CHAPTER 14-8
SALAMANDER MOSSY HABITATS

Janice M. Glime and William J. Boelema

TABLE OF CONTENTS

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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).

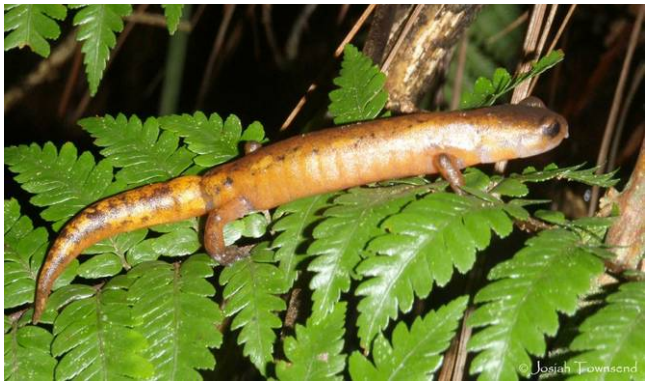

Figure 5. ***Bolitoglossa diaphora*** on a fern. Photo by Josiah Townsend, with permission.

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.

Figure 6. ***Bolitoglossa cf. hartwegi*** on a bed of ***Thuidium***. Photos by Sean Michael Rovito, with permission.

Figure 7. ***Bolitoglossa cf. hartwegi*** blending with mosses and lichens on a rock. Photos by Sean Michael Rovito, with permission.

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.

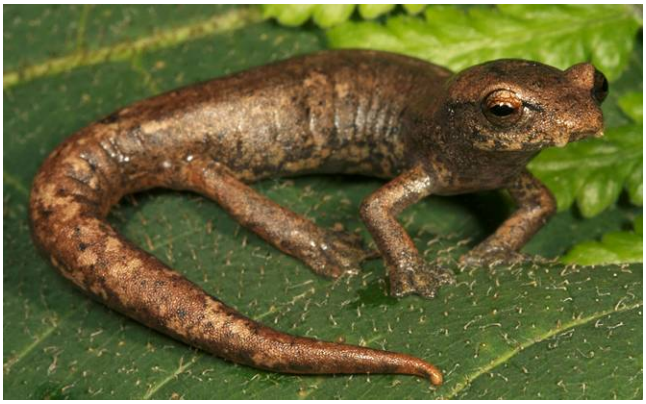

Figure 8. ***Bolitoglossa helmrichi*** resting on a leaf. Photo by Todd Pierson, with permission.

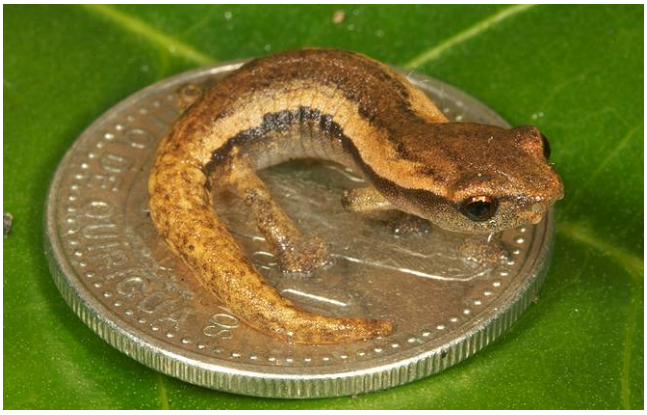

Figure 9. ***Bolitoglossa helmrichi***. The lower photo shows how small these salamanders are. Photo by Todd Pierson, with permission.

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.

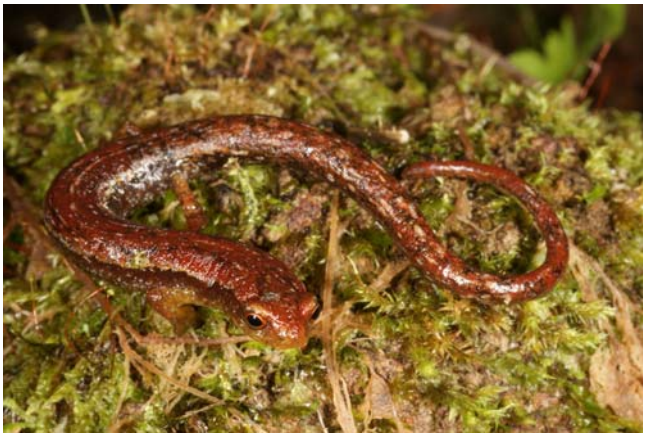

Figure 10. ***Bolitoglossa jugivagans*** exhibiting its daytime coloration while sitting on a moss. Photo by Andreas Hertz, with permission.

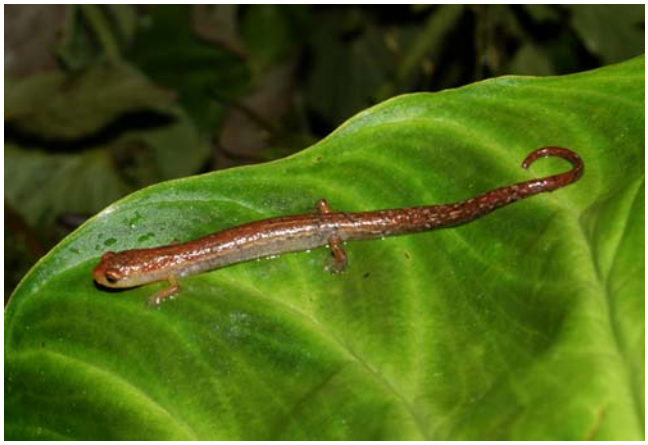

Figure 11. ***Bolitoglossa jugivagans*** exhibiting its nighttime coloration while sitting on a solid-colored leaf. Photo by Andreas Hertz, with permission.

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.

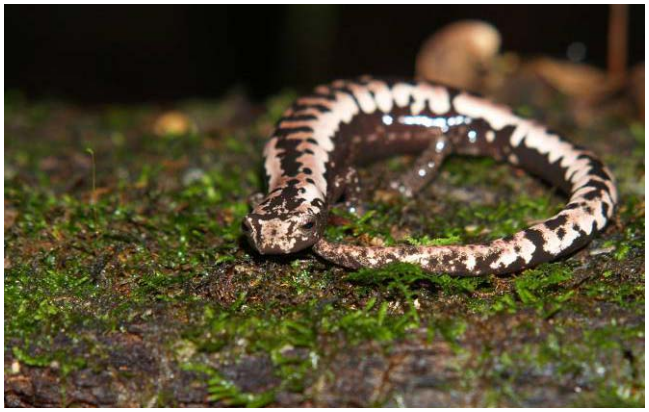

Figure 14. ***Bolitolgossa mexicana*** on mossy bark at Selva Lacandona, Chiapas, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

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).

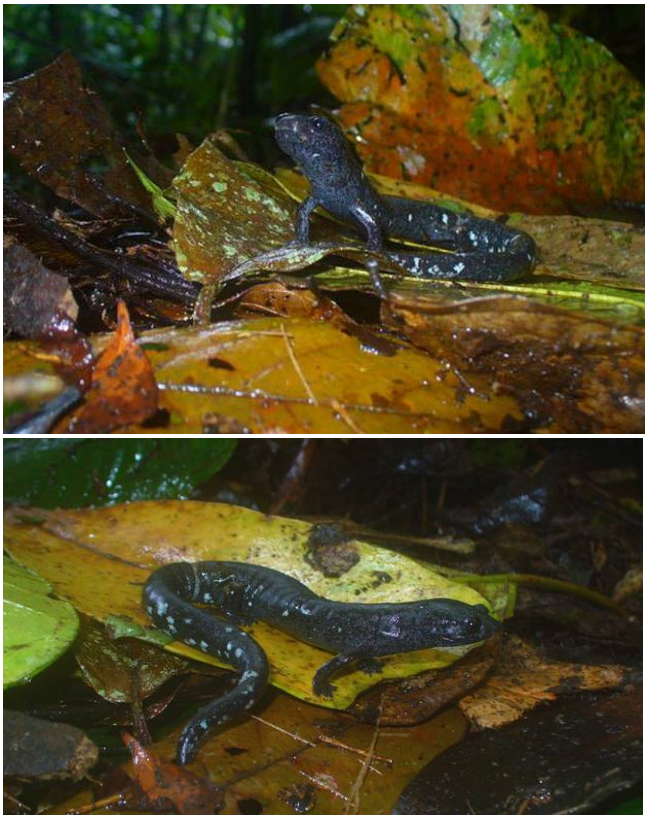

Figure 15. ***Bolitoglossa robusta***. Photos by Eduardo Bozo, with permission.

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.

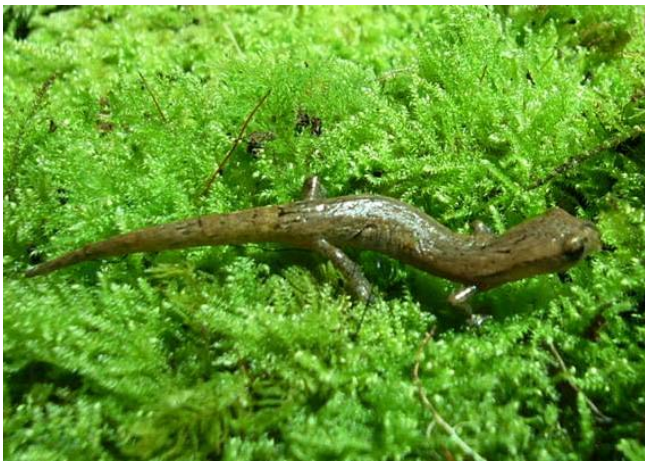

Figure 17. ***Bolitoglossa rufescens*** on a bed of mosses. Photo by Sean Michael Rovito, with permission.

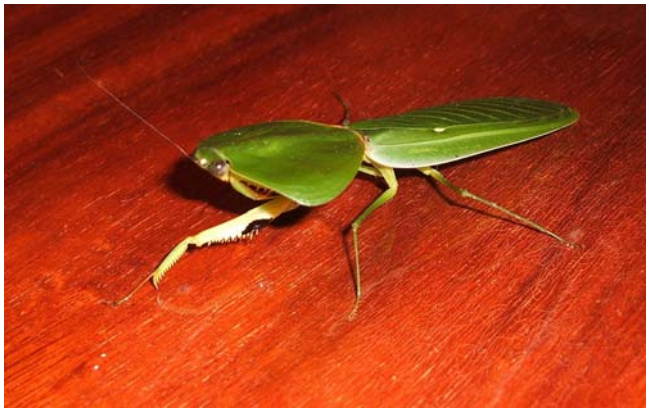

Figure 18. ***Choeradodis strumaria***, a mantid predator on ***Bolitoglossa rufescens***. Photo by C. Horwitz through Creative Commons.

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).

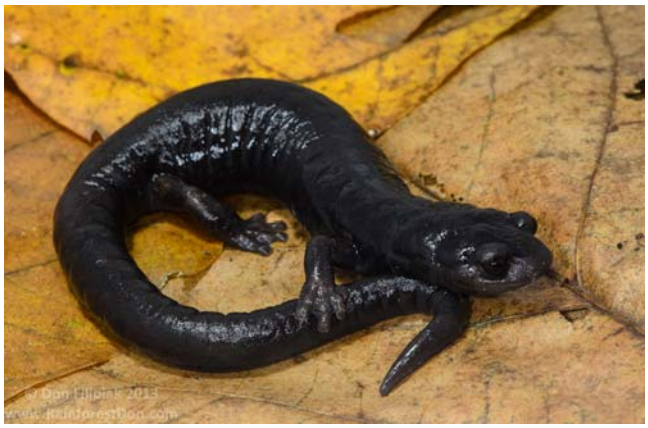

Figure 19. ***Bolitoglossa sombra***, a bryophyte dweller in the tropics. Photo © 2013 Don Filipiak, through online permission.

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).

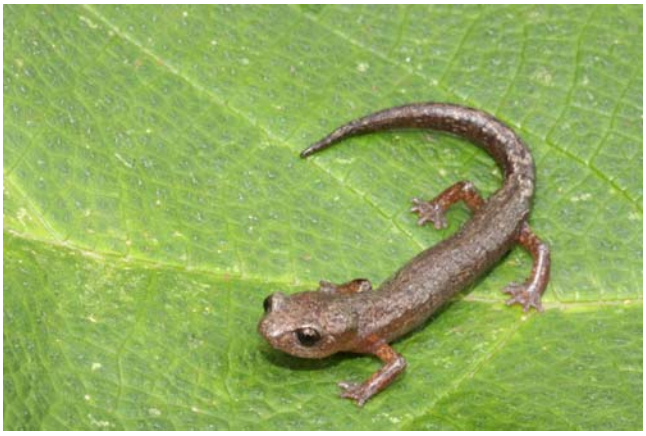

Figure 22. ***Bolitoglossa suchitanensis***, an inhabitant of mossy logs and forests. Photo by Sean Michael Rovito, through Creative Commons.

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.

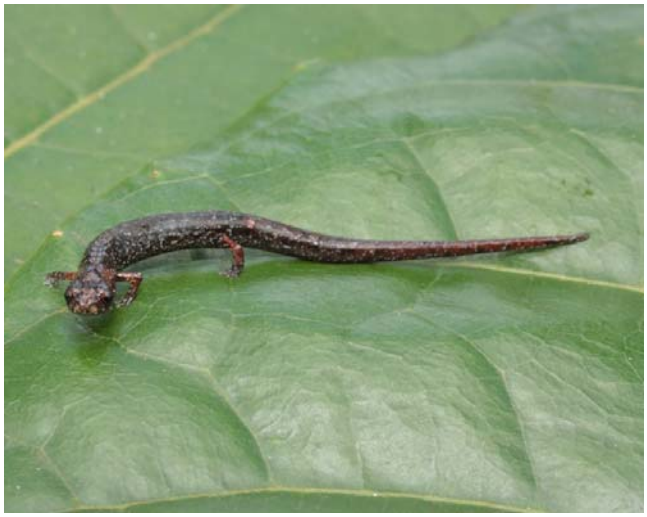

Figure 26. ***Cryptotriton alvarezdeltoroi***, a species that occurs among mosses in the cloud forest of Mexico. Photo by Sean Michael Rovito, through Creative Commons.

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.

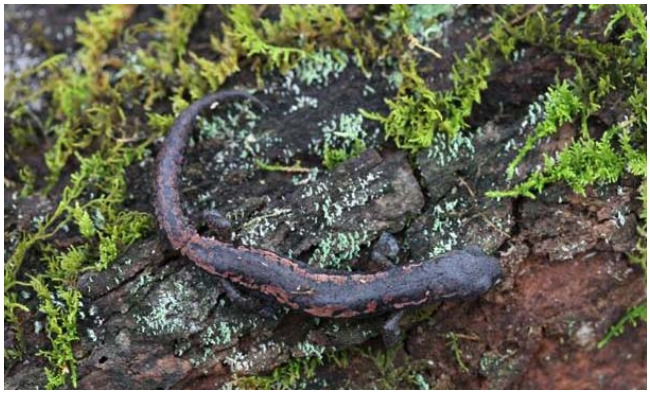

Figure 29. ***Dendrotriton cuchumatanus*** on a mossy log. Photo by Sean Michael Rovito, with permission.

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).

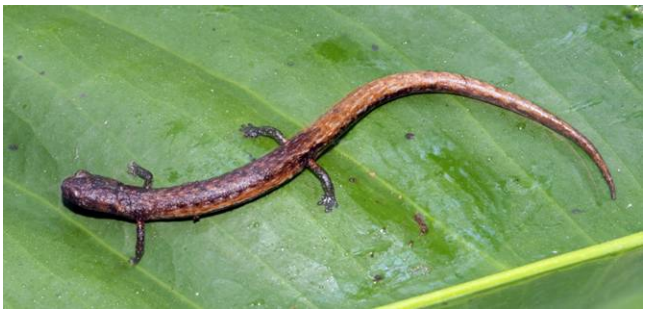

Figure 30. **Santa Barbara Moss Salamander**, ***Nototriton limnospectator***, a moss salamander of lower montane wet forests of the Parque Nacional Santa Barbara. It occurs at intermediate elevations (1640-1980 m asl) of the Montaña de Santa Bárbara on the Atlantic side of western Honduras where it 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).

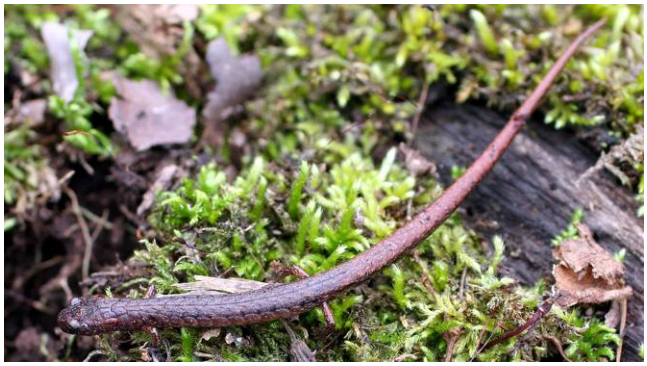

Figure 32. ***Nototriton barbouri*** on mosses covering decaying wood. Photo by Josiah Townsend, with permission.

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).

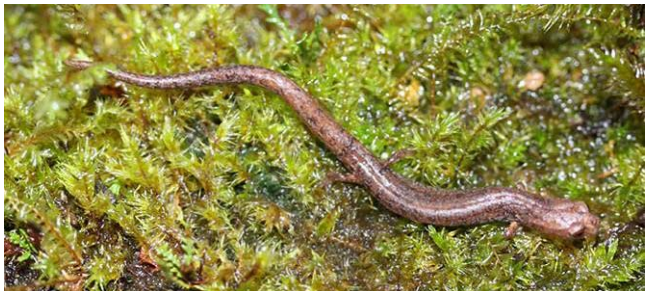

Figure 33. ***Nototriton gamezi***. Photo by Sean Michael Rovito, with permission.

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 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.

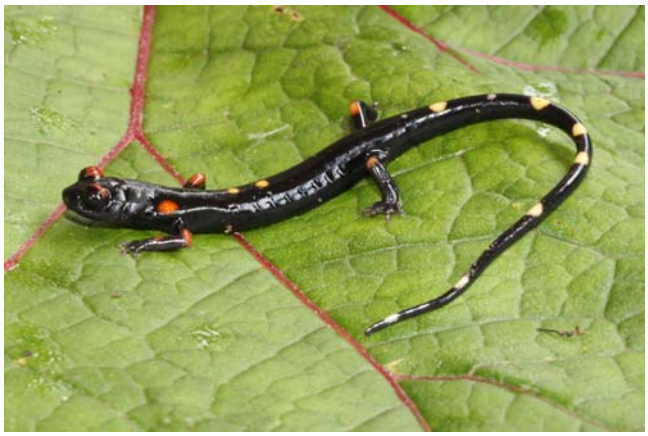

Figure 41. ***Nyctanolis pernix*** on a leaf. Photo by Sean Michael Rovito, with permission.

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.

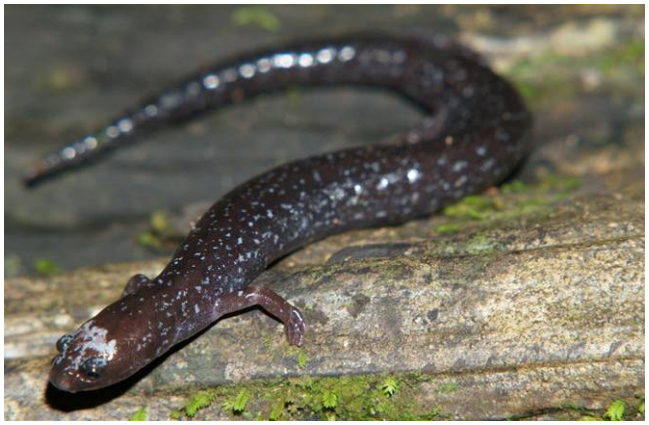

Figure 42. ***Oedipina elongata*** (**Central American Worm Salamander**), shown here on a log at Selva Lacandona, Chis, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

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.

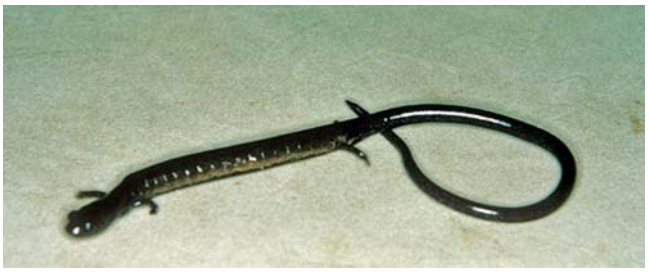

Figure 47. ***Oedipina poelzi***, a moss dweller in Costa Rica. Photo from Division of Herpetology at University of Kansas Biodiversity Institute, with permission through Rafe Brown.

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).

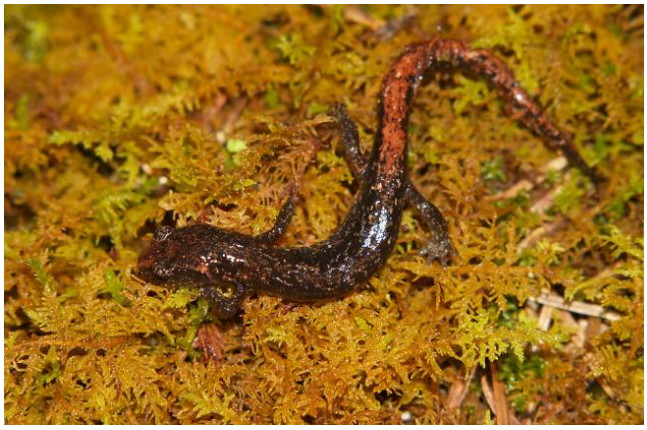

Figure 48. This ***Pseudoeurycea juarezi*** was located by lifting the moss at Sierra de Juarez Oaxaca, Mexico. Photo by Omar Hernandez-Ordoñez, with permission.

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).

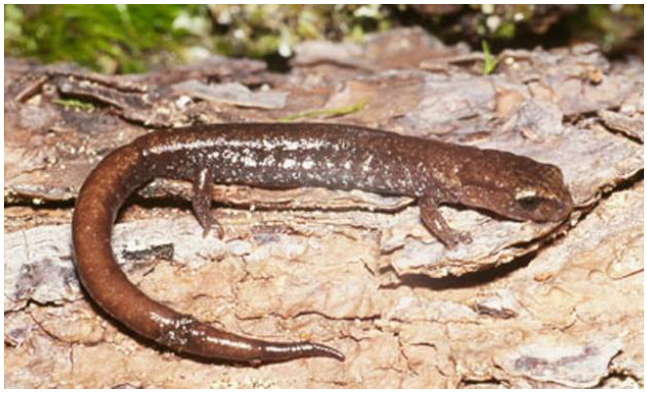

Figure 49. ***Pseudoeurycea rex*** on bark. Photo © 2003 Jonathan Campbell, with permission.

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.

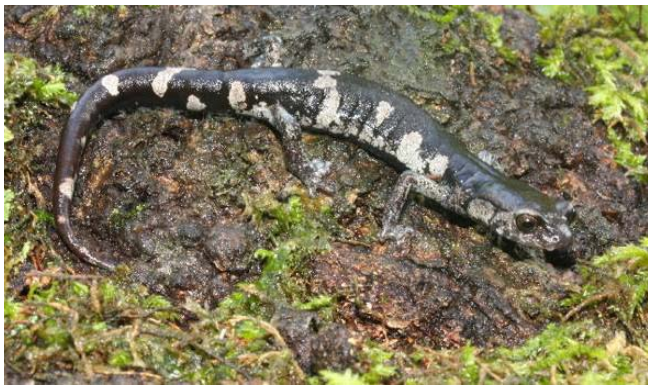

Figure 50. ***Pseudoeurycea scandens*** on moss-covered log where it blends well with the bark and the patchy environment. Photo by Sean Michael Rovito, with permission.

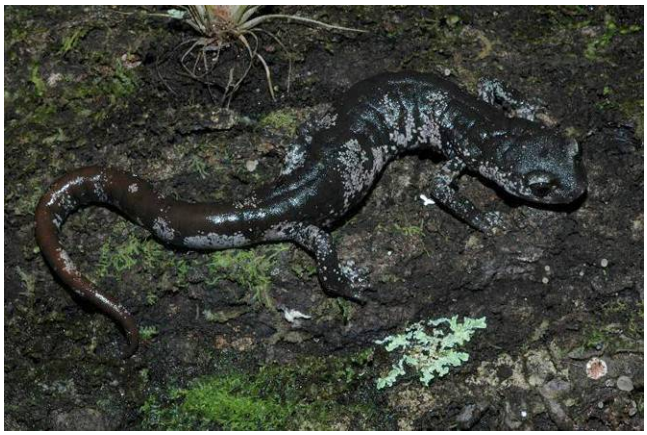

Figure 51. More muted color patterns on another ***Pseudoeurycea scandens*** (**Tamaulipan False Brook Salamander**) on bark where it blends well with the bark and lichens, permitting it to be inconspicuous among the patches of mosses as well. With no mating call and small size, these salamanders are 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.

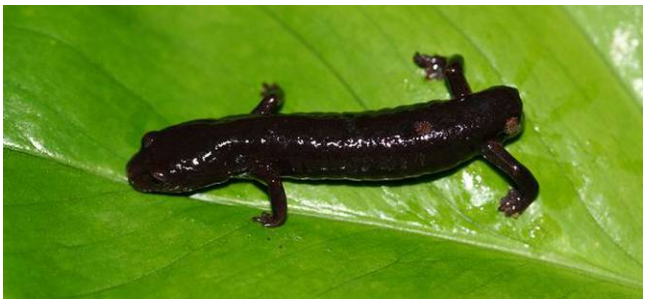

Figure 52. This ***Pseudoeurycea werleri*** came very close to being dinner, with its entire tail being disarticulated in an attack. Photo by Sean Michael Rovito, with permission.

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.

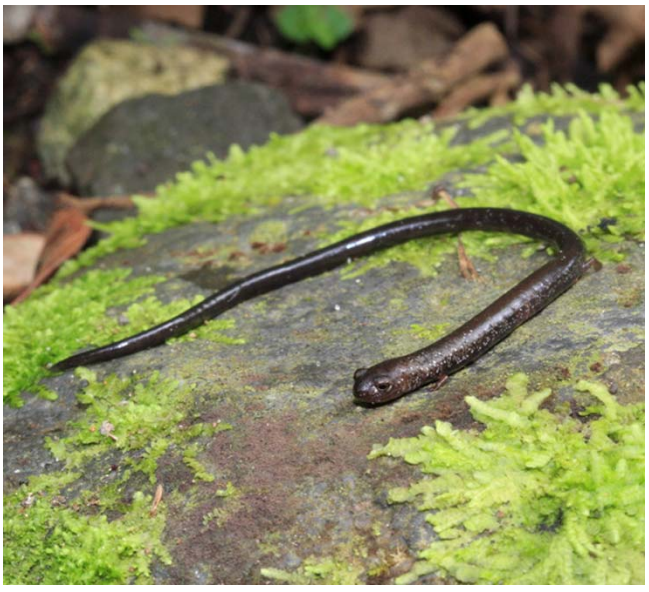

Figure 53. ***Pseudoeurycea lineola***. Photo by Sean Michael Rovito, with permission.

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).

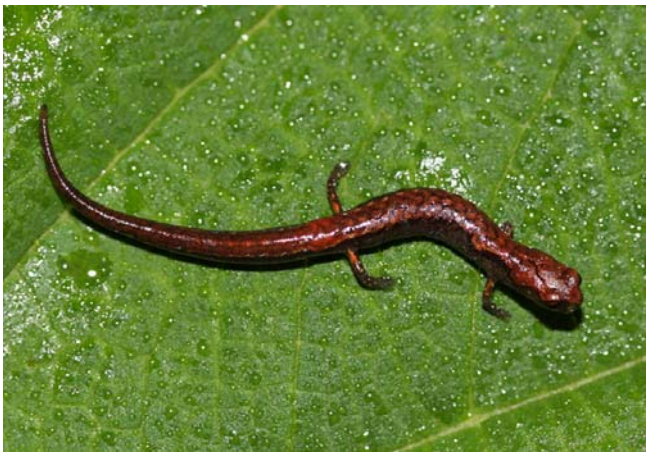

Figure 54. ***Thorius arboreus***, a relative of ***T. dubitus***, and possible a moss dweller. Photo by Sean Michael Rovito, with permission.

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.

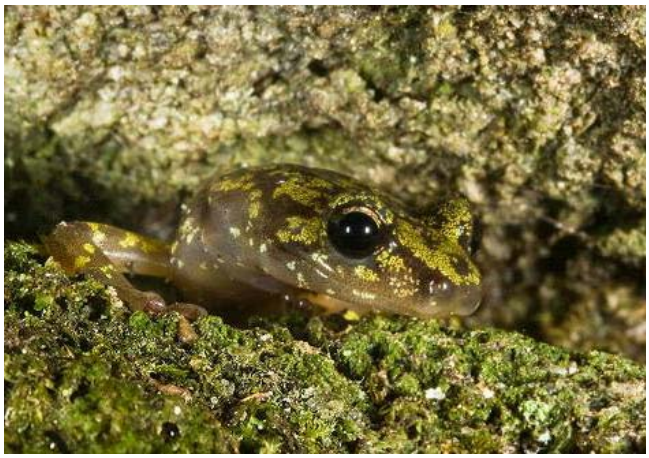

Figure 55. ***Aneides aeneus*** adult in crevice in its mossy habitat. Photo by Bill Peterman, with permission.

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).

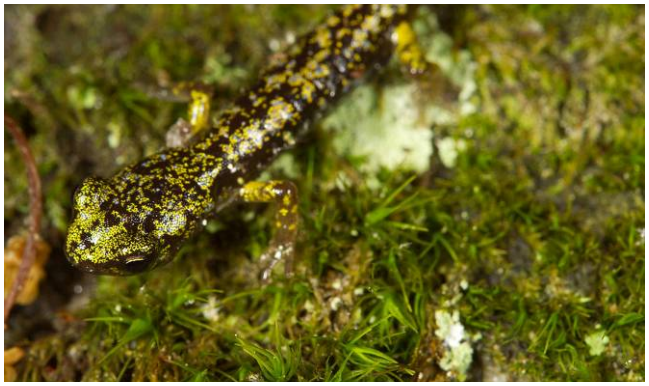

Figure 56. ***Aneides aeneus*** juvenile in its mossy habitat. Photo by Bill Peterman, with permission.

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.

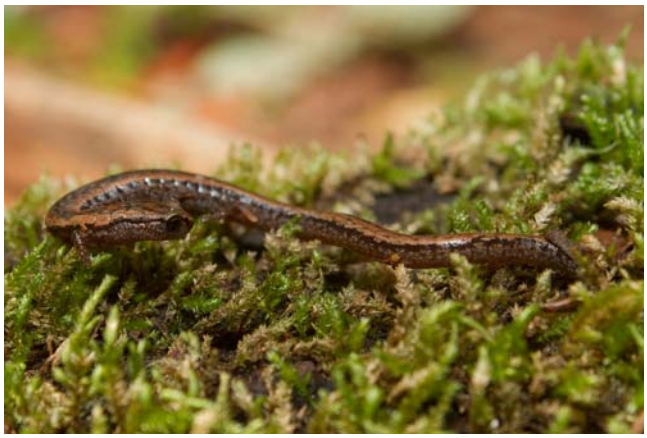

Figure 63. ***Batrachoseps attenuatus*** on moss. Photo by Brian Gratwicke, through Creative Commons.

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.

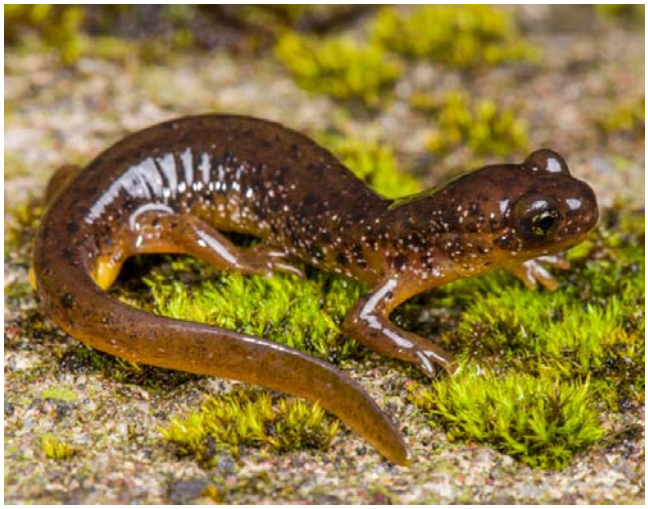

Figure 64. Cascade Torrent Salamander, ***Rhyacotriton cascadae***. Photo by John Clare, through Creative Commons.

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).

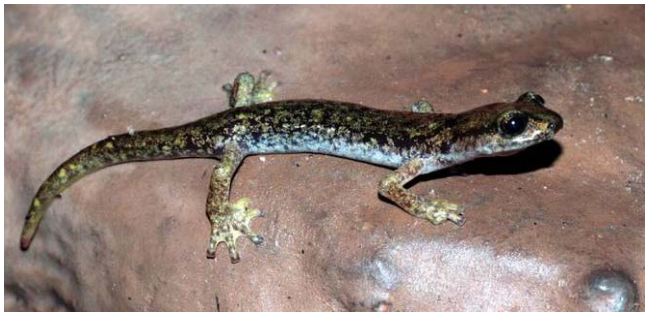

Figure 73. ***Speleomantes supramontis*** (**Supramonte Cave Salamander**) on a rock ledge. Photo by Franco Andreone, through Wikimedia Commons.

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).

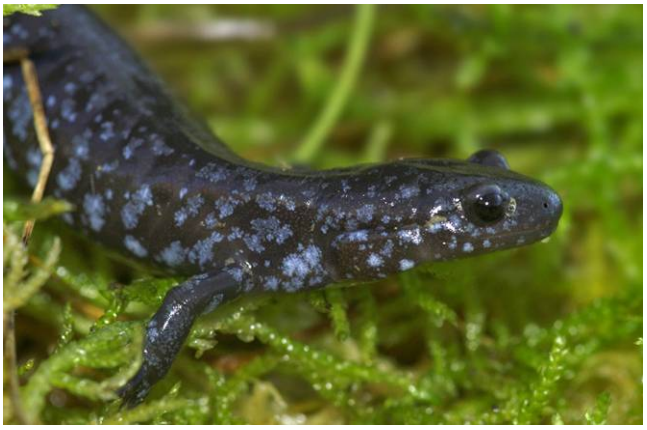

Figure 75. ***Ambystoma laterale*** (**Blue-spotted Salamander**), a peatland salamander that occurs in eastern USA and Canada (Frost 2011). Photo by Henk Wallays, through Creative Commons.

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.

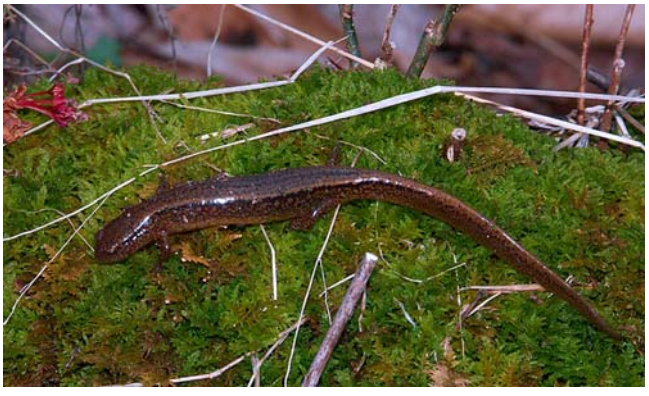

Figure 77. The Northern Two-lined Salamander, ***Eurycea bislineata***. Photo by Henk Wallays, through Creative Commons.

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.

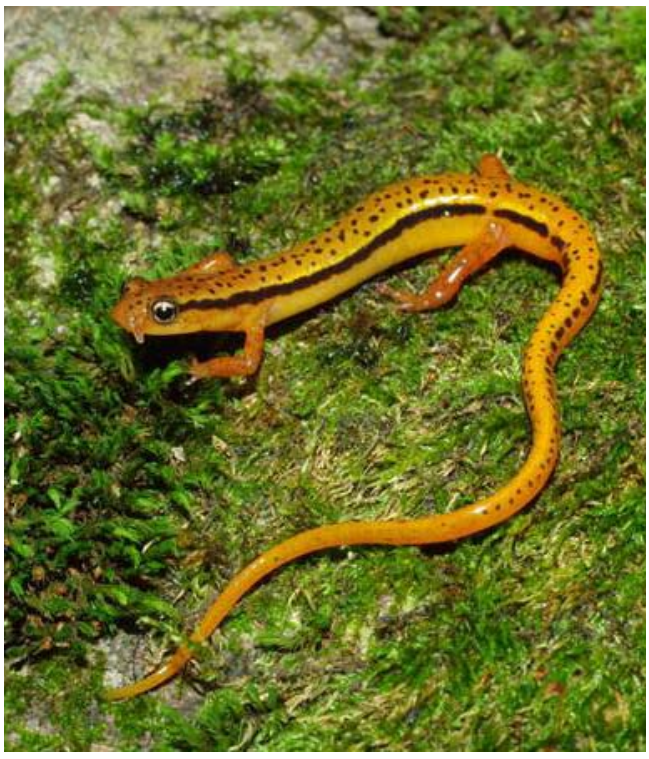

Figure 79. ***Eurycea wilderae*** on a mat of mosses. Photo by Michael Graziano, with permission.

Figure 80. ***Eurycea wilderae***, showing its small size compared to a US quarter. Photo by Todd Pierson, with permission.

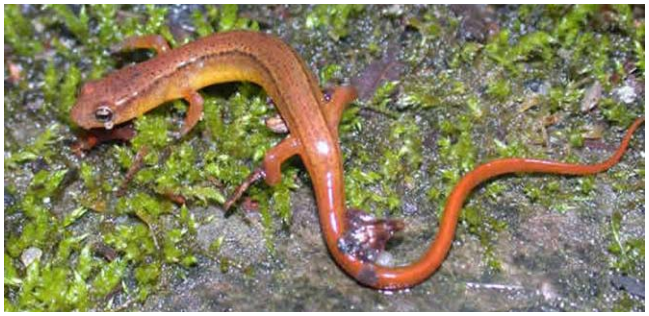

Figure 81. ***Eurycea wilderae***. Photo by John D. Willson, with permission.

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).

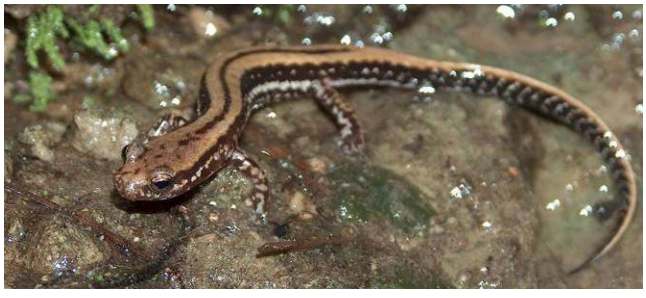

Figure 82. ***Eurycea guttolineata*** at the edge of a stream. Photo by Michael Graziano, with permission.

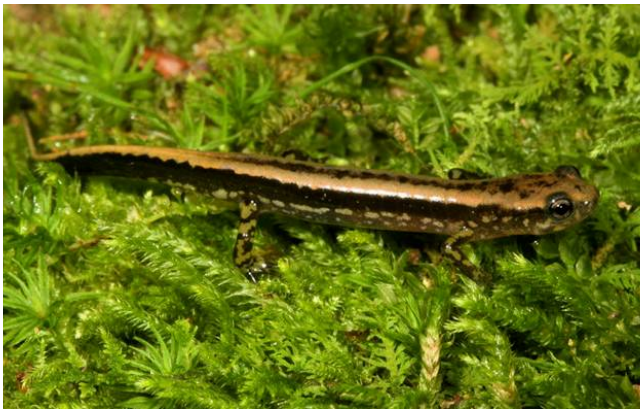

Figure 83. ***Eurycea guttolineata*** on a bed of mosses. Photo by Matthew Niemiller, with permission.

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.

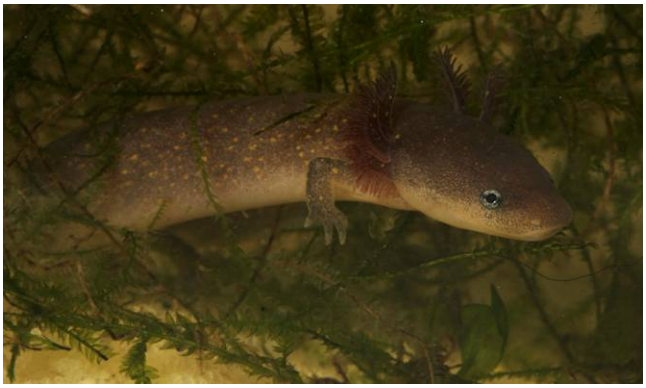

Figure 92. ***Necturus punctatus*** among mosses in water. Photo by Todd Pierson, with permission.

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.

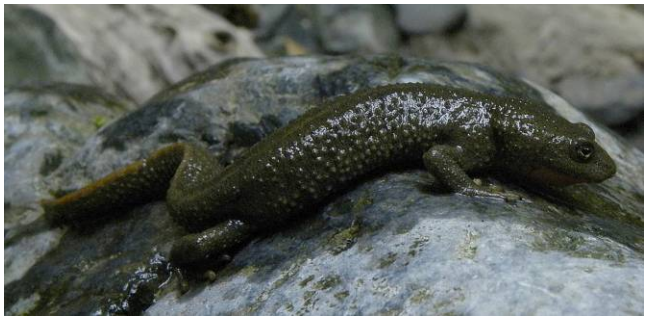

Figure 93. ***Calotriton asper*** that has been living among mosses in the Pyrenees. Photo by Michael Lüth, with permission.

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).

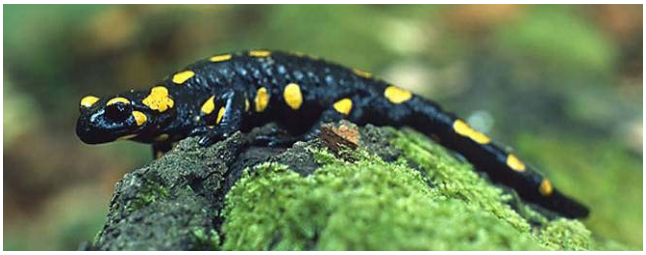

Figure 107. ***Salamandra salamandra*** on a mossy rock. Photo by Marek Szczepanek, through Wikimedia Commons.

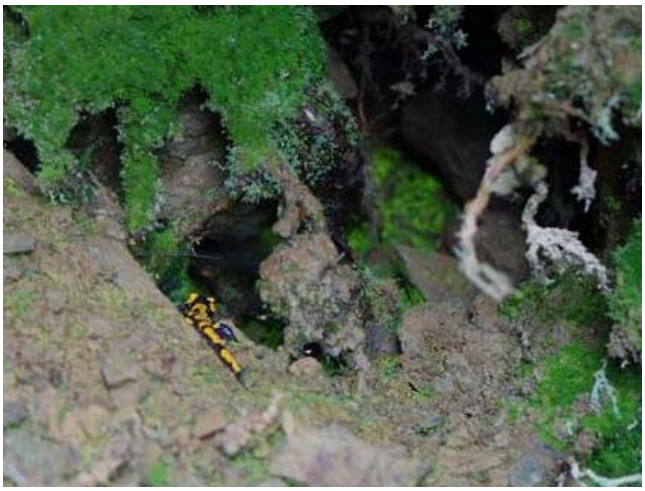

Figure 108. ***Salamandra salamandra*** on a wet day in the Harz National Park in central Germany. This colorful salamander is hiding in a minicave made by tree roots. The mosses are ***Schistostega pennata*** and ***Atrichum undulatum***. Photo by Katja Reichel, with permission.

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).

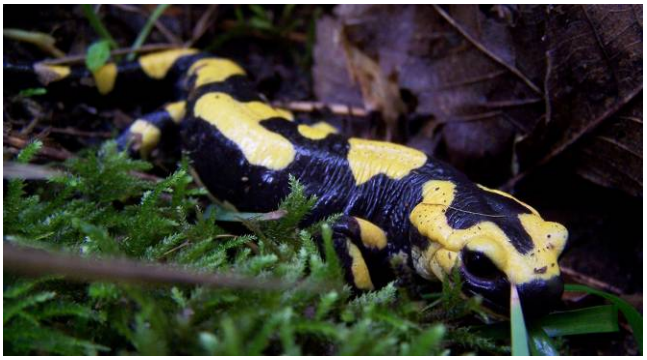

Figure 109. ***Salamandra salamandra*** on a bed of mosses, in plain view, advertising its warning coloration of black and yellow. Photo by Iocopo Buttini, through Creative Commons.

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.

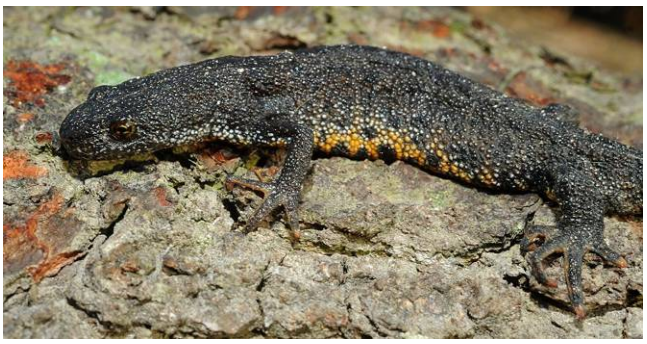

Figure 110. The **Great Crested Newt**, ***Triturus cristatus***. Photo by Milan Kořínek, with permission.

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.

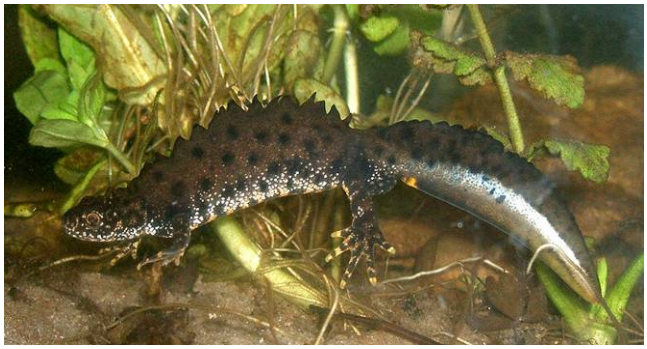

Figure 111. The **Great Crested Newt**, ***Triturus cristatus***. Photo from Wikimedia Commons.

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.

Acknowledgments

Most importantly, I thank herpetologists Edmund (Butch) Brodie for reading the salamander subchapters and offering his scientific comment and editorial advice. Herpetologists have been extremely helpful in answering my questions and providing images. David Wake helped me sort out the truth from a reference that overstated the role of poisons in salamanders, among other helpful comments. Sean Michael Rovito was helpful in providing images and anecdotal information about Guatemalan salamanders. Twan Leenders has been kind enough to provide me with original images. Eduardo Boza provided

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Literature Cited

Acevedo, M. and Wake, D. 2004. In: IUCN 2008. 2008 IUCN Red List of Threatened Species. IUCN RedList.org.

Altig, R. and McDiarmid, R. W. 2007. Morphological diversity and evolution of egg and clutch structure in amphibians. Herpetol. Monogr. 21: 1-32.

Amphibians: Tulula Wetlands. 2009. Accessed on 4 February 2009 at <http://orgs.unca.edu/tulula/amphibian.html>.

AmphibiaWeb. 2000. *Lissotriton boscai.* Accessed 1 April 2011 at <http://amphibiaweb.org/cgi/amphib_query?where-genus=Lissotriton&where-species=boscai>.

AmphibiaWeb. 2009a. Information on amphibian biology and conservation. Berkeley, California. Accessed on 7 February 2009 at <http://amphibiaweb.org/cgi-bin/amphib_query?query_src=aw_lists_genera_&table=amphib&where-genus=Rhyacotriton&where-species=cascadae>.

AmphibiaWeb. 2009b. Information on amphibian biology and conservation. *Triturus cristatus*. Great Crested Newt. Berkeley, California. Accessed on 6 February 2009 at <http://amphibiaweb.org/cgi-bin/amphib_query?where-genus=Triturus&where-species=cristatus>

AmphibiaWeb. 2009c. *Bolitoglossa marmorea*. Updated 11 March 2011. Accessed 1 April 2011 at <http://amphibiaweb.org/cgi/amphib_query?where-genus=Bolitoglossa&where-species=marmorea>.

AmphibiaWeb. 2009d. *Lissotriton vulgaris.* Accessed 1 April 2011 at <http://amphibiaweb.org/cgi-bin/amphib_query?query_src=aw_lists_genera_&table=amphib&where-genus=Lissotriton&where-species=vulgaris>.

AmphibiaWeb. 2010. Information on amphibian biology and conservation. Berkeley, California. Accessed 25 April 2010 at <http://amphibiaweb.org/>.

Anderson, J. D. 1968. *Rhyacotriton* and *R. olympicus*. Catalogue of American Amphibians and Reptiles 68.1-68.2.

Anderson, M. T. and Mathis, A. 1999. Diets of two sympatric neotropical salamanders, *Bolitoglossa mexicana* and *B. rufescens*, with notes on reproduction for *B. rufescens*. J. Herpetol. 33: 601-607.

Araujo, M. B. 1999. Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. Diversity Distrib. 5(4): 151-163.

Bahret, R. 1996. Ecology of lake dwelling *Eurycea bislineata* in the Shawangunk Mountains, New York. J. Herpetol. 30: 399-401.

Barrio, A. 1965. Cloricia fisiologica en batracios anuros. Physis 25: 137-142.

Bingham, B. B., and Sawyer, J. O. Jr. 1991. Distinctive features and definitions of young, mature, and old-growth Douglas-fir/hardwood forests. In: Ruggiero, L., Aubry, K., Carey, A., and Huff, M. (eds.). Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service Gen. Tech. Rpt. PNW-GTR-285, Pacific NW. Station, Portland, Oregon, pp. 362-377.

Boehme, W., Grossenbacher, K., and Thiesmeier, B. 1999. Handbuch der Reptilien und Amphibien Europas, band 4/I:Schwanzlurche (Urodela). Aula-Verlag, Wiesbaden.

Bolaños, F., Wake, D., and Savage, J. 2004. *Nototriton tapanti*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. Accessed 12 January 2012 at <www.iucnredlist.org>.

Bolaños, F., Wake, D., and Savage, J. 2008. *Nototriton tapanti*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. Accessed 21 March 2011 at <www.iucnredlist.org>.

Bragg, A. N. 1955. The Amphibia of Cherokee County, Oklahoma. Herpetologica 11: 25-30.

Brame, A. H. Jr. 1968. Systematics and evolution of the mesoAmerican salamander genus *Oedipina*. J. Herpetol 2: 1-64.

Brodie, E. D. Jr. 1968. Investigations on the skin toxin of the red-spotted newt, *Notophthalmus viridescens viridescens*. Amer. Midl. Nat. 80: 276-280.

Brodie, E. D. Jr. and Smatresk, N. J. 1990. The antipredator arsenal of fire salamanders: Spraying of secretions from highly pressurized dorsal skin glands. Herpetologica 46: 1-7.

Brodie, E. D. Jr., Ducey, P. K., and Lemos-Espinal, J. 1991. Antipredator behavior of the salamander *Bolitoglossa rufescens*: Effects of temperature and location of stimulus. J. Herpetol. 25: 99-101.

Brodie, E. D. Jr., Mendelson, J. R. III., and Campbell, J. A. 2002. Taxonomic revision of the Mexican plethodontid salamanders of the genus *Lineatriton*, with the description of two new species. Herpetologica 58: 194-204.

Bruce, R. C. 1998. Nesting habits, eggs, and hatchlings of the salamander *Nototriton picadoi* (Plethodontidae: Bolitoglossini). Herpetologica 54: 13-18.

Bruce, R. C. 1999. Life history attributes of a rare neotropical salamander, *Nototriton picadoi* (Plethodontidae: Bolitoglossini). Herpetol. Rev. 30: 76-78.

Bruce, R. C. 2003. Life Histories. In: Sever, D. M. (eds.). Reproductive Biology and Phylogeny of Urodela (Amphibia). Science Publishers, Inc., Enfield, New Hampshire, pp. 477-525.

Bury, R. B. 1988. Habitat relationships and ecological importance of amphibians and reptiles. In: Raedeke, K. (ed.). Streamside Management: Riparian Wildlife and Forestry Interactions. Institute of Forest Resources, Cont. No. 59. University of Washington, Seattle, pp. 61-76.

Bury, R. Bruce. 2011. AmphibiaWeb: *Batrachoseps wrighti*. Information on amphibian biology and conservation. [web application]. 2011. Berkeley, California: AmphibiaWeb. Accessed 21 March 2011 at <http://amphibiaweb.org/cgi/amphib_query?where-genus=Batrachoseps&where-species=wrighti&account=lannoo>.

Bury, R. B. and Corn, P. S. 1988. Responses of aquatic and streamside amphibians to timber harvest: A review. In: Raedeke, K. (ed.). Streamside Management: Riparian Wildlife and Forestry Interactions. Institute of Forest Resources, Cont. No. 59. University of Washington, Seattle, pp. 165-181.

Bury, R. B., Corn, P. S., Aubry, K. B., Gilbert, F. F., and Jones, L. C. 1991. Aquatic amphibian communities in Oregon and Washington. In: Ruggiero, L., Aubry, K., Carey, A., and Huff, M. (eds.).

Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service Gen. Tech. Rpt. PNW-GTR-285, Pacific NW Station, Portland, Oregon, pp. 362-377.

Buttenhoff, P. 1995. *Bolitoglossa rufescens* (Northern Banana Salamander) predation. Herpetol. Rev. 26: 197.

Campbell, J. A., Smith, E. N., Streicher, J., Acevedo, M. E., and Brodie, E. D. Jr. 2010. New salamanders (Caudata: Plethodontidae) from Guatemala, with miscellaneous notes on known species. Miscellaneous Publications, Museum of Zoology, University of Michigan. 200: 60 pp. <http://www.ummz.lsa.umich.edu/rep_amph/pdf/mp200_10-12-10.pdf>

Coniff, Richard. 2014. Salamander's Hefty Role in the Forest. New York Times 7 April 2014. Accessed 12 April 2014 at <http://www.nytimes.com/2014/04/08/science/salamanders-hefty-role-in-the-forest.html?_r=0#>.

Canterbury, R. A. 1991. Ecology of the green salamander, *Aneides aeneus* (Cope and Packard), in West Virginia. Master's thesis. Marshall University, Huntington, West Virginia.

Corn, P. S. and Bury, R. B. 1989. Logging in western Oregon: Responses of headwater habitats and stream amphibians. Forest Ecol. Mgmt. 29: 39-57.

Duellman, W. E. and Trueb, L. 1994. Biology of Amphibians. Johns Hopkins University Press, Baltimore, MD, p. 39.

Dundee, H. A. 1947. Notes on salamanders collected in Oklahoma. Copeia 1947: 117-120.

Edge. 2009. Amphibians: 53. Cerro de En Medio Moss Salamander (*Nototriton lignicola*). Accessed on 9 February 2009 at <http://www.edgeofexistence.org/amphibians/species_info.php?id=598>.

Elias, P. and Wake, D. 1983. *Nyctanolis pernix*, a new genus and species of plethodontid salamander from Northwestern Guatemala and Chiapas, Mexico. Rhodin, G. J. and Miyata, K. (eds.). Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. Museum of Comparative Zoology, Harvard, Cambridge.

Encyclopedia of Life. 2011. *Bolitoglossa hartwegi*. Accessed 4 September 2011 at <http://eol.org/pages/330812/overview>.

Flores-Villela, O. and Martínez-Salazar, E. A. 2009. Historical explanation of the origin of the herpetofauna of Mexico. Revista Mexicana de Biodiversidad 80: 817-833.

Frost, D. R. 2011. Amphibian Species of the World: An Online Reference. Version 5.5 (31 January 2011). Accessed 26 February 2011 at <http://research.amnh.org/vz/herpetology/amphibia/>. American Museum of Natural History, New York, USA.

García-París, M. and Wake, D. B. 2000. Molecular phylogenetic analysis of relationships of the tropical salamander genera *Oedipina* and *Nototriton*, with descriptions of a new genus and three new species. Copeia 2000: 42-70.

García-París, M., Good, D. A., Parra-Olea, G., and Wake, D. B. 2000a. Biodiversity of Costa Rican salamanders: Implications of high levels of genetic differentiation and phylogeographic structure for species formation. Proc. Natl. Acad. Sci. 97: 1640–1647.

García-París, M., Wake, D. B., and Price, A. H. 2000b. Molecular phylogenetic analysis of relationships of the tropical salamander genera *Oedipina* and *Nototriton*, with descriptions of a new genus and three new species. Copeia 2000: 42-70.

Good, A. and Wake, D. B. 1992. Geographic variation and speciation in the torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). Univ. California Publ. Zool. 126: 1-91.

Good, D. A. and Wake, D. B. 1993. Systematic studies of the Costa Rican moss salamander, genus *Nototriton*, with descriptions of three new species. Herpetol. Monogr. 7: 131-159.

Gordon, R. E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). Amer. Midl. Nat. 47: 666-701.

Goux, L. 1957. Contribution a l'etude ecologique, biologique et biogeographique de *Chioglossa lusitanica* Barb. (Urodela, Salamandridae). Bull. Soc. Zool. France 82: 361-377.

Guyer, C. and Donnelly, M. A. 2005. Amphibians and Reptiles of La Selva, Costa Rica and the Caribbean Slope: A Comprehensive Guide. University of California Press, Berkeley.

Hanken, J. 1983. Genetic variation in a dwarfed lineage, the Mexican Salamander genus *Thorius* (Amphibia: Plethodontidae): Taxonomic, ecologic and evolutionary implications. Copeia 1983: 1051-1073.

Hanken, J., Wake, D. B., and Savage, J. M. 2005. A solution to the large black salamander problem (genus *Bolitoglossa*) in Costa Rica and Panamá. Copeia 2005: 227-245.

Hassinger, D. D. 1970. Notes on the thermal properties of frog eggs. Herpetologica 26: 49-51.

HCT. 2009. The Great Crested Newt (*Triturus cristatus*). Accessed on 6 February 2009 at <http://www.herpconstrust.org.uk/animals/great_crested_newt.htm>.

Höbel, G. 2008. The amphibians and reptiles of the Golfo Dulce region. Stapfia 88, Neue Serie 80: 305-328. Available at <https://pantherfile.uwm.edu/hoebel/www/PDF/Hoebel2008_GolfoDulce_Survey.pdf>.

Houck, L. D. 1977. The reproductive biology of a neotropical salamander, *Bolitoglossa rostrata* (Urodela: Plethodontidae). Copeia 1977: 70-83.

Hunsinger, T. W. and Lannoo, M. J. 2011. AmphibiaWeb: *Notophthalmus viridescens*. Accessed 18 April 2011 at <http://amphibiaweb.org>.

Issartel, J., Voituron, Y., Guillaume, O., Clobert, J., and Hervant, F. 2010. Selection of physiological and metabolic adaptations to food deprivation in the Pyrenean newt *Calotriton asper* during cave colonisation. Compar. Biochem. Physiol. Part A: Molec. Integr. Physiol. 155: 77-83.

IUCN. 2010a. IUCN Red List of Threatened Species. Version 2010.1. Accessed 25 April 2010 at <www.iucnredlist.org>.

IUCN. 2010b. IUCN Red List of Threatened Species. Version 2010.4. Accessed 21 March 2011 at <www.iucnredlist.org>.

Jobson, H. G. M. 1940. Reptiles and amphibians from Georgetown County, South Carolina. Herpetologica 2: 39-43.

Jones, D. A. 1967. Green pigmentation in neotropical frogs. Ph.D. Dissertation, University of Florida, Gainesville, Florida, U.S.A.

Kinne, O. 2006. Successful re-introduction of the newts *Triturus cristatus* and *T. vulgaris.* Endang. Species Res. 1: 25-40.

Kirk, J. J. 1991. *Batrachoseps wrighti*. Catalogue of American Amphibians and Reptiles. Society for the Study of Amphibians and Reptiles, St. Louis. Missouri, pp. 506.1–506.3.

Kirk, J. J. and Forbes, R. B. 1991. Geographic distribution: *Batrachoseps wrighti* (Oregon Slender Salamander). Herpetol. Rev. 22: 22-23.

Köhler, G. 2002. A new species of salamander of the genus *Nototriton* from Nicaragua (Amphibia: Caudata: Plethodontidae). Herpetologica 58: 205-210.

Kubiki, Brian. 2011. Amphibian diversity in Guayacán, Limón Province, Costa Rica. Accessed 2 April 2011 at <http://www.amphibianark.org/Kevin/Amphibians-of-Guayacan.pdf>.

Kuzmin, S. L. 1999. AmphibiaWeb: *Salamandra salamandra*. Accessed 12 April 2011 at <http://amphibiaweb.org/cgi/amphib_query?where-genus=Salamandra&where-species=salamandra>.

Lannoo, M. (ed.). 2005. Amphibian Declines: The Conservation Status of United States Species. Regents of the University of California.

Lee, D. S. and Norden, A. W. 1973. A food study of the Green Salamander, *Aneides aeneus*. J. Herpetol. 7: 53-54.

Lee, J. C. 2000. A field Guide to the Amphibians and Reptiles of the Maya World: The Lowlands of Mexico, Northern Guatemala, and Belize. Cornell University Press, Ithaca, 402 pp.

Leenders, T. 2001. A Guide to Amphibians and Reptiles of Costa Rica. Zona Tropical, Miami.

Leenders, T. A. A. M. and Watkins-Colwell, G. J. 2003. Morphological and behavioral adaptations in *Bolitoglossa colonnea* (Caudata, Plethodontidae) in relation to habitat use and daily activity cycle. Phyllomedusa 2(2): 101-104.

Leonard, W. P., Brown, H. A., Jones, L. L. C., McAllister, K. R., and Storm, R. M. 1993. Amphibians of Washington and Oregon. Seattle Audubon Society, Seattle, Washington.

Lovelace, J. B. 2003. Environmental factors affecting the establishment, development, and growth of the epiphytic fern *Polypodium glycyrrhiza* in an old-growth redwood forest canopy. Thesis. Humboldt State University, Arcata, California, USA.

MacCracken, J. G. 2004. *Rhyacotriton cascadae* (Cascade torrent salamander) nest. Herpetol. Rev. 35: 367.

Manenti, R., Ficetola, G. F., Bernardi, F. De. 2009. Water, stream morphology and landscape: Complex habitat determinants for the fire salamander *Salamandra salamandra*. Amphibia-Reptilia 30: 7-15.

McCoy, C. J. 1990. Additions to the herpetofauna of Belize, Central America. Caribbean J. Sci. 26: 164-166.

McCranie, J. R. and Cruz, G. A. 1996. A new species of salamander of the *Bolitoglossa dunni* group (Caudata: Plethodontidae) from the Sierra de Agalta, Honduras. Caribbean J. Sci. 32: 195-200.

McCranie, J. R. and Wilson, L. D. 1992. Life history notes: *Nototriton barbouri*. Reproduction. Herpetol. Rev. 23: 115-116.

McCranie, J. R. and Wilson, L. D. 1995. A new species of salamander of the genus *Bolitoglossa* (Caudata: Plethodontidae) from Parque Nacional El Cusuco, Honduras. J. Herpetol. 29: 447-452.

McCranie, J. R., and Wilson, L. D. 2002. The Amphibians of Honduras. Contrib. Herpetol.19. Adler, K. and T. D. Perry, T. D. (eds.). Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Mebs, D. and Pogoda, W. 2005. Variability of alkaloids in the skin secretion of the European Fire Salamander (*Salamandra salamadra terrestris*). Toxicon 45: 603-606.

Meijden, A. van der. 1999. AmphibiaWeb: *Euproctus platycephalus*. Updated 25 May 2002. Accessed 28 March 2011 at <http://amphibiaweb.org/cgi/amphib_query?where-genus=Euproctus&where-species=platycephalus>.

Min, M. S., Yang, S. Y., Bonett, R. M., Vieites, D R., Brandon, R. A., and Wake, D. B. 2005. Discovery of the first Asian plethodontid salamander. Nature 435: 87-90.

Montori, A., Llorente, G. A., and Richter-Boix, À. 2008. Habitat features affecting the small-scale distribution and longitudinal migration patterns of Calotriton asper in a Pre-Pyrenean population. Amphibia-Reptilia 29: 371-381.

Müllner, A. 2001. Spatial patterns of migrating great crested newts and smooth newts: The importance of the terrestrial habitat surrounding the breeding pond. RANA, Sonderheft 4: 279-293.

National Geographic News. 29 January 2009. 3 new salamanders are "ballistic," bright, tiny. Accessed on 29 January 2009 at <http://news.nationalgeographic.com/news/2008/01/photogalleries/salamander-pictures/photo4.html>.

Neill, W. T. 1948. Hibernation of amphibians and reptiles in Richmond County, Georgia. Herpetologica 4: 107-114.

Nishikawa, K. 2009. The first specimen of *Karsenia koreana* (Caudata: Plethodontidae) collected 34 years before its descript. Current Herpetol. 28: 27-28.

Nöllert, A. and Nöllert, C. 1992. Die Amphibien Europas. Franckh-Kosmos Verlags-GmbH and Company, Stuttgart.

Nussbaum, R. A. and Tait, C. A. 1977. Aspects of the life history and ecology of the Olympic Salamander, *Rhyacotriton olympicus* (Gaige). Amer. Midl. Nat. 98: 176-199.

Nussbaum, R. A., Brodie, E. D., and Storm, R. M. 1983. Amphibians and Reptiles of the Pacific Northwest. Univ. Idaho Press, Moscow.

Oracle Thinkquest. 2000. Poisonous Plants and Animals. *Salamandra salamandra*. Accessed 31 March 2011 at <http://library.thinkquest.org/C007974/2_2sal.htm>.

Papenfuss, T. J. and Wake, D. B. 1987. Two new species of plethodontid salamanders (genus *Nototriton*) from Mexico. Acta Zool. Mex. 21: 1-16.

Parra-Olea, G., García-París, M., Hanke, J., and Wake, D. B. 2005. Two new species of *Pseudoeurycea* (Caudata: Plethodontidae) from the mountains of northern Oaxaca, Mexico. Copeia 2005: 461-469.

Peatlands. 2009. Accessed on 6 February 2009 at <http://www.peatlandsni.gov.uk/wildlife/amphibians/com_lizard.htm>.

Raffaëlli, J. 2011a. AmphibiaWeb: *Bolitoglossa rostrata*. Accessed 17 April 2011 at <http://amphibiaweb.org/>.

Raffaëlli, Jean. 2011b. Amphibia Web: *Cryptotriton alvarezdeltoroi*. Accessed 21 March at <http://amphibiaweb.org/cgi-bin/amphib_query?where-genus=Cryptotriton&where-species=alvarezdeltoroi>.

Ray, G. C. 1958. The vital limits and rates of desiccation in salamanders. Ecology 39: 75–83.

Richmond, N. D. 1945. Nesting of the Two-lined Salamander on the coastal plain. Copeia 1945: 170.

Robinson, D. C. 1976. A new dwarf salamander of the genus *Bolitoglossa* (Plethodontidae) from Costa Rica. Proc. Biol. Soc. Washington 89: 289-294.

Roe, A. W. and Grayson, K. L. 2008. Terrestrial movements and habitat use of juvenile and emigrating adult Eastern Red-Spotted Newts, *Notophthalmus viridescens.* J. Herpetol. 42: 22-30.

Rubin, D. 1969. Food habits of *Plethodon longicrus* Adler and Dennis. Herpetologica 25: 102-105.

Salamanders of Georgia and South Carolina. 2010. Accessed on 25 April 2010 at <http://www.uga.edu/srelherp/salamanders/eurgut.htm>.

Salthe, S. N. 1963. The egg capsules in the Amphibia. J. Morphol. 113: 161-171.

Sanders, R. 2005. Discovery of American salamander in Korea tells 100 million-year-old tale. U. C. Berkeley News 4 May

2005. Accessed 26 March 2011 at <http://berkeley.edu/news/media/releases/2005/05/04_korea.shtml>.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas. The University of Chicago Press, Chicago, IL, USA, 945 pp.

Sillett, S. C. 1995. Branch epiphytes assemblages in the forest interior and on the clearcut edge of a 700-year-old Douglas-fir canopy in western Oregon. Bryologist 98: 301-312.

Slater, J. R. 1933. Notes on Washington salamanders. Copeia 1933: 44.

Spickler, J. C., Sillett, S. C., Marks, S. B., and Welsh, H. H. Jr. 2006. Evidence of a new niche for a North American salamander: *Aneides vagrans* residing in the canopy of old-growth redwood forest. Herpetol. Conserv. Biol. 1: 16-27.

Stebbins, R. C. 1955. Southern occurrence of the Olympic Salamander *Rhyacotriton olympicus*. Herpetologica 11: 238-239.

Stebbins, R. C. 1985. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Company, Boston, Massachusetts.

Stein, K. F. 1938. Migration of *Triturus viridescens*. Copeia 1938: 86-88.

Stockwell, S. S. and Hunter, M. L. Jr. 1989. Relative abundance of herpetofauna among eight types of Maine peatland vegetation. J. Herpetol. 23: 409-414.

Storm, R. M. 1953. Range extension of the salamander *Batrachoseps wrighti*. Copeia 1953: 65-66.

Stuart, S., Hoffmann, M., Chanson, J., Cox, N., Berridge, R., Ramani, P., and Young, B. (eds.). 2008. Threatened Amphibians of the World. Lynx Edicions, IUCN, and Conservation International, Barcelona, Spain; Gland, Switzerland; and Arlington, Virginia, USA.

Taylor, E. R. 1954. Additions to the known herpetological fauna of Costa Rica with comments on other species. No. 1. Univ. Kans. Sci. Bull. 36: 597-639.

Tosi, J. 1969. Republica de Costa Rica. Mapa Ecologico. San José, Costa Rica.

Townsend, J. H., Nifong, J. C., and Downing, R. M. 2006. Oedipina elongata (Schmidt, 1936) in Honduras. Salamandra 42: 61-62.

UK Biodiversity Action Plan. 1995. Originally published as Biodiversity: The UK Steering Group Report - Volume II: Action Plans (December 1995, Tranche 1, Vol 2, p. 112). Accessed 6 February 2009 at <http://www.ukbap.org.uk/UKPlans.aspx?ID=619>.

Vial, J. L. 1968. The ecology of the tropical salamander, *Bolitoglossa subpalmata*, in Costa Rica. Rev. Biol. Trop. 15: 13-115.

Wake, D. B. 1987. Adaptive radiation of salamanders in Middle American cloud forests. Ann. Missouri Bot. Gard. 74: 242-264.

Wake, David B. 2005. AmphibiaWeb: *Karsenia koreana.* Last updated 9 November 2011. Berkeley, California: AmphibiaWeb. Accessed 26 March 2011 at <http://amphibiaweb.org/cgi/amphib_query?where-genus=Karsenia&where-species=koreana>.

Wake, D. B., Brame, A. H., and Duellman, W. E. 1973. New species of salamanders, genus *Bolitoglossa*, from Panama. Nat. Hist. Mus. Los Angeles Co. Contrib. Sci. 248: 1-19.

Wallace, H. W. and Wallace, B. M. N. 2000. Sex reversal of the newt *Triturus cristatus* reared at extreme temperatures. Internat. J. Devel. Biol. 44: 807-810.

Welsh, H. H. Jr. 1990. Relictual amphibians and old-growth forests. Conserv. Biol. 4: 309-319.

Welsh, H. H. Jr. and Lind, A. J. 1996. Habitat correlates of the Southern Torrent Salamander, *Rhyacotriton variegatus* (Caudata: Rhyacotritonidae), in northwestern California. J. Herpetol. 30: 385-398.

Whittaker, Kellie. 2010. Updated 25 December 2010. AmphibiaWeb: *Cryptotriton monzoni*. Accessed on 21 March 2011 at <http://amphibiaweb.org/cgi/amphib_query?where-genus=Cryptotriton&where-species=monzoni>.

Wikipedia. 2011a. *Bolitoglossa*. Updated 16 February 2011. Accessed 31 March 2011 at <http://en.wikipedia.org/wiki/Bolitoglossa>.

Wikipedia. 2011b. *Bolitoglossa marmorea*. Updated 18 March 2011. Accessed 1 April 2011 at <http://en.wikipedia.org/wiki/Bolitoglossa_marmorea>.

Wikipedia. 2011c. *Bolitoglossa subpalmata.* Updated 22 March 2011. Accessed 28 March 2011 at <http://en.wikipedia.org/wiki/Bolitoglossa_subpalmata>.

Wikipedia. 2011d. Fire Salamander. Last updated 23 March 2011. Accessed 26 March 2011 at <http://en.wikipedia.org/wiki/Fire_Salamander>.

Wikipedia. 2011e. Palmate Newt. Updated 7 January 2011. Accessed 19 April 2011 at <http://en.wikipedia.org/wiki/Palmate_Newt>.

Wikipedia. 2011f. *Pseudoeurycea rex.* Updated 22 March 2011. Accessed 29 May 2011 at <http://en.wikipedia.org/wiki/Pseudoeurycea_rex>.

Wikipedia. 2011g. *Thorius.* Updated 9 September 2011. Accessed 14 January 2012 at <http://en.wikipedia.org/wiki/Thorius>.

ZipcodeZoo.Com. 2008a. *Dendrotriton cuchumatanus.* Accessed on 8 February 2009 at <http://zipcodezoo.com/Animals/D/Dendrotriton_cuchumatanus/>.

ZipcodeZoo.Com. 2008b. *Nototriton barbouri.* Accessed on 8 February 2009 at <http://zipcodezoo.com/Animals/N/Nototriton_barbouri/>.

ZipcodeZoo. 2008c. *Nototriton richardi*. Accessed on 8 February 2009 at <http://zipcodezoo.com/Animals/N/Nototriton_richardi/>.

ZipcodeZoo. 2008d. *Nototriton saslaya*. Accessed on 29 January 2009 at <http://zipcodezoo.com/Animals/N/Nototriton_saslaya/>.