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Amphibians and reptiles of Guyana, South America: illustrated keys, annotated species accounts, and a biogeographic synopsis

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Abstract.—Guyana has a very distinctive herpetofauna. In this first ever detailed modern accounting, based on voucher specimens, we document the presence of 324 species of amphibians and reptiles in the country; 148 amphibians, 176 reptiles. Of these, we present species accounts for 317 species and color photographs of about 62% (Plates 1–40). At the rate that new species are being described and distributional records are being found for the first time, we suspect that at least 350 species will be documented in a few decades.

The diverse herpetofauna includes 137 species of frogs and toads, 11 caecilians, 4 crocodylians, 4 amphisbaenians, 56 lizards, 97 snakes, and 15 turtles. Endemic species, which occur nowhere else in the world, comprise 15% of the herpetofauna. Most of the endemics are amphibians, comprising 27% of the amphibian fauna. Type localities (where the type specimens or scientific name-bearers of species were found) are located within Guyana for 24% of the herpetofauna, or 36% of the amphibians. This diverse fauna results from the geographic position of Guyana on the Guiana Shield and the isolated highlands or tepuis of the eastern part of the Pantepui Region, which are surrounded by lowland rainforest and savannas. Consequently, there is a mixture of local endemic species and widespread species characteristic of Amazonia and the Guianan Region.

Although the size of this volume may mislead some people into thinking that a lot is known about the fauna of Guyana, the work has just begun. Many of the species are known from fewer than five individuals in scientific collections; for many the life history, distribution, ecology, and behavior remain poorly known; few resources in the country are devoted to developing such knowledge; and as far as we are aware, no other group of animals in the fauna of Guyana has been summarized in a volume such as this to document the biological resources.

We briefly discuss aspects of biogeography, as reflected in samples collected at seven lowland sites (in rainforest, savanna, and mixed habitats below 500 m elevation) and three isolated highland sites (in montane forest and evergreen high-tepui forest above 1400 m elevation). Comparisons of these sites are preliminary because sampling of the local faunas remains incomplete.

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Nevertheless, it is certain that areas of about 2.5 km^2 of lowland rainforest can support more than 130 species of amphibians and reptiles (perhaps actually more than 150), while many fewer species (fewer than 30 documented so far) occur in a comparable area of isolated highlands, where low temperatures, frequent cloudiness, and poor soils are relatively unfavorable for amphibians and reptiles. Furthermore, insufficient study has been done in upland sites of intermediate elevations, where lowland and highland faunas overlap significantly, although considerable work is being accomplished in Kaieteur National Park by other investigators.

Comparisons of the faunas of the lowland and isolated highland sites showed that very few species occur in common in both the lowlands and isolated highlands; that those few are widespread lowland species that tolerate highland environments; that many endemic species (mostly amphibians) occur in the isolated highlands of the Pakaraima Mountains; and that each of the isolated highlands, lowland savannas, and lowland rainforests at these 10 sites have distinctive faunal elements. No two sites were identical in species composition. Much more work is needed to compare a variety of sites, and especially to incorporate upland sites of intermediate elevations in such comparisons.

Five species of sea turtles utilize the limited areas of Atlantic coastal beaches to the northwest of Georgetown. All of these are listed by the International Union for the Conservation of Nature as being of global concern for long-term survival, mostly owing to human predation. The categories of Critically Endangered or Endangered are applied to four of the local sea turtles (80%). It is important to protect the few good nesting beaches for the sea turtles of Guyana.

We have documented each of the species now known to comprise the herpetofauna of Guyana by citing specimens that exist in scientific collections, many of which were collected and identified by us and colleagues, including students of the University of Guyana (UG). We also re-identified many old museum specimens collected by others in the past (e.g., collections of William Beebe) and we used documented publications and collection records of colleagues, most of whom have been working more recently.

We present dichotomous keys for identifying representatives of the species known to occur in Guyana, and we present brief annotated species accounts. The accounts provide the current scientific name, original name (with citation of the original description, which we personally examined in the literature), some outdated names used in the recent past, type specimens, type localities, general geographic distribution, examples of voucher specimens from Guyana, coloration in life (and often a color photograph), and comments pointing out interesting subjects for future research.

Keywords: amphibians, biogeography, Guyana, herpetology, keys, reptiles, South America.

Introduction

Amphibians and reptiles are of interest to humans for various reasons, ranging from their usefulness for biomedical research and development of pharmaceuticals to fascination with their diverse forms, colors, life histories and behavior, and as models for scientific research to better understand the nature of planet Earth. Amphibians of one kind or another have existed for the last 365 million yr, having evolved from fish. Subsequently, the reptiles evolved from an amphibian, and the mammals (including humans) from a reptile. These animals are part of our own ancestry, as all living things on Earth are part of one family tree that extends back for more than 3.5 billion yr. Amphibians were the first terrestrial vertebrates to appear in Earth history, and they and reptiles are important components of our terrestrial and aquatic ecosystems, especially in the tropics. In contrast, humans have existed for considerably less than the most recent 1 million yr and have had significant negative impact on planetary ecosystems, particularly in just the last 200 yr. In terms of the natural resources of Guyana, the amphibians and reptiles (herpetofauna) are among the most poorly known.

The first checklist of the herpetofauna of Guyana included a total of 164 species, including 50 frogs and toads, 2 caecilians, 1 amphisbaenian, 4 crocodilians, 33 lizards, 63 snakes, and 11 turtles (Beebe 1919). Today we are confident that twice as many species of amphibians and reptiles occur in Guyana. The present volume documents 324 species (plus 20 thought to occur in Guyana but not yet documented plus an unknown number of new species yet to be discovered), including 137 frogs and toads, 11 caecilians, 4 crocodylians, 4 amphisbaenians, 56 lizards, 97 snakes, and 15 turtles (about 62% are shown in color photographs in Plates 1–40). A total of 78 of these species were described based on samples collected at type localities within Guyana and 39 were described and named in the last 10 years.

The lack of a modern comprehensive volume dedicated to the herpetofauna of Guyana has been misunderstood by some people to mean that these organisms are unimportant and perhaps "nothing" was known about the species native to the country. Actually, the majority of the species have been known to science for decades or more (some going back to Linnaeus 1758), as they occur in adjacent countries or broadly across Amazonia. Consequently, this majority of species has been known to science, but most of what we know about them is based on research that was done in countries other than Guyana. In order to identify specimens found in Guyana, herpetologists have had to refer to diverse publications scattered widely in the technical literature, which can be a daunting task. Summary publications (with lists of possibly relevant species or comprehensive monographs) concerning the Guianan Region and South America that have been most broadly helpful to us include the following: Rivero (1961), Taylor (1968), Peters & Donoso-Barros (1970), Peters & Orejas-Miranda (1970), Brazaitis (1973), Hoogmoed (1973, 1979), Chippaux (1986), Ernst & Barbour (1989), Avila-Pires (1995, 2005), Barrio-Amorós (1998), Starace (1998), Gorzula & Señaris (1999), Lescure & Marty (2000), Reynolds et al. (2002), Savage (2002), Campbell & Lamar (2004), Duellman (2005), Señaris & MacCulloch (2005), and Frost (2011). Some of these papers provide skeleton lists of species of the herpetofauna of Guyana and adjacent areas, but none presents the perspective of Guyana on details for confirmed voucher specimens that were identified or re-identified recently, extensive literature citations, identification keys, illustrations of specimens, or suggestions for future research.

The present volume scratches the surface, as considerable research remains to be accomplished with the wildlife of Guyana, including the amphibians and reptiles. Consequently, we are pleased to see the growing appreciation of Guyana's biodiversity and relatively untouched natural environments, as shown in the recent outstanding book on the amphibians of Kaieteur National Park by Kok & Kalamandeen (2008) and the enthusiastic Guyanese students with whom we have worked.

In 1983 the National Museum of Natural History of the United States (Smithsonian Institution; NMNH) and the University of Guyana (UG) initiated a program now known as the Biological Diversity of the Guiana Shield Program (BDG), in order to improve knowledge of the biota and train students in such pursuits. That program, with major funding from the Smithsonian Institution, supplemented by the American Museum of Natural History (AMNH) and Royal Ontario Museum (ROM), was the foundation for developing this publication. In addition, this volume benefited greatly from the availability at the AMNH of significant herpetological collections from Guyana made early in the 1900s on various separate trips made by Robert Snedigar and William Beebe.

Objectives.—This volume is intended to provide the following: 1) a complete list of the species of amphibians and reptiles known to occur in Guyana through the year 2011 (Appendix 2); 2) keys and illustrations useful for identifying individuals of these species; 3) critical references to the primary literature; 4) citations of specimens in scientific collections that clearly document presence of the species in Guyana; 5) predictions about species of possible occurrence but not yet documented; 6) remarks about taxonomic and other problems that need additional research; and 7) preliminary comments on biogeography, faunal comparisons, and conservation.

This volume should be viewed as a progress report on the status of our knowledge today. It seems fitting to quote Parker (1935:505), who listed 209 species of frogs, lizards, and snakes from Guyana: "Many of the 'species' previously said to occur in the Guianas have already been relegated to synonymy, others have been questioned, and others, again, appear to be based on misidentifications or on specimens with wrong locality data." We have tried very hard not to perpetuate errors made previously by others and not to make new errors ourselves. There is still much work to be done.

Scholars should consider this volume as an effort upon which the next generation should improve. We hope that students and scholars will move quickly to make this volume obsolete, and we hope the citizens of Guyana will continue to conserve their biological resources. It would be a travesty if this volume were to become in the future only a record of what once existed.

Methods

Each author conducted considerable field work in Guyana in the last 20 years or so, making significant new collections from localities that were not well sampled previously. In the field, reptiles were euthanized with nembutal, amphibians with chloretone, usually after being photographed in life. Color notes and often tissue samples (temporarily stored in liquid nitrogen or 95% ethanol) were taken prior to preservation of the specimens in 10% formalin. Upon return to the laboratory, specimens were soaked in old 70% ethanol, then after a few days transferred to fresh 70% ethanol.

At each locality visited in the field, geographic coordinates and elevation were determined with a GPS receiver (CJC and

CRT used a Sony Pyxis; RPR used a Magellan and a Garmin; and RDM and AL used a Garmin); coordinates are presented in World Geodetic System 1984 (WGS 84). Many of our readings (particularly in the early to mid-1990s) were taken unavoidably on days when the satellite signals were not of the highest resolution so they include an unknown amount of error. To compensate for this, CJC and CRT took the mean of 10 readings per site, and in the process, considerable variation was observed. The worst examples noted are as follows: readings for N latitude at Konawaruk Camp (1998) varied over a span of 7.4″; W longitude at a spring on Dubulay Ranch (1995) over a span of 4.5″; and elevation at Dubulay Ranch (1994) over a span of −51 ft to +714 ft, where Alexander Mendes told us the elevation was mapped as about 100 ft.

We identified all of the newly collected specimens personally and cataloged them in the scientific collections at the AMNH, CSBD at UG (specimens specifically collected by us), ROM, and NMNH (=USNM catalog numbers; see below for a list of abbreviations for scientific collections). Literature that was most useful for identifying specimens is cited in the keys and annotated species accounts. In addition, we surveyed major collections that were known to have specimens from Guyana, and we personally examined specimens to confirm or correct identifications, where necessary.

It is important to note, however, that we listed each of the species of amphibians and reptiles that can be documented with voucher specimens as occurring in Guyana. We did not list every specimen in every collection around the world that has specimens from Guyana. Researchers wanting complete listings of all specimens for any taxon collected in Guyana will need to do their own global surveys of the various collections. In this context, it is important to realize that one cannot simply obtain a list of specimens from collections and expect the identification of specimens to be correct. In many instances the specimens, especially older ones, have not been identified or re-identified to modern standards, so names applied to specimens need confirmation or correction. This requires examining the specimens. A good example of what not to do was unintentionally provided in an appendix list of amphibians and reptiles from Kaieteur National Park, which was inappropriately attributed to CJC, CRT, and RPR (Kelloff 2003). Not only is that list far from complete in terms of what actually occurs at Kaieteur, but approximately half of the names listed are incomplete or simply wrong because old collection records were not verified prior to publication and the sources cited did not know that the list was being published.

We also examined each of the recently published lists of the herpetofauna of Guyana (Reynolds et al. 2002, Avila-Pires 2005, Señaris & MacCulloch 2005), and made sure we verified the occurrence of each taxon, although none of the previous lists actually cited individual specimens. Should users of this volume notice that a taxon listed previously for Guyana is not included here it is because we were unable to verify the record, specimens were re-identified to a different taxon, or taxonomic revisions resulted in recent name changes. This applies, for example, to the following: *Allobates brunneus*, *Anomaloglossus degranvillei*, *Arthrosaura versteegii*, *Atractus badius*, *Atractus zidoki*, *Centrolene papillahallicum*, *Chironius cochranae*, *Elachistocleis ovalis*, *Eleutherodactylus urichi*, *Helicops leopardinus*, *Hyalinobatrachium eccentricum*, *H. ignioculus*, *Mastigodryas bifossatus*, *Microcaecilia unicolor*, *Oxyrhopus formosus*, *Oxyrhopus trigeminus*, *Phyllomedusa tomopterna*, *Pipa aspera*, *Pristimantis fenestratus*, *Rhinella margaritifer*, *Rhinella typhonius*, *Thamnodynastes strigilis*, *Trachycephalus venulo-*

sus, *Typhlops lumbricalis*, and others. Comments on such details are presented in the species accounts, especially where we explain such matters as re-identification of specimens that were misidentified previously. Re-identifications applied mostly, but not only, to specimens that were collected decades or nearly a century ago and identified at that time on the basis of outdated literature. In addition, each of the bibliographic citations, including the oldest, going back to Linnaeus (1758), has been verified by at least one of us personally examining the actual publication cited.

Species Accounts

The brief species accounts are organized with several topics as follows.

Type material.—This includes the original name used for the taxon, the unique specimen(s) to which the scientific name is attached, and the type locality. Although some Amazonian species are currently thought to have a very wide distribution, especially the highly mobile species, the species of low vagility often become known as complexes of cryptic species with several yet to be named, following molecular analyses. Consequently, for example, if a Guyanan species has low vagility and a type locality in Bolivia or Peru, this may suggest that the specimens from Guyana are of a subtly different species, worthy of modern investigation.

Distribution.—This general statement of the overall range of the species allows one to gauge aspects of biogeography and to know whether a species is endemic to Guyana or the Guianan Region.

Vouchers for Guyana.—We personally examined and confirmed the identification of the specimens listed, with a few exceptions where knowledgeable scientists had done so. For example, we did not need to reconfirm identifications of a specimen of the caecilian *Typhlonectes compressicauda* at the UMMZ that was identified by Mark Wilkinson at the BMNH, or specimens of turtles identified by Peter C. H. Pritchard at the Chelonian Research Institute. Similarly, for species recently described by Philippe J. R. Kok at the IRSNB and collaborators, it was not necessary to reexamine every specimen, although in some instances we did. Suffice it to say that in the species accounts, we are quite confident of the accuracy of the identifications of the specimens listed in the vouchers for Guyana. Nevertheless, additional specimens may exist, and there is a great deal of additional herpetological work that needs to be done, including re-identification of older specimens, before the fauna of Guyana will be known reasonably well.

Coloration in life.—This is based primarily on our own field notes taken from animals while conducting field work in Guyana; the same applies to the photographs in this volume. Other sources are used and cited when necessary, including Beebe's color notes on specimens from Guyana. This category will be useful together with the keys and photographs for identifying specimens.

Comments.—This category is used to explain recent name-changes, to describe interesting aspects of life history, and to indicate areas where additional research is needed.

Major Collecting Sites

For most of our field work, we targeted localities where little or no previous scientific collecting had been done. Our goal for each trip was to make a general collection documenting what species of amphibians and reptiles occurred at the locality visited. Also, strategies of the coauthors differed a bit. For example, CJC and CRT visited sites expected to be best for studying the evolutionary biology

of unisexual species of lizards (thus staying in the lowlands), RDM and AL chose sites expected to reveal previously unknown species (thus mostly visiting the highlands), and RPR participated in multidisciplinary field trips of the BDG. Consequently, the herpetofauna of sites from which we made adequate new collections could be compared with the herpetofauna of sites that had been sampled well previously, and herpetofaunas from forest vs. savanna and from lowlands vs. isolated highlands can be compared to some extent, although considerable comparative work remains to be done. We hope that scholars at UG will be inspired to improve this effort.

Where logistically feasible, we spent about a month at each locality and collected both day and night. In addition, where feasible, we dug in pit-fall traps of 20-liter plastic buckets with open tops over which passed vertical plastic sheeting stapled to cut saplings, which formed a drift fence that guided animals into the traps 24 hours per day (Fig. 1). To prevent desiccation of specimens, traps were kept damp and checked at least twice a day. This field method provides far better sampling of the herpetofauna than simply walking and attempting to catch animals that happen to be seen, as in our experience, pit-falls produced specimens of species that we did not see otherwise. However, highland sites did not lend themselves logistically for long-term stays nor for installing pit-fall traps. Information on effort is provided in the following lists of the sites within Guyana (Figs. 2–4), and their herpetofaunas are compared following the species accounts (see Biogeography). These abbreviated site names are used to cite vouchers in the species accounts.

For general comparisons, we refer to lowland, upland, and isolated highland sites, similar to Gorzula & Señaris (1999), because biotic communities vary along elevational gradients. For convenience, suitable to the available sites within Guyana, we distinguish among the sites by elevation, as follows: lowland sites are those below 500 m elevation; upland sites are between 500 and 1400 m elevation; and isolated highland sites are above 1400 m. Future workers will want to refine this system. For example, elevation alone and air pressures associated with it are not as important to most organisms as the more-or-less elevation-correlated changes in temperature, rainfall, and soil moisture. Superimposed on this are additional effects, such as those based on the nature of the local substrate, slope exposure (including proximity of water fall spray and prevailing winds), and extent of mountain mass. Local plant communities often are more sensitive to these factors than animal communities, which are roughly correlated with the plants, so ideally, future workers may wish to compare herpetofaunal communities more closely with specified plant communities, and depending on all the physical characters mentioned, plant communities may differ even at the same elevation on different mountains or tepuis, or even on different slopes of the same mountain. Nevertheless, the sites we compare for now are the 10 lowland and isolated highland sites listed below.

Lowland sites (*below 500 m*).—The lowland sites are the following, going approximately from north to south (Figs. 3, 4). Details on each site follow.

Baramita (7°22′14″N, 60°29′28″W; ca. 120 m elevation): RDM collected here, including use of drift fences and pitfall traps, from 23 Sep–18 Oct 1992, and RPR collected here, without pitfall traps, from 10–18 Jun 1999. This was primarily a rainforest site.

Kartabo (6°21′N, 58°41′W according to AMNH catalog; ca.100 m elevation [Stephens & Traylor 1985]): William Beebe and colleagues from the New York Zoological Society collected "in one-quarter of a square mile of jungle" for parts of eight years from 1909–1926 (Beebe 1944:145).

Fig. 1. Trapline of drift fence (plastic sheeting stapled to cut saplings hammered into ground) and pitfall trap (arrow; 20 liter plastic bucket buried with brim flush to ground). Plastic sheeting crosses the middle of the open top of the bucket to allow catching things from either side.

Beebe also made collections in Trinidad and Venezuela. Many of the specimens he collected ultimately were received by the AMNH, but often the specimens and/or data arrived years or decades after collection, and this might explain problems associated with some of the specimens or data given for them (Barbour 1920). Identification of representatives of each taxon was confirmed recently by CJC. This

Fig. 2. South America; rectangle covers Guyana and areas shown in more detail in Figs. 3 and 4.

is the largest fauna known from a single site in Guyana, to our knowledge. As reported by Donnelly et al. (2005), the fauna at the Iwokrama Forest Reserve may be similar in diversity, and perhaps more diverse, but those collections were from a significantly larger area (including lowlands and uplands with different habitats); many species were listed with incomplete names, and representatives of some taxa were not available for our examination. Nevertheless, we examined the Iwokrama specimens that have USNM catalog numbers. The Kartabo collections were made without the benefit of drift fences and pitfall traps, which might explain the apparent absence of some species, and if Beebe had a special interest in large reptiles, that might explain the apparent absence from his collections of several species of small frogs that must occur at Kartabo.

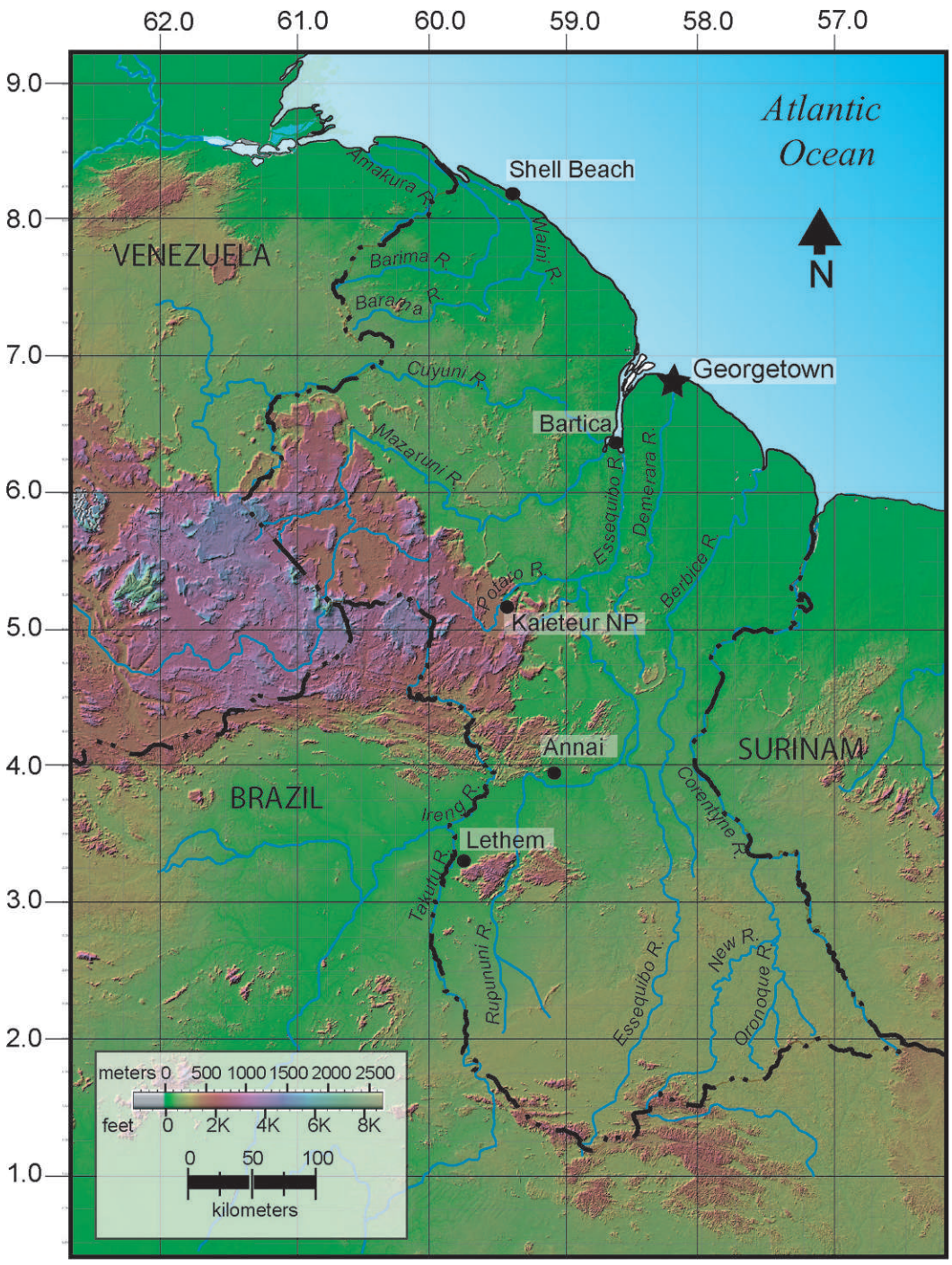

Fig. 3. Map of Guyana, color coded to show topography. The Pakaraima Mountains are west of Kaieteur NP (=National Park). We thank Ray Sterner, The Johns Hopkins University Applied Physics Laboratory for the satellite image base map.

Fig. 4. Map of Guyana, showing the 10 places for which faunas are compared (see Biogeography). Squares represent the 7 lowland sites, triangles the 3 isolated highland sites. See acknowledgement for Ray Sterner in Fig. 3.

Dubulay Ranch (5°40′55″N, 57°51′32″W; ca. 30 m elevation): CJC and CRT collected here from 25 Feb–24 Mar 1994 and 26 Aug–24 Sep 1995, including the use of drift fences and pitfall traps. RPR collected here without pitfall traps from 9–12 Apr 1994. Most collecting was done within a 1 km (linear) radius of the ranch house, at ca. 60 m elevation according to our GPS readings, but which Alexander Mendes reports is probably closer to 30 m. In addition, some specimens came from very small sites up to 12 km away. These sites include the following: Aramatani Creek (5°41′14″N, 57°54′59″W), ca. 12 km (linear) WNW the ranch house; a swamp along Aramatani Creek (5°40′22″N, 57°55′21″W); a spring (5°39′53″N, 57°54′31″W); Tableau Pond, ca. 6.5 km by road NW the ranch house; and Warniabo Creek (5°39′46″N, 57°53′24″W), ca. 6.5 km by road SW the ranch house. This was an area of mixed habitats, including gallery rainforest along waterways, and patches of savanna with bush or forest islands.

Berbice River Camp (5°05′06″N, 58°14′14″W; ca. 60 m elevation): CJC and CRT collected here from 14 Feb–15 Mar 1997 with Gerald and Wesley King, including the use of drift fences and pitfall traps. Most collecting was done within a 1 km (linear) radius of camp, which was on the east shore of the Berbice River. This was primarily a rainforest site, but highly selective logging had been done in the past in much of the area sampled.

Konawaruk Camp (5°13′07″N, 59°02′43″W; ca. 120 m elevation): CJC and CRT collected here with Gerald and Wesley King, including use of drift fences and pitfall traps, from 27 Feb–27 Mar 1998. Most collecting was done within a 1 km (linear) radius of camp. This was primarily a rainforest site, but our observations suffer because it was unusually dry while we were here, during an extreme El Niño event. The dry leaves on the forest floor crackled as we walked, sticks snapped when we stepped on them, and animal activity in general was low.

Karanambo (3°45′10″N, 59°18′33″W; ca. 115 m elevation): This is the McTurk Ranch and vicinity, sometimes spelled Karanambu, on the northern part of the Rupununi Savanna. CJC and CRT collected here and at the nearby village of Yupukari (ca. 11 km [linear] SSW Karanambo) from 15 Feb–13 Mar 1992, and RPR collected at Karanambo from 31 Mar–3 Apr 1994. In lieu of drift fences and pitfall traps, we had extensive assistance from local children at Yupukari. This is mostly savanna habitat, but there is gallery forest along the waterways, especially the Rupununi River.

Aishalton (2°28′31″N, 59°19′16″W; ca. 150 m elevation): This is a village on the southern part of the Rupununi Savanna. CJC and CRT collected here from 18 Mar–7 Apr 1993. In lieu of drift fences and pitfall traps, we had extensive assistance from local children. Most collecting was done within 1 km (linear) of the village. This is mostly savanna, but there is gallery forest along the waterways.

Isolated highland sites (*above 1400 m*).—Locations of these sites are shown in Fig. 4. Vegetation descriptions are from Huber (1995) and Huber et al. (1995). Because of the shallow soil, rocky terrain, and very dense vegetation, collections were made without the use of pitfall traps.

Mount Ayanganna (summit coordinates 5°23′N, 59°59′W; 2000 m): Mount Ayanganna is the highest peak located entirely within Guyana. It marks the divide between the headwaters of the Mazaruni, Potaro, and Ireng Rivers. Most collections were made on the northeast plateau of Ayanganna (5°24′N, 59°57′W; elevation 1490–1550 m), from 25 Oct–2 Nov 2000 by RDM, AL, and Carter Cox, with some help from guides and porters. Habitat on the northeast plateau is wet low evergreen high-tepui forest, dominated by *Bonnetia roraimae*, *Schefflera*, *Clusia* and *Ilex* spp.,

and large terrestrial bromeliads (*Brocchinia*). More details are provided by MacCulloch & Lathrop (2009).

Mount Wokomung (highest summit at 5°05′N, 59°50′W; 1700 m): Unlike Mount Ayanganna, which has a single peak, Wokomung is a massif with several connected peaks. Wokomung marks the divide between the headwaters of the Potaro and Ireng Rivers. Collections were made by RDM, AL, and Samir Khan, with some help from guides and porters, on the northeast slope (5°05′N, 59°51′W; 1411 m), 2–8 Nov 2004. One night, 6–7 November, was spent on the summit (5°05′N, 59°50′W; 1700 m). Slope habitat is montane forest with some epiphytes and understory. The summit is a shallow sloping bowl with very dense terrestrial bromeliads and woody shrubs in the center, stunted trees around the rim. Other collections have been made on Mount Wokomung, notably by D. B. Means (Means & Savage 2007).

Mount Roraima, summit, 2600–2810 m (5°12′N, 60°44′W): Roraima is the highest peak in the eastern Guiana Shield, and has been visited by numerous collectors. A history of the exploration of Roraima is in McDiarmid & Donnelly (2005). Collections were made on the slopes and summit, and specimens are deposited in many institutions. Most collecting was done on the Venezuelan portion of the mountain, where access is relatively easy. Two collections were made on the Guyanese portion of Roraima: one is at the BMNH (Warren 1973) and the other at the NMNH. For the present report we include all species collected above 1400 m on Mount Roraima, assuming that they occur in both Venezuela and Guyana, including those collected by other investigators. The herpetofauna of Roraima is summarized by MacCulloch et al. (2007).

Upland sites (*between 500–1400 m*).—Locations of these sites are shown on Figs. 3 and 4, although none of us spent sufficient time at these sites to include them in the faunal comparisons (see Biogeography, below).

Mount Ayanganna Base (870 m; 5°25′N, 59°58′W): RDM and AL collected here on 3 Nov 2000.

Mount Wokomung Slope (1234 m; 5°06′35″N, 59°49′15″W): RDM and AL collected here from 27 Oct–1 Nov 2004.

Mount Wokomung Base (698 m; 5°07′46″N, 59°48′37″W): RDM and AL collected here from 21–26 Oct 2004.

Kaieteur (above Kaieteur Falls; above 450 m; 5°10′N, 59°29′W): RPR collected here from 29 Mar–2 Apr 1989 and RDM collected here from 1–20 Jun 2005. This area has been visited much more frequently by other researchers, however (Kok & Kalamandeen 2008; their work is still in progress).

Abbreviations of Scientific Collections Used

Abbreviations are used in the species accounts to cite specimens in scientific collections that document occurrence in Guyana. We follow Sabaj Pérez (2012) for collections listed, with few exceptions (specified).

AMNH: American Museum of Natural History, New York, New York.

ANSP: Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania.

BMNH (=BM or NHMUK in some papers): Natural History Museum, London (formerly, British Museum of Natural History).

CPI: "D. Bruce Means field series, to be deposited at USNM" (Grant et al. 2006:45).

CSBD: see UG.

EBD: Estación Biológica de Doñana, Seville, Spain.

EBRG: Estación Biologia de Rancho Grande, Museo, Maracay, Venezuela.

FMNH: Field Museum of Natural History, Chicago, Illinois.
IBSP: Instituto Butantan, São Paulo, Brazil.
IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels.
KU: University of Kansas Biodiversity Institute, Lawrence, Kansas.
MBUCV: Museo de Biología, Universidad Central de Venezuela, Caracas.
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MHNLS: Museo de Historia Natural La Salle, Caracas, Venezuela.
MNHN (=MNHNP in some papers): Muséum national d'Histoire Naturelle, Paris.
MNRJ: Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil.
MSNM: Museo Civico di Storia Naturale di Milano, Italy.
MZUSP: Museu de Zoologia, Universidade de São Paulo, Brazil.
NHMW (=NMW in some papers): Naturhistorisches Museum, Wien (Vienna), Austria.
NMNH: National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM for specimen catalog numbers).
NRM (=NHRM in some papers): Naturhistoriska Riksmuseet, Stockholm, Sweden.
PCHP: Peter C. H. Pritchard, Chelonian Research Institute, Oviedo, Florida.
RMNH: Netherlands Centre for Biodiversity Naturalis, Leiden.
ROM: Royal Ontario Museum, Toronto, Canada.
SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany.
UF: University of Florida, Florida Museum of Natural History, Gainesville.
UG (=CSBD or HA in some papers): Centre for the Study of Biological Diversity, University of Guyana, Georgetown.
ULAM (=ULABG in some papers): Herpetological Collection, Laboratory of Biogeography, Universidad de Los Andes, Mérida, Venezuela.
UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Michigan.
UPRM (=UPR-M): University of Puerto Rico, Mayagüez.
USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UTA: University of Texas at Arlington, Department of Biology.
UUZM (=ZIUU or ZMUU in some papers): Uppsala University, Zoological Museum (=Zoologiska Museet), Sweden.
ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.
ZISP (=ZIN): Zoological Institute, Russian Academy of Sciences, St. Petersburg.
ZIUU: see UUZM.
ZMB: Museum für Naturkunde (formerly Zoologische Museum), Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität, Berlin, Germany.
ZMUU: see UUZM.
ZSM (=ZSMH in some papers): Zoologische Staatssammlung, Munich, Germany.
ZUU: Museo Academico Upsalensi, Sweden.

Identification of Specimens

For a variety of reasons, it is often desirable to identify animals that are under observation, whether in the laboratory or the field. The use of a dichotomous identification key (or several keys in succession) is an efficient way to accomplish this, although good magnification may be necessary to see some of the

characters, ideally with a dissecting microscope. A dichotomous key presents the user with a series of paired choices (couplets), beginning with pair number one (1) and continuing through a series of numbered choices. At the end of each paired set of statements, the user is led to either the next relevant couplet or the probable name of the taxon identified. At this point, it will be helpful to go to the relevant species account; each account has color notes and each account begins with a reference to the plate with the color photograph, if present. Once this process is completed, the identification obtained may or may not be correct, or there may be questions about why certain characters seen on the specimen do not fit some that were expected in using the keys.

When possible, follow-up should be done by comparing the specimen identified with either photographs or other specimens previously identified as belonging to the same species. Throughout this process, there are several possible sources of error, such as the following: 1) a mistake in observations or wrong turn in the key; 2) the specimen represents a taxon currently not known to occur in Guyana and therefore not included in the key; 3) the specimen represents a taxon unknown to science; 4) the specimens used for comparison may have been misidentified previously; 5) the specimen is abnormal in key characters; or 6) the key is faulty and does not work properly in some respect. In some cases, it may be useful to compare the specimen with the color plates, find a species that might be it, then find that species in the key and work backwards through the key to see where the difficulty occurs. Frustrating as it may be, it can be an interesting challenge to identify a difficult specimen when it does not key out directly and easily.

Initially, one must choose the right key with which to begin. In the context of this volume, our focus is on vertebrates (organisms with a backbone) that are not fish, birds (although birds are now classified as one of the major groups of reptiles), or mammals (which have a constant, warm body temperature, hair, and, in South America, give birth to living young). Once one has decided one has a vertebrate that is not one of these, it must be either an amphibian or reptile.

Reptiles have epidermal scales that are perfectly conspicuous and readily felt on the surface of their skin; amphibians do not (the hidden dermal scales of caecilians are very inconspicuous). For those reptiles that have legs, all of the fingers and toes almost invariably have claws; amphibian fingers and toes do not. If the animal looks like a frog or toad, it is an amphibian, even if it has a vocalization that sounds like the quack of a duck. However, if it looks very superficially like an earthworm, check it carefully, as there is a possibility that it is an amphibian or scaly reptile. Caecilians (Gymnophiona) are wormlike amphibians (see *Microcaecilia*, Plate 18F) that are legless, with a moist body that is not as limp in hand as an earthworm. Amphisbaenians (worm lizards) are legless reptiles that have epidermal scales and eyelids. Look and feel carefully to see if a wormlike animal has the following characters: a bone-hard head at one end, which is clearly different from the other end on close inspection; possibly vestigial eyes (if not absent or concealed by bone), a small mouth, with tiny teeth, and a vertebral column. Some species of caecilians are 30 cm or more in length and not readily confused with earthworms, but, as if to make matters worse, one species (see *Typhlonectes compressicauda*) is fully aquatic in fresh water and could be confused with an eel.

Our focus here is to understand the species that occur in Guyana, without emphasis on subspecies. In cases where there are significant issues with possible subspecies, these are discussed in the species accounts. Also, our focus is on adults and juveniles, excluding identifica-

tion of larval forms (e.g., tadpoles). We hope that soon someone will follow up with a volume dealing with the larval forms of all the amphibians of Guyana, as these are important components of the aquatic ecosystems, yet it will require considerable work to complete such a volume. Similarly, a volume on the vocalizations of the frogs, especially their advertisement calls, would be very useful to help in the identification of individuals, supported by recordings and print-outs of their acoustical characters (e.g., Kok & Kalamandeen 2008).

Key to the Orders of Amphibia of Guyana

1a. Legless amphibians ..... Gymnophiona (caecilians), p. 348
1b. Four-legged amphibians ..... Anura (frogs and toads), p. 332

Key to the Families and Many Species of Anura (Frogs and Toads) of Guyana

Many of the families and genera of anurans that occur in Guyana are represented by only one or a few species that occur in the country (e.g., *Atelopus*, *Pipa*). For those groups, the Guyanese species can be identified with this key. For most families and genera having more representatives in Guyana (e.g., Bufonidae, Hylidae), this key will lead users to relevant specific keys that follow.

This key is based largely on that of Lescure & Marty (2000). In addition, Dunn (1949), Trueb & Cannatella (1986), and Campbell & Clarke (1998) were especially helpful in places. Fingers and toes are numbered by counting from the innermost (thumb or big toe) as I to the outermost (pinky) as IV or V. Measurement of the body length is often from the tip of the snout to the vent, but some investigators measure to the end of the bone felt above the vent (urostyle).

1a. Body very flat; eyelids and tongue absent; fingertips star-shaped; aquatic, even as adults 2
1b. Not as 1a 3
2a (1). Irregular shaped dermal flap at angle of jaw; toes (hind feet) without keratinous tips..... ..... *Pipa pipa*, p. 435
2b. No dermal flaps at angle of jaw; tips of toes I–III with keratinous caps in adults..... ..... *Pipa arrabali*, p. 435
3a (1). Toes (hind feet) opposable; relative toe lengths, adpressed, IV>V> I>III≥II..... 4
3b. Toes not opposable; relative toe lengths, adpressed, IV>V≥III>II >I or IV>III>V>II>I..... 5
4a (3). Larger frogs with green backs, not with warty, toad-like appearance; eardrum (tympanum) distinct on side of head; pupil of eye vertical; toes IV and V not fused at base (Fig. 5B)..... see separate key for *Phyllomedusa*, p. 345
4b. Small, warty, toad-like appearance; tympanum not visible; pupil horizontal or round; toes IV and V fused at base (Fig. 5A)..... see separate key for Bufonidae, p. 338
5a (3). Discs of fingertips with two scale-like scutes on upper surface (Fig. 5D) ..... see separate key for Aromobatidae and Dendrobatidae, p. 336
5b. Not as 5a 6
6a (5). Conspicuous toad-like parotoid glands present (but may be small or large) on neck behind ears (Fig. 5E) and no black spot edged with red in groin..... 7
6b. No parotoid glands, or, if present, groin with large black spot edged with red 8
7a (6). Tympanum (eardrum) not evident (Fig. 5E); first toe somewhat indistinct, enclosed in skin .... *Atelopus spumarius*, p. 375

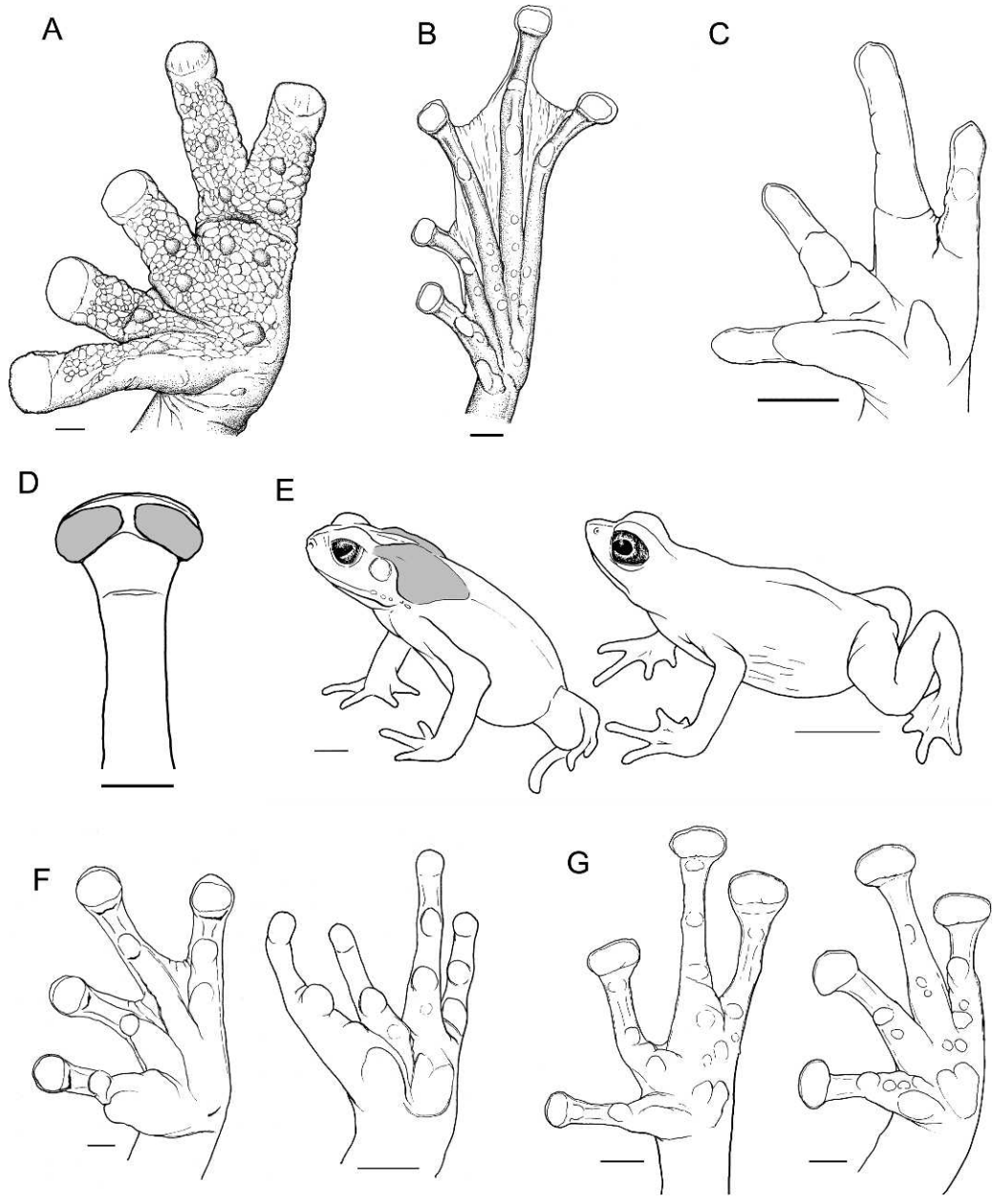

Fig. 5. A, Underside of foot, *Oreophrynella dendronastes*, toes IV+V fused at base (Lathrop & MacCulloch 2007:90). B, Underside of foot, *Scinax boesemani*, toes webbed, not fused. C, *Adelophryne patamona* hand, inconspicuous points on fingertips, pads beneath toes, not tubercles (MacCulloch et al. 2008a:40). D, Upper view, *Dendrobates leucomelas* toe, paired scale-like scutes shaded. E, Parotoid glands (shaded) behind tympanum in *Rhaebo guttatus* (left), neither conspicuous in *Atelopus spumarius* (right). F, Hand of *Hypsiboas* (left), fingertip discs; *Leptodactylus* (right) without discs. G, Hands of *Pristimantis* (left), *Scinax* (right), fingertip discs. Scale bars: A–D, F, G = 1 mm, E = 1 cm.

7b. Tympanum clearly visible; first toe distinct 9

8a (6). Body somewhat flattened (some species less so than others), with narrow head (although broad at neck); nose pointed (viewed from above); pupil round (some Bufonidae; all Microhylidae) 10

8b. Not as 8a 21

9a (7). Body length (snout-vent) usually more than 25 mm; crests on head; body thick or squat; warty skin on back..... see separate key for Bufonidae, p. 338

9b. Body length less than 25 mm; no cranial crests; body more slender; granular skin on back..... .... *Dendrophryniscus minutus*, p. 375

10a (8). Toes (on feet) essentially completely webbed..... 11

10b. Toes with incomplete or no webbing 12

11a (10). Belly white with large, irregular black spots; irregular black spot in groin..... .... *Chiasmocleis shudikarensis*, p. 430

11b. Belly dark brown with white spots; groin basically all dark brown to black, not just a spot... ..... *Ctenophryne geayi*, p. 431

12a (10). Tympanum as big as eye; behind eye, light-colored dorsolateral ridge or fold on skin along body..... 13

12b. Tympanum smaller than eye or concealed; no dorsolateral ridge or fold..... 15

13a (12). Dorsal body coloration (on back) black or dark gray, with yellow spots or blotches (usually red in Venezuela); rear of thigh with thin but distinct yellow line ..... *Otophryne steyermarki*, p. 434

13b. Dorsal coloration lighter, reddish brown to grayish yellow, with scattered pale tubercles; rear of thigh mottled or with pale tubercles connected by irregular, fine, pale line 14

14a (13). Upper surface of thigh and rear of thigh mottled with dark brown spots, with narrow dark brown line below; tip of snout rounded ..... *Otophryne robusta*, p. 433

14b. Upper surface and rear of thigh not mottled; rear of thigh with row of large, white tubercles, mostly connected by irregular, fine, pale line; pale color above this line, broad dark brown line below; tip of snout protrudes sharply .... *Otophryne pyburni*, p. 433

15a (12). Orange spot in groin .... *Elachistocleis surinamensis*, p. 431

15b. No orange spot in groin..... 16

16a (15). Snout projecting well past lower jaw (viewed from side) and curving downward; nostril beyond tip of lower jaw; snout blunt, distinctly light in color 17

16b. Not as 16a, snout projecting much less 18

17a (16). Back, sides, and limbs brown (gray-brown in life) with many light spots (cream to orange in life); belly uniform grayish white in life; distinct light stripe from snout over eye; ear (tympanum) concealed; body length of adult males less than 30 mm... *Synapturanus salseri*, p. 434

17b. Back brown (reddish brown in life) with no discrete spots (or only tiny flecks of white); brown mottled pattern on sides and limbs; belly yellow or tan in life; no light stripe from snout over eye; ear sometimes visible; body length of largest adult males greater than 30 mm..... .. *Synapturanus mirandaribeiroi*, p. 434

18a (16). Back light tan or brown with large, irregular, hourglass shaped darker brown area (which may fade in preservative); viewed from above, a dark brown spot at rear on back, in front of hip

(each side) . . . . . .
. . . . *Hamptophryne boliviana*, p. 432
18b. Not as 18a, although possibly brown 19
19a (18). No fingers or toes with swollen tips or discs (Fig. 5F); irregular black spot in groin. . . . . .
. . . . *Chiasmocleis shudikarensis*, p. 430
19b. Some fingers and toes with swollen tips; no black spot in groin 20
20a (19). First (inner) finger and first toe rudimentary; discs at tips of swollen fingers and toes with groove at tip, between upper and lower surfaces; belly white, with brown stippling on throat, brown reticulum on limbs . . . . . .
. . . . . *Chiasmocleis hudsoni*, p. 430
20b. First finger not rudimentary, although first toe reduced; swollen tips of fingers and toes without groove; belly cream, heavily spotted with gray . . . . . .
. . . . . *Chiasmocleis jimi*, p. 430
21a (8). In adults, belly skin translucent to transparent, some internal organs clearly visible . . . . . .
see separate key for Allophrynidae and Centrolenidae, p. 335
21b. Not as 21a 22
22a (21). Tips of fingers and toes with conspicuous disc (Fig. 5F, G) 23
22b. No discs at tips of fingers and toes (or only slightly expanded tips on animals with adult body length less than 20 mm). 24
23a (22). Toe webbing absent or rudimentary; finger discs wider than long . . . . . see separate key for Ceuthomantidae, Craugastoridae, Eleutherodactylidae, p. 339
23b. Toes webbed at least half way toward tips; toe discs rounded 28
24a (22). Toes webbed entirely to tips 25
24b. Toes not completely webbed. 27
25a (24). Body with dorsolateral fold or ridge of skin from behind eye toward rear . . . . . .
. . . . . *Lithobates palmipes*, p. 436
25b. No dorsolateral fold or ridge 26
26a (25). Adult body length (snout-vent) usually 50–65 mm; no cream stripe on side of body; rear of thighs with creamy yellow stripe; chest and belly with dark gray flecks . . . . . *Pseudis paradoxa*, p. 414
26b. Adult body length less than 30 mm; cream stripe on side of body; rear of thighs with cream dots; chest and belly with cream dots . .
. . . . . *Lysapsus laevis*, p. 408
27a (24). Conspicuous, flexible, dermal horn atop upper eyelid . . . . . .
. . . . . *Ceratophrys cornuta*, p. 385
27b. Not as 27a . . . . . see separate key for Leptodactylidae, p. 346
28a (23). Snout pointed (viewed from above), mouth not at tip; in life, body green above, with cream stripe (bordered below by brown stripe) from snout to eye; small dermal crest above vent . . . . . .
. . . . . *Sphaenorhynchus lacteus*, p. 418
28b. Not as 28a; if body green above, snout is rounded or truncate 29
29a (28). Finger I (innermost or thumb) shorter than finger II. . . . .
see separate key for Hylidae, p. 341
29b. Finger I longer than or equal in length to finger II . . . . . .
see separate key for Hemiphractidae (*Stefania*), p. 340

Key to Frogs of the Families Allophrynidae and Centrolenidae of Guyana

The following key is based primarily on information provided by Kok & Castroviejo-Fisher (2008). Additional information was obtained from Gorzula & Señaris (1999) and Lescure & Marty (2000), and we benefitted from editing and corrections provided by Santiago Castroviejo-Fisher (pers. comm.).

1a. Back brown with black spots;

viewed from above, head triangular, with narrow snout; back with hemispherical pustules having a central spinule; cream markings on lips, sides, arms, and legs .... *Allophryne ruthveni*, p. 370

1b. Back primarily green; viewed from above, snout wider, more rounded; otherwise also not as 1a..... 2

2a (1). Looking through translucent belly, anterior (front) one-third of internal parietal peritoneum (abdominal sheath) white; back light lime green with a few small black or dark brown flecks; bones green in life..... *Vitreorana helenae*, p. 384

2b. Parietal peritoneum transparent, viewed externally in life, although some visceral peritonea white; coloration basically green on back but not same as 2a..... 3

3a (2). Bony spine or protuberance at base of thumb (Fig. 6A) and on upper arm near shoulder in males (Fig. 6B); bones green in life; body all dark green above (with numerous subtle pale dots); heart covered with white pigment .... *Vitreorana gorzulae*, p. 384

3b. Thumb spine concealed and otherwise not as 3a..... 4

4a (3). Snout sloping in profile; bones green in life; back green with small or tiny pale whitish spots .... *Hyalinobatrachium taylori*, p. 383

4b. Snout truncate or round in profile; bones white in life; back green but otherwise not as in 4a..... 5

5a (4). Green back with round yellow spots (cream in preservative) 6

5b. Green back with irregular-shaped lime green areas (white in preservative) and scattered black dots .. .. *Hyalinobatrachium iaspidiense*, p. 382

6a (4). Snout truncate, viewed from above or side; body green above with somewhat subtle but large round yellow spots (cream in preservative) and small brown dots.. .. *Hyalinobatrachium cappellei*, p. 382

6b. Snout rounded; back green with small light yellow spots .... *Hyalinobatrachium mondolfii*, p. 383

Key to Frogs of the Families Aromobatidae and Dendrobatidae of Guyana

The monophyly and recognition of families and genera of these small frogs are strongly supported by molecular (DNA sequence) data, but in many cases there are no, or only inconspicuous, morphological characters to identify them (Grant et al. 2006). The following key is based on information provided by Rodríguez & Duellman (1994), Grant et al. (1997, 2006), Gorzula & Señaris (1999), Lescure & Marty (2000), Jungfer & Böhme (2004), Duellman (2005), Kok et al. (2006a, 2006b), and Kok et al. (2007).

1a. With fingers adpressed, finger I (innermost or thumb) clearly longer than finger II 2

1b. With fingers adpressed, finger I usually shorter than or equal in length to finger II (although may appear longer without adpressing).. 4

2a (1). Upper surfaces of arms and legs green; belly black with blue spots; broad yellow or greenish yellow dorsolateral stripe from snout to groin; adult body (snout-vent) length more than 35 mm ... . *Ameerega trivittata*, p. 391

2b. Not as 2a 3

3a (2). Brown mottling on chest or belly; adult males with throat dark gray, brown, or black; adult body length 20–34 mm .... *Allobates femoralis*, p. 370

3b. No mottling on chest or belly; adult males and females with very pale throat; adult body length less than

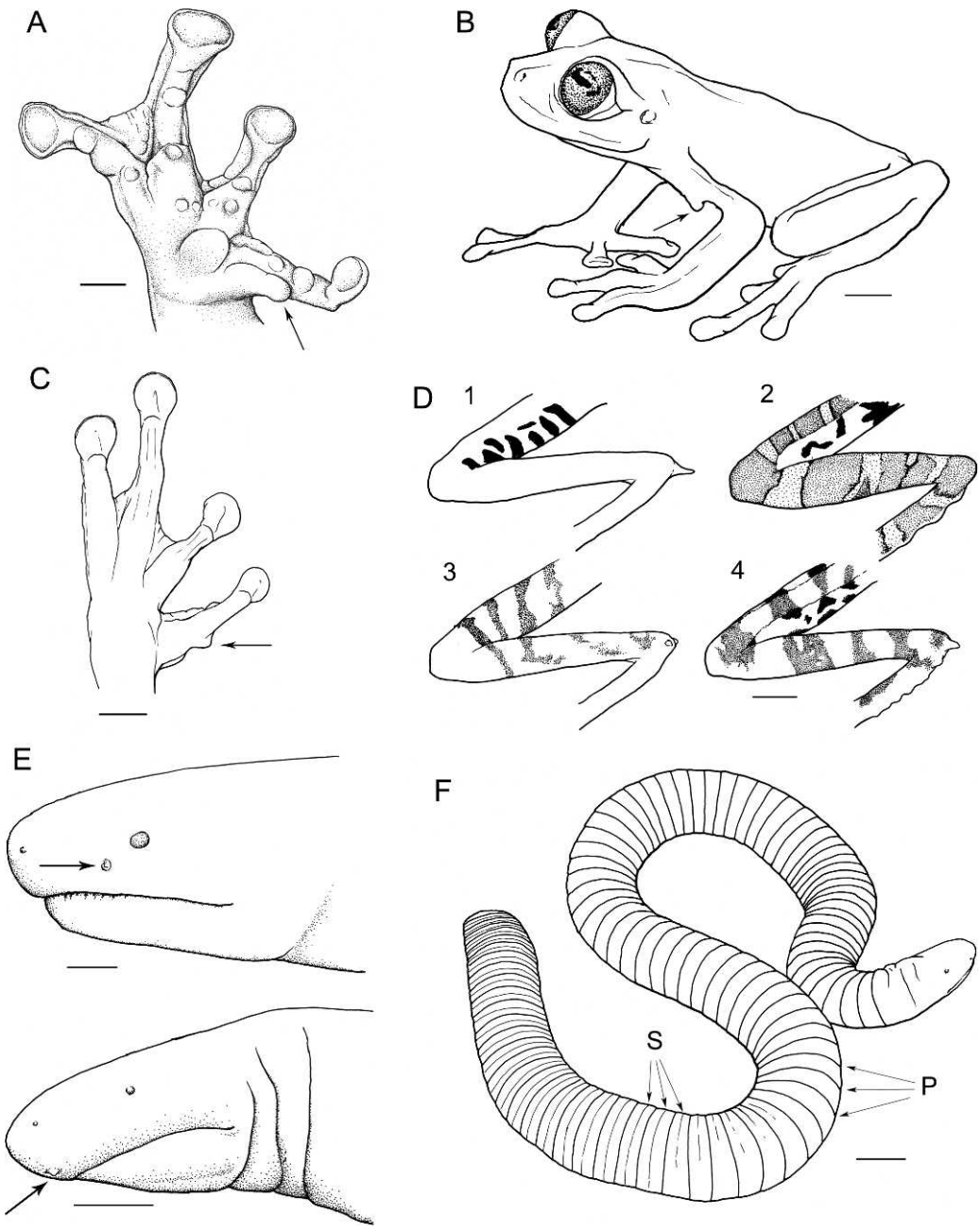

Fig. 6. A, *Vitreorana gorzulae* with thumb protuberance. B, *Vitreorana* with humeral spine. C, *Hypsiboas cinerascens* with prepollical spine. D, Calcars on tree frog heels; 1, elongate, pointed on *Hypsiboas calcaratus*; 2, absent on *Dendropsophus marmoratus*; 3, small, tubercular on *Myersiohyla kanaima*; 4, small, conical on *Hypsiboas roraima*. E, Caecilians, *Siphonops*, tentacle near eye (upper), *Caecilia*, tentacle below nostril (lower); see Acknowledgments. F, Primary (P) and secondary (S) grooves of *Caecilia*, marking folds or annuli; see Acknowledgments. Scale bars: A, C = 1 mm, B, E = 2 mm, D, F = 5 mm.

20 mm. . . . . *Allobates spumaponens*, p. 370

4a (1). With fingers adpressed, finger I equal in length to finger II 5

4b. With fingers adpressed, finger I usually shorter than finger II 7

5a (4). Tongue with pimple-like median lingual process; belly cream, yellow, or orange (although anterior belly may be gray with black blotches); toes (on feet) with only basal to moderate webbing 6

5b. Tongue without median lingual process; belly black or dark brown, marbled with light blue; no webbing on toes . . . . . *Ameerega hahneli*, p. 390

6a (5). Adult body length usually less than 20 mm or just a bit more; fingers II and III without fringing fold on side; dorsolateral stripe begins at posterior corner of eye; no black blotches on anterior part of belly; toes moderately webbed . . . . . *Anomaloglossus kaiei*, p. 372

6b. Adult body length usually 20 mm or more; fingers II and III with keel-like fringing fold on side; dorsolateral light stripe begins at tip of snout; anterior part of belly of males with black blotches; toes webbed only at base . . . . . *Anomaloglossus praderioi*, p. 373

7a (4). Coloration on back (dorsum) includes bright colors (gold, yellow, orange, bold white, blue, shiny black); tongue usually without pimple-like median lingual process (except in *A. beebei*). 8

7b. Dorsal coloration cryptic, dull brown or gray (sometimes black); tongue with pimple-like median lingual process 11

8a (7). Yellow or orange frog; small (adult body length 19 mm or less); toes with webbing; tongue with pimple-like median lingual process; lives in or near large terrestrial bromeliads. . . . . *Anomaloglossus beebei*, p. 371

8b. Not as 8a; adults larger; toes not webbed; tongue lacks median lingual process 9

9a (8). Back with scattered, small, roundish light spots; body length of adult males less than 30 mm . . . . . *Dendrobates nubeculosus*, p. 392

9b. Dorsum not as in 9a; body length of adult males 30 mm or more 10

10a (9). Viewed from above, conspicuous, broad, black band around neck region; toward rear, conspicuous, broad, yellow bands with black intrusions. . . . . *Dendrobates leucomelas*, p. 391

10b. Not as 10a; often with blue markings also. . . . . *Dendrobates tinctorius*, p. 392

11a (7). Adults of both sexes with body length of 21 mm or more (females to 28 mm) . . . . . *Anomaloglossus megacephalus*, p. 372

11b. Adult body length less than 20 mm. 12

12a (11). Back bright yellow or orange to pale tan; webbing between all toes (on feet); light dorsolateral stripe present, although may be obscure; throat and chest yellow . . . . . *Anomaloglossus beebei*, p. 371

12b. Back gray; no webbing between toes I–III; webbing nearly absent between toes III–V; no light dorsolateral stripe; undersides gray or brown, not yellow . . . . . *Anomaloglossus roraima*, p. 374

Key to Frogs and Toads of the Family Bufonidae of Guyana

This key includes bufonid genera and species that were not keyed out in the initial anuran key. The initial key covers *Atelopus spumarius* and *Dendrophryniscus minutus*. The following key is based on information provided by Hoogmoed (1977), Lescure & Marty (2000), Frost et

al. (2006), Fouquet et al. (2007a), and Lathrop & MacCulloch (2007).

1a. Conspicuous parotoid glands on neck; toes (on feet) not opposable; usually found in lowland or upland habitats 6
1b. No conspicuous parotoid glands; toes opposable; highland species, found above 1000 m elev. 2
2a (1). Extensive webbing on fingers and toes; distinct bony crest behind eye 3
2b. Webbing on fingers and toes only basal or moderate; bony crest behind eye indistinct or apparently absent 4
3a (2). Prominent, short bony crest below eye; back blackish brown without lengthwise line along middle (vertebral area); belly dark brownish orange with lengthwise black line along middle (midventral); palms of hands and soles of feet orange. . . . . *Oreophrynella seegobini*, p. 377
3b. Crest below eye indistinct; back reddish brown with dark markings and a thin, dark brown vertebral line; belly light reddish brown without black midventral line; palms and soles light brown. . . . . *Oreophrynella weiassipuensis*, p. 378
4a (2). Back covered with numerous, distinct, conical tubercles; fingers with only moderate webbing . . . . . *Oreophrynella quelchii*, p. 377
4b. Body with relatively few tubercles; only basal webbing on fingers 5
5a (4). Snout somewhat pointed in profile, projecting beyond front end of lower jaw . . . . . *Oreophrynella macconnelli*, p. 376
5b. Snout truncate, not projecting beyond lower jaw . . . . . *Oreophrynella dendronastes*, p. 376
6a (1). No conspicuous bony crests on head; sides (eye to groin) with broad, bold band of very dark brown to black, in some edged above by narrow cream stripe or row of cream warts . . . . . *Rhaebo guttatus*, p. 378
6b. Bony crests present on head, small in some species, very conspicuous in others; sides not as 6a 7
7a (6). Protruding bony knob at angle of jaws (rear of mouth, extending to side); bony crests on head most conspicuous . . . . . *Rhinella martyi*, p. 379
7b. No protruding bony knob at angle of jaws; crests present on head but not as prominent 8
8a (7). Edge of lower jaw with white stripe or row of white spots; parotoid glands on neck moderately large, longitudinally oval, about twice as long as wide; upper eyelid spiny, projecting over eye with distinct vertical surface on side; sharply pointed snout . . . . . *Rhaebo nasicus*, p. 378
8b. Not as 8a; parotoid glands large, triangular in shape 9
9a (8). Adults are largest toads in the world; warts on back without spinules; toes up to half webbed; belly light cream with gray or brown spots or mottling . . . . . *Rhinella marina*, p. 379
9b. Maximum adult body length, 45 mm; some warts on body with spinules; toes up to one-third webbed; belly grayish . . . . . *Rhinella merianae*, p. 381

Key to Frogs of the Families Ceuthomantidae, Craugastoridae, and Eleutherodactylidae of Guyana

The following key is based on information provided primarily by Lescure & Marty (2000), Means & Savage (2007), MacCulloch et al. (2008a), and Heinicke et al. (2009). Helpful information was also

obtained from Rivero (1968a) and Duellman (1997, 2005).

1a. Fingers and toes end in a point (Fig. 5C); subdigital pads (beneath toes) rather than tubercles; tiny frogs, adult snout-vent (body) length less than 25 mm. 2
1b. Fingers and toes end in discs (Fig. 5G); subdigital tubercles rather than pads; usually larger frogs, adult body length greater than 25 mm (but a few species are smaller) . . 3
2a (1). Maximum body length of 16 mm; side of face between eye and nostril (canthus rostralis) straight or flat; second segment of finger IV short, equal to width. . . . . *Adelophryne gutturosa*, p. 393
2b. Maximum body length more than 20 mm; canthus rostralis concave; second segment of finger IV longer, about twice width. . . . . *Adelophryne patamona*, p. 393
3a (1). Tiny frogs, adult body length usually less than 20 mm; paired gland-like protrusions on post-temporal and hip regions; viewed from above, digital discs notched at tip; prominent subconical tubercle on upper eyelid and heel; row of conical tubercles on outer edge of tarsus; bright green markings on head and body. . . . . *Ceuthomantis smaragdinus*, p. 385
3b. Not as 3a 4
4a (3), When adpressed, finger I (thumb) longer than finger II. 5
4b. When adpressed finger I shorter than finger II 6
5a (4). Upper body tan with a grayish tan or brown X across back. . . . . *Pristimantis chiastonotus*, p. 386
5b. No X across back; back dark brown with or without spots . . . . . *Pristimantis zeuctotylus*, p. 390
6a (4). Upper body with brilliant colors of red or green or both, in form of spots or larger markings (red becoming dull white to brown in preservative) 7
6b. Not as 6a, although a tannish orange vertebral stripe may be present 8
7a (6). Tympanum (eardrum) distinct; no bars on upper lip area but red spots may be present; back purplish-black with several large red spots; undersides bright red, without black . . . . . *Pristimantis dendrobatoides*, p. 387
7b. Tympanum not visible; bars on upper lip areas; back with brilliant green and red crossbands, possibly with an orange vertebral stripe; undersides mottled cream and black, possibly with cream stripe . . . . . *Pristimantis jester*, p. 388
8a (6). Yellow or orange spot in groin . . . . . *Pristimantis inguinalis*, p. 387
8b. Not as 8a 9
9a (8). Toes (on feet) with rudimentary, basal webbing . . . . . *Pristimantis marmoratus*, p. 388
9b. No webbing on toes 10
10a (9). Tympanum visible but indistinct . . . . . *Pristimantis saltissimus*, p. 389
10b. Tympanum prominent or clearly visible 11
11a (10). Large, transversely oval finger discs; disc on finger III larger than tympanum. . . . . *Pristimantis pulvinatus*, p. 389
11b. Smaller, rounded finger discs; disc on finger III about half diameter of tympanum. . . . . *Eleutherodactylus johnstonei*, p. 394

Key to Frogs of the Family Hemiphractidae (*Stefania*) of Guyana

The following key is based on information provided by Duellman & Hoogmoed (1984), MacCulloch & Lathrop (2002), and MacCulloch et al. (2006).

1a. Head wider than long; frontoparietal crests (atop head behind eyes)

very prominent .... *Stefania coxi*, p. 396

1b. Head length equal to or greater than width; frontoparietal crests low or absent 2

2a (1). Toe webbing (on foot) extensive, including all but the distalmost one (rarely two) phalange(s) or joints 3

2b. Toe webbing only basal, with at least two phalanges completely free of webbing..... 4

3a (2). Only one toe phalange free of webbing (but two on toe IV); frontoparietal crests visible; maximum adult body length (snout-vent) 97 mm; found below 900 m elev..... *Stefania evansi*, p. 396

3b. More than one toe phalange free of webbing (almost three on toe IV); frontoparietal crests absent; maximum adult body length 67 mm; found in Pakaraima highlands above 900 m .... *Stefania scalae*, p. 398

4a (2). Frontoparietal crests absent; skin on back smooth; conspicuous dorsolateral light stripes present, eye to groin..... ..... *Stefania roraimae*, p. 397

4b. Frontoparietal crests low; skin shagreened (textured between smooth and granular) or granular; bold dorsolateral stripes absent 5

5a (4). Mottled color pattern; skin shagreened to granular; found below 900 m .... *Stefania woodleyi*, p. 398

5b. Color pattern not mottled; skin shagreened but not granular; found above 1000 m 6

6a (5). When adpressed, finger II reaches base of disc or last joint of finger I; color pattern of dark chevrons on back; five vomerine teeth.... *Stefania ayangannae*, p. 395

6b. When adpressed, finger II does not reach terminal phalange of finger I; no chevrons on back; 6–9 vomerine teeth..... *Stefania ackawaio*, p. 395

Key to Frogs of the Family Hylidae of Guyana

This key includes hylid genera and species that were not keyed out to species in the initial anuran key. The initial key covers the two species of *Pseudis* and *Sphaenorhynchus lacteus*, and it directs users to a separate key for *Phyllomedusa*, which follows this key.

The following key is based largely on information provided by Lescure & Marty (2000). In addition, we used information provided by Duellman (2005), original descriptions of recently described species, and literature for highland species of Guyana and Venezuela that are not known to occur in French Guiana.

1a. Iris of eye (in moderate-sized treefrogs) with alternating narrow gold and black lines radiating from area of pupil..... 2

1b. Iris not as 1a, regardless of size, although a few dark lines may be in iris..... 3

2a (1). Largest *Osteocephalus*, adult body length reaching 100 mm or more; vocal sacs paired in males; cranial crests (longitudinal bony ridges between eyes) present; toes nearly fully webbed; no row of tubercles on outer edge of tarsus of foot..... ..... *Osteocephalus taurinus*, p. 412

2b. Smaller *Osteocephalus*, largest adults less than 65 mm; vocal sac single, medial, in males; cranial crests not apparent; toes about three-fourths webbed; low row of tarsal tubercles..... ..... *Osteocephalus oophagus*, p. 411

3a (1). Skin particularly thick and glandular; when handled in life, skin secretions copious, viscous, sticky..... 4

3b. Skin of usual thinness of most frogs; secretions not as noxious as in 3a. 7

4a (3). No brown bars across thighs; black or bluish-black spot behind insertion of arm; concealed parts beneath arms and legs and webbing on hands and feet bright red . . . . . *Trachycephalus coriaceus*, p. 418

4b. Brown bars across thighs; coloration not as 4a. 5

5a (4). Males with single, median vocal sac when expanded; belly with abundant brown speckling . . . . . *Trachycephalus hadroceps*, p. 419

5b. Males with apparently paired vocal sacs when expanded, one on each side at rear of mouth; belly lacks significant speckling 6

6a (5). Skin on back with low tubercles; iris with black flecks . . . . . *Trachycephalus typhonius*, p. 419

6b. Skin on back with numerous large tubercles; iris with dark cross or horizontal dark brown to black bars . . . . *Trachycephalus resinifictrix*, p. 419

7a (3). Skin of head co-ossified with skull; males with paired vocal sacs at rear of mouth, one on each side . . 8

7b. Skin of head as in most frogs not co-ossified with skull; males with single, median vocal sac. 12

8a (7). Smallest *Osteocephalus*, adult body length less than 43 mm; posterior surface of thighs black . . . . . *Osteocephalus exophthalmus*, p. 410

8b. Not as 8a 9

9a (8). Cranial crests present but low; distinct, large membrane in axilla (armpit) between body and upper arm; tympanum (ear drum) about half diameter of eye. . . . . *Osteocephalus phasmatus*, p. 412

9b. No cranial crests; axillary membrane absent or small; tympanum about three-fourths or more diameter of eye 10

10a (9). Tubercles absent from outer edge of tarsus and lower arm; back brown . . . . . *Osteocephalus leprieurii*, p. 411

10b. Prominent tubercles on outer edge of tarsus and lower arm; back green or brown with green on sides 11

11a (10). Back and head with prominent tubercles; toes nearly completely webbed; numerous prominent tubercles on outer edge of lower arm; back primarily mosslike green . . . . . *Osteocephalus cabrerai*, p. 410

11b. Tubercles on back and head not so prominent; toes about two-thirds webbed; few prominent tubercles on outer edge of lower arm; back green or brown, with green on sides. . . . . *Osteocephalus buckleyi*, p. 409

12a (7). Discs on fingers and toes truncate (viewed from above), wider than long (Fig. 5G); loreal region (between eye and nostril and down toward upper lip) concave or depressed; can bend finger I (innermost) and toe I off to side; fingers with webbing reduced or absent; webbing reduced or absent between first two toes. 13

12b. Discs on fingers and toes more rounded (viewed from above); otherwise not as 12a, although certain species with concave loreal region, certain species with webbing of fingers and toes similar to 12a. 19

13a (12). Snout very elongate and with narrow, projecting, pointed, cutaneous appendage; broad black bars over orange background on rear of thighs . . . . . *Scinax proboscideus*, p. 416

13b. Not as 13a 14

14a (13). Top of head, above ears, and back with conspicuous tubercles; black spots in groin; black bars over blue background on rear of thighs. . . . *Scinax nebulosus*, p. 415

14b. Small to moderate tubercles or pustules on head or back, if any; thigh coloration not as 14a..... 15

15a (14). Smallest *Scinax* of Guyana, adult body length less than 25 mm; three dark brown longitudinal stripes on back—one at middle of back (vertebral), which may be incomplete in length, and two dorsolateral (broad, from behind eye nearly to groin); indistinct paravertebral dark stripes present on some individuals..... ..... *Scinax trilineatus*, p. 417

15b. Pair of broad dorsolateral stripes may be present, but otherwise not as 15a 16

16a (15). Presence of yellow or orange coloration in groin; no light spots on back..... 18

16b. No yellow or orange coloration in groin..... 17

17a (16). Brown stripe, snout to shoulder; back with light spots on gray, beige, or brown background ..... *Scinax boesemani*, p. 415

17b. No brown stripe as in 17a; no light spots on back..... ..... *Scinax cruentommus*, p. 415

18a (16). Two or more dorsolateral, dark brown, longitudinal stripes on back; lighter brown on back; yellow coloration in groin and on rear surface of thighs, not orange..... ..... *Scinax ruber*, p. 416

18b. Darker brown on back, with darker markings but without stripes; vivid orange or reddish orange in groin and rear surface of thighs.... *Scinax* cf. *x-signatus*, p. 417

19a (12). Adult body length less than 25 mm..... 20

19b. Adult body length greater than 25 mm..... 24

20a (19). Deep green on back (brownish olive in preservative) with numerous well-defined brown spots; orange on thighs, hind feet and inner side of tarsus .... "*Hyla*" *helenae*, p. 402

20b. Tan or brown on back; otherwise not as 20a 21

21a (20). Dorsal (upper) surfaces of the upper arms brilliant white; in preservative, back dark brown; chin, throat, and belly gray..... .. *Dendropsophus grandisonae*, p. 400

21b. Not as 21a 22

22a (21). With legs pressed against body in normal resting position, cream or white line above vent appears similar to those on rear of ankles; back brown or beige, with dark brown markings (usually crossbars or chevrons) .... *Dendropsophus minutus*, p. 401

22b. No white line as in 22a, although back may appear similar (in *D. brevifrons*) 23

23a (22). Tympanum distinct; two small light cream spots or bars beneath eyes and a large one on each side of body; conspicuous dark brown crossbar and/or large dark brown patch on back..... ..... *Dendropsophus brevifrons*, p. 399

23b. Tympanum inconspicuous; back tan or beige, without conspicuous dark markings (except tiny brown dots)..... .... *Dendropsophus minusculus*, p. 401

24a (19). Dorsum (back) basically green (light or dark, rarely greenish brown, although may be white in preservative), with or without differently colored markings (*H. punctatus* vermillion on back at night, with green sides)..... 25

24b. Basically brown on back, with or without markings 30

25a (24). Skin on back granular..... 26

25b. Skin on back smooth or shagreened (with texture but not granular) 27

26a (25). Skin on back with fine granules; fingers II–IV about one-third webbed; adult males with spine at

base of thumb (Fig. 6C); belly pale green to bluish green; iris of eye orange or reddish orange. . . . . *Hypsiboas cinerascens*, p. 403

26b. Skin on back with coarse granules; no webbing on fingers; adult males lack spine at base of thumb; belly blue; iris silver (daytime) or bronze (night) . . . . . *Hypsiboas liliae*, p. 406

27a (25). Middle of back with reddish brown marking and longitudinal stripe . . . . . *Hypsiboas ornatissimus*, p. 407

27b. Not as 27a 28

28a (27). Narrow vermillion or purple dorsolateral stripe on narrow longitudinal ridge of skin (from eye toward hip), edged above by tan or yellow stripe . . . . . *Hypsiboas punctatus*, p. 407

28b. No dorsolateral ridge of skin or light stripes (although some *H. sibleszi* have a cream or yellow stripe) 29

29a (28). Adult body length less than 40 mm; found at localities above 400 m elev.; back with (or without) small reddish brown spots or flecks and, on some individuals, small white or yellow spots; belly pale green with blue tint; no white lines above vent or on rear of ankles but possible pale yellow line between eyes and from eye toward vent. . . . . *Hypsiboas sibleszi*, p. 408

29b. Adult body length up to 75 mm; found at lowland localities; back with or without small dark brown dots; belly orange; with legs pressed against body in normal resting position, white line above vent appears similar to those on rear of ankles. . . . . *Hypsiboas crepitans*, p. 404

30a (24). Back of heel of foot with a calcar—a dermal appendage (small, rounded, or conical to long, pointed, triangular; Fig. 6D) 31

30b. Back of heel rounded, without calcar. 36

31a (30). Calcar quite conspicuous, elongate, pointed, triangular 32

31b. Calcar shorter, although may be triangular. 33

32a (31). Fingers with only basal webbing on three outer fingers; sides with blue tint and, toward rear, dark brown vertical bars; lower eyelid without extensive light reticulation; belly whitish or translucent gray . . . . . *Hypsiboas calcaratus*, p. 403

32b. Three outer fingers almost but not completely webbed; blue sides without bars but with light speckles instead; lower eyelid covered with reticulum of light color; belly yellowish orange . . . . . *Hypsiboas geographicus*, p. 405

33a (31). Large treefrog, adult body length up to 132 mm; calcar short, triangular; three outer fingers and toes completely webbed; adult males with rounded spine at base of thumb . . . . *Hypsiboas boans*, p. 402

33b. Adult body length 50 mm or less; calcar tubercular or conical, not triangular; fingers with vestigial or no webbing; toes not completely webbed to discs; no spine on thumb 34

34a (33). Calcar small, conical (Fig. 6D); fingers with vestigial webbing; from high elevation or upland localities higher than 800 m . . . . . *Hypsiboas roraima*, p. 407

34b. Calcar small or medium, tubercular; fingers without webbing; from lowland or highland localities 35

35a (34). Calcar medium, tubercular; toes more than half webbed; eyes not completely black; from lowland localities. . . . . *Hypsiboas fasciatus*, p. 404

35b. Calcar small, blunt, tubercular (Fig. 6D); toes only about one-third webbed; eyes completely black; from highland or upland localities at 650 m or higher..... ..... *Myersiohyla kanaima*, p. 409

36a (30). Finger I half webbed, other fingers fully webbed; toes completely webbed; webbing black at base, yellowish orange distally; belly yellowish orange with numerous large black spots..... .... *Dendropsophus marmoratus*, p. 400

36b. Fingers and toes with less webbing; coloration not as 36a..... 37

37a (36). Upper surfaces of body, arms, and legs bright white to light beige with sharply contrasting brown patches; belly bright reddish orange..... ..... *Dendropsophus leucophyllatus*, p. 400

37b. Not as 37a..... 38

38a (37). Smaller frogs (maximum adult body length 32–42 mm); from upland to highland localities in Pakaraima Mountains..... 40

38b. Larger frogs (maximum adult body length up to 75 mm); from lowlands..... 39

39a (38). Toes about half webbed; brown crossbars on back (which is cream by day, light brown by night); rear of thighs beige or brown without markings..... ..... *Hypsiboas multifasciatus*, p. 406

39b. Toes about three-fourths webbed; no brown crossbars on back (which is pale cream, green, or gray by day, beige to brown at night); rear of thighs pale yellow with brown bars or spots .... *Hypsiboas crepitans*, p. 404

40a (38). Fingers about one-third webbed; toes about three-fourths webbed; snout rounded; smaller frogs, maximum adult body length 32 mm..... *Hypsiboas lemai*, p. 405

40b. Fingers without webbing or with basal webbing only; toes about half webbed; snout blunt or truncate; somewhat larger frogs, maximum adult body length 37–50 mm..... 41

41a (40). Tympanum (ear drum) about two-thirds diameter of eye; width of disc of finger III little more than half diameter of tympanum; with arm perpendicular to body, membrane in armpit extends to about one-third length of upper arm; undersides light, often without brown spots on throat or chest ..... *Tepuihyla talbergae*, p. 418

41b. Tympanum about half diameter of eye; width of disc of finger III about same diameter as tympanum; with arm perpendicular to body, membrane in armpit extends to about middle of upper arm; undersides light, with brown spots on throat (and sometimes chest and belly)..... ..... "*Hyla*" *warreni*, p. 402

Key to Hylid Frogs of the Genus *Phyllomedusa* of Guyana

The following key is based on information provided by Lescure & Marty (2000), primarily, and by Rodríguez & Duellman (1994).

1a. Dark vertical bars on sides of body toward rear (flanks) and on thighs ..... *Phyllomedusa hypochondrialis*, p. 413

1b. Not as 1a..... 2

2a (1). Throat, chest, and underside of arms and legs brown; flanks and hidden surfaces of limbs green with small light spots that are not edged with dark color..... ..... *Phyllomedusa tarsius*, p. 413

2b. Throat and chest gray or grayish brown; light spots on flanks edged with dark color..... 3

3a (2). The largest *Phyllomedusa*, maximum adult body length about 135 mm; thick glandular fold or ridge on each side of upper body (dorsolateral) extends to level of groin; discs on fingers large, about size of tympanum; first and second toes (hind foot) equal in length... ..... *Phyllomedusa bicolor*, p. 413

3b. Dorsolateral ridge extends toward rear only to about midbody; discs on fingers smaller than tympanum; first toe longer than second .... *Phyllomedusa vaillantii*, p. 414

Key to Frogs of the Family Leptodactylidae of Guyana

The following key is based largely on information provided by Lescure & Marty (2000). Additional information was obtained from Lynch (1970, 1989), Gorzula & Señaris (1999), Heyer & Thompson (2000), Heyer & Heyer (2006), and Kok et al. (2007).

1a. Tiny frogs, maximum body (snout-vent) length less than 20 mm and with one or two tubercles on outer side of lower arm, fringes on sides of toes, snout pointed (viewing head from above), tympanum (ear-drum) concealed beneath skin, toes only basally webbed, and several small tubercles on eyelids .... *Pseudopaludicola boliviana*, p. 429

1b. Frogs larger than 20 mm in body length, or if not, other characters in 1a not all present in that combination 2

2a (1). Side of body near rear with conspicuous eye-like swollen orbs, black with light gray or blue markings; bright orangish red flash-marks in groin, behind upper leg, behind knee, beneath lower leg, and on front of ankle..... ..... *Pleurodema brachyops*, p. 429

2b. Absence (usually) of bright flash-colors as in 2a, but if present (pinkish orange to red), no black swollen orbs on sides of body posteriorly 3

3a (2). Small frogs, maximum body length of adults 35 mm or less 4

3b. Larger frogs, adult body length greater than 35 mm 8

4a (3). Belly yellow in life; rear surface of thigh black with yellow, orange, or red spotting or mottling; dark brown or black triangular seat patch at vent .... *Adenomera lutzi*, p. 421

4b. Not as 4a 5

5a (4). Inconspicuous flattened discs at tips of toes; no dark spots on back..... *Adenomera andreae*, p. 420

5b. Toe tips slightly rounded but without discs; dark spots on back, although possibly few and widely scattered..... 6

6a (5). Small frogs, body length of adults less than 25 mm; conspicuous dark bar or two large dark spots between eyes on top of head; no tubercle on tarsus of foot..... ..... *Adenomera hylaedactyla*, p. 420

6b. Larger frogs, adult body length more than 25 mm; only very small dark spots, if any, between eyes atop head; rear of tarsus of foot with conical tubercle 7

7a (6). Skin of back basically smooth, with a few warts; no parotoid glands on neck; inconspicuous fold of skin from rear edge of eye to shoulder .... *Physalaemus cuvieri*, p. 428

7b. Numerous flat glands and pointed tubercles on back; elongate parotoid gland on each side of neck at shoulder; no fold of skin from rear of eye to shoulder..... .... *Engystomops* cf. *pustulosus*, p. 421

8a (3). Back essentially black with brightly contrasting golden yellow dorsolateral stripe on each side,

snout to groin; bright red spots in groin and on thighs ..... *Lithodytes lineatus*, p. 428

8b. Not as 8a 9

9a (8). Maximum adult body length more than 60 mm 10

9b. Maximum adult body length less than 60 mm 15

10a (9). Pattern of bars on upper lips 11

10b. No bars on upper lips, although an elongate spot may be present .. 13

11a (10). Behind eye, conspicuous dorsolateral ridge or fold on skin along body 12

11b. No dorsolateral fold, although a short warty ridge may occur on shoulder ..... *Leptodactylus rugosus*, p. 427

12a (11). Dorsolateral fold long, extending rearward to level of groin; a second fold from above ear (supratympanic) slants downward onto side, accompanied by a black stripe; reproductive males with one small black spine on thumb and no spines on chest; rear of thigh black with white dots ..... *Leptodactylus pentadactylus*, p. 425

12b. Dorsolateral fold usually shorter, extending only to sacrum; supratympanic fold and accompanying black stripe very short; reproductive males with black spines on thumbs and chest; rear of thigh black with orange bars ..... *Leptodactylus knudseni*, p. 423

13a (10). A dorsolateral fold on each side and light band on upper lip; back lacks paired brown spots 14

13b. Long ridges on back in addition to dorsolateral folds; elongate dark spot may be on upper lip; back with pattern of more-or-less paired, conspicuous roundish brown spots .... *Leptodactylus macrosternum*, p. 424

14a (13). Toes with lateral fringes and rudimentary webbing; rear of thigh yellowish, marbled with black .... *Leptodactylus guianensis*, p. 423

14b. Toes lack lateral fringes and rudimentary webbing; rear of thigh black, speckled with light spots... .... *Leptodactylus rhodomystax*, p. 426

15a (9). Behind eye, conspicuous dorsolateral ridge or fold on skin along body 16

15b. No dorsolateral folds, although a short warty ridge may occur on shoulder 18

16a (15). Only two distinct dorsolateral folds (one on each side); upper lip area very bright cream or white from snout, touching eye and tympanum, extending to angle of jaws ..... *Leptodactylus mystaceus*, p. 425

16b. More (4 to 6) dorsal and dorsolateral ridges on back, or if only two, upper lips not as 16a..... 17

17a (16). Upper lip area mostly dirty cream, snout to angle of jaws; rear of thigh dark brown or black, marbled with white and having a line of white dots between vent and knee .... *Leptodactylus fuscus*, p. 422

17b. Upper lip area light with pinkish coloration in life and possibly black markings; rear of thigh brown, marbled with white and having one or two yellow lines ... . *Leptodactylus longirostris*, p. 424

18a (15). Toes with slightly expanded, rounded tips; toes without fringes on sides; back very rough with warts .... *Leptodactylus rugosus*, p. 427

18b. Toe tips not expanded, more-or-less pointed; toes with fringes on sides; back less rugose, although warts may be present 19

19a (18). Undersides covered with black anastomosing spots .... *Leptodactylus petersii*, p. 426

19b. Not as 19a 20

20a (19). Maximum adult body length greater than 45 mm; often, indis-

tinct bars on upper lip area extending to rear edge of eye; often, light spots on throat .... *Leptodactylus leptodactyloides*, p. 424

20b. Maximum adult body length less than 45 mm; often, distinct bars on upper lip area extending to beneath eye; usually no light spots on throat .... *Leptodactylus validus*, p. 427

Key to the Gymnophiona (Caecilians) of Guyana

The characters used in the following key are based primarily on information presented by Taylor (1968).

1a. Posterior to vent, a distinct but short tail is present 2
1b. Tail absent or indistinct 3
2a (1). Unicolored body, purple to black; long axis of anal opening aligned with long axis of body ... . *Epicrionops niger*, p. 438
2b. Not unicolored, a yellow stripe low on each side of body; anal opening transverse, its long axis across body..... ..... *Rhinatrema shiv*, p. 438
3a (1). Fully aquatic; posterior part of body somewhat laterally compressed; primary annuli-like folds on body often difficult to see..... . *Typhlonectes compressicauda*, p. 440
3b. Not as 3a 4
4a (3). Nostrils present, although possibly small 5
4b. No external nostrils visible..... ..... *Caecilita iwokramae*, p. 438
5a (4). Eyes covered over by bone, although possibly partly visible..... 6
5b. Eyes in sockets not covered by bone..... 9
6a (5). Very small and slender animal, earthworm-like; tiny tentacle posterior to, not directly below nostril (Fig. 6E)..... 7
6b. Not so small, yet slender relative to length; tentacle essentially below nostril ..... *Oscaecilia zweifeli*, p. 437
7a (6). Secondary annular grooves on rear of body (Fig. 6F) number 21–34; body color purple in life..... ..... *Microcaecilia rabei*, p. 439
7b. Number of secondary annular grooves not in range of 7a; body color brown (may be reddish or grayish brown, approaching purple)..... 8
8a (7). Secondary annular grooves on rear of body number approximately 40..... *Microcaecilia iyob*, p. 439
8b. Secondary annular grooves fewer than 20 .... *Microcaecilia* cf. *rabei*, p. 440
9a (5). Body strongly laterally compressed ..... *Caecilia pressula*, p. 437
9b. Body round in cross-section 10
10a (9). Primary folds on body (Fig. 6F) more than 150; few secondary folds (numbering 2–25)..... ..... *Caecilia gracilis*, p. 437
10b. Primary folds fewer than 150; many secondary folds (25–100).... ..... *Caecilia tentaculata*, p. 437

Key to the Major Groups of Reptilia (Excluding Birds) of Guyana

The characters used in the following key are based on information presented by Savage (2002) and Duellman (2005).

1a. Body encased in a bony shell; no teeth on jaws .... Testudinata (turtles), p. 366
1b. No bony shell around body; teeth present 2
2a (1). Arms and legs present, although possibly quite small 3
2b. No arms or legs 4
3a (2). Long axis of anal opening aligned in same direction as long axis of body; toes (hind feet)

webbed; nostrils on top of elongate snout ..... Crocodylia, p. 349
3b. Long axis of anal opening perpendicular to long axis of body; toes not webbed; nostrils usually on side of less elongate face .... lizards, p. 350
4a (2). Eyelids absent; scales not rectangular and usually not equal in size around body (with exceptions) ..... snakes, p. 356
4b. Eyelids present; small rectangular scales around body .... amphisbaenians (worm lizards), p. 349

Key to the Crocodylia of Guyana

The characters used in the following key are based on information presented by Brazaitis (1973). The four species known from Guyana are in the family Alligatoridae.

1a. Transverse bony ridge, well-developed or weak, across face, between eyes anteriorly; iris of eyes yellowish or greenish in life; average total length of adults, including tail, greater than 1.5 m 2
1b. No bony ridge connecting eyes anteriorly; iris dark brown, reddish brown, or orange; average total length of adults usually less than 1.5 m 3
2a (1). Average total length of adults less than 2 m, maximum about 2.5 m; no large dark blotches on sides of jaws, although hatchlings have faint gray ones; no yellow or white crossbands on body; ventral (underside) collar (anterior to shoulder) a single transverse series of enlarged scales; ventral (belly) scales in 20–24 transverse rows (collar to vent); midbelly region cream or yellow; upper eyelids raised into a high point or tubercle ..... *Caiman crocodilus*, p. 441
2b. Average total length of adults greater than 3 m, maximum about 5 m; three or more large dark blotches on sides of jaws; body black, with yellow or white crossbands; ventral collar of 2 transverse rows of slightly enlarged scales; ventral scales in 25–29 transverse rows (collar to vent); midbelly region white, contrasting with black on sides; upper eyelids flat, striated..... ..... *Melanosuchus niger*, p. 442
3a (1). Ear coverlets colored similar to side of head; dorsal (upper) scales on body above hind leg inserts (hips) in a minimum of 4 longitudinal rows; dorsalmost two rows of body scales well keeled..... ..... *Paleosuchus palpebrosus*, p. 442
3b. Ear coverlets black or dark brown, darker than color of side of head; dorsal body scales above hind leg inserts in a minimum of 2 longitudinal rows; lateral body scales well-keeled but dorsalmost two rows of body scales often not so strongly keeled..... ..... *Paleosuchus trigonatus*, p. 442

Key to the Amphisbaenians (Worm Lizards) of Guyana

The characters used in the following key are based on information presented by Gans (1963) and Hoogmoed (1973). The four species known from Guyana are all of the family Amphisbaenidae.

1a. Scales around midbody 39 or fewer; preanal pores 6 or fewer (Fig. 7A) 2
1b. Scales around midbody 40 or more; preanal pores 7 or more 3
2a (1). Preanal pores 6; supralabial (upper lip) scales 3 (not counting rostral scale at tip of snout); body annuli more than 240; mental (foremost) and postmental scales

on chin fused .... *Amphisbaena stejnegeri*, p. 444

2b. Preanal pores 4; supralabial scales 2; body annuli fewer than 235; mental scale separate and distinct from postmental .... *Amphisbaena vanzolinii*, p. 444

3a (1). Scales around midbody 65 or more; supralabials 4; dorsal (upper) body color almost uniform tan to dark brown, but with a few light areas; belly light .... *Amphisbaena alba*, p. 444

3b. Scales around midbody fewer than 60; supralabials 3; body color, above and below, with patchwork of dark brown or black and light (whitish) contrasting areas .... *Amphisbaena fuliginosa*, p. 444

Key to the Lizards of Guyana

The following key is based largely on that of Avila-Pires (1995) for the lizards of Brazilian Amazonia. We followed her basic system even where no quotation marks are shown but modified wording for clarity, excluded species not documented to occur in Guyana, and added material for Guyanese lizards that were not included in Avila-Pires' book because they were not known to occur in Brazilian Amazonia. Additional references that were useful in preparing the key include Peters & Donoso-Barros (1970), Hoogmoed (1973), and Savage (2002).

1a. Top of head covered with very small, granular scales; eyelids absent, represented by a brille (disk of immovable transparent skin) covering eye..... 2

1b. Top of head with some large scales; movable eyelids usually present (although absent in *Gymnophthalmus*)..... 12

2a (1). Pupil vertical with lobed margins; toes broadened at least near base; body length (snout to vent, not including tail) may be greater than 60 mm 3

2b. Pupil round; toes not broadened at base or only slightly so; small lizards, adult snout-vent length less than 60 mm 5

3a (2). Toes broadened throughout their length; basal webbing between toes; scales on back small, of basically one size..... ..... *Thecadactylus rapicauda*, p. 447

3b. Toes broadened at base, not throughout length (Fig. 7B); no webbing between toes; scales on back (dorsum) include enlarged tubercles among the granules..... 4

4a (3). Base of fourth toe without enlarged subdigital lamellae, although present further along toe; nearly a 90° angle between fourth and fifth toes; distance between dorsal tubercles greater than width of tubercles .... *Hemidactylus mabouia*, p. 446

4b. Base of fourth toe with enlarged subdigital lamellae that continue along toe (Fig. 7B); very acute angle between fourth and fifth toes; dorsal (upper body) tubercles relatively large, distance between them equal to or less than width of tubercles..... ..... *Hemidactylus palaichthus*, p. 447

5a (2). Claws permanently exposed, with two to four scales at base (Fig. 7C); dorsal body scales granular..... 6

5b. Claws enclosed in a sheath of tiny scales, but one asymmetrically large scale may be part of sheath (or not); dorsal body scales either granular or flat and overlapping.... 9

6a (5). Ridge of skin above each eye with one very elongate spine ..... . *Gonatodes alexandermendesi*, p. 465

6b. No very elongate spine over eye ... 7

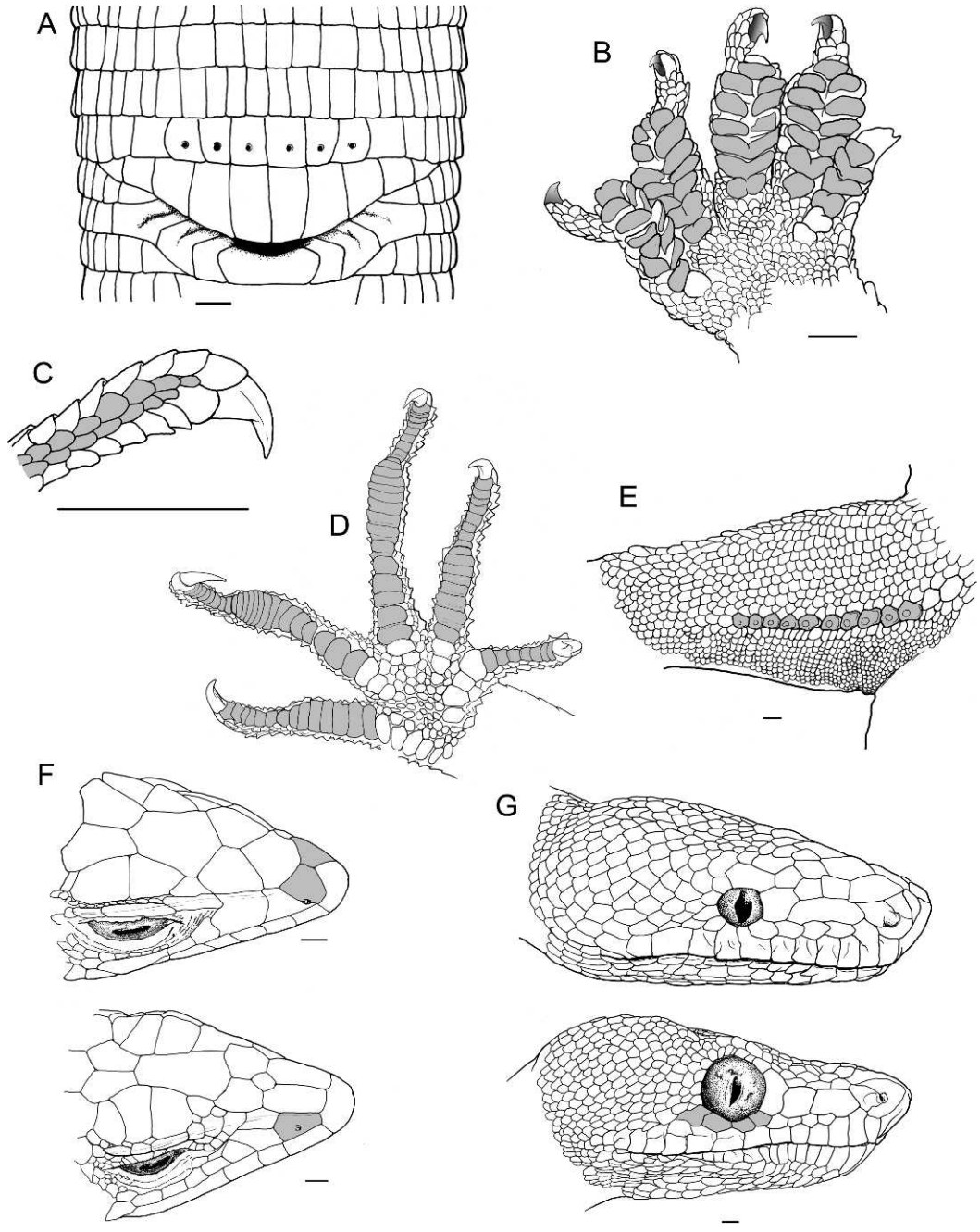

Fig. 7. A, Preanal pores, *Amphisbaena alba* (adapted from Gans 1962:11). B, Gekkonid subdigital lamellae (shaded; *Hemidactylus palaichthus*). C, Two rows of tiny scales on side of toe (shaded), *Gonatodes humeralis*. D, *Anolis planiceps* subdigital lamellae (shaded). E, Femoral pores (shaded), as in *Polychrus*. F, Nasal scales (shaded) either in contact atop snout in *Kentropyx calcarata* (above) or separated by frontonasal scales in *Neusticurus rudis* (below). G, *Epicrates cenchria* has some upper lip scales in contact with eye (above; drawing adapted from a photo by Philippe Macquet on the internet); *Corallus hortulanus* (below) does not (subocular scales shaded). Scale bars: 1 mm.

7a (6). At base of toes, scales beneath toes narrower than toes; three or four rows of tiny scales on sides of toes near toe tips; scales under tail moderately enlarged ..... *Gonatodes annularis*, p. 465

7b. At base of toes, scales beneath toes as wide as toes; two rows of tiny scales on side of toes near toe tips (Fig. 7C); scales under tail much wider than long 8

8a (7). More than 100 granules around midbody; no bold dorsal pale stripe on back; light bar near shoulder preceded by a black spot ..... *Gonatodes humeralis*, p. 466

8b. Fewer than 100 granules around midbody; light vertebral stripe (conspicuous white with black edges in males; tan or white edged with dark spots in females) from snout to base of tail..... *Gonatodes vittatus*, p. 467

9a (5). Dorsal scales, although very small, flat and overlapping 10

9b. Dorsal scales granular 11

10a (9). Dorsal scales keeled; claw sheath comprised of four scales .. .. *Chatogekko amazonicus*, p. 464

10b. Dorsal scales smooth; claw sheath comprised of five scales ... .. *Coleodactylus septentrionalis*, p. 464

11a (9). Claw sheath on toe tips includes one asymmetrically large scale; spine above eye; dorsal granular scales keeled .... *Sphaerodactylus molei*, p. 468

11b. Not as 11a .... *Pseudogonatodes guianensis*, p. 467

12a (1). Dorsal scales on head usually numerous, irregular, very small.... 13

12b. All or most dorsal head scales arranged in plates, relatively few in number and relatively large 26

13a (12). A very large, flat, round scale below ear ..... *Iguana iguana*, p. 458

13b. Not as 13a 14

14a (13). Three outer toes with projecting fringe of flat scales along their side; conspicuous, large, sail-like, narrow, dorsal fan of skin on body and tail of adult males .... *Basiliscus basiliscus*, p. 446

14b. Not as 14a 15

15a (14). Row of very distinctly enlarged scales or spines along vertebral area (middle of back)..... 24

15b. Not as 15a, although vertebral scales may be slightly enlarged in some species 16

16a (15). An extendable, thin, flat throat fan conspicuous in males (may be inconspicuous in females); most fingers and toes appear flattened top to bottom, along much of their length bearing flat pads below..... 17

16b. No throat fan, but a sac-like throat expansion may be present; toes not flattened 22

17a (16). Widened subdigital lamellae relatively narrow (usually less than twice width of toe; Fig. 7D); ventral (belly) scales relatively large, keeled, overlapping well..... 18

17b. Many subdigital lamellae very wide (clearly twice width of toe or more); ventral scales relatively small, usually smooth (but keeled in some species), overlapping little 19

18a (17). Vertebral area with 8–13 longitudinal rows of enlarged, keeled, overlapping scales, abruptly demarcated from small granular scales on sides of body; 60–90 scales around midbody..... ..... *Anolis auratus*, p. 460

18b. Two or more rows of somewhat but variably enlarged dorsal scales along vertebral area, grading in size to granules on sides; 103–175 scales around midbody..... ..... *Anolis planiceps*, p. 461

19a (17). Relatively small lizards (maximum snout-vent length 50–60 mm or less), with brown or gray body that is nearly cylindrical; tail round in cross section..... 20

19b. Relatively large (maximum snout-vent length greater than 70 mm), green or gray lizards; body and tail somewhat flattened side-to-side 21
20a (19). Enlarged scales on top of head between eyes (supraorbital semicircles) of each side of head broadly in contact between eyes; scales on posterior (rear) part of upper snout (posterior to swollen nasal regions) moderately large, smooth, and flat ..... *Anolis ortonii*, p. 461
20b. Supraorbital semicircles of each side of head separated from each other between eyes by 1–3 very small scales; scales on posterior part of upper snout relatively small or variable in size, mostly with small keels ..... *Anolis fuscoauratus*, p. 461
21a (19). Tail somewhat laterally compressed but without conspicuous crest of distinctive scales ..... *Anolis punctatus*, p. 462
21b. Tail quite laterally compressed and with conspicuous crest of enlarged scales on top ..... *Anolis aeneus*, p. 459
22a (16). Sac-like throat expansion present; crest of enlarged, pointed scales forming a central row on throat; femoral pores under thighs present (Fig. 7E); cone- or turret-shaped eyes, lids partially fused ..... *Polychrus marmoratus*, p. 462
22b. Not as 22a 23
23a (22). Tail shorter than body (snout-vent) length, somewhat flattened horizontally, very spiny ..... *Uracentron azureum*, p. 475
23b. Not as 23a ..... *Tropidurus hispidus*, p. 475
24a (15). Vertebral crest from neck to tip of tail; third and fourth fingers about of equal length ..... *Uranoscodon superciliosus*, p. 476
24b. Vertebral crest not extending beyond basal part of tail; fourth finger longer than third 25
25a (24). Body somewhat flattened horizontally; tufts of spinose scales on neck; scales around midbody 121–162 ..... *Plica plica*, p. 473
25b. Body basically cylindrical; no tufts of spinose scales on neck; scales around midbody 43–69 ..... *Plica umbra*, p. 474
26a (12). Body scales large, cycloid (with curved rear margin), overlapping, stiff, containing thin dermal bones; dorsal (upper surface) head scales also overlapping ..... *Mabuya nigropunctata*, p. 463
26b. Not as 26a; dorsal head scales not or only slightly overlapping 27
27a (26). Nasal scales (touching or containing nostrils) in contact on middorsal area of snout (Fig. 7F) .. 28
27b. Nasal scales separated by 1–2 frontonasal scales on top of snout (Fig. 7F) 33
28a (27). Ventral (belly) scales distinctly keeled 29
28b. Ventral scales smooth 31
29a (28). Median dorsal scales much larger than the lateral scales, strongly overlapping, keeled, in 13–27 longitudinal rows 30
29b. Median dorsal scales only slightly larger than the lateral scales, hexagonal, juxtaposed, keeled, not in longitudinal rows ..... *Kentropyx calcarata*, p. 471
30a (29). Enlarged dorsals slightly smaller than ventrals, the keels forming 13–17 continuous longitudinal ridges ..... *Kentropyx striata*, p. 472
30b. Enlarged dorsals much smaller than ventrals, in 22–27 longitudinal rows, keels not continuous and directed towards the median line of the back ..... *Kentropyx borckiana*, p. 471

31a (28). Maximum of ten enlarged ventrals in a row across midbody (not including smaller ventrolateral scales) 32

31b. More than 15 enlarged ventrals in a row across midbody..... ..... *Tupinambis teguixin*, p. 473

32a (31). Eight ventrals in a row across midbody .... *Cnemidophorus lemniscatus*, p. 470

32b. Ten ventrals in a row across midbody..... *Ameiva ameiva*, p. 469

33a (27). Small, almost worm-like in length, diameter, color; limbs very much reduced; no ear opening ... . *Bachia flavescens*, p. 450

33b. Not as 33a 34

34a (33). Inner finger absent or, if present, clawless 35

34b. All five fingers present, with claws 41

35a (34). Lower eyelids distinct, movable; snout-vent length may be longer than 50 mm..... 36

35b. Eyelids absent, an immovable brille (disk of transparent skin) covering eye; snout-vent length less than 50 mm 38

36a (35). Dorsal and ventral scales in two longitudinal rows of transversely enlarged scales .... *Iphisa elegans*, p. 454

36b. Dorsal, lateral, and ventral scales more similar in size 37

37a (36). Ventral scales quadrangular in shape, occurring in neat transverse and longitudinal rows .... *Riolama leucosticta*, p. 457

37b. Rear edge of ventral scales rounded or cycloid in shape..... ..... *Tretioscincus agilis*, p. 458

38a (35). Sides, arms, and legs in life coppery tan or brown, definitely not black; tail bright orange (salmon) above in females and juveniles (but tan or tannish gray in males or if regenerated or about to shed); occurs on Rupununi Savanna .... *Gymnophthalmus vanzoi*, p. 454

38b. Sides, arms, and legs in life very dark brown to black; tail gray, bluish gray, or tan above with gray iridescence; from Rupununi Savanna or not 39

39a (38). Anteriorly (toward head), dorsolateral light stripe vivid in life, yellow or pale gold; upper lip with white or otherwise light longitudinal stripe; occurs on Rupununi Savanna .... *Gymnophthalmus leucomystax*, p. 451

39b. Dorsolateral light stripe not vivid anteriorly, although more conspicuous than posteriorly; upper lip gray, black, or brown; from Rupununi Savanna and elsewhere 40

40a (39). In life, belly gray or bluish gray, with light copper iridescence; tail gray, bluish gray, rarely grayish tan above (varying with stage of molt); only females exist; from Rupununi Savanna or not ..... . *Gymnophthalmus underwoodi*, p. 452

40b. In life, belly cream to tan with copper iridescence; tail tan or reddish tan above, with gray iridescence; males and females exist; not from Rupununi Savanna, but localities north thereof .... *Gymnophthalmus* cf. *speciosus*, p. 452

41a (34). Dorsal body scales not of uniform size but with distinct enlarged tubercles or some longitudinal rows of enlarged scales; tail with a double dorsal crest or with transverse rows of tubercles 42

41b. Dorsal scales generally of uniform size; tail without crests or transverse rows of tubercles (although scales may be keeled)..... 44

42a (41). Rostral and mental scales (on frontmost tip of snout and of chin, respectively) with striations or grooves; three rows of similar-sized scales on snout between the rostral and frontal (large median

scale between eyes); a pair of scales behind the mental, not a single large postmental ..... *Echinosaura sulcarostrum*, p. 451

42b. Not as 42a 43

43a (42). Tubercles along dorsal surface of tail form a continuous double row; two transverse rows of scales on underside of tail correspond to two transverse rows on side of tail..... *Neusticurus bicarinatus*, p. 456

43b. Tubercles along dorsal surface of tail form a discontinuous row, with smaller scales in between; two transverse rows of scales on underside of tail correspond to 3–6 transverse rows on side of tail..... *Neusticurus rudis*, p. 456

44a (41). Dorsal scales in longitudinal rows on body..... *Cercosaura ocellata*, p. 451

44b. Dorsal scales in transverse rows across body or in diagonal rows on body..... 45

45a (44). Large scales atop back of head (parietals and interparietal) followed by smaller scales similar to dorsal body scales..... 46

45b. Not as 45a; distinct, somewhat enlarged occipital scales on nape of neck 48

46a (45). Large interparietal and parietal scales atop back of head form a straight margin across back of head ..... *Alopoglossus angulatus*, p. 448

46b. Interparietal and parietal scales form a curved margin across back of head 47

47a (46). Dorsal scales (on vertebral row from nape of neck back to rear edge of hind legs at hip) number 30–35; interparietal scale (largest scale atop back of head) very wide, with diverging lateral margins; males and females exist ..... *Leposoma guianense*, p. 455

47b. Dorsal scales number 35–40; interparietal scale usually not as wide, with lateral margins parallel or slightly diverging; only females exist ..... *Leposoma percarinatum*, p. 455

48a (45). Interparietal scale extends somewhat posteriorly beyond the parietal scales, these all followed by occipital scales on nape of neck, these in turn followed by smaller scales of back..... 49

48b. Interparietal and parietal scales forming a straight margin across back of head..... 50

49a (48). Head black, including upper lip scales; belly scales (ventrals) broadly keeled; one frontonasal scale atop snout between scales with nostrils ..... *Pantepuisaurus rodriguesi*, p. 457

49b. Head brown, but upper lip scales contrasting white; ventrals smooth; frontonasal scale divided, with one on each side of midline of snout ..... *Cercosaura argulus*, p. 450

50a (48). Nasal scales divided (=nostril between two scales); ventral scales hexagonal, in transverse rows but not longitudinal rows ..... *Kaieteurosaurus hindsi*, p. 455

50b. Nostril within one scale; ventrals quadrangular, in both transverse and longitudinal rows..... 51

51a (50). Four large supraocular scales (above eye) on each side 52

51b. Three large supraoculars, each side.... *Arthrosaura reticulata*, p. 449

52a (51). Lower eyelid with semitransparent disc; 45 scales around midbody; 40–42 keeled temporal scales (on side of head between postoculars and ear) ..... *Arthrosaura guianensis*, p. 448

52b. Lower eyelid with opaque disc; 37 scales around midbody; 32–33 smooth temporals..... *Arthrosaura hoogmoedi*, p. 449

Key to the Genera and Most Species of Snakes of Guyana

Be respectful in the presence of living snakes. Rattlesnakes, other pit vipers, and coral snakes, whether of colorful species or not, are highly venomous and dangerous to humans, as may be a few other species. Also, some of the characters used in this key require getting very close to the animal or picking it up. Therefore, people who are not fully familiar with proper procedures for safe handling of venomous snakes should not try to use this key to identify living snakes. In addition, snakes that were killed apparently recently, and perhaps found dead on the road, sometimes are capable of biting in a reflex action when handled, so these also should be handled only with the utmost care, to avoid a medical emergency.

Many of the genera of snakes that occur in Guyana are represented by only one or two species that occur in the country (e.g., *Boa*, *Crotalus*). For those genera, the Guyanese species can be identified with the key immediately below. For most genera having more representatives in Guyana (*Atractus*, *Chironius*, *Dipsas*, *Liophis*, *Micrurus*, and *Oxyrhopus*), this key will lead users to the relevant genus and then refer to specific generic keys that follow.

In some instances, a genus or species will appear in more than one place in the key. This reflects intrageneric or intraspecific variation in key characters, such as whether the number of scale rows around midbody is 17 or fewer. Variation in Guyanese snakes also necessitates using some characters that are difficult to see. While it would be convenient, it is not possible to design a key based only on conspicuous characters that are readily apparent to everyone, including non-specialists. Consequently, reference is of necessity made to some characters that are best viewed with magnification, preferably with a dissecting microscope (e.g., apical pits on upper body scales; grooves on rear maxillary teeth). Reference also is made to hemipenes. These are the copulatory organs of males, which are stored in the base of the tail, paired (one on each side), and may be everted through the anal opening of specimens found dead on the road or preserved in museum collections. Characteristics of hemipenes can be very important in snake taxonomy. When preserving specimens, it is advisable to fully evert the hemipenes so they will be visible for later examination.

This key is based largely on that of Peters & Orejas-Miranda (1970). In addition, the following references were especially helpful: Dixon & Hendricks (1979), Chippaux (1986), Savage (2002), Campbell & Lamar (2004), and Duellman (2005).

1a. One deep pit on each side of face between nostril and eye 2
1b. Not as 1a 6
2a (1). Rattle or button of keratin on tip of tail .... *Crotalus durissus*, p. 522
2b. No rattle or button of keratin on tip of tail 3
3a (2). Scales of posterior subcaudals (under tail, near tip) finely subdivided; keels on middorsals (upper body scales) tubercular or knobby ..... *Lachesis muta*, p. 523
3b. Posterior subcaudal scales single or paired across underside of distal tail; keels (ridges) on middorsal scales not knobby or tubercular 4
4a (3). Upper body background color green; yellow stripe low on each side of body .... *Bothriopsis bilineata*, p. 519
4b. Body not green above; no yellow stripe on each side 5
5a (4). Distinct dark stripe behind eye; usually fewer than 18 dark blotches on body (before vent) ... . *Bothrops atrox*, p. 520

5b. Stripe behind eye absent or indistinct; usually more than 18 dark blotches on body .... *Bothrops brazili*, p. 521
6a (1). More than 31 scales around midbody (between head and vent).. 7
6b. Scales around midbody 30 or fewer 11
7a (6). All scales on top of snout small, same size as those on top of head; one longitudinal dark stripe on top of head..... ..... *Boa constrictor*, p. 478
7b. Small scales on top of head, but with somewhat enlarged scales between and behind nostrils; head color pattern not as above 8
8a (7). No pits in labials (scales on lips); top of head dark brown with broad tan or orange stripe behind eye ..... *Eunectes murinus*, p. 480
8b. Pits in lip scales; head color pattern not as 8a..... 9
9a (8). Some scales of upper lip contact eye (Fig. 7G); fewer than 10 scales between the eyes across top of head ..... *Epicrates cenchria*, p. 480
9b. Upper lip scales separated from eye by small scales below eye (Fig. 7G); 10 scales or more between eyes across top of head 10
10a (9). Adults with green upper body (juveniles orange or yellow) with white cross-bars..... ..... *Corallus caninus*, p. 478
10b. Upper body brown, gray, or yellow, possibly with dark saddles edged in cream..... ..... *Corallus hortulanus*, p. 479
11a (6). Belly scales (ventrals) much wider than long; 4 scales or more around eye..... 20
11b. Belly scales same size as upper body scales or slightly widened; eye contained in or under a single scale..... 12
12a (11). Belly scales slightly widened; body color red with black rings .. .. *Anilius scytale*, p. 477
12b. Belly scales same size as upper body scales; body color not as above..... 13
13a (12). Scales around midbody 14; body very slender and short 14
13b. Scales around midbody 15 or more; usually stockier and longer snakes 17
14a (13). Enlarged supraocular scales (atop head, between eyes, and in contact with transparent scales covering eyes)..... 15
14b. Enlarged supraoculars absent; scales around middle of tail 10 to 12; upper body background color light, with dark brown stripes .... *Siagonodon septemstriatus*, p. 516
15a (14). Supraoculars rather large, larger than scales (prefrontal and frontal) centered on top of head; upper body color of wide dark stripes separated by inconspicuous, narrow light lines; small yellow spot on tip of snout and tip of tail ..... *Epictia albifrons*, p. 516
15b. Supraoculars smaller than prefrontal and frontal..... 16
16a (15). Four scales plus rostral (scale on tip of upper snout) form border of upper lip on each side; belly without reticulate color pattern ... . *Tricheilostoma dimidiatum*, p. 517
16b. Five scales plus rostral form border of upper lip on each side; reticulate color pattern on belly .. .... *Tricheilostoma macrolepis*, p. 517
17a (13). Head covered with small scales same size as those on body ..... *Typhlophis squamosus*, p. 477
17b. Head with plates larger than scales on body 18
18a (17). Scales around midbody 18. ..... *Typhlops minuisquamus*, p. 518
18b. Scales around midbody 20..... 19
19a (18). White snout and white tail ring; dorsum (upper body) dark brown to black; 9 upper rows of body scales pigmented .... *Typhlops reticulatus*, p. 518

19b. No white snout or tail ring; dorsum yellowish brown; usually 11 dorsal scale rows pigmented... ..... *Typhlops brongersmianus*, p. 517
20a (11). About one head length in front of vent, upper body (dorsal) scale rows at least 2 fewer than around midbody, not counting wide belly scale 21
20b. Dorsal scale rows same number throughout body, rarely reduced in number immediately before vent .. 23
21a (20). Dorsal scales in even number of rows around body, not counting wide belly scale..... 22
21b. Dorsal scales in odd number of rows around body 47
22a (21). Dorsal scale rows around midbody 12 or fewer ..... see separate key for genus *Chironius*, p. 364
22b. Dorsal scale rows around midbody 14 or more..... ..... *Spilotes pullatus*, p. 507
23a (20). More than 18 dorsal scale rows at midbody..... 24
23b. Fewer than 18 dorsal scale rows at midbody 25
24a (23). Fewer than 200 ventrals (wide belly scales from neck to vent); scales around midbody 21 ..... *Ninia hudsoni*, p. 500
24b. Ventrals more than 200; scales around midbody 19..... ..... *Clelia clelia*, p. 488
25a (23). Vent covered by one scale as wide as belly scales before it 36
25b. Anal scale divided into side-by-side halves..... 26
26a (25). Dorsal scale rows at midbody 17..... 27
26b. Dorsal scale rows at midbody fewer than 17..... 28
27a (26). Neck extremely thin, head very distinct from it; uppermost row of body scales distinctly wider than scales of adjacent rows..... ..... *Imantodes cenchoa*, p. 495
27b. Not as 27a .... *Mastigodryas boddaerti*, p. 499
28a (26). Rings of color completely, or nearly completely, encircle body..... 34
28b. Body without complete rings of color 29
29a (28). Venomous coral snake with upper body black or brown and, on belly, white or yellow half-rings (red under tail); frontmost upper tooth hollow (with venom canal) ..... *Micrurus collaris*, p. 512
29b. Not as 29a 30
30a (29). On each side, largest scale atop head behind eye (parietal scale) contacts some scales of upper lip (supralabials)..... ..... *Apostolepis nigrolineata*, p. 482
30b. Parietal scale separated from supralabials by one or two rows of scales 31
31a (30). Atop snout, internasal scales (between nostrils) fused into one plate across snout..... ..... *Pseudoeryx plicatilis*, p. 505
31b. Internasals paired, one on each side..... 32
32a (31). Neck extremely thin, with head very distinct from it; uppermost row of body scales distinctly wider than scales of adjacent rows ..... *Imantodes lentiferus*, p. 495
32b. Not as 32a 33
33a (32). Fewer than 170 wide belly scales (ventrals) from neck to vent ..... *Tantilla melanocephala*, p. 508
33b. Ventrals more than 170 ..... *Elapomorphus quinquelineatus*, p. 493
34a (28). Small scale (loreal) present (Fig. 8D) on side of face between nasal scale (enclosing or contacting nostril) and preocular scale (in front of eye) .... *Erythrolamprus aesculapii*, p. 493
34b. Loreal scale absent (Fig. 8D), nasal contacts preocular..... 35
35a (34). Venomous coral snake; frontmost upper tooth hollow

(with venom canal)..... see separate key for genus *Micrurus*, p. 366

35b. Frontmost upper tooth lacks venom canal ..... *Hydrops triangularis*, p. 495

36a (25). Upper body scale rows 17 around midbody 42

36b. Upper body scale rows fewer than 17 at midbody 37

37a (36). Uppermost longitudinal row of body scales (vertebrals) distinctly larger than scales of adjacent rows 38

37b. Scales of vertebral row on body about same size as those of adjacent rows 40

38a (37). Shallow longitudinal groove or depression (mental groove) present behind chin in middle of underside of head (Fig. 8A) 39

38b. Mental groove absent (Fig. 8A). .. see separate key for genus *Dipsas*, p. 365

39a (38). A labial scale (on upper lip) behind eye is enlarged (Fig. 8B), higher than other labials and in contact with postocular scale (immediately behind eye), anterior temporal (behind postocular), and posterior temporal (behind anterior temporal)..... *Sibon nebulatus*, p. 506

39b. Not as 39a ..... *Imantodes lentiferus*, p. 495

40a (37). Upper body scales with pair of small, subtle pits or depressions (apical pits) near rear of scale (Fig. 8C), best seen with magnification ..... *Drymoluber dichrous*, p. 493

40b. Apical pits absent 41

41a (40). Upper jaw teeth (on maxillary bone) solid, without hollow venom canal or open venom groove ..... *Drepanoides anomalus*, p. 492

41b. Venomous coral snake, with frontmost maxillary tooth hollow, with enclosed venom canal .... see separate key for genus *Micrurus*, p. 366

42a (36). Across top of snout, prefrontal scales (in front of frontal scale, the single large plate between the eyes) fused into one scale..... ..... *Xenopholis scalaris*, p. 511

42b. Prefrontals not fused, but paired, one on each side of snout 43

43a (42). Scales beneath tail (subcaudals) paired, one on each side 44

43b. Subcaudals single, one wide scale across underside of tail..... ..... *Pseudoboa coronata*, p. 504

44a (43). Upper body scales with a keel..... *Ninia hudsoni*, p. 500

44b. Upper body scales smooth, without a keel..... 45

45a (44). A labial scale (on upper lip) behind eye is enlarged (Fig. 8B), higher than other labials and in contact with postocular (immediately behind eye), anterior temporal (behind postocular), and posterior temporal (behind anterior temporal) ..... *Sibon nebulatus*, p. 506

45b. Not as 45a 46

46a (45). More than 200 wide belly scales (ventrals) neck to vent .... *Clelia clelia*, p. 488

46b. Fewer than 200 ventrals .... see separate key for genus *Atractus*, p. 364

47a (21). Some or all upper body scales with a keel 88

47b. Upper body scales smooth, without a keel..... 48

48a (47). Vent covered by one scale as wide as belly scales before it 65

48b. Anal scale divided into side-by-side halves 49

49a (48). Scales of uppermost longitudinal row on body (vertebrals) distinctly larger than scales of adjacent rows 50

49b. Scales of vertebral row about same size as those of adjacent rows 51

50a (49). Upper body scale rows 15 around midbody .... *Imantodes lentiferus*, p. 495

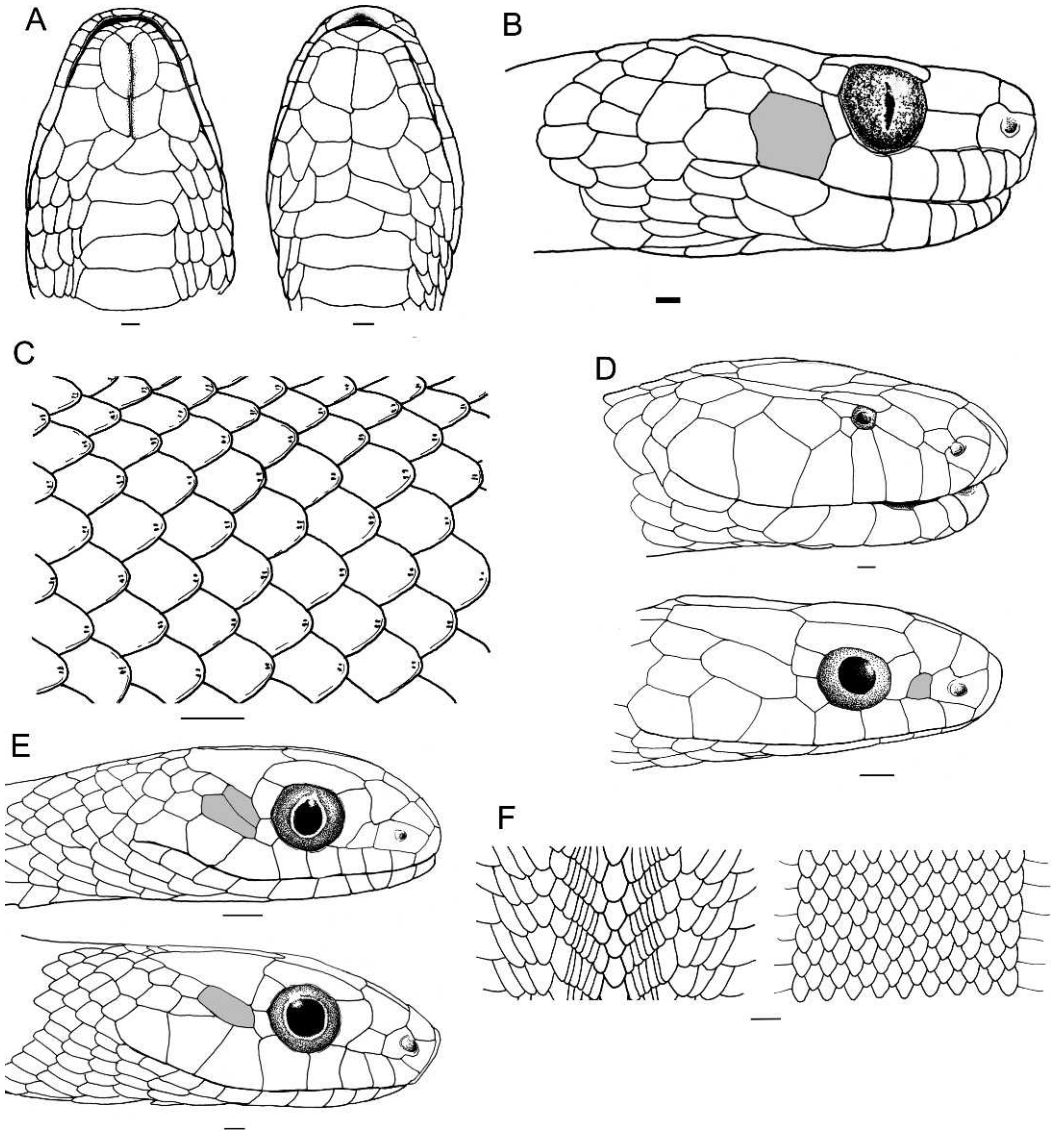

Fig. 8. A, Inconspicuous mental groove either present behind chin (shaded), *Sibon nebulatus* (left) or absent, *Dipsas catesbyi* (right). B, Enlarged labial scale (shaded) behind eye, *Sibon nebulatus*. C, Tiny apical pits on rear of body scales, *Philodryas*. D, Loreal scale (shaded) either present, *Erythrolamprus aesculapii* (below; with large eye) or absent, *Micrurus* (above; with small eye). E, Anterior temporal scales (shaded) either 2 as in a *Thamnodynastes* (above) or 1, *Philodryas* (below); both adapted from photos by W. Wüster on the internet. F, Body scales in either extremely oblique rows, *Xenodon* (left) or not, most snakes (right). Scale bars: A–D = 1 mm, E, F = 2 mm.

50b. Upper body scale rows 17 at midbody.... *Imantodes cenchoa*, p. 495

51a (49). Small scale (loreal) present (Fig. 8D) on side of face between nasal scales (enclosing or contacting nostril) and preocular scale (in front of eye) 54

51b. Loreal scale absent (Fig. 8D) 52

52a (51). Very elongate head with pointed snout 53

52b. Head and snout not as 52a .... *Hydrops triangularis*, p. 495
53a (52). Upper body color mainly tan or brown .... *Oxybelis aeneus*, p. 500
53b. Upper body color bright green . ..... *Oxybelis fulgidus*, p. 501
54a (51). Two or more anterior temporal scales (Fig. 8E), which are behind and in contact with postoculars (behind and in contact with eye) and between upper lip scales (supralabials) and parietal (rearmost large plate atop head) 61
54b. One anterior temporal (Fig. 8E) or none..... 55
55a (54). Upper body scale rows around midbody 17 or fewer..... 60
55b. Upper body scale rows at midbody more than 17..... 56
56a (55). Upper body scale rows extremely oblique (Fig. 8F), as scales of lateral rows (on sides) much narrower than those of upper and lower rows..... 57
56b. Upper body scale rows not so oblique, but as in most other snakes (Fig. 8F) 58
57a (56). Upper body scales in 19 or fewer rows at midbody..... ..... *Xenodon merremii*, p. 510
57b. Upper body scales in 21 or more rows at midbody..... ..... *Xenodon severus*, p. 510
58a (56). Upper body scales with one or two small, subtle pits or depressions (apical pits) near rear of scale (Fig. 8C), best seen with magnification 59
58b. Apical pits absent ..... see separate key for genus *Liophis*, p. 365
59a (58). Belly scales, neck to vent, more than 205 .... *Philodryas viridissimus*, p. 503
59b. Belly scales fewer than 205 .... *Philodryas olfersii*, p. 503
60a (55). Upper body scales with a pair of small, subtle pits or depressions (apical pits) near rear of scale (Fig. 8C), best seen with magnification..... *Leptodeira annulata*, p. 496
60b. Apical pits absent ..... see separate key for genus *Liophis*, p. 365
61a (54). Rearmost one or two teeth on maxillary bone with venom groove..... 62
61b. Rear maxillary teeth not grooved ..... *Mastigodryas boddaerti*, p. 499
62a (61). Upper body scales with one or two small, subtle pits or depressions (apical pits) near rear of scale (Fig. 8C), best seen with magnification 64
62b. Apical pits absent 63
63a (62). Usually 17 scales around midbody; paired scales beneath tail (subcaudals) of males 85–100, of females 78–97; male hemipenes lack enlarged basal hooks, but have numerous small spines..... ..... *Thamnodynastes pallidus*, p. 508
63b. Usually 19 scales around midbody; subcaudals of males 61–64, of females 54–61; male hemipenes have several basalmost spines noticeably enlarged..... ..... *Thamnodynastes ramonriveroi*, p. 509
64a (62). Belly scales, neck to vent, more than 205 .... *Philodryas viridissimus*, p. 503
64b. Belly scales fewer than 205 .... *Philodryas olfersii*, p. 503
65a (48). Upper body (dorsal) scale rows fewer than 17 around midbody..... see separate key for genus *Dipsas*, p. 365
65b. Dorsal scale rows 17 or more around midbody..... 66
66a (65). Dorsal scale rows 17 at midbody..... 67
66b. Dorsal scale rows 19 or more at midbody..... 73
67a (66). Body with longitudinal stripes, although may be subtle... ..... *Thamnodynastes pallidus*, p. 508
67b. Body without stripes 68

68a (67). Upper body scale rows extremely oblique (Fig. 8F), as scales of lateral rows (on side) much narrower than those of upper and lower rows. . . . . *Xenodon merremii*, p. 510

68b. Upper body scale rows not so oblique, but as in most other snakes (Fig. 8F) 69

69a (68). Shallow longitudinal groove or depression (mental groove) present behind chin in middle of underside of head (Fig. 8A) 70

69b. Mental groove absent (Fig. 8A) . . see separate key for genus *Dipsas*, p. 365

70a (69). Rearmost one or two teeth on maxillary bone (upper jaw) with venom groove 71

70b. Rear maxillary teeth not grooved 72

71a (70). Scales beneath tail (subcaudals) paired, one on each side . . . . . *Clelia clelia*, p. 488

71b. Subcaudals single, one wide scale across underside of tail. . . . . *Pseudoboa coronata*, p. 504

72a (70). Belly scales, neck to vent, more than 180 . . . . . *Drymarchon corais*, p. 492

72b. Belly scales, neck to vent, fewer than 180 . . . . . *Drymoluber dichrous*, p. 493

73a (66). Frontmost scale atop tip of snout turned up into a sharp point . . . . . *Phimophis guianensis*, p. 503

73b. Not as 73a 74

74a (73). Two or more anterior temporal scales (Fig. 8E), which are behind and in contact with postoculars (behind and in contact with eye) and between upper lip scales (supralabials) and parietal (rearmost large plate atop head) 79

74b. Only one anterior temporal scale on each side (Fig. 8E). 75

75a (74). Body relatively heavy; upper body scale rows extremely oblique (Fig. 8F), as scales of lateral rows much narrower than those of upper and lower rows. 77

75b. Body more slender; upper body scale rows not so oblique, as in most other snakes (Fig. 8F) 76

76a (75). Scales beneath tail (subcaudals) paired, one on each side . . . . see separate key for genus *Oxyrhopus*, p. 366

76b. Subcaudals single, one wide scale across underside of tail. . . . . *Pseudoboa neuwiedii*, p. 504

77a (75). Scales around midbody 17–19 78

77b. Scales around midbody 21–23 . . . . . *Xenodon severus*, p. 510

78a (77). Teeth on maxillary bone fewer than 10, including 2 enlarged ones at rear (ungrooved) . . . . . *Xenodon merremii*, p. 510

78b. Maxillary teeth 15 or more . . . . . *Xenodon rabdocephalus*, p. 510

79a (74). Rearmost one or two teeth on maxillary bone (upper jaw) with venom groove 80

79b. Rear maxillary teeth not grooved 85

80a (79). Uppermost longitudinal row of body scales (vertebrals) distinctly larger than scales of adjacent rows . . . . . *Siphlophis compressus*, p. 507

80b. Scales of vertebral row about the same size as those of adjacent rows 81

81a (80). Scales beneath tail (subcaudals) single, with one wide scale across underside of tail. . . . . *Pseudoboa neuwiedii*, p. 504

81b. Most or all subcaudals paired, one on each side 82

82a (81). All head scales with light edges; sides of body pale yellow with irregular vertical black marks; subtle diffuse orange-red middorsal stripe present length of body; on lower jaw (mandible), tooth numbers 3 through 5 (counted from front) very much enlarged . . . . . *Siphlophis cervinus*, p. 507

82b. Coloration not as 82a; frontmost mandibular teeth only somewhat enlarged if at all, tooth length decreasing toward rear of bone.... 83
83a (82). Belly scales (ventrals), neck to vent, more than 200; body coloration not a series of dark crossbands..... *Clelia clelia*, p. 488
83b. Ventrals fewer than 200, or if more, body coloration with dark crossbands that do not cross belly. 84
84a (83). Body coloration with dark crossbands that do not cross belly; belly unmarked ..... see separate key for genus *Oxyrhopus*, p. 366
84b. Body coloration with dark stripes or spots; belly with dark stripes .. .. *Thamnodynastes ramonriveroi*, p. 509
85a (79). Upper body scales with a pair of small, subtle pits or depressions (apical pits) near rear of scale (Fig. 8C), best seen with magnification 86
85b. Apical pits absent .... *Hydrodynastes bicinctus*, p. 494
86a (85). All upper body scales smooth, not keeled..... ..... *Xenodon rabdocephalus*, p. 510
86b. At least uppermost body scales keeled (with ridge) 87
87a (86). All upper body scales keeled except in lowermost row; usually 3 small scales contact rear edge of eye (postoculars); usually more than 210 belly scales, neck to vent ..... *Pseustes sulphureus*, p. 506
87b. Scales of several lower body rows usually smooth, not keeled; usually 2 postoculars; usually fewer than 210 belly scales .... *Pseustes poecilonotus*, p. 505
88a (47). Vent covered by one scale as wide as belly scales in front of it... 94
88b. Anal scale divided into side-by-side halves..... 89
89a (88). Upper body (dorsal) scale rows more than 17 around midbody..... 90
89b. Dorsal scale rows 17 or fewer at midbody..... 91
90a (89). Upper body pattern with colorful rings, including red, around body; upper body scales with a pair of small, subtle pits or depressions (apical pits) near rear of scale (Fig. 8C), best seen with magnification .... *Rhinobothryum lentiginosum*, p. 506
90b. Upper body coloration without colorful rings including red, but dark brown bands present; apical pits absent ..... *Helicops angulatus*, p. 494
91a (89). Upper body scale rows 17 around midbody 92
91b. Upper body scale rows 15 at midbody..... *Leptophis ahaetulla*, p. 496
92a (91). Very elongate head with pointed snout..... 93
92b. Head not as 92a..... ..... *Drymobius rhombifer*, p. 492
93a (92). Upper body color mainly tan or brown ..... *Oxybelis aeneus*, p. 500
93b. Upper body color bright green . ..... *Oxybelis fulgidus*, p. 501
94a (88). Upper body (dorsal) scale rows around midbody 17 95
94b. Dorsal scale rows at midbody more than 17 96
95a (94). Snout relatively very long and pointed; body with 3 conspicuous dark longitudinal stripes, one along vertebral area (atop body), one on each side..... ..... *Xenoxybelis argenteus*, p. 511
95b. Not as 95a .... *Dendrophidion dendrophis*, p. 489
96a (94). All dorsal scales keeled (with ridge) except in lowermost row; usually 3 small scales contact rear edge of eye (postoculars); usually more than 210 belly scales, neck to vent ..... *Pseustes sulphureus*, p. 506
96b. Scales of several lower rows of dorsals usually smooth, not keeled; usually 2 postoculars; usually fewer than 210 belly scales .... *Pseustes poecilonotus*, p. 505

Key to Snakes of the Genus *Atractus* of Guyana

The following key is based largely on information provided by Peters & Orejas-Miranda (1970), Chippaux (1986), and Kok (2006a).

1a. Upper body (dorsal) scale rows 15 around midbody, excluding wide belly scale 2
1b. Dorsal scales 17 around midbody .. 3
2a (1). Upper body color pattern with 3 or 4 longitudinal dark stripes; wide belly scales, neck to vent, 125–150; paired scales of underside of tail (subcaudals) fewer than 20 ..... *Atractus trilineatus*, p. 485
2b. Upper body pattern lacks well-defined dark stripes; wide belly scales 153–163; subcaudals more than 20 ... *Atractus tamessari*, p. 484
3a (1). Paired scales of underside of tail (subcaudals) more than 55; mental scale (foremost one on lower jaw) in contact at rear with paired, central chinshields; belly pattern of dark crossbands .... *Atractus favae*, p. 483
3b. Subcaudals fewer than 55; mental scale separated from chinshields by medial contact of first pair of lower lip scales (infralabials) on each side 4
4a (3). Usually two upper lip scales (supralabials) contact preocular (scale immediately in front of eye on side of face) 5
4b. Three supralabials contact preocular..... *Atractus torquatus*, p. 485
5a (4). Upper body color brown with black rectangular markings..... ..... *Atractus schach*, p. 483
5b. Upper body unicolor and dark (but broad dark stripes may appear over time in preservative) .... *Atractus steyermarki*, p. 484

Key to Snakes of the Genus *Chironius* of Guyana

The following key is based primarily on information provided by Dixon et al. (1993) and Kok (2010b).

1a. Upper body (dorsal) scales 10 around midbody, excluding wide belly scale 2
1b. Dorsal scales 12 at midbody 4
2a (1). Dorsal scales in longitudinal rows to each side of uppermost (vertebral) row with a keel (ridge; may be very subtle, but present) ..... *Chironius fuscus*, p. 487
2b. Dorsal scales smooth 3
3a (2). No light crossbands on body; loreal scale distinctly longer than high; small apical pits on scales on neck..... ..... *Chironius scurrulus*, p. 488
3b. Light crossbands on body; loreal about as high as long (perhaps slightly longer); no apical pits .... *Chironius challenger*, p. 486
4a (1). Anal plate entire..... ..... *Chironius exoletus*, p. 486
4b. Anal plate divided..... 5
5a (4). Subcaudal scales (beneath tail) yellow and outlined in black or dark brown; dorsal scales with light flecks or presence of a broad reddish brown stripe on each side on forward part of body .... *Chironius carinatus*, p. 485
5b. Subcaudals may be yellow, but not completely outlined in black or dark brown; dorsal coloration not as in 5a..... 6
6a (5). Dorsal color uniform, without distinct stripes or spots..... ..... *Chironius exoletus*, p. 486
6b. Dorsum brown or olive with light vertebral stripe edged in darker brown or olive..... ..... *Chironius multiventris*, p. 487

Key to Snakes of the Genus *Dipsas* of Guyana

The following key is based largely on information provided by Peters & Orejas-Miranda (1970) and MacCulloch & Lathrop (2004a).

1a. Dorsal (upper body) pattern of rounded, dark-brown or black blotches or saddles with interspaces tawny brown 2
1b. Not as 1a 4
2a (1). Dorsal scales 15 around midbody, not counting wide belly scale ..... *Dipsas copei*, p. 490
2b. Dorsal scales 13 at midbody 3
3a (2). Blotches saddle-shaped, wider at vertebral row (atop body) than laterally (on sides) .... *Dipsas pavonina*, p. 491
3b. Blotches narrower at vertebral row (may not meet there) than laterally ..... *Dipsas catesbyi*, p. 489
4a (1). Dorsal blotches triangular or lozenge-shaped, usually widest at ventrals (edges of wide belly scales), with yellow spot between corners of blotches at ventrals .. .. *Dipsas indica*, p. 490
4b. Not as 4a 5
5a (4). Dorsal ground color of light browns and tans, with narrow blotches higher than wide, much narrower than interspaces (at least posteriorly or toward rear); upper lip scales (supralabials) 7–10; chinshields (paired median scales of underside of head in front of wide belly scales) in 2 or 3 pairs .... *Dipsas variegata*, p. 491
5b. Dorsal color pattern not as 5a; supralabials 6, last elongate; chinshields in 4 pairs; from Mt. Ayanganna .... *Dipsas pakaraima*, p. 490

Key to Snakes of the Genus *Liophis* of Guyana

The following key is based largely on Dixon (1989).

1a. One head length in front of vent, scale rows around body at least 2 fewer than around midbody (between head and vent), excluding wide belly scale 2
1b. Scale rows one head length in front of vent same count as around midbody ..... *Liophis reginae*, p. 499
2a (1). Dorsal (upper) body scale rows 17 around midbody 3
2b. Dorsal scale rows 19 at midbody .. 8
3a (2). Upper lip scales (supralabials), not counting rostral scale (at tip of upper snout), usually 7 .... *Liophis breviceps*, p. 497
3b. Supralabials 8 4
4a (3). Belly with checkered pattern of black and red or yellow 5
4b. Belly not checkered with black and red or yellow, but occasionally with black marks on sides of ventrals (belly scales) 7
5a (4). Black stripe on side at rear of body, extending onto tail .... *Liophis reginae*, p. 499
5b. Not as 5a 6
6a (5). Upper body with pattern of bands, sometimes reticulations; belly and underside of tail checkered with black and red or yellow, seen as dark bands or partial bands in older preserved specimens .... *Liophis cobella*, p. 497
6b. Salt and pepper dorsal pattern, obscure in Amazon populations; belly and underside of tail not as 6a ..... *Liophis miliaris*, p. 498
7a (4). Belly scales edged with black on sides ..... *Liophis miliaris*, p. 498
7b. Belly scales unmarked on sides .. .. *Liophis reginae*, p. 499

8a (2). One head length in front of vent, scale rows around body only 2 fewer than around midbody .... *Liophis lineatus*, p. 498
8b. One head length in front of vent, scale rows around body 4 fewer than around midbody 9
9a (8). Upper body (dorsum) bright green ..... *Liophis typhlus*, p. 499
9b. Dorsum usually brown to nearly black, not green .... *Liophis poecilogyrus*, p. 498

Key to Most Snakes of the Genus *Micrurus* of Guyana

One of the species of coral snakes, *Micrurus collaris*, formerly placed in the genus *Leptomicrurus*, was included in the larger key to the snakes, above. The following key is based primarily on information provided by Campbell & Lamar (2004).

1a. Black rings in triads (groups of black-white [or yellow]-black-white-black) separated by red bands, perhaps best visible on belly 2
1b. Black rings not in triads 4
2a (1). Vent covered by one scale as wide as belly scales in front of it ..... *Micrurus hemprichii*, p. 513
2b. Anal plate divided into side-by-side halves 3
3a (2). Head scales red but outlined with black .... *Micrurus surinamensis*, p. 515
3b. Head scales not outlined with black ..... *Micrurus lemniscatus*, p. 514
4a (1). Red rings very wide; no black ring around neck right behind head; black rings on body relatively very narrow .... *Micrurus averyi*, p. 512
4b. Red rings about as wide as black rings but red ones may be apparently absent or reduced in size; black ring present around neck; black rings not relatively narrow, about as wide as red ones or wider ..... *Micrurus psyches*, p. 514

Key to Snakes of the Genus *Oxyrhopus* of Guyana

The following key is based primarily on information provided by Bailey (in Peters & Orejas-Miranda 1970), Starace (1998), and Zaher & Caramaschi (1992).

1a. Snout black, but may have light spots; preocular scale (in front of and contacting eye) in contact with frontal scale (large plate atop head between eyes); 10 scales along lower lip (infralabials), not counting median foremost scale (mental); adults with bands on body, but older adults may be melanistic 2
1b. Snout yellow or cream; supraocular scale (above eye) separates preocular from frontal; 9 infralabials; body reddish with cream bands in juveniles, but bands absent or obscure in adults .... *Oxyrhopus occipitalis*, p. 502
2a (1). Upper body (dorsal) black bands in triads (black-white-black-white-black, separated by red or yellow bands), at least toward rear of body .... *Oxyrhopus melanogenys*, p. 501
2b. Dorsal bands alternating red (may be orange or yellow) and black, not in triads .... *Oxyrhopus petolarius*, p. 502

Key to the Testudinata (Turtles and Tortoises) of Guyana

The characters used in the following key are based on information presented by Pritchard (1964), Ernst & Barbour (1989), and Duellman (2005).

1a. Arms and legs flattened as oar-like flippers (sea turtles) 2
1b. Not as 1a 6
2a (1). Top of shell covered with leathery skin and having 7 conspicuous longitudinal ridges. . . . . *Dermochelys coriacea*, p. 528
2b. Top of shell bone-hard and lacking 7 conspicuous longitudinal ridges. 3
3a (2). Pleural scutes on upper shell (scutes beside those along midline) 4 on each side; cervical scute (frontmost one on edge of upper shell) not in contact with first pleural on either side. 4
3b. Pleural scutes 5 or more on each side; cervical scute contacts first pleural on each side. 5
4a (3). One pair of elongate prefrontal scales atop head behind nasal scales and between eyes; large plates of upper shell not overlapping; rear edge of upper shell smooth; head broader, beak rounded (viewed from above) . . . . . *Chelonia mydas*, p. 526
4b. Two pairs of prefrontal scales; large plates of upper shell overlapping; rear edge of upper shell serrated; head narrower, beak bluntly pointed (viewed from above) . . . . . *Eretmochelys imbricata*, p. 527
5a (3). Underside of bridge (connecting upper and lower shells on sides) with 3 inframarginal scales (on bridge beside lower shell); upper shell somewhat elongate (viewed from above); head relatively large . . . . . *Caretta caretta*, p. 526
5b. Underside of bridge with 4 inframarginal scales; upper shell nearly round (viewed from above); head relatively small. . . . . *Lepidochelys olivacea*, p. 527
6a (1). To hide head, neck is pulled straight back into shell. 7
6b. To hide head, neck is bent sideways to lie along edge of shell. 10
7a (6). Webbing between toes; legs not elephantine or columnar 8
7b. Toes not webbed but stout; legs elephantine or columnar 9
8a (7). Red lines on head; 12 or 13 large scutes on lower shell. . . . . *Rhinoclemmys punctularia*, p. 528
8b. No red on head; large scutes on lower shell fewer than 12. . . . . *Kinosternon scorpioides*, p. 529
9a (7). Background color of upper shell brown; light spots on arms yellow or orange; viewed from above, sides of upper shell straight in both sexes. . . . . *Chelonoidis denticulata*, p. 531
9b. Background color of upper shell more of a black than brown; light spots on arms red; viewed from above, sides of upper shell of males indented as if constricted by a large rubber band . . . . . *Chelonoidis carbonaria*, p. 530
10a (6). A single, usually small, central, nuchal (=cervical) scute on front edge of upper shell (Fig. 9) . . 12
10b. No central nuchal scute on front edge of upper shell (Fig. 9). 11
11a (10). Upper shell relatively flat and widest posterior to (behind) center; usually two barbels on chin near front of lower jaw; upper jaw rather squared off, not notched in front; groove on head between eyes . . . . . *Podocnemis expansa*, p. 529
11b. Upper shell relatively domed and widest at midbody; usually one barbel on chin near front of lower jaw; upper jaw distinctly notched; no groove between eyes . . . . . *Podocnemis unifilis*, p. 530
12a (10). Bizarre turtle with enormous head of broadly triangular shape (viewed from above) and flattened; snout long, narrow, snorkel-like; upper shell with 3 conspicuous lengthwise knobby keels . . . . . *Chelus fimbriatus*, p. 524
12b. Head, snout, and shell not as 12a . . 13

13a (12). Upper shell with broad, lengthwise, round-bottomed, vertebral groove on middle of back ..... *Platemys platycephala*, p. 525

13b. Upper shell without vertebral groove..... 14

14a (13). Chin and throat yellow with black streaks; dark line on side of head, passing through eye..... ..... *Phrynops tuberosus*, p. 524

14b. Throat gray to pale yellow; no dark line through eye .... *Mesoclemmys gibba*, p. 524

Species Accounts: Amphibia

The approximately 6700 species of modern amphibians (Hoffmann et al. 2010) are remarkably diverse in body form, coloration (some being spectacularly beautiful), camouflage, life history, behavior, toxicity, actual and potential use to humans, and so-on. There are three major groups, as follows: Anura (frogs and toads); Caudata (salamanders, of which none occurs in Guyana); and Gymnophiona (the legless caecilians). The earliest origin(s) of amphibians from fish and the evolutionary relationships of the modern species have received extensive modern study (e.g., Frost et al. 2006, Anderson et al. 2008, Pyron & Wiens 2011), but there is not general agreement on their classification yet, and a great deal of work remains to be done. The on-line web reference by Frost (2011) is an exceedingly important resource for accessing the taxonomic literature on all species of amphibians of the world. Appendix 2 provides a complete list of the species we have documented as occurring in Guyana.

Species Accounts: Amphibia: Anura (Frogs and Toads)

The anurans have the legs modified for jumping, although the aquatic species use them for swimming. Adults are tailless. About 15 families, 46 genera, and 137 species of frogs and toads are known to occur in Guyana.

Allophrynidae

We follow Guayasamin et al. (2009) in recognizing this family and the Allocentroleniae, an unranked taxon above the family level that contains two families, the Allophrynidae and Centrolenidae. Their research agrees with several recent papers involving molecular phylogeny reconstruction (e.g., Faivovich et al. 2005, Frost et al. 2006) showing clearly that *Allophryne ruthveni* is the sister group of what traditionally had been called the Centrolenidae exclusive of the monotypic *Allophryne*. Consequently, Frost et al. (2006) combined the Allophrynidae with the Centrolenidae, which would eliminate a monotypic family (the former) and emphasize the sister group relationships of these organisms. However, glass frog specialists prefer retaining the two traditional family names and showing their close relationship by naming a new and unranked Allocentroleniae. What is important in the science involved is for the classification to most clearly reflect evolutionary relationships of monophyletic groups that are strongly supported by evidence, rather than have a classification that obscures or is inconsistent with relationships. One might still question whether the classification system of Frost et al. (2006) or Guayasamin et al. (2009) best accomplishes this for these frogs.

These animals can be difficult to find, even when males are calling. They are small and most often found on low vegetation at night, usually in primary forest "in the close vicinity of streams" (Kok & Kalamandeen 2008:111), often while it is raining. "Eggs are deposited on a leaf overhanging water, from which

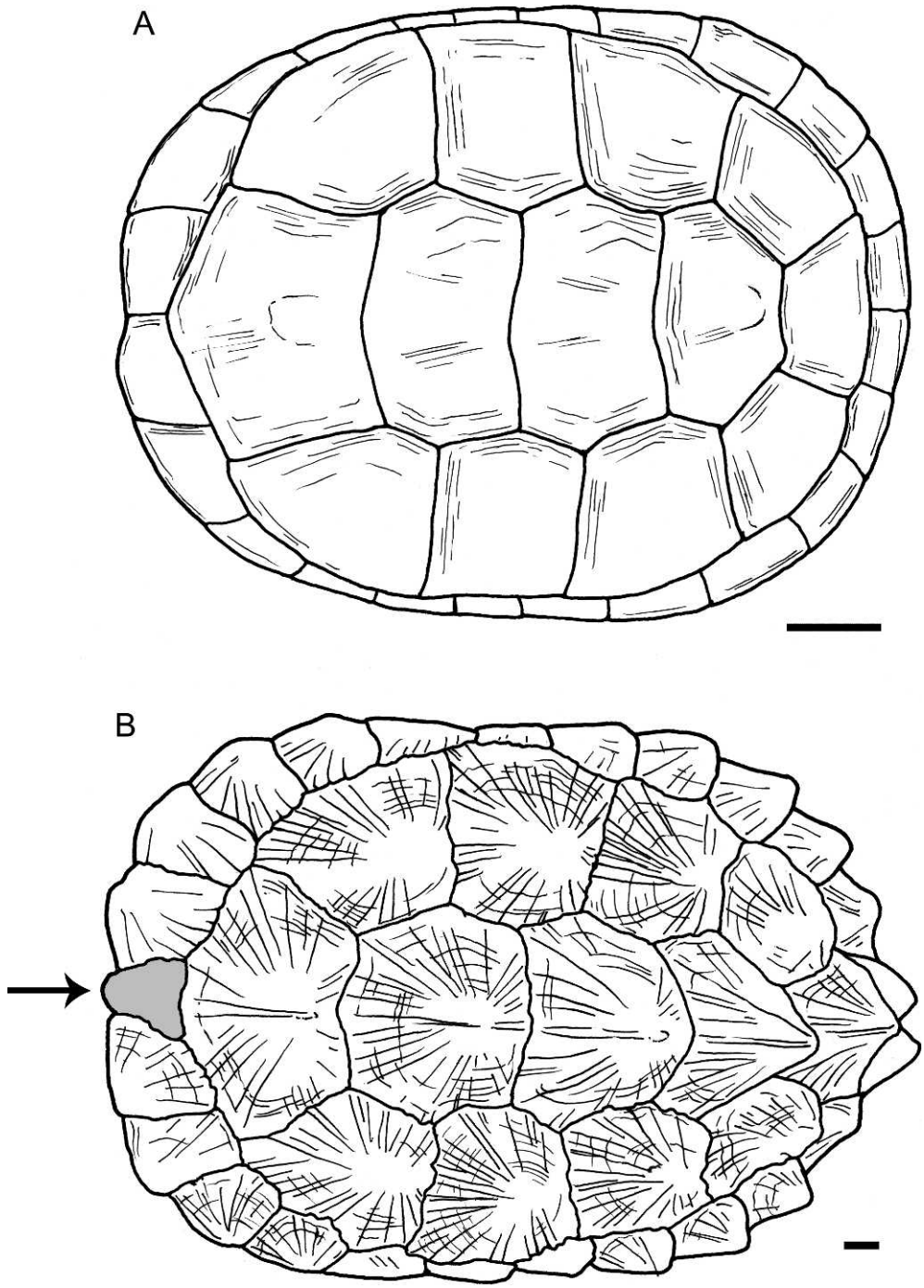

Fig. 9. Turtle shells; nuchal scute (shaded) either present on front edge of upper shell as in *Chelus* (below), or absent as in *Podocnemis* (above). Scale bars: 1 cm.

tadpoles will fall into the water as they hatch" (Kok & Kalamandeen 2008:112).

Allophryne ruthveni Gaige, 1926
Plate 1A, B

Type material.—The holotype is UMMZ 63419, adult female, from Tukeit Hill below Kaieteur Falls, Guyana.

Distribution.—The Guiana Shield region, including Venezuela, Guyana, French Guiana, Surinam, and Brazil (Frost 2011, Lescure & Marty 2000).

Vouchers for Guyana.—The holotype; and USNM 531291 from Iwokrama Forest Reserve, 5 hr downstream of Kurupukari Base Camp on the Essequibo River, Kabocali Camp.

Coloration in life.—The following quotations are from Kok & Kalamandeen (2008:112), for specimens from Kaieteur National Park. "Dorsal ground colour and pattern variable, ranging from greyish-brown to creamish bronze with dark irregular spots and/or reticulum; often a conspicuous cream spot on posterior face of upper arm;...Ventral surface ...translucent dark grey, with a whitish central area visible through the skin in males...Throat black with white spots...Iris dark reddish brown." Usually there are white or cream markings on the sides also (Lescure & Marty 2000).

Aromobatidae

We follow Grant et al. (2006) in recognizing this family, which is diagnosed solely on DNA sequence data. In the recent past, Guyanan species in this family have been assigned to the genera *Colostethus*, *Dendrobates*, or *Epipedobates*, but recently, generic assignments have been changed. These are rather small, inconspicuous frogs that usually occur on the ground or in low vegetation, such as terrestrial bromeliads. Eggs are laid hidden in moist situations on the ground or in vegetation, and for some species, after hatching, a parent carries the tadpoles to water.

Allobates femoralis (Boulenger, 1884)
Plate 1C

Type material.—Originally named *Prostherapis femoralis* based on two specimens, a male and female, from Yurimaguas, Huallaga River, northern Peru. BMNH 1947.2.14.21 was designated as the lectotype (Silverstone 1976).

Distribution.—Occurs widely in the Guiana Shield Region in eastern Venezuela, Guyana, French Guiana, Surinam, and Brazil; also in the Amazon drainage of Brazil, Colombia, Ecuador, Peru, and Bolivia (Frost 2011).

Vouchers for Guyana.—AMNH A-39679–39680, AMNH A-39687, AMNH A-39708, AMNH A-70991, AMNH A-70993, AMNH A-70994, and USNM 118075 from Kartabo; USNM 531354–531355 from Iwokrama Forest Reserve, 13 km S of Kurupukari Base Camp on Georgetown-Lethem Road; USNM 535737 from Baramita, on trail S to Baramita River; and USNM 566054 from the Marudi Mountains, about 24 km SE Aishalton.

Coloration in life.—The following is based on USNM 566054 (CJC field notes, 1993): dorsum black; dorsolateral light stripe pale metallic tan (very pale copper); lateral light stripe of similar color anterior to arm, very pale green posterior to arm; arms brown; orange spot in armpit, with yellow edging; femoral stripe orange with yellow center, within a black field; otherwise, legs brown with black spots; chin, throat, and chest black; beneath arms, abdomen, and legs gray with irregular black markings.

Allobates spumaponens Kok & Ernst, 2007
Plate 1D

Type material.—SMNS 12511, an adult male, from Mabura Hill Forest Reserve,

Upper Demerara-Berbice Region, Guyana (5°09′N, 58°41′W, elevation ca. 100 m).

Distribution.—Known only from central Guyana.

Vouchers for Guyana.—These include the holotype and paratopotypes (SMNS 12510, and 12512–12516); also AMNH A-166470–166475 from Berbice River Camp and AMNH A-166498 from Konawaruk Camp.

Coloration in life.—"Dorsal ground colour medium brown with several dark brown flecks on dorsum; dorsal surface of head slightly darker than dorsum. Wide lateral black band from tip of snout to vent, containing two-thirds of tympanum and not tapering posteriorly from axilla. Pale, narrow, diffuse dorsolateral stripe above the band, extending from tip of snout to vent. Diffuse, pale, partial oblique lateral stripe imbedded in the black band, extending from groin to about one-quarter of the distance to arm insertion. Flanks white with a few irregular brownish grey blotches; ventrolateral stripe present. Upper lip white, suffused with barely visible tiny melanophores. Throat hyaline white with barely visible tiny melanophores laterally and on the chin. Belly immaculate hyaline white. Upper surfaces of thighs and shanks brown with dark brown blotches, no crossbars discernible. Pale paracloacal mark present. Pale yellow spot on groin. Forelimbs light brown with a dark brown line posteriorly from elbow to wrist and a short dark brown line anteriorly discontinuous from arm insertion to elbow. Toes greyish with some light grey blotches. Fingers light brown with some pale blotches. Palm and sole dark brown. Iris golden bronze" (Kok & Ernst 2007: 27).

Specimens in the AMNH series from the Berbice River Camp noted by CJC in life (1997 field notes) had a translucent yellow venter (none white as Kok & Ernst [2007] noted for males, although translucent gray beneath arms and legs), with either the throat or abdomen of brighter color. CJC did not note the partial oblique pale lateral stripe as mentioned by Kok & Ernst (2007), although this is subtle (not very evident in their photos).

Comments.—At times in the recent past, this species was referred to as *Colostethus brunneus*.

Anomaloglossus beebei (Noble, 1923)
Plate 1E

Type material.—Originally named *Hyloxalus beebei* based on the holotype AMNH A-18683, an adult female from near Kaieteur Falls, Guyana.

Distribution.—Known only from the Pakaraima region of western Guyana.

Vouchers for Guyana.—The holotype; AMNH A-166132–166134 from the vicinity of Kaieteur Falls; IRSNB 13721–13726 and 13728–13753 from Kaieteur National Park; ROM 42994 and 43178–43197 from the Kaieteur plateau; ROM 39629–39636, and 42388 from Mount Ayanganna Plateau; and USNM 337769–337771 from the Kaieteur Savanna, Potaro River.

Coloration in life.—Adult coloration varies, with one of two ground colors; bright yellow to orange or pale brown. "Cream dorsolateral stripes and dark brown markings are present or absent, producing five color patterns, described in detail by Bourne (2001). In juveniles the background color is green by night and yellow-green by day, slightly darker than adult coloration. Palpebral membrane is unpigmented, with no dark line along its upper edge" (Kok et al. 2006a:58). "Ventral surface...immaculate yellow to yellowish orange in both sexes" (Kok & Kalamandeen 2008:116). In preservative the background color fades to pale dull yellow and the bright cream dorsolateral lines become white. Tadpoles are pale yellow with variable dark mottling.

Comments.—See Kok et al. (2006a) for a detailed redescription of this species and comments on past misuse of the name.

Also, MacCulloch & Lathrop (2009) discuss the specimens from Mount Ayanganna. Details of habitat, diet, vocalization, reproductive behavior and parental care are in Bourne et al. (2001), including a report that adult females will return to bromeliad leaf-axils containing water with their own tadpoles and deposit unfertilized eggs upon which their tadpoles will feed. Details of predator avoidance and foraging behavior are in Bourne et al. (2001) also.

Anomaloglossus kaiei (Kok, Sambhu, Roopsind, Lenglet, & Bourne, 2006b)
Plate 1F

Type material.—Originally named *Colostethus kaiei*, based on the holotype IRSNB 1938, adult male from Kaieteur National Park, Guyana, along Tukeit trail (5°11′06″N, 59°28′51″W, elevation ca. 400 m).

Distribution.—Pakaraima region, western Guyana.

Vouchers for Guyana.—These include the holotype and paratypes (IRSNB 1939–1964), all from Kaieteur National Park (Kok et al. 2006b:38–39); ROM 42999–43000, also from Kaieteur National Park; AMNH A-166483–166497 from Konawaruk Camp; IRSNB 14922–14924 from Wayalayeng; IRSNB 14925–14931 from Maringma Tepui; and ROM 43221, 43327, 43330, and 43333 from Mount Wokomung.

Coloration in life.—The holotype was described by Kok et al. (2006b:43–44) as follows: "Dorsal ground colour medium brown. A wide black band extending from tip of snout laterally around the body and above the vent, containing most of the tympanum and tapering posteriorly from axilla; a thin, white, partly broken dorsolateral stripe above this band, extending from posterior edge of orbit to vent. Upper lip bar dirty white with a few white and light blue dots. Flank same colour as upper lip. Chin same colour as upper lip; throat and chest medium pink, belly cream stippled with melanophores; underside of thigh and shank creamy yellow. Iris metallic reddish bronze. Upper arm and forearm orange, posterior edge of the latter with a black longitudinal stripe tapering from wrist to elbow. Dark spot on upper surface of wrist. Dorsal surfaces of thigh, shank and tarsus same colour as dorsum, with ill-defined black crossbars, more crossbars on tarsus. Pale paracloacal mark. Toes and digits with small light blue dots. Palms and soles black."

Coloration of the AMNH series from Konawaruk Camp was noted by CJC (field notes, 1998) as follows: brown above (all dorsal surfaces), with very dark brown to black sides; all ventral surfaces yellow (abdomen translucent); anal area dark brown to black, flanked by light tan line (slanted off vertical); some specimens with two or a few dark brown bands on legs.

Comments.—Details of habitat, diet, vocalization, tadpoles, and reproductive behavior are in Kok et al. (2006b).

Anomaloglossus megacephalus
Kok, MacCulloch, Lathrop, Willaert, & Bossuyt, 2010
Plate 2A

Type material.—The holotype is IRSNB 1986, adult female from the eastern base of Mount Maringma, Cuyuni-Mazaruni District, Guyana (05°12′37″N, 060°33′59″W, 1060 m elevation).

Distribution.—Only three specimens are known, all from the Pakaraima region of Guyana.

Vouchers for Guyana.—The holotype (see above) and two paratypes, ROM 39637–39638 from Mount Ayanganna (05°24′N, 59°57′W, 1490 m elevation).

Coloration in life.—"Dorsal ground colour medium brown, with a dark brown V-shaped interorbital bar slightly outlined with light creamish brown, followed by

two less defined dark brown bars, the first more or less V-shaped, at the level of arm insertion, the second just anterior to sacrum. Small, poorly defined, dark brown flecks on snout, between and on dorsal bars. Upper surface of arm light brown with well-defined dark brown transverse bands on forearm and wrist, a less defined one on elbow; upper surface of thigh, shank, and foot light brown with well-defined dark brown transverse bands. A yellow wash on the anterior face of the thigh. Flanks dark brown, slightly lighter ventrally with a few bluish irregular spots and a few whitish irregular blotches on the lower part forming a broken inconspicuous ventrolateral stripe. A few white spots (covering small tubercles) form a broken oblique lateral stripe that does not extend to arm insertion [but on some specimens the stripe is not broken]. No dorsolateral stripe. Upper lip creamish brown suffused with melanophores, two bluish marks below eye; loreal region and side of head dark brown; tympanum area light creamish brown concealed in a poorly defined light stripe from posterior corner of eye to arm insertion. A dark brown stripe is present on the anterior edge of upper arm, tapering from arm insertion to forearm. Throat light brown, blotched with white and dark brown; belly light grey, blotched with dark brown, blotches more numerous and larger laterally. Undersurface of upper arm light brown with a few dark markings; undersurface of forearm blackish; undersurface of thigh and shank light grey blotched with dark brown; rear of thigh and cloacal region blackish. Pale reddish orange paracloacal marks present. Tip of digits whitish. Palms and soles black. Iris mostly orange-bronze, darkened with black suffusion, with two oblique metallic white marks separated by a black triangular mark below pupil" (Kok et al. 2010:23).

Comments.—Previously, a specimen of the type series was reported tentatively as representing *A. tepuyensis*, with the prediction that additional work would discover that it was an undescribed species (Grant et al. 2006:120). Based on that tentative identification, tadpoles from Mount Ayanganna were described under the name *A. tepuyensis* by MacCulloch & Lathrop (2009:11).

Anomaloglossus praderioi (La Marca, 1997)

Type material.—Originally named *Colostethus praderioi* based on the holotype, UALBG 4196, adult male from Mount Roraima (5°10′N, 60°47′W; 1950 m), Estado Bolívar, Venezuela.

Distribution.—This species is known from only two localities in southeastern Venezuela and one in western Guyana (Kok 2010a).

Vouchers for Guyana.—IRSNB 11403–11413 "from the southeastern slope of Maringma Tepui (05°12′16″N, 060°34′39″W, 1376 m elevation...), Cuyuni-Mazaruni District, Guyana" (Kok 2010a:52). Considering that the type locality is on the Venezuelan part of Mount Roraima and that similar habitats occur on the Guyanan parts, we are certain that this species occurs here as well, but voucher specimens are needed.

Coloration in life.—"Dorsal ground color varies from light grayish brown to reddish brown or dark brown, usually with one to three dark brown to black triangular, diamond-shaped or diffuse hourglass markings from interorbital to presacral region. Upper surface of arm light brown to yellowish or orangish brown; upper surfaces of leg light grayish brown to dark gray with dark brown to black transverse bands on thigh, shank and foot; in most living specimens one of the transverse bands is larger and more conspicuous than others, which can sometimes be absent or barely visible... Adult males with gray to very dark gray throat,

almost solid black, with black blotches, throat color extending onto chest and anterior part of belly...; posterior part of belly bright orange... Adult female with bright orange throat, almost immaculate except a few lighter blotches and a few melanophores on chin and lower lip; belly bright orange... Flanks light gray to light reddish brown (males) or yellowish brown (female), usually with some small white or sky blue flecks more concentrated on the lower part, not forming a straight ventrolateral stripe... However, some inconspicuous yellowish elongate spots may occur and can be interpreted as a broken stripe... Distinct thin pale dorsolateral stripe present in both sexes,...extending from tip of snout to tip of urostyle, usually slightly narrower on body than on head... A wide dark brown band of variable width present below the dorsolateral stripe, extending from tip of snout laterally around the body and above the vent, containing most of the tympanum and usually tapering posteriorly from axilla. Upper lip light to dark gray, suffused with melanophores and sometimes with a few sky blue flecks in males, yellow with few melanophores in female. A black stripe extends from posterior margin of eye to axilla region and is usually underlined by a white to light gray (males) or bright yellow (females) line; a white or light gray (males) or yellow spot (female) at arm insertion. Usually a black stripe on anterior and posterior edges of forearm, tapering from arm insertion to forearm; dark area on upper surface of wrist. Undersurfaces of arm and thigh bright to dark orange, undersurface of shank yellowish brown with black flecks and spots (more extensive in males). Pale, creamish brown, paracloacal marks present. Toes and digits with sky blue dots... Palms and soles dark brown to black. Iris metallic reddish bronze in males, metallic bronze in female, with fine dark brown reticulation in both sexes'' (Kok 2010a:57–58).

Anomaloglossus roraima
(La Marca, 1997)

Type material.—Originally named *Colostethus roraima*, based on the holotype ULABG 4197, a juvenile female from "El Paso de La Muerte, a unos 60–70 m antes de la cumbre del tepuy, en el camino, 'La Rampa,' que conduce desde su base hasta cima del Monte Roraima, Estado Bolívar, Venezuela."

Distribution.—This species is known only from Mount Roraima, Guyana and Venezuela.

Vouchers for Guyana.—CPI 10212–10217, from "Mt. Roraima, 1860–2350 m" (Grant et al. 2006:242), which Grant et al. stated (p. 45) would be deposited at the USNM.

Coloration in life.—In the original description, La Marca (1997 [1996]) stated (as translated from Spanish) that photographs of the holotype show grayish dorsal tones and light brown ventral surfaces. There were no gaudy colors or yellow or reddish tones. Colors and pattern of the holotype in alcohol was also given in the original description (p. 41).

Comments.—This species was described from a single juvenile, but the CPI specimens collected recently in Guyana (see above) confirm its validity.

Bufonidae

This family, which includes the terrestrial, brown and warty anurans most often referred to as toads, was named about 185 yr ago (Gray 1825) and its composition has changed over many decades. Nevertheless, the family in its modern sense received strong support in recent molecular phylogenetic analyses (e.g., Frost et al. 2006, Pramuk 2006, Chaparro et al. 2007), although assignment of generic names in this large and complex family is still shifting as more and more is learned about relationships and synonymies. The family

probably originated in South America (Pramuk et al. 2008).

Most species of bufonids live on the ground, whether in savanna or forest, and many of them produce noxious secretions from their parotoid glands (on back of the head and/or neck) when disturbed. The species of one genus, however, are special in several respects. These are the five Guyanan species of *Oreophrynella*, a remarkable genus of montane species the total global distribution of which includes western Guyana, southeastern Venezuela, and northern Brazil. These are upland and highland species that occur at the highest elevations, are small, have opposable toes, and some of which are found on vegetation up to 3 m above the ground. They are among the least known frogs in the world. Of the five species of *Oreophrynella* that occur in Guyana, four are known from a total of 10 or fewer specimens (two species are known from only one or two specimens), and two species are endemic to Guyana.

Atelopus spumarius Cope, 1871
Plate 2B

Type material.—The neotype is MNHN 1979–8382, from "Colonia, bassin de la rivière Ampiyacu (Dpto Loreto, Pérou)" (Lescure 1981:894).

Distribution.—"Disjunct populations in Amazon lowlands of Ecuador and eastern Peru, to Amazonas, Pará, Amapá (Brazil), and the Guianas" (Frost 2011).

Vouchers for Guyana.—AMNH A-13528–13529, AMNH A-21332–21333, and AMNH A-53304–53305 from Kartabo; AMNH A-70997 from Kalacoon; and AMNH A-166066–166077 and USNM 566005–566010 from Konawaruk Camp.

Coloration in life.—The following is based on the AMNH and USNM specimens from Konawaruk Camp (CJC field notes, 1998). All dorsal surfaces black with bright orange, gold, or red markings (irregular circles, ellipses, reticulations); throat, chest, and anterior abdomen orange; remaining ventral surfaces yellow or pale orange, although pink with black spots in a small male. Kok & Kalamandeen (2008:122) add that the dorsal ground color is dark brown on some individuals and the light markings may have dark brown or black spots within them.

Comments.—The frogs currently covered by this name may be a complex of cryptic species. They occur widely across Amazonia and have a spotty distribution and low vagility, which promotes local differentiation. A thorough analysis of geographic variation is needed, following up on the recent work analyzing DNA sequences provided by Noonan & Gaucher (2005), which suggests that several taxa may be masquerading under this name. These authors and others (e.g., Lescure & Marty 2000, Kok & Kalamandeen 2008) have used various names, including *Atelopus spumarius hoogmoedi*, *Atelopus hoogmoedi*, and *Atelopus spumarius barbotini*, for different populations of these frogs from the Guianas, but we consider it to be premature to apply such names until additional studies are completed. See also comments by Frost (2011). If in the future it turns out that the name *A. barbotini* should be applied to some of the frogs we listed above (Vouchers), that name might apply to the series from Konawaruk Camp, a matter that needs additional investigation.

Daly et al. (1994) reported that the major component of the toxins in the skin of *A. spumarius* sampled in Brazil was the powerful tetrodotoxin.

Dendrophryniscus minutus (Melin, 1941)
Plate 2C, D

Type material.—Originally named *Atelopus minutus* based on specimens from Taracuá, Rio Uaupés, Brazil. The website

of the Göteborgs Naturhistoriska Museum (www.gnm.se) lists the holotype as Ba.Ex. 462.

Distribution.—Amazonian Colombia (from the llanos of Meta south to Amazonia), Ecuador, Peru, Bolivia, Brazil, and southern Guianas (Frost 2011).

Vouchers for Guyana.—AMNH A-166120–166125, 166130–166131 and USNM 566041–566044 from Berbice River Camp; USNM 200507 from 24-mile Forest Reserve south of Bartica; and USNM 531329–531353 from several sites within Iwokrama Forest Reserve.

Coloration in life.—The following is based on the AMNH and USNM series from Berbice River Camp (CJC field notes, 1997). Dorsum reddish brown or dark brown, with or without gray patches that may be in a reticulum, at times also numerous tiny gray or white dots; tan or light gray vertebral light line present or not; throat and chest black on some, reddish brown on others; belly white with black spots; beneath arms and legs may be translucent gray with dark gray or black spots; iris black with narrow copper inner ring.

Comments.—These are small toads with a maximum snout-vent length of about 24 mm (Lescure & Marty 2000) and a body shape somewhat similar to that of *Atelopus*.

Oreophrynella dendronastes Lathrop & MacCulloch, 2007 Plate 2E, F

Type material.—The holotype is ROM 39645, an adult female from the northeast slope of Mount Ayanganna, District 7, Guyana, 1490 m (5°24.11′N, 59°57.41′W).

Distribution.—Known only from Guyana, in the immediate vicinity of the type locality.

Vouchers for Guyana.—The holotype; ROM 39648–39655 from Mount Ayanganna; ROM 46398–46399, 46401–46402, 46409–46413, and 46417–46418 from Mount Wokomung; and IRSNB 1981.

Coloration in life.—"Dorsum, top of head, flanks and limbs uniformly brownish-orange. Throat, abdomen and ventral surfaces of limbs creamy yellow. Tip of snout, eyes and anterior flanks lighter shade of yellow. Flanks and upper portions of limbs covered in medium sized, yellow glandular spots. A loosely organized line of these spots extends from scapular region to groin. Posterior aspect of thighs and anal sheath with similar yellow glandular spots. Upper lip creamy yellow with diffuse brown mottling. Iris silvery orange with black reticulations" (Lathrop & MacCulloch 2007:90).

Comments.—These are small toads, males not exceeding a body size of 27 mm, females 38 mm. "All specimens were found on broad-leaf vegetation at a height of 1.5 m or more...[on] very humid evenings in which it had either rained all day, or was in the early stages of a downpour" (Lathrop & MacCulloch 2007:91). Additional research is warranted to clarify the differences between this species and *O. macconnelli* (Lathrop & MacCulloch 2007, Kok 2009a).

Oreophrynella macconnelli Boulenger, 1900

Type material.—The holotype is BMNH 1947.2.14.49 (formerly 99.3.25.17), from the base of Mt. Roraima, 3500 ft, reported originally as being from Guyana. However the locality is probably in Venezuela (Phelps 1938). See below (Vouchers) for definite records in Guyana.

Distribution.—This species is known only from Mt. Roraima and Maringma tepui, Guyana, on the Guyana-Brazil border (Kok 2009a), but it probably occurs in adjacent Brazil and Venezuela also.

Vouchers for Guyana.—BMNH 1976.700 and 1976.702 from northern slopes of Mount Roraima, 1460 m elevation; IRSNB

14333–14336 from "Maringma tepui, southeast slope, 1376 m asl (05°12′16″N, 060°34′39″W)" (Kok 2009a:49); USNM 549306 from the north slope of Mount Roraima, 05°16′N, 60°44′W, at 1300 m elevation.

Coloration in life.—"Adult dorsal colour is variable...ranging from light brownish orange...to olive brown with darker spotting...Olive brown specimens have distinct white spots on the lower flank, while in the orange specimen these spots are yellowish and less conspicuous. All adult specimens with a series of yellow...to brownish orange...spots forming a dorsolateral line, and series of similar spots on axilla, upper arm, groin and thigh forming short longitudinal stripes on limbs. All adult specimens have a white to yellow spot below the eye, although...inconspicuous [on some]. Adult ventral colour is creamy yellow with brown marbling; palm and sole are orange" (Kok 2009a:43–44).

Comments.—Individuals on Maringma Tepui were all "found active by night, walking on...epiphytic ferns...about 1.0–3.0 m above the ground, except...[one] collected on the ground at 17h00" (Kok 2009a:44–45). *Oreophrynella macconnelli* is more poorly known than *O. quelchii*.

Oreophrynella quelchii (Boulenger, 1895)

Type material.—Originally named *Oreophryne Quelchii* based on several specimens from the summit of Mount Roraima, at 8500 ft elevation. Apparently the type specimen was collected on the Venezuelan part of the summit (Phelps 1938). The syntypes include BMNH 95.4.19.1–5, 99.3.25.7–13, KU 126081–82 (formerly BMNH 99.3.25.14–15), and MCZ 3500–02 (Frost 2011). See below (Vouchers) for records from Guyana.

Distribution.—"Cerro Roraima, Venezuela and Guyana, presumably into Brazil on this same massif" (Frost 2011).

Vouchers for Guyana.—USNM 118230 is from Mount Roraima within the Guyana portion. In addition, Señaris et al. (2005:67) included the following: "GUYANA-BRAZIL: Wei-Assipu-tepui, (5°13′1″N, 60°42′19″W) 2400 m a.s.l.: MHNLS 15912."

Coloration in life.—Without specifying whether the color notes were taken in life or not, Boulenger (1895:521) stated the following: "black; throat and belly spotted or marbled with bright yellow." Kok (2009a: 39) stated that the belly in life is "bright orange with black mottling in *O. quelchii*."

Comments.—This species is very poorly known.

Oreophrynella seegobini Kok, 2009a

Type material.—The holotype is IRSNB 1979, an adult male from the summit plateau of Mount Maringma, Cuyuni-Mazaruni District, Guyana (05°12′59″N, 060°35′05″W, 2088 m elevation).

Distribution.—Known only from the type locality.

Vouchers for Guyana.—The holotype and a paratopotype, IRSNB 1980.

Coloration in life.—"Dorsum, top of head and flanks blackish brown, lower arm, hindlimbs and top of hands and feet slightly lighter than dorsum. A bright yellowish orange spot at arm insertion on the left side, lacking on the right side where the area is dark brownish orange. Upper eyelids and lateral surfaces of snout dark brownish orange. Throat, chest and anterior part of belly dark brownish orange, posterior part of belly and area below vent blackish brown. A black mid-ventral line running from tip of lower jaw to posterior part of belly, slightly curved sinistrally. Ventral surface of limbs brownish orange. Palms and soles orange...Iris dark greenish brown with inconspicuous dark grey streaks" (Kok 2009a:40).

Comments.—This is one of the least known species in the world, with only two

specimens known to science. One was found in late afternoon walking on muddy ground, the other hiding beneath a rotting bromeliad leaf (Kok 2009a).

Oreophrynella weiassipuensis Señaris, DoNascimiento, & Villarreal, 2005

Type material.—The holotype is MHNLS #15913 from Wei-Assipu-tepui, Sima de los Guácharos, 280 m north of the heliport, 2280 m a.s.l. (coordinates of the heliport 5°13′1″N, 60°42′19″W), Brazil-Guyana border.

Distribution.—Known only from the type locality.

Vouchers for Guyana.—The holotype from the Brazil-Guyana border is the only known specimen.

Coloration in life.—"Dorsum reddish brown with scattered darker brown marks and a fine dark mid-dorsal line; flanks dark brown; dorsum of hands light brown with minute reddish brown spots;...throat and chest reddish brown; belly slightly darker than the remaining ventral surface; fingers and toes light brown ventrally" (Señaris et al. 2005:62).

Comments.—This is one of the most poorly known animals in the world, being known to science by only a single specimen. The frog "was found in a forested area at the bottom of a large pit" (Señaris et al. 2005:66).

Rhaebo guttatus (Schneider, 1799) Plate 3A

Type material.—Originally named *Bufo guttatus* with the apparent holotype ZMB 3517 (Frost 2011). The type locality was restricted to Surinam (Rivero 1961).

Distribution.—Occurs widely throughout the Guianan Region and in Amazonian Brazil, Colombia, Ecuador, Peru, and Venezuela (Frost 2011).

Vouchers for Guyana.—AMNH A-136027 from Karanambo; AMNH A-141058–141060, AMNH 141063–141064, and USNM 497688 and 566020–566021 from Dubulay Ranch; AMNH A-166084 and A-166087 and USNM 566022–566023 from Berbice River Camp; and AMNH A-166089–166093 and USNM 566024–566025 from Konawaruk Camp. Also USNM 85013 from Pickersgill, Pomeroon River (07°16′N, 58°43′W); USNM 118068–118070 from Kartabo; USNM 291103 from Kato, Chiung River; and USNM 531292–531298 from several sites within Iwokrama Forest Reserve.

Coloration in life.—The following is based on the AMNH vouchers listed above from Karanambo and Dubulay Ranch, paraphrased from CJC's field notes (1992, 1994): Tan anterior to parotoid glands, with or without a few dots of rust; posterior body similar but warts are rust and there may be a wash of rust posteriorly; broad reddish brown lateral area from tip of snout nearly to groin; arms and legs dark brown or gray; ventral surfaces gray with cream spots; broad rust wash may be present on posterior belly, groin, and anal region, but on some individuals ventrally across thighs and hips is very pale tan instead. These notes compare well with those of Kok & Kalamandeen (2008:126).

Rhaebo nasicus (Werner, 1903) Plate 3B

Type material.—Originally named *Bufo nasicus*. The holotype is IRSNB 1.015 and the type locality was restricted to South America, probably along the Atlantic drainage by Smith & Laurent (1950).

Distribution.—The Pakaraima region of western Guyana and southeastern Venezuela, 100-1410 m elevation (Hoogmoed 1977).

Vouchers for Guyana.—AMNH A-3791 from Rockstone, Essequibo River, and A-

18986 and A-18988 from Kamakusa. Also a series of BMNH specimens cited by Hoogmoed (1977:267). Also ROM 20648–20650 from Tukeit; ROM 39445–39448 from Mount Ayanganna; and USNM 118071 from Kartabo.

Coloration in life.—The following is based on Hoogmoed (1977) and AL's color photos of specimens from Guyana: dorsal ground color reddish brown, often with darker spots, a dark brown hourglass patch and/or an ochre middorsal stripe. Sides dark brown. Limbs reddish brown with darker crossbands. Throat dark brown with white spots, venter white with brown mottling. Kok & Kalamandeen (2008:128) add that "the dorsal coloration can be variable, from grayish brown to reddish brown, and it may include pale blue spots (often present on flanks)."

Comments.—Essentially nothing is known about the life history of this species (Kok & Kalamandeen 2008).

Rhinella marina (Linnaeus, 1758)
Plate 3D

Type material.—Originally named *Rana marina* based on an illustration (Frost 2011). The type locality was restricted to Surinam by Müller & Hellmich (1936).

Distribution.—Occurs naturally widely throughout North America, Central America, and South America; introduced worldwide (Frost 2011).

Vouchers for Guyana.—AMNH A-24899–24900 from Kartabo; AMNH A-136024–136026 from Karanambo; AMNH A-139035–139039 and USNM 566026 from Aishalton; AMNH A-166079 and USNM 566027 from Berbice River Camp; and AMNH A-166080 and USNM 566028 from Konawaruk Camp. Also ROM 43998 (tadpoles) from Ayanganna; USNM 84491 from Linden; USNM 162894 from Atkinson (6°27′N, 58°15′W); USNM 162968–162974 from Enmore Estate (6°44′N, 57°59′W); USNM 291104 from Kato, Chiung River; USNM 291157–291171 from Paramaktoi; USNM 497694–497695 from Karanambo Ranch, Maricuba Lake (03°45′08″N, 59°18′36″W); USNM 497696 from Lethem, Takutu River (03°22′38″N, 59°48′13″W); USNM 497697 from Kaieteur National Park (near paved airstrip); USNM 497698 from Georgetown; USNM 531299–531303 from several sites within Iwokrama Forest Reserve; and USNM 535733–535736 from Baramita. In addition, CJC and CRT saw specimens (not collected) at Dubulay Ranch.

Coloration in life.—"Dorsal ground colour brown to greyish or reddish brown, with or without dark brown or black mottling and/or cream spots;...Ventral surface...creamy white, with or without a distinct pattern consisting in greyish brown, dark brown or black spots and/or mottling;...Flanks similar to dorsum" (Kok & Kalamandeen 2008:132).

Comments.—This is the largest species of toad in the world, the largest specimens being from the Guianan Region.

Rhinella martyi Fouquet, Gaucher, Blanc, & Vélez-Rodriquez, 2007a
Plate 3E, F

Type material.—The holotype is MNHN 2006.2601, an adult female from Brownsberg Nature Park, Suriname, Brokopondo district (4°56′N, 55°10′W), 510 m above sea level.

Distribution.—Guyana, Suriname, and southwestern French Guiana, "probably also present in adjacent areas of Brazil and may extend into...Venezuela" (Fouquet et al. 2007a:24).

Vouchers for Guyana.—AMNH A-24891 and A-39597 from Kartabo; AMNH A-49392 from Isheartun; AMNH A-141083–141085, 141089–141090, A-145164–145169, and USNM 566029–566034 from Dubulay Ranch; AMNH A-166096–166105 and USNM 566035–566037 from Berbice River Camp; AMNH

A-166109–166116 and USNM 566038–566040 from Konawaruk Camp; ROM 22813 and 22833 from Baramita (paratypes); ROM 20652–20654 from Kurupukari (4°40′N, 58°39′W; paratypes); USNM 164164 from Mabaruma Compound (08°12′N, 59°47′W); USNM 200506 from Bartica; USNM 531304–531328 from several sites within Iwokrama Forest Reserve; USNM 535732 from Baramita; USNM 549300 from Waruma River (05°20′N, 60°46′W); and USNM 549301–549303 from the north slope of Mount Roraima.

Coloration in life.—The following is quoted from the original description (Fouquet et al. 2007a:22), although the authors did not specify that these notes are from animals in life nor did they specify the series of specimens from which the notes were taken: "dorsum gray-brown with dark brown small patches; dark brown marks also on legs, tarsa and toes; belly cream slightly orange with more and more small grey spots going to the flanks; throat light grey; interior surface of the tarsa and feet dark brown (except the webbing); no middorsal stripe.'' Fouquet et al. (2007a:24) also noted that "this species is highly polymorphic...the back varies from dark brown to light gray and sometimes even reddish...the patterns...also variable with a variety of leaf like patterns and successive shades of dark to light brown or gray. A whitish middorsal stripe can occur and can be very thin to 5 mm wide."

The following notes are based on the AMNH series from Dubulay Ranch and Berbice River Camp (CJC field notes, 1994, 1997): tan above (reddish tan or reddish brown before chloretone) with or without light pale gray or tan vertebral line; some individuals with dark brown spots; line of tan or brown warts on sides; arms and legs may have dark brown bands; dark brown stripe on outer lower arm; reddish tan throat and anterior chest; other ventral surfaces pale yellow with black spots; iris a reticulum of black and gold. One individual from Berbice River Camp (AMNH A-166100) was noted separately as follows: black dorsum with gray mottling, the black being quite intense anteriorly, beneath the lateral row of warts; chin, throat and chest black with gray dots; anterior belly pale yellow with black mottling; pale yellow beneath arms and legs with very little pale black spotting; iris black and gold, with touch of pale copper.

Comments.—These toads are part of a group of cryptic species that occur in the Guianan Region and in the recent past certain populations have been referred to as *Bufo margaritifer* and *Rhinella margaritifera*. Fouquet et al. (2007b) showed with DNA sequence data and phylogenetic analyses that there are several lineages of this basic kind of toad in French Guiana, Suriname, and Guyana that appear to be on separate evolutionary tracks without evidence of interbreeding, which could signify that they are different cryptic species. Consequently, Fouquet et al. (2007a) named one of these lineages *R. martyi*, and they cited specimens from the following localities in Guyana: Bartica, Baramita, and Kurupukari. The other species they recognized were from Suriname, French Guiana, and the southern border region of these countries with Brazil. However, the confusion about these animals is such that there may still be unrecognized cryptic species among them. See Frost (2011) for further discussion.

Recently, Avila-Pires et al. (2010), unhappy with the changes in taxonomy and nomenclature, rejected the new information and returned to referring to all these toads as *Bufo margaritifer*, synonymizing *R. martyi* with that taxon, but they did so without any molecular data. In the long term, this could prove to be more confusing rather than enlightening for understanding these populations. Consequently, we follow Fouquet et al. (2007a) in referring the Guyanan samples they analyzed to *R. martyi*. Because there are not conspicuous reasons to use alternative

names on the other specimens of similar toads that we have seen from Guyana, from localities not represented in the study by Fouquet et al. (2007a), we tentatively use the same name for all the Guyanan specimens of this group. However, a thorough study of these toads throughout the Guianan Region is needed to clarify their status and determine whether there are additional cryptic species present. The future study should include morphology, vocalizations, and DNA sequences analyzed phylogenetically for samples from throughout the Guianas, including the entire *margaritifera* group.

Rhinella merianae (Gallardo, 1965)
Plate 3C

Type material.—Originally named *Bufo granulosus merianae*. The holotype, AMNH A-46531, is from Head Falls, Essequibo River, Guyana.

Distribution.—Brazil, north of the Amazon River, eastern Venezuela, Guyana, Surinam, and French Guiana (Narvaes & Rodrigues 2009).

Vouchers for Guyana.—AMNH A-70831 from Kartabo; AMNH A-139018–139025, A-139028, A-139031, A-139034, and USNM 566011–566016 from Aishalton; and AMNH A-141065–141073, A-141077–141082, A-167103–167104, and USNM 566017–566019 from Dubulay Ranch.

Coloration in life.—The following is based on the AMNH specimens from Aishalton (CJC field notes, 1993): Dorsum gray or pale tan with dark brown markings; pale yellow spot in anal region; ventral surfaces cream, abdomen of some individuals with gray, brown, or black spots (sometimes subtle); cream warts on posterior abdomen; throat and vocal pouch of males gold anteriorly, black posteriorly; chin and throat of females cream, with or without irregular gray spots.

Comments.—After we had reviewed specimens and written this part of our manuscript, Narvaes & Rodrigues (2009) published a morphological review of the toads in this complex, which were previously referred to as *Rhinella granulosa*. They concluded that there are 12 species throughout the overall range of the complex, many of which are similar to each other, and three occur in Guyana. According to their conclusions, most Guyanan localities are occupied by *R. merianae*, and these include the specimens from Aishalton and Dubulay Ranch cited above (AMNH and USNM catalog numbers). The other species they recorded from Guyana are *R. humboldti* and *R. nattereri*. The single Guyanan locality they cited for *R. nattereri* was from Cuyuni-Mazaruni, Mount Roraima, where they said it is sympatric with *R. merianae*. The only two Guyanan localities they cited for *R. humboldti* were from Cuyuni-Mazaruni, Bartica; and Upper Takutu-Upper Essequibo, Alto Rio Rupununi. We think it is timely for there to be a thorough review of the toads of this complex throughout Guyana, including ontogenetic development of morphology and DNA sequence analyses.

Centrolenidae

We follow Guayasamin et al. (2009) in recognizing this family. Its undisputed closest relative is the monotypic Allophrynidae (see above), in the account for which we discussed an alternative opinion of whether to include *Allophryne ruthveni* within the Centrolenidae, as recommended by Frost et al. (2006).

Frost et al. (2006) used quotation marks for the generic names "*Centrolene*" and "*Cochranella*" to indicate that species assigned to these genera at the time did not comprise monophyletic groups; this signified that generic assignments would change, but it would have been premature

to change them in their paper because considerably more research was needed. Subsequently, Guayasamin et al. (2008) showed that the genus *Hyalinobatrachium* was not monophyletic either. Taxonomic review of these frogs has been happening quickly, however, as shown by Guayasamin et al. (2009) and Castroviejo-Fisher et al. (2011). Considering the new generic arrangements proposed in the most recent papers, which are consistent with the results of their phylogenetic conclusions, we drop the use of quotation marks on the generic names and use *Vitreorana* where applicable because now the names reflect monophyletic groups.

These frogs are difficult to find. They are small and basically green with a high-pitched call produced by males perched on green leaves or moss overhanging water, often on the underside of a leaf and during a rain. Egg masses are deposited here, and, if successful, hatching tadpoles drop into the water below. In some species, particularly in the genus *Hyalinobatrachium*, the male will stay with his clutch of eggs during development. Recent research with a Costa Rican species has shown that clutches with the attendant male have better survival rates than those without, and perhaps the male helps discourage predation and prevent desiccation (Vockenhuber et al. 2009).

Hyalinobatrachium cappellei
Van Lidth de Jeude, 1904
Plate 4A

Type material.—The holotype is RMNH 4463 from the Saramacca River and vicinity (Gassó Miracle et al. 2007).

Distribution.—This species occurs widely in the Guiana Shield region, in Brazil, French Guiana, Guyana, Suriname, and Venezuela (Castroviejo-Fisher et al. 2011).

Vouchers for Guyana.—SMNS 12250–12254 from Mabura Hill Forest Reserve, Maiko Creek (05°09′19.30″N, 58°41′58.96″W; identification confirmed by Castroviejo-Fisher et al. 2011:44); UG HA 722 and UTA 51654–51664 from "a small stream on Peters Mountain, 3.6 km north of Imbaimadai in the Pacaraima Mountains, 600 m" (Noonan & Bonett 2003:92); also known from Kaieteur National Park (Kok & Kalamandeen 2008).

Coloration in life.—"Dorsum (including eyelid) light lime green with numerous yellow spots, giving appearance of a green 'net' over a yellow ground color; fine [dark brown] melanophores...in green areas; ventral surfaces...[transparent with] parietal peritoneum clear [translucent]; pericardial [peritoneum partly or totally white], visceral, and hepatic peritonea white; iris yellow...and [sometimes] a distinct red ring...encircling the pupil [complete or not]; bones white" (Noonan & Bonett 2003:94) [with some details from Kok & Kalamandeen 2008 or Castroviejo-Fisher et al. 2011, in brackets].

Comments.—The latest work on these frogs was done by Castroviejo-Fisher et al. (2011), who showed that *Hyalinobatrachium crurifasciatum* Myers & Donnelly (1997), *Hyalinobatrachium eccentricum* Myers & Donnelly (2001), and *Hyalinobatrachium ignioculus* Noonan & Bonett (2003) are junior synonyms of *H. cappellei*. The latter synonym was named based on specimens from Guyana (UG and UTA vouchers listed above).

Hyalinobatrachium iaspidiense
(Ayarzagüena, 1992)
Plate 4B–E

Type material.—The original name was *Centrolenella iaspidiensis*, based on the holotype EBD 28803, a male from Quebrada Jaspe, San Ignacio de Yuruaní, Bolivar, Venezuela.

Distribution.—This species occurs widely in the Guianan Region in Brazil, French Guiana, Guyana, Suriname, and Venezuela, and in the Amazonian lowlands of

Ecuador and Peru. Some records for Guyana are under the name *H. nouraguense* (see Comments, below).

Vouchers for Guyana.—SMNS 12242–12249 from Mabura Hill Forest Reserve, Maiko Creek (Kok & Castroviejo-Fisher 2008, Yánez-Muñoz et al. 2009, Castroviejo-Fisher et al. 2011).

Coloration in life.—Dorsum yellowish green with leaf green spots (but white in preservative; see also Yánez-Muñoz et al. 2009) and scattered black dots; belly and some peritoneum (e.g., pericardial) transparent (heart visible, red); visceral and parietal peritonea white; iris yellow to dull silver; bones white (Lescure & Marty 2000:75, under the junior synonym *H. nouraguensis*).

Comments.—Information on this species has appeared in the literature under the junior synonyms of *Hyalinobatrachium nouraguensis* Lescure & Marty, 2000 and *H. nouraguense*, but recent morphological research suggests that these names are junior synonyms of *H. iaspidiense* (e.g., Yánez-Muñoz et al. 2009). Nevertheless, DNA sequence data indicate there are two or more morphologically cryptic lineages that require more detailed analyses (Guayasamin et al. 2008). See Castroviejo-Fisher et al. (2011) for the latest information.

Hyalinobatrachium mondolfii
Señaris & Ayarzagüena, 2001
Plate 5A, B

Type material.—The holotype is MHNLS 12710, an adult male from "el Primer Raudal del Caño Acoima, afluente del Río Grande (8°22′N, 61°32′W), 15 msnm., estribaciones de la Serranía de Imataca, Estado Delta Amacuro, Venezuela" (Señaris & Ayarzagüena 2001:1084).

Distribution.—This species is known from Bolivia, Brazil, Colombia, French Guiana, Guyana, Suriname, and Venezuela (Castroviejo-Fisher et al. 2011).

Vouchers for Guyana.—SMNS 12255–12260 from Mabura Hill Forest Reserve, Maiko Creek (05°09′19.300″N, 58°41′58.96″W); and BMNH 1939.1.1.64 from the New River. A highly suggestive recording of an advertisement call (vocalizing male in Kaieteur National Park) has been analyzed and a color photograph has been published (see Comments, below).

Coloration in life.—Dorsum pale green with numerous tiny yellow dots; belly and parietal peritoneum transparent; pericardial, hepatic, and visceral peritonea white; iris golden; bones white (Señaris & Ayarzagüena 2001).

Comments.—Kok & Castroviejo-Fisher (2008:48) compared audiospectograms and oscillograms of an uncollected frog that was recorded in Kaieteur National Park with calls of *H. mondolfii* from Venezuela and concluded that they were so similar that "therefore we consider the presence of *H. mondolfii* in Guyana as likely." Kok & Kalamandeen (2008:143) also stated that "the presence of *Hyalinobatrachium mondolfii* in KNP [Kaieteur National Park] is probable." Voucher specimens are needed to confirm the presence of this species in Kaieteur National Park. In addition, the species has been reported for Iwokrama (Castroviejo-Fisher et al. 2011).

Hyalinobatrachium taylori (Goin, 1968)

Type material.—The original name was *Centrolenella taylori* based on BMNH 1939.1.1.65, an adult male from an elevation of 750 ft along the New River, Guyana. Frost (2011) noted Hoogmoed's comment in the 1985 edition of the amphibian checklist volume that the type locality is within an area that is in dispute with Suriname.

Distribution.—"Guianan Shield in southern Surinam, Guyana, French Guiana, and southeastern Venezuela; presumably in adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—The holotype from the New River (see above); and IRSNB 13981–13987 from Kaieteur National Park (Kok & Castroviejo-Fisher 2008).

Coloration in life.—"Dorsal ground colour dark green with pale green spots, usually bearing a white fleck in their centre [and perhaps some outside the spots], bronze flecks/lines sometimes present on dorsal surfaces; iris metallic lavender with dark brown reticulations; ventral surface...transparent, internal organs visible through the skin; parietal peritoneum transparent, pericardial peritoneum partly white, hepatic and visceral peritonea white... bones translucent green" (Kok & Kalamandeen 2008:146).

Comments.—Kok & Castroviejo-Fisher (2008) discussed taxonomic problems with this species, which are under review, and for which "at least two species" have been masquerading under this name recently. See Castroviejo-Fisher et al. (2011) for the latest information.

Vitreorana gorzulae (Ayarzagüena, 1992)
Plate 5C

Type material.—The original name was *Centrolenella gorzulae*, based on MHNLS 11221 from Cerro Auyantepuy (5°56′N, 62°34′W; 1850 m), Bolívar, Venezuela.

Distribution.—"Known from Auyantepui, Atapare, and Sierra de Lema, 1800–1900 m elevation, state of Bolívar, Venezuela, as well as Kaieteur National Park, Maringma Tepui, and Peters Mountain in Guyana; presumably to be found in adjacent areas of Brazil" (Frost 2011).

Vouchers for Guyana.—IRSNB 13974–13978 from Kaieteur National Park; ROM 43982 from Mount Wokomung. Also CSBD "HA 721" and UTA 52229–52247 from "Peters Mountain 3.6 km N of Imbaimadai in the Pacaraima Mountains, 600 m" (Noonan & Harvey 2000:295). See Castroviejo-Fisher et al. (2009) for additional localities.

Coloration in life.—"Dorsal surfaces dark green; upper lip yellow; hands and feet yellow green [or bluish green]; bones green; iris metallic copper with brown reticulations, yellow ring around pupil incomplete laterally; ventral surfaces cream; parietal peritoneum clear [transparent]; visceral peritoneum white; hepatic peritoneum white; pericardium white" (Noonan & Harvey 2000:299).

Comments.—Noonan & Harvey (2000) named *Centrolene papillahallicum* based on specimens from Guyana (UG and UTA vouchers listed above), but the frogs actually were misidentified specimens of *Centrolene* (=*Vitreorana*) *gorzulae* (Kok & Castroviejo-Fisher 2008). The specific epithet of this frog has been used by some authors with the ending *ai* instead of *ae* as used in the original description. This emendation was based on the assumption that the original authors either intended to or should have used that spelling. However, article 32.5.1 of The Code (ICZN 1999:39) states that the original spelling should be used in cases like this, even if certain errors were involved in forming the name. This phenomenon is discussed further by Dubois (2007:57). See Castroviejo-Fisher et al. (2009) for additional details on this species.

Vitreorana helenae (Ayarzagüena, 1992)
Plate 5D

Type material.—The original name was *Centrolenella helenae*, based on MHNLS 9431, a male from Quebrada Jaspe, San Ignacio de Yuruaní, Bolívar, Venezuela.

Distribution.—"Known from the type locality...and Salto Karuay, Bolívar, Venezuela, as well as Kaieteur National Park, Guyana" (Frost 2011).

Vouchers for Guyana.—IRSNB 13979–80 from Kaieteur National Park (Kok & Castroviejo-Fisher 2008); and ROM 43980

from the vicinity of the Potaro River (Wokomung Expedition).

Coloration in life.—Dorsal surfaces green to greenish yellow with scattered dark brown flecks; eyelids greenish yellow; fingers and toes bluish green; bones green, iris yellow; ventral surface transparent; parietal peritoneum white, heart not visible (Kok & Castroviejo-Fisher 2008:40).

Comments.—See Kok and Castroviejo-Fisher (2008:40) for comments on the value of certain characters for identifying this species.

Ceratophryidae

We follow Frost et al. (2006) in recognizing this family, which is diagnosed primarily on the basis of DNA sequence data.

Ceratophrys cornuta (Linnaeus, 1758)

Type material.—The original name was *Rana cornuta* for which the type can be seen on-line (http://linnaeus.nrm.se/zool/herp/madamph.html.en, image of NHRM type) (Frost 2011). The type was reported as being from Virginia, obviously in error as the species occurs only in South America.

Distribution.—Amazonian Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, and the Guianas (Frost 2011).

Vouchers for Guyana.—AMNH A-49247 from Shudikar-wau and A-70873–70874 from Kartabo.

Coloration in life.—"About 50% of the individuals are green with brown markings, whereas the others are tan with brown markings...The snout and side of the head usually are unicolor pale green or pale brown, but in a few individuals dark brown diagonal marks are present in the labial region. In brown individuals, the region demarcated by the interocular and paravertebral rows of tubercles is pale tan. Brown markings consist of irregular spots lateral to the paravertebral rows of tubercles and transverse bars on the limbs. The belly and ventral surfaces of the limbs are dull cream, and the throat is brown (black in calling males)" (Duellman 2005:263, based on frogs from Peru).

Comments.—These frogs of low-elevation rain forest have a conspicuous horn over each eye and a huge head and mouth. They are terrestrial sit-and-wait predators, and their exceptionally large gape enables them to include a wide variety of relatively large vertebrates and invertebrates as prey.

Ceuthomantidae

This recently named family (Heinicke et al. 2009) contains three species, all of which occur only in the Guianan Highlands of Venezuela and Guyana. On the basis of extensive DNA sequence data and phylogenetic analyses with related frogs, the ceuthomantids apparently have been evolving as a clade (branch) on the amphibian tree of life separated from their closest relatives for approximately 60 million yr. Only three species of ceuthomantids are known to survive today, with one of them endemic to Guyana. Among other Guyanan frogs, their closest relatives are the Craugastoridae, Eleutherodactylidae, and Hemiphractidae (Pyron & Wiens 2011).

Ceuthomantis smaragdinus Heinicke, Duellman, Trueb, Means, MacCulloch, & Hedges, 2009

Type material.—The holotype is KU 300000, an adult male from the top of Kamana Falls on Mt. Kopinang, part of the Wokomung Massif, Potaro-Siparuni District, Guyana (05°00′08″N, 59°52′47″W) at approximately 1540 m elevation.

Distribution.—This species is endemic to Guyana, known from only two localities at

high elevation (1490–1540 m) on Mount Wokomung and Mount Ayanganna (Heinicke et al. 2009).

Vouchers for Guyana.—Only three specimens are known as follows: the holotype; a paratopotype (KU 315000); and ROM 40161 from Mount Ayanganna (Heinicke et al. 2009:7).

Coloration in life.—"Dorsum dull olive-brown with diffuse black markings on body; black transverse bars on limbs; black longitudinal stripe on inner surface of forearm; black labial bars; broad black canthal stripe; bright, almost phosphorescent green interorbital bar; pair of diagonal marks in scapular region; spot on anterior surfaces of upper arm; distinct green bar below black canthal stripe...; dorsal surfaces of discs on fingers white; dorsal surfaces of toe pads creamy white with black suffusion in terminal notch; venter creamy gray, heavily mottled in black; throat nearly entirely black...; belly mottled black and gray; iris greenish bronze heavily flecked with black" (Heinicke et al. 2009:8).

Comments.—Essentially nothing is known about the biology of these frogs.

Craugastoridae

We follow Pyron & Wiens (2011) in recognizing this family, which is diagnosed primarily on the basis of DNA sequence data. Previously, these frogs were considered as part of the family Leptodactylidae, then Strabomantidae, but the current arrangement is based on the most recent phylogenetic analyses (Pyron & Wiens 2011). In addition, the generic name *Eleutherodactylus* was used previously for most of the species of craugastorids that occur in Guyana, and today these are all assigned to the genus *Pristimantis* (Heinicke et al. 2007), an ancient and diverse South American clade of more than 400 species. There is now one species of true *Eleutherodactylus* that occurs in Guyana (many others occur in the Caribbean), and that is treated in the recently-named family Eleutherodactylidae (see below).

These small to medium-sized frogs are primarily terrestrial but may be found low on vegetation and rocks. Their eggs are laid on land in moist situations (e.g., under cover on a humid forest floor), not necessarily near water. They have direct development; the hatchlings are froglets that immediately take on the terrestrial mode of life.

Pristimantis chiastonotus (Lynch & Hoogmoed, 1977)

Type material.—The original name was *Eleutherodactylus chiastonotus* and the holotype is RMNH 17614, an adult male from Brownsburg, Brokopondo District, Surinam, 500 m.

Distribution.—Guyana and "low elevation forests in northeastern Brazil, French Guiana, and Surinam (below 700 m)" (Frost 2011).

Vouchers for Guyana.—AMNH A-46564 from Marudi and A-46245 and A-91649 from Shudikarwau.

Coloration in life.—"Back and legs ochre-yellow, beige or yellow-orange, with a pattern of light-brown or beige-brown bands of varying width, forming a distinct X-shaped mark on the back, chevrons or oblique bands on the back and flanks, transverse bands on the legs, an interorbital bar, 2 spots on the snout and 2 bands radiating from the eye to the upper lip. The elements of the darker pattern are bordered by a narrow black or dark-brown and a narrow pale yellow line. Some specimens (from Löe Creek and Saül) have a cream-colored vertebral stripe from the tip of the snout to the vent. Canthal and supratympanic stripe dark brown. Dorsally this stripe is bordered by a narrow pale-brown to pale-yellow line passing over the canthus rostralis and the outer edge of the upper eyelid; ventrally there is no sharp border

anterior to the tympanum; in some specimens nearly the whole loreal region and the upper lip are dark-brown. Tympanum chestnut-brown to light brown. A dark-brown spot at the base of the forelimbs is sometimes present. Throat white, dirty-white or yellow with gray spots, belly yellowish-white. Groin, ventral, anterior and posterior surfaces of the thighs, posterior and ventral surfaces of the lower leg and palms bright orange. The soles may be orange, gray or dark-brown. Ventral surface of forelimbs transparent flesh-colored. Iris divided in 3 parts: an upper golden part, a silvery gray, gray-brown, or gray-green lower part, both parts separated by a horizontal reddish-brown bar. Around the pupil a narrow band, anteriorly reddish brown, posteriorly yellow" (Lynch & Hoogmoed 1977:429–430).

Pristimantis dendrobatoides
Means & Savage, 2007
Plate 17A

Type material.—The holotype is USNM 563662, an adult male from the Wokomung Massif, near Falls Camp, Potaro-Siparuni District, west-central Guyana (05°05′25″N, 59°50′18″W, 1385 m).

Distribution.—"Known only from the Wokomung Massif in west-central Guyana in cloud forest habitat (1385–1570 m)" (Means & Savage 2007:45).

Vouchers for Guyana.—ROM 43317, USNM 563661–563662 and USNM 564161–564164, all from the Wokomung Massif.

Coloration in life.—"Upper surfaces of head and body dark purple; head uniformly dark purple except for one or two small interorbital bright red spots and three or four bright red lip spots present in USNM 563661 but absent in the holotype (USNM 563662); one distinct, bright red, round middorsal, suprascapular spot on all seven specimens with 0–4 smaller, round, middorsal suprasacral spots; upper arm bright red or dark purple with several bright red spots; posterior of thigh bright red; lower arm and dorsal surfaces of hands, feet and toes dark purple with bright red spots, more prominent distally; hand red, finger discs purple; upper leg surface purple with small red spots; three obscure reddish cross bands on crus; toe discs outlined by purple. Undersurface of the skin over each dentary dark purple with four discrete, red spots; throat dark purple to black, extending onto the anterior pectoral area as a small bib. Venter below the bib uniformly bright red or, in some individuals, marked with a faint irregular, mid-ventral suffusion of black pigment from bib to hind limb insertions; in some of these, a faint black wash over red is present lateral to the mid-ventral darker pigment (the mid-ventral and lateral dark wash becoming much more pronounced in preservative); underside of legs sprinkled with tiny dark punctuations, most heavily on crus; palmar and plantar surfaces dark purple. Iris black with faint reddish punctations, but thin and continuously outlining the edge of the pupil. No color changes were noted between day and night. Specimens found with dry skin...had a blue-gray cast to their dorsal skin as opposed to wet frogs" (Means & Savage 2007:44).

Pristimantis inguinalis (Parker, 1940)
Plate 17B

Type material.—The original name was *Eleutherodactylus inguinalis* and the holotype is BMNH 1939.1.1.1, a female from the New River, Guyana. Frost (2011) noted that Hoogmoed (in the Frost 1985 version of the Amphibian Species of the World) mentioned that this locality is in an area under dispute between Surinam and Guyana.

Distribution.—"Several localities in Guyana, Surinam, and French Guiana" (Frost 2011).

Vouchers for Guyana.—The holotype; and ROM 40163–40164 from Mount Ayanganna.

Coloration in life.—The following is translated and paraphrased from Lescure & Marty (2000:208), based on specimens from French Guiana. Dorsal surface light brown with large brownish black spots, of which one behind the head is in the form of a W and another in the form of a chevron. Black supralabial bars. Ventral surface light gray with numerous small black dots. Yellowish orange spot in groin. Iris gray to reddish with fine, irregular black lines. Kok & Kalamandeen (2008:240) describe frogs from Kaieteur National Park as having a more variable dorsum ("greenish brown, brown or dark brown"); possible dorsolateral stripe; flecks on ventral surfaces dark brown or white; iris possibly gold in upper part, reddish gray in lower.

Pristimantis jester Means & Savage, 2007
Plate 17C, D

Type material.—The holotype is USNM 563631, an adult male from the summit of the Wokomung Massif called Mt. Wokomung, Potaro-Siparuni District, Guyana (05°04′03.3″N, 59°51′41.8″W, 1560 m).

Distribution.—Known from the slopes and tops of the highest peaks of the Wokomung Massif and from Mount Ayanganna (MacCulloch & Lathrop 2009).

Vouchers for Guyana.—ROM 43303, 43306, and USNM 563631–563633, holotype and paratypes, all from the Wokomung Massif; ROM 40169–40171 from Ayanganna.

Coloration in life.—"Upper surfaces of head and body extremely variable with dark red, light green, and black marbling. In some specimens the red predominates but in others the green and black are more extensive. In one specimen (USNM 563632) a bold, wide, pure orange stripe runs from the tip of the snout to the cloaca; another specimen (USNM 563633) was mostly yellow-green dorsally with four bright red lateral blotches; head olive green, mottled green and black, or with a broad orange medial stripe. Upper lips with red and olive green patches set off by thin yellow green vertical lines; upper arm olive green; lower arm with one or two red and green equally wide crossbands; finger and toe discs dark red to dark gray; upper leg surface with 3 or 4 alternating red and olive green crossbands continuing onto the crus when legs are folded against the body; ... throat, belly, and ventral surfaces of arms and legs mottled in cream and black except in the specimen with the bold middorsal stripe which had a cream colored, midventral longitudinal stripe; upper 2/5 of iris blue gray against the sclera, changing to metallic brown around and below the iris. No color changes were noted between day and night" (Means & Savage 2007:47).

Pristimantis marmoratus
(Boulenger, 1900a)
Plate 17E

Type material.—The original name was *Hylodes marmoratus* and the holotype is BMNH 1947.2.16.92 (formerly 99.3.25.19) from the foot of Mt. Roraima, 3500 ft, reported originally as being from Guyana. However, the type specimen was collected in adjacent Venezuela (Phelps 1938). See below (Vouchers) for records from Guyana.

Distribution.—Occurs widely in the Guiana Shield region in "eastern Venezuela, Guyana, Surinam, and French Guiana; presumably in adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—ROM 40159–40160 and 40162 from Mount Ayanganna; USNM 549318–549319 from the N slope of Mt. Roraima; and USNM 566156 from Ceiba Biological Station along the Madewini River, ca. 42 km S Georgetown on Linden Highway (06°29′57″N, 058°13′06″W).

Coloration in life.—The following is from Kok & Kalamandeen (2008:242), based on observations in Kaieteur National Park: dorsal color variable, brown, greenish brown, grayish brown, reddish brown, or dark brown, with dark markings (one W-shaped on neck); ventral surface grayish white; upper part of iris gray, lower part copper. Lescure & Marty (2000:212) said that the iris has black vermiculations.

Pristimantis pulvinatus (Rivero, 1968a)

Type material.—The original name was *Eleutherodactylus pulvinatus* and holotype is MCZ 64741, female from Paso del Danto, Región de La Escalera around 1400 m above San Isidro, road from El Dorado to Sta. Elena de Uairén, Bolivar, Venezuela.

Distribution.—Western Guyana and "La Escalera and the upland forests of the Gran Sabana region of southeastern Venezuela" (Frost 2011).

Vouchers for Guyana.—ROM 40156–40158 from Mount Ayanganna.

Coloration in life.—Dorsum medium brown, with a dark brown interorbital bar, a dark W-shaped mark on anterior back, and some large blotches and small spots on the posterior back; black supratympanic streak; flanks light brown with oblique gray bars; limbs medium brown with gray crossbands; upper lip with triangular brown blotches on gray background; dark canthal streak may be present. Ventral surfaces dirty white, darker on throat and distal portion of limbs (Rivero 1968a).

Pristimantis saltissimus
Means & Savage, 2007
Plate 17F

Type material.—The holotype is USNM 563639, an adult female from the Wokomung Massif, near Falls Camp, Potaro-Siparuni District, Guyana (05°05′25″N, 59°50′18″W, 1385 m).

Distribution.—Known only from the Wokomung Massif, Guyana.

Vouchers for Guyana.—USNM 563634–563651, 564165–564179, and ROM 43302, 43307, 43309, 43310, 43313, 43314. These are the holotype, paratypes, and referred specimens, all from the Wokomung Massif.

Coloration in life.—"Dorsal color pattern extremely variable due to pattern polymorphism as well as metachrosis... Frogs may be darker or lighter overall, as a result of handling, background coloration, temperature, or time of day. Upper surfaces of head and body light brown to tan with extremely variable dark brown markings that range from small spots or irregular blotches..., through single transverse suprascapular bar, to a series of several oblique bars that extend laterally onto the flanks... Many specimens have an unbroken, cream to light tannish orange colored middorsal stripe highlighted by a suffusion of black pigment laterally...; the stripe may be narrower than the width of a finger or half as wide as the interorbital distance; others have a broad middorsal light tan field bordered laterally by a black margin..., and a few have the dorsum marked with slightly irregular dark and light longitudinal stripes. Head in many individuals with a dark brown interorbital bar set off by tan color on snout...; canthus rostralis usually marked with a strong dark stripe; upper surfaces of arms and legs the same color as dorsum; finger and toe discs pinkish tan; upper and lower legs and crus on some specimens have a hint of three to four light gray and tan alternating crossbands and on others there are three dark brown bands; throat of males white with black smudging or mottling, often white in females; belly and undersurfaces of legs heavily marked with dark pigment sometimes mottles as on throat, but lighter overall...; individuals with a middorsal

stripe also have a mid-ventral, off-white streak...; upper two-fifths of iris dirty gold color, lower three fifths dark brown to black" (Means & Savage 2007:51).

Pristimantis zeuctotylus
(Lynch & Hoogmoed, 1977)
Plate 18A

Type material.—The original name was *Eleutherodactylus zeuctotylus* and holotype is RMNH 17701 from the west slope, Vier Gebroeders Mountain, Sipaliwini, Nickerie District, Suriname.

Distribution.—"Wet rainforests of northeastern South America from extreme southeastern Colombia through Amazonian Venezuela and the Guianas, as well as scattered records from northwestern Brazil and southwestern Brazil" (Frost 2011).

Vouchers for Guyana.—"Rupununi District: N of Acarai Mountains, W of New River, KU 69663; Shudikar-wau, AMNH 43680" (Lynch & Hoogmoed 1977:432); also AMNH A-166327–166336 and USNM 566157–566160 from Berbice River Camp.

Coloration in life.—"Back orange-brown, red-brown, brown, gray brown, or greenish-gray with an indistinct darker pattern of lines and spots; flanks sometimes yellowish-green; snout, in front of eyes, paler than dorsum; upper arm of juveniles orange-brown to yellow; venter dark gray to black; throat with white spots; upper lip spotted black and white; canthal and supratympanic stripe black; tympanum chestnut-brown; iris gold, divided horizontally by reddish-brown band (lower part of iris sometimes darker than upper part)" (Lynch & Hoogmoed 1977:436–437). Field notes of CJC (1997) on the AMNH and USNM series from the Berbice River Camp are consistent with the above and include the following: thin light yellow ring around outer edge of tympanum; iris copper.

Dendrobatidae

Although this family name has been used for about 135 yr (Cope 1865), the family has been reorganized and the Aromobatidae have been split out from within it. We follow Grant et al. (2006) in their revision of the family, which is diagnosed on the basis of five morphological characters as well as considerable DNA sequence data. In the recent past, the generic name *Epipedobates* has been improperly assigned to some of the Guyanan species currently assigned to *Ameerega* and *Dendrobates*.

These small frogs include some species with bright aposematic colors that signal to predators that they have skin glands with powerful toxins; these have potential for biomedical research (e.g., Daly et al. 2005). In many instances, the frogs do not synthesize the toxins but sequester them after they are obtained in small invertebrate prey (e.g., Daly et al. 2000, 2002). The mechanisms of sequestration are unknown. Eggs are laid hidden in moist situations on the ground or in vegetation, and for some species, after hatching, a parent carries the tadpoles to water. There are reports for several species in this family (e.g., Brust 1993, Summers et al. 1999) of females or pairs returning to places where they previously oviposited in nutrient-poor locations and depositing unfertilized or even fertilized eggs, which are consumed by their developing tadpoles.

Ameerega hahneli (Boulenger, 1884)

Type material.—The original name was *Dendrobates hahneli* and BMNH 1947.2.15.17 from Yurimaguas, Huallaga River, Northern Peru was designated lectotype by Silverstone (1976).

Distribution.—"Amazonian lowlands of...Peru, Ecuador, Colombia, Bolivia, Brazil, the extreme south of Venezuela,

French Guiana, and likely adjacent Surinam, and southern Guyana" (Frost 2011).

Vouchers for Guyana.—AMNH A-11667, A-13502–13503, A-23120–23121, A-23126–23127, A-39575–39576, A-39677–39678, A-39681–39686, A-39692–39695, A-39698, A-39702–39704, A-39706–39707, A-39709–39717, and A-70984–70987 all from "Essequibo: Kartabo" (quoted from the AMNH catalog).

Coloration in life.—The following is translated and paraphrased from Lescure & Marty (2000:96), based on specimens from French Guiana: Dorsum black; thin white dorsolateral stripe from snout to groin; fine white stripe edging lower lip, extending to shoulder; sides of body brownish black; small yellow or orange spot in axilla and groin; ventral surface brownish black to black, marbled laterally and posteriorly with light blue; yellow or orange spot on anterior surface of thighs, extending that of the groin and visible on the upper surface; yellow or orange spot on lower leg; iris dark chestnut.

Comments.—Specimens of this species from the Guiana Shield region previously were referred to as *Dendrobates* or *Epipedobates pictus*.

Ameerega trivittata (Spix, 1824)
Plate 5E

Type material.—The original name was *Hyla Trivittata* and RMNH 1836 from Rio Tefé, Brasil was designated as lectotype by Hoogmoed & Gruber (1983).

Distribution.—"Guianas and the Amazon drainage of Brazil, Peru, Bolivia (Pando), Colombia (Putumayo and Amazonia), and Venezuela; presumably in Amazonian Ecuador" (Frost 2011).

Vouchers for Guyana.—Silverstone (1976:48) listed 11 localities scattered around Guyana, each documented with specimens from various museums, including the following: AMNH A-13493, A-24925, and A-70988–70989 from Kartabo, AMNH A-21401 from Kamakusa, AMNH A-45774 from Wismar, AMNH A-46232 from Kuyuwini Landing, AMNH A-46236 from Parabam, and AMNH A-46570 from Marudi. Additional specimens are USNM 535738–535748 from Baramita and USNM 566055 from 6.4 km SE Aishalton.

Coloration in life.—The following notes were recorded on the USNM specimen from 6.4 km SE Aishalton (CJC field notes, 1993): Dorsum black; dorsolateral light stripe bright goldish yellow; lateral light stripe same color as this anterior to arms, but very pale yellow posterior to arms; arms and legs dark green above; hands and feet, above, green with irregular blue spots; posterior of thighs black with irregular blue spots; chin, throat, and chest black; abdomen black with irregular cream or pale blue spots; beneath arms and legs black with irregular blue spots.

Silverstone (1976:47) noted the following for specimens of the pattern type found in the Guianan Region: "The lateral stripes are green, yellow-green, yellow, or orange. The dorsum is black; there is no median dorsal stripe...Specimens from Suriname...[have] green spots...[on] the dorsal surface of the limbs; light blue spots adorned the belly and the ventral surface of the limbs."

Comments.—This species occurs in lowland forests, from "20 to 680 m" elevation (Silverstone 1976:47).

Dendrobates leucomelas Steindachner, 1864
Plate 5F

Type material.—The holotype from Colombia is NMW 19188, according to Häupl and Tiedemann, 1978.

Distribution.—"Guianan Orinoco drainage of Venezuela north to the Río Orinoco, east into Guyana to the Essequibo River, south into extreme northern Brazil, and west into eastern Amazonian Colombia" (Frost 2011).

Vouchers for Guyana.—AMNH A-43823–43825 from "Kopang River" (Silverstone 1975:26), but in the AMNH catalog as "Kumpang"; AMNH A-49942 from "Kurupung River" (Silverstone 1975:26), but in the AMNH catalog as "Kurupung, Upper Mazaruni"; AMNH A-70983 from Kartabo; and USNM 118044 from 16.1 km N Kaieteur Falls on Potaro River.

Coloration in life.—According to Silverstone (1975:26), "most Venezuelan specimens are black with three broad yellow [or orange] transverse dorsal bands containing black intrusions, bands, or spots. The limbs are yellow, spotted with black. The venter is black, sometimes with a yellow spot."

Comments.—This species inhabits lowland moist forests from "50 to 800 m" elevation (Silverstone 1975:26).

Dendrobates nubeculosus Jungfer & Böhme, 2004

Type material.—The holotype is ZFMK 45354, an adult male from Rockstone, Essequibo River, Mazaruni Potaro District, Guyana.

Distribution.—"The collecting site was noted as "Rockstone (5°58′N, 58°32′W) . . .7 m above sea level" (Jungfer & Böhme 2004:102).

Vouchers for Guyana.—Known only from the holotype.

Coloration.—The holotype was collected by ornithologists in the 1980s. "In alcohol, ground colouration of all surfaces dark brown. Dorsal surfaces of head and body with numerous irregular, ill-defined light grey spots (creamy white or yellow in life?), laterally on the body these spots merge to form an irregularly reticulate pattern. Legs and side of head uniformly dark brown, although a few small light spots may have darkened on the dorsal surfaces of the humeri. Ventrally two light brown spots in the pectoral area and a light grey spot on mid-venter. When the specimen is removed from preservative for a few minutes and starts to dry several reddish brown areas appear on the posterior part of the abdomen, dorsally and laterally on the thighs and in the interorbital area, which might indicate lighter reddish brown colouration in the living frog" (Jungfer & Böhme 2004:102).

Comments.—This is one of the most poorly known species in the world. Jungfer & Böhme (2004) suggested that it belongs to the *tinctorius* species group, and its closest relative may be *D. leucomelas*.

Dendrobates tinctorius (Cuvier, 1797)

Type material.—The original name was *Rana tinctoria*. The neotype designation has a complex history (Frost 2011).

Distribution.—"Lowland forests of the Guianas and adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-49301–49328 from Shudikar-wau and USNM 164813 from Kamoa Mountains.

Coloration in life.—Color and pattern are extremely variable. Lescure & Marty (2000) have color photographs of several very different colorations on frogs from French Guiana. The following quotes (Silverstone 1975:45–46) are for specimens geographically relevant to Guyana: "Specimens from the Kayser Mountains, Suriname, are black with dorsolateral stripes; these stripes are yellow on the snout and greenish white on the back, and connect with a greenish white reticulation on the sides of the body [these light areas being yellow or yellow-orange on specimens from French Guiana]. The digital disks are light blue. The limbs and venter are black with dark purplish blue reticulation...Most specimens from Guyana and a few specimens from Suriname have stripes composed of reticulation...Specimens from Shudikar-wau, Guyana, have a dorsal pattern transitional between stripes composed of reticulation and reticulation covering the whole back; some of these

specimens are similar in pattern and color (blue in life, no yellow [R. Snedigar, field notes at AMNH] to *D. azureus*, but the reticulation is broader (i.e., the interspaces are larger)."

Comments.—Silverstone (1975:46) noted similarities between the AMNH series from Shudikar-wau and *Dendrobates azureus* from Suriname (also see above for color) but "the tympanum is larger than in the type material of *D. azureus*. Provisionally, I include the Shudikar-wau population in *D. tinctorius*." Later, a molecular phylogenetic analysis (Wollenberg et al. 2006) confirmed the extreme variability in color and pattern and concluded that *D. azureus* is a junior synonym of the highly variable *D. tinctorius*.

Eleutherodactylidae

Frogs of this family, which is diagnosed primarily on DNA sequence data, until recently were included in the family Leptodactylidae, but molecular phylogenetic analyses have shown that this particular lineage should be split out taxonomically, consistent also with splitting out the Craugastoridae (e.g., Heinicke et al. 2007, Hedges et al. 2008, Pyron & Wiens 2011). These terrestrial frogs are tiny to rather small in size and, for the species studied so far, have direct development; hatchlings are froglets that immediately take on the terrestrial mode of life.

Adelophryne gutturosa Hoogmoed & Lescure, 1984

Type material.—The holotype is BMNH 1983.1139, a male from between camp IV and V, northern slopes of Mount Roraima, Guyana (5°17′N, 60°46′W, 3000 ft [914 m]).

Distribution.—"Guiana Shield, from Mount Roraima and Pakaraima Mountains, Guyana, nearby Venezuela (Bolívar), southern Surinam, southern French Guiana, and to Serra do Veado, Amapá, Brazil" (Frost 2011).

Vouchers for Guyana.—The holotype; IRSNB 13784–13793 from Kaieteur National Park; ROM 39578 from the base of Mount Ayanganna; ROM 43036–43037 from Mount Wokomung; ROM 44050–44051 from Meamu River (06°16′N, 060°30′W); and USNM 549315 from the N slope of Mt. Roraima (5°17′N, 60°45′W).

Coloration in life.—"Dorsal ground colour medium brown or grey. A middorsal black ")(", black canthal and supratympanic bars and other scattered black marks may be present; numerous irregular sky blue or white dots on dorsum and flanks; dorsal surfaces of hind limbs and forearms medium brown or grey, with or without black marks or crossbands and small irregular sky blue or white dots; upper arm orange...Venter brown or grey with small irregular sky blue or white dots; iris copper, with a red ring around pupil. In preservative the orange and sky blue colors become white, otherwise there is little change" (MacCulloch et al. 2008a:46).

Comments.—Although they may be locally abundant, the small size (maximum body length of 16 mm) and secretive habits of *Adelophryne gutturosa* make it difficult to find. It has been found at elevations ranging from 110-1234 m. This species produces large eggs and probably undergoes direct development (for a review of natural history, see MacCulloch et al. 2008a).

Adelophryne patamona MacCulloch, Lathrop, Kok, Minter, Khan, & Barrio-Amorós, 2008 Plate 6A

Type material.—The holotype is ROM 43034, an adult male from the north slope of Mount Wokomung, Guyana (05°06′ 35″N, 059°49′15″W, 1234 m).

Distribution.—This species is known only from Guyana, in the Pakaraima highlands at elevations ranging from 1060–1411 m, but probably also occurs in adjacent Brazil (MacCulloch et al. 2008a).

Vouchers for Guyana.—ROM 43034–43035 from Mount Wokomung. Also IRSNB 1971–1978 from two sites around Mount Maringma (see MacCulloch et al. 2008a:37 for details).

Coloration in life.—"Ground colour of dorsum, flanks and dorsal surfaces of limbs medium brown. Central part of dorsum dark brown, bounded by a black middorsal ")("-shaped mark and interorbital bar. Dorsum with a few other small, scattered black marks. Loreal and temporal regions dark brown. A black bar extending from tip of snout through eye to flank; another black bar in the inguinal region. Dorsal surfaces of limbs with black crossbands. Throat, chest and underside of arms dark grey with white or pale blue spots. Venter, underside of legs and rear of thighs reddish-brown with white or pale blue spots. A black anal spot. Palpebrum not reticulated, a black band along its upper rim. Iris copper with a red ring around pupil...In preservative the venter becomes brownish-grey with white spots" (MacCulloch et al. 2008a:39). "Black dorsal markings are variable; some specimens are darker with more pale blue spots...In the specimens from Maringma the throat, chest and underside of arms are black with white or pale blue spots and a few reddish-brown dots; the venter, underside of legs and rear of thighs are reddish-brown, sometimes with very few white or pale blue spots" (MacCulloch et al. 2008a:41).

Comments.—See MacCulloch et al. (2008a) for notes on natural history. This species reaches a body length of 23 mm, the largest known in the genus.

Eleutherodactylus johnstonei Barbour, 1914

Type material.—There are two syntypes, MCZ 2759 from St. Georges, Grenada.

Distribution.—"Lesser Antilles; likely originally from St. Lucia or the Antigua and Barbuda Bank but also known from the islands of St. Martin, Saba, St. Eustatius, St. Christopher, Nevis, Guadeloupe, Montserrat, Martinique, Bequia, Anguilla, St. Lucia, St. Vincent, Barbados, Grenada, Mustique, Canouan, and Carriacou; definitely introduced on Trinidad, Jamaica, Bermuda, Dominica, Venezuela, Panama, Barranquilla (Colombia), San José (Costa Rica), Curaçao, and Georgetown, Guyana, and coastal French Guiana; likely on coastal Surinam" (Frost 2011). In Guyana, this species is abundant in urban areas of Georgetown, Linden, and New Amsterdam (Bourne 1997).

Vouchers for Guyana.—AMNH A-18981–18982, A-21403–21404, and A-21413; UMMZ 80415, 80443, and 83576; and USNM 118685 and 194416–194428, all from Georgetown.

Coloration in life.—The following is translated and paraphrased from Lescure & Marty (2000:210): Dorsum brown with one or two darker brown chevrons, a W, or two dorsolateral stripes that may be either lighter or darker in color. Ventral surface whitish. Iris golden.

Comments.—Adults usually are smaller than 35 mm in body length. *Eleutherodactylus johnstonei* is a native of Caribbean islands and was introduced into Guyana prior to 1923 (Hardy & Harris 1979, Kaiser et al. 2002). Previously, some Guyanan specimens of this species were misidentified and incorrectly reported as *Eleutherodactylus urichi* (Kaiser et al. 1994); CJC also has re-examined many of these specimens (among the AMNH and UMMZ vouchers cited above), and we are confident that *E. urichi* does not occur in Guyana.

Hemiphractidae

We follow Guayasamin et al. (2008) in recognizing this family, which is diagnosed

primarily on the basis of DNA sequence data, although Frost (2011) commented that the question of monophyly for this group needs confirmation through additional research. Although these frogs appear superficially like large, agile tree frogs and previously were included in the Hylidae, it now appears that Hylidae is not their closest relative (see Guayasamin et al. 2008, Frost 2011, and Pyron & Wiens 2011 for summaries of recent research).

Stefania is the only genus of this family known to occur in Guyana, and it is represented here by seven species, six of which are endemic to Guyana. All other locality records for the genus are in southern and eastern Venezuela, with the exception of one Brazilian species recently described (Carvalho et al. 2010).

These frogs can be found on rocks, in trees, and on the ground in moist areas. For the species for which life history is known, females carry their clutch of relatively large fertilized eggs on their back; being large, the eggs are also few per clutch. There is no brood pouch holding the eggs in place; instead, they adhere by means of a mucoid glue-like substance. The adult female can jump for quite a distance and land abruptly, without the eggs becoming dislodged, so the adhesive and mechanics of the attachment warrant further study. During development, if the eggs become somewhat desiccated the female can rehydrate them in water. There is no free-living larval stage or metamorphosis, as tiny froglets emerge from the eggs. These remain on the back of the female (attached by seat-belt-like membranes) for a short while before dispersing.

Stefania ackawaio
MacCulloch & Lathrop, 2002
Plate 6B

Type material.—The holotype is ROM 39473, an adult male from the northeast plateau of Mount Ayanganna, Guyana (05°24′N, 059°57′W; elevation 1490 m).

Distribution.—Known only from Guyana (MacCulloch & Lathrop 2006a).

Vouchers for Guyana.—ROM 39473–39476 and ROM 40769 from Mount Ayanganna; and ROM 42804–42831 from Mount Wokomung.

Coloration in life.—"Dorsum, top of head and loreal region golden brown with numerous small orange spots. Lips and suborbital region light brown with distinct black mottling on lips and one vertical black bar extending from eye to lip. Ventral margin of supratympanic fold black; this line continues forward along canthus past nostrils to tip of snout. Temporal region and tympanum dark brown. Limbs bronze above, with orange flecks more concentrated on forearm. Transverse bars complete on thighs, incomplete on shanks, tarsi, and forelimbs. Flanks, belly, throat, posterior thigh and ventral surfaces of limbs purple-grey with creamy white mottling most concentrated on chest and throat region and reduced to irregular spots on flanks and limbs. Iris bicoloured, top third gold, lower two thirds reddish brown" (MacCulloch & Lathrop 2002:335–336). In some individuals the dorsal background is grey rather than brown (MacCulloch et al. 2006).

Comments.—There are no data on number of eggs or juveniles per clutch, and the call is unknown.

Stefania ayangannae
MacCulloch & Lathrop, 2002
Plate 6C

Type material.—The holotype is ROM 39501, an adult male from the northeast plateau of Mount Ayanganna, Guyana (05°24′N, 059°57′W; elevation 1490 m).

Distribution.—Known only from Guyana (MacCulloch et al. 2006).

Vouchers for Guyana.—ROM 39501–39551, ROM 39640, and USNM 561833–

561835 from Mount Ayanganna; and ROM 42893–42952 from Mount Wokomung.

Coloration in life.—"Dorsal color is yellowish-brown or yellowish-red with diagonal paravertebral dark brown marks, often joined to form chevrons. A dark brown patch is present on the head, bordered anteriorly by a cream interorbital bar. Canthal, supratympanic and lip bars are dark brown, with a cream vertical line on the tip of the snout. Flanks have five narrow diagonal dark brown bars. The venter is pale yellow with dark brown mottling on the throat. Limbs are yellowish-brown with dark brown crossbands dorsally, pale ventrally with increasing dark brown stippling distally. Palms and soles are darker brown, and the distal phalanges of the toes are red. In some individuals the markings are much less prominent" (MacCulloch & Lathrop 2006b:1).

Comments.—"Intra- and interpopulation variation in disc size, finger length, skin texture and coloration occurs in *Stefania ayangannae* from Wokomung and Ayanganna" (MacCulloch et al. 2006:35). The call is unknown. Number of eggs or juveniles ranges from four to nine per clutch. Means et al. (2008) describe amplexus and oviposition behavior, with photographs showing how the male and female cooperate in getting the eggs placed on the female's back.

Stefania coxi MacCulloch & Lathrop, 2002 Plate 6D

Type material.—The holotype is ROM 39477, an adult female from the northeast plateau of Mount Ayanganna, Guyana (05°24′N, 059°57′W; elevation 1550 m).

Distribution.—Known only from Guyana (MacCulloch et al. 2006).

Vouchers for Guyana.—ROM 39477–39480 from Mount Ayanganna; and ROM 42856–42860 from Mount Wokomung.

Coloration in life.—"The dorsum is medium brown or grey with a few scattered dark brown marks. Flanks are medium brown with darker brown mottling. The lower limbs, hands and feet are light brown with dark brown mottling. The distal phalanges of the toes have a red wash. Dark brown canthal and supratympanic stripes are present. The upper lip is creamy white with black mottling; the lower lip is black with a few white spots. The throat is brown or grey with white mottling; the venter and underside of thighs are white with a variable amount of brown or grey mottling...Neonates are dark grey with immaculate limbs and a cream interorbital bar; some have a dorsal chevron pattern" (MacCulloch & Lathrop 2006c:1).

Comments.—The number of eggs or juveniles ranges from four to six per clutch. The call is unknown.

Stefania evansi (Boulenger, 1904) Plate 6E

Type material.—The original name was *Hyla evansi* and the holotype is BMNH 1947.2.13.11 (formerly 1904.5.30.1; Condit 1964:89) from Groete Creek, Essequibo, Guyana.

Distribution.—This species is known only from "forested lowlands of west-central Guyana, up to 900 m" (MacCulloch & Lathrop 2006d:2).

Vouchers for Guyana.—The holotype; AMNH A-166292–166293, A-166297–166299, A-166302–166307, and USNM 566144–566148 from Konawaruk Camp; IRSNB 13673 and ROM 20555 and 20559 from Tukeit, Kaieteur National Park; ROM 39450–39463 from Mount Ayanganna; ROM 42861–42892 from Mount Wokomung; USNM 129530 from Karta-

bo; and USNM 531494–531499 from Iwokrama Forest Reserve, Sipuruni River, Pakatau Camp.

Coloration in life.—Adults have been reported (MacCulloch & Lathrop 2006d) as usually having one of two dorsal color patterns, either uniform medium brown or dark brown with cream dorsolateral and interorbital stripes. Juveniles may have dark brown dorsal chevrons, but these are rarely seen in adults. Black spots are on the distal portion of the anterior surface of the thighs. The venter is white, often with brown mottling.

The following notes are paraphrased from CJC's field notes (1998) for the AMNH and USNM series from Konawaruk Camp: Dorsum either brown or tan, at times with a wide postocular tan stripe and narrow tan interorbital line, and at times with dark or light brown spots on the back; darker brown mask aside face (nostril to past ear but not evident on every individual); canthal and postocular stripes (to beyond ear) darker brown yet; arms somewhat lighter brown than body, with few darker brown spots; lower legs similar to arms, upper legs of ground color similar to body, with a few more dark brown spots than arms, and very subtle brown bands on thighs; fingers and toes tan, fingers being lightest; toe webbing very dark brown; lips pale with few dark brown spots and a yellow wash that extends along the sides half way toward hip or all the way to groin; upper half of iris tan (metallic copper in sunlight), lower half bronze; venter cream, palest on throat (which may or may not have a copper wash), chest, abdomen, and, on some individuals, with extensive gray smudging; yellow wash ventrolaterally (sometimes extending to legs, abdomen, chest); pale gray mottling beneath legs and arms (less so); grayish brown beneath feet; tip of snout with yellowish tan vertical stripe. A male was noted to have extensive dark brown mottling on the dorsum, conspicuous bands on the legs and arms, and golden finger discs.

Comments.—*Stefania evansi* is the largest member of the genus, up to 97.5 mm snout-vent length, and the most widely distributed. Up to 25 eggs or 30 juveniles on a single female have been reported (Kok & Benjamin 2007, Kok et al. 2006c). For the AMNH series from Konawaruk Camp, the following data may someday be added to calculations of the relationship between female body size and number of eggs per clutch: AMNH A-166307, snout-urostyle length (sul; basically the snout-vent length, but using the firm posterior end of the urostyle bone as the rear point of the measurement) = 66 mm, 16 eggs in attached, intact mass on back; AMNH A-166306, sul = 69 mm, 17 eggs in attached, intact mass on back; AMNH A-166303, sul = 72 mm, 19 babies in clutch, most having been detached in preservative; AMNH A-166304, sul = 72 mm, 19 term embryos in attached, intact mass on back; AMNH A-166305, sul = 73 mm, 13 babies that had become detached in preservative.

Stefania roraimae
Duellman & Hoogmoed, 1984
Plate 6F

Type material.—The holotype is UG [=CSBD] 10, an adult female from Roraima, Guyana, 1402 m.

Distribution.—Known only from Guyana, as follows: "Mounts Roraima, Ayanganna and Wokomung, Pakaraima Mountains...at elevations of 1234–1550 m" (MacCulloch & Lathrop 2006e:1–2). We hypothesize that it also occurs in Venezuelan and Brazilian parts of Mount Roraima, where similar habitats occur.

Vouchers for Guyana.—The holotype; ROM 39466–39469 from Mount Ayanganna; ROM 42836–42855 from Mount Wokomung; and USNM 549313–549314 from Mount Roraima.

Coloration in life.—"The dorsum is dark brown or greyish brown. The top of the head and loreal region are golden brown speckled with orange. The canthus rostralis is outlined in black. The upper lip is mottled in black, with one or two irregular bars extending to the margin of the eye in some individuals. A black supratympanic bar extends halfway down the length of the body. Creamy yellow dorsolateral stripes, continuous with an interorbital bar of similar color, extend to the groin. Flanks are burnt orange fading to brown near belly. Belly, throat and thighs are light to medium brown or grey with white spots which are most numerous on throat and chest, and reduced to a few irregularly shaped spots on thighs, arms and flanks. Indistinct transverse bars are present on dorsal surfaces of shanks and forearms. The top third of the iris is golden, the lower two-thirds dark red. Juvenile coloration resembles that of adults by day. At night juveniles are uniformly yellow-green, with only the outline of the dorsolateral and interorbital stripes visible" (MacCulloch & Lathrop 2006e: 1).

Comments.—"No information is available on reproduction" (MacCulloch & Lathrop 2006e:2).

Stefania scalae Rivero, 1970
Plate 7A

Type material.—The holotype is MCZ 64373, a female from the region of La Escalera, road between El Dorado and Sta. Elena de Uairén, around 1200 m, Bolivar, Venezuela.

Distribution.—Known only from Guyana and Venezuela, in the uplands and highlands of the Pakaraima Mountains.

Voucher for Guyana.—ROM 39470 from Mount Ayanganna.

Coloration in life.—Dorsum medium brown with scattered dark brown spots and dark brown canthal and supratympanic bars. Venter white, possibly with brown mottling. This species is similar in appearance to *Stefania evansi*, but smaller.

Comments.—*Stefania scalae* was synonymized with *S. evansi* by Duellman & Hoogmoed (1984) but was restored to species status by Señaris et al. (1997).

Stefania woodleyi Rivero, 1968b

Type material.—The holotype is BMNH 1967.654, a female (MacCulloch & Lathrop 2006f:1) from a rocky stream on the slope of Mt. Kanaima, near the Potaro River, Guyana.

Distribution.—Known only from Guyana, in the "eastern portion of the Pakaraima Mountain region...at elevations from 200 to 870 m" (MacCulloch & Lathrop 2006f:2).

Vouchers for Guyana.—The holotype; ROM 20570 from Tukeit; ROM 28425–28426 and USNM 561836 from Paramakatoi; ROM 39465 from Mount Ayanganna; and ROM 42832–42835 from Mount Wokomung.

Coloration in life.—"Dorsal surfaces are medium brown with irregular ochre spots or reticulations. Some individuals have an ochre or cream interorbital bar and dorsolateral stripes. Laterally, the head is ochre with a dark brown canthal stripe and irregular medium brown spots in loreal and temporal regions. A dark brown supratympanic stripe continues to the groin. Flanks and groin are medium to dark brown with irregular ochre spots. Dorsal surfaces of thighs and arms are ochre with dark brown transverse bars continuing onto anterior surfaces of thighs; posterior surfaces of thighs are medium brown with white spots. Shanks and tarsi are ochre with dark brown spots or bars. Throat and ventral surfaces of thighs are medium brown with cream to ochre mottling; ventral surfaces of shanks, tarsi and arms are immaculate medium brown. The colour pattern on the chest and belly varies from medium brown with

ochre mottling to ochre with brown mottling...Juvenile coloration is similar to that of adults'' (MacCulloch & Lathrop 2006f:1).

Comments.—"Information on habitat and reproduction is in MacCulloch & Lathrop (2002), MacCulloch et al. (2006), and Rivero (1968b)'' (MacCulloch & Lathrop 2006f:2).

Hylidae

The family Hylidae was named about 100 yr ago (Rafinesque 1815). Its content (genera and species) has changed considerably over time, and recent name-changes, in order to reflect relationships of monophyletic groups, have occurred as a result of modern phylogenetic analyses based primarily, although not exclusively, on DNA sequence data (e.g., Faivovich et al. 2005, Frost et al. 2006). Consequently, significant recent changes in familial and generic names include the following: 1) many species that previously were included in the genus *Hyla* have been transferred to other genera (*Dendropsophus*, *Hypsiboas*, *Myersiohyla*, *Scinax*); 2) species previously in the genus *Ololygon* are now in *Scinax*; 3) species previously in the genus *Phrynohyas* are now *Trachycephalus*; 4) frogs of the genus *Pseudis* previously referred to the family Pseudidae are now in the Hylidae, including *Lysapsus laevis* (previously referred to as *Lysapsus limellus* or *Pseudis laevis*); and 5) the genus *Stefania* has been transferred to a different family, the Hemiphractidae (see above). In addition, a modern phylogenetic analysis on the charismatic poster frogs, or Phyllomedusinae, has provided "a historical framework for a discussion of the evolution of characters associated with reproductive biology, gliding behavior, the physiology of waterproofing, and bioactive peptides'' (Faivovich et al. 2010:227).

These are the frogs most commonly referred to as tree frogs, most of which spend much of their lives in trees or bushes, and they are exceptional climbers. Some of the species are so well adapted to arboreal life (e.g., *Trachycephalus resinifictrix*) that they can exist high in rain forest trees without coming to the ground, as they usually breed in treeholes that are filled with water, in which the tadpoles complete their larval life.

Dendropsophus brevifrons (Duellman & Crump, 1974)

Type material.—The original name was *Hyla brevifrons* and the holotype is KU 126370, an adult male from Santa Cecilia, Provincia Napo, Ecuador.

Distribution.—"The upper Amazon Basin in Ecuador, Perú, and probably western Brazil, to elevations of about 1300 m on the eastern slopes of the Andes. Additionally, the species is known from French Guiana and Belém, Brazil; it probably occurs throughout the Amazon Basin'' (Duellman & Crump 1974:17); Frost (2011) also included Amazonian Bolivia and Colombia.

Vouchers for Guyana.—USNM 566060 from Konawaruk Camp.

Coloration in life.—"The dorsum is olive-tan with brown markings and, in females, distinct creamy tan dorsolateral stripes. The thighs are dark brown; the spots on the thighs and the suborbital bars are creamy yellow. The venter is unpigmented except for the pectoral region and chin (in females), which is white; males have a pale yellow vocal sac. The iris is red medially and silvery gray peripherally'' (Duellman & Crump 1974:17), based on frogs from Ecuador. The following is added from Lescure & Marty (2000:156), based on frogs from French Guiana. Dorsum beige to brown; cream spot in groin; iris gray to chestnut, with a narrow edge of red at the pupil.

Dendropsophus grandisonae (Goin, 1966a)

Type material.—The original name was *Hyla grandisonae* and the holotype is BMNH 1938.10.3.25 from the forest at Mazaruni, British Guiana.

Distribution.—Known only from the type locality.

Vouchers for Guyana.—We are not aware of any specimens other than the holotype.

Coloration.—"Color in alcohol. A very strikingly marked little frog. The dorsal ground color is dark brown with the under surfaces of the chin, throat, and body gray. There is a rather distinct rounded white spot on the occipital region, and the dorsal surfaces of the upper arms are clear white. The patagium, while not white like the dorsal surfaces of the upper arms, is unpigmented. The left heel has been injured, but there is a short white line on the right heel" (Goin 1966a:40). This was published more than 25 yr after the frog was collected.

Comments.—This is one of the most poorly-known frogs in the world. Efforts should be expended to collect additional specimens for comparative analyses and to learn about the natural history of this frog. Faivovich et al. (2005:93) provisionally considered the species to be a member of the *parviceps* species group; their comment (p. 156) about the *microcephalus* group was an error (J. Faivovich pers. comm.).

Dendropsophus leucophyllatus
(Beireis, 1783)

Type material.—The original name was *Ranam leucophyllatam* and the holotype is lost (Frost 2011). The type locality is "unknown, but believed by Beireis to be from Surinam" (Frost 2011).

Distribution.—"The Amazon Basin (Colombia, Ecuador, Peru, Bolivia, and Brazil) and the Guianas; expected but not yet collected in Venezuela" (Frost 2011).

Vouchers for Guyana.—AMNH A-164124–164133 and USNM 531425–531434 from Iwokrama Forest Reserve (several localities); and USNM 129528–129529 from Kartabo.

Coloration in life.—The following is from Lescure & Marty (2000:138) based on frogs from French Guiana. Dorsum with light cream to yellowish tan vividly contrasting with chestnut or chocolate brown; arms and legs with similar colors; flanks chestnut; ventral surface and hidden parts of legs bright reddish orange; iris reddish chestnut.

Dendropsophus marmoratus
(Laurenti, 1768)
Plate 7B, D

Type material.—The original name was *Bufo marmoratus* and type(s) are frog(s) from Surinam "illustrated as *Rana surinamensis* by Seba, 1734, Locuplet. Rer. Nat. Thesaur. Descript. Icon. Exp. Univ. Phys. Hist., 1: pl. 71, figs. 4, 5" (Frost 2011).

Distribution.—"Amazon Basin in Brazil…, Colombia, Ecuador, Peru, Bolivia; southern Venezuela; Guianas" (Frost 2011).

Vouchers for Guyana.—AMNH A-18989 from Kamakusa; AMNH A-24914, A-25234, and A-70948 from Kartabo; USNM 102413 from Arakaka; USNM 284388–284389 from Takutu Mountains (6°15′N, 059°05′W); USNM 535749 from Baramita; and USNM 566092 from Konawaruk Camp.

Coloration in life.—The following is based on the USNM specimen from Konawaruk Camp (CJC field notes, 1998). Gray above, with very dark gray markings; orange axilla and groin; chin white with gray smudging and tiny black dots; chest yellow with black spots; abdomen, beneath upper arms, and beneath upper legs orange with black spots; beneath lower arms, hands, lower legs, and feet black; basal webbing (hands and feet) black, distal webbing bright yellow on

fingers, bright orange on toes; iris light gray with black lines. Kok & Kalamandeen (2008:160) added that the dorsal color may be brown in part, the pattern of coloration is "a network of dark lines and markings that resemble lichens or bird droppings," and the chest may be white with black spots.

Dendropsophus minusculus (Rivero, 1971)
Plate 7C

Type material.—The original name was *Hyla minuscula* and the holotype is UPRM 3377, a male from Nirgua, Yaracuy, Venezuela.

Distribution.—"Llanos of eastern Meta (Colombia) and lowland savannas of southeastern Venezuela eastward through Guianas to Belém, Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-139064–139067 from Aishalton; AMNH A-141041–141045, A-141050–141051, A-167099–167100, and USNM 566093–566096 from Dubulay Ranch. Also USNM 497715 from Karanambo Ranch; USNM 531435–531444 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton and Dubulay Ranch (CJC field notes, 1993, 1994). Dorsum tan or copper, with tiny dark brown dots and a broad darker brown or copper stripe on sides (snout almost to groin), lined above with cream; arms and legs similar in color, but thighs translucent yellow; hands and feet (most inner fingers and toes) pale yellow to gold; throat and abdomen cream to very pale yellow, but many males with a touch of green in the vocal sac; arms and legs translucent below.

Dendropsophus minutus (Peters, 1872)
Plate 7E, F

Type material.—The original name was *Hyla minuta* and the syntypes are ZMB 7456 "and possibly two unlocated specimens" (Frost 2011). The type locality is in Brazil (Frost 2011).

Distribution.—"Lowlands east of Andes from Colombia, Venezuela, and Trinidad southward through Ecuador, Peru and Brazil to Bolivia, eastern Paraguay, Uruguay, and Argentina, up to 2000 m elevation" (Frost 2011).

Vouchers for Guyana.—AMNH A-141033–141036, A-141038–141039, A-167097–167098, and USNM 566097 from Dubulay Ranch; AMNH A-166209–166211 from Konawaruk Camp. Also USNM 162854–162864 from Atkinson (=Timehri Airport); USNM 291171–291172 from Paramakatoi; USNM 531445–531454 from Iwokrama Forest Reserve (various localities); and USNM 535750–535759 from Baramita.

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch and Konawaruk Camp (CJC field notes, 1994–1998). This species has considerable variation in dorsal pattern. Usually the dorsal body, arms, and lower legs are dark tan with conspicuous brown bands on the back. On some individuals, the dorsum is tan with very subtle darker tan markings. One individual was basically patternless dark tan above with scattered pale yellowish gold flecks. Thighs yellow mottled with tan; short white or yellow bar atop vent and at each ankle; all ventral surfaces grayish white to pale yellow, but some individuals translucent tan beneath arms and legs or yellowish green beneath thighs; chin with gray smudges on some individuals; iris tan.

Comments.—All three of the AMNH specimens from Konawaruk Camp were of the patternless morph (one having numerous yellowish gold flecks), whereas those from Dubulay Ranch were of the morph with the conspicuous pattern on the back. Hawkins et al. (2007) reported that analyses of DNA sequences from nine populations sampled across much of the Guianan Region revealed two significant lineages

that differed from each other by 9%. One occurs in the western highlands, one spanned the whole area studied, and both occur "in the area surrounding Imbaimadai, Guyana" (p. 63). The authors found no differences in morphology, ecology, or behavior of these frogs, which may be part of a complex of cryptic species.

"*Hyla*" *helenae* Ruthven, 1919

Type material.—The holotype is UMMZ 52681 from Dunoon, valley of the Demerara River, Guyana.

Distribution.—Known only from the type locality (Frost 2011).

Vouchers for Guyana.—The type series included three adults from the type locality.

Coloration in life.—"Above deep green with numerous well-defined brown spots; thighs, hind feet and inner side of tarsus orange buff, tibiae javel green; fore limbs, except elbows and inner side of feet, asphodel green, elbows viridine yellow, inner side of fore feet orange buff; both fore limbs and hind limbs with light brown cross-bars; upper lip viridine yellow with vertical brown bars; belly white, immaculate. In alcohol the green has faded to a brownish olive, the light markings to dull white" (Ruthven 1919:11).

Comments.—Owing to the lack of specimens, Faivovich et al. (2005) and Frost et al. (2006) were unable to clarify the relationships of this species, so the generic name was placed in quotes to indicate that the taxon is known not to be a natural monophyletic group and future research will result in a change in the generic name.

"*Hyla*" *warreni* Duellman & Hoogmoed, 1992 Plate 8A

Type material.—BMNH 1979.561, an adult female from the north slope of Mt. Roraima (05°38′N, 60°44′W; elevation 1480 m), Rupununi District, Guyana. The quoted latitude corresponds to a location approximately 35 km north of Mt. Roraima and according to Warren (1973) the latitude should be 05°17′N.

Distribution.—Known only from highlands of Guyana (MacCulloch & Lathrop 2005).

Vouchers for Guyana.—The holotype; a paratopotype, KU 182471; ROM 39487–39496 from Mount Ayanganna; ROM 43500 from Mount Wokomung; and USNM 549312 from the north slope of Mount Roraima.

Coloration in life.—"Dorsum ground colour greenish-grey with medium brown blotches outlined in darker brown; fine dark brown or black reticulations between blotches on back. Dorsal dark blotches joined to form two irregular longitudinal stripes in one female. Dorsal pattern of diffuse brown reticulations and scattered dark brown spots on the ground color in two males. Axilla and flanks reddish-brown with dark brown blotches. Posterior thigh surface uniform medium brown with small white spots. Venter white with reddish-brown mottling on throat and chest, changing to small spots on belly. Underside of limbs white with reddish-brown wash. Iris gold to pale green with fine radiating black reticulations. Palpebral membrane not reticulated, upper edge with a broad black band containing tiny white specks" (MacCulloch & Lathrop 2005:24–25).

Comments.—Owing to the lack of specimens, Faivovich et al. (2005) and Frost et al. (2006) were unable to clarify the relationships of this species, so the generic name was placed in quotes to indicate that the taxon is known not to be a natural monophyletic group and future research will result in a change in the generic name.

Hypsiboas boans (Linnaeus, 1758) Plate 8B

Type material.—The original name was *Rana boans* and the types, from unspecified

localities, have had a complicated history (summarized by Frost 2011).

Distribution.—"Lower Amazon Basin, upper Orinoco and Magdalena Basins, Guianas, and Pacific lowlands of Colombia and adjacent Ecuador in South America; eastern Panama; Trinidad" (Frost 2011).

Vouchers for Guyana.—AMNH A-70929–70942 and USNM 118051 and 129535 from Kartabo; AMNH A-141014–141018, USNM 497704, and USNM 566056–566057 from Dubulay Ranch; AMNH A-166135–166137 from Berbice River Camp; AMNH A-166138–166139 and USNM 566058–566059 from Konawaruk Camp. Also ROM 22966 from Baramita; ROM 20556–20558 from Kurupukari; ROM 28420–28421 and USNM 291160 from Paramakatoi; USNM 284387 from Takutu Mountains (6°23′N, 059°05′W); USNM 291105 from Chiung River at Kato; USNM 291196 from Kaieteur; USNM 497699–497703 from Kumu (3°15′52″N, 059°43′34″W); USNM 497811 from Karanambo; USNM 497812–497813 from Moco Moco (3°18′12″N, 059°18′36″W); and USNM 531356–531365 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following notes are based on AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994). Dorsum brown with cream dots (plus darker brown spots and/or pale tan bands on some individuals); legs brown with paler tan bands across thighs; throat and beneath hands greenish gray; chest, abdomen and beneath thighs pale yellow; yellowish gray to pale tan bars on sides; bones green. Kok & Kalamandeen (2008:164) add the following for frogs from Kaieteur National Park: "Ventral surface...white to greenish white, throat white to greenish white in females, greyish in males. Iris bronze, lower eyelid reticulated with silvery gold."

Comments.—This is the largest species of tree frog in Guyana, with a maximum body length of about 132 mm, and males, at least at some localities, are known to defend their nests in basin-like depressions that they construct near water (Kok & Kalamandeen 2008).

Hypsiboas calcaratus (Troschel, 1848)
Plate 8C

Type material.—The original name was *Hyla calcarata* in a book about Guyana and based on a type or types "likely now lost" (Frost 2011).

Distribution.—"Guianas, Amazon Basin from southern Colombia and adjacent Ecuador south through Peru to Bolivia, and Orinoco Basin and delta in Venezuela and Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-166143–166144 and USNM 566061 from Konawaruk Camp. Also USNM 531366–531375 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following notes are based on AMNH and USNM specimens from Konawaruk Camp (CJC field notes, 1998). All dorsal surfaces very dark tan, with or without dark brown to black vertebral line from tip of snout to posterior body; posterior sides, groin, and rear of thigh light gray with chocolate brown bars; throat white; other ventral surfaces translucent gray or tan; very narrow pale yellow lines may be on upper and lower lips, rear of arms, and above vent; feet and spurs on ankles dark brown; iris tan.

Hypsiboas cinerascens (Spix, 1824)
Plate 8D

Type material.—The original name was *Hyla cinerascens* and the syntypes (from Brazil) are ZSM 2498/0, now lost (Glaw & Franzen 2006).

Distribution.—"Guianas and Amazon Basin in Brazil, Colombia, Venezuela, Ecuador, Peru, and Bolivia" (Frost 2011).

Vouchers for Guyana.—AMNH A-166182–166192 and USNM 566086–566090 from Berbice River Camp; AMNH A-166198–166200 and USNM 566091 from Konawaruk Camp; ROM 22750–22753 from Baramita; ROM 43208–43212 and USNM 291197–291211 from Kaieteur; USNM 118053–118054 from Kartabo; USNM 164178 from Mabaruma Compound (8°12′N, 059°47′W); and USNM 531405–531424 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following notes are based on AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1995). Dorsum light green, with conspicuous or inconspicuous yellow spots and possibly one or more irregular chestnut brown patches; chestnut brown bar often on head between eyes; chestnut brown horseshoe-shaped mark often on snout; arms and legs pale green; ventral surfaces translucent bluish green; iris pale coppery silver. Kok & Kalamandeen (2008:168) mentioned "outer edge of upper eyelid yellow," and referred to iris color as "light orange to reddish orange."

Comments.—Until recently, this species was referred to as *Hypsiboas granosus*. Kok (2006b) stated that there may be two or more cryptic species currently referred to as *H. cinerascens*.

Hypsiboas crepitans (Wied-Neuwied, 1824)
Plate 8E, F

Type material.—The original name was *Hyla crepitans* and the lectotype is AMNH 785 from a locality restricted to Tamburil, Bahia, Brazil (Frost 2011).

Distribution.—"Relatively dry habitats in eastern Panama,…Colombia, Venezuela, the Guianas…northern Brazil, below 1700 m elevation" (Frost 2011).

Vouchers for Guyana.—AMNH A-139041–139054, AMNH A-139060–139061, and USNM 566062–566068 from Aishalton; AMNH A-141019–141026, USNM 497705–497714, and USNM 566069–566072 from Dubulay Ranch; and AMNH A-145153 from Berbice River, 1.6 km downriver from Dubulay Ranch. Also ROM 20560 from Kurupukari; ROM 28436–28438 and USNM 291106 and USNM 291161–291168 from Paramakatoi; USNM 146365 from Lethem; USNM 162846–162853 from Atkinson (=Timehri Airport); USNM 291107–291108 from Kawa Valley east of Kato; USNM 291109–291113 from Chiung River at Kato; and USNM 531376–531380 from Iwokrama Forest Reserve, Muri Scrub Camp (4°25′12″N, 058°50′58″W).

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton and Dubulay Ranch (CJC field notes, 1993, 1994). Awake at night in the field, the dorsum is brown with darker brown markings. By day these frogs are very pale gray or green on the back; rear of thigh with bars of pale yellow and orangish yellow; sides with translucent orangish yellow bars; hands and feet orange above and below; throat extremely pale green; chest, abdomen, underside of hind legs and feet orange; bones green.

Hypsiboas fasciatus (Günther, 1858)

Type material.—The original name was *Hypsiboas fasciata* and the holotype from the Andes of Ecuador is BMNH 58.4.25.22 (Frost 2011).

Distribution.—"Guianas and upper Amazon Basin from southeastern Colombia and eastern Ecuador through eastern Peru to Bolivia; possibly to be found in southern Venezuela" (Frost 2011).

Vouchers for Guyana.—AMNH A-122257–122258 from Isheartun, identified by M. S. Hoogmoed; and USNM 531381–531384 from Iwokrama Forest Reserve, Cowfly Camp (4°20′15″N, 058°49′37″W).

Coloration in life.—The following is from Lescure & Marty (2000:128), based on frogs from French Guiana. Dorsal

surface grayish brown, yellowish brown, or chestnut, with subtle cross bands and small black spots; vertebral area may have black spots or a stripe. Flanks and anterior and posterior surfaces of thighs brownish gray, lightly tinged with black spots. Ventral surface whitish, translucent. Iris white to dull silver.

Hypsiboas geographicus (Spix, 1824)
Plate 9A

Type material.—The original name was *Hyla geographica* and the holotype is ZSM 35/0 from Brazil but now lost (Glaw & Franzen 2006).

Distribution.—Very widely distributed in "tropical South America east of the Andes, excluding coastal region from Alagoas to Santa Catarina, Brazil; including Trinidad" (Frost 2011).

Vouchers for Guyana.—AMNH A-70943 from Kartabo; AMNH A-141052–141054, AMNH A-141056, AMNH A-167108, USNM 497817, and USNM 566073 from Dubulay Ranch; AMNH A-166146–166157 and USNM 566074–566079 from Berbice River Camp; and AMNH A-166164–166175, AMNH A-166212–166213 (juveniles), and USNM 566080–566085 from Konawaruk Camp; ROM 28439–28449 and USNM 291169–291170 from Paramakatoi; USNM 163071 from Takama; USNM 291114 from 3.2 km E of Kato; USNM 531385–531404 from Iwokrama Forest Reserve (several localities); and USNM 564214 and 564218 from the summit of Mount Kopinang (5°00′08″N, 059°52′47″W, ca. 1538 m elevation).

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1994–1998). Upper surfaces orangish tan to brown with dark brown or light yellowish tan bands; flanks gray with cream dots and bars; dorsal surface of thigh as dorsal body or gray with lighter gray spots; hands and feet mostly yellowish tan; lips pale yellow, lower ones with gray speckling; throat very pale yellow; anterior chest cream; orange on abdomen and beneath thighs, hands, and feet, brighter on males than females; brown flecks on abdomen; cream to pale yellow beneath arms; dark brown middorsal stripe from snout to midbody; some individuals with several very pale yellow, lichen-like round spots on back; iris copper; bones green. Juveniles can look rather different from adults. AMNH A-166212 was young (SVL = 30 mm) and was noted as being tan above with very subtle darker tan markings; lower flanks black; anterior parts of the hands and feet black, but yellowish orange beneath innermost fingers and toes; webbing dark gray; black along anterior and posterior edges of the hind legs; throat and chest cream with gray smudging; abdomen cream with yellowish orange smudge; gray beneath arms; yellowish orange beneath thighs; iris copper.

Hypsiboas lemai (Rivero, 1972)

Type material.—The original name was *Hyla lemai* and the holotype is UPRM 3179, a female from "Paso del Danto, La Escalera, entre El Dorado y Sta. Elena de Uairén, Serranía de Lema," Bolivar, Venezuela, 1300–1400 m (Rivero 1972:183).

Distribution.—Eastern Venezuela, including Mount Roraima and Guyana (Frost 2011).

Vouchers for Guyana.—ROM 39567–39571 from Mount Ayanganna (MacCulloch & Lathrop 2005:37).

Coloration in life.—"Dorsum medium brown, with dense melanophores on back and upper surfaces of limbs, extending onto fingers III and IV, and toes IV and V; diffuse black interorbital and canthal lines and a faint black supratympanic line. Palpebral membrane unpigmented except for a thin dark brown line along upper

edge. Limbs with dark brown crossbands. Ventral surfaces white. Diffuse whitish patches present on dorsum and limbs of one individual, similar to the photograph in Rivero (1972:189). Scattered white spots present on dorsum in three specimens; one of these also has white dorsolateral lines extending almost to the groin, and anteriorly to the nostrils" (MacCulloch & Lathrop 2005:25–26).

Hypsiboas liliae Kok, 2006b
Plate 9B

Type material.—The holotype is IRSNB 1965, an adult male from between Boy Scout View and Johnson View on the Kaieteur Plateau (5°10′51″N, 59°28′57″W), 400 m elevation, Kaieteur National Park, Guyana.

Distribution.—Endemic to Guyana, known from only two localities.

Vouchers for Guyana.—IRSNB 1965–1968 from the Kaieteur plateau, and UTA A-53052–53054 from scrubby mountains NE of Imbaimadai, Mazaruni-Potaro, Guyana.

Coloration in life.—"Colouration is highly dependent on light intensity. By day: dorsal surfaces bright yellowish green; irregular brown blotch between the eyes; throat and venter blue; central portion of abdomen translucent, white peritoneum visible through ventral skin; posterior part of flank yellowish orange; ventral surfaces of limbs translucent greenish blue; webbing, fingers and disks greenish orange; palm greenish orange; sole greenish blue; upper eyelid yellow; iris silver with black periphery; bones green...At night: dorsum and dorsal surfaces of hind limbs greenish brown and iris bronze. At intermediate light levels, the granules may be greenish brown and brown dots may appear on snout, lips, and upper surfaces of arms and legs" (Kok 2006b:195–196).

Hypsiboas multifasciatus (Günther, 1859)
Plate 9C

Type material.—The original name was *Hyla multifasciata* and the holotype, from Belém, Pará, Brazil is BMNH 1947.2.23.6 (Condit 1964:93, Frost 2011).

Distribution.—"Lowlands of eastern Venezuela, through the Guianas to Ceará and Goiás, Brazil, limited by the Amazon, the Orinoco, and Rio Negro" (Frost 2011).

Vouchers for Guyana.—AMNH A-49360–49363 from Isheartun; AMNH A-141040 and A-167116–167118 from Ceiba Biological Station, Madewini River, ca. 4.8 km (linear) east of Timehri Airport (06°29′57″N, 058°13′06″W); AMNH A-145154 from Dubulay Ranch; AMNH A-166203–166206 and USNM 566098–566099 from Konawaruk Camp; ROM 22755–22759 and USNM 535760–535761 from Baramita; ROM 28435 and USNM 291173–291176 from Paramakatoi; USNM 118043 from Bartica; USNM 118049–118050 from Kartabo; USNM 291116–291121 from Chiung River at Kato; USNM 497716 from Moco Moco (3°18′12″N, 059°39′00″W); UTA A-55292–55293 from Mabaruma, ridge N side of town, NW District, and UTA A-55294–55295 from Mabaruma, along road NE of town ca. 2.0 km, NW District.

Coloration in life.—The following notes are based on AMNH and USNM specimens from Ceiba Biological Station, Dubulay Ranch, and Konawaruk Camp (CJC field notes, 1994–1998). Tan above (body, arms, legs) with darker tan bands and a brown face mask (snout through tympanum); a gray stripe over the tympanum fades quickly posteriorly; gray stripe around chin; darker tan to brown on posterior surface of thighs and on feet; dark brown on lateral edge of forearm and lower leg; anal region black with cream to orangish yellow stripe above vent; undersides yellow to orangish yellow, brightest on throat and chest, the throat having numerous tiny brown dots, but beneath

arms and legs, tan; iris copper or mixed gold and copper.

Hypsiboas ornatissimus (Noble, 1923)

Type material.—The original name was *Hyla ornatissima* and the holotype from Meamu, Mazaruni River, Guyana is AMNH A-13491, an adult female.

Distribution.—"Guianas and Amapá, Brazil, to Guainía, Colombia" (Frost 2011).

Vouchers for Guyana.—The holotype.

Coloration in life.—The following is from Lescure & Marty (2000:134) based on frogs from French Guiana. Dorsum light green to yellowish green, with small reddish brown to yellow spots; dark reddish brown bar edged with yellow across top of head from one eyelid to the other; similarly colored longitudinal vertebral stripe on body, split into a circle or diamond shape in the middle; dark reddish brown spot on nostrils; reddish brown spots on arms and legs; venter greenish yellow; iris reddish brown near pupil, with black outer edge.

Hypsiboas punctatus (Schneider, 1799)

Type material.—The original name was *Calamitae punctatus*. The syntypes from Surinam are at ZUU and ZISP (Frost 2011).

Distribution.—"The Amazon Basin of Ecuador, Peru, Bolivia, and Brazil and the Orinoco Basin...; Chaco of Paraguay, and Argentina; Guianas, northern Colombia in the Sierra Santa Marta, Venezuela (Amazonas, Apure, Bolívar, and Sucre), and Trinidad" (Frost 2011).

Vouchers for Guyana.—UMMZ 83552 from Yarikita River (2 specimens) and UMMZ 83553 from Yarikita River mouth (4 specimens), identified by M. S. Hoogmoed.

Coloration in life.—The following is from Lescure & Marty (2000:136) based on frogs from French Guiana. Dorsal surfaces yellowish green by day, vermillion at night; small yellow or sometimes vermillion spots on back; thin dorsolateral folds vermillion, edged with yellow; ventral surfaces bluish gray but belly yellow; iris grayish.

Hypsiboas roraima
(Duellman & Hoogmoed, 1992)
Plate 9E, F

Type material.—The original name was *Hyla roraima* and the holotype is BMNH 1979.560, an adult female from the north slope of Mt. Roraima (05°38′N, 60°44′W; elev. 1480 m), Rupununi District, Guyana. According to Warren (1973) the latitude should be 05°17′N, as the latitude quoted corresponds to a location some 35 km north of Roraima.

Distribution.—All known specimens are from Guyana, but the species probably also occurs in the Venezuelan part of Mount Roraima (MacCulloch & Lathrop 2005, MacCulloch et al. 2007).

Vouchers for Guyana.—The holotype; the paratypes, KU 182470 and UGDB 14 from Mount Roraima; and ROM 39596–39627 and USNM 561830–561831 from Mount Ayanganna (MacCulloch & Lathrop 2005:37).

Coloration in life.—The following is based on ROM specimens from Mount Ayanganna (MacCulloch & Lathrop 2005:26). "Dorsal ground colour medium reddish-brown with a pattern varying between two extremes: the first having four dark brown patches—on top of snout, between orbits, in scapular region, and in sacral region; the second having only a few small scattered dark brown marks. Dark brown middorsal stripe from tip of snout to posterior dorsum present in 12 individuals; usually, but not always, extending to the groin; middorsal

stripe never present on individuals with dorsal pattern of dark patches. Colour pattern not correlated with sex or size. Scattered dorsal white spots present in some individuals. Limbs with dark brown crossbands, usually most prominent on hind limbs; crossbands reduced to small dark brown spots in some individuals. Axilla pink, flanks pink with dark brown bars or spots and white spots posteriorly in some individuals. Rear of thigh pale brown with small dark brown spots. Upper lip yellow. Venter white; undersides of forearms, hands, tarsi and feet shading to reddish-brown. A row of dark spots along underside of tarsus and onto toe V. Iris pale green to yellow, pupil horizontal. Palpebral membrane with white reticulations, its upper edge with a brown-and-white speckled band."

Hypsiboas sibleszi (Rivero, 1972)
Plate 10A, B

Type material.—The original name was *Hyla sibleszi* and the holotype is UPRM 3177, a male from Paso del Danto, La Escalera, "entre El Dorado y Sta. Elena de Uairén, 1300–1400 m; Serranía de Lema," Bolívar, Venezuela (Rivero 1972:182).

Distribution.—"Moderate [to high] elevations (900-1850 m) in highlands in eastern Venezuela and adjacent Guyana" (Frost 2011).

Vouchers for Guyana.—ROM 39552–39566 and USNM 561832 from Mount Ayanganna; ROM 28450 from Paramakatoi; ROM 43229–43232 from the Kaieteur plateau; and ROM 43408–43409 and 43414 from Mount Wokomung.

Coloration in life.—The following is based on ROM specimens from Mount Ayanganna (MacCulloch & Lathrop 2005:29). "Dorsum greenish-yellow at night, green by day. Both sexes have small brown chromatophores of varying intensity on the dorsum and along upper surfaces of limbs, extending onto Toes IV and V, and Finger IV. Diffuse larger dark brown patches, made up of a concentration of minute spots, between orbits, on dorsum or on shanks in some individuals. Minute dark brown spots on the edge of the lower jaw below tympanum and eye, extending anteriorly to form a continuous line along edge of lower jaw in a few individuals. Scattered round white dorsal spots in several individuals. Pale yellow interorbital and dorsolateral lines present in two males. Digital discs and iris orange; limb bones green. In preservative the dorsal ground color is white and the interorbital and dorsolateral lines are barely visible." Kok & Kalamandeen (2008:174) presented the ventral coloration as "pale green to bluish green, translucent in the central portion of abdomen (internal organs visible)."

Lysapsus laevis Parker, 1935
Plate 9D

Type material.—The original name was *Pseudis laevis* and the holotype is a male, BMNH 1947.2.25.85 (Condit 1964) from the Rupununi Savannah, Guyana.

Distribution.—"Southwestern Guyana and adjacent northern Brazil" (Frost 2011).

Vouchers for Guyana.—The holotype; AMNH A-136028 and USNM 497779–497788 from Karanambo; AMNH A-139159–139170, A-139178–139181, and USNM 566237–566243 from Aishalton.

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo and Aishalton (CJC field notes, 1992, 1993). Pale olive green above (tan after immersion in chloretone), often with gray, brown, or black flecks forming an irregular pattern; some individuals with a rust or dark tan vertebral stripe; tiny cream dots around anal region and rear of thigh; cream stripe on side of body, broken or not; arms similar to body; legs paler, with darker bands of body

color; chin and throat pale green or greenish yellow with cream or yellow dots; chest and abdomen pale yellowish cream with white or cream dots extending rearward to hind legs; arms and legs translucent below; bones green.

Comments.—This aquatic species occurs in savannas, and in the recent past was referred to as *Pseudis laevis*.

Myersiohyla kanaima
(Goin & Woodley, 1969)
Plate 10C, D

Type material.—The original name was *Hyla kanaima* and the holotype is BMNH 1965.230, an adult female from Mt. Kanaima, near Amatuk Falls on the Potaro River, Guyana, at 2300 ft elevation.

Distribution.—Known only from Guyana (MacCulloch & Lathrop 2005).

Vouchers for Guyana.—The holotype; the paratypes; KU 182469 from Mount Kanaima; ROM 39272–39277, ROM 39279–39295, ROM 39580, ROM 39584–39585, ROM 39592, and USNM 561828–561829 from Mount Ayanganna; and USNM 549311 from the north slope of Mount Roraima.

Coloration in life.—"Dorsal background golden to medium brown with dark brown or black longitudinal lines. In many individuals the dark lines form a ")(" dorsal pattern, with additional scattered black marks and narrow canthal and interorbital lines; dorsal lines are broken and/or irregular in some individuals. Dark dorsal lines not present in juveniles. Upper eyelid and snout with small black specks. Scattered dorsal white spots present in some individuals. Flanks white to pale yellow with irregular black spots increasing in size posteriorly. Limbs with irregular black crossbands, most pronounced on dorsal surface of thighs, and small spots extending onto outer fingers and toes. Crossbands fade to fine mottling with small white pustules on posterior thigh surface. Axilla white with a reddish wash. Venter white with small brown spots on throat, variable diffuse brown blotches on chest and belly. Palpebral membrane with white reticulations, upper edge with a white band outlined in black. Iris black. In preservative dorsal ground color tan to medium brown" (MacCulloch & Lathrop 2005:30).

Osteocephalus buckleyi (Boulenger, 1882)

Type material.—The original name was *Hyla buckleyi* and the lectotype is BMNH 1947.2.13.44 with the type locality restricted to Canelos, Ecuador (Frost 2011).

Distribution.—"An arc around the periphery of the Amazon Basin from Colombia to east-central Bolivia, the Guianas and northeastern Brazil (Amapá), at elevations less than 700 m, and to the Orinoco Delta of Venezuela" (Frost 2011).

Vouchers for Guyana.—AMNH A-13492, A-144983, and A-70971 from Kartabo; AMNH A-46233 from Marudi; AMNH A-46283 from Kuyuwini Landing; and AMNH A-49252 from Shudikar-wau, mostly identified by W. E. Duellman and confirmed recently by CJC. Also UTA A-51630–51632 from 9.7 km (by road) S Bartica, near air strip, identified by Smith & Noonan (2001:356).

Coloration in life.—The following, based on frogs from Kaieteur National Park, is from Kok & Kalamandeen (2008:180). "Dorsal ground colour variable, from greenish brown to green, with dark brown markings often in the shape of a black inverted triangle between the eyes followed on the back by a ( ) or a X and two large dark lumbar spots; ventral surface...greyish white, with brown blotches located mainly on throat, chest, and sides of belly; ventral surface sometimes entirely covered by brown flecks. Broad, irregular, green subocular spot...Iris greenish bronze to gold without radiating black lines, but

with irregular black vermiculations...inguinal region and inner thigh blue."

Comments.—See comments in account for *O. oophagus*. In addition, in a recent review of frogs of this group, Jungfer (2010:46) stated that "*O. buckleyi* was believed to be a widespread Amazonian and Guianan species...but in fact it is a complex of several species. Four species in the *buckleyi* complex are dealt with here." However, Jungfer did not include any specimens of *O. buckleyi* from the Guiana Shield in his list of specimens examined. This would indicate that the specimens from the Guiana Shield need further study to determine whether they are in fact this species or an as yet unrecognized cryptic species.

Osteocephalus cabrerai
(Cochran & Goin, 1970)
Plate 10E

Type material.—The original name was *Hyla cabrerai* and the holotype is USNM 152759 from Caño Guacayá, a tributary of the lower Rio Apaporis, Amazonas, Colombia.

Distribution.—"Amazonian Colombia and Ecuador as well as adjacent northeastern Peru...; French Guiana and likely in adjacent Brazil and Surinam" (Frost 2011).

Vouchers for Guyana.—AMNH A-166220–166229 and USNM 566104–566108 from Konawaruk Camp. Also UTA A-51621–51623 from "Imbaimadai, ca. 0.8 km NW Mazaruni camp" (Smith & Noonan 2001:356).

Coloration in life.—The following is based on the AMNH and USNM specimens from Konawaruk Camp (CJC field notes, 1998). Dorsum and arms mottled very dark brown and moss green to light brown (but pale green on sides and anal area); legs and sometimes arms with same colors but patterned in bands; chin, throat, chest, beneath arms and abdomen white (or very pale tan) with distinct tan markings; tan beneath legs; posterior lateral body (anterior to groin) with black bars or other markings alternating with pale green; tympanum translucent copper; iris greenish gold; bones green. Lescure & Marty (2000:182) pointed out that there may be blue on the axillary membrane, in the groin, and on the posterior surface of the thigh.

Comments.—In a recent review of frogs of this group, Jungfer (2010:33) stated that "*Osteocephalus cabrerai* is known from...Colombia...and Peru...There are also specimens from the Guiana Shield and the Orinoco Delta...that I refrain from including in the present study." This would indicate that the specimens from the Guiana Shield need further study to determine whether they are in fact this species or an as yet unrecognized cryptic species.

Osteocephalus exophthalmus
Smith & Noonan, 2001

Type material.—The holotype is UG/CSBD HA-722, adult male cranium of UTA A-51620 from about 30 km SE Imbaimadai, Mazaruni-Potaro District, Guyana, about 585 m (5°37′30″N, 60°14′42″W).

Distribution.—Known only from Guyana (Kok & Kalamandeen 2008).

Vouchers for Guyana.—The holotype; and IRSNB 14644, 14662, and 14664–14665 from Kaieteur National Park.

Coloration in life.—"Light Buff (124) dorsum with suffusions of Raw Sienna (136); loreal area Raw Sienna; area below *canthus rostralis* and dorsal blotches and bars Vandyke Brown, somewhat dark edged; flanks Jet Black (89) with light Buff areolations; anterior area of insertion of limbs Jet Black; iris dark Buff with Jet Black cross radiation from black pupil; area below eye cream-white with small Vandyke Brown markings; Jet Black col-

oration behind posterior corner of eye, bordering transparent tympanum, and continuing to area of insertion of forelimbs; upper area of lower arms dark Buff (24); hand webbing transparent; anterior area of thighs, foot webbing, and anal patch Sepia (119), almost black; white coloration surrounding anal patch, including tubercles, and extending as lines of posterodorsal reticulations to about mid thigh; posterior area of thighs Jet Black; axillary and groin area Pearl Gray (81); throat white with Sepia (119) spotting, stronger on sides; chest, belly and arm ventral areas Drab-Gray (119D); chest with fine Natal Brown (219A) spotting on sides near insertion of limbs; palms Olive Brown (28); ventral surface of thighs Olive Brown (28); ventral shank and tarsal areas pearl Gray; sole of feet Hair Brown (119A); jaw and hind limb bones Emerald Green (163)" (Smith & Noonan 2001:351–352). The numbers associated with colors in the quote refer to "the *Naturalist's Color Guide* (Smithe 1975)" (Smith & Noonan 2001:348).

Osteocephalus leprieurii
(Duméril & Bibron, 1841)
Plate 10F

Type material.—The original name was *Hyla leprieurii* and the holotype from Cayenne, French Guiana is MNHN 4629 (Guibé 1950).

Distribution.—"It occurs on the Guiana Shield in French Guiana, Surinam, Guyana, Venezuela, and northern Brazil southward at least to the Rio Negro and Rio Uaupés" (Jungfer & Hödl 2002:34).

Vouchers for Guyana.—AMNH A-46387 from Onora; AMNH A-70967–70968, A-70976, and USNM 118052 from Kartabo; AMNH A-166235–166239, A-166247–166254, and USNM 566109–566115 from Berbice River Camp; AMNH A-166255 from Konawaruk Camp; and ROM 42997 from Kaieteur. In addition, Smith & Noonan (2001:356) identified the following specimens as this species: AMNH A-70967–70968 from Kartabo; UTA A-51618 from "Imbaimadai, ca 100 m W Mazaruni camp"; and UTA A-51619 from "Imbaimadai, Mt. NE Imbaimadai."

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). Brown above with darker brown markings; dark brown canthal stripe or face mask; anterior and posterior surfaces of thighs orange; varying degrees of translucent orange on ventral surfaces of legs and toe webbing; belly varies from light to bright yellow; iris gold and black on upper half, brown below. Kok & Kalamandeen (2008:184) referred to the dorsum as "ranging from ochre, tan or reddish tan to dark tan, usually with up to four narrow, usually fragmented, dark brown transverse lines, and a narrow dark brown interorbital bar."

Osteocephalus oophagus
Jungfer & Schiesari, 1995
Plate 11A

Type material.—The holotype is MZUSP 69852, an adult male from Reserva Florestal Adolfo Ducke (2°55′S, 59°59′W), km 26 on the Rodovia AM-010 (Manaus-Itacoatiara), Amazonas, Brazil.

Distribution.—"The species is found in the Guiana Shield and in the Amazon Basin, from east and north of State of Pará to eastern Colombia" (Kok & Kalamandeen 2008:186).

Vouchers for Guyana.—AMNH A-166214–166216 and USNM 566102 from Berbice River Camp; AMNH A-166219 and USNM 566103 from Konawaruk Camp; and ROM 44202–44230 from Kaieteur.

Coloration in life.—The following is based on the AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). Dorsum brown or grayish tan

with dark brown markings; all ventral surfaces tan, chin, throat, and chest with darker tan markings; iris gold, with contrasting black radiating lines. Kok & Kalamandeen (2008:186) stated that "individuals with white spots [on the dorsum] are reported."

Comments.—This species is smaller than *O. taurinus*, which also has the alternating gold and black radiating lines on the iris, but males of *oophagus* have a single, median vocal sac, not paired sacs as in *taurinus*. There are no supraorbital tubercles and there are small tarsal tubercles, but each of the latter usually has a white spot that makes it appear more conspicuous than the tubercle itself really is – not near as large as the tarsal tubercles of *O. buckleyi*, which also has 1–8 enlarged supraorbital tubercles.

Fertilized eggs are usually laid in small pockets of water in vegetation, where the tadpoles develop, although few nutrients may be present. However, the parents often return to the site, undergo amplexus again, and deposit fresh fertilized eggs, which the tadpoles consume (Jungfer & Weygoldt 1999).

Osteocephalus phasmatus MacCulloch & Lathrop, 2005 Plate 11B

Type material.—The holotype is ROM 39481, an adult female from the northeast plateau of Mount Ayanganna, Guyana, (05°24′N, 059°57′W; 1490–1550 m).

Distribution.—Known only from Guyana, in the Pakaraima highlands (MacCulloch & Lathrop 2005).

Vouchers for Guyana.—ROM 39481–39485 and ROM 43852 from Mount Ayanganna (MacCulloch & Lathrop 2005).

Coloration in life.—"Dorsum medium brown with scattered black flecks. Tympanic region and upper lip dark brown. Flanks and groin white with dark brown reticulations. Rear of thigh brown with small white spots. Venter white with dark brown reticulations on throat and chest. Palms and soles with scattered melanophores. Long limb bones green. Iris gold with dense black reticulations and a median horizontal brown bar" (MacCulloch & Lathrop 2005:22).

Osteocephalus taurinus Steindachner, 1862 Plate 11C

Type material.—The holotype is NHMW 16492 (Häupl & Tiedemann 1978) from Manáus, Brazil (Frost 2011).

Distribution.—"Amazon Basin of Ecuador, Brazil, Bolivia, Peru, Colombia, as well as the upper Orinoco Basin of Venezuela, and the Guianas" (Frost 2011).

Vouchers for Guyana.—AMNH A-145156–145158 and USNM 566166 from Dubulay Ranch; AMNH A-166256–166263, A-166268 and USNM 566117–566120 from Berbice River Camp; AMNH A-166269 and USNM 566121 from Konawaruk Camp; ROM 22737–22739 from Baramita; ROM 42996 from Kaieteur; USNM 118057 from Kartabo; USNM 291274–291275 from Paramakatoi; and USNM 531455–531474 from Iwokrama Forest Reserve (various localities). In addition, Smith & Noonan (2001:357) identified the following specimens as this species: AMNH A-21418–21419 from Kamakusa; UTA A-51628–51629 from ca. 1.0 km N Imbaimadai, Peters Mt.; UTA A-51625–51627 from ca. 3.4 km N Imbaimadai, Peters Mt.; and UTA A-51624 from 1.6 km (by road) W Kartabu Point.

Coloration in life.—The following notes are based on AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1995). Tan above, with brown markings; spots on sides and anal spot black; throat and chest cream with gray or brown spots, but throat pale yellow on some; bones green; iris gold with black radiating lines. Kok & Kalamandeen

(2008:188) noted that the dorsum may be dark brown and some individuals have a yellow middorsal stripe or small cream spots.

Phyllomedusa bicolor (Boddaert, 1772)
Plate 11D

Type material.—The original name was *Rana bicolor*, the type locality was restricted to Surinam, and the holotype is not known to exist (Frost 2011).

Distribution.—"Amazon Basin in Brazil, Colombia, Bolivia, and Peru; the Guianan region of Venezuela and the Guianas" (Frost 2011). Kok & Kalamandeen (2008) included Amazonian Ecuador also.

Vouchers for Guyana.—AMNH A-70978–70979 from Kartabo; ROM 22740 from Baramita; ROM 28419 from Paramakatoi; and USNM 531597–531606 from Iwokrama Forest Reserve (various localities).

Coloration in life.—"Dorsal colour green, dark green by night;...Ventral surface...light grey, sometimes with a few white ocelli. White ocelli on lower lip, flank, and hidden surfaces of thigh. Iris silvery grey" (Kok & Kalamandeen 2008:192).

Comments.—This species is the largest of the leaf frogs, attaining a body length of 115 mm (Kok & Kalamandeen 2008).

Phyllomedusa hypochondrialis (Daudin, 1800)
Plate 11E

Type material.—The original name was *Hyla hypochondrialis* based on material from Surinam. See Frost (2011) for a discussion about possible type specimens.

Distribution.—"Eastern Colombia east through northern and eastern Venezuela, through the Guianas and throughout Brazilian Amazonia; currently not known from Amazonian Colombia, Peru, Ecuador, or Bolivia" (Frost 2011).

Vouchers for Guyana.—AMNH A-70980 from Kartabo; AMNH A-141106 from Ceiba Biological Station, Madewini River, ca. 4.8 km (linear) east of Timehri Airport (06°29′57″N, 058°13′06″W); AMNH A-141107–141112, A-141115–141116, A-145152, and USNM 566124–566125 from Dubulay Ranch; AMNH A-166271–166276 and USNM 566126–566129 from Berbice River Camp; and AMNH A-166280–166281 from Konawaruk Camp.

Coloration in life.—The following is based on AMNH and USNM specimens from Ceiba Biological Station, Dubulay Ranch, and Konawaruk Camp (CJC field notes, 1994–1998). Leaf green above, set off on lower arms and legs by thin cream stripe; posterior half of sides, upper arms, and thighs (but for narrow green dorsalmost area) and feet bright orange with dark blue or purple bars and reticulate markings; lips cream, the lower lips edged posteriorly with row of black dots; chest very pale yellow or orange; abdomen and ventral surfaces of thighs pale yellow or darker pale orange; iris metallic tan with black reticulation.

Comments.—In the recent past, the specific epithet has been incorrectly spelled without the middle *h* as *hypocondrialis* (Lescure et al. 1995).

Phyllomedusa tarsius (Cope, 1869)

Type material.—The original name was *Pithecopus tarsius* and the holotype is USNM 6652 (now lost, according to Duellman 1974) from the Rio Napo, Departamento Loreto, Peru.

Distribution.—"Amazon Basin in southern Colombia, Ecuador, Peru, and Brazil, . . .as well as. . .eastern Venezuela" (Frost 2011); recently reported from Guyana (Forlani et al. 2012).

Vouchers for Guyana.—AMNH A-13552 from "British Guiana" (quoted from the AMNH catalog; no additional locality data). The specimen was collected by W. Beebe, identified by D. Cannatella in 1978, and recently confirmed by CJC. Most recently Forlani et al. (2012) reported specimens (with color photographs) from the vicinity of the hydropower dam site on the Kuribrong River, Potaro-Siparuni District, Guyana; vouchers are UG (=CSBD) HA 1000, 1001, 1100, and 1101.

Coloration in life.—The following is from Duellman (1978:178), based on specimens from Ecuador. "The dorsal surfaces and sides of the head are green. The flanks are dull green or bluish green with discreet or confluent cream, pink, or pale orange spots. The anterior and posterior surfaces of the thighs are brown or dull green with cream, pale orange, or bluish-gray spots. The throat, chest, and ventral surfaces of the limbs are dark brown or grayish-brown; the belly is gray or pale orange-brown. Ventral markings consist of a pair of white spots on the throat, a median white spot on the chest, and usually a pair of para-anal white spots. The iris is bright orange with bold black reticulations."

Phyllomedusa vaillantii Boulenger, 1882
Plate 11F

Type material.—The holotype is BMNH 1947.2.22.34 (Condit 1964:98), a female from Santarem, Brazil.

Distribution.—"Guianas and Amazon Basin from Guyana, Surinam, French Guiana, and northeastern Brazil to Colombia, Ecuador, Peru, and northern Bolivia; reported from Cerro Neblina, Amazonas, Venezuela" (Frost 2011).

Vouchers for Guyana.—AMNH A-166282, A-166286–166290, and USNM 566130–566132 from Berbice River Camp; USNM 531607–531616 from Iwokrama Forest Reserve (various localities); and USNM 531781–531783 from Baramita.

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). Green dorsum, but greenish brown on snout, blending gradually (posteriad) into the green of the midbody; yellow spots ventrolaterally, becoming orangish red in groin; orangish red on wrist, behind upper arms, on anterior and posterior surfaces of thighs, and anterior lower legs; chestnut brown posteriolaterally on lower arms and ventrally on lower legs and feet; chin, throat, chest, and abdomen pale chestnut brown; small white spots often on throat and chest; on body, inconspicuous dorsolateral line of tiny yellow dots; iris light copper. Kok & Kalamandeen (2008:194) refer to the iris as "silvery grey" and the lower lip as white.

Pseudis paradoxa (Linnaeus, 1758)

Type material.—The original name was *Rana paradoxa* and the syntypes from Surinam are NHRM 144–148 (Frost 2011).

Distribution.—"Lower Río Magdalena Valley as well as Arauca and Meta in Colombia; Guianas from northeastern Venezuela east through Guyana, Surinam, and French Guiana to the mouth of the Amazon, thence west in the Amazon Valley to northern Bolivia and southeastern Peru; Trinidad" (Frost 2011).

Vouchers for Guyana.—AMNH A-70918–70920 from Kartabo (identified by R. G. Zweifel); and USNM 162975–162981 from Enmore Estate (6°44′N, 057°59′W).

Coloration in life.—The following is from Lescure & Marty (2000:284) based on frogs from French Guiana. Dorsal surface green, especially in the anterior part, and brown, especially in the posterior part, speckled with dark spots; flanks, limbs, and posterior surface of thighs

brown, spotted with white; ventral surface white, more or less flecked with brown spots and with 3–4 brown lines more or less anastomosing or converging at the level of the thighs; brown reticulation on the underside of the limbs; iris golden yellow with a horizontal chestnut bar.

Comments.—"These are moderately large aquatic frogs; at least one species, *Pseudis paradoxa*, is well known for its gigantic tadpole" (Duellman 2005:261).

Scinax boesemani (Goin, 1966b)
Plate 12A

Type material.—The original name was *Hyla boesemani* and the holotype is RMNH 12601, an adult male found near Zanderij, Suriname District, Suriname.

Distribution.—"Northern Guyana, Surinam, and French Guiana, and Amazonas, Venezuela, to Amazonas and Pará, Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-145160, A-167101–167102, and USNM 566133 from Dubulay Ranch; ROM 43219–43228, USNM 291215–291219, 291221–291234, and 497717 from Kaieteur National Park; and USNM 531475–531492 from Iwokrama Forest Reserve (several sites).

Coloration in life.—The following is based on the AMNH specimens from Dubulay Ranch (CJC field notes, 1994). Brown above on all surfaces; dark brown mask from snout, through eye, over ear, then slanting downward and breaking up into spots; throat yellow; chest and abdomen cream; translucent tan beneath arms; translucent green beneath legs; iris copper speckled with black; bones green. Kok & Kalamandeen (2008:198) add that the dorsum may have cream or yellow spots, flanks may have dark brown spots, and the "hidden surfaces of thighs [are] greyish brown."

Scinax cruentommus (Duellman, 1972)

Type material.—The original name was *Hyla cruentomma* and the holotype is KU 126587, an adult male from Santa Cecilia on the Río Aguarico, Provincia Napo, Ecuador (0°02′N, 76°58′W; 340 m).

Distribution.—"Amazon Basin in Ecuador and northern Peru (drainages of the Río Napo, Río Marañon, and Río Ucayali); reported from 70–90 km north of Manaus, Brazil; possibly in Amazonian southeastern Colombia" (Frost 2011).

Vouchers for Guyana.—AMNH A-49447 from "British Guiana" (quoted from AMNH records, with no additional locality data available), collected by R. Snedigar on the Terry-Holden Expedition, 1937–1938, identified by Julian Faivovich.

Coloration in life.—"When collected [at night] pale yellow above with indistinct tan dorsolateral stripes. Later [day] changed to tan with olive-brown markings. Vocal sac bright yellow. Iris pale bronze with median horizontal reddish copper streak. Palpebrum clear. Bones green...[the foregoing for some individuals; the following for others] Dorsum varies from yellow to brown to tan to gray-green with or without distinct markings. Markings are brown to yellow-brown to greenish brown. Flanks yellow with or without brown spots. Iris silver with red horizontal streak. Posterior surfaces of thighs yellow-brown. Vocal sac deep yellow; venter pale yellow (males). Belly and throat of female white" (Duellman 1972:268).

Scinax nebulosus (Spix, 1824)

Type material.—The original name was *Hyla nebulosa* and the neotype is MNRJ 4055 from Belem, Para, Brazil (Hoogmoed & Gruber 1983, Glaw & Franzen 2006).

Distribution.—"Southeastern Venezuela, through the Guianas and the lower Amazon region to Alagoas in northeastern

Brazil; also Amazonian Bolivia" (Frost 2011).

Vouchers for Guyana.—AMNH A-46497 and A-93335–93336 from the "Upper Rupununi River"; and AMNH A-141126–141128, A-141131–141134 and USNM 566134–566135 from Dubulay Ranch, all identified by Julian Faivovich; USNM 129534 from Kartabo; USNM 162842–162845 from Atkinson (=Timehri Airport); USNM 162913–162914 from Enmore Estate (6°44′N, 057°59′W); and USNM 497718 from Kumu, at base of Kanuku Mountains (3°15′52″N, 059°43′34″W).

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994). Grayish tan to brown above (after chloretone; had looked gray at night); some individuals with dark brown markings, including bands on thighs; throat cream or pale gray, with dark gray or black speckles; abdomen cream or light gray; undersides of arms and legs translucent gray. Lescure & Marty (2000:164) add that specimens may be brown or brown and green above, with an inconspicuous interorbital triangle, there are black bars over dark blue on the hidden surfaces of the hind limbs, and there is a black spot in the groin.

Scinax proboscideus (Brongersma, 1933)

Type material.—The original name was *Hyla proboscidea* and the holotype from Surinam is number Z. 354 of the Zoological Museum of Amsterdam (in the process of being transferred to the RMNH).

Distribution.—"Interior of the Guianas" (Frost 2011) and Brazil (M. S. Hoogmoed, pers. comm.).

Vouchers for Guyana.—AMNH A-49248–49249, 49251, and 49254 from Shudikar-wau, identified by W. E. Duellman and confirmed recently by CJC; also USNM 531493 from Iwokrama Forest Reserve, Siparuni River, 4°45′17″N, 050°01′28″W.

Coloration in life.—The following is from Lescure & Marty (2000:166), based on frogs from French Guiana. Dorsum brown, with a darker interorbital triangle and bars; flanks and anterior surface of thighs greenish, more or less marbled with black; posterior surface of thighs orange with broad black bars, at times extending onto the posterior surface of the shank; ventral surface reddish brown, but the throat is white in females, grayish in males, and the belly is white; iris gold to silver with a horizontal brown band across the middle.

Scinax ruber (Laurenti, 1768)

Type material.—The original name was *Hyla rubra* and the neotype is RMNH 15292B from Paramaribo, Surinam (Frost 2011).

Distribution.—"Amazon Basin of Brazil, Peru, Colombia, and Ecuador; Guianas; coastal northern South America; eastern Panama; Tobago, Trinidad, and St. Lucia (Lesser Antilles). Introduced on Puerto Rico" (Frost 2011).

Vouchers for Guyana.—AMNH A-141121, A-141124, A-145161, and USNM 566136 from Dubulay Ranch; also USNM 118055 from Kartabo; USNM 162865–162871 from Atkinson (=Timehri Airport); USNM 162915–162938 from Enmore Estate (6°44′N, 057°59′W); USNM 164165–164177 from Mabaruma Compound (8°12′N, 059°47′W); USNM 284390–284391 from Takutu Mountains (6°15′N, 059°05′W); USNM 497719 from Karanambo Ranch; USNM 497720 from Georgetown, 300 New Garden Street (6°48′N, 058°10′W); and USNM 535762–535772 from Baramita.

Coloration in life.—The following is based on AMNH specimens from Dubulay Ranch (CJC field notes, 1994). Dorsum

tan, with dark brown stripes (two each side); arms and legs tan above with brown spots; yellow below (brightest on throat), but greenish yellow beneath hind legs.

Comments.—Following analyses of DNA sequences of frogs from the Guianan Region, Fouquet et al. (2007b) suggested that several cryptic species might be masquerading under the name *Scinax ruber*.

Scinax trilineatus (Hoogmoed & Gorzula, 1979)

Type material.—The original name was *Ololygon trilineata* and the holotype, from 12 km SE El Manteco, Bolivar, Venezuela, is RMNH 18257 a female.

Distribution.—"Scattered localities in the lowlands of eastern Venezuela and savannas of Guyana and Surinam, as well as adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-43673 from Isheartun; AMNH A-46248 from Rupununi River near Mora, east of Mt. Tirke; and AMNH A-97944–49 from Parabam, identified by M. S. Hoogmoed.

Coloration.—We found no description of coloration in life for these very small frogs. "Colour in preservative light brown to greyish brown with a pattern of dark brown longitudinal stripes: a narrow [dark brown] vertebral stripe, wider dorsolateral bands. Flanks either uniform dark brown or with a dark lateral band along the lower part. A dark brown canthal stripe. Ventral parts immaculate, white to pale brown" (Hoogmoed & Gorzula 1979:193).

Scinax cf. *x-signatus* (Spix, 1824) Plate 12C, D

Type material.—The original name was *Hyla x-signata* and the holotype is ZSM 2494/0, now lost (Glaw & Franzen 2006), from Provincia Bahia, Brazil.

Distribution.—"Non-forest habitats of northern Colombia and Venezuela to Surinam; eastern, southern, and southeastern Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-139068–139076, A-139086, and USNM 566137–566143 from Aishalton; AMNH A-141120, A-141123, A-141125, A-145162, and A-167107 from Dubulay Ranch, most of which were identified by Julian Faivovich; and ROM 22745–22749 from Baramita.

Coloration in life.—The following is based on AMNH specimens from Aishalton and Dubulay Ranch (CJC field notes, 1993, 1994). Brown or tannish gray above (body, arms, lower legs) with dark gray, brown, or black markings (although uniform dark brown when photographed); thighs with very narrow stripe colored as upper body, but anterior and posterior to this are black-edged yellow or gold spots or mottling (also below shanks and on anterior of ankle and upper foot); white or cream on chin and chest, chin with gray dots; abdomen translucent gray; fleshy pink where translucent (especially on thigh); iris copper with black reticulation. Lescure & Marty (2000:174) add that there are black and orange patches on the flanks and in the groin, and the ventral surface may be yellow in males from French Guiana.

Comments.—Application of the name *S. x-signatus* to specimens from Guyana needs additional research (J. Faivovich, pers. comm.).

Scinax sp. Plate 12B

Voucher for Guyana.—AMNH A-166499 from Berbice River Camp, identified by Julian Faivovich.

Coloration in life.—The following is based on the only known specimen (above; CJC field notes, 1997). All dorsal surfaces tan (darker and lighter); all ventral surfac-

es very pale translucent tan, but chin and throat yellow; iris a reticulation of black and copper.

Comments.—This is probably a new species. Additional specimens should be collected and studied, and the species should be named.

Sphaenorhynchus lacteus (Daudin, 1800)

Type material.—The original name was *Hyla lactea* and the holotype, from an unspecified locality in Amérique, is in the MNHN (Frost 2011).

Distribution.—"Amazon and Orinoco basins of Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil; Guianas, and Trinidad" (Frost 2011).

Vouchers for Guyana.—AMNH A-1327–1328 and A-13048 from "British Guiana" (no additional data in AMNH catalog); ROM 11081 and 11090 from the vicinity of Georgetown; USNM 127888 from Akyma, Demerara River (5°53′N, 059°18′W); and USNM 162942 from Enmore Estate (6°44′N, 057° 59′W).

Coloration in life.—The following is based on Lescure & Marty (2000:178) for frogs from French Guiana. Dorsal and lateral surfaces green to yellowish green, with a light dorsolateral line; thin brown stripe from snout to eye; ventral surfaces bluish gray, except belly white; males with yellow vocal sac; outer areas of limbs and above vent with light edging; iris orange.

Tepuihyla talbergae
Duellman & Yoshpa, 1996

Type material.—The holotype is CSBD 198920, an adult male from Kaieteur Falls, 366 m (05°10′N, 59°28′W), Mazaruni-Potaro District, Guyana.

Distribution.—Known only from Guyana, endemic to Kaieteur National Park (Kok & Kalamandeen 2008).

Vouchers for Guyana.—The holotype; BMNH 1938.10.3.26 from Kaieteur; KU 221735 collected with the holotype; and ROM 42983–42984 and USNM 291235–291237 from Kaieteur National Park.

Coloration in life.—"Dorsum grayish tan with minute dark brown flecks on body and faintly darker transverse bars on limbs—one on forearm, three on shank, and two on tarsus. Dark brown canthal stripe from nostril to eye; narrow dark brown line from posterior corner of orbit to point above tympanum; narrow creamy white labial stripe continuous with creamy white venter on anteroventral edge of insertion of arm. Tubercles in cloacal region and tips of discs on digits creamy white; iris pale silvery bronze with black flecks" (Duellman & Yoshpa 1996:278). Kok & Kalamandeen (2008:204) provide additional details on coloration.

Trachycephalus coriaceus (Peters, 1867)
Plate 12E

Type material.—The original name was *Hyla coriacea* and the syntypes are ZMB 5807 (3 specimens; Bauer et al. 1995) from Surinam.

Distribution.—"French Guiana, Surinam, and Upper Amazon Basin in Colombia, Ecuador, Peru, Bolivia, and downstream to near Manaus, Brazil" (Frost 2011).

Vouchers for Guyana.—IRSNB 13672 from Kaieteur National Park (Kok et al. 2005); USNM 566122 from Berbice River Camp.

Coloration in life.—The following is based on the USNM specimen from Berbice River Camp (CJC field notes, 1997). Dorsal surfaces tan, with greenish brown markings (including large dorsal hourglass); sides yellow; black patch on

shoulder; chin, throat, and chest yellow; abdomen of yellow warts surrounded by reticulation of bright orangish red; ventral posterior thigh area likewise; anterior of arms, hands, narrow throat band, narrow chest band, anterior and posterior of thighs, ventral surface of lower legs, and feet all bright orangish red; iris copper. Kok & Kalamandeen (2008:208) add that the dorsal ground color is reddish brown by night and there is "a saddle-shaped dark brown blotch over the sacrum."

Trachycephalus hadroceps
(Duellman & Hoogmoed, 1992)

Type material.—The original name was *Hyla hadroceps* and the holotype is KU 69720, an adult male from area north of Acarai Mountains, west of New River (ca. 02°N, 58°W), Rupununi District, Guyana.

Distribution.—"Extreme southern Guyana; French Guiana; presumably in adjacent Surinam" (Frost 2011).

Vouchers for Guyana.—The holotype is the only specimen known from Guyana.

Coloration in life.—The following is based on frogs from French Guiana (Lescure & Marty 2000:192). Dorsal surface light chestnut with a dark brown preorbital area and a large, equally dark brown dorsal area across middle of back and extending onto sides at axilla and groin; limbs with dark brown transversal bars; toe discs light green; ventral surface greenish, speckled with brown, almost marbled on throat; iris chestnut to beige, with a brown horizontal bar and at times a vertical one below the pupil, thus making an incomplete cross.

Trachycephalus resinifictrix (Goeldi, 1907)
Plate 12F

Type material.—The original name was *Hyla resinifictrix* and the holotype is BMNH 1947.2.23.24 (Condit 1964:94) from Mission of Santo Antonio do Prata at the River Maracanã (interior of the State of Pará).

Distribution.—"Widespread from eastern Ecuador, Peru and northern Bolivia through the Amazon Basin to the Guiana Shield" (Kok & Kalamandeen 2008:210).

Vouchers for Guyana.—IRSNB 14756 from Kaieteur National Park.

Coloration in life.—"Dorsal ground colour dark brown, with one large whitish, tan or greenish brown blotch narrowly outlined with a creamy border on the flank and another on the top of the head, the latter often having the shape of a triangle; tubercles [on back] usually with white tip; ventral surface...greenish white to light brown; iris golden with four radiating black lines (a black 'Maltese cross'); finger webbing...[and] toe webbing greenish blue" (Kok & Kalamandeen 2008:210).

Trachycephalus typhonius (Linnaeus, 1758)

Type material.—The original name was *Rana typhonia* and the holotype is UUZM 134; the type locality was restricted to the vicinity of Paramaribo, Surinam (Lavilla et al. 2010).

Distribution.—"Lowlands of Mexico, Central America (to 2500 m in Guatemala), to Amazon Basin of Colombia, Ecuador, Peru, Venezuela, and Brazil, Guianas, and south to Paraná (Brazil), Paraguay, northern Argentina; Trinidad and Tobago" (Frost 2011).

Vouchers for Guyana.—AMNH A-70977 from Kartabo; AMNH A-141142–141143, A-141145, A-167105–167106, and USNM 566123 from Dubulay Ranch; USNM 162939–162941 from Enmore Estate (6°44′N, 057°59′W); and USNM 164179 from Mabaruma (8°12′N, 059°47′W).

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994). Dark greenish brown above,

with tan or yellowish tan markings (body, arms, legs); yellow below, brightest ventrolaterally (and on chin of some). Using the name *Phrynohyas venulosa*, Lescure & Marty (2000:198) stated that the toe discs are emerald and iris is gold with black coalescing vermiculations.

Comments.—Until recently, this species was referred to as *Phrynohyas venulosa* or *Trachycephalus venulosus*.

Leptodactylidae

This essentially neotropical family of frogs was named more than 110 yr ago (Werner 1896) and its validity has been confirmed by phylogenetic analyses based on DNA sequence data, although composition of the family has changed significantly (Frost et al. 2006, Pyron & Wiens 2011).

These frogs range in size from tiny to very large. Most species are terrestrial or semi-aquatic, and, depending on the species, may be found in habitats ranging from savanna to primary forest. Breeding often involves depositing eggs in foam nests formed during amplexus, which may be in a burrow near the edge of a pond or depression such that subsequent rainfall may flood the nest and the tadpoles can swim out. *Pseudopaludicola boliviana* is an exception in this regard.

Adenomera andreae Müller, 1923

Type material.—Originally there were five specimens from the type locality of "Peixeboi (a. d. Bragançabahn) Staat Parà, Brasilien" (Müller 1923:41). Heyer (1973) designated ZSM 145/1911 as lectotype.

Distribution.—"Lowlands of northern South America east of the Andes including and limited to Amazonia to the south and east" (Frost 2011).

Vouchers for Guyana.—AMNH A-46264, 46268–46269, 46272–46273, 80028, and A-87877–87888 from Shudikar-Wau, identified by W. R. Heyer. Also AMNH A-166320 from Berbice River Camp, and USNM 531500 (identified by W. R. Heyer) from Iwokrama Mountain Gorge Trail, Iwokrama Forest Reserve.

Coloration in life.—According to Lescure & Marty (2000:224), based on specimens from French Guiana, the dorsum is grayish brown to beige, occasionally with dark brown spots (usually without), and rarely with a vertebral dark brown stripe and/or dorsolateral orangish yellow stripe. The ventral surfaces are white; iris chestnut.

Comments.—This species is so similar to *A. hylaedactyla* (see characters in the key) that some specimens are very difficult to identify. In southeastern Peru these two taxa are part of a complex of four cryptic species that were distinguished by vocalizations and subtle characters (Angulo et al. 2003). These are small frogs, usually less than 30 mm in adult body length.

Adenomera hylaedactyla Cope, 1868

Type material.—The original name was *Cystignathus Hylaedactylus* and the holotype is ANSP 2240 (Malnate 1971) from the Napo or upper Marañon River, Peru.

Distribution.—"Amazonian forests of southeastern Colombia and Venezuela east through the Guianas and south into northern, eastern, and central Brazil, and south through Amazonian Ecuador and Peru to Bolivia, 0–1000 m elevation" (Frost 2011).

Vouchers for Guyana.—AMNH A-39671 and A-39696 from Kartabo; and AMNH A-46565–46568 from Marudi, all identified by W. R. Heyer. Also AMNH A-13494 from Kartabo; and A-141118 and A-145151 from Dubulay Ranch. Also ROM 22760 from Baramita; UMMZ

52506 from Dunoon; UMMZ 85148–85149 from Membaru Creek, upper Mazaruni River; and UMMZ 83581–83582 from Yarikita River, mouth and Haul Over; USNM 163070 from Kamuni Creek; USNM 291122 from Chiung River at Kato; USNM 497721, 497723–497724, 497726–497729 from Karanambo; and USNM 566155 from Berbice River Camp, all identified by W. R. Heyer.

Coloration in life.—The following is based on frogs from French Guiana (Lescure & Marty 2000:226). Dorsum grayish brown to beige with a pattern of dark brown to black spots that may be discrete and oval or joined. Some individuals with dorsolateral or lateral light stripes. Dorsal surfaces of limbs usually lighter with dark brown bands. Ventral surfaces white. Iris chestnut.

Comments.—See the comments for *Adenomera andreae*.

Adenomera lutzi Heyer, 1975
Plate 14B

Type material.—The holotype is BMNH 1905.11.1.17, an adult male from Chinapoon R., upper Potaro (probably Chenapowu River), Guyana.

Distribution.—All specimens known are "from the Pakaraima Mountains of Guyana" (Kok & Kalamandeen 2008:220).

Vouchers for Guyana.—The holotype; the paratypes from Demerara Falls, Guyana (BMNH 1872.10.16.43–1872.10.16.44); AMNH A-3789 from Kai Camp, Kaieteur Region, identified by W. R. Heyer; ROM 40155, 40165, 40167, and USNM 546152 from Mount Ayanganna; ROM 43437–43455 from Mount Wokomung; ROM 44123–44125 from Partang; and ROM 44126–44127 from the Merume Mountains.

Coloration in life.—*Adenomera lutzi* "exhibits a remarkable color-pattern polymorphism. We recognize five major color patterns among our sample: (Pattern A) dorsal ground color dark brown, grey or black with no or a barely discernible pattern; (Pattern B) dorsal ground color light to medium grey with well-defined pattern, characterized by a strongly marked dark brown to black interorbital bar and postorbital ridges, chevron between shoulders almost continuous with round lumbar spots and irregular dark brown to black markings on back; (Pattern C) similar to the preceding pattern, but with dorsal ground color light grey, brown or reddish brown, with lighter, smaller, and much less evident markings on back (some of the markings may be absent); (Pattern D) rather similar to pattern B but with dark brown to black mottling on dorsum instead of well-defined markings; (Pattern E) dorsal ground color dark grey to black with large orange to orangish brown oblique lateral stripe; darker markings on back may be discernible or not" (Kok et al. 2007:49–50). In addition, these authors noted that many individuals have a narrow light yellow middorsal stripe; ventral surfaces are yellow to orangish yellow, usually with dark gray stippling on throat and chest; dorsal surfaces of arms and legs usually with dark bands; dark brown or black seat patch.

Engystomops cf. *pustulosus* (Cope, 1864)

Type material.—The original name was *Paludicola pustulosus* and the holotype is USNM 4339 (apparently lost) from New Grenada, on the River Truando, Colombia (Frost 2011).

Distribution.—"Eastern and southern Mexico (Veracruz and Oaxaca) south and east through Central America to Colombia and Venezuela" (Frost 2011).

Voucher for Guyana.—BMNH 1977.885 from Bartica District (no additional locality data).

Coloration in life.—The following is from Savage (2002:224) based on frogs from Costa Rica. "Ground color brownish to gray above, nearly uniform or with dark brown blotches, a narrow middorsal cream to orange stripe or paired dorsolateral light stripes or a combination of these; warts on anterior part of body usually reddish, orange or yellow; often an orange spot between shoulders; male vocal sac black with a medium [median?] light line when inflated; chest dark; upper surface of leg with several transverse dark bars; venter dirty white, usually with large black spots posteriorly; iris tan or pale brown."

Comments.—Colin McCarthy sent CJC photographs of the BMNH voucher from Guyana. These photographs were compared with specimens of several related frogs from Venezuela (Gorzula & Señaris 1999; also compared with AMNH A-70631, A-70635, and A-70639, *E. pustulosus* from Venezuela), and characters of the *pustulosus* species group as discussed by Lynch (1970) and Cannatella & Duellman (1984). The BMNH voucher clearly does not have the diagnostic characters of *Physalaemus cuvieri*, which also occurs in Guyana, and does have the following characters that fit *E. pustulosus*: dark markings above ankles and wrists; dark rounded markings on abdomen; presence of parotoid glands (possible, but photo not absolute); presence of elliptical flank glands (possible, but photo not absolute). The main character that is problematical is that the BMNH voucher does not appear to be sufficiently warty, although this could be affected by age and method of storage in preservative. Owing to the uncertainties, we refer to this taxon as cf. *pustulosus* and encourage future field work and collecting to confirm or reject the hypothesis that this species occurs in the Bartica District.

Leptodactylus fuscus (Schneider, 1799)
Plate 13E

Type material.—The original name was *Rana fusca* based on syntypes thought to be from Surinam (Frost 2011).

Distribution.—"Savannas from Panama throughout South America, east of the Andes, south to southern Brazil, Bolivia, Paraguay, and Argentina" (Frost 2011).

Vouchers for Guyana.—AMNH A-70909–70916 from Kartabo (identified by R. G. Zweifel); AMNH A-136031 and USNM 497732–497733 from Karanambo; AMNH A-139087–139099, A-139107, and USNM 566173–566179 from Aishalton; AMNH A-141091–141095, A-141098, A-145140–145146, A-167112–167113 and USNM 497735–497739 and 566180–566184 from Dubulay Ranch; USNM 162880–162893 from Atkinson (=Timehri Airport); USNM 162943–162965 from Enmore Estate (6°44′N, 057°59′W); USNM 497734 from Takutu River at Lethem.

Coloration in life.—The following is based on the AMNH and USNM specimens from Karanambo and Aishalton (CJC field notes, 1992, 1993). Dorsum reddish brown with dark brown spots and with or without a light gray vertebral stripe; lateral body greenish brown with dark brown spots; paravertebral ridges reddish brown; dorsolateral and lateral ridges yellowish tan; lateralmost warts cream; arms and legs yellowish tan with gray or black markings; posterior thigh warts pale yellow; chin and throat cream with gray specks; black line posteriorly on lower lip; chest pale yellow; abdomen brighter yellow; underneath arms and legs translucent pale yellow.

Comments.—This species is abundant in savannas and disturbed habitats. Analyses of DNA sequence data suggest that there are distinct evolutionary lineages of these frogs from localities north versus south of the Amazon, although no significant differences in morphology or vocalizations

have been found to distinguish these populations (Wynn & Heyer 2001, Camargo et al. 2006).

Leptodactylus guianensis
Heyer & de Sá, 2011
Plate 13B

Type material.—USNM 531509 from Pakatau Camp (4°45′17″N, 59°01′28″W; 85 m elevation), Sipuruni River, Iwokrama Forest Reserve, Guyana.

Distribution.—Lowlands of the Guiana Shield, in Brazil, Guyana, Suriname, and Venezuela.

Vouchers for Guyana.—Heyer & de Sá (2011) listed numerous specimens from Guyana in addition to the holotype, paratopotypes, and paratypes. The following are specimens that we examined: AMNH A-3990 from Kalacoon; AMNH A-10397, A-10423, and A-11709 from Kartabo; AMNH A-136032–136034 from Karanambo; AMNH A-145130–145131, A-145133–145134, and USNM 566161 from Dubulay Ranch; AMNH A-166341–166349, A-166356–166358, and USNM 566162–566167 from Berbice River Camp; AMNH A-166359–166366 and USNM 566168–566172 from Konawaruk Camp; ROM 20580–20590 from Kurupukari; USNM 146369–146374 and 497731 from Moco Moco, at the base of the Kanuku Mountains; USNM 497730 from Karanambo Ranch; and USNM 531501–531511 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on the AMNH and USNM specimens from Karanambo and Dubulay Ranch (CJC field notes, 1992–1995). Light brown with darker brown markings on upper surfaces of head, body, and arms; legs similar but also may have light olive green mottling and spots on rear of thigh and a pale yellow or olive green wash on thigh; dorsolateral folds with reddish brown stripe; light cream, tan, or rust line beneath eye and ear to corner of mouth, perhaps beyond; lower lips brown with cream spots; on some individuals, a rust, pale orange, or yellow wash also on uppermost arm, on light warts laterally on body, and as a streak on anterior of thigh; some warts cream in anal region; chin, throat, chest, and abdomen cream, yellowish cream, tan, or gray, with or without tan or gray mottling; translucent under legs and with or without yellow wash in groin.

Comments.—This species is morphologically similar to the other two species in the *bolivianus* complex, from which it differs significantly in molecular characters (Heyer & de Sá 2011). Adult males of *L. guianensis* differ from males of the others by having a single modestly chisel-shaped spine on each thumb. The other two species of the *bolivianus* complex do not occur in Guyana.

Leptodactylus knudseni Heyer, 1972
Plate 13F

Type material.—The holotype is LACM 72117, a juvenile female from Limoncocha (0°24′S, 76°37′W; 260 m), Provincia de Napo, Ecuador.

Distribution.—"Greater Amazon basin of Bolivia and Brazil north to Colombia, Venezuela, Trinidad, and the Guianas" (Frost 2011).

Vouchers for Guyana.—AMNH A-70880–70881 from Kartabo (identified by W. R. Heyer); AMNH A-141100–141104, and A-145136 from Dubulay Ranch; AMNH A-166372–166373 and USNM 566185–566186 from Berbice River Camp; and AMNH A-166376 and USNM 566187–566188 from Konawaruk Camp. Also ROM 22762–22765 and USNM 535773 from Baramita; and ROM 28451–28452 from Paramakatoi, identified by W. R. Heyer. Also USNM 531512–531520 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following is based on the AMNH specimens from Dubulay Ranch (CJC field notes, 1994). Brown above with light tan markings; upper arms black on rear, brown above with wash of rust; rust laterally on body; upper legs (thighs) brown above with light tan to black bands, black on rear with light orange-rust, reticulation, or bars; dorsal surface of lower legs as dorsal body; gray throat, chest, anterior abdomen; yellow area about waist; legs cream below, except thighs pink.

Comments.—These large frogs can grow to an adult body length of 170 mm (Kok & Kalamandeen 2008:214).

Leptodactylus leptodactyloides (Andersson, 1945)

Type material.—The original name was *Eleutherodactylus leptodactyloides* and the holotype, unnumbered at NHRM, was from the Rio Pastaza, eastern Ecuador (Andersson 1945).

Distribution.—"Greater Amazon Basin and the Guianas, 15–400 m elevation" (Frost 2011).

Vouchers for Guyana.—AMNH A-39625 from Kartabo, identified by W. R. Heyer.

Coloration in life.—The following (and quotes) are from Duellman (2005:284), based on frogs from Peru. Dorsum gray, tan, or reddish brown, darkest individuals with snout lighter than body; dorsolateral fold dark brown; narrow dark brown or black interorbital bar; most specimens with some irregular black spots on sides; indistinct light bars on lips, the posterior-most of which extends from the posterior corner of the eye; posterior of thigh mottled (dark brown to black with cream to pale tan), many individuals also having a distinct light stripe (mostly distally on thigh); "throat...brown or gray with cream flecks; ...rest of...venter...white with brown or dark gray reticulations on...hind limbs, chest, and in some individuals the anterior part of the belly. The iris is bronze with fine black reticulations."

Leptodactylus longirostris Boulenger, 1882

Type material.—BMNH 76.5.26.4 was designated as the lectotype reportedly from Santarem, Brazil, but see Frost (2011) for discussion.

Distribution.—"Guianas, eastern Venezuela, eastern Amazonian Colombia (Guainía), and Brazilian Amazonia" (Frost 2011).

Vouchers for Guyana.—AMNH A-139109–139112 and USNM 566189 from Aishalton; ROM 20591–20594, USNM 291238–291243 and 497740–497741 from Kaieteur; USNM 118065–118066 from Kartabo; USNM 291124–291126 from Chiung River at Kato; and USNM 291177 from Paramakatoi.

Coloration in life.—The following notes are from Kok & Kalamandeen (2008:218), based on specimens from Kaieteur National Park. "Dorsal ground colour and pattern very variable, light brown to reddish brown, sometimes greyish or dark brown, uniform or with irregular dark brown markings, middorsal and paravertebral stripes absent or present;...throat and chest cream or white, turning yellow on belly...upper lip with a white, cream, light brown or pinkish stripe below eye, always entering eye anteriorly. Black stripe from tip of snout to eye."

Comments.—"Found in open areas like savannah" (Kok & Kalamandeen 2008: 218).

Leptodactylus macrosternum Miranda-Ribeiro, 1926

Type material.—The original name was *Leptodactylus ocellatus macrosternus* and the holotype is MZUSP 448 (Frost 2011),

probably from Salvador, Bahia, Brazil (Frost 2011).

Distribution.—"Amazonian Colombia, most of Venezuela, and the Guianas south through Brazil to Bolivia; Trinidad" (Frost 2011).

Vouchers for Guyana.—AMNH A-136035–136038, USNM 497742–497763, and 566190–566192 from Karanambo; AMNH A-139114–139115 from Aishalton; and USNM 146368 from Lethem.

Coloration in life.—The following is based on the AMNH specimens from Karanambo (CJC field notes, 1992). Tan or greenish brown with darker brown spots on head, body, and arms; legs similar but wash of green superimposed (in groin also, and on some, posteriorlaterally on body); chin and throat cream, mottled with gray; chest and abdomen cream to pale yellow, sometimes with gray mottling, the latter and thighs with wash of pale greenish yellow; underside of lower legs translucent gray. Lescure & Marty (2000:242) stated that the rear of the thigh is spotted with black and yellow.

Comments.—Specimens of this species from the Guianas were formerly referred to as *Leptodactylus ocellatus*. It occurs in savannas.

Leptodactylus mystaceus (Spix, 1824)
Plate 14C

Type material.—The original name was *Rana mystaceus* and the lectotype, apparently lost, is ZSM 2504/0 (Hoogmoed & Gruber 1983), with the type locality restricted to Solimões, Brazil (Frost 2011).

Distribution.—"Amazon basin from its southern limit in Brazil to Bolivia, Peru, Ecuador, Colombia, Venezuela, and the Guianas" (Frost 2011).

Vouchers for Guyana.—AMNH A-141105 and A-145147 from Dubulay Ranch; AMNH A-166384–166393 and USNM 566193–566198 from Berbice River Camp; AMNH A-166401–166403 and USNM 566199 from Konawaruk Camp; ROM 22767 from Baramita; USNM 118058 from Kartabo; and USNM 531521–531541 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1994–1998). Dorsum reddish brown (possibly brighter on sides, but sides may be gray) to brown, with darker brown markings surrounded by a dirty cream line; arms and legs tan with brown bands, legs at times also with yellow wash; upper lip light tan, pinkish tan, or copper, above which is a dark brown or black mask from the snout through the eye and ear; a black stripe may be present on the posterior surfaces of the arms; rear of thigh may have a yellow stripe (possibly broken) with a thin very dark brown or black line above it; vent black with vertical yellow bar; ventral surfaces yellow (possibly brighter on abdomen and legs), with small gray or tan spots or flecks on the throat; possibly a few brown to black spots on underside of lower legs.

Leptodactylus pentadactylus (Laurenti, 1768)
Plate 14D

Type material.—The original name was *Rana pentadactyla* and a neotype (RMNH 29559) from Surinam, Marowijne, Lelygebergte, Suralcokamp V was designated by Heyer (2005).

Distribution.—"Amazon Basin from southern Colombia south to Peru, northern Bolivia, and northern Brazil to French Guiana; Honduras to western Colombia and northwestern Ecuador" (Frost 2011).

Vouchers for Guyana.—AMNH A-70118–20 from Shudikar-wau, a headwater stream of the Essequibo River (1°15′N, 58°35′W); these frogs were previously identified by W. R. Heyer (1978) and recently confirmed by CJC.

Coloration in life.—The following is based on Lescure & Marty (2000:248) for frogs from French Guiana. Dorsum reddish brown with 5 or 6 transversal, darker brown bands with light rims; sides lighter than the back, with some black tubercles; posterior surface of thighs black with white dots (but thighs banded above this); venter cream, marbled with black, especially toward the rear; iris reddish copper, except the upper third golden.

Comments.—These frogs, which usually occur in forest, become quite large, up to 185 mm in body length (Lescure & Marty 2000). They are similar to *Leptodactylus knudseni*.

Leptodactylus petersii (Steindachner, 1864)
Plate 14E

Type material.—The original name was *Platymantis Petersii* and the holotype from Marabitanas, Amazonas, Brazil has been lost (Frost 2011).

Distribution.—"Known from the Guianas, the Amazon basin (including one locality in Ecuador), and isolated localities from the Cerrado open formations in central Brazil reported from Pando and Santa Cruz, Bolivia" (Frost 2011).

Vouchers for Guyana.—AMNH A-39630–39631 and A-39633 from Kartabo (identified by W. R. Heyer); AMNH A-136050 and USNM 497725, 497775, and 566149–566154 from Karanambo; AMNH A-145150 from Dubulay Ranch; AMNH A-166308–166318 and A-166405–166406 from Berbice River Camp; AMNH A-166409–166411 and USNM 566202–566204 from Konawaruk Camp; ROM 20613–20616 from Kurupukari; USNM 162950 from Enmore Estate (6°44′N, 057°59′W); and USNM 531542–531557 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following is based on AMNH specimens from Dubulay Ranch and Berbice River Camp (CJC field notes, 1995–1997). Dorsum dark tan with brown markings on arms and legs, black spots on sides; light rust line below tympanum; throat, chest, and belly white or cream with gray spots, mottling, or reticulation; some with yellow in groin and on posterior surface of thigh; underside of legs with black reticulation. Kok & Kalamandeen (2008:224) stated that the ground color of the dorsum is more variable, from greenish or grayish brown to reddish brown.

Comments.—Previously this species was confused with *Leptodactylus podicipinus*.

Leptodactylus rhodomystax
Boulenger, 1884
Plate 14F

Type material.—BMNH 1947.12.17.81 from Yurimaguas, Huallaga River, Northern Peru was "designated lectotype by Heyer, 1979, Smithson. Contrib. Zool., 301: 30" (Frost 2011).

Distribution.—"Guianas through northern and central Brazil to Amazonian Ecuador, Peru, and Bolivia" (Frost 2011).

Vouchers for Guyana.—AMNH A-13489 and A-70903 from Kartabo; AMNH A-49246 and A-51942 from Shudikarwau (identified by W. R. Heyer); AMNH A-166412–166414, A-166418–166419, and USNM 566205–566207 from Berbice River Camp; AMNH A-166420 from Konawaruk Camp; ROM 40153–40154 from the base of Mount Ayanganna; and USNM 531558–531571 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp (CJC field notes,

1997). Dorsum reddish brown or tan, brightest on sides, with few (anterior) dark brown markings; tiny white specks on sides; snout and side of face dark brown; light stripe on lip tan, becoming white posteriorly; upper groin with black patch having white spots; upper surfaces of arms and legs reddish brown, arms with row of white specks posteriorly, from wrist to elbow; rear of thighs black with white, yellow, and/or gray spots; chin and throat very dark gray or grayish tan, with white spots; chest gray or grayish tan, with white spots or reticulation; some with gray reticulation on abdomen; lower groin and posterior abdomen yellow or orangish rust; translucent light tan or white beneath arms, light yellow beneath legs; black beneath feet; iris deep reddish brown on lower half, mixed copper and black above.

Leptodactylus rugosus Noble, 1923
Plate 15A

Type material.—The holotype is AMNH A-1169, an adult male from near Kaieteur Falls, Guyana.

Distribution.—"Southern Venezuela east to western Guyana; likely in intervening adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—Specimens in addition to the holotype include paratypes AMNH A-1166–1168 from Tukeit and Kaieteur, with identifications confirmed by W. R. Heyer. Also ROM 20597–20606, 43233–43252, USNM 291245–291266, and USNM 342151–342160 from Kaieteur National Park; ROM 40150–40151 from the base of Mount Ayanganna; USNM 118063–118064 and 129537–129538 from Kartabo; and USNM 118684 from Membaro Creek, Upper Mazaruni River.

Coloration in life.—"Dorsal ground colour variable, ranging from greyish or greyish brown to olive brown or reddish brown (dorsum bright red in some subadults), with irregular pale cream to greyish tan blotches and black markings;... ventral surface...variable in pattern, white to light greyish brown with diffuse brown mottling (...in juveniles and subadults... ventral surface of thighs orangish); throat white, heavily marked with grey mottling in juvenile and female, grey in adult male...dirty white, cream or brownish lines from eye to lip (ill-defined in some specimens)...dirty white, cream or brownish interorbital stripe," based on specimens from Kaieteur National Park (Kok & Kalamandeen 2008:228).

Leptodactylus validus Garman, 1888

Type material.—See Frost (2011) for a discussion of the many syntypes from Kingston, St. Vincent, and citation of Heyer's designation of MCZ 71920 as lectotype.

Distribution.—"Lowlands of Venezuela and the Guianas, and north-central Roraima, Brazil, and the continental islands of Tobago and Trinidad, from elevations of 0–360 m; Lesser Antillean islands of St. Vincent, Bequia, and Grenada" (Frost 2011).

Vouchers for Guyana.—AMNH A-53435–53437 from Isheartun (identified by W. R. Heyer); AMNH A-136043–136046, A-136049, USNM 497722, 497764–497774, and 566200–566201 from Karanambo; AMNH A-145148–145149 from Dubulay Ranch; ROM 20619–20632 from Kurupukari; ROM 40183–40187 from Baramita; USNM 118059–118062 from Kartabo; USNM 146366–146367 from Moco Moco (3°20′N, 059°39′W); USNM 162872–162879 from Atkinson (=Timehri Airport); and USNM 162966–162967 from Enmore Estate (6°44′N, 057°59′W).

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo (CJC field notes, 1992). Brown or greenish brown above, with inconspicuous black or blackish gray

bands on arms and legs; tan mottling on posterior of thighs; tips of fingers white; venter cream (but pale yellow on abdomen), mottled with dark gray, sometimes extensively on chin and throat; beneath arms and legs translucent pinkish gray; anal warts tan. The face may be gray anterior to the eyes and a short gray line may go posteromedially behind each eye; also there may be a black interorbital line.

Comments.—This species was referred to as *Leptodactylus pallidirostris*, but recent research, including DNA sequence comparisons, shows that *L. pallidirostris* is a junior synonym of *L. validus* (Yanek et al. 2006).

Lithodytes lineatus (Schneider, 1799)
Plate 14A

Type material.—The original name was *Rana Lineata* based on material in the "Musei Lampiani" with no locality information given.

Distribution.—"Eastern Peru, Ecuador, Bolivia, and Brazil through southern Venezuela to the Guianas; possibly Trinidad" (Frost 2011).

Vouchers for Guyana.—AMNH A-10408, A-11664–11666, A-13504, A-13564, A-23122, A-39589–39590, A-70917, and A-70992 from Kartabo; AMNH A-141147 from Dubulay Ranch; AMNH A-166428, AMNH A-166433–166435, and USNM 566208–566211 from Berbice River Camp; AMNH A-166436 from Konawaruk Camp; and ROM 22786–22787 from Baramita.

Coloration in life.—The following is based on the AMNH specimen from Dubulay Ranch (CJC field notes, 1994). Dorsum black, with pale tan to gold dorsolateral light stripe; small white spots on side of face and body; arms banded black and light tan; bright orangish red spot in groin and two on upper posterior thigh; rest of upper and anterior thigh black with light tan bars; lower legs black with light tan bands and spots; orangish red spots behind and below knee; all ventral surfaces dark gray to black with white spots.

Comments.—"Found exclusively in primary forest, often associated with large nests of leaf cutting ants (*Atta* spp.)" (Kok & Kalamandeen 2008:216).

Physalaemus cuvieri Fitzinger, 1826
Plate 13A

Type material.—"Type(s): [from Brazil] presumably originally in NHMW, but not noted in recent type lists" (Frost 2011).

Distribution.—"Northeastern, central, and southern Brazil; Misiones, Argentina; eastern Paraguay; Departments of Beni and Santa Cruz in Bolivia; possibly lowlands of southern Venezuela (see comment)" (Frost 2011).

Vouchers for Guyana.—AMNH A-52875 from Isheartun and A-52876 from Kuyuwini Landing, identified by A. J. Cardoso as "cf. *cuvieri*" (quoted from the AMNH catalog). Also USNM 291178–291183 from Paramakatoi; USNM 535775–535780 from Baramita; USNM 531577–531583 from Iwokrama Forest Reserve, ca. 3 mi S of Kurupukari base camp on Georgetown-Lethem Road; USNM 566212 from Dubulay Ranch; and UTA 55526 from Moses.

Coloration in life.—The following is based on USNM 566212 from Dubulay Ranch (CJC field notes, 1994). Brown above, with tan snout (anterior to eyes), tan spot on upper back, and, posteriorly, tan vertebral line starting at about midbody; dark brown stripe slants ventrally from behind eye past midbody, on side; arms and legs tan with brown bands, lower arms with dark brown stripe on outer edge; pinkish orange (bright) in groin, behind knee, down rear of lower leg, and anteriorly on ankle; throat, anterior chest, and beneath lower legs gray; abdomen and beneath and behind thigh very pale yellow.

Comments.—The vouchers for Guyana compare favorably with characters given by Gorzula & Señaris (1999:67–79) and also with AMNH A-23586 and A-54511 (*P. cuvieri* from Brazil).

Pleurodema brachyops (Cope, 1869) Plate 13C, D

Type material.—The original name was *Lystris brachyops* and syntypes (ANSP 2260–2264) were from the Magdalena River, New Grenada (Malnate 1971).

Distribution.—"Guyana and northern Brazil (Roraima) through Venezuela (including Isla Margarita) and Colombia into Panama in dry llanos and savanna areas; also Curaçao, Aruba, Bonaire, and Klein Bonaire in the Netherlands Antilles" (Frost 2011).

Vouchers for Guyana.—AMNH A-139116–139127, A-139134–139135, and USNM 566213–566218 from Aishalton.

Coloration in life.—The following is based on the AMNH and USNM specimens from Aishalton (CJC field notes, 1993). Dorsum yellowish tan or gray, with gray markings and some individuals having small orange dots; most individuals have a largely broken (clearest posteriorly) cream to orangish tan, thin vertebral stripe; posterior lateral abdomen with swollen orbs ("eyespots"), black with light gray markings; upper arms and legs as body, but on legs most marks are black; throat (all are males) gray or tan, with darker gray or tan speckling; abdomen cream, on some individuals translucent posteriorly (as legs), fleshy pink; bright orangish red flash marks in groin, behind thigh, behind knee, beneath lower leg, and on anterior of ankle.

Pseudopaludicola boliviana Parker, 1927a

Type material.—The holotype is BMNH 1927.8.1.1, a female from Santa Cruz, Bolivia.

Distribution.—"Disjunct regions of eastern Colombia, northern Brazil (Roraima), and Amazonian Venezuela through southern Guyana to southern Surinam; eastern Bolivia, Paraguay, southwestern Brazil, and northern Argentina" (Frost 2011).

Vouchers for Guyana.—AMNH A-136029–136030 and USNM 497776–497777 from Karanambo; AMNH A-139182–139191, A-139197–139198, and USNM 566219–566223 from Aishalton; and USNM 497778 from Moco Moco at base of Kanuku Mountains (3°18′12″N, 059°39′00″W).

Coloration in life.—The following is based on the AMNH and USNM specimens from Karanambo and Aishalton (CJC field notes, 1992, 1993). Dorsum light tan to dark grayish tan or tannish gray, with or without darker tan or brown markings; some individuals with cream, light tan, or rust vertebral stripe; side of face with very pale streaks; arms and legs pale tan with gray bands; conspicuous broad lateral tan stripe, complete from snout to vent; chin, throat, chest, and belly cream with tiny dark gray specks, although on some individuals chin and throat are gray or throat copper; translucent gray beneath arms and legs, the latter sometimes with tiny black specks.

Comments.—These are very small frogs, adults being less than 20 mm in body length.

Microhylidae

Both the intrafamilial and interfamilial relationships of this family have been discussed recently by Frost et al. (2006) and van der Meijden et al. (2007), based on phylogenetic analyses of DNA sequence data. Some of these frogs, especially of the genera *Synapturanus* and *Otophryne*, can be very difficult to find, as they live on or within the forest floor and are cryptically colored. Some, such as species of *Synapturanus* would appear to be rare, based on the few specimens in collections; yet they

may be abundant in nature but extremely hard to find as males vocalize from beneath the ground during rains and quickly escape in burrows as one tries to dig them up. We still have much to learn about the life history, ecology, and population genetics of these frogs.

Chiasmocleis hudsoni Parker, 1940

Type material.—The holotype is BMNH 1939.1.1.3, a male, from the New River, Guyana (750 ft elevation). This locality is in an area of dispute between Guyana and Surinam, but it is likely that any species occurring here occurs also at other localities in both countries.

Distribution.—"Cerro Neblina in Guianan Venezuela, as well as in Guyana, Surinam, and French Guiana; presumably to be found in adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—The holotype; paratypes, 3 males and 2 females with the same data as the holotype, BMNH 1939.1.1.4–1939.1.1.8.

Coloration in life.—The following is based on Lescure & Marty (2000:266) for frogs from French Guiana: dorsal surface chestnut with light markings at times forming a dorsolateral line from the snout to the flanks; ventral surface light, spotted with brown; sole of foot black.

We examined a preserved specimen (MNHN 2001.0322) from French Guiana. In alcohol, the dorsum is dark grayish tan, with numerous white dots. There is no light vertebral stripe nor is there one on the posterior surface of the thighs. The tan throat has irregularly shaped small light spots. The pale belly has a tan reticulation. Palmar and plantar surfaces of hands and feet, respectively, are very dark.

Comments.—These tiny frogs (maximum body length about 20 mm) live on the ground in primary forest (Lescure & Marty 2000:266).

Chiasmocleis jimi
Caramaschi & Cruz, 2001
Plate 15B

Type material.—The holotype is MNRJ 15459, an adult female from Brazil, Amazonas, Municipality of Humaitá, Igarapé do Banheiro (07°31′S, 63°00′W).

Distribution.—Known only from the vicinity of the type locality, in the states of Amazonas and Para, Brazil (Frost 2011) and Guyana.

Vouchers for Guyana.—AMNH A-166437–39 and USNM 566224 from Berbice River Camp.

Coloration in life.—"In life, color of dorsum of body, arms and legs uniform reddish brown with minute irregular white dots; no light mid-dorsal stripe; ventrolateral region and venter cream, heavily grayish spotted; gular region grayish, with irregular white dots; no femoral light stripe" (Caramaschi & Cruz 2001:3).

Individuals of the AMNH and USNM series from Berbice River Camp were noted in life (CJC field notes, 1997) as follows: "all dorsal surfaces chestnut brown; venter different shades of gray, throat being tannish gray, but hind legs with mottling of orange on the underside." USNM 566224 "differs in having a thin white stripe on the posterior femoral surfaces, continuous across the anus [=vent]; yellow ground [color] on throat and beneath arms; and white with black mottling beneath hind legs, abdomen, and chest."

Comments.—All individuals are smaller than 20 mm in body length.

Chiasmocleis shudikarensis Dunn, 1949

Type material.—AMNH A-43674 from Shudikar-wau, upper Essequibo River, Guyana.

Distribution.—Guyana, Surinam, French Guiana, and Brazil (Amazonas) (Frost 2011).

Vouchers for Guyana.—The holotype (see above) is the only specimen known from Guyana.

Coloration in life.—The following is based on Lescure & Marty (2000:268) for frogs from French Guiana: dorsal surfaces light brown to grayish brown, with or without a fine yellow vertebral line that meets a similar line on the posterior surfaces of the thighs; irregular black patch in groin; brown throat; venter and undersides of legs white with large irregular black patches; iris reddish chestnut.

Dunn (1949:8) stated the following in the original description, based on the holotype, probably in alcohol: "above gray with fine light flecking and a narrow, light, middorsal line; throat gray with a narrow light median line; belly and undersurfaces of limbs cream with black spotting or mottling, increasing in amount posteriorly; a black inguinal spot, rather vague and irregular."

We examined a series of French Guianan specimens in alcohol (MNHN 2001.0831–2001.0836), from which we took the following notes. The largest (2001.0836; SVL = 25 mm) is a female and it is the only one to have a very thin light vertebral stripe, as occurs on the holotype. It also has a light tan throat, whereas some of the smaller ones (e.g., 2001.0832) have a dark gray to black throat and may be males. The dorsum is dark grayish tan to dark tannish gray, covered with tiny light dots. The posterior of the thigh is dark with a thin light stripe along its length from the hip, which may continue down the leg to the foot. The throat and chest have irregular light stippling. A light V (apex to the rear) is on the chest of all specimens, but only on the large female is it bisected by a light midventral line that extends from the anterior edge of the lower jaw posteriorly to the rear of the abdomen. The basically white abdomen has very dark brown to black spots and reticulations, which also are on the ventral and anterior surfaces of the thighs. The palmar and plantar surfaces of the hands and feet, respectively, are very dark.

Ctenophryne geayi Mocquard, 1904
Plate 15C

Type material.—The holotype from the Sarare River, Colombia is registered as MNHN 1903.84 (Frost 2011).

Distribution.—"Northern South America from Surinam, Guyana, and Brazil to Amazonian Venezuela, Colombia, Ecuador, and Peru" (Frost 2011).

Vouchers for Guyana.—AMNH A-71399 from Kartabo (identified by R. G. Zweifel); AMNH A-145159 from Dubulay Ranch and AMNH A-166441–166446 and USNM 566225–566227 from Berbice River Camp. Also ROM 22769 from Baramita.

Coloration in life.—Specimens from the AMNH series from Berbice River Camp were noted in life (CJC field notes, 1997) as follows: grayish brown body with numerous tiny white dots; thin light tan vertebral line; dark chestnut brown on lateral surfaces beneath a white lateral stripe on head, arms, body, and legs; hands and feet with some yellowish tan; all ventral surfaces black with irregular white spots.

Elachistocleis surinamensis (Daudin, 1802a)
Plate 15D

Type material.—The original name was *Bufo surinamensis* based on an unspecified individual from Surinam.

Distribution.—Venezuela and Guyana to French Guiana; Trinidad (Frost 2011; M. S. Hoogmoed, pers. comm.).

Vouchers for Guyana.—AMNH A-139136–139147, A-139154–139155, and USNM 566228–566233 from Aishalton; AMNH A-141135–141137, A-141139–

141140, A-167110, and USNM 566234 from Dubulay Ranch.

Coloration in life.—The following is based on field notes of CJC (1993, 1994) for the AMNH and USNM specimens from Aishalton and Dubulay Ranch: dark gray above with very light gray speckling; mottled gold and gray below; orange spots in groin, behind knee (some becoming a stripe behind femur), and on upper side of foot, although this last spot may be gold in color.

Comments.—The following four names have been applied to *Elachistocleis*-like frogs of the Guianan Region and Trinidad for many years: *E. bicolor*, *E. ovalis*, *E. surinamensis*, and *Relictivomer* or *Elachistocleis pearsei*. Caramaschi (2010) added a new name to the list, *Elachistocleis surumu*, which he applied to frogs from the state of Roraima, Brazil; in the same paper he named what he called four additional new species from Brazil. The number of real species enveloped by all these names and how to apply the names remains unknown to us today.

For the Guianan Region, overall variation includes whether individuals have an immaculate venter or one with pronounced light spotting and dark reticulations; whether there are light spots in the groin and behind the knee; whether there is light striping behind the thigh; and whether there is a fine light (or dark) vertebral stripe. However, what is missing from most studies is careful analysis of local individual variation, geographic variation, and use of comparative samples from throughout the geographic ranges of the proposed species. None of the studies to date has involved modern molecular analyses.

All of the specimens we have seen from Guyana have the characters usually thought to represent *E. surinamensis*, which is consistent with the recent report of Lavilla et al. (2003). Contrary to Caramaschi's (2010) statements, Lavilla et al. (2003) did not state that *E. surinamensis* has a light vertebral stripe.

The AMNH specimens from Aishalton and Dubulay Ranch are in general similar to what has been described for *E. surinamensis* and *E. surumu*. However, they exhibit considerably more individual variation in ventral coloration than usually is attributed to local populations. After several years in preservative those with the lightest bellies have a rather abrupt transition on the sides between the darker dorsal coloration and lighter ventral coloration. These frogs also lack a vertebral stripe and have light spots in the groin and behind the knee plus light striping behind the thigh. The largest individual from Aishalton has a snout-vent length of 35 mm, that from Dubulay Ranch, 39 mm, which is larger than what Caramaschi (2010) reported for specimens from Roraima.

We conclude that the name *E. surinamensis* is most applicable to the specimens we have seen from Guyana. Furthermore, the taxonomic problems involving these frogs will be resolved only by doing extensive analyses of local variation, geographic variation, and DNA sequence data. In addition, specimens need to be analyzed from throughout the ranges of the so-called species without limitations of political boundaries.

Hamptophryne boliviana (Parker, 1927b)

Type material.—The original name was *Chiasmocleis boliviana* and the holotype is BMNH 1927.8.1.1, a female from Buena Vista, Santa Cruz, Bolivia.

Distribution.—"Northern and western sides of the Amazon basin: State of Bolivar (Venezuela), French Guiana, Surinam, Guyana, Brazil, Ecuador, Peru, Bolivia, and Colombia" (Frost 2011).

Vouchers for Guyana.—BMNH 1934.1.4.1 from Upper Cuyuni River (no additional locality data).

Coloration in life.—The following notes are from Lescure & Marty (2000:274), based on specimens from French Guiana:

Dorsum brown or light brown with a large darker brown middorsal area having an irregular edge (two wavy notches) that enlarges in width posteriorly; small black spot above groin; a blackish brown band from snout to cloacal area and on posterior surface of thigh neatly separates dorsal and ventral colorations; ventral surface white (but throat brownish), tinged with blue on the belly, and very spotted with brown; sole of the foot and tarsus blackish brown.

Otophryne pyburni Campbell & Clarke, 1998

Type material.—The holotype is UTA A-3814 from rainforest at 213 m elevation at Wacará, Vaupés Colombia. This site is east of Mitú and close to the Brazilian border at approximately 01°09′N, 69°55′W.

Distribution.—"From Vaupés and Amazonas, Colombia, across the lowlands of southern Venezuela and through the Guianan region to Amapás, Brazil" (Campbell & Clark 1998:311).

Vouchers for Guyana.—AMNH A-71015 from Kartabo.

Coloration in life.—"Dorsum...varying from reddish brown, brown, gray, grayish yellow...[or] yellow-ochre. The sides of the head and body and the concealed lower parts of the limbs are dark brown and sharply contrast with the pale dorsum. The exposed upper parts of the limbs are, for the most part, similar in color to the dorsum. A grayish, whitish, or pinkish, somewhat irregular line extends along the lateral ridge. The upper third of the iris is pale bronze and the lower portion is dark brown similar to the color on the side of the head. Most individuals have cream-colored dots (tubercles) scattered over the dorsum of the body and limbs. The vent is surrounded with a dark brown spot. The large tubercles on the posterior surface of the thigh are white or pinkish [in a row from below the vent toward the rear of the knee]. The throat is dark brown, grading to a paler brown on the chest and to orange at about the mid-belly. The abdomen and lower surface of the hind limb and foot are also orange" (Campbell & Clarke 1998:311).

Otophryne robusta Boulenger, 1900a Plate 15E, F

Type material.—The holotype is BMNH 1899.3.25.18 from the foot of Mt. Roraima, 3500 ft, reported originally as being from Guyana. However, the type locality is probably in Venezuela (Phelps 1938). See below (Vouchers) for specimens from Guyana.

Distribution.—The region of the Pakaraima Mountains of western Guyana and southeastern Venezuela, at elevations of approximately 400-1200 m; probably also in adjacent Brazil (Campbell & Clarke 1998).

Vouchers for Guyana.—Possibly the holotype; ROM 39678–39681 from Mount Ayanganna; ROM 42962–42963 from Mount Wokomung; ROM 44053–44054 from Meamu; UMMZ 85140 from Makreba Falls; and USNM 549320 from the north slope of Mount Roraima. For more details, see MacCulloch et al. (2008b).

Coloration in life.—The following notes are drawn from MacCulloch et al. (2008b:251). Dorsum variable, from dark orange with dark brown middorsal stripe and lateral bars to almost uniform dark brown with faint orange mottling; narrow pale yellow dorsolateral stripe from snout tip passing above eye to groin, continuing onto anterior thigh in some individuals; lateral surfaces dark orange with small black spots, some with white centers; dorsal surfaces of arms dark brown with small white spots; dorsal surfaces of thighs, shanks and feet dark orange with dark brown mottling and occasional dark brown bars; posterior thigh orange with

variable dark brown mottling and a few white spots, often connected by a white line; throat dark brown, chest orange with dense brown speckles in males; throat and venter orange with brown speckles in females; digits pink; upper third of iris pale yellow, matching color of dorsolateral stripe; remainder of iris dark orange with black reticulations.

Otophryne steyermarki Rivero, 1968c
Plate 16A, B

Type material.—The original name was *Otophryne robusta steyermarki* and the holotype is FMNH 74031, a male from the forest along Río Tiricaclusia, 5900 ft, falls below summit camp, Chimantatepui massif, Venezuela.

Distribution.—Western Guyana and southeastern Venezuela, at elevations of 1234–2140 m (MacCulloch et al. 2008b).

Vouchers for Guyana.—ROM 39677 from Mount Ayanganna; ROM 44052 from Partang; and ROM 42953–42961, 44778–44779, and 45271 from Mount Wokomung.

Coloration in life.—"Dorsum of body and limbs black or dark grey with irregular, variable yellow spots. A yellow line from tip of snout across eyelid to groin, continuing onto anterior thigh and sometimes onto shank. Lateral surfaces usually black or dark grey, occasionally dark orange, with yellow or orange spots, usually smaller than dorsal spots. Venter variable, ranging from black with small orange spots to orange with black or grey spots or mottling. Rear of thigh with a thin horizontal yellow line, continuing onto shanks and feet. Forelimbs with a thin pale yellow line on the anterior and posterior surfaces, from insertion of arm to toes. Palms and soles dark yellow or orange. Upper third of iris gold with black reticulations, remainder of iris dark red with black reticulations" (MacCulloch et al. 2008b:255).

Synapturanus mirandaribeiroi
Nelson & Lescure, 1975

Type material.—The holotype is MZUSP 49981, an adult female from Kanashen (a Waiwai Indian village and mission) on the Upper Essequibo River, Rupununi District, Guyana.

Distribution.—"Northern Brazil, Colombia, and the Guianas in humid tropical forests at low elevations" (Frost 2011).

Vouchers for Guyana.—The holotype; and paratopotypes include the following: AMNH A-90935–90943, MNHNP 1974–379, and UMMZ 136147.

Coloration in life.—"The dorsal coloration in life ranged from light yellowish brown to light reddish brown and to dark brown" (Nelson & Lescure 1975:396).

Synapturanus salseri Pyburn, 1975
Plate 16C

Type material.—The holotype is UTA A-4011, an adult male from Timbó, Vaupés, Colombia.

Distribution.—"Known from the type locality..., Cerro Neblina and 34 km south of Puerto Ayacucho, Amazonas, Venezuela; also reported from Kaieteur National Park, Guyana, and near Manaus, Amazonas, Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-166450 and USNM 566235 from Konawaruk Camp; IRSNB 14905–14911 (P. J. R. Kok, pers. comm.) and ROM 11731 from Kaieteur National Park; and USNM 118067 from Kartabo.

Coloration in life.—The following is from field notes of CJC (1998) based on the AMNH specimen from Konawaruk Camp: dark tan above with tiny light tan dots; venter light tan, but abdomen and posterior of chest translucent gray. "In life the dorsal aspect is medium brown with light cream to orange spots over the back, sides, arms and legs. There is a light cream line along the canthus rostralis and upper

eyelid that becomes a series of irregular spots from the eye to the shoulder. The venter is pearl white, has no pattern and the gula is light brown'' (Pyburn 1975:441). Individuals from Kaieteur National Park are the same, but the dorsum on some may be grayish brown (Kok & Kalamandeen 2008:232).

Comments.—Kok & Kalamandeen (2008:232) provided taxonomic comments and also stated the following: "Males call exclusively during rain, from small burrows in the ground, below the leaf litter. Eggs are laid in burrows below the soil surface; tadpoles do not feed and complete their development within the burrow."

Pipidae

This family of frogs has been taxonomically stable for a long time, and is based on many morphological and DNA sequence characters (Frost et al. 2006). The species in Guyana are highly aquatic frogs with rather flat bodies, and occur in ponds, ox-bow lakes, or slow-moving streams in low-elevation rain forest. Females carry their eggs embedded in their backs, from which froglets emerge.

Pipa arrabali Izecksohn, 1976
Plate 16D

Type material.—The holotype, from Vila Amazônia, Município de Parintins, Amazonas, Brasil, was a male in the author's private collection (EI 5311) and was destroyed (Frost 2011).

Distribution.—"Guyana, western Surinam, eastern Venezuela, and northern, central, and western Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-52829–52831 from Kartabo; ROM 22809 from Baramita, ROM 22379–22398 and USNM 291184 from Paramakatoi; ROM 43991 from Mount Wokomung; and USNM 284392 from Takutu Mountains.

Coloration in life.—Dorsal color medium brown, with irregular dark brown spots; a dark bar from eye to shoulder; ventral surface light brown, shaded with orange or pink, with irregular dark brown spots.

Comments.—*Pipa arrabali* and *Pipa aspera* (a rare frog known only from Suriname and French Guiana; Lescure & Marty 2000) were thought to be possibly conspecific, but Trueb & Massemin (2001) demonstrated that they are distinct species, despite their similarities.

Pipa pipa (Linnaeus, 1758)
Plate 16E

Type material.—The original name was *Rana Pipa* based on syntypes from Surinam (see http://linnaeus.nrm.se/zool/herp/madamph.html.en).

Distribution.—"Amazonian Bolivia to Colombia and the Guianas to Peru, Ecuador; Trinidad" (Frost 2011).

Vouchers for Guyana.—AMNH A-25191 from Kartabo, A-53492 from Marudi, A-53493–53494 from Onora, A-53495–53499 from Rupununi head; USNM 531587–531596 from Iwokrama Forest Reserve; and USNM 566236 from Berbice River Camp.

Coloration in life.—Dorsal surface dark brown to medium grayish brown, sometimes mottled; flanks and ventral surface light brown, with yellow or whitish mottling; at times, a large T-shaped ventral marking composed of a midventral black line from the cloaca forward to the middle of a ventral transverse black line between the head and chest (Trueb & Cannatella 1986:439, Lescure & Marty 2000:282).

Ranidae

Although this family was named nearly 200 yr ago (Rafinesque 1814), our understanding of relationships (both intrafamil-

ial and interfamilial) has greatly improved only recently (Hillis & Wilcox 2005, Frost et al. 2006). This has involved numerous name-changes, particularly among species previously included in the genus *Rana*.

Lithobates palmipes (Spix, 1824)
Plate 16F

Type material.—The original name was *Rana Palmipes* based on material from the Amazon River, Brazil. None of the types exist (Glaw & Franzen 2006).

Distribution.—"Northern and Amazonian South America east of the Andes, including Colombia, Ecuador, Peru, Bolivia, Venezuela, the Guianas, and Brazil south to Alagoas, Bahia, and Mato Grosso" (Frost 2011).

Vouchers for Guyana.—AMNH A-11655, A-11669–11671, and A-71006–71008 from Kartabo; AMNH A-139156 from Aishalton; AMNH A-166453–166459, A-166466–166469, and USNM 566244–566249 from Konawaruk Camp; ROM 28836–28970 from Paramakatoi; ROM 42641 from the Ayanganna airstrip (05°18′10″N, 059°49′55″W); USNM 291127–291128 and 291130 from Kato; USNM 497790 from Kumu at the base of the Kanuku Mountains (3°15′52″N, 059°43′34″W); and USNM 531617–531619 from Iwokrama Forest Reserve, Sipuruni River (4°45′17″N, 059°01′28″W).

Coloration in life.—The following notes were taken on specimens of the AMNH and USNM series from Konawaruk Camp (CJC field notes, 1998): top of head green, fading on body (from anterior to shoulders posteriorly to midbody) to become brown posteriorly on the dorsum with irregular black spots; arms brown; legs same as posterior dorsum and with dark brown subtle bands on lower legs; posterior of thighs black with contrasting reticulation of pale blue, cream, or tan; throat cream on smallest, extensively smudged with gray on largest; other ventral surfaces light gray with irregular darker gray or black spots.

Comments.—Most individuals in the AMNH and USNM series from Konawaruk Camp and the USNM specimens from Kato and Kumu were found in or near water flowing in streams. The ROM specimens from Paramakatoi are from a man-made pond.

Species Accounts: Amphibia: Gymnophiona (Caecillians)

Frost et al. (2006:165) obtained very strong support for this group, based on phylogenetic analyses of DNA sequence data, and characterized the group as follows: "Caecilians are a bizarre group of legless amphibians, primitively oviparous with aquatic larvae (Rhinatrematidae, Ichthyophiidae), although some species are ovoviparous (with or without direct development) and burrowing, as reflected by considerable numbers of osteological modifications." Superficially, individuals resemble earthworms (in some cases very large ones) more than they do other vertebrates, and it is unusual to find one crawling on the surface of the ground, except during or after a rain.

The most recent taxonomic revision, consistent with the phylogeny reconstruction, concluded that globally there are nine families that have existed for about 100 million yr (Wilkinson et al. 2011). Representatives of four families are known to occur in Guyana, including seven genera and 11 species.

Caeciliidae

Frost et al. (2006) and Wilkinson et al. (2011) found strong support for this family based on DNA sequence data and morphology. Most species are terrestrial, burrowing forms.

Caecilia gracilis Shaw, 1802

Type material.—Shaw (1802:598) stated: "In the Museum Adolphi Friderici it is figured under the name of *C. tentaculata*, and appears to be confounded with that species." It was said to be from South America.

Distribution.—"Surinam, and French Guiana; Pará and Maranhão, Brazil; northeastern Peru, presumably into adjacent southeastern Colombia, western Brazil, and eastern Guyana" (Frost 2011).

Vouchers for Guyana.—BMNH RR1987. 946 from Demerara and 1887.1.22.30 from Maccasseema. Also FMNH 35116 "from the Arenoque River," Guyana, 2°42′N Lat. (Taylor 1969:282); UMMZ 47410–47411 and 52507 from Dunoon; UMMZ 76676 from Wismar; and USNM 58750 from "Guyane" (no additional data).

Coloration in life.—The following is from Lescure & Marty (2000:290), based on specimens from French Guiana. Bluish lavender or lilac, a little lighter at the level of the head and on the belly. Nussbaum & Hoogmoed (1979:223) stated that a specimen from Surinam "RMNH 18696 was said to be 'dark purplish blue' in life."

Comment.—Diameter of the body is extremely slender relative to the body length in this species.

Caecilia pressula Taylor, 1968

Type material.—The holotype is AMNH A-49475, a male from the Marudi Mountains, Guyana.

Distribution.—Known only from Guyana, at the type locality (Frost 2011).

Vouchers for Guyana.—The holotype and AMNH A-49470–49474, 49476, all from the Marudi Mountains.

Coloration.—In preservative, "dorsally dark grayish-slate, the head olive; from high on the sides down to venter, yellowish-olive or olive-yellow, the dark lines following the grooves interrupting this on each fold. A median ventral gray-slate stripe, lighter than dorsum, scarcely distinguishable under neck. No light spots at vent, tentacle, eyes, lips, or nostrils" (Taylor 1968:433).

Caecilia tentaculata Linnaeus, 1758
Plate 18B

Type material.—See Frost (2011) for a discussion of the syntypes for which the only locality datum given was America.

Distribution.—"The greater part of wet-forested South America east of the Andes, south to central Peru and Amazonian Brazil" (Frost 2011).

Vouchers for Guyana.—AMNH A-49962 from Kamakusa; and USNM 566003 from Dubulay Ranch.

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1995). The animal was dark gun-metal blue, lighter below than above.

Oscaecilia zweifeli Taylor, 1968

Type material.—The holotype is AMNH A-20079 from a small creek tributary to Rio Mazaruni, Guyana.

Distribution.—Known from Guyana and the vicinity of Cayenne, French Guiana (Lescure & Marty 2000).

Vouchers for Guyana.—The holotype; and AMNH No. 20080 from the type locality.

Coloration.—The following is from Lescure & Marty (2000:296), without reference to source or whether it is coloration in life or in preservative. Dorsum grayish lavender; belly whitish with some gray specks; a yellowish spot near the nostril; a yellowish band on the side of the head, ending at the aperture for the tentacle.

Rhinatrematidae

Frost et al. (2006) and Wilkinson et al. (2011) found strong support for this family based on DNA sequence data and morphology. These are oviparous animals with aquatic larvae. Adults have conspicuous annuli and numerous secondary and tertiary grooves.

Epicrionops niger (Dunn, 1942)
Plate 18C, D

Type material.—The original name was *Rhinatrema nigrum* and the holotype was lost. The neotype is MBUCV 5360 from El Dorado, Bolivar, Venezuela (Taylor 1968).

Distribution.—"Central Guyana to northeastern Venezuela; presumably in adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—ROM 39682–39683 "from the northeast plateau of Mount Ayanganna, 1490 m" (MacCulloch & Lathrop 2009:16).

Coloration in life.—"The body is bluish-black...with diffuse medium-gray mottling on the sides of the head; a line of small blue spots laterally; chin with three longitudinal white bars, one at midline and one along the underside of each mandible; the anus [= vent] white" (MacCulloch & Lathrop 2009:17).

Rhinatrema shiv Gower, Wilkinson, Sherratt, & Kok, 2010
Plate 18E

Type material.—The holotype is IRSNB 1991, a transformed male (Gower et al. 2010:49) from Sir Donald's trail ca. 2 km from a tributary of the Elinkwa River, ESE Kaieteur National Park, Guyana, ca. 540 m elevation (5°08′N, 59°25′W) (Gower et al. 2010:49).

Distribution.—Known only from Guyana.

Vouchers for Guyana.—The holotype; BMNH 1976.102 from Winiperu, (6°10′N, 58°34′W); BMNH 2008.601, BMNH 2008.602, IRSNB 1992–1996, and IRSNB 1998–1999 from at or in the vicinity of the type locality; and USNM 566004 from Konawaruk Camp.

Coloration in life.—The following is based on the USNM specimen from Konawaruk Camp (CJC field notes, 1998). Brown above with tiny yellow speckles; yellow patch on head; yellow lateral stripe, with irregular edges; venter brown, gradually darkening to black posteriorly.

Comments.—Kok & Kalamandeen (2008:246) described specimens from Kaieteur National Park.

Siphonopidae

Wilkinson et al. (2011) recognized this neotropical family of oviparous species, of which the Guyanan forms are terrestrial burrowers.

Caecilita iwokramae Wake & Donnelly, 2010

Type material.—The holotype is CSBD HA 1500, an adult female from near Top Camp, Iwokrama Forest, Guyana (4°20′N, 58°48′W; ca. 1000 m).

Distribution.—Known only from Guyana.

Voucher for Guyana.—The holotype is the only specimen known.

Coloration.—Coloration in preservative only was given by Wake & Donnelly (2010:917). "Skin colour nearly uniform light yellow-brown dorsally and ventrally. Melanophore pattern mottled, surrounding light skin glands. Melanophores on dorsum of head more concentrated on snout, fewer over parietal region of head. Throat cream-coloured. Annuli slightly darker posteriorly adjacent to annular

groove. Annuli darker and much narrower posteriorly."

Comments.—This is one of the most poorly known species in the world, as it is known from only one extremely distinctive specimen. It was found in "mixed low-stature scrub forest on high hills" (Wake & Donnelly 2010:916) in a terrestrial, rather than aquatic, situation. The specimen is as small as the smallest species of caecilians known, and it is lungless, as is only one other species of caecilian in the world. We know essentially nothing about its biology.

Microcaecilia iyob Wilkinson & Kok, 2010

Type material.—The holotype is FMNH 35117, a mature male from the Oko River at Cuyuni River, Guyana.

Distribution.—Known only from Guyana.

Voucher for Guyana.—The holotype is the only specimen known.

Coloration in preservative.—"The specimen [FMNH 35117] is now nearly a uniform brown, the head somewhat clouded with yellowish-brown back to the collars, which are somewhat darker brown than the following annuli; chin and throat are very light brown to second collar; vent area whitish" (Taylor 1968:546). More than 40 yr later the same specimen was described (Wilkinson & Kok 2010:36–37) as follows: "Gray-brown, more brown anteriorly and where superficial epidermis missing, darker, more plumbous gray posteriorly, perhaps slightly paler on lateral flanks especially posteriorly where each annulus has a paler anterior and darker posterior half. Head paler than body especially ventrally, except for narrow darker lines, approximately level with medial aspect of mandibles, central pale colour extending onto C1 [first collar]. Collar grooves and AGs [annular grooves] edged in white, especially laterally. TAs [tentacular apertures] and nares lie within small pale spots. Cloacal disc, including small ventral area of terminal cap, pale."

Comments.—This is another of the most poorly known species in the world. The holotype and only known specimen was identified by Taylor (1968) as a representative of *Microcaecilia unicolor*. However, "Taylor's description of this species was based on a specimen from Guyana that differs so substantially from the type series [of *unicolor*]... that it most probably represents an as yet undescribed species" (Wilkinson et al. 2009:417).

Microcaecilia rabei (Roze & Solano, 1963)

Type material.—The original name was *Gymnopis rabei* and the holotype is MBUCV 5126 from the base of Cerro Lema, Río Chicanán, Bolívar, Venezuela.

Distribution.—"State of Bolívar, eastern Venezuela, and Surinam; presumably in intervening Guyana and adjacent Brazil" (Frost 2011).

Vouchers for Guyana.—BMNH 1968.1283 from Winiperu, identified by M. Wilkinson.

Coloration in life.—The following is from Nussbaum & Hoogmoed (1979:225), based on specimens from Surinam. "In life...snout pinkish, anterior part of the body purple-blue, darkening towards the posterior part of the body." "In preservative...blue-gray to slate above and below, somewhat lighter anteriorly. The tip and sides of the snout are cream. The chin and throat region is tan. The area immediately surrounding the vent is white. Apparently the Surinam and Venezuelan specimens are nearly identical in colour pattern" (cf. Taylor 1968:541).

Comments.—Most of the RMNH specimens from Surinam "were collected in the daytime by digging in the upper soil layer in rainforest, between the buttresses of trees'' (Nussbaum & Hoogmoed 1979:225).

Microcaecilia cf. *rabei*
Plate 18F

Vouchers for Guyana.—AMNH A-166045–166053 from Berbice River Camp and AMNH A-166054–166058 from Konawaruk Camp. These specimens superficially are similar to ones reported from Kaieteur National Park (Kok & Kalamandeen 2008:244–245).

Coloration in life.—The AMNH specimens from Berbice River Camp were noted in life (CJC field notes, 1997) as being reddish brown, but with the distal 20–25% being grayish brown. The AMNH specimens from Konawaruk Camp (CJC field notes, 1998) were noted in life (CJC field notes, 1998) as being similar, but with the additional note that the head was pink (lighter below), which, as recalled, seemed similar to those from Berbice River Camp as well; also, one was noted as having the distal 40% grayish brown. In alcohol, the head color is brown or yellowish brown; throat from snout through first collar is yellow; and the cloacal area is cream to pale yellow.

Comments.—These small caecilians generally have a body length of less than 160 mm; primary annuli numbering 101–109; and secondary annular grooves numbering 6–18, of which only 1–7 are complete. Teeth were counted on only one or two specimens as follows: premaxillary and maxillary teeth, 20–26; vomeropalatine teeth, 29; and dentary teeth, 15–19. These data are similar to those for *M. rabei*, although not identical in some comparisons, but one must allow for complications owing to possible geographic variation, small sample sizes, and data having been recorded by different specialists. Nevertheless, the range of primary annuli overlaps that of *M. rabei* from Suriname (and specimens from Konawaruk Camp fall entirely within the range for Suriname), and although the range of data for specimens from Venezuela is not overlapped by specimens from Berbice River Camp, it is by specimens from Konawaruk Camp. The range in number of secondary annular grooves for Guyanan specimens superficially appears not to overlap those for specimens from Venezuela and Suriname, but the differences are small and need confirmation. Considering that *Microcaecilia* are small burrowing animals, they may have low vagility, and they may be prone to local differentiation of cryptic species. Consequently, considerable molecular work is necessary to determine their evolutionary history and to estimate the number of species and how they differ from each other. One specimen from our Berbice River Camp was found burrowing in a sandy dirt pile.

Typhlonectidae

This is another strictly neotropical family (Wilkinson et al. 2011), of which the one species known from Guyana is aquatic, with a somewhat vertically compressed tail.

Typhlonectes compressicauda
(Duméril & Bibron, 1841)

Type material.—The original name was *Coecilia compressicauda* and MNHN 4269 from Cayenne, French Guiana is regarded as the lectotype (Frost 2011).

Distribution.—"Amazon Basin from the eastern coast of Brazil to the eastern slopes of Peruvian and Colombian Andes and the rivers of the Guyana Shield region" (Frost 2011).

Vouchers for Guyana.—UMMZ 82854 from "Demerara River Harauruni" (quoted from the UMMZ records, although cited by Taylor [1968:241] as "Hahauruni Creek, Demerara River, Guiana"); identification recently confirmed by Mark Wilkinson.

Coloration in life.—The following is from Lescure & Marty (2000:300). Bluish

gray to brownish gray; white spot tinged with blue at the level of the eyes and cloaca.

Comments.—This species is aquatic. Taylor (1968) used the UMMZ voucher cited above for his detailed description of the species.

Species Accounts: Reptilia

The approximately 9100 species of modern non-avian reptiles (Hoffmann et al. 2010) are remarkably diverse in body form, coloration (some being spectacularly beautiful), camouflage, life history, behavior, toxicity, and actual or potential use to humans. There are three major groups represented in Guyana, as follows: Crocodylia (crocodilians; 4 species); Squamata (amphisbaenians or worm lizards, lizards, and snakes; 157 species); and Testudinata (turtles and tortoises; 15 species). The earliest origin of reptiles from an amphibian approximately 300 million yr ago and the evolutionary relationships of the modern species have received extensive modern study, but a great deal of work remains to be done before we will adequately understand these organisms. Appendix 2 provides a complete list of the species we have documented as occurring in Guyana.

Species Accounts: Reptilia: Crocodylia

Molecular and morphological analyses indicate that there are three major groups of crocodilians (about two dozen species) that have survived to modern times (Gatesy et al. 2003, Harshman et al. 2003, Brochu et al. 2009). These are the alligators and caimans (primarily of the Western Hemisphere but including the Chinese alligator); crocodiles (pantropical in distribution); and the gavials or gharials (of southern Asia). Four species (3 genera) of 1 family of crocodilians are represented in Guyana. Today, none of these is considered to be critically endangered (http://www.iucncsg.org/).

Alligatoridae

Caiman crocodilus (Linnaeus, 1758)

Type material.—The original name was *Lacerta Crocodilus* and Hoogmoed & Gruber (1983) selected as lectotype the ZMUU specimen of a certain size and condition they specified. The type locality is unknown (Duellman 2005).

Distribution.—"Pacific lowlands from the Isthmus of Tehuantepec, Mexico, to southern Ecuador; Atlantic lowlands from extreme eastern Honduras to northern Colombia, Venezuela, and the Guianas and throughout the Amazon basin to eastern Peru and central Brazil" (Savage 2002:778). The subspecies *C. c. crocodilus* occurs in "Guiana, Venezuela, Trinidad, the Amazon drainage, eastern Colombia to Peru" (Brazaitis 1973:64).

Vouchers for Guyana.—AMNH R-32344 from Kartabo. In addition, CJC, RPR (USNM field series specimen number 207159 donated to UG), and CRT saw representatives of this species (not collected) at Dubulay Ranch and CJC and CRT saw them (not collected) at their Berbice River camp.

Coloration in life.—The following is from Brazaitis (1973:64): "Dorsally olive green [or brown] with numerous dark brown or black flecks on the head, body, and tail. Dark brown or black crossbands on the back and tail. Ventral surfaces are unpatterned, uniform cream, or yellow. No large dark blotches on the sides of the jaws...Hatchlings display a series of faded bars on the sides of the jaws, no longer visible at about 35 cm total length." Duellman (2005:328) described the dorsal coloration as "tan to pale olive-gray...Juveniles tend to be more tan...and small juveniles have distinct transverse dark

brown bars on the dorsum. The iris is pale brown with many black flecks."

Melanosuchus niger (Spix, 1825)
Plate 19A, B

Type material.—The original name was *Caiman niger* and ZSMH 2480/0 was designated as lectotype by Hoogmoed & Gruber (1983). The type locality is "fluminis Amazonium et Solimoëns [Brazil]" (Spix 1825:4).

Distribution.—"Eastern Colombia, Peru, south to Bolivia, the Brazilian Amazon basin north to Guiana'' (Brazaitis 1973:68).

Vouchers for Guyana.—AMNH R-15171 from Georgetown. In addition, CJC, RPR, and CRT saw representatives of this species (not collected) at Karanambo.

Coloration in life.—The following is from Brazaitis (1973:67): "Jet black above with narrow yellow crossbands on the body and tail, neck and base of skull light tan or yellow. From three to five large dark blotches on the sides of the jaws... Ear coverlets black, as is the median dorsal surface of the snout. Median ventral surfaces immaculate white bordered by jet black."

Paleosuchus palpebrosus (Cuvier, 1807)

Type material.—The original name was *Crocodilus palpebrosus* and type material from Cayenne, French Guiana, may be at the MNHN.

Distribution.—"The whole of tropical South America, from the Guianas in the north and Mexiana Island; south to Sao Paulo, Brazil; the Rio Pastaza in Ecuador to the east coast" (Brazaitis 1973:69).

Vouchers for Guyana.—UMMZ 46110 from Dunoon, Demerara River; UMMZ 55873 from Moruca River; and UMMZ 80435 from Wismar, with thanks to Greg Schneider, who confirmed identifications.

Coloration in life.—"Reddish brown above, blotched with brown on the ventral surfaces. Very dark, nearly black individuals are not uncommon. Light areas of the head and body may be light brown or yellow. The ear coverlets match the color of the cranial table which is noticeably reddish brown. The dorsal surface of the snout is uniform reddish brown. Some large red blotches on the sides of the jaws. The iris of the eyes are reddish brown or orange" (Brazaitis 1973:68).

Comments.—With respect to the two species of *Paleosuchus* that occur in Guyana, Brazaitis (1973:69) stated the following: "Both species appear to occupy the same habitat within the same distribution. Specific niches are not fully understood. Many individuals display overlapping physical characteristics, although *P. palpebrosus* shows a greater degree of dermal ossification."

Paleosuchus trigonatus (Schneider, 1801)
Plate 19C

Type material.—The original name was *Crocodilus trigonatus* and ZMB 243 from South America is the lectotype (Bauer & Günther 2006).

Distribution.—"South America. From Bahia, Brazil, in the south; west to northern Bolivia and the tributaries of the Amazon river in eastern Peru; north through Colombia to Ciudad Bolivar on the Rio Orinoco, Venezuela; eastward through Guiana, Surinam, and Mexiana Island" (Brazaitis 1973:69).

Vouchers for Guyana.—AMNH R-16048 and R-64823–64825 from Kartabo; BMNH 1872.10.16.89 from Demerara Falls; and UMMZ 86158 from Kurupung River, with thanks to Colin McCarthy and Greg Schneider for identifying the BMNH and UMMZ specimens, respectively. In addition, CJC and CRT saw representatives of this species (not collected) at their Konawaruk camp.

Coloration in life.—The following is from Duellman (2005:329–330), based on specimens from Peru: "Adults are dull brown with fainter darker brown crossbars on the body and tail, the posterior third of which is tan. The venter is cream, and the sides of the head are tan. Juveniles are reddish brown with irregular black transverse marks on the body and tail; the snout is black, and the parietal shelf is brown...The iris is brown." Brazaitis (1973:69) also noted "some individuals laterally tinged with yellow. Cranial table is dark brown, ear coverlets contrasting black or darker brown. A dark brown or black median dorsal stripe on the snout. Ventral surfaces densely blotched with brown. Iris of the eyes reddish brown or orange."

Comments.—Pritchard (1995:43) mentioned an individual (photo PCHP 002 deposited at UF) that he saw emerge from the sea and rest on Almond Beach near Waini Point, Guyana. He also noted that this was the "first marine record for species; closest records are from Lower Demerara and Lower Essequibo rivers, Guyana (Medem 1983, Crocodylia de Sur America, Vol. 2:95)."

Species Accounts: Reptilia: Squamata: Amphisbaenians or Worm Lizards

The Squamata is the largest group of reptiles (more than 8500 species) and includes the beak heads or tuataras of New Zealand, amphisbaenians or worm lizards, lizards, and snakes. Several modern studies based on phylogenetic analyses of morphology and/or DNA sequence data have shown clearly that the amphisbaenians and snakes are both monophyletic groups that have evolved from within the lizards (Kearney 2003, Townsend et al. 2004, Vidal & Hedges 2005, Conrad 2008, Wiens et al. 2010). However, there remain some uncertainties as to phylogenetically where the lineages of the Amphisbaenia and snakes split away from lizards. In addition, there are disagreements and new nomenclature for formal names to apply to the diverse higher-level taxonomic groups of lizards excluding amphisbaenians and snakes (see references above), as origins of the amphisbaenians and snakes within them could make the overall group of lizards paraphyletic. Nevertheless, we refer to lizards (excluding amphisbaenians and snakes) by their popular name, which, for present purposes, allows us to discuss in general the amphisbaenians or worm lizards, lizards, and snakes as separate groups within Squamata.

The amphisbaenians (worm lizards) are highly adapted to burrowing, and most species are limbless. They have a solid, compact skull, "an elongated body, short tail, and a unique modification of the inner ear that allows the detection of low frequency sounds" (Kearney 2003:1). They "burrow in loose or sandy soils [and riverbanks] and ostensibly come to the surface only rarely...Many species are only found serendipitously after heavy rains or when plowing or moving the soil. The ecology and life history of amphisbaenians are poorly known due to their fossorial lifestyle and the scarcity of researchers studying the group" (Kearney 2003:2). A recent phylogenetic analysis of many Brazilian amphisbaenians concluded that several genera recognized previously should be synonymized with the genus *Amphisbaena* (Mott & Vieites 2009). Presently, 1 family, 1 genus, and 4 species of amphisbaenians are known to occur in Guyana.

Amphisbaenidae

As for the species from Surinam (Hoogmoed 1973:371), the species from Guyana are "legless, having reduced eyes covered by the oculars and the scales arranged in annuli [around the body]."

Amphisbaena alba Linnaeus, 1758

Type material.—Gans (1967) cited syntypes from America in the Museum Drottningholm. Hoogmoed (1973) restricted the type locality to the confluence of the Cottica River and Perica Creek, Surinam.

Distribution.—"Forested lowlands of South America...Venezuela, Trinidad, and the Guianas; Colombia, Peru, and Bolivia east of the Andes; Brazil and northern Paraguay" (Gans 1962:16).

Vouchers for Guyana.—AMNH R-61223 from the Kuyuwini River and AMNH R-21279 from Kartabo.

Coloration in life.—"Light- to dark-brown above, fading to a dirty white on the ventral parts (Gans 1969). Juvenile specimens show white spots in the brown dorsal area, which, in adults, is uniform. Tip of the tail entirely white" (Hoogmoed 1973:376–377). Beebe (1945:29) described a specimen from Kartabo as follows. "Snout back to the eyes and the chin shields pale pink. Above dark brownish-yellow shading to old ivory below, the tail mottled with dead white. Eye showing pink beneath its scale."

Amphisbaena fuliginosa Linnaeus, 1758
Plate 19D, E

Type material.—Gans (1967) cited syntypes in the Stockholm Museum and Uppsala Museum from America. Hoogmoed (1973) restricted the type locality to the confluence of the Cottica River and Perica Creek, Surinam.

Distribution.—"Surinam, Guyana, French Guyana, Venezuela" (Hoogmoed 1973:383). Vanzolini (2002:625) included Brazil, Colombia, Ecuador, and Peru.

Vouchers for Guyana.—AMNH R-1085 from Kaieteur Falls; AMNH R-7295 and R-17688–17689 from Georgetown; AMNH R-25088 from Kamakusa; AMNH R-60907 from Marudi River; AMNH R-137423–137424 from Kartabo; AMNH R-140977, R-141875, and USNM 566299 from Dubulay Ranch; and USNM 164181 from Mabaruma Compound (8°12′N, 059°47′W).

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994). They are black and white, with more black above, more white below.

Amphisbaena stejnegeri Ruthven, 1922

Type material.—The holotype is UMMZ 55858, from a sand reef at Vreeden Rust, Demerara River, Guyana.

Distribution.—Known only from the type locality (Gans 1963:13).

Vouchers for Guyana.—The holotype is the only known specimen having locality data, and only one other specimen, without data, exists (Gans 1963).

Coloration.—The only color notes are for specimens in preservative, which are "yellowish, with an irregular dorsal scattering of individual dark segments...[more so on one specimen than the other], thinning out anteriorly toward an immaculate head. The anterior half of some [most] infracaudal segments is strongly pigmented, while the infracaudal segments of the ninth postcloacal annulus are entirely pigmented" (Gans 1963:6–7).

Amphisbaena vanzolinii Gans, 1963

Type material.—The holotype is AMNH R-60975, a female from "Marudi, British Guiana... Charles M. Bogert informs me that W. Hassler, who went over the route of the expedition, placed the locality as 'on a tributary of the Kuyuwini River, at 2°5′ North and 59° East'" (Gans 1963:13).

Distribution.—Brazil, Guyana, and Surinam (Hoogmoed 1973, Hoogmoed & Mott 2003).

Vouchers for Guyana.—The holotype; the paratopotype AMNH R-60778; and KU 69817–69818 from "Rupununi District, N. of Acarai Mountains, W. of New River" (Hoogmoed 1973:384).

Coloration.—The following is based on specimens from Surinam (Hoogmoed 1973:387). "RMNH 15144 from Paloemeu was purplish all over, slightly darker dorsally than ventrally. The specimens from Sipaliwini were light- to dark-brown above, with a transparent pink belly, the underside of the tail white. In preservative RMNH 15144 is dirty white all over, with a brown tinge on the dorsal parts. All Sipaliwini specimens are light- to dark-brown above, white below."

Comments.—"All Surinam specimens (except RMNH 15191) were collected in rotten logs lying on the rain-forest floor. RMNH 15191 (from Sipaliwini) was found while digging in the upper soil-layers. Only a special type of rotten log seems to be favoured by this species, namely logs that are very soft and when pulled apart rendered a pulp of small wood-fragments" (Hoogmoed 1973:387).

Species Accounts: Reptilia: Squamata: Lizards

Lizards are non-avian, non-crocodilian, and non-testudinatan reptiles (without a bony shell) that, for most species, are terrestrial or arboreal and have four legs and a tail. However, some lizards that lack limbs, and some of these and others are burrowing organisms. At the moment, at least 9 families, 34 genera, and 56 species of lizards are known to occur in Guyana.

Iguanian Lizards

Traditionally, until 1989, the Iguanidae was treated as a very large family of lizards that occur primarily in the Western Hemisphere. Frost & Etheridge (1989) conducted the first cladistic analysis of the group as a whole, and they partitioned the large traditional family into eight smaller families, many of which had been recognized previously as natural groups below the family level. By recognizing the eight families, Frost & Etheridge (1989) emphasized that they had strong evidence that each of these families represented a monophyletic group of genera and species; however, this also emphasized that at the time they could not establish firmly the monophyly of the larger group of those eight families with respect to other lizards.

Recently, the monophyly of the eight families partitioned from the larger, traditional Iguanidae has received improved support (e.g., Schulte et al. 2003, Townsend et al. 2004, 2011), and some authors have suggested returning to the original concept of one large family (e.g., Schulte et al. 2003), with the eight groups of Frost & Etheridge (1989) being treated as subfamilies. Both versions of family groupings proposed (Frost & Etheridge 1989 vs. Schulte et al. 2003) are consistent with formal taxonomic and nomenclatural procedures, so neither is conceptually flawed or necessarily wrong. However, the arrangement of families proposed by Frost & Etheridge (1989) has received such widespread use, including among authors writing about Guianan taxa (e.g., Avila-Pires 1995, Gorzula & Señaris 1999 [1998], Savage 2002, Conrad 2008), that we follow their usage of multiple smaller families. Most recently, the earlier Iguanidae has been divided up into even more than eight smaller families (Townsend et al. 2011).

The following four families of iguanian lizards have representatives living in Guyana: Corytophanidae (introduced by humans), Iguanidae, Polychrotidae, and Tropiduridae. Consistent with our treatment of families in this volume, these groups are considered below in alphabetical order by family. However, see Appen-

dix 1 for a most recent splitting of Dactyloidae (for *Anolis*) from the Polychrotidae (Townsend et al. 2011).

Corytophanidae

Representatives of this family of iguanian lizards occur in southern "Mexico, southward through Central America, to Ecuador and Venezuela" (Frost & Etheridge 1989:35). One species has been introduced to Guyana by humans (see Comments for *Basiliscus*).

Basiliscus basiliscus (Linnaeus, 1758)

Type material.—The original name was *Lacerta Basiliscus* and the type material from South America is not known to us.

Distribution.—"Lowlands and adjacent slopes on the Pacific versant from southwestern Nicaragua to northwestern Colombia, and on the Atlantic versant from central Panama to northwestern Venezuela'' (Savage 2002:430). Avila-Pires (2005:33) stated that this species was introduced into Guyana by humans (see Comments, below).

Vouchers for Guyana.—RMNH 40127 from Timehri Airport, identified by M. S. Hoogmoed.

Coloration in life.—The following is based on specimens from Costa Rica (Savage 2002:428–429). Adults with "body brown, olive, or bronze, with darker crossbands and usually cream to yellow light stripes along lips and a pair of similarly colored lateral stripes. Juveniles: yellowish green with brown cross-bands, lip and lateral stripes usually present, all markings more vivid than in adults; throat with three distinct longitudinal light lines...; iris brown to bronze in all age-classes."

Comments.—The RMNH voucher was collected by L. G. Hoevers in "swampy bush" (quoted from RMNH records). A photograph of the specimen was sent to CJC by M. S. Hoogmoed, according to whom (pers. comm.), Mr. Hoevers "said there was a reproducing population at the airport." The presence of this population should be confirmed.

Gekkonidae

Until recently, many genera of geckoes were included in the large family Gekkonidae (Gray 1825). However, recent phylogenetic analyses (Gamble et al. 2008), including considerable DNA sequence data, indicate that the geckoes of Guyana should now be considered as representative of the two following families: Gekkonidae (with *Hemidactylus* and *Thecadactylus*) and Sphaerodactylidae (with *Chatogekko*, *Coleodactylus*, *Gonatodes*, *Pseudogonatodes*, and *Sphaerodactylus*).

Hemidactylus mabouia (Moreau de Jonnès, 1818) Plate 20A

Type material.—The original name was *Gecko Mabouia* and the holotype is MNHN 6573 (Avila-Pires 1995:229). The type locality was restricted to St. Vincent Island, Lesser Antilles, according to Avila-Pires (1995).

Distribution.—Africa south of 10°N, Madagascar, the Antilles and South America, where it occurs in Brazil the Guianas, Ecuador, and Peru (Avila-Pires 1995:233). The species has been introduced to other localities in the Western Hemisphere also, although it was originally a "native to sub-Saharan Africa" (Bugoni & Welff-Neto 2008:226).

Vouchers for Guyana.—AMNH R-137421 from Kartabo; AMNH R-140930–140936, R-141899 and USNM 566313–566314 from Dubulay Ranch; USNM 162983–162999 from Enmore Estate (6°44′N, 057°59′W); and USNM 291268 and 497791 from Georgetown.

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994, 1995). Very light tan, yellowish tan, or grayish tan on body, arms, legs, and tail (the latter lighter), with dark gray, tan, brown, or black bands, which may be inconspicuous; venter translucent light gray, cream, or yellow.

Hemidactylus palaichthus Kluge, 1969
Plate 20B

Type material.—The holotype is AMNH R-60931, an adult male from Kurupukari, Guyana.

Distribution.—This species is known only from the Western Hemisphere, from "northern Brazil, coastal Suriname, Guyana, central and northeastern Venezuela, and on the islands of Trinidad and St. Lucia" (Avila-Pires 1995:237).

Vouchers for Guyana.—The holotype; AMNH R-60900–60906 from Isheartun (on the upper Rupununi River, about 30 km [linear] NW Kuyuwini Landing); AMNH R-137925–137926, R-137929, R-137931–137938, R-137940 and USNM 566315–566319 from Karanambo; AMNH R-138064 from Yupukari; AMNH R-139741–139753, 139759–139760, and USNM 566320–566326 from Aishalton; AMNH R-140948 from Dubulay Ranch; ROM 20521–20524 from Kurupukari.

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo, Aishalton, and Dubulay Ranch (CJC field notes, 1992–1994). Gray, pinkish gray tan or dark brown above (including body, arms, legs, tail) with grayish brown or dark gray, brown, or black markings (mostly bands) that are edged behind by light gray; ventral surfaces cream or pale yellow, with or without gray or tan specks, but with gray or brown flecks or mottling beneath tail, which may otherwise be gray or yellow.

Thecadactylus rapicauda (Houttuyn, 1782)
Plate 20C, D

Type material.—The original name was *Gekko Rapicauda* and type locality was restricted to Paramaribo, Surinam by Hoogmoed (1973). Avila-Pires (1995:239) stated that the "holotype is unknown, but possibly still preserved in the Zoological Museum Amsterdam" (M. S. Hoogmoed, pers. comm.).

Distribution.—"Venezuela, Guyana, Suriname, French Guiana, Brazil, on both sides of the Andes in Ecuador and Colombia, on eastern side in Peru and Bolivia; Central America north to Mexico; Lesser Antilles" (Avila-Pires 1995:245).

Vouchers for Guyana.—AMNH R-8106–8109 from Kalacoon; AMNH R-21302–21304 and R-46437–46438 from Kartabo; AMNH R-60914–60915 from Isheartun; AMNH R-60927–60928 from Onora; AMNH R-61382 from Marudi; AMNH R-140956–140959 from Dubulay Ranch; AMNH R-151743, R-151745, and USNM 566331 from Berbice River Camp; and AMNH R-151746–151753, R-151755, and USNM 566332–566336 from Konawaruk Camp. Also USNM 84486 from Tumatumari; USNM 164184–164185 from Mabaruma Compound (8°12′N, 059°47′W); USNM 531640–531641 from Iwokrama Forest Reserve; USNM 561449–561452 from CEIBA Biological Center, 26 mi S of Georgetown on Linden Highway (06°29′57″N, 058°13′06″W).

Coloration in life.—The following is based on AMNH specimens from Dubulay Ranch (CJC field notes, 1994). Yellowish tan above with brown markings (all dorsal surfaces); ventral surfaces yellow or very pale greenish yellow; regenerated tail (above and below) tan with dark brown markings.

Gymnophthalmidae

Until recently, the microteiid and macroteiid lizards were all included within the

large family Teiidae. However, recent phylogenetic analyses, including considerable data from DNA sequencing, have shown that the microteiids probably are a monophyletic group that can be treated as a separate family (Gymnophthalmidae), and its closest relatives are the Teiidae (Pellegrino et al. 2001, Castoe et al. 2004). Recent revisionary work has shown that one Guyanan species that formerly was assigned to the genus *Prionodactylus* is actually a member of the genus *Cercosaura* (*C. argulus*), and four new species and genera known only from Guyana have been described recently (*Arthrosaura hoogmoedi*, *Echinosaura sulcarostrum*, *Kaieteurosaurus hindsi*, and *Pantepuisaurus rodriguesi*).

There are approximately 200 species in approximately 45 genera of gymnophthalmids, and they occur primarily in South America. The group is exceedingly interesting because of its diversity, frequent examples of convergent evolution, and limited geographic ranges of many species. For taxa occurring in Guyana, there are examples of unisexual (all-female) species that reproduce by parthenogenetic cloning (by means of unfertilized eggs), and species with extreme elongation of the body, loss of limbs, and loss of eyelids, owing to multiple (convergent) origins of a burrowing life style. Most of the species, while being immensely interesting, are small and cryptic in the habitats in which they live, having secretive lives that are very difficult to study. As a consequence, of the 21 Guyanan species, 12 are known from only 5 specimens or fewer that have been found in Guyana, and about half of these are endemic to Guyana. In addition, some genera (e.g., *Gymnophthalmus* and *Leposoma*) have taxonomically cryptic species, which are morphologically so similar to one another that they are difficult to identify correctly to species.

Alopoglossus angulatus (Linnaeus, 1758)
Plate 20E

Type material.—The original name was *Lacerta angulata* and Hoogmoed (1973) designated RMNH 15200, a female, as the neotype. This specimen is from Brown's Mountain, Surinam.

Distribution.—"Amazonian region in Brazil..., French Guiana, Suriname, Guyana, Colombia, Ecuador and Peru" (Avila-Pires 1995:313).

Vouchers for Guyana.—AMNH R-61381 from Marudi; and USNM 566400 from Berbice River Camp.

Coloration in life.—The following is based on the USNM specimen from Berbice River Camp (CJC field notes, 1997). All dorsal surfaces dark brown, with very inconspicuous dark tan dorsolateral stripes, most visible on the neck and as spots on the hips and base of tail; all ventral surfaces very pale yellow, with dark gray to black spots on preanal area and base of tail. The following is from Hoogmoed (1973:222), based on specimens from Suriname. "In life dark-brown above with faint orange-brown dorsolateral stripes, tail with light-brown and dark-red spots. Ventral parts dirty white with two dark-brown spots on the preanal plate. Iris green. Tongue bluish black." Avila-Pires (1995) stated that males also have a light lateral stripe that is absent in females.

Arthrosaura guianensis
MacCulloch & Lathrop, 2001

Type material.—The holotype is ROM 39471, an adult male from the northeast plateau of Mount Ayanganna, Guyana (05°24′N, 059°57′W; 1490 m).

Distribution.—This species is known only from Guyana.

Vouchers for Guyana.—Only two specimens are known in addition to the holotype. These are ROM 39472 from

the type locality and USNM 549323 from the north slope of Mount Roraima (5°17′N, 060°45′W; 700 m).

Coloration in life.—"Dark brown dorsally and laterally, with a light dorsolateral line from above the eye to the groin. A fine line of small white dots from neck to midbody, parallel to dorsolateral line and passing just above forelimb. A second row of similar spots, also parallel to dorsolateral line, extending from behind forelimb insertion to about halfway to the hindlimb. Chin white, throat white with orange wash. Venter and underside of limbs and tail reddish-orange, fading to white distally on limbs and tail. Dark mottling extending from lateral surfaces onto ventral surfaces, decreasing in intensity so that midventral areas are immaculate or nearly so; dark mottling most intense in gular region. Underside of tail light with dark mottling proximally, becoming darker distally. Some irregular light mottling on sides of neck. Upper lips dark, with two vertical white bars below eye. Diffuse light markings on anterior supralabials, frenocular, and first subocular" (MacCulloch & Lathrop 2001:178).

Arthrosaura hoogmoedi Kok, 2008

Type material.—The holotype is IRSNB 2653, an adult female from the summit plateau of Mount Maringma, Cuyuni-Mazaruni District, Guyana (5°12′60″N, 60°35′06″W; 2112 m).

Distribution.—Known only from the type locality.

Vouchers for Guyana.—This is another of the least known species in the world, as it is known from only the type specimen.

Coloration in life.—"Dorsum dark brown, with a black middorsal stripe (about two–three dorsal scales wide) extending from nape to tail, where it quickly becomes inconspicuous due to the dark coloration of the tail; subtle, irregular, tan dorsolateral line extending from nape to about midbody; flanks black, lower part of flanks peppered with reddish brown, and with some small pale brown spots ventrolaterally, forming an irregular ventrolateral line. Axilla region and underside of arms marbled with reddish brown and black. Head blackish brown with tan dorsolateral lines extending above eyes, from the anterior part of the loreals to the parietals. Tip of snout paler; diffuse paler blotches on lower part of lateral surface of head. Tympanum black, surrounded by some tan scales. Arms black, legs and tail blackish brown. Iris black...Tongue dark gray. Palms and soles black. Chin, throat, chest, belly and ventral surface of upper legs [arms] cream with dark mottling; lower legs ventrally reddish brown with dark mottling; tail ventrally black, except proximally where it is dirty white peppered with black" (Kok 2008:11).

Arthrosaura reticulata (O'Shaughnessy, 1881) Plate 21A, B

Type material.—The original name was *Cercosaura* (*Pantodactylus*) *reticulata* and the holotype is BMNH 1946.9.1.5 (Avila-Pires 1995:335) from Canelos, Ecuador.

Distribution.—"Amazonian region in Brazil, French Guiana, Suriname, Guyana, southern Colombia, Ecuador and northern Peru" (Avila-Pires 1995:342).

Vouchers for Guyana.—AMNH R-57454 from Kuyuwini Landing; AMNH R-70623 from Isheartun; AMNH R-152005–009, R-152016, and USNM 566421 from Berbice River Camp.

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). Dark brown above, with three lighter brown stripes (one, the vertebral stripe, is very irregular on one individual, and all stripes can be very inconspicuous). Light gray spots on sides of lips and neck; light tan spots on sides of body. Top of

head, arms, and legs very dark brown; all ventral surfaces bright orange, throat with black spots. Hind legs above with inconspicuous tan dots. The coloration given by Hoogmoed & Avila-Pires (1992:466) is somewhat different, but within the realm of individual and geographic variation. They also noted the following: "iris brown, brown with an orange rim, or golden; tongue anteriorly blue-grey, posteriorly pink-white. Adult males may have brightly orange undersides, possibly related to breeding condition."

Bachia flavescens (Bonnaterre, 1789)
Plate 20F

Type material.—The original name was *Chalcides Flavescens* based on material from an unknown locality. Avila-Pires (1995:344) stated that the type was in the MNHN, but was lost.

Distribution.—"Brazil, French Guiana, Suriname, Guyana, and Colombia" (Avila-Pires 1995:349).

Vouchers for Guyana.—AMNH R-137365–137367 and R-137369 from Kartabo; AMNH R-140923–140927 and USNM 566422 from Dubulay Ranch; AMNH R-151916–151925 and USNM 566423–566426 from Berbice River Camp; AMNH R-151931–151932 and USNM 566427 from Konawaruk Camp; ROM 20515 from Tukeit; and USNM 85012 from Pickersgill, Pomeroon River.

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1994–1998). Brown above, with dark tan dorsolateral stripe bordered above and sometimes below by broken (dashed) fine dark brown or black lines; venter translucent pinkish gray or light to medium brown on body, brown on tail. Dorsally, the coloration may be intensified on the base of the tail. Ventrally, adult males have white to very pale blue spots on the preanal scales, posterior abdominals, and basal subcaudals.

Comments.—Avila-Pires (1995) discussed taxonomic problems and conclusions concerning this locally and geographically variable species.

Cercosaura argulus Peters, 1863a
Plate 21E

Type material.—The original name was *Cercosaura* (*Pantodactylus*) *argulus* and the holotype is ZMB 4555 from "mountainous regions around Santa Fé de Bogotá, Cundinamarca, Colombia" (Avila-Pires 1995:453).

Distribution.—"French Guiana, Colombia, Ecuador, Peru, Bolivia, and Brazil" (Avila-Pires 1995:458).

Vouchers for Guyana.—AMNH R-21265 from Bartica; AMNH R-61386 from Marudi; and AMNH R-61434 from Shudikar-wau, headwater stream, Essequibo River.

Coloration in life.—The following notes are based on AMNH R-119427 from Brownsberg Nature Park, Suriname (CJC field notes, 1980). Dorsum, posteriorly (including tail), brown; head and neck gray, grading into the brown dorsum posterior to shoulder; three largely complete rows (vertebral and dorsolateral) of tiny, black dots on back, fading on base of tail; dark brown lateral stripe on body originating at eye, followed below by a yellow stripe, in turn followed below by a thin black line originating anterior to arm; on body above arm are two tiny white dots encircled with black; one cream dot on each elbow plus one above humerus; venter beige, lightest anteriorly.

Comments.—Previously, this species was treated as being in the genus *Prionodactylus*, but Doan (2003) showed that this genus is a junior synonym of *Cercosaura*.

Cercosaura ocellata Wagler, 1830
Plate 21D

Type material.—Avila-Pires (1995) stated that the holotype is ZSMH 643/0 from "probably somewhere in northeastern South America; Surinam?" (Ruibal 1952:494).

Distribution.—"Eastern Amazonia, in Guyana, Suriname, French Guiana, and Brazil" (Avila-Pires 1995:364).

Vouchers for Guyana.—AMNH R-21264 from Kartabo; AMNH R-61385 from Marudi; AMNH R-139827–139830 and USNM 566428 from Aishalton; AMNH R-140947 from Ceiba Biological Station (Madewini River, ca. 5 km. E Timehri Airport; 06°29′57″N, 058°13′06″W); AMNH R-141877 from Dubulay Ranch; ROM 28352 from Paramakatoi; and UMMZ 46771–46772 from Dunoon, Demerara River.

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton, Ceiba Biological Station, and Dubulay Ranch (CJC field notes, 1993–1995). Dorsum brown or yellowish dark tan; orange lateral stripe or inconspicuous tan or cream dorsolateral stripe; sometimes black stripe to each side of dorsolateral stripe; sides green below this; head, arms, and legs brown or tan; sometimes black flecks on lips; chin, throat, and chest white or cream; abdomen and beneath arms, legs, and base of tail grayish tan or yellow; tail of adult male with orange on sides, pale yellow ventrally at base, grading into orange posteriorly.

Echinosaura sulcarostrum Donnelly, MacCulloch, Ugarte, & Kizirian, 2006
Plate 21F

Type material.—The holotype is ROM 22893, an adult male from Guyana, Baramita, approximately 1 km S airstrip (07°22′N, 060°29′W; 100 m).

Distribution.—Known only from Guyana.

Vouchers for Guyana.—The holotype; ROM 22892 and ROM 22894 from the type locality; and ROM 43805 from Mount Wokomung.

Coloration in life.—"Dark brown dorsally and laterally, with pale yellow spots. Spots join to form short longitudinal stripes on the nape and transverse blotches posteriorly. Venter mottled brown/yellow; chin and throat more yellow than brown, brown increasing posteriorly. Underside of limbs pale yellow with brown mottling. Proximal portion of ventral tail brown with yellow spots. Regenerated portion of tail uniform reddish brown" (Donnelly et al. 2006:400).

Gymnophthalmus leucomystax Vanzolini & Carvalho, 1991
Plate 21C

Type material.—The holotype is MZUSP 69301 from Fazenda Salvamento, Roraima, Brazil.

Distribution.—Known only from savanna regions in the Roraima area of northern Brazil and southern Guyana (within or near the Rupununi Savanna).

Vouchers for Guyana.—AMNH R-131991–93 from Isheartun; and AMNH R-139856–139860, AMNH R-139863–139866, and USNM 566453–566454 from Aishalton; both males and females are represented.

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton (CJC field notes, 1993). Dorsum grayish brown to shiny tan; dorsolateral light stripe distinct, yellow or pale gold anteriorly, becoming cream or tan posteriorly, continuous to base of tail; black stripe above and alongside the light stripe, becoming line of black dots posteriorly; sides very dark brown to black; cream to tan lateral (or essentially ventrolateral) light stripe, on some pres-

ent only anterior to arm, on others extending to midbody or hip; tail dark gray or bluish gray above (although may be tan at base), grayish blue below; arms and legs brown; females with chin and throat white, other ventral surfaces (excluding tail) gray with tiny black dots; adult males orange below.

Comments.—This species occurs on the southern part of the Rupununi Savanna in the vicinity of Aishalton, where the habitat is similar to that of localities where it occurs in Brazil.

Gymnophthalmus cf. *speciosus* (Hallowell, 1861) Plate 22C

Type material.—The original name was *Blepharactisis speciosa* and the type specimen(s) from Nicaragua are unknown to us.

Distribution.—Southern Mexico, Central America, and northern South America (Savage 2002:522), but see Comments, below.

Vouchers for Guyana.—AMNH R-140974–140975 from Dubulay Ranch; males.

Coloration in life.—The following is based on the AMNH specimens from Dubulay Ranch (CJC field notes, 1994). Dorsum copper; tip of snout very pale tan; sides, arms, and legs very dark brown (sides almost black); dorsolateral stripe light tan but posterior to midbody continuing to base of tail as dots; just above dorsolateral stripe on neck is a short series of black dots; tail tan or reddish tan above with gray iridescence (when viewed on an angle), having light tan dots aligned around tail appearing as inconspicuous, incomplete bands; belly cream or very pale tan, with tan or metallic copper iridescence; beneath tail tan becoming pale gray posteriorly.

Comments.—The more we study *Gymnophthalmus*, the more we realize that there are morphologically similar, cryptic species that are difficult to distinguish from each other and which usually have rather restricted geographic ranges. Consequently, most recent authors doubt that a single species, *G. speciosus*, actually ranges from southern Mexico to northern South America (e.g., Cole et al. 1990, Vanzolini & Carvalho 1991, Carvalho 1997, Kizirian & Cole 1999). Nevertheless, specimens from bisexual (gonochoristic) populations in northern South America are similar to those from Nicaragua, and there are no clear-cut objective data yet for concluding which populations should be named as a separate species. In fact, there may be several species masquerading under the name *G. speciosus* within its broad range. This will be resolved when somebody does careful comparative analyses of samples from throughout the range, including molecular work. The first work to be done with DNA sequence data showed that samples from Dubulay Ranch were most closely related to those from Chacachacare Island, Trinidad, that the next closest relative was from the Rupununi Savanna (now known as *Gymnophthalmus vanzoi*, see account and Comments below), and that these might be paraphyletic with respect to a sample from Venezuela (Kizirian & Cole 1999). No samples from Central America or Mexico were available for that study.

Gymnophthalmus underwoodi Grant, 1958 Plate 22A, B

Type material.—The holotype is UIMNH.42334 from Barbados.

Distribution.—Specimens identified with certainty are known from islands in the West Indies, Guyana, Suriname, and French Guiana (Cole et al. 1990). The species is expected to occur in Venezuela,

but no records are known as yet. For Brazil, specimens known may include both this species and an un-named cryptic species, which requires additional molecular analyses to confirm (see Comments, below).

Vouchers for Guyana.—AMNH R-137971–137972, R-137987–137993, R-137999, R-138010–138028, and USNM 566468–566482 from Karanambo and Yupukari; AMNH R-139879 from Aishalton; AMNH R-140976, R-141867–141868, R-141870, R-141872–141874, and USNM 566483–566485 from Dubulay Ranch; AMNH R-151933–151941 and USNM 566486–566489 from Berbice River Camp; and AMNH R-152338 from Ceiba Biological Station, Madewini River, ca. 5 km (linear) E Timehri Airport (06°29′57″N, 058°13′06″W).

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo (and Yupukari), Aishalton, Dubulay Ranch, and Berbice River Camp (CJC field notes, 1992–1997). Dorsum dark copper, extending well onto tail, may become grayish tan or tan with gray iridescence; sides, arms, and legs dark brown to black; light tan dorsolateral stripe fading posterior to shoulders; belly gray or bluish gray (paler anteriorly), with light coppery iridescence; posterior tail gray or bluish gray, especially below.

Comments.—This is a diploid, unisexual (all-female) species that had a hybrid origin (sympatric speciation) and of which females reproduce by parthenogenetic cloning (Hardy et al. 1989, Cole et al. 1990). The trigger for embryogenesis is unknown. The unisexual lineage arose from a female hybrid between *Gymnophthalmus cryptus* × *G*. cf. *speciosus* in the Guianan Region (Cole et al. 1993), and the female parent of the hybrid was the *G. cryptus* (see Kizirian & Cole 1999). Because members of the clone possess the F_1 generation combination of parental genes, the switch from gonochoristic reproduction to parthenogenetic cloning must have occurred in one generation. Analyses of DNA sequence data (more than 1800 nucleotides) indicated that specimens from Guyana, Suriname, Trinidad, and the type locality are of one clone (Kizirian & Cole 1999), so the name *G. underwoodi* is correctly applied to these populations.

At least two cryptic, unisexual species are masquerading under the name *G. underwoodi*, and there are also cryptic, bisexual (gonochoristic) species of which males (or possibly hybrids) have been misidentified as *G. underwoodi* (discussed by Cole et al. 1990). This is understandable because the species are difficult to identify, especially on the basis of external morphology of specimens that have been preserved for a long time. Of special interest is the Brazilian sample from Ilha da Maracá, Roraima, which Cole et al. (1990:12–15) referred to as "*G. underwoodi*?" On the basis of a few distinctive morphological characters, those authors stated: The lizards "could represent a distinctive clone of *G. underwoodi* or they could be a different species." Subsequently, Yonenaga-Yassuda et al. (1995) showed that these Brazilian lizards also have a karyotype rather different from that of *G. underwoodi*, so it would be appropriate to consider them as a separate species after all. In fact, the karyotype of the unisexual Brazilian sample is very similar to that of *G. cryptus* presented by Cole et al. (1993).

CJC compared 39 recently collected representatives of all known populations from Guyana with the Brazilian ones for a more-or-less diagnostic morphological character (number and size of infralabial scales from tip of snout to posterior edge of eye; Cole et al. 1990). Of these, 37 were typical of true *G. underwoodi*; 1 out of 7 from Dubulay Ranch (AMNH R-141874; mixed habitat) was like *underwoodi* on the right side but similar to Maracá specimens on the left, presumably owing to individual variation; and the only specimen from Aishalton (AMNH R-139879; savanna habitat) was similar to Maracá specimens

(of forest habitat) on both sides. Additional comparative work, including more extensive molecular analyses and direct comparisons of Brazilian and Guyanan samples are needed to confirm that the unisexual populations in these two countries had separate and independent hybrid origins and to determine the range of the species found at Ilha da Maracá.

At Dubulay Ranch, *G. underwoodi* is sympatric with *G.* cf. *speciosus*. At Karanambo and Yupukari it is sympatric with *Gymnophthalmus vanzoi* (see below). At Aishalton, it is sympatric with both *G. leucomystax* and *G. vanzoi* (see below). Because sympatry is rare among species of *Gymnophthalmus* and because *G. underwoodi* had an origin involving interspecific hybridization, detailed studies of ecology and behavior and the potential for hybridization should be conducted at localities where there are sympatric species of *Gymnophthalmus*.

Gymnophthalmus vanzoi Carvalho, 1997
Plate 22D

Type material.—The holotype is MZUSP 72598, a male from Brasil; Roraima: Fazenda Salvamento, Rio Uraricoera (03°20′N, 61°24′W).

Distribution.—Known only from savanna regions in the Roraima area of northern Brazil and southern Guyana (within or near the Rupununi Savanna).

Vouchers for Guyana.—AMNH R-137973 from Karanambo; AMNH R-138029–138034, R-138052–138056, and USNM 566455–566464 from Yupukari; and AMNH R-139867–139871, R-139875–139878, and USNM 566465–566467 from Aishalton; both sexes are represented.

Coloration in life.—The following is based on AMNH and USNM specimens from Yupukari and Aishalton (CJC field notes, 1992, 1993). Dorsum light copper (extending onto base of tail); sides, arms, legs darker coppery brown (not black); very pale copper dorsolateral stripe, inconspicuous or absent past midbody but sometimes continuing to hip; belly pale copper or coppery gray, but brighter in adult males, which may have bright orange on chin and throat (white, copper, or pale gray on some lizards); tail posterior to base bright orange or salmon, especially in juveniles and females; regenerated tails and those of males were noted as being tan or brownish gray (gray below), not as bright as in juveniles and females.

Comments.—This diploid, bisexual (gonochoristic) species is very similar to *G. speciosus* and specimens from northern Brazil and elsewhere have been identified as *G. speciosus* in the past (discussed by Carvalho 1997). The similarities between *G.* cf. *speciosus* and *G. vanzoi* in Guyana and elsewhere are so great that the species are not adequately diagnosed as yet.

Iphisa elegans Gray, 1851
Plate 22E

Type material.—The holotype is BMNH 1946.9.1.1, a male (Avila-Pires 1995) from within a circuit of about 300 miles of Belém, Para, Brazil (Avila-Pires 1995).

Distribution.—"Amazonia and some peripheral areas, in Brazil, French Guiana, Suriname, Guyana, southeastern Colombia, Ecuador, Peru, and Bolivia" (Avila-Pires 1995:388).

Vouchers for Guyana.—AMNH R-21294 and R-137363 from Kartabo; AMNH R-70624 from Kuyuwini Landing; AMNH R-151946–151949 and USNM 566490–566491 from Berbice River Camp; and USNM 531663 from Iwokrama Forest Reserve.

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). Brown above (darker on sides, but on some, uniform dark brown above and on sides) with inconspicuous

dark tan markings; venter translucent gray, but bluish gray beneath tail. An adult male also had an inconspicuous tan dorsolateral stripe anteriorly and bright orange ventral surfaces, including the arms, legs, and tail.

Kaieteurosaurus hindsi Kok, 2005

Type material.—The holotype is IRSNB 2628, an adult male from Tukeit trail, ca. 1250 m NEE from the beginning of the Kaieteur National Park airstrip (from point closest to the gorge), 420 m elevation, Kaieteur National Park, Potaro-Siparuni district, Guyana.

Distribution.—Known only from the type locality.

Vouchers for Guyana.—The holotype is the only known specimen.

Coloration in life.—"Dark brown dorsally and laterally. Chin whitish, venter and underside of limbs uniformly reddish orange. Proximal quarter of tail reddish orange, remaining distal part brownish speckled with whitish orange" (Kok 2005:41).

Comments.—Practically nothing is known about this species.

Leposoma guianense Ruibal, 1952
Plate 22G

Type material.—The holotype is UMMZ 46770, adult female from Dunoon, Demerara River, Guyana.

Distribution.—"...Guyana, Suriname, French Guiana, and Brazil" (Avila-Pires 1995:394).

Vouchers for Guyana.—The holotype; AMNH R-140962 from Ceiba Biological Station, Madewini River, ca. 5 km E Timehri Airport (06°29′57″N, 058°13′06″W); and UMMZ 46768 from the type locality (Ruibal 1952).

Coloration in life.—The following is based on the AMNH voucher, an adult male, from Ceiba Biological Station (CJC field notes, 1994). Dorsum medium brown with a light tan dorsolateral stripe, below which is dark brown; throat and chest orange, abdomen orangish yellow (probably not so brightly colored in females and juveniles).

Comments.—The karyotype of this diploid, bisexual (gonochoristic) species was described by Pellegrino et al. (1999). This is one of the cryptic species in *Leposoma*, of several that are extremely difficult to distinguish from each other, and is a candidate for being one of the ancestors for unisexual forms (see Comments for *Leposoma percarinatum*, below).

Leposoma percarinatum (Müller, 1923)
Plate 22F

Type material.—The original name was *Hylosaurus percarinatus* and Uzzell & Barry (1971) stated that the holotype, a female, was probably destroyed during World War II. It was from Peixeboi (a.d. Bragançabahn), Parà, Brazil.

Distribution.—"Northern South America east of the Andes, in French Guiana, Suriname, Guyana, Venezuela, southeastern Colombia, and Brazil" (Avila-Pires 1995:408).

Vouchers for Guyana.—AMNH R-139883 from forest 6.4 km SE Aishalton; AMNH R-140960, R-141888–141891, and USNM 566512 from Dubulay Ranch; AMNH R-152010–152015, R-152017–152020, and USNM 566513–566518 from Berbice River Camp; AMNH R-152027–152038 and USNM 566519–566524 from Konawaruk Camp; also UMMZ 58240 from Kartabo (thanks to information provided by Greg Schneider); USNM 531665–531673 from Iwokrama Forest Reserve (various sites); USNM 535792 from Baramita; and USNM 566511 from Ceiba Biological Station, Madewini River, ca. 5 km E Timehri Airport (06°29′57″N, 058°13′06″W).

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton, Ceiba Biological Station, Dubulay Ranch, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1993–1998). Brown above (all dorsal surfaces), with inconspicuous yellowish tan dorsolateral light stripe; some specimens with inconspicuous light tan to yellow spots on sides; chin translucent white; throat translucent very pale gray to pale yellow or orange; chest, abdomen, beneath arms, legs, and base of tail translucent pale yellow or gray.

Comments.—This is an all-female (unisexual) species, which probably includes at least two cryptic species, one of which remains un-named. See Avila-Pires (1995:411), Pellegrino et al. (2003, 2011), and Laguna et al. (2010) for discussions of the taxonomic difficulties involving several cryptic species of *Leposoma* that occur in Amazonia and that may be or may have been undergoing hybridization. The cryptic species include two unisexual forms, one diploid and one triploid (Laguna et al. 2010, Pellegrino et al. 2011). Specimens of this complex are extremely difficult to identify with confidence based on morphology alone. Extensive molecular research on the entire complex has recently been initiated by Pellegrino et al. (2011).

Neusticurus bicarinatus (Linnaeus, 1758)
Plate 23B

Type material.—The original name was *Lacerta bicarinata* and Avila-Pires (1995) stated that the holotype is UUZM 70. Hoogmoed (1973) restricted the type locality to the vicinity of Paramaribo, Surinam.

Distribution.—"...eastern Venezuela, Guyana, Suriname, French Guiana, and Brazil" (Avila-Pires 1995:426).

Vouchers for Guyana.—AMNH R-6138 from Marudi; AMNH R-21259 from Kartabo; AMNH R-61288–61290 from Onora; AMNH R-61361, R-61363, and R-61365–61366 from Shudikarwau; AMNH R-151983–151985 from Berbice River Camp; and USNM 497802 from Moco Moco at base of the Kanuku Mountains.

Coloration in life.—The following is based on the AMNH specimens from the Berbice River Camp (CJC field notes, 1997). Brown above (including arms, legs, and tail), with network of darker brown markings; dirty white to tan or pale yellow spots on sides; head brown; upper eyelid with thin edge of copper; lower eyelid with thin edge of white, extending upward posterior to eye; ventral surfaces very pale tan (but chin and throat may be white), with gray spots on chin and gray streaks on throat; one with yellow patch ventrolaterally on neck in front of arm; on some, most of distal tail black below (but tan with gray or brown dots beneath base, as beneath legs).

Neusticurus rudis Boulenger, 1900
Plate 23C

Type material.—The holotype is BMNH 1946.8.31.64 according to Avila-Pires (1995), from the foot of Mt. Roraima, 3500 ft, reported originally as being from Guyana. However, the type specimen was probably collected in Venezuela (Phelps 1938). See below (Vouchers) for records from Guyana.

Distribution.—"Guiana region, in Venezuela (Bolívar), Guyana, Suriname, French Guiana, and Brazil" (Avila-Pires 1995:446).

Vouchers for Guyana.—Possibly the holotype; AMNH R-29927 from Kartabo; AMNH R-151986–151998, R-152002–152004, and USNM 566525–566526 from Konawaruk Camp; ROM 39497–39500 from Mount Ayanganna; ROM 20514 and 20517 from Tukeit; and USNM 549324–549325 from the north slope of Mt. Roraima (5°17′N, 060°45′W; 800 m).

Coloration in life.—The following is based on AMNH and USNM specimens from Konawaruk Camp (CJC field notes, 1998). Dorsum dark brown, with dark yellowish tan squares and rectangles; head, arms, and legs dark brown (arms and legs with few yellowish tan spots); yellowish tan spot beneath eye; eyelids may be edged with yellow; tail, above, as dorsum; chin and throat orange, but throat may be tan or pale yellow; chest and beneath arms and legs yellow or orangish yellow; abdomen gray or grayish tan; very pale orangish tan beneath tail base, with numerous brown flecks, tail gradually becoming black posteriorly; on some, ventrolateral tail with row of tiny white dots.

Comments.—The vouchers from Guyana are of the morph that Avila-Pires (1995) discussed as having the tubercles scattered on the body (not in regular longitudinal rows) and having roundish and convex (not trihedral) gular scales. However, the Konawaruk lizards have significantly more femoral and preanal pores (both sexes) than reported by Avila-Pires, which could represent geographic variation or the presence of cryptic species yet to be diagnosed (see Remarks in Avila-Pires 1995).

Pantepuisaurus rodriguesi Kok, 2009b

Type material.—The holotype is IRSNB 2650, an adult male from the summit plateau of Mount Maringma, Cuyuni-Mazaruni District, Guyana (05°12′57″N, 060°35′07″W; 2080 m).

Distribution.—Known only from the type locality.

Vouchers for Guyana.—The holotype is the only specimen known.

Coloration in life.—"Dorsal and lateral surfaces completely black; closer examination shows that black scales on body and neck are peppered with brown or reddish brown. Upper surface of head black. Tympanum light pink. Arms legs and tail black. Iris red…Tongue dark gray in its anterior two-thirds, whitish with gray flecks on its posterior third. Palms and soles black. Underside of head and throat black with irregular light gray markings; venter orangish brown, ventral scales peppered with black; underside of upper legs [arms] black; underside of lower legs black with irregular orangish brown markings; underside of tail black, except proximally where some scales are white" (Kok 2009b:65).

Comments.—Essentially nothing is known about this species.

Riolama leucosticta (Boulenger, 1900)

Type material.—The original name was *Prionodactylus leucostictus* and Colin McCarthy informed us (pers. comm.) that the holotype was first cataloged as BMNH 99.3.25.4 and later, after World War II, "re-registered with the number BMNH 1946.8.2.8." The specimen was noted as being from the summit of Mt. Roraima, 8600 ft, Guyana, for which Colin McCarthy also informed us that "the original [catalog] entry (in Boulenger's handwriting) states 'Mt. Roraima, Brit. Guiana 8600 f (summit).'" However, the type specimen was probably collected on the Venezuelan part of the summit (Phelps 1938).

Distribution.—This species is known only from the summit of Mount Roraima and one or two additional tepuis in Venezuela (Gorzula & Señaris 1999 [1998], MacCulloch et al. 2007). We do not doubt that this species occurs in both Venezuela and Guyana on Mount Roraima, as the habitats are the same within the summit areas of both countries. We emphasize, however, that voucher specimens having localities clearly within Guyana are needed.

Vouchers for Guyana.—See above (Type Material and Distribution).

Coloration in life.—The following is from Gorzula & Señaris (1999 [1998]:142), based on specimens from Cerro Kukenán, Venezuela. "In life their ground color was shiny black with yellow-ochre speckling dorsally and dorsolaterally. The ventrals, anals and subcaudals had yellowish white speckles. Pale yellow mandibular stripes formed an inverted 'V.'"

Comments.—See above (Distribution) for comments on the need to clearly document the existence of this species in Guyana. As for most of the mountaintop fauna of Mount Roraima, practically nothing is known about the biology of this species.

Tretioscincus agilis (Ruthven, 1916)
Plate 23A

Type material.—The original name was *Calliscincopus agilis* and the holotype is UMMZ 47798 from a sand ridge near Dunoon, Guyana.

Distribution.—"Guyana, Suriname, French Guiana, and Brazil" (Avila-Pires 1995:482).

Vouchers for Guyana.—The holotype is the only specimen known from Guyana.

Coloration in life.—The following is from Avila-Pires (1995:482). "Brown on back, with dorsolateral stripe anteriorly salmon to pale orange, posteriorly yellowish or greenish, and blue on tail; [dorsolateral stripe]...may be bordered dorsally by a black stripe. Flanks black. Ventral region pearl-white or with a greenish shine, with centre of most scales, especially posteriorly, black-peppered. Tail mostly deep pastel blue, proximally with dorsal and lateral black stripes. Iris black." Hoogmoed (1973) stated that the ventral area may be greenish blue.

Iguanidae

This is one of the families of iguanian lizards (see Introduction above, before Corytophanidae). Representatives of this family occur in "tropical and subtropical America from the southwestern United States and eastern Mexico south to southern Brazil and Paraguay; Galapagos Islands; Antilles; Fiji and Tonga Islands" (Frost & Etheridge 1989:39). Although the occurrence of some iguanids in the Galapagos Islands undoubtedly resulted from over-water rafting, their occurrence in Fiji and the Tonga Islands may reflect their Gondwanan origins and ancient terrestrial connections (Noonan & Sites 2010).

Iguana iguana (Linnaeus, 1758)

Type material.—The original name was *Lacerta Iguana* and there are two syntypes, NRM 114 and UUZM Linnean collection no. 10 (Avila-Pires 1995). Hoogmoed (1973) restricted the type locality to the confluence of the Cottica River and Perica Creek, Surinam.

Distribution.—"From Mexico, though Central America and part of the Antilles, to central Brazil and Paraguay" (Avila-Pires 1995:47).

Vouchers for Guyana.—AMNH R-14111–14114, R-21289, and R-21330 from Kartabo; also CJC and CRT saw an individual (not collected) at Aishalton in 1993.

Coloration in life.—The following is based on specimens from Suriname (Hoogmoed 1973:155–156). "Grass-green all over, slightly lighter on the ventral parts. In old specimens the overall colour fades to a bluish grey. A distinct white line on the lower anterior surface of the upper arm, from the insertion to near the elbow. The upper surface of the head in adults may be bluish green or grayish. A number of more or less distinct vertical white stripes, accompanied by a black zone is present on the lower part of the flanks. Gular appendage with black and reddish brown stripes. Infra- and sublabials and anterior margin of gular appendage with

reddish brown spots. Tail with white and black transverse bands on a grass-green background. In old specimens the tail shows black bands, alternating with bluish grey bands. Iris brown with a golden rim around the pupil."

Comments.—This is the largest species of lizard in the Western Hemisphere. Savage (2002) mentioned an individual over 2 m in total length (body and tail), and weight of 4 kg. Avila-Pires (1995) mentioned a preserved specimen from Brazil with a total length of about 1.7 m. The species is primarily arboreal.

Polychrotidae

This is one of the families of iguanian lizards (see introduction above, before Corytophanidae). The family occurs in "southern North America to southern South America; West Indies" (Frost & Etheridge 1989:43). Representatives of two genera are known to occur in Guyana—*Anolis* and *Polychrus*. *Anolis* is a very large genus, which some recent authors have tried to partition into several smaller genera. However, the most recent phylogenetic analyses have shown that the smaller genera were largely not monophyletic groups and that retention of the single large genus concept is most consistent with evidence-based phylogenetic conclusions (Poe 2004). Townsend et al. (2011) split *Anolis* out to a new family, Dactyloidae.

Anolis aeneus Gray, 1840

Type material.—The holotype is BMNH 1946.8.28.7 and the type locality was restricted to Point Saline, Grenada (Lazell 1972).

Distribution.—Petit Martinique, Grenadines, Trinidad and Guyana (Peters & Donoso-Barros 1970); also, see Comments (below).

Vouchers for Guyana.—AMNH R-8087, R-60063–60066, R-60068–60070, R-60072–60074, R-60076–60086, R-60088–60090, and R-60333–60337 from Georgetown, identified by E. E. Williams. Also AMNH R-98386–98391 from near Kartabo, identified by E. E. Williams. Also AMNH R-84156–84157 from Rockstone Landing and AMNH R-38573 from Demerara River, Akyma, identified by E. E. Williams. Also AMNH R-139786, ROM 20571, and USNM 497793 and 566365 from Georgetown; and USNM 163000–163015 from Enmore Estate (6°44′N, 057°59′W).

Coloration in life.—The following is based on two AMNH and USNM specimens from Georgetown (CJC field notes, 1993). Greenish yellow above and below, including dewlap on large one, but dewlap with yellow scales and orange skin in between scales on smaller one.

Comments.—This species is abundant in Georgetown and Kartabo, but it is not part of the original, native herpetofauna of Guyana (Murphy 1996, Avila-Pires 2005). The species is a member of the *roquet* species group, which has a natural distribution on islands of the West Indies. Historically, three names are relevant to the taxon in Guyana: *Anolis roquet* (Lacépède 1788); *Anolis aeneus* Gray, 1840 (once treated as a variety of *roquet*); and *Anolis extremus* Garman, 1887 (originally named as a variety of *roquet*). The specific names applied in Guyana have been both *A. aeneus* and *A. extremus*, if not using names of subspecies, *A. roquet* if using subspecies. All three forms are very similar to each other, particularly *aeneus* and *extremus*.

Peters & Donoso-Barros (1970) stated that both *A. aeneus* and *A. roquet extremus* occur in Guyana, citing Underwood (1964) but not any individual specimens. They also gave key characters for distinguishing among these species, but the characters were wrong. Murphy (1997) said that both *aeneus* and *extremus* occur in Trinidad,

using a new character of the rostral scales to distinguish them, but this character also fails to work on AMNH specimens that CJC examined. The *roquet* group was last reviewed by Lazell (1972:80), who presented little morphological information and stated about coloration of *aeneus* that "there is so much variation that verbal description is wasteful." He also said "I have not seen Guyana...specimens alive, but MCZ 81283–92 (Georgetown) are precisely this anole." He gave no rationale for this determination, nor did he justify treating these forms as separate species. However, in a key Lazell (1972:23) said that *aeneus* has the "axilla without dark pigment," *extremus* has the "axilla with dark pigment."

For *A. aeneus*, Lazell (1972:81) stated that the main range is Grenada and the Grenadines, "...introduced into Trinidad and Guyana." For *extremus*, the range was given as Barbados and introduced into other islands and Caracas, Venezuela (no mention of Guyana). The diagnostic characters do not work, given variation observed on AMNH specimens that CJC examined, including no distinct difference in axillary coloration, despite Lazell's (1972:85) following statement: "The axillary pigmentation makes a simple distinction between *extremus* and *aeneus*, especially when specimens (even preserved) are compared directly." Our comparisons involved specimens from Barbados (*extremus*; AMNH R-14096–14101 and R-15105–15109), Grenada (*aeneus*; AMNH R-104731–104734), and Guyana (see Guyana Vouchers, above), and there was no clear resolution between *aeneus* and *extremus* using any of the characters mentioned by Peters & Donoso-Barros, Murphy, or Lazell. In general the armpit character looked a bit darker on most specimens from Barbados vs. Grenada, but it was subtle and relative, and not something that was applied easily on specimens from Guyana. More recently collected USNM specimens examined by RPR showed clearer, but not sharp, differences in axillary coloration.

AMNH has several series of *roquet* group anoles from Guyana, mostly old ones. All are identified as *A. aeneus*, and in each case where the determiner is recorded, it was Ernest E. Williams. These are the majority of those cited among the vouchers above. Clearly, the taxonomic status of *Anolis aeneus* versus *Anolis extremus* needs further investigation, both in areas where they occur in the West Indies and where they have been introduced on islands and the mainland of South America.

Anolis auratus Daudin, 1802b
Plate 23D

Type material.—The type material, from Surinam, is unknown (Avila-Pires 1995).

Distribution.—"...Brazil, French Guiana, Suriname, Guyana, Venezuela, and Colombia, northward to Panama" (Avila-Pires 1995:52).

Vouchers for Guyana.—AMNH R-137943–137948, R-137953, R-137959–137970, R-138063, R-138087, and USNM 566337–5663345 from Karanambo and Yupukari; AMNH R-139763–139775, R-139783–139784, and USNM 566346–566352 from Aishalton. Also USNM 163006–163007 from Enmore Estate, 6°44′N, 057°59′W; USNM 291131 from Kato; and USNM 291185 from Paramakatoi. In addition, "RMNH 26479" from "Berbice River, near Blairmont" (Avila-Pires 1995:49), and Mike Tamessar (pers. comm.) informed us that he has seen this species at Dubulay Ranch.

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo, Yupukari, and Aishalton (CJC field notes, 1992, 1993). All dorsal surfaces tan; cream or dark brown to black lateral stripe; if stripe cream, lined above and below by black flecks, but the lower edge may be a black stripe; some lizards also with a ventrolateral black stripe; rust-

orange spots on posterior of thigh; tail tan above with light gray bands, smudges, or indistinct, short black stripes; ventral surfaces cream, but orangish tan under tail; small dewlap of females with grayish blue skin between cream scales; larger dewlap of males similar but with yellow scales in center and at end beside base; tongue orange, brightly displayed when captured lizard gapes. On an adult male the lateral bright cream stripe was observed to change to black following capture.

Comments.—These little anoles often sleep at night on tall grass on the Rupununi Savanna.

Anolis fuscoauratus Duméril & Bibron, 1837 Plate 23F

Type material.—The original name was *Anolis fuscoauratus* and the holotype is MNHN 2420 (Avila-Pires 1995). The type locality is Rio Mamoré, between Loreto and the confluence of Rio Sara, Moxos province, Bolivia (Avila-Pires 1995).

Distribution.—"Northern South America east of the Andes, in Brazil, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru and Bolivia" (Avila-Pires 1995:64).

Vouchers for Guyana.—AMNH R-21306 and R-21324 from Kartabo; AMNH R-151828–151841 and USNM 566358–566363 from Konawaruk Camp; USNM 291267 from Kaieteur, near guest house; and USNM 531642–531644 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Konawaruk Camp (CJC field notes, 1998). Dark tan dorsum with subtle dark brown spots along vertebral area; tail similar, but with subtle dark brown bands instead of spots, and tail may become lighter distally; venter white to gray with extensive tan flecking; some males have very pale yellow iridescent ventrolateral wash on body and yellow beneath base of tail; dewlap of males light gray anteriorly, bright pink posteriorly.

Anolis ortonii Cope, 1868

Type material.—The holotype is ANSP 11404 (Avila-Pires 1995) from Napo or Upper Rio Marañon, Ecuador or Peru.

Distribution.—"Northern South America east of the Andes, in Brazil, French Guiana, Suriname, Guyana, Colombia, Ecuador, Peru, and Bolivia" (Avila-Pires 1995:94).

Vouchers for Guyana.—AMNH R-21292 from Kartabo; and AMNH R-25074 and R-25141 from Kamakusa, identified by E. E. Williams.

Coloration in life.—The following is based on a female from Suriname (Hoogmoed 1973:140). "Body yellowish grey, black to dark-brown on the vertebral region, a brown line between the eyes, upper surface of the head with a tinge of pink, flanks reticulated with dark-brown, tail grey with brownish transverse bands, belly grey, dewlap yellow-ochre with a few horizontal rows of white scales. Iris golden." Avila-Pires (1995:93) added that "no distinction in colour between sexes was observed."

Anolis planiceps Troschel, 1848 Plate 23E

Type material.—The holotype is ZMB 529 from Caracas, Venezuela.

Distribution.—This species occurs in much of the area of the Guiana Shield in northern Brazil, Guyana, and Venezuela, as well as Trinidad (D'Angiolella et al. 2011).

Vouchers for Guyana.—Vanzolini & Williams (1970:21) cited a long list of vouchers from Guyana, using the name *Anolis chrysolepis*, in the following collections: AMNH, BMNH, MCZ, and UMMZ. Specimens that we examined are

the following: AMNH R-15137–15142, R-21307–21308, R-21310–21314, R-32273–32278 from Kartabo; AMNH R-151810–151818, and USNM 566353–566356 from Berbice River Camp; AMNH R-151823–151825 and USNM 566357 from Konawaruk Camp; ROM 22853–22868 and USNM 535793–535794 from Baramita; USNM 200508 from Bartica; USNM 233871 from Kartabo Point (6°23′N, 058°42′W); USNM 497792 from CEIBA (6°29′55″N, 058°13′04″W); and USNM 549322 from the north slope of Mount Roraima.

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp and Konawaruk Camp (CJC field notes, 1997, 1998). The animal is covered with a pattern of browns and tans; with a fine vertebral light rust stripe, conspicuous in sacral region; on some, a wide tan vertebral stripe with dark brown edges; head brown, with dark brown patches, fine irregular rust-orange lines; some with pale yellow patches beneath eye; tail dark brown; venter white or yellowish tan, some with black specks; throat may be brown; dewlap orange or red, but may be purple at base.

Comments.—Avila-Pires (1995) treated this taxon as *A. nitens*, with priority over *A. chrysolepis*. However, in preparing our manuscript we followed Myers & Donnelly (1997) in accepting the name *Anolis chrysolepis* to represent a wide-ranging species with several subspecies. Most recently, D'Angiolella et al. (2011) concluded primarily from molecular analyses that each of the subspecies should be elevated to species status. Their interpretation is that two species (formerly subspecies) of this complex occur in Guyana, *A. planiceps* and *A. chrysolepis*. The former occurs widely in the northern and central part of Guyana, the latter is represented by a few specimens from the south (D'Angiolella et al. 2011). All the specimens we examined are *A. planiceps*. The best morphological character for distinguishing these species might be the size of the scales on the upper arm; if larger than the scales in the vertebral area, *A. planiceps*; if the same size or smaller, *A. chrysolepis*.

Anolis punctatus Daudin, 1802b
Plate 24A

Type material.—The holotype is MNHN 2340, a female from "South America" (Avila-Pires 1995:102).

Distribution.—"Widespread in Amazonia; present probably throughout French Guiana and Suriname, and in parts of Guyana, ...Colombia, Ecuador, Peru, Bolivia (Fugler 1988), and Brazil" (Avila-Pires 1995:109).

Vouchers for Guyana.—AMNH R-18185 and R-21293 from Kartabo; AMNH R-61237 from Kuyuwini Landing; AMNH R-61249 from Onora; AMNH R-98379–98380 from near Kartabo; and USNM 566364 from Berbice River Camp.

Coloration in life.—The following is based the USNM specimen from Berbice River Camp (CJC field notes, 1997). Bright green (can change at least in large part to brown), with small pale blue spots on sides; chin, throat, and chest light green; belly and beneath base of tail pale bluish gray, with tiny cream dots (most of tail regenerated). Hoogmoed (1973:147) added "Dewlap in males yellow-ochre with rows of white scales, in females the scales on the small dewlap are yellow. Iris orange-brown."

Polychrus marmoratus (Linnaeus, 1758)
Plate 24B

Type material.—The original name was *Lacerta marmorata* and the syntypes are UUZM Linnean collection nos. 14, 31 (Avila-Pires 1995). Hoogmoed (1973) restricted the type locality to the vicinity of Paramaribo, Surinam.

Distribution.—"Northern South America east of the Andes (French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, and Amazonian Brazil), and in the Atlantic forest [of Brazil]" (Avila-Pires 1995:142).

Vouchers for Guyana.—AMNH R-21315, R-32279–32281, and R-137404–137409 from Kartabo; AMNH R-139787 from Aishalton; and AMNH R-141901 from Dubulay Ranch; USNM 84487–84489 from Pomeroon; USNM 163053 from Enmore Estate (6°44′N, 057°59′W); and USNM 566374 from Yupukari.

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo or Yupukari, Aishalton, and Dubulay Ranch (CJC field notes, 1992–1995). Dorsum (body, arms, legs, tail) brown with dark brown bands and many scales green (the lizard becoming greener with thin black bands on body while being handled); top of head gray, with a few dark brown spots, short dark brown or black lines from eyes, and pale green wash; undersides all pale green, but darker on posterior abdomen, preanal area, hind legs, and base of tail; when excited and bright in color, orange patches on posterior of thigh and in axilla.

Scincidae

The Scincidae is a very large family. It has representatives basically all over the world wherever any kind of reptiles exist. Nevertheless, only one species is known to occur in Guyana. This is a member of the genus *Mabuya*, in which many of the species are very similar to each other and difficult to identify. Recent research based on morphology and phylogenetic analyses including DNA sequence data are beginning to improve our understanding of these lizards (e.g., Avila-Pires 1995, Mausfeld et al. 2002, Miralles et al. 2009), but a lot of work remains to be done.

Mabuya nigropunctata (Spix, 1825)
Plate 24D

Type material.—The original name was *Scincus Nigropunctatus* and the holotype was lost. Avila-Pires (1995) designated MPEG 15248 as neotype. It is from Santa Rita, Município de Maraã, left margin of Rio Japurá (Lago Paricá), Amazonas, Brasil.

Distribution.—"Throughout Brazilian Amazonia and most probably in the entire Amazonian region. Outside Amazonia, it seems to occur in the state of Mato Grosso..., and in part of the Atlantic Forest" (Avila-Pires 1995:590). Because of the difficulties of distinguishing among the similar species in this complex and the lack of a detailed analysis of geographic variation, the limits of the range of distribution remain unknown. Nevertheless, all specimens of *Mabuya* that we have examined from Guyana represent this species.

Vouchers for Guyana.—AMNH R-6785–6786 from Kaieteur; AMNH R-8543 and R-37550–37552 from Georgetown; AMNH R-15120–15122, R-18183, and R-21326 from Kartabo; AMNH R-25070 and R-25128 from Kamakusa; AMNH R-139814 and USNM 566395 from Aishalton; AMNH R-151880–151883, R-151888–151891, and USNM 566396–566399 from Berbice River Camp; AMNH R-151892 from Konawaruk Camp; ROM 22887–22891 and USNM 535801 from Baramita; ROM 20516 from Kurupukari; ROM 28349 from Paramakatoi; USNM 164190 from Mabaruma (8°12′N, 059°47′W); and USNM 531658–531662 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1993, 1997, 1998). Dorsum, including top of head and tail, copper or bronze, often with dark brown spots; pale coppery tan

dorsolateral light stripe may be present; arms, legs, side of face, and side of body dark brown; often a ventrolateral yellowish tan light stripe, with dark brown below; throat very pale yellow to yellowish green; beneath arms, chest, abdomen, legs, and base of tail yellow to yellowish green, brightest posteriorly; underside of hands, feet, fingers, and toes black; distal tail yellowish copper.

Comments.—See above (Distribution) for comments on the need for research on the overall distribution of this and related species in South America.

Sphaerodactylidae

Until recently, all Guyanan genera of geckoes were included in the large family Gekkonidae, as mentioned above (introduction to Gekkonidae). However, recent phylogenetic analyses (Gamble et al. 2008), including considerable DNA sequence data, indicated that Guyanan geckoes of the genera *Chatogekko*, *Coleodactylus*, *Gonatodes*, *Pseudogonatodes*, and *Sphaerodactylus* are appropriately considered as representatives of another family, Sphaerodactylidae. Individuals of most species of sphaerodactylid lizards are very small, including those that are among the smallest in Guyana.

Chatogekko amazonicus (Andersson, 1918)

Type material.—The original name was *Sphaerodactylus amazonicus* and the holotype from Amazonas, Manaos, Lago Poraquecuare, Brazil is NRM 3254 (Avila-Pires 1995).

Distribution.—"Eastern and central Amazonia, including Brazil, French Guiana, Suriname, southern Guyana, and Southern Venezuela (Amazonas)" (Avila-Pires 1995:250), south to northern Bolivia (Gamble et al. 2011).

Vouchers for Guyana.—AMNH R-144757–144759, R-144761, and R-144763 from Marudi; USNM 570538 from Gunn's Strip (01°36′46″N, 058°38′15″W).

Coloration in life.—The following is based on specimens from Brazil (Avila-Pires 1995:248). Dorsum reddish brown to brown; light spots on head and body cream, beige, yellow, or pale brown; on some, beige band on posterior head; posterior thigh and base of tail with short, light, beige to orange stripe; underside of head and belly white, but posterior belly pale pink or orange; underside of tail (and legs of some) pink to beige; "iris dark grayish-brown with an orange rim around pupil. Tongue grey anteriorly, white posteriorly."

Comments.—This species is similar to the following (*C. septentrionalis*), so the small specimens need to be identified with extra care (see key for characters). No comparative studies have been done on the life histories and ecology of these two species. This species formerly was in the genus *Coleodactylus*, but Gamble et al. (2011) named *Chatogekko* for this species, following morphological and DNA sequence analyses, because it is in a very distinctive lineage. They also noted that there probably are several cryptic species masquerading under the name *C. amazonicus*.

Coleodactylus septentrionalis Vanzolini, 1980
Plate 24C

Type material.—The holotype is MZUSP 52866, a male from Brasil, Roraima: Ilha de Maracá.

Distribution.—"Northern part of Roraima, Brazil; western Suriname...; Pacaraima foot hills, Guyana; Delta Amacuro, Venezuela" (Avila-Pires 1995:257).

Vouchers for Guyana.—AMNH R-132006 from Isheartun; AMNH R-137976-137977 and USNM 566300 from Karanambo; USNM 531620 from Iwokrama Forest Reserve, Burro Burro River; and AMNH R-148592–148594 and

USNM 531621–531622 from Iwokrama Forest Reserve (several localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo (CJC field notes, 1992). To the naked eye, this little lizard (maximum body length about 30 mm or less) may simply appear to be brown to dark brown above, with an inconspicuous light tan stripe dorsolaterally in hip area and on base of tail; venter translucent pinkish gray to gray with brown speckles. Avila-Pires (1995:254) stated that "the only colour description of living specimens available is that of O'Shea (1989:55), 'brown with a series of paired white dorsal spots and occasionally a pair of broken white dorso-lateral stripes.'" She also noted that other color descriptions in the literature were from preserved specimens (perhaps aided by microscopy), and she noted that there is significant variation in color pattern, including specimens with an apparent "absence of a pattern" (Avila-Pires 1995:257). Nevertheless, Avila-Pires noted that specimens from Roraima have a light band posteriorly on the head, and Vanzolini (1980:9) illustrated that on the holotype, which also showed the paired dorsal white spots.

CJC compared four preserved specimens from Brazil (AMNH R-131810–131813) with five from Guyana (AMNH R-132006, R-137976, and R-148592–148594; see Vouchers, above). The light spots or stripes were subtle to absent in Guyanan material, more evident in general but also variable in appearance in Brazilian material.

Comments.—We would not be surprised if there is more than one species of lizard masquerading under this name. Also, see Comments above for *Chatogekko amazonicus*.

Gonatodes alexandermendesi
Cole & Kok, 2006
Plate 25A, B

Type material.—The holotype is AMNH R-151805 an adult male from GUYANA: Magdalen's Creek Camp, near (ca. 275 m N) the NW bank of the Konawaruk River (ca. 40 km [linear] WSW Mabura Hill), 120 m elevation (5°13′07″N, 59°02′43″W) in WGS 84.

Distribution.—Known only from Guyana and eastern Venezuela (Schargel et al. 2010).

Vouchers for Guyana.—AMNH R-2714 from Kartabo; AMNH R-151804–151809 from the type locality; IRSNB 2630–2639 from several sites in Kaieteur National Park (Cole & Kok 2006:3); and UTA 57504 from "near Imbaimadai, Pacaraima Mountains, Guyana" (Schargel et al. 2010:327).

Coloration in life.—"Dorsum dark reddish brown [gray on some] through base of tail [grayish brown on some]; rest of tail gray; dorsum with tiny irregular black markings [not seen on some]; orange wash on side of face, around neck dorsally [yellowish orange on some], and on anterior surface of arms; yellowish orange beneath arms [or bright yellow, but not seen on some]; venter gray, but [underside of head and] throat bright orange [yellowish orange on some], chest bright yellow [orangish yellow on some]" (Cole & Kok 2006:6). Aspects of sexual dimorphism and possible seasonal variation in brightness of colors are also mentioned by Cole & Kok (2006:9). Schargel et al. (2010:327) described a new color morph with a "much darker body coloration...and...small ocelli on the sides of the neck and a yellow hood."

Comments.—Phylogenetic analyses including DNA sequence data confirm that *G. alexandermendesi* is a distinct species and that the Venezuelan *G. superciliaris* may be a junior synonym, but more work is needed to be certain (Schargel et al. 2010).

Gonatodes annularis Boulenger, 1887
Plate 24E, F

Type material.—The syntypes from Maccasseema (on the Pomeroon River),

Guyana are BMNH 1946.8.22.97–98 (Avila-Pires 1995:258).

Distribution.—"Rivero-Blanco (1979) reported the species for the wet tropical forests of eastern Venezuela (south of the Orinoco), Guyana, Suriname, French Guyana, and Amapá, Brazil. Here specimens are reported from the southern bank of Rio Trombetas, near Cruz Alta, close to Rio Amazonas" (Avila-Pires 1995:263).

Vouchers for Guyana.—AMNH R-21251, holotype of *Gonatodes beebei* Noble (1923; a junior synonym), R-2714, and R-137411 from Kartabo; AMNH R-17687 from Georgetown; AMNH R-151801–151802 and USNM 566301 from Berbice River Camp; ROM 22921–22964 and USNM 535784–535791 from Baramita; ROM 20518–20520 from Kurupukari; and USNM 164182–164183 from Mabaruma Compound (08°12′N, 059°47′W).

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). On one individual, dorsum was reticulation of dark and medium brown, with a few inconspicuous, irregular, light spots of yellow (anteriorly) or gray (posteriorly), their color transition being completed around the hips; arms and legs as body; iris dark brown with very thin inner ring of copper; ventral surfaces pale chestnut brown; chin, throat, and chest lighter, with small streaks and spots of very pale blue. Two other specimens (possibly males, indicating sexual dimorphism), had dorsal surfaces black with gold speckling, but hip and base of tail black with tan mottling and lower part of legs mostly dark brown (but tail of one animal brown with black reticulation); all ventral surfaces brownish orange, with, on throat only, gold streaks and spots (but one lizard with orange patch on throat and chest). Both Hoogmoed (1973) and Avila-Pires (1995) discuss sexual dichromatism and other color and pattern variants in this species.

Gonatodes humeralis (Guichenot, 1855)
Plate 25C, D

Type material.—The original name was *Gymnodactylus humeralis* and the six syntypes are MNHN 6745 (Avila-Pires 1995) from the edge of the Ucayali River, Mission de Sarayacu, Peru.

Distribution.—"Widespread in Amazonia and lowland surroundings, in Brazil, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, and Bolivia. In the Guianas, including the eastern part of Venezuela, it reaches the coast, as well as the islands of Trinidad and Tobago (Rivero-Blanco 1979)" (Avila-Pires 1995:281).

Vouchers for Guyana.—AMNH R-18193–18194, R-29922–29924, and R-137411 from Kartabo; AMNH R-61421 and R-131999–132001 from Isheartun; AMNH R-139740 from Aishalton; AMNH R-140952–140953, R-140955, and USNM 566302 from Dubulay Ranch; AMNH R-151772–151783 and USNM 566303–566309 from Berbice River Camp; AMNH R-151791–151797 and USNM 566310–566312 from Konawaruk Camp; ROM 43203–43204 from Kaieteur; and USNM 531623–531639 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton, Dubulay Ranch, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1993–1998). Dorsum brown with tan or lighter brown markings that become lighter posteriorly, including out to tip of tail; arms and legs similar; yellow collar anterior to arms; black dot anterior to collar; greenish yellow half-moon crescent across back of head, eye to eye; pale greenish yellow light spots on head; also metallic dark reddish brown spots on head; tiny pale yellow dots on side of neck; light tan spot at hip posterior to leg; undersides of body tan, but chest and abdomen may be light brown, throat may be yellowish tan; chin, throat, underside of

arms, and legs with black reticulation or streaks; beneath tail orange or orangish tan. Adult males have numerous green flecks and red spots on the body and hind legs; red spots atop head; green color to head markings, spots on side of neck, and shoulder bar; arms speckled brown with green; red flecks on tail; venter of body gray with green flecks; orange all along underside of tail. Sexual dichromatism is discussed in more detail by Hoogmoed (1973) and Avila-Pires (1995).

Gonatodes vittatus (Wiegmann, 1856)

Type material.—The original name was *Gymnodactylus vittatus* based on material from Laguayra, Puerto-Cabello, Caracas, Venezuela (Wiegmann 1856:6). The Type is unknown by us.

Distribution.—According to Avila-Pires (2005:31) this species was introduced onto continental South America and it occurs in Colombian Guayana and Bolivar, Venezuela. According to Gorzula & Señaris (1999 [1998]:113), "the distribution of this species is restricted to the dry Caribbean coastal areas of eastern Colombia, Venezuela, Trinidad and Tobago and the Antilles (Murphy 1997, Rivero-Blanco 1979)." Gorzula & Señaris discuss evidence that this was introduced into El Manteco, Bolívar State, Venezuela, but the population there has not survived.

Vouchers for Guyana.—AMNH R-61398 and R-132320–132321 from Rockstone Landing, Essequibo River (6°–′N, 58°35′W); UMMZ 82848–50 from Georgetown.

Coloration in life.—The following is quoted from Murphy (1997:126). "Males brown-grey or cinnamon-brown with bright white middorsal stripe bordered with black, and extending to tip of tail; females with white vertebral stripe [not so conspicuous as in males], and mottling on the sides. Venters of both sexes tend to be white or tan; males sometimes have a white chin with oblique stripes." The photographs in Murphy (1997:pls. 84–85) show a male with bright orange on the chin and throat and a female with a tan vertebral stripe bordered by dark brown, tan, and gray spots.

Comments.—The vouchers listed above compare favorably with specimens from Trinidad, including AMNH R-64454, R-72892, R-72900, and R-72903. This species, the natural distribution of which is primarily in the Antilles, probably arrived in Guyana as a result of human introduction. However, its continued presence in Guyana should be confirmed. There is a question of whether authorship of the specific name here is Wiegmann or Lichtenstein. We followed Kluge (1993) in citing Wiegmann.

Pseudogonatodes guianensis Parker, 1935

Type material.—The holotype, a pregnant female from the upper Cuyuni River, is now BMNH 1946.8.27.8 (Avila-Pires 1995), which would be the new number assigned after World War II.

Distribution.—"Widespread in a large part of Amazonia, in Brazil, French Guiana, Suriname, Guyana, Colombia, Ecuador, and Peru'' (Avila-Pires 1995:304).

Vouchers for Guyana.—"BM 1946.8.27.9 [from the type locality]; AMNH R-61433," six specimens from Shudikar-wau (Avila-Pires 1995:299). Also AMNH R-141886–141887 from Dubulay Ranch; AMNH R-151760–151765 and USNM 566327–566329 from Berbice River Camp; and AMNH R-151769–151770 and USNM 566330 from Konawaruk Camp.

Coloration in life.—The following is based on AMNH specimens from Dubulay Ranch and AMNH and USNM specimens from Berbice River Camp, and Konawaruk Camp (CJC field notes, 1995–1998). Dark brown above, with tan band across back of head and tan H across hip or base

of tail (sides of H essentially being dorsolateral stripes); throat white with irregular gray markings; gray beneath arms, legs, chest, abdomen, tail. Avila-Pires (1995:302) described a male from Brazil "with a middorsal dark stripe, more evident anteriorly."

Comments.—While preserving specimens, CJC and CRT noted that these lizards naturally float, apparently because structure of the surface of their scales prevents them from wetting. Upon submersion in formalin, a complete envelope of air instantly forms around them, floating them to the surface of the liquid. This must have survival benefits during times of heavy rains and sudden floods that might sweep these tiny lizards away in running water. This phenomenon, which has been observed in other lizards also, should be studied further, including examination of the skin with a scanning electron microscope.

Sphaerodactylus molei Boettger, 1894

Type material.—The lectotype is SMF 9611 and type locality is Caparo, Trinidad (Mertens 1967:60).

Distribution.—According to Gorzula & Señaris (1999 [1998]:114) "this species has been recorded from northern Colombia, Venezuela, Trinidad, Tobago and Guyana (Murphy 1997, Peters & Donoso-Barros 1970)."

Vouchers for Guyana.—AMNH R-15136, R-18192, R-21255–21257, R-21297–21298, R-32284, R-36249, and R-137419–137420 from Kartabo.

Coloration in life.—The following is based on Murphy (1997:131). Adult males usually have the top of the head conspicuously marked with "black [or dark brown] with bright white [or yellow] longitudinal stripes, with lower parts tan-yellow, with head pattern ending abruptly at back of head; [body with] dark stripes which edge lighter dorsolateral stripes which break up into spots toward the posterior of the body...Females tan above with a pair of yellow, dark-bordered dorsolateral stripes extending from eye to tail. Venter lighter in color, chin may be speckled." A color photograph (Murphy 1997:pl. 90) suggests that the dorsolateral light stripes can be inconspicuous and their dark borders can be dark brown or black spots.

The following is based on an adult male and female from Kartabo (Beebe 1944:154). Adult male: dorsum buff (brownish yellow) at times tinged with green; brown spots on body, becoming darker posteriorly and on base of tail; arms and legs similar but lighter; "top and sides of head and neck jet black, variegated with creamy white, chiefly in the form of two broken lines from the nostrils back over the eyes, forming an indefinite 'Y' on the neck"; . . .a solid broad white line from the eye back to the abrupt ending of the black nuchal area in front of the fore limb"; . . .tail abruptly ochracheous-orange. . .resulting from many large spots set close together both above and below; rostral, all labials, lower side of head and neck, the chin and throat yellow-green, remainder of ventral surface of body creamy-white; . . .iris ivory white, finely dotted with large, dark brown crescentic marks." Adult female: "buff with the head and neck rather indefinite gray. Apparently unmarked except for two light flank lines, down each side of the dorsal pelvic region. In the right light, however, all the broad cephalic lines of the male are visible as lighter brown, i.e., the two lateral lines and the central 'Y.' The lateral lines extend very faintly down the body and, becoming strong at the pelvic zone, die abruptly at the caudal change to coarser imbricated scalation, which marks the area of regeneration."

Teiidae

This group occurs in tropical to temperate regions of the New World from North America to South America. These are mostly medium-sized lizards that are

nervous, common, and frequently seen running rapidly on the ground in forest or savanna during warm to hot times of day. One species (*Tupinambis teguixin*) shares with *Iguana iguana* the title of being among the largest lizards in the Western Hemisphere. Two genera (*Cnemidophorus* and *Kentropyx*) have all-female (unisexual) species in the Guianan Region, one of which (*K. borckiana*) occurs in Guyana and can be seen on warm sunny days in the Botanical Gardens in Georgetown.

Ameiva ameiva (Linnaeus, 1758)
Plate 26A, B

Type material.—The original name was *Lacerta Ameiva* and there are three syntypes, NRM 120, NRM 124, and UUZM 12 (Avila-Pires 1995). Hoogmoed (1973) restricted the type locality to the confluence of the Cottica River and Perica Creek, Surinam.

Distribution.—"Panama and most of South America east of the Andes (Brazil, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina). Southern limits in southern Brazil and northern Argentina" (Avila-Pires 1995:499).

Vouchers for Guyana.—AMNH R-14118–14119, R-15125–15126, R-15130–15132, R-21295–21296, and R-46440 from Kartabo; AMNH R-25040–25042, R-25062–25063, R-25092, and R-25100–25102 from Kamakusa; AMNH R-137907, R-137910–137914, R-138095, and USNM 566401–566402 from Karanambo; AMNH R-139818–139826 and USNM 566403–566405 from Aishalton; AMNH R-140882–140888, R-140895–140896, R-141853-141855, and USNM 566406–566413 from Dubulay Ranch; AMNH R-151897–151903 and USNM 566414–566416 from Berbice River Camp; and AMNH R-151904–151911 and USNM 566417–566420 from Konawaruk Camp. Also ROM 20530–20533 from Tukeit; ROM 20535–20544 from Amatuk; ROM 20545–20554 from Kurupukari; ROM 22896–22900 and USNM 535802–535805 from Baramita; and ROM 28358–28366 and USNM 291186–291187 and 291189–291190 from Paramakatoi. In addition, USNM 162905 from Atkinson (=Timehri Airport); USNM 164191–164194 from Mabaruma (8°12′N, 059°47′W); USNM 257523–257524 and 257529–257531 from Kartabo Point (6°23′N, 058°41′W); USNM 291138 from Kato; and USNM 531674–531683 from Iwokrama Forest Reserve (various localities).

Coloration in life.—Colors and patterns on these lizards are complex and vary according to age, sex, season, and locality (geographic variation). The following is based on AMNH and USNM specimens from Karanambo, Aishalton, Dubulay Ranch, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1992–1998). Adult females have a tan or light brown dorsum (with green iridescence anteriorly if body sighted over from the rear), bright green on some from snout to midbody, if not to rump, often with black mottling; some with bright green on posterior body, hind legs, base of tail, with tail becoming turquoise blue posteriorly; row of brown spots (with lighter centers) on each side beside vertebral area; dark brown dorsolateral stripe with scalloped edges, on some blending below with brown sides, containing pale cream, yellow, tan or blue (on largest) spots or bars; inconspicuous pale greenish yellow stripe above eye along upper edge of dark brown dorsolateral stripe, fading posterior to arms; lateral light stripe from below eye, tan or yellow, often becoming cream or tan posterior to arms; top of head dark tan, sometimes with dark brown spots; lips cream to tan; arms and legs dark brown or tan with tan or brown spots, stripes, or reticulation (sometimes with few light dots of cream to pale tan); tail brown above, with irregular dark brown stripes (or not), spots, possibly bands; largest individuals with blue spots

on anterior of thighs and feet; chin and throat cream or tan; chest light tan to pale orange; underside of arms, abdomen, legs, feet, base of tail orange, paler anteriorly, darker posteriorly but underside of tail becoming very pale orange or gray posteriorly (turquoise blue on largest), sometimes with brown bands.

Adult males are similar to the above but differ as follows. Dorsum with conspicuous green superimposed on pattern, from back of head to hind legs; colors of scalloped dark brown dorsolateral stripe and brown sides blend together; all lateral area with pale yellow, green, or blue spots or bars; lateral light stripe from below eye is tan or green, extends beyond arms; tail with irregular dark brown spots, no stripes; throat with black specks; cream, pale greenish cream, or tan under arms, chest, anterior abdomen; abdomen on some with blue suffusion; pale yellow or orange under legs; blue spots anteriorly on legs, feet, side of tail; orange on posterior thigh, preanal area, undersides of feet, beneath base of tail; posteriorly, underside of tail very pale grayish green and orange; largest males with green obscuring the pattern over entire body above, legs, tail; no lateral stripe.

Cnemidophorus lemniscatus
(Linnaeus, 1758)
Plate 26C

Type material.—The original name was *Lacerta lemniscata*. Maslin & Secoy (1986) designated as lectotype ZMUU Linnaean Collection 15A, a male. This was overlooked by Cole & Dessauer (1993:18), so their later designation of a different lectotype is invalid (Markezich et al. 1997:51–54), although the invalid specimen is in outstanding condition and the lectotype is not. Cole & Dessauer (1993) restricted the type locality to Suriname: Marowijne: Christiaankondre and Langamankondre, on the west bank of the Marowijne River.

Distribution.—"The range includes northern Brazil, French Guiana, Suriname, Guyana, Venezuela, and Colombia, extending northward through Central America to Guatemala, plus the Republic of Trinidad and Tobago and other islands of the southern West Indies" (Cole & Dessauer 1993:20).

Vouchers for Guyana.—AMNH R-46441–46447 from Kartabo; AMNH R-138058–138062, R-138065–138069, R-138079, R-138081, and USNM 566429–566437 from Yupukari (on Rupununi River), 11 km (linear) SSW Karanambo, northern Rupununi Savanna; AMNH R-138099–138108 from Karasabai Village, 40 km (airline) NW Karanambo, northern Rupununi Savanna; AMNH R-139839–139855 and USNM 566440–566446 from Aishalton; and AMNH R-140862–140871, R-140873–140874, R-140880–140881, USNM 497801, and USNM 566447–566452 from Dubulay Ranch. Also USNM 162906–162912 from Atkinson (=Timehri Airport); USNM 257525–257528 from Kartabo Point (6°23′N, 058°41′W); USNM 291140–291150 from Kato; USNM 566438–566439 from Jouri, 32 km (linear) NW Karanambo.

Coloration in life.—Colors and patterns among these lizards vary according to age, sex, season, and locality (geographic variation). The following is based on AMNH and USNM specimens from Yupukari, Aishalton, and Dubulay Ranch (CJC field notes, 1992–1995). Dark brown dorsum with light tan stripes; lower sides dark tan in young males and females, tannish gray in adult males, with light tan and cream spots (some yellow, green, blue in adult males); top of head and arms brown, outer lower arm with tan outer stripe or row of spots (may fade in adults); legs brown with numerous conspicuous large light pale yellow to tan spots; tail brown; ventral surfaces (including beneath arms) cream,

tan, or greenish yellow on abdomen, preanal area, hind legs, base of tail (becoming gray near tip). Adult males much more colorful than young males or females, some with powder blue face (at times including chin and throat); dark brown dorsal stripes; with bright yellow, tan, or green dorsal and lateral wash on body, turquoise blue on anterior surface and underside of hind legs, groin (perhaps greenish yellow), posterior abdomen, and atop feet; bright bluish green or green on lateral aspect of tail (becoming turquoise distally); bright turquoise blue on midventral surface of tail (paler yellowish green in adult females). For comparisons with specimens from Suriname and Venezuela, see Cole & Dessauer (1993) and Markezich et al. (1997).

Comments.—Two closely related unisexual (all-female) species in the Guianan Region, one diploid and one triploid, had a hybrid origin in which *C. lemniscatus* was one of their ancestors (reviewed by Cole & Dessauer 1993). Consequently, these species are similar to *C. lemniscatus*. They occur in Venezuela, Brazil, and Suriname, so it seems possible that either or both might some day be found in Guyana. The diploid is *Cnemidophorus cryptus* and the triploid is *Cnemidophorus pseudolemniscatus*.

Kentropyx borckiana Peters, 1869a
Plate 26D

Type material.—The original name was *Centropyx Borckiana* and the lectotype is ZMB 897. The type locality is Guiana (Peters 1869a).

Distribution.—Guyana, Surinam, French Guiana, and Barbados (Gallagher & Dixon 1992:132, Fig. 3).

Vouchers for Guyana.—AMNH R-37457–37464 from Georgetown; AMNH R-138111–138115, AMNH R-138648, and USNM 566492–566493 from the Botanical Gardens in Georgetown; and USNM 163021–163052 from Enmore Estate (6°44′N, 057°59′W). In addition, Gallagher & Dixon (1992:163) listed specimens from Guyana with locality data from several collections.

Coloration in life.—The following is based on AMNH and USNM specimens from the Botanical Gardens in Georgetown (CJC field notes, 1992), and paraphrased from Cole et al. (1995:4–5). Dorsum brown with green wash anteriorly; short green middorsal stripe atop head and on nape of neck; cream, tan, or green (anteriorly) light stripes, one originating on temporal region, wavy on neck; dark brown stripe (anteriorly) becoming spots (posteriorly) above dorsolateral light stripe, dark brown area below; small light spots on dorsal surfaces of legs; dark brown spots dorsally on brown tail; cream stripes laterally on tail.

Comments.—This is an all-female species that had an origin resulting from hybridization between *K. calcarata* × *K. striata*, possibly in Guyana, and it appears to reproduce by parthenogenetic cloning (Cole et al. 1995). See Hoogmoed (1973:292–293) and Gallagher & Dixon (1992) for a discussion on the use of the name *K. borckiana*.

Kentropyx calcarata Spix, 1825
Plate 26E, F

Type material.—The original name was *Kentropyx calcaratus* based on material from flumen Itapicurú in provincia Maranhao, Brazil. The type material is "presumed lost" (Gallagher & Dixon 1992).

Distribution.—"Mainly in central and eastern Amazonia (Brazil, Guyana, French Guiana, and Suriname) and Atlantic Forest (coastal Brazil)" (Avila-Pires 1995:524).

Vouchers for Guyana.—AMNH R-8489 from near Georgetown; AMNH R-8563 from Georgetown; AMNH R-25065, R-25068, R-25090, and R-25111–25112 from

Kamakusa; AMNH R-21328, R-137358–137359, and R-137362 from Kartabo; AMNH R-57448–57449 and R-61459 from Karanambo; AMNH R-61255–61256 and R-61294–61295 from Kuyuwini Landing; AMNH R-60972–60973 from Marudi; AMNH R-61292–61293 from Onora; AMNH R-61378–61379 from Isheartun; AMNH R-140967–140968, R-141857, R-141861–141865, and USNM 566494–566496 from Dubulay Ranch; AMNH R-151957–151964 and USNM 566497–566501 from Berbice River Camp; AMNH R-151970–151978 and USNM 566502–566506 from Konawaruk Camp. Also ROM 20525–20528 from Amatuk; ROM 20529 from Kurupukari; ROM 22901–22920 and USNM 535806 from Baramita; and USNM 531684–531693 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The only notes taken in life in Guyana were based on a male at Dubulay Ranch (CJC field notes, 1994), noted to have green and cream spots on the sides. Detailed notes were not taken at that time because CJC and CRT recognized the Guyanan individuals as being like those with which they had experience previously in Suriname, so the following notes paraphrased from Cole et al. (1995:4–5) are relevant. Dorsum of adults brown with green wash anteriorly, with bright green (anteriorly) or cream to tan middorsal stripe from snout or top of head to about midbody; cream, tan, or green (anteriorly) dorsolateral light stripe; row of dark brown spots above the dorsolateral light stripe; some adults with pale cream, tan, green, gray, or blue spots on sides; tail brown with dark brown, sometimes also tan or cream, spots; on some individuals, tan or light brown spots on dorsal surface of hind legs.

Comments.—See comments above for the unisexual species, *K. borckiana*, and the discussion by Avila-Pires (1995) on the widespread use of the name *K. calcarata*.

Kentropyx striata (Daudin, 1802c)
Plate 27A

Type material.—The original name was *Lacerta striata* and holotype from Surinam is MNHN 4191 (Gallagher & Dixon 1992).

Distribution.—"Northern South America, in Brazil...Suriname, Guyana, Venezuela, and Colombia. Also in Trinidad" (Avila-Pires 1995:534).

Vouchers for Guyana.—AMNH R-61271–61272 from Wichabai; AMNH R-61331 from Marudi; AMNH R-61487–61488 from Haiowa Falls, Essequibo River; AMNH R-61377–61378 from Isheartun; AMNH R-138057 from Yupukari (on Rupununi River), 11 km (airline) SSW of Karanambo, northern Rupununi Savanna; AMNH R-138083–138085 from the Simoni area, about 16 km (by trail) E Yupukari; AMNH R-60881–60884, R-138088–138091, R-138096–138098, and USNM 566508–566510 from the Karanambo area; AMNH R-139880–139882 from Aishalton; ROM 28353–28357 from Paramakatoi; USNM 163018 and 163041–163044 from Enmore Estate (6°44′N, 057°59′W); and USNM 566507 from Dubulay Ranch. In addition, "RMNH 25405–406" "from Ogle, just W [sic] of Georgetown" (Avila-Pires 1995:530).

Coloration in life.—The following is based on AMNH and USNM specimens from the areas of Karanambo, Yupukari, Simoni, Aishalton, and Dubulay Ranch (CJC field notes, 1992–1995). On large adults, head and neck (to level of arms) washed with bright green dorsally and laterally, including lips; paler yellowish green on chin, throat; cream or tan light spots on sides. Otherwise, dorsum gray, grayish brown or brown, with paired paravertebral series of small dark brown spots; dorsolateral light stripe dirty cream (may be green anteriorly, tan posteriorly);

lateral light stripe gray; brown or reddish brown dark stripes, lower one with a black irregular streak or spots; brownish gray below lateral light stripe, with inconspicuous light tan stripe within; top of head brown; lips tan (or with green wash, perhaps bright); corner of mouth greenish yellow (color absent from smallest individuals); arms, legs, tail tannish gray to brown; legs sometimes with dark brown spots, tail usually with vertebral row of dark brown spots; chin white or pale tan; throat, chest, beneath arms, anterior abdomen tan (orange in large adults); posterior abdomen, beneath legs, preanal area, beneath tail pale tannish orange, brightest under legs and base of tail (bright orange on adult males and females); posterior underside of tail brown.

Comments.—See comments above for the unisexual species, *K. borckiana*.

Tupinambis teguixin (Linnaeus, 1758)
Plate 27B

Type material.—The original name was *Lacerta Teguixin* and the lectotype is UUZM, Linnaeus Coll. No. 14 (Presch 1973). Presch (1973) restricted the type locality to the vicinity of Paramaribo, Surinam.

Distribution.—"Northern South America (French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil)" (Avila-Pires 1995:563).

Vouchers for Guyana.—AMNH R-18190 and R-107640 from Kartabo; AMNH R-25039 from Kamakusa; AMNH R-140937–140938 from Dubulay Ranch; AMNH field number JC 7829 from Konawaruk Camp (given to UG); and USNM 84514–84515, 86869, 89368, and 94412–94414 from Pomeroon.

Coloration in life.—The following is based on AMNH and UG specimens from Dubulay Ranch and Konawaruk Camp (CJC field notes, 1994, 1998). Black above with tan to yellow or gold bands and, on some anteriorly, elliptical markings; arms similar but legs with tan spots instead of bands; on some, pale gold dots on body, arms, legs, tail; tail black with yellowish tan bands; head above mottled black and tan; venter yellow or orangish yellow with black spots on chin, throat, chest; black bands encircling tail.

Comments.—This is one of the largest species of lizards in the Western Hemisphere, although it is exceeded in length by *Iguana iguana*. Avila-Pires (1995) mentioned a preserved specimen from Brazil with a total length of about 1 m. This species is primarily terrestrial. In some literature in the recent past, the species was referred to as *T. nigropunctatus*, but that is a junior synonym, as discussed by Avila-Pires (1995).

Tropiduridae

This is one of the families of iguanian lizards (see introduction above, before Corytophanidae). Representatives of this family occur in "the Bahama Islands, Cuba and Hispaniola and associated banks; Cayman Islands; South America, excluding northern Colombia and northern Venezuela, southward to northern Tierra del Fuego; Galapagos Islands" (Frost & Etheridge 1989:45). At one point, the genera *Plica*, *Uracentron*, and *Uranoscodon* were synonymized with *Tropidurus*, but they have all been resurrected as they appear to be monophyletic groups after all (Frost et al. 2001).

Plica plica (Linnaeus, 1758)
Plate 27D

Type material.—The original name was *Lacerta Plica* and the holotype is NRM 112 (Avila-Pires 1995). Hoogmoed (1973) restricted the type locality to the confluence of the Cottica River and Perica Creek, Surinam.

Distribution.—"Northern South America east of the Andes, throughout most of the Amazonian region (Brazil, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, and Bolivia) and reaching the Atlantic coast in the Guianas and eastern Venezuela. Also in Trinidad" (Avila-Pires 1995:170).

Vouchers for Guyana.—AMNH R-8090 from Kamaria Landing, Cuyuni River; AMNH R-8091 from Groeta Creek, Essequibo River; AMNH R-14117, R-21290, and R-21331 from Kartabo; AMNH R-25071, R-25089, and R-25113–25115 from Kamakusa; AMNH R-61316 from Kuyuwini Landing; and AMNH R-151847–151849 and USNM 566366 from Konawaruk Camp. Also ROM 22850 and USNM 535795–535800 from Baramita; USNM 84492–84505 and 94408–94411 from Pomeroon; and USNM 164186–164188 from Mabaruma Compound (8°12′N, 059°47′W).

Coloration in life.—The following is based on AMNH and USNM specimens from Konawaruk Camp (CJC field notes, 1998). Brownish green with black markings on body and tail; arms, legs, hands, feet brownish green or gray, with black bands (not complete across undersides); chin and throat pale yellowish green with black markings; underside of neck subtle orange anterior to black patch; beneath arms, legs, chest, posterior abdomen, preanal area very pale yellowish green; orange on posterior chest, abdomen (perhaps with orangish yellow patch posteriorly), beneath hips, beneath base of tail (particularly bright ventrolaterally); iris copper.

Plica umbra (Linnaeus, 1758)
Plate 27E

Type material.—The original name was *Lacerta Umbra* and there are three syntypes, NRM 111 (2 specimens) and UUZM 73 (Avila-Pires 1995). Etheridge (1970) restricted the type locality to the vicinity of Paramaribo, Surinam.

Distribution.—"South America north of Rio Amazonas/Solimões and Rio Japurá, in Brazil, French Guiana, Suriname and Guyana" (Avila-Pires 1995:177). This range is for the subspecies Avila-Pires recognized as *P. umbra umbra*, which is the form that occurs in Guyana.

Vouchers for Guyana.—AMNH R-8097 from Kalacoon; AMNH R-14115–14116 and R-21316 from Kartabo; AMNH R-17690–17691 from Georgetown; AMNH R-25118 from Kamakusa; AMNH R-61436 from Isheartun; AMNH R-141879 from Dubulay Ranch; AMNH R-151851 from Berbice River Camp; AMNH R-151853–151863 and USNM 566367–566373 from Konawaruk Camp. Also ROM 22851–22852 from Baramita; ROM 20507–20508 from Tukeit; ROM 28350 from Paramakatoi; ROM 43206 from Kaieteur Plateau; USNM 164189 from Mabaruma Compound (8°12′N, 059°47′W); USNM 326119–326120 from Kwakwani (5°30′N, 058°00′W); and USNM 531645–531649 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on AMNH specimens from Dubulay Ranch and Berbice River Camp, and AMNH and USNM specimens from Konawaruk Camp (CJC field notes, 1995–1998). Brownish green or green above, including head, with dark brown or black markings (basically bands) on body, arms, legs, tail (ground color of tail on some light tan); lips possibly bluish green; orangish yellow beneath neck, becoming paler on throat and chin; orangish yellow patches on abdomen, thighs, preanal area, beneath tail (brightest at base); other ventral surfaces light tan to grayish orange. An adult male was noted specifically to have a bright yellowish orange throat, and an adult female as having only a trace of this color.

Tropidurus hispidus (Spix, 1825)
Plate 27C

Type material.—The original name was *Agama hispida* and the lectotype is RMNH 2912 (Hoogmoed & Gruber 1983). The type locality was "restricted by Rodrigues, 1987 to Salvador, Bahia, Brazil" (Avila-Pires 1995:186).

Distribution.—Avila-Pires (1995:190) stated that this species occurs in parts of Brazil, southern French Guiana, "Suriname, Guyana, and Venezuela."

Vouchers for Guyana.—AMNH R-137915, R-137920–137924, R-137927, and USNM 566375–566378 from Karanambo; AMNH 138086 from the Simoni area, about 16 km (by trail) E of Yupukari, northern Rupununi Savanna; AMNH R-139791–139803, R-139811–139812, and USNM 566379–566385 from Aishalton; and AMNH R-140906–140915, R-140921–140922, and USNM 497794–497797 and 566386–566390 from Dubulay Ranch. Also, USNM 146375 from Lethem; USNM 162895–162904 from Atkinson (=Timehri Airport); USNM 163054 from Enmore Estate (6°44′N, 057°59′W); USNM 291132 and 291134–291137 from Kato; and USNM 497798 from CEIBA Biological Station (06°29′57″N, 058°13′06″W).

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo, Yupukari, Aishalton, and Dubulay Ranch (CJC field notes, 1992–1994). Dorsum gray, tan, or brown, with indistinct dark brown to black or pale tan spots or bands and indistinct pale tan, orangish yellow, or greenish yellow wash; some individuals with indistinct, diffuse, very light gray dorsolateral stripe; top of head, arms, legs, tail similar to body; dark brown to black collar on neck; chin, throat, chest pale yellow or orange, on some with gray smudges or broad gray wash on throat; abdomen yellow to orange, paler posteriomedially; underside of arms and legs dirty cream with pale yellow to orange; underside of base of tail very pale yellow to orange, becoming cream then gray posteriorly; lips pale yellow or orange with gray smudges. Adult males have orange in the axilla and gray streaks on the chest. They also have dark patches of small, round black spots on the underside of the thighs and preanal area, which may be seasonal black patches correlated with the reproductive cycle, as noted for *T. semitaeniatus* by Ribeiro et al. (2010).

Comments.—We noted slight differences in coloration of the lizards from Dubulay Ranch versus the Rupununi Savanna, but this might have reflected seasonal or geographic variation.

Uracentron azureum (Linnaeus, 1758)

Type material.—The original name was *Lacerta azurea* and there are two syntypes, NRM 113 (Avila-Pires 1995). Hoogmoed (1973) restricted the type locality to the confluence of the Cottica River and Perica Creek, Surinam.

Distribution.—For *U. azureum azureum*, the form that occurs in Guyana, "eastern Amazonia, in Guyana, Suriname, French Guiana, and Brazil'' (Avila-Pires 1995:207).

Vouchers for Guyana.—BMNH 1905.10.21.1 and 62.12.15.36 from "British Guiana" (quoted from the BMNH catalog; no additional locality data). Colin McCarthy at the BMNH confirmed the catalog data and sent us digital photographs of both specimens for confirmation of the identification.

Coloration in life.—The following is from Hoogmoed (1973:196), based on a specimen from Suriname. "Colour in life of RMNH 15249, above bright grass-green with black cross-bands. Belly, throat and ventral surface of the fore-limbs yellow-green, chin green. Ventral surface of the hind limbs chrome-yellow. Scales on the dorsal surface of the tail

green, the outer and next to outer row with the tips of the spines yellow; scales under the tail yellow-ochre and green. Iris golden brown."

Comments.—Only two specimens are known from Guyana (see Vouchers, above). Little is known about the life history, behavior, and ecology of this species. Avila-Pires (1995:212) stated that "it is predominantly an arboreal forest inhabitant. Probably it mainly lives in the canopy, which could explain why it is only rarely observed."

Uranoscodon superciliosus
(Linnaeus, 1758)
Plate 28A

Type material.—The original name was *Lacerta superciliosa* and there are three syntypes, NRM 109–110, and UUZM Linnean collection no. 69 (Avila-Pires 1995). Hoogmoed (1973) restricted the type locality to the confluence of the Cottica River and Perica Creek, Surinam.

Distribution.—"Northern South America east of the Andes, in Brazil, French Guiana, Suriname, eastern Venezuela, eastern Colombia, and northeastern Peru" (Avila-Pires 1995:228).

Vouchers for Guyana.—AMNH R-15133–15135 and R-21317 from Kartabo; AMNH R-61306 from Isheartun; AMNH R-61390–61391 from Karanambo; AMNH R-139788–139790 from Aishalton; AMNH R-140949 from Dubulay Ranch; AMNH R-151871–151872 and USNM 566391 from Berbice River Camp; and AMNH R-151876, R-151878–151879, and USNM 566392–566394 from Konawaruk Camp. Also, ROM 20509 from Kurupukari; USNM 497799 from CEIBA Biological Station (06°29′57″N, 058°13′16″W); and USNM 531650–531657 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton, Dubulay Ranch, Berbice River Camp, and Konawaruk Camp (CJC field notes, 1993, 1994, 1996–1998). Dorsum, including head and tail, brown; alternating tan and black dashes or dark brown bands on vertebral line, continuing onto tail; arms and legs brown, with black bands and irregular spots; dark brown and tan lines radiating from eye; pale tan, tannish yellow, or orange flecks low on sides; chin may be dark grayish brown; white, dirty cream, or yellow on throat, chest, abdomen, and beneath arms, legs, and tail; some scattered brown to black spots or gray smudges on chest, posterior abdomen and beneath legs. A female had a broad orange streak on her sides.

Comments.—We usually found individuals of this species in trees that are in or adjacent to bodies of water. Massary & Ineich (1999:168) reported on an adult male that "was captured, photographed, measured, and released at 1545 h from a boat ca. 9 m from shore. The specimen dived just in front of us and remained at a depth of ca. 22 cm for 24 min 40 sec. The lizard then emerged for ca. 1 sec, took a single breath, and submerged a second time" for an unknown duration.

Species Accounts: Reptilia: Squamata: Snakes

Snakes of one kind or another have been around for at least 165 million yr, based on fossils and modern phylogenetic analyses using DNA sequence data (Vidal et al. 2010a). The oldest families in Guyana, those having the species among the first to evolve are the Aniliidae, Anomalepidae, Boidae, Leptotyphlopidae, and Typhlopidae. The modern snakes (of most recent origin) are the Colubridae sensu lato, Elapidae (coral snakes), and Viperidae. Despite the use of such words as "oldest" and "modern" here, every species alive today is a modern represen-

tative of its group, no matter how ancient the group's earliest representatives may have been.

Since 1995, several groups of investigators have been analyzing phylogenetic relationships of snakes using DNA sequence data, including Lawson et al. (2005), Vidal et al. (2007, 2010a), Zaher et al. (2009), and Pyron et al. (2011). The studies have involved numerous and varied samples of taxa among the many kinds of snakes in the world, different genes, and somewhat different techniques and philosophy. Consequently there are some differences in proposed revisions to the classification of snakes, including at the family level, and today there is not full agreement among specialists as to how many families of snakes there are and what names should be applied to them. As this is an active area of research with certainly more important changes to come in the near future, we adopt a rather conservative use of family names here. For now, at least 8 families, 52 genera, and 97 species of snakes are known to occur in Guyana.

Aniliidae

The species *Anilius scytale* is so distinctive morphologically among the snakes of the world that it has been assigned to a family of its own for nearly 200 yr and recent analyses of DNA sequence data indicate that this species belongs to an ancient lineage (Noonan & Sites 2010). It is not unusual to find this colorful snake in Guyana, although very little is known about its natural history.

Anilius scytale (Linnaeus, 1758)
Plate 28B

Type material.—The original name was *Anguis Scytale* and the holotype, which does not have reliable locality data, is NRM 13 (McDiarmid et al. 1999).

Distribution.—"Northern South America from southern and eastern Venezuela, Guyana, Suriname, French Guiana through the Amazon Basin of Colombia, Ecuador, and Brazil" (McDiarmid et al. 1999:157).

Vouchers for Guyana.—AMNH R-8162 from Kalacoon; AMNH R-21286 from Kartabo; USNM 85092 from McKenzie (=Linden); USNM 145457 from "Georgetown, 50 mi above, on the Abary River"; USNM 566250 from Berbice River Camp; and field number JC 8087 from Konawaruk Camp (given to UG).

Coloration in life.—The following notes are based on the USNM specimen from Berbice River Camp and the one from Konawaruk Camp (CJC field notes, 1997, 1998). Dorsum of alternating black and reddish orange bands; similar to this beneath head and tail (but reddish orange is paler); ventral surfaces of body pale yellow with black bands.

Comments.—These snakes eat primarily amphisbaenians, small snakes, and caecilians, most of which are burrowing; they forage "mainly on the ground, at night, as well as in aquatic environments" (Maschio et al. 2010:184).

Anomalepidae

These small burrowing snakes are superficially similar to worm snakes (Typhlopidae; see introduction to that family, below) but were recognized morphologically by Taylor (1939) as comprising a separate family. Only one of the few surviving species of this clade of snakes occurs in Guyana.

Typhlophis squamosus (Schlegel, 1839)

Type material.—The original name was *Typhlops squamosus* based on material

from Cayenne. Hahn (1980) stated the holotype was at the MNHN, now lost.

Distribution.—Atlantic lowlands of South America from French Guiana, Guyana, and Suriname south to northern Brazil (McDiarmid et al. 1999).

Vouchers for Guyana.—AMNH R-25051 from Kamakusa.

Coloration in life.—The following is from Starace (1998:68–69) based on specimens from French Guiana. "Dorsally, the body is toned from black to dark brown. The head is pinky-white, the eyes are barely visible. The belly is uniformly white." He also stated that his specimens had some small white spots toward the swollen rear of the snakes.

Comments.—Starace (1998:69) stated that this species is nocturnal and fossorial, "found in primary rainforests..., inside ant and termite nests. Feeds on ants, ant eggs and ant larva as well as on termites. Oviparous."

Boidae

These morphologically distinctive snakes have been recognized as a family separate from other snakes for nearly 200 yr. They use constriction to subdue their prey, give birth to living young, often are found in trees, can become quite large (including the largest snake in the Western Hemisphere, the anaconda, *Eunectes murinus*), and are fairly abundant in Guyana. The common ancestor of the Boidae existed approximately 70 million yr ago, so the modern distribution of the group as a whole (Western Hemisphere, Africa, Madagascar, Asia, southwestern Pacific islands) may reflect primarily a history of over-land dispersal within and on drifting parts of Gondwanaland, rather than more recent over-water dispersal or rafting across the Pacific Ocean (Noonan & Sites 2010).

Boa constrictor Linnaeus, 1758
Plate 28C

Type material.—According to McDiarmid et al. (1999:185) two syntypes exist: NRM 10 and NRM 20001, and a third is presumed lost. Credible locality data is lacking for the types.

Distribution.—"From northern México, through Central America ... to South America North of latitude 35°S...; Dominica and St. Lucia in the Lesser Antilles; San Andrés and Providencia Islands (Colombia), and many other continental islands along the Atlantic and Pacific coasts of Mexico, Central and South America" (McDiarmid et al. 1999:185).

Vouchers for Guyana.—AMNH R-65568 from Kartabo; USNM 164195–164196 from Mabaruma Compound (8°12′00″N, 059°47′00″W); USNM 497803 from Dubulay Ranch; and USNM 566251 from 24 km NE Aishalton. Also, RDM photographed and released an individual of this species at Baramita, and CJC and CRT photographed and released several at Dubulay Ranch and Berbice River Camp.

Coloration in life.—The following is from Starace (1998:92), based on specimens from French Guiana. "The dorsal [surface] is light brown, covered with dark [brown] geometric patterns while the tail is red-brick coloured [with cream areas in between]." There is a longitudinal mid-dorsal brown stripe on top of the head.

Comments.—The specimens seen at Berbice River Camp included a female more than 3 m in length. USNM 497803 was captured at 1815 h, ca. 6 m high in a tree while constricting/ingesting a kiskadee (*Pitangus sulphuratus*) it had just caught.

Corallus caninus (Linnaeus, 1758)
Plate 28D

Type material.—The original name was *Boa canina* and the holotype, known only

to be from America, is NRM "no. Lin. 8" (McDiarmid et al. 1999:190).

Distribution.—"Guyana, Suriname, French Guiana, eastern and southern Venezuela (states of Bolívar and Amazonas), and northeastern Brazil north of the Rio Amazonas and north and east of the Rio Negro (in the states of Amapá, Pará, Roraima, and Amazonas)," as restricted by Henderson et al. (2009:575; see Comments, below). For *C. caninus* sensu lato, include the broader Amazon Basin, south of the Amazon also, and "Amazonian Colombia, Ecuador, Peru, and Bolivia, as well as in northwestern Colombia north of the Andes" (Henderson et al. 2009:578).

Vouchers for Guyana.—AMNH R-8368 from Kalakun (Mazaruni River); AMNH R-14133 from Kartabo; AMNH R-25029 from Kamakusa (Mazaruni River); AMNH R-60835 without data additional to "British Guiana" (collected by R. Snedigar, Terry-Holden Expedition); BMNH 1929.7.13.5 from Demerara River; MCZ 33384 from Georgetown; and field number JC 8066 from Konawaruk Camp (given to UG). In addition, Alexander Mendes reports that this species occurs at Dubulay Ranch.

Coloration in life.—The following is based on the UG specimen from Konawaruk Camp (CJC field notes, 1998). Dorsum green (paler laterally) with light crossbars; anteriorly on body, crossbars gray with yellow spots at lateralmost ends; posteriorly on body, crossbars white or cream with yellow edging here and there; venter yellow; green and yellow colors of dorsum and venter interdigitate ventrolaterally; iris tan.

Comments.—Henderson et al. (2009) confirmed that *C. caninus* occurs in Guyana. They also named as a new species specimens from populations to the south and west, which previously had been included in *C. caninus*. The new species was diagnosed primarily on the basis of partitioning the range of variation of several variable characters in the absence of geographically-correlated analyses of clinal variation. Consequently, we personally still treat *C. caninus* as one widely distributed species, awaiting more convincing evidence that it should be partitioned into two. This species is arboreal.

Corallus hortulanus (Linnaeus, 1758)
Plate 28E, F

Type material.—The original name was *Boa Hortulana* and the holotype, from "America," is NRM "no. Lin. 7" (McDiarmid et al. 1999:192).

Distribution.—"South America: southern Colombia east of the Andes, southern Venezuela, Guyana, Suriname, French Guiana, and Amazonian Brazil, Ecuador, Peru and Bolivia" (McDiarmid et al. 1999:193).

Vouchers for Guyana.—AMNH R-8102 from Kalacoon; AMNH R-67869 from Kartabo; AMNH R-140234 and USNM 566252 from Dubulay Ranch; ROM 22849 from Baramita; USNM 141763 and 145462–145472 from "Georgetown, 50 mi above, on the Abary River"; USNM 166830 from Atkinson Airport (=Timehri Airport); and USNM 531694–531696 from Iwokrama Forest Reserve (various localities). In addition, CJC and CRT saw two individuals at their Berbice River Camp (not collected).

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994). Pale tan or gray above with brown markings that are darker brown dorsally than laterally; head yellowish tan or grayish tan with dark brown markings; iris rust; chin very pale yellow; anterior venter cream with tan or brown markings, posteriorly becoming dark tan or grayish tan. Some have a touch of orange among the facial pits and on the chin.

Comments.—This species frequently has been referred to as *Corallus enydris*, but *C. hortulanus* has precedence (McDiarmid et al. 1996). The species is arboreal.

Epicrates cenchria (Linnaeus, 1758)
Plate 29A

Type material.—The original name was *Boa Cenchria* and the holotype, from Surinam, is NRM "no. Lin. 6" (McDiarmid et al. 1999:196).

Distribution.—"Lower Central America in Costa Rica and Panama; South America east of the Andes in Colombia, Venezuela, Guayana [sic], Suriname, French Guiana, Brazil, Ecuador, Peru, Bolivia, Paraguay, and northern Argentina...; Trinidad and Tobago" (McDiarmid et al. 1999:196).

Vouchers for Guyana.—AMNH R-8102 from Kalacoon; AMNH R-21285 and R-31523 from Kartabo; AMNH R-98186 from near Kartabo; and AMNH R-28956 and R-60851 from "British Guiana" but with no additional locality data. Also, UMMZ 46676–46677 from Dunoon, Demerara River; UMMZ 66809 from Arakaka; USNM 566253 from Dubulay Ranch; and field number JC 7757 from Konawaruk Camp (given to UG).

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1994). Brown with dorsal circles, ellipses, and irregular ovals of tan edged in black; lateral spots black, lined above in light tan then black; ventrolaterally, spots very dark brown to black on light brown ground color; head brown with black stripes; chin and throat cream; rest of venter pale gray posteriorly through anal plate; mottled light gray and black beneath tail.

Comments.—Chippaux (1986), Starace (1998), and Passos & Fernandes (2008) treated the rainbow boas of the Guianan Region as two species, not two subspecies as per prior authors, elevating *Epicrates cenchria maurus* to specific status. They stated that *E. cenchria* occurs in humid forests and *E. maurus* occurs in drier savannas, but their data were limited, they studied no specimens from Guyana, they performed no geographically-correlated analyses of variation, and the meristic characters used to distinguish the forms were part of a continuum divided in the middle. We consider this to be an interesting working hypothesis rather than a matter that has been settled. Whether these authors are correct could be tested by obtaining samples along a north to south transect through Guyana, including humid forest and drier savanna habitats with gallery forests, and similar ecological transects in other areas of the Guianas and analyzing geographic variation. It also would be of interest to include molecular data.

We examined each of the Guyanan voucher specimens listed above for the characters used by Chippaux (1986), Starace (1998), and Passos & Fernandes (2008). The number of ventral scales ranged from 252–273 and subcaudals from 57–62, which is consistent with *E. c. cenchria*, as was the color pattern of each specimen. The loreal scales of these specimens included one elongate upper loreal (but 2 on the left side of one specimen) and 2–4 (usually 3) smaller ones below, which is more like *E. c. maurus*. This also indicates that more research is needed on these animals.

Eunectes murinus (Linnaeus, 1758)
Plate 29B

Type material.—The original name was *Boa murina* and the holotype, only known to be from America, is NRM "no. Lin. 9" (McDiarmid et al. 1999:201).

Distribution.—"South America east of the Andes in Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, and

Brazil; Trinidad'' (McDiarmid et al. 1999:201).

Vouchers for Guyana.—AMNH R-14266 from Kartabo; AMNH R-25032 from Kamakusa; USNM 85089–85091, 86640–86642, 89388–89389, and 90900 from McKenzie (=Linden); USNM 141764 from "Georgetown, 50 mi above, on the Abary River"; and USNM 497804 from Dubulay Ranch. Gerald and Wesley King (Amerindian field assistants of CJC and CRT) saw a large one (not collected) a short walking distance from our Konawaruk Camp.

Coloration in life.—The following is based on the juvenile USNM specimen from Dubulay Ranch (RPR field notes, 1994). "Dorsum olive green with dark brown spotting; venter pink cream with lateral dark spotting forming lines on lateral edge of ventrals." The following is from Starace (1998:111–113) based on specimens from French Guiana. "The dominant dorsal colouring is light greeny-brown with black oscillated patterns distributed on either side along the spinal axe." On each side of the head in the temporal region is a light orange elongate triangular area. The ventral surface is generally light green with some black spots.

The following is from Beebe (1946:20) based on specimens from Kartabo, Guyana, which he referred to as *Eunectes gigas*. "Top of head dark olive, almost black on orbits; side of face in front of eye, upper labials and post oculars dark olive; A broad cinnamon band equal in width to eye extends from eye to posterior point of jaw, becoming darker and narrower on side of neck. This cinnamon band is bounded below by a narrowed band of black which extends along the neck. Back olive green with many alternately placed, irregular, large, round and oval black spots. Sides buffy brown with smaller, more crowded spots of orange yellow, edged with black. The lowermost of these are much broken and extend in laces over the ventrals. Chin pale pinkish-cinnamon flecked laterally on the throat with gray and black. Ventrals warm buff with exceedingly variegated markings composed of small, black, geometrical patches, which frequently form two broken, longitudinal lines."

Comments.—This is the largest species of snake in the Western Hemisphere, and one of the largest in the world; adults can attain 10.5 m in length and have a heavy body. They are "generally found in watercourses and in marshlands" (Starace 1998:113). De Freitas (2009:98) reported that an individual of 5 m total length was swallowing an adult *Boa constrictor* of 1.8 m total length when found, which in turn had swallowed an *Iguana iguana*, "in the South Rupununi savannas of Guyana about 7 km N of Dadanawa Ranch (2.88°N, 59.53°W)."

Colubridae, sensu lato

Colubridae sensu lato is a very large family of snakes (more than 2400 species), including some representatives on nearly all of the continents that support snakes. Many recent papers on snake taxonomy and phylogeny, including those based on modern molecular and phylogenetic analyses, have suggested ways to subdivide the traditional Colubridae into smaller possibly monophyletic groups involving multiple smaller families and often more restricted geographic distributions (see introductory paragraph for the snakes, above). One partition uses the family Dipsadidae as a large family of primarily neotropical snakes. Two recent papers (Zaher et al. 2009, Vidal et al. 2010a) reviewed the earlier analyses and proposed different generic taxonomic conclusions of their own, based on extensive new analyses focused on South American species. These included 19 species of "colubrids" that occur in Guyana, and for which the authors supported revising the familial

classification to place most of them in the family Dipsadidae. Nevertheless, in the most recent paper with detailed phylogenetic analyses, Pyron et al. (2011:340) used the family Colubridae for the relevant South American snakes, consistent with "a conservative approach to taxonomic changes," which we follow here.

Zaher et al. (2009) also argued for changing the generic names applied to certain South American species, to be consistent with their understanding of monophyly and priority of authorship. This included four species that occur in Guyana. Consistent with Curcio et al. (2009) and Vidal et al. (2010a) we followed only one of these four suggestions, as discussed below. Interestingly, three of these four species have been jumping among genera for some time, which underscores the difficulties with colubrid classification.

1. Zaher et al. (2009) suggested changing the former name *Erythrolamprus aesculapii* to *Liophis aesculapii*. However, Curcio et al. (2009) and Vidal et al. (2010a) proposed that Zaher et al. had priority of authorship incorrect, that *Erythrolamprus* has priority over *Liophis*, that type species are available and should be included in the analyses, and that such a generic change should await "more analyses...with greater taxon and character sampling" (Vidal et al. 2010a:52), although there is apparently a problem with nonmonophyly of the traditional *Liophis*, *Erythrolamprus*, and *Umbrivaga*. We retain use of *Erythrolamprus aesculapii* and the genus *Liophis* here.
2. Zaher et al. (2009) suggested changing the name *Liophis lineatus* to *Lygophis lineatus*. Curcio et al. (2009) argued similar to the case with *Erythrolamprus*, that this change of generic name would be premature. We retain use of *Liophis lineatus* here.
3. Zaher et al. (2009) suggested changing the name *Waglerophis merremii* to *Xenodon merremii*. This seems reasonable and has not been opposed by other authors, so we use *Xenodon merremii* here.
4. Zaher et al. (2009) suggested changing the name *Xenoxybelis argenteus* to *Philodryas argenteus*. However, Vidal et al. (2010a:52) stated that "*Philodryas* appears to be paraphyletic with respect to *Xenoxybelis*, but with low support, and we recommend the recognition of the morphologically distinctive genus *Xenoxybelis* pending further studies with denser taxonomic and character sampling." We retain use of *Xenoxybelis argenteus* here.

Apostolepis nigrolineata (Peters, 1869b)

Type material.—The original name was *Elapomorphus nigrolineatus* and the holotype is ZMB 6447 (Bauer et al. 1995:71). The type locality was given as Guinea, "but assumed by Peters to be South America" (Peters & Orejas-Miranda 1970:22).

Distribution.—This species is known only from widely scattered localities in Guyana, French Guiana, and western and eastern Amazonian Brazil (Lema & Albuquerque 2010, Vidal et al. 1999 [1998]).

Voucher for Guyana.—Colin McCarthy of the BMNH provided us with the following details on the holotype for the junior synonym *Apostolepis quinquelineata* (see comment below). The specimen is BMNH 1946.1.9.59 (formerly 1889.9.30.12) from "Demerara," presented by J. Quelch. This is the only specimen from Guyana of which we are aware.

Coloration.—Lema & Albuquerque (2010:345), without specifying whether their notes were based on living individuals, stated the following: "dorsum reddish brown...; a blackish brown head...lacking a

pair of cream blotches on preocular scales...a pair of cream blotches [present] on neck covering the 3rd and 4th dorsal scales on 5th scale row on each side...The caudal band is dark brown...and covers only the dorsal surface of the end of the tail." Starace (1998:268), based on preserved specimens, added that there are five dark brown stripes on the body, the ventral surface is yellow, and the end of the tail can be black instead of dark brown.

Comments.—The genus *Apostolepis* is poorly known taxonomically, as well as in other aspects of its biology. In the last few years, the one species that occurs in Guyana has been referred to with three different names: *A. quinquelineata*, *A. flavotorquata*, and *A. nigrolineata*.

Atractus favae (Filippi, 1840)

Type material.—The original name was *Calamaria Favae* and type(s) and type locality are unknown to us.

Distribution.—Hoogmoed (1980:19) stated that the only known localities for this species are in Guyana and Surinam and that "probably this species is endemic to the Guiana Shield, possibly only to a small part of it in northern Suriname and Guyana."

Vouchers for Guyana.—AMNH R-17678 from Georgetown; AMNH R-61557 from Wismar, both identified by M. S. Hoogmoed (1980) and confirmed recently by CJC; BMNH 1934.11.1.132 from ''Demerara near Mackenzie'' (Hoogmoed 1980:16).

Coloration.—Hoogmoed (1980:19) stated that "according to Parker (1935) it is 'black above and banded black and coral-red beneath with a white spot around the vent.'" Hoogmoed (1980:18) described preserved specimens as being "brown with an indistinct dark-brown vertebral stripe. Light spots on snout...Rostral and median suture of internasals and prefrontals dark brown, separating the spots. A light spot on supralabials five and six. Belly...black cross-bars...frequently only extend to the middle [of the belly] and alternate with their counterparts."

Atractus schach (Boie, 1827)

Type material.—The original name was *Brachyorrhos schach* and Hoogmoed (1980) designated RMNH 119a as the lectotype. He also restricted the type locality to Mamadam, Saramacca River, Brokopondo, Surinam.

Distribution.—Known from western and central Surinam and Manaus, Brazil (Hoogmoed 1980); now widely in the Amazon Basin (Hoogmoed, pers. comm.).

Vouchers for Guyana.—BMNH 1939.1.1.95–1939.1.1.96 from "New River, Guiana, 750′," identified by F. Irish (quoted from catalog records of the BMNH; no additional data).

Coloration in life.—Hoogmoed (1980:34) described the coloration of a living individual from Surinam, based on color slides as: "The back is orange brown with black blotches. The belly is white with a median row of black spots, underside of tail grey." He also described (p. 33) the pattern of preserved specimens: "Snout and anterior part of head black, a light brown, transverse band on the back of the head, followed by a black band on the neck. Body light brown with rectangular black blotches, those of both flanks either alternating or confluent. A vague but distinct black vertebral line. Blotches on flanks often bifurcating near the ventrals. Belly immaculate or with a single row of brown or black spots down the middle, posteriorly accompanied by other brown or black spots. Underside of tail either completely grey or heavily mottled with brown." In life, the ground color of the belly is cream to yellow (Starace 1998:136).

Comments.—Colin McCarthy kindly sent photographs of the two BMNH

voucher specimens to CJC. They compare favorably with this species and with each other, so we accept this identification.

Atractus steyermarki Roze, 1958

Type material.—The holotype is CNHM 69920, a male from Chimantá Tepui, Bolívar, Venezuela; 1430 m (Roze 1958:301).

Distribution.—This species is known only from Guyana and Venezuela, from very few specimens.

Vouchers for Guyana.—BMNH 1976. 348 from "Roraima Guyana, 7500–8000′" (quoted from the BMNH records) and UF 150240 (six photographs of UG number HR 701) from "GUYANA: Potaro-Siparuni District, talus slope of Mt. Roraima beneath its northernmost promontory called 'The Prow,' (05°15′30″N, 60°43′30″W), ca. 2090 m elev." (Means 2007:484).

Coloration.—Roze (1958) described the type material from Venezuela as being dark gray above, the head similar to the body; white on the supralabials and lower secondary temporals (absent on a melanistic specimen); lateral ends of ventrals with black spots forming a ventrolateral row; light beneath head and anterior ventral surface, but soon with black spots on midventral line (with considerably more black on melanistic individual); midventral spots gradually increase in size posteriorly to occupy most of middle of ventrals; subcaudals black with light ends.

Comments.—Colin McCarthy of the BMNH and Kenneth L. Krysko of the UF provided CJC with nine digital photographs of the two Guyanan vouchers cited above. These were compared with AMNH specimens of various species of *Atractus* from the Guianan Region, including *A. zidoki* (AMNH R-131799 from Brazil, identified by M. Rodriguez, and AMNH R-108792 from Surinam, identified by M. S. Hoogmoed), and with descriptions of *A. steyermarki* in the literature (Roze 1958, Myers & Donnelly 2008). All important characters of scalation and color pattern visible on the photographs fit reasonably closely with *A. steyermarki* and not *A. zidoki* or any other species of the genus. This suggests that *A. steyermarki* has a wider geographic distribution than had been known and is consistent with Roze's (1961) comment about its possible occurrence on the Gran Sabana of eastern Venezuela, not far from Mt. Roraima. UF 150240 originally had been reported (Means 2007) incorrectly as representing *Atractus zidoki*.

Atractus tamessari Kok, 2006a
Plate 29C

Type material.—The holotype is IRSNB 2640, an adult male from along a tributary of Elinkwa River, within the ESE area of Kaieteur National Park, ca. 500 m elevation, Potaro-Siparuni District, Guyana (5°08′09″N, 59°25′28″W).

Distribution.—Known only from the type locality (Kok 2006a:25) and eastern Venezuela (Rivas et al. 2012).

Vouchers for Guyana.—The three specimens known are all from Kaieteur National Park, Guyana, the type locality (see above). This includes the holotype (see above) and two paratypes (IRSNB 2641–2642).

Coloration in life.—Kok (2006a:22–25) described coloration of the holotype as follows. "The dorsal ground color is brownish black with numerous irregular bright red and paler red markings. The tail is brownish black with a few bright red lateral markings. The top of the head is brownish black. The snout is lighter, with a slight yellow wash. The supralabials are mostly yellow with the upper third dark brown, except for the eighth, which is almost completely dark brown with a small yellow spot anteriorly, and the first and the second, which are speckled with

dark brown. The infralabials are mostly yellow with the lower third and posterior portion of each scale dark brown. The chinshields are mostly yellow with dark brown anteriorly and laterally. The mental groove area has a few dark brown speckles. The venter is yellowish cream with many irregular brownish black blotches, fewer blotches anteriorly, heavily mottled posteriorly. Underside of tail is brownish black with a few small irregular yellowish cream markings. The iris is brown." The paratypes showed variation in dorsal color tones and one specimen had two ventrolateral black stripes.

Comments.—Practically nothing is known about the biology of this snake.

Atractus torquatus (Duméril, Bibron, & Duméril, 1854) Plate 29D

Type material.—The original name was *Rabdosoma torquatum* and Hoogmoed (1980) designated RMNH 114, a male, as the lectotype. Hoogmoed (1980) restricted the type locality to Paramaribo, Surinam.

Distribution.—This species is known from Surinam, Guyana, French Guiana, Peru, and Bolivia according to Hoogmoed (1980:38); "Amazonian Colombia and Bolivia; Amazonas Brazil" according to Peters & Orejas-Miranda (1970:35).

Vouchers for Guyana.—AMNH R-60788 from Kuyuwini Landing; USNM 566254 from Dubulay Ranch; BMNH 72.10.16.72–72.10.16.73 from Demerara Falls (Hoogmoed 1980:36).

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1994). Dark brown above, with black markings that tend to form bands; ventral surface yellow, with black spots. Hoogmoed (1980:38) stated that specimens from Surinam had "upper parts iridescent dark greyish brown to reddish brown. Ventral parts creamish to yellow with brown spots. Underside of tail orange. Iris chestnut brown."

Atractus trilineatus Wagler, 1828 Plate 29E

Type material.—Hoogmoed (1982) designated RMNH 48 as the lectotype. There are no reliable data for the type locality.

Distribution.—"A lowland Guiana endemic, ranging from eastern Venezuela to the Guianas; and occurs on Trinidad, Tobago and Little Tobago" (Murphy 1997:166).

Vouchers for Guyana.—AMNH R-137334 from Kartabo, identified by A. L. Markezich; ROM 19197 from "Demerara" (quoted from catalog; no additional locality data); and USNM 566255 from Dubulay Ranch.

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1994). Brown above, with dark brown stripes; chin and anterior throat pinkish tan; rest of ventral surface lemon yellow. Beebe (1946:21) described a specimen from Kartabo as having the "head above cinnamon brown with distinct asymmetrical mottlings of mummy brown. Back hazel brown with three longitudinal stripes of dark clove brown. Upper labials citrine yellow. The upper side of body below the lateral dorsal stripes, tawny olive and below this a faint, narrow line of brown. Lower labials, chin and anterior ventrals lemon yellow. Remaining ventrals mustard yellow with pinkish tinge. Iris dark cinnamon brown."

Chironius carinatus (Linnaeus, 1758)

Type material.—The original name was *Coluber carinatus* and the holotype is NRM 33, which lacks reliable locality data

(http://linnaeus.nrm.se/zool/herp/madserp.html.en).

Distribution.—According to Dixon et al. (1993: 73) this species occurs in "northeastern Brazil...French Guiana, Surinam, Guyana, eastern Venezuela, and Trinidad." These authors recognized some subspecies, but it is the nominate form that occurs in Guyana, and the quote covers only that form (see Comments, below).

Vouchers for Guyana.—AMNH R-8705 from Kalacoon and AMNH R-60781 from Karanambo, identified by J. A. Wiest; and USNM 84520 from Pomeroon.

Coloration.—According to Dixon et al. (1993:75) "an ontogenetic change occurs, in which light brown or olive juveniles (some with faint flecking on dorsal scales or faint crossbands) become dark olive adults with distinct yellow spots on the first scale row of tail." Starace (1998:144) stated that this species is "olive green to brown, the sides are bluish and the belly is orange-yellow. Often light brown, the head is slightly lighter than the body."

Comments.—Dixon et al. (1993) recognized three subspecies, but Hollis (2006) elevated each of them to specific status. *Chironius carinatus* is the form that occurs in Guyana.

Chironius challenger Kok, 2010b
Plate 29F

Type material.—The holotype is IRSNB 2659, a subadult female from the southeastern slope of Maringma Tepui, Cuyuni-Mazaruni District, Guyana (05°12′N, 060°35′W; 1500 m) (Kok 2010b:32).

Distribution.—The four known specimens are from tepuis in Guyana and Venezuela (Kok 2010b).

Vouchers for Guyana.—The holotype; and ROM 42603 from Mount Wokomung, 1400 m elevation (Kok 2010b).

Coloration in life.—Kok (2010b:36–37) described the holotype from Guyana as follows. "Dorsolateral body ground colour light brown, darkening posteriorly, with a series of *ca*. 31 ill-defined greyish brown transverse bands (1, rarely 2 scales wide) outlined in black. Tail darker brown without conspicuous transverse bands. Dorsal scales with black edges, sometimes slightly peppered with dark brown or black; some dorsal scales yellow anteriorly, especially on anterior body and on lower flank. Skin between scales sky blue. Head light brown, supralabials yellow, with labials 2–3 having dark posterior edges; black postocular stripe from eye across lower part of primary temporal and upper part of ultimate supralabial reaching postcephalic scales then breaking into blotches on the lateral side of ventrals; iris dark copper; tongue black. Underside of head immaculate yellowish white; ventrals immaculate yellow until ca. the 36th, then posteriorly bordered by black, mottled with brown and black spots increasing in number posteriorly, becoming almost completely black near the vent; subcaudals similar in colour and pattern, but less heavily mottled by black than the posteriormost ventral scales."

Comments.—Kok (2010b) pointed out that this species is superficially similar to *Chironius fuscus*. Some specimens that were identified as *C. fuscus* before 2010 may actually be *C. challenger*.

Chironius exoletus (Linnaeus, 1758)
Plate 30A

Type material.—The original name was *Coluber exoletus* and the holotype is ZMUU 150 or 135 as discussed by Dixon et al. (1993:92–93). Data for the type locality are not reliable.

Distribution.—"Costa Rica south through western South America to Ecuador, northern South America, the Guianas, and the Amazon basin to Peru, southern Brazil, and extreme northeastern Argentina" (Savage 2002:650).

Vouchers for Guyana.—AMNH R-6801 from Rockstone; AMNH R-14261–14262, R-15150, R-18169, and R-44907 from Kartabo; AMNH R-25048 from Kamakusa; AMNH R-36107 from Lama Creek, Demerara River; AMNH R-57791 from Wismar; and AMNH R-60823 from Onora, all identified by J. A. Wiest. Also, AMNH R-137974 from Karanambo and USNM 566256 from Konawaruk Camp.

Coloration in life.—The following is based on the AMNH and USNM vouchers from Karanambo and Konawaruk Camp (CJC field notes, 1992, 1998). Dorsum brown or greenish brown; sides same or brownish green; dark brown dorsolateral stripe may be present anteriorly, disappearing on neck and midbody; keels on scales of midbody with thin dark brown line; snout tan; top of head brown; lips and neck yellow; white or yellow under head; yellow or orangish tan belly; yellowish tan or orangish yellow under tail, perhaps with brown stripe on underside; iris brown, with tan in uppermost and lowermost parts.

Chironius fuscus (Linnaeus, 1758)
Plate 30B

Type material.—The original name was *Coluber fuscus* and the holotype is NRM 34 (http://linnaeus.nrm.se/zool/herp/madserp.html.en), without reliable locality data.

Distribution.—"Amazonian Brazil, northern Bolivia, eastern Peru and Ecuador, southeastern Colombia, southern Venezuela, Guyana, Surinam, and French Guiana" (Dixon et al. 1993:115).

Vouchers for Guyana.—AMNH R-6080 from Shudikarwau; AMNH R-18171 and R-65561 from Kartabo; AMNH R-25033, R-25047, and R-25054 from Kamakusa; and AMNH R-152260–152261 and USNM 566257 from Berbice River Camp; ROM 39442–39444 from the base of Mount Ayanganna; ROM 42601–42602 from Mount Wokomung; ROM 22845–22846 from Baramita; and USNM 549326 from E bank of the Waruma River (5°23′00″N, 060°46′00″W).

Coloration in life.—The following is based on the AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). Dorsum chestnut brown with tan bands; chin and throat white; venter toward posterior becomes tan, then grayish tan, then tannish gray; iris copper. Starace (1998:150) presented a color photograph showing a light tan vertebral stripe on the anterior part of the body that is edged with dark brown.

Chironius multiventris
Schmidt & Walker, 1943
Plate 30C

Type material.—The holotype, from the Department of Madre de Dios, Peru, is FMNH 38250.

Distribution.—The map of Klaczko et al. (2010:477) and Starace (1998) give records for Amazonian Brazil; eastern Peru, Ecuador, and Colombia; then eastward through southeastern Venezuela, Guyana, Suriname, and French Guiana.

Vouchers for Guyana.—AMNH R-8216 and R-8991 from Kalacoon; AMNH R-15151, R-18174, and R-18175 from Kartabo; AMNH R-25030 from Kamakusa; AMNH R-36137 from Georgetown; AMNH R-60849 from lower Kuyuwini River; USNM 164212 from Mabaruma Compound (8°12′00″N, 059°47′00″W); and USNM 566258 from Berbice River Camp.

Coloration.—The following is based on the USNM specimen from Berbice River Camp (CJC field notes, 1997). Dorsum dark greenish brown; ventral surfaces yellow; iris mostly brown. In describing preserved specimens, Dixon et al. (1993:163) mentioned "a pale vertebral stripe." Klaczko et al. (2010:483) stated that there are "two dark brown lines

following the keels of the paravertebral scales."

Comments.—In the past, several subspecies were recognized. Recently, however, Hollis (2006), elevated the northern one that occurs in Guyana to a full species, *Chironius cochranae*, rather than *Chironius multiventris cochranae*. Most recently, Klaczko et al. (2010) concluded that *cochranae* is a junior synonym of *Chironius multiventris*, and there is no justification for treating it as a subspecies.

Chironius scurrulus (Wagler, 1824)
Plate 30D

Type material.—The original name was *Natrix scurrula* and the lectotype is ZSM 2628/0, a male (Hoogmoed & Gruber 1983). The type locality is the Japura River, Brazil or Colombia (Franzen & Glaw 2007).

Distribution.—"Amazonian Brazil, northern Bolivia, eastern Peru and Ecuador, southeastern Colombia, Trinidad, eastern Venezuela, Guyana, Surinam and French Guiana" (Dixon et al. 1993:190, map on p. 193).

Vouchers for Guyana.—AMNH R-8360 from Kalacoon; AMNH R-14132 and R-15154 from Kartabo; AMNH R-17677 from Georgetown; AMNH R-25037 from Kamakusa; AMNH R-60752 from Shudikarwau; AMNH R-60794 from Parabam; AMNH R-152263 and USNM 566259 from Berbice River Camp; AMNH R-152265 from Konawaruk Camp; ROM 28376–28377 from Paramakatoi; USNM 84519 from Pomeroon; USNM 531697 from Iwokrama Forest Reserve, Kurupukari Base Camp; and USNM 573506 from SW part of Wokomung Massif (5°00′08″N, 059°52′47″W).

Coloration in life.—The following is based on the AMNH and USNM vouchers from Berbice River Camp and Konawaruk Camp (CJC field notes, 1997, 1998). Dorsum leaf green (with black skin between the scales); no stripe on face; venter lighter green, bluish green anteriorly; lower lips, chin, and throat pale pastel blue or turquoise, some of which extends up to the supralabials below the eye. Dixon et al. (1993:192) stated that "AMNH 104608, a subadult from Surinam, had the following description on its attached field tag: above dark green, sides brown; below light green; eye pupil gray-green." Starace (1998:157) mentioned that individuals change ontogenetically from being green juveniles to become "adults...usually uniformly dark brick-red, while the belly is of a lighter orange in colour."

Clelia clelia (Daudin, 1803a)

Type material.—The original name was *Coluber clelia* based on MNHN material (now lost; Duellman 2005) from Surinam.

Distribution.—"Atlantic lowlands of Guatemala south on the Atlantic versant throughout Central America through Colombia, northern Venezuela, Trinidad and Grenada, and south from the Guianas to central Bolivia, and on the Pacific slope from Costa Rica to northern Peru" (Savage 2002:574).

Vouchers for Guyana.—AMNH R-14257–14258 and R-137337 from Kartabo.

Coloration in life.—The following is from Starace (1998:273), based on specimens from French Guiana. "Along the dorsum adults bear a uniformly charcoal grey to black colouring. The belly is blue grey...Newborns [and young] are red [on the dorsum] with black heads from the snout up to the [anterior] edges of the parietals. The rest of the head is white but becomes black again along 3 to 5 mm of the neck...[so that young with red bodies] closely resemble *Pseudoboa neuwiedii* and *Pseudoboa coronata*." The young also resemble *Drepanoides anomalus*. Beebe (1946:23–24) described indi-

viduals from Kartabo as "white or yellowish-white or rarely salmon colored below." Duellman (1978:235), describing specimens from Ecuador, mentioned that half-grown individuals have a dorsum of "dull reddish brown to brownish black" and "the ventrals and subcaudals...are immaculate cream throughout development."

Dendrophidion dendrophis (Schlegel, 1837)

Type material.—The original name was *Herpetodryas dendrophis* and the lectotype, from Cayenne, French Guiana is MNHN 41 (Lieb 1988).

Distribution.—As illustrated by Lieb's map (1988:167), this species occurs in far eastern Venezuela, Guyana, Suriname, western French Guiana, Amazonian Brazil, Amazonian Colombia, and Ecuador and Peru east of the Andes.

Vouchers for Guyana.—AMNH R-60820 and R-60833 from Parabam; AMNH R-60832 from Kuyuwini River. Also FMNH 30958 from "*Demerara*: Itabu Creek Head, Boundary Camp" (Lieb 1988:174).

Coloration in life.—The following is from Starace (1998:160), based on specimens from French Guiana. Dorsum "grey in colour, fading to dark grey towards the tail, the body is covered with...[dark] coloured spots along the dorsum and sides. The belly is distinctly...[pale]." The following is from Duellman (1978:237), based on specimens from Ecuador. "The top of the head is olive-brown. The body has 49–55 dark brown blotches 3 scales in width, separated by narrow (½ scale in width) creamy tan interspaces on the anterior half of the body. The anterior edge of each blotch is dark brown or black[;] posteriorly the pale interspaces do not extend across the body, so the blotches are delimited only by their dark anterior borders. Laterally the interspaces are orange. The dorsal scales on the anterior part of the body have faint blue edges. The chin and throat are white, and the belly is lemon yellow. The tongue is gray."

Dipsas catesbyi (Sentzen, 1796)
Plate 30E

Type material.—The original name was *Coluber Catesbyi* based on material from America, but "present location [of type material is] unknown" (Peters 1960:56).

Distribution.—"Amazonas region of South America, from Andean slopes of Bolivia, Peru, Ecuador, and Colombia to coast of Venezuela and British Guiana, and through northern half of Brazil" (Peters 1960:56).

Vouchers for Guyana.—AMNH R-17679 from Georgetown; AMNH R-18152, R-18153, R-21283, and R-98193 from Kartabo; AMNH R-25034 and R-25036 from Kamakusa; AMNH R-152267 and USNM 566260 from Berbice River Camp; ROM 39440 from Ayanganna; ROM 42597 from Potaro River; USNM 164203 from Mabaruma Compound (8°12′00″N, 059°47′00″W); USNM 200509–200510 from 24-Mile Forest Reserve south of Bartica.

Coloration in life.—The following is based on the AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). Dorsum with alternating black and brown bands (but white ventrolaterally); belly white with black markings that increase in number posteriorly; iris brown. The following is from Duellman (1978:237), based on specimens from Ecuador. "The head is black with a white line across the snout; usually the line continues across the chin. The dorsum is marked by paired elliptical dark brown blotches, meeting or not, middorsally. The dark chocolate brown blotches are bordered with white, especially anteriorly, and stand out in marked contrast with the reddish brown ground color. The venter is white with longitudinal black marks and

flecks, especially posteriorly. The iris is reddish brown."

Dipsas copei (Günther, 1872)

Type material.—The original name was *Leptognathus Copei* and the holotype is a male, probably from Surinam, in the BMNH (Peters 1960:58).

Distribution.—"Guianas and southern Venezuela" (Peters & Orejas-Miranda 1970:86).

Vouchers for Guyana.—BMNH 1920.1.13.2 from Georgetown, cited by Peters (1960).

Coloration in life.—The following is from Starace (1998:169), based on specimens from French Guiana. "The upper [anterior] quarter of the body is bright yellow fading into light brown in the lower [posterior] regions. The dorsal regions are covered with dark brown spots, [bordered]...with a very [narrow]...white [line]... Apart from a black band [connecting]...the eyes, the head is orange in colour...The belly is light brown."

Dipsas indica Laurenti, 1768

Type material.—"Unknown" (Peters 1960:68). The type locality was restricted by Peters (1960) to the Amazon region of South America.

Distribution.—"Amazon drainage in Brazil, Colombia, British Guiana, Ecuador and Peru" (Peters & Orejas-Miranda 1970:87). Also in French Guiana and Surinam (M. S. Hoogmoed, pers. comm.).

Vouchers for Guyana.—AMNH R-60857 from Marudi (2°07′N, 59°01′W) and AMNH R-137335 from Kartabo.

Coloration in life.—The following is from Starace (1998:171), based on specimens from French Guiana. "The [light]...-brown body is patterned with darker brown irregular saddle-shaped spots. Irregular white spots are also scattered across the dorsal... [surface]...[mostly on] the sides...The belly is light-coloured."

Dipsas pakaraima
MacCulloch & Lathrop, 2004a
Plate 30F

Type material.—The holotype is ROM 41233, an adult male from the northeast plateau of Mount Ayanganna, Guyana (05°24′N, 059°57′W; 1490 m).

Distribution.—Known only from the type locality (MacCulloch & Lathrop 2004a).

Vouchers for Guyana.—In addition to the holotype, the paratypes (ROM 41234, ROM 41236, and USNM 561837) are all from the vicinity of the type locality (MacCulloch & Lathrop 2004a:240).

Coloration in life.—"Dorsolateral ground colour light brown anteriorly, darkening posteriorly. A series of 22 pairs of medium brown dorso-lateral blotches, outlined in black, between neck and vent. Anteriorly the blotches are each about five scales long middorsally, lengthening to 8–9 scales dorsolaterally, then tapering to five scales on the first dorsal scale row. Posteriorly the blotches become shorter. Anteriorly the blotches are separated by one or two lateral scales; toward midbody this separation diminishes, and the black borders of adjacent blotches are in contact. In the five posteriormost blotches the black borders are reduced laterally, present only middorsally and on the ventrals. This results in a continuous uniform medium brown lateral colouration.

"Many pairs of blotches are not exactly opposite or symmetrical but rather alternating, creating a pattern of staggered blotches along the back. This asymmetry is caused by a blotch being a different length from its corresponding opposite blotch. In the holotype the blotch pairs change from opposite to alternating to opposite twice along the length of the body...

"Within the dorsal blotches the scales appear to have dark tips, the result of overlapping the next posterior scale. However, the lighter-coloured scales outside the blotches do not appear dark-tipped where they overlap the next scale. Between the blotches the light brown background creates a middorsal pattern of diamond shapes (or half-diamond where the blotches are not symmetrical): these diamonds contain small dark brown spots. The dorsal background colour becomes progressively darker posteriorly, converging with the blotch colour.

"Ventral background colour pale brown, the dorsolateral blotches extending to the midventral point, each covering two or three ventrals. Ventrals otherwise immaculate anteriorly, posteriorly with small black patches consisting of several juxtaposed or narrowly separated squarish to half-moon shaped marks. The ventral dark markings become more intense posteriorly...

"Tail with a narrow cream middorsal stripe flanked by narrow black stripes. Background colour is dark brown laterally and ventrally, with a few small cream-and-black lateral blotches proximally.

"Head dark brown dorsally and laterally. Lower labials with a narrow white band at lip. Chin medium brown with light brown mottling increasing posteriorly" (MacCulloch & Lathrop 2004a:241–242).

Dipsas pavonina Schlegel, 1837

Type material.—Types, "apparently from Guyanes" are in the MNHN and "Musée des Pay-Bas [= RMNH]" (Peters 1960:61).

Distribution.—"Guianas to Pará, Brazil, and to Amazonian slopes of Andes; Colombia to Bolivia, on eastern slope" (Peters 1960:61).

Vouchers for Guyana.—AMNH R-18154 and R-81424 from Kartabo; UMMZ 47747 from "Dunoon, Demerara River" (cited by Harvey 2009 [2008]:449).

Coloration in life.—The following is from Starace (1998:173), based on specimens from French Guiana. "Closely resembles *Dipsas catesbyi*. The [anterior]... third of the body is an off-white colour, fading [to]...beige [or]...brown [posteriorly]... Round black spots, with white-edges ...[mid-dorsally]. The black head is marked by a white crescent-shaped spot...[anterior to] the neck. A thin white line runs [across]...the snout to the supralabials. The light brown [or white] belly is covered with very fine dark brown spots."

Dipsas variegata (Duméril, Bibron, & Duméril, 1854) Plate 31A

Type material.—The original name was *Leptognathus variegatus* based on two specimens from Surinam; one in the MNHN, one in the RMNH (Peters 1960:132).

Distribution.—"Distributed from...Venezuela...to French Guiana,...thence southward to the mouth of the Amazon River in the state of Pará, Brazil" (Cadle & Myers 2003:5).

Vouchers for Guyana.—AMNH R-21275, R-81425, and R-98194 from Kartabo (as cited in Cadle & Myers 2003:44); ROM 28371 from Paramakatoi; ROM 42596 from Wokomung; and USNM 535807 from Baramita. Harvey (2009) cited UMMZ 47757–47758 from Dunoon; UMMZ 53900 from Demerara River; and UMMZ 76990 and 77504 from Wismar.

Coloration in life.—The following is from Starace (1998:176), based on specimens from French Guiana. "Light brown body along which are [irregularly alternating]...dark brown spots. On the [anterior]...third of the body the spots tend to be saddle-shaped, [becoming irregular ventrally]...as they join the white to off-yellow

coloured belly. [Small yellow spots]...cover the entire body."

Drepanoides anomalus (Jan, 1863)

Type material.—The original name was *Cloelia anomala* and the lectotype is MNHN 4 (Cat. 100) (Duellman 2005). See Peters & Orejas-Miranda (1970) for a discussion of the uncertain type locality.

Distribution.—"Central Bolivia north to Southern Colombia along Andean front" (Peters & Orejas-Miranda 1970:93). Avila-Pires (2005:36) listed this species as widespread in the Guiana Shield and Starace (1998:267) presented a map of its occurrence in French Guiana.

Vouchers for Guyana.—AMNH R-137569 from Guyana, with no additional data, collected by W. Beebe and identified by Roy W. McDiarmid.

Coloration in life.—The following is paraphrased from Starace (1998:267–268), based on material from French Guiana. The dorsum is basically uniform red, each scale with a dark border; sides of body generally lighter than uppermost body; head black; white collar in occipital region on rear of head; belly white. These snakes resemble juveniles of *Clelia clelia* and of both species of *Pseudoboa*.

Drymarchon corais (Boie, 1827)

Type material.—The original name was *Coluber corais* based on a specimen from "America." The type is unknown to us.

Distribution.—"...southern Sonora, Mexico, and southern Texas to extreme northwestern Peru on the Pacific versant, to southern Brazil, Paraguay, and extreme northern Argentina, including most of South America east of the Andes and Isla Margarita, Trinidad and Tobago on the Atlantic slope; disjunct populations in southeastern Georgia, Florida and southern Alabama [USA]" (Savage 2002:659).

Voucher for Guyana.—AMNH R-60821 from Parabam and USNM 84523 from Pomeroon.

Coloration in life.—The following is from Beebe (1946:27), who reported seeing the species at Kartabo, but whose color notes were based on a specimen from Caripito, Venezuela. "Above blue black as far back as 600 mm. before the tail, when the dorsal ground color changes to empire yellow and then to warm orange. The black is continued in this yellow area as paired bands. After four of these pairs, the bands begin to degenerate, diminishing in width and purity, but they continue in a succession of about 30 to the tip of the tail. The rostral, nasals, internasals, loreals and all the upper labials are ivory white, with a flecking of black on the loreals and [some]...labials. This white color continues on the chin, throat and ventrals, each of the latter with an invasion of black from each side, never meeting in the middle. The subcaudals are yellow orange like the upper side. The iris is dragon's blood red with a gold pupil ring." The photo in Starace (1998:181) shows the posterior body and tail and the side of the face as being basically bright yellow.

Comments.—Although Beebe (1946) mentioned seeing this species at Kartabo, and it is expected to occur there, the Beebe material at the AMNH does not include any specimens from this locality. Consequently, we have not listed this species in Table 1.

Drymobius rhombifer (Günther, 1860)

Type material.—The original name was *Coryphodon rhombifer* based on a specimen (unknown to us) from Esmeraldas, Ecuador.

Distribution.—"...Nicaragua south through Central America, Colombia, Venezuela, and the Guianas and over much of the upper Amazon basin to southern Peru and northern Bolivia on the Atlantic

versant and from central Costa Rica to western Ecuador on the pacific slope" (Savage 2002:663).

Vouchers for Guyana.—AMNH R-60783 from Kuyuwini Landing and AMNH R-60811 from Onora.

Coloration in life.—The following is from Starace (1998:185), based on specimens from French Guiana. "Colour varies from light brown to green with a series of distinct [dark brown] diamond shaped [markings]...with black edging distributed along the dorsum. The belly is off-yellow with black lateral markings."

Drymoluber dichrous (Peters, 1863b)
Plate 31B

Type material.—The original name was *Herpetodryas dichrous* and the syntypes, one from Brazil, one from Surinam, are ZMB 1661–2 (Bauer et al. 1995).

Distribution.—Widespread in the Guiana shield region (Avila-Pires 2005). Also "Colombia, Ecuador, eastern Peru, northern Brazil, Amazonian Venezuela" (Peters & Orejas-Miranda 1970:100).

Vouchers for Guyana.—AMNH R-18160 from Kartabo; USNM 549327 from East bank of Waruma River (05°20′00″N, 060°46′00″W; 550 m); and USNM 566261 from Berbice River Camp.

Coloration in life.—The following is based on the adult USNM specimen from Berbice River Camp (CJC field notes, 1997). Greenish black above (but head black); green laterally on neck; dark blackish green ventrolaterally on body; lips, chin, and anterior throat white; other ventral surfaces lemon yellow; iris mostly deep chestnut brown; anteriorly on dorsum very inconspicuous traces of dark brown bands; skin between scales gray. Starace (1998) points out that the young, being basically brown with numerous gray to tan bands, are very different in color from the adults.

Elapomorphus quinquelineatus
(Raddi, 1820)

Type material.—The original name was *Coluber 5-lineatus* based on two specimens from near Rio de Janeiro, Brazil. According to Lema (1984:58), Hoge (1958) stated that MNHN 3673 is one of the types.

Distribution.—"Eastern and central Brazil" (Peters & Orejas-Miranda 1970:105), and possibly the Guianas (see Voucher, below).

Voucher for Guyana.—USNM 6180 from "Guiana" (no additional data).

Coloration.—The following is based on a preserved specimen (AMNH R-131801) from Brazil. Dorsum light tan with five darker tan to brown stripes (one being vertebral); top of head brown; white patch on snout; supralabials tan; neck with wide tan collar, the two halves not quite meeting at nape of neck; venter tan anteriorly, unmarked, becoming lighter posteriorly, yellow beneath tail (which is very short).

Comments.—USNM 6180 is the only specimen reported as being from the Guianas. It was received by the NMNH in 1863 as part of an exchange with the "Paris Museum," so it is possible that the specimen was found in French Guiana. However, Starace (1998) does not include this species among the snakes known from French Guiana. Considering the uncertainties, the presence of this species in Guyana needs to be confirmed.

Erythrolamprus aesculapii (Linnaeus, 1758)
Plate 31C

Type material.—The original name was *Coluber Aesculapii* and the two types are NRM 95 and 84 (http://linnaeus.nrm.se/zool/herp/madserp.html.en). There are no reliable locality data for the types.

Distribution.—Peters & Orejas-Miranda (1970:111) stated that this inhabits "Ama-

zonian South America to central Brazil and Bolivia." It also has been described as occurring "from Trinidad southward to Argentina and Bolivia" (Murphy 1997:173).

Vouchers for Guyana.—AMNH R-98185 from near Kartabo; AMNH R-137333 from Kartabo; AMNH R-140941 and USNM 566262 from Dubulay Ranch; ROM 20504 from Kurupukari; USNM 55960 from Demerara (=Georgetown); and USNM 84528 from Pomeroon.

Coloration in life.—The following is based on the AMNH and USNM vouchers from Dubulay Ranch (CJC field notes, 1994). Body encircled with black, red, and white rings; white rings very narrow, bordered on both sides by black; snout tan; chin yellowish tan; throat orange; sixth infralabial each side white. On some individuals, the "white" bands are actually gray above, cream below, and the sixth infralabial is not so distinctive, although the lips are white, cream, or pale yellow. Starace (1998) presented several color photographs of specimens from French Guiana that showed a wide range of color and pattern variation.

Comments.—USNM 566262 (see Vouchers, above) was consuming an *Oxyrhopus melanogenys* (AMNH R-140898) when captured. The anterior 9 cm of the prey was yet to be swallowed.

Helicops angulatus (Linnaeus, 1758)
Plate 31D

Type material.—The original name was *Coluber angulatus* and Duellman (2005) stated that NRM 17 is a syntype. The same specimen is cited on the following web site: http://linnaeus.nrm.se/zool/herp/madserp.html.en. There are no reliable locality data associated with this.

Distribution.—"Venezuela and Colombia throughout South America to Bolivia; Trinidad, Ecuador and Peru" (Peters & Orejas-Miranda 1970:123).

Vouchers for Guyana.—AMNH R-8359 from Kalacoon; AMNH R-18150, R-36132, and R-36144 from Georgetown; AMNH R-65556 from Kartabo; MCZ R-24939 from Mahaica Creek; MCZ R-33360–33361 from Georgetown; USNM 85077–85084 from Pomeroon; USNM 145458 from 80 km above Georgetown on the Abary River; USNM 164205 from Mabaruma Compound (08°12′00″N, 059°47′00″W); USNM 531698–531699 from Iwokrama Forest Reserve, Three Mile Camp; and USNM 566263 from Berbice River Camp.

Coloration in life.—The following is based on the USNM specimen from Berbice River Camp (CJC field notes, 1997). Dorsum grayish tan (but yellow ventrolaterally), with dark brown bands; head greenish brown; chin white; venter yellow, becoming paler posteriorly; dirty cream beneath tail; body bands black on ventral surface. Starace (1998) reported that some specimens from French Guiana have a bright red belly.

Hydrodynastes bicinctus (Hermann, 1804)

Type material.—The original name was *Coluber bicinctus* and the holotype and type locality are unknown to us.

Distribution.—"Guianas, Amazon region of Brazil, Colombia and Venezuela" (Peters & Orejas-Miranda 1970:127).

Voucher for Guyana.—AMNH R-60798 from Onora Falls.

Coloration in life.—On individuals from French Guiana, "the body varies from light brown to yellow with 12 to 17 brown-black complete, but irregular rings. The head is yellow-beige [on the sides] with a longitudinal black band behind each eye" (Starace 1998:201). Starace's photograph (1998:200) shows dark brown as the predominant color on top of the head.

Hydrops triangularis (Wagler, 1824)

Type material.—The original name was *Elaps triangularis* and holotype originally was in the "Musee royal de Munic." The type locality, in the vicinity of "Ega," is presently Tefé, at (03°21′S, 64°42′W), on the inner mouth of the canal...that connects the lake of Tefé with the Solimões" (Vanzolini 1981:xxvi).

Distribution.—"From Venezuela, Guianas and Trinidad to eastern Peru and northern Bolivia" (Peters & Orejas-Miranda 1970:129).

Vouchers for Guyana.—AMNH R-25035, R-25053, and R-25056 from Kamakusa; and AMNH R-98196, R-14134–14141, and R-67874 from Kartabo.

Coloration in life.—Beebe (1946:28) described a specimen from Kartabo as follows. "Below, the ground color is pure white, with two series of dark brown blotches close together, sometimes opposite, sometimes alternate. These narrow suddenly and extend upward as scale-width vertical bands, not quite meeting on the mid-back. The back is red brown, while between each of the lateral, vertical lines is a conspicuous spot of bright coral red, suffusing from three to five scales over two rows.

"The head has four irregular cross bands of black, with inter-spaces, counting from the snout backward, of pale brown, dark brown, dark red and bright red. The succeeding nuchal band of black almost meets above, and is the broadest on the whole snake...the iris reddish. The general impression of the lateral pattern is of successive layers of red-brown, bright red and white, cut by numerous vertical black bands."

Comments.—Albuquerque & Lema (2008) examined a large number of specimens from widespread localities and concluded that the extensive variability of these snakes provides no justification for recognizing subspecies, although six had been described in the past.

Imantodes cenchoa (Linnaeus, 1758)
Plate 31E

Type material.—The original name was *Coluber Cenchoa* based on material from America and the type locality is unknown to us.

Distribution.—"...from southern Tamaulipas (Atlantic) and Oaxaca (Pacific), Mexico, south through Central America (exclusive of Pacific slope El Salvador, Honduras, and northwestern Costa Rica) to central Ecuador (Pacific) and Bolivia, Paraguay, and northeast Argentina (Atlantic)" (Savage 2002:608). The species also occurs on Trinidad and Tobago (Murphy 1997:177).

Vouchers for Guyana.—AMNH R-67875 and R-81432 from Kartabo; AMNH R-152271 from Konawaruk Camp; ROM 20502 from Kurupukari; ROM 42600 from Mount Wokomung; and USNM 566264 from Berbice River Camp.

Coloration in life.—The following is based on the AMNH and USNM specimens from Berbice River Camp and Konawaruk Camp (CJC field notes, 1997, 1998). Rusty tan with brown bands or spots; chin and throat white with tan flecks; venter light tan with brown flecks; iris copper. Beebe (1946:29) noted for a specimen from Kartabo that the iris is "golden, with irregular indistinct fleckings and streaks of orange and golden brown. Two narrow lines of light yellow along both sides of the pupil, and a small patch of dark brown at top and bottom."

Imantodes lentiferus (Cope, 1894)

Type material.—The original name was *Himantodes lentiferus* and the holotype is ANSP 11459 (Duellman 2005) from Pebas, Peru (Peters & Orejas-Miranda 1970).

Distribution.—"Amazonas, Brazil, Amazonian Colombia, Ecuador and Peru" (Peters & Orejas-Miranda 1970:135). The

species is also known from the Guianas (Starace 1998).

Vouchers for Guyana.—USNM 535808 from Baramita.

Coloration in life.—Starace (1998:284), based on specimens from French Guiana, noted that "the pattern closely resembles that of *Imantodes cenchoa* but is lighter (light beige to yellow)." Duellman (2005: 374) noted that on specimens from Peru there is "a Y-shaped mark on the top of the head, with the arms of the Y disjunct from the base on the suture of the parietals."

Comments.—The USNM specimen from Baramita (see Vouchers, above) was found at night on a branch 1.5 m above ground in primary forest.

Leptodeira annulata (Linnaeus, 1758)
Plate 31F

Type material.—The original name was *Coluber annulatus* and the holotype is "number 9 in the Zoologicka Institutionen Uppsala" (Duellman 1958:47). The type locality was restricted to the lower Rio Amazon, Pará, Brazil (Duellman 1958).

Distribution.—"The range of *Leptodeira annulata* extends from southern Tamaulipas and Guerrero southward at low and moderate elevations along both coasts of Mexico, excluding the wet forests of southern Veracruz and the Yucatan Peninsula, through the central plateaus and along the Pacific coast of Central America to Panama, thence through the interior valleys of Darien to northern Colombia, Venezuela, and the Guianas, including Isla de Margarita, Tobago, and Trinidad, and throughout the Amazon Basin, southward into the Chaco of Paraguay and northern Argentina, and along the Atlantic coast of Brazil southward to Sao Paulo" (Duellman 1958:28).

Vouchers for Guyana.—AMNH R-18155–18157 and R-67879–67880 from Kartabo; AMNH R-60784–60787 from Isheartun; AMNH R-137981–137984 and USNM 566265–566266 from Karanambo; AMNH R-140902–140904 and R-141893 from Dubulay Ranch; USNM 531700 from Iwokrama Forest Reserve, Burro Burro River; and USNM 566267 from Ceiba Biological Station, Madewini River, ca. 5 km E (linear) Timehri Airport (06°29′57″N, 058°13′06″W).

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo and Dubulay Ranch (CJC field notes, 1992, 1994, 1995). Dorsum light brown with darker brown blotches, but vertebral area tan; ventral surfaces white anteriorly, becoming tan posteriorly, with grayish brown speckling beneath tail.

Comments.—Duellman (1958) considered most specimens from Guyana as being intergrades between *L. a. annulata* and *L. a. ashmeadi*.

Leptophis ahaetulla (Linnaeus, 1758)
Plate 32A

Type material.—The original name was *Coluber Ahaetulla* and syntypes are NRM "37, 40, 41?" (Duellman 2005), from America.

Distribution.—"Lowlands and premontane areas from central Veracruz and Oaxaca, Mexico, on the Atlantic slope through Central and South America to northern Argentina; on the Pacific versant from Costa Rica to southwestern Ecuador" (Savage 2002:670).

Vouchers for Guyana.—AMNH R-21281 from Kartabo; AMNH R-60792 from Karanambo; AMNH R-140899 from Dubulay Ranch; USNM 84518 and USNM 85087 from Pomeroon; USNM 141762 from 50 miles above Georgetown on the Abary River; USNM 164218 from Kumaka (=Takama); USNM 535809–535810 from Baramita; and USNM 566268 from Konawaruk Camp.

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch and Konawaruk Camp (CJC field notes, 1994, 1998). Head green above, with black stripe through eye; lips cream; neck largely green, the color becoming dorsolateral stripes separated by yellowish tan vertebral area; green stripes becoming turquoise ca. midbody, green again posteriorly; lateral stripe gold anteriorly, yellowish tan posteriorly; tail mostly tan; chin cream; rest of venter tan, becoming more-so gradually posteriorly; iris yellow. Beebe (1946) and Starace (1998) stated that anteriorly the ventral surface is white.

Comments.—The specimen from Konawaruk Camp (see Vouchers, above) was found while it was consuming a tree frog, *Dendropsophus minutus* (AMNH A-166210).

Liophis breviceps Cope, 1860a
Plate 32B

Type material.—The holotype, from Surinam, is ANSP 3697 (Malnate 1971).

Distribution.—"Eastern flanks of the Andes of Ecuador and Perú, eastward to Obidos, Brasil; on the north from central Colombia and northern Guyana south to Río Mamoré (Trinidad) Bolivia, and Posto Diuarum Brasil" (Dixon 1989:9).

Vouchers for Guyana.—AMNH R-18159 and R-98203 from Kartabo; AMNH R-25052 from Kamakusa; AMNH R-140969–140970 and USNM 566269 from Dubulay Ranch; AMNH R-152273 from Konawaruk Camp; and BMNH 1976.1154 from Takama Village, Berbice River. See Dixon (1983a) for many additional specimens.

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch and Konawaruk Camp (CJC field notes, 1994, 1998). Dark brown to black above, with subtle tan or gray bands (not across belly) that fade and disappear past midbody (bands may be nearly white laterally or on neck, may persist posteriorly after dorsal part is obscure); chin cream, grayish white, or tan with dark gray to black spots; rest of venter (through anal plate) checkered with large squares of orange and black (often irregular pattern; banded in places); mostly mottled black and white beneath tail, where few pale orange spots may persist. Beebe (1946) and Starace (1998) referred to the colorful ventral areas as being red rather than orange.

Liophis cobella (Linnaeus, 1758)

Type material.—The original name was *Coluber Cobella* based on material from America. Dixon (1983a) discussed the confusion involved with the Linnaean specimens of this species.

Distribution.—"...from the eastern flanks of the Andes from near Villavicencio, Colombia, southward to Buenavista, Bolivia; from Caripito, Venezuela, southeastward to Bahia, Brasil" (Dixon 1983a:155, on p. 158 Dixon mapped the species in Trinidad also).

Vouchers for Guyana.—AMNH R-14263, R-18158, R-21336, and R-98204 from Kartabo; AMNH R-36135–36136, R-36142–36143, and MCZ R-33355–33359 from Georgetown; ROM 28372 from Paramakatoi; and USNM 145455 from 50 miles above Georgetown on the Abary River; and USNM 164198 from Mabaruma Compound (8°12′00″N, 059°47′00″W). See Dixon (1983a) for many additional specimens.

Coloration in life.—The following is from Starace (1998:215), based on specimens from French Guiana. "Body varies from dark grey to olive-green, speckled with small black marks and fine yellow-beige spots. The belly is off-white to yellow along which irregular dark markings form a chequered pattern." Beebe (1946:35) described specimens from Kartabo as

being brown or black above "with narrow white dorsal bands, scarlet below with broad bands of black; head and tail below whitish, the latter with imperfect black bands."

Comments.—Sometimes this species is referred to as *Liophis cobellus*, but Darrel Frost confirmed (pers. comm.) that our current spelling of the specific epithet, consistent with the original name and with some recent usage (e.g., Gorzula & Señaris 1999), is reasonable.

Liophis lineatus (Linnaeus, 1758)

Type material.—The original name was *Coluber lineatus* and the type material is unknown to us. The type locality information is not reliable.

Distribution.—"Central Panama eastward through Colombia, Venezuela, Guyana, Suriname, French Guiana, to the mouth of the Amazon River in Brazil" (Michaud & Dixon 1987:3).

Vouchers for Guyana.—AMNH R-14265 and R-98206 from Kartabo; AMNH R-2664 and R-137647 from Georgetown; AMNH R-60789 from Parabam; and AMNH R-60837–60838 from Isheartun.

Coloration in life.—The following is from Starace (1998:225), based on specimens from French Guiana. Light "brown to grey body with three characteristic dark brown lines running along the length of the dorsum. The two lateral lines are more distinct on the upper part [meaning anterior] of the body."

Liophis miliaris (Linnaeus, 1758)

Type material.—The original name was *Coluber miliaris* and the holotype is "N.R. [Naturhistoriska Riksmuseum, Stockholm, Sweden] No. 56" (Gans 1964:39). Dixon (1983b) restricted the type locality to Surinam.

Distribution.—"Eastern South America, from Guyana south to Buenos Aires, Argentina, with scattered records in the Amazon Basin and Cerrado of Brasil" (Dixon 1989:17).

Vouchers for Guyana.—AMNH R-8098 from Kalacoon; ROM 20502 from Kurupukari; and ROM 20505 from Tukeit. See Dixon (1983b) for additional specimens.

Coloration in life.—The following is from Starace (1998:217), based on specimens from French Guiana. "The body is bottle-green to black, splashed with faint yellow spots. The head is dark and reveals a small number of off-white fine spots. The belly is bright yellow."

Liophis poecilogyrus (Wied, 1824)

Type material.—The original name was *Coluber poecilogyrus* and there are two female syntypes, AMNH R-3593–3594 (Dixon & Markezich 1992), from Barra de Joucoú, assez près de la rivière Espirito santo [Brazil].

Distribution.—Eastern Venezuela eastward through the Guianas, south through the Amazon Basin to Bolivia, Argentina, and Uruguay (Dixon & Markezich 1992).

Vouchers for Guyana.—AMNH R-60803 from Kuyuwini, identified by J. R. Dixon; USNM 146376 from Lethem; and USNM 497805 from Karanambo.

Coloration in life.—Dixon & Markezich (1992:153–154) described extensive variation in coloration of this species, but without specifying whether the notes were based on specimens in life. Many specimens from the northern part of the range had a gray dorsum with or without dark brown or black markings. The ground color of the sides of the body was similar to that of the middorsal region or lighter. Middorsal scales were with or without white edges. Mottling of the venter was poorly defined.

Liophis reginae (Linnaeus, 1758)
Plate 32C

Type material.—The original name was *Coluber Reginae*. Dixon (1983c) discussed issues involved with designation of a lectotype at the Museum Regis Adolphi Friderici and he restricted the type locality to Suriname.

Distribution.—"Cis-Andean South America, from Colombia to northern Argentina; also Trinidad and Tobago" (Dixon 1989:21).

Vouchers for Guyana.—AMNH R-8095 from Kalacoon; AMNH R-17680 from Georgetown; AMNH R-18170, R-67876, and R-137348 from Kartabo; ROM 39441 from Mt. Ayanganna; USNM 164207–164210 from Mabaruma Compound (8°12′00″N, 059°47′00″W); USNM 549328–549329 from N slope of Mt. Roraima (5°17′00″N, 60°45′00″W); USNM 561439 from Washikura River (8°15′00″N, 059°44′00″W); and USNM 573507 from Wokomung Massif (5°00′08″N, 059°52′47″W).

Coloration in life.—The following is from Starace (1998:219), based on specimens from French Guiana. "The body varies from brown to olive green and is spotted with yellow scales. A dark brown line passes over the supralabials. Just behind the eyes run two light green triangular patterns, the apex pointing towards the neck. The belly is yellow with sundry [more-or-less rectangular] black markings."

Liophis typhlus (Linnaeus, 1758)
Plate 32D

Type material.—The original name was *Coluber Typhlus* and the syntypes are in the "Royal Museum, Stockholm" (Dixon 1987:173). There are no reliable locality data for them.

Distribution.—"Rainforests of the Guiana Shield and Amazon Basin, also the Chaco and Cerrado of Bolivia, Brasil, and Paraguay" (Dixon 1989:23).

Vouchers for Guyana.—AMNH R-21335 and R-98197–98198 from Kartabo; AMNH R-36106 from Lama Creek, Demerara River; ROM 20506 from Tukeit; ROM 22838 from Baramita; ROM 28375 from Paramakatoi; USNM 291151 from along trail from Kato to Paramakatoi; and USNM 566270 from Dubulay Ranch.

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1995). Body green above; subtle black markings visible at times on sides; lips greenish yellow; chin and throat yellow, then venter gradually becoming pale orange, then yellow again beneath tail. Starace (1998) stated that the dorsal color may be green, brown, or gray-blue, and there may be orange or blue speckling, especially on the neck.

Mastigodryas boddaerti (Sentzen, 1796)
Plate 32E

Type material.—The original name was *Coluber Boddaerti*. Location of the type specimen is unknown. Stuart (1941) and Merrem (1820) suggested that Surinam was the type locality.

Distribution.—"Tropical south America, from Colombia and Venezuela to Bolivia and western Brazil" (Peters & Orejas-Miranda 1970:192).

Vouchers for Guyana.—AMNH R-8092 from Georgetown; AMNH R-44920, R-14252, and R-18166–18167 from Kartabo; AMNH R-60791 from Karanambo; AMNH R-60840 from Isheartun; AMNH R-60852 from Kuyuwini River; AMNH R-152277 and USNM 566271 from Berbice River Camp; ROM 22840–22841 from Baramita, the last two identified by H. Zaher; and USNM 164199, 164206, and 164211 from Mabaruma Compound (8°12′00″N, 059°47′00″W).

Coloration in life.—The following is based on the AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). This species has ontogenetic

change in coloration. The juveniles from Berbice River Camp (see Vouchers, above) were described in life as follows. Dorsum brown with grayish tan bands; white spots ventrolaterally on ends of tan bands anteriorly on body; chin and throat white with dark brown irregular spots; venter tan. A larger individual from Berbice River Camp was described as follows. Nearly uniform brown dorsally, with traces of bands anteriorly; a lateral light tan stripe on anterior half of body; venter light gray with darker gray smudges on throat.

Ninia hudsoni Parker, 1940

Type material.—The holotype is BMNH 1946.1.15.38, a male from the New River, Guyana, within an area that is in dispute with Suriname.

Distribution.—"British Guiana; Amazonian Ecuador" (Peters & Orejas-Miranda 1970:222). Duellman (1978) described a specimen from Amazonian Ecuador and later (Duellman 2005:145) reported one from Amazonian Peru.

Vouchers for Guyana.—The holotype and the paratype (BMNH 1946.1.15.20), both from the type locality, are the only specimens known from Guyana.

Coloration in life.—The following is from Duellman (1978:250) based on a specimen from Ecuador. The individual "has a dark gray dorsum with a pale gray nape band and a creamy white venter." The following is from Parker (1940:270), but might be based on the preserved specimens. "Very dark purple-brown above, with a white nuchal collar...; lower surfaces white except the posterior half of the tail, which is brown-dusted."

Oxybelis aeneus (Wagler, 1824)

Type material.—The original name was *Dryinus aeneus* and the lectotype is ZSM 2645/0, female (Franzen & Glaw 2007:250). The type locality is the area of Ega, now known as Tefé, and "the locality (03°21′S, 64°42′W) is on the inner mouth of the canal..., a few kilometers long, that connects the lake of Tefé with the Solimões" (Vanzolini 1981:xxvi).

Distribution.—"Lowland and premontane zones from Arizona and Coahuila, Mexico, south to northern Peru on the Pacific versant and Bolivia east of the Andes; also on the islands of Trinidad and Tobago" (Savage 2002:677). The species also extends on the eastern part of the range to southeastern Brazil (Gorzula & Señaris 1999 [1998]).

Vouchers for Guyana.—AMNH R-8170 from Kalacoon; AMNH R-14260, R-18179–18180, R-98207–98209, and R-137326–137329 from Kartabo; AMNH R-60758–60766 and R-60770–60776 from Isheartun; AMNH R-60815 from Kuyuwini Landing; AMNH R-60839 from Wichabai; AMNH R-148587 from Iwokrama, Muri Scrub Camp; ROM 28374 from Paramakatoi; USNM 497820 from Pirara Ranch, ca. 25 mi N of Lethem (3°36′42″N, 059°40′30″W); and USNM 531701 from Iwokrama Forest Reserve, Three Mile Camp (4°37′59″N, 058°42′52″W).

Coloration in life.—Beebe (1946:36) described AMNH R-18179 from Kartabo, in life, as follows. "Top of head sepia. An indefinite streak along side of head which deepens to a narrow band of black just above the upper labials, and continues across the iris in two areas of dark green. The second to fifth upper labials with narrow shading of black along upper edge. A streak of pale vinaceous buff extends across the top of the preocular, tinging the lower portion of the supra ocular and continuing in a horizontal line a little back of eye, where it deepens to umber. Upper labials pale yellow, shading downward to bluish-white. Throat bluish-white with faint tinge of pink. Body above light ashy, ventral surface dark vinaceous brown. A

narrow rim of picric yellow extends around the lower four-fifths of the pupil, widening toward the top and shading to silver white, which extends over all the upper part of the iris. Large irregular patches of parrot green lie on either side of pupil flecked with black. The lower part of iris is silvery white flecked with maize yellow." Starace (1998:292) added that "the body is covered with very fine dark coloured patterns [markings]."

Oxybelis fulgidus (Daudin, 1803a)
Plate 32F

Type material.—The original name was *Coluber fulgidus* and the type material is unknown to us. The type locality was restricted to Chichen Itzá, Yucatán, Mexico by Smith & Taylor (1950a).

Distribution.—"Lowlands and adjacent slopes on the Pacific versant from the Isthmus of Tehuantepec to eastern Panama and on the Atlantic versant in southern Veracruz, Mexico, and then south from the Yucatán Peninsula through Central America and throughout South America, east of the Andes to northern Bolivia and extreme northeastern Argentina" (Savage 2002:679).

Vouchers for Guyana.—AMNH R-14259, R-16049, R-65553–65554, and R-137325 from Kartabo; AMNH R-25049 from Kamakusa; AMNH R-60847 from Isheartun; JC 8039 (AMNH field number) from Konawaruk Camp (given to UG); ROM 20501 from Kurupukari; USNM 84527 from McKenzie (=Linden); and USNM 566272 from Berbice River Camp.

Coloration in life.—The following is based on UG and USNM specimens from Berbice River Camp and Konawaruk Camp (CJC field notes, 1997, 1998). Leaf green above, with greenish yellow to white ventrolateral stripe; lips, chin, throat, and belly chartreuse; iris copper, black, tan on one specimen, brown, gold, and pale copper on another. Beebe (1946:37) noted on living individuals from Kartabo that when spreading the scales apart anteriorly on the body, one sees broad bands of orange and pale yellow on the skin between the scales.

Oxyrhopus melanogenys (Tschudi, 1845)
Plate 33A, B

Type material.—The original name was *Sphenocephalus melanogenys* and the holotype is "MHNN 14 (Cat. 99)" (Duellman 2005:379). The type locality is the Chanchamayo region, Peru (Peters & Orejas-Miranda 1970:232).

Distribution.—All records that we have seen for this species are from the Guianas and Amazon Basin.

Vouchers for Guyana.—AMNH R-8094 from Kalacoon; AMNH R-98211 from Kartabo; AMNH R-140898 from Dubulay Ranch; AMNH R-152279–152280 and USNM 566273 from Berbice River Camp; IRSNB 17912 and 17940–17941 from Kaieteur National Park; and ROM 39439 from Mt. Ayanganna. Additional details and localities are listed by MacCulloch et al. (2009:495).

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch and Berbice River Camp (CJC field notes, 1994, 1997). One specimen had the dorsum with alternating black (broadest), white (narrowest), and red bands; usually two white bands within a black one (triad pattern); red bands with black dots; bands not crossing belly; venter white (but gray on chin and throat), with gray marks beneath tail; top of head black; iris orange. Colors on two other individuals were similar, but with differences in the pattern. Anteriorly, these appeared to be predominantly black snakes with narrow white bands, but the middle of the broad black areas had a red triangle ventrolaterally, and those posteriorly on the body extended upward to become red bands with black spots. On the posterior belly there

were red and black mixed with the light coloration. Another specimen was noted as being similar to the last two, but with a conspicuous red band on the neck; without a triad pattern; and with the mix of red and black on the venter only on the posterior 25% of the body but more conspicuous beneath the tail. MacCulloch et al. (2009:491) gave more details and pointed out that older adults may be melanistic.

Comments.—When found on the forest floor at 1530 h, AMNH R-140898 (see Vouchers, above) was being consumed by another snake, an *Erythrolamprus aesculapii* (AMNH R-140942), tail first, with about 9 cm protruding from its mouth. In the recent past (see Zaher & Caramaschi 1992), Guyanan specimens of this species were misidentified as *Oxyrhopus trigeminus*, a species not known to occur in Guyana (MacCulloch et al. 2009).

Oxyrhopus occipitalis (Wagler, 1824)
Plate 33C

Type material.—The original name was *Natrix occipitalis* and the lectotype is ZSM 2053/0, a male (Franzen & Glaw 2007: 256), from the banks of the Solimöens River, Brazil.

Distribution.—This species occurs in Amazonas and Amapá, Brazil, Amazonas and Bolivar, Venezuela, Surinam, French Guiana, and Guyana (MacCulloch et al. 2009:490).

Vouchers for Guyana.—AMNH R-36102 from Lama Creek, Demerara River; IRSNB 17913 and ROM 42995 from Kaieteur National Park; and SMNS 12111 from Mabura Hill (5°09′N, 58°42′W).

Coloration in life.—"Dorsal ground colour red or reddish orange; snout and supralabials yellow; top of head medium to dark brown. A white anterior body band (sometimes obscure), 3–4 dorsal scales in width, approximately 2 cm behind the head. Faint, pale orange body bands with very narrow dark borders; width of pale orange bands equal to the length of 2–4 dorsal scales. Bands are usually symmetrical, but in one specimen there is a half-band, on one side only, between otherwise symmetrical bands...Underside of head yellowish orange. Venter white...Underside of tail banded orange and white, corresponding to dorsal pale orange bands and red ground respectively...Bands are prominent in juveniles but [usually] become inconspicuous in adults" (MacCulloch et al. 2009:489). Starace (1998:302) stated that "a dark band covering the [anterior]...half of the parietals crosses over the eyes."

Comments.—Formerly, snakes of this coloration and pattern were considered to be color pattern variants of a different species, *Oxyrhopus formosus*, which is a valid species also but not known from Guyana (Hoge et al. 1973, Jorge da Silva 1993, MacCulloch et al. 2009).

Oxyrhopus petolarius (Linnaeus, 1758)
Plate 33D

Type material.—The original name was *Coluber Petolarius*. The type material is unknown to us and the type locality lacks reliable data. Savage (2011; see Comments below) discussed why this specific epithet is preferred over *O. petola*, which was used previously.

Distribution.—"Tropical lowlands from Veracruz, Mexico, on the Atlantic versant and Costa Rica on the Pacific slope through Central America to western Ecuador and throughout northern South America and the Amazon basin to Brazil, Peru, and Bolivia" (Savage 2002:576).

Vouchers for Guyana.—AMNH R-18164 from Maripa; AMNH R-36099 and R-36524 from Lama Creek; AMNH 36140 from Georgetown; AMNH R-98210 from Kartabo; ROM 22843 (presently CSBD HR 89 at UG) and USNM 535811 from Baramita; USNM 164204

from Mabaruma Compound (8°12′00″N, 059°47′00″W); and USNM 566274 from Dubulay Ranch.

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1994). Dorsum with alternating bands (but not across belly) of black and red, the latter with black dots; top of head black; ventral surfaces white (gray near tip of tail). Beebe (1946:38) described living specimens from Kartabo as having the light bands anteriorly on the body white, transitioning through pink to red posteriorly. Additional details were presented by MacCulloch et al. (2009:493).

Comments.—Savage (2011) explained his conclusion that the appropriate name is *Oxyrhopus petolarius* for snakes that previously were called *O. petola*. The confusion stems from the fact that Linnaeus (1758) named and described both on the same page as if they were different species. Subsequent authors synonymized the two using one or the other name, and which name applies today hinges on who was determined to be the first reviser.

Philodryas olfersii (Lichtenstein, 1823)
Plate 33E

Type material.—The original name was *Coluber Olfersii* and the type specimen, from Brazil, is unknown to us.

Distribution.—"Western Brazil and eastern Peru through Bolivia and Paraguay to Uruguay and Argentina" (Peters & Orejas-Miranda 1970:244); also known from the Guianas (e.g., Starace 1998).

Vouchers for Guyana.—USNM 566275 from Aishalton; and AMNH R-140939–140940 from Dubulay Ranch.

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton and Dubulay Ranch (CJC field notes, 1993, 1994). Dark leaf green above; pale yellowish green below; fine (very thin) black line below eye, from midway between nostril and eye to temporal area, along upper sutures of supralabials.

Philodryas viridissimus (Linnaeus, 1758)

Type material.—The original name was *Coluber viridissimus* based on material from Surinam, but the type(s) are unknown to us.

Distribution.—"Amazonas and Paraguay valleys, from southern Venezuela and Guianas to Argentina" (Peters & Orejas-Miranda 1970:245).

Vouchers for Guyana.—AMNH R-60846 from Marudi; AMNH R-61540 from Matali; AMNH R-98212 from Kartabo; and USNM 84525 and 85088 from McKenzie (=Linden).

Coloration in life.—Beebe (1946:38) described one of two specimens from Kartabo as follows. "General body color lettuce green above, shading laterally to greenish-yellow on ventral scales. Top of head parrot green, two black spots on scales in front of eye and three behind, forming a broken facial band. Upper labials emerald green, shading posteriorly to light yellow green. Lower labials, chin and throat pale greenish-gray touched with pale cinnamon pink. Scales back of gape, along lateral neck and forming anterior border of the first fifty ventrals...a most delicate blue. This color occurs sporadically on other ventral scales and on all the caudal ventrals [= subcaudals]...Iris a tangled mesh of dark cinnamon brown with a sparse but conspicuous flecking of gold dots across the upper portion."

Phimophis guianensis (Troschel, 1848)
Plate 34A

Type material.—The original name was *Heterodon guianensis* based on a specimen

from the immediate vicinity of Pirara, Guyana. Location of the type is unknown to us.

Distribution.—"Cocle Province, Panama, to Surinam, in savannah and scrub areas" (Peters & Orejas-Miranda 1970: 246); also known from French Guiana (Starace 1998).

Vouchers for Guyana.—AMNH R-140943 from Ceiba Biological Station, Madewini River, ca. 5 km (linear) east of Timehri Airport (06°29′57″N, 058°13′ 06″W); and AMNH R-140944–140946, R-141896, and USNM 497806 and 566276–566277 from Dubulay Ranch.

Coloration in life.—The following is based on the AMNH and USNM specimens from Ceiba Biological Station and Dubulay Ranch (CJC field notes, 1994, 1995). Pale yellowish tan above (light orange in a juvenile) with dark brown to black speckling, sometimes extensive; snout often tan, but most of head brown; dark brown to black band on back of head to neck (but not across ventral aspect); venter translucent pinkish white or cream, becoming cream posteriorly, pale yellow out on tail. A juvenile had the black band on the back of the head and neck preceded by a contrasting white band.

Pseudoboa coronata Schneider, 1801
Plate 34B

Type material.—The type specimen was in the "Musei Heyeri" and no locality data were given.

Distribution.—"Guianas, Amazonian watershed in Brazil, Colombia, Ecuador, Peru and Bolivia" (Peters & Orejas-Miranda 1970:253).

Vouchers for Guyana.—AMNH R-152283 and USNM 566278 from Berbice River Camp; USNM 56167–56168 from "Guyane" (=Guyana, with no additional locality data).

Coloration in life.—Appearance of this species is similar to that of *Pseudoboa neuwiedii* (see below), and in the field the vouchers (see above) from Berbice River Camp were misidentified as such and no particular color differences were noted. However, color photographs were taken, and the following is based on them. Dorsum brownish red; top and sides of head black; conspicuous white collar on posterior head and neck, followed on neck by broad black area, soon fading on anterior body; venter light. Beebe (1946:39) described a specimen from Kartabo as having the light band around the neck "yellowish-white" and having "ventrals yellowish-white, tail grayish. Iris dark," but no voucher specimen from Kartabo occurs at the AMNH. Starace (1998:323) stated that not all individuals have the "white-yellow" collar on the neck and that "the belly is off-white."

Pseudoboa neuwiedii
(Duméril, Bibron, & Duméril, 1854)
Plate 34C, D

Type material.—The original name was *Scytale Neuwiedii* based on several specimens. The types are unknown to us, but the type locality was restricted to Cumaná, Venezuela (see Peters & Orejas-Miranda 1970:254).

Distribution.—"Pacific Panama from just west of Canal Zone through northern and interior Colombia to Surinam; south to Brazil, along Amazon River; Trinidad and Tobago Islands" (Peters & Orejas-Miranda 1970:254).

Vouchers for Guyana.—AMNH R-139737 from Aishalton; and AMNH R-140900–140901, R-141897, and USNM 566279 from Dubulay Ranch.

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994, 1995). In young individuals, top of head black; pale yellow band on neck and back of head, present or not,

followed by a black band on neck; rest of dorsum orangish red; ventral surfaces translucent white, but tail very pale orangish red below, perhaps distally. Adults are brown above, greenish yellow below.

Pseudoeryx plicatilis (Linnaeus, 1758)

Type material.—The original name was *Coluber plicatilis* and the holotype, from Ternataeis, is NRM 57 (Duellman 2005:382).

Distribution.—Colombia and Guianas to Bolivia, Paraguay and northern Argentina (Peters & Orejas-Miranda 1970:255).

Vouchers for Guyana.—ROM 5270 from "Guyana" (no additional data); and USNM 85075–85076 from Pomeroon.

Coloration in life.—The following is from Starace (1998:234), based on specimens from French Guiana. "The dorsum is [dark]...brown along which run two dark [yellow] longitudinal lines from the head along the sides...The belly is beige spotted with fine black marks on the sides." Starace's photo (p. 233) also shows a broad black stripe on the side of the head (also mentioned on his p. 234), which continues as a broad black stripe on the side of the body.

Pseustes poecilonotus (Günther, 1858b)
Plate 34E

Type material.—The original name was *Spilotes poecilonotus* and the holotype, from Honduras, is BMNH 1946.1.7.39 (Colin McCarthy, pers. comm.).

Distribution.—"Lowlands and premontane slopes of the Atlantic versant from San Luis Potosí, Mexico to Amazonian Peru, Bolivia, and Brazil; also on the Pacific versant in Oaxaca, Mexico, central and southern Costa Rica, Panama, and western Colombia and Ecuador" (Savage 2002:680).

Vouchers for Guyana.—AMNH R-21337 from Kartabo; AMNH R-60848 from the upper Rupununi River (collected by R. Snedigar); AMNH R-152285, AMNH field number JC 8057 (now at UG), and USNM 566280 from Konawaruk Camp; AMNH R-152286 from about 40 km (linear) southeast of Linden on Arakabusa Creek; USNM 85086 from Pomeroon; USNM 300656 from Bartica; and USNM 326121 from Kwakwani (5°30′00″N, 058°00′00″W).

Coloration in life.—The following is based on the AMNH, UG, and USNM vouchers (see above) from Konawaruk Camp (CJC field notes, 1998). On young snakes, dorsal ground color gray or tannish gray; vertebral area light tan; crossbands brown (gray or tannish gray within); venter mostly gray or grayish tan, anteriorly with cream showing through extensive gray flecking; lips mostly cream; cream lines on snout, nostril to lip; iris tan or pale copper. A larger adult from Arakabusa Creek, provided by Alexander Mendes (AMNH 152286; see Vouchers), was noted in the same field notes as follows: brownish green above; lips, chin, throat, and anterior venter orangish yellow; posterior venter greenish brown; iris brown.

Beebe (1946:39) reported seeing no fewer than 24 individuals at Kartabo. Adults were "monochrome above and below in two phases, one a deep olive green with lemon yellow lower head, chin and throat, and the other a rich red brown with yellowish-orange anterior lower parts. In the young...the variation is still more extreme, the basic colors being red brown, or gray or olive above, banded with darker shades of the ground color, with face and throat black-marked white or green-marked yellow. The iris is...mottled silvery, with dark pigmented areas fore and aft, which are crossed with about three, distinct, white, vein-like lines, radiating from a narrow area on the anterior and posterior equator of the

pupil, extending out to the external rim of the iris."

Pseustes sulphureus (Wagler, 1824)

Type material.—The original name was *Natrix sulphureus* and the lectotype is ZSM 1681/0, a male (Franzen & Glaw 2007:257). The type locality was along the Japura River, Brazil. According to Vanzolini (1981:xxvi), "Martius followed the Japurá from its mouth (03°08′S, 64°66′W), to the falls of Araracuara (00°24′S, 72°17′W), then in disputed territory, now in Colombia."

Distribution.—"Peru; Ecuador; Brazil; Guianas; Trinidad" (Peters & Orejas-Miranda 1970:259).

Vouchers for Guyana.—AMNH R-8349 from Kalacoon; AMNH R-60817 from Kuyuwini River; AMNH R-137349 from Kartabo, the last identified by R. W. McDiarmid; and UMMZ 53928 from Dunoon, Demerara River.

Coloration in life.—Beebe (1946:41) described specimens from Kartabo as follows. "While the dorsal coloring may be monochrome, olive, brown or yellow, this is not an adult pattern but may occur in an individual only one-third grown. The usual pattern shows a series of conspicuous dorsal cross markings, crescents or bands, single or double, or even more intricate figures. The general tendency is a gradual change from yellow background with black markings on the head and anterior body, to black with corresponding yellow markings posteriorly…The iris has a remarkably consistent pattern, the background brown-black, with a fine mist of paler brown lines radiating outward from the bright silver pupil ring to the outermost borders of the visible eyeball. It thus differs radically from the iris of the congeneric species." Starace (1998:243) stated that the belly is yellow anteriorly, black posteriorly, and his photos (on his pp. 240–241) show distinct black bars on the upper lips.

Rhinobothryum lentiginosum
(Scopoli, 1788)
Plate 34F

Type material.—The original name was *Coluber lentiginosus*. The holotype and type locality are not known to us.

Distribution.—"Basins of Ríos Amazon and Paraguay in tropical South America" (Peters & Orejas-Miranda 1970:269).

Vouchers for Guyana.—USNM 535812 from Baramita.

Coloration in life.—The following is based on Starace's (1998) description of specimens from French Guiana, and one (AMNH 119433) collected and photographed by CJC and CRT in Suriname, in 1980. The dorsum is a series of colorful rings of black (broadest), white (narrowest) and red (containing black spots). There is a narrow white ring on the neck, after which the sequence of rings is as follows, repeated along the body: black, white, red, white, etc. The venter is dark, except in areas of light rings. "The red [or light-colored] edging of each cephalic scale is a characteristic feature of this species" (Starace 1998:328), which otherwise basically has a dark head.

Comments.—In the past, two neotropical species were recognized in *Rhinobothryum*, the second of which was *R. bovallii*, which today is recognized as a junior synonym of *R. lentiginosum*. Consequently, the genus is monotypic.

Sibon nebulatus (Linnaeus, 1758)

Type material.—The original name was *Coluber nebulatus*. According to Peters (1960:199), the type is "one specimen in the Museum Regis Adolphi Friderici, Stockholm." The website of Museum Adolphi Friderici lists NRM numbers 60, 64, and 65 for this species at http://linnaeus.nrm.se/zool/herp/madserp.html.en. The type locality is America.

Distribution.—"Northern South America...lowland Central America to Michoacán...and Veracruz, Mexico, including Yucatán Peninsula" (Peters 1960:199).

Vouchers for Guyana.—AMNH R-36092 from Lama Creek, Demerara River; AMNH R-137340 from Kartabo (this one identified by R. W. McDiarmid); UMMZ 56463 from "Maruca River St Rosa" (quoted from UMMZ records); ROM 28373 from Paramakatoi; USNM 84524 from McKenzie (=Linden); and USNM 164202 from Mabaruma Compound (8°12′00″N, 059°47′00″W).

Coloration in life.—The following is from Starace (1998:179), based on specimens from French Guiana. "Closely resembles *Dipsas variegata*. The body colour varies from grey to brown and is covered with dark brown irregular bands, ring-like. Each band is edged by fine, irregular, beige spots. [Top of head brown with darker brown markings.] The belly ranges from white to beige, speckled with dark brown miniscule points [; darker under tail]."

Comments.—Often the spelling of the specific epithet for this species is *nebulata*, but recent authors (Harvey 2009, Zaher et al. 2009) have used *nebulatus* consistent with Linnaeus.

Siphlophis cervinus (Laurenti, 1768)

Type material.—The original name was *Coronella cervina* based on material (unknown to us) from America.

Distribution.—"Central Bolivia and Maranhão [northward] to the Canal Zone and Trinidad" (Peters & Orejas-Miranda 1970:281).

Vouchers for Guyana.—UMMZ 53967 from "Dunoon, Demerara River" (quoted from the UMMZ records).

Coloration in life.—The following is adapted from the description and photograph in Starace (1998:331), based on specimens from French Guiana. Body dark gray with numerous narrow yellow bands; irregular row of red scales along back, often extending onto sides; head scales dark with light borders; belly light with dark spots.

Siphlophis compressus (Daudin, 1803a)
Plate 35A

Type material.—The original name was *Coluber compressus* based on material (not known to us) from Surinam.

Distribution.—"Discontinuous. Coastal strip of Brazil from Rio de Janeiro (city) to Sergipe. Mouth of Amazon and central Bolivia to Trinidad and Panama" (Peters & Orejas-Miranda 1970:311).

Vouchers for Guyana.—AMNH R-18151 from Kartabo; AMNH R-25057 from Kamakusa; AMNH field number JC 7894 from Konawaruk Camp (given to UG); USNM 531702 from Iwokrama Forest Reserve (4°20′15″N, 058°49′37″W); USNM 535813 from Baramita; and USNM 566283 from Dubulay Ranch.

Coloration in life.—The following is based on the UG and USNM specimens from Dubulay Ranch and Konawaruk Camp (CJC field notes, 1994, 1998). Dusty pinkish red above, with black bands and spots; head orange; neck black; chin area white with orangish tinge on lips; rest of venter cream, with pink tinge posteriorly, but gray distally beneath tail; iris red.

Comments.—Until recently this species was considered to represent the genus *Tripanurgos*, which was monotypic (Zaher & Prudente 1999).

Spilotes pullatus (Linnaeus, 1758)

Type material.—The original name was *Coluber pullatas* and the holotype is listed as "NRM cat no 30" on the website of Museum Adolphi Friderici at http://linnaeus.nrm.se/zool/herp/madserp.html.

en. There are no reliable data for the type locality.

Distribution.—"Atlantic lowlands and premontane slopes from Tamaulipas, Mexico, south through Central America and northern South America to Bolivia, Paraguay, and extreme northeastern Argentina; on the Pacific versant from the Isthmus of Tehuantepec to western Ecuador" (Savage 2002:687).

Vouchers for Guyana.—AMNH R-60804 from Parabam; AMNH R-60824 from Wichabai; USNM 84522 from McKenzie (=Linden); USNM 145460 from 50 miles above Georgetown on the Abary River; USNM 164214 from Mabaruma Compound (8°12′00″N, 059°47′00″W); and USNM 291152 found on trail from Kato to Paramakatoi.

Coloration in life.—The following is from Starace (1998:250), based on specimens from French Guiana. "The body is shiny black, decorated with irregular yellow bands issuing from the belly which is also yellow. [Labials yellow and black.] The tail is often black...[without] the yellow markings." Some individuals are melanistic.

Tantilla melanocephala (Linnaeus, 1758)
Plate 35B

Type material.—The original name was *Coluber melanocephalus* based on material from America, and the types are listed as "NRM cat no 15 and 86" on the website of Museum Adolphi Friderici at http://linnaeus.nrm.se/zool/herp/madserp.html.en.

Distribution.—"Low to high elevations along both versants from Guatemala throughout Central America into South America as far south as southern Peru, Bolivia, northern Argentina, and Uruguay; also on the islands of Trinidad and Tobago" (Wilson 1999:11). However, Savage (2002:693) indicated that the Central American records noted by Wilson are actually based on two other species, *Tantilla armillata* and *Tantilla ruficeps*.

Vouchers for Guyana.—AMNH R-15147 and R-98216–98217 from Kartabo; AMNH R-139739 from Aishalton; AMNH R-140950–140951 from Dubulay Ranch; ROM 22839 from Baramita; USNM 164197 from Mabaruma Compound (8°12′00″N, 059°47′00″W); and USNM 566281 from Berbice River Camp.

Coloration in life.—The following is based on AMNH and USNM specimens from Aishalton, Dubulay Ranch, and Berbice River Camp (CJC field notes, 1992, 1994, 1997). Dorsum reddish brown; lower sides orangish brown; head and neck black, with tan spot on snout and tan parietal spots; white markings on face (side of head); chin white; white or cream beneath throat and neck; rest of ventral surfaces pale yellow. Starace (1998:334) added that there are "three to five black longitudinal lines running down the body of which the median is the most strongly marked."

Thamnodynastes pallidus (Linnaeus, 1758)

Type material.—The original name was *Coluber pallidus* and the neotype is ZMUU 292, an adult male (Bailey et al. 2005). The type locality is unknown (Bailey et al. 2005).

Distribution.—"The range of *T. pallidus* seems to be the Amazon and upper Orinoco watersheds from central Bolivia to eastern Colombia and Southern Venezuela and the Guianas, and to eastern Pará, Brazil" (Bailey et al. 2005:89).

Vouchers for Guyana.—AMNH R-2665 and R-36134 from Georgetown. Additional specimens from Guyana were listed by Bailey et al. (2005:101).

Coloration.—Based in part on the two preserved AMNH vouchers from Georgetown listed above, Bailey et al. (2005:88–89) stated the following: "chin and throat unmarked except for a few tiny dark dots...; on anterior ventrals a fine streak

on either side becomes a double (hollow) streak at about heart level; before midbody this has become a pair of double streaks which continue about to the cloaca where it becomes once more a double streak on each side of the tail venter...; in AMNH 36134 the double streak never becomes paired doubles; a variable amount of accessory pigment develops including another pair of double streaks medially in the most extreme specimens...; some general sprinkling of fine dots is sparse in AMNH 36134 to rather profuse in AMNH 101960; head pale, tan to brown on top, lighter elsewhere or with scattered dark dots; a double (dark-edged, pale-centered) dark streak extending from margins of the postoculars at rear center of eye through corner of mouth...disappearing on side of neck; this postocular bar slender...; [in some specimens] a similar anterior bar from center of orbit to top of nasal; also...[in some specimens] a single or double streak from top of eye across outer edge of parietals outlines the darker crown and joins a dark paravertebral line bordering a light nuchal stripe on the nape;...the five series of dark dorsal-spots are lost at about midbody and the lateralmost row becomes transformed, along with a double stripe on rows 1–2, into a series of lateral streaks resembling the ventral ones; the paravertebral spots become reduced to dark dots on every two or three scales of the 6th rows; the vertebral series is completely lost."

The following is from Gorzula & Señaris (1999:180) based on a living specimen from Venezuela. "Ventral surfaces lemon yellow in the anterior ¼, grading to pink in the posterior ¾; ventrals bordered laterally on each side with a double brown line, single anteriorly; hidden skin between the dorsals bright yellow; dark brown dorso-lateral line along dorsal scales 3 and lower 4; upper dorsal 4 and 5 and 6 are lighter; distinct post ocular stripe."

The following is from Starace (1998:337) based on living specimens from French Guiana. "Colouring ranges from yellow to light brown orange with two darker, ill-defined longitudinal bands running down the body. The scales are [speckled]...with copious fine black marks. Around the eyes are light brown markings which [extend posteriorly]...along the body. The belly is light yellow."

Comments.—Bailey et al. (2005) placed *Thamnodynastes strigilis* into the synonymy of *T. pallidus*, which was reported to be semi-aquatic (Starace 1998) and sympatric with *Thamnodynastes ramonriveroi* in Georgetown (Bailey & Thomas 2007). Comparative studies of sympatric populations of these two species may be worthwhile.

Thamnodynastes ramonriveroi
Manzanilla & Sánchez, 2005
Plate 35C

Type material.—The holotype is EBRG 3957, an adult male from Cerro La Laguna (10°01′27″N, 64°07′47″O [=W]) macizo del Turimiquire, municipio Freites, Anzoátegui, Venezuela, 2130 m (Manzanilla & Sánchez 2005).

Distribution.—This species occurs in northern and eastern Venezuela, Trinidad, Guyana, Suriname, and northern Brazil (Bailey & Thomas 2007).

Vouchers for Guyana.—"No [specific] locality: (AMNH 36117–20); Demerara (BMNH 1967.2201–03)" (Bailey & Thomas 2007 [2006]:26); USNM 566282 from Dubulay Ranch.

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1994). Tan above with small black spots and dorsolateral brown stripe; a darker tan stripe low on side; head tan with brown markings; venter yellow with brown stripes and spots, the lateralmost stripe of which becomes gray posteriorly.

Comments.—This species was reported to be semi-aquatic and sympatric with *Thamnodynastes pallidus* in Georgetown

(Bailey & Thomas 2007); comparative studies of sympatric populations may be worthwhile.

Xenodon merremii (Wagler, 1824)

Type material.—The original name was *Ophis merremii*, the type material disappeared (Hoogmoed & Gruber 1983), and the type locality is Bahia, Brazil, which is now the city of Salvador (13°00′S, 38°30′W) (Vanzolini 1981).

Distribution.—"Guianas, Brazil, Bolivia, Paraguay, central and northern Argentina" (Peters & Orejas-Miranda 1970:324).

Vouchers for Guyana.—AMNH R-8103 from Kalacoon.

Coloration in life.—The following is from Starace (1998:253) based on specimens from French Guiana. "The body colouring is light brown to beige with irregular dark brown markings [usually a pattern of alternating dark and light brown bands, with lighter borders]. The belly is light coloured."

Comments.—Until recently (Zaher et al. 2009), this species was treated as a representative of a different genus, *Waglerophis*.

Xenodon rabdocephalus (Wied, 1824)

Type material.—The original name was *Coluber rabdocephalus* based on material from Bahia, Brazil (see Peters & Orejas-Miranda 1970:324). The type material is unknown to us.

Distribution.—"Lowlands of tropical Mexico from Veracruz and Guerrero, south through Central America to northwestern Ecuador, west of the Andes, Amazonian Colombia, and Ecuador, the Guianas and the upper Amazon portion of Brazil, Peru, and Bolivia…" (Savage 2002:583).

Vouchers for Guyana.—AMNH R-18173, R-21338, and R-98219–98221 from Kartabo.

Coloration in life.—The following is from Starace (1998:257) based on specimens from French Guiana. "The body…is usually brown to grey along which are distributed fine, dark, complete cross-patterns…Closely resembles *Bothrops atrox*. The belly is light coloured." The following is from Savage (2002:582) based on specimens from Costa Rica. "Dorsum brown, usually with a series of 11 to 16 hourglass-shaped blotches [which may be broken up]; each blotch dark brown laterally and grayish brown medially, outlined by a pale brown border with some white areas;…head brown above, usually with a dark-outlined light lyre-shaped figure originating at the internasals with a branch running posteriorly above the eye and downward to the angle of jaw;…supralabials light brown, edged with dark; throat cream with very little dark pigment, which is usually restricted to scale margins; venter cream to beige with much light brown stippling and often with light brown irregular blotches as well; underside of tail cream, with little or no dark scale margins, contrasting sharply with venter; iris gray brown."

Comments.—It is likely that the specimens from Kartabo that Beebe (1946) described under the name *Xenodon colubrinus* were actually this species.

Xenodon severus (Linnaeus, 1758)

Type material.—The original name was *Coluber severus* the holotype is NRM 48 (http://linnaeus.nrm.se/zool/herp/madserp.html.en). The type locality was restricted to South America (see Duellman 2005).

Distribution.—"Amazonian South America" (Peters & Orejas-Miranda 1970:325).

Vouchers for Guyana.—AMNH R-8161 from Kalacoon; AMNH R-21284, R-98222–98223, and R-137332 from Kartabo; BMNH 1930.10.10.184-1930.10.10.185 and 1930.10.10.187 from Morabelli Creek, Essequibo River; BMNH 1934.11.1.29 from "Camaria, R. Cuyani" (Colin McCarthy, pers. comm., 20 October 2008);

BMNH 1971.1858 from Kamarang, Mazaruni District; ROM 22842 from Baramita; UMMZ 47743–47745 from Dunoon, Demerara River; UMMZ 55860 from Santa Rosa Island, Moruca River; UMMZ 65161 from Kartabo; UMMZ 77507 from Wismar; UMMZ 77820 from Malalli, Demerara River; UMMZ 83644–83645 from Kurupung Up, Mazaruni District; UMMZ 85284 from junction of Kamarang and Parvima Rivers, Parvima Mission; UMMZ 85285 from Kurupung River, Mackreba Falls; USNM 84521 from Pomeroon; and USNM 164200–164201 and USNM 164213 from Mabaruma Compound (8°12′00″N, 059°47′00″W).

Coloration in life.—Beebe (1946:44) summarized variation in specimens from Kartabo as follows. "The variety of pattern and coloring is almost indescribable. The adult snake tends to be monochrome, green, brown, black or rufous, and yellowish or gray below. But dorsal bands or spots may persist in large specimens, black-edged scales or more definite bands. The young usually have a complex angular pattern of bands and hourglass figures. One fairly consistent mark is a large central nuchal patch of pink, red, orange or rufous, surrounded by one or more concentric bands of the same color. This becomes very conspicuous when the snake flattens its neck, cobra-like," which other species of this genus do as well.

Xenopholis scalaris (Wucherer, 1861)

Type material.—The original name was *Elapomorphus scalaris* based on two specimens from Cañavieras, Matta de S. João, Bahia, Brazil. One is in the BMNH and location of the other is unknown to us.

Distribution.—"Amazonian Bolivia, Peru, Ecuador, and Brazil" (Peters & Orejas-Miranda 1970:326). More recently known from the Guianas (e.g., Starace 1998).

Vouchers for Guyana.—AMNH R-60799 from Shudikar-wau.

Coloration in life.—The following is adapted from Starace (1998:265) based on specimens from French Guiana. Body brick-red to light brown with a dark brown to black middorsal line; dark brown triangular markings extend laterally from the middorsal line; belly pale yellow.

Xenoxybelis argenteus (Daudin, 1803a)

Type material.—The original name was *Coluber argenteus* and the type locality and location of the type specimen are unknown to us.

Distribution.—"Lowlands of northern South America east of Andes" (Peters & Orejas-Miranda 1970:227).

Vouchers for Guyana.—AMNH R-60768 from Isheartun; AMNH R-60779 from Marudi; and AMNH R-60800 from Kuyuwini Landing.

Coloration in life.—The following is based on an individual collected by CJC and CRT in Suriname (AMNH R-133353; CJC field notes, 1986). Dorsum tan, but dark greenish tan on posterior half of tail; green lateral stripe from tip of snout, through eye, along body to fade on posterior half of tail; lighter green vertebral stripe on body, gradually fading past neck, terminating abruptly on base of tail; chin, throat, and ventral neck bright chartreuse with black spots; venter yellowish green posterior to neck, changing to cream with a midventral green stripe and lateral green stripe on each side; underside of tail cream, becoming yellowish, then chartreuse, with a green lateral stripe on each side; iris gold, peppered with copper but with a dark brown bar aligned with the lateral green body stripe; interior of mouth flesh pink; tongue yellow above, grayish tan with black flecks below.

Comments.—Previously, this species was assigned to two other genera, *Oxybelis* and *Philodryas* (see introduction to Colubridae,

above). Often when disturbed, an individual holds the tongue sticking straight forward from the mouth, motionless.

Elapidae

The families of snakes are discussed above in the introduction to the snakes. The Elapidae are usually quite colorful, mostly brightly ringed (black, yellow/white, red), highly venomous snakes, with relatively short fangs in a set or fixed position near the front of the upper jaw. The venoms of these and other venomous snakes are used and continue to have strong potential for pharmacological research, both for treatment of snakebite and development of new medicines.

In the recent past, some specialists (e.g., Campbell & Lamar 2004) put most species of South American coral snakes in the genus *Micrurus* and a few other species in another genus, *Leptomicrurus*, one species of which occurs in Guyana ("*L. collaris*"). However, Slowinski (1995:335) presented a phylogenetic analysis that suggested that *Leptomicrurus* clustered within *Micrurus*, so he concluded as follows: "the best course at present is to return *Leptomicrurus* to the synonymy of *Micrurus*." We follow Slowinski and recognize only one genus of coral snakes in the Guyanan herpetofauna, including the species *Micrurus collaris*.

Not all colorfully ringed snakes that superficially look similar to coral snakes are venomous, as several non-venomous species of Colubridae sensu lato have evolved color patterns that mimic those of coral snakes. Also, not every individual of venomous coral snake is colorfully ringed.

Micrurus averyi Schmidt, 1939

Type material.—The holotype is FMNH 30956, an adult female from the Courantyne District of Guyana, near the Brazilian border (1°40′N, 58°W). "The type locality may be further defined as the Boundary Commission's 'Boundary Camp' at about 2000 ft above sea level, at head of Itabu Creek. This creek enters the New River, an affluent of the Courantyne, at New River Depot" (Schmidt 1939:46).

Distribution.—"Known from the type locality in southern Guyana, southern Surinam, and the region around Manaus, Amazonas, Brazil" (Campbell & Lamar 2004:150).

Vouchers for Guyana.—The holotype is the only specimen known from Guyana.

Coloration in life.—The following is from Campbell & Lamar (2004:150). "This snake has rings of black, white, and intense red. The pattern does not consist of triads. The head is almost entirely black (sometimes with faint red markings on the snout) with a short white marking that partially covers the last 2–4 supralabials and the temporals, and borders the parietals. This pale marking may be red in some specimens; occasionally it may be interrupted by black. The black head coloration is present after the pale head ring but does not constitute a nuchal ring, an arrangement unique for the genus. Black is the predominant color on the venter of the head... There are 8–13 black body rings, 2 dorsal scales in length, on the body. These are bordered by very short white rings that are interrupted so frequently as to form series of spots. There are 4–7 black tail rings. The long red body rings (12–28 ventrals in length) are very intense in color and usually lack all traces of black stippling. On the tail the red rings are heavily melanic and shorter than the black rings; the yellow or white rings usually remain sharply demarcated but may be obscured."

Micrurus collaris (Schlegel, 1837)

Type material.—The original name was *Elaps collaris* and the lectotype is RMNH

1444 (Brongersma 1966). The type locality was restricted to the Guianas by Hoge & Romano (1966).

Distribution.—"Southeastern Venezuela through Guyana and Suriname to French Guiana and undoubtedly northern Brazil in the Guianan region" (Campbell & Lamar 2004:128).

Vouchers for Guyana.—Campbell & Lamar (2004:128) stated that the holotype for the subspecies *M. c. breviventris* is "FMNH 26658...[from] Oko Mountains, Essequibo, Guyana, 400 ms."

Coloration in life.—The following is from Campbell & Lamar (2004:129). "The head and dorsum are black or very dark brown. Usually there is a white, yellow, or red ring around the neck, passing just distal to the parietals or occasionally touching them; sometimes this ring is narrowly interrupted dorsally, with the black pigment of the head being continuous with that of the body.The [underside of the] body has a distinctive pattern of 35–50 oval whitish or yellowish blotches on a black or dark brown venter. These blotches are 2–4 ventrals in length and usually extend laterally to the first or second dorsal scale row but are not known to meet middorsally. The ventral blotches on the tail are usually reddish and often form 2–3 rings on the proximal portion of the tail."

Micrurus hemprichii (Jan, 1858)

Type material.—The original name was *Elaps Hemprichii* and the holotype was destroyed during World War II (Campbell & Lamar 2004). The type locality was restricted to Venezuela by Hoge & Lancini (1962).

Distribution.—"The Amazonian slopes of the Andes in Colombia, Ecuador, Peru, and Bolivia; the upper Amazon Basin, Guiana highlands, and upper Orinoco region from Vichada in eastern Colombia through southern Venezuela eastward, including Guyana, Suriname, and French Guiana, as well as all of Brazil north of the Amazon River in Amazonas, and probably Roraima and Amapá (it has not been recorded from the latter two regions)...and undoubtedly has a wider distribution in the Amazon Basin than has been recorded" (Campbell & Lamar 2004:218).

Vouchers for Guyana.—ROM 22836 from Baramita; UMMZ 80423 from Kermuri Creek, Demerara River; and UMMZ 82867 from Bartica.

Coloration in life.—The following is from Campbell & Lamar (2004:218–219). "The snout and top of head to the posterior edge of the parietals, the mental, and first pair of infralabials are black. This is followed by an orange occipital ring that covers the postoculars, temporals, last 2–3 labials, first few dorsals, and gular region, and occasionally encroaches on the parietals themselves. The ring is followed by 5–10 triads on the body and ⅔–2 on the tail. The first triad on the body is incomplete, and the primary and accessory black rings are subequal. These triads are composed of long black rings (4–10 dorsals...), of which the accessory rings are as long as or longer than the primary black rings; the black rings are separated by relatively short (2–5 dorsals) orange (sometimes brownish orange) rings. The triads contain short (1–3 dorsals) white rings. The orange scales are outlined faintly in black, as are the white scales of many specimens. An orange ring traverses the cloacal region, and it is sometimes interrupted by a black blotch. Occasionally an orange ring is melanized, resulting in the coalescing of two triads into a quincad."

Micrurus isozonus (Cope, 1860b)

Type material.—The original name was *Elaps isozonus* and the cotypes are ANSP 6804–6805 (Campbell & Lamar 2004). The type locality was restricted to Caracas, Venezuela (see Campbell & Lamar 2004).

Distribution.—"Semi-arid and seasonally dry regions in Colombia from east of the Andes throughout the Llanos Orientales eastward, the Llanos of central and southeastern Venezuela, humid forests of the Cordillera de la Costa in northern and central Venezuela, Isla Margarita and the Rio Cotinga region in Roraima, Brazil... [and] Guyana" (Kok et al. 2003:77).

Vouchers for Guyana.—IRSNB 16573 and 16575 from "*Region 9*, Dadanawa Ranch (N 02°49′30″W, 59°31′34″), South Rupununi Savannahs" (Kok et al. 2003:78).

Coloration in life.—The following is from Kok et al. (2003:73–74). "The two Guyanese specimens are similar...Both have 10+1 black triads on body and tail (10 triads on the body and one on the tail). The 10th body 'triad' of IRSNB 16573 is composed of 4 black bands. The first triad is complete and the pale yellow bands (white in preservative) are equal to or a little longer than the black bands. The black bands are 3–4 (generally 3) dorsal scales long; the yellow bands are 3–4 (generally 4) dorsals long, and the red bands are 2–6 (generally 5 or 6) dorsals. Red and yellow bands have black apical tips. The snout is predominantly black, spotted with white, followed by an irregular white band and an interorbital black band. The latter is followed by a red frontal band and a red parietal band."

Micrurus lemniscatus (Linnaeus, 1758)
Plate 35D

Type material.—The original name was *Coluber lemniscatus* and the lectotype is NRM 93 (Roze 1989; http://linnaeus.nrm.se/zool/herp/madserp.html.en). Roze (1967) stated: "The high number of black triads combined with ventral and subcaudal counts and the general coloration of the Linnaean syntypes conform to the populations of the northern Guianas. The restriction of the type locality to Belém, Pará, Brazil, by Schmidt & Walker (1943) does not correspond to the known distribution of *M. l. lemniscatus* and, therefore, should be considered invalid."

Distribution.—"The Amazonian slopes of the Andes in Bolivia, Peru, Ecuador; the Amazonian and Orinocoan watersheds of Colombia, southern and eastern Venezuela; Trinidad; Guyana; Suriname, and French Guiana; and the entire Amazon Basin south to the Brazilian states of Paraná, Mato Grosso do Sul and Minas Gerais..." (Campbell & Lamar 2004:223).

Vouchers for Guyana.—AMNH R-14142–14150 from Kartabo; ROM 11702 from "*Rupununi*: Ruawau River" (MacCulloch & Lathrop 2004b:143); ROM 22834–22835 from Baramita; USNM 145461 from "Georgetown, 50 mi above, on the Abary River;" USNM 164215 from Mabaruma Compound (8°12′00″N, 059°47′00″W); and USNM 566289 from Karanambo.

Coloration in life.—The following is based on the USNM specimen from Karanambo (CJC field notes, 1992). Body pattern consists of triads of solid black separated by narrow bands of cream (with black flecks); triads separated from each other by bands of red (with black flecks); tip of tail black; tip of snout black; cream band between nostrils and eye (but not around lower jaw—dorsally only); black band at eyes (dorsally only); red parietal band (completely around and forward below head so almost whole lower jaw and chin area is red, with a couple of black spots).

Comments.—ROM 11702 (see above) originally had been identified as an example of *Micrurus ibiboboca* but was recently re-identified (see MacCulloch & Lathrop 2004b).

Micrurus psyches (Daudin, 1803b)

Type material.—The original name was *Vipera psyches* and the holotype, from Surinam, is MNHN 7654 (Campbell & Lamar 2004).

Distribution.—"Northern South America from eastern Venezuela through northern Guyana to Suriname, French Guiana, and Brazil in the state of Amapá" (Campbell & Lamar 2004:189).

Vouchers for Guyana.—AMNH R-21333, R-110160–110162, and R-137321, all from Kartabo; ROM 28378 from Paramakatoi.

Coloration in life.—Campbell & Lamar (2004:189) stated that "this is a tricolored coralsnake with black rings arranged singly. There are 22–41 black body rings that are 3–4 dorsal and ventral scales long. The white or yellowish rings are 1 dorsal long or less; these rings are also sometimes obliterated on the dorsum owing to melanization, but they are evident across the venter. Red (melanic) body rings are usually about 3–7 dorsals and ventrals long, and are generally slightly longer than the primary black body rings. The red rings are so heavily melanized that they appear uniformly black and specimens appear to be bicolored. In some cases the red rings are only partially melanized and the rings are blackish red or purplish. Red rings are in evidence on the belly even in dark snakes on which the dorsal parts of the red rings have been totally obfuscated [by black]. The tail is patterned with black and white rings or with black, red, and white rings...The head is black, including all supracephalic scales; this black head cap usually coalesces with the black nuchal ring...The side of the head including the temporals and last 1–2 supralabials is white with considerable black markings. The white occipital ring is usually interrupted behind the parietals owing to the fusion of the black head coloration with the nuchal ring...All white scales [on the head] are tinged and edged with black. The chin is mostly black, including the infralabials and chinshields."

Comments.—A closely related species, *Micrurus circinalis*, previously treated as a subspecies of *M. psyches*, occurs in Venezuela and Trinidad (Campbell & Lamar 2004). Donnelly et al. (2005:457) reported that both *M. circinalis* and *M. psyches* were found at Iwokrama, but they did not cite specific specimens and our requests to examine vouchers were not answered (see Species Reported...Probably in Error, below).

Micrurus surinamensis (Cuvier, 1817)
Plate 35E

Type material.—The original name was *Elaps Surinamensis* and MNHN 3926 was designated as the lectotype by Schmidt (1952). The type locality is Surinam (see Campbell & Lamar 2004:230).

Distribution.—"The Orinocoan and Amazonian drainages of Colombia; Amazonian drainages of Ecuador, Peru, and Bolivia; the entire Amazon Basin of Brazil from northern Mato Grosso and Maranhão northward including Rondônia, Acre, Amazonas, Roraima, Pará, and Amapá; Guyana, Suriname, and French Guiana; and southern Venezuela" (Campbell & Lamar 2004:230–231).

Vouchers for Guyana.—AMNH R-152304–152305 and USNM 497807 from Berbice River Camp; and CJC and CRT saw a specimen (not collected) at Dubulay Ranch.

Coloration in life.—The following is based on the AMNH and USNM specimens from Berbice River Camp (CJC field notes, 1997). This species is distinctive in that the head is red but with the cephalic scales being edged with black. The pattern on the body is of triads of black. Red, black, and pale yellow bands completely encircle the body, the pale yellow ones being white on the belly and the red ones having black spots dorsally; tail tip black.

Comments.—This species is one of the longest and stoutest of all the coral snakes (Campbell & Lamar 2004:231).

Leptotyphlopidae

Leptotyphlopids have been recognized as a distinct family of snakes for well over 100 yr, based on morphology. Recent phylogenetic analyses of DNA sequence data indicate that these snakes have existed for perhaps 130 million yr (before the breakup of Gondwanaland, although the group has experienced over-water dispersal also), and that their closest living relatives may be the superficially similar Typhlopidae, which share a burrowing way of life, reduced eyes, and ecological association with ants and termites (Adalsteinsson et al. 2009, Vidal et al. 2010b). The Leptotyphlopidae includes about 116 species and the family has a pantropical to subtropical distribution. This family includes species that are among the world's "smallest and thinnest species of snakes, often called threadsnakes (or wormsnakes)" (Adalsteinsson et al. 2009:2), as does the family Typhlopidae. Until recently, the four species that occur in Guyana were all considered to be members of the very large genus *Leptotyphlops*, but phylogenetic analyses have resulted in taxonomic changes and now each of these four species is included in a different genus (Adalsteinsson et al. 2009). "The family is one of the most poorly known of all terrestrial vertebrates from the standpoint of systematics and ecology" (Adalsteinsson et al. 2009:2).

Epictia albifrons (Wagler, 1824)
Plate 36A, B

Type material.—The original name was *Stenostoma albifrons* and the holotype was destroyed during World War II (Hahn 1980). The type locality is the vicinity of Belém, Pará, Brazil (see Peters & Orejas-Miranda 1970).

Distribution.—"...Trinidad, Guyana, Suriname, French Guiana, southeastern Venezuela, northeastern Peru and possibly Ecuador, Amazonian Brazil south to Mato Grosso and Pará, Pernambuco, and Rio Grande do Norte, and Argentina" (McDiarmid et al. 1999:20), but see Comments, below.

Vouchers for Guyana.—AMNH R-14270 and R-137351 from Kartabo; AMNH R-98188 from near Kartabo; AMNH R-102569 from Camaria; AMNH R-141884–141885 from Dubulay Ranch; AMNH R-152310–152317 and USNM 566292–566295 from Berbice River Camp; ROM 20503 from Kurupukari; ROM 22847 and USNM 535814 from Baramita; and USNM 304357 from Kartabo Point (6°23′00″N, 058°41′00″W).

Coloration in life.—The following is based on AMNH and USNM specimens from Dubulay Ranch and Berbice River Camp (CJC field notes, 1995, 1997). Dark brown above and below; tip of tail (including "spine") bright yellow; less conspicuous yellow spot on snout.

Comments.—In the past, Guyanan specimens of this snake were referred to the species *Leptotyphlops tenellus* Klauber, 1939, with the type locality of Kartabo, Guyana. After discussing taxonomic problems of these small snakes, Hoogmoed & Gruber (1983:340) stated "that *L. tenella* Klauber, 1939 is nothing but a synonym of *S. albifrons* Wagler, 1824. The correct name for the taxon...actually is *L. albifrons* (Wagler, 1824)." However, McDiarmid et al. (1999:20) were not so certain that this matter was clearly resolved, and Franco & Pinto (2009) later decided that the appropriate name is *Leptotyphlops tenellus* after all, but this was not supported by Avila-Pires et al. (2010). Clearly, a thorough review of all known specimens, accompanied by molecular data from specimens representing the entire geographic range, would be appropriate.

Siagonodon septemstriatus (Schneider, 1801)

Type material.—The original name was *Anguis Septemstriatus* and the holotype,

from an unknown locality, is ZMB 3876 (Bauer et al. 2002).

Distribution.—"Southeastern Venezuela..., Guyana, Suriname, French Guiana, and northern Brazil" (McDiarmid et al. 1999:43).

Vouchers for Guyana.—AMNH R-98187 from Kartabo.

Coloration in life.—Beebe (1946:13) stated the following based on specimens from Kartabo. "The body color varies from pale lilac to rich golden orange with seven to nine dark lines down back and sides. In most specimens the lowermost line is broken or reduced to a fine thread of pigment." The following is from Starace (1998:80) based on specimens from French Guiana. "The dorsum is light yellow, striped with seven brown longitudinal lines, the belly is a shade lighter [yellow] in color."

Tricheilostoma dimidiatum (Jan, 1861)

Type material.—The original name was *Stenostoma dimidiatum* and the holotype was destroyed. The neotype is IBSP 24011, an adult female from São Marcos (03°05′N, 60°25′W; 75 m), Boa Vista Municipality, Roraima, Brazil (Pinto & Fernandes 2012).

Distribution.—"Guyana, Suriname, southeastern Venezuela, and northern Brazil in the Rupununi Savanna and its extensions, usually in only slightly elevated coastal areas" (McDiarmid et al. 1999:27).

Vouchers for Guyana.—AMNH R-137979 and USNM 566291 from Karanambo.

Coloration in life.—The following is based on AMNH and USNM specimens from Karanambo (CJC field notes, 1992). Brown dorsum; translucent pinkish gray ventral surface.

Tricheilostoma macrolepis (Peters, 1857)

Type material.—The original name was *Stenostoma macrolepis* and the lectotype is ZMB 1434 (Orejas-Miranda 1967). The type locality was restricted to Puerto Cabello, Venezuela (Orejas-Miranda 1967).

Distribution.—"Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, and northern Brazil" (McDiarmid et al. 1999:35).

Vouchers for Guyana.—ROM 28367 and USNM 291191 from Paramakatoi, the first of which was identified by Van Wallach.

Coloration in life.—The following is from Starace (1998:78) based on specimens from French Guiana. "The dorsum is grey-brown. Each dark-brown dorsal scale has a cream edging, forming a regular overall pattern. The belly is of a lighter brown."

Typhlopidae

There are about 260 species of typhlopid snakes, whose closest living relatives are the Leptotyphlopidae (see discussion of the family, above) and Anomalepididae. The common ancestor of these groups existed about 160 million yr ago, before the breakup of Gondwanaland, based on molecular phylogenetic analyses of DNA sequence data (Vidal et al. 2010b). Three species of this rather ancient family are known to occur in Guyana.

Typhlops brongersmianus Vanzolini, 1976
Plate 35F

Type material.—The original name was *Typhlops brongersmai* (Vanzolini, 1972) but it was preoccupied by the name of a different species, *Typhlops florensis brongersmai*. The replacement name was published by Vanzolini in 1976. The holotype is MZUSP 5218 and type locality is Barra de Itaipe, Ilheus, Bahia, Brazil (Vanzolini 1972).

Distribution.—"Trinidad south through South America (east of the Andes) to Buenos Aires Province, Argentina (Colombia, Trinidad, Venezuela, Guyana,

Suriname, Peru, Brazil, Bolivia, Paraguay, Argentina)" (McDiarmid et al. 1999:94).

Vouchers for Guyana.—AMNH R-140972 and USNM 566296 from Dubulay Ranch.

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994, 1995). Dark brown above, but very light tan on snout and on "spine" at tip of tail (or "spine" dark brown with tan band anterior to it); body at times with a few small irregular tan spots posteriorly; yellowish tan or translucent tan below, with increasing yellow posteriorly.

Typhlops minuisquamus
Dixon & Hendricks, 1979
Plate 36E

Type material.—The holotype is TCWC 39130, an adult female from Mishana, Loreto, Peru.

Distribution.—"Southeastern Colombia..., southern Venezuela..., northeastern Peru..., Brazil..., and Guyana (Kartabo, Kamakusa, and Tacoba)" (McDiarmid et al. 1999:111).

Vouchers for Guyana.—AMNH R-25050 from Kamakusa; AMNH R-25087 from Tacoba; AMNH R-98189 from near Kartabo; and USNM 566297 from Dubulay Ranch.

Coloration in life.—The following is based on the USNM specimen from Dubulay Ranch (CJC field notes, 1995). Dorsum (including tail and "spine") very dark brown; snout pale tan but tip with narrow, vertical, dark brown stripe; ventral surface translucent tan, lighter posteriorly than anteriorly.

Typhlops reticulatus (Linnaeus, 1758)
Plate 36C, D

Type material.—The original name was *Anguis reticulata* and the neotype, from Paramaribo, Surinam, is RMNH 7660, a subadult male (Dixon & Hendricks 1979).

Distribution.—"Tropical South America east of the Andes between 12°N and 14°S (Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Ecuador, Peru, and Bolivia); one specimen reported from coastal Ecuador" (McDiarmid et al. 1999:117).

Vouchers for Guyana.—AMNH R-8110 from Kalacoon; AMNH R-21280, R-21332, R-67882, and R-137350 from Kartabo; AMNH R-141881, AMNH R-141882, and USNM 566298 from Dubulay Ranch; ROM 28368 from Paramakatoi; and USNM 164216–164217 from Mabaruma (8°12′00″N, 059°47′00″W).

Coloration in life.—The following is based on the AMNH and USNM specimens from Dubulay Ranch (CJC field notes, 1994, 1995). The colors are similar to those of *T. brongersmianus*, with the dorsum black or very dark brown, but the "spine" at the tip of the tail is dark brown and there are two dorsal light tan patches; one posteriorly on the body; one just anterior to the "spine" on the tail. The ventral surface is light tan (darker anteriorly).

Viperidae

The families of snakes are discussed above in the introduction to Serpentes. Among these, the Viperidae are usually cryptically colored sit-and-wait predators that blend into their environment inconspicuously, whether on the ground or in vegetation. These are venomous snakes, some of which have venom that is dangerous to humans. The venom is delivered through relatively long, hollow fangs that can be swung forward into biting position near the front of the upper jaw; otherwise they lie back on the roof of the mouth. However, if one is bitten by a viper, that does not necessarily mean that one has been envenomated; many defen-

sive bites by pit vipers are not accompanied by injection of venom (so-called "dry bites").

The main function of the venom is to subdue prey. Occasionally it will be used for defense, particularly if a person steps on a snake or accidently hits it while working in vegetation. Otherwise, pit vipers usually allow very close approach by humans without revealing their presence and without striking, frequently allowing people to walk past them within inches, and without being aware of the snake (Hardy 1994). In fact, Hardy (1994:202) stated that in Costa Rica "biologists spent more than 1.5 million p-hr [=person hours] in the field with *B. asper* resulting in just three bites." The venoms of these and other venomous snakes have been successfully used for, and still have strong potential for, pharmacological research.

The six species of viperids that occur in Guyana all have an extremely sensitive heat-detecting pit on each side of the face between they eye and nostril (although often on a lower plane). Together with its interpretation center in the brain, this organ can accurately sense the presence, size, and location of nearby warm objects, such as warm-blooded prey, under conditions of absolute darkness (e.g., at night or in burrows).

Bothriopsis bilineata (Wied-Neuwied, 1821)

Type material.—The original name was *Cophias bilineatus* and the type specimen is "unlocated" (McDiarmid et al. 1999:248). The type locality was restricted to Vila Viçosa [Marobá], on Rio Peruhybe, Bahia, Brazil (see McDiarmid et al. 1999).

Distribution.—"Amazonian South America: Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Ecuador, Peru, and Bolivia. An isolated Atlantic slope population is known from southeastern Brazil" (McDiarmid et al. 1999:248).

Vouchers for Guyana.—AMNH R-60825 from "British Guiana" but without additional locality data, collected by R. Snedigar, Terry-Holden Expedition; AMNH R-98433 from near Kartabo; and UMMZ 65272 from Kartabo.

Coloration in life.—This is a colorful arboreal snake. "It is pale leaf green above, uniform or sparsely spotted with darker [areas], and yellow below" (Beebe 1946:50, summarizing three specimens from Kartabo). In following paragraphs on the same page, Beebe elaborated on one specimen as follows. "General color above lichen green, shading to grass green toward tail, which changes abruptly to pale pinkish-buff near the tip. Lateral line on side of head and about 40 sets of alternating, irregular, short, transverse dorsal marks light cadmium yellow, edged with black. Side of head greenish-yellow, shading into a wide patch of picric yellow on the side of the neck, which in turn merges into the lateral body line of straw deepening to citron toward the tail. Ventrals pale lumiere green lighter toward tail, touched with lighter greenish-yellow on the lateral edges of the ventrals. Iris light yellow green flecked with darker green, paler toward pupil." Beebe described other individuals as having black spots and orange coloration in places on the dorsum, including one with "blue green" on the belly.

Comments.—This is an arboreal pit viper with cryptic coloration and a prehensile tail, which is relatively longer than in other pit vipers. Is the distinctly colored end of the tail used as a caudal lure to attract prey, as in some other pit vipers?

Bothriopsis taeniata (Wagler, 1824)

Type material.—The original name was *Bothrops taeniatus*. Hoogmoed & Gruber (1983) designated MNHN 1582 as the

neotype. It is from Goiás, Brazil (see Campbell & Lamar 2004).

Distribution.—"Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, Ecuador, Peru, and Bolivia" (McDiarmid et al. 1999:252).

Vouchers for Guyana.—UF 142004, two photographs that document a specimen from "Mazaruni-Potaro District, Wokomung Massif, lat. 05°04′03.3″ by long. 59°51′44.8″, ca. 1135 m elev." (Means 2004:410).

Coloration in life.—The following is from Campbell & Lamar (2004:322). "The pattern [of adults] is exceedingly complex, and the overall color varies from lavender gray to yellow-green. The head is the same shade as the rest of the ground color, but with several black blotches on top and profuse black-and-yellow speckling overall. A black postocular stripe terminates at the angle of the mouth. The iris is speckled black and yellow. The chin is pale yellow, the dark speckling around the labials becoming heavier posteriorly such that the entire underside becomes predominantly maroon-brown with the yellow ground color showing through as specks. Dorsally the pattern consists of 26–40 black bands that are speckled throughout, often fail to meet middorsally, and may be divided on the sides, thus appearing to be divided into 4 parts. There are areas of concentrated black-and-yellow speckling midway between the dorsal bands. A series of 50–90 white or yellow spots is situated at the juncture of the dorsals and ventrals; each spot covers 1–2 dorsal scales and part of the adjacent 1–2 ventrals with an interspace of 1–4 ventrals between them. The distal third to half of the tail is often pink, and the tongue is black." Considerable ontogenetic change in colors and pattern exist.

Comments.—The UF voucher specimen was "collected about 1 m off the ground in cloud forest vegetation" (Means 2004:410). As the other species of *Bothriopsis* in Guyana, this arboreal species has a prehensile tail and cryptic coloration. Is the distinctly colored end of the tail used as a caudal lure to attract prey, as in some other vipers?

Bothrops atrox (Linnaeus, 1758)
Plate 36F

Type material.—The original name was *Coluber atrox* and the syntypes are NRM 100–101 (McDiarmid et al. 1999). The type locality was restricted to Surinam (Schmidt & Walker 1943).

Distribution.—"Tropical lowlands of South America east of the Andes;... southeastern Colombia, southern and eastern Venezuela, Guyana, Suriname, French Guiana, eastern Ecuador, eastern Peru, northern Bolivia, and the northern half of Brazil" (McDiarmid et al. 1999:257).

Vouchers for Guyana.—AMNH R-6803 from Libarria Savannah, Kaieteur; AMNH R-14254–14256, AMNH R-21287, and USNM 257527 from Kartabo; AMNH R-152293–152301 and USNM 566284–566288 from Berbice River Camp; AMNH 152302 from Dubulay Ranch; ROM 22848 from Baramita; ROM 43202 from Menzies Landing, Kaieteur; and USNM 531703–531705 from Iwokrama Forest Reserve (various localities).

Coloration in life.—The following is based on AMNH and USNM specimens from Berbice River Camp and Dubulay Ranch (CJC field notes, 1997). Dorsal colors of browns and tans; ventral surface brown with light gray spots; dark brown face mask; posterior 40% or so of tail yellow on juveniles. Colors and patterns can be variable, so we quote Beebe's (1946:49) descriptions of several specimens. A young snake was "reddish-brown above with cross bands of dark olive, each constricted at mid-back. Whitish below, thickly checkered with pinkish-brown. Iris golden yellow, covered with a vertically striated mesh of black." A larger specimen had "a series of transverse, broad, hour-

glass figures separated by narrow diamond interspaces. The boundaries are formed by narrow, yellowish-white lines. The anterior half of the body is of a general pale brown, the posterior half being much darker with a thick scattering of round, blackish-brown spots. Black, lateral head line and pale yellow tail as usual. Ventrals dominately black with many yellow spots." A larger breeding female had "head purplish gray, paler at the posterior sides and pinkish at snout. Sides of head also purple, all labials thickly mottled with dark brown, and the usual lateral dark line. Body purplish-gray with dark, transverse triangular markings of dark lilac, edged with smoke gray. Chin light buff tinged with purplish, ventrals naples yellow, upper edges with touches of pink, fading to cream color, and mottled more and more thickly with bluish-gray toward tail. Iris warm yellow with dense flecking of dark gray and brown all over, except for pupil rim."

Comments.—AMNH R-137323, cataloged only recently, was said to have been collected by W. Beebe at "Kartabo," decades prior to cataloging. Aspects of the anterior dorsal pattern of this specimen compare favorably with specimens identified as *B. venezuelensis* from Rancho Grande, Venezuela (AMNH R-137298–137299), where Beebe also collected. This Kartabo specimen is in poor condition, however, so not all characters are clear. Perhaps Beebe sent or took it to the New York Zoological Park alive, and, as for other specimens, the AMNH received it some time after it died and was retained in a freezer for an unknown period of time. This could have allowed for a mix-up in locality data, on which Barbour (1920) has commented, and which we question for some other Beebe records (e.g., *Tretioscincus bifasciatus*, see below). Nevertheless, this specimen has dark spots on the labial region, virtual absence of light stripes on the head, and a mix of pale and dark brown markings on the anterior ventral surface similar to specimens of *B. atrox* in the series of AMNH R-152293–302, so we prefer this identification. In addition, AMNH R-14254–14256 and 21287 are Beebe specimens from Kartabo, identified as *B. atrox*, which show variation in the anterior dorsal pattern. Combined modern morphological and genetic research on a large series of *Bothrops* from Kartabo might be worthwhile, to clarify the status of the population there. Is there one species, are there two, and are two taxa interbreeding in the vicinity of Kartabo?

Bothrops brazili Hoge, 1954

Type material.—The holotype, from Tomé Assú, Acará Mirim River, Pará, Brazil, is 14.721 in the Butantan Institute, Brazil.

Distribution.—"Equatorial forests of southern Colombia, eastern Ecuador, southern and eastern Venezuela, Guyana, Suriname, French Guiana, Brazil, eastern Peru, and northern Bolivia (McDiarmid et al. 1999:258).

Vouchers for Guyana.—AMNH R-8992 from Kalacoon, identified by M. S. Hoogmoed.

Coloration in life.—The following is from Campbell & Lamar (2004:383). "The dorsum of the head is pinkish tan to pinkish or reddish gray, usually uniform. In a few specimens a pale brown, poorly defined postocular stripe bordered below by a dark brown line extends from the eye to the angle of the mouth. The rostral and inferior edges of the supralabials are paler than the rest of the head. A lateral series of 9–19 dark ash gray bands or triangular Cs, alternating or opposite each other, crosses the dorsum of the body. The dorsal ground color is similar to that of the head but is usually darker with a pinkish or reddish cast. It appears that specimens from the northern portion of the range more frequently [than specimens from the south] have a pattern

of rectangular or slightly triangular crossbands...The vertebral region often has a rusty tinge. The dorsum of the tail is similar in color to that of the body but may be predominantly black. The venter is usually yellow or pinkish cream with slightly darker mottlings. Conspicuous gray splotches are present at the juncture of the ventral and dorsal scales, roughly on alternate ventrals. The first row of dorsals is usually the color of the ventrals. The iris is usually reddish, pinkish copper, or bronze. The tongue is brown with pink flecks."

Crotalus durissus Linnaeus, 1758
Plate 37A

Type material.—Savage et al. (2005:370) designated RMNH 12857, an adult male as the neotype. This specimen is from near 2.5 km east of Tibiti, Saramacca District, Suriname (ca. 5°33′N, 55°54′W).

Distribution.—"Mexico...to Costa Rica...; many disjunct populations in northern South America (Colombia, Venezuela, Guyana, Surinam, French Guiana, and northern Brazil); Colombia and eastern Brazil to southeastern Peru, Bolivia, Paraguay, Uruguay and northern Argentina..." (McDiarmid et al. 1999:283). The species also occurs in the West Indies (Campbell & Lamar 2004).

Vouchers for Guyana.—AMNH R-60754–60755 from Isheartun; AMNH R-60796 from Naju Creek, near Takutu River; AMNH R-60813 from Charwair Creek; AMNH R-60827 from Wichabai, 16 km N Dadanawa; UF 16157 and 16159–16161 from "the McTurk Homestead on the Rupununi River, about 3 mi E Karanambu, British Guiana (=Guyana)" (Harris & Simmons 1977:306); USNM 291153 from ca. 5 km N of Kato; and USNM 497808 from Karanambo Ranch. In addition, Beebe (1946:51) reported that the species is "very rare in the jungle at Kartabo"; Alexander Mendes has seen the species at Dubulay Ranch and Duane De Freitas (pers. comm.) has seen it at Dadanawa Ranch (Plate 37A).

Coloration in life.—Beebe (1946:51) stated the following about a specimen found at Kartabo. "Like the other Kartabo specimens this rattler was green in general coloring, with variegated shades from pale to deep forest green, with irregular dorsal markings of black. The eyes were connected by a black band, and from the eyes back, two broad bands of dark brown extended along the body for some distance. The iris was green with two large vertical patches of brown mottling on the central three-fifths...Below, the ventrals were creamy white, anteriorly deepening into greenish posteriorly."

Campbell & Lamar (2004:544–545) stated that "there are 18–32 rhombic or diamond-shaped dorsal body blotches... Middorsally, blotches are separated by 1 or 2 pale scales. The body blotches, at least anteriorly, are reddish-brown, dark brown, or black with paler interiors, usually tan to pale gray-brown except in some southern South American snakes. Posteriorly, dorsal blotches tend to become shorter and wider, in some populations coalescing with lateral body blotches and in others remaining discrete. The lateral blotches are below the lateral points of the dorsal series and usually comprise groups of 3–7 dark scales bordered by pale scales...Another secondary series of lateral blotches alternates between the primary lateral series; this series is usually more diffuse or less dark than the primary series and involves the outer edges of the ventrals...The chin and gular region is usually mostly white or yellowish, although some populations have dark flecking or mottling, especially on the infralabials. The belly is usually whitish, yellowish, or buff, and varies from nearly immaculate to white with pale

gray blotches or mottling that becomes progressively darker posteriorly."

Comments.—Harris & Simmons (1977) named a new subspecies as *Crotalus durissus trigonicus*, for which the UF vouchers cited above are paratypes. This subspecies was recognized by Campbell & Lamar (2004:546) who stated that it "is known with certainty only from the Rupununi savannas in southwestern Guyana, and probably from the adjacent Território Federal de Roraima, Brazil."

Lachesis muta (Linnaeus, 1766)

Type material.—The original name was *Crotalus mutus* and type material, from Surinam, is in the NRM (see McDiarmid et al. 1999).

Distribution.—"South America: *L. muta muta* occurs in equatorial forests east of the Andes (eastern Colombia, eastern Ecuador, Peru, northern Bolivia, eastern and southern Venezuela, Guyana, Suriname, French Guiana, and much of northern Brazil); *L. muta rhombeata* occurs in coastal forests of southeastern Brazil" (McDiarmid et al. 1999:313).

Vouchers for Guyana.—AMNH R-8172 from Kalacoon; AMNH R-60850 from Onora; AMNH R-98434–98435 from near Kartabo; and USNM 291192 from Paramakatoi. In addition, Alexander Mendes (pers. comm.) has seen this species at Dubulay Ranch.

Coloration in life.—Beebe (1946:48) described an individual from Kartabo as follows. "This was essentially a yellow brown phase and complete with the pattern of jungle debris when coiled as we first found it. The eye was scarlet, the head and much of the sides of the body pale wood brown. The postocular black band was very strongly marked. The dorsal diamonds were almost solid black, with a few rufous scales at their center, and each banded with a narrow frame of pale buff. The ventrals were yellowish-brown, and the dorsal markings became very irregular and whitish on the tail."

Campbell & Lamar (2004:447) stated that "the ground color is reddish brown, pinkish tan, orangish tan, yellow, or grayish yellow, and often obscurely mottled, especially posteriorly. There are 28–35 dark brown or blackish dorsal diamond-shaped blotches (forming triangles laterally)...The dark dorsal markings are often narrowly bordered by yellow or cream...The venter is white or ivory, with this color overlapping the first 1 or 2 rows of dorsals anteriorly but invaded by short brown intrusions (ends of dorsal bands) posteriorly."

Comments.—Three species of bushmasters are recognized today, two in Central America and one (*L. muta*) in South America (Zamudio & Greene 1997, Fernandes et al. 2004).

Species Accounts: Reptilia: Testudinata (Turtles and Tortoises)

These uniquely shelled vertebrates, which are toothless and have their shoulder and hip girdles inside their rib-cage, have a history that stretches back more than 200 million yr. In many species, as in crocodylians, the sex of a developing embryo is determined by the temperature of the egg's immediate environment in the nest at a critical point of development. We do not know what molecular phenomena control this.

All turtles reproduce by laying eggs, usually buried on land (few in open or simply covered nests), and several have become endangered owing to over-consumption of meat, eggs, tortoiseshell, and oil by humans. A modern phylogenetic analysis of the major groups of turtles of the world was provided by Shaffer et al. (1997), based on morphological (largely skeletal) and DNA sequence data.

Fifteen species representing seven families are known to occur in Guyana, and these include a spectrum of diversity from

sea turtles to freshwater aquatic turtles to terrestrial tortoises, as well as the remarkable turtle (leatherback sea turtle) that attains the greatest weight and longest carapace in the world today. Most of the literature concerning turtles specifically from Guyana has been published by Pritchard (e.g., 1964, 1966, 1969, 2005), with emphasis on sea turtles.

Chelidae

These are aquatic turtles that live in fresh water. They are called side-necked turtles because they bend the neck to the side when hiding the head. Representatives occur only in South America and the Australia-New Guinea areas.

Chelus fimbriatus (Schneider, 1783)
Plate 37E

Type material.—The original name was *Testudo Fimbriata*, the type material is unknown to us, but Fritz & Havaš (2006) gave the type locality as Surinam.

Distribution.—This species occurs in "...most major drainages in northern Bolivia, eastern Peru, Ecuador, eastern Colombia, Venezuela, the Guianas, and northern and central Brazil. It has also been found on Trinidad, apparently washed there by mainland floods" (Ernst & Barbour 1989:66).

Vouchers for Guyana.—PCHP 1823 from Essequibo, Rockstone; PCHP 2828 from Karanambo; PCHP 3909, 3933–3934, 3985, 5245–5246, 5460, and 5728 from Yupakari; and UTA R-37828–37829 from Guyana (no additional locality data).

Coloration in life.—The following is from Ernst & Barbour (1989:66). Carapace brown to black, often carrying aquatic algae; plastron and bridge cream to yellow, possibly brown. "Head, neck, limbs, and tail of adults are grayish brown."

Mesoclemmys gibba (Schweigger, 1812)
Plate 37B–D

Type material.—The original name was *Emys gibba* and the holotype is MNHN 8756, an adult female (Ernst 1981). The type locality was restricted to near Cayenne, French Guiana (see McCord et al. 2001).

Distribution.—Trinidad and northern South America, primarily in the Amazon and Orinoco drainage systems (Brazil, Colombia, Ecuador, the Guianas, Peru, and Venezuela; McCord et al. 2001).

Vouchers for Guyana.—AMNH R-64721 from Kartabo and PCHP 1820 from Mabura Pond, 10 mi SW Linden. In addition, CJC and CRT photographed and released a specimen at Dubulay Ranch (Plate 37B–D).

Coloration in life.—The following is from Ernst & Barbour (1989:53). "The carapace is chestnut brown to dark gray or black...The plastron is red brown to yellow with a brown blotch on each scute, and a narrow yellow border may occur anteriorly and posteriorly. Bridge and undersides of the marginals are brown to yellow...Head and neck are red brown to dark gray dorsolaterally and grayish to pale yellow ventrally; the jaw may contain dark spots and the two small chin barbells are yellow. The upper jaw is often yellow to white with black bars...Limbs and tail are gray black, [areas of] limb sockets yellow."

Comments.—This species formerly was included in the genus *Phrynops*, but McCord et al. (2001) treat *Mesoclemmys* as a separate monotypic genus.

Phrynops tuberosus (Peters, 1870)
Plate 37F

Type material.—The original name was *Platemys tuberose*, and the holotype, from Cotinga River, Mt. Roraima, Guyana, is ZMB 166 (McCord et al. 2001).

Distribution.—"Northeastern South America (eastern and southern Venezuela,

Guyanas, Surinam, northeastern Brazil)" (Fritz & Havaš 2006).

Vouchers for Guyana.—PCHP 4485 from the Ireng River; PCHP 4590, 4645, 4685, and 4917 from near Imbaimadai; and USNM 291154–291156 from Kato.

Coloration in life.—The following is from Ernst & Barbour (1989:59), in their account for *Phrynops geoffroanus* (see below). "The carapace is brown to black with gray mottlings and has a yellow border...In older adults, the undersides of the marginals, bridge, and plastron may be uniformly yellow to light brown; juveniles and young adults have an extensive red and black plastral pattern...the head is gray to olive dorsally, often with black vermiculations; a broad black stripe runs backward on each side from the nostril through or over the orbit and tympanum to the side of the neck, and a second black stripe runs along the upper jaw to the side of the neck; between these stripes is a yellow or cream-colored band. On the yellow chin and underside of the throat is a series of black streaks or stripes. The jaws are yellow...Limbs are gray to olive on the outside, but have cream-colored areas beneath; soles and palms of the feet may be black." The two chin barbells are yellow.

Comments.—Previously, these turtles were referred to as *Phrynops geoffroanus* and *P. geoffroanus tuberosus*, but McCord et al. (2001) concluded that the name *Phrynops tuberosus* applies.

Platemys platycephala (Schneider, 1792)
Plate 38A

Type material.—The original name was *Testudo platycephala* and type material is unknown to us. The type locality was restricted to Cayenne, French Guiana by Ernst (1983).

Distribution.—This species is "restricted to northern South America where it occurs in the Caribbean drainages of Venezuela and the Guianas and the Amazon drainages from northeastern Bolivia, eastern Ecuador and Peru and southeastern Colombia eastward to the vicinity of Belem, Brazil" (Ernst & Barbour 1989:62).

Vouchers for Guyana.—AMNH R-15145 from Kartabo; AMNH R-61523 and AMNH R-61531 from head of Rupununi River; AMNH R-61528–61529 from Shudikar-wau River; PCHP 0443 from NW District, near Mathews Ridge; and USNM 531706 from the Iwokrama Forest Reserve (04°25′12″N, 058°50′58″W).

Coloration in life.—The following is from Ernst & Barbour (1989:61–62). "The carapace is...yellow with dark-brown or black pigment covering varying amounts of the surface [see next paragraph]...The plastron is dark brown or black with a yellow border; the bridge is yellow with a dark transverse bar...The head is orange to yellow brown dorsally, but dark brown to black laterally and ventrally; the light dorsal pigment extends downward on the sides to the midpoint of the orbit and tympanum. The unnotched jaws are dark brown...Two small brown chin barbells are present, and the iris is brown. The neck is colored similarly to the head...Anterior surfaces of the black limbs are covered with large scales...The black tail is short."

The subspecies that occurs in the Guianas has "the dark pigment on the yellow carapace...restricted to the border of the seam separating the vertebrals and pleurals and to an incomplete band extending on each side of the medial groove downward through the 2d and 3d pleurals to the lateral carapacial rim (the medial groove remains yellow); the dark bar crosses less than 80% of the bridge."

Cheloniidae

These are sea turtles, with flipper-like arms and legs (see also Dermochelyidae,

below). Three of the species in this family are listed by the IUCN (2010) as being globally Endangered or Critically Endangered, owing to overharvesting by humans, and the fourth is listed as Vulnerable–Decreasing (see below, Endangered Species). Analyses of sequence data of mitochondrial DNA in Brazil (Lara-Ruiz et al. 2006) have shown that reasonably frequent hybridization occurs between *Eretmochelys imbricata* and two other species, *Caretta caretta* and *Lepidochelys olivacea*. Perhaps, if females of a species become depleted while nesting, the more abundant males offshore will have proportionally more females of other species with which to mate; this phenomenon of unusual hybridization may be a byproduct of human predation.

These turtles spend nearly 100% of their lives of many decades using vast areas of the world's oceans, mostly in the tropics, at times moving from one continent to another, although we still have much to learn about their navigation mechanisms and life histories. Four of the five species of sea turtles known to occur in Guyana are known to nest in very limited areas on and near Shell Beach, to the northwest of Georgetown (Pritchard 1964, 1966, 1969, 2005). After a hatchling emerges on the beach in Guyana and scrambles to the sea, where does it spend the rest of its life, including the 20 yr or so that may be required simply to reach maturity?

Caretta caretta (Linnaeus, 1758)

Type material.—The original name was *Testudo Caretta*, the type material is unknown to us, and the type locality was restricted Bimini, British Bahamas by Schmidt (1953).

Distribution.—This species occurs in the "Pacific, Indian, and Atlantic oceans from Washington, Japan, India, Kenya, the British Isles, and Newfoundland south to Chile, Australia, South Africa, tropical western Africa and Argentina. It also occurs in the Caribbean and Mediterranean seas" (Ernst & Barbour 1989:125).

Vouchers for Guyana.—PCHP 5697 from Guyana (no further data).

Coloration in life.—The following is from Ernst & Barbour (1989:124). "The carapace is reddish brown but may be tinged with olive; the scutes are often bordered with yellow. Bridge and plastron are yellow to cream colored...The head varies from reddish or yellow chestnut to olive brown, often with yellow-bordered scales...Limbs and tail are dark medially and yellow laterally and below."

Comments.—This species is not known to nest in Guyana, but occurs "as an occasional straggler'' (Pritchard 1964:26). The other four species of sea turtles documented for Guyana are known to nest on the beaches northwest of Georgetown (Pritchard 1964, 1966, 1969, 2005).

Chelonia mydas (Linnaeus, 1758)
Plate 38B

Type material.—The original name was *Testudo Mydas* based on type material (unknown to us) from Ascension Island (Smith & Taylor 1950b).

Distribution.—This species occurs in the Atlantic, Pacific, and Indian oceans, primarily in the tropics (Ernst & Barbour 1989).

Vouchers for Guyana.—The following specimens are primarily skeletal remains found dead on the beach. PCHP 0921 and 0923 from Shell Beach; PCHP 2027 from NW District, 8 mi E Waini Point; PCHP 2460–2462, 2469, 2504–2505, and many other PCHP specimens from NW District, Almond Beach.

Coloration in life.—The following is from Ernst & Barbour (1989:120). "Carapacial scutes are olive to brown and may contain a mottled, radiating, or wavy pattern...The [plastron is] immaculate

white or yellow…All skin is brown or, sometimes, gray to black, and many head scales may have yellow margins."

Eretmochelys imbricata (Linnaeus, 1766)
Plate 38C

Type material.—The original name was *Testudo imbricata* and the type material is unknown to us. The type locality was restricted to Belize by Schmidt (1953:106).

Distribution.—This species occurs in the "Atlantic, Pacific, and Indian oceans from California, Japan, the Red Sea, the British Isles, and Massachusetts south to Peru, Australia, Madagascar, northwestern Africa, and southern Brazil" (Ernst & Barbour 1989:123).

Vouchers for Guyana.—The following specimens are primarily skeletal remains found dead on the beach. PCHP 0817, 0951–0957, and 3880 from Shell Beach; PCHP 2025 from NW District, 10 mi E Waini Point; PCHP 2158–2162, 2501, 2506–2507, and many other PCHP specimens from Almond Beach; and USNM 163069 from Enmore Beach (06°44′00″N, 057°59′00″W).

Coloration in life.—The following is from Ernst & Barbour (1989:123). "The carapace is dark greenish brown; in the young it shows a tortoise-shell pattern…[the bridge and plastron are] yellow…Head scales are black to chestnut brown at the center and lighter at their margins; the jaws are yellow with some brown streaks or bars…The chin and throat are yellow, and the neck dark above." Juveniles may have a few dark spots on the plastron.

Lepidochelys olivacea (Eschscholtz, 1829)
Plate 38D

Type material.—The original name was *Chelonia olivacea* and the type material, from Manila Bay, Philippines, is lost (see Zug et al. 1998).

Distribution.—These turtles occur in "…tropical waters of the Pacific and Indian Oceans from Micronesia, Japan, India, and Arabia south to northern Australia and southern Africa; in the Atlantic Ocean off the western coast of Africa and the coasts of northern Brazil, French Guiana, Surinam, Guyana, and Venezuela in South America; and, occasionally, in the Caribbean Sea as far north as Puerto Rico. In the eastern Pacific it is found from the Galapagos northward to California" (Ernst & Barbour 1989:127).

Vouchers for Guyana.—The following specimens are primarily skeletal remains found dead on the beach. PCHP 0078, 0961–0977, 1005, and other PCHP specimens from Shell Beach; PCHP 2325–2328, 2503, 3182–3185, and other PCHP specimens from NW District, Almond Beach.

Coloration in life.—The following is from Zug et al. (1998:653.1). "General coloration is grayish-green to olive-brown dorsally. The carapace and upper surfaces of the limbs and head are uniformly pigmented, with the skin somewhat grayer than the shell. The plastron, bridge, and undersides of the limbs and head are creamy white.'' Ernst & Barbour (1989:127) referred to the bridge and plastron as being "greenish white or greenish yellow."

Dermochelyidae

As the Cheloniidae (see above), these are sea turtles with flipper-like limbs that come ashore in limited areas of coastal Guyana to lay eggs. The single species of this family is listed by the IUCN (2010) as being globally Critically Endangered, owing to overharvesting by humans. These turtles use vast areas of ocean, at times moving from one continent to another, although we still have much to learn about their navigation mechanisms and life histories. The species of this family is called the leatherback, because the outer

surface of its shell is not bone-hard, but leather-like to the touch. This is the turtle that attains the greatest weight (ca. 867 kg) and longest carapace (ca. 2.4 m) in the world (Ernst & Barbour 1989).

Dermochelys coriacea (Vandelli, 1761)
Plate 38E

Type material.—The original name was *Testudine coriacea* and "the specimen in the Museum of the Padova University, redescribed and figured by Fretey & Bour (1980), is the holotype and only type-specimen of this species" (Bour & Dubois 1983:358). The type locality is "Laurentum, between Lido di Ostia and Tor Paterno, shore of the Tyrrhenian Sea, Italy" (Bour & Dubois 1983:359).

Distribution.—This species "ranges throughout the waters of the Atlantic, Pacific, and Indian Oceans from Labrador, Iceland, the British Isles, Norway, Alaska, and Japan south to Argentina, Chile, Australia, and the Cape of Good Hope (Pritchard, 1980). It also enters the Mediterranean Sea" (Ernst & Barbour 1989:117).

Vouchers for Guyana.—The following specimens are primarily skeletal remains found dead on the beach. PCHP 1021 from Shell Beach; PCHP 2007 from 8 mi W Waini Point; PCHP 2467–2468, 3055–3058, and 3876 from NW District, Almond Beach; PCHP 4792 from Gwennie Beach; and PCHP 4793 from Kanwalla Beach.

Coloration in life.—The following is from Ernst & Barbour (1989:117). Carapace brown to black; plastron cream to white; head and neck dark brown to black with white to yellow blotches; upper jaw gray; limbs black with some light blotches.

Geoemydidae

In the past, turtles of the genus *Rhinoclemmys* were included in the families Bataguridae (see Shaffer et al. 1997) and Emydidae, but Fritz & Havaš (2006) referred to these and related turtles as the Geoemydidae; all other genera of this family occur in "northwest Africa, Europe to western Asia and the Middle East, across southern Asia to China, Japan, the Philippines, and islands of the Sunda Shelf" (Pough et al. 2004:109).

Rhinoclemmys punctularia (Daudin, 1802d)
Plate 38F

Type material.—The original name was *Testudo punctularia* and the holotype, from Cayenne, French Guiana, is MNHN 9130 (Fretey et al. 1977).

Distribution.—This species occurs "...from eastern Colombia, the Orinoco drainage of Venezuela, and Trinidad Island eastward through the Guianas and northeastern Brazil" (Ernst & Barbour 1989:182).

Vouchers for Guyana.—AMNH R-8080 from Kalacoon; AMNH R-61530 from Shudikar-wau River; PCHP 2878 from Barama River, Cariaco Mission; PCHP 4802 from Almond Beach (near Waini Point); USNM 85022 and 86861 from Pomeroon; and USNM 164180 from Mabaruma Compound (08°12′00″N, 059°47′00″W).

Coloration in life.—The following is from Ernst & Barbour (1989:182). Adults dark brown or black above, "but juveniles may have yellow to bronze radiations on each pleural [plate]...The plastron is red brown to black with a yellow border and seams. The bridge is yellow with two large dark blotches...The head is...black with...two longitudinal red or yellow stripes...or...a broad horseshoelike mark posterior to the orbit. Two light spots may occur on the nape...and stripes usually run between the orbit and tympanum and from the snout along the upper jaw to the tympanum. The iris is green to bronze. Forelimbs have large, yellow or red, black-spotted scales, and the

hind limbs are gray laterally and yellow with black spotting medially."

Kinosternidae

This family of aquatic turtles is restricted to North and South America.

Kinosternon scorpioides (Linnaeus, 1766) Plate 39A, B

Type material.—The original name was *Testudo scorpioides* and the holotype, from Surinam, has apparently been lost (see Berry & Iverson 2001).

Distribution.—This species "ranges at low elevations from southern Tamaulipas, Mexico, southward to northern Argentina, Bolivia, and northern Peru" (Ernst & Barbour 1989:83).

Vouchers for Guyana.—PCHP 0222 and 0431 from the Uitvlugt Sugar Estate; PCHP 2669 from NW District, 5 km SE Waini Point; PCHP 3709 from NW District, Almond Beach; PCHP 4221 from NW District, behind Almond Beach; and PCHP 5083–5113 and many other PCHP specimens discovered dead in the NW District, Avicennia forest behind Almond Beach, 6 km E Waini Point (died in a fire); and USNM 84582–84585 from Pomeroon.

Coloration in life.—The following is from Berry & Iverson (2001:725.3). "The carapace is highly variable in color, ranging from light brown to olive to black, with darker seams in all but the darkest individuals...The color of the plastron may be gray, yellow, orange, brown or black, usually with darker seams...The color pattern on the head is extremely variable, with a brown, gray, or black background and a reticulated or spotted pattern of cream, yellow, orange, pink, or red. The jaw sheaths are cream to yellow with darker vertical streaks most conspicuous in older males. The skin of other soft parts is gray or brown, usually with many small, darker spots."

Comments.—"This species lives in streams, rivers, lakes, and ponds. If its waterway dries up, it will bury itself in the mud bottom until the next rain...[It] is omnivorous" (Ernst & Barbour 1989:84).

Podocnemididae

These are large, aquatic, side-necked turtles that swim well, feed mostly on vegetation, live in rivers and lakes, and nest on sand banks, usually at night. The family occurs only in South America and Madagascar. Two species occur in Guyana, and both need conservation management activities.

Podocnemis expansa (Schweigger, 1812) Plate 39C

Type material.—The original name was *Emys expansa* and there are three types in the MNHN, from "America meridionali."

Distribution.—This species occurs in "Caribbean drainages of Guyana and Venezuela and in the upper Amazon tributaries in Bolivia, Peru, Colombia, Venezuela, and Brazil. It is also occasionally found on Trinidad, especially after floods of the adjacent mainland Orinoco River" (Ernst & Barbour 1989:27) and is found widely on the Amazon River, Brazil (M. S. Hoogmoed, pers. comm.).

Vouchers for Guyana.—The following are primarily skeletal remains of specimens found dead. PCHP 2779 from Rupununi River, Massala; PCHP 2827 from Rupununi River, Karanambo; PCHP 2884–2886, 3133–3134, and 4132 from Rupununi River, Apoteri; PCHP 4128 and 4148 from Rupununi River, Rewa mouth; and PCHP 4129 from Kwattanmang (near Annai), ex. Rewa River.

Coloration in life.—The following is from Ernst & Barbour (1989:26–27). "The carapace is olive to dark gray or brown and may have some dark spots and a light border in younger individuals. The plastron...bridge, and undersides of the marginals are yellow...The head is gray

brown with yellow markings. Two yellow spots occur on the interparietal scutes, and one on each side of the head; these spots fade with age. Jaws are tan; the chin yellow. The neck is gray dorsally and yellow ventrally...; limbs are gray."

Comments.—These giant river turtles have been overharvested by humans for consumption of eggs, meat, and oil. Consequently, populations have experienced dramatic declines. Analyses of mitochondrial DNA sequence data and nuclear microsatellites indicate that females practice natal-river homing and "that each major tributary [sampled] currently forms a semi-isolated reproductive population and should be managed accordingly" (Pearse et al. 2006:985).

Podocnemis unifilis Troschel, 1848
Plate 39D

Type material.—The holotype, from Guyana, was ZMB 142 but is now lost (Duellman 2005).

Distribution.—This species occurs in "Caribbean drainages of the Guianas, Venezuela and Colombia, and the upper tributaries of the Amazon River in Colombia, Ecuador, Peru, northern Bolivia, southern Venezuela, and Brazil" (Ernst & Barbour 1989:29). It is also found widely on the Amazon River, Brazil (M. S. Hoogmoed, pers. comm.).

Vouchers for Guyana.—The following are primarily skeletal remains of specimens found dead. AMNH R-8707 from Kalacoon; AMNH R-15144 from Kartabo; AMNH R-61524–61525 from Wichibei; AMNH R-61526 from Yupicari; PCHP 2775 and 2777 from Rupununi River, Massala; PCHP 2776 from Rupununi River, Karanambo; PCHP 2882 and 4131 from Rupununi River, Apoteri; PCHP 2883, 4134, and 4137–4138 from Rupununi River, mouth of Rewa River; and PCHP 5202–5203 from the Ireng River.

Coloration in life.—The following is from Ernst & Barbour (1989:29). "The carapace of juveniles is brown to greenish gray with a narrow yellow border, that of adults is olive to dark gray or brown...The yellow plastron and bridge may develop dark blotches with age...The head is gray to olive or brown with yellow spots–one on top of the snout, one on each side of the snout extending to the upper jaw rim, another on each side of the head extending from the lower posterior edge of the orbit to the corner of the mouth, and one on each tympanum. Jaws are dark brown or black, but the chin has a transverse yellow bar and a yellow spot on each side below the corner of the mouth. Limbs are gray to olive brown."

Testudinidae

These are the terrestrial tortoises with hard, high-domed shells and elephantine arms and legs. They are frequently preyed upon by humans. Until recently, the two species known to occur in Guyana were referred to the genus *Geochelone*, but now they are referred to *Chelonoidis*.

Chelonoidis carbonaria (Spix, 1824)
Plate 40A

Type material.—The original name was *Testudo carbonaria* based on material from Brazil. Hoogmoed & Gruber (1983:354) designated "pl. XVI in Spix (1824) as the lectotype." Vanzolini (1994:1–2) stated that the type locality probably is "the stretch of the Rio Amazonas between the mouth of the Negro, at 03°08′S, 59°55′W, and the mouth of the Furo do Tajapuru, at 01°02′S, 51°2′W."

Distribution.—This species occurs in "southeastern Panama and west of the Andes in Chocó of Colombia, but its main range is east of the Andes in eastern Colombia, Venezuela, and the Guianas

to eastern Brazil, south to Rio de Janeiro, and west to eastern Bolivia, Paraguay, and northern Argentina. It seems absent from almost all but the eastern parts of the Amazon Basin. This tortoise may occur naturally on Trinidad, and has been introduced on quite a few Caribbean Islands, including St. Croix in the Virgin Islands" (Ernst & Barbour 1989:253).

Vouchers for Guyana.—The following are primarily skeletal remains of specimens found dead. AMNH R-61522 from Head of Rupununi River; PCHP 2790–2801 from Rupununi, Yupakari; PCHP 2802 and 4146 from St. Cuthbert's Mission; PCHP 3052 from Mabaruma; USNM 85024 from "Georgetown, 70 mi from"; USNM 291193 from Paramakatoi; and USNM 291194 from Wandapa (04°32′ 00″N, 059°43′00″W). In addition, CJC and CRT saw specimens (not collected) at Dubulay Ranch, Karanambo, and Aishalton.

Coloration in life.—The following is from Ernst & Leuteritz (1999a:690.1). "The carapace is black, with the vertebral and pleural areolae yellow to reddish orange, and a light spot of the same color occurs at the base of each marginal...The plastron is yellowish brown with some dark pigment along the mid- and transverse seams...The head...scales are...yellow, red, or orange; the jaws are dark. The anterior surface of each forelimb is covered with large, red, and slightly or non-overlapping scales."

Chelonoidis denticulata (Linnaeus, 1766)
Plate 40B

Type material.—The original name was *Testudo denticulata* and the holotype is NRM De Greer 21 (see Ernst & Leuteritz 1999b). There are no reliable data on the type locality.

Distribution.—This species occurs in "southeastern Venezuela through the Caribbean lowlands of the Guianas to Brazil, where it occurs throughout the Amazon Basin to eastern Ecuador and Colombia, northeastern Peru, and northern and eastern Bolivia and on Trinidad" (Ernst & Barbour 1989:254).

Vouchers for Guyana.—The following are primarily skeletal remains of specimens found dead. AMNH R-15143 from Kartabo; AMNH R-25046 and R-44617–44618 from Kamakusa; AMNH R-128195 from Essequibo, Takutu Mts. (ca. 45 mi SE Itabali on W bank of Mazuruni River); PCHP 2108–2116 from NW District, Morawhanna (reportedly from lower Waini); PCHP 2181–2182 and 2306 from NW District, Mabaruma area; PCHP 2491 from Moruka River, Santa Rosa Mission; PCHP 2650–2651 from NW District, Mabaruma; PCHP 2832–2833 from Barama River, Cariaco (=Kariakau) Mission; PCHP 2834–2835 from NW District, Baramanni (Waini/R. Baramanni junction); PCHP 2886–2889 from Apoteri (Rupununi/Essequibo river junction); PCHP 2892 from Barama River, Iroma; PCHP 2979 from Barama, Towaka; PCHP 3053 from Rewa Mouth; PCHP 5333–5338 from Santa Rosa, Moruka River; and USNM 535818 from Baramita. In addition, CJC and CRT saw specimens (not collected) at Berbice River Camp and Konawaruk Camp.

Coloration in life.—The following is from Ernst & Leuteritz (1999b:691.1). "The carapace is brown with yellow to orange vertebral and pleural areolae; yellowish or orange pigment also occurs at the lower edge of each marginal...The plastron is yellowish brown with darker pigment along the seams. The head is brown with yellow dorsal scales... The...head scales are...yellow to orange with dark borders; the jaws are dark brown. The anterior surface of each forelimb is covered with large yellow or orange, non-or only slightly overlapping scales."

Species Reported from Guyana but Probably in Error

Tretioscincus bifasciatus (Duméril, 1851)

This species was described on the basis of a specimen from the vicinity of Madeleine (Nouvelle Grenade), Colombia (Peters & Donoso-Barros 1970:262). The general area of distribution is in arid habitats on the Caribbean coasts of Colombia and Venezuela, and on Isla Margarita and Dutch Leeward Islands (Gorzula & Señaris 1999).

We do not believe that this species occurs in Guyana despite the existence of one published report (Beebe 1945:23) and one AMNH specimen (R-137364), for which the catalog states "Guyana: [Mazaruni-Potaro]: Kartabo: 6°21′N 58°41′ W." A type-written note inside the jar states: "Near Kartabo, British Guiana." Another type-written note in the jar states: "*Tretioscincus bifasciatus* 3116. Kartabo." However, there is no field tag or label attached to the specimen itself. We suspect that the locality data associated with the specimen are incorrect.

The AMNH specimen was recorded as having been collected by W. Beebe in 1924, but it was not cataloged at the AMNH until 1991. The identification was confirmed by CJC as correct on 9 May 2007. However, there could be a problem with the association of the specimen and the locality data. We think that the occurrence of this species in Guyana is doubtful for the following reasons: no other specimens are known for Guyana; the species is present in Venezuela where Beebe collected also; the 67 yr delay in cataloging from the date of collection may reflect problems in transfer of data; and there are other problems associated with some of Beebe's specimens (Barbour 1920). Furthermore, Beebe (1945:23) stated the following: "captured or saw only five or six [individuals of *T. bifasciatus*] at Kartabo and the same number at Caripito [Venezuela]." The more detailed notes he presented in the publication were specifically based on specimens from Caripito, and he gave no indication that he was aware of the possibility that a different species, but similar congener, *Tretioscincus agilis*, does occur in Guyana and probably at Kartabo, although voucher specimens are needed to confirm this. Future workers should not list *T. bifasciatus* as a species that occurs in Guyana until it is confirmed and documented. Similarly, the presence of *T. agilis* at Kartabo should be confirmed.

Liophis juliae (Cope, 1879)

The AMNH has two specimens of *Liophis juliae* (R-6804–6805) that are noted as being from "Kaieteur." These were identified as *L. juliae* by J. R. Dixon, who stated "I recently examined two specimens from the American Museum of Natural History that were labeled from Guyana. I believe these to be mislabeled specimens" (Dixon 1981:303). No other specimens of this species are known from Guyana, and all other known specimens are from islands in the West Indies (type locality, Dominica). The collector of the AMNH specimens is given in the catalog as "Crampton."

The AMNH specimens cataloged as being from Guyana compare favorably with specimens of this species from Dominica (AMNH R-32889, R-44899–44900, and R-135273), as recently determined by CJC, which agrees with Dixon's earlier identification. Additional herpetological specimens at the AMNH were collected by "Crampton" in 1911, including specimens from Kaieteur that are credible. This collector presumably was Henry E. Crampton, who was at the time, among other things, a curator of invertebrates at the AMNH. Prior to collecting in Guyana, his field party stopped and collected in the

West Indies, apparently in transit to Guyana, and they collected in Dominica, which is the type locality for *L. juliae*. In addition, Philippe Kok (pers. comm.) stated that despite his extensive recent field work in Kaieteur National Park, he has seen no specimens that appear similar to *L. juliae*. We conclude that it is likely that there was a mix-up in locality data for AMNH R-6804–6805 and they probably were collected in Dominica, not at Kaieteur.

Micrurus circinalis (Duméril & Bibron, 1854)

Donnelly et al. (2005:457) reported that this species was found at Iwokrama, but we could not obtain voucher specimens to examine for confirmation. This is of interest as *M. circinalis* is known only from Trinidad and Venezuela (Campbell & Lamar 2004:157). It is intriguing also, as AMNH R-110163 appears to be an example of *M. circinalis*, and it is cataloged as being from Kartabo (collected by W. Beebe). As cited several times in this volume (and see account above for *Tretioscincus bifasciatus*), we are reluctant to accept records of Beebe that are open to question, especially for taxa that occur in Venezuela, where he collected also, and for which there was a long delay before his specimens were received or cataloged at the AMNH. Interestingly, the Beebe specimen had a paper tag tied to it saying "Kartabo," number "3263," and "Dept. Tropical Research of the N.Y. Zoological Society." As an alternative suggestion, one might question the status of our knowledge about intraspecific variation in *M. psyches*, of which *circinalis* was once treated as a subspecies. New studies based on larger collections, especially including specimens from strategically important localities, may show that *M. psyches* is more variable than we recognize today, perhaps dimorphic in coloration, with some individuals appearing to be of the *circinalis* type after all.

Typhlops lumbricalis (Linnaeus, 1766)

Although Hoogmoed (1983:235) said that this is the only species of snake to have been successfully introduced "into Guyana from the Antilles," Dixon & Hendricks (1979) cite Thomas' dissertation (1976) as being doubtful of the only known record for Guyana. The only reference specimen is AMNH R-67881, cataloged as having been collected by W. Beebe at Kartabo, and CJC recently confirmed the identification of the specimen. Considering that occasionally problems exist for specimens collected by Beebe (Barbour 1920; and see above discussion for *Tretioscincus bifasciatus*), and considering the lack of additional specimens from Guyana, we suggest that the record needs to be confirmed before concluding that the species occurs in Guyana. It seems more likely to us that this is another case of mislabeling of specimens.

Additional Species Possible (As Yet Undocumented)

New Species

Considerable research remains to be done on the amphibians and reptiles of Guyana. To date, the herpetofauna of Guyana includes at least 324 species (148 amphibians and 176 reptiles; Appendix 2). Of these, 39 (12%) were described and named since the year 2000. Most of the species described since 2000 are amphibians (17% of the amphibian fauna), most are from remote, isolated highland sites (see Biogeography, below), and most are endemic species that occur nowhere else in the world, except possibly in immediately adjacent uplands and isolated highlands of small areas of Venezuela and Brazil. Considering that 12% of the

herpetofauna (17% of the amphibians, 6% of the reptiles) were described between the years 2000–2011, undoubtedly additional undescribed species, including endemics, are yet to be discovered. We expect that most of the new species will still be found in the uplands and isolated highlands of the Pakaraima Mountains, but discoveries are to be made also in the lowlands (e.g., Jungfer & Böhme 2004, Kok 2005, Cole & Kok 2006, Donnelly et al. 2006, Kok & Ernst 2007).

Other Species

There are species known to occur in countries near Guyana but which are not yet known to occur in Guyana. Candidate species that may well be found in Guyana in the future are listed below in the same sequence as representatives of their families are listed in the species accounts above. The species that might some day be found in Guyana, however, are not strictly limited to those on these lists. It is not surprising that the majority of the species listed are snakes, as these can be most difficult to find and capture in tropical environments. Consequently, snakes usually are the most poorly represented group in scientific collections from the tropics.

Amphibians	Reptiles
Vitreorana oyampiensis	*Amapasaurus tetradactylus*
Dendropsophus luteoocellatus	*Arthrosaura kockii*
D. melanargyreus	*Atractus elaps*
Hypsiboas tepuianus	*A. flammigerus*
Phyllomedusa tomopterna	*A. latifrons*
Teratohyla midas	*A. zidoki*
Leptodactylus myersi	*Cercophis auratus*
Microcaecilia trombetas	*Helicops leopardinus*
	Mastigodryas bifossatus
	Taeniophallus brevirostris
	T. nicagus
	Xenodon werneri
	Mesoclemmys nasuta

Discussion

Biogeography

Comparisons of Faunas at Different Sites

There are several reasons to compare the lists of species that occur at different localities. Academics often use patterns of faunal similarities and differences to discover regions of historical significance in evolution and biogeography, and entrepreneurs often use unique biotas for ecotourism. The Guianan Region is recognized as having a fauna that is distinctive, large, and diverse among those of other regions in South America or Central America. This results from the geographic position of Guyana in Neotropica and on the Guiana Shield, including the isolated highlands or tepuis of the eastern part of the Pantepui Region, which are surrounded by lowland rainforest and savannas. Consequently, there is a mixture of local endemic species and widespread species characteristic of low elevation habitats of Amazonia and the Guianan Region. In the vicinity of the Pakaraima Mountains, the surrounding lowland fauna usually is quite different from adjacent isolated highland fauna. Comparing faunas is an important step in learning what patterns exist, which can be helpful in designating national parks or other preserves. Prior to comparing faunal lists, however, it helps to know whether the lists of local species are reasonably complete.

Estimating Effectiveness and Completeness of Sampling

How do investigators know whether the specimens they have studied are sufficient to accurately represent the biodiversity that occurs at a particular locality? Is the faunal list complete or not? Various authors have discussed methods to estimate this, and we found a good model in recent works on the mammals of Paracou,

French Guiana (Simmons & Voss 1998, Voss et al. 2001).

One method is to estimate effectiveness of sampling effort by keeping track of how many people hours (or days, weeks, months) were spent in the field and how many species were collected for the first time at the site during each period of time (also see Ernst et al. 2005). The resulting cumulative number of species (vertical axis) is plotted against the period of time (horizontal axis), and over time the plotted line approaches an asymptote. The results of this approach with mammals varied widely among analyses of six different collecting techniques at Paracou (Voss et al. 2001:167–177). We could not use this method because we did not track observations in ways that were consistent with drawing such plots (e.g., how many people hours or days were spent collecting, as opposed to writing notes and photography?). Furthermore, we had very unequal expenditure of efforts in different microhabitats (e.g., canopy, aquatic, subterranean) and in some areas we used pit-fall traps with drift fences, but not everywhere.

Another method for estimating completeness of the local sample (e.g., Voss et al. 2001:177–179), is to apply "Chao's (1984) estimator, which is based on the total number of observed species, S_{obs}, the number of singletons (species recorded only once), *a*, and the number of doubletons (species recorded only twice), *b*. The expected total number of species, S*, is...given by the expression $S^* = S_{obs} + (a^2/2b)$."

We performed this exercise for the two lowland sites that seemed most appropriate: Dubulay Ranch, and Berbice River Camp (see Methods for details on the localities). For Dubulay Ranch, we used observations for only the first sampling period, 1994, when we spent 26 nights, used drift fences and pitfall traps, did most of our work within about 1 km (linear) of the ranch house, and during which there was good rainfall, although there were only two field workers (CJC and CRT). For Berbice River Camp (1997), we spent 28 nights and the other conditions were similar, except that we also had the assistance of two American Indians, Gerald and Wesley King, who were outstanding in the field. At Dubulay Ranch in 1994, we recorded 46 species, of which 19 were singletons and 8 were doubletons, which resulted in an estimated fauna of 69 species of amphibians and reptiles. By this estimate, we recorded only 67% of the fauna around the ranch house. At Berbice River Camp, we recorded 65 species, of which 14 were singletons and 4 were doubletons, which resulted in an estimated fauna of 90 species of amphibians and reptiles. By this estimate, we recorded only 72% of the fauna. The results for the first sampling at Dubulay Ranch and Berbice River Camp indicate that our sampling was far from complete. This conclusion is supported by simply scanning Table 1. For example, incompleteness of sampling probably explains the following: apparent absence of *Allobates spumaponens* at Baramita and Kartabo; apparent absence of *Rhinella marina* at Konawaruk Camp; presence of *Ceratophrys cornuta* at only one of the sites; absence of *Hypsiboas boans* at Aishalton; presence of *Hypsiboas crepitans* at only two sites; presence of *Pipa pipa* at only two sites; and relatively few caecilians, amphisbaenians or worm lizards, snakes, and turtles in general. We conclude that considerably more effort is needed to accurately document the faunas at all the sites we visited.

Although the known herpetofauna for Kartabo is much larger than that for either Dubulay Ranch or Berbice River Camp, we could not calculate S* because we lack data on the numbers of singletons and doubletons observed by Beebe and his associates. However, we think the apparently larger fauna at Kartabo may be misleading, reflecting the more extensive time over eight field trips that Beebe and his colleagues spent there (Beebe 1946).

Table 1.—Herpetofaunal comparisons of seven lowland sites in Guyana. X indicates presence of the species, – indicates not documented. The sites are as follows: Ai, Aishalton; Ba, Baramita; Be, Berbice River Camp; Du, Dubulay Ranch; Ka, Karanambo; Ko, Konawaruk Camp; Kt, Kartabo. The habitats are as follows: F, forest; M, patchwork of forest, savanna, and gallery forest; S, savanna (but with gallery forest).

Taxon	BaF	KtF	KoF	DuM	BeF	KaS	AiS
Allobates femoralis	X	X	–	–	–	–	–
Allobates spumaponens	–	–	X	–	X	–	–
Anomaloglossus kaiei	–	–	X	–	–	–	–
Atelopus spumarius	–	X	X	–	–	–	–
Dendrophryniscus minutus	–	–	–	–	X	–	–
Rhaebo guttatus	–	X	X	X	X	X	–
Rhaebo nasicus	–	X	–	–	–	–	–
Rhinella merianae	–	X	–	X	–	–	X
Rhinella marina	X	X	–	X	X	X	X
Rhinella martyi	X	X	X	X	X	–	–
Ceratophrys cornuta	–	X	–	–	–	–	–
Pristimantis zeuctotylus	–	–	–	–	X	–	–
Ameerega hahneli	X	X	–	–	–	–	–
Ameerega trivittata	X	X	–	–	–	–	–
Dendrobates leucomelas	X	X	–	–	–	–	–
Stefania evansi	–	X	X	–	–	–	–
Dendropsophus brevifrons	–	–	X	–	–	–	–
Dendropsophus marmoratus	X	X	X	–	–	–	–
Dendropsophus minusculus	X	–	–	X	–	X	X
Dendropsophus minutus	–	–	X	X	–	–	–
Hypsiboas boans	X	X	X	X	X	X	–
Hypsiboas calcaratus	–	–	X	–	–	–	–
Hypsiboas cinerascens	X	X	X	–	X	–	–
Hypsiboas crepitans	–	–	–	X	–	–	X
Hypsiboas geographicus	X	X	X	X	X	–	–
Hypsiboas multifasciatus	X	X	X	X	–	–	–
Lysapsus laevis	–	–	–	–	–	X	X
Osteocephalus buckleyi	–	X	–	–	–	–	–
Osteocephalus cabrerai	–	–	X	–	–	–	–
Osteocephalus leprieurii	–	X	X	–	X	–	–
Osteocephalus oophagus	–	–	X	–	X	–	–
Osteocephalus taurinus	X	X	X	X	X	–	–
Phyllomedusa bicolor	X	X	–	–	–	–	–
Phyllomedusa hypochondrialis	–	X	X	X	X	–	–
Phyllomedusa vaillantii	X	–	–	–	X	–	–
Pseudis paradoxa	–	X	–	–	–	–	–
Scinax boesemani	–	–	–	X	–	–	–
Scinax nebulosus	–	–	–	X	–	–	–
Scinax ruber	X	X	–	X	–	X	–
Scinax cf. *x-signatus*	X	–	–	X	–	–	X
Scinax sp.	–	–	–	–	X	–	–
Trachycephalus coriaceus	–	–	–	–	X	–	–
Trachycephalus typhonius	–	X	–	X	–	–	–
Adenomera andreae	–	–	–	–	X	–	–
Adenomera hylaedactyla	X	X	–	X	X	X	–
Leptodactylus fuscus	–	X	–	X	–	X	X
Leptodactylus guianensis	–	X	X	X	X	X	–
Leptodactylus knudseni	X	X	X	X	X	–	–
Leptodactylus leptodactyloides	–	X	–	–	–	–	–
Leptodactylus longirostris	–	X	–	–	–	–	X
Leptodactylus macrosternum	–	–	–	–	–	X	X
Leptodactylus mystaceus	X	X	X	X	X	–	–

Table 1.—Continued.

Taxon	BaF	KtF	KoF	DuM	BeF	KaS	AiS
Leptodactylus petersii	–	X	X	X	X	X	–
Leptodactylus rhodomystax	–	X	X	–	X	–	–
Leptodactylus rugosus	–	X	–	–	–	–	–
Leptodactylus validus	X	X	–	X	–	X	–
Lithodytes lineatus	X	X	X	X	X	–	–
Physalaemus cuvieri	X	–	–	X	–	–	–
Pleurodema brachyops	–	–	–	–	–	X	X
Pseudopaludicola boliviana	–	–	–	–	–	X	X
Chiasmocleis jimi	–	–	–	–	X	–	–
Ctenophryne geayi	X	X	–	X	X	–	–
Elachistocleis surinamensis	–	–	–	X	–	–	X
Otophryne pyburni	–	X	–	–	–	–	–
Synapturanus salseri	–	X	X	–	–	–	–
Pipa arrabali	X	X	–	–	–	–	–
Pipa pipa	–	X	–	–	X	–	–
Lithobates palmipes	–	X	X	–	–	–	X
Caecilia tentaculata	–	–	–	X	–	–	–
Rhinatrema shiv	–	–	X	–	–	–	–
Microcaecilia sp.	–	–	X	–	X	–	–
Caiman crocodilus	–	X	–	X	X	–	–
Melanosuchus niger	–	–	–	–	–	X	–
Paleosuchus trigonatus	–	X	X	–	–	–	–
Amphisbaena alba	–	X	–	–	–	–	–
Amphisbaena fuliginosa	–	X	–	X	–	–	–
Hemidactylus mabouia	–	X	–	X	–	–	–
Hemidactylus palaichthus	–	–	–	X	–	X	X
Thecadactylus rapicauda	–	X	X	X	X	–	–
Alopoglossus angulatus	–	–	–	–	X	–	–
Arthrosaura reticulata	–	–	–	–	X	–	–
Bachia flavescens	–	X	X	X	X	–	–
Cercosaura ocellata	–	X	–	X	–	–	X
Echinosaura sulcarostrum	X	–	–	–	–	–	–
Gymnophthalmus leucomystax	–	–	–	–	–	–	X
Gymnophthalmus speciosus	–	–	–	X	–	–	–
Gymnophthalmus underwoodi	–	–	–	X	X	X	X
Gymnophthalmus vanzoi	–	–	–	–	–	X	X
Iphisa elegans	–	X	–	–	X	–	–
Leposoma percarinatum	X	X	X	X	X	–	–
Neusticurus bicarinatus	–	X	–	–	X	–	–
Neusticurus rudis	–	X	X	–	–	–	–
Iguana iguana	–	X	–	X	–	X	X
Anolis aeneus	–	X	–	–	–	–	–
Anolis auratus	–	–	–	X	–	X	X
Anolis fuscoauratus	X	X	X	–	–	–	–
Anolis ortonii	–	X	–	–	–	–	–
Anolis planiceps	X	X	X	–	X	–	–
Anolis punctatus	–	X	–	–	X	–	–
Polychrus marmoratus	–	X	–	X	–	X	X
Mabuya nigropunctata	X	X	X	–	X	–	X
Coleodactylus septentrionalis	–	–	–	–	–	X	–
Gonatodes alexandermendesi	–	X	X	–	–	–	–
Gonatodes annularis	X	X	–	–	X	–	–
Gonatodes humeralis	–	X	X	X	X	–	X
Pseudogonatodes guianensis	–	–	X	X	–	–	–
Sphaerodactylus molei	–	X	–	–	–	–	–

Table 1.—Continued.

Taxon	BaF	KtF	KoF	DuM	BeF	KaS	AiS
Ameiva ameiva	X	X	X	X	X	X	X
Cnemidophorus lemniscatus	–	X	–	X	–	X	X
Kentropyx calcarata	X	X	X	X	X	X	–
Kentropyx striata	–	–	–	X	–	X	X
Tupinambis teguixin	–	X	X	X	–	–	–
Plica plica	X	X	X	–	–	–	–
Plica umbra	X	X	X	X	X	–	–
Tropidurus hispidus	–	–	–	X	–	X	X
Uranoscodon superciliosus	–	X	X	X	X	X	X
Anilius scytale	–	X	X	–	X	–	–
Boa constrictor	X	X	–	X	X	–	–
Corallus caninus	–	X	X	X	–	–	–
Corallus hortulanus	X	X	–	X	X	–	–
Epicrates cenchria	–	X	X	X	–	–	–
Eunectes murinus	–	X	X	X	–	–	–
Atractus torquatus	–	–	–	X	–	–	–
Atractus trilineatus	–	X	–	X	–	–	–
Chironius carinatus	–	–	–	–	–	X	–
Chironius exoletus	–	X	X	–	–	–	–
Chironius fuscus	X	X	–	–	X	–	–
Chironius multiventris	–	X	–	–	X	–	–
Chironius scurrulus	–	X	X	–	X	–	–
Clelia clelia	–	X	–	–	–	–	–
Dipsas catesbyi	–	X	–	–	X	–	–
Dipsas indica	–	X	–	–	–	–	–
Dipsas pavonina	–	X	–	–	–	–	–
Dipsas variegata	X	X	–	–	–	–	–
Drymoluber dichrous	–	X	–	–	X	–	–
Erythrolamprus aesculapii	–	X	–	X	–	–	–
Helicops angulatus	–	X	–	–	X	–	–
Hydrops triangularis	–	X	–	–	–	–	–
Imantodes cenchoa	–	X	X	–	X	–	–
Imantodes lentiferus	X	–	–	–	–	–	–
Leptodeira annulata	–	X	–	X	–	X	–
Leptophis ahaetulla	X	X	X	X	–	X	–
Liophis breviceps	–	X	X	X	–	–	–
Liophis cobella	–	X	–	–	–	–	–
Liophis lineatus	–	X	–	–	–	–	–
Liophis miliaris	X	–	–	–	–	–	–
Liophis poecilogyrus	–	–	–	–	–	X	–
Liophis reginae	–	X	–	–	–	–	–
Liophis typhlus	X	X	–	X	–	–	–
Mastigodryas boddaerti	X	X	–	X	X	X	–
Oxybelis aeneus	–	X	–	–	–	–	–
Oxybelis fulgidus	–	X	X	–	X	–	–
Oxyrhopus melanogenys	–	X	–	X	X	–	–
Oxyrhopus petolarius	X	X	–	X	–	–	–
Philodryas olfersii	–	–	–	X	–	–	X
Philodryas viridissimus	–	X	–	–	–	–	–
Phimophis guianensis	–	–	–	X	–	–	–
Pseudoboa coronata	–	–	–	–	X	–	–
Pseudoboa neuwiedii	–	–	–	X	–	–	X
Pseustes poecilonotus	–	X	X	–	–	–	–
Pseustes sulphureus	–	X	–	–	–	–	–
Rhinobothryum lentiginosum	X	–	–	–	–	–	–

Table 1.—Continued.

Taxon	BaF	KtF	KoF	DuM	BeF	KaS	AiS
Siphlophis compressus	X	X	X	X	–	–	–
Tantilla melanocephala	X	X	–	X	X	–	X
Thamnodynastes ramonriveroi	–	–	–	X	–	–	–
Xenodon rabdocephalus	–	X	–	–	–	–	–
Xenodon severus	X	X	–	–	–	–	–
Micrurus hemprichii	X	–	–	–	–	–	–
Micrurus lemniscatus	X	X	–	–	–	X	–
Micrurus psyches	–	X	–	–	–	–	–
Micrurus surinamensis	–	–	–	X	X	–	–
Epictia albifrons	X	X	–	X	X	–	–
Siagonodon septemstriatus	–	X	–	–	–	–	–
Tricheilostoma dimidiatum	–	–	–	–	–	X	–
Typhlops brongersmianus	–	–	–	X	–	–	–
Typhlops minuisquamus	–	X	–	X	–	–	–
Typhlops reticulatus	–	X	–	X	–	–	–
Bothriopsis bilineata	–	X	–	–	–	–	–
Bothrops atrox	X	X	–	X	X	–	–
Crotalus durissus	–	–	–	X	–	X	–
Lachesis muta	–	X	–	X	–	–	–
Chelus fimbriatus	–	–	–	–	–	X	–
Mesoclemmys gibba	–	X	–	X	–	–	–
Platemys platycephala	–	X	–	–	–	–	–
Podocnemis expansa	–	–	–	–	–	X	–
Podocnemis unifilis	–	X	–	–	–	X	–
Chelonoidis carbonaria	–	–	–	X	–	X	X
Chelonoidis denticulata	X	X	X	–	X	–	–
Total (n = 188 species)	54	127	59	83	65	40	32

The Kartabo fauna appears to be closer in biodiversity to that of Iwokrama (Donnelly et al. 2005), but for Iwokrama many species remain unidentified and not available for examination by us.

Estimating Faunal Resemblance Between Various Localities

How similar (or dissimilar) are the faunas at two or more sites, such as Dubulay Ranch and Berbice River Camp? Simpson (1960) discussed alternative equations for calculating how similar two faunas are. The calculations were based on the total number of species known to occur in each fauna and the number of species known to be shared in common between those faunas, and comparisons were made on a pair-wise basis.

As Simpson (1960) pointed out, no one equation would apply necessarily as the most appropriate for all comparisons. For example, in ideal cases where the two faunas were reasonably well known (i.e., with little to no sampling error) and of similar size, the appropriate faunal resemblance index would be calculated as follows:

$$C/N_1 + N_2 - C \times 100,$$

where C = the number of species found in common at both sites, N_1 = the number of species at one site, and N_2 = the number of species at the other site. In this case, Simpson's equation (1), the resemblance index is "the percentage of taxa in common among the total taxa of the two faunas or samples in question," with possibilities ranging from 0–100% (Simpson 1960:300).

However, in many cases, as in Guyana, sampling of localities may be so inadequate that we do not have, for most sites, a complete inventory of the fauna, as discussed above. Sampling at one site or both may be so incomplete as to lead to very misleading indices with the above equation. To correct for this, at least in part, Simpson (1960) suggested an alternative index, calculated as follows:

$$C/N_1 \times 100,$$

where C = the number of species found in common at both sites and N_1 = the number of species at the site with the smallest fauna known, or presumably most incomplete sample. In this case, Simpson's equation (2), the index is a percentage of the smallest fauna sampled that is shared by both faunas, with possibilities ranging from 0–100%.

We used Simpson's equation (2), the one with correction for incomplete sampling, to compare samples of faunas within Guyana, despite the fact that many herpetologists follow Duellman (1965, 1979, and elsewhere), who used a different equation. The equation Duellman used drops off the % to give a fraction based on $2C/N_1 + N_2$, which is an alternative discussed by Simpson as his formula (4), and for which Simpson (1960:303) stated "it is hard to see a meaningful use for (4)." For faunal comparisons, Voss et al. (2001:182) used "Jaccard's coefficient," as did Silva & Sites (1995), which is the same as Simpson's equation (1), which can be used with or without expression as a percentage, but our incomplete samples did not lend themselves to this. Consequently, we also do not take the extra step taken by the other authors cited, to use UPGMA to produce a dendrogram of the sites and their similarities (e.g., Voss et al. 2001:182). This would be an appropriate future endeavor when more complete biodiversity data are available.

We made faunal comparisons between lowland sites separately from those between isolated highland sites. Differences in environments and habitats are so extensive that there are very few species shared between the lowlands and isolated highlands (see below), and this can be discussed effectively without calculating indices, especially based on the incomplete data that prevail today. When sites of intermediate elevations (upland sites) are involved, overlaps in shared fauna appear with both highland and lowland sites, but none of these intermediate sites in Guyana has been sampled sufficiently for such comparisons now. One such site, Kaieteur National Park, is currently receiving considerable important and careful work, thanks to the efforts of Kok, Kalamandeen, and their colleagues, but these studies are still in progress (see Kok & Kalamandeen 2008).

The Lowland Faunal Comparisons

We selected seven lowland sites to compare, although none has its herpetofauna completely known (see above). Each site is discussed above in Methods (Major Collecting Sites), its location is shown on a map (Fig. 4), and the herpetofauna known for each is listed in Table 1. Note that this table does not list all of the lowland species known for Guyana, but only those species known for the seven sites included in the table. The total number of species found at the various sites ranges from 32–127.

Table 2 shows the number of species known for each site (on the diagonal) and the number of species shared in common by each pair of sites (to upper right of the diagonal). Kartabo, with 127 known species, is the site where by far the most effort was expended, and yet the absence of certain species of small frogs that probably occur there indicates that even the Kartabo inventory is incomplete. The second largest herpetofauna known is for Dubulay Ranch, including the samples for both years we sampled there, which has mixed

Table 2.—Comparisons of number of species of amphibians and reptiles found at seven lowland localities in Guyana. Numbers in diagonal row (in bold italics) are numbers of species found at each site. Numbers to upper right of diagonal are numbers of species found in common at sites where rows and columns meet. Numbers to lower left of diagonal are faunal resemblance indices with correction for small samples (% of species in the smallest sample found in common between the two samples), or $C/N_1 \times 100$, comparing sites where rows and columns meet. The sites are as follows: Ai, Aishalton; Ba, Baramita; Be, Berbice River Camp; Du, Dubulay Ranch; Ka, Karanambo; Ko, Konawaruk Camp; Kt, Kartabo. The habitats are as follows: F, forest; M, patchwork of forest, savanna, and gallery forest; S, savanna (but with gallery forest).

	Ba F	Kt F	Ko F	Du M	Be F	Ka S	Ai S
Ba F	***54***	45	21	30	27	11	6
Kt F	83	***127***	49	58	50	20	14
Ko F	39	83	***59***	28	31	8	5
Du M	56	70	47	***83***	32	27	23
Be F	50	77	53	49	***65***	12	7
Ka S	29	50	21	68	32	***40***	19
Ai S	19	44	16	72	22	59	***32***

habitats. The two least diverse lowland faunas are the two sites on the Rupununi Savanna. What is interesting in this context, though, is that there are savanna species that do not occur in the rainforest, and vice-versa (see below).

Table 2 also shows the faunal resemblance indices (to the lower left of the diagonal) showing the percentage of the smallest sample that is shared by both faunas where rows and columns meet (equation with correction for small samples). The highest index is 83%, for two comparisons: Baramita vs. Kartabo and Konawaruk Camp vs. Kartabo. This is interesting because these three sites are in rainforest habitat and occur on the same side (west) of the Essequibo River, which may be a significant biogeographical item (Hoogmoed 1979). The lowest index is 16% (Aishalton vs. Konawaruk Camp) and close second lowest is 19% (Aishalton vs. Baramita). This is interesting because in both comparisons, one site is in savanna habitat and the other in rainforest, and it is well known that these different habitats have significant differences in faunas (e.g., Hoogmoed 1979). Comparing any two pairs of rainforest sites produced indices of 50% or more, except for one (Baramita vs. Konawaruk Camp, 39%), which is understandable because we worked at Konawaruk Camp (1998) during a major El Niño event and accompanying drought, which must have had a negative impact on our collecting. Comparison of the two savanna sites (Aishalton and Karanambo) produced an index of 59%. The site with mixed habitats (Dubulay Ranch) produced an index of 68–72% compared with the savanna sites and 47–70% compared with the rainforest sites. Indices for rainforest sites occurring to the east of the Essequibo River vs. those occurring to the west varied from 50–77%, demonstrating that many species are shared by faunas on both sides of this major river.

For information on general biogeography of the herpetofauna of the Guianan Region and for faunal differences among species occurring in rainforest vs. savanna habitats, see Hoogmoed (1979). Three very important details pertinent to the biogeography of Guyana are: occurrence of upland and isolated highland endemics in the unique habitats of the Pakaraima Mountains in western Guyana (see below), occupants of lowland rainforests vs. savannas, and the Essequibo [Rupununi]-Río Branco Depression as possibly both a historical barrier to terrestrial fauna (east/west) and a corridor for aquatic fauna (north/south). "The Essequibo-Río Branco Depression seems to have been a barrier to the eastward distribution of a number of species, mainly Pantepui species" (Hoogmoed 1979:257). "The Essequibo-Río Branco Depression forms a barrier for the distribution of a number of eastern forest species to the west and of western forest species to the east" (Hoogmoed 1979:264). "The Essequibo-Río Branco Depression also served as a route for lowland Amazo-

nian species invading the northern part of Guiana...The occurrence in Guyana of the aquatic *Melanosuchus niger* (the black caiman) and *Chelus fimbriatus* (the matamata [turtle]) apparently is the result of the rainy season connection between the Río Branco and the Essequibo River via the flooded Rupununi Savanna" (Hoogmoed 1979:257–258). In addition, the extensive tables provided by Señaris & MacCulloch (2005), on Guianan amphibians, and Avila-Pires (2005), on Guianan reptiles, are annotated with brief comments about endemism and general distribution of most of the species.

Isolated Highland Sites (Above 1400 m Elevation)

The isolated highlands are located in west-central Guyana, and constitute the highest parts of the Pakaraima Mountains, which stand on a base of uplands of intermediate elevations. Most highlands are sandstone mountains, often called tepuis, typical of the Guiana Shield. The highest peaks mark the borders with Venezuela and Brazil. Mount Roraima, the tallest peak in the Pakaraimas within Guyana, at 2810 m elevation, is at the point where Guyana, Brazil, and Venezuela meet. The highlands provide the headwaters of the Cuyuni, Ireng, Mazaruni, and Potaro rivers. Many of the higher peaks support cloud forest habitat, which is not found elsewhere in Guyana.

Herpetological collecting has been carried out primarily at three isolated highland sites (Fig. 4): Mounts Roraima, Ayanganna, and Wokomung. Mount Ayanganna is the highest peak that is entirely within Guyana, at 2000 m. Mount Wokomung, 37 km south of Ayanganna, has its summit at 1700 m. Ayanganna and Wokomung are some 80 km east of Roraima.

Habitats on the three tepuis are quite variable, depending on factors such as elevation, slope, soil depth, moisture, drainage, and exposure. Herpetofaunal collections were not made uniformly in all microhabitats; rather, most collections were made at or near locations suitable for camping, and visits to the high peaks were of relatively short duration. This uneven sampling is a probable cause for some of the apparent differences in faunal composition among the three mountains.

For purposes of comparison, we include only those species collected above 1400 m. In previous studies, highland locations have been considered as those above the arbitrarily chosen elevation of 1500 m (McDiarmid & Donnelly 2005, MacCulloch et al. 2007). However, in some cases major collecting sites of ours were located between 1400–1500 m, and these collections are included here as being from isolated highland sites. Species collected on the three mountains are shown in Table 3.

Composition and origin of tepui herpetofaunas can be complex. Isolated tepuis often support endemic species, some species may occur on two or more tepuis, and some lowland taxa can "invade" higher-elevation habitats. In addition, now isolated but adjacent peaks may once have been part of one high plateau from which the intervening material has eroded away. The degree of species overlap among mountains can depend on factors such as proximity, microhabitats, and local extirpations. Tepui herpetofaunal composition has been examined, for examples, by Myers & Donnelly (2001, 2008), McDiarmid & Donnelly (2005), MacCulloch et al. (2007), and MacCulloch & Lathrop (2009).

Calculations of estimated total number of species (S*) were made for Mounts Ayanganna and Wokomung, using Chao's estimator as for the lowland sites. Because we have no data on the numbers of singletons and doubletons collected on Roraima, we were unable to calculate S* for this location.

Table 3.—Herpetofaunal comparisons of three isolated highland sites in Guyana. X indicates presence of the species, – indicates not documented. The sites are Mounts Roraima, Ayanganna, and Wokomung. Only those specimens reported from above 1400 m are included. Locations are a mix of forest, low vegetation, and in some cases bare rock. Some data are from MacCulloch & Lathrop (2009), MacCulloch et al. (2007), and Means (2007).

Taxon	Roraima	Ayanganna	Wokomung
Anomaloglossus beebei	–	X	–
Anomaloglossus megacephalus	–	X	–
Anomaloglossus praderioi	X	–	–
Anomaloglossus cf. *praderioi*	–	–	X
Anomaloglossus roraimae	X	–	–
Anomaloglossus sp.	–	–	X
Oreophrynella dendronastes	–	X	X
Oreophrynella macconnelli	X	–	–
Oreophrynella quelchii	X	–	–
Rhaebo nasicus	–	–	X
Vitreorana gorzulae	–	–	X
Pristimantis dendrobatoides	–	–	X
Pristimantis inguinalis	–	X	–
Pristimantis jester	–	X	X
Pristimantis marmoratus	X	X	X
Pristimantis pulvinatus	–	X	–
Pristimantis saltissimus	–	–	X
Adelophryne patamona	–	–	X
Stefania ackawaio	–	X	X
Stefania ayangannae	–	X	X
Stefania coxi	–	X	X
Stefania roraimae	X	X	X
Stefania scalae	X	X	–
"*Hyla*" *warreni*	X	X	–
Hypsiboas roraima	X	X	X
Hypsiboas sibleszi	X	X	X
Myersiohyla kanaima	X	X	X
Osteocephalus phasmatus	–	X	X
Osteocephalus sp.	–	X	X
Adenomera lutzi	–	X	X
Leptodactylus fuscus	X	–	–
Pseudopaludicola sp.	X	–	–
Otophryne steyermarki	X	X	X
Epicrionops niger	–	X	–
Arthrosaura guianensis	–	X	–
Arthrosaura reticulata	–	–	X
Neusticurus rudis	X	X	–
Riolama leucosticta	X	–	–
Anolis planiceps	X	–	–
Mabuya nigropunctata	X	–	–
Tropidurus hispidus	X	–	–
Atractus steyermarki	X	–	–
Chironius challenger	–	–	X
Dipsas catesbyi	–	X	–
Dipsas pakaraima	–	X	–
Liophis breviceps	X	–	–
Liophis reginae	–	X	–
Bothriopsis taeniata	X	–	–
Crotalus durissus	X	–	–
Total ($n = 49$ species)	23	26	23

The Isolated Highland Faunal Comparisons

Similarities and differences among the faunas at the three locations are shown in Tables 3 and 4. The three sites are remarkably similar in numbers of species collected, despite the differences in collecting effort. Although all three sites produced 23–26 species, the highest number of species shared among sites is only 14. Species overlap between sites is strongly correlated with distance between the sites. Mounts Ayanganna and Wokomung, which are 37 km apart, have the greatest faunal resemblance (61%), while significantly fewer species are shared between these two sites and the more distant Roraima (both less than 40%). The number of species found at only one of the highland sites is especially striking, indicating a strong distinctiveness of each site.

Table 4.—Comparisons of number of species of amphibians and reptiles found at three isolated highland localities in Guyana. Numbers in diagonal row (in bold italics) are numbers of species found at each site. Numbers to upper right of diagonal are numbers of species found in common at sites where rows and columns meet. Numbers to lower left of diagonal are faunal resemblance indices with correction for small samples (% of species in the smallest sample found in common between the two samples), or $C/N_1 \times 100$, comparing sites where rows and columns meet.

	Roraima	Ayanganna	Wokomung
Roraima	***23***	9	6
Ayanganna	39	***26***	14
Wokomung	26	61	***23***

For Mount Roraima, 14 of 23 species were found only there (61%); for Mount Ayanganna, 8 of 26 species (31%); and for Mount Wokomung, 9 of 23 species (39%). Just as the highlands are important as significant watersheds for Guyana, they also support unique biotas.

Comparisons of Lowland vs. Isolated Highland Sites

At this point in time, only inadequate comparisons of the lowland and isolated highland faunas can be made because the faunal lists are incomplete and more sites need sampling in lowland, upland (intermediate elevations), and isolated highland areas. Consequently, we provide only a few general comments, hoping that future work will lead to rigorous comparisons and a better understanding of the biological phenomena involved.

For the seven lowland sites compared, a total of 188 species were listed (Table 1). For the three isolated highland sites, 49 species were listed (Table 3). Of these, only 11 species out of the total of 224 (5%) were shared between any lowland and highland sites, again showing how distinctive the isolated highland sites are. Those 11 species were *Rhaebo nasicus* (Wokomung and Kartabo), *Leptodactylus fuscus* (Roraima, Kartabo, Dubulay Ranch, Karanambo, and Aishalton), *Arthrosaura reticulata* (Wokomung and Berbice River Camp), *Neusticurus rudis* (Roraima, Ayanganna, Kartabo, and Konawaruk Camp), *Anolis planiceps* (Roraima, Baramita, Kartabo, Konawaruk Camp, and Berbice River Camp), *Mabuya nigropunctata* (Roraima, Baramita, Kartabo, Konawaruk Camp, Berbice River Camp, and Aishalton), *Tropidurus hispidus* (Roraima, Dubulay Ranch, Karanambo, and Aishalton), *Dipsas catesbyi* (Ayanganna, Kartabo, and Berbice River Camp), *Liophis breviceps* (Roraima, Kartabo, Konawaruk Camp, and Dubulay Ranch), *Liophis reginae* (Ayanganna and Kartabo), and *Crotalus durissus* (Roraima, Dubulay Ranch, and Karanambo). Many of these species apparently are widely distributed in the Guianan Region and they appear to have a wide range of tolerance for living in different environments, especially with different temperature regimes. However, one must bear in mind the state of our taxonomic knowledge and realize that some of the apparently wide-ranging taxa, such as *Leptodactylus fuscus*, may actually represent two or more cryptic species that have not yet been recognized as such (e.g., Wynn & Heyer 2001).

All 11 species shared between any lowland and isolated highland sites are species that are wide-ranging at low elevations. It appears as if these lowland species historically dispersed upward onto the mountains from below. Note also that of these 11 species only one, *Neusticurus rudis*, was found at more than one highland site. This suggests a haphazard, perhaps opportunistic, nature of lowland species successfully colonizing the highlands. None of the 11 shared species appears to be a high elevation form that has invaded the lowlands from above, although highland taxa did shift ranges downward in elevation during glacial maxima, which affected distribution of biota even in areas that lacked glaciers (e.g., Rull 2005). This also demonstrates the importance of each isolated highland as a unique area in which evolution has produced endemic novelties, although, paradoxically, the lineages of some highland endemics may be ancient, reflecting the deep history of the tepuis of the Guiana Shield, which has been above sea level for longer than the entire evolutionary history of the vertebrates. The Pakaraima Mountains have high peaks of distinctive habitats, including considerable bare rock, surrounded below by lowlands of tropical

Table 5.—Numbers of species shared in common between seven lowland and three isolated highland sites in Guyana. A total of 224 different species were found at these ten sites, showing that few species are shared between the lowlands and highlands. The sites are as follows: Ai, Aishalton; Ba, Baramita; Be, Berbice River Camp; Du, Dubulay Ranch; Ka, Karanambo; Ko, Konawaruk Camp; Kt, Kartabo.

Site	Ba	Kt	Ko	Du	Be	Ka	Ai
Roraima	2	5	4	4	2	3	3
Ayanganna	1	2	1	0	1	0	0
Wokomung	0	1	0	0	1	0	0

rainforest, like islands in the sea. As erosion of the highlands progresses, new species evolve on newly isolated peaks while the surrounding lowland species may remain relatively stable. In addition, the peaks are very small geographic areas and consequently, while their floras and faunas are distinctive and unique, the list of their species is relatively short.

Table 5 shows the number of species shared in the isolated highland vs. lowland sites. For 13 of the 21 comparisons (62%), 0 or only 1 species was shared, again showing how distinctive the isolated highlands are. The highest degree of shared highland and lowland species was between Roraima and Kartabo, with 22% of Roraima's fauna shared. The next highest were Roraima vs. Konawaruk Camp (17% of Roraima's) and Roraima vs. Dubulay Ranch (17% of Roraima's). These sites are all forested or with mixed habitats. Few species were shared between isolated highlands and the more distant sites on the low-elevation Rupununi Savanna.

The list of species for the seven lowland sites compared (Table 1) included 71 amphibians and 117 reptiles; or amphibians comprised 38%. In strong contrast, the list of species for the three isolated highland sites (Table 3) included 34 amphibians and only 15 reptiles; or amphibians comprised 69%. In general, this probably indicates that amphibians are better than reptiles at tolerating and adapting to relatively low temperature regimes within the tropics.

Areas of Endemism and Other Special Areas

The currently documented herpetofauna of Guyana includes 324 species (148 amphibians, 176 reptiles, including those in Appendix 1). Of these, 49 species (15%) are endemic or near-endemic species, found nowhere else in the world (or only marginally, in similar habitat of immediately adjacent areas, for example, the Pakaraima highlands of Brazil and Venezuela). For amphibians, the number of endemic species (27%) is much higher than for reptiles (5%). This is consistent with the observation that most of the endemic species are from isolated highlands, where amphibians apparently are better than reptiles at adapting to low temperatures (see Biogeography, above).

Table 6 lists the endemic species, their type localities, and also the type localities within Guyana for more wide-ranging species that were originally described primarily or only based on samples from Guyana. Type localities are within Guyana for 78 species of amphibians and reptiles, or 24% of the herpetofauna. This includes 53 amphibians (36%) and 25 reptiles (14%). The fact that one-third of the amphibians have their type localities in Guyana and more than one-quarter of the amphibians are endemic to Guyana attests to how special this fauna is in global terms.

Two of the species in Table 6 have yet to be described and named. For the 78 species with type localities in Guyana, 35 (45%) are from 6 areas in the Pakaraima uplands and isolated highlands, as follows: Kaieteur National Park (9 species, or 12%); Mt. Roraima (8 species, or 11%); Mt. Ayanganna (8 species, or

Table 6.—Endemic species (although these may occur in limited areas of adjacent countries in the Pakaraima Mountains) and type localities of amphibians and reptiles within Guyana. Type localities are abbreviated; see species accounts (in same sequence as given here) for details. + = yes; – = no.

Species	Endemic	Type locality
Amphibians		
Allophryne ruthveni	–	Tukeit Hill, below Kaieteur Falls
Allobates spumaponens	+	Mabura Hill Forest Reserve
Anomaloglossus beebei	+	Kaieteur National Park
Anomaloglossus kaiei	+	Kaieteur National Park
Anomaloglossus megacephalus	+	Mt. Ayanganna
Anomaloglossus roraima	+	Mt. Roraima
Oreophrynella dendronastes	+	Mt. Ayanganna
Oreophrynella macconnelli	+	Mt. Roraima
Oreophrynella quelchii	+	Mt. Roraima
Oreophrynella seegobini	+	Mt. Maringma
Oreophrynella weiassipuensis	+	Wei-Assipu-Tepui
Hyalinobatrachium taylori	–	New River area
Ceuthomantis smaragdinus	+	Mt. Kopinang, Wokomung Massif
Pristimantis aureoventris	+	Wei Assipu Tepui
Pristimantis dendrobatoides	+	Wokomung Massif
Pristimantis inguinalis	–	New River area
Pristimantis jester	+	Mt. Wokomung
Pristimantis saltissimus	+	Wokomung Massif
Dendrobates nubeculosus	+	Rockstone, Essequibo River
Adelophryne gutturosa	–	Mt. Roraima
Adelophryne patamona	+	Mt. Wokomung
Stefania ackawaio	+	Mt. Ayanganna
Stefania ayangannae	+	Mt. Ayanganna
Stefania coxi	+	Mt. Ayanganna
Stefania evansi	+	Groete Creek, Essequibo
Stefania roraimae	+	Mt. Roraima
Stefania woodleyi	+	Mt. Kanaima, Pakaraima Mts.
Dendropsophus grandisonae	+	Forest at Mazaruni
"*Hyla*" *helenae*	+	Dunoon, valley of Demerara River
"*Hyla*" *warreni*	+	Mt. Roraima
Hypsiboas calcaratus	–	"British Guiana"
Hypsiboas liliae	+	Kaieteur National Park
Hypsiboas ornatissimus	–	Meamu, Mazaruni River
Hypsiboas roraima	+	Mt. Roraima
Lysapsus laevis	–	Rupununi Savanna
Myersiohyla kanaima	+	Mt. Kanaima, Pakaraima Mts.
Osteocephalus exophthalmus	+	Pakaraima uplands
Osteocephalus phasmatus	+	Mt. Ayanganna
Scinax sp.	"+"	Undescribed, Berbice River Camp
Tepuihyla talbergae	+	Kaieteur National Park
Trachycephalus hadroceps	–	Acarai Mts., W of New River
Adenomera lutzi	+	Pakaraima uplands
Leptodactylus guianensis	–	Iwokrama Forest Reserve
Leptodactylus rugosus	–	Kaieteur National Park
Chiasmocleis shudikarensis	–	Shudikar-wau, upper Essequibo River
Synapturanus mirandaribeiroi	–	Kanashen, upper Essequibo River
Caecilia pressula	+	Marudi Mts.
Oscaecilia zweifeli	–	Tributary of Mazaruni River
Epicrionops niger	–	Arundabara uplands
Rhinatrema shiv	+	Kaieteur National Park
Caecilita iwokramae	+	Iwokrama uplands
Microcaecilia iyob	+	Oko River at Cuyuni River
Microcaecilia cf. *rabei*	"+"	Undescribed

Table 6.—Continued.

Species	Endemic	Type locality
Reptiles		
Amphisbaena stejnegeri	+	Vreeden Rust, Demerara River
Amphisbaena vanzolinii	–	Marudi Mts.
Hemidactylus palaichthus	–	Kurupukari
Arthrosaura guianensis	+	Mt. Ayanganna
Arthrosaura hoogmoedi	+	Mt. Maringma
Echinosaura sulcarostrum	+	Baramita
Kaieteurosaurus hindsi	+	Kaieteur National Park
Leposoma guianense	–	Dunoon, Demerara River
Neusticurus rudis	–	Foot of Mt. Roraima
Pantepuisaurus rodriguesi	+	Mt. Maringma
Ptychoglossus brevifrontalis	–	New River area
Riolama leucosticta	+	Mt. Roraima
Tretioscincus agilis	–	Near Dunoon
Gonatodes alexandermendesi	–	Konawaruk Camp
Gonatodes annularis	–	Maccasseema, Pomeroon River
Gonatodes timidus	+	Iwokrama Forest Reserve
Pseudogonatodes guianensis	–	Upper Cuyuni River
Atractus tamessari	+	Kaieteur National Park
Chironius challenger	–	Maringma Tepui
Dipsas pakaraima	+	Mt. Ayanganna
Ninia hudsoni	–	New River area
Phimophis guianensis	–	Savanna, vicinity of Pirara
Micrurus averyi	–	Head, Itabu Creek, New River area
Phrynops tuberosus	–	Cotinga River, Mt. Roraima
Podocnemis unifilis	–	Rupununi and Takutu rivers
Totals	49	78

11%); the Wokomung Massif (5 species, or 7%); Mt. Maringma (4 species, or 5%); and Wei Assipu Tepui (1 species, or 1%). It is noteworthy that the site representing the highest number of species in this context, Kaieteur National Park, is both a site of intermediate elevations and the one where the most extensive studies have been made (e.g., Kok & Kalamandeen 2008).

The numbers cited above show clearly that the Pakaraima uplands and isolated highlands are special for the biodiversity of Guyana. Nevertheless, the type localities (Table 6) also show that areas of special significance to biodiversity are scattered throughout the country, even in the lowlands, including the following sites: Baramita; Dunoon and Vreeden Rust, Demerara River; Iwokrama and Mabura Hill forest reserves; Berbice River and Konawaruk Camps; Groete Creek and Rockstone, Essequibo River; Kanashen and Shudikar-wau, upper Essequibo River; the Rupununi Savanna; Marudi Mountains; and the New River area.

Endangered Species

The Red List of the International Union for the Conservation of Nature (IUCN) includes a comprehensive assessment of the conservation status of the known species of amphibians of the world. The first assessment of all amphibians was completed as the Global Amphibian Assessment in 2004 (Chanson et al. 2008a), and the process is ongoing with periodic updates that incorporate new information, including newly described species. The

current Red List (IUCN 2010) uses the following categories of conservation status, listed from the least to greatest concern: Least Concern; Near Threatened; Vulnerable; Endangered; Critically Endangered; Extinct in the Wild; and Extinct. Another category, Data Deficient, is for species for which there is not yet sufficient information to make a judgment. Threatened species are included in the categories of Vulnerable, Endangered, and Critically Endangered.

The Neotropical Realm, which stretches from central Mexico southward throughout South America and includes all of the Caribbean Islands, has by far the greatest species richness of amphibians. This includes nearly half of the amphibians of the world, 96% of which are endemic to the Realm (Chanson et al. 2008b). This Realm also has the greatest proportion of threatened and extinct species of amphibians in the world, and it is the region that has been impacted hardest by the lethal amphibian fungal disease, chytridiomycosis. Whereas the overall threat level is high in Neotropica (60% of all globally threatened amphibians occur here) compared to the rest of the world, threat levels are comparatively low in the Guiana Shield (Bolaños et al. 2008), and in general, populations of amphibians in Guyana appear to be in good condition.

None of the modern species of amphibians that occur in Guyana is listed as Extinct or Extinct in the Wild. Similarly, none is listed as Critically Endangered, Endangered, or Near Threatened. Considering the species that occur in Guyana (and surrounding areas), 81% are listed as Least Concern, 16% are listed as Data Deficient, and only 3% are listed in the lowest threatened category of Vulnerable (Table 7, in which we did not include the species listed as of Least Concern). The following eight species that were described recently or have yet to be described were not included in the latest assessment (IUCN 2010): *Anomaloglossus megacephalus*, *Oreophrynella seegobini*, *Ceuthomantis smaragdinus*, *Scinax* sp., *Caecilita iwokramae*, *Microcaecilia iyob*, *Microcaecilia* cf. *rabei*, and *Rhinatrema shiv*.

Table 7.—Amphibians listed by the IUCN Red List (IUCN 2010) as species of concern for conservation, with the exception of species listed as Least Concern. DD = Data Deficient; VU = Vulnerable. Population Trend is indicated by Decreasing, Stable, or Unknown (Ukn).

Species of concern	Status	Population Trend
Anomaloglossus beebei	VU	Stable
Anomaloglossus praderioi	DD	Ukn
Anomaloglossus roraima	DD	Ukn
Atelopus spumarius	VU	Decreasing
Oreophrynella dendronastes	DD	Ukn
Oreophrynella macconnelli	VU	Stable
Oreophrynella quelchii	VU	Stable
Oreophrynella weiassipuensis	DD	Ukn
Vitreorana gorzulae	DD	Ukn
Vitreorana helenae	DD	Ukn
Hyalinobatrachium iaspidiense	DD	Ukn
Dendrobates nubeculosus	DD	Ukn
Adelophryne patamona	DD	Stable
Stefania roraimae	DD	Ukn
Dendropsophus grandisonae	DD	Ukn
"*Hyla*" *helenae*	DD	Ukn
"*Hyla*" *warreni*	DD	Ukn
Hypsiboas roraima	DD	Ukn
Osteocephalus exophthalmus	DD	Ukn
Osteocephalus phasmatus	DD	Ukn
Tepuihyla talbergae	DD	Ukn
Adenomera lutzi	DD	Ukn
Chiasmocleis jimi	DD	Ukn
Caecilia pressula	DD	Ukn
Oscaecilia zweifeli	DD	Ukn
Microcaecilia rabei	DD	Ukn

The IUCN has yet to complete a modern assessment of the conservation status of the reptiles of the world, comparable to that of the amphibians. The reptiles are the last group to be completed for the terrestrial vertebrates, and it has been initiated through a series of regional projects (IUCN 2010). Nevertheless, an earlier assessment had listed only the five sea turtles of Guyana (100% of them) as being of significant conservation concern among all the reptiles (excluding birds), with 40% of the sea turtles Critically Endangered, 40% Endangered, and 20%

Vulnerable–Decreasing. The status of these species is also under review.

Summary and Conclusions

We confirm that at least 324 species of amphibians and reptiles occur in Guyana. This includes 148 amphibians (137 frogs and toads, 11 caecilians) and 176 non-avian reptiles (4 crocodylians, 4 amphisbaenians, 56 lizards, 97 snakes, and 15 turtles). These are listed in Appendix 2.

Documentation of these species was accomplished through field work and identification of specimens that we and field associates including UG students collected; reidentifying old museum specimens collected by others in the past (e.g., William Beebe); and reviewing documented publications and collection records of colleagues (e.g., Pritchard 1969, Kok & Kalamandeen 2008; collection of Peter C. H. Pritchard's Chelonian Research Institute). Voucher specimens are cited in all our species accounts and references in Appendix 1. To date, no other large group of animals of Guyana has received such detailed treatment.

Undoubtedly, Guyana has additional species that remain to be discovered, named, and described, and perhaps 20 additional species known from adjacent countries will ultimately be found to occur in Guyana. Furthermore, future research, especially involving molecular genetics, undoubtedly will reveal that some populations interpreted today as representing wide-ranging species are actually comprised of multiple cryptic species yet to be recognized.

Consequently, we are confident that within a few decades the herpetofauna of Guyana will be confirmed at more than 350 species and this report will need updating.

We present dichotomous keys for identifying representatives of all the species known in the herpetofauna of Guyana, and we present brief annotated species accounts. However, some species are listed and discussed in Appendix 1, as they became known to us after we completed nearly all of our text in 2011. For the species accounts, we have examined and verified all the original literature references in which the species were named, but we have not tried to survey all scientific collections in the world to confirm every single specimen collected in Guyana in the past.

Aspects of biogeography are discussed based on collections made at seven lowland sites (4 in rainforest, 2 in savanna, 1 in mixed habitats; all below 500 m elevation) and three sites in isolated highlands (in montane forest and evergreen high-tepui forest; all above 1400 m elevation). This discussion presents preliminary comparisons because the sampling of each local fauna is incomplete; more field effort is necessary.

Although much remains to be learned, it is clear that an area of about 2.5 km^2 of lowland rainforest in Guyana probably supports more than 130 species of amphibians and reptiles, whereas many fewer species (fewer than 30 documented) live in a comparable area of the isolated highlands. Comparisons of the faunal lists of these 10 sites show that very few species occur in both the lowlands and isolated highlands (all are widespread lowland forms); that many endemic species occur in the isolated highlands (mostly amphibians); and that each of the isolated highlands, lowland savannas, and lowland rainforests at 10 sites have distinctive faunal elements. No two sites were identical in species composition. Much more work is needed to compare a variety of sites, and especially to incorporate upland sites of intermediate elevations in future comparisons.

Endemic species, which occur nowhere else in the world, comprise 15% of the herpetofauna of Guyana. Although some of the endemic species are lowland rainforest species, most are amphibians of the isolated highlands and uplands of the Pakaraima Mountains, where they live in headwaters of major watersheds. In fact, about 27% of the amphibian fauna is endemic to Guyana, or nearly so.

Another gauge of the distinctiveness of a fauna is to review the type localities in an area. These are the localities from which the population samples were collected that included the type specimens, which are the permanent, formal name-bearers for the species. For 24% of the herpetofauna (36% of amphibians, 13% of reptiles), the type locality of the species is within Guyana, and we discuss several specimens of amphibians in the species accounts that probably represent new species, as yet to be described and named.

Five species of sea turtles utilize the limited areas of Atlantic coastal beaches in Guyana, primarily to the northwest of Georgetown. All of these, (100%) are listed by the International Union for the Conservation of Nature as being of global concern for long-term survival, mostly owing to predation by humans (IUCN 2010): 2 species (40%) are listed as being Critically Endangered (*Eretmochelys imbricata* and *Dermochelys coriacea*); 2 (40%) are listed as Endangered (*Caretta caretta* and *Chelonia mydas*); and 1 (20%) is listed as Vulnerable–Decreasing (*Lepidochelys olivacea*). Clearly, it is important to protect the nesting beaches of the sea turtles.

It appears to us that Guyana is fortunate in having its native amphibian and reptilian faunas in very good shape in comparison to many other countries, particularly those elsewhere in which certain amphibians have become extinct and others are suffering dramatic losses. We hope that preservation of the original fauna and flora will continue to be an important goal within Guyana.

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This work was conducted in accordance with the national and international regulations that apply to travel in Guyana, wildlife protection, and humane euthanasia of samples with approved protocols of the various institutions involved. We also

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Appendix 1

Species Added to the Guyana Herpetofauna after Completion of Our Text

Amphibia, Anura, Craugastoridae

Pristimantis aureoventris.—This recently described species is known from only two isolated highland localities, from 2210–2305 m elevation. The type locality is on Wei Assipu Tepui on the border of Guyana and Brazil, and the other locality is on the Guyana portion of Mount Roraima. The description is very thorough, lavishly illustrated, and compares the new species with congeners from relevant localities (Kok et al. 2011).

Amphibia, Anura, Dendrobatidae

Ranitomeya amazonica.—Species of *Ranitomeya* are colorful, diminutive frogs that were previously included in the genus *Dendrobates*. In particular, *Ranitomeya* is a taxonomically difficult genus that has representatives basically throughout Amazonia, with many cryptic species. The most recent generic revision (Brown et al. 2011) shows that specimens are identified to species with the greatest confidence by using molecular data, but in many cases one can estimate an identification based only on old museum specimens or photographs. Brown et al. (2011:85) stated that "based on morphology" of a museum specimen, this species occurs at the following locality: "Guyana (Region: Upper Takutu-Upper Essequibo)" (Brown et al. 2011:86). On pages 117–120 they listed the museum specimens examined but did not give the locality data for them.

Ranitomeya uakarii.—Brown et al. (2011) on their page 51 showed (Fig. 17H) a frog photographed "in life, Iwokrama, Guyana (unknown photographer)." Apparently there is no voucher specimen. In their Fig. 22 (p. 56), this was mapped as *R. uakarii* "based on morphology" and on page 57 they stated that "we provisionally consider the Guyana population as *R. uakarii*." This needs to be confirmed, especially with molecular data, as all other specimens known are from southern Colombia, eastern Peru, or extreme western Brazil. This species is very similar to *Ranitomeya ventrimaculata* and names previously applied to it include *Dendrobates quinquevittatus* and *D. ventrimaculatus*.

Reptilia, Lizards, Gymnophthalmidae

Ptychoglossus brevifrontalis.—Peloso & Avila-Pires (2010:372) reported that BMNH 139.1.1.75 is a representative of this previously described species from "Suriname/Guyana: New River, 750 feet." Their determination was made from photographs. Very superficially (color, pattern, size), this species resembles *Arthrosaura reticulata* and to a lesser extent *Alopoglossus angulatus*, but there are considerable differences in scalation.

Reptilia, Lizards, Polychrotidae

Anolis chrysolepis.—See comments in the species account for *Anolis planiceps*. In the past, these two forms were treated as subspecies of one wide-ranging species, but recent molecular analyses indicated that the subspecies should be elevated to the species level, although some forms are not well-differentiated morphologically (D'Angiolella et al. 2011). These authors cited two specimens of *A. chrysolepis* from southern Guyana, and one was recently received at the ROM.

Anolis (sensu lato).—Townsend et al. (2011) performed extensive phylogenetic analyses of DNA sequence data and concluded that *Anolis* and *Polychrus* are not supported as each others' closest relative. As representatives of these genera clustered in different monophyletic groups, these authors proposed a new family, Dactyloidae, to accommodate the genus *Anolis*.

Reptilia, Lizards, Sphaerodactylidae

Gonatodes timidus.—This recently described species is known only from the base of the Iwokrama Mountains in the Iwokrama Forest Reserve, central Guyana (4°19′52″N, 58°47′58″W; 209 m elev.). The description is thorough, with extensive illustrations and detailed comparisons with congeners (Kok 2011).

Reptilia, Snakes, Colubridae

Mastigodryas moratoi.—Montingelli & Zaher (2011) described and named this new species, in part based on AMNH R-141798 from 3.2 km by road WNW Dubulay Ranch house (5°37′N, 57°53′W), Guyana. All known specimens are from Brazil and Guyana. On their page 119 and on map (p. 112) the authors included Kuyuwini Landing, Guyana in the range, but they did not cite any specimens from this locality. AMNH has specimens of *Mastigodryas* from Kuyuwini Landing, including R-60782 and R-60810, both or either of which might be the basis of the comment. CJC examined both of these specimens and confirmed that AMNH R-60810 is *M. moratoi*; AMNH R-60782 was not identified, as neither the light stripes nor hemipenes were visible (see below). Another AMNH specimen from Kuyuwini Landing, R-60852, is *M. boddaerti*, so the two species are sympatric at this locality. *Mastigodryas moratoi* is a member of the *pleei* species group, which "is distinguished from both [the] *melanolomus* and *boddaerti* groups by the length and position of the upper light lateral stripes...on the dorsum. In the former group, the larger upper light lateral stripes are formed by three dorsal scale rows that include the upper portion of row 3, [all of] row 4, and the inner [= lower] portion of row 5, whereas in the latter two groups the upper light lateral stripes are only two

dorsal scale rows wide, being formed by rows number 4 and 5…" (Montingelli & Zaher 2011:111). The adult from near Dubulay Ranch house (AMNH R-141798) was described in life by CJC (field notes, 1995) as follows. Anteriorly, dorsum light tan with brown and black contrasting stripes (the black only anteriorly on the dorsolateral stripe). Posteriorly, the pattern soon gradually becomes a broad brown stripe on a tan ground color. Further posteriorly, the dorsum becomes uniform dark tan, continuing through the tail. Top of head brown; lips white, with dark brown to black line from snout through eye, along top of labials; underside of head dark gray with white spots; throat and anterior ventral surfaces pale tan with extensive gray markings; rest of ventral surfaces orangish tan with gray markings becoming fewer posteriorly while orange becomes bolder, especially beneath base of tail, but turning yellow further posteriorly beneath tail.

Appendix 2

List of Currently Known Herpetofauna of Guyana (324 Species)

The following list includes all the species in our keys and species accounts, as well as those most recently discovered after our basic text was completed (Appendix 1).

Amphibia: 148 species:
- Anura (137 species of frogs and toads)
  - Allophrynidae:
    - *Allophryne ruthveni*
  - Aromobatidae (formerly in Dendrobatidae; genera formerly *Colostethus*, *Dendrobates*, *Epipedobates*):
    - *Allobates femoralis*
    - *Allobates spumaponens* (was *C. brunneus* in Guyana)
    - *Anomaloglossus beebei*
    - *Anomaloglossus kaiei*
    - *Anomaloglossus megacephalus*
    - *Anomaloglossus praderioi*
    - *Anomaloglossus roraima*
  - Bufonidae:
    - *Atelopus spumarius*
    - *Dendrophryniscus minutus*
    - *Oreophrynella dendronastes*
    - *Oreophrynella macconnelli*
    - *Oreophrynella quelchii*
    - *Oreophrynella seegobini*
    - *Oreophrynella weiassipuensi*s
    - *Rhaebo guttatus* (formerly *Bufo*)
    - *Rhaebo nasicus*
    - *Rhinella marina* (formerly *Bufo*)
    - *Rhinella martyi* (formerly *margaritifera*, *typhonius*)
    - *Rhinella merianae*
  - Centrolenidae (genera formerly *Centrolene, Cochranella*):
    - *Hyalinobatrachium cappellei* (sr. syn. *crurifasciatum* in Guyana)
    - *Hyalinobatrachium iaspidiense*
    - *Hyalinobatrachium mondolfii*
    - *Hyalinobatrachium taylori*
    - *Vitreorana gorzulae* (sr. syn. *papillahallicum*)
    - *Vitreorana helenae* (sr. syn. *oyampiensis* in Guyana)
  - Ceratophryidae (formerly in Leptodactylidae):
    - *Ceratophrys cornuta*
  - Ceuthomantidae:
    - *Ceuthomantis smaragdinus*
  - Craugastoridae: (formerly in Leptodactylidae; genus *Eleutherodactylus*):
    - *Pristimantis aureoventris*
    - *Pristimantis chiastonotus*
    - *Pristimantis dendrobatoides*
    - *Pristimantis inguinalis*
    - *Pristimantis jester*
    - *Pristimantis marmoratus*
    - *Pristimantis pulvinatus*
    - *Pristimantis saltissimus*
    - *Pristimantis zeuctotylus*
  - Dendrobatidae:
    - *Ameerega hahneli* (formerly *Dendrobates, Epipedobates pictus* in Guyana)
    - *Ameerega trivittata*
    - *Dendrobates leucomelas*
    - *Dendrobates nubeculosus*
    - *Dendrobates tinctorius*
    - *Ranitomeya amazonica*
    - *Ranitomeya uakarii*
  - Eleutherodactylidae (formerly in Leptodactylidae):
    - *Adelophryne gutturosa*
    - *Adelophryne patamona*
    - *Eleutherodactylus johnstonei*
  - Hemiphractidae (formerly in Hylidae):
    - *Stefania ackawaio*
    - *Stefania ayangannae*
    - *Stefania coxi*
    - *Stefania evansi*
    - *Stefania roraimae*
    - *Stefania scalae*
    - *Stefania woodleyi*
  - Hylidae:
    - *Dendropsophus brevifrons* (formerly *Hyla*)
    - *Dendropsophus grandisonae*
    - *Dendropsophus leucophyllatus*
    - *Dendropsophus marmoratus*
    - *Dendropsophus minusculus*
    - *Dendropsophus minutus*
    - "*Hyla*" *helenae*
    - "*Hyla*" *warreni*

- *Hypsiboas boans* (formerly *Hyla*)
- *Hypsiboas calcaratus*
- *Hypsiboas cinerascens* (formerly *granosa* in Guyana)
- *Hypsiboas crepitans*
- *Hypsiboas fasciatus*
- *Hypsiboas geographicus*
- *Hypsiboas lemai*
- *Hypsiboas liliae*
- *Hypsiboas multifasciatus*
- *Hypsiboas ornatissimus*
- *Hypsiboas punctatus*
- *Hypsiboas roraima*
- *Hypsiboas sibleszi*
- *Lysapsus laevis* (formerly *limellus*)
- *Myersiohyla kanaima* (formerly *Hyla*)
- *Osteocephalus buckleyi*
- *Osteocephalus cabrerai*
- *Osteocephalus exophthalmus*
- *Osteocephalus leprieurii*
- *Osteocephalus oophagus*
- *Osteocephalus phasmatus*
- *Osteocephalus taurinus*
- *Phyllomedusa bicolor*
- *Phyllomedusa hypochondrialis*
- *Phyllomedusa tarsius*
- *Phyllomedusa vaillantii*
- *Pseudis paradoxa*
- *Scinax boesemani* (formerly *Hyla*, *Ololygon*)
- *Scinax cruentommus*
- *Scinax nebulosus*
- *Scinax proboscideus*
- *Scinax ruber*
- *Scinax trilineatus*
- *Scinax* cf. *x-signatus*
- *Scinax* sp.
- *Sphaenorhynchus lacteus*
- *Tepuihyla talbergae*
- *Trachycephalus coriaceus* (formerly *Phrynohyas*)
- *Trachycephalus hadroceps*
- *Trachycephalus resinifictrix*
- *Trachycephalus typhonius* (formerly *venulosus*)

Leptodactylidae:

- *Adenomera andreae*
- *Adenomera hylaedactyla*
- *Adenomera lutzi*
- *Engystomops* cf. *pustulosus*
- *Leptodactylus fuscus*
- *Leptodactylus guianensis* (formerly *bolivianus*)
- *Leptodactylus knudseni*
- *Leptodactylus leptodactyloides*
- *Leptodactylus longirostris*
- *Leptodactylus macrosternum* (formerly *ocellatus*)
- *Leptodactylus mystaceus*
- *Leptodactylus pentadactylus*
- *Leptodactylus petersii* (formerly *podicipinus*)
- *Leptodactylus rhodomystax*
- *Leptodactylus rugosus*
- *Leptodactylus validus* (formerly *pallidirostris*)
- *Lithodytes lineatus*
- *Physalaemus cuvieri*
- *Pleurodema brachyops*
- *Pseudopaludicola boliviana*

Microhylidae:

- *Chiasmocleis hudsoni*
- *Chiasmocleis jimi*
- *Chiasmocleis shudikarensis*
- *Ctenophryne geayi*
- *Elachistocleis surinamensis* (formerly *ovalis*)
- *Hamptophryne boliviana*
- *Otophryne pyburni*
- *Otophryne robusta*
- *Otophryne steyermarki*
- *Synapturanus mirandaribeiroi*
- *Synapturanus salseri*

Pipidae:

- *Pipa arrabali*
- *Pipa pipa*

Ranidae:

- *Lithobates palmipes* (formerly *Rana*)

Gymnophiona (11 species of caecilians):

Caeciliidae:

- *Caecilia gracilis*
- *Caecilia pressula*
- *Caecilia tentaculata*
- *Oscaecilia zweifeli*

Rhinatrematidae:

- *Epicrionops niger*
- *Rhinatrema shiv*

Siphonopidae:

- *Caecilita iwokramae*
- *Microcaecilia iyob*
- *Microcaecilia rabei*
- *Microcaecilia* cf. *rabei*

Typhlonectidae:

- *Typhlonectes compressicauda*

Reptilia: 176 species:

Crocodylia (4 species):

Alligatoridae:

- *Caiman crocodilus*
- *Melanosuchus niger*
- *Paleosuchus palpebrosus*
- *Paleosuchus trigonatus*

Squamata: Amphisbaenians or worm lizards (4 species)

Amphisbaenidae:

- *Amphisbaena alba*
- *Amphisbaena fuliginosa*
- *Amphisbaena stejnegeri*
- *Amphisbaena vanzolinii*

Squamata: lizards (56 species)

Corytophanidae:

- *Basiliscus basiliscus*

Gekkonidae:

- *Hemidactylus mabouia*

- *Hemidactylus palaichthus*
- *Thecadactylus rapicauda*

Gymnophthalmidae (formerly within Teiidae):

- *Alopoglossus angulatus*
- *Arthrosaura guianensis*
- *Arthrosaura hoogmoedi*
- *Arthrosaura reticulata*
- *Bachia flavescens* (formerly *monodactylus*)
- *Cercosaura argulus* (formerly *Prionodactylus*)
- *Cercosaura ocellata*
- *Echinosaura sulcarostrum*
- *Gymnophthalmus leucomystax*
- *Gymnophthalmus* cf. *speciosus*
- *Gymnophthalmus underwoodi*
- *Gymnophthalmus vanzoi*
- *Iphisa elegans*
- *Kaieteurosaurus hindsi*
- *Leposoma guianense*
- *Leposoma percarinatum*
- *Neusticurus bicarinatus*
- *Neusticurus rudis*
- *Pantepuisaurus rodriguesi*
- *Ptychoglossus brevifrontalis*
- *Riolama leucosticta*
- *Tretioscincus agilis*

Iguanidae:

- *Iguana iguana*

Polychrotidae:

- *Anolis aeneus*
- *Anolis auratus*
- *Anolis chrysolepis*
- *Anolis fuscoauratus*
- *Anolis ortonii*
- *Anolis planiceps* (formerly *nitens*, *chrysolepis*)
- *Anolis punctatus*
- *Polychrus marmoratus*

Scincidae:

- *Mabuya nigropunctata* (formerly *mabouia*)

Sphaerodactylidae (formerly in Gekkonidae):

- *Chatogekko amazonicus* (formerly *Coleodactylus*)
- *Coleodactylus septentrionalis*
- *Gonatodes alexandermendesi*
- *Gonatodes annularis*
- *Gonatodes humeralis*
- *Gonatodes timidus*
- *Gonatodes vittatus*
- *Pseudogonatodes guianensis*
- *Sphaerodactylus molei*

Teiidae:

- *Ameiva ameiva*
- *Cnemidophorus lemniscatus*
- *Kentropyx borckiana*
- *Kentropyx calcarata*
- *Kentropyx striata*
- *Tupinambis teguixin*

Tropiduridae:

- *Plica plica*
- *Plica umbra*
- *Tropidurus hispidus*
- *Uracentron azureum*
- *Uranoscodon superciliosus*

Squamata: snakes (97 species):

Aniliidae:

- *Anilius scytale*

Anomalepidae:

- *Typhlophis squamosus*

Boidae:

- *Boa constrictor*
- *Corallus caninus*
- *Corallus hortulanus*
- *Epicrates cenchria*
- *Eunectes murinus*

Colubridae *sensu lato*:

- *Apostolepis nigrolineata*
- *Atractus favae*
- *Atractus schach*
- *Atractus steyermarki*
- *Atractus tamessari*
- *Atractus torquatus*
- *Atractus trilineatus*
- *Chironius carinatus*
- *Chironius challenger*
- *Chironius exoletus*
- *Chironius fuscus*
- *Chironius multiventris*
- *Chironius scurrulus*
- *Clelia clelia*
- *Dendrophidion dendrophis*
- *Dipsas catesbyi*
- *Dipsas copei*
- *Dipsas indica*
- *Dipsas pakaraima*
- *Dipsas pavonina*
- *Dipsas variegata*
- *Drepanoides anomalus*
- *Drymarchon corais*
- *Drymobius rhombifer*
- *Drymoluber dichrous*
- *Elapomorphus quinquelineatus*
- *Erythrolamprus aesculapii*
- *Helicops angulatus*
- *Hydrodynastes bicinctus*
- *Hydrops triangularis*
- *Imantodes cenchoa*
- *Imantodes lentiferus*
- *Leptodeira annulata*
- *Leptophis ahaetulla*
- *Liophis breviceps*
- *Liophis cobella*
- *Liophis lineatus*
- *Liophis miliaris*
- *Liophis poecilogyrus*
- *Liophis reginae*
- *Liophis typhlus*
- *Mastigodryas boddaerti*
- *Mastigodryas moratoi*
- *Ninia hudsoni*

- *Oxybelis aeneus*
- *Oxybelis fulgidus*
- *Oxyrhopus melanogenys*
- *Oxyrhopus occipitalis* (formerly *formosus* in Guyana)
- *Oxyrhopus petolarius*
- *Philodryas olfersii*
- *Philodryas viridissimus*
- *Phimophis guianensis*
- *Pseudoboa coronata*
- *Pseudoboa neuwiedii*
- *Pseudoeryx plicatilis*
- *Pseustes poecilonotus*
- *Pseustes sulphureus*
- *Rhinobothryum lentiginosum*
- *Sibon nebulatus*
- *Siphlophis cervinus*
- *Siphlophis compressus* (formerly *Tripanurgos*)
- *Spilotes pullatus*
- *Tantilla melanocephala*
- *Thamnodynastes pallidus*
- *Thamnodynastes ramonriveroi*
- *Xenodon merremii* (formerly *Waglerophis*)
- *Xenodon rabdocephalus*
- *Xenodon severus*
- *Xenopholis scalaris*
- *Xenoxybelis argenteus*

Elapidae:

- *Micrurus averyi*
- *Micrurus collaris* (formerly *Leptomicrurus*)
- *Micrurus hemprichii*
- *Micrurus isozonus*
- *Micrurus lemniscatus*
- *Micrurus psyches*
- *Micrurus surinamensis*

Leptotyphlopidae (genera formerly *Leptotyphlops*):

- *Epictia albifrons* (formerly *tenellus*)
- *Siagonodon septemstriatus*
- *Tricheilostoma dimidiatum*
- *Tricheilostoma macrolepis*

Typhlopidae:

- *Typhlops brongersmianus*
- *Typhlops minuisquamus*
- *Typhlops reticulatus*

Viperidae:

- *Bothriopsis bilineata*
- *Bothriopsis taeniata*
- *Bothrops atrox*
- *Bothrops brazili*
- *Crotalus durissus*
- *Lachesis muta*

Testudinata (15 species of turtles and tortoises):

Chelidae:

- *Chelus fimbriatus*
- *Mesoclemmys gibba* (formerly in *Phrynops*)
- *Phrynops tuberosus*
- *Platemys platycephala*

Cheloniidae:

- *Caretta caretta*
- *Chelonia mydas*
- *Eretmochelys imbricata*
- *Lepidochelys olivacea*

Dermochelyidae:

- *Dermochelys coriacea*

Emydidae:

- *Rhinoclemmys punctularia*

Kinosternidae:

- *Kinosternon scorpioides*

Podocnemididae (formerly in Pelomedusidae):

- *Podocnemis expansa*
- *Podocnemis unifilis*

Testudinidae:

- *Chelonoidis carbonaria* (formerly *Geochelone*)
- *Chelonoidis denticulata*