4. Distribution Patterns of Amphibians in the West Indies

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ABSTRACT   There are 174 species of amphibians known from the West Indies, 167 of these are native and eight introduced; 164 (98%) of the native species are endemic. The native fauna, all anurans, belongs to four families: Bufonidae (1 genus, 11 species), Dendrobatidae (1, 1), Hylidae (4, 11), and Leptodactylidae (2, 144). Most species (84%) of West Indian amphibians belong to the large leptodactylid genus *Eleutherodactylus*. The greatest diversity of bufonids (8 species) occurs in Cuba, and of hylids (5 species) in Jamaica. Except for two Cuban species occurring elsewhere, single-island endemism is 100% in the Greater Antilles, and most species are restricted to small areas (< 100 km^2) within an island, and 11 species (7%) are known from only type-localities. There are 50 native species (96% endemic) in Cuba, 22 species (100% endemic) in Jamaica, 63 species (100% endemic) in Hispaniola, 20 species (100% endemic) in the Puerto Rican Bank, and 10 species (90% endemic) in the Lesser Antilles. Only two species are native to the Bahamas Bank, and one species is native to the Cayman Islands; none is endemic. Ten percent of the amphibian fauna, including a new family for the West Indies, has been discovered in the last four years; this rate of discovery suggests that our knowledge of species diversity is far from complete.

Distributional data for West Indian amphibians are summarized and subjected to several analyses. Biogeographic regions (74) are defined for the Greater and Lesser Antilles and used in faunal similarity analyses to better understand regional patterns of distribution and endemism. Species density is mapped for the Greater Antilles in order to determine "hot spots" of species diversity. Altitudinal distributions are analyzed to search for possible trends in both species density and in body size, and distributional areas are examined to determine the typical extent of species distributions and possible taxonomic differences. Climatic, vegetational, topographic, and historical factors affecting distributional patterns are reviewed. Amphibian declines and extinctions are discussed, current conservation measures are reviewed, and recommendations are made to help protect the existing amphibian fauna.

Key words: Caribbean, Biogeography, Amphibia, Anura, Tropical, Conservation, Biodiversity, Islands.

INTRODUCTION

The West Indies are located between North and South America (12–27° N) and comprise a total land area of 223,846 km², which is similar to that of Great Britain. Historically, this region includes the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico), the Lesser Antilles, the Bahamas Bank, the Cayman Islands, and San Andrés and Providencia in the southwestern Caribbean (Fig. 4:1). These are the areas treated in this paper. Occasionally, some satellite islands of South America also are included in definitions of the West Indies, but these areas, such as Trinidad, Tobago, and the Netherlands Antilles, are zoogeographically more associated with the adjacent mainland. Because there are no amphibians endemic to the Bahamas or the Cayman Islands, the focus of this paper is on the amphibian fauna of the Greater and Lesser Antilles.

Climate in the West Indies is strongly influenced by the prevailing winds from the northeast, which typically bring moisture to the northern and eastern areas of each island and result in dry southern areas. The distribution and composition of the vegetation closely follows this rainfall pattern, often resulting in well-developed moist forests on northern and eastern slopes and dry, xerophytic vegetation in the south. Before human alteration, most islands were almost completely forested. Lowland rainforest with tall buttressed trees graded into montane rainforest on the lower slopes of mountains, with cloud forest at cloud level and elfin woodland on the summits. Wet limestone forest covered the karst regions, and dry scrub forest occupied the drier southern areas. Essentially no lowland rainforest remains anywhere in the West Indies, except for perhaps a few isolated buttressed trees (e.g., Cabezada, Guantánamo Province, Cuba); those forests were the first to disappear after discovery and colonization of these islands. Most other forest types are disappearing but still can be found in patches and isolated tracts throughout the Antilles. The destruction of wet limestone forest (with its sharp limestone rock substrate) and dry scrub forest (with its abundant spiny plants) has occurred at a slower pace partly because of the difficulty these pose for human access. For the same reason, some of the last remaining patches of montane rainforest (perhaps the most endangered forest type) exist only on the steepest mountain slopes.

The amphibian fauna of the West Indies (all anurans) is characterized by a relatively high number of native species (167 species) for its small land
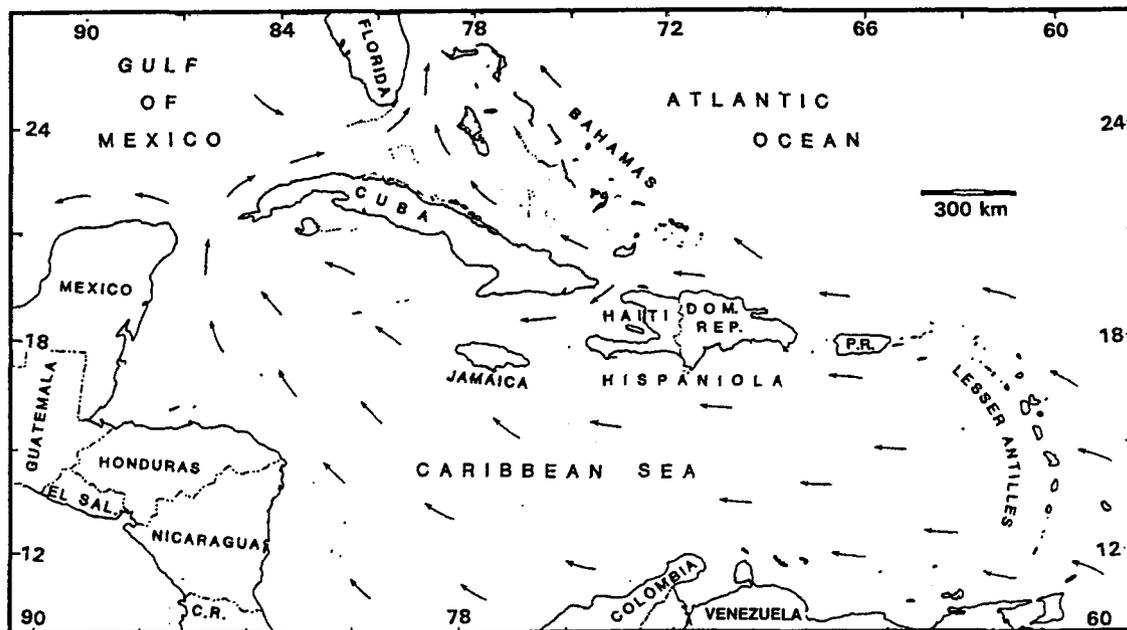

Fig. 4:1.   The West Indies, showing major water current patterns.

area, and a low number of genera (7) and families (4). The majority of species are in the single leptodactylid genus *Eleutherodactylus*. As terrestrial breeders with direct development (at least one species is ovoviviparous), the members of this genus have invaded a diversity of ecological niches including forest floor, leaf litter, rock outcrops, caves, burrows, streams, tree trunks, tree holes, bromeliads, root holes in elfin forest, and even coastal mangrove swamp (Hedges, 1989a; Hedges and Thomas, 1992). Nearly every species is endemic to a single island and usually to a small area on an island.

Previously, distributional data for the species have been summarized in the form of a checklist (Schwartz and Henderson, 1988), a supplement to the checklist (Hedges and Thomas, 1989), and distributional maps of individual species (Schwartz and Henderson, 1991). The amphibians of Hispaniola have been discussed in relation to the abundance of South Island species (Schwartz, 1973) and the recognition of two paleoislands (Schwartz, 1980). Some general taxonomic and distributional information also has been reviewed, in comparison with West Indian reptiles (Schwartz, 1978). Biogeographic studies on herpetofaunas of some selected areas in the West Indies include Cuba (Rodríguez-Schettino, 1993; reptiles only), Cuban satellite islands (Estrada, 1986, 1993a, b; Garrido et al., 1986), and the Puerto Rican Bank (Heatwole et al., 1981).

MATERIALS AND METHODS

The definition of the West Indies follows Bond (1979). Distributional data on West Indian amphibians were gleaned from the literature and from personal field notes. The distribution maps in Schwartz and Henderson (1991) summarize most locality records up to about 1989, including my specimen and locality data from 1981 through 1988. This has been supplemented by my unpublished field records gathered since that time (1988–1994), and by new published distributional information (e.g., Henderson et al., 1992; Kaiser, 1992; Powell et al., 1992; Thomas and Joglar, 1995). Elevational data for Cuban species were omitted from Schwartz and Henderson (1991) so those data reported here (and many new distributional records) are mostly from my field records. In cases where I believe published locality records are doubtful as to correct identification (taxon or locality), I have modified the distributions accordingly. An effort was made to include not only all described species, but also those currently being described (designated by first letter or letters of proposed name) for the benefit of completeness. After maps of locality records were gathered, species distributions were defined by circumscribing those records with a line or lines and adjusting for unsuitable habitat (e.g., a wide valley separating two montane populations). Small-scale changes in elevation creating unsuitable habitat were not taken into account.

Biogeographic regions were defined by considering their topographic, floristic, and faunistic distinctiveness. For reptiles or other groups, some of these regions may be combined, or require further subdivision. In the descriptions of these regions, their map location, relation to other regions, rainfall data, and areas (in the case of islands) have been omitted because this information is presented elsewhere in the paper.

Faunal similarity, or Coefficient of Biogeographic Resemblance (CBR; Duellman, 1990) was measured using the formula $CBR = 2C \div (N_1 + N_2)$, where C = number of species in common between two regions and N_1 and N_2 are the number of species present in each region; faunal distance (D) is $1 - CBR$. For comparison with other studies, cluster analysis of CBR values was done with the UPGMA algorithm (Sneath and Sokal, 1973). However, in addition, D values (no corrections were made) were used with the neighbor joining algorithm (Saitou and Nei, 1987). The latter method often performs better than UPGMA in computer simulations of phylogenetic data (Nei, 1991) so it was used here to explore its usefulness with faunal similarity analysis. If species are shared disproportionately among regions, a faunal similarity/distance tree might have unequal branch lengths as is common with phylogenetic data. In those cases, a clustering algorithm that does not equalize branch lengths (such as neighbor joining) should be at an advantage. Because it is a new application for neighbor joining, both trees are presented here for each comparison. The program MEGA (Kumar et al., 1994) was used for tree construction. To avoid spurious results, only regions containing more than one species were used in the analyses.

Native species are defined here as those that occur naturally, endemics are those native species that occur nowhere else other than the region under consideration (except as introductions), and percent endemism is number of endemic species divided by the number of native species. These terms are applied in this paper at three different levels: the West Indies, major divisions within Antilles (e.g., Cuba, Lesser Antilles), or biogeographic regions. In some cases (e.g., regions within Lesser Antilles) the biogeographic region is an island or island group. The classification of West Indian amphibians used here follows Duellman (1993) and Hedges (1996).

Species density is defined as the number of overlapping species distributions, and is approximately equal to the number of sympatric species (except in some areas of rapid elevational change) but often is greater than the number of syntopic species. By reference to species distribution maps, species density was determined for specific locations at a relatively fine scale throughout Cuba, Jamaica, Hispaniola, and Puerto Rico, and contours (interval = 2 species) were fitted. Species distributional areas were determined by weighing distributions that had been carefully traced and cut from a uniform medium (mylar) and applying a conversion factor calculated by application to regions of known area. Where body size is used, values are the maximum snout-vent length in mm, as reported in Schwartz and Henderson (1991); for nearly all species, the maximum value occurs in females.

Geographic, geologic, climatic, and vegetational data were taken from a variety of sources, including Asprey and Robbins (1953), Box and Cameron (1989), Caribbean and Latin American Action (1993), Instituto Cubano de Geodesia y Cartografía (1978), Johnson (1988), MacPherson (1980), Marrero (1946), Maurrasse (1982), National Geographic Society (1981), Núñez Jiménez (1972), Picó (1974), Rickards (1980), SEA/DVS (1990), Showker, (1989), Vickers (1979), Woodring et al. (1924), World Resources Institute (1992, 1994), and 1:1,000,000 scale topographic maps of the American Geographical Society, and various other topographic and road maps of the islands. Published values for island areas were found to vary slightly and sometimes the average or modal value was used. In the maps of elevation and rainfall for the Greater Antilles presented here, different contour intervals had to be used for different islands in order to high-

light variation (e.g., rainfall in Jamaica is higher than on other islands).

There are many different forest types described for the West Indies, partly reflecting the diversity of underlying rock types. However, much of the land area of the islands was covered with shallow marine waters at times during the Mesozoic and Cenozoic and therefore the predominate surface rock type is limestone. Forests overlying limestone are lower, have a more open canopy, and a greater number of vines and epiphytes than forests on other rock types. The forest types used here are from Asprey and Robbins (1953), Instituto Cubano de Geodesia y Cartografía (1978), Thompson et al. (1986a), and SEA/DVS (1990), with some modification. **Dry scrub forest** has a low canopy (2–10 m), often with thorny shrubs and cacti, and grows on bare rock or thin soil cover in areas receiving < 1 m rainfall annually; usually this is a coastal formation (low in elevation). **Wet limestone forest** essentially is rainforest growing on limestone rock, sometimes with a thin soil layer; the canopy is about 15–25 m and there are abundant vines and epiphytes; it usually occurs in areas of > 2 m rainfall annually. **Lowland rainforest** with high canopy and large, buttressed trees no longer exists in the West Indies (except in a few small patches); it was cleared in the early days of European colonization. **Montane rainforest** is characterized by a high (25–40 m), dense canopy and occurs on mountain slopes (typically 500–1500 m elevation) in areas receiving > 2 m rainfall annually. **Cloud forest** occurs in the upper elevations (usually > 1000 m) at the cloud level and thus it receives less light and greater humidity than other forest types. The canopy is low (10–15 m) and ferns (also tree ferns), mosses, and epiphytes are abundant. **Elfin woodland** also occurs at the cloud level on some ridges and mountain tops from as low as 750 m (Jamaica) to > 2400 m (Hispaniola). The vegetation is a low, windblown, tangle of mossy trees and shrubs about 5 m in height; ferns and epiphytes are abundant. **Pine forest** occurs naturally and in cultivation throughout the West Indies, but most often in the higher elevations (> 1000 m). **Mangrove woodland** (usually *Rhizophora mangle*) is a common forest type in coastal areas where trees average about 5 m in height.

The Cayman Islands have only a single, non-endemic, native amphibian species (*Osteopilus septentrionalis*) and the Bahamas Bank (including the Turks and Caicos Islands) also has a low diversity

of amphibians (two native species, neither endemic); both regions will be mentioned only briefly. The single native (but nonendemic) amphibian species on Isla de San Andrés and Isla de Providencia (off the east coast of Nicaragua), *Leptodactylus insularum*, is included in counts of species but is not discussed further.

DESCRIPTION OF REGION

Each of the major islands, or groups of islands, is defined below, with a definition of each of the biogeographic regions contained therein. Highest elevations are noted; unless otherwise indicated, the lowest elevation is approximately sea level. Relevant features of geology, physiography, and vegetation, including current extent of forest cover (if known), are described.

DEFINITION OF REGIONS

Cuba

This is the largest island (105,007 km^2) and makes up nearly one-half of the total area of the West Indies (Fig. 4:2). It is 1250 km long by 191 km at its widest point and 31 km at its narrowest point and has a maximum elevation of 1972 m. There are three major upland areas: the Cordillera de Guaniguanico in the west, Macizo del Escambray in the center, and the Sierra Maestra/Macizo de Sagua-Baracoa in the east. Most forest habitats are limited to those three areas; agriculture (especially sugar cane) predominates in the intervening lowland areas.

Península de Guanahacabibes: This low peninsula at the extreme western end of the island attains elevations of only 22 m. It is characterized by exposed dogtooth limestone rock (diente de perro), caves, and dry scrub forest.

Llanura Occidental: The western coastal plain at elevations of no more than 50 m is characterized by the near-absence of trees and the presence of extensive areas of sugar cane (*Saccharum officinarum*) and rice cultivation.

Cordillera de Guaniguanico: This interconnected upland region reaches 699 m in elevation and comprises two mountain chains with different soil, rock, and vegetation types. The western chain, the Sierra de los Organos (617 m), with its northern (Alturas Pizarrosas del Norte) and southern (Alturas Pizarrosas del Sur) adjoining ranges, primarily is an eroded limestone block with underlying metamorphic rocks of Jurassic age. It is dominated by pine (primarily *Pinus tropicalis*, but also *P. caribaea*) with dry scrub forest on the mogotes (limestone hillocks). The resulting "haystack" karst physiography, although similar to some areas in NW Puerto Rico, is unique in the West Indies and resembles some karst regions of southern China. The eastern chain, the Sierra del Rosario (699 m), is characterized by gently rolling hills, with outcrops of limestone, sedimentary, igneous, and metamorphic rocks.

Isla de Juventud and Archipiélago de los Canarreos: The largest satellite island, Isla de Juventud (formerly Isla de Pinos; 2,200 km^2) is composed of Jurassic metamorphic rocks similar to those underlying the western end of Cuba (Sierra de los Organos) and has a southern limestone plain. Most of the island is low in elevation, but a central upland area rises to 303 m. A long chain of low-lying islands, the Archipiélago de los Canarreos, extends to the east.

Alturas de la Habana-Matanzas: This upland area includes the Alturas de Bujucal-Madruga-Coliseo. These are mostly low limestone ridges and hills (no higher than 381 m) with some outcrops of serpentine.

Llanura de Zapata: This region includes an extensive swampland area (Ciénaga de Zapata) at or near sea level, and a slightly higher (10 m) central area of limestone supporting dry scrub forest. Dogtooth limestone is a common substrate.

Alturas Centrales: Included here are the Alturas de Santa Clara, Alturas del Nordeste, and Alturas del Noroeste. This upland region, mostly above 50 m but no higher than 487 m, is underlain by igneous and extrusive volcanic rock, and has limestone outcrops. The dominant vegetation is sugar cane and grassland with some tree savannas of palm (*Roystonea*) and ceiba (*Ceiba*).

Archipiélago Sabana-Camaguey: These northern satellite islands form a long (450 km) archipelago of low-lying islands composed of primarily Quaternary limestone and sediments. Mangrove woodland is the predominate vegetation on the smaller, western keys (Archipiélago de Sabana), whereas the larger keys in the eastern portion (Archipiélago de Camagüey) are dominated by dry scrub forest on limestone and attain an elevation of no more than 62 m.
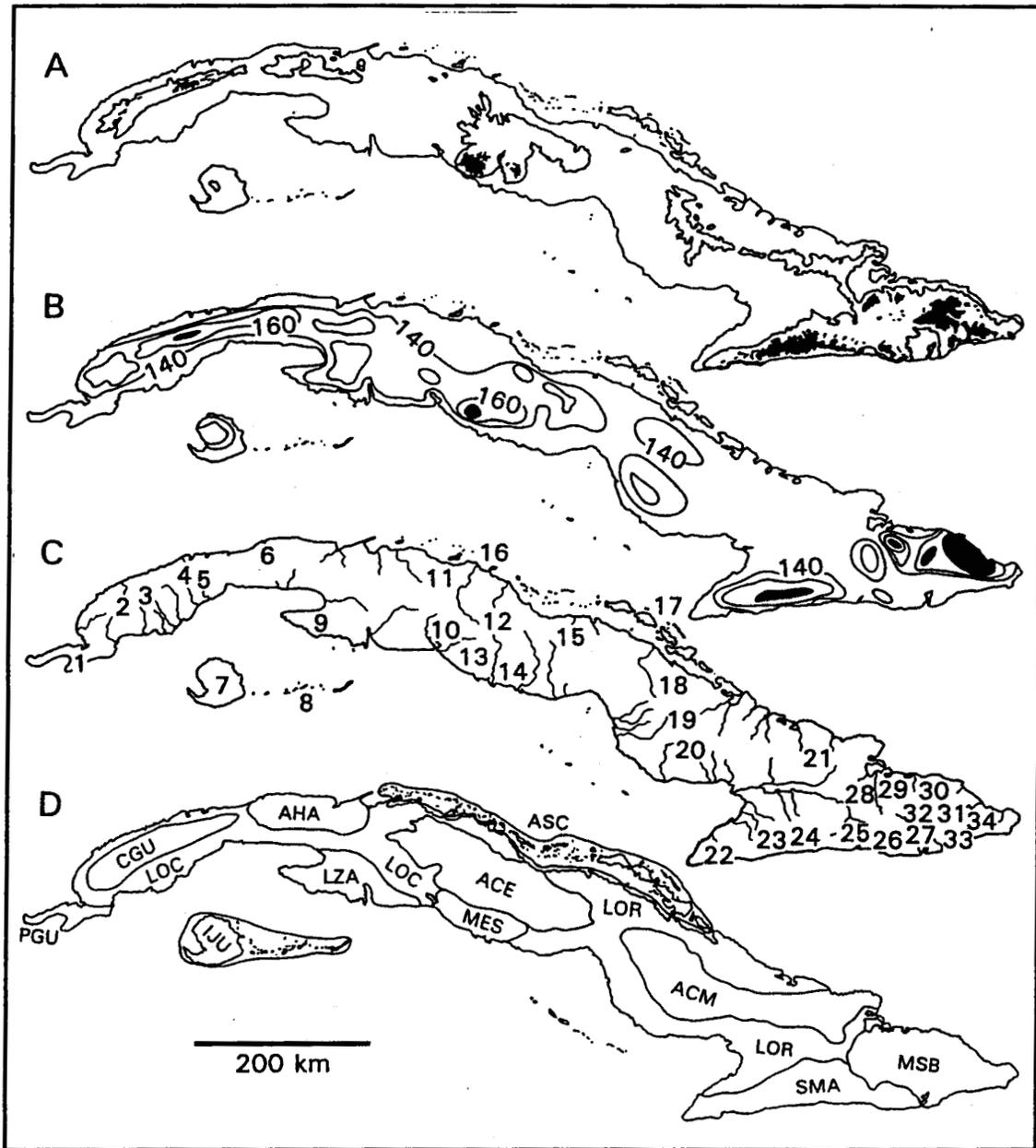
Fig. 4:2. Cuba. (A) Topographic map, showing the 100 m contour interval and areas above 500 m (black). (B) Rainfall map, showing contour intervals of 140 cm, 160 cm, and areas over 200 cm (black) annual precipitation. (C) Drainage map, showing major rivers. Numbers are locations of peaks, mountain ranges, major cities, and other geographic areas mentioned in text: Península de Guanahacabibes (1), Sierra de los Organos (2), Viñales (3), Sierra del Rosario (4), Soroa (5), La Habana (6), Isla de Juventud (7), Archipiélago de los Canarreos (8), Ciénaga de Zapata (9), Cienfuegos (10), Alturas del Noroeste (11), Alturas de Santa Clara (12), Alturas de Trinidad (13), Alturas de Sancti Spíritus (14), Alturas del Nordeste (15), Archipiélago de Sabana (16), Archipiélago de Camagüey (17), Sierra de Cubitas (18), Peniplano de Florida-Camagüey-Tunas (19), Sierra de Najasa (20), Grupo de Maniabón (21), Meseta de Cabo Cruz (22), Pico Turquino (23), Cordillera del Turquino (24), Santiago de Cuba (25), Cordillera de la Gran Piedra (26), Guantánamo (27), Altiplanicie de Nipe (28), Sierra del Cristal (29), Cuchillas de Moa (30), Cuchillas de Toa (31), Meseta del Guaso (32), Sierra de Mariana (33), and Sierra del Purial (34). (D) Biogeographic regions. Abbreviations: ACE Alturas de Central (Alturas de Santa Clara, Alturas del Nordeste, Alturas del Noroeste), ACM Alturas de Camaguey-Maniabón (Sierra de Cubitas, Peniplano de Florida-Camaguey-Tunas, Sierra de Najasa, Grupo de Maniabón), AHA Alturas de la Habana-Matanzas (including

Macizo del Escambray: This major central highland region includes a larger western area, the Alturas de Trinidad (1140 m), and a smaller eastern area, the Alturas de Sancti Spíritus (842 m), separated by the valley of the Río Agabama. Jurassic igneous rocks underlie both regions, but limestone outcrops occur throughout the region. Upper elevations are characterized by montane rainforest (now largely replaced by coffee, *Coffea arabica*).

Llanura Oriental: This low eastern coastal plain attains elevations of only 50 m. It is similar to the Llanura Occidental in being characterized by extensive areas of sugar cane cultivation and the near-absence of trees.

Alturas de Camagüey-Maniabón: Included in this region of moderate relief are the Sierra de Cubitas (330 m), Peniplano de Florida-Camagüey-Tunas (297 m), Sierra de Najasa (301 m), and Grupo de Maniabón (275 m). All primarily are underlain by igneous (serpentine and granite) rocks and extrusive volcanics. Vegetation is a mixture of mostly tree savanna and dry scrub forest, with sugar cane cultivation in the lower elevations.

Sierra Maestra: With a large area above 1000 m elevation, this is the major eastern highland region and it includes a large limestone platform (Meseta de Cabo Cruz, 401 m), a major central massif (Cordillera del Turquino, 1972 m), and a partially isolated eastern extension (Cordillera de la Gran Piedra, 1214 m). Pico Turquino (1972 m) is the highest point in Cuba. The underlying rocks primarily are Tertiary volcanic and sedimentary formations, including limestone. The dominant natural vegetation is montane rainforest (now mostly coffee cultivation on the northern slopes), and there is cloud forest and elfin woodland at the highest elevations.

Macizo de Sagua-Baracoa: Separated from the Sierra Maestra by the Río Guantánamo and Valle Central, this major upland region is a complex of seven smaller upland areas: the Altaplanicie de Nipe (995 m), the Sierra del Cristal (1231 m), Meseta del Guaso (862 m), Sierra de Mariana (747), Cuchillas de Moa (1175 m), Cuchillas de Toa (921 m), and the Sierra del Purial (1176 m). The underlying rocks primarily are a mixture of Mesozoic igneous and metamorphic rocks overlain by montane rainforest and pine forest (*Pinus cubensis*) and Cenozoic limestone overlain by pine forest and wet limestone forest. Cloud forest occurs in some of the higher elevations in the wettest areas.

Jamaica

With an area of 10,992 km², this island lies to the south of eastern Cuba; it is 230 km long by 80 km wide, and has a maximum elevation of 2256 m (Fig. 4:3). Most of the island is a dissected Tertiary limestone platform and therefore hilly and mountainous; a high mountain chain (Blue Mountains), involving other rock types, exists in the east. It is the wettest island in the Greater Antilles; some areas have more than 5 m of precipitation annually. Although Jamaica appears lush and green, this is due in large part to an introduced flora and high rainfall; few natural forests remain, and these are concentrated in the Cockpit Country of west-central Jamaica and in the Blue Mountains.

Western Lowlands: As in most of Jamaica, this region is largely underlain by mid-Tertiary limestone. There are a few patches of dry scrub forest and some coastal mangrove woodland, and a large (250 km²) fresh-water sedge marsh (Black River Morass), but most areas are under cultivation (primarily sugar cane). Elevations do not exceed 300 m.

Western Uplands: Although partly isolated from each other, these upland areas all lie on the western side (Hanover Block) of north-south trending fault zone (Montpelier-Newmarket Graben). Although the southern areas (801 m) are higher in elevation, Dolphin Head (545 m) has the better-developed wet limestone forest.

Santa Cruz Mountains: This is an isolated upland area in south-central Jamaica with little or no original wet limestone forest remaining. The highest elevation is 725 m.

Cockpit Country: This rugged karst plateau, with typical elevations of 600-700 m (946 m elevation at highest point), is the largest remaining area of wet limestone forest in Jamaica. It is bordered on the west by the Montpelier-Newmarket Graben, and on the north by the drier north coast, but the southern and eastern boundaries are less well defined.

North Coast: Coconut cultivation dominates the relatively dry north coast, but there are some occa-

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Alturas de Bujucal-Madruga-Coliseo), ASC Archipiélago Sabana-Camaguey, CGU Cordillera de Guaniguanico, IJU Isla de Juventud and Archipiélago de los Canarreos, LOC Llanura Occidental, LOR Llanura Oriental, LZA Llanura de Zapata (including Cienagas de Zapata), MES Macizo del Escambray, MSB Macizo de Sagua-Baracoa, PGU Península de Guanahacabibes, SMA Sierra Maestra.

sional patches of dry scrub forest. Elevations do not exceed 300 m.

Central Uplands: This region is similar in karst topography and elevation to the adjoining Cockpit Country, but with greater human population density and less wet limestone forest; the highest point is 838 m elevation. The eastern border is a major fault, the Wagwater Trough.

Manchester Plateau: This region includes the Don Figuero Mountains and is characterized by gently rolling hills (up to 995 m elevation) with less exposed rock and greater soil depth than the adjoining Central Uplands to the north. Some small patches of wet limestone forest remain; human population density is high, and most areas are cultivated.

Southern Lowlands: Because of the rainshadow effect of the Blue Mountains and Central Uplands, some of the driest areas in Jamaica are in this region, which includes areas below 300 m elevation. Cultivation and cattle grazing is extensive, although some small areas of dry scrub forest remain.

Portland Ridge Peninsula: This relatively low limestone ridge (up to 160 m elevation) with many caves is overlain by dry scrub forest on a dogtooth limestone substrate. It was an island during times of elevated sea level in the Pleistocene.

Hellshire Hills: Similar in some respects to the Portland Ridge Peninsula, this region largely is covered by dry scrub forest on limestone rock; the highest elevation is 258 m.

Blue Mountains: With several peaks above 2000 m, this is the major mountain chain of Jamaica; highest peak = Blue Mountain Peak (2256 m). The underlying rocks are igneous, metamorphic, and clastic sedimentaries; these are overlain by remnant montane rainforest (< 1350 m) grading to cloud forest (1350–1500 m) and elfin woodland (> 1500 m). Cultivation of pine and coffee is common at higher elevations. The northern slopes are considerably wetter and more forested than the southern slopes.

John Crow Mountains: The wettest areas in Jamaica are in this region, which is a northwest-southeast-oriented limestone block, tilted up to the southwest and separated (mostly) from the Blue Mountains by the Rio Grande Valley. Possibly because of the high rainfall in this region, the expected wet limestone forest is replaced by montane rainforest, and vegetational zones typical of the Blue Mountains (including elfin woodland) occur at low-

er elevations (Asprey and Robbins, 1953). The highest elevation is 1202 m.

Hispaniola

Lying between Cuba and Puerto Rico, Hispaniola has an area of 76,470 km²; it is 650 km long by 255 km wide with a maximum elevation of 3175 m (Fig. 4:4). The western one-third of the island is occupied by Haiti and the remainder by the Dominican Republic. Numerous mountain ranges and valleys dissect this island, which is divided into two faunistically defined paleoislands ("North Island" and "South Island"), separated by a below sea-level trough, the Cul de Sac and Valle de Neiba. Natural forests are essentially absent from Haiti, and this has caused widespread silting and destruction of the already overfished coral reefs. Most remaining forests in the Dominican Republic are confined to the Cordillera Central, but some relatively small tracts remain in other upland areas.

Navassa Island: This is a small island with a steep, rock shoreline located about 60 km west of the Tiburon Peninsula of Haiti.

Massif de la Hotte: The region defined here forms the core (Montagnes de la Hotte) of the more inclusive Massif de la Hotte, and includes the highest elevations (up to 2347 m). Lower elevations largely are barren, and remnants of montane rainforest and wet limestone forest exist on the slopes and foothills; some pine forest and cloud forest still may be present on the highest peaks.

Presqu'île de la Tiburon: The Tiburon Peninsula includes some limestone hills (up to 1340 m), representing the eastern extension of the Massif de la Hotte; at one time they may have been covered with wet limestone forest.

Massif de la Selle–Sierra de Baoruco: Two names have applied to this single mountain range that straddles the international border and is formed largely by an uplifted limestone platform that has been tilted up toward the north. This has resulted in a gradual southern incline and a steeper and more rugged northern slope; both have dry scrub forest at lower elevations. The mostly pine-clad ridge, rising up to 2690 m elevation, has occasional patches of cloud forest, especially in the extreme eastern end.

Península de Barahona: The dry southern peninsula of Hispaniola is a terraced limestone platform supporting dry scrub forest; the maximum elevation is 331 m.

Plaine du Cul de Sac–Valle de Neiba: Separating

Fig. 4:3. Jamaica. (A) Topographic map, showing 300 m contour interval and areas above 1,000 m (black). (B) Rainfall map, showing contour intervals of 180 cm, 250 cm, and areas over 380 cm (black) annual precipitation. (C) Drainage map, showing major rivers. Numbers are locations of peaks, mountain ranges, major cities, and other geographic areas mentioned in text: Dolphin Head (1), Montego Bay (2), Black River Morass (3), Cockpit Country (4), Quick Step (5), Santa Cruz Mountains (6), Don Figuerero Mountains (7), Portland Ridge Peninsula (8), Hellshire Hills (9), Kingston (10), Hardwar Gap (11), Blue Mountain Peak (12), and John Crow Mountains (13). (D) Biogeographic regions. Abbreviations: BMO Blue Mountains, CCO Cockpit Country, CUP Central Uplands, HHI Hellshire Hills, JCM John Crow Mountains, MPL Manchester Plateau, NCO North Coast, PRP Portland Ridge Peninsula, SCM Santa Cruz Mountains, SLO Southern Lowlands, WLO Western Lowlands, WUP Western Uplands.

the two paleoislands of Hispaniola along a major fault, this long, mostly barren valley (below 100 m elevation) with occasional patches of dry scrub forest lies below sea level in many places and has several large hypersaline lakes (e.g., Lago Enriquillo, –42 m).

Île Gonâve: This is the largest satellite island of Hispaniola and has an upland area (Montagnes de la Gonâve, rising to 702 m); the island is densely populated and largely devoid of natural vegetation.

Chaîne des Matheux–Sierra de Neiba: These ranges, and the Haitian Montagnes Trou D'eau, are oriented in a northwest-southeast direction and attain moderate to high elevations (1575 m and 2279 m, respectively). The Haitian ranges have been largely deforested, but some cloud forest and wet limestone forest are present in the Sierra de Neiba.

Sierra de Martín García: Surrounded by xeric lowlands in a region of relatively low rainfall, this isolated range with a maximum elevation of 1368 m supports some pine and hardwood forest at upper elevations.

Valle de San Juan: This relatively dry valley (below 400 m elevation) is the rain shadow of the Cordillera Central and presently an agricultural region with little remaining natural vegetation.

Plateau Central: At an elevation of about 300–400 m, this plateau is an extension of the Valle de San Juan and separates the Massif du Nord from the Montagnes Noires; there is little or no remaining natural vegetation.

Massif des Montagnes Noires: These are mostly limestone ridges rising to 1793 m elevation, now deforested.

Plaine de l'Artibonite: This floodplain of the large Rivière Artibonite, with elevations below 100 m, supports some agriculture but no natural vegetation.

Presqu'île du Nord Ouest: The dry northwest peninsula of Haiti resembles a barren lunar landscape when viewed from the air, but some small patches of secondary forest remain on steep slopes of the interior ranges; the maximum elevation is 840 m.

Île de la Tortue: Once thickly forested with large hardwood trees but now essentially barren, this large satellite island is mostly limestone; the maximum elevation is 378 m.

Massif du Nord: This is the major mountain range of northern Haiti and represents the northwest

extension of the Cordillera Central; the maximum elevation is 1210 m.

Cordillera Central: With many peaks above 2000 m, including the highest point in the West Indies (Pico Duarte, 3087 m), this is the major central mountain range of Hispaniola. Much of it has been deforested, but the core of this range and the highest elevations typically support pine (*Pinus occidentalis*) on a limestone substrate. Some cloud forest and montane rainforest exist in patches throughout the range, primarily in the northwest sector.

Plaine du Nord–Valle de Cibao: This is a mesic, fertile agricultural valley with elevations below 300 m and with essentially no remaining natural vegetation.

Cordillera Septentrional: The northern mountain range of the Dominican Republic is a nearly linear northwest-southeast-oriented ridge rising to 1249 m elevation and with scattered patches of montane rainforest.

Península de Samaná: This rugged, wet, limestone peninsula with several mountains has only secondary forest remaining; the maximum elevation is 606 m.

Los Haitises: Wedged between the Cordillera Central and the Cordillera Oriental, this highly dissected karst area is similar to the Cockpit Country of Jamaica but lower in elevation. Typical elevations are 150–250 m and wet limestone forest still exists, primarily on the tops of some mogotes; the maximum elevation is 467 m.

Cordillera Oriental: This eastern mountain chain of Hispaniola, attaining a maximum elevation of 736 m, is continuous with Los Haitises but has little remaining natural forest.

Llanura Costera del Caribe: In many places along the coast, this Caribbean coastal plain is characterized by low (0–20 m) limestone terraces with a substrate of dogtooth limestone. The depauperate flora of the terraces is characterized by *Bucida buceras,* whereas agriculture (primarily sugar cane) predominates in the more fertile inland areas; the maximum elevation is 200 m.

Puerto Rican Bank

This archipelago extends from the Isla Mona in the west to Anegada in the east. Except for Isla Mona and St. Croix, virtually all are separated by relatively shallow water. The main island of Puerto Rico is the largest in the chain but is the smallest of the Greater Antilles (8,768 km^2); it is 179 km long by 58 km
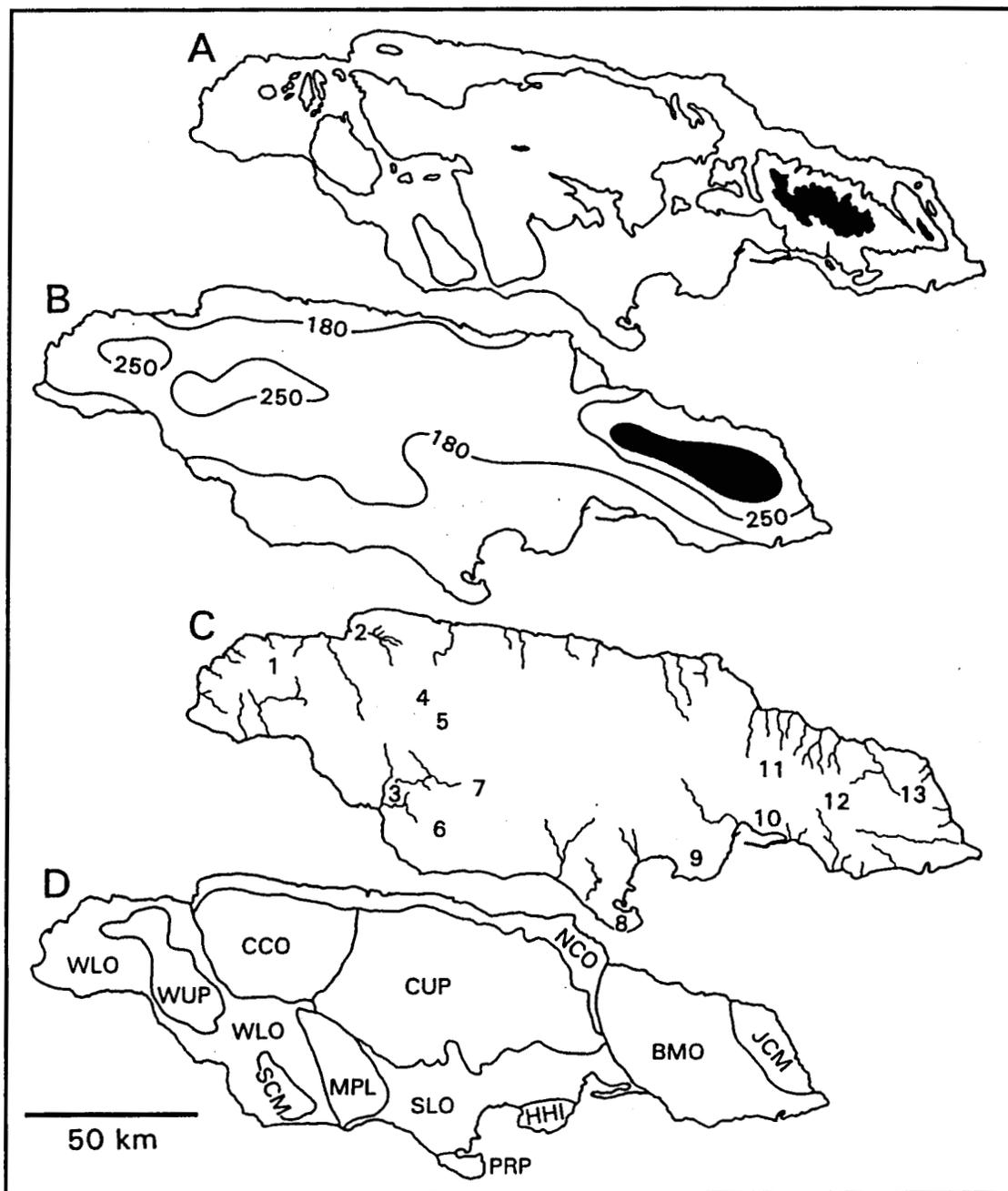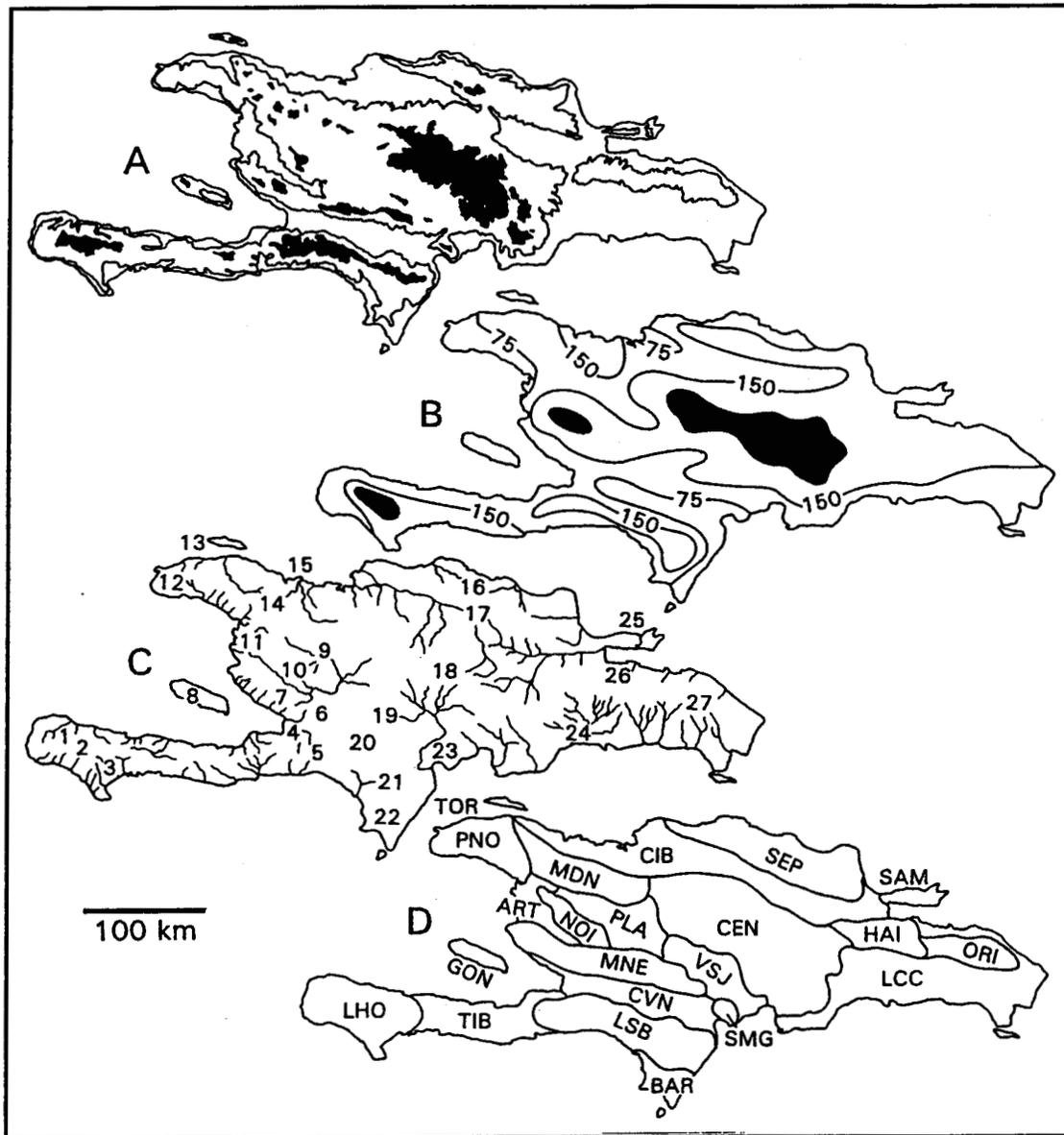
Fig. 4:4. Hispaniola. (A) Topographic map, showing 200 m contour interval and areas above 1,000 m (black). (B) Rainfall map, showing contour intervals of 75 cm, 150 cm, and areas over 225 cm (black) annual precipitation. (C) Drainage map, showing major rivers. Numbers are locations of peaks, mountain ranges, major cities, and other geographic areas mentioned in text: Castillon (1), Montagnes de la Hotte (2), Les Cayes (3), Port-au-Prince (4), Massif de la Selle (5), Montagnes Trou D'eau (6), Chaîne des Matheux (7), Île Gonâve (8), Plateau Central (9), Massif des Montagnes Noires (10), Plaine de l'Artibonite (11), Presqu'île du Nord Ouest (12), Île de la Tortue (13), Massif du Nord (14), Cap-Haïtien (15), Cordillera Septentrional (16), Santiago (17), Pico Duarte, Cordillera Central (18), Sierra de Neiba (19), Lago Enriquillo (20), Sierra de Baoruco, Sierra de Baoruco (21), Península de Barahona (22), Sierra de Martín García (23), Santo Domingo (24), Península de Samana (25), Los Haitises (26), and Cordillera Oriental (27). (D) Biogeographic regions. Abbreviations: ART Plaine de l'Artibonite, BAR Península de Barahona, CEN Cordillera Central, CIB Plaine du Nord-Valle de Cibao, CVN Plaine du Cul de Sac–Valle de Neiba, GON Île Gonâve, HAI Los Haitises, LCC Llanura Costera del Caribe, LHO Massif de la Hotte, LSB Massif de la Selle–Sierra de Baoruco, MDN Massif du Nord, MNE Chaîne des Matheux–Sierra de Neiba, NOI Massif des Montagnes Noires, ORI Cordillera Oriental, PLA Plateau Central, PNO Presqu'île du Nord Ouest, SAM Península de Samana, SEP Cordillera Septentrional, SMG Sierra de Martín García, TIB Presqu'île de la Tiburon, TOR Île de la Tortue, VSJ Valle de San Juan.

wide with a maximum elevation of 1338 m (Fig. 4:5). The physiography of this island is not as complex as that of the three larger islands of the Greater Antilles; it has a central cordillera and an isolated upland region (Sierra de Luquillo) in the northeast. Most natural forests, and one of the largest tracts of elfin woodland in the Caribbean, are in the Sierra de Luquillo.

Isla Mona: Although politically part of Puerto Rico, this island between Hispaniola and Puerto Rico is not part of the Puerto Rican Bank. It is a largely uninhabited limestone plateau attaining a maximum elevation of 85 m and with dry scrub forest.

Coastal Lowlands: These are the most densely populated areas in Puerto Rico, especially along the north coast; the maximum elevation is 100 m. Sugar cane cultivation is common along the southern coastal plain.

Central Uplands: The highland "backbone" of Puerto Rico, or Cordillera Central, extends in an east-west direction and includes a major region of serpentine rocks (Maricao forest) in the west; the maximum elevation is 1338 m. The northern, and especially northwestern, extension of the upland region is a dissected limestone plateau with karst topography similar to the Cockpit Country of Jamaica and Los Haitises of Hispaniola; in some areas, the wide separation of the mogotes resembles the Viñales region of western Cuba (although the mogotes are not as large). Montane rainforest has been replaced mostly by coffee cultivation in the upper elevations of the main cordillera, whereas wet limestone forest can be found on some mogotes in the karst areas.

Sierra de Cayey: This eastern extension of the Cordillera Central rising to 903 m elevation, sometimes referred to as the humid east-central mountains, is more densely populated and therefore less forested.

Cuchilla de Pandura: This relatively low range (up to 525 m elevation) consists mostly of weathered igneous rocks in the form of giant bolders (some > 10 m in diameter) which in turn form a network of bolder caves. Most natural forest has been removed, and human population density is high.

El Yunque: The largest area of natural forest in Puerto Rico is in this region, which takes the name of one of the three major peaks (El Yunque, 1065 m; highest peak = El Toro, 1074 m) in the Sierra de Luquillo. The mostly igneous rock supports mon-

tane rainforest in the lower elevations which grades into cloud forest and finally to elfin woodland on the peaks.

Vieques: The largest satellite island of Puerto Rico has moderate relief (up to 301 m elevation) and a mixture of dry scrub forest and cultivation (primarily sugar cane).

Culebra: This mostly limestone island also has moderate relief (up to 195 m elevation) and dry scrub forest along with cultivation and cattle farming.

St. Thomas: This volcanic and limestone island is characterized by highly dissected terrain, and includes the highest elevation in the U.S. Virgin Islands (474 m). There is very little agriculture because of the rugged terrain and poor soil.

St. John: Similar to St. Thomas in being rugged and mountainous, this island is less populated, has greater forest cover, and a National Park (The Virgin Islands National Park); maximum elevation is 389 m.

St. Croix: This, the largest of the U.S. Virgin Islands, is mountainous in the northeast and relatively flat along the south coast, with rolling hills throughout most of the central region; the maximum elevation is 355 m. Most rainfall occurs in the west leaving the eastern portion relatively arid. Some forests remain in the northwest, but most of the interior is used for agriculture.

Tortola: There are patches of rainforest on Mount Sage in the north (a "Protected Area"); dry scrub forest occurs mostly in the southern portion of this hilly island; the maximum elevation is 521 m.

Virgin Gorda: This is a geologically complex island with a small area of forest cover on Virgin Peak (414 m). Some secondary forests also occur in other high elevation areas and bordering drainage systems. The southwestern portion of the island is relatively flat and used for agriculture.

Anegada: This is a nearly flat limestone island attaining a maximum elevation of only 8 m.

Lesser Antilles

This chain of islands (5840 km² total) begins just east of the Puerto Rican Bank and extends in an arc southward to the continental shelf of South America at Trinidad and Tobago (Fig. 4:6). The largest island, Guadeloupe (1,510 km²), also is the highest (1467 m). Most islands have at least some small patches of forest remaining; Dominica is the most
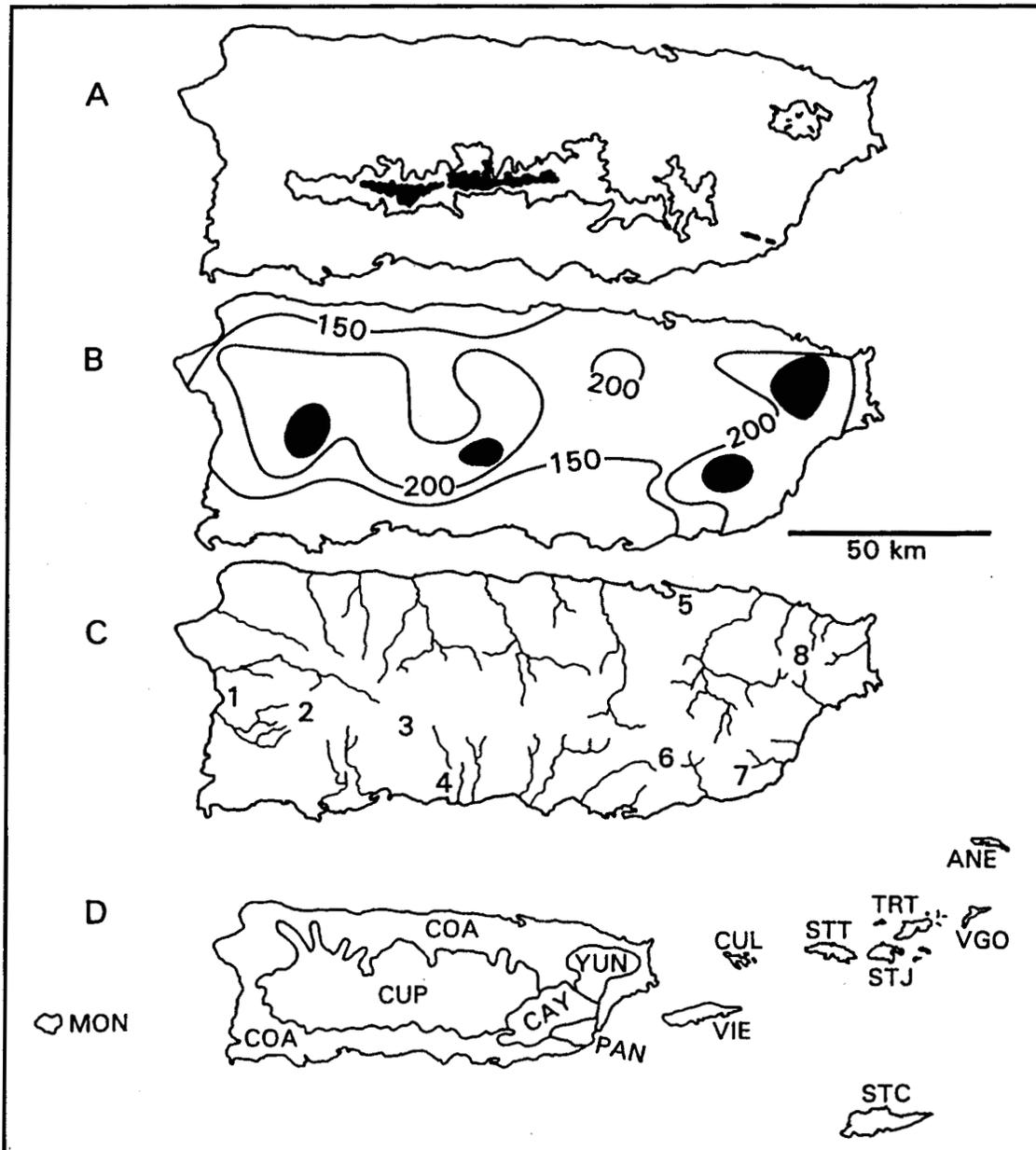
Fig. 4:5. Puerto Rican Bank. (A) Topographic map of Puerto Rico, showing 500 m contour interval and areas above 1,000 m (black). (B) Rainfall map of Puerto Rico, showing contour intervals of 150 cm, 200 cm, and areas over 250 cm (black) annual precipitation. (C) Drainage map of Puerto Rico, showing major rivers. Numbers are locations of peaks, mountain ranges, major cities, and other geographic areas mentioned in text: Mayaguez (1), Maricao forest (2), Cordillera Central (3), Ponce (4), San Juan (5), Sierra de Cayey (6), Cuchilla de Pandura (7), and El Yunque (8). (D) Biogeographic regions of the Puerto Rican Bank, including Mona Island and St. Croix. Abbreviations: ANE Anegada, CAY Sierra de Cayey, COA Coastal Lowlands, CUL Culebra, CUP Central Uplands, MON Isla Mona, PAN Cuchilla de Pandura, STC St. Croix, STJ St. John, STT St. Thomas, TRT Tortola, VGO Virgin Gorda, VIE Vieques, YUN El Yunque.

forested, Barbados the least. Hurricanes, and on a less-frequent time scale, volcanic eruptions, are natural causes of environmental perturbation in the Lesser Antilles.

Anguilla Bank: Included in this region are Anguilla (59 m maximum elevation), St. Martin (392 m), and St.-Barthélémy (424 m). These are three rocky islands of only moderate elevation. Anguilla is covered mostly with dry scrub forest.

Saba Bank: This is a small, rocky, volcanic island attaining a maximum elevation of 870 m.

St. Eustatius Bank: Included here are the islands of St. Eustatius (600 m maximum elevation), St. Christopher or "St. Kitts" (1156 m), and Nevis (985 m). All three are relatively rocky, volcanic islands with montane rainforest in the upper elevations and dry scrub forest along the coasts.

Barbuda Bank: Barbuda (62 m maximum elevation) and Antigua (402 m) are low, mostly denuded limestone islands with rolling hills and cattle farms.

Montserrat: Although primary forest has been removed from this volcanic island, there is some dry scrub forest (low elevations) secondary rainforest (mid-elevations of north slopes) and elfin woodland (summits); the maximum elevation is 914 m.

Guadeloupe Bank: The largest island, Basse-Terre (1467 m maximum elevation), is volcanic and has some montane rainforest; Grande-Terre is a low and essentially denuded limestone island; La Desirade (273 m) is a sharp ridge of limestone and exposed Jurassic rock.

Marie Galante: This is a low, deforested limestone island attaining a maximum elevation of only 204 m.

Dominica: The largest remaining tracts of primary forest in the Lesser Antilles are on this volcanic island, where 60% of the land is forested with either dry scrub forest (west coast), montane rainforest (south and central), or elfin woodland (summits); the maximum elevation is 1447 m.

Martinique: Moderately large tracts of forest, totalling 12% of land area, remain on this volcanic island which rises to 1397 m, but all have been affected by human activities. These tracts include dry scrub forest (south), montane rainforest (intermediate elevations), and cloud forest (Mt. Pelee and west-central).

St. Lucia: This volcanic island supports some forest habitats, including dry scrub forest (north, and
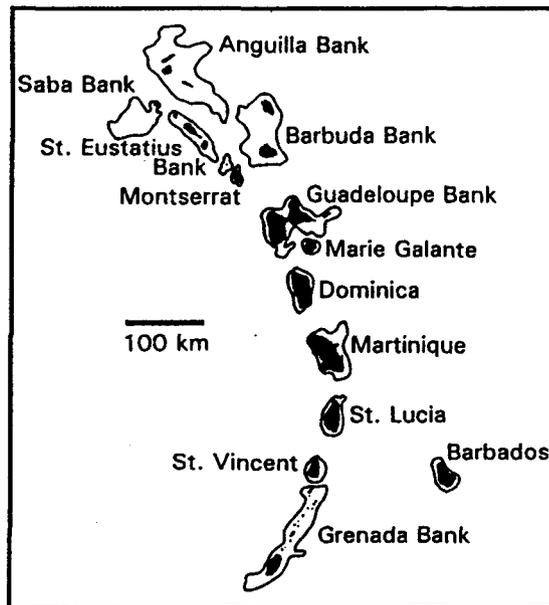
Fig. 4:6. Islands and island groups of the Lesser Antilles. Redonda, located between St. Eustatius and Montserrat, has no reported amphibian species.

lower elevations near coast), rainforest (slopes), and cloud forest (summits); the maximum elevation is 950 m.

St. Vincent: There are some secondary forests, but apparently there is only one remaining undisturbed montane rainforest area which is located along the ridge in the center of this volcanic island; the maximum elevation is 1234 m.

Grenada Bank: Grenada (840 m maximum elevation) is the largest of these volcanic islands; the Grenadines, including among others Carriacou (294 m), Ronde (164 m), and Union Island (305 m), is a chain of small, low islands between Grenada and St. Vincent. Forests on Grenada include dry scrub forest (south), secondary montane rainforest (intermediate elevations), and elfin woodland (summits).

Barbados: This densely populated low island, formed by uplifted ocean floor, is devoid of forest; the maximum elevation is 340 m.

Bahamas Bank

This cluster of islands lies to the north of Cuba and Hispaniola and to the east of the southern tip of Florida. It includes two political units, the Bahamas and the Turks and Caicos, which have a total area of 11,296 km². All of the thousands of islands on this bank are low (0–40 m elevation) and with a calcare-

ous substrate. Some well-developed lowland rain-forest existed at the time of discovery, but only secondary forests are present today.

Cayman Islands

These are three small islands (Grand Cayman, Cayman Brac, and Little Cayman) located about 250 km south of central Cuba and about 250 km northwest of Jamaica; the total area is about 260 km². They represent the emergent portion of the east-west-oriented Cayman Ridge (the southern edge of the North American tectonic plate) and lie immediately to the north of the Cayman Trough. The substrate is mostly coral and limestone and the highest point is only 45 m elevation (Cayman Brac). Dry scrub forest is the predominate vegetation, although a few pockets of primary hardwood forest (including mahogany) remain.

HISTORICAL GEOLOGY

The complex geologic history of the Caribbean still is the subject of intense study but some general features are evident. The Greater Antilles are old islands that originated in the early Cretaceous through island arc accretion in a zone between North and South America (Perfit and Williams, 1989; Pindell and Barrett, 1990). During the mid-Cretaceous, submarine basaltic extrusions in the eastern Pacific created an unusually thick and buoyant oceanic plate that later formed the Caribbean Plate after moving to the north and east behind the Greater Antillean arc (Burke et al., 1978). In the late Cretaceous (70 mya), the island arc connection between North and South America began to break apart as the northeastward movement progressed and a trailing subduction zone formed in the Pacific which would later become the isthmus of Central America. By the early Tertiary (60 mya), the Greater Antilles arc had reached the Bahamas Platform and started a collision which plugged the subduction zone and eventually (50 mya) sutured Cuba, northern Hispaniola, and Puerto Rico to the North American Plate. As a result, a fault zone and small spreading center (Cayman Trough) south of the arc now became the northern boundary of the Caribbean Plate and the direction of plate movement shifted from northeast to east. Jamaica and the southern portion of Hispaniola were carried eastward with the Caribbean Plate to their present locations; the two major portions of Hispaniola became sutured in the Miocene. Although volcanic rock is present, mountain building in the Great-

er Antilles largely has been caused by uplift as a result of compressional forces; there are no active volcanoes.

Subduction of the Atlantic Plate beneath the eastern edge of the Caribbean Plate initiated the Lesser Antillean arc system in the mid- or late Cretaceous. Back-arc spreading shortly after the Cretaceous-Tertiary boundary split the arc into the Aves Ridge (now inactive and almost completely submerged) and the present Lesser Antilles (Bouysse, 1988; Maury et al., 1990). Since then, there has been further subdivision within the Lesser Antilles. An older outer arc (Marie-Galante, Grande Terre of Guadeloupe, La Désirade, Antigua, Barbuda, St. Bartholemew, St. Martin, Dog, and Sombrero) is characterized by low limestone islands that are relatively flat, whereas most other islands (inner arc) in the Lesser Antilles are volcanic and some have active volcanos; there is one active submarine volcano north of Grenada (Maury et al., 1990). The two arcs diverge north of Martinique. This double arc pattern is the result of an initial period of volcanic activity in the Eocene (outer arc), a quiescent period for about 10 my in the late Oligocene and early Miocene, and then renewed volcanic activity since the mid-Miocene (Maury et al., 1990). Barbados differs from the other islands in being the emergent portion of the Lesser Antilles Accretionary Ridge and is, therefore, not volcanic. The presence of Mesozoic basement rocks at several locations in the Lesser Antilles supports a Mesozoic origin for the arc (Bouysse, 1988; Maury et al., 1990; Pindell and Barrett, 1990).

It was suggested recently that the northern (north of Martinique) and southern Lesser Antilles have had separate geologic histories that have influenced the evolution of anoline lizards in the West Indies (Roughgarden, 1995). The southern Lesser Antilles were proposed to be a separate plate "or piece of the South American Plate that has become sutured to the present-day eastward-moving Caribbean Plate." This was based in part on a suggestion in the geologic literature that the northern and southern portions of the Lesser Antilles were separated by a major east-west transform fault (Bouysse, 1984). Motion along the fault was believed to have caused the separation between the Aves arc and Lesser Antilles arc. However, the location of that proposed fault was north of Dominica (not Martinique) and Bouysse since has abandoned the hypothesis

Table 4:1. Numbers of species of anurans in the West Indies.

Taxon	Total	Native[1]	Endemic[2]	Introduced	%Endemic[3]
Bufonidae:					
Bufo	12	11	11	1	92
Dendrobatidae:					
Colostethus	1	1	1	0	100
Hylidae:					
Calyptahya	1	1	1	0	100
Hyla	7	5	5	2	100
Osteopilus	4	4	4	0	100
Pseudacris	1	0	0	1	0
Scinax	1	0	0	1	0
Leptodactylidae:					
Eleutherodactylus	139	139	139	0	100
Leptodactylus	5	5	3	0	60
Microhylidae:					
Gastrophryne	1	0	0	1	0
Ranidae:					
Rana	3	0	0	3	0
Total	174	167	164	8	98

[1]Occurs naturally within the West Indies.
[2]Occurs naturally within the West Indies and nowhere else (except as introduced).
[3]Number of endemic species divided by number of native species.

based on more recent geologic evidence that favors back-arc spreading of a single continuous island arc (Bouysse, 1988; Holcombe et al., 1990; Maury et al., 1990). A geologic model by Speed (1985) also was cited by Roughgarden (1995) as supporting evidence, but Speed's model indicates a different origin only for the extreme southern islands (e.g., Grenada) in the Lesser Antilles.

The location and extent of exposed land through time is important in understanding the historical biogeography of the West Indies. Unfortunately, very little of this information is known. In the mid- to late Cretaceous (90-70 mya), paleocoastline data suggest that areas in North and South America adjacent to the proto-Antilles were below sea level (Smith et al., 1994) suggesting that the proto-Antilles also were submerged, or at least did not form a land connection with the mainland. Jamaica is believed to have been completely (or nearly so) submerged during the Oligocene based on the extensive limestone sediments of that period virtually covering the island (reviewed in Hedges, 1989a). The southern portion of Hispaniola also may have been submerged during the Oligocene, although a large amount of subsequent mountain building since has erased much of that evidence (Maurrasse, 1982). Most of Cuba, northern Hispaniola, and Puerto Rico also were submerged during that time, although some areas appear to have been emergent throughout the Cenozoic (Bowin, 1975; Maurrasse, 1982; Ituralde-Vinent, 1988; Lewis and Draper, 1990). The Bahamas Bank, presently a low limestone platform, probably was completely submerged during the interglacial periods of the Pleistocene.

THE AMPHIBIAN FAUNA

The number of native amphibian species inhabiting the West Indies (167 species) is remarkably high considering the relatively small total area. Even more surprising is the small number of native families (4) and genera (7) represented; all are anurans (Table 4:1). Only two native West Indian species (*Leptodactylus insularum* and *L. validus*; Heyer, 1994) occur naturally outside the area. The majority of species (139 species or 84%) are from a single lepto-dactylid genus *Eleutherodactylus*, which also is the largest genus of vertebrates with over 500 species (Duellman, 1993). Other components of the amphibian fauna include: a relatively small radiation of bufonids (11 species: *Bufo peltocephalus* group), centered primarily in Cuba, but with representatives in Hispaniola and in the Puerto Rican Bank, some hylid frogs placed in three genera (10 species: *Calyptahyla, Hyla,* and *Osteopilus*), other leptodactylids (5

Table 4:2. Numbers of species of anurans on islands and island groups in the West Indies. Introduced taxa are noted by an asterisk.

Region	Total	Native	Endemic	Introduced	% Endemic
Cuba:	52	50	48	2	96
Bufo	8	8	8	0	100
Osteopilus	1	1	0	0	0
Pseudacris*	1	0	0	1	0
Eleutherodactylus	41	41	40	0	98
Rana*	1	0	0	1	0
Jamaica:	26	22	22	4	100
Bufo*	1	0	0	1	0
Calyptahyla	1	1	1	0	100
Hyla	2	2	2	0	100
Osteopilus	2	2	2	0	100
Eleutherodactylus	19	17	17	2	100
Rana*	1	0	0	1	0
Hispaniola:	65	63	63	2	100
Bufo	3	2	2	1	100
Hyla	3	3	3	0	100
Osteopilus	1	1	1	0	100
Eleutherodactylus	56	56	56	0	100
Leptodactylus	1	1	1	0	100
Rana*	1	0	0	1	0
Puerto Rican Bank:	25	20	20	5	100
Bufo	2	1	1	1	100
Hyla*	1	0	0	1	0
Osteopilus*	1	0	0	1	0
Scinax*	1	0	0	1	0
Eleutherodactylus	18	18	18	0	100
Leptodactylus	1	1	1	0	100
Rana*	1	0	0	1	0
Lesser Antilles:	14	10	9	4	90
Bufo*	1	0	0	1	0
Colostethus	1	1	1	0	100
Osteopilus*	1	0	0	1	0
Scinax*	1	0	0	1	0
Eleutherodactylus	8	7	7	1	100
Leptodactylus	2	2	1	0	50
Bahamas Bank:	6	2	0	4	0
Hyla*	1	0	0	1	0
Osteopilus	1	1	0	0	0
Eleutherodactylus	1	1	0	0	0
Gastrophryne*	1	0	0	1	0
Rana*	2	0	0	2	0

species: Leptodactylus), and a dendrobatid (Colostethus) on Martinique in the Lesser Antilles.

Introductions of plants and animals are common in the West Indies, and there are eight introduced amphibian species (Table 4:1). Unfortunately, two large species, Bufo marinus and Rana catesbeiana, have been introduced successfully on most of the major and many of the smaller islands.

The high level of endemism seen in the West Indian amphibian fauna also extends to the level of individual islands (Table 4:2), where completely endemic faunas are found in Jamaica (22 species), His-
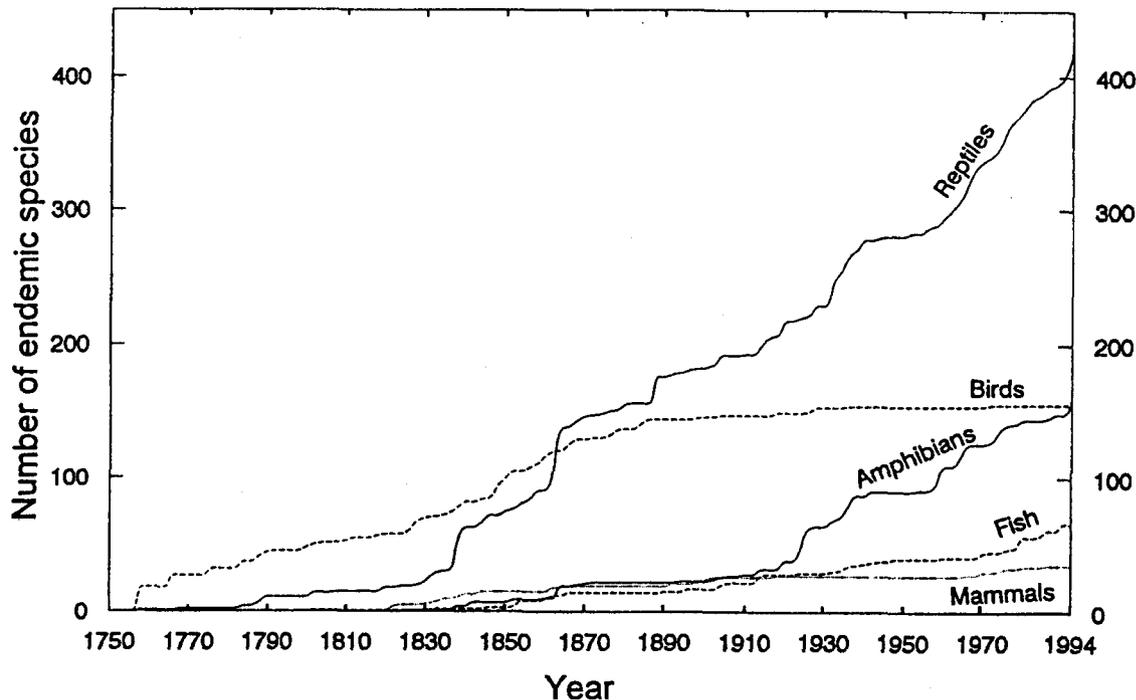
Fig. 4:7. Discovery curve of West Indian amphibian species in relation to curves of other West Indian vertebrate groups. Plotted is the number of species known at each time interval.

paniola (63 species), and the Puerto Rican Bank (20 species). High levels of endemism also are found in Cuba (96% of 50 species) and the Lesser Antilles (90% of 10 species). Only two species (*Eleuthero-dactylus planirostris* and *Osteopilus septentriona-lis*) are native to the Bahamas Bank and only one (*Osteopilus septentrionalis*) is native to the Cayman Islands; none is endemic. As with the amphibian fauna in general, the genus *Eleutherodactylus* is the major component of the amphibian fauna in each island, although there are some subtle differences. In Cuba, *Bufo* (8 species, 16% of total) is a significant component, whereas in Jamaica, it is the hylid frogs (5 species, 23% of total).

Trend curves of the rate of species description (Steyskal, 1965) can provide a gauge of our current understanding (in terms of species diversity) of a taxonomic group. Such discovery curves for West Indian vertebrates (Fig. 4:7) show that some groups, such as mammals and birds, have reached a plateau suggesting that nearly all of the extant species have been discovered. However, the curves for amphibians and reptiles rise steeply indicating that our knowledge of these groups is far from complete. For example, at least 16 new species of frogs have been discovered in the last four years; these represent 10% of the known amphibian fauna and include a family (Dendrobatidae) new to the West Indies.

PATTERNS OF DISTRIBUTION

CUBA

There are 50 native amphibian species in Cuba (Appendix 4:1), 48 of which are endemic (*Eleuth-erodactylus planirostris* and *Osteopilus septentrion-alis* also occur elsewhere). The total number of species inhabiting each biogeographic region of Cuba varies from five in the low Llanura de Zapata to highs of 26 and 27 in the two eastern highland regions (Sierra Maestra and Macizo de Sagua-Baracoa, re-

spectively). Three other regions with high numbers of species are the Cordillera de Guaniguanico (17 species), the Macizo del Escambray (17 species), and the Alturas de Camaguey-Maniabón (16 species). These five peaks also are seen in the species density map (Fig. 4:8). Steep gradients in species density (6–20 species) are evident along the northern edges of the two eastern regions and correspond closely to rainfall and elevation. The depression in species den-
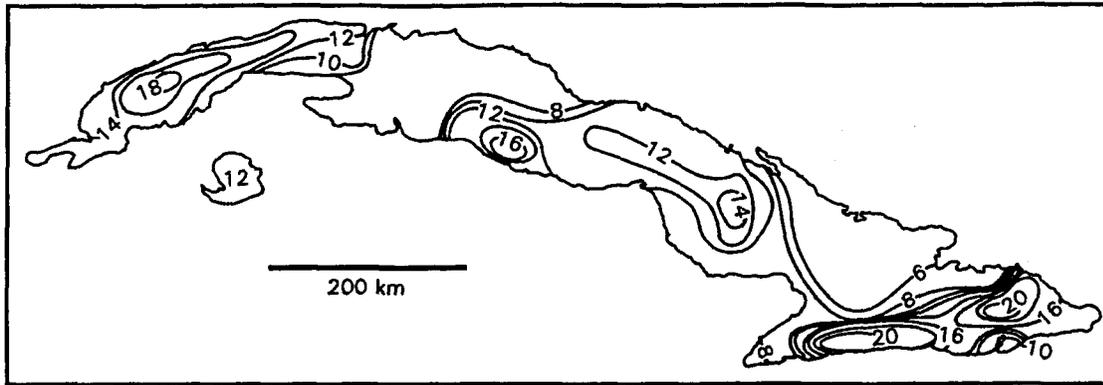
Fig. 4:8. Amphibian species density in Cuba (contour interval = two species).

sity between the two eastern peaks (Fig. 4:8) corresponds to the Valle Central, which separates the Sierra Maestra from the Macizo de Sagua-Baracoa. Noteworthy is the relatively high number of species (up to 15) occurring at low elevations in several parts of Cuba; this reflects the radiation of bufonids (*Bufo*) that mostly inhabit low areas on the island and possibly also reflects the high rainfall in some coastal regions of eastern Cuba.

Three of the five peaks in species density are not reflected in regional endemism (Appendix 4:1). The two eastern regions each have seven endemics; these account for 28% of the species on the island, whereas three other regions (Península de Guanahacabibes, Llanura de Zapata, and Macizo del Escambray) each have only one endemic species, and one region (Cordillera de Guaniguanico) has two endemics. The highest numbers of sympatric species at single localities are 16 at Soroa, Pinar del Río (200 m), and 13 at Gran Piedra, Santiago de Cuba (1100 m).

Analysis of amphibian faunal similarity identifies three major clusters corresponding to the western, central, and eastern regions (Fig. 4:9A). Amphibian faunal similarity among these clusters is low (CBR = 0.29–0.49). Even within these clusters, some adjacent regions have large differences in faunal composition. For example, the two eastern highland regions, separated by only 45 km, have only 68% (CBR = 0.68) of their species in common. The amphibian fauna in the Macizo del Escambray is more like that in the Alturas de Camaguey-Maniabón (CBR = 0.91) than in the adjacent Alturas Centrales (CBR = 0.66). The regions of western Cuba associate into two groups: the upland regions (Cordillera

de Guaniguanico, Alturas de la Habana-Matanzas) and the lowland regions (Península de Guanahacabibes, Llanura Occidental, Isla de Juventud). The position of the Llanura de Zapata differs between the two analyses (Fig. 4:9A, B), probably because of the small number of species (5) in that region. The relationships of the three major clusters (western, central, and eastern) also differs between the two trees.

JAMAICA

All 22 native amphibian species in Jamaica are endemic, and four other species are introduced (Ap-

Fig. 4:9. Relationships of the biogeographic regions of Cuba based on amphibian faunal similarity. (A) Neighbor-joining analysis (scale in distance units). (B) UPGMA analysis (scale in similarity units).
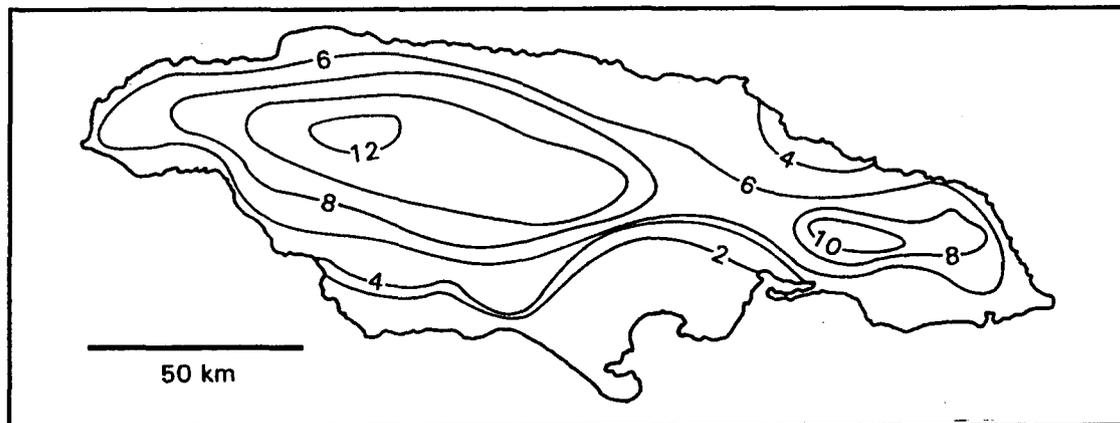
Fig. 4:10. Amphibian species density in Jamaica (contour interval = two species).

pendix 4:2). The total number of species inhabiting each biogeographic region of Jamaica ranges from one each in the three dry southern regions (Southern Lowlands, Portland Ridge Peninsula, and Hellshire Hills) to a high of 15 in the Cockpit Country of west-central Jamaica. The highland regions have considerably more species (5–15, $\bar{X}$ = 9.9) than the lowland regions (1–6, $\bar{X}$ = 2.4). This pattern also is seen in the species density map of Jamaica (Fig. 4:10), where overlapping ranges reach peaks of 12 species in the Cockpit Country and 10 species in the Blue Mountains. Three regions have endemic species: Cockpit Country (2), Portland Ridge Peninsula (1), and the Blue Mountains (2). The highest numbers of sympatric species at single localities are: 12 species at Quick Step, Trelawny (400 m) and 11 species at Hardwar Gap, St. Andrew/Portland (1200 m).

Analysis of faunal similarity defines two major clusters in Jamaica (Fig. 4:11): the western and central regions (CBR = 0.59) and the eastern regions (Blue Mountains and John Crow Mountains) (CBR = 0.70). The average similarity between these two clusters is only 0.35. This illustrates the strong regional endemism of amphibian species within Jamaica. Within the cluster of western and central regions, the neighbor-joining tree separates most of the upland regions (Western Uplands, Cockpit Country, Manchester Plateau, and Central Uplands) into one group and the two lowland regions (and Santa Cruz Mountains) into a separate cluster. Also, that analysis joins the Cockpit Country and Central Uplands together as "sister regions." These relationships, although concordant with geography and some

species distributions, were not seen in the UPGMA analysis (Fig. 4:11B).

HISPANIOLA

There are 63 endemic native amphibian species, and two introduced species in Hispaniola (Appendix 4:3). The number of species inhabiting each biogeographic region of Hispaniola ranges from only one in three Haitian regions (Île Gonâve, Plaine de l'Artibonite, Massif des Montagnes Noires) to the highest (32) in any region in the West Indies, in the
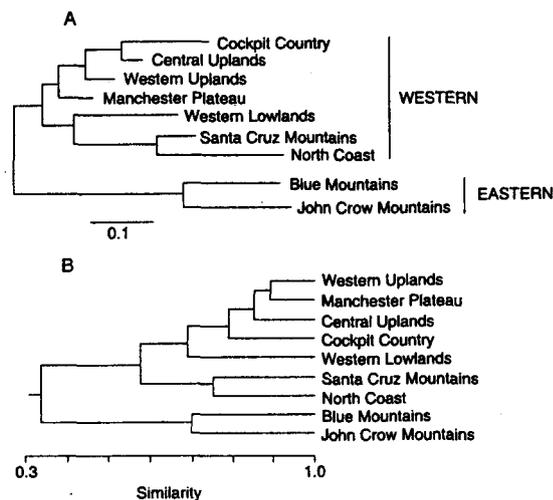
Fig. 4:11. Relationships of the biogeographic regions of Jamaica based on amphibian faunal similarity. (A) Neighbor-joining analysis (scale in distance units). (B) UPGMA analysis (scale in similarity units). Three regions with only one species in each were omitted.
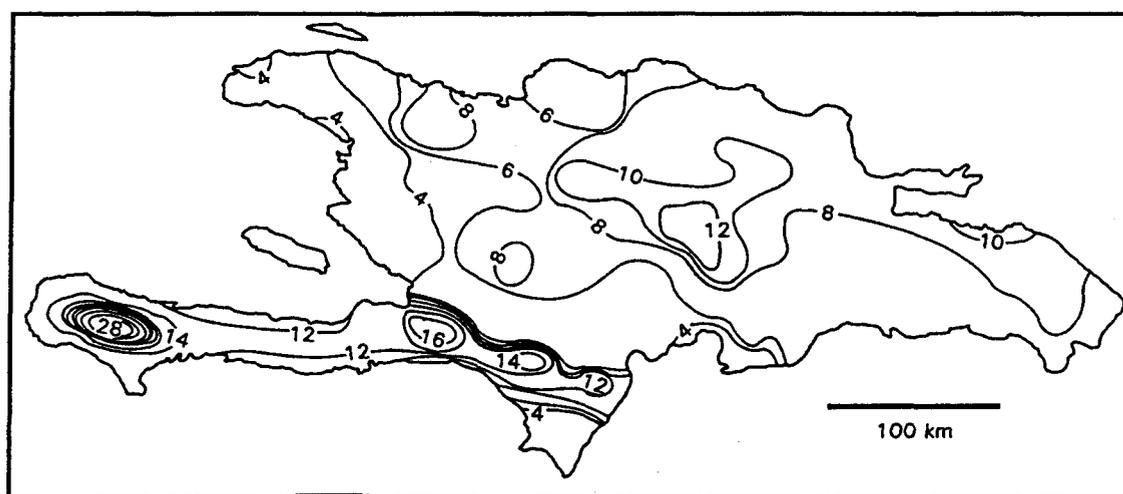
Fig. 4:12.   Amphibian species density in Hispaniola (contour interval = two species).

Massif de la Hotte (also in Haiti). Two other mountain ranges have at least 20 species: the Massif de la Selle–Sierra de Baoruco (26) and the Cordillera Central (20). Although these three regions represent the peaks of species diversity within Hispaniola, the species density map (Fig. 4:12) reveals that the high density of the Cordillera Central primarily is because of the large area of the defined region (Fig. 4:4), which encompasses species with nonoverlapping ranges. The actual species density of overlapping ranges does not exceed 12 (Fig. 4:12) and represents only a modest rise above the surrounding regions with 8–10 species. For similar reasons, species density reaches only 16 in the La Selle–Baoruco range. However, species density in the Massif de la Hotte drops only slightly, from 32 (regional) to 28 (species density); this rises steeply from the surrounding areas of the Tiburon Peninsula that have only 12 species.

Regional endemism within Hispaniola shows patterns similar to species density. Approximately one-fourth (16 species) of Hispaniolan amphibian species occur only in the Massif de la Hotte region, where they represent 50% of the anuran fauna. About 16% (10 species) and 10% (6 species), respectively, of Hispaniolan species occur in the Massif de la Selle–Sierra de Baoruco and Cordillera Central regions. In the poorly known northwest peninsula of Haiti, the Presqu'île du Nord Ouest, three of the five anurans are endemic species. Other regions with endemic species are the Chaîne des Matheux–Sierra de Neiba (2), the Llanura Costera del Caribe (2), Île de la Tortue (1), the Plaine du Nord–Valle de Cibao (1), and the Massif du Nord (1). The highest numbers of sympatric species at single localities are 24 at Castillon, Dept. de la Grande'Anse, Haiti (950 m) and 11 at Furcy, Dept. de l'Ouest, Haiti (1500 m).

The neighbor-joining analysis of faunal relationships of the biogeographic regions of Hispaniola (Fig. 4:13A) defines two major clusters (CBR approximately 0.50) which corresponds to the classical "North Island" and "South Island" of previous workers (Mertens, 1939; Williams, 1961; Schwartz, 1980) and is supported by molecular phylogenetic studies of amphibians (Hedges, 1989b; Hass and Hedges, 1991). The other regions not joining these two clusters have relatively small numbers of species (3–6) and primarily are low, dry regions. Strong regional differentiation is illustrated by the two major South Island regions which are separated by only 110 km. Although clustering as sister regions, they have a CBR of only 0.52. Relationships within the large cluster of North Island regions agrees closely with geography. For example, the four regions of eastern Hispaniola (Península de Samana, Haitises, Cordillera Oriental, and Llanura Costera del Caribe) form a cluster, as do two adjacent regions in the northern part of the island (Cordillera Septentrional and Plaine du Nord–Valle de Cibao). However, the UPGMA analysis (Fig. 4:13B) separates the two South Island upland regions and does not agree as well with geography as does the neighbor-joining analysis.

A

```
┌─ Península de Samana
│  ├─ Haitises
│  ├─ Ll. Costera del Caribe
├─ Cordillera Oriental
│  ├─ Plaine du Nord-Valle de Cibao    NORTH ISLAND
│  └─ Cordillera Septentrional
│     ├─ Ch. des Matheux-S. de Neiba
│     ├─ Cordillera Central
│     └─ Massif du Nord
├─ Presqu'Ile de la Tiburon
│  ├─ Massif de la Hotte              SOUTH ISLAND
│  └─ M. de la Selle-Baoruco
├─ Sierra Martín García
│  ├─ Île de la Tortue
├─ Cul de Sac-Valle de Neiba
│  ├─ Barahona
│  └─ Valle San Juan
├─ Plateau Central
└─ Presqu'Ile du Nord Ouest
```

0.2

B

```
┌─ Cordillera Septentrional
├─ Cordillera Oriental
├─ Península de Samana
├─ Plaine du Nord-Valle de Cibao
├─ Haitises
├─ Ll. Costera del Caribe
├─ Massif du Nord
├─ Presqu'Ile de la Tiburon
├─ Cordillera Central
├─ Massif de la Selle-Baoruco
├─ Ch. des Matheux-S. de Neiba
├─ Massif de la Hotte
├─ Île de la Tortue
├─ Barahona
├─ Cul de Sac-Valle de Neiba
├─ Sierra Martín García
├─ Valle San Juan
├─ Plateau Central
└─ Presqu'Ile du Nord Ouest
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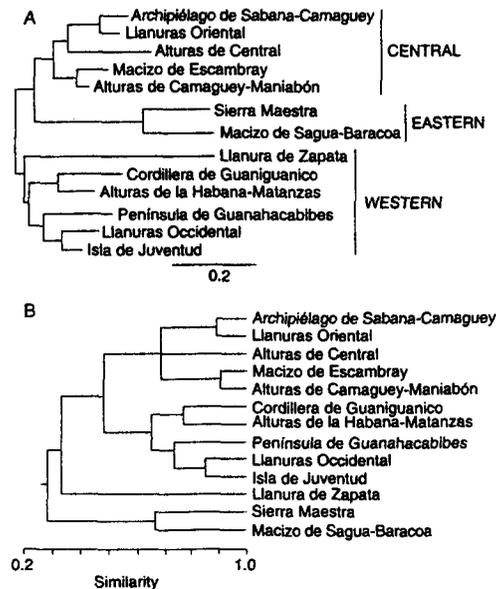0   1.0
            Similarity

Fig. 4:13. Relationships of the biogeographic regions of Hispaniola based on amphibian faunal similarity. (A) Neighbor-joining analysis (scale in distance units). (B) UPGMA analysis (scale in similarity units). Three regions with only one species in each were omitted.

PUERTO RICAN BANK

There are 20 endemic native amphibian species and five introduced species in the Puerto Rican Bank (Appendix 4:4). The number of species inhabiting each biogeographic region of the Puerto Rican Bank ranges from only one species on Mona and Anegada to 13 species in the Central Uplands and 14 species at El Yunque. The species density map of Puerto Rico (Fig. 4:14) also identifies those latter two regions as having high species density but with greater resolution; the high densities are shown to be associated with higher elevations on El Yunque, the Cordillera Central, and the Sierra de Cayey. The steepest contours of species density occur around El Yunque, where density ranges from 6 to 14 species in a distance of less than 10 km.

Regional endemism within the Puerto Rican Bank is relatively low compared to the other Great-

er Antillean islands; there is only one endemic species in each of the four regions (Island Mona, Sierra de Cayey, Cuchilla de Panduras, and El Yunque). Disjunct ranges, rather than regional endemism, explain the distinct peaks in species density seen in Puerto Rico (Fig. 4:14). The highest number of sympatric species at a single locality is 11 at El Yunque Peak (1065 m).

The neighbor-joining analysis of faunal similarity indicates that the biogeographic regions of the Puerto Rican Bank (Fig. 4:15A) form two major clusters corresponding to the regions of Puerto Rico and those of the islands to the east (Fig. 4:15A). The amphibian faunal similarity between these two clusters is low (CBR = 0.44–0.56). Within the Puerto Rican cluster, the three highland regions form a group, with a strong association between El Yunque and the Central Uplands (CBR = 0.96). The Sierra de Cayey, with its single endemic (*Eleutherodactylus jasperi*), is slightly more differentiated (CBR = 0.82). With the cluster of eastern islands (Fig. 4:15A), the two satellite islands of Puerto Rico (Vieques and Culebra) are identical in faunal similarity, as are St. Thomas and St. Croix. The three U.S. Virgin Islands form a group (CBR = 0.89 among islands) and the two British Virgin Islands form a group (CBR = 0.57 between islands). Some of these relationships, which are largely concordant with geography, are not evident in the UPGMA analysis (Fig. 4:15B).

LESSER ANTILLES

Ten of the 14 species inhabiting the Lesser Antilles are native (including nine endemics) and four are introduced (Appendix 4:5). The number of species inhabiting each biogeographic region of the Leser Antilles ranges from one species on five of the island banks to four species in Guadeloupe. Five island banks have endemic species: Guadeloupe (2), Dominica (1), Martinique (1), St. Vincent (1), and Grenada (1).

The relationships among island banks in the Lesser Antilles, based on faunal similarity, differ between the two analyses (Fig. 4:16). Both define a southern cluster containing St. Vincent and the Grenada Bank, and a northern-central cluster containing the Barbuda Bank, Marie Galante, Martinique, and the Guadeloupe Bank. However, the neighbor-joining analysis (Fig. 4:16A) joins Montserrat and Dominica and places them as the most diver-
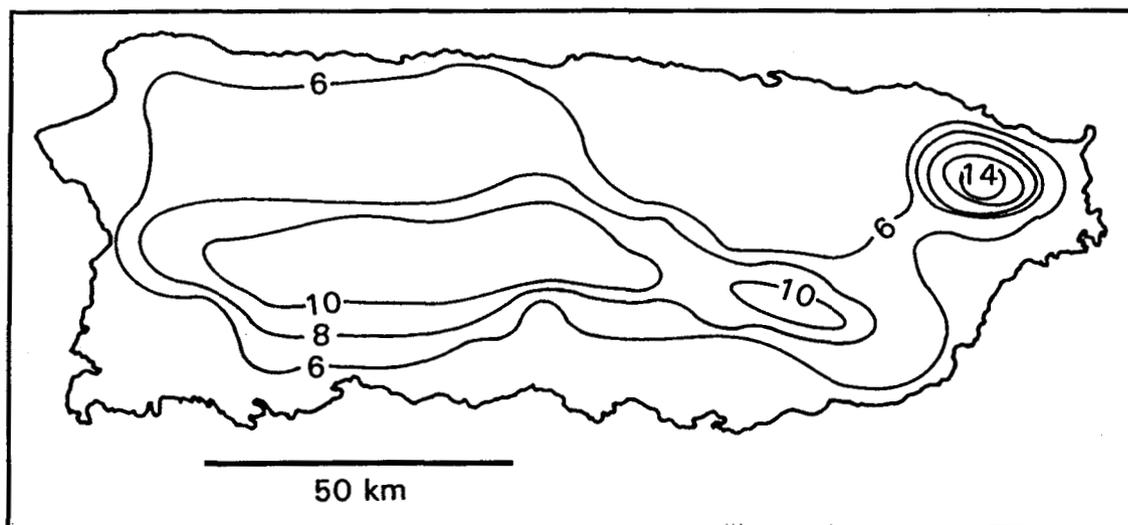
Fig. 4:14. Amphibian species density in Puerto Rico (contour interval = two species).

gent cluster, whereas the UPGMA analysis (Fig. 4:16B) places Montserrat as the sister region to the northern cluster, with Dominica joining that more inclusive group. The southern regions (St. Vincent and the Grenada Bank) have a CBR of only 0.32 with the other regions in the Lesser Antilles.

BAHAMAS BANK

Only two species of amphibians are native to the Bahamas Bank; neither is endemic. *Osteopilus septentrionalis* is distributed throughout the area, with the exception of Mayaguana Island and the Turks and Caicos Islands. *Eleutherodactylus planirostris* also is widely distributed, but apparent-
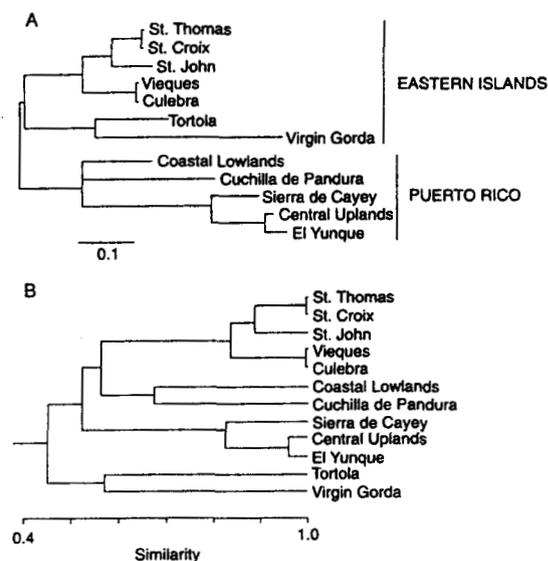
Fig. 4:15. Relationships of the biogeographic regions of the Puerto Rican Bank based on amphibian faunal similarity. (A) Neighbor-joining analysis (scale in distance units). (B) UPGMA analysis (scale in similarity units). Two regions with only one species in each were omitted.
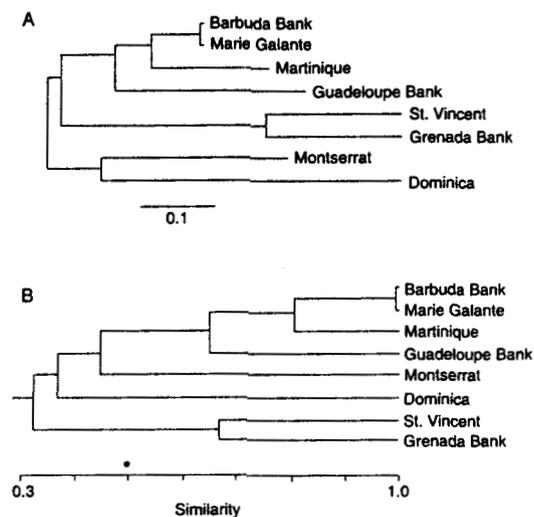
Fig. 4:16. Relationships of the biogeographic regions (islands and island banks) of Lesser Antilles based on amphibian faunal similarity. (A) Neighbor-joining analysis (scale in distance units). UPGMA analysis (scale in similarity units). Five regions with only one species in each were omitted.

ly is absent from Crooked Island, Acklins Island, and Mayaguana Island. Both are common and widespread species in Cuba. One hylid (*Hyla squirella*), one microhylid (*Gastrophryne carolinensis*), and two ranids (*Rana grylio* and *R. sphenocephala*) have been introduced to the Bahamas.

DISTRIBUTIONAL AREA

GEOGRAPHIC PATTERNS

Cuba

The total area of Cuba, including Isla de Juventud and other satellite islands, is 110,922 km². The average area of species distributions is 21,130 km², but one-half of the species (25) have distributions smaller than 6000 km² (5% of island area), and about one-quarter (13) have distributions occupying less than 1100 km² (1% of island area). Five species (8% of the amphibian fauna) are known only from their type localities (Appendix 4:1, Fig. 4:17; the single locality for *Eleutherodactylus pezopetrus* encompasses a range in elevation).

Jamaica

The total area of Jamaica is 10,990 km². The average area of species distributions is 2630 km², but one-half (11) of the species have distributions of less than 1000 km² (< 9% of the area of the island), and eight of those species inhabit areas less than 550 km² (Appendix 4:2, Fig. 4:17).

Hispaniola

The total area of Hispaniola (including satellite islands) is 76,470 km². The average area of species distributions is 9597 km², but one-half of the species have distributions smaller than 1330 km² (2% of the total island area), and one-third of the species occupy less than 1% of the total area of the island. Six species (10% of fauna) are known only from their type localities (Appendix 4:3, Fig. 4:17).

Puerto Rican Bank

The total area of the Puerto Rican Bank (including Isla Mona and St. Croix, which are not on the bank) is 9511 km² (Puerto Rico = 8768 km², Mona = 57 km², Vieques = 138 km², Culebra = 27 km², U.S. Virgin Islands = 347 km², British Virgin Islands = 174 km²). The average area of species distributions is 2567 km², although one half of the species have distributions smaller than 1050 km² (11% of

the total bank area). The distributions of six species (30% of fauna) are no larger than 160 km² or less than 1.7% of the total area (Appendix 4:4, Fig. 4:17).

Lesser Antilles

The total area of the Lesser Antilles is 5840 km². The average area of species distributions is 1029 km², this high figure is owing largely to the wide ranges of *Eleutherodactylus johnstonei* and *E. martinicensis*. Five species (50% of the fauna) have distributions no greater than 170 km² or 3% of the total area of the Lesser Antilles (Appendix 4:5).

GENERAL PATTERNS

Patterns of distributional area of individual islands are similar in that many species have small distributions, and only a few species are widespread. Considering all West Indian species, the same highly skewed pattern is evident; the median distributional area is 1545 km², and the mode is less than 100 km² (Fig. 4:17). If anuran families are examined separately, the median distributional area is 10,425 km² for the 11 bufonids, 25 km² for the single dendrobatid, 10,990–39,500 km² for the 10 hylids, and only 1250–1315 km² for the 143 leptodactylids.

The values of distributional area reported here have at least two sources of error. First, additional collecting almost certainly will reveal that some species have larger distributions. However, the second source of error is that much of the habitat contained within the distributional areas is unsuitable for the species because of deforestation or fine-scale elevational differences. This second source of error is likely to be much greater than the first; and therefore many of the distributional areas reported here probably are overestimates.

ALTITUDINAL DISTRIBUTION

GEOGRAPHIC PATTERNS

Cuba

Considering only altitude, amphibian species density in Cuba (n = 50 species) is highest (31) near sea level and then decreases with elevation to a low

of three species at the highest point in Cuba (Pico Turquino), near 2000 m (Fig. 4:18A). Concordant with this pattern is a decrease in mean maximum body size (SVL), from a high of 60.5 mm (n = 27) at sea level to 31.3 mm (n = 3) at 2000 m (Fig. 4:18A).

Fig. 4:18. Species density (shaded bars) and mean maximum body size (snout-vent length, SVL; white bars) at different elevational intervals in Cuba. Elevation is in 50 m intervals (e.g., 0-49, 50-99, etc.). (A) Islandwide. (B) Sierra Maestra.

Fig. 4:17. Histogram showing the number of species of West Indian amphibians at intervals of distributional area; intervals are 2,000 km² for Cuba and Hispaniola, and 500 km² for Jamaica and Puerto Rico. Arrows indicate the total area of each island. Combined analysis (West Indies) includes species with distributions less than 2,000 km² in area.

By restricting the analysis to the 26 species in the Sierra Maestra, a somewhat different pattern is seen (Fig. 4:18B); there species density increases slightly from 14 at sea level to 18 at 450 m, where it re-

mains relatively constant until about 1050 m, after which point it drops sharply to three species at 2000 m. The difference in species density pattern between the two analyses probably is because of the inclusion of the vast lowland areas of Cuba (and associated species) in the first analysis. However, body size shows the same trend (decreasing with increasing elevation) in the Sierra Maestra as for Cuba in general (Fig. 4:18B).

Jamaica

Amphibian species density in Jamaica ($n = 22$ species) increases from 10 at sea level to 17 species at 450-600 m and then decreases to one species at the highest point (Blue Mountain Peak), at about 2200 m (Fig. 4:19A). The peak at 450–600 m corresponds to the central limestone platform of Jamaica, and thus includes the endemic species of the Western Uplands, Cockpit Country, and Central Uplands. In general, body size decreases from 53.6 mm at sea level to 26.0 mm at 2200 m. However, there is a "depression" in the slope at about 450–600 m apparently caused by the inclusion of the small Cockpit endemics (especially *Eleutherodactylus griphus* and *E. sisyphodemus*). When the Blue Mountains

A Number of species

B Number of species
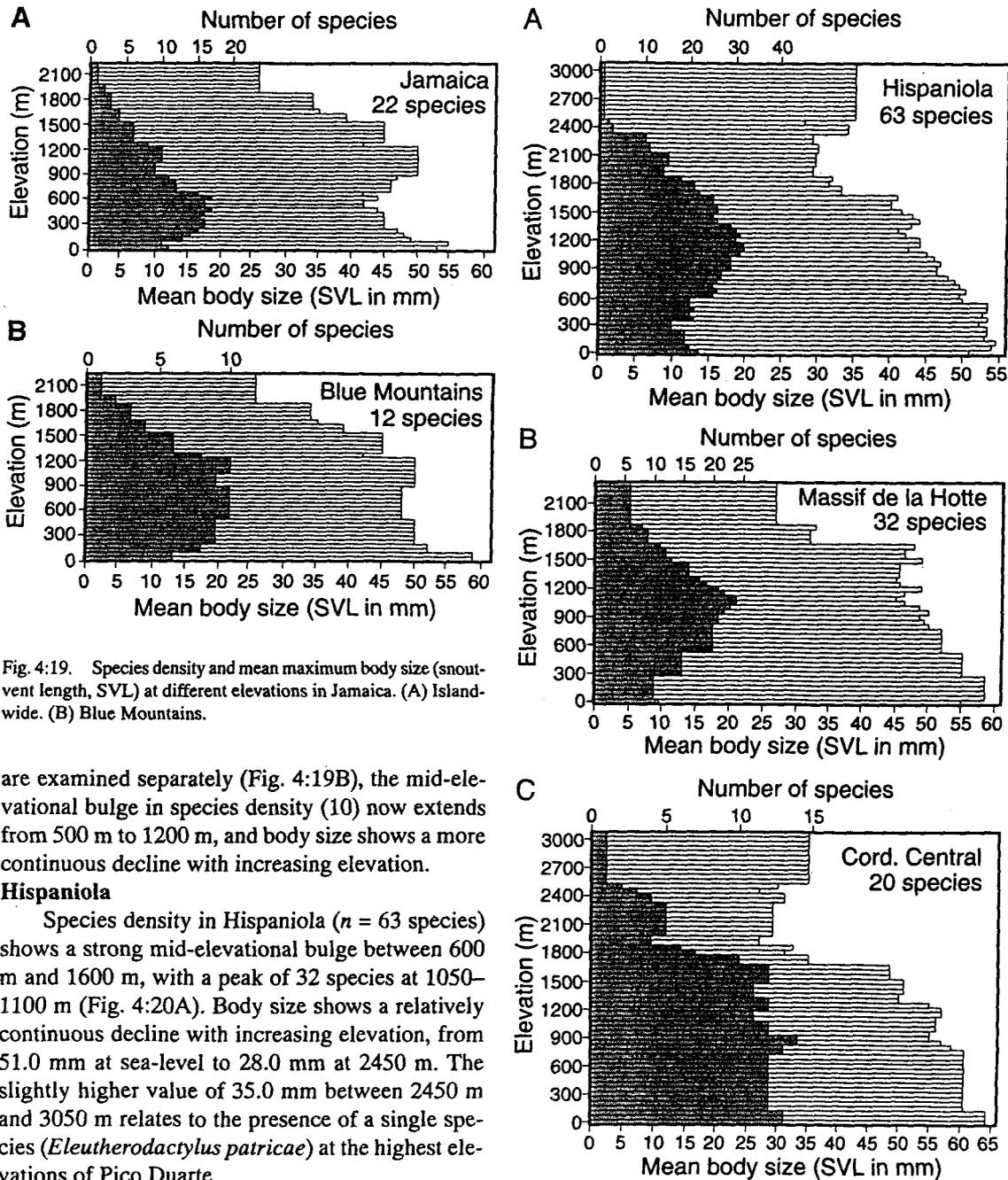
Fig. 4:19. Species density and mean maximum body size (snout-vent length, SVL) at different elevations in Jamaica. (A) Island-wide. (B) Blue Mountains.

are examined separately (Fig. 4:19B), the mid-elevational bulge in species density (10) now extends from 500 m to 1200 m, and body size shows a more continuous decline with increasing elevation.

Hispaniola

Species density in Hispaniola (n = 63 species) shows a strong mid-elevational bulge between 600 m and 1600 m, with a peak of 32 species at 1050–1100 m (Fig. 4:20A). Body size shows a relatively continuous decline with increasing elevation, from 51.0 mm at sea-level to 28.0 mm at 2450 m. The slightly higher value of 35.0 mm between 2450 m and 3050 m relates to the presence of a single species (*Eleutherodactylus patricae*) at the highest elevations of Pico Duarte.

The effect of elevation on species density and body size is perhaps best seen in the fauna of the Massif de la Hotte (Fig. 4:20B), because it is an isolated and well-defined massif that contains the highest density of amphibian species in the West Indies. Twelve species occur at sea-level; density increases to 24 species at 1050–1100 m before decreasing to six species at 2300 m. In contrast to the sharp mid-

A Number of species

B Number of species

C Number of species

Fig. 4:20. Species density and mean maximum body size (SVL) at different elevations in Hispaniola. (A) Islandwide. (B) Massif de la Hotte. (C) Cordillera Central.

elevation peak in species density, body size decreases more or less continuously with elevation, from 55.1 mm at sea-level to 26.5 mm at 2300 m.
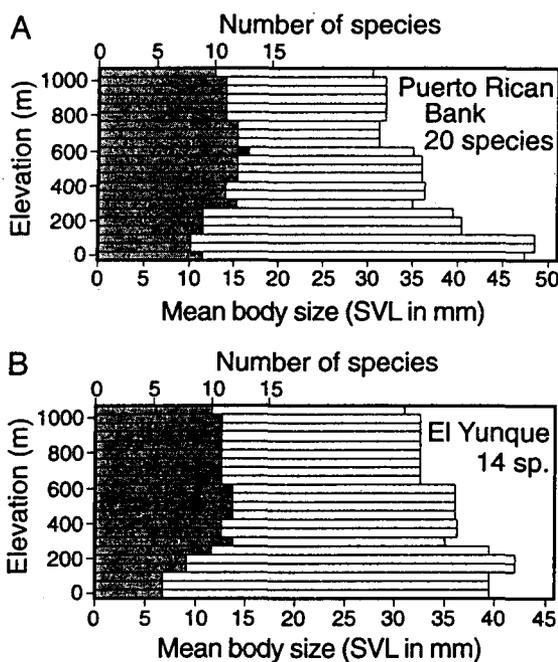
Fig. 4:21. Species density and mean maximum body size (SVL) at different elevations in the Puerto Rican Bank. (A) Puerto Rican Bank. (B) El Yunque.

Fig. 4:22. Species density and mean maximum body size (SVL) at different elevations throughout the West Indies.

The Cordillera Central exhibits a different pattern of species density change with elevation. Species density remains fairly constant (12–14) between sea level and 1650 m before decreasing to one species at 2550–3050 m. However, body size shows the typical decreasing trend (Fig. 4:20C).

Puerto Rican Bank

Analysis of the Puerto Rican Bank (*n* = 20 species) and a more restricted analysis of El Yunque (*n* = 14) both show species density increasing to a high of about 12–13 species at 500–600 m and decreasing only slightly (10 species) at the highest elevations (1050 m). Body size in both analyses decreases with increasing elevation, from 47.4 mm to 30.7 mm (Fig. 4:21A) and from 39.4 mm to 30.7 mm (Fig. 4:21B), respectively. This somewhat truncated pattern, with little decrease in the upper elevations, probably is because the highest elevations in Puerto Rico are lower than those on the other three large islands and that El Yunque Peak (1065 m) corresponds approximately to a general peak in species density with increasing elevation (see below).

Lesser Antilles

Although the total number of species (10 species) is relatively small, the same patterns that are seen in the larger island faunas are evident in the Lesser Antilles. There are more species (9) at middle elevations than at sea level (5) or at the highest elevations (1); mean body size shows a general decrease with increasing elevation (73.2 mm to 20.0 mm).

GENERAL PATTERNS

When all West Indian species are examined, a mid-elevational bulge in species density is seen: from 72 species (sea level) to 82–83 species (300–600 m) and then to 1 species at 3050 m (Fig. 4:22). However, this pattern is misrepresentative of the elevational pattern observed in a typical mountain range in the West Indies, where the mid-elevational increase in density occurs at higher elevations. A restricted but more representative analysis of 80 species in four upland areas (≥ 2000 m), including the Sierra Maestra, Blue Mountains, Massif de la Hotte, and Cordillera Central, shows that the mid-elevational bulge extends from 550 m to 1150 m, with a slight peak at 1050 m (Fig. 4:23). The reason for this difference between the complete analysis (Fig. 4:22) and the montane analysis (Fig. 4:23) is probably because the former includes lower elevation areas of locally high species density (e.g., as in the case of the Cockpit Country noted above) that cause an elevational "cap" in species density.

The relationship between mean maximum body size and elevation is virtually the same in all analyses: body size decreases with increasing elevation. When all West Indian species are considered (Fig. 4:22), body size decreases from 56.0 mm SVL (sea
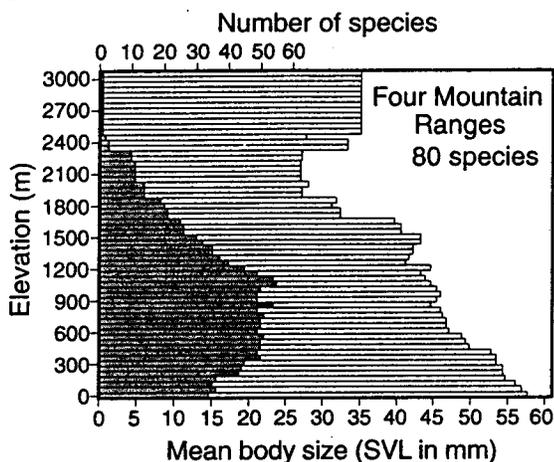
Fig. 4:23.   Species density and mean maximum body size (SVL) at different elevations in four montane areas in the West Indies: Sierra Maestra (Cuba), Blue Mountains (Jamaica), Massif de la Hotte and Cordillera Central (Hispaniola). Duplicate species within Hispaniola were excluded.

level) to 28.0 mm (2450 m), not considering the single species (35 mm) occurring above that elevation. The rate of decrease in body size is approximately 1 mm per 100 m of increasing elevation.

If the elevational limits (upper and/or lower) of species coincide, then it is possible that some ecological or topographical factor may be involved. An analysis of range limits for all West Indian species (n = 164 species) reveals one major and several minor peaks (Fig. 4:24). The major peak is the common lower elevational limit of sea level in 72 (44%) of the species. The next most significant peak is the upper elevational limit of 1050-1099 m found in 14 (8.5%) of the species. However, that peak is largely an expression of the fauna at El Yunque, Puerto Rico, the upper limit of which is restricted by the height of the mountain. An analysis of range limits of the 80 species in the four montane areas (≥ 2000 m) noted above does not show that peak. In general, range limits, although not completely random, do not seem to be significantly clumped.
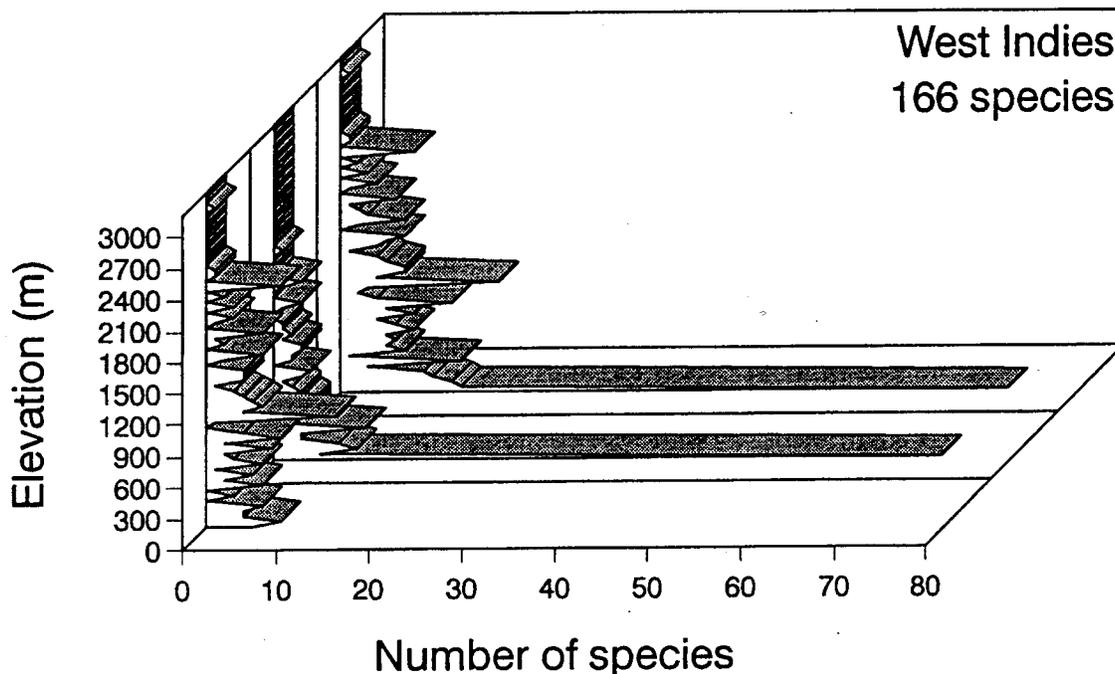
Fig. 4:24.   Elevational limits of amphibian species in the West Indies; front = upper limits, middle = lower limits, and back = combined range limits.

CORRELATIONS OF DISTRIBUTION PATTERNS

TOPOGRAPHY AND CLIMATE

Amphibian distribution in the West Indies is closely associated with both topography and rainfall. This is evident in comparing the species density maps (Figs. 4:8, 4:10, 4:12, and 4:14) with corresponding maps of topography and rainfall (Figs. 4:2–5), and in the altitudinal analysis. However, because of the relationship between topography and rainfall, it is difficult to separate these two variables to determine the exact relationship of each to species density and distribution.

The fact that high species density occurs near sea level only in regions of high rainfall (e.g., northern slopes of Cuchillas de Moa and Cuchillas de Toa in Cuba; northern slopes of Blue Mountains and John Crow Mountains in Jamaica) suggests that rainfall is an important factor in the distribution of these amphibians, and that high elevation is not required. Supporting that contention is the near-absence of amphibian species in the driest areas (e.g., Hellshire Hills of Jamaica; Barahona Peninsula of Hispaniola). However, this relationship between rainfall and amphibian distribution is not tied to a requirement for reproduction in water, because the majority (84%) of West Indian amphibians have direct development and can reproduce far away from standing water.

VEGETATION

Most of the West Indies were at one time covered with forests, and virtually all extant West Indian taxa can be considered forest-dwelling species. Because 80–99% of the original forest has been removed from the Greater Antilles (see below), most amphibians presently are found in forest remnants and are not distributed evenly throughout their geographic ranges. Next to nothing is known about the ecological requirements of most West Indian amphibians; therefore, presently it is not possible to ascertain the association of species with vegetation types except in a general or anecdotal way. However, my impression, gained through field work, is that most species are not closely tied to specific species of trees or vegetational zones. Examples of some possible exceptions are *Hyla marianae* (*Tillandsia* bromeliads), *Eleutherodactylus unicolor* (elfin woodland of Puerto Rico) and *E. caribe* (mangrove forest of southwestern Haiti).

HISTORICAL PHENOMENA

Mesozoic

The origin of the West Indian biota has been a topic of considerable interest over the years (literature reviewed in Williams, 1989; Hedges, 1996). The recognition that the geologic history of the Antilles extends back into the Mesozoic, and that there has been considerable plate movement within the Caribbean, led Rosen (1975) to propose a vicariance theory for the origin of the biota. A review of the extensive literature on the debate over the vicariance versus dispersal theories for the origin of the Antillean biota is beyond the scope of this paper. Several studies of West Indian amphibians have addressed phylogeny with morphological data (e.g., Joglar, 1989; Pregill, 1981). However, pertinent to this discussion are the studies that provide estimates of time of divergence from molecular data (there are no Mesozoic fossils of West Indian amphibians).

Hedges (1989b) examined variation in slow-evolving protein loci in 82 species of West Indian *Eleutherodactylus* (and two mainland species). Phylogenetic analysis defined three major groups within the West Indies, and each was assigned the rank of subgenus. The subgenus *Euhyas* (83 species) primarily is a western Caribbean group that includes all Jamaican, most Cuban and most South Island (Hispaniola) species that are mostly terrestrial. The subgenus *Eleutherodactylus* includes mostly arboreal species (50) and is distributed throughout the West Indies; it includes all taxa in the Puerto Rican Bank and Lesser Antilles. *Pelorius* is a subgenus of six large species on Hispaniola. Indications from DNA sequence data are that these three West Indian subgenera (and possibly *Syrrhophus* of Central America) form a single monophyletic group within the genus (Hedges and Youngblood, in prep.).

It was proposed that the large amount of molecular divergence between the subgenera *Euhyas* and *Eleutherodactylus* represents a phylogenetic divergence event in the late Mesozoic, possibly related to the breakup of the proto-Antilles (Hedges, 1989b). Albumin immunological data on West Indian and mainland *Eleutherodactylus* indicated that this divergence event probably occurred in the late Cretaceous, ca. 70 mya (Hass and Hedges, 1991). A review of the origin of all West Indian amphibians and

reptiles indicates that the genus *Eleutherodactylus* is one of the few groups, if not the only group, to show a Mesozoic origin (Hedges, 1996).

Tertiary

The only known Tertiary fossil amphibians from the West Indies are those specimens of *Eleutherodactylus* embedded in Hispaniolan amber, Oligocene to mid-Miocene in age (Poinar and Cannatella, 1987; Poinar, 1992). These fossils establish the presence of amphibians in the West Indies by the mid-Tertiary.

Albumin immunological data suggested that the hylid, bufonid, and leptodactyline frogs all arrived to the Antilles by overwater dispersal (on flotsam) from South America in the Tertiary (Hedges et al., 1992b; Hedges, 1996). Most reptile lineages in the West Indies also show an origin in South America, and this pattern probably is due to the direction of water currents (Hedges, 1996). It was suggested that this predominant pattern of dispersal, rather than vicariance, may have been related to extinctions caused by the bolide impact that occurred in the Caribbean region at 65 mya (Hedges et al., 1992b).

In *Eleutherodactylus,* dispersal from the Antilles (subgenus *Euhyas*) to Central America (subgenus *Syrrhophus*) during the Tertiary has been suggested (Hass and Hedges, 1991; Hedges, 1996). No albumin immunological data are available for the recently described dendrobatid species, although indirect evidence from albumin IDs in the genus *Colostethus,* relationships, and distributions, suggest that it originated by dispersal from South America in the Tertiary (Hedges, 1996).

Hedges (1989b) proposed a biogeographic scenario to explain the distribution and relationships of *Eleutherodactylus* in the western Caribbean; this was based on allozyme and immunological data (Hedges, 1989a,b; Hass and Hedges, 1991) and is supported by chromosome data (Bogart and Hedges, 1995). In the early Miocene (20 mya), the South Island of Hispaniola had not yet collided with the remainder of Hispaniola, and dispersal of the subgenus *Euhyas* to Jamaica and the South Island probably occurred. Speciation during the late Miocene and Pliocene led to the large radiation of *Euhyas* existing today in these two areas. Collision of the South Island with the North Island of Hispaniola (containing frogs of the subgenus *Eleutherodactylus*) in the late Miocene (7 mya) led to limited dispersal between the North and South Islands. Jamaican *Eleuth-*

erodactylus thus represent a monophyletic group within the subgenus *Euhyas,* and most Cuban and South Island species belong to that subgenus. Therefore the major differences seen between the North and South Island amphibian faunas probably are not the result of sea-level changes in the Quaternary (see below), but rather are the consequence of completely isolated islands colliding in the Tertiary with minimal subsequent exchange of faunas.

Quaternary

Pregill and Olson (1981) suggested that arid savanna, grassland, and xeric scrub forest habitats predominated in the West Indies during the Pleistocene glaciations. This conclusion primarily was based on evidence from palynological and climatic studies of areas adjacent to the West Indies, and from some West Indian deposits indicating frequent fires during that period. Because West Indian amphibians predominantly are forest-dwelling animals, these vegetational changes would have resulted in a significant reduction in the area occupied by species, and probably would have led to extinctions. At the same time, this reduction in area would have increased isolation of populations and may have led to geographic differentiation and possibly to speciation.

Besides the climatic and vegetation changes, sea-level fluctuation both joined and isolated land areas during the Pleistocene. Estimates of sea-level change suggest dramatic changes in exposed land area. Pregill and Olson (1981) speculated that the diversity of species within *Eleutherodactylus* in the South Island of Hispaniola largely is the result of Pleistocene climatic cycles and fragmentation of ranges leading to speciation. Although it is likely that climatic cycles were important in the speciation and radiation of West Indian amphibians, immunological distances > 3 (1.8 mya) between species suggest that most divergences predated the Pleistocene (Hedges, 1989a, b; Hass and Hedges, 1991; Hedges et al., 1992b); this agrees with molecular data from most South American amphibians examined (Duellman et al., 1988; Maxson and Heyer, 1988; Hass et al., 1995), although speciation may have been more recent in the high Andes (Duellman et al., 1988). It is more likely that intraspecific variation seen in some West Indian amphibians (e.g., *Eleutherodactylus audanti, E. ruthae, E. schmidti, Bufo longinasus*) is the result of differentiation associated with Pleistocene climatic cycles.

The absence of endemic amphibians in the Bahamas may provide additional support for the importance of pre-Quaternary speciation in West Indian amphibians. These islands were submerged, either mostly or entirely, during interglacial periods and therefore their present terrestrial flora and fauna probably arrived since that time and could provide a "gauge" of the time required for speciation. Some geographic differentiation in one of the two native species (*Eleutherodactylus planirostris*) has taken place to the extent that an endemic subspecies is recognized, but there does not seem to have been enough time for speciation to have occurred. The presence of endemic species of reptiles in the Bahamas suggests that speciation may occur more rapidly in reptiles than in amphibians, but also it could simply mean that reptiles were able to colonize the Bahamas more quickly than amphibians. Nonetheless, this concept of finding an area that was "wiped clean" at a known time period and examining rates of colonization and speciation in different groups might be useful in other regions of the world.

Disjunct Distributions

Typically, West Indian amphibians have well-defined distributions restricted to a particular area on an island. The few distributions that can be unambiguously characterized as disjunct tend to be upland species isolated in different mountain ranges within an island. For example, in Cuba, this includes *Eleutherodactylus limbatus, Bufo longinasus,* and *B. taladai.* Some Cuban species that appeared to have disjunct distributions (Schwartz and Henderson, 1991) now are known to have wider distributions based on recent collections (e.g., *E. varians;* Hedges, unpubl.).

In Hispaniola, several species (*Eleutherodactylus nortoni, E. oxyrhynchus,* and *E. semipalma-*

tus) are found only in the Massif de la Hotte and Massif de la Selle, but not in the intervening area of the Tiburon Peninsula. This may be due to ecological requirements, or more likely, due to the fact that little more than barren rock and dirt now exists in the intervening areas of suitable elevation because of deforestation. The distribution of the burrowing species *E. ruthae* appears to be truly disjunct, and four subspecies have been described to recognize geographic variation in the species. It is a species of low to moderate elevations, and it is possible that upland areas have posed barriers to gene flow. This is almost certainly the explanation for the disjunct distributions of the Hispaniolan toad *Bufo guentheri* and the Puerto Rican toad, *B. lemur,* both of which are restricted to low elevations. One high elevation species of Hispaniola, *E. audanti,* is distributed in disjunct populations on the North and South Islands and has differentiated into three recognized subspecies.

COLLECTING BIAS

For reasons of economics, politics, and accessibility, collecting activities in the West Indies have not been evenly distributed throughout the region; this fact may introduce a bias in the analysis of distributions. Puerto Rico, Jamaica, and the Lesser Antilles have received greater attention than Hispaniola, whereas Cuba has received by far the least amount of attention by collectors. Within Hispaniola, the much more difficult logistics, greater expense, and greater personal risk of an expedition to Haiti has resulted in a far greater amount of attention given to the Dominican Republic. The result of this type of bias is an underestimation of distributions, including area and elevational range, in more poorly known countries such as Cuba and Haiti.

ISLAND BIOGEOGRAPHY

The number of species on an island is a product of many factors, but usually it is positively correlated, to some degree, with island area. Based on empirical plots of this relationship, Darlington (1957) discovered that a tenfold increase in the area typically leads to a doubling of the number of species. In an effort to explain this general relationship, an equilibrium model of biogeography was proposed (MacArthur and Wilson, 1963) which suggests that rates of colonization and extinction are the primary factors determining the number of species present.

Other factors include distance from source area and the size of the island. More recently, environmental heterogeneity has been suggested as the primary factor responsible for the species-area effect (Williamson, 1981, 1988).

Darlington's (1957) example of the species-area effect was the amphibians and reptiles of the West Indies, and this data set, unrevised, has been reproduced repeatedly (e.g., MacArthur and Wilson, 1967:8; Cox et al., 1976:103; Wilson, 1992:222). Because the original data on species abundance on

Fig. 4: 25.   Relationship between island area and number of native amphibian species in the West Indies (areas as in Table 4:3).

each island are nearly four decades old, a revised plot of this relationship in West Indian amphibians is shown here (Fig. 4:25; Table 4:3). Although the number of species of West Indian amphibians is correlated with island area, this relationship is unlikely to be explained by MacArthur and Wilson's (1967) equilibrium model of immigration and extinction or by extinction alone (Jones, 1980). For example, all 17 native Jamaican species of *Eleutherodactylus* are the result of a single colonization event and subsequent adaptive radiation (Hedges, 1989a, b). Although not yet confirmed, preliminary data suggest that the amphibian faunas of the other Greater Antillean islands represent one or a few large adaptive radiations (Hedges, 1989b; Hass and Hedges, 1991). As noted earlier, Hispaniola is a composite of two

islands; it is likely that considerable speciation took place prior to the collision of the North and South Islands (the postcollision exchange of species poses difficulties in treating these two areas as separate islands in a species-area analysis). The West Indian bufonids apparently represent a single colonization from the mainland (Pregill, 1981); there is no phylogenetic evidence of any dispersal of *Eleutherodactylus* from the mainland to the Greater Antilles during the entire Cenozoic. In fact, dispersal in the reverse direction has been proposed to explain the origin of the subgenus *Syrrhophus* in Central America (Hedges, 1989b). The increased topographic variability and greater availability of niches for adaptive radiation on larger islands is the most likely explanation for the species-area relationship in West Indian amphibians.

CONSERVATION OF THE AMPHIBIAN FAUNA

CURRENT STATUS

In response to current concerns over the possible disappearance of some amphibian species in several regions of the world, the conservation status of West Indian amphibians was reviewed by Hedges (1993). Each species was listed, along with the year that it was most recently encountered. No general

decline at the species level was found, although eight species were listed that had not been seen in recent years: *Eleutherodactylus orcutti* (Jamaica); *E. lucioi, E. neodreptus, E. warreni,* and *Bufo fluviatica* (Hispaniola), and *E. jasperi, E. karlschmidti,* and *E. lentus* (Puerto Rican Bank). However, sufficient information was available for only one of those species

Table 4:3. Numbers of species of native amphibians on islands in the West Indies (> 10 km²).

Island	Island Area (km²)	No. Species
Cuba	105,007	50
Hispaniola	76,470	63
Jamaica	10,992	22
Puerto Rico	8,768	17
Isla de Juventud	2,200	12
Guadeloupe	1,510	4
Martinique	1,079	3
Dominica	790	3
Île Gonâve	702	1
St. Lucia	616	1
Barbados	430	1
St. Vincent	345	3
Grenada	311	3
Antigua	280	2
St. Croix	218	3
Île de la Tortue	209	3
Grand Cayman	184	1
St. Kitts	166	1
Barbuda	161	1
Marie Galante	149	2
Isla Vieques	138	3
Isla Saona	114	1
Montserrat	102	2
Nevis	93	1
Anguilla	91	1
St. Martin	88	1
St. Thomas	77	4
Isla Mona	57	1
Tortola	54	4
St. John	52	5
Ile à Vache	47	2
Ile Grand·Cayemite	47	1
Isla Beata	47	1
Anegada	39	1
Isla Culebra	27	3
La Desirade	27	1
Virgin Gorda	21	3
St. Eustatius	21	1
St. Barthélémy	21	1
Saba	13	1

(*E. karlschmidti*) to conclude that it has probably disappeared. At the population level, virtually all West Indian amphibians presumably have declined substantially as a consequence of deforestation and the resulting loss of habitat. Introduced predators such as the mongoose (*Herpestes auropunctatus*),

black rat (*Rattus rattus*), and feral cat (*Felis domesticus*) have been linked to the extinction of species of West Indian reptiles (Henderson, 1992) and also may be adversely affecting native amphibians, even in undisturbed forest (Hedges and Thomas, 1991; Hedges, 1993). The large introduced amphibians, *Rana catesbeiana* and *Bufo marinus* known to prey on smaller amphibians, are well-established on most islands and probably have adversely affected the native species. Population level surveys have been conducted for some Puerto Rican species, although there is no agreement as to the reasons for the declines (Burrowes and Joglar, 1991; Joglar and Burrowes, 1991; Moreno, 1991; Rivero, 1991).

The list of last reported records (Hedges, 1993: Table 1) requires some revision following recent field work in Hispaniola (1993) and Cuba (1994). In northern Hispaniola, nine species were encountered (*Eleutherodactylus abbotti, E. audanti, E. flavescens, E. inoptatus, E. montanus, E. patricae, E. pictissimus, E. weinlandi,* and *Osteopilus dominicensis*). In Cuba, 26 described species were encountered: *Bufo empusa, B. gundlachi, B. peltocephalus, B. taladai, Eleutherodactylus acmonis, E. albipes, E. atkinsi, E. auriculatus, E. cubanus, E. cuneatus, E. dimidiatus, E. guantanamera, E. gundlachi, E. intermedius, E. ionthus, E. leberi, E. limbatus, E. melacara, E. planirostris, E. ricordii, E. ronaldi, E. toa, E. turquinensis, E. varians, E. varleyi,* and *Osteopilus septentrionalis.* No species was conspicuously absent in areas where it was expected to occur. Noteworthy was the rediscovery in 1994 (Hedges et al., 1996) of two Cuban species, *E. cubanus* and *E. turquinensis,* previously known only from the type series collected in the mid-1930s (although these two species were cited in Hedges, 1993, as having been collected recently, that material has been reidentified as a new species and *E. cuneatus,* respectively).

Estimates of forest cover for islands of the West Indies are among the lowest in the world, and this is tied to relatively high human population densities in the region (Hedges and Woods, 1993; Fig. 4:26). Of the ten tropical countries with the highest rates of net annual deforestation during 1981–1990, three are in the West Indies: Dominican Republic (2.5%), Haiti (3.9%), and Jamaica (5.3%); Jamaica's is the highest in the world (World Resources Institute, 1994). Because of the fact that a species will "exist" until its last population disappears, the decline in forest cover has not been accompanied by a similar
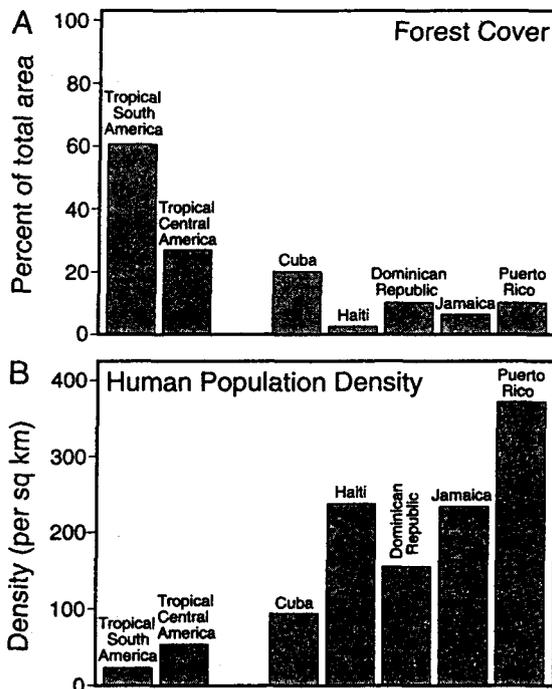
Fig. 4:26. Forest cover and human population size in the West Indies, Central America, and South America. After Hedges and Woods (1993); original sources are Caribbean/Latin American Action (1993), Cohen (1984), Johnson (1988), Paryski et al. (1989), and World Resources Institute (1992). The figure of 5% for Jamaica was disputed (Goreau, 1993) in favor of a much higher value, 46% published elsewhere (Rampair, 1986). However, that higher value was not included in the reports by the Tropical Forests Resource Assessment Project of the Food and Agriculture Organization of the United Nations, and the United Nations Environment Programme, summarized in World Resources Institute (1992) as 6% closed forest for Jamaica. Another study of Jamaican forest cover (Thompson et al., 1986b) reported a value of 7% for "fully stocked Broadleaf Forest," which is in close agreement with the value accepted by the United Nations. More recent information on forest cover is available (World Resources Institute, 1994), but closed forest ("trees cover a high proportion of the ground") is not distinguished from open forest ("at least 10% tree cover and a continuous grass layer on the forest floor"), so the earlier values are shown here.

decline in species (Hedges, 1993). However, the critically low levels of forest cover remaining in some areas, such as in Jamaica (5%) and Haiti (1%), indicate that species extinctions will occur in the near future unless the trend is reversed. It was suggested that Haiti may soon become the Earth's "first major biodiversity disaster" (Hedges, 1993).

Nearly all countries in the West Indies currently have some protected areas that typically encom-

pass the largest or last remaining stands of natural vegetation. For amphibian species diversity and endemism, some of the most important of these protected areas are: Parque Nacional Sierra Maestra (Cuba), Blue Mountains National Park (Jamaica), Parc National Pic Macaya and Parc National Morne la Visite (Haiti), Parque Nacional Sierra de Baoruco, Parque Nacional Armando Bermudez, and Parque Nacional José del Carmen Ramírez (Dominican Republic), and Caribbean National Forest (Puerto Rico).

Unfortunately, protection of the natural resources is not complete in any of these areas, and it essentially doesn't exist in some areas such as the Haitian national parks. In Cuba, the severe economic difficulties of the last several years has taken a toll on the forests. Felling of trees for firewood, charcoal, and building materials is taking place in the Sierra Maestra National Park and other protected areas in Cuba. Jamaica has only recently established a system of protected areas, and it remains to be seen whether or not they will be effective. Haiti is the poorest country in the Western Hemisphere ($400 per capita annual income), has a burgeoning human population of 7 million, and has exhausted virtually all of its forests. On an expedition in 1991 to the center of Pic Macaya National Park, Richard Thomas and I saw trees being cut and removed from one of the last remaining stands of natural forest in the country. Although it is illegal to fell trees in the Dominican Republic, clearing and burning is widespread and common, and trees are being cut within the National Parks. Protection of the forests in Puerto Rico has been more effective than elsewhere, although the Caribbean National Forest has "lost its virginity" because of the abundance of introduced predators.

RECOMMENDATIONS

General

It cannot be overstated that the loss of biodiversity in the West Indies, as in other regions, is closely tied to the loss of forest cover, and therefore it is of prime importance to halt the deforestation. Greater efforts should be made to enforce park boundaries and prevent illegal felling of trees. For the longterm, some form of human population control must be implemented or else the economic pressures and demands of a growing population will lead to continued deforestation.

Specific

Additional protected areas: Many "hot spots" of West Indian amphibian diversity and endemism already are contained within protected areas, and therefore emphasis should be placed on enforcement. Important areas for amphibian diversity not yet protected (including proposed areas) are: in Cuba, (1) Sierra de los Organos (including region of Viñales), (2) Sierra del Rosario (including region of Soroa), (3) Macizo del Escambray, (4) Macizo de Sagua-Baracoa (including the Meseta del Guaso, Cuchillas de Toa, Cuchillas de Moa, and Sierra del Purial); in Jamaica, (5) Dolphin Head National Park, and (6) Cockpit Country National Park; in Haiti, (7) enlargement of Parc National Pic Macaya and Parc National Morne La Visite; in the Dominican Republic, (8) Sierra de Neiba National Park, (9) eastward extension of Sierra de Baoruco National Park (including Loma Remigio and Loma Trocha de Pey); and in Puerto Rico, (11) Cuchilla de Panduras.

Removal of introduced predators: In view of the disappearance of *Eleutherodactylus karlschmidti* and apparent decline of several amphibian species in undisturbed forest on El Yunque, the U.S. Forest Service should make feral animal removal/extirpation a major concern for the Caribbean National Forest. Removal of introduced predators also should be a concern in other areas of the West Indies.

Promotion of scientific collecting: All species of West Indian amphibians were described from specimens that had been collected and preserved, and in most cases, those specimens were exported to another country for study. Despite the obvious importance of this activity, it is discouraged by the governments of both the country of origin of the specimens and the country of origin of the researcher through unrealistic restrictions and permit procedures (Hedges and Thomas, 1991). Often, collection of only a few specimens of each species is permitted even though additional specimens would cause no harm to populations or species and would increase the quality of the information gathered (Hedges and Thomas, 1991). It is not uncommon to spend one week out of a four-week expedition simply to obtain a collecting or export permit for a small number of specimens while, at the same time, thousands or millions of these organisms have perished in that country through deforestation.

The majority of researchers surveying tropical biodiversity are not required to do so as part of their employment. Many are university professors whose primary obligations are to teaching, and are free to choose any research topic or location. For this reason, countries that have excessively complicated and stringent permitting procedures suffer because scientists simply avoid them and focus their attention on other countries.

Scientific collecting should be promoted, rather than discouraged. The immediate benefit for the country is a much greater knowledge of its biodiversity, which will aid in planning and implementing conservation policies. Regulation is important, but permit procedures should be streamlined and have greater flexibility so that legitimate scientists can obtain permits quickly and collect and export a sufficient number of specimens for systematic study. Importation procedures also should be improved so that scientists with proper documentation can enter any port without encountering long, unnecessary delays.

LITERATURE CITED

ARDEN, D. D. 1975. The geology of Jamaica and the Nicara-guan Rise. Pp. 617–661 in Nairn, A. E. M. and F. G. Stehli (eds.), *Ocean Basins and Margins, Vol. 3, Gulf Coast, Mexico, and the Caribbean.* Plenum Press, New York.

ASPREY, G. F., AND R. G. ROBBINS. 1953. The vegetation of Jamaica. Ecol. Monogr. 23:359–413.

BOGART, J. P., AND S. B. HEDGES. 1995. Rapid chromosome evolution in Jamaican frogs of the genus *Eleutherodactylus* (Leptodactylidae). J. Zool. (London) 235:9–31.

BOND, J. 1979. *Birds of the West Indies.* London, England: Collins Publishers.

BOUYSSE, PH. 1984. The Lesser Antilles arc: structure and geo-dynamic evolution. Pp. 83–103 in B. Biju-Duval, J. C. Moore, et al. (eds.), *Initial Reports of the Deep Sea Drilling Project, Vol. 78A.* Washington, D.C.: U. S. Government Printing Office.

BOUYSSE, PH. 1988. Opening of the Grenada back-arc basin and evolution of the Caribbean during the Mesozoic and early Paleogene. Tectonophysics 149:121–143.

BOWIN, C. 1975. The geology of Hispaniola. Pp. 501–522 in Nairn, A.E.M. and F.G. Stehli (eds.), *Ocean Basins and Margins, Vol. 3, Gulf Coast, Mexico, and the Caribbean.* New York, NY: Plenum Press.

BOX, B., AND S. CAMERON (eds.). 1989. *Caribbean Islands Handbook.* New York, NY: Prentice-Hall.

BURKE, K., P. J. FOX, AND A. M. C. SENGOR. 1978. Buoyant ocean floor and the evolution of the Caribbean. J. Geophys. Res. 83:3949–3954.

BURROWES, P. AND R. JOGLAR. 1991. A survey of the population status and an ecological evaluation of three Puerto Rican frogs. Pp. 42–46 in J. A. Moreno (ed.), Status y Distribución de los Reptiles y Anfibios de la Región de Puerto Rico. Depart. Recur. Nat. Puerto Rico, Pub. Cien. Misc. 1:1–67.

CARIBBEAN AND LATIN AMERICAN ACTION. 1993. *Caribbean Basin Databook.* Washington, D.C.: Caribbean and Latin American Action.

COHEN, W. B. 1984. *Environmental Degradation in Haiti: An Analysis of Aerial Photography.* Port-au-Prince, Haiti: Report, USAID/Haiti.

COX, C. B., I. N. HEALEY, AND P. D. MOORE. 1976. *Biogeography.* New York: John Wiley and Sons.

DARLINGTON, P. J. 1957. *Zoogeography: The Geographical Distribution of Animals.* New York, NY: Wiley.

DUELLMAN, W. E. 1990. Herpetofaunas in Neotropical rainforests: comparative composition, history, and resource use. Pp. 455–505 in A. H. Gentry (ed.), *Four Neotropical Rainforests.* New Haven, CT: Yale University Press.

DUELLMAN, W. E. 1993. *Amphibian Species of the World: Additions and Corrections.* Spec. Publ. Univ. Kansas, Mus. Nat. Hist. 21:1–372.

DUELLMAN, W. E., L. R. MAXSON, AND C. JESIOLOWSKI. 1988. Evolution of marsupial frogs (Hylidae: Hemiphractinae): immunological evidence. Copeia 1988:527–543.

ESTRADA, A. R. 1986. Anfibios, reptiles, y aves de Cayo Guajaba, Archipiélago Sabana-Camaguey, Cuba. Poeyana 328:1–34.

ESTRADA, A. R. 1993a. Herpetofauna del Archipiélago de los Canarreos, Cuba. Poeyana 431:1–19.

ESTRADA, A. R.. 1993b. Anfibios y reptiles de Cayo Coco, Archipiélago de Sabana-Camaguey, Cuba. Poeyana 432:1–21.

GARRIDO, O. H., A. R. ESTRADA, AND A. LLANES. 1986. Anfibios, reptiles y aves de Cayo Guajaba, Archipiélago de Sabana-Camagüey, Cuba. Poeyana 328:1–34.

GOREAU, T. J. 1993. Forest Cover. Nature 365:688.

HASS, C. A., J. F. DUNSKI, L. R. MAXSON, AND M. S. HOOGMOED. 1995. Divergent lineages within the *Bufo margaritifera* complex (Amphibia: Anura; Bufonidae) revealed by albumin immunology. Biotropica 27:238–249.

HASS, C. A., AND S. B. HEDGES. 1991. Albumin evolution in West Indian frogs of the genus *Eleutherodactylus* (Leptodactylidae): Caribbean biogeography and a calibration of the albumin immunological clock. J. Zool. (London) 225:413–426.

HEATWOLE, H., R. LEVINS, AND M. D. BYER. 1981. Biogeography of the Puerto Rican Bank. Atoll Research Bull. 251:1–55.

HEDGES, S. B. 1989a. An island radiation: allozyme evolution in Jamaican frogs of the genus *Eleutherodactylus* (Anura, Leptodactylidae). Carib. J. Sci. 25:123–147.

HEDGES, S. B. 1989b. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus:* slow-evolving loci and the major groups. Pp. 305–370 in C. A. Woods (ed.), *Biogeography of the West Indies: Past, Present, and Future.* Gainesville, FL: Sandhill Crane Press.

HEDGES, S. B. 1993. Global amphibian declines: a perspective from the Caribbean. Biodiversity and Conservation 2:290–303.

HEDGES, S. B. 1996. The origin of West Indian amphibians and reptiles. Pp. 95–128 in R. Powell and R. W. Henderson (eds), *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz.* Ithaca, NY: Society for the Study of Amphibians and Reptiles.

HEDGES, S. B., A. R. ESTRADA, AND R. THOMAS. 1992a. Three new species of *Eleutherodactylus* from eastern Cuba, with notes on vocalizations of other species (Anura, Leptodactylidae). Herpetol. Monogr. 6:68–83.

HEDGES, S. B., L. GONZALEZ, AND A. R. ESTRADA. 1996. Rediscovery of the Cuban frogs *Eleutherodactylus cubanus* and *E. turquinensis* (Anura: Leptodactylidae). Carib. J. Sci. 31:327–322.

HEDGES, S. B., C. A. HASS, AND L. R. MAXSON. 1992b. Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. Proc. Natl. Acad. Sci. (U.S.A.) 89:1909–1913.

HEDGES, S. B., AND R. THOMAS. 1989. Supplement to West Indian Amphibians and Reptiles: a checklist. Milwaukee Publ. Mus. Contr. Biol. Geol. 77:1–11.

HEDGES, S. B., AND R. THOMAS. 1991. The importance of systematic research in the conservation of amphibian and reptile populations. Pp. 56–61 in J. A. Moreno (ed.), Status y Distribución de los Reptiles y Anfibios de la Región de Puerto Rico. Depart. Recur. Nat. Puerto Rico, Pub. Cien. Misc. 1:1–67.

HEDGES, S. B., AND R. THOMAS. 1992. A new marsh-dwelling species of *Eleutherodactylus* from Haiti (Anura: Leptodactylidae). J. Herpetol. 26:191–195.

HEDGES, S. B., AND C. A. WOODS. 1993. Caribbean hot spot. Nature 364:375.

HENDERSON, R. W. 1992. Consequenses of predator introductions and habitat destruction on amphibians and reptiles in the post-Columbus West Indies. Carib. J. Sci. 28:1–10.

HENDERSON, R. W., J. DAUDIN, G. T. HAAS, AND T. J. McCARTHY. 1992. Significant distribution records for some amphibians and reptiles in the Lesser Antilles. Carib. J. Sci. 28:101–103.

HEYER, W. R. 1994. Variation within the Leptodactylus podicipinus-wagneri complex of frogs (Amphibia: Leptodactylidae). Smithsonian Contr. Zool. 546:1–124.

HOLCOMBE, T. L., J. W. LADD, G. WESTBROOK, N. T. EDGAR, AND C. L. BOWLAND. 1990. Caribbean marine geology; ridges and basins of the plate interior. Pp. 231–260 in G. Dengo and J. E. Case (eds.), The Caribbean Region. Boulder, CO: Geological Society of America.

INSTITUTO CUBANO DE GEODESIA Y CARTOGRAFÍA. 1978. Atlas de Cuba. Havana, Cuba: Instituto Cubano de Geodesia y Cartografía.

ITURALDE-VINENT, M. A. 1988. Naturaleza Geológica de Cuba. Havana, Cuba: Editorial Científico-Técnica.

JOGLAR, R. L. 1989. Phylogenetic relationships of the West Indian frogs of the genus Eleutherodactylus: a morphological analysis. Pp. 371–408 in C. A. Woods (ed.), Biogeography of the West Indies: Past, Present, and Future. Gainesville, FL: Sandhill Crane Press.

JOGLAR, R. L., AND P. BURROWES. 1991. El efecto del Huracan Hugo sobre una communidad de anfibios en El Yunque, Puerto Rico y algunas recomendaciones para la proteccion de las especies del genero Eleutherodactylus. Pp. 47–53 in J. A. Moreno (ed.), Status y distribución de los reptiles y anfibios de la región de Puerto Rico. Depart. Recur. Nat. Puerto Rico, Pub. Cien. Misc. 1:1–67.

JOHNSON, T. H. 1988. Biodiversity and conservation in the Caribbean: profiles of selected islands. Intern. Coun. for Bird Preser., Monogr. 1:1–144.

JONES, K. L. 1980. Frog diversity in the Lesser Antilles. Carib. J. Sci. 16:19–22.

KAISER, H. 1992. The trade-mediated introduction of Eleutherodactylus martinicensis (Anura: Leptodactylidae) on St. Barthélémy, French Antilles and its implications for Lesser Antillean biogeography. J. Herpetol. 26:264–273.

KAISER, H., L. A. COLOMA, AND H. M. GRAY. 1994. A new species of Colostethus (Anura: Dendrobatidae) from Martinique, French Antilles. Herpetologica 50:23–32.

KAISER, H., D. M. GREEN, AND M. SCHMID. 1994. Systematics and biogeography of eastern Caribbean frogs (Eleutherodactylus: Leptodactylidae), with a description of a new species from Dominica. Canadian J. Zool. 72:2217–2237.

KUMAR, S., K. TAMURA, AND M. NEI. 1994. MEGA: Molecular Evolutionary Genetics Analysis software for microcomputers. CABIOS 10:189–191.

LEWIS, J. F., AND G. DRAPER. 1990. Geology and tectonic evolution of the northern Caribbean margin. Pp. 77–140 in G. Dengo and J. E. Case (eds.), The Caribbean Region. Boulder, CO: Geological Society of America.

MACARTHUR, R. H., AND E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373–387.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The Theory of Island Biogeography. Princeton, NJ: Princeton University Press.

MACPHERSON, J. 1980. Caribbean Lands. Essex, England: Longman.

MARRERO, L. 1946. Elementos de Geografía de Cuba. Havana, Cuba: Editorial Minerva.

MAURRASSE, F. J-M. R. 1982. Survey of the Geology of Haiti. Miami, FL: Miami Geological Society.

MAURY, R. C., G. K. WESTBROOK, P. E. BAKER, PH. BOUYSSE, AND D. WESTERCAMP. 1990. Geology of the Lesser Antilles. Pp. 141–166 in G. Dengo and J. E. Case (eds.), The Caribbean Region. Boulder, CO: Geological Society of America.

MAXSON, L. R., AND W. R. HEYER. 1988. Molecular systematics of the frog genus Leptodactylus (Amphibia: Leptodactylidae). Fieldiana: Zool. 41:1–13.

MERTENS, R. 1939. Herpetologische Ergebnisse einer Reise nach der Insel Hispaniola Westindien. Abh. Senckenberg. Naturf. Ges. 449:1–84.

MORENO, J. 1991. Status survey of the Golden Coqui Eleutherodactylus jasperi. Pp. 37–41 in J. A. Moreno (ed.), Status y Distribución de los Reptiles y Anfibios de la Región de Puerto Rico. Depart. Recur. Nat. Puerto Rico, Pub. Cien. Misc. 1:1–67.

NATIONAL GEOGRAPHIC SOCIETY. 1981. National Geographic Atlas of the World. Washington, D. C.: National Geographic Society.

NEI, M. 1991. Relative efficiencies of different tree-making methods for molecular data. Pp. 90–128 in M. M. Miyamoto and J. Cracraft (eds.), Phylogenetic Analysis of DNA Sequences. Oxford, England: Oxford University Press.

NÚÑEZ JIMÉNEZ, A. 1972. Geografía de Cuba. Havana, Cuba: Pueblo y Educación.

PARYSKI, C. A. WOODS, AND F. SERGILE. 1989. Conservation strategies and the preservation of biological diversity in Haiti. Pp. 855–78 in C. A. Woods (ed.), Biogeography of the West Indies: Past, Present, and Future. Gainesville, FL: Sandhill Crane Press.

PERFIT, M. R., AND E. E. WILLIAMS. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean Sea and its islands. Pp. 47–102 in C. A. Woods (ed.), Biogeography of the West Indies: Past, Present, and Future. Gainesville, FL: Sandhill Crane Press.

PICÓ, R. 1974. The Geography of Puerto Rico. Chicago, IL: Aldine Publ. Co.

PINDELL, J. L., AND S. F. BARRETT. 1990. Geological evolution of the Caribbean region: A plate-tectonic perspective. Pp. 405–432 in G. Dengo and J. E. Case (eds.), The Geology of North America. Vol. H. The Caribbean Region. Boulder, CO: Geological Society of America.

POINAR, G. O., JR. 1992. Life in Amber. Stanford, CA: Stanford University Press.

POINAR, G. O., JR., AND D. C. CANNATELLA. 1987. An upper Eocene frog from the Dominican Republic and its implication for Caribbean biogeography. Science 237:1215–1216.

POWELL, R., R. J. PASSARO, AND R. W. HENDERSON. 1992. Noteworthy herpetological records from Saint Maarten, Netherlands Antilles. Carib. J. Sci. 28:234–235.

PREGILL, G. K. 1981. Cranial morphology and the evolution of West Indian toads (Salientia: Bufonidae): resurrection of the genus Peltophryne Fitzinger. Copeia 1981:273–285.

PREGILL, G. K. AND S. L. OLSON. 1981. Zoogeography of the West Indian vertebrates in relation to Pleistocene climatic cycles. Ann. Rev. Ecol. Syst. 12:75–98.

RAMPAIR, S. 1986. Jamaica Resource Assessment-1980. Pp. 77–80 in D. A. Thompson, P. K. Bretting, and M. Humphreys (eds.), Forests of Jamaica. Kingston, Jamaica: Jamaican Soc. Scientists and Technol.

RICKARDS, C. (ed.). 1980. Caribbean Year Book. Toronto, Canada: Caribook Limited.

RIVERO, J. A. 1991. Divagaciones sobre las especies de coquies

en peligro de extincion y las causas posibles de esa situacion. Pp 54–55 *in* J. A. Moreno (ed.), Status y distribución de los reptiles y anfibios de la región de Puerto Rico. Depart. Recur. Nat. Puerto Rico, Pub. Cien. Misc. 1:1–67.

RODRÍGUEZ-SCHETTINO, L. 1993. Areas faunísticas de Cuba según la distribución ecogeográfica actual y el endemismo de los reptiles. Poeyana 436:1–17.

ROSEN, D. E. 1975. A vicariance model of Caribbean biogeography. Syst. Zool. 24:431–464.

ROUGHGARDEN, J. 1995. *Anolis lizards of the Caribbean.* New York, NY: Oxford Univ. Press.

SAITOU, N. AND M. NEI. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 4:406–425.

SCHWARTZ, A. 1973. Six new species of *Eleutherodactylus* (Anura, Leptodactylidae) from Hispaniola. J. Herpetology 7:249–273.

SCHWARTZ, A. 1978. Some aspects of the herpetogeography of the West Indies. Acad. Nat. Sci. Phila. Spec. Publ. 13:31–51.

SCHWARTZ, A. 1980. The herpetogeography of Hispaniola, West Indies. Stud. Faun. Curaçao Other Carib. Islands 189:86–127.

SCHWARTZ, A., AND R. W. HENDERSON. 1988. West Indian amphibians and reptiles: a checklist. Milwaukee Publ. Mus. Contr. Biol. Geol. 74:1–264.

SCHWARTZ, A., AND R. W. HENDERSON. 1991. *West Indian Amphibians and Reptiles: Distributions, Descriptions, and Natural History.* Gainesville, FL: University of Florida Press.

SEA/DVS. 1990. *La Biodiversidad Biológica en la República Dominicana.* Santo Domingo, Dominican Republic: Secretaría de Estado de Agricultura, SURENA/DVS.

SHOWKER, K. 1989. *Caribbean.* New York, NY: Stewart, Tabori, and Chang.

SMITH, A. G., D. G. SMITH, AND B. M. FUNNEL. 1994. *Atlas of Mesozoic and Cenozoic Coastlines.* Cambridge, England: Cambridge Univ. Press.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. *Numerical Taxonomy.* San Francisco, CA: W. H. Freeman.

SPEED, R. C. 1985. Cenozoic collision of the Lesser Antilles Arc and continental South America and the origin of the El Pilar Fault. Tectonophysics 4:41–69.

STEYSKAL, G. C. 1965. Trend curves of the rate of species description in zoology. Science 149:880–882.

THOMAS, R., AND R. JOGLAR. 1995. *The Herpetology of Puerto Rico: Past, Present, and Future.* Publ. New York Acad. Sci., in press.

THOMPSON, D. A., P. K. BRETTING, AND M. HUMPHREYS. (eds.), 1986a. *Forests of Jamaica.* Kingston, Jamaica: Jamaican Soc. Scientists Technol.

THOMPSON, D. A., D. L. WRIGHT, AND O. EVELYN. 1986b. Forest resources in Jamaica. Pp. 81–90 *in* D. A. Thompson, P. K. Bretting, and M. Humphreys (eds.), *Forests of Jamaica.* Kingston, Jamaica: Jamaican Soc. Scientists Technol.

VICKERS, D. O. 1979. The rainfall of Jamaica. J. Geol. Soc. Jamaica 18:5–26.

WILLIAMS, E. E. 1961. Notes on Hispaniolan herpetology. 3. The evolution and relationships of the *Anolis semilineatus* group. Breviora 136:1–8.

WILLIAMS, E. E. 1989. Old problems and new opportunities in West Indian biogeography. Pp. 1–46 *in* C. A. Woods (ed.), *Biogeography of the West Indies: Past, Present, and Future.* Gainesville, FL: Sandhill Crane Press.

WILLIAMSON, M. 1981. *Island Populations.* Oxford, England: Oxford Univ. Press.

WILLIAMSON, M. 1988. Relationships of species number to area, distance and other variables. Pp. 91–115 *in* A. A. Myers and P. S. Giller (eds.), *Analytical Biogeography.* New York, NY: Chapman and Hall.

WILSON, E. O. 1992. *The Diversity of Life.* Cambridge, MA: Harvard Univ. Press.

WOODRING, W. P., J. S. BROWN, AND W. S. BURBANK. 1924. *Geology of the Republic of Haiti.* Port-au-Prince, Haiti: Dept. Public Works.

WORLD RESOURCES INSTITUTE. 1992. *World Resources 1992–93.* New York, NY: Oxford Univ. Press.

WORLD RESOURCES INSTITUTE. 1994. *World Resources 1994–95.* New York, NY: Oxford Univ. Press.

APPENDIX 4:1

DISTRIBUTION OF SPECIES OF AMPHIBIANS IN CUBA

Symbols in columns: − absent, + present (native), I introduced. Abbreviations for regions: AC Alturas de Central (Alturas de Santa Clara, Alturas del Nordeste, Alturas del Noroeste), AH Alturas de la Habana-Matanzas (including Alturas de Bujucal-Madruga-Coliseo), AS Archipiélago Sabana-Camaguey, CG Cordillera de Guaniguanico, CM Alturas de Camaguey-Maniabón (Sierra de Cubitas, Peniplano de Florida-Camaguey-Tunas, Sierra de Nejasa, Grupo de Maniabón), IJ Isla de Juventud and Archipiélago de los Canarreos, LC Llanura Occidental, LR Llanura Oriental, LZ Llanura de Zapata (including Cienagas de Zapata), ME Macizo del Escambray, MS Macizo de Sagua-Baracoa, PG Península de Guanahacabibes, SM Sierra Maestra.

Taxon	Elevation (meters)	Distribution Area (km²)	PG	LC	CG	IJ	AH	LZ	AC	AS	ME	LR	CM	SM	MS
BUFONIDAE:															
Bufo cataulaciceps	0–50	6,950	+	+	−	+	−	−	−	−	−	−	−	−	−
Bufo empusa	0–70	73,360	−	+	−	+	+	+	−	+	−	+	+	−	+
Bufo fustiger	0–155	16,600	+	+	+	−	+	−	−	−	−	−	−	−	−
Bufo gundlachi	0–70	75,290	+	+	−	+	+	−	−	+	+	+	+	−	−
Bufo longinasus	100–820	1,545	−	−	+	−	−	−	−	−	+	−	−	−	+
Bufo peltocephalus	0–410	70,270	−	−	−	+	−	−	+	+	+	+	+	+	+
Bufo taladai	0–560	10,425	−	−	−	−	−	−	−	−	+	−	+	+	+
Bufo species "Z"	0–50	1	−	−	−	−	−	+	−	−	−	−	−	−	−
HYLIDAE:															
Osteopilus septentrionalis	0–1110	110,922	+	+	+	+	+	+	+	+	+	+	+	+	+
Pseudacris crucifer (I)	0	—	−	−	−	−	I	−	−	−	−	−	−	−	−
LEPTODACTYLIDAE:															
Eleutherodactylus acmonis	30–1150	10,810	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus albipes	1300–1974	385	−	−	−	−	−	−	−	−	−	−	−	+	−
Eleutherodactylus atkinsi	0–1212	93,365	+	+	+	+	−	−	−	+	+	+	+	+	+
Eleutherodactylus auriculatus	0–1150	33,205	+	+	+	+	+	−	−	−	+	−	+	+	+
Eleutherodactylus bartonsmithi	30–212	2,315	−	−	−	−	−	−	−	−	−	−	−	−	+
Eleutherodactylus bresslerae	30–212	1,160	−	−	−	−	−	−	−	−	−	−	−	−	+
Eleutherodactylus cubanus	1060–1400	385	−	−	−	−	−	−	−	−	−	−	−	+	−
Eleutherodactylus cuneatus	0–1515	16,215	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus dimidiatus	0–1375	75,290	+	−	+	−	−	−	−	−	+	+	+	+	+
Eleutherodactylus eileenae	0–700	36,680	+	−	+	−	+	−	+	−	+	−	+	−	−
Eleutherodactylus emiliae	350–400	385	−	−	−	−	−	−	−	−	+	−	−	−	−
Eleutherodactylus etheridgei	0–151	1,160	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus glamyrus	800–1972	1,160	−	−	−	−	−	−	−	−	−	−	−	+	−
Eleutherodactylus greyi	0–820	18,530	−	−	−	−	−	+	+	+	+	−	+	−	−
Eleutherodactylus guanahacabibes	0–20	1,350	+	−	−	−	−	−	−	−	−	−	−	−	−
Eleutherodactylus guantanamera	60–1150	7,335	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus gundlachi	650–1375	3,860	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus iberia	600	1	−	−	−	−	−	−	−	−	−	−	−	−	+
Eleutherodactylus intermedius	454–1818	1,930	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus ionthus	0–1230	3,090	−	−	−	−	−	−	−	−	−	−	−	+	−
Eleutherodactylus klinikowskii	75–182	3,090	−	−	+	−	−	−	−	−	−	−	−	−	−
Eleutherodactylus leberi	394–465	2,700	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus limbatus	50–1150	24,710	−	−	+	−	+	−	−	−	+	−	+	+	+
Eleutherodactylus mariposa	720	1	−	−	−	−	−	−	−	−	−	−	−	−	+
Eleutherodactylus melacara	845–1974	1,160	−	−	−	−	−	−	−	−	−	−	−	+	−
Eleutherodactylus pezopetrus	100–270	1	−	−	−	−	−	−	−	−	−	−	−	−	+
Eleutherodactylus pinarensis	0–381	20,850	+	+	+	+	+	+	−	−	−	−	−	−	−
Eleutherodactylus planirostris	0–727	110,922	+	+	+	+	+	−	+	+	+	+	+	+	+
Eleutherodactylus ricordii	290–1150	8,495	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus species"R"	0–830	75,290	+	+	+	+	+	−	+	+	+	+	+	+	−
Eleutherodactylus ronaldi	212–1060	9,650	−	−	−	−	−	−	−	−	−	−	−	+	+
Eleutherodactylus symingtoni	70–155	8,880	−	−	+	−	+	−	−	−	−	−	−	−	−
Eleutherodactylus tetajulia	600	1	−	−	−	−	−	−	−	−	−	−	−	−	+
Eleutherodactylus thomasi	0–390	10,425	−	−	−	−	−	−	+	+	+	+	+	−	−
Eleutherodactylus toa	195–900	5,405	−	−	−	−	−	−	−	−	−	−	−	−	+
Eleutherodactylus tonyi	10–50	1,350	−	−	−	−	−	−	−	−	−	−	−	+	−
Eleutherodactylus turquinensis	455–1400	770	−	−	−	−	−	−	−	−	−	−	−	+	−
Eleutherodactylus varians	0–845	38,220	+	−	+	+	+	+	+	−	+	−	+	−	−
Eleutherodactylus varleyi	0–845	55,985	−	+	+	+	+	−	+	+	+	+	+	+	+
Eleutherodactylus zeus	75–182	3,090	−	−	+	−	−	−	−	−	−	−	−	−	−
Eleutherodactylus zugi	155–390	1,545	−	−	+	−	+	−	−	−	−	−	−	−	−
RANIDAE:															
Rana catesbeiana (I)	0	—	−	−	−	I	I	−	−	−	−	−	−	−	−
Total native species in region (A)			13	11	17	12	14	5	9	10	17	10	16	26	27
Endemic species in region (B)			1	0	2	0	0	1	0	0	1	0	0	7	7
Percent regional endemism (B/A)			8	0	12	0	0	20	0	0	6	0	0	27	26
Percent total endemism (B/50)			2	0	4	0	0	2	0	0	2	0	0	14	14

APPENDIX 4:2

DISTRIBUTION OF SPECIES OF AMPHIBIANS IN JAMAICA

Symbols in columns: – absent, + present (native), I introduced. Abbreviations for regions: BM Blue Mountains, CC Cockpit Country, CU Central Uplands, HH Hellshire Hills, JC John Crow Mountains, MP Manchester Plateau, NC North Coast, PR Portland Ridge Peninsula, SC Santa Cruz Mountains, SL Southern Lowlands, WL Western Lowlands, WU Western Uplands.

Taxon	Elevation (meters)	Distribution Area (km²)	Biogeographic Region											
			WL	WU	SC	CC	NC	CU	MP	SL	PR	HH	BM	JC
BUFONIDAE:														
Bufo marinus (I)	0–?	—	I	–	–	–	I	–	–	–	–	–	–	–
HYLIDAE:														
Calyptahyla crucialis	0–1200	10,990	–	+	+	+	–	+	+	–	–	–	+	–
Hyla marianae	121–879	1595	–	–	–	+	–	+	–	–	–	–	–	–
Hyla wilderi	121–879	4540	–	+	+	+	–	+	+	–	–	–	+	+
Osteopilus brunneus	0–1515	8430	+	+	+	+	+	+	+	–	–	–	+	+
Osteopilus new species	0–450	240?	–	–	–	+	–	–	–	–	–	+	–	+
LEPTODACTYLIDAE:														
Eleutherodactylus alticola	1650–2248	80	–	–	–	–	–	–	–	–	–	–	+	–
Eleutherodactylus andrewsi	545–1970	485	–	–	–	–	–	–	–	–	–	–	+	+
Eleutherodactylus cavernicola	10–15	55	–	–	–	–	–	–	–	–	+	–	–	–
Eleutherodactylus cundalli	0–636	6325	+	+	+	+	+	+	+	–	–	–	–	–
Eleutherodactylus fuscus	121–682	700	–	+	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus glaucoreius	0–1652	1515	–	–	–	–	–	–	–	–	–	–	+	+
Eleutherodactylus gossei	0–1515	8350	+	+	+	+	+	+	+	+	–	–	+	+
Eleutherodactylus grabhami	152–667	2675	+	+	–	+	–	+	+	–	–	–	–	–
Eleutherodactylus griphus	250–636	160	–	–	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus jamaicensis	121–1288	3405	–	+	–	+	–	+	+	–	–	–	+	+
Eleutherodactylus johnstonei (I)	0–1200	—	I	–	–	I	I	I	I	I	–	–	I	I
Eleutherodactylus junori	606–833	945	–	–	–	+	–	+	–	–	–	–	–	–
Eleutherodactylus luteolus	0–682	1810	+	+	–	+	–	+	–	–	–	–	–	–
Eleutherodactylus nubicola	1061–1879	160	–	–	–	–	–	–	–	–	–	–	+	–
Eleutherodactylus orcutti	227–1212	485	–	–	–	–	–	–	–	–	–	–	+	+
Eleutherodactylus pantoni	0–1636	4135	+	+	–	+	–	+	+	–	–	–	+	–
Eleutherodactylus pentasyringos	0–1273	730	–	–	–	–	–	–	–	–	–	–	+	+
Eleutherodactylus planirostris (I)	0–100?	—	I	I	I	I	I	I	I	I	–	–	I	I
Eleutherodactylus sisyphodemus	450	40	–	–	–	+	–	–	–	–	–	–	–	–
RANIDAE:														
Rana catesbeiana (I)	0–?	—	I	–	–	–	–	–	–	–	–	–	–	–
Total species native to region (A)			6	10	5	15	3	11	8	1	1	1	12	9
Endemic species in region (B)			0	0	0	2	0	0	0	0	1	0	2	0
Percent regional endemism (B/A)			0	0	0	13	0	0	0	0	100	0	17	0
Percent total endemism (B/22)			0	0	0	9	0	0	0	0	5	0	9	0

APPENDIX 4:3

DISTRIBUTION OF SPECIES OF AMPHIBIANS IN HISPANIOLA

Symbols in columns: – absent,+ present (native), I introduced. Abbreviations for regions: AR Plaine de l'Artibonite, BA Península de Barahona, CE Cordillera Central, CI Plaine du Nord–Valle de Cibao, CV Plaine du Cul de Sac–Valle de Neiba, GO Île Gonâve, HA Los Haitises, LC Llanura Costera del Caribe, LH Massif de la Hotte, LS Massif de la Selle–Sierra de Baoruco, MD Massif du Nord, MN Chaîne des Matheux–Sierra de Neiba, NO Massif des Montagnes Noires, OR Cordillera Oriental, PL Plateau Central, PN Presqu'île du Nord Ouest, PS Península de Samana, SE Cordillera Septentrional, SM Sierra de Martín García, TI Presqu'île de la Tiburon, TO Île de la Tortue, VS Valle de San Juan. No species of amphibians are known from Navassa Island.

Taxon	Elevation (meters)	Distribution Area (km²)	LH	TI	LS	BA	CV	GO	MN	SM	VS	PL	NO	AR	PN	TO	MD	CE	CI	SE	PS	HA	OR	LC
BUFONIDAE:																								
Bufo fluviatica	150–175	625	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Bufo guentheri	0–107	24,135	–	+	–	–	+	–	–	–	+	+	–	+	+	–	–	+	+	–	–	–	–	+
Bufo marinus (I)	0	—	–	–	–	–	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
HYLIDAE:																								
Hyla heilprini	0–1856	74,275	+	+	+	–	–	–	+	–	–	+	–	–	+	–	+	+	+	+	–	–	+	–
Hyla pulchrilineata	0–1091	39,500	+	+	+	–	–	–	+	–	+	+	–	–	–	–	+	+	+	+	+	+	+	+
Hyla vasta	0–1697	74,590	+	+	+	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	–	+	+
Osteopilus dominicensis	0–1212	70,690	+	+	+	+	+	+	+	+	+	+	–	–	–	+	+	+	+	+	+	+	+	+
LEPTODACTYLIDAE:																								
Eleutherodactylus abbotti	0–1818	67,555	+	+	+	–	+	–	+	+	–	–	–	–	–	–	–	+	+	+	+	+	+	+
Eleuth. alcoae	0–606	2,300	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. amadeus	1000–2340	390	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. apostates	333–1640	815	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. armstrongi	152–1697	2,190	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. audanti	800–2500	4,700	+	–	+	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Eleuth. auriculatoides	788–1879	3,760	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Eleuth. bakeri	890–2325	815	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. brevirostris	575–2375	920	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. caribe	0	1	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. chlorophenax	990–1290	910	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. corona	1120	1	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. counouspeus	303–760	4,075	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. darlingtoni	1720–2200	235	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. dolomedes	1120–1120	1	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. eunaster	575–1300	890	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. flavescens	0–909	22,730	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+
Eleuth. fowleri	1045–1303	815	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. furcyensis	803–2100	1,960	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. glandulifer	303–1886	1,330	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. glanduliferoides	1515–2121	280	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. glaphycompus	576–1480	5,640	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Taxon	Elevation	Distribution	LH	TI	LS	BA	CV	GO	MN	SM	VS	PL	NO	AR	PN	TO	MD	CE	CI	SE	PS	HA	OR	LC
Eleuth. grahami	20–330	78	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Eleuth. haitianus	1545–2455	1,72	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Eleuth. heminota	0–1697	10,660	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. hypostenor	667–1061	2,040	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. inoptatus	0–1697	69,580	+	+	+	–	–	–	+	+	–	+	–	–	–	+	+	+	+	+	+	+	+	+
Eleuth. jugans	1242–2146	1,220	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. lamprotes	818–1455	750	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. leoncei	1182–2303	1,315	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. lucioi	100	1	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Eleuth. minutus	879–2300	2,115	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Eleuth. montanus	1270–2424	2,540	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Eleuth. sp "N"	1500–1800	440	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. neodreptus	1121	1	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. nortoni	576–1515	2,350	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. oxyrhynchus	333–1212	1,680	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. parabates	1455–1870	440	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. parapelates	950–1050	470	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. patricae	2000–3050	4,700	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Eleuth. paulsoni	0–750	8,780	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. pictissimus	0–1758	20,380	+	+	+	+	+	–	–	+	+	+	–	–	–	–	–	+	–	–	–	–	–	+
Eleuth. pituinus	1212–1770	1,065	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Eleuth. poolei	550–650	310	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
Eleuth. probolaeus	0–60	1,490	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Eleuth. rhodesi	30	45	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Eleuth. rufifemoralis	727–1370	550	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. ruthae	0–900	12,85	+	+	+	–	–	–	+	–	–	–	–	–	–	–	–	+	–	+	+	–	+	+
Eleuth. schmidti	0–1758	11,600	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	–	–	–	–
Eleuth. sciagraphus	1060–1181	80	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. semipalmatus	303–1697	1,250	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. thorectes	1700–2340	4	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. ventrilineatus	1700–2340	45	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleuth. warreni	400	1	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Eleuth. weinlandi	0–788	24,610	–	–	–	–	+	–	+	–	–	–	+	–	–	–	–	+	+	+	+	+	+	+
Eleuth. wetmorei	0–1324	12,070	+	+	+	–	–	–	+	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–
Leptodactylus dominicensis	0–60	1,220	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
RANIDAE:																								
Rana catesbeiana (I)	0	—	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	–	I	–	I
Total native species in region (A)			32	13	26	3	5	1	10	4	4	6	1	1	5	3	9	20	11	10	8	6	9	12
Endemic species in region (B)			16	0	10	0	0	0	2	0	0	0	0	0	3	1	1	6	1	0	0	0	0	2
Percent regional endemism (B/A)			50	0	39	0	0·	0	20	0	0	0	0	0	60	33	11	30	9	0	0	0	0	17
Percent total endemism (B/63)			25	0	16	0	0	0	3	0	0	0	0	0	5	2	2	10	2	0	0	0	0	3

APPENDIX 4:4

DISTRIBUTION OF SPECIES OF AMPHIBIANS IN THE PUERTO RICAN BANK

Symbols in columns: – absent, + present (native), I introduced. Abbreviations for regions: ANE Anegada, CAY Sierra de Cayey, COA Coastal Lowlands, CUL Culebra, CUP Central Uplands, MON Isla Mona, PAN Cuchilla de Pandura, STC St. Croix, STJ St. John, STT St. Thomas, TRT Tortola, VGO Virgin Gorda, VIE Vieques, YUN El Yunque.

Taxon	Elevation (meters)	Distribution Area (km²)	MON	COA	CUP	CAY	PAN	YUN	VIE	CUL	STT	STJ	STC	TRT	VGO	ANE
BUFONIDAE:															
Bufo lemur	0–50	1000	–	+	–	–	–	–	–	–	–	–	–	–	+	–
Bufo marinus (I)	0	—	–	I	–	–	–	–	–	–	I	I	I	–	–	–
HYLIDAE:															
Hyla cinerea (I)	0	—	–	I	–	–	–	–	–	–	–	–	–	–	–	–
Osteopilus septentrionalis (I)	0	—	–	I	–	–	–	–	–	–	I	–	I	–	–	–
Scinax rubra (I)	0	—	–	I	–	–	–	–	–	–	–	–	–	–	–	–
LEPTODACTYLIDAE:															
Eleutherodactylus antillensis	0–1212	9355	–	+	+	+	+	+	+	+	+	+	+	+	+	–
Eleutherodactylus brittoni	100–636	2500	–	+	+	–	–	+	–	–	–	–	–	+	–	–
Eleutherodactylus cochranae	0–333	9059	–	+	+	+	–	+	+	+	+	+	–	–	–	–
Eleutherodactylus cooki	91–242	135	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Eleutherodactylus coqui	0–1128	8768	–	+	+	+	+	+	–	–	I	–	I	–	–	–
Eleutherodactylus eneidae	303–1151	1725	–	–	+	+	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus gryllus	303–1182	1050	–	–	+	–	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus hedricki	455–1152	160	–	–	+	–	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus jasperi	647–785	110	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Eleutherodactylus karlschmidti	182–630	1050	–	–	+	+	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus lentus	0–10	347	–	–	–	–	–	–	–	–	+	+	+	–	–	–
Eleutherodactylus locustus	273–1050	565	–	–	+	+	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus monensis	0–10	25	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Eleutherodactylus portoricensis	273–1182	1480	–	–	+	+	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus richmondi	40–1152	3395	–	+	+	+	+	+	–	–	–	–	–	–	–	–
Eleutherodactylus schwartzi	0–227	130	–	–	–	–	–	–	–	–	–	+	–	+	+	–
Eleutherodactylus unicolor	670–1039	40	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Eleutherodactylus wightmanae	303–1182	2020	–	–	+	+	–	+	–	–	–	–	–	–	–	–
Leptodactylus albilabris	0–1030	9433	–	+	+	+	+	+	+	+	+	+	+	+	–	+
RANIDAE:															
Rana catesbeiana (I)	0	—	–	I	–	–	–	–	–	–	–	–	–	–	–	–
Total native species in region (A)			1	7	13	11	5	14	3	3	4	5	3	4	3	1
Endemic species in region (B)			1	0	0	1	1	1	0	0	0	0	0	0	0	0
Percent regional endemism (B/A)			100	0	0	9	20	7	0	0	0	0	0	0	0	0
Percent total endemism (B/20)			5	0	0	5	5	5	0	0	0	0	0	0	0	0

APPENDIX 4:5

DISTRIBUTION OF SPECIES OF AMPHIBIANS IN THE LESSER ANTILLES

Symbols in columns: – absent, + present (native), E extirpated, I introduced. Abbreviations for regions: AN Anguilla Bank, BB Barbuda Bank, BA Barbados, DO Dominica, GR Grenada Bank, GU Guadeloupe Bank, MG Marie Galante, MA Martinique, MO Montserrat, SA Saba Bank, SE St. Eustatius Bank, SL St. Lucia, SV St. Vincent.

Taxon	Elevation (meters)	Distribution Area (km²)	AN	SA	SE	BB	MO	GU	MG	DO	MA	SL	SV	GR	BA
BUFONIDAE:															
Bufo marinus (I)	0	—	–	–	I	I	I	I	–	–	I	I	I	I	I
DENDROBATIDAE:															
Colostethus chalcopis	500	25	–	–	–	–	–	–	–	–	+	–	–	–	–
HYLIDAE:															
Osteopilus septentrionalis (I)	0	—	I	–	–	–	–	–	–	–	–	–	–	–	–
Scinax rubra (I)	0	—	–	–	–	–	–	–	–	–	–	I	–	–	–
LEPTODACTYLIDAE:															
Eleutherodactylus amplinympha	300–1200	150	–	–	–	–	–	–	–	+	–	–	–	–	–
Eleutherodactylus barlagnei	121–1200	530	–	–	–	–	–	+	–	–	–	–	–	–	–
Eleutherodactylus euphronides	300–840	16	–	–	–	–	–	–	–	–	–	–	–	+	–
Eleutherodactylus johnstonei	0–922	5050	+	+	+	+	+	+	+	–	+	+	+	+	+
Eleutherodactylus martinicensis	0–1200	2860	I	–	–	+	–	+	+	+	+	–	–	–	–
Eleutherodactylus pinchoni	182–1467	855	–	–	–	–	–	+	–	–	–	–	–	–	–
Eleutherodactylus planirostris (I)	0	—	–	–	–	–	–	–	–	–	–	–	–	I	–
Eleutherodactylus shrevei	275–922	90	–	–	–	–	–	–	–	–	–	–	+	–	–
Leptodactylus fallax	0–300	17	–	–	E	–	+	–	–	+	E	–	–	–	–
Leptodactylus validus	0–735	395	–	–	–	–	–	–	–	–	–	–	+	+	–
Total native species in region (A)			1	1	1	2	2	4	2	3	3	1	3	3	1
Endemic species in region (B)			0	0	0	0	0	2	0	1	1	0	1	1	0
Percent regional endemism (B/A)			0	0	0	0	0	50	0	33	33	0	33	33	0
Percent total endemism (B/10)			0	0	0	0	0	20	0	10	10	0	10	10	0

ADDENDUM

Subsequent to my reading proof, two additional species of *Eleutherodactylus* have been named from Cuba. Their elevational range, distribution area, and biogeographic region (see Appendix 4:1) are, respectively: *E. jaumei*—150–200 m, 1 km², SM; *E. principalis*—300–1000 m, 468 km², MS.