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CHAPTER 14-7
HYNOBIIDAE, AMBYSTOMATIDAE, AND PLETHODONTIDAE

Janice M. Glime and William J. Boelema

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

Hynobiidae

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

Hynobius tokyoensis (Tokyo Salamander)

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

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

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

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

Salamandrella keyserlingii (Siberian Salamander, Hynobiidae)

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

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

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

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

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

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

Ambystomatidae (Mole Salamanders)

Ambystoma laterale (Blue-spotted Salamander)

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

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

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

Ambystoma maculatum (Spotted Salamander)

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

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

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

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

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

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

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

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

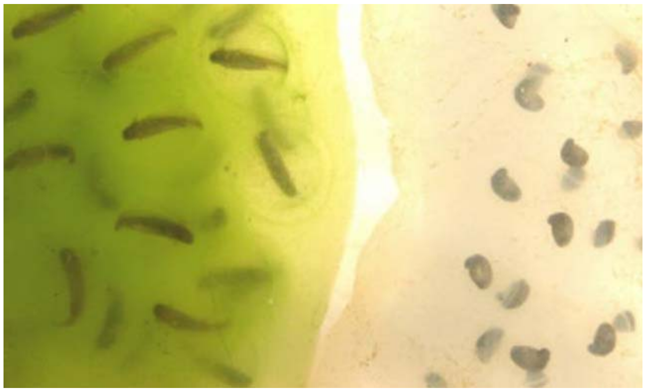

Figure 10. Comparison of embryos of ***Ambystoma maculatum*** that have symbiotic algae, ***Oophila amblystomatis***, on the **left** and no symbionts on the **right**. Photo by Renn Tumlison, with permission.

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

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

Ambystoma jeffersonianum (Jefferson Salamander)

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

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

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

Plethodontidae (Lungless Salamanders)

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

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

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

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

Plethodon serratus (Southern Red-backed Salamander)

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

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

Plethodon nettingi (Cheat Mountain Salamander)

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

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

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

Plethodon cinereus (Eastern Red-backed Salamander, Plethodontidae)

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

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

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

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

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

Plethodon dorsalis (Northern Zigzag Salamander)

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

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

Plethodon welleri (Weller's Salamander)

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

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

Plethodon elongatus (Del Norte Salamander)

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

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

Plethodon idahoensis (Coeur d'Alene Salamander)

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

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

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

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

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

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

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

Plethodon vandykei complex (Van Dyke's Salamander)

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

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

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

Plethodon larselli (Larch Mountain Salamander)

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

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

Plethodon glutinosus (Northern Slimy Salamander)

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

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

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

Plethodon richmondi (Southern Ravine Salamander)

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

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

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

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

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

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

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

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

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

Plethodon shermani (Red-legged Salamander)

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

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

Plethodon stormi (Siskiyou Mountains Salamander)

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

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

Plethodon asupak (Scott Bar Salamander)

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

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

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

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

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

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

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

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

Pseudotriton ruber (Red Salamander)

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

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

Hemidactylium scutatum (Four-toed Salamander)

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

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

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

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

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

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

Habitat Characteristics

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

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

Mating

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

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

Nest Sites

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Stereochilus marginatus (Many-lined Salamander, Plethodontidae)

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

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

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

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

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

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

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

Desmognathus fuscus (Northern Dusky Salamander)

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

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

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

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

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

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

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

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

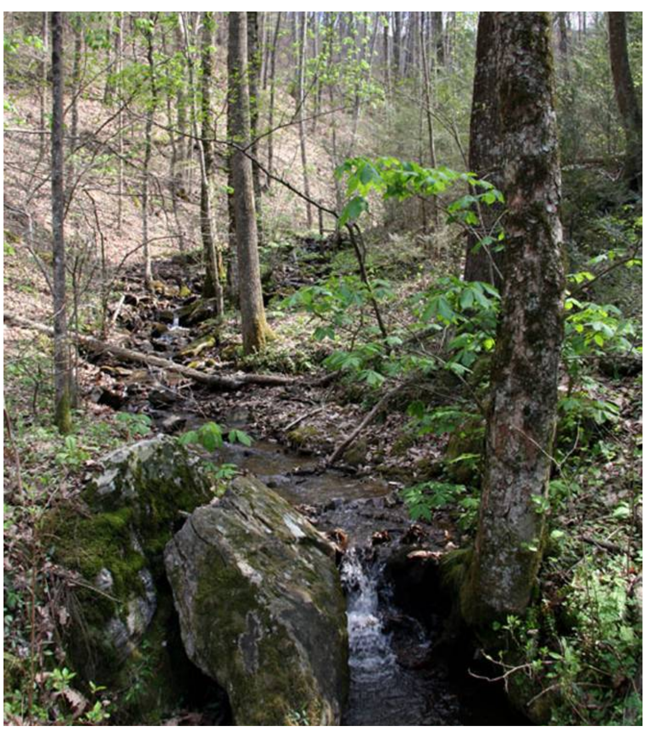

Figure 48. Habitat of ***Desmognathus fuscus***, Lumpkin County, Georgia, USA. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

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

Desmognathus ochrophaeus (Allegheny Mountain Dusky Salamander, Plethodontidae)

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

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

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

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

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

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

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

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

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

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

Desmognathus monticola (Seal Salamander)

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

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

Desmognathus santeetlah (Santeetlah Dusky Salamander, Plethodontidae)

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

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

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

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

Desmognathus aeneus (Seepage Salamander)

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

The 11-14 eggs of ***D. aeneus*** are deposited under mosses, as well as under logs, leaf litter, and mats of roots in seepage or wet areas near streams (Figure 56) (Bishop & Valentine 1950; Valentine 1963; Harrison 1967; Jones 1981; Collazo & Marks 1994). Females remain with the eggs during incubation (Brown & Bishop 1948; Bishop & Valentine 1950). Although this species is not considered a climber, Wilson (1984) observed them jumping from branch to branch in bushes and climbing up grasses. They feed mostly on insects, but their diet also includes nematodes, earthworms, land snails, isopods, amphipods, centipedes, arachnids, and millipedes, all items that can be found among mosses as well as leaf litter (Folkerts 1968; Donovan & Folkerts 1972; Jones 1981).

Figure 55. **Seepage Salamander**, ***Desmognathus aeneus*** on ***Atrichum***. Photo by Todd Pierson, with permission.

Figure 56. Habitat of the **Seepage Salamander** ***Desmognathus aeneus*** in Georgia, USA. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Desmognathus wrighti (Pygmy Salamander)

Known as the **Pigmy Salamander** (Figure 57), this small species occurs in woodland areas, especially above 1400 m asl within the southern Appalachians, including the Great Smoky Mountains of North Carolina and Tennessee, the Plott Balsam Mountains and Great Balsam Mountains of North Carolina, USA; it is also common between 950 m and 1400 m asl within the Cowee Mountains, Nantahala Mountains, and Unicoi Mountains of North Carolina, USA.

In the southern Nantahala Mountains, North Carolina, USA, ***Desmognathus aeneus*** (**Seepage Salamander**; Figure 55) and ***D. wrighti*** (**Pygmy Salamander**; Figure 57-Figure 58) are **sympatric** (ranges overlap) in high elevations (Hining & Bruce 2005). Both occupy clumps of moss, damp leaf litter, or shelter under stones or logs near streams and seepages in the deciduous forest during the spring (Figure 56). ***Desmognathus wrighti*** not only occupies wet areas, but can also be found up to two meters high in a tree on its leaves (Hairston, 1949; Organ, 1961). The two species manage to remain distinct by having different oviposition times, early May for ***D. aeneus*** and early August for ***D. wrighti*** (Harrison 2009).

Figure 57. **Pygmy Salamander**, ***Desmognathus wrighti***. Photo by Michael Graziano, with permission.

Richard Bruce (pers. comm. 10 August 2019; Bruce 2019) describes his experience with the Pygmy Salamanders: "I find the salamanders under moss cushions (especially ***Thuidium delicatulum***; Figure 58) on the soil but also in the mosses among the rhizoids, stems, and leaves. I find them in loosely organized mosses with a lot

of internal space, as opposed to more compact mosses. But the salamanders also occur in leaf litter and under logs. Of the 3 miniaturized species of ***Desmognathus***, ***D. aeneus*** seems to have the greatest affinity for moss, but the other two also occur frequently in mosses. Mosses provide shelter and moisture, but also an abundance of food, especially oribatid mites, as well as other mites, springtails, and other tiny arthropods. A recent paper by Bruckner *et al*. (1918), based on research in a German forest, reported that oribatids were more abundant in moss than in either leaf litter or dead wood. Pore size (spaces within the moss clump) can be an important factor in mobility as well as moisture retention.

Figure 58. ***Desmognathus wrighti*** that lives within the mats of ***Thuidium delicatulum*** and ***Atrichum*** sp. seen here. Photo courtesy of Richard Bruce.

Desmognathus quadramaculatus (Black-bellied Salamander)

From Monroe County, West Virginia eastward to Henry County, Virginia, and southward through eastern Tennessee, western North and South Carolina to northeastern Georgia, in the Appalachian Mountains, USA. Peatlands are good habitats for salamanders, and ***Desmognathus*** is certainly represented there. In the ***Sphagnum*** habitat of the Tulula Wetland, North Carolina, USA, one can find ***Desmognathus quadramaculatus*** (**Black-bellied Salamander**; Figure 59), typically in streams (Amphibians: Tulula Wetlands 2009). In North Carolina, it is known from among mosses in streams (LeGrand *et al*. 2001).

This species has a somewhat longer development time than some of the other ***Desmognathus*** species, requiring six years in males and seven in females to reach first reproduction in the southern Blue Ridge Mountains (Bruce 1988).

Beachy (1997) reported that ***D. quadramaculatus*** co-occurred with the salamander ***Eurycea wilderae***, another bryophyte dweller. Unfortunately for ***E. wilderae***, it provides dinner for ***D. quadramaculatus***. Larval growth rates of ***E. wilderae*** differed with different predator densities, but survivorship did not differ, suggesting that provided no advantage in the low productivity of Appalachian streams.

Figure 59. ***Desmognathus quadramaculatus*** (**Black-bellied Salamander**). Photo by Bill Peterman.

Desmognathus ocoee (Ocoee Salamander)

The **Ocoee Salamander** (Figure 60) occurs in two **allopatric** (non-overlapping) units, one in the Appalachian Plateau of northeastern Alabama and adjacent Tennessee, and the other in the southwestern Blue Ridge Physiographic Province of western North Carolina, eastern Tennessee, extreme western South Carolina, and northern Georgia, south of the Pigeon River (Balsam, Blue Ridge, Cowee, Great Smoky, Nantahala, Snowbird, Tusquitee, and Unicoi Mountains), USA (Frost 2011).

Along with ***D. quadramaculatus***, one can find ***D. ocoee*** in the ***Sphagnum*** habitat of the Tulula Wetland, North Carolina, USA (Amphibians: Tulula Wetlands 2009), where their typical habitat is streams. Petranka *et al*. (1993) estimated that timber-harvesting rates of the 1980's and early 1990's caused an annual loss of at least 14 million salamanders of all species in western North Carolina, increasing the importance of peatland refugia.

Typical predators on ***D. ocoee*** include beetles, but Hess and Harris (2000) showed that pond beetles did not eat their eggs. However, beetles from a stream punctured and consumed a large number of ***D. ocoee*** eggs.

Figure 60. ***Desmognathus ocoee*** (**Ocoee Salamander**). Photo by John D. Willson, with permission.

In Macon County, North Carolina, eggs were mostly in nests embedded in mosses growing on rocks on the stream

bank or in the stream (Hess & Harris 2000). Bruce (1996) likewise found that most of the eggs of this species were located under moss on logs, soil, or rocks at the edges of streams, where females care for the eggs.

Phaeognathus hubrichti (Red Hills Salamander)

The **Red Hills Salamanders** (Figure 61) occur in the wooded Alabama Coastal Plain, southern edge of the Red Hills region, USA (Frost 2011). They generally stay in burrows where the humidity is high (Dodd 2011), but when they leave the burrows to forage they can encounter mosses in their habitat and may use them as foraging sites. Their diet of mostly land snails, ants, beetles, and spiders are all likely moss dwellers and perhaps account for the mosses found in some fecal pellets (Gunzburger 1999).

Figure 61. ***Phaeognathus hubrichti***. Photo by John P. Clare, through Creative Commons.

Ensatina eschscholtzii (Monterey Ensatina)

When I was teaching species concepts, this was always one of my favorite examples. Armed with a film loop that showed the morphs and their habitats, I could introduce the difficulty in defining species in any practical way. At that time, several species were recognized, as suggested by breeding incompatibility between some populations, but now they are listed by Frost (2011) as a single species, ***Ensatina eschscholtzii*** (Figure 62), and, like Christopher (2005), Frost treats them as seven distinct subspecies.

The distribution of this superspecies is in Southwestern British Columbia and Vancouver Island, Canada, south through mesic Washington, Oregon, and California, USA, to northern Baja California, Mexico, in the Sierra San Pedro Martír and Sierra Juárez. Its distribution around the mountain range in western USA led to its designation as a **Rassenkreis**, a circle of races (Figure 70).

Hence, current thinking is that there is only one species within the genus. The subspecies are distributed up the Pacific coast of the USA, across the northern Central Valley, and south through the Sierras. The coastal and Sierran subspecies meet in the mountains of southern California and they behave as separate species. Nevertheless, although some of these subspecies look quite different in the pictures that follow, adjacent salamanders recognize each other and can hybridize. For example, ***Ensatina eschscholtzii eschscholtzii*** hybridizes with ***E. e. xanthoptica*** and ***E. e. klauberi***.

Figure 71 demonstrates the habitat of ***Ensatina eschscholtzii oregonensis***. The recognized variants of ***Ensatina eschscholtzii***, not including hybrids, are:

Ensatina eschscholtzii eschscholtzii (Figure 62)
Ensatina eschscholtzii klauberi (Figure 64)
Ensatina eschscholtzii xanthoptica (Figure 63)
Ensatina eschscholtzii picta (Figure 65)
Ensatina eschscholtzii oregonensis (Figure 66-Figure 67)
Ensatina eschscholtzii platensis (Figure 68)
Ensatina eschscholtzii croceater (Figure 69)

Figure 62. ***Ensatina eschscholtzii eschscholtzii***. Photo by William Flaxington, with permission.

Figure 63. ***Ensatina eschscholtzii xanthoptica*** on moss. Photo by William Leonard, with permission.

Figure 64. ***Ensatina eschscholtzii klauberi***. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 65. ***Ensatina eschscholtzii picta.*** Photo by William Flaxington, with permission.

Figure 66. ***Ensatina eschscholtzii oregonensis.*** Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 67. ***Ensatina eschscholtzii oregonensis*** amid mosses. Photo by Henk Wallays, through Creative Commons.

Figure 68. ***Ensatina eschscholtzii platensis.*** Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 69. ***Ensatina eschscholtzii croceator.*** Photo © Gary Nafis at CaliforniaHerps.com, with permission.

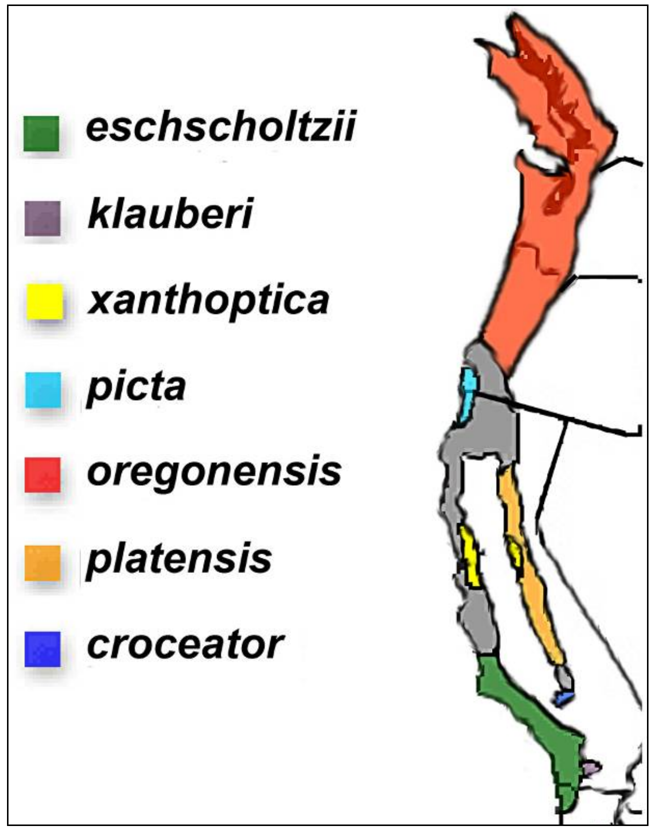

Figure 70. *Rassenkreis* of subspecies of ***Ensatina eschscholtzii.*** Redrawn from Gary Nafis, © Gary Nafis at CaliforniaHerps.com, with permission.

Figure 71. ***Ensatina eschscholtzii oregonensis*** habitat. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Gnaedinger and Reed (1948) pointed out that the importance of the moss habitat for ***Ensatina eschscholtzii*** had apparently been overlooked. At that time, several species were recognized, and when we combine them we need to recognize that the former species did not all have the same habitat, hence requiring caution in applying species habitat descriptions. Gnaedinger and Reed reported the salamander to occur between the moss and the ground, easily visible when the moss was removed. Such moss cover was found in 31.5% of their observations, exceeded only by the grouping of leaves, grass, and twigs. Relative numbers of those individuals found under mosses were 52.4% young, 16.7% juvenile, and 13.6% adults. This suggests that eggs may be laid on or in moss patches. The mosses may have been important in temperature regulation. The young were active under mosses at 1.2°C when the air temperature was -3.3°C, suggesting an insulating effect. The ground where salamanders were located was not frozen, apparently due to the protective cover of mosses. Unprotected soil, leaf litter, and surface of the mosses were frozen to a depth of about 1 cm and almost to the depth where the salamanders were active.

Hydromantes brunus (Limestone Salamander)

This species is known only from the area along the Merced River and North Fork Merced River, Mariposa County, California, USA, at 300-760 m asl (Frost 2011). The type was found under a moss-covered rock in Mariposa County, California, USA (Gorman 1954).

Hydromantes shastae (Shasta Salamander)

This species (Figure 72) is an endemic to the limestone substrates south of Mount Shasta near the Shasta Reservoir, Shasta County, California, USA at 300-910 m asl (Frost 2011). The type specimen was found under a small mossy log at a cave entrance (Gorman & Camp 1953). Eggs are terrestrial and have only been found in caves.

Road construction, quarrying, and changes in water levels cause this species to be vulnerable (IUCN 2010).

Figure 72. ***Hydromantes shastae*** on mosses. Photo by Henk Wallays, through Creative Commons.

Hydromantes ambrosii

Andreas Nöllert kindly sent me images of two subspecies of this salamander from mossy habitats. He found both in northwestern Italy. ***Hydromantes ambrosii ambrosii*** was living on a mossy cliff and ***H. a. blanchii*** was living in a mossy forest.

Figure 73. ***Hydromantes ambrosii ambrosii***, a cliff dweller. Photo by Andreas Nöllert, with permission.

Figure 74. ***Hydromantes ambrosii ambrosii*** habitat in NW Italy. Photo by Andreas Nöllert, with permission.

Figure 75. ***Hydromantes ambrosii blanchii***. Photo by Andreas Nöllert, with permission.

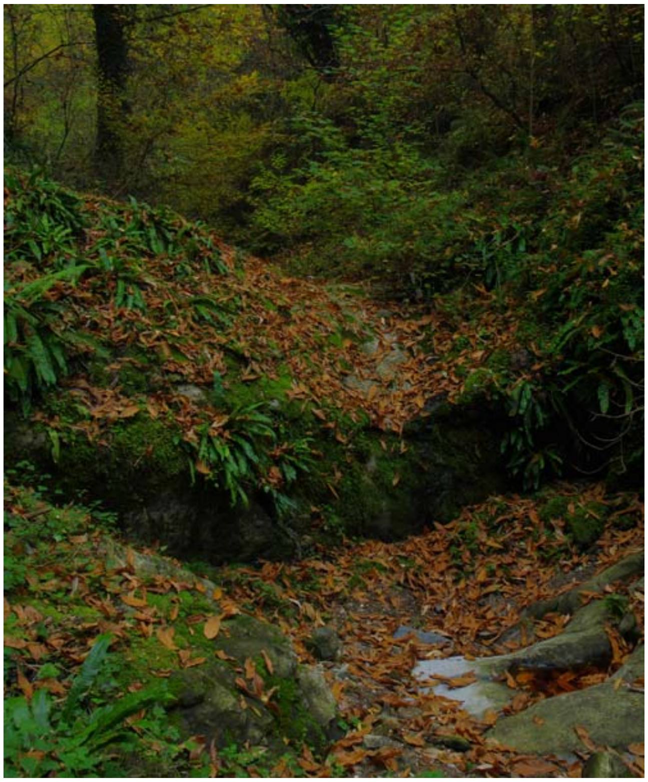

Figure 76. ***Hydromantes ambrosii bianchii*** habitat in Italy. Photo by Andreas Nöllert, with permission.

Summary

The Hynobiidae is a small family in Asia and Europe, with ***Hynobius tokyoensis*** migrating to the forest floor where mosses are among its hiding places. ***Salamandrella keyserlingii*** is also Asian and European and is one of the most cold-tolerant species of salamanders, spending winter in moss **hibernacula** and even surviving freezing in the permafrost for many years.

The Ambystomatidae extend from southern Canada to Mexico, living under mosses, among other forest floor habitats. Some species (*e.g.* ***Ambystoma maculatum***) are common in peatlands. This species provides oxygen to its jelly-coated eggs by partnering them with the green alga ***Oophila amblystomatis***.

In the Western Hemisphere, the Plethodontidae, including the large genus ***Plethodon***, is a large family of temperate zone salamanders. Many of these are bryophyte dwellers. The **Cheat Mountain Salamander** (***Plethodon nettingi***) is usually associated with the leafy liverwort ***Bazzania trilobata***, a rare example of a salamander associated with a specific bryophyte other than the genus ***Sphagnum***. ***Plethodon cinereus*** often lives in ***Sphagnum*** peat, where it attempts to rob the pitcher plant leaves of the invertebrates living there. But it can also live under forest floor mosses such as ***Leucobryum glaucum***. ***Desmognathus*** is found with mosses both in peatlands and in old-growth forests.

Peatlands are especially important for some species, such as members of ***Plethodon*** and ***Ambystoma***. Nevertheless, ***Sphagnum*** and associated ponds are typically too acid for most salamanders. ***Hemidactylium scutatum*** (**Four-toed Salamander**) apparently uses ***Sphagnum***. The **Four-toed Salamander** is the best known of the bryophyte dwellers, depositing its eggs under a variety of bryophytes, especially ***Thuidium*** and ***Sphagnum***. Mosses appear to be critical in its habitat, and loss of wetlands is a threat to its existence.

Stereochilus marginatus lays its eggs underwater on the moss ***Fontinalis***. ***Desmognathus fuscus*** lays eggs in the moist soil of stream banks, under mosses; a number of ***Desmognathus*** species use mosses for egg-laying sites.

Ensatina eschscholtzii subspecies form a **Rassenkreis** in California, USA, and mosses are often an important niche, where they can be found on the soil surface just under the moss.

Unknown species like ***Hydromantes brunus*** are likely to be living among mosses, invisible to the collector.

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