

# **CHAPTER 11-5**

## **AQUATIC INSECTS: HEMIMETABOLA – ODONATA**

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# CHAPTER 11-5

## AQUATIC INSECTS: HEMIMETABOLA – ODONATA



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

### 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 (Thorpe & Covich 1991) and the naiads 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). Dragonflies 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, with permission.



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, with permission.



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, with permission.



Figure 7. *Lestes* (damselfly; **Lestidae**) showing extended labium. Photo by Dana R. Denson, Florida Association of Benthologists, with permission.





Figure 8. *Cordulegaster boltonii* (dragonfly; **Cordulegasteridae**) jaws on exuvia. Photo by Tim Faasen, with permission.

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.

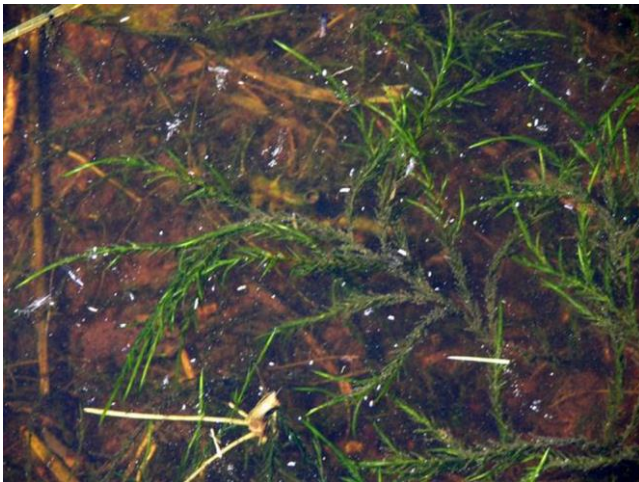


Figure 9. *Fontinalis dalecarlica*, a moss often less preferred than sand, at least in Quebec streams. Photo by J. C. Schou, with permission.

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 10. *Cordulegaster erronea* (dragonfly; **Cordulegastridae**) naiad, an occasional dragonfly genus among bryophytes in mid-Appalachian Mountain streams. Photo by Richard Orr, with permission.



Figure 11. *Gomphus lividus* (dragonfly; **Gomphidae**) naiad, a genus that is a rare bryophyte inhabitant in the mid-Appalachian Mountain streams. Photo by Richard Orr, with permission.



Figure 12. *Octogomphus specularis* (dragonfly; **Gomphidae**) naiad, a genus that is a rare bryophyte inhabitant in the mid-Appalachian Mountain streams. Photo by Mark Melton, with permission.





Figure 13. *Gomphus exilis* (dragonfly; **Gomphidae**) female adult, a species that uses mosses for emergence. Photo by Sheryl Pollock through Discover Life, with permission.



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



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

## Suborder Zygoptera – Damselflies

Specific records of damselfly naiads living among bryophytes 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, with permission.



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** or **Megapodagrionidae**; damselflies; Figure 18) in Papua New Guinea are known only from shaded areas of water courses; *Argiolestes fornicatus* avoids sunny areas of the watercourses and occurs primarily in areas with high moss cover (Michalski & Oppel 2010). *Argiolestes tuberculiferus* (Figure 19) 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**. (**Lestidae** hold them at 45° angles.) Photo by Vincent J. Kalkman.



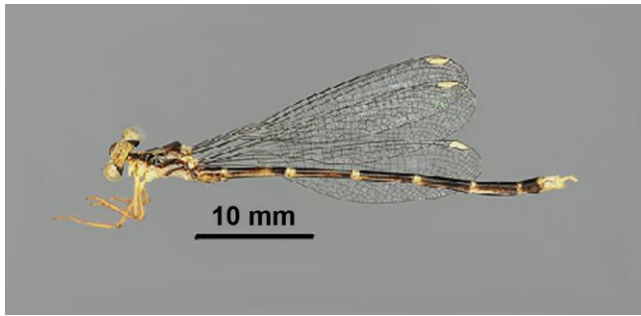


Figure 19. *Argiolestes tuberculiferus* adult. Photo by Naturalis Biodiversity Centre through Creative Commons.

## 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 20-Figure 21) 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* (Figure 79-Figure 80) and *Libellula quadrimaculata* (Figure 22), neither of which seems to live among bryophytes.



Figure 20. *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.

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 23) occurred in a small lake inlet in southeastern USA, where *Sphagnum* (e.g. Figure 24) provided a border (Tennessen 1975). The naiads were common in the flowing water, but were hanging out near that *Sphagnum* cover.



Figure 21. *Somatochlora linearis* (dragonfly; Corduliidae) naiad. Some species in this genus retreat to bryophytes when their water body dries up. Photo by Richard Orr.



Figure 22. *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 23. *Somatochlora provocans* (dragonfly; Corduliidae) adult. Naiads of this species stay near the *Sphagnum* cover in pools. Photo by Mike Ostrowski through Creative Commons.





Figure 24. *Sphagnum* peatland in Alaska, USA. Photo by Vita Plasek.

*Oplonaeschna armata* (Figure 25), a member of the **Aeshnidae** – hawkers 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).



Figure 25. *Oplonaeschna armata* (dragonfly; **Aeshnidae**) adult, a species that climbs to mosses a meter above water to emerge from the naiad state. Photo by Greg Lasley through Creative Commons.

## 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 27) in northwestern Wisconsin flies along the northwest shoreline, the sunny side, where there is a mat of

floating mosses and sedges (DuBois *et al.* 1999). While they submerge the ends of their abdomens into the moist *Sphagnum* (Figure 27) they are not ready for a quick getaway. Naiads of this species require submerged mosses in their habitat. *Aeshna sitchensis* (Figure 61) does not distinguish between *Sphagnum* bog pools and pools of fens with *Drepanocladus* (Figure 59) (Cannings *et al.* 2004). In the muskeg, *Aeshna coerulea septentrionalis* (dragonfly; **Aeshnidae**) (Figure 62) 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). During mating and oviposition is a good time to catch the **Odonata** because they are occupied in laying eggs and not in flying.

The female of *Argia moesta* (damselfly; **Coenagrionidae**; Figure 26), in Ohio, USA, deposits her eggs on submerged mosses, logs, and algae-covered stones (Kellicott 1899). *Tanypteryx hageni* was once thought to insert eggs into plant tissues, but in a closer examination Svihla (1959) found that these were deposited below the water among mosses, liverworts, and other bog plants.



Figure 26. *Argia moesta* adult, a species that lays its eggs on submerged mosses. Photo by Richard Murphy through Creative Commons.

Corbet (1999) specifically reports naiads of *Thaumatoneura inopinata* (**Megapodagrionidae**), the giant water damselfly, as moss dwellers. This species oviposits among mosses that grow adjacent to, but not within, the main current.

*Leucorrhinia hudsonica* (dragonfly; **Libellulidae** – skimmers; Figure 29) at a black spruce *Sphagnum* bog (Figure 30) 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 51). Males hover nearby to guard the females during this process, chasing off competing males. In Illinois, USA, when females of *Leucorrhinia* are pursued by too many males, they land on the mosses and deposit their eggs (Needham & Hart 1901).





Figure 27. *Aeshna subarctica* (dragonfly; **Aeshnidae**) female laying eggs in *Sphagnum*. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

Some species use terrestrial mosses for egg deposition. For example, one female *Tetracanthagyna plagiata* (**Aeshnidae**; Figure 28), the heaviest of all extant **Odonata**, deposited eggs on a moss-covered log adjacent to a stream, arching its abdomen to insert its ovipositor into the soft substrate (Leong & Tay 2009).



Figure 28. *Tetracanthagyna plagiata* (dragonfly; **Aeshnidae**) adult in Malaysia. Photo by Keith Wilson, through Creative Commons.



Figure 29. *Leucorrhinia hudsonica* (dragonfly; **Libellulidae**) female adult. Photo by Richard Orr, with permission.



Figure 30. 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 31) dipped her ovipositor into the stream water, avoiding the danger of being washed away and helpless against the current (Opler 2013).



Figure 31. *Octogomphus specularis* (dragonfly; **Gomphidae**) clinging to moss while ovipositing in the water. Photo by Jim Johnson, with permission.

Temperature plays a major role in the timing and coordination of emergence in *Somatochlora alpestris* (dragonfly; **Corduliidae**) (Figure 34) and *S. arctica* (Figure 35-Figure 36) (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 the season in *S. alpestris* and from 0 to 18% in *S. arctica*. Depending on the temperature during development, egg development requires 17 to 38 days. Dark mosses and dark bog water help to increase the ambient temperature and hasten development.

Few studies have identified egg-laying locations in streams. Bryophytes would seem to be ideal, even if the naiads leave soon after hatching to chase food items in open water. Askew (1988) did in fact observe *Caliaeschna microstigma* (**Aeshnidae**; Figure 32-Figure 33) depositing eggs in mosses on boulders of a stream in Europe.





Figure 32. *Caliaeschna microstigma* adult. Photo by Cosmin O. Mancu, with permission.



Figure 33. *Caliaeschna microstigma* exuvia. Photo by Cosmin O. Mancu, with permission.

### Emergence

Donnelly (1990) reported with implied amazement a finding of naiads of a species of the damselfly *Nesobasis* (Coenagrionidae; Figure 37) 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 38-Figure 40) were present on mosses under underhanging foliage at Godbout, Quebec, Canada, where they were a meter or more from the present waterline.



Figure 34. *Somatochlora alpestris* (dragonfly; Corduliidae) adult, a dragonfly whose egg maturation time depends on the temperature. Photo by Gilles San Martin, through Creative Commons.



Figure 35. *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 36. *Somatochlora arctica* (dragonfly; Corduliidae) naiad exuvia. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.





Figure 37. *Nesobasis erythropis* (damselfly; **Coenagrionidae**) adult, a genus whose naiads climb across wet mosses in the Fijian Islands. Photo by Mark O'Brien, through Creative Commons.



Figure 38. 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, with permission.



Figure 39. *Ophiogomphus cecilia* (dragonfly; **Gomphidae**) exuvia, a genus with some members that crawl onto overhanging mosses to emerge. Photo by Tim Faasen, with permission.



Figure 40. *Ophiogomphus cecilia* (dragonfly; **Gomphidae**) adult, a genus that apparently uses mosses for emergence. Photo by Varel, through Creative Commons.

*Somatochlora elongata* (dragonfly; **Corduliidae**) (Figure 41) sometimes sheds its exuvia on mosses at the edge of ponds (Needham *et al.* 1901). *Somatochlora semicircularis* (Figure 20) 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 42-Figure 48.



Figure 41. *Somatochlora elongata* (dragonfly; **Corduliidae**) male adult, a species that may shed its naiad exuvia on mosses bordering ponds. Photo by Denis A. Doucet, with permission.



## Life Cycle Stages of the Damselfly *Coenagrion scitulum*



Figure 42. *Coenagrion scitulum* naiad, illustrating the three anal gills of the **Zygoptera**. Photo by Tim Faasen, with permission.



Figure 43. Naiad climbing up a plant to emerge to adulthood. Photo by Tim Faasen, with permission.



Figure 44. Adult emerging from exuvia. Photo by Tim Faasen, with permission.



Figure 45. Exuvia of emerged adult. Photo by Tim Faasen, with permission.



Figure 46. Adult *Coenagrion scitulum* ready to mate. Photo by Tim Faasen, with permission.



Figure 47. Mating *Coenagrion scitulum* pair, male on top, female below. Photo by Tim Faasen, with permission.





Figure 48. Male (left) and female (right) *Coenagrion scitulum* in tandem following copulation. They are most likely looking for a suitable site to lay eggs. Photo by Tim Faasen, with permission.

### Safety in Numbers

The dragonfly *Sympetrum vicinum* (Libellulidae – skimmers; Figure 49) 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 49) grouping together in a single 1 m<sup>2</sup> 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.



Figure 49. *Sympetrum vicinum* (dragonfly; Corduliidae) adults mating. Photo by Phil Myers, through Creative Commons.

*Sympetrum danae* (dragonfly; Corduliidae) (Figure 50-Figure 52) does not remain in tandem pairs (compare to Figure 48) like *S. vicinum* (Figure 49). 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 24), 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.



Figure 50. *Sympetrum danae* (dragonfly; Corduliidae) naiad. Photo by Tim Faasen, with permission.



Figure 51. The male dragonfly *Sympetrum danae* (dragonfly; Corduliidae) resting on *Sphagnum* in the habitat it prefers for mating. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.





Figure 52. *Sympetrum danae* (dragonfly; **Corduliidae**) mating. Once mating is completed, this species separates and does not fly in tandem. Photo by Tim Faasen, with permission.

## 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 53) in the Adirondack Mountains of eastern North America.



Figure 53. *Cordulia shurtleffi* (American emerald dragonfly) adult, a species that forages and plays around bog pools. Photo by Richard Orr, with permission.

But is this habitat equally suitable for the naiads? As Krebs (2001) reminded us, habitat heterogeneity provides more ecological niches, and bogs fit that heterogeneity of moisture and temperature as well as differences in microtopography. Some of these may use the mosses as occasional cover in the naiad stage (Figure 54).



Figure 54. *Cordulia aenea* (downy emerald dragonfly) naiad with mosses. This species is a relative of *C. shurtleffi*, a bog species. Photo by Tim Faasen, with permission.

In Ontario, Canada, naiads of *Williamsonia fletcheri* (**Corduliidae**; Figure 55) live among the dead *Sphagnum* stems (Charlton & Cannings 1993). They matched the *Sphagnum* and rarely moved, giving them excellent camouflage. In Maine, USA, the males perch on *Sphagnum* hummocks in spruce bogs.



Figure 55. *Williamsonia fletcheri*, a species whose naiads live among dead *Sphagnum* stems. Photo by Diana-Terry Hibbitts, through Creative Commons.

**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 56-Figure 62) – 11 species) and *Somatochlora* (**Corduliidae**; Figure 20-Figure 21) – 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).



Figure 56. *Aeshna juncea* (dragonfly; **Aeshnidae**) depositing eggs among the *Polytrichum* plants. It is common in small acid pools of bogs. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.

*Aeshna juncea* (dragonfly; **Aeshnidae**) (Figure 56-Figure 57) prefers the acid water of bog pools and lays its eggs among the bog bryophytes (Figure 56). *Aeshna subarctica* (Figure 27) likewise lays its eggs among *Sphagnum* (Figure 24), but in the northern Cordilleran peatlands, *A. subarctica* (Figure 58) is more commonly associated with *Drepanocladus* (*s.l.*) (Figure 59) and *Scorpidium* (Figure 60) (Cannings & Cannings 1997). Its males patrol only the floating mats in search of females; the females lay their eggs directly on these mats. *Aeshna sitchensis* (Figure 61) lives where the peatlands have filled-in depressions. The mossy fen ponds of the Yukon include *Aeshna septentrionalis* (Figure 62) and *A. subarctica* among their fauna. *Aeshna septentrionalis* females use the sedge-moss habitat for oviposition.



Figure 57. *Aeshna juncea* (dragonfly; **Aeshnidae**) naiad, a species of acid bog pools, with mosses. Photo by Tim Faasen, with permission.



Figure 58. *Aeshna subarctica* (dragonfly; **Aeshnidae**) adult, a bog dweller. Photo by Arnold Sennhauser, through Creative Commons.



Figure 59. *Drepanocladus aduncus* var. *polycarpon*, home for species of *Aeshna*, *Somatochlora*, and *Leucorrhinia* in the Yukon. Photo by Michael Lüth, with permission.



Figure 60. *Scorpidium scorpioides*, home for species of *Aeshna*, *Somatochlora*, and *Leucorrhinia* in the Yukon. Photo by Michael Lüth, with permission.





Figure 61. *Aeshna sitchensis* (dragonfly; **Aeshnidae**) adult, a bog dweller. Photo by Five Acre Geographic, through Creative Commons.



Figure 62. *Aeshna caerulea* (dragonfly; **Aeshnidae**) male adult. Photo by Guillaume Doucet <guillaume.doucet.free.fr>, with permission.

In the Czech Republic, *Aeshna caerulea* (Figure 62) 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 63-Figure 64) and dragonfly *Somatochlora sahlbergi* (**Corduliidae**; Figure 65; see Figure 66 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 sitchensis* (Figure 61), *Somatochlora franklini* (Figure 67), *S. kennedyi* (Figure 82), *S. whitehousei* (Figure 83), and *Leucorrhinia patricia* (**Libellulidae**; Figure 84). These dragonfly males patrol the floating mats of mosses that include *Drepanocladus* (*s.l.*) (Figure 59) and *Scorpidium* (Figure 60). *Leucorrhinia patricia* (Figure 84) is restricted to water bodies that have aquatic mosses either floating or near the surface. In Sweden, *Leucorrhinia rubicunda* (Figure 85-Figure 86) 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 63. *Coenagrion interrogatum* (dragonfly; **Coenagrionidae**) adult, an inhabitant of mossy fen ponds in the Yukon, Canada. Photo by Jim Johnson, with permission.



Figure 64. *Coenagrion* (damselfly; **Coenagrionidae**) naiad, genus that sometimes lives in mossy fen ponds. Photo by Gerard H. Visser <www.microcosmos.nl>, with permission.





Figure 65. *Somatochlora sahlbergi* (dragonfly; **Corduliidae**) adult, a bog dweller. Photo by Mark Zekhuis, with online permission.



Figure 66. *Somatochlora metallica* (dragonfly; **Corduliidae**) naiad. Several species in this genus live in bogs. Photo by Tim Faasen, with permission.



Figure 67. *Somatochlora franklini* (dragonfly; **Corduliidae**) adult, a bog dweller. Photo by Larry deMarch, through Creative Commons.

In northern British Columbia, Canada, species are similar to those of the Yukon. In standing open water with submerged mosses provides a suitable naiad home for many species with wide ecological tolerances: *Coenagrion interrogatum* (Figure 63-Figure 64), *Aeshna septentrionalis* (Figure 62), *A. subarctica* (Figure 27), *Somatochlora kennedyi* (Figure 82), *S. septentrionalis*, *Leucorrhinia patricia* (Figure 84). In slender sedge fens with *Drepanocladus* (Figure 59), one can find *Lestes disjunctus* (Figure 101), *Coenagrion interrogatum*, *C. resolutum* (Figure 68), *Nehalennia irene* (Figure 69), *Aeshna juncea* (Figure 56-Figure 57), *Aeshna subarctica*, *Leucorrhinia hudsonica* (Figure 29), *L. proxima* (Figure 70), and *Sympetrum obtrusum* (Figure 71-Figure 72) (Cannings *et al.* 2004). In shallow sedge-moss fens, typical of patterned fens with *Drepanocladus*, *Lestes disjunctus*, *L. congener* (Figure 73), *L. forcipatus* (Figure 102), *Enallagma boreale* (Figure 74), *Coenagrion resolutum*, *Nehalennia irene*, *Aeshna septentrionalis*, *A. sitchensis* (Figure 61), *A. tuberculifera* (Figure 75), *Somatochlora brevicincta*, *S. franklini* (Figure 76), *S. kennedyi*, *S. semicircularis* (Figure 87), *S. whitehousei* (Figure 83), *Leucorrhinia hudsonica*, and *Sympetrum danae* (Figure 50-Figure 52) occur. The outer coastal bogs have a communities of *Pinus contorta* – *Empetrum nigrum* – *Sphagnum austini* (Figure 77) and *Juniperus communis* – *Trichoporum cespitosum* – *Racomitrium lanuginosum* (Figure 78). These are suitable habitats for *Lestes disjunctus*, *Enallagma boreale*, *Aeshna interrupta* (Figure 79-Figure 80), *Aeshna sitchensis*, *Cordulia shurtleffii* (Figure 53), *Somatochlora albicincta* (Figure 88), *Leucorrhinia hudsonica*, *Libellula quadrimaculata* (Figure 22), and *Sympetrum danae*. The seepages and springs of coastal fen associations with *Eriophorum angustifolium* and *Sphagnum* are typical habitats for *Tanypteryx hageni* (Figure 81), which burrows into the seepage.



Figure 68. *Coenagrion resolutum* laying eggs. Photo by D. Gordon E. Robertson, through Creative Commons.





Figure 69. *Nehalennia irene* male adult. Photo by Rsbernard, through Creative Commons.



Figure 72. *Sympetrum obtrusum* male, a species that occurs in sedge fens with *Drepanocladus*. Photo by D. Gordon E. Robertson, through Creative Commons.



Figure 70. *Leucorrhinia proxima* adult, a fen species. Photo by Ed McAskill, through Creative Commons.



Figure 73. *Lestes congener* adult. Photo by Richard Orr, with permission.

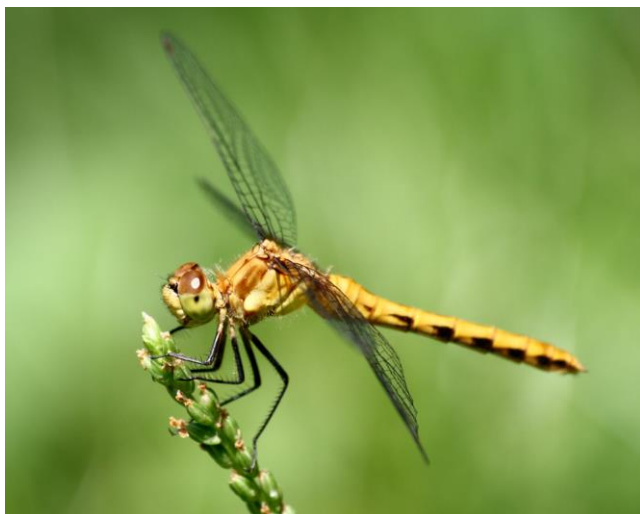


Figure 71. *Sympetrum obtrusum* female in central Connecticut. Photo by Sage Ross, through Wikimedia Commons.



Figure 74. *Enallagma boreale* adult, a species of patterned fens with *Drepanocladus*. Photo by Mike Ostrowski, through Creative Commons.





Figure 75. *Aeshna tuberculifera* adult flying, a species of patterned fens with *Drepanocladus*. Photo by Mike Ostrowski, through Creative Commons.



Figure 76. *Somatochlora franklini* male adult. Photo by Denis A. Doucet, with permission.



Figure 77. *Sphagnum austinii*, outer coastal species that is home to a number of **Odonata** species. Photo by Michael Lüth, with permission.



Figure 78. *Racomitrium lanuginosum*, outer coastal species that is home to a number of **Odonata** species. Photo by Juan Larrain, with permission.



Figure 79. *Aeshna interrupta* naiad, a species that lives in habitats with *Sphagnum austinii* and *Racomitrium lanuginosum*. Photo by Donald S. Chandler, with permission.





Figure 80. *Aeshna interrupta* adult, a species that lives in habitats with *Sphagnum austini* and *Racomitrium lanuginosum*. Photo by Kam's World, through Creative Commons.



Figure 82. *Somatochlora kennedyi* (dragonfly; Corduliidae) male adult, a species that patrols the *Sphagnum* mats to find a female. Photo by Denis A. Doucet, with permission.



Figure 81. *Tanypteryx hageni* adults mating. Photo by Roy J. Beckemeyer, with permission.



Figure 83. *Somatochlora whitehousei* (dragonfly; Corduliidae) adult, a species that patrols the *Sphagnum* mats to find a female. Photo by Jim Johnson, with permission.

*Somatochlora franklini* (Figure 76) patrols over *Sphagnum* (Figure 24) in bogs and over water-soaked mosses in fens, preferring spring-fed *Sphagnum* fens. *Somatochlora sahlbergi* (Figure 65) naiads (see Figure 66) 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 87) and *S. albicincta* (Figure 88) prefer mossy substrata, the former in a sedge-moss marsh and the latter in mud-bottomed, mossy fen ponds. *Somatochlora semicircularis* (Figure 89) flies low over bogs in search of egg-laying sites among the pools; naiads develop in the spring pools and swamps (Usinger 1974).



Figure 84. *Leucorrhinia patricia* (dragonfly; Libellulidae) adult male, a species restricted to water bodies with mosses near the surface. Photo by Denis A. Doucet, with permission.





Figure 85. *Leucorrhinia rubicunda* (dragonfly; **Libellulidae**) male, a species that hunts in bogs. Photo by Guido Gerding, through GNU Free Documentation.



Figure 88. *Somatochlora albicincta* (dragonfly; **Corduliidae**) adult, an inhabitant of mud-bottomed, mossy fen ponds. Photo by Chuunen Baka, through Creative Commons.



Figure 86. *Leucorrhinia rubicunda* (dragonfly; **Libellulidae**) naiad on *Sphagnum*. Photo by Tim Faasen, with permission.



Figure 89. *Somatochlora artica* (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>, with permission.



Figure 87. *Somatochlora semicircularis* (dragonfly; **Corduliidae**) adult, a species that prefers a mossy fen-marsh. Photo by Leslie Flint, through Creative Commons.

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 90-Figure 93) from Europe (Matthey 1971) and *Calicnemia miles* (**Platycnemididae** – white-legged damselflies; Figure 94) from the Himalayan Mountains (Kumar & Prasad 1977).

Macan (1962) attempted to explain why (and how) *Leucorrhinia dubia* (Figure 90-Figure 93), 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 51) pool (68%) to tap water, but considered this to be inconclusive. It is likely that water chemistry plays a role.





Figure 90. *Leucorrhinia dubia* (Libellulidae) naiad, a dragonfly species that changes color in late naiad stages to blend with the surrounding *Sphagnum* (Figure 51). Photo by Tim Faasen, with permission.



Figure 91. *Leucorrhinia dubia* (Libellulidae) emergent adult dragonfly and exuvia. Photo by Tim Faasen, with permission.



Figure 92. Female white-faced darter, *Leucorrhinia dubia* (dragonfly; Libellulidae). Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 93. Male white-faced darter, *Leucorrhinia dubia* (Libellulidae), a bog-dwelling dragonfly. Photo copyright by David Kitching <<http://www.brocross.com/dfly/dfly.htm>>, with permission.



Figure 94. *Calicnemis miles* (Platynemididae) adult female damselfly who often lays eggs among wet mosses in the Himalayas. Photo by Davidvraju, through Creative Commons.

The dragonfly *Leucorrhinia dubia* (white-faced darter; dragonfly; Libellulidae) (Figure 90-Figure 93) is so well adapted to the *Sphagnum* (Figure 24) habitat that the late instar naiads (immature stages) actually change color to blend with the brown and green color of *Sphagnum* (Figure 95) (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 96). 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 95. *Sphagnum angustifolium* showing brown and green colors that *Leucorrhinia dubia* dragonfly naiads can mimic. Photo by Michael Lüth, with permission.



Figure 96. *Asellus aquaticus*, food of *Leucorrhinia dubia*. Photo by Niels Sloth, with permission.

*Tanypteryx hageni* (Figure 97-Figure 99) (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 97. *Tanypteryx hageni* (dragonfly; **Petaluridae**) naiad clinging to mosses. Photo by Greg Courtney, with permission.



Figure 98. *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 99. *Tanypteryx* (dragonfly; **Petaluridae**) burrows amid mosses and swamp litter. Note the holes. Photo by Greg Courtney, with permission.

Damselflies (**Zygoptera**) seem less common among the bog fauna than dragonflies. The common genus *Lestes* (**Lestidae** – spreadwings; Figure 100-Figure 102), a damselfly, includes bogs among its many habitats. In British Columbia, Canada, *Lestes disjunctus* (Figure 101) is common in several bog types whereas *L. forcipatus* (Figure 102) 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 100. *Lestes viridis* (damselfly; **Lestidae**) naiad, a bog inhabitant, among *Sphagnum* mosses. Photo by Tim Faasen, with permission.





Figure 101. *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 102. *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, with permission.

## Summary

The **Odonata** are **hemimetabolous**, having egg, naiad, and adult stages. They are comprised of dragonflies (**Anisoptera**) and damselflies (**Zygoptera**). Neither is common among bryophytes, most likely due to their large labium used for catching prey and to their large size. Nevertheless, some occur among the bryophytes as naiads, some lay their eggs there, and some gather on bryophytes to emerge to the adult stage.

The **Odonata** are common in bogs and fens, with naiads living among the many pools, sometimes darting into the dangling mosses for cover. The form and structure of the bryophytes may be important determinants in where they live. At mating time, some of the **Odonata** increase the safety of the species by forming aggregations – safety in numbers. *Aeshna* and *Somatochlora* are the most common genera in the bogs. In both the naiad and adult stages the **Odonata** are voracious carnivores and thus have a major impact, especially in the bog ecosystem.

The typical bog inhabitants include members of **Aeshnidae**, **Coenagrionidae**, **Corduliidae**, **Lestidae**, **Libellulidae**, **Platynemididae**, and **Petaluridae**. Other families that may be found among bryophytes include **Argiolestidae**, **Cordulegastridae**, and **Gomphidae**.

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## Literature Cited

- Askew, R. R. 1988. The Dragonflies of Europe. Harley Books, Martins, Great Horkesley, Colchester, Essex, England, 291 pp.
- Boudot, J.-P., Jacquemin, G., and Goutet, P. 1990. Odonates des lacs et tourbières à sphaignes des Hautes-Vosges, France. Opuscula Zoologica Fluminensia 52: 1-11.
- Cannings, S. G. and Cannings, R. A. 1994. The Odonata of the northern Cordilleran peatlands of North America. Mem. Entomol. Soc. Can. 126: 89-110.
- Cannings, S. G. and Cannings, R. A. 1997. Dragonflies (Odonata) of the Yukon. Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, pp. 169-200.
- Cannings, R. A. and Simaika, J. P. 2005. *Lestes disjunctus* and *L. forcipatus* (Odonata: Lestidae): An evaluation of status and distribution in British Columbia. J. Entomol. Soc. Brit. Columb. 102: 57-64.
- Cannings, R. A., Ramsay, L. R., Cannings, S. G., Yukon, N., and Copley, C. R. 2004. The dragonflies (Insecta: Odonata) of Northern British Columbia: Field surveys, collections



- development and public education. Report to the Habitat Conservation Trust Fund. Royal British Columbia Museum and BC Ministry of Sustainable Resource Management, Victoria, BC. unpaginated.
- Cattaneo, A., Cloutier, L., and Méthot, G. 2004. The response of invertebrates in moss and in gravel to water level fluctuations in a Québec stream. *Arch. Hydrobiol.* 161: 21-43.
- Charlton, R. E. and Cannings, R. A. 1993. The larva of *Williamsonia fletcheri* Williamson (Anisoptera: Corduliidae). *Odonatologica* 22: 335-343.
- Corbet, P. S. 1999. Dragonflies. Behavior and Ecology of Odonata. Cornell University Press, Ithaca.
- Desrochers, A. and Duinen, G.-J. van. 2006. Peatland fauna. In: Weider, R. K. and Vitt, D. H. (eds.). Boreal Peatland Ecosystems. Ecological Studies 188. Springer-Verlag, Heidelberg, Germany, pp. 67-100.
- Dolný, A. 2013. Population size estimation of *Aeshna caerulea* (Odonata: Aeshnidae) in the Czech part of Úpské rašeliniště bog (Giant Mountains). *Casopis slezského zemskeho muzea (A)* 62: 83-89.
- Donnelly, T. W. 1990. The Fijian genus *Nesobasis* Part 1: Species of Viti Levu, Ovalau, and Kadavu (Odonata: Coenagrionidae). *N. Z. J. Zool.* 17: 87-117.
- Dragonfly. 2015. Wikipedia. Accessed 12 February 2015 at <[http://en.wikipedia.org/wiki/Dragonfly#Life\\_cycle](http://en.wikipedia.org/wiki/Dragonfly#Life_cycle)>.
- DuBois, R. B., Johnson, R., and Putz, S. 1999. *Aeshna subarctica* (Odonata: Aeshnidae) in northwestern Wisconsin. *Great Lakes Entomol.* 32: 29-31.
- Gerson, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman & Hall, New York. pp. 291-332.
- Glime, J. M. 1968. Aquatic Insect Communities among Appalachian Stream Bryophytes. Ph.D. Dissertation, Michigan State University, East Lansing, MI, 180 pp.
- González Soriano, E. and Novelo Gutiérrez, R. 1998. *Oploniaeschna magna* sp. nov. (Odonata: Aeshnidae), from Mexico with a description of its larva. *Rev. Biol. Trop.* 46: 705-715.
- Henrikson, B.-I. 1993. *Sphagnum* mosses as a microhabitat for invertebrates in acidified lakes and the color adaptation and substrate preference in *Leucorrhinia dubia* (Odonata, Anisoptera). *Ecography* 16: 143-153.
- Hilton, D. F. 1984. Reproductive behavior of *Leucorrhinia hudsonica* (Selys) (Odonata: Libellulidae). *J. Kans. Entomol. Soc.* 57: 580-590.
- Kellicott, D. S. 1899. The Odonata of Ohio. Academy of Science. Press of the Clapper Printing Co., Wooster, OH.
- Krebs, Ch. J. 2001. Ecology. The Experimental Analysis of Distribution and Abundance. Wydawnictwo Naukowe PWN, Warszawa, Poland, 734 pp.
- Kumar, A. and Prasad, M. 1977. Last instar larvae of two Odonata species from Western Himalaya. *Entomon* 2: 225-230.
- Larson, D. J. and House, N. L. 1990. Insect communities of Newfoundland bog pools with emphasis on the Odonata. *Can. Entomol.* 122: 469-501.
- Leong, T. M. and Tay, S. L. 2009. Encounters with *Tetracanthagyna plagiata* (Waterhouse) in Singapore, with an observation of oviposition (Odonata: Anisoptera: Aeshnidae). *Nat. Singapore* 2: 115-119.
- Macan, T. T. 1962. Ecology of aquatic insects. *Ann. Rev. Entomol.* 7: 261-287.
- Macan, T. T. 1963. Freshwater Ecology. Longmans, London.
- Matthey, W. 1971. Ecologie des insectes aquatiques d'une tourbière du Haut-Jura. *Rev. Suisse Zool.* 78: 367-536.
- McMillan, V. E. 2000. Aggregating behavior during oviposition in the dragonfly *Sympetrum vicinum* (Hagen) (Odonata: Libellulidae). *Amer. Midl. Nat.* 144: 11-18.
- Michalski, J. and Oppel, S. 2010. Two new species of *Argiolestes* from Papua New Guinea (Odonata: Megapodagrionidae). *Internat. J. Odonatol.* 13: 63-74.
- Michiels, N. K. and Dhondt, A. A. 1990. Costs and benefits associated with oviposition site selection in the dragonfly *Sympetrum danae* (Odonata: Libellulidae). *Anim. Behav.* 40: 668-678.
- Needham, J. G. and Hart, C. A. 1901. The dragon-flies (Odonata) of Illinois, with descriptions of the immature stages. Part I. Petaluridae, Aeshnidae, and Gomphidae. *Bull. Ill. State Lab. Nat. Hist.* 6: 1-94.
- Needham, J. G., Betten, C., MacGillivray, A. D., Coquillett, D. W., and Ashmead, W. H. 1901. Aquatic Insects in the Adirondacks. *N. Y. State Mus. Bull.* 47: 1-612.
- Opler, Paul A. 2013. Dragonflies and Damselflies (Odonata) of the United States. Odonata of California. Grappletail (*Octogomphus specularis*). Accessed 4 January 2015 at <<http://www.npwrc.usgs.gov/resource/distr/insects/dfly/ca/230.htm>>.
- Paulson, D. R. and Buden, D. W. 2003. The Odonata of Pohnpei, Eastern Caroline Islands, Micronesia. *Internat. J. Odonatol.* 6: 39-64.
- Schiemenz, H. 1954. Über die angebliche Bindung der Libelle *Leucorrhinia dubia* v.d.L. an das Hochmoor. *Zool. Jahrb. Abt. Systematik* 82: 473-480.
- Scholl, C. 2002. Report of The Dragonflies at Store Mosse National Park 2001. Johan Rova. Landsbygdsavdelningen.
- Sternberg, K. 1995. Influence of oviposition date and temperature upon embryonic development in *Somatochlora alpestris* and *S. arctica* (Odonata: Corduliidae). *J. Zool.* 235: 163-174.
- Svihla, A. 1959. The life history of *Tanypteryx hageni* Selys (Odonata). *Trans. Amer. Entomol. Soc.* 85: 219-232.
- Tennessen, K. J. 1975. Description of the nymph of *Somatochlora provocans* Calvert (Odonata: Corduliidae). *Fla. Entomol.* 58: 105-110.
- Thorp, J. H. and Covich, A. P. 1991. Ecology and classification of North American Freshwater Invertebrates. Academic Press, New York, Boston, et al., 754 pp.
- Usinger, R. L. 1974. Aquatic Insects of California. University of California Press, Berkeley.
- Walker, E. M. 1923. Notes on the Odonata of Godbout, Quebec. *Can. Entomol.* 55: 5-12.
- Whitehouse, F. C. and Walker, E. M. 1941. British Columbia dragonflies (Odonata), with notes on distribution and habits. *Amer. Midl. Nat.* 26: 488-557.
- Wiley, R. L. 1974. Emergence pattern of the subalpine dragonfly, *Somatochlora semicircularis* (Odonata: Corduliidae). *Psyche* 81: 121-133.
- Wiley, R. L. and Eiler, H. O. 1972. Drought resistance in subalpine nymphs of *Somatochlora semicircularis* Selys (Odonata: Corduliidae). *Amer. Midl. Nat.* 87: 215-221.