= Mayfly =

Mayflies also known as shadflies or fishflies in Canada , are aquatic insects belonging to the order Ephemeroptera . This order is part of an ancient group of insects termed the Palaeoptera , which also contains dragonflies and damselflies . Over 3 @,@ 000 species of mayfly are known worldwide , grouped into over 400 genera in 42 families .

Mayflies are relatively primitive insects and exhibit a number of ancestral traits that were probably present in the first flying insects , such as long tails and wings that do not fold flat over the abdomen . They are aquatic insects whose immature stages (called " naiads " or " nymphs ") live in fresh water , where their presence indicates a clean , unpolluted environment . They are unique among insect orders in having a fully winged terrestrial adult stage , the subimago , which moults into a sexually mature adult , the imago .

Mayflies " hatch " (emerge as adults) from spring to autumn , not necessarily in May , in enormous numbers . Some hatches attract tourists . Fly fishermen make use of mayfly hatches by choosing artificial fishing flies that resemble the species in question . One of the most famous English mayflies is Rhithrogena germanica , the fisherman 's " March brown mayfly " .

The brief lives of mayfly adults have been noted by naturalists and encyclopaedists since Aristotle and Pliny the Elder in classical times . The German engraver Albrecht Dürer included a mayfly in his 1495 engraving The Holy Family with the Mayfly to suggest a link between heaven and earth . The English poet George Crabbe compared the brief life of a newspaper with that of a mayfly , both being called " Ephemera " , in 1785 .

= = Description = =

= = = Nymph = = =

Immature mayflies are aquatic , and are known as nymphs or naiads . They have an elongated , cylindrical or somewhat flattened body that passes through a number of instars (stages) , moulting and increasing in size each time . When ready to emerge from the water , nymphs vary in length , depending on species , from 3 to 30 mm (0 @.@ 12 to 1 @.@ 18 in) . The head has a tough outer covering of sclerotin , often with various hard ridges and projections ; it points either forwards or downwards , with the mouth at the front . There are two large compound eyes , three ocelli (simple eyes) and a pair of antennae of variable lengths , set between or in front of the eyes . The mouthparts are designed for chewing and consist of a flap @-@ like labrum , a pair of strong mandibles , a pair of maxillae , a membranous hypopharynx and a labium .

The thorax consists of three segments , the hindmost two , the mesothorax and metathorax being fused . Each segment bears a pair of legs which usually terminate in a single claw . The legs are robust and often clad in bristles , hairs or spines . Wing pads develop on the mesothorax , and in some species , hind wing pads develop on the metathorax .

The abdomen consists of ten segments , some of which may be obscured by a large pair of operculate gills , a thoracic shield (expanded part of the prothorax) or the developing wingpads . In most taxa up to seven pairs of gills arise from the top or sides of the abdomen , but in some species they are under the abdomen , and in a very few species the gills are instead located on the coxae of the legs , or the bases of the maxillae . The abdomen terminates in a pair of , or three , slender thread @-@ like projections .

= = = Subimago = = =

The final moult of the nymph is not to the full adult form , but to a winged stage called a subimago that physically resembles the adult , but which is usually sexually immature and duller in colour . The subimago often has partially cloudy wings fringed with minute hairs ; its eyes , legs and genitalia are not fully developed . Subimagos are generally poor fliers , and typically lack the colour patterns used

to attract mates . After a period , usually lasting one or two days but in some species only a few minutes , the subimago moults to the full adult form , making mayflies the only insects where a winged form undergoes a further moult .

= = = Imago = = =

Adult mayflies , or imagos , are relatively primitive in structure , exhibiting traits that were probably present in the first flying insects . These include long tails and wings that do not fold flat over the abdomen . Mayflies are delicate @-@ looking insects with one or two pairs of membranous , triangular wings , which are extensively covered with veins . At rest , the wings are held upright , like those of a butterfly . The hindwings are much smaller than the forewings , and may be vestigial or absent . The second segment of the thorax , which bears the forewings , is enlarged to hold the main flight muscles . Adults have short , flexible antennae , large compound eyes , three ocelli and non @-@ functional mouthparts . In most species , the males ' eyes are large and the front legs unusually long , for use in locating and grasping females during the mid @-@ air mating . In the males of some families there are two large cylindrical " turban " eyes that face upwards in addition to the lateral eyes . They are capable of detecting ultraviolet light and are thought to be used during courtship to detect females flying above them . In some species , all the legs are functionless , apart from the front pair in males . The abdomen is long and roughly cylindrical , with ten segments and two or three long cerci (tail @-@ like appendages) at the tip . Uniquely among insects , mayflies possess paired genitalia , with the male having two aedeagi (penis @-@ like organs) and the female two gonopores (sexual openings) .

= = Biology = =

= = = Reproduction and life cycle = = =

Mayflies are hemimetabolous (they have " incomplete metamorphosis ") . They are unique among insects in that they moult one more time after acquiring functional wings ; this last @-@ but @-@ one winged (alate) instar usually lives a very short time and is known as an imago , or to fly fishermen as a spinner . Mayflies at the imago stage are a favourite food of many fish , and many fishing flies are modelled to resemble them . The imago stage does not survive for long , rarely for more than 24 hours . In some species , it may last for just a few minutes , while the mayflies in the family Palingeniidae have sexually mature subimagos and no true adult form at all .

Often , all the mayflies in a population mature at once (a hatch) , and for a day or two in the spring or autumn , mayflies are everywhere , dancing around each other in large groups , or resting on every available surface . In many species the emergence is synchronised with dawn or dusk , and light intensity seems to be an important cue for emergence , but other factors may also be involved . Baetis intercalaris , for example , usually emerges just after sunset in July and August , but in one year , a large hatch was observed at midday in June . The soft @-@ bodied subimagos are very attractive to predators . Synchronous emergence is probably an adaptive strategy that reduces the individual 's risk of being eaten . The lifespan of an adult mayfly is very short , varying with the species . The primary function of the adult is reproduction ; adults do not feed , and have only vestigial (unusable) mouthparts , while their digestive systems are filled with air . Dolania americana has the shortest lifespan of any mayfly : the adult females of the species live for less than five minutes .

Male adults may patrol individually , but most congregate in swarms a few metres above water with clear open sky above it , and perform a nuptial (courtship) dance . Each insect has a characteristic up @-@ and @-@ down pattern of movement ; strong wingbeats propel it upwards and forwards with the tail sloping down ; when it stops moving its wings , it falls passively with the abdomen tilted upwards . Females fly into these swarms , and mating takes place in the air . A rising male clasps the thorax of a female from below using his front legs bent upwards , and inseminates her .

Copulation may last just a few seconds , but occasionally a pair remains in tandem and flutters to the ground . Males may spend the night in vegetation and return to the nuptial dance the following day . Although they do not feed , some briefly touch the surface to drink a little water before flying off .

Females typically lay between four hundred and three thousand eggs . The eggs are often dropped onto the surface of the water ; sometimes the female deposits them by dipping the tip of her abdomen into the water during flight , releasing a small batch of eggs each time , or deposits them in bulk while standing next to the water . In a few species , the female submerges and places the eggs among plants or in crevices underwater , but in general , they sink to the bottom . The incubation time is variable , depending at least in part on temperature , and may be anything from a few days to nearly a year . Eggs can go into a quiet dormant phase or diapause . The larval growth rate is also temperature @-@ dependent , as is the number of moults . At anywhere between ten and fifty , these post @-@ embryonic moults are more numerous in mayflies than in most other insect orders . The nymphal stage of mayflies may last from several months to several years , depending on species and environmental conditions .

Many species breed in moving water , where there is a tendency for the eggs and nymphs to get washed downstream . To counteract this , females may fly upriver before depositing their eggs . For example , the female Tisza mayfly , the largest European species with a length of 10 cm (4 in) , flies up to 3 kilometres (1 @.@ 9 mi) upstream before depositing eggs on the water surface . These sink to the bottom and hatch after 45 days , the nymphs burrowing their way into the sediment where they spend two or three years before hatching into subimagos .

When ready to emerge , several different strategies are used . In some species , the transformation of the nymph occurs underwater and the subimago swims to the surface and launches itself into the air . In other species , the nymph rises to the surface , bursts out of its skin , remains quiescent for a minute or two resting on the exuviae (cast skin) and then flies upwards , and in some , the nymph climbs out of the water before transforming .

= = = Ecology = = =

Nymphs live primarily in streams under rocks , in decaying vegetation , or in sediments . Few species live in lakes , but they are among the most prolific . For example , the emergence of one species of Hexagenia was recorded on Doppler weather radar by the shoreline of Lake Erie in 2003 . In the nymphs of most mayfly species , the paddle @-@ like gills do not function as respiratory surfaces because sufficient oxygen is absorbed through the integument , instead serving to create a respiratory current . However , in low @-@ oxygen environments such as the mud at the bottom of ponds in which Ephemera vulgata burrows , the filamentous gills act as true accessory respiratory organs and are used in gaseous exchange .

In most species , the nymphs are herbivores or detritivores , feeding on algae , diatoms or detritus , but in a few species , they are predators of chironomid and other small insect larvae and nymphs . Nymphs of Povilla burrow into submerged wood and can be problem for boat owners in Asia . Some are able to shift from one feeding group to another as they grow , thus enabling them to utilise a variety of food resources . They process a great quantity of organic matter as nymphs and transfer a lot of phosphates and nitrates to terrestrial environments when they emerge from the water , thus helping to remove pollutants from aqueous systems . Along with caddisfly larvae and gastropod molluscs , the grazing of mayfly nymphs has a significant impact on the primary producers , the plants and algae , on the bed of streams and rivers .

The nymphs are eaten by a wide range of predators and form an important part of the aquatic food chain . Fish are among the main predators , picking nymphs off the bottom or ingesting them in the water column , and feeding on emerging nymphs and adults on the water surface . Carnivorous stonefly , caddisfly , alderfly and dragonfly larvae feed on bottom @-@ dwelling mayfly nymphs , as do aquatic beetles , leeches , crayfish and amphibians . Besides the direct mortality caused by these predators , the behaviour of their potential prey is also affected , with the nymphs ' growth rate being slowed by the need to hide rather than feed . The nymphs are highly susceptible to pollution

and can be useful in the biomonitoring of water bodies . Once they have emerged , large numbers are preyed on by birds , bats and by other insects .

Mayfly nymphs may serve as hosts for parasites such as nematodes and trematodes . Some of these affect the nymphs ' behaviour in such a way that they become more likely to be predated . Other nematodes turn adult male mayflies into quasi @-@ females which haunt the edges of streams , enabling the parasites to break their way out into the aqueous environment they need to complete their life cycles . The nymphs can also serve as intermediate hosts for the horsehair worm Paragordius varius , which causes its definitive host , a grasshopper , to jump into water and drown .

= = = = Effects on ecosystem functioning = = = =

Mayflies are involved in both primary production and bioturbation . A study in laboratory simulated streams revealed that the Centroptilum genus of the mayfly increased the export of periphyton , thus indirectly affecting primary production positively , which is essential process for ecosystems . The mayfly can also reallocate and alter the nutrient availability in aquatic habitats through the process of bioturbation . By burrowing in the bottom of lakes and redistributing nutrients , mayflies indirectly regulate phytoplankton and epibenthic primary production . Once burrowing to the bottom of the lake , mayfly nymphs begin to billow their respiratory gills . This motion creates current that carries food particles through the burrow and allows the nymph to filter feed . Other mayfly nymphs possess elaborate filter feeding mechanisms like that of the genus Isonychia . The nymph have forelegs that contain long bristle @-@ like structures that have two rows of hairs . Interlocking hairs form the filter by which the insect traps food particles . The action of filter feeding has a small impact on water purification but an even larger impact on the convergence of small particulate matter into matter of a more complex form that goes on to benefit consumers later in the food chain .

= = = Distribution = = =

Mayflies are distributed all over the world in clean freshwater habitats , though absent from Antarctica . They tend to be absent from oceanic islands or represented by one or two species that have dispersed from nearby mainland . Female mayflies may be dispersed by wind , and eggs may be transferred by adhesion to the legs of waterbirds . The greatest generic diversity is found in the Neotropic ecozone , while the Holarctic has a smaller number of genera but a high degree of speciation . Some thirteen families are restricted to a single bioregion . The main families have some general habitat preferences : the Baetidae favour warm water ; the Heptageniidae live under stones and prefer fast @-@ flowing water ; and the relatively large Ephemeridae make burrows in sandy lake or river beds .

= = Conservation = =

The nymph is the dominant life history stage of the mayfly . Different insect species vary in their tolerance to water pollution , but in general , the larval stages of mayflies , stoneflies (Plecoptera) and caddis flies (Trichoptera) are susceptible to a number of pollutants including sewage , pesticides and industrial effluent . In general , mayflies are particularly sensitive to acidification , but tolerances vary , and certain species are exceptionally tolerant to heavy metal contamination and to low pH levels . Ephemerellidae are among the most tolerant groups and Siphlonuridae and Caenidae the least . The adverse effects on the insects of pollution may be either lethal or sub @-@ lethal , in the latter case resulting in altered enzyme function , poor growth , changed behaviour or lack of reproductive success . As important parts of the food chain , pollution can cause knock @-@ on effects to other organisms ; a dearth of herbivorous nymphs can cause overgrowth of algae , and a scarcity of predacious nymphs can result in an over @-@ abundance of their prey species . Fish that feed on mayfly nymphs that have bioaccumulated heavy metals are themselves at risk . Adult female mayflies find water by detecting the polarization of reflected light . They are easily fooled by

other polished surfaces which can act as traps for swarming mayflies .

The status of many species of mayflies is unknown because they are known from only the original collection data . Four North American species are believed to be extinct . Among these , Pentagenia robusta was originally collected from the Ohio River near Cincinnati , but this species has not been seen since its original collection in the 1800s . Ephemera compar is known from a single specimen , collected from the " foothills of Colorado " in 1873 , but despite intensive surveys of the Colorado mayflies reported in 1984 , it has not been rediscovered .

The International Union for Conservation of Nature (IUCN) red list of threatened species includes one mayfly : Tasmanophlebi lacuscoerulei , the large blue lake mayfly , which is a native of Australia and is listed as endangered because its alpine habitat is vulnerable to climate change .

= = Taxonomy and phylogeny = =

Over 3 @,@ 000 species of mayfly in 42 families and over 400 genera are known worldwide , including about 630 species in North America . Mayflies are an ancient group of winged (pterygote) insects . Putative fossil stem group representatives (e.g. Syntonopteroidea like Lithoneura lameerrei) are already known from the late Carboniferous . The largest mayfly of all times may have been Bojophlebia prokopi from the Upper Carboniferous of Moravia with a wing span of 45 cm (18 in) . The name Ephemeroptera is from the Greek ???????? , ephemeros = " short @-@ lived " (literally " lasting a day " , cf . English " ephemeral ") , and ?????? , pteron = " wing " , referring to the brief lifespan of adults . The English common name is for the insect 's emergence in or around the month of May in the UK . The name shadfly is from the Atlantic fish the shad , which runs up American East Coast rivers at the same time as many mayflies emerge .

From the Permian , numerous stem group representatives of mayflies are known , which are often lumped into a separate taxon Permoplectoptera (e.g. including Protereisma permianum in the Protereismatidae , and Misthodotidae) . The larvae of Permoplectoptera still had 9 pairs of abdominal gills , and the adults still had long hind wings . Maybe the fossil family Cretereismatidae from the Lower Cretaceous Crato Formation of Brazil also belongs as the last offshoot to Permoplectoptera . The Crato outcrops otherwise yielded fossil specimens of modern mayfly families or the extinct (but modern) family Hexagenitidae . However , from the same locality the strange larvae and adults of the extinct family Mickoleitiidae (order Coxoplectoptera) have been described , which represents the fossil sister group of modern mayflies , even though they had very peculiar adaptations such as raptorial forelegs .

The oldest mayfly inclusion in amber is Cretoneta zherichini (Leptophlebiidae) from the Lower Cretaceous of Siberia . In the much younger Baltic amber numerous inclusions of several modern families of mayflies have been found (Ephemeridae , Potamanthidae , Leptophlebiidae , Ametropodidae , Siphlonuridae , Isonychiidae , Heptageniidae , and Ephemerellidae) . The modern genus Neoephemera is represented in the fossil record by the Ypresian species N. antiqua from Washington State .

Grimaldi and Engel , reviewing the phylogeny in 2005 , commented that many cladistic studies had been made with no stability in Ephemeroptera suborders and infraorders ; the traditional division into Schistonota and Pannota was wrong because Pannota is derived from the Schistonota . The phylogeny of the Ephemeroptera was first studied using molecular analysis by Ogden and Whiting in 2005 . They recovered the Baetidae as sister to the other clades . Mayfly phylogeny was further studied using morphological and molecular analyses by Ogden and others in 2009 . They found that the Asian genus Siphluriscus was sister to all other mayflies . Some existing lineages such as Ephemeroidea , and families such as Ameletopsidae , were found not to be monophyletic , through convergence among nymphal features .

The following traditional classification is based on Peters and Campbell (1991) , in Insects of Australia .

= = In human culture = =

= = = In art and literature = = =

The Ancient Greek naturalist and philosopher Aristotle wrote in his History of Animals that

Bloodless and many footed animals , whether furnished with wings or feet , move with more than four points of motion ; as , for instance , the dayfly (ephemeron) moves with four feet and four wings : and , I may observe in passing , this creature is exceptional not only in regard to the duration of its existence , whence it receives its name , but also because though a quadruped it has wings also .

The Ancient Roman encyclopaedist Pliny the Elder described the mayfly as the " hemerobius " in his Natural History :

The River Bug on the Black Sea at midsummer brings down some thin membranes that look like berries out of which burst a four @-@ legged caterpillar in the manner of the creature mentioned above , but it does not live beyond one day , owing to which it is called the hemerobius .

The Dutch Golden Age author Augerius Clutius (Outgert Cluyt) illustrated some mayflies in his 1634 De Hemerobio (" On the Mayfly ") , the earliest book written on the group . Maerten de Vos similarly illustrated a mayfly in his 1587 depiction of the fifth day of creation , amongst an assortment of fish and water birds .

In 1495 Albrecht Dürer included a mayfly in his engraving The Holy Family with the Mayfly . The critics Larry Silver and Pamela H. Smith argue that the image provides " an explicit link between heaven and earth .. to suggest a cosmic resonance between sacred and profane , celestial and terrestrial , macrocosm and microcosm . "

In his 1789 book The Natural History and Antiquities of Selborne , Gilbert White described in the entry for " June 10th , 1771 " how

Myriads of May @-@ flies appear for the first time on the Alresford stream . The air was crowded with them , and the surface of the water covered . Large trouts sucked them in as they lay struggling on the surface of the stream , unable to rise till their wings were dried ... Their motions are very peculiar , up and down for so many yards almost in a perpendicular line .

The mayfly has come to symbolise the transitoriness and brevity of life . The English poet George Crabbe , known to have been interested in insects , compared the brief life of a newspaper with that of mayflies , both being known as " Ephemera " , things that live for a day :

The theme of brief life is echoed in the artist Douglas Florian 's 1998 poem , " The Mayfly " . The American Poet Laureate Richard Wilbur 's 2005 poem " Mayflies " includes the lines " I saw from unseen pools a mist of flies , In their quadrillions rise , And animate a ragged patch of glow , With sudden glittering " .

Another literary reference to mayflies is seen in The Epic of Gilgamesh , one of the earliest surviving great works of literature . The briefness of Gilgamesh 's life is compared to that of the adult mayfly .

In Szeged , Hungary , mayflies are celebrated in two monuments , one by Pal Farkas , and another on the Belvárosi bridge , symbolizing freedom .

= = = In fly fishing = = =

Mayflies are the primary source of models for artificial flies , hooks tied with coloured materials such as threads and feathers , used in fly fishing . These are based on different life @-@ cycle stages of mayflies . For example , the flies known as " emergers " in North America are designed by fly fishermen to resemble subimago mayflies , and are intended to lure freshwater trout . In 1983 , Patrick McCafferty recorded that artificial flies had been based on 36 genera of North American mayfly , from a total of 63 western species and 103 eastern / central species . A large number of these species have common names among fly fishermen , who need to develop a substantial knowledge of mayfly " habitat , distribution , seasonality , morphology and behavior " in order to match precisely the look and movements of the insects that the local trout are expecting .

Izaak Walton describes the use of mayflies for catching trout in his 1653 book The Compleat Angler

; for example , he names the " Green @-@ drake " for use as a natural fly , and " duns " (mayfly subimagos) as artificial flies . These include for example the " Great Dun " and the " Great Blue Dun " in February ; the " Whitish Dun " in March ; the " Whirling Dun " and the " Yellow Dun " in April ; the " Green @-@ drake " , the " Little Yellow May @-@ Fly " and the " Grey @-@ Drake " in May ; and the " Black @-@ Blue Dun " in July . Nymph or " wet fly " fishing was restored to popularity on the chalk streams of England by G.E.M. Skues with his 1910 book Minor Tactics of the Chalk Stream . In the book , Skues discusses the use of duns to catch trout . The March brown is " probably the most famous of all British mayflies " , having been copied by anglers to catch trout for over 500 years .

Some English public houses beside trout streams such as the River Test in Hampshire are named " The Mayfly " .

= = = As a spectacle = = =

The hatch of the giant mayfly Palingenia longicauda on the Tisza and Mure? Rivers in Hungary and Serbia , known as " Tisza blooming " , is a tourist attraction . The 2014 hatch of the large black @-@ brown mayfly Hexagenia bilineata on the Mississippi River in the US was imaged on weather radar ; the swarm flew up to 760 m (2500 feet) above the ground near La Crosse , Wisconsin , creating a radar signature that resembled a " significant rain storm " , and the mass of dead insects covering roads , cars and buildings caused a " slimy mess " .

= = = As food = = =

Mayflies are consumed in several cultures and are estimated to contain the most raw protein content of any edible insect by dry weight . In Malawi , kungu , a paste of mayflies (Caenis kungu) and mosquito is made into a cake for eating . Adult mayflies are collected and eaten in many parts of China and Japan . Near Lake Victoria , Povilla mayflies are collected , dried and preserved for use in food preparations .

= = = As a name for ships and aircraft = = =

" Mayfly " was the crew 's nickname for His Majesty 's Airship No. 1 , an aerial scout airship built by Vickers but wrecked by strong winds in 1911 before her trial flights .

Two vessels of the Royal Navy were named HMS Mayfly : a torpedo boat launched in January 1907 , and a Fly @-@ class river gunboat constructed in sections at Yarrow in 1915 .

The Seddon Mayfly , which was constructed in 1908 , was an aircraft that was unsuccessful in early flight . The first aircraft designed by a woman , Lillian Bland , was titled the Bland Mayfly .

= = = Other human uses = = =

In pre @-@ 1950 France , " chute de manne " was obtained by pressing mayflies into cakes and using them as bird food and fishbait . From an economic standpoint , mayflies also provide fisheries with an excellent diet for fish . Mayflies could find uses in the biomedical , pharmaceutical , and cosmetic industries . Their exoskeleton contains chitin , which has applications in these industries .

Mayfly larvae do not survive in polluted aquatic habitats and , thus , have been chosen as bioindicators , markers of water quality in ecological assessments .

In marketing , Nike produced a line of running shoes in 2003 titled " Mayfly " . The shoes were designed with a wing venation pattern like the mayfly and were also said to have a finite lifetime . The telecommunication company Vodafone featured mayflies in a 2006 branding campaign , telling consumers to " make the most of now " .