

The ventral fur of *brosseti* (including that covering the neck and throat) is either pale gray or pale buff, whereas that of *megalotis*

and *microtis* is brown (approximately the same shade as the dorsal fur). The underparts of *schmidtorum* and *minuta* are also pale (gray or buff), like *brosseti*, but *sanborni* has bright white ventral fur.

All of the Paracou specimens of *brosseti* have a pale gray venter, as do some specimens from Peru (e.g., MUSM 5528). However, some older and somewhat faded Peruvian specimens of *brosseti* have pale buff venters (e.g., AMNH 73495–73499, collected in 1926). It is not clear if the buff color is the result of postmortem alteration or within-species variation. Both ventral fur-color variants can be observed among museum series of other species (e.g., *minuta* and *schmidtorum*), so this variation (whatever its cause) is evidently not peculiar to *brosseti*.

The fur on the outside of the medial third of the ear pinna is short (≤ 3 mm) and dense in *brosseti*, similar to the condition seen in *microtis*, *minuta*, and *sanborni*. By contrast, the auricular fur of *megalotis*, *schmidtorum*, and *homezi* is much longer (5–8 mm).

As in all other species of *Micronycteris*, the ears of *brosseti* are connected across the crown of the head by an interauricular band of skin. In *brosseti*, this band is low and nearly horizontal in profile, and is marked at the midline by a shallow notch; a similar condition is seen in *megalotis* and *microtis*. This morphology contrasts sharply with the interauricular band in *minuta*, *sanborni*, and *homezi*, which is much higher and divided by a deep median notch into two roughly triangular flaps (see species account for *homezi* below). The interauricular band of *schmidtorum* is of intermediate height with a moderately deep median notch.

The second phalanx of wing digit IV is shorter than the first in *brosseti*, as it is also in *megalotis*, *microtis*, *schmidtorum*, and *homezi*. By contrast, the first and second phalanges of digit IV are subequal in *minuta* and *sanborni*.

The calcar is distinctly longer than the hindfoot in *brosseti*, resembling the condition seen in *megalotis*, *microtis*, and *schmidtorum*. The calcar is approximately equal in length to the hindfoot in *sanborni*, however, and the calcar is shorter than the foot in *minuta* and *homezi*.

As noted by Simmons (1996b), cranial

morphology is remarkably similar in all species of *Micronycteris*. Like other members of the genus, *brosseti* has a relatively long rostrum, no anteorbital inflation, a large braincase, and shallow basisphenoid pits. Mastoid breadth is less than zygomatic breadth in *brosseti*, as it is likewise in *megalotis*, *microtis*, and *schmidtorum*; mastoid breadth is greater than zygomatic breadth in *minuta*, *sanborni*, and *homezi*.

Like all other congeneric species, *brosseti* has a dental formula of I 2/2, C 1/1, P 2/3, $M \frac{3}{3} \times 2 = 34$. The crown height of the upper incisors is not reduced, and no gap is present between the outer upper incisor and the canine. In this respect, *brosseti* resembles most species of *Micronycteris*; the contrasting morphology is seen only in *sanborni*.

Although differences in the upper premolar dentition are subtle, variation in this region provides an important means of distinguishing species of *Micronycteris* (see Simmons, 1996b). In *brosseti*, P3 and P4 are subequal in anteroposterior length, and the height of P3 is very slightly less than that of P4. This is similar to the condition seen in *megalotis*, *microtis*, *schmidtorum*, and *homezi*. Some variation is known in the former three species, with P3 and P4 subequal in height in some individuals and P3 slightly smaller than P4 in others. Although we did not observe such variation in *brosseti* (or *homezi*, known from only one specimen), it would not be unexpected. In contrast to the conditions described above, P3 is noticeably smaller than P4 in both length and height in *minuta* and *sanborni*.

The degree of development of the postero-lingual heel and lingual cusp on P4 varies among and within species of *Micronycteris*. In *brosseti*, P4 has a small lingual heel and a poorly developed lingual cusp. The lingual heel of P4 in *brosseti* is similar in size to those of *megalotis*, *microtis*, *schmidtorum*, and *homezi*, but the lingual heel is generally smaller in *minuta* and larger in *sanborni*. The lingual cusp of P4, which is formed from the raised edge of the tooth, is poorly developed and lacks a sharp point in *brosseti*, *homezi*, *minuta*, and *sanborni*, and it is entirely lacking in many specimens of *schmidtorum*. By contrast, this cusp is better developed and tapers to a sharp point in most specimens of

microtis and *megalotis*; however, some individuals of both species have a poorly developed cusp, while this cusp may be lacking entirely in others.

The first upper molar is noticeably narrower than M2 in *brosseti* as it is in most other species of *Micronycteris*. Uniquely, the lingual portion of M1 is expanded so that M1 and M2 are subequal in width in *sanborni*, which also differs from all other species in having a large gap visible between the posterior edge of the cingulum of M2 and the anterolingual edge of M3 when the toothrow is seen in occlusal view.

The lower dentition of *brosseti* closely resembles that of most other species, with minor differences apparent only in the premolars. In *brosseti* and *schmidtorum*, p2 and p4 are subequal in anteroposterior length and in height, while p3 is slightly smaller in both dimensions. In *minuta*, *sanborni*, and *homezi*, p3 is further reduced relative to p2 and p4, which are large and subequal. By contrast, p3 is a larger tooth (approximately the same size as p4) in *microtis* and *megalotis*; in these taxa, p2 is often slightly larger than either p3 or p4, although there is some within-species variation in this trait and all three lower premolars are subequal in some individuals of both species.

The coronoid process in *brosseti* is high, and the upper margin of the ascending process has a steep slope (25–30°), similar to the mandibular morphology of *megalotis*, *microtis*, and *schmidtorum*. In contrast, the coronoid process is comparatively low and the upper margin of the ascending ramus has a shallow slope (16–18°) in *minuta*, *sanborni*, and *homezi*.

FIELD OBSERVATIONS: Of the eight specimens of *Micronycteris brossei* that we collected at Paracou, one was taken in a ground-level mistnet and the remaining seven from a single roost in a hollow tree; both capture sites were in well-drained primary forest. The roost tree, about 1 m in diameter at breast height, had a single entrance hole (about 20 cm in diameter) 1 m above the ground. A mistnet enclosure around the base of the tree captured seven of the eight bats that emerged (between 18:45 and 19:15 hours) on 19 August 1991; the captured animals consisted of four adult males and three

adult females. In addition, the mistnet enclosure captured two *Phyllostomus elongatus* on the outside as they came swooping toward the roost opening, obviously intending to ambush the much smaller emerging bats. We were unable to revisit this roost in subsequent years because the site was cleared for agricultural research in 1992.

Micronycteris hirsuta (Peters)

VOUCHER MATERIAL: 3 females (AMNH *267857, *267858; MNHN *1995.800) and 6 males (AMNH *267093, *267894, *267096, 267860; MNHN *1995.801, 1995.802); see table 24 for measurements.

IDENTIFICATION: *Micronycteris hirsuta* is easy to identify owing to its large size (see Simmons [1996b] and tables 23–25) and uniquely high-crowned lower incisors (figured by Genoways and Williams, 1986). Descriptions and comparative measurements of *M. hirsuta* from the Guianas and elsewhere were provided by Sanborn (1949), Goodwin and Greenhall (1961), Hill (1964), Davis (1976a), Genoways and Williams (1986), Brosset and Charles-Dominique (1990), and Simmons (1996b). No subspecies are currently recognized (Simmons, 1996b).

Our specimens of *Micronycteris hirsuta* conform in all respects to previous descriptions of the species.

FIELD OBSERVATIONS: We captured nine individuals of *Micronycteris hirsuta* at Paracou, three of which were taken in ground-level mistnets (two in well-drained primary forest and one in swampy primary forest), and the other six at roosts. The two roosts we found were similar: both were hollow trees near streams in primary forest, both trees had sloping trunks, and the central cavity of each tree had a lower entrance 1–2 m above the ground and another smaller aperture several meters higher up the trunk. From one tree (fig. 21) we collected an adult male and an adult female (probably not the entire roosting group); from the other (fig. 29) we collected two adult males, one adult female, and one subadult male (possibly the entire roosting group). The floor of the latter roost was littered with the wings of large orthopterans, presumably the remains of prey car-



Fig. 29. Roost of *Micronycteris hirsuta* in swampy primary forest at Paracou. Like the roost illustrated in figure 21, this is an inclined tree (sloping away from the camera in this view) with a hollow central cavity accessed by a large lower aperture (arrow) and a second smaller opening much higher up the trunk (not visible). The presence of bats in this roost was inferred from a pile of large orthopteran wings found at the base of the lower aperture. In the foreground are cut palm fronds that we used to thatch a mistnet enclosure in which four emerging bats were captured.

ried back to the roost and eaten by the inhabitants.

Micronycteris homezi Pirlot

Figures 30–32

VOUCHER MATERIAL: 1 male (AMNH *267414); see table 25 for measurements.

IDENTIFICATION: *Micronycteris homezi* was originally described by Pirlot (1967), who considered it a subspecies of *M. megalotis*. Prior to the present study, the only specimens referred to *homezi* were those of Pirlot's type series from the Maracaibo Basin of northwestern Venezuela (ca. 2200 km WNW of Paracou). Simmons (1996b: 4) discussed the brief history of this taxon:

Micronycteris megalotis homezi Pirlot, 1967, was named based on three specimens collected in the western Venezuelan state of Zulia. These specimens (including the holotype) were destroyed along with the rest of Pirlot's collection sometime during the 1970s (Pirlot, phone conversation with T. Griffiths). The published description of *homezi* is incomplete, but several features described by Pirlot (e.g., pale venter, deep notch in ear membrane) suggest that *homezi* is not related to *megalotis*. It is not clear from the type description if *homezi* represents a distinct species or is synonymous with *minuta*, *schmidtorum*, or *sanborni*.

Simmons (1996b) found Pirlot's description of *homezi* to be inadequate for several reasons, including (1) no description of the dentition, (2) no measurements other than length of the forearm, and (3) no mention of relative size of the calcar. The only truly distinctive character of *homezi* described by Pirlot was a "creux cutané glabre" (smooth cutaneous fossa) on the top of the head between the ears behind the interauricular band. Pirlot (1967: 265) described this peculiar structure as follows:

C'est une petite plage subovale, partiellement glabre, limitée par un bourrelet très net. Les deux versants antérieur et postérieur de cette plage se terminent dans le sillon transversal qui va d'une oreille à l'autre. Sur le versant antérieur, une rangée de poils relativement longs est implantée.

An accompanying drawing of the dorsum of the head with the ears and interauricular band folded forward (op. cit.: fig. 1) shows little more than the location of the structure in question. Although Pirlot did not explicitly discuss sexual dimorphism, he apparently

had both male and female examples of *homezi* in hand (op. cit.: 262), suggesting that the cutaneous fossa is present in both sexes.

Having never seen a structure resembling Pirlot's cutaneous fossa, Simmons (1996b) inferred that he was just describing the naked patch of skin that lies underneath the interauricular band and the attached hair tuft in all *Micronycteris* species. The interauricular band is normally folded back against the top of the head so that the posterior (ventral) surface of the band is closely appressed to the skin of the head. The cranial skin covered by the band appears naked (although a sparse coat of fine hairs can be seen under magnification), and it is fully exposed only when the ears are drawn forward. This naked patch varies in size among species of *Micronycteris*, being largest in species with a high interauricular band (e.g., *minuta*, *sanborni*) and smallest in those with a low interauricular band (e.g., *megalotis*, *microtis*). However, this interpretation of Pirlot's "creux cutané glabre" now appears incorrect.

One of the specimens that we collected at Paracou—AMNH 267414, an adult male—has a well-defined, hairless fossa on the top of the head between the ears and behind the interauricular band (fig. 30). Smooth and glabrous inside, this pit is surrounded by a rim of skin with coarse projecting hairs, exactly as Pirlot described. Although no histological work has yet been done, this structure appears to be a glandular pouch or a pouch in which glandular secretions might be stored. To the best of our knowledge, this structure is unique among bats (for a summary of known chiropteran glandular structures, see Quay, 1970).

Several other characters of our specimen correspond with Pirlot's (1967) description of *homezi*, including (1) small size (forearm length 36.5 mm in Paracou specimen, 31.4–37.4 mm in Pirlot's series), (2) a pale venter (much lighter than the dorsal fur), and (3) a high interauricular band divided into roughly triangular flaps by a deep median notch. Because our material agrees closely with Pirlot's description, and because of its clear distinctness from any other named congeneric form, we conclude that AMNH 267414 represents a valid species that should be called *Micronycteris homezi*.



Fig. 30. Live views of *Micronycteris homezi* (AMNH 267414; male). Note the pale ventral fur, the long hairs on the leading edge of each pinna, and the very deep, V-shaped notch in the interauricular band; the cutaneous fossa is visible through the notch in the interauricular band. The hairs covering the fossa in this view are rooted in the skin surrounding the fossa, and on the underside (posterior surface) of the interauricular band; the fossa itself is hairless.

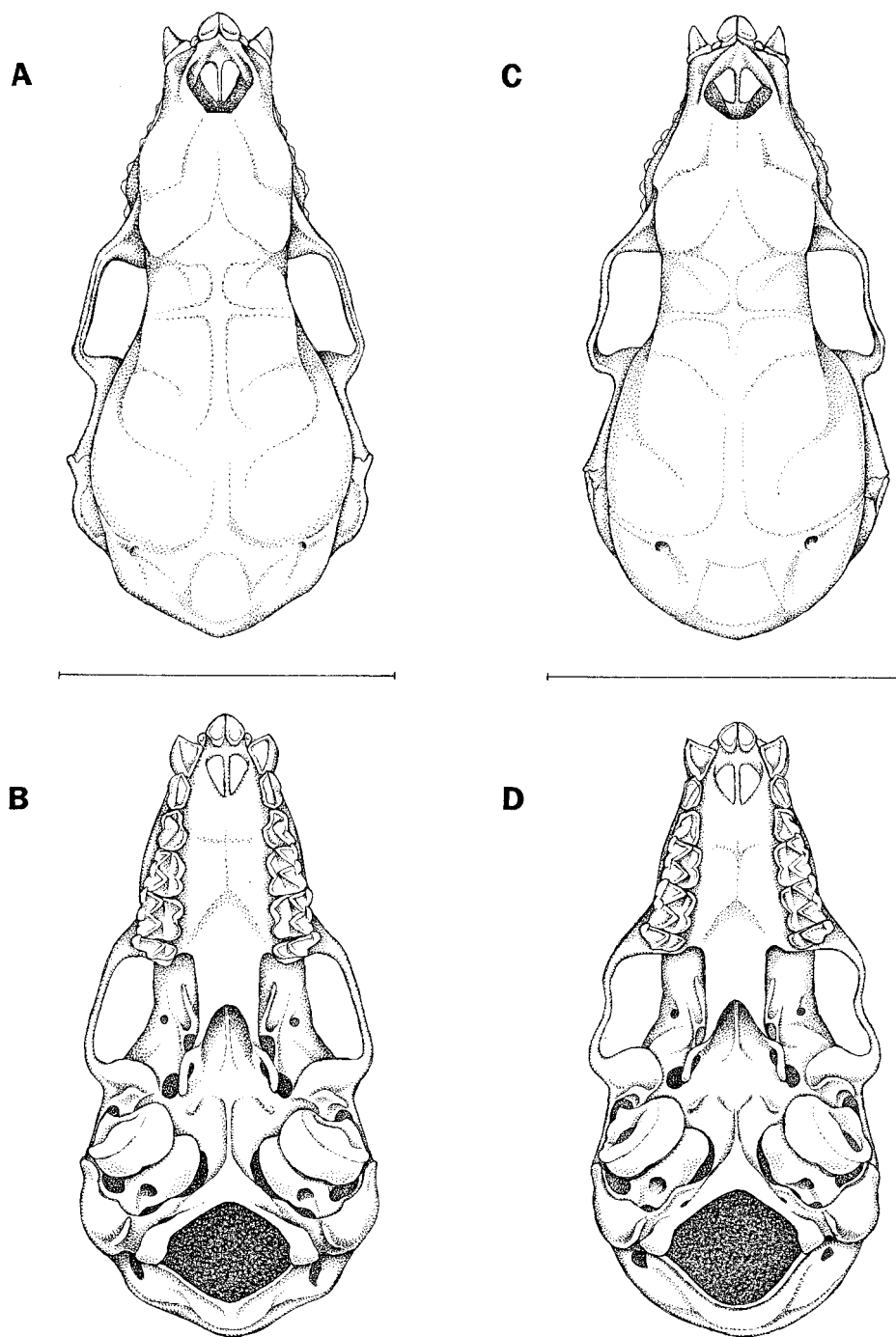


Fig. 31. Dorsal (A) and ventral (B) views of the skull of *Micronycteris homezi* (AMNH 267414; male). Dorsal (C) and ventral (D) views of the skull of *M. minuta* (AMNH 267875; male). Scale bars = 10 mm.

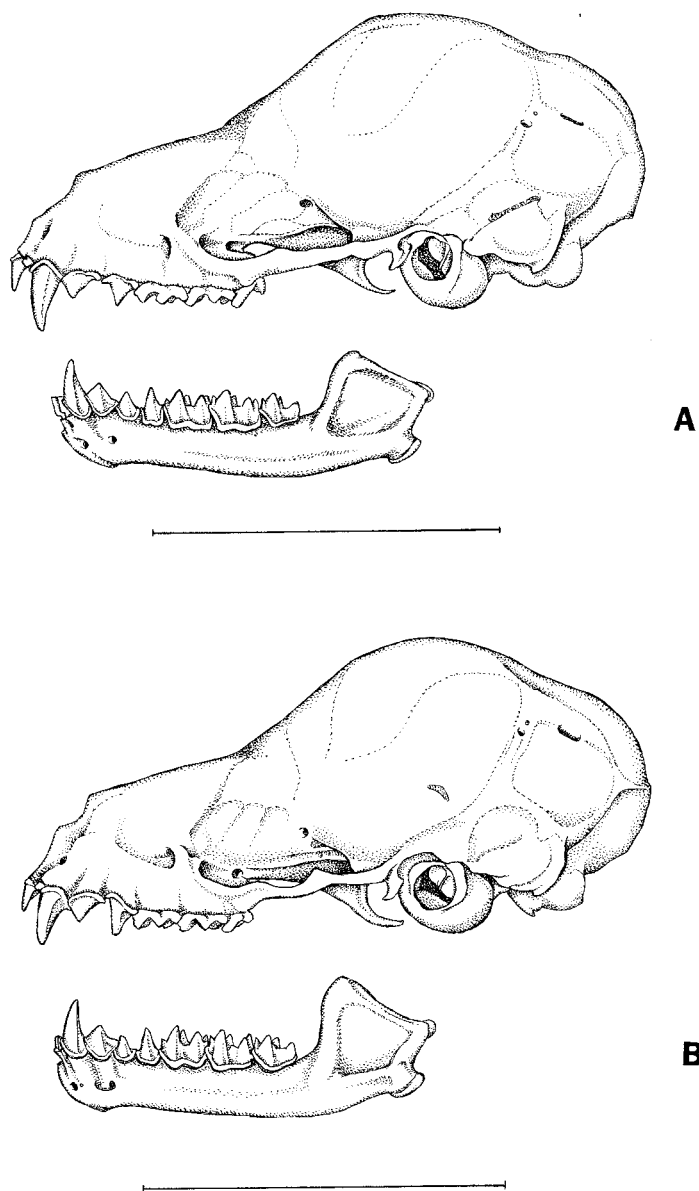


Fig. 32. Lateral views of the skull and lower jaw of (A) *Micronycteris homezi* (AMNH 267414; male) and (B) *M. minuta* (AMNH 267875; male). Note the species difference in premolar proportions. Scale bars = 10 mm.

The congeneric species that most closely resembles *homezi* in external morphology is *minuta*. In addition to similar size, fur color, and form of the interauricular band, both *homezi* and *minuta* have a calcar that is noticeably shorter than the hindfoot. The latter character was previously thought to be

uniquely diagnostic of *minuta* within *Micronycteris* (e.g., see key to species in Simmons, 1996b: table 3). Indeed, we initially misidentified our specimen of *homezi* as *minuta* before noticing the cutaneous fossa and other differences. Comparisons of our material from Paracou indicate that *homezi* and

minuta are distinguished by numerous features, including the following: (1) a cutaneous fossa is present on the top of the head in *homezi* but absent in *minuta*; (2) the triangular skin flaps that comprise the interauricular band are higher in *homezi* (height of flap equal to width of flap at base) than in *minuta* (height of flap slightly less than width at base); (3) the white base of each hair in the pelage of the upper back comprises approximately $\frac{1}{4}$ – $\frac{1}{2}$ of the length of each hair in *homezi*, whereas the white base comprises $\frac{1}{2}$ – $\frac{2}{3}$ of each hair in *minuta*; (4) the length of the fur over the upper back is approximately 7–8 mm in *homezi*, while it is shorter (5–7 mm) in *minuta*; (5) the fur on the outside of the medial third of the pinna is long (7–8 mm) in *homezi*, but is much shorter (≤ 3 mm) in *minuta*; (6) the second phalanx of wing digit IV is shorter than the first in *homezi*, while these phalanges are subequal in *minuta*; and (7) P3 and P4 are subequal in anteroposterior length and the height of P3 is very slightly less than that of P4 in *homezi*, but P3 is noticeably smaller than P4 in *minuta*.

There are also size differences between *Micronycteris homezi* and *M. minuta* where they occur sympatrically at Paracou (table 25), although the small sample sizes must be noted. In our material, *homezi* appears slightly larger than *minuta* in body weight, forearm length, tibia length, and in all craniodental measurements. Some of these differences are trivial, but we expect that others (e.g., differences in tibia length, greatest length of skull, postorbital breadth) will be shown ultimately to represent consistent species differences.

Comparisons with congeneric species other than *Micronycteris minuta* can be found under the species account for *brosseti* (above) and will not be repeated here (see tables 23–25 for comparative measurements). To summarize the distinctive characters of *homezi* (as represented by Pirlot's original description and our single specimen), we provide an emended diagnosis below.

EMENDED DIAGNOSIS OF *MICRONYCTERIS HOMEZI*: A small species of *Micronycteris* with dark brown dorsal fur and pale (gray or buff) ventral fur; dorsal hairs bicolored, 7–8 mm long in shoulder region, with white bas-

es comprising $\frac{1}{4}$ – $\frac{1}{2}$ of each hair; fur on outside of medial third of pinna long (7–8 mm); ears connected by high interauricular band with a deep midline notch (resultant skin flaps triangular, height of each flap equal to width at base); cutaneous fossa present on top of head just posterior to interauricular band; second phalanx of wing digit IV shorter than first; calcar shorter than foot; mastoid breadth greater than zygomatic breadth; crown height of upper incisors not reduced; no gap between outer upper incisor and canine; P3 and P4 subequal in anteroposterior length, height of P3 slightly less than that of P4; P4 with small lingual heel and poorly developed lingual cusp; M1 narrower than M2; no noticeable gap between posterior edge of cingulum of M2 and anterolingual edge of M3 when toothrow seen in occlusal view; lower incisors small and bilobed; p2 and p4 subequal in anteroposterior length and height, p3 smaller in both dimensions; coronoid process high, upper margin of ascending process with steep slope (25–30°).

FIELD OBSERVATIONS: Our single specimen of *Micronycteris homezi* was captured in a mistnet suspended 18–21 m above a narrow dirt road through well-drained primary forest. Interestingly, this was the only example of *Micronycteris* that we took in an elevated mistnet at Paracou.

Micronycteris megalotis (Gray)

VOUCHER MATERIAL: 4 females (AMNH *267092, *267862; MNHN *1995.809, *1995.811) and 7 males (AMNH *266020, *267090, *267091, 267863; MNHN *1995.803, *1995.804, 1995.810); see table 24 for measurements.

IDENTIFICATION: Characters distinguishing *Micronycteris megalotis* from other congeneric species were summarized under the species account for *M. brosetti* (above); additional diagnostic information can be found in Simmons (1996b). Comparative measurements of *megalotis* from the Guianas can be found in Husson (1962, 1978) and Brosset and Charles-Dominique (1990). Many previous accounts of *megalotis* (e.g., Sanborn, 1949; Swanepoel and Genoways, 1979; Hall, 1981; Koopman, 1994) treated *microtis* as a subspecies, so such references must be used

with care. No subspecies of *M. megalotis* are presently recognized (Simmons, 1996b).

Handley (1976) reported that *Micronycteris megalotis* and *M. microtis* occur sympatrically in Venezuela, but Brosset and Charles-Dominique (1990) were the first authors to discuss diagnostic characters. They noted that, although the dentition is similar in *megalotis* and *microtis*, these species can be distinguished easily on the basis of ear length (longer in *megalotis*). According to Brosset and Charles-Dominique, the palate is also slightly longer and wider and the braincase is slightly higher in *megalotis* than in *microtis*. Palatal shape differences were attributed by these authors to differences in length and width of the maxillary toothrow, although the measurements they reported indicated species overlap in both dimensions. In addition to ear and craniodental differences, Brosset and Charles-Dominique (1990: 522) observed that "the ventral surface of *megalotis* is lighter than the dorsal surface, but this is not the case for *microtis*, which is grey brown above and below."

Simmons (1996b) agreed that *Micronycteris megalotis* and *M. microtis* are distinct species based on her examination of specimens from Paracou and elsewhere. She found that ear length is indeed different in these species although some overlap in measurements is apparent when the smallest specimens of *megalotis* are compared with the largest specimens of *microtis*. No consistent differences in craniodental measurements or fur color were found when large samples of *megalotis* and *microtis* from many different localities were compared. However, Simmons identified one obvious difference between these species: the length of the hair on the leading edge of the pinna is relatively long (7–8 mm) in *megalotis* but is much shorter (≤ 3 mm) in *microtis*.

Our comparisons of specimens of *Micronycteris megalotis* and *M. microtis* collected at Paracou indicate that several features distinguish these species where they occur sympatrically in French Guiana: (1) length of dorsal fur over the upper back (long in *megalotis* [8–11 mm], shorter in *microtis* [7–8 mm]), (2) color of the dorsal and ventral fur (dark gray-brown in *microtis*, more reddish in *megalotis*), (3) length of the fur on the

outside of the medial third of the ear pinna (long in *megalotis* [7–8 mm], much shorter in *microtis* [≤ 3 mm]), (4) ear length (greater in *megalotis* [22–23 mm], shorter in *microtis* [19–21 mm]), and (5) maxillary toothrow length (males only; long in *megalotis* [6.90–7.15 mm], shorter in *microtis* [6.45–6.75 mm]). We found overlap in all other external and craniodental measurements although mean values for *megalotis* are somewhat larger than mean values for *microtis* for several dimensions (e.g., greatest length of skull, condyloincisive length; table 24).

Contra Brosset and Charles-Dominique (1990), we did not find that the ventral fur is noticeably paler than the dorsal fur in *megalotis*. In our experience, dorsal and ventral fur is approximately the same color in all individuals of both *megalotis* and *microtis*. However, the reddish fur of *megalotis* appears lighter in contrast to the dark wing membranes than does the gray-brown ventral fur of *microtis*. The differences in fur color in *megalotis* and *microtis* that we observed at Paracou are subtle and not discernable in wet specimens. These differences may also be obscured by bleaching in older material, possibly the reason for Simmons' (1996b) previous inability to distinguish consistent pelage color contrasts between *megalotis* and *microtis* in her preliminary survey of specimens collected at different times and places. Alternatively, the differences we observed at Paracou might be geographically variable.

FIELD OBSERVATIONS: We captured 11 *Micronycteris megalotis* at Paracou, of which 8 were taken in ground-level mistnets (1 in well-drained primary forest and 7 in swampy primary forest) and the other 3 at a roost. The single roost we found was in the central cavity of a large buttressed tree growing in well-drained primary forest (fig. 25). The roosting group consisted of four bats hanging together in a tight cluster from the roof of the cavernous lower chamber about 2.5 m above the ground; two adult males and one adult female were captured and one bat escaped. A solitary adult male *Carollia perspicillata* was simultaneously found roosting in the same chamber.

Micronycteris microtis Miller

VOUCHER MATERIAL: 9 females (AMNH *266025, 266026, *266027, *266030,

*267868, *267869, *267872; MNHN *1995.805, *1995.807) and 13 males (AMNH *266024, 266028, *266029, 266031, *267097, *267866, *267867, *267870, *267871, *267873; MNHN *1995.806, 1995.808, 1995.812); see table 24 for measurements.

IDENTIFICATION: The characters that distinguish *Micronycteris microtis* from other congeners are explained in the preceding species accounts for *M. brosetti* and *M. megalotis* and need not be repeated here. Additional observations and comparative measurements can be found in Brosset and Charles-Dominique (1990) and Simmons (1996b). Two subspecies of *M. microtis* are currently recognized: *M. m. mexicana* (Mexico south to the Pacific coast of Costa Rica) and *M. m. microtis* (Atlantic coast of Nicaragua south to Colombia, Venezuela, the Guianas, and northern Brazil) (Simmons, 1996a, 1996b).

Our specimens of *Micronycteris microtis* conform in all respects to previous descriptions of this species and fall within the range of size variation that Simmons (1996b) described for *M. m. microtis*.

FIELD OBSERVATIONS: Of the 22 *Micronycteris microtis* we captured at Paracou, 3 were taken in ground-level mistnets (1 in well-drained primary forest and 2 in swampy primary forest), 17 were taken at day roosts, 1 was shot at a night roost, and 1 was caught in a harp trap set across a trail through closed-canopy secondary vegetation.

The four roosts in which we found *Micronycteris microtis* were all at or below ground level. One day roost and the night roost were in small (50–70 cm diameter) metal culverts under dirt roads; another roost was a hollow log with an inside diameter of ca. 50 cm; and another was a shallow vertical chamber in the partially rotted buttress of a very large tree (fig. 33). The hollow-log roosting group (which was captured in its entirety) consisted of three adult males, three adult females, and one subadult male. The roosting group occupying the buttress cavity shown in figure 33 included two adult males, three adult females, and three juveniles (one or more members of this group may have escaped). The culvert day roost contained only a lactating adult female carrying a juvenile. The culvert night roost contained an

adult male, but other occupants might have escaped detection. *Carollia perspicillata* was the only species we found roosting together with *Micronycteris microtis* (in the buttress cavity and in a culvert).

Micronycteris minuta (Gervais)

Figures 31, 32

VOUCHER MATERIAL: 3 females (AMNH *267098, *267874; MNHN *1995.814) and 3 males (AMNH *267415, *267875; MNHN *1995.813); see table 25 for measurements.

IDENTIFICATION: Close relatives of *Micronycteris minuta* with which it may be easily confused include *M. homezi* (described above), *M. sanborni* (described by Simmons, 1996b), and *M. schmidtorum* (discussed below). Accounts of *M. minuta* by Sanborn (1949), Goodwin and Greenhall (1961), and Genoways and Williams (1986) provide accurate descriptions and useful summaries of comparative measurements, but Willig's (1983) discussion of *M. minuta* must be disregarded because his composite sample minimally included specimens of two other species (*M. sanborni* and *M. schmidtorum*) and may have contained no true *M. minuta* at all (see discussion in Ascorra et al. [1991a] and Simmons [1996b]). No subspecies of *M. minuta* are currently recognized (Simmons, 1996b).

Our specimens of *Micronycteris minuta* from Paracou conform in all respects to previous valid descriptions of this species.

FIELD OBSERVATIONS: All of the six specimens of *Micronycteris minuta* that we captured at Paracou were taken in ground-level mistnets: one in well-drained primary forest, four in swampy primary forest, and one in a manmade clearing.

Micronycteris schmidtorum Sanborn

VOUCHER MATERIAL: 2 males (AMNH *267853; MNHN *1995.818); see table 25 for measurements.

IDENTIFICATION: Characters distinguishing *Micronycteris schmidtorum* from other congeneric species were summarized in the preceding account for *M. brosetti* and will not be repeated here. Ascorra et al. (1991a) reviewed *M. schmidtorum* but referred some specimens to this species that we subsequent-

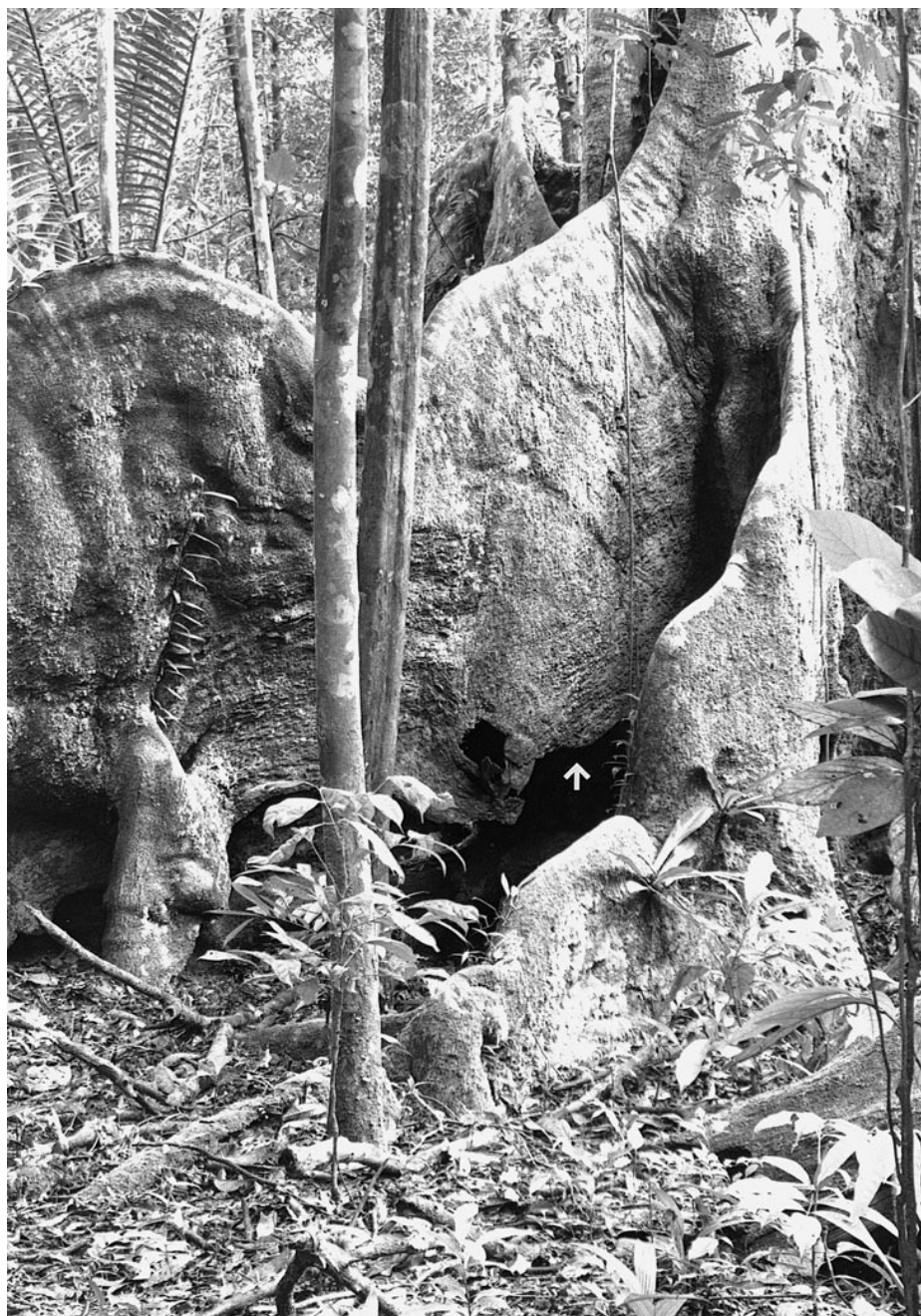


Fig. 33. Roost of *Micronycteris microtis* and *Carollia perspicillata* in a partially rotted buttress of the large tree shown in figure 3. From the upper edge of the opening visible in this view (arrow), a dark chamber extended upward less than a meter. In 1991 this small cavity contained 13–14 bats, of which 8 *M. microtis* and 2 *C. perspicillata* were captured; 3–4 unidentified bats escaped. This roost was not revisited in subsequent years.

ly reidentified as either *M. sanborni* (Simmons, 1996b) or *M. brosetti* (see above). Simmons (1996b) provided a summary of measurements of *Micronycteris schmidtorum* sensu stricto from throughout its known geographic range. No subspecies are currently recognized (Simmons, 1996b).

Although our voucher material generally agrees with previous descriptions of *Micronycteris schmidtorum*, Paracou specimens have pale gray ventral fur rather than the pale buff venters seen in specimens from other localities. Because we did not find any other consistent differences, and because other congeners with pale ventral fur (e.g., *M. brosetti* and *M. minuta*) exhibit similar chromatic variability, we conclude that this represents normal intraspecific variation.

In addition to characters discussed previously, we found that tibia length was helpful for distinguishing *Micronycteris schmidtorum* from sympatric species in the hand, at least at Paracou. Whereas both *M. schmidtorum* and *M. homezi* have long tibias (15.3–15.8 mm), the lower leg is consistently shorter (12.8–14.6 mm) in *M. brosetti*, *M. megalotis*, *M. microtis*, and *M. minuta*.

FIELD OBSERVATIONS: Our two examples of *Micronycteris schmidtorum* were both taken in ground-level mistnets in well-drained primary forest.

Mimon bennettii (Gray)

Figures 34–37

VOUCHER MATERIAL: 1 female (AMNH *267109) and 1 male (MNHN *1995.988); see table 26 for measurements.

IDENTIFICATION: Although Koopman (1993, 1994) considered *Mimon bennettii* and *M. cozumelae* to be conspecific, many other authors have recognized them as distinct species (Dalquest, 1957; Handley, 1960; Carter et al., 1966; Gardner and Patton, 1972; Jones and Carter, 1976; Swanepoel and Genoways, 1979; McCarthy, 1987; McCarthy et al., 1993). Whereas the restricted type locality of *M. bennettii* is Ipanema in the Brazilian state of São Paulo (Hershkovitz, 1951), the type locality of *M. cozumelae* is Cozumel Island in the Mexican state of Quintana Roo (Goldman, 1914). Currently, the known range of *cozumelae* extends from

southern Mexico to northwestern Colombia, and that of *bennettii* extends from the Guianas to southeastern Brazil (Koopman, 1994).

Dalquest (1957) reported additional specimens of *Mimon cozumelae* collected in the decades following Goldman's (1914) original description, and discussed differences between *cozumelae* and *bennettii*, which he treated as distinct species. However, as Handley (1960) subsequently noted, Dalquest's only comparative example of *bennettii* was a juvenile. Schaldach (1964) subsequently summarized characters supposedly distinguishing these taxa, including size (smaller in *bennettii*), dorsal pelage color (darker in *bennettii*, brighter in *cozumelae*), and length and woolliness of the middorsal hairs (long and not woolly in *bennettii*, short and woolly in *cozumelae*). Like Dalquest's (1957) account, however, Schaldach's description of the pelage of *bennettii* seems to have been based on juvenile or subadult specimens. Despite the morphological differences he noted, Schaldach concluded that *bennettii* and *cozumelae* are conspecific, a decision based in large part on the geographic gap between their known geographic ranges. Hall (1981) and Koopman (1993, 1994) followed Schaldach (1964) without additional discussion.

Contra Schaldach (1964), Hall (1981), and Koopman (1993, 1994), we consider *Mimon bennettii* and *M. cozumelae* to represent distinct species based on apparently consistent differences in the following characters: (1) dorsal pelage color (more reddish in adult *bennettii*, less reddish in *cozumelae*), (2) color of the wingtip (dark in *bennettii*, white in *cozumelae*), (3) shape of the middle upper incisors (tapering to points in *bennettii*, more spatulate in *cozumelae*), (4) form of the lower incisors (narrower in *bennettii*), (5) morphology of m3 (taloid larger and better developed in *bennettii*), and (6) morphology of the posterior palatal margin (broader with U-shaped mesopterygoid notch in *bennettii*, narrower with V-shaped notch in *cozumelae*).⁸ Although some overlap exists, *bennet-*

⁸ This list of characters is based on both literature accounts and our examination of voucher specimens. Specimens examined in addition to those from Paracou: *Mimon bennettii* (Brazil: USNM 123393, 391027); *Mimon cozumelae* (Mexico: AMNH 144508, 185862–185872).

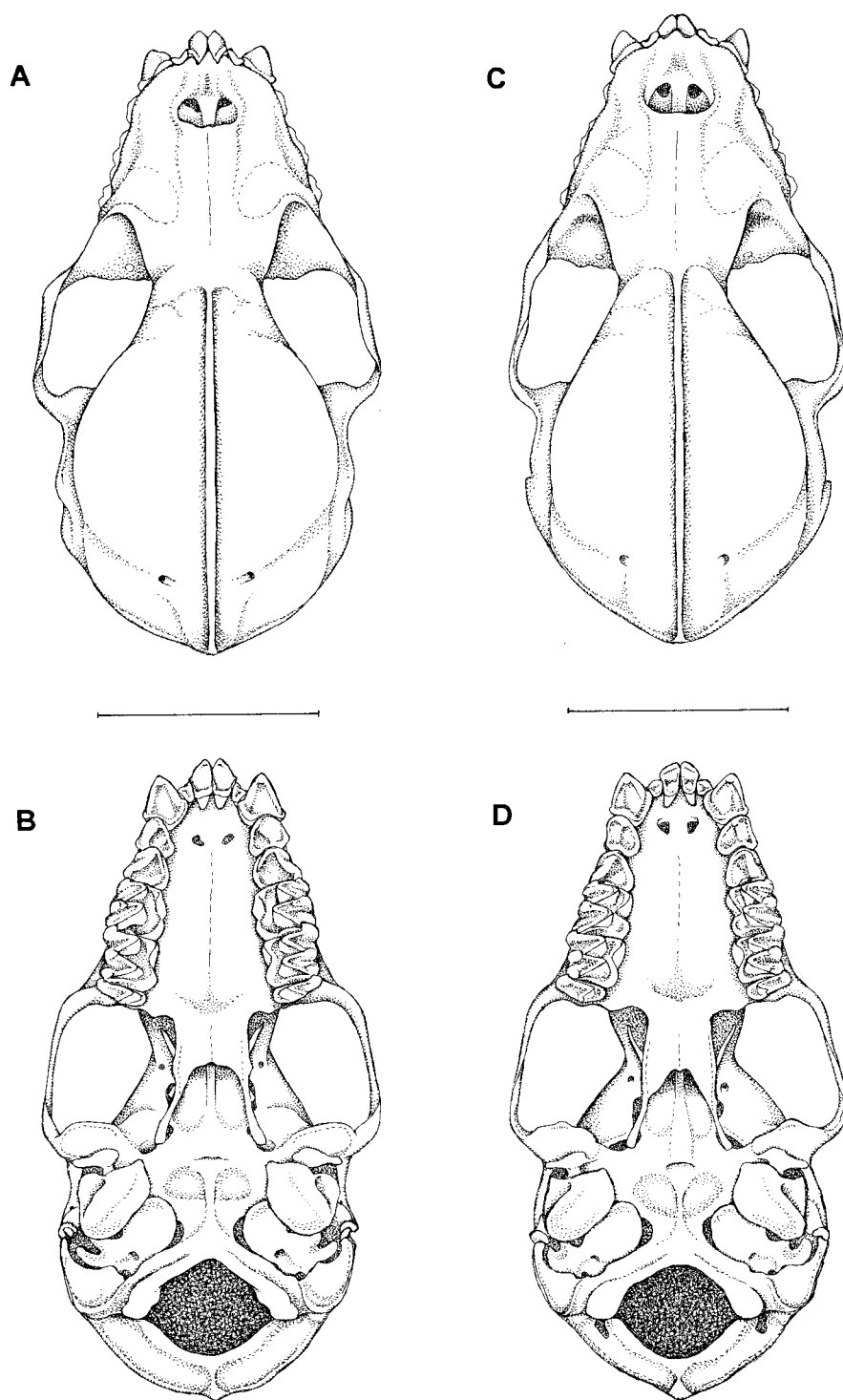


Fig. 34. Dorsal (A) and ventral (B) views of the skull of *Mimon bennettii* (MNHN 1995.988; male) from Paracou. Dorsal (C) and ventral (D) views of the skull of *M. cozumelae* (AMNH 265107; male) from Guatemala. Note the species differences in incisor morphology and in the shape of the mesopterygoid notch of the posterior palate. Scale bars = 10 mm.

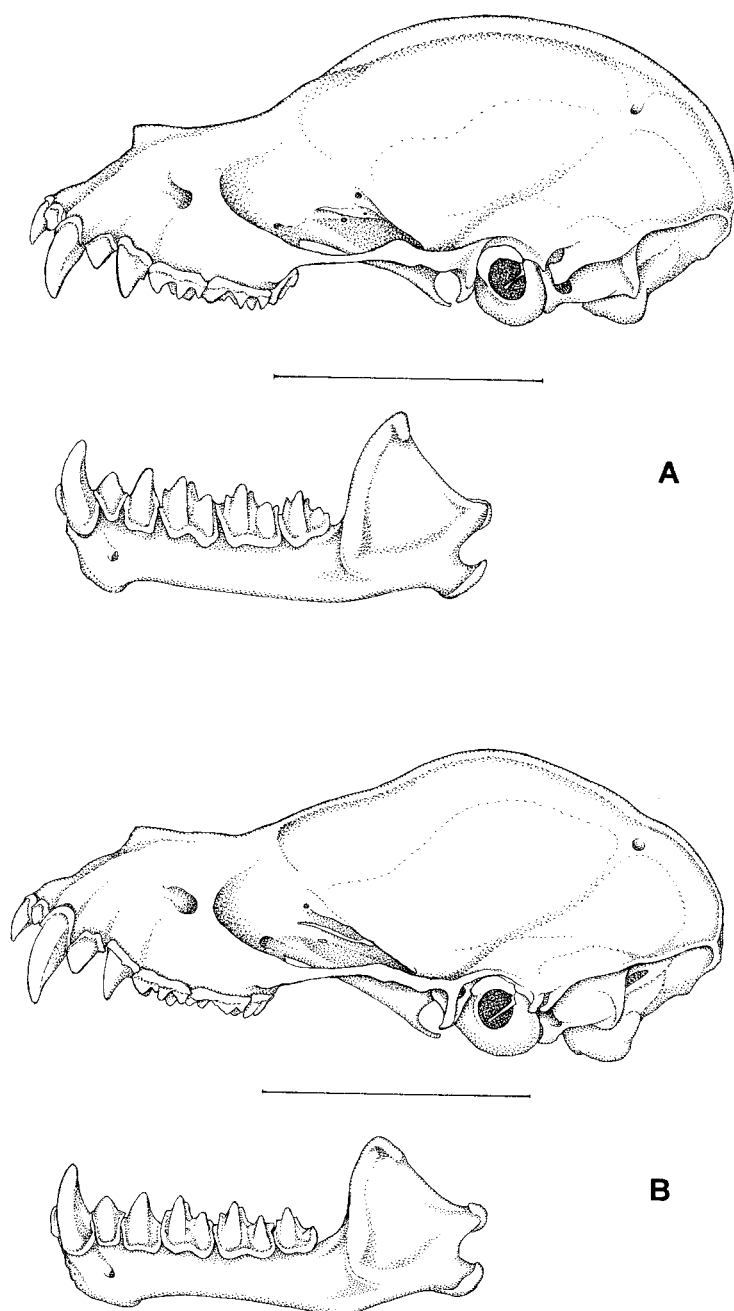


Fig. 35. Lateral views of the skull and lower jaw of (A) *Mimon bennettii* (MNHN 1995.988; male) and (B) *M. cozumelae* (AMNH 265107; male). Scale bars = 10 mm.

tii is generally smaller than *cozumelae* (e.g., forearm length of 50.0–56.6 mm in *bennettii*, 54.6–60.7 mm in *cozumelae*; Swanepoel and Genoways, 1979; Hall, 1981; Brosset and

Charles-Dominique, 1990). Although these taxa have not been collected in sympatry, it is counterproductive to regard them as sub-species given the magnitude of their mor-

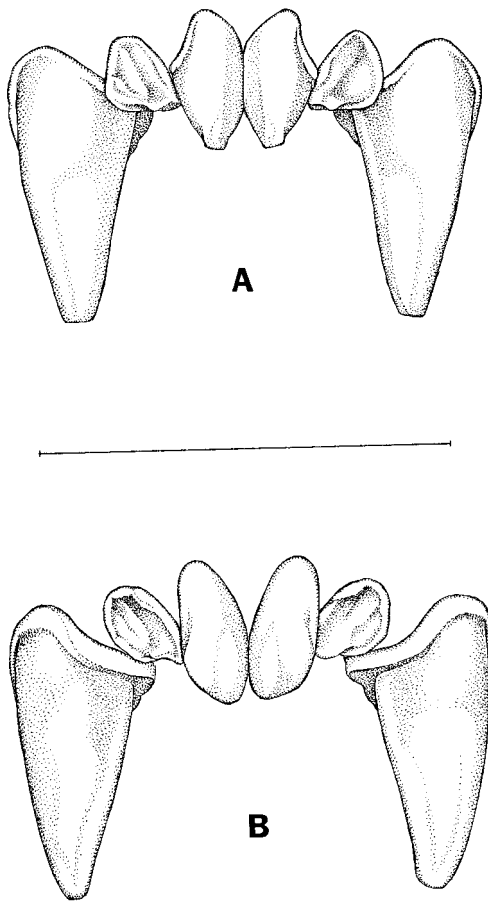


Fig. 36. Anterior views of the upper and lower dentition of (A) *Mimon bennettii* (MNHN 1995.988; male) and (B) *M. cozumelae* (AMNH 265107; male). Note that the middle upper incisors of *bennettii* taper to points, whereas these teeth are more spatulate in *cozumelae*. Scale bars = 5 mm.

phological divergence; until proven false, the appropriate null hypothesis is that they represent distinct species.

Descriptions and measurements of *Mimon bennettii* sensu stricto were provided by Gray (1838), Dalquest (1957), Husson (1962, 1978), Hill (1964), Swanepoel and Genoways (1979), and Brosset and Charles-Dominique (1990). Our specimens closely resemble others previously reported from Guianas, particularly the bright orange-russet adults described by Brosset and Charles-Dominique (1990). Based on our limited comparisons,

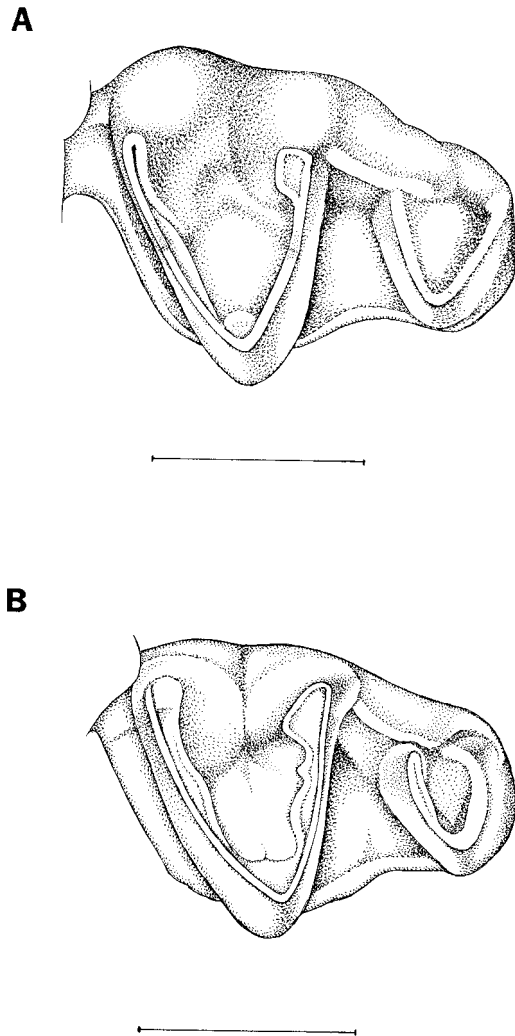


Fig. 37. Occlusal views of the crown of the right m3 in (A) *Mimon bennettii* (MNHN 1995.988; male) and (B) *M. cozumelae* (AMNH 265107; male). Note that the talonid is larger and better developed in *bennettii* than it is in *cozumelae*. Scale bars = 1 mm.

recognition of subspecies does not seem warranted.

FIELD OBSERVATIONS: One of our two specimens of *Mimon bennettii* was captured in a ground-level mistnet and the other was taken at a roost; both captures were in creekside primary forest. The roost site was a large tree (ca. 1.5 m in diameter at breast height) with a central cavity extending from ground level to near the crown. We surrounded the only

TABLE 26
Measurements^a of *Mimon* Collected at Paracou

	<i>Mimon bennetti</i>		<i>Mimon crenulatum</i>	
	1 female	1 male	6 females	7 males
Number/Sex				
Weight	21.9	19.7	11.8 (10.7–13.1) 6	11.4 (9.8–11.8) 7
Total length	90.0	91.0	86.2 (76.0–92.0) 6	83.0 (76.0–90.0) 7
Tail length	25.0	23.0	26.0 (23.0–28.0) 6	23.7 (20.0–28.0) 7
Hind foot length	17.0	15.0	12.0 (11.0–13.0) 6	12.1 (12.0–13.0) 7
Ear length	35.0	35.0	25.7 (25.0–26.0) 6	25.4 (24.5–27.5) 7
Forearm length	54.0	54.0	50.0 (47.2–53.5) 6	48.7 (47.0–50.2) 7
Greatest length of skull	—	25.37	21.77 (21.35–22.05) 4	21.11 (20.57–21.66) 4
Condylolincisive length	—	23.29	19.69 (19.46–20.09) 4	18.91 (18.25–19.49) 4
Postorbital breadth	—	4.77	4.28 (4.03–4.46) 4	4.04 (3.91–4.24) 4
Braincase breadth	—	10.05	8.87 (8.65–9.12) 4	8.25 (8.00–8.51) 4
Mastoid breadth ^b	—	11.67	11.34 (10.86–11.79) 4	10.74 (10.16–11.17) 4
Zygomatic breadth	—	13.92	12.49 (11.96–12.97) 4	11.84 (10.94–12.32) 4
Maxillary toothrow length	—	9.48	7.81 (7.52–8.06) 4	7.48 (7.40–7.53) 4
Breadth across molars	—	5.56	8.56 (8.39–8.71) 3	8.22 (7.52–8.60) 4

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

^b Mastoid breadth in *Mimon crenulatum* does not include the width of the enlarged bulla, which extends laterally beyond the edge of the mastoid.

roost opening at ground level, a small hole ca. 15 cm in diameter, with a mistnet enclosure that caught one adult male *Mimon bennettii* and 27 adult male *Carollia perspicillata* between 18:10 and 18:35 hours on 17 November 1992 (the *Mimon bennettii* emerged at 18:25 hours); no emerging bats escaped. We did not revisit this roost in subsequent years.

Mimon crenulatum (E. Geoffroy)

VOUCHER MATERIAL: 7 females (AMNH *267114, *267115, *267437, *267887, *267889; MNHN *1995.1032, 1995.1033) and 10 males (AMNH *267111, 267113, *267880, 267884, *267885, *267886, 267888; MNHN *1995.1034, *1995.1035, *1995.1036); see table 26 for measurements.

IDENTIFICATION: Useful descriptions and measurements of *Mimon crenulatum* were provided by Handley (1960), Goodwin and Greenhall (1961), Husson (1962, 1978), Hill (1964), Genoways and Williams (1979), Swanepoel and Genoways (1979), Gardner and Patton (1972), Hall (1981), Brosset and Charles-Dominique (1990), and Pedro et al. (1994). Of the five subspecies recognized by

Koopman (1994), *M. c. crenulatum* occurs from Trinidad and eastern Venezuela throughout the Guianas to southern Amazonian Brazil. However, we follow Gardner and Patton (1972) in regarding *M. koepckeae* (from the highlands of central Peru) as a distinct species contra Koopman (1978, 1993, 1994).

Our voucher material conforms with previous descriptions of *Mimon crenulatum crenulatum*. Measurements of Paracou specimens generally fall within the range of variation previously documented for Guianan populations (Husson, 1962, 1978; Hill, 1964; Genoways and Williams, 1979; Brosset and Charles-Dominique, 1990), although some of our males are slightly smaller in some dimensions than specimens previously reported from the region.

FIELD OBSERVATIONS: All of the 17 *Mimon crenulatum* we captured at Paracou were taken in ground-level mistnets: 9 in well-drained primary forest, 4 in swampy primary forest, and 4 in creekside primary forest. An unusually large proportion (88%) of captures were in the very early evening, before 19:00 hours.

TABLE 27
Measurements^a of *Phylloderma stenops* Collected at Paracou

Number/Sex	3 females	5 males
Weight	49.2 (44.5–57.5) 3	42.0 (40.0–43.5) 3
Total length	117.3 (115.0–119.0) 3	110.6 (100.0–124.0) 5
Tail length	20.3 (19.0–22.0) 3	18.2 (13.0–24.0) 5
Hind foot length	20.0 (18.0–22.0) 3	19.6 (19.0–21.0) 5
Ear length	25.5 (25.0–26.0) 2	25.8 (25.0–27.0) 5
Forearm length	69.0 (67.0–71.0) 3	69.8 (69.0–72.0) 5
Greatest length of skull	29.16 (29.16) 1	29.82 (29.45–30.06) 3
Condylolincisive length	26.22 (26.22) 1	27.08 (26.88–27.30) 3
Postorbital breadth	8.72 (8.72) 1	8.80 (8.58–8.87) 3
Braincase breadth	12.49 (12.49) 1	12.73 (12.43–13.06) 3
Mastoid breadth	13.32 (13.32) 1	13.69 (13.59–13.85) 3
Zygomatic breadth	14.90 (14.90) 1	14.92 (14.90–14.95) 3
Maxillary tooththrow length	9.55 (9.55) 1	9.84 (9.74–9.86) 3
Breadth across molars	9.77 (9.77) 1	9.63 (9.59–9.69) 3

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

Phylloderma stenops Peters

VOUCHER MATERIAL: 3 females (AMNH *266078, *267441; MNHN *1995.1075) and 5 males (AMNH *266077, *267440, *267890, *267891; MNHN *1995.1076); see table 27 for measurements.

IDENTIFICATION: Descriptions and measurements of *Phylloderma stenops* from the Guianas and elsewhere were provided by Husson (1962, 1978), Hill (1964), Gardner (1976), Genoways and Williams (1979), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Brosset and Charles-Dominique (1990), and Anderson (1997). Three subspecies are currently recognized: *P. s. septentrionalis* (southern Mexico to Costa Rica), *P. s. stenops* (Panama to southern Brazil), and *P. s. boliviensis* (central Bolivia) (Barquez and Ojeda, 1979; Koopman, 1994; Anderson, 1997).

Our voucher material conforms in all respects to previous descriptions of *Phylloderma stenops stenops*, and measurements fall within the range of variation reported previously for this taxon.

FIELD OBSERVATIONS: All eight of the *Phylloderma stenops* we captured at Paracou were taken in ground-level mistnets: two in well-drained primary forest, three in swampy primary forest, two in creekside primary for-

est, and one in closed-canopy secondary growth.

Phyllostomus discolor Wagner

VOUCHER MATERIAL: 10 females (AMNH *267116, *267118, *267120, *267121, *267123, *267124; MNHN *1995.1077, *1995.1078, *1995.1079, *1995.1080) and 5 males (AMNH *267117, *267119, *267984, *267986; MNHN *1995.1081); see table 28 for measurements.

IDENTIFICATION: Useful descriptions and measurements of *Phyllostomus discolor* may be found in Goodwin and Greenhall (1961), Husson (1962, 1978), Power and Tamsitt (1973), Taddei (1975a), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), and Anderson (1997). Two subspecies are often recognized: *P. d. verrucosus* (Mexico to northwestern Peru) and *P. d. discolor* (South America east of the Andes to northwestern Argentina; Margarita Island; Trinidad) (Koopman, 1994). Power and Tamsitt (1973), however, questioned the recognition of these taxa based on comparisons of specimens from near the supposed contact zone in Colombia.

Our Paracou specimens conform closely with previous descriptions of *Phyllostomus discolor*, and measurements fall within the

TABLE 28
Measurements^a of *Phyllostomus* Collected at Paracou

	<i>Phyllostomus discolor</i>		<i>Phyllostomus elongatus</i>	
	10 females	5 males	14 females	12 males
Number/Sex				
Weight	34.8 (29.4–47.0) 10	34.1 (32.0–36.0) 5	36.6 (30.0–51.0) 14	38.8 (32.0–42.0) 12
Total length	100.3 (95.0–110.0) 10	102.2 (100.0–106.0) 5	105.0 (99.0–112.0) 14	106.9 (101.0–115.0) 12
Tail length	15.1 (12.0–16.0) 10	18.8 (16.0–21.0) 5	21.4 (17.0–27.0) 14	21.8 (18.0–26.0) 12
Hind foot length	17.0 (16.0–18.0) 10	16.8 (16.0–18.0) 5	17.8 (13.0–22.0) 14	18.3 (15.0–23.0) 12
Ear length	22.3 (19.0–25.0) 10	22.0 (21.0–23.0) 5	29.1 (26.0–31.5) 14	29.6 (27.0–32.0) 12
Forearm length	61.7 (60.0–65.0) 10	63.0 (61.0–65.0) 5	66.8 (64.0–69.0) 14	66.5 (65.0–68.0) 10
Greatest length of skull	29.16 (28.68–29.84) 6	29.52 (29.03–29.85) 3	29.04 (28.64–29.91) 6	29.32 (28.73–29.81) 4
Condylolincisive length	26.69 (26.04–27.53) 6	26.89 (26.46–27.26) 3	26.21 (25.93–26.70) 6	26.48 (25.99–26.87) 4
Postorbital breadth	6.36 (6.12–6.73) 6	6.47 (6.35–6.62) 3	5.47 (5.30–5.61) 6	5.48 (5.32–5.60) 4
Braincase breadth	11.95 (11.49–12.38) 6	12.07 (11.73–12.41) 3	11.16 (11.01–11.36) 6	11.07 (10.83–11.47) 4
Mastoid breadth	14.31 (14.07–14.56) 6	14.83 (14.72–15.02) 3	14.40 (13.97–14.85) 6	14.72 (14.54–14.87) 4
Zygomatic breadth	15.12 (14.80–15.38) 6	15.39 (15.15–15.52) 3	16.01 (15.54–16.29) 6	16.58 (16.48–16.76) 4
Maxillary toothrow length	9.32 (9.11–9.60) 6	9.43 (9.13–9.60) 3	10.66 (10.49–10.83) 6	10.66 (10.46–10.79) 4
Breadth across molars	9.78 (9.36–9.96) 6	9.75 (9.64–9.89) 3	11.21 (11.07–11.39) 6	11.24 (10.84–11.45) 4

	<i>Phyllostomus hastatus</i>	
	11 females	8 males
Number/Sex		
Weight	77.5 (64.0–90.0) 11	88.2 (78.0–100.0) 8
Total length	130.8 (123.0–138.0) 11	135.6 (130.0–142.0) 8
Tail length	20.2 (17.0–26.0) 11	22.0 (17.0–29.0) 8
Hind foot length	22.5 (19.0–25.0) 11	22.9 (22.0–24.0) 8
Ear length	30.2 (27.0–32.0) 11	30.3 (28.0–32.0) 8
Forearm length	84.3 (82.5–89.0) 11	83.9 (77.5–87.0) 8
Greatest length of skull	35.71 (34.72–36.16) 7	37.27 (35.48–38.29) 5
Condylolincisive length	31.99 (31.56–32.39) 7	33.20 (32.10–34.23) 5
Postorbital breadth	6.82 (6.40–7.06) 7	6.94 (6.65–7.31) 5
Braincase breadth	13.74 (13.47–14.05) 7	13.96 (13.66–14.38) 5
Mastoid breadth	18.55 (17.99–18.90) 7	19.72 (19.26–20.30) 5
Zygomatic breadth	19.84 (19.44–20.17) 7	21.07 (20.58–21.65) 5
Maxillary toothrow length	12.53 (12.23–12.75) 7	13.03 (12.43–13.74) 5
Breadth across molars	13.18 (12.75–13.60) 7	13.59 (13.21–13.94) 5

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

range of variation previously reported from the Guiana region. Our comparisons of published measurements from throughout the known geographic range of *P. discolor* suggest that Power and Tamsitt (1973) were correct and that there is no current justification for recognizing subspecies.

FIELD OBSERVATIONS: We captured 17 *Phyllostomus discolor* at Paracou: 14 in ground-level mistnets and 3 in elevated nets. Four of the ground-level captures were in well-drained primary forest, eight were in

swampy primary forest, and two were in creekside primary forest. One of the elevated mistnet captures was made at 18–21 m over a narrow dirt road and two were made at 10–13 m above a treefall gap in creekside primary forest. Several individuals netted in the dry season were covered with pollen. Most bats were caught singly, but two adult males and two adult females (possibly members of a foraging flock) were taken within a 10-minute interval at one mistnetting site in swampy primary forest on 24 October 1992, and an-

other adult female was caught a few hours later at the same place.

Phyllostomus elongatus (E. Geoffroy)

VOUCHER MATERIAL: 14 females (AMNH *266051, *266055, *266058, *266062, *266063, *266064, *266067, *266068, *267152, *267897; MNHN *1995.1082, *1995.1083, *1995.1084, *1995.1085) and 12 males (AMNH *266050, *266052, *266053, *266054, *266065, *266066, *266069, *267127; MNHN *1995.1086, *1995.1087, *1995.1088, *1995.1089); see table 28 for measurements.

IDENTIFICATION: Descriptions and measurements of *Phyllostomus elongatus* from the Guianas and elsewhere were provided by Husson (1962, 1978), Hill (1964), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), and Anderson (1997). No subspecies are currently recognized (Koopman, 1994).

Our material from Paracou agrees in all respects with previous descriptions of *Phyllostomus elongatus*. Like other conspecific material from the Guiana region, our specimens fall near the upper end of the known range of size variation for *P. elongatus*.

FIELD OBSERVATIONS: We recorded 162 captures (probably including some recaptures) of *Phyllostomus elongatus* at Paracou. One hundred fifty-nine captures were in ground-level mistnets,⁹ one was in a mistnet suspended 13–16 m above a narrow dirt road, and two were at roosts. Seventy-four of the ground-level mistnet captures were in well-drained primary forest, 45 were in swampy primary forest, 27 were in creekside primary forest, 1 was in a natural treefall opening in primary forest, 7 were in man-made clearings, and 5 were in closed-canopy secondary growth. The two bats taken at roosts were both solitary males; one was collected from a tree cavity with a single large opening about 5 m above the ground (fig. 26), the other from the central shaft of a hol-

low tree with a large lower entrance at ground level and second smaller aperture ca. 15–20 m farther up the trunk (this roost was shared with *Saccopteryx bilineata* and *Carollia perspicillata*). Both roosts were in well-drained primary forest.

By contrast with the multiple elevated-mistnet captures we recorded for *Phyllostomus discolor* and *P. hastatus* (see above and below), the almost complete absence of *P. elongatus* in nets suspended more than a few meters above the ground is noteworthy.

Phyllostomus hastatus (Pallas)

VOUCHER MATERIAL: 11 females (AMNH *266071, *266072, *266073, *266075, *267433, *267901, *267902, *267903; MNHN *1995.1090, *1995.1091, *1995.1092) and 8 males (AMNH *266070, *266074, *267434, *267904, *267907; MNHN *1995.1093, *1995.1094, *1995.1095); see table 28 for measurements.

IDENTIFICATION: Descriptions and measurements of *Phyllostomus hastatus* have appeared in many publications; we consulted those in Goodwin and Greenhall (1961), Husson (1962, 1978), Taddei (1975a), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), and Anderson (1997). Two subspecies of are currently recognized: *P. h. panamensis* (Honduras to Peru and east to Venezuela) and *P. h. hastatus* (eastern Venezuela south to northern Bolivia and southeastern Brazil) (Koopman, 1994). These are distinguished principally on the basis of size, with *P. h. hastatus* being the smaller form.

Our voucher material conforms closely with previous descriptions of *Phyllostomus hastatus hastatus*, with measurements generally falling within the range of variation previously reported from the Guianas. One exception is a particularly small adult male (AMNH 267907), some measurements of which are less than any previously reported for the species (e.g., forearm length of 77.5 mm, compared with 79.0 mm for the smallest male reported by Taddei [1975a]). Comparisons of this diminutive individual with other specimens in our sample, however, failed to reveal any morphological differences other than size.

⁹ This figure includes two bats caught on the outside of the mistnet enclosure described above in the account for *Micronycteris brosetti*. However, because those captures were incidental to roost sampling, they are excluded from the quantitative analysis of mistnetting results below.

FIELD OBSERVATIONS: We recorded 56 captures (possibly including some recaptures) of *Phyllostomus hastatus*, of which 34 were in ground-level mistnets and 22 were in elevated mistnets. The 34 ground-level captures included 9 in well-drained primary forest, 11 in swampy primary forest, 6 in creekside primary forest, and 8 in manmade clearings (7 were taken in a banana/cacao plantation on a single night). Of the 22 elevated mistnet captures, 17 were in nets suspended 10–23 m above a narrow dirt road, 4 were made at 20–38 m above a treefall gap in well-drained primary forest, and 1 was at 7–10 m above a treefall in creekside primary forest.

Tonatia

Although keys to the species of *Tonatia* provided by Genoways and Williams (1984) and Medellín and Arita (1989) are useful tools for identification, neither is complete; the former covers only the species known from Surinam, and the latter was published before *T. bidens* and *T. saurophila* were recognized as distinct species (see below). All of the five species of *Tonatia* known from the Guiana subregion of Amazonia are sympatric (and apparently syntopic) at Paracou.

Tonatia brasiliense (Peters)

VOUCHER MATERIAL: 3 females (AMNH *267103, *267104; MNHN *1995.1052) and 6 males (AMNH *267101, *267102, *267916, *267917; MNHN *1995.1053, *1995.1054); see table 29 for measurements.

IDENTIFICATION: Descriptions and measurements of *Tonatia brasiliense* from the Guianas and elsewhere can be found in Goodwin (1942), Swanepoel and Genoways (1979), Genoways and Williams (1984), and Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Genoways and Williams, 1984; Koopman, 1994).

As the smallest member of its genus, *Tonatia brasiliense* is most likely to be confused with species of *Micronycteris*, which are also small gray-brown phyllostomines with large, rounded ears. Genoways and Williams (1984) mentioned several craniodental characters that can be used to distinguish these taxa, but failed to note one obvious external character: whereas all species of *Micronycteris*

have a pair of large dermal pads forming a “V” on the tip of the chin, the tip of the chin in *T. brasiliense* (and other congeners) has a U-shaped row of tiny dermal papillae (Emmons, 1990, 1997). We also observed that *T. brasiliense* folds its ears back against the crown of the head when touched, a behavior seen in several other species of *Tonatia* (see below) but not in *Micronycteris*.

Our voucher material conforms closely with previous descriptions of *Tonatia brasiliense*, particularly those based on material from the Guianas. Probably because our series contains more individuals than do earlier collections from the region, it exhibits somewhat greater size variability than previously reported. However, measurements of our specimens fall within the range of variation previously documented for the species as a whole.

As remarked by Genoways and Williams (1984), *Tonatia brasiliense* as currently recognized may be composite. Should this prove to be the case, comparisons with published measurements (e.g., those in Goodwin [1942] and Swanepoel and Genoways [1979]) suggest that our specimens, along with others from the Guianas, would be referred to *T. brasiliense* rather than to other taxa currently treated as synonyms (e.g., *minuta*, *nicaraguae*, and *venezuelae*; Handley [1966], Gardner [1976], Jones and Carter [1976], Genoways and Williams [1984], Medellín and Arita [1989], Koopman [1993, 1994]).

FIELD OBSERVATIONS: All of the nine specimens of *Tonatia brasiliense* that we caught at Paracou were taken in ground-level mistnets: six in swampy primary forest and three in creekside primary forest.

Tonatia carrikeri (J. A. Allen)

VOUCHER MATERIAL: 1 female (AMNH *267918); see table 29 for measurements.

IDENTIFICATION: *Tonatia carrikeri* has been collected only rarely, so descriptions and measurements of most known specimens have been reported in the literature, for example, by Goodwin (1942), Husson (1962, 1978), Gardner (1976), Swanepoel and Genoways (1979), McCarthy et al. (1983, 1992), Genoways and Williams (1984), and McCar-

TABLE 29
Measurements^a of Smaller Species of *Tonatia* Collected at Paracou

	<i>Tonatia brasiliense</i>		<i>Tonatia carrikeri</i>
Number/Sex	3 females	6 males	1 female
Weight	8.6 (8.6–8.7) 3	9.3 (8.3–9.9) 6	20.8
Total length	67.0 (66.0–68.0) 3	64.7 (61.0–68.0) 6	80.0
Tail length	10.3 (8.0–13.0) 3	10.0 (8.0–14.0) 6	17.0
Hind foot length	11.3 (11.0–12.0) 3	11.6 (11.0–13.0) 6	14.0
Ear length	23.7 (23.0–24.0) 3	23.8 (23.0–25.0) 6	27.0
Forearm length	35.7 (35.0–36.0) 3	35.8 (34.0–38.0) 6	48.5
Greatest length of skull	18.90 (18.50–19.30) 2	19.49 (19.14–19.83) 6	—
Condylolincisive length	17.27 (17.03–17.50) 2	17.45 (17.19–17.71) 2	—
Postorbital breadth	3.02 (2.98–3.06) 2	3.24 (3.13–3.34) 2	—
Braincase breadth	7.94 (7.91–7.97) 2	8.11 (8.00–8.22) 2	—
Mastoid breadth	8.95 (8.92–8.98) 2	9.35 (9.10–9.60) 2	—
Zygomatic breadth	9.20 (9.18–9.22) 2	9.52 (9.48–9.55) 2	—
Maxillary tooththrow length	6.73 (6.59–6.87) 2	6.70 (6.64–6.75) 2	—
Breadth across molars	6.14 (6.13–6.14) 2	6.30 (6.27–6.32) 2	—
	<i>Tonatia schulzi</i>		
Number/Sex	2 females	2 males	
Weight	19.2 (18.4–19.9) 2	18.7 (17.6–19.8) 2	
Total length	78.5 (77.0–80.0) 2	77.0 (76.0–78.0) 2	
Tail length	13.0 (11.0–15.0) 2	11.0 (7.0–15.0) 2	
Hind foot length	13.0 (12.0–14.0) 2	14.5 (14.0–15.0) 2	
Ear length	29.0 (28.0–30.0) 2	31.0 (30.0–32.0) 2	
Forearm length	44.5 (44.0–45.0) 2	42.8 (42.5–43.0) 2	
Greatest length of skull	23.12 (23.03–23.20) 2	22.79 (22.51–23.07) 2	
Condylolincisive length	20.23 (20.14–20.32) 2	20.14 (19.65–20.63) 2	
Postorbital breadth	3.80 (3.75–3.84) 2	3.87 (3.78–3.95) 2	
Braincase breadth	9.59 (9.51–9.66) 2	9.63 (9.35–9.90) 2	
Mastoid breadth	12.00 (11.91–12.08) 2	11.87 (11.63–12.11) 2	
Zygomatic breadth	11.60 (11.58–11.61) 2	11.54 (11.27–11.80) 2	
Maxillary tooththrow length	7.96 (7.83–8.09) 2	7.88 (7.67–8.08) 2	
Breadth across molars	7.49 (7.37–7.60) 2	7.44 (7.24–7.63) 2	

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

thy and Handley (1987). No subspecies are currently recognized (Koopman, 1994).

Our single female specimen of *Tonatia carrikeri* agrees with previous descriptions of the species in all respects. Like several other congeners, *T. carrikeri* folds its ears back over the crown of the head when they are touched.

FIELD OBSERVATIONS: The single example of *Tonatia carrikeri* we captured at Paracou was taken in a ground-level mistnet in

swampy primary forest dominated by the palm *Euterpe oleracea*.

Tonatia saurophila
Koopman and Williams

VOUCHER MATERIAL: 10 females (AMNH *266044, *266045, *266046, *266047, *267429, *267908, *267914; MNHN *1995.1060, *1995.1061, *1995.1062) and 11 males (AMNH *266049, *267099,

TABLE 30
Measurements^a of Larger Species of *Tonatia* Collected at Paracou

	<i>Tonatia saurophila</i>		<i>Tonatia silvicola</i>	
Number/Sex	10 females	11 males	4 females	6 males
Weight	28.1 (24.9–33.0) 10	25.1 (21.4–28.0) 11	34.9 (29.4–44.0) 4	36.7 (33.0–41.0) 6
Total length	96.9 (92.0–101.0) 9	96.0 (84.0–103.0) 11	103.0 (98.0–107.0) 4	103.3 (98.0–107.0) 6
Tail length	20.0 (18.0–23.0) 10	18.5 (15.0–23.0) 11	21.5 (19.0–26.0) 4	17.5 (15.0–23.0) 6
Hind foot length	16.4 (15.0–18.0) 10	15.5 (13.0–17.0) 10	18.0 (16.0–20.0) 4	18.7 (17.0–20.0) 6
Ear length	29.9 (29.0–33.0) 9	30.3 (29.0–34.0) 11	37.9 (36.0–39.0) 4	37.8 (36.0–41.0) 6
Forearm length	57.3 (55.0–59.0) 10	55.9 (54.0–58.0) 11	59.5 (59.0–61.0) 4	59.0 (56.0–61.0) 6
Greatest length of skull	27.51 (26.98–28.03) 5	27.22 (26.83–27.58) 6	27.50 (27.50) 1	28.39 (27.21–29.24) 3
Condylolincisive length	24.36 (23.73–24.95) 5	24.09 (23.73–24.48) 6	24.58 (24.58) 1	25.23 (24.77–25.81) 3
Postorbital breadth	5.36 (5.15–5.55) 5	5.48 (5.33–5.66) 6	4.04 (4.04) 1	4.12 (3.95–4.32) 3
Braincase breadth	10.26 (10.17–10.44) 5	10.36 (10.24–10.55) 6	10.67 (10.67) 1	10.80 (10.43–11.10) 3
Mastoid breadth	12.77 (12.50–13.13) 5	12.47 (12.10–12.73) 6	14.61 (14.61) 1	14.48 (13.95–14.93) 3
Zygomatic breadth	13.58 (13.20–14.11) 5	13.58 (13.25–13.83) 6	13.89 (13.89) 1	14.46 (14.13–14.70) 3
Maxillary tooththrow length	9.34 (9.21–9.45) 5	9.33 (9.15–9.49) 6	9.65 (9.65) 1	10.08 (10.03–10.14) 3
Breadth across molars	8.27 (7.96–8.58) 5	8.41 (8.00–8.86) 6	9.20 (9.20) 1	9.34 (9.00–9.73) 3

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

*267909, *267430, *267431, *267912, *267915; MNHN *1995.1063, *1995.1064, *1995.1065, *1995.1066); see table 30 for measurements.

IDENTIFICATION: Species identification within the *Tonatia bidens* complex, which includes *T. saurophila*, requires reference to craniodental characters described by Williams et al. (1995). Other useful descriptions and comparative measurements of *T. saurophila* from the Guianas may be found (incorrectly listed under *T. bidens*) in Husson (1962, 1978), Hill (1964), Genoways and Williams (1984), and Brosset and Charles-Dominique (1990). Williams et al. (1995) summarized measurements of *T. saurophila* from throughout its known geographic range. Three subspecies of *T. saurophila* are presently recognized: *T. s. bakeri* (southern Mexico to northern Colombia and northwestern Venezuela), *T. s. maresi* (southern and northeastern Venezuela, eastern Colombia, Ecuador, and Peru, the Guianas, and eastern Brazil), and *T. s. saurophila* (Jamaica) (Williams et al., 1995).

Our voucher material corresponds closely to Williams et al.'s (1995) description of *Tonatia saurophila maresi*, with measurement data generally falling within the range

of variation they reported; the only exception is the forearm length of one of our females, which slightly exceeds the largest value previously reported for the subspecies. As *T. s. maresi* is the smaller of the two mainland forms, however, this measurement falls within the known range of variation for the species *T. saurophila* as a whole.

None of the individuals of *Tonatia saurophila* that we captured at Paracou folded its ears over the crown of the head when touched.

FIELD OBSERVATIONS: We recorded 61 captures (possibly including some recaptures) of *Tonatia saurophila* at Paracou, of which 60 were in ground-level mistnets and 1 was in an elevated net. Of the 60 ground-level mistnet captures, 23 were in well-drained primary forest, 26 were in swampy primary forest, 8 were in creekside primary forest, 2 were in closed-canopy secondary growth, and 1 was in a manmade clearing. The only capture we recorded in an elevated net was made at 7–10 m above a treefall in creekside primary forest.

Tonatia schulzi
Genoways and Williams

VOUCHER MATERIAL: 3 females (AMNH *267105, *267420, *267421) and 4 males (A-

MNH *267106, *267920; MNHN 1995.1055, 1995.1056); see table 29 for measurements.

IDENTIFICATION: Descriptions and comparative measurements of *Tonatia schulzi* can be found in Genoways and Williams (1980, 1984), Marques and Oren (1987), Gribel and Taddei (1989), and McCarthy et al. (1988). This species is easy to recognize in the field owing to the unique warty skin covering the forearms, fingers, ears, and noseleaf. No subspecies are currently recognized (Koopman, 1994).

Tonatia schulzi was originally described in 1980, and only a few specimens exist in museum collections. Our seven specimens almost double the number reported in the literature, and constitute the largest series available from a single locality. Although our material generally agrees with previous descriptions, some specimens are slightly larger than any previously reported. We also found a surprising amount of variation in ventral pelage color among our adults, with the venter ranging from medium gray (comparable to that seen in *T. saurophila*) to almost white (approaching that seen in *T. carrikeri*). In the original description of *T. schulzi*, the venter was said to be "slightly paler than dorsum but not white" (Genoways and Williams, 1980: 205). Comparisons of dental wear among our specimens suggest that the example with the palest ventral fur, an adult female (AMNH 267105), is also the oldest, whereas younger adults have darker venters; our two subadults have dark gray venters. Apparently the ventral pelage becomes paler with age in *Tonatia schulzi*.

Our material confirms the observations made by McCarthy et al. (1988) concerning the morphology of the clitoris in *Tonatia schulzi*. The clitoris is elongate in all of our females, resembling a penis upon casual inspection; indeed, we incorrectly recorded the sex of one individual in the field, an error that might not have been detected had the specimen been made into a skin rather than preserved in fluid. As McCarthy et al. (1988) remarked, careful examination of the genitalia before specimen preparation is crucial for accurate sex identification in this species.

As in *Tonatia brasiliense*, *T. carrikeri*, and *T. silvicola*, we found that all individuals of

T. schulzi folded their ears back over the crown of the head when they were touched.

FIELD OBSERVATIONS: All seven *Tonatia schulzi* captured at Paracou were taken in ground-level mistnets: five in well-drained primary forest, one in swampy primary forest, and one in creekside primary forest.

Tonatia silvicola

VOUCHER MATERIAL: 4 females (AMNH *267108, *267422, *267924; MNHN *1995.1057) and 6 males (AMNH *267107, *267922, *267923, *267925; MNHN *1995.1058, *1995.1059); see table 30 for measurements.

IDENTIFICATION: Useful descriptions and comparative measurements of *Tonatia silvicola*¹⁰ can be found in Husson (1962, 1978), Davis and Carter (1978), Swanepoel and Genoways (1979), Genoways and Williams (1984), and Medellín and Arita (1989). Four subspecies are currently recognized, of which *T. s. laephotis* is the Guianan form (Koopman, 1994).

Our voucher material conforms closely with descriptions of *Tonatia silvicola* in the literature cited above. Like the holotype of *T. s. laephotis* (from Guyana; Thomas, 1910) and specimens from Guyana and Surinam subsequently referred to *T. s. laephotis* by Hill (1964) and Genoways and Williams (1984), measurements of our material (table 30) fall at the upper end of the size range known for *T. silvicola*. A few specimens in our series have measurements slightly in excess of previously reported values.

As in *Tonatia brasiliense*, *T. carrikeri*, and *T. schulzi*, we found that all individuals of *T. silvicola* folded their ears back over the crown of the head when the pinnae were touched. This is an easy way to distinguish *T. silvicola* from *T. saurophila* in the hand. Another useful field character is ear length (table 30): *T. silvicola* has very large ears (36.0–41.0 mm), while those of *T. saurophila* are substantially smaller (29.0–34.0 mm).

¹⁰ Patterson (1992) argued that the correct spelling of the specific epithet is "sylvicola," but we have not formed a definite opinion about the relevant nomenclatural issues and therefore follow current usage (Koopman, 1993).

TABLE 31
Measurements^a of *Trachops cirrhosus* Collected at Paracou

Number/Sex	8 females	16 males
Weight	36.7 (32.0–44.6) 8	37.6 (29.5–44.0) 16
Total length	104.4 (95.0–110.0) 8	101.6 (93.0–107.0) 16
Tail length	18.8 (17.0–21.0) 8	18.4 (13.0–29.0) 16
Hind foot length	21.1 (20.0–22.0) 8	20.0 (15.0–23.0) 16
Ear length	35.1 (34.0–36.0) 8	34.9 (33.0–37.5) 16
Forearm length	63.6 (62.0–66.0) 8	63.2 (60.0–65.5) 15
Greatest length of skull	29.16 (29.01–29.42) 4	29.78 (28.43–30.29) 11
Condylolincisive length	26.77 (26.02–27.43) 4	27.20 (26.12–28.04) 11
Postorbital breadth	5.26 (5.09–5.41) 4	5.41 (5.22–5.60) 11
Braincase breadth	11.63 (11.41–11.93) 4	11.93 (11.21–12.40) 11
Mastoid breadth	14.16 (14.01–14.32) 4	14.37 (13.53–14.94) 11
Zygomatic breadth	15.02 (14.81–15.30) 4	15.31 (14.70–15.96) 11
Maxillary tooththrow length	10.81 (10.36–11.17) 4	10.88 (10.52–11.21) 11
Breadth across molars	10.61 (10.32–10.85) 4	10.64 (10.33–11.01) 11

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

FIELD OBSERVATIONS: All of the 11 *Tonatia silvicola* we captured at Paracou were taken in ground-level mistnets: 6 in well-drained primary forest, 3 in swampy primary forest, and 2 in creekside primary forest.

Trachops cirrhosus (Spix)

VOUCHER MATERIAL: 8 females (AMNH *266080, *266081, *266082, *267928, *267936; MNHN *1995.1067, *1995.1068, *1995.1069) and 16 males (AMNH *266079, *266084, *266089, *267129, *267442, *267929, *267930, *267932, *267933, *267934, *267935; MNHN *1995.1070, *1995.1071, *1995.1072, *1995.1073, *1995.1074); see table 31 for measurements.

IDENTIFICATION: Descriptions and measurements of *Trachops cirrhosus* from the Guianas and elsewhere may be found in Goodwin and Greenhall (1961), Husson (1962, 1978), Swanepoel and Genoways (1979), Hall (1981), and Brosset and Charles-Dominique (1990). Three subspecies are currently recognized: *T. c. cirrhosus* (Costa Rica to Amazonian Brazil and Bolivia, east of the Andes to Ecuador), *T. c. coffini* (southern Mexico to Nicaragua), and *T. c. ehrhardti* (Atlantic Forest of southeastern Brazil, and possibly parts of Bolivia) (Koopman, 1994).

Our Paracou specimens agree well with

previous descriptions of *Trachops cirrhosus cirrhosus*. Like other material with published measurements from the Guianas, our vouchers are among the largest known for the species. In particular, a few forearm measurements from our series slightly exceed the largest values previously reported for *T. cirrhosus*.

FIELD OBSERVATIONS: We recorded 58 captures (possibly including some recaptures) of *Trachops cirrhosus* at Paracou, of which 53 were in ground-level mistnets and 5 were at roosts. Of the 53 mistnet captures, 16 were in well-drained primary forest, 25 were in swampy primary forest, 11 were in creekside primary forest (many over streams), and 1 was over a roadside puddle adjacent to well-drained primary forest. Both of the roosts we found were over water in large (2.5 m in diameter) culverts; one roosting group captured in its entirety consisted of four adult males. Most mistnet captures were of solitary individuals, but we once saw a flock of five bats collide with a net set across a small stream; two individuals, both adult females, were captured but the other three escaped. A mistnet enclosure built around a hollow tree occupied by *Mimon bennettii* and *Carollia perspicillata* (described in the account for the former species, above) caught a single adult female *Trachops* that flew directly toward

TABLE 32
Measurements^a of *Trinycteris nicefori* Collected at Paracou

Number/Sex	4 females	5 males
Weight	8.2 (7.2–8.9) 4	7.4 (7.0–8.0) 5
Total length	64.3 (60.0–68.0) 4	61.0 (55.0–64.0) 5
Tail length	10.0 (9.0–13.0) 4	9.4 (9.0–10.0) 5
Hind foot length	13.0 (12.0–14.0) 4	13.4 (13.0–14.0) 5
Ear length	18.8 (18.0–20.0) 4	18.2 (17.0–19.0) 5
Forearm length	39.5 (38.0–41.0) 4	37.2 (36.0–38.0) 5
Tibia length	15.9 (15.4–16.4) 2	15.5 (15.0–15.9) 3
Thumb length	9.6 (9.5–9.6) 2	9.7 (9.1–10.5) 3
Greatest length of skull	20.10 (19.71–20.49) 2	20.10 (19.54–20.39) 3
Condylolincisive length	18.53 (17.99–19.07) 2	18.50 (18.06–18.72) 3
Postorbital breadth	4.21 (4.21) 1	4.03 (3.92–4.11) 3
Braincase breadth	8.12 (7.97–8.26) 2	8.12 (7.92–8.22) 3
Mastoid breadth	8.53 (8.43–8.62) 2	8.67 (8.74–9.05) 3
Zygomatic breadth	9.10 (9.05–9.14) 2	9.13 (8.84–9.51) 3
Maxillary toothrow length	7.28 (6.99–7.56) 2	7.29 (7.14–7.45) 3
Breadth across molars	6.05 (5.99–6.10) 2	5.99 (5.84–6.13) 3

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

the roost opening from the outside, possibly attempting to ambush the emerging *C. perspicillata*.

Trinycteris

As discussed in the accounts for *Glyphoncteris* and *Micronycteris* (above), we follow Peffley et al. (MS) in elevating *Trinycteris* to generic rank. As recognized herein, *Trinycteris* is monotypic, containing only *T. nicefori*. Although Sanborn (1949) diagnosed *Trinycteris*, he did not include all of the characters that we consider useful for distinguishing phyllostomine genera. We therefore provide an emended diagnosis below.

EMENDED DIAGNOSIS OF *TRINYCTERIS*: Dorsal fur tricolored (each hair with dark base, pale median band, and dark tip); ventral fur dark; fur on external surface of leading edge of ear pinna short (≤ 4 mm); pinna pointed (not rounded) with concavity on posterior border near tip; interauricular band absent; ventral margin of narial horseshoe confluent with upper lip (boundary between horseshoe and lip not defined by a ridge or free flap of skin); chin with a pair of dermal pads arranged in a “V” with no central papilla; fourth metacarpal shortest, third longest; second phalanx of wing digits III and IV longer

than first phalanx of same digits; calcar markedly shorter than hind foot; rostrum and anterior orbital region not inflated; basisphenoid pits deep; mastoid breadth less than zygomatic breadth; dental formula I 2/2, C 1/1, P 2/3, M 3/3 $\times 2 = 34$; upper canine much less than twice the height of the inner upper incisor; outer upper incisor in normal position between inner incisor and canine, not excluded from occlusion with lower incisors; P3 not molariform, lingual cingulum and cusp absent; P4 lingual cingulum with convex outline and raised edge, lingual cusp small or absent; crown height of P3 less than that of P4; lower incisors trifid; p3 much smaller than p2 or p4; lower premolars aligned in row on mandible, none excluded from toothrow; coronoid process high, with relatively steep slope along upper margin from anterior to posterior.

Trinycteris nicefori

VOUCHER MATERIAL: 4 females (AMNH *267877, *267878; MNHN *1995.815, *1995.817) and 5 males (AMNH *266017, *266019, *267410, *267876; MNHN *1995.816); see table 32 for measurements.

IDENTIFICATION: Descriptions and comparative measurements of *Trinycteris nicefori*

TABLE 33
Measurements^a of *Vampyrum spectrum* Collected at Paracou

Number/Sex	2 females	1 male
Weight	153.0 (134.0–172.0) 2	138.0
Total length	146.0 (145.0–147.0) 2	135.0
Tail length	0.0 (0.0–0.0) 2	0.0
Hind foot length	35.5 (35.0–36.0) 2	34.0
Ear length	48.0 (48.0–48.0) 2	48.0
Forearm length	107.5 (105.0–110.0) 2	105.0
Greatest length of skull	50.19 (50.19) 1	—
Condylolincisive length	42.86 (42.86) 1	—
Postorbital breadth	8.16 (8.16) 1	—
Braincase breadth	15.87 (15.87) 1	—
Mastoid breadth	21.80 (21.80) 1	—
Zygomatic breadth	24.06 (24.06) 1	—
Maxillary toothrow length	20.77 (20.77) 1	—
Breadth across molars	14.66 (14.66) 1	—

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

from the Guianas and elsewhere can be found in Sanborn (1949), Goodwin and Greenhall (1961), Hill (1964), Genoways and Williams (1979, 1986), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Brosset and Charles-Dominique (1990), and Simmons (1996b). No subspecies are currently recognized (Sanborn, 1949; Jones and Carter, 1976; Koopman, 1994).

Our voucher specimens conform closely with descriptions of *Trinycteris nicefori* in the literature cited above, with measurements (table 32) falling within the range of variation previously reported for Guianan populations. It is noteworthy that both of the pelage color phases described by Sanborn (1949) are present in our Paracou series, as they are in other Guianan samples reported by Hill (1964) and Williams and Genoways (1980a). Eight of our vouchers (including all the all females) represent Sanborn's "gray phase," having tricolored gray-brown dorsal pelage and a pale gray stripe on the lower back. The brightness of the stripe varies among individuals; in some the stripe is bright and clearly distinct from the surrounding fur, while in others the stripe is only barely discernable. A single male in our series (AMNH 267876) represents Sanborn's "red phase." The dorsal fur in this individual is bright orange-brown, contrasting sharply with the dark brown wing membranes. As in

gray-phase specimens, the dorsal hairs of our red-phase specimen are tricolored with a dark base, pale median band, and dark tip. A pale middorsal stripe is just barely visible in our one red example.

FIELD OBSERVATIONS: The nine individuals of *Trinycteris nicefori* that we captured at Paracou were all taken in ground-level mist-nets. Two were netted in well-drained primary forest, two in swampy primary forest, and four at the margins of manmade clearings. One of the latter was captured next to a fruiting shrub, *Vismia* sp. (Clusiaceae), growing beside a narrow dirt road through the forest. The mistnet we erected in front of this shrub to intercept foraging frugivores otherwise caught only carollines and stenodermatines (*Carollia perspicillata*, *Rhinophylla pumilio*, *Artibeus obscurus*, *A. gnomus*, *A. concolor*, and *Sturnira tildae*).

Vampyrum spectrum (Linnaeus)

VOUCHER MATERIAL: 2 females (AMNH *267446; MNHN *1995.1051) and 1 male (AMNH *267132); see table 33 for measurements.

IDENTIFICATION: *Vampyrum spectrum* is the largest bat in the Neotropics and is easily identified by size alone. Descriptions and measurements have been provided by Goodwin and Greenhall (1961), Husson (1962,

TABLE 34
Measurements^a of *Carollia perspicillata* Collected at Paracou

Number/Sex	23 females	33 males
Weight	15.6 (13.0–20.3) 23	15.3 (11.0–17.1) 33
Total length	69.2 (65.0–85.5) 23	69.6 (62.0–79.0) 33
Tail length	9.0 (6.0–15.0) 23	8.6 (6.0–13.0) 33
Hind foot length	14.1 (12.0–19.0) 21	14.3 (11.0–15.0) 33
Ear length	19.7 (16.0–22.0) 23	19.9 (15.0–23.0) 32
Forearm length	41.9 (39.0–45.0) 23	41.6 (39.0–44.0) 33
Greatest length of skull	22.22 (21.12–23.16) 14	22.54 (21.91–23.12) 15
Condylolincisive length	20.59 (19.75–21.04) 14	20.89 (20.01–21.47) 15
Postorbital breadth	5.49 (5.19–5.92) 14	5.51 (5.23–5.93) 15
Braincase breadth	9.51 (9.25–9.91) 14	9.65 (9.24–10.10) 15
Mastoid breadth	10.84 (10.41–11.27) 14	11.14 (10.64–11.57) 15
Zygomatic breadth	10.88 (10.35–11.53) 14	11.23 (10.95–11.66) 15
Maxillary tooththrow length	7.50 (7.03–7.96) 14	7.61 (7.37–8.14) 15
Breadth across molars	7.61 (7.03–7.88) 14	7.67 (7.31–8.12) 15

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

1978), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Navarro and Wilson (1982), and Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Navarro and Wilson, 1982; Koopman, 1994).

Our voucher material conforms in all respects to previous descriptions of the species.

FIELD OBSERVATIONS: All four *Vampyrus spectrum* we captured at Paracou were taken in ground-level mistnets: two in creekside primary forest and two in manmade clearings bordered by welldrained primary forest. One individual was obviously attracted to the net by the squeals of an entangled *Uroderma bilobatum*, around which it swooped several times before becoming entangled itself.

CAROLLIINAE

By contrast with other Amazonian sites that may have as many as five sympatric carolliines, we collected only two species of this phyllostomid subfamily at Paracou. A third species, however, has been reported from other French Guianan and Surinamese localities (appendix 1).

Carollia perspicillata (Linnaeus)

VOUCHER MATERIAL: 24 females (AMNH *266141, *266145, *266151, *266152, *266155, *266160, *266162, *266378,

*267962, *267965, *267967, *267969, *267970; MNHN *1998.641, *1998.642, *1998.643, *1998.644, *1998.645, *1998.646, *1998.647, *1998.648, *1998.649, *1998.650, *1998.651) and 33 males (AMNH *266126, *266127, *266134, *266153, *266156, *266157, *266158, *266159, *266161, *266163, *266164, *267454, *267961, *267964, *267966, *267968, 269116; MNHN *1998.652, *1998.653, *1998.654, *1998.655, *1998.656, *1998.657, *1998.658, *1998.659, *1998.660, *1998.661, *1998.662, *1998.663, *1998.664, *1998.665, *1998.666, *1998.667); see table 34 for measurements.

IDENTIFICATION: The most useful resources for identification of *Carollia* species are Pine (1972) and Cloutier and Thomas (1992), with the latter containing a key. Other descriptions and comparative measurements of *C. perspicillata* can be found in Goodwin and Greenhall (1961), Husson (1962, 1978), Swanepoel and Genoways (1979), Hall (1981), and Brosset and Charles-Dominique (1990). Although three subspecies of *C. perspicillata* are recognized by some authors (*azteca*, *perspicillata*, and *tricolor*), Pine (1972) found that these taxa intergrade, McLellan (1984) concluded that no subspecies can be distinguished by craniodental measurement data, and Koopman (1994: 84) noted that “subspecies boundaries are not

clear." Although the use of trinomial nomenclature for *Carollia perspicillata* is not currently justified, future morphological or molecular studies may yet show that some subspecific distinctions are warranted.

Our specimens of *Carollia perspicillata* conform in all respects to previous descriptions of the species.

FIELD OBSERVATIONS: We recorded 1142 captures (including recaptures) of *Carollia perspicillata* at Paracou, of which 1048 were in ground-level mistnets, 18 were in elevated mistnets, 75 were at roosts, and 1 was in a harp trap. Of the 1049 ground-level mistnet and harp-trap captures, 252 were in well-drained primary forest, 279 were in swampy primary forest, 110 were in creekside primary forest, 1 was in a treefall opening in primary forest, 325 were in manmade clearings, 9 were in closed-canopy secondary growth, and 73 were over roadside puddles. The 18 captures in elevated mistnets were made between 5 and 13 m above the ground: 7 over a narrow dirt road, 7 over treefalls, and 4 in the subcanopy of swampy primary forest.

Of the 11 roosts at which we captured or observed *Carollia perspicillata* at Paracou, 4 were in culverts under roads, 1 was under a bridge, and 6 were in tree cavities (e.g., figs. 21, 25, 26, 33). We never found *C. perspicillata* under fallen trees, inside hollow logs, or in foliage of any kind. Other bats observed roosting with *C. perspicillata* included *Rhynchonycteris naso*, *Saccopteryx bilineata*, *Micronycteris megalotis*, *M. microtis*, *Mimon bennettii*, *Phyllostomus elongatus*, *Trachops cirrhosus*, and *Glossophaga soricina*. *Carollia perspicillata* was the only species that we found roosting in large bachelor groups; for example, 27 males were captured in a mistnet enclosure as they emerged from an opening in the base of a large hollow tree (a roost shared with *Mimon bennettii*, see above). Another tree-cavity roosting group that we captured in its entirety consisted of two adult males, two lactating adult females, and two juveniles.

Rhinophylla pumilio Peters

VOUCHER MATERIAL: 25 females (AMNH *266168, *266171, *266178, *266184,

*266186, *266188, *266189, *266193, *266196, *266198, *267159, *267456, *267457, *267458, *267459, *267971; MNHN *1998.623, *1998.624, *1998.625, *1998.626, *1998.627, *1998.628, *1998.629, *1998.630, *1998.631) and 24 males (AMNH *266174, *266175, *266179, *266180, *266181, *266182, *266183, *266185, *266187, *266190, *266191, *266192, *266194, *266197, *267158; MNHN *1998.632, *1998.633, *1998.634, *1998.635, *1998.636, *1998.637, *1998.638, *1998.639, *1998.640); see table 35 for measurements.

IDENTIFICATION: Descriptions and comparative measurements of *Rhinophylla pumilio* that we consulted to identify our material included those in Husson (1962, 1978), Hill (1964), Carter (1966), Swanepoel and Genoways (1979), Williams and Genoways (1980a), and Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Koopman, 1994).

Our Paracou specimens conform closely with previous qualitative descriptions of *Rhinophylla pumilio* in the literature cited above. Likewise, measurements of our series generally fall within the known range of variation for the species, although a few are slightly smaller than any previously reported. Because the small individuals in our collection are similar in all other respects to larger examples, we attribute this minor discrepancy to within-population morphometric variation. Like other collections of *R. pumilio* from the Guianas, our Paracou vouchers fall at the lower end of the known range of size variation for the species.

FIELD OBSERVATIONS: We recorded 128 captures (probably including some recaptures) of *Rhinophylla pumilio* at Paracou, of which 106 were in ground-level mistnets, 2 were in elevated mistnets, 19 were at roosts, and 1 was in a harp trap near ground level. Of the 107 ground-level mistnet and harp-trap captures, 22 were in well-drained primary forest, 44 were in swampy primary forest, 14 were in creekside primary forest, 4 were in treefall openings in primary forest, 19 were in manmade clearings, and 4 were in closed-canopy secondary growth. The two bats captured in elevated mistnets were taken

TABLE 35
Measurements^a of *Rhinophylla pumilio* Collected at Paracou

Number/Sex	25 females	24 males
Weight	9.5 (8.0–13.5) 25	8.3 (7.0–10.0) 23
Total length	50.1 (41.0–54.0) 25	48.5 (45.0–52.0) 24
Tail length	0.0 (0.0–0.0) 25	0.0 (0.0–0.0) 24
Hind foot length	10.0 (9.0–11.0) 25	10.0 (9.0–11.0) 23
Ear length	15.2 (14.0–16.0) 25	14.6 (13.0–16.0) 24
Forearm length	34.1 (33.0–36.0) 25	33.5 (32.0–35.0) 23
Greatest length of skull	18.35 (17.64–18.86) 8	18.05 (17.78–18.44) 5
Condylolincisive length	16.88 (16.20–17.53) 8	16.47 (15.96–16.85) 5
Postorbital breadth	5.28 (5.00–5.45) 8	5.29 (5.10–5.51) 5
Braincase breadth	8.22 (8.00–8.47) 8	8.36 (8.17–8.40) 5
Mastoid breadth	9.06 (8.83–9.31) 8	9.02 (8.76–9.27) 5
Zygomatic breadth	9.63 (9.27–10.04) 8	9.50 (9.34–9.84) 5
Maxillary tooththrow length	4.96 (4.71–5.28) 8	4.91 (4.60–5.11) 5
Breadth across molars	6.31 (6.15–6.55) 8	6.30 (5.92–6.74) 5

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

5–10 m above a treefall opening in creekside primary forest.

We found eight roosting groups of *Rhinophylla pumilio* at six unique roost sites (one roost was revisited twice). All of the roosts we found were in foliage between 1.5 and 5 m above the ground. Six roosting groups of *R. pumilio* occupied “bifid” tents (sensu Kunz et al., 1994) made from the terminal leaflets of fronds of immature understory palms that we provisionally identified as *Astrocaryum sciophilum*.¹¹ In all recorded construction details, these tents exactly resembled those in which we also found *Artibeus cinereus* (see figs. 43–45) and *Ectophylla macconnelli* (see fig. 47). Although we do not know which (if any) of these bats was actually responsible for making such tents, we once collected (on 6 August 1993) a group of three *R. pumilio* from a tent previously occupied (on 30 July 1993) by seven *E. macconnelli*. By contrast, we never ob-

served other species of bats in tents previously found occupied by *R. pumilio*. For this reason, and because the delicate anterior dentition of *Rhinophylla* seems inadequate to the task of chewing through the tough lateral veins of *Astrocaryum* leaves, we favor the hypothesis suggested by Charles-Dominique (1993) that *R. pumilio* is a roost parasite that uses tents made by other bats.

In addition to finding roosts of *Rhinophylla pumilio* in bifid *Astrocaryum* leaf-tents, we disturbed one group of three individuals from an unidentified location in a clump of *Phenakospermum guyannense* (Strelitzaceae) that contained an “apical” tent (Kunz et al., 1994) similar in construction to those in which we found *Uroderma bilobatum* at other sites (see fig. 51). On another occasion we found an adult male *R. pumilio* roosting alone beneath an unmodified leaf of *P. guyannense*.

Of the four *Astrocaryum* leaf-tents in which we found *Rhinophylla pumilio*, two were in well-drained primary forest, one was in closed-canopy secondary growth, and one was in primary forest at the edge of a swampy area. The two *Phenakospermum* roosts were both in swampy primary forest. None of the roosting groups we found at Paracou (table 36) contained more than one adult male.

¹¹ We base this identification on vegetative characters described by Henderson et al. (1995) and de Granville (1997): the plicate and subcoriaceous leaflets, regularly arranged and spreading in one plane, have nonspinous margins, and the long spines on the rachis lack basal wings (see figs. 44, 45). However, none of the plants in which we found bat tents at Paracou were fertile, so diagnostic reproductive characters could not be determined.

TABLE 36
Roosting Groups of *Rhinophylla pumilio* Observed at Paracou

Date	Roost site ^a	Group size	Entire group captured?	Age and sex of captured group members
29 Oct 1992	<i>Astrocaryum</i> ^b	2	yes	2 ad. females
2 Nov 1992	<i>Astrocaryum</i>	2	yes	1 ad. male, 1 ad. female
7 Nov 1992	<i>Astrocaryum</i> ^b	4	yes	1 ad. male, 3 ad. females
12 Nov 1992	<i>Astrocaryum</i>	1	yes	1 ad. male
6 Aug 1993	<i>Astrocaryum</i>	3	yes	3 ad. females
29 Aug 1993	<i>Astrocaryum</i> ^b	5	yes	1 ad. male, 4 ad. females
5 Sep 1993	<i>Phenakospermum</i>	3?	no	none aged or sexed
6 Sep 1993	<i>Phenakospermum</i>	1	yes	1 ad. male

^a Plant taxon with occupied foliage (see text).

^b Roosting groups collected and preserved as vouchers on 29 October 1992, 7 November 1992, and 29 August 1993 were found occupying the same leaf-tent.

STENODERMATINAE

Although other Amazonian sites are known to have more than 20 sympatric species of Stenodermatinae, we captured only 15 species of this phyllostomid subfamily at Paracou. Following the taxonomic usage recommended by Peffley et al. (MS), the Paracou species represent eight genera: *Ametrida*, *Artibeus* (including *Dermanura* and *Koopmania*), *Chiroderma*, *Ectophylla* (including *Mesophylla*), *Platyrrhinus* (formerly *Vampyrus*), *Sturnira*, *Uroderma*, and *Vampyressa*. Collections from other localities in French Guiana and Surinam include an additional

seven stenodermatine species (appendix 1), but for reasons explained below (see Analyses of Sampling: Estimating Completeness) we doubt that any of these normally occur within our study area.

Ametrida centurio Gray

VOUCHER MATERIAL: 7 females (AMNH *267973, *267274, *267275, *267276, *267278; MNHN *1995.1037, *1995.1038) and 3 males (AMNH *267279, *267976; MNHN *1995.1039); see table 37 for measurements.

IDENTIFICATION: Peterson's (1965a) revi-

TABLE 37
Measurements^a of *Ametrida centurio* Collected at Paracou

Number/Sex	7 females	3 males
Weight	10.8 (9.3–14.2) 7	7.7 (7.2–8.0) 3
Total length	49.4 (46.0–52.0) 7	44.0 (43.0–45.0) 3
Tail length	0.0 (0.0–0.0) 7	0.0 (0.0–0.0) 3
Hind foot length	11.2 (10.0–12.0) 7	10.2 (10.0–10.5) 3
Ear length	15.0 (15.0–15.0) 7	14.3 (14.0–15.0) 3
Forearm length	32.3 (31.0–33.0) 7	25.8 (25.5–26.0) 3
Greatest length of skull	16.04 (15.62–16.32) 2	14.55 (14.25–14.84) 2
Condylolincisive length	13.71 (13.52–13.90) 2	12.10 (11.94–12.25) 2
Braincase breadth	8.94 (8.77–9.11) 2	8.51 (8.35–8.66) 2
Mastoid breadth	9.83 (9.79–9.86) 2	8.93 (8.84–9.01) 2
Zygomatic breadth	11.23 (11.19–11.26) 2	10.57 (10.43–10.71) 2
Maxillary toothrow length	4.53 (4.43–4.62) 2	3.99 (3.87–4.10) 2
Breadth across molars	7.93 (7.89–7.97) 2	7.22 (7.04–7.39) 2

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

sion remains the principal reference on *Ametrida centurio*. Measurements for specimens previously collected in the Guianas can also be found in Husson (1962, 1978), Swanepoel and Genoways (1979), and Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Peterson, 1965a; Jones and Carter, 1976; Koopman, 1994).

Paracou specimens of *Ametrida centurio* conform in all respects to Peterson's (1965a) account of this species, with measurements falling within the range of variation previously reported in the literature. In particular, morphometric data from our series (table 37) provide compelling confirmation of the remarkable sexual size dimorphism of *A. centurio*, in which females are substantially larger than males. Measurements of Paracou males and females are completely nonoverlapping in 11 of 13 dimensions, with slight overlap occurring only in hindfoot length and length of ear.

FIELD OBSERVATIONS: Of the 10 individuals of *Ametrida centurio* captured at Paracou, 6 were taken in ground-level mistnets and 4 in elevated mistnets. Of the six ground-level captures, two were in swampy primary forest, one was in creekside primary forest, and three were in manmade clearings. Two individuals were captured between 5 and 20 m over a narrow dirt road, and two were captured 34–37 m above a treefall clearing in well-drained primary forest.

Artibeus

Reliable species identifications within the genus *Artibeus* as recognized herein (including *Dermanura* and *Koopmania*) requires reference to Handley (1987) and Marques-Aguiar (1994). Although Lim and Wilson's (1993) concept of *Artibeus jamaicensis* differs from ours, their keys are also useful for distinguishing the larger species of *Artibeus* (subgenus *Artibeus*) in northern South America.

Artibeus (Artibeus) jamaicensis Leach

Figures 38, 39

VOUCHER MATERIAL: 23 females (AMNH *266322, *266331, *266333, *266334, *266335, *266336, *266337, *266338, *266344, *267998, *268503, *268505,

*268508, *268528, *268529; MNHN *1995.1139, *1995.1140, *1995.1141, *1995.1142, *1995.1143, *1995.1144, *1995.1145, *1995.1146) and 12 males (AMNH *266321, *266332, *266341, *266345, *267202, *267999, *268502, *268504; MNHN *1995.1147, *1995.1148, *1995.1149, *1995.1150); see table 38 for measurements.

IDENTIFICATION: We follow Handley (1987) and Marques-Aguiar (1994) in regarding *Artibeus jamaicensis* as the senior synonym of *A. planirostris* (contra Lim and Wilson [1993] and Koopman [1993, 1994]). Descriptions and comparative measurements can be found in Goodwin and Greenhall (1961), Swanepoel and Genoways (1979), Koepcke and Kraft (1984), Handley (1987), Brosset and Charles-Dominique (1990), Lim and Wilson (1993), and Marques-Aguiar (1994). Although Husson (1962, 1978) provided a detailed account of "*Artibeus lituratus fallax*" (= *A. jamaicensis*) from Surinam, his sample may have included specimens of both *A. jamaicensis* and true *A. lituratus*.

Between 10 and 13 subspecies of *Artibeus jamaicensis* (including *planirostris*) are currently recognized (see Hall, 1981; Davis, 1984; Handley, 1987; Marques-Aguiar, 1994; Koopman, 1994), of which 5 occur in South America: *A. j. aequatorialis* (Pacific slope of the Andes from southern Colombia to northern Peru), *A. j. hercules* (eastern Ecuador and Peru), *A. j. trinitatis* (central Colombia and Venezuela north of the Orinoco), *A. j. fallax* (Venezuela south of the Orinoco throughout the Guianas, thence southward through central Brazil to Bolivia), and *A. j. planirostris* (eastern Brazil and Paraguay).

Our Paracou material conforms closely to published qualitative descriptions of *Artibeus jamaicensis fallax*, although we observed somewhat more variation in pelage color than previously described for Guianan specimens (see below). Measurements of our material fall within the range of variation previously reported by most authors for *A. j. fallax*, including specimens referred to *A. planirostris* by Lim and Wilson (1993).

Despite our best efforts to correctly identify large *Artibeus* in the field, subsequent museum study showed that we initially mis-

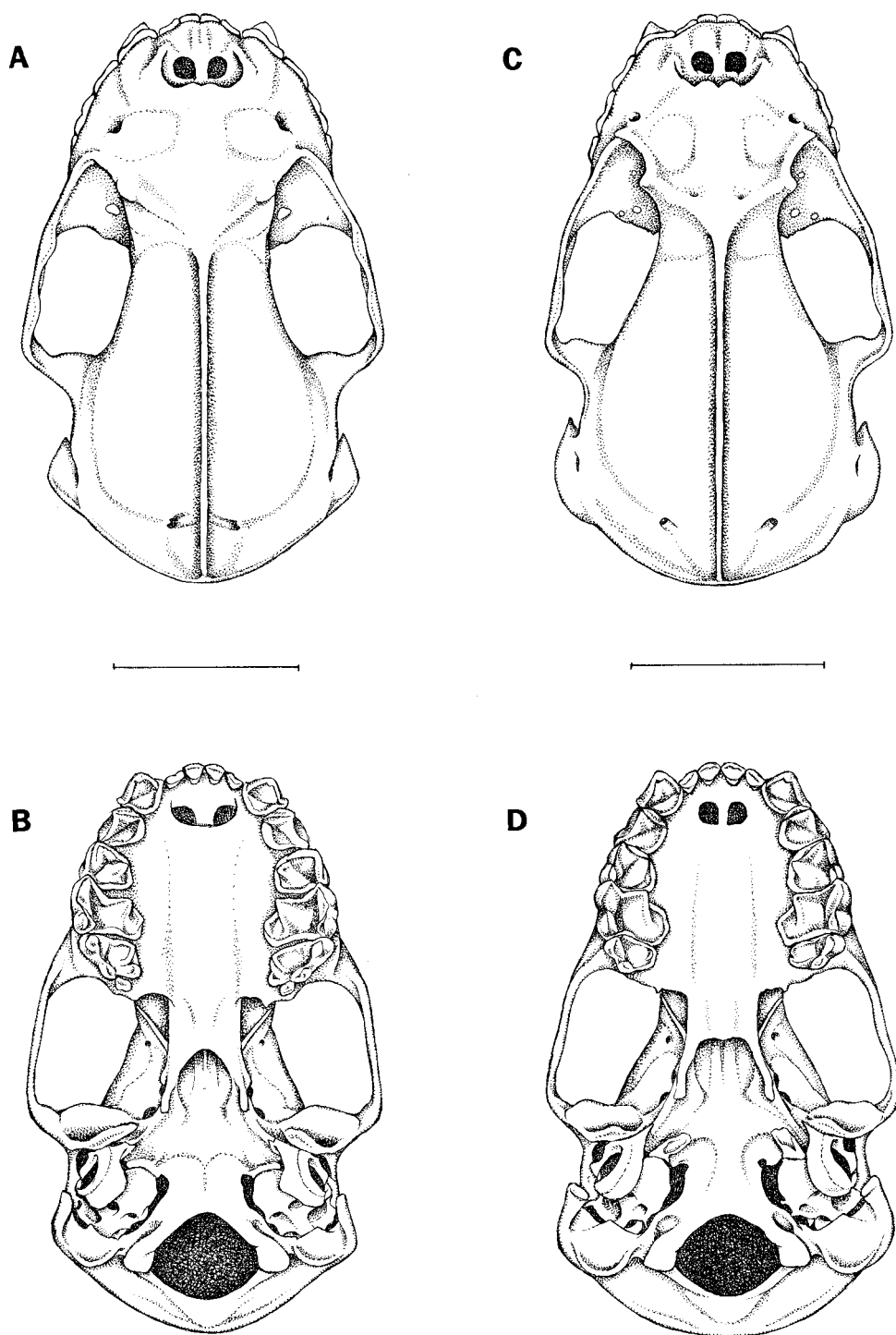


Fig. 38. Dorsal (A) and ventral (B) views of the skull of *Artibeus jamaicensis* (AMNH 266321; male) from Paracou. Dorsal (C) and ventral (D) views of the skull of *A. lituratus* (AMNH 267492; male) from Paracou. Note that *jamaicensis* has a broad interorbital region, small postorbital processes, and three molars, whereas *lituratus* has a narrower interorbit, better developed postorbital processes, and lacks M3. Scale bars = 10 mm.

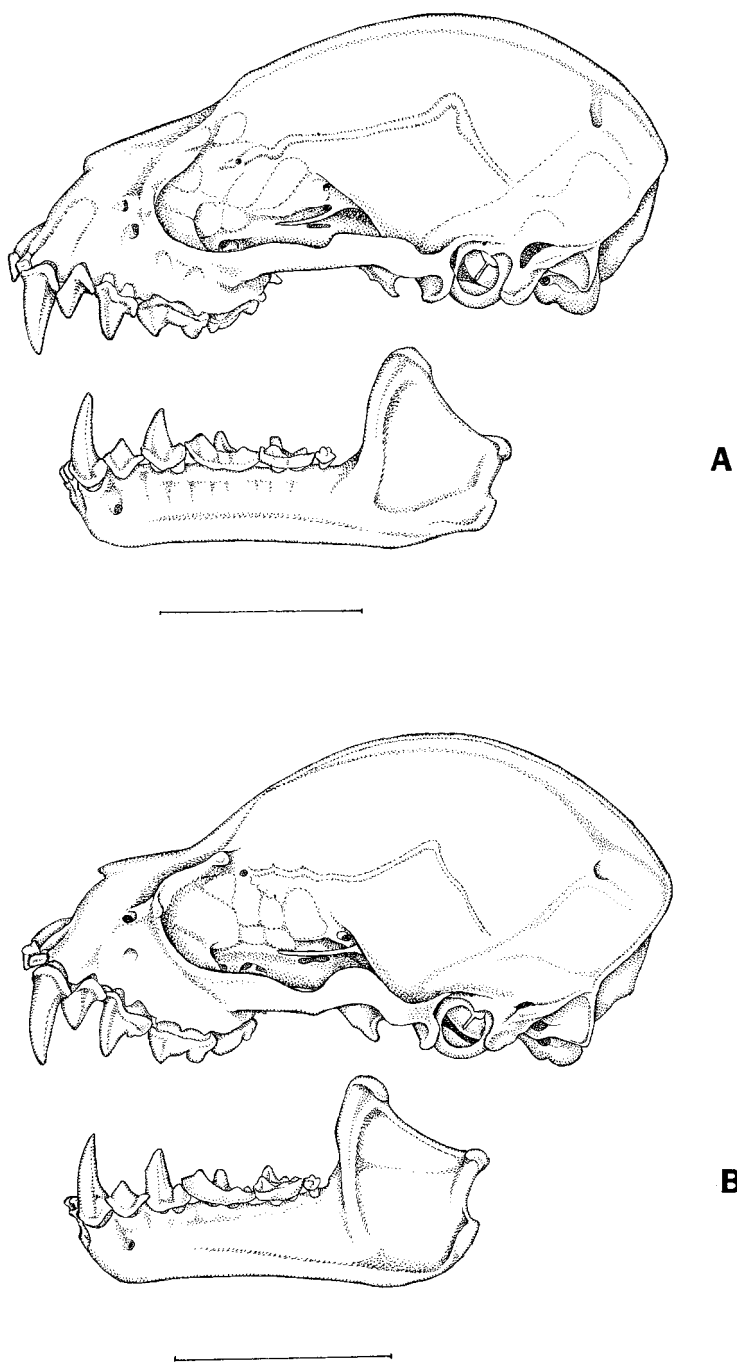


Fig. 39. Lateral views of the skull and lower jaw of (A) *Artibeus jamaicensis* (AMNH 266321; male) and (B) *A. lituratus* (AMNH 267492; male). Scale bars = 10 mm.

identified 6 specimens (6%) out of 94 adults preserved as vouchers. While we never confused specimens of *lituratus* and *obscurus*, we initially misidentified one specimen of *jamaicensis* as *lituratus*, two specimens of *jamaicensis* as *obscurus*, and three specimens of *obscurus* as *jamaicensis*. All of our identification errors involved females. Most of our identification mistakes involved individuals somewhat larger or smaller than the species norm, or those with ambiguous pelage colors and facial markings. For example, most specimens of *lituratus* have much brighter facial stripes than those typical of *jamaicensis*, but we found some *jamaicensis* with bright stripes and some *lituratus* with pale stripes. We also found intraspecific variation in dorsal pelage color in all three species, with some individuals having blacker or browner fur than that reported as typical in the literature.

Unambiguous identifications of our voucher material were ultimately based on the qualitative craniodental characters described by Handley (1987), Brosset and Charles-Dominique (1990), and Marques-Aguiar (1994). In particular, Paracou specimens of *Artibeus jamaicensis* are uniformly distinguished by a broad postorbital region with poorly developed postorbital processes (fig. 38), and M3 is always present. By contrast, the postorbital region is always narrower (table 38) and the postorbital processes are well developed in our specimens of *A. lituratus*, which uniformly lack M3. Subsequent examination of our measurement data (table 38) showed that whereas mean values for external dimensions of *jamaicensis* are smaller than those of *lituratus*, these species have overlapping ranges of morphometric variation at Paracou.

Marques-Aguiar (1994) cited two pelage characters as particularly useful for distinguishing *Artibeus jamaicensis* from *A. lituratus*: (1) the dorsal surface of the base of the forearm is very sparsely furred (almost naked) in *jamaicensis* versus densely furred in *lituratus*; and (2) the ventral fur is frosted (with white or pale gray) in adult *jamaicensis*, whereas *lituratus* has completely dark (unfrosted) ventral fur. Examination of our vouchers confirms that these traits are unambiguously diagnostic for *jamaicensis* and

lituratus at Paracou. Unfortunately, we were not aware of these helpful identification criteria in the field.

Numerous cranial characters cited by Handley (1989) consistently separate *Artibeus jamaicensis* and *A. obscurus*, but these are obviously not useful in the field. Our morphometric data, however, indicate that *jamaicensis* and *obscurus* can be separated unambiguously (at least in French Guiana) on the basis of body weight, total length, and forearm length, in all of which dimensions *obscurus* is substantially smaller. As noted by Handley (1989), *jamaicensis* has shorter fur than *obscurus*, but at Paracou this difference is slight (7 mm versus 8–9 mm) and requires careful measurement to be useful for identification. Both taxa, in our judgment, have equally “soft” fur, contra Handley’s observations. Dorsal fur color is typically much darker in *obscurus* than in *jamaicensis*, but (as previously noted) we found enough overlapping variation in this character to compromise its usefulness in the field. Handley (1989: 450) also noted that *obscurus* has “fewer and smaller ornamental warts on [the] chin,” but we did not find this to be consistently true in our material. Most individuals of both species have the same number of chin papillae (nine small papillae arranged in a “U” around a larger central papilla), with considerable variation in papillary size.

As noted above, we suspect that Husson’s (1962, 1978) sample of “*Artibeus lituratus fallax*” was a composite of individuals properly referred to *jamaicensis* and *lituratus*. This conclusion is based on two observations. First, Husson (1962, 1978) reported that M3 was present in 26 of his 34 specimens, and absent in 7 specimens. By contrast, we found M3 to be uniformly present in *jamaicensis* and uniformly absent in *lituratus*, a pattern that was also observed by Brosset and Charles-Dominique (1990). Second, Husson (1962: table XX) provided measurements of 10 individuals, 9 of which fall within the range of variation that we observed for *jamaicensis*, but 1 of which does not. The latter individual (a female from the Stuttgart museum, SNM 686.1) was reported to have a postorbital breadth of 6.3 mm, a value falling well below the range of varia-

tion in our series of *jamaicensis*, but agreeing perfectly with our measurement data for *lituratus*.

FIELD OBSERVATIONS: We recorded 73 captures (possibly including some recaptures) of *Artibeus jamaicensis* at Paracou, of which 71 were in ground-level mistnets and 2 were in elevated mistnets. The 71 ground-level captures included 18 in well-drained primary forest, 38 in swampy primary forest, and 15 in creekside primary forest. The two elevated net captures were made 5–10 m above the ground in the subcanopy of swampy primary forest.

Artibeus (Artibeus) lituratus (Olfers)

Figures 38, 39

VOUCHER MATERIAL: 15 females (AMNH *267204, *267495, *267496, *267497, *268506, *268507, *268509, *268510, *268512, *268513; MNHN *1995.1151, *1995.1152, *1995.1153, *1995.1154, *1995.1155) and 10 males (AMNH *266346, *267206, *267492, *268511, *268514, *268515; MNHN *1995.1156, *1995.1157, *1995.1158, *1995.1159); see table 38 for measurements.

IDENTIFICATION: Characters useful for separating *Artibeus lituratus* from *A. jamaicensis* at Paracou are discussed in the preceding species account. Descriptions and comparative measurements of *A. lituratus* can also be found in Goodwin and Greenhall (1961), Hill (1964), Tamsitt and Valdivieso (1966), Swanepoel and Genoways (1979), Davis (1984), Koepcke and Kraft (1984), Handley (1987), Brosset and Charles-Dominique (1990), Lim and Wilson (1993), and Marques-Aguiar (1994). As noted earlier, Husson's (1962, 1978) account of "*Artibeus lituratus fallax*" was apparently based on a composite series of *A. lituratus* and *A. jamaicensis*.

Two subspecies of *Artibeus lituratus* are generally recognized: *A. l. palmarum* (Central America to northwestern Peru, northern Colombia, northern Venezuela, Trinidad to St. Vincent) and *A. l. lituratus* (throughout Amazonia to northern Argentina) (Davis, 1984; Koopman, 1994; Marques-Aguiar, 1994). *Artibeus intermedius*, considered a distinct species by many authors (e.g., Davis,

1984; Koopman, 1993, 1994), may represent a subspecies of *A. lituratus* endemic to Mexico and Central America (Marques-Aguiar, 1994).

Our voucher material conforms closely with most previous qualitative descriptions of *Artibeus lituratus* (except Husson's) in the literature cited above. In particular, measurements of our specimens fall within the range of variation previously reported for *A. l. lituratus* in the Guianas and elsewhere in northern South America.

FIELD OBSERVATIONS: We recorded 53 captures (possibly including some recaptures) of *Artibeus lituratus* at Paracou, of which 40 were in ground-level mistnets and 12 were in elevated mistnets; in addition, 1 individual was shot at night. Of the 40 ground-level mistnet captures, 17 were in well-drained primary forest, 8 were in swampy primary forest, 3 were in creekside primary forest, 3 were in manmade clearings, and 9 were over roadside puddles. Of the 12 individuals captured in elevated nets, 11 were taken between 10 and 23 m above a narrow dirt road, and 1 was taken at 5–8 m in the subcanopy of swampy primary forest. The shot bat was found hanging from a palm frond about 10 m above the ground in well-drained primary forest.

Artibeus (Artibeus) obscurus (Schinz)

VOUCHER MATERIAL: 27 females (AMNH *266271, *266273, *266279, *266281, *266287, *267997, *268000, *268501, *268516, *268518, *268520, *268522, *268523, *268524, *268525, *268526, *268527; MNHN *1995.1160, *1995.1161, *1995.1162, *1995.1163, *1995.1164, *1995.1165, *1995.1166, *1995.1167, *1995.1168, *1995.1169) and 10 males (AMNH *266272, *266286, *266288, *267208, *267210, *268517, *268519; MNHN *1995.1170, *1995.1171, *1995.1172); see table 38 for measurements.

IDENTIFICATION: We follow Handley (1989) in using the name *Artibeus obscurus* instead of *A. fuliginosus* for the smallest and darkest member of the subgenus *Artibeus* found throughout the wet South American lowlands east of the Andes. *Artibeus obscurus* is best identified by reference to Handley (1987,

TABLE 38
Measurements^a of *Artibeus (Artibeus)* Collected at Paracou

	<i>Artibeus lituratus</i>		<i>Artibeus jamaicensis</i>	
Number/Sex	14 females	10 males	23 females	12 males
Weight	70.8 (60.0–94.0) 14	61.0 (55.0–66.0) 10	56.7 (48.0–66.0) 23	53.75 (41.0–66.0) 12
Total length	97.1 (92.0–103.0) 14	94.3 (85.0–104.0) 10	91.5 (84.0–98.0) 23	90.5 (84.0–99.0) 12
Tail length	0.0 (0.0–0.0) 14	0.0 (0.0–0.0) 10	0.0 (0.0–0.0) 23	0.0 (0.0–0.0) 12
Hind foot length	20.4 (17.5–24.0) 14	19.9 (17.5–22.0) 10	19.7 (16.0–22.0) 23	19.8 (18.0–22.0) 12
Ear length	23.7 (21.0–26.0) 14	23.2 (21.0–26.0) 10	22.8 (21.0–25.0) 23	23.2 (22.0–24.0) 12
Forearm length	72.3 (69.0–75.0) 14	71.5 (67.0–74.0) 10	67.5 (63.0–71.0) 23	67.6 (64.4–69.8) 12
Greatest length of skull	31.02 (30.15–32.05) 6	30.41 (30.13–30.69) 4	30.58 (29.93–31.62) 5	31.38 (31.18–31.57) 2
Condylolincisive length	27.66 (27.07–28.70) 6	27.08 (27.00–27.20) 4	27.70 (27.18–28.40) 5	28.24 (27.94–28.54) 2
Postorbital breadth	6.40 (6.08–6.70) 6	6.35 (6.10–6.46) 4	7.35 (6.92–7.63) 5	7.51 (7.48–7.54) 2
Braincase breadth	13.48 (12.94–14.20) 6	13.35 (13.06–13.82) 4	13.36 (13.03–13.75) 5	13.28 (13.02–13.53) 2
Mastoid breadth	16.83 (16.13–17.61) 6	16.78 (16.34–17.36) 4	16.53 (15.78–17.04) 5	16.87 (16.59–17.14) 2
Zygomatic breadth	19.10 (18.63–20.00) 6	18.55 (18.20–18.94) 4	19.79 (19.38–20.03) 4	19.64 (19.47–19.81) 2
Maxillary tooththrow length	10.89 (10.34–11.29) 6	10.77 (10.71–10.89) 4	11.16 (10.80–11.44) 5	11.75 (11.59–11.91) 2
Breadth across molars	13.66 (12.62–14.49) 13	13.58 (13.24–13.92) 10	14.17 (13.48–14.91) 11	14.46 (14.18–14.72) 7

	<i>Artibeus obscurus</i>	
Number/Sex	25 females	9 males
Weight	37.7 (28.0–52.5) 25	33.9 (30.5–39.2) 9
Total length	80.8 (74.0–87.0) 25	79.1 (75.0–84.0) 9
Tail length	0.0 (0.0–0.0) 25	0.0 (0.0–0.0) 9
Hind foot length	16.1 (13.0–19.0) 25	17.0 (15.0–19.0) 9
Ear length	22.6 (21.0–24.0) 25	22.6 (22.0–24.0) 8
Forearm length	61.0 (55.4–64.0) 25	62.3 (60.0–65.0) 9
Greatest length of skull	27.61 (26.66–28.28) 8	27.96 (27.91–28.01) 2
Condylolincisive length	24.70 (23.82–25.21) 8	25.41 (25.16–25.65) 2
Postorbital breadth	6.59 (6.27–7.09) 8	6.44 (6.43–6.45) 2
Braincase breadth	12.07 (11.31–12.71) 8	12.32 (12.17–12.47) 2
Mastoid breadth	14.60 (14.17–15.24) 8	14.69 (14.67–14.71) 2
Zygomatic breadth	16.99 (16.64–17.66) 8	16.95 (16.87–17.03) 2
Maxillary tooththrow length	9.94 (9.73–10.28) 8	10.13 (10.12–10.14) 2
Breadth across molars	12.61 (12.25–13.10) 14	12.38 (12.34–12.41) 2

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

1989), Lim and Wilson (1993), and Marques-Aguiar (1994). Additional descriptions and comparative measurements can also be found (under the name *A. fuliginosus*) in Swanepoel and Genoways (1979), Koepcke and Kraft (1984), and Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Handley, 1987, 1989; Marques-Aguiar, 1994).

Although our voucher material generally agrees with previous qualitative descriptions of *Artibeus obscurus*, three of our specimens lack M3 completely, a polymorphism noted

by Handley (1989) and Marques-Aguiar (1994), but not by Handley (1987) or Lim and Wilson (1993). Measurements of the Paracou series likewise fall within the known range of variation for this species with the exception of our largest specimens, which have slightly longer forearms than previously reported.

FIELD OBSERVATIONS: We recorded 117 captures (probably including some recaptures) of *Artibeus obscurus* at Paracou, of which 104 were in ground-level mistnets, 7 were in elevated mistnets, and 6 were at

roosts. Of the 104 ground-level mistnet captures, 42 were in well-drained primary forest, 37 were in swampy primary forest, 19 were in creekside primary forest, 4 were in man-made clearings, 1 was in closed-canopy secondary growth, and 1 was over a roadside puddle. Of the seven elevated mistnet captures, five were made between 7 and 20 m above a narrow dirt road, one was 10 m above a treefall in well-drained primary forest, and one was 5–8 m above the ground in the subcanopy of swampy primary forest.

We found three roosting groups of *Artibeus obscurus* under exfoliating pieces of bark 6–7 m above the ground on the trunks of grignon trees, *Ocotea rubra* (Lauraceae), in well-drained primary forest (fig. 40). One of these groups consisted of an adult female with a nursing juvenile; another consisted of an adult female, a nursing juvenile, and an escaped adult of unknown sex; and the third was a solitary near-term pregnant female. We also found a solitary adult male *Artibeus obscurus* roosting beneath an unmodified leaf of *Phenakospermum guyannense* (Strelitziaceae) about 4 m above the ground at the edge of a clearing in secondary vegetation.

Artibeus (Dermanura) cinereus (Gervais)

Figures 41, 42

VOUCHER MATERIAL: 9 females (AMNH *266259, *266265, *266266, *266270, *267499, *267991; MNHN *1995.1108, *1995.1109, *1995.1110) and 16 males (AMNH *266260, *266261, *266290, *266291, *266302, *266306, *266307, *266320, *267196, *267978, *267980; MNHN *1995.1111, *1995.1112, *1995.1113, *1995.1114, *1995.1115); see table 39 for measurements.

IDENTIFICATION: The most recent revision of the smaller species of *Artibeus* (subgenus *Dermanura*) is Handley's (1987), whose meticulous species comparisons and key were our primary resource for identification. Additional comparative measurements of *A. cinereus* and *A. gnomus* from French Guiana provided by Brosset and Charles-Dominique (1990) were also helpful. Although both species probably occur in Surinam and may have been mixed in earlier collections, Husson's (1962, 1978) account of *A. cinereus*

seems to have been based entirely upon specimens properly referred to that species. Koopman (1994) listed seven subspecies of *A. cinereus*, however all but two of these appear to represent other species (see Handley, 1987, and below).

Our voucher material, one of the largest series of *Artibeus cinereus* reported from a single locality, conforms in all respects to Handley's (1987) description of the species. Although our specimens generally fall within the range of morphometric variation previously reported in the literature, a few individuals of both sexes are slightly smaller in some dimensions than those documented from the Guianas by Husson (1962, 1978) and Brosset and Charles-Dominique (1990).

As with the larger species of *Artibeus* (subgenus *Artibeus*), we found that we could not always distinguish species of *Dermanura* in the field. Most individuals of *cinereus* are larger than most specimens of *gnomus* (table 39), and most *cinereus* have cream-colored ear margins and tragus while those structures are bright yellow in most *gnomus*. However, we captured some individuals that we initially misidentified using these characters. Of 67 collected specimens of *Dermanura*, 65 (97%) were correctly identified in the field; two individuals (3%) were initially identified incorrectly, both cases involving specimens of *A. cinereus* (one male and one female) misidentified as *A. gnomus*. We had to clean the skulls of these and several other specimens that fell in the zone of size overlap between *A. cinereus* and *A. gnomus* (see table 39) in order to determine their correct identifications.

We are unaware of any external characters that allow unequivocal identification of *Artibeus cinereus* and *A. gnomus* where these taxa occur in sympatry, but the number of lower molars appears to be reliable in our Paracou sample: all individuals with two lower molars present on *both* sides proved to be *A. cinereus* upon subsequent examination, and all individuals with three lower molars on *both* sides were *A. gnomus* (one individual of *cinereus* had two lower molars on one side and three on the other). Although the number of lower molars is perhaps the best single character for distinguishing these taxa in the field, it is not very useful for nonde-



Fig. 40. Roost of *Artibeus obscurus* in well-drained primary forest at Paracou. An adult female with a nursing juvenile and another adult bat of unknown sex (which escaped capture) were found clustered beneath this sheet of bark (arrow), about 6 m above the ground on the trunk of a grignon tree (Lauraceae: *Ocotea rubra*). Two additional roosting groups of *A. obscurus* were found on successive weeks in a similar shelter beneath the exfoliating bark of another grignon nearby.

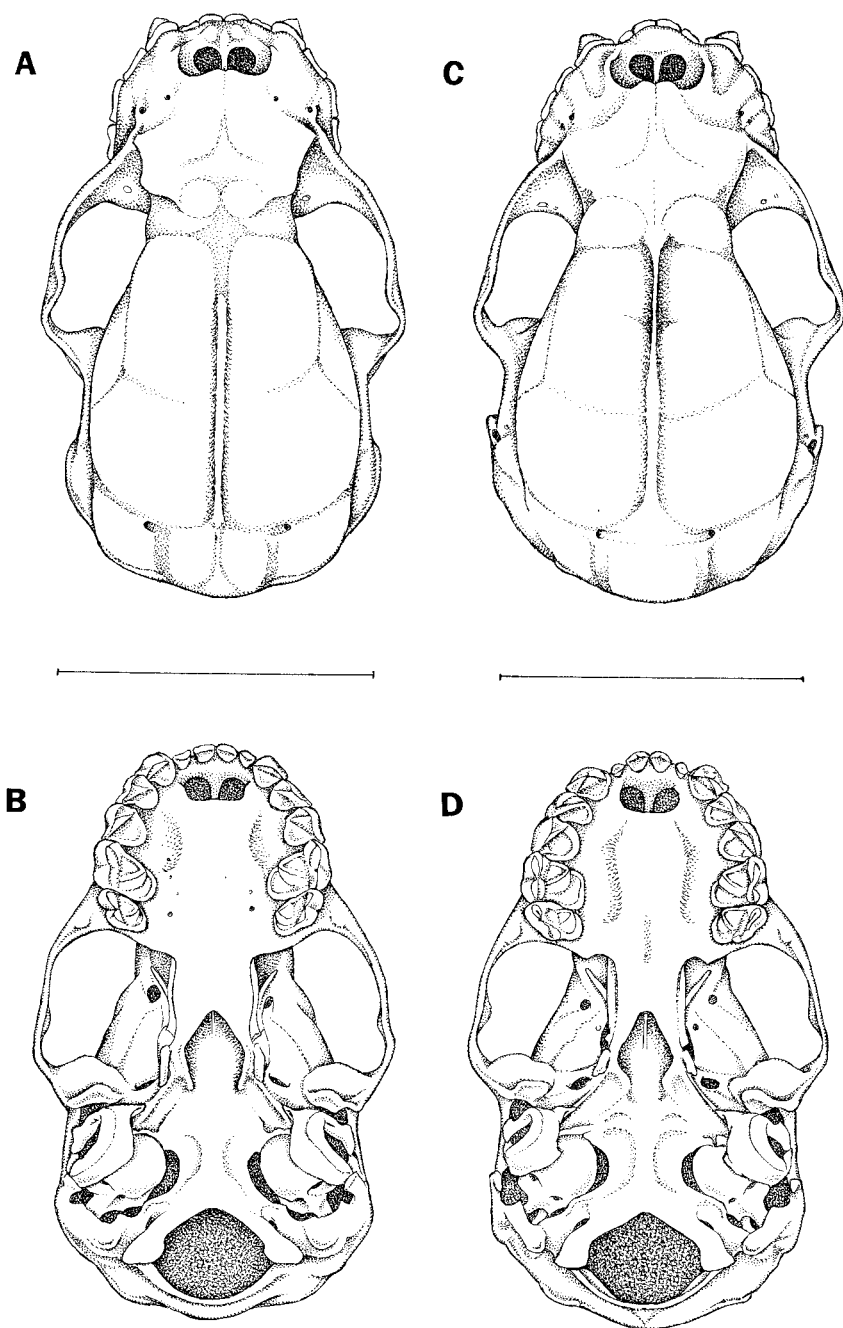


Fig. 41. Dorsal (A) and ventral (B) views of the skull of *Artibeus cinereus* (MNHN 1995.1112; male) from Paracou. Dorsal (C) and ventral (D) views of the skull of *A. gnomus* (AMNH 266314; male) from Paracou. Among other features, *gnomus* is distinguished from *cinereus* by its inflated anteorbital region and posteriorly constricted mesopterygoid fossa. Scale bars = 10 mm.

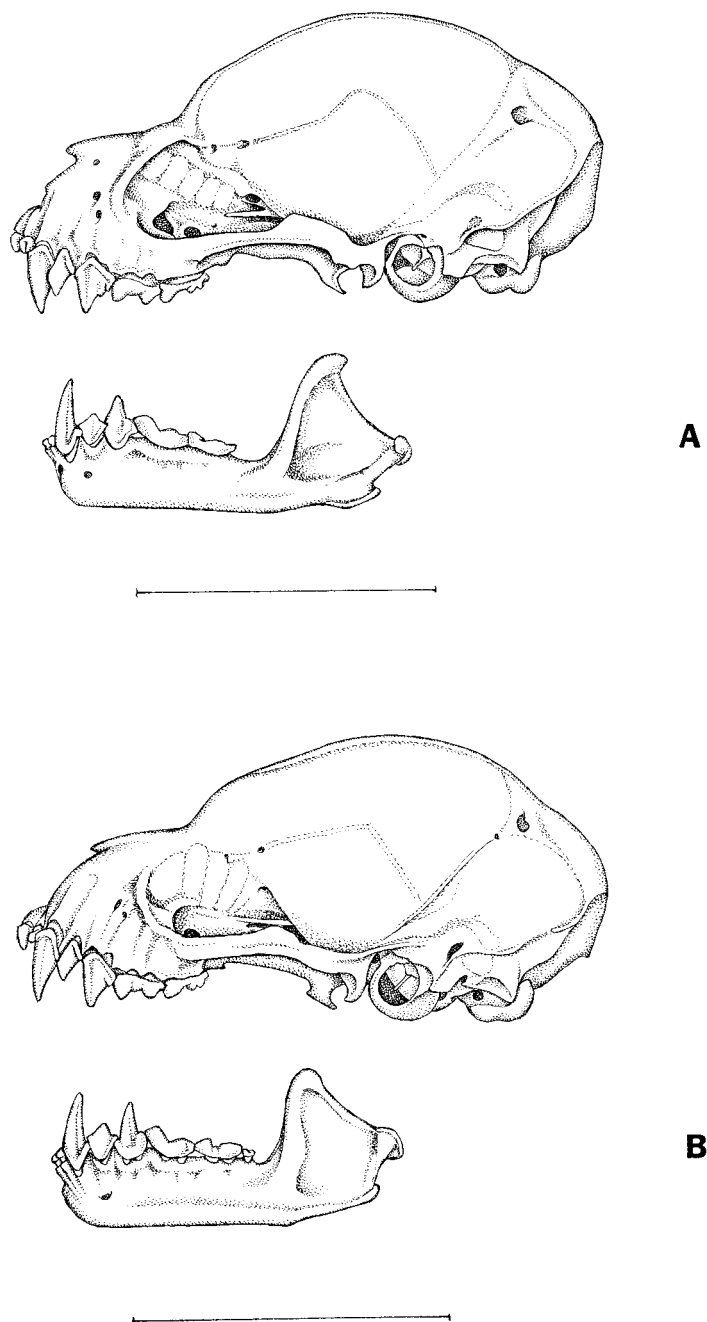


Fig. 42. Lateral views of the skull and lower jaw of (A) *Artibeus cinereus* (MNHN 1995.1112; male) and (B) *A. gnomus* (AMNH 266314; male). Note the species difference in number of lower molars. Scale bars = 10 mm.

TABLE 39
Measurements^a of *Artibeus (Dermanura)* Collected at Paracou

	<i>Artibeus cinereus</i>		<i>Artibeus gnomus</i>	
Number/Sex	9 females	15 males	18 females	24 males
Weight	12.0 (10.0–15.4) 9	10.7 (9.0–12.0) 15	10.0 (8.5–13.0) 18	9.2 (7.5–10.2) 24
Total length	54.6 (48.0–58.0) 9	53.7 (49.0–59.0) 15	51.9 (48.0–51.0) 18	50.5 (46.0–54.0) 24
Tail length	0.0 (0.0–0.0) 9	0.0 (0.0–0.0) 15	0.0 (0.0–0.0) 18	0.0 (0.0–0.0) 24
Hind foot length	10.9 (10.0–13.0) 9	11.3 (10.0–12.0) 13	10.1 (7.5–11.0) 18	10.5 (9.0–12.0) 24
Ear length	16.7 (16.0–17.0) 9	16.7 (16.0–18.0) 15	16.2 (15.0–17.0) 18	16.3 (15.0–17.5) 24
Forearm length	40.9 (38.0–42.0) 9	39.7 (37.0–42.0) 15	37.8 (34.5–39.0) 18	37.6 (35.5–40.0) 24
Greatest length of skull	19.59 (19.16–19.94) 6	19.47 (18.79–20.15) 13	18.46 (18.05–19.09) 14	18.60 (18.24–19.03) 18
Condylolincisive length	17.71 (17.01–18.18) 6	17.50 (16.84–18.07) 13	16.61 (16.27–17.32) 14	16.71 (16.40–17.48) 18
Postorbital breadth	4.69 (4.36–5.07) 6	4.61 (4.24–4.86) 13	4.90 (4.77–5.31) 14	4.87 (4.49–5.19) 17
Braincase breadth	8.87 (8.60–9.17) 6	8.96 (8.55–9.36) 13	8.66 (8.48–8.93) 13	8.67 (8.41–8.93) 17
Mastoid breadth	10.35 (10.06–10.65) 6	10.29 (9.58–10.84) 13	9.97 (9.60–10.38) 13	9.86 (9.45–10.23) 18
Zygomatic breadth	12.02 (11.67–12.46) 6	11.78 (11.12–12.24) 13	10.96 (10.36–11.56) 14	11.03 (10.66–11.47) 17
Maxillary toothrow length	6.28 (6.11–6.56) 6	6.26 (5.85–6.67) 13	5.70 (5.41–6.04) 14	5.72 (5.48–6.08) 18
Breadth across molars	8.67 (8.32–8.90) 9	8.33 (7.90–8.54) 15	7.82 (7.48–8.10) 18	7.79 (7.29–8.10) 23

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

structive research projects because m3 (when present) is small, translucent, and easily obscured by saliva; hence, we found it almost impossible to unambiguously determine if m3 was present in living bats.

Handley (1987) recognized two subspecies of *Artibeus cinereus* but did not discuss their distinguishing characteristics. Whereas specimens he identified as *A. c. cinereus* were listed from localities in central Amazonia on both sides of the river, specimens he assigned to *A. c. quadrivittatus* were from eastern Venezuela, Surinam, eastern Amazonia, and the northernmost part of the Brazilian Atlantic forest. Presumably, our material is referable to the latter taxon, the type locality of which is Surinam (Husson, 1962, 1978). Measurements of the holotype of *quadrivittatus* provided by Husson (1962) fall entirely within the range of variation in our sample from Paracou.

FIELD OBSERVATIONS: We recorded 41 captures (possibly including some recaptures) of *Artibeus cinereus* at Paracou, of which 37 were in ground-level mistnets, 1 was in an elevated mistnet, and 3 were at roosts. Of the 37 ground-level mistnet captures, 1 was in well-drained primary forest, 5 were in swampy primary forest, 3 were in creekside

primary forest, 1 was in a treefall opening in primary forest, 22 were in manmade clearings, and 5 were over roadside puddles. The single example taken in an elevated mistnet was captured 5–8 m above the ground in the subcanopy of swampy primary forest.

We found only a single roosting group of *Artibeus cinereus*, in a leaf-tent constructed from the bifid terminal leaflet of an immature understory palm provisionally identified as *Astrocaryum sciophilum* (figs. 43–45).

Artibeus (Dermanura) gnomus Handley

Figures 41, 42

VOUCHER MATERIAL: 18 females (AMNH *266195, *266239, *266301, *266303, *266308, *266309, *266310, *267199, *267979, *267988, *267989; MNHN *1995.1124, *1995.1125, *1995.1126, *1995.1127, *1995.1128, *1995.1129, *1995.1130) and 24 males (AMNH *266304, *266314, *266316, *266317, *266318, *267200, *267984, *267985, *267986, *267987, *267990, *267992, *267993, *267994, *267995, *267996; MNHN *1995.1131, *1995.1132, *1995.1133, *1995.1134, *1995.1135, *1995.1136,



Fig. 43. Leaf-tent roost of *Artibeus cinereus* in closed-canopy secondary vegetation at Paracou. Formed of the bifid terminal leaflet of an immature understory palm (*Astrocaryum* cf. *sciophilum*), this roost contained at least four bats, of which three (an adult male, an adult female, and one juvenile) were collected as vouchers. The roosting bats, hanging in a tight cluster from the midrib of the leaf about 1.5 m above the ground (arrow), were invisible from any vantage point except directly underneath. Some six to eight abandoned roosts of identical construction were found within about 100 m of this example. See figures 44 and 45 for close-ups.

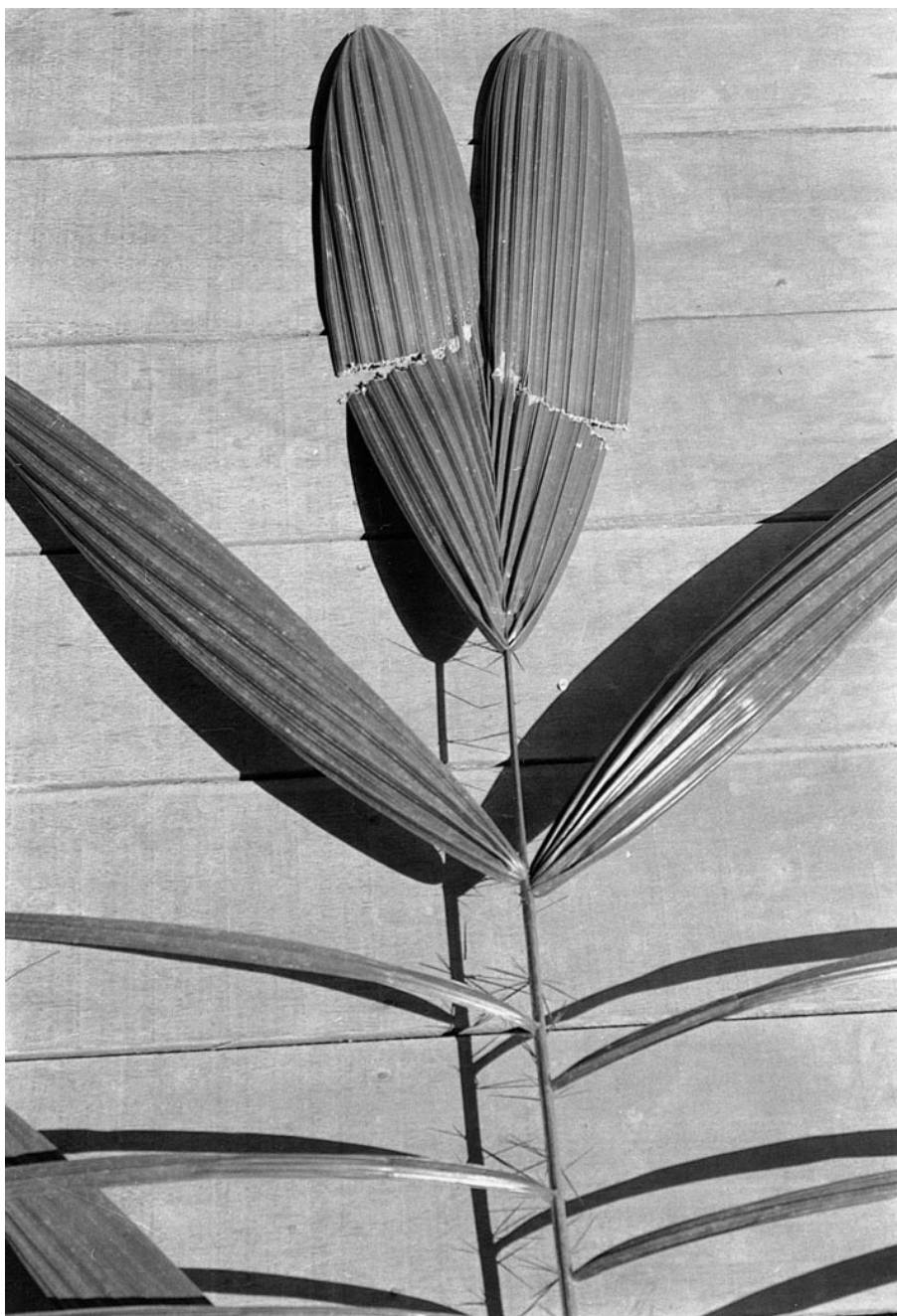


Fig. 44. Detail of the leaf-tent roost of *Artibeus cinereus* shown in figure 43. This is the dark green upper surface of the leaf, the bifid terminal leaflet of which had been cut from each outer margin in a curving line toward the midrib.

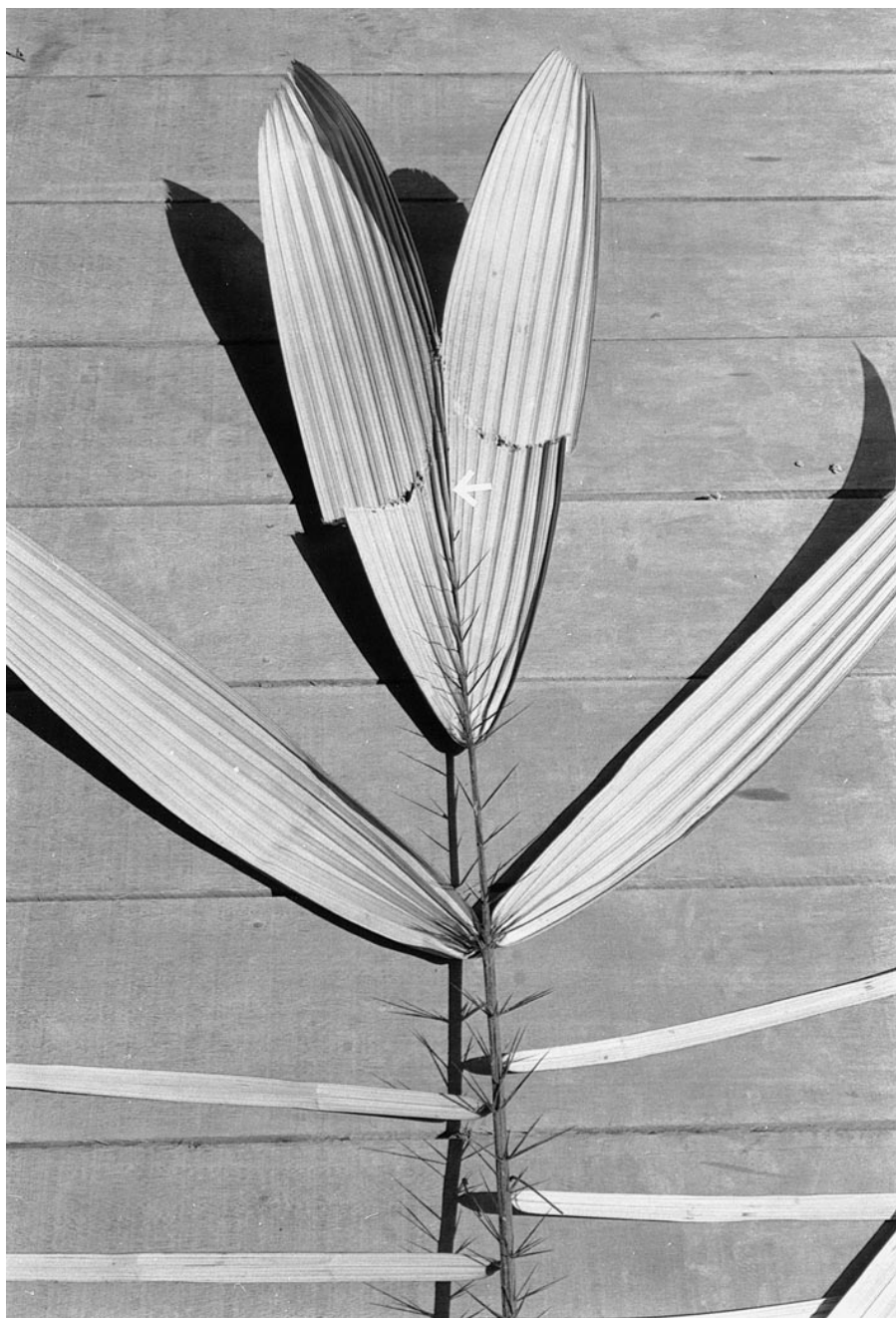


Fig. 45. Detail of the leaf-tent roost of *Artibeus cinereus* shown in figure 43. This is the lower surface of the leaf, which is conspicuously whitish by contrast with the dark green upper surface (facing page). The long black spines, grouped in clusters all along the midrib, had been chewed to short stubs for the distalmost 15 cm or so, near the apex of the tent where the bats were hanging (arrow).

*1995.1137, *1995.1138); see table 39 for measurements.

IDENTIFICATION: The original description of *Artibeus gnomus* by Handley (1987) is still the basic reference for this species, although the measurements tabulated by Brosset and Charles-Dominique (1990) for their French Guianan material are also helpful. The few problems we encountered in distinguishing *A. gnomus* from *A. cinereus* were discussed in the preceeding species account. No subspecies of *Artibeus gnomus* are recognized (Handley, 1987).

Our voucher material corresponds closely with Handley's (1987) description of *Artibeus gnomus*, and measurements of our specimens generally fall within the range of variation previously reported for the species. One exception is a particularly large male (AMNH 267987), whose measurements in several dimensions exceed any previously reported in the literature (e.g., length of maxillary toothrow, 6.08 mm; breadth across molars, 8.30 mm; zygomatic breadth, 11.47 mm). Except in size, however, this specimen agrees morphologically with the remainder of our specimens, and we conclude that it simply represents an unusually large example. Unpublished measurement data from other localities (in Venezuela, Guyana, Peru, and Brazil; Handley, personal commun.) indicate that AMNH 267987 is not unique in this respect, and that the normal range of size variation in *A. gnomus* is somewhat greater than that originally reported by Handley (1987).

FIELD OBSERVATIONS: We recorded 59 captures (possibly including some recaptures) of *Artibeus gnomus* at Paracou: 51 in ground-level mistnets, 4 in elevated mistnets, and another 4 at roosts. Of the 51 ground-level mistnet captures, 6 were in well-drained primary forest, 17 were in swampy primary forest, 5 were in creekside primary forest, 22 were in manmade clearings, and 1 was in closed-canopy secondary growth. It is noteworthy that of the 22 ground-level mistnet captures in manmade clearings, 18 were taken in nets erected around small fruiting trees, *Vismia* sp. (Clusiaceae), growing along a narrow road through well-drained primary forest; none were made in large clearings far removed from primary forest. Of the elevat-

ed mistnet captures, two were made between 4 and 21 m above a narrow dirt road and two were made at 7–10 m in the subcanopy of swampy primary forest.

We found four roosting groups of *Artibeus gnomus*, all of which occupied leaf-tents. Two large roosting groups (one with 4–8 individuals, the other with perhaps 6–10) each inhabited a single modified leaf of the giant herb *Phenakospermum guyannense* (Strelitziaceae); both roosts were hard to see, about 3 m above the ground in the densely cluttered understory of swampy primary forest (fig. 46). We captured (and preserved as vouchers) only a single adult female from each of these roosting groups, the age and sex composition of which are otherwise unknown.

The other two roosts, inhabited by solitary adult males, were "apical" tents (sensu Kunz et al., 1994) made from the spade-shaped leaves of epiphytic *Philodendron* sp. (Araceae). One of these roosts was about 5 m above the ground in well-drained disturbed forest, the other about 10 m above the ground in well-drained primary forest. We found many epiphytic *Philodendron* plants with similarly modified leaves throughout our study area, but only these two examples were occupied by bats (wasp nests were found under the modified leaves of a few plants).

Although *Artibeus gnomus* and *A. cinereus* are morphologically similar, our data suggest they are ecologically divergent. Consistent with Brosset and Charles-Dominique's (1990) generalizations concerning habitat use in these species, an analysis of ground-level capture frequency data from Paracou (table 40) suggests that *A. gnomus* is more abundant in primary forest than *A. cinereus*, which apparently favors the early-successional vegetation of modified habitats. Whether or not *A. cinereus* consistently inhabits bifid palm-leaf tents whereas *A. gnomus* uses differently designed tents made from the leaves of large herbs is unknown, but this hypothetical difference could easily be tested by following the movements of positively identified bats fitted with radio transmitters. Because *A. gnomus* was only recently recognized as taxonomically distinct from *A. cinereus*, and because they are hard



Fig. 46. Roost of *Artibeus gnomus* in swampy primary forest at Paracou. As many as eight individuals may have inhabited the dark apex of this leaf-tent (arrow), but it was impossible to obtain a clear view to make an accurate count. *Phenakospermum guyannense* (Strelitziaceae) is moderately common in swampy primary forest and secondary vegetation at Paracou, where tent-roosts made from its large leaves are also inhabited by *Uroderma bilobatum* (fig. 51). This tent was made by cuts in the lateral veins and interstitial tissue along both sides of the midrib causing the sides of the leaf to droop (as in the “boat” tents described and illustrated by Kunz et al., 1994), and by a deep cut through the midrib, causing the apex of the leaf to hang straight down (a characteristic of “apical” tents described by the same authors). A similar roost inhabited by another large group of *A. gnomus* was found several kilometers from this site.

TABLE 40
Comparison of Capture-Habitat Frequencies
Between *Artibeus cinereus* and *A. gnomus*
Taken in Ground-Level Mistnets at Paracou^a

	Capture habitats		Totals
	Primary	Modified	
<i>A. cinereus</i>	10	27	37
<i>A. gnomus</i>	28	23	51
Totals	38	50	88

$\chi^2 = 6.8$, $df = 1$, $p < 0.01$

^a Table entries are numbers of captures (possibly including some recaptures). The chi-square value calculated from these data tests the null hypothesis of no interspecific difference in proportions of captures by habitat.

(but not impossible) to distinguish in the field, unvouchered ecological observations reported in the literature for these species should be regarded with caution.

Artibeus (Koopmania) concolor Peters

VOUCHER MATERIAL: 17 females (AMNH *266267, *266269, *267192, *267194, *267476, *267478, *267479, *267487, *267488, *267981, *267982, *267983; MNHN *1995.1116, *1995.1117, *1995.1118, *1995.1119, *1995.1120) and 7 males (AMNH *267193, *267195, *267477,

*267502; MNHN *1995.1121, *1995.1122, *1995.1123); see table 41 for measurements.

IDENTIFICATION: Features useful for identifying *Artibeus concolor* were summarized by Handley (1987) and Acosta and Owen (1993); additional descriptions and measurements can be found in Husson (1962, 1978), Hill (1964), Barriga-Bonilla (1965), Linares (1969), Genoways and Williams (1979), Swanepoel and Genoways (1979), and Brosset and Charles-Dominique (1990). In contrast to the situation with most other species of *Artibeus*, no taxonomic problems are apparently associated with *A. concolor*, so identification is relatively straightforward. No subspecies are currently recognized (Handley, 1987; Acosta and Owen, 1993; Koopman, 1994).

Our voucher material, apparently the largest series available from any single locality, conforms closely with previous qualitative and morphometric descriptions of *Artibeus concolor*. In particular, measurements of our specimens confirm Brosset and Charles-Dominique's (1990) report of considerable size variation within French Guianan populations of this species. The size range among our specimens is even greater than they reported, yet we found no evidence that the Paracou sample includes more than one taxon.

TABLE 41
Measurements^a of *Artibeus (Koopmania) concolor* Collected at Paracou

Number/Sex	17 females	7 males
Weight	19.3 (15.8–24.4) 17	15.7 (13.4–19.0) 7
Total length	67.5 (62.0–71.0) 17	62.8 (61.0–65.0) 7
Tail length	0.0 (0.0–0.0) 17	0.0 (0.0–0.0) 7
Hind foot length	12.6 (10.0–15.0) 17	11.6 (11.0–14.0) 7
Ear length	18.0 (15.5–19.0) 17	17.5 (17.0–19.0) 6
Forearm length	48.5 (45.0–52.0) 17	45.8 (43.0–49.0) 7
Greatest length of skull	21.37 (20.70–22.08) 6	20.93 (20.71–21.41) 4
Condylolincisive length	19.19 (18.70–19.70) 6	18.70 (18.34–19.14) 4
Postorbital breadth	5.60 (5.54–5.76) 6	5.40 (5.23–5.53) 4
Braincase breadth	9.99 (9.78–10.51) 6	9.74 (9.64–9.92) 4
Mastoid breadth	11.41 (11.10–11.98) 6	11.37 (11.02–11.77) 4
Zygomatic breadth	13.20 (12.59–13.53) 6	12.64 (12.05–13.00) 4
Maxillary toothrow length	7.06 (6.90–7.43) 6	6.87 (6.69–6.99) 4
Breadth across molars	9.39 (8.92–9.96) 6	8.82 (8.54–9.10) 3

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

TABLE 42
Measurements^a of *Chiroderma* Collected at Paracou

Number/Sex	<i>Chiroderma trinitatum</i>		<i>Chiroderma villosum</i>	
	8 females	4 males	3 females	5 males
Weight	13.7 (12.0–16.0) 8	12.5 (12.0–13.2) 4	25.9 (24.4–27.0) 3	20.6 (20.0–21.5) 5
Total length	60.1 (55.0–67.0) 8	56.8 (55.0–58.0) 4	71.3 (69.0–74.0) 3	68.5 (62.0–76.0) 5
Tail length	0.0 (0.0–0.0) 8	0.0 (0.0–0.0) 4	0.0 (0.0–0.0) 3	0.0 (0.0–0.0) 5
Hind foot length	10.5 (9.0–12.0) 8	11.3 (11.0–12.0) 4	13.3 (13.0–14.0) 3	12.1 (11.0–13.0) 5
Ear length	16.6 (16.0–17.0) 8	15.8 (15.5–16.0) 4	19.0 (19.0–19.0) 3	17.4 (16.0–18.5) 5
Forearm length	40.1 (38.0–42.0) 8	38.1 (38.0–38.5) 4	48.3 (48.0–49.0) 3	45.5 (45.0–46.5) 5
Greatest length of skull	21.33 (21.20–21.40) 3	21.28 (21.20–21.37) 3	24.93 (24.70–25.16) 2	24.23 (23.86–24.78) 4
Condylolincisive length	19.39 (19.16–19.72) 3	19.16 (18.93–19.38) 3	22.83 (22.69–22.96) 2	22.09 (21.56–22.56) 4
Postorbital breadth	5.17 (4.89–5.32) 3	5.25 (5.15–5.30) 3	5.74 (5.49–5.98) 2	5.82 (5.63–6.06) 4
Braincase breadth	9.74 (9.68–9.78) 3	9.50 (9.33–9.72) 3	10.54 (10.48–10.60) 2	10.62 (10.52–10.73) 4
Mastoid breadth	10.75 (10.71–10.80) 3	10.43 (10.28–10.59) 3	12.49 (12.43–12.54) 2	11.77 (11.48–12.17) 4
Zygomatic breadth	13.16 (12.95–13.30) 3	12.87 (12.75–13.07) 3	16.06 (15.99–16.13) 2	15.34 (15.12–15.62) 4
Maxillary tooththrow length	6.82 (6.67–6.96) 3	6.76 (6.58–6.89) 3	8.53 (8.48–8.57) 2	8.23 (7.96–8.66) 4
Breadth across molars	9.31 (9.26–9.40) 3	9.48 (9.32–9.64) 3	11.58 (11.55–11.61) 2	10.91 (10.55–11.31) 4

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

FIELD OBSERVATIONS: We caught 24 *Artibeus concolor* at Paracou, of which 22 were taken in ground-level mistnets and 2 in elevated mistnets. Of the 22 ground-level captures, 3 were in well-drained primary forest, 7 were in swampy primary forest, 3 were in creekside primary forest, 7 were in manmade clearings, and 2 were over roadside puddles. The two elevated mistnet captures were made between 10 and 21 m over a narrow dirt road.

Chiroderma trinitatum Goodwin

VOUCHER MATERIAL: 8 females (AMNH *266255, *267189, *267473, *268531, *269117; MNHN *1995.1191, *1995.1192, *1995.1193) and 4 males (AMNH *266256, *268532, *269118; MNHN *1995.1194); see table 42 for measurements.

IDENTIFICATION: Descriptions and measurements of *Chiroderma trinitatum* from the Guianas and elsewhere can be found in Goodwin (1958), Goodwin and Greenhall (1961), Ojasti and Linares (1971), Gardner (1976), Genoways and Williams (1979), Swanepoel and Genoways (1979), and Brosset and Charles-Dominique (1990). Although subspecies of *C. trinitatum* have been recognized by some authors (e.g., Jones and

Carter, 1976), increased sampling throughout the range of this species has demonstrated more within-population variation than previously suspected (see discussion in Williams and Genoways, 1980a). Pending a thorough systematic review, no trinomial nomenclature seems warranted (Koopman, 1994).

Our Paracou specimens conform in all respects to previous qualitative and morphometric descriptions of *Chiroderma trinitatum*.

FIELD OBSERVATIONS: We caught 13 *Chiroderma trinitatum* at Paracou, of which 11 were taken in ground-level mistnets and 2 in elevated mistnets. Four of the ground-level captures were made in swampy primary forest and the other seven in manmade clearings. The elevated mistnet captures were made at 17–20 m above a narrow dirt road.

Chiroderma villosum Peters

VOUCHER MATERIAL: 3 females (AMNH *267191, *267474, *268536) and 5 males (AMNH *267190, *267475, *268535; MNHN *1995.1195, *1995.1196); see table 42 for measurements.

IDENTIFICATION: Descriptions and comparative measurements of *Chiroderma villosum* can be found in Goodwin and Greenhall

(1961), Husson (1962, 1978), Hill (1964), Genoways and Williams (1979), Swanepoel and Genoways (1979), Hall (1981), Brosset and Charles-Dominique (1990), and Anderson (1997). Two subspecies are currently recognized: *C. v. jesupi* (Mexico to northern Colombia) and *C. v. villosum* (tropical South America east of the Andes from Colombia to southeastern Brazil, including Trinidad and Tobago) (Koopman, 1994).

Although our Paracou series of *Chiroderma villosum* agrees in qualitative and quantitative characters with previous descriptions of the species as a whole, craniodental measurement comparisons indicate that our specimens are substantially smaller than most of those previously reported from the Guianas. For example, the observed range in length of the maxillary toothrow is 7.96–8.66 mm at Paracou versus 8.6–10.2 mm at other Guianan localities from which measured specimens are reported in the literature cited above. An apparently individual anomaly is represented by one of our male specimens, AMNH 268535, which has only one pair of upper and lower incisors; all of our remaining specimens have two pairs in both jaws, the normal formula for *Chiroderma* (see Koopman, 1994).

FIELD OBSERVATIONS: We caught eight *Chiroderma villosum* at Paracou, of which four were taken in ground-level mistnets and four in elevated nets. Two ground-level captures were made in well-drained primary forest, one in swampy primary forest, and one in creekside primary forest. Two specimens were captured 34–37 m above a treefall opening in well-drained primary forest and two others were netted 17–20 m above a narrow dirt road.

Ectophylla

Phylogenetic relationships between *Ectophylla*, *Mesophylla*, and *Vampyressa* have been the subject of much debate in the literature. Most workers have retained all three as distinct genera (e.g., Hall, 1981; Koopman, 1993, 1994), but some authors have considered *Mesophylla* to be a junior synonym of *Vampyressa* (e.g., Owen, 1987) or of *Ectophylla* (e.g., Goodwin and Greenhall, 1962; Handley, 1976). Recently, Peffley et

al. (MS) found strong support for a sister-group relationship between *Ectophylla* and *Mesophylla*, both of which are monotypic, and argued that *Ectophylla alba* H. Allen (1892) and *Mesophylla macconnelli* Thomas (1901a) should be placed in a single genus to reflect this relationship. We therefore use the older generic name for both species, and provide a formal diagnosis for *Ectophylla* as so defined.

EMENDED DIAGNOSIS OF *ECTOPHYLLA*: Size small (weight less than 11 g and forearm length less than 35 mm); dorsal and ventral fur pale buff, grayish white, or white; no white facial stripes or middorsal stripe; skin of noseleaf, ears, and thumb bright yellow; ventral border of narial horseshoe defined by a free flap of skin; uropatagium short, naked, translucent; length of calcar less than one-half length of hindfoot; dental formula I 2/2, C 2/2, P 2/2, M 2/2–3 × 2 = 28–30; rostrum approximately three-fourths the length of the braincase; rostrum not inflated and without a deep depression or long nasal emargination; interpterygoid space not extended by a deep palatal emargination; inner upper incisors elongate, unworn crown height more than twice that of outer incisors; inner upper incisors not deeply bifid; m1 without posterolingual cusp (crown resembles that of last premolar); lingual cusps of m2 vestigial or absent.

Ectophylla macconnelli (Thomas)

VOUCHER MATERIAL: 9 females (AMNH *267281, *267537, *267538, *267556, *267558, *267559; MNHN *1995.1181, *1995.1182, *1995.1183) and 4 males (AMNH *267557, *267562, *268539; MNHN *1995.1184); see table 43 for measurements.

IDENTIFICATION: We consulted descriptions and measurements of *Ectophylla macconnelli* provided by Goodwin and Greenhall (1962), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Brosset and Charles-Dominique (1990), and Kunz and Pena (1992). Two subspecies are currently recognized, of which the nominate form occurs throughout most of the humid Neotropical lowlands, including the Guianas (Koopman, 1994).

TABLE 43
Measurements^a of *Ectophylla macconnelli* Collected at Paracou

Number/Sex	9 females	4 males
Weight	8.4 (7.1–10.4) 9	7.6 (6.9–8.2) 4
Total length	49.4 (45.0–50.0) 9	48.3 (47.0–49.0) 3
Tail length	0.0 (0.0–0.0) 9	0.0 (0.0–0.0) 4
Hind foot length	9.9 (9.0–11.0) 9	9.8 (9.0–11.0) 4
Ear length	14.9 (13.0–16.0) 9	14.5 (13.0–15.0) 4
Forearm length	32.0 (32.0–32.0) 4	31.0 (29.0–32.0) 3
Greatest length of skull	18.04 (17.75–18.21) 3	18.04 (17.56–18.52) 3
Condylolincisive length	16.54 (16.50–16.57) 2	15.73 (15.48–15.97) 2
Postorbital breadth	4.46 (4.29–4.60) 6	4.58 (4.24–4.60) 3
Braincase breadth	8.20 (7.88–8.09) 4	8.06 (7.68–8.44) 3
Mastoid breadth	9.36 (9.18–9.60) 3	9.12 (8.73–9.50) 2
Zygomatic breadth	10.42 (10.19–10.68) 3	10.21 (10.04–10.36) 3
Maxillary tooththrow length	5.89 (5.65–6.09) 5	5.82 (5.61–5.99) 4
Breadth across molars	7.06 (6.63–7.61) 5	6.74 (6.72–6.77) 4

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

Our Paracou series conforms in all respects to previous descriptions of *Ectophylla macconnelli* except that of Brosset and Charles-Dominique (1990), who reported unusually high values for length of the maxillary tooththrow (6.7–7.4 mm) in their French Guianan material. By contrast, the observed range for this measurement in our series (5.61–6.09 mm) falls within the range previously reported by other authors (5.5–6.6 mm). Because the other external and craniodental measurements reported by Brosset and Charles-Dominique are not aberrant, we presume that their maxillary tooththrow measurements were erroneously reported.

FIELD OBSERVATIONS: We caught 13 *Ectophylla macconnelli* at Paracou, of which only 1 was taken in a mistnet; the remaining 12 were caught at roosts. Our single mistnet capture was at ground level in swampy primary forest.

We found three roosting groups of *Ectophylla macconnelli*, all of which inhabited leaf-tents (fig. 47) made from the bifid terminal leaflets of fronds of young understory palms provisionally identified as *Astrocaryum sciophilum*. In all construction details that we noted, these tents exactly resembled those described above in the accounts for *Rhinophylla pumilio* and *Artibeus cinereus*. All three roosts were in well-drained primary forest. One roosting group of seven bats, col-

lected in its entirety, consisted of two adult males and five adult females. Another entire group of three consisted of one adult male and two adult females.

Our roost observations, together with those reported by Foster (1992) and Charles-Dominique (1993), suggest that *Ectophylla macconnelli* regularly inhabits tents manufactured from the leaves of *Astrocaryum* palms.¹² Because the undersurfaces of *Astrocaryum* leaves are characteristically whitish (Henderson et al., 1995), we agree with Hingston (1932) that the unusually pale fur of

¹² Emmons (1990) was apparently the first to report that *Ectophylla macconnelli* inhabits palm-leaf tents, but she did not identify the host plant. Roosts have been reported in the foliage of other palms (and aroids), but multiple independent observations of occupied bifid tents in *Astrocaryum* spp. from opposite ends of Amazonia suggest that this genus is favored by *Ectophylla macconnelli*. Emmons' (1990, 1997) suggestion that *E. macconnelli* sometimes inhabits hollow trees was based on Handley's (1976: 30) report of one individual "found roosting in a tree." However, the original field record for the specimen in question (USNM 405185) notes "shot in tree after frightened up"—the bat having presumably been dislodged from an unobserved roost in the undergrowth. All other published accounts (including Beebe [1925], Hingston [1932], Charles-Dominique [1993], and Kunz et al. [1994] in addition to references cited by Foster [1992]) explicitly identify foliage as the roosting substrate of *E. macconnelli*.



Fig. 47. Roost of *Ectophylla macconnelli* in well-drained primary forest at Paracou. Made from the bifid terminal leaflet of a young palm (*Astrocaryum* cf. *sciophilum*), this shelter contained three *E. macconnelli* (one adult male and two adult females) hanging in a tight cluster from the midrib about 1.5 m above the ground (arrow). Note the much sparser undergrowth at this primary-forest site than that surrounding an otherwise similar roost in secondary vegetation (figure 43).

TABLE 44
Measurements^a of *Platyrrhinus helleri* Collected at Paracou

Number/Sex	9 females	5 males
Weight	13.6 (11.2–15.4) 9	12.6 (12.0–13.4) 5
Total length	61.6 (55.0–65.0) 9	59.2 (56.0–61.0) 5
Tail length	0.0 (0.0–0.0) 9	0.0 (0.0–0.0) 5
Hind foot length	11.8 (10.0–13.0) 9	10.6 (10.0–11.0) 5
Ear length	16.7 (15.0–19.0) 9	16.6 (16.0–17.0) 5
Forearm length	38.5 (38.0–40.0) 9	38.5 (38.0–39.0) 5
Greatest length of skull	22.02 (21.52–22.78) 4	21.66 (21.66) 1
Condylolincisive length	20.00 (19.50–20.73) 4	19.78 (19.78) 1
Postorbital breadth	5.43 (5.07–5.57) 4	5.24 (5.24) 1
Braincase breadth	9.54 (9.33–9.74) 4	9.32 (9.32) 1
Mastoid breadth	10.87 (10.63–11.16) 4	10.78 (10.78) 1
Zygomatic breadth	12.37 (12.13–12.64) 4	12.10 (12.10) 1
Maxillary tooththrow length	7.63 (7.38–7.94) 4	7.33 (7.33) 1
Breadth across molars	9.04 (8.87–9.26) 4	8.92 (8.92) 1

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

E. macconnelli is correlated with the background color of its typical roosts, perhaps making the bats less conspicuous to diurnal predators.

Platyrrhinus helleri (Peters)

VOUCHER MATERIAL: 9 females (AMNH *266254, *267182, *267551, *267554, *267555, *268540; MNHN *1995.1187, *1995.1188, *1995.1189) and 5 males (AMNH *267179, *267550, *268541, *268542; MNHN *1995.1190); see table 44 for measurements.

IDENTIFICATION: A key to the species of *Platyrrhinus* was provided by Ferrell and Wilson (1991), and Anderson (1996) helpfully reviewed characters distinguishing *P. helleri* from *P. brachycephalus* (see also Rouk and Carter, 1972). Other useful descriptions and measurements of *P. helleri* can be found in Sanborn (1955), Goodwin and Greenhall (1961), Husson (1962, 1978), Gardner and Carter (1972), Rouk and Carter (1972), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), and Anderson (1997). Two subspecies of *P. helleri* are currently recognized, of which *P. h. incarum* ranges throughout Amazonia, including the Guianas (Koopman, 1994).

Our Paracou specimens conform closely with previous descriptions of *Platyrrhinus*

helleri. Although some populations (e.g., in Bolivia; Anderson, 1996) exhibit variation in the number of accessory cusps present on the anterior margin of the second lower premolar, all of our vouchers have only a single accessory cusp in this location. Measurements of the Paracou series (table 44) fall within the range of variation previously reported for *P. h. incarum*.

FIELD OBSERVATIONS: We captured 14 individuals of *Platyrrhinus helleri* at Paracou, of which 11 were taken in ground-level mist-nets and 3 in elevated mist-nets. Four ground-level captures were in well-drained primary forest, one in swampy primary forest, two in creekside primary forest, two in manmade clearings, and two over roadside puddles. The three elevated net captures were made between 6 and 21 m above a narrow dirt road.

Sturnira lilium (E. Geoffroy)

Figures 48–50

VOUCHER MATERIAL: 19 females (AMNH *266210, *266226, *266231, *266234, *266235, *266236, *267170, *268543, *268546, *268549, *268552, *268553; MNHN *1995.1197, *1995.1198, *1995.1199, *1995.1200, *1998.600, *1998.601, *1998.602) and 35 males (AMNH *266199, *266200, *266201, *266203, *266205,

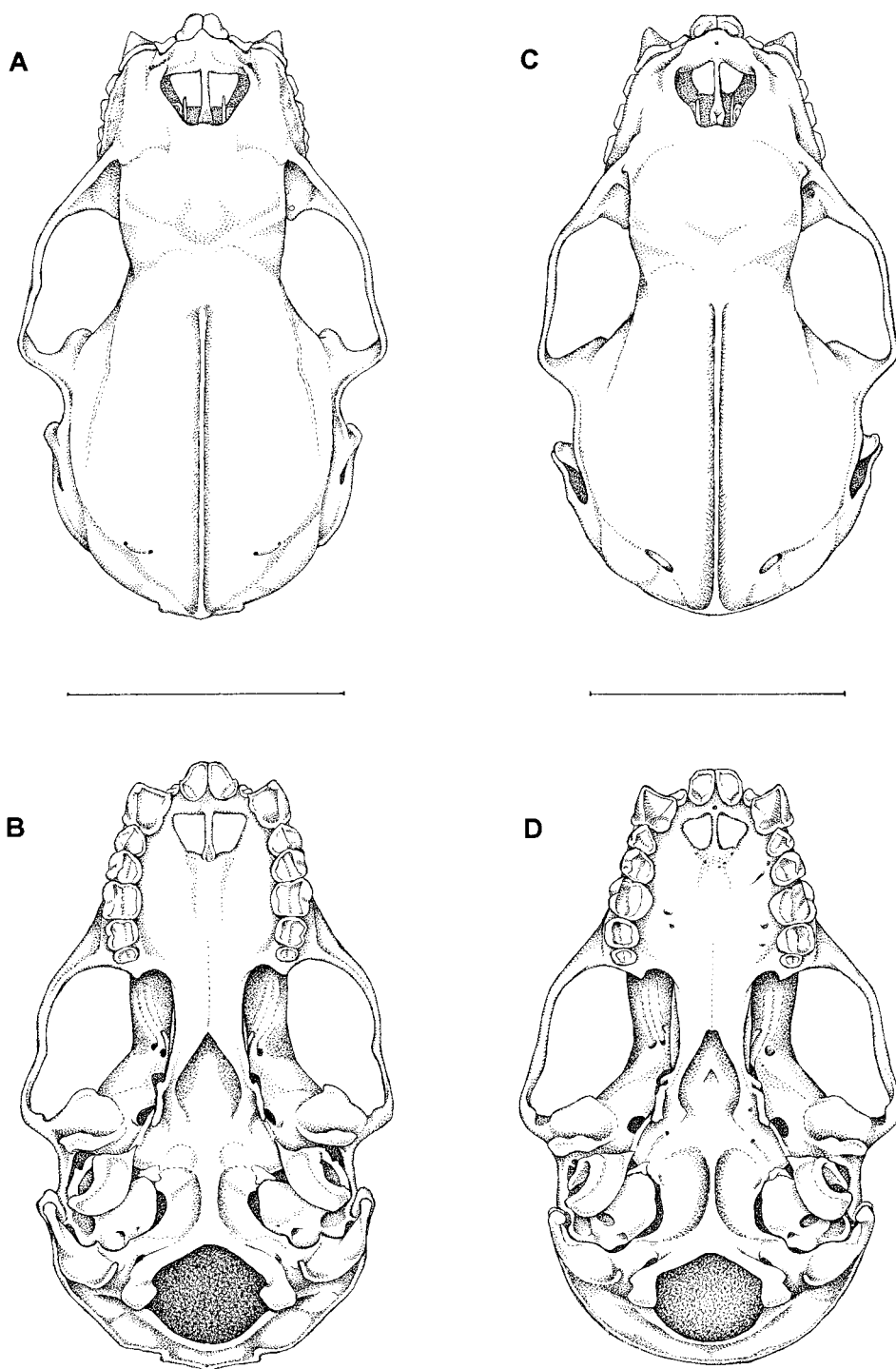


Fig. 48. Dorsal (A) and ventral (B) views of the skull of *Sturnira lilium* (AMNH 266232; male) from Paracou. Dorsal (C) and ventral (D) views of the skull of *S. tildae* (AMNH 267461; male) from Paracou. Note the species differences in incisor morphology, size and shape of the molars, and relative breadth of the mesopterygoid fossa and mastoid region. Scale bars = 10 mm.

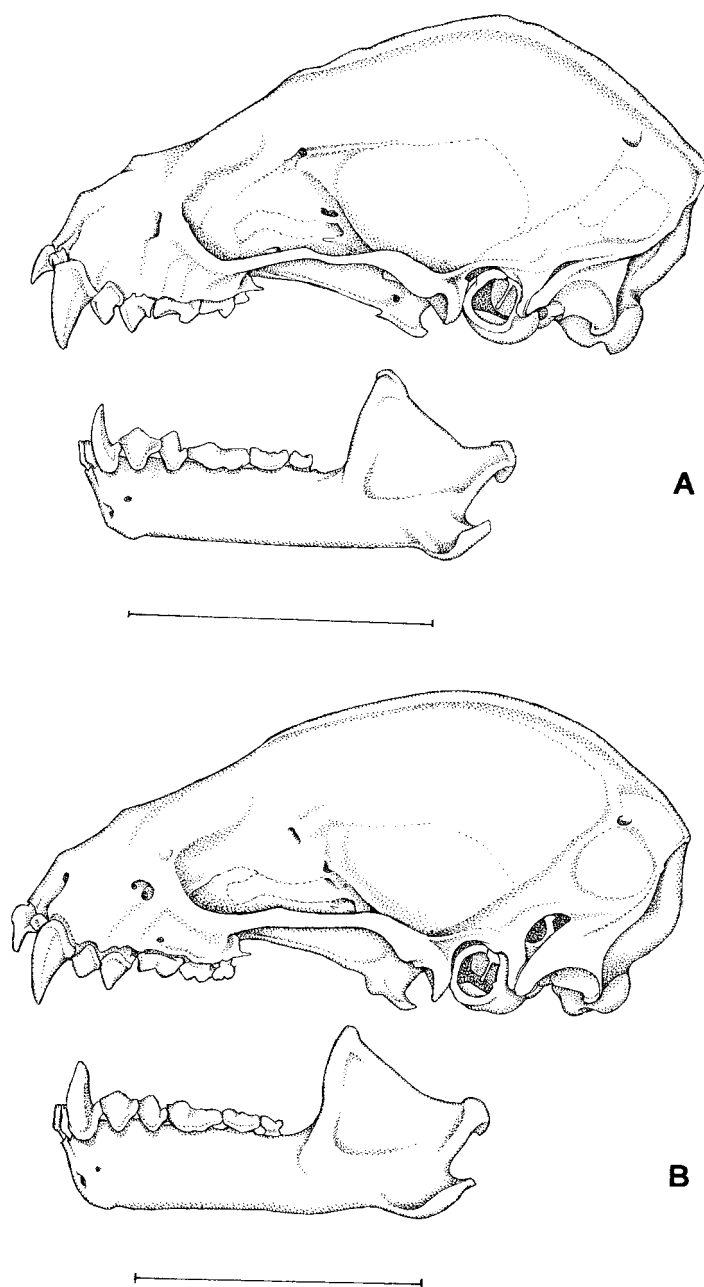


Fig. 49. Lateral views of the skull and lower jaw of (A) *Sturnira lilium* (AMNH 266232; male) and (B) *S. tildae* (AMNH 267461; male). Scale bars = 10 mm.

*266206, *266207, *266224, *266225, *1998.604, *1998.605, *1998.606, *1998.607,
 *266227, *266228, *266230, *266232, *1998.608, *1998.609, *1998.610, *1998.611,
 *266233, *266237, *266238, *267197, *1998.612, *1998.613, *1998.614); see table
 *268544, *268545, *268547, 268548, 45 for measurements.
 *268550, *268551; MNHN *1998.603, IDENTIFICATION: References that we found

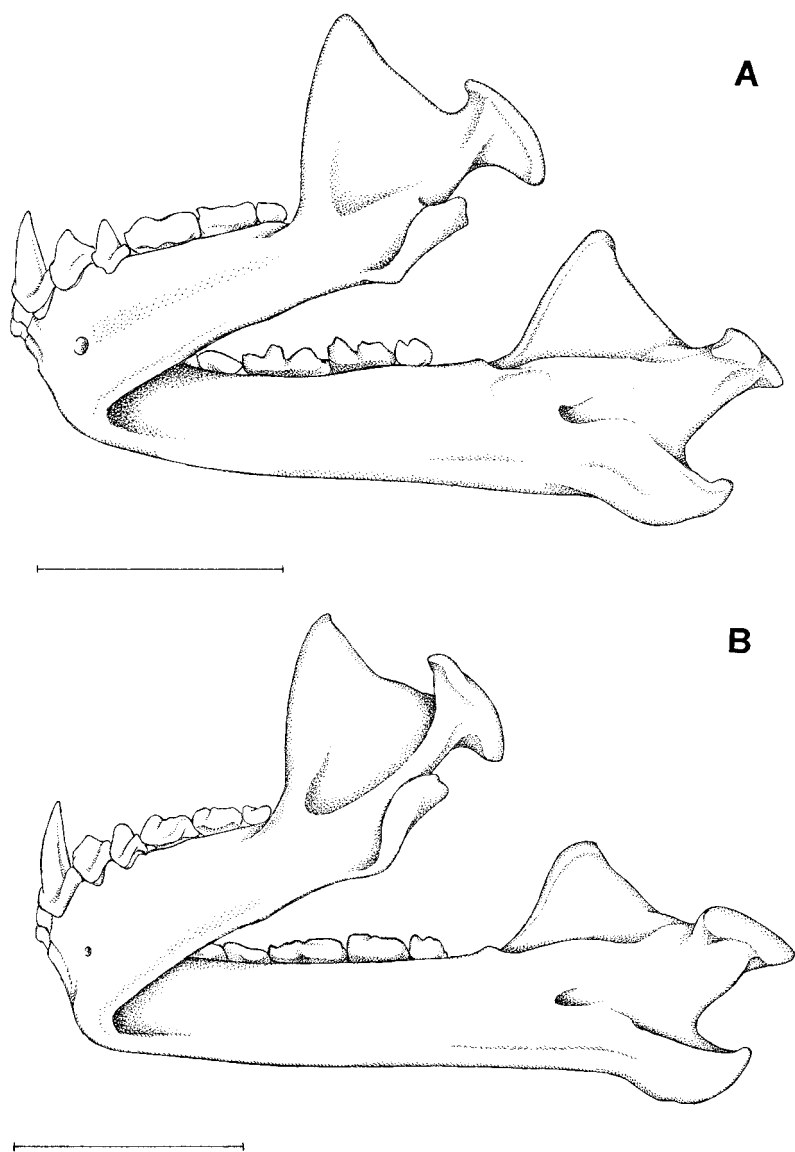


Fig. 50. Oblique view of the lower jaw of (A) *Sturnira lilium* (AMNH 266232; male) and (B) *S. tildae* (AMNH 267461; male). Note the different morphologies of the lingual cusps on the molar teeth: *lilium* is characterized by tall lingual cusps that are separated by a deep vertical notch on m1 and m2; by contrast, these cusps are lower and separated by shallower notches in *tildae*. Scale bars = 10 mm.

useful for distinguishing the smaller species of *Sturnira* include Goodwin and Greenhall (1961), Husson (1978), Davis (1980), and Gannon et al. (1989). Other descriptions and comparative measurements of *S. lilium* can be found in Taddei (1975b), Swanepoel and Genoways (1979), and Brosset and Charles-Dominique (1990). Six subspecies of *S. lil-*

ium are currently recognized, of which the nominate form occurs throughout tropical South America east of the Andes, including the continental islands of Trinidad and Tobago (Koopman, 1994).

Our voucher material generally conforms with published descriptions and measurements of *Sturnira lilium*, although a few Par-

TABLE 45
Measurements^a of *Sturnira* Collected at Paracou

Number/Sex	<i>Sturnira lilium</i>		<i>Sturnira tildae</i>	
	19 females	34 males	13 females	11 males
Weight	19.3 (15.0–25.5) 19	19.7 (15.0–25.3) 34	22.5 (15.8–33.5) 13	22.3 (18.0–24.0) 11
Total length	64.5 (60.0–70.0) 19	65.5 (61.0–73.0) 34	69.8 (64.0–72.0) 13	71.3 (67.0–74.0) 11
Tail length	0.0 (0.0–0.0) 19	0.0 (0.0–0.0) 34	0.0 (0.0–0.0) 13	0.0 (0.0–0.0) 11
Hind foot length	14.5 (13.0–15.0) 19	15.0 (13.0–16.0) 34	15.8 (15.0–17.0) 12	15.2 (13.0–17.0) 11
Ear length	16.4 (15.0–18.0) 19	16.4 (15.0–18.0) 34	18.1 (17.0–20.0) 13	16.9 (16.0–20.0) 11
Forearm length	41.9 (39.5–44.4) 19	42.6 (39.3–44.5) 34	46.1 (44.0–47.0) 13	46.4 (44.2–48.0) 11
Greatest length of skull	21.77 (20.79–22.59) 11	22.21 (21.39–23.04) 13	22.76 (22.22–23.52) 5	23.30 (23.16–23.49) 4
Condylolincisive length	20.05 (19.49–20.88) 11	20.52 (19.41–21.39) 13	21.26 (20.63–22.18) 5	21.65 (21.29–21.90) 4
Postorbital breadth	5.79 (5.45–6.37) 11	5.37 (5.25–6.12) 13	6.16 (6.01–6.34) 5	6.21 (6.10–6.28) 4
Braincase breadth	10.18 (9.78–10.67) 11	10.42 (10.09–10.70) 13	10.80 (10.64–10.94) 5	10.94 (10.75–11.09) 4
Mastoid breadth	11.92 (11.22–12.37) 11	12.00 (11.50–12.55) 13	12.76 (12.48–13.14) 5	12.96 (12.90–13.02) 4
Zygomatic breadth	13.42 (12.90–13.87) 11	13.91 (13.57–14.28) 13	14.15 (13.82–14.47) 5	14.37 (14.35–14.87) 4
Maxillary tooththrow length	6.46 (6.15–6.60) 11	6.58 (6.05–6.93) 13	6.87 (6.72–7.04) 5	6.81 (6.59–7.13) 4
Breadth across molars	8.00 (7.62–8.47) 11	8.13 (7.81–8.59) 13	8.21 (7.94–8.54) 5	8.02 (7.76–8.47) 4

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

acou specimens are slightly smaller than any previously reported from the Guianas. As noted by previous authors (e.g., Peterson and Tamsitt, 1968), the presence and development of “epaulettes” (patches of shoulder hairs stained dark brown by glandular secretions) varies in both sexes, with epaulettes present in virtually all older adults in our series but faint in some younger adults; subadults (with grayer pelage than the yellow-gray adults) frequently lack epaulettes. The same ontogenetic patterns of pelage variation occur in *S. tildae*, which occurs sympatrically with *S. lilium* at Paracou.

In the field we had some difficulty distinguishing *Sturnira lilium* from *S. tildae*; most of our problems involved subadults, very old animals, and a few individuals that fell near the zone of species overlap in size (table 45). We found no consistent pelage differences to distinguish these species. Although Goodwin and Greenhall (1961: figs. 55, 56) illustrated incisor differences between *lilium* and *tildae* that we found helpful for field identification, this character is not 100% reliable. Incisor morphology can be misleading in older individuals with worn teeth, and we found cases in which the incisors were morphologically intermediate to the conditions suppos-

edly diagnostic of *lilium* and *tildae*. Out of 79 specimens of *Sturnira* that we identified in the field using incisor morphology, we misidentified 1 female *lilium* as *tildae* and 1 female *tildae* as *lilium*, an error rate of 2.5%.

A more useful character for distinguishing *Sturnira lilium* and *S. tildae* in the field, one that we “discovered” only late in our study, is morphology of the lingual cusps on m1 and m2 (fig. 50). In our material, the lingual cusps on m1 and m2 are always tall and separated by a deep vertical notch in *lilium*, whereas *tildae* always has lower cusps separated by a shallow notch lacking vertical edges. On cleaned cranial material, this contrast is best seen when viewing the tooththrow medially from below (i.e., tilting the lower jaw and viewing from underneath the opposing ramus, as in fig. 50). With a little experience, however, cusp morphology is also readily apparent when looking into a living animal’s mouth. Morphology of the lingual cusps was dismissed as a useless character by Marin-kelle and Cadena (1971: 237), who assumed that previous descriptions noting this distinction between *lilium* and *tildae* (e.g., Hill, 1964) were based on specimens of the latter taxon with “unusually worn teeth.” However, we found this character to be useful even in

older individuals: in our material there is little evidence of wear on the lingual cusps of the lower molars in any specimens. Morphology of the lingual cusps on m1 and m2 is strongly correlated with other diagnostic traits and, at least in the Guianas, it appears to be a reliable field character for separating *lilium* and *tildae* (for similar observations on Surinamese material, see Genoways and Williams, 1979).

Given the preceding observations, we cannot account for the small specimens of *Sturnira* "*tildae*" that Brosset and Charles-Dominique (1990: 536) reported as having lower molar lingual margins with "the serrated condition" (i.e., with tall cusps separated by deep vertical notches). If the specimens in question are not, in fact, referable to *S. lilium*, then a third species of *Sturnira* (hitherto unsuspected in the Guianas) may be present in their material. For additional comments on this problem, see the account for *S. tildae* (below).

After confirming identifications of our specimens by the qualitative characters reported in the literature cited above, we found that *Sturnira lilium* and *S. tildae* broadly overlap at Paracou in all external measurements except forearm length. All specimens with forearm length ≤ 44.0 mm in our series were found to represent *lilium* and all individuals with forearms ≥ 45.0 mm proved to be *tildae*. Specimens with forearm measurements between 44.0 and 45.0 mm included representatives of both species. Because we measured the forearms of most of the *Sturnira* that we released in the course of our fieldwork, we were able to make retrospective identifications from these data if other identification criteria were ambiguous or unrecorded. However, a few unvouchered capture records remain identified only as "*Sturnira* sp."

FIELD OBSERVATIONS: We recorded 83 captures (probably including some recaptures) of *Sturnira lilium* at Paracou, all in ground-level mistnets. One capture was in well-drained primary forest, 1 was in swampy primary forest, 6 were in creekside primary forest, 74 were in manmade clearings, and 1 was over a roadside puddle. Of all the bats we captured at Paracou, *S. lilium* was the species most strongly associated with the early-successional vegetation bordering roads, gardens, and other artificial openings in the forest.

Sturnira tildae de la Torre

Figures 48–50

VOUCHER MATERIAL: 14 females (AMNH *266240, *266241, *266251, *267167, *267460, *268554, *268556, *268557, *268560, 268561; MNHN *1998.615, *1998.616, *1998.617, *1998.618) and 11 males (AMNH *266243, *266244, *266247, *266253, *267461, *268558, *268559; MNHN *1998.619, *1998.620, *1998.621, *1998.622); see table 45 for measurements.

IDENTIFICATION: Characters that we found useful for distinguishing *Sturnira tildae* from *S. lilium* are discussed in the preceding species account and will not be repeated here. Descriptions and comparative measurements of *S. tildae* can be found in Goodwin and Greenhall (1961), Hill (1964), Marinkelle and Cadena (1971), Husson (1978), Genoways and Williams (1979), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), and Ochoa et al. (1993). No subspecies of *S. tildae* are currently recognized (Koopman, 1994).

Our Paracou material agrees well with most (not all, see below) previous qualitative descriptions of *Sturnira tildae*, and measurements of our vouchers fall within the range of size variation previously reported for the species. In all of our specimens, m1 and m2 have low lingual cusps separated by a shallow notch.

As noted in the preceding account, Brosset and Charles-Dominique (1990: 536) indicated that some of the smaller French Guianan specimens they identified as *Sturnira tildae* had lower molars with "serrated" lingual margins (i.e., with tall cusps separated by a deep vertical notch on each tooth), a condition not seen in our material. Their systematic conclusions also differed significantly from ours:

Several of our specimens share the measurements and characteristics of a third species described in 1980 by Davis, *Sturnira luisi*. Davis compares the morphology of *luisi* with that of *lilium*, but, concerning *tildae*, says nothing more than [that] *luisi* is smaller than *tildae*. The specimens collected by us which correspond to the description of *luisi* are in fact *tildae* of small size . . . in our series of *tildae*, a continuum exists between these small specimens and the bigger ones, whose size corresponds to the classical descriptions. The serrated condition of the lingual edges of the lower molars is given as distinctive of *luisi* by

Davis; the lower molars of our small specimens of *tildae* show the same characteristics . . . This feature is characteristic of both *luisi* and *tildae*. *Sturnira luisi* probably represents *tildae* of small size, the taxon *luisi* being synonymous with *tildae*.

We are not convinced by this argument, which seems to be based entirely on molar morphology and body size. The form of the skull, particularly of the zygomatic arches, is very different in *tildae* and *luisi*. As described and figured by Davis (1980) and confirmed by our observations, *luisi* is characterized by zygomatic arches with maxillary processes that are not bowed outward, producing a triangular appearance when the arches are seen in dorsal or ventral view. In contrast, both *tildae* and *lilium* have outwardly bowed maxillary processes, so that the zygomatic outline appears much less triangular. The shape of the dental arcade also differs among these taxa: whereas the maxillary tooththrows arch outward in *tildae* and *lilium*, the upper tooththrows are nearly parallel in *luisi* (Davis, 1980; personal obs.). Pending documentation of a graded series of intermediates between *tildae* and *luisi*, these morphologically distinctive taxa should still be regarded as valid species.

FIELD OBSERVATIONS: We recorded 54 captures (possibly including some recaptures) of *Sturnira tildae* at Paracou, of which 51 were in ground-level mistnets and 3 were in elevated nets. Of the 51 ground-level captures, 1 was in well-drained primary forest, 7 were in swampy primary forest, 11 were in creek-side primary forest, 1 was in closed-canopy secondary growth, 27 were in manmade clearings, and 4 were over roadside puddles. Of the three elevated-net captures, one was at 5–8 m above a treefall in creek-side primary forest, and the other two were at 10–13 m above a narrow dirt road.

Comparing ground-level capture-habitat frequencies between *Sturnira* species at Paracou (table 46), we note that *S. tildae* was captured significantly more often in primary forest than was *S. lilium*, a result consistent with Brosset and Charles-Dominique's (1990) conclusions about these species based on sampling at other French Guianan localities.

In addition to captures positively identified as either *Sturnira lilium* or *S. tildae* by the

TABLE 46
Comparison of Capture-Habitat Frequencies
Between *Sturnira lilium* and *S. tildae* Taken in
Ground-Level Mistnets at Paracou^a

	Capture habitats		Totals
	Primary	Modified	
<i>S. lilium</i>	8	75	83
<i>S. tildae</i>	19	32	51
Totals	27	107	134

$$\chi^2 = 15.0, df = 1, p \ll 0.01$$

^a Table entries are numbers of captures (possibly including some recaptures). The chi-square value calculated from these data tests the null hypothesis of no interspecific difference in proportions of captures by habitat.

characters described above, we also recorded 10 unvouchered captures of "*Sturnira* sp." in ground-level mistnets: 2 in well-drained primary forest, 2 in swampy primary forest, 2 in creek-side primary forest, 3 in manmade clearings, and 1 over a roadside puddle. Presumably these bats represented one or both of the species documented by our voucher material, but diagnostic traits were not recorded before the animals were released.

Uroderma bilobatum Peters

VOUCHER MATERIAL: 10 females (AMNH *266257, *267174, *267177, *267178, *267465, *267469; MNHN 1995.1173, *1995.1174, *1995.1175, *1995.1176) and 13 males (AMNH *267171, *267175, *267176, *267183, *267463, *267464, *267470, *268563, *268565; MNHN *1995.1177, *1995.1178, *1995.1179, *1995.1180); see table 47 for measurements.

IDENTIFICATION: The principal reference on bats of the genus *Uroderma* is Davis (1968), who described the species in detail and provided figures and measurements. Helpful descriptions and comparative measurements of *U. bilobatum* can also be found in Goodwin and Greenhall (1961), Husson (1962, 1978), Swanepoel and Genoways (1979), Baker and Clark (1987), and Brosset and Charles-Dominique (1990). Six subspecies of *U. bilobatum* are currently recognized, of which the nominate form occurs throughout Amazonia, including the Guianas (Davis, 1968; Baker et

TABLE 47
Measurements^a of *Uroderma bilobatum* Collected at Paracou

Number/Sex	9 females	13 males
Weight	18.6 (17.6–22.0) 9	16.1 (14.5–18.2) 13
Total length	65.2 (61.0–70.0) 9	64.0 (55.0–71.0) 13
Tail length	0.0 (0.0–0.0) 9	0.0 (0.0–0.0) 13
Hind foot length	12.3 (12.0–13.0) 8	11.8 (10.0–13.0) 13
Ear length	18.0 (17.0–20.0) 9	17.7 (16.0–19.0) 13
Forearm length	43.4 (42.0–45.0) 9	42.9 (42.0–44.0) 13
Greatest length of skull	23.21 (22.56–23.95) 5	23.57 (23.11–23.97) 5
Condylolincisive length	20.97 (20.52–21.86) 5	21.42 (20.97–21.68) 5
Postorbital breadth	5.43 (5.18–5.63) 5	5.43 (5.21–5.68) 4
Braincase breadth	9.82 (9.48–10.27) 5	9.78 (9.47–10.16) 5
Mastoid breadth	11.21 (10.76–11.70) 5	11.08 (10.82–11.13) 5
Zygomatic breadth	12.94 (12.47–13.61) 5	12.92 (12.38–13.26) 5
Maxillary tooththrow length	7.92 (7.65–8.12) 5	8.08 (7.71–8.35) 5
Breadth across molars	9.10 (8.86–9.43) 5	9.05 (8.70–9.38) 4

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

al., 1972; Baker and Clark, 1987; Koopman, 1994).

Our voucher material conforms in all respects with published descriptions of this species, and our measurement data fall within the range of variation previously reported for *U. b. bilobatum*.

FIELD OBSERVATIONS: We captured 25 individuals of *Uroderma bilobatum* at Paracou, of which 21 were taken in ground-level mist-nets and 4 at roosts. Of the 21 ground-level mistnet captures, 6 were in swampy primary forest, 5 were in creekside primary forest, 6 were in manmade clearings, and 4 were over roadside puddles.

We found two roosting groups, each in an “apical” tent (sensu Kunz et al., 1994) made by chewing through the midrib of a large leaf of *Phenakospermum guyannense* (Strelitzia-ceae) (fig. 51). A roosting group of three bats collected in its entirety consisted of an adult male, a lactating adult female, and a juvenile. Both roosts were in swampy primary forest; one tent was 3.5 m and the other 5 m above the ground.

Vampyressa (Metavampyressa) brocki
Peterson

VOUCHER MATERIAL: 6 females (AMNH *266311, *267471, *268566, *268567; MNHN *1995.1185, *1995.1186) and 1

male (AMNH *267184); see table 48 for measurements.

IDENTIFICATION: As currently defined (Koopman, 1993), *Vampyressa* includes three subgenera and five species: *Metavampyressa* (including *brocki* and *nymphaea*), *Vampyressa* (including *melissa* and *pusilla*), and *Vampyriscus* (including *bidens* only). In part because of confusion in the literature regarding middorsal stripes in *Vampyressa* (see discussion below), unambiguous identifications must still be based on Peterson’s (1968) review, which included a key (subsequently reproduced by Lewis and Wilson, 1987). Information about specimens of *V. brocki* collected after 1968 can be found in Baker and Genoways (1972), Swanepoel and Genoways (1979), and Williams and Genoways (1980a). No subspecies of *V. brocki* are currently recognized (Koopman, 1994).

Our voucher material, apparently the largest series of *Vampyressa brocki* collected at a single locality, conforms in all respects with Peterson’s (1968) original description. Although our measurement data broadly overlap those previously reported for the species, some Paracou specimens are slightly smaller than any hitherto reported in the literature.

Peterson’s original description of *Vampyressa brocki* was not ambiguous, but discrep-



Fig. 51. Leaf-tent roost of the type inhabited by *Uroderma bilobatum*, in a wet opening in swampy primary forest at Paracou. This simple conical shelter, made by cutting the midrib of a *Phenakospermum guyanense* frond (arrow), was unoccupied when we found it, but an identical tent nearby contained three bats. Because it is difficult to approach such roosts without alarming the inhabitants, we found many empty tents that might have contained bats only moments before.

TABLE 48
Measurements^a of *Vampyressa brocki* Collected at Paracou

Number/Sex	6 females	1 male
Weight	10.1 (8.6–11.8) 6	8.1
Total length	52.5 (49.0–54.0) 6	50.0
Tail length	0.0 (0.0–0.0) 6	0.0
Hind foot length	10.2 (9.0–11.0) 6	10.0
Ear length	15.7 (15.0–16.0) 6	16.0
Forearm length	33.0 (29.7–35.0) 6	33.0
Greatest length of skull	18.56 (18.35–18.79) 4	18.13
Condylolincisive length	16.50 (15.80–16.76) 4	16.32
Postorbital breadth	5.13 (5.00–5.32) 5	4.98
Braincase breadth	8.42 (8.15–8.63) 5	7.96
Mastoid breadth	9.56 (9.40–9.84) 4	9.13
Zygomatic breadth	10.90 (10.59–11.21) 5	10.65
Maxillary tooththrow length	5.64 (5.45–5.80) 5	5.63
Breadth across molars	7.74 (7.64–7.96) 5	7.35

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

ant readings are current in the literature. Thus, Williams and Genoways (1980a) stated that *V. brocki* lacks a middorsal stripe, citing Peterson as their authority, whereas other authors have evidently interpreted Peterson to mean that a stripe is present in this species (e.g., Lewis and Wilson, 1987). Peterson (1968: 1) himself clearly stated that the holotype of *brocki* is “greyish brown above with a faint indistinct dorsal whitish stripe.” A diagrammatic character summary accompanying the original description (op. cit.: fig. 6), however, does not distinguish between the faint middorsal stripe of *brocki* and the much brighter markings of two other congeners (*nymphaea* and *bidens*).

Our Paracou vouchers have a middorsal stripe, but it is extremely faint and is visible only when the dry dorsal pelage is carefully brushed. The stripe is hard to see under any conditions because it is only slightly paler than the surrounding fur, and it becomes quite invisible when the fur is wet (precluding observation in alcohol-preserved specimens).

Because the dorsal stripe is hard to see, *Vampyressa brocki* externally resembles *V. pusilla*, with which it might be confused in the field. The latter species entirely lacks a dorsal stripe and shares several traits with *brocki*, including small size, two pairs of lower incisors, and absence of m3 (Peterson,

1968). Characters that unambiguously distinguish *brocki* and *pusilla* include a suite of craniodental features (op. cit.), of which the most useful include: (1) form of the inner upper incisors (tapering to a point in *brocki*, bilobed in *pusilla*), (2) shape of the anterior lower premolar (low-crowned and bladelike in *brocki*, with higher crown and spearlike anterior cusp in *pusilla*), and (3) shape of the nasal aperture (with straight ventral border in *brocki*, V-shaped ventral border in *pusilla*). The latter character is visible only on cleaned skulls, but the distinction is unambiguous and provides a means of unequivocally identifying old individuals with worn or broken teeth.

FIELD OBSERVATIONS: Of the seven *Vampyressa brocki* we captured at Paracou, four were taken in ground-level mistnets and three in elevated nets. One of the ground-level captures was in well-drained primary forest, two were in creekside primary forest, and one was in a manmade clearing. The elevated net captures were made 17–21 m over a narrow dirt road.

FURIPTERIDAE

We captured a single furipterid species at Paracou, the only member of its family known to occur in rainforest habitats.

TABLE 49
Measurements^a of *Furipterus horrens* Collected at Paracou

Number/Sex	7 females	3 males
Weight	3.8 (3.2–4.2) 7	3.3 (3.1–3.6) 3
Total length	65.1 (54.0–74.0) 7	62.0 (54.0–69.0) 3
Tail length	26.4 (21.0–38.0) 7	24.3 (20.0–28.0) 3
Hind foot length	8.0 (7.0–9.0) 7	7.7 (7.0–8.0) 3
Ear length	10.5 (10.0–11.0) 7	10.3 (10.0–11.0) 3
Forearm length	37.3 (36.5–38.5) 6	36.0 (35.0–37.0) 3
Greatest length of skull	12.01 (11.86–12.19) 3	—
Condylolincisive length	11.25 (10.85–11.45) 3	—
Zygomatic breadth	7.57 (7.33–7.85) 3	—
Maxillary tooththrow length	4.76 (4.67–4.85) 3	—
Breadth across molars	4.95 (4.89–5.04) 5	—

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

Furipterus horrens (F. Cuvier)

VOUCHER MATERIAL: 9 females (AMNH *265975, *265979, 265980, *267213, *267214, *268572, 268573; MNHN *1995.870, *1995.871) and 4 males (AMNH *267212, *267507; MNHN *1995.872, 1995.873); see table 49 for measurements.

IDENTIFICATION: Husson (1962, 1978) provided a detailed description and measurements of *Furipterus horrens*, and additional morphometric data were published by Brosset and Charles-Dominique (1990). No subspecies are recognized (Koopman, 1994).

Although our voucher material does not differ in any respect from Husson's (1962, 1978) careful qualitative description of *Furipterus horrens*, measurements of the Paracou series document a greater range of size variation than that previously reported from the Guianas. Our measurement data (table 49) additionally suggest that the species may be sexually dimorphic (females averaging slightly larger than males in most dimensions), an observation that tends to corroborate Uieda et al.'s (1980) report of sexual dimorphism in a northeastern Brazilian population. In her otherwise excellent external descriptions of *Furipterus horrens*, Emmons stated that the thumb has "no claw" (1990: 82) or "almost no claw" (1997: 91). The thumb, small and enclosed in the wing membrane, bears a tiny but distinct claw in all the specimens we examined.

FIELD OBSERVATIONS: We collected 13

specimens of *Furipterus horrens* at Paracou, of which 12 were taken at roosts and 1 was shot as it flew back and forth along a regular beat about a meter above the ground in well-drained primary forest at night. The nine roosting groups we found consisted of one to two individuals, either solitary adults (of both sexes) or lactating females with nursing juveniles. In no case did we find more than one adult occupying a roost. All of the roosts we found were in or under fallen trees in various stages of decomposition. One roost was a small cavity in the broken end of a rotting log (fig. 52), but most were on the undersides of trunks or in dark chambers between buttresses (fig. 17). Four roosts were in well-drained primary forest, one was in swampy primary forest, two were in primary forest of unrecorded character, one was in selectively logged forest, and one was in closed-canopy secondary growth. Small, dark, solitary bats that flew away unidentified from refugia in or under woody debris on many occasions throughout the course of our fieldwork at Paracou were probably *F. horrens*. Although we never caught this species in mistnets, our impression was that roosts of *F. horrens* could be found by careful searching almost anywhere in the forest.

THYROPTERIDAE

Although we caught only one thyropterid species at Paracou, a second is known from



Fig. 52. Roost of *Furipterus horrens* in well-drained primary forest at Paracou. An adult female with her nursing offspring inhabited this dark but shallow cavity in the broken end of a rotting log, about 40 cm above the ground (arrow). Such inconspicuous refugia occur everywhere in the forest and we probably overlooked many *F. horrens* roosts even along frequently traveled trails through our study area.

French Guiana and might also be expected to occur in our study area (appendix 1).

Thyroptera tricolor Spix

VOUCHER MATERIAL: 16 females (AMNH *266348, *266356, *266358, 266359, *266364, *267215, *267216, *267217, *267218, *268576; MNHN *1995.874, *1995.875, *1995.876, *1995.877, 1995.878, *1995.879) and 12 males (AMNH *266352, 266355, 266357, *266361, *266363, 266365, *268574, 268577; MNHN 1995.880, *1995.881, 1995.882, 1995.883); see table 50 for measurements.

IDENTIFICATION: We consulted the descriptions and measurements of *Thypotera tricolor* provided by Husson (1962, 1978), Brosset and Charles-Dominique (1990), and Pine (1993) to confirm the identification of our material. Although three subspecies were

recognized by Wilson and Findley (1977) and Koopman (1994), the morphological justification for a trinomial classification is not clear. Furthermore, Pine (1993) suggested that some published observations of geographic variation within *T. tricolor* may have been based on material that was not correctly identified to species. Pending a thorough review of the problem, it currently seems pointless to employ subspecific nomenclature.

Our material from Paracou conforms with published descriptions of *Thyroptera tricolor* in all respects. Although Pine (1993) noted some variation in the number of lappets on the calcar in some populations of this species, all of our specimens have two lappets on the calcar. The free portion of the tail is relatively long in all our fluid-preserved material, which conforms to Pine's (1993) ob-

TABLE 50
Measurements^a of *Thyroptera tricolor* Collected at Paracou

Number/Sex	14 females	5 males
Weight	4.3 (3.7–5.5) 14	3.5 (2.6–4.0) 5
Total length	73.4 (67.0–77.0) 14	69.2 (65.0–74.0) 5
Tail length	29.6 (25.0–36.0) 14	27.6 (24.0–30.0) 5
Hind foot length	5.8 (5.0–6.0) 14	5.9 (5.0–6.0) 5
Ear length	12.7 (12.0–14.0) 13	12.6 (12.0–13.0) 5
Forearm length	36.4 (35.0–38.0) 14	36.2 (34.5–37.5) 5
Greatest length of skull	14.73 (14.44–15.02) 6	14.75 (14.59–14.90) 2
Condylolincisive length	13.86 (13.53–14.20) 6	13.75 (13.57–13.93) 2
Zygomatic breadth	7.58 (7.41–7.71) 6	7.45 (7.42–7.47) 2
Maxillary tooththrow length	5.93 (5.78–6.07) 6	5.91 (5.86–5.96) 2
Breadth across molars	5.30 (5.19–5.41) 6	5.35 (5.22–5.47) 2

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

servations. We note, however, that the free portion of the tail appears quite short in our skins, an artifact that resulted from pinning the specimens to dry with the uropatagium maximally extended.

The size range documented by our voucher specimens (table 50) is somewhat greater than that previously reported from Surinamese and French Guianan populations of *Thyroptera tricolor* by Husson (1962, 1978) and Brosset and Charles-Dominique (1990).

In addition, the Paracou measurement data suggest some slight sexual dimorphism, with females exceeding males in average body weight and total length.

FIELD OBSERVATIONS: We recorded 40 captures (possibly including some recaptures) of *Thyroptera tricolor* at Paracou, of which 3 were in ground-level mistnets, 1 was in an elevated net, and 36 were at roosts. One ground-level mistnet capture was in well-drained primary forest, one was in swampy

TABLE 51
Roosting Groups of *Thyroptera tricolor* Observed at Paracou

Date	Roost site ^a	Group size	Entire group captured?	Age and sex of captured group members
21 Jul 1991	<i>Heliconia</i>	3	yes	2 ad. females, 1 juv.
22 Jul 1991	<i>Phenakospermum</i>	4	no	1 ad. male
8 Aug 1991	<i>Phenakospermum</i>	6	yes	1 ad. male, 2 ad. females, 1 subad. male, 2 juv.
20 Aug 1991	<i>Phenakospermum</i>	4	yes	1 ad. male, 2 ad. females, 1 juv.
23 Aug 1991	<i>Phenakospermum</i> ^b	4?	no	1 ad. female
23 Aug 1991	<i>Phenakospermum</i>	3	yes	1 ad. male, 1 ad. female, 1 juv.
3 Nov 1992	<i>Heliconia</i>	4	yes	2 ad. females, 2 juv.
20 Jul 1993	<i>Heliconia</i>	4	no	2 males ^c , 1 ad. female
1 Aug 1993	<i>Heliconia</i>	4?	no	2 adults ^d , 1 juv
7 Sep 1993	<i>Heliconia</i>	4	yes	1 ad. male, 3 ad. females
24 Sep 1994	<i>Phenakospermum</i> ^b	6?	no	1 ad. male, 1 ad. female
21 Oct 1994	<i>Phenakospermum</i> ^b	5–6	no	1 juv.

^a Plant taxon with occupied foliage. Except as noted, bats were found in erect, half-unrolled new leaves.

^b In scrolled dead leaf hanging from plant.

^c Age not recorded, but presumably not juveniles; not preserved as vouchers.

^d Sex not recorded; not preserved as vouchers.



Fig. 53. Roost of *Thyroptera tricolor* in the half-unrolled new leaf of a small *Heliconia* growing in swampy primary forest at Paracou. The adhesive suckers of the roosting bats are visible as dark spots through the translucent tissue of the leaf; the bats themselves (an adult male and three adult females) form a dark mass inside their tubular shelter (arrow).



Fig. 54. Roost of *Thyroptera tricolor* in a scrolled dead leaf of *Phenakospermum guyannense* (arrow) in secondary vegetation at Paracou. We found two other roosts of *T. tricolor* in dead leaves like this one, which is hanging downward from its broken petiole. This roost contained about four bats, one of which was collected as a voucher.

primary forest, and one was in a manmade clearing. Our single elevated mistnet capture was made at 7–8 m above the ground in the subcanopy of swampy primary forest.

We found 12 roosting groups of *Thyroptera tricolor*, all of them in foliage (table 51). Most (nine) roosts were in the erect, half-unrolled new leaves of heliconias, *Heliconia* sp. (Heliconiaceae) (fig. 53), or *Phenakospermum guyannense* (Strelitziaceae), but three roosting groups occupied scrolled dead leaves hanging from large *Phenakospermum* plants (fig. 54). Of the five *Heliconia* roosts we found, one was in well-drained primary forest, two were in swampy primary forest, and two were in creekside primary forest. Five *Phenakospermum* roosts were in secondary vegetation (especially along the margins of a small savanna enclave) and two were in wet glades surrounded by swampy primary forest. All of the leaves that we found used by *T. tricolor* as roosts were shaded; none was in direct sunlight. The number of bats per roost varied from one to six with a well-defined mode of four. We did not record more than a single adult male in any roost.

VESPERTILIONIDAE

We captured five vespertilionid species at Paracou belonging to the genera *Eptesicus*, *Lasiurus*, and *Myotis*. Of the six other vespertilionids known from French Guiana and Surinam, four could plausibly be expected to occur in our study area also (appendix 1).

Eptesicus chiriquinus Thomas

Figures 55, 56

VOUCHER MATERIAL: 2 females (AMNH *267531, *268584) and 4 males (AMNH *267234, *267530; MNHN *1995.961, 1995.962); see table 52 for measurements.

IDENTIFICATION: In his revision of the South American species of *Eptesicus*, Davis (1966) recognized an *andinus* group of species with long blackish fur. Several taxa were included in this complex: *andinus* Allen (1914), *chiriquinus* Thomas (1920b), *inca* Thomas (1920b), *montosus* Thomas (1920b) and *chiralensis* Anthony (1926). Of these, Davis considered *inca* and *chiriquinus* to be

strict junior synonyms of *E. andinus*, the larger of the two species he recognized; the smaller species, *E. montosus*, included *chiralensis* as a valid subspecies.

Koopman (1978) disagreed, claiming that the long-haired forms of Neotropical *Eptesicus* are restricted to cool highland areas, whereas the short-haired forms occur in the warm lowlands. By his interpretation, the long-haired taxa are local variants of short-haired species that have adapted to cooler conditions at higher elevations. Accordingly, Koopman (1978, 1993, 1994) treated the members of Davis' (1966) *andinus* group as subspecies of nomenclaturally older short-haired species based on size, assigning *andinus* to *E. brasiliensis*, and *montosus* and *chiralensis* to *E. furinalis*. However, Koopman's adaptive scenario concerning hair length is refuted by the occurrence of long-haired *Eptesicus*—clearly referable to Davis' *andinus* group—in lowland areas of Brazil, Panama, Venezuela, and French Guiana.¹³ In addition, the sympatric occurrence in northeastern Venezuela of *E. brasiliensis*, *E. furinalis*, and a third species that Ochoa et al. (1993) identified as *E. andinus* definitely indicates that *Eptesicus* species with different pelage types can coexist at the same elevation.

Specimen data cited by Davis (1966), together with other collections subsequently reported in the literature (e.g., by Handley, 1976), provide compelling evidence that two species referable to the *andinus* group are sympatric at several South American localities. However, Davis did not personally examine any of the relevant holotypes in this complex, so his decisions about synonymies

¹³ We examined dark, long-furred specimens of *Eptesicus*, clearly referable to Davis' *andinus* group, from lowland areas of Brazil (Amazonas, Rio Madeira, Santo Antonio do Guajará [ca. 25 m]: AMNH 92251, 93787), French Guiana (Paracou [ca. 30 m]: AMNH 267234, 267530, 267531, 268584; MNHN 1995.961, 1995.962), and Panama (San Blas, Armila, Quebrada Venado [sea level]: USNM 335411). In addition, unambiguous descriptions of *andinus*-group specimens have been reported in the literature from a lowland site in Venezuela (Bolívar, Imataca Forest Reserve [180 m]; Ochoa et al., 1993) and another in French Guiana (Piste Saint-Élie [ca. 45 m]; Brosset and Charles-Dominique, 1990).

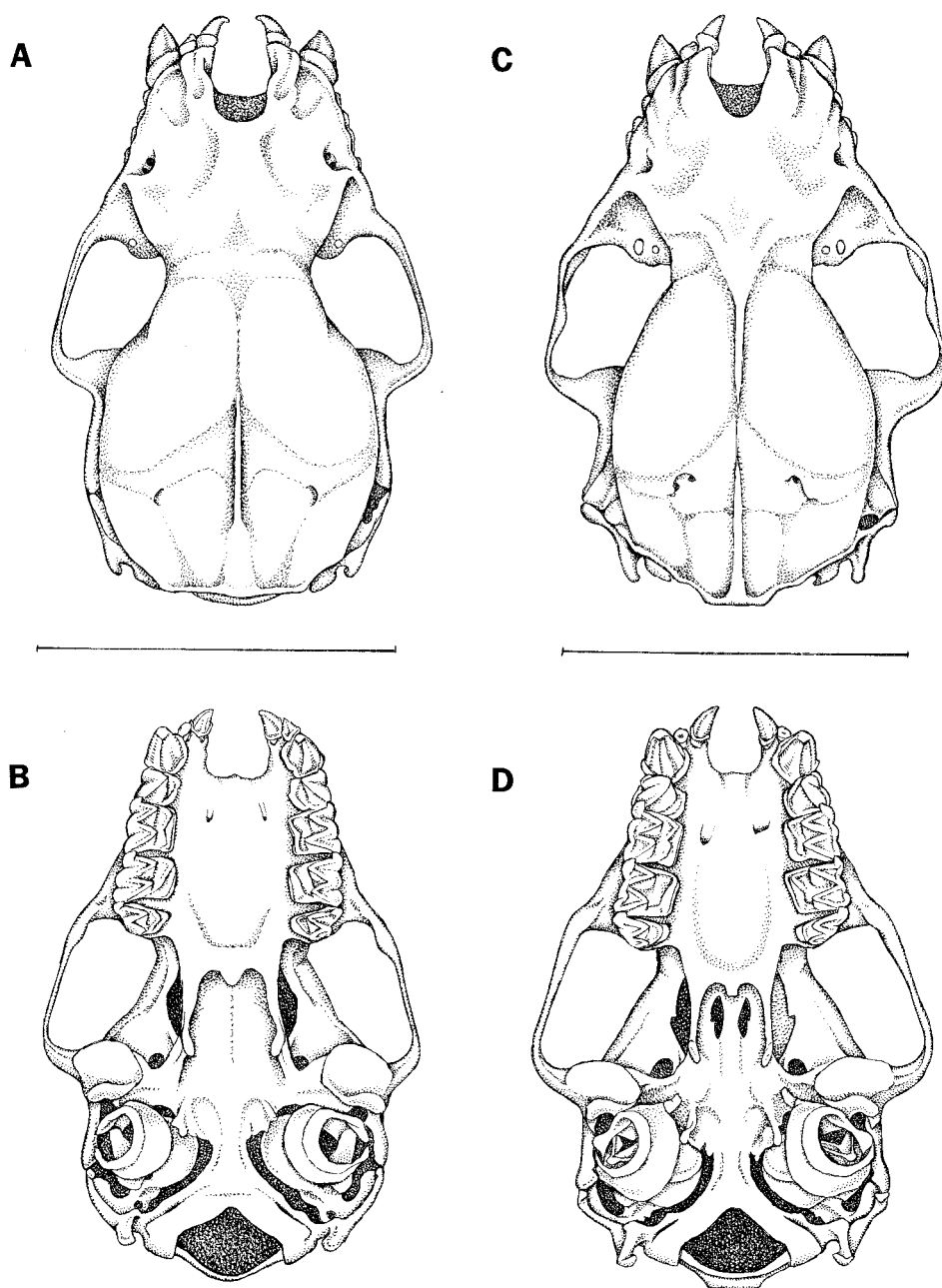


Fig. 55. Dorsal (A) and ventral (B) views of the skull of the holotype of *Eptesicus andinus* (AMNH 33807; male) from Colombia. Dorsal (C) and ventral (D) views of the skull of *E. chiriquinus* (AMNH 267234; male) from Paracou. *E. chiriquinus* has a consistently larger and more heavily built skull than does *E. andinus*. Also note the flattened, triangular bony plate at the intersection of the sagittal and nuchal crests in *andinus*, a structure never present in *chiriquinus*. Scale bars = 10 mm.

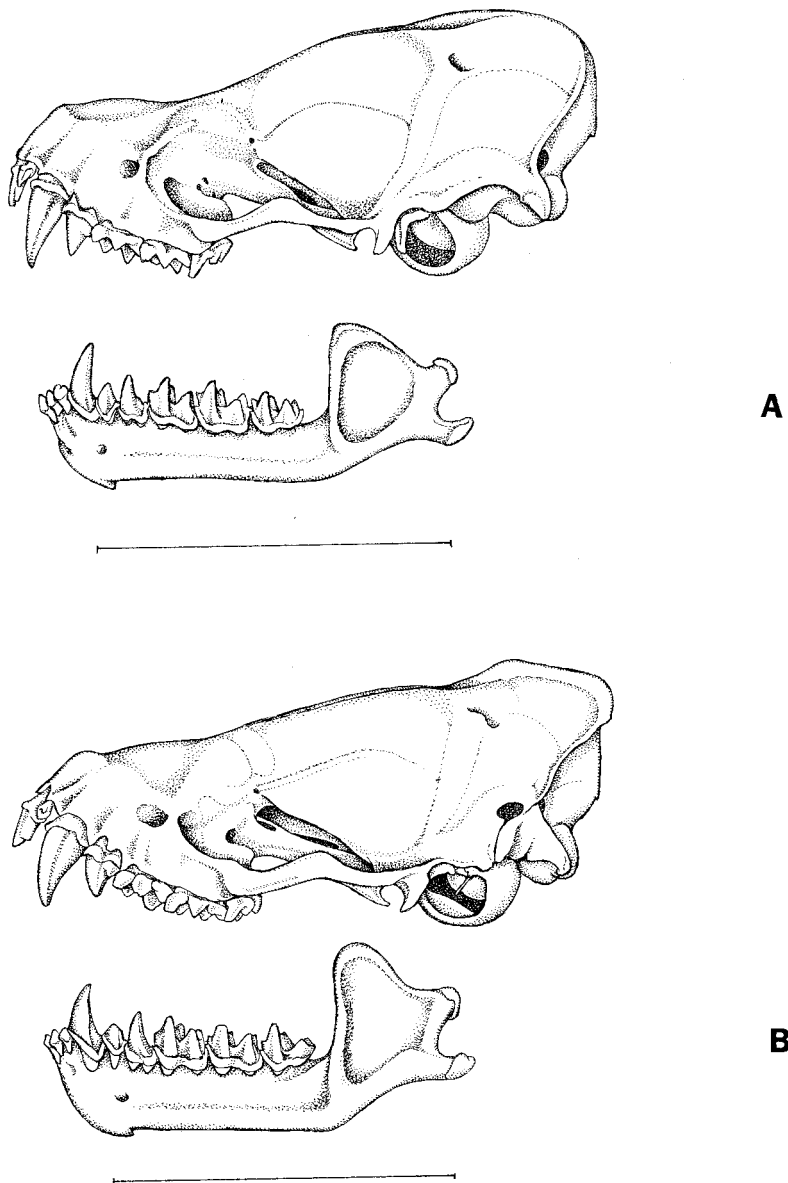


Fig. 56. Lateral views of the skull and lower jaw of (A) the holotype of *Eptesicus andinus* (AMNH 33807; male) and (B) *E. chiriquinus* from Paracou (AMNH 267234; male). Note the species difference in development of the sagittal crest. Scale bars = 10 mm.

are problematic. Because Koopman's (1978) review of the situation was obviously not an improvement, a fresh appraisal of the systematics of Neotropical *Eptesicus* is necessary.

To determine the correct identification of several blackish, long-haired specimens of *Eptesicus* captured at Paracou, we examined the holotypes of *E. andinus* and *E. chiriquinus* as well as 136 other specimens of Neo-

TABLE 52
Measurements^a of *Eptesicus chiriquinus* Collected at Paracou

Number/Sex	3 males	2 females
Weight	10.9 (10.4–11.6) 3	12.3 (11.1–13.4) 2
Total length	108.7 (107.0–111.0) 3	114.0 (112.0–116.0) 2
Tail length	45.7 (45.0–46.0) 3	48.0 (45.0–51.0) 2
Hind foot length	11.3 (10.0–13.0) 3	12.0 (11.0–13.0) 2
Ear length	13.9 (13.5–14.3) 3	15.8 (15.5–16.0) 2
Forearm length	46.6 (45.1–48.3) 3	47.6 (47.0–48.2) 2
Greatest length of skull	17.29 (17.06–17.52) 2	17.34 (17.32–17.35) 2
Condylolincisive length	16.96 (16.86–17.05) 2	17.22 (16.88–17.56) 2
Postorbital breadth	4.12 (4.07–4.16) 2	3.95 (3.94–3.96) 2
Zygomatic breadth	12.24 (12.04–12.44) 2	12.04 (11.62–12.46) 2
Braincase breadth	8.07 (8.01–8.12) 2	8.04 (7.79–8.28) 2
Mastoid breadth	9.07 (8.94–9.19) 2	9.30 (9.22–9.38) 2
Maxillary toothrow length	6.88 (6.86–6.90) 2	6.87 (6.83–6.91) 2
Breadth across molars	7.47 (7.43–7.51) 2	7.58 (7.42–7.73) 2

^a Summary statistics (mean, observed range, and sample size) of measurements for each sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

tropical *Eptesicus* in the collections of the AMNH, FMNH, and USNM.¹⁴ We also consulted the original descriptions of *E. chiriquinus*, *E. inca*, and *E. montosus* (Thomas, 1920b), and we compared our observations with those reported by Davis (1965, 1966), Williams (1978), Brosset and Charles-Dominique (1990), and Ochoa et al. (1993). Our conclusions, which differ substantially from those previously expressed in the literature, are explained below.

¹⁴ Specimens examined in addition to those from Paracou are listed here by species based on our revised identifications. *Eptesicus andinus*: Brazil (AMNH 134910), Colombia (AMNH 32671, 32802, 33807 [holotype]), Ecuador (AMNH 47218–47220), Peru (AMNH 23780, FMNH 123953), Venezuela (USNM 370934–370938, 370943–370947, 370949–370953, 370955, 370962–370963, 387732, 441755, 441764). *Eptesicus brasiliensis*: Brazil (AMNH 78868–78871, 79535–79538, 79645–79647), Colombia (AMNH 239096–239098), Ecuador (AMNH 67606), Peru (AMNH 67232–67233, 74016), Venezuela (78387–78401). *Eptesicus chiriquinus*: Brazil (AMNH 92251, 93787), Colombia (AMNH 33806, USNM 483952), Costa Rica (USNM 566457), Ecuador (AMNH 47217, 47221–47223, 67608; USNM 513502, 548349), Panama (USNM 306809–306810, 310258–310260, 319504, 331958–331968, 335411, 338098–338100, 387728, 387730–387731, 518026–518027, 520577–520579, 526246, 541105, 567879–567880, 575587–575590), Venezuela (USNM 387728, 387730–387731, 441765).

Our side-by-side comparisons of the holotypes of *Eptesicus andinus* (AMNH 33807, from Valle de las Papas, Colombia) and *E. chiralensis* (AMNH 47219, from El Chiral, Ecuador) indicate that these forms are conspecific. Although the holotype of *andinus* is slightly larger than that of *chiralensis* (table 53), both share a similar skull morphology that is unusual in *Eptesicus*: the braincase appears domed rather than flattened when seen in profile, the sagittal and nuchal crests are very poorly developed, and the intersection of the sagittal and nuchal crests is marked by a flattened triangular plate of bone that is thicker than the surrounding braincase. The dorsal pelage of both holotypes is the same dark brown color (although the tips of the hairs are slightly lighter over the lower back in the holotype of *andinus*), the length of the dorsal fur is the same (ca. 9 mm), and the length and coloration of the bicolored ventral fur (hairs with dark bases and tan tips) are also similar. In our view, these specimens represent a single species, the oldest name for which is *Eptesicus andinus* Allen (1914).

Although we have not examined the holotype of *Eptesicus montosus*, the original description and accompanying measurements suggest that it too is conspecific with *E. andinus*. Collected at El Choro, Bolivia, this specimen (BMNH 2.1.1.1) was described by

TABLE 53
Measurements^a of Holotypes in the *Eptesicus andinus* Species Complex

	<i>andinus</i> AMNH 33807	<i>chiralisensis</i> AMNH 47219	<i>montosus</i> ^b BMNH 2.1.1.1	<i>inca</i> ^b BMNH 94.8.6.1	<i>chiriquinus</i> ^b BMNH 3.3.3.1
Sex	male	male	male	male	male
Total length	100.0	97.0	98.0	99.0	120.0
Tail length	35.0	38.0	43.0	44.0	50.0
Hind foot length	8.0	10.0	—	—	—
Ear length	—	—	—	—	14.0
Forearm length	43.6	41.1	43.0	46.0	46.5
Greatest length of skull	16.01	15.22	15.6	16.2	16.2
Condylolincisive length	15.75	15.15	—	—	—
Postorbital breadth	4.24	4.04	4.2	4.5	4.0
Zygomatic breadth	10.55	10.34	10.3	10.8	11.1
Braincase breadth	7.85	7.63	8.0	8.0	7.8
Mastoid breadth	8.40	8.10	—	—	—
Maxillary toothrow length	6.07	5.83	6.0	6.3	6.3
Breadth across molars	6.62	6.69	—	—	—

^a See text for a description of measurement methods.

^b Measurements from Thomas (1920).

Thomas (1920b: 363) as follows: "Fur very long and fine, hairs of back about 9 mm. in length. General colour blackish brown, lightened on the posterior back by the Prout's brown of the tips of the hairs . . . skull, as compared with that of *E. brasiliensis*, conspicuously more swollen, higher in the braincase . . . the whole skull less flattened and less ridged." Measurements of BMNH 2.1.1.1, a male, indicate that it is intermediate in size between the male holotypes of *chiralisensis* and *andinus* (table 53).

Also apparently referable to *Eptesicus andinus* are two small specimens so identified by Thomas (1920b) from Chanchamayo, Peru, that Davis (1966) subsequently reidentified as *E. montosus chiralisensis* (we have not seen these, but base our identification on their size and morphology as reported by Thomas and Davis). By contrast, another specimen (BMNH 94.8.6.1) collected at the same locality, the holotype of *Eptesicus inca* Thomas (1920b), is clearly distinct. *Eptesicus inca* is larger than *E. andinus* in most dimensions (table 53) and, unlike the latter species, it has a well-defined sagittal ridge.

A third *andinus*-group taxon named by Thomas (1920b) was *E. chiriquinus*, based on a specimen from Cerro Chiriquí, Panama (BMNH 3.3.3.1). The holotypes of *chiriquin-*

us and *inca* are similar in most dimensions (table 53), and Thomas did not explain why he thought they were different species. In comparing their respective descriptions, only a 0.5-mm difference in postorbital breadth and a possible difference in wooliness of the pelage appear noteworthy. Although we have not seen these types, our examination of other specimens convinces us that the same large-bodied species of *Eptesicus* with long blackish fur occurs in Central and South America, and that such character differences do not hold up on examination of large series. Accordingly, we conclude, like Davis (1966), that *chiriquinus* and *inca* are conspecific. Since both *chiriquinus* and *inca* were named in the same publication, and because their relative precedence has not previously been established, we select *chiriquinus* as the senior epithet.

Based on the preceding inferences from examination of specimens and from the literature, we offer the following revised diagnosis of *Eptesicus chiriquinus*: a large species (for the genus) with long (8.0–10.0 mm) dark brown or blackish dorsal fur that appears oily in living individuals; ventral fur bicolored (each hair with a dark brown base and tan tip); skull with sagittal and nuchal crests well developed (even in smaller indi-

TABLE 54
Measurements^a of *Eptesicus andinus* and *Eptesicus chiriquinus*

	<i>Eptesicus andinus</i> (multiple localities ^b)		<i>Eptesicus chiriquinus</i> (multiple localities including Paracou ^b)	
Number/Sex	10 males	16 females	24 males	30 males
Weight	8.2 (7.0–10.2) 3	10.4 (10.4) 1	10.7 (9.0–14.0) 7	11.8 (9.9–14.0) 8
Total length	91.2 (83.0–100.0) 9	92.5 (87.0–101.0) 14	102.9 (93.0–111.0) 24	106.3 (95.0–116.0) 28
Tail length	36.4 (31.0–39.0) 9	37.3 (34.0–41.0) 14	43.2 (36.0–48.0) 24	43.3 (35.0–51.0) 28
Hind foot length	9.2 (8.0–10.0) 9	10.1 (9.0–11.0) 16	10.4 (9.0–13.0) 24	10.4 (9.0–13.0) 28
Ear length	13.9 (11.0–15.0) 6	14.4 (13.0–16.0) 13	13.9 (12.0–16.0) 21	14.7 (12.0–17.0) 22
Forearm length	40.2 (37.2–44.4) 9	40.0 (37.7–42.0) 16	45.0 (42.5–48.3) 24	45.7 (42.7–48.9) 28
Greatest length of skull	15.19 (14.37–16.01) 9	15.05 (14.17–15.72) 16	16.52 (16.04–17.52) 22	16.67 (15.81–17.39) 23
Condylolincisive length	15.15 (14.54–15.89) 8	14.86 (14.58–15.18) 13	16.30 (15.94–17.05) 22	16.42 (15.63–17.56) 24
Postorbital breadth	3.99 (3.67–4.32) 9	3.93 (3.77–4.14) 16	4.01 (3.72–4.17) 9	3.96 (3.09–4.33) 17
Zygomatic breadth	10.25 (9.71–10.71) 8	10.28 (10.04–10.86) 11	11.33 (10.75–12.44) 18	11.65 (10.97–12.46) 23
Braincase breadth	7.53 (7.15–7.85) 9	7.36 (7.19–7.93) 16	7.92 (7.30–8.50) 22	7.87 (7.37–8.28) 24
Mastoid breadth	8.22 (7.89–8.60) 7	8.15 (7.77–8.65) 16	8.72 (8.41–9.19) 23	8.91 (8.49–9.38) 24
Maxillary tooththrow length	5.81 (5.53–6.07) 9	5.77 (5.51–5.93) 16	6.47 (6.22–6.90) 23	6.53 (6.15–7.11) 29
Breadth across molars	6.42 (6.27–6.69) 9	6.62 (6.38–6.92) 16	7.09 (6.76–7.57) 23	7.25 (6.78–7.79) 27

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

^b See footnote 12 in the text for a list of specimens examined.

viduals); rostrum not laterally inflated; braincase high, not flattened, with well-defined dish-shaped facial profile; length of forearm > 42.0 mm; greatest length of skull > 15.80 mm; zygomatic breadth > 10.70 mm; mastoid breadth > 8.40 mm; length of maxillary tooththrow > 6.10 mm; breadth across molars > 6.75 mm.

Eptesicus chiriquinus can be distinguished unambiguously from *E. andinus* on the basis of size (generally larger in *chiriquinus*; see table 54), presence of well-developed sagittal and nuchal crests (absent in *andinus*), and absence of a flattened, triangular plate of bone at the intersection of the sagittal and nuchal crests (present in *andinus*). *Eptesicus chiriquinus* and *E. andinus* exhibit nonoverlapping measurements in the following dimensions: forearm length (females only), greatest length of skull, condylolincisive length, zygomatic breadth, maxillary tooththrow length, and breadth across molars (males only). *Eptesicus chiriquinus* can be distinguished from *E. brasiliensis* on the basis of pelage (always longer and usually darker in *chiriquinus*) and skull morphology (rostrum less inflated, braincase higher, and dish-

shaped facial profile more strongly developed in *chiriquinus*).

Based on our examination of material in the USNM collected by the Smithsonian Venezuela Project, the specimens referred to *Eptesicus montosus* by Handley (1976) represent *E. andinus* in our usage, and the specimens he referred to *E. andinus* represent *E. chiriquinus* as diagnosed above (see footnote 14 for specimens examined). Based on published measurements, specimens of *Eptesicus* “*andinus*” reported from French Guiana by Brosset and Charles-Dominique (1990) and from Venezuela by Ochoa et al. (1993) probably represent *E. chiriquinus*.

The specimens of *Eptesicus chiriquinus* that we collected at Paracou are among the largest known representatives of this taxon (see tables 52–54). Although our preliminary comparisons suggested that the Paracou specimens might represent a distinct taxon, consideration of additional material (particularly from Panama) blurred all distinctions initially detected between the larger and smaller specimens referable to this species. In the absence of any clear pattern of geo-

TABLE 55
Measurements^a of *Eptesicus furi*

	Paracou, French Guiana		Holotype of <i>E. f. gaumeri</i> AMNH 11040/12753	Holotype of <i>E. f. chapmani</i> AMNH 37057
Number/Sex	8 males	10 females	female	female
Weight	8.5 (7.5–9.5) 8	8.7 (7.5–12.0) 10	—	—
Total length	96.6 (93.0–99.0) 8	97.2 (92.0–103.0) 10	95.0	95.0
Tail length	40.1 (37.0–46.0) 8	40.4 (35.0–48.0) 10	39.6	40.0
Hind foot length	9.8 (9.0–10.0) 8	10.0 (8.5–11.0) 10	9.4	8.5
Ear length	13.3 (12.0–14.0) 8	13.3 (12.5–15.0) 10	—	—
Forearm length	40.4 (39.5–42.0) 8	40.7 (40.0–42.4) 10	39.7	40.2
Greatest length of skull	15.47 (15.08–15.91) 4	15.85 (15.23–16.13) 4	15.34	15.63
Condylolincisive length	15.11 (14.93–15.26) 4	15.12 (14.45–15.73) 4	14.95	15.16
Zygomatic breadth	10.84 (10.44–11.28) 4	10.76 (10.51–11.09) 3	10.61	10.70
Braincase breadth	7.19 (7.01–7.40) 4	7.27 (7.19–7.37) 4	7.22	7.44
Mastoid breadth	8.42 (8.05–8.90) 4	8.46 (8.22–8.78) 4	8.47	8.54
Maxillary toothrow length	5.67 (5.58–5.77) 4	5.76 (5.55–5.93) 4	5.57	5.72
Breadth across molars	6.63 (6.37–6.81) 4	6.74 (6.54–6.98) 4	6.24	6.58

^a Summary statistics (mean, observed range, and sample size) of measurements for each taxon and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

graphic variation, we do not recognize any subspecies of *E. chiriquinus*.

FIELD OBSERVATIONS: Two of the six *Eptesicus chiriquinus* that we captured at Paracou were taken in ground-level mistnets and four were taken in elevated nets. Of the two ground-level captures, one was in a man-made clearing and one was over a roadside puddle. The four elevated mistnet captures were made between 4 and 23 m over a narrow dirt road. Although all of our vouchered captures were in modified habitats, we once caught a large, blackish vespertilionid in the uppermost mesh of a ground-level mistnet in swampy primary forest. Briefly entangled in full view but just out of reach before escaping, this bat closely resembled *E. chiriquinus* and differed in external appearance from other species known to occur at Paracou.

Eptesicus furi (d'Orbigny)

VOUCHER MATERIAL: 12 females (AMNH *266368, 267236, *267238, *267525, *267526, *268581, *268582, *268583; MNHN *1995.887, *1995.888, 1995.889, *1995.890) and 10 males (AMNH 266367, *266369, *266373, *267235, *267237, *267529, *268580; MNHN 1995.891, *1995.892, *1995.893); see table 55 for measurements.

IDENTIFICATION: Useful descriptions and measurements of *Eptesicus furi* were provided by Davis (1966), Williams (1978), Brosset and Charles-Dominique (1990), and Ochoa et al. (1993). Four subspecies are currently recognized in South America: *E. f. gaumeri* (tropical Mexico through Central America to northern Colombia, Venezuela, and the Guianas), *E. f. chapmani* (Amazonian Colombia, Brazil, and Bolivia), *E. f. furi* (southeastern Brazil to southern Bolivia and northeastern Argentina), and *E. f. findleyi* (northwestern Argentina) (Davis, 1966; Williams, 1978).¹⁵

Our voucher material conforms in all respects to previous descriptions of *Eptesicus furi*, but our initial attempt to make a subspecific determination was not successful. We compared our material to measurements of *E. f. gaumeri* and *E. f. chapmani* provided by Davis (1966), and were dismayed to discover that these taxa appear to have almost completely overlapping ranges of size variation (op. cit.: table 3). The range of varia-

¹⁵ Koopman (1994) additionally included *chiralensis* Anthony (1926) and *montosus* Thomas (1920b) as subspecies of *Eptesicus furi*, but we agree with Davis (1966) that those forms are instead conspecific with *E. andinus* (see discussion in the preceding account for *E. chiriquinus*).

tion in the Paracou series (table 55) could easily be interpreted as corresponding to either subspecies.

Although Davis (1966) published measurements of the holotypes of *Eptesicus furinalis gaumeri* and *E. f. chapmani* that suggested a significant size difference, he did not personally examine the specimens; instead, these data were provided by two different colleagues. We therefore remeasured and compared the types of *gaumeri* (AMNH 11040/12753) and *chapmani* (AMNH 37057) ourselves and found that they are more similar than previously reported (table 55). Indeed, both fall within the range of variation found in our Paracou sample in almost every dimension. Moreover, the types of *gaumeri* and *chapmani* and the Paracou specimens are all the same dark brown color above and have similar bicolored ventral fur with dark bases and tan tips. We conclude that *gaumeri* and *chapmani* cannot usefully be distinguished even at the level of subspecies. The correct name for this taxon—which seems distinct from the other South American subspecies of *E. furinalis* (see Williams, 1978)—is *Eptesicus furinalis gaumeri* Allen.

FIELD OBSERVATIONS: We captured 23 *Eptesicus furinalis* at Paracou, of which 14 were taken in ground-level mistnets, 8 in elevated mistnets, and 1 at a roost. Of our 14 ground-level mistnet captures, 6 were in manmade clearings and 8 were over roadside puddles. Seven of our elevated mistnet captures were made between 5 and 20 m over a narrow dirt road, and one was made at 34–37 m over a treefall in well-drained primary forest. Our single roosting example was found behind a window shutter.

Lasiurus blossevillii (Lesson and Garnot)

VOUCHER MATERIAL: 1 female (MNHN *1995.936) and 1 male (AMNH *267533); see table 56 for measurements.

IDENTIFICATION: Characters and measurements necessary for unambiguous identification of *Lasiurus blossevillii* were given by Handley (1960, 1996). Husson (1962, 1978) provided a detailed description of Surinamese specimens of this taxon under the name *L. borealis frantzii*. *Lasiurus blossevillii* was considered to represent a subspecies of *L. bo-*

TABLE 56
Measurements^a of *Lasiurus blossevillii*
Collected at Paracou

Number/Sex	1 female	1 male
Weight	8.2	7.2
Total length	109.0	99.0
Tail length	53.0	46.0
Hind foot length	10.0	10.0
Ear length	10.0	11.0
Forearm length	40.6	38.5
Greatest length of skull	11.46	11.38
Condylolincisive length	11.72	11.45
Zygomatic breadth	8.74	8.49
Maxillary tooththrow length	4.02	3.89
Breadth across molars	5.53	5.28

^a Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

realis by most workers (e.g., Handley, 1960; Goodwin and Greenhall, 1961) until the publication of morphometric and allozyme data on *Lasiurus* by Schmidly and Hendricks (1984) and Baker et al. (1988). Based on morphological and allelic traits, Baker et al. restricted *L. borealis* to eastern North American populations and proposed use of *L. blossevillii* for populations from western North America, Central America, and South America. As thus defined, *L. blossevillii* contains several mainland subspecies: *L. b. teliotis* (southeastern Canada to southcentral Mexico), *L. b. frantzii* (southern Mexico to Amazonian Brazil, including Trinidad and Tobago), *L. b. blossevillii* (eastern Brazil to northern Argentina), and *L. b. varius* (Chile and southern Argentina) (ranges from Koopman, 1994).

Morales and Bickham (1995) analyzed mitochondrial rDNA restriction site data from more than 50 individuals of *Lasiurus* and found compelling evidence for the separation of *L. borealis* and *L. blossevillii* at the species level. Within *L. blossevillii*, they demonstrated very strong support (bootstrap values of 100%) for a clade including specimens from Argentina, Bolivia, and Guyana, and for a second clade comprising specimens from Mexico and Belize. Interestingly, specimens identified as *teliotus* from Mexico and as *frantzii* from Belize were found to have identical haplotypes. On this basis, Morales and Bickham suggested that *frantzii* and *te-*

liotus should be synonymized as subspecies (of these, *frantzii* Peters is the oldest name). However, Morales and Bickham did not address the morphological characters of *teliotus* and *frantzii*, nor did their biochemical comparisons include any material from Costa Rica, the type locality of *frantzii*.

Problems also remain with the South American forms of *Lasiurus blossevillii*. Specimens from Colombia, Peru, Venezuela, Trinidad and Tobago, Surinam, and Brazil have traditionally been referred to *frantzii* on morphological grounds (Handley, 1960; Goodwin and Greenhall, 1961; Husson, 1962, 1978; Koopman, 1994), yet the rDNA data of Morales and Bickham (1995) unambiguously place a specimen from Guyana in a clade with Argentinian and Bolivian specimens referable to the nominate subspecies *L. b. blossevillii*. Thus, the rDNA data suggest that at least two species may be present in the *L. blossevillii* complex, a northern form in northern Central America, and a southern form that extends at least as far north as the Guianas. However, rDNA data are not available from populations in intervening regions, and patterns of morphological variation have yet to be analyzed. A thorough revision of the Neotropical red bats is clearly needed to resolve species and subspecies limits within this group.

Our material from Paracou conforms to previous descriptions of *Lasiurus blossevillii* from the Guianan region (Husson, 1962, 1978; Handley, 1996), although measurements in some dimensions fall slightly outside the reported range of variation (e.g., greatest length of skull, smaller in our specimens).

FIELD OBSERVATIONS: One of our two individuals of *Lasiurus blossevillii* was caught in a ground-level mistnet over a roadside puddle, and the other was taken in a net suspended 10–13 m over a narrow dirt road.

Myotis nigricans (Schinz)

Figures 57, 58

VOUCHER MATERIAL: 27 females (AMNH *267223, *267225, *267227, *267228, *267229, 267230, *267231, *267509, *267510, *267511, *267512, *267514, *267516, *267517, *267519, *267520,

*267522, *268539; MNHN *1995.937, *1995.938, *1995.939, *1995.940, *1995.941, *1995.942, *1995.943, *1995.944, *1995.945) and 2 males (AMNH *267221, *267513); see table 57 for measurements.

IDENTIFICATION: LaVal's (1973) revision is still the standard reference for Neotropical *Myotis*, but descriptions and measurements useful for identifying *M. nigricans* can also be found in Goodwin and Greenhall (1961), Husson (1962, 1978), Wilson and LaVal (1974), and Brosset and Charles-Dominique (1990). *Myotis nigricans* as currently recognized is a highly variable species. As noted by LaVal (1973: 6), "Any specimen [of Neotropical *Myotis*] that does not seem to fit the diagnosis of another species is probably *nigricans*." Four or five subspecies of *Myotis nigricans* are currently recognized, of which the nominate form *M. n. nigricans* occurs throughout Central America and most of tropical South America (LaVal, 1973; Wilson and LaVal, 1974; Koopman, 1994).

Despite confusion concerning the limits and diagnosis of *Myotis nigricans*, specimens from the Guianan region (presumably referable to the nominate subspecies) share a common craniodental morphology (described by Husson, 1962, 1978). Given appropriate specimen preparations (see below), this species can be easily distinguished from *M. riparius* and *M. albescens*, both of which also occur in the region (see below and appendix 1).

We found that specimens of *Myotis* from Paracou could not be identified unambiguously without extracting and cleaning skulls. Although pelage characters (e.g., color, banding and/or frosting, degree of "silkeness" or "woolliness") and measurements (e.g., forearm length) have been cited previously as morphological criteria for identifying *Myotis* species (e.g., by LaVal, 1973; Brosset and Charles-Dominique, 1990), we found considerable overlap between *M. nigricans* and *M. riparius* with respect to all of these features (see below). By contrast, *M. nigricans* and *M. riparius* are easily distinguished by craniodental morphology (figures 57, 58), and we found no species overlap in five of seven craniodental measurements (table 57).

Myotis nigricans can be distinguished from *M. albescens* throughout South Amer-

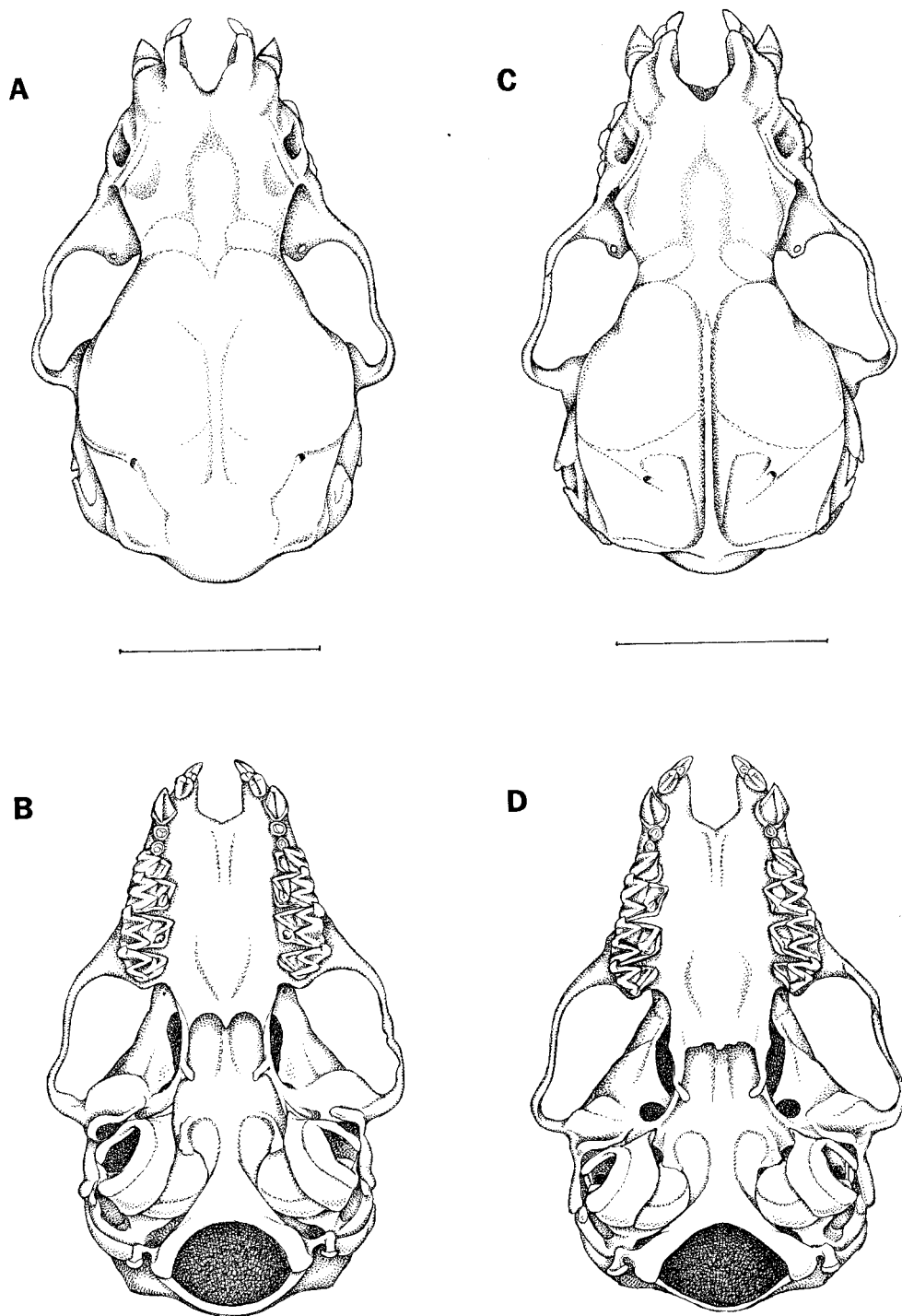


Fig. 57. Dorsal (A) and ventral (B) views of the skull of *Myotis nigricans* (AMNH 267228; female) from Paracou. Dorsal (C) and ventral (D) views of the skull of *M. riparius* (AMNH 268591; female) from Paracou. Note differences in structure of the anterior braincase, palate, and auditory region. Scale bars = 5 mm.

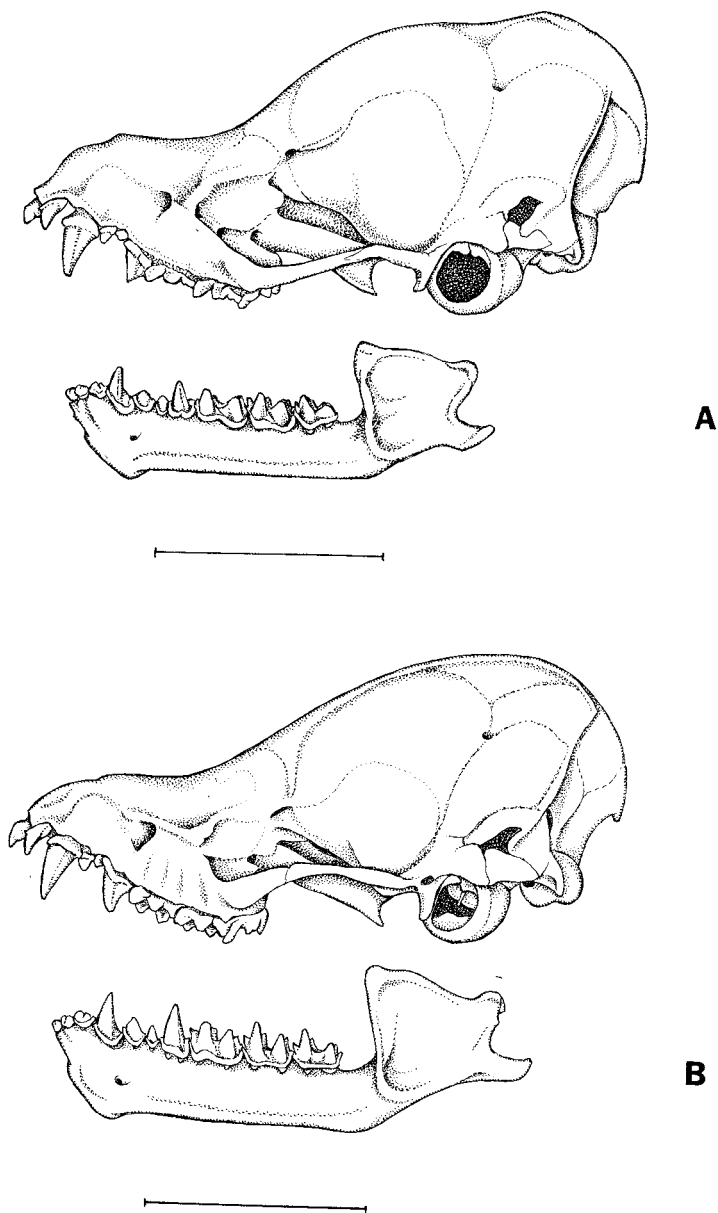


Fig. 58. Lateral views of the skull and lower jaw of (A) *Myotis nigricans* (AMNH 267228; female) and (B) *M. riparius* (AMNH 268591; female). Scale bars = 5 mm.

ica based on postorbital breadth and braincase breadth, both of which are greater in *M. albescens* where these taxa occur in sympatry or near-sympatry (Husson, 1962, 1978; LaVal, 1973; Baud and Menu, 1993). Husson (1962, 1978) noted that Surinamese specimens of *M. albescens* have a braincase

breadth > 6.8 mm and a postorbital breadth > 3.6 mm, whereas these dimensions are smaller in *M. nigricans* from Surinam. None of our specimens from Paracou has a braincase breadth > 6.75 mm, and only one specimen has a postorbital breadth > 3.50 mm (table 57). In our sample of 29 individuals,

TABLE 57
Measurements^a of *Myotis* Collected at Paracou

	<i>Myotis nigricans</i>		<i>Myotis riparius</i>	
Number/Sex	26 females	2 males	6 females	6 males
Weight	4.7 (3.9–5.6) 26	3.7 (3.5–3.9) 2	5.6 (5.2–6.5) 6	5.5 (4.8–6.2) 6
Total length	81.5 (78.0–85.0) 26	80.0 (78.0–82.0) 2	88.3 (83.0–91.0) 6	84.7 (83.0–86.0) 6
Tail length	35.4 (31.0–40.0) 26	35.5 (34.0–37.0) 2	41.3 (39.0–44.0) 6	36.8 (36.0–38.0) 6
Hind foot length	8.0 (7.0–9.0) 26	7.5 (7.0–8.0) 2	8.3 (7.0–9.0) 6	8.5 (7.0–10.0) 6
Ear length	12.5 (11.0–13.0) 26	12.5 (12.0–13.0) 2	13.1 (12.0–14.0) 6	12.7 (12.0–13.0) 6
Forearm length	33.7 (32.0–35.0) 26	32.8 (32.5–33.0) 2	36.7 (34.2–38.0) 6	35.3 (33.5–36.0) 6
Greatest length of skull	13.19 (12.78–13.58) 26	13.07 (12.97–13.16) 2	13.98 (13.76–14.31) 6	14.05 (13.83–14.32) 6
Condylolincisive length	12.65 (12.24–12.97) 26	12.55 (12.48–12.61) 2	13.62 (13.34–13.99) 6	13.63 (13.33–13.92) 6
Postorbital breadth	3.24 (3.22–3.65) 26	3.39 (3.30–3.48) 2	3.51 (3.33–3.68) 6	3.43 (3.22–3.59) 6
Braincase breadth	6.41 (6.16–6.75) 26	6.47 (6.47–6.48) 2	6.72 (6.65–6.87) 6	6.65 (6.57–6.77) 6
Zygomatic breadth	8.12 (7.85–8.55) 16	7.94 (7.94) 1	9.32 (8.98–9.60) 6	9.17 (8.91–9.51) 6
Maxillary tooththrow length	4.86 (4.68–5.01) 26	4.83 (4.78–4.87) 2	5.34 (5.25–5.40) 6	5.39 (5.21–5.59) 6
Breadth across molars	5.24 (5.00–5.49) 26	5.27 (5.25–5.28) 2	5.73 (5.64–5.88) 6	5.82 (5.50–5.97) 6

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

the specimen with the largest postorbital breadth (MNH 1995.943, postorbital breadth 3.65 mm) has a braincase breadth identical to the sample mean (6.41 mm). Based on these data and comparisons of external morphology, we are confident that none of the *Myotis* collected at Paracou represents *M. albescentis*. *Myotis albescentis* has yet to be reported in French Guiana despite its occurrence in Surinam and northeastern Brazil. However, we note that several specimens identified as *M. nigricans* by Brosset and Charles-Dominique were reported to have postorbital breadth ≥ 3.7 mm, and it is possible that one or more of these specimens may represent *M. albescentis*. Although *M. albescentis* generally has a distinctively “frosted” pelage, LaVal (1973) noted that some specimens lack this feature and externally resemble *M. nigricans*.

Our voucher material of *Myotis nigricans* falls within the lower range of size variation previously reported for this species (e.g., by LaVal, 1973; Wilson and LaVal, 1974). With the exception of postorbital breadth (noted above), the Paracou specimens are similar in all dimensions to specimens reported from other localities in French Guiana and Surinam (Husson, 1962, 1978; Brosset and Charles-Dominique, 1990). Most of our

specimens have long, silky, brownish dorsal fur. However, several have fur that is brownish but woollier in texture, and one individual (a male) has almost black fur. The ventral fur is always slightly lighter in color than the dorsal fur, appearing frosted in many specimens.

FIELD OBSERVATIONS: We made 29 vouchered captures of *Myotis nigricans* at Paracou, 25 of which were in ground-level mistnets and 4 of which were in elevated nets. Of the 25 ground-level captures, 3 were in creekside primary forest, 9 were in manmade clearings, and 13 were over roadside puddles. The elevated net captures were made between 4 and 13 m above a narrow dirt road.

See the following species account for habitat comparisons with *Myotis riparius* and for information about captures of unidentified *Myotis*.

Myotis riparius Handley

Figures 57, 58

VOUCHER MATERIAL: 6 females (AMNH *267224, *267524, *268591, *268592; MNHN *1995.946, *1995.947) and 6 males (AMNH *266366, *266376, *267523, *268589; MNHN *1995.948, *1995.949); see table 57 for measurements.

IDENTIFICATION: As noted above, identification of species of Neotropical *Myotis* requires reference to LaVal (1973). Descriptions and measurements of *Myotis riparius* can also be found in Handley (1960) and Brosset and Charles-Dominique (1990). No subspecies of *M. riparius* are currently recognized (Koopman, 1994).

Our specimens of *Myotis riparius* conform to the description provided by LaVal (1973). A sagittal crest is present in all individuals, although it is poorly developed in two specimens; P3 is less than one-fourth the height of P4 in all individuals with both teeth (P3 is missing in one individual); and P3 is shifted to the inside of the tooththrow in 64% of our specimens. Most of our specimens of *M. riparius* have woolly brown dorsal fur and slightly lighter ventral fur. However, some individuals have fur that is silkier in texture, and one specimen (clearly adult based on epiphyseal fusion) is gray-brown with slightly darker underparts. Measurements of our material resemble those reported by Brosset and Charles-Dominique (1990) for French Guianan *M. riparius*, although our larger series exhibits somewhat more size variation (table 57).

FIELD OBSERVATIONS: We made 12 vouchered captures of *Myotis riparius* at Paracou: 11 individuals were taken in ground-level mistnets and 1 was shot as it flew back and forth in a regular beat about 5 m above a narrow dirt road at night. Of the 11 ground-level mistnet captures, 5 were in well-drained primary forest, 4 were in swampy primary forest, 1 was in creekside primary forest, and 1 was in a manmade clearing.

The observed habitat difference in ground-level mistnet capture frequencies between *Myotis nigricans* and *M. riparius* is noteworthy despite the rather small numbers of vouchered captures available for comparison (table 58). Apparently, *M. nigricans* favors clearings whereas *M. riparius* is more commonly found beneath the primary forest canopy. To our knowledge, ecological differences between sympatric populations of these species have not previously been reported in the literature, possibly due to the difficulty of field identification.

In addition to the vouchered captures of *Myotis nigricans* and *M. riparius* reported

TABLE 58
Comparison of Capture-Habitat Frequencies
Between *Myotis nigricans* and *Myotis riparius*
Taken in Ground-Level Mistnets at Paracou^a

	Capture habitats		Totals
	Primary	Modified	
<i>M. nigricans</i>	3	22	25
<i>M. riparius</i>	10	1	11
Totals	13	23	36

$\chi^2 = 20.6$, $df = 1$, $p \ll 0.01$
 $\chi_c^2 = 17.3$, $df = 1$, $p \ll 0.01$
 $p = 0.00001$ by Fisher's Exact Test

^a Table entries are numbers of captures. The chi-square value calculated from these data tests the null hypothesis of no inter-specific difference in proportions of captures by habitat. Because of the small number of observations in two frequency classes, we also tabulate chi-square with Yate's correction for continuity and the exact probability calculated by Fisher's method.

above, we recorded five unvouchered captures of *Myotis* in ground-level mistnets over roadside puddles. These bats were identified in the field as representing either *M. nigricans* or *M. riparius*, but were released without adequate confirmation of identification.

MOLOSSIDAE

We captured nine molossid species at Paracou, including members of the genera *Eumops*, *Molossops*, *Molossus*, and *Promops*. Four of these species have not been reported previously from French Guiana, and another, originally described from the department, has long been lost in synonymy. Another eight molossids known from elsewhere in French Guiana or Surinam might also occur in our study area (appendix 1).

Eumops auripendulus (Shaw)

VOUCHER MATERIAL: 2 females (AMNH *267537, *268594) and 1 male (MNHN *1995.950); see table 59 for measurements.

IDENTIFICATION: Eger (1977) provided species diagnoses and a key in her revision of the genus *Eumops*, which has not been superseded by any comparably comprehensive study. Husson (1962, 1978) gave a detailed description and comparative measurements

TABLE 59
Measurements^a of *Eumops* Collected at Paracou

Number/Sex	<i>Eumops auripendulus</i>		<i>Eumops hansae</i>
	2 females	1 male	1 female
Weight	29.3 (23.6–35.0) 2	29.5	13.2
Total length	129.0 (126.0–132.0) 2	141.0	103.0
Tail length	46.5 (43.0–50.0) 2	48.0	32.0
Hind foot length	15.0 (15.0–15.0) 2	13.0	10.0
Ear length	19.5 (18.0–21.0) 2	24.0	20.0
Forearm length	58.5 (58.0–59.0) 2	59.0	38.5
Greatest length of skull	22.96 (22.96) 1	—	18.80
Condylolincisive length	22.70 (22.70) 1	—	18.09
Postorbital breadth	4.61 (4.61) 1	—	4.15
Zygomatic breadth	14.03 (14.03) 1	—	10.81
Mastoid breadth	11.70 (11.70) 1	—	10.16
Maxillary tooththrow length	8.96 (8.96) 1	—	6.96
Breadth across molars	9.59 (9.59) 1	—	7.81

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

of *E. auripendulus* from Surinam, and additional information can be found in Sanborn (1932) under the account for *E. abrasus* (now considered a junior synonym of *auripendulus*; see Goodwin, 1960; Husson, 1962, 1978; Eger, 1974, 1977). Two subspecies of *E. auripendulus* are currently recognized with the following continental distributions (Eger, 1974, 1977; Koopman, 1994): *E. a. auripendulus* (southern Mexico to Amazonia, including the Guianas) and *E. a. major* (northern Argentina, southern Paraguay, and eastern Brazil). These taxa are distinguished on the basis of size, with *major* being the larger of the two.

Our voucher material conforms in all respects to Eger's (1977) description of *Eumops auripendulus auripendulus*. The Paracou specimens are also comparable in size to those reported from Surinam by Husson (1962, 1978), although one of our females has a shorter maxillary tooththrow and narrower skull than either of the females whose measurements he published (op. cit.: table 32).

FIELD OBSERVATIONS: Our three specimens of *Eumops auripendulus* from Paracou were captured in mistnets suspended 17–23 m above a narrow dirt road through the forest.

Eumops hansae Sanborn

VOUCHER MATERIAL: 1 female (AMNH *267538); see table 59 for measurements.

IDENTIFICATION: Diagnostic characters and measurements of *Eumops hansae* have been discussed by Gardner et al. (1970), Eger (1977), and Brosset and Charles-Dominique (1990). No subspecies are currently recognized (Eger, 1977; Koopman, 1994).

Our Paracou specimen conforms to published descriptions of *Eumops hansae* and falls within the range of size variation previously reported by Gardner et al. (1970), Eger (1977), and Brosset and Charles-Dominique (1990).

FIELD OBSERVATIONS: Our single specimen of *Eumops hansae* was caught in a mistnet suspended 10–13 m over a narrow dirt road.

Molossops

Both of the species of *Molossops* that we captured at Paracou belong to the subgenus *Cynomops*, the contents of which have never been subjected to modern revisionary treatment. Table 60 summarizes the diagnostic traits of the four species that we recognize based on the literature and our examination of representative museum specimens. All of

TABLE 60
 Characters Distinguishing Species of *Molossops* (subgenus *Cynomops*)^a

<i>Molossops abrasus</i>	<i>Molossops greenhalli^b</i>	<i>Molossops paranus^c</i>	<i>Molossops planirostris</i>
<i>Dorsal fur</i> unicolor dark brown, brown, or chestnut	<i>Dorsal fur</i> dark brown or blackish with pale hair base	<i>Dorsal fur</i> dark brown or blackish with pale hair base	<i>Dorsal fur</i> brown or reddish-brown with pale hair base
<i>Ventral fur</i> dark brown, brown, or chestnut, similar in color to dorsal fur	<i>Ventral fur</i> brown along sides of body, somewhat paler (sometimes grayish) on throat and along broad band down midline of chest and abdomen, no sharp line of transition between brown fur along sides and paler fur down midline of body	<i>Ventral fur</i> brown, only slightly paler than dorsal fur, no sharp line of transition present between fur on sides and along midline of body	<i>Ventral fur</i> brown along sides of body, fur on throat and along broad band down midline of chest and abdomen very pale (white, yellowish, buffy, or grayish), sharp line of transition between brown fur along sides and pale fur down midline present in adults; OR entire venter pale grayish, buffy, or pinkish
<i>Dense patch of dark brown fur</i> along anterodorsal surface of proximal 1/3 of forearm and adjacent propatagial membrane; second patch present along posterodorsal surface of distal 3/4 of forearm, extends across patagium near wrist to base of metacarpal IV; fur patches darker than wing membrane, clearly visible without magnification	<i>Patch of wooly brown fur</i> along anterodorsal surface of proximal 1/3 of forearm and adjacent propatagial membrane; second patch present along posterodorsal surface of distal 2/3 of forearm, extends across patagium near wrist to base of metacarpal IV; fur patches darker than wing membrane, clearly visible without magnification	<i>Dense patch of dark brown fur</i> along anterodorsal surface of proximal 1/3 of forearm and adjacent propatagial membrane; second patch present along posterodorsal surface of distal 3/4 of forearm, extends across patagium near wrist to base of metacarpal IV; fur patches darker than wing membrane, clearly visible without magnification	<i>Patch of wooly brown fur</i> along anterodorsal surface of proximal 1/3 of forearm and adjacent propatagial membrane; second patch present along posterodorsal surface of distal 2/3 of forearm, extends across patagium near wrist to base of metacarpal IV; fur patches roughly the same color as wing membrane, may not be visible without magnification
<i>Lateral lower incisor</i> always present	<i>Lateral lower incisor</i> sometimes absent	<i>Lateral lower incisor</i> always present	<i>Lateral lower incisor</i> always present
<i>Forearm length</i> 44.2–49.0 mm (males), 41.0–45.0 (females)	<i>Forearm length</i> 35.6–38.2 mm (males), 33.4–37.8 (females)	<i>Forearm length</i> 33.8–36.3 mm (males), 29.9–33.1 (females)	<i>Forearm length</i> 30.0–34.9 mm (males), 29.0–34.6 (females)
<i>Greatest length of skull</i> 19.50–24.30 mm (males), 18.40–21.50 (females)	<i>Greatest length of skull</i> 17.44–20.60 mm (males), 16.22–17.68 (females)	<i>Greatest length of skull</i> 16.73–18.09 mm (males), 15.50–16.00 (females)	<i>Greatest length of skull</i> 14.90–17.50 mm (males), 14.10–16.74 (females)
<i>Zygomatic breadth</i> 13.70–16.50 mm (males), 12.70–14.30 (females)	<i>Zygomatic breadth</i> 11.89–13.54 mm (males), 11.16–12.80 (females)	<i>Zygomatic breadth</i> 11.53–11.80 mm (males), 10.50–11.13 (females)	<i>Zygomatic breadth</i> 10.00–11.77 mm (males), 9.70–11.37 (females)
<i>Mastoid breadth</i> 12.90–16.20 mm (males), 12.70–14.40 (females)	<i>Mastoid breadth</i> 11.94–13.60 mm (males), 10.50–12.84 (females)	<i>Mastoid breadth</i> 10.88–11.52 mm (males), 10.30–11.02 (females)	<i>Mastoid breadth</i> 9.44–11.85 mm (males), 8.90–12.70 (females)
<i>Lacrimial breadth</i> 9.80–11.00 mm (males), 8.17–9.00 (females)	<i>Lacrimial breadth</i> 7.60–8.99 mm (males), 7.09–8.40 (females)	<i>Lacrimial breadth</i> 6.91–7.66 mm (males), 6.60–7.00 (females)	<i>Lacrimial breadth</i> 6.96–7.92 mm (males), 6.00–6.90 (females)
<i>Length of maxillary toothrow</i> 7.40–8.80 mm (males), 6.80–7.85 (females)	<i>Length of maxillary toothrow</i> 6.53–7.60 mm (males), 6.04–7.20 (females)	<i>Length of maxillary toothrow</i> 6.31–6.87 mm (males), 5.70–6.00 (females)	<i>Length of maxillary toothrow</i> 5.60–6.68 mm (males), 5.30–6.38 (females)
<i>Breadth across molars</i> 9.30–10.17 mm (males), 8.50–9.60 (females)	<i>Breadth across molars</i> 8.03–8.90 mm (males), 7.40–8.70 (females)	<i>Breadth across molars</i> 7.69–8.10 mm (males), 7.10–7.82 (females)	<i>Breadth across molars</i> 6.80–7.92 mm (males), 6.70–7.63 (females)

TABLE 60
(Continued)

^a All members of the subgenus *Cynomops* share the following: ears well separated on crown, do not meet in center of forehead; hair of crown ends abruptly, usually on line between ears; ears rounded, folded longitudinally to form compartment over eye; when flattened, ears reach forward to midway between eye and nose; rear edge of ear slightly folded backward; muzzle broad, chin broad, rounded in profile; no wrinkles on upper lip; upper lip slightly "puckered in" to meet lower lip; distinct patch of dense fur along anterodorsal surface of forearm and adjacent propatagial membrane, extends from elbow along approximately $1/3-1/2$ of the forearm; distinct patch of dense fur on posterodorsal surface of forearm, extends along distal $2/3-3/4$ of forearm to wrist, covers base of metacarpal V and surrounding patagial membrane, extends across patagial membrane to (but does not cover) base of metacarpal IV; 2nd phalanx of digit IV of wing = 6.9–8.5% of total length of digit IV; wing tips relatively narrow; basisphenoid pits absent; upper incisors fairly long and in contact only near their bases; anterior upper premolar absent; last upper molar greatly reduced, v-shaped, with no third commissure; sexually dimorphic, males larger than females in many dimensions. Sources of data: Peters (1865b); Dobson (1878); Thomas (1901b, 1911, 1920a); Goodwin (1958); Goodwin and Greenhall (1961); Husson (1962); Jones and Dunnigan (1965); Gardner et al. (1970); Taddei et al. (1976); Vizotto and Taddei (1976); Williams and Genoways (1980a, 1980b); Brosset and Charles-Dominique (1990); Emmons (1990); Koopman (1994), personal obs. (see footnote 14 in text for a list of specimens examined).

^b Including *mexicanus* Jones and Genoways, 1967. *M. mexicanus* may represent a species distinct from *greenhalli*; however, we have not examined this problem in depth, so we follow previous authors in recognizing *mexicanus* as a subspecies of *greenhalli*.

^c Including *milleri* Osgood, 1914.

the substantive taxonomic difficulties we encountered concern the three smaller species, an extended commentary on which is provided below in the account for *M. paranus*.

Molossops (Cynomops) abrasus
(Temminck)

VOUCHER MATERIAL: 1 female (AMNH *267534); see table 62 for measurements.

IDENTIFICATION: *Molossops abrasus* is easily identified by size and other morphological traits from other members of the subgenus *Cynomops* (tables 60, 61). Four subspecies are currently recognized (Williams and Genoways, 1980a; Koopman, 1994): *M. a. mastivus* (Venezuela and the Guianas), *M. a. brachymeles* (eastern Peru), *M. a. abrasus* (eastern Brazil), and *M. a. cerastes* (Paraguay and northern Argentina). These taxa are distinguished principally on the basis of size, with *mastivus* being the largest (Goodwin, 1958; Taddei et al., 1976; Williams and Genoways, 1980a, 1980b).

Our Paracou voucher, apparently the first record from French Guiana, conforms to previous qualitative descriptions of *Molossops abrasus* and falls within the range of size variation previously reported for the species (Goodwin, 1958; Taddei et al., 1976; Williams and Genoways, 1980a, 1980b; Koopman, 1994). Our specimen, a female, is

somewhat smaller than a male identified as *M. a. mastivus* that Williams and Genoways (1980a) reported from Surinam, but this difference is of the same magnitude as the sexual dimorphism that Taddei et al. (1976) documented in a collection of *M. abrasus* from eastern Brazil.

FIELD OBSERVATIONS: We caught our only specimen of *Molossops abrasus* in a mistnet suspended 18–21 m above a narrow dirt road.

Molossops (Cynomops) paranus (Thomas)
Figures 59, 60

VOUCHER MATERIAL: 1 male (AMNH *267535); see table 62 for measurements.

IDENTIFICATION: *Molossops paranus*, originally described as *Molossus planirostris paranus* by Thomas (1901b), continues to be recognized as a subspecies of *Molossops planirostris* by authors (e.g., Koopman, 1978, 1993, 1994). Although Handley (1976) reported specimens identified as *Molossops paranus*, *M. planirostris*, and *M. greenhalli* from the Venezuelan state of Bolívar, he did not comment on the criteria he used to distinguish these taxa. Partial diagnoses and descriptions of the species and subspecies of *Cynomops* occur throughout the literature, but significant inconsistencies exist among published accounts. Conflicting descriptions

TABLE 61
Measurements^a of Holotypes of Selected Named Forms of *Molossops* (*Cynomops*)

	<i>Molossops abrasus</i> ^b RNM 17374	<i>Molossops planirostris</i> ^c ZMB 2513	<i>Molossops paranus</i> ^d BMNH 1.7.11.15	<i>Molossops milleri</i> ^e FMNH 19652	<i>Molossops greenhalli</i> ^f AMNH 175326	<i>Molossops greenhalli mexicanus</i> ^g KU 108609
Sex	female	male	male	female	male	male
Total length	—	78.0	86.0	83.0	—	107.0
Tail length	—	26.0	28.0	26.0	—	33.0
Hind foot length	—	8.0	—	6.5	10.5	12.0
Ear length	—	—	—	—	—	17.5
Forearm length	42.0	32.5	35.1	29.9	36.6	36.8
Greatest length of skull	—	—	16.9	15.5	17.72	19.0
Condylolincisive length	—	16.5	—	—	17.84	—
Lacrimal breadth	—	—	7.1	6.6	8.10	8.6
Postorbital breadth	—	4.1	4.6	4.4	4.53	4.6
Mastoid breadth	—	10.9	11.5	—	11.94	13.1
Zygomatic breadth	—	—	11.8	10.5	12.46	13.1
Maxillary tooththrow length	7.5	6.5	6.5	5.9	6.53	7.6
Breadth across molars	9.3	7.3	7.7	—	8.07	8.8

^a All measurements are recorded in millimeters. See text for a description of measurement methods.

^b Data from Carter and Dolan (1978).

^c Data from Peters (1865b) and Carter and Dolan (1978).

^d Data from Thomas (1901b), amended based on measurements taken by C. O. Handley, Jr. (personal commun.).

^e Data from Osgood (1914), amended based on measurements taken by C. O. Handley, Jr. (personal commun.).

^f Measurements taken by NBS.

^g Data from Jones and Genoways (1967).

TABLE 62
Measurements^a of *Molossops* (*Cynomops*)
Collected at Paracou

	<i>Molossops abrasus</i>	<i>Molossops paranus</i>
Number/Sex	1 female	1 male
Weight	28.7	16.2
Total length	123.0	101.0
Tail length	35.0	29.0
Hind foot length	12.0	11.0
Ear length	20.0	15.0
Forearm length	44.3	35.8
Greatest length of skull	20.86	17.59
Condylolincisive length	20.90	17.40
Lacrimal breadth	8.71	7.19
Postorbital breadth	5.22	4.84
Zygomatic breadth	14.19	11.53
Mastoid breadth	14.26	10.88
Maxillary tooththrow length	7.85	6.38
Breadth across molars	9.43	7.83

^a Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

of ventral coloration, presence or absence of white hair bases, and degree of development of hair patches on the wings make unambiguous identification difficult. To address this problem, we consulted original taxonomic descriptions, literature accounts of additional material, and examined representative specimens of all of the smaller species to develop working diagnoses for identification.¹⁶

¹⁶ The specimens we examined in addition to those from Paracou are: *Molossops greenhalli* (Mexico: USNM 511543, 523453; Panama: USNM 310264–310268, 310270–310275, 368108, 396481, 449875; Venezuela: USNM 387745, 517509; Trinidad: AMNH 175326 [holotype], 176285, 207071); *Molossops paranus* (Panama: AMNH 183868, USNM 317627; Colombia: ROM 41479; Venezuela: USNM 387744; Guyana: ROM 32426, 57337–57338, 57375; Brazil: AMNH 79744–79745); *Molossops planirostris* (Panama: AMNH 183161, 183863; Venezuela: AMNH 17096–17097; Brazil: AMNH 37043–37049, 37050–37052, 79725, 79727, 79731, 79733, 93879–93886, 92971, 92753–92755, 94630–94653, 236221; Paraguay: 234455–234459)

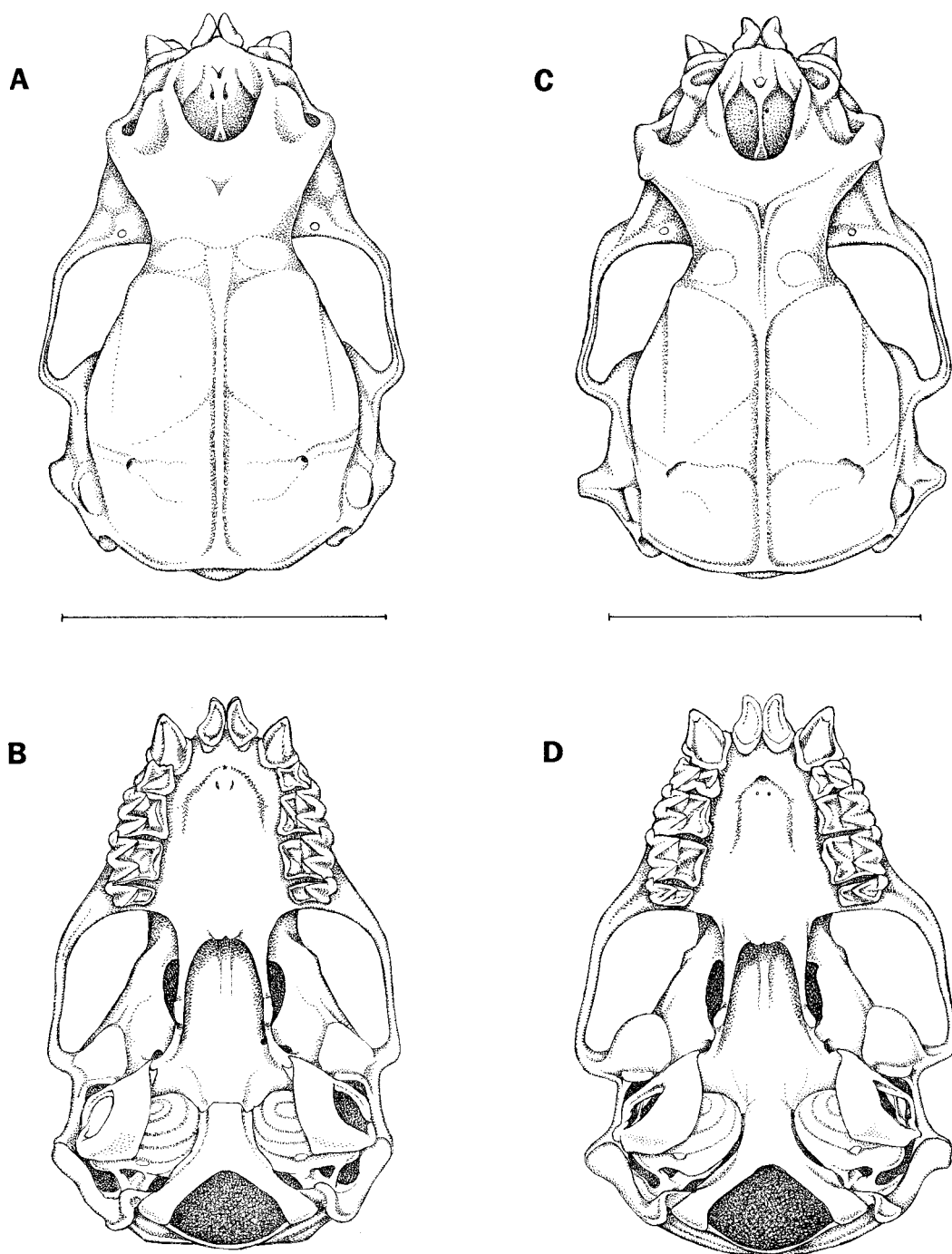


Fig. 59. Dorsal (A) and ventral (B) views of the skull of *Molossops pararus* (AMNH 267535; male) from Paracou. Dorsal (C) and ventral (D) views of the skull of the holotype of *M. greenhalli* (AMNH 175326; male) from Trinidad. Note species differences in size and cranial proportions. Scale bars = 10 mm.

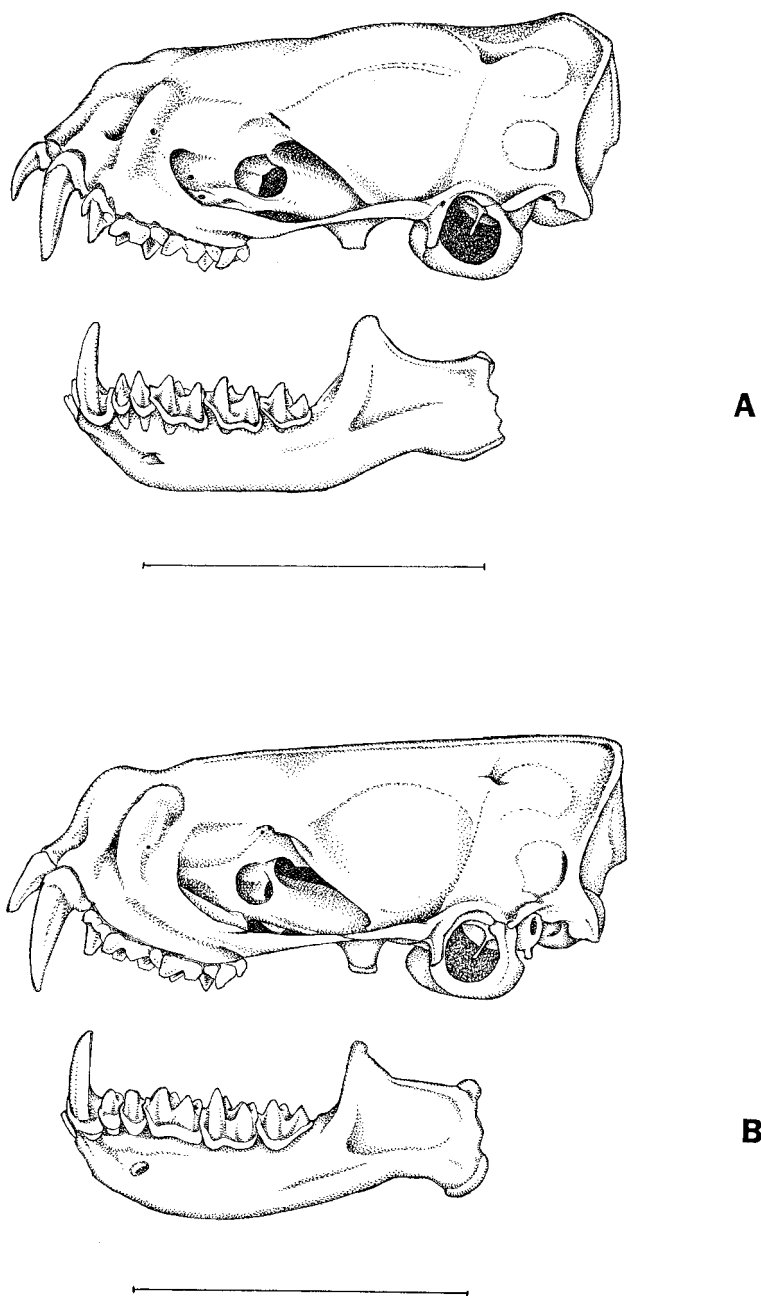


Fig. 60. Lateral views of the skull and lower jaw of (A) *Molossops paranus* (AMNH 267535; male) and (B) the holotype *M. greenhalli* (AMNH 175326; male). Scale bars = 10 mm.

Molossops paranus can be distinguished unambiguously from other members of the subgenus *Cynomops* by external and craniodental traits summarized in table 60. *Molossops paranus* differs from *M. abrasus* in size and dorsal fur pattern, and it differs from *M. greenhalli* in the development of fur patches on the forearm and wing membranes and in many skull dimensions. Finally, *M. paranus* differs from *M. planirostris* in coloration of the ventral fur and in the development of fur patches on the forearm and wing membranes.

Another named form that requires consideration is *Molossops milleri* Osgood, which was based on a single female with a dark venter collected in Peru. Osgood (1914) distinguished *milleri* from *paranus* on the basis of size; however, the holotype of *milleri* is a female and that of *paranus* a male, so sexual dimorphism could be an alternative explanation. This hypothesis seems supported by our examination of a small series of *M. paranus* collected at one locality in Guyana by Brock Fenton and his students in 1970. These specimens appear identical in terms of pelage color, development of fur patches on the wings, and other qualitative features. However, the single female (ROM 57337) is much smaller than the two males (ROM 57338, 57375). Measurements of the Guyanan female correspond closely to those of the holotype of *milleri*, while those of the Guyanan males are very similar to those of the holotype of *paranus*. Accordingly, we conclude that *milleri* and *paranus* represent a single species for which the oldest name is *Molossops paranus* Thomas.

Our Paracou specimen agrees closely with Thomas's (1901b) original description of *Molossops paranus*, and clearly differs from the original descriptions of *M. planirostris* (Peters, 1865b) and *M. greenhalli* (Goodwin, 1958). Two females (CM 64378, 64379) from Grassalco, Surinam, referred to *M. greenhalli* by Williams and Genoways (1980a, 1980b) and another (AMNH 79745) from near Manaus, Brazil, referred to *M. planirostris* by Williams and Genoways (1980b) appear to represent *M. paranus* based on ventral coloration and cranial dimensions.

Although our Paracou specimen represents the first report of *Molossops paranus* from

French Guiana, it may not be the first time that this species has been collected there. Brosset and Charles-Dominique (1990: 544) described a peculiarly dimorphic series of male *Molossops* collected at one locality, noting that "when considered separately, the larger and smaller specimens could be classified at first glance as different species." Despite striking differences in cranial morphology and body weight that permitted subdivision of the series into "type A" and "type B" groups, Brosset and Charles-Dominique identified all seven individuals as *M. greenhalli*. This was justified as follows: "We place in the same taxonomic unity these dissimilar specimens because in both types, the color of the fur, the shape of the ears, tragus, antitragus, tail, wings, the length of the tooth-rows, the shape and size of the molars are similar."

We are unaware of any consistent differences among *Molossops greenhalli*, *M. paranus*, and *M. planirostris* in shape of the ears, tragus, antitragus, tail, wings, length of the toothrows, or shape or size of the molars, and conclude that these features are not useful for distinguishing the smaller species of the subgenus *Cynomops*. The cranial characters that are useful for distinguishing some species involve dimensions of the skull other than those of the dentition (tables 60, 61). Our examination of Brosset and Charles-Dominique's (1990) illustrations and measurements suggest that the smaller form ("type A") probably represents *M. paranus*, while the larger form ("type B") probably represents *M. greenhalli*. A specimen identified as *Molossops planirostris* was also collected (op. cit.) at the same locality, so more detailed comparisons of this material, which is remarkably extensive for a single-locality sample of *Cynomops*, may be particularly informative about species limits in the subgenus.

FIELD OBSERVATIONS: Our single specimen of *Molossops paranus* was caught in a mist-net 18–21 m above a narrow dirt road.

Molossus

The lack of modern revisionary treatment of the South American forms of *Molossus* is a major impediment for identification. We

found several references to be useful, however, including Miller (1913), Goodwin and Greenhall (1961, 1964), Husson (1962, 1978) and, especially, Dolan (1989). In addition, we consulted original descriptions and available holotypes to confirm our species determinations.

Molossus barnesi Thomas

Figures 61–63

VOUCHER MATERIAL: 2 females (AMNH *269105; MNHN *1995.951); see table 63 for measurements.

IDENTIFICATION: Thomas (1905a) originally described *Molossus barnesi*¹⁷ from a single female specimen collected at Cayenne, French Guiana. Thomas noted that *M. barnesi* could be distinguished from other small *Molossus* species based on length of the dorsal fur (shorter in *barnesi*), color of the fur (lighter in *barnesi*), height and ribbing of the muzzle (both less pronounced in *barnesi*), length of the forearm and hind leg (both shorter in *barnesi*), and degree of inflation of the braincase (greater in *barnesi*). Thomas (1905a) particularly noted that *barnesi* could be easily distinguished from specimens of *M. obscurus* (= *M. molossus*) collected in the same area based on length of the forearm (33.7 mm in *barnesi*, 39.0–40.0 in *obscurus*).

No specimens other than the holotype have been referred directly to *Molossus barnesi*. However, Cabrera (1958) suggested that *M. cherriei* Allen (1916) from the Mato Grosso might be a junior synonym based on the published description. Cabrera likewise noted that a small specimen identified by Vieira (1942) as *M. obscurus* from Manaus might also represent *M. barnesi*.

Although Cabrera (1958) and Husson (1962) recognized *Molossus barnesi* as a distinct species, several recent authors have not.

¹⁷ The specific epithet was spelled two ways in Thomas's (1905a) account: "*Burnesi*" (p. 584) and "*Barnesi*" (p. 585). As indicated by Cabrera (1958), the former was clearly a typographic error and as such must be considered an incorrect original spelling (see also Carter and Dolan, 1978). According to Gardner and Farrell (1990), Cabrera was the first reviser, so Miller's (1913) prior use of *burnesi* is nomenclaturally irrelevant (contra Husson, 1962).

Freeman (1981) listed *barnesi* (which she spelled "*burnsei*") as a synonym of *M. molossus*, Brosset and Charles-Dominique (1990) considered *barnesi* a synonym of *M. m. crassicaudatus*, and Koopman (1994) listed *barnesi* as a valid subspecies of *M. molossus*. However, none of these authors presented any justification for treating *M. barnesi* and *M. molossus* as conspecific.

In contrast to these taxonomic assessments, we conclude that *Molossus barnesi* and *M. molossus* are distinct species. Among other characters, these species can be distinguished by their upper incisors, which taper to a set of pincers in *molossus*, whereas in *barnesi* they form a flattened bladelike or spatulate array (figs. 61, 63). Measurement comparisons (table 63) demonstrate that our Paracou specimens of *barnesi* and *molossus* can be distinguished unambiguously by forearm length, tibia length, tail length, condyloincisive length, mastoid breadth, and length of the maxillary tooththrow. *Molossus barnesi* is the smaller of the two species in all dimensions except tail length and mastoid breadth. There is at least some overlap in the other measurements we recorded, but comparisons of mean values suggest that *molossus* has a longer hindfoot, longer skull, narrower braincase, and narrower postorbital region than does *barnesi* (table 63). In addition, length of the dorsal fur is different (3–4 mm in *molossus*, ≤ 2 mm in *barnesi*), as is color and banding of the fur. In our Paracou material of *molossus*, the dorsal fur is dark brown with a white base that comprises roughly two-thirds the length of the hairs in the shoulder region and one-half the length of the hairs over the lower back; the ventral fur is slightly lighter brown, also with an extensive white base. In contrast, the dorsal fur in our specimens of *barnesi* is reddish brown with a white base that comprises approximately one-half the length of the hairs in the shoulder region and somewhat less over the lower back; the ventral fur is a slightly paler reddish brown with little or no white base except in the throat region. We found no obvious differences between these species in ear or facial morphology.

In her revision of the Central American species of *Molossus*, Dolan (1989) treated *barnesi* as a junior synonym of *M. coibensis*

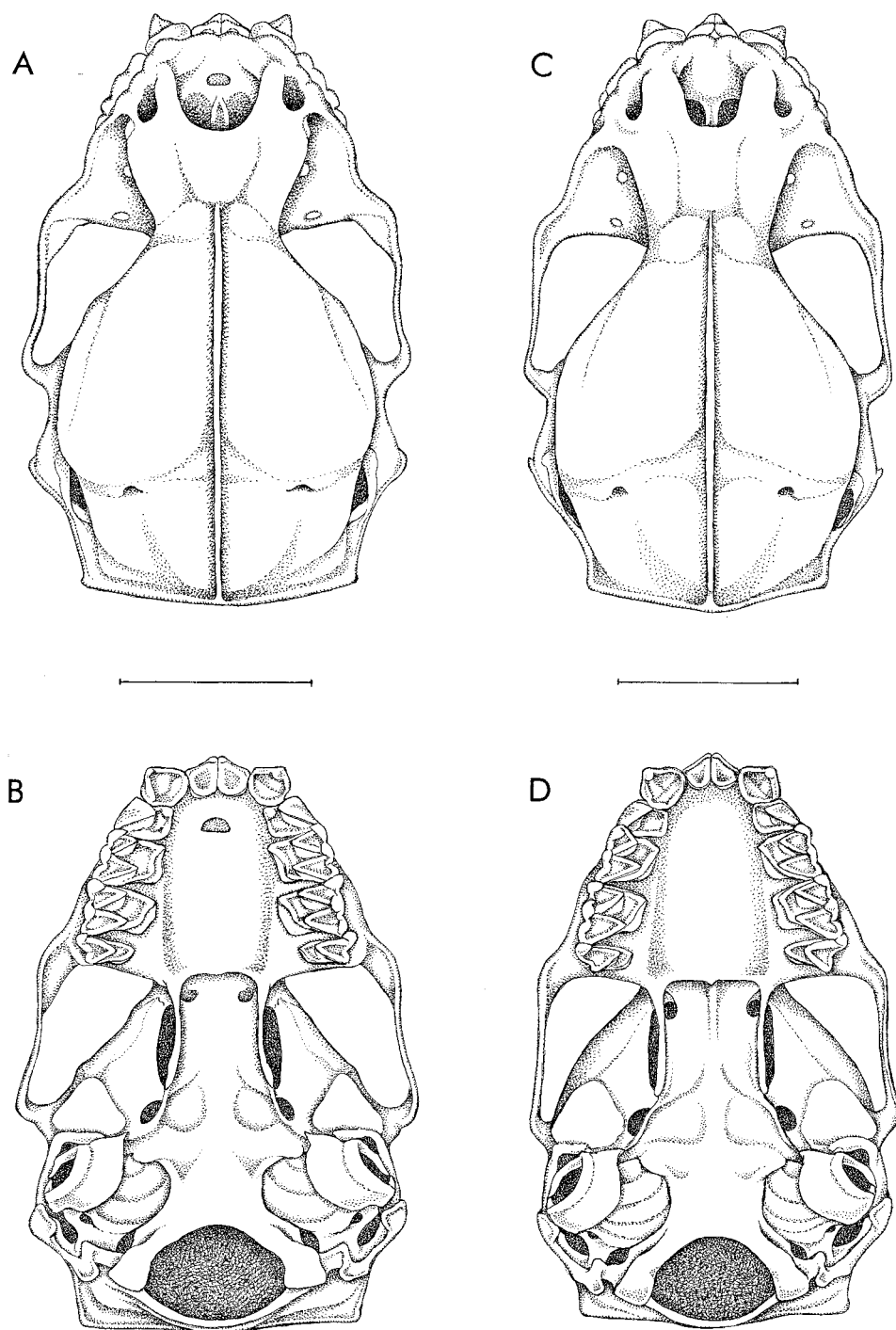


Fig. 61. Dorsal (A) and ventral (B) views of the skull of *Molossus barnesi* (AMNH 269105; female) from Paracou. Dorsal (C) and ventral (D) views of the skull of *M. molossus* (AMNH 269102; female) from Paracou. Note species differences in size, relative breadths of the postorbital region and braincase, and incisor morphology. Scale bars = 10 mm.

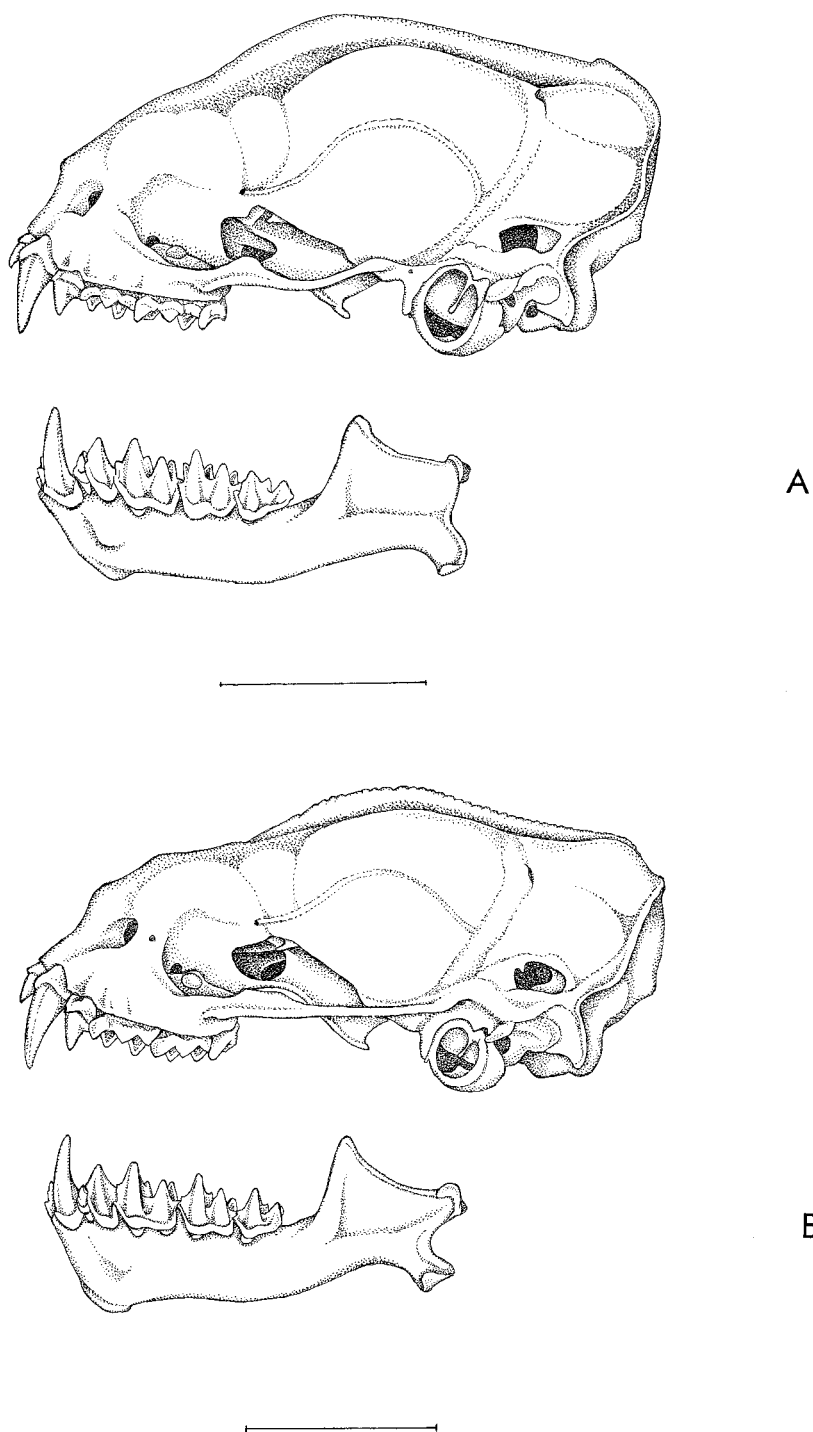


Fig. 62. Lateral views of the skull and lower jaw of (A) *Molossus barnesi* (AMNH 269105; female) and (B) *M. molossus* (AMNH 269102; female). Scale bars = 10 mm.

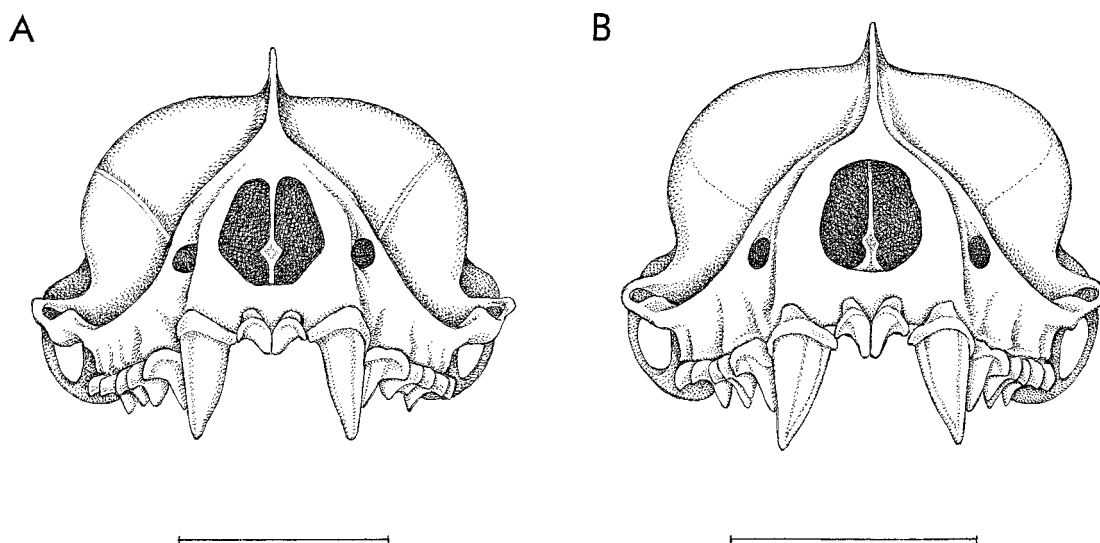


Fig. 63. Anterior view of the skull and upper dentition of (A) *Molossus barnesi* (AMNH 269105; female) and (B) *M. molossus* (AMNH 269102; female). Note the species difference in shape of the upper incisors, which are spatulate in *barnesi* but taper to pincerlike points in *molossus*. Scale bars = 5 mm.

TABLE 63
Measurements^a of Small *Molossus* Collected at Paracou

	<i>Molossus barnesi</i>	<i>Molossus molossus</i>
Number/Sex	2 females	17 females 8 males
Weight	14.8 (13.2–16.4) 2	13.5 (11.3–15.2) 17 14.9 (12.7–17.4) 8
Total length	98.0 (93.0–103.0) 2	100.5 (96.0–105.0) 17 100.8 (95.0–105.0) 8
Tail length	43.0 (43.0–43.0) 2	37.5 (35.0–40.0) 17 37.8 (34.0–44.0) 8
Hind foot length	10.0 (9.0–11.0) 2	11.8 (10.0–13.0) 17 11.3 (9.0–13.0) 8
Ear length	13.0 (13.0–13.0) 2	12.7 (12.0–13.0) 17 13.0 (13.0–13.0) 8
Forearm length	34.7 (34.4–35.0) 2	38.8 (37.6–39.7) 17 38.8 (37.6–39.9) 8
Tibia length	10.9 (10.8–10.9) 2	13.5 (11.3–15.2) 17 12.2 (11.5–12.5) 17
Greatest length of skull	16.14 (16.09–16.19) 2	16.37 (16.06–16.75) 8 17.06 (16.74–17.55) 5
Condylolincisive length	14.78 (14.70–14.85) 2	15.33 (14.92–15.72) 8 15.88 (15.70–16.08) 5
Postorbital breadth	3.80 (3.75–3.85) 2	3.62 (3.45–3.75) 8 3.60 (3.41–3.77) 5
Braincase breadth	8.93 (8.83–9.03) 2	8.71 (8.45–9.03) 8 8.94 (8.70–9.15) 5
Mastoid breadth	10.52 (10.50–10.53) 2	9.93 (9.67–10.11) 8 10.30 (9.98–10.63) 5
Zygomatic breadth	10.64 (10.61–10.66) 2	10.40 (10.02–10.70) 8 10.81 (10.36–11.07) 5
Maxillary tooththrow length	5.56 (5.53–5.58) 2	5.86 (5.74–5.99) 8 5.87 (5.71–5.97) 5
Breadth across molars	7.64 (7.59–7.68) 2	7.60 (7.44–7.77) 8 7.68 (7.41–7.77) 5

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

TABLE 64
Measurements^a of Holotypes of Selected Named Forms of Small *Molossus*

	<i>Molossus barnesi</i> ^b BMNH 5.1.8.7	<i>Molossus cherriei</i> ^c AMNH 36669	<i>Molossus coibensis</i> ^c AMNH 18731	<i>Molossus bondae</i> ^c AMNH 23661	<i>Molossus daulensis</i> ^c AMNH 36257	<i>Molossus debilis</i> ^c USNM 110935	<i>Molossus pygmaeus</i> ^c USNM 102104	<i>Molossus verrilli</i> ^c AMNH 25764
Sex	female	female	male	female	male	female	female	male
Total length	84.0	—	—	—	—	—	—	—
Tail length	31.0	—	—	—	—	—	—	—
Hind foot length	—	8.0	8.0	11.0	9.0	—	—	—
Ear length	—	—	—	—	—	—	—	—
Forearm length	33.8	33.3	35.5	40.1	—	38.3	36.1	38.9
Tibia length	11.6	—	—	—	12.0	12.6	11.5	—
Greatest length of skull	16.6	—	15.90	17.89	16.60	15.13	14.72	16.61
Condylolincisive length	—	—	14.88	16.52	15.20	14.06	13.55	—
Postorbital breadth	3.9	—	3.86	4.00	3.63	3.18	3.02	3.90
Braincase breadth	8.8	—	8.36	9.42	8.70	8.35	7.69	8.95
Mastoid breadth	10.0	—	—	11.13	9.71	9.19	9.03	10.38
Zygomatic breadth	10.7	—	10.57	11.46	10.07	—	—	—
Maxillary toothrow length	5.9	—	5.99	6.61	5.74	5.16	5.31	5.56
Breadth across molars	7.3	—	7.95	8.30	7.32	6.75	6.79	7.68

^a All measurements are recorded in millimeters. See text for a description of measurement methods.

^b Measurements reported by Thomas (1905a) and Carter and Dolan (1978).

^c All craniodental, hind foot, forearm, and tibia measurements were made by NBS; other external measurements were taken from original tags.

Allen (1904) based on measurement data and the unusual spatulate form of the upper incisors. Our comparisons of Thomas' (1905a) measurements of the female holotype of *barnesi* (table 64) with measurements of female *coibensis* from Central America (in Dolan, 1989) confirm that *barnesi* falls within the range of variation reported for *coibensis* in all standard measurements. However, Dolan (1989: 59) also noted that

J. E. Hill of the British Museum graciously compared Panamanian *coibensis* collected during this investigation with the holotype of *M. barnesi* and noted no differences in the construction of the upper incisors (personal communication). However, based on variation in the extent of the white basal band in the dorsal fur, features of the basisphenoid pits, breadth of the mesopterygoid canal, and absence of geographically intermediate populations, Hill argued for continued recognition of *M. barnesi*.

We compared our material of *Molossus barnesi* with the holotype of *M. coibensis* (AMNH 18731) and with 10 additional specimens of *coibensis* from Panama (AMNH 18732, 18733, 18738, 31432, 31435, 31436, 63800, 173919, 183864, 183867) and found

consistent differences in the same pelage and cranial features mentioned by Hill. The white base of the dorsal fur over the shoulders comprises less than one-fourth of the length of the hair in *coibensis*, but approximately one-half in *barnesi*. The mesopterygoid canal is wider in *barnesi* than in *coibensis*, and the bony ridge separating the right and left basisphenoid pits is also wider in *barnesi* than in *coibensis*. On the basis of these features, we agree with Hill and conclude that *coibensis* and *barnesi* represent distinct species.

To further check the identity of our material, we examined the holotypes of *Molossus bondae* (AMNH 23661), *M. cherriei* (AMNH 36669), *M. daulensis* (AMNH 36257), *M. debilis* (USNM 110935), *M. pygmaeus* (USNM 102104), and *M. verrilli* (AMNH 25764), and reviewed literature accounts for these taxa as well as for *M. aztecus*, *M. crassicaudatus*, *M. fuliginosus*, *M. fortis*, *M. lambi*, *M. longicaudatus*, *M. minor*, *M. major*, *M. molossus*, *M. obscurus*, and *M. tropidorhynchus* (Saussure, 1860; Miller,

1900, 1913; Allen, 1904, 1916; Thomas, 1905a; Husson, 1962, 1978; Gardner, 1966; Carter and Dolan, 1978; Genoways et al., 1981; Dolan, 1989; Brosset and Charles-Dominique, 1990). The taxonomic history of *M. molossus* is complex, and we did not attempt to address the many problems of synonymy that remain unresolved (see summaries in Husson [1962] and Dolan [1989]). Instead, we followed Dolan (1989) in recognizing the following as synonyms of *Molossus molossus*: *crassicaudatus*, *daulensis*, *debilis*, *fortis*, *fuliginosus*, *longicaudatus*, *milleri*, *minor*, *major*, *obscurus*, *pygmaeus*, *tropidorhynchus*, and *verrilli*.

Morphological features distinguishing *Molossus barnesi* from all named forms of *M. molossus* include the differences in fur length, extent of banding of the dorsal fur, and incisor morphology mentioned earlier; differences in external and craniodental measurements likewise separate these species where they occur sympatrically (see summary above). *Molossus bondae* resembles *M. coibensis* and *M. barnesi* in length and color of the fur, general shape of the skull, and incisor morphology; however, *bondae* differs from both *barnesi* and *coibensis* by its larger size and unicolored dorsal fur (Dolan, 1989). The affinities of *M. cherriei* are difficult to assess since the skull of the holotype is missing, but we agree with Dolan's observation that forearm length, pelage length and coloration, and presence of a minute white band at the base of the hairs suggest that *cherriei* is a junior synonym of *coibensis*. *Molossus aztecus* from northern Central America apparently represents a distinct species distinguished from *barnesi* by larger size in most dimensions and by having shorter white bases on the dorsal hairs (for a summary of characters of *aztecus* see Dolan, 1989). The status of *M. lambi* is more difficult to assess. Originally named by Gardner (1966) as a subspecies of *aztecus*, *lambi* was recognized as a junior synonym of *coibensis* by Dolan (1989) based on pelage similarity and measurement data. We tentatively agree with Dolan's assessment although we have not seen the holotype of *lambi*.

FIELD OBSERVATIONS: Both of our specimens of *Molossus barnesi* were captured in ground-level mistnets over roadside puddles.

Molossus molossus (Pallas)

Figures 61–63

VOUCHER MATERIAL: 18 females (AMNH *267242, *267243, *267244, *267245, *267246, *267247, *267252, *267253, *267254, *267255, *267256, *269102; MNHN 1995.964, *1995.965, *1995.966, *1995.967, *1995.968, *1995.969), 8 males (AMNH *266374, *267241, *267248, *267250, *267251, *267261; MNHN *1995.970, *1995.971), and 1 individual of indeterminate sex (MNHN 1995.963; individual found dead); see table 63 for measurements.

IDENTIFICATION: As described above, our collections from Paracou include two small *Molossus* species, *M. barnesi* and *M. molossus*, that can be easily distinguished based on features of the pelage and dentition, and by craniodental and external measurements. Our voucher material of *Molossus molossus* corresponds closely with Husson's (1962, 1978) description of this species in Surinam, although our 25 adults include a few individuals that are slightly smaller than any in his series.

The subspecies nomenclature for *Molossus molossus* is complex (see discussion in Dolan, 1989) and has been confused by the inclusion of several distinct species (e.g., *M. aztecus*, *M. barnesi*, *M. coibensis*) in recent classifications (e.g., Freeman, 1981; Hall, 1981; Koopman, 1994). Husson (1962) restricted the type locality of *M. molossus* to Martinique, so *M. m. molossus* is clearly the appropriate name for populations in the southern Lesser Antilles (Hall, 1981; Dolan, 1989). Hall (1981) and Dolan (1989) also applied this name to populations on the north coast of South America (e.g., in Venezuela). However, Dolan (1989: 64) noted that, should additional collecting demonstrate differences between populations in the Lesser Antilles and those on the adjacent mainland, then the correct subspecies name for the latter "would be *M. m. minor* Kerr, 1792, with *M. longicaudatus* Geoffroy, 1805, *M. pygmaeus* Miller, 1900, and *M. daulensis* J. A. Allen, 1916 as junior synonyms."

We compared measurements of our Paracou material (table 63) with published measurements of several large series of *M. mol-*

losus from populations in the Lesser Antilles (in Genoways et al., 1981) and found few differences. Measurements of males and females from Paracou fall within the range of variation reported for each sex in the Lesser Antilles. However, mean values of several measurements (forearm length, postorbital breadth, mastoid breadth, zygomatic breadth, maxillary tooththrow length) for Paracou females slightly exceed (by 0.1–0.2 mm) the corresponding means reported by Genoways et al. (1981) for Lesser Antillean females. No such pattern was seen with male measurements. In our view, this is trivial geographic variation that does not deserve recognition at any taxonomic level. Although we do not advocate any trinomial nomenclature for *M. molossus*, if subspecies were to be recognized the French Guianan population would presumably be referable to the nominate form in recognition of the similarities described above.

One final problem involves the specimens referred to this species by Brosset and Charles-Dominique (1990: 547), who noted that “the *Molossus molossus* from French Guiana are remarkable by their small size.” Examination of the measurements they published for five specimens from Piste St.-Élie reveals that one male and two females are much smaller than any in our Paracou sample of *M. molossus* for forearm length and length of the maxillary tooththrow. Measurements of these same individuals, however, compare favorably with our specimens of *M. barnesi*. For example, female forearm length at Paracou is 34.4–35.0 mm for *barnesi* and 37.6–39.7 mm for *molossus*; the two small females from Piste St.-Élie have forearms measuring 34.5–35.2 mm (Brosset and Charles-Dominique, 1990). The small male from St.-Élie has a forearm of 35.0 mm, compared to 37.6–39.9 mm for *molossus* males at Paracou. By contrast, two larger specimens from St.-Élie fall well within the range of variation we observed for *molossus* at Paracou. Plausibly, Brosset and Charles-Dominique’s sample of “*Molossus molossus*” is composed of individuals representing both *M. molossus* and *M. barnesi*.

FIELD OBSERVATIONS: We recorded 222 captures (probably including some recaptures) of *Molossus molossus* at Paracou, of

which 93 were in ground-level mistnets, 104 were in elevated nets, and 24 were at roosts; additionally, we were given a skull found in a storage shed. Of the 93 ground-level mistnet captures, 6 were in manmade clearings and 87 were over roadside puddles. Of the 104 elevated net captures, 97 were made between 7 and 23 m over a narrow dirt road and 7 were made at 35–38 m over a treefall in well-drained primary forest.

Two separate roosting groups were found simultaneously occupying a small wooden shed in a large clearing: one group of 11 females and 4 males was found under the corrugated metal roof, and another group of 8 males and 1 female was found in a box half-filled with tools on the floor (one unsexed bat escaped from this group). All of the bats found in the shed were adults.

Molossus rufus (E. Geoffroy)

Figures 64, 65, 67

VOUCHER MATERIAL: 10 females (AMNH *267266, *267267, *267273, *267539, *268597, *268600, *269101; MNHN *1995.976, *1995.977, *1995.978) and 13 males (AMNH *267263, *267264, *267268, *267269, *267270, *267546, *268595, *268596, *268598; MNHN *1995.979, *1995.980, 1995.981, 1995.982); see table 65 for measurements.

IDENTIFICATION: The history of nomenclature applied to the largest species of *Molossus* is complex, with different authors alternatively recognizing either *M. ater* or *M. rufus* as the correct name. Whereas the epithet *ater* was used by Goodwin (1960), Husson (1962, 1978), Handley (1976), Freeman (1981), Hill (1981), Brosset and Charles-Dominique (1990), and Koopman (1993, 1994) among others, the name *rufus* was applied by Cabrera (1958), Dolan (1989), and Brosset et al. (1996). Both names originate from the same publication (Geoffroy, 1805a). We follow Dolan (1989) in using *rufus* for the largest species of *Molossus* based on her lucid discussion of the historical confusion that led to the *rufus/ater* controversy.

The type locality of *Molossus rufus* was restricted by Miller (1913) to Cayenne, French Guiana. Measurements of the lectotype and paralectotype (both adult males)

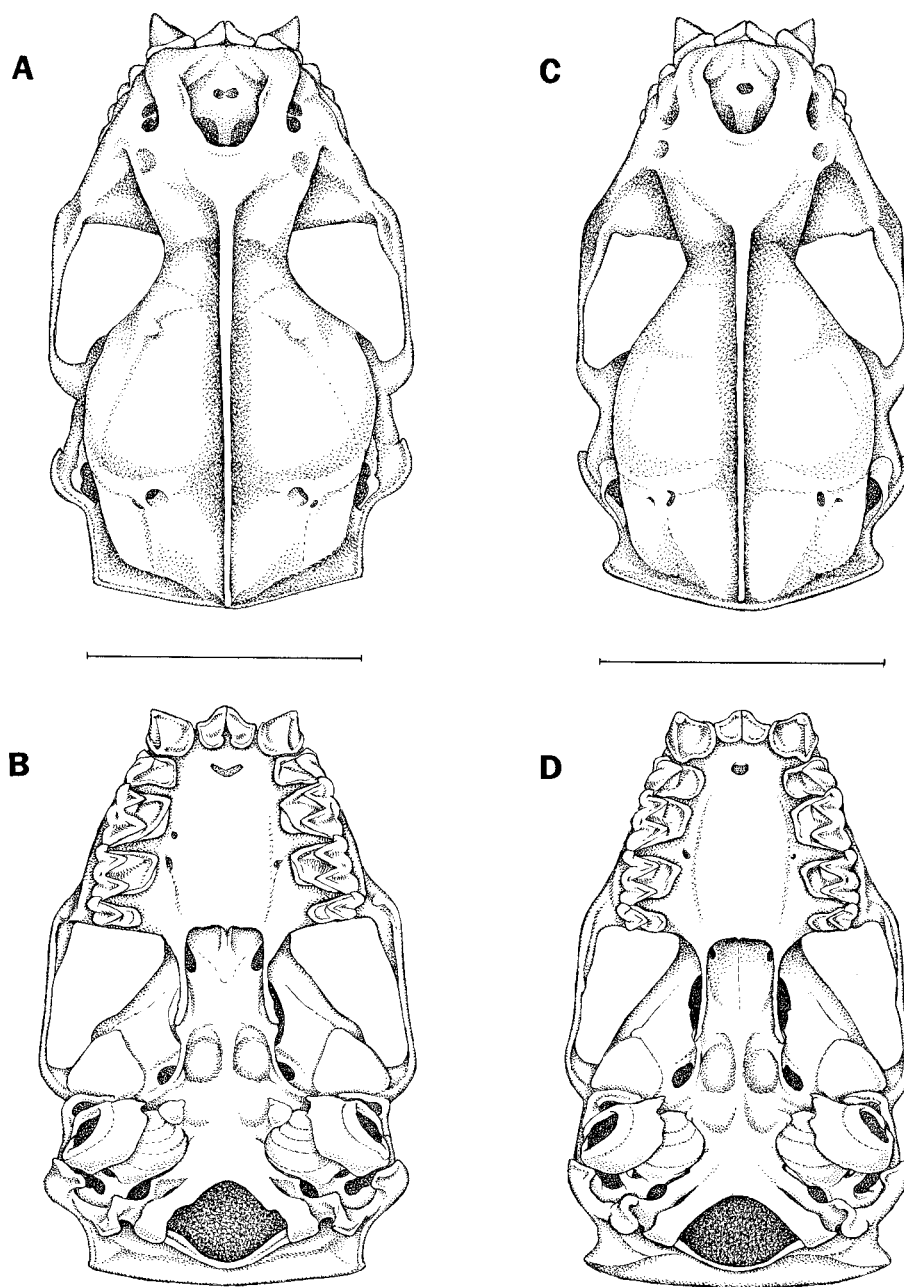


Fig. 64. Dorsal (A) and ventral (B) views of the skull of *Molossus rufus* (AMNH 269101; female) from Paracou. Dorsal (C) and ventral (D) views of the skull of *M. sinaloae* (AMNH 269107; female) from Paracou. Scale bars = 10 mm.

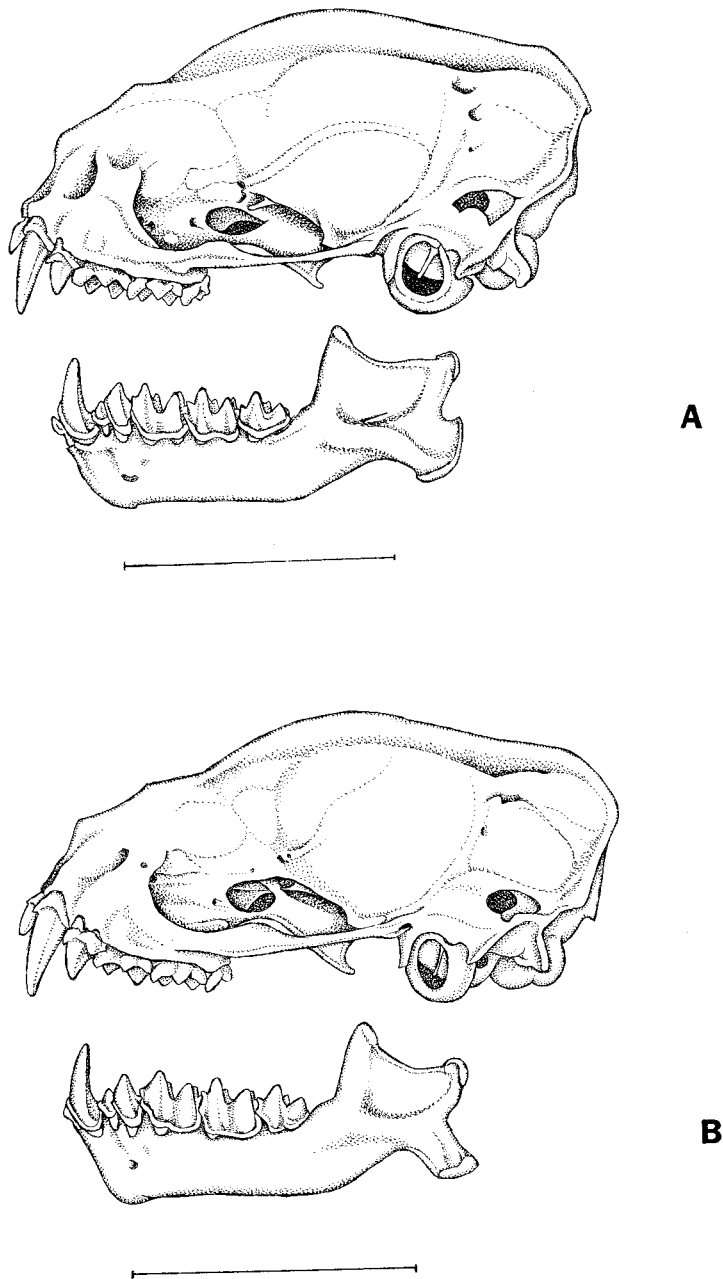


Fig. 65. Lateral views of the skull and lower jaw of (A) *Molossus rufus* (AMNH 269101; female) and (B) *M. sinaloae* (AMNH 269107; female). Scale bars = 10 mm.

provided by Carter and Dolan (1978) fall slightly outside the range of variation among our male specimens from Paracou (tables 65, 66) in some dimensions. Compared with the Paracou males, the lectotype of *rufus* has a

slightly narrower skull (cf. braincase breadth, mastoid breadth, zygomatic breadth, breadth across molars), and its tooththrow is slightly longer. However, this degree of variation is comparable to that found by Dolan (1989)

TABLE 65
Measurements^a of Large *Molossus* Collected at Paracou

	<i>Molossus rufus</i>		<i>Molossus sinaloae</i>	
Number/Sex	10 females	11 males	6 females	6 males
Weight	34.7 (30.5–39.3) 10	40.0 (34.8–42.7) 10	23.1 (18.0–28.8) 6	27.2 (26.0–29.8) 6
Total length	137.8 (131.0–147.0) 10	138.5 (130.0–149.0) 10	127.8 (124.0–130.0) 6	135.5 (129.0–143.0) 6
Tail length	54.9 (47.0–68.0) 10	51.0 (47.0–60.0) 9	48.8 (43.0–58.0) 6	52.7 (45.0–62.0) 6
Hind foot length	15.2 (13.5–16.0) 10	15.7 (14.0–17.0) 10	11.3 (10.0–13.0) 6	13.4 (12.5–14.0) 6
Ear length	16.6 (16.0–17.5) 10	16.8 (15.0–18.0) 10	14.3 (12.0–15.0) 6	14.5 (13.0–15.0) 6
Forearm length	51.4 (50.0–53.4) 10	51.4 (49.4–54.4) 11	49.0 (48.2–49.7) 6	48.5 (47.2–50.0) 6
Tibia length	20.1 (18.5–21.3) 8	19.2 (18.5–20.9) 11	17.0 (16.7–17.2) 6	17.3 (16.8–18.1) 6
Greatest length of skull	21.84 (21.08–22.56) 5	23.12 (22.35–23.72) 8	20.12 (20.02–20.20) 4	20.95 (20.69–21.38) 4
Condylolincisive length	20.07 (19.42–20.57) 5	21.09 (20.58–21.69) 8	18.97 (18.81–19.08) 4	19.68 (19.28–20.10) 4
Postorbital breadth	4.47 (4.39–4.53) 5	4.58 (4.22–4.81) 8	3.98 (3.97–3.98) 4	4.00 (3.90–4.07) 4
Braincase breadth	11.04 (10.87–11.30) 5	11.44 (11.13–11.79) 8	9.72 (9.60–9.89) 4	9.87 (9.66–10.05) 4
Mastoid breadth	13.52 (13.07–13.84) 5	14.20 (13.67–14.57) 8	11.69 (11.52–11.79) 4	12.33 (12.19–12.40) 4
Zygomatic breadth	13.97 (13.46–14.28) 5	14.43 (14.13–14.69) 8	12.11 (12.03–12.18) 4	12.66 (12.22–12.89) 4
Maxillary tooththrow length	7.60 (7.39–7.74) 5	7.85 (7.64–8.19) 8	7.46 (7.35–7.60) 4	7.62 (7.39–7.81) 4
Breadth across molars	10.02 (9.76–10.30) 5	10.24 (10.15–10.34) 8	8.88 (8.76–9.03) 4	9.12 (8.81–9.34) 4

^a Summary statistics (mean, observed range, and sample size) of measurements for each species and sex. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

TABLE 66
Measurements^a of Type Material and Topotypes of Selected Large Species of *Molossus*

	<i>Molossus sinaloae</i> (holotype)	<i>Molossus trinitatus</i> (topotype ^b)	<i>Molossus trinitatus</i> (topotype ^b)	<i>Molossus trinitatus</i> (holotype)	<i>Molossus rufus</i> (lectotype ^c)	<i>Molossus rufus</i> (paralectotype ^c)
	AMNH 24524	AMNH 256340	AMNH 188264	AMNH 179987	MNHN A.428/224	MNHN A.428/224a
Sex	female	female	male	male	male	male
Weight	—	16.0	—	19.0	—	—
Total length	108.0	—	—	—	—	—
Tail length	38.0	—	—	—	—	—
Hind foot length	—	—	—	—	—	—
Ear length	—	—	—	—	—	—
Forearm length	46.2	48.9	50.1	49.4	50.9	49.4
Tibia length	—	—	—	18.6	17.8	17.5
Greatest length of skull	19.54	—	—	21.22	—	—
Condylolincisive length	18.14	18.63	—	19.83	20.8	—
Postorbital breadth	4.01	—	—	4.12	4.4	—
Braincase breadth	9.83	—	—	9.89	11.0	—
Mastoid breadth	11.34	—	—	12.14	13.3	—
Zygomatic breadth	12.23	—	—	12.64	13.8	—
Maxillary tooththrow length	7.07	7.33	7.84	7.78	8.3	—
Breadth across molars	8.88	8.92	—	9.29	9.8	—

^a Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods. All forearm, tibia, and craniodental measurements were made by NBS; other external measurements were taken from original tags.

^b Trinidad and Tobago: Trinidad, Port of Spain.

^c Measurements from Carter and Dolan (1978).

within large series of *rufus* from Central America. Measurements of both sexes of *rufus* from Paracou (table 65) fall within the range of variation of Central American *rufus* measured by Dolan (1989), confirming her observation that this species appears to be morphologically homogeneous across a wide geographic area.

A species similar to and sometimes confused with *Molossus rufus* is *M. pretiosus*. Both are large bats with dark, unicolored pelage that may be brown, red, or black; both have spatulate upper incisors; and both have skulls of similar shape with equivalently developed sagittal crests (Miller, 1902; Dolan, 1989). However, recent authors agree that consistent size differences indicate that *rufus* and *pretiosus* are distinct species (Jones et al., 1971; Freeman, 1981; Dolan, 1989; Koopman, 1994). In South America, *pretiosus* has been reported from Colombia, Venezuela, and Guyana, but not from localities farther east or south (Dolan, 1989; Koopman, 1994). Even the smallest of our specimens of *rufus* from Paracou are too large to be referred to *pretiosus* (for comparative measurements, see Miller, 1902; Jones et al., 1971; Freeman, 1981; Dolan, 1989).

Instead, our collections from Paracou include a different large *Molossus* species, *M. sinaloae*. Although *rufus* and *sinaloae* exhibit overlapping forearm measurements, they can be immediately and unambiguously identified in the field by pelage characters. Whereas the dorsal fur of *rufus* is unicolored brown, black, or red, *sinaloae* has dorsal fur that is bicolored dark brown or reddish brown with a white base comprising approximately one-half of the length of each hair (the base of the fur may appear gray in subadult *sinaloae*, but the dorsal pelage it is still clearly bicolored). Also, whereas adult male *rufus* are either black or red (the two color morphs occurring with roughly equal frequency), male *sinaloae* are brown or reddish brown (never black in our experience, and probably never the rich red color of many male *rufus*). The fur over the shoulders is the same length (2–4 mm) as the rest of the dorsal fur in *rufus*, but a distinct ruff of longer fur (6–7 mm) is present over the neck and shoulders in *sinaloae*. The ventral fur is the same color as the dorsal fur, and the throat

never appears pale in *rufus*, whereas the ventral fur is slightly paler than the dorsal fur and the white hair bases show through the fur of the throat in *sinaloae*. These species additionally exhibit nonoverlapping ranges of variation in body weight and many craniodental measurements (greatest length of skull, condyloincisive length, postorbital breadth, braincase breadth, mastoid breadth, zygomatic breadth, and breadth across molars), with *rufus* consistently larger than *sinaloae* (tables 65, 66).

A confusing case is presented by the measurement data and pelage variation reported for *Molossus "ater"* by Husson (1962). Several specimens referred to *M. ater* by Husson exhibit measurements that fall in the range of *M. sinaloae*, not *M. rufus* (i.e., the two smallest males and the two smallest females in his table XXXI: RMNH 12998, 12999, 13001; ZMH 1632). Husson (1962: 262) also described another specimen (RMNH 13010, for which no measurements were provided) as having "dorsal fur . . . dark brown, the ventral surface being light brown with the exception of the chin and the area surrounding the gular sac, which are whitish as in *Molossus molossus*." In our experience, this description fits *M. sinaloae* but not *M. rufus*. The pelage patterns described by Husson for other specimens in his sample correspond closely with our observations of *M. rufus*. Unfortunately, Husson did not discuss banding (or lack of banding) of the fur in his 1962 discussion of these bats.

Husson (1962) was apparently unaware of Goodwin's (1959) description of *Molossus trinitatus* (which we recognize as a subspecies of *M. sinaloae*; see below) from Trinidad. Husson regularly mentioned extralimital species that might eventually be found in Surinam, and had he known of *M. trinitatus* he would likely have done so. We suspect that Husson, unaware of the potential existence of another large species of *Molossus* in northern South America, actually described a mixed collection of *M. rufus* and *M. sinaloae trinitatus* in his 1962 account of *M. ater*. This hypothesis is supported by close examination of Husson (1978), which was compiled by L. B. Holthuis and M. Boeseman (op. cit.: xiii–xv) from Husson's 1962 monograph and later notes. The 1978 volume

reported two specimens of *M. trinitatus* from Surinam (RMNH 13010 and 13014), both of which had been included in Husson's 1962 treatment of *M. ater*. In what must have been an editorial oversight, however, the description of the pelage of one of these specimens (RMNH 13010) was still included in the 1978 account of *M. ater*.

One effect of the mistakes in Husson's 1962 and 1978 accounts is that the range of size and pelage variation of *Molossus rufus* in the Guiana region has been overestimated, possibly leading to misidentifications in the subsequent literature. For example, Brosset and Charles-Dominique (1990: 546) referred three French Guianan specimens from Piste St.-Élie to this species, a large black male and two much smaller "light brown" females; citing Husson (1962), they attributed the disparities in color and size among these specimens to sexual dimorphism. Comparisons of the published measurements of these individuals with our Paracou data, however, suggest that Brosset and Charles-Dominique's collection of *Molossus* "*ater*" is a mixed series. Whereas the black male from Piste St.-Élie clearly represents *M. rufus* (measurements of this individual falling in every case within 0.1 mm of the range of variation among male *rufus* from Paracou), the "light brown" females from the same locality probably represent *M. sinaloae* (being much smaller than female *rufus* from Paracou in most dimensions).

In our experience, correct identification of females is often more difficult than identification of males since female *Molossus rufus* lack the distinctive red or black pelage of adult males; specimens that we misidentified in the field were invariably female *M. sinaloae* that we initially attributed to *M. rufus*. In contrast to other molossid species that can be distinguished on the basis of forearm measurements, we found that the best way to quickly identify large *Molossus* species was to look for the white hair bases characteristic of both sexes in *M. sinaloae*.

In the event that a trinomial nomenclature for *Molossus rufus* seems warranted, our Paracou material would be unambiguously referable to the nominate form.

FIELD OBSERVATIONS: We recorded 47 captures (possibly including some recaptures) of

Molossus rufus at Paracou, of which 19 were in ground-level mistnets over roadside puddles and 28 were in nets suspended between 13 and 23 m over a narrow dirt road.

Molossus sinaloae J. A. Allen

Figures 64, 65, 67

VOUCHER MATERIAL: 6 females (AMNH *267542, *267543, *269107, *269109; MNHN *1995.974, *1995.975) and 6 males (AMNH *267547, *267549, *269110, *269112; MNHN *1995.972, *1995.973); see table 65 for measurements.

IDENTIFICATION: *Molossus sinaloae* was named by Allen (1906) based on a specimen collected in the Mexican state of Sinaloa, and Goodwin (1959) described *M. trinitatus* from a specimen collected at Port of Spain, Trinidad. Although Goodwin noted that his specimen resembled *sinaloae* in having long bicolored fur, he emphasized differences in size (*trinitatus* is larger) and cranial breadth (the skull is narrower in *trinitatus*). However, the holotype of *sinaloae* (AMNH 24524) is a female while the holotype of *trinitatus* (AMNH 179987) is a male, making such comparisons hard to interpret given the sexual dimorphism characteristic of *Molossus*. Five years later, Goodwin and Greenhall (1964) reported more material of *trinitatus* (including adult male and female topotypes), and reiterated that *trinitatus* and *sinaloae* appeared clearly distinguishable. However, collections of additional material from southern Central America and northern South America have subsequently blurred the distinctions Goodwin observed. Most recent authors have considered *trinitatus* and *sinaloae* to be no more than subspecifically distinct (e.g., Handley, 1966; Ojasti and Linares, 1971; Hall, 1981; Dolan, 1989; Koopman, 1993, 1994).

Contra those authors listed above, Freeman (1981) concluded that *Molossus trinitatus* was clearly distinct from *M. sinaloae* on the basis of a morphometric analysis. In addition to her own observations, Freeman (1981) cited the work of Brown (1967), who noted that the baculum of *trinitatus* is somewhat longer than that of *sinaloae*, and that the base of the baculum in *trinitatus* is more pointed than in any other species of *Molossus*. However, both of these studies were

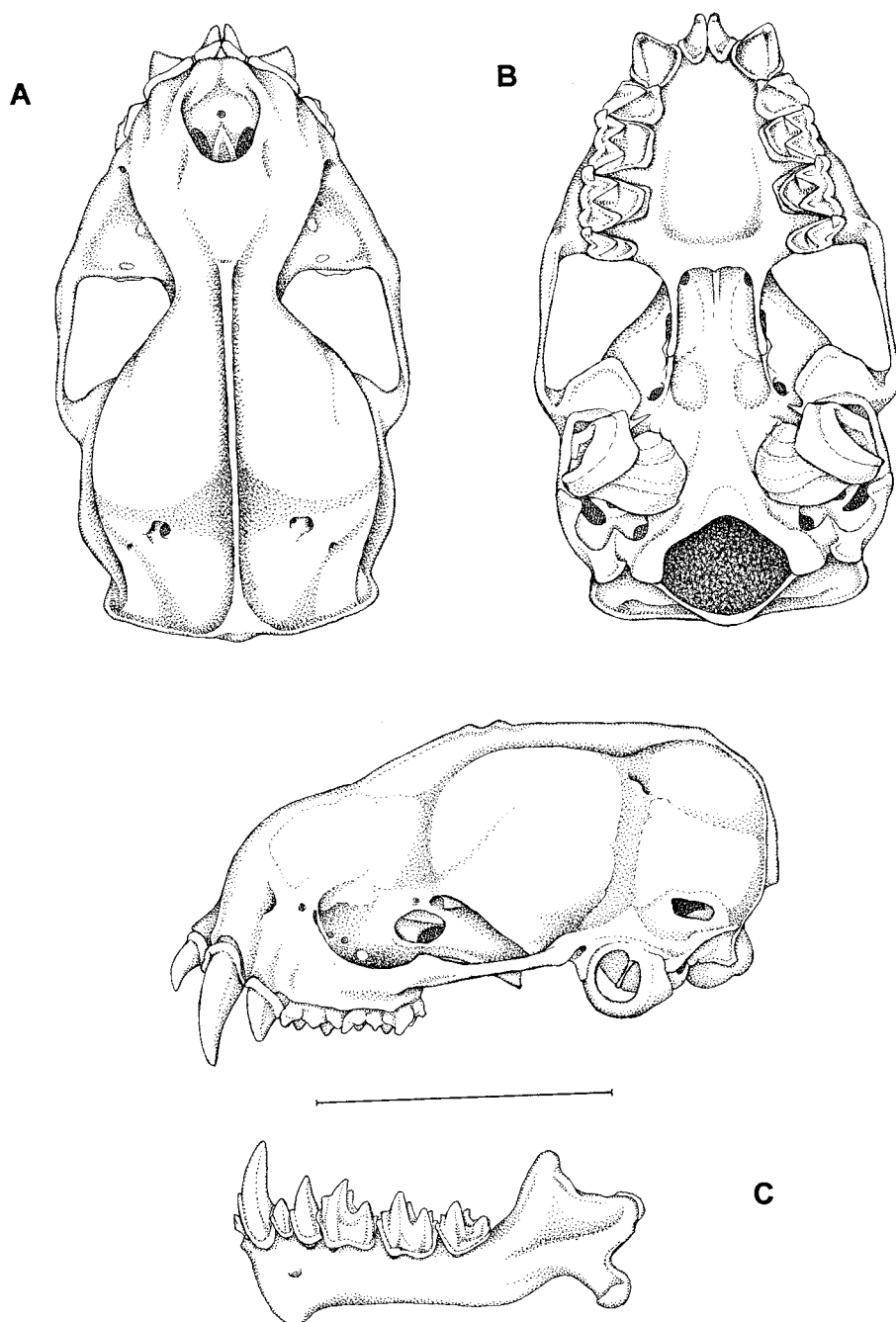


Fig. 66. Dorsal (A), ventral (B), and lateral (C) views of the skull of *Promops centralis* (AMNH 269114; female) from Paracou. Scale bar = 10 mm.

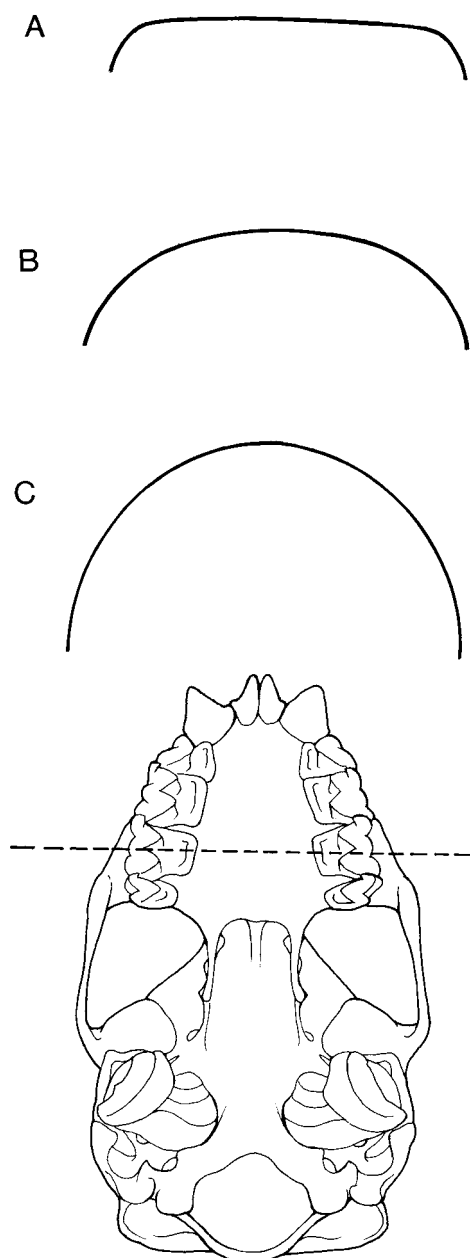


Fig. 67. Comparative palatal cross sections of (A) *Molossus rufus* (AMNH 269101; female), (B) *M. sinaloae* (AMNH 269107; female), and (C) *Promops centralis* (AMNH 269114; female).

based on very small samples of each species drawn from extremes of the geographic range. Dolan (1989) included many more specimens of *sinaloae* in her morphometric analyses, and concluded (op. cit.: 56) that “the position of the holotype of *M. trinitatus*

clearly within the *M. sinaloae* cluster . . . argues against specific recognition.”

To identify our material from Paracou, we compared our specimens (table 65) with the holotypes of *sinaloae* and *trinitatus* (table 66), two topotypes of *trinitatus* (table 66),

specimens of *sinaloae* from Mexico (AMNH 204985, 204986), Honduras (AMNH 265132, 1265133), and Nicaragua (AMNH 41190, 41193, 41195), and measurements of *sinaloae* and *trinitatus* published by Alvarez and Aviña (1964), Jones et al. (1971), Ojasti and Linares (1971), Marinkelle and Cadena (1972), Husson (1978), and Dolan (1989). We were unable to find any characters that unambiguously separate *sinaloae* and *trinitatus*. Although specimens referred to *trinitatus* are usually larger than those referred to *sinaloae*, measurements of our Paracou material overlap in all dimensions with measurements of specimens from Nicaragua reported by Jones et al. (1971). In the absence of a thorough revision, we therefore follow the current consensus and treat *trinitatus* and *sinaloae* as conspecific. Given apparent size differences, recognition of two subspecies (*M. s. sinaloae* and *M. s. trinitatus*) might be justified; if so, our material from Paracou represents the latter.

FIELD OBSERVATIONS: We captured 12 *Molossus sinaloae* at Paracou, all of which were taken in nets suspended 17–23 m over a narrow dirt road.

Promops centralis Thomas

Figures 66, 67

VOUCHER MATERIAL: 2 females (AMNH *269114; MNHN *1995.983); see table 67 for measurements.

IDENTIFICATION: References useful for identifying species of *Promops* include Goodwin and Greenhall (1961, 1962), Ojasti and Linares (1971), and Genoways and Williams (1979), all of which include comparative measurements. Unfortunately, the genus has received no modern revisionary treatment and some vexing taxonomic problems remain.

Promops centralis was originally described by Thomas (1915) based on three specimens from “N. Yucatan,” Mexico. Handley (1966) suggested that *P. occultus* Thomas (1915) from Paraguay and *P. davisoni* Thomas (1921) from Peru might be conspecific with *P. centralis*, but provided no supporting data. Although subsequent authors have accepted this synonymy, most have expressed doubts about the affinities of

TABLE 67
Measurements^a of *Promops centralis*
Collected at Paracou

Number/Sex	2 females
Weight	22.9 (22.8–30.0) 2
Total length	137.5 (130.0–145.0) 2
Tail length	56.0 (46.0–66.0) 2
Hind foot length	13.0 (13.0–13.0) 2
Ear length	14.5 (14.0–15.0) 2
Forearm length	52.8 (52.0–53.5) 2
Tibia length	17.1 (17.0–17.2) 2
Greatest length of skull	20.02 (20.02) 1
Condylolincisive length	19.63 (19.63) 1
Postorbital breadth	3.72 (3.72) 1
Braincase breadth	10.13 (10.13) 1
Mastoid breadth	11.34 (11.34) 1
Zygomatic breadth	12.37 (12.37) 1
Maxillary toothrow length	7.70 (7.70) 1
Breadth across molars	9.13 (8.89–9.36) 2

^a Summary statistics (mean, observed range, and sample size) of measurements. Weight is given in grams; all other measurements are recorded in millimeters. See text for a description of measurement methods.

P. davisoni, which may have affinities with *P. nasutus* instead (Freeman, 1981; Genoways and Williams, 1979; Koopman, 1994). Setting aside specimens from the Pacific coast of Ecuador and Peru (referrable to *davisoni*; Koopman, 1978, 1994), *P. centralis* is now believed to range throughout much of the Neotropics. Whereas *P. c. centralis* is said to occur from Mexico to Surinam (Ojasti and Linares, 1971; Genoways and Williams, 1979; Koopman, 1994), populations from eastern Peru to northern Argentina have been identified as *P. c. occultus* (see Goodwin and Greenhall, 1962; Koopman, 1994).

Our voucher material corresponds closely to published descriptions of *Promops centralis centralis* (e.g., Goodwin and Greenhall, 1961, 1962; Ojasti and Linares, 1971; Genoways and Williams, 1979). The dorsal fur, bicolored dark brown with white only at the base, is longer over the neck and shoulders (ca. 7 mm) than it is over the lower back (4–5 mm). The ventral fur, slightly paler brown in mass effect, is likewise bicolored, with a white base that comprises approximately one-fourth of each hair. The morphology and measurements of the skull and dentition of our specimens fall within the range of vari-

ation described by previous authors (e.g., Goodwin and Greenhall, 1961, 1962; Alvarez and Aviña, 1964; LaVal, 1969; Ojasti and Linares, 1971; Genoways and Williams, 1979). Ojasti and Linares (1971) noted that the tiny anterior upper premolar is absent in the holotype of *P. centralis*, but is present in one paratype and in their specimen from Venezuela. The anterior upper premolar is present on both sides in one of our specimens (AMNH 269114) but is bilaterally absent in the other (MNHN 1995.983).

In the field we initially had difficulty distinguishing female *Molossus rufus* from *Promops centralis* because these bats have a similar dark brown dorsal pelage, and the pale hair bases in our *Promops* were very

short and hard to detect. We also found it hard to see the tiny lower incisors (one pair in *Molossus*, two pairs in *Promops*) in living bats even with the help of a hand lens. However, we found that we could easily separate these species based on the ventral pelage (unicolored brown in *M. rufus*, bicolored brown with distinct white hair bases in *P. centralis*), morphology of the upper incisors (short and spatulate in *M. rufus*, very long and pincerlike in *P. centralis*), and form of the anterior palate (gently arching in *Molossus*, very strongly arched in *Promops*; fig. 67).

FIELD OBSERVATIONS: Both of our specimens of *Promops centralis* were taken in mistnets suspended 17–21 m over a narrow dirt road.

ANALYSES OF SAMPLING

Over the four-year course of our fieldwork we recorded a total of 3126 bat captures at Paracou, of which about 78% were in ground-level mistnets, 10% in elevated mistnets, and 12% at roosts (table 68). Counting only those dates on which we actually captured bats, our total effective inventory time amounted to 168 sampling days. From one to four persons worked together on the bat inventory on any given sampling date, for an aggregate labor total of about 12 person-months from 1991 to 1994.

Combining results from all methods (fig. 68), we initially encountered new species at a rapid and fairly constant average rate of about 0.75 species per sampling day after day 1, producing a nearly linear species accumulation plot for 1991 and 1992. However, new records were added much more slowly in 1993 (0.19 species/day) and 1994 (0.13 species/day), when we experienced many intervals of several consecutive sampling days with no additional species. Because our effective effort per sampling day actually increased from 1991 to 1994 (see below), this decreasing rate presumably resulted from the dwindling number of undetected species that remained in our study area. In total, we captured 78 species of bats at Paracou, the last of which (*Dididurus scutatus*) was taken on sampling day 155.

Although convenient for the purpose of a general overview, graphing species accumulation as the sum of results from all methods over time is not informative about crucial aspects of inventory completeness. In particular, figure 68 is useless for extrapolation or for comparisons with the results of other inventories because days do not represent a uniform sampling process (*sensu* Colwell and Coddington, 1994): we used different methods with varying intensity from day to day, we worked in different habitats on different days, and we worked in different seasons in different years. If distinct sets of species are effectively sampled by using different methods, by working in different habitats, or by working in different seasons, such heterogeneity must be taken into account in assessing species richness and in comparing our results with those of other studies.

SAMPLING RESULTS FROM DIFFERENT METHODS

None of our inventory methods captured all of the bat species known to occur at Paracou (table 69), so exclusive reliance on the results from any one method would necessarily give an incomplete picture of the whole fauna. Beyond this obvious fact, several patterns of methodological bias in our data are noteworthy.

TABLE 68
Summary by Year of Bat Sampling at Paracou

	Sampling days ^a	Mistnet captures ^b			Other captures		Total captures	Species
		Ground ^c	Elevated ^d	Total	Roosts	Misc. ^e		
1991	49	537	0	537	143	5	685	42 ^f
1992	27	591	19	610	95	7	712	55 ^f
1993	47	769	128	897	80	1	978	61 ^f
1994	45	547	157	704	43	4	751	63 ^f
Totals	168	2444	304	2748	361	17	3126	78 ^g

^a Counting only those dates on which bats were actually captured (omitting field time devoted to other inventory activities).

^b Including recaptures (released bats were not marked for identification).

^c 0–3 m above the ground.

^d More than 3 m above the ground.

^e Including captures in harp-traps, specimens shot in flight, salvaged material (e.g., from the digestive tracts of predators), and other miscellaneous records mentioned in the species accounts.

^f Annual total.

^g Project total (1991–1994).

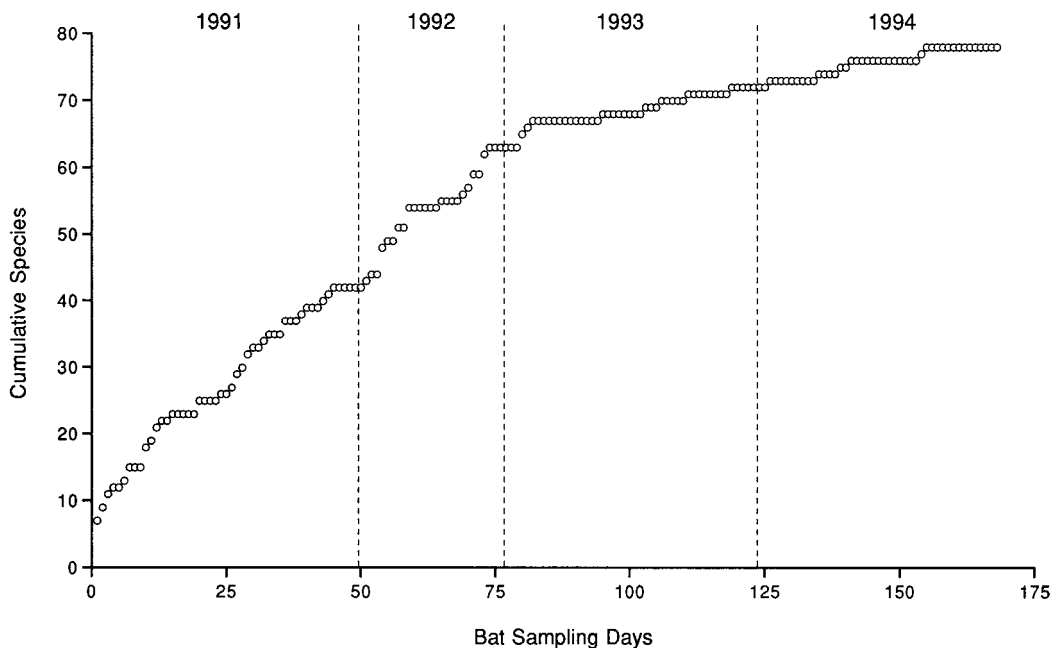


Fig. 68. Species accumulation of bats at Paracou, where we captured 78 species in 168 days of sampling from 1991 to 1994. The results of sampling using all methods (ground-level and elevated mistnetting, searching for roosts, and miscellaneous) are represented in this graph, wherein each plotted point represents one bat-sampling date. We use days as proxy units of sampling effort in order to combine the results of methods that are better represented by other units in figures 69–71. We did not plot our combined results against person-days (an alternative proxy unit of sampling effort) because the participation of different personnel in the bat inventory was hard to quantify meaningfully on a day-to-day basis; had we done so, the flatter terminal phase of our sampling curve would be much extended because more people worked together on bats in 1993–1994 than in 1991–1992.

TABLE 69
Summary of Bat Captures at Paracou by Species^a and Method

Mistnets						Mistnets							
		Ele-							Ele-				
	Ground	vated	Roosts	Misc.	Total		Ground	vated	Roosts	Misc.	Total		
<i>Centronycteris maxi-</i>						<i>Tonatia carrikeri</i>	1	0	0	0	1		
<i>miliani</i>	0	0	1	0	1	<i>Tonatia saurophila</i> ^b	60	1	0	0	61		
<i>Cormura brevirostris</i> ^b	7	12	23	0	42	<i>Tonatia schulzi</i>	7	0	0	0	7		
<i>Diclidurus scutatus</i>	0	1	0	0	1	<i>Tonatia silvicola</i>	11	0	0	0	11		
<i>Peropteryx kappleri</i>	4	5	17	0	26	<i>Trachops cirrhosus</i> ^b	52	0	5	1	58		
<i>Peropteryx leucoptera</i>	1	0	13	0	14	<i>Trinycteris nicefori</i>	9	0	0	0	9		
<i>Peropteryx macrotis</i>	0	0	5	0	5	<i>Vampyrum spectrum</i>	4	0	0	0	4		
<i>Rhynchonycteris naso</i>	0	0	10	0	10	<i>Carollia perspicillata</i> ^b	1049	18	75	2	1144		
<i>Saccopteryx bilineata</i> ^b	14	11	9	1	35	<i>Rhinophylla pumilio</i> ^b	106	2	19	1	128		
<i>Saccopteryx gymnura</i>	2	0	0	0	2	<i>Ametrida centurio</i>	6	4	0	0	10		
<i>Saccopteryx leptura</i> ^b	10	6	9	1	26	<i>Artibeus jamaicensis</i> ^b	71	2	0	0	73		
<i>Pteronotus parnellii</i>	18	0	0	2	20	<i>Artibeus lituratus</i> ^b	40	12	0	1	53		
<i>Noctilio albiventris</i>	1	0	0	0	1	<i>Artibeus obscurus</i> ^b	104	7	6	0	117		
<i>Noctilio leporinus</i>	3	0	0	0	3	<i>Artibeus cinereus</i> ^b	37	1	3	0	41		
<i>Desmodus rotundus</i>	5	0	0	0	5	<i>Artibeus gnomus</i> ^b	51	4	3	1	59		
<i>Diaemus youngi</i>	2	1	0	0	3	<i>Artibeus concolor</i>	22	2	0	0	24		
<i>Anoura caudifera</i>	1	0	0	0	1	<i>Chiroderma trinitatum</i>	11	2	0	0	13		
<i>Choeroniscus minor</i>	7	0	6	0	13	<i>Chiroderma villosus</i>	4	4	0	0	8		
<i>Glossophaga soricina</i> ^b	45	0	11	0	56	<i>Ectophylla macconnelli</i>	1	0	12	0	13		
<i>Lichonycteris obscura</i>	1	0	0	0	1	<i>Platyrrhinus helleri</i>	11	3	0	0	14		
<i>Lonchophylla thomasi</i> ^b	36	1	18	0	55	<i>Sturnira lilium</i> ^b	83	0	0	0	83		
<i>Chrotopterus auritus</i>	5	0	0	0	5	<i>Sturnira tildae</i> ^b	51	3	0	0	54		
<i>Glyphonycteris daviesi</i>	2	0	0	0	2	<i>Uroderma bilobatum</i>	21	0	4	0	25		
<i>Glyphonycteris sylvestris</i>	1	0	0	0	1	<i>Vampyressa brocki</i>	4	3	0	0	7		
<i>Macrophyllum macro-</i>						<i>Furipterus horrens</i>	0	0	12	1	13		
<i>phyllum</i>	0	0	3	0	3	<i>Thyroptera tricolor</i> ^b	3	1	36	0	40		
<i>Micronycteris brosetti</i>	1	0	7	0	8	<i>Eptesicus chiriquinus</i>	2	4	0	0	6		
<i>Micronycteris hirsuta</i>	3	0	6	0	9	<i>Eptesicus furinalis</i>	14	8	1	0	23		
<i>Micronycteris homezi</i>	0	1	0	0	1	<i>Lasiurus blossevillei</i>	1	1	0	0	2		
<i>Micronycteris megalotis</i>	8	0	3	0	11	<i>Myotis nigricans</i>	25	4	0	0	29		
<i>Micronycteris microtis</i>	3	0	17	2	22	<i>Myotis riparius</i>	11	0	0	1	12		
<i>Micronycteris minuta</i>	6	0	0	0	6	<i>Eumops auripendulus</i>	0	3	0	0	3		
<i>Micronycteris schmidt-</i>						<i>Eumops hansae</i>	0	1	0	0	1		
<i>orum</i>	2	0	0	0	2	<i>Molossops abrasus</i>	0	1	0	0	1		
<i>Mimon bennettii</i>	1	0	1	0	2	<i>Molossops paranus</i>	0	1	0	0	1		
<i>Mimon crenulatum</i>	17	0	0	0	17	<i>Molossus barnesi</i>	2	0	0	0	2		
<i>Phylloderma stenops</i>	8	0	0	0	8	<i>Molossus molossus</i> ^b	93	104	24	1	222		
<i>Phyllostomus discolor</i>	14	3	0	0	17	<i>Molossus rufus</i> ^b	19	28	0	0	47		
<i>Phyllostomus elongatus</i> ^b	157	1	2	2	162	<i>Molossus sinaloae</i>	0	12	0	0	12		
<i>Phyllostomus hastatus</i> ^b	34	22	0	0	56	<i>Promops centralis</i>	0	2	0	0	2		
<i>Tonatia brasiliense</i>	9	0	0	0	9								

^a Captures of incompletely identified bats (*Dermanura* spp., *Sturnira* spp., *Myotis* spp.) are not tabulated.

^b Tabulated captures may include some recaptures.

GROUND-LEVEL MISTNETTING: This was by far the most intensively used method at Paracou, where we recorded 2444 captures in 24,957 net-meter-hours (nmh) at ground lev-

el (table 70). From 1991 to 1994 we used ground-level nets on 112 nights at 42 different netting sites, for an average usage of about 2.7 nights per site; site usage was high-

TABLE 70
Summary of Mistnet Sampling at Paracou by Net Height and Habitat

	Net-m-hrs	Number of captures ^a	Capture rate ^b	Number of species
Ground-level nets				
Primary forest				
Well-drained forest	6808	567	0.83	41
Swampy forest	8451	659	0.78	43
Creekside forest ^c	2833	309	1.09	41
Treefall openings	533	10	0.19	6
TOTALS, PRIMARY FOREST	18,625	1545	0.83	57
Modified habitats				
Manmade clearings ^d	5288	627	1.19	36
Secondary growth ^e	769	28	0.36	8
Roadside puddles	275	244	8.87	19
TOTALS, MODIFIED HABITATS	6332	899	1.42	42
TOTALS, GROUND-LEVEL	24,957	2444	0.98	65
Elevated nets				
Swampy forest	182	19	1.04	12
Natural openings	590	37	0.63	12
Manmade clearings	1950	248	1.27	34
TOTALS, ELEVATED NETS	2722	304	1.12	39
GRAND TOTALS	27,679	2748	0.99	73

^a Including recaptures.

^b Number of bats per 10 net-m-hrs.

^c Many nets in this habitat were set across streams.

^d Including gardens, plantations, roadways, and clearings around houses.

^e With a closed canopy; including forest disturbed by selective logging.

ly skewed, however, because some productive and convenient locations (e.g., our camp clearing, fig. 2) were netted many times whereas 25 unproductive or remote sites were only netted once. About 75% of our ground-level netting effort (18,625 nmh) and about 63% of our recorded captures in ground-level nets were in primary forest, with the remaining effort and captures distributed among several categories of more-or-less disturbed sites (table 70). On average we captured about one bat per 10 nmh at ground level, but capture rates were notably higher over roadside puddles than in other habitats.

Combining ground-level mistnet records from all habitats (fig. 69), we observed a fluctuating but nonetheless rather steady initial rate of species accumulation (about 1

new species per 20 captures after sampling day 1) until we had recorded 58 species and 1054 captures in 57 nights of ground-level netting. Subsequent netting more than doubled the number of ground-level captures but produced only seven additional species. In total, we captured 65 species in ground-level mistnets at Paracou.

Familial representation in our ground-level mistnet data is highly uneven: phyllostomids accounted for 2184 recorded captures (89% of the total), followed distantly by molossids with 114 captures (5%), vespertilionids with 53 captures (2%), emballonurids with 38 captures (2%), and mormoopids with 18 captures (<1%). Noctilionids and thyropterids were seldom captured, and furipterids were never caught.

Of the 65 species taken in ground-level

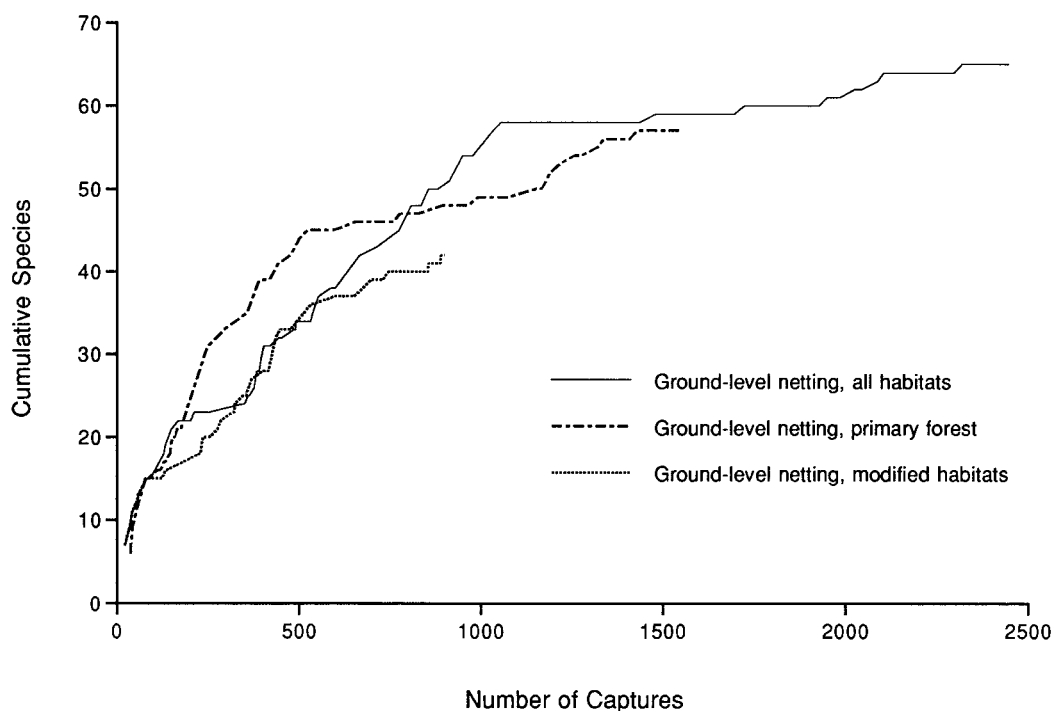


Fig. 69. Species accumulation by ground-level mistnetting at Paracou from 1991 to 1994. Number of captures is the appropriate measure of sampling effort for this method because each captured bat is equally informative about local diversity. By contrast, plotting species accumulation against net-nights or net-hours would be misleading because nets vary tremendously in sampling effectiveness depending on when and where they are used.

mistnets, *Carollia perspicillata* was by far the most frequently recorded, with 1049 recorded captures (43% of the total), followed by *Phyllostomus elongatus* with 157 (6%), *Rhinophylla pumilio* with 106 (4%), *Artibeus obscurus* with 104 (4%), *Molossus molossus* with 93 (4%), and *Sturnira lilium* with 83 (3%). Other than *M. molossus*, the only non-phyllotomid species accounting for 1% or more of captures in ground-level nets was *Myotis nigricans*. Significantly, both *M. molossus* and *M. nigricans* were taken almost exclusively over roadside puddles.

Twenty-three species captured in ground-level mistnets at Paracou were not taken by elevated mistnetting or by searching for roosts. Whereas most of these were uncommon species, *Sturnira lilium* is a conspicuous exception. Frequently captured in ground-level nets in modified habitats, *S. lilium* was never taken in high nets or at roosts. Other

taxa that were often captured in ground-level nets but were seldom or never captured in elevated nets or at roosts include *Pteronotus parnellii*, *Mimon crenulatum*, *Phyllostomus elongatus*, *Tonatia saurophila*, *Trachops cirrhosus*, *Artibeus jamaicensis*, and *Sturnira tildae*.

Of 13 species captured in elevated nets or at roosts but not in ground-level nets, only two (*Macrophyllum macrophyllum* and *Microonycteris homezi*) are phyllostomids. The remainder (four emballonurids, *Furipterus horrens*, and six molossids) are all aerial insectivores. Seven of these (*Diclidurus scutatus* and all six molossids) usually fly above the range of ground-level nets, and the other four (*Centronycteris maximiliani*, *Peropteryx macrotis*, *Rhynchonycteris naso*, *Furipterus horrens*) are very small-bodied species that are seldom caught in nets for reasons that are not well understood.

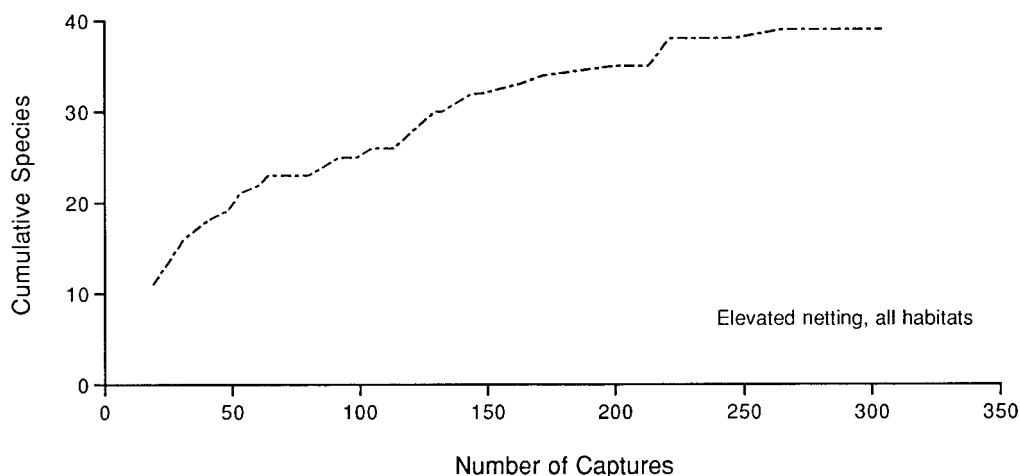


Fig. 70. Species accumulation by elevated mistnetting at Paracou. We first used elevated mistnets in 1992, but most of these data were obtained in 1993–1994. Note the difference in scale between the horizontal axis of this graph and that of figure 69.

ELEVATED MISTNETTING: We recorded 304 captures in 2722 nmh of elevated mistnetting at Paracou (table 70). We first used elevated nets in 1992 (for one night only) and did not begin regular elevated mistnetting until 1993. From 1992 to 1994 we used elevated nets on 46 nights at 8 different netting sites, for an average usage of about 5.8 nights per site. About 82% of our elevated net captures and 72% of our elevated netting effort (1950 nmh) were made at several points along a single road through the forest (fig. 11). Elevated netting over natural treefall openings accounted for only about 12% of our captures and 22% of our effort (590 nmh); we also netted once in the subcanopy of swampy forest. Overall, we made about 1.1 captures per 10 nmh in elevated nets, about the same average rate as in ground-level nets.

Our species accumulation curve for elevated netting in all habitats (fig. 70) illustrates a gradually declining rate without any abrupt transition from an initially steep slope to a well-defined plateau. After our first night of elevated netting, we recorded an average of about 1 new species per 10 captures, or approximately twice the high initial rate of species accumulation in ground-level nets. However, as only one elevated net was generally used per night, our chronological rate of species accumulation in elevated nets was

somewhat slower (about 0.8 species/night) than we experienced using ground-level nets in the early phase of our fieldwork (about 1.0 species/night for 1991–1992).

In contrast to the higher taxonomic composition of ground-level netting records, Molossidae was the family most frequently taken in elevated nets, accounting for 152 captures or about 50% of the total. Phyllostomids were next in frequency, with 97 captures (32%), followed by emballonurids with 35 captures (12%), and vespertilionids with 17 captures (6%). Only one thyropterid was netted above ground level. Mormoopids, noctilionids, and furipterids were never caught in elevated nets.

Tabulating elevated netting records by species and capture height (table 71) reveals that the fauna above ground level is really a mix of understory species that seldom fly much above 10 m and a distinctive assemblage of high-flying bats. *Carollia perspicillata*, for example, was by far the most common species captured in nets suspended between 4 and 10 m above the ground, but we never caught it above 15 m. *Phyllostomus elongatus*, *Tonatia saurophila*, *Rhinophylla pumilio*, *Artibeus jamaicensis*, *A. cinereus*, and *Thyroptera tricolor*, all commonly taken in mistnets or at roosts near ground level, were likewise never taken above 15 m.

TABLE 71
Distribution of Elevated Mistnet Records by
Species and Capture Height^a

	Capture height (m)				Total captures
	4-10	11-15	16-20	>20	
<i>Cormura brevirostris</i>	0	6	3	3	12
<i>Didlidurus scutatus</i>	0	0	1	0	1
<i>Pteropteryx kappleri</i>	0	1	4	0	5
<i>Saccopteryx bilineata</i>	5	4	2	0	11
<i>Saccopteryx leptura</i>	2	1	1	2	6
<i>Diademus youngi</i>	0	0	1	0	1
<i>Lonchophylla thomasi</i>	0	0	1	0	1
<i>Micronycteris homezi</i>	0	0	1	0	1
<i>Phyllostomus discolor</i>	0	2	1	0	3
<i>Phyllostomus elongatus</i>	0	1	0	0	1
<i>Phyllostomus hastatus</i>	2	8	4	8	22
<i>Tonatia saurophila</i>	1	0	0	0	1
<i>Carollia perspicillata</i>	16	2	0	0	18
<i>Rhinophylla pumilio</i>	2	0	0	0	2
<i>Ametrida centurio</i>	1	0	1	2	4
<i>Artibeus jamaicensis</i>	2	0	0	0	2
<i>Artibeus lituratus</i>	1	7	3	1	12
<i>Artibeus obscurus</i>	3	3	1	0	7
<i>Artibeus cinereus</i>	1	0	0	0	1
<i>Artibeus gnomus</i>	3	0	1	0	4
<i>Artibeus sp.^b</i>	0	1	1	0	2
<i>Artibeus concolor</i>	0	1	1	0	2
<i>Chiroderma trinitatum</i>	0	0	2	0	2
<i>Chiroderma villosus</i>	0	0	2	2	4
<i>Platyrrhinus helleri</i>	2	0	1	0	3
<i>Sturnira tildae</i>	1	2	0	0	3
<i>Vampyressa brocki</i>	0	0	3	0	3
<i>Thyroptera tricolor</i>	1	0	0	0	1
<i>Eptesicus chiriquinus</i>	1	1	1	1	4
<i>Eptesicus furinalis</i>	5	1	1	1	8
<i>Lasiurus blossevillii</i>	1	0	0	0	1
<i>Myotis nigricans</i>	2	2	0	0	4
<i>Eumops auripendulus</i>	0	0	1	2	3
<i>Eumops hansae</i>	0	1	0	0	1
<i>Molossops abrasus</i>	0	0	1	0	1
<i>Molossops parvus</i>	0	0	1	0	1
<i>Molossus molossus</i>	2	27	56	19	104
<i>Molossus rufus</i>	0	2	19	7	28
<i>Molossus sinaloae</i>	0	0	9	3	12
<i>Promops centralis</i>	0	0	2	0	2
Totals	54	73	126	51	304

^a Tabulated values are numbers of captures, which may include recaptures for species indicated as possible recaptures in table 69.

^b Subgenus *Dermanura*.

Of the 177 captures we recorded in elevated nets above 15 m, *Molossus molossus* was overwhelmingly the most common bat, with 75 recorded captures (about 42% of the total), followed by *Molossus rufus* with 26 records (15%), and *M. sinaloae* and *Phyllostomus hastatus* with 12 records (7%) each. Two emballonurid species (*Cormura brevirostris*, *Saccopteryx leptura*), four phyllostomids (*Phyllostomus hastatus*, *Ametrida centurio*, *Artibeus lituratus*, *Chiroderma villosus*), two vespertilionids (*Eptesicus chiriquinus*, *E. furinalis*), and four molossids (*Eumops auripendulus*, *Molossus molossus*, *M. rufus*, *M. sinaloae*) were taken at or near canopy level (>20 m), but so few captures (51) were made at this height that our species list of canopy bats must be very incomplete. For example, we presume that *Didlidurus scutatus*, *Lasiurus blossevillii*, *Eumops hansae*, *Molossops abrasus*, *M. parvus*, *Molossus barnesi*, and *Promops centralis* typically forage above 20 m although we never caught them that high.

Of the eight species that we caught only in elevated nets at Paracou, six (75%) were molossids (*Eumops auripendulus*, *E. hansae*, *Molossops abrasus*, *M. parvus*, *Molossus sinaloae*, *Promops centralis*) and one was an emballonurid (*Didlidurus scutatus*). Only a single phyllostomid species (*Micronycteris homezi*) was taken exclusively in elevated nets.

The absence of species in elevated nets at Paracou is hard to interpret because of our small effective effort (as quantified by number of captures). It seems likely that most understory bats at least occasionally fly above the 3 m level that we arbitrarily used to define the lower limit of elevated netting, but we seldom netted in the 4- to 10-m interval where many species are probably active. Additionally, because most of our elevated netting effort was in manmade or natural openings, we probably missed some species that favor the middle levels of unbroken forest.

SEARCHING FOR ROOSTS: Although we often found different species in sequential visits to the same roost in different years (see captions to figs. 16, 21, 25, 26), most roosts were inhabited by only one species at a time. Because captures made at the same roost on

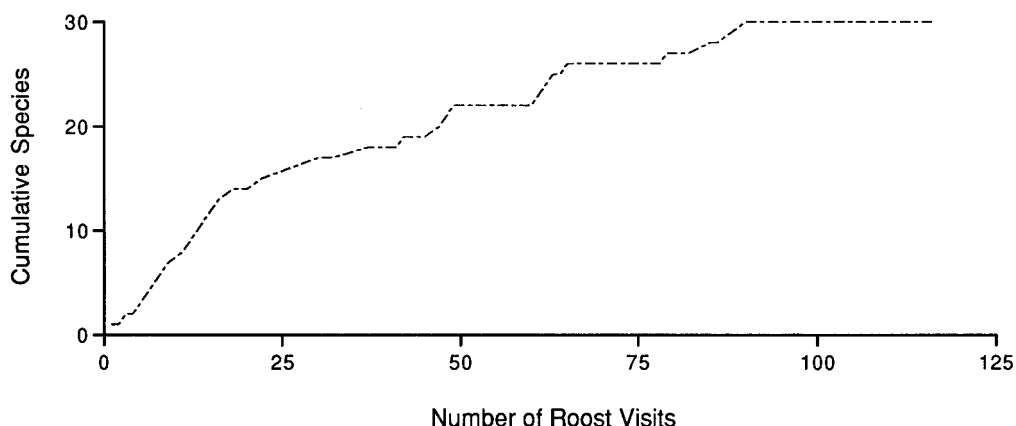


Fig. 71. Species accumulation by searching for roosts at Paracou from 1991 to 1994. Because captures at the same roost on the same date are not independent sampling events, the appropriate unit of effort for this method is the roost visit (see text).

the same date cannot be counted as independent events, the most appropriate unit for quantifying roost sampling effort is the roost visit. From 1991 to 1994 we captured a total of 361 bats during 116 visits to 85 different roosts on 68 sampling dates. On days that we searched for roosts, we made from one to five roost visits; the mean number of roosts visited per search date was 1.7, but few days were completely devoted to roosts.

Of the 85 roosts we found at Paracou, only 9 were in manmade structures (culverts, bridges, and buildings). The remaining 76 roosts were natural shelters that we classified in the following categories: under fallen trees (18 roosts), inside hollow logs (8), between buttresses of standing trees (4), under bark chips on standing trees (2), inside cavities of standing trees (12), in unmodified foliage (4), in leaf tents (13), in rolled new leaves of *Phenakospermum* or *Heliconia* (9), in scrolled dead leaves of *Phenakospermum* (3), and miscellaneous (3). Almost all of the roosts we found were within a few meters of the ground. We made 62 visits to roosts in well-drained primary forest, 11 visits to roosts in swampy primary forest, 12 visits to roosts in creekside primary forest, and 31 visits to roosts in more-or-less disturbed habitats.

We combined data from all habitats to plot species accumulation by roost-searching as a function of effort. The resulting graph (fig.

71) indicates that new species accumulated at an average rate of about one for every three roost visits until we had recorded 30 species on 90 visits to 66 different roosts in 50 days of searching. We subsequently made 26 more roost visits, 19 of which were to newly discovered roosts, without adding any more species.

Of the 30 species captured or positively identified by observation at roosts, phyllostomids were the most frequently encountered, representing 58 (46%) of the 127 roosting groups found.¹⁸ Next in abundance were emballonurids with 45 roosting groups found (35% of the total), thyropterids with 12 (9%), and furipterids with 9 (7%). We found only one roost used by a vespertilionid, and one used by molossids, both in manmade structures. Noctilionids and mormoopids were never found at roosts.

The species most commonly found at roosts were *Thyroptera tricolor* (12 roosting

¹⁸ We define roosting groups for the purpose of this tally as a group of conspecific bats found roosting together at the same time (on the same roost visit). Occasionally, two conspecific roosting groups were counted at the same roost on the same visit; for example, solitary males roosting apart in different chambers (between buttresses) on opposite sides of the same fallen tree. However, groups of apparently identical composition observed at the same roost on different visits in the same field season (a rare occurrence) were not counted as different roosting groups.

groups), *Peropteryx kappleri* (11), *Carollia perspicillata* (11), *Cormura brevirostris* (10), *Furipterus horrens* (9), *Lonchophylla thomasi* (8), and *Rhinophylla pumilio* (8). Together, these seven species accounted for just over half of the roosting groups we found at Paracou. Only a few (3–6) roosting groups were found for each of nine other species (*Peropteryx leucoptera*, *Rhynchonycteris naso*, *Saccopteryx bilineata*, *S. leptura*, *Glossophaga soricina*, *Micronycteris microtis*, *Artibeus obscurus*, *A. gnomus*, *Ectophylla macconnelli*), two groups were found for each of seven species (*Peropteryx macrotis*, *Choeroniscus minor*, *Micronycteris hirsuta*, *Phyllostomus elongatus*, *Trachops cirrhosus*, *Uroderma bilobatum*, *Molossus molossus*), and just one group was found for each of another seven species (*Centronycteris maximiliani*, *Macrophyllum macrophyllum*, *Micronycteris brosetti*, *M. megalotis*, *Mimon bennettii*, *Artibeus cinereus*, *Eptesicus furin- alis*).

Five species found by searching for roosts were never captured by any other method: *Centronycteris maximiliani*, *Peropteryx macrotis*, *Rhynchonycteris naso*, *Macrophyllum macrophyllum*, and *Furipterus horrens*. Notably much more commonly captured at roosts than in mistnets were *Peropteryx leucoptera*, *Micronycteris microtis*, *Ectophylla macconnelli*, and *Thyroptera tricolor*. Two other species captured at roosts, *Micronycteris brosetti* and *Mimon bennettii*, were only represented by singletons in our mistnet data.

By contrast, many species commonly captured in mistnets were never found by searching for roosts. The most conspicuous examples are (in order of decreasing abundance in the mistnet data): *Sturnira lilium*, *Artibeus jamaicensis*, *Tonatia saurophila*, *Phyllostomus hastatus*, *Sturnira tildae*, *Artibeus lituratus*, and *Molossus rufus*. Presumably, roosts of these species are either unusually cryptic or they are located in the canopy or subcanopy, habitats that we were unable to search effectively.

We found 22 roosts in the 25-ha plot (Parcel 16) that was systematically covered by four searchers in 1994 (see Methods), giving an estimated average density of about 0.9 roosts/ha near ground level in primary forest at Paracou. Three of the searchers found

about the same number of roosts per hectare, but searcher #4 found only two roosts in 6 ha. The six quadrats originally covered by searcher #4 were subsequently re-searched by the others, who found three additional roosts, bringing the total to five (approximately the same density as found in the remaining 19 ha). It is noteworthy that searcher #4 is deaf to higher frequency sounds and was unable to hear the faint vocalizations and muffled wing-beats that often alerted other searchers to the presence of bats in the dimly lit interiors of most roosts.

Most (17) of the roosts we found by systematically searching Parcel 16 were in durable structures (fallen or standing trees and woody debris), but a few (5) were found in foliage, a ratio of 3.4:1. By contrast, the 76 natural roosts we found by haphazard (not deliberately standardized) searching elsewhere at Paracou included 46 in durable shelters and 30 in foliage (a ratio of 1.5:1), probably because we often searched in secondary vegetation where large-leaved plants favored by some foliage-roosting bats are common. Unfortunately, our inability to identify most of the bats we found roosting on Parcel 16 precludes comparisons of systematic versus haphazard searching in taxonomic terms.

SAMPLING RESULTS IN DIFFERENT HABITATS

Although we used elevated nets and searched for roosts in several different habitats, our data from these methods are too unevenly distributed for meaningful habitat comparisons. For example, we made 62 roost visits in well-drained primary forest, but only 11 in swampy primary forest. Similarly, over 80% of our elevated-net captures were made in manmade clearings. Comparing habitats in terms of the species found by searching for roosts or by elevated netting would certainly be biased by such disparities in sampling. Only our ground-level mistnet data are extensive enough for meaningful habitat comparisons, but not all habitats were adequately sampled even by ground-level mistnetting.

PRIMARY FOREST: Well-drained and swampy sites were the most intensively sampled primary forest habitats at Paracou, rep-

resented in our data by 567 and 659 captures, respectively (table 70). Capture frequencies for the commonest species in these two forest types are strikingly similar: *Carollia perspicillata* was the most frequently captured by a substantial margin, followed by the same set of five species (*Phyllostomus elongatus*, *Artibeus obscurus*, *Rhinophylla pumilio*, *Artibeus jamaicensis*, and *Tonatia saurophila*) with only minor differences in rank ordering (e.g., *Rhinophylla pumilio* was the fifth most frequently captured species in well-drained forest, but ranked third in our records for swampy forest). Similar numbers of species (16–17) accounted for 90% of recorded captures in both habitats.

Although a few uncommon species were netted in well-drained forest but not in swampy forest (and vice versa), such results could have been obtained by chance even if the habitats were inhabited by identical faunas. On the other hand, it is possible that well-drained and swampy forest could have very different faunas without a corresponding difference in our sampling results because it is impossible to distinguish captures of bats residing in the habitat where nets were located on a given night from captures of nonresident bats commuting through the netting site. Because of the hilly topography at Paracou, no hillside is very far (more than a few hundred meters) from a swampy valley bottom, and no swampy site is far from a well-drained slope. Furthermore, the presence of an annectant habitat category (creekside forest) blurs an otherwise obvious edaphic dichotomy among the undisturbed sites we sampled by ground-level netting.

Because our capture-frequency data exhibit broadly similar patterns in well-drained and swampy forest, and because of the interpretive ambiguities mentioned above, it seems reasonable to pool all of our records from undisturbed net locations (including captures in creekside forest and treefall gaps, most of which were unremarkable) to characterize ground-level mistnet capture frequencies in primary forest at Paracou (table 72; fig. 72, top chart). Twenty-one species account for 90% of these data, with the residual 10% of captures distributed among another 36 species. As in the separately compiled records for well-drained and swampy

sites, *Carollia perspicillata* predominates in the combined data, followed by six other phyllostomids that are locally common in all primary forest types: *Phyllostomus elongatus*, *Artibeus obscurus*, *Rhinophylla pumilio*, *Artibeus jamaicensis*, *Tonatia saurophila*, and *Trachops cirrhosus*. Among nonphyllostomids, *Pteronotus parnellii* was the most commonly netted in the primary forest understory, followed by *Myotis riparius* and *Saccopteryx bilineata*; however, none of these species individually accounts for even 1% of our capture data.

Combining records from all sampling methods, we counted 21 species that were exclusively captured in primary forest at Paracou: *Centronycteris maximiliani*, *Peropteryx macrotis*, *Noctilio leporinus*, *Anoura caudifera*, *Lichonycteris obscura*, *Chrotopterus auritus*, *Glyphonycteris daviesi*, *G. sylvestris*, *Micronycteris brosetti*, *M. hirsuta*, *M. megalotis*, *M. schmidtorum*, *Mimon bennettii*, *M. crenulatum*, *Tonatia brasiliense*, *T. carrikeri*, *T. schulzi*, *T. silvicola*, *Artibeus jamaicensis*, *Chiroderma villosum*, and *Ectophylla macconnelli*. Notably dominating this list are uncommon bats, a category that includes many phyllostomines. By contrast, most stenodermatines and most common nonphyllostomid taxa were taken at least occasionally in manmade clearings and other modified habitats.

MODIFIED HABITATS: The only modified habitat that we sampled intensively by ground-level mistnetting at Paracou was manmade clearings (fig. 72, bottom chart). As in primary forest, *Carollia perspicillata* was the most frequently captured species by a wide margin. However, the next most frequently captured species in manmade clearings, *Sturnira lilium*, was rarely captured in primary forest, and the relative capture frequencies of several other species were notably higher in roadways, gardens, and similar artificial openings than in primary forest (*Sturnira tildae*, *Glossophaga soricina*, and *Artibeus cinereus*). By contrast, some species commonly captured in the primary forest understory were seldom or never captured in nearby clearings (e.g., *Phyllostomus elongatus*, *Artibeus obscurus*, *A. jamaicensis*, *Tonatia saurophila*, and *Trachops cirrhosus*). Fourteen species accounted for 90% of our

TABLE 72
Frequency Data for Species Taken in Ground-Level Mistnets in Primary Forest^a at Paracou

	Captures ^b		Nights ^c			Captures ^b		Nights ^c	
	Frequency	%	Frequency	%		Frequency	%	Frequency	%
<i>Carollia perspicillata</i>	638	41	59	95	<i>Choeroniscus minor</i>	6	<1	5	8
<i>Phyllostomus elongatus</i>	145	9	46	74	<i>Sturnira</i> sp. ^e	6	<1	5	8
<i>Artibeus obscurus</i>	98	6	34	55	<i>Chrotopterus auritus</i>	5	<1	4	6
<i>Rhinophylla pumilio</i>	84	5	39	63	<i>Micronycteris minuta</i>	5	<1	4	6
<i>Artibeus jamaicensis</i>	71	5	22	35	<i>Peropteryx kappleri</i>	4	<1	2	3
<i>Tonatia saurophila</i>	57	4	32	52	<i>Trinycteris nicefori</i>	4	<1	4	6
<i>Trachops cirrhosus</i>	51	3	28	45	<i>Chiroderma trinitatum</i>	4	<1	3	5
<i>Lonchophylla thomasi</i>	28	2	20	32	<i>Chiroderma villosus</i>	4	<1	3	5
<i>Artibeus lituratus</i>	28	2	18	29	<i>Desmodus rotundus</i>	4	<1	4	6
<i>Artibeus gnomus</i>	28	2	18	29	<i>Noctilio leporinus</i>	3	<1	2	3
<i>Phyllostomus hastatus</i>	26	2	16	26	<i>Micronycteris hirsuta</i>	3	<1	3	5
<i>Glossophaga soricina</i>	21	1	10	16	<i>Micronycteris microtis</i>	3	<1	3	5
<i>Sturnira tildae</i>	19	1	11	18	<i>Ametrida centurio</i>	3	<1	3	5
<i>Mimon crenulatum</i>	17	1	10	16	<i>Vampyressa brocki</i>	3	<1	3	5
<i>Pteronotus parnellii</i>	15	1	11	18	<i>Myotis nigricans</i>	3	<1	1	2
<i>Phyllostomus discolor</i>	14	1	10	16	<i>Saccopteryx leptura</i>	2	<1	2	3
<i>Artibeus concolor</i>	13	1	9	15	<i>Glyphonhycteris daviesi</i>	2	<1	1	2
<i>Tonatia silvicola</i>	11	1	10	16	<i>Micronycteris schmidtorum</i>	2	<1	2	3
<i>Uroderma bilobatum</i>	11	1	5	8	<i>Vampyrum spectrum</i>	2	<1	2	3
<i>Artibeus cinereus</i>	10	1	9	15	<i>Thyroptera tricolor</i>	2	<1	2	3
<i>Artibeus</i> sp. ^d	10	1	6	10	<i>Peropteryx leucoptera</i>	1	<1	1	2
<i>Myotis riparius</i>	10	1	8	13	<i>Glyphonhycteris sylvestris</i>	1	<1	1	2
<i>Saccopteryx bilineata</i>	9	1	6	10	<i>Micronycteris brosetti</i>	1	<1	1	2
<i>Tonatia brasiliense</i>	9	1	7	11	<i>Mimon bennettii</i>	1	<1	1	2
<i>Micronycteris megalotis</i>	8	1	6	10	<i>Tonatia carrikerei</i>	1	<1	1	2
<i>Sturnira lilium</i>	8	1	6	10	<i>Anoura caudifera</i>	1	<1	1	2
<i>Phylloderma stenops</i>	7	<1	7	11	<i>Lichonycteris obscura</i>	1	<1	1	2
<i>Tonatia schulzi</i>	7	<1	7	11	<i>Ectophylla macconnelli</i>	1	<1	1	2
<i>Platyrrhinus helleri</i>	7	<1	6	10	<i>Diaemus youngi</i>	1	<1	1	2
<i>Cormura brevirostris</i>	6	<1	5	8					

^a Well-drained primary forest, swampy primary forest, creekside primary forest, and natural treefall openings.

^b Tabulated frequencies may include recaptures for species indicated by a superscript in table 69. Percentages are of 1545 total ground-level mistnet captures in primary forest from 1991 to 1994.

^c Tabulated frequencies are the number of nights on which each species was captured. Percentages are of 62 total nights of ground-level netting in primary forest from 1991 to 1994.

^d *Artibeus cinereus* or *A. gnomus*.

^e *Sturnira lilium* or *S. tildae*.

recorded captures in manmade clearings, with the residual 10% distributed among another 28 species.

Although we netted over roadside puddles on just six sampling dates, we recorded 244 captures representing 22 species, of which the following account for 90% of our records: *Molossus molossus* (87 captures), *Carollia perspicillata* (73), *Molossus rufus* (19), *Myotis nigricans* (13), *Artibeus lituratus* (9), *Eptesicus furinalis* (8), *Artibeus cinereus* (5),

Sturnira tildae (4), and *Uroderma bilobatum* (4). Despite the small sample, these relative frequencies clearly differ from those recorded at ground level in other local habitats, especially by the large proportion of nonphyllostomids. Molossids alone accounted for 44% of the captures we recorded over roadside puddles, as compared with 1% at ground level in manmade clearings and none in the primary forest understory.

We recorded only 27 ground-level mistnet

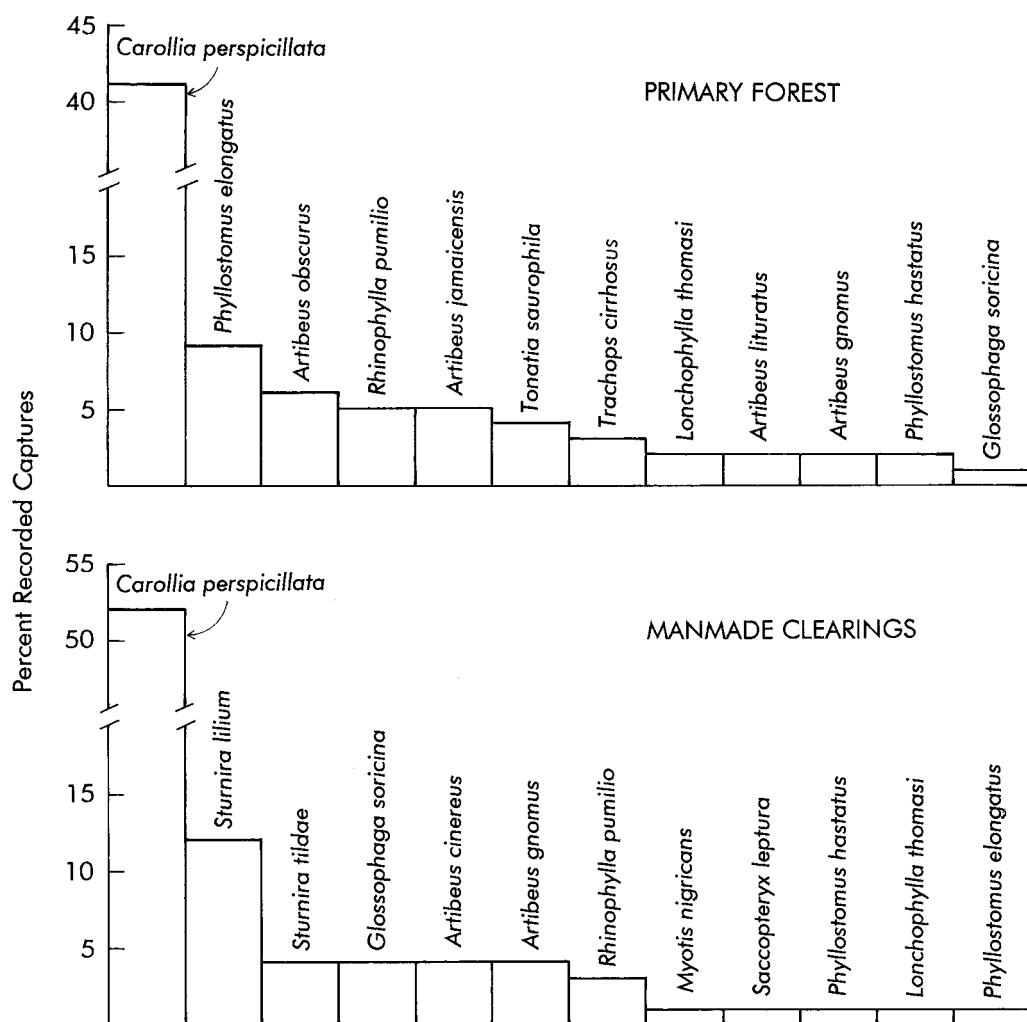


Fig. 72. Species frequency histograms of recorded captures in ground-level mistnets in primary forest and in manmade clearings at Paracou from 1991 to 1994. Only the 12 most frequently captured species in each habitat are shown; these account for 82% of 1545 total captures in primary forest and 88% of 627 total captures in manmade clearings.

captures in disturbed forest and closed-canopy secondary growth at Paracou, far too few to be informative about the fauna (which presumably resembles that of the primary forest in most respects). However, we found 19 roosts in these habitats, mostly under felled trees and in the foliage of early-successional plant species.

Sixteen species of bats were taken only in modified habitats at Paracou, of which 12 were captured in elevated nets over roadways

and/or in ground-level nets over roadside puddles: *Didelphis scutatus*, *Noctilio albigentris*, *Micronycteris homezi*, *Lasiurus blossevillii*, *Eumops auripendulus*, *E. hansae*, *Molossops abrasus*, *M. parvus*, *Molossus barnesi*, *M. rufus*, *M. sinaloae*, and *Promops centralis*. Two species, *Rhynchonycteris naso* and *Macrophyllum macrophyllum*, were captured only at roosts in manmade shelters. *Saccopteryx gymnura* was captured twice in ground-level mistnets in manmade clearings,

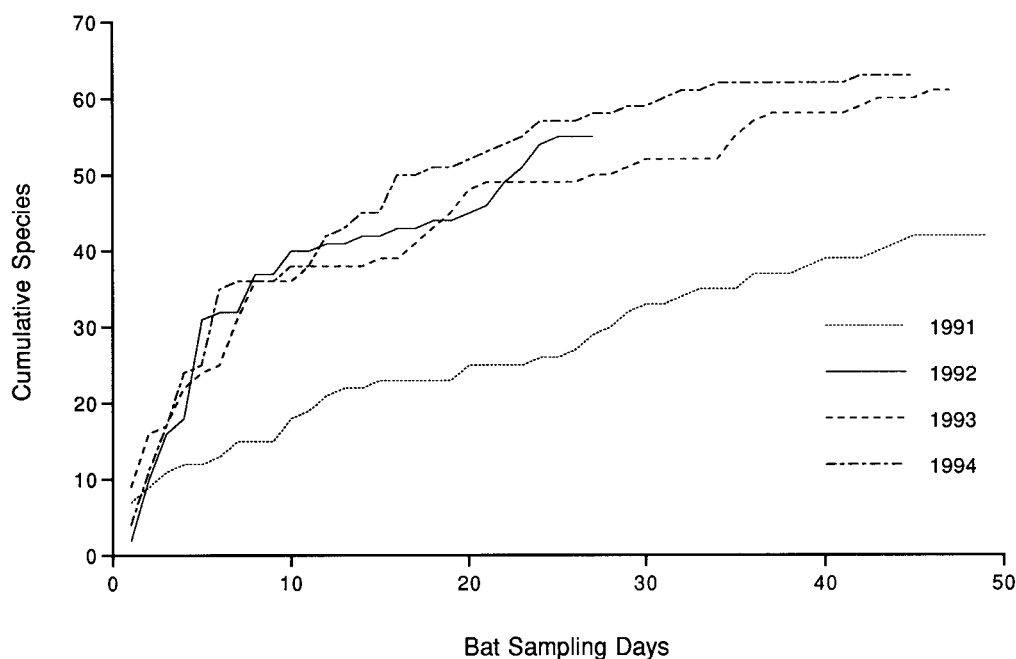


Fig. 73. Species accumulation curves representing sampling results using all methods in all habitats for each of the four years we worked at Paracou.

and *Eptesicus chiroquinus* was netted at ground-level in manmade clearings as well as over puddles and in elevated nets over roadways.

SAMPLING RESULTS IN DIFFERENT YEARS

Comparing the species lists we obtained by sampling the Paracou bat fauna in different years is complicated by changes in the methodological and ecological scope of our fieldwork. For example, our species accumulation curve from sampling with all methods in all habitats for 1991 is conspicuously different from the accumulation curves for later years (fig. 73): on any given sampling day after the first week, we recorded about 20–25 fewer species in 1991 than we did in 1992–1994. However, we captured fewer individuals per day in our first field season than in later years, we moved our nets less often, we did not net over roadside puddles, and we did not use elevated nets (table 73). Therefore, no valid conclusions regarding temporal

variation in local bat communities are possible from such incommensurate results.

Restricting annual comparisons to results obtained by our most intensively used method (ground-level mistnetting) in the best sampled local habitat (primary forest) suggests that the Paracou bat fauna was not unusually depauperate in our first field season (fig. 74). Instead, the species accumulation curves representing ground-level netting in primary forest for 1991 and 1993 appear remarkably similar despite differences in the net weights and acoustical attractants used in those years (table 73). The higher species accumulation curves for 1992 and 1994, however, suggest either richer understory faunas or more effective sampling in those years.

Perhaps significantly, our fieldwork in 1991 and 1993 began in the late wet season and ended in the early dry season, whereas our 1992 and 1994 fieldwork was in the late dry season. Comparing species lists obtained by ground-level mistnetting in primary forest among years, however, does not suggest any consistent pattern of taxonomic or trophic

TABLE 73
Methods Used to Capture Bats at Paracou, 1991–1994

	Ground-level netting					Roost searching?	Elevated netting?	Captures/day ^c
	Net weight	Net-meters ^a	Nights per site	ABC ^b used?	Puddles netted?			
1991	70	38 ± 3	2.4	no	no	yes	none	14 ± 2
1992	30	39 ± 7	1.5	yes	yes	yes	once	26 ± 4
1993	30	29 ± 4	1.8	yes	yes	yes	often	21 ± 3
1994	30	48 ± 4	1.2	yes	yes	yes	often	17 ± 2

^a Mean length of nets deployed per night (± 1 SE).

^b Audubon Bird Call (see Methods).

^c All methods combined (mean ± 1 SE).

differences between the late-wet/early-dry season samples on the one hand and the late dry season samples on the other; only five species with no obvious behavioral traits in common (*Micronycteris hirsuta*, *Phyllostomus discolor*, *Ametrida centurio*, *Chiroderma trinitatum*, *C. villosum*) were netted in the primary forest understory in 1992 and 1994 but not in 1991 or 1993. Possibly, the high species accumulation rates for 1992 and 1994 reflect the more experienced personnel who chose netting sites and tended the nets in those years.

Because we only netted for bats in the primary forest understory for a few (11–18) nights each year, the chance positioning of nets on a single night could have a large effect on annual capture frequencies for species attracted to clumped resources. For example, 23 of the 25 *Artibeus jamaicensis* that we netted in 1991 (when this species ranked second in capture frequency) were taken on a single night when our nets were located near a fruiting fig tree. In our view, meaningful tests for homogeneity of species frequency distributions among years would require much more extensive sampling (more netting nights) to overcome the effects of such haphazard variation. Therefore, we are reduced to a more-or-less subjective evaluation of the limited data at hand.

Although we cannot rule out the possibility that some infrequently captured species are seasonally or annually missing from the Paracou bat fauna, our impression is that the fauna was essentially similar throughout the course of our fieldwork. Certainly the com-

monest species in our combined records for 1991–1994 were frequently captured every year, and in roughly the same proportions using the same method in the same habitat. Thus, 7 of the 10 species most frequently netted in the primary forest understory each year were the same: *Carollia perspicillata*, *Phyllostomus elongatus*, *Artibeus obscurus*, *Rhinophylla pumilio*, *Artibeus jamaicensis*, *Tonatia saurophila*, and *Trachops cirrhosus*. Of these, *C. perspicillata* was always first by a wide margin, followed by *P. elongatus* (except in 1991, as noted above); either *R. pumilio* or one of the *Artibeus* species was always in third place. Together, these seven species accounted for 66–85% of the mistnet captures recorded in the primary forest understory every year, so capture frequencies for most of the remaining 50 species known to use this habitat at Paracou were obviously subject to considerable random sampling variation. Comparisons of annual capture frequencies for ground-level netting in man-made clearings (1991–1994), for ground-level netting over roadside puddles (1992–1994), and for elevated netting over roadways (1993, 1994) likewise suggest that essentially the same fauna was sampled by the same method in the same habitat from year to year with no more variation than could plausibly be explained by chance.

ESTIMATING COMPLETENESS

We see no evidence in our species accumulation results (figs. 68–71) that we exhaustively inventoried the Paracou bat fauna.

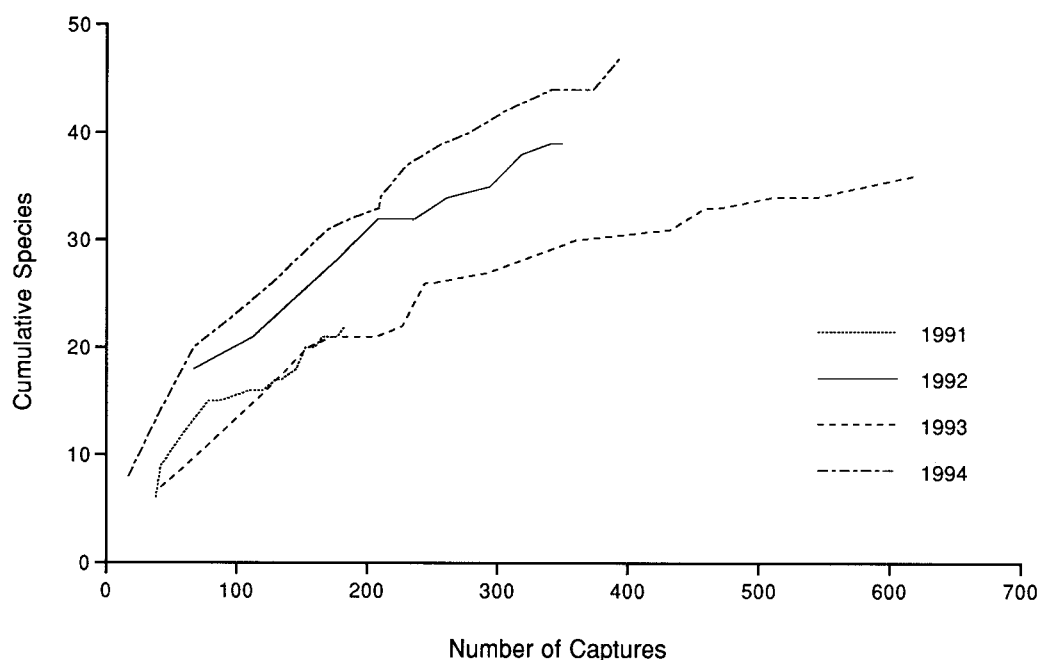


Fig. 74. Species accumulation by ground-level mistnetting in primary forest for each of the four years we worked at Paracou.

Although all of the graphs show a declining rate of discovery of new species with time, none shows a convincing asymptote. Presumably, we could have captured more species had we returned for another field season, and the question therefore arises of how to estimate the completeness of our survey. Equivalently, how can we extrapolate our sampling results to estimate the true number of species in the fauna as a whole, or in methodologically or ecologically defined subsets of the fauna?

Of the many extrapolation procedures for estimating species richness suggested in the literature (helpfully reviewed by Colwell and Coddington, 1994), several nonparametric methods seem readily applicable to our data. Certainly they are computationally convenient. Using Colwell and Coddington's notation, Chao's (1984) estimator is based on the observed number of species, S_{obs} , the number of "singletons" (species observed exactly once), a , and the number of "doubletons" (species observed exactly twice), b . The expected number of species, S^* , is then given by the expression

$$S^* = S_{\text{obs}} + (a^2/2b).$$

Thus, the quantity by which S^* exceeds S_{obs} is largely determined by the number of singletons. When there are no singletons in the data ($a = 0$), the fauna may be presumed to be completely inventoried (because $S^* = S_{\text{obs}}$). Sampling data with many singletons, however, suggest that the inventory is not complete (because $S^* > S_{\text{obs}}$). Intuitively, if many species were observed only once in an inventory, other local species probably remained unobserved.

As a heuristic exercise, we counted S_{obs} , a , and b for the whole Paracou bat inventory, as well as for several methodologically defined partitions of our sampling data. From these counts we estimated S^* by the expression given above, and we estimated the standard deviation of S^* using the formula for the variance given by Colwell and Coddington (1994) and Chao (1987); confidence intervals were computed assuming the approximate normality of S^* (after Chao, 1987). We estimated completeness as the percentage $(S_{\text{obs}}/S^*) \times 100$.

TABLE 74
**Analysis of Sampling Completeness for Methodologically Defined
 Partitions of the Paracou Bat Inventory**
 (See text for explanation)

	S_{obs}	a	b	S^*	Confidence interval	Percent complete
Ground-level mistnetting	65	10	6	73	(62, 84)	89
Elevated mistnetting	39	12	5	53	(36, 70)	74
Searching for roosts ^a	30	7	7	34	(28, 40)	88
ALL METHODS ^b	78	12	9	86	(76, 96)	91

^a Singletons are species represented by one roosting group, doubletons by two roosting groups.

^b Singletons are species represented by one sampling event (mistnet capture or roosting group found), doubletons by two events.

The results of our analysis (table 74) suggest that more species could be obtained by additional sampling using each method, but the confidence intervals for S^* are wide and include the observed number of species in every case. Sampling by elevated mistnetting would appear to be the least complete of the three data subsets analyzed, a result consistent with our judgment based on species accumulation curves (see above). Overall, Chao's estimator suggests that the Paracou bat inventory is about 90% complete. However, the predicted total number of species in the fauna, 86, is perhaps too low given that S^* estimated by this method is really a lower bound (Chao, 1984). Other nonparametric extrapolation methods based on sample coverage (counting dates as samples) give higher predictions (e.g., $S^* = 91$ species by Heltshe and Forrester's [1983] jackknife estimator) that approach the upper 95% confidence limit on Chao's estimate (table 74).

Although the identities of the local species that are missing from our inventory cannot be known with certainty, some useful indications are provided by the list of singletons and doubletons in our combined sampling data (from all methods). Twelve species were effectively observed only once in our fieldwork (either by single mistnet captures or on single roost visits): *Centronycteris maximiliani*, *Diclidurus scutatus*, *Noctilio albiventris*, *Anoura caudifera*, *Lichonycteris obscura*, *Glyphoncteris sylvestris*, *Macrophyllum macrophyllum*, *Micronycteris homezi*, *Tonatia carrikeri*, *Eumops hansae*, *Molossops abrasus*, and *Molossops parvus*. Our nine

doubletons (species that were effectively observed twice) include *Peropteryx macrotis*, *Saccopteryx gymnura*, *Glyphoncteris daviesi*, *Micronycteris brosetti*, *Micronycteris schmidtorum*, *Mimon bennettii*, *Lasiurus blossevillei*, *Molossus barnesi*, and *Promops centralis*. Conspicuously absent from these lists are frugivores (carolline and stenodermatine phyllostomids), all of which are represented by seven or more observations (mistnet captures or roost visits) in our sampling data. Indeed, the last new frugivorous species added to our inventory (*Ectophylla macconnelli*) was captured on 12 November 1992, less than halfway through our fieldwork. Presumably, our inventory of the local frugivore fauna is essentially complete.

Instead, the singletons and doubletons in our data are (to judge from known habits, morphology, and taxonomic affinity) either aerial insectivores (11 spp.), gleaning insectivores (8 spp.), or nectarivores (2 spp.). It would be reasonable to suppose that most of the local species missing from our inventory belong to these trophic categories, all of which are well represented among the list of taxa known from elsewhere in French Guiana and Surinam (appendix 1). At least seven singletons or doubletons are species that probably forage above the level of the forest canopy, where our inventory efforts were least effective (table 74). Therefore, at least some future additions to the Paracou fauna will probably come from elevated mistnetting or other methods of sampling the high-flying fauna.

DISCUSSION

Paracou is apparently the first Neotropical rainforest locality at which bat diversity has been assessed by sustained sampling over several years with ground-level mistnets, elevated mistnets, and roost surveys.¹⁹ Although the preceding analyses of sampling suggest that the local fauna is still incompletely known, the number of missing species would appear to be small in proportion to the 78 species identified from morphological voucher material (table 69). Inferences about taxonomic composition, biogeographic relationships, species richness, and other topics based on the data at hand are therefore unlikely to be substantially altered by additional inventory efforts at Paracou.

Unfortunately, the intensity and methodological scope of inventory fieldwork at other Neotropical rainforest localities has been highly uneven, making valid comparisons difficult. Nevertheless, it is useful to evaluate our results in a comparative context where similarities and differences can be identified and discussed with respect to sampling artifacts, biogeography, ecology, and other causal factors. Accordingly, we surveyed the literature and identified 13 other Neotropical rainforest sites, 3 in Central America and 10 in Amazonia, from which large species lists of bats have been published. These localities are mapped in figure 75, the taxonomic distribution of bat species richness for each inventory is summarized in table 75, and a complete species-by-locality matrix is provided in appendix 2.

TAXONOMIC COMPOSITION AND BIOGEOGRAPHY

In terms of higher taxonomic composition, the Paracou bats represent a typical Neotropical lowland fauna. All eight families commonly found in Central and South American rainforests (Emballonuridae, Noctilionidae, Mormoopidae, Phyllostomidae, Thyropteridae, Furipteridae, Vespertilionidae, and Molossidae) are represented. Similarly, all of the

five phyllostomid subfamilies ubiquitous at other rainforested sites on the Neotropical mainland (Desmodontinae, Glossophaginae, Phyllostominae, Carolliinae, and Stenodermatinae) are present at Paracou.

In terms of species composition, the Paracou bat inventory clusters (fig. 76) with five other faunas from the Guiana subregion of Amazonia, next with an additional five Amazonian sites representing the southeastern and western subregions, and finally with a discrete grouping of three Central American faunas. Pairwise coefficients of faunal similarity (table 76) indicate that the Paracou inventory is most similar in species composition to Brosset and Charles-Dominique's (1990) list from Piste Saint-Élie (an adjacent locality in northern French Guiana), and least similar to Medellín's (1993) list from Chajul (in Chiapas, Mexico). Clearly, the overall pattern in these results suggests that bat faunal similarity within the Neotropical rainforest biome is positively correlated with geographic proximity, and that the Paracou fauna in particular closely resembles others previously reported from northeastern Amazonia.

Paracou bats can be sorted into eight groups (table 77) based on their known patterns of distribution among the four Neotropical lowland rainforest regions recognized by Voss and Emmons (1996).²⁰ By far the commonest distribution category (pattern 1) includes species that occur in all four regions; members of this very widespread fauna include *Peropteryx kappleri*, *P. macrotis*, *Rhynchonycteris naso*, *Saccopteryx bilineata*,

¹⁹ All three methods have been used at some inventory sites (Voss and Emmons, 1996: table 6), but published accounts of fieldwork do not document sustained effort by all methods over multiple years.

²⁰ Our classification of Paracou bat distributional patterns is based primarily on manuscript compilations of locality data by the late Karl F. Koopman, which reflect his identifications of specimens in the AMNH and other museums, computerized records of FMNH material, and the literature published prior to 1997. For the distribution of *Artibeus* species, however, we relied on an unpublished review of South American locality records by Suely Marques, whose species concepts followed Handley (1987, 1989) rather than Koopman (1993, 1994). In a few other cases (e.g., for *Centronycteris maximiliani*, *Mimon bennettii*, and *Eptesicus chiriquinus*) our distributional classifications follow the revised species taxonomy suggested in this report.

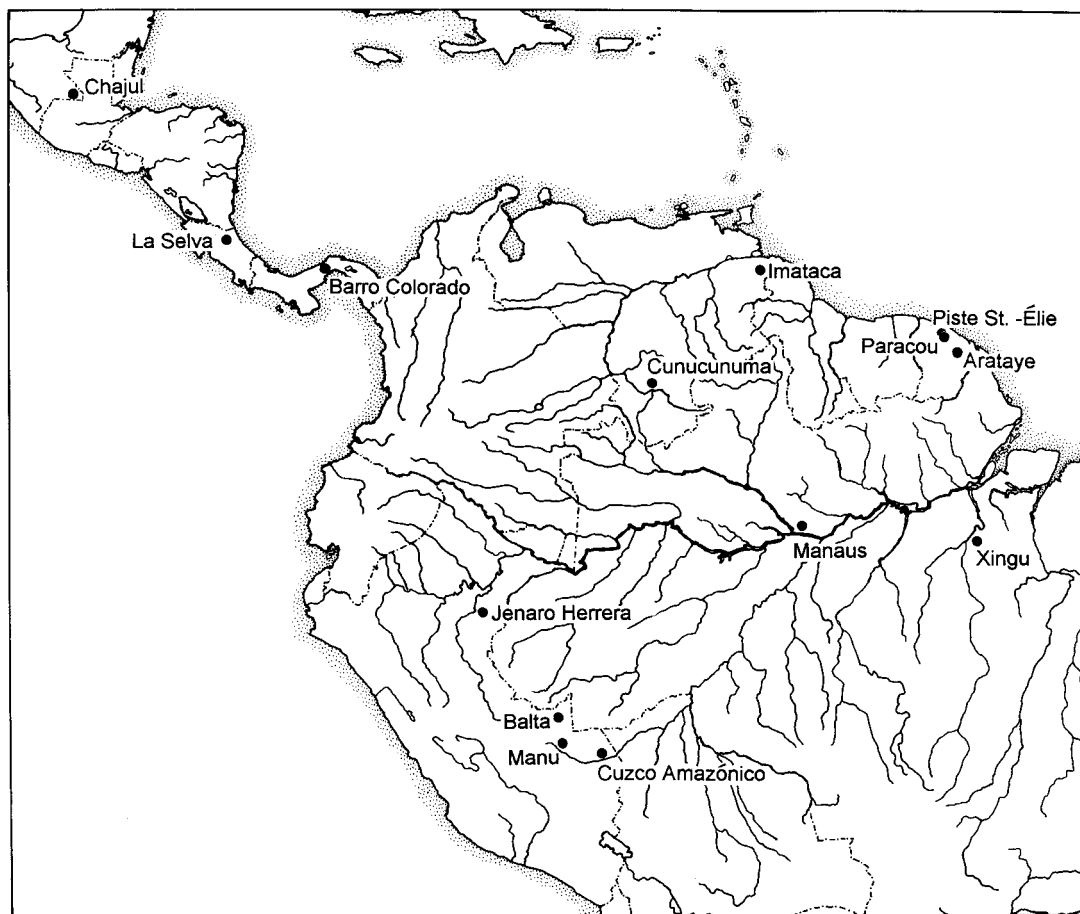


Fig. 75. Fourteen Neotropical rainforest bat inventory sites. See footnotes to table 75 for geographic coordinates and references.

S. leptura, *Noctilio albiventris*, *N. leporinus*, *Desmodus rotundus*, *Diaemus youngi*, *Glossophaga soricina*, *Chrotopterus auritus*, *Glyphoncyteris sylvestris*, *Macrophyllum macrophyllum*, *Micronycteris megalotis*, *M. minuta*, *M. schmidtorum*, *Mimon crenulatum*, *Phylloderma stenops*, *Phyllostomus discolor*, *P. hastatus*, *Tonatia brasiliense*, *T. silvicola*, *Trachops cirrhosus*, *Trinycteris nicefori*, *Carollia perspicillata*, *Artibeus jamaicensis*, *A. lituratus*, *Chiroderma villosus*, *Sturnira lilium*, *Uroderma bilobatum*, *Eptesicus furinalis*, *Lasiurus blossevillii*, *Myotis nigricans*, *Eumops auripendulus*, *E. hansae*, *Molossus molossus*, and *M. rufus*. Therefore, a large fraction (47%) of the Paracou species list is essentially pan-Neotropical and biogeographically uninformative.

The next most frequent distributional category among Paracou bats (pattern 2) consists of species known to occur in trans-Andean, coastal Venezuelan, and Amazonian rainforests, but not in the Atlantic forest of southeastern Brazil. The 13 species with this distribution include *Cormura brevirostris*, *Pteronotus parnellii*, *Micronycteris hirsuta*, *M. microtis*, *Tonatia saurophila*, *Vampyrus spectrum*, *Ametrida centurio*, *Chiroderma trinitatum*, *Platyrrhinus helleri*, *Eptesicus chiriquinus*, *Molossops parvus*, *Molossus sinaloae*, and *Promops centralis*. By contrast, 10 species occur in Amazonia and the Atlantic rainforest, but apparently not in trans-Andean or coastal Venezuelan rainforests (pattern 3): *Centronycteris maximiliani*, *Peropteryx leucoptera*, *Micronycteris bros-*

TABLE 75
Taxonomic Distribution of Bat Species Richness in 14 Neotropical Rainforest Faunas
 (Table entries are numbers of species present)

	Bat families and subfamilies ^a													Total spp
	Emb	Noc	Mor	Phyllostomidae					Nat	Thy	Fur	Ves	Mol	
				Des	Glo	Phy	Car	Ste						
CENTRAL AMERICA														
Chajul ^b	3	1	2	3	2	13	2	11	1	1	0	8	3	50
La Selva ^c	8	2	2	1	6	19	3	13	0	1	1	7	2	65
Barro Colorado ^d	7	2	3	1	3	16	3	16	1	2	0	6	6	66
AMAZONIA														
Imataca ^e	8	2	1	1	4	15	3	17	0	0	0	6	5	62
Piste St.-Elie ^f	6	0	0	1	5	17	2	15	0	1	1	4	2	54
Paracou	10	2	1	2	5	25	2	15	0	1	1	5	9	78
Arataye ^g	5	0	1	1	6	18	3	18	0	1	0	2	6	61
Cunucunuma ^h	5	1	1	1	4	10	3	17	0	1	1	3	3	50
Manaus ⁱ	8	2	1	1	5	11	3	11	0	1	0	5	4	52
Xingu ^j	5	1	1	2	4	13	3	14	0	0	1	2	1	47
Jenaro Hererra ^k	5	1	0	1	5	15	5	19	0	1	1	5	4	62
Balta ^l	3	1	0	1	5	11	4	19	0	1	0	8	3	56
Manu ^m	3	2	0	2	5	14	4	21	0	1	1	5	2	60
Cuzco Amazónico ⁿ	4	1	0	1	3	9	4	15	0	1	0	5	1	44

^a Abbreviations: Emb, Emballonuridae; Noc, Noctilionidae; Mor, Mormoopidae; Des, Desmodontinae; Glo, Glossophaginae; Phy, Phyllostominae; Car, Carollinae; Ste, Stenodermatinae; Nat, Natalidae; Thy, Thyropteridae; Fur, Furipteridae; Ves, Vespertilionidae (sensu lato); Mol, Molossidae.

^b Chajul (16°06'N, 90°57'W) is a research station in the Lacandon rainforest of the Mexican state of Chiapas (Medellín, 1993).

^c La Selva (10°26'N, 83°59'W) is a research station in the Caribbean lowlands of Provincia Heredia, Costa Rica (Voss and Emmons, 1996: appendix 2).

^d Barro Colorado Island (9°09'N, 79°51'W) is a research station in the former Canal Zone of central Panama (Voss and Emmons, 1996: appendix 3; Kalko et al., 1996).

^e The Reserva Forestal de Imataca is in the Venezuelan states of Delta Amacuro and Bolívar (Ochoa, 1995); the species counts are from "Unidad V," Ochoa's (1995) inventory area, centered at ca. 7°45'N, 61°10'W.

^f A research station (also known by the acronym "ECEREX") on the road (piste) to Saint-Élie at 5°18'N, 53°04'W in northern French Guiana (Brosset and Charles-Dominique, 1990; Masson and Cosson, 1992).

^g We combine inventory data from two research stations, Les Nouragues (4°05'N, 52°40'W) and Saut Pararé (4°02'N, 52°42'W) in the lower Arataye catchment of east-central French Guiana (Voss and Emmons, 1996: appendix 5).

^h We combine inventory data from Culebra (3°39'N, 65°46'W) and Acanaña (3°32'N, 65°48'W), two Yekuana villages on the Río Cunucunuma in the Venezuelan federal territory of Amazonas (Voss and Emmons, 1996: appendix 6).

ⁱ Manaus (3°08'S, 60°01'W) is near the confluence of the Río Negro and the Río Solimões in the Brazilian state of Amazonas (Reis and Peracchi, 1987).

^j A Smithsonian collecting locality on the right (east) bank of the lower Río Xingu (at 3°39'S, 52°22'W) in the Brazilian state of Pará (Voss and Emmons, 1996: appendix 8).

^k Jenaro Herrera (4°55'S, 73°45'W) is a research station on the right (east) bank of the Río Ucayali in Departamento Loreto, Peru (Ascorra et al., 1993).

^l Balta (10°08'S, 71°13'W) is a Cashinahua village on the Río Curanja in Departamento Ucayali, Peru (Voss and Emmons, 1996: appendix 9).

^m We combine inventory data from Cocha Cashu (11°54'S, 71°22'W) and Pakitzu (11°57'S, 71°17'W), adjacent inventory sites on the left (north) bank of the Río Manu in Departamento Madre de Dios, Peru (Voss and Emmons, 1996: appendix 10).

ⁿ Cuzco Amazónico (12°33'S, 69°03'W) is an ecotourist lodge on the left (north) bank of the Río Madre de Dios in Departamento Madre de Dios, Peru (Voss and Emmons, 1996: appendix 11).

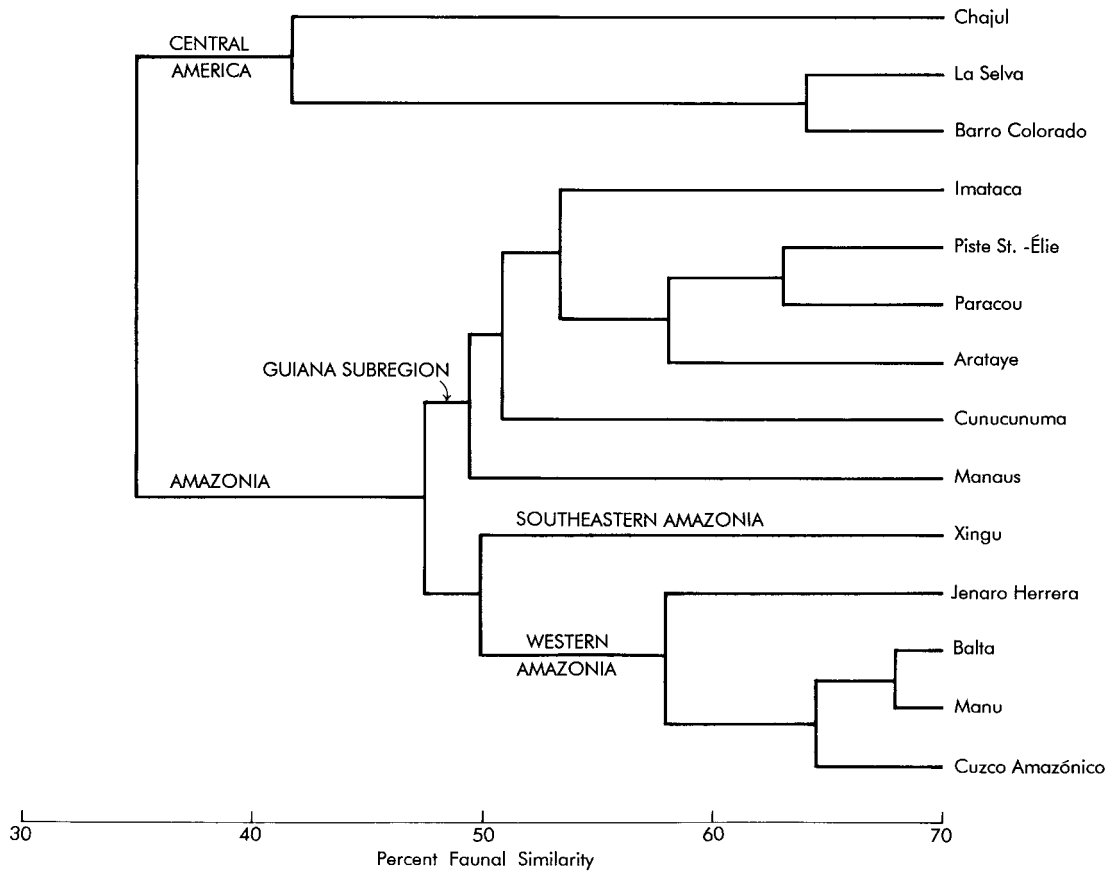


Fig. 76. Analysis of faunal relationships among 14 Neotropical rainforest bat inventories. Faunal similarity was quantified between each pair of localities (i, j) by Jaccard's coefficient, $J_{ij} = C_{ij}/T_{ij}$, where C_{ij} is the number of species common to both faunas and T_{ij} is the total number of species in both faunas combined ($T_{ij} = N_i + N_j - C_{ij}$). Localities were clustered by the unweighted pair-group method using arithmetic averages (Sneath and Sokal, 1993) for comparability with other recent biogeographic analyses of Neotropical vertebrates (e.g., da Silva and Sites, 1995). The bottom scale shows the clustering level in units of percent faunal similarity ($J \times 100$). Obviously, no historical or other causal interpretation is implied by these results, nor do we assume that a hierarchical model is necessarily appropriate except as a convenient summary graphic.

seti, *Mimon bennettii*, *Phyllostomus elongatus*, *Rhinophylla pumilio*, *Artibeus obscurus*, *A. cinereus*, *Sturnira tildae*, and *Molossops abrasus*.

Only about 10% of the Paracou bat fauna consists of species with known rainforest distributions restricted to Amazonia (pattern 4); these include six species that seem to be true Amazonian endemics (*Diclidurus scutatus*, *Saccopteryx gymnura*, *Tonatia carrikeri*, *T. schulzi*, *Artibeus gnomus*, *Vampyressa brocki*), one species that also occurs in adjacent cerrado habitats (*Artibeus concolor*),

and one species known from so few localities that its true range is difficult to evaluate (*Molossus barnesi*). The remainder of the fauna consists of species known from all rainforested regions but coastal Venezuela (pattern 5: *Choeroniscus minor*, *Lichonycteris obscura*, *Thyroptera tricolor*, *Furipterus horrens*, *Myotis riparius*), trans-Andean and Amazonian rainforests only (pattern 6: *Lonchophylla thomasi*, *Glyphonhycteris daviesi*, *Mesophylla macconnelli*), all rainforested regions but the trans-Andean (pattern 7: *Anoura caudifera*), and the coastal Venezuelan and Am-

TABLE 76
Percent Faunal Similarity Among 14 Neotropical Rainforest Bat Faunas^a
(Table entries are Jaccard's coefficient $\times 100$)

LSe	42												
BCo	41	64											
Ima	33	46	44										
PSE	28	40	36	55									
Par	29	42	38	56	63								
Ara	29	30	35	50	62	54							
Cun	30	32	36	49	53	44	54						
Man	31	34	39	50	51	53	49	48					
Xin	28	32	31	47	53	49	48	43	48				
JHe	29	34	37	49	53	51	48	42	48	54			
Bal	34	33	37	49	49	44	48	43	54	49	59		
CCP	36	40	43	51	52	45	48	53	45	51	58	68	
CAM	29	33	35	45	48	39	42	40	50	47	56	64	65
	Cha	LSe	BCo	Ima	PSE	Par	Ara	Cun	Man	Xin	JHe	Bal	CCP

^a Abbreviations: Cha, Chajul (Mexico); LSe, La Selva (Costa Rica); BCo, Barro Colorado (Panama); Ima, Imataca (Venezuela); PSE, Piste St.-Élie (French Guiana); Par, Paracou (French Guiana); Ara, Arataye (French Guiana); Cun, Cunucunuma (Venezuela); Man, Manaus (Brazil); Xin, Xingu (Brazil); JHe, Jenaro Herrera (Peru); Bal, Balta (Peru); CCP, Cocha Cashu/Pakitzta (= Manu, Peru); CAM, Cuzco Amazónico (Peru). See footnotes to table 75 for geographic information and references.

The calculation of Jaccard's coefficient of faunal similarity is explained in the caption to figure 76, and the original (presence/absence) data are provided in appendix 2. Note that incomplete sampling generally underestimates biotic similarity, for the same reasons that complementarity is generally overestimated by incomplete samples (Colwell and Coddington, 1994). Because complementarity can be expressed as the one-complement of Jaccard's coefficient (op. cit.), the values in this table can be subtracted from 100 to obtain percent complementarity (the fraction of the combined fauna from two sites that is not shared between them).

azonian regions only (pattern 8: *Micronycteris homezi*).

In effect, the Paracou fauna is composed of species representing every possible pattern

TABLE 77
Rainforest Distribution Patterns of Paracou Bats

Pattern	Rainforest distribution ^a				Number of species
	trAnd	CoVen	Ama	Atl	
1	X	X	X	X	37
2	X	X	X		13
3			X	X	10
4			X		8
5	X		X	X	5
6	X		X		3
7		X	X	X	1
8		X	X		1

^a Abbreviations of Neotropical lowland rainforest regions as defined by Voss and Emmons (1996): trAnd, trans-Andean (including Central America and the Chocó); CoVen, Coastal Venezuelan; Ama, Amazonian; Atl, Atlantic (southeastern Brazil).

of distribution among the disjunct rainforested regions of the Neotropical mainland. Of course, many of the widespread species are eurytopic and occur in other habitats besides rainforest. For example, 28 of the 37 species in the Paracou fauna with distribution pattern 1 are also known from the Llanos (Ibáñez, 1981), the Caatinga (Willig and Mares, 1989), or the Chaco (Myers and Wetzel, 1983). Conspicuously absent from the Paracou fauna, however, are any species consistently associated elsewhere with open (non-forest) habitats. Indeed, such species are apparently unknown in French Guiana or Surinam, although several occur farther west in Venezuela and Guyana (e.g., *Glossophaga longirostris*, *Eptesicus diminutus*, *Molossus pretiosus*). In summary, despite the location of our study site at the periphery of Amazonia and adjacent to coastal savannas, there is no evidence that the Paracou bat fauna is composed of any species other than those known or expected to occur in rainforested landscapes.

SPECIES RICHNESS

Comparisons of species richness among Neotropical rainforest bat inventories are complicated by problems related to the methods, ecological scope, and intensity of faunal sampling at different sites. As explained above in the context of analyzing our own sampling data from Paracou, different capture methods effectively sample different sets of species, samples obtained by the same capture method in different habitats can differ significantly in species composition, and increased effort using any capture method usually produces more species. Explicit reporting of inventory results by capture method and habitat, together with appropriate quantification of sampling effort, are therefore crucial for meaningful intersite comparisons of bat species richness.

Although all the inventories we reviewed used ground-level mistnetting as the primary sampling method, most published reports either (1) did not distinguish species obtained by ground-level netting from those obtained by other methods (e.g., searching for roosts, harp-trapping, or elevated netting), (2) combined ground-level netting results from two or more distinct habitats (e.g., mature forest, successional vegetation, artificial clearings), (3) did not report ground-level netting results in sufficient quantitative detail to adjust intersite comparisons for sampling effort (e.g., no capture frequencies provided), or (4) used ground-level nets primarily in habitats that were not sampled at other sites (e.g., over open water). For these reasons, tabulated species counts (table 75) are undoubtedly affected by sampling artifacts to an extent that is hard to evaluate.

The apparently unusual richness of emballonurids, phyllostomines, and molossids in the Paracou fauna is a case in point. Because most emballonurids and many small phyllostomines are difficult to capture with mistnets, short-term inventory projects based largely or entirely on mistnet sampling might be expected to obtain fewer species in these groups than long-term projects, or than projects that incorporate supplementary sampling methods. Also, because molossids and some emballonurids (e.g., *Diclidurus* spp.) are primarily active above the forest canopy,

these bats are seldom caught except by netting over water (where they come to drink), by using elevated nets in canopy gaps, by shooting on the wing, or by discovering roosts (Voss and Emmons, 1996).

Published descriptions of inventory fieldwork (cited in the footnotes to table 75) generally support the artifactual interpretation of observed differences in emballonurid, phyllostomine, and molossid species richness outlined above. Low reported diversity for these groups is usually associated with short-term mistnet sampling at ground level only (e.g., on the Rio Xingu and at Cuzco Amazónico). By contrast, most reports of high emballonurid diversity are either from research stations with long histories of bat research (e.g., La Selva, Barro Colorado), and/or include data from acoustical monitoring (e.g., Barro Colorado, Imataca). After Paracou, the Amazonian site with the highest reported phyllostomine and molossid diversity is Arataye, where systematic roost searching and elevated mistnetting were also carried out (Brosset and Charles-Dominique, 1990).

Our own sampling data underscore the effects of supplementing mistnetting at ground level with other sampling methods. Thus, we captured only six emballonurids and three molossids (table 69) in ground-level nets, completely unremarkable counts by comparison with those from other inventory sites. The unusually large number of phyllostomines (23 species) netted at ground-level at Paracou is perhaps attributable to the lightweight (30 d) nets that we used in combination with an audible lure (the Audubon Bird Call), equipment not used together by any other Neotropical rainforest bat inventory project of which we are aware.

A different situation, however, is presented by the comparatively low diversity of carollines and stenodermatines at Paracou, which does not appear to have any plausible methodological explanation (all carollines and most stenodermatines are easy to catch in ground-level mistnets). We presume that our inventory is complete for these groups because every species is represented in our data by multiple (>7) observations (see Analyses of Sampling: Estimating Completeness, above), and because no new species were encountered in the last 116 days of our field-

work. It therefore seems reasonable to conclude that carollines and stenodermatines are less speciose at Paracou than they are at many other Amazonian (especially western Amazonian) sites. Possible explanations for this result are considered below.

The frequency data for ground-level mist-net sampling on Barro Colorado Island (BCI) published by Handley et al. (1991: table 1-2) provide the only approximately valid basis for statistical comparisons of species richness with our Paracou results.²¹ Barro Colorado Island is almost completely covered by tall lowland forest, of which that sampled by the BCI Bat Project is late successional growth about 100 years old (Kalko et al., 1996). Presumably, ground-level mistnetting on BCI primarily samples the forest understory and merits close comparison with our ground-level mistnet sampling of the primary forest at Paracou.

Relevant quantities from both sampling projects are summarized in table 78 together with species richness estimators. Although Handley et al. (1991) recorded 9118 captures (including recaptures) in ground-level mist-nets on 157 nights in 1979 on BCI, they encountered only 39 species. By contrast, we recorded just 1545 captures in ground-level mistnets on 63 nights from 1991 to 1994 at Paracou, but caught 57 species. Given the considerable disparity in sampling effort (almost 600% more captures and 250% more nights on BCI), these results clearly require adjustment by extrapolation. By Chao's (1984, 1987) methods, the estimated richness of understory species is about 65–67 at Paracou and about 40–41 on BCI. Although the confidence intervals around these point estimates are wide, they do not overlap between the two sites. Jackknife estimates of species richness (Heltshe and Forrester, 1983) are very similar to Chao's: 68 for Paracou and 42 for BCI. All extrapolations from the 1979

TABLE 78
Bat Sampling Results Using Ground-Level Mistnets in Primary Forest at Paracou and in Late Successional Forest on Barro Colorado Island (BCI)

	Paracou ^a	BCI ^b
Recorded captures ^c	1545	9118
Netting nights	62	157
Observed species	57	39
Singles ^d	9	3
Doubletons ^e	5	2
Uniques ^f	11	3
Duplicates ^g	6	3
Estimated species richness ^h		
S^*_1 (individuals)	65 ± 12	41 ± 6
S^*_2 (nights)	67 ± 13	40 ± 4

^a See tables 70 and 72.

^b See Handley et al. (1991: table 1-2).

^c Including recaptures.

^d Species for which only one individual was captured.

^e Species for which only two individuals were captured.

^f Species captured on only one night.

^g Species captured on only two nights.

^h Estimated species richness (S^*) was calculated by Chao's (1984, 1987) method from frequencies of (1) individuals (singletons and doubletons) or (2) nights (uniques and duplicates). Each point estimate is accompanied by its approximate 95% confidence interval (± 2 SD). All statistics have been rounded to the nearest integer.

BCI data agree closely with the total observed richness (43 species) in a representative set of 210 nights from 7 years of ground-level netting by the BCI Bat Project (Kalko et al., 1996). Sampling on this scale seems likely to have detected nearly every bat species normally active in the forest understory, from which we infer that the remaining 20-odd species in the known BCI fauna are either rare vagrants, are primarily active over water or in clearings, or normally fly well above the reach of ground-level nets.

Although geographic range data (summarized by Voss and Emmons, 1996) predict that Central American rainforest bat communities should be less diverse than Amazonian communities, the estimated difference in understory bat species richness between Paracou and BCI is unexpectedly large. Possibly, the same factors invoked to explain the island's conspicuously depauperate avifauna (extinctions plus habitat uniformity; see Wil-

²¹ Other published capture-frequency data from Neotropical bat inventories are not analyzable because they combine sampling results by different methods (e.g., ground-level and elevated netting; Brosset et al., 1996) and/or combine sampling results from different habitats (e.g., manmade clearings, river beaches, nonforest riparian vegetation, and primary forest; Ascorra et al., 1996). Such heterogeneity is irreducible by any statistical method and precludes valid intersite comparisons.

lis, 1974; Karr, 1982; Karr et al., 1990) may also have depleted the chiropteran community on BCI, but intensive comparative sampling on the adjacent mainland is needed to determine whether or not there really is an insular diversity deficit for bats. If not, then the large increase in understory bat species richness from BCI to Paracou suggests that species interactions in Amazonia are likely to be significantly more complex than those in Central American habitats, perhaps with important consequences for the behavior and demography of many bats hitherto studied primarily in Panama or Costa Rica.

TROPHIC GUILDS, HABITAT USE, AND OTHER TOPICS

Progress in the ecological classification of bats has generally consisted in subdividing the coarse dietary categories of older schemes by incorporating relevant observations or inferences about behavior. For example, whereas Fleming et al. (1972) treated all insectivorous species as one dietary class, Wilson (1973) distinguished aerial insectivores and foliage gleaners as distinct trophic categories, Bonaccorso (1979) divided aerial ("hawking") insectivores into separate "slow-flying" and "fast-flying" guilds, and Kalko et al. (1996) recognized three guilds of aerial insectivores based on the acoustical discrimination necessary to locate airborne prey in different habitats. The obvious result has been a proliferation of classes defined by criteria that, unfortunately, are difficult to determine for species with unstudied behaviors.

Lacking relevant information about the behavior of many species, and acknowledging the genuinely ambiguous dietary habits of others, we sorted Paracou bats into the following broad trophic categories using the published literature (e.g., Fleming et al., 1972; Gardner, 1977; Bonaccorso, 1979; Humphrey et al., 1983) as our primary basis for inference about diets: (1) aerial insectivores (all nonphyllostomids except *Noctilio leporinus*), (2) frugivores (carollines and stenodermatines), (3) gleaning animalivores (all phyllostomines except *Phylloderma stenops*, *Phyllostomus discolor*, and *P. hastatus*), (4) nectarivores (glossophagines), (5) omnivores (*Phylloderma stenops*, *Phyllostomus*

discolor, *P. hastatus*), (6) piscivores (*Noctilio leporinus*), and (7) sanguivores (desmodontines). For the most part, our trophic assignments are not problematic, particularly as they affect the principal points that we wish to make below. We acknowledge the heterogeneous nature of our gleaning-animalivorous group, but the sparsely documented (or completely unknown) food habits of several phyllostomine species in the Paracou fauna (e.g., *Glyphoncteris daviesi*, *Mimon bennettii*, *Tonatia carrikeri*, *T. schulzi*) would leave them otherwise unclassifiable. Also, numerous literature accounts (e.g., those cited by Gardner, 1977; Norberg and Fenton, 1988) suggest that many predatory phyllostomines are opportunistic foragers that do not discriminate between large insects and small vertebrates as acceptable items of diet.

For comparison with the Paracou fauna, we used the same criteria to identify trophic categories in other Neotropical rainforest bat inventories (table 79). To obtain an estimate of the relative importance of different trophic classes in local faunas, we divided the number of species in each category by the total known species richness at each site and multiplied by 100 to scale this quotient as a percentage. However, when scanning these figures it is important to recognize the well-known tendency of mistnet data to overestimate the richness of frugivores relative to most other feeding guilds (Handley, 1967; Tamsitt, 1967; Fleming et al., 1972; LaVal and Fitch, 1977; Kalko et al., 1996). Although this bias can be substantially reduced by sustained inventory effort using supplementary capture methods (fig. 77), many of the inventories we reviewed were short-term surveys and/or primarily used mistnets to capture bats.

AERIAL INSECTIVORES: This is the most speciose feeding guild at Paracou, where 28 members represent about 36% of the known fauna. At the other Neotropical rainforest sites we reviewed (table 79), aerial insectivores constitute 22–39% of the known species, with the lower numbers generally from short-term or methodologically limited surveys and the higher values mostly from well-studied sites or sites where ground-level mistnetting was supplemented by other col-

TABLE 79
**Numbers and Proportions of Species Assignable to Four Trophic Categories in
 14 Neotropical Rainforest Bat Faunas^a**
 (See text for definitions of trophic categories)

	Aerial insectivores	Frugivores	Gleaning animalivores	Nectarivores	Others	Total species
CENTRAL AMERICA						
Chajul	18 (36%)	13 (26%)	11 (22%)	2 (4%)	6 (12%)	50
La Selva	22 (34%)	16 (25%)	16 (25%)	6 (9%)	5 (8%)	65
Barro Colorado	26 (39%)	19 (29%)	13 (20%)	3 (5%)	5 (8%)	66
AMAZONIA						
Imataca	21 (34%)	20 (32%)	13 (21%)	4 (6%)	4 (6%)	62
Piste St.-Élie	14 (26%)	17 (31%)	14 (26%)	5 (9%)	4 (7%)	54
Paracou	28 (36%)	17 (22%)	22 (28%)	5 (6%)	6 (8%)	78
Arataye	15 (25%)	21 (34%)	15 (25%)	6 (10%)	4 (7%)	61
Cunucunuma	14 (28%)	20 (40%)	8 (16%)	4 (8%)	4 (8%)	50
Manaus	20 (38%)	14 (27%)	9 (17%)	5 (10%)	4 (8%)	52
Xingu	11 (23%)	17 (36%)	11 (23%)	4 (9%)	4 (9%)	47
Jenaro Herrera	17 (27%)	24 (39%)	12 (19%)	5 (8%)	4 (6%)	62
Balta	16 (29%)	23 (41%)	10 (18%)	5 (9%)	2 (4%)	56
Manu	13 (22%)	25 (42%)	12 (20%)	5 (8%)	5 (8%)	60
Cuzco Amazónico	12 (27%)	19 (43%)	8 (18%)	3 (7%)	2 (5%)	44

^a Inventory sites from which faunal data were obtained are identified in the footnotes to table 75.

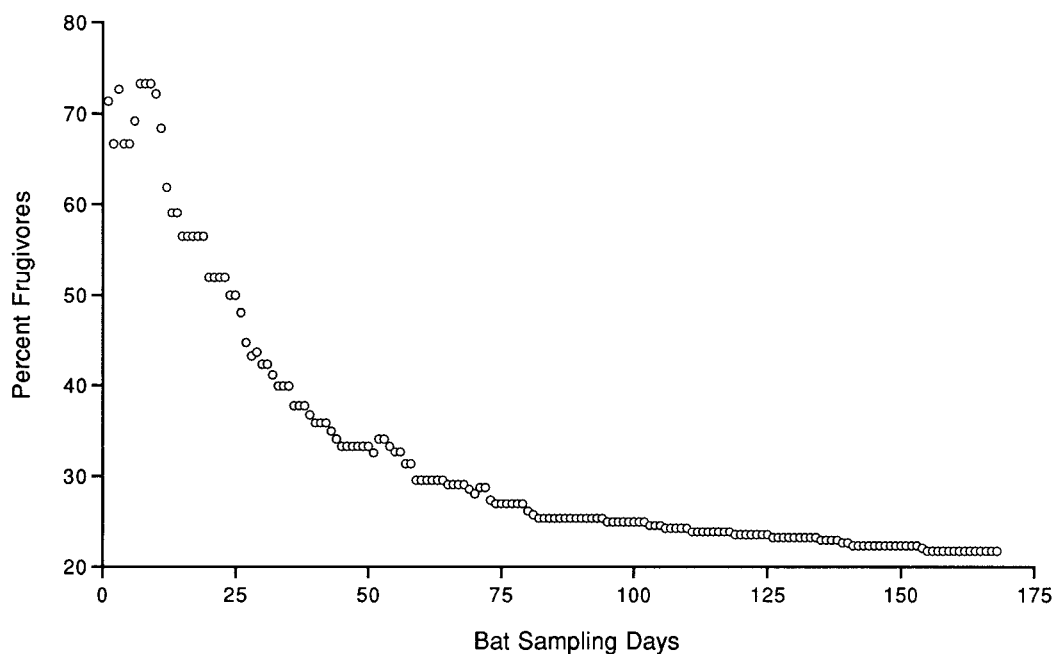


Fig. 77. Percent frugivore species in the known bat fauna at Paracou on each sampling day of our inventory from 1991 to 1994. From a maximal value of 73% after the first week of fieldwork, percent frugivory declined almost monotonically to a final value of 22% (see text). If our conjectures about inventory completeness are correct, frugivores probably constitute only about 19% of the local fauna.

lecting methods. Aerial insectivores are probably more speciose than other feeding guilds at all rainforest localities, although the inventory data at hand do not convincingly document such predominance.

Aerial insectivores are not randomly distributed among local habitats at Paracou. Instead, some species seem to be restricted to the forest understory, whereas others range into the upper levels of the forest or use small openings like treefalls. A distinct set of species appears to use exclusively the unobstructed airspace outside or above the forest. Although bats with apparently similar patterns of habitat use are not necessarily closely related phylogenetically, it is useful to review the aerial insectivore fauna family by family to identify systematic trends and highlight exceptions.

Most Paracou emballonurids use durable roosts (standing and fallen trees, hollow logs, or other woody shelters, not foliage) in the primary forest understory, although *Saccopteryx bilineata* and *S. leptura* also use subcanopy roosts. All of the emballonurid species we netted most frequently (*Cormura brevirostris*, *Peropteryx kappleri*, *Saccopteryx bilineata*, *S. leptura*) are apparently active above ground level in both manmade and natural clearings as well as in the forest understory (table 71). Although it is possible that many (perhaps most) of our ground-level mistnet captures of these species were individuals commuting to or from their diurnal retreats, Bradbury and Vehrencamp (1976) and Kalko (1995) observed *Saccopteryx bilineata* and *S. leptura* actively foraging in the forest understory at twilight, a temporal pattern consistent with our netting results.

Direct evidence of habitat use by other Paracou emballonurids is limited. Although we found several roosts of *Peropteryx leucoptera* in the forest, our observations suggest this species forages near ground level in treefalls and other small openings. We did not find any roosts of *Saccopteryx gymnura*, which we only netted twice, both times at ground level in clearings. Although the two understory roosts we found of *Peropteryx macrotis* resembled those of other *Peropteryx* species and *Cormura brevirostris*, we have no idea where this species is active because we never caught it in nets. Two tiny

bats that we once observed foraging for gnats just above the surface of a small stream were probably *Rhynchonycteris naso* (see Bradbury and Vehrencamp, 1976; Kalko, 1995), but they evaded our nets and we never actually caught this species except at culvert roosts. The habits of *Centronycteris maxmilianii* are a complete mystery. Although we found this species perched under a large leaf in the late afternoon, and although C. O. Handley, Jr. made a similar observation of a related species (*C. centralis*; see Simmons and Handley, 1998) in Panama, it is possible that both bats had just emerged from some other refuge; to date, nothing has been published concerning the foraging behavior of either species.

In striking contrast to other emballonurids, species of *Diclidurus* roost in foliage and fly in unobstructed airspace above the forest canopy or over water. Our single capture of *Diclidurus scutatus* suggests that even the highest elevated nets at Paracou barely intersected the foraging range of these bats.

The single mormoopid species known to occur at Paracou, *Pteronotus parnellii*, was only netted in the forest understory and (less commonly) at ground level in clearings. Bonaccorso's (1979) and Kalko et al.'s (1996) observations from Barro Colorado Island provide strong corroborative evidence that *P. parnellii* is exclusively an understory species in rainforest. Since there are no caves (reputedly the normal diurnal retreat of this species; Herd, 1983) in the vicinity of Paracou, we assume that the local population inhabits tree cavities, although we never found any roosts.

The two tiny nataloid species whose roosts we often found in the forest understory, *Furipterus horrens* and *Thyroptera tricolor*, probably forage primarily near ground level in the forest, but we have scant evidence to suggest that this is true, nor does anything appear to have been published concerning the nocturnal activities of these interesting bats.

With one exception, all vespertilionid species at Paracou were captured primarily or exclusively outside the forest. The exception, *Myotis riparius*, appears to be a true understory species that is replaced by its externally indistinguishable congener *M. nigricans* at

the forest edge; neither species of *Myotis* was commonly captured more than a few meters above the ground. By contrast, both *Eptesicus chiriquinus* and *E. furinalis* were netted from ground level to canopy height. *Lasiurus blossevillei* is perhaps active primarily above ground level except when it descends to drink at pools. We did not encounter the natural roosts of any vespertilionid at Paracou.

Out of almost 300 recorded captures representing nine species of molossids at Paracou, not one was inside the forest. Instead, our capture data strongly support the prevailing consensus (e.g., Wilson, 1989; Brosset and Charles-Dominique, 1990; Kalko et al., 1996) that in rainforested landscapes these fast-flying bats forage above the canopy, usually descending to ground level (if at all) only to drink or roost. By far the most frequently captured molossid at Paracou was *Molossus molossus*, which was the only species we ever took in ground-level nets away from water. It is perhaps noteworthy that although roadside puddles provided the only open water within our study area, only three molossid species (*Molossus barnesi*, *M. molossus*, and *M. rufus*) were netted in such situations. Very large fast-flying bats that might have been *Eumops trumbulli* were seen passing far above our highest elevated nets on several nights, and we assume that our molossid inventory is incomplete. We did not find the natural roost of any molossid species at Paracou.

GLEANNING ANIMALIVORES: Gleaning animalivores represent the second most speciose trophic category at Paracou, where they are represented by 22 species that constitute 28% of the known fauna. The proportions of gleaning animalivores in the other Neotropical rainforest bat inventories we reviewed are 16–26%, with most of the higher values from the better sampled sites and the lower values generally from short-term mistnet surveys. Although their proportion in the Paracou fauna might be unusually high, it seems probable that gleaning-animalivorous species constitute a large fraction of all Neotropical rainforest bat communities. In fact, the real trophic signature of Neotropical rainforest bat faunas may consist as much in the high diversity of gleaning animalivores as in the

TABLE 80
Comparison of Capture-Habitat Frequencies
Between Gleaning Animalivores and Frugivores
Taken in Mistnets at Paracou^a

	Capture habitats		Totals
	Primary forest	Modified habitats	
Gleaning animalivores	336	27	363
Frugivores	1069	688	1757
Totals	1405	715	2120

$$\chi^2 = 135.4, df = 1, p \ll 0.01$$

^a Table entries are numbers of captures (including recaptures). The chi-square value calculated from these data tests the null hypothesis of no guild difference in proportions of captures by habitat.

high frugivore diversity frequently emphasized in the literature.

A striking aspect of our sampling results is that almost all of our recorded captures of gleaning animalivorous bats were in the primary forest understory: only a few captures were in manmade clearings and almost none were in elevated nets. The latter observation, however, is hard to interpret because much of our elevated netting (72% in terms of net-meter-hours, table 70) was in manmade clearing; hence, the scarcity of captures in high nets may simply reflect an avoidance of artificial openings. Also, many gleaning animalivores were attracted to ground-level nets by squeaking with Audubon Bird Calls (e.g., *Chrotopterus auritus*, *Glyphonycteris daviesi*, *Micronycteris hirsuta*, *Trinycteris nicefori*, *Mimon crenulatum*, *Phyllostomus elongatus*, *Tonatia carrikeri*, *T. saurophila*, *T. schulzi*, *T. silvicola*, *Trachops cirrhosus*, *Vampyrus spectrum*), so our mistnet data cannot be interpreted as providing a random sample of vertical activity patterns for such species. Finally, most gleaning animalivores were infrequently netted under any circumstances, so their vertical activity ranges were doubtless undersampled by our inventory.

On the other hand, it is difficult to avoid the conclusion that most gleaning animalivores seldom venture outside the primary forest. Statistical comparisons of habitat capture frequencies among feeding guilds (e.g., table 80) simply reinforce our nightly field

experience that these bats do not commonly occur in modified habitats. That this is a guild phenomenon and not a trait of phyllostomines in general is suggested by our multiple captures of the omnivorous species *Phyllostomus hastatus* in manmade clearings, as well as by numerous literature accounts (e.g., LaVal, 1970) of *P. discolor* in similar situations.

Although LaVal and Fitch (1977), Belwood and Morris (1987), Fenton et al. (1992), and Wilson et al. (1996) previously reported that gleaning animalivorous bats are significantly more frequently captured in primary forest than in adjacent clearings or secondary vegetation at other Neotropical localities, the causes for this apparently widespread phenomenon are unclear. As remarked by LaVal and Fitch (1977), seemingly suitable food resources for gleaning animalivores are not absent in secondary growth. Belwood and Morris (1987) implied that gleaning animalivores do not occur in habitats lacking suitable woody supports to use as feeding perches, but some frugivores that are common in young secondary growth also use feeding perches (e.g., *Carollia perspicillata*; Charles-Dominique, 1991), so this behavior alone does not seem to be an adequate explanation.

Whatever sampling artifact or ecological variable might explain the restricted spatial distribution of gleaning animalivorous bat captures at Paracou, the fact remains that our mistnet data are not very informative about patterns of habitat use within this feeding guild. With only nine records of *Tonatia brasiliense*, we can only speculate that this species might favor swampy and creekside forest over well-drained formations. Other guild members were either captured in different primary forest habitats in roughly the same proportions expected from the distribution of netting effort, or were netted so infrequently that nothing can be inferred about their habits. The few natural roosts we found (of *Micronycteris brosetti*, *M. hirsuta*, *M. megalotis*, *M. microtis*, *Mimon bennettii*, and *Phyllostomus elongatus*) were in tree cavities or hollow logs.

Scattered dietary and behavioral observations in the literature suggest that the predatory habits of these bats may be richly di-

versified, but most dietary studies (e.g., those cited by Humphrey et al., 1983) have been carried out at Central American localities with relatively depauperate faunas where feeding niches are perhaps not maximally differentiated. Such studies might be particularly informative in Amazonia, where our results indicate that as many as five species of *Tonatia* and seven species of *Micronycteris* (sensu stricto) can be sympatric. However, it is possible that roosts, not food resources, are limiting for these small gleaners, a conjecture that also invites field testing in areas of maximal sympatric diversity.

FRUGIVORES: Next in richness at Paracou are frugivores, represented by 17 species, about 22% of the known fauna. By contrast, all of the other Neotropical rainforest bat inventories we reviewed have higher proportions of frugivorous species, ranging from 25% to 43% of the known fauna at each site. Although the highest values in this range are almost certainly attributable to undersampling of the aerial insectivore and gleaning animalivore communities, the actual numbers of frugivores at some western Amazonian sites (e.g., 23–25 species at Jenaro Herrera, Balta, and Manu; table 75) are remarkable.

Why the Paracou fauna is depauperate in species of frugivorous bats by comparison with other Amazonian (especially western Amazonian) inventories is an interesting question that may relate to the seasonal availability, diversity, and quantity of local fruit resources. Both at Paracou and at nearby Piste St.-Élie (with the same number of frugivorous bat species), fruit virtually disappears from the forest during the dry season (Sabatier, 1985; Henry, 1994), a 3- to 4-month annual bottleneck for resident frugivore populations that may exclude some species. Although dry-season fruit shortages also occur at western Amazonian inventory sites, asynchronous peaks of fruit production in adjacent floodplain habitats created by river meanders might be important for sustaining high frugivore diversity at some riparian localities (Terborgh, 1983; Janson and Emons, 1990). Poor local soils may also be a factor, perhaps constraining the diversity and density of fruit-producing plants at Paracou. Although we did not gather quantitative data on fruit production for comparisons with oth-

er inventory sites, the average count of 21 individual fruiting understory plants per 500-m transect that Gentry and Emmons (1987) reported for Manu (a western Amazonian inventory site with rich alluvial soils) seems much higher than anything we might have obtained by similar surveys in our study area, where fruiting understory plants were seldom seen in primary forest.

The results of our mistnet sampling strongly suggest that the two carollines at Paracou, *Carollia perspicillata* and *Rhinophylla pumilio*, are preeminently understory bats: abundant throughout the primary forest undergrowth, neither was commonly captured more than a few meters above the ground. In other important respects, however, these species differ conspicuously in habitat use. Whereas *Carollia perspicillata* is abundant in manmade clearings (presumably attracted by the high density of fruiting plants in early-successional vegetation along the margins), *Rhinophylla pumilio* was more frequently netted inside the primary forest, a habitat association previously noted by Brosset and Charles-Dominique (1990). Also, whereas *C. perspicillata* roosts in tree cavities and manmade structures, *R. pumilio* apparently roosts only in foliage.

All of the 15 stenodermatine species we encountered at Paracou were taken in ground-level mistnets, but our capture data for many species that were sometimes attracted by squeaking or by the cries of conspecifics tangled in ground-level nets (*Artibeus jamaicensis*, *A. lituratus*, *A. obscurus*, *A. gnomus*, *A. concolor*, *Chiroderma villosum*, *Uroderma bilobatum*) probably give a biased picture of vertical activity range. For example, although we seldom caught *Artibeus jamaicensis* (a well-known canopy frugivore) more than a few meters above the ground, most of the individuals netted at ground level were observed to descend from the canopy or subcanopy in response to real or simulated distress calls. Nevertheless, the scarcity of elevated net captures for some common species and the complete absence of such records for others suggest that they are seldom, if ever, active far above ground level; notable examples are *Artibeus cinereus*, *Sturnira lilium*, and *S. tildae*. By contrast, we recorded multiple elevated net captures, in-

cluding one or more above 15 m, for *Ametrida centurio*, *Artibeus lituratus*, *A. obscurus*, *A. gnomus*, *A. concolor*, *Chiroderma trinitatum*, *C. villosum*, *Platyrrhinus helleri*, and *Vampyressa brockii*; of these, however, only *A. centurio* and *C. villosum* were taken in our highest nets (34–37 m).

Our results support Brosset and Charles-Dominiques' (1990) hypothesis that two congeneric pairs of small stenodermatines differ significantly by their use of primary versus secondary vegetation in French Guiana (see also Brosset et al., 1995, 1996). In their data and in ours, *Artibeus (Dermanura) cinereus* and *Sturnira lilium* are mostly active in the early-successional growth along the margins of manmade clearings, whereas *A. (D.) gnomus* and *S. tildae* are more often associated with primary forest. It would be interesting to know in what natural habitats the former two species and other small plant-visiting bats highly characteristic of young secondary growth (*Carollia perspicillata*, *Glossophaga soricina*) are found in pristine landscapes where manmade clearings do not exist. Possibly they are most abundant along rivers, in the pioneering riparian vegetation that colonizes beaches and eroded banks; treefall openings are another possibility (Charles-Dominique, 1991). Rather than being restricted to modified habitats per se, it seems likely that the abundance of *A. cinereus*, *S. lilium*, and *C. perspicillata* is simply correlated with the local density of the heliophilous shrubs and small trees whose fruits they prefer: *Piper*, *Solanum*, and *Vismia* (de Foresta et al., 1984; Charles-Dominique, 1986).

The results of our roost survey confirm previous observations (reviewed by Kunz et al., 1994) that *Artibeus cinereus*, *A. gnomus*, *Ectophylla macconnelli*, and *Uroderma bilobatum* roost in leaf-tents. The only other stenodermatine roosts we found were of *Artibeus obscurus* (females under bark chips, one male under an unmodified leaf), apparently the first to be reported for this species. Our extensive searching at ground level also tends to support Emmons' (1990, 1997) speculation that *Sturnira* species roost in the canopy, as may well be true for all of the other Paracou stenodermatines whose diurnal retreats were not found.

Although frugivores comprise only 22% of the known species in the Paracou fauna, they accounted for 63% of our total recorded mistnet captures at all heights and in all habitats sampled from 1991 to 1994. In the primary forest understory, frugivores accounted for an even higher fraction (68%) of recorded mistnet captures. From these numbers we conclude merely that frugivores blunder into mistnets more frequently than do members of other feeding guilds. Given the plethora of confounding behavioral variables that can affect mistnet capture frequencies for birds (Remsen and Good, 1996), and presumably for bats too, no valid conclusions about relative abundance from such data seem possible. Whether or not frugivores account for more individuals or more biomass than do members of other feeding guilds can only be answered by real census data (actual counts of individuals in a delimited study area), information that can be obtained with extraordinary effort for rainforest birds (Terborgh et al., 1990), but that seems logistically prohibitive for community-level studies of rainforest bats.

NECTARIVORES: Nectarivores rank a distant fourth in guild richness at Paracou, including only five known species, a mere 6% of the fauna. Essentially similar numbers and proportions are documented at most of the other Neotropical rainforest localities we reviewed (table 79).

Only two nectarivorous species were netted frequently in our study area, one of which was taken exclusively at ground level (*Glossophaga soricina*) and the other (*Lonchophylla thomasi*) with only a single unvouchered capture recorded in an elevated net. At Paracou, these two common understory nectarivores seem to be partially segregated by successional stage, with *L. thomasi* occurring mostly in primary forest and *G. soricina* more commonly in modified habitats (an ecological association previously documented by Brosset et al. [1996: table 1]). Also,

whereas *L. thomasi* roosts under fallen trees and in hollow logs, *G. soricina* apparently roosts in cavities in standing trees and in manmade structures. A third species, *Chorioniscus minor*, appears to resemble *L. thomasi* in favoring primary forest, where one roost was found under a fallen tree. The remaining two species (*Anoura caudifera* and *Lichonycteris obscura*) were each captured only once, in ground-level mistnets in primary forest, from which nothing but their presence in the area can be inferred.

OTHER FEEDING GUILDS: The remaining guilds are represented by very few species at Paracou as they are at all other Neotropical rainforest localities. Of the three omnivores found in our study area, *Phyllostomus hastatus* was the most frequently captured, both at ground level and at the very highest level of the canopy, in both primary forest and in manmade clearings. Although *P. discolor* was less frequently captured, it too was repeatedly taken in elevated nets as well as in the forest understory. *Phylloderma stenops* was rarely captured as it apparently is everywhere within its geographic range; our scant data suggest that it favors the primary forest understory. We did not find roosts of any omnivorous species at Paracou.

As at all other Neotropical rainforest localities lacking local concentrations of domesticated animals, vampires are rare at Paracou. In fact, both *Desmodus rotundus* and *Diaemus youngi* were captured so infrequently that almost nothing about their local patterns of habitat use can be inferred. However, our single elevated-net capture of *D. youngi* is apparently the first direct evidence that this vampire is active in the rainforest subcanopy. We never found the local roosts of either species.

Noctilio leporinus, apparently the only known species of Neotropical rainforest piscivore, was infrequently captured only in nets set across the largest stream in our study area.

SUGGESTIONS FOR FUTURE WORK

Given current rates of habitat destruction in Central and South America, opportunities for rainforest inventory fieldwork in many

zoogeographically important areas may disappear forever over the next few decades. In the trans-Andean, coastal Venezuelan, and

Atlantic rainforests (*sensu* Voss and Emmons, 1996), few localities with pristine habitat remain, and any that do should be targeted immediately for comprehensive biological surveys. Although much of the Amazonian rainforest remains intact, biological survey work in advance of large-scale development projects (hydroelectric dams, mining, commercial logging, etc.) is urgently needed at many sites.

Inevitably, money, personnel, and logistics will constrain the duration of inventory fieldwork everywhere, so maximizing the efficiency of faunal sampling is a clear priority. Equally important is the effective dissemination of results in the literature, for which certain reporting standards are desirable. In addition, quantitative methods suitable for analyzing the less-than-ideal sampling data obtained by inventory fieldwork at remote localities should be adopted to formalize intersite diversity comparisons. Finally, the feasibility of rapid diversity assessment at sites where prolonged inventory work is impossible needs to be evaluated. We offer suggestions on these four topics as they apply to bat research below.

IMPROVING INVENTORY EFFICIENCY

Our results clearly show that supplementing ground-level mistnetting with elevated netting and roost surveys can substantially increase bat inventory efficiency. In our last field season (1994), the equivalent of two persons working full time captured 63 species in just 45 days, a rate of accumulation apparently unmatched by any previous inventory but probably achievable (or surpassable) with equivalent effort almost anywhere in Amazonia. Although we have not completed an exhaustive efficiency analysis of our sampling data, certain factors are obviously important for the effectiveness of each method.

GROUND-LEVEL MISTNETTING: In our results, the single best predictor of the number of species netted at ground level on a given night is the number of individuals captured ($r^2 = 0.56$), and (all else being equal) the single most important determinant of the number of captured individuals is the number of meters of net deployed. However, capture

rates were almost always depressed by bright moonlight and by using the same net setup for more than a single night (second-night captures are about 50–60% fewer, on average, than first-night captures in the same nets). Most bats are caught early in the evening, and some species are only active in the understory at dusk. Therefore, maximally effective ground-level netting is achieved by using many nets, moving them every night, opening the nets before it is fully dark, and by scheduling mistnet sampling (if tradeoffs with other inventory activities are necessary) in the first three lunar quarters (when there is no bright moonlight in the early evening). The Audubon Bird Call should be part of every inventory field kit, but analyses of our data do not indicate any significant sampling difference between lightweight (30 d) and standard-weight (70 d) mistnets, which appear to be roughly equivalent in terms of numbers of individual bats captured per net-meter-hour and in the number of species represented per captured individual.

ELEVATED NETTING: Our crude method of suspending mistnets above ground level had nothing but simplicity and expediency to recommend it; any of the alternative systems described in the literature (e.g., by Humphrey et al., 1968; Whitaker, 1972; Dejonghe and Cornuet, 1983; Ingle, 1993) would probably have worked as well. However, lacking detailed information about where elevated nets were suspended in relation to canopy gaps at other rainforest localities, we cannot explain why such disparate results for this method have been reported in the literature. For example, we captured many molossids in our elevated nets as Brosset and Charles-Dominique (1990) did in theirs, but no molossids were caught in the elevated nets used by Handley (1967) or Ascorra et al. (1996). It is probably important to suspend nets in unobstructed airspace, either as high as possible above large treefalls or across open corridors through the forest such as roadways and streams.

ROOST SURVEYS: Based on our density estimate of 0.9 bat roosts/ha near ground level in primary forest, and assuming that most roosts can be detected at a distance of 10–15 m, it would be reasonable to expect to find about two to three roosts per kilometer

of searched trail or transect. A well-developed trail system is therefore a great advantage in searching for roosts (as it is for mist-netting and other inventory activities as well; Voss and Emmons, 1996). In our experience, developing an effective search image for the types of structures used as shelters by bats is the most important determinant of success in finding roosts. The ability to hear high-pitched vocalizations and muffled wing-beats is also important when inspecting potential roost sites where visibility is limited. Probably, any active person with sharp eyes and ears can learn to search effectively for bat roosts after several weeks in the forest.

STANDARDS FOR REPORTING INVENTORY DATA

In reviewing the literature on Neotropical rainforest bats, we found many important diversity studies that would have been even more useful if additional information about specimen identification and sampling results were provided. The adoption of the following minimal reporting standards would greatly increase the utility of published inventory reports.

VOUCHERED TAXONOMIC IDENTIFICATIONS: Some species of rainforest bats are impossible to identify except from cleaned cranial material, and many others have such subtle field characters that inattention could easily lead to errors in identification. Even experienced taxonomists make mistakes in the field, and the only way to resolve doubtful issues of identification is to check voucher material. Obviously it is neither necessary nor justifiable to kill every individual bat in order to identify it; most species can be reliably identified in the hand once some familiarity with the local fauna is gained. However, new Neotropical rainforest species are being described at the rate of several each year, and many taxa long ignored as synonyms or nomina dubia (e.g., *Peropteryx trinitatis*, *Micronycteris homezi*, *M. microtis*, *Molossus barnesi*) are increasingly being recognized as valid species. Therefore, all species identifications in published inventory reports should be documented by museum specimens cited by catalog number to provide a permanent basis for subsequent eval-

uation. Species lists based largely on unvouchered identifications (e.g., Smith and Kerry, 1996; Robinson, 1998) are essentially worthless for the purposes either of research or conservation.

ECOLOGICAL DESCRIPTIONS: The local environment where bats were captured should be described in sufficient detail for ecologically meaningful comparisons with inventory results from elsewhere. Site descriptions should minimally include accounts of local topography, climate, and soils, as well as an explicit statement about what habitats were actually sampled for bats (e.g., primary forest, secondary growth, savannas, swamps, canebrakes, river beaches, lakeshores). Habitat accounts should be informative about the successional stage and physiognomy of major vegetation types. For bats, the presence or absence of caves and rocky outcrops is an important ecological factor that should always be mentioned.

SPECIES ACCUMULATION CURVES: Graphs of species accumulation are essential tools for assessing inventory completeness, but Fleming et al. (1972), Medellín (1993), Brosset et al. (1996), and Kalko et al. (1996) are among the few investigators who have used this method to evaluate bat sampling results. Ideally, species accumulation should be graphed against appropriate measures of sampling effort for each capture method used and for each major habitat sampled. For intersite comparisons of mistnet surveys (e.g., Karr et al., 1990), number of captures is much to be preferred as a measure of effort over such proxy units as nights of netting, net-nights, or net-hours.

TABULATIONS OF CAPTURE FREQUENCIES: Full frequency data broken down by capture method and habitat are extremely useful for inventory comparisons. However, such tabulations are expensive to typeset and take up considerable page space, so editors will probably discourage complete documentation. Furthermore, habitats that do not support distinctive faunas are of limited interest, and some heterogeneous categories (e.g., "man-made clearings") are hard to compare meaningfully from site to site. As a standard for intersite comparisons of bat faunas within the Neotropical rainforest biome, we suggest publishing complete capture frequency data

for ground-level mistnetting in mature (late successional or primary) forest (e.g., table 72). Such data lend themselves to statistical treatment by extrapolation or rarefaction, quantitative methods that should be used routinely to reduce bias and subjectivity in comparing samples of unequal size from different sites (see below).

QUANTITATIVE METHODS FOR DIVERSITY COMPARISONS

Meaningful intersite comparisons of species richness require that some correction be made for unequal sampling because, all else being equal, more intensively sampled sites will always tend to have larger species lists than will sites where sampling was less intensive. Extrapolation is one statistical approach to this problem (e.g., table 78) in which the standard of faunal comparison is true species richness at each site, which can be estimated in many ways (Colwell and Coddington, 1994). Of primary interest for comparing Neotropical rainforest bat faunas are robust estimators that can provide approximately valid extrapolations from data collectible in the course of inventory fieldwork by limited personnel working at remote sites. The constraints on data collection imposed by field logistics and other considerations are significant.

Accurate counts of individuals are not obtainable unless (1) all captured bats are killed, or (2) all released bats are marked for subsequent recognition. The first alternative is repugnant to many investigators (including ourselves) and would require devoting an enormous amount of field time to specimen preparation. To be humane and effective, the second alternative requires necklacing (Handley et al., 1991: appendix), which is labor-intensive and does not seem feasible for inventory work except at well-appointed field stations where a sufficient number of assistants can be housed and fed.

Capture-frequency data from most inventory projects will therefore consist, like ours, of an unknown number of recaptures for the common species and counts of individuals (preserved as specimens) for the rare species. This is not a problem for some nonparametric extrapolation methods (e.g., those that only re-

quire counts of singletons and doubletons), but it does preclude extrapolations based on fitting parametric models of relative abundance (which require more-or-less accurate individual counts for all species). Extrapolating species accumulation graphs (as by Medellín, 1993) is another option, but different mathematical functions fitted to the same empirical curve can give very different estimates of the asymptote, and we do not see how such functions can be chosen a priori by biological criteria (as recommended by Soberon and Llorente, 1991). Furthermore, a recent simulation study of the most popular function fitted to species accumulation data does not encourage confidence in practical applications (Keating and Quinn, 1998).

An alternative to extrapolation is rarefaction, which estimates the expected number of species, $E(S_n)$, in a sample of n observations drawn at random from a larger collection with N observations of S species (Hurlbert, 1971; Heck et al., 1975; Simberloff, 1979; James and Rathbun, 1981). For example, to compare 500 captures of 27 species at site A with 2000 captures of 31 species at site B, the rarefaction method calculates $E(S_{500})$ from the capture-frequency data for site B. If actual counts of individuals belonging to each species are available from both sites (by removal or by marking), the sampling is without replacement and $E(S_n)$ is calculated from the hypergeometric distribution; if individuals were not removed (or marked), however, the sampling is with replacement and $E(S_n)$ can be calculated from the multinomial distribution (Hurlbert, 1971). Perhaps the latter method would be appropriate if most captured individuals were released unmarked, but no statistician will be happy about analyzing mixed frequency data that include recaptures of common species but not of rare species.

Many statistical improprieties are likely to be involved in any quantitative analysis of rainforest mammal inventory data. Our samples are perhaps never random with respect to any underlying probability distribution, and they may seldom (if ever) be truly independent. Nevertheless, even flawed applications of extrapolation or rarefaction methods to the data at hand seem preferable to merely ad hoc inference.

PROSPECTS FOR RAPID DIVERSITY ASSESSMENT

Exhaustive inventories of Neotropical rainforest bat faunas are not feasible objectives for short-term fieldwork: too many species are rare or hard to capture. Perhaps the most methodologically accessible bat taxa in Neotropical rainforest faunas are carollines and stenodermatines, all of which can probably be captured with ground-level mistnets and by searching for roosts. However, it still took us the equivalent of more than two months in the field (71 bat sampling days) to collect the last stenodermatine species found at Paracou, and it took considerably longer to convince us that our stenodermatine inventory was probably complete. Exhaustive enumeration of the members of any speciose taxonomic group (or trophic category) of Neotropical rainforest bats is therefore likely to be a lengthy process.

A possibly feasible option for gathering meaningful data on Neotropical rainforest bat diversity by short-term fieldwork would involve sampling by some standard protocol to obtain data that could be analyzed by extrapolation or rarefaction to make statistical comparisons between sites. However, extensive replicated sampling would be required to determine how much effort and what degree of standardization are necessary to obtain consistent results at the same site before any short-term protocol could be validly used as a basis for intersite comparisons. For example, Chao's (1984) extrapolation method applied to ground-level mistnet samples from different field seasons at Paracou gives wide-

ly varying estimates of bat species richness in the primary forest understory (36–82 species).

Another problem is the extent to which sampling just one component of the fauna permits valid conclusions about the whole. Perhaps the understory bats sampled by ground-level mistnetting respond to zoogeographic or rainfall gradients in a completely different way than do high-flying aerial insectivores. Rapid assessment protocols focused on one capture method, one habitat, or one trophic group may therefore miss important heterogeneity in geographic diversity patterns of rainforest bats. Ideally, any diversity assessment protocol, rapid nor not, should include complementary methods to maximize the fraction of the fauna effectively sampled. Fortunately, it is not necessary to choose between rapid assessment on the one hand and a decades-long commitment to exhaustive inventory on the other.

As this report demonstrates, it is possible to obtain a reasonably complete survey of a Neotropical rainforest bat fauna in only a few field seasons, and we think that the time necessary to achieve comparable results could be substantially shortened. Indeed, from our 1994 results it seems plausible that 90% completeness might be attainable in less than six months with experienced personnel using all methods with maximal efficiency. Ninety percent inventory completeness is probably good enough for most research and conservation objectives, and the fieldwork necessary to accomplish it is well within the means of many small funding agencies.

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APPENDIX 1

Bats Previously Reported from French Guiana or Surinam, But Not Captured at Paracou

Among the bats that we did not capture in the course of our 1991–1994 fieldwork at Paracou are 37 species previously reported from other localities in French Guiana or Surinam. We list the original published records of these taxa below, providing comments where necessary to explain relevant issues of identification or habitat association. French Guianan collection localities are mapped in figure 1. Bats are identified as rainforest species if they are known from humid lowland sites (in the eastern Guianas or elsewhere) where rainforest is the predominant natural vegetation; in a few cases, we cite literature to support habitat associations, but the species matrix of rainforest inventory sites in appendix 2 provides adequate documentation in most cases. Our list does not include several problematic Surinamese records whose doubtful validity has been discussed elsewhere: *Pygoderma bilabiatum* (see Voss and Emons, 1996: table 1, footnote k), *Myotis surinamensis* (see Carter and Dolan, 1978: 72–73), and *Eumops glaucinus* (see Husson, 1962: 239–240; Eger, 1977: 39).

Of the species listed below, eight (*Anoura geoffroyi*, *Lonchorhina aurita*, *L. fernandesi*, *Phyllostomus latifolius*, *Platyrrhinus aurarius*, *P. brachycephalus*, *Natalus tumidirostris*, *Myotis albescentis*) seem unlikely to occur at Paracou because their known habits or published distributions suggest consistent associations with habitats that do not occur in our study area (e.g., mountains, caves, rock outcrops, open water). Another six species, all frugivores (*Carollia brevicauda*, *Platyrrhinus lineatus*, *Vampyressa bidens*, *V. melissa*, *V. pusilla*, *Vampyrodes caraccioli*), seem unlikely

to be local residents (although they might occur as rare vagrants) because our inventory is apparently complete for this trophic category (see Analyses of Sampling: Estimating Completeness, above). The remaining 23 species are those that could plausibly be detected with additional inventory effort at Paracou: *Diclidurus albus*, *Cyttarops alecto*, *Peropteryx trinitatis*, *Saccopteryx canescens*, *Pteronotus gymnotus*, *P. personatus*, *Choeroniscus godmani*, *Lionycteris spurrelli*, *Lamproncycteris brachyotis*, *Thyroptera discifera*, *Eptesicus brasiliensis*, *Lasiurus atratus*, *L. ega*, *L. egregius*, *Rhogeessa hussoni*, *Eumops maurus*, *E. trumbulli*, *Molossops greenhalli*, *M. neglectus*, *M. planirostris*, *Nyctinomops laticaudatus*, *N. macrotis*, *Promops nasutus*.

1. *Diclidurus albus*: Ojasti and Linares (1971) reported this widespread rainforest bat from Surinam, but the species is apparently unknown in French Guiana.

2. *Cyttarops alecto*: A single specimen of this rarely collected rainforest species was reported from Piste St.-Élie, French Guiana, by Masson and Cosson (1992). It has apparently not been collected in Surinam.

3. *Peropteryx trinitatis*: This species was reported by Brosset and Charles-Dominique (1990) from Cayenne, French Guiana. Although all known French Guianan material is apparently from urban areas (Brosset et al., 1996), Venezuelan collection data reported by Handley (1976) suggest that this species could be expected in rainforest habitats.

4. *Saccopteryx canescens*: Brosset and Charles-Dominique (1990) reported this widespread and

possibly eurytopic species from Cayenne, French Guiana. Surinamese records were summarized by Husson (1962, 1978).

5. *Pteronotus gymnonotus*: Brosset et al. (1996) reported a single specimen of this widespread rainforest bat from primary forest "at the Regina-St. Georges road project," presumably somewhere between the rivers Approuague and Oyapock in northeastern French Guiana. To date, *P. gymnonotus* has not been recorded from Surinam.

6. *Pteronotus personatus*: This widespread rainforest species was reported by Brosset and Charles-Dominique (1990) and Williams et al. (1990) from Kaw, Rémire, and Stoupan, French Guiana. Williams and Genoways (1980a) reported *P. personatus* in Surinam.

7. *Anoura geoffroyi*: This rainforest species was reported from French Guiana at Cayenne, Fourgassie, Les Nouragues, and Saül by Brosset and Charles-Dominique (1990). Specimens from Surinam were reported by Husson (1962, 1978). Descriptions of roosting habits (e.g., by Handley, 1976; Brosset and Charles-Dominique, 1990) and the geographic distribution of collection localities for *A. geoffroyi* suggest that it is restricted to the vicinity of caves and rock outcrops.

8. *Choeroniscus godmani*: This widespread rainforest bat is known from Surinam (Williams and Genoways, 1980a) but has apparently never been captured in French Guiana.

9. *Lionycteris spurrelli*: Webster and McGillivray (1984) reported French Guianan specimens of this widespread rainforest species from Saül, and Brosset and Charles-Dominique (1990) reported additional material from Les Nouragues, Montagne de Kaw, and Piste St.-Élie, French Guiana. Husson (1962, 1978) and Williams and Genoways (1980a) described specimens from Surinam.

10. *Lamproncycteris brachyotis*: This uncommonly collected but widespread rainforest bat (formerly placed in the genus *Microncycteris*) was originally described from Cayenne, French Guiana, by Dobson (1878), and an additional French Guianan specimen from an unidentified locality was reported by Brosset et al. (1996). Specimens from Surinam were reported by Husson (1978).

11. *Lonchorhina aurita*: Genoways et al. (1981) reported this widespread rainforest bat from Surinam, but it has not been collected in French Guiana. Literature accounts (e.g., Goodwin and Greenhall, 1961; Handley, 1976; Lassieur and Wilson, 1989) consistently indicate that *L. aurita* roosts in caves, abandoned mine shafts, or other rocky refugia.

12. *Lonchorhina fernandesi*: Specimens originally reported from Les Nouragues, French Guiana, as *L. marinkellei* (Brosset and Charles-Dom-

inique, 1990) were subsequently reidentified as *L. fernandesi* by Brosset et al. (1996). The French Guianan population was collected from a cave, and the species is presumably restricted to the vicinity of caves or rock outcrops like other congeners (Ochoa and Sanchez, 1988).

13. *Phyllostomus latifolius*: Brosset and Charles-Dominique (1990) reported this rainforest species from Kaw and Les Nouragues, French Guiana. Williams and Genoways (1980a) reported material from Surinam. Apparently, all known collection localities are near mountains or rock outcrops, where Brosset and Charles-Dominique's observations suggest they roost in caves.

14. *Carollia brevicauda*: Brosset and Charles-Dominique (1990) reported French Guianan specimens or observations of this common rainforest species from Armontabo, Les Nouragues, Petit Saut, Saut Pararé, and Saül. Genoways and Williams (1979) and Williams and Genoways (1980a) described specimens from Surinam.

Carollia castanea was reported from Saül, French Guiana, by Brosset and Dubost (1967) based on specimens that Brosset and Charles-Dominique (1990) later reidentified as *C. brevicauda*. Similarly, Husson (1962, 1978) reported material identified as *C. castanea* from Surinam, but Genoways and Williams (1979) observed that the published measurements of Husson's specimens resembled measurements of *C. brevicauda*. In fact, any identifications of small *Carollia* prior to Pine's (1972) revision are suspect, and Husson's 1978 text did not take that revision into account (op. cit.: 128); although Husson's material has not been reexamined, we assume that it was misidentified. Apparently, Webster and McGillivray (1984) were also mistaken in reporting *C. castanea* from French Guiana because their voucher material (at KU) has since been reidentified as *C. brevicauda* (R. M. Timm, personal commun.). No valid records of *C. castanea* are currently known from either French Guiana or Surinam.

15. *Platyrrhinus aurarius*: This species was reported from the Tafelberg in Surinam by Williams et al. (1983). All known collection localities for *P. aurarius* are in montane or premontane forest on the eroded, rocky highlands of Pantepui (Handley, 1976; Gardner, 1989).

16. *Platyrrhinus brachycephalus*: Brosset and Charles-Dominique (1990), Williams et al. (1990), and Brosset et al. (1995) reported specimens from Anse de Sinnamary, Cayenne, Rémire, and Sinnamary, French Guiana. Surinamese material was described by Williams and Genoways (1980a). The maritime situation of all known collection localities in both French Guiana and Surinam, together with the explicit habitat observa-

tions of Brosset et al. (1995, 1996), suggest that the distribution of *P. brachycephalus* in the eastern Guianas is restricted to coastal vegetation; no rainforest records are apparently known.

17. *Platyrrhinus lineatus*: This species was reported from Les Nouragues, French Guiana by Brosset and Charles-Dominique (1990), and from Surinam by Williams et al. (1983). As the taxonomic limits of this species are currently understood (following Koopman, 1978), *P. lineatus* is widespread in savannas, dry forests, and subtropical forest south of the Amazon, and in montane Andean forests (Willig and Hollander, 1987). Apparently, Brosset and Charles-Dominique's specimen is the only known example of *P. lineatus* collected in Amazonian rainforest (the Surinam record is from savanna).

18. *Vampyressa bidens*: This widespread Amazonian rainforest species was reported from Les Nouragues, French Guiana, by Brosset and Charles-Dominique (1990) and from Surinam by Genoways and Williams (1979) and Williams and Genoways (1980a).

19. *Vampyressa melissa*: Brosset and Charles-Dominique (1990) reported two specimens from Les Nouragues, French Guiana. All other known records of this species are from montane forest in the Andes.

20. *Vampyressa pusilla*: Brosset and Charles-Dominique (1990) reported French Guianan material of this rainforest species from Piste St.-Élie and Les Nouragues. Apparently, *V. pusilla* is unknown from Surinam.

21. *Vampyrodes caraccioli*: This widespread rainforest bat was first reported from French Guiana by Brosset et al. (1995), who caught a single specimen in coastal swamps at Anse de Sinnamary. Brosset et al. (1996) reported additional material from primary forest at an undisclosed locality. Surinamese specimens were reported by Genoways et al. (1981).

22. *Natalus tumidirostris*: A single specimen of this species was reported from secondary coastal forest near Montjoly, French Guiana (Brosset et al., 1996) and another from a savanna locality in Surinam (Williams et al., 1983). Accounts of roosting habits (e.g., Goodwin and Greenhall, 1961; Handley, 1976) suggest that the distribution of *N. tumidirostris*, like those of other natalids, is probably restricted to the vicinity of caves.

23. *Thyroptera discifera*: Thomas's (1928b) passing mention of specimens from Cayenne is apparently the only published record of this widespread but seldom collected rainforest species in French Guiana. A single Surinamese specimen was reported by Genoways et al. (1981).

24. *Eptesicus brasiliensis*: Specimens of this widespread rainforest species were reported from

Surinam (as *E. melanopterus*) by Husson (1962, 1978). The species is apparently unknown from French Guiana.

25. *Lasiurus atratus*: This rainforest species was recently described from a Surinamese type by Handley (1996), who also reidentified as *L. atratus* a single specimen from Saül, French Guiana, originally reported as *L. castaneus* by Masson and Cosson (1992).

26. *Lasiurus ega*: This very widespread and possibly eurytopic species was reported from Surinam by Husson (1962, 1978) and Williams and Genoways (1980a). It is apparently unknown from French Guiana.

27. *Lasiurus egregius*: This rare but widespread species was reported by Williams et al. (1990) from the vicinity of Piste St.-Élie, French Guiana. The predominant natural vegetation of at least two of the four known collection localities is rainforest.

28. *Myotis albescens*: Husson (1962, 1978) reported specimens of this very widespread species from Surinam, but *M. albescens* is currently unknown in French Guiana. Although commonly collected at rainforested sites, most explicit descriptions of captures or behavior (e.g., Handley, 1976; Ascorra et al., 1996; Kalko et al., 1996) suggest that *M. albescens* is primarily associated with open water.

29. *Rhogeessa hussoni*: Recently described by Genoways and Baker (1996) based on one specimen from Surinam and another from southeastern Brazil, this species is not currently known from French Guiana. The holotype of *R. hussoni*, originally misidentified as *R. tumida* by Williams and Genoways (1980a) and Honeycutt et al. (1980), was collected in an area of mixed savanna and gallery forest, but the ecological distribution of the species is otherwise unknown.

30. *Eumops maurus*: This species (which includes *E. geijskesi* as a junior synonym; Eger, 1977), was reported from Surinam by Husson (1962, 1978). It has not been reported from French Guiana, and its habitat associations are apparently unknown.

31. *Eumops trumbulli*: This species, which appears to be distinct from *E. perotis* according to Eger's (1977) revisionary study (contra Koopman, 1978), was reported from Surinam by Husson (1962, 1978). Geographic information summarized by Eger document the occurrence of *E. trumbulli* throughout Amazonia, and many collection records are from sites where rainforest vegetation predominates.

32. *Molossops greenhalli*: This apparently widespread rainforest species was reported from Les Nouragues, French Guiana, by Brosset and

Charles-Dominique (1990), and from Surinam by Williams and Genoways (1980a).

33. *Molossops neglectus*: Originally described from a Surinamese holotype (Williams and Genoways, 1980b), *M. neglectus* is still unknown from French Guiana. Although the type was collected in savanna, subsequently identified material convincingly documents the occurrence of this species in rainforest (Ascorra et al., 1991b, 1993).

34. *Molossops planirostris*: This rainforest species has been reported from Les Nouragues and Saül, French Guiana (Webster and McGillivray, 1984; Brosset and Charles-Dominique, 1990), and from Surinam (Husson, 1962, 1978).

35. *Nyctinomops laticaudatus*: Brosset and Dubost (1966) and Brosset and Charles-Dominique (1990) reported this widespread rainforest species (as *Tadarida europs*) from Camopi and Les Nouragues, French Guiana. Husson (1962,

1978) described specimens from Surinam (also as *T. europs*).

36. *Nyctinomops macrotis*: The only known record of this species from the eastern Guianas is the holotype of *Nyctinomops megalotis* Dobson (a junior synonym of *Nyctinomops macrotis* Gray), which was said to have come from "Surinam" (Husson, 1962, 1978). *Nyctinomops macrotis* is known from a very wide range of habitats (Milner et al., 1990); collection localities in predominantly rainforested areas have been reported from Ecuador (Albuja, 1982) and Brazil (Piccinini, 1974).

37. *Promops nasutus*: This rarely collected species was reported from Surinam by Genoways and Williams (1979) but it is not known from French Guiana. The habitat affinities of *P. nasutus* are not well understood, but some referred material is known from rainforested Amazonian localities (Goodwin and Greenhall, 1962; Handley, 1976).

APPENDIX 2

Species Matrix for 14 Neotropical Rainforest Bat Inventories

Below we provide the data on which our quantitative comparisons of Neotropical rainforest bat faunas are based. The matrix consists of binary presence/absence records (0 = absent, 1 = present) for 146 species at 14 localities. From left to right, the matrix columns represent Chajul, La Selva, Barro Colorado, Imataca, Piste Saint-Élie, Paracou, Arataye, Cunucunuma, Manaus, Xingu, Jenaro Herrera, Balta, Cocha Cashu/Pakitza, and Cuzco Amazónico (see table 75 for geographic data and references).

1. *Centronycteris centralis*: 01100 00000 0000
2. *Centronycteris maximiliani*: 00000 10010 0000
3. *Cormura brevirostris*: 01111 11110 0000
4. *Cyttarops alecto*: 01001 00000 0000
5. *Diclidurus albus*: 01110 00010 0000
6. *Diclidurus scutatus*: 00010 11000 0000
7. *Peropteryx kappleri*: 11010 10000 1000
8. *Peropteryx leucoptera*: 00001 10010 1001
9. *Peropteryx macrotis*: 00001 11111 0000
10. *Rhynchonycteris naso*: 11110 10111 1111
11. *Saccopteryx bilineata*: 11111 11111 1111
12. *Saccopteryx canescens*: 00010 00001 0000
13. *Saccopteryx gymnura*: 00000 10000 0000
14. *Saccopteryx leptura*: 01111 11111 1111
15. *Noctilio albiventris*: 01110 10011 1111
16. *Noctilio leporinus*: 11110 10110 0010
17. *Pteronotus davyi*: 11000 00000 0000
18. *Pteronotus gymnotus*: 00100 00000 0000
19. *Pteronotus parnellii*: 11110 11111 0000
20. *Desmodus rotundus*: 11111 11111 1111
21. *Diaemus youngi*: 10000 10000 0000
22. *Diphylla ecaudata*: 10000 00001 0010
23. *Anoura caudifera*: 00001 11111 1110
24. *Anoura geoffroyi*: 00000 01000 0100

25. *Choeroniscus godmani*: 01010 00000 0000
26. *Choeroniscus minor*: 00001 11011 1111
27. *Glossophaga commissarisi*: 11100 00000 0010
28. *Glossophaga soricina*: 11111 11111 1111
29. *Hylonycteris underwoodi*: 01000 00000 0000
30. *Lichonycteris obscura*: 01010 10010 0000
31. *Lionycteris spurrelli*: 00001 01100 0000
32. *Lonchophylla mordax*: 00000 00000 1000
33. *Lonchophylla robusta*: 01100 00000 0000
34. *Lonchophylla thomasi*: 00011 11011 1111
35. *Scleronycteris ega*: 00000 00100 0000
36. *Chrotopterus auritus*: 11111 11101 1011
37. *Glyphonycteris daviesi*: 01011 10001 0000
38. *Glyphonycteris sylvestris*: 00000 11001 0000
39. *Lampronnycteris brachyotis*: 11100 00000 0000
40. *Lonchorhina aurita*: 10000 00000 0000
41. *Lonchorhina* sp. nov.: 00000 01100 0000
42. *Macrophyllum macrophyllum*: 11111 11111 0110
43. *Micronycteris brosetti*: 00000 10000 1000
44. *Micronycteris hirsuta*: 01100 10000 0000
45. *Micronycteris homezi*: 00000 10000 0000
46. *Micronycteris megalotis*: 10011 11111 1111
47. *Micronycteris microtis*: 01111 10100 0000
48. *Micronycteris minuta*: 01001 10000 0011
49. *Micronycteris schmidtorum*: 01100 10100 0010
50. *Mimon bennettii*: 00000 11000 0000
51. *Mimon cozumelae*: 11000 00000 0000
52. *Mimon crenulatum*: 11111 11010 1111
53. *Phylloderma stenops*: 11111 11100 1010
54. *Phyllostomus discolor*: 11101 11011 1000
55. *Phyllostomus elongatus*: 00011 11111 1111
56. *Phyllostomus hastatus*: 01111 11111 1111
57. *Phyllostomus latifolius*: 00000 01000 0000
58. *Tonatia brasiliense*: 11111 10001 1110
59. *Tonatia carrikeri*: 00000 10000 1100
60. *Tonatia evotis*: 10000 00000 0000
61. *Tonatia saurophila*: 11111 11011 1110

62. *Tonatia schulzi*: 00001 11000 0000
63. *Tonatia silvicola*: 01111 11111 1111
64. *Trachops cirrhosus*: 11110 11011 1111
65. *Trinycteris nicefori*: 01111 11011 1100
66. *Vampyrum spectrum*: 01111 11010 1011
67. *Carollia brevicauda*: 11110 01110 1111
68. *Carollia castanea*: 01100 00000 1111
69. *Carollia perspicillata*: 11111 11111 1111
70. *Rhinophylla fischeriae*: 00000 00001 1000
71. *Rhinophylla pumilio*: 00011 11111 1111
72. *Ametrida centurio*: 00111 11110 0000
73. *Artibeus amplus*: 00000 00100 0000
74. *Artibeus jamaicensis*: 11111 11111 1111
75. *Artibeus lituratus*: 11111 11111 1111
76. *Artibeus obscurus*: 00011 11101 1111
77. *Artibeus anderseni*: 00000 00000 1111
78. *Artibeus cinereus*: 00011 10011 0111
79. *Artibeus glaucus*: 00010 00100 0010
80. *Artibeus gnomus*: 00011 11101 1010
81. *Artibeus phaeotis*: 11100 00000 0000
82. *Artibeus watsoni*: 11100 00000 0000
83. *Artibeus concolor*: 00011 11111 1100
84. *Centurio senex*: 10100 00000 0000
85. *Chiroderma salvini*: 00000 00000 0001
86. *Chiroderma trinitatum*: 00001 11110 1110
87. *Chiroderma villosus*: 11111 11101 1111
88. *Ectophylla alba*: 01000 00000 0000
89. *Ectophylla macconnelli*: 00101 11111 1111
90. *Enchisthenes hartii*: 00100 00000 1000
91. *Platyrrhinus brachycephalus*: 00000 00000 1110
92. *Platyrrhinus helleri*: 11111 11111 1111
93. *Platyrrhinus infuscus*: 00000 00000 0111
94. *Platyrrhinus lineatus*: 00000 01000 0000
95. *Sphaeronycteris toxophyllum*: 00000 00000 0010
96. *Sturnira lilium*: 11011 11111 1111
97. *Sturnira ludovici*: 01000 00000 0000
98. *Sturnira luisi*: 00100 00000 0000
99. *Sturnira magna*: 00000 00000 1000
100. *Sturnira tildae*: 00011 11101 1111
101. *Uroderma bilobatum*: 11111 11111 1111
102. *Uroderma magnirostrum*: 00110 00011 1111
103. *Vampyressa bidens*: 00010 01100 0110
104. *Vampyressa brocki*: 00000 11001 1000
105. *Vampyressa melissa*: 00000 01000 0000
106. *Vampyressa nymphaea*: 01100 00000 0000
107. *Vampyressa pusilla*: 11111 01000 1111
108. *Vampyrodes caraccioli*: 11110 00100 0110
109. *Natalus stramineus*: 10100 00000 0000
110. *Furipterus horrens*: 01001 10101 1010
111. *Thyroptera discifera*: 00100 00000 1000
112. *Thyroptera tricolor*: 11101 11110 0111
113. *Eptesicus brasiliensis*: 00010 00110 1101
114. *Eptesicus chiriquinus*: 01011 10000 0000
115. *Eptesicus furinalis*: 11111 10000 0100
116. *Eptesicus melanopterus*: 00000 00010 0000
117. *Lasiurus atratus*: 00010 00000 0000
118. *Lasiurus blossevillii*: 10000 10010 0100
119. *Lasiurus ega*: 10000 00000 0111
120. *Myotis albescens*: 11100 00111 1111
121. *Myotis elegans*: 01000 00000 0000
122. *Myotis fortidens*: 10000 00000 0000
123. *Myotis keaysi*: 10000 00000 0000
124. *Myotis nigricans*: 01111 11110 1111
125. *Myotis riparius*: 01111 11001 1111
126. *Myotis simus*: 00000 00000 1110
127. *Pipistrellus subflavus*: 10000 00000 0000
128. *Rhogeessa tumida*: 01100 00000 0000
129. *Bauerus dubiaquercus*: 10000 00000 0000
130. *Eumops auripendulus*: 00110 10000 0000
131. *Eumops hansae*: 00010 11000 0000
132. *Eumops trumbulli*: 00000 00010 0000
133. *Molossops abrasus*: 00000 10010 0100
134. *Molossops greenhalli*: 10000 01000 0100
135. *Molossops parvus*: 00000 10000 0000
136. *Molossops planirostris*: 00000 01000 0000
137. *Molossops neglectus*: 00010 00000 1000
138. *Molossus barnesi*: 00000 10000 0000
139. *Molossus bondae*: 01100 00000 0000
140. *Molossus coibensis*: 00100 00000 0000
141. *Molossus molossus*: 10111 11110 1111
142. *Molossus rufus*: 10011 11110 1000
143. *Molossus sinaloae*: 01100 10000 0000
144. *Neoplatymops mattogrossensis*: 00000 00001 0000
145. *Nyctinomops laticaudatus*: 00100 01100 0010
146. *Promops centralis*: 00000 10000 1000