

CHAPTER 12-3 TERRESTRIAL INSECTS: HEMIMETABOLA – ODONATA

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CHAPTER 12-3

TERRESTRIAL INSECTS: HEMIMETABOLA – ODONATA



Figure 1. *Uropetala chiltoni* naiad emerging from burrow hidden among leafy liverworts. Photo by Rod Morris, with permission.

ODONATA – DRAGONFLIES AND DAMSELFLIES

Most of the **Odonata** are discussed in Chapter 11-5 with the aquatic insects, but some are terrestrial even as naiads and are appropriately discussed here. The **Odonata** are **hemimetabolous**. That is, they have an incomplete life cycle, one in which the immature animal resembles the adult and has no **larval** or **pupal** stage. Rather, the **naiad** (Figure 2), or **nymph**, develops directly into the adult. Naiads are the aquatic nymphs and thus the term doesn't apply in the strict sense to the terrestrial species. The large eyes (Figure 3) and scoop mouth enable these to be formidable carnivores. The odonate wings develop within the wingpads of the nymphs/naiads and expand when the last nymphal skin is shed. These adults must climb upward and pump fluids into the wing veins to expand them. They are vulnerable at this time because they are not yet ready to fly. Refer to Chapter 11-5 for more detailed discussion of this order of insects.



Figure 2. *Aeshna interrupta* naiad, a species whose naiads are not tolerant to drying. Photo by Donald S. Chandler <www.discoverlife.org>, with permission.



Figure 3. *Sympetrum striolatum* head showing large eyes. Photo by Anki Engström <www.krypinauren.se>, with permission.

Both dragonflies (**Anisoptera**) and damselflies (**Zygoptera**) have members that spend their nymphal life among bryophytes on land. These habitats provide cover and help the **Odonata** retain moisture. Others deposit eggs among mosses near water bodies where it is easy for nymphs to reach water through flooding, crawling, and/or dropping into the water.

Biology

The **Odonata** are voracious carnivores and are preyed upon as naiads primarily by fish in their aquatic habitat. On land, this larger predator is absent and birds and amphibians are the most likely predators for both nymphs and adults. But their larger danger as nymphs on land is drying out. Hence, enter the bryophytes.

Paulson and Buden (2003) collected **Odonata** on the Eastern Caroline Islands of Micronesia, bagging 448 specimens. These comprised 15 species, six of which were damselflies in the genus *Teinobasis* (**Coenagrionidae**), a genus with known bryophyte dwellers. *Teinobasis ponapensis* (see Figure 4) was taken only in areas with moss and fern cover, suggesting that even adults can find some advantage in association with bryophytes. On that island they found that body size increases with an increase in altitude.



Figure 4. *Teinobasis sjupp* adult. *Teinobasis ponapensis* is a species whose adults live only in areas with mosses and ferns. Photo by V. J. Kalkman, through Creative Commons.

Terrestrial Naiads

Terrestrial nymphs are known for some families of **Odonata**, and moist forests, especially montane rainforests, seem especially suited for the moisture needs of this

"aquatic" insect. Oppel (2005) reported on the **Odonata** of Papua New Guinea, where its 61 species were predominately among the **Zygoptera** (damselflies). Most were associated with moving or standing water, but one group was associated with temporary water sources or forest sites with high non-seasonal rainfall and high humidity. No **Anisoptera** (dragonflies) were among these terrestrial associations. Surprisingly to me, there was a negative correlation between the **Odonata** and mosses among this group.

Nevertheless, bryophytes can play an important role for some species. In Australia, the nymphs of *Pseudocordulia* (**Corduliidae** or **Pseudocorduliidae** – dragonflies) occur among leaf litter in the rain forests and moss forests of northern Queensland far from water (Watson 1982). Thus it should be no surprise to find **Odonata** nymphs among mosses as well, and many records of **Odonata** in litter may include mosses – soil biologists typically include mosses as part of the litter layer. *Austropetalia patricia* and *A. tonyana* (Figure 5-Figure 6) (**Austropetaliidae** – dragonflies) nymphs live on logs or among mosses in waterfalls and on streambanks (Theischinger & Hawking 2006). These alpine species are often rare due to limited habitat.



Figure 5. *Austropetalia tonyana* adult, a species whose nymphs can live among terrestrial mosses. Photo by Reiner Richter, with permission.



Figure 6. *Austropetalia tonyana* habitat where nymphs live above water among mosses. Photo by Reiner Richter, with permission.

Some **Odonata** use water-filled tree holes for their naiads. It is interesting that the rare damselfly naiads of *Podopteryx selysi* (**Megapodagrionidae** – damselflies; Figure 7) occur in such tree holes in the rainforest of north Queensland, Australia, but Watson and Dyce (1978) surmise that this species must lay its eggs on moss-covered stones or bushes. They apparently base this on finding the adults clinging to shrubs along paths and to the use of mosses for egg laying by other rainforest **Odonata**.



Figure 7. *Podopteryx selysi* adult, a species that may lay its eggs among mosses near tree holes in the rainforest. Photo by Reiner Richter, with permission.

In the Northern Sierra Madre Natural Park, Philippines, *Risicnemis elegans* (**Cordulegasteridae** – dragonflies; Figure 8) nymphs occur in shaded seepages and on the moist forest floor several meters from water (Villanueva *et al.* 2009). In these locations, the females lay eggs on moist mosses.



Figure 8. *Risicnemis cf. elegans*, a species that lays its eggs on moist mosses. Photo through Project Noah, with permission.

The genus *Gomphomacromia* (**Corduliidae** – dragonflies) also has at least semi-terrestrial nymphs. Von Ellenrieder and Garrison (2005) found nymphs under stones about 3 m from a moist, rocky area in Chile. Louten *et al.* (1996) found *G. cf. fallax* (Figure 9) on a moist, moss-covered slope along a dirt trail in Pakitza, Peru. That Beckemeyer (2002) found *Gomphomacromia fallax* laying eggs in dripping mosses on a cliffside suggests that nymphs of this species live there as well.



Figure 9. *Gomphomacromia cf. fallax* adult, a species that sometimes lays eggs in dripping mosses. Photo by Roy J. Beckemeyer, with permission.

Bryophytes can be a refuge for aquatic **Odonata** naiads when their habitat dries up. Willey and Eiler (1972) observed this in *Somatochlora semicircularis* (**Corduliidae**; Figure 10) from subalpine pools in Colorado, USA. When their pond dried up, they could be found under rocks, in moss mats, under logs, and at the bases of sedge clumps. This species dries more slowly than the dragonflies *Aeshna interrupta interna* (Figure 2, Figure 11) and *Libellula quadrimaculata* (Figure 12). It takes *S. semicircularis* twice as long to reach the same lethal state of dryness as that experienced by these two less tolerant species. This advantage seems to be incurred by a lower transpiration rate, and further protection is afforded by the early formation of snow pack over the dry pond. The mosses and other substrata are sufficient to protect the naiads from drought until the snow arrives.



Figure 10. *Somatochlora semicircularis* adult; this species has naiads that use wet mosses when its pond dries up. Photo by Belinda Lo through Creative Commons.



Figure 11. *Aeshna interrupta* adult. Photo by Kam's World, through Creative Commons.



Figure 12. *Libellula quadrimaculata* adult, a species with poor desiccation tolerance as a naiad. Photo by Böhringer Friedrich, through Creative Commons.

Donnelly (1990) found damselfly naiads of the dominant Fijian genus *Nesobasis* (Coenagrionidae; Figure 13) near a stream, crawling over wet mosses. As Donnelly cautiously pointed out, these may not be truly terrestrial. Rather, normally aquatic insects often climb above the water level in search of food, or perhaps to avoid excessive flow – or just because they can. In other cases, receding water levels after a rainstorm may leave them above the water surface. There is sufficient moisture for them to maintain hydration until they return to the water. But naiads must leave the water to shed their naiadal skin and emerge as adults, perhaps also explaining this above-water observation.



Figure 13. *Nesobasis* sp., a species whose naiads are known to crawl over wet mosses occasionally. Photo through Creative Commons.

Mosses may aid in the selection of burrowing sites of terrestrial dragonflies. Rod Morris (2010) shows the giant mountain dragonfly (*Uropetala chiltoni*; Figure 1, Figure 14) nymph poking its head out of its burrow in the soil and into a bed of mosses in a small wetland in New Zealand.



Figure 14. *Uropetala chiltoni* nymph emerging from burrow to a bed of mosses. Photo by Rod Morris, with permission.

Emergence

Terrestrial bryophytes can serve as emergence sites where the naiads shed their exoskeleton, leaving it behind as an **exuvia** (Figure 15-Figure 16), to become adults (Needham *et al.* 1901). These researchers found layers of shed exuviae of both *Gomphus exilis* (Figure 17) and *G. spicatus* (Gomphidae – dragonflies; Figure 18-Figure 19) among the mosses on logs at the edge of a pond. Similarly, *Somatochlora elongata* (Corduliidae – dragonflies; Figure 20; see also Figure 21-Figure 22) left exuviae on mosses at the edge of a pond. Soriano and Gutiérrez (1998) found the exuviae of *Oplonaeschna magna* (Aeshnidae – dragonflies; see Figure 23-Figure 24), a new species at the time, clinging to mosses on the vertical rock walls of a canyon in Mexico. These exuviae were 0.80-1.25 m above the water, reaching as much as 3 m on tree trunks and shrubs. Bryophytes are easy to climb, provide moisture, and permit at times a refuge or limited camouflage.



Figure 15. *Lestes* sp. emerging on a reed, leaving behind its shed **exuvia**. Photo by Richard Orr, with permission.



Figure 16. *Tetragoneuria cynosura* emerging. Photo by Richard Orr, with permission.



Figure 17. *Gomphus exilis* adult, a species that uses mosses as emergence sites. Photo by Richard Orr, with permission.



Figure 18. *Gomphus spicatus* naiad, a species known to emerge among mosses on logs near water. Photo by Donald S. Chandler, with permission.



Figure 19. *Gomphus spicatus* male adult. Photo by Richard Orr, with permission.



Figure 20. *Somatochlora elongata* male, a species that emerges on mosses. Photo by Denis A. Doucet, with permission.



Figure 21. *Somatochlora tenebrosa* exuvia, shed here on a moss-covered surface. Photo by Richard Orr, with permission.



Figure 22. *Somatochlora tenebrosa* male adult. Photo by Richard Orr, with permission.



Figure 23. *Oplonaeschna armata* adult, a species that uses mosses for emergence. Photo by Jerry Oldenettel, through Creative Commons.



Figure 24. *Oplonaeschna armata* adult ovipositing in mud. Photo by Jerry Oldenettel, through Creative Commons.

Once the dragonflies shed their naiad exoskeleton, the newly emerged adults must climb or hang in place to spread their wings and pump fluids into those veins (Figure 25). I have watched them climb *Eleocharis* to the top, then climb down and climb another, apparently in search of a minimum height where they finally stayed to emerge. In the Huron Mountains of the Upper Peninsula of Michigan, USA, Kielb *et al.* (1996) observed emergent adults of *Stylogomphus albistylus* (Gomphidae – dragonflies; Figure 26) resting on vertical moss-covered rock faces below waterfalls and on nearby trees.

But not all naiads must assume a vertical position to emerge. *Aeshna juncea* (Figure 28-Figure 29) is able to emerge in a horizontal position on *Sphagnum* (Figure 33) (Maitland 1967).



Figure 25. *Anax junius* on *Eleocharis*, where it is has emerged and is preparing to pump fluids into its wings. Photo by Richard Orr, with permission.



Figure 26. *Stylogomphus albistylus* adult, a species that can emerge on vertical rocks covered by mosses. Photo by Richard Orr, with permission.

Perching and Mating

Although the adults are strong fliers, even they must rest at times. For some, mosses seem to be suitable sites (Figure 27), especially in bogs.



Figure 27. *Celtithemis martha tenera* adult resting on male *Polytrichum*. Photo by Richard Orr, with permission.



Figure 28. *Aeshna juncea* naiad with mosses. Photo by Tim Faasen, with permission.



Figure 29. *Aeshna juncea* in flight. Photo by Jens Nielsen Buurgaard, through Creative Commons.

Adults no longer must live in the water and these strong fliers (Figure 29) can often stray far from their naiadal home. For example, members of *Enallagma* (Figure 30) occasionally travel up to 1 km to a different lake to lay eggs (McPeck 1989). But some exhibit mass annual migrations of a much greater distance, a phenomenon noted as early as 1494 in Europe! (Calvert 1893; May 2013). Matthews (2007) used a hydrogen isotope ratio to track migrations of *Anax junius* from Ontario, Canada, to Veracruz, Mexico in late August to

October. Matthews found that about 90% of the individuals moved southward for a mean distance of ca. 900 km, but exhibited a maximum of nearly 3,000 km. During these migrations they often stop to feed, mate, or lay eggs (Russell *et al.* 1998; Wikelski *et al.* 2006; Matthews 2007). Distance travelled depends on species, sex, age, size, and weather (Angelibert & Giani 2003). They may seek a particular habitat as adults that differs from that adjacent to the water, at least in part to avoid predators such as frogs while mating.



Figure 30. *Enallagma divagans* mating pair. Photo by Richard Orr, with permission.

In New Guinea, the genus *Lathanusa* (Libellulidae – dragonflies) is restricted to high elevations above 1350 m (Lieftinck 1955). *Lathanusa lamberti* occurs in the moss forests at 2800-2850 m, the highest known elevation of any Libellulidae in New Guinea. The mosses there may simply like the same atmospheric conditions and habitat as the odonates, but the presence of the moss could also provide some aspect of the habitat that makes it more suitable for these dragonflies. One such possibility could be as sites for egg deposition and nymphal development.

Beckemeyer (2002) found *Gomphomacromia fallax* (Figure 9) adult males perching on mosses beneath cliff sides where there was dripping water. Females were flitting about nearby and flicking their abdomens to deposit eggs toward the mosses. A discussion of perching and mating in bogs (Figure 31) is in Chapter 11-5 of this volume.



Figure 31. The dragonfly *Sympetrum danae* rests here on the moss *Polytrichum*. It prefers *Sphagnum* peatlands for mating. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.

Oviposition

If a nymph is terrestrial, then the eggs must also be laid in a terrestrial habitat, although the converse is not necessarily true. (Hatched naiads could drop into the water from overhanging plants or crawl to the water.) Most aquatic Odonata are not moss inhabitants, but the female may nevertheless lay her eggs among mosses, providing them with a secure and hidden location for development. Such is the case for *Austroargiolestes chrysoides* (Figure 32) in Australian rainforest streams (Theischinger & Hawking 2006).

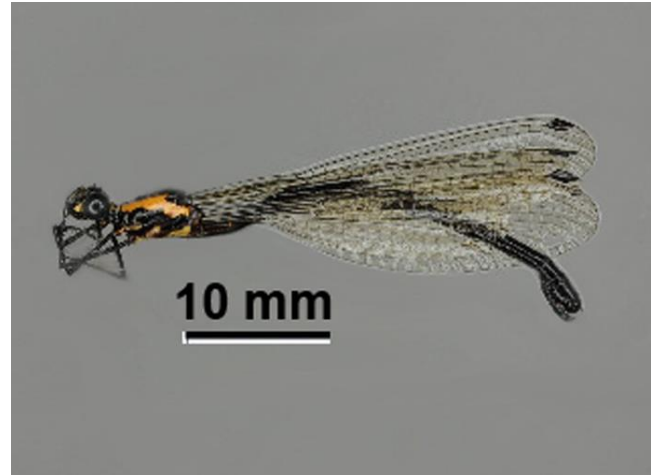


Figure 32. *Austroargiolestes chrysoides* adult, a species that lays its eggs among mosses in Australian rainforest streams. Photo from Biodiversity Centre, through Creative Commons.

Michiels and Dhondt (1990) described the selection of the oviposition site by the dragonfly *Sympetrum danae* (Libellulidae; Figure 33). This species deposits its eggs among *Sphagnum* (Figure 33), but given the choice of *Sphagnum* and *Mnium hornum* (Figure 34-Figure 35), some females will deposit eggs in the latter as well. Michiels and Dhondt attempt to explain the choice of these mosses, considering them to have similar form but distinctly different odors, at least to humans. They thus eliminate odors as determining the choice and consider moss form to be a more likely determining factor. They derived a list of advantages for depositing eggs among *Sphagnum*, based on a number of literature references:

1. Wet *Sphagnum* prevents summer drying of eggs and is likely to be submerged in the spring when eggs hatch and naiads develop.
2. Acid water associated with *Sphagnum* has fewer fish and other predator species.
3. Conditions are optimal for mycobacteria that feed Cladocera that in turn feed naiad Odonata.
4. *Sympetrum danae* (Figure 33) naiads are sprawling and need support and shelter found among *Sphagnum* (Figure 33).



Figure 33. *Sympetrum danae* male on *Sphagnum*, a suitable egg deposition site. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 34. *Mnium hornum* hummock, giving a superficial similarity to *Sphagnum*. Photo by Michael Lüth, with permission.



Figure 35. *Mnium hornum* up close, showing that it is quite different from *Sphagnum*. Photo by Bob Klips, with permission.

These advantages would not be present in the terrestrial moss *Mnium hornum* (Figure 34-Figure 35), so the choice of *Sphagnum* for egg deposition is also dependent on its availability in the proximal habitat to that of the naiads. Nevertheless, mosses near water bodies and in rain forests do afford more limited protection from drying. One must wonder how the terrestrial nymphs are adapted for obtaining prey. The large jaws and watch and

wait behavior should still work on land, but the prey items will be different.

Egg-laying among bryophytes has been observed for a long time. Lucas (1900) noted that *Aeshna caerulea* (Aeshnidae – dragonfly) occurred on "moss-hags" around peaty tarns and laid its eggs in wet, mossy ground. A female *Aeshna juncea* (Figure 36) on the Brooks Peninsula of Vancouver Island, Canada, oviposited into the wet mosses clinging to a vertical rock surface at the edge of a drying pool (Cannings & Cannings 1983).

Wang (2000, in Reels & Dow 2006) found that *Bayadera brevicauda brevicauda* (Euphaeidae – damselflies; Figure 37) from Taiwan uses moss-covered stones or fallen leaves, often at some distance from water, as oviposition sites.

In Hawaii, the seepage damselfly *Megalagrion hawaiiense* (Coenagrionidae; Figure 38) deposits her eggs in dripping moss banks (Williams 1936). These damselflies are territorial (Moore 1983) and males guard the females while they lay eggs (Williams 1936; Polhemus 1994). The eggs hatch in about ten days.



Figure 36. *Aeshna juncea* ovipositing in *Polytrichum*. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 37. *Bayadera brevicauda*, a species that uses moss-covered stones away from water for oviposition. Photo by Cao Heihua, through Creative Commons.



Figure 38. *Megalagrion hawaiiense*, a species that lays its eggs in dripping moss banks. Photo by Karl Magnacca, with permission.

The heaviest of all dragonflies, females of *Tetracanthagyna plagiata* (Aeshnidae; Figure 39-Figure 40), seem to prefer soft substrates (Leong & Tay 2009). One such substrate is decaying logs kept moist and soft by moss cover. Leong and Tay observed this behavior on a log next to a stream in Singapore.



Figure 39. *Tetracanthagyna plagiata* (dragonfly; Aeshnidae) adult in Malaysia. This is the heaviest of the dragonflies. Photo by Keith Wilson, through Creative Commons.

Matushkina and Klass (2011) suggest that the ovipositor of female *Phenes raptor* (Petaluridae; Figure 41) is particularly adapted for the substrate where the eggs are to be laid. This ovipositor (Figure 42) has numerous sensilla of different shapes and Matushkina and Klass suggest these may be able to detect suitable places for depositing eggs. These females choose loose substrata, including mosses, grass roots, and decaying plant matter. The ovipositor also lacks serration and the interlocking mechanism that connects the first two valves medially is reduced, both adaptations they suggest to relate to depositing eggs within soft substrata, including mosses.



Figure 40. *Tetracanthagyna plagiata* showing oviposition into soft wood. Photo by Marcus Ng, with permission.



Figure 41. *Phenes raptor* ovipositing into the soft end tissue of log. Mosses help to keep logs moist so they become soft. Photo by Eric LoPresti, with permission.



Figure 42. *Phenes raptor* female showing ovipositor. Photo by Eric LoPresti, with permission.

It would be interesting to see if the **Odonata** have preferences for growth forms of mosses. Dense cushions would seem appropriate for those adapted to a soft but solid substrate. Others that drop or "throw" the eggs to the substrate may prefer loose, thick mats, or at least be able to use them. If such correlations exist, the structure of the ovipositor may tell us the kinds of mosses or liverworts they would prefer.

Sampling

These nymphs are worth bringing home live for a closer look, but bring some smaller food items for observations of the interesting feeding. Keep them separate until you are ready to watch! Lucas (1900) suggests carrying the live specimens home in wet moss to avoid the jostling they would get in a jar. They can live this way for several hours to several days. Winstanley *et al.* (1981) were able to keep nymphs of *Uropetala carovei carovei* (**Petaluridae**; Figure 43) from New Zealand alive and rear them through emergence to adults by filling 2-liter containers with leaf mold, moss, and water.



Figure 43. *Uropetala carovei*, a species that can be reared using mosses, leaf mold, and water. Photo by Geoff Tutty, through Creative Commons.

Collection of terrestrial nymphs that live among bryophytes is a matter of collecting the bryophytes. Some may be collected by using traps, but small ones may not leave the bryophyte. Adults are usually collected with insect nets.

Life in a Thallus

Some of the **Odonata** use bryophytes as food for larvae and pupae, providing a safe, moist habitat for their survival in semiterrestrial habitats. For the dragonfly *Epiophlebia superstes* (**Epiophlebiidae**; Figure 44), an **endemic** (restricted to certain area or country) in Japan (Asahina & Eda 1982; Inoue 1983; Tabaru 1984), it appears that bryophytes also provide egg-laying substrata. This dragonfly is often confused with damselflies because

its hind wings are nearly equal to the forewings and it folds its wings over its back at rest like damselflies do. Furthermore, it lacks the jet propulsion typical of dragonflies but absent in damselflies (Tabaru 1984). But it has apparently branched from a dragonfly, then become separated from them when the Himalayas uplifted. Normally the adult lays her eggs in vegetation alongside a waterfall (Asahina & Sugimura 1981). However, in the absence of any nearby tracheophytes, females in locations in Nakamura, Kochi Prefecture, Japan, used bryophytes on the nearby rocks. The eggs were injected into the thallose tissues of the thallose liverworts *Dumortiera hirsuta* (Figure 45), *Conocephalum* (Figure 46), and *Pellia* (Figure 48). In China, *Epiophlebia diana* selects tracheophytes, and Carle (2012) considers the preferred plants of *E. superstes* there to be tracheophytes as well as the liverworts *Dumortiera*, *Conocephalum*, and *Pellia* (Asahina 1934, 1950; Asahina & Eda 1958, 1982; Asahina & Sugimura 1981; Tamiya & Miyakawa 1984; Tokunaga & Odagaki 1939).

In fact, it appears that the dragonfly *Epiophlebia superstes* (Figure 44) actually prefers the liverworts (Asahina & Eda 1958, 1982) for oviposition. Males stake out a "territory" over a patch of *Conocephalum conicum* (Figure 46), despite the presence of the usual tracheophyte egg depositories of *Petasites japonica* and *Eutrema wasabi*. Subsequently the female deposits her eggs in the tissues of this thallose liverwort (Figure 47). Upon dissection Asahina and Eda discovered that the eggs were precisely deposited in the air chambers of the thallus. Further egg deposits are also made into another thallose liverwort, *Pellia endiviifolia* (Figure 48). Because the liverwort thallus has an irregular shape compared to the symmetry of the tracheophyte leaves, the female has to keep changing her position relative to the surface, resulting in some of the eggs being laid in nearby tracheophytes.



Figure 44. *Epiophlebia superstes* (**Epiophlebiidae**) adult, a dragonfly that lays its eggs in thallose liverworts. Photo through Creative Commons.



Figure 45. *Dumortiera hirsuta*, a thallose liverwort that houses eggs injected into it by the dragonfly *Epiophlebia superstes*. Photo by Li Zhang, with permission.



Figure 46. *Conocephalum conicum* thallus, species where *Epiophlebia superstes* deposits its eggs. Photo by Li Zhang, with permission.

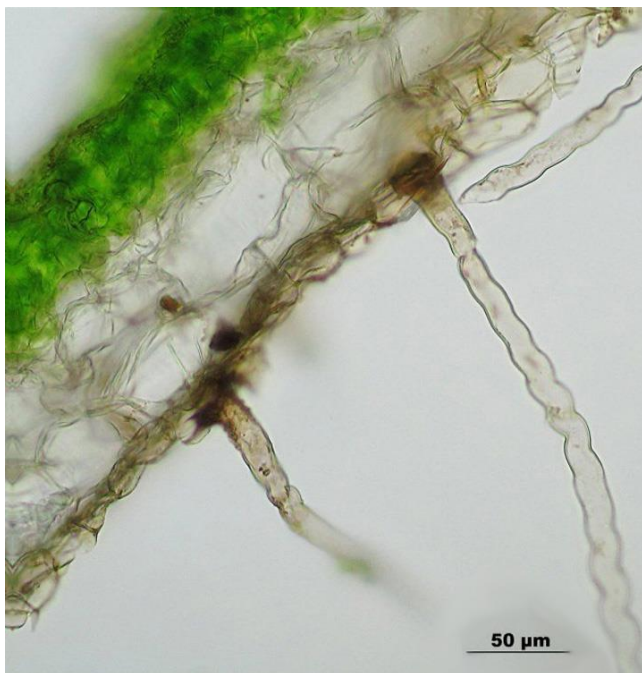


Figure 47. *Conocephalum conicum* thallus cross section showing chambering where nymphs of *Epiophlebia superstes* are able to live. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 48. *Pellia endiviifolia*, site of egg deposition for the dragonfly *Epiophlebia superstes*. Photo by Michael Lüth, with permission.

The ovipositor leaves a small "scar" on the liverwort thallus and the young nymphs later hatch through this hole. These holes permitted the researcher to identify thalli containing eggs and to count them. One thallus had 175 eggs! Others had lesser numbers of 24, 51, and 100. Development of the nymphs to become adults requires 5-8 years, perhaps setting the record for **Odonata** (Tabaru 1984). Use of the liverworts seems to vary between locations, with females in some areas seemingly avoiding the liverworts despite their suitable availability.

Asahina and Eda (1982) suggest that the related *Epiophlebia laidlawi* (Epiophlebiidae; Figure 49), a relict species from the Himalayas, might also use bryophytes for egg-laying. Now one can find in Wikipedia the statement that bryophytes are the preferred egg-laying substrate for that species, citing information from Silby (2001). At these high altitudes, mostly above 2000 m, the nymphs can take up to six years to develop before they emerge as adults.

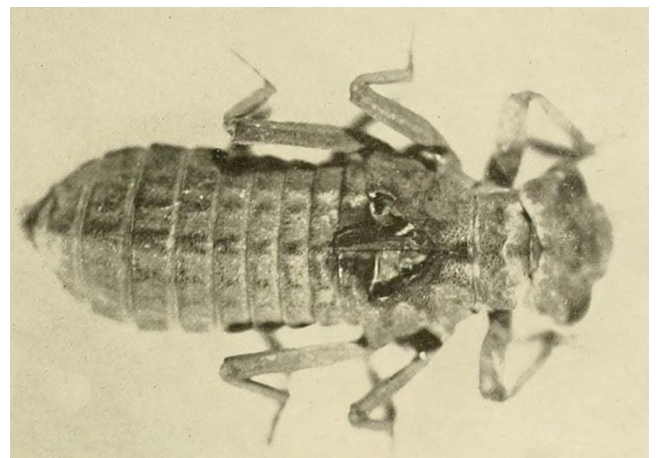


Figure 49. *Epiophlebia laidlawi*, dragonfly nymph that hatches from eggs laid in thallose liverworts. Photo by Shyamal, through Creative Commons.

It appears that *Epiophlebia* (Figure 44, Figure 49), which has only four species (Wikipedia 2007) and these are restricted to Asia, may not be the only odonate that uses a bryophyte thallus for oviposition (Villareal 2009). It's not

water, but it offers similar protection from desiccation – what better place than within the tissues of a plant that is seldom eaten? In this case, the nymphs were damselflies (**Zygoptera**; Figure 50-Figure 55), but their identity remains unknown. Although *Nothoceros aenigmaticus* (Figure 53) is not a true liverwort, but rather is a hornwort, its thalloid structure is similar to that of liverworts. This species is endemic to the southern Appalachian Mountains, USA, where, sadly, it is threatened to extinction resulting from a plague of hemlock woolly adelgids (*Adelges tsugae* – Hemiptera) on the hemlocks (*Tsuga canadensis*) that make its environment suitable for the hornworts (Jacobs 2005; Hyatt 2006).



Figure 50. Young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.



Figure 51. Anal gills and abdomen of a young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.



Figure 52. Young damselfly from within the thallus of a hornwort. Photo courtesy of Juan Carlos Villareal.

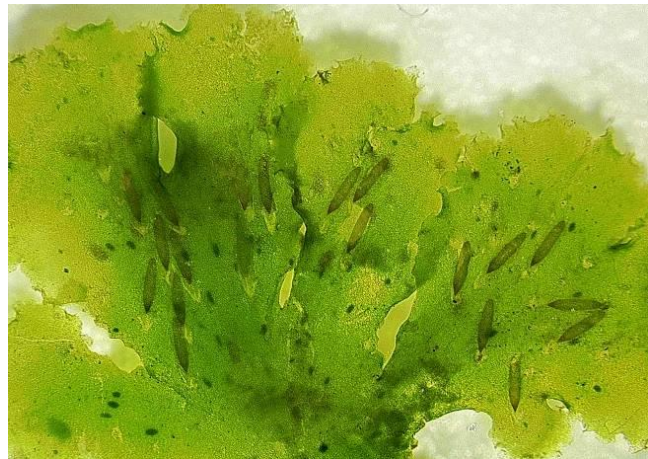


Figure 53. *Nothoceros aenigmaticus* thallus, a hornwort, with eggs that are probably those of a dragonfly or damselfly. Note that the small dark-green patches are *Nostoc* symbionts (blue-green bacteria that live in partnership with the hornwort, contributing converted atmospheric nitrogen). Dragonfly identification is by K. Tennessen. Photo courtesy of Juan Carlos Villareal.



Figure 54. Damselfly egg cases in *Nothoceros aenigmaticus*. Photo courtesy of Chris Cargill.



Figure 55. Damselfly egg case from *Nothoceros aenigmaticus*. Photo courtesy of Chris Cargill.

Juan Carlos Villareal (pers. comm. 23 December 2008) made a similar find in Mexican populations where the developing larvae were leaf miners on the thallus. The damselflies, identified by Ken Tennessen, were in the *Coenagrionidae*, possibly the genus *Argia* (Figure 56).



Figure 56. *Argia tibialis* adult, member of a genus whose nymphs may be one of those that live in hornwort thalli. Photo by Richard Orr, with permission.

I could find no observations on feeding by these thallus dwellers. How long do they remain in the thallus? What do they eat while they are there? This order of insects is highly adapted to be carnivorous. The chances that they find animal food items within the thallus seem slim.

Summary

The **Odonata** are predominately aquatic in the immature stage, but some nymphs are terrestrial, and some of these use bryophytes to protect themselves and to maintain moisture. These carnivores can find food among the bryophytes, including spiders, while hiding from their own predators – mostly amphibians and birds.

Bryophytes provide a good site for egg laying, and even aquatic species may lay eggs on streamside or poolside bryophytes. Some naiads may seek bryophytes as their water body dries up. Many more species climb to the banks of streams and lakes to

emerge from their nymphal skins, leaving behind evidence as numerous **exuviae** on the bryophytes. Others use moss hummocks as perching sites.

Live **Odonata** nymphs, including aquatic species, may be kept alive by placing wet moss in the container with them. Adults can be collected with insect nets.

A few **Odonata** actually live within the thalli of liverworts and hornworts. In particular, *Epiophlebia superstes* in Asia lays its eggs in several liverwort species and nymphs develop there. An unidentified damselfly develops within hornwort thalli; others appear to be in the genus *Argia*.

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