CHAPTER 11-5
AQUATIC INSECTS: HEMIMETABOLA – ODONATA

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Figure 1. *Lanthus vernalis* (Gomphidae) exuviae on the terrestrial moss *Thuidium* sp. Photo by Richard Orr.

**ODONATA – Dragonflies and Damselflies**

This order contains both dragonflies (*Anisoptera*; Figure 2-Figure 4) and damselflies (*Zygoptera*). You can recognize adult dragonflies by their wings at rest (Figure 2) – they are spread horizontally; the term *anisoptera* means uneven wings. The damselflies, by contrast, usually fold the wings together above the body at rest (Figure 5); their wings are of equal size (*Zygoptera*). Both dragonflies and damselflies have an aquatic stage, the *naiad* (gilled nymph). Dragonflies can be recognized in the naiad stage by having internal anal gills and relatively stout bodies (Figure 3). Damselflies have three blade-like external anal gills and slender bodies (Figure 6).

Both groups are predators (Thorp & Covich 1991) and have a large, scooplike *labium* (mouth part; Figure 4 & Figure 8, Figure 7) that extends to capture the prey. These giant jaws are formidable and the *Odonata* are efficient in catching prey.

The naiads climb out of the water and must climb up rocks or vegetation before they split their exoskeleton and emerge (Figure 1). They must then pump fluids into their wings before they fly away. Unlike the mayflies, the dragonfly naiads live as long as 5-6 years and adults for 5-6 months (Dragonfly 2015). *Odonata* are among the strongest fliers in the insect world – just try to catch one!
Figure 2. Dragonfly adult with spread wings. Photo by Eileen Dumire.

Figure 3. *Anax junius* (dragonfly; Aeshnidae) naiad showing stout body and anal opening that surrounds internal gills. Photo by Tom Murray through Creative Commons.

Figure 4. *Diplacodes* (dragonfly; Libellulidae) young naiad showing extended labium. Photo by Stephen Moore, Landcare Research, NZ.

Figure 5. *Enallagma cyathigerum* (Coenagrionidae) Blue Damselfly adult illustrating the wings folded above the abdomen. Photo by Umberto Salvagnin through Creative Commons.

Figure 6. *Argia* (Coenagrionidae) naiad showing three external anal gills typical of damselfly naiads. Photo by Bob Henricks.

Figure 7. *Lestes* (damselfly; Lestidae) showing extended labium. Photo by Dana R. Denson, Florida Association of Benthologists.
Bryophytes are not the usual homes of Odonata naiads in lakes, ponds, and streams. In a Québec, Canada stream, Odonata preferred gravel to the moss Fontinalis dalecarlica (Figure 9) (Cattaneo et al. 2004). These carnivores preferred places where they could remain hydrated as the water level decreased and were not tied to the bryophytes for obtaining the periphyton required by many other orders.

But bryophytes do seem to hold importance for some Odonata. In my studies of Appalachian Mountain, USA, streams, the dragonfly genus Cordulegaster (Cordulegastridae – spiketail dragonflies; Figure 10) was occasionally present among bryophytes (Glime 1968). The gomphids Gomphus (Gomphidae – clubtail dragonflies; Figure 11) and Octogomphus (Gomphidae; Figure 12) also occurred among the bryophytes, both rarely, representing the dragonfly naiads (Glime 1968).

The presence of exuviae provides indirect evidence that the Odonata use bryophytes for emergence (Needham et al. 1901). Both Gomphus exilis (dragonfly; Gomphidae) (Figure 13) and G. spicatus (Figure 14) exuviae (Figure 15) appeared in layers among mosses at the edge of a pond in the Adirondack Mountains of New York, USA.
Figure 13. *Gomphus exilis* (dragonfly; *Gomphidae*) female adult, a species that uses mosses for emergence. Photo by Sheryl Pollock through Discover Life.

Figure 14. *Gomphus spicatus* (dragonfly; *Gomphidae*) adult, a species that uses mosses for emergence. Photo by Creative Commons

Figure 15. *Somatochlora tenebrosa* (dragonfly; *Corduliidae*) exuvia. Photo by Richard Orr.

**Suborder Zygoptera – Damselflies**

Specific records of damselflies outside of bogs and fens are few, partly because they do not tend to inhabit the types of habitats where many of the aquatic bryophytes grow. But it seems more likely that the bryophytes do not afford a suitable habitat for their elongate labium to catch prey.

In the Red Cedar River, East Lansing, MI, I found a number of damselfly naiads early in the spring in large clumps of *Fontinalis* (Figure 16). *Teinobasis ponapensis* (see Figure 17), in the *Coenagrionidae* – narrow-winged damselflies, a damselfly from the eastern Caroline Islands of Micronesia, occurred as adults only near mosses (Paulson & Buden 2003).

Figure 16. *Fontinalis antipyretica*, home for damselfly naiads in early spring. Photo by Michael Lüth.

Figure 17. *Teinobasis sjupp* (damselfly; *Coenagrionidae*) adult, relative of *T. ponapensis* that is known as adults only near mosses in the Caroline Islands of Micronesia. Photo by V. J. Kalkman through Creative Commons.

But there appear to be interesting relationships still waiting for us. Two new species of the genus *Argiolestes* (*Argiolestidae*; damselflies; Figure 18) are known only from shaded areas of water courses where there is a high moss cover (Michalski & Oppel 2010). *Argiolestes tuberculiferus* and *A. verrucatus* were discovered only recently in Papua New Guinea. Other bryophyte relationships most likely remain for discovery in less studied parts of the world.

Figure 18. *Argiolestes ornatus* (damselflies; *Megapodagrionidae*) male adult from Papua, Indonesia. Note that the wing position at rest is spreading, unlike other members of *Zygoptera*. Photo by Vincent J. Kalkman.
Suborder Anisoptera – Dragonflies

Direct usage of bryophytes by Odonata naiads is not well documented, but there seems to be more usage for the dragonflies than for the damselflies. It appears that mosses, as well as other protective pond locations, can protect some species when their ponds dry up. *Somatochlora semicircularis* (*Corduliidae* – emerald dragonflies; Figure 19) uses mosses, as well as rocks, logs, and deep in the bases of sedge clumps, to escape the drying conditions of exposure when their Colorado, USA, ponds dry up in late August and September (Willey & Eiler 1972). This species has the further advantage that it loses water more slowly than other dragonflies such as *Aeshna interrupta interna* and *Libellula quadrimaculata* (Figure 21), neither of which seems to live among bryophytes.

Even if Odonata are unable to live among bryophytes where their large size would make movement and prey capture more difficult, they may still take advantage of them for cover. *Somatochlora provocans* (*dragonfly; Corduliidae*) (Figure 22) occurred in a small lake inlet in southeastern USA, where *Sphagnum* (e.g. Figure 23) provided a border (Tennesen 1975). The naiads were common in the flowing water, but were hanging out near that *Sphagnum* cover.

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Figure 19. *Somatochlora semicircularis* (dragonfly; *Corduliidae*) adult whose survival could depend on naiads seeking shelter in mosses when their ponds dry up. Photo by Belinda Lo through Creative Commons.

Figure 20. *Somatochlora linearis* (dragonfly; *Corduliidae*) naiad. Some species in this genus retreat to bryophytes when their water body dries up. Photo by Richard Orr.

Figure 21. *Libellula quadrimaculata* (dragonfly; *Libellulidae*) naiad, a species that loses water rapidly and cannot survive when its aquatic habitat dries up. Photo by Tim Faasen.

Figure 22. *Somatochlora provocans* (dragonfly; *Corduliidae*) adult. Naiads of this species stay near the *Sphagnum* cover in pools. Photo by Mike Ostrowski through Creative Commons.

Figure 23. *Sphagnum* peatland in Alaska, USA. Photo by Vita Plasek.
**Oplonaeschna armata** (Figure 24), a member of the *Aeshnidae* – hawks or darners, may not live among mosses, but the species still finds them useful. Some individuals of this dragonfly left traces of their behavior behind as exuviae clinging to mosses 0.8-1.25 m above the water on vertical rocky walls of a canyon (González Soriano & Novelo Gutiérrez 1998).

**Life Cycle Considerations**

Bryophytes can actually provide several functions for *Odonata*, from wet habitats in waterfalls to safe sites or cover at the margins of streams, ponds, and lakes. The most important of these uses seems to be for egg depositories.

**Mating and Egg-Laying**

Mosses may not house naiads in many habitats, but they are a preferred site for egg deposition in many bogs and fens. *Aeshna subarctica* (dragonfly; *Aeshnidae*) (Figure 25) in northwestern Wisconsin flies along the northwest shoreline, again the sunny side, where there is a mat of floating mosses and sedges (DuBois 1999). Females land there to oviposit in the openings among the mosses, submerging the ends of their abdomens into wet *Sphagnum* (Figure 25). In the muskeg, *Aeshna coerulescens septentrionalis* (dragonfly; *Aeshnidae*) (Figure 57) uses wet moss patches between tufts of scant grass as well as the muskeg "slime" as deposition sites in small pools, or in the creamy-pink muskeg slime bordering small pools (Whitehouse & Walker 1941).

*Leucorrhinia hudsonica* (dragonfly; *Libellulidae* – skimmers; Figure 27) at a black spruce *Sphagnum* bog (Figure 28) in Québec, Canada, uses that habitat for egg deposition (Hilton 1984). The males first establish territories, then perch there except for short attack flights against intruders. Females visit those sites to deposit eggs and are intercepted by the males who enter into tandem formation and copulate with them. Unlike many of the other *Odonata*, they perch near the egg-laying sites during copulation. Once copulation is completed, the females dip their abdominal tips in rapid succession into the small pools of water associated with the saturated *Sphagnum* (Figure 47). Males hover nearby to guard the females during this process, chasing off competing males.
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Figure 28. Spruce bog in Pennsylvania, USA. Photo by Nicholas A. Tonelli through Creative Commons.

One smart dragonfly in Oregon, USA, used mosses to make egg-laying a safer venture. Using her legs to cling to streambank mosses, *Octogomphus specularis* (dragonfly; Gomphidae) (Figure 29) dipped her ovipositor into the stream water, avoiding the danger of being washed away and helpless against the current (Opler 2013).

Figure 29. *Octogomphus specularis* (dragonfly; Gomphidae) clinging to moss while ovipositing in the water. Photo by Jim Johnson.

Temperature plays a major role in the timing and coordination of emergence in *Somatochlora alpestris* (dragonfly; Corduliidae) (Figure 30) and *S. arctica* (Figure 31-Figure 32) (Sternberg 1995). Eggs can hatch the same season or go into diapause and remain in their aquatic habitat throughout the winter. This is a facultative response that causes eggs deposited late in the season to increase from 0 diapausal eggs early in the season to 37% later in *S. alpestris* and to 18% in *S. arctica*. Depending on the temperature during development, egg development requires 17 to 38 days.

**Emergence**

Donnelly (1990) reported with implied amazement a finding of naiads of a species of the damselfly *Nesobasis* (Coenagrionidae; Figure 33) crawling over wet mosses near a stream in the Fijian Islands, but it was not clear if they lived there or were seeking an emergence site to climb. It appears that mosses are among the sites used for emergence (Walker 1923). Exuviae from several species of the dragonfly *Ophiogomphus* (Gomphidae; Figure 34-Figure 36) were present on mosses under underhanging foliage at Godbout, Quebec, Canada, where they were a meter or more from the present waterline.

Figure 30. *Somatochlora alpestris* (dragonfly; Corduliidae) adult, a dragonfly whose egg maturation time depends on the temperature. Photo by Gilles San Martin through Creative Commons.

Figure 31. *Somatochlora arctica* (dragonfly; Corduliidae) adult male, a species whose egg maturation time depends on temperature, permitting it to keep its niche separate from that of *S. alpestris*. Photo by Piet Spaans through Creative Commons.

Figure 32. *Somatochlora arctica* (dragonfly; Corduliidae) naiad exuvia. Photo by Guillaume Doucet <guillaume.doucet.free.fr>.
Figure 33. *Nesobasis erythrops* (damselfly; *Coenagrionidae*) adult, a genus whose naiads climb across wet mosses in the Fijian Islands. Photo by Mark O’Brien through Creative Commons.

Figure 34. Adult *Ophiogomphus cecilia* (dragonfly; *Gomphidae*) that has just emerged from its exuvia, a genus that sometimes emerges on overhanging mosses by streams. Photo by Tim Faasen.

Figure 35. *Ophiogomphus cecilia* (dragonfly; *Gomphidae*) exuvia, a genus with some members that crawl onto overhanging mosses to emerge. Photo by Tim Faasen.

Figure 36. *Ophiogomphus cecilia* (dragonfly; *Gomphidae*) adult, a genus that apparently uses mosses for emergence. Photo by Varel through Creative Commons.

**Somatochlora elongata** (dragonfly; *Corduliidae*) (Figure 37) sometimes sheds its exuvia on mosses at the edge of ponds (Needham *et al.* 1901). *Somatochlora semicircularis* (Figure 19) faces imminent danger as it emerges. First, it must find a suitable site for climbing out of the water, and if these sites are scarce, they may all be occupied (Willey 1974). Then, it is vulnerable while it is emerging because it can neither fly nor return to the safety of cover. At this time it is especially vulnerable to birds, and its relatively large size can make a hearty meal. Once free of its nymphal skin, its maiden flight easily draws the attention of hungry predators. At this time, it gains the advantage of safety in numbers. Emergence is highly synchronized, and although many die, the emergence of 50% of the adults within the first three to six days prevents birds from capturing all of them. Considerable space is needed for catching these strong fliers in the air, limiting the number of predators. Life cycle processes from naiad to adult to egg laying can be seen in Figure 38-Figure 44.
Life Cycle Stages of the Damselfly *Coenagrion scitulum*

Figure 38. *Coenagrion scitulum* naiad, illustrating the three anal gills of the *Zygoptera*. Photo by Tim Faasen.

Figure 39. Naiad climbing up a plant to emerge to adulthood. Photo by Tim Faasen.

Figure 40. Adult emerging from exuvia. Photo by Tim Faasen.

Figure 41. Exuvia of emerged adult. Photo by Tim Faasen.

Figure 42. Adult *Coenagrion scitulum* ready to mate. Photo by Tim Faasen.

Figure 43. Mating *Coenagrion scitulum* pair, male on top, female below. Photo by Tim Faasen.
Safety in Numbers

The dragonfly *Sympetrum vicinum* (Libellulidae – skimmers; Figure 45) typically uses wet mosses at the edge of a lake for depositing eggs (Whitehouse & Walker 1941). Mating and egg laying can be particularly dangerous for the **Odonata**. These able fliers are at a disadvantage when coupled during mating and when dipping into the water to lay eggs. One strategy for reducing chances of becoming frog dinner is for the mating pair to join other mating pairs, with up to seven pairs of *Sympetrum vicinum* (Figure 45) grouping together in a single 1 m² plot (McMillan 2000). Interestingly, frogs attacked lone pairs more frequently than they attacked pairs in aggregations. On the other hand, the presence of multiple pairs may have signalled a safe site against the predation.

*Sympetrum danae* (dragonfly; *Corduliidae*) (Figure 46–Figure 48) does not remain in tandem pairs (compare to Figure 44) like *S. vicinum* (Figure 45). In the field, 14% of females that started oviposition while still in tandem and 10% of those that had separated from the males were killed by frogs (Michiels & Dhondt 1990). A curious observation is that separated ovipositing females were attacked less often by the frogs than were those females that were not observed mating previously. Females of this species preferred sites with *Sphagnum* (Figure 23), but when non-aquatic mosses with a similar structure were substituted, they were selected equally, suggesting that selection was based on surface characteristics of the mosses. Within the bog, temperature played a role in oviposition location. In the cooler part of the season the females selected the south-facing side of a hummock, whereas in the warmer part of the season they selected the cooler north-facing side of the hummock.
Bogs and Fens

Bogs and fens in many ways offer ideal conditions for adult Odonata. These strong fliers prefer bright sunshine and become quiet when the weather is cloudy. Sunny, open bogs are thus best suited for them, compared to other kinds of habitats. As discussed earlier regarding bog habitats (Chapter 11-2), the adults are easily seen flying about in bogs (Boudot et al. 1990).

Some Odonata seem to prefer bogs as adults, using them as a place to forage and for "sport" (Needham et al. 1901). One such dragonfly is *Cordulia shurtleffi* (American emerald – *Corduliidae*; Figure 49) in the Adirondack Mountains of eastern North America.

Odonata can have a strong impact on the communities where they live. The naiads are efficient carnivores with highly specialized scoops for capturing prey. Larson and House (1990) concluded that they may be the principal organism determining abundance and distribution of potential prey organisms in the bog pool system.

Normally bogs and fens have rather different flora and fauna from each other. But Cannings and Cannings (1994) concluded that there were no clear differences between the Odonata in these two habitat categories. Rather than responding to acidity or nutrient levels, they seem to respond to the form and structure that is similar in these two habitats.

In a study of the northern Cordilleran peatlands, Cannings and Cannings (1994) found that of 40 species there, 8 are obligate peatland inhabitants and another 4 almost always occur there. The most common genera there are *Aeshna* (*Aeshnidae*; Figure 51-Figure 57) – 11 species) and *Somatochlora* (*Corduliidae*; Figure 19-Figure 20) – 10 species, both dragonflies. The peatlands serve as refugial habitats (having isolated populations of once more widespread species, i.e. relict populations), with 25 species that are restricted to boreal regions and six that are Holarctic (majority of habitats found throughout the northern continents of the world).
**Aeshna juncea** (dragonfly; **Aeshnidae**) (Figure 51-Figure 52) prefers the acid water of bog pools and lays its eggs among the bog bryophytes (Figure 51). **Aeshna subarctica** (Figure 25) likewise lays its eggs among Sphagnum (Figure 23), but in the northern Cordilleran peatlands, **A. subarctica** (Figure 53) is more commonly associated with Drepanoclados (s.l.) (Figure 54) and Scorpidium (Figure 55) (Cannings & Cannings 1997). Its males patrol only the floating mats in search of females; the females lay their eggs directly on these mats. **Aeshna setchensis** (Figure 56) lives where the peatlands have filled-in depressions. The mossy fen ponds of the Yukon include Aeshna septentrionalis and **A. subarctica** among their fauna. **Aeshna septentrionalis** females use the sedge-moss habitat for oviposition.

**Figure 52.** *Aeshna juncea* (dragonfly; **Aeshnidae**) naiad, a species of acid bog pools, with mosses. Photo by Tim Faasen.

**Figure 53.** *Aeshna subarctica* (dragonfly; **Aeshnidae**) adult, a bog dweller. Photo by Arnold Sennhauser.

**Figure 54.** *Drepanoclados aduncus* var. polycarpum, home for species of *Aeshna, Somatochlora*, and *Leucorrhinia* in the Yukon. Photo by Michael Lüth.

In the Czech Republic, *Aeshna caerulea* (Figure 57) is a relict, living in bogs that are drying up, suffering from nitrogen deposition, suffering from global warming – all factors contributing to the disappearance of the bogs that serve as its habitat (Dolný 2013).

Mossy fen ponds in the Yukon, Canada, provide us with some idea of the dominant **Odonata** in northern habitats (Cannings & Cannings 1997). In addition to *Aeshna* species, their distinctive fauna includes the damselfly *Coenagrion interrogatum* (*Coenagrionidae*; Figure 58-Figure 59) and dragonfly *Somatochlora sahlbergii* (*Corduliidae*; Figure 60; see Figure 61 for *Somatochlora* naiad). *Coenagrion interrogatum* is only common where the aquatic mosses are abundant. Where the peatlands have filled in depressions the habitat is characterized by *Aeshna stichensis* (Figure 56), *Somatochlora franklini* (Figure 62), *S. kennedyi* (Figure 63), *S. whitehousei* (Figure 64), and *Leucorrhinia patricia* (*Libellulidae*; Figure 65). These dragonfly males patrol...
the floating mats of mosses that include *Drepanocladus* (s.l.) (Figure 54) and *Scorpidium* (Figure 55). *Leucorrhinia patricia* (Figure 65) is restricted to water bodies that have aquatic mosses either floating or near the surface. In Sweden, *Leucorrhinia rubicunda* (Figure 66- Figure 67) hunts for its food in bogs as adults (Scholl 2002). In the boreal ecosystems this species occurs only in transitional mires, but in the Netherlands it is the most abundant species of *Odonata* in the spring in degraded and rewetted mires (Desrochers & van Duinen 2006).

![Figure 57. *Aeshna caerulea* (dragonfly; *Aeshnidae*) male adult. Photo by Guillaume Doucet <guillaume.doucet.free.fr>.

![Figure 58. *Coenagrion interrogatum* (dragonfly; *Coenagrionidae*) adult, an inhabitant of mossy fen ponds in the Yukon, Canada. Photo by Jim Johnson.

![Figure 59. *Coenagrion* (damselfly; *Coenagrionidae*) naiad, genus that sometimes lives in mossy fen ponds. Photo by Gerard H. Visser.

![Figure 60. *Somatochlora sahlbergi* (dragonfly; *Corduliidae*) adult, a bog dweller. Photo by Mark Zekhuis.

![Figure 61. *Somatochlora metallic* (dragonfly; *Corduliidae*) naiad. Several species in this genus live in bogs. Photo by Tim Faasen.

![Figure 62. *Somatochlora franklini* (dragonfly; *Corduliidae*) adult, a bog dweller. Photo by Larry deMarch.

*Somatochlora franklini* patrols over *Sphagnum* (Figure 23) in bogs and over water-soaked mosses in fens, preferring spring-fed *Sphagnum* fens. *Somatochlora sahlbergi* (Figure 60) naiads (see Figure 61) live where the water is underlain with mosses. As adults they drop their eggs into the water, but again in sites underlain with mosses. Both *S. semicircularis* (Figure 68) and *S. albicincta* (Figure 69) prefer mossy substrata, the former in a sedge-moss marsh and the latter in mud-bottomed, mossy fen ponds. *Somatochlora semicircularis* (Figure 70) flies low over bogs in search of egg-laying sites among the pools; naiads develop in the spring pools and swamps (Usinger 1974).
Figure 63. *Somatochlora kennedyi* (dragonfly; Corduliidae) male adult, a species that patrols the *Sphagnum* mats to find a female. Photo by Denis A. Doucet.

Figure 64. *Somatochlora whitehousei* (dragonfly; Corduliidae) adult, a species that patrols the *Sphagnum* mats to find a female. Photo by Jim Johnson.

Figure 65. *Leucorrhinia patricia* (dragonfly; Libellulidae) adult male, a species restricted to water bodies with mosses near the surface. Photo by Denis A Doucet.

Figure 66. *Leucorrhinia rubicunda* (dragonfly; Libellulidae) male, a species that hunts in bogs. Photo by Guido Gerding through GNU Free Documentation.

Figure 67. *Leucorrhinia rubicunda* (dragonfly; Libellulidae) naiad on *Sphagnum*. Photo by Tim Faasen.

Figure 68. *Somatochlora semicircularis* (dragonfly; Corduliidae) adult, a species that prefers a mossy fen-marsh. Photo by Leslie Flint through Creative Commons.
Figure 69. *Somatochlora albicincta* (dragonfly; *Corduliidae*) adult, an inhabitant of mud-bottomed, mossy fen ponds. Photo by Chuunen Baka through Creative Commons.

Figure 70. *Somatochlora arctica* (dragonfly; *Corduliidae*) adult; the female flies low over bogs to find a suitable place to lay eggs. Naiads develop in pools there. Photo by Guillaume Doucet <guillaume.doucet.free.fr>.

Dragonflies often deposit their eggs among bryophytes (Macan 1963), with the naiads subsequently living there (Gerson 1982). These bryophyte dwellers include *Leucorrhinia dubia* (*Libellulidae* – skimmers; Figure 71-Figure 74) from Europe (Matthey 1971) and *Calicnemia miles* (*Platycnemididae* – white-legged damselflies; Figure 75) from the Himalayan Mountains (Kumar & Prasad 1977).

Macan (1962) attempted to explain why (and how) *Leucorrhinia dubia* (Figure 71-Figure 74), a *Libellulidae* dragonfly, chose bog pools for laying eggs. He found that this genus was attracted to a white surface on the ground, but that hardly explained anything since *Leucorrhinia* species lay eggs by flying and dipping to deposit the eggs in the water during flight. Schiemenz (1954) found that it preferred a *Sphagnum* (Figure 47) pool (68%) to tap water, but considered this to be inconclusive. It is likely that water chemistry plays a role.

Figure 71. *Leucorrhinia dubia* (*Libellulidae*) naiad, a dragonfly species that changes color in late naiad stages to blend with the surrounding *Sphagnum* (Figure 47). Photo by Tim Faasen.

Figure 72. *Leucorrhinia dubia* (*Libellulidae*) emergent adult dragonfly and exuvia. Photo by Tim Faasen.

Figure 73. Female white-faced darter, *Leucorrhinia dubia* (dragonfly; *Libellulidae*). Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>. 

Figure 74. *Leucorrhinia dubia* (dragonfly; *Libellulidae*) naiad, a dragonfly species that changes color in late naiad stages to blend with the surrounding *Sphagnum* (Figure 47). Photo by Tim Faasen.
Figure 74. Male white-faced darter, *Leucorrhinia dubia* (Libellulidae), a bog-dwelling dragonfly. Photo copyright by David Kitching <http://www.brocross.com/dfly/dfly.htm>.

Figure 75. *Calicnemia miles* (Platycnemididae) adult female damselfly who often lays eggs among wet mosses in the Himalayas. Photo by Dennis Farrell.

The dragonfly *Leucorrhinia dubia* (white-faced darter; dragonfly; Libellulidae) (Figure 71-Figure 74) is so well adapted to the *Sphagnum* (Figure 23) habitat that the late instar naiads (immature stages) actually change color to blend with the brown and green color of *Sphagnum* (Figure 76) (Henrikson 1993). These naiads show preference for the *Sphagnum* substrate over debris in laboratory tests, a behavior that seems to permit them to be more successful in preying on aquatic pillbugs, *Asellus aquaticus* (Figure 77). Henrikson suggested that the complex habitat of *Sphagnum* serves both as shelter and as a foraging site; the *Sphagnum* apparently provides a safe habitat against predators – where large mats of this moss exist, *Leucorrhinia dubia* is able to coexist with the fish without becoming dinner.

Figure 76. *Sphagnum angustifolium* showing brown and green colors that *Leucorrhinia dubia* dragonfly naiads can mimic. Photo by Michael Lüth.

Figure 77. *Asellus aquaticus*, food of *Leucorrhinia dubia*. Photo by Niels Sloth.

*Tanypteryx hageni* (Figure 78-Figure 80) (dragonfly; Petaluridae – petaltails) adults are most common in alpine bogs. Naiads have been found in mosses in seepage along the west coast of USA (Usinger 1974).

Figure 78. *Tanypteryx hageni* (dragonfly; Petaluridae) naiad clinging to mosses. Photo by Greg Courtney.
Figure 79. *Tanypteryx hageni* (*Petaluridae*) adult, a dragonfly that lives in alpine bogs; naiads can be found among mosses in seepage. Photo by Dana Kenneth Johnson through Creative Commons.

Figure 80. *Tanypteryx* (dragonfly; *Petaluridae*) burrows amid mosses and swamp litter. Note the holes. Photo by Greg Courtney.

Damselflies (*Zygoptera*) seem less common among the bog fauna than dragonflies. The common genus *Lestes* (*Lestidae* – spreadwings; Figure 81-Figure 83), a damselfly, includes bogs among its many habitats. In British Columbia, Canada, *Lestes disjunctus* (Figure 82) is common in several bog types whereas *L. forcipatus* (Figure 83) is uncommon in one type and absent in the others (Cannings & Simaika 2005). *Lestes forcipatus* is most common in the cold sedge and moss fens and is relatively rare in warmer habitats.

Figure 81. *Lestes viridis* (damselfly; *Lestidae*) naiad, a bog inhabitant, among *Sphagnum* mosses. Photo by Tim Faasen.

Figure 82. *Lestes disjunctus* (damselfly; *Lestidae*) adult, a species common in several types of bogs in British Columbia, Canada. Photo by Phil Myers through Creative Commons.

Figure 83. *Lestes forcipatus* (damselfly; *Lestidae*) pair mating; the upper male clasps the female at the neck. Note the posterior ovipositor on the female. Photo by Richard Orr.
Life in a Liverwort 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 84), an endemic in Japan (Inoue 1983; Tabaru 1984), it appears that bryophytes may be emergency, or at least alternative, 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 liverwort Dumortiera hirsuta (Figure 85).

In later observations, however, it appeared that the dragonfly Epiophlebia superstes (Figure 84) actually preferred the liverworts (Asahina & Eda 1982). Males staked out a "territory" over a patch of Conocephalum conicum (Figure 86), despite the presence of the usual tracheophyte egg depositories of Petasites japonica and Eutrema wasabi. Subsequently the female deposited her eggs in the tissues of this thallose liverwort (Figure 87). Upon dissection Asahina and Eda discovered that the eggs were precisely deposited in the air chambers of the thallus. Further egg deposits were also made into another thallose liverwort, Pellia endiviifolia (Figure 88). Because the liverwort thallus has an irregular shape compared to the symmetry of the tracheophyte leaves, the female had to keep changing her position relative to the surface, resulting in some of the eggs being laid in nearby tracheophytes.
The ovipositor leaves a small "scar" on the liverwort thallus and the young naiads 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 naiads 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 89), 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 naiads can take up to six years to develop before they emerge as adults.

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An unusual association of bryophytes and Odonata is that of the dragonfly Epiophlebia superstes and thalllose bryophytes (liverworts and hornworts). This species lays its eggs within the thallus. The naiads live there, eating it, and later emerging from it.
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Literature Cited


