BATS OF JAMAICA

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Introduction

The modern history of Jamaica is entwined with European exploration of the New World beginning with the landing of Columbus at Discovery Bay on 4 May 1494, during his second voyage to the Americas. Since that time the word Jamaica has conjured thoughts of tropical beaches, trade winds, pleasant tropical nights, Spaniards, British navy, Empire, sugar, rum, plantations, slavery, revolt, maroons, pirates, Port Royal, disasters, hurricanes, and in more recent years independence, tourism, Reggae, and welcoming and happy residents. Our knowledge of Jamaican natural history begins with Browne (1789). He and other early naturalists displayed a broad interest in plants and animals, including bats, but thorough surveys of the island's chiropteran fauna were not accomplished until the 1960s when mist nets came into general use. Following Browne (1789), the general natural history of Jamaica and of bats of the island were described by Gosse (1851), Osburn (1865), G. M. Allen (1911), Anthony (1920), Palmer (1940), Sanderson (1941), Asprey and Robbins (1953), Goodwin (1970), Adams (1972), McFarlane (1985, 1986), and Fincham (1997).

Our main goal in writing *Bats of Jamaica* was to pull together all of the credible—and sometimes highly disparate—natural history and scientific information about the species of bats that live on the island. The authors have worked together, and individually, and with other collaborators on the subject of the biology of Jamaican bats for nearly 30 years. Our collective and individual field work on Jamaica was conducted in four separate years—1974, 1977, 1984, and 1985**.** To write *Bats of Jamaica* we also made use of a small collection of Jamaican bats deposited in the Museum of Texas Tech University by Brent L. Davis while he was a student there. This collection was made between 27 June and 2 July 1969 and has been incorporated with our materials in this publication. Our field work involved the setting of mist nets in areas where bats would be moving, foraging, or coming to drink. Nets also were set near the entrance of selected caves to sample the resident species and night-time visitors. We explored known caves on the island to obtain samples of selected species of bats and also visited man-made structures with known or suspected colonies of bats.

All of our data are based on voucher specimens, which were deposited in the collections of the Museum of Texas Tech University or the Carnegie Museum of Natural History. Throughout our field work, we made a substantial effort to obtain the maximum amount of data from each bat specimen. Many were karyotyped and tissue samples were frozen in liquid nitrogen and/or fixed for transmission electron microscopic (TEM) study, immunohistochemistry, or standard histology and histochemistry. These various samples were returned to laboratories at Texas Tech University, Texas A&M University, Hofstra University, Case-Western Reserve University, and the University of West Virginia for subsequent and ongoing research. Because our Jamaican fieldwork was a test bed for developing new field techniques (Phillips, 1985, 1988), there is a substantial amount of published information on comparative cell structure in bat salivary glands and digestive tract microanatomy from Jamaican bat specimens. Some of this information is summarized in the species accounts; additional data from Jamaican bat species and an explanation of evolutionary context and theory can be found in reviews (Phillips et al., 1977; Forman et al., 1979; Phillips and Tandler, 1987; Tandler et al., 1989, 1990, 1998, 2001).

Combining our results with those of earlier researchers, we now believe that 21 species of bats currently occur on Jamaica. These 21 species represent six families—Noctilionidae, 1 species; Mormoopidae, 4; Phyllostomidae, 7; Natalidae, 2; Vespertilionidae, 2; Molossidae, 5. Three additional modern species of bats are known from Jamaica based solely on fossil remains. One of these species is a member of the family Mormoopidae and the other two belong to the family Phyllostomidae.

Geography

The island of Jamaica is located in the Caribbean Sea 150 km south of Cuba, 190 km west of the southwestern coast of Hispaniola, and 625 km northeast of the nearest point on the mainland—the eastern end of the boundary between Honduras and Nicaragua. The island falls between 17°07' N and 18°05' N latitude and 76°11' W and 78°22' W longitude. Jamaica has an area of 11,424 square km, making it the third largest island in West Indies (Fig. 1). It is grouped with Cuba, Hispaniola, and Puerto Rico as the Greater Antillean islands. The island measures 240 km from west to east and has a maximum north-south width of 80 km. The highest point on Jamaica is Blue Mountain Peak at 2257 m (Blume 1974).

Geology

Jamaica is a geologically complex, mountainous island; nearly 50% of its surface area is above 300 m elevation. The interior mountain ranges form an east-west backbone for the island. The highest portion of the interior ranges is the "Blue Mountain Range" toward the eastern end of the island. These mountains are composed of Cretaceous igneous and metamorphic rocks. There are at least seven peaks that exceed 1500 m. These rugged mountains divide the north and south sides of the island and are crossed by passes at only a few points. Hardwar Gap at 1200 m has the only paved mountain road connecting Buff Bay and Kingston. To the northeast of the Blue Mountain Range are the John Crow Mountains, which are composed of limestone and reach a height of 1060 m. The 1500 m high Port Royal Mountains behind Kingston form a subsidiary ridge to the south and east of the Blue Mountains (Floyd 1979).

In the central and western parts of Jamaica, the elevations are lower than in the Blue Mountains, ranging from 600 m to 900 m. The inconspicuous Central Range is composed of the same rocks as the Blue Mountains. A white limestone plateau of Eocene and Miocene origin surrounds the Central Range. The limestone plateau composes nearly 65% of the island and has an undulating to hilly relief where various types of karst features have developed (Floyd 1979).

The most extensive karst area is the Cockpit Country southeast of Montego Bay. The Cockpit Country is composed of innumerable conical and tower-shaped hills that surround depressions, sinkholes, or solution holes. The sides of these depressions are sharp, often precipitous, making the Cockpit Country inaccessible and undeveloped. The Cockpit Country is the area where runaway slaves—Maroons—took

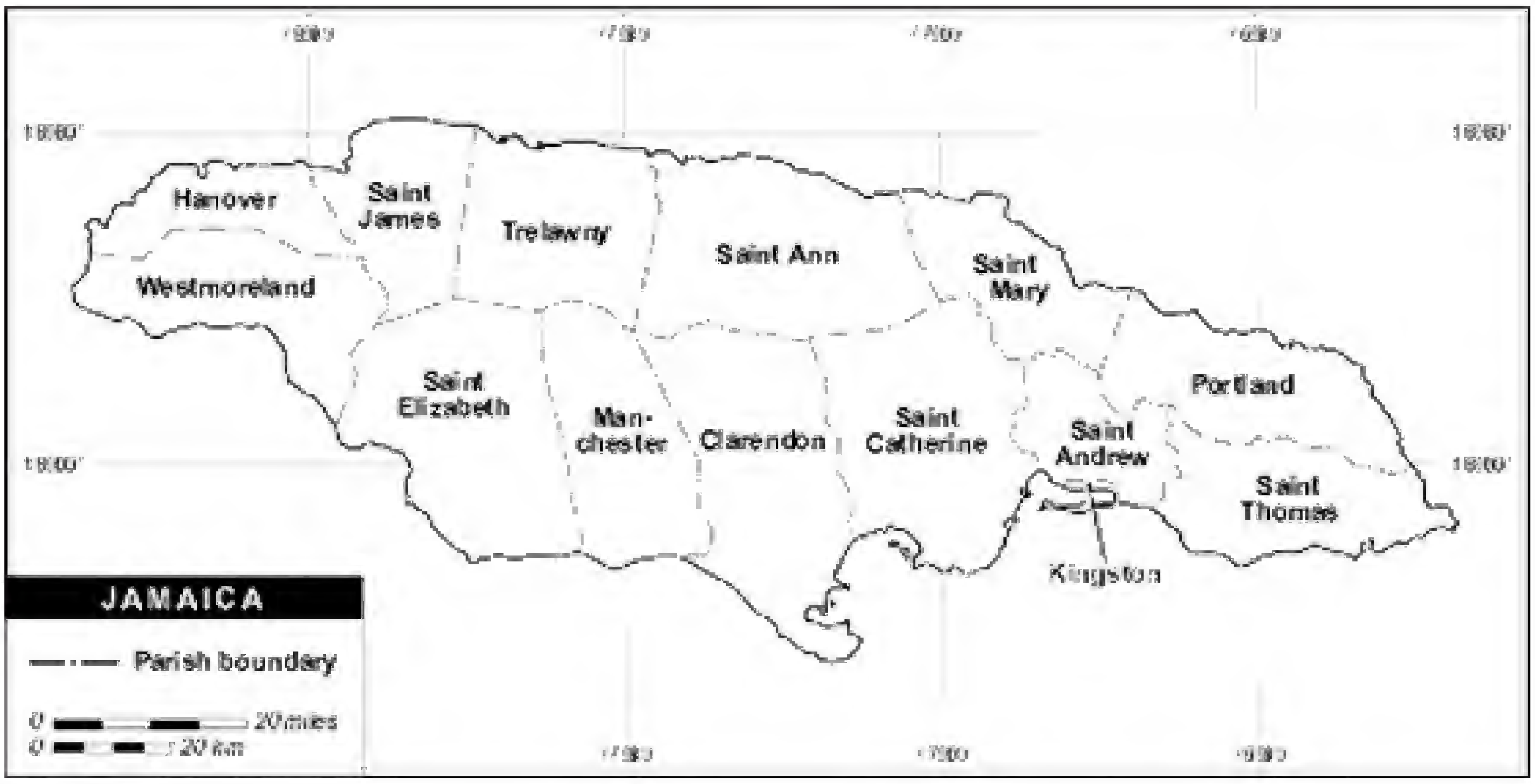

Fig. 1. Map of Jamaica indicating parish names and boundaries.

refuge during colonial times. The southern part of the Cockpit Country in Trelawny Parish still is called "The Land of Look Behind" giving a vivid memory of the conflicts between the British military and Maroons (Floyd 1979).

More than 1100 caves have been found on Jamaica, primarily associated with the limestone areas (Fincham 1997). These caves are extremely important for the survival of a number of the bats species occurring on Jamaica. Elsewhere in the central and western uplands are a number of interior valleys and plains that provide flatter land, which have been converted for settlement and agricultural purposes (Floyd 1979). Even in these areas are scattered limestone hills with precipitous sides that maintain a partial assemblage of native vegetation.

The coastal plain, which surrounds the island, is broadest in areas along the southern coast of the island where it may extend 8 to 20 km inland, whereas along the northern coast the plain usually is no more than 2 km wide. The contact between the coastal plain and the inland plateau and mountains is abrupt, indicating a former coastline. The coastal plain is composed of recent alluvial sands, gravels, and loams. These represent rich, cultivable soils that have been significantly altered for growing of sugarcane, bananas, and vegetables (Bent and Bent-Golding 1966; Floyd 1979).

The growing knowledge of plate tectonics in the Caribbean region is providing evidence of a much more complex early geological history for Jamaica than previously believed. There are recent data, which still need further confirmation, that Jamaica may have had a dual origin rather than originating as a single crustal unit in the Cretaceous as currently accepted (Pindell 1994). The Western Jamaica Block may have arisen along with the Nicaraguan Rise (situated between modern Jamaica and northern Central America) as part of a Mesozoic volcanic arc between the Chortis Block that forms modern northern Central America and the Caribbean Plate. The final uplift of the Western Jamaica Block that created most of Jamaica probably occurred during the Middle Miocene (Iturralde-Vinent and MacPhee 1999).

The Blue Mountain Block, which forms the eastern 25% of Jamaica under the new theory of origins of the island, formed as part of the northern Greater Antilles. There was a possible land connection between the southern peninsula of Hispaniola and the Blue Mountain Block in the Eocene-Oligocene periods. The two blocks that form Jamaica may have conjoined in the Middle Miocene resulting in tectonic deformations on the island (Iturralde-Vinent and MacPhee 1999). This new concept of the geological history of Jamaica is resulting in a reassessment of the biogeography of early land mammals on the island (Domning et al. 1997; MacPhee et al. 1983, 1989; MacPhee and Fleague 1991; MacPhee and Iturralde-Vinent 1994, 1995; MacPhee 1996), but has not yet been considered in the biogeography of the chiropteran fauna of the island.

Climate

Jamaica has a tropical maritime climate characterized by warm average temperatures throughout the year and relatively high local rainfall. Prevailing wind is on-shore from the northeast, which creates a modest rain shadow on the southern side of the island. The most serious climatic upheaval on the island is caused by hurricanes, which are a perennial threat between July and November.

Temperatures on Jamaica are warmest near sea level and become cooler inland with distance from the sea and increases in elevation. This trend can be seen in comparing the average maximum and minimum temperatures for July at three localities on the island—Kingston (6 m elevation), 31.2° C, 25.3° C; Stony Hill (425 m), 30° C, 20° C; Blue Mountain Peak (2257 m), 20.5° C, 8.2° C (Bent and Bent-Golding 1966).

The annual rainfall for the island is approximately 2000 mm, but this is unevenly distributed over the island. The northeast prevailing winds drive moisture-laden tropical air masses into the northern slope of the Blue Mountains and John Crow Mountains creating the wettest areas on the island with over 5000 mm of rain annually. The leeward side—south side—of the island in the rain shadow of the central mountains is the driest area of the island. This trend in rainfall can be seen by comparing that received annually by Kingston (750 mm) on the south side of the island with that at Port Antonio (3500 mm) on the northeastern coast and Montego Bay (1300 mm) on the northwestern coast (Bent and Bent-Golding 1966; Floyd 1979). Rainfall records reveal that the wettest months of the year on Jamaica are October and May, whereas the major dry period is from January to March.

Vegetation

The vegetational communities of Jamaica were described in detail by Asprey and Robbins (1953) and a survey of flowering plants of the island was completed by Adams (1972; floral taxonomy and common names, when available, from this publication are used throughout the current paper). Before European colonization, Jamaica was forested and lacked natural savannas (Beard 1953). The current vegetation of Jamaica can be divided into three categories—coastal, lowland, and montane. The vegetational communities are determined by the interplay of a combination of factors including soil, rainfall, topography, and prevailing winds.

The coastal vegetation is primarily associated with beach, strand, and cay situations, with very low vegetation of little significance to the chiropteran fauna except for the strand woodland where trees can reach 8 to 10 m. The broom thatch palm (*Thrinax parviflora*) dominates these woodlands, with other larger trees including manchineel (*Hippomane mancinella*), seaside grape (*Coccoloba uvifera*), and seaside mahoe (*Thespesia populnea*). Larger trees are found only in mangrove swamps, which are dominated by red (*Rhizophora mangle*), white (*Laguncularia racemosa*), black (*Avicennia germinans*), and button (*Conocarpus erectus*) mangroves, and other swamp situations, which are dominated by swamp cabbage palm (*Roystonea princeps*), long thatch palm (*Calyptronoma occidentalis*), hog gum (*Symphonia globulifera*), and figs (*Ficus* sp.).

The lowland vegetation is primarily associated with the limestone areas that cover a large part of the island. The blue mahoe tree (*Hibiscus elatus*) is common throughout the lowlands and lower montane areas because of planting activities. Coastal limestone hills are occupied by a Dry Limestone Scrub Forest such as on Portland Point where trees form a canopy at 15 to 18 m, including red birch (*Bursera simaruba*), white cedar (*Tabebuia riparia*), ketto (*Hypelate trifoliata*), in the deeper ravines silk cotton tree (*Ceiba pentandra*), and a subcanopy at 6 to 10 m, with such species as *Piper amalago*. In drier situations a similar, but shorter, vegetation type is present—Arid Limestone Scrub Forest—including such typical coastal trees as scarlet cordia (*Cordia sebestana*), dogwood (*Piscidia piscipula*), velvet-leaved maiden plum (*Comocladia velutina*), coco plum (*Chrysobalanus icaco*), and yellow fiddlewood (*Citharexylum fruticosum*). Both of these areas have been impacted by human activities. In the driest areas of the lowlands, Cactus Thorn Scrub Forest prevails, characterized by abundant stands of the columnar dildo cactus (*Stenocereus hystrix*), which reach heights of 6 m. The alluvial plains in Jamaica have been totally converted to agriculture and other development, but probably supported forest before settlement.

Wet Limestone Forest is found in areas where rainfall exceeds 2500 mm and now can best be seen in the Cockpit Country. This is a luxuriant evergreen forest with many tall trees (> 30 m), including broadleaf (*Terminalia latifolia*), galba (*Calophyllum calaba*), silk cotton tree (*Ceiba pentandra*), West Indian cedar (*Cedrela odorata*), and shagbark (*Pithecellobium alexandri*). Frequent dominant trees of the canopy layer are breadnut (*Brosimum alicastrum*), yellow sweetwood (*Nectandra antillana*), small-leaved sweetwood (*Nectandra coriacea*), black bulletwood (*Bumelia nigra*), wild tamarind (*Pithecellobium arboreum*), cogwood (*Ziziphus chloroxylon*), and pruan tree (*Prunus occidentalis*).

There is no typical Tropical Rain Forest remaining on Jamaica, but it probably was present prior to settlement. The Lower Montane Rain Forest still is found in the less accessible wet northern slopes of the Blue Mountains and western slopes of the John Crow Mountains. This is a mixed forest dominated by tall, straight-boled trees, including such species of trees as mountain guava (*Psidium montanum*), galba (*Calophyllum calaba*), coby wood (*Matayba apetala*), and hog gum (*Symphonia globulifera*). Montane Sclerophyll Forest is found along the drier southern slopes of the Blue Mountains between 750 m and 1200 m. Two characteristic shrubs of this zone are mountain broom (*Baccharis scoparia*) and switch sorrel (*Dodonaea viscosa*), with a more open canopy of small trees and tall, slender shrubs including beet wood (*Cyrilla racemiflora*), soapwood (*Clethra occidentalis*), bilberry (*Vaccinium meridionale*), wild pear (*Persea alpigena*), balsam fig (*Clusia rosea*), capberry sweetwood (*Nectandra patens*), and John Crow bush (*Bocconia frutescens*). At lower elevations, this area is characterized by shifting cultivation and burning that prevents invasion of shrubs and allows invasion of introduced grasses. Above this zone is an area of sclerophyllous thickets in which beet wood (*Cyrilla racemiflora*), soapwood (*Clethra occidentalis*), mountain broom (*Baccharis scoparia*), switch sorrel (*Dodonaea viscosa*), and bilberry (*Vaccinium meridionale*) are conspicuous.

Montane Mist Forest occurs in areas on the Blue Mountains above 1200 m. As the name implies this area is shrouded in mist, with a low-canopied forest of evergreen trees in association with abundant undershrubs, ferns, bryophytes, and lichens. Common trees of the canopy layer include the gymnosperm *Podocarpus urbani*, beet wood (*Cyrilla racemiflora*), dovewood (*Alchornea latifolia*), West Indian sumach (*Brunellia comocladiifolia*), bloodwood (*Laplacea haematoxylon*), fig (*Ficus membranacea*), and alligator wood (*Guarea swartzii*). This vegetation type in exposed ridges and summits is called Elfin Woodland. The canopy in this area is reduced to 6 m or less with gnarled and stunted trees from lower elevations such as *Vaccinium, Podocarpus, Cyrilla*, and *Guarea*. The dominant trees are *Clethra alexandri* and *Clusia havetioides*. Other common trees and shrubs include soapwood (*Clethra occidentalis*), wild mammee (*Garcinia humilis*), *Sciadophyllum sciadophyllum*, and Jamaican rose (*Blakea trinerva*).

Ruinate is the appropriately descriptive Jamaican term for lands undergoing secondary succession from agricultural use to natural regeneration. The type of ruinate vegetation that develops depends on the previous use of the land and the current climatic regimen. The ruinate vegetation typically progresses from pioneer weeds to scrub and tree saplings becoming thicker and taller over the years, including such species as lignum vitae (*Guaiacum officinale*), guava (*Psidium guajava*), logwood (*Haematoxylon campechianum*), Cayenne pepper (*Capsicum frutescens*), cassie flower (*Acacia farnesiana*), park nut (*Acacia macracantha*), wild poponax (*Acacia tortuosa*), and cashaw (*Prosopis juliflora*). Finally, a forest that has a similar appearance to climax or natural forest is present, but these forests do differ from the original vegetation in its floral composition. Unfortunately, a large portion of the vegetation of Jamaica today would fall into some stage of ruinate vegetation (Asprey and Robbins 1953; Floyd 1979).

Agricultural activities occupy nearly 50% of the island of Jamaica. The types of crops and plantations certainly have impacted the chiropteran fauna of the island. These changes have favored some species of bats, while negatively impacting others. In the late 1960s, the agricultural uses of the land were, in order beginning with the most common, as follows: pastures; sugar cane; coconut; bananas; citrus; coffee; maize; cocoa; rice (Blume 1974). Typical subsistence gardens include such crops as yams (*Dioscorea cayenensis, D. rotundata*), yampies (*Dioscorea trifida*), cassava (*Manihot esculenta*), gungo peas (*Cajanus cajan*), and beans (*Mucuna, Phaseolus, Pachyrhizus*) (Floyd 1979). Significant introduced and native fruit trees that can be of value both to humans and many species of bats on the island include banana (*Musa*), mango (*Mangifera indica*), peach (*Prunus persica*), apple (*Malus domestica*), breadfruit (*Artocarpus altilis*), jackfruit (*A. heterophyllus*), edible fig (*Ficus carica*), papaya (*Carica papaya*), cashew (*Anacardium occidentalis*), cocoa (*Theobroma cacao*), coconut (*Cocos nucifera*), custard apple (*Annona reticulata*), sour sop (*A. muricata*), sweet sop (*A. squamosa*), fustic tree (*Chlorophora tinctoria*), guava (*Psidium guajava, P. montanum, P. cattleianum),* naseberry (*Manilkara zapota*), star apple (*Chrysophyllum cainito*), rose apple (*Syzygium jambos*), and otaheite apple (*S. malaccense*).

METHODS AND MATERIALS

The Species Accounts that follow are arranged in systematic order and are intended to be as comprehensive as possible. We thus have included a list of specimens examined along with additional records, known geographic distribution, systematics, morphometrics, natural history, genetic data, and information obtained from microscopic studies of cells and organs. All measurements were taken with a dial or digital caliper and are recorded in millimeters (mm). Only adult specimens (phalangeal epiphyses completely fused) were measured in this study unless otherwise noted. All weights are recorded in grams (g). All measurements of embryos are of crown-rump length. Distances are recorded in kilometers (km) or miles (mi.) as they appear on the original specimen tags. All elevations are in meters (m).

Our measurements were taken as follows:

Length of forearm—measured from the posterior extension of the radius-ulna to the anterior extension of the carpels;

Greatest length of skull—measured from the posterior-most projection of the skull to the anterior surface of the incisors;

Condylobasal length—measured from the posterior-most projection of the exoccipital condyles to the anterior-most projection of the premaxillae;

Zygomatic breadth—greatest distance across the zygomatic arches measured at right angles to the longitudinal axis of the cranium;

Interorbital constriction—least distance between the orbits measured at right angles to the longitudinal axis of the cranium;

Postorbital constriction—least distance across the postorbital constriction measured at right angles to the longitudinal axis of the cranium;

Mastoid breadth—greatest distance across the mastoid processes measured at right angles to the longitudinal axis of the cranium;

Palatal length—measured from the anterior-most point of the posterior margin of the palate to the anterior-most projection of the premaxillae;

Length of maxillary toothrow—measured from the posterior rim of the alveolus of M3 to the anterior rim of the alveolus of C1;

Breadth across upper molars—greatest distance across the upper molars measured at right angles to the longitudinal axis of the cranium.

Non-differentially stained karyotypes were prepared for 20 of the 21 species of bats on the island during the course of our field work in 1974 and 1978. The only species not studied was *Nyctinomops macrotis,* which was never obtained during our field work. Karyotypes were prepared either by the in vivo bone marrow method (Baker 1970b) or from fibroblasts cultured in vitro (Bickham 1979b).

Field collecting was accomplished primarily by catching the bats in Japanese mist nets. Caves and man-made structures also were explored for colonies of bats. Museum voucher specimens were prepared in the field as skins with skulls, skeletons only, or by preservation in 10% buffered formalin. Tissue samples for microscopic studies were dissected and fixed for TEM or various optical microscopic procedures by means of field techniques and fixatives described in Phillips (1985, 1988) or Forman and Phillips (1988).

Floral taxonomy and common names, when available, used throughout this paper are from Adams (1972). Site numbers given for caves in text are those of the Jamaican Cave Register as detailed by Fincham (1997). Localities printed in italics in the specimens examined and additional records are those not represented on the maps for the species to avoid undue crowding of map symbols. Statistical analyses were performed using StatView® software package (Sager 1992). The unpaired t-test gave standard statistics for each sample and statistical significance of differences in group means.

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KEY TO THE BATS OF JAMAICA

This key to the bats of Jamaica was prepared using only external characteristics and measurements of the bats. The key is prepared primarily for individuals who are not familiar with Antillean bats, but it will be useful to chiropterologists as well. The key was adapted from earlier keys by Pine (1980) and Baker et al. (1984).

Tail vertebrae visible and extending into uropatagium 3

Tail vertebrae absent, not visible in uropatagium 2

Dorsal surface of uropatagium between hind legs heavily furred . . . .*Ariteus flavescens*

Dorsal surface of uropatagium between hind legs essentially naked. . . . . *Artibeus jamaicensis*

Tail vertebrae not "free," that is, they do not extend beyond the posterior margin of the uropatagium for more than 10 mm 4

Tail vertebrae "free," that is, extending more than 10 mm beyond the posterior margin of the uropatagium 17

Nose leaf present 5

Nose leaf absent 9

Ears enlarged, more than 20 mm; ears united across top of head. . . . . *Macrotus waterhousii*

Ears not enlarged, less than 20 mm; ears separated 6

Tail vertebrae present, but not extending beyond uropatagium .. . . *Glossophaga soricina*

Tail vertebrae extending beyond uropatagium (less than 10 mm) 7

Calcar absent . . . . *Phyllonycteris aphylla*

Calcar present 8

Nose leaf short; ventral fur tan to pale brown . . . . *Erophylla sezekorni*

Nose leaf attenuated; ventral fur dark silvery gray . . . . *Monophyllus redmani*

Tail longer than head and body; fringe of hair along posterior border of uropatagium 10

Tail shorter than head and body; no fringe of hair along posterior border of uropatagium, unless entire dorsal surface of uropatagium heavily furred 11

Length of forearm more than 40 mm . . . . *Natalus stramineus*

Length of forearm less than 40 mm . . . . *Natalus micropus*

Hind feet and claws greatly enlarged, exceeding 20 mm . . . . *Noctilio leporinus*

Hind feet and claws not greatly enlarged, not exceeding 20 mm 12

Distal portion of the tail perforating the dorsal surface of the uropatagium near its center 13

Distal portion of the tail not perforating the dorsal surface of the uropatagium near its center 16

Ears short, broad, and round, joined across head; nose and chin complex; hair long, lax . . . . *Mormoops blainvillii*

Ears pointed and separated; nose simple; hair relatively short. 14

Forearm greater than 50 mm . . . . *Pteronotus parnellii*

Forearm less than 50 mm 15

Forearm more than 41 mm . . . . *Pteronotus macleayii*

Forearm less than 41 mm . . . . *Pteronotus quadridens*

Dorsal color reddish; white spot on shoulder where antebrachial membrane joins body; uropatagium covered with hair . . . .*Lasiurus degelidus*

Dorsal color a dark chocolate brown; no white spot on shoulder; uropatagium not covered with hair . . . . *Eptesicus lynni*

Upper lip wrinkled 18

Upper lip smooth 19

Forearm more than 50 mm . . . . *Nyctinomops macrotis*

Forearm less than 50 mm . . . . *Tadarida brasiliensis*

Forearm more than 50 mm 20

Forearm less than 50 mm . . . . *Molossus molossus*

Hairs bicolored with a dark grayish brown at the tip and pale to white base, giving an overall color of chocolate brown; ears extending to, or beyond, nose when viewed from above; tragus blunt and broad . . . . *Eumops glaucinus*

Hairs dark to their base, giving an overall color appearance of black; ears not extending to nose when viewed from above; tragus pointed and relatively small. . . . .*Eumops auripendulus*

Species Accounts

Noctilio leporinus mastivus (Vahl, 1797)
Greater Fishing Bat

Specimens examined (31).—HANOVER PARISH: Flint River, 1.5 mi. E Sandy Bay, 2 (CM). PORTLAND PARISH: Hectors River, 3 (JMM). ST. ANDREW PARISH: *Hope Garden, Kingston*, 1 (NMNH); Kingston, 1 (MCZ). ST. ANN PARISH: Queenhythe, 7 (2 CM, 5 TTU). ST CATHERINE PARISH: Deanery, Hellshire Fish Farm, near Salt Island Lagoon, approximately 6.5 mi. S, 3 mi. W Spanish Town, 1 (UF); near Spanish Town, 1 (NMNH); Two Sisters Cave, Louzy Bay, Hillshire Park Estate, Hellshire Hills [17º54′ N, 76º54′ W], 3 (UF); 0.2 mi. E Watermount, 4 (CM). ST. ELIZABETH PARISH: Long Hill, 1 (BMNH). ST. THOMAS PARISH: Yallahs, 1 (TTU). WESTMORELAND PARISH: Mount Edgecombe, 1 (BMNH). PARISH UNKNOWN: no specific locality, 5 (3 BMNH, 2 NMMH).

Additional records (McFarlane 1997).—CLARENDON PARISH: Portland Cave-1. ST. CATHERINE PARISH: St. Clair Cave. TRELAWNY PARISH: Windsor Cave. WESTMORELAND PARISH: Monarva Cave [1.2 km ENE Brighton, in Negril Hills].

Distribution.— Figure 2 shows collecting localities for *Noctilio leporinus* on Jamaica. The species can be expected in the coastal and lowland areas throughout the island and anywhere there are large ponds and slow moving rivers where it can "fish" for food. The greater fishing bat occurs throughout the tropical areas of the Americas. The subspecies *N. l. mastivus* occurs in Mexico, Central America, northern South America, and throughout the Antillean islands (Davis 1973).

Systematics.—Davis (1973) studied geographic variation throughout the range of *Noctilio leporinus*. He recognized three subspecies, assigning specimens from Jamaica to *N. l. mastivus*, which was originally described from St. Croix in the Virgin Islands. Davis (1973) characterized this subspecies by its large size and usual presence of a whitish middorsal stripe.

Morphometrics.—Table 1 presents length of forearm and nine cranial measurements of samples of nine male and six female *Noctilio leporinus* from Jamaica. Males averaged larger than females in all 10 measurements. For three of the measurements—condylobasal length, zygomatic breadth, and length of maxillary toothrow—the differences were significant at *P* =

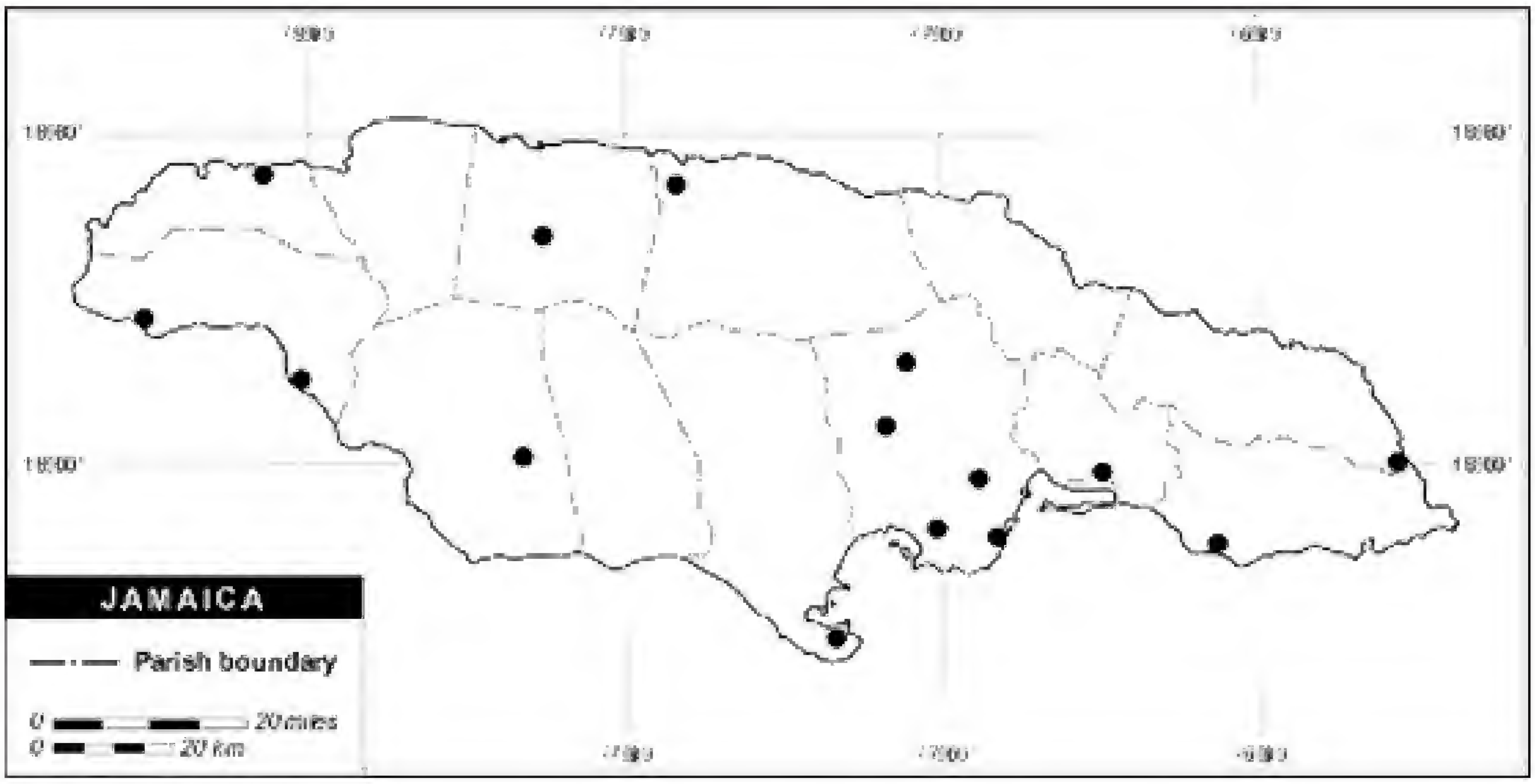

Fig. 2. Map of Jamaica showing the locations where specimens of the greater fishing bat, ***Noctilio leporinus***, have been collected.

Table 1.—Length of forearm and nine cranial measurements for five species of the families Noctilionidae and Mormoopidae occurring on Jamaica.

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
				Noctilio leporinus mastivus						
Males										
N	6	6	6	4	5	6	5	6	6	6
Mean	85.8	28.3	24.3	19.9	10.8	7.2	18.3	13.1	10.1	12.8
Minimum	82.6	25.8	23.6	19.7	9.2	6.7	16.9	11.9	9.9	11.6
Maximum	88.3	29.8	24.7	20.1	11.7	7.5	20.0	13.6	10.4	13.2
SE	±0.81	±0.61	±0.17	±0.08	±0.44	±0.12	±0.50	±0.26	±0.08	±0.25
Females										
N	6	5	5	6	6	6	4	6	6	6
Mean	85.6	26.8	23.5	18.7	10.4	7.0	17.2	12.8	9.8	12.6
Minimum	84.4	26.4	23.2	18.5	10.2	6.8	17.0	12.5	9.5	12.4
Maximum	87.0	27.3	23.8	19.1	10.7	7.1	17.3	12.9	10.0	13.0
SE	±0.35	±0.15	±0.11	±0.11	±0.07	±0.04	±0.07	±0.06	±0.08	±0.09
				Pteronotus macleayii grisea						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	44.0	16.7	15.4	8.3	5.5	3.3	8.5	8.2	6.8	5.8
Minimum	43.5	16.4	15.2	8.0	5.2	3.1	8.1	8.1	6.7	5.6
Maximum	45.2	17.0	15.9	8.5	5.8	3.5	8.8	8.4	7.0	6.1
SE	±0.20	±0.06	±0.07	±0.05	±0.07	±0.04	±0.08	±0.04	±0.03	±0.04
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	44.0	16.4	15.1	8.0	5.4	3.2	8.1	8.0	6.7	5.7
Minimum	42.3	16.1	15.0	7.8	5.2	3.1	7.8	8.0	6.6	5.5
Maximum	45.0	16.8	15.3	8.3	5.5	3.3	8.5	8.2	6.8	5.9
SE	±0.28	±0.07	±0.03	±0.05	±0.04	±0.02	±0.08	±0.02	±0.02	±0.04
				Pteronotus parnellii parnellii						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	53.2	20.6	19.2	11.3	7.2	3.9	10.7	10.2	8.9	7.4
Minimum	52.0	20.5	19.1	11.0	6.8	3.7	10.5	10.0	8.7	7.2
Maximum	55.2	20.9	19.5	11.5	7.7	4.0	10.8	10.3	9.0	7.8
SE	±0.30	±0.04	±0.04	±0.04	±0.11	±0.04	±0.03	±0.03	±0.03	±0.05
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	53.4	20.4	18.9	11.0	6.9	3.9	10.4	10.1	8.7	7.3
Minimum	52.6	20.0	18.4	10.9	6.6	3.7	10.2	9.9	8.5	7.1
Maximum	55.1	20.6	19.1	11.2	7.4	4.0	10.7	10.3	8.9	7.4
SE	±0.25	±0.06	±0.07	±0.04	±0.09	±0.03	±0.04	±0.04	±0.04	±0.03

Table 1. (cont.)

Sex and statistics forearm	Length of of skull	Greatest length length	Condylo-basal breadth	Zygomatic constriction	Interobital constriction	Postoribtal breadth	Mastoid length	Palatal toothrow	Length of maxillary upper molars	Breadth across
					Pteronotus quadridens fuliginosus					
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	39.1	14.9	13.7	7.8	5.2	3.0	7.9	7.2	6.0	5.4
Minimum	38.0	14.6	13.4	7.4	5.0	2.8	7.6	7.0	5.9	5.2
Maximum	40.1	15.3	14.2	8.1	5.3	3.1	8.1	7.3	6.2	5.5
SE	±0.23	±0.06	±0.08	±0.06	±0.04	±0.03	±0.06	±0.04	±0.03	±0.03
Females										
N	5	5	5	5	5	5	5	5	5	5
Mean	37.9	14.5	13.2	7.5	5.1	2.9	7.7	7.1	5.9	5.2
Minimum	37.0	14.3	13.0	7.4	4.8	2.8	7.6	6.9	5.8	5.2
Maximum	38.9	14.8	13.4	7.6	5.4	3.0	7.9	7.4	6.0	5.3
SE	±0.33	±0.09	±0.08	±0.04	±0.10	±0.04	±0.06	±0.08	±0.04	±0.02
					Mormoops blainvillii					
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	46.7	14.1	13.8	8.6	6.2	4.3	7.4	8.9	7.5	6.0
Minimum	46.2	13.8	13.4	8.3	6.0	4.2	7.2	8.6	7.3	5.9
Maximum	47.7	14.3	14.0	8.8	6.3	4.5	7.6	9.0	7.6	6.1
SE	±0.17	±0.06	±0.06	±0.06	±0.03	±0.04	±0.04	±0.05	±0.03	±0.02
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	46.5	14.0	13.6	8.5	6.1	4.2	7.2	8.8	7.4	6.0
Minimum	44.5	13.7	13.4	8.3	5.9	4.1	7.2	8.4	7.3	5.8
Maximum	47.5	14.3	14.0	8.6	6.4	4.3	7.4	9.1	7.5	6.1
SE	±0.33	±0.06	±0.07	±0.04	±0.05	±0.02	±0.02	±0.06	±0.0.3	±0.3

0.001. For three additional measurements (greatest length of skull, mastoid breadth, and palatal length), the sexes differed at $P = 0.05$. The mean values for the sexes approach each other most closely for length of forearm and breadth across upper molars where the differences are 0.3 mm or less.

Gosse (1847) gives an interesting description of the external characteristics of a living specimen from Mount Edgecombe (Fig. 3).

Natural History.—Specimens collected near Hector's River, Sandy Bay, and Queenhythe were all netted over water as the bats were attempting to feed on small fish or invertebrates. At Queenhythe nets were placed over a large earthen tank used as the village's source of water for its livestock (Figs. 4-5). The pool was approximately 30 m wide and 75 m long. A few trees were located near one end of the pool, but elsewhere there was only a grassy open field. The water in the pool at the time that the bats were netted was about 0.5 m deep with an additional 0.5 m of soft mud below it. The coastal forest formed a closed canopy over the Flint River at the point where a male and a female were netted on the night of 28 July 1997. The individual from Yallahs was netted early in the evening in a mango and banana plantation. The bat was probably moving from its day roost to feed over the nearby coast and river.

Two Sisters Cave (cave 122), located near Louzy Bay, is a shaft to a pool type of cave (Fincham 1997). The cave is 15 m deep and 60 m in length. In the cave opening installed stairs lead to a boulder pile with a pool on each side. Dávalos and Erikkson (2003) describe standing on a platform at this point and observing as many as 20 *Noctilio* "fishing immediately after dusk."

Figure 3. View of the head of *Noctilio leporinus*.

Figure 4. A view of the earthen tank at Queenhythe, St. Ann Parish, Jamaica.

Figure 5. A view of the earthen tank at Queenhythe, St. Ann Parish, Jamaica.

An historically interesting account of feeding by this species can be read in Gosse (1847). Here, he described the capture of several fishing bats from a roost inside of a "gigantic cotton-tree" (*Ceiba pentandra*) on 18 October 1845. The tree was situated in a "grass-piece of Mount Edgecombe." The opening in the tree was large enough to allow Gosse and another person to enter and examine it for bats. The hollow of the tree formed a chimney that was high enough that he could not discern any bats until he discharged his "fowling-piece" at random into the cavity. Ultimately, he obtained four or five specimens and several individuals escaped.

An individual kept in captivity by Gosse (1847) readily consumed a large cockroach that he offered to it. Gosse reports that on being offered the cockroach the bat "seized greedily and munched up, moving the jaws only vertically." He described the progression of mastication of the insect with parts being placed into the internal cheek-pouches, which ultimately became distended. After the initial mastication was completed, the bat using its jaw and muscles of the pouch removed portions of the contents, which were re-masticated and swallowed. The process was repeated until the pouches appeared to be empty and had disappeared from sight. Gosse (1847) likened the process to rumination. One of us (Phillips, previously unpublished observations) followed up on these observations in 1972. Histological examination of two specimens revealed that the "cheek pouch" observed when the bat is chewing consists of distended buccal epithelium. The epidermal component of the integument is extraordinarily thick and heavily keratinized in comparison to typical oral epithelium in the buccal cavity of bats. With histochemical techniques, a substantial abundance of elastic fibers can be demonstrated in the dermis, which is consistent with the capability of the "pouches" to distend and then collapse and retract when the bat swallows. The most important histological observation, however, involved the salivary glands. In *Noctilio leporinus,* the parotid salivary gland main duct empties directly into the portion of the buccal cavity that acts as a pouch. Therefore, the pouch is a container that holds the food bolus while it is bathed in parotid gland secretions. This is the only known example of this anatomical-feeding behavior association in mammals. The association is so dramatic that one could hypothesize that the parotid gland secretions in *Noctilio leporinus* probably are unusually rich in digestive enzymes such as proteinases. To date, however, the secretory proteins have not been isolated and identified.

No pregnant females were taken during our work on Jamaica, but three females taken on 23 July (2) and 27 July were lactating. Three individuals taken on 8 July (2) and 23 July were juveniles as indicated by their unfused phalangeal epiphyses. This would indicate that young are being born in June and early July. Six July-taken adult males had testes lengths that averaged 6.3 (3-9). Three adult females taken on 18 December weighed 50, 54, and 58 g.

Genetics.—The karyotype of *N. leporinus* has 2n = 34 and FN = 58 (Fig. 6). There are 26 biarmed autosomes in a graded series from large to small, and 6 medium-sized to small acrocentric autosomes. The X is medium-sized and metacentric, and the Y is small and acrocentric. Karyotypes were obtained from two males and one female from Queenhythe.

The karyotype of *N. leporinus* reported here is identical to those reported for specimens from Brazil (Yonenega et al. 1969), Trinidad (Baker and Jordan 1970), and Mexico (Baker 1970a). *Noctilio albiventris* (= *labialis*) appears to have an identical karyotype (Baker and Jordan 1970; Patton and Baker 1978).

Lewis-Oritt et al. (2001b) examined the mitochondrial cytochrome *b* gene and the nuclear recombination activating gene 2 (RAG 2) for zoogeographic and population studies of this species (but not including Jamaica). These authors concluded that *N. leporinus* is a younger species than *N. albiventris,* which implies that piscivory is a recently evolved feeding strategy for this genus. Further, they concluded that populations ranging from Peru to Middle America and throughout the Caribbean show very low levels of genetic distance, which is compatible with the hypothesis that the current geographic range represents a recent expansion. The authors estimate the time since divergence for this species is between 0.28-0.7 million years ago.

Remarks.—We were unable to locate Mount Edgecombe [= Mount Edgecumbe] on modern maps

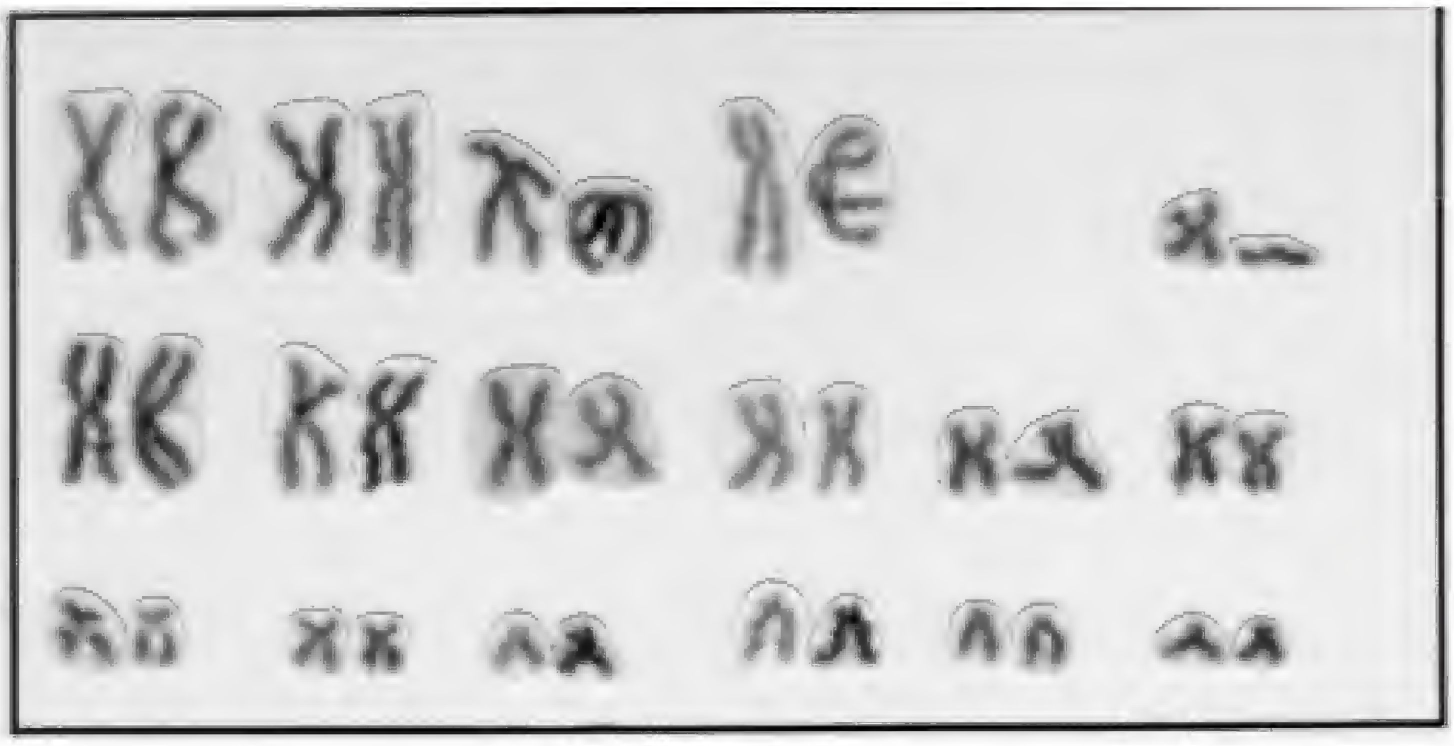

Figure 6. Karyotype of a male *Noctilio leporinus* from Queenhythe, St. Ann Parish (TK 8129; TTU 21135).

of Jamaica, but according to Gosse (1851:36, 50) the "park-like estate of Mount Edgecumbe" is reached by travelling along "The great post-road of the southern side, after passing Bluefields (supposing the traveller to be proceeding eastward), runs along the coast to Belmont, Mount Edgecumbe, &c., often at the very water's edge, and sometimes separated from the sea only by a narrow belt of woods." We estimate its location to be approximately 18°08' N, 78°01' W in Westmoreland Parish.

Pteronotus macleayii grisea (Gosse, 1851)
Macleay's Mustached Bat

Specimens examined (400).—CLARENDON PARISH: Douglas Castle Cave, 4 mi. W Kellits, 12 (TTU). HANOVER PARISH: Lucea, 4 (AMNH); Flint River, 1.5 mi. E Sandy Bay, 1 (CM). MANCHESTER PARISH: Oxford Cave, 2 (IJ); *Oxford Cave, Balaclava* [given as St. Elizabeth Parish], 51 (44 AMNH, 7 BMNH). ST. ANDREW PARISH: Brentford Rd., Kingston, 1 (NMNH). ST. ANN PARISH: Green Grotto, 2 mi. E Discovery Bay, 1 (CM); Queenhythe, 1 (CM). ST. CATHERINE PARISH: St. Clair Cave, 2 mi. S Ewarton, 93 (1 BMNH, 30 CM, 16 COLU, 1 JMM, 15 ROM, 30 TTU); Spanish Town, 1 (NMNH); 0.2 mi. E Watermount, 4 (CM). ST. ELIZABETH PARISH: Balaclava, 96 (AMNH). ST. JAMES PARISH: Montego Bay, 77 (AMNH); *Providence Cave, Montego Bay*, 43 (30 AMNH, 13 NMNH); *cave near Montego Bay*, 7 (MCZ). TRELAWNY PARISH: Freeman's Hall, 1 (BMNH); Windsor Cave, 1 (TTU). WESTMORELAND PARISH: Phœnix Park [18°13'N, 78°08'W], near Savanna-La-Mar, 1 (BMNH[holotype of *Chilonycteris grisea* Gosse]). PARISH UNKNOWN: no specific locality, 3 (2 BMNH, 1 MCZ).

Additional records.—ST. ANN PARISH: Mount Plenty Cave (Goodwin 1970; McFarlane 1997). WESTMORELAND PARISH: Monarva Cave (Dávalos and Erikkson 2003).

Distribution.—Figure 7 shows collecting localities for *Pteronotus macleayii* on Jamaica. Macleay's mustached bat is present at low to moderate elevations wherever appropriate roost caves are found. There are no records from the eastern-most two parishes—Portland and St. Thomas. The species occurs only on Cuba, Isle of Pines, and Jamaica. The subspecies *P. m. grisea* is endemic on Jamaica (Smith 1972).

Systematics.—Rehn (1904a) first reviewed this species under the name *Chilonycteris macleayii*. Subsequently, the systematics of *Pteronotus macleayii* was reviewed by Smith (1972). Smith recognized the Jamaican and Cuban populations as separate subspecies, applying the name *P. macleayii grisea*, originally described from Phœnix Park, Westmoreland Parish, by Gosse (1851), to bats from Jamaica. Smith (1972) distinguished *P. m. grisea* on the basis of its larger external and cranial size. Smith (1972:83) was im-

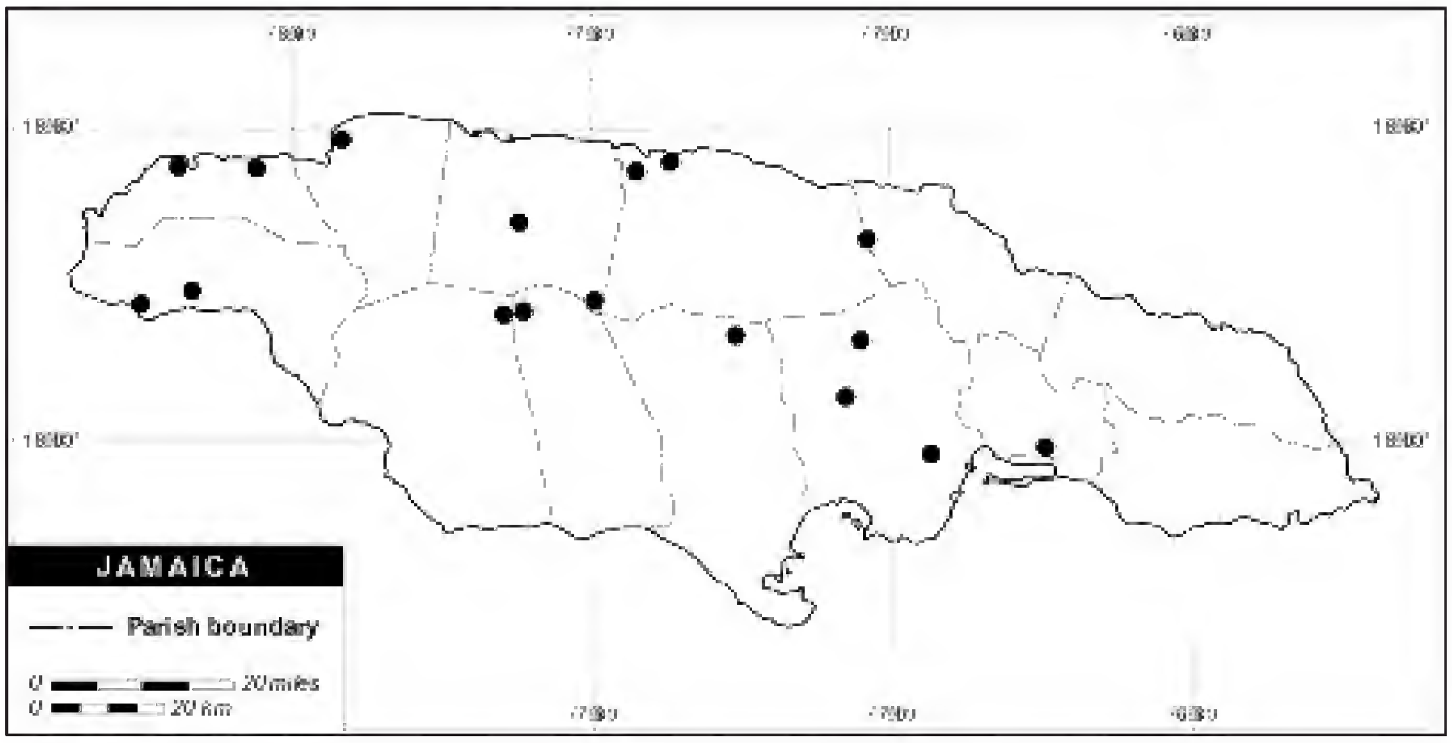

Figure 7. Map of Jamaica showing the locations where specimens of Macleay's mustached bat, *Pteronotus macleayii*, have been collected.

pressed by the differences between the two subspecies and opined that "it is doubtful that any substantial gene flow now exists between these two races." Simmons and Conway (2001) recently confirmed Smith's conclusions regarding the presence of two subspecies.

On Jamaica, *P. macleayii* can be confused with *P. quadridens* in the field (Fig. 8). The two species are both relatively small and their color is not substantially different. However, *P. macleayii* has a consistently longer forearm with the shortest length of 170 individuals measured being 41.3 (AMNH 60678, male from Providence Cave) as opposed to the longest forearm measure for *P. quadridens* of 41.2 and larger greatest length of skull (16.1 to 17.0 as opposed to 14.3 to 15.3) than *P. quadridens* (Table 1).

Morphometrics.—Table 1 gives the length of forearm and nine cranial measurements for samples of 10 males and 10 females from St. Clair Cave. Males averaged larger than females in all nine cranial measurements. The males were significantly larger than females at the $P = 0.01$ level for greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, and palatal length and at the $P = 0.05$ level for postorbital constriction and length of the maxillary toothrow. The only measurements for which no significant differences were found were interorbital constriction, breadth across upper molars, and length of forearm, which was the only measurement in which males were not larger than females as the means were equal.

Smith (1972) reports the cranial measurement of 19 males and the external measurements of 6 males and 6 females of *P. m. grisea*. Gosse (1851) gives measurements of the holotype of *C. [= P.] m. grisea* and an excellent description of its external morphology (Fig. 9). Rehn (1904a) gives the external measurements of four individuals and cranial measurements of two from Lucea as well as a description of external and cranial characteristics of *P. m. grisea*.

Natural history.—McFarlane (1986) considered Macleay's mustached bat to be one of the obligate cave-dwelling species living on Jamaica. Our observations support this classification because we collected all but six specimens during our work on Jamaica in or near caves. The species has been taken in association with nine caves on the island, including the following five. Douglas Castle Cave (cave 256) is a small dry chamber cave with two entrances that is 40 m in length (Fincham 1997). Nets were placed covering one of the entrances, capturing bats as they entered and exited the cave. The flight of bats began about 7:30 PM with *P. macleayii* beginning to exit the cave about 30 to 45 minutes later. Oxford Cave (cave 192) is a dry passage cave over 750 m in length. The passage is generally 10 m wide and 8 m high, with a mud, boul-

Figure 8. View of the dorsal surface of three species of *Pteronotus* giving a comparison of their overall size. The species are (from left to right) *P. parnellii*, *P. macleayii*, and *P. quadridens*.

Figure 9. View of the head of *Pteronotus macleayii*.

der, stalagmite, and bat guano floor (Fincham 1997). Just inside the entrance, the passage constricts to an opening of about 0.6 m by 1 m. D. A. McFarlane reports seeing a "solid column of bats pouring from the entrance" (Fincham 1997:279). The colony is composed of several species that occupy a large portion of the cave. The single specimen of *P. macleayii* taken at the Green Grotto cave was a male captured in a net set near one of the cave entrances. Providence Cave (cave 1037) has not been found since visited by H. E. Anthony in 1920. It is believed to be a chamber cave, with side chambers containing bat colonies (Fincham 1997). A full description of St. Clair Cave is given in the account for *Phyllonycteris aphylla*. Most of our specimens of Macleay's mustached bat were captured in the huge Junction Chamber of this cave (Fig. 10). Mist nets simply held in the air in this area caught a large number of individuals as did a net erected for a few minutes near the exit leading into the Main Passage. Bats in the Junction Chamber seemed to be disturbed by our initial entry into the area. We became aware immediately on entering the space of many bats, including this species and several others flying in circles high in the chamber.

Goodwin (1970) found Macleay's mustached bats to be abundant during his December-January surveys in Mount Plenty Cave, St. Clair Cave, and Windsor Great Cave. He believed that the species exhibited "a strong preference for extensive, deep, wet cave systems and for large high-domed chambers located well back from the entrances." He found that *P. macleayii* formed small to medium-sized clusters located at the highest points of the chambers. He discovered *P. macleayii* in close association with *P. parnellii* and *Monophyllus redmani* and believed that the three species required essentially the same cave environments. Goodwin (1970) found that even though these three species were associated in the caves that they formed single species clusters.

Figure 10. Photograph of John Bickham and Hugh Genoways collecting bats, particularly mormoopids in the Junction Chamber, St. Clair Cave, St. Catharine Parish, Jamaica.

Aside from specimens collected in caves, we also captured this bat species along the Flint River east of Sandy Bay, at Queenhythe, and near Watermount. In each of these situations, individuals were captured over watercourses or ponds. At Queenhythe, the individual probably was coming to drink from the pond or was hawking insects over it. At Flint River and Watermount, the individuals were probably using the river courses as flyways during their nightly movements. The male holotype of *C. m. grisea* was captured by Gosse (1851) after it flew through an open window into his room where he was staying at Phœnix Park.

The length of testes of 18 July-taken males averaged 2.44 (2-3). Goodwin (1970) found a mean length of testes for 12 males taken on 1 January to be 4.2 (2-5). Of 21 females taken on 17 and 18 July, only one was lactating when obtained on 18 July. None of the females taken on 23 July (2) or on 28-29 July (14) was reproductively active. None of the four females captured by Goodwin (1970) on 1 January carried embryos. Based on these field observations it is difficult to draw many conclusions about reproduction in this species. Our best guess is that they breed annually, probably in late winter. A male from St. Clair Cave weighed 5.9 g.

Kössl et al. (1999) studied the echolocation calls of *P. macleayii* from Runaway Bay Caves. They learned that the bats used both pure frequency-modulated and short constant-frequency/frequency-modulated calls. The otoacoustic emission-threshold curves showed the most sensitivity between 30 and 50 kHz. The threshold curve for *P. macleayii* is comparable to those of unspecialized frequency-modulated species of bats (Kössl et al. 1999).

Webster (1971) discovered two species of trematodes infesting *Pteronotus macleayii* from St. Clair Cave. He found *Limatulum gastroides* Macy 1935 in eight of 29 specimens examined and *Urotrema scabridum* Braum 1900 in four of the 29 specimens.

Genetics.—The karyotype of *P. macleayii* has 2n = 38 and FN = 60 (Fig. 11). There are 24 biarmed autosomes in a graded series from large to medium-sized, and 12 acrocentric autosomes graded from medium-sized to small. The X is medium-sized and submetacentric, and the Y is minute and biarmed. Karyotypes were obtained from two females from St. Clair Cave and one male from Queenhythe. This is the first report of the standard karyotype of *P. macleayii*. It is identical to karyotypes reported for *P. parnellii*

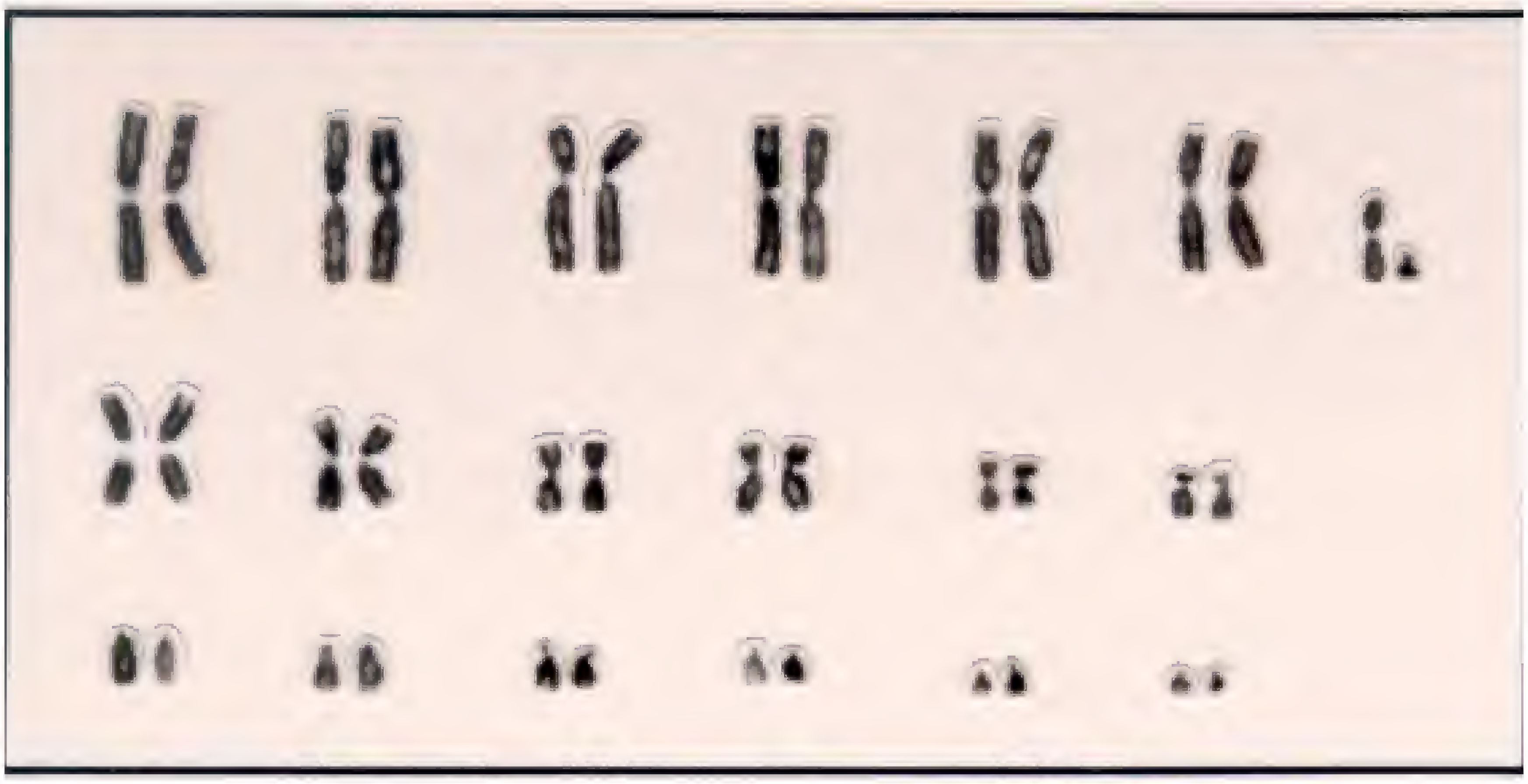

Figure 11. Karyotype of a male *Pteronotus macleayii* from Queenhythe, St. Ann Parish (TK 9386; CM 44155).

(Baker, 1967 1970a; Baker and Lopez 1970), *P. fuliginosus* [= *quadridens*] (Baker and Lopez 1970), *P. davyi* (Baker 1967), and *P. psilotus* [= *personatus*] (Baker 1967).

Sites et al. (1981) studied the G-band patterns of the chromosomes of *P. macleayii* from Jamaica. The pattern appeared to be identical for all species of *Pteronotus* studied, including the Jamaican species *P. parnellii* and *P. quadridens*. Members of the genus *Pteronotus* differ from members of the genus *Mormoops* in G-band pattern, but only in that the latter has a prominent G-positive region proximal to the centromere of arm 2.

Molecular data (Lewis-Oritt et al. 2001a) show *P. macleayii* to be sister to *P. quadridens* (see genetics section of *P. quadridens*). Furthermore, the Jamaican and Cuban populations show low genetic distance and thus likely have shared a recent common ancestry.

Remarks.—The holotype of *Chilonycteris grisea* Gosse in the British Museum (Natural History) does not have a locality listed, but as Smith (1972:83) reported, the unregistered specimen is from Phœnix Park, near Savanna-La-Mar, Westmoreland Parish (approximately 18°13' N, 78°08' W). Gosse (1851:326) stated in the introduction to the description of this bat: "*May 24th, 1846*.—A pretty and interesting little Bat came into my hands, a species of the curious genus *Chilonycteris*. It flew in at an open window at Phœnix Park in the evening, but was not captured until after a very tedious pursuit, manifesting great agility on the wing." Elsewhere in his book Gosse (1851:155) describes the location of Phœnix Park as follows: "Many of the opulent merchants of Savanna le Mar have pleasant country seats, a few miles out of town. At one of these, the residence of a kind friend, I frequently spent a few days; though the neighbourhood was not particularly favourable to my pursuits." The holotype is an adult male preserved in fluid without the skull removed. The specimen is in excellent condition. Its forearm measured 45.5, which is consistent with other specimens assigned to the taxon.

The locality known as "Freeman's Hall" is an enigma. We have been unable to precisely locate it, although specimens of another species of bat, *Mormoops blainvillii,* in the British Museum (Natural History) and Osburn's writing (1859a) indicate that Freeman's Hall was in Trelawny Parish. However, by piecing together information in Osburn (1859a, 1859b), the location actually can be delimited even further. Osburn (1859b), describing the taking of a bird on the Greenock estate in the mountains on the border between St. Ann's and Clarendon parishes, stated that he expected to find the same species of bird at Freeman's Hall, which was located "only ten or twelve miles westward on the same ridge." The current gazetteer gives the location of Greenock at 18°12′ N, 77°22′ W, which would place this location almost exactly on the border of the two parishes where it is crossed by Jamaican highway "B3." This would place Freeman's Hall in the extreme southeastern corner of Trelawny Parish in the vicinity of the modern settlements of Lorrimers, Lowe River, and Wait-A-Bit. Further confirmation that this is probably the correct location of Freeman's Hall can be found in Osburn (1859a). Osburn, in describing a trip leaving Freeman's Hall, stated: "My first day was across a forest district of the Black Grounds, partially cleared and known as Hector's River. As my first stage was to Oxford . . . ." The border between southeastern Trelawny and Manchester parishes is formed by Hector's River and Oxford is located along the border between Manchester and St. Elizabeth parishes only a short distance to the southwest of this region.

There is some confusion as to the exact location of Oxford Cave. Some early specimens at the American Museum of Natural History reference the location from Balaclava and place the location in St. Elizabeth Parish (Koopman and Williams 1951), whereas more recent specimens including those at the Institute of Jamaica and Goodwin (1970) reference the cave from Auchtembeddie and place the location in Manchester Parish. We have followed Goodwin (1970) throughout this manuscript in placing Oxford Cave in Manchester Parish, but have maintained the original reference points.

Pteronotus parnellii parnellii (Gray, 1843)
Parnell's Mustached Bat

Specimens examined (297).—CLARENDON PARISH: Douglas Castle Cave, 4 mi. W Kellits, 29 (TTU). HANOVER PARISH: Lucea, 9 (8 AMNH, 1 MCZ); Flint River, 1.5 mi. E Sandy Bay, 1 (CM).

MANCHESTER PARISH: Oxford Cave, 1 (IJ); *Oxford Cave, Balaclava* [given as St. Elizabeth Parish], 27 (25 AMNH, 2 BMNH). PORTLAND PARISH: 0.8 mi. W Drapers, 4 (CM); Green Hill, 2 (TTU); along Williamsfield River, 1.5 mi. NW Hectors River, 2 (UF); Happy Grove School, Hectors River, 1 (JMM); 27 mi. from Kingston [in St. Andrew Parish] on Newcastle Highway, 5000 ft., 1 (ROM). ST. ANN PARISH: Green Grotto, 2 mi. E Discovery Bay, 3 (2 CM, 1 HZM); Orange Valley, 1 (CM); Circle B Plantation, 2 km SW Priory, 2 (TTU); Queenhythe, 1 (CM); 4 mi. E Runaway Bay, 1 (TTU). ST. CATHERINE PARISH: Healthshire Hills, 1 (AMNH); St. Clair Cave, 2 mi. S Ewarton, 45 (1 BMNH, 7 CM, 3 COLU, 4 IJ, 1 JMM, 12 ROM, 17 TTU); Swansea Cave, Worthy Park Factory Ltd., Lluidas Vale, 2 (TTU); 0.2 mi. E Watermount, 17 (CM); Worthy Park, 1 (BMNH). ST. ELIZABETH PARISH: Wallingford Cave, Balaclava, 4 (AMNH); Peru Cave, Goshen 1 (AMNH); Pedro Bluffs, 1 (AMNH). ST. JAMES PARISH: Montego Bay, 1 (MCZ); *Providence Cave, Montego Bay*, 10 (AMNH). ST. THOMAS PARISH: Whitfield Hall, Penlyne, 4300 ft., 1 (JMM). TRELAWNY PARISH: Duanvale, 1 (TTU); *Cock Pit Cave, 5 mi. N, 2.5 mi. WNW Quick Step, 280 m*, 6 (NMNH); Cock Pit Cave, 4 mi. NNW Quick Step, 14 (NMNH); *cave north and west of Quick Step*, 5 (NMNH); Windsor Cave, 91 (6 AMNH, 7 KU, 78 TTU). WESTMORELAND PARISH: Wakefield, 1 (CM). PARISH UNKNOWN: *Sportsman's Hall Cave*, 3 (BMNH); no specific locality, 7 (3 BMNH, 2 MCZ, 2 NMNH).

Additional records.—CLARENDON PARISH: Jackson's Bay Cave [near Jackson's Bay] (McFarlane 1997); Pedro Cave [Pedro River area] (McFarlane 1997). ST. ANN PARISH: Ewart Town Bat Cave [Claremont area] (McFarlane 1997); *Golden Grove Cave* (Webster 1971); Moseley Hall Cave (Goodwin 1970; McFarlane 1997); Mount Plenty Cave (Goodwin 1970; McFarlane 1997); Thatchfield Great Cave [near Philadelphia] (McFarlane 1997). ST. CATHERINE PARISH: *Riverhead Cave* (McNab 1976; McFarlane 1997). ST. ELIZABETH PARISH: *Pedro Bluff Cave* (McFarlane 1997)*;* *Spaniards Cave* [Great Pedro Bluff] (McFarlane, 1997). ST. JAMES PARISH: *Sewell Cave* [Montego Bay] (Goodwin 1970; McFarlane,1997). ST. THOMAS PARISH: Ratbat Hole [17°52′12" N, 76°29′24" W] (Dávalos and Erikkson 2003). TRELAWNY PARISH: Belmont Cave [near Stewart Town] (McFarlane 1997). WESTMORELAND PARISH: Geneva Mountain Rat Bat Cave [18°21′01" N, 78°09′10.5" W] (Dávalos and Erikkson 2003); Monarva Cave (Dávalos and Erikkson 2003).

Distribution.—Figure 12 shows the collecting localities for *Pteronotus parnellii* on Jamaica. This bat is a common and widespread species on Jamaica. It can be found from sea level to over 1500 m and can be expected throughout the island. Parnell's mustached bat is found throughout much of Mexico, Central America, the northern third of South America, Greater Antilles, and St. Vincent in the Lesser Antilles. The nominate subspecies is confined to Jamaica and Cuba (Smith 1972).

Systematics.—Gray (1843) described *Phyllodia parnellii* based on a small collection of Jamaican bats that he received from Dr. Richard Parnell. Gray (1843) recognized that this new genus "has much resemblance with *Mormoops*, and especially *Chilonycteris*." This species was moved to the genus *Chilonycteris* when revised by Rehn (1904a). However, we follow Smith (1972) in placing it in the genus *Pteronotus* and recognizing *P. parnellii* as the sole representative of the subgenus *Phyllodia*. Recently, Simmons and Conway (2001) also agreed with Smith's conclusions.

Smith (1972) indicates that there are two syntypes for the species in the British Museum (Natural History)—BMNH 43.6.15.6-7, unsexed specimens in alcohol with the skulls not removed. Subsequent to the description by Gray, Tomes (1861a) described *Chilonycteris osburni*, on the basis of six specimens from Sportsman's Hall Cave. It subsequently was shown by Smith (1972) and others that Tomes' species is identical with *P. parnellii* and, therefore, is a junior synonym of that name. Smith (1972) lists the type locality for *C. osburni* as "Sportsman Hall and Oxford cave, Manchester, Jamaica" and lists the syntypes as "BM 7.1.1.626 (male) and 7.1.1.632 (sex unknown)." After re-reading Tomes (1861a), we believe that the type locality should be restricted to Sportsman's Hall Cave because Tomes states "The present species, of which six examples are in the collection obtained at Sportsman's Cave in Dec. 1858." There is no mention of Oxford Cave in the description. In Osburn's (1865:68) posthumous publication on this collection of bats, he gives this collection in-

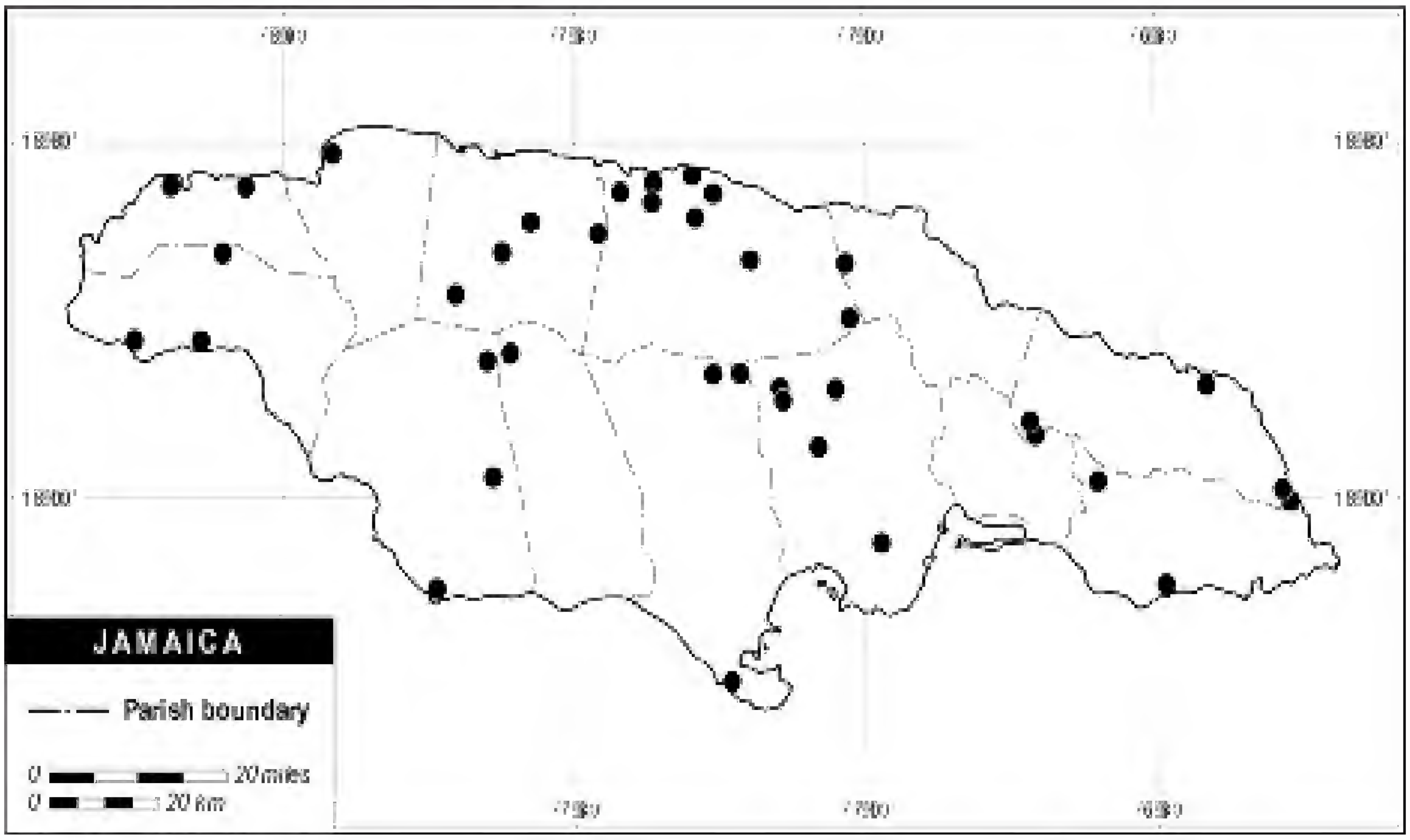

Figure 12. Map of Jamaica showing the locations where specimens of Parnell's mustached bat, *Pteronotus parnellii*, have been collected.

formation as "Sportsman's Hall Cave, 30th November, 1858. Two males and one female" and then as "Sportsman's Hall Cave, 15th December, 1858. Two males, one female, stuffed; one in spirits, injured in bring home; four males , one female." Although the numbers of specimens do not add up, it is clear that Sportsman's Hall Cave was the locality he visited.

Unfortunately, Sportsman's Hall Cave is one of a few localities of Osburn that we have not been able to precisely locate, but it can be hoped that one day this mystery will be solved. The only hint in Osburn's (1865:69) publication about the site of Sportsman's Hall Cave is in the account for *Monophyllus redmani* where he states "a large cave at the summit of the steep hill that overlooks Sportsman's Hall Works." Sportsman's Hall Cave is not listed in the recent survey of Jamaican caves (Fincham 1997). Smith's (1972) confusion over Oxford Cave might have resulted from Osburn's (1865:69) listing of a specimen under the heading of *Chilonycteris* sp. from "Oxford Cave, Manchester, 22nd February, 1859." However, Tomes (1861a:65) associated this specimen and four other specimens listed by Osburn (1865:78) as *Chilonycteris grisea* from "Oxford Cave, Manchester, 29th February, 1859" as a single species under the name *Chilonycteris quadridens*. Examination of the specimens (7.1.1.627-29, 7.1.1.631) reveals that they are properly assigned to *Pteronotus macleayii*.

Smith (1972) listed two syntypes for *Chilonycteris osburni* Tomes, 1861a and gave length of forearm for each as 52.3. Our reading of Tomes (1861a:66-68) leads us to conclude that all six specimens in his hypodigm should be considered syntypes. The remaining four specimens are still in the British Museum (Natural History) as follows: 7.1.1.624, male, collected 15 December 1858, skin in good condition with broken skull attached, length of forearm, 55.1; 7.1.1.625, male, 30 November 1858, skin in good condition with broken skull attached, length of forearm, 54.0; unregistered, female, 15 December 1858, skin in good condition, but skull not found, length of forearm, 53.0, notes associated with the skin state "To Be Figured" and "Type of *Chilonycteris osburni* Tomes;" 32.11.58, male, no date of capture, skin in fair condition, but skull not found, length of forearm, 53.9, note associated with skin states "To be figured with assistance of a second specimen." Tomes (1861a) does figure the skin, skull, and dentition of *Chilonycteris* *osburni*, but the specimen or specimens are not identified. All of the four additional specimens have lengths of forearm that are longer than those of the syntypes listed by Smith (1972). These measurements clearly indicate that Tomes' hypodigm includes only a single species, which can be identified with *Pteronotus parnellii*.

The question may be raised as to why Tomes (1861a) redescribed a taxon that less than 20 years earlier had been described by Gray (1843) from the same island. Tomes (1861a) did not compare *Chilonycteris osburni* with *Phyllodia parnellii.* His only comparisons were made with *Chilonycteris gymnonota* (= *Pteronotus gymnonotus*, occurring from southern Mexico into northern South America), *Chilonycteris rubiginosa* (= *Pteronotus parnellii rubiginosus*, occurring in the Caribbean versant of Central America into the Amazonian lowlands), and *Chilonycteris quadridens* (= *Pteronotus quadridens*, occurring in the Greater Antilles).

Morphometrics.—Table 1 gives measurements for samples of 10 males and 10 females from St. Clair and Windsor caves. Males averaged larger than females in eight of the nine cranial measurements, with the mean being the same for both for postorbital constriction. The males were significantly larger than females at the $P = 0.001$ level for condylobasal length, zygomatic breadth, and mastoid breadth and at the $P = 0.01$ level for greatest length of skull and length of the maxillary toothrow. In addition to postorbital constriction, the means for the sexes did not differ significantly for length of forearm, interorbital constriction, palatal length and breadth across upper molars. Only in length of forearm did females average larger than males.

Smith (1972) gave mean and range of four external measurements of a sample of eight males and four females from St. Clair Cave. Rehn (1904a) gives the external measurements of eight specimens and the cranial measurements of three from Lucea as well as descriptions of the external, cranial, and dental characteristics of this taxon. Tomes (1861a) gave an extensive and detailed description of the pelage and other external morphology of this species (Fig. 13). Dobson (1878) also gave a description of the external characteristics of this species and external and wing measurements for the holotype.

Natural history.—McFarlane (1986) lists Parnell's mustached bat as one of the obligate cave dwelling species on Jamaica. We concur in this observation because the species is known to use at least 26 caves on the island as roost sites. Nine of these caves are described in detail here and the others are described elsewhere in this publication.

Wallingford Roadside Cave (cave 854) is a small chamber cave of about 10 m in length. It is a steeply descending passage with an earth and flowstone floor leads to a small chamber (Fincham 1997). According to Fincham (1997), this is the "Wallingford Cave" visited by H. E. Anthony in 1920. It was here that Anthony collected Recent owl pellets with bat remains and observed a small colony of *Artibeus*. Peru Cave (cave 94) is a labyrinth type cave with a total length of approximately 215 m. A large open entrance leads to a chamber with a lighthole 25 m above. Two passages lead from this chamber—one to a small chamber and the other to a series of chambers with lightholes (Fincham 1997). Anthony's 1920 field notes indicates that he encountered bats near the entrance to Peru Cave, whereas Frank's notes from 1971 indicate that "The S. E. passage soon led into a large chamber with bat population and rich guano deposits" (Fincham 1997). Pedro Bluff Caves (cave 93) is a series of dry chamber caves located on Pedro Bluff (Fincham 1997). Spaniard's Cave (cave 164) is a complex-type cave about 45 m long. It is located on Great Pedro Bluff near the sea. A boulder chamber entrance leads to several dry, choked grottos and passages (Fincham 1997). According to McFarlane (1997), *P. parnellii* occupied these two caves only with *Monophyllus redmani* and *Artibeus jamaicensi*s.

Sewell Cave (cave 681, St. James Parish) is a large chamber cave with two entrances. The cave is located at the eastern end of Poorly Street in Montego Bay. The single chamber is about 128 m long (Fincham 1997). Only *Artibeus jamaicensis* and *Eumops glaucinus* are reported from Sewell Cave in addition to *P. parnellii* (McFarlane 1997). Belmont Cave (cave 260) is a dry passage cave of about 300 m length. The walk-in entrance leads to a domed chamber with a lighthole. The cave eventually connects to Drip Cave (cave 401) (Fincham 1997). Parnell's mustached bat was the only species observed here by McFarlane (1997). Thatchfield Great Cave (cave 275, also called Light Hole Sink) is a complex-type cave of about 1400

Figure 13. View of the head of *Pteronotus parnellii*.

m in length. The cave has two entrances at the base of a low hill. The western entrance leads directly under the Lighthole, which is an opening to the surface about 50 m above. The opening at the surface is over 10 m wide and located in a clump of trees. The last 40 m below this opening are a sheer drop. Beyond the Lighthole the passage leads to a crawl that opens into a huge descending tunnel with mud and guano covering the floor that ends in a 45 m shaft with four guano cover ledges. About 300 m beyond the crawl, the North Passage leads about 200 m to the left ending in an aven (vertical shafts leading upward from the cave passage) with a series of ledges that extends at least 20 m (Fincham 1997). Thatchfield Great Cave has a large bat population that include four species in addition to *P. parnellii*—*Pteronotus quadridens, Macrotus waterhousii, Monophyllus redmani,* and *Artibeus jamaicensis* (McFarlane 1997). Pedro Cave (cave 175, St. Catherine Parish) is a dry passage cave with a length of 460 m. At about 250 m, Three Way Chamber is entered with passages leading away in three directions. Bats of two species (*P. parnellii* and *Phyllonycteris aphylla*) were observed coming from the right hand exit of Three Way Chamber (Fincham 1997).

In St. Clair Cave, we collected *P. parnellii* in the Junction Chamber under conditions described in the account of *P. macleayii*. Goodwin (1970) also found this species in St. Clair Cave, Windsor Cave, Oxford Cave, Moseley Hall Cave, Mount Plenty Cave, and Sewell Cave. In all of the caves except Sewell, he found Parnell's mustached bats in close association with *Monophyllus redmani*. Although the species seems to prefer to roost in large, humid chambers of caves, it also has been found in small chambers and hanging along the walls of passages. Goodwin (1970) found that *Pteronotus parnellii* and *Monophyllus* emerge from caves in mixed flocks beginning just after dark with activity continuing until at least midnight. He found that in collections made in five caves throughout the month of January the sex ratio for *P. parnellii* was consistently 1:1. Osburn (1865) commenting on Sportsman's Hall Cave found *P. parnellii* to be the most abundant of the three species present, with it occupying the area around one entrance and the center of the cave with *M. redmani* and *M. blainvillii* being taken near a second entrance. Dávalos and Erikkson (2003) believed that Geneva Mountain Rat Bat Cave harbored "several thousand *Pteronotus* *quadridens* and *P. parnellii,*" which were easily captured as they returned at dawn to the 5-m wide entrance to the cave on 4 December 2001.

Away from cave situations, Parnell's mustached bats generally are represented by a single or a very few individuals in collections with the exception of the site at 0.2 mi. E Watermount. Here we took 17 specimens as they flew over a stream canopied by tall trees. These bats were undoubtedly moving from day-roosts in nearby caves to foraging areas. This species displays a wide range of elevation when foraging, having been netted in a coffee plantation at 1300 m along the southern slope of the Blue Mountains at Penlyne and at a similar elevation along the north slope of these mountains at Green Hill. On the other hand, these bats have been netted near sea level in a coconut and banana plantation in the vicinity of Hectors River, over the Flint River near Sandy Bay, in an area of gallery forest that was about 100 m wide with a fast moving stream with many waterfalls at 4 mi. E Runaway Bay, and over a small canopied stream near Drapers. At Orange Valley, a single *P. parnellii* was netted under some isolated trees in a pasture area. Another individual was netted over a large pool in a pasture at the edge of the village of Queenhythe. A single *P. parnellii* was taken in nets set in an orchard including banana, several types of fruit trees, and palm trees at Duanvale. We believe that these last three individuals were in their foraging areas or coming to drink at the pond.

Goodwin (1970) found seven adult males taken on 4 January had testes that averaged 4.6 (2.5-6) in length. Three males obtained on 9 April had testes lengths of 4, 4, and 4.5, five males taken on 11 June had testes that averaged 3.2 (2-4) in length, and 22 July-taken males had testes that averaged 3.1 (2-5) in length. Two males taken on 2 November had testes that measured 3 and 4 in length.

Eight females examined by Goodwin (1970) on 4 January were nonpregnant, whereas McNab (1976) found that one (possibly three) female of 10 from the Worthy Park area was pregnant when captured between 23 February and 2 March. Dávalos and Erikkson (2003) described 27 of 30 *P. parnellii* as "heavily pregnant females" when they were captured on 23 March 2002 at Ratbat Hole, St. Thomas Parish. All seven females taken at Cock Pit Cave on 8-9 April were pregnant. The embryos averaged 17 (15-19) in crown-rump length. The only female captured on 14 June at this same locality was lactating as were the two females taken on 12 July. A female taken north of Kingston on the Newcastle Road on 7 May was determined by the field collector to be "pregnant with near-term embryo." Fifteen of the 81 additional July-taken females were lactating (14 taken on 14 July and 1 taken on 19 July), whereas the remaining 66 females evinced no gross reproductive activity. Collectively, these data support the conclusion that *P. parnellii* is a highly synchronous breeder. Young are born in April, May, and early June and lactating females can be found at least into late July.

Kanwal et al. (1994) studied the communication calls (as opposed to echolocation) of individuals of *P. parnellii* from Windsor Cave on Jamaica. They concluded "that this species uses a structurally complex repertoire of sounds that is no less elaborate than that of any other mammalian species." Its calls consist of one or more of 33 different types of discrete sounds. Kössl et al. (1999) studied the echolocation system of the four species of mormoopids occurring on Jamaica. They found that *P. parnellii* was the only species to use a constant-frequency as opposed to a frequency-modulated echolocation signal. The inner ear in Parnell's mustached bat is maximally sensitive at 62 kHz, which is the dominant constant-frequency of the echolocation call. It is believed that the auditory frequency resolution for this species is among the highest for any mammal (Kössl and Russell 1995), which allows it to resolve fine frequency modulations caused by the wing beats of its prey insects. The constant frequency echolocation calls allow Parnell's mustached bats to hunt insects within the forest canopy by distinguishing the insect against the acoustic clutter of the dense foliage of the canopy. Osborn (1865) stated that in specimens he examined from Sportsman's Hall Cave that "stomachs contained minute fragments of insects" and later commented that "fragments in stomach appeared to be those of Coleoptera principally."

Studying the annual variation in fat reserves of eight species of bats on Jamaica, McNab (1976) found that *Pteronotus parnellii* had significantly less fat deposits in the dry season as compared with the wet season. This also was true of other insectivorous bats. Females had significantly more fat than males during time of maximum fat reserves in the wet season, but this difference normally disappeared in the dry season. McNab's (1976) findings were consistent with the interpretation that insectivorous bats face the greatest seasonal variation in food availability because the number of flying insects is reduced during the dry season. Weights of seven April-taken males averaged 13.9 (12.5-15.6), five June-taken males 11.5 (10.5-12.5), and a December-taken male was 13.2. A lactating female taken on 14 June weighed 11 and a non-pregnant female weighed 12.2 on 19 December.

Webster (1971) discovered three species of nematodes infesting *Pteronotus parnellii* from two caves on Jamaica. He found *Capillaria* sp. [near *C. martinezi* Caballero 1942] in the stomach of one of six bats from Golden Grove Cave and two of six bats from St. Clair Cave. He found *Litomosoides guiterasi* (Perez Vigueras 1934) Sandground 1934 in two of six bats from Golden Grove Cave and one of six from St. Clair Cave. Webster (1971) described a new species of trichostrongylid, *Histiostrongylus parnelli*, based on two specimens discovered in the small intestine of two of six bats from Golden Grove Cave. Phillips and Jones (1969) found no dental abnormalities in five specimens that they examined from Jamaica.

Specimens examined from Peru Cave, Healthshire Hills, and Wallingford [Roadside] Cave were all recovered from owl pellets obtained within the caves.

Genetics.—The karyotype of *P. parnellii* has 2n = 38 and FN = 60 (Fig. 14). There are 24 biarmed autosomes in a graded series from large to medium-sized, and 12 acrocentric autosomes graded from medium-sized to small. The X is medium-sized and submetacentric, and the Y is minute and biarmed. Karyotypes were obtained from one female from Duanvale, one male from Douglas Castle Cave, and two males from St. Clair Cave.

Baker (1967), Baker and Jordan (1970), and Patton and Baker (1978), reported 2n = 38 and FN = 60 for populations of *P. parnellii* from Mexico, Puerto Rico, and Trinidad. The karyotype of *P. parnellii* was shown to share a high degree of homology with the karyotypes of *Noctilio* and several phyllostomatids, based on G- and C-band analyses (Patton and Baker 1978). The karyotype of *P. parnellii* is identical to those of species of *Mormoops* and the other species of *Pteronotus*. Sites et al. (1981) studied the G-band patterns of the chromosomes of *P. parnellii* from Jamaica. The pattern appeared to be identical for all

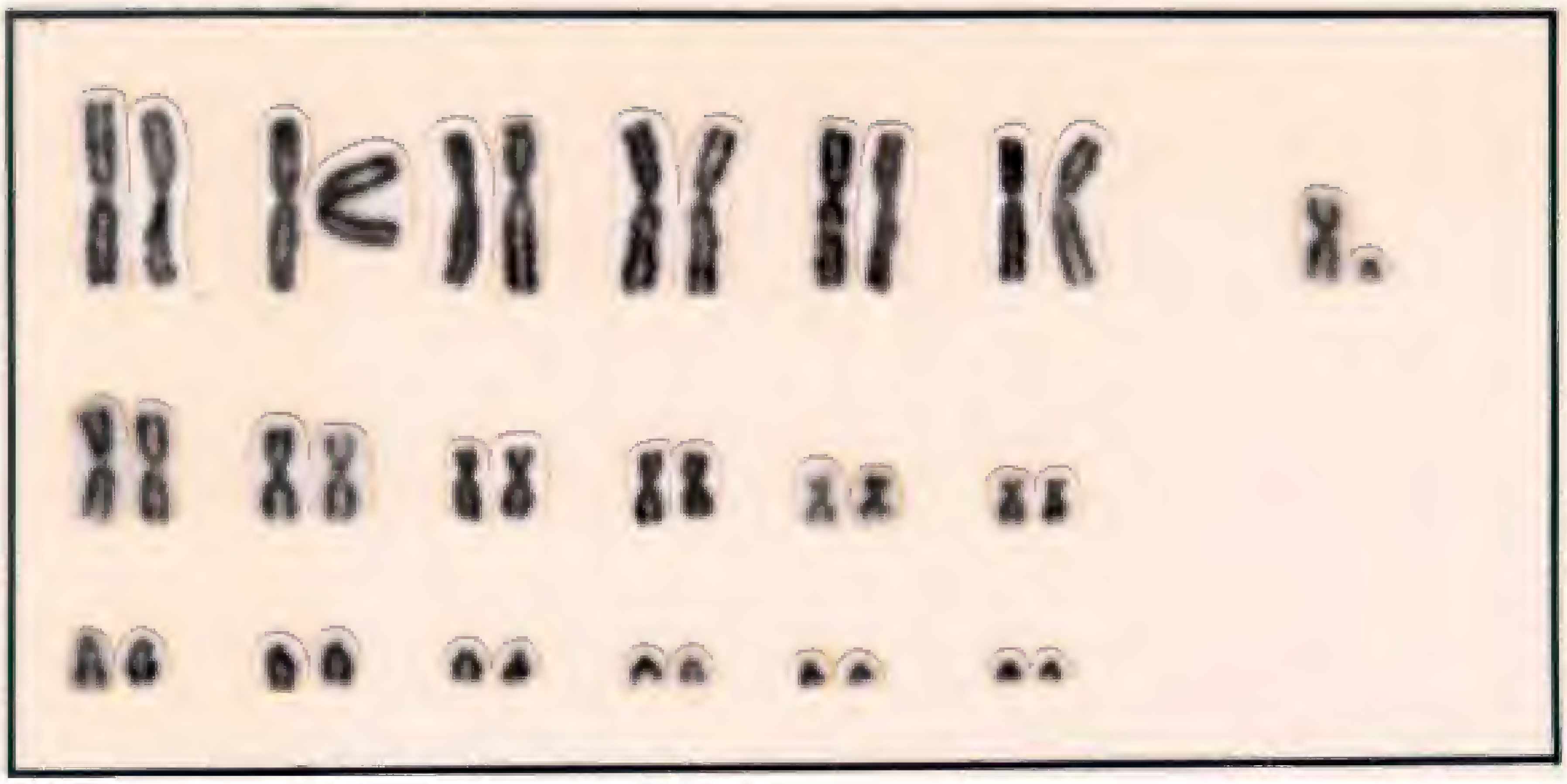

Figure 14. Karyotype of a male *Pteronotus parnellii* from St. Clair Cave, St. Catherine Parish (TK 9445; CM 44202).

species of *Pteronotus* studied, including the Jamaican species *P. macleayii* and *P. quadridens*. Members of the genus *Pteronotus* differ from members of the genus *Mormoops* in G-band pattern, but only in that the latter has a prominent G-positive region proximal to the centromere of arm 2.

The molecular systematics of *Pteronotus* was investigated by Lewis-Oritt et al. (2001a) and Van Den Bussche and Weyandt (2003). *Pteronotus parnellii* was found to be the most basal species in the genus, and sister to a monophyletic clade composed of the other five species in the genus (*P. personatus, P. davyi, P. gymnonotus, P. macleayii,* and *P. quadridens*). Lewis-Oritt et al. (2001a) further showed that *P. parnellii* has two maternal lineages, one of which is represented on Jamaica, Puerto Rico, and Suriname. The other maternal lineage is found in Honduras, Mexico, and Guyana. Given the genetic distance between the mitochondrial cytochrome *b* gene in these two lineages, they could represent two biological species based on the model proposed by Bradley and Baker (2001).

Concerning the zoogeographic affinities of *Pteronotus parnellii* populations, molecular data are consistent with a South American origin for this species because representatives of both mitochondrial gene clades occur in South America. Furthermore, the basal branch in each lineage is from South America. The sister relationship between the Jamaican and Puerto Rican specimens and the genetic distance in the cytochrome *b* gene (7.6%) suggest a substantial diversification among island populations of this species. The exact implications of a genetic distance value of >7% is difficult to ascertain in isolated populations but clearly values this high usually indicate different biological species (Bradley and Baker 2001). It is obvious from a distance value of 7% that the Jamaican and Puerto Rican populations have been separated in the Caribbean for a substantial amount of time between one million to 2.5 million years. The distance values that separate the island populations from the mainland populations (11%) also documents that the island populations have been separated from the mainland populations for greater than two million years (assuming a rate of change of 5% per million years). We know of no example where intraspecific variation in bats is greater than 10% in the cytochrome *b* gene. Therefore the default mode would be to recognize the forms in the Antilles as being distinct from the mainland forms. If that is true, then the correct name for the Antillean form would remain *Pteronotus parnellii* and the oldest available name for mainland populations would be *Pteronotus rubiginosus* (Wagner, 1843) with a type locality of Caicara, Mato Grosso, Brazil. Further, the closest relationship in the cytochrome *b* gene in the island forms and the mainland forms is to a specimen collected from Suriname. This relation suggests a South American origin, probably through the Lesser Antilles, for *Pteronotus parnellii*.

Remarks.—Healthshire Hills are marked on many recent maps as the Hellshire Hills and are located in southern St. Catharine Parish south of Spanish Town. Cock Pit Cave located 4 mi. NNW Quick Step also is given on specimen labels as "Cave north and west of Quick Step" and "Cock Pit Cave, 5 mi. N, 2.5 mi. WNW Quick Step." We have been unable to find Whitfield Hall, Penlyne, 4300 ft., on any of our Jamaican maps nor is it listed in the gazetteer for Jamaica from U. S. Board on Geographic Names. However, the collectors recorded that Whitfield Hall was a coffee plantation house on the slopes of Blue Mountain Peak. Penlyne should have been Penlyne Castle, a tiny settlement just down the road from Whitfield Hall. Both of these places are uphill from Hagley Gap [18°01' N, 76°37' W] in the Blue Mountains, amazingly close to Kingston [~ 13 km east of Kingston].

Pteronotus quadridens fuliginosus (Gray, 1843)
Sooty Mustached Bat

Specimens examined (163).—CLARENDON PARISH: Portland Point Lighthouse, 1 (TTU). HANOVER PARISH: Flint River, 1.5 mi. E Sandy Bay, 1 (CM). MANCHESTER PARISH: Oxford Cave, Balaclava [given as St. Elizabeth Parish], 27 (AMNH). PORTLAND PARISH: 0.8 mi. W Drapers, 1 (CM). ST. ANN PARISH: Circle B Plantation, 2 km SW Priory, 2 (1 CM, 1 TTU). ST. CATHERINE PARISH: St. Clair Cave, 2 mi. S Ewarton, 83 (46 CM, 3 COLU, 1 JMM, 27 ROM, 4 TTU, 2 UF); 0.2 mi. E Watermount, 1 (CM). ST. ELIZABETH PARISH: Balaclava, 3 (2 AMNH, 1 MCZ). TRELAWNY PARISH: Windsor Cave, 40 (2 AMNH, 2 NMNH, 36 TTU). WESTMORELAND PARISH: Wakefield, 1 (CM). PARISH UNKNOWN: no specific locality , 3 (2 BMNH, 1 MCZ).

Additional record.—ST. ANN PARISH: Thatchfield Great Cave (McFarlane 1997). WESTMORELAND PARISH: Geneva Mountain Rat Bat Cave [18°21′01" N, 78°09′10.5" W] (Dávalos and Erikkson 2003); Monarva Cave (Dávalos and Erikkson 2003).

Distribution.—Figure 15 shows the collecting localities for *Pteronotus quadridens* on Jamaica. This species is the least common member of the Mormoopidae on Jamaica and appears to have a restricted distribution on the island. It was found to be common only in the vicinity of the three large caves on the island—Oxford, St. Clair, and Windsor. The sooty mustached bat is confined to the islands of the Greater Antilles, with *P. q. fuliginosus* occurring on Jamaica, Hispaniola, and Puerto Rico (Smith 1972).

Systematics.—Smith (1972) reviewed this species under the name *Pteronotus fuliginosus* and Simmons and Conway (2001) recently confirmed his conclusions. Smith (1972) recognized two subspecies—*fuliginosus* from Jamaica, Hispaniola, and Puerto Rico, and *torrei* from Cuba. Silva Taboada (1976) examined the holotype of *Lobostoma quadridens* (which was described by Gundlach in 1840) in the collection of Humboldt University in Berlin and presented evidence that this name applies to the smallest of the mormoopids occurring in the Greater Antilles. Subsequent authors have followed this taxonomic arrangement, applying the names *Pteronotus quadridens quadridens* to the population on Cuba and *P. q. fuliginosus* to those populations on Jamaica, Hispaniola, and Puerto Rico.

On Jamaica, *P. quadridens* can be confused with *P. macleayii* in the field (Fig. 8). The two species are both relatively small and their color is not substantially different. However, *P. quadridens* has a consistently shorter forearm with the longest length of 70 individuals measured being 41.2 (AMNH 60668, female from Oxford Cave) as opposed to the shortest forearm measured for *P. macleayii* of 41.3 and smaller greatest length of skull (14.3 to 15.3 as opposed to 16.1 to 17.0) than *P. macleayii* (Table 1).

Morphometrics.—The length of forearm and nine cranial measurements of 10 male *P. quadridens* from Windsor Cave and of five females from St. Clair Cave are presented in Table 1. A comparison of measurements for males and females reveals that males are significantly larger than females in six of the 10 measurements studied. Males were significantly larger than females at the $P = 0.001$ level for condylobasal length in which the sexes only overlapped at 13.4 in this sample. Males were significantly larger at the $P = 0.01$ level for length of forearm, greatest length of skull, and length of maxillary toothrow and at the $P = 0.05$ level for zygomatic breadth and breadth across upper molars. In the other four characters—interor-

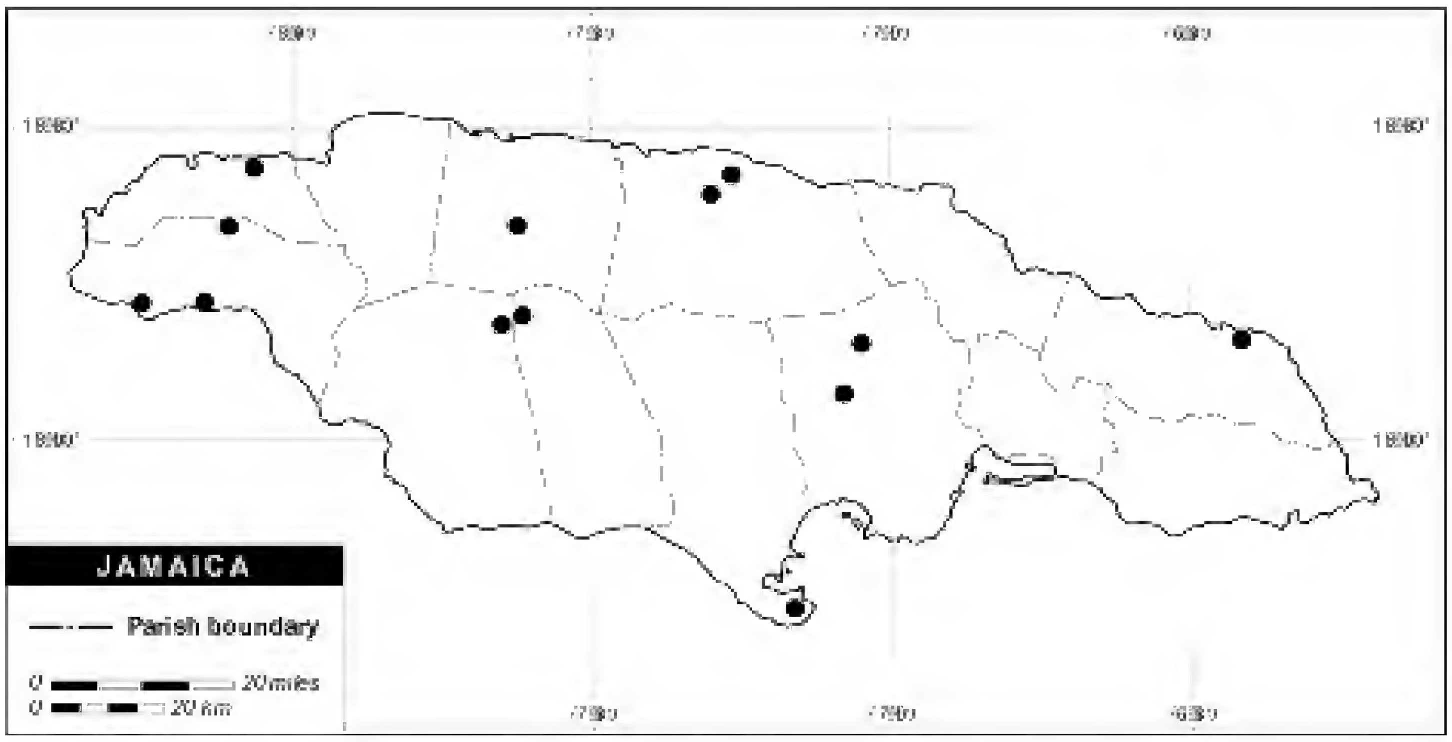

Figure 15. Map of Jamaica showing the locations where specimens of the sooty mustached bat, *Pteronotus quadridens*, have been collected.

bital constriction, postorbital constriction, mastoid breadth, and palatal length—the measurements of the two sexes display broad overlap and reveal no significant differences.

Smith (1972) presented external measurements for 13 males and 13 females from St. Clair Cave. He also gave cranial measurements for eight males from Jamaica.

Natural history.—The sooty mustached bat (Fig. 16) has been found in only six caves on Jamaica—Geneva Mountain Rat Bat Cave, Monarva Cave, Oxford Cave, St. Clair Cave, Windsor Cave, and Thatchfield Great Cave. This limited number of caves being used by this species indicates that it could be quite vulnerable to extirpation on Jamaica because we agree with McFarlane (1986) that *P. quadridens* is an obligate cave roosting species. This would indicate a much narrower range of roost condition tolerance than found for its congeners *P. parnellii* (known from 26 caves) and *P. macleayii* (known from nine). Specimens taken in St. Clair Cave were captured in the Junction Chamber under conditions described in accounts for *P. parnellii* and *P. macleayii* (Fig. 17). At Windsor Cave a single 6 m mist net was used at the main north entrance. Windsor Cave (cave 123) is a complex-type cave over 2980 m in length located near Windsor Great House. Passages lead to several chambers, which reach 25 m in height and 55 m in width. One passage ultimately leads to a second entrance in Bamboo Bottom Glade (Fincham 1997). On the night of 11 July 1974, the single net took 36 individuals of sooty mustached bats, which were all males. Other species of bats taken in this same small net in addition to *P. quadridens* were *P. parnellii, P. macleayii, Mormoops blainvillii, Macrotus waterhousii, Monophyllus redmani, Artibeus jamaicensis*, and *Natalus micropus* (Fig. 18). Prior and Gibson (1997) report observations on a juvenile female Jamaican boa (*Epicrates subflavus*) attempting to catch bats as they exited and entered the mouth of Windsor Cave. The snake was hanging from vegetation above the cave mouth with about two-thirds of its body length extended into the flight path of the bats. They did not observe any bats being captured, but heard reports of similar behavior

Figure 16. View of the head of *Pteronotus quadridens*.

Figure 17. Photographof a recess in the ceiling of the Junction Chamber, St. Clair Cave, St. Catharine Parish, Jamaica, containing a tightly packed group of mormoopid bats.

Figure 18. Photographof the main north entrance of Windsor Cave, Trelawny Parish, Jamaica.

by snakes at several other caves (see Dávalos and Erikkson 2003).

Although Koopman and Williams (1951) were the first to report this species from Jamaica, Goodwin (1970) was the first to discuss the natural history of the species based upon the specimens that he obtained in St. Clair Cave. He found *P. quadridens* in the same area of the cave that we found them. *Pteronotus quadridens* was in close association with *Monophyllus redmani* as well as with *P. macleayii* and *P. parnellii*. Goodwin (1970) estimated the total population of these four species to be about 5000 individuals with *M. redmani* the most abundant species and *P. quadridens* the least abundant, occurring in a ratio of about 10 to 1. Dávalos and Erikkson (2003) reported a population of "several thousand *Pteronotus quadridens* and *P. parnellii*" at Geneva Mountain Rat Bat Cave on 4 December 2001, whereas a survey of this same cave on 27 April 2001 had recorded only "19 *Mormoops blainvillii* and 16 *P. quadridens*."

Away from cave situations, sooty mustached bats have only been taken as single individuals, with the exception of three from Balaclava and these may well have been taken in association with the Oxford and Wallingford cave complexes. Near Priory we took two specimens but one was taken in 1984 and the other in 1985. At three sites (Flint River, near Drapers, and near Watermount), we took single individuals in mist nets as the bat was moving along a tree-lined river. At Wakefield, the single individual was netted as it flew among the trees of a fruit orchard containing mango, cashew, breadfruit, and citrus tree. The only other bats taken in the five nets that we set at this place were a single *P. parnellii* and two *Artibeus jamaicensis*.

Twenty-one July-taken males had testes that averaged 2.7 (2-3) in length, whereas three males taken by Goodwin (1970) on 29 December had testes that measured 5, 5, and 3. A male taken on 3 November had testes that were 1.5 in length. None of the 15 adult females taken in July (17 July, 1; 18 July, 3; 23 July, 1; 24 July, 1; 28 July, 1; 29 July, 8) evinced any gross reproductive activity nor did one taken during our work on 13 December or four females taken by Goodwin (1970) on 29 December. A non-pregnant adult female taken on 23 December weighed 4.2.

Kössl et al. (1999) investigated the echolocation calls of *P. quadridens* from Runaway Bay Caves and learned that they used both pure frequency-modulated and short constant-frequency/frequency-modulated calls. The otoacoustic emission-threshold curves showed the most sensitivity between 30 and 50 kHz. The authors concluded that the threshold curve for *P. quadridens* was comparable to those of unspecialized frequency-modulated species of bats.

Genetics.—The karyotype of *P. quadridens* has 2n = 38 and FN = 60 (Fig. 19). There are 24 biarmed autosomes in a graded series from large to medium sized, and 12 acrocentrics graded from medium-sized to small. The X is medium-sized and submetacentric, and the Y is minute and biarmed. Karyotypes were obtained from four males and five females from St. Clair Cave. This is the first report of the karyotype of *P. quadridens*. It is identical to the karyotypes reported for all species of *Mormoops* and *Pteronotus*.

Sites et al. (1981) studied the G-band patterns of the chromosomes of *P. quadridens* from Jamaica. The pattern appeared to be identical for all species of *Pteronotus* studied, including the Jamaican species *P. macleayii* and *P. parnellii*. Members of the genus *Pteronotus* differ from members of the genus *Mormoops* in G-band pattern, but only in that the latter has a prominent G-positive region proximal to the centromere of arm 2.

The molecular data of Lewis-Oritt et al. (2001a) and Van Den Bussche and Weyandt (2003) document a sister relationship for *P. quadridens* and *P. macleayii*. The observation that these two species are restricted to the Caribbean and that they are sisters is consistent with the hypothesis that their speciation occurred in the Greater Antilles. This particular speciation event(s) and the previously discussed genetic differentiation between the two maternal lineages in Antillean *Pteronotus parnellii* indicate that the Caribbean islands were a center for diversification in this genus. Exactly why this would be the case is unknown, but population instability (especially frequent drastic declines) within island populations and low frequency of inter-island movements are two factors consistent with the data.

Figure 19. Karytotype of a male *Pteronotus quadridens* from St. Clair Cave, St. Catharine Parish (TK 9487; CM 44226).

Mormoops blainvillii (Leach, 1821)
Antillean Ghost-faced Bat

Specimens examined (249).—CLARENDON PARISH: Douglas Castle Cave, 4 mi. W Kellits, 73 (TTU). HANOVER PARISH: Lucea, 1 (AMNH); Flint River, 1.5 mi. E Sandy River, 2 (CM). MANCHESTER PARISH: Gut River, sea level, 1 (UF); Oxford Cave, Balaclava [given as St. Elizabeth Parish], 16 (12 AMNH, 4 BMNH). PORTLAND PARISH: 0.8 mi. W Drapers, 1 (CM); Green Hill, 2 (TTU); Port Antonio, 1 (NMNH). ST. ANDREW PARISH: *Half Way Tree*, 1 (IJ); Kingston, 1 (NMNH). ST. ANN PARISH: Dairy Cave, Discovery Bay [= Dry Harbor], 2 (AMNH); Green Grotto, 2 mi. E Discovery Bay, 1 (TTU); Orange Valley, 2 (TTU); Moneague, 1 (NMNH); Queenhythe, 1 (TTU); *24 km W St. Ann's Bay*, 1 (TTU). ST. CATHERINE PARISH: River Sink Cave [near Worthy Park], 1 (TTU); St. Clair Cave, 2 mi. S Ewarton, 109 (1 BMNH, 34 CM, 28 COLU, 4 IJ, 4 JMM, 2 NMNH, 5 ROM, 29 TTU, 2 UF); 0.2 mi. E Watermount, 3 (CM). ST. MARY PARISH: Coldspring [18°12'N, 76°54'W], 1 (BMNH); Lucky Hill, 1 (COLU). TRELAWNY PARISH: Freeman's Hall, 3 (BMNH); cave N and W Quick Step, 4 (NMNH); Windsor Cave, 14 (4 NMNH, 10 TTU). PARISH UNKNOWN: *Sportsman's Hall Cave*, 1 (BMNH); no specific locality, 5 (3 BMNH, 2 NMNH).

Additional records.—CLARENDON PARISH: Jackson's Bay Cave (McFarlane 1997); Portland Cave-1 (McFarlane 1997). ST ANN PARISH: Moseley Hall Cave (Goodwin 1970; McFarlane 1997); Mount Plenty Cave (Goodwin 1970; McFarlane 1985); Ocho Rios (Goodwin 1970). ST. CATHERINE PARISH: *Riverhead Cave* (Henson and Novick 1966; McNab 1976; McFarlane 1997); Spanish Town (Gosse 1851:327). WESTMORELAND PARISH: Geneva Mountain Rat Bat Cave [18°21′01" N, 78°09′10.5" W] (Dávalos and Erikkson 2003); Monarva Cave (Dávalos and Erikkson 2003).

Distribution.—Figure 20 shows the collecting localities for *Mormoops blainvillii* on Jamaica. The records for this species are clustered in central Jamaica, with no records from the parishes of St. Elizabeth, St. James, St. Thomas, and eastern Portland. It is unknown if this clustering reflects a biological phenomenon or is simply an artifact of only capturing it at certain caves. The Antillean ghost-faced bat is an obligate cave-roosting species and its distribution on Jamaica could be limited by the availability of appropriate roost sites.

Systematics.—The correct generic and species names for this taxon were called into question by Hall (1981:96-97) when he used the name *Aëllo cuvieri* Leach, 1821. Leach (1821a, 1821b) described both *Aëllo cuvieri* from an unknown location and *Mormoops blainvillii* from Jamaica in the same volume of the *Transactions of the Linnean Society of London*. The papers were read on separate dates—22 February 1820

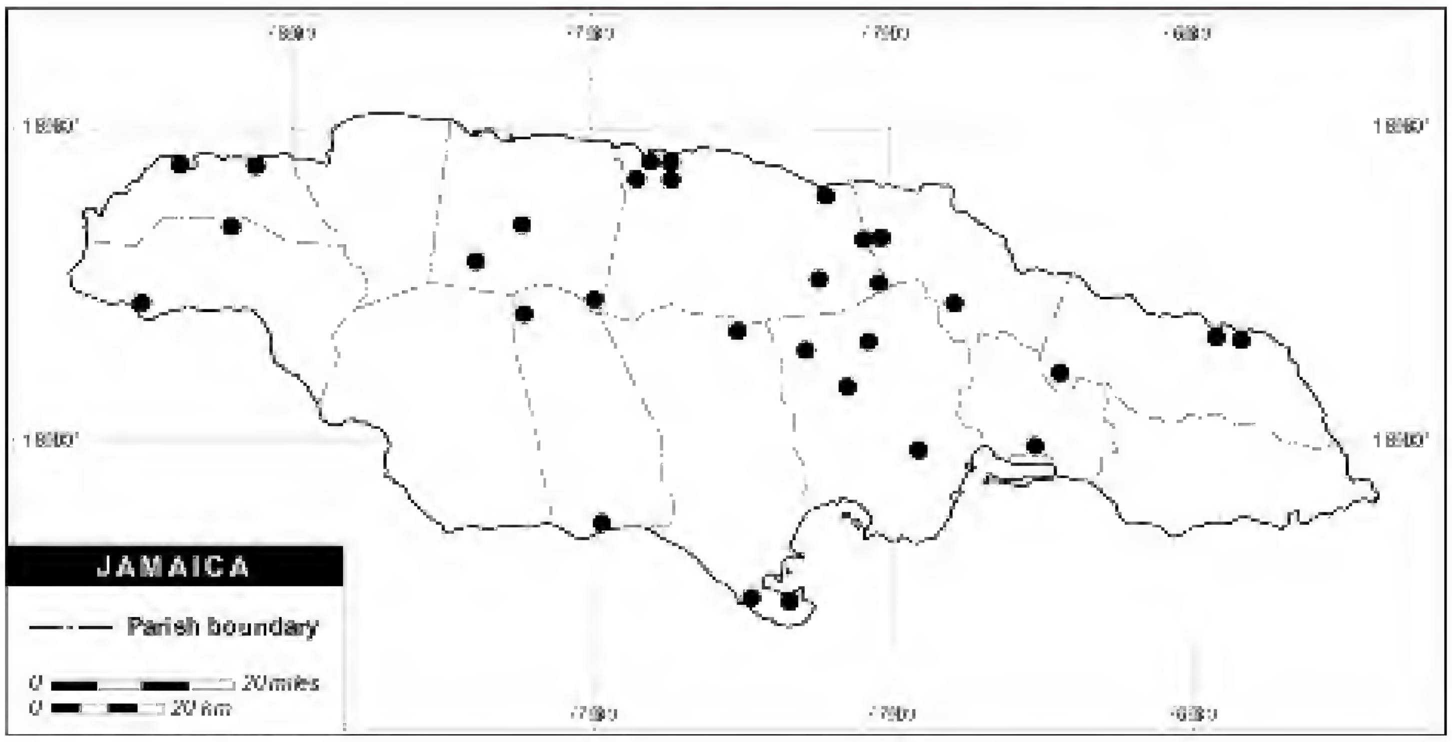

Figure 20. Map of Jamaica showing the locations where specimens of the Antillean ghost-faced bat, *Mormoops blainvillii*, have been collected.

for *Aëllo* and 7 March 1820 for *Mormoops*—but available evidence is that all articles in Part 1 of Volume 13, in which both descriptions appeared, of the *Transactions* were published at the same time in 1821. This gives *Aëllo cuvieri* page priority as Hall (1981) correctly notes. Hall (1981) attributes the use of *Mormoops* in preference to *Aëllo* by recent authors to Opinion 462 of the International Commission on Zoological Nomenclature. However, a review of the relevant literature reveals that this is a practice of long standing and that the use of *Mormoops* is supported strongly by the Code of Zoological Nomenclature.

Dobson (1878:454) was the first to note that the name *Aëllo cuvieri* referred to the same taxon as *Mormoops blainvillii*. He states the following in reference to *Aëllo*: "the definition of the genus is quite incorrect, as the type specimen from which it was taken had lost all trace of the cutaneous processes on the muzzle, and the number of teeth is incorrectly given. Therefore, although the name *Aëllo* has precedence of *Mormoops*, I retain the latter, which was published at the same time and has the advantage of correct definition." There can be no question, but that Dobson (1878) understood the problem and he made a clear decision on the resolution of the problem. As Dobson (1878) noted, Leach (1821a) gives the total number of incisors of *Aëllo* as 2 above and 4 below and the total premolars and molars as 8 above and 12 below, whereas he (Leach 1821b) gives the same for *Mormoops* as 4 and 4 for incisors and 10 and 12 for premolars/molars. The counts given for *Mormoops* match those for the genus and species at hand, whereas those for *Aëllo* do not. An external dorsal view, face, and cranium of the type of *Mormoops blainvillii* are beautifully figured by Leach (1821b) leaving no doubt as to the identity of the species, whereas no drawings are provided for *Aëllo cuvieri* (Leach 1821a).

Subsequent revisers of this genus, Rehn (1902b) and Smith (1972), also have chosen to follow this same course of action using the name *Mormoops blainvillii*. Under the International of Zoological Nomenclature for 2000 and earlier versions of the Code, the principal of First Reviser is stated in Article 24.2.2: "If two or more names, different or identical, and based on the same or different types, or two nomenclatural acts, are published on the same date in the same or different works, the precedence of the names or acts is fixed by the First Reviser . . . ." We believe that Dobson (1878) fulfills the requirement for a "First Reviser" and if not Dobson (1878) then Rehn (1902b) certainly fulfills this role. Therefore, based upon Opinion 462 of the International Commission and the principal of First Reviser as defined by International Code, we reject the action of Hall (1981) and urge other authors to do same by using the name *Mormoops blainvillii* for this taxon.

Mormoops blainvillii is monotypic and living populations only occur on islands in the Greater Antilles (Smith 1972). Although two subspecies were recognized prior to the study by Smith (1972), his morphometric analysis revealed "relatively continuous clinal variation between these population" rather than the discontinuity associated with subspeciation. Smith thus concluded that it was best to consider *M. blainvillii* to be monotypic based on the available data. Recently, Simmons and Conway (2001) also agreed with Smith's conclusions on the relationships of the genera *Mormoops* and *Pteronotus*.

Morphometrics.—Length of forearm and nine cranial measurements of 10 males and 10 females from Douglas Castle Cave are given in Table 1. Significant secondary sexual variation was detected in only three of these measurements—condylobasal length, mastoid breadth, and length of maxillary toothrow. For these three measurements, males were found to be significantly larger than females at the $P = 0.05$ level. In the other seven measurements, males were found to average slightly larger than females. Smith (1972) presented length of forearm and cranial measurements of eight males from Jamaica. Carter and Dolan (1978) gave wing and cranial measurements for the holotype of *Aëllo cuvieri*, which is presumed to have been obtained on Jamaica.

Rehn (1902b) gave a detailed description of the external (Fig. 21), cranial, and dental characteristics of this species as well as the external measurements of two Jamaican specimens. Rehn (1902b) mentioned the potential for this species to have two color phases. Individuals clearly can have quite different pelage colors, but whether these are color phases or the result of changes between new and older pelage is uncertain.

Gosse (1851:327-328) received a specimen captured in Spanish Town and described its pelage as being "a delicate light rufous hue" and its texture being

Figure 21. View of the head of *Mormoops blainvillii*.

"particularly fine, soft, and silky." Tomes (1861a) commented on the lighter color of specimens from Jamaica in which the under parts were "a pale rusty-red colour." Osburn (1865) described in detail the external and dental characteristics of this species. He also commented on the color of animals stating: "There is a great difference in the shade of chestnut-colour, which varies from a sandy buff to deep reddish brown."

Natural History.—Our records indicate that *Mormoops blainvillii* has been taken in at least 15 caves on Jamaica, which leads us to agree with McFarlane (1986) that the Antillean ghost-faced bat is an obligate cave dweller on the island. Most of these cave situations are described elsewhere in this paper, but two of the sites include River Sink Cave and Jackson's Bay Cave. River Sink Cave is near Worthy Park, according to McNab (1976) but is not listed by Fincham (1997). It is believed that it is probably one of the three Worthy Park Caves, most likely Worthy Park Cave No. 3 (cave 236), which is a stream passage cave of about 400 m length (Fincham 1997). Jackson's Bay Cave (cave 168), located on the dry south-central coast, is a complex cave with nine entrances and a length of approximately 3360 m. There are both wet and dry chambers present (Fincham 1997). Goodwin (1970) took this species in four caves—Oxford, Moseley Hall, Mount Plenty, and St. Clair. He estimated the population in Oxford Cave on 30 January 1966 to include 3000 individuals. On 27 April 2001, 19 individuals of *M. blainvillii* were taken at Geneva Mountain Rat Bat Cave, but on 4 December 2001 no individuals of this species were taken at this cave, which at that time held a large population of *Pteronotus quadridens* and *P. parnellii* (Dávalos and Erikkson 2003).

Goodwin (1970) remarked about the swift flight of this species "attaining extraordinary speed even in the narrow passages of a cave." Osburn (1865) also stated that "it flies with great agility and rapidity." We made the same observation when capturing this species in St. Clair Cave. We first encountered this species in the huge Junction Chamber where bats seemed to be disturbed by our initial entry into the area. However, we took the majority of the specimens of this species when a mist net was erected for a few minutes just inside the entrance of the Main Passage leading away from the Junction Chamber. In this area the net quickly filled, primarily with Antillean ghost-faced bats. In an attempt to prevent the onslaught from destroying the net, we laid it against the wall of the passage. This slowed the number of captures, but they continued to occur, including some where the only way that they could enter the net was to fly for a short distance between the wall and net. All of this occurred at very high speed because it was impossible to distinguish individual bats as they flew by. As Goodwin (1970) pointed out, "the vibration of the wings membranes of this species often produces a characteristic humming sound." Goodwin (1970) found that Antillean ghost-faced bats penetrated deeper into caves on Jamaica than any other species of bat, freely entering small crawlways and small chambers. In Oxford Cave he found them in a chamber that they could have accessed only by passing through an entrance that was 1 m high and 0.2 m wide.

Goodwin (1970) believed that *Mormoops* inhabited only the larger cave systems on Jamaica. It is true that many of the caves in which this species was taken were among the largest on Jamaica; however, we also caught it at Douglas Castle Cave (cave 256), which is a small dry chamber cave that is 40 m in length and has two entrances (Fincham 1997). The interesting point here is that specimens of *Mormoops blainvillii* were taken entering the cave rather than exiting it. This flight of *Mormoops* arrived at the cave about one hour after dark. The sex ratio of this group of bats was approximately two males to every female. However, Goodwin (1970) found the sex ratio of populations in the four caves in which he captured the species in January to be "near one to one."

During our field work on Jamaica, we netted ghost-faced bats in seven foraging situations away from caves. At 0.2 mi. E Watermount, we took three individuals, whereas at three other sites two specimens were captured and at the other three sites only single individuals were taken. The majority of these sites (Flint River, Drapers, Queenhythe, west of St. Ann's Bay, and near Watermount) are associated with water in the form of rivers or large ponds, which were being used as foraging sites, watering sites, or as routes for moving from day roosts to foraging areas. The highest point from which we recorded the species was at Green Hill along the north side of the Blue Mountains along the road to Kingston. The two individuals from

Orange Valley were netted in a pasture near a tree where considerable bat activity was occurring.

Salivary glands from one of our specimens were successfully field-fixed for transmission electron microscopy. Subsequent analysis revealed that the submandibular gland striated ducts in this bat have significant unique features (in comparison to about 250 other species of bats). In *Mormoops*, the striated ducts are highly convoluted and have a physically intimate association with a dense capillary network (Tandler et al. 1989). The physiological significance of this unique arrangement is unknown, although based upon the extensive experimental research on striated ducts in laboratory mammals (Tandler et al. 1989, 2001) it seems likely that there is a metabolic or excretory explanation.

Sixty-two females collected in July lacked any obvious evidence of reproductive activity. The same was true for another 24 adult females taken in St. Clair Cave on 4 January (Goodwin 1970) and a female taken on 27 January at Mt. Plenty Cave. Osburn (1865) believed that one of 12 females that he captured on 22 February 1859 at Oxford Cave was pregnant. Thirty adult males taken in July had testes lengths that averaged 2.34 (1-3.5). A male taken on 5 November had testes that were 3 in length. Goodwin (1970) found the average testis length of 20 males taken in St. Clair Cave on 4 January 1966 to be 3.0 (2-4).

Kössl et al. (1999) studied the echolocation calls of *Mormoops blainvillii* from Runaway Bay Caves and reported that they used only frequency-modulated calls. The otoacoustic emission-threshold curves showed the most sensitivity between 30 and 50 kHz. Kössl et al. (1999) found that the ghost-faced bat "emits downward-swept multiharmonic frequency-modulated signals." These signals start at frequencies of approximately 35, 70, and 105 kHz and the total call covers a wide frequency range from 20 kHz and beyond. They concluded that the threshold curve for *M. blainvillii* was comparable to those of unspecialized frequency-modulated species of bats.

An adult male captured on 29 December along the Gut River weighed 8.6. Two adult females taken in St. Clair Cave on 23 December weighed 8.0 and 7.9, whereas one taken here on 4 January weighed 5.3. The two specimens from Diary Cave were recovered from owl pellets (Koopman and Williams 1951; Williams 1952).

Genetics.—The karyotype of *M. blainvillii* has 2n = 38 and FN = 60 (Fig. 22). There are 24 biarmed autosomes in a graded series from large to medium-sized, and 12 acrocentric autosomes graded from medium-sized to small. The X is medium-sized and submetacentric, and the Y is minute and biarmed. Karyotypes were obtained from one male from St. Clair Cave, 2 mi. S Ewarton, three males from Windsor Cave, one male from Green Grotto, and one female from Orange Valley.

Nagorsen and Peterson (1975) reported 2n = 38 and FN = 60 for *M. blainvillii* from Hispaniola. The karyotype of *M. blainvillii* is identical to that of the mainland species *M. megalophylla* (Baker and Hsu 1970) and to species of the genus *Pteronotus* (Baker 1967).

Sites et al. (1981) studied the G-band patterns of the chromosomes of *M. blainvillii* from Jamaica. The pattern was unique among the mormoopid species studied. It agreed with *M. megalophylla* and differed from the species of *Pteronotus* in having a prominent G-positive region proximal to the centromere of arm 2. However, it differed from *M. megalophylla* and *Pteronotus* in having a prominent G-positive band in the distal end of arm 9 that stains lightly in all other species.

DNA sequences from the mitochondrial cytochrome *b* gene imply that *M. blainvillii* and *M. megalophylla* represent an early colonization event for the Caribbean (Lewis-Oritt et al. 2001a). The gene sequences from the two species differ by 14%. Although the divergence of these two species is relatively old, the sequence difference between specimens from Cuba and Jamaica (0.88%) suggests a recent common ancestry for the populations on these two islands.

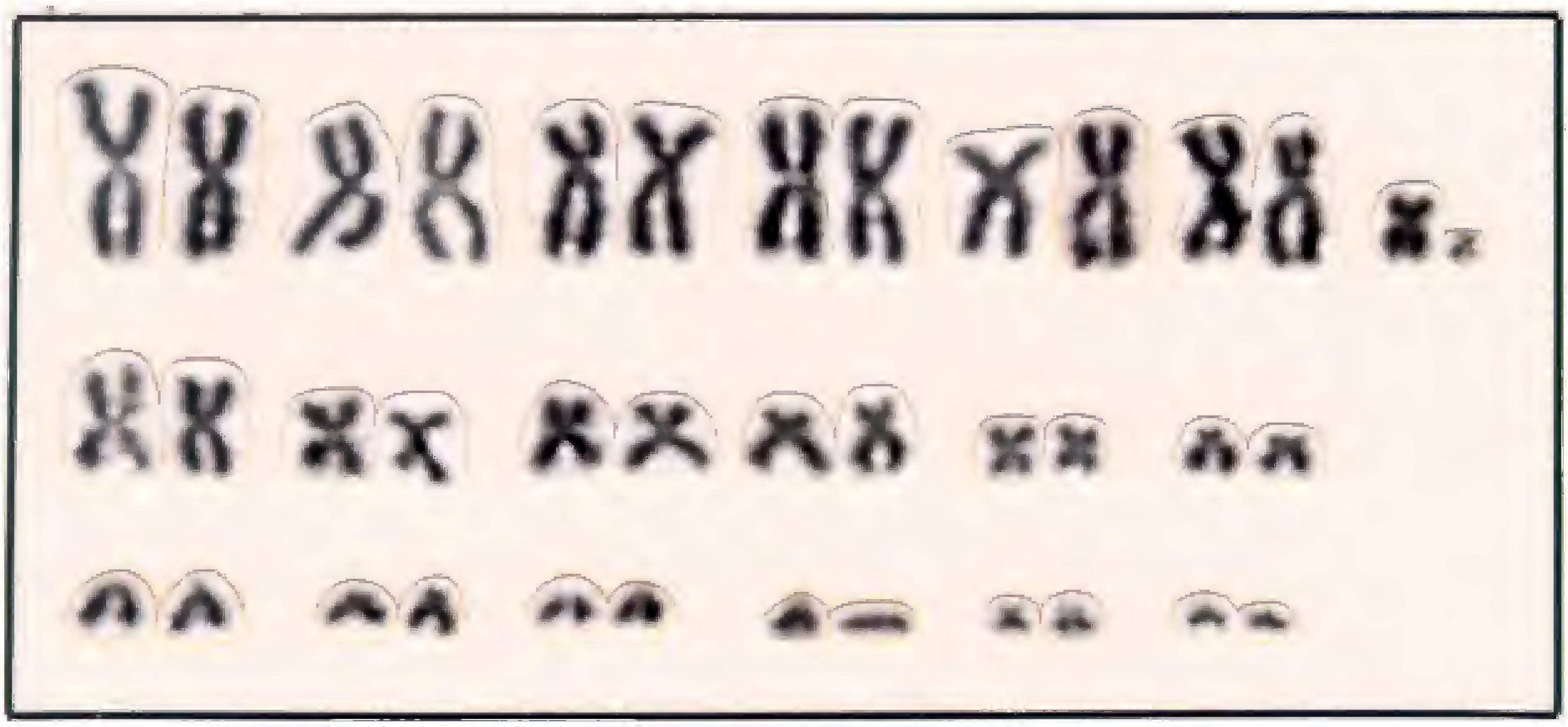

Figure 22. Karyotype of a male *Mormoops blainvillii* from Windsor Cave, Trelawny Parish (TK 8171; TTU 21254).

Macrotus waterhousii jamaicensis Rehn, 1904
Waterhouse's Leaf-nosed Bat

Specimens examined (334).—CLARENDON PARISH: Portland Cave, 3 (BMNH); *Portland Cave, 1 mi. W Mahoe Gardens*, 3 (NMNH); *5.6 mi. SE Portland Cottage*, 8 (KU); *Portland Ridge*, 9 (AMNH); Portland Ridge Cave, Portland Point, 5 (2 COLU, 3 IJ); *Portland Point Lighthouse*, 13 (4 FMNH, 9 TTU). MANCHESTER PARISH: 2 mi. NE Alligator Pond, 1 (AMNH); Gut River, sea level, 1 (JMM); Oxford Cave, Balaclava [given as St. Elizabeth Parish], 2 (AMNH). PORTLAND PARISH: Port Antonio, 3 (1 KU, 2 MCZ). ST. ANDREW PARISH: Kingston, 1 (NMNH). ST. ANN PARISH: Dry Harbour [= Discovery Bay], 2 (AMNH); Green Grotto, 2 mi. E Discovery Bay, 133 (21 CM, 17 HZM, 95 TTU); Orange Valley, 1 (CM); *1.5 km S Orange Valley*, 10 (CM); 1.2 km W Priory, 4 (CM); *24 km W St. Ann's Bay*, 21 (TTU). ST. CATHERINE PARISH: ruins of Colbeck Castle, 2 (1 IJ, 1 ROM); Fort Clarence, 3 (1 BMNH, 1 HZM, 1 ROM); Healthshire Hills, 1 (AMNH); Port Henderson, 1 (IJ); Spanish Town, 1 (NMNH); Swansea Cave, Worthy Park Factory Limited, Lluidas Vale, 2 (TTU). ST. ELIZABETH PARISH: Wallingford Cave, Balaclava, 1 (AMNH); Bryan Cave, Brompton, 3 (BMNH); Money Cave, Hounslow [near Malvern], 1 (AMNH); 3 mi. SE Whitehouse [*in* Westmoreland Parish], 4 (KU). ST. JAMES PARISH: Cambridge, 1 (AMNH)); 7-rivers Cave, Lapland, 1 (AMNH); Providence Cave, 4 mi. NE Montego Bay, 6 (5 AMNH, 1 NMNH); Montego Bay, 1 (ROM); *Sweetwater*, 1 (UF). ST. MARY PARISH: Port Maria, 50 (KU). TRELAWNY PARISH: Cock Pit Cave, 4 mi. NNW Quick Step, 280 m, 1 (NMNH); *cave N and W Quick Step*, 2 (NMNH); 3.2 mi. N Good Hope Estate, 1 (NMNH); Kinloss, 1 (KU); Windsor Cave, 15 (7 AMNH, 3 NMNH, 5 TTU). WESTMORELAND PARISH: Bluefields, 1 (BMNH); Negril, large cave in town, 1 (KU). PARISH UNKNOWN: no specific locality, 13 (8 BMNH, 2 MCZ, 3 NMNH).

Additional records (McFarlane 1997, unless otherwise noted).—CLARENDON PARISH: Lloyd's Cave [Jackson's Bay]; *Portland Cave 1* (Dávalos and Erikkson 2003); *Portland Cave 2* (Dávalos and Erikkson 2003); *Portland Cave 9* [17°45′12.1" N, 77°09′28.4" W] (Dávalos and Erikkson 2003). PORTLAND PARISH: Grove Cave [2 mi. SW Sherwood Forest] (Goodwin 1970). ST. ANN PARISH: Ewart Town Bat Cave; Moseley Hall Cave; Mount Plenty Cave; Ocho Rios (Goodwin 1970); Thatchfield Great Cave. ST. CATHERINE PARISH: *Riverhead Cave*; St. Clair Cave. TRELAWNY PARISH: Carambie Cave [Spring Garden area].

Distribution.—Figure 23 shows the collecting localities for *Macrotus waterhousii* on Jamaica. This

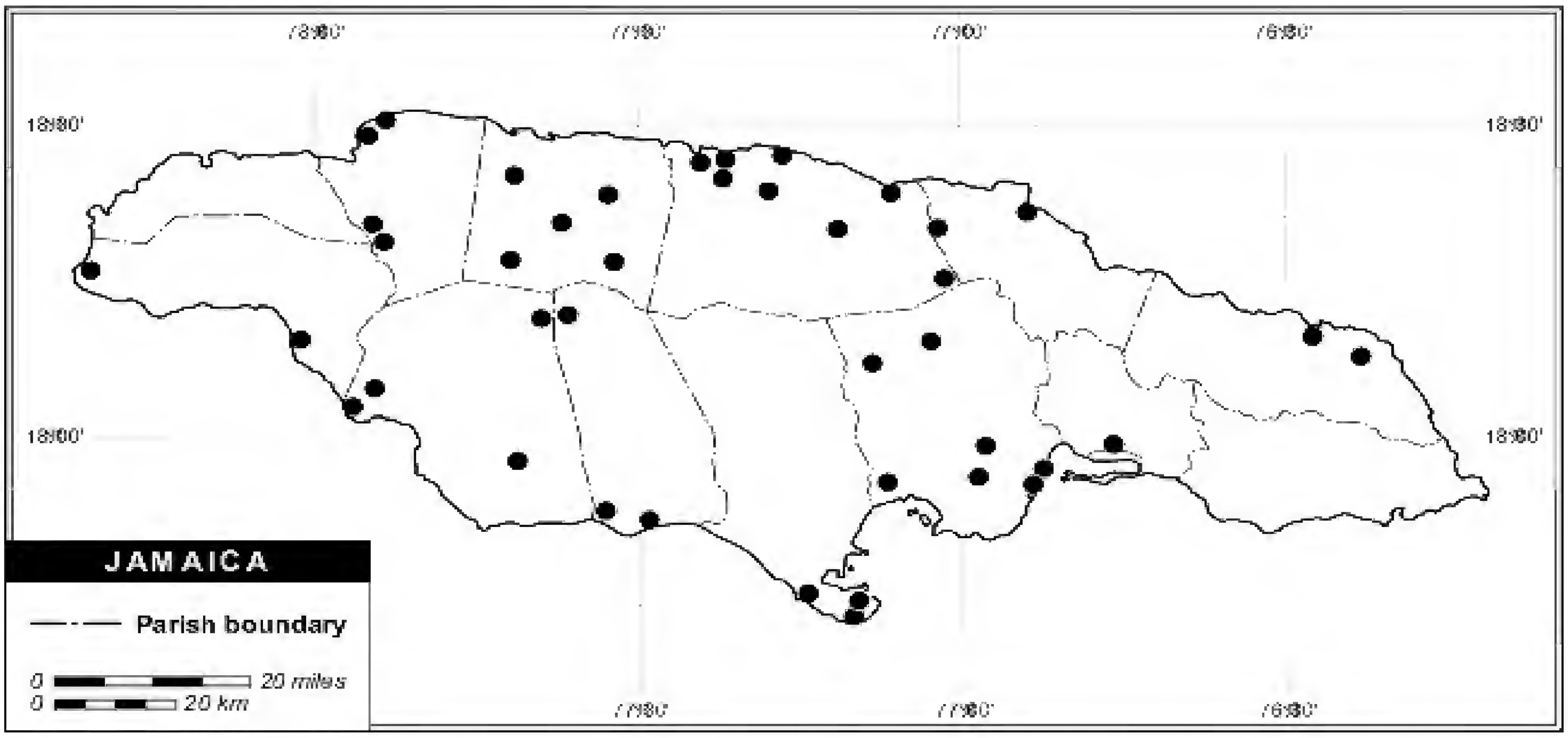

Figure 23. Map of Jamaica showing the locations where specimens of Waterhouse's leaf-nosed bat, *Macrotus waterhousii*, have been collected.

is a widespread species most commonly found in association with caves and subterranean human-constructed habitats. Waterhouse's leaf-nosed bats may be absent at sites above 500-600 m in elevation. The species ranges from northwestern Mexico and some areas of southern Mexico to the islands of the Greater Antilles and many of the Bahamas. The Jamaican bats have been assigned to an endemic subspecies, *M. w. jamaicensis* (Anderson and Nelson 1965).

Systematics.—The subspecies *M. w. jamaicensis* was originally described by Rehn (1904b) with a holotype from Spanish Town. He distinguished this new taxon from *M. w. waterhousii* from Hispaniola based upon duller coloration, smaller skull, and narrower and "weaker" (meaning smaller and more delicate-looking) upper toothrow. A revision of *Macrotus waterhousii* by Anderson and Nelson (1965) continued to recognize *M. w. jamaicensis* as a valid taxon. They confirmed Rehn's conclusion that *jamaicensis* is indeed smaller than *waterhousii* from Hispaniola and has a smaller less crowded upper toothrow. Compared to *M. w. minor* from Cuba, Anderson and Nelson (1965) found *jamaicensis* to be larger and darker. They concluded that "In size *jamaicensis* is intermediate between *minor* and *waterhousii*, but is closer to *waterhousii*." In another recent review of Antillean populations of this species, Buden (1975) recognized only two subspecies in this region, placing the material from Jamaica into the subspecies *M. w. waterhousii* along with populations from Hispaniola and the southern Bahamas. Buden (1975) made this arrangement even though in his analyses the sample from Jamaica differed significantly from Hispaniolan specimens in all six cranial measurements presented and length of forearm. The Jamaican sample also differed significantly from a combined sample of specimens from Hispaniola and the southern Bahamas in four of the cranial measurements. We do not agree with conclusions drawn by Buden (1975) based on his analyses. Instead, we think that his results further confirm the unique character of the *M. w. jamaicensis* and therefore we continue to recognize it as the appropriate trinomial for the Jamaican population

Morphometrics.—Table 2 compares 10 males and 10 females from the Green Grotto and generally agrees with measurements given by Anderson and Nelson (1965) who found no secondary sexual differences in size. We found significant size differences in only two measurements—interorbital breadth (P = 0.05) and postorbital constriction (P = 0.001). In six of the remaining measurements, males and females either averaged the same or 0.1 mm different. In only length of forearm and palatal length were the differences in the means of males and females 0.2 mm or more. Our

Table 2.—Length of forearm and nine cranial measurements for six species of the family Phyllostomidae occurring on Jamaica.

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
				Macrotus waterhousii jamaicensis						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	52.8	25.9	22.0	12.3	5.4	4.5	11.1	11.4	9.6	7.8
Minimum	50.4	25.0	21.0	11.8	5.1	4.3	10.7	10.8	9.4	7.6
Maximum	55.5	26.4	22.6	12.8	5.7	4.6	11.5	12.0	10.0	8.1
SE	±0.40	±0.13	±0.13	±0.09	±0.06	±0.03	±0.08	±0.13	±0.06	±0.5
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	53.9	25.8	22.0	12.2	5.2	4.2	11.0	11.6	9.6	7.8
Minimum	52.5	25.1	21.7	11.9	5.0	4.2	10.7	11.0	9.1	6.9
Maximum	55.0	26.4	22.2	12.5	5.6	4.3	11.4	12.0	9.9	8.1
SE	±0.36	±0.12	±0.10	±0.07	±0.06	±0.02	±0.07	±0.09	±0.07	±0.11
				Glossophaga soricina antillarum						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	36.7	22.1	20.5	9.6	4.2	4.7	9.0	12.0	7.6	5.7
Minimum	35.6	21.3	19.7	9.0	4.1	4.5	8.6	11.5	7.4	5.2
Maximum	37.6	22.8	21.2	9.9	4.3	4.8	9.1	12.3	8.1	5.9
SE	±0.16	±0.14	±0.13	±0.08	±0.03	±0.03	±0.05	±0.08	±0.07	±0.6
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	37.4	22.1	20.6	9.5	4.2	4.7	9.0	12.0	7.7	5.7
Minimum	36.0	21.5	20.1	9.1	4.1	4.6	8.9	11.5	7.5	5.3
Maximum	37.9	22.5	21.0	9.8	4.4	4.9	9.1	12.3	8.0	5.9
SE	±0.20	±0.12	±0.10	±0.07	±0.03	±0.03	±0.02	±0.09	±0.08	±0.06
				Monophyllus redmani redmani						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	40.4	23.0	21.5	10.0	4.1	4.3	9.7	11.8	8.3	5.3
Minimum	38.6	22.5	21.0	9.5	3.9	4.0	9.4	11.5	7.9	5.1
Maximum	42.5	23.4	21.9	10.2	4.3	4.5	9.8	12.2	8.5	5.9
SE	±0.33	±0.11	±0.09	±0.06	±0.04	±0.04	±0.05	±0.09	±0.06	±0.07

Table 2. (cont.)

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	40.1	23.1	21.6	9.5	4.1	4.4	9.3	11.8	8.5	5.4
Minimum	38.8	22.5	21.1	9.1	3.9	4.3	8.8	11.5	8.2	5.1
Maximum	41.3	23.6	22.1	9.8	4.4	4.6	9.6	12.3	9.0	5.6
SE	±0.24	±0.12	±0.09	±0.07	±0.05	±0.04	±0.08	±0.09	±0.09	±0.05
Erophylla sezekorni syops										
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	46.7	24.9	22.6	11.5	5.4	4.6	11.0	11.0	8.1	6.6
Minimum	45.4	24.1	22.2	11.2	5.1	4.5	10.8	10.6	7.8	6.2
Maximum	48.9	25.7	23.3	11.8	5.7	4.8	11.3	11.5	8.4	7.0
SE	±0.39	±0.16	±0.11	±0.08	±0.05	±0.03	±0.05	±0.09	±0.05	±0.08
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	47.4	24.6	22.6	11.3	5.4	4.5	10.8	11.1	8.2	6.5
Minimum	44.3	24.0	22.0	11.0	5.1	4.1	10.7	10.7	8.0	6.3
Maximum	49.1	25.3	23.2	11.5	5.5	4.7	11.0	11.4	8.3	6.8
SE	±0.51	±0.12	±0.13	±0.06	±0.05	±0.06	±0.03	±0.08	±0.03	±0.05
Phyllonycteris aphylla										
Males										
N	10	10	10	—	10	10	10	10	10	10
Mean	46.6	25.5	23.1	—	5.7	5.0	11.5	11.0	7.8	7.0
Minimum	44.3	24.8	22.6	—	5.4	4.7	11.2	10.4	7.7	6.8
Maximum	48.3	26.1	23.6	—	5.9	5.2	11.7	11.5	8.0	7.0
SE	±0.38	±0.12	±0.09	—	±0.05	±0.05	±0.05	±0.11	±0.03	±0.02
Females										
N	10	10	10	—	10	10	10	10	10	10
Mean	45.6	24.7	22.6	—	5.5	5.0	11.0	10.7	7.9	6.9
Minimum	44.8	24.0	21.8	—	5.2	4.8	10.5	10.4	7.4	6.7
Maximum	47.2	25.1	23.2	—	6.0	5.2	11.4	10.9	8.2	7.2
SE	±0.22	±0.11	±0.12	—	±0.08	±0.04	±0.09	±0.06	±0.08	±0.05

Table 2. (cont.)

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
				Ariteus flavescens						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	38.7	18.8	15.6	13.1	4.8	4.7	11.1	3.4	5.3	8.1
Minimum	37.0	18.4	15.3	12.7	4.6	4.4	10.7	3.2	5.2	7.9
Maximum	39.9	19.5	16.2	13.5	5.1	5.0	11.6	3.6	5.5	8.5
SE	±0.30	±0.10	±0.08	±0.08	±0.06	±0.07	±0.08	±0.04	±0.04	±0.05
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	42.0	20.6	17.2	14.1	5.2	4.9	11.7	4.0	6.0	9.0
Minimum	41.1	20.0	16.9	13.6	4.9	4.6	11.4	3.8	5.8	8.6
Maximum	42.8	21.3	17.6	14.7	5.4	5.1	12.0	4.3	6.2	9.2
SE	±0.24	±0.12	±0.8	±0.10	±0.05	±0.05	±0.08	±0.05	±0.05	±0.06
				Artibeus jamaicensis jamaicensis						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	59.4	28.2	25.0	16.4	7.9	7.2	14.6	13.5	9.9	12.1
Minimum	57.8	27.4	24.1	15.9	7.4	7.0	14.1	13.0	9.7	11.4
Maximum	61.9	29.0	26.1	17.3	8.4	7.6	15.4	14.0	10.5	12.9
SE	±0.36	±0.19	±0.20	±0.16	±0.11	±0.07	±0.13	±0.11	±0.09	±0.14
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	60.5	28.4	25.2	16.9	8.1	7.2	14.8	13.5	9.8	12.3
Minimum	57.6	27.1	24.2	15.5	7.7	7.1	14.0	12.7	9.4	11.8
Maximum	63.7	29.5	26.1	17.7	9.0	7.5	15.7	14.2	10.4	13.0
SE	±0.80	±0.23	±0.20	±0.23	±0.12	±0.04	±0.17	±0.17	±0.10	±0.13

sample from Jamaica averaged slightly larger in cranial measurements than the sample used by Anderson and Nelson (1965), but the length of forearm of our sample of males averaged smaller than their Jamaican sample.

Anderson and Nelson (1965) gave external measurements for five individuals and cranial measurements of four individuals from Jamaica. Buden (1975) presented cranial and external measurements from a sample of 24 specimens drawn from throughout Jamaica. Rehn (1904b) gave external and cranial measurements of the holotype of *M. w. jamaicensis* as well as the mean and range of a larger sample from Jamaica. Swanepoel and Genoways (1979) reported the forearm and seven cranial measurements of three females and one male from Jamaica. Osburn (1865) gave external measurements of one individual and detailed descriptions of external (Fig. 24) and dental characters of this species. Dobson (1878) also gave a description of the external characteristics of this species along with external and wing measurements.

Based on individuals from Portland Cave, Osburn (1865) described the pelages as "Males yellowish; females dark grey; some females show both tints in patches." Tomes (1861a) on examining the specimens obtained by Osburn noted that "the older ones are of a more decidedly rufous tint than the younger ones." Buden (1975) observed that color is extremely variable in this species, with "light (= reddish-brown) and dark (= brown or grayish-brown) color phases and occasional intermediate shades occur in both sexes from single localities." In contrast to Buden's (1975) observations on pelage color, Goodwin (1970) believed that this species was the only one on Jamaica that exhibited sexual dichromatism. To his eyes, adult females were gray and males had a more distinctly reddish cast.

Figure 24. View of the head of *Macrotus waterhousii*.

Natural History.—Gosse (1851) believed that "One of the most common of the Jamaican *Cheiroptera* is the Great-eared Leaf-bat (*Macrotus Waterhousii*)." This impression was probably enhanced by the fact that all of these bats that he captured on Jamaica "were taken by their flying into lighted rooms at night." Certainly, Waterhouse's leaf-nosed bat was a relatively common species on Jamaica during our work, although several other species seemed to be more abundant. However, Goodwin (1970) during his work in the mid-1960s found them only in two places. A colony of about 150 individuals was observed in Portland Cave and two individuals were taken from Grove Cave. Collectively, this information gives the impression of dramatic changes in population density.

Although we have records of this species from at least 23 caves on Jamaica, we would agree with McFarlane (1986) that this species is probably not an obligate cave dweller on Jamaica, at least at the present time. Prior to human occupation of the island this leaf-nosed species may well have been confined to caves for day roosts, but as noted by Osburn (1865) as early as 1859 "They inhabit houses sometimes, but always the cellars, below ground, never the roofs." During our work on Jamaica, we observed a colony of *Macrotus* under the headquarter house at Orange Valley on 8 July 1974. We later caught an individual under a large fustic tree in a pasture not far from the building. It was the only representative of this species that we captured away from a roost site.

The majority of the caves where *Macrotus waterhousii* was captured on Jamaica are discussed elsewhere in this publication, but the following five caves are typical of the type used by this species. Green Grotto (cave 228) where our largest sample of *M. waterhousii* was obtained is part of the Runaway Bay Caves complex. The section of the cave that was visited was nearest the highway and is a dry labyrinth type of cave with several entrances (Figs. 25-26) and light holes (Fincham 1997). Carambie Cave (cave 108) is a labyrinth-type cave with a total length of 335 m. The main entrance, which is located at the base of an overhanging cliff, leads to an irregular chamber about 30 m wide and 20 m high. There is a lighthole in the chamber and passages leading to two additional entrances (Fincham 1997). Lloyd's Cave (cave 364) is a complex cave with seven entrances and an approximate length of 1840 m in the vicinity of many other caves in the Jackson's Bay area. The cave consists of a complex series of dusty galleries with fossil guano and dry chambers. The cave has seven entrances as well as a number of skylights. In the Guano Crawl in Lloyd's Cave, McFarlane et al. (2002) found guano deposits that aged at the surface 1750±80 years BP, at 30-40 cm deep 10,440±100, and at 95-100 cm deep 16,400±110, which is the oldest guano deposit found in their study of caves in the Jackson's Bay area. Bryan Cave near Brompton was described by Osburn (1865) as follows: "The mouth is in an angle of perpendicular rock, which, through a small aperture, leads to a circular space with a vaulted roof, as smooth as if chiselled . . . . A strong smell announced the presence of Bats." They quickly caught 10 individuals of *Macrotus waterhousii*. Dávalos and Erikkson (2003) discussed capturing *M. waterhousii* along with *Erophylla sezekorni* and *Glossophaga soricina* at the entrance of the newly discovered Portland Cave 9. They described the entrance as 3 m wide and 1.5 m high located in "overgrown secondary scrub." Osburn (1865) also found this species to be abundant in an unnamed cave near Dry Harbour, which may have been the Green Grotto. At Portland Cave, Goodwin (1970) found this species roosting "across the low ceiling of a wide lens-shaped chamber in the twilight zone of the cave." This species does seem to be relatively tolerant of light in its day roosts.

Osburn (1865) in examining the stomach contents of a Waterhouse's leaf-nosed bat found chitinus insect exoskeletons and two short legs with powerful claws attached. He identified the insect as an orthopteran and this seemed to be confirmed by other observations that he made. At Mount Pleasant, these long-eared bats were using the veranda as a night roost to consume prey items. One of the bats dropped "the wings and legs of a large grasshopper." Also on the veranda, he found dropping containing the seeds of the fustic berry (*Maclura* [= *Chlorophora*] *tinctoria*). Osburn (1865) described how individuals of this species viciously attacked each other when held in captivity. He even believed that one might have "sucked" blood from another, but this behavior has not been verified. We did, to our horror, verify that members of this species will attack and kill each other when held in close confinement. After holding a number of these bats in a large cloth bag overnight, only two or

Figure 25. Photograph of one of several entrances to the Green Grotto Cave, St. Ann Parish, Jamaica. Note the dry ruinate vegetation surrounding the entrance.

Figure 26. Photograph of bats being netted at night at an entrance to the Green Grotto Cave, St. Ann Parish, Jamaica.

three individuals remained alive and they were badly bitten and battered. We have not had this experience with any other species of Jamaican bats held in a similar manner.

Fifteen males taken between 24 June and 1 August had testes lengths that averaged 4.1 (2-6). Five males taken on 5 November at 24 km east of St. Ann's Bay had testes lengths that averaged 4.2 (2.5-5.0). Six taken on 14 and 15 December had a mean testes length of 4.8 (3-6.5). Two males taken by Goodwin (1970) at Portland Cave on 31 December had testes lengths of 6 and 7.

Ten of the 36 females taken between 6 to 12 July at the Green Grotto Cave and Windsor Cave were lactating. A female taken on 24 October at Portland Ridge cave carried a single embryo. Two females taken on 5 November evinced no reproductive activity. One of three females taken on 14 December that were examined for reproductive activity was noted by the field collector as having a single embryo. At Bryan Cave, nine of the 10 bats that Osburn (1865) captured on 17 December 1858 were females and of these "seven had young of differing ages, but about half-grown, clinging to them." More than 100 years later, Goodwin (1970) found a breeding colony in Portland Cave on 31 December. The three nursery clusters were located at the center of the roosting area of the adults. Each cluster consisted of 10 to 20 immature animals. Six subadult individuals had an average forearm length of 47 as compared to an average of 55 for six adults. The females appeared to moving back and forth between the clusters and the peripheral roosting areas. The sex ratio among adults in this colony was 1 male to 4 females. At Portland Cave 9, Dávalos and Erikkson (2003) took 14 female *M. waterhousii* on 9 December that were "all in late gestation," as were 13 females captured at Portland Cave 1 on 14 December. Also on 14 December, they (Dávalos and Erikkson 2003) observed at least 10 females with relatively small young in Portland Cave 2.

Collectively, the foregoing data indicates that the Jamaican population reproduces at times of the year that are different from the reproductive season in Mexico and even elsewhere in the Antilles. Wilson (1979) summarized data for Mexican populations by stating that parturition occurs in May. Silva Taboada (1979) in a study involving 283 females from Cuba found pregnant females from February to April with lactating females being found beginning in April and occurring into August. The Cuban data would support the observations of Buden (1975) who found three pregnant females in the Caicos Islands on 27 February, each with an embryo of less than 2 mm in crown-rump length, and one female from Crooked Island on 11 April with a fetus with a crown-rump length of 17.8. In summary, the Jamaican population produces young earlier in the year than other populations and given the duration of reproductive activity (probably from late October to July) either two young are produced annually or the reproductive period is long and non-synchronous. It is unknown whether or not this species undergoes delayed development as in *Macrotus californicus* (Wilson 1979).

Studying the annual variation in fat reserves of eight species of bats on Jamaica, McNab (1976) found that *Macrotus waterhousii* had significantly less fat deposits in the dry season as compared with the wet season. A non-pregnant female captured at Cock Pit Cave on 9 April weighed 17.8, whereas a male taken near Good Hope Estate on 24 June weighed 16.5.

A female taken on 1 August was molting over its dorsum, whereas three other females and two males taken at this same place and time were not molting. Individuals reported from Wallingford Cave, Healthshire Hills, Portland Ridge, Money Cave, and 7-rivers Cave were recovered from owl pellets. Koopman and Williams (1951) and Williams (1952) report subfossil material of *Macrotus waterhousii* from Jamaica. Williams (1952) was of the opinion that the cave deposit material documented a replacement of *Tonatia saurophila* by *Macrotus* on the island at a time of cooling climate. McFarlane et al. (2002) report fossil and subfossil remains of *Macrotus* from the Jackson's Bay caves that were approximately 10,000 years old.

Genetics.—The karyotype of *M. waterhousii* has 2n = 46 and FN = 60 (Fig. 27). There are 16 biarmed autosomes in a graded series from large to small and 28 acrocentric autosomes in a graded series from medium-sized to small. The X is medium-sized and submetacentric, and the Y is minute and acrocentric. Karyotypes were obtained from four males and one female from Green Grotto, 2 mi. E Discovery Bay.

The karyotype of *M. waterhousii* from Jamaica was first reported by Greenbaum and Baker (1976) and is identical to karyotypes reported for populations from Hispaniola (Greenbaum and Baker 1976; Nagorsen and Peterson 1975) and Mexico (Baker 1967; Hsu et al. 1968; Nelson-Rees et al. 1968; Davis and Baker 1974). Banded karyotypes of *M. waterhousii* were described by Patton and Baker (1978) and Baker (1979). These authors presented evidence that the karyotype of *M. waterhousii* is primitive for the family Phyllostomidae. Baker et al. (2003) presented DNA sequence data from the mitochondrial ribosomal genes and the nuclear RAG 2 gene, which show that *Macrotus* is the sister taxon to the remainder of the family. Consequently, these authors placed *Macrotus* in its own subfamily (Macrotinae). As currently understood, the Jamaican bats are conspecific with *M. waterhousii* on Cuba, Hispaniola, and in central Mexico. If this is the correct interpretation, the most parsimonious explanation is that the Antillean populations were derived from Mexican mainland.

Davis and Baker (1974) recognized two mainland species of *Macrotus, M. waterhousii* (2n = 46; FN = 60) and *M. californicus* (2n = 40; FN = 60). These species are distinguished based on karyotype and morphology and exhibit parapatric distributions. The genetic relationships of these species were investigated indirectly by Greenbaum and Baker (1976) using electrophoretic techniques. Phenotypic similarity was shown to be higher among mainland populations of *M. waterhousii* than between Jamaican and mainland populations. They concluded that although the differences were not so great as to indicate different species, the Jamaican population is sufficiently different to warrant recognition as a subspecies distinct from the mainland populations. Average heterozygosity values ranged from 0.00 to 0.043 among four populations of *M. waterhousii*. The average heterozygosity of the Jamaican population was 0.040.

Figure 27. Karyotype of a female *Macrotus waterhousii* from Green Grotto, 2 mi E Discovery Bay, St. Ann Parish (TK 8055; TTU 21538).

Eyes and vision.—Studholme et al. (1987) used immunohistochemical techniques to compare retinal neurotransmitters in four genera of bats: *Macrotus*, *Artibeus*, *Anoura*, and *Glossophaga* collected on Jamaica. All the bats were successfully tested for glutamic acid decarboxylase, tyrosine hydroxylase, substance P; and 5-hydroxytryptamine. The retina in *Macrotus waterhousii* was unique relative to the other bats; 5-HT-immunoreactivity was found in a narrow band of fibers and punctate processes in the distal portion of the inner plexiform layer, outer plexiform layer, and inner nuclear layer in this species. Overall, the patterns of neurotransmitter immunoreactivity observed matched the hypothesized phylogenetic relationships among the bats (Studholme et al., 1987). This is the first and only example in which species within a family of mammals have been shown to exhibit diversity this type of neurotransmitter diversity. Given the ecological and behavioral differences among these Jamaican bats, it is reasonable to conclude that the retinal neurological differences might have adaptive significance.

Glossophaga soricina antillarum Rehn, 1902
Pallas' Long-tongued Bat

Specimens examined (168).—CLARENDON PARISH: Mason River Research Station, 2.5 mi. W Kellits, 2300 ft., 1 (TTU); Portland Cave, 1 mi. W Mahoe Gardens, 5 (NMNH); *5.6 mi. SE Portland Cottage,* 3 (KU); Portland Point, 3 (TTU); *Portland Ridge*, 2 (AMNH); *Portland Ridge Cave*, 1 (IJ). PORTLAND PARISH: 0.8 mi. W Drapers, 2 (CM); along Williamsfield River, 1.5 mi. NW Hectors River, 3 (2 JMM, 1 UF); *along Hectors River, Hectors River*, 1 (UF); Hectors River, 2 (1 IJ, 1 JMM); caves of Nonsuch, 1 (HZM); Port Antonio, 6 (1 ANSP [holotype], 5 NMNH). ST. ANDREW PARISH: Kingston, 2 (1 BMNH, 1 IJ). ST. ANN PARISH: Green Grotto, 2 mi. E Discovery Bay, 70 (16 CM, 28 HZM, 26 TTU); Mount Plenty Cave, Goshen/Lucky Hill, 3 (HZM); Moseley Hall Cave, Moseley Hall [near Blackstonedge], 1 (AMNH); Orange Valley, 7 (CM); Circle B Plantation, 2 km SW Priory, 2 (TTU); Queenhythe, 1 (TTU); 4 mi. E Runaway Bay, 5 (TTU); *0.5 mi. S, 0.5 mi. W Runaway Bay*, 1 (TTU). ST. CATHERINE PARISH: 0.2 mi. E Watermount, 1 (CM). ST. ELIZABETH PARISH: Money Cave, Hounslow [near Malvern], 1 (AMNH); Pedro Bluffs, 1 (AMNH); 3 mi. SE Whitehouse [*in* Westmoreland Parish], 4 (KU). ST. JAMES PARISH: Montego Bay, 17 (NMNH); *cave east of Montego Bay*, 2 (NMNH); *Sewell Cave, Montego Bay*, 1 (AMNH). ST. MARY PARISH: Highgate, 3 (ROM); Port Maria, 1 (KU). ST. THOMAS PARISH: Amity Hall, 1 (AMNH); *Four Mile Wood*, 1 (IJ); Yallahs, 4 (TTU). TRELAWNY PARISH: Cock Pit Cave, 5 mi.

N, 2.5 mi. WNW Quick Step, 2 (NMNH); *cave N and W Quick Step*, 1 (NMNH); Good Hope Estate, 2 (NMNH); 4.9 mi. N Quick Step, 360 m, 1 (NMNH). WESTMORELAND PARISH: Bluefields, 2 (CM); Negril, 1 (KU).

Additional records.— CLARENDON PARISH: *Portland Cave 9* [17º45´12.1" N, 77º09´28.4" W] (Dávalos and Erikkson 2003). ST. CATHERINE PARISH: Riverhead Cave [also called Braham Cave, near Ewarton] (Henson and Novick 1966; McNab 1976; McFarlane 1997); River Sink Cave [Worthy Park] (McNab 1976); Two Sisters Cave [17º54´ N, 76º54´ W] (Dávalos and Erikkson 2003). ST. JAMES PARISH: *Sewell* (Goodwin 1970). ST. MARY PARISH: *Idlewild Caves* [6 mi. E Oracabessa]; 4 mi. E Oracabessa (Goodwin 1970). TRELAWNY PARISH: Windsor Cave (Dávalos and Erikkson 2003).

Distribution.—Figure 28 shows the collecting localities for *Glossophaga soricina* on Jamaica. The species is widely distributed although it might be absent from localities above 750 m. According to Webster (1993), *Glossophaga soricina* is the only species of the genus to occur on Jamaica and Jamaica is the only island in the West Indies where the species occurs. The subspecies *G. s. antillarum* is endemic on Jamaica (Webster 1993).

Systematics.—Webster (1993) reviewed members of the genus *Glossophaga.* He recognized five species—*commissarisi, leachii, longirostris, morenoi*, and *soricina*. He distinguished *G. soricina* from others by its moderately elongated rostrum, procumbent upper incisors, and relatively large lower incisors. Webster (1993) recognized the Jamaican population as a distinct subspecies under the name *G. s. antillarum.* The subspecies is distinguished by it large external and cranial size, extremely procumbent upper incisors, well-developed postpalatal processes, zygoma that converge anteriorly, and paler pelage. A recent analysis of the mitochondrial cytochrome *b* gene by Hoffmann and Baker (2001) agreed with Webster's morphological analysis and indicated that the Jamaican population is related to those in Mexico and Central America.

Peters (1869) reviewed members of the subfamily Glossophaginae and recognized Geoffroy St. Hilaire as the author of the generic name *Glossophaga.* Peters gave an extensive review of the early taxonomy of *G. soricina* fixing Pallas 1766 as the correct author of the species name.

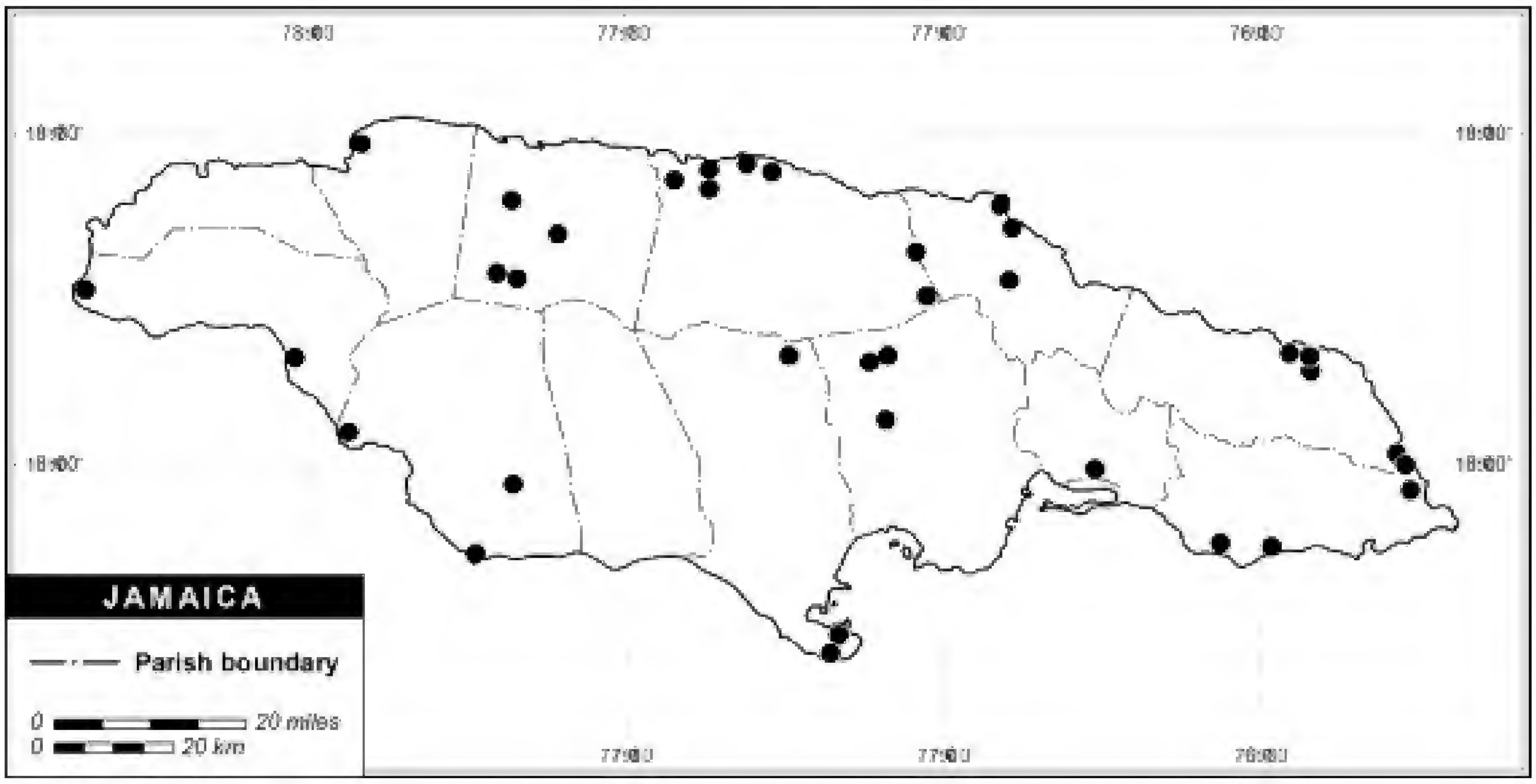

Figure 28. Map of Jamaica showing the locations where specimens of Pallas' long-tongued bat, *Glossophaga soricina*, have been collected.

Morphometrics.—Length of forearm and nine cranial measurements of 10 males and 10 females from Jamaica are given in Table 2. Females are significantly larger than males in length of forearm at the $P = 0.05$ level. No significant secondary variation was detected in cranial measurements in our samples; in fact the sexes averaged the same size in six measurements. Females averaged larger in two measurements (condylobasal length and length of maxillary toothrow) and males in one measurement (zygomatic breadth).

Rehn (1902a) gave external (Fig. 29) and cranial measurements of the female holotype; some of these measurements are repeated by G. M. Allen (1911). Webster (1993) presented measurements of the holotype and also gave measurements from samples of 8 males and 10 females from Jamaica (named sample 31 in his paper). Forearm and cranial measurements of the holotype (ANSP 6618) are as follows: forearm, 37.3; greatest length of skull, 22.3; condylobasal length, 20.7; postorbital constriction, 4.8; breadth of braincase, 8.8; length of maxillary toothrow, 7.6; breadth across upper molars, 5.7.

Natural history.—The largest sample of Pallas' long-tongued bats taken during our work on Jamaica came from Green Grotto, 2 mi. E Discovery Bay. Bats were captured in nets at the entrance of this lowland, dry cave (Fig. 26). Beyond the parking lot for the cave was a typical, dense ruinate lowland scrub forest. Specimens of this species also were taken at two nearby localities along the north coast of Jamaica. At 4 mi. E Runaway Bay, long-tongued bats were taken over a large, fast moving river, surrounded by a narrow corridor of large tropical forest trees. The situation at 0.5 mi. S, 0.5 mi. W Runaway Bay was much drier with the specimen being netted in a palm plantation. Further to the east along the north coast, specimens were taken in Portland Parish at 0.8 mi. W Drapers in a situation similar to 4 mi. E Runaway Bay except that the stream was somewhat smaller and slower moving. Along the southwestern coast near Bluefields, specimens were netted in relatively open ruinate lowland scrub forest. There were a few larger trees in the area especially along a nearby small stream. At Yallahs along the southeastern coast long-tongued bats were taken in nets placed under the large trees in a commer-

Figure 29. View of the head of *Glossophaga soricina*.

cial orchard that included bananas, mangos (*Mangifera indica*), papaya (*Carica papaya*), nutmeg (*Myristica fragrans*), almond (*Terminalia catappa*), and naseberries (*Manilkara zapota*). At the eastern extreme of the island, long-tongued bats were taken in a coconut-banana plantation.

Away from the coast at elevations of approximately 300 m, this species was captured in mist nets at three localities. Near Watermount, a specimen was taken over a stream in a heavily forested area. The areas at Queenhythe and Orange Valley, in contrast, have been heavily impacted by human activities. At Orange Valley, specimens were taken in nets set around a large fustic tree (*Maclura* [= *Chlorophora*] *tinctoria*) in the middle of a pasture with a nearby livestock pond. At Queenhythe, a single individual was netted over a large earthen tank used for watering the community animals and domestic purposes. The area surrounding the tank was an open soccer field and pastures. The highest elevation from which we have recorded this species on Jamaica was at approximately 700 m near Kellits where a female was netted over an open pond. There were no trees in the vicinity of the pond, but a large growth of cattails did grow at one end. The surrounding area (Fig. 30) was in heavy agriculture use, growing bananas, hops, gardens, subsistence gardens, and plants for personal smoking for medicinal and religious purposes.

Figure 30. Photograph of hte general habitat in the vicinity of Kellits, Clarendon Parish, Jamaica.

Goodwin (1970) in a survey of the ecology of bats in caves on Jamaica found that *G. soricina* was generally absent from the large cave systems on the island and preferred the smaller dry cave systems, which is in agreement with our finding at the Green Grotto, where the portion of the cave being netted was relative small and dry. In most situations, he found this species in small clusters of individuals near the entrance of the cave where considerable light penetrated. However, at Moseley Hall Cave, Goodwin (1970) found a group of seven individuals in a small depression in the ceiling of the cave approximately 100 m from the entrance. Other species associated with long-tongued bats in caves were *Artibeus jamaicensis* and *Macrotus waterhousii*. Goodwin (1970) found two *Glossophaga* roosting in the same room with a maternity colony of 150 *Macrotus* in the twilight zone of Portland Cave. Henson and Novick (1966) noted that on 19 June *Glossophaga* had exited Riverhead Cave by 9 PM.

McFarlane (1986) believed that *G. s. antillarum* is an obligate cave dweller on Jamaica, but elsewhere in the Antilles we have found *Glossophaga longirostris* roosting in buildings. However, there are records of Pallas' long-tongued bats from at least 16 caves on Jamaica so clearly, it regularly used these sites as day roosts. Three of the relatively small caves from which this species has been recorded are as follows—Money Cave (cave 335) is a shelter cave about 10 m high and 10 m deep in a hillside (Fincham 1997), Idlewild Caves (cave 283) are three small dry passage caves of which the largest is about 30 m long (Fincham 1997), and Nonsuch Caves (cave 90) are chamber-type caves of about 76 m length (Fincham 1997).

Wilson (1979) believed that this species was polyestrous, with pregnant individuals present in the population throughout the year. We found pregnant females on Jamaica on the following dates (crown-rump length of fetus in parentheses): 9 June, 1 of 1 examined (23); 5 July, 2 of 3 (8, 9); 6 July, 0 of 8; 7 July, 2 of 3 (4, 5); 11 July, 1 of 1 (8); 17 July, 2 of 5 (4, 12); 25 July, 2 of 2 (4, 11); 26 July, 2 of 5 (6, 11); 30 July, 1 of 11 (17); 9 August, 1 of 1 (13.8); 26 December, 0 of 1. Lactating females were taken on 8 and 10 June. Goodwin (1970) recorded that 1 of 2 females taken on 29 January was pregnant with a single fetus measuring 6 in crown-rump length, whereas none of 3 females taken on 7 January was pregnant.

Length of testes were recorded for male long-tongued bats on the following dates: 28 March, 4.1; 29 March, 4.2; 24 June, 2, 2.5; 2 July, 4, 4; 5 July, 3; 6 July, 3, 3, 3, 3, 4, 4; 7 July, 1, 1, 4; 3 August, 2.5; 26 December, 2.8, 4.3. Four males taken by Goodwin (1970) in December and January had testes that measured 2.5 to 5 in length (average 3.5). We examined four pre-volant individuals taken on the following dates: 27 May (length of forearm, 33.8, 34.8); 23 June (32.8); 9 August (--). Individuals that were netted, but still exhibited unfused phalangeal epiphyses, were taken on 6 (length of forearm, 36.9, 37.1) and 7 (36.3, 37.0) July.

Two adult males weighed 9.2 and 9.3 on 24 June, whereas males taken on 19 and 26 December weighed 10.2 and 9.1, respectively. Two lactating females taken on 8 and 10 June weighed 10 and 11, respectively. McNab (1976) noted that fat reserves of *Glossophaga* from Jamaica significantly decreased from December at the beginning of the dry season to July in the middle of the wet season. The largest fat reserves were noted in specimens from the end of the dry season/beginning of the dry season. McNab (1976) found that *Glossophaga* collected in the much wetter areas around Worthy Park did not have significantly larger fat deposits than specimens taken from the dry southern coast on Portland Point.

Of 32 individuals taken in January, March, August, and December, only 6 males captured on 3 August exhibited molt of the dorsal and ventral pelage. The specimen from Money Cave actually consisted of remains that were recovered from an owl pellet obtained at the cave.

Genetics.—The karyotype of *G. soricina* has 2n = 32 and FN = 60 (Fig. 31). There are 30 biarmed autosomes in a graded series from large to small. The X is medium sized and metacentric, and the Y is minute and acrocentric. Karyotypes were obtained from 1 male from 0.5 mi. S, 0.5 mi. W Runaway Bay, 1 female from Queenhythe, 1 male from Orange Valley, and 2 males from Green Grotto.

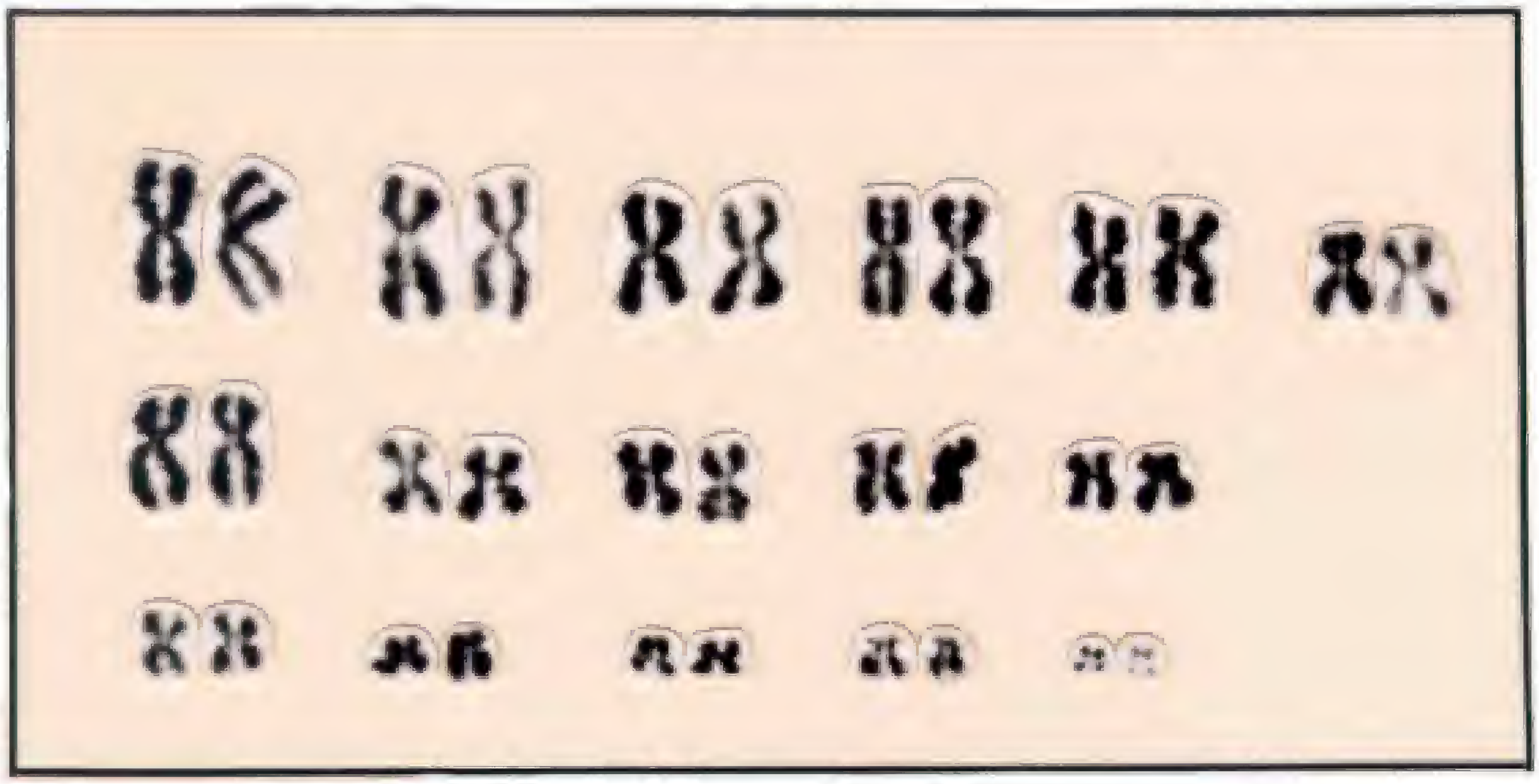

Figure 31. Karyotype of a female *Glossophaga soricina* from Queenhythe, St. Ann Parish (TK 8167; TTU 21591).

The karyotype of *Glossophaga soricina* reported here is identical to previous reports for this species from Mexico (Baker 1967; Baker and Hsu 1970) and Trinidad (Hsu et al. 1968). The karyotype of this species is also identical to that of *G. alticola* [= *leachii*], *G. commissarisi,* and *G. longirostris* (Baker 1979). Results of G- and C-band studies reported by Baker and Bass (1979) indicate that heterochromatin is restricted to the centromeric regions and that the karyotype of *G. soricina* is identical in banding pattern to those of species in the genera *Monophyllus, Brachyphylla, Erophylla*, and *Phyllonycteris*.

Hoffmann and Baker (2001) sequenced the mitochondrial cytochrome *b* gene within and among physically separated populations of *G. soricina.* This species is basal for the genus and is comprised of two major maternal lineages. One lineage is found in South America primarily east of the Andes Mountains and the other includes populations from Middle America, Peru west of the Andes, and Jamaica. It is likely that this major subdivision is indicative of two biological species and that they are sympatric in western Peru. The affinities of the Jamaican population, and its probable origin, clearly lie with the Middle American populations.

Remarks.—Rehn (1902a) designated ANSP 6619 as the holotype of *Glossophaga soricina antillarum*, but according to Koopman (1976b) this was a *lapsus calami* by Rehn because ANSP 6619 is an *Artibeus* and ANSP 6618 is given as the type in the museum's catalog. Rehn (1902a) and Miller (1913b) gave the type locality simply as "Port Antonio, Jamaica," whereas Webster (1993) further specifies that the locality is in St. Thomas Parish. This in turn appears to be a *lapsus calami* by Webster because the city of Port Antonio is located along the northeastern coast of Jamaica in Portland Parish.

Monophyllus redmani redmani Leach, 1821
Leach's Long-tongued Bat

Specimens examined (388).—CLARENDON PARISH: Douglas Castle Cave, 4 mi. W Kellits, 33 (TTU); *Mason River Research Station, 2.5 mi. W Kellits, 2300 ft.,* 1 (TTU). HANOVER PARISH: Flint River, 1.5 mi. E Sandy Bay, 1 (CM). MANCHESTER PARISH: Oxford Cave, 16 (11 BMNH , 3 COLU, 2 IJ); *Oxford Cave, Balaclava* [given as St Elizabeth Parish], 14 (AMNH). PORTLAND PARISH: 0.8 mi. W Drapers, 6 (CM); Green Hill, 2 (TTU); Hardwar Gap, 1090 m, 6 (NMNH); along Williamsfield River, 1.5 km. NW Hectors River, 8 (6 JMM, 2 UF); *Buttonwood River, Hectors River*, 1 (JMM); Happy Grove, Hectors River, 1 (JMM); *27 mi. from Kingston on Newcastle Highway*, 1 (ROM). ST. ANDREW PARISH: *Hardwar Gap, 5000 ft.,* 1 (UF); Kingston, 1 (IJ);

St. Ann's, Kingston, 1 (NMNH); Botanical Gardens, Mona Campus of the University of the West Indies, 2 (ROM). ST. ANN PARISH: Green Grotto, 2 mi. E Discovery Bay, 2 (1 CM, 1 TTU); *4 mi. E Runaway Bay*, 14 (TTU); Mount Plenty Cave, Goshen/Lucky Hill, 26 (5 COLU, 21 HZM); Orange Valley, 36 (35 CM, 1 TTU); *1.2 km W Priory*, 3 (CM); Circle B Plantation, 2 km SW Priory, 34 (17 CM, 17 TTU); Queenhythe, 1 (CM); 0.5 mi. S, 0.5 mi. W Runaway Bay, 2 (TTU). ST. CATHERINE PARISH: St. Clair Cave, 2 mi. S Ewarton, 81 (1 BMNH, 26 COLU, 5 IJ, 5 NMNH, 20 ROM, 1 TCWC, 23 TTU); Healthshire Hills, 4 (AMNH); Swansea Cave, Worthy Park Factory Ltd., Lluidas Vale, 2 (TTU); 0.2 mi. E Watermount, 4 (CM); Worthy Park, 1 (BMNH). ST. ELIZABETH PARISH: Balaclava, 9 (AMNH); *Hutchinson's Meadow, Balaclava,* 1 (AMNH); *Wallingford Cave, Balaclava,* 1 (AMNH); Peru Cave, Goshen, 5 (AMNH); Malvern, 1 (AMNH). ST. JAMES PARISH: 7-rivers Cave, Lapland, 2 (AMNH). ST. THOMAS PARISH: Whitfield Hall, Penlyne, 4300 ft., 2 (1 JMM, 1 UF); Yallahs, 12 (TTU). TRELAWNY PARISH: Duanvale, 1 (TTU); Good Hope Estate, 2 (NMNH); Windsor Cave, 41 (19 AMNH, 4 KU, 1 NMNH, 17 TTU). WESTMORELAND PARISH: Bluefields, 1 (CM). PARISH UNKNOWN: *Sportsman's Hall Cave,* 2 (BMNH); no specific locality, 3 (2 BMNH [including holotype], 1 MCZ).

Additional records (McFarlane 1997, unless otherwise noted).— CLARENDON PARISH: *Jackson's Bay* (McFarlane and Garrett 1989); Jackson's Bay Cave; *Portland Cave* (Fincham 1997); *Skeleton Cave*. ST. ANN PARISH: Ewart Town Bat Cave; Moseley Hall Cave (Goodwin 1970; McFarlane 1986); Thatchfield Great Cave. ST. CATHERINE PARISH: *Riverhead Cave* (McNab 1976). ST. ELIZABETH CAVE: Pedro Bluff Cave; *Spaniards Cave*. ST. MARY PARISH: San Souci Grotto [along north coast just west of Frankfort and 4 mi. E Ocho Rios] (Goodwin 1970; McFarlane 1986). ST. THOMAS PARISH: Ratbat Hole [17°52′12" N, 76°29′24" W] (Dávalos and Erikkson 2003).

Distribution.—Figure 32 shows the collecting localities for *Monophyllus redmani* on Jamaica. Leach's long-tongued bat is a common and widely distributed species on the island. There are records from sea level to over 1500 m along the slopes of the Blue Mountains. The species can be expected throughout the island, with the exception of the highest elevations in the Blue Mountains. *Monophyllus redmani* occurs only

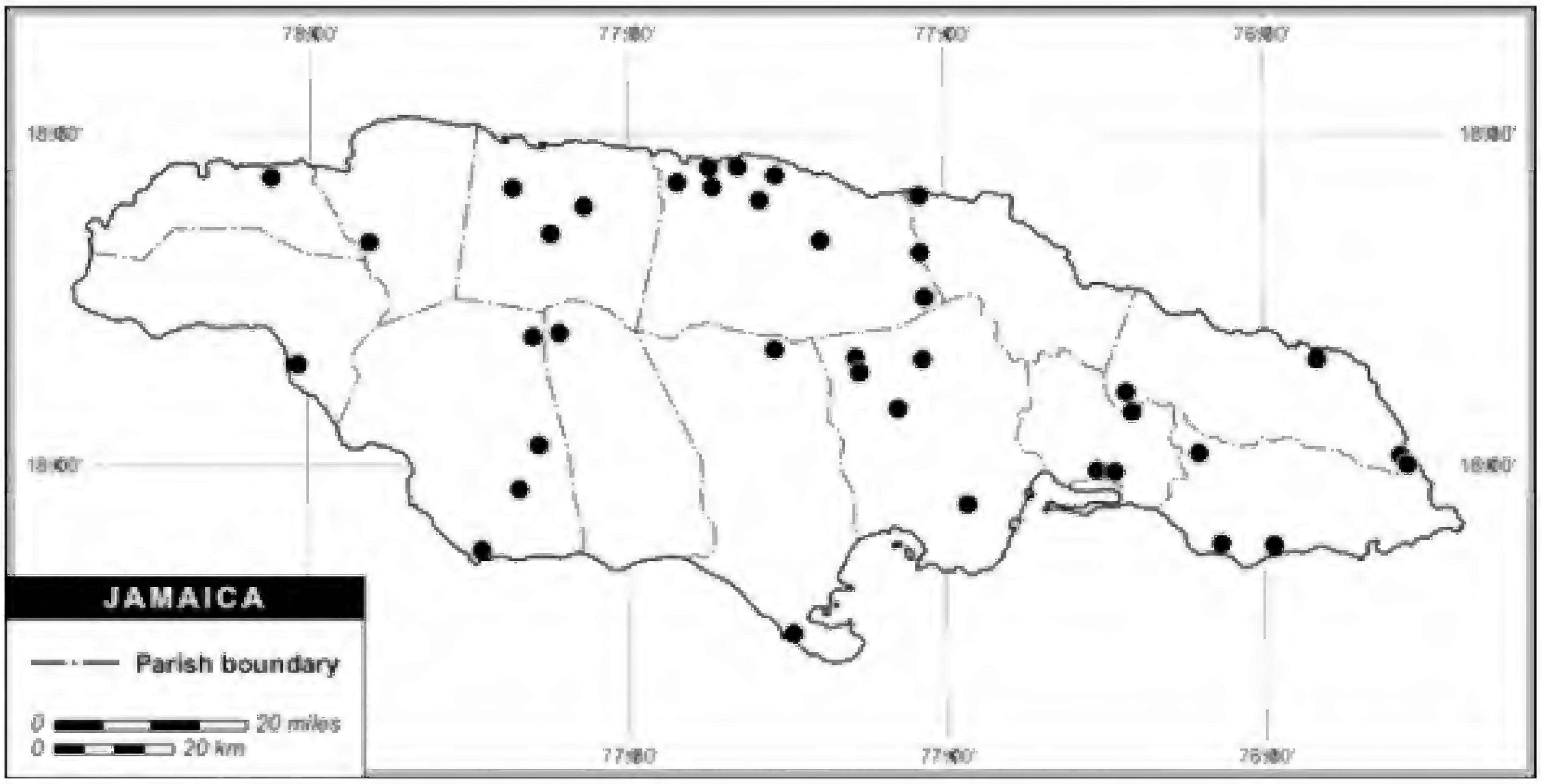

Figure 32. Map of Jamaica showing the locations where specimens of Leach's long-tongued bat, *Monophyllus redmani*, have been collected.

on the islands of the Greater Antilles, with the nominate subspecies being endemic to Jamaica (Schwartz and Jones 1967).

Systematics.—The species *M. redmani* was originally described by Leach (1821b) based on a specimen received from R. S. Redman from an unspecified locality on Jamaica. Although the species was mentioned by Gosse (1851:328), specimens of the species were not reported again until the work of Tomes (1861b) based on specimens obtained by Osburn (1865) at Sportsman's Cave and Oxford Cave in 1858-1859. Tomes gave an extensive redescription of *M. redmani* based on the new material. Peters (1869) reviewed the history of the species and continued to recognize it as a valid member of the subfamily Glossophaginae.

Miller (1900) first reviewed the genus *Monophyllus*, describing three new species in addition to recognizing *M. redmani* from Jamaica. Subsequently, Schwartz and Jones (1967) recognized two species in their systematic revision of the genus *Monophyllus*. The two species were distinguished based upon the size of the diastema between the first and second upper premolars (P2 and P3). The diastema between these teeth is less than one-half of the length of the first premolar (P2) in *M. plethodon* from the Lesser Antilles and equal to or longer than one-half the length of the first premolar in *M. redmani* from the Greater Antilles. The two species demonstrate sympatry in fossil deposits on Puerto Rico.

Schwartz and Jones (1967) distinguished the nominate subspecies from others within *M. redmani* by its relatively short forearm, large skull with broad postorbital, mastoid, and zygomatic regions, and a long toothrow. They (Schwartz and Jones 1967) further stated "The degree of differentiation of the subspecies of *M. redmani* is striking. The races of *M. redmani* all are distinctly different, the primary difference being overall size and concomitantly in size of skull."

Morphometrics.—Available measurements of the holotype (unregistered BMNH, unsexed) are as follows: length of forearm, 38.2; interorbital constriction, 4.3, postorbital constriction, 4.4; palatal length, 11.3; length of maxillary toothrow, 8.5; breadth across upper molars, 5.6. These measurements agree well with those for our sample from Jamaica (Table 2), although the length of the forearm and palatal length do fall slightly below the range of these specimens.

The comparison of combined samples of 10 males and 10 females from Douglas Castle Cave, Green Grotto, and St. Clair Cave reveals some interesting patterns of secondary sexual variation (Table 2). Six of the 10 measurements show no significant secondary variation. Of these, only for length of forearm, where the difference was 0.3 mm, did the differences between means exceed 0.1 mm. Of the four cranial length measurements, only one—length of maxillary toothrow—displayed any significant secondary sexual variation and this was at the $P = 0.05$ level. In contrast, three of the five cranial breadth measurements revealed significant secondary sexual variation—zygomatic breadth and mastoid breadth at the $P = 0.001$ level, and postorbital constriction at the $P = 0.01$. Clearly, secondary sexual variation in this species is associated primarily with cranial width.

Tomes (1861b), Dobson (1878), and Miller (1900) gave detailed descriptions of the external (Fig. 33), wing, and cranial morphology of this species. Each of these authors also gave external and wing measurements of individual specimens and Tomes (1861b) and Miller (1900, 1902) gave cranial measurements for single individuals, with Miller's specimen being from Kingston. Schwartz and Jones (1967) gave the mean and range of external and cranial measurements for 15 specimens from Oxford Cave and Windsor Cave.

In the field on Jamaica, *M. redmani* can be confused with *G. soricina* (Fig. 34). However, *M. redmani* is larger than *G. soricina;* for example, the length of forearm of the former is more than 38.0, whereas the latter is always less. For condylobasal length there is only slight overlap, with the smallest measurement for *M. redmani* at 21.0 and the largest for *G. soricina* at 21.2. The uropatagium of *M. redmani* is reduced and deeply emarginate with the tail free beyond its posterior margin, whereas the uropatagium in *G. soricina* is not reduced or emarginate and the tail does not reach its posterior margin.

Natural history.—Goodwin (1970) believed that Leach's long-tongued bat was one of the three most

Figure 33. View of the head of *Monophyllus redmani*.

Figure 34. View of the dorsal surface of *Glossophaga soricina* (left) and *Monophyllus redmani* (right) giving a comparison of their overall size. Note the deep emargination of the uropatagium of *Monophyllus* as compared to *Glossophaga* and the present of a tail extending beyond the uropatagium in *Monophyllus* that is not present in *Glossophaga*.

abundant species of bats on Jamaica. He found that the species showed a distinct preference for "large, deep caves with high humidity" and within these caves it seemed to prefer "large dome-shaped rooms with high ceilings" although it did enter smaller chambers and passageways. Goodwin (1970) found colonies in excess of 1000 individuals in the following caves: Windsor, Oxford, Moseley Hall, Mount Plenty, and St. Clair. The colonies of these bats were broken into many small and medium-sized clusters. He did find a group of less than 10 individuals in the small San Souci Grotto, but believed this to be an atypical situation for the species. Goodwin (1970) observed, as did Osburn (1865) over 100 years earlier, that Leach's long-tongued bats are often found in close association with *Pteronotus parnellii* and *Mormoops blainvillii* within caves.

Based on these excellent observations McFarlane (1986) concluded that *Monophyllus redmani* is an obligate cave dweller on Jamaica. In addition to the six caves visited by Goodwin (1970), we have records of this species from 16 other caves on Jamaica. Descriptions of four of these 22 caves give an idea of the variety of the types of caves where the species has been found. Portland Cave-2 (cave 701) is a dry passage-type of cave about 300 m in length. The double entrance leads to an earthen-floored passage that leads to the west-northwest for about 185 m. H. E. Anthony writing in his 1920 field notes stated that the two Portland Caves "are fairly large, dry, and with a few bats in them, mostly *Otoplerus* [= *Macrotus*] and *Artibeus* although *Monophyllus* was present in small numbers" (Fincham 1997). Seven Rivers Cave (also called Hazelymph Cave; cave 37) is a dry passage cave that is 45 m long. This is a funnel-shaped passage that starts at 5 m wide and 8 m high and narrows inwardly (Fincham 1997). Skeleton Cave (cave 524) is a chamber cave with a length of about 35 m. This is a boulder-filled, dry cave, with a main chamber and two smaller side chambers (Fincham 1997). Moseley Hall Cave (cave 278) is a dry passage cave with a total length of about 245 m. The cave has four entrances and extends beneath a low hill and joins two cockpits (Fincham 1997). Schwartz and Jones (1967) describe the capture of *Monophyllus* at Windsor Cave where the bats were found well back from the entrance. The bats were observed clinging to and flying just below the high ceiling of this moist cave.

During our work on Jamaica, *M. redmani* always was abundant and widespread. It was captured from near sea level to at least 5000 feet [1515 m] at Hardwar Gap. We took the species at two of the caves where Goodwin (1970) found them—St. Clair and Windsor—as well as three others—Douglas Castle, Green Grotto, and Swansea. At Douglas Castle Cave, *M. redmani* shared the day roost with *P. macleayi* and *P. parnellii*. *Pteronotus parnellii* was the first species to exit the cave, with the *M. redmani* starting to leave about one hour after dark. In St. Clair Cave the largest numbers of this species were taken in the Junction Chamber (see Figs. 10, 17) along with the three species of *Pteronotus*.

This cave roosting species was easily taken in mist nets set in foraging areas. Large numbers were taken at Circle B Plantation, Orange Valley, 4 miles east of Runaway Bay, Yallahs, and near Drapers. The specimens from east of Runaway Bay and near Drapers were taken over a large stream with swiftly moving water as were the specimens collected in the vicinity of Hectors River. There was gallery forest along the streams with agriculture lands beyond the forest. At Yallahs, Leach's long-tongued bats were taken in nets placed under the large trees in a commercial plantation of bananas and mangos, which included other types of fruit trees such as naseberries. The banana plants were in flower and certainly were being visited by this species. At Orange Valley, specimens were taken in nets set around a large fustic tree (*Maclura* [= *Chlorophora*] *tinctoria*) in the middle of a pasture. This tree was covered with fruits and may still have been blooming as well. At the Circle B Plantation specimens were netted under the trees of an orchard of introduced fruit trees. The surrounding hills were covered with native trees and secondary brush. Many of the other situations in which we took this species involved netting over water such as the ponds at 2.5 mi. W Kellits, Queenhythe, and 1/2 mi. S, 1/2 mi. W Runaway Bay, or rivers and streams near Sandy Bay, near Watermount, and Bluefields. In these situations we believe that the bats were coming to drink or were using the watercourses as their nightly flyways. The single male captured at Whitfield Hall was taken in a plantation of coffee and bananas. The collector noted that the specimen was covered with pollen.

Four males taken on 13-14 April had testes lengths of 2, 3, 3.5, and 4 and one taken 23 June had testes that measured 2.5 in length. The mean testes length of 45 July-taken males was 2.4 (1-5). A male captured on 9 August had testes that measured 3.8 in length. Six males obtained on 2 November had testes that averaged 3.3 (3-4) in length. Five males taken during our work between 13 to 15 December had a mean testes length of 3.8 (2-5). Seven males taken by Goodwin (1970) at St. Clair Cave on 29 December had testes lengths that averaged 3.0 (2-4).

Two of three females taken on 6 January at Mt. Plenty Cave were noted by the collector as being in the early stages of pregnancy, whereas one taken on 7 January had a single embryo that measured 10 in crown–rump length. Two of three females taken at this place on 20 January were pregnant with single embryos each measuring 14. Two of three females captured at Oxford Cave on 30 January were pregnant with embryos measuring 16 and 18. All 11 females taken by Osburn (1865) on 22 February also at Oxford Cave were pregnant. McNab (1976) found six females of 10 from the Worthy Park area to be pregnant when captured between 23 February and 2 March. Two females taken on 12 April evinced no reproductive activity, whereas three of five females captured at St. Clair Cave on 18 April were noted as lactating and another of the individuals was considered to be post-lactating by the collector. A female taken on 24 June and one of three females taken at Windsor Cave on 10 July were lactating. None of the other 75 July-taken females that we examined evinced any gross reproductive activity nor did 10 females taken on 2 November. Two of nine females captured between 13 to 15 December were noted as being pregnant with single embryos that each measured 3. Fifteen of 19 females collected by Goodwin (1970) on 29 December at St. Clair Cave were pregnant with embryos averaging 8.4 (3-11.5) in crown-rump length.

The reproductive cycle of *M. redmani* most closely fits the monestry pattern as detailed by Wilson (1979). The cycle would seem to differ from that proposed by Wilson (1979) only by being moved to late in the calendar year. Gestation would appear to begin in late November. Parturition must occur from March into May, with lactation lasting from March until July. The cycle appears to be highly synchronous, with only two females from late June and early July from a large number examined still lactating. The remaining females from June and July evinced no gross reproductive activity.

Studying the annual variation in fat reserves of eight species of bats on Jamaica, McNab (1976) found that *Monophyllus redmani* was the only species that did not reveal significant differences between wet and dry seasons. He concluded that nectivorous species have significantly smaller amplitudes in fat reserves than do bats with other food habits. Two females obtained at Hardwar Gap on 12 April weighed 11.7 and 11.9, whereas four males taken there on 13 April weighed 14.2, 15, 15, and 15.5. A male captured at Good Hope Estate on 23 June weighed 10.5 and a lactating female from 24 June weighed 9.9. A male and female netted northwest of Hectors River on 18 December weighed 13.4 and 12.3, respectively. A female *M. redmani* taken in St. Clair Cave on 29 December weighed 11.4.

Webster (1971) reported the nematode *Capillaria* sp. from the one individual of Leach's long-tongued bat that he examined from St. Clair Cave. Phillips (1971) found that mite-caused periodontal disease was geographically variable in *M. redmani*, being highest on Cuba with an occurrence rate of 94%, lowest on Jamaica at 17.6%, and Puerto Rico with an intermediate rate of 33.3% of specimens examined. A female taken at Mount Plenty Cave on 9 August was molting over its entire dorsum, whereas 10 other males and females taken on this date displayed no molting.

Specimens from Healthshire Hills, Hutchinson's Meadow, Wallingford Cave, Peru Cave, and Seven-Rivers Cave were recovered from subfossil owl pellets. McFarlane et al. (2002) report fossil and subfossil remains of *Monophyllus* from the Jackson's Bay caves that were approximately 10,000 years old. McFarlane and Garrett (1989) reported a minimum of 2 individuals of *Monophyllus redmani* from contemporary Barn Owl (*Tyto alba*) pellets found in caves in the Jackson's Bay area. This species constituted 2.4% of the non-rodent remains found in the pellets.

Genetics.—The karyotype of *M. redmani* has 2n = 32 and FN = 60 (Fig. 35). There are 30 biarmed autosomes in a graded series from large to small. The

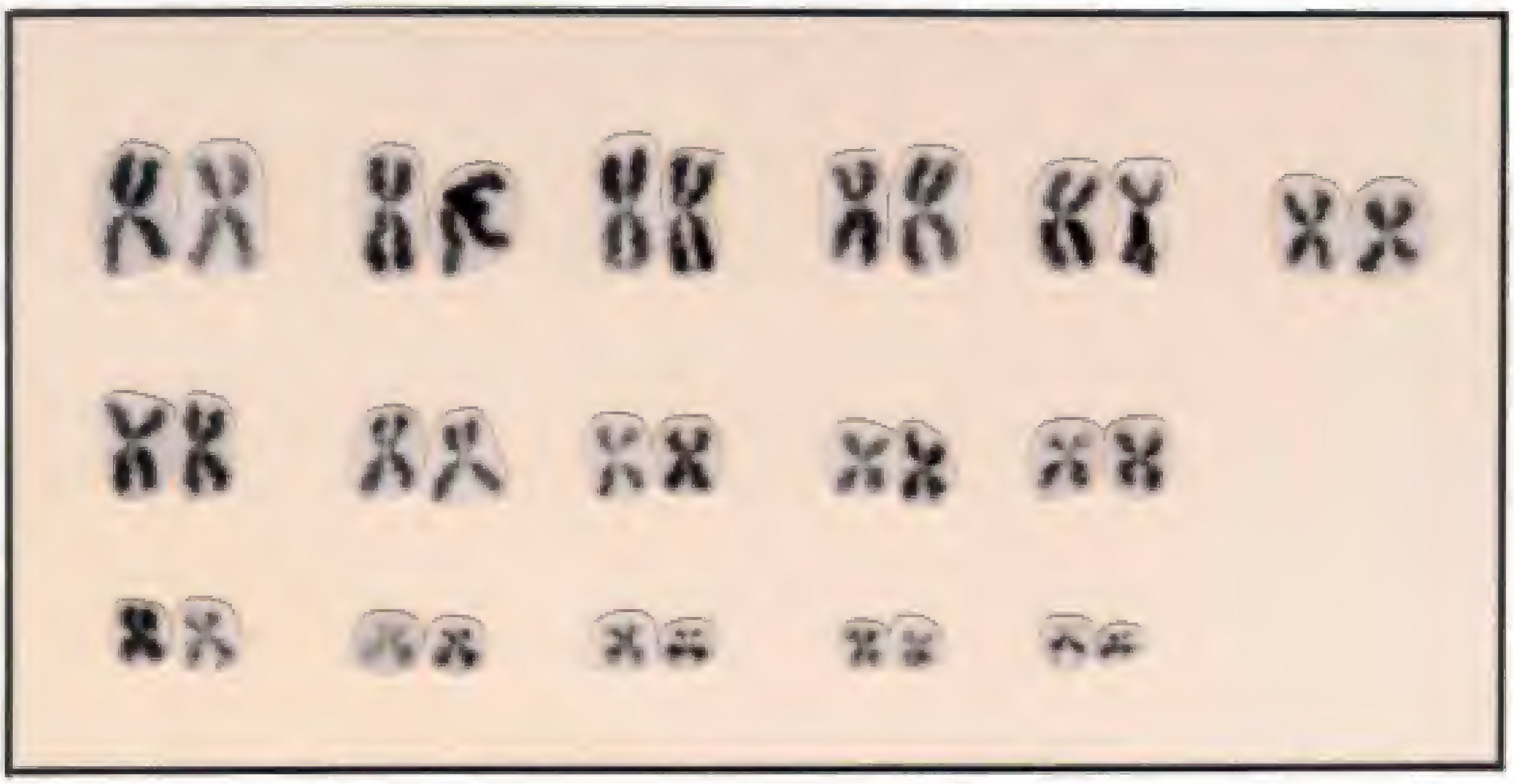

Figure 35. Karyotype of a female *Monophyllus redmani* from 0.5 mi S, 0.5 mi W Runaway Bay, St. Ann Parish (TK 8002; TTU 21653).

X is medium sized and metacentric, and the Y is minute and acrocentric. Karyotypes were obtained from one male and one female from 0.5 mi. S, 0.5 mi. W Runaway Bay, four males and one female from Orange Valley, and one female from Bluefields.

Baker and Jordan (1970) reported 2n = 32 and FN = 60 for *M. redmani* from Puerto Rico. The karyotype of *M. redmani* is identical to that reported for *Monophyllus plethodon* (Baker 1979). Baker and Bass (1979) reported the karyotype of *M. redmani* to be identical to that of *Glossophaga soricina* based on G- and C-band analyses.

Baker et al**.** (2003) sequenced DNA from the mitochondrial ribosomal genes and the nuclear RAG 2 gene from *Monophyllus* and representatives of the other genera of Glossophaginae. Based on these data, *Monophyllus* was placed in a lineage with the other Antillean glossophagines (*Brachyphylla* and *Erophylla*) and the two mainland genera *Leptonycteris* and *Glossophaga.*

Erophylla sezekorni syops G. M. Allen, 1917
Buffy Flower Bat

Specimens examined (156).—CLARENDON PARISH: Kemps Hill, 1 (AMNH); Portland Cave, 1 mi. W Mahoe Gardens, 2 (NMNH); *Portland Point Lighthouse*, 1 (TTU); Portland Ridge, 1 (AMNH). HANOVER PARISH: Flint River, 1.5 mi. E Sandy Bay, 1 (CM). PORTLAND PARISH: 0.8 mi. W Drapers, 6 (CM); Williamsfield River, 1.5 km NW Hectors River, 8 (5 JMM, 3 UF); *Buttonwood River, Hectors River*, 3 (1 IJ, 2 JMM). ST. ANN PARISH: Orange Valley, 8 (4 CM, 4 TTU); *1.5 km S Orange Valley*, 10 (CM); Circle B Plantation, 2 km SW Priory, 3 (TTU); 4 mi. E Runaway Bay, 1 (TTU). ST. CATHERINE PARISH: St. Clair Cave, 2 mi. S Ewarton, 7 (5 IJ, 2 ROM); Healthshire Hills, 1 (AMNH); River Head Cave, 1 (AMNH); 0.2 mi. E Watermount, 1 (CM). ST. ELIZABETH PARISH: Money Cave, Hounslow [near Malvern], 1 (AMNH); 3 mi. SE Whitehouse [*in* Westmoreland Parish], 6 (KU). ST. JAMES PARISH: Montego Bay, 60 (49 AMNH, 5 MCZ, 6 NMNH); Providence Cave, Montego Bay, 35 (17 AMNH, 18 NMNH). ST. THOMAS PARISH: Whitfield Hall, Penlyne, 4300 ft., 1 (JMM). TRELAWNY PARISH: Harmony Hall [18º28'N, 77º31'W], 4 (BMNH); 4 mi. NNW Quick Step, 370 m, 1 (NMNH). WESTMORELAND PARISH: Bluefields, 1 (CM).

Additional records.—CLARENDON PARISH: Jackson's Bay (McFarlane and Garrett 1989); *Portland Cave 9* [17º45′12.1" N, 77º09′28.4" W] (Dávalos and Erikkson 2003). ST. ANN PARISH: Mount Plenty

Cave (Goodwin 1970; McFarlane 1986, 1997); Runaway Bay Caves (McFarlane 1997). ST. JAMES PARISH: *Sewell Cave* (Goodwin 1970; McFarlane 1986). ST. THOMAS PARISH: Ratbat Hole [17°52′12" N, 76°29′24" W] (Dávalos and Erikkson 2003). TRELAWNY PARISH: Windsor Cave (Dávalos and Erikkson 2003).

Distribution.—Figure 36 shows collecting localities for *Erophylla sezekorni* on Jamaica. There are records of the buffy flower bat from all but three of the parishes, but we did not find the species to be abundant in any particular place. There are records of the species from sea level to 1300 m, but we would not expect to find it at elevations higher than this. The genus *Erophylla* is endemic to the Greater Antilles and Bahama Islands. The species *E. sezekorni* occurs on Jamaica, Cuba, Isle of Pines, and Bahamas, with the subspecies *syops* endemic to Jamaica.

Systematics.—The genus *Erophylla* was described and named by Miller (1906). Most species of *Erophylla* had initially been described as members of the genus *Phyllonycteris*. Miller (1906) distinguished members of the genus *Erophylla* because they possessed short, though evident, calcars, which are absent in species of *Phyllonycteris*, and because they possess complete zygomatic arches, which are incomplete in *Phyllonycteris* species.

Allen (1917) first reported *Erophylla* from the island of Jamaica. He reviewed the known taxa of the genus and reduced them to two species—*sezekorni* and *bombifrons*. He described the Jamaican specimens under the new subspecific name *syops,* which he placed in the species *E. sezekorni* known from Cuba and the Bahamas. The description indicates that the Jamaican specimens are most closely related to Cuban populations from which they differed “conspicuously in its wider rostrum with molar rows nearly parallel instead of converging anteriorly.” Allen also believed that *E. s. syops* had a more swollen lachrymal region and slightly broader teeth.

Buden (1976) reviewed the taxa in the genus *Erophylla*, reducing them to a single species and two subspecies. Under Buden’s arrangement, buffy flower bats from Jamaica would be known under the name *Erophylla sezekorni sezekorni*. We have not followed Buden’s (1976) arrangement because of a number of problems with his analyses. The first serious technical problem is that all analyses and comparisons were done solely with one-way analyses of variance. In our opinion, the only method to get an acceptable sta-

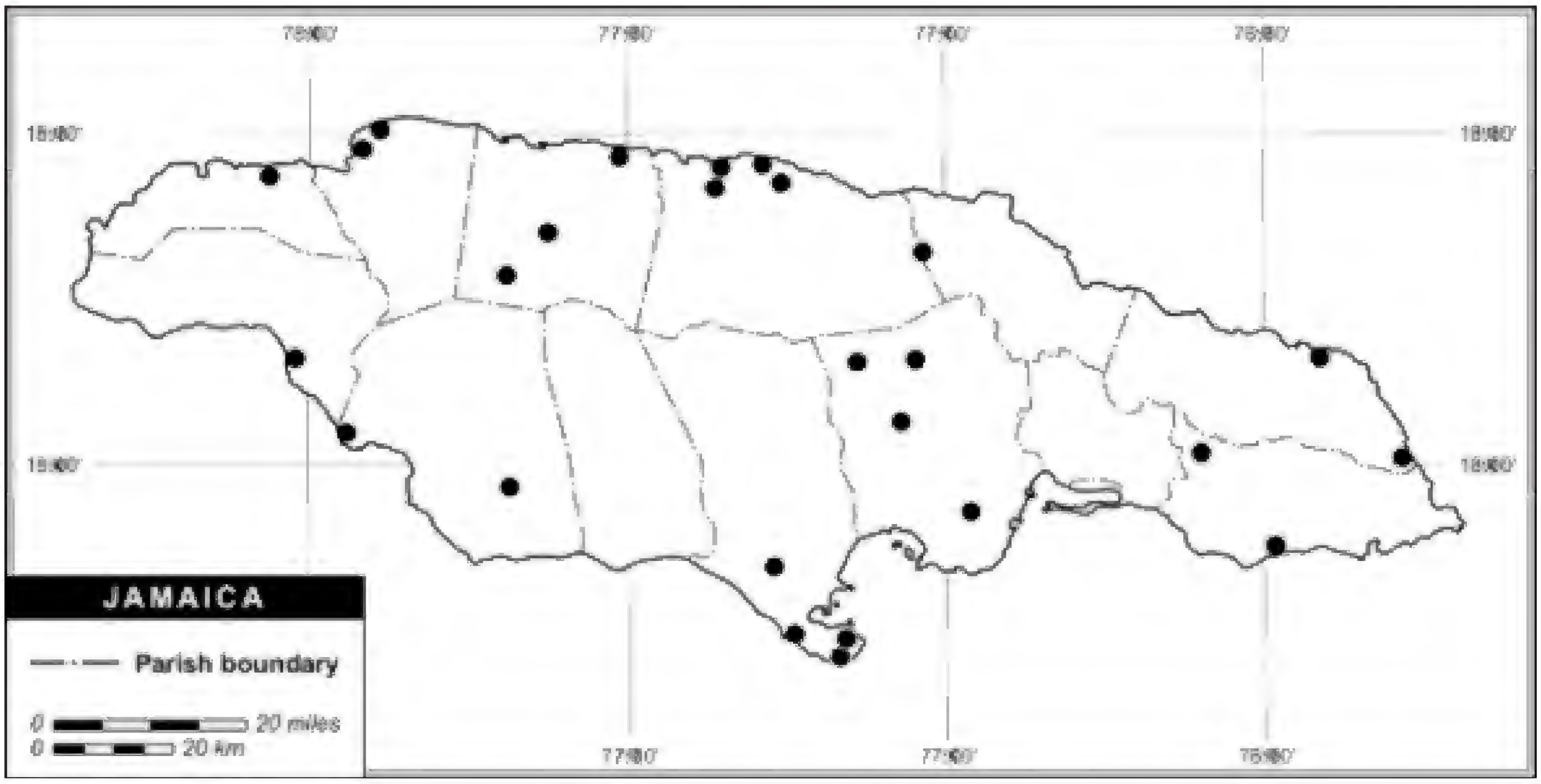

Figure 36. Map of Jamaica showing the locations where specimens of the buffy flower bat, *Erophylla sezekorni*, have been collected.

tistical comparison among the island populations would be through use of multivariate techniques, such as principal components or discriminant functions. Buden stated that "Mensural comparisons include specimens from 17 localities" and that he studied 15 characters. However, mensural data for only six localities and four characters are presented in the publication, making it impossible to assess his data. Among the characters used by Buden (1976), two are ratios, which are not normally distributed as required by many statistical tests such as analysis of variance (Sokal and Rohlf 1969), and three are standard external measurements taken by many different field collectors, which are known to be highly variable because of the differences among collectors' methods. In the remaining eight cranial and two external characters (tibia length and forearm length) that would have been taken by Buden), the populations from Jamaica (*syops*) and Cuba (*sezekorni*) differ significantly in results for four characters—skull length, condylobasal length, forearm length, and tibia length. In view of all of these considerations, we have maintained the taxonomic arrangement for the Jamaican populations as it was prior to Buden's work (as did Hall 1981), pending a comprehensive multivariate analysis of all *Erophylla* populations.

Morphometrics.—Table 2 gives the measurements for length of forearm and nine cranial measurements for samples of 10 males and 10 females drawn from localities throughout the island. The sexes differed significantly in only two of these measurements—zygomatic breadth ($P = 0.05$) and mastoid breadth ($P = 0.01$). In both of these measurements, males averaged larger than females. In those measurements not displaying significant secondary sexual variation, the sexes averaged the same in two (condylobasal length and interorbital breadth), males averaged larger in three (greatest length of skull, postorbital constriction, and breadth across upper molars), and females averaged larger in the remaining three measurements (length of forearm, palatal length, and length of maxillary toothrow).

Osburn (1865) gave some external measurements of this species and an extensive description of external characteristics (Fig. 37). Allen (1917) gave the external and cranial measurements of the male holotype of *E. s. syops* from Montego Bay. Buden (1976) presented data for four measurements for *Erophylla* from Jamaica (number of specimens in parentheses): skull length (29); cranial height (29); forearm length (66);

Figure 37. View of the head of *Erophylla sezekorni*.

ear length (43). Swanepoel and Genoways (1979) reported the forearm and seven cranial measurements of four females and four males from Jamaica.

Natural history.— During our field work we never encountered buffy flower bats in large numbers. Likewise, Goodwin (1970) stated "This is an uncommon species in Jamaica." The largest group that Goodwin encountered was a colony of approximately 25 individuals in St. Clair Cave. Examination of the list of the specimens that we examined reveals that largest numbers were taken in the vicinity of Montego Bay, including Providence Cave. These records date to between 1910 and 1920. The apparent rarity of this species on Jamaica and the possibility that its numbers have declined since early in the 20th Century make *E. sezekorni* a prime candidate for additional field studies on Jamaica. Recently, however, Dávalos and Erikkson (2003) took 33 individuals of the buffy flower bat at the Ratbat Hole in St. Thomas Parish, which indicates that there is still much to be learned about the ecology and roosting behavior of this species.

Although the majority of our records of *E. sezekorni* on Jamaica are from foraging sites, we do agree with McFarlane (1986) that it is an obligate cave roosting species. There are currently records of buffy flower bats being taken in 11 caves on Jamaica. Mount Plenty Cave (cave 279) is typical of caves in which the species has been found. Mount Plenty is a dry passage cave about 160 m in length. The large entrance leads to two branches. The west passage is 100 m long and up to 20 m wide. The south branch leads to a large chamber that is 20 m by 40 m across (Fincham 1997). In St. Clair Cave, Goodwin (1970) found a mixed colony of approximately100 individuals of *E. sezekorni* and *Phyllonycteris aphylla* deep in the cave. A small sample revealed a ratio of one *Erophylla* to every three *Phyllonycteris*. The colony was located in a portion of the passageway that had "rough, irregular ceiling and walls." At Sewell Cave, Goodwin (1970) documented this species based upon two males that were netted at 8 PM on 7 January as they attempted to enter the cave. A thorough search of the cave yielded no additional bats. The newly reported Ratbat Hole in St. Thomas Parish is a karst cave with a 5-m wide entrance that leads to a vertical drop of 15 to 20 m. Dávalos and Erikkson (2003) captured numerous *Erophylla sezekorni* along with *Pteronotus parnellii*, *Monophyllus redmani*, and *Artibeus jamaicensis* at the Ratbat Hole on 16 December 2001. However, when they returned to this cave on 23 March 2002, they captured no *M. redmani* and only 5 *E. sezekorni* along with the other two species. This represented an 84% reduction in the *Erophylla* population, which they attributed to changing plant resources in the area (Dávalos and Erikkson 2003).

Osburn (1865) gave an early account of this species in a cave on Harmony Hall Estate, Trelawny Parish, which he visited on 4 June 1859. He described the entrance of the cave as being in a rock wall shrouded by a thicket. The cave was "not very extensive, and not thoroughly dark." The bats were present in "immense numbers, flying about and swarming on the walls and roof like bees." Osburn (1865) found no species of bat in the cave except *Erophylla sezekorni.* Among the 17 individuals that Osburn collected "the sexes were pretty equal and the number of young very great." Each female carried a single young. He described one young as "quite naked and blind, and about two inches long, but clung with great tenacity" to its mother. "From a portion of an umbilical cord still attached to one mother, I conclude one had only been born quite recently."

Osburn (1865) found the floor of the cave to be littered with kernels of the breadnut (*Brosimim alicastrum*), which is a yellow fruit about 1.5 to 2.5 cm in diameter, and the remains of the clammy cherry (*Cordia collococca).* The captive animals readily ate the clammy cherry fruits. Osburn was surprised when the bats held and easily manipulated the fruit between their wrists and thumbs. The bats moved the fruit until all of the pulp was eaten from the central seed, which was then discarded.

Away from caves buffy flower bats were taken in mist nets in a variety of situations, including a coffee plantation near Penlyne, coconut and banana plantations near Hectors River, and over the Buttonwood River, Williamsfield River, Flint River, and smaller, fast moving streams near Drapers, near Watermount, and east of Runaway Bay. At Orange Valley, individuals were taken in nets set in a pasture near a fruiting fustic tree that also attracted many other species of phyllostomids. Nets were set at Bluefields in a dry ravine with scattered large trees that formed no definable flyway. There was no understory but the trees did contain a variety of wild fruits. Five species of phyllostomids in addition to *Erophylla sezekorni* were taken here including *Glossophaga soricina, Monophyllus redmani, Phyllonycteris aphylla, Ariteus flavescens*, and *Artibeus jamaicensis.*

A female taken on 7 April contained a single embryo that measured 18.5 in crown-rump length, whereas single females taken on 14 March, 2 July, and 25 July were noted as displaying no gross reproductive activity. Lactating females were taken on 5 July (1), 9 July (2), and 31 July (6). Two males taken at 1.5 km S Orange Valley had testes lengths of 4 and 4.5. Four males taken in December/January had testes that averaged 3.9 (2.5-5) in length (Goodwin 1970), whereas four July-taken males had testes lengths of 2.5, 3, 3, and 3. Buden (1976) recorded an immature individual of nearly adult size on 20 August. During our field work four individuals taken on 26 July were found to have unfused phalangeal epiphyses. The length of forearm for these four individuals averaged 45.3 (44.5-45.8), which is only slightly smaller than the average for adults (Table 2). Although these reproductive data are limited, they fit closely the monestry pattern described by Wilson (1979).

Erophylla mating behavior has not been studied, but probably will be found to be very interesting if some enterprising individual develops the appropriate techniques to observe it in the wild. Sexually mature males have a large, green-colored salivary gland. This gland is physically present in sexually immature males and in adult females, but is so small that it is almost unnoticeable. Moreover, it is beige in color and has the gross appearance of a typical phyllostomid submandiblar gland. This sexually dimorphic gland is regarded to be an accessory submandibular (Phillips et al. 1993) and so far it is the only example of such a sexual difference in the salivary glands of any group of mammals. Transmission electron microscopic analysis revealed that the male gland consists of elongate tubules with unusual secretory cells. The secretory products(s) are completely unknown, but pheromones or regulatory peptides or some combination would not be surprising. Indeed, these glands might contribute to the odor associated with these bats. The striking green color of the gland in mature males might be due to an abundance of catylase, but even this has not yet been confirmed (Phillips et al. 1993).

Studying the annual variation in fat reserves of eight species of bats on Jamaica, McNab (1976) found that *Erophylla sezekorni* had significantly less fat deposits in the dry season as compared with the wet season. Two males captured on 18-19 December weighed 15.4 and 14.6, respectively, whereas a female taken on the latter date weighed 16.5.

Single males taken on 9 and 10 July evidenced molt on the anterior half of the dorsum, but showed no molt on the venter. On the dorsum much darker new hair was replacing the old. Three individuals in our sample of *E. sezekorni* had dental abnormalities. One individual (CM 44512) was missing the left upper and lower first incisors. In the upper jaw the alveolar bone in which this tooth would have been rooted had been resorbed. The remaining three upper and lower incisors were evenly spaced between the canines. The second individual (CM 44509) was missing the upper right M2, which was probably lost during life. The third bat (CM 44511) exhibited the most extensive dental problems, missing the upper right M1 and M2, left M2, and lower left m3. There was no evidence of alveoli for any of these teeth.

Single specimens in the American Museum of Natural History from Healthshire Hills, Money Cave, and Portland Ridge were recovered from subfossil owl pellets. McFarlane et al. (2002) reported fossil and subfossil remains of *Erophylla* from the Jackson's Bay caves that were approximately 10,000 years old. McFarlane and Garrett (1989) reported a minimum of 8 individuals of *Erophylla sezekorni* from contemporary Barn Owl (*Tyto alba*) pellets found in caves in the Jackson's Bay area. This species constituted 9.7% of the non-rodent remains found in the pellets.

Genetics.—The karyotype of *E. sezekorni* has 2n = 32 and FN = 60 (Fig. 38). There are 30 biarmed autosomes in a graded series from large to small. The X is medium sized and metacentric, and the Y is minute and acrocentric. Karyotypes were obtained from one female from 4 mi. E Runaway Bay, one male and four females from Orange Valley, and one female from Bluefields. Baker and Lopez (1970) and Nagorsen and Peterson (1975) reported 2n = 32 and FN = 60 for *E.*

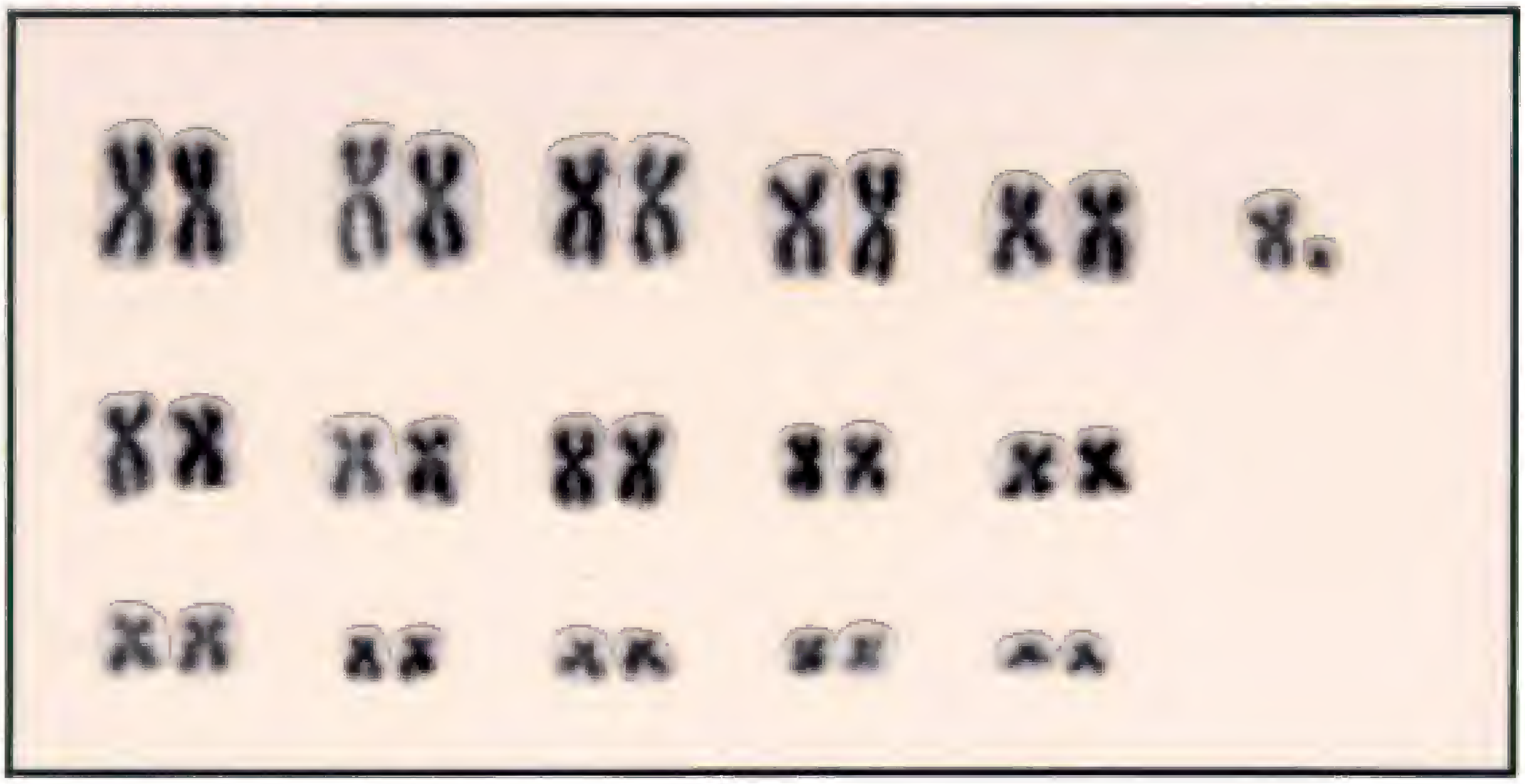

Figure 38. Karyotype of a male *Erophylla sezekorni* from Orange Valley, St. Ann Parish (TK 8136; TTU 21894).

sezekorni (= *E. bombifrons*) from Puerto Rico and Hispaniola. Baker and Bass (1979) reported the karyotype of *E. sezekorni* to be identical to that of *Phyllonycteris aphylla* based on G- and C-band analyses.

Baker et al. (2003) sequenced DNA from the mitochondrial ribosomal genes and the nuclear RAG 2 gene from *Erophylla* and representatives of other genera of Glossophaginae. On the basis of these molecular data, *Erophylla* is included in a lineage with the other Antillean glossophagines (*Brachyphylla*, *Monophyllus*, and *Erophylla*) and the two mainland genera *Leptonycteris* and *Glossophaga*.

Remarks.—The specimens at the National Museum of Natural History catalogued as from "Providence Cave, Montego Bay" have the following note associated with them: large cave on "Providence" 3 miles east of Snug Harbor. The collector, E. A. Andrews, is assumed to have left this note, which gives the most precise available location of Providence Cave.

Phyllonycteris aphylla (Miller, 1898)
Jamaican Flower Bat

Specimens examined (102).—HANOVER PARISH: Flint River, Sandy Bay, 2 (CM). PORTLAND PARISH: *1.5 km NW Hectors River*, 4 (3 JMM, 1 UF); Hectors River, 3 (JMM). ST. ANDREW PARISH: Kingston, 1 (MCZ). ST. ANN PARISH: Antrim, near Runaway Bay, 1 (MCZ); Dairy Cave, Dry Harbour [= Discovery Bay], 3 (AMNH); Mount Plenty Cave, Goshen/Lucky Hill, 1 (AMNH); Orange Valley, 52 (13 CM, 39 TTU); *1.5 km S Orange Valley*, 3 (CM); Circle B Plantation, 2 km SW Priory, 9 (2 CM, 7 TTU); Queenhythe, 1 (TTU); 4 mi. E Runaway Bay, 5 (TTU). ST. CATHERINE PARISH: St. Clair Cave, 2 mi. S. Ewarton, 11 (1 AMNH, 1 CM, 1 IJ, 1 MCZ, 6 ROM, 1 TTU); River Head Cave [near Ewarton], 1 (AMNH). ST. ELIZABETH PARISH: Wallingford Cave, Balaclava, 1 (AMNH). TRELAWNY PARISH: Cock Pit Cave, 5 mi. N, 2.5 mi. WNW Quick Step, 280 m, 2 (NMNH); Duanvale, 1 (TTU). WESTMORELAND PARISH: Bluefields, 1 (CM). PARISH UNKNOWN: no specific locality, 1 (NMNH [holotype]).

Additional records (McFarlane 1997).—MANCHESTER PARISH: Oxford Cave. ST. CATHERINE PARISH: Pedro Cave. TRELAWNY PARISH: Windsor Cave.

Distribution.—Figure 39 shows the collecting localities for *Phyllonycteris aphylla* on Jamaica. Until the early 1960s this species was thought to be extinct on Jamaica. But we have found it to be relatively com-

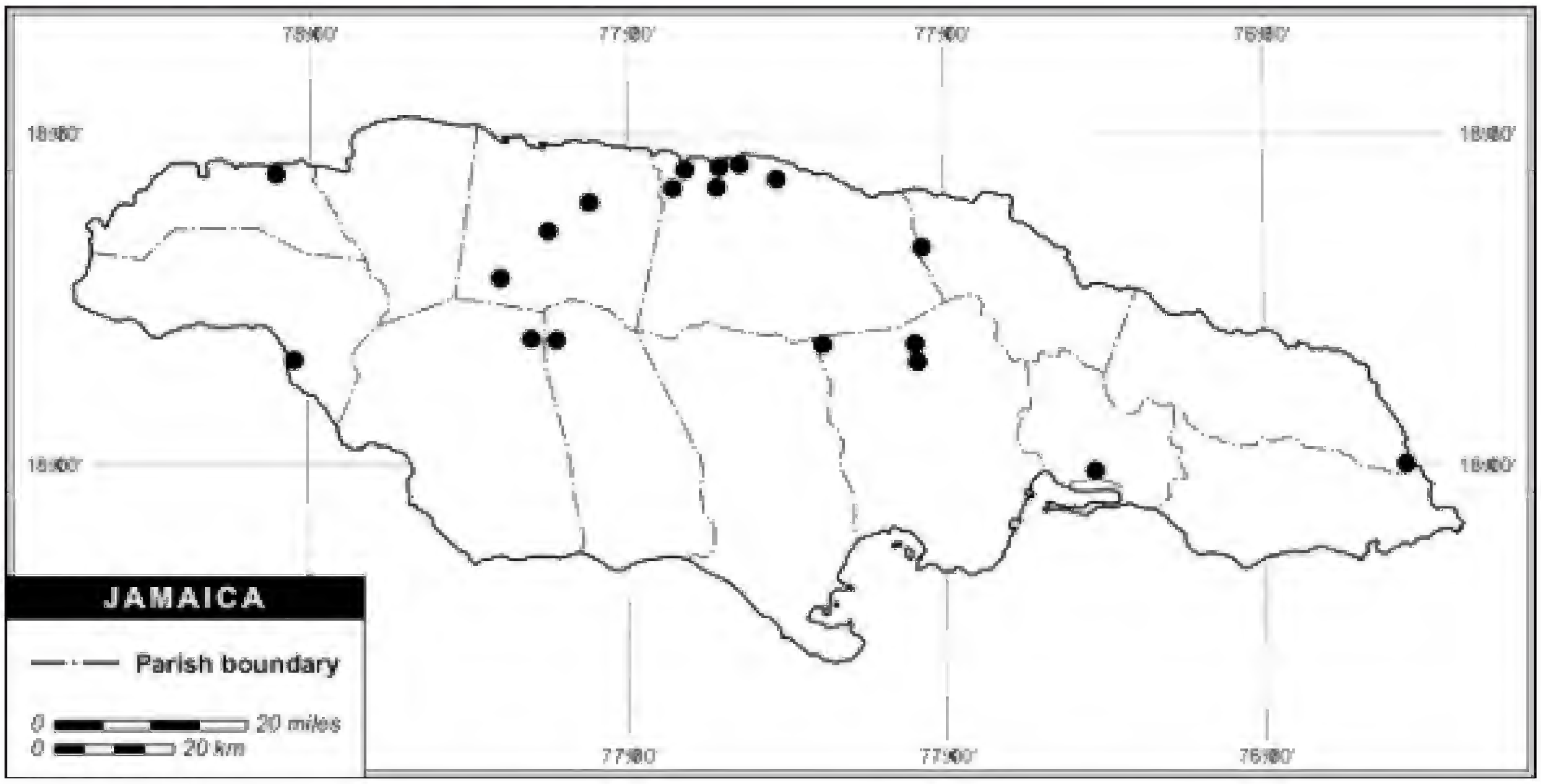

Figure 39. Map of Jamaica showing the locations where specimens of the Jamaican flower bat, *Phyllonycteris aphylla*, have been collected.

mon in areas of the Central Range where appropriate cave habitats can be found. Its apparent absence from the southern coast south of the Central Range and Blue Mountains (except for in the Kingston area) probably is not an artifact because considerable bat collecting has been done in this area. The southern coast might be too hot and dry for the species to inhabit most of the year. The genus *Phyllonycteris* is endemic to the Greater Antilles and *P. aphylla* is endemic to Jamaica.

Systematics.—The Jamaican flower bat was described as *Reithronycteris aphylla* by Miller (1898), with the species serving as the type species for the new genus *Reithronycteris*. The holotype was the only known representative of the species. Miller (1907) partially re-described the genus in view of his recognition of the genus *Erophylla* and a better understanding of the characteristics of the genus *Phyllonycteris*. The anatomy of the basicranial region was the primary characteristics used by Miller (1907) to separate *Phyllonycteris* from *Reithronycteris.* This region in *Reithronycteris* is unique among mammals because the floor of the braincase is elevated out of its normal position with the roof of the posterior nares being formed by two longitudinal folds probably formed by the pterygoid bones and nearly meeting along the median line of the region. The roof of the posterior nares normally is formed by the basisphenoid and presphenoid in this region of the cranium of other mammals. Koopman (1952) acknowledged these cranial differences, but he believed that the relationships among phyllonycterine genera could be represented by placing *Reithronycteris* as a subgenus of *Phyllonycteris* thus making the correct name of the Jamaican flower bat *Phyllonycteris (Reithronycteris) aphylla.* This is the taxonomic arrangement that we have followed here.

A misreading of a statement in Koopman (1952) led some authors (Henson and Novick 1966; Goodwin 1970, for example) to state that the holotype of *P. aphylla*, which was originally in the Institute of Jamaica, has been lost. However, a complete reading of Koopman (1952) reveals that he examined the holotype now deposited in the National Museum of Natural History as Poole and Schantz (1942) had noted earlier. The holotype remains in the National Museum of Natural History with the catalog number 255514. The male holotype has the following external and cranial measurements: length of forearm, 47.8; greatest length of skull, 25.8; condylobasal length, 23.2; interorbital constriction, 6.0; postorbital constriction, 5.3; mastoid breadth, 12.0; palatal length, 10.9; length of maxillary toothrow, 7.6; breadth across upper molars, 7.2.

Morphometrics.—Table 2 presents the measurements of 10 males and 10 females from Orange Valley and 4 mi. east of Runaway Bay. No zygomatic breadth is given because this structure is incomplete in members of the genus *Phyllonycteris*, which distinguishes the genus from all other phyllonycterines and most other phyllostomatids. Males were significantly larger than females in four of the nine measurements, including greatest length of skull ($P = 0.001$), condylobasal length ($P = 0.01$), mastoid breadth ($P = 0.001$), and palatal length ($P = 0.05$). Males also averaged larger than females in length of foreman, interorbital breadth, and breadth across the upper molars, whereas females averaged slightly larger than males for length of maxillary toothrow. The samples for the sexes had the same mean value for postorbital constriction.

Miller (1898) presented an array of external and cranial measurements of the holotype. Henson and Novick (1966) and Howe (1974) present external measurements of four females from Riverhead Cave and near Hector's River, respectively. Swanepoel and Genoways (1979) reported the forearm and seven cranial measurements of four females and four males from Jamaica.

Natural history.—Between the time of the original description of the species by Miller in 1898 and 1957 (Henson and Novick 1966) no living representatives (Fig. 40) of this species were captured. In the intervening years, fossil and subfossil remains of *P. aphylla* were discovered in a number of caves, including two along the north coast—Dairy (Koopman and Williams 1951; Williams 1952) and Antrim (Koopman 1952)—one in west-central Jamaica—Wallingford Cave (Koopman and Williams 1951; Williams 1952)—and one from along the southern coast—Portland (Williams 1952). The presence of fossils and the inability to catch living specimens led these authors to speculate that the species recently had become extinct. However, a living specimen was captured at St. Clair Cave in 1957 (Henson and Novick 1966) and at several localities throughout the island in

Figure 40. View of the head of *Phyllonycteris aphylla*.

the 1960s and early 1970s (Henson and Novick 1966; Goodwin 1970; Howe 1974).

St. Clair Cave, where the species was rediscovered by Goodwin (1970) and also found by our field parties, is the single most important cave on Jamaica for the safe future of a large portion of the chiropteran fauna of the island. St. Clair Cave (cave 306) is some 2900 m in length and is a river passage type of cave for the above-ground Black River. There is a steep descent entrance of 5 m down tree roots to a collapsed shaft entrance (Figs. 41-42). A descending passage over large boulders leads to the huge Junction Chamber, which approaches 30 m in height and nearly 90 m in width. To the southwest is the Inferno Passage where the primary bat colony is located. This passage extends nearly 400 m through pools and around boulders. Air temperature in the Inferno Passage is elevated by the large bat colony and at times ammonia and hydrogen sulfide fill the air. To the northeast extends the Main Passage 1740 m before reaching an area of water approximately 75 m in length that is deep enough that swimming is required. Ultimately this passage ends in a muddy slope that leads to the second entrance of the cave (Fincham 1997; Zans 1954).

D. A. McFarlane (1985) gave a description of the Inferno Passage that is worthy of repeating: "Inferno Passage is home to tens of thousands of bats. The floor of the passage is largely occupied by thigh-deep pools of fetid water and liquid guano. The walls are a living carpet of scavenging invertebrates—cockroaches, cave crickets, millipedes, and innumerable smaller forms. The air, vibrating with the beat of a myriad of unseen wings and raised some five or six degrees by the heat of the bats' bodies, resembles some kind of Stygian sauna bath and is filled with a rain of bat urine and excrement. Sick and young bats that lose their grip and fall to the floor are rapidly consumed by carnivorous insects, while their more fortunate colleagues host clouds of parasitic flies that show an unwholesome attraction to visiting cavers' lights."

Our experience was much the same as McFarlane's when we first visited the cave in 1974. Any flat or sloping areas of the passage were covered with 0.5 m or more layer of bat guano. The air quality was very poor with high levels of ammonia and hydrogen sulfide, which was luminescent in our lights as it bubbled up from the water filling the bottom of the passage. The rain of pestilence from the air also included larval dermestid beetles that were quite happy to begin feeding on the ears or other exposed areas of the bodies of bat biologists. When we visited the cave again in 1977, conditions had changed considerably. The pools of water in the bottom of the Inferno Passage were much shallower and had lost most of their fetid nature. Most of the guano deposit was gone. It was our assumption that the Black River had flooded recently flushing out most of this debris. The condition of the bat colony seemed as good as in our previous visit. The air temperature was high as was the relative humidity. The air quality in the passage deteriorated as one moved deeper in the passage until the ammonia levels were dangerously high and the oxygen levels were dangerously low, at least for human beings.

When Goodwin visited St. Clair cave on 29 December and 4 January he found a mixed colony of about 100 *Phyllonycteris* and *Erophylla* in the Inferno Passage about 1350 m from the entrance of the cave. He estimated that about 75 *P. aphylla* were in this colony. The roosting site was in a long, straight portion of the passageway with a width varying from 6 to 15 m and a height of 9 to 12 m. The temperature of the passageway was measured at 30° C and the air was saturated with water vapor (Goodwin 1970). Other species of bats known to inhabit this passageway include *Pteronotus macleayi, P. parnellii, P. quadridens, Mormoops blainvillii, Monophyllus redmani, Natalus micropus, N. stramineus*, and *Erophylla sezekorni*.

Riverhead Cave (also called Braham Cave; cave 226), where the second recent specimen was captured by Henson and Novick (1966), is a large, complex sumped-rising type of cave with an approximate length of 2500 m. The Black River that flows from the 10-m wide entrance of the cave is subject to rapid flooding. The cave contains a number of chambers as well as the main passage, an arched tunnel, with pools, sinks, and sumps. Some of the chambers are oxygen depleted of which the Anoxia Chamber is the first encountered along the main passage (Fincham 1997). The Jamaican flower bat obtained here was a female that was captured about 9 PM in a mist net placed at the cave entrance. Most of the other species of bats

Figure 41. Photograph of the cockpit entrance leading to St. Clair Cave, St. Catharine Parish, Jamaica.

Figure 42. Photograph of members of our field party climbing down the roots of a fig tree to gain access to the entrance to St. Clair Cave, St. Catharine Parish, Jamaica.

in the cave, *Pteronotus, Mormoops, Glossophaga*, and *Artibeus,* had already exited the cave by the time the *Phyllonycteris* specimen was netted (Henson and Novick 1966). At Mount Plenty Cave a male was captured between 1 and 8 AM on 20 January in a mist net set across the entrance of the cave and a female was taken in the same manner between 9 and 11 PM on 27 January (Goodwin 1970). Howe (1974) was the first to report the capture of *Phyllonycteris aphylla* in foraging areas away from caves. He captured three adult females in a mist net on the night of 25 December 1967 between 6 and 9:30 PM. The net was set in a clearing at the end of a service road adjacent to the Williamfield River near Hector's River at the extreme eastern end of Jamaica. An adult male was taken in a mist net in a coconut and banana plantation at this same locality on 19 December 1975 at 11 PM.

Our largest sample of *P. aphylla* came from Orange Valley where specimens were taken in nets set around a large fustic tree (*Maclura* [= *Chlorophora*] *tinctoria*) in the middle of a pasture with a nearby livestock pond. There was no doubt that the Jamaican flower bats were coming to feed on the ripening fruits of the fustic tree. The first species of bat taken was *Ariteus flavescens*, which began arriving in large numbers just at dusk on the evening of 8 July. The large numbers of *Phyllonycteris* began arriving about one hour later. At the height of activity we estimated that there were several hundred bats of these two species and *Artibeus jamaicensis* feeding in the tree. Large numbers of *Monophyllus redmani* also were taken and they may well have been attracted in part by the fruits. *Pteronotus parnellii, Mormoops blainvillii, Macrotus waterhousii, Glossophaga soricina*, and *Erophylla sezekorni* also were collected at the same time. At Duanvale a single individual was netted in an orchard of native and cultivated fruit trees, and at Bluefields an individual was netted along a dry ravine with adjacent native fruit trees. The conditions at the Circle B Plantation where 12 individuals were captured included an orchard with introduced fruit trees—mango, banana, papaya and others—and native trees on the surrounding steep-sided hills. At the remaining three locations where we captured Jamaican flower bats (Flint River, 4 mi. E Runaway Bay, and Queenhythe), specimens were taken in association with water, either rivers (the first two places) or a large pond (the last place).

Males with testes lengths of 6 and 3 were taken on 4 and 20 January, respectively (Goodwin 1970). A male taken on 13 June had testes that measured 3.5 in length. Twenty males captured between 5 to 11 July had testes that averaged 3.8 (2-5) in length, as did five males taken on 25-26 July 3.8 (3.5-4.5). Males taken on 2-3 November had testes lengths of 3, 5, 5, and 5.5. Two males taken on 13 December and one taken on 15 December had testes lengths of 2.5, 4.5, and 4.5, respectively.

A female carrying a single embryo, measuring 4 in crown-rump length, was taken at Mount Plenty Cave on 27 January (Goodwin 1970). The only other pregnant female recorded for this species was taken on 19 June at Riverhead Cave. The embryo measured 32.6 in crown-rump length. The remaining females for which we have data were either lactating or evinced no gross reproductive activity as follows (number lactating of number examined): 10 January, 1 of 1; 4 July, 1 of 1; 5 July, 3 of 3; 9 July 2 of 14; 17 July, 0 of 1; 25 July, 1 of 2; 26 July, 3 of 9; 28 July, 0 of 2; 3 November 0 of 2; 15 December, 0 of 2; 25 December, 0 of 3 (Howe 1974). These limited reproductive data do not fit precisely any of the patterns for bats discussed by Wilson (1979). With gestation occurring in both January and June and lactation occurring in January and July, it would appear that Jamaican flower bats are polyestrous, but whether this is an aseasonal or bimodal pattern can not be determined at this time.

A male obtained on 20 January weighed 13.3, one taken on 13 June weighed 19, and one taken on 19 December weighed 18.7. A lactating female captured on 10 January weighed 20.

Three specimens listed above from Dairy Cave as well as single specimens from Wallingford Cave, Antrim, and St. Clair Cave were recovered from cave deposits. The specimens from Dairy and Wallingford caves were from the older layers of the cave and were considered to be fossils (Koopman and Williams 1951; Williams 1952); however, the deposit at Antrim was considered to be only 50 to 400 years old (Koopman, 1952). It is believed that all of these specimens reached the caves as owl pellets.

Two of the specimens collected at Orange Valley had dental abnormalities. One male (CM 44522) is missing the lower right m2, but pieces of the root are still visible in the lower jaw indicating that the crown of the tooth was lost in life. Another male (CM 44532) is missing the right I2, i1, and i2. There is no indication of an alveolus for the missing upper tooth, but roots are still partially visible for the lower teeth. The upper right I1 has been slightly displaced anteriorly. The lower canines are heavily worn, especially the right tooth. This abnormality appears to be the result of an injury that resulted in malocclusion.

Genetics.—The karyotype of *P. aphylla* has 2n = 32 and FN = 60 (Fig. 43). There are 30 biarmed autosomes in a graded series from large to small. The X is medium sized and metacentric, and the Y is minute and acrocentric. Karyotypes were obtained from two males and four females from 4 mi. E Runaway Bay, six males from Orange Valley, and one male from Bluefields.

Baker and Bass (1979) reported the karyotype of *P. aphylla* to be identical to species of *Glossophaga, Monophyllus, Brachyphylla*, and *Erophylla* based on G- and C-band analyses. They suggested a close relationship between the Glossophaginae and Brachyphyllinae based on the sharing among these genera of a karyotype considered to be highly derived. Nagorsen and Peterson (1975) and Baker (1979) reported the karyotype of *P. obtusa* to be 2n = 32 and FN = 60; identical to that of *P. aphylla* presented here.

Baker et al. (2000) examined the relationships of *Erophylla sezekorni* and *P. aphylla* to other genera of Phyllostomidae using DNA sequence data from the nuclear RAG 2 gene. *Phyllonycteris* was found to be sister to *Erophylla* and a member of a clade including the other Antillean endemic glossophagines (*Brachyphylla* and *Monophyllus*) as well as the mainland *Glossophaga* and *Leptonycteris*.

Figure 43. Karyotype of a female *Phyllonycteris aphylla* from 4 mi E Runaway Bay, St. Ann Parish (TK 8029; TTU 21943).

Ariteus flavescens (Gray, 1831)
Jamaican Fig-eating Bat

Specimens examined (406).—CLARENDON PARISH: Kemps Hill, 1 (AMNH); Portland Ridge, 4 (AMNH). HANOVER PARISH: Long Bay, 4 mi. N Negril [*in* Westmoreland Parish], 1 (KU); Flint River, 1.5 mi. E Sandy Bay, 15 (CM). MANCHESTER PARISH: Gut River, sea level, 1 (JMM); Mandeville, 2 (BMNH); *near Mandeville*, 1 (AMNH). PORTLAND PARISH: 0.8 mi. W Drapers, 5 (CM); Green Hill, 1 (TTU); Hardwar Gap, 1090 m, 1 (NMNH); along Williamsfield River, 1.5 km. NW Hectors River, 8 (6 JMM, 2 UF); Hectors River, 4 (JMM). ST. ANDREW PARISH: *Half Way Tree*, 1 (IJ); Kingston, 6 (1 IJ, 1 HZM, 1 JMM, 2 NMNH, 1 ROM). ST. ANN PARISH: Dairy Cave, Dry Harbour [=Discovery Bay], 12 (AMNH); Mount Plenty Cave, Goshen/Lucky Hill, 1 (AMNH); Moneague, 1 (BMNH); Orange Valley, 70 (10 CM, 60 TTU); *1.5 km S Orange Valley*, 16 (CM); *1.2 km W Priory*, 2 (CM); Circle B Plantation, 2 km SW Priory, 4 (TTU); Queenhythe, 5 (2 CM, 3 TTU); 4 mi. E Runaway Bay, 1 (TTU). ST. CATHERINE PARISH: Ferry Cave, 7 (AMNH); Healthshire Hills, 3 (AMNH); Riverhead Cave [also called Braham Cave], near Ewarton, 1 (UF); 0.2 mi. E Watermount, 7 (CM). ST. ELIZABETH PARISH: *Hutchinson's Meadow Cave, Balaclava*, 4 (AMNH); Hounslow Money Cave, near Malvern, 78 (AMNH); Peru Cave, Goshen, 28 (AMNH); Wallingford Cave, 4 (AMNH). ST. JAMES PARISH: 7-rivers Cave, Lapland, 43 (AMNH). ST. THOMAS PARISH: Arntully, 2 (NMNH); Eleven Mile, 5 (4 BMNH, 1 UF); *Penlyne, Whitfield Hall, 4300 ft.*, 1 (UF); *Rock Shelter, 4-mile Wood*, 2 (1 FMNH, 1 UF); Yallahs, 3 (TTU). TRELAWNY PARISH: *Cock Pit Cave, 5 mi. N, 2.5 mi. WNW Quick Step, 280 m*, 9 (NMNH); Duanvale, 3 (TTU); Fowl House Cave, Windsor, 1 (AMNH); *Pen House Cave, Windsor*, 1 (AMNH); 4.9 mi. N Quick Step, 369 m, 2 (NMNH); 4 mi. NNW Quick Step, 370 m, 2 (NMNH). WESTMORELAND PARISH: Bluefields, 19 (CM); Content, 3 (BMNH); Savanna-La-Mar, 2 (BMNH). PARISH UNKNOWN: no specific locality, 13 (1 AMNH, 5 BMNH, 1 MCZ, 6 NMNH).

Additional records.—CLARENDON PARISH: Jackson's Bay (McFarlane and Garrett 1989); *Portland Cave 9 entrance* [17°45′12.1" N, 77°09′28.4" W] (Dávalos and Erikkson 2003). ST. ELIZABETH PARISH: Vineyard, near Black River (Gosse 1851:267). TRELAWNY PARISH: *Windsor Cave entrance* (Dávalos and Erikkson 2003). WESTMORELAND PARISH: Monarva Cave entrance (Dávalos and Erikkson 2003).

Distribution.—Figure 44 shows the collecting localities for *Ariteus flavescens* on Jamaica. The Jamaican fig-eating bat is a common, widespread species found in forested areas throughout the island with exception of elevations above 1500 m. The genus and species are endemic to Jamaica.

Systematics.—Genoways (2001) reviewed the taxonomic history and systematics of this endemic Jamaican species. The genus *Ariteus* is closely related to three other endemic Antillean genera—*Ardops, Phyllops*, and *Stenoderma*. All of these bats are characterized by a greatly shortened rostrum and a white spot on each shoulder. Some biologists have treated all of these genera as a single genus under the name *Stenoderma* (Varona 1974). But members of the genus *Ariteus* are distinguished from other members of this group by the lack of an upper third molar and the presence of a metaconid on the first lower molar (Miller 1907; Genoways 2001).

Gray (1831) described *Ariteus flavescens* based on a single specimen from an unknown location. Gosse (1851) was the first to obtain specimens now identified as this species from Jamaica. In doing so, he described two new species that are now considered to be junior synonyms of *Ariteus flavescens*—*Artibeus achradophilus* and *Artibeus sulphureus* (Genoways 2001).

Morphometrics.—Table 2 presents measurements of 10 males and 10 females from Orange Valley. In all measurements females are significantly larger than males at the $P = 0.001$ level, except for postorbital constriction in which the significance level was $P = 0.05$. In fact, in this sample there is no overlap in the measurements of males and females in all but three measurements—interorbital breadth, postorbital constriction, and mastoid breadth. This species clearly exhibits more secondary sexual variation than any other species of bat occurring on Jamaica. As Genoways (2001) discussed, this degree of secondary variation is displayed in only a few other species of New Word bats. Two other species of white-shouldered bats from the Antilles—*Stenoderma rufum* and *Ardops nichollsi*—display secondary sexual variation that approaches that in *Ariteus* as do the members of the mainland species *Ametrida centurio* (Genoways et al. 2001; Jones et al. 1971; Peterson 1965).

Genoways (2001) described individual and geographic variation in the Jamaican fig-eating bat. He found that the coefficient of variation for *Ariteus* was low for mammals in general, but comparable to other

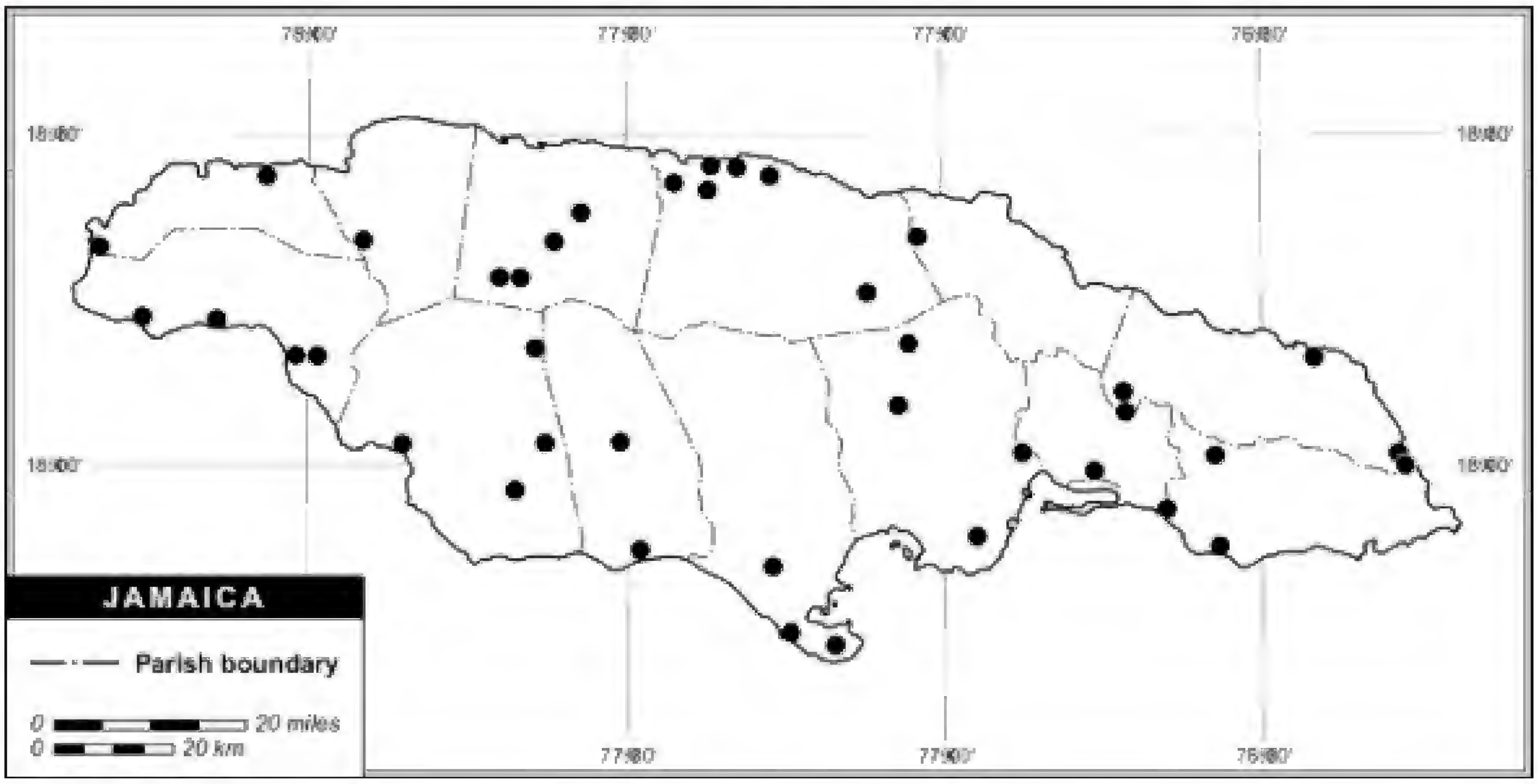

Figure 44. Map of Jamaica showing the locations where specimens of the Jamaican fig-eating bat, *Ariteus flavescens*, have been collected.

species of bats. In contrast to other wild mammals that have been studied, Genoways (2001) found that male *Ariteus* were more variable than females. In other mammals, the sexes do not display differences in variability. Whether this phenomenon is or is not related to the high degree of secondary sexual variation in *Ariteus* will await studies of other species of bats that show similar levels of secondary sexual variation. Genoways (2001) found that *Ariteus flavescens* possessed little geographic variation among populations and the variation present followed no distinct pattern. Based on these data, *A. flavescens* is considered to be a monotypic species.

Genoways (2001) presented the following measurements for the female neotype (TTU 21721): length of forearm, 42.7; greatest length of skull, 20.7; condylobasal length, 17.1; zygomatic breadth, 14.2; interorbital constriction, 5.2; postorbital constriction, 4.9; mastoid breadth, 11.9; palatal length, 4.0; length of the maxillary toothrow, 6.0; breadth across upper molars, 9.1. Dobson (1878) presented some external measurements of the female holotype of *Ariteus achradolphilus*. Swanepoel and Genoways (1979) reported the forearm and seven cranial measurements of four females and four males from Jamaica.

Natural history.—*Ariteus flavescens* is a tree-roosting species (Fig. 45) on Jamaica. Little information has been recorded about its natural history because earlier work has concentrated on cave-dwelling species. This might be surprising because as many as 192 specimens from 13 localities listed above (Dairy Cave, Eleven Mile, Ferry Cave, Fowl House cave, Healthshire Hills, Hounslow Money Cave, Hutchinson's Meadow Cave, Pen House Cave, Peru Cave, Portland Ridge, Wallingford Cave, 4-mile Wood, and 7-rivers Cave) are from cave localities. However, all of these specimens were recovered from deposits in caves, rock ledges, and rock shelters that are believed to represent the degraded remains of owl pellets. These deposits represent a range of time of undetermined length because a definite age for the oldest material has not been precisely determined, but the newest material was probably not over 50 years old when collected (Koopman 1952). McFarlane and Garrett (1989) reported a minimum of 22 individuals of *Ariteus flavescens* from contemporary Barn Owl (*Tyto alba*) pellets found in caves in the Jackson's Bay area. This species constituted 26.8% of the non-rodent remains found in the pellets.

Figure 45. View of the head of *Ariteus flavescens*.

Based on fossils (Koopman and Williams 1951; Williams 1952), it has been postulated that *Ariteus* out competed *Brachyphylla* on Jamaica with the latter becoming extinct. We find the postulation of a direct displacement of *Brachyphylla* by *Ariteus* difficult to accept. Close relatives of *Ariteus*—*Phyllops, Stenoderma*, and *Ardops*—co-occur with *Brachyphylla* throughout much of the Greater and Lesser Antilles, with no obvious competition. As an alternative to direct competition, we favor the idea that some environmental shift favored *Ariteus* over *Brachyphylla*. Williams (1952) also believed there was a striking shift in the abundance of *Ariteus* versus *Artibeus* between fossil deposits and the Recent fauna. He hypothesized that this shift—if real—was caused by human disturbance of the native flora and its ultimate replacement by exotic plants. Williams (1952) thought that introduction of domestic tropical fruits and logging of native trees would have favored *Artibeus*. He also acknowledged that the loss of roost sites could impact a tree-roosting species. Based on our field studies in Jamaica, we believe that the difference between the representation of *Ariteus* in fossil deposits and the modern fauna is really a collecting artifact. Past field studies have primarily focused on the cave roosting species of bats on Jamaica, with the use of mist nets only coming into use in the mid-1960s. The populations of *Ariteus* may be somewhat lower than indicated by the fossil record for the reasons stated by Williams (1952), but clearly the species is at least locally abundant and is widespread on the island. McFarlane et al. (2002) report fossil and subfossil remains of *Ariteus* from the Jackson's Bay caves that were approximately 10,000 years old.

We have locality records for the species from at, or near, sea level at such places as Gut River and Hector's River to at least 1300 m elevation at Penlyne. There are records of the species from Long Bay at the western tip of the island, from the vicinity of Hector's River near the east end of the island, from near Runaway Bay along the north coast, and Gut River along the southern coast. Howe (1974) reported some of the earliest mist-netting results from Jamaica when he took four individuals of *Ariteus* in banana-coconut plantations in the vicinity of Hector's River, with no extensive representation of native vegetation in the area. All specimens were captured between 6 and 10 PM in December.

During our field work on Jamaica, *Ariteus flavescens* were taken at 11 localities. Our largest sample came from Orange Valley where specimens were taken in mist nets set around a large fustic tree (*Maclura* [= *Chlorophora*] *tinctoria*) in the middle of a pasture with a nearby livestock pond (Fig. 46). There was no doubt that the Jamaican fig-eating bats were coming to feed on the ripening fruits of the fustic tree. Individuals of *Ariteus flavescens* were the first species of bats taken, with large numbers arriving just at dusk on the evening of 8 July. At the height of activity we estimated that there were several hundred bats of this species and two others—*Phyllonycteris aphylla* and *Artibeus jamaicensis*—feeding in the tree. Other species taken include *Pteronotus parnellii, Mormoops blainvillii, Macrotus waterhousii, Glossophaga soricina*, *Monophyllus redmani*, and *Erophylla sezekorni*. In a similar situation at Bluefields, 19 individuals were netted on one night along a dry ravine with adjacent native fruit trees.

Sixteen specimens were collected at 1.5 km S Orange Valley. This was the third largest collection of individuals of *A. flavescens* captured at a single place. The area is characterized by a mosaic of pastures, some of which were being grazed by cattle, fringes of tropical second growth, and remnants of old forest with open understory. At five other locations, we captured Jamaican fig-eating bats associated with rivers (0.8 mi. W Drapers, Flint River, 4 mi. E Runaway Bay, and 0.2 mi. E Watermount) and a large earthen tank (Queenhythe). As with many bat species, *A. flavescens* probably uses rivers as fly-ways. The large number of Jamaican fig-eating bats taken on a single night along the Flint River probably resulted from a nearby fruiting tree. At Duanvale three individuals were netted in an orchard of native and cultivated fruit trees, including bananas, rose apple (*Syzygium jambos*), cashew (*Anacardium occidentale*), cocoa (*Theobroma cacao*), and naseberry (*Manilkara zapota*). The steep-sided karst-formation hills in the immediate area were covered with native vegetation (Fig. 47). At Yallahs three individuals were taken in a commercial orchard that included bananas, mangos, and naseberries. A single individual was taken at Green Hill at a relatively high elevation along the north slope of the Blue Mountains in an area with scattered introduced fruit trees such as mangos.

Figure 46. Photograph of the pond and surrounding habitat where bats were netted at Orange Valley, St. Ann Parish, Jamaica.

Figure 47. Photograph of the orchards with the native vegetation on the steep hills in the background near Duanvale, Trelawny Parish, Jamaica.

Gosse (1851:267-272) was the first to describe some aspects of the natural history of this species, which he termed the "naseberry bat." Gosse (1851) described a naseberry tree as large and spreading with leaves forming into rosettes and large white fleshy flowers forming bunches. He described the fruits when ripe as "firm and fleshy, of a rich sugary sweetness" and each containing "a large flat oval black seed." Gosse (1851) observed Jamaican fig-eating bats coming to a naseberry tree (*Manilkara zapota*) at Content just at sunset. Activity increased with the increasing darkness until "many dusky forms are discerned flitting round and round." The bats would momentarily alight among the leaves and then swiftly fly away. On occasion ripe fruits were dislodged revealing that pieces had been bitten away by the bats. Gosse (1851) also found the delicately scented rose apple (*Syzygium jambos*) was "a favourite fruit of these winged quadrupeds." Dávalos and Erikkson (2003) during their work on cave bats on Jamaica took this species in the vicinity of the entrances to three caves. Near Monarva Cave *Ariteus* was taken in "early secondary stands" of vegetation, whereas near Windsor Cave they were taken in "primary forest" and near Portland Cave 9 the vegetation was a "late successional stand."

Although these incidental observations seem to imply that *Ariteus* and *Artibeus jamaicensis* have similar or even the same diets, there are anatomical and histological similarities, but also striking differences in their digestive tracts. Generally speaking, the gastric mucosa in all of the stenodermatine bats is characterized by huge numbers of highly active acid-producing parietal cells (Forman et al. 1979; Phillips et al. 1984). One statistically significant difference is in the relative numbers (density per unit volume of gastric pylorus) of gastrin-producing G-cells (Mennone et al. 1986). Another difference is in stomach structure and in histology of the fundus. In *Ariteus* the cardiac and fundic portion of the stomach is subdivided into two seemingly identical chambers connected by a small passage, whereas in *Artibeus* the stomach is a more typical single chambered structure (Phillips, unpublished data; Forman et al. 1979). The stomach walls and the septum that creates the anatomically unique stomach in *Ariteus* contain skeletal muscle fibers, which extend down into the stomach from the esophagus (Phillips, unpublished data). The presence of skeletal muscle in the stomach wall is, of course, unique relative to all other mammals (although one could reasonably predict that it will be found in relatives of *Ariteus*).

No single explanation accounts for the collective differences in fruit bats stomachs but the first impression is that these two fruit bats (*A. jamaicensis* and *A. flavescens*) must have completely different diets. If there really is broad overlap in diet, then it must be that metabolic or other basic physiological differences between the species necessitate radically different biological approaches to the same nutritional problem.

A male taken on 6 April had testes that measured 5 in length, whereas five males taken between 9 to 17 June had testes that averaged 4.4 (3-5.5) in length. July-taken males had the following average testes lengths (number of individuals in brackets): 4-10 July [16], 4.25 (4-5); 17-19 July [4], 4.0 (3-5); 23-25 July [11], 3.7 (2.5-4.5). Two males taken on 2 November had testes that measured 3 and 6. Seven males obtained on 14-15 December had an average testes length of 4.1 (3.5-5).

A female captured on 9 April contained an embryo that measured 27.5 in crown-rump length and one taken on 14 April contained an embryo measuring 15. Of six females taken between 8 to 17 June one was lactating and four contained embryos measuring 10, 10, 12, and 15. Of the 46 females taken between 4 and 12 July that were examined for reproductive data, one was lactating, three were noted as postpartum, five evinced no gross reproductive activity, and 37 contained single embryos. These embryos averaged 18.4 (6-28) in crown-rump length. Of the 20 females taken between 23 and 27 July that were examined for reproductive data, two were lactating, four were noted as postpartum, four evinced no gross reproductive activity, and 10 contained single embryos. These embryos averaged 14.8 (3-26.5) in crown-rump length. Single females taken on 2 November and 20 and 29 December showed no signs of gross reproductive activity (Howe 1974) nor did eight females taken on 14-15 December.

Although the reproductive data for *Ariteus flavescens* are incomplete, some conclusions can be drawn. The species is almost certainly polyestrous. The fact that we have pregnant females from at least early April until late July would support this conclusion. There seems to be a high amount of synchrony in breeding with most of the females in April, June, and July being pregnant. With three females being taken on 25-26 July having embryos of 3, 3, and 5 crown-rump lengths, reproductive activity will extend well into September. Whether observed polyestry is aseasonal or some other pattern can not be determined with certainty.

A male captured on 6 April weighed 16.9; the weights of five males taken between 9-17 June were 11.0, 11.5, 12.0, 12.5, and 13.0; and the weights of two taken on 22 December were 9.2 and 12.9 (Howe 1974). A lactating female taken on 14 June weighed 15.5, whereas females taken on 20 and 29 December weighed, respectively, 12.4 and 13.1 (Howe 1974).

Phillips et al. (1987) studied the ultrastructure of the parotid salivary glands of *Ariteus flavescens* captured on Jamaica. As is the case in nearly every bat species, *Ariteus flavescens* has its own unique secretory granule ultrastructure. The microscopic appearance of the secretory contents probably is due to a combination of physio-chemical properties and the presence or absence of particular proteins and differences in their primary structure. Species-specificity documents that the secretory products or their packaging (the process by which the cells make and store the product) evolves relatively quickly in bats (Phillips 1996).

Two specimens in our collection from Jamaica exhibit dental abnormalities that probably resulted from disease. A female from Queenhythe (CM 44401) is missing i1-2 (right and left), p3 (right), and m3 (right and left). The root surfaces of the remaining mandibular teeth are exposed where the mandibular bone was resorbed, possibly as a result of periodontal disease. In this same individual the upper incisors are misaligned. A female from Bluefields (CM 44412) is missing the right i1 and lateral surface of the mandible at the base of the left i1 shows evidence of resorption. This condition was probably the result of gingivitis.

Genetics.—The karyotype of *A. flavescens* has 2n = 30 females, 31 males and FN = 56 (Fig. 48). There are 28 biarmed autosomes in a graded series from large to small; four medium-sized pairs are subtelocentric, and the remaining pairs are metacentric. The X is medium sized and submetacentric, the Y1 is small and subtelocentric, and the Y2 is minute and acrocentric. Karyotypes were obtained from one male and two females from Duanvale, one male from Queenhythe, and seven males and two females from Orange Valley.

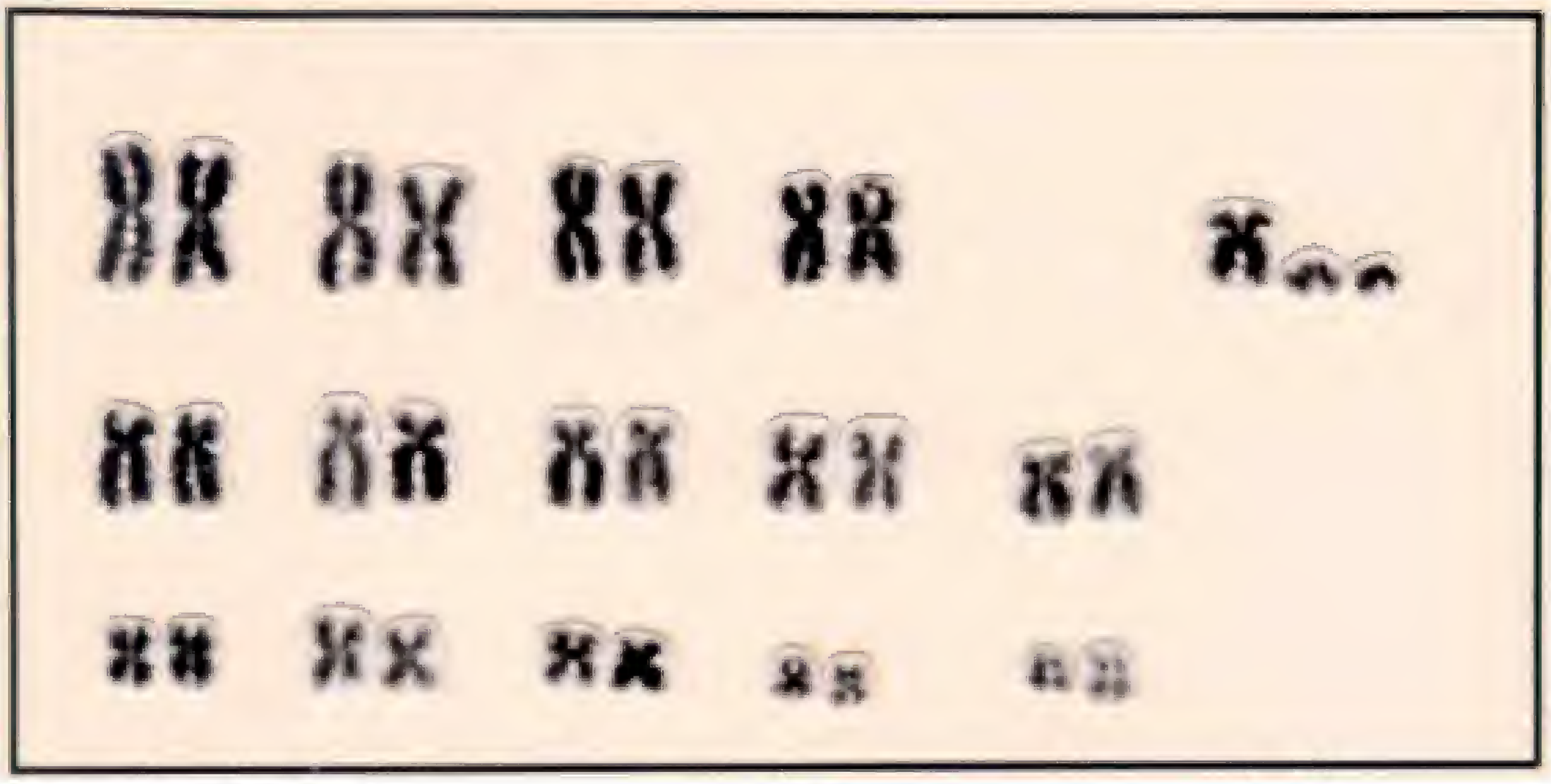

Figure 48. Karyotype of a male *Ariteus flavescens* from Queenhythe, St. Ann Parish (TK 8128; TTU 21774).

The karyotype of *A. flavescens* was previously reported by Greenbaum et al. (1975). They reported identical karyotypes among the endemic Antillean genera *Ariteus, Ardops*, and *Phyllops* and the previously reported *Stenoderma* (Baker 1973) and concluded these genera to be closely related and to represent a single invasion of the Antilles. The karyotype of *A. flavescens* also is identical to those of species of the mainland genera *Ametrida, Artibeus*, and *Enchisthenes* (Baker 1979).

Baker et al. (2003) sequenced DNA from the mitochondrial ribosomal genes and the nuclear RAG 2 gene in *Ariteus* and representatives of other genera of Stenodermatinae. *Ariteus* is a member of the short-faced stenodermatines and was found to be the sister taxon to the Lesser Antillean endemic genus *Ardops.* The *Ardops-Ariteus* clade is sister to a clade that includes *Stenoderma, Centurio, Pygoderma, Sphaeronycteris, and Ametrida.* It is significant that *Stenoderma* is the basal taxon for the latter clade. Varona (1974) placed all of the Caribbean short-faced stenodermatines into the genus *Stenoderma.* However, analysis of the DNA sequence data of Baker et al. (2003) shows that *Stenoderma* would be paraphyletic if Varona's taxonomy were used. For this reason, we retain the generic distinction for *Ariteus.*

Remarks.—Based on Gosse (1851: 271-272) "Content" is 3 miles east of Bluefields, Westmoreland Parish, on recent maps of Jamaica (see Genoways 2001).

Artibeus jamaicensis jamaicensis (Leach, 1821)
Jamaican Fruit-eating Bat

Specimens examined (721).—CLARENDON PARISH: Mason River Research Station, 2.5 mi. W Kellits, 2300 ft., 1 (TTU); Portland Ridge, 2 (AMNH). HANOVER PARISH: Long Bay, north of Negril [*in* Westmoreland Parish], 2 (KU); Cousin's Cave, 6 mi. W Lucea, 9 (AMNH); Lucea, 14 (AMNH); Flint River, 1.5 mi. E Sandy Bay, 8 (CM). MANCHESTER PARISH: 0.5 km E Gut River, 1 (JMM). PORTLAND PARISH: 0.8 mi. W Drapers, 12 (CM); Hectors River, 2 (JMM); Port Antonio, 12 (7 ANSP, 5 KU). ST. ANDREW PARISH: Constant Spring, 22 (BMNH); Kingston, 5 (1 FMNH, 1 MCZ, 3 NMNH); *Hope Gardens, Kingston,* 56 (NMNH); *Montenegro Bay, Kingston*, 5 (AMNH). ST. ANN PARISH: Brown's Town, 17 (AMNH); *Cardiff Hall* [18°27'N, 77°19'], 1 (AMNH); Discovery Bay, 4 (AMNH); *Dairy Cave, Discovery Bay*, 1 (AMNH); Green Grotto, 2 mi. E Discovery Bay, 43 (3 CM, 40 HZM); Moseley Hall Cave, Guys Hill, 1 (ROM); "Seven C's" Mammee Bay [18°25'N, 77°10'W], 2 (HZM); Mount Plenty Cave, Goshen/Lucky Hill, 8 (2 COLU, 6 HZM); Orange Valley, 41 (40 CM, 1 TTU); *1.5 km S Orange Valley*, 5 (CM); *1.2 km W Priory*, 1 (CM); Circle B Plantation, 2 km SW Priory, 44 (10 CM, 34 TTU); Queenhythe, 14 (7 CM, 7 TTU); 4 mi. E Runaway Bay, 34 (TTU); *0.5 mi. S, 0.5 mi. W Runaway Bay*, 3 (TTU); *24 km W St. Ann's Bay*, 1 (TTU); Thunder Cave, St. Ann's Bay, 2 (UF). ST CATHERINE PARISH: St. Clair Cave, 2 mi. S. Ewarton, 1 (IJ); Ferry, 4 (IJ); *Ferry Cave, Kingston-Spanish Town Road at the boundary of St. Andrew and St. Catherine Parishes*, 29 (AMNH); Healthshire Hills, 18 (AMNH); Worthy Park, 8 (1 BMNH, 6 COLU, 1 KU). ST. ELIZABETH PARISH: Appleton, 1 (AMNH); Balaclava, 9 (AMNH); *Hutchinson's Meadow, Balaclava*, 1 (AMNH); *Wallingford Cave, Balaclava*, 15 (AMNH); Pedro Bluffs, 2 (AMNH); Peru Cave, Goshen, 28 (16 AMNH, 12 NMNH); Hounslow [near Malvern], 4 (AMNH); *Money Cave, Hounslow*, 11 (AMNH); *Peru [near Malvern],* 1 (AMNH). ST. JAMES PARISH: Cambridge, 15 (AMNH); *cave near Cambridge*, 1 (AMNH); *Lapland,* 1 (AMNH); 7-rivers Cave, Lapland, 16 (AMNH); *Cereal Cave, Montego Bay*, 1 (COLU); Providence Cave, Montego Bay, 18 (12 AMNH, 5 BMNH, 1 NMNH); Montego Bay, 17 (6 AMNH, 6 NMNH, 5 UF); *cave east of Montego Bay,* 1 (NMNH); *Norwood Caves*, 1 (UF). ST. MARY PARISH: *Aguatta [Agualta] Vale, Metcalfe*, 2 (BMNH); Annotto Bay, 5 (ROM); 5 mi. E Ocho Rios [*in* St. Ann Parish], 1 (COLU); Oracabessa, 3 (1 BMNH, 2 FMNH); 2 mi. W Port Maria, 1 (AMNH). ST. THOMAS PARISH: Bath, 1 (MCZ); Eleven Mile, 1 (BMNH); Yallahs, 1 (TTU). TRELAWNY PARISH: Duanvale, 57 (TTU); Good Hope Estate, 2 (NMNH); Kinloss, 4 (KU); Mahogany Hall [18°23'N, 77°28'W], 4 (BMNH); Windsor Cave, 8 (2 NMNH, 6 TTU). WESTMORELAND PARISH: Bluefields, 6 (CM); Content, 1 (BMNH [holotype of *Artibeus capeolegus*]); Roaring River near Shrewsbury, 7 mi. NE Savanna-La-Mar, 11 (AMNH); Wakefield, 2 (CM). PARISH UNKNOWN: *Montserrat*, 2 (NMNH); *Page's Mount*, 1 (NMNH); no specific locality, 12 (5 BMNH [including holotype], 7 NMNH).

Additional records (McFarlane 1997 unless otherwise noted).—CLARENDON PARISH: *Drum Cave* [Jackson's Bay area]; *Jackson's Bay* (McFarlane and Garrett 1989); Jackson's Bay Cave; Portland Cave-1; *Portland Cave-2*. PORTLAND PARISH: near Sherwood Forest (Sanderson 1941: 28). ST. ANN PARISH: Chesterfield Cave [1.1 km SW Higgin Town]; Claremont Cave [1 mi. N Claremont] (Goodwin 1970); *Ewart Town Bat Cave*; Ramble Bat Hole [Alderton area]; Thatchfield Great Cave. ST. CATHERINE PARISH: *Riverhead Cave* (Henson and Novick 1966; McNab 1976); *River Sink Cave* [Worthy Park] (McNab 1976). ST. ELIZABETH PARISH: *Pedro Bluff Cave; Spaniards Cave*; Wondrous Cave [near Elderslie]. ST JAMES PARISH: Big Bottom Cave [in Big Bottom]; *Sewell Cave* (Goodwin, 1970). ST. MARY PARISH: *Sans Souci Grotto* (Goodwin 1970). ST. THOMAS PARISH: Ratbat Hole [17°52′12" N, 76°29′24" W] (Dávalos and Erikkson 2003). TRELAWNY PARISH: Carambie Cave; Johnston Pen [18º28'N, 77º33'W] (Osburn 1865). WESTMORELAND PARISH: Ratbat Cave, Little Bay [18°12′ N, 78°14′24" W] (Dávalos and Erikkson 2003).

Distribution.—Figure 49 shows the collecting localities for *Artibeus jamaicensis* on Jamaica. The Jamaican fruit-eating bat is one of the most common and widely distributed species of bats in the New World tropics. This is generally the same for the distribution of the species on Jamaica although it has not been captured at high elevations along the slopes of the Blue Mountains and it would appear that the species should not be expected above 1000 m in these areas. The subspecies *A. j. jamaicensis* is found on Jamaica, Hispaniola, Puerto Rico, Virgin Islands, the Lesser Antillean islands as far south as St. Lucia, and two small isolated islands in the southwestern Caribbean Sea—Providencia and San Andrés (Hall 1981).

Systematics.—*Artibeus jamaicensis* was originally described by William E. Leach (1821b:75) based on a specimen from Jamaica submitted to the British Museum (Natural History) by J. S. Redman. The paper was read before the Linnean Society of London on 7 March 1820, but the paper did not appear in print until 1821. In the same publication, Leach (1821b:82) also described another species, *Madatæus lewisii,* based on specimens from Jamaica submitted by W. Lewis. As discussed by Andersen (1908), the characteristics that led Leach to regard the latter "as a distinct species (and genus) are due to the immaturity of the individual." The name *jamaicensis* enjoys page priority over *lewisii* and thus is the appropriate name to use for this taxon. Gosse (1851) described *Artibeus carpolegus* based on

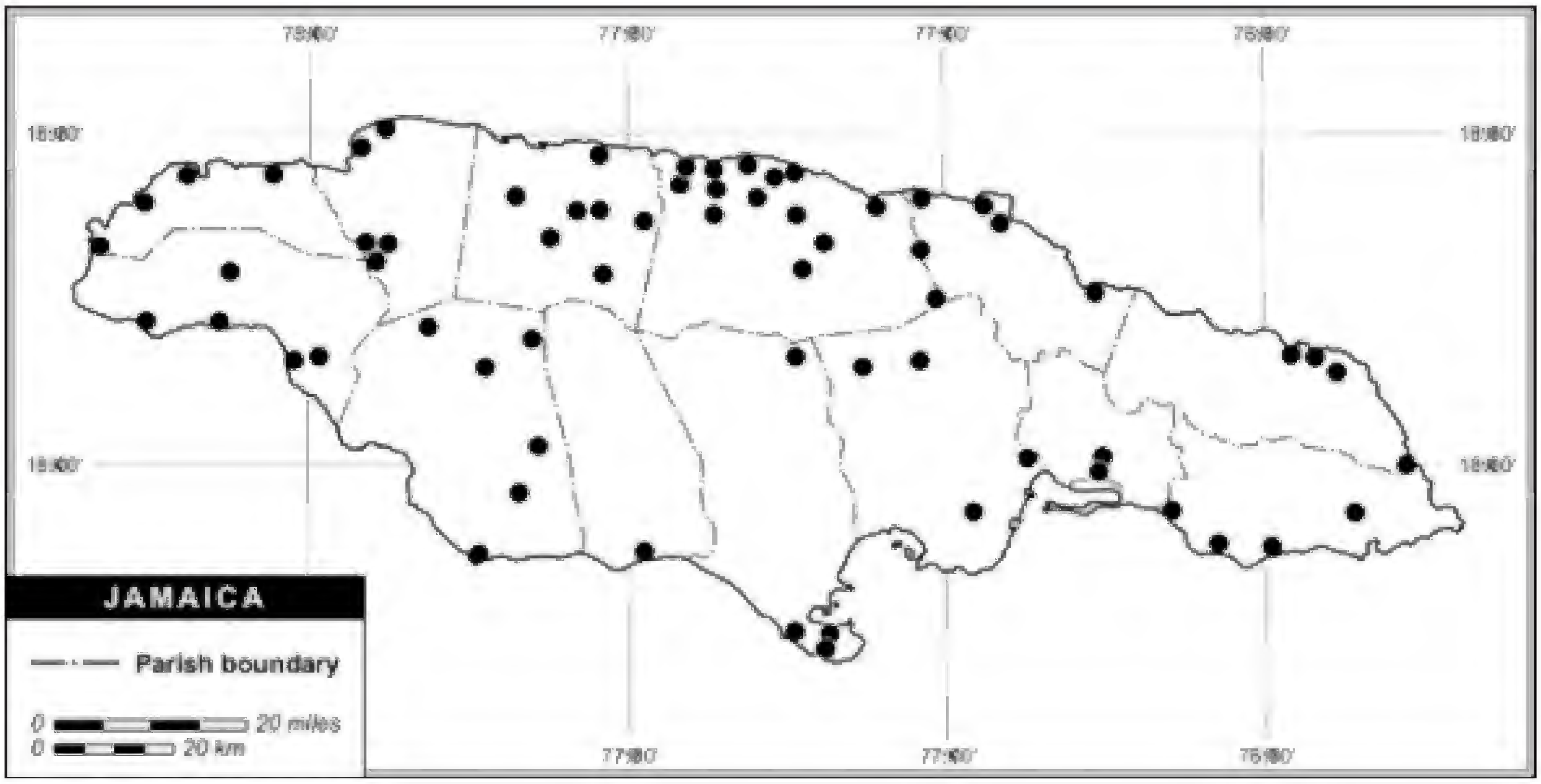

Figure 49. Map of Jamaica showing the locations where specimens of the Jamaican fruit-eating bat, *Artibeus jamaicensis*, have been collected.

a specimen that he obtained at Content, Westmoreland Parish.

As early as Dobson (1878), all three of these taxa were being treated under a single scientific name, *Artibeus perspicillatus.* Tomes (1861a) was the first to apply this name to Jamaican bats because he believed that the Linnean name *Vespertilio perspicillatus* should be applied to this species. This name of Linneaus is currently applied to *Carollia perspicillata* (see Pine 1972, for a discussion of the complicated nomenclatural history of this Linnean name) and thus is not available to apply to this species of *Artibeus.* The confusion over the appropriate name to apply to *A. jamaicensis* persisted for a number of years as illustrated by Allen and Chapman (1897) and Miller and Rehn (1901). Oldfield Thomas (1901) was first to again use the name *Artibeus jamaicensis* for this taxon because he (Thomas 1892) had earlier determined that the specimen that formed the basis of Linneaus's name was in reality *Hemiderma* [= *Carollia*] *brevicaudatum.* It was under this name that Andersen (1908) revised the species. Andersen (1908) gives a detailed description of the external (Fig. 50), cranial, and dental characteristics of the species, but this must be used with caution because at least two species—*A. jamaicensis* and *A. lituratus*—form the basis of his description. Nevertheless, the name used by Andersen (1908), *Artibeus jamaicensis jamaicensis*, remains the appropriate scientific name to apply to the Jamaican population.

Morphometrics.—Measurements of 10 males from 4 mi. E Runaway Bay and 10 females from Duanvale and Port Antonio are given in Table 2. Comparing the measurements of the sexes revealed that this species does not exhibit secondary sexual variation in size. The sexes did not evince significant differences in size in any of the measurements tested; however, females averaged larger than males in all but three measurements. Males averaged larger than females in length of the maxillary toothrow and the sexes

Figure 50. View of the head of *Artibeus jamaicensis*.

had the same means for postorbital constriction and palatal length.

Rehn (1902c) gave external measurements of a specimen from Port Antonio. G. M. Allen (1908) gave the external and wing measurements of a specimen from Kingston. Andersen (1908) gave the external and cranial measurements of 21 specimens from Jamaica. Swanepoel and Genoways (1979) reported the forearm and seven cranial measurements of two females and two males from Jamaica. Carter and Dolan (1978) gave wing and cranial measurements for the holotype of *Artibeus carpolegus* Gosse 1851 from Content, Jamaica, length of forearm for the holotype of *Madatœus lewisii* Leach 1821, and selected wing measurements for the holotype of *Artibeus jamaicensis* Leach, 1821.

Natural history.—The Jamaican fruit bat is the most widespread and common of the frugivorous species occurring on Jamaica, which reflects its abundance and widespread distribution elsewhere in the Neotropics. We are in agreement with McFarlane (1986) that *A. jamaicensis* is not an obligate cave dweller on Jamaica; however, these bats do make extensive use of caves and rock shelters for roosting sites. Goodwin (1970) seldom found other species of bats sharing roosting sites with *Artibeus*, which might be because this species roosts in areas where considerable light penetrates. Goodwin (1970) did not find the species in the three largest caves he visited—Oxford, St. Clair, and Windsor. Our survey of museum collections found only a single specimen labeled as coming from St. Clair Cave and only eight from Windsor Cave, including six taken during our field work. These latter specimens were netted at night at the entrance to the cave.

Descriptions of a series of caves used solely by *Artibeus* as a roost will illustrate the types of cave habitats sought by Jamaican fruit bats. Big Bottom Cave (cave 82) is a dry passage cave about 200 m in length. The passage is up to 12 m high. This is probably Cambridge Cave of Anthony (1920) according to Fincham (1997)—Anthony stated it was located 2 1/2 miles from Cambridge in a northeastern direction. Chesterfield Cave (cave 267) is a complex-type of cave that is about 245 m in length. The primary part of the cave is reached from the large descending entrance to the boulder-strewn chamber where the bat colony is located (Fincham 1997). Cousin's Cave (called Cousin's Cove Cave; cave 359) is a labyrinth-type cave about 300 m long. The cave has two branches that are up to 25 m wide—the west branch is flooded in areas and the east branch was mined for guano between 1944 and 1960 (Fincham 1997). Drum Cave (cave 737) is a large complex-type cave in the Jackson's Bay area. The total length of the cave is over 600 m. The cave has four entrances, which interconnect to a number of chambers and passages. Parts of the cave were recently excavated for fossils. McFarlane et al. (2002) found fossil guano deposits in Drum Cave that aged from as old as 11,980±80 at the base of Guano II layer to as young as 10,250±80 at the surface of Guano I layer. Ferry Cave (cave 963) is a shelter cave in a cliff beside the Ferry River (Fincham 1997). In this cave, Goodwin (1970) found bats roosting in an area where they could be seen without the aid of a flashlight. Norwood caves are probably the same as the Norwood Ratbat Hole (cave 201), which is a dry passage cave about 135 m in length. A 30 m deep collapsed entrance leads to a large passage up to 20 m wide (Fincham 1997). Guano deposits would indicate that the roosting area for bats was found near the entrance to the passage. Ramble Bat Hole (cave 722) is a dry passage cave that has a slippery descent to a level passage with a large bat colony [probably *Artibeus*] and much guano (Fincham 1997). Thunder Cave (cave 400) is a silt-floored dry passage cave about 45 m in length. The cave is a tubular passage about 3 m in diameter with smooth walls sloping up to a terminal chamber (Fincham 1997). Wondrous Cave (cave 354) is a complex type of cave with a length of about 430 m. The cave has four entrances and a cliff window reached by a relatively level floor. The bats evidently enter and exit the cave through the large ratbat entrance, which is to the left of the main entrance (Fincham 1997). Worthy Park Cave-1 (Water Sink Caves and Lluidas Vale Cave; cave 234) is a dry passage cave that extends for about 125 m. The large cliff-face entrance leads into three dry chambers. A large number of sprouting seeds were found in the final chamber, indicating that this was the *Artibeus* roost area (Fincham 1997). Dávalos and Erikkson (2003) found that the Ratbat Cave at Little Bay provided a day roost for "hundreds" of *Artibeus* and no other species when it was visited on 5 December 2001. This is a large cave with an entrance that is 25 m wide and 3 m high leading to a chamber that is 75 m in diameter. The authors believe that the exposure and light conditions made the cave unsuited for other species of bats. Cruz (1976) reported two bats without specifying the species as part of the diet of the American Kestrel (*Falco sparverius*) in a study conducted in the Worthy Park area. These two bats constituted 5.8% of the biomass taken by the kestrels.

The holotype of *Artibeus carpolegus,* which we now know represents *A. jamaicensis*, was captured by Gosse (1851) at Content, Westmoreland Parish. He believed that the bat had a "predilection for the luscious naseberry" (*Manilkara zapota*), which flowers and produces fruit throughout the year.

Osburn (1859a, 1865) is the first to write extensive natural history notes for this species on Jamaica. He found Jamaican fruit bats to be abundant in Mahogany Hall Cave in Trelawny Parish where the floor of the cave was covered with kernels of breadnut (*Brosimum alicastrum*), which were germinating in the piles of guano. In a small cave near Montego Bay, Osburn found them roosting in a place with sufficient light for him to shoot specimens. Here the floor was strewn with the pits of the clammy cherry (*Cordia collococca*). Near Kinloss, Trelawny Parish, Osburn discovered a colony of *Artibeus* in the narrow crevices and solution hole in the ceiling of a rock overhang. The rock overhang was about 6 m high and the hollowed out area at the base was about 2.5 to 3 m deep. Osburn realized that bats were present because he found a pile of "dried seed, berries, husks, with some fresh ones on top," and bat guano. Among the food items that he was able to identify were unripe mangoes (*Mangifera indica*) and pieces of rose apple (*Syzygium jambos*) fruits, which are 3 to 6 cm in diameter, light yellow in color, and rose scented. Osburn (1865) concluded that *Artibeus* "certainly does not seem such a lover of darkness as the generality of the family." This thought was further strengthened when Osburn later found members of this species at Aquatta Vale [not precisely located but believed to be in the vicinity of Dover in extreme northeastern St. Mary Parish] roosting under the fronds of coconut palms (*Cocos nucifera*). Osburn observed that bats were so tightly clustered "that at a single shot I brought down twenty-two, while many flew off and took refuge in the neighbouring tree." When he examined the stomachs and intestines of some of these individuals, he found seed that he believed were from the fruits of the fustic tree (*Chlorophora tinctoria*).

Sanderson (1941) described the capture of Jamaican fruit bats at Constant Spring and near Sherwood Forest. At both locations, these bats were taken in cave-type situations; however, at Constant Spring (see also Hershkovitz 1951) the bats were located in an area of an overhanging cliff into "which road workers had burrowed to get stones and lime. The place was full of daylight, but never the less several dozen large bats hung chattering in clusters . . ." Near Sherwood Forest *Artibeus* were captured in a "perfectly enormous cave" with crumbling limestone walls.

Goodwin (1970) found *Artibeus* hanging in small loose clusters or singly from the high entrances of smaller cave systems. The one exception was a small cave in the Worthy Park area where a colony of about 30 individuals was found in a small room about 68 m from the entrance. The populations of Jamaican fruit bats varied from one to 30 in the seven caves that Goodwin (1970) visited, with a sex ratio of about one male to two females. In several caves Goodwin found the seeds of cabbage bark tree (*Andira inermis*) littering the floor in some cases to the depth of several inches. Goodwin (1970) believed that "fruits of this tree are a staple food of *Artibeus*, at least during the winter months." The bats were bringing the fruits, which are ellipsoid in shape and 3.5 cm long, into the cave to eat the fleshy pericarp and then dropping the seeds.

Our experience using mist nets away from caves on Jamaica was that anywhere a net is set at an elevation under 1000 m that catches bats, it will take *Artibeus jamaicensis*. We caught them over water and in areas having fruiting trees. Jamaican fruit bats were taken over rivers that they were using as flyways (Flint River, near Drapers, and 4 mi. E Runaway Bay) and over ponds (2.5 mi. W Kellits, Queenhythe, and 1/2 mi. S, 1/2 mi. W Runaway Bay). Whether the bats were coming to drink at the rivers and pond or simply moving through the area was difficult to determine. The area 4 mi E Runaway Bay where a large series of these fruit bats was obtained is typical of these situations. This was an area of gallery forest that was about 100 m wide, with a fast moving stream running over waterfalls and among many large boulders and fallen trees. Beyond the gallery forest on both sides of the stream were open sugarcane fields. The gallery forest was composed of many large trees, including blue mahoe, white cedar, silk cotton trees, hog gum, breadnut, naseberry, and large stands of bamboo (Fig. 51). Jamaican fruit bats also were abundant in commercial and local fruit orchards containing many imported species that we visited including Circle B Plantation, Duanvale, Wakefield, and Yallahs. At Orange Valley and Bluefields, they were visiting native fruit trees in the vicinity of nets.

The reproductive cycle of mainland populations of this species have been extensively studied. These populations have a bimodal polyestrous cycle in which a peak of parturition occurs in March and April and a second peak occurs in July and August. Testes size also has been shown to follow reproductive activity in males (Wilson 1979). There have been no extensive studies of island populations of *A. jamaicensis* to determine if they follow a similar reproductive cycle.

Males taken on 6 January and 28 March had testes lengths of 4.5 and 6, respectively. The field collectors judged 10 adult males taken at the Ratbat Hole on 23 March 2003 to be in "reproductive condition" (Dávalos and Erikkson 2003). Twenty-one males taken between 3-12 July had testes that averaged 4.3 (3-10) in length. Fifteen males taken between 24-31 July had testes that averaged 5.8 (3.5-9) in length. Males taken on 3 August had testes lengths of 7.8, 8, 8, and 9.8. Ten males taken on 3 November had testes that averaged 7 (4.5-9) in length and seven taken on 13 December averaged 6 (4.5-7). Males taken on 26 December had testes lengths of 3.2, 4, 4.8, and 5.2.

Five of nine females captured by Goodwin (1970) between 7 and 24 January were pregnant with embryos that averaged 21.6 (12-26) in crown-rump length. McNab (1976) found five females to be in late pregnancy, one in early pregnancy, and three to be non-pregnant when captured in the Worthy Park area between 23 February and 2 March. All six females captured on 17 March were pregnant with embryos that averaged 34.5 (31-38.2) in crown-rump length.

Figure 51. Photograph of a portion of the stream and surrounding gallery forest at 4 mi E Runaway Bay, St. Ann Parish, Jamaica.

Of 43 bats netted on 27 April, six were females of which five were lactating and one evinced no gross reproductive activity. Single females taken 28 March and 28 April were recorded as carrying newborn young when captured. Of the 63 females captured between 3 and 12 July, 32 were carrying embryos that averaged 23 (7-35) in crown-rump length and an additional seven of the females were noted as having an enlarged uterus and probably had recently given birth. The remaining 24 female evinced no gross reproductive activity. The same was true of a female taken on 17 July. Of 27 females captured between 24 and 31 July, seven were pregnant with embryos that measured 24.9 (9-40) in crown-rump length, whereas the remaining 20 females evinced no gross reproductive data. Of 10 females taken between 1 and 9 August, seven evinced no gross reproductive activity, one was lactating, and three carried embryos that measured 3.2, 26.3, and 35 in crown-rump length. Five females taken on 1 November, five taken on 3 November, and seven taken 13-15 December evinced no gross reproductive data.

Immature individuals with open phalangeal epiphyses were taken on the following dates (length of forearm, when available, in parentheses): 28 March, 2 individuals; 29 March, 1; 27 April, 9 (34.5, 39.0, 45.0, 45.0, 49.2, 55.0, 58.5, 59.5, 60.0); 6 May, 1; 16 May, 3; 27 May, 1 (44.0); 23 June, 2 (58.8, 59.3); 3 July, 1; 5 July, 2 (54.5, 57.0); 29 July, 4 (35, 37, 39.4, 43); 31 July, 6; 1 August, 1; 2 August, 4 (34.8, 35.8, 37.9, 38.0); 3 August, 5; 9 August, 1; 1 November, 3 (48.6, 49.1, 59.8); 26 December, 1. The individuals with forearm lengths of 34.5, 39.0, and 44.0 were noted as being unfurred. The individuals with forearm lengths of 45.0, 48.6 and 49.1 were lightly furred. The individual with a forearm length of 59.8 was fully furred and matched adults in appearance.

On Jamaica, there are pregnant females present in January, February, and March and in July and August. Parturition should be occurring in March, April, and early May and in July, August, and September. The only individual that does not seem to fit within this pattern is the juvenile taken on 26 December. These data would indicate that the reproductive cycle of Jamaican fruit bats on Jamaica is similar to that of the Central American mainland. Clearly, young are being produced twice a year and the pattern that this follows most closely is bimodal polyestry (Wilson 1979).

Studying the annual variation in fat reserves of eight species of bats on Jamaica, McNab (1976) found that *Artibeus jamaicensis* had significantly less fat deposits in the dry season as compared with the wet season. A female captured on 7 January weighed 37.4.

Specimens from the following localities were from cave deposits: cave near Cambridge; Dairy Cave; Eleven Mile; Ferry Cave; Healthshire Hills; Hutchinson's Meadow Cave; Money Cave; Montego Bay (5 UF); Peru Cave; Seven-Rivers Cave; Wallingford Cave. It is believed that these deposits resulted from weathered owl pellets (Koopman and Williams 1951; Williams 1952). McFarlane et al. (2002) report fossil and subfossil remains of *Artibeus* from the Jackson's Bay caves that were approximately 10,000 years old. McFarlane and Garrett (1989) reported a minimum of 16 individuals of *Artibeus jamaicensis* from modern Barn Owl (*Tyto alba*) pellets found in caves in the Jackson's Bay area. This species constituted 19.5% of the non-rodent remains found in the pellets.

Jamaican *A. j. jamaicensis* lack the upper third molar (M3), which is a geographically variable characteristic (Genoways et al. 2001). The lower third molar (m3) is generally present in these bats. In 46 individuals examined for the presence of m3, these teeth were missing in both left and right dentaries in two individuals (TTU 21844, CM 110280) or 4.3% of the sample. The m3 was missing only in the left dentary in one additional specimen (TTU 21806) or an additional 2.1% of the sample. Because there is a geographic pattern to the presence or absence of third molars, it has been assumed for many years that this variation has a genetic basis. Not surprisingly, therefore, we now know that the dental data are consistent with genetic data obtained from studying mitochondrial DNA. This is an important observation because the mitochondrial genome does not control dental development and therefore is an independent marker.

Genetics.—The karyotype of *A. jamaicensis* has 2n = 30 females, 31 males, and FN = 56 (Fig. 52). There are 28 biarmed autosomes in a graded series from large to small; four medium-sized pairs are subtelocentric, and the remaining pairs are metacentric. The X is medium-sized and submetacentric, the Y1 is small and subtelocentric, and the Y2 is minute and acrocentric. Karyotypes were obtained from one male and one female from 0.5 mi. S, 0.5 mi. W Run-

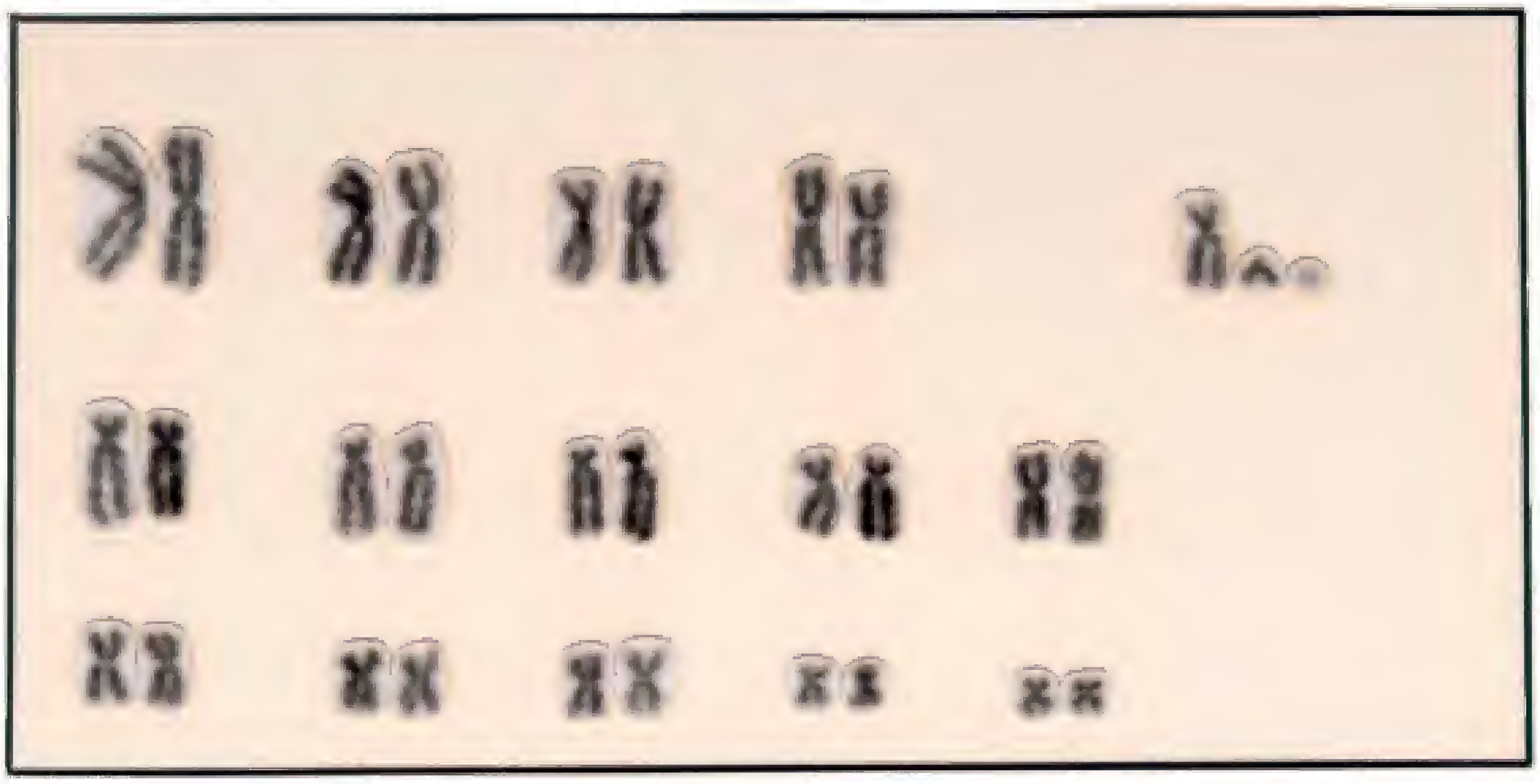

Figure 52. Karyotype of a male *Artibeus jamaicensis* from 4 mi E Runaway Bay, St. Ann Parish (TK 8051; TTU 21820).

away Bay, and four males and one female from 4 mi. E Runaway Bay.

The karyotype of this species was first reported by Baker (1967) from Mexican populations. The karyotype of *A. jamaicensis* appears identical to those reported for seven other species in the genus (Baker 1979). G- and C-band studies were reported by Baker et al. (1979) and revealed the karyotype of *A. jamaicensis* is nearly identical to that of the genus *Sturnira*, differing only in the centromere position of one pair of small autosomes. Heterochromatin is restricted to the centromeric area in *A. jamaicensis*.

Valdivieso and Tamsitt (1974) and Straney et al. (1979) conducted studies of biochemical genetics in *A. jamaicensis*. Straney et al. (1979) sampled 3 localities on Trinidad and reported 24% of the loci examined to be polymorphic and the average heterozygosity to be 0.80. *Artibeus jamaicensis* on Trinidad had the highest average heterozygosity among six phyllostomid species studied or reported in the literature. This finding is consistent with the genetic variation calculated from restriction site polymorphism in mitochondrial DNA recovered from bats living on Grenada, which is just to the north of Trinidad (Pumo et al. 1988; Phillips et al. 1989). The genetic variation in *A. jamaicensis* in the southern-most Caribbean might be the consequence of multiple arrivals of distantly related individuals rather than genetic diversity intrinsic to the southern islands (Phillips et al. 1989; Pumo et al. 1996). Alternatively, it might be the case that our concept of *A. jamaicensis* as a single species in the Caribbean needs to be reconsidered. Mitochondrial DNA data from St. Vincent might support this alternative explanation (Pumo et al. 1996).

A considerable number of scientists have directly investigated or even speculated on the history of *Artibeus jamaicensis* in the Caribbean. These fruit bats have been a popular topic because (a) they usually are common and easy to collect, (b) they vary morphologically across the Antilles, and (c) they were thought to be common on the adjacent Mexican, Central American, and South American mainland. The first two points are valid, but the third "given" might not be supported by genetic analyses of *A. jamaicensis*-like bats from the mainland. In northern South America specimens of bats traditionally identified as *jamaicensis* or *jamaicensis*-like probably represent an unknown number of morphologically similar species. Genetic data from the bats living on Jamaica and the Yucatan peninsula of Mexico support the hypothesis that the Jamaican population was probably derived fairly recently (Late Pleistocene) from Mexico or Central America (Phillips et al. 1991). Indeed, the data basically support a zoogeographic explanation in which the bats first spread through the Greater Antilles and only recently dispersed as far south as Grenada in the Lesser Antilles. In the southern Caribbean, the northern Antillean *A. jamaicensis* overlap with distantly related South American relatives. Interbreeding apparently occurs, at least in some places, but it also is possible that several non-interbreeding species are involved in this complex story (Pumo et al. 1996).

On Jamaica, the genetic data and the fossil evidence are consistent: *A. jamaicensis* from the Mexican or Central American mainland probably arrived late in the Pleistocene, possibly about 12,000 years ago. In a Caribbean geological and ecological context, these fruit bats are clearly "new" to the scene, especially in comparison to the fruit bat genera endemic to the Antilles.

Finally, because *Artibeus jamaicensis* is commonplace on Jamaica, specimens collected from there (and Puerto Rico) were the basis for sequencing the entire mitochondrial genome (Pumo et al. 1998). Thus, this species was the first bat for which the genome structure and entire sequence were determined.

Salivary glands.—The histochemistry and ultrastructure of salivary glands of bats in the genus *Artibeus* have been used as models for comparison to other bat species (Phillips et al., 1977; Phillips and Tandler, 1987; Phillips et al., 1993; Phillips, 1996). Acinar secretory cells in the submandibular salivary gland in species of *Artibeus* produce a product that exhibits species-specific substructure, apparently as a reflection of species differences in the secretory proteins (Tandler et al., 1986).

Remarks.—The locality Agualta Vale is spelled Aguatta Vale in the catalogue of the British Museum and Osburn (1865). A place with either of these spellings is not found on current maps or gazetteers. These specimens were obtained by W. Osburn (1860) and his description of the site permits a relatively close determination of its geographic location on the island. The name of this estate is Agualta Vale from the Spanish name for the area and river "Agua Alta." The English name for this river is the Wag Water River, which empties into Annotto Bay just to the west of the town of this name. This places the locality in St. Mary Parish. Osburn's description indicates that the estate is not on the narrow coastal plain in this area, but is along the steeply rising highlands inland from the town, but close enough to see the masts on the ships in Annotto Bay. The locality probably is not far from the modern town of Chovey.

Natalus micropus micropus Dobson, 1880
Cuban Funnel-eared Bat

Specimens examined (241).—CLARENDON PARISH: near end Jackson's Bay [17°44'N, 77°14'W], 2 (ROM); North Kellits, 1 (IJ). HANOVER PARISH: Lucea, 1 (AMNH). MANCHESTER PARISH: Oxford Cave, Balaclava [given as St. Elizabeth Parish], 7 (3 AMNH, 4 BMNH). PORTLAND PARISH: Paradise, 1 (UF); Port Antonio, 4 (NMNH). ST. ANDREW PARISH: environs of Kingston, 1 (BMNH [holotype]). ST. ANN PARISH: Moneague, 1 (NMNH). ST. CATHERINE PARISH: Bog Walk, 1 (FMNH); St. Clair Cave, 2 mi. S Ewarton, 191 (1 AMNH, 33 CM, 4 COLU, 6 HZM, 4 IJ, 7 JMM, 42 ROM, 88 TTU, 6 UF). ST. JAMES PARISH: Montego Bay, 2 (NMNH). TRELAWNY PARISH: Mahogany Hall Cave [18°23'N, 77°28'W], 1 (BMNH); Windsor Cave, 26 (3 FMNH, 22 NMNH, 1 TTU). PARISH UNKNOWN: no specific locality, 2 (NMNH).

Additional record.—WESTMORELAND PARISH: Monarva Cave (McFarlane 1985, 1986, 1997).

Distribution.—Figure 53 shows the collecting localities for *Natalus micropus* on Jamaica. The Cuban funnel-eared bat can be expected throughout Jamaica at low to intermediate elevations; however, nowhere is the species abundant except in direct association with three major caves—Oxford, St. Clair, and Windsor. The species *N. micropus* occurs only on the three largest islands in the Greater Antilles, with the nominate subspecies being found on Jamaica and Hispaniola (Ottenwalder and Genoways 1982).

Systematics.—The small-sized bats of the *Natalus micropus*-complex were reviewed by Ottenwalder and Genoways (1982). Varona (1974) and Hall (1981) had treated the four nominal taxa in this complex as subspecies of a single species under the name *Natalus micropus.* However, Ottenwalder and Genoways (1982) demonstrated that two species—*N. micropus* and *N. tumidifrons*—should be recognized based on the much larger size of *N.*

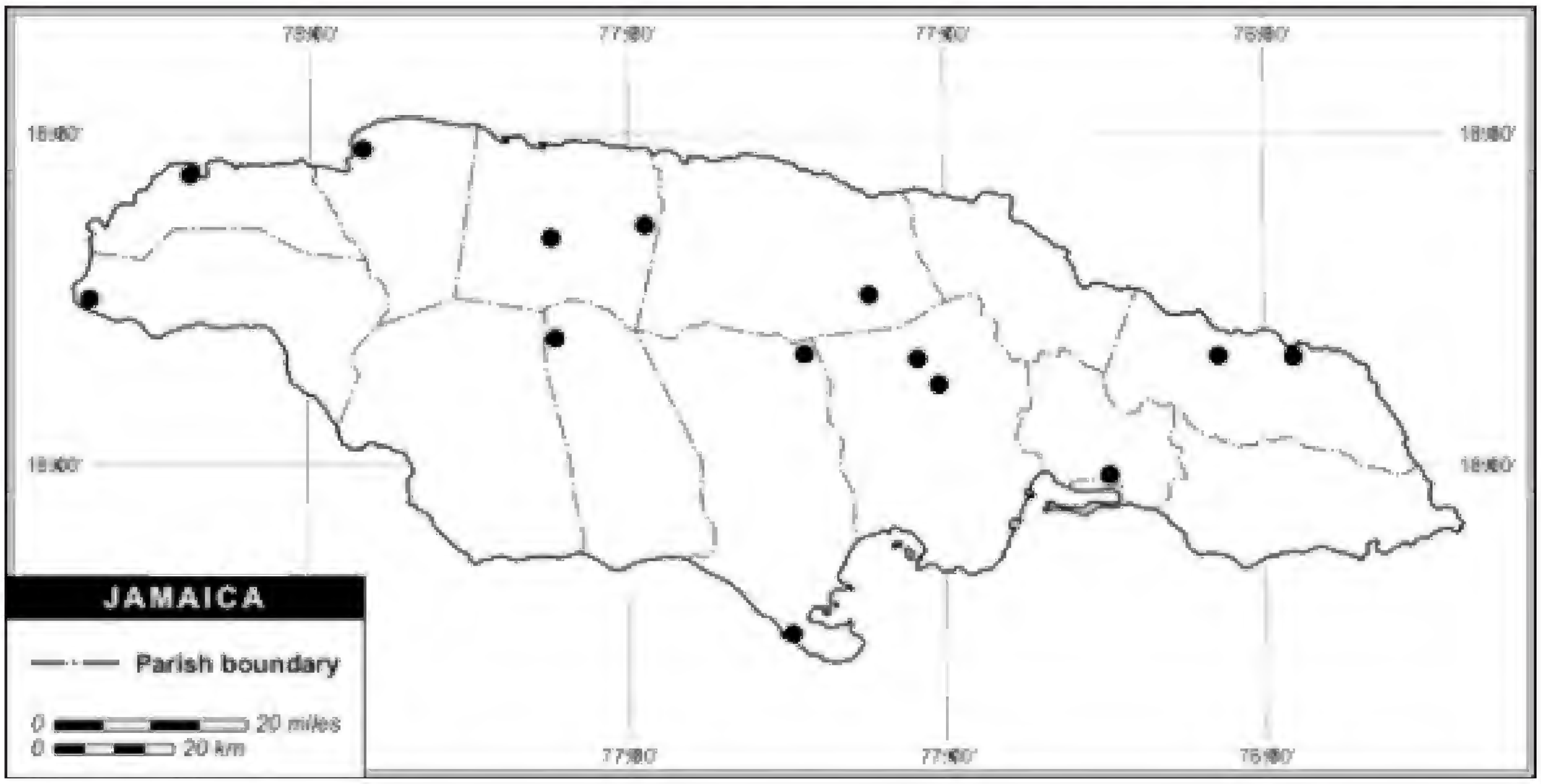

Figure 53. Map of Jamaica showing the locations where specimens of the Cuban funnel-eared bat, *Natalus micropus*, have been collected.

tumidifrons, which exhibited no overlap in the range of half or more of the measurements with samples of *N. micropus*. *N. tumidifrons* occurs only in the Bahamas and is monotypic.

Ottenwalder and Genoways (1982) recognized two subspecies within populations of *N. micropus*—*macer* and *micropus*. These two subspecies can be distinguished based on the longer length of phalanx 1 (digit III) and a relatively shorter forearm length of the Cuban populations representing *N. m. macer*. Populations from Jamaica, Hispaniola, and Old Providence Island are assigned to nominate subspecies *N. m. micropus*, originally described by Dobson (1880) from the environs of Kingston.

Morphometrics.—Table 3 presents the external and cranial measurements of 10 males and 10 females from St. Clair Cave. Significant secondary sexual variation was found only in greatest length of skull ($P = 0.05$) and condylobasal length ($P = 0.01$). In both of these measurements, females averaged larger than males. Ottenwalder and Genoways (1982) found females to be significantly (P 0.05) larger than males in length of forearm. Of the remaining measurements, females in our sample averaged slightly larger in four of which two are measurements of cranial length—length of forearm, mastoid breadth, palatal length, and length of maxillary toothrow. The sexes averaged the same in four measurements of cranial breadth—zygomatic breadth, interorbital breadth, postorbital constriction, and breadth across upper molars. Ottenwalder and Genoways (1982) found relatively low levels of individual variation in a sample from Jamaica, with the coefficient of variation ranging from 1.3 for greatest length of skull for a sample of 38 females to a high of 3.8 for postorbital breadth for a sample of 16 males.

Miller (1898) gave the external measurements of two males and a female from Jamaica. Ottenwalder and Genoways (1982) gave values for three external and nine cranial measurements for a sample from Jamaica. External and cranial measurements of the male holotype (BMNH 80.12.14.1) from the environs of Kingston are as follows: length of forearm, 33.5; greatest length of skull, 14.5; condylobasal length, 13.3; zygomatic breadth, 6.5; interorbital breadth, 3.4; postorbital constriction, 2.6; mastoid breadth, 6.3; palatal length, 7.1; length of maxillary toothrow, 6.1; breadth across upper molars, 4.4.

The two species of *Natalus* occurring on Jamaica easily are distinguished by size alone (Fig. 54). None of the *Natalus micropus* had a length of forearm

Table 3.—Length of forearm and nine cranial measurements for two species of the family Natalidae and two species of the family Vespertilionidae occurring on Jamaica.

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
				Natalus micropus micropus						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	34.1	14.3	13.2	6.7	3.4	2.7	6.3	7.3	5.9	4.3
Minimum	33.6	14.1	13.0	6.4	3.2	2.6	6.2	7.0	5.8	4.1
Maximum	34.8	14.6	13.6	6.8	3.5	2.8	6.4	7.8	6.0	4.5
SE	±0.13	±0.06	±0.06	±0.03	±0.04	±0.02	±0.02	±0.10	±0.02	±0.04
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	34.5	14.5	13.5	6.7	3.4	2.7	6.4	7.4	6.0	4.3
Minimum	33.6	14.4	13.3	6.4	3.2	2.6	6.3	6.9	5.9	3.8
Maximum	35.9	14.8	13.7	6.7	3.6	2.8	6.5	8.0	6.1	5.0
SE	±0.24	±0.04	±0.04	±0.03	±0.04	±0.02	±0.03	±0.10	±0.02	±0.10
				Natalus stramineus jamaicensis						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	44.4	17.8	16.1	9.1	4.7	2.9	7.9	9.9	7.9	5.8
Minimum	43.7	17.3	15.6	8.8	3.5	2.8	7.6	9.4	7.6	5.4
Maximum	45.8	18.2	16.6	9.5	5.1	3.0	8.2	10.2	8.1	6.1
SE	±0.23	±0.10	±0.10	±0.08	±0.15	±0.03	±0.06	±0.06	±0.05	±0.7
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	44.3	17.6	15.9	9.0	4.7	2.9	7.8	9.7	7.7	5.7
Minimum	43.7	17.2	15.6	8.6	4.2	2.8	7.6	9.2	7.5	4.9
Maximum	45.0	18.0	16.2	9.3	5.1	3.0	8.1	10.1	7.8	6.1
SE	±0.16	±0.08	±0.06	±0.07	±0.08	±0.03	±0.06	±0.10	±0.04	±0.11
				Eptesicus lynni						
Males										
N	5	5	5	4	5	5	5	5	5	5
Mean	44.5	16.5	15.3	10.6	6.1	4.0	8.4	7.3	5.8	6.6
Minimum	43.2	15.9	14.7	10.1	5.8	3.9	7.8	6.1	5.5	6.4
Maximum	46.0	17.1	15.8	11.1	6.3	4.0	8.7	8.0	6.0	7.0
SE	±0.54	±0.21	±0.19	±0.21	±0.09	±0.02	±0.17	±0.36	±0.09	±0.12

Table 2. (cont.)

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
				Eptesicus lynni						
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	46.6	17.3	16.3	11.5	6.4	4.0	9.1	8.3	6.1	7.0
Minimum	43.5	16.8	15.9	10.9	6.2	3.8	8.8	7.8	5.8	6.8
Maximum	48.3	17.7	16.7	12.0	6.7	4.2	9.3	9.3	8.5	7.5
SE	±0.46	±0.10	±0.10	±0.12	±0.04	±0.03	±0.05	±0.08	±0.05	±0.07
				Lasiurus degelidus						
Males										
TTU 22080	41.3	12.9	12.4	9.2	6.0	4.3	7.5	4.6	4.4	5.8
CM 44608	42.9	13.1	12.5	9.7	5.9	4.2	8.0	5.7	4.6	6.4
Females										
CM 44609	46.9	13.9	13.1	10.1	6.3	4.3	8.2	6.2	4.8	6.8
NMNH 96188 (holotype)	45.3	14.2	13.7	---	6.6	4.2	8.3	6.3	4.8	6.7

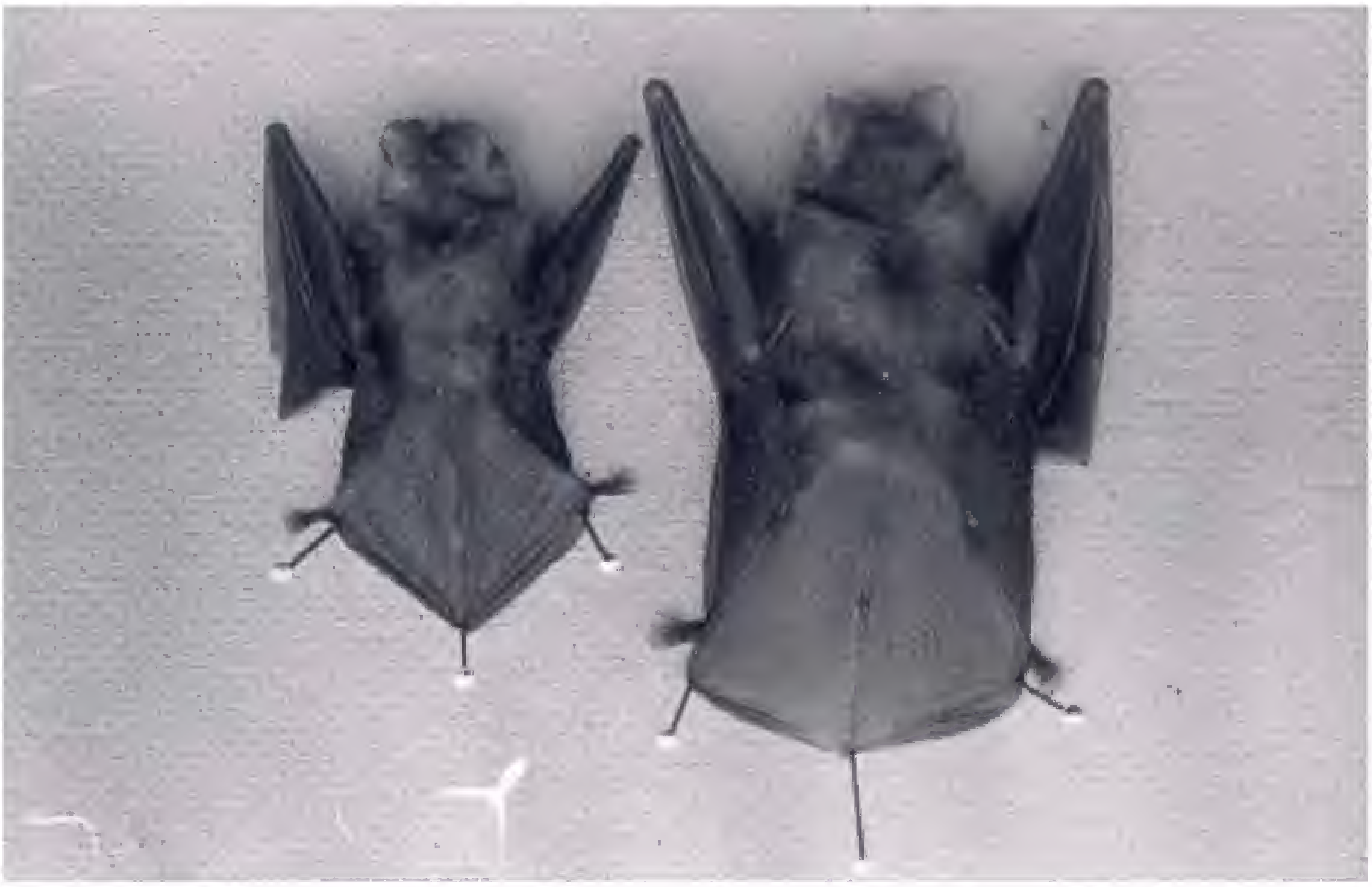

Figure 54. View of the dorsal surface of *Natalus micropus* (left) and *Natalus stramineus* (right) giving a comparison of their overall size.

over 36.0 and none of the *N. stramineus* had a measurement of less than 43.0. The same is true for greatest length of skull where the largest *N. micropus* is 14.8 and the smallest *N. stramineus* is 17.2 (Table 3).

Natural history.—We agree with McFarlane's (1986) conclusion that the Cuban funnel-eared bat (Fig. 55) is an obligate cave roosting species. However, we have records for the species from only five caves of which three—Oxford, St. Clair, and Windsor—are among the largest on the island. These caves are described elsewhere in this publication. McFarlane (1985) described the capture of this species in Monarva Cave (cave 142), which is a dry passage cave with a length of 305 m. A short drop-in entrance gives access to a steeply descending passage that leads to a series of low, guano-filled chambers (Fincham 1997). It was in these chambers that McFarlane captured specimens of *N. micropus* and *Molossus molossus*. He described the chambers as "filled with multitudes of bats". . . "The air temperature was noticeably elevated, humidity approached 100 percent, and . . . an uncomfortably high carbon dioxide concentration."

Osburn (1865) described capturing Cuban funnel-eared bats while in Mahogany Hall Cave catching *Artibeus*. He "discovered them clustering like bees in a little recess with a high domed roof. They seemed driven here by the larger Bats." In the Inferno Passage of St. Clair Cave, we found them forming similar clusters hanging from the ceiling. They appeared to form a single species cluster of 10 to 20 individuals, but they were in the main passageway and not in recesses. Specimens were easily captured in large numbers with the use of a small hand net. In contrast to our experience, Goodwin (1970) found a colony of 200 individuals in a ratio of three *N. micropus* to one *N. stramineus* roosting in a side chamber off of the Inferno Passage. The chamber was 6 m by 6 m and 3 m high and was located behind a ledge that was 4 m above the floor. Conditions in the chamber were similar to those in the Passage. Although both species were occupying the chamber, Goodwin (1970) believed that they were segregated into species flocks as they fluttered about the chamber. Goodwin's (1970) observation was that the bats did not form tight clusters when roosting, with 7 to 10 cm between individu-

Figure 55. View of the head of *Natalus micropus.*

als. When disturbed in the side chamber, the bats returned to the main passage where "they flew about in a relatively tight flock like a mass of large moths" (Goodwin 1970).

Our single specimen from Windsor Cave was taken in a short mist net set at one of the entrances to the cave. The specimen from Paradise was captured on 4 April 1965 when it flew inside of a house.

The reproductive data for *N. micropus* on Jamaica are very inadequate as are the data for the species in Cuba (Silva Taboada 1979). Males taken on 18 and 29 July had testes that were highly regressed and at best 10 males each had a testes length of 1. Four males taken by Goodwin (1970) on 29 December had testes that averaged 2.6 (2-3) in length. Of 75 females taken on 18 July, only two revealed gross reproductive activity and these were lactating. Fourteen females taken 29 July evinced no gross reproductive activity. A female taken by Goodwin (1970) on 29 December contained no embryo.

Four adult males captured on 23 December weighed 2.82, 2.90, 3.16, and 3.32 and two taken on 4 January weighed 2.3 and 2.6. A female weighed 2.88 when captured in St. Clair Cave on 23 December and one taken there on 4 January weighed 2.8. Osburn (1865) described the color polymorphism present in this species. At Oxford Cave he found individuals varying in color "from brownish grey to yellowish chestnut."

Genetics.—The karyotype of *N. micropus* has 2n = 36 and FN = 54 (Fig. 56). There are 20 biarmed autosomes in a gradual series, the smallest pair being distinctly subtelocentric, and 14 acrocentric autosomes. The X is medium-sized and submetacentric, the Y is minute and acrocentric. Karyotypes were obtained from a total of five males and four females from Windsor Cave and St. Clair Cave. The karyotype of *N. micropus* appears identical to that of *N. stramineus* discussed next.

Arroyo-Cabrales et al. (1997) used protein electrophoresis to study the relationships of mainland and

Figure 56. Karyotype of a male *Natalus micropus* from St. Clair Cave, St. Catharine Parish (TK 9447; CM44571).

island populations of *N. micropus* and *N. stramineus*. Thirty-four loci were examined of which 20 were variable within or between the species. They examined 10 specimens of *N. micropus* from St. Clair Cave and found five variable loci. They interpreted these limited data as indicative of a relatively low level of genetic variability for this species. Interspecific comparison to *N. stramineus*, however, showed that the specimens of *N. micropus* were well differentiated from the sample representing *N. stramineus.*

Salivary glands.—Phillips et al. (1998) used immunohistochemical techniques and light microscopy to look for the presence of a lysozyme-like enzyme in the salivary glands of *Natalus micropus* and 11 other bat species. In *Natalus micropus* some of the parotid gland intercalated duct cells and the demilune secretory cells of the submandibular gland were shown to exhibit lysozyme-like reactivity. Collectively, the comparative data from bats with divergent diets support the hypothesis that lysozyme might serve as a dietary chitinase in insectivorous species such as *Natalus micropus.*

Remarks.—The specimens in the British Museum (Natural History) from Oxford Cave and Mahogany Hall Cave were reported by their collector Mr. W. Osburn (1865) under the name *Lasiurus rufus*, but Tomes (1861a) reported the same specimens under the name *Natalus stramineus.* However, examination of four of the specimens (BMNH 7.1.1.546-549) from the former locality collected by Osburn on 22 February 1859 and one from the latter locality (BMNH 7.1.1.545) obtained on 24 November 1858 in the collections of the British Museum (Natural History) reveals that these individual are representatives of the current species, *Natalus micropus*.

Natalus stramineus jamaicensis Goodwin, 1959
Mexican Funnel-eared Bat

Specimens examined (109).—ST. CATHERINE PARISH: St. Clair Cave, 2 mi. S. Ewarton, 108 (3 AMNH [including holotype], 33 CM, 2 COLU, 1 FMNH, 2 IJ, 9 JMM, 4 ROM, 49 TTU, 5 UF). ST. ELIZABETH PARISH: Wallingford Cave, Balaclava, 1 (AMNH).

Additional record.—CLARENDON PARISH: Portland Cave-1 (McFarlane 1997).

Distribution.—Figure 57 shows the collecting localities for *Natalus stramineus* on Jamaica. This species has the most restricted distribution of any bat on the island; it is known for certain only from contemporary specimens from St. Clair Cave. The specimen from Wallingford Cave was recovered from a cave deposit and the occurrence of the species in Portland Cave is not verified by a voucher specimen.

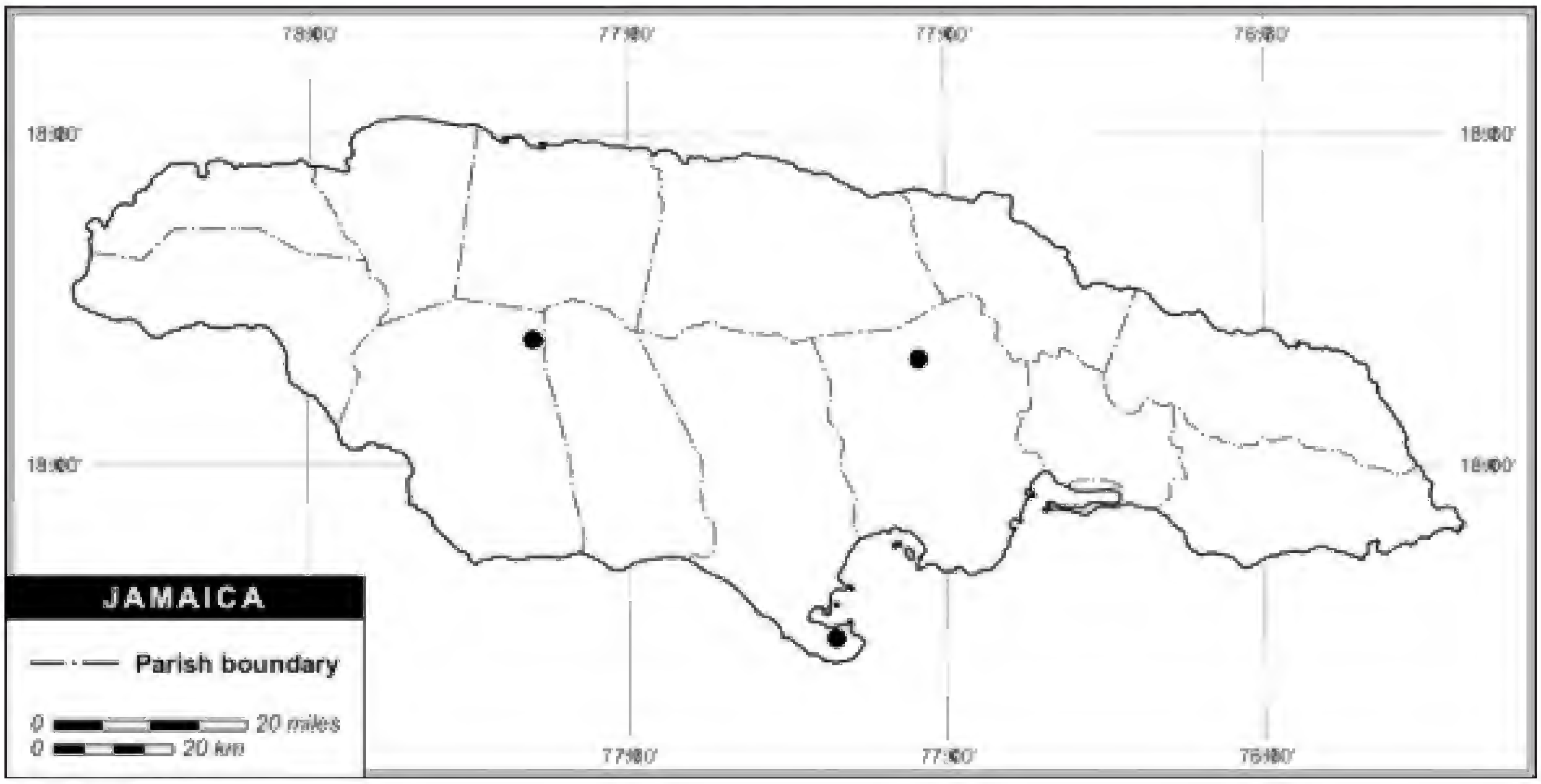

Figure 57. Map of Jamaica showing the locations where specimens of the Mexican funnel-eared bat, *Natalus strimineus*, have been collected.

On the Meso-American mainland *N. stramineus* ranges from the Mexican states of Sonora and Nuevo Leon to the north, southward into Panama. In South America, it occurs in possibly isolated populations in Venezuela and Brazil. It also is known from the three largest of the Greater Antillean islands and in the northern Lesser Antilles from Anguilla to Dominica (Goodwin 1959). The subspecies *N. s. jamaicensis* is endemic on Jamaica.

Systematics.—The systematic status of the large species of *Natalus* in the Greater Antilles is probably more uncertain than for any other bat species on Jamaica. The Antillean island populations were originally described by Miller (1902) under the name *N. major* based on two specimens from Hispaniola. Goodwin (1959) later described specimens from Jamaica under the name *Natalus major jamaicensis*. In this same publication Goodwin (1959) provided evidence that the type locality of *Natalus stramineus* was not Lagoa Santa, Minas Gerais, Brazil, and fixed the type locality as Antigua in the Lesser Antilles. Handley and Gardner (1990) made a more detailed investigation of this situation, but ultimately they agreed with Goodwin's decisions. Varona (1974) was the first author to treat the taxa associated with *Natalus major* as subspecies of *Natalus stramineus*, which also was done by Koopman (1975, 1993), Silva Taboada (1979), and Hall (1981), but not by Hoyt and Baker (1980). Arroyo-Cabrales et al. (1997) used genic data to study the relationship among island (*N. major*) and mainland (*N. stramineus*) populations. They concluded "that the allozymic data are conservatively interpreted as supporting subspecific recognition of *N. stramineus* occurring in the Greater Antilles to which the name *N. stramineus major* applies."

We tentatively use the name *Natalus stramineus jamaicensis* here. It should be fully recognized that the issues of the systematic relationships of the large-sized *Natalus* living in the Greater and Lesser Antilles are yet to be resolved. Morphometric analyses of specimens from the islands would be an excellent initial step and molecular genetic data obviously would be helpful.

Morphometrics.—Measurements of 10 males and 10 females of *N. stramineus* from St. Clair Cave are presented in Table 3. Significant ($P = 0.05$) secondary sexual variation was found only in length of maxillary toothrow, with males averaging larger. In two other measurements—interorbital constriction and postorbital constriction—males and females averaged the same. In the seven other measurements, males averaged slightly larger than females.

Goodwin (1959) presented length of forearm and eight cranial measurements for four males from St. Clair Cave. External measurements of two males and two females from St. Clair Cave were given by Hoyt and Baker (1980). External and cranial measurements of the male holotype of *Natalus major jamaicensis* Goodwin, 1959, are as follows: length of forearm, 45.2; greatest length of skull, 18.2; condylobasal length, 16.6; zygomatic breadth, 9.5; interorbital constriction, 5.1; postorbital constriction, 3.0; mastoid breadth, 8.0; palatal length, 10.1; length of maxillary toothrow, 8.1; breadth across upper molars, 6.0.

On Jamaica, some species of *Natalus* can be confused with species of *Pteronotus* in the field (Fig. 58). However, in *Natalus* the wing membranes attach lower along the sides than in *Pteronotus* and the pelage is long and lax in *Natalus*, whereas in *Pteronotus* the hair on the back is short and bristle-like. In *Natalus* the tail vertebrae extend to the posterior margin of the uropatagium, whereas in *Pteronotus* the distal portion of the tail vertebrae perforate and are free on the dorsal surface of the uropatagium near its center. Finally, the ears of *Natalus* are larger and rounded into a funnel-shape, in comparison the ears of *Pteronotus* are smaller and more lanceolate in overall shape.

Natural history.— St. Clair Cave is the only locality from which Recent specimens of *N. s. jamaicensis* (Fig. 59) are available. This fact led Goodwin (1970) and us to think that this species requires large caves with high humidity. This seems logical given the high surface to body mass ratio of this species. Moreover, its long limbs and large patagium probably are subject to rapid dehydration. At the same time, the locality record of this species from Portland Cave-1 reported by McFarlane (1997) does not support this idea because Portland Cave-1 (cave 6) is a dry passage cave approximately 150 m in length. The entrance leads to an arched tunnel extending about 75 m to the right and left. Guano was mined from this cave in the 1940s (Fincham, 1997). H. E. Anthony's 1920 daily journal described this area as "very dry and arid and the vegetation is about as xerophytic as any I

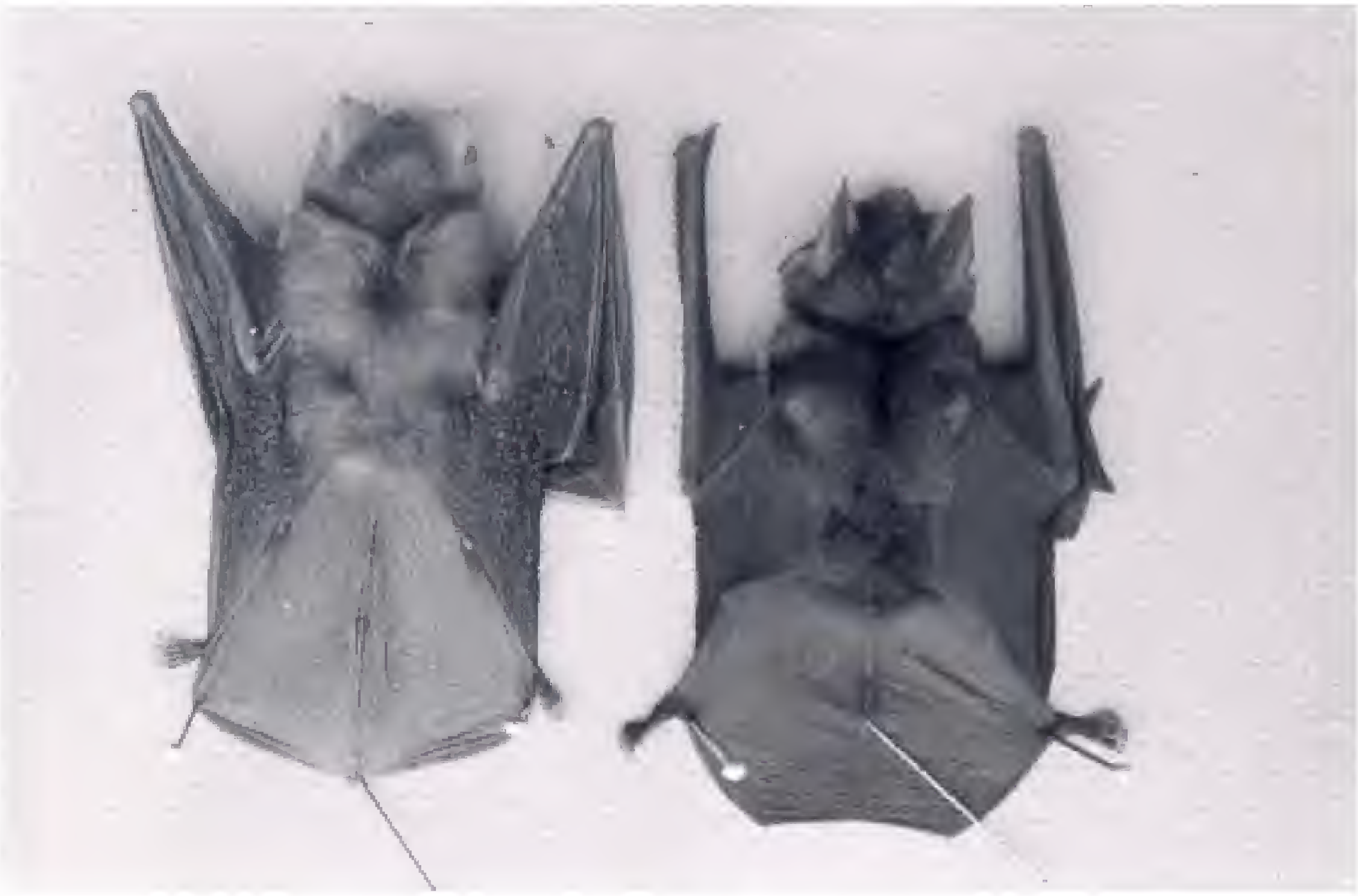

Figure 58. View of the dorsal surface of *Natalus stramineus* (left) and *Pteronotus macleayii* (right). Note that the tail vertebrae in *Natalus* extend to the posterior edge of the uropatagium, whereas in *Pteronotus* the distal portion of the tail vertebrae perforate the dorsal surface of the uropatagium near its center.

Figure 59. View of the head of *Natalus strimineus*.

have encountered on the island." The presence of a colony of *N. s. jamaicensis* in Portland Cave-1 is still uncertain because as far as we are aware no voucher specimen was preserved (also see Dávalos and Erikkson 2003, on this point). However, we do know that *N. micropus* occurs in this area because there are two voucher specimens from the Jackson's Bay area preserved in the Royal Ontario Museum. Perhaps, the individual seen by McFarlane (1997) was a *N. micropus* that was mis-identified as *N. stramineus*. Alternatively, it is difficult to understand how the much smaller *N. micropus*, which faces the same physiological dehydration problems, could survive in this xeric area and *N. stramineus* could not.

The environmental conditions in the Inferno Passage of St. Clair Cave are described in detail in the account for *Phyllonycteris aphylla*. Goodwin's (1970) description of his experience with this species and *N. micropus* is detailed in the account of the latter species. In the small side chamber where Goodwin found both species of *Natalus*, he believed that approximately 50 of the 200 bats present were *N. stramineus*. He found that *N. stramineus* congregated near to the entrance of this side chamber to rest singly with individuals about 7 to 10 cm apart, but they finally returned to the main passage with disturbance. We found them within the first 50 m of the Inferno Passage (Hoyt and Baker 1980) where they formed tight clusters so that several individuals were captured at one time in a hand net.

Twenty-five July-taken females showed no gross evidence of reproductive activity. Twenty males taken at the same time had testes that were noted as being highly "regressed" and not exceeding 1 in length. An adult female taken on 29 December did not contain an embryo (Goodwin 1970). Two males taken on the same date had testes that measured 2.5 and 3 in length. These scant reproductive data give no insight into the reproductive cycle of the species beyond documenting periods when reproduction is not occurring.

Two males taken on 23 December weighed 6.66 and 6.76 and two taken on 29 December weighed 6.0 and 6.5. Two females taken on 23 December weighed 6.83 and 7.28.

The record from Wallingford Cave is based on a partial left mandible (Koopman and Williams 1951). The specimen comes from the next to the oldest level of the cave's deposits. It is believed that these deposits originated from owl pellets.

Genetics.—The karyotype of *N. stramineus* has 2n = 36 and FN = 54 (Fig. 60). There are 20 biarmed autosomes in a graded series, the smallest pair being distinctly subtelocentric, and 14 acrocentric autosomes. The X is medium sized and submetacentric, and the Y is minute and acrocentric. Karyotypes were obtained from five males and one female from St. Clair Cave.

Baker and Jordan (1970) reported 2n = 36 and FN = 56 for *Natalus tumidirostris* from Trinidad. The karyotype of *N. stramineus* is apparently identical to that of *N. tumidirostris* but we interpret the second smallest biarmed chromosome in the figure reported by Baker and Jordan (1970) to be acrocentric. This reduces the FN to 54. The karyotype of *N. stramineus* from Mexico was reported by Baker (1970a) to be 2n = 36 and FN = 56. This differs from the karyotype of the Antillean populations of *N. stramineus* and *N. tumidirostris* by possessing an additional small biarmed pair and one fewer small acrocentric pairs. It is possible, however, that this could merely be due to a difference in interpretation of centromere position in the small chromosome.

Arroyo-Cabrales et al. (1997) used protein electrophoresis to estimate relationships among mainland and island populations of *N. micropus* and *N. stramineus*. Five population samples of *N. stramineus* were examined including island populations on Jamaica and Dominica in the Caribbean and mainland samples from Belize and northern and southern Mexico. Thirty-four presumptive loci were examined of which 20 were variable within or between the species. Thirteen loci were variable within or among populations of *N. stramineus*. These data were interpreted to imply a moderate level of genetic variation. Regarding the relationships among geographic samples of *N. stramineus,* two main branches were observed in a UPGMA dendrogram based on Nei's genetic distances. The two island populations are closely related to each other and comprise one branch of the tree. The three mainland populations form the other branch. A phylogenetic analysis showed the Jamaican population to be basal to a lineage that includes the remainder of the populations. In biogeographic terms the outcome of this analysis is interesting because it could be interpreted as evidence in favor of an Antillean island origin for *N. stramineus*. If the protein mobility data are supported by molecular genetic data, *N. stramineus* might be an unusual example of a species originating on islands and moving to adjacent mainland. The fact that all other natalids are distributed in the Antilles is compatible with this conclusion.

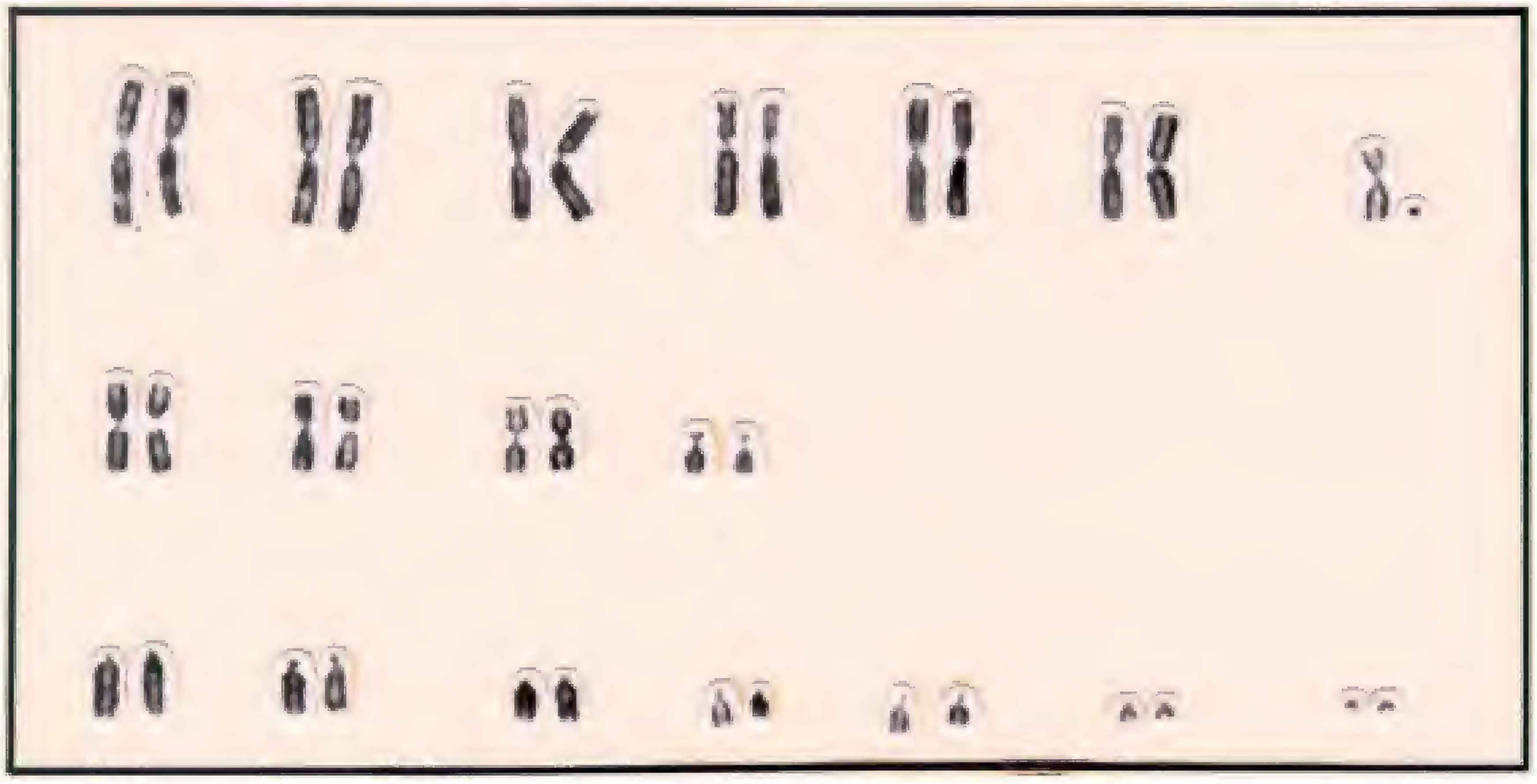

Figure 60. Karyotype of a male *Natalus strimineus* from St. Clair Cave, St. Catharine Parish (TK 9421; TTU 29110).

Eptesicus lynni Shamel, 1945
Jamaican Brown Bat

Specimens examined (37).—CLARENDON PARISH: Portland Point Lighthouse, 1 (TTU). PORTLAND PARISH: Sherwood Forest, 1 (BMNH). ST. ANDREW PARISH: Chincona [probably = Cinchona], 2 (1 BMNH, 1 FMNH). ST. ANN PARISH: Green Grotto, 2 mi. E Discovery Bay, 19 (4 CM, 1 HZM, 14 TTU); Queenhythe, 1 (TTU). ST. JAMES PARISH: cave east of Montego Bay, 13 (NMNH [including holotype]).

Additional records.—CLARENDON PARISH: Jackson's Bay (McFarlane and Garrett 1989). ST. CATHERINE PARISH: Riverhead Cave (McFarlane 1997). ST. ELIZABETH PARISH: Wallingford Cave (Koopman and Williams 1951). ST JAMES PARISH: Cambridge Cave (Koopman and Williams 1951). TRELAWNY PARISH: Windsor Cave (McFarlane 1997).

Distribution.—Figure 61 shows collecting localities for *Eptesicus lynni* on Jamaica. The Jamaican brown bat has been recorded throughout Jamaica, but is abundant at only at two sites—Green Grotto and a cave near Montego Bay. Both of these north shore caves are at or near sea level in areas characterized by ruinate vegetation. The Jamaican brown bat also has been collected at several other lowland locations including the arid areas of Portland Point. It also has been taken from high on the southern slope of the Blue Mountains at Cinchona at an elevation approaching 1500 m. This monotypic species is endemic to Jamaica.

Systematics.—This species was described by Shamel (1945) based upon a series of 27 bats taken from an unspecified cave east of Montego Bay. Shamel (1945) placed *E. lynni* in his *brasiliensis*-group in the genus. This group included many of the medium- to small-sized species occurring in Middle and South America. The large-sized species from North America and elsewhere in the Antilles were placed into the *fuscus*-group. Arnold et al. (1980) used allozyme analysis to investigate the systematic relationships and found that regardless of size, *lynni* was more closely related to *E. fuscus* than to either *E. brasiliensis* or *E. diminutus* (representing Shamel's third group). Their conclusions were that *E. lynni* was a member of the *fuscus*-group and most likely originated on Jamaica. Whether to consider *E. lynni* a species or subspecies of *E. fuscus* was a more difficult decision for Arnold and his colleagues. Generally, with allozyme analyses intraspecific populations do not differ from each other at more than the 15% level. In the present case *E. lynni* differed from *E. fuscus* at about 20%. Arnold et al. (1980)

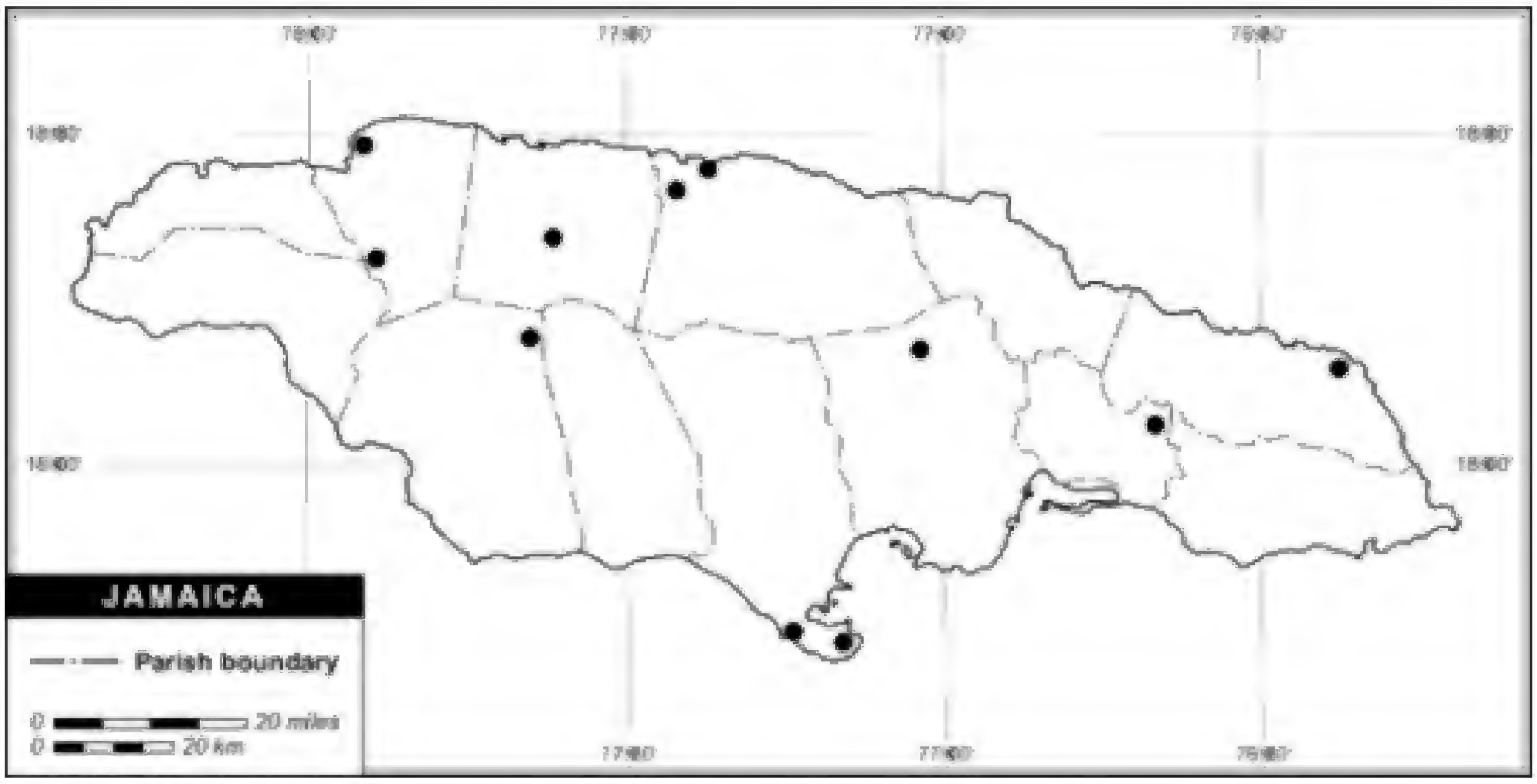

Figure 61. Map of Jamaica showing the locations where specimens of the Jamaican brown bat, *Eptesicus lynni*, have been collected.

concluded that *E. lynni* is a separate species. Hopefully this hypothesis eventually will be tested through a molecular genetic comparison of *E. lynni* and *E. fuscus hispaniolae.*

Koopman (1989, 1993) apparently disagreed with Arnold et al. (1980) because he listed *E. lynni* as a subspecies of *E. fuscus*, although he presented no data to support this conclusion. At about the same time Kurta and Baker (1990) maintained *E. lynni* as a distinct species. We still agree that *E. lynni* should be maintained as a distinct species endemic to Jamaica until data to the contrary are presented and an analysis of geographic variation in Antillean *Eptesicus* is undertaken.

Sanborn (1941) reported three Jamaican specimens of *Eptesicus* from Sherwood Forest under the name *E. fuscus hispaniolae.* Arnold et al. (1980) subsequently examined these specimens and assigned them to *E. lynni*.

Morphometrics.—Table 3 presents external and cranial measurements of samples of five males and 10 females of *Eptesicus lynni* from the type locality and the Green Grotto. The sexes of this species show considerable secondary sexual variation, with only postorbital constriction not displaying significant variation. Females were significantly larger than males in all other measurements. Only for length of forearm was the difference at the $P = 0.05$ level. For two other measurements—condylobasal length and mastoid breadth—the significance level was $P = 0.001$, with the remaining six measurements showing differences at a significance level of $P = 0.01$.

Measurements of the female holotype included the following: length of forearm, 43.5; greatest length of skull, 16.3; condylobasal length, 14.9; zygomatic breadth, 10.5; interorbital constriction, 5.9; postorbital constriction, 4.0; mastoid breadth, 8.0; palatal length, 6.1; length of maxillary toothrow, 5.1; breadth across upper molars, 6.4. This specimen is unusually small when compared to our sample of individuals given in Table 3. The values for all measurements of the holotype except length of forearm and postorbital constriction fall below the range of measurements listed for females in Table 3. The length of forearm falls at the minimum of the size range of the sample and the postorbital constriction falls at the mean of the sample. The unusually small size of the holotype might have led Shamel (1945) to the erroneous conclusion that *E. lynni* should be associated with the *brasiliensis*-group.

Natural history.—Very little is known about the natural history of this species on Jamaica (Fig. 62), but McFarlane (1986) lists it as probably an obligate cave roosting species. Certainly, the majority of our specimens come from or physically near to caves, such as the type locality and the Green Grotto, and McFarlane (1997) lists them from two additional caves. At the Green Grotto specimens were netted at the entrance of the cave (Fig. 20), although a search inside the cave did not locate any roosting individuals. This could indicate that the Jamaican brown bat only was using the cave as a night roost. The individual from Queenhythe was taken in a mist net set over a large open earthen tank (Figs. 4-5).

Testes lengths were taken from males captured on the following dates: 6 July, 2, 3; 7 July, 2, 5; 8 July, 3. Females taken on the following dates displayed no gross evidence of reproductive activity: 2 July (1); 7 July (7); 3 November (1). These negative reproductive data give no real insight into the breeding cycle of this species.

Specimens from Wallingford Cave and Cambridge Cave consist of fragmentary lower jaws recovered from subfossil deposits in the caves (Koopman and Williams, 1951). Although the fragmentary nature of the material made positive identification impossible, Koopman and Williams concluded that both specimens more closely resembled *E. lynni* than *E. fuscus hispaniolae*. McFarlane et al. (2002) reported fossil and subfossil remains of *Eptesicus lynni* from the Jackson's Bay caves that were approximately 10,000 years old. McFarlane and Garrett (1989) reported a minimum of 4 individuals of *Eptesicus lynni* from contemporary Barn Owl (*Tyto alba*) pellets found in caves in the Jackson's Bay area. This species constituted 4.8% of the non-rodent remains found in the pellets.

Because field fixation techniques for transmission electron microscopy (TEM) were successfully developed during our joint field work with Jamaican bats (Phillips, in press), the salivary glands of *Eptesicus*

Figure 62. View of the head of *Eptesicus lynni*.

lynni are among those that have been examined ultrastructurally. Salivary gland acinar cells typically produce, temporarily store, and then release membrane-bound granules containing enzymes, glycoproteins, and other formative constituents of saliva. With TEM, stored (mature) granules can be observed in acinar cell cytoplasm. The physical appearance of such secretory granules in one species then can be compared to granules in homologous cells in other species. One this basis, it has been shown that the parotid gland acinar cell granules in *E. lynni* have unique substructure that is clearly different from either *E. fuscus* or *E. brasiliensis* (Phillips et al. 1987; Phillips and Tandler unpublished data). Additionally, subtle secretory differences in the salivary gland striated ducts also were discovered in a comparison of *E. lynni* to *E. fuscus* (Tandler et al. 2001). Collectively, these ultrastructural data are consistent with the systematic arrangement of *E. lynni* as a species of bat endemic to Jamaica. This is an important point because the ultrastructural appearance of secretory products often is species-specific (based on comparative data from hundreds of mammal species) and probably a physiochemical representation of genetic differences between species (Phillips 1996).

Genetics.—The karyotype of *E. lynni* has 2n = 50 and FN = 48 (Fig. 63). There are 48 acrocentric autosomes in a graded series. The X is submetacentric and the Y is a minute acrocentric. One pair of medium-sized autosomes bears a distinct secondary constriction proximal to the centromere. Karyotypes were obtained from one male and two females from Green Grotto, 2 mi. E Runaway Bay (TK8123-8125).

Bickham (1979a) reported the G-band karyotype of *E. lynni* and concluded it was identical to that of *E. fuscus* from Texas and New Mexico. Constitutive heterochromatin is restricted to the centromeric region in both species. The standard karyotype of *E. lynni* is identical to that of other New World and Old World species of *Eptesicus* (Ando et al. 1977; Baker and Patton 1967; Baker et al. 1974; Genoways and Baker 1975; Peterson and Nagorsen 1975; Rautenbach et al. 1993; Williams 1978), and *Histiotus montenus* (Williams and Mares 1978). Previously, *Eptesicus* was

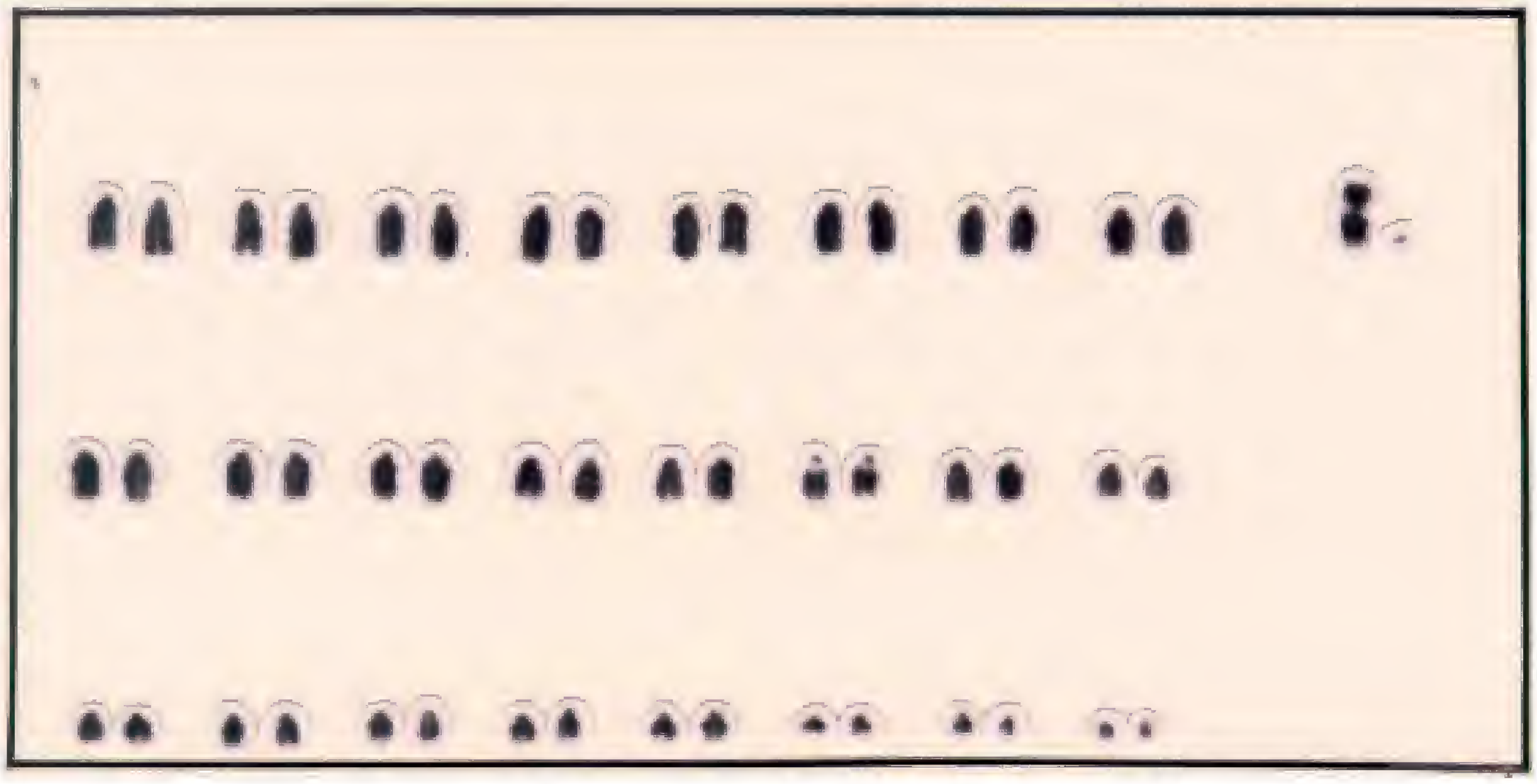

Figure 63. Karyotype of a male *Eptesicus lynni* from Green Grotto, 2 mi E Discovery Bay, St. Ann Parish (TK 8123; TTU 22066).

considered karyotypically variable because of diverse karyotypes in some Old World taxa in the subgenera *Neomoricia*, such as the African *Eptesicus capensis* (2n = 32; Peterson and Nagorsen 1975) and *Vespadelus*, such as the Australian *Eptesicus volturnus* (2n = 44; Volleth and Tideman 1989). However, chromosomal, genic (Morales et al. 1991), molecular (Hoofer and Van Den Bussche 2003), and bacular morphology (Hill and Harrison 1987) all indicate that these taxa are not members of the genus *Eptesicus* and that the genus *Eptesicus* should be considered to be comprised only of those species, such as *E. lynni*, with 2n = 50. Presently, *Vespadelus* and *Neomoricia* are considered genera (Hoofer and Van Den Bussche 2003).

Arnold et al. (1980) used protein electrophroesis to explore the relationships among four species of the genus *Eptesicus*. It was found that *E. lynni* and *E. fuscus* cluster together and are significantly distant from *E. brasiliensis* and *E. diminutus*, which formed a second cluster. The sample of *E. lynni* shared about 80% of its alleles with samples of *E. fuscus*. Among those tested, allele frequency differences were found at the following allozyme loci: Albumin; Malate dehydrogenase-1; -Glycerophosphate dehydrogenase; and 6-Phosphogluconate dehydrogenase.

Lasiurus degelidus Miller, 1931
Jamaican Red Bat

Specimens examined (6).—CLARENDON PARISH: Sutton's, District of Vere, 1 (NMNH [holotype]). ST. ANDREW PARISH: Kingston, 1 (IJ). ST. ANN PARISH: Queenhythe, 3 (CM); 0.5 mi. S, 0.5 mi. W Runaway Bay, 1 (TTU).

Additional records.—ST. CATHERINE PARISH: Spanish Town (Miller 1897, 1931). WESTMORELAND PARISH: near Bluefields (Gosse 1851:279-281).

Distribution.—Figure 64 shows collecting localities for *Lasiurus degelidus* on Jamaica. Specimens of this species are few in number and have been collected at widely scattered sites below 400 m. This monotypic species is endemic to Jamaica.

Systematics.—Miller (1931) described *Lasiurus degelidus* based on three specimens from Sutton's and one from Spanishtown. He characterized the species based on the larger size of females of *L. degelidus* as compared to two males of *L. pfeifferi* from Cuba and with the cheekteeth of *L. degelidus* also being con-

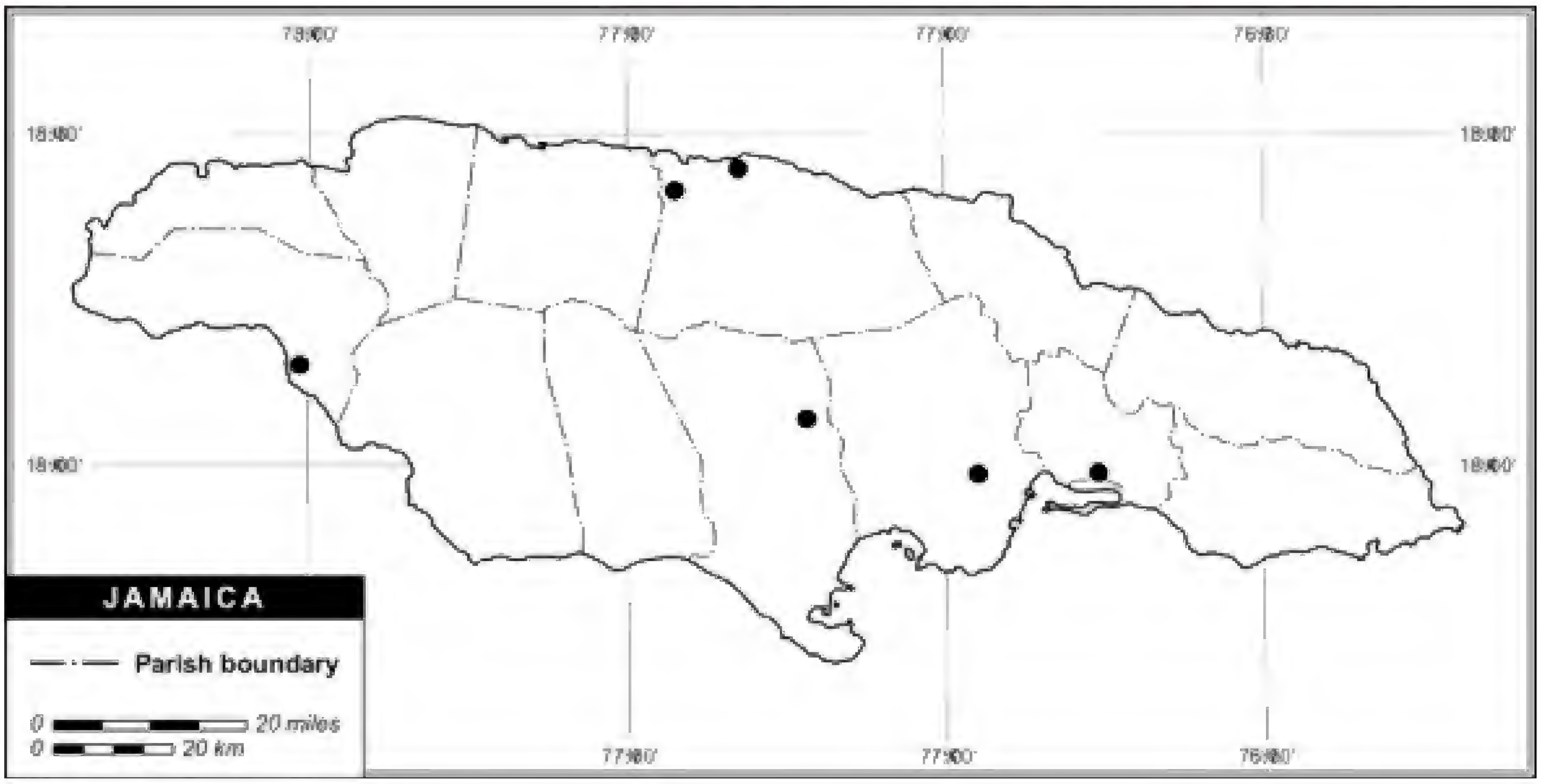

Figure 64. Map of Jamaica showing the locations where specimens of the Jamaican red bat, *Lasiurus degelidus*, have been collected.

spicuously larger. Externally the upper parts lack the grayish frosting typical of *L. borealis* and the underparts are darker than mainland *L. borealis borealis*.

Given the apparent size difference between males and females (see morphometric data below), Miller's small sample could have been misleading so the relationship of *L. degelidus* to *L. pfeifferi* must be reexamined. Varona (1974) reduced all named taxa of red bats in the West Indies to subspecies of *L. borealis*. Baker et al. (1988) used allozymes to study the relationships among eight species of *Lasiurus*, including *L. degelidus*. Unfortunately, the results of this study, for the present time, have further clouded its relationship to *L. degelidus*. First, they restricted the name *L. borealis* to those populations living in eastern North America and applied the name *L. blossevillii* to populations in western North America, Middle America, and South America. This decision was based on a combination of allozyme differences (Baker et al. 1988), morphological differences (Schmidly and Hendricks 1984), and sympatry (Genoways and Baker 1988). The allozyme data suggested a somewhat closer relationship between *L. degelidus* and *L. seminolus* of the southeastern United States than to either *L. borealis* or *L. blossevillii*. Also, *degelidus* and *seminolus* share the morphological characteristic of a well-developed lacrimal ridge, which is the primary morphological characteristic that distinguishes *L. seminolus* from *L. borealis*. Morales and Bickham (1995) studied the molecular systematics of the genus *Lasiurus* using the mitochondrial 12S and 16S ribosomal genes. Although their study did not include *L. degelidus*, they did support the separation of *L. blossevillii* and *L. borealis* as suggested by Baker et al. (1988). Moreover, they obtained strong support for a close relationship between the Cuban *L. pfeifferi* and *L. seminolus*.

Koopman and McCracken (1998) suggested placing all of the recognized taxa of red bats, including *L. degelidus, L. pfeifferi, L. seminolus, L. blossevillii, L. frantzii, L. minor, L. teliotis, L. brachyotis*, and *L. varius*, into the species *L. borealis*. Their reasoning for this was based solely upon morphological comparisons of these taxa. Moreover, they discounted the distributional overlap among some of the taxa, such as *L. borealis* and *L. seminolus*, saying that it has not been demonstrated that overlap during the breeding season occurs between any members of the group. We reject the single-species arrangement of the red bats proposed by Koopman and McCracken (1998) because it ignored genetic divergence observed among members of the group (Baker et al. 1988; Morales and Bickham 1995) as well as the recognized morphological differentiation of the taxa. Moreover, it would obscure the biologically interesting and well documented—but complex—interrelationships among these bats.

The morphological and genetic data leave at least three scenarios for the origin and relationships of *L. degelidus* from Jamaica. The relationship of *L. degelidus* could be with *L. borealis* of eastern North America as Miller's (1931) comparisons would indicate and Varona's (1974) systematic arrangement established. The relationship could be with *L. seminolus* as the allozymic and some morphological characters would indicate or the relationship could be with *L. blossevillii*, at least on zoogeographic grounds. The red bats occurring in southern Mexico and Central America are *L. blossevillii*. This is the region from which populations of several others species of bats have reached Jamaica; therefore, the possible origin of red bats from this area should not be overlooked. With current data, we can not select one of these scenarios over the others; therefore, we conclude that it is best to maintain *L. degelidus* as a species, as did Baker et al. (1988). We predict that with additional data *L. degelidus* will be taxonomically united with one of the three more widespread species of *Lasiurus.*

Morphometrics.—The measurements of two male and two female Jamaican red bats are presented in Table 3. Because of this small sample, no significance testing can be done, but the two females are larger than the males in all measurements except postorbital constriction. This would suggest to us that there might be secondary sexual variation in size in this species. Miller (1931) presents measurements for two specimens from Sutton's.

Natural history.—This is certainly one of the rarest and poorest known species on Jamaica (Fig. 65). No specimens have been recorded from within caves or near caves so we expect that this is a tree-roosting species as are most other members of the genus. The four specimens taken during our field work on Jamaica all were netted over water. At Queenhythe, three individuals were taken over a large rectangular-shaped earthen tank filled with muddy water (Figs. 4-5). The pond was located in a large open grassy area with low trees only near one corner. The specimen from near Runaway Bay was taken in a net set over another earthen tank in an area with coconuts and ruinate vegetation typical of the dry lowland north coast. The individual from Kingston was an adult male that was found on the driveway of a family home.

Figure 65. Dorsal view of the back of *Lasiurus degelidus.*

On successive evenings in early December, Gosse (1851) captured single individuals of *Lasiurus degelidus* near a small river just inland from Bluefields. At least one of the specimens deposited in the British Museum of Natural History is an adult male (Dobson 1878). The specimens were caught in a hand net as they flew just "a little before sunset under the Avocada Peartrees" (Gosse 1851:280). Gosse's (1851) description of the bats is excellent and makes identification quite easy. One of the bats was captured unharmed and ate a fly and its maggots from his hand. When held by the wing tips above some water it drank by touching its muzzle to the surface. This led Gosse (1851:281) to speculate "that in a state of freedom, this, and perhaps other Bats, drink on the wing, like swallows, sweeping down, and just touching the surface with the mouth." Gosse (1851:281) also observed that: "Both specimens were infested with numbers of a parasite (*Nycteribius*) rather large for the size of the Bat."

A male captured on 3 July and two taken on 27 July had testes that were 2, 2, and 4, respectively, in length. A female netted on 27 July evinced no gross reproductive activity.

Genetics.—The karyotype of *L. degelidus* has 2n = 28 and FN = 48 (Fig. 66). There are 22 biarmed autosomes in a graded series, the smallest being distinctly subtelocentric, and 4 small acrocentric autosomes. The X is submetacentric and the Y is a minute acrocentric. Karyotypes were obtained from one male from 0.5 mi. S, 0.5 mi. W Runaway Bay (TK 8001).

Bickham (1987) reported the G-band karyotype for *L. degelidus* and concluded it was identical to the karyotypes of *L. borealis, L. minor, L. seminolus*, and *L. cinereus*, but differed from that of Honduran *L. ega* (also 2n = 28) by centromere placement of the X chromosome. Studies of standard karyotypes have varied in regard to the FN of *Lasiurus* species, probably because of the difficulty in resolving the short arm of the smallest biarmed autosome (Baker and Patton 1967; Baker and Mascarello 1969; Baker et al. 1971).

Remarks.—There is evidently a *lapis* in the original description of this species by Miller (1931). Miller lists the catalogue number of the holotype as NMNH 96187, but later in the same paper, he lists the catalog number of a second female that he measured as also being NMNH 96187. In the collection of the National Museum of Natural History, an adult female catalog number NMNH 96188 is labeled as the holotype and should be considered as such.

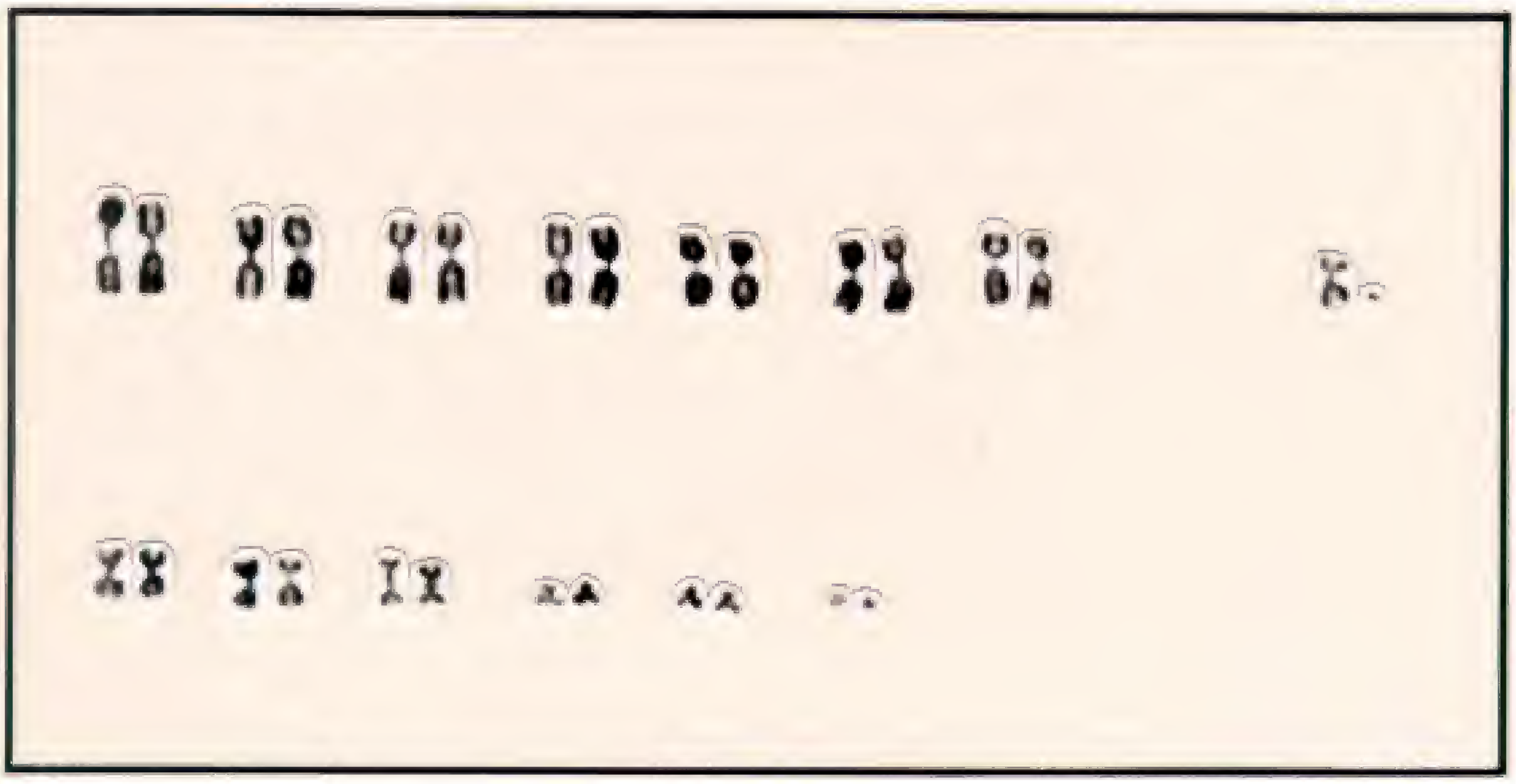

Figure 66. Karyotype of a male *Lasiurus degelidus* from 0.5 mi S, 0.5 mi W Runaway Bay, St Ann Parish (TK 8001; TTU 22080).

See the account of *Natalus micropus* for a discussion of the specimens reported by Osburn (1865) as *Lasiurus rufus*.

Eumops auripendulus auripendulus (Shaw, 1800)
Shaw's Mastiff Bat

Specimens examined (6).— MANCHESTER PARISH: 6.5 mi. SE Alligator Pond, 2 (KU). ST. ANN PARISH: Queenhythe, 4 (2 CM, 2 TTU).

Additional records (Eger 1977).—ST. ANDREW PARISH: Kingston. PARISH UNKNOWN: no specific locality.

Distribution.—Figure 67 shows the collecting localities for *Eumops auripendulus* on Jamaica. Shaw's mastiff bat is known from only three localities on the island. These sites are located at elevations under 400 m. The nominate subspecies is known from southern Mexico, Central America, and northern South America. Another subspecies occurs in eastern South America. The population on Jamaica is the only one on any Antillean island (Eger 1977).

Systematics.—Eger (1977) reviewed members of the genus *Eumops* including *E. auripendulus.* She recognized two subspecies in the species with *Eumops auripendulus auripendulus* having a type locality of French Guiana being the name used for all populations in northern South America, Central America, southern Mexico, and Jamaica. We have followed this arrangement here.

According to Freeman (1981), *E. auripendulus* groups most closely with *E. glaucinus* within the genus. The two species do look much alike, which can present real challenges to field and laboratory studies of the species. This is certainly true on Jamaica where these two species are the only members of the genus in the bat fauna. The quickest and easiest way to distinguish these species is based on the color of the dorsal pelage. In *E. auripendulus*, the hairs are dark to their base giving an overall color appearance of black or dark brown, whereas in *E. glaucinus*, the hairs are bicolored with a dark grayish brown at the tip and pale to white at the base giving an overall color appearance of chocolate brown. The tragus in *E. auripendulus* is small and pointed, whereas in *E. glaucinus* it is square

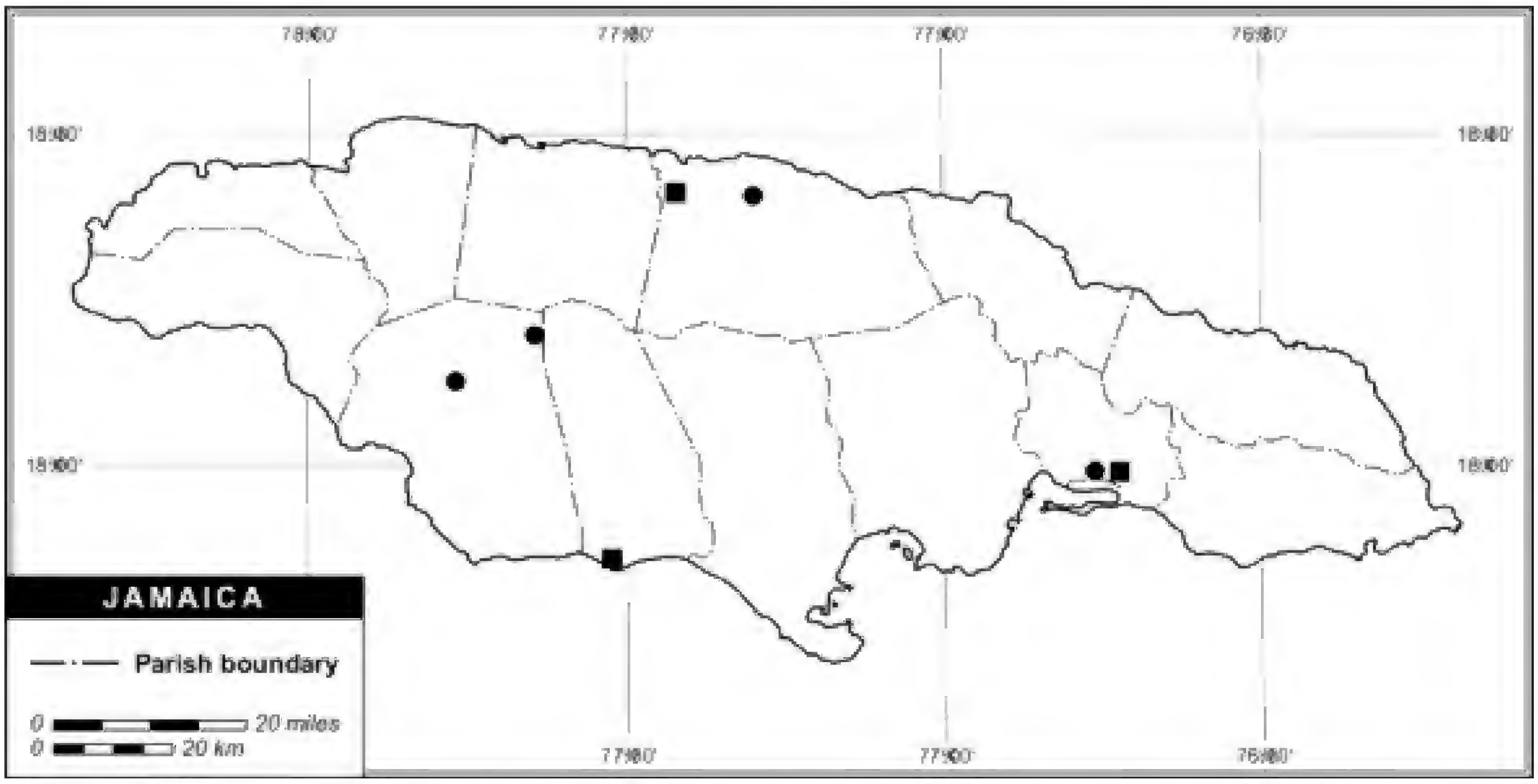

Figure 67. Map of Jamaica showing the locations where specimens of Shaw's mastiff bat, *Eumops auripendulus* (represent by closed squares), and the big free-tailed bat, *Nyctinomops macrotis* (represented by closed circles), have been collected.

and broad. Finally, the ears of *E. glaucinus* are larger extending to the level of the anterior tip of the nose when viewed from above, whereas the smaller ears of *E. auripendulus* do not extend to the level of the anterior tip of the nose when viewed from above (Fig. 68). Cranially, the basisphenoid pits in *E. glaucinus* are larger and better defined than in *E. auripendulus* (Eger 1977).

Morphometrics.—Table 4 gives the length of forearm and nine cranial measurements for two males and two females from Queenhythe and a third female from near Alligator Pond. The length of forearm measurements of the males and females seem to be in the same range, but the males appear slightly larger than the females in cranial measurements although there is overlap in several of the measurements.

Natural history.—This species was first reported from Jamaica by Eger (1977) based on specimens (Fig. 69) from Queenhythe and Kingston. However, the first specimens to enter scientific collections may have been those from near Alligator Pond, which were obtained 2 August 1961. These specimens were obtained by collectors working for Albert Schwartz and remained in his collection mis-identified as *E. glaucinus* until recently when this collection was transferred to the University of Kansas. A note by the field collector indicates that these specimens were shot from dead palm fronds that also were occupied by Antillean Palm Swifts (*Tachornis phoenicobia*). The swifts are colonial nesters in dead hollow palm trees and among the dead drooping palm fronds.

The specimens from Queenhythe were taken in mist nets set over a large earthen tank filled with muddy water and surrounded by a large grassy area. Almost certainly the bats were coming to drink. The high-pitched clicks of this species and *E. glaucinus* could be heard as the bats circled high above the pond. These clicks became much more rapid as the bats swooped toward the pond and were taken in the nets.

Figure 68. View of the dorsal surface of *Eumops glaucinus* (left) and *E. auripendulus* (right). Note that the ears of *E. glaucinus* are larger extending to the level of the tip of the nose when viewed from above, whereas the smaller ears of *E. auripendulus* do not extend to the level of the tip of the nose when viewed from above.

Table 4.—Length of forearm and nine cranial measurements for five species of the family Molossidae occurring on Jamaica.

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
Eumops auripendulus auripendulus										
Males										
TTU 22081	58.4	25.4	21.7	14.3	8.0	4.5	12.5	9.8	9.2	9.9
CM 44611	58.2	25.5	21.9	14.5	7.9	4.8	12.3	10.9	9.2	10.0
Females										
TTU 22082	56.9	24.3	20.7	13.8	7.9	4.5	12.1	9.6	8.7	9.7
CM 44610	59.4	24.6	21.37	14.2	7.7	4.7	12.3	10.9	9.2	9.4
KU 150206	57.2	24.1	21.4	13.7	7.6	4.5	12.0	9.8	8.8	9.5
Eumops glaucinus glaucinus										
Males										
N	4	4	4	4	4	4	4	4	4	4
Mean	60.7	24.7	23.1	14.5	7.6	4.8	13.2	9.9	9.4	10.0
Minimum	60.1	24.3	22.8	14.0	7.5	4.7	12.9	9.8	9.3	9.8
Maximum	61.0	25.0	23.5	15.1	7.6	4.9	13.4	10.1	9.6	10.2
SE	±0.19	±0.15	±0.19	±0.24	±0.03	±0.04	±0.11	±0.07	±0.07	±0.08
Females										
N	6	6	6	7	7	7	7	7	7	7
Mean	59.8	24.1	22.5	14.5	7.2	4.7	13.0	9.7	9.1	9.8
Minimum	58.7	23.8	21.9	13.8	6.7	4.6	12.5	9.1	8.8	9.5
Maximum	60.6	24.7	22.9	14.7	7.4	4.9	13.2	10.4	9.3	10.0
SE	±0.32	±0.13	±0.16	±0.12	±0.09	±0.04	±0.09	±0.15	±0.06	±0.06
Nyctinomops macrotis										
Males										
NMNH 122655	57.9	22.3	21.9	12.0	4.3	3.9	10.9	9.3	8.5	8.4
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	40.2	15.9	14.7	9.3	4.6	3.8	8.9	6.3	5.5	6.7
Minimum	38.3	15.3	14.0	9.0	4.1	3.7	8.5	6.0	5.2	6.4
Maximum	41.6	16.2	15.1	9.7	4.8	3.9	9.1	6.5	5.7	7.0
SE	±0.32	±0.09	±0.10	±0.08	±0.06	±0.02	±0.06	±0.07	±0.05	±0.05

Table 4. (cont.)

Sex and statistics	Length of forearm	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Interobital constriction	Postoribtal constriction	Mastoid breadth	Palatal length	Length of maxillary toothrow	Breadth across upper molars
				Tadarida brasiliensis murina						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	40.2	15.9	14.7	9.3	4.6	3.8	8.9	6.3	5.5	6.7
Minimum	38.3	15.3	14.0	9.0	4.1	3.7	8.5	6.0	5.2	6.4
Maximum	41.6	16.2	15.1	9.7	4.8	3.9	9.1	6.5	5.7	7.0
SE	±0.32	±0.09	±0.10	±0.08	±0.03	±0.02	±0.06	±0.07	±0.05	±0.05
Females										
N	7	6	7	5	6	7	6	7	7	7
Mean	39.9	16.0	14.6	9.4	4.6	3.8	8.8	6.2	5.5	6.6
Minimum	38.3	15.6	14.4	9.3	4.5	3.6	8.5	5.9	5.4	6.3
Maximum	41.1	16.1	15.1	9.5	4.9	3.9	9.0	6.6	5.6	7.0
SE	±0.47	±0.09	±0.10	±0.03	±0.09	±0.04	±0.07	±0.09	±0.04	±0.09
				Molossus molossus milleri						
Males										
N	10	10	10	10	10	10	10	10	10	10
Mean	39.0	17.2	17.0	11.0	5.6	4.1	10.8	6.1	6.0	7.9
Minimum	38.3	16.8	16.7	10.8	5.3	4.0	10.5	5.8	5.8	7.7
Maximum	39.8	17.5	17.3	11.4	6.0	4.2	11.1	6.3	6.4	8.0
SE	±0.14	±0.08	±0.07	±0.06	±0.07	±0.02	±0.06	±0.06	±0.06	±0.03
Females										
N	10	10	10	10	10	10	10	10	10	10
Mean	38.5	16.7	16.5	10.6	5.3	4.0	10.3	5.9	5.8	7.7
Minimum	37.4	16.5	16.3	10.3	5.2	3.8	10.0	5.8	5.6	7.3
Maximum	39.0	16.9	16.7	10.7	5.6	4.1	10.5	6.1	6.0	7.9
SE	±0.17	±0.05	±0.04	±0.05	±0.04	±0.03	±0.05	±0.03	±0.06	±0.06

Figure 69. View of the head of *Eumops auripendulus*.

Males taken on 11 July and 27 July had testes lengths of 7 and 6, respectively. Females captured on 12 July and 27 July were lactating.

McDaniel and Webb (1982) reported two specimens of the labidocarpine bat-mite *Parakosa tadarida* McDaniel and Lawrence 1962 from a bat captured at Queenhythe.

Genetics.—The karyotype of *E. auripendulus* has 2n = 42 and FN = 62 (Fig. 70). There are 12 large biarmed autosomes, 10 medium sized biarmed autosomes (the last 2 pairs are distinctly subtelocentric), and a graded series of 18 medium-sized to small acrocentric autosomes. The X is medium sized and submetacentric and the Y is small and biarmed. Karyotypes were obtained from 2 males and 2 females from Queenhythe. The karyotype of *E. auripendulus* from Jamaica is identical to that described but not figured by Warner et al. (1974) for this species from Trinidad.

Eumops glaucinus glaucinus (Wagner, 1843)
Wagner's Mastiff Bat

Specimens examined (29).—ST. ANDREW PARISH: Half Way Tree, 3 (NMNH); *12 Stoney Hill Road, Kingston*, 2 (IJ). ST. ANN PARISH: Queenhythe, 12 (6 CM, 6 TTU). ST. CATHERINE PARISH: Spanish Town, 3 (1 BMNH, 2 NMNH). WESTMORELAND PARISH: Savanna-La-Mar, 1 (BMNH). PARISH UNKNOWN: no specific locality, 8 (2 ANSP, 3 BMNH, 1 MCZ, 2 NMNH).

Additional records (McFarlane 1997, unless otherwise noted).—ST. ANN PARISH: Ewart Town Bat Cave; Mount Plenty Cave; Runaway Bay Caves. ST. CATHERINE PARISH: St. Clair Cave. ST. JAMES PARISH: Sewell Cave. WESTMORELAND PARISH: *Phœnix Park* [18°13'N, 78°08'W] (Gosse 1851:159-163).

Figure 70. Karyotype of a male *Eumops auripendulus* from Queenhythe, St. Ann Parish (TK 9385; CM 44611).

Distribution.—Figure 71 shows the collecting localities for *Eumops glaucinus* on Jamaica. Wagner's mastiff bats can be expected at any locality on Jamaica that is under 500 m and has appropriate roosting sites. The nominate subspecies can be found in southern Mexico, Central America, and the northern half of South America. In the West Indies, Wagner's mastiff bats occur on Cuba as well as on Jamaica (Eger 1977).

Systematics.—Miller (1906) created the genus *Eumops* to hold 10 species of molossids described at that time. He distinguished the members of the genus *Eumops* based on a combination of the following characteristics: skull hour-glass shaped; no distinct sagittal crest; incisors 2/2; premolars 2/2; upper incisor with slender curved shaft; M1 and M2 with well-developed hypocone.

Eumops glaucinus originally was described based on a specimen from Cuibana, Mato Grosso, Brazil. This name has been applied to all populations of the species in South America, Central America, southern Mexico, and the Greater Antilles. With the inclusion of *Eumops floridanus* in this species (Koopman 1971), the trinomial *E. g. glaucinus* has been applied to these populations. Eger (1977) reviewed this species and maintained the existing taxonomy. We have followed this arrangement here. However, the genetic data discussed below indicate that the systematics of this species may not be as clear as this arrangement would indicate.

H. Allen in 1889 described *Nyctinomus orthotis* based on a single specimen received from Spanishtown, Jamaica. The genus *Nyctinomus* at the time constituted species now commonly associated with *Tadarida* and closely related genera. His (H. Allen 1889) primary comparisons for the new taxon were with two species now called *Tadarida brasiliensis* and *Nyctinomops macrotis* (Freeman 1981). Miller (1906) lists "*E. orthotis* (H. Allen)" among the species included in his newly described genus *Eumops*. The exact relationships of this taxon were not known until Sanborn's (1932) revision of the genus *Eumops*. In this paper Sanborn (1932) stated: "Comparison of the type of *Nyctinomus orthotis* H. Allen . . . shows no characters to distinguish it from *Eumops glaucinus*." Thus, *Nyctinomus orthotis* was placed as a junior synonym of *Eumops glaucinus* and it continues to be treated as such.

Morphometrics.—Table 4 presents the length of forearm and nine cranial measurements for four male and seven female Wagner's mastiff bats from Jamaica. Males averaged larger than females in all measurements

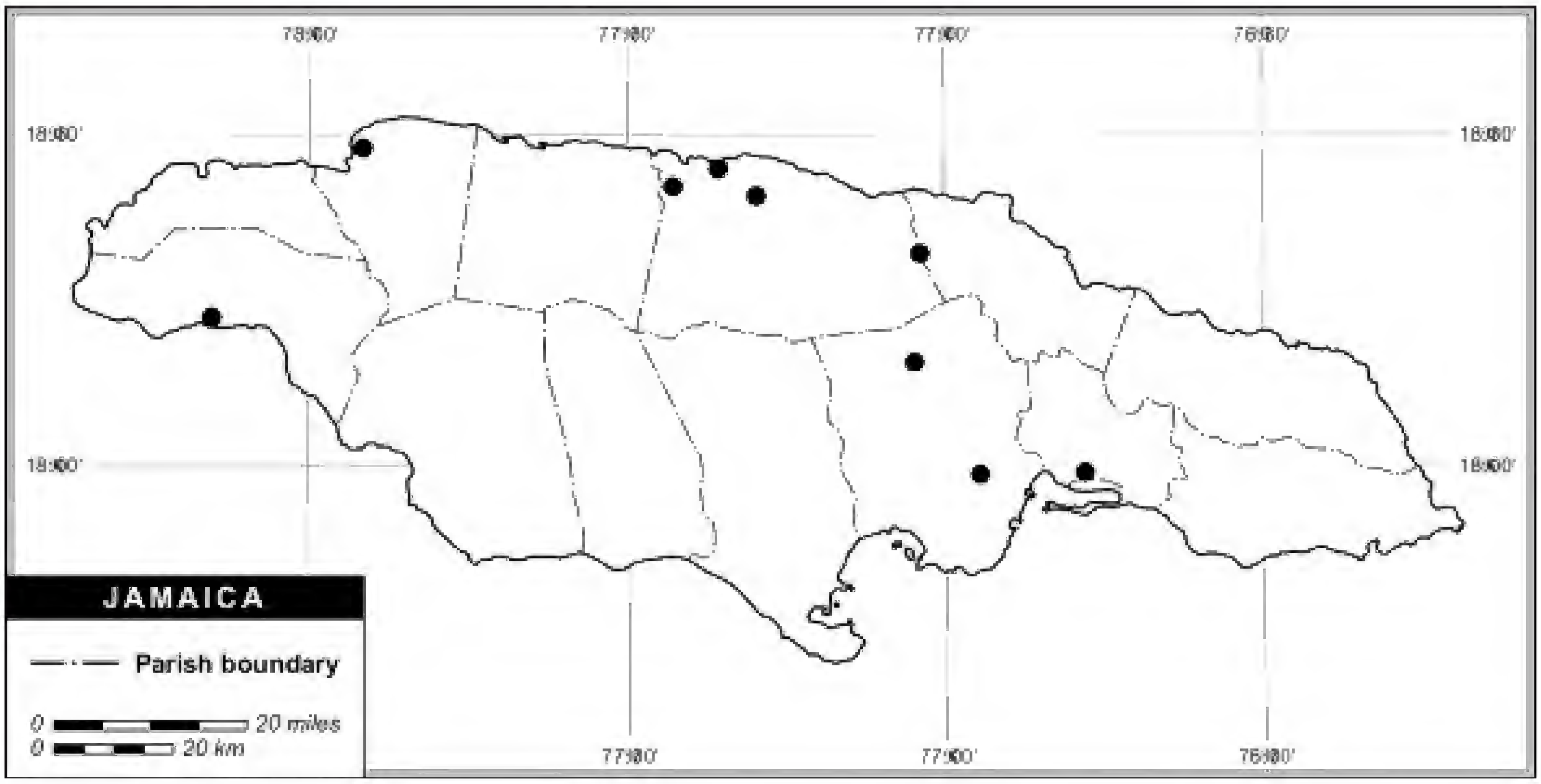

Figure 71. Map of Jamaica showing the locations where specimens of Wagner's mastiff bat, *Eumops glaucinus*, have been collected.

except zygomatic breadth in which the sexes had the same mean. Males were significantly larger than females in four measurements, including greatest length of skull, condylobasal length, interorbital constriction, and length of maxillary toothrow. The significance level for each of these measurements was $P = 0.05$, which should not be surprising given the small samples, especially of males.

Some of the comparative differences between *Eumops glaucinus* and *E. auripendulus* are discussed in the account for the latter species. According to Eger (1977), these species are similar in size; however, examination of Table 4 hints at some interesting morphometric differences in the Jamaican material, with the caveat that sample sizes are small. Comparing measurements of the sexes respectively, *Eumops glaucinus* is larger than *E. auripendulus* with no overlap for both sexes in three measurements—length of forearm, condylobasal length, and mastoid breadth. In addition, there is no overlap in the measurements of breadth across upper molars in females and length of maxillary toothrow in males, with *E. glaucinus* being the larger. Interestingly, interorbital breadth does not overlap between sexes, but *E. auripendulus* is the larger sized. Clearly, *E. auripendulus* must be proportionally much broader in the interorbital region than *E. glaucinus*. Males of *E. auripendulus* are larger than *E. glaucinus* with no overlap for greatest length of skull. It will be interesting to note whether these differences remain as additional specimens of these species from Jamaica become available.

H. Allen (1889) presents extensive external and wing measurements for the holotype of *Nyctinomus orthotis*.

Natural history.— Wagner's mastiff bats have been taken on Jamaica in a variety of ecological situations (Fig. 72). They have been recorded as roosting in five caves on the island. These range from the large and well-known St. Clair Cave to the much smaller Ewart Town Bat Cave (cave 1065), which may be the same as Goodwin's (1970) Claremont Cave, although he did not record this species in his studies on Jamaica. At Ewart Town Bat Cave a large entrance leads to 30 m of passage ending at an unexplored drop of 5 m or more (Fincham 1997). A large bat colony is recorded to be present with as many as five species of bats in addition to *E. glaucinus*, including *Pteronotus parnellii, Macrotus waterhousii, Monophyllus redmani, Artibeus jamaicensis*, and *Nyctinomops macrotis* (Fincham 1997).

Figure 72. View of the head of *Eumops glaucinus*.

Gosse (1851) described the capture of this species, recording them as the chestnut mastiff-bat, from a home in Phœnix Park, Westmoreland Parish (see Dobson 1878, for the confirmation of this identification). The bats evidently were roosting between the ceiling and the roof of the home and emerging from a small hole just below the eaves. Gosse (1851) recorded that they began to emerge "just as the stars begin to come out." They emerged in groups of three or four, one bat following the other, until about 15 had emerged. Gosse (1851) also was able to observe the bats returning and re-entering the hole between 8 and 9 PM and the family living in the home assured him that this was the bats' normal routine

All the specimens taken during our work came from Queenhythe where they were taken in mist nets set over a large earthen tank filled with muddy water and surrounded by a large grassy area (Fig. 73). Almost certainly the bats were coming to drink. The high-pitched clicks of this species and *E. auripendulus* could be heard as the bats circled from high above the pond. These clicks became much more rapid as the bats swooped toward the pond and were taken in the nets. These individuals were taken late in the evening compared to other species, with all being netted between 9:30 and 11:15 PM.

Two adult males taken on 12 July had testes measuring 5 and 9, whereas two taken on 27 July had lengths of 5 and 10. Females carrying single embryos were taken on 12 July (crown-rump length, 7) and 27 July (13). Lactating females were taken on 11 July and 27 July. Individuals still possessing unfused phalangeal epiphyses were taken on 12 July (female, length of forearm, 58.3) and 27 July (female, 57.1).

Genetics.—The karyotype of *E. glaucinus* has 2n = 38 and FN = 64 (Fig. 74). There are 28 biarmed autosomes in a graded series from large to medium sized, the smallest is distinctly subtelocentric, and 8 small acrocentric autosomes. The X is medium sized and submetacentric, the Y is small and acrocentric. Karyotypes were obtained for 2 males and 5 females from Queenhythe.

This species shows a considerable amount of chromosomal variability. Specimens from Colombia possess 2n = 40 and FN = 64 (Warner et al. 1974). The differences in diploid numbers between Colombian specimens and Jamaican specimens could best be explained by centric fusion of 2 pairs of acrocentrics present in the Colombian specimens. There also appears to be a difference in size of the X chromosomes in these two chromosomal races. Specimens

Figure 73. A view of the eathern tank at Queenhythe, St. Ann Parish, Jamaica.

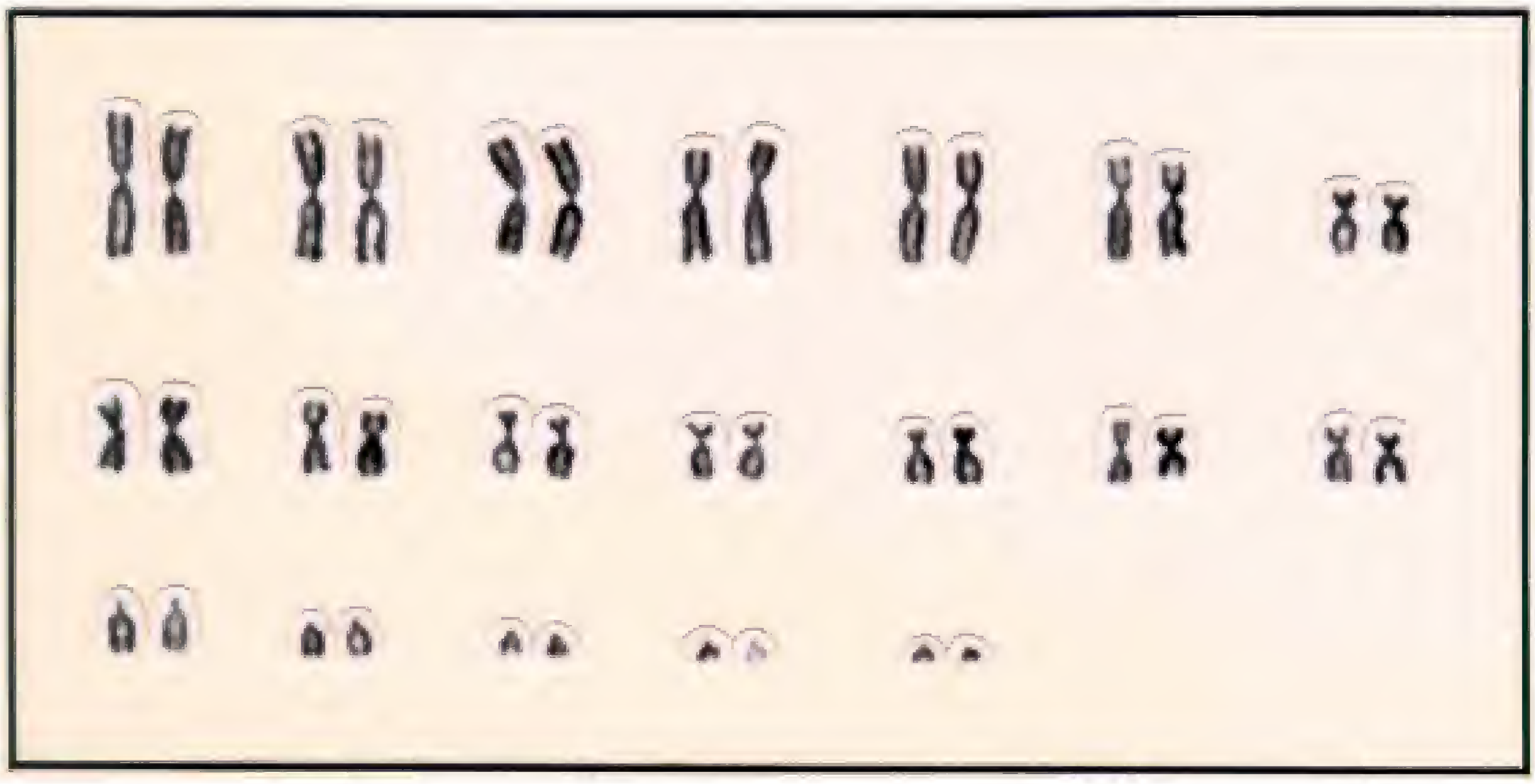

Figure 74. Karyotype of a female *Eumops glaucinus* from Queenhythe, St. Ann Parish (TK 9380; CM 44614).

from Mexico and Central America possess a 2n = 38, FN = 64 karyotype in which the autosomes are identical to those of *E. glaucinus* from Jamaica. There is, however, variation in centromere placement of the X in the Mexico and Central American populations. Both acrocentric and submetacentric X's are present in these populations; it is not clear if this represents a population polymorphism or the existence of geographic races (Warner et al. 1974). Karyological data suggest that the Jamaican population of *E. glaucinus* has affinities with the Mexican and Central American populations of this species, rather than the South American population.

Salivary glands.-- The submandibular gland demilune secretory cells have been show to exhibit intense lysozyme-like immunoreactivity in *Eumops glaucinus* (Phillips et al., 1998). Similar (but not identical) results were obtained from *Tadarida brasiliensis.* In the context of diet and in comparison to 11 other bat species, it appears that lysozyme-like immunoreactivity is associated with feeding on chitinous insects. On this basis it was hypothesized that lysozyme might serve as a salivary chitinase (Phillips et al., 1998).

Nyctinomops macrotis (Gray, 1839)
Big Free-tailed Bat

Specimens examined (34).—ST. ANDREW PARISH: Kingston, 22 (2 BMNH, 20 NMNH). ST. ELIZABETH PARISH: Grove Cave, 1 mi. E Balaclava, 4 (NMNH); Bagdale Cave, 1 1/4 mi. E, 3/4 mi. N Maggotty, approx. 750 ft., 1 (UF). PARISH UNKNOWN: no specific locality, 7 (1 BMNH, 6 NMNH).

Additional records (McFarlane 1997).—ST. ANN PARISH: Ewart Town Bat Cave. ST. ELIZABETH PARISH: *Wallingford Roadside Cave*.

Distribution.—Figure 67 shows the collecting localities for *Nyctinomops macrotis* on Jamaica. With only five known sites of occurrence, it is difficult to comment on the overall distribution of the big free-tailed bat on Jamaica. The recent records seem to be centered in intermediate elevations in St. Ann and St. Elizabeth parishes. The big free-tailed bat is known from the southwestern United States, the northern two-thirds of Mexico, and tropical areas of South America (Koopman 1982). There are populations on the three largest islands in the Greater Antilles—Jamaica, Cuba, and Hispaniola.

Systematics.—Freeman (1981) presented evidence for reviving the use of the generic name *Nyctinomops* for this species that long had been treated in the literature as *Tadarida macrotis* (Shamel 1931; Husson 1962). Freeman (1981) included four species in the genus that originally was described by Miller (1902) to include these species and some that are now treated as synonyms. *Nyctinomops macrotis* traditionally has been treated as a monotypic species and we have followed this arrangement here.

Morphometrics.—Table 4 presents external and cranial measurements for one male and five female big free-tailed bats from Jamaica. Only the measurements for length of forearm and condylobasal length of the male lie outside the upper range of measurements for the five females.

Natural history.—This species was not taken by Goodwin's (1970) or by our various expeditions to Jamaica. Consequently, little is known of the natural history of the species on the island. The most recently captured Jamaican specimens were four females taken on 18 June 1983 by a group from the National Museum of Natural History that intended to collect fossil specimens of mammals. One collector noted that the bat specimens were taken by hand as they roosted in Grove Cave near Balaclava. Three of the females were pregnant with embryos that measured 29, 29, and 30 in crown-rump length. These females weighed 24.0, 25.5, and 22.0, respectively. A single female taken in Bagdale Cave on 22 June 1980 did not evince gross reproductive activity. Bagdale Cave (also known as Vauxhall Cave and Red Hill Ratbat Cave; cave 488) is a cave-to-a-shaft cave located about 1.2 km NNE of the bauxite plant in Maggotty. The cave, which is 90 m long and about 15 m deep, has a steep drop from the entrance to a sandy floor and then an ascent to a 7-m drop to a second entrance. Guano has been mined from the cave (Fincham 1997:364). The field collector noted that the bat was "knocked from cave ceiling with a small rock."

Genetics.—This is the only species for which we have been unable to obtain a karyotype from a Jamaican specimen. However, specimens from

Sonora, Mexico, have a karyotype identical to that presented here for *Molossus molossus* and *Tadarida brasiliensis* (Baker 1970a; Warner et al. 1974).

Remarks.—The tags for the specimens from Grove Cave list it as being in Trelawny Parish; however, Balaclava is clearly in St. Elizabeth Parish. We believe that this is a simple *lapses* because the field expedition was conducting most of its work in Trelawny Parish. Fincham (1997) does not list a Grove Cave in either Trelawny or St. Elizabeth parishes, but only lists Grove Cave, Portland Parish, Grove Land Well, Westmoreland Parish, and Grove Road Cave, Manchester Parish. We, therefore, are not able to exactly locate Grove Cave, but we assume that it must be in the area of Wallingford caves.

Tadarida brasiliensis murina (Gray, 1827)
Brazilian Free-tailed Bat

Specimens examined (296).—CLARENDON PARISH: *Cumberland District, 3000 ft.*, 2 (AMNH); Mason River Research Station, 2.5 mi. W Kellits, 3 (TTU); Tweedside, 3 (NMNH). KINGSTON PARISH: Institute of Jamaica, 4 (IJ); *Hanover Street, Kingston*, 1 (IJ). MANCHESTER PARISH: Mandeville, 1 (NMNH). PORTLAND PARISH: Green Hill, 7 (TTU); Hardwar Gap, 1090 m, 14 (1 BMNH, 13 NMNH); *Happy Grove, Hectors River*, 1 (JMM); Hectors River, 6 (JMM); Port Antonio, 2 (KU). ST. ANDREW PARISH: *Chestervale*, 1 (UF): Cinchona, 5 (1 AMNH, 4 NMNH); *Raetown, Kingston*, 1 (NMNH); *Rock Fort, Kingston*, 1 (BMNH); Kingston, 2 (NMNH); *University of the West Indies, Mona*, 6 (COLU); Mona, 1 (BMNH); Newcastle, 8 (JMM); Silver Hill Mill, 4 (UF). ST. ANN PARISH: Cardiff Hall, 1 (AMNH); Green Grotto, 2 mi. E Discovery Bay, 52 (1 CM, 51 TTU). ST. CATHERINE PARISH: Bog Walk, 20 (17 FMNH, 3 MCZ); Spanish Town, 1 (NMNH); *Swansea Cave, Worthy Park Factory Ltd., Lluidas Vale*, 6 (1 ROM, 5 TTU); 0.2 mi. E Watermount, 20 (CM); Worthy Park, 1 (AMNH). ST. ELIZABETH PARISH: Appleton, 2 (AMNH); Balaclava, 28 (AMNH); *Wallingford Cave, Balaclava*, 1 (AMNH); Pepper, 1 (NMNH); Peru Cave, Goshen, 46 (33 AMNH, 13 NMNH). ST. JAMES PARISH: *Lapland*, 9 (AMNH); 7-rivers Cave, Lapland, 1 (AMNH); Montego Bay, 11 (1 BMNH, 10 MCZ). ST. MARY PARISH: Highgate, 2 (ROM). ST. THOMAS PARISH: Whitfield Hall, Penlyne, 4300 ft., 1 (JMM). TRELAWNY PARISH: Mahogany Hall [18°23'N, 77°28'W], 2 (BMNH). PARISH UNKNOWN: no specific locality, 18 (1 ANSP, 1 BMNH, 16 NMNH).

Additional records.—CLARENDON PARISH: *Rowington Park (Vere)* [17°54′ N, 77°19′ W] (Osburn 1865). ST. ANN PARISH: Golden Grove Cave (Webster 1971). ST. ELIZABETH PARISH: Salmon Gully Cave [near Merrywood] (McFarlane 1997). TRELAWNY PARISH: Windsor Cave (Dávalos and Erikkson 2003).

Distribution.—Figure 75 shows collecting localities for *Tadarida brasiliensis* on Jamaica. The Brazilian free-tailed bat has an interesting distribution on Jamaica because locality records are largely concentrated between intermediate and the highest elevations that have been sampled. Except for records concentrated around Kingston, the species does not occur on the dry, hotter southern coast. The species has been taken at a few sites along the northern coast, but these are relatively rare given the amount of fieldwork concentrated in these areas. There are no records of Brazilian free-tailed bats from the two western-most parishes of Westmoreland and Hanover, which at this point is difficult to explain. The species also has no modern records from some of the largest caves on the islands such as St. Clair, Oxford, Wallingford, and Mount Plenty. The Brazilian free-tailed bat has one of the most extensive geographic ranges of any New World bat, being found from the central United States southward through Mexico and Central America into western and central South America (Koopman 1982). In the West Indies, the species has been recorded from the islands of the Greater Antilles, Bahamas, Virgin Islands, and as far south in the Lesser Antilles as St. Vincent. The subspecies *T. b. murina* is endemic to Jamaica (Hall 1981).

Systematics.—Gray originally described *Nyctinomus murinus* based on a specimen submitted by J. S. Redman from Jamaica (Dobson 1878). Gray (1838) characterized the species as follows: "upper lip simple in front; ears round, separated at base in front; tragus slender." The holotype was present at the time that Dobson (1878) prepared his catalog of the Chiroptera in the British Museum; however, we did not locate it in the collection during our visit in the late

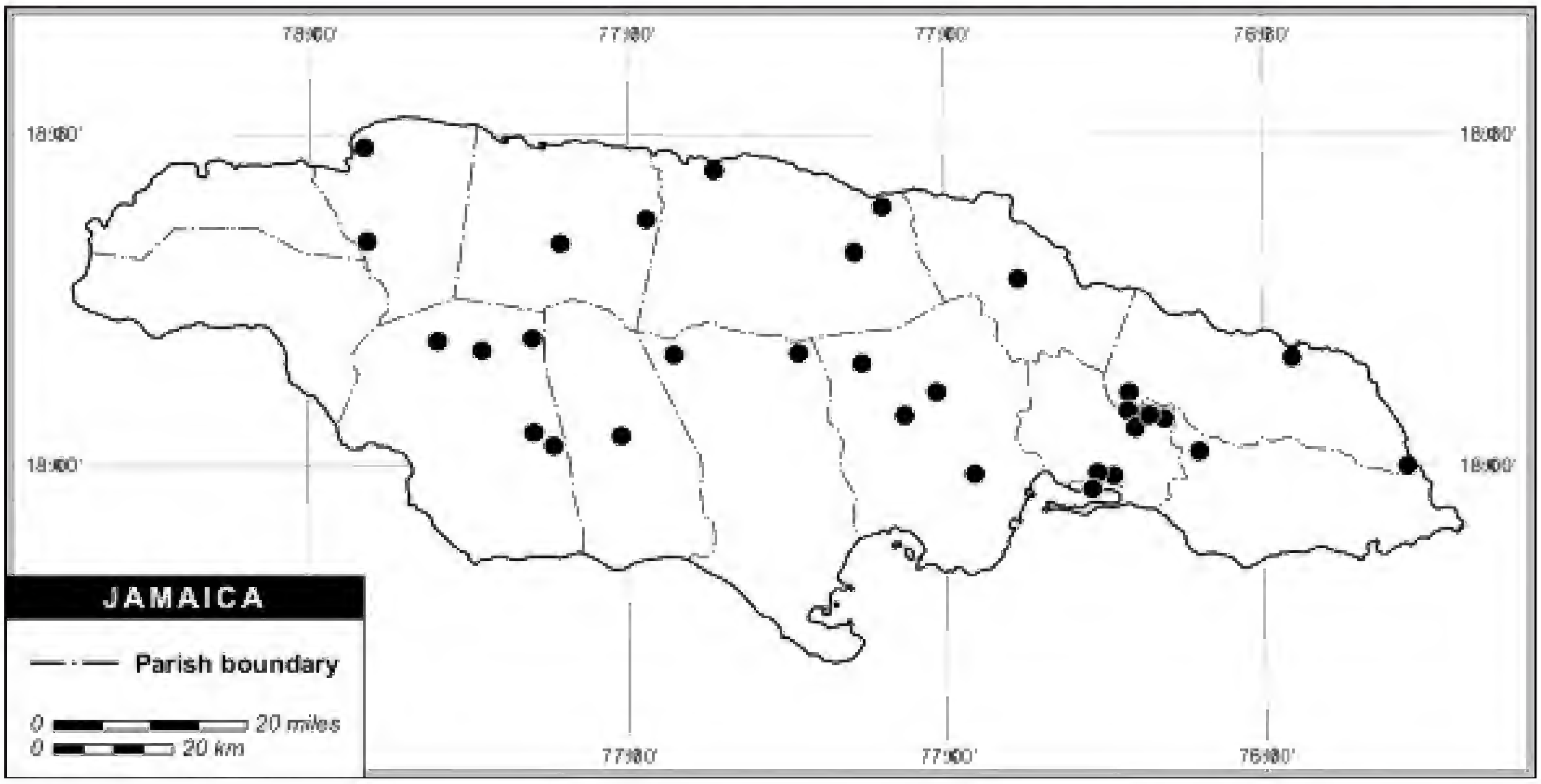

Figure 75. Map of Jamaica showing the locations where specimens of the Brazilian free-tailed bat, *Tadarida brasiliensis*, have been collected.

1970s nor did Carter and Dolan (1978) during their visit in 1976. Dobson (1878) treated *N. murinus* as a synonym of *N. brasiliensis*. G. M. Allen (1911) reported three specimens from Jamaica under the name *Nyctinomus brasiliensis musculus*, seeming to be unaware of the older name *N. murinus*. The next use of *Nyctinomus murinus* was by Anthony (1918) when he applied the name to all populations in the Greater Antilles. Shamel (1931) used the name *Tadarida murina* for this taxon in his revision of the American members of the genus. He restricted the species to Jamaica, characterizing it by smaller size, shorter ear, and reddish chocolate brown color. In 1955, Schwartz (1955) reviewed taxa of the "*brasiliensis*" group of the genus *Tadarida*. He concluded that all members of the group should be considered to be a single species with nine subspecies. Schwartz (1955) used the name *Tadarida brasiliensis murina* for the Jamaican populations of the group and that is the arrangement that we follow here.

Morphometrics.—Table 4 presents external and cranial measurements of 10 male and seven female Brazilian free-tailed bats from Jamaica. There is no significant secondary sexual variation between the males and females. The sexes average the same for three of the measurements—interorbital constriction, postorbital constriction, and length of the maxillary toothrow. Males average slightly larger for four of the measurements (length of forearm, mastoid breadth, palatal length, and breadth across the upper molars) and females for three (greatest length of skull, condylobasal length, and zygomatic breadth).

Shamel (1931) gives external measurements for eight males and two females and cranial measurements for three males and two females from Jamaica.

Natural history.—Although Brazilian free-tailed bats (Fig. 76) probably were primarily cave-dwellers prior to human occupation of the island, they are now most frequently found in buildings. Our large sample from the Green Grotto (see account for *Pteronotus macleayi* for full description of this cave) consisted of males, all of which were captured at the entrance of the cave (Figs. 25-26). In addition to this sample, we have examined contemporary specimens from at least four other caves. Two of these caves for which some information is available are Swansea Cave and Salmon Gully Cave, whereas Peru Cave (NMNH specimens) is discussed in the *Pteronotus parnellii* account, and we know nothing of the situation at Golden Grove Cave. Swansea Cave (cave 232) is a dry passage cave of some 1170 m. There are at least three major ceiling

Figure 76. View of the head of *Tadarida brasiliensis*.

collapses or cockpits that must be traversed, with the first reaching daylight (Fincham 1997). The bat colony is located between the second and third collapses, which are in the longest section of the cave. This portion of the cave is described as "an enormous 'railway-tunnel' with a floor of guano-covered mud" (Fincham 1997). Salmon Gully Cave (cave 100) is a chamber-type cave about 66 m in length. The entrance is a 20 m descent into a collapse. There is a large cave opening on the northeast side of the collapse, which leads to an ascending passage that is up to 30 m wide (Fincham 1997). The floor of most of the chamber is covered with guano from the colony of Brazilian free-tailed bats.

Both Osburn (1865) and Goodwin (1970) present excellent descriptions of colonies of Brazilian free-tailed bats in or around buildings. At Mahogany Hall, Osburn (1865) caught several individuals as they entered a house at night. They were roosting beneath the shingles of the house and finding their way inside through chinks. In early December Osburn (1865) observed they became active between 5:30 and 6:00 PM, just after sundown, and returned as late as 10 PM.

At Rowington Park, Osburn (1865, see Tomes 1861a) had the opportunity to observe a colony of Brazilian free-tailed bats that occupied the attic and also lived under roof shingles. The bats gained access to the attic via a crack in the boarding that crossed a gable. Although the attic was extremely hot in day time, the bats roosted in tight clusters. One of these clusters had 14 individuals. Osburn (1865) observed that not all of the bats were asleep with several at any one time stretching and grooming. He noted that in late March the bats exited about 6:30 PM and returned between and 8 and 9 PM. However, the bats remained active all night and probably indulged in a second round of feeding, returning to roost between 5 and 6 AM "in the grey of the morning." Osburn (1865) found that as many as a "half a dozen may often be found behind pictures in houses not much disturbed by housemaids."

Goodwin (1970) found two colonies during his work on Jamaica. One colony of about 75 individuals was found behind a window shutter on a frame house in Hardwar Gap. This location is at 1330 m in a rainforest where the temperature was about 18° C at 3 PM when the colony was discovered on 27 January.

The torpid bats were tightly packed in a small area behind the shutter. It took 10 minutes or more before they were able to fly away. The second colony was found on the campus of the University of the West Indies in Mona. This colony of 20 to 30 individuals was observed to exit just after sunset from a crack in a wall in a concrete building. The sex ratio at each site was three males to four females (Goodwin 1970).

Notes accompanying some of the museum specimens examined by us indicated that the individuals were taken from an old building in Hector's River and another was caught in a bedroom. A specimen from Whitfield Hall, Penlyne, was removed from a colony in the roof of Whitfield Hall. The elevation of this site is about 1300 m, which is similar to Hardwar Gap. Specimens from Newcastle were removed from a rock crevice. The specimens taken in our field work from near Watermount were all netted over a large, tree-lined stream on the night of 23 July. The sample of 20 individuals consisted of three males and 17 females. Many of the females were reproductively active, which we interpret to indicate that a maternity colony was nearby. This locality was near Swansea Cave so these individuals might have come from there. The three specimens from Mason River Research Station were two males and one female netted over a pond that was approximately 15 m in diameter. This was an area in intense agricultural use and there were no trees in the vicinity of the pond. Other species taken on the night of 13 July were *Glossophaga soricina, Monophyllus redmani, Artibeus jamaicensis*, and *Molossus molossus*, which was by far the most abundant species.

Four males taken 12 April all had testes that measured 5 in length. The average testes length of 10 males taken on 6-7 July was 2.7 (2-4) and that of nine males taken between 14 and 23 July was 2.9 (1.5-4). A male obtained on 3 November had testes that were 4.5 long and two captured on 28 December both had testes measuring 4 (Goodwin 1970). None of nine females collected on 12-13 April evinced any gross reproductive activity. A female taken on 24 June contained a single well-developed male embryo with a crown-rump length of 27. Of five females netted on 27 June, four carried embryos that measured 18, 20, 21, and 22. A female obtained on 7 July carried an embryo measuring 29, whereas a female taken 14 July and two taken on 19 July evinced no gross reproductive activity. Thirteen of the 17 females netted on 23 July were lactating. The other four females evinced no gross reproductive activity. None of the females collected on 28 December contained an embryo (Goodwin 1970). Although these data are far from adequate, the reproductive pattern of the Brazilian free-tailed bat on Jamaica most closely resembles that of monestry (Wilson 1979).

Studying the annual variation in fat reserves of eight species of bats on Jamaica, McNab (1976) found that *Tadarida brasiliensis*, as other insectivorous species, had significantly less fat deposits in the dry season as compared with the wet season. Females had significantly more fat than males during the time of maximum fat reserves during the wet season, but this difference normally disappeared during the dry season. McNab's (1976) findings were consistent with the interpretation that insectivorous bats face the greatest seasonal variation in food availability because the number of flying insects is reduced during the dry season. Four males taken on 12 April had an average weight of 10.1 (9.6-10.5), whereas nine non-pregnant females taken on 12-13 April had an average weight of 9.5 (8.8-10.7).

Webster (1971) discovered two species of trematodes and one species of nematode infesting *Tadarida brasiliensis* from Golden Grove Cave. The trematode *Prosthodendrium (P.) swansoni* Macy 1936 was found in eight of 15 bats examined and *Urotrema scabridum* Braum 1900 was found in four of the 15 specimens. Webster (1971) described a new species of nematode, *Capillaria jamaicensis*, based on specimens recovered from the stomachs of nine of 15 hosts examined.

Specimens listed above from Peru Cave (33 AMNH), Wallingford Cave, and 7-rivers Cave are from owl pellet remains found in the caves (Koopman and Williams 1951).

Genetics.—The karyotype of *T. brasiliensis* has 2n = 48 and FN = 56 (Fig. 77). There is one large metacentric pair and 4 medium-sized pairs of biarmed autosomes, one of which is distinctly subtelocentric. There are eighteen pairs of acrocentric autosomes in a graded series from medium sized to minute. One of the largest pairs has a distinct secondary constriction proximal to the centromere. The X is medium sized

Figure 77. Karyotype of a male *Tadarida brasiliensis* from Green Grotto, 2 mi E Discovery Bay, St. Ann Parish (TK 8076; TTU 22267).

and metacentric, the Y is minute and acrocentric. Karyotypes were obtained from five males from Green Grotto, 2 mi E Discover Bay, St. Ann Parish.

Warner et al. (1974) also reported 2n = 48 and FN = 56 for *T. brasiliensis* from Texas, New Mexico, Arizona, and Louisiana in the United States. Our specimens from Jamaica have a karyotype that differs by the presence of one additional medium-sized biarmed pair and one fewer acrocentric pair. Warner et al. (1974) also consider one of the small acrocentric pairs to be subtelocentric thus resulting in identical FN counts between our study and theirs. We interpret the karyotype of Jamaican *T. brasiliensis* as being identical to that of *M. molossus* described next.

Molossus molossus milleri Johnson, 1952
Pallas' Mastiff Bat

Specimens examined (343).—CLARENDON PARISH: Mason River Research Station, 2.5 mi. W Kellits, 2300 ft., 2 (TTU). HANOVER PARISH: Flint River, 1.5 mi. E Sandy Bay, 13 (CM). KINGSTON PARISH: Tower Street, Kingston, 1 (IJ); *Kingston*, 1 (IJ). MANCHESTER PARISH: Mandeville, 5 (MCZ). ST. ANDREW PARISH: August Town, 3 (2 HZM, 1 ROM); *Havendale, Kingston*, 2 (ROM); *Hope Garden, Kingston*, 30 (AMNH); Kingston, 21 (20 AMNH, 1 IJ). ST. ANN PARISH: Queenhythe, 122 (20 CM, 102 TTU); 4 mi. E Runaway Bay, 1 (TTU); 0.5 mi. S, 0.5 mi. W Runaway Bay, 22 (TTU). ST. CATHERINE PARISH: 0.2 mi. E Watermount, 33 (CM). ST. ELIZABETH PARISH: Accompong Town, 1500 ft., 2 (NMNH); Balaclava, 3 (AMNH); Pepper, 2 (NMNH); Peru Cave, Goshen, 1 (AMNH). ST. JAMES PARISH: *Snug Harbor, Montego Bay*, 1 (NMNH); Montego Bay, 2 (NMNH). ST. MARY PARISH: Frankfort, 29 (COLU); Retreat, 1 (BMNH). TRELAWNY PARISH: Commondo, ca. 1.5 mi. NW Quick Step, 7 (NMNH); Duanvale, 18 (TTU). WESTMORELAND PARISH: Lochiel, 2 mi. E Savanna-La-Mar, 2 (AMNH); Mount Edgecombe, 1 (BMNH). PARISH UNKNOWN: no specific locality, 20 (7 BMNH, 12 NMNH, 1 ROM).

Additional records.—HANOVER PARISH: Shettlewood (Osburn 1865). ST. ANN PARISH: *Mount Pleasant* (Osburn 1865). TRELAWNY PARISH: Windsor (Osburn 1865). WESTMORELAND PARISH: *Belmont* (Gosse 1851:295); Monarva Cave (McFarlane 1985, 1997).

Distribution.—Figure 78 shows collecting localities for *Molossus molossus* on Jamaica. The distribution of the Pallas' mastiff bat on Jamaica is interesting, especially in comparison to that of the other small molossid, *Tadarida brasiliensis*. Pallas' mastiff bat is

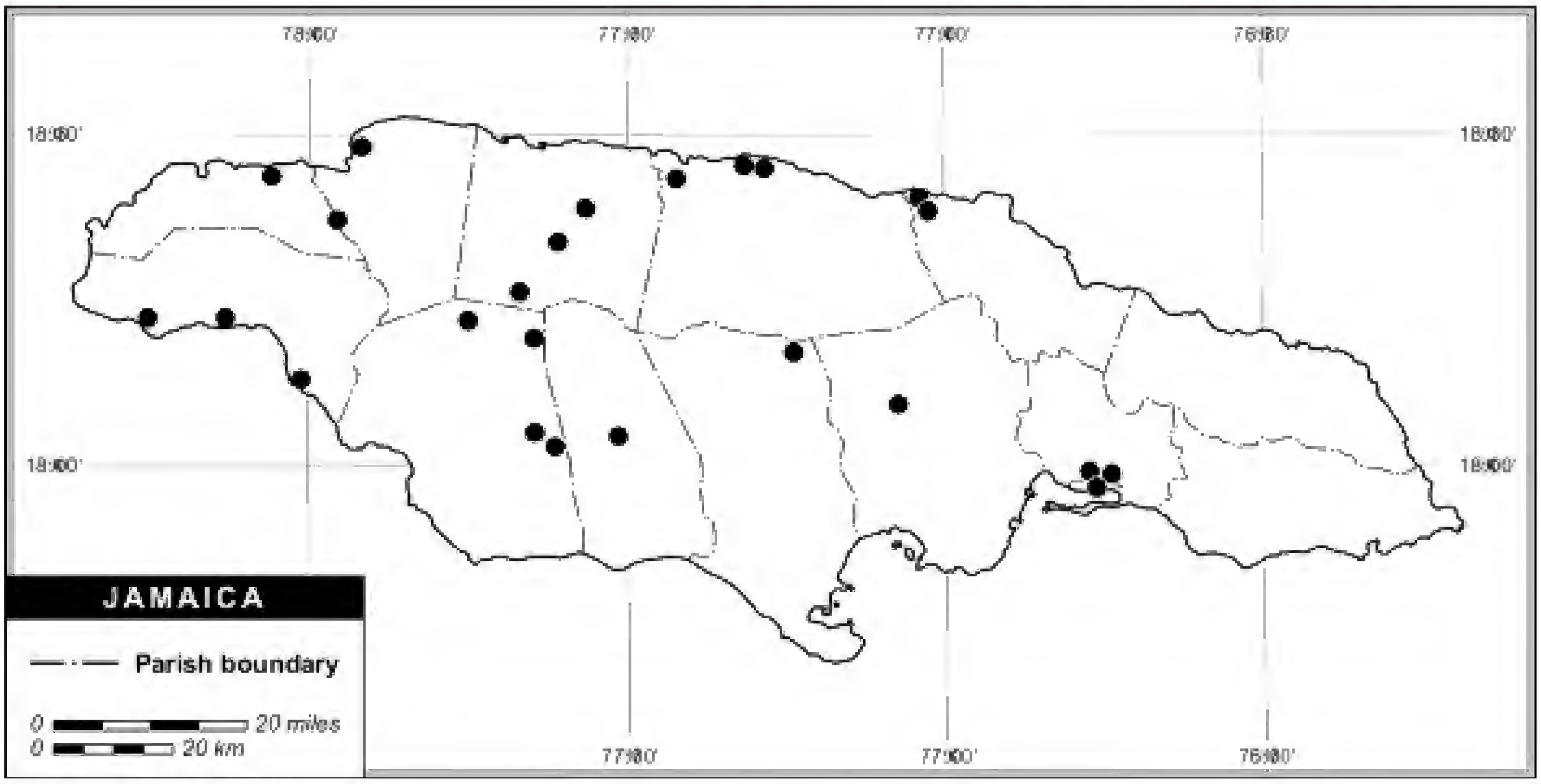

Figure 78. Map of Jamaica showing the locations where specimens of Pallas' mastiff bat, *Molossus molussus*, have been collected.

found at low and intermediate elevations on the island, but it is absent from elevations as high as where *T. brasiliensis* occurs . Both species are absent from the dry, hot southern coast, with exception of the Kingston area. There are records of this species from both Westmoreland and Hanover parishes, but there are no records from the eastern-most parishes of Portland and St. Thomas, which is difficult to explain given the considerable collecting effort in these areas. Pallas' mastiff bats occur on most of the islands in the West Indies except the Bahamas. On the mainland the species occurs from northern Mexico through Central America (Hall 1981) into the northern two-thirds of South America (Koopman 1982). The subspecies *M. m. milleri* is endemic to Jamaica (Hall 1981).

Systematics.—Our understanding of the systematics of both island and mainland populations of small bats of the genus *Molossus* remains in a state of flux with considerable disagreement among experts. This problem is compounded by confusion concerning the nomenclature of the group (Hershkovitz 1949; Miller 1913a). Husson (1962) wrote an excellent discussion of the issues and selected a lectotype for the name *Vespertilio Molossus* Pallas, 1766, thereby affixing the name to the present species and fixing the type locality for the species as Martinique. The small-sized members of the genus in the Antilles are now considered to be members of a single species to which the name *Molossus molossus* should apply.

Miller (1913a) in his review of the genus *Molossus* treated the described taxa at that time as distinct species. He applied the name *Molossus fuliginosus* to bats from Jamaica based on a taxon described earlier by Gray (1838). Gray (1838) did not indicate the geographic origin of the holotype for this taxon, but Dobson (1878) indicated that it was a Jamaican specimen submitted by "J. Bell, Eq." Hershkovitz (1949) questioned the validity of many of the species of small *Molossus* recognized by Miller (1913a) even at the subspecific level. However, Hershkovitz recommend preservation of the names at the subspecific level under *Molossus major* pending a revision of the group.

Johnson (1952) presented evidence that the name *Molossus fuliginosus*, Gray 1838, is preoccupied by *Molossus fuliginosus* (Cooper 1837), which is a bat from Milledgeville, Georgia, currently treated as a junior synonym of *Tadarida brasiliensis cynocephala*. Johnson (1952) could find no other valid name for the Jamaican population so proposed the name *Molossus milleri*. This name has the same lectotype and type locality as Gray's name. Carter and Dolan (1978) examined types in European museums and discussed the situation with the three potential specimens that could be selected as the lectotype and agreed that a specimen from Jamaica was selected by Dobson (1878) for this designation. However, they could not locate the lectotype so they listed a paralectotype from "Bermuda" submitted by Thomas Cottle. Independently, the lectotype was found during a visit to the British Museum (Natural History) by one of us (Genoways) in the mid-1970s. It is an unregistered female preserved in fluid (as indicated by Dobson) with the skull not removed. The label says that the specimen was presented by T. Bell (name is believed to be Thomas and not "J." as reported by Dobson). Examination of this specimen indicated that it is a small-sized member of the genus *Molossus* for which we think the correct trinomial at this time is *Molossus molossus milleri*.

Antillean island populations of *Molossus molossus* are badly in need of taxonomic revision. Both Genoways et al. (1981) and Dolan (1989) found significant morphological differences among some of these island populations, but a more comprehensive analysis is needed, using samples from all of the Antilles.

Morphometrics.—Table 4 presents the external and cranial measurements of 10 male and 10 female Pallas' mastiff bats from 1/2 mi S, 1/2 mi W Runaway Bay. Males were found to be significantly larger than females in all measurements. The differences were significant ($P = 0.05$) for two measurements (length of forearm and postorbital constriction), at the $P = 0.01$ level for three measurements (palatal length, length of maxillary toothrow, and breadth across upper molars), and at the $P = 0.001$ level for the remaining five measurements. Similar levels of secondary sexual variation were found by Genoways et al. (1981) for samples from Jamaica, Guadeloupe, and Trinidad. The highest degree of secondary sexual variation was found in the samples from Guadeloupe.

When they compared males among three separate samples of specimens collected on Jamaica, Genoways et al. (1981) found that there were significant differences in three of the measurements—greatest length of skull, zygomatic breadth, and length of the maxillary toothrow. When the females from these same three samples were compared, they differed significantly in greatest length of skull. Whether or not these morphological differences among samples have biological importance is unknown. But at the least such intraisland geographic differentiation is expected to complicate analyses of interisland geographic variation.

G. M. Allen (1911) presents the measurements of a specimen from Mandeville. Genoways et al. (1981) present data for external and cranial measurements of three samples of Pallas' mastiff bat from Jamaica, including those from Duanvale, 1/2 mi S, 1/2 mi W Runaway Bay, and Queenhythe.

Natural history.—Although Pallas' mastiff bat (Fig. 79) along with the Jamaican fruit-eating bat are the most abundant species of bats on the island, we know relatively little about the habitat preferences of *M. molossus* beyond the use of anthropogenic structures. We have only one record of the species from a cave on Jamaica. The conditions under which the specimen was taken in Monarva Cave is discussed in detail in McFarlane (1985) and presented in his account of *Natalus micropus*. The single specimen from Peru Cave is based on a partial cranium recovered from an owl pellet.

Early accounts of the capture of this species on Jamaica could provide clues to the original roosting habitat used by *M. molossus*. Gosse (1851) discussed the first specimen that he examined, which was obtained in late January at Mount Edgecombe when "Some labourers, felling a decayed Thatch-Palm (*Thrinax*), found the hollow trunk to be tenanted by Bats." About a month later another thatch-palm was knocked down and a large group of bats was found in a hollow in the trunk. Gosse (1851) examined 43 of these specimens and they were all males. At Belmont in May 1846, Gosse (1851) examined two females of *M. molossus* that had been caught by a servant in the evening inside the house. Osburn (1865) described going with local residents to cut down dead coconut palms trees that had lost their tops and had holes in the trunk drilled by woodpeckers. From one tree near Windsor, they recovered three individuals, but from another tree between 150 and 200 bats were discovered. Osburn (1865) described the bats as occurring in two holes in the trunk. He believed that the upper hole contained only males and the lower predominantly was occupied by females. Osburn (1865) examined

Figure 79. View of the head of *Molossus molossus*.

some powder found associated with these colonies and found it to be "entirely composed of fragments of the harder portions of insects." Osburn (1865) also found mastiff bats occupying the roofs of houses at Shettlewood and Mount Pleasant. If, as these data may indicate, tree holes were the prime roosting sites for Pallas' mastiff bats prior to human occupation of Jamaica, we can surmise that the species is now far more abundant than in the past given the fact that they typically use buildings as roost sites.

Goodwin (1970) gives a detailed description of a colony of mastiff bats in the attic of an old beach house on the Prospect Estate in Frankfort. Approximately 300 bats occupied an attic space that was 12 m by 6 m and 2 m at the peak. Most of the bats were clustered in two large groups located at the ends of the room. Some individuals were wedged in cracks and the angles of the rafters, but none was found hanging free. Goodwin (1970) described the attic as "unbearably hot and dry" with the floor covered in guano "that consisted of fragments of insect integument." Goodwin (1970) also found a colony in the hollow trunk of a dead coconut palm near Retreat. The colony, which consisted of approximately 50 individuals, was located about 6 m above the ground. In both colonies Goodwin (1970) found the sex ratio to be about one male to three females with no apparent segregation of the sexes.

We collected mastiff bats in Duanvale as they exited from a number of buildings in town (Fig. 80), particularly from under the eaves of the large stone church. The bats appeared to be exiting all along the south side of the church where we were stationed with our nets. The church was about two stories tall and the bats could be seen dropping out from holes and opening their wings as they fell toward the ground. At several locations such as Flint River, 4 mi. E of Runaway Bay, and near Watermount, mastiff bats were netted over large rivers and streams. In these situations, we believe that the bats were using these as flyway to move between roosts and foraging areas. At Mason River Station, 1/2 mi. S, 1/2 mi. W Runaway Bay, and Queenhythe, mastiff bats were netted over ponds where we believe they were coming to

Figure 80. Photograph of some of the buildings in Duanvale, Trelawny Parish, Jamaica, from which *Molossus molossus* were observed exiting.

drink. This was particularly evident at the ponds at Queenhythe where these bats arrived in swarms just at dusk. There was still enough light that individual bats could be observed swooping down to touch the surface of water on repeated passes. The intense activity continued until about one hour after dark.

Seven males captured on 12 January had testes that averaged 5.7 (3-8) in length (Goodwin 1970). The average length of testes for 15 males collected on 3-4 July was 5.2 (4-7), for 10 taken on 12 July 4.8 (4-7), and for nine taken on 23 and 27 July 4.4 (3.5-5.5).

None of 22 females taken on 12 January contained embryos (Goodwin 1970). Females carrying single embryos were obtained on the following dates (crown-rump length in parentheses): 23 June (--); 4 July (22, 28); 12 July (14, 24, 25); 27 July (8). Lactating females were taken on 3 July (4 females), 4 July (8), and 5 July (1). Females evincing no gross reproductive activity were taken on the following dates: 3 July (9 females); 4 July (2); 5 July (1); 8 July (30); 12 July (31);14 July (1); 23 July (10); 27 July (15); 28 July (3). Because there is a lack of synchrony displayed by these females with some individuals at various stages of reproduction and others reproductively inactive during the same period, a reproductive pattern of aseasonal polyestry or continuous breeding is suggested (Wilson 1979).

McDaniel and Webb (1982) reported six specimens of the labidocarpine bat-mite *Parakosa tadarida* McDaniel and Lawrence 1962 from a bat captured at 1/2 mi. S, 1/2 mi. W Runaway Bay. Gosse (1851) found this species “infested with a curious parasitic insect, a species of *Trichodectes*.”

An adult male taken on 18 June weighed 18.5. A non-pregnant female captured on 21 January weighed 13.3.

Genetics.—The karyotype of *M. molossus* has 2n = 48 and FN = 56 (Fig. 81). There is one large metacentric pair and 4 medium-sized pairs of biarmed autosomes, one of which is distinctly subtelocentric. There are 18 pairs of acrocentric autosomes in a graded

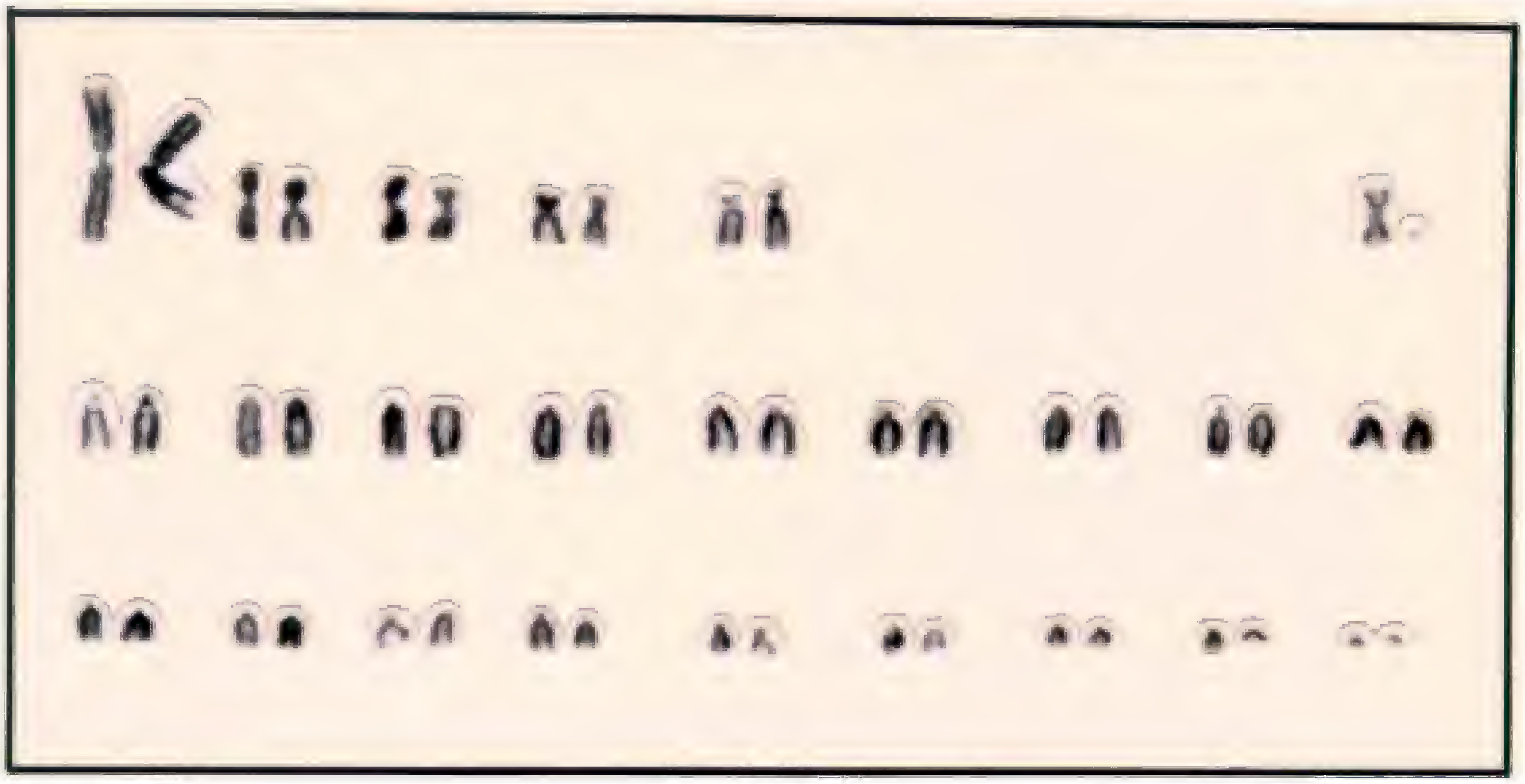

Figure 81. Karyotype of a male *Molossus molossus* from Queenhythe, St. Ann Parish (TK 9391; CM 44632).

series from medium sized to minute. One of the largest pairs has a distinct secondary constriction proximal to the centromere. The X is medium sized and metacentric, the Y is minute and acrocentric. Karyotypes were obtained from six males and three females from 0.5 mi. S, 0.5 mi. W Runaway Bay and two males from Queenhythe.

Warner et al. (1974) reported 2n = 48 and FN = 58 for *M. molossus* from Trinidad, Puerto Rico, Nicaragua, Columbia, and Peru. They also report identical karyotypes for *M. ater, M. sinaloae, M. aztecus,* and *M.* cf. *pygmaeus*. The karyotype we report for *M. molossus* from Jamaica is identical to those of the above species (Warner et al. 1974). We consider the FN of *M. molossus* and presumably the other species mentioned above to be 56 rather than 58 because the identification of one of the smallest autosomes as subtelocentric rather than acrocentric is variable due to the stage of contraction.

Remarks.—Osburn (1865) places Shettlewood in St. James Parish, but modern maps of Jamaica show the town in Hanover Parish.

RECENT SPECIES KNOWN ONLY FROM FOSSIL REMAINS

Koopman and Williams (1951) and Williams (1952) reported 11 species of bats from fossil and subfossil deposit in four caves (Wallingford Roadside Cave, Diary Cave = Runaway Bay Caves, Cambridge Cave, and Portland Cave) on Jamaica. Of these species, nine species remain part of the modern chiropteran fauna of the island, including *Pteronotus parnellii, Mormoops blainvillii, Macrotus waterhousii, Monophyllus redmani, Erophylla sezekorni, Phyllonycteris aphylla, Ariteus flavescens, Natalus stramineus*, and *Eptesicus* sp. Four additional species—*Glossophaga soricina, Artibeus jamaicensis, Molossus molossus*, and *Tadarida brasiliensis*—also were recovered, but only in surface and subsurface deposits. The authors believe that all of the deposits represented ancient owl pellets.

Among older fossils (Koopman and Williams 1951; Williams 1952) from Wallingford and Diary caves was a specimen that was used to describe and name a new species—*Tonatia saurophila* (Koopman and Williams 1951; Williams 1952). This new species was considered to be related to *Tonatia bidens* of the Central American mainland. Specimens of a second species, *Brachyphylla nana*, which is not extant on Jamaica, were recovered from deposits in three of the caves. These two species are discussed in more detail below.

Morgan (1989) was the first to report a third Recent species, *Mormoops megalophylla,* known only from fossil deposits on Jamaica. He (Morgan 1993, 2001) subsequently published two summaries of the 16 species of bats known from fossil deposits on Jamaica.

Mormoops megalophylla

Mormoops megalophylla is known on Jamaica from a single distal end of a humerus recovered from Swansea Cave, St. Catherine Parish (Morgan 1993, 2001). Although the stratum from which the specimen was recovered is undated, it contained "only indigenous Jamaican vertebrates." Modern populations of *Mormoops megalophylla* occur from southern Arizona and Texas to Honduras and El Salvador in Middle America. Elsewhere, in the West Indies *M. megalophylla* also has been reported from fossil deposits on Cuba, Hispaniola, Abaco, and Andros. Morgan (1993, 2001) in attempting to explain the extinction of this species in the West Indies cited environmental changes including rising sea level as factors in the loss of this cave-dwelling species. The ages of these deposits have been estimated to be late Pleistocene to early Holocene (40,000 to 4500 BP) according to Morgan and Woods (1986) and Morgan (1993).

Tonatia saurophila saurophila

Koopman and Williams (1951) described *Tonatia saurophila* based on two partial mandibles from Wallingford Roadside Cave and three rostra from Diary Cave (= Runaway Bay Cave). The ages of these deposits were estimated as Late Pleistocene to early Holocene (40,000 to 4500 BP) according to Morgan and Woods (1986) and Morgan (1993). Koopman and Williams (1951) distinguished *T. saurophila* from *T. bidens* of the mainland based on its slightly smaller size, slightly lower coronoid process, slightly more bulbous forehead, and details of the upper and lower dentitions. After he examined more specimens of *T. saurophila,* Koopman (1976a) reduced its status to a subspecies of *T. bidens*. Subsequently, Williams et al. (1995) demonstrated that two different species of *Tonatia* had been combined under a single name *T. bidens.* One result was that the name *T. bidens* now is geographically restricted to the population spread through Brazil, Paraguay, and northern Argentina.

Tonatia saurophila is the oldest available name for the remaining group of bats, which formerly were identified as *T. bidens* based on the Jamaican fossils. Williams et al. (1995) placed bats from Central America and northwestern South America under the name *Tonatia saurophila bakeri.* They used the name *T. s. maresi* for the population that occurs from Venezuela eastward through the Guianas into northern Brazil and southward along the eastern slope of the Andes to southern Peru. They then restricted the name *T. s. saurophila* to the fossil specimens known only from Jamaica.

Williams (1952) speculated on the possibility that *Tonatia* was directly replaced by *Macrotus* on Jamaica. His supposition was based on the limited sample of fossils. Both species feed on insects and fruit (Gardner 1977), but neither of these resources would seem to be limiting on an island the size of Jamaica. Alternatively, we hypothesize that *Tonatia* was not successful on Jamaica for reasons other than direct competition. This hypothesis is based on the fact that the genus is absent on all islands except Trinidad (Carter et al. 1981), which essentially has a mainland chiropteran fauna. The genus *Macrotus*, on the other hand, has been quite successful in island faunas occurring throughout the Greater Antilles and on many of the small islands in the Bahamas as well as islands off of the west coast of Mexico (Hall 1981). It should also be noted that Jamaica lies near the northern limit of the geographic ranges of members of the genus *Tonatia* and that shifting environmental conditions may have led to its extinction on Jamaica.

Brachyphylla nana

Koopman and Williams (1951) reported *Brachyphylla pumila* from Jamaica based on eight partial mandibles and three rostra from Dairy Cave on the north side of the island. Williams (1952) reported an additional unspecified number of specimens of this species from Portland Cave on the south side of the island. The age of these deposits was estimated to be

Late Pleistocene to early Holocene (40,000 to 4500 BP) according to Morgan and Woods (1986) and Morgan (1993). McFarlane et al. (2002) reported fossil and subfossil remains of *B. nana* from the Jackson's Bay caves that were approximately 10,000 years old. *Brachyphylla pumila* was originally described from Hispaniola and at the time of the reports by Koopman and Williams (1951) and Williams (1952) the species was believed to be confined to that island. Swanepoel and Genoways (1978) analyzed geographic variation in the genus, recognizing two species—*B. cavernarum* and *B. nana*. *Brachyphylla pumila* was considered to be a junior synonym of the monotypic species *B. nana*. As currently understood, *B. nana* occurs on Cuba, Isle of Pines, Grand Cayman, Middle Caicos, and Hispaniola as well as the fossils on Jamaica.

Williams (1952) tried to explain the loss of *Brachyphylla* from the Jamaican fauna by arguing that there might have been competition between *Brachyphylla* and *Ariteus*. Subsequent to the arrival of the widespread *Artibeus jamaicensis, Ariteus* then became rare because of competition. We can find no support for these ideas. The genus *Brachyphylla* is an Antillean endemic. The species *Brachyphylla nana* occurs on Cuba, Hispaniola, Isle of Pines, and Grand Cayman with *Artibeus jamaicensis* and *Phyllops*, which is a close relative of *Ariteus*. The closely related *B. cavernarum* occurs together with *Artibeus jamaicensis* and other genera closely related to *Ariteus*—*Stenoderma* and *Ardops*—on Puerto Rico, the Virgin Islands, and most of the Lesser Antilles. We can see no reason why competition among these species should have functioned differently on Jamaica than on many of these much smaller islands.

Unfortunately, we do not have any really good explanation for the extinction of *B. nana* from Jamaica. The species was widely distributed on Jamaica at one time, which is reflected in the cave deposits on both the north and south shores of the island. Elsewhere in the Antilles, *B. nana* and *B. cavernarum* remain among the commonest bats in the chiropteran fauna. This enigma must, at least for now, be listed along with many others concerning the geographic distribution of species of bats in the West Indies.

SPECIES OF DUBIOUS OCCURRENCE

There are specimens of five species of bats in museum collections that are labeled as coming from Jamaica but are of species that have not been obtained during recent surveys of caves and using mist nets. Because many of these specimens are very old, the status of these species in relationship to the chiropteran fauna of Jamaica is difficult to assess. The temptation is to attribute these records to erroneous locality data or mixing of specimens before their arrival in the museums; however, there are at least two additional possibilities that must be considered. These might represent "accidental" or rare chance occurrences on Jamaica. One example is a natural arrival of individuals on the island followed by failure to colonize. Another example is bats that arrived on the island via indirect human assistance, such as traveling among food stores transported to the island by ships. Unfortunately, there are no hard data on such events and virtually no way to estimate how often individual bats reach the island alone or with members of their own sex and, thus, have no chance to colonize. On the other hand, unusual specimens might simply represent species that did colonize Jamaica but later went extinct. It should be noted that none of these rare specimens have been found among fossil remains from the island, so that fact might be construed as evidence that they did not colonize. We have included these species in this account because the status of these species remains to be determined

Vampyrum spectrum

Dobson (1878; G. M. Allen 1911) reported two specimens—one skin only and one skull—of *Vampyrum spectrum* in the collections of the British Museum (Natural History) from Jamaica. These specimens were both submitted to the collection by J. S. Redman, Esq. Examination of the material leads us to the conclusion that this skin and skull represent a single, unregistered individual. The numbers 3a, 70a, and 73a all seem to be associated with the specimen. The skin is in very poor condition giving the appearance that it may have been prepared from a specimen preserved in fluid or the relaxing of a taxidermy mount. The skull is that of an adult and is in good condition. External and cranial measurements of the specimen are as follows: length of forearm, 102.5; greatest length of skull, 51.3; condylobasal length, 42.5; zygomatic breadth, 23.3; interorbital constriction, 103; postorbital constriction, 7.7; mastoid breadth, 21.4; palatal length, 25.0; length of maxillary toothrow, 19.9; breadth across upper molars, 14.4.

The sole locality information associated with the specimen is "Jamaica." It must be remembered that J. S. Redman did submit specimens of bats from Jamaica to the British Museum (Natural History), which were being described as early as 1821 by W. E. Leach. We are confident that this large, conspicuous bat is not part of the current fauna of Jamaica, but its earlier status is unclear at this time.

Anoura geoffroyi

There are two specimens of *Anoura geoffroyi* in the collection of the Royal Ontario Museum (ROM 67558-59) from an unknown place on Jamaica. The information associated with the specimens indicates that the museum obtained the specimens from the University of the West Indies. *Anoura geoffroyi* is known in the West Indies only from Grenada at the opposite end of the arc of islands. The species is easily taken on Grenada in mist nets (Genoways et al. 1998) so we are relatively confident that this species is not present on Jamaica. Further, we believe that these specimens are an example of the mixing of locality data before the specimens reached the museum and that this species was never part of the Jamaican fauna.

Brachyphylla cavernarum

There is a single specimen (BMNH 9.1.4.59) of *Brachyphylla cavernarum* in the collection of the British Museum (Natural History) that indicates that it originated from Jamaica. The collector of the specimen is noted as "Surg. G. E. Dobson." Dobson did visit Jamaica before 1880 (Dobson 1880). The specimen is an adult female preserved in fluid with the skull not removed. The length of forearm of the specimen is 64.8 clearly indicating that it is *B. cavernarum* and not *B. nana* (Swanepoel and Genoways 1978). The latter species is known on Jamaica from fossil remains (Koopman and Williams 1951) and based upon its geographic distribution, including Cuba and Hispaniola, is the species that would be expected on Jamaica. We believe that the data associated with this specimen are erroneous and that this species has never occurred on Jamaica.

Carollia perspicillata

Dobson (1878) reported a single specimen of *Carollia perspicillata* in the collections of the British Museum (Natural History) that was obtained from Jamaica. This specimen is an adult female registered as number BMNH 48.7.17.4 that was obtained from Dr. A. Smith. The skin is stored in fluid with the skull removed. Pine (1972) assigned the specimen to *Carollia perspicillata* and we agree with that assignment. This species, which is widespread and common in Central America and South America, is known elsewhere in the West Indies only based upon six specimens from Redonda and one from Grenada. Pine (1972) considered the record from Redonda as doubtful. We are confident that *Carollia* does not currently occur on Jamaica; as with the individual from Grenada (Genoways et al. 1998) the specimen from Jamaica also must be considered as either an erroneous record or an accidental occurrence. The data are currently insufficient to select between these alternatives. Available cranial measurements for the specimen are as follows: greatest length of skull, 23.4; condylobasal length, 20.7; interorbital breadth, 5.9; postorbital constriction, 5.5; mastoid breadth, 11.5; palatal length, 10.3; length of maxillary toothrow, 7.6; breadth across upper molars, 8.4.

Sturnira lilium

Dobson (1878; G. M. Allen 1911) recorded two specimens of *Sturnira lilium* in the collection of the British Museum (Natural History) from Jamaica. One of the specimens was received from P. H. Gosse and one from J. Gould. A search of these collections revealed a skin and a skull still in the collection labeled from Jamaica, which were given separate registration numbers, respectively, BMNH 49.5.30.12 and BMNH 49.5.30.3. Examination of the data associated with the two items leads us to the conclusion that they pertain to a single individual and are the one deposited by P. H. Gosse. The location of the Gould specimen is unknown. The skin is in poor condition, but it is recognizable as *Sturnira lilium*. The skull is badly broken, consisting only of the rostral, orbital, and palatal regions. The lower jaw is complete and most of the teeth are still in place. Available external and cranial measurements are as follows: length of forearm, 41.9; interorbital constriction, 5.4; postorbital constriction, 5.4; length of maxillary toothrow, 6.5; breadth across upper molars, 7.4.

Elsewhere in the Antilles, *Sturnira lilium* is known from the southern Lesser Antilles as far north as Dominica (Genoways et al. 2001) and is then replaced on Guadeloupe and Montserrat by *Sturnira thomasi* (Genoways 1998). No member of the genus is known to be part of either the Recent or fossil faunas of any island in the Greater Antilles. Gosse (1851) gives a detailed account of his natural history findings on Jamaica. He recognized species of bats that he was capturing with excellent accuracy for the time. He gives detailed descriptions of the specimens and their capture for each species that he obtained. There is nothing in his account that can be associated with *Sturnira lilium.* This leads us to the conclusion that the specimen associated with Gosse has erroneous locality information. However, the final determination of the status of *Sturnira lilium* on Jamaica must await the rediscovery and study of the specimen submitted to the museum by J. Gould.

DISCUSSION

Island populations of bats are intrinsically interesting and scientifically important. In the overview, there are basic questions of what are the bat faunas of individual islands, how do the faunas of islands differ, how do island faunas compare to the fauna of mainland regions, and what factors contributed to the current faunal compositions? At another level there are questions about speciation processes, historical zoogeographic patterns, and population sizes and dynamics Jamaica is a relatively large, ecologically complex island that geographically is one of two main portals into the Antilles from the Mesoamerican mainland (Cuba being the other). Thus, in addition to the usual interesting questions about its bats, there also is the possibility that studies of the Jamaican fauna will shed some light on the dispersal and colonization process. Collectively, these questions and topics combine into a complex biological problem. With this in mind, we have organized the following discussion of the Jamaican fauna around a series of subsections that consider traditional aspects of island biogeography.

Diversity of the Chiropteran Fauna

Potentially, an island fauna could be identical to the fauna of a nearby mainland region; however, island faunas rarely are identical or are as diverse as mainland faunas. From an ecological perspective island habitat structure, diversity, and food resources typically do not mimic the mainland and if this is the case, one would not expect the bat faunas to be identical. Alternatively, if an island is large and complex enough to approximate the adjacent mainland, differences in the bat faunal composition might be attributable to species differences in dispersal and colonization potential. Trinidad with 64 species comes nearest to approximating the mainland bat fauna of any island in the Caribbean and adjoining regions (Carter et al. 1981).

Wilson (1973) recognized seven trophic guilds in Neotropical Chiroptera. We have used Wilson's system of analyzing trophic structure because it seems more appropriate for an island fauna than are the more complicated systems introduced in recent years (Findley 1993; Willig 1986; Willig and Moulton 1989; Willig et al. 1993; Willig and Gannon 1996). Five of Wilson's seven guilds are represented in the modern fauna of Jamaica. Only the trophic guilds of carnivores and sanguinivores are absent.

In general, most papers on Caribbean bat faunas focus on the currently known distributions and a primary goal of collecting has been to identify and document the presence of species on an island-by-island basis. As our knowledge of island bat faunas becomes more complete, the apparent absence of certain species or groups of species takes on added importance as a biological and zoogeographic issue. In the present case, we are left to hypothesize why neither saguinivorous nor carnivorous bats occur on Jamaica. Presumably, the absence of such species tells us something about their biology or historical factors on Jamaica, or both.

In historically modern times, vampire bats are abundant members of the chiropteran fauna of tropical mainland bordering the Caribbean. They also are common on the island of Trinidad. The current absence of vampire bats on Cuba, Jamaica, and other islands thus is interesting. McNab (1971) attributed this absence to a lack of large mammals on the islands. Support for this explanation comes from fossil evidence, which documents that vampire bats were present on Cuba at the time that ground sloths and large rodents occurred there (Genoways et al. 2001; Morgan 2001; Rodríguez-Durán and Kunz 2001). Loss or even reduction in abundance of potential food sources therefore might be one explanation for the disappearance of vampire bats from the Cuban fauna and the absence of vampire bats from Jamaica and other islands in the Greater Antilles. At the same time, cattle and other livestock have been kept in substantial numbers on Jamaica and most other islands since colonial times. Northward dispersal from Trinidad into the Lesser Antilles would be a logical pathway for vampire bats to colonize the West Indian islands. The absence—or lack of documentation—of such movement in the last 500 years might be interpreted as evidence that vampire bats do not easily or quickly overcome the saltwater barrier.

The absence of a chiropteran carnivore guild on West Indian islands is at first more difficult to explain than is the absence of vampire bats. Because of the abundance of terrestrial vertebrates such as frogs, lizards, birds, and other bats (McNab 1971; Humphrey and Bonaccorso 1979), we think that the absence of carnivorous bats can be attributed to the small pool of species available for colonization. There are four candidate species—*Chrotopterus auritus*, *Phyllostomus hastatus, Trachops cirrhosus,* and *Vampyrum spectrum*—to fill this guild (Gardner 1977). All of these species currently occur in the Nicaraguan-Honduran portions of Central America. If their current distribution is indicative of their distribution in the Late Pleistocene, they should have been available geographically to reach Jamaica. However, three of these four species are among the largest sized New World bats, so perhaps their metabolic requirements limit over-water dispersal and successful colonization of islands, even large islands such as Jamaica. As is typical of top carnivores, three of these four species have low local population densities thereby further decreasing the statistical probability of their dispersal to Jamaica and the Greater Antilles. At the same time, perhaps one or more of these species did reach Jamaica but the island population failed to persist. An old British Museum specimen of *V. spectrum* is labeled as being from Jamaica and this raises the question whether or not the species once occurred there. If the locality information is correct, this species was present and persisted into the 19th century on Jamaica. If it ever did exist on Jamaica, the population eventually went extinct because it clearly is absent now. Moreover, another of the carnivorous species, *Phyllostomus hastatus*, is established on Trinidad. Although the over-water dispersal from South America to Trinidad is not equivalent to reaching Jamaica from Central America, its presence on Trinidad nevertheless documents dispersal and colonization by a carnivorous bat. Finally, among the carnivorous bats, we think that *Trachops cirrhosus,* which feeds on tropical frogs, would be the most logical candidate species that could fill the carnivore guild and survive on some of the large West Indian islands. Its absence cannot be explained in terms of scarcity of food resources so other factors probably affect its capacity to disperse and colonize. In the end, it is difficult to develop a testable hypothesis to explain the absence of a carnivore guild on Jamaica. In the overview it is clear that carnivorous bats have not exploited habitats and food resources in the Antilles. But the reasons are unknown and perhaps multiple. The list of reasons logically could include (1) low mainland source population densities, (2) metabolic requirements associated with body size, (3) foraging behaviors that make long distance flights unlikely, and (4) time span of a species presence on adjacent mainland.

Aerial insectivores dominate the trophic guilds of the Jamaican chiropteran fauna. At least 13 species would be primarily classified in this trophic guild including *Mormoops blainvillii, Pteronotus macleayii, P. parnellii, P. quadridens, Natalus micropus, N. stramineus, Lasiurus degelidus, Eptesicus lynni, Eumops auripendulus, E. glaucinus, Tadarida brasiliensis, Nyctinomops macrotis,* and *Molossus molossus.* Also, *Macrotus waterhousii* could be placed in this group because Wilson (1973) split its trophic role into three guilds—0.5 aerial insectivore, 0.3 foliage gleaner, and 0.2 frugivore. Aerial insectivores have been found in earlier studies to dominate the chiropteran faunas of all four of the Greater Antillean islands (Genoways et al. 2001; Rodríguez-Durán and Kunz 2001) and this pattern would not change even if the fossil species were added to the modern fauna. The percentage of aerial insectivores on these four islands is over 50% and is far higher than in four mainland areas that are potential source areas in northern South America, Central America, and Mexico. Only the chiropteran faunas of the dry coastal islands off northern South America and the island of Dominica approach these levels of aerial insectivores. Our explanation for this guild's dominance is that the chiropteran fauna developed under drier conditions that favored this guild. Further, aerial insectivores spend substantial time flying and are more likely to disperse than most bats. Pregill and Olsen (1981) examining data from other vertebrate groups in the West Indies concluded that the region was drier during the last Pleistocene glaciation than it is now. During this period, they believed that xeric scrub forest predominated, with areas of arid savannahs and grasslands. These conditions apparently favored survival and colonization by aerial insectivores that reached Jamaica.

Nectivory is the guild with the next highest number of members with four species—*Glossophaga soricina, Monophyllus redmani, Erophylla sezekorni*, and *Phyllonycteris aphylla*. A chiropteran fauna having nectivory as the second largest guild also is characteristic of the other three Greater Antillean islands and unlike the four mainland areas studied by Genoways et al. (2001) where this guild is in fourth place or lower. However, comparison to suitable mainland regions is complicated by the fact that three of the Jamaican nectivores—*M. redmani*, *E. sezekorni*, and *P. aphylla*—do not occur on the mainland. The evolution of three endemic Antillean genera of nectivores suggests that historical opportunities favored nectivory and that the Jamaican ecosystem is not historically or biologically comparable to the mainland, even though there is superficial physical similarity.

The frugivore guild on Jamaica constitutes only 9% of the extant fauna and is represented by only two species—*Artibeus jamaicensis*, a common and geographically widespread mainland species, and *Ariteus flavescens*, a genus endemic to Jamaica. Among localities studied by Genoways et al. (2001), 9% is the lowest percentage for any of the other Greater Antillean, Lesser Antillean, and coastal South American islands except Aruba. The Jamaican fauna also is very different from four mainland regions studied by Genoways et al. (2001). In these mainland regions the lowest percentage of frugivores was 23.9% (of 48 species) on the Yucatan Peninsula.

Collectively, the Jamaican frugivore and nectivore guilds illustrate the challenge that arises in island studies. In the frugivore guild one species (*Artibeus jamaicensis*) is a mainland disperser, whereas the other (*Ariteus flavescens*) is a Jamaican endemic. In the nectivore guild three of the four species are Antillean endemics. What affect does the presence of a fruit bat and three species of nectivores that do not occur on the mainland have on the trophic structure of Jamaica? At the very least these endemics complicate direct comparison to the mainland. More importantly perhaps, is the fact that none of these endemics is simply an endemic Jamaican or Antillean species of a geographically widespread mainland genus. Instead, these are four endemic genera, three of which are monotypic. Moreover, two of the endemics (*A. flavescens* and *E. sezekorni*) are not merely run-of-the-mill phyllostomid fruit- or nectar-feeding bats. As discussed in the individual species accounts, *A. flavescens* has an unique two-chambered stomach and a modified pyloris with a substantial number of gastrin cells (Menone et al. 1986). *Erophylla sezekorni* has a type of sexually dimorphic salivary gland that is unique among all studied mammals (Phillips et al. 1993). It could be coincidental, but at the least it is noteworthy that two of the endemics thus exhibit extraordinary specializations in organs linked to diet. At best we can only speculate about selection pressures and circumstances that led to the origin and evolution of endemic genera, but in a theoretical sense the Jamaica data would be consistent with the idea that the island trophic guilds are historically and ecologically unique relative to any mainland region. Moreover, the island trophic guilds quite possibly were more dynamic—less stable—than mainland systems. All of this is important because there are two possible ways to visualize island ecosystems: (1) a duplicate of the mainland system occurs on an island and thus awaits exploitation by mainland species able to disperse and colonize; and (2) the island system is independent from the mainland and dynamic over time so that the fauna at any given time will be a combination of colonizers and locally adapted specialists. In the case of Jamaica, the data are more consistent with the second of these two options.

Unusual ecological circumstances and a dynamic situation also are consistent with the loss of at least one frugivorous species, *Brachyphylla nana,* from the Jamaican bat fauna. It also makes it difficult to argue that the local extinction of *B. nana* from the Jamaican fauna resulted from competition with other frugivores as proposed by earlier authors (Koopman and Williams 1951; Williams 1952). Most of the other Greater Antillean island faunas have at least three species of frugivores and most of these are the same species or close relatives of those that historically occurred on Jamaica.

The greater fishing bat, *Noctilio leporinus*, constitutes the piscivore guild on Jamaica as it does on the other West Indian and coastal islands and surrounding mainland. Because the piscivore guild is comprised of a single species, its percentage of the fauna is a function of the number of species in the fauna. Molecular data (Lewis Oritt et al. 2001) indicate that this guild only recently invaded the islands (within the last million years), therefore, any ecological interactions helping shape the Jamaican bat fauna could be new to the islands relative to the age of other members of the bat fauna.

No single species in the Jamaican chiropteran fauna can be assigned as primarily belonging to the foliage-gleaning guild. Several species are believed to do some gleaning of insects from foliage as part of their overall feeding strategy, which Genoways et al. (2001) estimated as 5.7% of the trophic structure on Jamaica. The leading species with this feeding strategy is *Macrotus waterhousii*, which was assigned a value of 0.3 for foliage gleaning by Wilson (1973). The other species believed to supplement their diets with foliage gleaning include *Glossophaga soricina, Monophyllus redmani, Phyllonycteris aphylla*, and *Artibeus jamaicensis.*

In summary, the trophic structures of the chiropteran faunas on Greater Antillean islands are quite similar to each other but substantially different from potential source areas on mainland. How the differences in trophic structure developed are not exactly known but undoubtedly can be attributed to several factors including biogeographic history, shifting climates, and resource availability. The presence of endemic species, including some unusual bats with unique diet-associated features, implies that island trophic structures are the consequence of dramatic evolutionary processes rather than simple haphazard dispersal and colonization events.

Local Extinctions in the Jamaican Fauna

It is difficult to explain local extinctions if Jamaican ecosystems are thought of as stable living opportunities and if one imagines that some trophic levels are available but either unfilled (for example, carnivores) or partially occupied (for example, frugivores) relative to what we find on the mainland. However, if dynamic processes were involved in the historical development of trophic structure on Jamaica, one should expect to find evidence of local (island) extinctions along with the previously discussed presence of specialized endemic species. Events on the island of Jamaica thus are seen as actively selecting and shaping the fauna rather than as passively preparing a landscape awaiting colonization.

Fossil evidence from cave deposits on several Greater Antillean islands document local extinctions as well as recent arrivals. It is clear from data obtained on Cuba, Jamaica, Puerto Rico, and the Bahamas, that changes have occurred in island bat faunas since the Pleistocene. Some of the local extinctions might have been the result of specific environmental shifts in the transition into the Holocene (Morgan 2001). Competition between ecologically similar species is another possibility that has been suggested by earlier authors (Koopman and Williams 1951; Williams 1952; Pumo et al. 1996).

Morgan (2001) explained the loss of obligate cave-dwelling bats in the West Indies as a result of rising sea levels. Two of the species of bats—*Mormoops megalophylla* and *Brachyphylla nana*—lost from the bat fauna of Jamaica could fall into this category. Fortunately for biologists studying bats on Jamaica, a fairly detailed paleoenvironmental reconstruction for the last 125,000 years is available based on deposits from Wallywash Great Pond in St. Elizabeth Parish (Curtis et al. 2001; Holmes et al. 1995; Holmes 1998; Street-Perrott et al. 1993). This research (Holmes 1998; Street-Perrott et al. 1993) has shown that the time from 125,000 years BP to 106,000 years BP was a dry period followed by a stable, wet, warm period until 93,000 years BP. McFarlane and Lundberg (2004) present evidence based on vertebrate fossil-bearing cave deposits of late Sangamonian age (prior to 100,000 years ago) that this period was characterized by enhanced storm or hurricane activity resulting in "hyper-flood" events. These events were relatively rare but widespread in the West Indies. From 93,000 years BP to at least 9500 years BP was a long dry cool period during which the fossil chiropteran assemblage probably developed and these conditions may explain the dominance of aerial insectivorous species in the fauna. The Wallywash Great Pond data (Holmes 1998; Street-Perrott et al. 1993) indicate three cycles of wet and dry conditions since 9500 years BP, but these are not precisely dated. However, McFarlane et al. (2002) working on cave deposits in the Portland Ridge area of southern Jamaica have described four paleoclimatic phases, including 16,500 to 10,000 years ago a dry period, 10,000 to 2000 intermittently wet, 2000 to 700 wet and humid, and 700 to present returning to a dry climate. This information supports Morgan's claim that changing environmental conditions could have played a role in the extirpation of the three species on Jamaica, especially during the Holocene.

Morgan (2001) calculated that the postglacial rise in sea levels at the end of the Pleistocene could have flooded seashore caves, which typically are found in weathered volcanic outcrops that form points of land extending beyond the beaches. Such flooding would impact obligate cave dwelling bats, especially those dependent on large, hot, humid caves, by loss of habitat. The Post-Pleistocene rise in sea level also could have had an environmental impact by reducing the overall sizes of islands and thus the habitat resources available to all species. Loss of caves could be a plausible explanation for the extinctions of island populations of *Mormoops megalophylla* throughout the Greater Antilles and Florida. The applicability of this explanation to the loss of *Brachyphylla nana,* which went extinct on Jamaica and three small dry islands (Andros, New Providence, and Cayman Brac), seems less probable. If sea level affect on shore caves were important, we would expect that *B. nana* also would have gone extinct on Cuba and Hispaniola and certainly on the small islands such as Grand Cayman, Grand Caicos, and Isla de Pinos where virtually all caves are at low elevation or sea level. For *Brachyphylla,* we propose a more complex set of environmental circumstances involving conditions unique to Jamaica, such as major hurricanes, at the time of local extinction.

Tonatia saurophila is another bat species that went extinct on Jamaica (Morgan 2001). This species takes a diet combining insects and fruit (Gardner 1977) and it is not an obligate cave dweller. It could be described as a "generalist" and generalist habits usually are believed to be an advantage for a species living in a variable environment. The reasons for the local extinction of this species might lie within short-term environmental impacts—such as tropical storms and hurricanes—rather than long-term changes (Zimmerman et al. 1996). Bellingham et al. (1992) documented the damage done to forests on Jamaica by Hurricane Gilbert in 1988. They found tree mortality to be patchy with as much as 30% severe damage in some areas on the Blue Mountains. They concluded that in areas "Where substantial numbers of seedlings [of gap-demanding species] become established the hurricane will have measurable effects for several centuries." Lugo et al. (2000) make the point that hurricanes damage rainforests in valleys and on slopes more than those on ridges, which would seem to maximize the impact on bat populations that forage more often in the valleys. They also make the point that "The most important result of hurricane damage in rainforests is a dramatic change in microenvironments of the forest." This is because much of the canopy is destroyed by hurricanes, with "Fruits, flowers, and leaves disappear[ing] for varying periods of time."

Hurricanes are known to significantly reduce bat populations on West Indian islands (Rodríguez-Durán and Kunz 2001). Hurricane Hugo was documented to have decreased bat populations on Puerto Rico (Gannon and Willig 1994) and Montserrat (Pedersen et al. 1996). Pedersen et al. (2005) raised this same issue in relation to the low levels of bat populations on St. Kitts following Hurricane Georges. Adams and Pedersen (1999) and Pedersen (2001) also have documented the impact of volcanic eruptions on Montserrat on the island's bat populations. They propose that some of the species with low population numbers (*Sturnira thomasi* and *Chiroderma improvisum*) prior to the most recent eruptions were extirpated from the island. Such local, short-term catastrophic events might be responsible for the loss of *Tonatia* on Jamaica, but local environmental catastrophes leave little or no evidence in the fossil record based on cave deposits.

Finally, as mentioned previously, there is questionable 19th Century evidence that *Vampyrum spectrum* occurred on Jamaica. If so, it is yet another species that is now extinct from the island fauna. Logging, clearing, and tropical agriculture are human activities that potentially could have affected these large-sized carnivorous bats if they indeed lived on Jamaica in historical times.

Island Size as a Factor in the Jamaican Bat Fauna

Species-area analyses have been used to examine the relationship between island area and the number of species present on an island (MacArthur 1972; Wright 1981). Our analyses of West Indian bat faunas (Fig. 82) gives a value $z = 0.21$ where z is the slope of the species-area relationship. Morgan and Woods (1986) and Griffiths and Klingener (1988) also reported a slope of $z = 0.21$ for West Indian mammal and bat faunas, respectively, whereas Wilcox (1980) reported $z = 0.24$ for bats, and 0.48 for land mammals in the West Indies. Wilcox reported a slope of $z = 0.24$ for breeding land birds and 0.38 for reptiles and amphibians and Davies and Smith (1998) reported z-values of 0.34 for beetles and 0.20 for butterflies in the West Indies. Davies and Smith (1998) noted that the slope

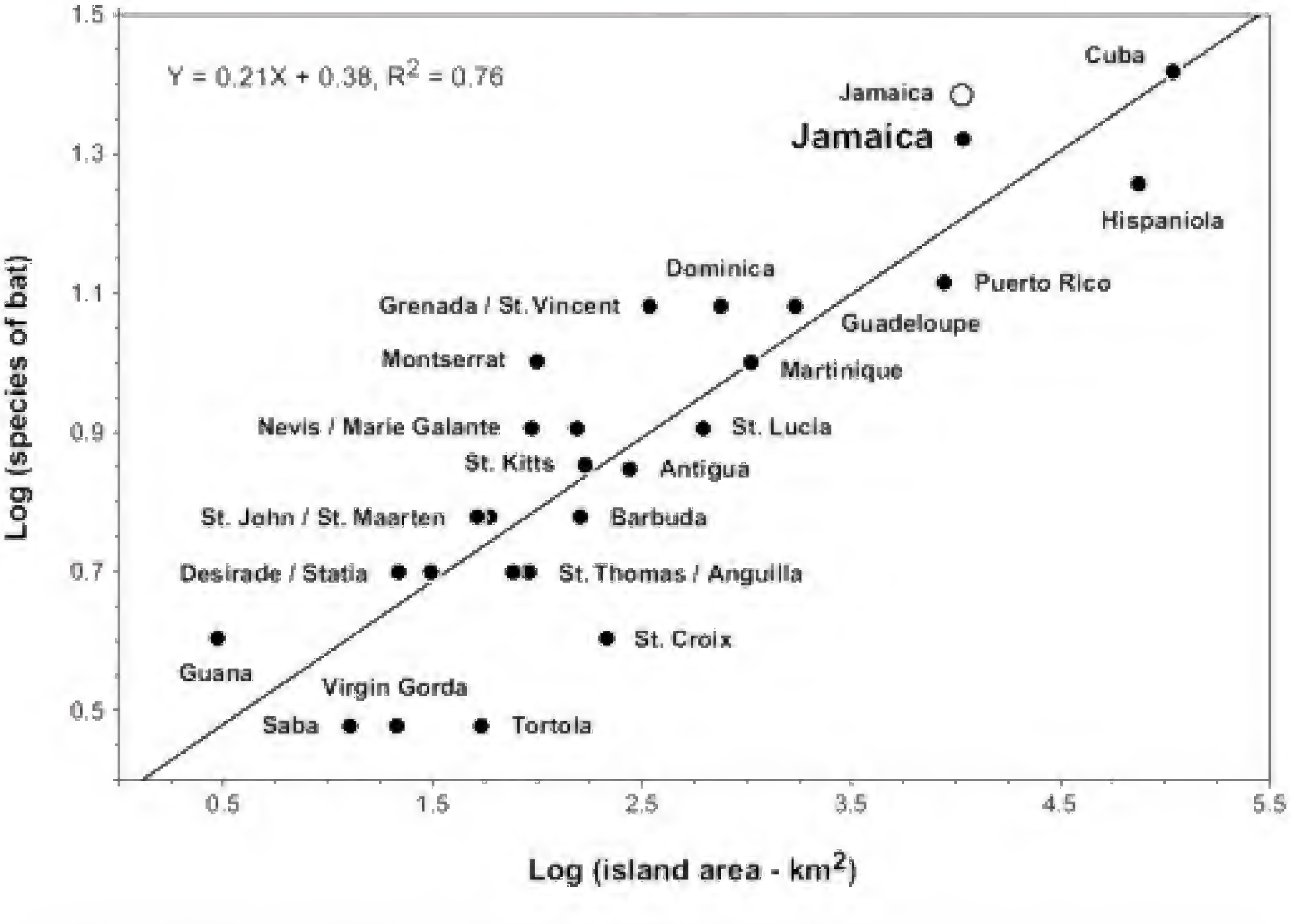

Figure 82. Species/area curve based on the published data (December 2003) for the chiropteran fauna on islands in the West Indies. "Jamaica" written in larger letters on the figure represents the living fauna of 21 species and in the smaller lettering it represents the fossil fauna of 24 species.

for butterflies was the flattest thus far reported for West Indian biota. Our analysis and that of Morgan and Woods (1986) show that bats have a similarly flat slope. Davies and Smith (1998) proposed that their data for butterflies could be interpreted to mean that butterflies had a propensity for dispersal and colonization or alternatively that butterflies have low extinction rates relative to other West Indian biota. Based on our knowledge of the fossil record for bats in the West Indies, the first explanation seems most plausible. Wilcox (1980) observed that "more highly vagile" species produce lower *z*-values.

Variance (R^2) estimates the amount of species diversity that can be explained by area alone. Our value of 76% for West Indian bats falls between the values of 69% found by Morgan and Woods (1986) for West Indian mammals generally and 88% found by Griffiths and Klingener (1988) for the West Indian bat faunas. The variance value for West Indian butterflies was even lower than any of mammal estimates at 64%. The position of Jamaica on Fig. 82 indicates that there are more species of bats on the island than the species-area curve would predict. This becomes even more exaggerated if fossil species are included (Fig. 82). In our analyses, Cuba falls as would be predicted and Puerto Rico and Hispaniola have less species than expected. These inter-island differences are likely explained by dispersal distances from the mainland sources of bats to the islands. The position of Jamaica above the curve may indicate that during Pleistocene glaciation and lowered sea level it was physically closer to mainland source populations and thus received more species than predicted by its area and current isolation from mainlands (Griffiths and Klingener 1988).

With 24% of the variance dependent on factors other than area, it is interesting to examine a species-altitude curve (Fig. 83, log of species number versus

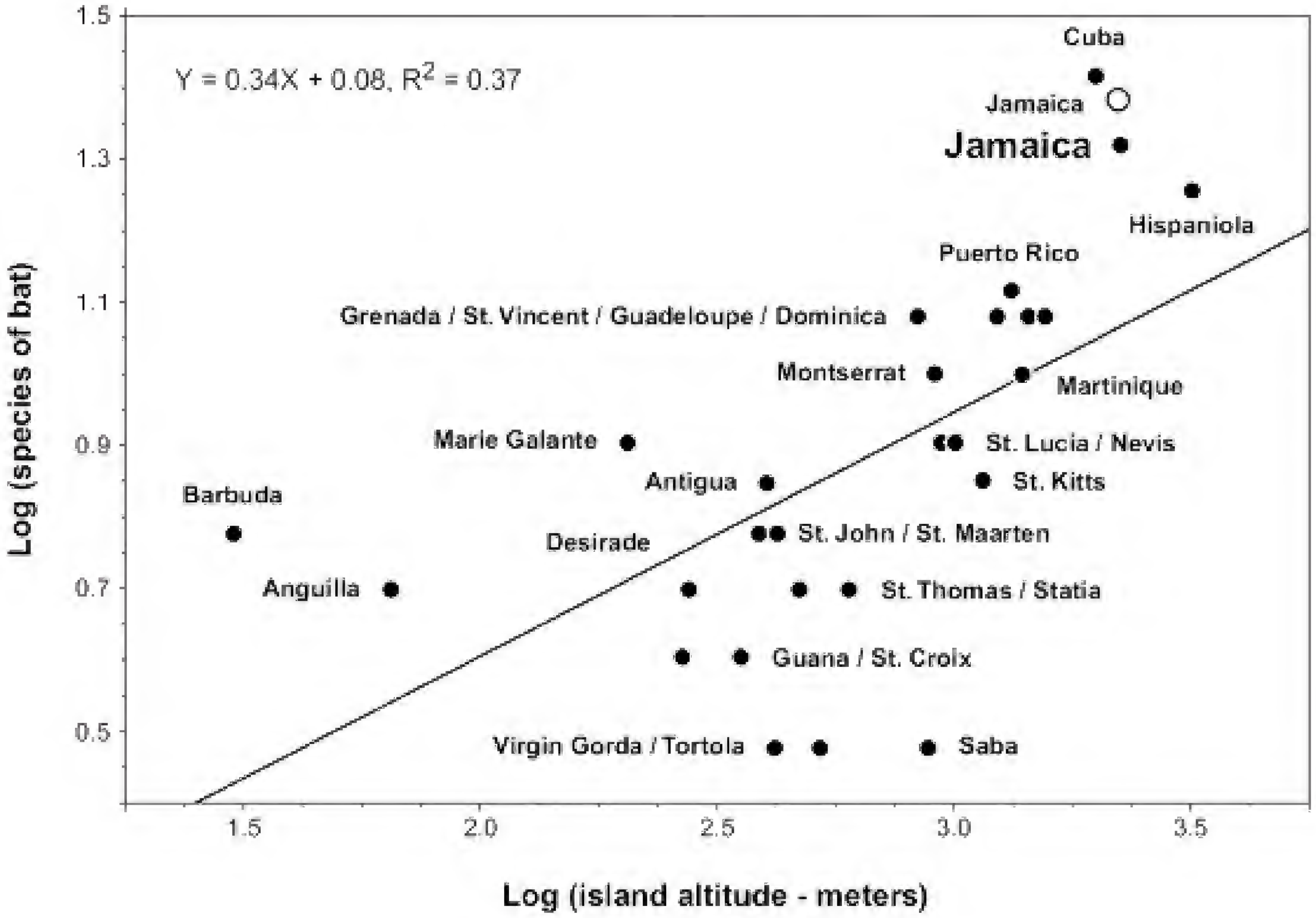

Figure 83. Species/altitude curve based on the published data (December 2003) for the chiropteran fauna on islands in the West Indies. "Jamaica" written in larger letters on the figure represents the living fauna of 21 species and in the smaller lettering it represents the fossil fauna of 24 species.

log of altitude in meters) for West Indian bats. This analysis should give a better estimate of available habitat diversity than simply area of the island because plant communities in the West Indies are highly influenced by altitude. This analysis gives a $z = 0.34$ and $R^2 = 37\%$. Although this indicates that altitude can certainly be an influence on the number of species of bats on islands, altitude has much less influence than area. Figure 83 reveals that the faunas of the four islands of the Greater Antilles have more species than is predicted by the species-altitude curve for each island. The islands below the curve are, for the most part, the low-lying limestone islands of the Virgin Islands and Lesser Antilles.

Similarities Among Caribbean Island Bat Faunas

The chiropteran fauna of Cuba is most similar to the chiropteran fauna of Jamaica (Figure 84 and Table 5). Jamaica and Cuba share fifteen species when only living species are considered and 17 are shared when fossils are included. Griffiths and Klingener (1988) accounted for this pattern, which they termed the Western Antillean pattern, because both of these islands received more recent mainland immigrants than other Antillean islands. Of the seven species not shared with Cuba, four are endemic to Jamaica—*Phyllonycteris aphylla, Ariteus flavescens, Eptesicus lynni*, and *Lasiurus degelidus*. The other three species—*Tonatia saurophila, Glossophaga soricina*, and *Eumops auripendulus*—occur on Jamaica and have wide distributions on the mainland of Mexico, Central America, and northern South America, but are found nowhere else in the West Indies. After Cuba, the next highest number of shared species is between Jamaica and the mainland of Mexico and Central America—11 extant species and 13 species if Jamaican fossils are included. Many of the shared species have broad geographic distributions and are considered to be part of a more general Neotropical chiropteran fauna (Genoways et al. 2001)—*Noctilio leporinus, Pteronotus parnellii, Mormoops megalophylla, Tonatia saurophila, Glossophaga soricina, Artibeus jamaicensis, Natalus*

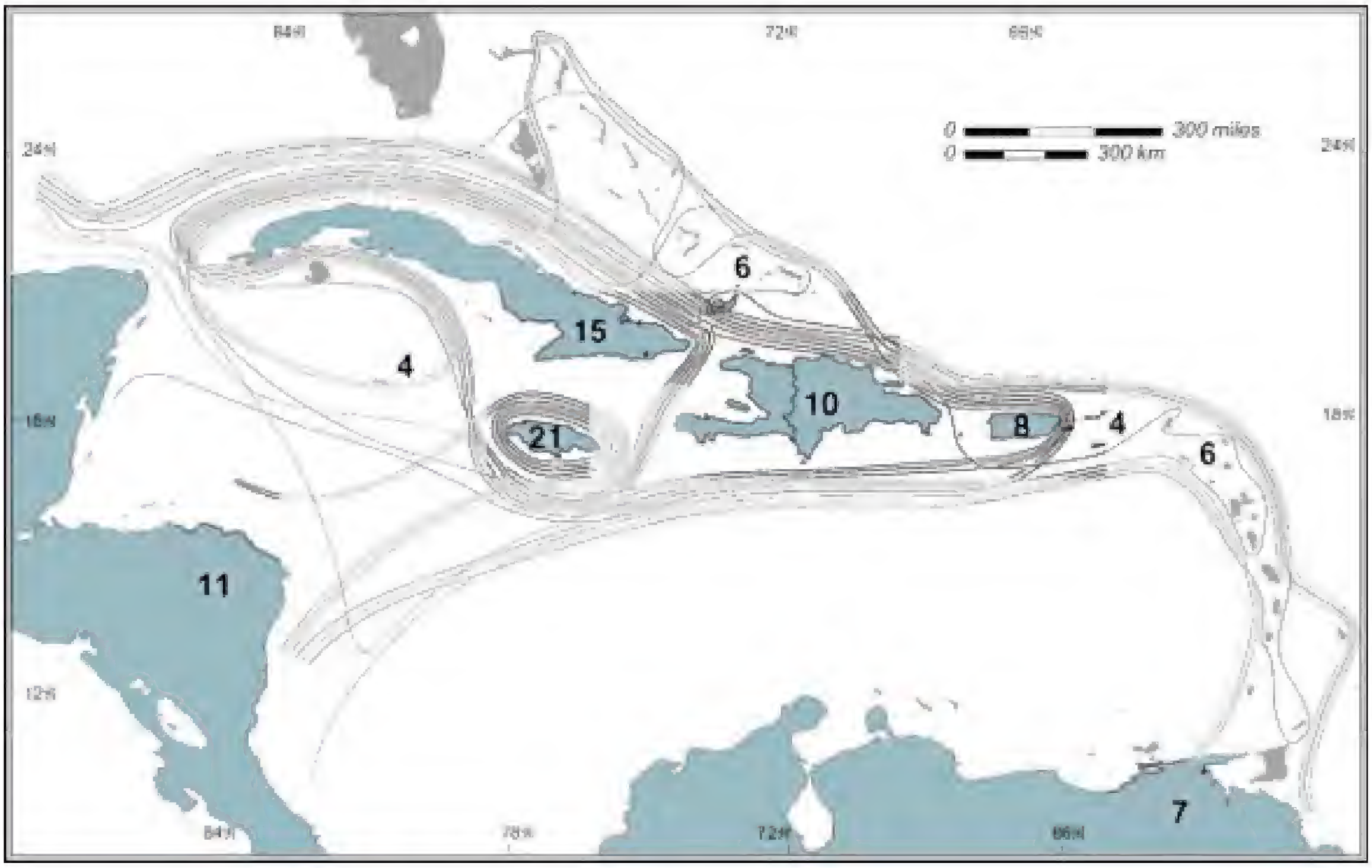

Figure 84. An areographic map for the living chiropteran fauna (21 species) of Jamaica. Numbers indicate total shared species living in the area indicated (see also Table 5).

Table 5.—Species of bats occurring on Jamaica compared with the chiropteran faunas from nine other geo-
living species of bats known from that place.

Species occurring on Jamaica	Species Shared with Central American/ Mexican Mainland (85)	Species Shared with Cuba (26)	Species Shared with Cayman Islands (8)	Species Shared with Hispaniola (18)
Noctilio leporinus	+	+	-	+
Pteronotus macleayii	-	+	-	-
Pteronotus parnellii	+	+	†	+
Pteronotus quadridens	-	+	-	+
Mormoops blainvillii	-	+	-	+
Macrotus waterhousii	+	+	+	+
Monophyllus redmani	-	+	†	+
Glossophaga soricina	+	-	-	-
Erophylla sezekorni	-	+	+	-
Phyllonycteris aphylla	-	-	-	-
Artibeus jamaicensis	+	+	+	+
Ariteus flavescens	-	-	-	-
Natalus micropus	-	+	†	-
Natalus stramineus	+	+	†	+
Eptesicus lynni	-	-	-	-
Lasiurus degelidus	-	-	-	-
Tadarida brasiliensis	+	+	+	+
Nyctinomops macrotis	+	+	-	-
Eumops auripendulus	+	-	-	-
Eumops glaucinus	+	+	-	-
Molossus molossus	+	+	-	+
Total living species of bats (total 21 species) shared with Jamaica (including fossils in parentheses)	11	15	4 (7)	10
Fossil species on Jamaica				
Mormoops megalophylla	+	†	-	†
Tonatia saurophila	+	-	-	-
Brachyphylla nana	-	+	+	+
Total living and fossil species of bats shared with Jamaica (24 species total)	13	17	8	12

† = known from this geographic area only from fossil remains.

[1] Data from Baker et al. (1978); Birney et al. (1974); Buden (1985); Carter et al. (1981); Genoways et al. (1998, 2001); Hall (1981); Stephan (1986); Koopman (1989); Koopman et al. (1957); Linares (1998); Morgan (1993, 1994, 2001); Morgan and Woods (1986); (1996).

graphic areas.[1] The number following the location names in the heading of the table indicates the number of

Species Shared with Puerto Rico (13)	Species Shared with Virgin Islands (5)	Species Shared with Bahamas (16)	Species Shared with Antilles	Species Shared with Northeastern South America (64)
+	+	+	+	+
-	-	†	-	-
+	-	†	+	+
+	-	†	-	-
+	-	†	†	-
†	-	+	†	-
+	-	+	-	-
-	-	-	-	+
-	-	+	-	-
-	-	-	-	-
+	+	+	+	+
-	-	-	-	-
-	-	-	-	-
-	-	†	+	-
-	-	-	-	-
-	-	-	-	-
+	+	+	+	-
-	-	-	-	-
-	-	-	-	+
-	-	-	-	+
+	+	-	+	+
8 (9)	4	6 (11)	6 (8)	7
-	-	†	-	+
-	-	-	-	+
-	-	+	-	-
9	4	13	8	9

Husson (1960); Handley (1976); Jones (1989); Jones and Baker (1979); Jones et al. (1971, 1973); Jones and Owens (1986); Kock and Pedersen et al. (1996, 2003, 2004); Pregill et al. (1988, 1994); Sanchez-Herrera et al. (1986); Steadman et al. (1984); Vaughan and Hill *stramineus, Tadarida brasiliensis, Eumops auripendulus, Eumops glaucinus*, and *Molossus molossus*. Most of these are species in which the geographic range extends at least from Mexico to northeastern South America.

The Bahamas present an interesting situation because although only 6 extant species are shared with Jamaica, the number more than doubles (13) when fossils are considered. This is as many species as are shared between Jamaica and the mainland of Central America and Mexico. All of the species (extant and locally extinct) in the Bahamas that are shared with Jamaica also are shared with Cuba. Cuba or Jamaica, or both, might have served as sources for the Bahamian fauna. However, the Bahamas offer substantially less shelter than either Jamaica or Cuba and less than 50% of the species known to have been established on these small islands have survived. The shared species between the Bahamas and Jamaica undoubtedly is a result of Cuba's central location between them.

The number of species shared between Jamaica and Hispaniola (10) is surprisingly low given that (a) Hispaniola is only 50 km farther from Jamaica than is Cuba and (b) the prevailing wind would seem to favor dispersal from Jamaica to Hispaniola. Hispaniola and Jamaica share less than 50% of the Jamaican chiropteran fauna, and only about 55% of the Hispaniolan fauna. However, Jamaica shares 62% of the 13 species of bats in the Puerto Rican fauna. We believe that the anomalous relationship here is between Jamaica and Hispaniola. The faunal similarity between Jamaica and Puerto Rico is the result of the reduced diversity of bats on Puerto Rico combined with the sharing of species that are widely distributed in the Greater Antilles. Griffiths and Klingener (1988) account for the higher similarity between Cuban and Hispaniolan bat faunas than between Jamaica and Hispaniola because Cuba and Hispaniola previously were contiguous or linked by an archipelago. Jamaica is surrounded by deep water. In fact, the trench between Jamaica and Cuba is one of the deepest in the hemisphere. It is unlikely that Jamaica was connected to other islands during the Pleistocene.

All of the species shared between the Cayman Islands and Jamaica also are shared with Cuba. This clearly indicates that the chiropteran fauna of the Cayman Islands is a depauperate sampling from the two large islands lying to the north and south. The four species of bats shared between Jamaica and the Virgin Islands are species with widespread geographic ranges that include most of the Caribbean Islands and circum-Caribbean mainland.

The only Antillean endemic species shared between the Lesser Antillean islands and Jamaica is *Mormoops blainvillii*, which is known in the Lesser Antilles only from fossil remains. The other seven species shared between these areas have broad geographic ranges including other Greater Antillean islands and extensive areas on the mainland.

Only a modest number of species are shared between northeastern South America and Jamaica. The nine-shared species constitute only 14% of the chiropteran fauna of Trinidad (64 species total). Although a map of the Antilles gives the impression that Jamaica is connected in stepping stone fashion to Trinidad and northeastern South America, bats clearly have not easily dispersed from south to north throughout the islands. Generally, northward dispersal from Trinidad and South America stops at Grenada and the Grenadines, although we now believe that *Pteronotus parnellii* may be an exception to this rule. This zoogeographical phenomenon is referred to as Koopman's Line (Genoways et al. 1998). Southward dispersal of bats also dwindles in the vicinity of Grenada. Genetic data from the mitochondrial genome of the Jamaican fruit bat, *Artibeus jamaicensis*, documents that the Jamaican island haplotype (known as J-1) becomes rarer and rarer between St. Lucia and Grenada (Phillips et al. 1989; Phillips et al. 1991). The inhospitality of the Grenadines (small sizes, low elevation, and lack of freshwater) is one explanation for this limitation on northward and southward dispersal by bats (Phillips et al. 1989).

Vicariance and Dispersal as Origins

Baker and Genoways (1978) discussed potential Caribbean radiations and these authors concluded that the oldest lineage of bats to be isolated in the Caribbean region was the *Brachyphylla, Phyllonycteris,* and *Erophylla* clade (see Baker et al. 2003, for the position of this clade within the family Phyllostomidae). They also concluded that the second oldest assemblage was the *Ardops, Ariteus, Stenoderma,* and *Phyllops* clade.

As we discuss herein, the members of the family Natalidae also should be placed among these older lineages. Baker and Genoways (1978) noted there are three hypotheses to explain the modern day Caribbean bat fauna. They are 1) over-water dispersal (Hedges 1996a, 1996b, 2001), 2) vicariance (Bussing 1975; Rossen 1976), and 3) land bridges (G. M. Allen 1911). At the time Baker and Genoways (1978) wrote their paper, the land bridge hypothesis was not supported by the current interpretations of the geological evidence (Woodring 1954). Baker and Genoways (1978) concluded that essentially all of the fauna in the Caribbean could be explained by over-water dispersal and by inter-island radiations. They concluded that if any taxa were explained by the vicariance model (Bussing 1975; Rossen 1976) it would be the *Brachyphylla, Phyllonycteris,* and *Erophylla* radiation and less likely *Ariteus, Ardops, Phyllops,* and *Stenoderma.* Further, they pointed out that if the ancestor of either of these groups occupied the islands through a vicariant origin, then inter-island over-water dispersal is required to explain present day distribution. See also Davalos (2004) for similar discussions that relate to these taxa as well as modifications for the vicariance model and land bridge model (MacPhee and Iturralde-Vinent 1994, 1995; Iturralde-Vinent and MacPhee 1999). This model hypothesizes a land bridge or landspan from South America to the Greater Antilles along the Aves Ridge and this bridge is referred to as Gaarlandia (Greater Antilles and Aves Ridge). We follow Baker and Genoways (1978) and conclude that if Gaarlandia is functional relative to the present day fauna, it only can account for the *Brachyphylla* complex and less likely the *Stenoderma* complex. *Natalus* appears to have originated in the Antilles and its closest relative on the mainland appears to be a clade that gave rise to the Vespertilionid*a*e and the Molossidae (Hoofer et al. 2003; Hoofer and Van den Bussche 2003). If the Natalidae has an origin in the Antilles ranging back to the common ancestor with the Vespertilionidae/Molossidae clade then *Natalus* becomes a candidate to be the oldest lineage with continual distribution in the Antilles. See Davalos (2004) for additional comments and ideas on the phylogeography of *Natalus.*

The remaining two explanations, therefore, for the geographic origins of the bat fauna of the Caribbean are over-water dispersal and vicariance. It has been established that most of the Greater Antilles originated more than 100 million years ago through fragmentation of the formative Mesoamerican mainland and subsequent drift of the Caribbean geological plate (Iturrade-Vinent and MacPhee 1999; Graham 2003). By way of contrast, most of the Lesser Antilles (Barbados being the main exception) were formed volcanically along the Lesser Antilles arc where the Caribbean and North American plates met (Iturrade-Vinent and MacPhee 1999; MacPhee et al. 2000). The component of the Caribbean island fauna that has a vicariant origin would be those species derived from land masses prior to fragmentation and subsequent movement of the Caribbean plate and its islands into the present day location. The attractiveness of the vicariant model to zoogeographers comes from its simplicity. One can imagine that at the time of fragmentation the complete flora and fauna with all of the ecological potential would be found intact on the newly created island. But, for vicariance to explain the biological diversity in the Caribbean, the divergence times of the Caribbean taxa must predate the geological time since fragmentation of the formative Mesoamerican mainland and all available data, especially the molecular data (Baker et al. 2003; Hoofer et al. 2003; Hoofer and Van den Bussche 2003; Pumo et al. 1996) indicate that no lineage present in the Caribbean predate this time.

Although vicariance provides a suitable explanation for some Antillean vertebrate species—especially some fresh water fish species, amphibians, and some reptiles—the timing is problematic when it comes to mammals. Indeed, the geological evidence places the fragmentation in the Cretaceous and the earliest mammalian fossils found in the islands are from the Eocene (Domning et al. 1997; MacPhee and Wyss 1990; MacPhee and Iturralde-Vinent 1995; Iturrade-Vinent and MacPhee 1999). Taxa comprising such a fauna would have had to diverge more than 65 million years ago. However, the Order Chiroptera is not known to have had a pre-Cenozoic origin, and modern families of bats did not arise prior to the middle Eocene (McKenna and Bell 1997). If any component of the bat fauna of the Caribbean has a vicariance origin it would be expected to be the deepest node within the Order (Simmons, 1998; Teeling et al., 2002; Hoofer and Van den Bussche, 2003). Since this is not the case, we think that it is highly improbable that vicariance played any role in the origin of the Caribbean bat fauna (Baker and Genoways, 1978). Nonetheless, while we reject the notion that the original vicariant event that created the Caribbean islands played a role in the diversity of the present-day bat fauna, it is possible that more recent vicariant events involving pairs of islands could have played a role (Griffiths and Klingener 1988; MacPhee and Iturralde-Vinent 1995; Iturrade-Vinent and MacPhee 1999).

Over-water dispersal involves the movement of animals between and among a mainland and islands. Over-water dispersal from mainland areas is probably the best explanation for the origins of Caribbean bat distributions. Given the likelihood that over-water dispersal explains the presence of bats on islands, it is tempting to embrace the conclusion that flight makes over-water dispersal easy. But as Phillips et al. (1989; see also Baker and Genoways 1978; Morgan and Woods 1986; Griffiths and Klingener 1988; Hedges et al. 1992; Hedges 1996a, 2001) have discussed, the evidence does not suggest that such is the case. The complex species distributional patterns, the genetic data sets, and the presence and distributional patterns of endemic subspecies, species, and even genera, collectively signal that inter-island movement and colonization are neither commonplace nor frequently successful (Phillips et al. 1989; Pumo et al. 1996). However, it is clear some species of bats such as *Noctilio leporinus, Pteronotus parnellii, Artibeus jamaicensis*, and *Molossus molossus* have been better over-water dispersers than other species of bats. Although in theory over-water dispersal could include inter-island, mainland to island, and island to mainland movement, it does not appear that these events are co-equal. In the Antilles, at least, the main movement has been from mainland onto islands. On the other hand, there also is evidence that several genera of bats might have originated in the Antilles and might be the ancestors of mainland species. Based on the phylogenetic tree published by Baker et al. (2004) the two best examples would be the mainland genera *Leptonycteris* and *Glossophaga* evolving from a common ancestor shared with *Monophyllus* and the mainland genera *Centurio, Sphaeronycteris, Ametrida,* and *Pygoderma,* which reached the mainland and radiated after evolving from a common ancestor shared with *Stenoderma, Ardops,* and *Ariteus* in the islands. As discussed herein, evidence of inter-island movement is highly patterned—some islands apparently exchange bats, whereas others either do not or at least colonization does not occur.

In summary, numerous authors (Baker and Genoways 1978; Morgan and Woods 1986; Pumo et al. 1988; Griffiths and Klingener 1988; Phillips et al. 1989; Hedges et al. 1992; Hedges 1996a, 1996b; Davalos 2004) have discussed evidence that most vertebrates, including bats, entered the West Indies via over-water dispersal rather than vicariance. An additional line of evidence for over-water dispersal is that the island faunal compositions appear to have passed through a dispersal filter, which becomes more intense with greater distance from the mainland. Certainly the chiropteran fauna of Jamaica is not a replication of the mainland fauna of the Nicaragua-Honduras region of Central America. Furthermore, the bat faunas become more attenuated with greater distances from the mainland, such as revealed by comparing the faunas of Puerto Rico and Jamaica. Vicariance would predict the faunas of the two islands would be nearly the same, whereas the over-water dispersal model would predict that the fauna of Jamaica would be more diverse because it is closer to the source mainland areas thus having less of a dispersal filter through which to pass. We observed higher bat diversity in Jamaica than Puerto Rico as discussed above.

Anderson (1994) examined the concept of endemism and factors that affect endemism, which provides another approach to measuring vagility and over-water dispersal, in many parts of the world. His analyses included the percent of insular endemic mammals, bats, and birds on the four Greater Antillean islands and found that there was less endemism in bats than in birds in the region (Cuba, 22% bats and 28% birds; Hispaniola, 13%, 26%; Puerto Rico, 7%, 18%; Jamaica, 22%, 37%). Our data would put the value for bats on Jamaica at 19% rather than 22% thus making the difference even larger. Our interpretation of these data is that either bats are more highly vagile than birds in the West Indies and thus forming fewer endemic species, or conversely, the extinction rate is higher for bats and thus endemic species of bats are lost more quickly than are endemic species of birds. However, Alcover et al. (1998) found that on a worldwide basis Chiroptera had the extinction rate of 6% for insular species, which was the lowest for any mammalian group considered. On Jamaica none of the endemic species of bats are extinct and the extirpation rate for bats is 12.5% (3 of 24 species). The extinction rate of endemic birds (Johnson and Stattersfield 1990; Douglas 2001; Lepage 2004) on Jamaica appears to be about 14.3% (5 of 35 species), thus higher than the rate for bats and even exceeding the extirpation rate for bats. It would appear based on these data that bats are more vagile than are birds in the West Indies.

Invasion Routes

Various authors (Jones and Phillips 1970; Baker and Genoways 1978; Jones 1989; Koopman 1989; Rodríguez-Durán and Kunz 2001) have discussed the potential over-water invasion routes by which bats could have reached the West Indies. Based on their conclusions and new data now available, it is clear that the majority of the Jamaican bat fauna reached the island from the west either from the Nicaragua-Honduran area or from Yucatan or elsewhere in southern Mexico. During the height of Pleistocene glaciation, the lowered sea levels would have greatly reduced the distance between Central America and Jamaica by the emergence of the Nicaraguan Plateau and Seranilla, Rosilind, and Pedro banks (Griffiths and Klingener 1988). Hedges (1996a, 1996b) agrees that the Nicaragua-Honduras area is the source area for bats in the West Indies, but points out that nonvolant vertebrates probably entered the area primarily from northeastern South America. At least seven species living on Jamaica are likely invaders from the west, including *Macrotus waterhousii, Glossophaga soricina, Artibeus jamaicensis, Tadarida brasiliensis, Nyctinomops macrotis, Eumops auripendulus*, and *E. glaucinus*. The two fossil species *Mormoops megalophylla* and *Tonatia saurophila* also can be added to this list. Traditionally, *Natalus stramineus* has been included within this group, but we now believe that this species may have an Antillean origin and has subsequently invaded the mainland. The ancestors of at least three of the endemic species on Jamaica—*Pteronotus macleayii, P. quadridens*, and *Mormoops blainvillii*—also probably entered the West Indies from the west. This leaves three widespread species (*Noctilio leporinus, Pteronotus parnellii,* and *Molossus molossus*), which could have entered the area from the west or the south, as the only potential representatives with possible southern origins. There are five Antillean endemic species on Jamaica (*Monophyllus redmani, Ariteus flavescens, Erophylla sezekorni, Phyllonycteris aphylla*, and *Natalus micropus*) and the fossil *Brachyphylla nana* in which the source of the ancestral stock cannot be identified.

The two remaining species known from Jamaica—*Eptesicus lynni* and *Lasiurus degelidus*—are endemic to the island but present some interesting challenges and potentials when their origins are considered. Molecular analyses of *E. lynni* indicates that it is most closely related to *E. fuscus*, which occurs on the Mexican-Central American mainland, but also could have entered the West Indies from the north from Florida to Cuba or islands in the Bahamas. Earlier authors related *L. degelidus* to *L. borealis* occurring in the United States and throughout Central America. However, as Baker et al. (1988) and Genoways and Baker (1988) have demonstrated, *L. borealis* is confined to the eastern United States, with a closely related species—*Lasiurus blossevillii*—occurring in the western United States and through Middle America into South America. If *L. degelidus* followed the pattern of other Jamaican bats then its ancestor would be expected to be *L. blossevillii,* which entered the West Indies from the west. However, our genic and some morphological characters indicate that the closest relative of *L. degelidus* is a second species of red bats occurring in the southeastern United States, *L. seminolus* (Baker et al. 1988). This is further supported by the fact that Morales and Bickham (1995) showed the Cuban red bat (*L. pfeifferi*) to be most closely related to *L. seminolus* in a molecular study of mtDNA. If these data remain the best explanation for the ancestry of *L. degelidus*, then it likely entered the West Indies from the north.

The traditional view of the West Indian chiropteran fauna has been that species entered the area, became established, and in some cases underwent some evolutionary diversification. However, the emerging evidence, as discussed below, is that the biogeographic history of bats in this region is far more complex with genera such as *Brachyphylla, Monophyllus, Phyllonycteris, Erophylla*, and the *Stenoderma-Ariteus-Phyllops-Ardops* complex and even higher-level groups of bats having their diversification in the Greater Antilles (Baker et al. 2003).

Geographic Origins

Species that compose the Jamaican bat fauna could have originated on the island or, alternatively, they originated elsewhere and dispersed to Jamaica. Recent genic and molecular studies provide insights into these alternatives that were not available only a few years ago. To discuss these alternatives, we have divided the bats on Jamaica into four categories—1) those that share conspecific populations with mainland localities, 2) species that share conspecific populations with other Antillean islands but not with any mainland populations, 3) endemic species that share congeneric associations with mainland species, and 4) species belonging to genera endemic to Jamaica.

In category 1, 11 species share a conspecific relationship with mainland populations: *Noctilio leporinus, Pteronotus parnellii, Macrotus waterhousii, Glossophaga soricina, Artibeus jamaicensis, Natalus stramineus, Tadarida brasiliensis, Nyctinomops macrotis, Eumops auripendulus, E. glaucinus*, and *Molossus molossus*. Most of these species undoubtedly originated on the mainland and subsequently became distributed in the Caribbean (Baker and Genoways 1978). The one potential example to the contrary is *Natalus stramineus*. Comments on the geographic origin of each of the species follow.

Noctilio leporinus.—The molecular data suggest that this species evolved recently (within the last million years), that piscivory evolved from the more generalized insectivorous lifestyle, and that the Caribbean populations are a recent extension of the mainland geographic range (Lewis-Oritt et al. 2001a). The evidence that *N. leporinus* originated on the mainland includes the observation that its sister taxon (*N. albiventris*) also is distributed on the mainland but not in the Antilles. Molecular data from nuclear and mitochondrial genes suggest that *N. albiventris* is composed of two species and that *N. leporinus* is more closely related to one than to the other. If this complex arrangement is accurate, then the origin of *N. leporinus* would be most parsimoniously described by a mainland origin. Further, there is more haplotype diversity present in mainland populations of *N. leporinus* than is present from a limited sample from the Caribbean. These data are comparable with the hypothesis that *N. leporinus* has had a longer evolutionary history on the mainland than in the Caribbean.

Pteronotus parnellii.—*P. parnellii* is distributed in the Greater and Lesser Antilles as well as on the mainland. The molecular data (Lewis-Oritt et al. 2001b) indicates that *P. parnellii* from Jamaica is most closely related to *P. parnellii* from Puerto Rico. Although these authors sampled Antillean specimens only from Jamaica and Puerto Rico, it is probable that all of the Greater Antillean material is more closely related to each other than to mainland populations. In the study of Lewis-Oritt et al. (2001b), mainland populations of *P. parnellii* included specimens from Suriname, Guyana, Honduras, and Mexico in which there is a major subdivision in the sequence values for the cytochrome *b* gene. These distance values are greater than 10%, which usually indicates the presence of two biological species (Bradley and Baker 2001). The specimen most closely related to the Caribbean *P. parnellii* was collected in Suriname. If there are two species within what is currently recognized as *P. parnellii*, one species is distributed in northern South America throughout Middle America and the other is distributed in northern South America and throughout the Caribbean. If two species are involved, both are distributed in South America, which we interpret as suggesting that the Caribbean populations originated in South America, dispersed northward through the Lesser Antilles and throughout the Greater Antilles. This implies that *P. parnellii* is in reality from the south and reached the Greater Antilles after island hopping through the Lesser Antilles. This example demonstrates that cases must be examined on their own merits with no single pattern successfully predicting all inter-island relationships.

Macrotus waterhousii.—According to the molecular trees proposed in Baker et al. (2003) the genus *Macrotus* is the basal clade that is sister to the lineage that gave rise to the remainder of phyllostomid bats, including the vampires. The implications are that the morphology associated with this genus could have been present at the basal radiation for all phyllostomid bats and potentially there could be a subtropical time during which *M. waterhousii* was experiencing stabilizing selection (Baker et al. 2003). The distribution of *M. waterhousii* across northern and central Mexico and the distribution of *M. californicus* in northern Mexico and southwestern United States is most parsimoniously explained by *M. waterhousii* having a mainland origin from northern Mexico and subsequently reaching and colonizing Jamaica.

Glossophaga soricina.—This species is distributed from the western side of South America to northern Mexico. All other species within this genus are distributed on the mainland. The only other species entering the Antilles is *G. longirostris*, which is found in the southern Lesser Antillean islands of St. Vincent, the Grenadines, and Grenada. This information is most parsimoniously explained by *Glossophaga soricina* having a mainland origin. Based on the genetic distance in the cytochrome *b* gene (Hoffmann and Baker 2001), it is probable that *Glossophaga soricina* is composed of two biological species, one of which is distributed across northern South America, including Trinidad, to Peru. The second species is distributed on the western versant of the Andes on South America, northward throughout Middle America. The molecular data (Hoffmann and Baker 2001) suggests that the Jamaican populations of *G. soricina* have a Central American origin.

Artibeus jamaicensis.—This is a widely distributed species; it occurs throughout the Antilles and on the mainland from Mexico to northern South America. The Jamaican population is recently derived; fossil evidence of *A. jamaicensis* first appears in Late Pleistocene cave deposits (Koopman and Williams 1951; Williams 1952) and extensive sampling (more than 40 individuals) of the current population has uncovered only a single restriction enzyme mitochondrial DNA haplotype (Pumo et al. 1988; Phillips et al. 1989). All of the available genetic data support the conclusion that *A. jamaicensis* dispersed to Jamaica and Cuba from the Mexican or Central American mainland and that the species subsequently spread through the Greater Antilles and southward to Grenada, where it is uncommon (Phillips et al. 1991; Pumo et al. 1996).

Natalus stramineus.—This species is distributed from northern Mexico to Panama and on the Lesser and Greater Antilles. From this standpoint, a mainland origin for this species is parsimonious and that interpretation was followed by Baker and Genoways (1978) and most other authors until the work of Arroyo-Cabrales et al. (1997). The biogeographic data that contradict this are that all other species except *N. tumidirostris* of the genus *Natalus* are distributed in the Antilles and this suggests a radiation in the Antilles for the genus, which would then suggest that *stramineus* had an Antillean origin and subsequently became distributed in Central America. Arroyo-Cabrales et al. (1997) produced two alternative trees to explain electrophoretic variability in *Natalus micropus* and *N. stramineus*. In both of these trees, the basal radiation involved Caribbean populations and the derived populations were in Mexico and Belize. The most parsimonious explanation for these data is that the Antillean islands were the center for diversification and the mainland populations were derived from Antillean ancestors. Davalos (2004), on the other hand, concluded that "*Natalus stramineus* shows a relationship between the continent and the Lesser Antilles pointing to dispersal from northern South America." Morgan and Czaplewski (2003) studying a new genus and species of natalid from Florida believe that the Natalidae evolved in North America before the late Oligocene and "probably reached the Antilles by overwater dispersal from tropical North America early in their evolutionary history, presumably in the Oligocene or Miocene." They believe that the family entered South America comparatively recently, possibly in the Pliocene after the formation of the Panamanian Isthmus. We hypothesize that the natalids originated and radiated in the Antilles. From this radiation they dispersed to North America (Morgan and Czaplewski, 2003) and to elsewhere on the mainland. This is obviously a complex story that will possibly be resolved in the future with additional molecular data.

Nyctinomops macrotis.—Other species of *Nyctinomops* are found on the mainland, although *N. laticaudata* has a population on Cuba. Additionally, *N. macrotis* has populations throughout much of Mexico and the southwestern United States and we conclude that a mainland origin is probable.

Molossus molossus.—The geographic origin of this species has been considered to be from the west, but the possibility of a South American origin and expansion to the north or an invasion from both the west and south should not be overlooked. All explanations involve a mainland origin.

Eumops auripendulus.—This is an extremely widespread species ranging from Peru to Trinidad, southern Mexico, and Jamaica. It is our opinion that this species has a mainland origin. There are 11 recognized species in the genus *Eumops* and nine of those are restricted to a distribution on the mainland (Timm and Genoways 2004).

Eumops glaucinus.—The logic that *Eumops glaucinus* has a mainland geographic origin is the same as *Eumops auripendulus*.

Category 2 contains species that share conspecific populations with other Antillean islands but not with any mainland populations. There are seven species that fit this geographic distributions. They are *Pteronotus macleayii, Pteronotus quadridens, Mormoops blainvillii, Monophyllus redmani, Erophylla sezekorni, Phyllonycteris aphylla,* and *Natalus micropus.* We conclude that all of these species evolved in the Caribbean because that is the current distribution of the species. In the case of *Monophyllus, Erophylla, Phyllonycteris*, and *Natalus*, their respective sister taxa also are distributed in the Antilles, which strengthens this conclusion. There are as many species in the genus *Pteronotus* distributed in the Caribbean as are distributed on the mainland. Clearly, *Pteronotus* has diversified in the Caribbean, although Lewis-Oritt et. al. (2001a) concluded *parnellii* to have involved a mainland ancestry due to the higher genetic diversity of mainland population.

Category 3 species are unique to Jamaica but share congeneric associations with mainland species. Species that fit this geographic pattern are *Eptesicus lynni* and *Lasiurus degelidus*. The logic for the geographic origin of these two species is that some of their congeneric species are distributed in the mainland and that a mainland origin explains this distribution. The genus *Eptesicus* is distributed throughout the New World mainland as well as Africa and Eurasia. *Lasiurus* is distributed over the New World mainland. Arnold et al. (1980) present genic data indicating that *E. lynni* evolved from the *E. fuscus* complex. *Eptesicus fuscus* is widely distributed on the mainland of the United States, Mexico, and Central America as well as occurring on all of the Greater Antillean islands except Jamaica and several islands in the Bahamas. The genic data indicated that the ancestor of *E. lynni* reached Jamaica from the mainland, but they do not indicate whether this was from Florida via Cuba or directly from Central America. Earlier authors related *L. degelidus* to *L. borealis* occurring in the United States and throughout Central America. However, Baker et al. (1988) and Genoways and Baker (1988) have demonstrated *L. borealis* is confined to the eastern United States, with a closely related species—*Lasiurus blossevillii*—occurring in the western United States and through Middle America into South America. If *L. degelidus* followed the pattern of a western origin then its ancestor would be expected to be *L. blossevillii*. However, the genic and some morphological characters indicate that the closest mainland relative of *L. degelidus* is a second species of red bats occurring in the southeastern United States, *L. seminolus* (Baker et al., 1988). *L. seminolus* was also shown to be the most closely related mainland species to the Cuban red bat *L. pfeifferi* (Morales and Bickham 1995). If these data remain the best explanation for the ancestry of *L. degelidus*, then it had a mainland origin with an invasion from the north via Florida and Cuba to reach Jamaica.

Category 4 contains only a single species belonging to a Jamaican endemic genus, *Ariteus flavescens.* Based on the analyses of Baker et al. (2003), *Ariteus* shares a close relationship to *Ardops nichollsi*, which is endemic to the Lesser Antilles. These genera fall into a group placed in the subtribe Stenodermatina, which is ". . . defined as the clade. . . arising from the last common ancestor of *Ariteus, Stenoderma,* and *Ametrida.*" Given the basal position of *Ariteus* and *Stenoderma* and the geographic distribution of members of this subtribe, we believe the group originated and underwent initial diversification in the West Indies before invading the mainland.

The most powerful way to view the biogeography and origin of the fauna of Jamaica is in a phylogenetic context. Unfortunately, well-resolved evolutionary trees do not exist for most major taxa of bats, although there is a well-supported tree for phyllostomid bats (Baker et al. 2003). Using this tree (Baker et al 2003: 10, Fig. 5), we can make the following observations. From an overview, two examples *(Macrotus waterhousii* and *Artibeus jamaicensis*) represent species that occur on Jamaica as well as the mainland and other islands. As noted above, this is most parsimoniously explained by over-water dispersal from the mainland and each species requires a different dispersal event to account for the biogeographically defined fauna.

Within this phylogenetic tree, there are two groups that appear to have had substantial radiations that were a product of isolation on the Caribbean islands. The greatest magnitude of morphological radiation to have occurred in the Caribbean is present in clade 34 (Baker et al. 2003:10-11, Fig 5, node 34). Two genera distributed on Jamaica (*Phyllonycteris* and *Brachyphylla*-only found as a fossil species on Jamaica) in the phylogenetic tree involve a clade that contains *Phyllonycteris, Brachyphylla,* and *Erophylla* (Baker et al. 2003, Fig. 5, node 37). This fascinating assemblage of primarily nectar feeding species is most parsimoniously explained as having a basal radiation in the Caribbean that produced two sub-nodes. *Brachyphylla, Erophylla,* and *Phyllonycteris* are presently Caribbean in their distribution. The sister node to the *Brachyphylla, Erophylla,* and *Phyllonycteris* clade (node 35) produced *Monophyllus,* which is the basal branch that subsequently produced *Leptonycteris* and *Glossophaga*. The most parsimonious explanation of this arrangement is the ancestors of nodes 37 and 35 were Caribbean. This is the first time that a Caribbean origin for this portion (node 35) of the Glossophaginae has been proposed. This arrangement implies that *Glossophaga* evolved on the mainland and that *soricina* dispersed into the Antilles. The remainder of the Glossophaginae (Baker et al. 2003, Fig.5, node 38) probably had a mainland origin.

The endemic Jamaican monotypic genus, *Ariteus flavescens*, is part of a clade (Baker et al. 2003, Fig. 5, node 15) in which the basal taxa are all Caribbean and the derived taxa (*Centurio, Pygoderma, Sphaeronycteris,* and *Ametrida)* are distributed on the mainland. The most parsimonious explanation for the zoogeographic pattern is that the Caribbean fauna radiated before reinvasion of the mainland and that the derived mainland genera are the descendants of Caribbean island endemics.

Conservation

Topographic and vegetational factors contribute to the structure of the habitat used by tropical bat faunas (McNab 1971). On Jamaica caves probably represent the single must important topographic feature for bats. Another obviously important feature to the conservation of bats on Jamaica is the preservation of large areas of native vegetation. In general, the bat populations on Jamaica are healthy, but during our work some species of the genera *Eumops, Lasiurus, Natalus,* and *Nyctinomops* were rare and limited in distribution on the island. Although these species appear to be rare on Jamaica, there is little evidence that these small populations have resulted from human activities. On the other hand, it must be remembered that at least three species occurring on Jamaica have been extirpated in the last 10,000 years. The health of many bat populations on Jamaica, as everywhere, is dependent on the continued availability of native habitats. These habitats include caves where many species roost, as well as native plant and insect communities that supply the critical foods of Jamaican bats. There are some species that have obviously benefited from human activities on Jamaica. Such species would include *Artibeus jamaicensis*, which clearly has benefited from human agricultural practices and the planting of exotic fruit trees, and *Molossus molossus*, which has benefited from the greatly expanded roosting sites provided by human habitations.

Most of the bats on Jamaica are either obligate or opportunistic cave-roosting species (McFarlane 1985, 1986). We urge the government of Jamaica to protect, at least, five of the largest caves, including St Clair Cave, Windsor Cave, Oxford Cave, Portland caves, and Mount Plenty Cave. Protection should include limiting, but not excluding, human activity in the caves. Other caves on the island have already been developed for tourism purposes and the five caves noted above should not undergo similar development. We urge official protection for several smaller caves including Bagdale Cave, Cousin's Cave, Ferry Cave, Monarva Cave, Ramble Bat Hole, Two Sisters Cave, and Wallingford Cave. Protection of these caves will afford a number of high quality bat cave habitats to assure the survival of populations of most species on Jamaica.

One of the unique threats to bat caves is posed by *Cannabis* growers on Jamaica. It appears that these highly specialized farmers are known to site their fields near caves because the bat guano is used as a high quality fertilizer. Also, the caves can serve to give temporary shelter to the *Cannabis* growers while they are resting from tending their fields or escaping adverse weather conditions (Lee 1988).

There are large areas of native vegetation remaining on Jamaica in the Cockpit region, along the Blue Mountains, and John Crow Mountains. We also observed native vegetation being preserved on steep-sided hills even in agricultural areas. This preservation must be continued and encouraged. Of particular importance to the continued health of bat populations on Jamaica is the preservation of native fruit trees and shrubs such as breadnut, cabbage bark tree, clammy cherry, fustic tree, mountain guava, naseberry, piper, rose apple, khaki tree, and silk cotton tree. These plants provide food that is necessary for the fruit- and pollen-eating species as well providing part of the habitat to maintain a robust native insect fauna necessary for the insect-eating species.

The bat fauna of Jamaica is a national and natural treasure. This fauna is the result of generations of adaptation to the rigors of the environment of Jamaica. Stored in the gene pool of these species is the ability to traverse broad expanses of water, to endure the periodic devastation of hurricanes, to endure climate shifts between warm, humid conditions and cool, dry conditions, and numerous other factors that have shaped the modern Jamaica. This is a unique genetic resource that is not replicated elsewhere on Earth. Bats play a vital role in the numerous cave ecosystems found on Jamaica. Bats essentially serve as the "green plants" of these systems, being the primary source of energy entering these ecosystems through dropped food items and accumulations of guano. The organisms living in these caves represent source of genetic biodiversity unique to Jamaica. Bats play a role in the pollination and seed dispersal for many of the native plants on the island, thereby keeping these terrestrial ecosystems functioning and healthy. Bats add to human health and recreational enjoyment for both native Jamaicans and their worldwide visitors by consuming vast quantities of insects on a daily basis. Jamaica will be well served by the chiropteran members of its native fauna and will repay conservation efforts many times over.

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