

# The Herpetofauna of the Guayana Highlands: Amphibians and Reptiles of the Lost World

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South America has an extremely diverse herpetofauna that includes about one-third of all living amphibian and one-fifth of all living reptile species (Duellman 1979b, 1999; Uetz 2000). The rate of discovery and description of amphibian and reptile species, unlike that of birds and mammals, continues to increase. Many of these new taxa are from South America (Bauer 1998; Glaw and Köhler 1998), a continent for which 60% of the species of amphibians have been described in the past 40 years (Duellman 1999). In contrast to other continents, South America has only moderate topographic complexity. Lowlands cover about half of the continent and are associated primarily with the major drainage systems of the Orinoco, Amazon, and Paraná rivers. The highland regions are generally discrete and occur in the northeast (Guayana Shield), the southeast (Brazilian Shield), and along the western margin of the continent (Andes). Narrow coastal lowlands fringe these upland areas in the east and west. Even though the tropical lowland regions and their wet forests contribute substantially to herpetofaunal species diversity, species diversity among amphibians is highest in montane regions, where the numbers of endemics are high (usually above 75%; Duellman 1999). Comparable data for species of reptiles are not available, but typically, species diversity of reptiles in montane regions lags behind that of amphibians (e.g., amphibians make up 64% of the Andean herpetofauna; Duellman 1979c). In contrast, reptile diversity in lowland Neotropical regions may be 20%–30% higher than that of amphibians in any particular area (e.g., Hoogmoed 1979a; Duellman 1990).

In 1979, Hoogmoed reviewed the Guianan herpetofauna and published a list of species of amphibians and reptiles known from the region. Hoogmoed pointed out the relatively high degree of endemism in highland components of the fauna. He evaluated the distributional patterns of the endemics in light of various hypotheses that had been used to explain distributions of other organisms from the same region. The appearance of that seminal publication, which coincided with early work by McDiarmid on the eastern tepuis, provided a starting point for our efforts and those of others to document the herpetofauna of the Guayana Highlands. Recently, Gorzula and Señaris (1998) published an account of the species of amphibians and reptiles collected by Gorzula from 1974 to 1990, largely in the Río Caroní watershed in Bolívar state. Although restricted to the Venezuelan Guayana, that treatment made another important contribution to our understanding of the distributions and species diversities of the amphibians and reptiles of the region. Gorzula and Señaris (1998, 1) expressed the hope that “these raw data could provide both a stimulus and a starting point for others to attempt a more definitive account of the herpetofauna of this region.” Their statement, combined with the natural appeal of the region, our research interests, and past and on-going field investigations, served as the stimulus for this review. In this chapter we briefly describe the physical and biological characteristics of the Guayana Highlands, review the fieldwork and publications that have appeared since Hoogmoed’s pioneering contribution, compile a list of the highland herpetofauna by massif/tepui, identify patterns reflected in the distributions of the component species, and offer some explanation for those patterns.

### *The Guayana Region*

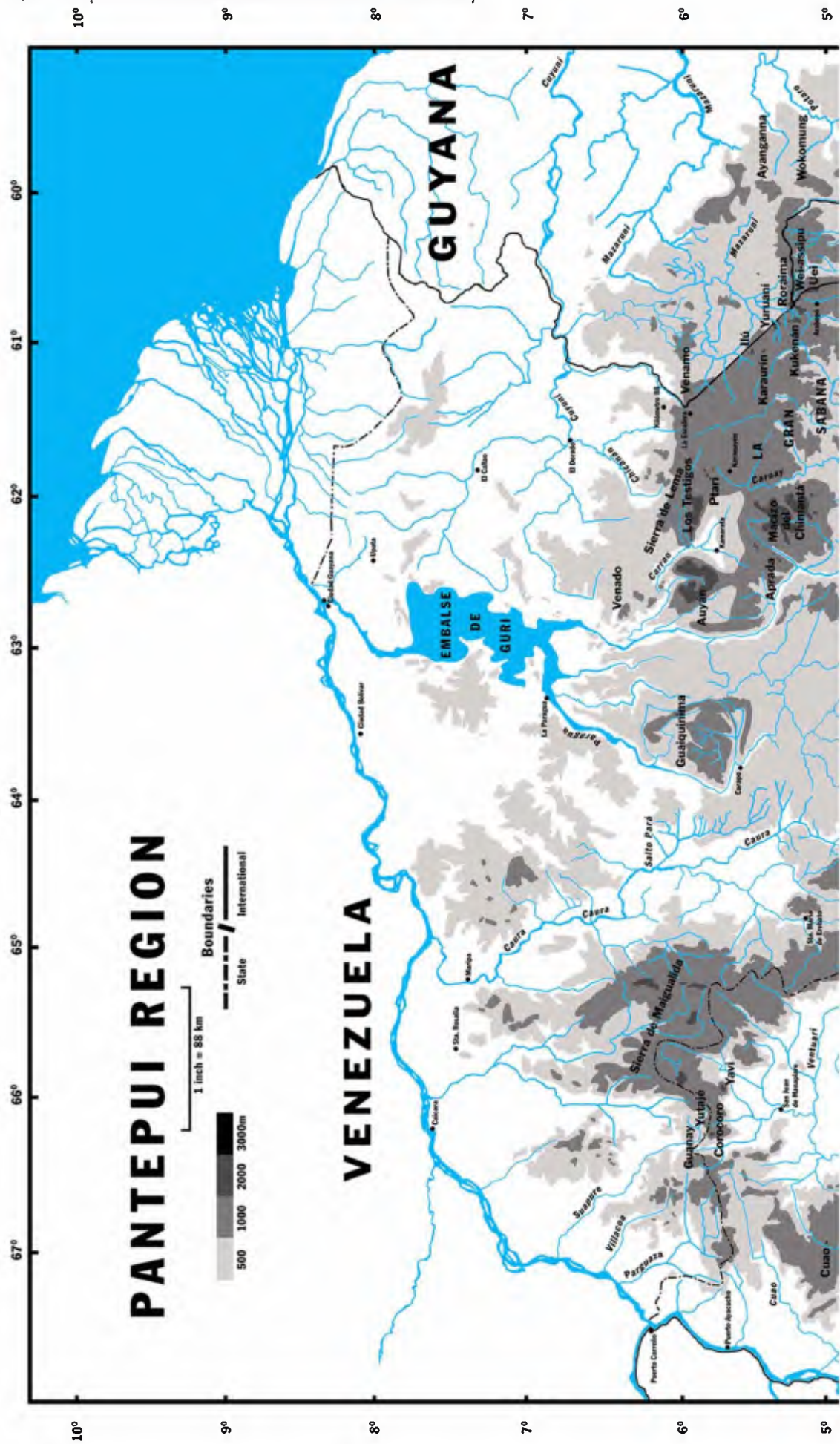
A brief comparison of the three highland areas of South America will help to put our discussion of the Guayana Highlands in perspective. Each has a complex and contrasting history, provides an array of different habitats, and harbors a diverse and highly endemic fauna. The series of meridionally oriented Andean mountain chains that extend along the entire western edge of the continent (Tierra del Fuego in the south to Panama in the north) forms the most obvious and most extensive highland area. The Andes include some of the highest mountains in the world and exert a primary influence on the climates of western South America. Compared with the other two upland areas, the Andes are relatively young. Lundberg et al. (1998) gave a detailed reconstruction of the Andean orogeny through its 90-million-year history and focused on the complex geologic history of the continent relative to its major river systems. They showed unequivocally that the current patterns of west-to-east flow of the Amazon and Orinoco rivers resulted from the final uplift of the Mérida Andes and Eastern Cordillera of Colombia approximately 8 million years ago.

Two immense and older upland areas, the Brazilian and Guayana shields,

occupy the eastern parts of South America and are essentially Precambrian in age (Simpson 1979). These areas, derived from the western section of Gondwanaland, contain some of the oldest terrestrial habitats on the continent. The Brazilian Shield covers much of the continent south of the Amazon and north and east of the Paraná. Although more extensive, the Brazilian Shield tends to be lower, supports drier habitats, and lacks the distinctive, isolated mountains characteristic of the Guayana region. Together with the Andes, the Guayana and Brazilian shields contribute noticeably to the geographic layout of the continent (Lundberg et al. 1998) and have affected the composition and distribution of its biota both historically and ecologically.

The Guayana Shield occupies a vast area that extends approximately 1,500 km in an east-to-west direction from the coast of Suriname to southwestern Venezuela and adjacent Colombia and covers much of the southern portions of Venezuela, Guyana, and Suriname as well as portions of French Guiana and extreme northern Brazil. Extensive lowland forests and savannas, as defined by the Orinoco, Negro, and Amazon rivers, separate this region from the Andean highlands to the north and west and from the northern portions of the Brazilian Shield to the south (Lundberg et al. 1998). Various authors have used the terms *Guiana*, *Guyana*, and *Guayana* and their derivatives to refer to the entire region or to parts of it, and three countries in the region have had or currently use some form of the word in their names. In this chapter, we follow an author's usage when referring to his or her work (see Berry, Holst, et al. 1995). Otherwise, we use *Guayana* because it has a broader and less political meaning.

The Guianan region was broadly delimited by Hoogmoed (1979a) as the area south of the Río Orinoco, east of the Cassiquiare Canal and the Río Negro, north of the Río Amazonas, and west and south of the Atlantic Ocean. From a phytogeographical perspective, the Guayana region encompasses the area from central French Guiana, Suriname, and Guyana, westward through the northern portions of the Brazilian states of Pará, Roraima, and Amazonas, most of the Venezuelan states of Bolívar and Amazonas, and parts of the southeastern Colombian departments of Guainía, Vichada, and Vaupés (Huber 1994; Berry, Huber, et al. 1995). Contrary to treatments by certain authors (e.g., Maguire 1979), that of Berry, Huber, et al. (1995) specifically excluded the Cordillera de Macarena located in Meta at the base of the Colombian Andes, and we concur. Topographically, the Guayana region is marked by extensive uplands (500–1,500 m), isolated highlands (> 1,500 m), and peripheral lowlands (< 500 m) that occur along the rivers and on the coastal plain. This region is mostly characterized by nutrient-poor soils and a flora of notable species richness (approximately 15,000 species), high endemism, and diversity of growth forms. The most significant geographic feature of the Guayana region is the presence of mid- to high-elevation areas that make up its physiographic core. These highlands, collectively called the Guayana Highlands or Pantepui (fig. 18.1), consist of loosely clustered groups of isolated mountains that range





from approximately 1,300 to more than 3,000 m in elevation and harbor a diverse and highly endemic herpetofauna.

### *Pantepui: The Guayana Highlands*

#### HISTORY

Mayr and Phelps (1955) first used the term *pantepui* in the title of a paper they gave in 1954. In a subsequent paper, Mayr and Phelps (1967, 275) explicitly proposed *Pantepui* as an arbitrary name to refer collectively to “the sandstone tabletop mountains in the Venezuelan Territorio Amazonas and Estado Bolívar and in the adjacent border regions of Brasil and Guyana.” Although Mayr and Phelps (1967) specifically stated that Cerro el Negro (a granite mountain of 1,200 m elevation in northern Amazonas) and Cerro de la Neblina (600 km to the south on the Brazilian border) were not tabletop mountains, they included them in their treatment of the Pantepui mountains on faunistic grounds.

Maguire (1970, 1972, 1979) used *Guayana* in a general sense to refer to the region overlain by the Roraima Formation (see the section titled “Geology”) and its outwash sediments, but restricted *Guayana* as a floristic province to those parts of the Guayana Shield that included tepuis; he considered the Tafelberg in Suriname and the Cordillera (Sierra) de Macarena in Colombia to be the easternmost and westernmost sites, respectively, in that province.

Müller (1973) used *Pantepui* and *Roraima* as names for two dispersal centers for terrestrial vertebrates in the region, and Brown (1975, 1987) used *Pantepui* as a name for a center of endemism of lowland forest butterflies in the southeastern part of Bolívar state. Relatively few workers have used Müller’s classification, and like Huber (1987), we find it difficult to incorporate Brown’s concepts, derived from forest butterflies, into a broader biogeographic pattern for Pantepui.

Steyermark (1982, 200) expanded Mayr and Phelps’s definition of Pantepui to include “not only the sandstone tabletop mountains in the Venezuelan Territorio Amazonas and Estado Bolívar and in the adjacent border regions of Brazil and Guyana, . . . but also the Gran Sabana at the base of the eastern Venezuelan tepuis, the edaphic lowland sand savannas and igneous ‘laja’ formations of the western part of the Territorio Federal Amazonas, and the extreme northeastern sector drained by the Río Venamo and tributaries.” In so doing, he included lowlands in his notion of Pantepui, in contrast to Mayr and Phelps (1967), who specifically defined the term to accommodate only the mountains. Steyermark (1982) argued that because the flora of the Guayana Highlands appears to be unified but also differentiated, it was preferable to maintain it as a single large unit but recognize eastern and western subdivisions. In this sense, he followed the lead of Mayr and Phelps (1967), who divided Pantepui into eastern and western subdivisions separated primarily by the Río

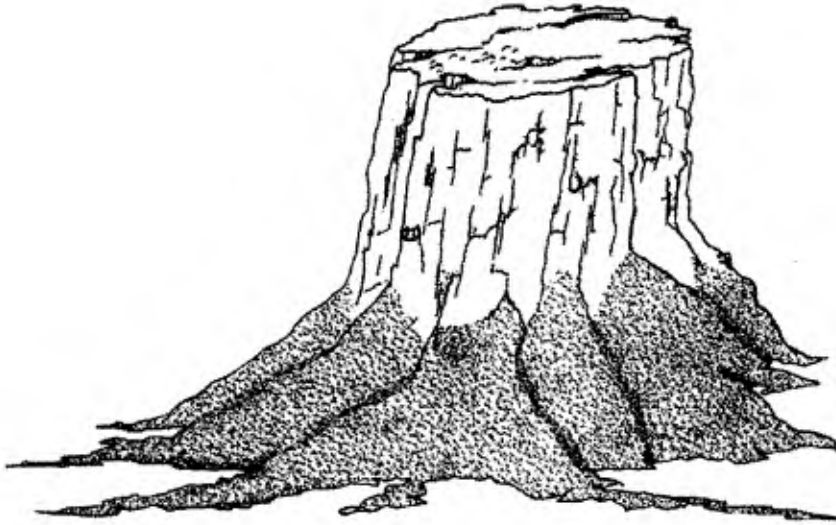


Figure 18.2 Schematic representation of a typical tepui with forested slopes and surrounding savannas (modified from a figure in Means 1995).

Caroní. Mayr and Phelps (1967) also noted that the Pantepui avifauna was not evenly distributed, despite the relatively high vagility of birds, and that species differed between the two divisions.

Huber (1987) recommended use of the term *Pantepui* to refer to the complex of mountains in the Guayana region of southern Venezuela, northeastern Guyana, southern Suriname, and northern Brazil whose major components were derived from the sandstone of the Roraima Group that lies atop the Guayana Shield. The majority of these mountains (fig. 18.2) are relatively isolated, have summits that today are above 1,200 m elevation, and share a common geological history. Huber's concept of Pantepui was more than a geographically based entity; he reasoned that because Pantepui has common geological, geomorphological, chemical, and biological attributes, it is distinct from the surrounding lowland ecosystems. In this chapter, we use Huber's concept of Pantepui.

#### PHYSIOGRAPHY

The Guayana region has been divided into subregions that differ among authors (e.g., Maguire 1979; Huber 1987, 1995a). In the most recent phytogeographical treatment, Berry, Huber, et al. (1995) recognized four provinces: Pantepui, and Eastern, Central, and Western Guayana. The Pantepui Province comprises the central highlands, whereas the latter three include lowlands with some scattered upland regions. Huber (1987) initially subdivided the Pantepui Province into five geographically defined sectors, but subsequently Berry, Huber, et al. (1995) modified that scheme and recognized four districts defined primarily by geographical criteria (major drainages) and floristics. We follow their

arrangement, with only minor modifications, because it has a strong geographical component and treats lowlands and highlands separately (appendix 18.1).

The Eastern Pantepui District includes those highlands that occur east of the Río Caroní, a major drainage that flows north into the lower Río Orinoco (fig. 18.1). Most of these tepuis are in the Caroní basin, but those in western Guyana are drained by the Mazaruni and Essequibo rivers. Maguire (1979) indicated that the Guyana tepuis might deserve separate treatment when they are better known. Tepuis in Brazil are in the drainage of the Río Branco, a tributary of the Amazon. Water from the summit of Roraima flows into all three drainages. We recognize three subdistricts, Roraima, Los Testigos, and Chimantá, for the eastern, north central, and western tepuis, respectively. We separated the Los Testigos group from the Chimantá group because of its geographically intermediate position. Berry, Huber, et al. (1995) also commented on the transitional nature of these tepuis.

The Western Pantepui District is the most extensive and includes sandstone and granite mountains whose summits reach between 1,300 and 2,350 m elevation; it is bounded by the Río Caura, Río Orinoco, and Río Ventuari systems (fig. 18.1). The summits (between 1,800 and 2,350 m) of the granitic Sierra Maigualida and other high mountains along the eastern edge of the district are mostly forested and make up the Maigualida Subdistrict. The Yutajé Subdistrict includes Guanay, Yaví, Corocoro, and Yutajé tepuis, the summits of which lie at elevations from 1,800 to 2,300 m and have a high diversity of shrubland (M. A. Donnelly, pers. obs.). Cerro Yaví and Cerro Yutajé are relatively dry tepuis with little or no peat on their summits. The Cuaó-Sipapo Subdistrict includes several small sandstone tepuis and granitic mountaintops that reach elevations between 1,400 and 2,000 m. Tepuis in this subdistrict are poorly explored and have wet meadows, high-tepui shrub, and open rock habitats.

The Central Pantepui District (the Jaua-Duida District of Berry, Huber, et al. 1995) includes a number of large sandstone massifs in southwestern Bolívar and east-central Amazonas states, Venezuela (fig. 18.1). The summits of most of these tepuis are between 1,500 and 2,800 m. We recognize four subdistricts rather than three (Berry, Huber, et al. 1995), tentatively placing Cerro Guaiquinima in its own subdistrict. Cerro Guaiquinima is a centrally located, well-defined large tepui that lies in the Paragua drainage well to the west (> 100 km) of the Chimantá-Auyán massifs of the Eastern Pantepui District. Berry, Huber, et al. (1995, 173, 175) placed Guaiquinima, along with Cerro Yapacana, the Tafelberg (a Suriname outlier), and other uplands with summits above 1,500 m elevation, in the Central Guayana Province. However, the summit of Cerro Guaiquinima lies at 1,650 m (Huber 1995a) and thus, by their own definition, should be in Pantepui; accordingly, we place Cerro Guaiquinima in its own subdistrict within the Central Pantepui District. The other three subdistricts are Jaua-Sarisariñama, in the upper Paragua and Caura river drainages (we also place the



Sierra Marutaní here); Asisa, which includes the poorly explored Parú Massif at approximately 2,200 m elevation, and the lower (up to 1,300 m), forested Parima uplands in the Río Ventuari system; and Duida-Marahuaka in the upper Río Orinoco drainage. The latter subdistrict includes the moderately well-explored Cerro Duida and an adjacent tepui, Cerro Marahuaka; together with Cerro Huachamacari to the north, these tepuis have summits that lie between 1,900 and 2,800 m, are somewhat isolated, and have several distinctive vegetation types. We have included the much lower (1,300 m) Cerro Yapacana here as well, because of geographic location.

The Southern Pantepui District includes some high sandstone tepuis and granitic mountains along the southern border of Venezuela (fig. 18.1). For the most part, these highlands, whose summits range from 1,600 to 3,014 m, are drained by tributaries of the Río Negro. This region is complex geologically and consists of both quartzitic and igneous units (Berry, Huber, et al. 1995). Extensive shrublands and broad-leaved, high-tepui meadows occur on Neblina, which has been well explored compared with the other highlands in this district. Although poorly known as a whole, this region has the highest number of endemic plant taxa of the entire Guayana region.

The major tepuis and other uplands and highlands that make up Pantepui of the Guayana region are listed in appendix 18.1; most are shown on the map in figure 18.1. If the maximum elevation of a tepui was less than 1,500 m (i.e., an upland, not a highland), we usually added it to our list. Thus, some uplands whose highest elevations do not exceed 1,500 m are included (e.g., Cerro Venado in the Chimantá Subdistrict). When known, the approximate elevational range for each tepui is included in appendix 18.1 (data from Huber 1987, 1995a; T. Hollowell, pers. comm.; available maps).

## GEOLOGY

The Guayana Shield is made up of igneous and metamorphic rock (granites, gneisses, schists) of Proterozoic age. A thick layer of sedimentary rock (sandstone and quartzite) called the Roraima Group (also Series or Formation) lies atop this crystalline basement. Younger intrusive rocks (diabases and granites) have penetrated the basement and sedimentary layers, and their sills are scattered throughout the formation. The granitic basement apparently formed during four orogenic events between 0.8 and 3.6 billion years ago. Geologic evidence argues that the multiple layers of sand that were heavily compressed and cemented together to form the Roraima Group, which must have been thousands of meters deep in some areas, were deposited atop the granite between 1.5 and 1.8 billion years ago (Ghosh 1985). The absence of fossil material also supports a Precambrian age. Ghosh (1985) noted that the original Roraima sediments could have had a minimal surface area of approximately 250,000 km<sup>2</sup>.

Extensive ripple marks and cross-bedded sections in freshly exposed sandstone surfaces on the summits of several eastern tepuis attest to several periods of deposition (in a shallow sea or large inland lake [S. Ghosh, pers. comm.]; Huber 1995a), probably beginning in the east and later filling in western and southern basins. Whatever the case, the Roraima sandstone has been in place much longer than most terrestrial life. Huber (1995a), Maguire (1970), Schubert and Briceño (1987), and Steyermark (1986) summarized the geologic history of the region, and detailed treatments were written by Gansser (1974) and Ghosh (1977, 1985).

Reid (1974) delineated four strata of the Roraima Formation whose distinctive thicknesses and compositions are easily seen on Mount Roraima. Rock in each stratum differs in color and hardness, evidently reflecting compositional differences. Strata on eastern tepuis are often level-bedded (e.g., Roraima) or gently sloped (e.g., Auyán), whereas those on western tepuis, where visible (e.g., Duida), are largely deformed. The four stratigraphic patterns described for the eastern tepuis are not evident on many western, central, and southern tepuis that we have visited. These differences may reflect variations in patterns of deposition in eastern versus western tepuis. If so, then the eastern strata are likely older than western and southern ones, and the older granitic mountains of Parima and Maigualida may have separated the different sedimentation basins (Huber 1995a). Given the extreme age of these events, it seems unlikely that any separation would be reflected in present-day patterns of herpetofaunal diversity. If, however, the distinct rocky habitats characteristic of the summits of the eastern tepuis are a consequence of differential patterns of deposition and subsequent erosion of the sandstone, then the occupation of these habitats should be manifest in the evolutionary history of the herpetofauna.

The initial uplift of the granitic base and roofing sandstone of the Guayana Highlands probably occurred more than 2 billion years ago (Schubert and Briceño 1987). Three other periods of uplift have been reported, one each in the Mesozoic, the Paleocene, and the later Tertiary. Recent history has been marked by intense erosion and minor eustatic changes (Simpson 1979). A schematic model that describes the erosional surfaces seen at different elevations on tepuis is available (Schubert and Briceño 1987). The flat-topped summits that characterize many tepuis (fig. 18.3) apparently are the result of horizontally layered sandstone and quartzite strata. Most summits occur at elevations between 2,000 and 2,600 m, with several in the eastern chain being higher. Occasionally, the flat summits are surmounted by higher conical peaks that rise to over 3,000 m, as occurs in the Sierra de la Neblina. Most tepuis have sculpted, vertical walls, or escarpments, that drop 300–700 m, and sometimes more than 1,000 m, to the surrounding lowlands; some (e.g., Auyán) have a series of vertical drops that form step-like sides (fig. 18.4). Several larger massifs (e.g., Auyán, Jaua, Duida) have sizable streams that may flow continuously; others (e.g., Roraima,



Figure 18.3 Aerial view of Aparamán-tepui looking west from Murisipán-tepui, in the Los Testigos Massif. Murochiopán is the small tepui in the foreground between Murisipán and Aparamán, and Padapué-tepui of the Los Hermanos group is to the left and beyond Aparamán. The northwest extent of Auyán-tepui appears in the distance.

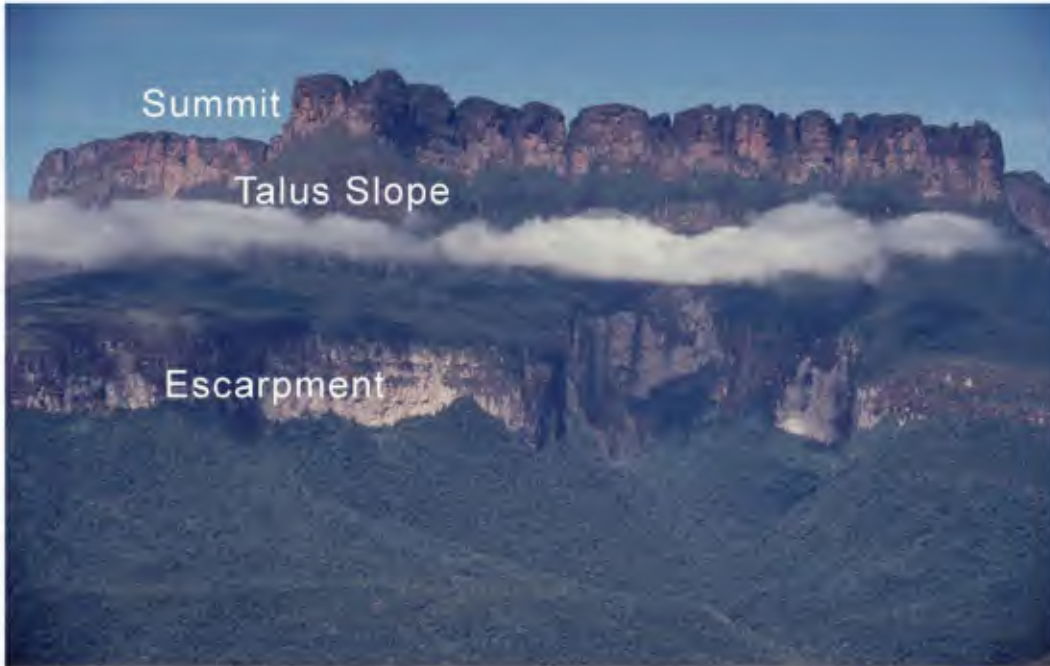


Figure 18.4 The step-like escarpments of Auyán-tepui as seen from the south.

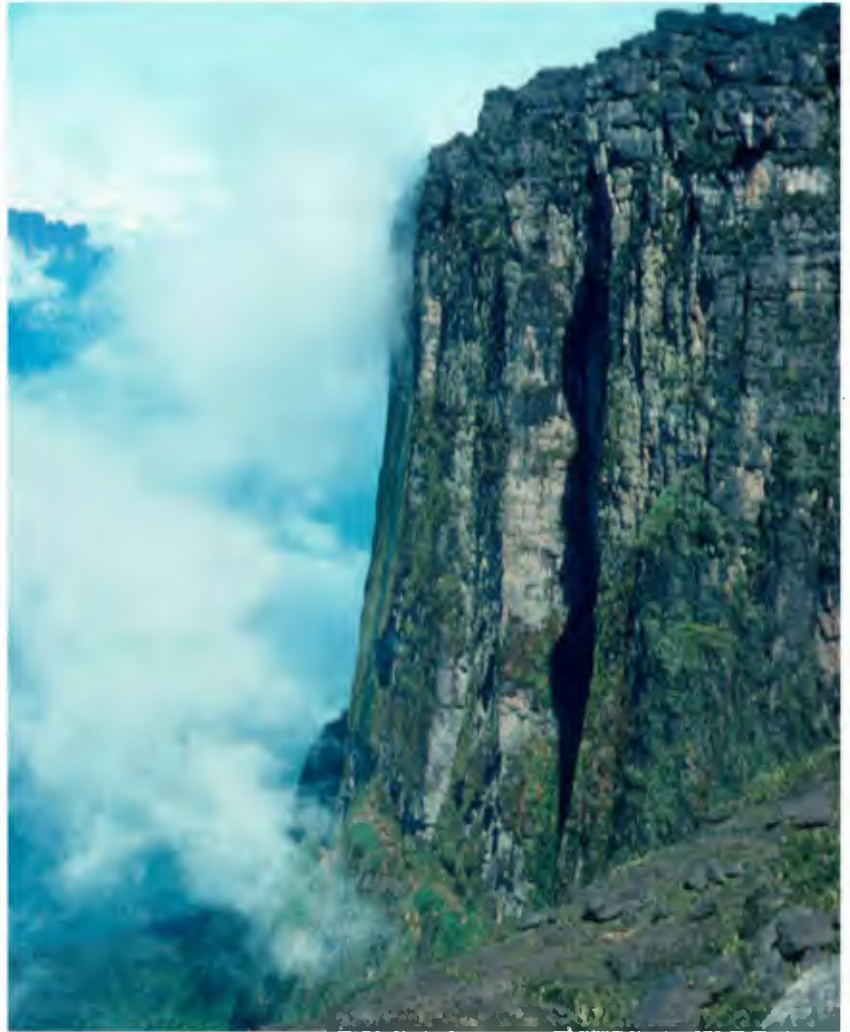
Kukenán, Ptari, Yaví) accumulate rainwater in shallow depressions, some of which may be of considerable expanse, and drain through a few nonpermanent streams that plunge as intermittent waterfalls over the escarpment. The lower slopes and the talus that forms at the base of these cliffs often include very large blocks of stone and rocky debris that have separated and fallen from the escarpment. The slopes often are steep and covered by a dense mossy forest that is bathed by moisture from dense clouds that form along their cliffs. Summits are often deeply cut by streams that follow rock crevices and contact zones between strata (e.g., Auyán-tepui). Presumably, valleys between adjacent tepuis within some massifs (e.g., Chimantá) were formed by rivers that began as small water courses on their summits.

The principal consequences of this long erosional history are the flat-topped mountains with vertical pink cliffs and cascading waterfalls. This type of highland is what Pemón Amerindians of southeastern Venezuela call a *tepui*. Appropriately, this term has been added as a suffix to many specifically named mountains in the region. Tepuis have provided the settings for some exciting science and science fiction (e.g., *The Lost World* by Arthur Conan Doyle, 1912; see fig. 18.5) and likely will continue to do so for decades to come.

## SOILS

The soils of the Guayana Highlands are moderately diverse, highly acidic, and generally low in nutrients. Poor soil quality is the result of low mineral content

Figure 18.5 (Right) View of the western flank of Roraima with Kukenán in the background. (Below) The Eastern Tepui Chain from the Gran Savanna. From the left, the eastern tepuis are Tramen, Ilú, and Karaurín, with the pinnacle of Wadakapiapué lying in the gap (left of center), followed (at right) by Yuruani, Kukenán, and Roraima.



of the parent rock as well as the long and extreme weathering to which they have been subjected. The following comments are based on Huber (1995a) and our observations. Many tepui summits have relatively little soil, and summits of many eastern tepuis are largely bare sandstone. Here, plants grow wherever they can get a start, often in shallow sand derived from weathered rock, and some plants respond to nutrient limitation by trapping insects or nutrients (e.g., sundews and bromeliads; Huber 1995a). On other tepuis (e.g., Duida), deep (up to 2 m) layers of decomposing organic materials (peat) form histosols atop rocky substrates. These boggy areas are generally open and devoid of trees, provide easy helicopter access, and frequently are used for campsites (e.g., Neblina). Entisols are characteristic of the extensive savannas that surround many tepuis and are made up of fine- to coarse-grained white sands. These soils are often high in iron and aluminum and are known for their poor quality (Huber 1995a). The soils (e.g., oxisols) that support forests in the region are composed of white sand with varying amounts of clay.

#### CLIMATE

The climate of the Guayana Highlands environment is the result of the interplay between the trade winds and the annual oscillations of the Intertropical Convergence. Trade winds carry cool moisture-laden air onto the warm continent, and the eastern tepuis are among the first major upland areas contacted in Guayana. As a result, mean annual rainfall decreases from east to west and south to north. The Sierra de la Maigualida may cause a local rain shadow on its western slopes and on tepuis to the west (e.g., Cerro Yaví); similar effects are seen at sites in the southern Gran Sabana. The mean annual temperature in the lowlands (0–500 m) is always greater than 24°C, and the annual rainfall varies from approximately 2,000 mm in the north to 4,200 mm in the upper Caroní, Paragua, and Caura river basins. A distinct dry season occurs from December through February in northern areas and is almost imperceptible in December and January to the south. Mean annual temperatures at upland elevations (500–1,200 m) range from 18° to 24°C, and mean annual rainfall is 2,000 mm or higher (data are sparse for the region). Mean annual temperatures at sites above 1,500 m elevation (highlands) are cool, between 12° and 18°C, and the mean annual precipitation is high (2,500–3,500 mm). Dense clouds and prolonged mist are common and provide additional moisture at highland sites. Precipitation is less common from December through February, when insolation is high. Because rainy weather makes helicopter access difficult, most work has been done on the summits of higher tepuis from December through March. The highest tepuis (summits > 2,350 m) probably have a mean annual temperature below 10°C. Frost is unknown on tepuis, but freezing temperatures occasionally occur; one of us (RWM) found ice in a metal drinking cup outside his

tent one January morning on Roraima. A detailed treatment of the climate of the Guayana Highlands is provided by Huber (1995a).

#### VEGETATION

The Guayana Highlands are characterized by high floristic diversity and high ecological diversity in both physiognomy of the plant communities and their distributions. The vegetation relevant to our analyses includes zones of montane (800–1,500 m elevation) forest on tepui slopes and upper-montane (cloud) forests that develop near or along bases of vertical cliffs at approximately 1,500–2,000 m. Epiphytic mosses, ferns, lichens, and orchids are common in the upper-montane forests. On some tepui slopes (e.g., Roraima, Auyán, Uei), forests have been destroyed by locally set fires (Means 1995). The summit vegetation (2,000–3,000 m) includes low-growing tepui forest, tepui scrub, and high mountain meadows and grasslands. Leaves of most trees and shrubs are small and sclerophyllous, whereas those of most herbs are thick and coriaceous (Huber 1995c; R. W. McDiarmid, pers. obs.; see Steyermark et al. 1995a for vegetation map).

Low, evergreen forests grow in sheltered areas on some tepui summits, usually on peat overlying sandstone or on mineral soils generated from weathering of diabasic intrusions (Huber 1995c). On the eastern tepuis, such evergreen forests are often low (tree layer of 6–12 m) and species poor, and the undergrowth is dominated by large rosette-forming herbs (e.g., bromeliads of the genus *Brocchinia*). Montane forest on the summits of other tepuis (e.g., Sarisariñama) are taller (15–25 m) and have a well-developed, species-rich understory. Low (7–10 m), evergreen upper-montane forests cover the central and southern sections of Cerro Duida between 1,500 and 2,200 m, whereas a low, evergreen high-tepui forest occurs in occasional depressions on the summit of Marahuaka above 2,600 m. Low (8–15 m), evergreen upper-montane forest occurs between 1,500 and 2,000 m on Cerro de la Neblina, and a taller, evergreen, montane forest type occurs at lower elevations (800–1,500 m) on Neblina's slopes.

Shrublands are important components of the Guayana environments. Most of the shrubs are less than 5 m tall and have woody stems and leaves that are distributed along the stem or concentrated as a terminal rosette. The makeup and distribution of shrubland habitats probably reflect local edaphic conditions more than do those of either forest or grassland. Shrublands (1–3 m tall) occur on the summits of Auyán and Chimantá massifs, sometimes on peat soils and sometimes on rocky slopes and outcrops. Areas of well-developed shrublands occur on rocky soils in the Jaua-Sarisariñama Massif, and dense sclerophyllous scrub (usually < 4 m) is found on the summits of Guanay, Yutajé, and Duida. A peculiar shrubland grows on shallow organic soils between 1,600 and

2,000 m elevation on Cerro de la Neblina. This “Neblinaria scrub” is composed primarily of a single species (*Bonnetia maguireorum*, Theaceae), which forms dense stands of plants 2–3 m tall. The plants have terminal rosettes of leathery leaves that can hold considerable water. Fire has been shown to play a role in maintenance of these shrublands (Givnish et al. 1986; Means 1995).

Grass-dominated meadows (savannas) are common in the lowlands but less so on tepuis. Highland meadows comprise nongramineous plants with a variety of growth forms. Broad-leaved meadows vary floristically and physiognomically on different tepuis. In some places (e.g., between 2,400 and 2,750 m on Roraima), the meadows consist of isolated clumps of mixed species on exposed rocky surfaces. Meadows grow in dense patches on dead peat on Auyán (1,600–1,900 m) and on Guaiquinima (1,200–1,600 m). Species of *Stegolepis* (Rapateaceae) are often found in these meadows. Eastern tepui (e.g., Ptari, Ilú) meadows are dominated by species in the Xyridaceae and Ericaulaceae. Tubiform bromeliads (*Brocchinia*) and tubiform pitcher plants (*Heliamphora*, Sarracenaceae) are also found in some tepui meadows. High-tepui grasslands are rare and have been found in waterlogged or flooded sites on Auyán, Chimantá, Sierra de Maigualida, and Cerro Marahuaka (Huber 1995c).

Pioneer plant formations occur throughout the Guayana Shield on granite outcrops at low elevations and on exposed sandstone in the highlands. Early colonizers include the cyanobacteria *Stigonema panniforme*, which gives rise to the black color of the rock surfaces, many lichens, a few mosses, and several kinds of vascular plants. These plants often grow in small, elongate vegetation islands (up to 300 m<sup>2</sup>) and form over depressions in which sand and organic materials have accumulated (Michelangeli 2000).

### *The Pantepui Herpetofauna*

#### CREATING A LIST

Current knowledge of the Pantepui biota comes from publications and materials collected by a series of expeditions, the history of which we summarize in appendix 18.5. We compiled a species list of amphibians and reptiles known to be above 1,500 m on tepuis, on the basis of previously published summaries (e.g., Hoogmoed 1979a; Duellman 1999; Gorzula and Señaris 1998), other published literature (e.g., Donnelly and Myers 1991; Avila-Pires 1995; Myers and Donnelly 1996, 1997, 2001; Barrio 1998; Galán 2000), and known specimens in museum collections. Reports of the occurrence of widespread, lowland species on tepuis that were based on specimens unaccompanied by specific locality and/or elevation data (e.g., Roze’s [1958a, 1958b] papers reporting on material collected by others from Auyán and Chimantá tepuis) were evaluated individually. Elevation and/or precise locality data were available for a few specimens in museum catalog records; if these records indicated an occurrence above



1,500 m, the species was included in our list. In other instances where precise data were not available, a decision to include or exclude a specific record was based on other considerations (e.g., the distribution of the species elsewhere and our experience with it in the Guayana region). Although we did exclude a few records (e.g., *Anolis auratus*, *Anilius scytale*) as likely having been collected from a locality near the tepui but in the surrounding lowlands and below 1,500 m, we made such decisions cautiously.

Hoogmoed (1979a, appendix) gave an elevational range for each amphibian and reptile species from Guayana and assigned each to one of 12 general categories of distribution. Of the 55 species of frogs reported from localities above 1,000 m, 18 were known only from localities above 1,000 m and were called highland endemics by Hoogmoed. He listed 9 of 38 species of reptiles from above 1,000 m in the same category. Many (perhaps most) of the highland species that Hoogmoed listed as "sp." (i.e., unidentified) in his 1979 compilation have now been identified and/or described (e.g., for *Stefania* sp. A–C, see Duellman and Hoogmoed 1984; Señaris et al. 1996).

Duellman (1999, table 5.2) reported 76 species (74 in his appendix 5.1) of anurans from the Guayana Highlands, including several taxa known primarily from upland sites near La Escalera in Venezuela, the north slope of Roraima in Guyana, and possibly elsewhere (see Duellman and Hoogmoed 1992; Duellman 1997). The following species have not been found on the summit of any tepui and are not included in our list: *Oreophrynella macconnelli*, *Cochranella helenae*, *C. oyampiensis*, *Hyalinobatrachium iaspidiensis*, *H. ostracodermoides*, *Colostethus parimae*, *C. parkerae*, *Hyla kanaima*, *H. lemai*, *H. loveridgei*, *H. ornaticissima*, *H. pulidoi*, *H. roraima*, *H. warreni*, *Scinax danae*, *S. exigua*, *Stefania roraimae*, *S. scalae*, *S. woodleyi*, *Tepuihyla galani*, *T. rodriguezii*, *T. talbergae*, *Eleutherodactylus pulvinatus*, *Leptodactylus sabanensis*, and *Otophryne robusta*. Duellman (1999, appendix 5.1) also included a few more-widespread forms that occur at localities above and below 1,000 m. We assume (no elevational data were given) that Duellman's count of 76 species was comparable to Hoogmoed's general value of 55 species. However, Duellman's (1999, appendix 5.1) Guayana Highlands list does not include many of the 37 species that Hoogmoed (1979a) reported from the highlands (above 1,000 m) and from localities below 1,000 m. Duellman listed many of those 37 species in his Amazon basin–Guiana lowlands category, rather than in both categories, as would have been appropriate based on their elevational range. Five species that Duellman (1999) omitted from his Guayana Highlands list (*Hyla boans*, *H. minuta*, *Osteocephalus taurinus*, *Leptodactylus longirostris*, and *L. rugosus*) had been reported from the top of Cerro Guaiquinima (Donnelly and Myers 1991; Mägdefrau et al. 1991; Schlüter 1994). Thus, Duellman's Guayana Highlands amphibian fauna is not the same as Hoogmoed's highland endemic group. Duellman's count(s) represents about a 30% increase in the total known anuran diversity for the Guayana Highlands in the 20-year period since Hoogmoed's (1979a) treatment.

We included records of some species that had been collected from uplands (1,000–1,500 m) rather than highlands ( $> 1,500$  m), when such sites had been treated as tepuis (see previous discussion of physiography; also Huber 1995a). Accordingly, species collected at moderate elevations but from the tops of Guaiquinima (e.g., *Hyla boans* at 780 m and *Hyla crepitans* at 930 m; Schlüter 1994) and Cerro Yapacana (*Minyobates steyermarki* described from a single specimen collected at 1,200 m near the summit) were added to the list, even though these and other species records from similar upland and slope elevations (but not on tepui tops) were not included. Likewise, species collected at localities of moderate to high elevations in the Sierras Maigualida, Marutaní, and Tapirapecó, primarily granitic mountains within the Guayana Highlands, were included. Finally, we added RWM's unpublished records of taxa encountered during fieldwork on the tepuis and those of others with which we were familiar.

We had a more difficult time deciding how to treat species reports from localities at intermediate elevations (up to 1,500 m) on tepui slopes, given our adoption of 1,500 m elevation as a workable though completely arbitrary lower limit for a highland to qualify as a tepui. An often-used approach is to include any species that has been taken at a locality above some minimal elevation (i.e., the lowest elevation used in defining the highlands) as a member of the highland assemblage (e.g., Chapman 1931). Such an approach certainly facilitates species assignments and in some studies may be appropriate. On the other hand, when the decision to add a species is based on specimen availability (e.g., Chapman 1931) rather than some biologically meaningful elevational limit, it deserves scrutiny. In instances in which a species occurrence can be documented by numerous samples taken along elevational transects, one may be able to detect natural breaks or discontinuities in species distributions by using statistical approaches. Such a statistically defined limit could then be applied to the distribution of the same species in comparable sites with some confidence. Given the inadequacy of sampling on tepui slopes, such an approach currently is not possible. Ultimately, we excluded species that had been reported from localities below but near 1,500 m, if the bulk of other evidence indicated that the species occurs primarily at lower elevations. On the other hand, we always included a primarily lowland species if it had been collected from a locality above 1,500 m on a tepui slope.

Most troublesome were reports of species collected from the “base” or “foot” of Roraima (e.g., certain species collected by Quelch and McConnell and described in Boulenger 1900a, 1900b). The “base” of Roraima is somewhat variable, and accessible localities above 1,500 m occur in this area (see Chapman 1931). However, most reports of specimens from the base of Roraima use 3,500 ft. (approximately 1,067 m) as the elevation, and we did not include those records in our compilation. Many of the same species, as well as several others,

have been collected from montane forest sites on the north slope of Roraima (August–September 1971) at camps reportedly located between approximately 3,000 ft. (camp 5, approximately 915 m) and 6,700 ft. (camp 9, approximately 2,040 m), and possibly higher (Warren 1973). Unfortunately, Warren did not list all species collected or clearly indicate which species came from which camp or at which elevation. As a result, we were forced to determine specific locations from his narrative, which is somewhat problematic. Certain frogs collected by Warren and his associates were described by Duellman and Hoogmoed (1992) and listed as coming from localities between 1,430 and 1,480 m. Two years after Warren's trip (October–November 1973), Michael Tamessar of Georgetown, Guyana, accompanied a British climbing expedition to Roraima's summit (MacInnes 1976). They made use of the camps and trails prepared by Warren's group (appendix 18.5). Tamessar collected the holotype of *Stefania roraimae* at 1,402 m (Duellman and Hoogmoed 1984) and a paratype of *Hyla roraima* and another specimen of *Hyla kanaima* at 1,430 m, reportedly at the same place that Warren had collected these two species (Duellman and Hoogmoed 1992). Warren reported elevations for his camps (1–4) along the Waruma at above 2,000 ft. (2,100–2,300 ft., 640–700 m), but current maps and recent GPS readings indicate that the entire stretch of the river where the trails and camps were located is actually between 1,600 and 1,700 ft. (488–520 m; C. Milensky, pers. comm.). On the basis of these reports, comparisons of elevations given by Warren with those on topographic maps (not available in 1971), and recent measures with GPS devices, it seems likely that Warren's elevations were too high, perhaps by as much as 150 m. Confusion about elevations and the locations at which specimens had been collected, and knowledge that other specimens from the same region collected by Warren and others (e.g., Smithsonian Guyana Expedition, 2001) have been neither identified nor reported in the literature, led to the decision to exclude records of species from the north slope of Roraima from our list. Future work will show which, if any, of these species are members of the Pantepui herpetofauna.

Our final list of amphibians and reptiles from the Guayana Highlands includes 159 species, of which 61% are amphibians and 39% are reptiles (appendix 18.3). A recent collection from Mount Ayanganna in Guyana (Royal Ontario Museum Ayanganna Expedition [2000], Biological Diversity of the Guianas Program) contains some species on our list, others not currently treated in our compilation and known previously only from the slopes of Roraima, as well as undescribed species of *Oreophrynella*, *Stefania*, *Arthrosaura*, and possibly others (A. Lathrop and R. MacCulloch, pers. comm.). We have not included those records in our list but refer to species when appropriate. The pattern of species accumulation over time indicates that herpetofaunal species of Pantepui remain to be discovered (fig. 18.6). We are convinced that additional fieldwork at higher elevations on this and other tepuis in Guyana and

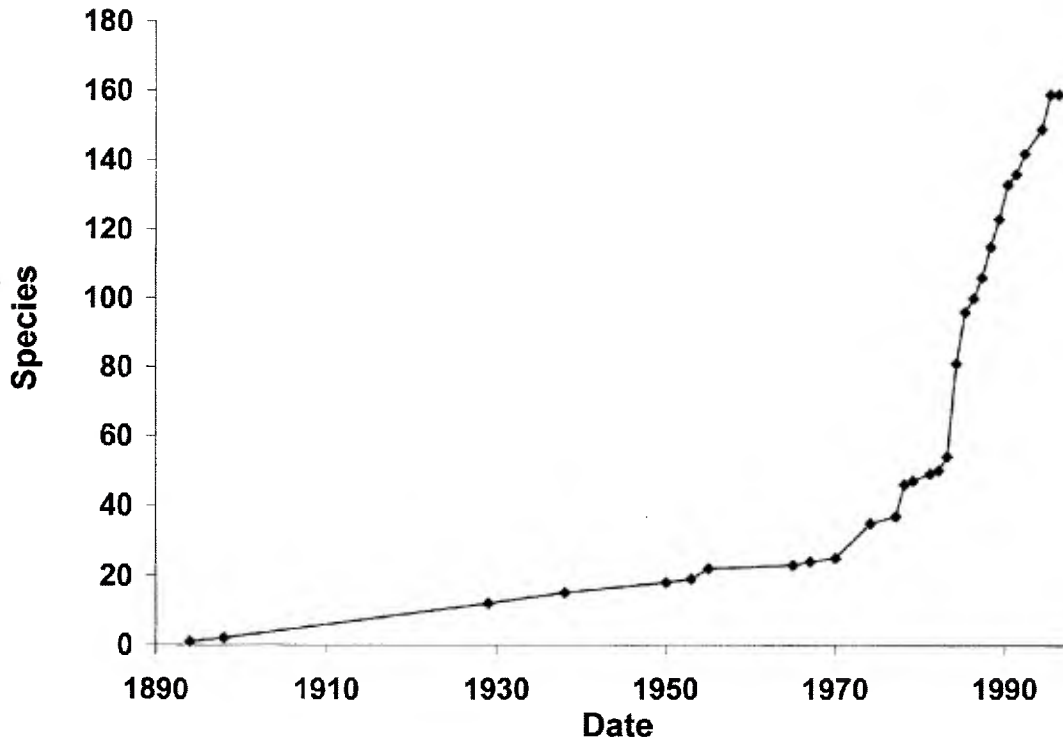


Figure 18.6 Accumulation curve for the 159 species of amphibians and reptiles from Pantepui.

Brazil (e.g., Uei, Wei-assipu, Wokomung), as well as on the slopes and summits of many of the poorly sampled Venezuelan tepuis, will increase the Pantepui herpetofauna to more than 200 species.

From our lists of amphibians and reptiles (appendix 18.3) and tepuis (appendix 18.1), we compiled a list of amphibians and reptiles for each tepui (appendix 18.4). Forty of 72 tepuis (approximately 55%) have some herpetological records, but certain tepuis are better known than others. We arranged tepuis and massifs into 12 groups (subdistricts), which we combined into four regional clusters (districts), generally following the phytogeographical system devised for the Guayana region (Berry, Huber, et al. 1995). For each tepui, we included select information about its geography, physical and biological features, and the date of the first herpetological sample. We indicated which species were endemic, listed pertinent general and herpetological references, and provided other relevant comments.

## FACTORS AFFECTING SPECIES DISTRIBUTIONS

### *Assumptions*

Both historical and contemporary factors affect the distributions of amphibians and reptiles of the Lost World. Aside from inferences derived from geological

and geographical attributes of tepuis, historical influences await elucidation of phylogenetic relationships among tepui taxa. Given the absence of historical information, we used multivariate statistical methods to determine which ecological and geographic factors are associated with the observed patterns of amphibian and reptile diversity on tepuis. We assumed that tepuis are habitat islands and, therefore, that island size, elevation, slope (an indication of relative accessibility), distance from neighboring "islands," ecological complexity, and other such factors interact to determine diversity. Further, we assumed that all tepuis were of approximately the same age and older than any significant component of their summit biota. Finally, we assumed that any large-scale environmental change would have affected the evolutionary history of the biota on each tepui in more or less the same fashion and at about the same time(s).

### *Abiotic Factors*

We derived data on abiotic (physical) features of the tepuis from Huber (1995a) or other published sources. Tepui/massif size was based on measures of summit and slope areas. Tepuis with large slope areas often have more gradual rises (i.e., slope habitat) and potentially easier access to their summits. Those with a smaller slope–summit area relationship often have steeper slopes with prominent vertical cliffs; slope habitats suitable for amphibians and reptiles often are lacking, and access by lowland species is difficult. Slope area is not known for all tepuis (i.e., some tepuis were too close together to have individual slope areas); in those instances we used slope values that were provided by Huber (1995a) for a massif rather than an individual tepui. Slope or summit area estimates were not available for three southern sierras (Marutaní, Maigualida, and Tamacuari), and they were excluded from the multivariate analyses. We used the maximum elevation recorded for a tepui as an index of the degree of isolation from the surrounding lowlands and of habitat diversity on the mountain. In our experience, flat-topped tepuis (e.g., Roraima) generally have fewer habitats than those with distinct peaks (e.g., Neblina).

Sampling effort was not equal among adjacent or connected tepuis. For this and other reasons (e.g., geographical proximity and lack of slope data for individual tepuis [Huber 1995a]), we combined neighboring tepuis into single massifs for analysis. For example, ten tepuis make up the Chimantá Massif (appendix 18.1; Huber 1995a, fig. 1.27), and some are interconnected; each of the Chimantá tepuis has been sampled disproportionately (Huber 1992), and one (Agparamán) has no reported records of amphibians and reptiles (Gorzula and Señaris 1998). For our analyses, all Chimantá tepuis were treated as a single massif. In some instances, a massif (e.g., Guaiquinima) consists of a single tepui; in others, a massif (e.g., Eastern Tepui Chain) includes several discrete tepuis. Some massifs contain tepuis each with a different but closely related species, whereas others show little or no inter-tepui differentiation (appendix 18.4).

Chimantá Massif is interesting because only 6 of the 17 species recorded from the massif are known from single tepuis, whereas 7 others occur on four or more tepuis within the Chimantá Massif. Given the disproportionate sampling and our combining of data for massifs rather than individual tepuis, we felt compelled to include some measure of this geographical reality in our analysis. In the absence of knowledge of the timing of fragmentation of a massif into discrete tepuis (e.g., seemingly a more recent event within the Chimantá Massif than within the Eastern Tepui Chain), and of the responses of different taxa to such a vicariant event(s), we used the number of tepuis with species of amphibians and reptiles that make up each massif as a variable in our analyses.

As an estimator of geographic isolation, we measured the nearest neighbor distance for each tepui by using the map of Mayr and Phelps (1967; modified and reproduced here as fig. 18.1). For each massif we calculated the nearest-neighbor distance as the average of the nearest-neighbor distance for each contained tepui.

### *Biotic Factors*

The number and kinds of animals at any site are influenced by their interactions with each other and with other biological components of the environment. We used two approaches to incorporate some independent measures of the biological complexity of each tepui into our analyses. We used the number of vegetation types documented from the slopes and summit of tepuis (from the vegetation map in Steyermark et al. 1995a; see appendix 18.2) as an indicator of habitat diversity. We gathered distributional data for several vascular plant taxa from the accounts in the published volumes of the *Flora of the Venezuelan Guayana* (Steyermark et al. 1995b, 1997, 1998, 1999) with the idea that plant diversity and distribution patterns might reflect factors that have contributed to the diversity and distribution patterns of the amphibians and reptiles. We included a taxon in our plant data set when its occurrence on a specific massif was noted; we did not include species whose ranges were described in general terms (e.g., “found on tepuis in Bolívar state”). Four values were scored for each massif: total number of primitive vascular plant species, total number of endemic primitive vascular plant species, total number of angiosperm plant species (as taken from the alphabetical listing of families [A–L] in the published volumes), and total number of endemic angiosperm species (families A–L).

Montane herpetofaunas are aggregates of species with different elevational ranges and distributions. We reasoned that tepuis have faunas composed of different assortments of taxa, reflecting their relative degrees of temporal and spatial isolation, and that the patterns of distributions of their component species result from such isolation. Hoogmoed (1979a) recognized the importance of these patterns and provided an elevational range for each species; he also as-

signed species to specific distributional categories (e.g., lowland endemic, widespread, disjunct Amazonian, highland endemic, and so forth). In our analysis we augmented Hoogmoed's data with our own and with those from the literature and determined the elevational and distributional ranges for each taxon (see table 18A.1 in appendix 18.3).

Tepui herpetofaunas often include species with narrow elevational ranges (i.e., known from a single locality on the summit or from a narrow range of slope elevations), species with moderate elevational ranges (i.e., they occur on the slopes and on the summit), and a few species that occur in the surrounding lowlands, on the slopes, and on the summit. To characterize each tepui fauna on the basis of the elevational ranges of its component species, we generated an elevational range (ER) for each species by subtracting the minimum from the maximum known elevation (table 18A.1) and then assigned each species to one of four categories: (1) 0–500 m (the elevational range is 0 when a taxon is known only from a single locality); (2) 501–1,000 m; (3) 1,001–1,600 m; and (4) 1,601–2,300 m. We calculated a value for each tepui by summing the number of species in each category, which we weighted by multiplying each by 1, 2, 10, and 100, respectively, or,  $SUMER = ER_1(1) + ER_2(2) + ER_3(10) + ER_4(100)$ , where  $ER_1$  is the number of taxa known from the massif in category 1,  $ER_2$  is the number of taxa in category 2,  $ER_3$  is the number of taxa in category 3, and  $ER_4$  is the number of taxa in category 4. We chose our weighting factors to reflect the observation that available geographic range increases as a power of elevational range. The SUMER values range from 1 (Angasima, Upuigma, and Yapacana) to 728 (Auyán). The SUMER values reflect observed differences among massifs with similar species diversities but different compositions of species from the four ER groups. For example, Cerro Guaiquinima, Duida, and Auyán massifs have faunas of similar size (22, 23, and 24 species, respectively), but they have very different SUMER values (Guaiquinima = 520; Duida = 150; Auyán = 728). The herpetofaunas of the Cerro Guaiquinima and Auyán massifs include several taxa with wide elevational ranges, whereas that of the Duida Massif includes more taxa with narrow elevational ranges. The SUMER value likely will change with more complete sampling, but we believe that similar differences will remain.

Species in the Pantepui herpetofauna vary from forms that are narrowly restricted in their distributions (i.e., known from a single locality) to forms that are more widespread (i.e., occur over much of the continent). In an attempt to capture these differences, we assigned each species to one of the following distributional pattern (DP; table 18A.1) categories: (1) known from a single tepui (highly restricted); (2) known from localities on two or more tepuis (moderately restricted); (3) broadly distributed across, but still restricted to, the Guayana region (Guayanan endemic); and (4) wide ranging in South America (widespread). From these data we generated the following weighted distribu-

tional range score for each massif:  $SUMDP = DP_1(1) + DP_2(2) + DP_3(10) + DP_4(100)$ , where  $DP_x$  values represent the number of species in that particular category on each tepui or massif. Again, our weighting factors reflect the increase in surface area covered by each successive category. Values ranged from 1 (Yapacana) to 1,336 (Guaiquinima) and were 226 (Neblina), 457 (Auyán), 1,336 (Guaiquinima), and 324 (Duida) for the tepuis with high species diversity (27, 24, 23, and 22, respectively). SUMDP values (226–457) for Neblina, Auyán, and Duida massifs are more tightly clustered than are their SUMER values (60–728), reflecting the relative differences among their respective herpetofaunas as revealed by the elevational and distributional distribution data.

### *Sampling Effort*

We incorporated a measure of sampling effort into the analysis by scoring each tepui or massif with a value derived from our estimate of the total number of sampling days devoted to herpetological exploration on each tepui. These data were taken from the literature and from our field notes. Although crude in some instances (e.g., the high Duida value was influenced by the estimate of three months spent by Tate and his associates on Duida although we have little knowledge of the actual time spent collecting amphibians and reptiles), the values (1–131 days) provide an index to actual sampling effort on each tepui/massif. The temporal bias (most sampling has been done during the dry season) often has a major impact on results obtained at lowland sites, but few data are available to gauge its impact on tepui summits.

## ANALYSES

To understand the sources of variance in the total number of species among massifs, we used Principal Component Analysis (PCA; SAS Institute 2000) to reduce 13 independent variables (table 18.1) to a smaller set of orthogonal (uncorrelated) factors. We deleted three massifs (Tamacuari, Marutaní, and Maigualida) from this analysis because of missing data (Tamacuari and Maigualida lack slope area estimates, and Marutaní lacks a summit area estimate). We used variance maximizing (varimax) rotation of the original variable space. The varimax rotation maximizes the variability of the factor while minimizing the variance around the factor (Statsoft 1994).

The PCA identified three factors with Eigenvalues greater than 1.0 (factor I = 8.03, accounting for 61.8% of variation; factor II = 2.28, 17.5%; factor III = 1.06, 8.1%). Several variables loaded heavily on factor I. The highest values (table 18.2), in decreasing order, were the number of endemic primitive vascular plant species, the number of primitive vascular plant species, the number of endemic angiosperm plant species, the number of angiosperm plant species,



Table 18.1 Variables used in the PCA

LOC	TOT	REP	AMP	TEP	ELE	SUM	SLOP	NN	FT	DC	VPT	VPE	PPT	PPE	ER	DR
ETC	9	1	8	4	2,810	70	320	383	1	50	135	56	112	19	9	11
PTA	2	0	2	1	2,400	2.5	28	290	2	2	94	28	71	10	2	2
LT	5	1	4	3	2,400	12	116	317	1	3	33	13	46	10	6	8
AUY	24	11	13	3	2,450	667.7	715	272	4	54	165	76	83	17	728	457
APR	2	0	2	1	2,500	6	210	264	1	6	17	9	15	5	2	3
CHI	17	11	6	9	2,650	615	915	268	4	81	242	129	156	28	426	340
ANG	1	0	1	1	2,250	2	32	270	1	3	7	5	0	0	1	2
UPU	1	0	1	1	2,100	0.6	13	281	1	1	5	0	0	0	1	2
GUQ	22	13	9	1	1,650	1,096	410	260	3	28	111	40	41	4	520	1,336
MAR	1	1	0	1	1,500	n.a.	740	278	2	1	20	4	17	0	101	101
COC	1	0	1	1	1,500	526	400	249	2	1	8	5	4	0	100	100
JAU	18	6	12	2	2,350	1,170	770	259	4	29	113	63	53	7	236	327
MAI	2	0	2	1	2,400	440	n.a.	303	2	7	39	26	22	0	11	11
YAV	7	4	3	1	2,300	5.6	70	331	2	9	19	13	6	3	7	10
YUT	10	5	5	2	2,400	275	143	361	3	17	108	61	28	4	127	212

(continued)

Table 18.1 (continued)

LOC	TOT	REP	AMP	TEP	ELE	SUM	SLOP	NN	FT	DC	VPT	VPE	PPT	PPE	ER	DR
GUY	8	3	5	1	2,080	165	113	367	1	11	36	22	5	3	233	225
YAP	1	0	1	1	1,300	10.5	38	421	1	7	28	13	5	0	1	1
DUI	23	9	14	3	2,800	1,219	1,100	346	7	131	220	135	187	28	150	324
TAM	11	4	7	1	2,340	0.01	n.a.	466	1	8	8	1	0	0	137	228
NEB	27	9	18	2	3,014	473	1,515	538	5	69	199	118	180	23	246	226

Note: The 13 variables used in the analysis are those in cols. 5–17. Column headings are abbreviated as follows: LOC, massif or tepui; TOT, total number of amphibian and reptile species known from each massif; REP, number of reptile species known from each massif; AMP, number of amphibian species known from each massif; TEP, number of tepuis in each massif known to have amphibians and reptiles; ELE, maximum elevation (m); SUM, summit area (m<sup>2</sup>); SLOP, slope area (m<sup>2</sup>); NN, average nearest-neighbor distance between each massif known to have amphibians and reptiles; FT, number of forest/vegetation types from each massif; DC, days spent collecting; VPT, total number of vascular plants known from each massif; VPE, number of endemic primitive plants known from each massif; PPT, total number of primitive plants known from each massif; PPE, number of endemic primitive plants known from each massif; ER, summed elevation range variable; DP, summed distribution variable. Missing data are indicated by n.a. (not available). Massifs or tepuis used in the analysis are abbreviated as follows: ETC, Eastern Tepui Chain; PTA, Ptari; LT, Los Testigos; AUY, Auyán; APR, Aprada; CHI, Chimantá; ANG, Angasima-tepui; UPU, Upuigma-tepui; GUQ, Cerro Guaiquinima; MAR, Sierra Marutani; COC, Cerro Guanacoco; JAU, Jaua; MAI, Sierra de Maiqualda; YAV, Cerro Yavi; YUT, Yutajé; GUY, Cerro Guanay; YAP, Cerro Yapacana; DUI, Duida-Marahuaka; TAM, Cerro Tamacuari; NEB, Neblina-Aracamuni.

the number of tepuis in a massif known to support amphibians and reptiles, the maximum elevation of a massif, the number of collecting days, the slope area, and the number of forest types. Three variables, distributional patterns (SUMDP), summit area, and elevational range (SUMER) loaded heavily (and negatively) on factor II (table 18.2). Average nearest-neighbor distance was the only variable that loaded heavily on factor III.

We used the rotated PCA factor scores in three multiple regression analyses to describe the sources of variance in total number of amphibians and reptiles known from tepui massifs, total number of reptiles alone, and total number of amphibians alone. For all amphibians and reptiles (i.e., total number of species), the multiple regression was statistically significant ( $F_{3,13} = 43.93$ ,  $p < .0001$ ), and the three factors explained 88.9% of the variance in observed species richness. All three factors were significant in the effect tests (factor I:  $F = 42.58$ ,  $p < .0001$ ; factor II:  $F = 80.02$ ,  $p < .0001$ ; factor III:  $F = 9.19$ ,  $p = .0096$ ). For reptiles, the multiple regression was statistically significant ( $F_{3,13} = 29.84$ ,  $p < .0001$ ), and the three factors explained 84.4% of the variance in the number of reptile species among massifs. The effect tests showed that factor I ( $F = 20.68$ ,  $p = .0005$ ) and factor II ( $F = 68.84$ ,  $p < .0001$ ) were significant, but factor III ( $F = 0.0021$ ,  $p = .9638$ ) was not. For amphibians, the multiple regression model was statistically significant ( $F_{3,13} = 25.03$ ,  $p < .0001$ ), and the

Table 18.2 Factor-loading scores (varimax normalized) for variables used in the PCA

Original variable	Factor I	Factor II	Factor III
No. tepuis with amphibians and reptiles	.828*	-.055	-.411
Maximum elevation (m)	.821*	.173	.167
Summit area (m <sup>2</sup> )	.270	-.896*	.021
Slope area (m <sup>2</sup> )	.681*	-.527	.362
Nearest-neighbor distance (km)	.233	.180	.860*
No. forest types	.603*	-.648	.296
Days spent collecting	.790*	-.480	.208
No. vascular plant species	.847*	-.472	.115
No. vascular plant endemics	.852*	-.447	.217
No. primitive vascular plants	.901*	-.269	.273
No. primitive vascular endemics	.956*	-.199	.107
SUMER	.249	-.796*	-.228
SUMDP	-.048	-.903*	-.121

Note: An asterisk indicates that the original variable loads heavily on the PCA factor, and the loadings are similar to correlation coefficients. The abbreviations SUMER and SUMDP indicate the loadings for the summed elevational range variable and the summed distribution pattern variable, respectively.

three factors explained 81.8% of the variance in the number of amphibian species among massifs. All three PCA factors were significant in the effect tests (factor I:  $F = 27.59$ ,  $p = .0002$ ; factor II:  $F = 30.53$ ,  $p < .0001$ ; factor III:  $F = 16.97$ ,  $p = .0012$ ).

Factor I is an index of habitat diversity. The positive relationship between amphibian and reptile diversity and the four measures of plant diversity, the number of forest types, and probably the slope area together show that habitat diversity has a positive influence on species richness. One might argue that factors affecting plant species distributions and diversity are likely to influence amphibian and reptile diversity in a similar manner. Even though certain plants (e.g., those with wind-dispersed spores and seeds) may move easily among tepuis and between tepuis and other montane habitats, we believe that plant diversity itself positively influences amphibian and reptile species diversity. The varied and unusual growth forms of many tepui plants (e.g., *Brocchinia*, Bromeliaceae) are important contributors to the life history and ecology of many amphibians and reptiles on tepuis. The abrupt, insular nature of tepuis (elevated rocky mesas rising from a sea of lowland forest) is revealed in the high number of endemic taxa of amphibians and reptiles characteristic of Pantepui environments and dependent on two other variables that loaded heavily on factor I—the number of discrete tepuis in a massif and their maximum elevations. As each increases, the chance of adding different habitats rises. These variables have a positive affect on herpetofaunal diversity. It is interesting that factor-loading scores for endemic plants are higher in both categories than for non-endemic plants and that the highest values are for primitive vascular species rather than for angiosperms.

The relatively well-sampled massifs with high factor II scores have large summit areas and faunas that include several geographically and elevationally widespread taxa. Most of these massifs (e.g., Guaiquinima, Auyán, Jaua, Duida) also have large slope areas. Accordingly, we interpret factor II as an index of “accessibility” because the variables that loaded heavily on this factor were generally associated with surface area. We suggest that the probability of a lowland species of amphibian or reptile becoming established on a tepui summit is inversely related to summit elevation and extent of vertical cliffs, and directly related to summit and slope areas.

High factor III scores are associated with variables that measure distance among massifs and, hence, isolation. The relative degree of isolation of certain massifs (e.g., Duida, Neblina) explains some of the species diversity and endemism characteristic of these massifs (appendix 18.4).

Results from the multivariate analyses indicate that the biotic and abiotic factors we examined explain a substantial amount of the variance seen in the number of species known from the massifs included in our analysis. For two of the larger tepuis (Auyán and Guaiquinima), species richness is higher than might be expected based on habitat diversity alone (see factor II scores). An

examination of the species lists from these two tepuis (appendix 18.4) confirms the presence of several lowland species in their faunas. Although Auyán is a high tepui (up to 2,450 m) with impressive cliffs (Angel Falls is on the north side) and has a slope area that is only slightly larger than its summit (table 18.1), a series of step-like escarpments (fig. 18.4) on the southern and eastern sides support forest and savanna-type habitats and provide relatively easy access to the top (R. W. McDiarmid and M. A. Donnelly, pers. obs.). Auyán also is relatively well sampled and has a multibranching river complex on its summit (see Huber 1995a, fig. 1.25; R. W. McDiarmid and M. A. Donnelly, pers. obs.) that provides additional habitats uncommon on many other high tepuis. In contrast, Guaiquinima is a low tepui whose summit ranges from 730 m in the south to 1,650 m in the northeast. Although its surface area is larger than that of Auyán (1,096 vs. 667 km<sup>2</sup>), its slope area is only approximately 40% of that of the summit and consists of a series of circular piedmont escarpments. Dense forest alternating with scrub and herbaceous vegetation covers much of the summit plains (Huber 1995a), a feature that presumably provides relatively easy access for lowland species. Two major streams drain Guaiquinima's summit to the south, and like Auyán, this tepui has been relatively well sampled. This combination of unusual traits may help explain why these two massifs differ from the general trends described by the principal components analysis.

### *Origin of the Herpetofauna*

#### PATTERNS OF ENDEMISM AND DIVERSITY

Hoogmoed (1979a) was the first to comment on the high levels of endemism characteristic of the herpetofauna of the Guayana region. Of the 55 species of amphibians then known from highland localities (> 1,000 m), he noted that 18 (33%) occurred exclusively above 1,000 m and referred to them as highland endemics. Comparable data for reptiles identified 9 of 38 species (24%) as highland endemics. Hoogmoed remarked that most of the sampling of amphibians and reptiles on tepuis since 1894 had been done by explorers and scientists other than herpetologists (see appendix 18.5), and he speculated that the scanty information at the time was a reflection of inadequate sampling rather than geographically limited species distributions. Twenty years later, Duellman (1999) noted that 71 of 76 species of amphibians that he recorded from the Guayana Highlands were endemic and that this represented the highest endemism value (93%) for amphibians in South America. Although Duellman did not specify his criteria, we assume that his Guayana Highlands species were those occurring at localities above 1,000 m.

Our data support assertions of high endemism on tepuis. We define endemics relatively rigidly, however, restricting the term to those species known only from a single tepui (i.e., they are highly restricted). We recorded 159 spe-

cies (appendix 18.3) from tepuis in the Guayana Highlands. Of those, 109 are known from the slope or summit of only a single tepui (i.e., 68.5% of the Pantepui herpetofauna is highly restricted). Levels of endemism differ between amphibians and reptiles ( $G_{\text{idf}} = 8.76$ ,  $p = .003$ ); there are more highly restricted species of amphibians (75 of 97 known species, 77.3%) than reptiles (34 of 62 known species, 54.8%). The observation that the percentage of highly restricted reptiles is considerably lower than that for amphibians suggests that amphibians tend to have smaller ranges than do reptiles in the Pantepui and that moderate- to wide-ranging reptiles are more likely to invade tepui habitats than are moderate- to wide-ranging amphibians. Even though more species of amphibians compared with reptiles occur in the Guayana Highlands, reptile species outnumber amphibian species throughout the Venezuelan portion of Guayana (Péfaur and Rivero 2000). We classified 13 other species that are known from more than one tepui within one of five massifs as moderately restricted: *Epipedobates rufulus*, *Stefania ginesi*, *Anadia* sp. A, *Arthrosaura* sp. A, *Atractus steyermarki*, and *Thamnodynastes chimanta* (Chimantá); *Oreophrynella nigra* and *Riolama leucosticta* (Eastern Tepui Chain); *Colostethus shrevei*, *Stefania goini*, *Atractus riveroi* (Duida); *Arthrosaura testigensis* (Los Testigos); and *Prionodactylus phelpsorum* (Jaua). We also considered 9 species that occur on more than one massif to be moderately restricted: *Stefania satelles* (Angasima, Aprada, Los Testigos, and Upuigma); *Tepuihyla edelcae* (Auyán, Chimantá, and Los Testigos); *Otophryne steyermarki* (Chimantá, Jaua, and Eastern Tepui Chain [Mount Ayanganna; A. Lathrop and R. MacCulloch, pers. comm.]); *Eleutherodactylus cantitans*, *E. yaviensis*, and *Prionodactylus goeleti* (Yaví and Yutajé); *Arthrosaura synaptolepis* (Neblina and Tamacuari); *Arthrosaura tyleri* (Duida and Jaua); and *Plica pansticta* (Guanay and Yutajé). If we relax our definition of endemism to include the moderately restricted forms as well (i.e., those 22 species restricted to tepuis and/or massifs), then we would treat 131 Pantepui species as highland endemics. That is 82.4% of the entire Guayana Highlands herpetofauna as we have defined it and represents 87.6% of the amphibians and 74.2% of the reptiles. As was pointed out earlier, amphibians in tropical highland faunas (e.g., tropical parts of the Andes) may outnumber reptiles between 1.5:1 to 2:1, and endemic species of amphibians may outnumber endemic reptiles even more. As expected, the Pantepui amphibian-to-reptile ratio (1.56:1) is similar to that in portions of the Andes, and the inclusive endemicity values also are higher (1.85:1).

A brief review of appendix 18.3 shows that species of centrolenids, *Colostethus*, and *Eleutherodactylus* are especially numerous and together make up more than half of the anuran fauna. These three taxa contribute significantly to the species diversity of frog faunas in tropical South America, and their numerical contributions are relatively similar to those reported for the same groups in the Andes (Duellman 1999). Inclusion of the endemic radiations of

bufonids (7 species), *Stefania* (9 species), *Tepuihyla* (4 species), and certain hylids (8 species) accounts for more than 80% of the fauna. Other noteworthy and distinctive components of the amphibian fauna are manifest in species of *Adelophryne* (2), *Dischidiodactylus* (2), and *Otophryne* (1). Among reptiles, species of gymnophthalmids are dominant and represent 66% of the lizard fauna, and a few of them (e.g., *Adercosaurus* and *Riolama*) are endemic to the region. Other genera are more widely distributed (e.g., *Anadia*, *Arthrosaura*, *Neusticurus*, and *Prionodactylus*), but they include Pantepui species. Another noteworthy tepui clade is represented by the three species of *Phenacosaurus*, all of which have been described in the last decade. It will be interesting to learn how the Pantepui clade is related to the Andean *Phenacosaurus*. Among snakes, a few species of *Atractus* and *Thamnodynastes* are noteworthy for their limited distributions, but these genera also are widespread in South America.

Given the long evolutionary history of Pantepui and its biota, one might expect to find unusual life-history traits, interesting behaviors, peculiar morphological characteristics, and other such distinguishing features that serve to differentiate taxa of the Guayana Highlands from relatives found in other habitats and regions on the continent. Reproductive modes are diverse among South American anurans, and examination of reproductive patterns in tepui anurans might explain some of the observed patterns. As currently understood, several species of tepui bufonids (in contrast to most other South American bufonids), species of the Guayanan endemic *Stefania* (Hylidae), those of the wide-ranging genus *Eleutherodactylus*, and likely the two species of *Dischidiodactylus* (Leptodactylidae) all have some form of independently derived direct development. The Pantepui species of *Adelophryne* may also fit this pattern. The presence of relatively permanent streams on several tepui summits has provided interesting evolutionary challenges manifest in the larvae of some frogs. Species of centrolenids, *Colostethus*, certain hylids, and *Otophryne* generally breed in or along streams, and the tadpoles of some of these taxa are modified for specific tepui habitats. For example, the larvae of the stream-breeding hylids have a complex oral disc with many rows of labial teeth that facilitate their feeding in high-energy rocky streams (Ayarzagüena and Señaris 1993; R. W. McDiarmid and M. A. Donnelly, pers. obs.), and the tadpoles of *Otophryne* have curious modifications of the jaw sheaths and an elongate spiracular tube that purportedly are associated with feeding beneath the fine Roraima sands on the bottoms of shallows and seeps of small streams in the Guayana uplands (Wassersug and Pyburn 1987). The rock-climbing habits and peculiar tumbling behavior of species of *Oreophrynella* seemingly are unique among South American amphibians (McDiarmid and Gorzula 1989). Although less is known about the natural history of most tepui reptiles, a few observations are notable. Certain arboreal snakes (species of *Leptophis*) have been observed foraging across the tops of and searching among the leaves of several tepui plants (e.g., *Brocchinia*, Bromeli-

aceae; *Neblinaria celiae*, Theaceae); the overlapping leaves and water-holding capacities of these plants provide ample retreats for amphibians and foraging areas for frog-eating snakes. Likewise, wet meadows on the summits of some tepuis (e.g., Duida) often support populations of large earthworms, thereby providing good foraging habitat for worm-eating snakes (e.g., *Atractus*; B. Means, pers. comm.; R. W. McDiarmid, pers. obs.).

#### BIOGEOGRAPHIC HYPOTHESES

In many ways, amphibians and reptiles are better subjects for biogeographical study than are other terrestrial vertebrates. They are usually less vagile than birds and most mammals, and may be closely tied to specific habitats. Given the age and degree of isolation of Pantepui habitats, we expected the herpetofauna to reflect some generalized biogeographic patterns not duplicated in younger faunas at comparable elevations (e.g., Andes).

In their analysis of the origin of the bird fauna of the Venezuelan highlands, Mayr and Phelps (1967) predicted a greater similarity between western tepui and Andean faunas than between the eastern tepui and Andean faunas, and found higher endemism and species diversity in the eastern than in the western avifaunas. Mayr and Phelps (1967, 289) attributed this to "greater ecological opportunities" in the tepuis and highlands around the Gran Sabana, as compared with those of the more isolated western tepuis. They also noted that the eastern tepuis were more closely aggregated, which might have provided more opportunities to birds than were available with the more dispersed western tepuis. Finally, they hypothesized that the more clumped eastern tepuis may have represented a sort of reservoir for highland elements, whereas the western tepuis were more like isolated towers in a vast area of lowlands. Accordingly, they posited that the eastern tepuis were more suitable for the development and maintenance of a highland fauna.

Mayr and Phelps (1967, 289) examined five hypotheses to explain the origin of the Pantepui bird fauna: Distance Dispersal, Cool Climate, Habitat Shift, Specialized Habitat, and Plateau. Hoogmoed (1979a) assessed four of these (excluding the Specialized Habitat hypothesis) together with a Mountain Bridge hypothesis. No geological evidence supports the notion of a physical connection between the tepuis and the Andes; hence, the Mountain Bridge hypothesis is not considered here. The Specialized Habitat idea may explain the presence of some birds (swifts and swallows along cliffs and in canyons) but seems to have little relevance to amphibians and reptiles, with the possible exception of species of rock-dwelling lizards of the genera *Plica* and *Tropidurus*, which must have been derived independently from lowland ancestors (Frost et al. 2001). The other four hypotheses deserve more attention.



### *Distance Dispersal*

The Distance Dispersal hypothesis was considered important relative to the origin of the Pantepui bird fauna, accounting for 50% of the 96 species treated by Mayr and Phelps (1967). Some Andean bird species are active colonizers; they or their ancestors presumably crossed the valleys of the Orinoco and Negro rivers to become established on some of the western tepuis, from whence they "island hopped" across Pantepui to the eastern massifs. Mayr and Phelps (1967) and others (e.g., Cook 1974) presented evidence that supported this notion and indicated that eastern tepuis had a higher diversity than western ones, a relationship contrary to predictions derived from measures of distance to source. Mayr and Phelps (1967) argued that the eastern tepuis provided greater ecological opportunities for bird colonists and thereby retained more species (i.e., fewer went extinct), even though the distance from the Andes was greater. Although this is an interesting idea and may well explain some diversity patterns exemplified by tepui birds, no evidence on species turnover rates was presented. Immigration rates may be high, as indicated by reports of several accidental and chance occurrences among Neblina birds (Willard et al. 1991).

Mindful of the inappropriateness of this idea for amphibians and reptiles (i.e., they do not island hop by flying long distances), we examined the presence of highly and moderately restricted taxa (appendix 18.3) across the four Pantepui districts (table 18.3) for comparison with the bird data. A similar pattern emerges from our data. The eastern tepuis as a group have an equivalent or higher number of amphibian (except for the central tepuis, which have one more amphibian) and reptile genera, the highest number of amphibian species, and the second highest number of reptile species (equivalent in number to the central tepuis), when compared with any of the more western districts. Tepuis in the Western District (nearest straight-line distance to an Andean source) have the lowest number of endemic amphibians (genera and species). Reptile genera are more numerous than amphibian genera in the Western District. Additionally, the number of species of reptiles (8) is equivalent in the Western and Southern districts, and this value is about half that of the Central and Eastern districts (15 species). However, if one were to sum the numbers for the western tepuis (Western, Central, and Southern districts), those tepuis would have about twice the number of endemic species as found in the eastern tepuis (58/28 for amphibians, 31/15 for reptiles; table 18.3). These results are in sharp contrast to those reported by Mayr and Phelps (1967) for birds.

In considering the similarities and differences between the amphibian/reptile and bird comparisons, we considered the discrepancy of samples between summits and slopes, and the elevational limits of tepui samples for the bird data. Mayr and Phelps (1967, table 1) were cognizant of these sampling

Table 18.3 Occurrence of endemic (highly and moderately restricted) taxa of amphibians and reptiles in the four Pantepui districts

	Pantepui District							
	Eastern		Western		Central		Southern	
	A	R	A	R	A	R	A	R
Genera	10 (4)	10 (2)	4 (0)	6 (2)	11 (6)	10 (1)	8 (4)	6 (2)
Species	28	15	8	8	26	15	24	8

Note: A, amphibians; R, reptiles. Values for genera include Pantepui endemics/clades in parentheses.

issues but performed the analysis because they considered the Pantepui bird fauna to be reasonably well known. They (Mayr and Phelps 1967, 283) commented further that future fieldwork undoubtedly would turn up new records, new subspecies, and possibly even species, but that those additions would not modify their picture of this fauna to any major extent. Two points relative to Mayr and Phelps's views deserve comment. First, Roraima has the longest history of exploration and the greatest bird diversity (76, 78, or 84 species [Mayr and Phelps 1967; Cook 1974; Willard et al. 1991, respectively]). Many of these collections were made on the slopes of Roraima in forest, a large part of which on the southern and eastern sides was destroyed by fire in 1926 (Tate 1932). The forest apparently is extensive and continuous on the northern side of Roraima in Guyana. On the basis of our experience with Roraima and its herpetofauna, we question the validity of conclusions derived from comparisons between sites at which sampling over time and space differed substantially. In our experience, vertical cliffs of many tepuis separate slope from summit herpetofaunas with little or no overlap in species. We do not know if this is true for birds, but habitats differ considerably on the slopes and summit of Roraima. Second, Mayr and Phelps (1967) reported 38 different Pantepui bird species from Neblina and considered the degree of exploration to be good (in their five-position scale: very poor, poor, fair, good, very good) for both the summit and slopes. Cook (1974) stated that Neblina had only 36 species, less than half the number predicted by his regression of species number against elevation. Cook attributed this peculiarity to Neblina's isolation and noted its high proportion of endemic taxa (19%) compared with other tepuis (0%–9%). Willard et al. (1991) increased the number of montane (above 750 m) species from Neblina to 65, a value more in line with Cook's expectation. These values (very poor to good) represent an informed guess; they are therefore arbitrary and may mislead some workers who are looking for data about a fauna. Had the value "good" been deemed sufficient to those trying to make an informed decision about the

value of more bird work on Neblina, we might not have learned that the previous estimate was only 60% of the currently reported diversity. To the best of our knowledge, the only tepui that Mayr and Phelps (1967) cited as having been re-sampled was Cerro Duida. Over a three-month period in 1928–29, personnel from the Tyler Duida Expedition (American Museum of Natural History) collected 52 different species from localities above 1,000 m. In November 1950, an ornithological team from the Phelps Collection secured 38 species, none of which was new to Duida. Accordingly, Duida was rated as “very good” by Mayr and Phelps (1967). In their characterization of the tepui avifauna, Willard et al. (1991) reported 64 species from Duida, an increase of approximately 23% above the diversity suggested in the analysis of Mayr and Phelps.

### *Cool Climate*

Chapman (1931) proposed the Cool Climate hypothesis for birds, and Tate (1939) proposed it for Pantepui mammals. Their arguments were based on the idea that cool temperatures during glacial periods shifted subtropical (montane and upper-montane) habitats down mountains and thereby formed habitat connections between tepuis that previously had been separated by warmer lowland environments. Mayr and Phelps (1967) argued that temperature depressions as great as those proposed by Chapman and Tate (up to 9°C) would have resulted in considerable loss of the lowland fauna, for which there are no convincing data. They also pointed out that virtually no evidence exists in support of a habitat connection between the Andes and Pantepui during glacial periods, and that such would have resulted in a more or less uniform fauna throughout Pantepui. Hoogmoed (1979a) proposed a Modified Cool Climate hypothesis under which subtropical habitats would have been somewhat depressed (with a temperature depression of perhaps 3°C), thereby permitting some upland and highland organisms to occur at sites from which they previously had been absent.

The high level of endemism among amphibian and reptile species seems to argue against the Cool Climate hypothesis. Only a few species occur on more than one tepui (i.e., moderately restricted, in table 18A.1), and most of those 22 species occur on neighboring tepuis. We argue that such a distribution pattern is more likely the result of fragmentation of a continuous population on a plateau than depression of habitats to the lowlands and dispersal to adjacent isolates. Additional sampling of suitable habitat at lower elevations and between tepuis should shed light on this issue.

A few species occur on the slopes of some tepuis and at lower elevations between tepuis. Although samples from low or moderate elevations between tepuis are rare, the detection of species in these areas that previously were known only from the slopes or summits of adjacent tepuis would indicate wider

distributions that may have been associated with temperature depressions. Likely candidates for consideration are *Colostethus shrevei*, some species of *Stefania* and *Tepuihyla*, *Otophryne*, possibly some species of *Eleutherodactylus* (e.g., *E. cantitans* and *E. yaviensis*), *Arthrosaura tyleri*, perhaps some species of *Prionodactylus*, and *Atractus riveroi*.

### **Habitat Shift**

The Habitat Shift hypothesis was used to explain the origins of more than 36% of the Pantepui avifauna (Mayr and Phelps 1967), and Hoogmoed (1979a, 256) advanced this idea for amphibians and reptiles by stating that it “serves to explain the distribution and occurrence of the majority of the taxa living at higher elevations.” Basically, this concept assumes that elements of the Pantepui fauna were derived from lowland ancestors that adjusted to intermediate and highland habitats and subsequently differentiated into distinct species. Among amphibians, many of the endemic species of centrolenids, *Colostethus*, and certain *Eleutherodactylus* seem to fit this pattern. With reptiles, we suggest that *Arthrosaura*, *Neusticurus*, *Prionodactylus*, *Tropidurus*, *Dipsas*, *Leptophis*, *Liophis*, and *Thamnodynastes* also fit this pattern.

Presumably all upland taxa at some point in their evolution can be traced to lowland ancestors. Given the age of the Guayana Shield and its associated Roraima Formation, it seems safe to say that in Guayana some type of uplands has been available for colonization from lowland stocks for a very long period. Such colonization probably has been ongoing for the past 100 million years and certainly for much of the Cenozoic. Only two taxa of endemic Pantepui amphibians seem likely to predate this period, and they have arisen from Gondwanaland stocks (also see Rachowiecki 1988, 48–49); these are bufonid frogs of the genera *Oreophrynella*, *Metaphryniscus*, and their relatives, and microhylid frogs of the genus *Otophryne*. Graybeal (1997) showed that the Pantepui bufonids are most closely allied with African genera other than *Bufo*; we predict that a similar pattern will be found with *Otophryne* (but see Wild 1995). Other amphibian species on tepuis presumably were derived from South American ancestors that were lowland species or that reached Pantepui through the lowlands. If these derivations occurred before the last major uplift (later Tertiary) and the subsequent major erosional events that have configured Pantepui today, then some elements of the fauna likely were distributed more or less continuously on a large plateau or on large blocks of a plateau, and fragmentation of that plateau and its fauna (vicariance) may account for many of the Pantepui endemics seen today (see section titled “Plateau Hypothesis”). Thus, ignoring the temporal component with regard to derivations of highland forms may make the Habitat Shift hypothesis more encompassing than it really is.

Second, Hoogmoed (1979a) suggested that the presence of widespread low-

land forms in the herpetofauna of some tepuis supports the Habitat Shift hypothesis. It is true that lowland species are conspicuous components of the herpetofaunas on some tepuis (e.g., Guaiquinima). Mere presence, however, does not provide evidence to support the hypothesis; rather, differentiation (i.e., actual habitat shifts) rather than wide ecological tolerances must be demonstrated. That both Guayanan endemic and widespread forms (appendix 18.4) occur on the tepuis supports the notion that invasions of the highlands are continuing. If highland forms are being derived independently from some widely distributed lowland species, then it should be possible to detect local geographic differentiation within certain taxa (e.g., *Hyalinobatrachium orientale*, *Hyla benitezi*, *H. minuta*, *H. sibleszi*, *Leptodactylus rugosus*, *Arthrosaura tyleri*, *Neusticurus racenisi*, *N. rudis*, *Anolis nitens*, and *Tropidurus hispidus*).

### *Plateau Hypothesis*

The last hypothesis asserts that the Pantepui herpetofauna consists of remnants of a herpetofauna that occupied a plateau that has been dissected by uplift and erosion into discrete tepuis. Chapman (1931) wrote about the tepuis as remnants of a more extensive tableland and the fauna as being more extensive than it is today. Tate (1938), in contrast, talked about in situ adaptations to changing environments associated with a slowly rising plateau. That might seem to support the Habitat Shift hypothesis, but he also noted that little change had occurred among the species after the dissection of the plateau into its numerous faunal islands. Tate maintained that the absence of a species from a mountain could only be accounted for by some inimical condition that caused it to die out (i.e., extirpation). Mayr and Phelps (1967) argued that considerable evidence contradicted the Plateau hypothesis, primarily the ancient age of the plateau, which they argued was dissected into its component tepuis long before most of the bird fauna evolved. They suggested that the irregular distributions of species, and their different levels of differentiation from nearest relatives and among themselves, argued against the notion that the present Pantepui bird fauna is a remnant of an old, formerly uniform plateau fauna. Although those arguments may be appropriate in assessing the origin of a vagile Pantepui avifauna, they do not seem appropriate for amphibians and reptiles. The observation that few genera and only a small number of species of birds and mammals are endemic to the Pantepui fauna contrasts markedly with the situation among amphibians and reptiles.

Hoogmoed (1979a) noted that a modified version of the Plateau hypothesis explains the distribution of the hylid genus *Stefania*. We believe that several other genera can be added to that list and argue that events proposed by the Plateau hypothesis have contributed significantly to the herpetofaunal diversity of Pantepui. The complex patterns of differentiation and distribution of certain

species of hylid frogs on adjacent tepuis within the Chimantá Massif and of species of *Oreophrynella* and *Riolama* in the Eastern Tepui Chain lend support to the Plateau hypothesis. Likewise, erosional fragmentation of massifs into separate, isolated tepuis results in an increase in the number of isolated, related populations and, in terms of species diversity, approximates patterns seen among islands of some archipelagos. The difference here is that vicariance likely has played a more important role in total herpetofaunal diversity than has dispersal. Recolonizations after local extinctions may be less probable because access to some tepuis is difficult compared with other montane environments. More thorough sampling of the Pantepui herpetofauna and development of phylogenetic hypotheses about the relationships among the endemic taxa are required to gauge the importance of various processes in the origin of the Pantepui herpetofauna.

#### DISTRIBUTION PATTERNS

We suggest that if species known only from the summits of tepuis are found on more than one tepui, this is evidence that these tepuis were probably connected in the past—that is, that the tepuis were part of a larger physical unit (Pantepui Plateau) that was subsequently fragmented. Individual species known from lowland, intermediate, and upland sites could represent colonization from the lowlands upward or from the summit downward. The former seems more likely because lowland species often have wider geographic ranges and may have greater ecological tolerance than upland forms. Distinguishing between these two alternatives, however, is difficult. If upland populations on separate tepuis are more closely related to each other than they are to lowland populations, then vicariance explains their origins better than independent upland derivations from lowland ancestors. Unfortunately, our knowledge of the phylogenetic relationships of tepui taxa is nonexistent; hence, we lack a basis for making historical arguments. Although several species from tepuis have been described, no phylogenetic treatment includes all known species for any Pantepui lineage.

Only 33 species are known from more than a single tepui (excluding the 17 species that are treated as lowland taxa and have only been collected on the summit of a single tepui: *Colostethus brunneus*, *Hyalinobatrachium orientale*, *Hyla boans*, *H. crepitans*, *Leptodactylus longirostris*, *Osteocephalus taurinus*, *Pseudopaludicola llanera*, *Ameiva ameiva*, *Anolis fuscoauratus*, *Mabuya bistriata*, *Chironius exoletus*, *C. fuscus*, *Imantodes lentiferus*, *Leptophis ahaetulla*, *Leptotyphlops albifrons*, *Thamnodynastes pallidus*, and *Bothriopsis taeniata*). Fourteen of the 33 species are known to have narrow elevational ranges (elevational range < 500 m; see “Biotic Factors” for definition of elevational range used in this chapter): *Oreophrynella nigra*, *Epipedobates rufulus* (listed as *Dendrobates rufu-*

lus in Duellman 1999), *Eleutherodactylus cantitans*, *E. yaviensis*, *Stefania goini*, *S. satelles*, *Otophryne steyermarki*, *Anadia* sp. A, *Arthrosaura* sp. A, *A. synaptolepis*, *A. testigensis*, *Prionodactylus goeleti*, *Riolama leucosticta*, and *Atractus riveroi*. Six species have moderate elevational ranges (501–1,000 m): *Stefania ginesi*, *Tepuihyla edelcae*, *Arthrosaura tyleri*, *Prionodactylus phelpsorum*, *Atractus steyermarki*, and *Thamnodynastes chimanta*. Six species, *Colostethus shrevei*, *Hyla benitezi*, *H. sibleszi*, *Neusticurus racenisi*, *Tropidurus hispidus*, and *T. panstictus*, have moderately wide elevational ranges (1,001–1,600 m), and seven, *Hyalinobatrachium taylori*, *Hyla minuta*, *Leptodactylus rugosus*, *Anolis nitens* ssp., *Neusticurus rudis*, *Leptodeira annulata*, and *Mastigodryas boddaerti*, have extremely wide elevational ranges (> 1,600 m).

Six of the 14 species with narrow elevational ranges (*Eleutherodactylus cantitans*, *E. yaviensis*, *Stefania satelles*, *Otophryne steyermarki*, *Arthrosaura synaptolepis*, and *Prionodactylus goeleti*) occur on more than one massif. Populations of *E. yaviensis* and *P. goeleti* are known from Cerro Yaví and from Yutajé and Corocoro of the Yutajé Massif, whereas *E. cantitans* is known from Yaví and Yutajé. *Otophryne steyermarki* has been taken on Jaua and Chimantá massifs and recently from Mount Ayanganna, in the Eastern Tepui Chain, and *A. synaptolepis* is known from Neblina and Tamacuari. *Stefania satelles* is known from the Angasima, Aprada, Upuigma, and Los Testigos massifs but, interestingly, not from the Chimantá Massif (see fig. 18.1). Specimens of *S. satelles* from Los Testigos differ from those of other localities (see comments under “Kamarkawarai-tepui” in appendix 18.4 and in Señaris et al. 1996, 37). This suggests that the Los Testigos frogs (on two tepuis) may have been separated from those on the other tepuis at an earlier time. Molecular studies could clarify relationships among these populations. Because these six species are known only from tepui summits, we argue that their distribution patterns are reflective of history, and these highlands at one time must have been parts of larger units that subsequently fragmented.

Each of the eight remaining species of amphibians and reptiles with narrow elevational ranges is found on more than one tepui but always within a single massif (*Oreophrynella nigra* and *Riolama leucosticta* in the Eastern Tepui Chain; *Epipedobates rufulus*, *Anadia* sp. A, and *Arthrosaura* sp. A on the Chimantá Massif; *Stefania goini* and *Atractus riveroi* on the Duida Massif; and *Arthrosaura testigensis* from the Los Testigos Massif). We suggest that the presence of a species on more than one tepui within a massif indicates a past physical connection between tepuis.

The six species with moderate elevational ranges (501–1,000 m) exhibit similar patterns. *Tepuihyla edelcae* has been recorded from eight of the nine tepuis that have been sampled in the Chimantá Massif, as well as from the Auyán (two tepuis) and Los Testigos (one tepui) massifs. The distribution of this frog, together with those of the frog *Stefania ginesi* (known from seven of nine Chi-

mantá tepuis) and the snakes *Thamnodynastes chimanta* (six Chimantá tepuis) and *Atractus steyermarki* (two Chimantá tepuis), provides ample evidence that most elements of the Chimantá Massif share a common history. With few exceptions, absences of particular species from individual tepuis within the Chimantá Massif probably reflect inadequate sampling. In a few instances, lack of suitable habitat may explain an absence (e.g., *A. steyermarki*). It seems likely that the Chimantá Massif was at one time a single sandstone block with its own fauna that was divided into separate entities by erosional forces associated with streams draining in different directions. That relatively little differentiation is evident among the populations on the tepuis of the Chimantá Massif suggests a more recent separation than has occurred among tepuis in other massifs (e.g., Eastern Tepui Chain). Whether the Chimantá Massif was connected to the Auyán and Los Testigos massifs, as is suggested by their common faunal components, remains to be determined. Given their physical proximity, it is likely that these massifs were once part of a single unit. Genetic studies would be useful in determining the relationships among the populations of *Tepuihyla edelcae* and among the populations of *Stefania ginesi* and its presumed close relatives, *S. satelles* and *S. schuberti*, deciphering the sequences of taxon differentiation and elucidating the geographic history of the region.

The other two species with moderate elevational ranges and distributions on more than one tepui are *Arthrosaura tyleri* (Duida and Jaua) and *Prionodactylus phelpsorum* (Sarisariñama and Jaua, according to our treatment). On the basis of our knowledge of other species in these two genera, we suspect that the Pantepui taxa are more widely distributed at intermediate elevations than currently reported (e.g., *A. tyleri*) and may be closely related to other taxa endemic to the Guayana Highlands. Increased sampling at intermediate elevations and phylogenetic analyses of these lizards and their relatives should provide much needed biogeographic insight.

Six of the 13 species with moderately wide (1,001–1,600 m) or very wide (> 1,600 m) elevational ranges are ecologically associated with streams: *Hyalinobatrachium taylori*, *Hyla benítezi*, *H. sibleszi*, *Leptodactylus rugosus* (see Heyer 1995), *Neusticurus racenisi*, and *N. rudis*. We expect that if these species, all of which are Guayanan endemics (appendix 18.3), occur on other tepuis, they will be found only on tepuis with persistent streams and relatively easy access. Hoogmoed (1979a) considered five of the species to be endemic to the lowlands of Guayana; *Hyalinobatrachium taylori* was not described until after his study, but it would also fit the category. These taxa could have moved from the surrounding lowlands to the summits of tepuis or moved from the summits to the lowlands. Hoogmoed (1979a) suggested *Neusticurus*, *Stefania*, and *Otophryne* as examples of organisms that originated in the highlands and subsequently invaded the lowlands. Donnelly and Myers (1991) referred to *Neusticurus racenisi* as a tepui species but later (Myers and Donnelly 1997) suggested that it was likely a lowland form that had moved upward. On the basis of the lowland dis-



tributions of other species of *Neusticurus*, the latter seems a more reasonable explanation. Nearly all of the lizard and snake species with wide or very wide elevational ranges that have been collected on more than one tepui are lowland species, suggesting that they have successfully moved from the lowlands onto the summits of certain tepuis. We are not surprised that amphibians and reptiles have been able to disperse upward into these amazing mountains. None of the “lowland invaders” is known from tepuis with sheer escarpments (e.g., Roraima); rather, they occur on mountains with low elevations (e.g., Guaiquinima, Tamacuari) or on those with extensive, less abruptly rising slope areas (e.g., Auyán-tepui).

### *Conclusions*

The increase in knowledge about the Pantepui herpetofauna over the past 20 years has been remarkable. We now have a working list of the species of amphibians and reptiles known from the Guayana Highlands and some knowledge of the distributions of species among tepuis. Although appreciation of the herpetofauna of several areas clearly would benefit from additional fieldwork, our compilation provides a baseline inventory of taxa from some tepuis (e.g., Roraima, Auyán), and future work should concentrate on tepuis and regions in which collections are either scarce or nonexistent. Primary targets include Ayanganna, Karaurín, Uei, Wei-assipu, and Wokomung in the Eastern Tepui Chain; Soropán and Carrao in the Ptari Massif; Aparamán and others in the Los Testigos Massif; Araopán in the Aprada Massif; any tepui above 1,800 m in the Cuao-Sipapo and Parú massifs; and Avispa, Aracamuni, and other uplands between Neblina and Duida. We are not suggesting that work on other tepuis (e.g., Duida, Marahuaka, Jaua, Sarisariñama) is complete but rather that information from other sites is more important at this time. In addition to the summits of select tepuis and specific summit habitats (e.g., bogs), slope habitats of most tepuis, where accessible, need to be explored.

Throughout this analysis we have stressed the need for detailed phylogenetic studies of Pantepui taxa to hypothesize about the evolutionary history of the herpetofauna. Molecular data would provide an additional and potentially informative perspective, and we recommend that tissues be sampled at every opportunity. Future tepui explorations should include scientists from several disciplines (e.g., malacology, arachnology, botany) with specific goals to collect tissues and produce phylogenetic hypotheses of groups with ages and vagility similar to those of amphibians and reptiles. Such phylogenetic studies would permit cross-group comparisons and potentially produce patterns of geographic congruence. Results also should clarify the relative importance of the Plateau and Habitat Shift hypotheses with regard to understanding the origin of the Pantepui herpetofauna.

An unresolved issue that we encountered during our analyses of distribu-

tional patterns among elements of the Pantepui herpetofauna was the potential importance of extinctions and our ability to detect them. Two aspects of this problem deserve mention. First, it seems likely that extinction of some highland populations of amphibians and reptiles occurred as a consequence of differential uplift and erosion of the Pantepui Plateau and the habitat changes that resulted from these processes. Guaiquinima is a large tepui and presumably was part of the Pantepui Plateau, so therefore it must have been much higher than it is today (ranges from 730 to 1,650 m). If true, its geographic location (fig. 18.1) suggests that some Pantepui endemics (e.g., species of *Oreophrynella* or a related bufonid, *Stefania*, *Tepuihyla*) may have occurred there. The fauna today (appendix 18.4) has none of these taxa. Instead, it is dominated by wide-ranging, lowland forms (e.g., species of *Hyla*, *Leptodactylus*, *Anolis*) and a few endemic taxa that likely were derived from lowland ancestors (e.g., species of *Eleutherodactylus*, *Liophis*, *Philodryas*). Whether these lowland species contributed to extirpations through biological interactions (e.g., competition, predation) or whether abiotic factors (e.g., increasing aridity, warmer temperatures) and habitat changes were the principal causes of species loss is immaterial. What seems likely is that extinctions of highland populations must have occurred, and with few chances of recolonization, their faunas gradually changed.

Second, the relatively small area and isolated nature of most tepuis suggest that extinction rates may have been higher there than elsewhere. Even though we are beginning to understand which species occur on which tepuis (appendix 18.4) and may actually know the fauna of certain better-sampled summits (e.g., Roraima, Auyán), the history of herpetofaunal sampling in the Guayana Highlands indicates that our knowledge is incomplete (fig. 18.6). We lack repeated samples from most tepuis over adequate time periods and know relatively little about population sizes. In our experience, certain frogs (e.g., species of *Oreophrynella*, *Eleutherodactylus*, *Tepuihyla*) are moderately abundant and, if present, may be relatively easy to detect directly or through their vocalizations. With adequate sampling on targeted tepuis, statements about actual absence, as compared with lack of detection, may be possible for some species. For other, less-abundant, nonvocalizing species, documentation of an absence is more difficult. Such a reality leads to another question. How likely is the absence of a species in an area where it is expected to occur attributable to local extinction? If one accepts our premise that a tepui is relatively difficult to colonize from another highland area, then our ability to detect historical extinctions of amphibian and reptile species on tepuis may be higher than for other groups. Although hypotheses of phylogenetic relationships of Pantepui endemics are wanting, we remain optimistic that future studies will show congruence among area cladograms and thereby provide insight about past distributions and likely extinctions. Such notions almost certainly will furnish direction about where sampling needs to be done, and we remain confident that repeated sampling of

tepuis eventually will allow us to make definitive statements about the origins of their herpetofaunas.

In summary, through the efforts of many herpetologists and countless other field biologists, we currently have a much better idea of the composition and diversity of the Pantepui herpetofauna. Many tepuis are unexplored herpetologically, and we advocate an expanded program of exploration and field research. New ideas and biogeographical predictions made during this study need testing, and we look forward to refinements that will come with additional data for species that live in the Lost World.

## Appendix 18.1 Tepuis of the Guayana Highlands

Major tepuis and other uplands and highlands that make up Pantepui of the Guayana region (also see fig. 18.1) are listed in this appendix. The approximate elevational range (m), when known, is included. Tepuis from which herpetological specimens have been collected are indicated with an asterisk (\*). Data are from Huber (1987, 1995a), T. Hollowell (pers. comm.), and field notes (RWM).

### Eastern Pantepui District

#### Roraima Subdistrict

##### Eastern Tepui Chain

Ilú/Tramen, 1,000–2,400/2,700 m\*

Karaurín, 1,000–2,500 m

Kukenán, 1,000–2,600 m\*

Roraima, 1,000–2,723 m\*

Uei, 1,000–2,150 m

Wadakapiapué, 1,000–2,000 m

Yuruaní, 1,000–2,400 m\*

Ayanganna, 550–2,043 m

Wei-assipu, 1,000–2,772 m

Wokomung, 550–1,650? m

#### Los Testigos Subdistrict

##### Isolates

Cerro Venamo, ?–1,600 m

Sierra de Lema, ?–1,650 m

##### Ptari Massif

Carrao, 1,200 ± 2,200 m

Sororopán, 1,200–2,050 m

Ptari, 1,200–2,400 m\*

Los Testigos Massif

Aparamán, 400–2,200 m

Kamarkawarai, 400–2,400 m\*

Murisipán, 400–2,400 m\*

Tereke-yurén, 400–1,900 m\*

Chimantá Subdistrict

Isolates

Cerro Venado, 400–1,300 m

Kurún-tepui, 400–1,300 m

Angasima, 500–2,250 m\*

Upuigma, 500–2,100 m\*

Auyán Massif

Auyán, 400–2,400 m\*

Cerro El Sol, 400–1,750 m\*

Cerro La Luna, 400–1,650 m\*

Uaipán, 400–1,950 m

Aprada Massif

Aprada, 400–2,500 m\*

Araopán, 400–2,450 m

Chimantá Massif

Abacapá, 500–2,400 m\*

Acopán, 500–2,200 m\*

Agparamán, 500–2,400 m

Amurí, 500–2,200 m\*

Apacará, 500–2,450 m\*

Chimantá, 500–2,550 m\*

Churí, 500–2,500 m\*

Murey (Eruoda), 500–2,650 m\*

Tirepón, 500–2,600 m\*

Toronó, 500–2,500 m\*

Western Pantepui District

Maigualida Subdistrict

Sierra de Maigualida (Cerro Yudi, Serranía Uasadi, and others),

?–2,400 m\*

Yutajé Subdistrict

Isolates

Cerro Camani, 100–1,800 m

Cerro Guanay, 100–1,500/2,080 m\*

Cerro Yaví, 100–2,300 m\*

Yutajé Massif

Cerro Corocoro, 100–1,500/2,400 m\*

Serranía Yutajé, 100–1,300/2,140 m\*

Cuaio-Sipapo Subdistrict

Isolates

Cerro Moriche, 100 to  $\pm$  1,250 m

Cerro Ovana, ? to  $\pm$  1,800 m

Cuaio-Sipapo Massif

Cerro Autana, 100–1,375 m

Cerro Cuaio, 100–2,000 m

Cerro Sipapo, 100 to  $\pm$  1,800 m

Central Pantepui District

Guaiquinima Subdistrict

Cerro Guaiquinima, 300–1,650 m\*

Jaua-Sarisariñama Subdistrict

Isolates

Cerro Guanacoco, 300 to  $\pm$  1,500 m\*

Cerro Ichún, 500 to  $\pm$  1,500? m

Sierra Marutaní, 500 to  $\pm$  1,500 m\*

Jaua Massif

Cerro Jaua, 300–1,300/2,250 m\*

Cerro Sarisariñama, 300–1,250/2,350 m\*

Asisa Subdistrict

Parú Massif

Cerro Asisa, 100 to  $\pm$  2,200 m

Cerro Euaja, 100 to  $\pm$  2,000 m

Cerro Parú, 100–900/2,200 m

Parima uplands

Sierra Parima, ?–750/1,300 m

Duida-Marahuaka Subdistrict

Isolate

Cerro Yapacana, 100–1,300 m\*

Duida-Marahuaka Massif

Cerro Duida, 100–2,358 m\*

Cerro Huachamacari, 100–1,900 m\*

Cerro Marahuaka, 100 to  $\pm$  2,800 m\*

Southern Pantepui District

Isolates

Cerro Aratityope, ?–1,700 m

Sierra Unturán, ? to  $\pm$  1,600 m

Sierra Tapirapeco

Cerro Tamacuari, ?–2,340 m\*

Sierra Urucusiro, ?–?

Sierra Curupira, ?–?

Neblina-Aracamuni Massif

Cerro Aracamuni, 400–1,200/1,500 m\*

Cerro Avispa, 400–1,500 m

Cerro de la Neblina, 400–1,800/3,045 m\*

## Appendix 18.2 Pantepui Plant Formations

Pantepui plant formations are listed in this appendix; their occurrence on tepuis with amphibians and reptiles is listed in appendix 18.4. Numbers of species are from the vegetation map that accompanies volume 1 of *Flora of the Venezuelan Guayana* (Steyermark et al. 1995a).

### Upland and Highland Forests

- Low evergreen upper-montane forests (eastern tepuis, Auyán, Chimantá)—22
- Low evergreen high-tepui forests (Auyán, Chimantá)—23
- Medium evergreen montane forest (Guaiquinima type)—26
- Medium evergreen montane forest (Guanacoco, Jaua, Sarisariñama, Marutaní type)—27
- Medium evergreen upper-montane forest (Jaua, Sarisariñama)—28
- Low to medium evergreen upper-montane forest (Sierra de Maigualida)—30
- Low evergreen upper-montane forest (Yaví, Corocoro, and Yutajé summits)—37
- Low evergreen montane forest (Cerro Yapacana summit)—41
- Tall evergreen lower-montane forest (Duida, Marahuaka, and Huachamacari slopes)—44
- Medium evergreen montane forest (Duida-Marahuaka Massif)—45
- Low evergreen upper-montane forest (Duida, Marahuaka, and Huachamacari)—46
- Low evergreen high-tepui forest (Marahuaka summit)—47
- Medium to tall evergreen montane forest (Aracamuni and Neblina, upper slopes)—53
- Low evergreen upper-montane forest (Neblina, Tapirapecó)—54

### Shrublands

- Tall upland scrub on rock (Guaiquinima uplands type)—57
- Tall upland scrub on rock (Marutaní type)—58
- Low tepui-summit scrub and meadows on peat and rock (Auyán, Chimantá summits)—59
- Tall upland scrub on rock (Sarisariñama uplands type)—60

- Low high-tepui scrub on peat and rock (Jaua)—61
- Low to tall tepui scrub on rock (Guanay, Corocoro, Yutajé)—62
- Low to tall upland and high-tepui scrub (Duida and Huachamacari summits)—68
- Low high-tepui scrub on peat (Neblina)—69

#### Herbaceous Formations

- Broad-leaved, shrubby upland meadows on peat (Guaiquinima)—89
- Tubiform, shrubby highland meadows on rock and peat (Guanacoco, Jaua, Sarisariñama)—90
- Broad-leaved, shrubby upland and highland meadows on rock and peat (Sierra de Maigualida, Yaví, Corocoro, Yutajé)—91
- Broad-leaved, shrubby highland meadows on peat (Duida type)—93
- Broad-leaved, shrubby high-tepui meadows on peat and rock (Marahuaka)—94
- Broad-leaved, shrubby highland meadows on peat (Huachamacari type)—95
- Broad-leaved, shrubby upland meadows on peat (Aracamuni)—97
- Broad-leaved, shrubby upland and high-tepui meadows on peat (Neblina)—98

#### Pioneer Formations

- Pioneer vegetation on sandstone summits (Ilú, Yuruaní, Kukenán, Roraima, Los Testigos, Ptari, eastern Auyán, Aprada, Murey, and Tirepón tepuis in the Chimantá Massif, others?)—102

## Appendix 18.3 Herpetofauna of the Guayana Highlands

The 159 species of amphibians and reptiles known from the Guayana Highlands are listed in table 18A.1 at the end of this appendix. Data on elevational range (minimum elevation–maximum elevation, or elevation at type locality) were taken from the literature and from field notes (RWM). Distribution patterns are as follows: highly restricted (HR) = known only from a single tepui; moderately restricted (MR) = known from two or more tepuis or massifs; Guayanian endemic (GE) = known only from localities in the Guayana region (see text for definition of Guayana); widespread (WS) = also known from areas of South America outside of Guayana. Numbers in parentheses represent the number of species in that group.

Our treatment of the distribution and identification of certain tepui taxa requires some explanation. We have confirmed records of *Otophryne steyermarki* from Apacará-tepui and Jaua (appendix 18.4) and reliable reports from Mount Ayanganna; Gorzula (1985) and Campbell and Clarke (1998) also reported a population (males heard calling but none collected) from Acopán-tepui, near the type locality in the Chimantá Massif. Gorzula and Señaris (1998) mentioned a specimen of *O. steyermarki* that had been collected from the talus slope (no elevation given) of Roraima during a La Salle expedition, but they did not give a museum number. We have not examined that specimen and defer from including it in our Roraima list. The type specimen of *Otophryne robusta* was collected at the base of Roraima, and other specimens have been taken on the slopes (see "Remarks" for Roraima, appendix 18.4). We are concerned that the specimen reported by Gorzula and Señaris (1998) may be *O. robusta* and not *O. steyermarki*. However, both *O. robusta* and *O. steyermarki* have been collected on Mount Ayanganna (A. Lathrop and R. MacCulloch, pers. comm.), and they may both occur on the slopes of Roraima at elevations compelling their inclusion in that fauna.

Considerable confusion exists both with the identification of specimens and the application of names for certain Pantepui lizards of the genus *Anolis*. The proposed use of the generic name *Norops* is a third issue that adds to the confusion. Although we agree philosophically with many of the points to partition the genus *Anolis* (Guyer and Savage 1986; Savage and Guyer 1989), in this treatment we follow the lead of other students of the Pantepui herpetofauna and use the name *Anolis* rather than *Norops*.

Part of the confusion involves the distinctiveness of *Anolis eewi*, a species Roze (1958b) described from the summit of the Toronó-tepui (Chimantá Massif). Roze compared the unique type to specimens of *Anolis fuscoauratus kugleri*, at the time the only other anole from Chimantá but from lower elevations; he did not compare the Toronó specimen to *A. nitens* (Wagler 1830), which Roze (1958a) had previously reported from Auyán-tepui to the north. Most other authors (e.g., Peters and Donoso-Barros 1970) recognized *A. eewi* and *A. nitens* as distinct species. In a key paper on geographic variation in this group of anoles, Vanzolini and Williams (1970) asserted that only a single species was involved (they examined the holotype of *A. eewi*) and used the name *Anolis chrysolepis* Dumeril and Bibron 1837 for these lizards (they assigned the few Pantepui anoles available to them to the subspecies *A. c. planiceps*). They opted for *chrysolepis* rather than *nitens* (the older name) because the type of *nitens* is lost and the locality ("America") is imprecise. Vanzolini and Williams noted that the original description was inadequate and that the name *nitens* had been used primarily for a color morph of *chrysolepis* group animals (Shreve 1947). Vanzolini and Williams (1970, 84) commented further that the type of *nitens* "is probably, but hardly with certainty, applicable to some member of the *chryso-*



lepis group." Setting aside the propriety of the name *chrysolepis* (see below), most workers have considered anoles in this group from Pantepui to be one species. However, Mägdefrau et al. (1991) referred specimens from Guaiquinima to both *A. c. planiceps* (camp 5, at 1,520 m) and *A. c. scypheus* (camp 4, at 980 m). Specimens from Guaiquinima (1,030 m; Donnelly and Myers 1991) and Pico Tamacuari (1,270 m; Myers and Donnelly 1997) were referred to *A. c. planiceps*. Gorzula and Señaris (1998) used ratios of tibia to body length and argued that *Anolis eewi* was distinct from *A. nitens*; their sample of seven specimens (two from an upland south of Marutaní, five from the Chimantá Massif, and two from 1,650 m on Cerro Guanay) supposedly showed that *A. eewi* has shorter legs than *A. nitens* (*A. chrysolepis* data from Vanzolini and Williams 1970). Proportional data of this kind that are gathered by different people from few individuals of widely spaced samples are subject to considerable variation, and the resulting analyses are fraught with problems. Also, a plot of tibia length versus snout-vent length for several specimens of *A. nitens* (Avila-Pires 1995, fig. 22) seems to encompass the differences reported by Gorzula and Señaris (1998). Accordingly, we believe it is prudent to treat all of these populations as representative of a single species, pending detailed study of available material. What this taxon should be called is a second problem.

After Vanzolini and Williams (1970), most authors used *Anolis chrysolepis* for these lizards. Hoogmoed (1973) did as well, but correctly pointed out that stability would be best served if Vanzolini and Williams would request that the International Commission of Zoological Nomenclature use its plenary powers to suppress *nitens* Wagler 1830 in favor of *chrysolepis* Dumeril and Bibron 1837. Apparently no request was made. Subsequently, various authors (e.g., Savage and Guyer 1991; Avila-Pires 1995) argued for retention of the name *nitens*. Gorzula and Señaris (1998) also called some of the Pantepui anoles *A. n. nitens*. Myers and Donnelly (1997) raised some concerns about the suitability of applying Wagler's *nitens*, which was described as greenish-, to brownish-colored anoles. Although we agree with the concern about coloration and recognize the disquiet caused by Wagler's (1830) inadequate description, some populations of this lizard in the Kartabo area of Guyana were described as greenish above (Beebe 1944, 197).

In our opinion, the lack of adequate samples from the Guayana Highlands has hindered previous analyses and makes current determinations difficult. Until results from a detailed study of material from lowland and highland sites throughout Pantepui are available, we prefer to consider all populations as representative of a single species; in this regard, we are in agreement with most authors. In this chapter we ignore assignment of populations to subspecies and, for reasons of priority, use the name *Anolis nitens* ssp. for these lizards.

Another taxonomic problem exists with gymnophthalmid lizards of the genus *Prionodactylus*. An understanding of the distributions of Pantepui spe-

cies of these lizards is confounded by conflicting taxonomic opinions. Lancini (1968) described *Euspondylus phelpsi* from a single specimen purportedly collected during the Phelps Expedition of 1967 from the top of Cerro Jaua. Steyermark and Brewer-Carías (1976, 180) pointed out that the expedition never visited Cerro Jaua; rather, personnel collected only on the western summit of Sarisariñama. We therefore assume, as did Gorzula and Señaris (1998), that the type of *E. phelpsi* also was from Sarisariñama, not Jaua. That was confirmed by Phelps (1977), who changed his specimen data from Jaua to Sarisariñama (Myers and Donnelly 2001 n. 26). About 30 years later, Myers and Donnelly (1996) described *Euspondylus goeleti* from six specimens taken at 2,150 m on Cerro Yaví, and they pointed out that the name that Lancini had proposed for the Sarisariñama lizard, *E. phelpsi*, needed to be changed to *Euspondylus phelpsum* to meet the requirements of the *International Code of Zoological Nomenclature*. In their description of *Euspondylus goeleti*, Myers and Donnelly compared the Yaví specimens to Lancini's description of *E. phelpsum* and concluded that the two were distinct. Gorzula and Señaris (1998) described *Prionodactylus nigroventris* on the basis of three specimens from 1,650 m on Cerro Guanay and considered all three Pantepui taxa to be in the genus *Prionodactylus*. Gorzula and Señaris distinguished *P. nigroviridis* and *P. phelpsum* on the basis of ventral coloration and the number of temporal scales. They also suggested that *E. goeleti* from Cerro Yaví was the same as *P. phelpsum*. Gorzula and Señaris reported five other specimens of what they called *P. phelpsum* from Cerro Corocoro, Serranía de Yutajé, and Cerro Yaví (specimen[s] from Corocoro and Yutajé listed with same catalog number; also see comment in Myers and Donnelly 2001, 60). According to their interpretation, *P. phelpsum* occurs on Sarisariñama and Jaua (Jaua Massif, Jaua-Sarisariñama Subdistrict of Central Pantepui District) and on Yutajé, Yaví, and Corocoro (Yutajé Subdistrict of Western Pantepui District; fig. 18.1). Mijares-Urrutia (2000) examined specimens of *P. goeleti* and reviewed the evidence relative to recognition of one or two species. Although the type of *P. phelpsum* is lost, Mijares-Urrutia concluded that two species were represented, and he resurrected *P. goeleti* from synonymy. Myers and Donnelly (2001) reported another juvenile from Cerro Yutajé that they called *P. goeleti*, thereby independently rejecting the conclusion of Gorzula and Señaris (1998). Because the holotype of *P. phelpsum* is lost and other specimens from the Jaua-Sarisariñama area are not available for study, further comment on the status of these two species is pointless. If *P. goeleti* proves to be conspecific with *P. phelpsum*, then the distribution pattern described above suggests a link between the Yutajé Massif, Cerro Yaví, and the Jaua Massif. If the taxa are distinct, then *P. phelpsum* is restricted to the Jaua Massif and *P. goeleti* links the Yutajé Massif (Yutajé and Corocoro) to Cerro Yaví. At this time we prefer to use the name *P. goeleti* for the species on Yaví, Yutajé, and possibly Corocoro, and restrict *P. phelpsum* to those lizards from the Jaua Massif.

Confusion besets the systematics of snakes in the genus *Thamnodynastes*, and determining the number of Pantepui species is somewhat problematic. We include six species in appendix 18.3, one of which (*T. pallidus*) is a widespread, lowland species that gets onto a few tepuis at lower elevations (1,270 m on Tamacuari [Myers and Donnelly 1997]; 1,370 m on Cerro Guaiquinima [Gorzula and Ayarzagüena 1995; Gorzula and Señaris 1998]). The other five are small species known from specific tepuis. Myers and Donnelly (1996) described *T. yavi* from three specimens taken at 2,150 m on the summit of Cerro Yaví in 1995 and *T. duida* from a single male collected in 1929 at 2,015 m on the south end of the summit of Cerro Duida. That same year, Gorzula and Ayarzagüena (1995) described *T. marahuaquensis* from a single female taken at 2,500 m on Tepui Marahuaka Norte (Cerro Marahuaka) and *T. corocoroensis* also from a single female collected at 2,150 m on Tepui Corocoro (Cerro Corocoro). Gorzula and Señaris (1998) considered *T. yavi* Myers and Donnelly to be a junior synonym of *T. corocoroensis* Gorzula and Ayarzagüena. Setting aside the problem of name priority (publication date of the Gorzula and Ayarzagüena paper is controversial; Myers and Donnelly 1997, 63 n. 19; 2001, 78–79), Myers and Donnelly (2001) concluded that *T. yavi* and *T. corocoroensis* probably were distinct species but that *T. duida* and *T. marahuaquensis* were more problematic. We do not know why Gorzula and Señaris (1998) did not include *T. marahuaquensis* in their compilation of taxa known from the Venezuelan Guayana. Until more material from Duida and Marahuaka becomes available, we recommend the species be treated as separate.

Three species of reptiles on our list (appendices 18.3 and 18.4) are known from parts of shed skins: Gymnophthalmid sp. B, Tirepón-tepui; *Chironius* sp., Sarisariñama; and Colubrid sp., Auyán-tepui. Two of these sheds were collected by McDiarmid, who has examined all three. Although we think the snake sheds are not of new species, that of the lizard represents the only reptile record from Tirepón-tepui; we therefore scored Gymnophthalmid sp. B as endemic. Detailed comparisons may yet show that it is a shed from one of the other gymnophthalmid species known from the Chimantá Massif (*Anadia* sp. A, *Arthrosaura* sp. A., *Neusticurus rudis*). Additionally, two other lizard taxa, Gymnophthalmid sp. A (*Arthrosaura*?, Cerro Yaví) and *Riolama* sp. C (Cerro Duida), are based on partially digested specimens taken from the stomachs of snakes (Myers and Donnelly 1996). A tail of Gymnophthalmid sp. A was in the stomach of a female *Thamnodynastes yavi* (296 mm total length [TL]), and a specimen of *Riolama* sp. C was taken from the stomach of the male holotype of *T. duida* (455 mm TL). These species “records” demonstrate that even relatively well-explored mountains harbor additional species and that snakes of the genus *Thamnodynastes* are effective lizard collectors.

According to our best estimates, only approximately 61% of the 97 species of amphibians and approximately 71% of the 62 species of reptiles recorded from the Guayana Highlands can be assigned to currently known species. Interest-

ingly, only about 39% of the 18 species of amphibians that Hoogmoed (1979a) listed as highland endemics were known at the time, whereas nearly all (8 of 9 species) of reptiles were known. Although most of the unknown species recorded by Hoogmoed more than 20 years ago have been identified or described since then, the current proportion of undescribed to described taxa is significant and reflects both the high levels of endemism and the incredible rate of discovery of new taxa in the Guayana Highlands. Much remains to be done.

Table 18A.1 Amphibia and Reptilia of the Guayana Highlands

	Elevational range (m)	Distribution pattern
Amphibia		
Anura (97)		
Bufonidae (7)		
Bufonid sp. (Neblina)	2,000–2,400	HR
<i>Metaphryniscus sosai</i>	2,600–2,800	HR
<i>Oreophrynella cryptica</i>	1,750	HR
<i>Oreophrynella huberi</i>	1,700	HR
<i>Oreophrynella nigra</i>	2,300–2,600	MR
<i>Oreophrynella quelchii</i>	2,600–2,800	HR
<i>Oreophrynella vasquezii</i>	2,500	HR
Centrolenidae (12)		
<i>Centrolene gorzulae</i>	1,850	HR
<i>Cochranella duidaeana</i>	2,140	HR
<i>Cochranella riveroi</i>	1,600	HR
<i>Cochranella</i> sp. (Neblina)	1,390–2,100	HR
<i>Hyalinobatrachium auyantepuianum</i>	1,850	HR
<i>Hyalinobatrachium crurifasciatum</i>	1,160–1,200	HR
<i>Hyalinobatrachium eccentricum</i>	1,700	HR
<i>Hyalinobatrachium orientale</i>	100–1,650	WS
<i>Hyalinobatrachium</i> cf. <i>orientale</i>	1,800–1,900	HR
<i>Hyalinobatrachium taylori</i>	200–1,900	GE
<i>Hyalinobatrachium</i> sp. A (Guaiquinima) <sup>a</sup>	1,400	HR
<i>Hyalinobatrachium</i> sp. B (Jaua)	1,750–1,800	HR
Dendrobatidae (14)		
<i>Colostethus ayarzaguenai</i>	1,600 <sup>b</sup>	HR
<i>Colostethus brunneus</i>	0–1,524	WS
<i>Colostethus guanayensis</i>	1,650	HR
<i>Colostethus murisipanensis</i>	2,350	HR
<i>Colostethus praderioi</i>	1,800–1,950	HR
<i>Colostethus roraima</i>	2,700	HR
<i>Colostethus shrevei</i>	350–1,829	MR
<i>Colostethus tamacuarensis</i>	1,160–1,200	HR
<i>Colostethus tepuyensis</i> <sup>c</sup>	1,600–1,850	HR

Table 18A.1 (continued)

	Elevational range (m)	Distribution pattern
<i>Colostethus undulatus</i>	1,750	HR
<i>Colostethus</i> sp. A (Jaua)	1,750–1,800	HR
<i>Colostethus</i> sp. B (Neblina)	140–1,250	HR
<i>Epipedobates rufulus</i>	2,100–2,600	MR
<i>Minyobates steyermarki</i>	1,200	HR
Hylidae (28)		
<i>Hyla aromatica</i>	1,700	HR
<i>Hyla benitezi</i>	800–1,801	GE
<i>Hyla boans</i>	0–1,216	WS
<i>Hyla crepitans</i>	0–1,420	WS
<i>Hyla inparquesi</i>	2,600	HR
<i>Hyla minuta</i>	0–1,800	WS
<i>Hyla sibleszi</i>	900–2,100	GE
<i>Osteocephalus taurinus</i>	10–1,250	WS
<i>Stefania ginesi</i>	1,850–2,600	MR
<i>Stefania goini</i>	1,402–1,700	MR
<i>Stefania oculosa</i>	1,600	HR
<i>Stefania percristata</i>	1,600	HR
<i>Stefania riae</i>	1,400	HR
<i>Stefania riveroi</i>	2,300	HR
<i>Stefania satelles</i>	2,000–2,500	MR
<i>Stefania schuberti</i>	1,750–1,970	HR
<i>Stefania tamacuarina</i>	1,270	HR
<i>Tepuihyla aecii</i>	2,150	HR
<i>Tepuihyla edelcae</i>	1,630–2,600	MR
<i>Tepuihyla luteolabris</i>	2,550	HR
<i>Tepuihyla rimarum</i>	2,400	HR
Hylid sp. A (Maigualida) <sup>d</sup>	2,100	HR
Hylid sp. B (Auyán) <sup>e</sup>	1,600	HR
Hylid sp. C (Neblina)	1,450–2,100	HR
Hylid sp. D (Neblina)	1,450–1,880	HR
Hylid sp. E (Neblina)	1,250	HR
Hylid sp. F (Duida)	1,850	HR
Hylid sp. G (Jaua)	1,750–1,800	HR
Leptodactylidae (35)		
<i>Adelophryne</i> sp. A (Neblina)	1,390–1,515	HR
<i>Adelophryne</i> sp. B (Neblina)	1,730–2,100	HR
<i>Dischidiodactylus colonnelloi</i>	2,550	HR
<i>Dischidiodactylus duidensis</i>	1,402	HR
<i>Eleutherodactylus avius</i>	1,160–1,460	HR
<i>Eleutherodactylus cantitans</i>	1,750–2,150	MR

(continued)

Table 18A.1 (continued)

	Elevational range (m)	Distribution pattern
<i>Eleutherodactylus cavernibardus</i>	1,160–1,200	HR
<i>Eleutherodactylus memorans</i>	1,160–1,270	HR
<i>Eleutherodactylus pruinatus</i>	2,150	HR
<i>Eleutherodactylus yaviensis</i> <sup>f</sup>	1,700–2,150	MR
<i>Eleutherodactylus</i> sp. A (Guanay) <sup>g</sup>	1,650	HR
<i>Eleutherodactylus</i> sp. B (Aprada) <sup>h</sup>	2,500	HR
<i>Eleutherodactylus</i> sp. C (Auyán) <sup>h</sup>	1,860	HR
<i>Eleutherodactylus</i> sp. D (Murisipán) <sup>h</sup>	2,350	HR
<i>Eleutherodactylus</i> sp. E (Yuruaní) <sup>h</sup>	2,300	HR
<i>Eleutherodactylus</i> sp. F (Jaua)	1,750–1,800	HR
<i>Eleutherodactylus</i> sp. G (Saritariñama)	1,380–1,420	HR
<i>Eleutherodactylus</i> sp. H (Ptari)	2,350	HR
<i>Eleutherodactylus</i> sp. I (Murey)	2,350	HR
<i>Eleutherodactylus</i> sp. J (Roraima)	2,600–2,620	HR
<i>Eleutherodactylus</i> sp. K (Duida)	1,850	HR
<i>Eleutherodactylus</i> sp. L (Neblina)	1,730–2,100	HR
<i>Eleutherodactylus</i> sp. M (Neblina)	1,390–2,100	HR
<i>Eleutherodactylus</i> sp. N (Neblina)	1,390–1,515	HR
<i>Eleutherodactylus</i> sp. O (Neblina)	1,730–1,850	HR
<i>Eleutherodactylus</i> sp. P (Neblina)	1,390–1,850	HR
<i>Eleutherodactylus</i> sp. Q (Neblina)	1,250	HR
<i>Eleutherodactylus</i> sp. R (Neblina)	1,390–1,850	HR
<i>Eleutherodactylus</i> sp. S (Guaiquinima) <sup>i</sup>	780–1,520	HR
<i>Eleutherodactylus</i> sp. T (Marahuaka)	2,450	HR
<i>Leptodactylus longirostris</i>	0–1,520	WS
<i>Leptodactylus rugosus</i>	90–1,720	GE
<i>Leptodactylus</i> sp. (Neblina)	2,085–2,100	HR
Leptodactylid sp. (Neblina)	2,085–2,100	HR
<i>Pseudopaludicola llanera</i>	100–1,220	WS
Microhylidae (1)		
<i>Otophryne steyermarki</i>	1,800–2,150	MR
Reptilia (62)		
Squamata (Lizards) (35)		
Gymnophthalmidae (23)		
<i>Adercosaurus vixadnexus</i>	1,700	HR
<i>Anadia</i> sp. A (Chimantá) <sup>j</sup>	2,100–2,600	MR
<i>Anadia</i> sp. B (Auyán) <sup>k</sup>	1,970	HR
<i>Arthrosaura synaptolepis</i>	1,200–1,450	MR
<i>Arthrosaura testigensis</i>	1,800–2,300	MR
<i>Arthrosaura tyleri</i>	1,402–2,164	MR
<i>Arthrosaura</i> sp. A (Chimantá) <sup>l</sup>	1,950–2,250	MR
<i>Arthrosaura</i> sp. B (Auyán) <sup>m</sup>	2,100	HR

Table 18A.1 (continued)

	Elevational range (m)	Distribution pattern
<i>Neusticurus racenisi</i>	134–1,234	GE
<i>Neusticurus rudis</i>	0–2,100	GE
<i>Neusticurus tatei</i>	1,402	HR
<i>Neusticurus</i> sp. A (Guaquinima) <sup>n</sup>	1,030–1,520	HR
<i>Neusticurus</i> sp. B (Marutaní)	1,200	HR
<i>Neusticurus</i> sp. C (Jaua) <sup>o</sup>	1,600	HR
<i>Prionodactylus goeleti</i>	1,700–2,150	MR
<i>Prionodactylus nigroventris</i>	1,650	HR
<i>Prionodactylus phelporum</i>	1,380–1,917	MR
<i>Riolama leucosticta</i>	2,500–2,700	MR
<i>Riolama</i> sp. A (Neblina)	2,085–2,100	HR
<i>Riolama</i> sp. B (Neblina)	1,730–2,100	HR
<i>Riolama</i> sp. C (Duida) <sup>p</sup>	2,015	HR
Gymnophthalmid sp. A (Yaví) <sup>q</sup>	2,150	HR
Gymnophthalmid sp. B (Tirepón)	2,450	HR
Polychrotidae (5)		
<i>Anolis nitens</i> ssp. <sup>r</sup>	0–2,200	WS
<i>Anolis fuscoauratus</i>	0–1,030	WS
<i>Phenacosaurus bellipeniculus</i>	2,150	HR
<i>Phenacosaurus carlostoddi</i>	2,200	HR
<i>Phenacosaurus neblininus</i>	1,690–2,100	HR
Scincidae (2)		
<i>Mabuya bistrriata</i>	0–1,800	WS
<i>Mabuya</i> sp. (Neblina)	140–1,880	HR
Teiidae (1)		
<i>Ameiva ameiva</i>	0–1,180	WS
Tropiduridae (4)		
<i>Plica lumaria</i>	780–1,380	HR
<i>Plica pansticta</i>	180–1,220	MR
<i>Tropidurus bogerti</i>	1,600–2,080	HR
<i>Tropidurus hispidus</i>	20–1,420	WS
Squamata (Snakes) (27)		
Leptotyphlopidae (1)		
<i>Leptotyphlops albifrons</i>	0–1,380	WS
Colubridae (25)		
<i>Atractus duidensis</i>	2,050–2,150	HR
<i>Atractus riveroi</i>	1,300–1,800	MR
<i>Atractus steyermarki</i>	1,430–2,250	MR
<i>Atractus</i> sp. (Auyán) <sup>s</sup>	2,100	HR
<i>Chironius exoletus</i>	200–1,402	WS
<i>Chironius fuscus</i>	0–2,283	WS
<i>Chironius</i> sp. (Sarisariñama)	1,380–1,420	HR

(continued)

Table 18A.1 (continued)

	Elevational range (m)	Distribution pattern
<i>Dipsas</i> cf. <i>indica</i>	1,515	HR
<i>Dipsas</i> sp. (Neblina)	1,250	HR
<i>Imantodes lentiferus</i>	100–1,030	WS
<i>Leptodeira annulata</i>	0–2,150	WS
<i>Leptophis ahaetulla</i>	0–1,850	WS
<i>Leptophis</i> sp. (Neblina)	1,820	HR
<i>Liophis ingeri</i>	1,900	HR
<i>Liophis torrenicola</i>	1,030–1,180	HR
<i>Liophis trebbauai</i>	1,020–1,938	HR
<i>Mastigodryas boddaerti</i>	0–2,200	WS
<i>Philodryas cordata</i>	1,030–1,520	HR
<i>Thamnodynastes chimanta</i>	1,920–2,600	MR
<i>Thamnodynastes corocoroensis</i>	2,150	HR
<i>Thamnodynastes duida</i>	2,015	HR
<i>Thamnodynastes marahuaquensis</i>	2,500	HR
<i>Thamnodynastes pallidus</i>	0–1,370	WS
<i>Thamnodynastes yavi</i>	2,150	HR
Colubrid sp. (Auyán)	1,940	HR
Viperidae (1)		
<i>Bothriopsis taeniata</i>	0–2,000	WS

Source: Data on elevational range were taken from the literature and from RWM's field notes.

Note: In this list of the 159 species known to occur on tepuis in the Guayana Highlands, the numbers in parentheses represent the numbers of species in the particular group. The elevational range represents the minimum elevation–maximum elevation or elevation at a type/single locality. Distribution patterns are as follows: HR, highly restricted, known only from a single tepui; MR, moderately restricted, known from two or more tepuis or massifs; GE, Guayanian endemic, known only from localities in the Guayana region; WS, widespread, also known from areas of South America outside of Guayana.

<sup>a</sup> *Hyalinobatrachium* sp. of Gorzula and Señaris 1998, 32.

<sup>b</sup> Elevation derived from other source (see remarks concerning Jaua in appendix 18.4).

<sup>c</sup> Includes the *Colostethus* sp. of Myers 1997, 3 (C. Myers, pers. comm.).

<sup>d</sup> Hylid sp. A of Gorzula and Señaris 1998, 36.

<sup>e</sup> Hylid sp. B of Gorzula and Señaris 1998, 37.

<sup>f</sup> Includes Eleutherodactylinae series b (Corocoro) of Gorzula and Señaris 1998, 55, according to Myers and Donnelly 2001, 39.

<sup>g</sup> Eleutherodactylinae series a (Corocoro) of Gorzula and Señaris 1998, 55.

<sup>h</sup> Eleutherodactylinae series b (Corocoro) of Gorzula and Señaris 1998, 55.

<sup>i</sup> *Eleutherodactylus* spp. of Mägdefrau et al. 1991, 16, and Schlüter 1994, 79, 83.

<sup>j</sup> *Anadia* sp. A of Gorzula and Señaris 1998, 114.

<sup>k</sup> *Anadia* sp. B of Gorzula and Señaris 1998, 115.

<sup>l</sup> *Arthrosaura* sp. A of Gorzula and Señaris 1998, 124.

<sup>m</sup> Refers to an undescribed species of *Arthrosaura* mentioned in Myers 1997, 4.

<sup>n</sup> *Neusticurus* sp. of Donnelly and Myers 1991, 38; *Neusticurus rudis* of Mägdefrau 1991, 21, and Gorzula and Señaris 1998, 127–28.



Table 18A.1 (continued)

<sup>o</sup> *Neusticurus cf. rudis* of Señaris et al. 1996, 24.

<sup>p</sup> *Riolama* sp. of Myers and Donnelly 1996, 52. Molina and Señaris (2001) described *Riolama uzzelli* from two sites on Cerro Marahuaka (1,850 and 2,600 m). We suspect that future work will show that the Duida and Marahuaka specimens represent a single species.

<sup>q</sup> *Arthrosaura* (?) species of Myers and Donnelly 1996, 22.

<sup>r</sup> Includes *Anolis eewi*, *Anolis nitens nitens*, and *Anolis chrysolepis planiceps* of the authors.

<sup>s</sup> Refers to a specimen of *Atractus* mentioned in Myers 1997, 4.

## Appendix 18.4 Tepuis of the Guayana Highlands and Their Herpetofaunas

The major tepuis of the Guayana Highlands from which species of amphibians and/or reptiles are known are listed by district and, where appropriate, by massifs within districts. Arrangement is in a general east-to-west and north-to-south sequence. Tepuis within each of the four districts are listed in alphabetical order by subdistrict, massif, or individually, whichever is appropriate. Unless otherwise specified, much of the tepui data come from Huber (1995a). Endemic species are indicated with an asterisk (\*). Pertinent general and herpetological references are listed, as are various clarifying remarks.

### *Eastern Pantepui District*

#### RORAIMA SUBDISTRICT

### *Eastern Tepui Chain*

#### Ilú-tepui and Tramen-tepui

Venezuela (Bolívar); latitude × longitude: 05°27' N 61°03' W and 05°40' N 62°37' W (U.S. Board on Geographic Names [USBGN] 1961); maximum elevation: 2,700 m; summit area: 5.63 km<sup>2</sup>; slope area: not available, 300 km<sup>2</sup> for all tepuis in Eastern Tepui Chain except Uei-tepui; massif: Eastern Tepui Chain; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1977.

Herpetofauna: 2 species, 1 endemic: Amphibia (1)—*Oreophrynella vasquezii*\*; Reptilia (1) *Riolama leucosticta*.

Pertinent literature: Gorzula and Señaris 1998; Señaris et al. 1994.

Remarks: McDiarmid accompanied Charles Brewer-Carías here and made collections one day in January 1977. Gorzula visited the tepuis at three different sites; one day in April 1984 and another two in June 1985. The three collection

sites had the following coordinates: 05°25' N 60°58' W, 05°26' N 60°59' W, and 05°25' N 60°59' W (Gorzula and Señaris 1998). *Riolama leucosticta* is endemic to the Eastern Tepui Chain.

### Kukenán

Venezuela (Bolívar); latitude × longitude: 05°13' N 60°51' W (Paynter 1982; USBGN 1961, spelled Cuquenán); maximum elevation: 2,650 m; summit area: 20.63 km<sup>2</sup>; slope area: not available, 300 km<sup>2</sup> for all tepuis in Eastern Tepui Chain except Uei-tepui; massif: Eastern Tepui Chain; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1977.

Herpetofauna: 2 species, 0 endemics: Amphibia (1)—*Oreophrynella nigra*; Reptilia (1)—*Riolama leucosticta*.

Pertinent literature: General: Brewer-Carías 1978b; Mayr and Phelps 1967. Herpetological: Gorzula and Señaris 1998; McDiarmid and Gorzula 1989; Señaris et al. 1994.

Remarks: McDiarmid collected on this tepui for three days in January 1977 with Charles Brewer-Carías and others, and Gorzula visited it for one day in April 1984 and for one day in April 1985. Gorzula and Señaris (1998) listed coordinates for the two collection sites as 05°17' N 60°48' W and 05°11' N 60°49' W. This tepui has also been called Kukenán-, Mataui-, and Matawi-tepui (Huber 1995a), Kukenám and Monte Kukenám (Brewer-Carías 1978a, 1978b), Cuquenán (USBGN 1961), Cuquenám (Mayr and Phelps 1967), Mt. Kukenaam (McConnell 1916, map), and Mount Kukenaam (Warren 1973). The two recorded species, *Riolama leucosticta* and *Oreophrynella nigra*, are endemic to the Eastern Tepui Chain. Mayr and Phelps (1967) listed the elevation at 2,680 m, and Brewer-Carías (1978b) reported 2,600 m and coordinates of 05°12' N and 60°45' W for the site of McDiarmid's collections.

### Roraima

Venezuela (Bolívar), Brazil (Roraima), and Guyana (Cuyuni-Mazaruni); 05°12' N 60°44' W (Paynter 1982; Stephens and Traylor 1985; Paynter and Traylor 1991; USBGN 1961); maximum elevation: 2,810 m; summit area: 34.38 km<sup>2</sup>; slope area: not available, 300 km<sup>2</sup> for all tepuis in Eastern Tepui Chain except Uei-tepui; massif: Eastern Tepui Chain; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1894.

Herpetofauna: 5 species, 4 endemics: Amphibia (5)—*Colostethus praderioi*\*, *Colostethus roraima*\*, *Eleutherodactylus* sp. J\*, *Oreophrynella quelchii*\*; Reptiles (1)—*Riolama leucosticta*.

Pertinent literature: General: Brewer-Carías 1978a; Clementi 1920; Im Thurn 1885; Mayr and Phelps 1967; Quelch 1921; Tate 1928, 1930; Warren 1973. Her-

petological: Boulenger 1895a, 1895b, 1900a, 1900b; Gorzula and Señaris 1998; La Marca 1996; McDiarmid and Gorzula 1989.

Remarks: This was the first tepui to be explored (appendix 18.5), and because of the moderately easy access to the summit, it probably is one of the best known. Several herpetologists have worked on Roraima. McDiarmid spent three days with Charles Brewer-Carías on the summit in January 1977, five days in February 1979, and one day in 1988. Even so, new species are still being found on its top. Also known in the literature as Roraima-tepui (Huber 1995a), Monte Roraima (Brewer-Carías 1978a), Mt. Roraima (McConnell 1916, map), and Mount Roraima (Warren 1973). The single collection cited by Gorzula and Señaris (1998) was made at 2,750 m at 05°11' N 60°45' W. USBGN (1961) and Stephens and Traylor (1985) gave Mazaruni-Potaro as the administrative unit in Guyana, but this has recently changed to Cuyuni-Mazaruni (*Times Atlas of the World* 1999). Huber (1995a) listed the maximum elevation for the Venezuelan part of Roraima as 2,723 m; the highest part of Roraima may be on the northern end of the tepui and in Guyana. Other elevations reported are 9,094 ft. (~2,771 m; Warren 1973) and 2,810 m (Paynter 1982; *Merriam-Webster's Geographical Dictionary* 1997). The type locality of *Colostethus praderioi* (La Marca 1996) apparently is in the third and highest quebrada crossed by the summit trail; we include it here because the given elevations were 1,800 and 1,950 m. Several examples of *Otophryne robusta* were reported by M. J. Praderio (pers. comm. in La Marca 1996, 37); we have not examined those specimens and accordingly have not included *Otophryne robusta* in the Roraima compilation. Gorzula and Señaris (1998) mentioned a specimen of *O. steyermarki*, purportedly from the talus slope of Roraima (no elevation given), but we are reluctant to accept this record without verification. Future work may confirm their presence (see appendix 18.3). The report of *Tepuihyla edelcae* from Roraima (Gorzula and Señaris 1998, 255; Galán 2000) apparently is an error; no specimens of this frog are listed in the species account by Gorzula and Señaris, and none is known to us. Specimens of *Bothriopsis taeniata*, previously known from Pantepui only from the holotype of *Bothrops lichenosa* from Chimantá (Roze 1958b), have been collected along the summit trail at the base of Roraima (Lancini 1978; Peter McIntyre, pers. comm.). A few species collected by McConnell and Quelch (appendix 18.5) and described by Boulenger (1900a, 1900b) were listed as coming from the base of Roraima; included are *Oreophrynella macconnelli*, *Eleutherodactylus marmoratus*, *Otophryne robusta*, and *Neusticurus rudis*. These and a few other species have been collected from the north slopes in Guyana (appendix 18.5); some were listed by Warren (1973) and others described by Duellman and Hoogmoed (1984, 1992) and Hoogmoed and Lescure (1984). Most, perhaps all, of these records are from localities below 1,500 m and have not been incorporated into this study (see the section titled "Creating a List"). Excluded were *Adelophryne gutturosa*, *Hyla kanaima*, *H. roraima*,

*H. warreni*, *Stefania roraimae*, *Oreophrynella macconnelli*, *Eleutherodactylus marmoratus*, *Otophryne robusta*, and *Neusticurus rudis*. Vegetation on the slopes is low evergreen, upper-montane forest. A lake (Lago Gladys) occurs on the northern end of the summit at about 2,700 m in Guyana (photographs in Brewer-Carías 1978a, 59; Huber 1995c, pl. 27). As currently understood, *Riolama leucosticta* is endemic to the Eastern Tepui Chain.

### Yuruaní-tepui

Venezuela (Bolívar); latitude × longitude: 05°16' N 60°51' W (USBGN 1961); maximum elevation: 2,400 m; summit area: 4.38 km<sup>2</sup>; slope area: not available, 300 km<sup>2</sup> for all tepuis in Eastern Tepui Chain except Uei-tepui; massif: Eastern Tepui Chain; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1977.

Herpetofauna: 3 species, 2 endemics: Amphibia (3)—*Eleutherodactylus* sp. E\*, *Oreophrynella nigra*, *Stefania riveroi*\*.

Pertinent literature: Gorzula and Señaris 1998; Mägdefrau and Mägdefrau 1994; Señaris et al. 1994, 1996.

Remarks: McDiarmid collected here for one day on the summit in January 1977 with Charles Brewer-Carías. Yuruaní has also been called Iwara-Karima (Brewer-Carías 1978b) and Mt. Iwalkarima (McConnell 1916, map; Warren 1973). Gorzula and Señaris (1998) listed the coordinates for a collection made over two days in April 1984 at 2,300 m as: 05°19' N 60°51' W. We are unable to verify if the *Eleutherodactylus* sp. E (a specimen in series B reported by Gorzula and Señaris 1998, 55) is the same as that represented in the photograph in Mägdefrau and Mägdefrau (1994, 100). We list only a single species from Yuruaní-tepui, pending clarification and additional material. *Oreophrynella nigra* is known from here and Kukenán to the south; such a distribution suggests a former connection between the tepuis or a more extensive distribution of the species.

## LOS TESTIGOS SUBDISTRICT

### Ptari Massif

#### Ptari-tepui

Venezuela (Bolívar); latitude × longitude: 05°46' N, 61°46' W (Paynter 1982), 05°47' N 61°47' W (USBGN 1961); maximum elevation: 2,400 m; summit area: 1.25 km<sup>2</sup>; slope area: not available, 28 km<sup>2</sup> for Carrao-tepui and Ptari-tepui; massif: Ptari; number of vegetation types for massif: 2—pioneer vegetation on sandstone summits; low evergreen, upper-montane forests on slopes; date of first herpetological collection-exploration: 1978.

Herpetofauna: 2 species, 2 endemics: Amphibia (2)—*Eleutherodactylus* sp. H\*, *Tepuihyla rimarum*\*.

Pertinent literature: General: Brewer-Carías 1978b; Mayr and Phelps 1967. Herpetological: Ayarzagüena et al. 1992a, 1992b.

Remarks: McDiarmid accompanied Charles Brewer-Carías and collected one day in February 1978. Brewer-Carías (1978b) reported the collecting locality as 05°47' N 61°47' W and 2,400 m. Gorzula visited the summit on a November day in 1984 and collected 16 amphibians at approximately 2,400 m at a site with coordinates of 05°47' N 61°47' W. Mayr and Phelps (1967) listed the elevation as 2,620 m, but the summit had not been visited at that time.

### *Los Testigos Massif*

#### Kamarkawarai-tepui

Venezuela (Bolívar); latitude × longitude: 05°53' N 61°59' W (Gorzula and Señaris 1998); maximum elevation: 2,400 m; summit area: 5.00 km<sup>2</sup>; slope area: not available, 88 km<sup>2</sup> for Los Testigos Massif except Aparamán-tepui; massif: Los Testigos; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1986.

Herpetofauna: 1 species, 0 endemics: Amphibia (1)—*Stefania satelles*.

Pertinent literature: Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: Señaris et al. (1996, 37) did not include the Los Testigos specimens in their description of *Stefania satelles*, commenting that the specimens had much larger tympana than specimens from other localities. Gorzula and Señaris (1998, 47) later commented on their initial reluctance to treat those frogs as *S. satelles*, and then included them in that species. Collectors spent one day in January 1986 on this tepui.

#### Murisipán-tepui

Venezuela (Bolívar); latitude × longitude: 05°53' N 62°05' W (estimated from Huber 1995a, fig. 1.19); maximum elevation: 2,350 m; summit area: 5.00 km<sup>2</sup>; slope area: not available, 88 km<sup>2</sup> for Los Testigos Massif except Aparamán-tepui; massif: Los Testigos; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1988.

Herpetofauna: 4 species, 2 endemics: Amphibia (3)—*Colostethus murisipanensis*\*, *Eleutherodactylus* sp. D\*, *Stefania satelles*; Reptilia (1)—*Arthrosaura testigensis*.

Pertinent literature: Gorzula and Señaris 1998; La Marca 1996.

Remarks: Also known as Murosipán, according to La Marca (1996). Confusion exists about the exact location of collecting sites on this tepui. Gorzula and

Señaris (1998, 257) listed coordinates of 05°53' N 62°03' W for a collection made by Gorzula and others at a site on "Terekyurén (Murisipán)" at 2,350 m. According to Huber (1995a, fig. 1.19), this locality has to be on Murisipán, because the maximum elevation of Tereke-yurén is 1,900 m. Therefore, we have decided that the amphibians reported by Gorzula and Señaris (1998, 257) as collected on 2–3 March 1988 from Terekyurén were actually collected on Murisipán. La Marca (1996) also listed coordinates 05°53' N 62°04' W and 2,350 m for the holotype of *Colostethus murisipanensis* that Gorzula collected on Murisipán on 2 March 1988. If our deductions about localities are true, only the westernmost Aparamán, of the tepuis making up the Los Testigos Massif, has not been sampled. USBGN (1961) listed the coordinates for Murisipán at 05°51' N 62°00' W, which is clearly incorrect according to Huber's map. *Arthrosaura testigensis* is endemic to the Los Testigos Massif.

### Tereke-yurén-tepui

Venezuela (Bolívar); latitude × longitude: 05°53' N 62°02' W (estimated from Huber 1995a, fig. 1.19; Gorzula and Señaris 1998); maximum elevation: 1,900 m; summit area: 0.63 km<sup>2</sup>; slope area: not available, 88 km<sup>2</sup> for Los Testigos Massif except Aparamán-tepui; massif: Los Testigos; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1988.

Herpetofauna: 2 species, 0 endemics: Amphibia (1)—*Tepuihyla edelcae*; Reptilia (1)—*Arthrosaura testigensis*.

Pertinent literature: Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: According to Gorzula and Señaris (1998, 117), the holotype of *Arthrosaura testigensis* was collected at 1,800 m at 05°52' N 62°03' W on the south side of the massif on 15 January 1986, as was a single specimen of *Tepuihyla edelcae*. See remarks for Murisipán-tepui regarding the location of reported localities.

## CHIMANTÁ SUBDISTRICT

### *Auyán Massif*

#### Auyán-tepui

Venezuela (Bolívar); latitude × longitude: 05°55' N 62°32' W (Paynter 1982; USBGN 1961); maximum elevation: 2,450 m; summit area: 667.7 km<sup>2</sup> excluding Uaipán; slope area: not available, 715 km<sup>2</sup> for Auyán-tepui, Cerro La Luna, Cerro El Sol; massif: Auyán; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows, on peat and rock; low evergreen, high-tepui forests; low evergreen, upper-montane forests on slopes; date of first herpetological collection-exploration: 1956.

Herpetofauna: 23 species, 12 endemics: Amphibia (12)—*Centrolene gorzulae*\*, *Colostethus tepuyensis*\*, *Eleutherodactylus* sp. C\*, *Hyalinobatrachium auyantepuianum*\*, *Hyalinobatrachium* cf. *orientale*\*, *Hyalinobatrachium taylori*, *Hyla sibleszi*, Hylid sp. B\*, *Leptodactylus rugosus*, *Oreophrynella cryptica*\*, *Stefania schuberti*\*, *Tepuihyla edelcae*; Reptilia (11)—*Anadia* sp. B\*, *Anolis nitens* ssp., *Arthrosaura* sp. B\*, *Neusticurus rudis*, *Tropidurus bogerti*\*, *Atractus* sp.\*, *Chironius fuscus*, Colubrid sp., *Leptodeira annulata*, *Liophis trebbau*, *Mastigodryas boddaerti*.

Pertinent literature: General: Brewer-Carías 1978b; Buchsbaum 1969; Barrowclough et al. 1997; Jirak et al. 1968; Mayr and Phelps 1967; Tate 1938. Herpetological: Ayarzagüena 1992; Ayarzagüena et al. 1992a, 1992b; Ayarzagüena and Señaris 1996; Gorzula and Señaris 1998; La Marca 1996; Myers 1997; Roze 1958a; Señaris 1993; Señaris and Ayarzagüena 1993; Señaris et al. 1996.

Remarks: Gorzula and Señaris (1998) listed the following coordinates for their nine collecting sites on this tepui: 05°48' N 62°32' W, 05°54' N 62°38' W, 05°56' N 62°33' W, 05°58' N 62°29' W, 06°00' N 62°35' W, 06°01' N 62°26' W, 06°01' N 62°37' W, 06°02' N 62°40' W, and 06°03' N 62°35' W. Myers (1997) briefly reviewed the history of herpetological investigations on Auyán-tepui and referred to some specimens collected during the American Museum of Natural History–Terramar Expedition of 1994. Among species collected at or near five helicopter-supported camps (camp I, 05°51' N 62°32' W, 1,700 m; camp II, 05°54' N 62°29' W, 1,750 m; camp III, 05°53' N 62°38' W, 1,850 m; camp IV, 05°58' N 62°33' W, 1,700 m; camp V, 05°46' N 62°32' W, 2,200 m) were specimens of an undescribed *Arthrosaura* (sp. B); a snake of the genus *Atractus* had been collected previously. Even though the specimen of *Atractus* sp. has not been compared with other forms (Myers 1997), we treat it and the *Arthrosaura* sp. B as endemic forms in our analysis. Several lowland species, including *Anolis auratus*, *Ameiva ameiva*, *Cnemidophorus lemniscatus*, *Tropidurus hispidus*, *Leptotyphlops albifrons*, *Chironius carinatus*, *Oxybelis aeneus*, *Liophis lineatus*, and *Erythrolamprus aesculapii* were reported by Roze (1958a) from Auyán-tepui but without specific locality or elevation. Specimens of these species reported by Roze and in the collections of the American Museum of Natural History have no additional data pertinent to elevation. Accordingly, we assume they were collected near the base of the tepui and exclude them from our treatment. The unidentified colubrid is known from parts of a shed skin and has not been counted as endemic. Ayarzagüena and Señaris (1996) transferred their species *Centrolenella auyantepuiana* to the genus *Hyalinobatrachium* (also see Myers and Donnelly 1997, 71, note added in proof).

### Cerro el Sol

Venezuela (Bolívar); latitude × longitude: 06°06' N 62°32' W (Gorzula and Señaris 1998); maximum elevation: 1,750 m; summit area: 0.60 km<sup>2</sup>; slope area: not available, 715 km<sup>2</sup> for Auyán-tepui, Cerro La Luna, Cerro El Sol; massif:

Auyán; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows, on peat and rock; low evergreen, high-tepui forests; low evergreen, upper-montane forests on slopes; date of first herpetological collection-exploration: 1987.

Herpetofauna: 1 species, 1 endemic: Amphibia (1)—*Oreophrynella huberi*\*.

Pertinent literature: Diego-Aransay and Gorzula 1987.

Remarks: Three specimens of *Oreophrynella huberi* reportedly were captured in high, dense herbaceous vegetation at 1,700 m on the summit; two among the several scattered males heard calling during the day were collected on 7 May 1987. Cerro El Sol is the name that has been applied to Uei-tepui in the Eastern Tepui Chain by some authors (e.g., Huber 1995a, 36); a locality with this name is listed as Uei-tepui in USBGN (1961) with coordinates 05°01' N 60°37' W.

### Cerro La Luna

Venezuela (Bolívar); latitude × longitude: 06°05' N 62°31' W (Gorzula and Señaris 1998); maximum elevation: 1,650 m; summit area: 0.20 km<sup>2</sup>; slope area: not available, 715 km<sup>2</sup> for Auyán-tepui, Cerro La Luna, Cerro El Sol; massif: Auyán; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows, on peat and rock; low evergreen, high-tepui forests; low evergreen, upper-montane forests on slopes; date of first herpetological collection-exploration: 1986.

Herpetofauna: 1 species, 0 endemics: Amphibia (1)—*Tepuihyla edelcae*.

Pertinent literature: Ayarzagüena et al. 1992a, 1992b.

Remarks: Cerros La Luna and El Sol exist as two tower-like tepuis at the end of a long, forested ridge extending off the north end of Auyán-tepui (Huber 1995a, fig. 1.25).

### *Aprada Massif*

#### Aprada-tepui

Venezuela (Bolívar); latitude × longitude: 05°26' N 62°25' W (Paynter 1982; USBGN 1961); maximum elevation: 2,500 m; summit area: 4.37 km<sup>2</sup>; slope area: not available; 210 km<sup>2</sup> for Aprada Massif; massif: Aprada; number of vegetation types for massif: 1—pioneer vegetation on sandstone summits; date of first herpetological collection-exploration: 1984.

Herpetofauna: 2 species, 1 endemic: Amphibia (2)—*Eleutherodactylus* sp. B\*, *Stefania satelles*.

Pertinent literature: General: Brewer-Carías 1978b; Mayr and Phelps 1967. Herpetological: Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: McDiarmid accompanied Charles Brewer-Carías and collected here in 1978; Brewer-Carías (1978b) reported coordinates as 05°26' N 62°26' W



at 2,450 m elevation. Gorzula and Señaris (1998) listed two other localities for this tepui: 05°24' N 62°27' W at 2,500 m and 05°27' N 62°23' W at 2,050 m. Mayr and Phelps (1967) gave 2,400 m as the elevation, but this must have been an estimate.

### *Chimantá Massif*

#### *Abacapá-tepui*

Venezuela (Bolívar); latitude × longitude: 05°13' N 62°15' W (USBGN 1961); maximum elevation: 2,400 m; summit area: 28.13 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1984.

Herpetofauna: 6 species, 1 endemics: Amphibia (2)—*Stefania ginesi*, *Tepuihyla edelcae*; Reptilia (4)—*Anadia* sp. A, *Arthrosaura* sp. A, *Anolis nitens* ssp., *Phenacosaurus carlostoddi*\*

Pertinent literature: General: Huber 1992. Herpetological: Gorzula 1992; Gorzula and Señaris 1998; Señaris et al. 1996; Williams et al. 1996.

Remarks: Gorzula and Señaris (1998) listed 05°12' N 62°19' W as coordinates for their collecting site. We use the name *Anolis nitens* ssp., rather than *Anolis eewi*, contrary to the treatment in Gorzula and Señaris (1998); see appendix 18.3 for explanation. *Stefania ginesi*, *Anadia* sp. A, and *Arthrosaura* sp. A are endemic to the Chimantá Massif.

#### *Acopán-tepui*

Venezuela (Bolívar); latitude × longitude: 05°12' N 62°04' W (USBGN 1961); maximum elevation: 2,200 m; summit area: 92.50 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1984.

Herpetofauna: 6 species, 0 endemics: Amphibia (2)—*Stefania ginesi*, *Tepuihyla edelcae*; Reptilia (4)—*Arthrosaura* sp. A, *Neusticurus rudis*, *Leptodeira annulata*, *Thamnodynastes chimanta*.

Pertinent literature: General: Huber 1992; Mayr and Phelps 1967. Herpetological: Barreát et al. 1986; Gorzula 1985, 1992; Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: Paynter (1982) gave coordinates for this locality as 05°12' N 62°14' W. Gorzula and Señaris (1998) had four coordinates for collection sites on this tepui: 05°11' N 62°02' W, 05°13' N 62°05' W, 05°10' N 61°59' W, and 05°12' N

62°05' W. This site was listed as Akopan-tepui by Huber (1992) and Señaris et al. (1996). Three (*Stefania ginesi*, *Arthrosaura* sp. A, and *Thamnodynastes chimanta*) of the six species known from this tepui are endemic to the Chimantá Massif. Gorzula (1985) and Campbell and Clarke (1998) also reported hearing *Otophryne steyermarki* calling from this tepui.

### Amurí-tepui

Venezuela (Bolívar); latitude × longitude: 05°10' N 62°07' W (USBGN 1961); maximum elevation: 2,200 m; summit area: 36.88 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows, on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1983.

Herpetofauna: 7 species, 0 endemics: Amphibia (3)—*Epipedobates rufulus*, *Stefania ginesi*, *Tepuihyla edelcae*; Reptilia (4)—*Anadia* sp. A, *Neusticurus rudis*, *Leptodeira annulata*, *Thamnodynastes chimanta*.

Pertinent literature: General: Huber 1992. Herpetological: Barreát et al. 1986; Gorzula 1988, 1992; Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: Gorzula and Señaris (1998) listed 05°12' N 62°06' W, 05°08' N 62°07' W, and 05°08' N 62°08' W as collection sites on this tepui. *Epipedobates rufulus*, *Stefania ginesi*, *Anadia* sp. A, and *Thamnodynastes chimanta* are endemic to the Chimantá Massif.

### Apacará-tepui

Venezuela (Bolívar); latitude × longitude: 05°18' N 62°13' W (USBGN 1961); maximum elevation: 2,450 m; summit area: 173.12 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1983.

Herpetofauna: 5 species, 0 endemic: Amphibia (2)—*Otophryne steyermarki*, *Tepuihyla edelcae*; Reptilia (3)—*Anolis nitens* ssp., *Leptodeira annulata*, *Thamnodynastes chimanta*.

Pertinent literature: General: Huber 1992. Herpetological: Barreát et al. 1986; Campbell and Clarke 1998; Gorzula 1992; Gorzula and Señaris 1998; Rivero 1967; Roze 1958b.

Remarks: Huber (1992) and Gorzula and Señaris (1998) listed five collection sites with the following coordinates: 05°20' N 62°12' W, 05°25' N 62°11' W, 05°19' N 62°10' W, 05°19' N 62°12' W, and 05°17' N 62°16' W for this tepui. A sixth site (camp XIX; Huber 1992) lies between this and the adjacent Murey-

tepui in the headwaters of the Río Apakará near 05°22' N 62°08' W. *Thamnodynastes chimanta* is endemic to the Chimantá Massif. We use the name *Anolis nitens* ssp., rather than *Anolis eewi* (contra Gorzula and Señaris 1998; see appendix 18.3).

### Chimantá-tepui

Venezuela (Bolívar); latitude × longitude: 05°18' N 62°10' W (Paynter 1982; USBGN 1961); maximum elevation: 2,550 m; summit area: 93.75 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1953.

Herpetofauna: 11 species, 1 endemic: Amphibia (3)—*Hyla sibleszi*, *Stefania ginesi*, *Tepuihyla edelcae*; Reptilia (8)—*Anolis nitens* ssp., *Arthrosaura* sp. A, *Neusticurus rudis*, *Atractus steyermarki*, *Leptodeira annulata*, *Liophis ingeri*<sup>\*</sup>, *Thamnodynastes chimanta*, *Bothriopsis taeniata*.

Pertinent literature: General: Huber 1992; Mayr and Phelps 1967. Herpetological: Barreát et al. 1986; Gorzula 1992; Gorzula and Señaris 1998; Roze 1958b; Señaris et al. 1996.

Remarks: Gorzula and Señaris (1998) listed three collecting localities on Chimantá proper: 05°16' N 62°09' W, 05°18' N 62°03' W, and 05°22' N 62°08' W. We use the name *Anolis nitens* ssp., rather than *Anolis eewi* (contra Gorzula and Señaris 1998; see appendix 18.3). *Stefania ginesi*, *Arthrosaura* sp. A, *Atractus steyermarki*, and *Thamnodynastes chimanta* are endemic to the Chimantá Massif.

### Churi-tepui

Venezuela (Bolívar); latitude × longitude: 05°13' N 61°54' W (Paynter 1982; USBGN 1961); maximum elevation: 2,500 m; summit area: 47.50 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1985.

Herpetofauna: 5 species, 0 endemics: Amphibia (2)—*Stefania ginesi*, *Tepuihyla edelcae*; Reptilia (3)—*Arthrosaura* sp. A, *Atractus steyermarki*, *Thamnodynastes chimanta*.

Pertinent literature: General: Huber 1992. Herpetological: Barreát et al. 1986; Gorzula 1992; Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: Gorzula and Señaris (1998) listed 05°15' N 62°01' W as coordinates for their collection site. *Arthrosaura* sp. A, *Atractus steyermarki*, and *Thamnodynastes chimanta* are endemic to the Chimantá Massif. A single site on this

tepui in the Chimantá Massif was sampled on three different occasions for a total of 11 days (Gorzula and Señaris 1998).

### Murey-tepui

Venezuela (Bolívar); latitude  $\times$  longitude: 05°22' N 62°05' W (camp XVIII) from Huber (1992) and Gorzula and Señaris (1998); maximum elevation: 2,650 m; summit area: 51.25 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1978.

Herpetofauna: 6 species, 1 endemic: Amphibia (4)—*Eleutherodactylus* sp. I\*, *Epipedobates rufulus*, *Stefania ginesi*, *Tepuihyla edelcae*; Reptilia (2)—*Anadia* sp. A, *Thamnodynastes chimanta*.

Pertinent literature: General: Huber 1992. Herpetological: Barreát et al. 1986; Duellman and Hoogmoed 1984; Gorzula 1988, 1992; Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: McDiarmid collected on this tepui in 1978 with Charles Brewer-Carías, and they called it Eruoda-tepui (also see Duellman and Hoogmoed 1984); Brewer-Carías (1978b) subsequently adopted Murey-tepui for the site. Others also have used two names for this tepui. Initially, Huber (1992) used Eruoda-tepui but later recommended Murey-tepui (Huber 1995a). USBGN (1961) listed Eruoda-tepui as the preferred name (but also listed Eruoda-tepui) and gave coordinates as 05°26' N 62°03' W. If these coordinates are accurate, this site is at the northern tip of Murey (= Eruoda) and represents the northernmost locality on the Chimantá Massif (see Huber 1992; Gorzula and Señaris 1998). The following species are endemic to the Chimantá Massif: *Epipedobates rufulus*, *Stefania ginesi*, *Anadia* sp. A, and *Thamnodynastes chimanta*.

### Tirepón-tepui

Venezuela (Bolívar); latitude  $\times$  longitude: ~05°23' N 62°02' W based on extrapolation from Huber's map (1995a, fig. 1.27) and a description in McDiarmid's field notes; maximum elevation: 2,650 m; summit area: 8.75 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1978.

Herpetofauna: 4 species, 1 endemic: Amphibia (3)—*Epipedobates rufulus*, *Stefania ginesi*, *Tepuihyla edelcae*; Reptilia (1)—Gymnophthalmid sp. B\*.

Pertinent literature: General: Huber 1992. Herpetological: Duellman and Hoogmoed 1984.

Remarks: McDiarmid collected here in 1978 with Charles Brewer-Carías. In the field they referred to this site as Toroná-tepui (different from Toronó); later they realized that Tirepón was the more appropriate name and made pertinent corrections to the field catalog. Unfortunately, specimens of *Stefania ginesi* that had been collected by McDiarmid from this tepui were loaned to Duellman with the original field locality information. This has been subsequently corrected so that the specimens of *Stefania ginesi* (USNM 212041-43) reported by Duellman and Hoogmoed (1984, 17, 37) as coming from a locality at 2,450 m on Toroná-tepui are actually from Tirepón-tepui. *Stefania ginesi* and *Epipedobates rufulus* are endemic to the Chimantá Massif. Gymnophthalmid sp. B is known from a shed skin. This isolated, eastern tepui in the Chimantá Massif has been sampled only for a few hours on one day.

### Toronó-tepui

Venezuela (Bolívar); latitude × longitude: 05°12' N 62°10' W based on an approximation from Huber's map (1995a, fig. 1.27); maximum elevation: 2,500 m; summit area: 59.38 km<sup>2</sup>; slope area: not available, 915 km<sup>2</sup> for Chimantá Massif; massif: Chimantá; number of vegetation types for massif: 4—pioneer vegetation on sandstone summits; low tepui-summit scrub and meadows on peat and rock; low evergreen, high-tepui forests; and low evergreen, upper-montane forests on slopes and in valleys between tepuis; date of first herpetological collection-exploration: 1955.

Herpetofauna: 1 species, 0 endemics: Reptilia (1)—*Anolis nitens* ssp.

Pertinent literature: General: Huber 1992. Herpetological: Roze 1958b.

Remarks: Apparently the only herpetological material known from this tepui is the type specimen of *Anolis eewi* Roze 1958, that was collected by Julian Steyermark and John Wurdack during their botanical explorations of the Chimantá Massif in the period of January through March 1955. We use the name *Anolis nitens* ssp., rather than *Anolis eewi* (contra Gorzula and Señaris 1998; see appendix 18.3). The coordinates listed for Toronó-tepui in USBGN (1961) are 05°24' N 62°00' W; these are incorrect and contributed to the confusion with an early name for Tirepón-tepui (see earlier remarks).

### Angasima-tepui

Venezuela (Bolívar); latitude × longitude: 05°05' N 62°03' W (USBGN 1961); maximum elevation: 2,250 m; summit area: 2.00 km<sup>2</sup>; slope area: 32 km<sup>2</sup>; massif: not part of a massif; number of vegetation types: 1—low tepui-summit scrub and meadows on peat and rock; date of first herpetological collection-exploration: 1986.

Herpetofauna: 1 species, 0 endemics: Amphibia (1)—*Stefania satelles*.

Pertinent literature: Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: Gorzula and Señaris (1998) included two localities, 05°03' N 62°04' W and 05°03' N 62°07' W, that were sampled for two days in August and one day in March.

### Upuigma-tepui

Venezuela (Bolívar); latitude × longitude: 05°07' N 61°56' W (Paynter 1982; USBGN 1961); maximum elevation: 2,100 m; summit area: 0.63 km<sup>2</sup>; slope area: 13 km<sup>2</sup>; massif: not part of a massif; number of vegetation types for massif: 1—low tepui-summit scrub and meadows on peat and rock; date of first herpetological collection-exploration: 1986.

Herpetofauna: 1 species, 0 endemics: Amphibia (1)—*Stefania satelles*.

Pertinent literature: General: Mayr and Phelps 1967. Herpetological: Gorzula and Señaris 1998; Señaris et al. 1996.

Remarks: The collection site described by Gorzula and Señaris (1998) was listed at 05°05' N 61°57' W and sampled once in March. Mayr and Phelps (1967) estimated the summit elevation at 2,200 m. This site is also called El Castillo.

## Western Pantepui District

### MAIGUALIDA SUBDISTRICT

#### Isolates

##### Sierra de Maigualida

Venezuela (Bolívar); latitude × longitude: 05°30' N 65°10' W (USBGN 1961); maximum elevation: 2,400 m; summit area: 440 km<sup>2</sup>; slope area: not available; massif: none; number of vegetation types: 2—broad-leaved, shrubby upland and highland meadows on rock and peat and low to medium upper-montane evergreen forest; date of first herpetological collection-exploration: 1988.

Herpetofauna: 2 species, 1 endemic: Amphibia (2)—Hylid sp. A\*, *Leptodactylus rugosus*.

Pertinent literature: Gorzula and Señaris 1998.

Remarks: Gorzula and Señaris (1998) listed one set of coordinates (05°43' N 65°19' W) for a site in Bolívar state and another (05°33' N 65°13' W) for an Amazonas site. As currently known, Maigualida is primarily granitic and has little or none of the Roraima sandstone characteristic of tepuis. This extensive area has received little work (7 days at two sites in March).

## YUTAJÉ SUBDISTRICT

*Isolates***Cerro Guanay**

Venezuela (Amazonas); latitude × longitude: 05°51' N 66°18' W (Paynter 1982; USBGN 1961); maximum elevation: 2,080 m; summit area: 165 km<sup>2</sup>; slope area: 113 km<sup>2</sup>; massif: none; number of vegetation types: 1—low to tall tepui scrub on rock; date of first herpetological collection-exploration: 1985.

Herpetofauna: 8 species, 3 endemics: Amphibia (5)—*Colostethus guanayensis*\*, *Eleutherodactylus* sp. A\*, *Hyalinobatrachium orientale*, *Hyla sibleszi*, *Leptodactylus rugosus*; Reptilia (3)—*Anolis nitens* ssp., *Plica pansticta*, *Prionodactylus nigroventris*\*.

Pertinent literature: General: Mayr and Phelps 1967. Herpetological: Gorzula and Señaris 1998; La Marca 1996.

Remarks: Gorzula and Señaris (1998) reported on collections made at and near a camp with the following coordinates: 05°55' N 66°23' W at 1,650 m. La Marca (1996) reported an elevation of 1,800 m for a topoparatype of *Colostethus guanayensis* and referred to the tepui as Serranía de Guanay. Myers and Donnelly (2001, 75) reported *Plica pansticta* (as *Tropidurus panstictus*) from Guanay and gave an indication of work in progress. We use the name *Anolis nitens* ssp. rather than *Anolis eewi* (contra Gorzula and Señaris 1998; see appendix 18.3).

**Cerro Yaví**

Venezuela (Amazonas); latitude × longitude: 05°32' N 65°59' W (Paynter 1982; USBGN 1961); maximum elevation: 2,300 m; summit area: 5.62 km<sup>2</sup>; slope area: 70 km<sup>2</sup>; massif: none; number of vegetation types: 2—broad-leaved, shrubby upland and highland meadows on rock and peat, and low evergreen, upper-montane forest; date of first herpetological collection-exploration: 1986.

Herpetofauna: 7 species, 5 endemics: Amphibia (3)—*Eleutherodactylus cantitans*, *Eleutherodactylus pruinatus*\*, *Eleutherodactylus yaviensis*; Reptilia (4)—Gymnophthalmid sp. A\*, *Phenacosaurus bellipeniculus*\*, *Prionodactylus goeleti*\*, *Thamnodynastes yavi*\*.

Pertinent literature: General: Hitchcock 1947; Mayr and Phelps 1967. Herpetological: Gorzula and Señaris 1998; Myers and Donnelly 1996.

Remarks: The collection of 63 specimens described by Myers and Donnelly (1996) was made during five days in February 1995 in the vicinity of a summit camp at 2,150 m and coordinates of 05°43' N 65°54' W. Gorzula and Señaris (1998) reported eight specimens collected over four days in October at a locality at 2,100 m elevation and coordinates of 05°42' N 65°53' W. Given this level of sampling, we think the herpetofauna of Yaví is reasonably well known compared with that of many tepuis in the Western Pantepui District, some of which

(e.g., Cuao-Sipapo Massif) have not been sampled for amphibians and reptiles. The record for Gymnophthalmid sp. A is based on the tail of a lizard removed from the stomach of a specimen of *Thamnodynastes yavi*. Myers and Donnelly (1996) compared the tail to those of *Prionodactylus goeleti* and found that they were different; they suggested that the tail might belong to a species of *Arthrosaura*. Four habitat pictures, one showing a lake, were published in Myers and Donnelly (1996).

### *Yutajé Massif*

#### Cerro Corocoro

Venezuela (Amazonas); latitude × longitude: 05°46' N 66°11' W (Gorzula and Señaris 1998); maximum elevation: 2,400 m; summit area: 179.38 km<sup>2</sup>; slope area: not available, 143 km<sup>2</sup> for Yutajé Massif; massif: Yutajé; number of vegetation types for massif: 3—low evergreen, upper-montane forest; broad-leaved, shrubby upland and highland meadows on rock and peat; and low to tall tepui scrub on rock; date of first herpetological collection-exploration: 1987.

Herpetofauna: 5 species, 1 endemic: Amphibia (2)—*Eleutherodactylus yawiensis*, *Pseudopaludicola llanera*; Reptilia (3)—*Plica pansticta*, *Prionodactylus goeleti*, *Thamnodynastes corocoroensis*\*.

Pertinent literature: Gorzula and Ayarzagüena 1995; Gorzula and Señaris 1998; Myers and Donnelly 2001.

Remarks: This tepui was called Cerro Coro Coro by Huber and other authors in various chapters in *Flora of the Venezuelan Guayana* (Steyermark et al. 1995a). For purposes of utility we have used the orthography (Corocoro) found on some older maps and recently adopted by Gorzula and Señaris (1998) and Myers and Donnelly (2001). Myers and Donnelly (2001) noted that a single specimen from Corocoro called *Eleutherodactylinae* series b by Gorzula and Señaris (1998, 55) likely represented *Eleutherodactylus yawiensis*, and we have followed that suggestion. Myers and Donnelly (2001) also reported the frog *Pseudopaludicola llanera* and a new lizard they called *Tropidurus panstictus* (= *Plica pansticta*, following Frost et al. 2001) that were taken along a small rocky stream bordered by a narrow strip of gallery forest on a small plateau at 1,220 m (1,400 m on some maps) and coordinates of 05°42' N 66°10' W on the south end of Cerro Corocoro. Although they were taken from a relatively low site, we have included these two species in the Pantepui list (appendix 18.1) but do so cautiously because of the relatively low elevation and some concern about the lower elevational limits of Cerro Corocoro. For additional comments on *Thamnodynastes corocoroensis*, see remarks under Cerro Yaví.

#### Serranía Yutajé

Venezuela (Amazonas); latitude × longitude: 05°45' N 66°03' W (Gorzula and Señaris 1998); maximum elevation: 2,140 m; summit area: 95.63 km<sup>2</sup>; slope area:



143 km<sup>2</sup> for Yutajé Massif; massif: Yutajé; number of vegetation types for massif: 3—low evergreen, upper-montane forest; broad-leaved, shrubby upland and highland meadows on rock and peat; and low to tall tepui scrub on rock; date of first herpetological collection-exploration: 1988.

Herpetofauna: 7 species, 3 endemics: Amphibia (4)—*Colostethus undulatus*\*, *Eleutherodactylus cantitans*, *Eleutherodactylus yaviensis*, *Hyalinobatrachium eccentricum*\*; Reptilia (3)—*Adercosaurus vixadnexus*\*, *Mabuya bistrata*, *Prionodactylus goeleti*.

Pertinent literature: Gorzula and Señaris 1998; Myers and Donnelly 2001.

Remarks: The collecting site listed by Myers and Donnelly was on a branch of the upper Río Corocoro at about 1,700 m (1,920 m on some maps) on the north end of Serrania Yutajé (see map in Myers and Donnelly 2001, 5) at 05°46' N 66°08' W. The area has a mosaic of dense scrub on the rocky, exposed western side of the river and low, wet mossy forest along the eastern side. These forests are extensions of the medium, evergreen, lower-montane to montane forests that surround the uplands in the Yaví-Corocoro-Yutajé-Guanay mountain complex and reach into the highlands in wetter places (Huber 1995c).

## Central Pantepui District

### GUAIQUINIMA SUBDISTRICT

#### Isolates

#### Cerro Guaiquinima

Venezuela (Bolívar); latitude × longitude: 05°49' N 63°40' W (Paynter 1982; USBGN 1961); maximum elevation: 1,650 m; summit area: 1,096.26 km<sup>2</sup>; slope area: 410 km<sup>2</sup>; massif: none; number of vegetation types: 3—broad-leaved, shrubby upland meadows on peat; tall, upland scrub on rock; and medium, evergreen montane forest; date of first herpetological collection-exploration: 1984.

Herpetofauna: 22 species, 5 endemics: Amphibia (9)—*Eleutherodactylus* sp. S\*, *Hyalinobatrachium* sp. A\*, *Hyla benitezi*, *Hyla boans*, *Hyla crepitans*, *Hyla minuta*, *Leptodactylus longirostris*, *Leptodactylus rugosus*, *Osteocephalus taurinus*; Reptilia (13)—*Ameiva ameiva*, *Anolis nitens* ssp., *Anolis fuscoauratus*, *Neusticurus racenisi*, *Neusticurus* sp. A\*, *Plica lumaria*\*, *Tropidurus hispidus*, *Imantodes lentiferus*, *Leptotyphlops albifrons*, *Liophis torrenicola*, *Mastigodryas boddaerti*, *Philodryas cordata*\*, *Thamnodynastes pallidus*.

Pertinent literature: Donnelly and Myers 1991; Gorzula and Señaris 1998; Mägdefrau et al. 1991; Schlüter 1994.

Remarks: Huber (1995a) treated Guaiquinima as an upland rather than a highland tepui, presumably because most of the cerro is below 1,500 m. Huber's definition of highlands (above 1,500 m) results in a somewhat subjective deci-

sion to treat Guaiquinima separately from most other tepuis (see text for discussion). We place Guaiquinima in the Central District primarily because of its geographic position. Donnelly and Myers (1991) listed approximate coordinates for this extensive tepui as 05°46' N 63°36' W. Gorzula and Señaris (1998) listed four localities at which collections of amphibians and reptiles were made on this tepui: 05°53' N 63°41' W, 05°58' N 63°29' W, 05°54' N 63°26' W, and 05°47' N 63°48' W. Mägdefrau et al. (1991) and Schlüter (1994) gave coordinates and elevations for four other sites at which they collected: 05°54'50" N 63°28' W, 1,180 m; 05°45'50" N 63°33'40" W, 780 m; 05°44'10" N 63°38' W, 980 m; and 05°47'10" N 63°50'30" W, 1,520 m. Mägdefrau et al. (1991) used *Neusticurus rudis* for the taxon referred to here as *Neusticurus* sp. A, but the species from Guaiquinima is distinct from *N. rudis* and an undescribed form from Marutaní. Preliminary reports seem to suggest that more than a single species is represented by *Eleutherodactylus* sp. S (= *Eleutherodactylus* spp. of Mägdefrau et al. 1991 and Schlüter 1994); we prefer to list only one pending publication of descriptions or additional information.

#### JAU A SARISARIÑAMA SUBDISTRICT

##### *Isolates*

##### **Cerro Guanacoco**

Venezuela (Bolívar); latitude × longitude: 04°40' N 63°51' W (Paynter 1982; USBGN 1961); maximum elevation: 1,500 m; summit area: 526.25 km<sup>2</sup>; slope area: 400 km<sup>2</sup>; massif: none; number of vegetation types: 2—tubiform, shrubby highland meadows on rock and peat and medium, evergreen upper-montane forest; date of first herpetological collection-exploration: 1974.

Herpetofauna: 1 species, 0 endemics: Amphibia (1)—*Hyla minuta*.

Pertinent literature: General: Orejas-Miranda and Quesada 1976.

Remarks: Braulio Orejas Miranda visited this tepui for one day in 1974 with Charles Brewer-Carías during the Jaua-Sarisariñama Expedition.

##### **Sierra Marutaní**

Venezuela (Bolívar); latitude × longitude: 03°46' N 63°03' W (Paynter 1982 as Cerro Urutaní; USBGN 1961 as Sierra Marutaní); maximum elevation: 1,500 m; summit area: not available; slope area: 740 km<sup>2</sup>; massif: none; number of vegetation types: 2—tall, upland scrub on rock and medium, evergreen montane forest; date of first herpetological collection-exploration: 1981.

Herpetofauna: 2 species, 1 endemic: Reptilia (2)—*Anolis nitens* ssp., *Neusticurus* sp. B\*.

Pertinent literature: Gorzula and Señaris 1998.

Remarks: This tepui is included in the Jaua Sarisariñama subdistrict primar-

ily because of geography, but as noted by Huber (1995a), this serranía is so poorly known that placement is preliminary. Julian Steyermark gave McDiar-mid a specimen of *Neusticurus* that he had collected on Marutaní in 1981. Hu-ber (1995a) noted that the toponymy for this area is unreliable; other names for the mountain range (cerro or serranía) include Urutaní, Pia-Zoi, Piazoí, and Pia Soi. We use the name *Anolis nitens* ssp. rather than *Anolis eewi* (contra Gorzula and Señaris 1998; see appendix 18.3). As currently known, Marutaní is primarily granitic, with little or none of the Roraima sandstone characteristic of tepuis.

### *Jaua Massif*

#### Cerro Jaua

Venezuela (Bolívar); latitude × longitude: 04°48' N 64°26' W (Paynter 1982; USBGN 1961); maximum elevation: 2,250 m; summit area: 625.62 km<sup>2</sup>; slope area: 482 km<sup>2</sup>; massif: Jaua; number of vegetation types for massif: 4—low, high-tepui scrub on peat and rock; tubiform, shrubby highland meadows on rock and peat; medium, evergreen montane forest; and medium, evergreen upper-montane forest; date of first herpetological collection-exploration: 1967.

Herpetofauna: 14 species, 8 endemics: Amphibia (10)—*Colostethus ayarzaguenai*\*, *Colostethus* sp. A\*, *Eleutherodactylus* sp. F\*, *Hyalinobatrachium* sp. B\*, *Hyla benitezi*, *Hyla minuta*, Hylid sp. G\*, *Otophryne steyermarki*, *Stefania oculosa*\*, *Stefania percristata*\*; Reptilia (4)—*Anolis nitens* ssp., *Arthrosaura tyleri*, *Neusticurus* sp. C\*, *Prionodactylus phelpsorum*.

Pertinent literature: General: Orejas-Miranda and Quesada 1976. Herpeto-logical: Barrio 1998, 1999; Donnelly et al. 1992; La Marca 1996; Lancini 1968; Señaris et al. 1996.

Remarks: Braulio Orejas-Miranda visited this tepui in 1974 as part of the Charles Brewer-Carías Expedition and collected several species, including *Pri-onodactylus phelpsorum*. Unfortunately, only a few species from this collection have been described. Señaris and Ayarzagüena collected at two sites in the cen-tral part of the tepui at 1,600 m during 10–12 June 1994. Coordinates listed for the type locality of *Colostethus ayarzaguenai* and *Stefania oculosa* are 04°49'55" N 64°25'54" W; those for that of *Stefania percristata* are 04°49'55" N 64°25'59" W. La Marca (1996) did not give an elevation for the type locality of *Colostethus ayarzaguenai*; however, he did list the collectors (Ayarzagüena and Señaris), the date (10 June 1994), and a set of coordinates. The latter match exactly those given by Señaris et al. (1996) in the description of *Stefania oculosa*, the type of which was collected at 1,600 m on 11 June 1994. Accordingly, we list 1,600 m as the elevation at the type locality of *Colostethus ayarzaguenai*. Other specimens of amphibians and reptiles have been collected incidental to botanical and or-nithological interests on Jaua. Two major streams that make up the Río Mara-

jano drain Jaua from its high point ( $\sim 2,250$  m) in the south to about 1,400 m in the north; gallery forests alternate with tepui meadows along the river on the south half of the tepui (Huber 1995a).

### Cerro Sarisariñama

Venezuela (Bolívar); latitude  $\times$  longitude:  $04^{\circ}30'$  N  $64^{\circ}14'$  W (Paynter 1982; USBGN 1961); maximum elevation: 2,350 m; summit area: 546.88 km<sup>2</sup>; slope area: 482 km<sup>2</sup>; massif: Jaua; number of vegetation types for massif: 4—tall, upland scrub on rock; tubiform, shrubby highland meadows on rock and peat; medium, evergreen upper-montane forest; and medium, evergreen montane forest; date of first herpetological collection-exploration: 1974.

Herpetofauna: 5 species, 2 endemics: Amphibia (2)—*Eleutherodactylus* sp. G\*, *Stefania riae*\*; Reptilia (3)—*Prionodactylus phelpsorum*, *Tropidurus hispidus*, *Chironius* sp.

Pertinent literature: General: Brewer-Carías 1976, 1983; Mayr and Phelps 1967. Herpetological: Duellman and Hoogmoed 1984; Orejas-Miranda and Quesada 1976.

Remarks: Braulio Orejas-Miranda visited this tepui in 1974 with Charles Brewer-Carías and collected a few species of amphibians and reptiles. Although Lancini (1968) listed the type locality for *Prionodactylus phelpsorum* as Cerro Jaua, Gorzula and Señaris (1998) corrected the type locality to Sarisariñama. In this action, they accepted the correction provided by Steyermark (Steyermark and Brewer-Carías 1976, 180) for all material collected during the Phelps Expedition of 1967, which incidentally was the first expedition to use helicopters in support of scientific collecting on tepui summits (J. Steyermark, pers. comm., as cited in Huber 1995b). According to Steyermark, who was the botanist on the Phelps Expedition, all botanical specimens were collected from the western summit of Sarisariñama, not Jaua as originally reported; apparently the expedition never reached the real Meseta Jaua. Consequently, one assumes that the holotype of *Prionodactylus phelpsorum* also was from Sarisariñama. As pointed out by Myers and Donnelly (2001), this was confirmed by Phelps (1977), who changed the Jaua locality to Cumbre Occidental, Meseta de Sarisariñama, at approximately  $04^{\circ}45'$  N  $64^{\circ}26'$  W (new coordinates seem unlikely according to a map in Huber 1995a, fig. 1.29). The *Chironius* sp. record is based on a piece of a shed skin.

## DUIDA-MARAHUAKA SUBDISTRICT

### *Duida-Marahuaka Massif*

#### Cerro Duida

Venezuela (Amazonas); latitude  $\times$  longitude:  $03^{\circ}25'$  N  $65^{\circ}40'$  W (Paynter 1982; USBGN 1961); maximum elevation: 2,358 m; summit area: 1,089.00 km<sup>2</sup>; slope

area: 715 km<sup>2</sup>; massif: Duida-Marahuaka; number of vegetation types for massif: 7—broad-leaved, shrubby highland meadows on peat; broad-leaved, shrubby high-tepui meadows on peat and rock; low to tall upland and high-tepui scrub; low evergreen high-tepui forest; low evergreen upper-montane forest; medium evergreen montane forest; tall evergreen lower-montane forest; date of first herpetological collection-exploration: 1928.

Herpetofauna: 15 species, 10 endemics: Amphibia (7)—*Cochranella duidaeana*\*, *Colostethus shrevei*, *Dischidiodytes duidensis*\*, *Eleutherodactylus* sp. K\*, Hylid sp. F\*, *Stefania goini*, *Tepuihyla aecii*\*; Reptilia (8)—*Anolis nitens* ssp., *Arthrosaura tyleri*, *Neusticurus tatei*\*, *Riolama* sp. C\*, *Atractus duidensis*\*, *Atractus riveroi*\*, *Chironius exoletus*, *Thamnodynastes duida*\*.

Pertinent literature: General: Mayr and Phelps 1967; Tate and Hitchcock 1930. Herpetological: Ayarzagüena 1992; Ayarzagüena et al. 1992a, 1992b; Burt and Burt 1931; Duellman and Hoogmoed 1984; Myers and Donnelly 1996; Rivero 1966, 1968; Roze 1961; Señaris et al. 1996; Vanzolini and Williams 1970; Van Devender 1969.

Remarks: *Stefania goini* is endemic to the Duida Massif. We follow La Marca (1996), who considered *Colostethus shrevei* to be endemic to the Duida Massif and surrounding region, in contrast to the earlier treatment of Hoogmoed (1979a), who assessed the species as peripheral amazonian. The record for *Riolama* sp. C is based on a partially digested lizard removed from the stomach of the holotype of *Thamnodynastes duida* (Myers and Donnelly 1996). *Stefania marahuacuensis* and *Neusticurus racenisi* are known from intermediate elevations (near 600 m) on Cerro Duida and at higher elevations on Marahuaka but are not included in this analysis pending their collection from elevations above 1,500 m. Duida and Marahuaka are joined by upland, but Huachamacari is separated from them by a considerable expanse (10–20 km) of lowland (< 500 m) tree and shrub savanna that apparently does not flood. A map and information about the geography and habitats on the southern portion of the summit are available in Tate and Hitchcock (1930). Myers and Donnelly (1996) described the area near the type locality of *Thamnodynastes duida* as a broad ravine at 2,015 m that lies between peaks 7 and 16 on the southeastern side of the south end of the massif at approximate coordinates of 03°20' N 65°35' W.

### Cerro Huachamacari

Venezuela (Amazonas); latitude × longitude: 03°48' N 65°46' W (Paynter 1982; USBGN 1961); maximum elevation: 1,900 m; summit area: 8.75 km<sup>2</sup>; slope area: 60 km<sup>2</sup>; massif: Duida-Marahuaka; number of vegetation types for massif: 7—broad-leaved, shrubby highland meadows on peat; broad-leaved, shrubby high-tepui meadows on peat and rock; low to tall upland and high-tepui scrub; low evergreen high-tepui forest; low evergreen upper-montane forest; medium evergreen montane forest; and tall evergreen lower-montane forest; date for first herpetological collection-exploration: 1992.

Herpetofauna: 2 species, 1 endemic: Amphibia (2)—*Hyla aromatica*\*, *Stefania goini*.

Pertinent literature: General: Mayr and Phelps 1967. Herpetological: Ayarzagüena and Señaris 1993; Rivero 1966; Señaris et al. 1996.

Remarks: *Stefania goini* is endemic to the Duida-Marahuaka Massif. Huachamacari is the smallest, lowest, and least studied of the three tepuis in the massif.

### Cerro Marahuaka

Venezuela (Amazonas); latitude × longitude: 03°34' N 65°27' W (Paynter 1982; USBGN 1961); maximum elevation: 2,800 m; summit area: 121.00 km<sup>2</sup>; slope area: 325 km<sup>2</sup>; massif: Duida-Marahuaka; number of vegetation types for massif: 7—broad-leaved, shrubby highland meadows on peat; broad-leaved, shrubby high-tepui meadows on peat and rock; low to tall upland and high-tepui scrub; low evergreen high-tepui forest; low evergreen upper-montane forest; medium evergreen montane forest; and tall evergreen lower-montane forest; date for first herpetological collection-exploration: 1950.

Herpetofauna: 8 species, 6 endemics: Amphibia (7)—*Colostethus brunneus*, *Colostethus shrevei*, *Dischidiodactylus colonnelloi*\*, *Eleutherodactylus* sp. T\*, *Hyla inparquesi*\*, *Metaphryniscus sosai*\*, *Tepuihyla luteolabris*\*; Reptilia (1)—*Thamnodynastes marahuaguensis*\*.

Pertinent literature: Ayarzagüena 1983; Ayarzagüena and Señaris 1993; Ayarzagüena et al. 1992a, 1992b; Duellman and Hoogmoed 1984; Gorzula and Ayarzagüena 1995; Rivero 1961, 1966; Señaris et al. 1994, 1996.

Remarks: A common, alternate spelling for this tepui is Marahuaca. The frogs *Eleutherodactylus marmoratus* and *Stefania marahuaguensis*, and the lizard *Neusticurus racenisi* have been reported from elevations near 1,200 m on Cerro Marahuaka; they are excluded from our analysis pending their collection from higher elevations. Also, the snake *Atractus riveroi* has been collected at Temiche, a camp on the southern slope of Marahuaka at 1,300 m (Roze 1961); also given as 4,050 ft. (1,234 m) by Rivero (1961). We did not include the *Atractus* in the Marahuaka fauna because of the elevation; it also is known from Cerro Duida. Broad-leaved, shrubby high-tepui meadows on peat and rock are known only from Marahuaka, and low evergreen high-tepui forest is restricted to the summit. Molina and Señaris (2001) recently described *Riolama uzzelli* from two sites on Cerro Marahuaka (1,850 and 2,600 m). We do not know if *R. uzzelli* is the same as *Riolama* sp. C from Duida, but we treat them as the same species in this chapter.

### Cerro Yapacana

Venezuela (Amazonas); latitude × longitude: approximately 03°42' N 66°45' W (Paynter 1982); maximum elevation: 1,300 m; summit area: 10.50 km<sup>2</sup>; slope

area: 38 km<sup>2</sup>; massif: none; number of vegetation types: 1—low evergreen montane forest; date of first herpetological collection-exploration: 1970.

Herpetofauna: 1 species, 1 endemic: Amphibia (1)—*Minyobates steyermarki*\*.

Pertinent literature: General: Mayr and Phelps 1967. Herpetological: Gorzula and Señaris 1998; Rivero 1971.

Remarks: Huber (1995a) considered Yapacana as an upland rather than highland tepui because of its low maximum elevation (given as 1,345 m in Mayr and Phelps 1967, map 1). Although we understand the need for specific definitions and elevational limits for physiographic units, we include Yapacana here because it is a sandstone mountain, was considered a low-elevation tepui by Huber (1995a), and has had some herpetological attention. We provisionally place it in the Duida-Marahuaka Subdistrict strictly on the basis of its geographic position. Additional samples of the herpetofauna should provide some guidance relative to the future treatment of Cerro Yapacana and its fauna. Paynter (1982) listed an approximate locality for this mountain. Gorzula and Señaris (1998) listed 03°42' N 66°46' W as the coordinates for the dendrobatid collection.

### *Southern Pantepui District*

#### SIERRA TAPIRAPECÓ

##### *Cerro Tamacuari*

Venezuela (Amazonas); latitude × longitude: 01°13' N 64°42' W (Myers and Donnelly 1997); maximum elevation: 2,340 m; summit area: < 0.01 km<sup>2</sup>; slope area: not available; massif: none; number of vegetation types: 1—low evergreen upper-montane forest; date of first herpetological collection-exploration: 1989.

Herpetofauna: 11 species, 6 endemics: Amphibia (7)—*Colostethus tamacuarensis*\*, *Eleutherodactylus avius*\*, *Eleutherodactylus cavernibardus*\*, *Eleutherodactylus memorans*\*, *Hyalinobatrachium crurifasciatum*\*, *Hyla benitezi*, *Stefania tamacuarina*\*; Reptilia (4)—*Anolis nitens* ssp., *Arthrosaura synaptolepis*, *Neusticurus racenisi*, *Thamnodynastes pallidus*.

Pertinent literature: Myers and Donnelly 1997.

Remarks: This locality, also known as Pico Tamacuari (Mayr and Phelps 1967, map 1), is a conical granite mountain in the poorly explored Sierra Tapirapecó (Huber 1995a), which, as currently known, has little or none of the Roraima sandstone characteristic of tepuis. The immediate region near Cerro Tamacuari has received reasonable attention (Myers and Donnelly 1997), but the Sierra Tapirapecó, which extends for about 100 km along the Venezuelan–Brazilian border, is unknown from a herpetological perspective.

## NEBLINA-ARACAMUNI MASSIF

*Cerro Aracamuni-Avispa*

Venezuela (Amazonas); latitude  $\times$  longitude: 01°14' N 65°26' W (USBGN 1961); maximum elevation: 1,600 m; summit area: 238 km<sup>2</sup>; slope area: 658 km<sup>2</sup>; massif: Neblina-Aracamuni; number of vegetation types for massif: 5—low, high-tepui scrub on peat; broad-leaved, shrubby upland and high-tepui meadows on peat; broad-leaved, shrubby upland meadows on peat; medium to tall evergreen montane forest; and low evergreen upper-montane forest; date of first herpetological collection-exploration: 1987.

Herpetofauna: 1 species, 1 endemic: Amphibia (1)—*Cochranella riveroi*\*.

Pertinent literature: Ayarzagüena 1992.

Remarks: Cerro Avispa is the larger, more southern section of this largely unexplored system. This tepui complex is virtually unknown and compared with its neighbors (Duida to the north and Neblina to the south) deserves much more herpetological work.

*Cerro de la Neblina*

Venezuela (Amazonas) and Brazil (Amazonas); latitude  $\times$  longitude: 00°48' N 65°59' W (Brewer-Cariás 1978b); maximum elevation: 3,014 m; summit area: 235 km<sup>2</sup>; slope area: 857 km<sup>2</sup>; massif: Neblina-Aracamuni; number of vegetation types for massif: 5—low, high-tepui scrub on peat; broad-leaved, shrubby upland and high-tepui meadows on peat; broad-leaved, shrubby upland meadows on peat; medium to tall evergreen montane forest; and low evergreen upper-montane forest; date of first herpetological collection-exploration: 1984.

Herpetofauna: 26 species, 20 endemics: Amphibia (17)—*Adelophryne* sp. A\*, *Adelophryne* sp. B\*, Bufonid sp.\*, *Cochranella* sp.\*, *Colostethus* sp. B\*, *Eleutherodactylus* sp. L\*, *Eleutherodactylus* sp. M\*, *Eleutherodactylus* sp. N\*, *Eleutherodactylus* sp. O\*, *Eleutherodactylus* sp. P\*, *Eleutherodactylus* sp. Q\*, *Eleutherodactylus* sp. R\*, Hylid sp. C\*, Hylid sp. D\*, Hylid sp. E\*, Leptodactylid sp.\*, *Leptodactylus* sp.\*; Reptilia (9)—*Arthrosaura synaptolepis*, *Mabuya* sp., *Phenacosaurus neblininus*\*, *Riolama* sp. A\*, *Riolama* sp. B\*, *Dipsas* cf. *indica*, *Dipsas* sp., *Leptophis ahaetulla*, *Leptophis* sp.

Pertinent literature: General: Brewer-Cariás 1978b, 1988; Maguire 1955; Mayr and Phelps 1967; Ort 1965; Givnish et al. 1986; Willard et al. 1991. Herpetological: Donnelly et al. 1992; McDiarmid and Paolillo 1988; Myers et al. 1993.

Remarks: Also known as the Sierra de la Neblina (Huber 1995a); contains Pico da Neblina (3,014 m), the highest mountain in Brazil and the Guayana Highlands. Maguire and Wurdack (1959) listed 00°59'26" N 65°58'05" W for their summit camp at 1,800 m on the northeastern part of the complex. Coor-



dinates and elevations for the camps established during the Neblina Expedition (Brewer-Cariás 1988) are as follows: camp 1— $00^{\circ}52'10''$  N  $66^{\circ}05'25''$  W, 1,820–1,880 m elevation; camp 2— $00^{\circ}50'00''$  N  $66^{\circ}58'48''$  W, 2,085–2,100 m; camp 3— $00^{\circ}54'10''$  N  $66^{\circ}03'50''$  W, 1,820 m; camp 4— $00^{\circ}56'20''$  N  $65^{\circ}56'50''$  W, 2,085–2,770 m; camp 5— $00^{\circ}49'10''$  N  $66^{\circ}00'02''$  W, 1,250 m; camp 6— $00^{\circ}52'20''$  N  $65^{\circ}56'20''$  W, 2,000 m; camp 7— $00^{\circ}50'40''$  N  $65^{\circ}58'10''$  W, 1,730–1,850 m; camp 8— $00^{\circ}50'00''$  N  $65^{\circ}57'30''$  W, 2,300–2,400 m; camp 9— $01^{\circ}00'00''$  N  $65^{\circ}53'00''$  W, 1,780–1,830 m; camp 10— $00^{\circ}54'40''$  N  $66^{\circ}02'30''$  W, 1,690 m; camp 11— $00^{\circ}51'45''$  N  $65^{\circ}58'52''$  W, 1,390–1,515 m; camp 12— $00^{\circ}47'50''$  N  $66^{\circ}00'10''$  W, 1,950–2,000 m.

## Appendix 18.5 History of Exploration

The isolated nature of the Guayana Highlands has made exploration of the tepuis and sampling of its herpetofauna a difficult and sporadic endeavor. General accounts of some nineteenth-century explorations serve to introduce the region, and when combined with reports resulting from the significant, though primarily botanical and ornithological, expeditions made during the mid-twentieth century and those from recent interdisciplinary field efforts when the collection of amphibians and reptiles was a primary goal, they provide ample material for our review. We briefly review the history of exploration to augment understanding of the region and to provide a historical context for our treatment of the Pantepui herpetofauna.

Scientific exploration of the interior Guayana region began in the eighteenth century and was concentrated primarily in lowland areas. Huber and Wurdack (1984) and Huber (1995b) provided interesting accounts of the history of botanical exploration in the Venezuelan Guayana. Prominent among the early explorers were the German naturalist Alexander von Humboldt and the French botanist Aimé Bonpland, who, as near as we can tell, may have been the first scientists to actually see a tepui. In May 1800, during their epic explorations of the upper Orinoco and Cassiquiare rivers, Humboldt (1907) described the “solemn grandeur” of Cerro Duida as seen from the small mission settlement of Esmeralda (fig. 18.1). Another remarkable explorer was Robert H. Schomburgk, who reached Esmeralda, which by then had dwindled to a single family, 39 years after Humboldt. His travels (Schomburgk 1841) from Roraima to Duida (approximately 600 km of straight-line distance) took him through parts of the Serra Pacaraima (in northern Roraima, Brazil), along the southern reaches of Sarisariñama, through the northern portions of the Sierra Parima, and along the eastern side of Cerro Marahuaka (fig. 18.1). Schomburgk also was impressed by the view of Duida and noted that Nature had remained the same. Schom-

burgk (1841, 245) wrote, "Duida still raises its lofty summit to the clouds, and flat savannahs, interspersed with tufts of trees and the majestic *Mauritia* palm stretch from the banks of the Orinoco to the foot of the mountains beyond, giving to the landscape that grand and animated appearance which so much delighted Humboldt." More than 11 years later, Richard Spruce reached Esmeralda by boat from the Cassiquiare. In December 1853, he described Duida from about the same spot as had Humboldt and Schomburgk; Spruce provided an illustration of Cerro Duida (Spruce 1908). As far as we know, none of these explorers actually collected material on Duida.

Exploration of specific tepuis became the goal of explorers and scientists in the mid- to late 1800s. At that time, travel in this part of the world and especially to the Guayana Highlands was arduous and time-consuming. Field logistical support for these early expeditions usually was nonexistent; nearly everything had to be carried, initially by river and then on foot, sometimes over considerable distances. Food frequently was a major limiting factor, and success often depended on weather, the knowledge and hunting skills of local guides, and luck. Accounts of these early explorations make for exciting reading (e.g., Schomburgk 1841; Quelch 1921). Not surprisingly, the first tepuis to be explored were located close to major rivers, and mostly appeared on some general maps. Specimens were collected in the surrounding lowlands and on the slopes of a few tepuis, but access to summits often was limited or impossible. Conditions on tepuis whose summits were reachable were harsh, and relatively little time was available for collecting. Even so, scientific discoveries were frequent and important enough to convince a few scientists and explorers that the tepuis deserved a lot more attention.

An intensive period of exploration of the tepuis, driven primarily by a few prominent scientists/explorers (e.g., George Tate, William H. Phelps Sr., William H. Phelps Jr., Julian Steyermark, Bassett Maguire, John Wurdack) associated with certain museums and botanical gardens, began around 1930. In addition to basic exploration and description of the geography and geology of this area, the goal of these individuals and their institutions was to amass collections of specific biotic groups adequate to serve as a baseline for future studies on the ecology and evolution of the flora and fauna of the tepuis. Most of these expeditions were major undertakings and sometimes involved weeks to months in the field. Although birds and plants were the target organisms for much of the early work, an occasional herpetological specimen found its way back to a museum. The resulting collections and publications set the stage for the next phase of scientific exploration, which began in the late 1960s. The goals of earlier investigators (i.e., to understand the biota of the region and elucidate the factors that played prominent roles in its evolution) continue to drive much of the science in the region.

Exploration since the early 1970s has focused on tepuis whose summits had

never been explored or were poorly known. Fieldwork often involves multiple visits to specific tepuis, usually with helicopter support. In contrast to most previous work, these expeditions frequently involve botanists and zoologists, often with a major contingent of Venezuelan scientists. Recent expeditions have been sponsored by scientific societies, government agencies, private foundations, and other entities. Helicopters have enabled scientists to access formerly unexplored areas and have facilitated visits to multiple sites on each tepui, leading to broader coverage than was previously possible. Also, the significant decrease in travel time and improved logistical support meant that more sites could be visited and more time spent searching for organisms in field situations. Even though helicopters require considerable logistical support and fuel, are sometimes plagued by mechanical problems, and are especially susceptible to changes in local weather conditions, helicopter access allows scientists to commence fieldwork almost immediately upon arriving at a site. As a result, the numbers of scientific visits made and samples collected on tepuis in the past 20 years far exceed those made in all the previous explorations combined, and the number of tepuis visited has increased dramatically. This increased activity is clearly reflected in the dramatic rise in the species accumulation curve for amphibians and reptiles from Pantepui (fig. 18.6). Even so, most tepuis have been sampled relatively few times, and several are completely unknown herpetologically (appendix 18.1).

We review the exploration of Roraima in more detail not only because of its long history but also because its patterns of investigation reflect those characteristic of most of the highlands of Pantepui. In writing about explorations of interior British Guiana, Sir Walter Raleigh (1848) referred to a mountain of Christall (Crystal) with a large waterfall plummeting from its summit. He indicated that he had seen this from a great distance and described the noise from the falls. We suspect that Raleigh may have been reporting what someone told him rather than describing what he actually saw. Warren (1973) suggested that if true, Raleigh's account almost certainly represented the first sighting of Roraima by someone other than an Amerindian.

The first known description of the environs of Roraima was by the German geographer Robert H. Schomburgk, who explored the interior of Guayana for the British Crown. He reached the southern flank of Roraima in November 1838 and for the next 25 days explored the surrounding region. On his approach from the south, Schomburgk reported visiting a small hillock (about 35 miles south of Roraima), which his guides called the Crystal Mountain. Here, a layer of short and greatly weathered crystals, an intrusive characteristic of Roraima Sandstone, covered the surface. According to the local Arecunas, some Portuguese had previously carried away crystals that were clear as water and four to five inches long. Those sorts of exposed strata, several of which occur on the summit, account for Roraima being known as the Crystal Mountain. In

1842 Robert Schomburgk and his brother Richard returned to Roraima and made extensive plant collections in the region. The results of that work were published in *Reisen in Britisch-Guiana* (Schomburgk 1847–48) and included some of the first descriptions of plants and animals from that part of the world. The only reptile from the region specifically mentioned by Schomburgk (1841) was a rattlesnake (*Crotalus durissus*) that bit one of his men. Vivid accounts by other explorers and sporadic descriptions of new taxa based on samples supplied by purveyors of natural history specimens sparked the curiosity of key individuals in the scientific community, especially in British Guiana. Over the next 40 years, a number of explorers and collectors tried to get to Roraima with the goal of reaching the top. Many of them approached Roraima from the north and east and concentrated their efforts along the eastern and southern slopes of the mountain. Nearly all pronounced the summit inaccessible (Warren 1973), and a few even suggested that a balloon might provide the only access to the top (Whitley 1884). Almost all of those explorers and scientists mentioned that a lack of provisions cut short the time available to explore Roraima's vertical faces, and some indicated that dense forests along the north side made that approach especially challenging. Most of them also commented that poor weather and dense cloud cover often made visual inspections difficult. In September 1883, Henry Whitley, who had spent considerable time over the past three years collecting birds in the environs of Roraima, spied a spot on the southwest side where the vertical cliff seemed to have broken away and possibly offered a route to the top. He learned from some of the locals who had accompanied Schomburgk some years earlier that Schomburgk also had seen the route but had not explored it, thinking the precipice halfway up would be insuperable. The ledge depicted in Whitley's (1884) drawing (fig. 18A.1) ascends to the left at a moderate slope across part of the southwest face of Roraima's cliffs; it also seems to have been depicted on the face of the mountain shown to the right in Schomburgk's (1841, 207) drawing (fig. 18A.1). Whitley's assistants spent nearly six days cutting a trail through dense undergrowth and around large boulders to the base of the southwest cliff face near where he thought passage might begin. Unfortunately, dense mist and a misjudgment relative to the point of access prevented further exploration.

Word about a possible route to the summit apparently spread quickly through British Guiana and, after Whitley's account of his explorations were published in the *Proceedings of the Royal Geographical Society* in August 1884, through London as well. The year after Whitley's explorations, a German orchid collector named Seidel, who was on his second trip to Roraima, met Everard Im Thurn, curator at the Georgetown Museum, and Harry I. Perkins, assistant Crown surveyor, on the southwest side of Mount Roraima. Both groups had departed from the mouth of the Mazaruni River on 17 October; Seidel followed the northern route, while Im Thurn and Perkins headed south on the

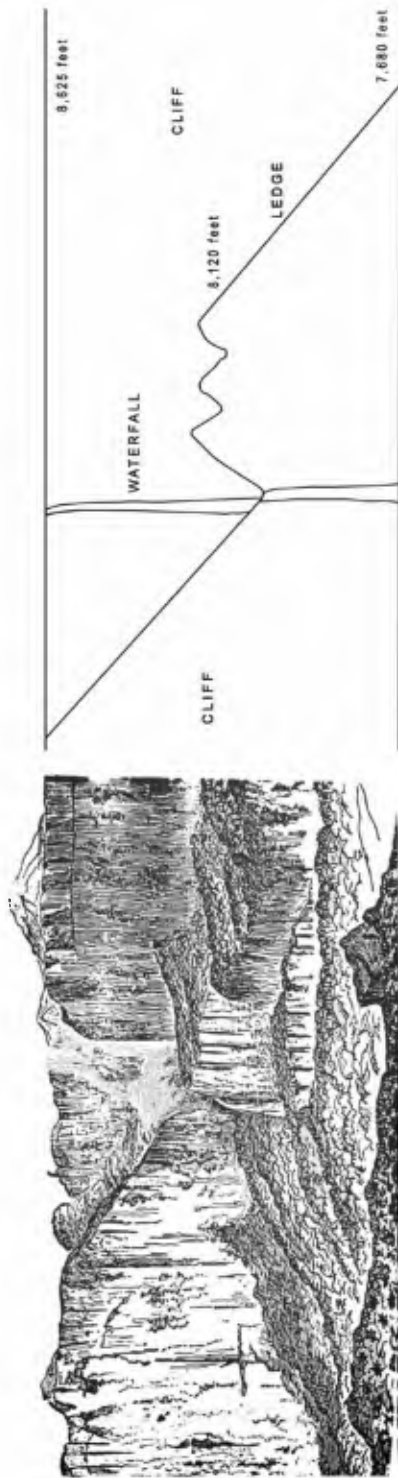


Figure 18A.1 (Top) Reproduction of Whitley's (1884) drawing that Im Thurn subsequently used to reach the top. (Lower left) Sketch (from Warren 1973) of the route along the ledge to the summit; this image is similar to a photograph by McConnell (1916). (Lower right) Line drawing (adapted from Clementi 1920) depicting the path to the top.

Essequibo River (fig. 18A.2). The primary goal of the Im Thurn and Perkins Expedition, which had been supported in part by the Royal Geographical Society, was to reach Roraima's summit. Im Thurn and Perkins traveled up the Essequibo and Potaro rivers to Chinebowie (= Chenapou) and then overland through forest and savanna, crossing the Ireng, Cotinga, and Arapu rivers to Roraima. They arrived at the small village of Teruta, 3–4 miles south of the Roraima and Kukenán massifs on 4 December, one day after Seidel. On 7 December, they moved closer to Roraima and built a hut near Seidel's. For the next week they collected plants and explored the region. On 14 December, with extensive cutting of new trail, they intercepted Whitley's trail near the base of the cliff and had a good view of the ledge (fig. 18A.1). After cutting additional trail to the ledge and waiting a few days for the weather to clear, they attempted on the bright morning of 18 December 1884 to reach the top (Perkins 1885; Im Thurn 1885). The trail passes over three rounded spurs and then descends to a point where the waterfall from above contacts the ledge. The first part of their ascent (about two-thirds of the distance) was slippery because of the recent rains and reportedly especially treacherous in many areas because the cut and previously trodden plants were slippery. In many places they described climbing on all fours over masses of vegetation dense enough to bear their weight and over and under high-piled rocks and tree stumps covered with moss and filmy ferns. After walking about 150 yards beneath the waterfall, whose flow was relatively light on that particular morning, they made their way up a relatively steep (about 30°) rocky slope to the ledge and then through dense vegetation to the final rise, which was easier than the previous parts, and gradually merged onto the relatively barren summit.

The following excerpt from Im Thurn's account of 18 December (1885, 517) more than adequately captures the excitement and emotion of the moment:

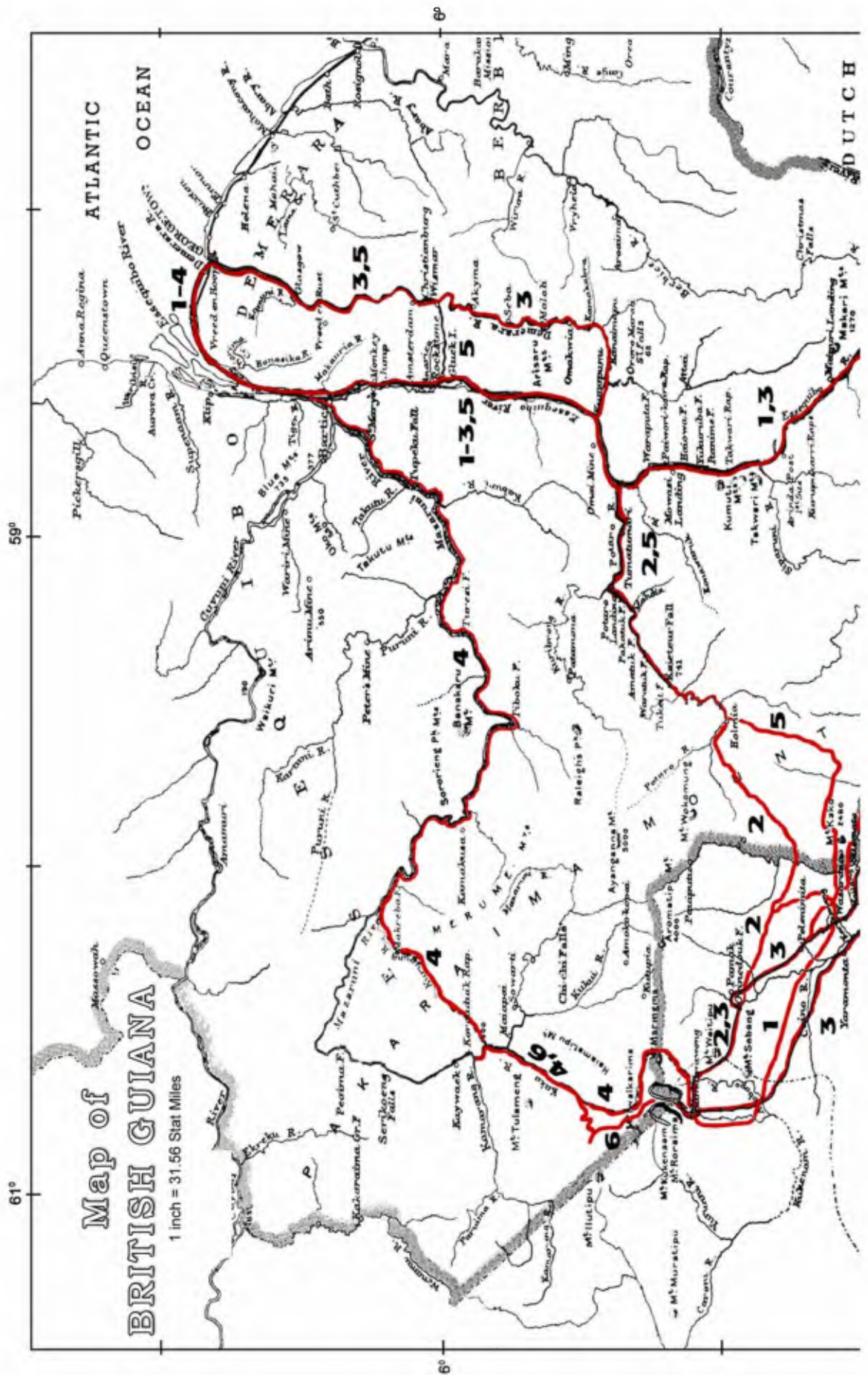
Up this part of the slope we made our way with comparative ease till we reached a point where one step would bring our eyes on a level with the top—and we should see what never had been seen since the world began; should see that of which, if it cannot be said all the world has wondered, at least many people have long and earnestly wondered; should see that of which all the few, white men or red, whose eyes have ever rested on the mountain had declared would never be seen while the world lasts—should learn what is on top of Roraima.

Then the step was taken—and we saw surely as strange a sight, regarded simply as a product of nature, as may be seen in this world; nay, it would probably not be rash to assert that very few sights even as strange can be seen. The first impression was one of inability mentally to grasp such surroundings; the next that one was entering on some strange country of nightmares for which an appropriate and wildly fantastic landscape had been formed, some dreadful and stormy day, when, in their mid ca-

reer, the broken and chaotic clouds had been stiffened in a single instant into stone. For all around were rocks and pinnacles of rocks of seemingly impossible fantastic forms, standing in apparently impossible fantastic ways—nay, placed one on or next to the other in positions seeming to defy every law of gravity—rocks in groups, rocks standing singly, rocks in terraces, rocks as columns, rocks as walls and rocks as pyramids, rocks ridiculous at every point with countless apparent caricatures of the faces and forms of men and animals, apparent caricatures of umbrellas, tortoises, churches, cannons, and of innumerable other incongruous and unexpected objects. And between the rocks were level spaces, never of great extent, of pure yellow sand, with streamlets and little waterfalls and pools and shallow lakelets of pure water; and in some places there were little marshes filled with low scanty and bristling vegetation. And here and there, alike on level space and jutting from some crevice in the rock, were small shrubs, in form like miniature trees, but all apparently of one species. Not a tree was there; no animal life was visible, or it seemed, so intensely quiet and undisturbed did the place look, ever had been there. Look where one would, on every side it was the same; and climb what high rock one liked, in every direction as far as the eye could see was the same wildly extraordinary scenery.

Other than describing small fleeting masses of clouds, Im Thurn made no mention of the weather on the summit, but Perkins (1885, 532) noted that shortly after arriving on top, the mist closed in and prevented them from exploring much of the summit. They returned to the hut that afternoon, where they remained preparing specimens and collecting on the slopes. On 24 December they returned to Teruta, where they spent Christmas day, departing for home on the following day. They arrived at the junction of the Mazaruni and Essequibo rivers on 28 January. Mr. Seidel left Roraima on 28 December and, following the northern route, arrived at the same river junction two days later than Im Thurn and Perkins.

The accounts of this and other explorations in the Roraima region that appeared in the publications of the Royal Geographic Society and elsewhere served to feed the imagination of many Londoners. The following editorial appeared in *The Spectator* in April 1877 and perhaps reflects some of the attitudes at the time: “Will no one explore Roraima and bring back the tidings which it has been waiting these thousands of years to give us? One of the great marvels of the mysteries of the Earth lies on the outskirts of one of our colonies—British Guiana—and we leave the mystery unsolved, the marvel uncared for.” As Warren (1973) pointed out, many people at the time were attracted by the idea that some place on earth might still harbor remnants of prehistoric life. This notion caught on when someone suggested that Roraima had been cut off from the rest of the world for millions of years and that life on its





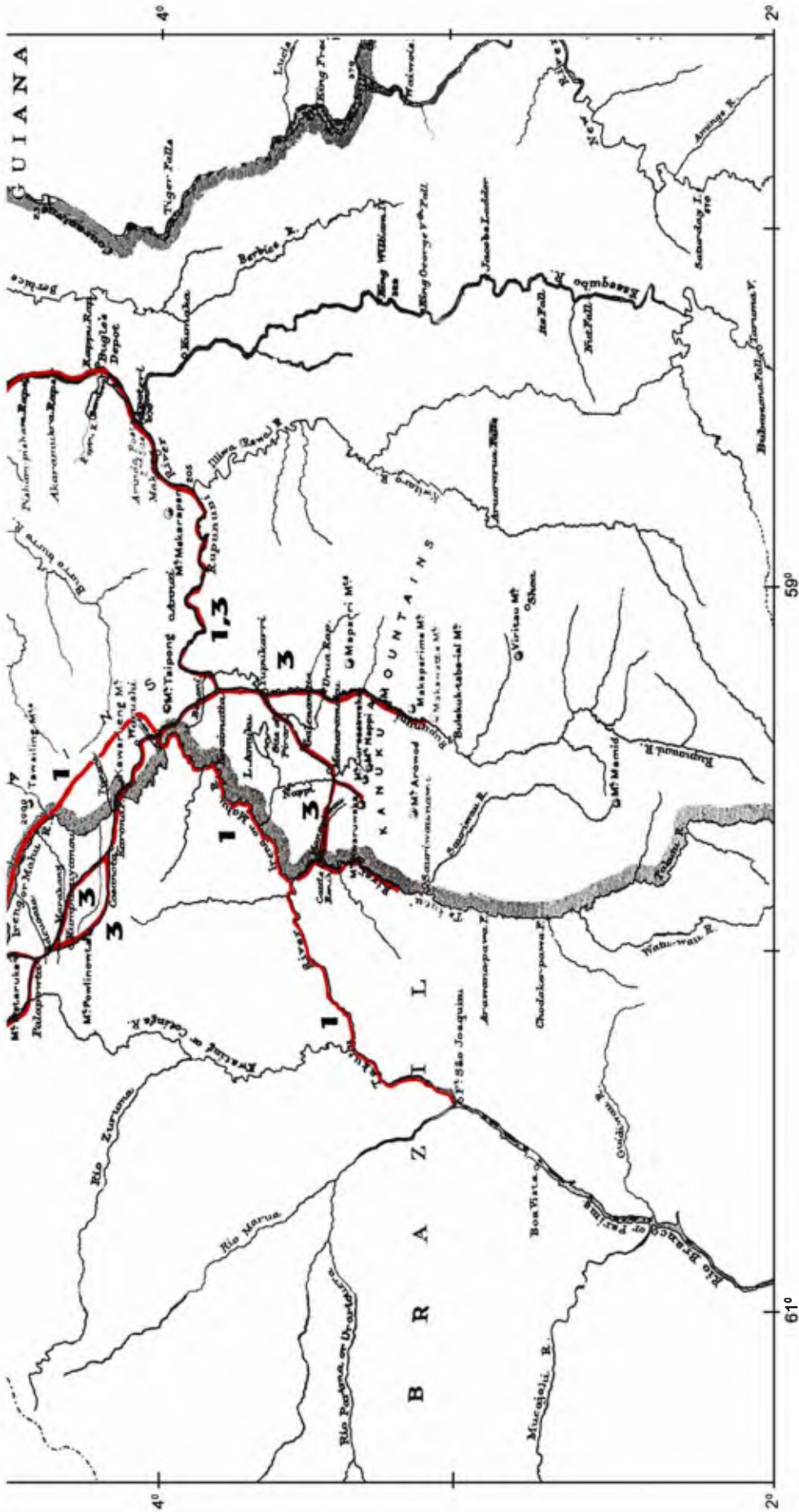


Figure 18A.2 Map of British Guiana modified from that in Chubb's two-volume work *The Birds of British Guiana*, which included McConnell's (1916) and Quelch's (1921) accounts of their expeditions. The primary routes used by explorers in their approaches to Roraima are indicated by number, as follows: 1, Schomburgk (1838); 2, Im Thurn and Perkins (1884); 3, McConnell and Quelch (1894); 4, McConnell and Quelch (1898); 5, Clementi party (1916); and 6, Warren group (1971). The latter has become known as the Waruma route.

summit might be suspended in evolutionary time. Sir Joseph Hooker's comment in 1884 (Warren 1973) that a detailed examination of the top would provide some interesting results and probably would show a flora that was similar to that which had existed in the old times, only raised expectations in some people's minds; perhaps dinosaurs and pterodactyls lived on Roraima's summit! Some say that publications and public presentations at Royal Geographical Society meetings around this time provided ample material for Arthur Conan Doyle to write *The Lost World* (Doyle 1912).

Publications resulting from ornithological and botanical collections from the area served as an incentive to others to get to Roraima and collect their favorite group. This scientific inquisitiveness, coupled with a desire to learn more about the native populations in the area, or to establish a political and economic presence in a region where country boundaries were not well established, resulted in a considerable increase of exploration of the region. From a herpetological perspective, the most important expeditions were those led by John J. Quelch, a curator of zoology at the Georgetown Museum, and Frederick V. McConnell, a collector of birds in British Guiana. The itineraries of their two expeditions were published in the preface of volume 1 (McConnell 1916) and the introduction of volume 2 (Quelch 1921) of Chubb's *The Birds of British Guiana*. The first expedition was sponsored by the Royal Agricultural Society of British Guiana and led by Quelch; it departed Georgetown on 7 July 1894. The group followed the southern route to Roraima (fig. 18A.2), traveling south up the Essequibo and Rupununi rivers, and after a few side trips reached Kwaimatta on 6 September. That village of about 200 inhabitants was located at the eastern edge of extensive savannas and served as the base of operations for the next six weeks. On 16 October they started north on foot into Brazil and then Venezuela on trails that generally tracked the courses of the Ireng, Cotinga, and Arabato rivers. On 3 November they reached Kamaiwawong, a little village at the end of the valley between Roraima and Kukuenaam. After two days of exploration and clearing trails through the dense bush and forest on Roraima's slope, they established a rough camp near the base of the cliff. The next morning they reached the cliff and began moving up the ledge. The descent into the gully with the waterfall was made in a sitting position, and the climb out was oftentimes on all fours. From this point the climb to the summit, though initially steep, was not arduous. Once on top, Quelch and one worker decided to stay the night and maximize the time for collecting. McConnell returned to the camp for blankets, food, and photographic equipment and returned the next day. All three spent the second night on the summit and returned to Kamaiwawong the following day. Shortly thereafter, they returned to Georgetown. Although time on top was short, Quelch and McConnell made some collections, among which were several specimens of a tepui toad that Boulenger (1895a) described as a new genus and species, *Oreophryne quelchii*, later changed to *Oreophrynella quelchii*, for reasons of preoccupation (Boulenger 1895b).

The second expedition to Roraima was led by McConnell and was organized specifically to explore the mountain and spend more time on the summit. For various reasons, McConnell and Quelch decided to follow the northern route going west up the Mazaruni River (fig. 18A.2). They left Bartika at the junction of the Mazaruni and Essequibo rivers on 20 August 1898 and, making reasonable time, reached the headwaters of the Kurubung River in slightly less than three weeks. From this point they began a seven-day trek on bad trail over the Pacaraima Mountains. After descending again to the Mazaruni River, they obtained small woodskins (bark-covered canoes) and continued upstream via the Kako River and then a smaller creek, the Aruparu, for three days to a point where the overland trek began. After several (3–5) days moving east around Marima Mountain and then south and west primarily through forest and small savannas, they approached Roraima's eastern flank between "other smaller Roraimas" (likely Wei-assipu, Appokailang, and Yakontipu) to the north and Mount Weitipu (Uei) to the south. From there they headed southwest toward the village of Kamaiwawong at the base of Roraima, which they reached early in October, 40 days after their departure.

Preparations for the summit ascent began immediately. Old trails were overgrown and had to be cleared. Some new trails were cut, and a temporary camp was established at the cliff base. On the fourth day they reached the top. The plan was for Quelch to spend as much time as possible collecting and exploring on Roraima, while McConnell would take a series of photographs on the summit and then concentrate his efforts on the forested slopes and savannas below, making the best collection possible, chiefly of birds. On this trip they brought a small tent and were able to establish a camp near their previous camp. Over the next two days McConnell took photographs of the terrain and vegetation (fig. 18A.3) and collected several specimens of the only bird seen on the summit (subsequently named *Zonotrichia macconnelli*), after which he went down off the mountain. Quelch on the other hand spent the next nine days on top, completely caught up in making collections and exploring the mountain. When discovery of new materials slowed, Quelch decided to join McConnell below and work the sunny slopes of Kukuenaam, the agricultural clearings, and possibly the unexplored gorge between the two mountains. Unfortunately, the cold, wet climate on top had taken its toll. Quelch was suffering from stiffness in the back and joints and had a hard time descending the steep slippery trails. On top of this, he had to cover the final two miles back to the village in a cold, drenching rain. He spent the next week nearly helpless in his hammock and a second week regaining strength for the return trip. Finally, at the end of October they departed Roraima, retracing their steps to Bartika.

Among the herpetological material collected by Quelch on Roraima's top were additional specimens of *Oreophrynella quelchii* and a single lizard later described as *Prionodactylus* (= *Riolama*) *leucostictus*. McConnell and others collected herpetological material from the base of Roraima at approximately

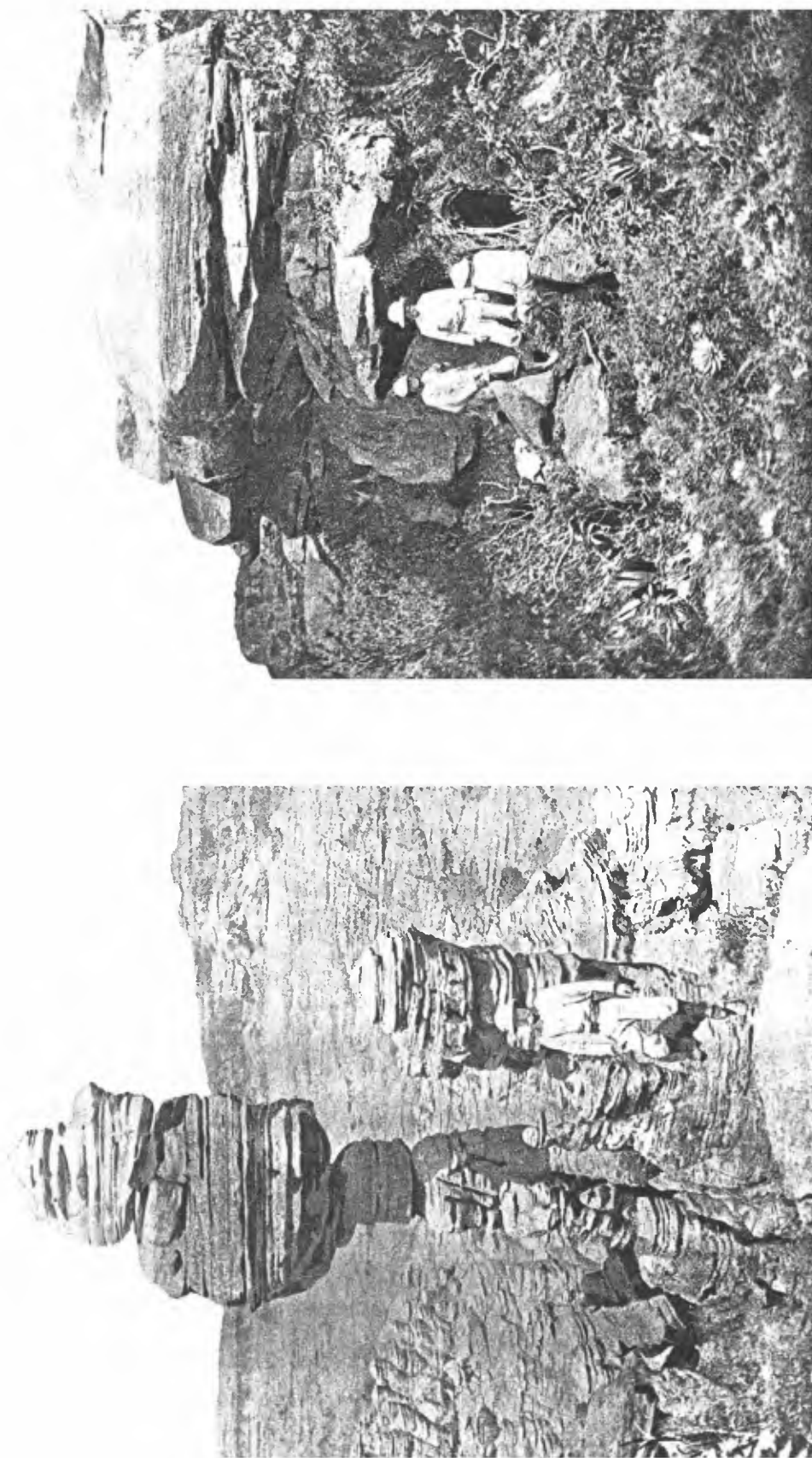
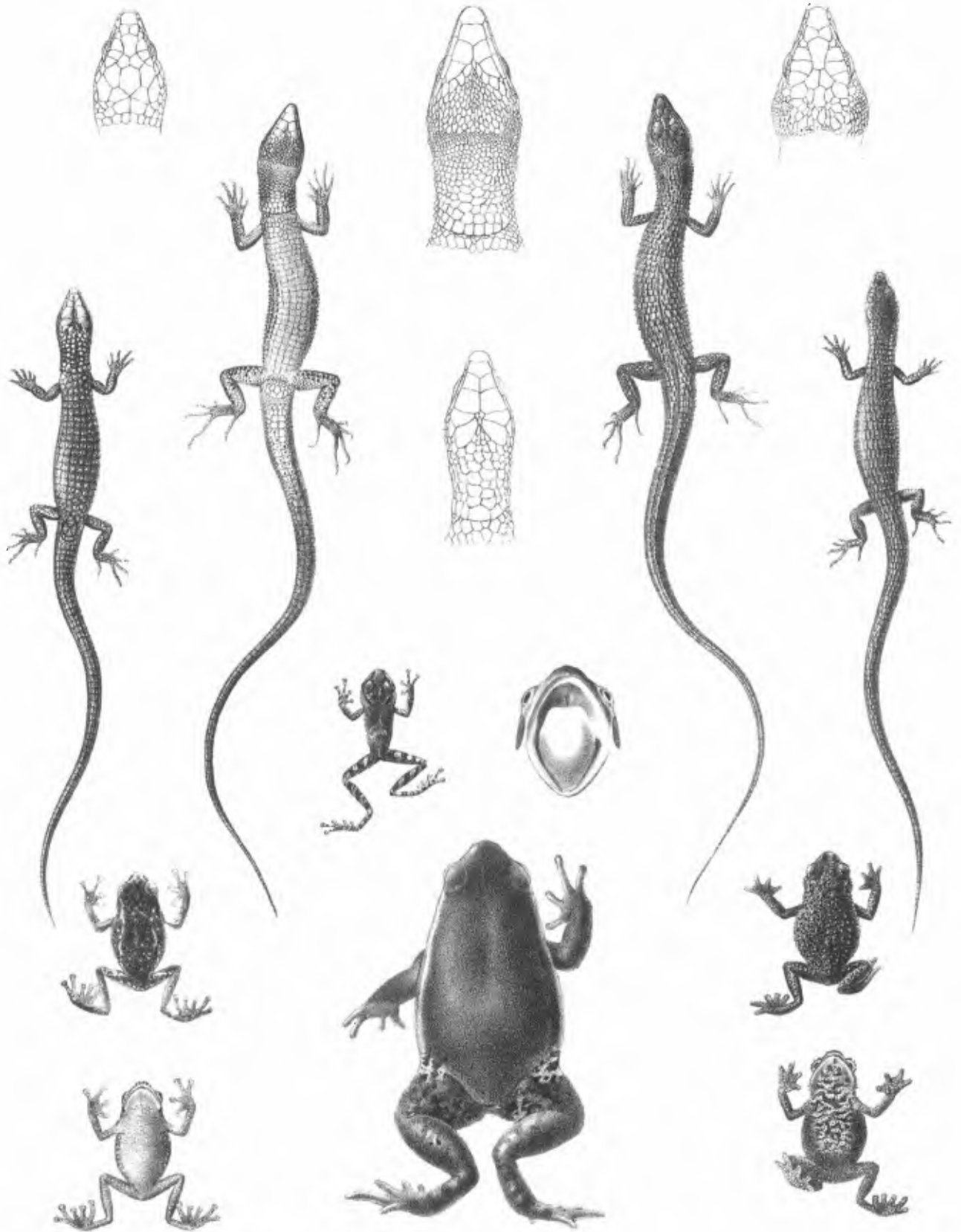


Figure 18A.3 Two photographs taken by McConnell (1916) on the summit of Roraima in 1898. McConnell near sculptured rocks (*left*) and with Quelch and assistant at their primitive camp (*right*).

3,500 ft. (~1,067 m). Among these were unique specimens of the following taxa: *Neusticurus rudis*, *Oreophrynella macconnelli*, *Hylodes* (= *Eleutherodactylus*) *marmoratus*, and *Otophryne robusta* (Boulenger 1900a, 1900b; see fig. 18A.4). All are recognized species today. Quelch and McConnell were especially successful in adding to the herpetological knowledge of the region. In the 100 years following their expeditions, only one other species of amphibian (*Eleutherodactylus* sp.) has been collected on the summit and two others (*Colostethus praderioi* and *Colostethus roraima*) taken from the southwestern slopes of Roraima (appendix 18.4).

During the next twenty years, several other expeditions reached the summit of Roraima, including three to document national borders (see Warren 1973 and Huber 1995b for brief reviews). Although of minimal herpetological interest, one of the better-documented trips during this time was that undertaken by Cecil Clementi, his wife, and John C. Menzies, a prospector and rancher. Their goal was to reach the interior tablelands of British Guiana and to see the forests and savannas of the interior and perhaps even to make their way to "Mount Roraima, of which the residents in British Guiana hear so much and see so little" (Clementi 1920). The Clementi party traveled by steamer up the Demerara River south from Georgetown, crossed to the Essequibo by railroad, and continued up the Essequibo River by launches to a major cataract on the Potaro River. Here they met Menzies and continued up the Potaro; after several portages they reached Holmia, a place above Kaieteur Falls. From there they walked southwest through the forests, then across the tablelands and savannas of the eastern part of the country through the village of Puwa to the Ireng River, where they turned to the northwest and continued toward Roraima (fig. 18A.2). On the day after their arrival at Kamaiwawong, the same village that Quelch and McConnell had used as their base of operation at Roraima, they climbed to the summit and spent that afternoon, night, and part of the next day on top. On the day after their descent to the village, they departed for the Ireng River, following a slightly different route, and from there retraced their steps along the previously traversed Potaro route. The entire trip from Georgetown to Roraima and back following the Potaro route was accomplished in 46 days, which was quite an undertaking and, as pointed out by Quelch (1921, lxxviii), "to say the least of it, is an exceedingly fine feat for a lady." The account of this exploration was effectively captured by Mrs. Clementi's (1920) book titled *Through British Guiana to the Summit of Roraima*.

The next major exploration of Roraima probably was that accomplished by the Lee Garnett Day Roraima Expedition of the American Museum of Natural History, which was led by the American mammalogist G. H. H. Tate (Tate 1928). Tate and his party reached Roraima on 21 October 1927, traveling by boat up the Río Branco from Brazil. Tate (1930) lamented the common practice of the Arekuna Indians of setting fire to grasslands in their territory; he noted that



1900b) descriptions of specimens collected by Quelch and McConnell on their second Roraima expedition in 1898. *Oreophrynella quelchii* is shown at lower left, and *Riolama leucosticta*, the smaller of the two lizards, is shown on the outside left and right.

during a period of extreme drought some two years before their arrival, a fire started on the savanna had burned onto the slopes of the mountain, destroying the greater part of the forests therein (Means 1995 discussed the role of fire in the region). Tate's party was able to establish three camps in the upper savannas and in patches of forest on the slopes and one on top of Roraima. In total, they spent about 80 days in the region, 13 of which were on the summit. In the history of herpetology at the American Museum of Natural History, Myers (2000) included three previously unpublished pictures from the Tate Expedition, two of which were taken on top. The Tate party returned through British Guiana by following a trail that started on the southeastern side of Roraima near the village of Arabopo, headed south around the western side of Weitipu (Uei), and from there continued east through open savannas and across the upper reaches of the Cotinga and Ireng rivers. Soon they crossed the high sandstone divide (southern part of the Pacaraima Mountains) that separates the upper drainages of the Ireng and Potaro rivers north of Mount Kowatipu and descended to the Chenapowu (= Chenapou) River, from whence they traveled by canoe down to the Potaro River and the Kaieteur Falls area.

In the 1970s, several groups explored Roraima and its surroundings and made important collections of amphibian and reptiles. The British Roraima Expedition, led by Adrian Warren (1973), explored the northern slopes of Roraima, following what has come to be known as the Waruma route (fig. 18A.2). They reached Kamarang, where the Kako and Kamarang rivers join the Mazaruni, by plane and established their main camp. From there they moved up the Kako by longboat to a previously established base camp on a savanna at Makuripai. From that camp they moved farther up the Kako to the Waruma River and then headed due south toward Roraima, establishing a series of camps along the Waruma River and onto the northern slopes. They reportedly reached a high point of 7,700 ft. (2,346 m) on the north slope before being forced to turn back. They collected more than 2,500 scientific specimens of plants and animals, including more than 130 amphibians and 28 reptiles. At camps above 3,000 ft. (914 m), they collected specimens of most of the taxa first collected by McConnell and Quelch some 75 years earlier from the southwestern side of Roraima, including the frogs *Oreophrynella macconnelli*, *Otophryne robusta*, *Eleutherodactylus marmoratus*, and the lizard *Neusticurus rudis*, all described as new by Boulenger (1900a, 1900b). At localities later reported as lying between 1,430 and 1,480 m, Warren and his group collected two specimens each of hylid frogs that were described as *Hyla roraima* and *Hyla warreni* by Duellman and Hoogmoed (1992).

In the three decades since the Warren Expedition, other groups have explored the slopes of Roraima from the north; some of those expeditions were reviewed briefly by Gradstein (1985). Two expeditions are important from a herpetological perspective. Two years after the Warren explorations, a British

climbing group following the Waruma route successfully reached the north side of Roraima and climbed to the summit (MacInnes 1976). Michael Tamesar collected anurans on that trip, including specimens of what were subsequently described as *Stefania roraimae* (Duellman and Hoogmoed 1984) and *Hyla roraima* (Duellman and Hoogmoed 1992). Early in 2001, scientists from the Smithsonian Institution and the University of Kansas conducted an ornithological survey of the north slope of Roraima, with funding from the National Geographic Society (Smithsonian Guyana Expedition, 2001). That group followed the same path and used some of the same camps established by Warren's party. In addition to birds, they collected several interesting specimens of amphibians and reptiles that remain to be studied. Thus, our knowledge of the slope fauna is gradually improving, but much work remains.

As was the case with other tepuis, the summit of Roraima received additional attention with the increase in the availability of helicopters for scientific exploration. In 1977 (January) and 1978 (February) Charles Brewer-Carías (1978a) led expeditions sponsored by the Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR) that visited Roraima. McDiarmid was the herpetologist on those expeditions and collected specimens of *Oreophrynella quelchii* and *Riolama leucosticta* on the summit. Field observations of the former species were reported by McDiarmid and Gorzula (1989). On a subsequent trip to Roraima, Brewer-Carías was stranded on the mountain for a day and night; during that episode he collected an undescribed species of *Eleutherodactylus* (table 18A.1).

In the last 20 years, several individuals and groups have visited Roraima, either by helicopter or on foot. Carlos Galán, a biologist with the Electrificación del Caroní project of the Corporación Venezolana de Guayana, reportedly has visited Roraima several times (Galán 2000); in April 1985 he collected a series of 33 *Oreophrynella quelchii* from the summit (Gorzula and Señaris 1998). The report of *Tepuihyla edelcae* from Roraima from the Galán collection (Galán 2000; Gorzula and Señaris 1998, 255) is probably an error; no other records of this species from Roraima are known, and Gorzula and Señaris (1998, 49) made no further mention of a Roraima specimen in their account of the species. Scientists working with the Fundación Terramar visited the summits of Roraima, Kukenán, and Ilú-tepui in 1989 (Huber 1995b), and it seems likely that herpetological specimens, if encountered, would have been collected. In August 1996, two species of dendrobatid frogs were collected along the southwestern cliff face on the trail to the summit. La Marca (1996) described two specimens, one from a quebrada at 1,950 m and another from 1,800 m, as *Colostethus praderioi*, and a single specimen taken in the trail at about 2,700 m (60–70 m before the summit) as *Colostethus roraima*. We suspect that other specimens from the slopes and summit of Roraima may reside in collections in Venezuela and elsewhere.

The expeditions and collectors who have contributed to our understanding



of the herpetofauna of Roraima are summarized in the following chronological list of principal explorers and expeditions to Mount Roraima and vicinity, the year the expedition took place, and the nature of the exploration. Similar chronologies and patterns of investigation could be compiled for certain of the other, better-known tepuis (e.g., Auyán, Duida), and details can be garnered from references presented for specific sites in appendix 18.4. Data are derived from Huber (1995a), Perkins (1885), Warren (1973), and other sources.

- Robert H. Schomburgk; 1838; discovery and exploration, some plant collecting on southern flank; 25 days in November.
- Robert H. Schomburgk and M. Richard Schomburgk; 1842; extensive collections of plants and of some animals from the region.
- Karl Ferdinand Appun; 1864; German botanist worked the eastern and southern flanks for a month; declared summit inaccessible.
- Charles Barrington Brown; 1869 and 1872; geological survey of the area along the southern route; lack of food forced the expedition's return; viewed Mount Roraima on his second trip, this one from the northeast; concluded that a balloon was needed to reach the summit.
- Messrs. Flint and Edgington; 1877; 18 days on foot from the Rupununi Savanna; lack of provisions hampered exploration.
- Messrs. Boddam-Wetham and McTurk; 1878; approached from Mazaruni and explored the north, west, and south sides; ascent was impractical.
- Henry Whitley; 1881–83; several trips collecting birds near Roraima; cut a path to the cliff base and observed a ledge in September 1883; published description and sketches in 1884.
- Mr. Siedel; 1884; orchid collector; two trips to same area as Whitley; joined by Im Thurn's party in early December.
- Everard F. Im Thurn and Harry I. Perkins; Royal Geographical Society; 1884; traveled overland from Kaieteur Falls; first summit ascent; 1 day on top; plant collections; published descriptions and maps.
- John J. Quelch and Frederick V. McConnell; first Roraima expedition; 1894; southern route to the southwestern slopes; 2 nights and 3 days on summit (November); first collection of *Oreophrynella*; detailed account of approach.
- Frederick V. McConnell and John J. Quelch; second Roraima expedition; 1898; northern route via Mazaruni, along the eastern side to southwest ledge; 9 days on summit (October); major collections from summit and slopes, with several new amphibians and reptiles.
- Mr. and Mrs. Cecil Clementi; 1913; no collections; first woman on summit; wrote a book about her experiences.
- G. H. H. Tate and others; American Museum of Natural History Lee Garnett Day Cerro Roraima Expedition; 1927–28; well-documented expedition of

80 days in the region and 13 on the summit; made extensive collections of birds and mammals.

Julian A. Steyermark; Field Museum of Natural History Roraima Expedition; 1944; climbed and collected botanical material from the summit in September; often collected amphibians and reptiles from tepui summits (e.g., Chimantá).

Adrian Warren; British expedition to Mount Roraima; 1971; approached north side along the Waruma route; extensive herpetological collections.

Michael Tamessar; British Climbing Group; 1973; used Waruma route; several new frog species; first successful ascent of Roraima from the north.

Charles Brewer-Carías and Roy McDiarmid; Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas Expedition I; 1977; general collections, including herpetological material for 3 days in January; three other tepuis visited on this expedition.

Charles Brewer-Carías and Roy McDiarmid; Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas Expedition II; 1978; herpetological specimens collected over 5 days in February; general collections by several scientists on Roraima and four other tepuis.

Carlos Galán; 1985; 33 *Oreophrynella quelchii* collected in April.

Fundación Terramar Eastern Tepui Expedition; 1989; some herpetological materials collected here and on other eastern tepuis.

Smithsonian Guyana Expedition; 2001; Waruma route; ornithologists from Smithsonian and University of Kansas also collected amphibians and reptiles.

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