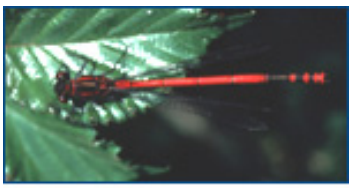
A Natural History of Dragonflies, Mayflies and Stoneflies

Editor's Introduction | Dragonflies, mayflies and stoneflies form a diverse group of species. What they all have in common is that their lives are centred around water. Many of them are stunningly beautiful, and hover in the air with elegance and acrobatic skill. Steve Brooks, a researcher in the department of entomology at The Natural History Museum, London, introduces these remarkable members of the insect world.

Dragonflies, mayflies and stoneflies are amongst the most primitive groups of freshwater insects. Each group has adapted in different ways to the aquatic lifestyle. Dragonflies are noted for their striking colours and aerial agility; mayflies are known for their short life-span and are mimicked by the artificial lures of fly-fishermen, while stoneflies are among the largest freshwater insects known. But all three groups spend most of their lives as larvae below the water, and go unnoticed by most people.



Ann Brooks

Adult, largered damselfly, *Phyrrhosomoa nymphula*.

Dragonflies belong to the order Odonata ('toothed jaw'), which has three suborders. The Zygoptera (meaning equal wings--the fore and hind wings are a similar shape), also called damselflies, is the most primitive group. They have a narrow body, the eyes are positioned on either side of the head, the wings are held over the body when at rest and they have a weak, fluttering flight. There are 20 families of Zygoptera and about 2,500 species world-wide. The second suborder, the Anisoptera (meaning unequal wings because the fore wings are much narrower than the hind wings), also known as dragonflies, have large eyes which occupy most of the head, the wings are held open when the insect is at rest, and they have a powerful flight. There are only eight families of Anisoptera, and about 2,700 species. The third suborder is the Anisozygoptera, which includes only two living species--one in the Himalayas and the other in Japan--although the fossil record shows that they were diverse in the past. Their wings are similar to those of damselflies, but the body and eyes are reminiscent of Anisoptera.

Ann Brooks

Adult common darter dragonfly, *Sympetrum striolatum*.

The modern families of dragonflies appeared in the Permian period, about 250 million years ago, but their ancestors, the giant Protodonata, were alive 300 million years ago and were much larger, with wingspans of up to one metre. Today there are about 5,500 species of dragonfly, most of which are tropical. There are about 120 known from Europe, some of which have dark colours, and a hairy thorax for warmth in their cold environment,.

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Anisozygopteran dragonfly, *Epiophlebia superstes*.

A dragonfly senses the world through its eyes. The two huge eyes have very good colour vision and are sensitive to movement in order to detect prey, potential mates and rivals. The largest eyes are found in dragonflies that live in dense tropical forest and those species that fly at dawn and

dusk. Dragonflies additionally have three simple eyes (ocelli) positioned on the top of the head which are connected directly by nerves to the wing muscles. They detect the position of the horizon, so a dragonfly can continually adjust its orientation while in flight.

The fastest speed recorded for a dragonfly is 38 kilometres an hour, despite the relatively slow motion of about 30 wing-beats per second, which means they do not make a buzzing sound. The wings beat and twist independently of each other in a figure-of-eight motion, which makes dragonflies very aerobatic. The wing veins have a corrugated arrangement to provide strength and lift, but the trailing edge of the wing is also very flexible.

Ken King

Dragonfly in flight.

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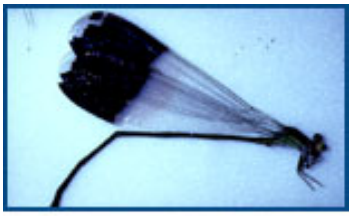
Jaws and spine-covered legs of an adult southern hawker dragonfly, *Aeshna cyanea*.

Dragonflies can fly forwards, backwards, sideways, and can hover. Hovering enables them to hold their heads still and spot mates and small insect prey more easily. Migratory dragonflies have a broad wing base, enabling them to glide and so conserve energy. Some even cross the Pacific Ocean. The thorax of a dragonfly is slanted so that the upper surface is inclined backwards, and the legs are brought forward. Although this prevents them from walking, it does mean that the spiny legs can be held in front of the head, where they are used to scoop up other insects which are caught and often devoured in flight.

Dragonflies are hemimetabolous (they do not have a pupal stage), and most have an aquatic larval stage. There are a few truly marine species, several that live in brackish water, and many that survive in arid regions where the larvae can develop quickly in the warm waters of temporary ponds before they dry up. Others live in flowing water, some even in waterfalls, where the larvae cling to moss on the rocky surface. Yet others, like the giant helicopter damselfly of Central America, live in tree rot-holes. One Hawaiian species has a terrestrial larva which lives in damp leaf litter.



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Helicopter damselfly from Costa Rica, *Megaloprepus caerulea*.

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Anisopteran dragonfly larva, *Libellula sp.*

Anisopteran larvae have two basic body forms which are adaptions to their specific environment. Larvae which live on the bottom of ponds, such as those from the family Libellulidae, have small eyes, long antennae and long legs covered in fine hairs (setae) covering the often flattened body. The long legs and flat body help prevent them sinking into the mud. The setae act to clothe the insect in debris, helping to conceal it. Because their environment is gloomy, bottom-dwelling larvae must detect their prey by touch rather than by sight, so they do not need particularly large eyes but long antennae are an asset. In contrast, larvae of the aeshnid family live amongst plants higher in the water column. They have a streamlined body, because they swim rather than crawl, larger eyes and small antennae, because they locate prey visually.

Anisopteran larvae breathe underwater using gills inside the abdomen. A current of water is sucked into the end of the abdomen and passed over the gills. By contracting the abdominal muscles and expelling the water, dragonflies can jet-propel themselves if they are threatened by predators or are chasing fast-moving prey. Some species of bottom-living larvae have a a cylindrical body with a long siphon at the end of the abdomen so they can stay hidden below the mud while reaching oxygenated water to breathe.

Damselfly larvae have three plate-like structures at the tip of the abdomen, known as caudal lamellae. They are covered with a thin membrane that allows oxygen to pass into the large number of tracheae (the branched hollow tubes that allow oxygen to diffuse around the body) in each lamella. The caudal lamellae also function as paddles when the larva swims with a sinuous motion through the water. Finally, the caudal lamellae can function as decoys to divert the attention of predators away from the body. A dragonfly can shed the lamellae very readily, but continue to breathe through the body wall.

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Larva of the red-eyed damselfy, *Erythroma najas*.

To feed, dragonfly larvae use a modification of the lower lip (the labium). The labium has a pair of spines at the tip and it is hinged at the base so it can be withdrawn under the head. When the larva is within range of prey it is shot out at high speed and the prey is impaled on the spines. The labium is then retracted to below the mouth and the prey can be devoured.

Adult dragonflies emerge after the fully developed larva has climbed up a stem or rock near the water's edge. It can take up to two hours for the adult to emerge and be ready for flight so, to avoid predators, this process usually happens at night. It is quicker in small dragonflies and damselflies, so they tend to emerge very early in the morning.

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Male broad-bodied chaser, *Libellula depressa*, holding territory.

Dragonflies have a adopted a range of strategies to find mates. Some males, including the broad-bodied chaser Libellula depressa, guard a territory from a suitable perch such as a reed stem. They wait for females and chase off rival males that enter the territory. The male will remain in the territory as long as it is successful in attracting females. After about two days, if it has been unsuccessful, it will move off and establish a territory elsewhere. The size of the territory is inversely related to the number of adult males in the vicinity, because the male finds it difficult to maintain a large territory in the face of a lot of competition. Some species, like the downy emerald Cordulia aenea, actually time share their territories. Males occupy the territory for about 20 minutes before moving off to feed, when they are replaced by another male for a short period. In this way a large number of males can share a small area.

The emerald damselfly *Lestes dryas* does not hold a territory at all, but it is very unusual to find females at a pond which are not already in tandem with a male. The females gather away from the pond in the surrounding countryside, where the males search for them. Any single adult males present at a pond have been unsuccessful at finding females and are hoping to seize a female that has been brought in by another male, although this strategy is usually unsuccessful.

Unlike most dragonflies, the Calopterygidae have a pre-mating courtship display. Initially a female perches in the male's territory. The male then takes off and hovers in front of the female displaying his coloured wings, or may land on the water to demonstrate the speed of current flow and the suitability of his territory for egg-laying. Prior to mating, male dragonflies grasp the female with two pairs of claspers at the tip of the abdomen. In damselflies the male grasps the female by the neck, whereas in Anisoptera the female is held by the head. Occasionally the eyes of the female can be damaged by the male's claspers leaving tell-tale mating scars. Once a male has a female in tandem it is very difficult for another male to mate with that female. When the female accepts the male, they adopt the wheel position for mating, a position unique to dragonflies. Sperm is produced at the tip of the abdomen, and the male uses a series of hooks and claspers at the base of the abdomen to pass the sperm across to the female.

Ann Brooks

Mating common blue damselflies, *Coenagrion puella* in the wheel position.

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Secondary male sex organs at the base of the abdomen in male Orthetrum (Libellulidae) dragonfly.

The blue-tailed damselfly Ischnura elegans maintains the wheel position for up to ten hours, which prevents other males from mating with the female. It also gives him plenty of time to use his long, barbed, whip-like penis to remove the sperm of rival males before inserting his own sperm and taking the female to oviposit (lay her eggs), thus ensuring that most of them were fertilised by him. Other dragonflies, for example Libellulidae, copulate very rapidly, perhaps spending just a few seconds while in flight. In these species, the penis is bulbous in shape and is used to push aside the sperm of rivals to ensure that the male fertilises a large percentage of the eggs. This strategy allows the male to mate with many females, but each female will lay only a small percentage of eggs fertilised by any single male. Selection pressure has resulted in an increase in the size and complexity of the female subgenital plate to ensure that only male conspecifics can mate successfully with her and also that they are prevented from displacing all the sperm. This in turn has resulted in an enlargement of the male penis.

Most damselflies stay together during oviposition so that the male can guard the female against predators and rival males. In damselflies and many dragonflies, the elongate eggs are laid inside a plant stem, cut with the ovipositor (the blade-like, tubular structure through which the eggs are laid), to protect the eggs from predators and desiccation. During oviposition, the female often climbs down the stem and completely submerges herself in the part of the plant which is underwater. Air is trapped between the wings so she can continue to breathe. Water is circulated over the bubble when the female rolls her body. Some species like the emperor dragonfly *Anax imperator* oviposit completely alone. In Libellulidae the spherical eggs are laid in a clump of jelly which sticks them to plants and helps to protect them from predators. They are washed off the tip of the female's abdomen when she dips it in the water while in hovering flight. The male and female begin oviposition in tandem, but when most of the eggs are laid, the male lets go and hovers above her, looking out for other females, while still being close enough to drive off other males.

Ovipositor at the tip of the abdomen of a female southern hawker dragonfly, *Aeshna cyanea*.

Most dragonfly larvae complete their development within a year, but large species may take two years or, if they live in cool water, up to five years to develop. Adult damselflies live from two to four weeks, while the larger Anisoptera may survive four to eight weeks. Two European species of damselfly can survive the whole winter in the adult stage, and several tropical dragonflies aestivate (become dormant) for several months throughout the dry season.

Mayfly larva, *Cloeon dipterum*.

Mayflies, with dragonflies, belong to the Palaeoptera, the most primitive group of winged insects. There are about 4,000 species in the world, divided amongst 20 families. The adults have two pairs of membranous wings, which are held upright above the body, two or three long tails at the tip of the abdomen, short antennae and relatively large eyes. The mouthparts are non-functional, and most adult mayflies survive for just a few days. The aquatic larvae have large gills along each side of the abdomen, and three tails. The body shape adapts them to their habitat. Clingers, such as Ecdyonuridae, live in fast-flowing streams. They have a streamlined, flattened body, long claws, and gills that act like suckers to help adhere them to stones. In swimmers, such as Baetidae, the tail is fringed with hairs and acts as a paddle. By flexing the abdomen up and down they swim rapidly in short bursts and stop suddenly. This helps them to avoid the attention of predators that are attuned to movements. Caenids live in the mud on the bottom of ponds. They are poor swimmers, and their gills are covered by a pair of large plates that prevent them being clogged by silt. Ephemerids are burrowers that have fringed gills, expanded front legs, tusks and a cylindrical body which all help them to burrow quickly into the sand of the slow-flowing rivers in which they live.

All mayfly larvae are herbivorous and feed on detritus or on microbes growing on the surface of stones and plants. To breathe they draw a current of water over the gills which beat continuously. Some species are very sensitive to pollutants, and so are useful indicators of water quality. The larvae of most species take one year to complete development, but a few species complete several generations in one year. Mayflies are unique among insects in being the only group which moult once they have reached a fully functional flying stage. The wings of the immature dun stage are dull because the wing membrane is double and is clothed in fine hairs that repel water. The mature imago (the reproductively mature adult insect) emerges when the dun has successfully flown from the water.

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Blue-winged olive dun, *Centroptilum luteolum*.

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Male blue-winged olive imago, *Centroptilum luteolum*. The shed skin of the dun stage is next to the adult imago.

Adult male mayflies have long forelegs, a pair of claspers at the tip of the abdomen and, in several families, the upper eye is enormously enlarged. Females have small eyes and short forelegs. The males congregate over trees and bushes by rivers and ponds, in an undulating flight from the top to the bottom of the swarm, waiting for females to arrive. When a female enters the swarm, a male approaches from below using his enlarged eyes to spot her. He grasps the base of the female's wings with his long forelegs and grips the tip of her abdomen with his claspers. Mating is completed before the couple fall to the ground. In most species, the female releases her eggs by flying over the water and dipping her abdomen to wash the eggs off. Other species land on stones and plants where they lay their eggs. A few develop the eggs within their body for up to two weeks and release live larvae into the water.

The word Plecoptera means "fan-shaped wing", which describes the way the hind wing is folded below the forewing in the adult insect. Stoneflies are divided into two suborders, the Antarctoperlaria and the Arctoperlaria. There are 1,700 species world-wide and 34 species in Britain. Adults are characterised by paired tails, small eyes and long antennae, and rely mainly on touch rather than sight. Like dragonflies and mayflies, they too are a primitive group of insects, thought to be distantly related to cockroaches.

The aquatic larvae also have two tails and a tuft of gills underneath the thorax. Most live in cool, torrential upland streams and are among the largest freshwater insects. Others live in lowland rivers and some in ponds. They are important as bio-indicators of water quality. The larvae are flat and seldom swim but creep around on stones or burrow into the silt and detritus. The smaller species feed on algae, detritus and debris, while the larger species are carnivorous. Most spend the winter as larvae and complete development in one year, but in cool, northern upland streams they can take several years to develop. When development is complete, the larvae crawl to shore and the adults quickly emerge on stones or vegetation. The freshly emerged adults fly straight into the trees.

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Stonefly larva, *Dinocras cephalotes*.

The adults settle with their wings folded flat over the top of the abdomen or rolled around the abdomen. They have a weak flight and poor powers of dispersal which has led to isolated populations having a distinct morphology. They tend to fly only on warm, still days and otherwise run around on foliage and even underneath stones by the stream-side. As an adaptation to windy upland conditions, some adults are brachipterous--that is, the wings are not fully developed. Adults that develop from carnivorous larvae lack functional mouthparts and so are unable to feed. The adults of other taxa feed on algae and lichens and can survive for a few weeks. Stoneflies mate on the ground where the males drum their abdomens in order to attract females. During oviposition the females either fly above the stream, dipping the abdomen onto the surface of the water to wash off the eggs or, in larger species, they land on the water and run across the surface releasing their eggs.

The morphology and biology of dragonflies, mayflies and stoneflies have all adapted them to the demands of aquatic life in different ways, but the longevity of their fossil records is a testament to how successful they have been.

British Dragonfly Society (www.dragonflysoc.org.uk) The Dragonfly Project (www.natdragonflymuseum.org.uk)

Books:

Title: Dragonflies
Format: Hardcover
Author: Miller, P.L.
Date: 01-DEC-87
ISBN: 0855463007

Title: Field Guide to the Dragonflies and Damselflies of Great Britain and Ireland
Format: Paperback
Author: Brooks, Steve
Date: 01-JAN-00
ISBN: 0953139905

Title: A Key to the Adults of the British Ephemeroptera
Format: Paperback
Author: Elliot, J. M.; Humpesch, U. H.
Date: 30-DEC-83
ISBN: 0900386452