CHAPTER 14-4
ANURANS: WATERFALLS, TREEFROGS, AND MOSSY HABITATS

Janice M. Glime and William J. Boelema

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Figure 1. Honduran cloud forest at Parque Nacional Montana de Santa Barbara at 2180 m asl that is habitat to many tropical anurans. Photo by Josiah Townsend, with permission.

Waterfalls

Sachatamia ilex (formerly *Centrolene ilex*) (Limon Giant Glass Frog, Centrolenidae)

A number of glass frogs are native to Central and South America where they live in streams and in subtropical or tropical moist lowland and moist montane forests. The Limon Giant Glass Frog, ***Sachatamia ilex*** (Figure 2), is also known as the Ghost Glass Frog and is nocturnal and **arboreal** (lives in trees) (Leenders 2001). It sleeps during the day on the upper surfaces of leaves where its green coloration makes it inconspicuous. Its habitat is in both primary and secondary wet forests where it often occurs in the spray zone of waterfalls and rapids of streams. Its color makes it inconspicuous when its perches are covered with mosses and it may be more common there than observations would indicate.

Figure 2. The **Limon Giant Glass Frog**, ***Sachatamia ilex*** (formerly *Centrolene ilex*). Its pose here makes one wonder if it is watching for dinner among the mosses, a place where insects often hide. Photo by Twan Leenders, with permission.

Frogs in the Trees

We know that mosses that live in trees must have xerophytic adaptations to survive the periods of no rain. The frogs that live there are most abundant and have the most species in the tropics (as will be seen below), where they share their habitat with epiphytes, including bryophytes (Figure 1). We can presume that bryophytes hold moisture and protect against UV light in these arboreal habitats, permitting at least some species to have a better survival chance than would be possible with no bryophytes.

Espadarana prosoblepon (formerly *Centrolenella prosoblepon*) (Emerald Glass Frog, Centrolenidae)

The Emerald Glass Frog, ***Espadarana prosoblepon*** (=*Centrolenella prosoblepon*) (Figure 3), is an arboreal frog (WWW.WildHerps.Com 2009). It has the coloration needed to blend with the many epiphytes, including bryophytes, on the mossy branches. These frogs take advantage of this coloration in their nest sites and calling locations among mosses and leaves. Jacobson (1985) studied this species at the Gaucimal River in Monteverde, Puntarenas Province, Costa Rica, at an elevation of 1360 m asl. She found that females deposit their eggs on leaf tops, moss-covered rocks, and moss-covered branches, where they attend the eggs immediately after depositing them (Jacobson 1985; Ryan & Lips 2004). Although in some species, attendance of eggs is important for removal of bacteria and fungi, it did not seem to improve larval survival for this species. Jacobson found 50 clutches of eggs, and these demonstrated a choice of moist micro-habitats. Five of the clutches were on constantly wet, mossy rocks on a river bank. Three were in water-laden mosses in forks of tree branches.

Figure 3. The Emerald Glass Frog, ***Espadarana prosoblepon*** (formerly *Centrolene prosoblepon*), blending in with the light green color of the mosses and liverworts. Photo by Twan Leenders, with permission.

Unlike many of the tropical arboreal frogs, ***Sachatamia ilex*** and ***Espadarana prosoblepon*** are not on the IUCN (2015) protected list and are not considered to be endangered (WWW.WildHerps.Com: *Centrolene prosoblepon*, Emerald Glass Frog).

Hylidae: North Temperate Treefrogs

The Britannica Online Encyclopedia defines the treefrogs as any frogs living in trees. Hence, they encompass several families. Among these, the **Hylidae** (Figure 4) are considered to be the "true" treefrogs, a taxonomic distinction rather than an ecological one. We prefer the definition from <dictionary.com> "any arboreal frog of the family Hylidae... They are strong jumpers and have long toes ending in adhesive discs, which assist in climbing," but common names ignore those requirements.

Figure 4. ***Hyla arborea*** (**Hylidae**) on moss. Photo by Milan Kořínek, with permission.

While some amphibians are most likely casual visitors, treefrogs in the tropics necessarily encounter bryophytes frequently. In tropical forests, biodiversity can be high, but many of these habitats remain unexplored (Tennesen 1998). Among these seemingly unknown habitats are the arboreal mosses – habitats where new species of frogs can be discovered on nearly every collecting trip to new areas. Each location may act like an island where contact with other such "islands" has been cut off by topography for a long enough period of time for genetic drift, differing selection pressures, and new mutations to create new species or variants. Such tiny frogs as are typical of these arboreal locations most likely don't travel far across open habitats without trees. Much like the human aborigines in some parts of the world, I doubt that they travel to a new mountain range very often.

The ground of many Peruvian forests is covered with wet ***Sphagnum***, and epiphytes abound on the trees. Although treefrogs need to maintain moist skin, there seems to be little direct evidence linking them to the use of these bryophytes to maintain moisture in their aerial habitat. Nevertheless, cryptic coloration that blends well with moss- and liverwort-covered branches suggests that such locations may be favorable resting places and may account for the limited observations that have been made of many species. Johannes Foufopoulos tells me he would never have discovered one of the new species in New Guinea (Foufopoulos & Brown 2004) if the frog hadn't called from its mossy perch. He had walked right by it without seeing it. It appears that some, perhaps many, can change colors to blend with their backgrounds or select backgrounds where their colors blend in. They become invisible to most searching eyes, especially those of the herpetologists.

Furthermore, nesting requirements and locations of eggs are virtually unknown in many of these species (*e.g.* Foufopoulos & Brown 2004). The same moisture advantage is offered to eggs and it is likely that eggs of

many species hide among the bryophytes and litter on the trees and forest floor.

We know that in the tropics, at least some treefrogs lay eggs among the mosses on the trees (Filipe Osorio pers. comm.). In Figure 5 the eggs resemble *Nostoc* balls and may thus be ignored by some carnivores because *Nostoc* has an unpleasant taste or just because they don't look like eggs. The terrestrial young of these species could remain protected from predators and desiccation within the mossy chambers until they develop to a sufficient size to move about easily.

Figure 5. Eggs of frogs on the tropical epiphytic liverwort ***Plagiochila* sp.** Can you find them in the upper picture? Photos by Filipe Osorio, with permission.

In these forests, animals have evolved reproductive specializations to the plants they live on, often being highly adapted to a single species or group of species. Frogs in particular have some special advantages that permit them to survive in an aerial habitat. Some sit on their eggs to incubate them. Others carry their tadpoles on their backs. And others lay eggs on leaves so that the young will fall into the river when they hatch. Most either have warning colors to threaten predators or have mottled colors that serve as camouflage (Figure 6).

Figure 6. This dart frog is not difficult to see when resting on epiphytic moss, but it is protected by its warning coloration of black and white and its poisonous skin. In some locations, its light and dark patches may hide it among sunflecks. Photo by Nate Warner, with permission.

At Monteverde, Costa Rica, temperatures in a sunlit moss mat or bromeliad basin may exceed the lethal temperature for the endangered tree-dwelling frogs that inhabit them (Pounds *et al*. 2006). Fortunately, these habitats are usually shaded, affording the frogs a safe place to live most of the time.

A variety of breeding niche diversifications, including mouth breeding, permit up to 80 different species of frogs and toads to co-occupy the same small forests in southern Chile, despite the absence of standing water in the treetops (Fogden & Fogden 1989). Their small size and susceptibility to dehydration causes the treefrogs to have narrow distributions, and many are **endemic** [exclusively occurring in just one locale (country, province, mountain, etc)] to a single or small group of mountains. Navas (2006) suggests the long history of amphibians at mid elevations in the Andes has permitted the many populations to adapt independently to the lower temperatures of the higher elevations. But high elevations require adaptations to other stressors as well, including UV radiation, especially for eggs. More recently, the more successful spread of chytridiomycosis in the lower temperatures at higher elevations has further reduced taxa there.

Hyla chrysoscelis (Cope's Gray Treefrog, Hylidae)

The Cope's Gray Treefrog (***Hyla chrysoscelis***; Figure 7-Figure 8) is a native American treefrog that lives on the bole and branches of trees. This species is listed as endangered in New Jersey, USA, but it is not federally listed (Southern Gray Treefrog, *Hyla chrysoscelis* 2011). It can change color from green to gray in only a few seconds to blend with its substrate (Reptiles and Amphibians of Minnesota 2009). It tends to occur in habitats with lots of mosses as ground cover, and moss is a recommended substrate for keeping the species in captivity [Costanzo *et al*. 1992; Girgenrath & Marsh 2003; Pollywog 2009]. Its coloration permits it to blend in with the lichens and mosses on tree bark. Despite its small size, ***Hyla chrysoscelis*** is able to withstand freezing, but where does it spend the winter? What use does it make of mosses and liverworts during its life cycle?

Figure 7. The Cope's Gray Treefrog, ***Hyla chrysoscelis*** in its grey coloration. When on a green substrate such as mosses, it can change rapidly to green. Photo by John D. Willson, with permission.

Figure 8. ***Hyla chrysoscelis*** (Cope's Gray Treefrog) in its greenish coloration, here blending with the bryophytes on the branch. This mossy branch seems to be a good night-calling position. Photo by Kerry Kriger, through SaveTheFrogs.com, for public use only.

Hyla versicolor (Gray Treefrog)

The specific name of ***Hyla versicolor*** means changing color, a capability of a number of treefrogs. ***Hyla versicolor*** is a similar species to ***H. chrysoscelis***, differing only in its call and its ploidy number, but lives farther north, overlapping with it at the southern end of its range. These species differ not only in range, but also in chromosome number, with ***H. chrysoscelis*** being diploid and ***H. versicolor*** being tetraploid (Ptacek *et al*. 1994). Like ***H. chrysoscelis***, it blends with the mosses of its tree bark environment (Rhode Island Vernal Ponds 2009; Figure 9). The AnimalsandEarth (2011) website describes ***Hyla versicolor*** as camouflaged on a moss-covered tree.

Figure 9. ***Hyla versicolor*** on a bed of moss. Photo by Brian Gratwicke, through Creative Commons.

Hyla arborea (Common Treefrog, Hylidae)

Hyla arborea, the Common Treefrog (Figure 10-Figure 11), typically occurs in open forests and open areas in Europe (Wikipedia: European Treefrog 2008). However, in Poland it is one of the species to be found in high elevational and transition bogs (Stachyra & Tchórzewski 2004). It is the only indigenous treefrog in mainland Europe and is endangered due to habitat loss and pollution (Wikipedia 2008).

Figure 10. Young ***Hyla arborea***, the Common Tree Frog, on a finger, demonstrating its tiny size. Photo by Christian Fischer, through Wikimedia Commons.

Figure 11. ***Hyla arborea*** on a bed of moss. Photo by Milan Kořínek, with permission.

Hyla gratiosa (Barking Treefrog, Hylidae)

Hyla gratiosa (Figure 12) is one of the larger hylids and is known from southeastern USA (Frost 2011). Wright (2002) reported it from a "moss-laden" black gum (*Nyssa sylvatica*) tree in Okefinokee Swamp, Georgia, USA.

Figure 12. ***Hyla gratiosa***, the **Barking Treefrog**, on a bed of bryophytes, where it sometimes calls to attract females. Photo by Brian Gratwicke, through Creative Commons.

Hylidae: Tropical Treefrogs

Ptychohyla dendrophasma (formerly *Hyla dendrophasma*) and *Ecnomiohyla minera* (formerly *Hyla minera*) (Fringe-Limbed Treefrogs, Hylidae)

The trunks of tropical cloud forest trees are typically covered with bryophytes. There hide numerous

inconspicuous frogs, still unknown to the world. Among these, ***Ptychohyla dendrophasma*** (formerly ***Hyla dendrophasma*** (a name meaning tree ghost) was discovered in 2000 from the Sierra Los Cuchumatanes in northwestern Guatemala (Campbell *et al*. 2000). This is a surprisingly large frog (84.1 mm) for bryophyte habitation, but it was hanging from a moss-covered tree branch about 1.2 m above a stream. At the same location, ***Ecnomiohyla minera*** spends its nights on the sides of moss-covered tree trunks and on branches. Duellman (1970) suggested that the resistance to desiccation and arboreal lifestyle of the Central American ***Ecnomiohyla miliaria*** (Figure 13) are evidence that its home is in the forest canopy. Its coloration would help to camouflage it among the canopy mosses. The large toe pads and scallops along the legs help it to maintain its hold in the canopy.

Figure 13. ***Ecnomiohyla miliaria*** blending with the multicolored bark of the branch. It occurs in humid rainforests and wet forested highlands of Colombia, Costa Rica, Nicaragua, and Panama. Note the fringes on the legs that may be helpful in holding onto branches, where it flattens itself against the substrate. Or perhaps they help it to glide. Photo by Joseph H. Townsend, through Wikimedia Commons.

Isthmohyla lancasteri (formerly *Hyla lancasteri*) (Lancaster's Treefrog, Hylidae) – Why Have Tubercles?

As noted earlier, the brown splotchy pattern on the green-colored ***Isthmohyla lancasteri*** (formerly *Hyla lancasteri*; Figure 14) should serve it well as camouflage among the mosses. But as elevation levels increase (to 1920 m asl in Panama), so do the elevations on the frog. That is, instead of the smooth skin seen at elevations between 650 and 910 m in Panama and Costa Rica (Figure 14), this higher elevation frog gets dorsal warts that are increasingly greater in size as elevation rises (Figure 15; Trueb 1968). It looks a bit like a miniature field of volcanoes.

One can only speculate on the selection pressure behind retention of such an innovation. Why should higher elevations favor conservation of larger tubercles? One might consider camouflage amid the moss or perhaps added protection against UV radiation. Or might it be a deterrent to would-be predators? Trueb (1968) seems to think that the protuberances provide cryptic coloration: "At 1920 m on Cerro Pando, the frogs were perched on branches covered with deep moss. The frogs were difficult to see because of their **tuberculate** skin and cryptic coloration – green, white, and brown mottling. At 1450 m, less moss is present and the frogs are correspondingly less tuberculate. Moss is less common at lower elevations, and frogs have fewer and less prominent protuberances and more subtle dorsal mottling. At elevations less than 910 m, the frogs are smooth, and the dorsal mottling is replaced by blotches on a unicolor background; these frogs are typically found on or near the ground, perched on leaves, branches, and stones." But Trueb also suggests that the protuberances on the legs and feet may help the frogs to hold onto the slippery branches. One might also speculate that they would help to keep a slippery, sleeping frog from falling through the mosses to the ground.

Figure 14. ***Isthmohyla lancasteri*** showing the low elevation (550 m asl) morph at Guayacan, Limon Province, Costa Rica. Note the color splotches and almost no tubercles. Photo by Brian Kubicki, with permission.

Figure 15. This is a higher elevation form of ***Isthmohyla lancasteri*** showing prominent tubercles. The photo was taken in Panama at Bocas del Toro Province, Parque Internacional La Amistad Caribbean side, Cerro Frío, at 1000 m asl. Photo by Angel Solís, with permission.

Agalychnis (Hylidae)

Agalychnis saltator (Misfit Leaf Frog; Figure 16-Figure 17) is one of those adorable green frogs with red eyes and large suction pads on its toes. It can be found in the Caribbean lowlands of northeastern Honduras, Nicaragua, and east-central Costa Rica at 15-1300 m asl. Pictures of frogs like this one frequently adorn ads, calendars, and other decorative positions. Bryophytes can provide a suitable substrate for laying its eggs, spread in a layer over the bryophyte mat (Figure 18). This species adds to its charm by **parachuting** (a free-fall descent that is less than 45° from the vertical) (Roberts 1994)!

Parachuting frogs display a tropical novelty that is part of the breeding activity. Males and females of ***Agalychnis saltator*** (Figure 16) gather in breeding aggregations on **lianas** (vines) above temporary swamps (Roberts 1994). From there, both genders parachute to the ground to join breeding aggregations there. They return to the canopy rapidly by a hand-over-hand movement up the **lianas** (vines). They lay grey eggs during the daylight hours, packed into the mosses that surround the lianas. They eggs are vulnerable to mortality caused by desiccation, submergence in water, and predation by ants, snakes, and birds. Roberts suggests that the parachuting behavior, followed by walking, may permit these frogs to live in the canopy where they are widely dispersed, then to gather in a short burst to breed in large numbers in isolated ponds.

Figure 16. ***Agalychnis saltator*** (Misfit Leaf Frog), a parachuting frog on a mossy branch. Photo by Twan Leenders, with permission.

Figure 17. ***Agalychnis saltator*** showing its greenish coloration patterning that blends with its aerial or ground mossy habitat. Photo by Jason Folt, through Creative Commons.

Figure 18. Eggs of ***Agalychnis saltator*** on leaf. Photo by Peter Janzen, with permission.

The related species ***Agalychnis spurrelli*** only occasionally lays eggs among the mosses (Gomez-Mestre & Warkentin 2007). These are laid in an irregular X shape only one layer deep (rarely in 2 layers). The tadpoles (Figure 19) drop into the water when they hatch. The eggs are subject to predation by egg-eating snakes. Tadpoles may be eaten by fish.

Figure 19. ***Agalychnis callidryas*** eggs – a treefrog that does not use mosses for oviposition. Photo by Geoff Gallice, through Creative Commons.

Charadrahyla nephila (Oaxacan Cloud-forest Treefrog, Hylidae)

Charadrahyla nephila (Figure 20) is endemic to Mexico, where it lives in subtropical or tropical moist lowland forests and moist montanes (cloud forests), and rivers at 680-2256 m asl, habitats that are all being destroyed, thus threatening its existence (Santos-Barrera & Canseco-Márquez 2004). It seems further to be suffering from **chytridiomycosis**, a fungal disease caused by ***Batrachochytrium dendrobatidis***, as suggested by the loss of keratinized mouthparts in tadpoles of southern Mexico. (See subchapter 14-2 for a discussion of this fungus disease.)

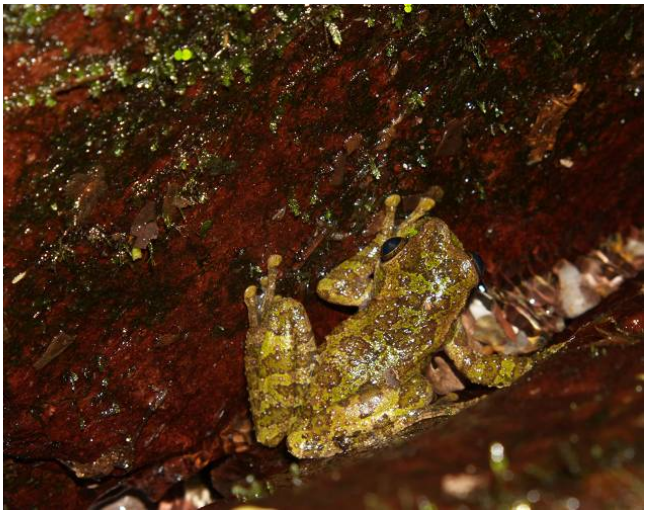

Figure 20. ***Charadrahyla nephila*** (Oaxacan Cloud-forest Treefrog) clinging to a tree and surrounded by bryophytes at La Chinantla, Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Anotheca spinosa (Spine-headed Tree Frog, Hylidae)

Anotheca is a **monotypic** hylid genus. That is, there is only one species in the genus, ***Anotheca spinosa*** (Spine-headed Tree Frog, Figure 21). It is distributed in Costa Rica, Honduras, Mexico, and Panama in subtropical or tropical moist lowland forest and montane regions (Santos-Barrera *et al*. 2004) where it lives in cloud forests (Duellman 1970). It is active year-round, requiring it to choose habitats where it can maintain moisture through dry seasons. Unlike the tiny ***Eleutherodactylus***, this relatively large 80 mm species lays an average of 158 eggs per clutch (Jungfer 1996), keeping them wet in the basin of a bromeliad or a tree hole. The female stays with her eggs, and when she feels the tadpoles swimming against her, she releases a second set of eggs that serve as nutrient sources for the tadpoles.

The branches that hold these bromeliads in a cloud forest are typically covered with bryophytes, so being adapted to sit among them is beneficial. The bryophytes are most likely important in providing both camouflage and in maintaining moisture. For some they might provide sites for eggs that are adapted to the terrestrial environment. And the bryophytes hold numerous arthropods that serve as potential food items.

Figure 21. ***Anotheca spinosa*** (Spine-headed Tree Frog), shown here amid bryophytes on a tree at La Chinantla, Oaxaca, Mexico. It appears that looking like a leaf or bark is useful when bryophytes are sparse. Photo by Omar Hernandez-Ordoñez, with permission.

Litoria serrata (Green-eyed Treefrog, Hylidae)

Litoria serrata (Figure 22-Figure 23) lives in northeastern Queensland, Australia. Ross Alford (pers. comm. 28 March 2011) states that this species looks quite inconspicuous when it rests on mosses, which it often does in its natural habitat. This is facilitated by its tubercles and its brown-grey-green coloring.

Figure 22. ***Litoria serrata*** in its brown and green camouflage form. Photo by Jean-Marc Hero, with permission.

Figure 23. ***Litoria serrata*** in its lichen/moss camouflage form. Note the fringe projections on the legs that help hold it in place on tree branches and trunks. Photo by Jean-Marc Hero, with permission.

Ecnomiohyla miliaria (Cope's Brown Treefrog, Hylidae)

Ecnomiohyla miliaria (Figure 24) lives in rainforests in humid lowlands and premontane slopes from eastern Honduras and southeastern Nicaragua and central Colombia (Duellman 1970) to southeastern Costa Rica on the Atlantic slope (20-900 m) and on the Pacific slope in humid premontane areas of southwestern Costa Rica and western Panama at 600-1300 m asl (Frost 2011).

Figure 24. ***Ecnomiohyla miliaria***, demonstrating the flattened position that helps to make it inconspicuous. Its coloration helps to hide it among the lichens and mosses. Its large toes and fringes on the legs help it to clasp its arboreal substrate. Photo by Josiah H. Townsend, through Creative Commons.

Its actual habitat is unknown, although its thick, roughened skin, large toe suction pads, and fringes on the legs, as well as its ability to flatten its body, suggest that it is an arboreal species (Schoville 2000). Its coloration and tubercles suggest that it would blend well among bryophytes. It is listed as vulnerable because it is distributed over less than 20,000 km^2, its distribution is severely fragmented, and the extent and quality of its forest habitat in Nicaragua, Costa Rica, and Panama are in continued decline (IUCN 2010).

Smilisca sila (Panama Cross-banded Treefrog, Hylidae)

This Panama Cross-banded Treefrog lives in Colombia, Costa Rica, and Panama in subtropical or tropical moist lowland forests, rivers, and freshwater marshes (Frost 2011). These include mossy habitats, where it often traverses the bryophytes on the soil and trees (Figure 27). But its actual use of these substrata and their importance to its habitat have not been investigated. Habitat loss threatens its existence, so it is important to understand if this if bryophytes are a vital part of its niche.

Mantellidae

Spinomantis aglavei (Anamalozoatra Madagascar Frog, Mantellidae)

Spinomantis aglavei (Figure 25-Figure 26) is known from the Andringitra Mountains and eastern forests of Madagascar (Frost 2011). It occurs from sea level to 1500 m asl in slow-flowing streams, swamps, and fast-flowing streams of the rainforest, but does not tolerate secondary forests (Nussbaum & Vallan 2008). It is medium-sized (40-50 mm), greenish brown, and resembles tree bark with epiphytes (Glaw & Vences 2007). Its calls are emitted from the canopy, 1.5-3 m above ground, necessitating its travel up the tree where its coloration serves as camouflage. It deposits 30-38 eggs on leaves above streams and the hatching tadpoles drop into the streams to complete their development. Adults rest on the tree trunks during the day, relying on their cryptic coloration and skin fringes to hide them from harm. It is listed as a species of least concern because it is widely distributed and presumed to have a large population (IUCN 2010). It is likely that other species in this genus also use mosses (Figure 27).

Figure 25. ***Spinomantis aglavei***, showing the large toe suction pads and leg fringes typical or frogs living high in trees. Photo by Jörn Köhler, with permission.

Figure 26. ***Spinomantis aglavei*** at night on a tree trunk. Note how the large feet and fringe can help to hold this frog to this smooth bark while the colors serve as camouflage. Photo by Franco Andreaone, through Wikimedia Commons.

Figure 27. ***Smilisca sila*** (Panama Cross-banded Treefrog, **Hylidae**) climbing on roots and moss in Costa Rica. Photo by Brian Gratwicke, through Creative Commons.

Cloud Forests and Other Mossy Habitats

As I worked on this chapter, I discovered an interesting co-incidence that may actually reveal evolutionary adaptations. Based on concerns by an anuran systematist who was not accustomed to seeing my included taxa arranged in non-phylogenetic order, I rearranged

everything to a semblance of their current phylogenetic positions. I later decided this did not accomplish the ecological purpose of the book and began grouping the stories by habitat. By the time I finished the frogs and toads and was wrapping up the **Hylidae**, I realized that this chapter was mostly in habitat order already. Hence, as we end the discussion of the **Hylidae** and their close relatives, which are mostly tree-dwellers, (arboreal) we begin a group of families associated with bryophytes on the ground, rocks, or low branches (<2 m), but in "mossy" habitats they occur on trees as well. Note that I refer to bryophytes here and not just mosses because I believe that liverworts are often the substrate as well. However, most folks studying anurans are not bryophyte taxonomists and do not take note of the distinction, hence, I suspect, grouping the leafy liverworts into the broad category of mosses. Thus, as you read "mosses" below, keep in mind that they may include liverworts.

In tropical cloud forests, biodiversity can be high, but many of these habitats remain unexplored (Tennesen 1998). Many of the species are known from only one or two collections, and information on their biology and ecological preferences is extremely limited.

Cape Horn, South America

In her visit to the Cape Horn area, Blanka Shaw observed frogs among the very mossy habitats there (Figure 28-Figure 30). It's too bad we don't have joint herpetological and bryological field trips so that we can describe the habitats of these frogs more completely and so bryologists can be more familiar with the roles that bryophytes play in many mossy ecosystems.

Figure 28. Habitat for small frogs among liverworts in ***Nothofagus betuloides*** forest at Fjord Agostini, Provincia Magallanes, Chile. Photo by Blanka Shaw, with permission.

Microhylidae

The Microhylidae is a large family in the tropics and spans both eastern and western hemispheres. The species frequent mossy forests, among other habitats.

Albericus valkuriarum (Microhylidae)

Albericus valkuriarum inhabits the mid-montane rainforest and forest edge (Richards & Allison 2004) above 2000 m asl in Papua New Guinea (Frost 2011). Habitat degradation usually results in its disappearance (Richards & Allison 2004). Its breeding is unknown, but Richards and Allison suggest that it probably lays its eggs on the ground or in mosses on tree trunks. Richards and Zweifel (2004) make a similar statement about ***Albericus fafniri***.

Cophixalus *(Rainforest Frog, Microhylidae)*

With a name like **Microhylidae**, one would expect the tiny members of this family to be among the bryophyte fauna, taking advantage of the bryophyte moisture buffering to conserve moisture in the tiny animals with their large surface area to volume ratio.

Cophixalus sphagnicola lives in moss and leaf litter (Zweifel & Allison 1982; Kraus & Allison 2000) in very mossy rainforests near Wau, Morobe Province, Papua New Guinea. In Australia, ***Cophixalus ornatus*** (Figure 29) is an **arboreal** (tree-dwelling) frog that lives under logs and leaf litter in its New Guinea rainforest home. However, it often lays its eggs in moss (Figure 30) (Online Field Guide: Ornate Nursery Frog; Hoskin 2004). In one observation in Australia, the male attending the eggs began moving them when disturbed (Hoskin 2004). However, before moving them, he consumed some of them, then moved about half of those remaining to a more moist location. Those left behind failed to hatch. The male attendants apparently feed on ants that threaten survival of the eggs. The clutch size of this species is the largest of any known for Australian microhylids, with up to 22 eggs recorded.

Figure 29. ***Cophixalus ornatus***, a species wherein some females lay their eggs among mosses. The male is shown here in calling mode with an inflated vocal sac. Its relative, ***Cophixalus sphagnicola***, lives among the mosses. Photo by Jean-Marc Hero, with permission.

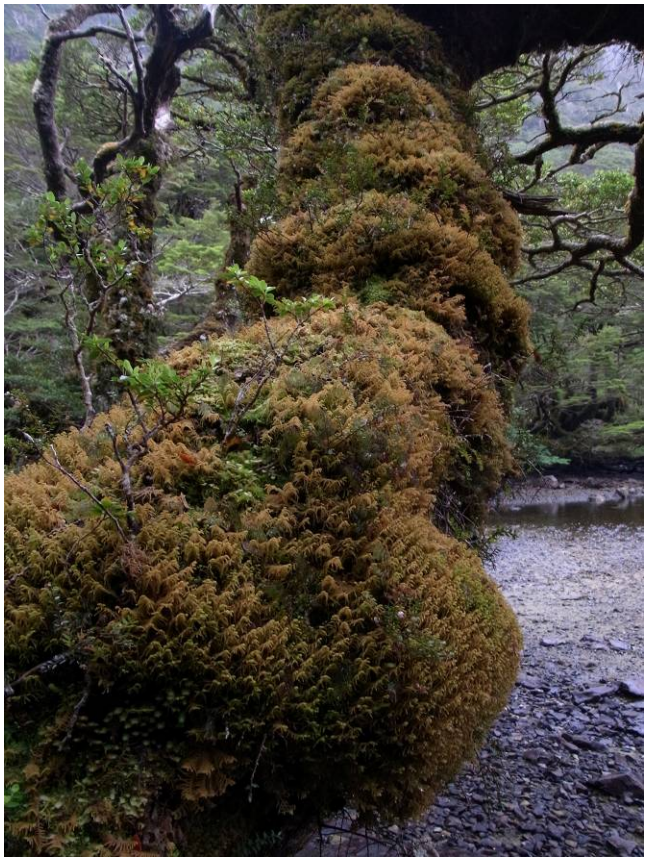

Figure 30. Leafy liverwort ***Lepicolea*** on bole at Tierra del Fuego, Peninsula Edwards, Cape Horn, Chile. This dense cover of epiphytic bryophytes provides ideal habitat where small frogs can hide. Photo by Blanka Shaw, with permission.

Choerophryne (Microhylidae)

Species of ***Choerophryne*** (Torricelli Mountain Frogs), a genus endemic to New Guinea, live on the forest floor and on leaves of shrubs, but also among mosses on steep rocky cliff faces, where they can be heard calling (Kraus & Allison 2001).

Dyscophus guineti (Sambava Tomato Frog, Microhylidae)

Dyscophus guineti (Figure 31-Figure 32) is broadly distributed beside slow-moving streams in the eastern rainforest belt of Madagascar from 150 to 900 m asl (Nussbaum *et al*. 2008). This is a very secretive species, making it difficult to locate. These are somewhat easier to find at night when they travel about on the forest floor. They lay hundreds of sticky eggs that are deposited in ponds (Glaw & Vences 2007), rendering sharp contrast to the single-digit egg clutches of terrestrial egg-layers.

Evans and Brodie (1994) used this frog (and others) in experiments to determine the ability of the surface secretions to slow down predators by creating a glue. But for our purposes, this is more interesting because these secretions make the frog sticky, permitting it to be a dispersal agent of bryophytes. In their discussion of the adhesive strength of these secretions, Evans and Brodie (1994) stated that they first washed the amphibians in their study to remove soil, debris, mosses, and other adhering substances. In this experiment, ***Dyscophus antongilii*** and ***D. guineti*** had the strongest glue among the eleven amphibians tested. The Common Garter Snake, ***Thamnophis sirtalis***, was able to free itself from secretions by ***Dyscophus*** in 7-39 seconds, a sufficient time for the frog to achieve some distance from its predator.

In an email discussion with Butch Brodie, he stated that he had not paid attention to bryophyte adherence in the field; the experiments were in the lab. But this sticky surface can indeed glue substances to the frogs, permitting such things as bryophytes to travel with the frog and potentially get dropped off elsewhere (see image of ***Ceuthomantis smaragdinus***, Figure 37). In my garden room, my Green Frog (***Lithobates clamitans***) was usually covered with bird seed shells because it spent much time under the bird feeder where fermenting seed shells nourished fruit flies.

Figure 31. ***Dyscophus guineti*** (**Sambava Tomato Frog**) male showing its duller coloration compared to the female. Photo by Franco Andreone, through Wikimedia Commons.

Figure 32. ***Dyscophus guineti*** female peering out from a seclusive spot among bryophytes. Photo by Tim Vickers, through Public Domain.

While getting these secretions on the belly of a snake in a place where it might be glued down seems a bit of a stretch, these secretions can be useful tactics against some animals. When encountering these frogs, the Lesser Hedgehog Tenrec, a mammal (***Echinops telfairi***) got its lips glued together and one eye and its toes were stuck together for the full thirty minutes of the trial (Evans & Brodie 1994). Furthermore, contact with the secretion caused the tenrec to turn in circles, snuffling and salivating profusely and rubbing the substrate with its head.

It appears that part of the strange behavior that permits ***Dyscophus guineti*** to escape predators could be the result of a trypsin inhibitor in the skin secretions (Conlon & Kim 2002). This differs from the α-helical antimicrobial peptides used by many frogs as a defense strategy, so Conlon and Kim speculated that it may be part of an alternative strategy of defense against microorganisms. But could it be part of a strategy against predators?

Platypelis grandis (Boulenger's Giant Treefrog, Microhylidae)

Platypelis grandis (Figure 33) lives in eastern and northwestern Madagascar (Frost 2011). Its habitat is subtropical or tropical moist lowland forests and moist montanes where it is threatened by habitat loss. It is usually arboreal, although it is occasionally found on the ground (IUCN 2010). It needs mature forest and breeds in tree holes. Its coloration and tubercles provide camouflage that help to protect it as it climbs on tree trunks and branches.

Figure 33. ***Platypelis grandis*** on tree bark with bryophytes and lichens. Photo by Jörn Köhler, with permission.

Hypopachus barberi (Barber's Sheep Frog, Microhylidae)

Hypopachus barberi (Figure 35) lives at 1470-2070 asl in the tropical countries of El Salvador, Guatemala, Honduras, and Mexico (Frost 2011). Its limited distribution is threatened by habitat loss in its native habitats of subtropical and tropical moist montane areas and freshwater marshes, although it is also able to live in plantations and rural gardens (Wikipedia 2011b).

Figure 34. ***Hypopachus barberi*** on a bed of moss where it is able to maintain hydration. Photos by Josiah Townsend, through Wikimedia Commons.

Figure 35. ***Hypopachus barberi*** from Guisayote Honduras on a bed of moss where it is able to maintain hydration. Photos by Josiah Townsend, through Wikimedia Commons.

Xenorhina (Snouted Frog, Microhylidae)

From the North Coast Ranges of Papua New Guinea, ***Xenorhina arboricola*** (Figure 36) is unique among members of ***Xenorhina*** there in being **arboreal** (tree-dwelling) (Allison & Kraus 2000). It lives among leaf litter collected in *Asplenium* (bird's nest fern) and in the mosses that surround the trees and epiphytes. Allison and Kraus found one frog guarding a clutch of 11 eggs that were "connected together by a single filament into a pearl-like string." ***Xenorhina zweifeli*** (formerly *Xenobatrachus zweifeli*) lives in the same North Coast range, where trees are covered with mosses (Kraus & Allison 2002). Like many of the frogs in that area, the extent of its use of mosses is unknown.

Ceuthomantidae

Ceuthomantis duellmani

New records of tiny, moss-dwelling frogs are common in the less-explored portions of the world. In 2010, Barrio-Amorós described a new species of ***Ceuthomantis*** from Sarisariñama Tepui, southern Venezuela. This species occurred in a dwarf forest that was completely covered by mosses and other epiphytes. ***Ceuthomantis duellmani*** called from within holes and hiding places in tree buttresses, undoubtedly taking advantage of the mosses as cover. It would be interesting to determine the density of these frogs within the moss mats during the daytime when moisture may be a problem elsewhere.

Figure 36. ***Xenorhina arboricola*** from New Guinea, a species that often lives among epiphytic mosses. Photo from Bishop Museum, with permission from Barbara Kennedy.

Ceuthomantis smaragdinus

Ceuthomantis smaragdinus (Figure 37) occurs at 1490-1540 m asl in Guyana (Heinicke *et al*. 2009). Its cloud forest habitat has broad-leafed trees up to 12 m tall, shrubs, and small tree ferns. These are covered with epiphytic bryophytes and bromeliads. Little is known about this frog, but it lives in a mossy habitat where it is likely to encounter bryophytes during its daily activities.

Figure 37. ***Ceuthomantis smaragdinus*** transporting what appear to be pieces of mosses. See discussion above on ***Dyscophus guineti*.** Photo by D. Bruce Means, through Public Domain.

Hemiphractidae

Gastrotheca pacchamama (Ayacucho Marsupial Frog, Hemiphractidae)

Gastrotheca pacchamama (*cf*. Figure 38) is an endemic found along the Amazonian slopes of the Andes, known from three different areas: Machu Picchu, San Luis, and San Pedro in southern Peru (Frost 2011). It is known from 2000-3000 m asl. It is one of the **marsupial** frogs (direct-developing frogs that carry their developing eggs on their backs in a pouch until the eggs hatch) (Wikipedia 2015). The marsupial method in frogs is an adaptation to living in a terrestrial habitat. This species was found under rocks in wet grassland at Abra Tapuna in Peru (Duellman 1987). During the day, some of the males were calling from moss-covered talus. Presumably, the moss reduced the moisture loss and possibly provided camouflage.

Figure 38. Female ***Gastrotheca cornuta***, showing eggs in pouches on her back. Photo © Danté Fenolio <www.anotheca.com>, with permission.

Gastrotheca excubitor (Abra Acanacu Marsupial Frog, Hemiphractidae)

Gastrotheca excubitor (Figure 39) lives on the Amazonian slopes of the Andes in southern Peru at 2000-3000 m asl. It exhibits a green and brown pattern that would help make it less conspicuous among mosses, but there seems to be no verification that it lives among the mosses, where it may only be a casual visitor.

Figure 39. ***Gastrotheca excubitor*** on a bed of moss. The coloration would make this frog less conspicuous to its flying predators. Photo by Alessandro Catenazzi, with permission.

Stefania (Stefania Treefrogs, Hemiphractidae)

There are a number of records of collections of ***Stefania*** from mossy habitats in the tropics and subtropics. ***Stefania evansi*** (Figure 40) occurs in Guyana in tropical and subtropical moist lowland forests or moist montane forests up to 1400 m asl and in rivers (Wikipedia 2010). It carries its eggs on its back, and likewise carries the tadpoles, hence providing parental care. In Guyana, MacCulloch and Lathrop (2002) found several species of ***Stefania*** at night, sitting on moss-covered branches 1-4 m above the ground. Others were found in bromeliads, and one was collected from a mossy tree trunk. At the summit of Cerro Autana, Estado Amazonas, Venezuela, Barrio-Amorós and Fuentes (2003) found ***Stefania ginesi***, ***S. satelles***, and ***S. schuberti***, mossy inhabitants of the high summits of Tepui from 1750-2600 m. In addition to mossy habitats, these species occur along creeks, under rocks, and in bromeliads (*Brocchinia*) (Duellman & Hoogmoed 1984; Gorzula & Señaris 1998; Señaris *et al*. 1996).

Figure 40. ***Stefania evansi*** from Guyana carrying its eggs on its back. This is a strategy practiced by a number of arboreal frogs and permits them to move to places with sufficient moisture for the eggs. Photo by Philippe Kok, with permission.

Dendrobatidae

Oophaga pumilio (formerly *Dendrobates pumilio*) (Strawberry Poison-dart Frog, Dendrobatidae)

The Strawberry Poison Dart Frog is a small frog (17.5-22 mm) from Central America, where it lives in humid lowlands and premontane forest (Savage 2002; Wikipedia 2011c).

Frogs can be territorial over their personal patch of ***Sphagnum*** (or other substrate). The Strawberry Poison-dart Frog ***Oophaga pumilio*** (Figure 41-Figure 43) even exhibited dominance over intruders when it was placed into a new aquarium with the ***Sphagnum*** it had inhabited in its previous captive home (Figure 42; Baugh & Forester 1994), suggesting chemical markers were left in the moss. An earlier experiment (Forester & Wisnieski 1991) had demonstrated that, given a choice, these frogs exhibited a preference for their home aquarium, which had been lined with ***Sphagnum*** and contained a bromeliad. On Isla Colón, Bocas del Toro archipelago, Panama, this brightly colored frog can hide inconspicuously within the moss mat covering the trees (Sirota 2011). The males often use tree bases as calling places, likewise often being inconspicuous among the mosses (Pröhl & Ostrowski 2010).

Figure 41. The Strawberry Poison-dart Frog, ***Oophaga pumilio*** on a bed of *Selaginella*. Photo by Jason Folt, through Creative Commons.

Figure 42. Strawberry Poison-dart Frog, ***Oophaga pumilio***, in a chamber with ***Sphagnum*** where it had been previously, showing aggression toward the newcomer frog. Photo by Don Forester, with permission.

Figure 43. Strawberry Poison-dart Frog, ***Oophaga pumilio***, sitting on a tree trunk with bryophytes. Photo by John D. Willson, with permission.

The female Strawberry Poison-dart Frog deposits her tadpoles singly at each location and expends a great deal of energy to care for them (Savage, 2002; Wikipedia 2011c). She visits each tadpole every few days and deposits several of her unfertilized eggs to serve as food. This seems to be an essential food, as no other food form seems to work. The male contributes by transporting water in his **cloaca** (combined cavity used to release both excretory and genital products in amphibians, reptiles, fish, birds, and a few other groups) and watering the eggs to keep them hydrated (Wikipedia 2011c). Even so, success of the tadpoles is only 5-12%. The tadpoles take about one month to develop into young adults, but remain near their water sources a few more days while they absorb what remains of their tails.

These day-active Strawberry Poison-dart Frogs derive their poison from their diet of beetles and ants, primarily formicine ants (Daly & Myers 1967). Thus, the frog is harmless if its diet is confined to other foods, such as that of the ones kept for pets (Wikipedia 2010c).

This species has 15-30 color morphs, as discussed in Chapter 14-1 on adaptations. Among these, the green morphs typically remain within the moss mats and spend less time foraging compared to the more active, brightly colored morphs that advertise their poisons with their warning coloration (Pröhl & Ostrowski 2010).

Phyllobates (Poison-arrow Frog, Dendrobatidae)

Other wet forest frogs that may spend some of their time on or in mosses are even more poisonous [***Phyllobates terribilis*** (Golden Poison Frog; Figure 44-Figure 45), ***P. bicolor***, ***P. aurotaenia***] (Dumbacher *et al*. 2000). Among these, ***P. terribilis*** (Figure 44) is the most poisonous; natives that use poison darts need only touch a dart to this frog to make it poisonous for a year! (Wikipedia: Golden Poison Frog 2011). Even touching the frog can be lethal for humans (Daly & Witkop 1971; Wikipedia: Golden Poison Frog 2011).

Figure 44. ***Phyllobates terribilus***, a very poisonous tree frog that has been used to make poison darts. Photo by Milan Kořínek, with permission.

Phyllobates terribilis lives in rainforests with 5 m or more rainfall! (Wikimedia 2011a). They occur at 100-200 m asl where the temperature is at least 26°C and relative humidity 80-90%. A large portion of the diet consists of ground-dwelling ants in the genera ***Brachymyrmex*** and ***Paratrechina***, contributing to their poisons. These frogs live in social groups of up to six individuals, perhaps protecting each other through their severe poisons. Surely only one would be eaten.

Figure 45. ***Phyllobates terribilus*** from the Pacific Coast of Colombia showing a color morph that serves as a warning color. Photo by Wilfried Berns, through Wikimedia Commons.

Silverstoneia flotator (Rainforest Rocket Frog, Dendrobatidae)

The tiny Rainforest Rocket Frog (Figure 46-Figure 48) lives in lowland rainforests and semideciduous forests in Panama and Costa Rica at elevations of 10-865 m asl. It is diurnal and hides among the leaf litter, but must often traverse bryophyte-covered areas to move around. The adults tend to hang out on the rocky sections of forest streams, but they deposit their eggs in leaf litter (Solís *et al*. 2004). The males transport the hatchling tadpoles to the streams where these young develop into adults (Figure 48).

Figure 46. ***Silverstoneia flotator*** on a bryophyte substrate. Photo by Brian Gratwicke, through Creative Commons.

Figure 47. ***Silverstoneia flotator*** (Rainforest Rocket Frog) jumping from a bryophyte substrate. Photo by Brian Gratwicke, through Creative Commons.

Figure 48. ***Silverstoneia flotator*** (Rainforest Rocket Frog) male with tadpoles on its back. Photo by Brian Gratwicke, through Creative Commons.

Leptodactylidae

This was once a much larger family that included the huge genus ***Eleutherodactylus*** (now in Eleutherodactylidae). Current thinking has divided the family and its largest genus.

Within the Leptodactylidae, some members make foam nests for their eggs, an adaptation to terrestrial life. Tadpoles remain in this frothy mass without eating, not exiting until they have completed metamorphosis. Their **development** is **direct** and they hatch into miniature frogs. That is, they have no tadpole stage.

In Brazil, the Marbled Tropical Bullfrog, ***Leptodactylus marmoratus*** (**Leptodactylidae**; Figure 49),

used mosses as cover for a foam nest on a road cut (Wassersug & Heyer 1988). However, nothing else is known that relates this frog to mosses (Mauro Teixeira pers. comm. 8 February 2009).

Figure 49. The Marbled Tropical Bullfrog, ***Leptodactylus marmoratus***, a frog known to nest under mosses. Photo © Mauro Teixeira Jr, with permission.

Eleutherodactylidae

This family lives in the tropics and subtropics of the western hemisphere. The genus ***Eleutherodactylus*** (Robber Frogs, Figure 50; **Eleutherodactylidae**) was the largest genus of frogs. However, many of the species have been placed in other genera and some in other families. It is interesting to see how many of these have gone back to the generic distinctions recognized in the 1800's. Our genetic information seems to have taken us full circle in many cases. What wonderful powers of observation those early herpetologists must have had!

Figure 50. ***Eleutherodactylus limbatus*** amid lichens and mosses on a tree branch at Gran Piedra, Cuba. Photo by Ariel Rodriguez, for educational use.

This family abounds from the ground to the treetops. The tiny size of the members of Eleutherodactylidae permits these species to live among mosses, especially in the canopy and on tree trunks. Some call from a perch on mosses (Figure 51). Many more may exist there unknown because many surveys don't seem to include searching among the bryophytes. Others seem only to lump the bryophytes into vegetation. When the habitat is a cloud forest, it is usually safe to assume that bryophytes are abundant.

Figure 51. ***Eleutherodactylus richmondi*** calling from a perch on mosses. Photo by Luis J. Villanueva-Rivera, with permission.

The Burrowing Frog **(*Eleutherodactylus parapelates*, Eleutherodactylidae**, formerly in Leptodactylidae), despite being a ground frog, was calling from within a large moss clump at 3 m high in a tree at the Massif de la Hotte of the Haitian Tiburon Peninsula, southwestern Haiti (Hedges & Thomas 1987).

Eleutherodactylus dolomedes (Figure 52) (Hedge's Robber Frog, Hispaniolan Ventriloquial Frog), likewise from Haiti, is difficult to locate, even when it is calling. It is a ventriloquist! Its 7-note call sounds a bit like a chirping bird and the ability of this frog to make it sound like the call is coming from somewhere else makes it difficult to locate the frog; its original finders spent an hour locating one calling specimen (Hedges & Thomas 1992).

Figure 52. ***Eleutherodactylus dolomedes***, the Hispaniolan Ventriloquial Frog, sitting on a fern frond in the mountains of Haiti. Photo from mongabay.com © Robin MooreiLCP, for educational use.

It is endemic to the high-elevation (1120 m asl) cloud forest of Massif de la Hotte, Haiti (Frost 2011) and had not been seen since 1991. But it was discovered again in 2010 in the mountains of southern Haiti (Burton 2011). Nevertheless, it is critically endangered. The IUCN report projects a population decline of greater than 80% over the next ten years because of the severe degradation of habitat in Haiti (IUCN 2010). Only 2% of the rainforest there remains.

While it has been recorded from forest edge, this is probably not suitable habitat (IUCN 2010). Eggs are laid on the ground, and it breeds by direct development.

The arguably smallest frog in the world (males 9.6-9.8 mm long, females 10.5 mm long) (Endangered Species

International: The World's Smallest Frog 2011), ***Eleutherodactylus iberia*** (Figure 53), was first discovered in 1996 in Monte Iberia, Cuba (Wikipedia 2010a). It seems to be the smallest known frog in the Northern Hemisphere, whereas the smallest in the Southern Hemisphere is the Gold Frog [***Brachycephalus didactylus*** (formerly *Psyllophryne didactyla*)] from Brazil (Allaboutfrogs.org 2011). Together they are tied for smallest frog and smallest tetrapod in the world. ***Brachycephalus didactylus*** may actually be smaller, with known males averaging 8-9 mm (Estrada & Hedges 1996).

Figure 53. ***Eleutherodactylus iberia***, the smallest known frog in the northern hemisphere, on a leaf. Photograph by Thomas Brown, through Wikimedia Commons.

Eleutherodactylus iberia (Figure 53) lives on the forest floor and requires a high humidity, so it stands to reason that habitats (rainforests) suitable for bryophytes in Cuba are also suitable for this frog (Allaboutfrogs.org). Only two populations are known, both in Holguín Province of eastern Cuba at elevations less than 600 m (Wikipedia 2010), making it critically endangered (Endangered Species International: The World's Smallest Frog 2011). One female has been found guarding a single egg. A small clutch size is common in the tiny frogs (Estrada & Hedges 1996), permitting more energy to be stored in each. It appears that the female of ***Eleutherodactylus iberia*** guards the eggs and may care for the young. Although the young are unknown, Estrada and Hedges (1996) suggest that the young may be as small as those in ***Stumpffia*** (**Microhylidae**), *i.e.* only 3 mm long!

The saga of this frog and its adaptations don't end with being small and inconspicuous. Did you wonder why it has the coloration of a bee or wasp (and a number of other poisonous beings)? This condition, known as **aposemitism**, is the familiar warning coloration that a number of poisonous, often unrelated, organisms share. Once a predator learns to recognize the color mix through a bad experience, it will avoid other potential prey items with that same color mix, just as we avoid several kinds of bees by recognizing the array of black mixed with yellow, orange, or red. It is noteworthy that this color combination prevails from tiny mites to large snakes. But some animals are **mimics**, displaying the colors without the poison or bad taste, thus taking advantage of the bad experiences with the truly nasty ones. These mimics must be in smaller numbers than their **models** (the ones with the real poison/bad taste) so that the predator is more likely to encounter the **model** first. Thus, the black, yellow, and white ***Eleutherodactylus iberia*** (Figure 53) could be a nasty model or an edible mimic.

A slight alkaloid odor among the collected ***E. iberia*** (Figure 53) frogs led Rodriguez *et al*. (2010) to test them and their close relatives in the area for poisonous alkaloids. They discovered that the skin of these frogs is endowed with a variety of poisonous alkaloids. They hypothesized that the poisons might originate from their diet, a convenient way to save your own energy and let someone else make your poisons. Indeed, they found that the diet consisted primarily of mites, ants, and springtails (Collembola). Among the 62 prey items in the gut, 71% were mites. Mites are known to contribute toxins used by other amphibians as skin toxins.

It appears that miniaturization in many of these frogs has been accompanied by a diet where mites play a major role (Caldwell 1996; Vences *et al*. 1998; Saporito *et al*. 2004; Rodriguez *et al*. 2010). Becoming smaller means the food items must also be smaller, and a smaller tongue can't reach as far to catch things. This switch to mites has resulted in the source of the sequestered alkaloids. Given the primary sources of food for ***E. iberia*** (Figure 53) – mites, ants, Collembola – one would expect these frogs to find bryophytes a particularly suitable foraging location because bryophytes often serve as a habitat for large numbers of these food items. Hence, tiny frogs most likely eat tiny mites that live among the tiniest of plants, the bryophytes.

This still very large genus of very tiny frogs in the **Eleutherodactylidae** extends from the ground to the treetops. The morphological variations also change through this vertical range, as shown by the ground to treetop array of ***Eleutherodactylus unicolor unicolor***, ***Eleutherodactylus wightmanae***, ***E. brittoni***, ***E. richmondi***, ***E. locustus***, ***E. antillensis***, ***E. portoricensis***, ***E. coqui***, ***E. cochranae***, ***E. gryllus***, and ***E. hedricki*** (Figure 54), with toe pads becoming larger as the height in the tree increases (pers. comm. Father Alejandro Sanchez, 24 February 2011). Although the moss often becomes dry and brittle, it serves as a suitably moist site for eggs in their season in the cloud forest.

In the Luquillo Experimental Forest of Puerto Rico, the well-known Coqui (***Eleutherodactylus coqui***; Figure 55-Figure 59) does a daily migration that must itself be a significant feat as they attempt to avoid predation by the whip scorpion ***Phrynus gervaisii*** (=*Phrynus palmatus*) (Formanowicz *et al*. 1981), tarantulas, snakes, screech owls, and other birds (Stewart 1985). At dusk the Coqui climb the tree trunks to search for food in the canopy. Often within minutes of peak climbing, the arachnid predators make their appearance. During this time, most adult male **Coqui** remain on understory call sites, but the others typically engage in this migration. At daybreak, the frogs return to the ground quickly by parachuting downward. A dry atmosphere reduces the number of frogs making this nightly migration. It appears that mosses contribute to the choice of climbing trees: those with more than 10 climbing frogs had either rough bark or the bark was covered with mosses. Could this correlation be due to hiding advantages, greater moisture, or both?

Figure 54. Toe pad sizes as they increase from ground level (**top left**) to treetop (**bottom right**) in the ***Eleutherodactylus***, a genus whose members commonly lay their eggs among the bryophytes.
Top from left to right: ***Eleutherodactylus unicolor***, ***Eleutherodactylus wightmanae***, ***Eleutherodactylus brittoni***,
Second row from left to right: ***Eleutherodactylus richmondi***, ***Eleutherodactylus locustus***, ***Eleutherodactylus antillensis***,
Third row from left to right: ***Eleutherodactylus portoricensis***, ***Eleutherodactylus coqui***, ***Eleutherodactylus cochranae***,
Fourth row from left to right: ***Eleutherodactylus gryllus***, ***Eleutherodactylus hedricki***.
Photos by Father Alejandro J. Sánchez Muñoz, with permission.

Figure 55. **Coqui**, ***Eleutherodactylus coqui***. Photo by Father Alejandro J. Sánchez Muñoz, with permission.

Figure 56. Coqui (***Eleutherodactylus coqui***) with eggs in a bromeliad basin. Photo by Rafael I. Marquez, with permission.

Figure 57. ***Eleutherodactylus coqui*** in its nest under mosses as it was uncovered on a tree in El Yunque, Puerto Rico. Photo by Father Alejandro Sanchez, with permission.

Figure 58. ***Eleutherodactylus*** with a set of eggs from an unknown species in the genus. Photos by Father Alejandro Sanchez, with permission.

Figure 59. ***Eleutherodactylus coqui*** eggs with a fully formed frog emerging from an egg. Photo by Father Alejandro Sanchez, with permission.

In a different Puerto Rican study, Drewry and Rand (1953) reported members of ***Eleutherodactylus*** (*sensu lato*; Figure 60-Figure 61) in high elevation mossy forests and the upper montane forest just below it. In Haiti, ***Eleutherodactylus limbensis*** spent the night on the wall of a ravine where there was a lush growth of moss (Lynn 1958).

Eleutherodactylus longipes (Figure 60) is endemic to Mexico. Its natural habitats are temperate, subtropical, or tropical dry pine-oak forests, subtropical or tropical moist montanes, and caves from 650-2000 m asl (Santos-Barrera & Canseco-Márquez 2010). It is threatened by habitat loss.

Eleutherodactylus gryllus (Cricket Coqui) is endemic to Puerto Rico. It lives in forest edge habitats or openings of subtropical or tropical moist lowland forests and subtropical or tropical moist montanes at 300-1182 m asl (Hedges & Rios-López 2008). During the day it hides in bromeliads or under mosses or rocks. Males call from bromeliads, most intensely at dawn (Villanueva-Rivera 2005), and eggs are laid in bromeliad basins, but development is direct into hatching froglets (Hedges & Rios-López 2008).

Figure 60. ***Eleutherodactylus longipes*** from ca. 2590 m on the N side of Cerro Pena Nevada near the community of Dulces Nombres in SE Nuevo Leon, Mexico (pers. comm. from Timothy Burkhardt, 17 February 2011). This frog may be taking advantage of the damp moss while blending in with the white lichens. Photo by Timothy Burkhardt <www.mexico-herps.com>, with permission.

Figure 61. ***Eleutherodactylus gryllus*** (Cricket Coqui) from El Yunque National Forest, Puerto Rico, sitting on a leaf covered with epiphyllous bryophytes. Such leaves are likely to maintain higher moisture levels than leaves without epiphyllous bryophytes. And these epiphylls are almost certainly liverworts. Photo by Luis J. Villanueva-Rivera, with permission.

To many people, ***Eleutherodactylus planirostris*** (Greenhouse Frog; Figure 62) is best known as an alien in greenhouses, where it was introduced in potted plants. ***Eleutherodactylus planirostris*** occurs in Cuba, the Bahamas, Grand Cayman, and Cayman Brac (AmphibiaWeb 2011). It has been introduced to Jamaica, and to Florida, Alabama, Georgia (Winn *et al.* 1999), Louisiana (Platt & Fontenot 1993), and Hawaii (Kraus *et al.* 1999), USA, and to Guam (Christy *et al.* 2007). Its altitudinal range is from sea level up to 727 m asl (AmphibiaWeb: *Eleutherodactylus planirostris* 2011).

Figure 62. ***Eleutherodactylus planirostris*** (Greenhouse Frog) on moss. Photo by Brian Gratwicke, through Creative Commons.

In Gainesville, Florida, USA, males of ***E. planirostris*** (Figure 62) call from April–September; breeding occurs under moist cover from late May to late September, peaking in July (Carr 1940; Goin 1947). Its 3-16 eggs are laid in moist depressions in the earth or in moist debris (Goin 1947; Lazell 1989; Bartlett & Bartlett 1999). These experience direct development and hatch as miniature froglets (Lazell 1989; Bartlett & Bartlett 1999) in June in Gainesville (Goin 1947) and from late May to early June in Key West, Florida (Lazell 1989). The adults are secretive and nocturnal except on warm, overcast, or rainy days (Carr 1940; Bartlett & Bartlett 1999). Their food depends on availability. In Florida they eat ants, beetles, and roaches, as well as other types of small invertebrates (Goin 1947; Duellman & Schwartz 1958; Lazell 1989). In Jamaica, they did not eat roaches, but instead ate numerous ants, mites, spiders, and harvestmen (Stewart 1979). In Hawaii, with densities in places of 12,500 frogs ha^{-1}, they have been known to consume up 129,000 invertebrates ha^{-1} $night^{-1}$ (Olson *et al.* 2011).

Diasporus hylaeformis (Pico Blanco Robber Frog; Figure 63), previously known as *Eleutherodactylus hylaeformis*, is a nocturnal species that lives at 1,500-2,500 m, where it can be found among the mosses and low vegetation in its native Costa Rica and Panama (Savage 2002). It includes mosses as egg-laying sites. Unlike most of the small bryophyte-dwelling frogs in the tropics, this one is relatively abundant and not endangered.

Figure 63. ***Diasporus hylaeformis*** among vegetation. Photo by Angel Solis, with permission.

Summary

Little seems to be known about treefrogs and their use of bryophytes, but it seems likely that bryophytes provide moisture and safe sites in an otherwise dry arboreal habitat. Life cycles are modified to accommodate the terrestrial habitat, including caring for eggs, carrying the eggs, supplying new eggs to tadpoles for food, and emergence of fully formed frogs from the eggs. Many of the tree frogs are tiny (including the smallest tetrapods) and produce only one to a few large eggs. Most have cryptic coloration that makes them nearly invisible among the bryophytes. Tubercles seem to aid some in camouflage. Some, however, have bright colors that advertise that they are poisonous (**aposemitism**), a result of their diet of ants, beetles, and/or mites that live on the ground or among the bryophytes.

Arboreal frogs have special behavioral and morphological adaptations to their lofty habitat. Females may sit on their eggs or carry them on their backs. Some lay eggs on low leaves where the young can fall into the river. Toe pads in ***Eleutherodactylus***, and probably other genera, increase in size as the habitat becomes more arboreal.

Cloud forests and other mossy habitats, especially in the tropics, house a large number of species of small to medium frogs. Some frogs hide deep within mosses to make their mating calls. Many lay their eggs on mosses. Like the treefrogs, these are poorly known and their relationships to mosses are often just speculation. They, like the treefrogs, have adaptations in their life cycles that conserve moisture for the eggs and tadpoles, including live birth of froglets or carrying tadpoles on their backs.

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