13 ISLANDS IN THE SKY

SNAKES ON SOUTH AMERICAN TEPUIS

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Introduction

Consider volcanoes building up from great depth over a hot spot under an oceanic crust. Eventually rising above sea level, each island grows in elevation and areal extent, and then a younger island forms as the crust continues to move over the hotspot. This process goes on until an archipelago is formed, with the older islands now volcanically inactive and the youngest island still developing. Lying astride the Equator, one such archipelago exists—the Galapagos Islands. The oldest island formed approximately 5 million years ago, and the newest one has been above the sea for less than 1 million years (Cox 1983; Grehan 2001). These islands support a snake fauna currently consisting of six species in the genus *Pseudoalsophis* whose ancestor probably arrived as waif disperser on floating vegetation from the closest continental land mass of South America (Thomas 1997).

Now consider another archipelago of tropical islands separated from each other not by water but by elevation. They formed as a sandstone landscape that was uplifted tectonically. Slowly over eons, rivers cut into the rising landscape and carried away much of the original sandstone sediments, isolating flat-topped mesas of varying elevations up to the present highest of 3,014 m. The summits of almost all the mesas are protected by 300+ m high vertical cliffs. Between 2,500 and 3,500 mm of annual rainfall (Huber 1995a; McDiarmid and Donnelly 2005) plunges off the cliffs in spectacular waterfalls, including Angel Falls, the world's tallest (979 m). Approximately 100 such mesas rise from the Guiana Shield (Figure

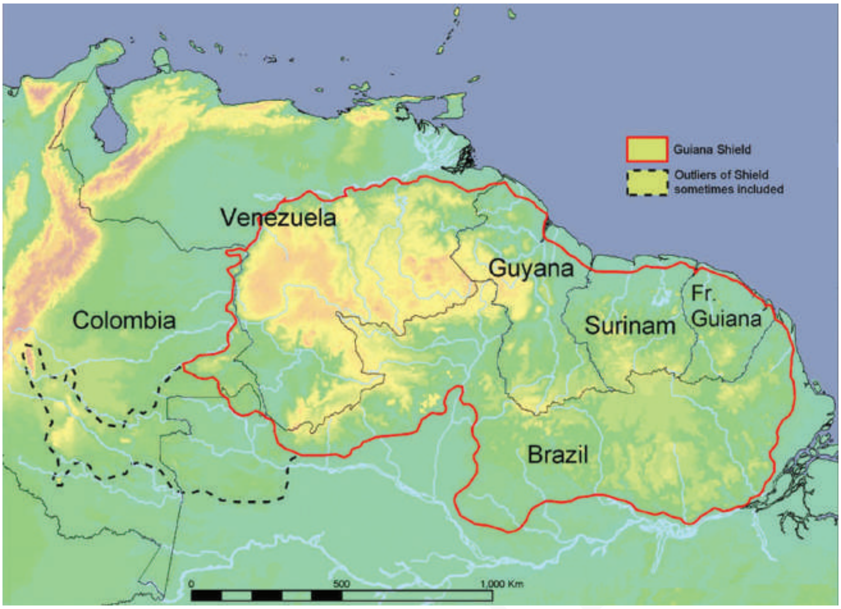

FIGURE 13.1 Map of the Guiana Shield of northern South America. Highlands along the left side are the northern Andes.

13.1), an ancient Gondwanan component of the South American continent in southeastern Venezuela and running along its border with Brazil and Guyana (George 1991; McPherson 2008; Aubrecht *et al*. 2012).

These tropical mesas in the Pemon Amerindian language are called *tepuis* (meaning mountain). The most famous, Mt. Roraima, straddles the triple drainage divide where rainfall flows off the tepui into three of the world's largest rivers. Northward, water cascades off Roraima's cliffs and flows into Guyana's Essequibo River. Southward, Roraima's waters flow into Venezuela's Orinoco River, the world's third largest by volume. And waters flowing eastward off of Mt. Roraima eventually make their way through Brazil and into the mighty Amazon River. For these reasons, Mt. Roraima is called the "Mother of Waters."

Exploration and Discovery

Tepuis have had a long and romantic history of exploration and discovery. Sir Walter Raleigh remarked about a "Mountain of Christall" that he claimed to have seen "farre off" during his two ill-fated attempts to locate the fabled city of Manoa, home of the king that "the Spaniards call El Dorado" (Raleigh 1596).

He never got close to Roraima. Later expeditions were based out of British Guiana (now Guyana), and in November 1838, Robert Schomburgk (1840) became the first recorded white man to see the Mother of Waters. Without climbing the tepui, as the government-appointed Boundary Commissioner in 1841, Schomburgk established the so-called "Schomburgk Line" that ran northwest from the center of Mt. Roraima. By 1874, a dozen explorers who had made the long journey to Mt. Roraima still had not been able to reach the forbidding summit. The British sensationalist newspapers of the day whipped up public excitement that prehistoric creatures, "maybe dinosaurs," might still be found on the cliff-protected tepui summits. Finally, in December 1884, a local British Guiana magistrate named Everard im Thurn succeeded.

Back in England listening avidly to Everard im Thurn's lectures was a writer, none other than Arthur Conan Doyle, conjuring up the basis for an exciting novel—a change of pace from his normal detective stories. Im Thurn's account of the cliff-protected summit of Roraima—an ancient land locked away from the rest of the world, with holdover monsters from the distant past—supplied Doyle with ample fodder for his 1912 book, *The Lost World: Being an Account of the Recent Amazing Adventures of Professor E. Challenger, Lord John Broxton, Professor Summerlee, and Mr. Ed Malone of the Daily Gazette*. The novel was an immediate and perennial success, considered by many as Conan Doyle's finest piece of fiction. The *Lost World* novel was not based exclusively on Mt. Roraima, but the idea stuck, and from that time on, the public has associated the mountain with Doyle's *Lost World*.

The Guiana Shield forms the northern one-half of the ancient heartland of the South American continent. All continents have shield areas that are generally centrally located and represent the oldest exposed rocks of continental plates. Over eons, continental plates drift about and collide with other continental and oceanic plates. At their edges where these plates come together, mountains are formed by uplift as heavier oceanic plates subduct under the lighter continental plates where volcanoes add lava and ash to the surface of the continental plate. The shield areas of continental plates may rise and fall in elevation as sediments eroding from mountainous areas are deposited on top of them or eroded off of them. Such movements are called tectonic activity.

In the case of the Guiana Shield, sands from ancient eroding mountains were piled up on old bedrock beneath a shallow sea. As the weight of the deepening sands depressed the shield area, more sand was allowed to accrete. For a 200-million-year period (from 1.8 to 1.6 billion years ago), thousands of feet of sand was laid down on the Guiana Shield and became hard-packed sandstone now called the Roraima Supergroup (Priem *et al*. 1973; Gibbs

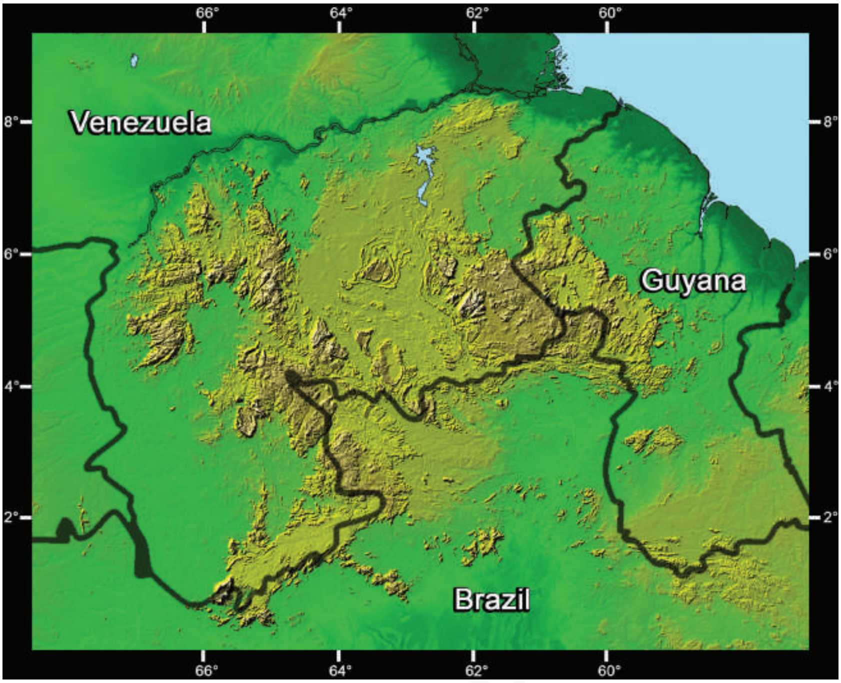

FIGURE 13.2 Map showing the Guayana Highlands (Pantepui), mostly in southern Venezuela and western Guyana, with its southern fringes in Roraima State of Brazil. Pantepui supports the highest elevations on the South American continent east of the Andes.

Source: Map courtesy of Charles Brewer-Carías.

and Barron 1993; Santos *et al*. 2003). Geologists do not know how long the Roraima Supergroup lay relatively low in elevation, but eventually the Guiana Shield began to rise. As it did, creeks and rivers began cutting down into the rising landscape and carrying away the ancient sediments. The once contiguous landscape became a series of disconnected mesas separated by deep and sometimes wide valleys (Figure 13.2).

Herpetology of Tepuis

The first amphibians and reptiles of tepuis were collected by F. V. MacConnell and J. J. Quelch on their 1894 expedition to Mt. Roraima. Boulenger (1900) named two pebble toads after them, *Oreophrynella quelchii* from the summit and *Oreophrynella macconnellii* from the fringing cloud forest below the base of Roraima's ultimate cliffs. Exploration of tepui summits did not really get underway until the middle of the 20th century (Huber and Wurdack

1984; Huber 1995b; Myers and Donnelly 1996, 2001, 2008; Barrio-Amorós and Brewer-Carías 2008). Botanists and ornithologists led the way, at first in expensive and time-consuming ground expeditions, but then helicopters entered the scene and have facilitated most of the summit explorations to the present day. Herpetological sampling was basically limited to an occasional frog or snake inadvertently collected by other specialists; eventually, however, a few herpetologists made quick forays to some tepuis by helicopter, often as adjuncts to larger botanical expeditions. The history of herpetology of tepuis with a focus on expeditions to Mt. Roraima through 2005 can be found in McDiarmid and Donnelly (2005), MacCulloch *et al.* (2007), and Barrio-Amorós and Fuentes (2012). Here, we summarize their data and add data of herpetological fieldwork since then.

As ecological islands, tepuis are highly diverse. Their summit elevations range from approximately 800 m (Cerro Supamo) to just over 3,000 m (Cerro de la Neblina). Elevation in the tropics is highly correlated with plant and animal distributions (Humboldt and Bonpland 2009). As elevation rises, oxygen content of the air decreases, ultraviolet intensity increases, temperature drops, and rainfall usually increases. Tepuis are also highly variable in their summit areas, ranging from a few hectares (Autana, El Sol, and La Luna) to approximately 1,000 km^2 (Duida and Auyantepui). The high, rocky summits of the eastern tepuis along the border with Guyana (Roraima, Kukenan, Yuruani, and Ilu-Tramen) are so inhospitable that no snakes have been recorded from them (see Figure 13.2). The summit areas of these tepuis are relatively small (34.4, 20.6, 4.4, and 5.6 km^2, respectively). On the other hand, high tepuis with large summit areas (Chimantá Massif, Duida, and Auyantepui) have great habitat diversity (interior cliffs, rivers, ponds, seepage slopes, forested declivities, and bogs; Figures 13.3–13.5).

The high-elevation summits of the small to medium-sized tepuis do not support high vertebrate species richness because of their small sizes, harsh climates, and lack of nutrients. These tepuis have been relatively well explored because biologists can access them via helicopters. However, most of the biodiversity of tepuis lies on the mid-elevation slopes (~1,200 to ~1,500 m elevation) that are vegetated with montane forests (here called cloud forests) rich in tree species and epiphytes. Such forests and their biotic richness are impossible to reach by helicopter and often inaccessible on foot (Figure 13.6). Because the base-to-peak elevations can rise through more than 2,000 m on some tepuis, transects often pass through several ecological zones. Several decades ago, Janzen (1967) noted that because tropical species are often narrowly adapted to the climatic zones along mountainside transects, the

FIGURE 13.3 Many of the higher tepuis of Estado Bolivar have bare rocky terrains with patches of shallow water following rainfall. During seasonal drought, most lentic habitats dry up. This is the summit of Ilu Tepui in Venezuela.

Source: Photograph by Bruce Means.

FIGURE 13.4 Summit of Cerro Kukenan, showing habitat diversity including open water, marshes, rocky labyrinths, bare rock, and cliff faces.

Source: Photograph by Bruce Means.

FIGURE 13.5 Nearly the entire summit of Cerro Duida in Venezuela's Amazonas State is densely vegetated with shrubs of the family Theaceae. The leaves of tepui shrubs, especially *Bonnetia roraimae*, reflect an olive color. Deep canyons harbor completely different plants and animals and high biodiversity. Duida is the most diverse tepui in herpetofauna.

Source: Photograph by Bruce Means.

FIGURE 13.6 Quaking bog on Weiassipu Tepui in Guyana, dominated by carnivorous plants (red and green upright pitcher plants in foreground, family Sarraceniaceae; red sundews in right middle ground, family Droseraceae; in the background yellow-green tubes of the carnivorous *Brocchinia reducta*, family Bromeliaceae).

Source: Photograph by Bruce Means.

elevational distributions of vertebrates including snakes can be quite narrow (Figure 13.7).

Snakes of the Tepuis

Of a total of 27 snakes listed from tepuis by McDiarmid and Donnelly (2005), they were either highly restricted to a single tepui (*n* = 15) or moderately restricted to two or more tepuis or massifs (*n* = 3, Figure 13.8a). McDiarmid and Donnelly (2005) considered only nine species of snakes reported from tepuis to be widespread and on several tepuis or beyond (Table 13.1). All of these nine species have elevational ranges that extend upward from near sea level, so they cannot be considered tepui specialists or endemic species (Figure 13.8b).

Most of the moderately or highly restricted species of snakes are endemics to specific tepuis, but they belong to more wide-ranging South American genera (*Atractus, Chironius, Dipsas, Leptophis, Liophis, Oxyrhopus,* and *Philodryas*; Figure 13.9a). Of approximately 19 species of *Thamnodynastes*, 5 are endemic to one or more tepui summits (Figure 13.9b). Since the McDiarmid and Donnelly (2005) tally, several recent expeditions have added to the list of tepui snakes (Figure 13.9c). Barrio-Amorós and Brewer-Carías (2008) reviewed the herpetofauna of Sarisariñama, a tepui in southeastern Bolivar state (Venezuela), mentioning 4 species from the surrounding lowlands (*Helicops angulatus, Imantodes cenchoa, Erythrolamprus typhlus*, and *Phrynonax polylepis;* Figure 13.9d) and 3 from the uplands and summit area (*Liophis torrenicola, Chironius* sp., and *Bothrops atrox*). Myers and Donnelly (2008) reported 4 species from their 1994 expedition to Auyantepui, including *Chironius fuscus* from 2,088 m (later demonstrated to be *Chironius challenger* by Kok 2010), *Liophis trebbaui* from 1,750 m, and *Mastigodryas boddaerti* from 1,750 m, and provided a photo of what seems to be a *Bothrops atrox* from 1,600 m (Figure 13.10a). They also described a new species, *Atractus guerreroi* from 2,100 m, that was synonymized later by Passos *et al.* (2013) with *Atractus steyermarki*. Kok (2010) described *C. challenger*, a tepui endemic that was confused previously with *C. fuscus* in honor of Professor Challenger from Conan Doyle's *Lost World* novel. It occurs from 1,400 to 2,088 m on Maringma and Wokomung tepuis in Guyana and Auyan and Guaquinima in Venezuela. Barrio-Amorós and Fuentes (2012) mentioned two snakes—*Epictia albifrons* and *Liophis reginae cf. semilineata*—that were collected by Oswaldo Fuentes on the summit of Autana at 1,250 m. Only one species of snake, *Thamnodynastes chimanta*, was seen by CBA on Chimantá (see Figure 13.9b), but it proved to be quite abundant.

FIGURE 13.7 Elevational transects such as this one on the southern side of Churi, an arm of the Chimantá Massif, are characteristic of tepuis. The transects are aligned from seasonal rainforest at the base of the tepui, pass through a montane cloud forest on the first terrace, and then spread out among numerous habitats on the table-top summit. Cliff faces are also habitats with their own unique biota.

Source: Photograph by Bruce Means.

FIGURE 13.8 (a) *Atractus steyermarki*; (b) *Leptodeira annulata*. Both from the summit of Toronó-tepui of the Chimantá Massif, elevation approximately 2,100 m.
Source: Photographs by Bruce Means.

No snakes are known from the tops of the rocky eastern tepuis such as Roraima, Kukenan, or Yuruani, but the viper *Bothriopsis taeniata* is commonly seen in the cloud forests surrounding those tepuis between 1,220 and 1,800 m (Figure 13.10b). Passos *et al.* (2013), in their review of the genus *Atractus* from the Guiana Shield, found several unreported specimens from the summits of Chimantá (*A. steyermarki*) and Uei tepui (*Atractus tamessari*). In addition, MacCulloch and Lathrop (2004, 2009) reported three species of snakes on Ayanganna tepui in Guyana; only one is apparently endemic (*Dipsas pakaraimae*) and two others, *Dipsas catesbyi* and *Liophis miliaris*,

Table 13.1 Pantepuian Snakes Listed in Alphabetical Order[a]

Snake Species	Tepui on Which Found	Level of Endemism	Authority
Atractus duidensis	Duida	1	Roze (1961)
Atractus riveroi	Duida, Marahuaka	2	Roze (1961)
Atractus steyermarki	Chimantá, Auyan, Roraima, Weiassipu	2	Roze (1958)
Atractus tamessari	Uei tepui	2	Kok (2006)
Atractus zidoki	Below Roraima's cliff	4	Means (2007)
Bothriopsis taeniata	Roraima, Kukenan, Weiassipu, Chimantá	4	Means (2004), McDiarmid and Donnelly (2005)
Bothrops atrox	Auyan, Sarisariñama	4	Myers and Donnelly (2008), Barrio-Amorós and Brewer-Carías (2008)
Chironius challenger	Auyan, Maringma, Wokomung	2	Kok (2010)
Chironius exoletus	Duida	4	McDiarmid and Donnelly (2005)
Chironius fuscus	Auyantepui	4	Myers and Donnelly (2008)
Chironius sp.	Sarisariñama	1	McDiarmid and Donnelly (2005), Barrio-Amorós and Brewer-Carías (2008)
Dipsas catesbyi	Below Roraima's cliff	3	D. B. Means (personal observation)
Dipsas cf. *indica*	Neblina	1	McDiarmid and Donnelly (2005)
Dipsas pakaraima	Ayanganna	1	MacCulloch and Lathrop (2004)

Table 13.1 Continued

Snake Species	Tepui on Which Found	Level of Endemism	Authority
Dipsas sp.	Neblina	1	McDiarmid and Donnelly (2005)
Epictia albifrons	Guaiquinima, Autana	4	Barrio-Amorós and Fuentes (2012)
Imantodes lentiferus	Below Roraima's cliff	4	D. B. Means (personal observation)
Lachesis muta	Wokomung Massif	4	D. B. Means (personal observation)
Leptodeira annulata	Roraima, Chimanta Massif	4	Gorzula (1992), D. B. Means (personal observation)
Leptophis ahaetulla	Neblina	4	McDiarmid and Donnelly (2005)
Leptophis sp.	Neblina	1	McDiarmid and Donnelly (2005)
Liophis ingeri	Chimantá	1	Roze (1958)
Liophis reginae	Autana, Wokomung	4	Barrio-Amorós and Fuentes (2012), D. B. Means (personal observation)
Liophis torrenicola	Guaquinima, Sarisariñama	2	Donnelly and Myers (1991), Barrio-Amorós and Brewer-Carías (2008)
Liophis trebbaui	Auyan	2	Myers and Donnelly (2008)
Mastigodryas boddaerti	Auyan, Guaquinima	4	Myers and Donnelly (2008)
Oxyrhophis melanogenys	Wokomung Massif	2	Means and Kalamandeen (2007)
Philodryas cordata	Guaquinima	1	McDiarmid and Donnelly (2005)

(*continued*)

Table 13.1 Continued

Snake Species	Tepui on Which Found	Level of Endemism	Authority
Thamnodynastes chimanta	Acopan, Amuri, Apacará, Chimantá, Churi, Murey	2	McDiarmid and Donnelly (2005)
Thamnodynastes corocoroensis	Corocoro	1	Myers and Donnelly (2001)
Thamnodynastes duida	Duida	1	Franco and Ferreira (2003)
Thamnodynastes marahuaquensis	Marahuaka	1	McDiarmid and Donnelly (2005)
Thamnodynastes pallidus	Guaiquinima, Tamacuari	4	McDiarmid and Donnelly (2005)
Thamnodynastes yavi	Yaví	1	Myers and Donnelly (1996)

[a]The list of species is based on the literature (McDiarmid and Donnelly 2005; Rivas *et al.* 2012), other authorities, and personal observations. With some exceptions, we consider mostly species inhabiting the Pantepui summits and slopes above 1,500 m above sea level. On tepuis with summits lower than 1,500 m (*e.g.*, Autana and Sarisariñama), we included species seen or collected on their summits as well. Endemicity on tepui summits, in the Guiana Shield, or ranging more widespread is ranked as follows: 1, endemic to a single tepui; 2, endemic to more than one tepui; 3, Guianan endemic (not restricted to tepui summits) on tepuis and beyond; and 4, widespread (Guiana and Amazon, both on tepuis and lowlands).

are widespread Amazonian elements, as is *Lachesis muta* reported here from the Wokoming Massif in Guyana (Figure 13.10c). In our summary, we include these snakes, those reported in geographical distribution papers since the review of McDiarmid and Donnelly (2005), and a few unpublished observations of our own and substantiated by photographs. See Table 13.1 for the list of known tepui snakes as of the end of 2016.

Conclusions and Prospectus

Although tepuis are known to harbor a highly endemic fauna of amphibians and lizards, just a few species of snakes are known to be endemic to a single tepui summit (*Atractus duidensis* from Duida, *D. pakaraimae* from Ayanganna, *Thamnodynastes corocoro* from Corocoro, *Thamnodynastes*

FIGURE 13.9 (a) *Oxyrhopus melanogenys* from a vegetated island in a creek on the Wokomung Massif, Guyana, approximately 1,200 m elevation. (b) *Thamnodynastes chimanta*, Churi-tepui, an arm of the Chimantá Massif, 2,400 m elevation. (c) *Dipsas catesbyi*, found in branches 1.5 m off the ground in cloud forest below the ultimate cliff of Mt. Roraima's "Prow" in Guyana, approximately 1,200 m elevation. (d) *Imantodes lentiferus*, from cloud forest below the ultimate cliff of Mt. Roraima's "Prow" in Guyana, approximately 1,200 m elevation.

Source: Photographs by Bruce Means (a, c, and d) and César Barrio-Amorós (b).

duida from Duida, *Thamnodynastes marahuaquensis* from Marahuaka, and *Thamnodynastes yavi* from Yaví). A few others are known from several tepuis and nearby granitic mountain summits or slopes above 1,500 m; these include *Atractus riveroi, A. steyermarki,* and *T. chimanta*. As far as we know, Duida and Neblina are the most diverse tepuis in number of species, with four snakes currently reported from each. From Neblina, three of the four species remain to be identified to species and could be new, endemic forms; two from Duida are restricted endemics (*A. duidensis* and *Thamnodynastes duida*), and one, *A. riveroi*, is known also on neighboring Marahuaka.

FIGURE 13.10 (a) *Bothrops atrox* from the southern summit of Sarisariñama, approximately 1,300 m elevation; a terrestrial species whose color pattern blends it well in dappled light on dead-leaf-littered ground surfaces. (b) *Bothriopsis taeniata* from the montane gap between Mt. Roraima and Cerro Kukenan, Venezuela, approximately 1,900 m elevation; an arboreal species that color matches the chiaroscuro light of branches, twigs, moss, and other epiphytes. (c) Bushmaster, *Lachesis muta*, found crossing footpath approximately 1,500 m elevation on the Wokomung Massif, Guyana, a high elevation record for the species.

Source: Photographs by César Barrio-Amorós (a), Bruce Means (b), and Joe Riis (c), with permission.

Snakes in general are difficult to find, and tropical South American snakes might be even less frequently encountered than those in the temperate zones of the earth (Means 1994). In addition to their morphological crypticity, tropical snakes are often nocturnal, although on high-elevation tepuis, one might expect ectothermic snakes to be most active during daytime. On the other hand, because birds and small mammals are relatively rare on tepuis, the principal potential vertebrate food for snakes on tepui summits would seem to be frogs, most of which are nocturnal (*e.g.*, species of *Tepuihyla, Stefania, Hypsiboas, Myersiohyla,* and *Pristimantis*). In our experience, comparing the species richness of amphibians and reptiles among tepuis, we find that species numbers of both frogs and snakes are higher in the mid-elevation cloud forests fringing the higher tepuis (*e.g.*, Roraima) and on extensive summits of low-elevation tepuis (*e.g.*, Wokomung) or on large tepuis with complex and diversified summit landscapes (*e.g.*, Auyantepui and Chimantá). The food habits of tepui snakes are unknown, but in our experience, the most common potential vertebrate food items are frogs (especially species of the genera *Stefania, Tepuihyla, Pristimantis, Anomaloglossus*, and *Otophryne*). Other vertebrates, such as mammals and birds, are quite rare on tepui summits, but invertebrates that we have seen—especially earthworms and arthropods—might be sufficiently abundant to support a snake specialist. The arthropods, at least, support the frog fauna.

Unfortunately, the snake fauna of tepuis is so poorly known that we cannot make meaningful comparisons with evolutionary features of snakes on other islands. In our own experiences, finding a single specimen of a single snake species during a 2-week stay on the summit of a larger tepui was usually a rare event. Species of *Thamnodynastes, Atractus*, and *Liophis* were the most commonly encountered snakes on tepui summits (see Table 13.1). *Thamnodynastes* has the most endemic tepui species, whereas the other two genera are more widespread elevationally and geographically. We expect that documentation of the diversity of snake faunas of tepuis will increase in time as more tepuis are explored.

The snake fauna of tepui summits seems not likely to be hiding any spectacular discoveries of ancient lineages as is known for frogs such as the adaptive radiations of carrying frogs of the genus *Stefania* or pebble toads of the genus *Oreophrynella* (Kok *et al.* 2012, 2016). However, tepuis are such spectacular examples of ecological islands with sharp elevational features that continuing research on the distribution and ecology of snakes might eventually enable evolutionary comparisons with other terrestrial "island" systems (*e.g.*, the "sky islands" of the southwestern United States and northwestern Mexico; Favé *et al.* 2015).

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