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CHAPTER 14-1
AMPHIBIANS: ANURAN ADAPTATIONS

Janice M. Glime and William J. Boelema

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Figure 1. ***Dendrobates tinctorius*** (Dyeing Poison Frog), perched on a bed of mosses. Many species in the tropics use bryophytes to maintain hydration. This species is named for the use of the poisons in its skin. Its specific name, *tinctorius*, refers to the way indigenous tribes of Amerindians of the Amazon drainage and the Guianas rub the frogs' skin or blood onto the skin of plucked parrots, toxifying the skin and causing the new feathers to develop with a variety of different colors (Métraux 1944). Photo © Henk Wallays, through Creative Commons.

Bryophytes and Amphibians Share Commonalities

In searching for information on bryophytes and their amphibian inhabitants (frogs, toads, salamanders; Figure 1), I ran into Wachman's (2010) interesting question: "In what way are the bryophyte plants and the amphibian animals alike?" Wachman points out that bryophytes have shared the planet with amphibians since the Carboniferous era. Both are transitional organisms from living entirely in water to living at least part of their life cycle on land, a shift that occurred around 360–290 mya. Wachman claims both need a moist environment (I think most bryologists would take exception to that claim, and many treefrogs likewise have found ways around that requirement, although they do use mosses and other moist places to keep their skin moist). While it is true that most amphibians must find water to reproduce, this can be the basin of a bromeliad or tree hole, and a number of them lay their eggs on mosses or other vegetation in trees or on the ground.

Bryophytes need water to maintain the viability of their male gametes (sperm) while they travel to female reproductive organs, taking advantage of rainwater or dew in most cases. Both bryophytes and most amphibians have two distinctive phases of development – bryophytes have haploid leafy gametophytes and diploid sporophytes with a capsule; amphibians have larvae (not always free-living; usually known as tadpoles in frogs and toads) and adults. (But certain salamanders are neotenic in that they stay aquatic and have gills all their lives. Newts have three life phases: larva, then eft, then aquatic adult. They are somewhat able to go back to the eft stage if the standing water disappears – their skin becomes less permeable to water.) And both bryophytes and amphibians thrive best when far from populated areas. But bryophytes seem to be well armed against disease by their secondary compounds, whereas amphibians seem very susceptible to diseases. Since bryophytes are able to grow well in some areas, becoming a major part of the flora, it is to their credit that they provide cover and moisture for the amphibians there.

But in one way, bryophytes differ greatly from amphibians. Bryophytes have tolerance to extreme cold, occupying the northernmost and southernmost locations on the planet, sometimes even surviving on glaciers, whereas amphibians have very poor cold tolerance and most cannot occupy areas with permafrost. In central Alaska, only the Wood Frog (***Lithobates sylvaticus***) and Boreal Toad (***Anaxyrus boreas boreas***) occur, surviving the winter buried in frozen mud (National Park Service 2013).

Anura – Frogs and Toads

The tailless amphibians (Figure 1) are in the order **Anura**, a word that literally means without a tail. These include the frogs and toads. Most of the more familiar temperate frogs were included in the family **Ranidae** in the genus ***Rana***. The family occurs on all continents except Antarctica. However, only the Australian Wood Frog (***Hylarana daemeli***) represents this family in Australia, where it is restricted to the far north. The family has been revised and many of the familiar species are no longer in the genus ***Rana***.

Standard English names used here are according to Crother (2008) for North American species. **Common names** are local and not at all standardized, whereas the **Standard English names** have legal standing through an official published list (Crother 2007, 2008). Scientific (Latin) names are based on Frost (2011), using classification concepts based largely on recent molecular studies. Where possible, I have tried also to provide the older, more familiar names.

Ranid frogs range in size from the Wood Frog (***Lithobates sylvaticus***, previously *Rana sylvatica*; 2.5-7 cm long; Figure 2) to the Goliath Frog (***Conraua goliath***; up to 45 cm long).

Figure 2. ***Lithobates sylvaticus*** on a bed of mosses, the smallest of the "true" frogs (Ranidae). Photo © John White, with permission.

Role of Bryophytes for Anurans

Amphibians utilize bryophytes in a variety of ways, from nesting sites to substrata for maintaining or replenishing moisture to perches for calling to winter hibernacula. One of the more amazing discoveries I have made is to pick up a moss clump in late fall and discover a torpid toad beneath it. Indeed, many herpetologists seek out mossy sites when they are on amphibian hunts, as I well remember from my undergraduate days when I had the privilege to go in the field with a well-known **herpetologist** (one who studies amphibians and reptiles). But often the use of the bryophytes is passive or difficult to perceive. The bryophytes grow in the same sorts of habitats where these amphibians can survive, but does the bryophyte really contribute?

The evidence of bryophyte-amphibian interaction is modest and experiments to demonstrate the importance of the bryophytes are all but non-existent. Most of the reports on anurans only mention bryophytes casually. For example, Bosch and Martínez-Solano (2003) describe the factors that influence the presence of montane frogs in ponds and describe their study area as having moss with underwater caves. In many of the contacts I have made with herpetologists they have commented that the area (especially in the tropics) was covered with bryophytes and that surely the frogs make use of that habitat, but often published documentation is lacking. Nevertheless, it appears that loss of bryophytes could seriously impair many species in this highly vulnerable group of vertebrates that already are disappearing from the planet at an extraordinary rate.

Bryophytes provide a number of possible advantages to the anurans. For the tiny species, the bryophytes may be a full-time or part-time home where they can move about unseen by large predators like birds. As we wend our way through the many species that have been collected among the bryophytes, we will find that they provide mating and nesting sites, cover, calling sites, oxygen under water, and even food sources – both as food themselves and as sites for more traditional food items.

Bryophytes harbor many endangered species whose disappearance will increase with the loss of the bryophyte habitat. Some of these are tiny tropical anuran species that have not even been identified or named. Those that stay within the bryophyte mat are the least likely to have been collected (except perhaps by bryologists☺). Many occur on the IUCN (2011) list of endangered species.

Safe Sites

Safe sites, sometimes also known as predator-free sites, are important for amphibians, especially when they are calling or hibernating or nesting. Anurans are vulnerable to all sorts of predators, depending on their size. Large ones can suffer a brutal death by ducks that beat them to death on the water surface. Small ones can even become prey to insects, including those that can inhabit bryophytes, both on land (Figure 3) and in the water (Figure 4), or spiders (Figure 5) that lurk on ground and in the trees. Snakes lurk among the branches and leaf litter (Figure 6-Figure 7). For the amphibians, having colors of green, brown, and black can protect them when living among bryophytes, serving as camouflage. Furthermore, a large number of would-be predators are unable to maneuver among the small spaces provided among the bryophyte branches and leaves. Hence, for small frogs and salamanders the bryophytes provide safe sites. And for winter even larger amphibians can hide under them.

Figure 3. ***Pristimantis ridens*** that has fallen prey to an ant. This tiny frog most likely would have been just as vulnerable to ants within a mat of bryophytes, but would perhaps have been less obvious during its movements. Photo by Tobias Eisenberg, through Creative Commons.

Figure 4. ***Dytiscus*** (diving beetle) larva attacking the frog ***Xenopus***. This freshwater larva can be a threat to small frogs and tadpoles in pools and lakes. Photo by Brian Gratwicke, through Creative Commons.

Figure 5. Toad being eaten by spider in Costa Rica. Photo by Brian Gratwicke, through Creative Commons.

Figure 6. The Lora or Parrot Snake (***Leptophis ahaetulla***) eating the Evergreen Robber Frog (***Craugastor gollmeri***) with a much greater diameter than the snake. Photo by Brian Gratwicke, through Creative Commons.

Figure 7. ***Craugastor gollmeri***, a species adapted primarily for leaf litter, and resembling leaves. Photo by Brian Gratwicke, through Creative Commons.

Moisture and Temperature Conservation

Frogs and toads must maintain **moisture** without drowning, and mosses can provide that balance. As lung and skin breathers, it is more difficult for most anurans to obtain oxygen in water than in air, but the skin must remain moist to keep the cells functional and pliable. The moisture and temperature of the frogs are also important in attaining maximum jumping distance to avoid predators (Walvoord 2003).

Mosses can provide a moist environment at times when other habitats might be dry, playing a major role in the moisture conservation of many amphibians. Mazerolle (2001) demonstrated that the Wood Frog (***Lithobates sylvaticus***; Figure 2) had more predictable activity, based on weather, near the fragmented edges than in pristine bogs. This greater activity seemed to be more related to the amount of precipitation in the fragments than it was in the bogs, suggesting that the bogs are able to buffer the moisture changes for the frogs living there.

Walvoord (2003) demonstrated that for Cricket Frogs (***Acris crepitans*, Hylidae**) maximum jumping distance requires maintenance of appropriate interplay between

temperature and hydration. In lab experiments at 30°C, jumping distances of frogs at hydration levels of 85-95% significantly exceeded those at 75%. Furthermore, when the temperature was lowered to 15°C, the frogs had significantly poorer performance. However, at 15°C and 85% hydration, the frogs jumped as well as those at 95% hydration at 30°C. Air temperature was the best predictor of frog body temperature, and sky condition (sunny, cloudy) was the best predictor of hydration. The frogs are able to behaviorally modify their body temperature and their hydration to near optimum by choosing their location, thus permitting them maximal jumping distance and increasing their chances to avoid predators. In the field, the mean body temperature of 55 Cricket Frogs was 28.0°C and hydration was 97.4%. As we shall see, some frogs burrow into mosses during the day or go underground or under mosses, presumably optimizing their temperature and state of hydration.

Calling Sites

In anurans, calling by males is used as a means to attract females. But it also calls attention them by would-be predators (not to mention humans). In the cypress swamps of Georgia, USA, frogs often perch on mounds of moss in summer, using these as locations for breeding calls (Wright 2002), and possibly increasing the distance the call will travel by using an elevated location. But in the tropics, calling sites are often elevated on tree branches and leaves (Figure 8), or even located **within** bryophyte clumps. Presumably, this affords a place to hide while the frog is otherwise making itself more noticeable by calling.

Figure 8. ***Eleutherodactylus eileenae*** (Eileen's Robber Frog) perched on a tree leaf in Cuba to call during breeding season. Photo by Ariel Rodríguez, with permission.

One of the common genera calling from within mosses is ***Bryophryne*** (Figure 9). In southern Peru, at elevations of 3800-3850 m asl, Lehr and Catenazzi (2010) found ***Bryophryne abramalagae*** **(Strabomantidae)** calling from inside Peruvian feather grass clumps and in mosses at 11:00-13:00 hours. Likewise in Peru, ***Bryophryne cophites*** (Figure 9) calls from within moss clumps, despite its absence of a **tympanum** (exposed outer surface of ear drum).

Figure 9. ***Bryophryne cophites*** on a bed of mosses. Note the absence of a tympanum, the external evidence of an ear. Photo by Alessandro Catenazzi, with permission.

In the same location as ***Bryophryne abramalagae***, ***B. flammiventris*** called at 10:00-16:00 hours, again from within large moss mats (Lehr & Catenazzi 2010). Another species of ***Bryophryne*** (***B. gymnotis*;** Figure 10) and a different genus of strabomantid (***Psychrophrynella*** sp.; Figure 11) also call from moss hideouts. These calls were often heard from the opposite side of the valley, suggesting that the moss cover was likely to be an important safe site during calling, protecting them against detection and possible predation when they were making such loud sounds.

Figure 10. ***Bryophryne gymnotis***, a Peruvian frog that calls from within moss mats. Photo by Alessandro Catenazzi, with permission.

In Bolivia, as in Peru, the genus ***Psychrophrynella*** (syn. = *Phrynopus***)** (**Strabomantidae**, formerly in Leptodactylidae) has a number of species that call from mosses (De la Riva 2007). At Cotapata, ***P. guillei*** begins as the mist rolls over the vegetation, calling from 5-10 cm deep within the mosses. ***Psychrophrynella iani*** calls from under stones and among the mosses. ***Psychrophrynella iatamasi*** (Figure 11) seems to stay in the forest floor mosses for its daytime calling (Aguayo & Harvey 2001). All of the Bolivian **páramo** ***Psychrophrynella*** species seem to call from secluded places such as mosses, with time of day or night depending on the species. The

páramo (Figure 12) is a misty alpine plateau with stunted trees and wide daily temperature fluctuations, creating a severe habitat. Luteyn (2011) describes the páramo as high, cold, inhospitable, wind and rain swept. I think I would seek shelter too.

Figure 11. ***Psychrophrynella*** (=*Phrynopus*) ***iatamasi*** on a bed of mosses. Photo by Ignacio de la Riva, with permission.

Figure 12. Chingaza páramo in the Eastern Cordillera of the Andes, Colombia. Photo by Andres Baron Lopez, with permission.

Peru seems to be one of the best-studied tropical countries for calling sites. ***Gastrotheca pacchamama*** (Ayacucho Marsupial Frog, **Hemiphractidae**; see Figure 13) males were found during the day, calling from moss-covered talus (Duellman 1987).

Figure 13. ***Gastrotheca testudinea***. Photo by Tiffany Kosch, with permission.

In east of Tanzania, from the moss forests at the summit of Morne Seychellois (1000 m), ***Sooglossus*** (=***Nesomantis***) ***thomasseti*** (**Sooglossidae**; Figure 16) calls from under objects, on cliff faces and boulders. Naomi Doak (pers. comm. 24 February 2011) reports that the three species of sooglossids that she studied [***Sooglossus sechellensis*** (Figure 14), ***S. gardineri*** (Figure 15), ***S. thomasseti*** (Figure 16)] call from mosses, and despite sooglossids being ground-dwelling frogs, they sometimes call from mosses on tree trunks.

Figure 14. ***Sooglossus sechellensis***, a species that sometimes calls from epiphytic mosses. Photo by Naomi Doak, with pernission.

Figure 15. Perhaps the world's tiniest frog, ***Sooglossus gardineri*** sits on a bed of moss in the Seychelles. Photo by Naomi Doak, with permission.

Figure 16. ***Sooglossus thomasseti*** sometimes calls from mosses on tree trunks. Photo by Naomi Doak, with permission.

In New Guinea, ***Choerophryne*** species (**Microhylidae**) call from steep, mossy-covered rocky cliff faces, as well as the forest floor and leaves of shrubs (Kraus & Allison 2001).

In a temperate forest in southern Chile, ***Eupsophus emiliopugini*** (Figure 17) (**Cycloramphidae,** formerly in Leptodactylidae**)** and its close relatives excavate burrows in mosses in bogs, from which they make their calls (Penna *et*

al. 2005). This species also calls from burrows hidden in the moss ***Racomitrium*** (Figure 18-Figure 19) and grasses or ferns on the margins of small streams. Stimuli from calls of nearest neighbors increase the calling intensity, creating a chorus, hence making a larger concentration of frogs that is advantageous for mating.

Figure 17. ***Eupsophus emiliopugini*** on a bed of mosses, probably ***Racomitrium*** sp. Photo by Rafael I. Marquez, with permission.

Figure 18. ***Racomitrium lanuginosum*** in Europe. Photo by Michael Lüth, with permission.

Figure 19. ***Racomitrium lanuginosum*** showing spaces where tiny frogs can hide while they call. Photo by Michael Lüth, with permission.

Males of ***Eupsophus calcaratus*** (Figure 20) use cavities within mosses to alter the resonance of their calls (Márquez *et al*. 2005). Hence, the females learn to recognize the resonance characteristics of the mossy burrow-like cavities where the males call. This moss cavity resonance contributes to the recognition by females of the males of their own species in an environment where several species may be calling at the same time.

Figure 20. ***Eupsophus calcaratus***, a frog that uses cavities among mosses to modulate its call resonance. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

It is somewhat of a surprise to find that a Macaya Burrowing Frog (***Eleutherodactylus parapelates***, **Eleutherodactylidae**, formerly in Leptodactylidae) 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). Many members of this genus call from mosses on the ground or on trees (*e.g.* ***E. richmondi***, Figure 21). One must interpret general references to the genus ***Eleutherodactylus*** with caution. This genus has recently been divided based on molecular evidence and some members now reside in different families and genera.

Even the larger frogs, in Ranidae, may call from within moss mats. In southwestern Sulawesi, Indonesia, ***Limnonectes*** (=***Rana***) ***arathooni*** calls from 4-10 cm depths within mosses, as well as from leaf litter and rotting roots (Brown & Iskandar 2000).

Figure 21. ***Eleutherodactylus richmondi*** calling from a bed of mosses. Note the really narrow toes that would be of little help in swimming. Photo by Luis J. Villanueva-Rivera, with permission.

Nesting and Reproduction

Some frogs and toads make use of bryophytes as **nesting sites**. Many more species for which the nesting sites are unknown, especially in the tropics, are likely to make use of bryophytes. Altig and McDiarmid (2007) described the arrangement of deposited eggs in amphibians, stating that semiterrestrial eggs need a source of free water without being submerged. Mosses at the edge of a bog or seepy talus often fulfill this need, where some frogs deposit their eggs in wet moss (McDiarmid & Heyer 1994). When the larvae of these species hatch, they do not feed, and they undergo their development right there in the moss bed.

For example, in the Philippines ***Limnonectes* (=*Rana*) *magnus* (Dicroglossidae)**, which is threatened by habitat loss, lays her eggs on rocks and moss (Wells 2007). ***Limnonectes*** (=***Rana***) ***leytensis*** (Swamp Frog, **Dicroglossidae;** Figure 22) also occurs in the Philippines, where it is endemic. The female most frequently deposits her eggs on mosses attached to roots or rocks, although she may also use leaves (Alcala 1962). Males call from the nest and guard the nest until the tadpoles hatch. By placing the eggs near the water, the female provides for the tadpoles to be washed into the water by rain – or to scramble there when disturbed.

Figure 22. The Swamp Frog, ***Limnonectes leytensis***. Photo by Wouter Beukema, with permission.

Frogs that call from mosses often lay their eggs there as well. Figure 23 shows ***Bryophryne cophites*** (**Strabomantidae**) tending her eggs on a bed of moss, perhaps at the same place the male has called to her.

Figure 23. ***Bryophryne cophites*** tending a clutch of eggs laid among mosses. Photos by Alessandro Catenazzi, with permission.

Experimental observations on ***Sooglossus gardineri*** (**Sooglossidae**; Figure 15), an endemic species from the moss forests of Mahe, Seychelles, suggest that wet substrata may be preferred in that species (Nussbaum 1980). In terraria, all observed **amplexus** (mating stage in which a male amphibian grasps a female with his front legs prior to depositing sperm on her eggs; Figure 24) occurred on damp paper towels or mosses. This is one of the tiniest frogs in the world at 9-12 mm long. This small size suggests that it would easily be at home within the epiphytic and ground bryophytes in the mossy forests where it lives. Fortunately, it is relatively widespread in the Seychelles and is not endangered in the way many of these tiny frogs are.

Figure 24. ***Hylarana temporalis*** in amplexus. The smaller frog on top is the male. Photo by Sandilya Theuerkauf, through Wikimedia Commons.

Living in a tree has unique environmental problems for young tadpoles that can't escape or change environmental conditions by swimming. Some species, like tree-dwelling ***Sooglossus seychelles***, have solved the problem by carrying the tadpoles on their backs (Figure 25). Bryophytes in their habitat may help to maintain their moisture.

Figure 25. ***Sooglossus sechellensis*** carrying its tadpoles on its back. Photo by Naomi Doak, with pernission.

Limnonectes* (=*Rana*) *arathooni (Djikoro Wart Frog, **Dicroglossidae)** in Indonesia, where it is endemic (BioDiversity Hotspots), deposits eggs under 4-10 cm of mosses, leaf litter, and rotting roots (Brown & Iskandar 2000). The male guards the eggs until they hatch and calls from within the nest while sitting on top of the eggs. When disturbed, nearly mature larvae can rapidly emerge from

the eggs and bounce down rocks, banks, etc to reach the nearby stream water. A further advantage of these streamside nest sites is that the splash of water from the stream keeps them humid, a necessity for these eggs and hatchlings. The height above the water protects the eggs from being washed away during high water periods. ***Limnonectes poilani*** (Figure 26) lives in streams and along their borders in the highlands of central and southern Vietnam and eastern Cambodia. As shown in Figure 26, bryophytes are often common in these habitats.

Figure 26. ***Limnonectes poilani*** **(Dicroglossidae)** on bryophytes in a stream, where its coloration matches that of the rocks. This is a member of a genus that often lays eggs among streamside mosses. Photo by W. Djatmiko, through Wikimedia Commons.

A Cuban species of the widespread bryophyte inhabitant ***Eleutherodactylus*** **(*E. rivularis*;** Figure 27), laid its eggs, a clutch of 42, 4 m from the edge of the Jibacoa River at Las Mercedes (Díaz *et al*. 2001). These eggs where in a hole that had been excavated, presumably by the frog, under a piece of cloth and "moss sheaths."

Figure 27. ***Eleutherodactylus rivularis*** calling to attract a female. Photo by Ariel Rodríguez, with permission.

Many tropical treefrogs deposit their eggs in mosses. The extent of these occurrences is not well documented, and almost no experimental evidence exists to demonstrate any preference. ***Dendropsophus sarayacuensis*** (formerly *Hyla sarayacuensis*; **Hylidae**) (Shreve's Sarayacu Treefrog; Figure 28) from Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela will lay its eggs on either leaves (Figure 29-Figure 30) or moss-covered trees (Henzi 1987).

Figure 28. ***Dendropsophus sarayacuensis*** (Shreve's Sarayacu Treefrog) is adapted by its coloration to sitting on a tree branch and looking like lichens or dying leaves that have insect damage. Nevertheless, it also uses mosses as egg-laying substrate. Photo by Andreas Schlüter, through Wikimedia Commons.

Figure 29. Eggs of ***Dendropsophus sarayacuensis*** hanging from the underside of a leaf. Note how easily these masses can break and "drip" the froglets to the ground or water beneath. Photo by Andreas Schlüter, through Wikimedia Commons.

Figure 30. ***Teratohyla*** (formerly *Cochranella*) ***spinosa*** (**Glass Frog**) eggs dripping. Photo by Brian Gratwicke, through Creative Commons.

In North America, the east coast of the USA has several terrestrial species. Among these, we know that the Chorus Frog (***Pseudacris feriarum***; Figure 32) (central Pennsylvania inland south to southern Alabama and Georgia) deposits eggs in February to mid-May at the edge of wet patches (ponds and marshes), often on mosses (Livezey & Wright 1947).

Figure 31. ***Teratohyla*** (formerly *Cochranella*) ***spinosa*** (Glass Frog) on a leaf covered with lichen and liverwort epiphytes. Epiphytes hold moisture and help to keep the frogs moist. Photo by Brian Gratwicke, through Creative Commons.

Figure 32. ***Pseudacris feriarum***, a Chorus Frog that often deposits its eggs on mosses. Photo by John D. Willson, with permission.

The genus ***Mantella*** (Malagasy Poison Frog, Mantellidae) is endemic to Madagascar. It lays clutches of up to 130 eggs that are deposited under moss layers and other hidden places in their captive terrarium, but nesting behavior in the wild may differ (Glaw et al. 2000). ***Mantella laevigata*** (Figure 33) are **oophages** – they eat tadpole eggs, and these may be delivered to them by adult females, providing a type of parental care. Members of the genus ***Mantella*** frequently hybridize with each other, suggesting they aren't quite species yet (see Figure 34 for a member of this group).

Figure 33. ***Mantella aurantiaca*** (golden mantella) on a bed of bryophytes. Photo by Robert Lawton, through Wikimedia Commons.

Overwintering

Many frogs and toads use bryophytes for **cover** from cold and drought, especially in winter or dry weather. It is not uncommon to pick up a moss clump late in the fall and find a hibernating frog or toad under it (personal observation). For some frogs, the bryophytes are a hiding place, and an array of adaptive coloration patterns helps to disguise these amphibians, especially among the tree frogs, as discussed later.

Peatlands may be important temperature mediators for amphibians. Their openness permits warming in the sun, but their branches with air spaces provide a thick insulation from both heat and cold. Toads in north central Alberta, Canada, take advantage of this temperature buffering for hibernation locations (Browne & Paszkowski 2010). In the boreal forest there, 14 out of 21 hibernation sites were in cavities in peat hummocks (Table 1). Other locations were decayed root channels and red squirrel middens (refuse heaps).

Figure 34. ***Mantella expectata***, a species known to hybridize with ***Mantella laevigata***, on a bed of bryophytes. Photo by Paddy Ryan, with permission.

Peatlands in northern areas are known to freeze down to 80 cm. Toads are known to die at temperatures between

-1.5 and -5.2°C (Swanson *et al*. 1996). It is noteworthy that the hibernacula selected by toads in north central Alberta, Canada, rarely or never had temperatures below -5.2°C (Browne & Paszkowski 2010; Table 1). Furthermore, the toads hibernated in communal groups of up to 29 toads, most likely providing further insulation that was not detected by the temperature recorders, although groups of 2-5 were more common. By regularly exchanging positions, they could keep each other from freezing.

The importance of these sites is suggested by their use at distances ranging up to 1020 m from the breeding pond (Browne & Paszkowski 2010). It is likely that the insulation supplied by these peatland sites is crucial for overwintering in these northern sites that mark the limits of tolerance for temperature in ***Anaxyrus***. At the boreal forest site, the toads had a significantly higher selection for black spruce/tamarack stands than for other available habitats, with 79% of the toads hibernating there. Thus it appears that the peat/moss configuration of the forest floor provides the most important overwintering habitat in these northern locations.

Table 1. Site temperature characteristics of paired hibernation and reference sites for Western Toads (***Anaxyrus boreas***). Modified from Browne & Paszkowski 2010.

hibernation or reference	shelter type	depth (cm)	min (C)	consecutive days <0C	<-1.5C	<-5.2C
hibernation	red squirrel tunnel	45	-2.44	176	0.7	0
reference	organic soil under spruce	45	-1.06	154	0	0
hibernation	peat hummock cavities	53	-2.40	149	4.7	0
reference	peat hummock, no cavities	53	-3.37	176	22.2	0
hibernation	burned peat, cavities	47	-8.38	191	10.7	0.6
reference	burned peat, cavities	47	-1.40	163	0	0
hibernation	peat hummock, cavities	62	-9.46	175	41.9	3.2
reference	peat hummock, cavities	62	-6.31	150	21.7	0.7

Undulating Mosses and *Lithobates* (=*Rana*) *sylvaticus* (Wood Frog, Ranidae)

Imagine the mosses around you suddenly heaving and rising! The earliest known report of frogs freezing in winter is that of the Arctic explorer, Samuel Hearne (1769 in Hearne 1911). He reported that he frequently saw Wood Frogs, ***Lithobates sylvaticus*** (Ranidae; formerly placed in *Rana*; Figure 35) that were dug up with the moss when they pitched tents. These seemingly dead frogs could be "brought back to life" by wrapping them in skins and warming them slowly by the fire. For ***Lithobates sylvaticus***, the mosses not only ameliorate the temperature fluctuations, but also greatly reduce the water loss (Churchill & Storey 1993). And, these frogs may very well be frozen, only to start hopping around again in the spring! Despite being the smallest ranid, they are the only frog to be found north of the Arctic Circle (Conant & Collins 1998). Unprotected, the frozen frogs could die in 7-9 days from dehydration, so the moss is an important contributor to their survival.

Figure 35. Wood Frog, ***Lithobates*** (=*Rana*) ***sylvaticus***, among woodland **Polytrichaceae**. Photo by Michael Zahniser, through Wikimedia Commons.

It is not surprising that peatlands are one of the habitats providing a winter home for Wood Frogs. (Wikipedia 2008). Richard Andrus relays "a curious thing I've seen with Wood Frogs in our area (Adirondacks, New York, USA). These critters are explosive breeders in vernal pools for which the eggs and tadpoles are susceptible to predation. So they have a need to find pools that won't support larger frogs and fish. Several years ago I was at a floating mat bog in late April just as the ice was melting. There was ice and snow in the spruce forest around the pond but the mat itself had melted. When we reached the open mat we saw literally 1000's of Wood Frogs all over the mat, in the water, and pouring out of the forest. The reason for this huge number was apparently that the *p*H of the water (ca 4.0) was too low for fish and Green Frog tadpoles (***Lithobates clamitans***; Figure 36) but not too low for Wood Frogs (***Lithobates sylvaticus***; Figure 35). So this was a huge 'safety zone' for them to breed without these predators. They were coming from the north side as its southern exposure caused this to warm up first. On a hunch, the very next week I went out to another floating ***Sphagnum*** (Figure 37) mat I knew of and saw exactly the same thing repeated!! So apparently at least this species can escape egg and tadpole predation by using ***Sphagnum***-acidified ponds."

Figure 36. ***Lithobates clamitans*** (Green Frog) sitting on mosses. Photo by Matthew Niemiller, with permission.

Figure 37. ***Sphagnum lindbergii*** and ***S. balticum*** in Alaska. Photo by Matthew Johnson, for fair use.

Cold Water – *Rana temporaria* (Common Frog, Ranidae)

Despite their **ectothermic** (cold-blooded) nature, many frogs are able to survive winters that take them to below freezing (Koskela & Pasanen 1974). ***Rana temporaria*** (the European Common Frog; Ranidae; Figure 38-Figure 39) is not freeze-tolerant (Voituron *et al.* 2009a). Instead, as is common in northern Finland, ***Rana temporaria*** spends its winters under water to avoid freezing (Koskela & Pasanen 1974). From the time these frogs enter their winter habitat until they leave in April (mature individuals) or May (immature frogs), they disappear into the bottom muds or under bottom moss carpets, stones, or other hiding places. They are not in hibernation, and they can become active if disturbed, but they do not feed. When the air temperature exceeds 5ºC, the adult frogs emerge to land, with the juveniles emerging 1-3 weeks later. Following mating, a large mass of eggs with up to 2000 individuals is produced (Peatlands 2009). The eggs hatch into tadpoles within a week. In Northern Ireland the species is declining due to loss of peatlands and other wetlands. Hence, the species has been legally protected from capture for sale.

Figure 38. European Common Frog (grass frog, brown frog), ***Rana temporaria*** (Ranidae). Photo through Czech Wikipedia GNU Free Documentation License.

Figure 39. European Common Frogs, ***Rana temporaria***, amid their eggs at Cambourne, Cambridgeshire. Photo by Brian Eversham, with permission.

Freeze Tolerance – *Rana arvalis*

In contrast to ***Rana temporaria***, ***Rana arvalis*** (Moor Frog, **Ranidae**; Figure 40) is **freeze-tolerant** (Voituron *et al*. 2009a). It spends the winter not in the water, but in the soil under litter or mosses. The juveniles can survive freezing temperatures for about 72 hours at body temperatures of -3°C (Voituron *et al*. 2009b). In nature, they prepare for this when the temperature drops to the range of 4 to -1°C. In this temperature range, glucose increases 14-fold in the liver and 4-fold in the muscles. **Aerobic** metabolism (using oxygen) persists at a low level, decreasing with temperature, thus preventing the toxic conditions that would arise from **lactate** accumulation. Voituron *et al*. (2009b) suggest that their terrestrial habitat beneath mosses and litter layers provides a temperature regime that shortens the time they spend frozen. Allowance for temperatures to -3°C would permit them to live without freezing under the insulation of snow with the added insulation of the litter, including mosses.

Figure 40. ***Rana arvalis*** (Moor Frog) on a bed of mosses. Photo by Petr Balej, with permission.

Despite this cold tolerance, ***Rana arvalis*** (Figure 40) seems to be rare in the Czech Republic (Šandera *et al*.

2008). It requires nearby water with emergent vegetation where it can attach its eggs (Martin Šandera, pers. comm. 20 February 2011). Its breeding period is a short one week, and that is the time it is best to observe it. After that, even if found, it is difficult to identify.

Under Woodland Bryophytes - *Pelophylax* (Ranidae)

Other frogs **hibernate** in woodlands. ***Pelophylax lessonae*** (Pool Frog; Figure 41) and ***P. ridibundus*** (Edible Frog; Figure 42-Figure 43), both formerly placed in *Rana*, leave the ponds to prepare for winter (Holenweg & Reyer 2000). ***Pelophylax esculentus*** (Figure 44) is a hybrid of ***Pelophylax lessonae*** (Figure 41) and ***Pelophylax ridibundus*** (Marsh Frog, also formerly included in *Rana*), (Figure 42-Figure 43), but it is no longer recognized as a separate species by Frost (2011). In the woodlands, members of this frog group hibernate 3-7 cm below the surface, often under mosses, fallen leaves, or soil. Interestingly, they change hibernation sites during the winter, sometimes more than once. They seem able to find warmer spots – the hibernation sites had warmer temperatures than other spots that were sampled.

Figure 41. The Pool Frog (***Pelophylax lessonae***) from Europe. Photo by M. Betley, through Wikimedia Commons.

Figure 42. Marsh Frog, ***Pelophylax ridibundus***. Photo by Christian Fischer, through Creative Commons.

Figure 43. Marsh Frog, ***Pelophylax ridibundus***, with secreted white mucous that is most likely poisonous or distasteful to some of its would-be predators. Photo by Piet Spaans, through Creative Commons.

Figure 44. The Edible Frog, ***Pelophylax esculentus*** group. Photo by Leo Bogert, through Wikimedia Commons.

Bryophytes for Food and Food Locations

Strangely enough, Ting (1950) found that ***Sphagnum*** (Figure 37) mixed with egg yolk could serve as a food source when rearing various species of tadpoles. It has the added advantage of reducing the bacterial growth. Hartmann (1971) discovered that certain mosses produced **neurohormones** that stimulate frog hearts much like the action of **acetylcholine** (and have the same RF value). However, there is no conclusive evidence that mosses serve as an intended food source for adult frogs in nature.

Tadpoles may, however, consume at least some bryophytes in nature. We generally think of tadpoles as being algal and detrital feeders. However, at least in the terrestrial habitat, bryophytes may form part of the diet (Wickramasinghe *et al*. 2007). The semi-terrestrial tadpoles of ***Nannophrys ceylonensis*** (Ceylon Streamlined Frog, **Dicroglossidae**; Figure 45) in Sri Lanka, like most tadpoles, shift from a scraping food strategy as larvae to catching live prey as adults. During their larval stage, algae are an important part of their diet, with the majority of diatoms being ***Selenastrum*** (Figure 46). Surprisingly, in

the population studied by Wickramasinghe *et al*., ***Barbula*** sp. (*sensu lato*; Figure 47) accounted for most of the moss consumption. As the body size increases, the consumption of mosses decreases significantly, as does the consumption of diatoms. At the same time the mosses and diatoms diminish in the diet, so does the gut size. (Longer guts are needed to absorb nutrients from food organisms with cell walls, like algae and mosses.)

Figure 45. ***Nannophrys ceylonensis*** among the small plants of the moss ***Fissidens*** on the rock. Photo by Peter Janzen, with permission.

Figure 46. ***Selenastrum***, an alga that provides food for larval ***Nannophrys ceylonensis***. Photo by Yuuji Tsukii, with permission.

Figure 47. ***Barbula convoluta*** from Europe, member of a genus that can provide food for frogs. Photo by Michael Lüth, with permission.

Stebbins (1955) found the Tailed Frog ***Ascaphus truei*** (Figure 48) (Leiopelmatidae) in company of the Olympic Salamander ***Rhyacotriton olympicus*** under moss-covered rocks along the Pacific coast. Since the seepage where they were found was nearly completely hidden by the mosses, it is not clear that presence of the moss on the rocks was an important habitat consideration or simply that both frogs and mosses preferred the same conditions. But it seems that the two amphibians prefer the same food (Bury 1970). More specifically, young frogs eat a diet similar to that of the salamander. ***Ascaphus truei*** shifts from having mostly **Collembola** in the diet when young to eating more amphipods at older stages. But even when both are eating the same foods, the abundance of food items among the mosses prevents competition. ***Ascaphus truei*** climbs on rocks that are covered with mosses and algae, and Noble and Putnam (1931) suggested that these moss-covered rocks might provide a richer food source than locations within the rapid flow of the stream. Bury (1970) indicated that this habitat of ***Ascaphus truei*** was consistent throughout their range, where they lived in association with "small, water-washed or moss-covered rocks" in running water or along its borders.

Figure 48. Coastal Tailed Frog, ***Ascaphus truei***. Photo by James Bettaso, with permission.

Occasional Usage – A Place to Travel

In Panama, aerial frogs like the Banded Horned Treefrogs, ***Hemiphractus fasciatus*** (formerly ***Cerathyla panamensis*; Hemiphractidae**) (Figure 49-Figure 53) may make indirect or intermittent use of bryophytes. This frog lives among **bromeliads** – those basket-shaped plants that capture water and live in trees (Stejneger 1917). The female ***Hemiphractus fasciatus*** carries her eggs and her young on her back (Myers 1966; Figure 49-Figure 50), suggesting that desiccation could become a problem. The bromeliads are abundant on both trees and the ground, and mosses are frequently present around them. It is difficult to imagine that these frogs do not take advantage of the cover, camouflage, and moisture of the mosses as they move from place to place. At the very least, one might expect to find these frogs when looking for bryophytic treasure on tropical tree branches. However, it appears that this species does not need to hide from many kinds of predators.

Instead, it rears up, arches its body, and throws up its head (Figure 51). The yellowish-orange tongue and large mouth present an imposing image (Figure 53). If a would-be predator makes contact, the frog has further defense by clamping two sharp tooth-like projections (Figure 53) into the attacker and hanging on with a strong grip (Figure 52), a painful experience that Myers knew all too well. The frog had to be pried loose!

Figure 49. ***Hemiphractus fasciatus*** female carrying eggs on her back. Photo by Edgardo J. Griffith, El Valle Amphibian Conservation Center (EVACC), Director, with permission.

Figure 50. ***Hemiphractus fasciatus*** female with juvenile frogs on its back. Eggs are retained in patches until the larvae develop into young adults, then remain for some time with the mother after hatching (Myers 1966). This behavior permits the adult to carry the young to locations with sufficient moisture. Photo by Brian Gratwicke, through Wikimedia Commons.

Figure 51. ***Hemiphractus fasciatus*** rearing up in a defensive position. Photo by Brian Gratwicke, through Creative Commons.

Figure 52. ***Hemiphractus fasciatus*** eating an earthworm. Note the two sharp teeth just to the right of the worm on the lower jaw. Photo by Edgardo J. Griffith, El Valle Amphibian Conservation Center (EVACC), Director, with permission.

Figure 53. ***Hemiphractus fasciatus*** with open mouth, showing yellow tongue and two sharp front teeth (in front lower jaw). Photo by Marcos Guerra, through fair use copyright.

Adaptations to Bryophyte Habitats

It is interesting that so many species of anurans exist sympatrically (same geographic area) in "mossy" habitats such as the mountain tops of tropical areas. Hofer *et al.* (2004) paraphrased Gause's Rule by stating that "If interspecific competition is a strong structuring force of

communities, ecologically similar species should tend to have spatial ranges at local scale that do not overlap." They used collected data to test the hypothesis and were surprised to find that whereas lizards and birds exhibited adjustments that reduced the potential for interspecific competition, the frogs did the opposite – there was a greater than chance co-occurrence of ecologically similar frog species. They suggested that resource requirements such as breeding sites may be more important for frogs than competition.

With this in mind, we can see that bryophytes can play a role in providing breeding sites that maintain moisture and provide cover that contributes to keeping the eggs safe. They furthermore provide moist respites for travelling anurans, and for many species can provide hiding places. Given this usage of bryophytes to define part of the anuran niche, we should expect adaptations to have evolved that make this bryological life somewhat easier.

An Altered Life Cycle

Alcala (1962) divided the tadpoles of anurans into three environmental categories. Stream dwellers have depressed bodies, strong tail muscles, and reduced body and tail fins (Figure 54); pond tadpoles have subspherical bodies, weak tail muscles, and high body and tail fins (Figure 55). Both of these aquatic larvae come from small eggs laid in large clutches. Larvae with direct development (out of water) have altered larval structures, including abdominal sacs instead of gills, and derive from large eggs in small clutches. A fourth category is those anurans that have no tadpoles at all, but that hatch directly into froglets.

Figure 54. ***Atelopus limosus***, showing the flattened body of a stream tadpole. Photo by Brian Gratwicke, through Creative Commons.

Figure 55. ***Paracrinia haswelli*** (**Haswell's Frog**) tadpole showing the high body and tail fins typical of pond tadpoles. Photo through Wikimedia Commons.

In the study area of Negros, Philippine Islands, more than 50% of the eggs are laid out of water (Alcala 1962). Among those in the study, some eggs were attached to mosses growing on rocks above a pool in a mountain stream, including ***Platymantis dorsalis*** (=*Cornufer meyeri*; **Ceratobatrachidae**; Figure 56) whose adults live on the montane forest floor, sometimes under moss mats.

Figure 56. ***Platymantis dorsalis***, a frog that seeks refuge under moss mats on the forest floor. Photo by Amir Hamidy, with permission.

Food Capture

Terrestrial adults require different adaptations to capture their food than do the aquatic larvae of their ancestors. One of these adaptations is an extremely fast tongue (O'Reilly & Nishikawa 1995). The anuran tongue is attached at the front, permitting a rapid and extended unfolding.

Escaping Predators and Flying Moss Frogs

When hiding among the mosses is not an option for avoiding predators, then a fast getaway might work. ***Ecnomiohyla rabborum*** (**Rabb's Fringe-limbed Treefrog**, **Hylidae**) is only known from the cloud forest in the mountains near El Valle de Anton, Panama, in the narrow elevational range of 900-1150 m asl (Mendelson *et al*. 2008; Mendelson 2009), where it lives in the canopy. Its large feet (Figure 57) permit it to glide downward from its arboreal habitat, effecting a rapid escape route. It lays its eggs in tree holes, just above the water line. Males remain near the eggs and defend them (Frost 2011). Although I could find no documentation that this species uses mosses, its habitat in the canopy of the cloud forest almost assures that it does.

Figure 57. ***Ecnomiohyla rabborum*** (**Rabb's Fringe-limbed Treefrog**, Hylidae), illustrating the large, very webbed feet used for gliding in the Costa Rican forest. Photo by Brian Gratwicke, through Creative Commons.

I thought I had finished adding new species to this chapter when I ran into "moss frogs." None of the names I had seen used this terminology except for the "mossy frogs" that mimicked mosses. But these were a whole new group of frogs, the genus ***Arthroleptella*** (**Moss Frogs, Pyxicephalidae**; southern Africa) and the family **Rhacophoridae** (Old World Tropics) (Wikipedia 2015a). Well – not quite all were new. ***Theloderma***, the genus of the Vietnamese Mossy Frog, is in the **Rhacophoridae** and will be discussed below.

Of interest is that some members of the genus ***Rhacophorus*** are known as **Flying Frogs** or **Parachuting Frogs**. ***Rhacophorus malabaricus*** (**Malabar Flying Frog**, **Rhacophoridae**; Figure 58-Figure 59) lives in the Western Ghats of India with an altitudinal range of 300-1200 m asl (Biju *et al*. 2004).

Rhacophorus malabaricus lives in tropical moist evergreen and deciduous forests as well as secondary forests and agricultural forests such as coffee plantations (Wikipedia 2011b). It spends its time in the lower canopy or understory and breeds in overhanging vegetation where tadpoles can drop from the foam nests into ponds and pools.

Rhacophorus malabaricus frogs are known as flying frogs because of their ability to glide from their arboreal habitat to the ground. Using their leg and toe spread (Figure 60) and unique morphology, they are able to minimize their descent (falling/gliding) speed and maximize their descent time (Emerson & Koehl 1990). Rather than relying on increasing horizontal travelling distance, their particular maneuverability permits them to actually decrease horizontal distance during descent. These gliding pathways can carry them 9-12 m, about 115 times their length (Wikipedia 2011b). Webbing between the toes further increases their gliding ability.

Figure 58. ***Rhacophorus malabaricus*** showing its narrow legs. Photo by L. Shyamal, through Wikimedia Commons.

Rhacophorus arboreus (**Japanese Green Treefrog**; **Kinugasa Flying Frog**; Figure 61-Figure 62) lives in Honshu, Japan, from sea level to 2000 m asl (Chantasirivisal 2011). It is a comparatively large treefrog; adult males are smaller (42-60 mm) than females (59-82 mm). During breeding season, they live in ponds and rice fields. Otherwise, they live in trees and leaf litter. They hibernate through the winter under moss or shallow soil. Unlike the moss frogs of ***Arthroleptella***, ***Rhacophorus arboreus*** females deposit eggs in a foam nest on vegetation near standing water where the larvae can easily enter the water. To protect the eggs, the female excretes an albumin-based fluid from her cloaca. She creates the foam by beating her hind legs, forming a nest to protect the 300-800 eggs. The male then fertilizes the eggs and the foam hardens, protecting the eggs from water loss and predators.

Figure 59. ***Rhacophorus malabaricus*** showing its ability to flatten against its substrate. Photo by L. Shyamal, through Wikimedia Commons.

Figure 60. ***Rhacophorus malabaricus*** in amplexus. Note the webbing between the toes that helps it to glide and maneuver to the ground. Photo by Sandilya Theuerkauf, through Wikipedia Commons

Figure 61. ***Rhacophorus arboreus*** (**Japanese Green Tree Frog; Kinugasa Flying Frog**). Photo by Peter Janzen, with permission.

Figure 62. ***Rhacophorus arboreus*** (**Japanese Green Tree Frog**) in its arboreal home. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

Arthroleptella bicolor (**Bainskloof Moss Frog**, **Pyxicephalidae**) lives in fynbos and heathland of Western Cape Province, South Africa at 300-2000 m asl (IUCN 2011). This species breeds in wet mossy areas usually near water, where it lays 8-10 eggs in terrestrial mosses or similar vegetation. Nevertheless, its eggs do not hatch into tadpoles, but develop directly into froglets.

Arthroleptella drewesii (**Drewe's Moss Frog, Pyxicephalidae**; Figure 63) is endemic to Table Mountain and other mountains, up to 1,000 m asl, in the Cape Peninsula of South Africa (IUCN 2011). It lives in fynbos and heathland, as well as forest. It lays its 5-12 unpigmented eggs in moss or similar vegetation in wet mossy areas similar to those of ***A. bicolor***. As in ***A. bicolor***, the eggs hatch directly into froglets.

Arthroleptella lightfooti (**Lightfoot's Moss Frog** or **Cape Chirping Frog**, **Pyxicephalidae**) is endemic to Table Mountain and to the other mountains of the Cape Peninsula, South Africa, where it occurs from sea level up to 1000 m asl (Frost 2011). Like the other ***Arthroleptella*** species thus far, it lives in fynbos, heathland, and forest (IUCN 2011). It lays its 5-12 eggs in mosses or similar vegetation in wet mossy areas, and likewise chooses locations near wet areas and streams (Rose 1929; Livezey & Wright 1947; Frost 2011). It, too, has direct development into froglets. Metamorphosis to adults occurs there on the mosses (Livezey & Wright 1947).

Figure 63. ***Arthroleptella drewesii*** on a bed of moss. Photo by Robert C. Drewes, with permission.

Arthroleptella villiersi (**De Villiers' Moss Frog, Pyxicephalidae**) is endemic to the western cape of South Africa, from sea level up to 1,000 m asl (IUCN 2011). It lives in lowland and montane fynbos and heathland, where it breeds in wet mossy areas similar to those of the other ***Arthroleptella*** species mentioned here. It lays its 10 eggs in moss and similar vegetation.

Anhydrophryne hewitti (**Hewitt's Moss Frog, Pyxicephalidae**; Figure 64) lives in forest and dense vegetation in the Drakensberg and midlands of Kwa-Zulu Natal, South Africa (IUCN 2011). Its breeding habitat is in wet mossy areas of riverine bush and forest near waterfalls and rapids. The 14-40 eggs are laid in moss and leaf-litter on edges of streams. Despite its preference for streamside habitats, the eggs develop directly without a larval stage.

Figure 64. ***Anhydrophryne rattrayi***, here blending with the leaf litter, shows the small size of these frogs. Another member of its genus, *A. hewitti*, lays its eggs in wet mossy areas along streams. Photo by Robert C. Drewes, with permission.

But most frogs don't glide. Some can hop quite high. I had a pet **Green Frog** (***Lithobates clamitans***) I soon named Mr. Wanderlust. He lived in my garden room on the main floor of the house, but he would often escape. I found him hopping across the TV room at the other end of the house several times, at the top of the stairs on the second story several times, and once I found him on top of the open door! I watched him jump one time as I saw him on the floor beside me at my desk. Then suddenly, he was on the desk beside me! But despite our usual vision of hopping frogs, many of them spend more time creeping and

climbing (Figure 65). That is how Mr. Wanderlust escaped under the hanging screen to get free from the garden room.

Figure 65. ***Lithobates clamitans*** attempting to climb a soil bank. Photo by Sheryl Pollock, with permission.

Camouflage and Mimicry

When you make a good dinner, it is helpful to be invisible. A number of species of frogs have disruptive coloration that would make them less conspicuous than a solid color. Greens and browns are common colors among frogs, again providing good camouflage for moss dwellers. But some have disruptive skin surfaces with warts and other extensions, making them blend with the mosses even more.

Importance of Being Still

One reason we know so little about the moss-dwelling frogs is that they do camouflage so well. Cooper *et al.* (2008) noted that camouflaged frogs should limit their movement to avoid detection by disrupting their crypsis. They experimented with ***Craugastor fitzingeri*** (formerly *Eleutherodactylus fitzingeri*; **Craugastoridae**; Figure 66-Figure 67) and demonstrated that when the frogs were motionless, four humans were able to detect only 60% of them in a 2 m diameter circle within 60 seconds. Over 90% of the individuals of five species of ***Craugastor*** remained motionless until the potential predator reached them.

Disruptive Coloration - *Boophis*

Vallan *et al.* (1998) reported on a new tree frog in the genus ***Boophis*** (**Bright-eyed Frogs**, **Mantellidae**; Figure 68) from Madagascar. This frog was especially adapted to blending with tree bark covered with lichens – it has tubercles and fringes and flattens against the branch when it is disturbed. It can change colors from whitish to brown, thus making it also camouflaged on some bryophytes. This mimicry makes it very different in appearance from other members of the genus, such as ***B. viridis*** (**Green Bright-eyed Frog**; Figure 69).

Figure 66. ***Craugastor fitzingeri*** on mosses. Photo by Brian P. Folt, with permission.

Figure 67. ***Craugastor fitzingeri***, with colors that blend with the soil. This one seems to be eyeing an ant, a potential food source. Sitting quietly not only protects it from being preyed upon, but also permits it to lie in wait for food organisms without being noticed. Photo by William Leonard, with permission.

Figure 68. ***Boophis lichenoides*** showing small tubercles, fringes and mottled (disruptive) coloration that help it to be inconspicuous among lichens on bark. Photo by Franco Andreone, through Creative Commons.

Figure 69. ***Boophis viridis*** (**Green Bright-eyed Frog**), a greenish member of the genus that looks very different from the lichen mimic, ***B. lichenoides***. Photo by Franco Andreone, through Creative Commons.

Ceratophrys ornata, A Bryophyte Mimic

Some frogs and toads really play it safe with both disruptive coloration and tubercles, making them look like the light and dark patches of a bryophyte clump. Such is the case for ***Ceratophrys ornata*** (up to 16.5 cm long), the Argentine Horned Frog, but it appears that this frog typically spends its time in grassland (except in captivity). In fact, moss in a terrarium can cause impaction if the frogs eat it. These frogs are unusual in having teeth and a strong jaw – strong enough to inflict pain on animals that attack them. The mouth is extremely large, and they feed on rodents, small reptiles, large spiders, and insects. Gut analysis of thirty-four specimens from Uruguay included 78.5% anurans, 11.7% passerine birds, 7.7% rodents, and 0.3% snakes, leaving only 1.8% as "other" (Basso 1990). They use a "lie-in-wait" strategy that is facilitated by their similarity to the bryophyte (or other) background. There are several color forms, ranging from mostly green to mostly brown. The larvae are also unusual – these are the only vertebrates to make calls in the larval state.

Figure 70. ***Ceratophrys ornata*** in a bed of moss. Photo through Flickr Creative Commons.

Figure 71. ***Ceratophrys ornata*** squatted among bryophytes. Photo by John White, from Wikimedia Commons.

Tubercles – *Theloderma corticale* (Vietnamese Mossy Frog, Rhacophoridae)

The **Vietnamese Mossy Frog, *Theloderma corticale*** (Figure 72-Figure 73), is one of many moss mimics among the amphibians, and perhaps the most famous. Literally translated from medical terminology, its generic name means nipple skin. Although it resembles a toad, it is not one. This strange animal can mimics both mosses and bird droppings, sometimes in the same animal! (Indraneil Das, pers. comm. 8 January 2012).

Figure 72. **Vietnamese Mossy Frogs**, ***Theloderma corticale***. Photo by Milan Kořínek, with permission.

It is an inhabitant of the karst zones of northern Vietnam, where it lives in flooded caves and other deep holes on the banks of mountain streams (Ryboltovsky 1999). Its skin is a mottled black and green that resembles a "bunch of moss." Numerous spines and tubercles add to the disruptive pattern that makes it quite invisible among the dense moss and lichen cover (Figure 73).

These frogs remain quiet in the daytime and hunt at night (Figure 73). When frightened, they will roll into a ball and play dead (Figure 74) (Wikipedia 2015b). They also avoid detection by being ventriloquists – throwing their voice to another location so they cannot be found while calling. This rare frog is now being bred as a terrarium pet. It appears that the starter pair has been

rescued from an area that is rapidly becoming unsuitable as a home. Despite its broad habitat range, it is threatened by habitat loss (Animal Photo Album 2007).

Figure 73. ***Theloderma corticale*** (**Vietnamese Mossy Frog**) camouflaged among bryophytes. Photo by Brian Gratwicke, through Creative Commons.

Figure 74. ***Theloderma corticale*** (**Vietnamese Mossy Frog**) on its back, feigning death. Photo © Chris Mattison <http://www.agefotostock.com/age/ingles/home01b.asp>, with permission.

Green and Wet – *Centrolene geckoideum* (Pacific Giant Glass Frog, Centrolenidae)

The Pacific Giant Glass Frog, ***Centrolene geckoideum*** (Figure 75), lives in tropical and South American cloud forests of Ecuador and Colombia (Glass Frogs: Centrolenidae), especially near waterfalls or rapids, where traversing mossy substrata must surely be a necessity in some locales. This is the largest of the glass frogs and its coloration of dark green to lime green, and skin covered with tubercles, most likely helps it to be inconspicuous among wet bryophytes and rocks. Clearing of forests for farming and chemical sprays from agriculture have reduced numbers so that this is listed as an IUCN vulnerable species (IUCN 2011).

Figure 75. ***Centrolene geckoideum***, the Pacific Giant Glass Frog, from near Tandayapa, Province of Pichincha, Ecuador. Note the tubercles and greenish color that helpsto camouflage this frog among bryophytes and lichens. Photo by William Duellman, courtesy of Biodiversity Institute, University of Kansas, with permission.

Changing Colors – *Platymantis* spp. (Ground Frogs, Ceratobatrachidae)

Platymantis macrosceles (Figure 76), endemic to Papua New Guinea, where it lives in montane forests, is not known for its arboreal behavior. However, when Foufopoulos and Brown (2004) found them in New Britain, two of them were perched on moss-covered branches of shrubs about 1 m above the ground and 2 m from a small stream. Their tubercles, combined with brown spots on green backs, made them all but invisible on their mossy perch. Interestingly, when removed from the mosses, they lost their patterned colors and became a yellowish green color (Figure 76; Johannes Foufopoulos pers. comm. 10 February 2009).

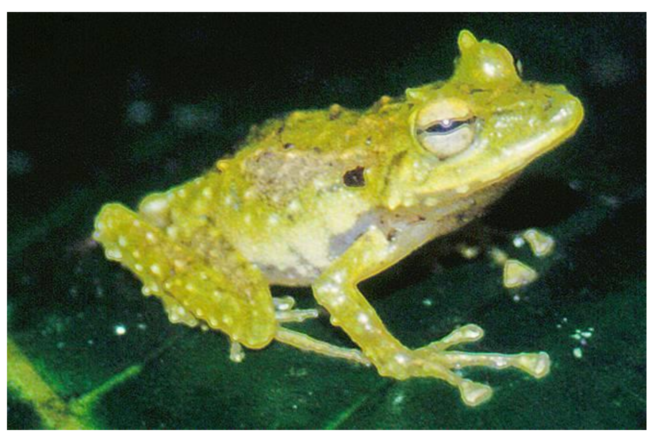

Figure 76. ***Platymantis macrosceles***, after losing its color when removed from its mossy perch. Photo by Johannes Foufopoulos, with permission.

Platymantis mamusiorum (**Ceratobatrachidae**; Figure 77), another little-known frog from the Nakanai Mountains of New Britain, Papua New Guinea, lives in montane rainforests where the ground and logs are thickly covered with moss (Foufopoulos & Brown 2004). It spends resting time on bushes and low branches up to about 1 m from the ground, but its cryptic coloration permits it to remain unseen against a mossy background. It is not as well camouflaged as the former species, lacking the brown spots and tubercles (Johannes Foufopoulos pers. comm. 10 February 2009).

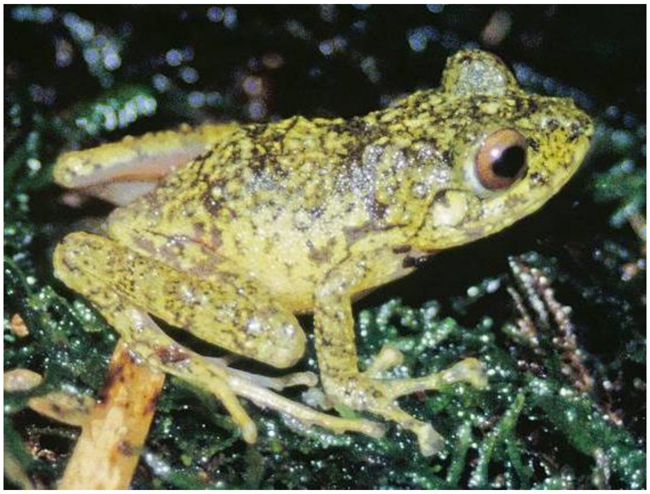

Figure 77. A ground frog, ***Platymantis mamusiorum*** showing cryptic coloration on a bryophyte-covered perch. Photo by Johannes Foufopoulos, with permission.

Colors Matter

As seen by the foregoing discussion, cryptic and disruptive coloration permit frogs to sit quietly without being seen. But it is not just blending with one particular substrate that provides an advantage. Having multiple color forms within a species increases chances for the species to survive. Forsman and Hagman (2009) demonstrated this in their studies of 194 species of Australian frogs. The polymorphic color patterns afforded larger ranges, more survival habitats, less negative population trends, and less vulnerability to extinction compared to species with non-variable color patterns. Among these, we can assume, is the ability for some color forms to utilize bryophyte habitats to their advantage where they are available. is a good example of multiple color morphs.

Oophaga pumilio has many color morphs (Pröhl & Ostrowski 2011; Figure 78-Figure 81) with estimates of 15-30 different forms (Summers *et al*. 2003). The green morphs typically remain within the moss mats and spend less time foraging compared to the brightly colored morphs that are more active (Pröhl & Ostrowski 2010). This dual strategy in a highly poisonous frog permits two different kinds of adaptations to operate in the same population. The brightly colored morphs advertise their poisonous nature through their warning coloration, whereas the green morphs are less conspicuous to us, to predators, and apparently also to potential mates.

Figure 78. Orange color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 79. White color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 80. Yellow color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 81. Blue color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Does Size Matter?

Although some large frogs and toads make use of mosses for nesting and moisture retention, those that live within the mosses terrestrially are typically quite small. Bryophytes, particularly mosses, provide them with small spaces where they can navigate without being seen by hungry predators. But it appears that bryophytes might have had a role in their evolution and size characteristics.

The tiny ***Noblella pygmaea*** (**Noble's Pygmy Frog, Strabomantidae**; Figure 82) was found for the first time in southern Peru, where it occupied two habitat types, one along the montane ridge and the other in the elfin forest where moss cover was abundant (Lehr & Catenazzi 2009). This frog is the smallest in the Andes (females 12.5 mm, males 10 mm) and one of the smallest in the world. (Note that members of **Leptodactylidae** and related families have many small members and will be discussed later). Having a small size, while beneficial for hiding in mosses, is detrimental for venturing away from the moss during the drying heat of day. As size decreases, the surface area to volume ratio increases, providing relatively more surface area for losing water.

To understand the role of size and other parameters in the evolution of Neotropical amphibians, Gonzalez-Voyer *et al*. (2011) examined the correlates of species richness with habitat parameters and body morphology. They found that a greater age of the clade did not increase richness. Rather, ecological and morphological traits seemed most important. One of these traits that correlated well with greater terrestrialization and ability to live at high altitudes was the presence of greater vascularization in the ventral skin. This, presumably, may aid in moistening the body by ventral contact with moist substrates such as bryophytes.

Figure 82. Adult ***Noblella pygmaea*** on what appears to be a liverwort. Photo by Alessandro Catenazzi, with permission.

Since being small can also be a problem for eggs, having only two eggs permits ***Noblella pygmaea*** to make larger eggs with less relative surface area to suffer drying out (Figure 83) (Gonzalez-Voyer *et al*. 2011). The moss cover should help to protect both eggs and adults against water loss as well as provide camouflage, but the preferred egg-laying locations of many of these small species, including ***Noblella pygmaea***, are not known.

Figure 83. Adult ***Noblella pygmaea*** with its two eggs. Photo by Alessandro Catenazzi, with permission.

Although Gonzalez-Voyer *et al.* (2011) found no correlation between latitude and richness, Wiens (2007) and Moore and Donoghue (2007) found greater diversification rates in amphibians in lower latitudes. Amphibians seem to have evolved in contrast to **Bergmann's** (1847) **rule** (species of larger size are found in colder environments; usually applied to endotherms), having greater body size farther from the poles and small size at high elevations in the tropics (Feder *et al*. 1982; Adams & Church 2007; Lehr & Catenazzi 2009). Geist (1987) disagreed with Bergmann's rule and instead claimed that in mammals body size initially increases with latitude, but at latitudes of 53-65°N it reverses, with the result being small body sizes at the lowest and highest latitudes.

But does this relationship apply to ectotherms like anurans? Ashton (2002) found a distinct body size relationship with latitude and elevation in salamanders, with 13 of 18 species being larger in higher latitudes and elevations. But anurans seemed less likely to conform, with only 10 of 16 species showing these trends.

Part of the disagreement lies in what is being compared. The within species comparison of Ashton (2002) is not the same as comparing among species and genera. Blackburn and Hawkins (2004) quote Bergmann as saying that "on the whole. . . larger **species** live farther north and the smaller ones farther south."

For terrestrial frogs, Gonzalez-Voyer *et al*. (2011) found that larger body size correlated only marginally with latitude and elevation. In fact, they suggested that small-bodied species may diversify more than larger ones in the Neotropics, at least in the Andes, because they are able to partition the niches on a finer scale (see also Lomolino 1985; Purvis *et al*. 2003).

The first explanation that comes to mind regarding Bergmann's rule is that a larger body is less susceptible to losing heat due to a smaller surface area to volume ratio. While this is a reasonable explanation for endotherms, there does not seem to be any reason to assume this for ectotherms. In fact, Ashton (2002) found no clear relationship between body size of salamanders and environmental temperature.

One explanation for the ability of small frogs to survive at high altitudes is their ability to make a physiological activity shift in response to lower temperatures (Navas 1996, 2006; Lehr & Catenazzi 2009).

This ability permits them to occupy the "mosaic" of small patches where the habitat is suitable and a food source is available (Hutchinson & MacArthur 1959). These terrestrial frogs have the advantage that they do not need to migrate to water to lay their eggs, and generally their home range is small, sparing them of the dangers of moving among a patchwork of unfavorable habitats. Such small patches would be unsuitable for larger frogs with greater food demands and need for moisture.

Let us consider the genus ***Pristimantis***, a genus that includes arboreal bryophyte dwellers, in this discussion. ***Pristimantis*** (Figure 84) represents the clade with the greatest number of terrestrial species (Gonzalez-Voyer *et al*. 2011). Lynch and Duellman (1997) reported a correlation between small body size and arboreal species richness in this genus. Concomitantly, prey size correlates with body size, a phenomenon which Duellman (2005) suggested might indicate competitive release through resource partitioning, subsequently explaining high local diversity that can reach as high as 139 species in 6.5 km^2 in the Amazon (Bass *et al*. 2010).

One explanation for the successful niche partitioning is that large amphibians retain water more easily and maintain body heat at a more constant temperature (Shoemaker 1992). The presence of many body sizes permits greater niche partitioning, with each size group locating where moisture and temperature are optimal. In this regard, the variety of bryophyte growth forms available can provide a wide range of niches with different moisture and insulating abilities. Conversely, the divergent niches offered create divergent selection pressures that, coupled with the geographic isolation afforded by ridge and valley topography, provide suitable conditions for speciation (Lynch 1986; Lynch & Duellman 1997).

Figure 84. ***Pristimantis bacchus*** on a bed of mosses. Photo by Esteban Alzte, through Creative Commons.

One peculiar habit noted for small frogs in marshy areas of Suryamaninagar, Tripura, India, is that they form small groups as rain approaches, effectively becoming a large animal, but after it stops they separate from each other (Acharya 2011). One could hypothesize that this behavior may help to prevent overcooling during the rain, so it would be interesting to know if the same behavior would occur if they were able to sit within the cover of bryophytes.

The Frog or the Egg?

When frogs invaded bryophytes, whether on the ground or in the trees, did they invade because they were small, or did they become smaller as they adapted more and more to terrestrial living and bryophytic habitats? Did the tiny frogs invade first, or did they begin using bryophytes as egg-laying sites, taking advantage of UV protection, moisture, and protection from larger predators? If the latter, did birth among the mosses direct more and more of them to seek shelter there later in life, creating greater survival for those that did, and driving selection toward those with that behavior and miniature size? Did bryophytes drive anuran evolution in the tropics, or were they just convenient co-evolvers in time? In any event, being small permits a wider range of uses of bryophytes by anurans.

Enter the Bryophytes – and *Eleutherodactylus* (Eleutherodactylidae)

The genus ***Eleutherodactylus*** has many species of very small frogs associated with mosses. Their subtle coloring, often with disruptive patterns, makes them inconspicuous in a variety of habitats, including bryophytes. This is clearly demonstrated for ***E. cuneatus*** in Figure 85. So far, we do not know much about the moss interactions of this species. Is it pre-adaptive to becoming a moss-dweller when its environment becomes too dry for open exposure? Or is its coloration already an adaptation to the multiple habitats it must cross during its daily activities?

Figure 85. Some frogs, like this Cuban endemic ***Eleutherodactylus cuneatus***, blend in well with the mosses they cross by having a disruptive pattern of light and dark browns. This same coloration would serve it well as it crosses forest soil and patchy, decomposing leaf litter. Nevertheless, it is on the IUCN red list. Is it rare because it is disappearing, or only because we seldom see it due to its coloration? Photo by Ansel Fong, with permission.

Being tiny is one adaptation that permits some members of this genus to inhabit mosses. The smallest frogs known in the world are in this genus, measuring only 8.5 mm long (Wikipedia 2011a). The tiny ***Eleutherodactylus coqui*** (Figure 86) has invaded Hawaii, where it competes with native species (Kreaser *et al*. 2007). Frogs of this small size are likely invaders in the moss

trade, where they can travel unnoticed among the imported moss species. But of even greater concern is the trafficking of these tiny frogs in the plant trade.

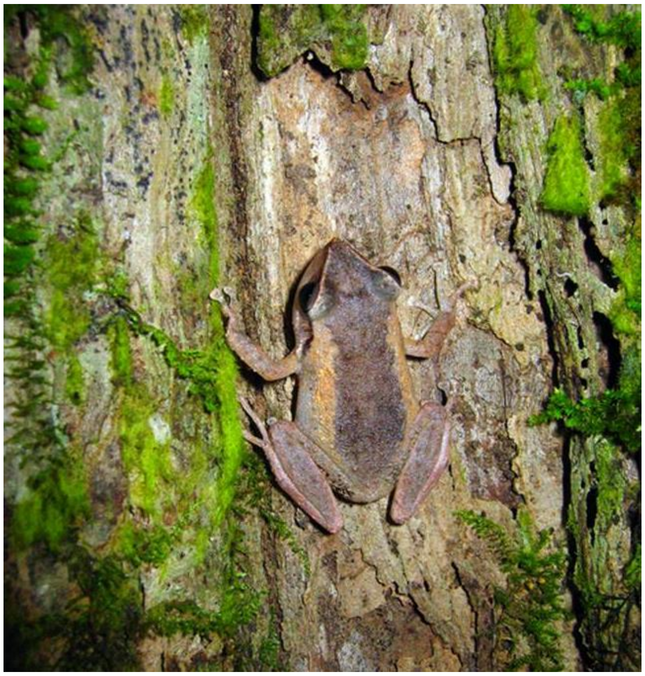

Figure 86. ***Eleutherodactylus coqui*** on a tree bole, surrounded by bryophyte and algae growth. Photo by Alan Cressler, with permission.

One species of *Eleutherodactylus* appears in greenhouses so commonly through plant transport that it has been named the **Greenhouse Frog** (***Eleutherodactylus planirostris***; Figure 87) (Frost 2011). The natural distribution of this species is in Cuba, and the Isla de Juventud (0-720 m asl), Cayman Islands, and Caicos Islands. But they have been introduced into Florida, southern Louisiana, southern Georgia, Oahu, and the island of Hawaii, USA, and to Guam, Jamaica, Honduras, and Veracruz, Mexico. This terrestrial species lives in both mesic and xeric habitats, including forests, caves, beaches, nurseries, gardens, and urban areas (Hedges *et al*. 2004). In the Cayman Islands it has naturalized in bromeliads. No surprise, it is categorized as least concern by the IUCN.

Figure 87. ***Eleutherodactylus planirostris*** on moss. Photo by Brian Gratwicke, through Creative Commons.

When you are as small as these ***Eleutherodactylus*** species, even thin mats of bryophytes can help maintain moisture. Note in Figure 88 the wet leafy liverworts that are epiphyllous on the leaf, maintaining a moist location for this tiny ***Eleutherodactylus gryllus*** (**Cricket Robber Frog**; Figure 88-Figure 89). A native of interior uplands in Puerto Rico from 300-1182 m asl, it is known from only a few localities and is considered endangered (IUCN 2011). Mosses provide daytime retreats in its forest home. It calls from perches in trees and shrubs (Figure 88). Eggs still require water and are laid in basins of bromeliads, but Father Alejandro Sánchez found them under bryophytes (Figure 90). These develop young froglets, with no tadpole stage.

Figure 88. ***Eleutherodactylus gryllus*** (**Cricket Robber Frog**) calling from a leaf covered with epiphylls. Photo by Luis J. Villanueva-Rivera, USDA, with permission.

Figure 89. ***Eleutherodactylus*** sp. calling from a plant. Photo by Brian Gratwicke, through Creative Commons.

Figure 90. Eggs of ***Eleutherodactylus*** sp. under layer of moss on a tree trunk, El Yunque National Forest, Puerto Rico. Photo by Father Alejandro Sánchez, with permission.

Most of these species don't bear any coloration patterns that distinguish them as bryophyte dwellers. However, ***Pristimantis galdi*** (formerly *Eleutherodactylus galdi*) (Espada's Robber Frog; Figure 91) has both color patterns and tubercles to render it invisible in the right setting; *i.e.*, it is a moss mimic. This species lives in both secondary and old-growth humid evergreen forests in Peru and the Cordillera of Ecuador from 1000 to 1740 m asl (Frost 2011; Rodríguez *et al*. 2004). It seems to prefer leaves at 1-2 m above the ground (Lynch & Duellman 1980). Its habitat is threatened by livestock farming, agriculture, and logging, classifying it at near threatened (Rodríguez *et al*. 2004).

Figure 91. ***Pristimantis galdi***, showing its tubercles from an arboreal branch. Photo © 2007 German Chavez, with permission for educational use.

Summary

Bryophytes and amphibians are both transitional organisms that have adapted to land. Their life cycles are characterized by two phases that have different requirements. Frogs need to maintain moist skin, so bryophytes can provide them with a suitable habitat. Mosses provide moist safe sites from the drying sun during the day and serve as mating and calling sites for many species. *Sphagnum* can offer a moisture refugium for migrating amphibians. The same moisture advantage is offered to eggs. The male Leyte Wart Frogs (***Limnonectes leytensis***) stay under the mosses with their eggs; tadpoles can later be washed into the nearby water by rain. In winter, the bryophytes can provide insulation for hibernating anurans that can become frozen up to 60%, as well as reducing the risk of desiccation. And some bryophytes can serve as food and even sources of oxygen. ***Sphagnum***, mixed with egg yolk, can even serve as food for rearing several species of tadpoles. At the very least, mosses provide refuge for a number of invertebrates that are suitable food for the anurans. For some species, using mosses as cover during overwintering may save their lives. In summer, some frogs may even return day after day to the same spot among the mosses.

Some Anura seem to be well adapted for the bryophyte habitat. Small size is an advantage for living among the stems or climbing across epiphytes on branches. Many have disruptive coloration of browns and greens. And some have protuberances that further disrupt the shiny surface, serving as additional camouflage. Some even change their color to blend with their substrate. Altered life cycles are adaptations to land in general, with such modifications as parental care of eggs, carrying eggs on their backs, having large but few eggs, and burying the eggs in mossy nests. Because of these anuran traits, bryophytes offer them **safe sites** against not only environmental conditions, but also against predation.

One means of escape for Moss Frogs and others is "flying." This is actually gliding, and some of these frogs have modified muscle placement that permits them to maneuver to a selected landing spot. Others simply hop or crawl.

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the images, email addresses, and literature, making possible wonderful stories that would not have been included otherwise. Without the kind cooperation of many, many people, this chapter could not have been written. The herpetologists have been incredible in encouraging us on the project and in providing images, especially for the tropical frogs. Wikipedia and Wikimedia helped us find biological information and nomenclature synonyms for the included species.

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CHAPTER 14-2
ANURAN CONSERVATION ISSUES

Janice M. Glime and William J. Boelema

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Figure 1. ***Atelopus certus*** in its natural setting, streamside on a mossy rock. This species may soon only exist in captivity and is the object of a rescue operation. Photo by Brian Gratwicke, through Creative Commons.

Conservation Issues and Endangered Species

Many species of anurans, especially in the tropics, are disappearing because their ranges are small, restricted to mountain tops separated by uninhabitable valleys, preventing them from spreading to new locations (Figure 1). For some, extinction is imminent because their small range of habitat is being destroyed. Blaustein *et al*. (1994) suggest that amphibian species may not be able to recolonize areas where they have become extinct because of physiological constraints, low mobility, and site fidelity.

Knutson *et al*. (1999) examined landscape effects and wetland fragmentation on anuran abundance and species richness in Iowa and Wisconsin, USA. They found that there was a negative association with the presence of urban land, but a positive association with emergent wetlands and upland and wetland forests. For these larger species, a complex of habitats including wetlands is the best combination for success of the amphibian populations.

But amphibians are declining at an alarming rate worldwide. Factors of disease, parasites, deforestation, agriculture, heavy metals, herbicides, pesticides, increasing UV radiation, acid rain, fire, and other environmental changes all seem to have contributed to a rapid decline in anuran species.

Although the decline of amphibians is well known throughout the world, the causes are not so clear. It appears that the causes are multiple and that the tadpole stage, in particular, is very sensitive. This helps to explain why amphibians are endangered from pesticides, heavy metals, organic compounds, parasites (Figure 2), and bacteria. Tadpoles of many species are sensitive to low *p*H (Freda *et al*. 1991). Rising temperatures may play a role by increasing likelihood of bacterial, fungal (Halliday 1998), or parasitic infection (Blaustein & Dobson 2006). The rich diversity of arboreal amphibians in the tropics is particularly at risk, and we know almost nothing about where they place their eggs or how bryophytes may be essential in their life cycle survival. Meanwhile, their habitats are disappearing (Mazerolle 2003).

The anurans are negatively associated with urban development. This group of organisms often requires different habitats for breeding, hibernation, and summer feeding. When one of these habitats disappears or becomes inaccessible, the amphibians will disappear from the others as well. The genus ***Lithobates*** is a common peatland visitor that exemplifies common characteristics among disappearing anuran species: aquatic habit, montane distribution, and large body size (Lips *et al*. 2003).

Figure 2. ***Bufo bufo*** infected with parasitic fly larvae. Photo © Henk Wallays, with permission.

The amphibians are further limited by their latitudinal restrictions. While species richness decreases from low to high latitudes for all animal groups but birds and sawflies, the amphibians are nearly absent in the Arctic (Kouki 1999).

One contributing factor to the absence of amphibians at high latitudes, in addition to the short food season and cold temperatures, is the lack of canopy and higher levels of UV. As the ozone in the stratosphere diminishes, more UV-B radiation is able to penetrate the atmosphere and reach the Earth. Several researchers have hypothesized that it is increased levels of UV-B that have precipitated the massive losses of amphibians. This suggestion is in part due to the much greater decline in amphibians than that seen in birds or mammals (Bancroft *et al*. 2008). Bancroft *et al*. showed that UV-B radiation reduced amphibian survival by 1.9-fold compared to controls, with larvae (tadpoles) being more susceptible than embryos. Salamanders were even more susceptible than frogs. They concluded that the UV-B acted synergistically with other environmental stressors, such as those mentioned above. However, the results of multiple studies have been conflicting, with the same species acting differently at different life stages and even at the same life stage in the same population at the same time.

The complicating factor in explaining amphibian decline seems to be that there are multiple causes. For example, the Boreal Toad ***Anaxyrus boreas boreas*** (Figure 3) suffered total loss of 11 populations in the West Elk Mountains of Colorado between 1974 and 1982 (Carey 1993). In this case, it was the bacterium ***Aeromonas hydrophila*** that seemed to be the culprit. Carey concluded that stress caused a suppression of the immune system, increasing the sensitivity to infection. Such suppression would make the amphibians more susceptible to fungal, bacterial, viral, and parasite attacks.

Red leg: *Aeromonas hydrophila*

One of the most common infections of frogs in the lab, in my experience, is red leg, caused by a heterotrophic, Gram-negative, rod-shaped bacterium, ***Aeromonas hydrophila***. This bacterium travels through the bloodstream to the first available organ, where it produces an Aerolysin Cytotoxic Enterotoxin (ACT) (Wikipedia 2011a). Its very toxic infections are common in fish and amphibians, and can also affect humans. It is most likely to infect during times of environmental change, stress, temperature change, pollution, or in an otherwise unhealthy animal. One reason for the name of red leg is that the disease can cause internal hemorrhaging, a problem that can lead to death. For the disease to become manifest, both hemolysin and the endotoxin must be present (Rigney *et al*. 1978), resulting in bloating, lesions, hemorrhaging, and other serious problems in the frogs.

Figure 3. ***Anaxyrus boreas*** on a bed of mosses. Photo by William Flaxington, with permission.

Red leg may be a somewhat seasonal infection. Emerson and Norris (1905) observed more incidence of the disease in the warm weather of September and October, claiming that short periods in the cold chamber would delay death by the disease in infected frogs. But in 14 sites in Minnesota, USA, there were more infections in ***Lithobates pipiens*** (Leopard Frog; formerly ***Rana pipiens***) in March-June than in August-November (Hird *et al*. 1981), suggesting that either these frogs were more stressed early in the season after a winter of little food, or that the disease could grow better under spring conditions, possibly in lower temperatures. In that study, red-leg infections could not account for the declining populations of ***Lithobates pipiens*** (Hird *et al*. 1981).

Frogs are actually rather well protected from diseases such as those caused by ***Aeromonas*** species. Glands in their skin produce secretions containing a multitude of peptides with antimicrobial prosperities (Simmaco *et al* 1998). In ***Pelophylax lessonae*** (Edible Frog; formerly ***Rana esculenta***), 20-30 different peptides are secreted. Although these bacteria can grow freely in the blood of the frog, those in contact with the skin toxins are killed within 10 minutes.

Peatland Conservation

One might argue that the tropics and the peatlands are the two most vulnerable ecosystems under current circumstances. Peatlands are disappearing through mining and draining, and if they are replaced, it is frequently by a different vegetation type and hydrologic regime. But even when peatland pools are retained, lack of suitable habitat for summer retreats may cause amphibian losses (Marsh & Trenham 2001). Baldwin *et al*. (2006) and Bellis (1965) likewise concluded that summer refugia in peatlands were important for the Wood Frog (***Lithobates sylvaticus***; Figure 4), providing shade and moisture-laden ***Sphagnum*** (Figure 5).

Figure 4. ***Lithobates sylvaticus***, a frog with short lifespan and high fecundity. Photo by Bill Peterman, with permission.

Figure 5. Mer Bleue Bog with ***Sphagnum*** near Ottawa, Canada. Photo through Creative Commons.

Harper *et al*. (2008) concluded that current federal wetland law is inadequate to protect the amphibians, partly because it lacks protection for surrounding areas. They contend that state wetland regulations that protect no more than 30 m from the breeding pool cannot support the terrestrial habitat needs.

Life span can play a role in amphibian sensitivity, with a short life span and high fecundity, like that of the Wood Frog (***Lithobates sylvaticus***; Figure 4), being most sensitive to habitat loss and isolation. On the other hand, long life and low fecundity, like that of the Spotted Salamander (***Ambystoma maculata***), can lead to greater sensitivity to habitat degradation and lower adult survival. Furthermore, connections between wetlands are needed for recovery after population crashes (Baldwin *et al.* 2006; Harper *et al.* 2008).

Mining

Mining of peat changes the gross morphology of the peatland, removes the more open upper layers where it is easy for frogs and toads to nestle among the stems, and alters the hydrology. Such changes are likely to remove the aspects of peatlands that make these favorable habitats for amphibians.

Mazerolle (2003) demonstrated the negative impact of peat mining on amphibian abundance and diversity. Species richness and numbers of individuals both were lower in bog remnants (after mining) than in unmined bogs. The Wood Frog (***Lithobates sylvaticus***; Figure 4) was most abundant in areas far from the ponds when the area had not been mined. Only ***Anaxyrus americanus*** (formerly *Bufo americanus*; Figure 6) appeared to benefit from the increase in habitat complexity resulting from mined edges in fragmented peatlands. Knutson *et al.* (2000) suggest that more wetland patches are likely to increase the probability that at least one of those sites will be suitable for amphibian habitation. Mazerolle (2003) contended that amphibians would benefit from a management plan that maintained a complex mosaic of bog ponds, shrubs, and forest patches. Since peatlands are such important habitats for many amphibians, it is essential that we understand the role of their bryophytes in our attempts to restore their fauna along with wetland restoration (Mazerolle *et al*. 2006).

Figure 6. ***Anaxyrus americanus*** amid mosses and rocks. Photo by John D. Willson, with permission.

We can surmise from the foregoing information that some anurans would suffer from the loss of peatland habitat due to water loss during travels and daytime activity and to loss of egg-laying sites. Bellis (1962) stressed the importance of moisture provided by a spruce and tamarack bog in northern Minnesota, especially for smaller frogs.

But it appears there may be other consequences that result from mined peatlands. Mazerolle (2001) examined effects of fragmented bogs in southeastern New Brunswick, Canada. He found that the Wood Frogs (***Lithobates sylvaticus***; Figure 4) that occurred in fragments were actually larger than those in pristine bogs. Leopard Frogs had a similar size relationship, but only in the 1998 year of study. Mazerolle attributed this relationship to be the result of larger frogs having a better chance of surviving than small frogs in the disturbed habitat of mined peatlands. Larger frogs would have a smaller surface area to volume ratio, thus decreasing their sensitivity to desiccation.

Old-growth Forests

Old-growth forests (Figure 7) with mature trees, continuous canopy, logs, snags, and often well-developed moss beds on the ground, logs, and branches, are likely to represent the third major habitat type where amphibians are rapidly disappearing. Logging and clearing for harvest or

agriculture greatly alters the old-growth habitat, eliminating vast acreage and replacing it with a drier cover with fewer niches.

Figure 7. Old-growth habitat of ***Ascaphus truei***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Dupuis *et al*. (1995) demonstrated the importance of stand age in providing suitable habitat for amphibians. They found that logging could reduce terrestrial amphibian populations by up to 70% in old-growth forests in Canadian forests. Logging reduced the availability of moist habitats such as snags and logs, reduced shade, and often lost streamside buffer zones. As in peatland studies, they found that having connectivity between patches of suitable habitat was important. Bryophytes can play a role in these connections and in creating microhabitats that are moist and provide protection against UV-B radiation.

One of these disappearing species (the Coastal Tailed Frog, ***Ascaphus truei***; **Leiopelmatidae**; Figure 9) has been discussed earlier because it seems to find a rich food source among the streamside mosses. This is an unusual frog that can unlock keys to evolutionary processes. Although it is "tailed," it does not break the anuran rule of no tails because its "tail" lacks bone and is thus not a true tail. This is the only genus of frogs with internal fertilization (California Herps.com 2011).

Figure 8. ***Ascaphus truei*** tadpole in a stream with leafy liverworts. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Welsh (1990) found that the Coastal Tailed Frog occurred primarily in old-growth forests – those primeval coniferous forests that are disappearing rapidly from the Pacific Northwest in North America. Younger forests do not offer the needed microclimate required. It is only in the older forests that the preferred cover of the Coastal Tailed Frog (moss, rocks, and organic matter) exists. Their sucker-like mouths permit them to hang onto the rocks, where they presumably eat the attached algae. The importance of the bryophytes has not been studied experimentally, but Noble and Putnam (1931) suggested that these mossy habitats might provide an enriched food source for them. The tadpoles (Figure 8-Figure 10) occur in fast melt-water streams.

Figure 9. ***Ascaphus truei*** showing its fleshy tail. Stream edges such as this provide suitable feeding areas for the adults. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 10. ***Ascaphus truei*** tadpole showing its rasping suction cup mouth. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Tropics

There are possibly the greatest numbers of endangered amphibians in the tropics. That is where the smallest of vertebrate species live among bryophytes, lichens, and other epiphytes in the canopy, on tree trunks, and on the ground. Many of the anuran species remain to be described. But this habitat is in great danger of destruction to make way for farming and managed forestry, depleting the sites with bryophyte-covered habitats and replacing them with non-forest or with young trees that do not have established bryophyte cover.

A rapid decline in tropical anurans was first noticed in the 1980's (Bustamante *et al*. 2005; La Marca *et al*. 2005). Bustamonte *et al*. noted that 24 anuran species in the Ecuadorian Andes were in decline or had become extinct since the late 1980's. But the decline was not prevalent in

all species. Between 1988 and early 2000's, 56 of 73 species had declines, but 27 had increased in relative abundance. In six of seven localities, fewer species could be located, despite greater capture effort. It is noteworthy that they found greater differences for species with aquatic larvae (reduction from 34 to 17 species) than for those terrestrial species having direct development. For example, the genus ***Eleutherodactylus*** presented 28 species in both the earlier and recent surveys. Furthermore, six species had expanded their distributions to higher altitudes.

Fong and Hero (2006) explored eastern Cuba in an effort to document the extant anuran species so that losses with habitat destruction could be measured. They cited ***Eleutherodactylus cuneatus*** (Figure 11) as a species that is at high risk of disappearance if habitat loss were to occur in Cuba (Williams & Hero 1998; Lips *et al*. 2003; Hero *et al*. 2005; Fong & Hero 2006). In the tropics, at least in Latin America, species living close to streams seem to be the most vulnerable (Young *et al*. 2001).

Figure 11. ***Eleutherodactylus cuneatus***, a species that is at risk due to limited distribution. Photo by Ansel Fong, with permission.

Despite forest habitat destruction, Lips (1998) had also surmised that it was species with aquatic eggs and larvae that were most vulnerable to decline. Those with direct development such as ***Eleutherodactylus*** and some salamanders (***Bolitoglossa minutula***), both bryophyte inhabitants, typically arboreal, do not seem to be in decline. Lips further concluded that based on evidence in Australia, Brazil, and Costa Rica, it was an environmental contaminant such as chemicals or biotic pathogens, or a combination of factors that might include climate change. Laurance *et al*. (1996) concluded, based on worldwide spread patterns and presence of the disease in pristine environments that lacked environmental contamination, that the problem was caused by a disease.

Atelopus (Bufonidae)

The genus ***Atelopus*** (**Bufonidae**), the Neotropical Harlequin Frog – but actually a toad – seems to be particularly vulnerable. Of the known 113 species, 42 species have been reduced by at least 50% since earlier surveys, and only ten have stable populations (La Marca *et al*. 2005). Many of the species could not be relocated, and 30 have been missing from all previously known localities for at least 8 years. In this case, it seems to be those at higher elevations (above 1000 m) that are most vulnerable, with 75% disappearance, compared to 58% disappearance among lowland ***Atelopus*** species. Habitat loss did not seem to be the causal factor. Climate change may have played a role, but environmental contamination, pet trade, and introduction of competitor or predator species did not seem to have any role. Rather, 22 species had disappeared from protected areas! There is some good news, however. ***Atelopus varius*** (Figure 12) has recently been located in Costa Rica in a mossy stream (Solano Cascante *et al*. 2014).

Figure 12. ***Atelopus varius***, known from a mossy stream in Costa Rica. Photo by Brian Gratwicke, through Creative Commons.

Atelopus certus (Darien Stubfoot Toad; Toad Mountain Harlequin Frog; Figure 13-Figure 16) is an endemic to Panama, where it occurs at 500-1150 m asl. This golden-colored frog with spots like a giraffe is disappearing from Panama. It is one of the frogs targetted for a rescue operation to breed the frogs in captivity (Amphibian Rescue and Conservation Project 2011). On an expedition to capture these frogs for rescue, Mark Cheater (2011) reported finding the first few of these frogs on mosses, including a pair in amplexus. The frogs were placed in plastic cups lined with damp moss for transport.

Figure 13. ***Atelopus certus*** at edge of stream where wet mosses can keep it hydrated when it ventures landward. Photos by Brian Gratwicke, through Wikimedia Commons.

Figure 14. ***Atelopus certus*** male. These males climb shrubs and trees at night. Photo by Brian Gratwicke, through Creative Commons.

Figure 15. ***Atelopus certus*** (Darien Stubfoot Toad; Toad Mountain Harlequin Frog) male calling near stream. Photo by Brian Gratwicke, through Creative Commons.

Figure 16. ***Atelopus certus*** male calling. Its coloration serves it better as camouflage in its stream home than aloft on a mossy perch when calling. Photo by Brian Gratwicke, through Creative Commons.

An alarming factor was beginning to emerge. ***Batrachochytrium dendrobatidis***, a fungal disease organism that causes **chytridiomycosis** in amphibians and other animals, had arrived. And this fungus was present in populations of nine of the ***Atelopus*** species that have declined.

Chytridiomycosis

Although loss of cover and moisture will surely have a great impact on the anuran fauna, it appears that another serious threat is the rapid spread of the fungal disease **chytridiomycosis**. Anurans seem to be defenseless against fungi that are causing whole populations to disappear (Thompson 2010).

Catenazzi *et al*. (2011) found that the introduced fungal pathogen ***Batrachochytrium dendrobatidis*** caused the **chytridiomycosis** that accounted for a large portion of amphibian decline in the Andes of Peru. In its short known history, it has been responsible for both extinctions and **extirpations** (local extinctions) in Central America. In Peru, the overall number of species declined by 47%. The fungus seems to have a greater effect on aquatic and arboreal species (declined by 55% between 1999 and 2008) than on the terrestrial species. Abundance of frogs also declined during that period, following its discovery by Longcore *et al*. in 1999. The declines correspond with increases in the fungus (Catenazzi *et al*. 2011).

The fungus adheres to the skin of the amphibians, causing it to thicken, thus interfering with respiration (Denton 2008). That thickened skin inhibits the animal's ability to take in water and interferes with the salt-water balance in the body of the frog (Voyles *et al.* 2007). Furthermore, the fungus damages the nervous system (Denton 2008). This causes lethargy and ultimately death.

This fungal disease seems to be associated with a large number of amphibian declines worldwide (Berger *et al*. 1998; Piotrowski *et al*. 2004; Bovero *et al*. 2008; Brodman & Briggler 2008; Byrne *et al*. 2008; Reeves 2008; Gaertner *et al.* 2009), but the greater incidence of the disease could have multiple causes that weaken the amphibian resistance to the disease. Furthermore, it seems clear that chytridiomycosis is not the only cause of the decline (Daszak *et al*. 2003; Di Rosa *et al.* 2007).

In a summit-type meeting of herpetologists regarding the threat of amphibian extinctions in Latin America, 88 Latin American herpetologists and conservationists concluded that "at least 13 countries have experienced declines, and in 40 cases species are now thought to be extinct or extirpated in a country where they once occurred. Declines or extinctions have affected 30 genera and nine families of amphibians. Most declines have occurred in remote highlands, above 500 m in elevation in Central America and above 1000 m in the Andes. ...Climate Change appears to be important at one site and chytrid fungal disease has been identified at sites in three countries." (Young *et al*. 2001). Recognizing the importance of *in situ* studies, they concluded that it would be important to rear species in captivity to avoid imminent extinction.

One species targetted for *in situ* studies is ***Atelopus limosus*** (Limosa Harlequin Frog; Figure 17-Figure 22), an endemic to Panama, where it lives on stream banks in subtropical or tropical moist lowland forests and rivers (Wikipedia 2011b; Figure 13). Once a thriving species, it is now endangered by chytridiomycosis (Figure 21-Figure 22) as well as habitat destruction (IUCN 2011).

Figure 17. ***Atelopus limosus*** in its natural habitat. Photo by Brian Gratwicke, through Creative Commons.

Figure 18. A once healthy, reproductive species, ***Atelopus limosus*** is now endangered due to chytridiomycosis. Here it blends with mosses in its terrestrial habitat. Photo by Brian Gratwicke, through Creative Commons.

Figure 19. ***Atelopus limosus*** male and female in amplexus. Note the size differences between the male (smaller) and female in this lowland color form. Photo by Brian Gratwicke, through Creative Commons.

The Limosa Harlequin Frog has two color forms, a brown form with yellow nose and finger tips in the lowlands, and a green form with black patches on its back in the uplands (Wikipedia 2011b). The upland form is in the greatest danger, and the Amphibian Rescue and Conservation Project (2011) targeted this species and managed to maintain one upland female in captivity (Estrada 2011). They successfully bred the Limosa Harlequin Frog in captivity – no small feat.

This species, particularly the green and black upland variety, has been described several times as being camouflaged among the mosses and dark rocks (Amphibian Rescue and Conservation Project 2011; Price 2011). This ability to blend makes them difficult to locate, hence making the rescue operation difficult. Typical food for the genus includes beetles, ants, flies, and mites (Durant & Dole 1974), all of which can be found among and near bryophytes.

But they must leave these bryological hiding places during the dry season and return to fast-flowing rainforest streams (Amphibian Rescue and Conservation Project. 2011). It is here that the females lay their eggs. The rapidly moving water helps to protect the eggs from predation. Once the tadpoles emerge, they cling to the rocks with their suction cup mouths.

A more fundamental question is why this disease has suddenly become so widespread. One might look at acidification as a contributor, with frogs being more vulnerable and fungi typically being favored by a lower *p*H.

Figure 20. ***Atelopus limosus*** dead from chytridiomycosis caused by ***Batrachochytrium dendrobatidis***. Photo by Brian Gratwicke, through Creative Commons.

Figure 21. ***Atelopus limosus*** dead from chytridiomycosis caused by ***Batrachochytrium dendrobatidis***. Photo by Brian Gratwicke, through Creative Commons.

Figure 22. Dead ***Atelopus limosus***, a typical result of chytridiomycosis. Photo by Brian Gratwicke, through Creative Commons.

The danger from chytridiomycosis has gotten so severe that several scientists travelled to Panama to rescue as many frogs as they could (Goodman 2006; Figure 24-Figure 25). According to models of the spread of the fungus causing chytridiomycosis, attack on these

populations was imminent. So they packed hundreds of frogs into deli containers with wet mosses, placed them in carry-on suitcases, and began their adventure through airport customs back to Atlanta where they would attempt to breed them in captivity.

Figure 23. Swabbing a tropical frog for chytridiomycosis. Photo by Brian Gratwicke, through Creative Commons.

Figure 24. Swabbing a tropical frog for chytridiomycosis. Photo by Brian Gratwicke, through Creative Commons.

Figure 25. Testing a new and faster test for ***Batrachochytrium dendrobatidis***, the chytridiomycosis fungus. Photo by Brian Gratwicke, through Creative Commons.

Diagnosis

When organisms are under stress, whether it be temperature, pollution, or disease, one measure of the severity of that stress is an instability in development (St. Amour *et al*. 2010). The assumption is that it is costly to control symmetry (I am reminded of so many things that develop in a spiral, including at least some protonemata from spores imbedded in agar, and rhizoids before they touch a substrate). Therefore, the greater the evidence of asymmetry, the greater the indication of stress. In their study of asymmetry, St. Amour *et al*. found that ***Lithobates clamitans*** (Green Frog; Figure 4) had significantly higher levels of fluctuating asymmetry in individuals infected with chytridiomycosis.

A Cure?

One of the first steps in combating chytridiomycosis is to determine what conditions the fungus likes. Puschendorf *et al*. (2011) studied several species of the tree frog ***Litoria*** (Hylidae). They found that the fungus thrives where the environment is cool and moist, causing the highest outbreaks to occur in such areas. To support this conclusion, they demonstrated that in species with greater elevational ranges, populations disappeared at the higher elevations while surviving in the lowlands. To their surprise, they found a population of ***Litoria lorica*** and one of ***Litoria nannotis*** (Figure 26-Figure 27) in a stream at high elevation in a dry sclerophyll forest. In that and six additional surveys, 82.9% of the frogs had ***Batrachochytrium dendrobatidis*** (Figure 28). Among tadpoles of both species, 100% were infected. BUT none of the individuals had any signs of chytridiomycosis. This site had little canopy cover, low annual precipitation, and a more defined dry season than a nearby rainforest site. In that nearby site, ***L. nannotis*** was negatively affected by the disease chytridiomycosis. They hypothesized that the open habitat permitted the rocks where the frogs perched to warm up, having negative effects on growth and reproduction of the fungus.

Figure 26. ***Litoria nannotis***, an active frog that has frequent contact with habitats of other frogs. Note the color pattern that can easily blend with bryophytes during its travels. Photo through Wikimedia Commons.

Figure 27. ***Litoria nannotis*** tadpole. Photo by Jean-Marc Hero, through Wikimedia Commons.

Litoria nannotis (Figure 26-Figure 27) lives in fast streams, waterfalls, and cascades in the rainforest or wet sclerophyll forest of Australia (Liem 1974; McDonald 1992), where it is endemic (Williams & Hero 1998, 2001; Hodgkison & Hero 2001). The tadpoles are specially adapted to living in these torrents, including a streamlined body shape, large sucking mouthparts, and a muscular tail (Liem 1974; Richards 1992). At night, the frogs may venture up to 15 m from the stream in search of food, returning to the stream before dawn (Hodgkison & Hero 2001).

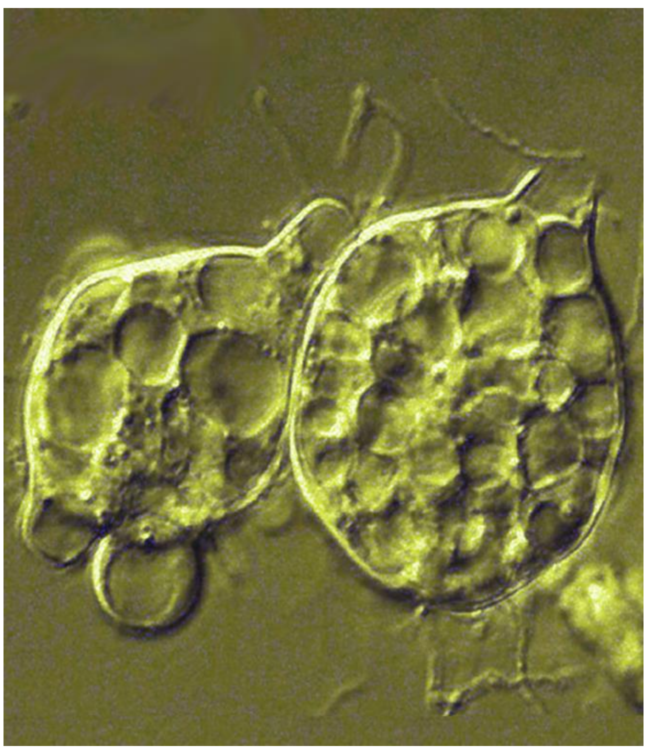

Figure 28. ***Batrachochytrium dendrobatidis***, a fungus causing chytridiomycosis. Photo by A. J. Cann, through Creative Commons.

Rowley (2006), and later Searle *et al*. (2011) found that some anuran species may be severely affected by chytridiomycosis while others in the same area are unaffected. Rowley suggested that behavior of the frogs played a role. Such factors as physical contact between frogs, contact with infected water, and contact with terrestrial substrates that serve as reservoirs all contribute to the likelihood of contracting an infection. In other words, the microenvironment plays a role. As in other studies, Rowley found that at elevations above 400 m asl the populations were more likely to decline due to chytridiomycosis, even while populations of the same species in the lowlands contracted no infection. Among three species of ***Litoria***, ***L. nannotis*** became locally extinct at all known high elevation sites. ***Litoria genimaculata*** (Figure 29) declined at the high elevation sites, then recovered. The third species, ***L. lesueurii*** (Stoney Creek Frog; Figure 30), had no known infection at any elevation. Ouellet *et al*. (2005) found similar confounding indications in Quebec, Canada. They examined specimens spanning the years 1895 to 2001 from 25 countries, totalling 3371 specimens. In recent studies, they found no evidence of mortality from chytridiomycosis in amphibians from Québec, despite the presence of the fungus in 17.8% of the amphibians from 1990-2001. Furthermore, epidermal infections were apparently absent in 440 amphibians from 23 other countries. It appears that despite the internal infection in seemingly healthy amphibians from eastern North America, the lethal expression of chytridiomycosis has complex causes that may require a predisposition to contract the disease.

Figure 29. ***Litoria genimaculata*** showing cryptic coloration and pronounced tubercles that permit it to blend with mosses and lichens. Photo by Jean-Marc Hero, with permission.

Figure 30. ***Litoria lesueurii*** in its stream home, exhibiting much smaller tubercles than its terrestrial congenerics. Photo through Wikimedia Commons.

Rowley (2006) demonstrated that the frequency of contact with other frogs and with water was greatest for ***L. nannotis*** (Figure 26), intermediate for ***L. genimaculata*** (Figure 29), and least for ***L. lesueurii*** (Figure 30), corresponding with the degree of infection mentioned above. Furthermore, ***L. lesueurii*** travelled farthest from the stream, whereas ***L. nannotis*** remained in the stream all day, moving only a short distance from the streams. These "travelling" patterns further separated the environment created for the fungus by creating temperature differences. For the most susceptible species, ***L. nannotis*** (Figure 26), the frogs rarely moved outside the temperature range that was optimum for the fungus. On the other hand, the uninfected species, ***L. lesueurii*** (Figure 30), were frequently at sites with temperatures above the temperature optimum and even the thermal tolerance for the fungus. ***Litoria nannotis*** even had the most suitable hydric conditions for development of the fungus. Hence, the "predisposition" seems to be the behavior of these three species. From our bryological perspective, the substrate used by the frogs can also play a role. Dewel *et al.* (1985) found that zoospores of chytrids are common on moss-covered rocks, and Letcher and Powell (2002) suggested that distance from moss could affect the safety of a given substrate where the frogs might sit.

Searle *et al*. (2011) looked at the differences between species somewhat differently, showing that even with the same degree of ***Batrachochytrium dendrobatidis***, the mortality rates differed among species. This would eliminate dispersal and contact as causal factors. Temperature seems to be emerging as an important distinction, but the work of Searle *et al*. seems to suggest that there is also a difference in immunity.

The spread of this disease around the world has been rapid. One contributing factor, perhaps the primary one, has been the human factor. Among these has been international trade in aquarium fish (Laurance *et al.* 1996). But even plant trade, with frogs as hitchhikers, contributes to the problem. And if the zoospores survive on mosses, then the moss trade can also spread the disease, either by spreading the zoospores, or by transport of infected frogs.

One interesting aspect of survival of the ***Batrachochytrium dendrobatidis*** is that rising temperatures, often viewed as a cause for disease increase, may actually improve the resistance of tadpoles to the disease. In experiments on tadpoles of ***Rana muscosa*** (Mountain Yellow-legged Frog; Figure 31-Figure 32), at 22°C, 50% died within 35 days, while 95% of those maintained at 17°C died (Andre *et al*. 2008). Nevertheless, Piotrowski *et al*. (2004) showed that growth of the chytrid fungus from the zoospores (Figure 33) was maximal in the range of 17-25°C.

There is perhaps some hope for at least some of the amphibians in this chytridiomycosis epidemic. There is strong evidence that some species of amphibians survive because of a co-habiting bacterium, dubbed the **anti-Bd skin bacterium** (Lam *et al*. 2009). The resistance seems to result from antimicrobial skin peptides and these anti-Bd skin bacteria. I have to wonder if any of the bryophyte antibiotic properties might help their inhabitants avoid fungal and other infectious invasions.

Figure 31. ***Rana muscosa*** (Mountain Yellow-legged Frog), a species whose tadpoles are susceptible to death from chytridiomycosis at temperatures of 17-25°C. Photo by USGS, through public domain.

Figure 32. ***Rana muscosa*** (Mountain Yellow-legged Frog) that has died from chytridiomycosis. Photo by Vance Vredenburg, NSF.gov website, through public domain.

Figure 33. Zoospores of the fungus ***Batrachochytrium dendrobatidis*** that causes **chytridiomycosis** in amphibians and other animals, in this case living on an arthropod. Photo by A. J. Cann, through public domain.

In summary, chytridiomycosis seems to be a major player in the decline of amphibians, but it is not the only cause. Amphibians are sensitive to stress, and stress can

exacerbate chytridiomycosis, but this same stress may be the primary cause. Furthermore, as will become obvious in the rest of this chapter, loss of habitat is a severe problem in parts of the world, particularly the Neotropics. In the Neotropics, it is likely that many species will disappear before they will even be described, and many of these are bryophyte inhabitants.

Moss Use in Captivity

Use of frogs in the pet industry is one of the causes for amphibian decline, but for most species this use may be minor compared to spread of disease and habitat loss. Nevertheless, it appears that the pet industry has helped in the spread of the disease.

Certain frogs have been targetted for rescue from tropical areas where their demise seems imminent (Amphibian Rescue and Conservation Project 2011). In the rescue efforts, bryophytes are often placed in plastic containers to provide a moist environment with cover that helps to keep the amphibians alive, especially during transport (Amphibian Rescue and Conservation Project 2011). In searching for various species and their relationships to mosses, I found many descriptions for preparing terraria for pets, including mosses as part of the habitat. Even biological supply companies often package frogs in mosses, especially ***Sphagnum*** (Figure 34), for shipping.

Figure 34. ***Sphagnum***, suitable packaging for amphibians. Photo by Hermann Schachner, through Wikimedia Commons.

Many species of anurans have suffered the fate of becoming pets. To this end, they are frequently sold along with a species of moss, often ***Sphagnum*** (Figure 34), to be placed with them in a terrarium or other container. The mosses can help to maintain moisture. ***Sphagnum***, in particular, can provide antibiotics that reduce chances of infections like red leg, a bacterial disease caused by any of several genera (***Aeromonas***, ***Citrobacter***, ***Escherichia coli***, ***Proteus***, ***Pseudomonas***, ***Salmonella***) (Hadfield & Whitaker 2005; PetEducation.com 2011). In the lab, we found presence of ***Sphagnum*** (Figure 34) in the aquarium/terrarium to prolong the life of the frogs and reduce incidence of red leg. It also reduced the effects of excreted ammonia and gave the frogs a place to get out of the water.

Making a Home – *Scaphiopus holbrookii* (Eastern Spadefoot, Scaphiopidae)

Like the fire-bellied toads, the Eastern Spadefoot (***Scaphiopus holbrookii***), often called the spadefoot toad, is not a member of the toad family Bufonidae. Its English name indicates its habit of using its hind feet to dig a hole in the sandy ground typical of its home, where it escapes the heat and drying atmosphere. My first experience with this unique animal was at a Girl Scout camp on the Eastern Shore of Maryland, USA, where we found it on the outdoor shower floor after dark. We put it in a jar for the night and released it the next day. To our amazement, it immediately dug a hole and disappeared! And its disappearance was rapid. Only a bit of disturbed soil indicated its former presence (Figure 35-Figure 37).

Figure 35. The Eastern Spadefoot Toad, ***Scaphiopus holbrookii***, begins to dig a hole in the ground in Maryland, USA. Photo by Janice Glime.

Figure 36. The Eastern Spadefoot Toad, ***Scaphiopus holbrookii***, digging a hole in the ground. Photo by Janice Glime.

Figure 37. The Eastern Spadefoot Toad, ***Scaphiopus holbrookii***, as it ultimately leaves only a bit of raised, disturbed soil. Photo by Janice Glime.

I don't know of any evidence that the Eastern Spadefoot uses bryophytes in its natural home, but it can make good use of them in captivity. Wright (2002) tells about a pet Eastern Spadefoot (***Scaphiopus holbrookii***; Figure 38) that made the most of the mosses provided for it as a winter home. The first batch of mosses seemed too wet, so Wright provided an additional set of dry ones. The spadefoot immediately began work and arranged the moss into an enclosure. At the rear was a thick pile of mosses, but the front had only a thin film through which the spadefoot could still see. Such instinctive behavior suggests that it may use mosses or similar vegetation structures in nature.

Figure 38. Eastern Spadefoot, ***Scaphiopus holbrookii***, on a bed of mosses. Photo © John White, with permission.

In the Aquarium - *Trachycephalus resinifictrix* (Amazon Milk Frog, Hylidae)

In aquaria, mosses such as Java moss serve as nesting substrata and hiding places for tadpoles. In Figure 39, the tadpoles of ***Trachycephalus resinifictrix*** (Amazon Milk Frog; **Hylidae**; Figure 40-Figure 42) are in the shelter of aquarium mosses. The milk frog derives its name from its habit of exuding a toxic, milky-white substance when threatened (Amphibian Rescue and Conservation Project 2010). Not only does this substance deter predators, but it helps to keep the frog hydrated, although it would seem to be stealing from itself to do so. This is one of the largest of the South American treefrogs, with males up to 10 cm and females 11.4 cm vent to snout. Their large size and concomitant large vocal sacs permit them to make very loud calls.

Figure 39. Tadpoles of the Amazonian Milk Frog ***Trachycephalus resinifictrix*** using mosses for cover in an aquarium. Photo by Milan Kořínek, with permission.

Figure 40. ***Trachycephalus resinifictrix*** adult. Photo by Milan Kořínek, with permission.

Figure 41. Adult ***Trachycephalus resinifictrix*** (Amazon Milk Frog) in amplexus. Photo by Milan Kořínek, with permission.

Figure 42. Adult ***Trachycephalus resinifictrix*** on a moss in nature at last! Note how different this morph is from the ones in the photo above. Photo by Philippe Kok, with permission.

Summary

Many of these anurans, especially in the tropics, are on the IUCN protected list, largely due to habitat loss and pollution. Stresses due to habitat changes most likely contribute to the increasing occurrences of the fungal disease **chytridiomycosis**. Most of the tropical anurans lack legal protection because they are so poorly

known, but they may be rapidly disappearing due to habitat loss and pollution. Peatland species may be especially vulnerable as the area of peatlands on the planet continues to diminish and become fragmented. Species in tropical forests may disappear due to habitat destruction before we even know they exist. Our lack of knowledge about the role of bryophytes in the various life stages of amphibians could hinder our ability to preserve these fascinating species.

Since most of these frogs have cryptic coloration that makes them almost invisible among lichens and bryophytes on trees, they are likely to be further endangered by air pollution that causes loss of this cryptogamic flora. Furthermore, in areas of deforestation, it will be many years before new forests develop the kind of epiphytic flora in which they are so well camouflaged. Under these circumstances they are likely to experience the same sorts of selection pressures for loss of some color variants as that seen in the classic example of the peppered moths (*Biston betularia*) due to loss of lichens.

Stresses make the amphibians more susceptible to disease. Among these is red leg, a common bacterial disease caused by ***Aeromonas hydrophila***. Its ability to cause hemorrhaging causes the legs to become red.

Chytridiomycosis, a fungal disease caused by ***Batrachochytrium dendrobatidis***, has been causing severe declines. In the tropics, it is the higher elevation populations that are most susceptible, offering the optimal temperature conditions. Hence, in these bryologically dense habitats, the anuran inhabitants may disappear. In some habitats, bryophytes may provide a safe resting place for chytrid zoospores that can eventually infect amphibians that journey across them. For frogs that are more mobile, there is more opportunity for contact with infected frogs or with deposits of zoospores on bryophytes and other substrates.

Mosses are used to provide suitable conditions for anurans in captivity. In experiments with spadefoot toads (***Scaphiopus holbrookii***), the toads rearranged the mosses to create their "comfortable" moisture level. Amphibian pet trade accounts for some of the losses of the colorful anurans. Mosses are often used in both transport containers and terraria for keeping these pets.

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CHAPTER 14-3
GROUND-DWELLING ANURANS

Janice M. Glime and William J. Boelema

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Figure 1. ***Nannophryne variegata*** (previously *Bufo variegatus*) peering from a bed of the dung moss ***Tetraplodon mnioides*** in southern Chile. This toad is most likely only a casual visitor to the ***Tetraplodon***, although the attraction of these moss capsules for flies might make it an attractive feeding location for the toad. Photo by Filipe Osorio, with permission.

Peatland Habitats

Peatland habitats have been considered inhospitable for many species of frogs due to their acidity. Some frogs are tolerant enough to breed in the ***Sphagnum*** pools, but for others, mortality is too high. However, the ***Sphagnum*** mat and associated bryophyte serve other roles in the life cycles of these amphibians (Figure 1).

In Australia, the **Sphagnum Frog**, ***Philoria sphagnicolus*** (**Limnodynastidae**; Figure 2), has good reason for its name. This frog produces large eggs that are embedded in a foamy jelly (Debavay 1993). The male excavates a shallow burrow in clumps of ***Sphagnum*** or under stones on the forest floor. The females deposit the eggs in these burrows. The tadpoles complete development into adults within the nest. It is in small numbers worldwide and is on the IUCN red list of endangered species.

Figure 2. ***Philoria sphagnicolus***, the **Sphagnum Frog**. Photo by Evan, through Wikimedia Commons.

Mazerolle (2005) determined that male calling indicated that upland ponds were preferred by frogs over bog ponds, with calls emanating from 75% of the upland ponds, but only from 25% of the bog ponds, supporting the notion that the bog ponds may be too acid. None of the minnow traps in bog ponds caught tadpoles, whereas 58% of the upland ponds had at least one trapped tadpole. Several other studies likewise found few successful attempts of amphibians to breed in peatlands (Saber & Dunson 1978; Dale *et al*. 1985; Karns 1992b).

Furthermore, Mazerolle (2005) found no evidence that frogs moved from the forest to the bog in the summer, suggesting that the bog was not a significant refuge. However, there was back and forth movement between the bog and the upland, suggesting that the bog may provide a site for rehydration at times. Karns (1992a) and Mazerolle (2001), observing a number of amphibians, found that amphibians increased in bogs following the breeding season, so perhaps at least some frogs and other amphibians use them as summer sites.

But, it appears that **Green Frogs (*Lithobates clamitans*; **Figure 3**)** will use ***Sphagnum*** for rehydration (Mazerolle 2005). In an experiment where frogs were given the choice of ***Sphagnum***, upland sifted sandy loam, and well water with a *p*H of ~6.5 (upland pond water), the frogs showed no discrimination between the ***Sphagnum*** and the upland media as a source for rehydration.

Figure 3. ***Lithobates clamitans*** sitting among ***Sphagnum***. Photo by Alexander McKelvy, with permission.

Nevertheless, it appears that ***Sphagnum*** (Figure 4) peatlands are not as inhospitable to amphibians as formerly thought. In the boreal peatlands of North America, one might find the **Northern Leopard Frog** (***L. pipiens***; Figure 4), **Wood Frog** (***Lithobates sylvaticus***; Figure 5), **Green Frog** (***L. clamitans***; Figure 3), **Mink Frog** (***L. septentrionalis***; Figure 6), **Spring Peeper** (***Pseudacris crucifer***; Figure 7), **Western Chorus Frog** (***P. triseriata***; Figure 8), and **Gray Treefrog** (***Hyla versicolor***; Figure 9-Figure 10) (Desrochers & van Duinen 2006).

In Maine, the **American Bullfrog** (***Lithobates catesbeianus***; Figure 11) and **Pickerel Frog** (***Lithobates palustris***; Figure 12) are often found, as well as **Wood Frog** (***L. sylvaticus***; Figure 5), **Green Frog** (***L. clamitans***; Figure 3), **Northern Leopard Frog** (***L. pipiens***; Figure 4), **Spring Peeper** (***Pseudacris crucifer***; Figure 7), and **Gray Treefrog** (***Hyla versicolor***; Figure 9-Figure 10) (Desrochers & van Duinen 2006). Stockwell and Hunter (1989) also examined peatland amphibians in Maine, USA, and found twelve amphibian species. Of these, 94% of the captures were anurans. The most abundant of these was ***Lithobates sylvaticus*** (**Wood Frog**; Figure 5), comprising 59% of the captures. ***Lithobates clamitans*** (**Green Frog**; Figure 3) was the second most abundant, with 30% of the captures. Despite the presence of both sexes among adults in the Maine peatlands, Stockwell and Hunter concluded that none of the frogs except ***Lithobates sylvaticus*** (Figure 5) laid eggs in the peatlands. In Minnesota, the **American Toad** (***Anaxyrus americanus***; Figure 14) is added to the previous lists as one of the dominant species (Karns 1992a; Figure 13).

Figure 4. **Pickerel Frog**, ***Lithobates pipiens*** (Ranidae), among ***Sphagnum***. Photos by Janice Glime.

Figure 5. ***Lithobates sylvaticus*** on the moss ***Atrichum***. Photo by © John White, with permission.

Figure 6. **Mink Frog**, ***Lithobates septentrionalis*** (Ranidae). Photo by Twan Leenders, with permission.

Figure 7. **Spring Peeper**, ***Pseudacris crucifer*** (Hylidae). Photo by Matthew Niemiller, with permission.

Figure 8. **Mink Frog**, ***Pseudacris triseriata*** (Hylidae). Photo by Twan Leenders, with permission.

Figure 9. **Gray Treefrog**, ***Hyla versicolor*** (Hylidae). Photo by Janice Glime.

Figure 10. **Gray Treefrog**, ***Hyla versicolor*** (Hylidae), ventral view. Photo by Twan Leenders, with permission.

Figure 11. **American Bullfrog**, ***Lithobates catesbeianus*** (Ranidae). Photo by John D. Willson, with permission.

Figure 12. The **Pickerel Frog**, ***Lithobates palustris*** (Ranidae), on a bed of terrestrial mosses. Photo by Janice Glime.

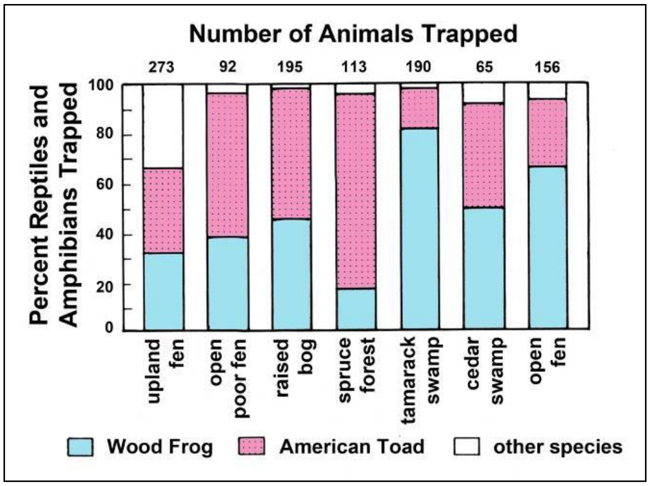

Figure 13. Comparison of percentage of **Wood Frogs** (***Lithobates sylvaticus***) with **American Toads** (***Anaxyrus americanus***) and other reptile and amphibian species trapped in various types of Minnesota peatlands. Redrawn from Karns 1992a.

The Tulula Wetlands, North Carolina, USA, have similar species to the boreal peatlands: **American Toad** (***Anaxyrus americanus***; **Bufonidae**; Figure 14), **Cope's Gray Treefrog** (***Hyla chrysoscelis***; Figure 15), **Green Frog** (***Lithobates clamitans***; Figure 3), **American Bullfrog** (***Lithobates catesbeianus***; Figure 11), **Wood Frog** (***Lithobates sylvaticus***; Figure 5), and **Spring Peeper** (***Pseudacris crucifer***; Figure 7) (Amphibians: Tulula Wetlands 2009). Knutson *et al*. (2000) suggest that the presence of **Pickerel Frog** (***Lithobates palustris***; Figure 12) is the best indicator of habitat quality in cold wetlands. Bog ponds can be especially enticing for amphibians because they harbor numerous insects and other invertebrates that serve as food (Desrochers & van Duinen 2006). Nevertheless, not all bogs seem to hold this attraction; in Estonia, frogs and toads are rare in bogs (H. Strijbosch in Desrochers & van Duinen 2006).

Figure 14. ***Anaxyrus americanus*** (**American Toad**) sitting on mosses. Photo by John D. Willson, with permission.

Figure 15. **Cope's Gray Treefrog**, ***Hyla chrysoscelis*** (Hylidae) with throat inflated while calling. Photo from US Geological Survey, through public domain.

Effects of *Sphagnum* Acidity

Because of its nearly continuous moisture, ***Sphagnum*** would seem to be an ideal habitat for frogs. But there is a caveat. ***Sphagnum*** acidifies its environment. And adult frogs typically avoid acidic conditions (Karns 1992a; Vatnick *et al*. 1999). Acidity can interfere with their development (Pough 1985; Leuven *et al*. 1986). Hence, it appears that low *p*H bog ponds might be of little or no importance in successful breeding and reproduction, but can be detrimental or lethal during tadpole development for most anurans (Gosner & Black 1957).

Rorabaugh (2008) found that the use of New Brunswick peatlands by the juvenile and adult **Northern Leopard Frogs** (***Lithobates pipiens***; Figure 4) peaked in August, a time when juveniles disperse from the breeding ponds (Mazerolle 2001). But *p*H is a problem for them. Tadpoles were unable to survive at *p*H less than 4, and even at less than *p*H 5.6 for more than 24 hours, mortality was high (Rorabaugh 2008).

As already suggested, ***Sphagnum*** can present problems for frogs because of the low *p*H conditions it creates. The **Wood Frog**, ***Lithobates sylvaticus*** (Figure 5), has tolerance to the lowest *p*H values measured in the New Jersey Pine Barrens, USA (Johnson 1985; Freda & Dunson 1986). In nine Maine bogs, Stockwell and Hunter (1985) found the **Wood Frog** to be the most common of the amphibians (59% of amphibians and reptiles). Karns (1979) never found tadpoles of this species at a *p*H lower than 5.0, although Johnson (1985) determined that eggs could develop normally at *p*H 4.0. Freda and Dunson (1985) showed that tadpoles of ***L. sylvaticus*** experienced lower sodium, chloride, and water concentrations in a low-*p*H pond (4.05-4.90) than did those from a nearby pond with a *p*H of 5.74-6.37. Higher sodium efflux occurred in both populations when placed in the lower *p*H pond, demonstrating the effect of low *p*H on ionic regulation in the tadpoles. This ability to exist in low *p*H water gives them an advantage – their predators are unable to survive the low *p*H, giving the tadpoles a huge advantage (See

discussion of overwintering and the anecdotal story by Dick Andrus).

Mazerolle and Cormier (2003) reported that they had captured **Green Frog** tadpoles in some of the bog ponds. However, they considered these ponds to be marginal, with an average *p*H of 3.67 (Mazerolle 2005), whereas the LC_{50} (*p*H at which 50% of frogs died) for **Green Frog** tadpoles in one study was 3.36 (Freda & Taylor 1992). Hence, the habitat was indeed marginal and indicated its importance despite its near-lethal *p*H. On the other hand, ***Lithobates clamitans*** (**Green Frog**; Figure 3) was among the most common (29%) of the amphibians and reptiles trapped in nine Maine, USA, bogs (Stockwell & Hunter 1985). In contrast, Brooks *et al*. (1987) found 13 amphibians and reptiles in peatlands of the Pocono Mountain region of Pennsylvania, USA, but none was common. The **Green frog** and ***Lithobates sylvaticus*** (**Wood Frog**; Figure 5) were not among the most common there. In Minnesota, the **Wood Frog** was the dominant amphibian (47% of all amphibian and reptile captures), but the **Green Frog** was conspicuously absent (Karns 1992a). Rather, in the Minnesota peatlands the **American Toad** (***Anaxyrus americanus***; Figure 14) was among the most common. Karns attributed this to more pools in the Maine peatlands, favoring the more aquatic **Green Frog**.

Not all amphibians are equally susceptible to the effects of low *p*H. Freda and Dunson (1986) found that in central Pennsylvania and the New Jersey Pine Barrens, USA, the **Jefferson Salamander** (***Ambystoma jeffersonianum*; Ambystomatidae**) and **Fowler's toad** (***Anaxyrus fowleri***, formerly *Bufo woodhousei*; Figure 16) were intolerant of water with a low *p*H. These two species had significantly higher mortality in ponds with low *p*H. In addition, ***Pseudacris triseriata***, ***P. crucifer***, ***Lithobates pipiens*** (Figure 4), ***Hyla versicolor*** (Figure 9-Figure 10), and ***Anaxyrus*** (=*Bufo*) ***americanus*** (Figure 14) were negatively affected by low *p*H water found in bog lakes. In laboratory experiments, ***Anaxyrus fowleri*** (Figure 16 and ***Hyla andersonii*** (**Pine Barren Treefrog**; Figure 17) exhibited significantly slower growth under acidic conditions, perhaps helping to explain the global decline in amphibians under the bombardment of acid rain. Freda and Dunson suggested that the small but erratic fluctuations of *p*H in the New Jersey ponds could contribute to their demise. They found that a *p*H change of only 0.2 units could alter hatching success. Contributions from acid rain could alter the *p*H sufficiently to kill sensitive eggs and larvae if the event were to occur at a critical time. In ponds where ***Sphagnum*** or other mosses are contributing H^+ ions, this additional input could to be lethal.

On the other hand, in these same locations the **Wood Frog** (***Lithobates sylvaticus***; Figure 5) and the **Pine Barrens Treefrog** (***Hyla andersonii***; Figure 17) tadpoles occurred in ponds with the lowest *p*H values, with the latter hatching at a *p*H as low as 3.70 (Freda & Dunson 1986). Ling *et al*. (1986) in Marquette County, Michigan, and Karns (1992b) in northern Minnesota, USA, found a similar tolerance for low *p*H in tadpoles of ***Lithobates sylvaticus*** (Figure 5). The larvae were seemingly unaffected when reared at *p*H as low as 3.0 (Ling *et al.* 1986). But further study is needed to explain the survival of ***Hyla andersonii*** at such low *p*H levels when the same authors (Freda & Dunson 1986) have demonstrated that low *p*H has a negative effect on its growth.

Figure 16. **Fowler's Toad** (***Anaxyrus fowleri***) sitting on ***Plagiomnium***. Photo by Twan Leenders, with permission.

Figure 17. ***Hyla andersonii*** (**Pine Barrens Treefrog**). Photo by Bruce Means, US Fish & Wildlife Service, with permission.

It is perhaps encouraging that proximal populations of ***L. sylvaticus*** (Figure 5) may differ. Karns (1992b) found that both embryos and larvae of ***L. sylvaticus*** from northern Minnesota peatlands had a greater tolerance for the low *p*H of bog water than did those that came from a circumneutral marsh in southern Minnesota. However, Karns concluded that the preference of this species for fen sites (higher *p*H) was due to being born there and not to avoidance of bog water.

Acid as a Refuge - *Rana arvalis* (Moor Frog, Ranidae)

The Moor Frog (***Rana arvalis***; Figure 18) occurs in many European countries. This frog can be the only frog species in some upland Lithuanian bogs (Ðireika & Staðaitis 1999). As many as 20 individuals may be found in 0.1 hectare. However, throughout Europe it inhabits a wide range of habitats. In Siberia it occurs primarily in open swamps.

Figure 18. The **Moor Frog**, ***Rana arvalis*** on ***Sphagnum***. Photo by Piet Spaans, through Creative Commons.

This is one of the few species that is able to breed in acid peat bogs (Figure 19) because the acidic water is not suitable for frog egg development in most species (Klaus Weddeling, Bryonet 26 March 2011). Šandera (pers. comm. 20 February 2011) suggested that the frogs may hide in mosses in the summer to maintain moisture. Extensive fishery and agriculture threaten the future of ***Rana arvalis*** (Figure 18) (Šandera *et al*. 2008.

Figure 19. ***Rana arvalis*** in amplexus with the male on top. Notice the difference in coloration between the male and female. Photo by Martin Šandera, with permission.

Moisture Refuge

The **Wood Frog** (***Lithobates sylvaticus***; Figure 5) also may use ***Sphagnum*** as a "refugium" when it is migrating to its summer habitat and during the daytime in forested wetlands (Baldwin *et al*. 2006). The moisture and protection from the sun permit it to survive its trek to its new home. At least in Maine, USA, forested wetlands with *Sphagnum* are important in their migratory success. It is time to let the world know that to save the frogs we may need to save the mosses!

As already discussed, frogs need moisture. Hence, Mazerolle (2005) investigated the use of ***Sphagnum*** bogs (peatlands) by **Northern Green Frogs, *Lithobates*** (=*Rana*) ***clamitans melanota*** (Figure 20), in New Brunswick, Canada, to look for indications that the low *p*H would deter them from use of the moist habitat of the bog.

Figure 20. **Green Frog**, ***Lithobates clamitans***. Photo by Tony Swinehart, with permission.

Burrows in the Bog Moss

The **Common Frog** in Europe (***Rana temporaria***; Figure 21) inhabits raised bogs, blanket bogs, and fens (Peatlands 2009). Ida Bruggeman (pers. comm. 5 February 2009) observed them in her own Netherlands garden peatland, where they sometimes would burrow into holes dug by **Green Frogs** (***Pelophylax***). They never seemed to dig their own holes, however. She was able to observe ***P. rubicundus*** digging a burrow in which it would sit for hours (Figure 22-Figure 24). It would return to the same burrow for several consecutive days.

Figure 21. ***Rana temporaria*** (**Common Frog**) mating. Photo by Richard Bartz, through Wikimedia Commons.

Figure 22. A green frog, ***Pelophylax ridibundus***, in a ***Sphagnum*** bank in the garden of Ida Bruggeman in The Netherlands. This one is resting in the burrow it dug. Photo by Ida Bruggeman, with permission.

Figure 23. **Marsh Frog**, ***Pelophylax ridibundus*** peering out of resting burrow in ***Sphagnum***. Photo by Ida Bruggeman, with permission.

Figure 24. An empty burrow of the green frog, ***Pelophylax ridibundus***, in a ***Sphagnum*** bank in the garden of Ida Bruggeman in The Netherlands. Photo by Ida Bruggeman, with permission.

Figure 25. **European Common Spadefoot Toad** (***Pelobates fuscus***). Photo by Christian Fischer, through Wikimedia Commons.

Retreats – Mosses Instead of Sand

The **European Common Spadefoot** (***Pelobates fuscus***; Pelobatidae; Figure 25) can occur in ***Sphagnum*** peatlands, where its retreat-making behavior might be useful (Stachyra & Tchórzewski 2004). But its typical habitat is farmland, dunes, and pinewoods (Bosman & van den Munckhof 2006). This spadefoot is also known as the garlic toad because of the odor it emits as part of its noxious exudation defense mechanism. Like so many species of amphibians, this one is also disappearing. Its need for a suitable terrestrial habitat is emphasized by its predominantly beetle diet (Nicoară *et al*. 2005).

A Toxic Bog-dweller – *Bombina bombina* (European Fire-bellied Toad, Bombinatoridae)

Native to lowland swamps and wetlands (IUCN 2011), the **European Fire-bellied Toad** is named ***Bombina bombina*** (Figure 26). [**Tautonyms** (specific name repeats the generic name) are acceptable in zoological nomenclature, but are cause for rejection in botanical nomenclature and word processor grammar checkers!] ***Bombina bombina***, common in eastern and central Europe (IUCN 2011) and from the Balkans across central and eastern Asia (Staniszewski 1998), is one of the amphibians that inhabit the highland and transitional ***Sphagnum*** peatlands in Poland (Stachyra & Tchórzewski 2004), as well as bogs in other areas. It is not a true toad, but does have a warty skin. Its name derives from its bright red-orange belly that acts as warning coloration against predators, especially as it rears up to expose its bright underbelly. Despite its toxic skin, this and several other species of fire-bellied toads are kept as pets.

When it is time to shed its skin, this slightly toxic (to humans) toad first bloats itself, making a coughing sound, then tears off its skin with its mouth and eats it for added nutrition (Wikipedia 2008). When endangered, it rolls over, exposing its colorful belly, and covers its eyes with its feet (AmphibiaWeb: *Bombina bombina* 1999). In other cases, it may arch its back and expose its brightly colored underside (Wikipedia 2010). Despite its threatening color display and distasteful poison, it still is frequently eaten.

Figure 26. **European Fire-bellied Toad** (***Bombina bombina***). Photo by Mark Szczepanek, through Wikimedia Commons.

BSTI is a protease in the skin of these frogs that is a trypsin and thrombin inhibitor (Mignogna *et al*. 1996). Mignogna and coworkers suggest that the role of this protease in the skin is to prevent the premature release or breakdown of skin peptides. But it seems likely that the protease may also have toxic properties against predators. Certainly, inhibition of thrombin can cause excessive

bleeding, but the authors did not test this possibility in would-be predators. Despite its use of many kinds of habitats, the disappearance of wetlands is the greatest threat to this species (AmphibiaWeb: *Bombina bombina* 1999).

Ground-Dwellers: Bufonidae (Toads)

Although a number of amphibians have the common name of toad, only members of the Bufonidae are true toads. They differ from all other amphibian families by the presence of a pair of **parotoid** glands (Figure 27) at the back of the head, behind the eyes. Most of the Bufonidae have conspicuous warts, but so do members of many other Anuran species. Otherwise, they generally resemble frogs.

North American toads have recently been moved to a different genus, based on genetics and cladistics (Naish 2009), from the well known genus ***Bufo*** to ***Anaxyrus***, a genus restricted to the North American continent. However, this move is not acceptable to all herpetologists because it makes the remaining genus ***Bufo*** paraphyletic (Pauly *et al*. 2004, 2009). Furthermore, morphological characters that unite the genus ***Anaxyrus*** and separate it from ***Bufo*** have not yet been elaborated. Nevertheless, I shall use ***Anaxyrus*** for the North American members where it is appropriate, but be aware that other genera have also been split off from ***Bufo*** as well.

Most of us know the toads from childhood and may have been told that we would get warts from handling them. But toads don't cause warts. They do, however, emit secretions that can be irritants to some people. Toads have a pair of **parotoid glands** (Figure 27) on the backs of their heads. These excrete an alkaloid poison when the animals are stressed. There is a variety of compounds in these, differing among species. The term **bufotoxin** refers to any of these. The most toxic of these is from the Cane Toad, *Rhinella marina* (previously *Bufo marinus*).

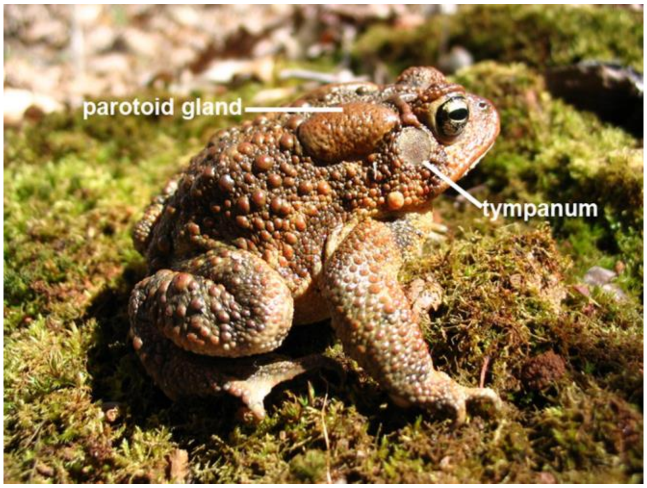

Figure 27. Head and thorax of the American Toad, ***Anaxyrus americanus***, illustrating the location of the parotoid gland and the tympanum, the external portion of the ear drum. Photo © Jason Gibson, with permission for academic use.

As already seen, toads certainly make use of bryophytes as hibernacula, where they spend the winter under the insulating blanket of clumps and thick mats. Toads spend less time in the water than do the true frogs. Hence, in addition to casual use, as is likely for ***Nannophryne variegata*** (previously *Bufo variegatus*) in Figure 1**,** we might expect somewhat different uses of the bryophytes than that seen for frogs.

Most toads lay their eggs in paired strings in open water (Figure 28) (Wikipedia 2015b). These eggs hatch into tadpoles except in ***Nectophrynoides***, whose eggs hatch directly into tiny toads.

Figure 28. ***Rhinella arunco*** (Bufonidae) strings of eggs. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

One of the strangest characteristics for toads is the ability of the male to change sex! These males have a **Bidder's organ** that can become an ovary under the right conditions (Wikipedia 2015b). But apparently this organ only becomes functional as an ovary when the testes are destroyed – an event most likely to occur in the lab (Wikipedia 2014). But it can also become functional when the testes are rendered non-functional by exposure to endocrine-disrupting chemicals. This may be somewhat adaptive in our polluted world.

Anaxyrus americanus (American Toad, Bufonidae)

Among the amphibians of the boreal peatlands in North America (Desrochers & van Duinen 2006) and the Tulula Wetlands in North Carolina, USA (Amphibians: Tulula Wetlands), one can find the widespread American Toad, ***Anaxyrus americanus*** (Figure 29-Figure 32). In Maine, USA, wetlands this species likewise occurred, but it was not abundant (Desrochers & van Duinen 2006).

It is likely that toads use bryophytes as part of a mosaic habitat. Their mottled browns and grays make them inconspicuous on the intermittent patches of soil. They can burrow under the bryophytes in winter to hibernate or burrow into them in summer to get cool or remain hydrated (Figure 30).

Terrestrial mosses may be more important than wetlands for toads. In the late autumn, I have more than once lifted a clump of moss for a collection, only to find a very quiet toad (**American Toad**, ***Anaxyrus americanus***; Figure 29) under the moss. I presumed that these animals were spending the winter there. It would seem likely that the moss would help to protect them from desiccation and cold during the winter months, and perhaps even lessen evaporative cooling. Kate Frego (personal communication 12 January 2008 and Bryonet 3 February 2009) relays this interesting story from Crepieul Township, northern Ontario (near town of Chapleau), Canada. She was working in an

upland white spruce post-fire forest, ~130 years old, with a thick carpet of ***Pleurozium schreberi*** (Figure 33). "It was quite startling! I arrived at my site before the snow melted (on purpose) and watched everything come to life. One day the ***Pleurozium*** carpet around some tree bases was literally pulsating. I was somewhat spooked, and watched for some time, from a distance!! Eventually there was a little break in the moss, and these toad feet 'swam' out, and a great fat **American Toad** pulled itself out of the opening it had made." The toad sat on the moss in the warm sun, then hopped off toward the pond. She estimates that the toad had been about 12 cm below the surface of the mosses. The pond nearby was full of **American Toad** tadpoles every year she was there, suggesting that this was an important breeding and overwintering habitat.

Figure 29. **American Toad**, ***Anaxyrus americanus***, peering through the sporophytes of ***Polytrichum***. Photo by Josh Vandermeulen, with permission.

Figure 30. Toad (***Anaxyrus***) burrowed into moss in July in the Adirondacks, eastern USA, perhaps to keep its skin moist. Photo by Sean Robinson, with permission.

To be of use to the toads, breeding habitats must be near water – ditches, pools, even vernal ponds. Eggs are laid in a long string or tube and young are hatched as tadpoles (Figure 34).

Figure 31. The common **American Toad**, ***Anaxyrus americanus***, on a bed of the moss ***Atrichum***. Photo by Twan Leenders, with permission.

Figure 32. **American Toad**, ***Anaxyrus americanus***, showing nostril, eye, tympanum, and warts. Photo by Janice Glime.

Figure 33. ***Pleurozium schreberi***, a moss where toads can emerge in the spring. Photo by Janice Glime.

Figure 34. Eggs and tadpoles of the common **American Toad *Anaxyrus americanus*** in a shallow pool. Photo by Janice Glime.

Anaxyrus boreas (Western Toad, Bufonidae)

Bartelt *et al.* (2004) used radio transmitters to demonstrate the movement patterns of 18 **Western Toads** (***Anaxyrus boreas***, previously *Bufo boreas*; Figure 35). The toads seemed to move at times and through habitats that maximized moisture conservation and selected moss cover for their movements 1.8% of the time, despite a frequency of this cover type that was near zero. Browne and Paszkowski (2010a) found that in north-central Alberta, Canada, this species used moss-covered peatland, among other habitats, during the foraging period, but they did not report use of mosses for hibernation (Browne 2010; Browne & Paszkowski 2010b).

Figure 35. ***Anaxyrus boreas*** on the forest floor where moss cover can help to maintain skin moisture. Photo by William Flaxington, with permission.

Bull (2009) found a similar preference by juveniles for mossy areas in Oregon. Young toads dispersed up to 2720 m from their site of birth within only 8 weeks after entering their adult stage. During their movement to their new summer home, they were subject to desiccation, predation (especially by birds), death by car, cattle trampling, and chytridiomycosis infection. Having mosses at 85% of the plots where juveniles occurred, compared to presence of mosses in only 3% of the area may only be a correlation with the need for the water. Mosses may have occurred in wetter areas. Nevertheless, Bull suggested that the mosses helped to provide protection from desiccation.

Bufo bufo (European Common Toad, Bufonidae)

The **European Common Toad** (***Bufo bufo***; Figure 36), which also extends into northern Africa, may be one of the few amphibians to eat bryophytes. Javier Martínez Abaigar (February 2009 pers. comm.) tells of finding bits of leaves of aquatic bryophytes, such as ***Fontinalis antipyretica*** (Figure 37), ***Chiloscyphus polyanthos*** (Figure 38), and other unidentified species, in the guts of tadpoles of this toad. Was this truly intended as food? Or did the rasping mouth tear these as it scraped algae from the leaves, or did they enter as detritus among the other edibles nestled among the bryophytes or on the bottom? In any event, I thought this would be worth exploring as a potential dispersal mechanism for the moss, but Javier says the tadpoles are confined to small, quiet pools and would provide no more dispersal than the fragment would have without the help of the tadpole, unless of course, the tadpole gets eaten.

Figure 36. Brown expression of the **European Common Toad**, ***Bufo bufo***, amid herbaceous plants and bryophytes. Photo by Milan Kořínek, with permission.

Figure 37. ***Fontinalis antipyretica***, shown here exposed out of water in early autumn, is an occasional food source for the **European Common Toad**, ***Bufo bufo***. Photo by Janice Glime.

Figure 38. ***Chiloscyphus polyanthos***, an occasional food source for the **European Common Toad**, ***Bufo bufo***. Photo by Des Callaghan, with permission.

This **European Common Toad** excretes a **bufagin** toxin that deters most predators. Unfortunately for the toad, grass snakes and hedgehogs, both predators on toads, are immune to it (Wikipedia 2015a). Females typically return to the pond where they were born to lay eggs in the spring. As adults, they are land-born, eating insects and other small invertebrates, but turnabout is fair play – larger toads may also eat grass snakes. These toads are on the IUCN (2010) red list of endangered species. They are often vulnerable when crossing roads to reach breeding grounds, causing some environmental groups to build tunnels under the road to permit safe crossing (Figure 39). Mazerolle (2005) indicates that drainage ditches may offer similar facilitation for frogs.

Figure 39. Tunnel under road to permit safe passage of the **European Common Toad *Bufo bufo*** to and from its breeding grounds. Photo by Christian Fischer, through Wikimedia Commons.

Incilius coniferus (formerly *Bufo coniferus*, Evergreen Toad, Bufonidae)

Incilius coniferus (formerly *Bufo coniferus*; **Evergreen Toad)** (Figure 40) is listed as a species of least concern (IUCN 2011), but it seems to be largely ignored. A Google search found nothing except its occurrence on several species lists. Its known distribution was on both Atlantic and Pacific slopes in east-central Nicaragua, Costa Rica, and Panama and into the Pacific lowlands of Colombia and northern Ecuador (Frost 2011).

Figure 40. ***Incilius coniferus*** (**Evergreen Toad**) blending with a bed of mosses and liverworts. Photo by Brian Gratwicke, through Creative Commons.

I could find nothing to indicate this species makes use of bryophytes for a habitat element, but the picture shown here (Figure 40) suggests that it might, and that it certainly would have good camouflage if it did. But this is not its only coloration. Most individuals are yellow-green to olive green, or even dull brown or gray, with little mottling, or sometimes with white or dark blotches (Savage 2002). The presence of warts helps to disrupt its coloration and facilitate blending with its environment. This individual seems to have combined these in just the right way to blend with the surrounding bryophytes. These color patterns help it to blend with its humid lowland forest and premontane habitat, where it is known up to 1550 m (Savage 2002). But it most likely also helps make it less conspicuous when it climbs, as much as several meters (Duellman & Schulte 1992; Savage 2002).

A further suggestion, besides its coloration, that bryophytes might be an important part of its habitat is that it eats ants and mites (Toft 1981), both of which can be abundant among bryophytes. Its oviposition doesn't offer any clues – it occurs at the beginning of the wet season, and the frogs place the eggs in temporary pools or depressions (Crump 1989). Tadpoles emerge from the eggs five days later, attesting to its aquatic, rather than terrestrial, affiliations. Is the coloration of ***Incilius coniferus*** (**Evergreen Toad;** Figure 40) just a co-incidence?

Pseudepidalea viridis (Green Toad, Bufonidae)

The green toad, ***Pseudepidalea viridis*** (previously *Bufo viridis*) (Figure 41) is a common inhabitant of peatlands in high elevation and transitional peat bogs in Poland (Stachyra & Tchórzewski 2004). This frog breeds over several months, presumably as a mechanism for greater survival in habitats that may dry up before tadpoles mature (Kovács & Sas 2009). When food gets scarce, the tadpoles may become cannibalistic, a phenomenon known in other tadpoles such as ***Anaxyrus boreas*** (Figure 35) (Jordan *et al*. 2004).

Figure 41. The **Green Toad**, ***Pseudepidalea viridis***, a peatland inhabitant. Its coloration suggests it might blend well with the mix of moss tops and dark spaces in the peatland. Photo by © John White, with permission.

Epidalea calamita (Natterjack Toad, Bufonidae)

Although this European frog, a close relative of ***Pseudepidalea viridis*** (Figure 41), inhabits sand dunes and gravel quarries (AmphibiaWeb: *Bufo calamita* 2006), the **Natterjack toad**, ***Epidalea calamita*** (previously *Bufo calamita*) (Figure 42-Figure 43), is likewise a common inhabitant of peatlands in high elevation and transitional peat bogs in Poland (Stachyra & Tchórzewski 2004). This is the only species of toad native to Ireland, where it lives near pools that stay warm (Wikipedia 2016). In The Netherlands, Strijbosch (1979) found this species selected the most eutrophic sites during its aquatic stage. Elsewhere in Europe it is common in heathlands.

Figure 42. Very young **Natterjack Toad**, ***Epidalea calamita*** climbing among the mosses. Photo by Piet Spaans, through Creative Commons.

In southern Britain, these toads avoid *Calluna* heaths, but they spend their entire lives in open areas where bare sand or short bryophyte turf dominates the landscape (Banks *et al*. 1993). It is interesting that introducing the cyprinid fish known as **ide** or **orfe** (***Leuciscus idus***; Figure 44) to the breeding pools reduced the predatory invertebrates, increasing survival of the tadpoles. Unfortunately, adults, especially males, fell prey to the grass snake (***Natrix natrix***; Figure 45).

Figure 43. Adult **Natterjack Toad**, ***Epidalea calamita***, at night. Photo by Christian Fischer, through GNU Free Documentation License.

Figure 44, ***Leuciscus idus*** (**ide** or **orfe**), a fish that reduces predators on the tadpoles of ***Epidalea calamita*** by eating the predators. Photo through Wikimedia Commons.

Figure 45. ***Natrix natrix*** (**Grass Snake**), a predator on adult **Natterjack Toads** (***Epidalea calamita***). Photo by Karl Larsaeus, through Wikimedia Commons.

Beebee (1977) attempted to determine the cause of 40 years of decline in this species. It is interesting that it was the inland heaths that had the greater decline, compared to the dunes. Climate change, human activity, and development did not seem to be a problem. Rather, large-scale changes in the heathland flora were responsible. Grazing stopped and forestry activity increased, permitting the invasion by taller vegetation and greater shade. These conditions were unsuitable for the **Natterjack Toad**, but a greater problem was the invasion of its competitor, ***Bufo bufo*** (Figure 36).

Leptophryne cruentata (Indonesia Tree Toad, Bleeding Toad, Bufonidae)

Leptophryne cruentata (Figure 46-Figure 47) is a true toad distributed in Southeast Asia, primarily Indonesia. Kusrini *et al*. (2007) found fifteen frogs hidden in a crevice covered by mosses in the wall of a waterfall. Its habit of hiding could explain its elusiveness. It is listed as critically endangered, at least partly because of the volcanic eruption of Mount Galunggung in 1982 (Wikipedia: Bleeding Toad 2008) that buried a large part of its range.

Figure 46. **Indonesian Tree Toad**, ***Leptophryne cruentata***, showing a pink-purple variety. Photo by Frank Yuwono, with permission.

Figure 47. ***Leptophryne cruentata***, the **Indonesian Tree Toad**, showing a red and yellow spotted variety. Photo by Georg Moser, with permission.

Atelopus zeteki (Panamanian Golden Frog, Bufonidae)

In tropical wet forest stream habitats, the critically endangered Panamanian Golden Frogs (***Atelopus zeteki***; Figure 48-Figure 49) can be found among mosses (Hong 2007; Lindquist *et al*. 2007). Technically a toad (Bufonidae), these amphibians look more like a tree frog. They may climb as much as 3 m near water falls, where they perch on large moss-covered boulders. But beware of these beautiful frogs. Their skin contains a highly toxic alkaloid that is an analog of **saxitoxin** (Fuhrman *et al*. 1969; Brown *et al*. 1977) and has the ability to block sodium channels in the nervous system (Yotsu-Yamashita *et al*. 2004).

Figure 48. **Panamanian Golden Frog** (***Atelopus zeteki***) sitting among bryophytes and ferns beside a stream. Photos by © John White, with permission.

Figure 49. ***Atelopus zeteki*** (**Panamanian Golden Frog**) with a conspicuous yellow dorsal view while sitting on a bed of moss. Photo by Dave Pape, through Wikimedia Commons.

Figure 50. Habitat of ***Atelopus zeteki*** (**Panamanian Golden Frog**). Photo by Brian Gratwicke, through Creative Commons.

Atelopus loettersi (Bufonidae)

This newly described species was located on the Amazonian slopes of southern Peru at 400-1000 m asl (De la Riva *et al*. 2011). Only tiny juveniles could be found, dwelling on mosses covering a large rock wall along a river bank. That appears to be all that is known about this species at this time.

Toads in the Trees: Bufonidae

Rhinella tacana (formerly *Chaunus tacana*, Bufonidae)

First named in 2006 (Padial *et al* 2006), ***Rhinella tacana*** (Figure 51) lives in the humid forest at only one known location in Bolivia at 1500 m asl (Frost 2011). It lives in Andean valleys and Amazonian slopes. Within its habitat, it climbs moss-covered tree trunks and rests on leaves or trunks at 1-4 m height (Padial *et al*. 2006). Its reproduction is unknown and too little is known about it for classification in the IUCN redlisting (IUCN 2011).

Figure 51. ***Rhinella tacana***, a toad that climbs mossy tree trunks in Bolivia. Photo by Sean Michael Rovito, with permission.

Ansonia latidisca (Borneo Rainbow Toad, Sambas Stream Toad, Bufonidae)

The **Sambas Stream Toad** (Figure 52) had not been seen since 1924 when Dr. Indraneil Das and his research team set out in 2011 to find it (Lin 2011). Just imagine the excitement of his graduate student, Pui Yong Min, who discovered it near the border of Indonesia and Malaysia, perched 2 m above ground on a moss-covered branch. But at this time, that is about all we know about it, except that it is a beautiful toad that would be a desirable pet for that reason. Therefore, to protect it, the location will not be published.

Figure 52. ***Ansonia latidisca***, **Borneo Rainbow Toad**, perched on mosses 2 m up in a tree. Photo by Indraneil Das, with permission.

Eastern Hemisphere Mossy Habitats

Arthroleptidae

Leptodactylodon albiventris (**Whitebelly Egg Frog;** see Figure 53) is endemic to Cameroon, Africa, in subtropical and tropical moist lowland forests, moist montane areas, rivers, and rocky areas (Amiet 2004). Living at 300-1000 m asl (Frost 2011), this species calls day and night from hidden locations; it finds a thin layer of water flowing under rocks or other cover and can only be located by removing the rocks, mosses, or looking among submerged roots (De la Riva *et al*. 2001).

Figure 53. ***Leptodactylodon*** sp. (**Whitebelly Egg Frog**) on leaf, member of a genus where some species hide under mosses in flowing water. Photo by Ignacio De la Riva, with permission.

Myobatrachidae

Pseudophryne (Myobatrachidae)

Several species in this genus, which is endemic to Australia, are known to be bryophyte inhabitants. Unique

to ***Pseudophryne*** species among the anurans, part of their defense is accomplished by a class of indolic alkaloids called **pseudophrynamines** (PS's). These compounds appear to be produced internally, either by the frog itself or by symbiotic organisms living within the frog (Smith et al 2002). In addition to these toxic alkaloids, they also possess **pumiliotoxins** (PTX's). The latter are found in all genera worldwide if those anurans (frogs & toads) contain lipophilic alkaloids. The PTX's appear to have a dietary source, with lab-reared animals lacking the compound. It is subsequently incorporated into the skin. An interesting consequence of high levels of this skin toxin is that it seems to inhibit the production of PS.

Pseudophryne corroboree & *P. pengilleyi* (Corroboree Frogs, Myobatrachidae)

The genus ***Pseudophryne*** is known only from Australia. The alpine species ***Pseudophryne corroboree*** (Figure 54) in New South Wales, Australia, has been split into two species with the northern one separated into ***P. pengilleyi*** (Osborne *et al.* 1996; Figure 55). Corroboree is the aboriginal name for a group meeting and the name of the frogs refers to the habit of gathering in large groups to form a chorus.

Figure 54. ***Pseudophryne corroboree***, an alpine corroboree frog from New South Wales, Australian, shown here in its peat moss (***Sphagnum***) habitat. Its bumblebee coloration is a better warning coloration than a camouflage. Photo by Scott Robinson <www.ifrog.us>, with permission.

Figure 55. The **Northern Corroboree Frog**, ***Pseudophryne pengilleyi***, in its native peatland habitat in northern New South Wales, Australia. Photo by Ken Thomas, with permission.

Both live in peatlands and often deposit their 10-38 eggs there (Pengilley 1973) in locations that become seasonally inundated. The male makes deep burrows in the ***Sphagnum*** or other substrate and proceeds to call from there to attract females. Males generally stay with the eggs for two-four weeks. Like several other moss-dwelling frogs, females may deposit several clutches of eggs, thus making smaller clutches and increasing the oxygen availability to all the eggs (Woodruff 1976). The southern species, ***P. corroboree*** (Figure 54), is in danger of extinction (Project Corroboree). Efforts to save the species include captive breeding.

Pseudophryne semimarmorata (formerly *Pseudophryne bibroni*) (Southern Toadlet, Myobatrachidae)

Pseudophryne semimarmorata (Figure 56) occurs in the extreme southeast of South Australia, southern Victoria, and eastern Tasmania, where it enjoys the status of least concern – an unusually safe designation for a small frog (IUCN 2010). It is called a toadlet due to its warty appearance, but it is not a true toad. Its typical habitats are dry forest, woodland, shrubland, grassland, and heath (Frogs of Australia 2011). The frogs hide under leaf litter or other debris (a designation that includes bryophytes) in depressions and other moist areas. They move about in their habitat by walking instead of the familiar hop we typically think of for frogs, but then many (most?) frogs walk or crawl when not trying to escape something.

Figure 56. ***Pseudophryne semimarmorata***, a species that hides under mosses in southern Australia. Note the absence of a tympanum behind the eye. Photo by John Wombey, through Creative Commons.

Males call, from burrows that the males construct, in late summer and autumn (FrogsAustralia 2005). But this species lacks any structural hearing organ (Figure 57) (Loftus-Hills 1973b; Parks & Wildlife Service, Tasmania 2010). One hypothesis is that they sense the sounds through the vibrations of the skull bones, a concept supported by the correlation between head width and auditory threshold (Loftus-Hills 1973a). They cease calling if ***Crinia victoriana*** begins calling nearby, and resume when this competing species stops (Littlejohn & Martin 1969). These two species use the same frequency band (~2500 Hz), so cessation of the call increases the efficiency of their communication.

Figure 57. ***Pseudophryne semimarmorata*** on a bed of mosses. Note the absence of a tympanum behind the eye. Photo by John Wombey, through Creative Commons.

It has an unusual reproductive behavior that befits its amphibious habitat. The nesting burrows, dug by the males, are located near water or boggy ground (FrogsAustralia 2005). The females lay their large eggs in loose clumps under litter in these shallow burrows (Frogs of Australia 2011). These must be located where they will later be flooded so that the aquatic tadpoles have a place to swim. The unusual aspect is that the eggs of one female may have up to eight different fathers and be placed in as many different nests (O'Brien 2011). These fathers stay with their fertilized eggs until they have developed into tadpoles (O'Brien 2011), a duty that lasts for at least 42 days (Parks & Wildlife Service Tasmania 2010). This promiscuous strategy by the females increases the chances that some of her eggs will be in nests that are suitably positioned for flooding at the right time (O'Brien 2011). If they are flooded too early, the eggs could be washed away, whereas if flooding is too late, the eggs can dry out. Since mosses often grow in such amphibious locations, they may play a role in the "debris" used for nesting and adult habitat.

Crinia nimbus & C. georgiana (Australian Moss Froglet, Myobatrachidae)

In Tasmania, you might hear what sounds like a ping-pong ball dropped on wood: took-tok-tok-tok-tok-tok, the call of the endemic **Australian Moss Froglet**, ***Crinia nimbus***, a cloud forest froglet (Wildlife Management 2014; Figure 58). The call of this common but narrowly distributed frog (southern mountains of Tasmania) is likely to come from its position under mosses or lichens in its nest, thus muffled by the overlying cover (Sopory & Hero 2008).

In ***Crinia nimbus***, the larval development time is greatly benefitted by temperatures as they increase from 5 to 15ºC (Mitchell & Seymour 2003). It would be interesting to learn whether the dark-colored mosses serve as black bodies to warm the habitat for these larvae in winter. If so, they could significantly increase survival because the larvae do not feed, and at 5ºC they can run out of yolk and die before reaching adulthood and food intake.

The **Australian Moss Froglet** requires mosses or lichens to maintain sufficient moisture for the development of its embryos (Mitchell 2002a). The female deposits 4-16 large eggs (Figure 59) in nests made from these in the subalpine regions of southern Tasmania (Mitchell & Seymour 2000). The frogs spend one year as larvae within any of about 10 species of mosses, lichens, and lycopods (Mitchell 2002b), and in southern Tasmania, this occurs under the snow (Mitchell & Seymour 2000). In laboratory experiments, embryos that experienced more drying than that experienced among the mosses had asymmetrical deformities and lower survivorship (Mitchell 2002a).

Figure 58. The **Australian Moss Froglet**, ***Crinia nimbus***, a small (up to 30 mm length) Tasmanian endemic that sounds like a ping-pong ball calling from its nest under mosses. Photo by Gerry Marantelli, compliments of the Amphibian Research Centre <http://www.frogs.org.au/>, with permission.

Figure 59. **Australian Moss Froglet**, ***Crinia nimbus***, eggs in their nest under mosses. Photo by Gerry Marantelli, compliments of the Amphibian Research Centre <http://www.frogs.org.au/>, with permission.

But moisture is not the only contribution of the moss. The thick gelatinous capsule around the eggs in this species affords further protection from desiccation, but it creates a formidable barrier to the entrance of oxygen (Mitchell & Seymour 2003). Models predict that the frogs should die at temperatures above 5ºC due to insufficient oxygen, but in reality, the frogs have an added advantage in the moss layers and rarely die at any of their natural temperatures (Mitchell 2002a). Not only does the moss permit aeration of both lower and upper surfaces, but the photosynthetic

oxygen production further supplements the oxygen available. At night it is safer for the frog to roam away from the protection of the moss. In the daytime, the nest of ***Crinia georgiana*** (Figure 60) in a moss bed had double the oxygen it had during pre-dawn hours (Seymour *et al*. 2000).

Figure 60. Two frogs of ***Crinia georgiana***, looking very much like two humans doing a dance! Photo by Jean-Marc Hero, with permission.

Byrne (2002) found ***Crinia georgiana*** (Figure 60) breeding in shallow temporary pools by a sloping, moss-covered granite outcrop where it "enjoys" the privilege of having a testes size at least four times that of any other species of ***Crinia***. This unusual size may be an adaptation to its habit of multiple matings (1-9) with a single female, creating sperm competition (Birkhead 1995; Byrne 2002).

Crinia tasmaniensis (Tasmanian Froglet, Myobatrachidae)

Crinia tasmaniensis, the **Tasmanian Froglet** (Figure 61), is endemic to Tasmania and must always be near water (ZipcodeZoo.com: ***Crinia tasmaniensis*** 2009). This requirement takes it to alpine areas, rainforests, bogs, swamps, fens, and peatlands, where mosses are part of its environment. Its call sounds like a bleating sheep.

Figure 61. The **Tasmanian Froglet**, ***Crinia tasmaniensis***, an inhabitant of bogs, swamps, and peatlands, among others. Photo through GNU Free Documentation License.

Geocrinia victoriana (Victoria Ground Froglet, Myobatrachidae)

Gollmann and Gollmann (1996) collected ***Geocrinia victoriana*** (Figure 62) in southwestern Victoria and from 180-1300 m in central Victoria from mosses in a roadside ditch and under grass tussocks. In laboratory experiments they demonstrated that populations from the mountains were larger when they hatched and grew faster than those from the lowland sites, but those from the southwest were similar to their counterparts at higher altitudes in central Victoria.

Figure 62. ***Geocrinia victoriana*** adult. Photo by Matt, through Creative Commons.

Summary

Although peatlands provide moist sites for adults to rest, bog ponds are often too acid. Acidification has resulted in extirpation of many species of frogs, interfering with development, but apparently the Wood Frog (***Lithobates sylvaticus***) is more tolerant and thus can inhabit low *p*H ponds without risk of predation by other amphibians. The tadpoles of the Green Frog (***Lithobates clamitans***) are apparently unsuccessful in surviving the low *p*H of bog ponds. ***Rana arvalis*** is one of the few species that is able to breed in acid peat bogs. Nevertheless, many frogs use peatlands in summer. Frogs such as ***Rana temporaria*** (European Common Frog) and ***Pelophylax*** spp. (green frogs) often make burrows in *Sphagnum* banks as a resting place in summer; other frogs may use those same burrows or tunnels and burrows made by small mammals. The ***Sphagnum*** Frog (***Philoria sphagnicolus***) male excavates a nest where the female deposits the eggs; the tadpoles remain in the nest. The destruction of peatlands can result in decreases in both numbers and diversity of anurans.

The **American Toad** (***Anaxyrus americanus***) is common in wetlands, including peatlands, as well as forests. Toads often spend the winter under bryophytes where both temperature and humidity are modulated. The bryophytes may be especially important during migrations. Some toads, such as tadpoles of the European common toad (***Bufo bufo***), may eat bryophytes, but it is possible these bryophyte fragments

come along with bacteria, algae, and other food items being scraped from their surfaces.

The Cloud Froglet Tadpoles (***Crinia*** spp.) require the moisture of mosses or lichens for the larvae to develop. The mosses also provide oxygen to the eggs and adults. Panamanian Golden Frogs (***Atelopus zeteki***) perch on mosses near waterfalls to maintain their moisture.

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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.)

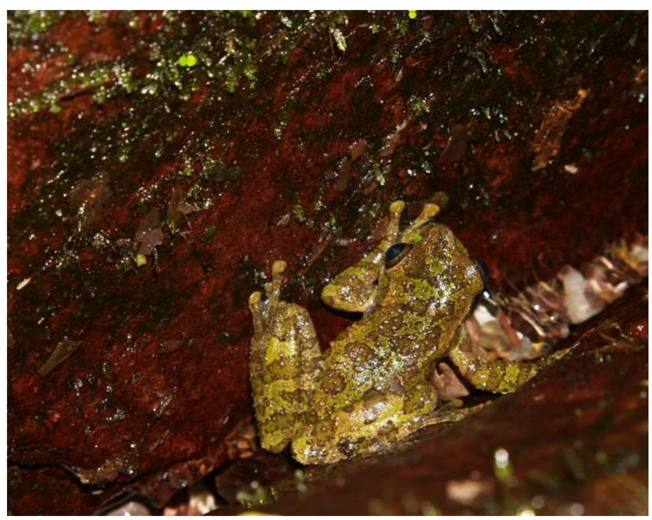

Figure 20. ***Charadrahyla nephila*** (Oaxacan Cloud-forest Treefrog) clinging to a tree and surrounded by bryophytes at La Chinantla, Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

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.

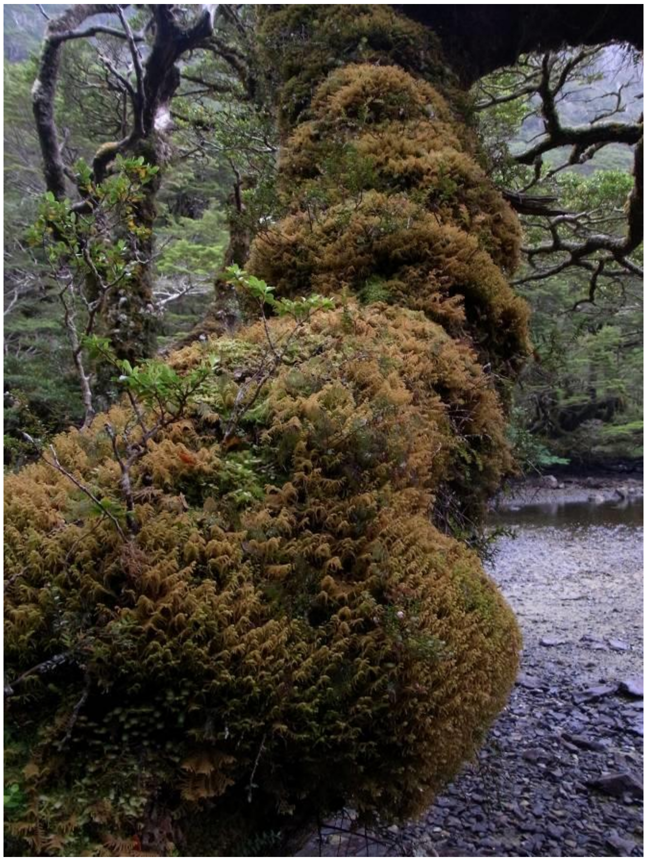

Figure 30. Leafy liverwort ***Lepicolea*** on bole at Tierra del Fuego, Peninsula Edwards, Cape Horn, Chile. This dense cover of epiphytic bryophytes provides ideal habitat where small frogs can hide. Photo by Blanka Shaw, with permission.

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?

The Coqui, in turn, contribute to the nutrient dynamics of the forest. Beard *et al*. (2002) experimented with these frogs by using cubic meter enclosures and exclosures of the frogs. When Coqui were excluded, leaf washes had 83% less dissolved organic C, 71% less NH_4^+, 33% less NO_3^-, 60% less dissolved organic N, and 60-100% less Ca, Fe, Mg, Mn, P, K, and Zn. Exclusion of the Coqui had no effect on the foliar chemistry of plants transplanted into the exclosures. However, it did decrease nutrients available from decomposing leaf litter by 12% for K and 14% for P. C:N ratios increased by 13% in the litter. These changes appear to result from Coqui waste products, resulting from the conversion of their insect diet into nutrient forms that are more accessible for microbes and plants.

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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CHAPTER 14-5
ANURANS: CENTRAL AND SOUTH AMERICAN MOSSY HABITATS

Janice M. Glime and William J. Boelema

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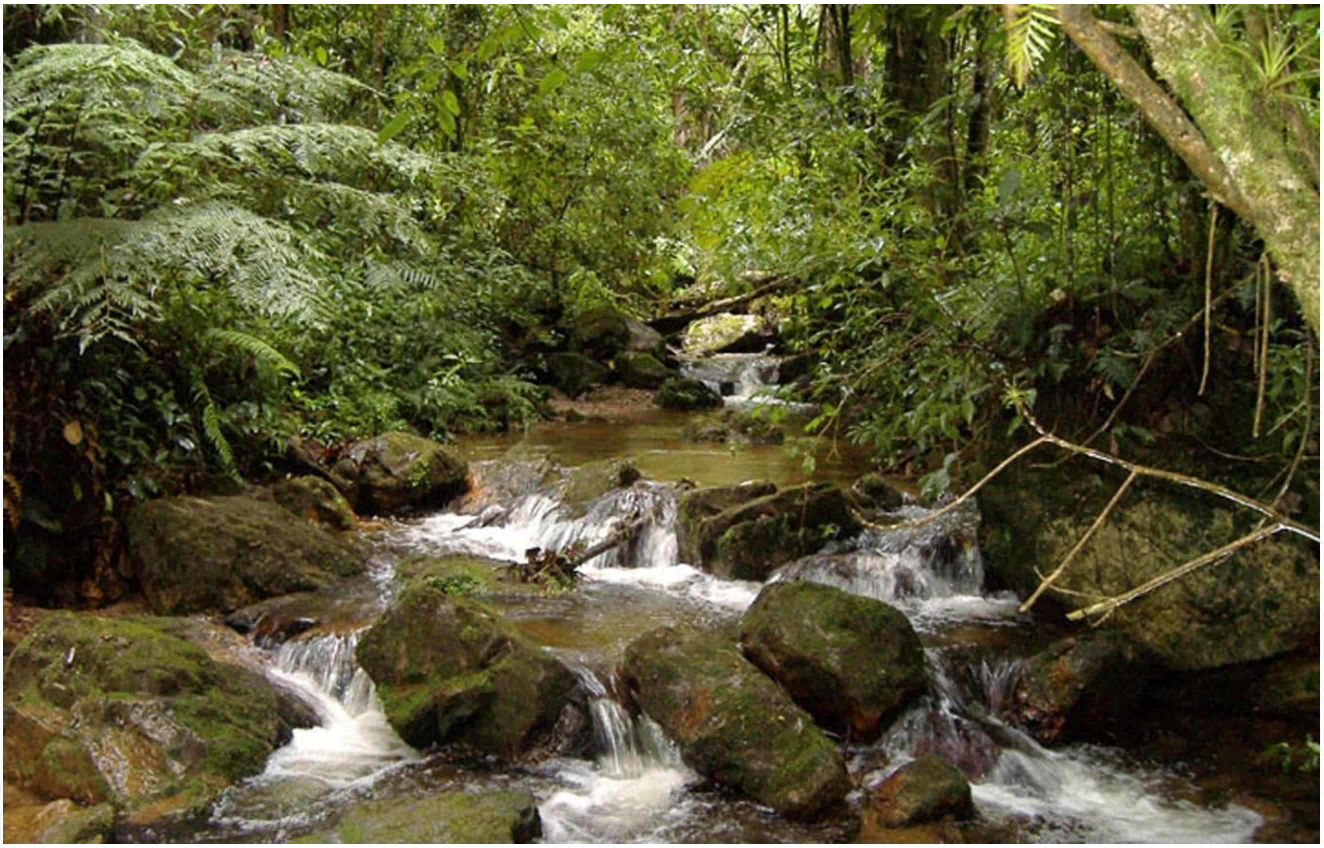

Figure 1. Waterfalls at Quebrada Cataguana Honduras, home to many disappearing anurans. Photo by Josiah Townsend, with permission.

Central and South American mossy habitats provide good places for tiny frogs. Some of these frogs are primarily stream dwellers that go ashore to feed as adults (Figure 1). Others live on the forest floor of mossy forests, or in the Páramo. But the most elusive are the ones that live in trees where mosses provide cover and moisture, as well as protection from UV light.

Strabomantidae

The giant genus ***Eleutherodactylus*** has been divided not only into a number of smaller genera, but also into several families. One of these is the **Strabomantidae**.

Bryophryne abramalagae (Strabomantidae)

Bryophryne species inhabit the cloud forests in Peru, on the eastern slopes of the Andes (Leandro 2011). ***Bryophryne abramalagae*** is primarily known from its type locality of Abra Málaga at 4000 m asl, in the puna, Provincia de La Convención, Región Cusco, Peru (Lehr & Catenazzi 2010). The males call from inside moss, maintaining their cover during this vulnerable time. The mosses also provide a reproductive site for members of the genus.

Bryophryne flammiventris (Strabomantidae)

This species occurs along the road between Vilcabamba and Pampaconas, Provincia de La Convención, Región Cusco, Peru, at 3800-3850 m asl (Lehr & Catenazzi 2010). There is some suggestion that ***B. flammiventris*** was adapted to the habitat by having coloration on the ventral side similar to that of the tree roots where the mosses were providing habitats. The male calls, made at 10:00-16:00 hours, were made from within the moss clumps and could be heard on the other side of the valley.

Bryophryne bustamantei (Strabomantidae)

Bryophryne bustamantei (Figure 2) inhabits the transitional zone from the cloud forest to the humid grassy puna in the Umasbamba Valley, Provincia de La Convención, Peru, at 3555-3950 m asl (Lehr & Catenazzi 2008; Frost 2011). The frogs are active in both the rainy and dry seasons, living under stones, in bushes and grass, and under mosses (Chaparro *et al.* 2007; Lehr & Catenazzi 2008). They lack a tympanum, separating them from several members of the genus (Lehr & Catenazzi 2008). Despite the lack of this special hearing organ, the males

call from bushes (Chaparro 2008), suggesting they are still able to hear. Like many other terrestrial anurans, their development is presumed to be direct, lacking a tadpole stage. The species is endangered due to encroachment of human activities in its narrow habitat range.

Figure 2. ***Bryophryne bustamantei*** on a leaf. Note the absence of a tympanum. Photo by Alessandro Catenazzi, with permission.

Bryophryne zonalis (Strabomantidae)

Bryophryne zonalis (Figure 3) lives in the upper Marcapata valley, at elevations of 3129-3285 m asl along the road from Huallahualla to Quincemil, Quispicanchis, Peru (Frost 2011). This frog lays her eggs in moist habitats such as under mosses (Leandro 2011). The embryos do not become tadpoles, but rather become minute terrestrial froglets. The female remains nearby the eggs to tend them, protecting them from predation and desiccation. The 18-25 eggs are only 4-5 mm in diameter, with the hatchlings measuring about 5 mm snout to vent.

Figure 3. ***Bryophryne zonalis*** on a leaf. Photo by Alessandro Catenazzi, with permission.

Bryophryne gymnotis (Strabomantidae)

Bryophryne gymnotis (Figure 4) is known only from the montane cloud forest in its type locality, San Luis, at 3272-3354 m asl, Provincia de La Convención, Región Cusco, Peru (IUCN 2013). Its habitat is mossy and it calls from mosses, like other members of its genus (Lehr & Catenazzi 2010). Leandro (2011) reported that it is the only member of the genus with a tympanum. And like ***B. zonalis***, the female tends the eggs, which hatch into froglets, often among mosses (Leandro 2011).

Figure 4. ***Bryophryne gymnotis***. Photo by Alessandro Catenazzi, with permission.

Bryophryne cophites (formerly *Phrynopus cophites)* (Cuzco Andes Frog, Strabomantidae)

In the species ***Bryophryne cophites***, the name *cophites* means "deaf" and refers to the absence of the middle and external ear (tympanum) in this species (Figure 5), separating it from several other members of the genus.

Figure 5. ***Bryophryne cophites*** on bark, showing the absence of a tympanum. Photo by Tiffany Kosch, with permission.

The species is endemic to its type locality in the Páramo and elfin forest habitats on both north and south slopes of the Abra Acanacu on the northwestern end of the Cordillera Carabaya, Peru, at 3400-3450 m asl (Frost 2011). Mosses serve as a substrate for the eggs. Its narrow distribution and continuing decline of its Peruvian Andes habitat cause it to be classified as endangered (IUCN 2010).

Catenazzi *et al*. (2011) found that the introduced fungal pathogen ***Batrachochytrium dendrobatidis*** (see Chapter 14-1) caused **chytridiomycosis**, which accounted for a large portion of amphibian decline in the Andes of Peru, further endangering this species.

Bryophryne hanssaueri (Strabomantidae)

The endemic species ***Bryophryne hanssaueri*** (Figure 6) is known only from the immediate vicinity of the type

locality (Acjanaco, Manu National Park, Paucartambo, Peru) at 3266-3430 m asl (Frost 2011). The female tends her eggs (Figure 7), which develop directly into froglets (Figure 8). It lives in mossy habitats but, like many of these tropical species, its use of the moss remains a matter of speculation.

Figure 6. ***Bryophryne hanssaueri***, an endemic species from cloud forests in southeastern Peru. Photo by Alessandro Catenazzi, with permission.

Figure 7. ***Bryophryne hanssaueri*** female tending her eggs. Photo by Alessandro Catenazzi, with permission.

Figure 8. ***Bryophryne hanssaueri*** hatching froglet. Photo by Alessandro Catenazzi, with permission.

Bryophryne nubilosus (Strabomantidae)

Bryophryne nubilosus (Figure 9) lives in the mossy montane cloud forest and montane scrub at 2350-3215 m asl in the vicinity of Esperanza, in the Cosñipata Valley, Provincia de Paucartambo, Región Cusco, Peru (Frost 2011). Its relationship to mosses needs to be verified, but it seems to be sitting on a liverwort in the picture by Alessandro Catenazzi (Figure 9).

Figure 9. ***Bryophryne nubilosus***. Photo by Alessandro Catenazzi, with permission.

Noblella pygmaea (Noble's Pygmy Frog, Strabomantidae)

Noble's Pygmy Frog (Figure 10) has already been discussed in Chapter 14-1. This tiny frog is known only from its type locality in the Cusco Region, Peru, 3100 m asl (Frost 2011). It has not yet been rated by the IUCN (2012), but it is certainly endangered with such a small distribution. However, its tiny size and presence among mosses (Lehr & Catenazzi 2009) suggest it might be more widespread but not yet detected.

Figure 10. ***Noblella pygmaea*** (**Noble's Pygmy Frog**), a tiny moss-dweller. Photo by Alessandro Catenazzin, with permission.

Psychrophrynella (formerly *Phrynopus)* (Andes Frogs, Strabomantidae)

This genus has already been discussed because many of its species call from bryophytes, often from within the moss mat. The eggs are laid under mosses and stones, where they are seldom found. They presumably undergo direct development.

The **páramo** occurs at high elevations from about 2000 m asl (the upper forest line) to 5000 m (the permanent snow line), creating a uniquely harsh environment. In the páramo at Cotapata, Bolivia, members of ***Psychrophrynella*** (**Strabomantidae**, formerly members of *Phrynopus*) live under stones or among the grasses and mosses (De la Riva 2007). For example, ***P. condoriri*** spends the day under stones in a humid area of the páramo that has abundant mosses; ***P. illimani*** lives at the border of the elfin forest and wet páramo where both the ground and rocks are covered with mosses; ***P. katantika*** was even found among mosses and ferns on old walls and ruins. Likewise at Cotapata, ***P. guillei*** calls from deep within moss clumps and ***P. iani*** calls from under stones and among mosses. But ***P. iatamasi*** stays in the forest floor mosses, calling from there during the day (Aguayo & Harvey 2001). This genus deposits its eggs under mosses and stones, but these are rarely found (De la Riva 2007). As noted earlier, the mosses provide cover for calling males, who call day or night or both.

Psychrophrynella kempffi (Figure 11) usually occurs among the mosses or under stones and logs of the cloud forest. The latter species calls with a short whistle and is difficult to locate (De la Riva 1992), perhaps because it is hidden by the mosses.

Figure 11. ***Psychrophrynella kempffi***. Photo by Ignacio De la Riva, with permission.

Psychrophrynella usurpator (Strabomantidae)

Psychrophrynella usurpator (Figure 12) is another tropical frog, known only from the vicinity of Abra Acjanacu Peru at 3270-3539 m asl, a high pass in the Cordillera de Paucartambo, which is the easternmost Andean range facing the Amazonian lowlands in Departamento Cusco, Peru (Frost 2011).

Figure 12. ***Psychrophrynella usurpator*** on a bed of mosses. Photo by Alessandro Catenazzi, with permission.

Pristimantis (South American Rain Frogs; Strabomantidae)

If you do your searching in the daytime, you might miss some of the moss dwellers. At elevations of 2500-3275 m in the Cordillera Oriental of the central Peruvian Departamentos Huainuco, Junin and Pasco, Lehr *et al*. (2006) found ***Pristimantis platydactylus*** (formerly *Eleutherodactylus platydactylus*) **(Strabomantidae)** on low vegetation and moist moss at night. However, during the day they were under dry leaves on the ground or in terrestrial bromeliads. In western Ecuador, ***Pristimantis quinquagesimus*** (previously *Eleutherodactylus quinquagesimus*) has been seen at night on leaves and mossy branches less than 2 m above the ground in cloud forests between 2000 and 2700 m asl in Provincias Imbabura and Pichincha (Lynch & Trueb 1980). Many of these frogs are nocturnal, as witnessed by their night-time calling.

One adult female of ***Pristimantis vanadise*** (formerly *Eleutherodactylus vanadise*) (**Strabomantidae)** was captured on mosses on the walls of a creek canyon in the cloud forest of the mountains of Merida, western Venezuela (La Marca 1984). All the males and some juvenile females, on the other hand, were found among the litter on the forest floor, possibly including mosses, but not near the stream.

In Ecuador, ***Pristimantis simonbolivari*** (formerly *Eleutherodactylus simonbolivari*) spends the daytime under mosses on logs as well as in leaf litter and under rotten logs (Wiens & Coloma 1992). Near a small creek, ***Pristimantis appendiculatus*** (formerly *Eleutherodactylus appendiculatus*) (Figure 13) sits on moss-covered stems or exposed fern fronds at the edge of the road at night (Miyata 1980).

Figure 13. ***Pristimantis appendiculatus*** (**Pacific Robber Frog**) on a moss-covered tree trunk. Photo by William Duellman, courtesy of Biodiversity Institute, University of Kansas.

Some species rest on leaves that have **epiphylls** (plants living on leaves), including bryophytes, especially leafy liverworts in the **Lejeuneaceae**. The ability of epiphylls to hold moisture may provide a moist niche for some frogs. ***Pristimantis ridens*** (Figure 14) is a tiny frog that spends time on epiphyll-covered leaves in Costa Rica, Honduras, and Colombia from sea level to 1600 m asl (Solís *et al*. 2010a).

Figure 14. ***Pristimantis ridens*** with epiphylls on a palm leaf. Photo by Jason Folt, through Creative Commons.

Duellman and Hedges (2005) found ***Pristimantis stictogaster*** (formerly *Eleutherodactylus stictogaster*) on the western slopes of the Cordillera Yanachago in central Peru nestled under a moss on the ground. ***Pristimantis aniptopalmatus*** (formerly *Eleutherodactylus aniptopalmatus*) occurred at 2300-2600 m, also on the western slopes, where it is known only from under moss on tree trunks and under moss on the ground in the cloud forest.

The **Santa Cecilia Robber Frog** (***Pristimantis croceoinguinis***; Figure 15) is a nocturnal frog that lives in the eastern Amazonian lowland rainforest of Ecuador and central Peru (Panguana, 200 m asl, Huanuco, southern Peru; Pakitza, 350 m asl (Madre de Dios); and Tavara (Puno) (Castro *et al*. 2004b). In Colombia it occurs mostly in the Departamento de Putumayo at 400 m asl, but also is able to survive in the low cloud forest at the base of the Pastaza trench. Although its primary habitat is the lowland primary rainforest, it is able to invade low cloud forests as well. Typically, it occurs on low vegetation 0.5-1.5 m from the ground. Its development is unknown, but it is most likely directly into tiny frogs with no free-living tadpole stage.

Figure 15. ***Pristimantis croceoinguinis*** (**Santa Cecilia Robber Frog**) in a bed of mosses. Photo by Andreas Nöllert, with permission.

In Panama, ***Pristimantis museosus*** (**Robber Frog**; Figure 16-Figure 18) is a moss-dweller whose name (*museosus*) means mossy. Also named the Vanishing Frog, it is a moss mimic, with disruptive warts, green body, and disruptive patches of darker green and brown (Figure 16-Figure 17). I suspect it can vanish in plain view among the bryophytes. It lives among low vegetation, including the mossy forest floor of humid montane forests (IUCN 2010) of the Cordillera Central of Panama at 700-1000 m asl (Frost 2011). Its egg deposition niche is unknown. This unique frog is on the IUCN endangered list due to a fragmented habitat and narrow distribution (IUCN 2010).

Figure 16. ***Pristimantis museosus***, a Panamanian moss mimic. Photo by Justin Touchon, Smithsonian Tropical Research Institute, through Public Domain.

Figure 17. ***Pristimantis museosus*** on a twig, exposing the white ventral side. If this works as it is supposed to in birds, it would make the frog less conspicuous when viewed from below against a light-colored sky, while maintaining camouflage above against moss-covered bark. Photo by Marcos Guerra, Smithsonian Tropical Research Institute, through public domain.

Figure 18. ***Pristimantis museosus*** head, showing the tubercles and color patterning that provide it with good camouflage among the bryophytes. Photo by Justin Touchon, Smithsonian Tropical Research Institute, through public domain.

Pristimantis nervicus (Figure 19) lives in extreme southeastern Costa Rica to eastern Panama, and central Colombia from 20 to 200 m asl (Savage 2002). It maintains its moisture by being night-active and living in primary humid lowland and secondary forest. Adults live under surface debris (presumably including bryophytes) and in leaf litter, often near or in caves and rocky streambanks. Its development is directly from egg to froglet.

Figure 19. ***Pristimantis nervicus*** among mosses (***Thuidium*** sp.). Photo by Rafael Marquez, with permission.

Pristimantis gaigei (**Fort Randolph Robber Frog**; Figure 20) lives in drainage lowlands in extreme southeastern Costa Rica to Panama and central Colombia (Frost 2011) from 20-200 m asl (Savage 2002). This nocturnal species occupies humid lowland and secondary forests under surface debris and leaf litter near rocky stream banks where it is likely to encounter bryophytes.

Figure 20. ***Pristimantis gaigei*** (**Fort Randolph Robber Frog**). Photo by Esteban Alzate, through Creative Commons.

Pristimantis cerasinus (**Limon Robber Frog**; Figure 21-Figure 22) lives in Atlantic lowlands and premontane slopes of Nicaragua, Costa Rica, and Panama, western and central Panama, and northeastern Honduras at 19-1500 m asl (Savage 2002; Frost 2011). The adults live among the leaf litter in the daytime, but at night they roam among the vegetation, most likely including bryophytes (Pounds *et al.* 2004). They deposit their eggs on this low vegetation.

Figure 21. ***Pristimantis cerasinus*** (**Limon Robber Frog**). Is that a bryophyte or a fern under it? Photo by Jason Folt, through Creative Commons.

Figure 22. ***Pristimantis cerasinus*** (**Limon Robber Frog**). Photo by Brian Gratwicke, through Creative Commons.

Pristimantis bacchus (**Wine Robber Frog**; Figure 23) lives in Colombia at 1740-2300 m asl. This rare species was last seen in 2002 (Castro *et al.* 2004a). Its home among ground vegetation of cloud forests makes it difficult to locate. It is unlikely that it can avoid travelling among bryophytes in this habitat, but its further use is not known.

Figure 23. ***Pristimantis bacchus*** (**Wine Robber Frog**) on a thick moss bed. Photo by Esteban Alzate, through Creative Commons.

Pristimantis mutabilis **(Strabomantidae) – A new kind of camouflage**

This unusual frog stumped its collectors. They found it among mosses in the Ecuadorian Andes and brought it back to the house in a cup (Quenqua 2015). It was unusual in having tubercles that helped it blend in with its mossy habitat (Figure 24). But when they next looked in the cup, the tubercles were gone (Figure 25) and they at first thought they had collected the wrong frog. But when they added some mosses to the cup, the tubercles returned.

Figure 24. ***Pristimantis mutabilis*** on mosses, showing the protruding tubercles. Photo by Tim Krynak, with permission.

Figure 25. ***Pristimantis mutabilis*** on a leaf, showing the disappearance of tubercles. Photo by Tim Krynak, with permission.

Ranging 17-23 mm, this frog was a new species and an interesting anomaly (Guayasamin 2015). But the researchers wondered if this anomaly occurred elsewhere. Hence, they re-examined ***Pristimantis sobetes***, a member of a different species group. And there were the tubercles when the frog sat among mosses, but gone they were on other types of substrata. Might there be other moss mimics with this peculiar behavior?

Both species live in montane cloud forests that have abundant epiphytes and bryophytes.

Yunganastes ashkapara **(Strabomantidae)**

In Peru and Bolivia, ***Yunganastes ashkapara*** (formerly *Eleutherodactylus ashkapara*; **Strabomantidae**; Figure 26) in the ***Yunganastes fraudator*** group is a **nocturnal arboreal** species that apparently finds some advantage other than moisture among the mosses. This species calls from 2.5-10 m height during the rainy season, sitting inside mosses of the cloud forest canopy (Köhler 2000; Padial *et al*. 2007). Little information seems to be available on ***Y. pluvicanorus*** (Figure 27), but it appears to occupy similar mossy habitats.

Figure 26. ***Yunganastes ashkapara*** on a bed of mosses. This species calls from within thick moss mats. Photo by Jörn Köhler, with permission.

Craugastoridae

Other members of the former *Eleutherodactylus* genus, such as ***Craugastor catalinae*** (formerly *Eleutherodactylus catalinae*) (**Craugastoridae**) in Middle America (Panama to Mexico), may conserve their moisture when they sit at night on moss-covered boulders midstream where a rapid retreat into the water is possible (Campbell & Savage 2000).

Figure 27. ***Yunganastes pluvicanorus*** on a bed of mosses. This species calls from within thick moss mats. Photo by Jörn Köhler, with permission.

Craugastor lineatus (**Montane Robber Frog**; Figure 28) has been recorded from elevations of 300-2000 m asl on the Atlantic side from Guerrero, Oaxaca, and Chiapas, Mexico, southeast to Guatemala. On the Pacific side it occurs from eastern Oaxaca through Chiapas to the southwestern highlands of Guatemala, at elevations of 300-2000 m asl (Santos-Barrera *et al.* 2004). It occupies lower montane evergreen forests and requires nearby streams for development. Unfortunately, it is rapidly declining in

Mexico, probably due to the fungal infection **chytridiomycosis.** Habitat loss through agriculture, logging, and urbanization also threaten its survival.

Figure 28. ***Craugastor lineatus*** sitting on a bed of ***Sphagnum*** at La Chinantla, Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Craugastor noblei (**Noble's Robber Frog**; Figure 29) lives in lowland and premontane evergreen forests of extreme eastern Honduras, through Nicaragua and Costa Rica, both slopes in central Panama, and in the lower portion of the premontane zone of southwestern Costa Rica, at 4-1200 m asl (Frost 2011). With its diurnal habit (Solís *et al*. 2010b) and brown color, it is dangerously visible on bryophytes, although its shape makes it look like a leaf.

Figure 29. ***Craugastor noblei*** (**Noble's Robber Frog**) on a mat of mosses in Costa Rica. Photo by Andrew J. Crawford, through Creative Commons.

Craugastor bransfordii (**Bransford's Robber Frog**; Figure 30-Figure 31) lives in humid lowlands and adjacent premontane slopes on the Atlantic mountainside from eastern Honduras and Nicaragua to central Costa Rica, 60-880 m asl (Frost 2011). It is a forest floor species, where it typically lives among leaf litter. However, as seen in Figure 30-Figure 31, it can traverse bryophytes and most likely finds a moist resting spot there.

Figure 30. ***Craugastor bransfordii*** (**Bransford's Robber Frog**) on a bed of mosses. Photo by Jason Folt, through Creative Commons.

Figure 31. ***Craugastor bransfordii*** (**Bransford's Robber Frog**) on a bed of mosses. Photo by Brian Gratwicke, through Creative Commons.

Craugastor crassidigitus (**Isla Bonita Robber Frog**; Figure 32) lives in northern Costa Rica, through Panama to the extreme northwestern border of Colombia, at 10-2000 m asl (Frost 2011). Its habitat is the humid lowland and premontane forests (Solís *et al*. 2004a).

Figure 32. ***Craugastor crassidigitus*** (**Isla Bonita Robber Frog**) on a bed of mosses. Photo by Sean Michael Rovito, through Creative Commons.

Craugastor gollmeri (**Evergreen Robber Frog**; Figure 33-Figure 35) lives in the lowland and premontane humid forests of Panama at 10-850 m asl and in eastern Costa Rica at 10-1520 m asl (Savage 2002). It lives among the leaf litter (Solís *et al.* 2004b), but where bryophytes are present they too can serve as cover or substrate during travels. Females attend the nest in this genus, but nesting sites of this species are not known.

Figure 33. ***Craugastor gollmeri*** (**Evergreen Robber Frog**) showing its leaf-like appearance. Photo by Brian Gratwicke, through Creative Commons.

Figure 34. ***Craugastor gollmeri*** (**Evergreen Robber Frog**) sitting on bryophytes. Photo by Brian Gratwicke, through Creative Commons.

Figure 35. ***Craugastor gollmeri*** (**Evergreen Robber Frog**) showing its underbelly coloration. Photo by Brian Gratwicke, through Creative Commons.

Cycloramphidae

Alsodes vittatus (Cycloramphidae)

It appears that some genera of **Cycloramphidae** in La Picada, Chile, may be dependent on mosses. ***Alsodes vittatus*** (formerly *Eupsophus vittatus*) (**Malleco Spiny-chest Frog**; see Figure 36) and ***Eupsophus roseus*** (**Cycloramphidae**; Figure 37) can be found under mosses, predominantly ***Hygroamblystegium*** (Figure 38; Formas & Vera 1980). The males of ***Alsodes vittatus*** (**Cycloramphidae**) occur under ***Sphagnum*** in water-filled cavities. Tadpoles were collected in water-filled cavities (*p*H 5.0) under ***Hygroamblystegium*** at the edge of a stream, with fifty tadpoles in one and sixteen in another cavity (Formas & Pugin 1978). Two clutches of eggs were found in similar ***Sphagnum***-covered water-filled cavities. Formas and Vera (1980) considered these two species to be derived from pond breeders, with the deposition of eggs and development of tadpoles in water-filled cavities under mosses as a derived character.

Figure 36. ***Alsodes igneus*** on a bed of bryophytes. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

Figure 37. ***Eupsophus roseus*** on a bed of bryophytes. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

Figure 38. ***Hygroamblystegium tenax*** from a dry streambed in a north-temperate stream. Photo by Janice Glime.

Eupsophus (Cycloramphidae)

In a temperate forest in southern Chile, ***Eupsophus emiliopugini*** calls from within clumps of the moss ***Racomitrium*** (Figure 39), and in bogs they excavate burrows where they can make their calls without being seen (Penna *et al*. 2005).

Figure 39. ***Racomitrium canescens*** in Iceland, demonstrating the types of mounds it can make – suitable for frogs to hide and call. Photo by Janice Glime.

Rhinoderma darwinii (Darwin's Frog, Cycloramphidae)

Protection of eggs from desiccation seems to have been one of the primary drivers in the evolution of terrestrial frogs. One of the strangest egg incubation techniques is that of the Darwin's Frog (***Rhinoderma darwinii***; Figure 40-Figure 46), a vulnerable species from Argentina and Chile. In southern Chile, these frogs live in the beech forests (Fogden & Fogden 1989). The female lays her eggs where it is somewhat damp, under litter or mosses. She abandons the eggs and several males take over the care for about 20 days (Vocal Sac-Brooding Frogs: Rhinodermatidae 2011), an unusual trait in itself. The males then each put a few eggs into their vocal sacs. Since calling season is over, the vocal sac is no longer needed for calling, so it makes a moist incubation pouch. The larvae feed on their own yolk (Jorquera 1982), but Goicoechea *et al*. (1986) used tracers to demonstrate that there is also a transfer of substances from the male to the developing larvae. In the sac for the next 50-70 days, these eggs hatch and the tadpoles complete their juvenile development (talk about a tickle in your throat!), leaving the males' mouths as froglets! (Vocal Sac-Brooding Frogs: Rhinodermatidae 2011). The males may gather a few eggs from several different clutches and not all the young will be at the same developmental stage. Meanwhile, the presence of the developing frogs makes the male look as if he is pregnant! (Figure 40).

The **Darwin's Frog** is a prey organism to birds, rodents, and snakes (Wikipedia 2011). It is protected from such attacks by camouflage. It comes in many combinations of greens and browns, typically looking like a leaf fallen on a moss, or just a leaf (Figure 46). Crump (2002) demonstrated that it selected substrate color based on its own color. Brown frogs selected brown substrata significantly more often than they selected green, and bicolored frogs likewise selected substrata that matched their color patterns. Green **Darwin's Frogs** (Figure 41), however, actually occurred less often on a green substrate, perhaps gaining an advantage by looking like a fallen green leaf or a plant on soil or other brown surface. Brooding males appeared on warmer surfaces than did non-brooding males or females.

Figure 40. Male **Darwin's Frog** (***Rhinoderma darwinii***) carrying developing tadpoles in its vocal sac, hence appearing to be pregnant. Photo by Claudio Soto-Azat, with permission.

Figure 41. Green variant of ***Rhinoderma darwinii***, blending in with the mosses and liverworts. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

This camouflage serves a second purpose. These frogs are ambush hunters, so they are able to sit undetected among the bryophytes to watch and wait for their own dinner (Figure 42).

One might ask why so many different patterns are necessary, but perhaps the predator would be able to learn a pattern if only one existed. If the frog is detected, it rolls over on its back and plays dead (Figure 43). The underside is black with white spots, a pattern recognized as warning coloration. If water is nearby, the frog jumps into the water, then floats downstream – on its back!

Figure 42. Darwin's frog (***Rhinoderma darwinii***) sitting on damp mosses in Chile. While this animal "leaf" sits still, an insect may land, unaware of the danger. At the same time, its predators often pass it by without noticing that it is a frog. Photo by Filipe Osorio, with permission.

Ceratophryidae

In Peru and Bolivia, ***Telmatobius timens*** (**Ceratophryidae**; similar species in Figure 44-Figure 45) lives in the páramo, where it spends the night sitting on rocks, on the ground, or in crevices and under mats of mosses along streams (Riva *et al*. 2005).

The specific name *timens* means frightened, scared, or alarmed (timid) and refers to the possible arrival of the infectious fungal disease **chytridiomycosis** to Bolivia (Riva *et al*. 2005). This disease has already devastated many amphibian species, including ***Telmatobius*** in Ecuador and Peru.

Figure 43. Darwin's Frog (***Rhinoderma darwinii***) playing dead by rolling on its back and exposing its black and white warning coloration. Photo by Claudio Soto-Azat, with permission.

Figure 44. ***Telmatobius culeus*** (Titicaca water frog) juvenile. Photo by Joshua Stone, through Wikimedia Commons.

Figure 45. ***Telmatobius*** sp. from northern Chile. Some members of this genus spend the night under mats of mosses near streams. Photo by José Grau de Puerto Montt, through Wikimedia Commons.

Figure 46. Color and pattern variants of Darwin's Frog, ***Rhinoderma darwinii***. Some color forms blend well with bryophytes while others are more suitable for leaf litter or other substrata. Photos by Claudio Soto-Azat, with permission.

Summary

Bryophytes offer opportunities for anurans to live in places where they might not otherwise survive. Among these are waterfalls where bryophytes provide a foothold and place to deposit eggs.

Pristimantis mutabilis is especially adapted to living among mosses by projecting tubercles that help it blend in with mosses, but withdrawing then when it is on a smooth substrate. In the cloud forests, genera such as ***Bryophryne***, ***Noblella***, ***Psychrophrynella***, ***Pristimantis***, ***Yunganastes*** use bryophytes for egg-laying, calling sites, and cover. ***Craugastor*** is more common in lowland and premontane forests where bryophytes can be common ground cover, providing moisture during travels. ***Alsodes vittatus*** lives under ***Sphagnum*** in water-filled cavities. ***Eusophus*** species call from within clumps of mosses in temperate forests in Chile. **Darwin's Frog** (***Rhinoderma darwinii***) has multiple color phases that permit the species to blend with a wide range of habitats, including bryophytes. In the páramo, ***Telmatobius timens*** finds refuge under moss mats.

In Australia, the Darwin's Frog (***Rhinoderma darwinii***) lays eggs in the mosses, then leaves them for the male to incubate, which they do in their vocal sacs after about a week of maternal care.

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CHAPTER 14-6
SALAMANDERS AND ADAPTATIONS

Janice M. Glime and William J. Boelema

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CHAPTER 14-6 SALAMANDERS AND ADAPTATIONS

Figure 1. **Four-toed Salamander** (***Hemidactylium scutatum***), predominantly a moss dweller, in a bed of mosses. Photo by John D. Willson, with permission.

Caudata (Urodela) – Salamanders

The term Caudata refers to having a tail (Figure 1), so the Caudata are the amphibians with tails. Caudata have four legs positioned at right angles to the body, and moist, smooth skin (except in newts). Some live entirely in the water, some live part of their life cycle in water and part on land, and others are entirely terrestrial or **arboreal** (in trees). Newts are salamanders that spend part of their adult life on land and part in the water.

Many salamanders live among bryophytes, and many live in areas where bryophytes form a dominant feature of the landscape. Others live in places where bryophytes are present, but scattered. Casual observations include finding salamanders in bryophyte collections, but we seldom know if this is a casual/accidental association, or if salamanders actually prefer the bryophyte habitat. Does the bryophyte offer any advantage to the salamander? There is no collection of data on the broad role of bryophytes, and most information is observational, thus not providing preferences or causality. The salamander sub-chapters represent an attempt to challenge researchers to make detailed studies on the relationships between bryophytes and salamanders.

In an attempt to be consistent with a worldwide fauna, Latin nomenclature in this chapter follows Frost (2011). English names are mostly based on the SSAR names list (Crother 2008) for North America north of Mexico, and AmphibiaWeb (Sandmeier 2010) or Frost (2011) for species that do not occur in North America north of Mexico. The order of families follows proposed phylogeny presented by Pearson and Pearson (2010), but the species presented do not, but rather one of related habitats and of convenience.

Distribution

The majority of species of salamanders occur in North America, with the largest family, Plethodontidae, being almost restricted to the western hemisphere. Of the ten families, only the Plethodontidae have a significant number of species that live in areas outside the temperate regions, *i.e.*, in the Neotropics.

If you live in the North Temperate Zone of North America, it is difficult to imagine that large parts of the world do not have salamanders. As somewhat late arrivals on the tree of life, salamanders are absent in Australia (Marc P. Hayes, pers. comm. 26 March 2011; Stan A. Orchard, pers. comm. 27 March 2011; Frost 2011) and in most of India, South America, Africa (Marc P. Hayes, pers. comm. 26 March 2011), and parts of Southeast Asia [Edmund (Butch) Brodie, Jr., pers. comm. 7 June 2011] and of course Antarctica (Frost 2011). The most species-rich areas are the Appalachian and Ozark Mountains, USA,

the Pacific coast of North America, western Europe, Japan, and China (Wake 2011). Only the Salamandridae extend into Northern Africa, southern foothills of the Himalayas, northern Vietnam, and southern islands of Japan.

The largest concentration of salamander species is in the Appalachian Mountains in eastern North America. Perhaps more striking is the distribution of the Plethodontidae, containing 70% of all salamander species. This large family is restricted to the USA, southern Canada, Mediterranean Europe, and the Korean Peninsula (1 species!). In Europe and Asia, the only plethodontids present are the limestone cave dwellers in the genus ***Speleomantes***, and only one of these (***S. supramontis***) is known to be associated with a mossy habitat. So, salamanders do not have worldwide distribution, and my North American bias in this presentation is justified.

Descriptions of salamander habitats often seem to lack detail. This is partly justifiable in that often a single individual represents the species when it is described for the first time. Even in surveys, it is typical to describe the general habitat and mention logs and rocks, but omit any mention of bryophytes. Salamanders that hide under bryophytes in the soil are treated as soil organisms and the bryophytes may or may not be mentioned. Epiphytic bryophytes that must be crossed to traverse the arboreal habitat are likewise often not mentioned. In some cases, these omissions are probably true representations of absence, but often they are in old-growth forests, cloud forests, and rainforests where this is unlikely to be the case.

I found it encouraging that Bryce A. Maxell (2005) of the Wildlife Biology Program, University of Montana, Missoula, MT, USA, not only recommended looking on and under bryophyte mats for amphibians, but the sample data sheet for ***Plethodon idahoensis*** specifically listed it among the habitats to record:

under wood/vegetation
under 4-20cm rock fragments
under >20cm rock fragments
under bryophyte mat
on bryophyte mat
in rock fracture
other_______________

This list would insure that habitat information on the bryophytes would be included in any survey using the form. On the other hand, encouraging searching of bryophytes could be seriously destructive to the bryophyte habitat. This seems to be a tricky problem.

Adaptations to Bryophytes

If you have to move through moss mats, it doesn't hurt to be shaped like a worm (Figure 2). For a salamander, that includes having short legs on an elongate body (Figure 2). Your diet necessarily changes to the mites, ants, beetles, and other small invertebrates (mostly arthropods) available. And if you wiggle and move, you attract attention, so your color should either blend in with the bryophytes or you should warn predators to beware by having bright colors that suggest you are poisonous. And if you fail to blend and someone grabs your tail, disengaging your tail while you run off can confuse your predator (Figure 3-Figure 5) (Wikipedia 2011a), especially if the detached tail continues to wiggle.

Figure 2. ***Oedipina pacificensis*** showing its small size, reduced appendages, and wormlike body that adapt it to maneuvering among mosses. Photo by Vide Ohlin, with permission for education.

Of these adaptations, most are adaptations to terrestrial living in general. Small size, short limbs, and cryptic (camouflage) coloration are the most bryological. Need for moisture is not an adaptation, but it increases the utility of the bryophytes in some habitats.

Tail Autotomy

Tail autotomy is the ability to drop the tail. Often if the salamander tail is simply dropped, it can continue to move and wiggle (Figure 3), providing a distraction that might permit the rest of the body to escape (Jim McCormac, pers. comm. April 2011). Not only that, but apparently some predators prefer the tail; consumption of the disengaged tail permits the remainder of the body more time for escape (Beneski 1989).

Figure 3. The Greenmountain Slender Salamander, ***Batrachoseps altasierrae***, with a waving disarticulated tail on the left and the escaping body in the upper left of the photo. Photo by Gary Nafis, © Gary Nafis at CaliforniaHerps.com, with permission.

And it doesn't hurt to be able to regenerate lost parts. But regeneration requires energy, and this apparently results in loss of reproductive capacity, at least in the salamander ***Batrachoseps attenuatus*** (California Slender Salamander; Maiorana 1977). On the other hand, Smits and Brodie (1995) demonstrated that in the moss-dwelling ***Oedipina uniformis*** (**Cienega Colorado Worm Salamander**) it does not appear to cause any increase in

respiratory cost. They measured respiration before and after activity of this salamander with and without an autotomized tail. Results suggest that the tail accomplishes the oxygen exchange/respiration the tail needs, but the tail is not needed to supply the rest of the salamander.

Figure 4. ***Bolitoglossa lincolni***, **Lincoln's Mushroomtongue Salamander**, with a complete tail. Note the constriction at the base of the tail that permits it to release. Photo by Sean Michael Rovito, with permission.

Salamanders have remarkable abilities to regenerate lost tissues (Figure 5), including other limbs as well as the tail (Endo *et al*. 2007; Keim 2009; Garza-García 2010). The exposed tissue after losing a tail is undoubtedly subject to bacterial infection, but following this self-amputation (**autotomy**), epidermal tissue migrates within 12 hours to cover the remaining stump (Mullen *et al*. 1996; Bryant, *et al*. 2002). In as little as twelve weeks after tail loss, some salamanders are able to achieve coordinated swimming behavior with their newly developing tails (Davis *et al.* 1990). It appears that the only serious price is loss of reproduction.

Figure 5. ***Bolitoglossa lincolni*** with short tail, suggesting it has been attacked by a predator and lost its tail, which is now regenerating. Photo by Sean Michael Rovito, with permission.

Toxicity

Living on land can often make salamanders more vulnerable to predation. They are more easily seen and more easily caught by small mammals, birds, and snakes than those in water where glares, shadows, and silt can make visibility poor. The salamanders have varying degrees of being poisonous through glands in their skin, and many either have no poison or it is too weak to be effective [Edmund (Butch) Brodie, Jr., pers. comm. 22 April 2011]. Fortunately for herpetologists, the poison is not a contact poison, but must be eaten to become noxious or dangerous. But when a snake flicks its tongue against this would-be dinner, it feels the effects of the poison from the more toxic ones.

Unfortunately for the salamander, it appears that not every snake is affected by the poison. In some cases, one or more species occurring in the same range, and with historically overlapping habitats to the salamander, have evolved immunity to the poison (Brodie *et al*. 2002; Williams *et al*. 2003; Ridenhour *et al*. 2004). For example, the garter snake (***Thamnophis*** spp.) has developed resistance to the neurotoxin **tetrodotoxin** (**TTX**). This resistance seems to have evolved independently in both related and unrelated snakes. The Sierra Gartersnake, ***Thamnophis couchii***, has elevated resistance to TTX, a toxin present in the **sympatric** (having overlapping distribution) newt ***Taricha torosa*** (**California Newt**, Salamandridae; Brodie *et al.* 2005). But the distantly related ***Thamnophis sirtalis*** (**Common Gartersnake**) also coevolved with its very poisonous sympatric newt prey, ***Taricha granulosa***, **Rough-skinned Newt**. These multiple predator-prey co-evolutions in ***Thamnophis*** seem to result from the simplicity of the genetic structure of TTX resistance in that genus, permitting the evolution of "extreme phenotypes" (Feldman *et al*. 2010), in this case, TTX resistance.

Not only does the ***Thamnophis*** snake with immunity have a broadened diet that includes newts, it becomes endowed with a bit of protection of its own! Some of these highly resistant snakes are able to ingest multiple newts safely in one meal (Williams *et al*. 2004). Williams *et al*. (2010) found that after consuming only one newt of ***Taricha granulosa***, the **Common Gartersnake** ***Thamnophis sirtalis*** retained significant amounts of active TTX in its liver for one month or more. The 42 µg in the liver that remained after three weeks is sufficient to incapacitate or even kill avian predators, and possibly also mammalian predators (Williams *et al.* 2010). Hence, the bryophytes in the ecosystem, through their housing of newts, could increase the number of snakes in the area through these interactions. ***Taricha torosa***, and all ***Taricha*** species, can dwell in bryophytes [Edmund (Butch) Brodie, pers. comm. 7 June 2011]. It is likely that other bryophyte-dwelling salamanders could be victims or promulgators of similar, as yet unexplored, relationships.

Several authors have attempted to determine the origin of the poison TTX. Possible sources include diet of poisonous arthropods, bacteria that manufacture the poison within the salamander, and manufacture by the salamander itself.

Some arthropods living among mosses are poisonous when eaten, especially mites and ants, and we know these can impart their poisons to some of the poisonous frogs that consume them (Daly & Myers 1967). Although Cardiff (2011) states that the same is true for salamanders, few salamanders eat the beetles, mites, or ants that are poisonous (David Wake, pers. comm. 21 April 2011), and no peer-reviewed study seems to be published to support this poison transfer claim.

Lehman *et al*. (2004) examined the possibility of bacterial origin of the poison TTX. Using PCR primers that amplify 16S rRNA genes, they were unable to detect any bacterial DNA in skin samples from the toxic ***Taricha***

granulosa. This provides a strong suggestion that bacteria are not involved.

Hanifin *et al*. (2002) examined the ability of ***Taricha granulosa*** to manufacture its own TTX by maintaining the newts in captivity. These newts were fed non-toxic earthworms, ***Tubifex*** worms, and crickets weekly. The levels of TTX actually increased by 20.7% after one year. Since none of these food items is poisonous, these results suggest that the newts manufacture their own poisons. Cardall *et al*. (2004) supported this view by stimulating the release of TTX in ***Taricha granulosa*** with a mild electric stimulation. Following reductions of 21-90% in TTX levels, these newts regenerated their original TTX levels in the skin during the next nine months in captivity.

It appears that toxins may be rare among the members of the largest family of salamanders, the Plethodontidae. Brandon and Huheey (1981) were the first to identify the composition of a skin toxin in the family Plethodontidae, a family with many bryophyte-dwelling species. This toxin, identified by them in ***Pseudotriton ruber*** (Figure 13) and ***P. montanus***, occurs in the skin and some organs but is most concentrated on the **dorsal** (back) surface. They determined this to be a **pseudotritontoxin**, a proteinaceous **neurotoxin**. When they experimented with its effects on mice, the mice responded by exhibiting hyperextension of their hind legs and lower back, having severe **hypothermia** (body temperature below normal), prolonged debility, coma, and death usually in 12 to 48 hours. Larger doses caused convulsions and death within as little as one hour. Young chickens, perhaps a closer model for their natural predators of reptiles and birds, had convulsions and death within minutes.

But reports of toxins in other plethodontid salamanders are rare. These salamanders are not as easy to experiment with as newts because of their small size, and for many tropical species, rarity. Brodie *et al*. (1991) have found toxicity in ***Bolitoglossa huehuetenanguensis*** (formerly *B. rostrata*), and ***B. subpalmata*** (Figure 6-Figure 7), so poisons may exist elsewhere.

Bolitoglossa subpalmata not only produces toxins, but also has behavioral responses to predators (snakes) that deter the predator (Brodie 1977; Ducey & Brodie 1991). In this case, the salamander rolls onto its back. Those salamanders from alpine areas where there were no snakes were less likely to respond with this behavior when making contact with a snake tongue.

Figure 6. ***Bolitoglossa subpalmata*** on its back in a defensive posture. Photo by Edmund (Butch) Brodie, with permission.

Figure 7. ***Bolitoglossa subpalmata*** adult with eggs. Photo by Edmund (Butch) Brodie, with permission.

Predator Avoidance

There is some suggestion that some sort of chemical cues may exist that warn other salamanders because at least some members of the family Plethodontidae are sensitive to skin chemicals from other salamanders, both their own species and others in their genus, that have been attacked. These are not documented as being poisonous, but rather elicit avoidance behavior in those salamanders sensing this danger signal (Lutterschmidt *et al*. 1994). Lutterschmidt *et al*. (1994) demonstrated this response for ***Desmognathus ochrophaeus*** (sometimes a moss-dweller) toward other ***D. ochrophaeus*** and also to others in its genus, but not to ***Plethodon richmondi*** skin extracts. This chemical does not seem to be present in the viscera of the salamanders or in damaged mealworms. Recognition of the released chemical from attacked individuals signals the nearby salamanders to flee or take cover.

Warning Coloration and Mimicry

A type of mimicry known as **disruptive coloration** helps to hide organisms in plain view and involves having a color pattern that resembles their surroundings. This is well known in the clothing worn by soldiers who need to blend with their surroundings. You probably noticed that the colors changed when the soldiers started fighting in desert habitats with little vegetation. Greens were replaced by grays.

For bryophyte-dwelling salamanders mimicry can involve resembling the bryophytes that surround them. Disruptive patterns of green, brown, and black give them the appearance of the bryophytes (Figure 8), at least from a distance. Nevertheless, most bryophyte-dwelling salamanders do not seem to mimic bryophytes. Instead, the non-colorful ones are typically shades of brown, instead mimicking the soil, bark, or a stick. This is perhaps reasonable since they could move within moss mats with little visibility, but would be conspicuous on the soil or bark where catching dinner may dictate surface movement. And brown salamanders on green moss do resemble a stick from a distance. I have not located any information to indicate that any salamanders have outgrowths that resemble moss or lichen growths, such as those seen on some frogs.

Figure 8. ***Aneides aeneus*** (**Green Salamander**) juvenile somewhat resembling its mossy habitat. However, one could argue that the blackish and yellow colors are also warning colors. Photo by Bill Peterman, with permission.

Some salamanders take advantage of camouflage on top so they are not noticed from a distance, but if a predator draws near, they can rear up and show a bright warning color on the ventral (lower) side, such as that seen for ***Taricha granulosa*** in Figure 9, or roll over onto their backs (Figure 10-Figure 11). If the predator has had a bad experience with that color combination, it is likely to retreat.

Figure 9. **Adult Rough-skinned Newt** (***Taricha granulosa***) demonstrating a defensive posture that is practiced by a number of the larger salamander species. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 10. The **Cascade Torrent Salamander**, ***Rhyacotriton cascadae***, demonstrating the brown dorsal surface that blends with the twigs among the mosses. Photo © Henk Wallays, through Creative Commons.

Figure 11. The **Cascade Torrent Salamander**, ***Rhyacotriton cascadae***. Behavior of rolling onto its back and revealing the warning color of yellow. Photo by Henk Wallays, through Creative Commons for educational use.

Müllerian mimicry is common among salamanders. **Müllerian mimicry** permits species that look like each other to protect each other through similar warning coloration. Less or non-poisonous species enjoy less predation because they look like a species that is highly poisonous. Thus a predator has a higher probability of encountering the highly poisonous common species first and learns to avoid things that look like it, including the less common weakly poisonous or non-poisonous species. Both relatively common, highly poisonous species and slightly poisonous species with small numbers can have varying degrees of red, yellow, and black warning color combinations. Interestingly, the same color combinations are prevalent among hurtful and toxic species elsewhere in the animal kingdom, including snakes, bees, and frogs.

Howard and Brodie (1971) first demonstrated the **Batesian mimetic** relationships of two toxic salamander species in the area at Highlands, North Carolina, USA. **Batesian mimicry** is the case where there is a toxic model and a non-toxic mimic that gains benefit by looking like a toxic species. It works best when the model is abundant and the mimic at least less abundant so that the predator is more likely to experience the model first. In the experiments by Howard and Brodie (1971), the highly toxic red **eft** (immature) stage of the **Eastern Newt**, ***Notophthalmus viridescens viridescens*** (Figure 12), a common moss visitor and a species that is both noxious and toxic, served as a model for the **Red Salamander**, ***Pseudotriton ruber schencki*** (Figure 13-Figure 15), a moss hibernator. After experiencing a noxious red eft, previously inexperienced chickens avoided the **Red Salamander** as well as the red eft. They still readily ate non-toxic species of ***Desmognathus***. Brandon and Huheey (1981) suggested that a **Müllerian mimicry** complex exists that has a variety of palatability levels. In **Müllerian mimicry**, a number of species, often unrelated, resemble each other and thus gain predation protection when a predator experiences another member of the group. This enhances the effectiveness of **Batesian mimics** as well because it increases the size of the pool of models. In the study by Brandon and Huheey, the poisonous (Müllerian) group includes the red eft of the **Eastern Newt** and at least some members of the **Red Salamander**; the non-poisonous Batesian species include such moss dwellers as the **Spring Salamander**, ***Gyrinophilus porphyriticus*** (Figure 16).

Figure 12. Red eft stage, ***Notophthalmus viridescens***, example of **Müllerian mimicry**. Photo by Alan Cressler, with permission.

Figure 13. ***Pseudotriton ruber***, a salamander with a strong neurotoxin, a Muellerian mimic of the red eft. This species is known to hibernate under mosses in ***Sphagnum*** peatlands. Photo by Mike Graziano, with permission.

Figure 14. ***Pseudotriton ruber***, where it is conspicuous on mosses. Photo by John White, through Creative Commons.

Figure 15. ***Pseudotriton ruber*** on mushrooms, where it is somewhat less conspicuous. Photo by John White, through Creative Commons.

Figure 16. ***Gyrinophilus porphyriticus***, a non-toxic Müllerian mimic of ***Pseudotriton ruber*** (Figure 13-Figure 15), giving it the advantage of looking like a poisonous species. Photo by Todd Pierson, with permission.

If you have no warning coloration and you are edible, it is not a good idea to advertise your presence. Instead, being still works well. And if the predator gets too close, try to look bigger or more dangerous – or drop your tail and run!

Locomotion

Locomotion provides an interesting story for bryophyte-dwelling salamanders. Limbs provide means of climbing trees and running across rocks, with arboreal species at times having large footpads that help them to cling to slippery surfaces (Wake 2011). But they also use sinuous body movements for rapid locomotion. For example, the genera ***Batrachoseps***, ***Oedipina***, ***Pseudoeurycea*** (formerly in ***Lineatriton***), and ***Phaeognathus*** have bryophyte-dwelling members with reduced limbs, and they use body movements for rapid locomotion. Some members of the often bryophyte-dwelling genus ***Bolitoglossa*** have highly webbed feet with nearly fused toes (Figure 17) that permit them to move across wet leaves and other smooth surfaces like bark. ***Aneides***, ***Chiropterotriton*** (Figure 18), ***Dendrotriton***, ***Nyctanolis*** (Figure 19), and ***Pseudoeurycea*** have bryophyte-dwelling species that are arboreal and use their long legs and toes with expanded tips to climb, but they are also aided by **prehensile tails** (tails that can be used to grasp, like that of a monkey) (Figure 18).

Figure 17. ***Bolitoglossa*** sp., illustrating the webbing on the foot that permits moving about on smooth surfaces. Photo by Ira Richling, <www.helicina.de >, with permission.

Figure 18. ***Chiropterotriton*** sp., demonstrating the long legs and prehensile tail that permit them to maneuver arboreal habitats. Photo by Timothy Burkhardt, with permission.

Figure 19. ***Nyctanolis pernix***. Photo by Todd Pierson, with permission.

Life Cycle

Having a life cycle with no aquatic stage is critical for tree dwellers, but many other species are restricted to living near water where they can lay their eggs (Figure 20-Figure 21). This is particularly true for the larger salamanders (newts) in the Salamandridae. For completely terrestrial species, having eggs that hatch into young salamanders (**direct development**) instead of tadpoles (Figure 22) facilitates this terrestrial transition. Others lay eggs near water where the larvae can easily drop or slither in.

Figure 20. Breeding adult **California Newts** (***Taricha torosa***). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Role of Bryophytes

"One does not know whether a man killing an elephant or setting fire to the grassland is harming others until one knows the total system in which his act appears." Whereas this quote from Hardin (1968) was intended to illustrate the folly of our exploitations against whole ecosystems, it also characterizes our knowledge about the interaction of bryophytes with other members of the ecosystem. The salamanders are a group of organisms that is rapidly disappearing from the planet. As I researched this chapter, it became clear to me that for salamanders in particular, there is a huge gap in our knowledge. Many species live in "mossy" habitats, but little seems to be known about their use of the bryophytes.

Figure 21. Eggs of the **California Newt** (***Taricha torosa***). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 22. Tadpole (aquatic) of **California Newt** (***Taricha torosa***). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Pictures of salamanders on bryophytes abound on the web. But beware! Bryophytes are a favorite substrate for the photographers who often take these animals to the lab to be photographed. The bryophyte in the picture does not necessarily indicate that it is a preference for the salamander.

It is difficult to find documentation that salamanders actually depend on bryophytes, even when they are often found on or among mosses and liverworts (Figure 1). Others hide there in trees or peatlands. For example, Wilson (1992) reported finding one immature salamander

under a bryophyte mat at the base of a rock face in Idaho, USA. What does that really mean? Nevertheless, there is evidence that mosses can be beneficial to salamanders for maintaining moisture, camouflage, cover during hibernation and aestivation, nests, and in a few cases foraging sites.

Moisture

Salamanders have mucous-secreting glands that help to moisten and lubricate the skin. But these are insufficient to keep the skin moist in drier habitats, and not all salamanders are equally endowed with these glands.

The need of salamanders for moisture suggests that the bryophytes might play a vital role, albeit in a spurious way. When the soil is moist and the air is cool, bryophytes may simply be there, occasionally stepped on, and probably more often avoided because the soil and litter are easier to traverse. But when conditions begin to dry, the bryophyte offers a place to replenish moisture or a wetter place to take cover. Even for those species living in the soil, a bryophyte reduces water loss, making the soil more hospitable.

Almost no experiments exist to support the role of bryophytes in the habitat of salamanders. Using the **California Newt *Taricha torosa*** (Figure 23-Figure 25), Brown and Brown (1980) demonstrated the usefulness of mosses in hydrating salamanders. This animal can be up to 20 cm long (Wikipedia 2011b), and water maintenance is important, as it is to all salamanders. In their experiments, Brown and Brown (1980) found that water uptake from wet moss equalled 66% of that in fully submersed members of the species. Furthermore, external movement of water occurred along skin channels from the ventral (lower) to the dorsal (upper) surface, suggesting that a damp substrate such as moss could hydrate an animal resting on it or walking across it (Figure 23-Figure 25).

Figure 23. Adult **California Newt** (***Taricha torosa***) posed on a bed of mosses. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 24. Front view of adult **California Newt** (***Taricha torosa***) posed on a bed of mosses. Note its low profile, permitting the abdomen to contact the moss as it moves. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Despite the wonderful pictures above by Gary Nafis, it appears that ***Taricha torosa*** often lives in habitats lacking bryophytes. David Wake (pers. comm. 31 March 2011) concurs. Nevertheless, some ***T. torosa*** and ***T. granulosa*** do indeed live where the forest is humid and epiphytic mosses are common. In these locations, this newt lives among the mosses (Gary Nafis, pers. comm. 27 April 2011; Edmund (Butch) Brodie, pers. comm. 7 June 2011). In general, however, it appears that ***Taricha torosa*** prefers less humid climates than many of the other newt species (Wikipedia 2011b). Too bad – there has been a lot of research on this species. ***Taricha torosa*** further conserves water by storing it in the bladder (Brown & Brown 1980).

Figure 25. Adult **California Newt** (***Taricha torosa***) posed on a bed of mosses where it is able to replenish its water supply. Note the rough skin. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

This research on an animal of relatively dry habitats suggests that mosses could be critically important rehydration sources for other salamander taxa with higher moisture requirements. It is interesting that for their experiments Brown and Brown (1980) chose this species, which rarely encounters bryophytes in its California coastline and in the Sierra Nevada, USA, habitats. One must wonder if the species living in habitats with bryophytes have even better ability to make use of damp bryophytes for moisture regulation. Hopefully someone will investigate this role for salamanders in the "mossy" habitats occupied by amphibians, especially in the Neotropics.

Nesting Sites

Salamander nests are common among mosses, as well as grasses, sedges, and rotting logs (Wood 1955; Salthe 1967; Harris & Gill 1980). Studlar (Bryonet 8 September 2004) shared her observations that lungless salamanders (**Plethodontidae**) may lay their eggs in moss mats in the Appalachian Mountains, USA. Bryophytes help to maintain moisture as well as to provide cover that decreases visibility of the eggs. I wonder if they provide any antibiotic service? This could be especially helpful in preventing molds from developing on the eggs since many, perhaps most, bryophytes produce secondary compounds that have antibiotic properties. On the other hand, large areas of the eggs would not be in direct contact with the bryophytes and may, therefore, derive no antibiotic benefit from their bryological neighbors.

Food Source

As you will see later in this chapter, mosses are at least occasionally consumed by a few salamanders. But are they consumed as food, or merely ingested along with invertebrates or other food matter associated with them? No experimental work seems to be available to address this question.

On the other hand, bryophytes can be home to a number of food organisms, both in the water and on land. In peatlands, one attraction for salamanders in that mossy habitat is the presence of pools that harbor numerous insects, hence providing food (Desrochers & van Duinen 2006). Searching for the food available in the terrestrial bryophytes may impart cover as protection for them during foraging. Their predators may include reptiles, fish, birds, small mammals, and even spiders, with all but the latter being prevented from entering the small spaces within moss clumps.

Hibernation and Aestivation

When one considers **hibernation** (animal state of inactivity and metabolic depression, characterized by lower body temperature and slower breathing; used for passing winter) and **aestivation** (cessation or slowing of activity during summer, especially slowing of metabolism during a hot or dry period) sites, it appears that even less is known. Some salamanders in cooler climates hibernate in the winter and may seek the shelter of bryophytes for that purpose. However, as will be seen in the table at the end of this chapter, there seems to be documentation of this use for only a few species of salamanders. In many cases, the hibernation site is simply unknown.

Most salamander species are night-active. Some may spend the day among bryophytes, where they are less likely to be detected and where moisture is greater than on rocks or even in soil. In habitats where the summer is hot and dry most of the time, aestivation can occur. This likewise is not well documented, but at least a few species are known to use mosses as a summer refuge.

Bryophytes can help to buffer the temperature, maintaining a safer range for the salamanders. Vial (1968) found that ***Sphagnum*** in the mountains of Costa Rica maintained a relatively low range of stable temperatures (9.8-16°C). Peatland mosses, in particular, may help to cool the habitat through evaporative cooling. Gnaedinger and Reed (1948) found a temperature of 1.2°C under mosses while the air temperature was -3.3°C. The mosses apparently kept the soil from freezing, although the mosses themselves were frozen to a depth of 1 cm, as was the soil where mosses were absent.

This subchapter and the next will necessarily include a lot of anecdotal information and speculation in the hope that the information will stimulate further study. I hope in the following pages to suggest species that are worthy of further investigation to determine the role that bryophytes play in their life cycle – as hibernation sites, aestivation sites, remoistening sites, cover, and nesting sites.

Summary

Newts and salamanders are known as Caudata, a term referring to their tails. The majority are distributed in the Western Hemisphere. Lungless species (**Plethodontidae**) are almost completely restricted to North America and the Neotropics.

Salamander Adaptations: Arboreal bryophyte-dwelling salamanders tend to be small, shaped like a worm, with an elongate body and short legs. Their movements are often sinuous – they slither through a moss like a snake. And some have **prehensile tails** like a monkey, adding a fifth appendage for climbing, hanging, or clinging. Their colors are typically brown with various patterns of other colors (including **disruptive coloration**), and the ventral surface may be endowed with warning coloration. Hence, their defensive behavior may be to rear up or roll on their backs, exposing the **warning colors**. Some species are poisonous and colorful, and other species living in the same area may mimic their warning coloration (**Müllerian mimicry**). When attacked on the tail, salamanders can disarticulate the tail, which may continue wiggling, distracting the predator. They typically feed on ants, beetles, mites, and other small invertebrates. Their life cycle is either fully terrestrial, often with eggs hatching into young salamanders instead of tadpoles (**direct development**), or females locate their eggs near water where the larvae can easily drop or slither into the water when they hatch. Females often defend and tend the eggs, rotating them or cleaning them to reduce bacterial and fungal infection.

Role of Bryophytes: Bryophytes are important moisture reservoirs for salamanders, and at least some have channels in the skin that direct water, gained from bryophytes, upward to their backs. The plethodontid salamanders often lay eggs in mosses, thus satisfying their need for a wet or at least moist incubation environment. Some species use bryophytes exclusively for egg laying and are true **bryobionts**. Some use mosses for winter **hibernacula**, whereas others use them as summer retreats for aestivation. Thick bryophyte mats can buffer the temperature, providing soil that is frost-free longer, or cooled by evaporative cooling and shading. At least a few use the bryophytes as foraging sites.

Specific uses are often unknown, but the co-occurrence of certain salamanders with bryophytes in most of their known habitats suggests that the bryophytes may play an important role in their lives. At the very least, they can serve as indicators of the likely presence of salamanders.

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Brodie kindly reviewed the two salamander sub-chapters and offered many suggestions and references. Gary Nafis not only gave me permission for use of numerous of his images, but he also suggested additional species I had not yet found. The CalPhoto and CaliforniaHerps websites have been invaluable for finding images **and** email addresses of the photographers, permitting me to gain permission and make contacts with the wonderfully helpful community of herpetologists. Wikipedia, AmphibiaWeb, and the IUCN websites have been invaluable for general habitat and distribution summaries and often for life history and other biological information as well, not to mention Google's fantastic search engine for both websites and published literature to verify the website information. Bryonetters, as usual, have been very helpful in seeking out other scientists and sending me anecdotal information that have made this and the succeeding subchapter as complete as they are. Others who gave permission for images are credited under the pictures. Not only have these people been helpful in providing pictures, but they have been very encouraging in the overall endeavor of these amphibian chapters. I appreciate all the individuals who placed images in the public domain where permission was not required.

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CHAPTER 14-7
HYNOBIIDAE, AMBYSTOMATIDAE, AND PLETHODONTIDAE

Janice M. Glime and William J. Boelema

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Figure 1. ***Desmognathus wrighti*** on a bed of moss, probably ***Hypnum* sp.** Photo by Bill Peterman, with permission.

Hynobiidae

This is a family of ca 36 species of medium-sized (to ~250 mm) terrestrial and semi-aquatic salamanders (Wake 2011). They occur in parts of Asia, south to Japan, and European Russia (Wikipedia 2011a). I could, however, find little information on their associations with bryophytes.

Hynobius tokyoensis (Tokyo Salamander)

Google made a link between ***Hynobius tokyoensis*** (**Tokyo Salamander**; Figure 2-Figure 3) and mosses, stating that when this species occurs on the forest floor, it can be found at the entrance of burrows, and under decayed logs, rocks, leaf litter, and moss mats (Kusano & Miyashita 1984). The eggs are deposited in water and the larvae are aquatic. The adults disperse up to 100 m from their breeding site by the time they are 4 years old, suggesting the importance of a suitable forest floor within that proximity.

This species has two completely disjunct distributions in Japan: Fukushima Prefecture southwestward to Kanagawa Prefecture and Aichi Prefecture of the Chubu District of Honshu (Matsui & Nishikawa 2001). It may be, however, that the Aichi population is actually ***Hynobius nebulosus*** (Matsui *et al*. 2001). This discontinuous distribution pattern is related to their need for areas kept moist by underground water oozing to the surface, a habitat found only in hills or small mountains (Ihara 2002). Its limited distribution makes it vulnerable to extinction (IUCN 2010).

Figure 2. ***Hynobius tokyoensis*** on a bed of moss. Photo by Henk Wallays, through Creative Commons.

Figure 3. ***Hynobius tokyoensis*** on a bed of moss. Photos © Henk Wallays, through Creative Commons.

Salamandrella keyserlingii (Siberian Salamander, Hynobiidae)

The **Siberian Salamander** seems to be the one Asian representative that has a notable association with bryophytes. It is distributed in northern Asia from Northern Hokkaido, Japan, and Sakhalin and Kurile Islands, Russia, from Kamchatka to eastern European Russia (to 45° E), south to northern Mongolia, northeastern China, and northern and northwestern Korea (Frost 2011).

It is an inhabitant of wet coniferous forests and mixed deciduous forests of the taiga, as well as riparian groves of the tundra and forest steppe (Kuzmin 1999).

This is one of the few amphibians to survive the cold of northernmost habitats. However, some salamanders do take advantage of mosses to provide their winter **hibernacula**. The **Siberian Salamanders** (***Salamandrella keyserlingii***; Figure 4), also known as Dybowski's Salamander, Manchurian Salamander, and Siberian Newt, are among the most cold-tolerant species (Potapov 1993). They can freeze for many years in the permafrost, then thaw out and go merrily on their way. Some may have been frozen for 10,000 years (Meat on the Web 2008)! This unusual animal can survive temperatures down to -50ºC, and they have been found preserved in ice with the wooly mammoth. However, there is no scientific evidence to support that ancient age for the salamanders. Rather, they probably fell into a crevasse.

Figure 4. ***Salamandrella keyserlingii***, the **Siberian Salamander**. Photo by Milŏs Anděra, with permission.

The young **Siberian Salamanders** seek out vegetation where the temperature remains above -15ºC, but adults spend the winter in moss cushions near ponds and seldom experience temperatures below -3ºC (Potapov 1993). Nonetheless, adults can actually survive several weeks of temperatures below -50ºC. Amphibians use such cryoprotectants as glucose and glycerol, but the mechanism in this salamander is unknown. The nearness to ponds is critical when they do thaw because a moist salamander, caught in the freezing temperatures, is likely to die as ice crystals draw water out of the body. Nearness to the pond permits it to seek the safety of the water.

In summer, refugia under cover are important to modulate the temperature and maintain humidity (Hasumi *et al*. 2009). For example, at Shaamar, Mongolia, humidity under logs was 85.5% while the ambient air temperature was 48.3%. Light intensity in burrows and under logs was 27 lux compared to 17,000 lux at the surface. Some of these salamanders take cover in moss mats where they are seldom found by collectors. When captured and kept in the lab, ***Sphagnum*** will help to prevent desiccation.

Ambystomatidae (Mole Salamanders)

Ambystoma laterale (Blue-spotted Salamander)

This species is distributed from southern Canada and Alaska, USA, south to the southern edge of the Mexican Plateau. It lives under logs, mosses, and damp leaves or in burrows (LeClere 2011; NatureWorks 2011). The species migrates from wetlands to the forest floor where it spends the winter in underground retreats (Douglas & Monroe 1981). The migrants typically must travel 250 m or more to these sites.

The **Blue-spotted Salamander**, ***Ambystoma laterale***, also known as Lateral Salamander, Slender Salamander, Silvery Salamander, and Tremblay's Salamander (Figure 5), occurs in central and eastern North America, but it has become endangered in the lower part of its range (Ohio, Iowa) and is listed as a species of special concern in Indiana (Center for Reptile and Amphibian Conservation and Management). However, the IUCN (2010) lists it as a species of least concern. Clearcutting has been a major contributor to its increasing rarity, but acid precipitation also contributes to embryo mortality (Pough 1976). In northeastern North America it is threatened by acid rain (DeGraaf & Rudis 1983; Knox 1999). Not only is the *p*H detrimental to its development, but larval activity is lowered at *p*H levels less than 4.5-5.0, causing larvae to be preyed upon more easily (Brodman 1993; Kutka 1994).

Figure 5. The **Blue-spotted Salamander**, ***Ambystoma laterale***. Photo by Tony Swinehart, with permission.

Ambystoma maculatum (Spotted Salamander)

The **Spotted Salamander** occurs from Nova Scotia and Gaspe Peninsula west to central Ontario, Canada, and south through the eastern USA from Wisconsin to eastern Texas and east to southern Georgia, excluding the peninsula of Florida (Frost 2011).

The **Spotted Salamander, *Ambystoma maculatum*** (Figure 6-Figure 7), also known as Brown-spotted Salamander, Violet-colored Salamander, Yellow-spotted Salamander, Spotted Eft, Large Spotted Salamander is common in peatlands (Amphibians). Their typical home is in the deciduous forest, but they need vernal pools or ponds with no fish so that their eggs can avoid predation (Wikipedia: Spotted Salamander 2008; Figure 7). Oxygen is often a problem for salamander eggs, but ***A. maculatum*** has solved this problem by having a partner (Orr 1888; Gilbert 1944; Anderson 1971).

Figure 6. ***Ambystoma maculatum*** on mosses. Photo by John D. Willson, with permission.

Figure 7. Eggs of the Spotted Salamander, ***Ambystoma maculatum***. Photo by John D. Willson, with permission.

The salamander's eggs have a jelly coat that protects the eggs from drying out. However, this coating interferes with oxygen diffusion to the developing embryo. The salamander can solve the problem by partnering with the green alga ***Oophila amblystomatis*** (Figure 8-Figure 9) (name meaning "loves salamander eggs") (Hammen 1962; Bachmann *et al.* 1986). Through photosynthesis of the alga, the eggs obtain oxygen. The salamander returns the favor by providing the alga with much-needed CO_2 for photosynthesis (Figure 10). Ryan Kerney of Dalhousie University in Halifax, Nova Scotia, Canada, carried this story further, demonstrating that the algae were actually within the cells of the embryos, closely associated with the mitochondria, and that they benefitted from the nitrogen-rich waste produced by the embryos (Petherick 2010; Thoughtnomics 2011).

Researchers have questioned how these algae become associated and enter the cells, particularly in view of the typical immune response known for vertebrates. Kerney found that the algae could be present in the oviducts of adult females, the place where the jelly sacs that surround the embryos form. This suggests the possibility that the algae are passed to the embryos by the mother, but it does not explain how they enter the cells or what prevents the immune system from attacking them. Perhaps they, like the salamanders' own cells, are recognized as part of self at the time the embryo begins to form – an hypothesis that if true could be of tremendous benefit in our understanding of immunity.

Figure 8. Embryos of ***Ambystoma maculatum*** that have symbiotic algae, ***Oophila amblystomatis***, living with them. Photo by Renn Tumlison, with permission.

Figure 9. Embryo of ***Ambystoma maculatum*** showing the symbiotic algae, ***Oophila amblystomatis***, living within its egg. Photo by Renn Tumlison, with permission.

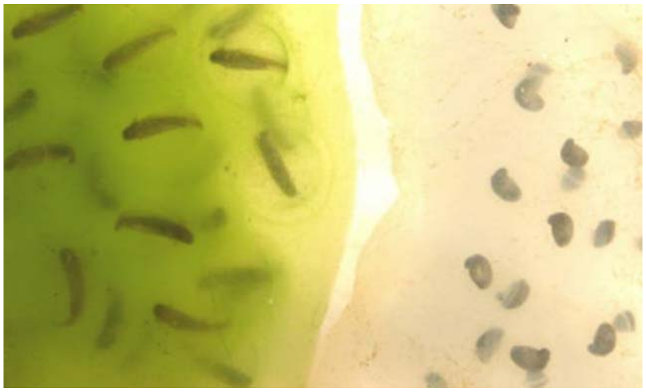

Figure 10. Comparison of embryos of ***Ambystoma maculatum*** that have symbiotic algae, ***Oophila amblystomatis***, on the **left** and no symbionts on the **right**. Photo by Renn Tumlison, with permission.

Embryos that were raised in continuous light hatched synchronously and at somewhat earlier developmental stages than those in either 12- or 24-hour darkness per day (Tattersall & Spiegelaar 2008). Those embryos without algae or in the dark moved more frequently than those with symbionts in the light. However, in later developmental stages, those in the light had more movements, suggesting that perhaps those without supplemental oxygen were conserving energy by not moving as much.

Like the frogs, larvae of salamanders are sensitive to low *p*H water. ***Ambystoma maculatum*** from three ponds in Marquette County, Michigan, USA, were raised at *p*H 3, 4, and 5 and in pond water *p*H (Ling *et al*. 1986). It took only 12 hours for the larvae to die at *p*H 3. At 4 and 5 the rates of development were significantly slower than those raised at *p*H above 5. Ling *et al*. (1986) found that 42% of the ponds in their study had *p*H levels below 5.5. Some of these were surrounded by a mat of ***Sphagnum***. In the pond with a central ***Sphagnum*** mat, and the lowest mean *p*H at 4.6, the researchers observed a slower rate of development. It is possible that under the stresses of laboratory conditions they were less tolerant of the lower *p*H than in their native ponds.

Ambystoma jeffersonianum (Jefferson Salamander)

The **Jefferson Salamander** (Figure 11) extends from central New Hampshire, USA, and southern Quebec, Canada, southwest to southern Indiana, and east to central Kentucky, western Virginia and West Virginia, USA (Frost 2011). Through a large part of this range it is able to hybridize with ***A. laterale***, complicating identification.

The Jefferson Salamander (*Ambystoma jeffersonianum*; Figure 11), also known as Granulated Salamander, Jefferson's Salamander, Plumbeous Salamander, and Brown Salamander, is among the many amphibians sensitive to conditions of low *p*H. In a study in central Pennsylvania and New Jersey Pine Barrens, USA, eggs could not hatch at *p*H below 4.5 (Freda & Dunson 1986). Those ponds with the lowest *p*H levels typically had abundant ***Sphagnum***. ***Sphagnum*** lowers the *p*H of the environment around it through cation exchange, releasing H^+ ions in exchange for cations such as Ca^{++} and Mg^{++} (Clymo 1963). In transplant experiments with embryos, mortality of ***A. jeffersonianum*** increased significantly as pond *p*H declined (Freda & Dunson 1986). The sensitivity helps to explain amphibian decline in the many sensitive species living with acid rain. A change of only 0.2 *p*H units can determine whether hatching occurs, making timing of the life cycle crucial for survival of the species.

Figure 11. ***Ambystoma jeffersonianum***. Photo by Todd Pierson, with permission.

Plethodontidae (Lungless Salamanders)

This large family is distributed on both sides of the Atlantic, from southern Alaska, USA, and Nova Scotia, Canada, south to eastern Brazil and central Bolivia, and in southern Europe and Korea (Frost 2011). But North America has most of the species. The family comprises 70% of the world's salamanders. These are known as **lungless salamanders** because they lack lungs and breathe through their skin. Most members of the large genus ***Plethodon*** prefer moist substrates (Taub 1961; Sugalski & Claussen 1997; Moore *et al*. 2001), hence making mosses near streams an ideal location for them. Nevertheless, in the tropics many species are land breeders, including many arboreal species. Bryophytes often play a role in keeping them moist as well as providing cover that hides them from predators. Their need for moisture is likely to be one reason for the preponderance of **nocturnal** (nighttime) activity among the plethodontid species.

Plethodon teyahalee, formerly *Plethodon oconaluftee* (Southern Appalachian Salamander)

Both ***Plethodon teyahalee*** (**Southern Appalachian Salamander**; also known as Teyahalee Salamander, Southern Appalachian Slimy Salamander, Balsam Mountains Salamander; Figure 12) and ***P. serratus*** (**Southern Red-backed Salamander**; Figure 13) may occur in peatlands (Amphibians: Tulula Wetlands 2009). ***Plethodon teyahalee*** is endemic to the United States, where it occurs at high elevations in the southern Appalachians, eastern USA, in other habitats as well as peatlands. Ash (1997) suggests that adults of the species may move into dry, clearcut areas to avoid competition with the smaller, immature salamanders of the same and other species in the more moist forest sites.

Figure 12. **Southern Appalachian Salamander** (***Plethodon teyahalee***). Photo by U. S. Geological Survey, through public domain.

Plethodon serratus (Southern Red-backed Salamander)

This species is also known as Ouachita Red-backed Salamander, Southern Redback Salamander, and Georgia Red-backed Salamander. The **Southern Red-backed Salamander** (Figure 13) is scattered into **disjunct** (disconnected) populations throughout southeastern USA (Frost 2011) where it hides under moss, as well as rocks and rotten logs, and migrates to seeps and springs during dry periods (Aardema 1999).

Figure 13. **Southern Red-backed Salamander** (***Plethodon serratus***). Photo by Henk Wallays, through Creative Commons.

Plethodon nettingi (Cheat Mountain Salamander)

The endangered relict **Cheat Mountain Salamander** (***Plethodon nettingi,* Plethodontidae**; Figure 14), an **endemic** in the Appalachian Mountains, West Virginia, USA, depends on bryophytes, especially the leafy liverwort ***Bazzania trilobata*** (Figure 15) (NationMaster 2008; Pauley 1985). While in the bryophyte mats, these amphibians feed on small invertebrates. Their territories are small and they seldom move more than a few meters in their lifetimes. Brooks (1945, 1948) reported finding 33 individuals on Cheat Mountain, crawling on moss-covered logs in dense stands of sapling and pole red spruce, sometimes with birch mixed in. On Bickle's Knob, West Virginia, these salamanders began appearing from mosses and under logs just after twilight (Brooks 1945).

Figure 14. **Cheat Mountain Salamander** (***Plethodon nettingi***) on bed of ***Bazzania trilobata***. Photo by Michael Graziano, with permission.

Figure 15. Branches of ***Bazzania trilobata***, home to the **Cheat Mountain Salamander**. Photo by Michael Lüth, with permission.

Plethodon cinereus (Eastern Red-backed Salamander, Plethodontidae)

The **Eastern Red-backed Salamander** (Figure 16) occurs in the northeastern USA and southeastern Canada, south through northeastern Wisconsin to southern Indiana, southern Ohio, and east of the Appalachian Divide south to northern North Carolina.

Plethodon cinereus poses a danger to the **Cheat Mountain Salamander** through competition with this much more widespread **Eastern Red-backed Salamander** (NationMaster 2008). The widespread distribution of ***Plethodon cinereus*** is reflected in having 18 English names listed by Frost (2011). This common salamander includes bogs among its habitats, where it can sometimes be found attempting to rob the pitcher plant leaves of their inhabitants (Hughes *et al*. unpubl.). Analysis of gut contents indicate a diet of midge larvae, ants, mites, and other small invertebrates that live in the bogs. I wonder if this diet makes it poisonous? The red-backed salamander can often be found under a clump of moss such as ***Leucobryum glaucum*** (Figure 17). At Cap des Rosiers, eastern Quebec, Canada, this salamander was mostly under stones and logs, but one specimen was under moss on a vertical limestone cliff face (Trapido & Clausen 1938).

Figure 16. ***Plethodon cinereus***, the **Eastern Red-backed Salamander**. Photo by Tony Swinehart, with permission.

Figure 17. ***Leucobryum glaucum*** cushions that provide suitable shelters for the **Eastern Red-backed Salamander**. Photo by Michael Lüth, with permission.

In this species, adults typically defend the territories surrounding their offspring. However, it appears that mothers cannot recognize their own offspring, nor could the offspring recognize their mothers (Gibbons *et al*. 2003). The young salamander offspring did not distinguish between mosses scented by their mothers and those with no scent or with scents of unfamiliar females. On the other hand, females chose unrelated offspring significantly more often over their own for acts of cannibalism.

Plethodon dorsalis (Northern Zigzag Salamander)

This salamander (Figure 18) often poses in a Z formation, hence its name. Other English names include Ashy Lizard, Zigzag Salamander, and Eastern Zigzag Salamander. It occurs in lower Midwestern USA from southern Indiana and southern and eastern Illinois to western Kentucky, central Tennessee, northern and western Alabama, and northeastern Mississippi (Frost 2011). Although Brode (1957) found it under sandstone slabs, Ferguson (1961) reported it from the bases of cliffs in Tishomingo County, Mississippi, USA, where it was under moist mosses, or from leaf litter.

Figure 18. ***Plethodon dorsalis***. Photo by Todd Pierson, with permission.

Plethodon welleri (Weller's Salamander)

Other English names for ***Plethodon welleri*** (Figure 19) include Spot-bellied Salamander and Spotbelly Salamander. **Weller's Salamander** occurs at higher elevations in Tennessee, north to mountains in Virginia (Frost 2011). Organ (1960) reported eight nests of this salamander, located from mid-August to early September between the upper rotting surfaces of conifer logs and the mat of 5-10 cm of mosses.

Figure 19. ***Plethodon welleri*** on a bed of mosses. Photo by Todd Pierson, with permission.

Plethodon elongatus (Del Norte Salamander)

In southwestern Oregon and northwestern California, USA, the **Del Norte Salamander** (***Plethodon elongatus***; Figure 20) is restricted to old-growth forests (Welsh 1990) and may require the moss cover that develops there. These forests range up to 560 years old and have more favorable microclimates than do the young forests. The **Del Norte Salamander** (***Plethodon elongatus***) rarely occurs in open water and seems to require the moisture of mosses, rocks, and organic matter. In northwestern California, Welsh and Lind (1995) sampled 57 sites and found a mean of 20 individuals at sites with moss as ground cover, but only 6.9 individuals at sites with none. The need for mosses meant that these salamanders also needed late successional stage forests where mosses had had time to develop significant cover. These habitats tended to be cooler with more moist microclimates among the mosses.

Figure 20. The **Del Norte Salamander**, ***Plethodon elongatus***. Photo by Henk Wallays, through Creative Commons.

Plethodon idahoensis (Coeur d'Alene Salamander)

Plethodon idahoensis (formerly *Plethodon vandykei idahoensis*), the **Coeur d'Alene Salamander** (Figure 21), lives further east in the drainage areas of the Selway River

of northern Idaho and the Bitterroot River of extreme western Montana, USA, as well as in the Duncan and Columbia River drainages of southeastern British Columbia, Canada (Frost 2011). The **Coeur d'Alene Salamander**, ***Plethodon idahoensis***, is the only plethodontid in the northern Rocky Mountains (AmphibiaWeb 2004).

This salamander can be found in springs, seepages, streamside, or spray zones of waterfalls (Discover Life 2012; Figure 21-Figure 22). These habitats often have bryophytes and the **Coeur d'Alene Salamander** can most likely be found on and under these bryophytes. Wilson (1990) reports one such case under bryophyte mats on cobbles along a stream at ~540 m in the Nez Perce National Forest, Idaho, USA.

The eggs of the **Coeur d'Alene Salamander** are produced in grapelike clusters, and larvae of this species develop within the eggs; thus, no tadpoles exist (Wikipedia 2011b).

Figure 21. The **Coeur d'Alene Salamander**, ***Plethodon idahoensis***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

At Beauty Bay on Coeur d'Alene Lake, Idaho, USA, Dumas (1957) found two females and two immatures under moist moss on a stable talus slope. In the following year he found another immature under wet moss in a small seepage area on the south shore of the Chatcolet Lake.

Figure 22. Color variant of **Coeur d'Alene Salamander**, ***Plethodon idahoensis***. Photo by William Leonard, with permission.

Plethodon vandykei complex (Van Dyke's Salamander)

The **Van Dyke's Salamander** (Figure 23), also known as Van Dyke Salamander and Washington Salamander, occurs on the Olympic Peninsula and in the southern Cascade Range of western Washington, USA, at 0-1550 m asl (Frost 2011). This species, along with other members of its species complex, is frequent under moss mats (Slater 1933). ***Plethodon vandykei***, *sensu stricto*, is most common near streams, where it uses the mosses and moist slabs of bark at tree bases for cover.

During the day these salamanders are typically found under stones and mosses within streams, but when they search for food after dark they wander out of the water and hunt streamside. McIntyre *et al*. (2006) suggested that ***P. vandykei*** (Figure 23) is most common in habitats that are able to maintain both cool and hydric conditions; this species is sensitive to both heat and desiccation. Mosses provide such habitats, particularly in seeps. McIntyre and coworkers hypothesized that this would result in a positive association of this species with early successional stages that were dominated by bryophytes and graminoids, while having a negative association with leaf litter. Typically, in the Cascade Range of Washington State, USA, the mosses were associated with bedrock and small cobble, not soil. Surroundings of moist bryophytes would permit this and other members of the genus to absorb water directly through their skin (Spotila 1972). Seeps typically provide these ideal habitats by providing stability of both temperature and moisture (Hynes 1970; Huheey & Brandon 1973).

Figure 23. **Van Dyke's Salamander**, ***Plethodon vandykei*** on a log covered with mosses. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Plethodon larselli (Larch Mountain Salamander)

The **Larch Mountain Salamander**, ***Plethodon larselli*** (formerly *Plethodon vandykei larselli;* Figure 24), occurs in the Lower Columbia River Gorge of Oregon and Washington, USA (Frost 2011). It inhabits the lava talus slopes, and Burns (1962) found it among mosses on the side of a steep **andesite** (dark grey fine-grained volcanic rock) cliff.

Figure 24. ***Plethodon larselli***, the **Larch Mountain Salamander**. Photo © Henk Wallays, through Creative Commons.

Plethodon glutinosus (Northern Slimy Salamander)

The **Northern Slimy Salamander** (Figure 25) is a large (11.5-20.5 cm total length) terrestrial salamander (Virginia Department of Game and Inland Fisheries 2011a) that lives mostly in bottomland and wet hardwood forests of eastern USA (Beamer & Lannoo 2011a). This species lives under logs, rocks, and in tunnels in the soil; there seems to be no documentation that it lives among bryophytes. At night it traverses the forest floor, hunting for food. At that time, mosses may aid in rehydration, but this theory has not been tested. However, it does at times deposit eggs under mosses (Virginia Department of Game and Inland Fisheries 2011a). The eggs are a creamy white with an average of 5.5 mm diameter.

When handled, the **Northern Slimy Salamander** secretes a noxious sticky substance from its tail, a protection against predators (Virginia Department of Game and Inland Fisheries 2011a). Brodie *et al.* (1979) found that this secretion deterred shrews, causing them to avoid the salamander or to spend more time to kill it, resulting in less predation than that on the non-noxious ***Desmognathus ochrophaeus***. As an added deterrent it lashes its tail, further exposing the secreting glands.

Figure 25. ***Plethodon glutinosus*** on mosses. Photo by Henk Wallays, through Creative Commons.

Plethodon richmondi (Southern Ravine Salamander)

This salamander can be found in parts of Pennsylvania, Ohio, Kentucky, Indiana, and West Virginia (Pauley & Watson 2011). It is restricted to woodlands (Duellman 1954). Sexual maturity requires three years in males and four years in females (Nagel 1979). The Virginia Department of Game and Inland Fisheries (2011b) reports that this species has a spring courtship, followed by laying its eggs in damp logs and mosses in the early summer. On the other hand, Nagel (1979) found that in northeastern Tennessee, mating occurred from November to March, with a mean of 8.3 eggs deposited in May.

Plethodon metcalfi, formerly *Plethodon jordani metcalfi* (Southern Gray-cheeked Salamander)

The **Southern Gray-cheeked Salamander**, ***Plethodon metcalfi*** (Figure 26), is also known as Unspotted Salamander, Metcalf's Salamander, Clemson's Salamander, Clemson Salamander, Highland's Salamander, Highlands Salamander, Rabun Bald Salamander, Rabun Salamander, Frosted Salamander, and Southern Graycheek Salamander. It is surprising to have so many English names for a salamander that ranges only from the southwestern corner of North Carolina and extreme northwestern South Carolina into extreme northeastern Georgia, USA (Frost 2011). Organ (1958) found a courting pair on moss of the forest floor in mid August, but little else seems to be known of its relationship with bryophytes. The food of this species (snails, mites, spiders, insect larvae, springtails, millipedes, and centipedes) suggest that it could subsist on organisms found among bryophytes, making them potential hunting grounds (Whitaker & Rubin 1971).

Figure 26. ***Plethodon metcalfi***, the **Southern Gray-cheeked Salamander**, on a bed of mosses. Photo by Bill Peterman, with permission.

Plethodon jordani (Red-cheeked Salamander; Jordan's Salamander)

In the higher elevations of the Great Smoky Mountains, this species (Figure 27-Figure 28) is most abundant in the red spruce-Fraser's fir forest where the forest floor is covered with a heavy layer of mosses and little soil (King 1939). Its greater abundance in forests with a predominant bryophyte cover suggests that bryophytes may be important in maintaining the moisture required in its niche.

Although its range is somewhat small, it is widespread within that range and does not appear to be endangered (Beamer & Lannoo 2011b). Nevertheless, despite its protection within the Great Smoky Mountain National Forest, it could be endangered by the infestation of the balsam woolly adelgid beetle (***Adelges piceae***, Adelgidae, Hemiptera) that has caused considerable canopy changes. As new openings impact the bryophytes (Stehn *et al*. 2010a, b) by creating more light, potentially reducing their cover, this species could lose considerable habitat.

Figure 27. **Red-cheeked Salamander**, ***Plethodon jordani***, on a bed of ***Thuidium***. Photo by Matthew Niemiller, with permission.

Figure 28. ***Plethodon jordani*** on a bed of bryophytes. Photo by Bill Peterman, with permission.

Plethodon shermani (Red-legged Salamander)

Richard Bruce is an avid salamander hunter and has become interested in their mossy habitats. He has just sent me another picture, this time of ***Plethodon shermani***, adding another species to the list of bryophyte dwellers. The salamander was living in a species of ***Hypnum*** on a slope above the Nantahala River, North Carolina, USA. The species is mainly found under logs in daytime, and emerges on humid and rainy nights to forage on the forest floor (Richard Bruce, pers. comm. 4 November 2020). They are only occasionally found under moss cushions (unlike ***Desmognathus aeneus*** which is a moss specialist, and which co-occurs in forests with ***P. shermani***).

Figure 29. ***Plethodon shermani*** crawling on the moss ***Hypnum*** sp. where it lives. Photo courtesy of Richard Bruce.

Plethodon stormi (Siskiyou Mountains Salamander)

The **Siskiyou Mountains Salamander** (Figure 30) has a narrow distribution in southwestern Jackson County, Oregon, and northern Siskiyou County, California, USA (Frost 2011). Its narrow distribution and loss of habitat cause it to be listed as endangered (IUCN 2010). It is associated with moss-covered rocks (Gary Nafis, pers. comm. 28 April 2011). It appears that nothing is known about nests, eggs, or young (see Bury & Welsh 2011). Adults sit quietly and wait for their prey of collembolans, termites, beetles, moths, spiders, and mites (Nussbaum *et al*. 1983). They dart out from whatever cover they are using, so it is likely that some take advantages of the humidity and cooling ability of the mosses that abound in some of their talus habitats, using them as cover and re-moistening sites.

Figure 30. ***Plethodon stormi***. on a rock with mossy patches. Spotted coloration blends somewhat with the rock, but not with the moss. Photo © Gary Nafis through CaliforniaHerps.com, with permission.

Plethodon asupak (Scott Bar Salamander)

Like the previous species, the **Scott Bar Salamander** (Figure 31-Figure 32) is associated with moss-covered talus rocks (Figure 33; Gary Nafis, pers. comm. 28 April 2011), and it likewise has a restricted distribution, occurring in the Siskiyou Mountains (700-1300 m asl) at Muck-a-Muck Creek above Scott Bar, Siskiyou County, California, USA. ***Plethodon asupak*** is listed only as vulnerable (IUCN 2010),

being threatened by habitat loss (Lu 2009). It prefers north-facing slopes with closed canopy and talus rock (Lu 2009).

Figure 31. ***Plethodon asupak*** on a bed of mosses. Photo © Gary Nafis through CaliforniaHerps.com, with permission.

Figure 32. ***Plethodon asupak*** adult and juvenile. Photo by Timothy Burkhardt, with permission.

Figure 33. Rocky forest floor where mosses contribute to the habitat of ***Plethodon asupak***. Photo © Gary Nafis through CaliforniaHerps.com, with permission.

Gyrinophilus porphyriticus, formerly *Pseudotriton porphyriticus* (Spring Salamander)

This common species (Figure 34) has 25 English names in the 2011 list of Frost, even though its range is in just one area of North America: eastern USA from Canada to Georgia-Mississippi (Frost 2011). The most common alternative name among these is Blue Ridge Spring Salamander. The number may not be so surprising when one recognizes that there have been 34 Latin synonyms – it seems to be rather misunderstood. In Tishomingo County, Mississippi, Ferguson (1961) found a single salamander "resting" on a mat of mosses by a spring at the base of an over-hanging cliff. Scott LaGrecca (pers. comm. 11 August 2014) found "a couple" of them among ***Fontinalis*** in a stream in the Berkshires, Massachusetts, USA.

Figure 34. ***Gyrinophilus porphyriticus***, the **Blue Ridge Spring Salamander**, on a bed of mixed mosses. Photo by Bill Peterman, with permission.

Pseudotriton ruber (Red Salamander)

The **Red Salamander** (Figure 35) occurs from southern New York to northwestern Florida and west to eastern Ohio, central Kentucky and southeastern Louisiana, USA. Burger (1933) found a single adult in torpor under mosses of a drying bog in Pennsylvania in mid-summer. Bishop (1941) also observed adults under mats of ***Sphagnum***. As discussed earlier, this salamander has a complex of mimics that take advantage of its poisonous skin secretions.

Figure 35. The **Red Salamander**, ***Pseudotriton ruber***, on a bed of terrestrial mosses. Photo by John White, with permission.

Hemidactylium scutatum (Four-toed Salamander)

This seems to be the most famous of salamanders for dependence on mosses. Whenever I ask a North American herpetologist about salamanders associated with mosses, this species is mentioned, usually first. The **Four-toed Salamander** (Figure 36) is also known as Scaly Salamander, Scaly Lizard, and Eastern Four-toed Salamander. Its distribution is fairly continuous from

extreme southern Maine, USA, and extreme southern Quebec and Ontario, Canada, west to northern Wisconsin, USA, south to the **fall line** [area where an upland region (continental bedrock) and a coastal plain (coastal alluvia) meet; an unconformity] in North Carolina, South Carolina, Georgia, Alabama, and Tennessee, USA (Frost 2011). There may be additional disjunct populations in nearby areas.

Figure 36. ***Hemidactylium scutatum*** (**Four-toed Salamander**) on a bed of mosses. Photo by John D. Willson, with permission.

The **Four-toed Salamander** (***Hemidactylium scutatum***, Plethodontidae; Figure 37) is one of the best known of the amphibian moss inhabitants. Blanchard (1923) reported that all of his finds near Ann Arbor, Michigan, USA, were among ***Sphagnum*** clumps of woody bog shrubs within 15 cm above the water surface. the need for deep moss may be explained by the critical temperature maximum (CTM) for this species. In experiments, Hutchinson (1961) found the CTM to be 36.74°C, a temperature easily exceeded at the moss surface on a sunny day, but not likely to be achieved 15 cm below. The **Four-toed Salamander**, ***Hemidactylium scutatum*** (Figure 36), had a CTM of 36.7 + 0.11 C.

But, as early as 1918, Wright reported that this species was disappearing from New York due to draining of wetlands. Today the species is listed as endangered or rare in a number of states (Harris 2011), but is listed as a species of least concern on the 2010 IUCN Red List.

Fowler (1942) found a single adult under a ***Sphagnum*** mat in a shoreline bog of a lake in a Maine coniferous forest. King (1944) found it on fallen tree trunks and logs in a gum swamp in the Great Smoky Mountains National Park. Burger (1933) found two inactive individuals during the last week of March in Pennsylvania, again in swampy conditions. But apparently it has a broader habitat than just boggy or swampy land. Blanchard (1928) reported one adult male in ***Sphagnum*** in Reese's Bog, northern Michigan, USA, and argued that the apparent scarcity of the species may be due to its secretive habit of hiding among the ***Sphagnum***.

Habitat Characteristics

Bleakney (1953) revealed the role that mosses could play in the distribution of this species: "The first record for the province dates back to 1934 when the Arthur Dean's Nursery in Halifax sent a specimen to the Nova Scotia Museum of Science in Halifax. The salamander was correctly identified, but, because the northern limit of its range was believed to be southern Maine, the occurrence of this specimen was credited to introduction via ship's cargo. However, when in 1951 the nursery records were consulted, it was revealed that this **Four-toed Salamander** (Figure 36) had actually come from a load of moss gathered for the nursery from just outside the city."

Because so little was known of the habitat use of this species, Chalmers and Loftin (2006) investigated these relationships in order to build a predictive model of habitat. Among the predictors, a shoreline of ***Sphagnum*** species was important, along with wood substrate, water flow, and several plants. Interestingly, the shrub sheep laurel (*Kalmia angustifolia*) was a negative predictor, as was deciduous forest canopy. In Canaan Valley, West Virginia, USA, this species is likewise common in pond habitats with mosses, typically ***Sphagnum***, or loose bark on logs that can provide nest cover (Pauley 2007). After breeding season, the **Four-toed Salamanders** (Figure 36) leave the aquatic habitat to forage among the forest litter.

Mating

The species mates in late summer and into fall or even early winter. Courtship is an entertaining set of activities and responses, often occurring on peat mosses. The story reminds me of what we as children called Eskimo kisses. The male rubs his nose on the female's nose (Harding 1997; Petranka 1998). Then he circles her with his tail bent at a sharp right angle. If he is lucky, the female straddles his tail and presses her snout on the base of his tail. After a time, the male begins to move forward, tail undulating, and starts to deposit spermatophores. The female follows close behind, picking up the sticky spermatophores. With her snout still against the male's tail, she deposits the spermatophores in her **cloaca** (posterior opening for the intestinal, reproductive, and urinary tracts) while doing a straddle walk. After about 20 minutes the mating and fertilization are completed. It is not until spring that the female searches for a suitable nesting site to lay her eggs.

Figure 37. ***Hemidactylium scutatum*** (**Four-toed Salamander**) on mosses, ventral view. Flipping onto its back is one mechanism of responding to potential predators. Photo by John D. Willson, with permission.

Nest Sites

Numerous studies indicate that mosses are preferred nest sites for laying eggs. Wahl *et al*. (2008) found that when choices of moss, grasses, and sedges were available 89% of the nests at three montane pond sites in Virginia, USA, were in clumps of ***Sphagnum***. These sites had steeper banks, lower *p*H, and faced north more often than expected by chance. These three factors were correlated with embryonic survival. North-facing nests were cooler than those facing south.

The female typically lays her eggs among mosses at the edge of forest ponds and water holes (David Taylor, Bryonet 3 February 2009) where spaces will allow the larvae to wiggle down to the water (Linton & Gascho Landis 2005). Headstrom (1970) tells us that this salamander makes a simple cavity in ***Sphagnum*** (Figure 38-Figure 39), sometimes making use of a natural opening. Each cavity takes several minutes to construct, and it may take hours to provide for the entire clutch (Gates 2002). It is usually not far from open water and may be along the sides of a moss-covered rock that projects into the water. The eggs are sticky and adhere to the mosses. They have an added advantage – the eggs are unpalatable to insects, giving them protection in the mossy habitat that often houses insects (Hess & Harris 2000).

As already suggested, this species is best known for its occurrence among mosses in bogs and poor fens. Bleakney and Cook (1957) reported two females in Nova Scotia with eggs under ***Sphagnum*** mosses on logs. The logs hung over a stream and the two egg clutches had 36 eggs. It appears that the number of eggs in the clutch may be diminishing. Bishop (in Gilbert 1941) considered clutch sizes to range 40-60, with an average of 50 per female. But Cornell researchers found that after 1920 the averages were less than 50.

Figure 38. Female **Four-toed Salamander** (***Hemidactylium scutatum***) guarding her eggs in her nest of ***Sphagnum***. The ***Sphagnum*** has been parted so that the picture could be taken. Photo from Minnesota DNR, through public domain.

The females typically lay their eggs in such mosses as ***Sphagnum*** and ***Thuidium*** spp. (Wood 1955; Harris 2005). Chalmers (2004) found 238 nests in 36 wetlands in Maine, a state where the species is listed as one of Special Concern, along with eleven other states. Furthermore, it is listed as Threatened in Illinois and as Endangered in Indiana. Chalmers was able to locate these 36 new sites by using the predictive ability of shorelines with ***Sphagnum***. The nests were more common on shorelines with steeper slopes and deeper nesting vegetation, especially with moss and *Ilex verticillata* (winterberry), but were negatively associated with *Spiraea alba*, *Chamaedaphne calyculata*, and *Kalmia angustifolia* when they were within 1 m of the shoreline.

Figure 39. Eggs of ***Hemidactylium scutatum*** among non-***Sphagnum*** mosses. Photo by Jim McCormac <http://jimmccormac.blogspot.com>, with permission.

Wood (1955) reported that the **Four-toed Salamander** surrounds its nest with liverworts, as well as many species of ***Sphagnum***. ***Sphagnum*** is an important nest material (Wallace 1984), where the female deposits its eggs in mossy hummocks above the waterline where the eggs remain moist but don't drown (NJ Division of Fish & Wildlife 2009; Richard Andrus, pers. comm.; David Taylor, Bryonet 3 February 2009). Although many herpetologists assume that ***Sphagnum*** is preferred for nesting (Figure 38), females also deposit eggs under other species such as those of ***Atrichum*** (Figure 40) (David Taylor, Bryonet 3 February 2009), ***Sphagnum palustre*** (David Taylor, pers. comm. 25 October 2011), ***Thuidium*** (Figure 41), ***Mnium*** (probably now ***Plagiomnium*** or ***Rhizomnium***), ***Climacium*** (Gilbert 1941; Wood 1955; Easterla 1971; Petranka 1998; Harris 2009), ***Thamnobryum alleghaniense***, ***Hypnum*** sp., and in, as well as under, ***Aulacomnium palustre*** (Figure 42) (David Taylor, Bryonet 3 February 2009). In fact, in Kentucky, USA, John MacGregor (pers. comm. 4 February 2009) finds that most of the nests are under ***Thuidium*** (Figure 41). Many taxa of both mosses and liverworts surround the nests, contributing to the content of the nests (Harris 2009). The female often remains with the eggs until they hatch (Figure 40).

Figure 40. Female **Four-toed Salamander** (***Hemidactylium scutatum***) guarding her eggs in her nest amid the moss ***Atrichum* sp**. Photo by John D. Willson, with permission.

Figure 41. ***Thuidium delicatulum***, a common nest moss for the **Four-toed Salamander** (***Hemidactylium scutatum***). Photo by Michael Lüth, with permission.

Figure 42. ***Aulacomnium palustre***, a suitable moss for egg deposition by the **Four-toed Salamander**. Photo by Janice Glime.

Despite the numerous reports on eggs of this species in ***Sphagnum***, Wood (1953) found greater mortality for eggs in ***Sphagnum*** than for those laid on other genera. Overcrowding in large nests resulted in more dead eggs than for loosely placed eggs of small nests. Breitenbach (1982) found that solitary brooding was more likely to occur when there were abundant suitable nesting sites. In a Michigan study, only 12% of 109 nests were communal, with 13 of 14 nests in ***Sphagnum*** (Breitenbach 1982). Hence, greater reproductive success is likely to occur when there is more moss habitat available for cover. Nest disturbance can cause desertion of the nest, so nests hidden among mosses are less likely to be abandoned.

Wood (1955) found that the salamanders preferred thick mosses that contained many natural crevices where eggs could be placed, compared to shallow, thin mosses lacking such depressions. Gilbert (1941) similarly found that dense mosses such as those at tree bases and stumps or around hummocks did not seem to be desirable, whereas 27 out of 32 nests were in loose mosses along logs.

Hmmm...It appears that the habitat may alter the preferences for growth form and species. Gilbert (1941) found only five of these nests in ***Sphagnum***. He described the mosses being used as "loose and fluffy." But another factor could be temperature. Wood (1955) found that nest temperatures were warmer in the two ***Sphagnum*** habitats than in the seven ***Thuidium*** hummocks.

Gilbert (1941) found that the logs were located where water was within 7-10 cm. No nests were found where the water had completely dried up. Boyle (1914) found this species in Long Island, New York, by tearing mosses apart at the bases of dead trees at the edge of a pool. Green (1941) found a nest of 12 eggs in Kentucky, covered by a moss mat where a constant drip from a cliff face kept it continuously wet. These collections indicate that bogs are not essential for this species, but mosses apparently are.

Humphrey (1928) actually observed the female laying eggs in captivity. She had available to her ***Sphagnum*** in a dish. She actually turned upside down to lay the eggs on the overlying ***Sphagnum***. On a North Carolina, USA, coastal plain, three out of twenty **Four-toed Salamanders** laid their eggs on the underside of "sheet" moss (Schwartz & Etheridge 1954). Typically, the female repeatedly turns onto her back before laying eggs, perhaps to ensure the eggs are attached to the mosses instead of the underlying substrate (Noble & Richards 1932; Bishop 1941).

One problem that could further endanger such diminishing species as ***Hemidactylium scutatum*** is predation by inhabitants of the moss. Hess and Harris (2000) experimented with palatability of eggs and found that carabid beetles from the pond did not eat the eggs, but beetles from a stream punctured the eggs. However, they ate few of them. As noted earlier, Hess and Harris suggested that the eggs might contain a toxic or noxious chemical in their gelatinous layer. This avoidance of egg predation helps to explain the lack of nest defense and desertion of nests by this species. However, we have seen that the females seem to stay with the eggs at least some of the time.

Stereochilus marginatus (Many-lined Salamander, Plethodontidae)

The **Many-lined Salamander** (Figure 43), also known as Margined Triton and Margined Salamander, occurs on the Atlantic coastal plain from southeastern Virginia to northeastern Florida, USA (Frost 2011). Gerhardt (1967) found this species in a cypress swamp in Georgia, USA, among the ***Sphagnum*** in pine flatwoods, where it cohabited in the mosses with the **Broad-striped Dwarf Siren** (***Pseudobranchus striatus***), **Carpenter Frog** (***Lithobates virgatipes***) larvae, **Easter Lesser Siren** (***Siren intermedia***), and the **Mud Snake** (***Farancia abacura***).

Hatching can be fun to watch for both the **Four-toed Salamander *Hemidactylium scutatum*** and **Many-lined Salamander *Stereochilus marginatus*** (Figure 43) (both **Plethodontidae**) when they make their nests in ***Sphagnum*** or rotting wood (Blanchard 1934; Duellman & Trueb 1986). When the larvae hatch, they wriggle down the moss to the water. These larvae need to beware of cohabiting newts that like to have them for dinner (Wells & Harris 2001).

Adults of ***Stereochilus marginatus*** are somewhat safer than the larvae due to several anti-predator mechanisms. They secrete a glandular substance from the dorsal part of the tail, "threaten" by raising and undulating the tail, flip

over to expose the yellow venter with black spots (warning colors), secrete noxious substances from the skin, and lose their tails. The tail is lost when the salamander is attacked, even if the salamander has not been captured (Brodie 1977). The tail continues to wiggle after it has been detached (Gates 2002), possibly attracting the attention of the would-be predator.

Figure 43. The **Many-lined Salamander**, ***Stereochilus marginatus***. Photo by Michael Graziano, with permission.

In the Dismal Swamp, Virginia, where ***Sphagnum*** spp. are common, females seem to prefer laying their eggs on the brook moss ***Fontinalis*** sp. (Figure 44) (Wood & Rageot 1963; Rabb 1966). Bruce (1971) reported that females of ***Stereochilus marginatus*** in the Croatan National Forest in eastern North Carolina, USA, laid eggs underwater or just above the surface, with those underwater being laid singly or in small groups attached to stems of mosses.

Figure 44. ***Fontinalis antipyretica*** in a dry stream bed. During seasons of good flow, this is a suitable site for eggs of the **Many-lined Salamander**. Photo by Janice Glime.

Desmognathus fuscus (Northern Dusky Salamander)

The well-known salamander ***Desmognathus fuscus*** (Figure 45-Figure 47) occurs in Southern New Brunswick and southern Quebec, Canada, south of the Great Lakes to southeastern Indiana, western Kentucky, eastern Tennessee, and northeastern Georgia (excluding the coastal plain of North Carolina and South Carolina), USA.

Figure 45. The **Northern Dusky Salamander**, ***Desmognathus fuscus***. Photo by John D. Willson, with permission.

Figure 46. ***Desmognathus fuscus***. Photo by Todd Pierson, with permission.

The genus ***Desmognathus*** seems to be a common one under bryophytes. Adults may be located under mats of moss and other cover (Hom 1987). Their typical strategy when disturbed is to disappear into the mud (Tilley 1981). In New York, the Northern Dusky Salamander was the most common salamander species when Bishop compiled his list in 1922 (Bishop 1923). But lack of suitable sites may limit breeding and population growth throughout much of its range.

Figure 47. ***Desmognathus fuscus***. Photo by Bill Peterman, with permission.

In Tennessee, USA, Hom (1987) found nests mostly on the banks of streams (Figure 48) in moist soil under mosses [***Atrichum undulatum*** (Figure 51), ***Mnium affine***, ***Thuidium delicatulum*** (Figure 41)] and the leafy liverwort ***Trichocolea tomentella***, accounting for 85-95% of the observations over a three-year period.

Unlike many amphibians, most ***Desmognathus*** species do not have a larval stage, but instead begin life as miniature adults (Chippindale & Wiens 2005); *i.e.*, they have **direct development**. It appears that the most advanced forms have a larval stage that may have secondarily returned to the water, as in the Northern Dusky Salamander. The **Northern Dusky Salamander**, ***Desmognathus fuscus*** (Figure 47), selects sites in advance for laying eggs (Hom 1988). Burger (1933) found a cluster of eleven eggs under moss on a mountain slope in Lebanon County, Pennsylvania, USA, during the first week of September. These larvae were just ready to emerge, and when disturbed several did break through the egg membrane.

Females can occur in clusters, such as the three females hiding with their egg clusters under a 20-cm square of moss covering mucky soil of a springy swamp (Bishop 1923). Females of the species tended to brood their egg clutches under mosses (Hom 1987). Montague (1977) showed experimentally that ***Sphagnum*** served as a sufficiently moist site for a clutch of eggs in an environmental chamber at 14°C. Eggs are deposited in moist soil under mosses (Figure 49), rotting logs, rocks, and leaf litter (Dennis 1962; Snodgrass *et al*. 2007). Clutch size typically ranges 5-34 with a mean in the mid 20's (Means 2011). Hatching requires 45-60 days, and the female remains with the eggs during this time (Snodgrass *et al*. 2007). Females seem to recognize tradeoffs in parental care (Forester *et al*. 2005). In an experiment where eggs of several clutches were divided and placed at 13 and 21°C, those at the higher temperature developed faster. When the female was introduced to her two sets of eggs, she spent most of her time caring for those that were further developed. But when the young hatch, she leaves them to fend for themselves.

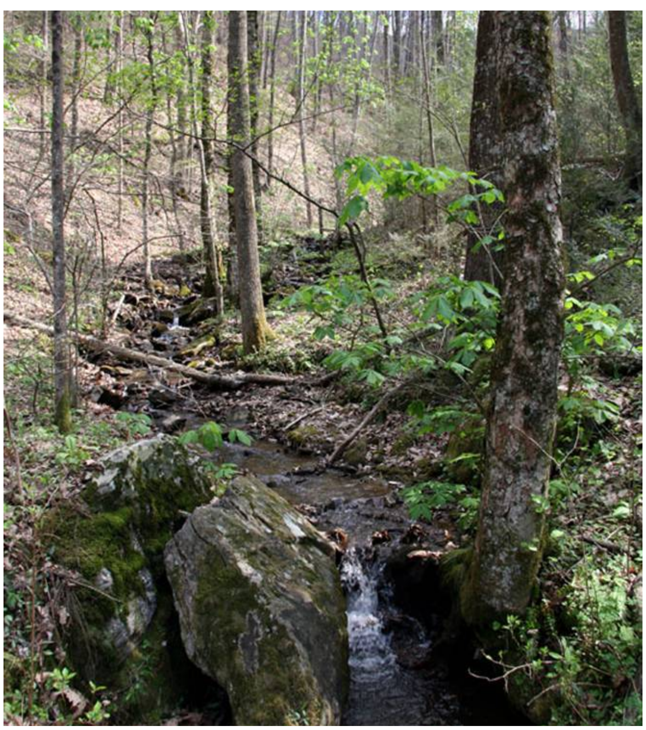

Figure 48. Habitat of ***Desmognathus fuscus***, Lumpkin County, Georgia, USA. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 49. ***Desmognathus fuscus*** that has been uncovered with its eggs. Photo by Todd Pierson, with permission.

Desmognathus ochrophaeus (Allegheny Mountain Dusky Salamander, Plethodontidae)

The **Allegheny Mountain Dusky Salamander** (Figure 50) occurs from the mountains of southeastern Kentucky, through the Adirondack Mountains, USA, to southern Quebec, Canada.

As for many salamanders, seeps provide this species with both moisture and temperature stability (Huheey & Brandon 1973). This is true even on rock faces, where they are able to maintain moisture among mosses. But this highly variable species also inhabits forest streambanks where it lives among mosses, under rocks, leaves, bark, and logs, and in rock crevices (Tilley 1972; Mushinsky 1976). Experiments indicate that the adults will select some habitats based on the one in which they experienced early development.

Figure 50. ***Desmognathus ochrophaeus*** (**Allegheny Mountain Dusky Salamander**) on a bed of ***Atrichum* sp**. Photo by John White, with permission.

Bruce (1990) tried to explain the selection pressures accounting for size differences between ***D. ochrophaeus*** and ***D. monticola*** (**Seal Salamander**). The more aquatic ***D. monticola*** is larger than ***D. ochrophaeus***. Bruce located most of the egg clutches under mosses at Wolf Creek in the Appalachian Mountains. Eggs of ***D. ochrophaeus*** were significantly smaller than those of ***D. monticola*** and also experienced earlier maturation, making them smaller as adults. Bruce suggested that the decrease in age at maturation in ***D. ochrophaeus*** accompanied the shift to a terrestrial habitat. The selection pressure could be competition or predation – or both.

Whereas Bruce suggests that the smaller size leads to greater predation, Forester (1979a) suggests that the predation is reduced by greater parental care of egg clutches in this species. Furthermore, those clutches unprotected by females were more susceptible to phycomycete fungi, in as little as 12 days after they were deposited. It appears that the female uses her head and mouth to remove infected eggs and to gently oscillate them through movements of the throat (**gular**) region; mechanically vibrated clutches likewise had a higher percentage of survival than non-vibrated controls. Females were able to defend their eggs against other members of their own species and against ground beetles, but were not so successful against larger salamanders or **Ringneck Snakes** (***Diadophis punctatus***). Nests often occurred under mats of the mosses ***Thuidium delicatulum*** (Figure 41), ***Atrichum undulatum*** (Figure 51), and ***Plagiomnium ciliare*** (Figure 52).

Figure 51. ***Atrichum undulatum***, a moss that provides a nesting site for several species of salamanders, including ***Desmognathus ochrophaeus***. Photo by Michael Lüth, with permission.

Figure 52. ***Plagiomnium ciliare***, a moss that is often home to eggs of ***Desmognathus ochrophaeus***. Photo by Annie Martin, Mountain Moss Enterprises, with permission.

Females in this species have a homing instinct for their own nests, at least over short distances (Forester 1974, 1979b). When 117 females were moved 2 m from their nests, 78% returned to their nests within 24 hours. They were attracted to unattended eggs, but were able to distinguish their own nests from others with unattended eggs, only occasionally selecting the eggs of another female in preference to their own. For example, seven females were nesting on a single moss-covered rock. When they were marked and moved, five of the seven returned to their own eggs. Females typically remain with their eggs and do not forage while attending them.

In an experiment, females were offered sites with depressions in soil, but only half of them were covered with moss (Forester 1979b). Females preferred holes with moss cover in all arrangements tested. That is some of the best evidence I have found indicating preference for bryophytes.

This species is known to avoid predation by early detection of a nearby predator. Chemicals released by wounded members of its own species and others in the genus serve as a warning to take cover (Lutterschmidt *et al*. 1994).

Desmognathus monticola (Seal Salamander)

This species (Figure 53) ranges from the central and southern Appalachians of western Pennsylvania to central Alabama (Camp & Tilley 2011) and is more aquatic than is ***Desmognathus ochrophaeus*** (Bruce 1990). It is typically found among mosses on rocks in streams (LeGrand *et al.* 2001). It lays its eggs in rapid streams where they are sometimes placed under mosses (Camp & Tilley 2011).

Figure 53. ***Desmognathus monticola*** on a bed of streamside mosses. Photo by Bill Peterman, with permission.

Desmognathus santeetlah (Santeetlah Dusky Salamander, Plethodontidae)

The **Santeetlah Dusky Salamander** (Figure 54) is restricted to the Great Smoky, Great Balsam, and Unicoi Mountains of the southwestern Blue Ridge Mountains in Tennessee and North Carolina, USA. ***Desmognathus santeetlah*** (Figure 54) is a higher elevation segregate of the **Northern Dusky Salamander** (***Desmognathus fuscus***) in the southern Appalachians, USA. One of the factors that maintains it as a separate species is that it has a different larval environment (Beachy 1993). This species broods its ca 20 eggs under mosses on logs and rocks at the edges of headwater streams (Jones 1986; Tilley 1988; Beachy 1993), compared to the soil depository under mosses, logs, and rocks for eggs of ***Desmognathus fuscus*** (Tilley 1973).

Instead of scurrying into the mud to hide, like ***D. ochrophaeus*** (**Allegheny Mountain Dusky Salamander**; Figure 50), this one remains motionless (Tilley 1981). Both ***D. santeetlah*** and ***D. ochrophaeus*** occur in the Southern Appalachians (Tilley 1973) and both seem to prefer brooding sites under mosses on logs or rocks. In some locations, only ***D. santeetlah*** nesting sites can be found (Tilley *et al*. 1978), but in others both species occur, suggesting that under some conditions there may be competition for suitable nesting sites. However, ***D.***

santeetlah oviposits mostly under mosses on rocks or logs in seepage areas.

Figure 54. ***Desmognathus santeetlah*** (**Santeetlah Dusky Salamander**), a high elevation salamander from the southern Appalachians. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Desmognathus aeneus (Seepage Salamander)

Also known as the Cherokee Salamander and Alabama Salamander, the **Seepage Salamander** (Figure 55) occurs from extreme southwestern North Carolina, adjacent Tennessee, and southwestward through northern Georgia (Figure 56) to north central Alabama, USA. In Georgia, Martof and Humphries (1955) found it under leaves, mosses, and stones, especially near seepages and other places of high humidity (Figure 56).

The 11-14 eggs of ***D. aeneus*** are deposited under mosses, as well as under logs, leaf litter, and mats of roots in seepage or wet areas near streams (Figure 56) (Bishop & Valentine 1950; Valentine 1963; Harrison 1967; Jones 1981; Collazo & Marks 1994). Females remain with the eggs during incubation (Brown & Bishop 1948; Bishop & Valentine 1950). Although this species is not considered a climber, Wilson (1984) observed them jumping from branch to branch in bushes and climbing up grasses. They feed mostly on insects, but their diet also includes nematodes, earthworms, land snails, isopods, amphipods, centipedes, arachnids, and millipedes, all items that can be found among mosses as well as leaf litter (Folkerts 1968; Donovan & Folkerts 1972; Jones 1981).

Figure 55. **Seepage Salamander**, ***Desmognathus aeneus*** on ***Atrichum***. Photo by Todd Pierson, with permission.

Figure 56. Habitat of the **Seepage Salamander** ***Desmognathus aeneus*** in Georgia, USA. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Desmognathus wrighti (Pygmy Salamander)

Known as the **Pigmy Salamander** (Figure 57), this small species occurs in woodland areas, especially above 1400 m asl within the southern Appalachians, including the Great Smoky Mountains of North Carolina and Tennessee, the Plott Balsam Mountains and Great Balsam Mountains of North Carolina, USA; it is also common between 950 m and 1400 m asl within the Cowee Mountains, Nantahala Mountains, and Unicoi Mountains of North Carolina, USA.

In the southern Nantahala Mountains, North Carolina, USA, ***Desmognathus aeneus*** (**Seepage Salamander**; Figure 55) and ***D. wrighti*** (**Pygmy Salamander**; Figure 57-Figure 58) are **sympatric** (ranges overlap) in high elevations (Hining & Bruce 2005). Both occupy clumps of moss, damp leaf litter, or shelter under stones or logs near streams and seepages in the deciduous forest during the spring (Figure 56). ***Desmognathus wrighti*** not only occupies wet areas, but can also be found up to two meters high in a tree on its leaves (Hairston, 1949; Organ, 1961). The two species manage to remain distinct by having different oviposition times, early May for ***D. aeneus*** and early August for ***D. wrighti*** (Harrison 2009).

Figure 57. **Pygmy Salamander**, ***Desmognathus wrighti***. Photo by Michael Graziano, with permission.

Richard Bruce (pers. comm. 10 August 2019; Bruce 2019) describes his experience with the Pygmy Salamanders: "I find the salamanders under moss cushions (especially ***Thuidium delicatulum***; Figure 58) on the soil but also in the mosses among the rhizoids, stems, and leaves. I find them in loosely organized mosses with a lot

of internal space, as opposed to more compact mosses. But the salamanders also occur in leaf litter and under logs. Of the 3 miniaturized species of ***Desmognathus***, ***D. aeneus*** seems to have the greatest affinity for moss, but the other two also occur frequently in mosses. Mosses provide shelter and moisture, but also an abundance of food, especially oribatid mites, as well as other mites, springtails, and other tiny arthropods. A recent paper by Bruckner *et al*. (1918), based on research in a German forest, reported that oribatids were more abundant in moss than in either leaf litter or dead wood. Pore size (spaces within the moss clump) can be an important factor in mobility as well as moisture retention.

Figure 58. ***Desmognathus wrighti*** that lives within the mats of ***Thuidium delicatulum*** and ***Atrichum*** sp. seen here. Photo courtesy of Richard Bruce.

Desmognathus quadramaculatus (Black-bellied Salamander)

From Monroe County, West Virginia eastward to Henry County, Virginia, and southward through eastern Tennessee, western North and South Carolina to northeastern Georgia, in the Appalachian Mountains, USA. Peatlands are good habitats for salamanders, and ***Desmognathus*** is certainly represented there. In the ***Sphagnum*** habitat of the Tulula Wetland, North Carolina, USA, one can find ***Desmognathus quadramaculatus*** (**Black-bellied Salamander**; Figure 59), typically in streams (Amphibians: Tulula Wetlands 2009). In North Carolina, it is known from among mosses in streams (LeGrand *et al*. 2001).

This species has a somewhat longer development time than some of the other ***Desmognathus*** species, requiring six years in males and seven in females to reach first reproduction in the southern Blue Ridge Mountains (Bruce 1988).

Beachy (1997) reported that ***D. quadramaculatus*** co-occurred with the salamander ***Eurycea wilderae***, another bryophyte dweller. Unfortunately for ***E. wilderae***, it provides dinner for ***D. quadramaculatus***. Larval growth rates of ***E. wilderae*** differed with different predator densities, but survivorship did not differ, suggesting that provided no advantage in the low productivity of Appalachian streams.

Figure 59. ***Desmognathus quadramaculatus*** (**Black-bellied Salamander**). Photo by Bill Peterman.

Desmognathus ocoee (Ocoee Salamander)

The **Ocoee Salamander** (Figure 60) occurs in two **allopatric** (non-overlapping) units, one in the Appalachian Plateau of northeastern Alabama and adjacent Tennessee, and the other in the southwestern Blue Ridge Physiographic Province of western North Carolina, eastern Tennessee, extreme western South Carolina, and northern Georgia, south of the Pigeon River (Balsam, Blue Ridge, Cowee, Great Smoky, Nantahala, Snowbird, Tusquitee, and Unicoi Mountains), USA (Frost 2011).

Along with ***D. quadramaculatus***, one can find ***D. ocoee*** in the ***Sphagnum*** habitat of the Tulula Wetland, North Carolina, USA (Amphibians: Tulula Wetlands 2009), where their typical habitat is streams. Petranka *et al*. (1993) estimated that timber-harvesting rates of the 1980's and early 1990's caused an annual loss of at least 14 million salamanders of all species in western North Carolina, increasing the importance of peatland refugia.

Typical predators on ***D. ocoee*** include beetles, but Hess and Harris (2000) showed that pond beetles did not eat their eggs. However, beetles from a stream punctured and consumed a large number of ***D. ocoee*** eggs.

Figure 60. ***Desmognathus ocoee*** (**Ocoee Salamander**). Photo by John D. Willson, with permission.

In Macon County, North Carolina, eggs were mostly in nests embedded in mosses growing on rocks on the stream

bank or in the stream (Hess & Harris 2000). Bruce (1996) likewise found that most of the eggs of this species were located under moss on logs, soil, or rocks at the edges of streams, where females care for the eggs.

Phaeognathus hubrichti (Red Hills Salamander)

The **Red Hills Salamanders** (Figure 61) occur in the wooded Alabama Coastal Plain, southern edge of the Red Hills region, USA (Frost 2011). They generally stay in burrows where the humidity is high (Dodd 2011), but when they leave the burrows to forage they can encounter mosses in their habitat and may use them as foraging sites. Their diet of mostly land snails, ants, beetles, and spiders are all likely moss dwellers and perhaps account for the mosses found in some fecal pellets (Gunzburger 1999).

Figure 61. ***Phaeognathus hubrichti***. Photo by John P. Clare, through Creative Commons.

Ensatina eschscholtzii (Monterey Ensatina)

When I was teaching species concepts, this was always one of my favorite examples. Armed with a film loop that showed the morphs and their habitats, I could introduce the difficulty in defining species in any practical way. At that time, several species were recognized, as suggested by breeding incompatibility between some populations, but now they are listed by Frost (2011) as a single species, ***Ensatina eschscholtzii*** (Figure 62), and, like Christopher (2005), Frost treats them as seven distinct subspecies.

The distribution of this superspecies is in Southwestern British Columbia and Vancouver Island, Canada, south through mesic Washington, Oregon, and California, USA, to northern Baja California, Mexico, in the Sierra San Pedro Martír and Sierra Juárez. Its distribution around the mountain range in western USA led to its designation as a **Rassenkreis**, a circle of races (Figure 70).

Hence, current thinking is that there is only one species within the genus. The subspecies are distributed up the Pacific coast of the USA, across the northern Central Valley, and south through the Sierras. The coastal and Sierran subspecies meet in the mountains of southern California and they behave as separate species. Nevertheless, although some of these subspecies look quite different in the pictures that follow, adjacent salamanders recognize each other and can hybridize. For example, ***Ensatina eschscholtzii eschscholtzii*** hybridizes with ***E. e. xanthoptica*** and ***E. e. klauberi***.

Figure 71 demonstrates the habitat of ***Ensatina eschscholtzii oregonensis***. The recognized variants of ***Ensatina eschscholtzii***, not including hybrids, are:

Ensatina eschscholtzii eschscholtzii (Figure 62)
Ensatina eschscholtzii klauberi (Figure 64)
Ensatina eschscholtzii xanthoptica (Figure 63)
Ensatina eschscholtzii picta (Figure 65)
Ensatina eschscholtzii oregonensis (Figure 66-Figure 67)
Ensatina eschscholtzii platensis (Figure 68)
Ensatina eschscholtzii croceater (Figure 69)

Figure 62. ***Ensatina eschscholtzii eschscholtzii***. Photo by William Flaxington, with permission.

Figure 63. ***Ensatina eschscholtzii xanthoptica*** on moss. Photo by William Leonard, with permission.

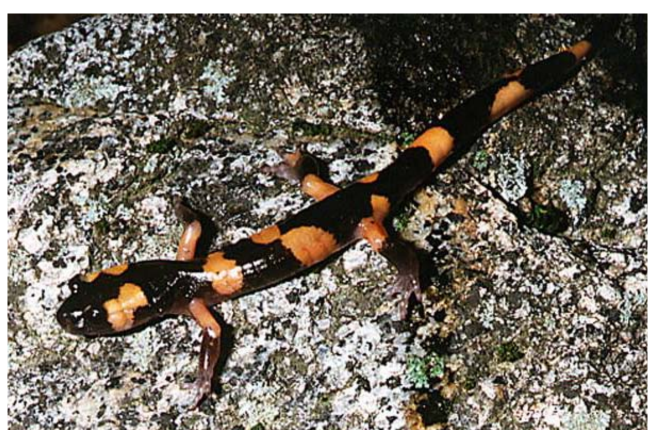

Figure 64. ***Ensatina eschscholtzii klauberi.*** Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 65. ***Ensatina eschscholtzii picta.*** Photo by William Flaxington, with permission.

Figure 66. ***Ensatina eschscholtzii oregonensis.*** Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 67. ***Ensatina eschscholtzii oregonensis*** amid mosses. Photo by Henk Wallays, through Creative Commons.

Figure 68. ***Ensatina eschscholtzii platensis.*** Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 69. ***Ensatina eschscholtzii croceator.*** Photo © Gary Nafis at CaliforniaHerps.com, with permission.

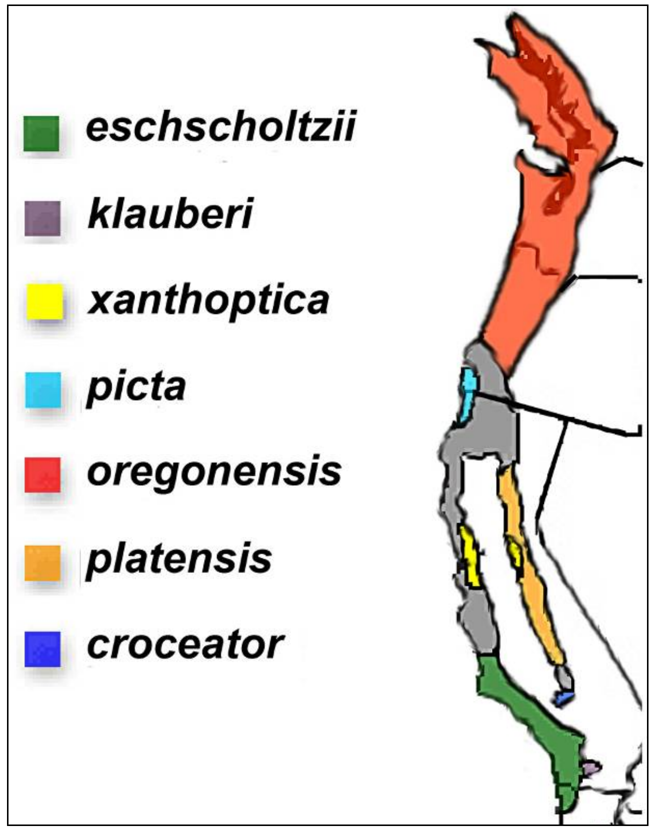

Figure 70. *Rassenkreis* of subspecies of ***Ensatina eschscholtzii***. Redrawn from Gary Nafis, © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 71. ***Ensatina eschscholtzii oregonensis*** habitat. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Gnaedinger and Reed (1948) pointed out that the importance of the moss habitat for ***Ensatina eschscholtzii*** had apparently been overlooked. At that time, several species were recognized, and when we combine them we need to recognize that the former species did not all have the same habitat, hence requiring caution in applying species habitat descriptions. Gnaedinger and Reed reported the salamander to occur between the moss and the ground, easily visible when the moss was removed. Such moss cover was found in 31.5% of their observations, exceeded only by the grouping of leaves, grass, and twigs. Relative numbers of those individuals found under mosses were 52.4% young, 16.7% juvenile, and 13.6% adults. This suggests that eggs may be laid on or in moss patches. The mosses may have been important in temperature regulation. The young were active under mosses at 1.2°C when the air temperature was -3.3°C, suggesting an insulating effect. The ground where salamanders were located was not frozen, apparently due to the protective cover of mosses. Unprotected soil, leaf litter, and surface of the mosses were frozen to a depth of about 1 cm and almost to the depth where the salamanders were active.

Hydromantes brunus (Limestone Salamander)

This species is known only from the area along the Merced River and North Fork Merced River, Mariposa County, California, USA, at 300-760 m asl (Frost 2011). The type was found under a moss-covered rock in Mariposa County, California, USA (Gorman 1954).

Hydromantes shastae (Shasta Salamander)

This species (Figure 72) is an endemic to the limestone substrates south of Mount Shasta near the Shasta Reservoir, Shasta County, California, USA at 300-910 m asl (Frost 2011). The type specimen was found under a small mossy log at a cave entrance (Gorman & Camp 1953). Eggs are terrestrial and have only been found in caves.

Road construction, quarrying, and changes in water levels cause this species to be vulnerable (IUCN 2010).

Figure 72. ***Hydromantes shastae*** on mosses. Photo by Henk Wallays, through Creative Commons.

Hydromantes ambrosii

Andreas Nöllert kindly sent me images of two subspecies of this salamander from mossy habitats. He found both in northwestern Italy. ***Hydromantes ambrosii ambrosii*** was living on a mossy cliff and ***H. a. blanchii*** was living in a mossy forest.

Figure 73. ***Hydromantes ambrosii ambrosii***, a cliff dweller. Photo by Andreas Nöllert, with permission.

Figure 74. ***Hydromantes ambrosii ambrosii*** habitat in NW Italy. Photo by Andreas Nöllert, with permission.

Figure 75. ***Hydromantes ambrosii blanchii***. Photo by Andreas Nöllert, with permission.

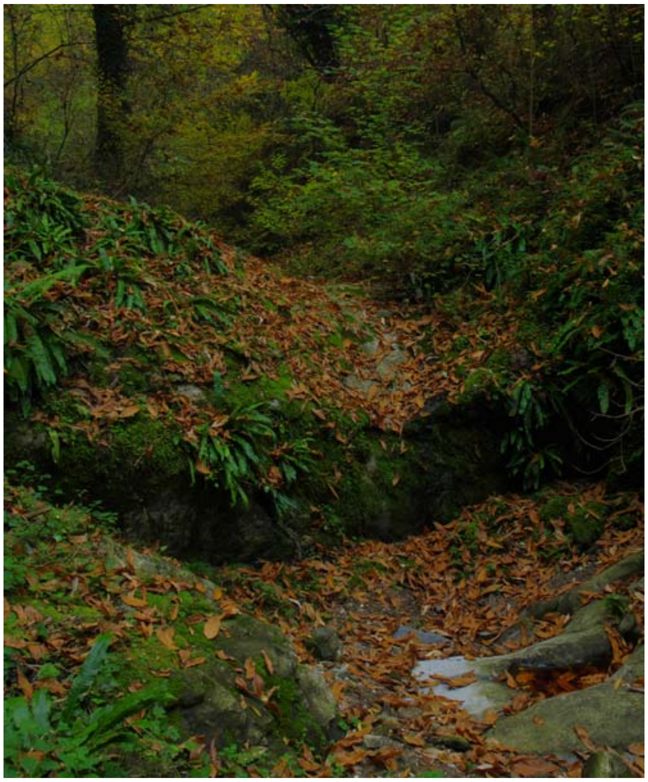

Figure 76. ***Hydromantes ambrosii bianchii*** habitat in Italy. Photo by Andreas Nöllert, with permission.

Summary

The Hynobiidae is a small family in Asia and Europe, with ***Hynobius tokyoensis*** migrating to the forest floor where mosses are among its hiding places. ***Salamandrella keyserlingii*** is also Asian and European and is one of the most cold-tolerant species of salamanders, spending winter in moss **hibernacula** and even surviving freezing in the permafrost for many years.

The Ambystomatidae extend from southern Canada to Mexico, living under mosses, among other forest floor habitats. Some species (*e.g.* ***Ambystoma maculatum***) are common in peatlands. This species provides oxygen to its jelly-coated eggs by partnering them with the green alga ***Oophila amblystomatis***.

In the Western Hemisphere, the Plethodontidae, including the large genus ***Plethodon***, is a large family of temperate zone salamanders. Many of these are bryophyte dwellers. The **Cheat Mountain Salamander** (***Plethodon nettingi***) is usually associated with the leafy liverwort ***Bazzania trilobata***, a rare example of a salamander associated with a specific bryophyte other than the genus ***Sphagnum***. ***Plethodon cinereus*** often lives in ***Sphagnum*** peat, where it attempts to rob the pitcher plant leaves of the invertebrates living there. But it can also live under forest floor mosses such as ***Leucobryum glaucum***. ***Desmognathus*** is found with mosses both in peatlands and in old-growth forests.

Peatlands are especially important for some species, such as members of ***Plethodon*** and ***Ambystoma***. Nevertheless, ***Sphagnum*** and associated ponds are typically too acid for most salamanders. ***Hemidactylium scutatum*** (**Four-toed Salamander**) apparently uses ***Sphagnum***. The **Four-toed Salamander** is the best known of the bryophyte dwellers, depositing its eggs under a variety of bryophytes, especially ***Thuidium*** and ***Sphagnum***. Mosses appear to be critical in its habitat, and loss of wetlands is a threat to its existence.

Stereochilus marginatus lays its eggs underwater on the moss ***Fontinalis***. ***Desmognathus fuscus*** lays eggs in the moist soil of stream banks, under mosses; a number of ***Desmognathus*** species use mosses for egg-laying sites.

Ensatina eschscholtzii subspecies form a **Rassenkreis** in California, USA, and mosses are often an important niche, where they can be found on the soil surface just under the moss.

Unknown species like ***Hydromantes brunus*** are likely to be living among mosses, invisible to the collector.

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CHAPTER 14-8
SALAMANDER MOSSY HABITATS

Janice M. Glime and William J. Boelema

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SALAMANDER MOSSY HABITATS

Figure 1. ***Bolitoglossa rostrata*** on the moss ***Thuidium*** sp. Photo by Sean Michael Rovito, with permission.

There are a number of habitats where bryophytes dominate either the ground cover (Figure 1) or the arboreal portion. In these, traversing bryophytes by salamanders is unavoidable. Since the Plethodontidae bryophyte inhabitants are too numerous for one subchapter of downloadable size, I have chosen to subdivide them into the mosses present vs mosses dominant and discuss them in these habitats. Please keep in mind that reference to "mosses" might actually include liverworts as well because the collectors were not trained to recognize the difference.

Tropical Mossy Habitats - Plethodontidae

The Neotropics provide a wide array of niches for bryophytes in trees, and elfin cloud forests literally look as if they have been draped by a bryophytic mat. The epiphytic bryophytes provide moisture-holding capacity that enables bromeliads and other epiphytes to be successful there. This arboreal system is home to a myriad of salamander species that use bryophytes for homes, cover, nests, moisture, and foraging sites. Small size and limited mobility have contributed to the evolution of many related species on mountains separated by valleys that prohibit their interbreeding, resulting in numerous microspecies and more conspicuous species.

Rich salamander fauna is associated with bryophyte mats in cloud forests of Talamancan central America, where they can sometimes be very abundant in the cloud forests. In Costa Rica salamanders use moss mats more commonly than do salamanders farther north and west. This is especially true for ***Nototriton*** and ***Oedipina***. Fossorial ***Lineatriton*** (now ***Pseudoeurycea***) and ***Oedipina*** occur only below the lower elevational limit of cloud forests in Veracruz, Mexico, and in Nuclear Central America. On the other hand, in cloud forests of Costa Rica and Panama, elongate members of ***Oedipina*** are common in moss mats covering soil banks, downed logs, and stumps at elevations up to at least 2000 m. Likewise, in Costa Rica ***Nototriton*** species, as well as at least two species of ***Bolitoglossa*** (Figure 1), occur among cloud forest mosses. The mid-elevational cloud forest locations tend to have the most salamanders, and at that elevation, mosses are the more commonly used habitat.

Terrestrial and Arboreal Adaptations

Wake (1987) considers mid-elevation cloud forests to have been critical in the evolution of Neotropical salamanders. Salamanders in the arboreal habitat of the Neotropics represent the epitome of adaptations for salamanders living on land. Wake (1987) considers the epiphytic habitat for tropical salamanders to have diverged into two habitat groups: mosses and bromeliads (Figure 3). The epiphytic bryophyte habitat is actually a composite including roots, club mosses, stems, ferns, and small flowering plants. Altig and McDiarmid (2007) summarized the terrestrial adaptations, which are largely coincidental to adaptations for living among terrestrial bryophytes, especially in the arboreal habitat. Epiphytic bryophyte-dwelling salamanders are not as easy to characterize as the bromeliad dwellers (Wake 1987). They are typically slender with short legs, presumably making movement within the moss mat easier. But living on land, especially in trees, made life cycle adaptations essential.

Nests need to be placed where they have both cover/camouflage and moisture maintenance. Bryophytes can provide both, so their use in arboreal habitats, especially for live-bearers, is a viable option for those not using bromeliad basins.

Eggs (Figure 2) cannot move about to adjust to the changes in their environment, hence they exhibit some of the most important of the terrestrial adaptations. They require tradeoffs among need for gas exchange, need for mechanical support, same-species sperm attraction, other species sperm avoidance, heat conservation or cooling, predator defense, moisture retention, UV light protection, prevention of polyspermy (multiple fertilizations by sperm), and protection from bacteria and the water molds ***Saprolegnia*** and ***Achlys*** (Altig & McDiarmid 2007). Together, these needs influence the number of layers, thickness, and physical characteristics of the layers of the eggs. Salthe (1963) suggests that having 8 jelly layers is the primitive condition and that changes in number of layers can occur through the loss of the most external layers (*e.g.* **Ambystomatidae**), loss of more internal layers (especially **Plethodontidae**), or having eggs with three layers for which we do not understand the homologies. Salthe further suggested that loss of layers of terrestrial eggs in **Plethodontidae** results from changes of internal layers whereas the tough outer layer remains for protection.

Figure 2. ***Bolitoglossa hartwegi***, a moss dweller, tending its eggs. Photo by Bill Peterman, with permission.

Figure 3. Bromeliads and mosses on the floor of the cloud forest in Puerto Rico, illustrating the types of habitats available to small salamanders such as ***Nototriton*** species. Photo by Janice Glime.

Important adaptive features of the jelly layer include elasticity, stickiness, toughness, turgidity, and wateriness. Those eggs laid in the water are typically spherical in the water but sag on surfaces in the air. Terrestrial eggs typically have jelly that is turgid and retains its spherical shape in air. Terrestrial salamanders and frogs that experience direct development to adults lay eggs that have a tough outer jelly that permits proper development, oxygenation, and protection from trampling by the parents. Pigmentation has received insufficient study. However, there is evidence that those eggs laid in the open have melanic pigments at the animal pole (Altig & McDiarmid 2007). Buried eggs usually are pale or lack pigmentation. Pigments can absorb heat and increase rate of development, protect against heat, and protect against specific wavelengths (Barrio 1965; Jones 1967; Hassinger 1970).

Egg placement (Figure 2) necessarily must protect eggs from desiccation. The semiterrestrial eggs have not yet abandoned their aquatic history. These are usually deposited adjacent to a water source, not submerged, where hatchlings can easily move or drop into the water (Altig & McDiarmid 2007). They frequently are laid among mosses in seeps or beside bog ponds.

Development and hatching of eggs is often modified from that of aquatic species. Females of many terrestrial species care for the eggs, cleaning and turning them – an activity that seems to reduce the bacterial and fungal colonization. Some species are **viviparous** (have live birth). Some have embryos that develop directly into young salamanders with no larval stage. But some still require water for development of their larvae and therefore lay their eggs near water where larvae have easy access.

Hatching is similar among most salamanders, using an enzyme to break through the jelly, but in some terrestrial salamanders there is an egg tooth similar to that in birds.

Bolitoglossa (Tropical Climbing Salamanders, Plethodontidae)

Sean Rovito has told me about finding several species of tropical climbing salamanders (***Bolitoglossa***; Figure 4) in the páramo in the Cordillera de Talamanca, Costa Rica, under thick mats of moss. Wake (1987) reported that members of this genus use mats of vegetation, including mosses and liverworts surrounding tree branches and twigs.

Species in this genus are able to propel themselves forward by an "explosive tail flip" that carries them off the vegetation – a protective device when in danger during its daylight resting hours (Leenders & Watkins-Colwell 2003). Another protective behavior is to raise its tail as an offering to a predator. If the tail is grabbed, the salamander can **disarticulate** and run off, leaving the predator with only the tail (Lee 2000).

Figure 4. **La Loma Salamander**, also known as the Ridge-headed Salamander, ***Bolitoglossa colonnea*** occurs in Costa Rica and Panama. Photo by Twan Leenders, with permission.

Arboreal adaptations include elongated fingers, contrasting with webbing used by aquatic species to move through water, and increased efficiency of the suction cups (Wikipedia 2011a). The arboreal body size is smaller, making it easier to cling (and easier to move through moss mats).

Bolitoglossa diaphora (Plethodontidae)

Although ***Bolitoglossa diaphora*** (Figure 5) was described by McCranie and Wilson in 1995, it still has no English name (Frost 2011). It is known from 1470-2200 m asl in cloud forests of the Sierra de Omoa on the Atlantic side of the mountains of northwestern Honduras. It was described as a species based on a specimen at Cerro Jilinco at 2200 m asl from under a moss mat in a small hole. Its decreasing population is listed as critically endangered (IUCN 2010b).

Figure 6. ***Bolitoglossa*** *cf.* ***hartwegi*** on a bed of ***Thuidium***. Photos by Sean Michael Rovito, with permission.

Figure 5. ***Bolitoglossa diaphora*** on a fern. Photo by Josiah Townsend, with permission.

Figure 7. ***Bolitoglossa*** *cf.* ***hartwegi*** blending with mosses and lichens on a rock. Photos by Sean Michael Rovito, with permission.

Bolitoglossa diminuta (Quebrada Valverde Salamander, Plethodontidae)

This is a tiny (35 mm) bryophyte-mat-inhabiting Costa Rican salamander, known only from the type locality of lower montane rain forest, near Quebrada Valverde, Cartago Province, on the Atlantic slope of Costa Rica at 1300-1650 m asl. For a long time the only known adult was collected with its egg mass in a mat of liverworts (Robinson 1976; Wake 1987). Wake (pers. comm. 31 March 2011) says that this species specializes in living in balls of mosses attached to vines suspended far from the ground or the trees to which the vines are attached. Eggs are typically laid in these moss balls. This salamander is considered vulnerable because it is known from only one location (IUCN 2010b).

Bolitoglossa hartwegi (Hartweg's Mushroomtongue Salamander, Plethodontidae)

Bolitoglossa hartwegi (Figure 2, Figure 6-Figure 7) lives in Guatemala and Mexico in subtropical and tropical moist montane forests (IUCN 2010b; Frost 2011), 1200-2800 m asl (Encyclopedia of Life 2011). It is also able to live in heavily degraded forests, but loss of habitat still renders it threatened. Its presence in moist montane forests suggests that it might be an occasional moss dweller, or use them at moist sites.

Bolitoglossa helmrichi (Plethodontidae)

The tiny ***Bolitoglossa helmrichi*** (Figure 8-Figure 9) is near threatened in its arboreal home in the cloud forests of Guatemala (IUCN 2010b). Its scarcity accounts for the little information we have on it, but its small size and habitat suggest it spends at least part of its time among mosses.

Figure 8. ***Bolitoglossa helmrichi*** resting on a leaf. Photo by Todd Pierson, with permission.

Figure 9. ***Bolitoglossa helmrichi***. The lower photo shows how small these salamanders are. Photo by Todd Pierson, with permission.

Bolitoglossa jugivagans (Plethodontidae)

The species ***Bolitoglossa jugivagans*** (Figure 10-Figure 11) causes one to ask about potential adaptations among these mossy habitat salamanders. This is a newly described species from Panama, where it lives in a mossy habitat (Hertz *et al*. 2013). Its life habits are poorly known, but it has one habit that offers possibilities as an adaptation to its mossy neighborhood – it changes from a highly patterned coloration during the day (Figure 10) to a more uniform coloration at night (Figure 11). Andreas Hertz (pers. comm. 14 January 2016) tells me that the trigger(s) for its change in coloration are currently unknown, but other salamanders are known to respond to changes in light, background coloration, temperature, and stress. Such ability could provide adaptations for salamanders living within bryophyte mats or running about and resting on top of them. He pointed out that while we know about mechanisms for these changes in only a few species, we know that these mechanisms do differ among species.

Figure 10. ***Bolitoglossa jugivagans*** exhibiting its daytime coloration while sitting on a moss. Photo by Andreas Hertz, with permission.

Figure 11. ***Bolitoglossa jugivagans*** exhibiting its nighttime coloration while sitting on a solid-colored leaf. Photo by Andreas Hertz, with permission.

Bolitoglossa lincolni (Lincoln's Mushroomtongue Salamander, Plethodontidae)

Bolitoglossa lincolni (Figure 12) is known from the central plateau of the Chiapas, Mexico, and mountainous areas of western Guatemala at 1200-3000 m asl (IUCN 2010b). It lives in low vegetation (probably including mosses), under bark, and in bromeliads, with a broad enough habitat that its populations are not declining. However, due to destruction of habitat, it is listed as a species near threatened on the IUCN list.

Figure 12. ***Bolitoglossa lincolni*** (**Lincoln's Mushroomtongue Salamander**). Photo by Bill Peterman, with permission.

Bolitoglossa longissima (Plethodontidae)

Bolitoglossa longissima is restricted to intermediate elevations (1840-2240 m asl) on the Atlantic side of Pico La Picucha in the Sierra de Agalta, Honduras (Frost 2011) where it is critically endangered (IUCN 2010b). This species is known from under leaves and moss on the ground and from moss-covered tree trunks at ~2.0-3.5 m above the ground (McCranie & Cruz 1996).

Bolitoglossa marmorea (Crater Salamander, Plethodontidae)

This species (Figure 13) is distributed in Costa Rica and Panama, where it lives in subtropical or tropical moist

montane regions and areas where the forest has been highly degraded (Wikipedia 2011b) at 1,920-3,444 m asl (IUCN 2010b). It hides under rocks in the daytime, but climbs over moss mats on tree trunks and branches at night (Wake *et al.* 1973). It is moderately sized – large for a moss dweller (adults range 128-134 mm in total length), and has long limbs (AmphibiaWeb 2009c). Habitat loss and degradation due to agricultural expansion threaten its existence, causing it to be listed as endangered (IUCN 2010b).

Figure 13. ***Bolitoglossa marmorea***, a species that traverses mosses on tree trunks at night in the Neotropics. Photo from Division of Herpetology, University of Kansas, permission through Rafe Brown.

Bolitoglossa mexicana (Mexican Mushroomtongue Salamander, Plethodontidae)

Bolitoglossa mexicana (Figure 14) occurs from the Chiapas, Mexico, to the Honduras (IUCN 2010b). It primarily lives in trees where it hangs out in bromeliads and other epiphytes, presumably including bryophytes. Their broad distribution and abundance cause them to be classified as a species of least concern.

Figure 14. ***Bolitolgossa mexicana*** on mossy bark at Selva Lacandona, Chiapas, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Bolitoglossa obscura (Tapantí Giant Salamander, Plethodontidae)

Hanken *et al.* (2005) examined the members of ***Bolitoglossa*** in Costa Rica and Panama in an effort to understand the taxonomy there. They found that ***Bolitoglossa obscura***, known only from the type locality in the Parque Nacional Tapanti, Provincia Cartago, Costa Rica., is **sympatric** (having overlapped distributions) with two other tiny (35 mm) moss-mat-inhabiting plethodontid species, ***B. diminuta*** **(Quebrada Valverde Salamander)** and ***Nototriton picadoi*** (discussed below). The existence of ***Bolitoglossa obscura*** is vulnerable, but its population trend is unknown (IUCN 2010b).

Bolitoglossa robusta (Robust Mushroomtongue Salamander, Plethodontidae)

The **Robust Mushroomtongue Salamander** (Figure 15), also known as the Ringtail Salamander, occupies humid premontane and lower montane areas in the mountains of north-central and eastern Costa Rica at 500-2048 m asl and in Bocas del Toro Province, Panama at 50-2100 m asl (Frost 2011). It is often found under fallen logs, in thick leaf litter, or under mosses (Hanken *et al.* 2005). Although its populations are decreasing, it is still listed as a species of least concern (IUCN 2010b).

Figure 15. ***Bolitoglossa robusta***. Photos by Eduardo Bozo, with permission.

Bolitoglossa rostrata (Longnose Mushroomtongue Salamander, Plethodontidae)

The species ***Bolitoglossa rostrata*** (Figure 16) of Guatemala and Mexico occurs in high elevation forests and is often arboreal (Raffaëlli 2011a). One could expect to find it among epiphytic bryophytes since the genus is well adapted to the small spaces provided by them. The species is vulnerable and decreasing in population size (IUCN 2010b).

Figure 16. ***Bolitoglossa rostrata*** on ***Thuidium***. Photo by Sean Michael Rovito, with permission.

Bolitoglossa rufescens (Northern Banana Salamander, Plethodontidae)

Bolitoglossa rufescens (Figure 17) is distributed from Mexico to Honduras (Frost 2011) where it occupies rainforests in lowlands (sea level to 1500 m asl) (McCoy 1990). It is arboreal and night active (McCoy 1990), living mostly in bromeliads (Frost 2011). The bryophytes in its habitat most likely contribute to keeping it hydrated when it moves about in search of food. Ants are the most important food source (Anderson & Mathis 1999), thus we should expect it to venture away from the bromeliads to find them. It is listed as a species of least concern (IUCN 2010b). It defends itself by flicking its tail, a behavior that distracts the predator, usually a snake, from the more vulnerable parts of the body (Brodie *et al*. 1991). If deemed necessary, it will **disarticulate** its tail (Lee 2000). Unlike ***B. palmata*** and ***B. rostrata***, this species is not noxious to snakes. In one case, Buttenhoff (1995) observed an attack by the mantid ***Choeradodis strumaria*** (see Figure 18) on an adult ***B. rufescens***. Although mantids would not seem to have much connection to bryophytes, some are excellent bryophyte mimics and hang out among the arboreal bryophytes.

Figure 17. ***Bolitoglossa rufescens*** on a bed of mosses. Photo by Sean Michael Rovito, with permission.

Figure 18. ***Choeradodis strumaria***, a mantid predator on ***Bolitoglossa rufescens***. Photo by C. Horwitz through Creative Commons.

Bolitoglossa sombra (Shadowy Web-footed Salamander, Plethodontidae)

Bolitoglossa sombra (Figure 19) occurs on Pacific slopes of the Cordillera de Talamanca of Costa Rica and extreme western Panama at 1500-2300 m asl (Frost 2011) and is found on moss-covered tree trunks, under mosses on tree trunks, and on stumps at 0.6-2.0 m above the ground, but was also found on a concrete structure providing access to an underground aqueduct and between mossy buttresses of a tree on top of leaf litter (Hanken *et al*. 2005). Like most of the tropical amphibians, it is red-listed, but is listed only as vulnerable (IUCN 2010b).

Figure 19. ***Bolitoglossa sombra***, a bryophyte dweller in the tropics. Photo © 2013 Don Filipiak, through online permission.

Bolitoglossa subpalmato (La Palma Salamander, Plethodontidae)

The **La Palma Salamander** (Figure 20) occurs in humid lower montane and montane zones, marginally into the premontane belt on both slopes of the Cordillera de Guanacaste, Cordillera de Tilarán, Cordillera Central to central and northern Costa Rica at 1245-2900 m asl (Frost 2011). Its habitat is subtropical or tropical moist montane regions, pastureland, plantations, rural gardens, and heavily degraded former forests (Wikipedia 2011c), where its habitat is threatened by habitat loss and fragmentation due to the encroachment of agriculture, causing it to be listed as endangered by the IUCN (IUCN 2010b).

Figure 20. ***Bolitoglossa subpalmata*** on a leaf. Photo by Ira Richling, <www.helicina.de>, with permission.

This species enjoys one of the most extensive studies done on tropical salamanders. Vial (1968) found that its niche changes with elevation in Costa Rica. In the middle portion of its elevational range (2400-2700 m asl), its most frequent microhabitat is in the dense carpet of ***Sphagnum*** (Figure 21) and club mosses, where it is able to maintain its hydration. These salamanders are not active when the humidity is less than 51%. The mossy habitats also afford a relatively low, stable temperature (9.8-16°C).

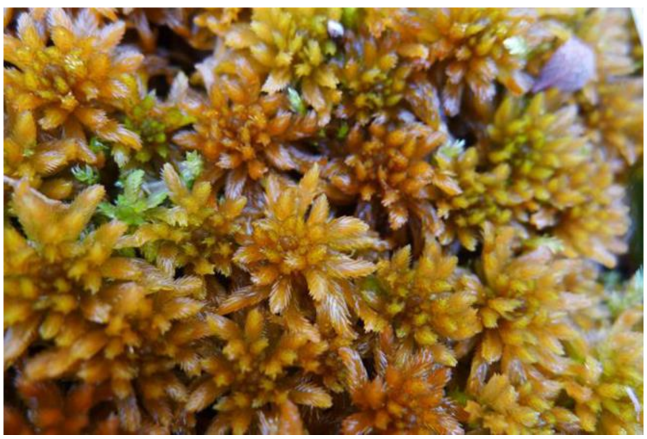

Figure 21. ***Sphagnum balticum*** from Costa Rica, home for a variety of salamanders. Photo from Biopix, through Creative Commons.

The species is nocturnal, spending the day under rocks, mosses, and plant debris where these are either deeply imbedded in the soil or have well-developed borders of lichens and mosses (Vial 1968). At night they may climb branches of moss-covered trees to 2 m above ground. They nest under well-imbedded rocks or in decaying logs. Adults attend the eggs (Houck 1977). When the nest is disturbed, the adults abandon the eggs and development ceases. They require a site that has been undisturbed for several years, permitting it to develop a good cover of lichens and mosses. Mosses clearly play a role in maintaining the species in at least the middle elevations of its range.

This species seems to be ideal prey for small snakes, but it has an effective defense mechanism (Wikipedia: *Bolitoglossa* 2011). It, and ***B. subpalmata***, are poisonous. The skin secretes a toxin that is effective on particular snake species. The initial contact causes the snake to become immobile and unable to respond to its prey. The salamander remains still, taking advantage of the behavior of the snake to contact the salamander when the snake flicks its tongue. This contact paralyzes the snake and permits the salamander to run.

Bolitoglossa suchitanensis (Plethodontidae)

The type specimen of ***Bolitoglossa suchitanensis*** (Figure 22), buried in moss on a log, was collected in Guatemala in 1999 (Campbell *et al*. 2010). However, it was not named and described until 2010. Subsequent collections came from tree trunks and under logs, but not in mosses. Its known habitat is a humid deciduous forest with abundant mosses and epiphytes. It lacks an IUCN status evaluation (IUCN 2010b).

Figure 22. ***Bolitoglossa suchitanensis***, an inhabitant of mossy logs and forests. Photo by Sean Michael Rovito, through Creative Commons.

Bolitoglossa xibalba (Plethodontidae)

Campbell *et al*. (2010) reported that most of the individuals of ***Bolitoglossa xibalba*** (Figure 23) were taken from under loose bark or mosses at bases of rotting tree trunks. These were found at 1980-2760 m asl in wet montane forests of Guatemala. Little seems to be known about the species, and it lacks an IUCN status evaluation (IUCN 2010b).

Figure 23. ***Bolitoglossa xibalba***. Note the webbing of the feet. Photo © Jonathan Campbell, with permission.

Chiropterotriton (Splayfoot Salamanders, Plethodontidae)

This genus of twelve species is known from West-central Tamaulipas in the north to the mountains of northern Oaxaca in the south, Mexico (Frost 2011). Tim Burkhardt (pers. comm. 17 February 2011) found an unidentified member of ***Chiropterotriton*** (Figure 24) at 2440 m asl on the NW slope of Cerro Cofre de Perote, Veracruz, Mexico. It was beneath a mat of mosses on the rocky wall of a ravine.

Figure 24. ***Chiropterotriton*** sp. from the wall of a ravine where it was beneath sheets of moss on Cerro Cofre de Perote, Veracruz, Mexico. Photo by Timothy Burkhardt <www.mexico-herps.com>, with permission.

Chiropterotriton chiropterus (Common Splayfoot Salamander, Plethodontidae)

Chiropterotriton chiropterus (Figure 25) is known only from central Veracruz, near Huatusco, Mexico, at 1000-1200 m asl (IUCN 2010b). Its niche includes mosses and bromeliads and it has direct development. IUCN lists it as critically endangered and possibly extinct, although it was once abundant. It seems unable to live in degraded habitats.

Figure 25. ***Chiropterotriton chiropterus***, a moss dweller in Mexico. Photo by César L. Barrio Amorós, with online permission for educational use.

Cryptotriton alvarezdeltoroi (Alvarez del Toro's Salamander, Plethodontidae)

Timothy Burkhardt (pers. comm. 17 February 2011) suggested to me that the salamanders in ***Nototriton*** and ***Cryptotriton*** are the ones most closely associated with mosses. ***Cryptotriton*** is a recent segregate of the genus ***Nototriton***.

In Mexico, ***Cryptotriton*** (formerly *Nototriton*) ***alvarezdeltoroi*** (**Alvarez del Toro's Salamander**; Figure 26), a salamander of ~2.6 cm length (Raffaëlli 2011b), was found at 1200-1550 m asl in the cloud forest of the Chiapas, climbing up a moss bank at night (Papenfuss & Wake 1987). It is known only from this type locality. The IUCN Red List of this species has been changed from endangered (2004) to vulnerable (2008) (IUCN 2010b). This change is because it is now known in less than 20,000 km^2, all individuals are known in fewer than five locations, and there is continuing decline in the extent and quality of its habitat in Chiapas, Mexico. Its known habitat is restricted to the cloud forest, where it seems to require microhabitats with very high humidity. Like many terrestrial salamanders, it has direct development into froglets that hatch from the eggs.

Figure 26. ***Cryptotriton alvarezdeltoroi***, a species that occurs among mosses in the cloud forest of Mexico. Photo by Sean Michael Rovito, through Creative Commons.

Cryptotriton monzoni (Monzon's Hidden Salamander, Plethodontidae)

This little fellow, ***Cryptotriton monzoni*** (Figure 27), measures only 2.2 cm (Whittaker 2010) and is listed as critically endangered by the IUCN Red List (IUCN 2010b). It is known only from its type locality at 1570 m asl in Zacapa, Guatemala, thus occurring in less than 100 km^2 and fewer than five localities, while suffering from a continuing decline in its habitat, especially due to deforestation. Its known habitat is in the cloud forest, and it may occur in additional, unexplored sites of cloud forest. The type specimen was found in a bromeliad and its use of mosses is unknown. Most likely they contribute to keeping it moist while it is foraging.

Figure 27. ***Cryptotriton monzoni***, known only from lower montane wet forest at its type locality in lower montane wet forest, near La Unión, Zacapa, Guatemala, at 1570 m asl. Photo by Sean Michael Rovito, with permission.

Dendrotriton cuchumatanus (Forest Bromeliad Salamander, Plethodontidae)

In Guatemala, ***Dendrotriton cuchumatanus*** (also known as Cuchumatanas Bromeliad Salamander; Figure 28-Figure 29) lives under moss mats on oak trees (Sean Michael Rovito pers. comm. 7 February 2009). It is endemic to its type locality in Guatemala (Acevedo & Wake 2004) at Sierra de los Cuchumatanes southwest of San Juan Ixcoy (Frost 2011). Despite its common name, it is not known to inhabit bromeliads, but does live both in moss banks and under mosses on fallen trees (ZipcodeZoo.Com 2008a).

Figure 28. Cuchumatanas Bromeliad Salamander, ***Dendrotriton cuchumatanus*** on a leaf covered with epiphyllous algae and bryophytes. Photo © Jonathan Campbell, with permission.

Figure 29. ***Dendrotriton cuchumatanus*** on a mossy log. Photo by Sean Michael Rovito, with permission.

Nototriton (Moss Salamanders)

In Costa Rica, and other neotropical countries, a genus of tiny **Moss Salamanders** (***Nototriton***; Figure 30) lives among mosses on trees as well as among leaf litter on the ground (Good & Wake 1993; García-París *et al.* 2000a). Seven species of **Moss Salamanders** have been discovered among the mossy habitats in diversity hotspots in Costa Rica (ZipcodeZoo.Com 2008d). In the cloud forest they can be abundant in moss clumps (Taylor 1954), where they are difficult to find (Good & Wake). In other Neotropical countries, most of the species live in bromeliads (Good & Wake 1993). Some species of ***Nototriton*** are so small that young ones can fit completely on a man's thumbnail (National Geographic News 2009)! The long, thin bodies maximize surface area for oxygen exchange in this lungless salamander (Edge 2009).

Figure 30. **Santa Barbara Moss Salamander**, ***Nototriton limnospectator***, a moss salamander of lower montane wet forests of the Parque Nacional Santa Barbara. It occurs at intermediate elevations (1640-1980 m asl) of the Montaña de Santa Bárbara on the Atlantic side of western Honduras where it is threatened by habitat loss. That, plus its limited distribution, cause it to be listed as endangered (IUCN 2010b). Its use of mosses is unknown. Photo by Sean Michael Rovito, with permission.

This genus, as currently configured, is the result of an evolutionary radiation of bolitoglossine salamanders (**Plethodontidae**) that has tremendous diversification of both form and ecology (García-París & Wake 2000). They range from the large, robust terrestrial taxa such as ***Pseudoeurycea bellii*** to the much smaller moss dwellers of ***Nototriton*** such as ***N. abscondens*** (Figure 31).

The genus ***Nototriton*** is small and slender, with a long tail and moderately long to short legs, with moss dwellers having short legs (García-París & Wake 2000). The feet are small, especially in the arboreal moss dwellers. This is an interesting contrast to the tree-dwelling frogs, where the foot pads are larger with increasing elevation above the ground, providing better suction for holding on. One can assume that such suction ability is not needed for wormlike salamanders that live within the moss mat.

This genus differs from many of the terrestrial plethodontid salamanders in its care of the eggs. Instead of guarding them, the females deposit the eggs in clumps of bryophytes in trees and abandon them (McCranie & Wilson 1992; Good & Wake 1993). This suggests that the bryophytes provide sufficient moisture. But does this suggest that the bryophytes afford such good protection that parental care is unnecessary? Might the bryophytes provide antibiotics that keep the eggs safe from disease?

The larvae of ***Nototriton*** develop completely within the eggs, and the eggs hatch into small salamanders, not tadpoles. Papenfuss and Wake (1987) describe members of this diverse genus as "rare, secretive, and poorly known." ***Nototriton*** is characterized by a delicate pattern of colors that are quite beautiful under the dissecting microscope, but to the unaided eye, these colors usually blend to create a dull brown (Figure 37). Wake suggests that miniaturization in this genus permits its members to occupy habitats not available to other species. For some, the habitat appears to be the spaces among bryophytes (see Figure 3).

Nototriton abscondens (Plethodontidae)

Like many of the moss-dwelling salamanders that have been seen only a few times, ***Nototriton abscondens*** (Figure 31) has no English name. It is known from sub-humid and humid premontane and humid montane forests of the Cordillera de Tilarán and Cordillera Central of Costa Rica, 960-2050 m asl (Good & Wake 1993). This one has been known longer than most, with Taylor (1954) reporting them from moss mats hanging from trees and bushes, occasionally horizontal limbs, and mosses that cover dirt banks, large boulders, or stumps. They also seem to be common in lightly disturbed areas along trails and roads, again in clumps of moss. Good and Wake (1993) found them again in these habitats, but also in mosses on tree trunks and branches in the cloud forest and on mosses on logs. They consider this to be a species that specializes on mosses (**bryobiont**).

Figure 31. ***Nototriton abscondens***. Photo by Eduardo Boza Oviedo, with permission.

Nototriton barbouri (Yoro Salamander, Plethodontidae)

Nototriton barbouri (Figure 32) is an endemic living at moderate and intermediate elevations (860-1990 m asl) on the Atlantic mountainside from northwestern to north-central Honduras (Frost 2011). This species occurs in an area of less than 5000 km^2, has fewer than ten known locations, and suffers from continuous decline of its habitat, making it an endangered species on the IUCN Red List (IUCN 2010b). In this lower montane forest, it lives among moss, low vegetation, on the forest floor, and on tree trunks (ZipcodeZoo.Com 2008b). Its clutch size of 5-19 eggs is a bit larger than that of ***Nototriton picadoi*** (McCranie & Wilson 2002).

Figure 32. ***Nototriton barbouri*** on mosses covering decaying wood. Photo by Josiah Townsend, with permission.

Nototriton gamezi (Monteverde Moss Salamander, Plethodontidae)

This species (Figure 33) lives in the premontane and lower montane rainforests of the Reserva Biologica Monteverde, Cordillera de Tilarán, Costa Rica, at 1550-1650 m asl. The species is listed as vulnerable, but stable (IUCN 2010b).

Figure 33. ***Nototriton gamezi***. Photo by Sean Michael Rovito, with permission.

Two specimens of ***Nototriton gamezi*** (Monteverde Moss Salamander**,** Figure 33-Figure 36) were collected in thick mats of moss in Monteverde Cloud Forest Reserve, Costa Rica, in August, 1987, in forest openings near the divide (García-París & Wake 2000). The type specimen and one other were collected nearby from mosses growing on a tree. García-París and Wake (2000) found specimens by searching through heavy moss mats in openings in the forest. The temperatures within the mats ranged 20.0-21.5°C.

Figure 34. ***Nototriton gamezi*** on a bed of mosses. Photo by Sean Michael Rovito, with permission.

Figure 35. ***Nototriton gamezi***. Photo by Sean Michael Rovito, with permission.

Figure 36. ***Nototriton gamezi***. Photo by Eduardo Boza Oviedo, with permission.

Nototriton guanacaste (Guanacaste Moss Salamander, Plethodontidae)

Nototriton guanacaste (also known as Volcan Cacao moss salamander) is known primarily from collections of moss from tree trunks and branches, up to 4 m from the ground, in the cloud forests and premontane rainforests of Costa Rica (Tosi 1969; Good & Wake 1993). It is known only from humid, lower montane moss-laden, low-stature forests near the summits of Volcán Orosí and Cerro Cacao, in the Cordillera de Guanacaste, Province of Guanacaste, northwestern Costa Rica, at 1420 and 1580 m asl (Frost 2011). It has a narrow temperature activity range of 17.1-18.1°C (Good & Wake 1993), suggesting that the bryophytes may serve to buffer its temperature climate, or at least provide a safe haven during inactivity.

Figure 37. ***Nototriton guanacaste***. Photo by Javier Sunyer, with permission.

Nototriton picadoi (Picado's Moss Salamander, Plethodontidae)

Nototriton picadoi (Picado's Moss Salamander) is restricted to premontane and lower montane wet forest (in the northern end of the Cordillera de Talamanca in cloud forest, Costa Rica, at 1200-2200 m asl (Frost 2011). Although a few individuals have been found in moss balls up to 8 m high, associated with vines (Wake 1987; David Wake, pers. comm. 31 March 2011), most ***Nototriton picadoi*** seem to be almost restricted to hanging mosses on tree limbs and tree trunks, but they have also been collected in bromeliads (Good & Wake 1993; Savage 2002). Bruce (1999) considers the species to be a "specialist on moss." In a collecting trip to Tapanti, Bruce was able to locate only 38 individuals in 270 person hours. Of these, three were in moss mats on the ground and 35 were above ground to about 8 cm, all but one being in mosses.

Eggs of ***Nototriton picadoi*** have been found only in and under mosses in the same habitats where adults are known (Good & Wake 1993; Savage 2002). Nevertheless, it appears that the adults do not attend their eggs (Bruce 1998), an unusual behavioral omission for terrestrial salamanders (Duellman & Trueb 1994). Bruce (1998) suggests that this lack of care may represent a tradeoff with other adaptations that minimize desiccation, predation, and fungal infections in the eggs. Like the tiny frogs, this species has few eggs (1-8), permitting eggs to be larger and more protected. The eggs are laid over an extended period of several months that begins with the wet season in May. All hatching is completed before the dry season, ending in December. Development of the embryos requires 2.5-3 months.

Nototriton richardi (Richard's Salamander, Plethodontidae)

Nototriton richardi (Figure 38-Figure 39) lives in moss banks (Wake 1987) and leaf litter of the humid lower montane rainforest and to a lesser degree in upper premontane rainforest of higher altitudes (1370-1800 m asl) on the Atlantic slopes of the Cordillera Central of Costa Rica (Good & Wake 1993; ZipcodeZoo.Com 2008c; Frost 2011). Good and Wake (1993) also found it among mosses covering tree trunks and stumps in Costa Rica. It is listed as near threatened on the IUCN red list (IUCN 2010b).

Figure 38. ***Nototriton richardi***. Photo by Eduardo Boza Oviedo, with permission.

Figure 39. ***Nototriton richardi***. Photo by Eduardo Boza Oviedo, with permission.

Nototriton saslaya (Plethodontidae)

Nototriton saslaya (Figure 40) is an endemic known only from the cloud forest near its type locality on the south slope of Cerro Saslaya, Atlántico, Nicaragua, at 1280-1370 m asl (Köhler 2002; IUCN 2010a; Frost 2011). The cloud forest is characterized by an abundant bryophyte cover, so it is almost inevitable that the salamanders will traverse them. They would make ideal safe spots for eggs, but the location of eggs has not been documented. The species is listed as vulnerable (IUCN 2010b).

The species ***Nototriton saslaya*** not only lives in moss, but the eggs hatch there and juveniles develop there; *i.e.*, they are not dependent upon submersion as are eggs of many salamanders (ZipcodeZoo.Com 2008d).

Figure 40. ***Nototriton saslaya*** on leaf. Photo by Gunther Koehler, with permission.

Nototriton tapanti (Tapanti Moss Salamander, Plethodontidae)

This species is known only from its type locality, the humid premontane Atlantic slope forest near Tapanti, Costa Rica, where it lives in the humid premontane Atlantic slope at the north end of the Cordillera de Talamanca (Frost 2011). It lives among mosses that cover tree trunks and stumps, on road banks, and probably in leaf litter in the Orosi River Valley (Savage 2002). This and other recent species in Costa Rica suggest that a number of species have evolved there through miniaturization, a good adaptation to living among mosses (Good & Wake 1993). In other locations, the species of ***Nototriton*** are primarily bromeliad dwellers. This species is currently listed as endangered on the IUCN Red List due to its very restricted distribution and may possibly be critically endangered due to continued habitat loss (Bolaños *et al*. 2004, 2008). However, lack of data makes it hard to assess its status.

Nyctanolis pernix (Nimble Long-limbed Salamander, Plethodontidae)

Nyctanolis pernix (Figure 41) occurs in Guatemala and Mexico in subtropical or tropical moist montanes (IUCN 2010b) at 1200-1610 m asl (Frost 2011). It is listed as endangered due to its small distribution and threatened habitat (IUCN 2010b). It is not found in disturbed habitats. Its habitat is humid pine-oak forests and cloud forests, where it lives under moss and bark and is most active on rainy evenings (Elias & Wake 1983; Stuart *et al.* 2008), suggesting it has high sensitivity to moisture loss. Breeding is direct with no tadpole stage.

Figure 41. ***Nyctanolis pernix*** on a leaf. Photo by Sean Michael Rovito, with permission.

Oedipina (Plethodontidae)

The genus ***Oedipina*** has also been segregated from the genus ***Nototriton***, based on both molecular and morphological characteristics (García-París *et al*. 2000b).

This genus has fifteen recognized species and is the most specialized genus in the Plethodontidae (Brame 1968). It seems to have evolved around Costa Rica and western Panama, then extended southward from Estado de Chiapas, Mexico, southward through western Colombia to extreme northwestern Ecuador. It occurs primarily in lowlands or low montane areas up to 2286 m asl. The genus is primarily **fossorial** (adapted to digging and living underground) and is often found under very wet mosses along road cuts or in and under rotting logs in pastures of forested areas.

Species of ***Oedipina*** at intermediate altitudes occur in cloud forests, typically in moss mats covering downed vegetation and soil banks (Wake 1987).

Oedipina carablanca (Los Diamantes Worm Salamander, Plethodontidae)

In Guayacan, Limon Province, Costa Rica, this species occurs in humid Atlantic lowlands (Frost 2011) in places like rotting logs and under moss mats (Kubiki 2011). It is barely known and its population status is known. IUCN (2010b) lists it as endangered.

Oedipina elongata **(Central American Worm Salamander, Plethodontidae)**

Oedipina elongata (Figure 42-Figure 43), also known as Galliwasp and White-crowned Worm Salamander, occurs at low and moderate elevations from north-central Chiapas, Mexico, and near the Caribbean coast of eastern Belize, across the Guatemalan Atlantic foothills to the Montañas del Mico and into adjacent northwestern Honduras (Townsend *et al*. 2006; Frost 2011). It is known from elevations up to 1035 m asl in Honduras, where it occupies channels within logs, termite nests, leaf litter, and tree stumps (IUCN 2010b). Its preference for moist microhabitats suggests that one should also seek it in mosses. Its development is direct. This lucky salamander is listed by IUCN as one of "least concern" (IUCN 2010b). Nevertheless, like its sister species, it is threatened by deforestation. Fortunately, it does tolerate modest disturbance.

Figure 42. ***Oedipina elongata*** (**Central American Worm Salamander**), shown here on a log at Selva Lacandona, Chis, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Figure 43. ***Oedipina elongata*** (**Central American Worm Salamander**). Photo by Edmund (Butch) Brodie, with permission.

Oedipina gracilis **(Long-tailed Worm Salamander, Plethodontidae)**

Oedipina gracilis (Figure 44) lives in low to moderately high elevation (3-710 m asl) in Costa Rica along the Caribbean coast and into Panama (Savage 2002; Guyer & Donnelly 2005). Habitat destruction is causing populations to decrease and it is listed as endangered (IUCN 2010b).

Figure 44. ***Oedipina gracilis*** (Long-tailed Worm Salamander) on ***Monoclea***, probably ***M. gottschei***. Photo by William Leonard, with permission.

Oedipina gracilis (Figure 44) is nocturnal (Bruce 2003) and inhabits predominantly moist, hidden environments, such as leaf litter, burrows made by insects, and underneath or near rotting logs (Leenders 2001). It finds these habitats in humid Atlantic lowlands of Costa Rica and extreme northwestern Panama (Frost 2011). The eggs occur in the same places as adults, but degree of parental care is unknown (Bruce 2003). Its use of bryophytes is unknown, but likely.

Oedipina pacificensis **(Plethodontidae)**

Oedipina pacificensis (Figure 45-Figure 46) is known from the humid lowlands and premontane slopes of southwestern Costa Rica and adjacent southwestern Panama at 5-730 m asl (Frost 2011). The pictures below demonstrate its tiny diameter (Figure 45-Figure 46). Its wormlike morphology is suitable for its habit of burrowing underground, sometimes going under mats of wet moss or rotten logs (Höbel 2008).

Figure 45. ***Oedipina pacificensis*** showing its small size. Photo by Angel Solis, with permission.

Figure 46. Close view of ***Oedipina pacificensis***. Photo by Angel Solis, with permission.

Oedipina poelzi (Quarry Worm Salamander, Plethodontidae)

Oedipina poelzi (Quarry Worm Salamander; Figure 47) occurs in the Cordillera de Tilarán, Cordillera Central, and Cordillera de Talamanca of Costa Rica at 775-2050 m asl (Frost 2011). Individuals were taken from moss and lichen mats covering the road cuts near the falls where water seepage was constant (Wake 1987). This species occurs in subtropical or tropical moist montanes, rivers, and previously forested land (Frost 2011). It is threatened by habitat loss.

Figure 47. ***Oedipina poelzi***, a moss dweller in Costa Rica. Photo from Division of Herpetology at University of Kansas Biodiversity Institute, with permission through Rafe Brown.

Oedipina pseudouniformis (Plethodontidae)

Oedipina pseudouniformis lives in humid lowland and premontane areas of the Atlantic slope of central Costa Rica and on both slopes in northern Costa Rica at 19-1213 m asl, and in Nicaragua at 730-945 m asl (Frost 2011). It was described from a salamander taken from moss growing beneath bushes on a steep, sloping hill about 0. 25 km north of a swamp (Brame 1968). Wake (1987) lists it as an arboreal moss dweller. Additional specimens of ***O. pseudouniformis***, in large numbers, were in or under moss covering the east facing slopes, north of the swamp, or under logs in the deep woods to the northwest of the swamp. Its small population size and human activity have caused its populations to grow even smaller, causing it to be listed as endangered (IUCN 2010b).

Oedipina uniformis (Cienega Colorado Worm Salamander, Plethodontidae)

This worm salamander lives in the mountains and lowlands of central Costa Rica (Volcan Tenorio, Meseta Central) to the Panama border at 750-2150 m asl. It is an arboreal moss dweller (Wake 1987) that is decreasing in population size and is near threatened (IUCN 2010b).

Pseudoeurycea juarezi (Juarez Salamander, Plethodontidae)

The **Juarez Salamander** (Figure 48) occurs in the cloud forests of the Sierra Juárez and Sierra Mixe, Oaxaca, Mexico at 2400-3000 m asl (IUCN 2010b). It inhabits pristine moist forests under loose bark, under fallen trees, and under mosses on rocks and logs. Its development is direct, with no tadpoles. Logging, agricultural expansion, and human settlement threaten it with habitat loss. Parra-Olea *et al*. (2008) suggest that it has declined by 80% in the last ten years, and the IUCN has listed it as critically endangered (IUCN 2010b).

Figure 48. This ***Pseudoeurycea juarezi*** was located by lifting the moss at Sierra de Juarez Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

Pseudoeurycea rex (Royal False Brook Salamander, Plethodontidae)

Pseudoeurycea rex (Figure 49) lives in the high elevations (2450-4000 m asl) of western Guatemala (Frost 2011) and Mexico (although that may prove to be a different species) and is known to live predominantly in arboreal mosses (Wake 1987). This species has direct development and therefore does not depend upon open water for larval development.

Although it was formerly listed as a species of least concern by IUCN (Wikipedia 2011f), it is threatened by habitat loss. But the whole cause of its decline is unknown; it is declining or disappearing even in areas that still maintain the habitat of former populations. It was once considered to be the most abundant species in Guatemala, but now it is extremely rare, with its population size dropping by 80% in ten years, and its status has been changed to that of critically endangered (IUCN 2010b).

Figure 49. ***Pseudoeurycea rex*** on bark. Photo © 2003 Jonathan Campbell, with permission.

Pseudoeurycea scandens (Tamaulipan False Brook Salamander, Plethodontidae)

The Tamaulipan False Brook Salamander (Figure 50-Figure 51) lives in Southwestern Tamaulipas in the caves of the Biósfera El Cielo, Mexico, at 1050-1800 m asl, and from the type locality at ~28 km northeast of Ciudad del Maiz in San Luis Potosí, Mexico (Frost 2011). This

species can also live among arboreal mosses (Wake 1987), presumably benefitting from the moisture and cover they provide. Its direct development precludes the need for open water.

This species has fared better than most and is listed only as vulnerable by IUCN (2010b). Nevertheless, it has not been seen since the mid 1980's, but this may be due to limited searching. Its mossy habitat can easily hide it from an undiscerning eye.

Figure 50. ***Pseudoeurycea scandens*** on moss-covered log where it blends well with the bark and the patchy environment. Photo by Sean Michael Rovito, with permission.

Figure 51. More muted color patterns on another ***Pseudoeurycea scandens*** (**Tamaulipan False Brook Salamander**) on bark where it blends well with the bark and lichens, permitting it to be inconspicuous among the patches of mosses as well. With no mating call and small size, these salamanders are difficult to locate and may be lurking nearby undetected. Photo by Timothy Burkhardt, with permission.

Pseudoeurycea werleri (False Brook Salamander, Plethodontidae)

Pseudoeurycea werleri (Figure 52), a lower elevation salamander, lives in the rainforest and cloud forest from 900-1500 m asl on Sierra de los Tuxtlas, Veracruz, Mexico, where it is endangered due to its small distribution and declining habitat (Flores-Villela & Martínez-Salazar 2009; IUCN 2010b). Its home is in the arboreal mosses, where its direct development permits it to survive without pools of water.

Wake (1987) stated that bromeliads and moss mats in mid-elevational wet and rain forests provide "ideal" microhabitats for insectivorous, direct developing amphibians. This suggests that we may be overlooking such secretive species as this one.

Figure 52. This ***Pseudoeurycea werleri*** came very close to being dinner, with its entire tail being disarticulated in an attack. Photo by Sean Michael Rovito, with permission.

Lineatriton (placed in *Pseudoeurycea* by Frost 2011) (Plethodontidae)

This genus is combined into ***Pseudoeurycea*** by Frost (2011). In its narrow ***Lineatriton*** sense, it is a relatively rare Mexican genus with three described species. The systematics of these species is uncertain and they may actually represent more or fewer species. It uses moss mats to some degree (Wake 1987) and is secretive, nearly always under cover in the rainforest floor (Brodie *et al*. 2002 for ***L. orchimelas***). When predators approach, it propels itself by coiling and uncoiling its body rapidly.

Pseudoeurycea lineola (Veracruz Worm Salamander; Figure 53) lives only at 800-1250 m asl in a small area of oak-pine forest in the Sierra Madre Oriental of Veracruz, Mexico (Frost 2011). It lives under stones, logs, and debris, possibly including mosses, and in subterranean hideouts. Its need for moisture suggests that mosses might be a suitable habitat. This species is endangered due to its small, fragmented distribution and continuing loss of habitat (IUCN 2010b). None of its known locations is protected by law.

Figure 53. ***Pseudoeurycea lineola***. Photo by Sean Michael Rovito, with permission.

Pseudoeurycea orchileucos (Sierra de Juárez Worm Salamander) lives around Yetla and Vista Hermosaat 800-1390 m asl on the humid northern slope of the Sierra de Juárez, Oaxaca, Mexico (Frost 2011). In these cloud forests it can live below ground (**fossorial**), making it difficult to locate. It does not survive in disturbed habitats, probably due to its need for moisture (IUCN 2010b). Its development is direct, so pools of water are not needed. Hence, mosses might be used to keep its body moist. The species is endangered due to its small population size and limited distribution; logging contributes to its loss of habitat (IUCN 2010b). None of its habitats is on protected land.

Pseudoeurycea orchimelas (San Martin Worm Salamander) lives at 100-1300 m asl in the Sierra de Los Tuxtlas and adjacent Sierra de Santa Marta, Veracruz, Mexico (IUCN 2010b). It is fossorial (lives below ground) in leaf litter. Its direct development does not necessitate open water. Its relationship to bryophytic habitats is unclear. Wake (1987) considered the genus to make some use of bryophytes, but there is no specific mention for this species. This species likewise is endangered because of its small population, limited distribution, and habitat destruction, despite being abundant within its distribution (IUCN 2010b). Unlike the other two species of the former ***Lineatriton***, it is protected where it occurs in the Reserva de la Biósfera Los Tuxtlas.

Thorius (Mexican Pigmy Salamanders, Plethodontidae)

Thorius dubitus (Acultzingo Pigmy Salamander, Plethodontidae)

Thorius (Figure 54) represents the smallest of the tailed amphibians (Hanken 1983), with some members less than 2 cm, including the tail (Wikipedia 2010). The genus occurs in the pine-oak cloud forest on high mountain crests of west-central Veracruz and adjacent Puebla, Mexico at 2475-2800 m asl (Frost 2011). ***Thorius dubitus*** occurred under mosses (Wake 1987) and other plants and occurred at slightly higher elevations than the other salamander species of the area (Hanken 1983).

Figure 54. ***Thorius arboreus***, a relative of ***T. dubitus***, and possible a moss dweller. Photo by Sean Michael Rovito, with permission.

Old-growth Temperate Habitats

Old growth forests offer a variety of microhabitats not available in younger secondary forests. Dense growths of bryophytes there ameliorate the temperature, providing safe sites that help to cool by evaporation as well as provide dense shade from the dangers of the sun. These same bryophytes likewise provide a haven of moisture when bare soil and branches become dry (Figure 28). Hence, they are able to harbor an array of interesting miniature communities about which we really know very little.

Aneides aeneus (Green Salamander, Plethodontidae)

Aneides aeneus (Figure 55-Figure 57), also known as Web-footed Salamander, Bronzy Salamander, or Bronzed Salamander, lives in the Appalachian region from southern Ohio, southern Indiana, and southwestern Pennsylvania to western South Carolina, Tennessee, northern Georgia, northern Alabama, and northeastern Mississippi, USA (Frost 2011). It eats a diet that can easily be found among, under, or on top of mosses. In Bat Cave, North Carolina, USA, Rubin (1969) found that one individual had eaten 53% ants, 32% spiders, 13% shed salamander skin, and 2% unidentified insect larvae. But when Lee and Norden (1973) examined gut contents of 25 individuals from Coopers Rock, West Virginia, USA (at the northern limit of their range), they found some interesting organic matter – leaf fragments, humus, mosses, and hemlock needles, as well as sand grains.

Figure 55. ***Aneides aeneus*** adult in crevice in its mossy habitat. Photo by Bill Peterman, with permission.

Canterbury (1991) found that juveniles remained with their mother for about a month. They climbed up the rock faces from their birth crevices toward moss-covered ledges. Cryptic coloration of mottled green and dark colors would render these youngsters almost invisible (Figure 56). Adults live in crevices in boulders and retreat deep into the crevice to hibernate for the winter (Figure 57) (Gordon 1952).

Figure 56. ***Aneides aeneus*** juvenile in its mossy habitat. Photo by Bill Peterman, with permission.

Figure 57. ***Aneides aeneus*** adults with eggs in crevice in its mossy habitat, North Carolina, USA. Photo by Bill Peterman, with permission.

Aneides vagrans (Wandering Salamander, Plethodontidae)

Aneides vagrans (Figure 58) lives in coastal northern California, USA, from northwestern Sonoma County to Smith River near Crescent City, and has been introduced and is widespread on Vancouver Island, British Columbia, Canada (Frost 2011). Nevertheless, its populations are decreasing and its IUCN status is near threatened (IUCN 2010b).

Although the ground-dwelling **Wandering Salamander**, ***Aneides vagrans*** (Plethodontidae) (Figure 58) lives under bark of fallen trees, arboreal members living on large coast redwoods (*Sequoia sempervirens*; Figure 67) may inhabit mosses as well (Spickler *et al*. 2006). Like most of the arboreal salamanders, the species is lungless and the young are hatched fully formed, *i.e.*, they do not form larvae first. Hence, they require high moisture and high oxygen levels. Sillett (1995) found this species among the branches of the moss ***Antitrichia curtipendula*** (Figure 59-Figure 61) at 30 m above ground. However, the moss study was not designed to be quantitative, and the more quantitative study on mats of the epiphytic fern *Polypodium scouleri* suggests that ***A. vagrans*** spends much time among the fern mats, occupying tunnels and cavities left by dead roots and rhizomes (Spickler *et al*. 2006). (I have to guess that these tunnels may actually be in mosses.) Nevertheless, the moist habitat and production of photosynthetic oxygen provided by mosses suggest that mosses should be suitable habitats for these salamanders as well. In any event, the salamanders are at least indirectly dependent on the bryophytes. *Polypodium scouleri* requires either bryophytes or litter to provide the moist substrate needed for their gametophytes to establish (Lovelace 2003).

Figure 58. The **Wandering Salamander**, ***Aneides vagrans***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 59. ***Antitrichia curtipendula***, a good candidate for protection of small organisms in mature forests of the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 60. ***Antitrichia curtipendula***, moist and expanded. Photo by Michael Lüth, with permission.

Figure 61. ***Antitrichia curtipendula***, dry, with capsules. Photo by Michael Lüth, with permission.

Batrachoseps wrighti, formerly *B. wrightorum* (Oregon Slender Salamander, Plethodontidae)

Batrachoseps wrighti (**Plethodontidae**; Figure 62-Figure 63) [85-120 mm total length (Bury 2011)] is also known as the Western Four-toed Salamander. It is endemic to the northwestern USA, where it occurs from the Columbia River Gorge of northwestern Oregon, USA, southward along the slopes of the Cascade Mountains in Oregon, from sea level to about 1430 m asl (Kirk 1991; Kirk & Forbes 1991; Frost 2011). It lives in temperate zone forests of moist Douglas fir (*Pseudotsuga menziesii*), maple (*Acer*), and red cedar (*Juniperus*) (Bury 2011) and is considered vulnerable on the IUCN Red List due to continuing habitat loss (IUCN 2010b).

Figure 62. ***Batrachoseps wrighti*** on a bed of mosses. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

The specific habitats of these salamanders include decayed logs and stumps, especially in older decay classes (Bury 2011). However, they have also been found under moss-covered bark in termite channels in decaying logs (Storm 1953) and under large rocks that are moss covered (Bury 2011). It is possible that they require the mosses when they venture out for food, using the mosses to maintain their moisture. On the other hand, as far as we know, they seem to spend their time in burrows underground or deep within large logs except in early spring just after snowmelt.

They develop without a larval stage, emerging from eggs as froglets (Lannoo 2005), an adaptation to terrestrial living.

Figure 63. ***Batrachoseps attenuatus*** on moss. Photo by Brian Gratwicke, through Creative Commons.

Rhyacotriton cascadae (Cascade Torrent Salamander, Rhyacotritonidae)

The Cascade Torrent Salamander (***Rhyacotriton cascadae***; Figure 64-Figure 65), also known as Cascade Salamander and Cascades Torrent Salamander, lives in torrents (AmphibiaWeb 2009a) on the western slope of the Cascade Mountains from just north of Mount St. Helens, Washington, south to northeastern Lane County, Oregon, USA (Frost 2011). Although it seems to occur where there are lots of mosses, documentation of its actual use of the moss as a place of shelter or laying eggs is lacking. There is only one published record of its nest, which was under cobble in a quiet area of a small stream (MacCracken 2004). Since this genus is apparently the least desiccation-tolerant genus of salamanders (Ray 1958), it is likely that the salamanders migrate to mosses during times of diminished flow.

Figure 64. Cascade Torrent Salamander, ***Rhyacotriton cascadae***. Photo by John Clare, through Creative Commons.

Figure 65. Ventral side of the Cascade Torrent Salamander, ***Rhyacotriton cascadae***. Photo by Henk Wallays, through Creative Commons.

Rhyacotriton olympicus (Olympic Torrent Salamander, Rhyacotritonidae)

The Olympic Torrent Salamander (***Rhyacotriton olympicus***; Figure 66), also known as Mountain Salamander, Olympic Salamander, Olympic Mountain Salamander, and Northern Olympic Salamander, is another inhabitant restricted to old-growth forests of northern California and southwestern Oregon (Anderson 1968; Welsh 1990). The Olympic Torrent Salamander (***Rhyacotriton olympicus***), like ***Plethodon elongatus***, rarely occurs in open water and likewise seems to require the moisture of mosses, rocks, and organic matter (Welsh 1990) (Figure 67-Figure 68).

Figure 66. ***Rhyacotriton olympicus***, the Olympic Torrent Salamander. Photo by Michael Graziano, with permission.

As we have seen in other taxa, ***R. olympicus*** (Figure 66) often occurs under moss-covered stones in both larval and adult stages, particularly in seepage areas (Stebbins 1955). Stebbins found that the stream was mostly hidden by the moss-covered rocks. Slater (1933) noted that collectors generally hunt for them only during the day. On his night trips he noted that they were on stones and moss a meter or so away from the water (Figure 68). He suggested that they made these excursions onto the mosses in search of food. The mossy habitat would help to conserve their moisture during these wanderings.

Figure 67. Coast redwood forest (*Sequoia sempervirens*), home of ***Rhyacotriton*** and ***Dendrotriton*** salamanders. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 68. Rainforest in the Olympic National Park, Washington, USA, home of ***Rhyacotriton olympicus***. Photo by Andreas Nöllert and published in a calendar by Druckhaus Gera GmbH, Jacob-A.-Morand-Strasse 16, D-07552 Gera, Thuringia, Germany, with permission.

Rhyacotriton variegatus (Southern Torrent Salamander, Rhyacotritonidae)

The Southern Torrent Salamander (Figure 69-Figure 70) is also known as the Southern Olympic Salamander and the California Mountain Salamander. As its name implies, it has a more southerly distribution in the coast ranges from southern Mendocino County, California, north to the Little

Nestucca River and the Grande Ronde Valley in Polk, Tillamook, and Yamhill counties, Oregon and the western slope of the Cascade Mountains near Steamboat, Oregon, USA (Frost 2011).

Figure 69. ***Rhyacotriton variegatus*** on a bed of mixed mosses. Photo by Henk Wallays, through Creative Commons.

Figure 70. ***Rhyacotriton variegatus*** creeping across a moss. Photo by William Flaxington, with permission.

Welsh and Lind (1996) conducted an extensive survey of ***Rhyacotriton variegatus*** (Figure 69-Figure 70) in northwestern California to identify those attributes most important to its location. They determined that it has a rather narrowly defined niche that is encompassed by cold, clear headwaters to low-order streams that have loose, coarse substrata (little sedimentation), in humid forests with large conifers affording more than 80% canopy closure and abundant ground-layer moss. That defines old-growth, undisturbed forest. Their preference for shallow, cold, percolating water with cover of moss and rocks is supported by observations of Anderson (1968), Nussbaum & Tait (1977), Nussbaum *et al.* 1983, Stebbins (1985), Bury (1988), Bury & Corn (1988), Corn & Bury (1989), Welsh (1990), Bury *et al.* (1991), Good & Wake (1992), and Leonard *et al.* (1993). Large conifers, moss, and high canopy closure indicated sites with this species, whereas those with grass and stumps lacked the species (Welsh & Lind 1996). As reported by Bingham and Sawyer (1991), significantly greater moss abundance occurs in old-growth compared with young forests in northwestern California. The moss appears to be important in maintaining moisture in this salamander, but so far there seems to be no direct evidence they live there.

Asia – One Plethodontid!

I was nearly finished with this chapter when I suddenly realized that the salamander chapter had a strong western hemisphere bias. A little checking revealed that the eastern hemisphere does not have many species of these little 4-footed creatures, but I was certain at least some might make use of mosses. Google didn't get me very far, so I appealed to bryonetters for help.

Karsenia koreana (Korean Crevice Salamander, Plethodontidae)

Known in Korea as the Moss Salamander (Figure 71) (Hiromi Matsui, pers. comm. 25 March 2011), or Ikkee dorongyong (Wake 2005), ***Karsenia koreana*** is a disjunct curiosity. But what is so special about this salamander? It is the first and only plethodontid salamander found in Asia (Min *et al*. 2005)! The world plethodontid specialist David Wake is quoted as saying, "I've discovered and named nearly 50 species of salamanders – more than 10 percent of the total in the world. I've discovered new genera in Guatemala and Costa Rica. But this tops everything I've ever found by a long ways. For me, this is the most stunning discovery in the field of herpetology during my lifetime. It's so utterly unexpected, so completely unexpected." (Sanders 2005).

Figure 71. ***Karsenia koreana***, the only known plethodontid in Asia. Photo by Todd Pierson, with permission.

Figure 72. ***Karsenia koreana*** in a mossy habitat in Asia. Photo by Todd Pierson, with permission.

But that is not the only remarkable circumstance. It was not described until 2005 (Min *et al.* 2005) when a high school teacher from Illinois, Stephen J. Karsen, was on a field trip with his Korean students looking for salamanders in the same sorts of places (Figure 72) he might find them in Illinois (Wake 2005). But in South Korea, this was not considered as a likely habitat because the terrestrial plethodontid species so common in North America were totally unknown and thought to be absent here. Discovered at 210 m asl (Min *et al*. 2005) and endemic to the middle portion of the Korean Peninsula, South Korea, the species is now known from 16 locations in three provinces of South Korea (Wake 2005). With this many locations, it is listed as a species of least concern on IUCN Red List (IUCN 2010b).

This was not, however, the first find of the species. It had been collected 34 years earlier by a Japanese-Korean collecting team but never described as a species (Nishikawa 2009).

Karsenia koreana (Figure 71) was both a new species and a new genus in the family Plethodontidae, representing a considerable disjunction from this predominantly western hemisphere family, and raising questions about its venture to Asia 100 million years ago (Sanders 2005). It averages 42 mm snout to vent length and only superficially resembles the North American ***Plethodon*** (Wake 2005). It occurs in rock slides and on damp, mossy slopes, causing the Koreans to call it the moss salamander. Its habitat is young forests of hardwoods and pines, 15-50 years old, in limestone areas. Its resting habitat seems to be under small rocks and slices of limestone in areas with fine-grained soil. Since it requires moisture, bryophytes are likely to play a role in maintaining its hydration.

Europe – One Plethodontid Genus

Speleomantes supramontis (Supramonte Cave Salamander, Plethodontidae)

The Plethodontidae in Eurasia are limited to ***Karsenia koreana*** in Korea and ***Speleomantes***, a genus of six limestone cave dwellers (Marc P. Hayes, pers. comm. 26 March 2011). Of these six, it appears that ***S. supramontis*** (Figure 73) from east Sardinia (around the Gulf of Orosei, Italy, from 100-1360 m asl) is the only one frequently associated with bryophytes. In the Mediterranean oak forests it occurs under mosses on rocks near streams (Nöllert & Nöllert 1992). Not surprisingly, a species such as this with a limited habitat and distribution is endangered (IUCN 2010b).

Figure 73. ***Speleomantes supramontis*** (**Supramonte Cave Salamander**) on a rock ledge. Photo by Franco Andreone, through Wikimedia Commons.

Peatlands and Wetlands

Peatlands would seem to provide an ideal habitat for many kinds of amphibians. They have open areas where the amphibians can bask, they have open water for tadpoles and larvae, and they provide moist mosses that keep the amphibians hydrated (Figure 74). This combination also makes them ideal sites for nesting for some species. But there is a caveat – acidity!

Stan A. Orchard of BulfrogControl.com Inc. (pers. comm. 27 March 2011) gave me this summation of his observations: "I have routinely found amphibians (toads, frogs, semi-aquatic salamanders, newts) in and around ***Sphagnum*** bogs, but they tend to be found in and around open water pools (Figure 74) that are used for spawning, larval stage development, and over-wintering. Amphibian associations with ***Sphagnum*** (Figure 21) bogs seem to me to be co-incidental and the result of a need by both for damp conditions. However, Plethodontid salamanders, for example, that require damp, shady conditions but reproduce on land are not so likely to be found in a peat bog as on a damp shaded forest floor. Conversely, amphibian species that are found in bogs tend to have migrated in specifically to escape summer dehydration, to forage, and to utilize permanent or seasonal pools for reproduction. ***Sphagnum*** patches do not seem to be attractive sites for over-wintering for semi-terrestrial species because they are too water soaked in the winter and subject to water table fluctuations, as opposed to damp but drained upland habitats. It is also possible that peat bogs may be uncomfortably acidic for some species."

Figure 74. Developing peatland, seen from upland at Lawrence Lake, Michigan, USA. Photo by Janice Glime.

Despite the acidity, some salamanders are able to tolerate ***Sphagnum*** habitats. Most of these have been discussed in the subchapter on Ground-dwelling Anurans, including results of various experiments on acidity. In peatlands of Maine, USA, twelve species of amphibians appeared in traps (Stockwell & Hunter 1989). Of the 2179 amphibians captured, only 4.5% were salamanders. Nevertheless, four species were present: ***Ambystoma laterale*** (Blue-spotted Salamander; Figure 75), ***Desmognathus fuscus*** (Northern Dusky Salamander; Figure 76), ***Eurycea bislineata*** (Northern Two-lined Salamander; Figure 77), and ***Notophthalmus viridescens*** (Eastern Newt **- Salamandridae**; Figure 106).

Figure 75. ***Ambystoma laterale*** (**Blue-spotted Salamander**), a peatland salamander that occurs in eastern USA and Canada (Frost 2011). Photo by Henk Wallays, through Creative Commons.

In addition to the salamanders just mentioned, at least occasional ***Sphagnum*** (Figure 21) dwellers include some members of the genera ***Bolitoglossa***, ***Eurycea***, ***Hemidactylium***, ***Lissotriton***, ***Pseudotriton***, ***Stereochilus***, and ***Triturus***. Some ***Ambystoma*** species in ***Sphagnum*** waters seem to suffer lower developmental rates and reduced activity, but survive; some, however, suffer death in the acid water (see chapter on Ground-dwelling Anurans). The relationship of some ***Eurycea*** species to wetlands with ***Sphagnum*** are discussed here, and later those of the Salamandridae.

Figure 76. Northern Dusky Salamander, ***Desmognathus fuscus***. Photo by Janice Glime.

Figure 77. The Northern Two-lined Salamander, ***Eurycea bislineata***. Photo by Henk Wallays, through Creative Commons.

Eurycea wilderae (Blue Ridge Two-lined Salamander, Plethodontidae)

The Blue Ridge Two-lined Salamander lives in the Southern Appalachian Mountains, USA. In the Tulula Wetlands, North Carolina, USA, one can find ***Eurycea wilderae*** (Blue Ridge Two-lined Salamander, Figure 78-Figure 81) and ***E. guttolineata*** (Three-lined Salamander; Figure 82-Figure 83) among the ***Sphagnum*** (Amphibians: Tulula Wetlands 2009). Although it would seem that ***Sphagnum*** would provide a safe site for eggs, both lay their eggs in the water, presumably because they have aquatic larvae. Instead, their preferred habitat for egg laying appears to be streams and stream banks (AmphibiaWeb 2010).

Figure 78. ***Eurycea wilderae*** on a moss mat. Photo by Todd Pierson, with permission.

Figure 79. ***Eurycea wilderae*** on a mat of mosses. Photo by Michael Graziano, with permission.

Figure 80. ***Eurycea wilderae***, showing its small size compared to a US quarter. Photo by Todd Pierson, with permission.

Figure 81. ***Eurycea wilderae***. Photo by John D. Willson, with permission.

Eurycea guttolineata (Three-lined Salamander, Plethodontidae)

Eurycea guttolineata (Figure 82-Figure 83) is also known as Holbrook's Triton and Southern Long-tailed Salamander. It lives in the southeastern USA where it is found in the Mississippi Embayment from eastern Louisiana to extreme western Kentucky and western Tennessee, throughout most of Mississippi and Alabama, the panhandle of Florida and northward through Georgia, South Carolina, North Carolina, to the eastern half of Virginia (Frost 2011).

In the Tulula Wetlands, North Carolina, USA, it lives among the ***Sphagnum*** (Figure 74) (Amphibians: Tulula Wetlands). Nevertheless, it lays its eggs in the water, presumably because the larvae are aquatic, preferring streams and stream banks (AmphibiaWeb 2010). This very long-tailed ***Eurycea guttolineata*** is common in swampy areas and along the margins of sluggish streams in Georgia, USA (Salamanders of Georgia and South Carolina 2010).

Figure 82. ***Eurycea guttolineata*** at the edge of a stream. Photo by Michael Graziano, with permission.

Figure 83. ***Eurycea guttolineata*** on a bed of mosses. Photo by Matthew Niemiller, with permission.

Streams and Springs

Eurycea bislineata (Northern Two-lined Salamander, Plethodontidae)

Eurycea bislineata (Figure 84-Figure 85) lives in eastern North America from the St. Lawrence River in Canada and northeastern Ohio, USA, to northern Virginia, USA. It is widespread and known enough to have ten additional English names (Frost 2011). This species frequently uses mosses for nests and shelter. Eggs may be laid on rocks and logs, but Bahret (1996) found clutches of eggs, fully exposed, on the uppermost leaves of an aquatic moss, ***Sphagnum trinitense*** (Figure 86-Figure 88). Jobson (1940) found larvae and adults in patches of moss in a swift stream. Richmond (1945) found a nest with 42 eggs among underwater roots under a clump of mosses and other plants. When he turned the mosses back and left them undisturbed for an hour, he returned to find that the salamander had returned to its nest.

Figure 84. ***Eurycea bislineata***. Photo by Twan Leenders, with permission.

Figure 85. Aquatic larva of ***Eurycea bislineata***. Photo by John White, with permission.

Figure 86. Habitat of ***Sphagnum trinitense*** in South Carolina, USA. Photo by Blanka Shaw, with permission.

Figure 87. Emergent ***Sphagnum trinitense***. Photo by Jan Janssens, with permission.

Figure 88. Close view of submerged ***Sphagnum trinitense*** in South Carolina, USA. Photo by Blanka Shaw, with permission.

Eurycea lucifuga (Cave Salamander, Plethodontidae)

The Cave Salamander (Figure 89) is also known as the Spotted Tailed Triton, Hoosier Salamander, and Spotted-tail Salamander. It appears to be limited to limestone areas near and in limestone caves at higher elevations of the Appalachian Mountains from eastern Tennessee northward almost to Maryland, USA, and in the Ozark uplift of northeastern Oklahoma, southeastern Kansas, northern Arkansas and central and southern Missouri, southern Illinois, southern Indiana and southwestern Ohio through Kentucky and Tennessee to northeastern Mississippi, northern Alabama, and northwestern Georgia (Frost 2011). This species is common in large springs in Oklahoma, hiding in wet mosses and other vegetation (Bragg 1955).

Figure 89. ***Eurycea lucifuga***. Photo by Danté Fenolio, with permission.

Eurycea multiplicata (Many-ribbed Salamander, Plethodontidae)

Also known as the **Many-ribbed Triton**, the species ***Eurycea multiplicata*** (Figure 90) occurs in the Ouachita Mountains of west-central Arkansas and southeastern Oklahoma, USA (Frost 2011). Its apparent avoidance of acidic conditions was exemplified by Bragg (1955) when he placed them in an aquarium with peat moss (***Sphagnum***) at one end. The entire aquarium, including the sand, was moistened, but after two days of drying, the salamanders had not collected in the peat moss as expected, but rather were curled up on the dry limestone from their native habitat. After several more days they died from desiccation. A limestone rock-dwelling moss may have been a more appropriate choice, but the ***Sphagnum*** avoidance suggests that it has properties that keep these salamanders away from it, possibly its acidity due to its cation exchange ability.

Figure 90. ***Eurycea multiplicata***, a ***Sphagnum*** avoider. Photo by Michael Graziano, with permission.

The natural habitat of this species is cave springs, cave runs, and cold streams (IUCN 2010b). Despite its apparent aversion to peat mosses in the experiments of Bragg (1955), some mosses do seem to play a role in its life. Dundee (1947) reported that during winter these salamanders remain active, taking cover under rocks, logs, and mosses near streams. It is only during extreme cold that they actually go into **torpor** (state of inactivity), and this may occur under mosses.

Eurycea tynerensis, formerly *Eurycea griseogaster* (Oklahoma Salamander, Plethodontidae)

Eurycea tynerensis (Figure 91) (formerly *Eurycea griseogaster*), was once considered part of ***E. multiplicata***. This species likewise occurs on the Ozark Plateau of southwestern Missouri, extreme southeastern Kansas, northern Arkansas, and northeastern Oklahoma, USA, where it lives in streams, springs, and seeps. Dundee (1947) found the species under rocks, logs, and clumps of moss at the edges of streams.

Figure 91. ***Eurycea tynerensis*** (**Oklahoma Salamander**) on a liverwort, ***Conocephalum* sp**. Photo by Michael Graziano, with permission.

Proteidae

This is a small family of salamanders with only one known representative that makes use of bryophytes.

Necturus punctatus (Dwarf Waterdog, Proteidae)

Necturus punctatus (Figure 92) ranges along the coastal plain from southeastern Virginia to central Georgia, USA. This species is unusual in retaining its gills as an adult. Its typical habitats are slow-moving muddy or sandy streams, deep irrigation ditches, cypress swamps, stream-fed rice fields, and mill ponds (IUCN 2010b).

Neill (1948) found as many as twelve individuals of this species hibernating in decaying hardwood logs, under bark, or in beetle tunnels, but also in insect burrows under thick moss on sunny slopes in Richmond County, Georgia, USA.

Figure 92. ***Necturus punctatus*** among mosses in water. Photo by Todd Pierson, with permission.

Salamandridae

The **Salamandridae** are the newts, a naming choice that will always be a mystery, or at least a point of consternation, for me. But a newt is really just a salamander that differs enough from members of the large **Plethodontidae** family to be distinguished by its own family. One major difference is the life cycle of newts. They have three stages rather than two. Their **larval** stage is aquatic. They then metamorphose into juveniles that are terrestrial, known as the **eft** stage. Finally, as **adults**, they return to the water, but can at times venture onto land, often including peatlands. In their adult stage, a number of them are sold as aquarium pets, but they need a way to get above water occasionally.

Newts are more common than other salamanders in Eurasia, and they often live in mossy habitats or make use of them at times during their wanderings (Marc P. Hayes, pers. comm. 26 March 2011). The newt family **Salamandridae** occurs in Africa in the Mediterranean fringe (Stan A. Orchard, pers. comm. 27 March 2011). Asia has an endemic newt family, the Hynobiidae, mostly known from Japan.

Klaus Weddeling (Bryonet 26 March 2011) informed me that all the European species of salamanders use mosses for shelter during hibernation and during dry periods. Young adults use the wet mosses and soil as shelter for 2-3 years while they mature. But that doesn't mean you are likely to find one. Des Callaghan (Bryonet 26 March 2011) reported that there are only three species of salamanders in Britain, all of them newts in the **Salamandridae**. Although these might traverse bryophytes, they are not particularly associated with them.

Calotriton asper, formerly *Euproctus asper* (Pyrenean Brook Salamander, Salamandridae)

In the French Pyrenees, Michael Lüth and fellow bryologists found the endemic ***Calotriton asper*** (Figure 93-Figure 94) among mosses close to a waterfall (Figure 94; Bryonet 26 March 2011). Its distribution is the Pyrenees Mountains of France, Spain, and Andorra at 175-3000 m asl. This species is also known as Pyrenean Mountain Newt, Pyrenean Mountain Salamander, Pyrenees Mountain Newt, Pyrenees Mountain Salamander, Pyrenean Salamander, and Pyrenean Newt.

Figure 93. ***Calotriton asper*** that has been living among mosses in the Pyrenees. Photo by Michael Lüth, with permission.

Figure 94. Habitats of ***Calotriton asper*** in the French Pyrenees. Photos by Michael Lüth, with permission.

As a cave dweller, this species faces food deprivation for extended periods up to a year. Issartel *et al.* (2010) attempted to follow the physiological responses to 42 days of fasting, followed by 10 days of refeeding in a subterranean and an epigean population of ***Calotriton asper***. The control subterranean population exhibited hypometabolism together with higher glycogen (+ 25% in liver and muscles) and triglyceride stores (+ 50% in muscles), suggesting it was ready to fast. While fasting, the subterranean cave individuals had a 20% decrease in $\mathbf{VO_2}$ (liters of oxygen used per minute) while epigean individuals showed little change. Furthermore, the underground population maintained a higher energetic reserve. It appears that the cave population is genetically better adapted to fasting, inducing a decrease in metabolism and greater capacity to accumulate energy reserves. But one must ask if this is, rather than a genetic change, one that has been induced by the prior experiences in the cave. In either case, those organisms with this ability to retain reserves are the ones who will be more likely to survive to breed.

This advantage is almost ensured by the limited dispersion of individuals. Montori *et al.* (2008) demonstrated that the mean distance this species migrated in a year was less than 50 m. There did not seem to be any seasonal migration. Suitable habitats that favored abundance relate to the number of refugia: woody debris, stones, and fissures, places where the salamander can hide and remain hydrated. Larval abundance is correlated with streambed structure. With the limited movement in this species, suitable adult and larval habitats must be in close proximity.

Chioglossa lusitanica (Golden-striped Salamander, Salamandridae)

Chioglossa lusitanica (

Figure 95-Figure 96) is known from northwestern Spain (Iberian Peninsula) and the northern-central part of Portugal (Frost 2011) where it occurs in forested streams (IUCN 2010b) and uses mosses as a refuge (Goux 1957; Marc P. Hayes, pers. comm. 26 March 2011; Iñigo Martínez-Solano, pers. comm. 30 March 2011).

Its limited distribution, pollution, and loss of habitat contribute to its listing as vulnerable (IUCN 2010b).

Figure 95. The **Golden-striped Salamander**, ***Chioglossa lusitanica***. Photo by Andreas and Christel Nöllert, with permission.

Figure 96. Close view of the **Golden-striped Salamander**, ***Chioglossa lusitanica***. Photo by Andreas and Christel Nöllert, with permission.

Euproctus platycephalus (Sardinian Mountain Newt, Salamandridae)

In Sardinia, Italy, there seems to be a salamander species that makes use of mosses. Michael Lüth (Bryonet 26 March 2011) informed me of ***Euproctus platycephalus*** (Figure 97); a group of bryologists disturbed one in wet mosses, ***Thamnobryum alopecurum*** (Figure 98). In the hot, dry summer of the Mediterranean (Figure 99), mosses provide a place to aestivate.

Figure 97. ***Euproctus platycephalus*** photographed on the leafy liverwort ***Porella platyphylla***, but it was under a moss when it was disturbed. Photo by Michael Lüth, with permission.

Figure 98. ***Thamnobryum alopecurum***, home to a population of ***Euproctus platycephalus***. Photo by Michael Lüth, with permission.

The **Sardinian Mountain Salamander** is also known as Sardinian Newt, Pyrenean Brook Salamander, Sardinia Mountain Salamander, Sardinian Brook Salamander, and Flat-headed Salamander. It is endemic to the mountains of Sardinia, Italy, at 50-1800 m asl (Frost 2011). This rare species is red-listed as endangered (IUCN 2010b). It is threatened by treatment of water bodies with DDT in the 1950's in the battle against malaria, introduction of trout that may eat the larval and possibly adult salamanders or compete with them for food, and reduction of water levels due to increasing pressures from human activities including tourism and agriculture (Boehme *et al.* 1999).

Figure 99. Habitat of ***Euproctus platycephalus*** in Sardinia, Italy. Photo by Michael Lüth, with permission.

This salamander spends its larval stage in primarily calm, but also running water (Meijden 1999). The terrestrial phase is always near water, under stones, but also in root zones of bushes and trees and under mosses. The size is 120-140 mm for males and 100-130 for females, total length. This is the opposite of many species of salamanders where the female is the larger gender.

Eggs are only 3 mm in diameter, achieving 4-5 mm with the gelatinous envelope (Meijden 1999). The female lays them over a 3-5.6 month period and development averages 37.6 days at 15°C, or 12.7 days at 14.5°C. Larval development can take 376-453 days at 15°C, exposing the small larvae to predation for a dangerously long time. Even at 20.5°C, development takes 184-260 days.

Lissotriton boscai (Bosca's Newt)

This species (Figure 100) is endemic in the western Iberian Peninsula, excluding southwestern Portugal, and southernmost Spain from sea level to 1800 m asl (Frost 2011). Its habitats include peat moss, running water, and deep, still waters, but it prefers small, shallow ponds with aquatic plants (AmphibiaWeb 2000). In its terrestrial phase, it lives near ponds and hides in humid, shady places under roots, stones, mosses, and trees.

Figure 100. ***Lissotriton boscai***, a peatmoss dweller in the Iberian Peninsula. Image through public domain.

***Lissotriton helveticus*, formerly *Triturus helveticus* (Palmate Newt, Salamandridae)**

This species (Figure 101) occurs in western Europe, including Great Britain (Wikipedia 2011e). Smaller than most newts, males reach only 8.5 cm and females 9.5 cm. It has a wide range of habitats, including terrestrial forests, pastures, and agricultural land, as well as aquatic ponds, lakes, canals, and marshes. It is more tolerant of lower *p*H levels than most amphibians, permitting it to range into more habitats. In the moorlands it can occupy acid pools, and it occurs in peatlands, so Marc P. Hayes (pers. comm. 26 March 2011) suggested that it might make some use of mosses. It is likely that this mostly aquatic species uses the mosses to maintain hydration when it ventures onto land.

Figure 101. Water form of a male **Palmate Newt**, ***Lissotriton helveticus***. Photo by H. Krisp, through Creative Commons.

***Lissotriton montandoni*, formerly *Triturus montandoni* (Carpathian Newt, Salamandridae)**

This newt, also known as Montadon's Newt (Figure 102), lives in the Carpathian and Tatra Mountains of Europe, where it makes use of streams (Frost 2011), but also forest habitats rich in mosses (Marc P. Hayes, pers. comm. 26 March 2011). Like ***L. helveticus***, it tolerates acid more than most other amphibians, permitting it to occupy a wider range of habitats.

Figure 102. ***Lissotriton montandoni***, a moss dweller in European forests. Photo by Maciej Pabijan, through Creative Commons.

***Lissotriton vulgaris*, formerly *Triturus vulgaris* (Smooth Newt, Salamandridae)**

The **Smooth Newt** (Figure 103) has pages of Latin synonyms and a good share of English names. It occurs in Europe in the British Isles and western France west through southern Norway and southern Finland to the Urals and south to the northern Balkans, northwestern Turkey, and Kazakhstan (Frost 2011). Forests are critical to its existence, but it can occur in meadows and shrub land where forests existed previously, and even occurs in gardens, parks, and fields (AmphibiaWeb 2009d). In the steppe zone it is present in wooded river valleys. In Northern Ireland, this species is legally protected, but it is listed as a species of least concern worldwide (IUCN 2010b).

Figure 103. ***Lissotriton vulgaris***, the **Smooth Newt**. Photo by Andreas & Christel Nöllert, with permission.

Newts are not common among mosses, with adults needing a place to swim, but peatlands with open water seem suitable for some. In Ireland, the Smooth Newt (***Lissotriton vulgaris***; Figure 103) prefers the moist habitat of peatlands (Peatlands 2009). After courtship and mating, the female gathers the sperm packets and lays her eggs on aquatic plant leaves that she rolls around the sticky eggs, thus necessitating peatlands that have open water.

This species is rapidly disappearing. Kinne (2006) attempted to determine factors that would improve its habitat and foster greater survival. He determined that the terrestrial phase would hide, especially in the daytime, under mosses, as well as rotting wood, roots of trees and bushes, log piles, and earth holes. When this species was maintained in a terrarium, it chose mosses for its overwintering habitat. There seems to be no documentation of its overwintering activities among mosses in nature.

***Notophthalmus viridescens* (Eastern Newt, Salamandridae)**

This species of newt (Figure 104-Figure 106) is widespread in the eastern USA and into the Midwest (Hunsinger & Lannoo 2011). Its life cycle is unusual, taking it to a variety of habitats. The eggs (Figure 104) are laid in streams, where the larvae develop. Juveniles migrate to land where they may spend 2-7 years in the red eft stage (Figure 105. As mature adults (Figure 106), they are amphibious, spending most of their time in water, but also traversing the land.

Figure 104. Eggs of ***Notophthalmus viridescens***. Photo by Tom Murray, with permission.

Figure 105. Terrestrial red eft stage of the **Eastern Newt**, ***Notophthalmus viridescens***, displaying warning coloration and Muellerian mimicry that announce its toxic skin. Photo by Janice Glime.

Figure 106. Aquatic adult stage of **Eastern Newt**, ***Notophthalmus viridescens***. Photo by Janice Glime.

The eft and adults both make use of mosses for cover, as well as a variety of other cover types (leaves, branches, logs, rocks, grass) (Roe & Grayson 2008). The bright orange coloration of the red eft contrasts sharply against the green bryophytes, but acts as a warning coloration to ward off predators who could have a bad experience with the toxins in the skin (Brodie 1968). The brightly colored efts are more than 10X as toxic as the adults. Only 0.005 cc of eft back skin killed white mice in 10 minutes.

Salamandra salamandra (European Fire Salamander, Salamandridae)

European Fire Salamanders occur in central and southern Europe, from the Iberian Peninsula to Iran and North Germany to North Africa (Kuzmin 1999), mostly at altitudes of 400-1000 m asl (Wikipedia: Fire Salamander 2011). In the Balkans and Spain, they can be at even higher altitudes. Of these, ***Salamandra salamandra*** (Figure 107-Figure 109) is the best known species, living in deciduous forests in hilly areas. Its abundance classifies it as a species of least concern (IUCN 2010b). Although its primary habitat is among fallen leaves, it also lives on mossy tree trunks (Wikipedia 2011d).

Figure 107. ***Salamandra salamandra*** on a mossy rock. Photo by Marek Szczepanek, through Wikimedia Commons.

Figure 108. ***Salamandra salamandra*** on a wet day in the Harz National Park in central Germany. This colorful salamander is hiding in a minicave made by tree roots. The mosses are ***Schistostega pennata*** and ***Atrichum undulatum***. Photo by Katja Reichel, with permission.

This species gets its English name of fire not from its yellow spots, but from its behavior (Wikimedia: Fire Salamander 2011). Adults often hide in crevices in logs. When the logs are used as fire wood, the heat drives them from their hiding places and a number of them may appear "from the flames." Hence, they have earned the name of Fire Salamander.

As Klaus Weddeling pointed out on Bryonet (26 March 2011), the adults of ***Salamandra*** species are completely terrestrial, using terrestrial habitats even for spawning, having no need for spawning waters any more. Eggs are developed internally and larvae are deposited into the water as they "hatch" (Manenti *et al*. 2009; Wikipedia: Fire Salamander 2011). Adult life spans are known up to 50 years.

You might ask why this salamander has such a bright black and yellow coloration, thus advertising its presence (Figure 109). This is one of the **warning color** combinations, also seen in a number of species of bees, butterflies, and snakes. And yes, this is a poisonous species. But many salamanders are poisonous when consumed. This one is, however, one of the most, perhaps the most, poisonous (Mebs & Pogoda 2005). Its poison glands are concentrated around its head and are usually associated with the colored spots. When disturbed, it assumes a defensive posture and actually sprays, at high velocity (>3 m s^{-1}), defensive alkaloid poisons and **salamandrin** (Brodie & Smatresk 1990; Oracle Thinkquest 2000). **Salamandrin** is a strong alkaloid neurotoxin that usually causes convulsions (Oracle Thinkquest 2000; Wikipedia: Fire Salamander 2011), hypertension, and hyperventilation in all vertebrates (Wikipedia: Fire Salamander 2011). However, it is only dangerous if swallowed, thus not dangerous to humans, but washing one's hands after handling it is highly advisable (Oracle Thinkquest 2000). The secretions probably do double duty in protecting against bacteria and fungi (Wikipedia: Fire Salamander 2011).

Figure 109. ***Salamandra salamandra*** on a bed of mosses, in plain view, advertising its warning coloration of black and yellow. Photo by Iocopo Buttini, through Creative Commons.

Triturus cristatus (Great Crested Newt, Salamandridae)

This species (Figure 110), with at least ten English names, occurs in northern and middle Europe to the Alps, westward to middle and eastern France, and eastward to central Russia (Frost 2011). This species is diminishing, despite considerable protection of its habitats in many countries in Europe.

Figure 110. The **Great Crested Newt**, ***Triturus cristatus***. Photo by Milan Kořínek, with permission.

Müllner (2001) found a distinct preference for forested sites over grassland, attributing this to increased structural diversity that offered better shelter and higher humidity. In the highland and transitional peatlands of Poland, ***Triturus cristatus*** (Figure 111) inhabits the peatlands. In their land phase, the newts hide in the daytime, using stones, mosses, dead or rotting wood, tree roots, shrubs, log piles, and holes to hide in or under (Kinne 2006). In Europe this **Great Crested Newt** (***Triturus cristatus***; Figure 110-Figure 111) uses mossy habitats from June until March (Klaus Weddeling, Bryonet 26 March 2011). In winter, the adult newts move to land where they hide in mosses and moist grasses (Kinne 2006).

During breeding season, peat mosses may again become important, but in the water. Dag Dolmen (pers. comm. through Karen Thingsgaard 4 April 2011) of NTNU The Museum, Trondheim, Norway, advised me that both ***Triturus cristatus*** (Figure 110-Figure 111) and ***Lissotriton vulgaris*** (Figure 103) often attach eggs to ***Sphagnum*** (Figure 21) in the ponds where they breed.

This species seems to be rapidly disappearing, largely due to disappearance of its habitat (UK Biodiversity Action Plan 1995). This newt was fairly common in Europe and has been protected by law in England and elsewhere in Europe (HCT 2009), including prohibition of habitat destruction. Nevertheless, both its terrestrial habitat and ponds needed for its young are disappearing rapidly (AmphibiaWeb 2009b). Protected peatlands may be its last holdout.

Global warming is also likely to impact this species by changing the sex ratio (Wallace & Wallace 2000). At temperatures of 18-24°C the sex ratio is generally 1:1. At higher temperatures, the population develops more males than females, whereas at lower temperatures than 18°C, the number of females increases significantly. Thus, at higher temperatures one might expect a lower reproductive rate due to the smaller number of females.

Figure 111. The **Great Crested Newt**, ***Triturus cristatus***. Photo from Wikimedia Commons.

This newt seems to be one of the species that utilizes the moist mosses during migrations. Stein (1938) observed "great numbers" near Sunderland, Massachusetts, USA, during their migration toward a pond. Many were on the moist mossy bank. As they climbed out of the stream, they travelled along the projecting mosses toward the top of a waterfall. Stein was able to collect over 1000 individuals without exhausting the population. At the very end of their journey the newts had to ascend a dam with a perpendicular wall. It seems that the mosses permitted them to maintain a foothold against the force of the water.

Importance of the Bryophyte Amphibian Community

The bryophytes not only support large amphibians and reptiles like green frogs and rattlesnakes, but more importantly, they provide critical habitat for a number of smaller amphibians and reptiles. Araujo (1999), working in Portugal, concluded that these small amphibians and reptiles may be better indicators of biodiversity than the larger, more conspicuous species. That suggestion is even more applicable in the tropics among the arboreal bryophyte fauna.

Salamanders may play a much greater role in the ecosystem than most of us realize (Conniff 2014). Conniff considers them to be at least one of the top predators in North American forests. In many locations, they have a high abundance and eat a lot. He reports that an average salamander eats 20 ants, 2 flies or beetle larvae, 1 adult beetle, and half a springtail in a single day. But this is an ecosystem, and nothing acts alone. Their food consists almost entirely of shredding invertebrates – those organisms that shred and eat the leaf litter. And when these shredders eat, they release carbon from the leaves, carbon that comprises 47.5% of the litter. When the shredders are eaten by the salamanders, less carbon is released to the atmosphere.

To assess the importance of salamanders in the carbon cycle, Dr. Hartwell H. Welsh Jr., a herpetologist at the United States Forest Service research station in Arcata, California, and Dr. Michael L. Best, currently at the College of the Redwoods in Eureka, California, built exclosures that permitted free access to invertebrates but kept salamanders out of half of them (Conniff 2014). The results – fly and beetle larvae and adult beetles and springtails declined significantly when in enclosures with salamanders. Welsh and Best calculated that the density of salamanders in their study would account for 179 pounds (81.2 kg) of carbon per forest acre being stored in the soil instead of contributing to atmospheric gases that affect global climate.

The small size and lack of lungs in most salamanders translates to a small caloric need. This permits them to eat really small invertebrates that provide insufficient calories for birds and mammals. Bryophytes contribute part of the habitat where many of these salamanders reside.

Summary

Bryophyte-dwelling terrestrial salamanders, particularly arboreal ones, are typically slender with short legs, presumably making movement within the moss mat easier. Terrestrial life cycle adaptations are essential. Egg construction requires tradeoffs among need for gas exchange, need for mechanical support, same-species sperm attraction, other species sperm avoidance, heat conservation or cooling, predator defense, moisture retention, UV light protection, prevention of polyspermy, and protection from bacteria and fungi. Terrestrial eggs are turgid compared to aquatic eggs, usually have a tough outer layer, and may have pigments. Parental care of eggs helps to minimize bacteria and fungi. Eggs may hatch into tadpoles, but many hatch directly into young salamanders, skipping the larval stage.

Many undescribed species of tiny salamanders most likely lurk among the mosses in the tropical forests. Those that are known are limited in distribution and are threatened by habitat loss. In Costa Rica, the moss salamander ***Nototriton*** and the climbing salamander ***Bolitoglossa*** can be found in such habitats, and in Mexico ***Cryptotriton*** occupies bryophytes in the cloud forest. These three genera are tiny and seem to be moss specialists, with large eggs, long development times, and no larval stages. In Guatemala, the similarly adapted ***Dendrotriton cuchumatanus*** may occupy moss mats. ***Oedipina*** species, a Central American group, may live on the ground or be arboreal, using bryophytes for moisture and cover.

In the temperate zones, old growth forests are likely to have more developed bryophyte communities than younger forests. Bryophyte growths are often well developed in old growth, and small amphibians can find refuge from desiccation and predation and in some cases use them as an oxygen source. In old-growth forests of northern California and southwestern Oregon, moss dwellers include species of ***Batrachoseps***, ***Rhyacotriton***, and ***Plethodon***. The wandering salamander ***Aneides vagrans*** seems to be dependent on mosses among the coast redwoods. ***Aneides vagrans*** salamanders benefit from the photosynthetic oxygen produced by the bryophytes, while remaining moist among their masses. They also use tunnels made by rhizomes and roots of the fern *Polypodium scouleri*, which seems to depend on the bryophytes to develop its gametophytes successfully.

Asia has only one Plethodontid species; Europe has one genus, of which only ***Speleomantes supramontis*** has known bryophyte associations.

North American streams and springs can have species of ***Eurycea*** among the bryophytes, especially on streambanks.

Peatlands support salamanders and newts, including ***Eurycea*** species (lined salamanders), ***Necturus punctatus*** (Dwarf Waterdog), ***Lissotriton vulgaris*** (Smooth Newts), ***Triturus cristatus*** (Great Crested Newt), ***Notophthalmus viridescens*** (Eastern Newt), ***Ambystoma laterale*** (Blue-spotted Salamander), and ***Desmognathus fuscus*** (Northern Dusky Salamander).

The bryophyte amphibian fauna, especially the small species, are good indicators of biodiversity.

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Bryophyte-dwelling Salamander Checklist

species	distribution	habitat	bryophyte use: mossy habitats	under or in mosses	nests	aestivation	hibernation	foraging	source
Hynobiidae									
Hynobius tokyoensis Tokyo Salamander	Japan	forest floor		x					Kusano & Miyashita 1984
Salamandrella keyserlingii Siberian Salamander	northern Asia	wet forest of taiga		x		x	x		Potapov 1993; Hasumi *et al*. 2009
Ambystomatidae									
Ambystoma laterale Blue-spotted Salamander	western N. Amer.	deciduous & mixed forest		x					LeClere 2011
Ambystoma maculatum Spotted Salamander	eastern N. Amer.	peatlands	x						Amphibians: Tulula Wetlands
Ambystoma jeffersonianum Jefferson Salamander	central E. N. Amer.	forest floor & wetlands	x						Freda & Dunson 1986
Plethodontidae									
Plethodon teyahalee Southern Appalachian Salamander	high elev S. Appalachians	decid. forest & peatlands	x						Amphibians: Tulula Wetlands
Plethodon serratus S. Red-backed Salamander	SE USA	forest floor			x				Aarademа 1999
Plethodon nettingi Cheat Mountain Salamander	Cheat Mtn, WVa, USA	red spruce forest floor		x	x		?		Pauley 1985
Plethodon cinereus E. Red-backed Salamander	NE USA, SE Canada	peatlands, forest floor	x	x					Hughes *et al*. unpubl.
Plethodon dorsalis Northern Zigzag Salamander	lower midwest USA	rocky slopes		x					Ferguson 1961
Plethodon welleri Weller's Salamander	mtns of TN to VA, USA	conifer logs		x					Organ 1960
Plethodon elongatus Del Norte Salamander	SW OR to NW CA	old growth forest	x						Welsh & Lind 1995
Plethodon idahoensis Coeur d'Alene Salamander	northern Rocky Mtns	seeps, springs, waterfalls		x					Wilson 1990; Dumas 1957
Plethodon vandykei Van Dyke's Salamander	Washington, USA	coniferous forest floor		x					Slater 1933
Plethodon larselli Larch Mountain Salamander	Columbia R Gorge USA	talus slopes		x					Burns 1962
Plethodon glutinosus Northern Slimy Salamander	eastern USA	bottomland			x				VA Dept Game Inland Fish 2011
Plethodon richmondi Southern Ravine Salamander	eastern USA	ravines, hillsides, mesic forest			x				VA Dept Game Inland Fish 2011
Plethodon metcalfi Southern Gray-cheeked Salamander	S Blue Ridge Mtns USA	forest floor	x						Organ 1958
Plethodon jordani Red-cheeked Salamander	Great Smoky Mtns	spruce-fir forest	x	x					King 1939
Plethodon stormi Siskiyou Mountains Salamander	S Oregon, N California	talus		x					Gary Nafis 28 April 2011
Plethodon asupak Scott Bar Salamander	S Oregon, N California	talus		x					Gary Nafis 28 April 2011
Gyrinophilus porphyriticus Spring Salamander	eastern N Amer	mature hdwd forest	x						Ferguson 1961
Pseudotriton ruber Red Salamander	eastern USA	tamarack wetlands	x	x			x		Burger 1933
Hemidactylium scutatum Four-toed Salamander	eastern N Amer	mature forest, peatlands	x	x	x				Gilbert 1941; Wood 1955; Petranka 1998; Harris 2009
Stereochilus marginatus Many-lined Salamander	Atlantic coastal plain, USA	wetlands	x	x	x				Blanchard 1934; Duellman & Trueb 1986

Desmognathus fuscus Northern Dusky Salamander	eastern N Amer	forest streams			x				Burger 1933; Hom 1987
Desmognathus ochrophaeus Alleghany Mountain Dusky	Appalachian Mtns, USA	seeps	x	x	x				Tilley 1972; Mushinsky 1976
Desmognathus monticola Seal Salamander	central & S Appalachians	streams			x				Camp & Tilley 2011
Desmognathus santeetlah Santeetlah Dusky Salamander	SW Blueridge Mtns	headwater streams			x				Beachy 1993
Desmognathus aeneus Seepage Salamander	SE USA	seepage in deciduous forest			x				Martof & Humphries 1955; Jones 1981
Desmognathus wrighti Pygmy Salamander	S Nantahala Mtns, NC, USA	deciduous & spruce-fir forest		x					Hining & Bruce 2005
Desmognathus quadramaculatus Black-bellied Salamander	Appalachian Mtns, USA	cool steep streams, peatlands	x						Amphibians: Tulula Wetlands
Desmognathus ocoee Ocoee Salamander	SW Blue Ridge; Piedmont Physiogr	peatlands; streams	x		x				Amphibians: Tulula Wetlands
Phaeognathus hubrichti Red Hills Salamander	Alabama coastal plain USA	forest						x	Gunzberger 1999
Ensatina eschscholtzii Monterey Ensatina	W N Amer	mossy ground		x					Gnaedinger & Reed 1948
Hydromantes brunus Limestone Salamander	Mariposa Co, CA, USA	limestone rock		x					Gorman 1954
Hydromantes shastae Shasta Salamander	Shasta Co, CA, USA	limestone rock		x					Gorman & Camp 1953
Hydromantes ambrosii	Italy	forest, cliffs	x						Andreas Nöllert, pers. comm. 22 January 2016
Nototriton abscondens	Costa Rica	premontane & humid montane	x	x	?				Taylor 1954
Nototriton guanacaste Guanacaste Moss Salamander	Costa Rica	cloud forest	x	x	?				Tosi 1969; Good & Wake 1993
Nototriton picadoi Picado's Moss Salamander	Costa Rica	cloud forest	x	x	x			?	Good & Wake 1993; Savage 2002
Nototriton saslaya	Nicaragua	cloud forest	x	x	x				ZipcodeZoo.Com 2008c
Nototriton gamezi Monteverde Moss Salamander	Costa Rica	rainforest	x	x	?				García-Paris & Wake 2000
Nototriton ricardi Richard's Salamander	Costa Rica	rainforest	x	x	?				Good & Wake 1993
Nototriton tapanti Tapanti Moss Salamander	Costa Rica	humid premontane	x	x	?				Savage 2002
Nototriton barbouri Yoro Salamander	Honduras	lower montane forest floor	x	x	?				ZipcodeZoo.Com 2008b
Chiropterotriton chiropterus Common Splayfoot Salamander	Veracruz, Mexico	arboreal	x						IUCN 2010
Cryptotriton alvarezdeltoroi Alvarez del Toro's Salamander	Chiapas, Mexico	cloud forest		x					Papenfuss & Wake 1987
Cryptotriton monzoni Monzon's Hidden Salamander	Zacapa, Guatemala	cloud forest	x						IUCN 2010
Oedipina poelzi Quarry Worm Salamander	Costa Rica	moist montanes	x	x	?				Wake 1987
Oedipina uniformis Cienega Colorado Worm Salamander	Costa Rica; Nicaragua	arboreal	x	x					Wake 1987
Oedipina pseudouniformis Cienega Colorado Worm Salamander	Costa Rica & Nicaragua	arboreal		x					Brame 1968
Oedipina elongata Central American Worm Salamander	Mexico to Honduras	soil & wood channels	x						IUCN 2010
Oedipina gracilis Long-tailed Worm Salamander	Costa Rica; Panama	moist litter & burrows	x						Leenders 2001
Oedipina pacificensis	SW Costa Rica & Panama	lowlands	?	?					Frost 2011
Oedipina carablanca Los Diamantes Worm Salamander	Costa Rica	lowlands		x					Kubiki 2011
Bolitoglossa obscura Tapanti Giant Salamander	Costa Rica & Panama	arboreal		x					Wake 1987
Bolitoglossa diminuta Quebrada Valverde Salamander	Costa Rica	arboreal		x					Wake 1987

Bolitoglossa sombra Shadowy Web-footed Salamander	Costa Rica; Panama	arboreal		x					Hanken *et al*. 2005
Bolitoglossa robusta Robust Mushroom-tongue Salamander	Costa Rica; Panama	ground in lower montane		x					Hanken et al. 2005
Bolitoglossa diaphora	Honduras	cloud forest	?						McCranie & Wilson 2009
Bolitoglossa rostrata Longnose Mushroomtongue Salamander	Guatemala; Mexico	arboreal high mountain	x						Raffaëlli 2011
Bolitoglossa longissima	Honduras	ground & arboreal		x					McCranie & Cruz 1996
Bolitoglossa mexicana Mexican Mushroomtongue Salamander	Veracruz, Mexico to Honduras	arboreal in rainforest	x						IUCN 2010
Bolitoglossa subpalmato La Palma Salamander	Costa Rica	moist montane		x	x				Robinson 1976; Wake 1987
Bolitoglossa marmorea Crater Salamander	Costa Rica; Panama	moist montane	x						Wake *et al.* 1973
Bolitoglossa hartwegi Hartweg's Mushroomtongue Salamander	Guatemala; Mexico	moist montane forest	?						IUCN 2010
Bolitoglossa helmrichi	Guatemala	arboreal in cloud forest	?						IUCN 2010
Bolitoglossa lincolni Lincoln's Mushroomtongue Salamander	Guatemala; Mexico	forest, somewhat arboreal	?						IUCN 2010
Bolitoglossa rufescens Northern Banana Salamander	Mexico to Honduras	bromeliads in wet forest	?						McCoy 1990
Bolitoglossa suchitanensis	Guatemala	humid deciduous forest	x	x					Campbell *et al*. 2010
Bolitoglossa xibalba	Guatemala	wet montane forest	x	x					Campbell *et al*. 2010
Thorius dubitus Acultzingo Pigmy Salamander	Veracruz & Puebla Mexico	pine-oak cloud forest		x					Hanken 1983; Wake 1987
Pseudoeurycea juarezi Juarez Salamander	Oaxaca, Mexico	cloud forest	x	x					IUCN 2010
Pseudoeurycea rex Royal False Brook Salamander	western Guatemala	arboreal		x					Wake 1987
Pseudoeurycea scandens Tamaulipan False Brook Salamander	Mexico	arboreal		x					Wake 1987
Pseudoeurycea werleri Werler's False Brook Salamander	Veracruz Mexico	arboreal; rainforest & cloud forest		x					IUCN 2010
Pseudoeurycea lineola Veracruz Worm Salamander	Veracruz Mexico	oak-pine forest	x	?					Frost 2011
Pseudoeurycea orchileucos Sierra de Juárez Worm Salamander	Oaxaca Mexico	cloud forest	x						IUCN 2010
Pseudoeurycea orchimelas San Martin Worm Salamander	Veracruz Mexico	litter	?						IUCN 2010
Nyctanolis pernix Nimble Long-limbed Salamanders	Mexico; Guatemala	humid pine-oak & cloud forest		x					Elias & Wake 1983; Stuart *et al.* 2008
Dendrotriton cuchumatanus Forest Bromeliad Salamander	Guatemala	oak forest		x					ZipcodeZoo.Com 2008a
Batrachoceps wrighti Oregon Slender Salamander	NW USA	temperate forest	x						Storm 1953; Bury 2011
Aneides vagrans Wandering Salamander	N coastal CA, USA; BC, Canada	redwood forest		x					Sillett 1995; Spickler *et al*. 2006
Aneides aeneus Green Salamander	mid - E USA	boulders & rock cliffs		x				x	Gordon 1952; Lee & Norden 1973; Canterbury 1991
Rhyacotriton olympicus Olympic Torrent Salamander	N CA, SW OR, USA	old growth forest	x	x					Slater 1933; Welsh 1990
Rhyacotriton cascadae Cascade Torrent Salamander	Cascade Mtns, USA	riffles; underground streams	x	?					Frost 2011
Rhyacotriton variegatus Southern Torrent Salamander	Cascade Mtns CA; OR USA	humid forest headwaters	x	?					Welsh & Lind 1996
Karsenia koreana Korean Crevice Salamander	Korea	rock slides in young forest	x						Wake 2005
Speleomontes supramontis Supramonte Cave Salamander	east Sardinia, Italy	caves; oak forest		x					Nöllert & Nöllert 1992
Eurycea wilderae Blue Ridge Two-lined Salamander	S Appalachian Mtns	peatlands	x	x					Amphibians: Tulula Wetlands

Eurycea guttolineata Three-lined Salamander	SE USA	swampy areas	x	x					Amphibians: Tulula Wetlands
Eurycea multiplicata Many-ribbed Salamander	Ouichita Mtns, USA	limestone streams						x	Dundee 1947
Eurycea tynerensis Oklahoma Salamander	Ozark Plateau, USA	streams, springs, seeps		x					Dundee 1947
Eurycea bislineata Northern Two-lined Salamander	E USA	peatlands, small streams	x	x	x				Jobson 1940; Richmond 1945; Bahret 1996
Eurycea lucifuga Cave Salamander	mid-S Appalachian Mtns, USA	limestone caves, springs		x					Bragg 1955
Proteidae									
Necturus punctatus Dwarf Waterdog	SE coastal plain, USA	hardwoods		x					Neill 1948
Salamandridae									
Notophthalmus viridescens Eastern Newt	Eastern USA	streams; forest floor		x					Roe & Grayson 2008
Salamandra salamandra European Fire Salamander	Central & S Europe	deciduous forest		x					Wikipedia: Fire Salamander 2011
Euproctus platycephalus Sardinian Mountain Newt	Sardinia, Italy	rivers		x		x	?		Michael Lüth (Bryonet 26 March 2011)
Calotriton asper Pyrenean Brook Salamander	Pyrenees	streams & lakes		x					Michael Lüth (Bryonet 26 March 2011)
Triturus cristatus Great Crested Newt	Europe	forest & peatlands	x	x	x	?	x		Kinne 2006
Taricha torosa California Newt	Coastal California, USA	epiphytic mosses; dry forest	x	x					Gary Nafis, 27 Apr 2011; Edmund Brodie, 7 Jun 2011
Lissotriton helveticus Palmate Newt	W Europe	peatlands	x						Wikipedia: Palmate Newt 2011
Lissotriton montandoni Carpathian Newt	Carpathian & Tatra Mtns	forest; rivers	x						Marc Hayes pers. comm. 26 March 2011
Lissotriton vulgaris Smooth Newt	Europe	forest	x						Peatlands 2009
Lissotriton boscai Bosca's Newt	W Iberian Peninsula	shallow ponds; peatlands	x	x					AmphibiaWeb: *Lissotriton boscai* 2000

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