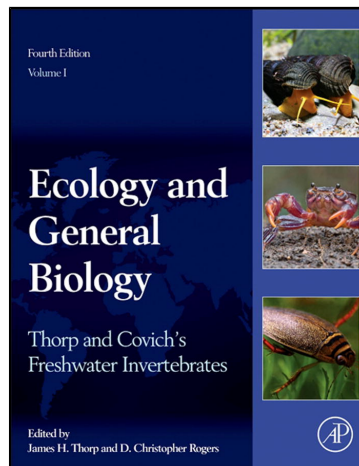


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# Order Ephemeroptera

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## INTRODUCTION TO MAYFLIES (EPHEMEROPTERA)

### Brief History and Paleontology

Extant Ephemeroptera represent what is left of a much diversified group of primitive flying insects (Ephemera), the origin of which goes back to the Carboniferous. Permian data confirm that the group was already present at the end of the Paleozoic. Ephemera reached their greatest diversity during the Mesozoic, mainly in the Jurassic and Cretaceous. All of these species share the presence of a costal brace at the base of the forewing and a reduction in the anal region of the hindwing with modern mayflies. However, contrary to them, they had homonomous wings (i.e., fore- and hindwing of the same size), and their aquatic stages could possess up to nine pairs of abdominal gills (compared with a

maximum of seven in extant species). Some species also had a wing span over 90 mm. All of these lineages, including Permian Ephemera (e.g., Protoneuridae or Mithridatidae), went extinct by the end of the late Jurassic. A recent study described adults and nymphs of a peculiar fossil insect order, the Coxoptera, which could be the true sister group of modern Ephemera (Staniczek et al., 2011). Although the adults have homonomous wings, the nymphs possess seven pair of gills as in the modern mayflies, a single tarsal segment (compared with five tarsal segments in the nymphs of Protoneuridae), and a single pretarsal claw (compared with paired claws in Protoneuridae). Heteronomous mayflies with reduced hindwings had appeared by the end of the Jurassic. The Tertiary fauna, as documented by fossils in Baltic or Dominican amber, is definitely contemporary with the presence of extinct and living genera of modern families.

## General Systematics

Ephemeroptera constitutes a small order of extant insects, with approximately 40 families, 440 genera, and 3330 species (Table 34.1). The state of our knowledge varies considerably depending on the geographic region. Some areas of North America and Europe are well known, whereas others, such as Southeast Asia or the Neotropics, still harbor numerous undescribed species. Within the period 2009–2011, almost 150 new species were described: more than 70 from South America and only 8 from North America. This can also be seen by comparing Table 34.1 with those published in Barber-James et al. (2008) and Brittain and Sartori (2003, 2009). We estimate that around 1000 species are still waiting to be described worldwide. The increasing use of genetic tools is also bringing new insight into mayfly systematics, which may potentially boost the number of taxa (Monaghan and Sartori, 2009). The supraspecific taxonomy has been the subject of major changes during the last 20 years, mainly because of the gathering of species into a more phylogenetic system, leading to a narrower concept of genus and family. As a result, the number of genera increased by 30% during this period because of the phylogenetic rearrangement of species groups, together with the discovery of new taxa, especially in the tropics. As shown in Table 34.1, the distribution of species among families is rather unequal. Because of their ancient origin (see previous section), we can represent ephemeropteran evolution as a baobab tree, with a large trunk, numerous broken ramifications, but few actual branches, some with very few leaves and others with bunches of boughs and dense foliage. Hence, fewer than 50% of the known species and genera belong to the families Baetidae and Leptophlebiidae, whereas 17 families are monogeneric, 8 of which are also monospecific. Several genera are particularly species rich, and the 12 richest encompass approximately one third of all known species (Table 34.2).

## Phylogenetic Relationships

The relationships of Ephemeroptera, Odonata, and Neoptera are one of the major unsolved problems in entomology (Blanke et al., 2012). Traditionally, Ephemeroptera and Odonata were clustered in the clade Paleoptera, characterized by wings unable to be folded against the body at rest. This clade was considered as the sister group of Neoptera. However, alternative theories have also been proposed, including the Metapterygota and Chiastomyaria hypotheses. The former suggests a basal position of Ephemeroptera compared with Odonata + Neoptera, whereas the latter hypothesizes that Odonata occupies a basal position compared with Ephemeroptera + Neoptera.

All of these hypotheses were proposed on morphological and/or molecular data, but no consensus exists at the moment, although recent studies bring new evidences for the Paleoptera hypothesis (Blanke et al., 2013; Thomas et al., 2013).

Deciphering the relationships among extant Ephemeroptera still attracts attention, and the higher classification is also now a matter of debate. McCafferty and Edmunds (1979) proposed two suborders: Schistonota (nymphs with free wing pads) and Pannota (nymphs with basally fused wing pads). It soon transpired that the Schistonota was paraphyletic, and McCafferty (1991) proposed a new classification, including three suborders (Setisura, Pisciforma and Rechtracheata, with the infraorder Pannota). Several modifications were put forward by McCafferty in subsequent years, in addition to the work of Kluge (e.g., 2004). All of these studies were based on morphology. The results were quite congruent and are summarized in Ogden and Whiting (2005) and Ogden et al. (2009). McCafferty and Kluge recognize a basal suborder, including the families Baetiscidae and Prosopistomatidae, characterized by the development of a mesonotal shield in the nymphs (hence the name Carapacea given by McCafferty) and the peculiar position of the anal veins in the forewings (hence the name Posteritorna given by Kluge). Three other suborders were then redefined as Furcatergalia (including Pannota, Ephemeroidea and Leptophlebiidae), Setisura (Heptagenioidea) and Pisciforma (including Baetoidea and Siphonuroidea). Ogden and Whiting (2005) proposed the first molecular phylogeny, followed by Ogden et al. (2009), who performed a combined analysis of five genes (5880 bp) and 101 morphological characters on 112 species in 107 genera and 42 families. The results are quite different from those that are based solely on morphology, although taxa such as Furcatergalia or Pannota were found to be monophyletic (Figure 34.1). The suborder Carapacea is not basal, but nested with the family Oligoneuriidae at the base of Furcatergalia, whereas the suborders Setisura and Pisciforma are highly paraphyletic, as is the well-established superfamily Baetoidea (Baetidae + Siphonuridae). Three families are basal to the leftover taxa: Siphuriscidae, Baetidae (Pisciforma), and Isonychiidae (Setisura). The nymph of *Siphuriscus chinensis* Ulmer, 1920 (Siphuriscidae) has been described recently and exhibits archaic morphological conditions, making it a good candidate to represent the oldest extant lineage (Zhou and Peters, 2003), confirmed by its position as the sister taxon to all other Ephemeroptera. The position of Baetidae and Isonychiidae is contradictory to previous hypotheses; however, as demonstrated by Ogden et al. (2009), the inclusion of these families in Pisciforma and Setisura, respectively, is based on homoplasies or plesiomorphic conditions. One of the main conclusions is that

**TABLE 34.1** List of the Extant Families, with Number of Genera and Species in the Different Biogeographic Realms, According to Barber-James et al. (2008), as of July 2012

Family	# Genera	PAL	NEA	NEO	ORI	AFR	AUS	PAC	# Species	Distribution Complement
Acanthametropodidae	2	1	2	0	0	0	0	0	3	Amphinotic
Ameletidae	2	17	35	0	5	0	0	0	56	
Ameletopsidae	4	0	0	2	0	0	4	0	6	
Ametropodidae	1	1	3	0	0	0	0	0	3	
Austremerellidae	1	0	0	0	0	0	1	0	1	Australia
Baetidae	104	212	137	239	150	194	43	3	956	
Baetiscidae	1	0	12	0	0	0	0	0	12	
Behningiidae	3	3	1	0	2	0	0	0	6	
Caenidae	26	43	36	37	33	61	13	1	221	Amphinotic
Coloburiscidae	3	0	0	1	0	0	6	0	7	
Coryphoridae	1	0	0	1	0	0	0	0	1	
Dicercomyzidae	1	0	0	0	0	4	0	0	4	
Dipteromimidae	1	2	0	0	0	0	0	0	2	Japan
Ephemerellidae	22	53	65	0	32	0	0	0	148	
Ephemeridae	7	11	16	3	39	13	0	0	80	
Ephemerythidae	1	0	0	0	0	3	0	0	3	
Euthyplociidae	7	0	0	7	3	10	0	0	20	Continental Africa
Heptageniidae	33	306	128	5	140	21	1	0	598	
Ichthybotidae	1	0	0	0	0	0	2	0	2	
Isonychiidae	1	14	16	1	4	0	0	0	34	
Leptohyphidae	14	0	29	124	0	0	0	0	145	New Zealand
Leptophlebiidae	141	58	69	247	68	52	120	38	643	
Machadorythidae	1	0	0	0	0	1	0	0	1	
Melanemerellidae	1	0	0	1	0	0	0	0	1	
Metretopodidae	3	4	9	0	0	0	0	0	11	Amphinotic
Neophemeridae	3	4	4	0	6	0	0	0	14	
Nesameletidae	3	0	0	1	0	0	6	0	7	
Oligoneuriidae	12	12	8	23	2	11	0	0	55	
Oniscigastridae	3	0	0	2	0	0	6	0	8	Amphinotic
Palingeniidae	6	10	0	0	14	4	4	0	32	
Polymitarciidae	6	6	7	60	12	2	0	0	85	
Potamanthidae	3	7	4	0	13	0	0	0	24	
Prosopistomatidae	1	3	0	0	11	6	2	0	22	New Zealand
Rallidentidae	1	0	0	0	0	0	1	0	1	
Siphlaenigmatidae	1	0	0	0	0	0	1	0	1	
Siphonuridae	4	25	25	0	0	0	0	0	48	

Continued

**TABLE 34.1** List of the Extant Families, with Number of Genera and Species in the Different Biogeographic Realms, According to Barber-James et al. (2008), as of July 2012—cont'd

Family	# Genera	PAL	NEA	NEO	ORI	AFR	AUS	PAC	# Species	Distribution Complement
Siphuriscidae	1	1	0	0	0	0	0	0	1	China
Teloganellidae	1	0	0	0	1	0	0	0	1	
Teloganodidae	8	0	0	0	13	8	1	0	22	
Tricorythidae	5	0	0	0	7	29	1	0	37	
Vietnamellidae	1	0	0	0	6	0	0	0	6	Southeast Asia
Total	441	793	606	754	561	419	212	42	3328	

PAL, Palaearctic; NEA, Nearctic; NEO, Neotropical; ORI, Oriental; AFR, Afrotropical; AUS, Australasian; PAC, Pacific Islands. Note that the total numbers of species in rows and columns are not necessarily equal because of the occurrence of some species in several realms.

**TABLE 34.2** The Twelve Most Speciose Mayfly Genera as of July 2012

Genus	Family	Species #	Distribution
<i>Baetis</i> Leach, 1815	Baetidae	152	Worldwide
<i>Rhithrogena</i> Eaton, 1881	Heptageniidae	152	Holarctic and Oriental
<i>Caenis</i> Stephens, 1835	Caenidae	141	Worldwide
<i>Epeorus</i> Eaton, 1881	Heptageniidae	93	Holarctic and Oriental
<i>Cloeon</i> Leach, 1815	Baetidae	74	Worldwide
<i>Pseudocloeon</i> Klapalek, 1905/ <i>Labiobaetis</i> Kluge and Novikova, 1987	Baetidae	73	Worldwide except Neotropical
<i>Afronurus</i> Lestage, 1924	Heptageniidae	64	Oriental; Afrotropical and Palaearctic
<i>Ecdyonurus</i> Eaton, 1868	Heptageniidae	61	Holarctic and Oriental
<i>Tricorythodes</i> Ulmer, 1920	Leptohyphidae	59	Panamerica
<i>Thraulodes</i> Ulmer, 1920	Leptophlebiidae	55	Panamerica
<i>Paraleptophlebia</i> Lestage, 1917	Leptophlebiidae	54	Holarctic and Oriental
<i>Ameletus</i> Eaton, 1885	Ameletidae	53	Holarctic and Oriental
Total		1031	

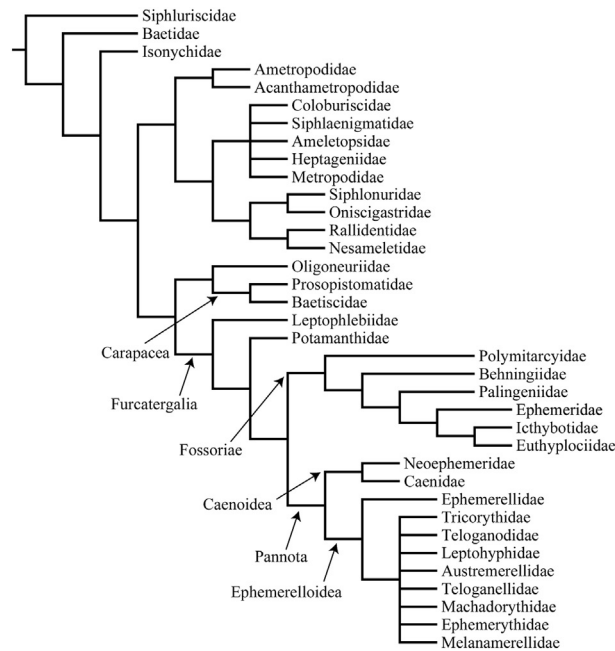
our understanding of mayfly phylogeny is hampered by morphological convergences in many features. The exact status of “Siphonuroidea” and “Heptagenioidea” still needs to be resolved, and further studies including more genes are necessary.

### Distribution, Diversity, and Endemism

Mayflies are distributed throughout the world, colonizing freshwater and sometimes brackish waters on all continents except Antarctica. Their presence on islands is explained on one hand by vicariance processes, induced, for instance, by the

Gondwana break up (New Caledonia, Seychelles, Sri Lanka), but also by dispersal events on continental islands (i.e., Madagascar) or oceanic islands (e.g., Macaronesia, la Reunion). Dispersal by mayflies and colonization of new habitats has long been considered a rare phenomenon, but there is a growing record of data that prove some species can disperse over at least 700 km. Thus, mayflies are only absent from remote islands, such as the Tristan da Cunha Archipelago and Gough Island (Barber-James, 2007) in the southern Atlantic Ocean or the Galapagos Islands and Polynesia in the Pacific Ocean, where distance and the lack of suitable habitats explain their probable absence. Accidental introduction by human activities





**FIGURE 34.1** Phylogenetic relationships among extant mayfly families; nodes with former appropriate names are mentioned. From Ogden et al., 2009.

and transportation is another way of colonizing new territories for animals and plants. The Hawaiian Archipelago seems to have been colonized by a single species of *Caenis* introduced during World War II from Southeast Asia (Smith, 2000) and an African species has been recently reported as introduced in Brazil (Salles et al., 2014).

At the family level, we can see that some have a cosmopolitan distribution (Baetidae, Caenidae, Leptophlebiidae) whereas others are restricted to a single continent (Baetiscidae in North America, Teloganellidae in Southeast Asia, Diceromyzidae in Africa) or even a single island group (Rallidentidae in New Zealand, Dipteromimidae in Japan). Some of them show a characteristic amphinotic distribution (i.e., a vicariant distribution in Australia, New Zealand, and Southern South America after the break off of Gondwanaland, such as the Ameletopsidae, Coloburiscidae, Nesameletidae and Oniscigastriidae). The Amazon basin seems to be the only home of peculiar families, such as Coryphoridae or Melanemerellidae. Some closely related families present interesting vicariance, such as Tricorythidae in Africa and Southeast Asia on one hand, and its sister group, the Leptohyphidae in the Americas on the other hand. Thus, the distribution of extant families is basically the result of the continental drift since the break off of Pangea, more than 200 mya.

Mayflies are especially diversified in temperate piedmont areas and tropical environments. Because of their ecological requirements, they are less diversified in arid or high-altitude areas, although endemism can be high.

Endemism in mayflies is a function of the history of the lineage under study and the ecological requirement of their nymphs. A good example is provided by Malagasy fauna, in which the Baetidae have been genetically studied (Monaghan et al., 2005a). If all but one species are endemic to the island, the lineages that are issued from vicariant processes are composed of endemic genera (paleoendemism), whereas those issued from dispersal processes included cosmopolitan or tropical genera (neoendemism). The nonendemic species is member of the genus *Cloeon*, the nymphs of which inhabit pools, swamps, or even water tanks. The females are ovoviviparous, living unusually longer than other species and thus are more amenable to disperse actively or passively. Species endemism is high in mayflies, reaching almost 100% in Australasia and Africa. Fewer than 60 species (<2%) occur in two different realms, most (~40) exhibiting a Panamerican distribution as a consequence of the Great American interchange (McCafferty, 1998). On a smaller scale, endemism is particularly pronounced in and within mountain ranges as well as in islands, even for those of oceanic origin and less than 2 mya old, such as Madeira (Gattolliat et al., 2008).

## GENERAL BIOLOGY

### External Anatomy of Imagos and Nymphs

#### Winged Stages

The general structure of mayfly adults and subadults is fairly constant throughout the diverse lineages. Differences between subimagos and imagos rely mainly on the opaqueness of wings and the presence of a fringe of setae along wing margins, the coloration of the abdomen, the length of the cerci and terminal filament, and the length of the fore legs of the males (Figures 34.2 and 34.3).

#### Head

The head is always small and bears dorsally a pair of short antennae, three ocelli, and two compound eyes. Mouthparts are vestigial because these stages do not feed; some larval structures (e.g., palpi) may be present but are nonfunctional. Compound eyes often present a strong sexual dimorphism, with males having larger eyes than females (exception in the Caenidae for instance). In some families, the male eyes are divided in two parts of different coloration (e.g., Leptophlebiidae, Ephemerellidae, Teloganodidae); in the Baetidae, the dorsal part is hyperdeveloped and forms a structure called *turbinate eyes* (Figure 34.4).

#### Thorax

Legs are composed of the following basic parts: coxa, trochanter, femur, tibia, tarsi, and a double claw, the last of which can be formed of two ungulates or one ungulate

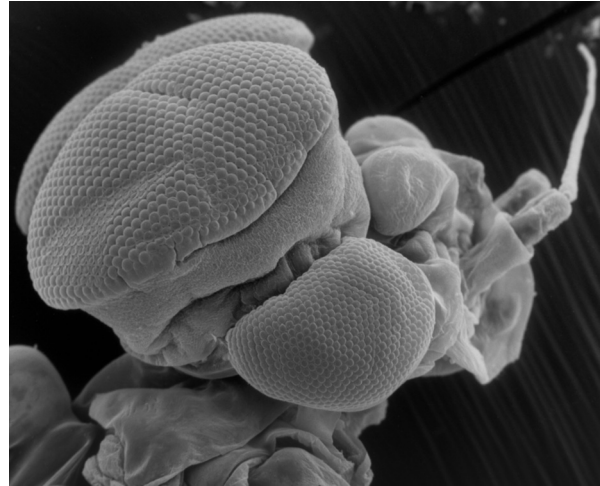


**FIGURE 34.2** Male subimago of *Ephemera danica*. Photograph courtesy of Sandro Marcacci, Aqualogue project.



**FIGURE 34.3** Male imago of *Ephemera danica*. Photograph courtesy of Sandro Marcacci, Aqualogue project.

and one paddle. In some burrowing mayflies (e.g., Polymitarcyidae) abortion of middle and hind legs can be seen, especially in females. Male fore legs are longer than the others and are used to grasp the female in flight for mating. The mesothorax is always more developed than the metathorax and bears the forewings which are larger than the hind ones. Wing venation differs considerably from one lineage to another and offers useful hints to separate families. The number of longitudinal and transversal veins can vary from the most complete set (e.g., as found in Siphonuridae or Ephemeridae) to highly reduced venation as in Caenidae and Leptohyphidae. Venation may also slightly differ



**FIGURE 34.4** Scanning electron microscopy picture of the head of *Alainites albinatii* (Baetidae) in lateral view; the elevated turbinated eye is characteristic of baetid male eyes. Photograph Michel Sartori, Microscopic Center, Lausanne University.

between males and females and rarely offers specific features for identification. Hindwings have a more reduced venation, but their shape may present specific characters. In several independent lineages (e.g., Baetidae, Caenidae, Leptophlebiidae), some or even all species lack hind wings.

### Abdomen

The abdomen is primitive and constitutes 10 segments that are identical and formed by a tergite and a sternite, at least for segments 1–6. On sternite 7, females often bear subgenital plate that covers the gonopore through which the eggs are extruded. Male genitalia are located on sternite 9 and constitute a styliger plate, which bears generally segmented forceps, and a double penis, more or less fused, the shape of which is of great taxonomic importance. Tergite 10 bears the two cerci and the terminal filament (three-tailed mayflies), the latter being highly reduced in some families (two-tailed mayflies).

### Nymphs

Contrary to the winged stages, mayfly nymphs are extremely diverse in shape and structure, reflecting their highly diverse habitats, locomotion, and feeding behavior. Some families are flattened dorsoventrally (e.g., Heptageniidae) and live under the stones and pebbles in the currents of streams (clingers) (Figure 34.5), others are pisciform (Baetidae, Siphonuroidea) and actively swim in lentic or lotic habitats (swimmers) (Figure 34.6), and some present highly transformed morphology such as sand-dwellers (Behningiidae).

### Head

All nymphs have one pair of antennae, three ocelli, and two compound eyes. Antenna length is variable among families, and the sexual dimorphism and special structure found in



**FIGURE 34.5** Nymph of *Rhithrogena semicolorata* (Heptageniidae). Photograph courtesy of Cyril Bennett.



**FIGURE 34.6** Nymph of *Baetis fuscatus* (Baetidae). Photograph courtesy of Cyril Bennett.

the adult compound eyes are already visible in half-grown nymphs. Mouthparts are highly diverse in shape and size, although the ground plan is always the same from dorsal to ventral: a single labrum, two mandibles, two maxillae (generally with palpi), one hypopharynx, and a labium with palpi. In burrowers, mandibles bear tusks for digging (Figure 34.7). Depending on the feeding habits of the nymphs, some mouthparts are more developed than others. For example, the maxillary and labial palps can be long and densely covered with setae in filter-feeding species, the mandibles can be sharp and acute in carnivorous species, and the apex of the maxillae is covered with special setae in scraping species. Some mouthparts may be highly transformed, such as the maxillae of Acanthametropodidae, which mimic a second pair of mandibles. Accessory tubular gills may be present at the base of the labium or on maxillae, as found in Oligoneuriidae, Nesa-meletidae, or Baetidae, but this is rather uncommon. All in all, mouthparts offer a significant set of characters to identify mayfly species.



**FIGURE 34.7** Nymph of *Ephemerella lineata* (Ephemeridae). Photograph courtesy of Cyril Bennett.

### Thorax

Numerous sclerites form the various parts of the meso- and metathorax. In one lineage, the whole thorax is covered by a notal shield (Baetiscidae, Prosopistomatidae). Wingpads develop progressively from one instar to the other. Forewing pads can be more or less fused; however, in all mature nymphs, they appear blackish just before the last molt, a stage that is often called “mature nymphs.” The three pairs of legs are built as in the imagos, except that the tarsi are unsegmented (segmented in Ameletopsidae) and the claw is always simple (but forked in Metretopodidae or absent in Behningiidae). Fore legs are sometimes transformed in relation to feeding habits or habitats. The most striking examples involve the presence of filtering setae on the femur and/or tibia, as in Isonychiidae or Oligoneuriidae, and the shovel-like legs of some burrowing species (Euthyplociidae, Palingeniidae). Species living in fast-flowing streams possess widened femora that allow the nymph to cling to stony substrates. Accessory gills may be found on the fore coxae in some species (Siphuriscidae, Isonychiidae). In general, nymphal legs offer a wide range of characters useful for species identification.

### Abdomen

Except for the genus *Murphyella* from southern South America (Coloburiscidae), all nymphs possess abdominal gills, the position and shape of which vary enormously between families or genera—hence, their taxonomic importance. They are normally fixed laterally to the abdomen (Figure 34.8), but they can be dorsal (Figure 34.9) or even ventral in some genera. Gills are originally present on segments 1–7, with almost all other combinations. They can be platelike, bilamellate, or bifurcate and mobile or not mobile. In some Heptageniidae, the first pair is transformed into a suction disk; in Caenidae and some other sprawlers in the infraorder Pannota, the second gill is modified into an operculum protecting the delicate remaining gills (Figure 34.10). Gills are not only used for respiration, but in some burrowing genera they also create a flux of water into the burrow that brings oxygen and fine particulate organic matter. The 10th segment bears the cerci





**FIGURE 34.8** Nymph of *Paraleptophlebia submarginata* (Leptophlebiidae). Photograph courtesy of Cyril Bennett.



**FIGURE 34.9** Nymph of *Serratella ignita* (Ephemerellidae). Photograph courtesy of Cyril Bennett.

and the terminal filament, which can be reduced and almost invisible. Cerci length is variable, from less than one third of the body length to more than 2 times. They can be covered with swimming setae or with whorls of stout setae. In some Ephemerellidae, the nymphs use them as a defense mechanism against predators by adopting a scorpion-like posture with cerci bent forward over the abdomen.

### Internal Anatomy of Nymphs

Mayfly nymphs possess a well-known internal anatomy that has been used for drawing phylogenetic evidences among lineages. Comprehensive information can be found in [Landa and Soldán \(1985\)](#). The nervous system is primitive and constitutes the brain, the subesophagal ganglion, three thoracic ganglia, and seven to eight abdominal ganglia. The ventral nerve cord can show several fusions in the abdomen, leading in some lineages to the reduction of



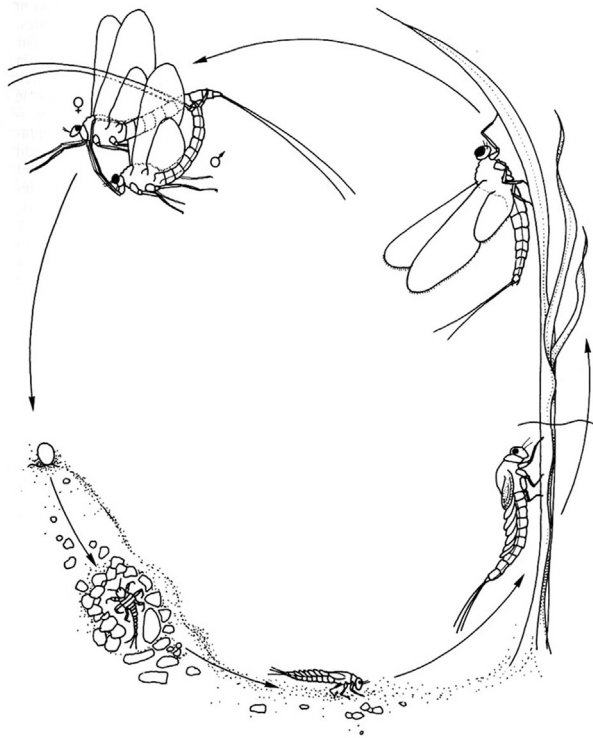
**FIGURE 34.10** Nymph of *Caenis horaria* (Caenidae). Photograph courtesy of Cyril Bennett.

the number of ganglia. The most derived example is displayed by the families Baetiscidae and Prosopistomatidae, in which abdominal ganglia are fused with the thoracic ones. The tracheal system is especially complicated in the head, where four major tracheae form what is known as the Palmen body. This structure consists of several concentric rings of intima, left behind at successive ecdyses, one layer being secreted during each instar. Microtome preparations of thin layers of this organ allow estimation of the number of instars the nymph has been through ([Ruffieux et al., 1996](#)). Reproductive organs generally occupy a large part of the internal body cavity; for instance, with ovaries being developed up to the head in *Caenis*. Ephemeroptera display unique gametogenesis because spermatozoa and eggs are all produced simultaneously and are functional at the end of the larval stage, indicating a tendency toward neoteny.

### Life Cycle

The life cycle of mayflies entails an aquatic and a terrestrial phase. However, they spend most of their life in the aquatic environment, only briefly emerging as winged adults to mate and lay eggs ([Figure 34.11](#)). The length of egg development varies from that characteristic of ovoviviparity—the release of live offspring—to a period of up to approximately 10 months in certain Arctic/alpine species. The duration of the nymphal stage ranges from a few weeks in some tropical species up to approximately 3 years in some of the larger, more long-lived northern temperate species. Estimates of the number of nymphal instars vary between 10 and 50; most are in the range 15–25. The number of instars for a particular species does not seem to be constant, but it probably varies within certain limits according to environmental conditions, such as food quality and temperature.

The major regulator of nymphal growth rates is water temperature. Other factors, such as food and current velocity, may exert a modifying influence on growth rates. No true diapausing nymphal stage has been reported in the Ephemeroptera, although growth rates can be very low



**FIGURE 34.11** Schematic representation of a mayfly life cycle. From Studemann et al., 1992.

during the winter, especially in Arctic/alpine regions. Egg diapause occurs, but it is uncommon (Elliott and Humpesch, 1980). The absence of small nymphs in field collections is often due to their occurrence deep in the substrate or their being too small to be detected by the sampling method used.

Most mayfly eggs hatch at temperatures in the range of 3–25°C, although there is considerable variation (Brittain, 1990). For example, in the North American *Hexagenia rigida* McDunnough, 1924, the eggs hatch successfully between 12°C and 32°C and even at 36°C if incubation is started at lower temperatures. In *Tricorythodes minutus* Traver, 1935, nymphs hatch between 7.5°C and 23°C, but mortality is least at 23°C. Hatching success is variable, ranging from over 90% in several *Baetis* and *Hexagenia* species to less than 50% in the Heptageniidae studied. The actual period over which the eggs hatch can be quite short. For example, most eggs of *Baetis rhodani* (Pictet, 1843) hatch in less than 10 days at temperatures above 10°C, although in certain species extended hatching has been demonstrated in the laboratory and the field (Knispel et al., 2006). Temperature is the major factor determining the length of the period of egg development in mayflies, and the incubation period in many species is well expressed by a positive power law relationship with water temperature (Elliott and Humpesch, 1980). Ovoviviparity is rare in the mayflies, found only in the family Baetidae, and is restricted in North America to some species of *Callibaetis* and most *Cloeon* species in the Old World.

There is an extensive literature on mayfly life cycles, although mostly from temperate areas of Europe and North America (Clifford, 1982). Care should be taken in the interpretation of mayfly life cycles, especially when based solely on field observations. Particular care is necessary in interpreting the duration of egg development from field data. Multivoltine species usually have two or three generations in temperate regions, often a slowly growing winter generation and one or two rapidly growing summer generations. Data from the tropics, where many species are nonseasonal and have overlapping cohorts, indicate that some species have very rapid growth and possibly go through up to 10 generations during the course of a year (e.g., Vasquez et al., 2009). There are two main types of univoltine cycle: when overwintering occurs during the nymphal stage after a relatively short egg developmental period and when hatching occurs in the spring after a long period of egg development.

Mayfly life cycles show a distinct trend from the tropics to Arctic/alpine regions. In the tropics, nonseasonal multivoltine cycles predominate, with seasonality becoming more distinct in mountainous and continental areas. In cool temperate regions, univoltine cycles dominate. Some mayflies, such as the widespread *Leptophlebia cupida* (Say, 1823), have a univoltine winter cycle over a wide range of latitudes and climates whereas other common and widespread species exhibit a substantial degree of life-cycle flexibility throughout their distributional range. This is perhaps best exemplified by many Baetidae. They have the ability to switch from multivoltine to univoltine, or even semivoltine in northern mountains, depending on water temperatures and food availability (Sand and Brittain, 2009). The North American *Hexagenia* show a similar flexibility over a wide latitudinal range from less than 1 year in the south to at least 3 years in the far north (Giberson and Rosenberg, 1992). There may also be differences in life-cycle duration between the sexes, with some males in a population emerging a year earlier in some populations of the ephemerid, *Ephemera danica* Müller, 1775 (Tokeshi, 1985). However, semivoltine life cycles, with generation times up to 3 years, are uncommon in mayflies and are often but not exclusively associated with large size. Earlier estimates (Clifford, 1982) indicated that only approximately 4% of mayfly life cycles were semivoltine, and this figure is unlikely to be exceeded as more information is published from tropical regions.

## Behavior of the Winged Stages

### Emergence

The process of emergence is a critical time because the insect is especially vulnerable to predation. In general, three main patterns can be observed. One group emerges from the water surface, where the subimago emerges from

its exuvia in the current and uses it as a raft before flying off. This behavior is found in many families, such as Baetidae, Ephemerellidae, Heptageniidae, and most burrowing families (e.g., Ephemeridae). The nymph may also crawl out of the water, completely or partially, onto stones or vegetation, and then molt. This is found in Siphonuridae and allied families, in Baetiscidae, and in some Leptophlebiidae (Figure 34.12). Finally, some species go through emergence underwater, as in some *Electrogena* (Heptageniidae) and *Caenis* species (Caenidae). All subimagos possess hydrofugous setae on their wings and body, allowing them to escape the water surface tension.

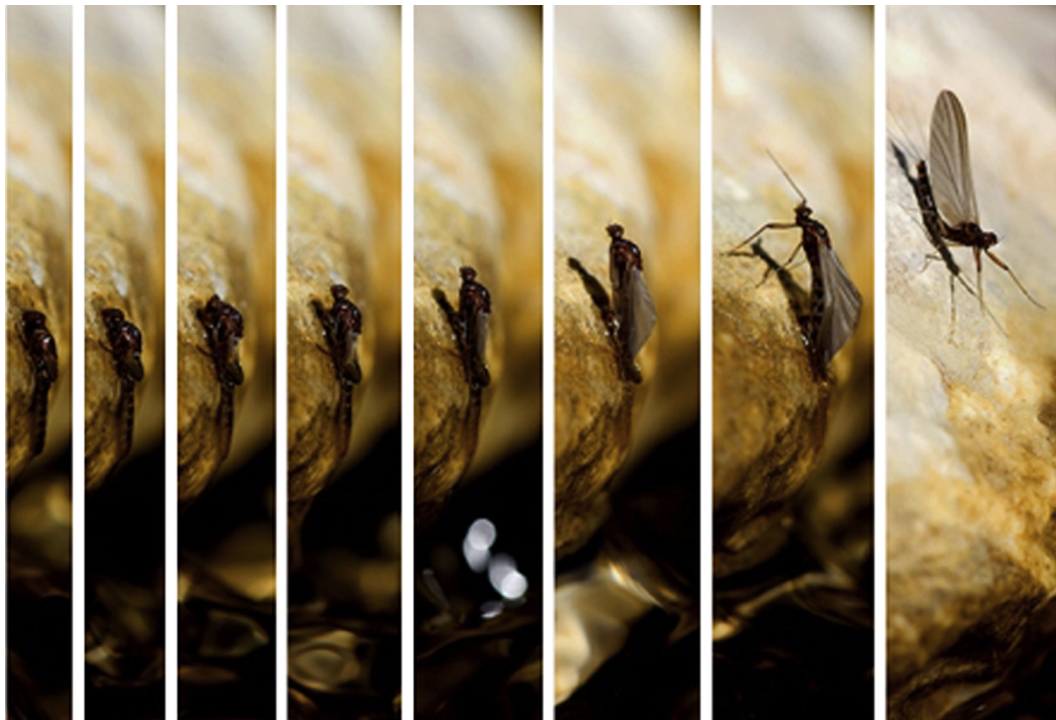
### Diel Patterns

Emergence time seems to be driven by temperature and light intensity. In temperate areas, emergence takes place during daytime whereas in the tropics, it is generally after dusk or before dawn. Short-lived species of *Caenis* behave like tropical species even in temperate regions. There is no sex-bias in the emergence pattern of most species, except for a marked early emergence of males in species for which females remain in the subimaginal stage for mating.

### Seasonal Patterns

In temperate and arctic areas, the different mayfly species usually have distinct and finite emergence periods whereas in the tropics, emergence is often nonseasonal.

An exception is the well-known lunar rhythm of emergence in the African species *Povilla adusta* Navás, 1912. Within a single species there are often latitudinal and altitudinal gradients in the timing of emergence. For example, in North American and European *Leptophlebia*, emergence occurs progressively later northward and at increasing altitudes. In habitats with several mayfly species, peak emergence of the major species is usually separated in time, especially in congeneric species (Brittain, 1982). It has been suggested that emergence falls into two main categories—synchronized and dispersed—and it represents two approaches for reducing adult mortality. Synchronous emergence attempts to saturate a potential predator, and dispersed emergence seeks to lower the possibility of predator-prey encounters (Sweeney and Vannote, 1982). Synchronous mass emergence is common in the burrowing mayflies such as *Hexagenia* (Ephemeridae), *Ephoron* (Polymitarcyidae), or *Palingenia* species (Palingeniidae), which emerge en masse (up to millions of individuals) during a short period, sometimes less than 1 hr, and for a couple of successive days each year. It has been shown that this synchronization in the Japanese species *Ephoron shigae* (Takahashi, 1924) takes place in the last nymphal instar. The size of last instar nymphs decreases as emergence approaches, and the smaller nymphs require fewer degree-days to complete development compared with the larger ones (Watanabe and Ohkita, 2000).



**FIGURE 34.12** Emergence process in *Habrophlebia lauta* (Leptophlebiidae). Photograph courtesy of Nadia Vuilleumier, Aqualogue project.



### Subimaginal Stage

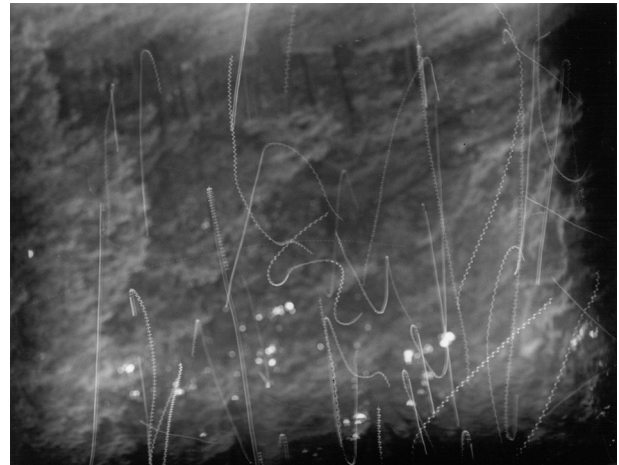
Mayflies are unique among extant insects because the winged stage arising from the aquatic nymph is a preadult that will molt once more into the reproductive adult stage. This transitional stage is called the subimago. Several explanations have been proposed, including a plesiomorphic condition lost in all other winged insects, or an apomorphy unique to this order (see [Edmunds and McCafferty, 1988](#) for a review). However, the subimago seems necessary for the mayfly to acquire fully developed genitalia, cerci, and fore legs (especially in males) to copulate. These characters could not be developed in an aquatic stage because they would compromise the survival of the mayfly. The subimago is a still stage, flying directly to riverine vegetation and waiting until the final molt. The duration of the subimaginal stage varies to some extent, but it is generally fixed within a species, genus, or even family. Air temperature and relative humidity are the key factors in this process. The subimaginal stage can last for more than 3 days in some Siphonuridae and Heptageniidae in springtime or in montane environments. In contrast, most tropical subimagos only last a few hours. In palingeniid mayflies (*Palinogenia* or *Cheirogenesia*), the subimaginal stage lasts only a couple of minutes. Molt to imago generally takes place in the vegetation; however, in some species, such as *Caenis*, or Oligoneuriidae, it takes place in the air, although molting is often only partial (only ventral part of the thorax and the abdomen).

### Flight Activity

Flight of mayfly adults is linked exclusively to reproduction because they do not feed. Swarming, mating, dispersal, and oviposition are the main sequences generally observed. Diel patterns of flight activity are rather specific, but they depend also on the local conditions. In cool environments (Arctic/alpine), flight tends to take place during the warm hours whereas in temperate zones, it is displaced to the end of the day, in late afternoon, or before sunset. Some species (e.g., *Baetis*) can be seen flying all day long. In tropical areas, most of the species fly during the first hour after dusk or before dawn.

Males usually exhibit a particular courtship, with a vertical active flight followed by a passive drop ([Figure 34.13](#)). This nuptial flight can be performed individually, in small groups of tens of males, or in huge swarms depending of the life history, atmospheric conditions, and landscape features. Other species may exhibit a horizontal flight or even a patrolling flight over the watercourse, as occurs in Oligoneuriidae and Palingeniidae.

Females generally enter the swarm and are grabbed by the first male; there is no chemical cue in the attraction of partners, and vision seems to be the only signal. Mating



**FIGURE 34.13** Long exposure against the light of male swarming mayflies; helicoidal marking indicates the active ascendant flight whereas the straight line represents the passive drop flight. Photograph courtesy of Pedro Galliker ([www.pedrogalliker.ch](http://www.pedrogalliker.ch)).

occurs most often in the air, but sometimes it can be on the ground or on the water surface. Once copulated, females leave the swarm whereas males reenter it and continue their courtship flight until exhaustion.

In several species, although not all, females fly predominantly upstream. This is seen as a compensation for downstream drift in the nymphal stage, thus completing what is known as the colonization cycle of lotic invertebrates. In a few species, such as *Dolania americana*, two female morphs are present, with one laying eggs immediately after copulation at the mating site and the other undergoing a dispersal flight ([Peters and Peters, 1995](#)).

Dispersal within and among watersheds has been the subject of several recent studies and shows that manmade obstacles, such as dams or bridges, may have important consequences for the genetic diversity of mayfly populations ([Monaghan et al., 2005b](#); [Malnas et al., 2011](#)). Genetic analyses have also indicated that recruitment at the reach scale is the result of few matings and oviposition by few females and that there may be differences in dispersal between males and females (e.g., [Bunn and Hughes, 1997](#)).

Mayflies display positive polarotaxis, and males and females are sometimes lured by manmade artifacts, such as asphalt roads or solar panels, which mimic the polarized light of the water (e.g., [Horvath et al., 2010](#)).

Oviposition can be performed by releasing eggs when flying (Palingeniidae), by touching the water surface and releasing a few eggs at a time (Heptageniidae, Oligoneuriidae), depositing a single batch of eggs on the water surface (Ephemerellidae), or dipping the abdomen under the water line when resting on the bank and releasing eggs (e.g., Leptophlebiidae, Heptageniidae, [Figure 34.14](#)). *Baetis* females actively enter the water ([Figure 34.15](#)) and



**FIGURE 34.14** Female of *Ecdyonurus* sp. (Heptageniidae) with a batch of eggs ready to be dipped into the water. Photograph courtesy of Sandro Marcacci, Aqualogue project



**FIGURE 34.15** A rare picture of a *Baetis* female entering the water to stick its eggs on a stone. Photograph courtesy of Nadia Vuilleumier, Aqualogue project.

crawl around until they can fix their eggs on the underside of suitable stones, the lack of which may limit egg supply (Lancaster et al., 2010). Females of ovoviparous species (e.g., *Cloeon*) find a resting place in the vegetation or any shelter (including human houses), where they wait for the completion of the offspring's embryogenesis before returning to the water to deposit the neonates. Because both sexes do not feed in the winged stages, they rely on the energetic reserves accumulated during their nymphal life. Flight activities are energetically demanding, and they store much of their reserves as lipids, which are more efficient for long sustainable flight than carbohydrates (Sartori et al., 1992). An exception is the flightless genus *Cheirogenesia* in Madagascar, which has switched from lipids to carbohydrates for skimming the water surface, a less energy-demanding activity (Ruffieux et al., 1998). Mayfly adult longevity is rather short, not exceeding one nuptial flight for most. Some tropical species of Tricorythidae and Leptohyphidae as well as species of Oligoneuriidae, Palingeniidae, and Caenidae are

especially short lived; the entire winged stages lasting less than 1 h.

## Reproduction

Most species produce 500–3000 eggs, but values range from less than 100 in *Dolania* to 12,000 in *Palingenia* (Brittain and Sartori, 2009). The fecundity values recorded for the females of the larger species of mayfly are higher than in most other insect groups except the social Hymenoptera. Most studies have shown a positive correlation between adult size and the number of eggs within a given population. In species with a long emergence period or with a bivoltine life cycle, early emerging females are larger; therefore, they are more fecund than those emerging later.

Parthenogenesis has been reported in many mayfly species (Brittain, 1982), although it is not generally obligatory. In nonobligatory parthenogenesis, the eggs develop more slowly and hatching success is often, but not always, low (Funk et al., 2010). In contrast, hatching success is high in species or populations in which parthenogenesis is obligatory. In several cases, parthenogenetic populations arise at the edge of a species' distribution, although not always (Tojo et al., 2006). It is interesting to note that the emergence period of the parthenogenetic North American *Cenotritium triangulifer* McDunnough, 1931 is unusually long, indicating the absence of a need for synchronization of emergence.

## GENERAL ECOLOGY AND BEHAVIOR

### Habitat Selection

Mayflies constitute a major part of the macroinvertebrate biomass and production in freshwater habitats. Seasonal variation in density, biomass, and annual production are strongly influenced by life-cycle parameters, such as generation time. Mayflies are found in almost all types of freshwater habitat, although they are more abundant and species rich in the tropics and warm temperate regions. Although the number of mayfly species usually decreases with increasing altitude and latitude, there are mayflies in ponds across the Arctic tundra and immediately downstream of glaciers in the Southern Hemisphere (Milner et al., 2001). Because of their winged adult stage and a propensity for downstream drift as nymphs, mayflies are often among the first macroinvertebrates to colonize virgin habitats. However, over longer distances their dispersal capacity is limited because of their fragility and short adult life. Within these basic zoogeographical limitations, abiotic factors (notably temperature, substrate, water quality, and, in running water, current velocity) seem to be the most important. Other factors such as ice, floods, drought, food, and competition may also influence abundance and distribution.



Many lotic mayflies are either dorsoventrally flattened, as in Heptageniidae, or streamlined as in *Baetis*—both of which are seen adaptations to life in swift currents. The physical substrate traps different amounts of detritus and silt, and this is a major factor influencing microdistribution within the stream or river. The richest mayfly community is often found in association with aquatic vegetation, which functions as a detrital trap and as a substrate for periphyton as well as providing shelter. For burrowing mayflies, the presence of the correct substrate is obviously a major determinant of macro- and microdistribution. In lakes, the highest mayfly diversity occurs in the shallow littoral areas. At deeper levels, the mayfly fauna, although often reaching high densities, is usually poor in species. Mayflies are generally absent from the profundal zone of lakes. Several species tolerate a wide range of salinities, and a few species within the Baetidae, Caenidae, and Leptophlebiidae occur in brackish waters.

### Physiological Constraints

High rates of oxygen consumption are often reported in association with emergence and gonad maturation. Nevertheless, many burrowing Ephemeridae and pond-dwelling Baetidae can survive moderately low oxygen concentrations, especially for short periods. However, so far only the European baetid, *Cloeon dipterum* (Linnaeus, 1761), has been shown to survive long-term anoxia (Nagell, 1980), although several species move into particular microhabitats more likely to contain oxygen, such as meltwater cracks in winter ice cover (Brittain and Nagell, 1981). Most of the lentic species are respiratory regulators, whereas most running water species cannot physiologically regulate oxygen consumption over concentration gradients, although they can usually position themselves in relation to the current, thereby regulating oxygen uptake.

### Feeding Behavior

Most mayfly nymphs are herbivores, feeding on detritus and periphyton. The herbivorous mayflies fall into two main categories: collectors and scrapers. Among the collectors, several genera are filter collectors, with setae on the mouthparts (e.g., Leptophlebiidae) or fore legs acting as filters (e.g., Isonychiidae, Oligoneuriidae). By using their gills to produce a current of water through their burrows, several Ephemeridae and Polymitarcyidae may also be regarded as filter collectors, at least for part of their food supply. They may also leave their burrows at night and graze on periphyton. Many mayflies are fine-particle detritivores. The other major feeding group within the mayflies, the scrapers, feed on the periphyton. For example, compared with stoneflies, the shredding habit is uncommon in mayflies. However, a species of *Paraleptophlebia* has been shown to shred leaves, but it depends on the fine organic matter produced

by shredding along with colonizing microorganisms to successfully complete development (Dieterisch et al., 1997).

Several species are opportunistic in their feeding habits, especially in harsh environments (Füreder et al., 2003). True omnivory is of limited occurrence, and the predatory habit is also relatively uncommon in the mayflies. In North America, *Dolania*, *Anaetris*, and the heptageniids *Pseudiron*, *Spinadis*, and *Anepeorus* feed largely on chironomids. The baetid genera, *Centroptiloides*, *Guloptiloides*, and *Raptobaetopus*, have carnivorous nymphs and some *Prosoptoma*. Several species, such as *Siphonurus occidentalis* (Eaton, 1885), *Herbrossus elouardi* Gattolliat and Sartori, 1998, and *Maccaffertium vicarium* (Walker, 1853), may shift from a predominantly detrital diet in the early instars to one containing a significant proportion or even a dominance of animal material in the mature nymphs. Seasonal differences are frequently a reflection of food availability, emphasizing the opportunistic nature of nutrition in many mayflies.

The time for food to pass through the gut is often short, and in *Baetis*, *Cloeon*, and *Tricorythodes* it has been shown to be only about 30 min. *Hexagenia* nymphs feed continuously during the day and night; and at most temperatures, they ingest over 100% of their dry body weight per day. In contrast, values for the surface-dwelling collector *Stenonema* are much lower and vary between 2% and 22% of dry body weight per day. The carnivorous *Dolania*, feeding more intermittently but on a higher energy diet, has consumption indices similar to those of *Stenonema*. Studies have shown little or no cellulase activity in mayflies, whereas the proteolytic activity of trypsin- and pepsin-like enzymes is very high (Brittain and Sartori, 2009). Some species have been observed to eat their own feces—a mechanism to increase the utilization of food resources.

### Other Relevant Behavior

Mayflies, especially Baetidae, are a major component of invertebrate drift in running waters (Brittain and Eikeland, 1988). Their drift shows a strong diel periodicity, with most activity during the hours of darkness and peaks at dusk and dawn. Drift rates are not constant for a particular species, and the larger size classes are usually more in evidence, especially as emergence approaches. Other factors that have been shown to influence mayfly drift include changes in current velocity and discharge, increased sediment loading, pollutants, temperature changes, oxygen conditions, density, food availability, and predators. Drift is a means by which nymphs can move to more optimal habitats. It also serves to disperse the early instar nymphs and is an important aspect of the colonization of new habitats downstream, notably after spates and pollution incidents (Gayraud et al., 2000).

Stream mayflies usually establish themselves after such events with a few weeks largely through the medium of drift, although oviposition by flying adults and movement of early instar nymphs from the deeper substrate layers may also contribute.

During the final stages of nymphal life there is a movement to and a concentration in the shallower areas of lakes and rivers. In running waters, springtime mass movements of mayfly nymphs along the banks of the main river and into slower flowing tributary streams or into areas flooded by spring snowmelt have been observed. In running water, mayfly nymphs may move down into the substrate in response to spates or as part of a daily rhythm. However, mayflies generally do not extend far down into the hyporheic zone (Boulton et al., 2010), although there are exceptions (Collier et al., 2004).

### Predators

Mayfly nymphs are eaten by a wide range of predators (Grant, 2001). Among the aquatic invertebrate predators are stoneflies, caddisflies, alderflies, dragonflies, water beetles, leeches, triclads, and crayfishes. Mayflies are also important food organisms for fish. Birds and winged insects, such as Odonata, also prey on mayfly adults. Several other animal groups, including spiders, amphibians, marsupials, and insectivorous mammals such as bats and shrews, have also been reported to take mayflies. The degree of predation on mayflies will vary with season, size of the nymphs, and the behavior patterns at that particular time. For example, mayfly nymphs are especially vulnerable when emerging. Drift patterns in mayflies may also change in relation to the presence and density of fish populations (Forrester, 1994). It has been demonstrated that populations of *Baetis* living in fish and fishless streams are not genetically distinct, but rather that traits associated with such contrasting environments are phenotypically plastic (Peckarsky et al., 2005). Predator detection appears to require visual or hydrodynamic cues in addition to chemical ones for an accurate assessment of predator risk (Tikkanen et al., 1994).

Predation may have major effects on mayfly population dynamics. In a Norwegian mountain lake, it was estimated that trout consumed 30–40% of the total annual mayfly production, whereas studies in experimental stream channels have demonstrated that avoidance of stonefly predators has dramatic consequences for mayfly fitness, including reduced fecundity (Peckarsky et al., 1993). There are alternative strategies by mayflies in response to stonefly predators in terms of mobility. *Baetis* species escape by entering the drift whereas *Ephemerella* relies on morphological defense, normally freezing, posturing, and crawling away (Peckarsky, 1996).

### Parasitic and Commensal Relationships

There is a wide range of organisms that live on or in mayflies, including a spectrum of bacterial, protozoan, nematode, cestode, and trematode parasites. As well as being final hosts for parasites, mayflies act as intermediate hosts, notably for fish parasites. Parasite infections may cause infertility or sex reversal in the mayfly host (Vance, 1996), in addition to behavioral changes that increase mortality (Vance and Peckarsky, 1997). For example, infection by mermithid nematodes may increase drift in mayflies, leading to greater susceptibility to fish predation (Williams et al., 2001). Ectoparasitic chironomids in the genera *Symbiocladius* and *Epoicocladius* attach to mayflies, feed on the host's hemolymph, and may cause sterility (Jacobsen, 1995).

Phoretic and commensal relationships with other organisms also occur. For example, blackflies are phoretic on mayflies, and two baetid genera—*Symbiocloeon* from Thailand and *Mutelocloeon* from West Africa—are commensal on freshwater mussels.

### Environmental Changes and Human Effects

Human activities have had and continue to have a significant effect on mayfly diversity throughout the world (Landa and Soldán, 1995). Several mayfly species have become extinct, and many are endangered and figure in the national Red Lists. The fragmentation of river networks either through physical barriers or through riparian agriculture and urbanization also hinders recovery (Alexander and Lamp, 2008). Nevertheless, colonization of restored habitats by mayflies usually takes place fairly rapidly, either through drift or from ovipositing adults, although it depends on the distance to existing populations.

By virtue of their widespread occurrence and importance in aquatic food webs and particularly in fish production, mayflies have been widely used as indicators of water quality and are frequently an important component of biomonitoring protocols (e.g., Buffagni, 1997). The mass emergence of burrowing mayflies from Lake Erie has provided a sensitive barometer of water quality (Schloesser and Nalepa, 2001). Organic and nutrient enrichment of Lake Erie in the 1940 and 1950s led to an increase in the intensity and frequency of mass emergence of *Hexagenia* until 1953, when prolonged periods of oxygen depletion in the lake hypolimnion caused the population to crash to virtual extinction. However, improvements in water quality have now led to a resurgence of emerging swarms, although contaminated sediments still hamper full recovery (Edsall et al., 2005). Nymphs of *Hexagenia* are also used in several bioassays for a range of contaminants, including detergents and heavy metals.

Pesticides also affect nontarget organisms such as mayflies, and studies in connection with blackfly control have demonstrated catastrophic drift and reduced biomass in mayfly populations in rivers treated with the insecticide, methoxychlor. The piscicide, rotenone, has been shown to cause mortality and increased drift in mayflies (Arnekleiv et al., 2001). Contamination by oil and gas exploration, as well as petroleum products, is also a threat to mayfly communities (Novikova and Kluge, 1997). Although most mayflies are adversely affected, a few species may show increases because of the extensive algal growth that often occurs on oiled substrates.

Acidification, either through long-range atmospheric dispersal or industrial discharges directly to the aquatic environments, in addition to the extensive planting of conifers, is a major threat to freshwater communities. Many mayflies are affected adversely by low pH, and emergence has been shown to be a particularly critical period. *Baetis* is especially sensitive, whereas other genera, such as *Lepophlebia*, are frequently encountered in acidic waters. The range in tolerance to low pH among mayflies has led to the development of acidification indices that are based on the species composition of the mayfly fauna, together with other aquatic insects such as stoneflies and caddisflies (Fjellheim and Raddum, 1990). Some degree of recovery has been registered in some of the areas affected by acidification as discharges are reduced. However, full recovery of mayfly communities, if attained at all, may take many years (Monteith et al., 2005).

River and lake regulation for water supply and hydropower can have a major effect on mayfly communities (Brittain and Saltveit, 1989). For example, an increase in winter temperatures and a fall in summer temperatures as a result of the release of hypolimnion waters may remove obligatory life-cycle thresholds, leading to extinction. Fecundity may also be influenced by changes in water temperature. Successive run-of-the-river power plants can substantially reduce the fast-flowing reaches of large rivers, increasing sedimentation and reducing the riffle species (Usseglio-Polatera, 1997; Medina and Vallania, 2001). In reservoirs themselves, lentic conditions and increased water level fluctuations usually lead to a reduction of species typical of stony substrates and macrophyte belts, although there may be an increase in the abundance of burrowing and silt-dwelling species in deeper waters. In many of the large African reservoirs, the mayfly *Povilla adusta* has developed substantial populations that burrow into the submerged trees and play an important role in tree breakdown.

Catchment land-use changes have effects on the mayfly fauna. Deforestation, often accompanied by the development of agriculture, is a major threat to mayfly biodiversity, especially in the tropics (Benstead and Pringle,

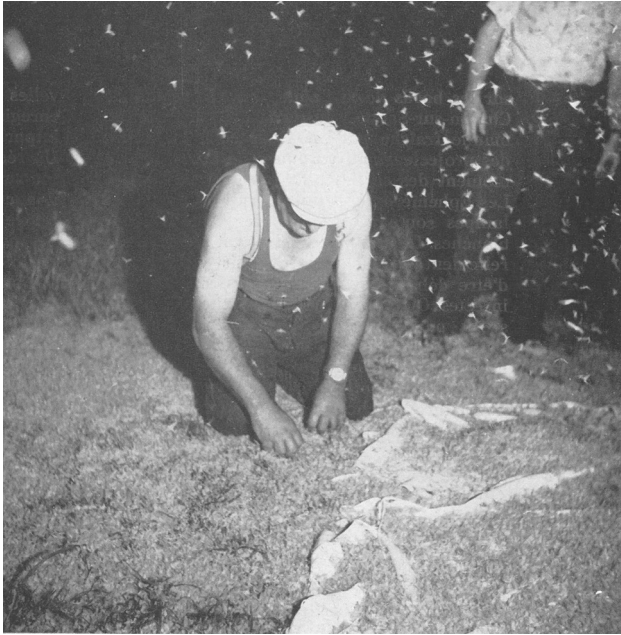
2004). Other important factors in the tropics associated with a drastic decrease in mayfly diversity include water abstraction for irrigation and human consumption, pollution, and alteration in riverine connectivity (Ramirez et al., 2008).

On a global scale, climate change will undoubtedly lead to significant changes in mayfly communities (Brittain, 2008). Suboptimal temperatures have been shown to result in smaller adult size in mayflies and thus lower fecundity (Sweeney and Vannote, 1978). This is likely to lead to changed mayfly distributions under global warming. During periods of rapid environmental transition, certain species traits will be beneficial. For example, some species will be able to adapt to warmer conditions by changing their life cycle from univoltine to bivoltine whereas others will be unable to adapt and will become extinct. In general, it is the widespread, generalist species that have the ability to adapt, resulting in decreased species richness. Nevertheless, some species will be able to extend their distribution to higher latitudes and altitudes as temperatures rise, although this depends on the availability of suitable and accessible habitats at higher altitudes. In the cold regions of the world, changes in water source because of the melting of glaciers and changes in the distribution of permafrost will affect mayfly distribution. Dispersal ability is also an important trait in a climate change scenario, and those mayfly species with good dispersal powers will have an advantage and are more likely to survive.

## Mayfly Interactions with Humans

Ephemeroptera are generally unknown to the public who call “mayflies” any fragile insect they encounter, such as chironomids and lacewings. On the contrary, mayfly nymphs, subimagos (duns), and imagos (spinners) are well known to anglers and fishermen in general, who imitate their shape and different stages to catch fish, especially salmonids. Huge emergences (e.g., *Hexagenia* or *Ephoron*) can be a problem in some occasions; for example, when the number of mayflies attracted by urban lights on bridges is so enormous that they cover roads like snow and can cause car accidents. This behavior has been exploited in France until the 1950s by farmers to collect this “chute de manne” (Figure 34.16), and once dried, sold it as a food for birds or as fish bait (Fontaine, 1959). The same emergence may lead to asthmatic problems in sensitive people because of the inhalation of cast skins or body fragments but not more than for other mass flying insects (Henson, 1966). In tropical Africa and Southeast Asia, nymphs of the burrowing *Povilla* tunnel holes in canoes and boats, which can be seriously damaged (Hartland-Rowe, 1958). However, the same mayfly is used in the making of a dried cake by the residents on the shores of the Lakes Victoria





**FIGURE 34.16** *Ephoron virgo* (Polymitarcyidae) “chute de manne” near the Marne River, France, in 1955. From Fontaine, 1959.

and Tanganyika (Bergeron et al., 1988). Mayflies also are part of human diet in South America and in Papua New Guinea (Grant, 2001). In Madagascar, nymphs of *Elassoneuria* (Oligoneuriidae) are collected and sold in the markets as “shrimps” (M. Sartori, personal observation). Finally, it should be noted that mayflies can be part of the intangible cultural heritage. In Hungary, *Palingenia longicauda* (Olivier, 1791), the largest and most spectacular European species, is at the origin of songs, poems, and even a festival that is held in Szolnok during the emergence period of the species (<http://www.tiszaviragfesztival.hu>). The same also happens in the United States (<http://www.mayflymusicfestival.com>).

## COLLECTING, REARING, AND SPECIMEN PREPARATION

Mayfly larvae and nymphs can be collected by a large range of devices, similar to other macroinvertebrates. Details can be found in Merritt et al. (2008). Adult mayflies are generally caught using a hand net with a telescopic handle and large opening to catch swarming adults. Beating the vegetation with a stick can also be used to collect resting imagoes and subimagoes in a hand net or a “Japanese umbrella.” Tent traps, such as the Malaise traps, can also be used but give differing results. Emergence traps can also be used, but they need to be checked regularly to remove subimagoes, preventing them from drowning and enabling rearing to the adult stage. Light traps at dusk and dawn, especially in the tropics, give significant results.

Rearing is an important procedure because it allows the association between nymphal and adult characteristics. Several techniques exist, but the most useful is to select a single mature nymph and put it in a rearing cage, either in situ or in a suitably equipped laboratory. Cages should be checked regularly for the emergence of the subimago. Once emerged, the nymphal skin must be placed in a vial with ethanol, and the subimago placed in another cage without direct sunlight and a relative humidity of more than 50%. Once the imago has molted, it is necessary to wait for a couple of hours for the teguments to dry and the final coloration to be fixed. The specimen can then be placed in ethanol with its nymphal and subimaginal exuviae for further study. Nowadays, molecular techniques using a barcode gene are more and more frequently used to associate adult and nymphal stages (Monaghan and Sartori, 2009).

Because of their soft cuticle and long appendices, mayflies are fragile insects and, as such, nymphs and adults should be preserved in ethanol. The ethanol concentration should be approximately 80% for long-term conservation but 100% if genetic studies are planned. If nymphs are fixed in 80% ethanol in the field, then the medium should be changed when arriving in the laboratory because of the high water and lipid concentration in the body. Ideally, specimens should be kept at negative or low temperatures (<6°C) and definitely never in a warm place, which will rapidly fade the colors. Some small specimens (e.g., *Caenis*) can also be mounted entirely on a slide according to an appropriate protocol for slide preparation. For morphological examination and species identification, slide preparation of nymphal mouthparts and appendices as well as male genitalia and wings is often necessary.

## REFERENCES

- Alexander, L.C., Lamp, W.O., 2008. Mayfly population density, persistence and genetic structure in fragmented headwaters habitats. In: Hauer, F.R., Stanford, J.A., Newell, R.L. (Eds.), *International Advances in the ecology, Zoogeography and Systematics of Mayflies and Stoneflies*. University of California Press, Berkeley, pp. 39–50.
- Arnekleiv, J.V., Dolmen, D., Ronning, L., 2001. Effects of rotenone treatment on mayfly drift and standing stocks in two Norwegian rivers. In: Dominguez, E. (Ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, pp. 77–88.
- Barber-James, H.M., 2007. Freshwater invertebrate fauna of the Tristan da Cunha islands (South Atlantic Ocean), with new records for Inaccessible and Nightingale Islands. *Trans. Roy. Soc. S. Afr.* 62, 24–36.
- Barber-James, H.M., Gattolliat, J.L., Sartori, M., Hubbard, M.D., 2008. Global diversity of mayflies (Ephemeroptera, Insecta) in freshwater. *Hydrobiologia* 595, 339–350.
- Benstead, J.P., Pringle, C.M., 2004. Deforestation alters the resource base and biomass of endemic stream insects in Eastern Madagascar. *Freshw. Biol.* 49, 490–501.

- Bergeron, D., Bushway, R.J., Roberts, F.L., Kornfield, I., Okedi, J., 1988. The nutrient composition of an insect flour sample from Lake Victoria, Uganda. *J. Food Compos. Anal.* 1, 371–377.
- Blanke, A., Greve, C., Wipfler, B., Beutel, R.G., Holland, B.R., Misof, B., 2013. The identification of concerted convergence in insect heads corroborates Palaeoptera. *Syst. Biol.* 62, 250–263.
- Blanke, A., Wipfler, B., Letsch, H., Koch, M., Beckmann, F., Beutel, R., Misof, B., 2012. Revival of Palaeoptera-head characters support a monophyletic origin of Odonata and Ephemeroptera (Insecta). *Cladistics* 28, 560–581.
- Boulton, A.J., Thibault, D., Kasahara, T., Mutz, M., Stanford, J.A., 2010. Ecology and management of the hyporheic zone: stream groundwater interactions of running waters and their floodplains. *J. North Am. Benthol. Soc.* 29, 26–40.
- Brittain, J.E., 1982. Biology of mayflies. *Annu. Rev. Entomol.* 27, 119–147.
- Brittain, J.E., 1990. Life history strategies in Ephemeroptera and Plecoptera. In: Campbell, I.C. (Ed.), *Mayflies and Stoneflies: Life Story and Biology*. Kluwer Academic Publishers, Dordrecht, pp. 1–12.
- Brittain, J.E., 2008. Mayflies, biodiversity and climate change. In: Hauer, F.R., Stanford, J.A., Newell, R.L. (Eds.), *International Advances in the Ecology, Zoogeography and Systematics of Mayflies and Stoneflies*. University of California Press, Berkeley, pp. 1–14.
- Brittain, J.E., Eikeland, T.J., 1988. Invertebrate drift - a review. *Hydrobiologia* 166, 77–93.
- Brittain, J.E., Nagell, B., 1981. Overwintering at low oxygen concentrations in the mayfly *Leptophlebia vesperina*. *Oikos* 36, 45–50.
- Brittain, J.E., Saltveit, S.J., 1989. A review of the effect of river regulation on mayflies (Ephemeroptera). *Regulated Rivers. Res. Manag.* 3, 191–204.
- Brittain, J.E., Sartori, M., 2003. Ephemeroptera. In: Resh, V.H., Cardé, R. (Eds.), *Encyclopedia of Insects*. Academic Press, New York, pp. 373–380.
- Brittain, J.E., Sartori, M., 2009. Ephemeroptera. In: Resh, V.H., Cardé, R. (Eds.), *Encyclopedia of Insects*, second ed. Academic Press, New York, pp. 328–333.
- Buffagni, A., 1997. Mayfly community composition and the biological quality of streams. In: Landolt, P., Sartori, M. (Eds.), *Ephemeroptera & Plecoptera Biology-Ecology-Systematics*. Mauron+Tinguely & Lachat SA, Fribourg, pp. 235–246.
- Bunn, S.E., Hughes, J.M., 1997. Dispersal and recruitment in streams: evidence from genetic studies. *J. North Am. Benthol. Soc.* 16, 338–346.
- Clifford, H.F., 1982. Life cycles of mayflies (Ephemeroptera) with special reference to voltinism. *Quaest. Entomol.* 18, 15–90.
- Collier, K.J., Wright-Stowe, A.E., Smith, B.J., 2004. Trophic basis of production for a mayfly in a North Island, New Zealand, forest stream: contributions of benthic versus hyporheic habitats and implications for restoration. *N. Z. J. Mar. Freshw. Res.* 38, 301–314.
- Dieterich, M., Anderson, N.H., Anderson, T.M., 1997. Shredder-collector interactions in temporary streams of western Oregon. *Freshw. Biol.* 38, 387–393.
- Edmunds, G.F., McCafferty, W.P., 1988. The mayfly subimago. *Annu. Rev. Entomol.* 33, 509–529.
- Edsall, T.A., Bur, M.T., Gorman, O.T., Schaeffer, J.S., 2005. Burrowing mayflies as indicators of ecosystem health: status of populations in western Lake Erie, Saginaw Bay and Green Bay. *Aquat. Ecosyst. Health Manag.* 8, 107–116.
- Elliott, J.M., Humpesch, U., 1980. Eggs of Ephemeroptera. *Annu. Rep. Freshw. Biol. Assoc.* 48, 41–52.
- Fjellheim, A., Raddum, G.G., 1990. Acid precipitation: biological monitoring of streams and lakes. *Sci. Total Environ.* 96, 57–66.
- Fontaine, J., 1959. Les chutes de manne. *Sci. Et. Nat.* 32, 1–6.
- Forrester, G.E., 1994. Diel patterns of drift by five species of mayfly at different levels of fish predation. *Can. J. Fish. Aquat. Sci.* 51, 2549–2557.
- Funk, D.H., Sweeney, B.W., Jackson, J.K., 2010. Why stream mayflies can reproduce without males but remain bisexual: a case of lost genetic variation. *J. North Am. Benthol. Soc.* 29, 1258–1266.
- Füreder, L., Welter, C., Jackson, J.K., 2003. Dietary and stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) analyses in alpine Ephemeroptera and Plecoptera. In: Gaino, E. (Ed.), *Research Update on Ephemeroptera and Plecoptera*. University of Perugia, Perugia, Italy, pp. 39–46.
- Gattolliat, J.-L., Hughes, S.J., Monaghan, M.T., Sartori, M., 2008. Revision of Madeiran mayflies (Insecta, Ephemeroptera). *Zootaxa*, 52–68.
- Gayraud, S., Philipp, M., Laurence, T.L., Maridet, L., 2000. The response of benthic macroinvertebrates to artificial disturbance: drift or vertical movement in the gravel bed of two sub-alpine streams. *Arch. für Hydrobiol.* 147, 431–446.
- Giberson, D.J., Rosenberg, D.M., 1992. Effects of temperature, food quality and nymphal rearing density on life history traits of a northern population of *Hexagenia* (Ephemeroptera: Ephemeridae). *J. North Am. Benthol. Soc.* 11, 181–193.
- Grant, P.M., 2001. Mayflies as food. In: Dominguez, E. (Ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, pp. 107–124.
- Hartland-Rowe, R., 1958. The biology of a tropical mayfly *Povilla adusta* Navàs (Ephemeroptera, Polymitarcidae) with special reference to the lunar rhythm of emergence. *Rev. Zool. Bot. Afr.* 58, 185–202.
- Henson, E.B., 1966. Aquatic insects as inhalant allergens: a review of American literature. *Ohio J. Sci.* 66, 529–532.
- Horvath, G., Blaho, M., Egri, A., Kriska, G., Seres, I., Robertson, B., 2010. Reducing the maladaptive attractiveness of solar panels to polarotactic insects. *Conserv. Biol.* 24, 1644–1653.
- Jacobsen, R.E., 1995. Symbiotic associations between Chironomidae (Diptera) and Ephemeroptera. In: Corkum, L.D., Ciborowski, J.J.H. (Eds.), *Current Directions in Research on Ephemeroptera*. Canadian Scholars' Press Inc., Toronto, pp. 317–332.
- Kluge, N.J., 2004. *The Phylogenetic System of Ephemeroptera*. Kluwer Academic Publishers, Dordrecht. 442 pp.
- Knispel, S., Sartori, M., Brittain, J.E., 2006. Egg development in the mayflies of a Swiss glacial floodplain. *J. North Am. Benthol. Soc.* 25, 430–443.
- Lancaster, J., Downes, B.J., Arnold, A., 2010. Environmental constraints on oviposition limit egg supply of a stream insect at multiple scales. *Oecologia* 163, 373–384.
- Landa, V., Soldán, T., 1985. Phylogeny and Higher Classification of the Order Ephemeroptera: A Discussion from the Comparative Anatomical Point of View. CSAV, Praha. 121 pp.
- Landa, V., Soldán, T., 1995. Mayflies as bioindicators of water quality and environmental change on a regional and global scale. In: Corkum, L.D., Ciborowski, J.J.H. (Eds.), *Current Directions in Research on Ephemeroptera*. Canadian Scholars' Press Inc., Toronto, pp. 21–29.
- Malnas, K., Polyak, L., Prill, E., Hegedus, R., Kriska, G., Devai, G., Horvath, G., Lengyel, S., 2011. Bridges as optical barriers and population disruptors for the mayfly *Palingenia longicauda*: an overlooked threat to freshwater biodiversity? *J. Insect Conserv.* 15, 823–832.
- McCafferty, W.P., 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. *Ann. Entomol. Soc. Am.* 84, 343–360.



- McCafferty, W.P., 1998. Ephemeroptera and the great American inter-change. *J. North Am. Benthol. Soc.* 17, 1–20.
- McCafferty, W.P., Edmunds, G.F., 1979. The higher classification of the Ephemeroptera and its evolutionary basis. *Ann. Entomol. Soc. Am.* 72, 5–12.
- Medina, A.I., Vallania, E.A., 2001. Ephemeroptera: abundance and distribution in regulated streams (San Luis, Argentina). In: Dominguez, E. (Ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, pp. 143–148.
- Merritt, R.W., Cummins, K.W., Resh, V.H., Batzer, D.P., 2008. Sampling aquatic insects: collection devices, statistical considerations, and rearing procedures. In: Merritt, R.W., Cummins, K.W., Berg, M.B. (Eds.), *An Introduction of the Aquatic Insects of North America*. Kendall/Hunt Publishing Company, Dubuque, Iowa, pp. 15–37. 1158 pp.
- Milner, A.M., Brittain, J.E., Castella, E., Petts, G.E., 2001. Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: a synthesis. *Freshw. Biol.* 46, 1833–1847.
- Monaghan, M.T., Gattolliat, J.L., Sartori, M., Elouard, J.M., James, H., Derleth, P., Glaizot, O., de Moor, F., Vogler, A.P., 2005a. Trans-oceanic and endemic origins of the small minnow mayflies (Ephemeroptera, Baetidae) of Madagascar. *Proc. Roy. Soc. B Biol. Sci.* 272, 1829–1836.
- Monaghan, M.T., Robinson, C.T., Spaak, P., Ward, J.V., 2005b. Macroinvertebrate diversity in fragmented Alpine streams: implications for freshwater conservation. *Aquat. Sci.* 67, 454–464.
- Monaghan, M.T., Sartori, M., 2009. Genetic contributions to the study of taxonomy, ecology, and evolution of mayflies (Ephemeroptera): review and future perspectives. *Aquat. Insects* 31, 19–39.
- Monteith, D.T., Hildrew, A.G., Flower, R.J., Raven, P.J., Beaumont, W.R.B., Collen, P., Kreiser, A.M., Shilland, E.M., Winterbottom, J.H., 2005. Biological responses to the chemical recovery of acidified fresh waters in the UK. *Environ. Pollut.* 137, 83–101.
- Nagell, B., 1980. Overwintering strategy of *Cloeon dipterum* (L.) larvae. In: Flannagan, J.F., Marshall, K.E. (Eds.), *Advances in Ephemeroptera Biology*. Plenum Press, New York, pp. 259–264.
- Novikova, E.A., Kluge, N.J., 1997. Mayflies (Ephemeroptera) of the Western Siberian lowland and oil pollution. In: Landolt, P., Sartori, M. (Eds.), *Ephemeroptera & Plecoptera: Biology–Ecology–Systematics*. Mauron+Tinguely & Lachat SA, Fribourg, pp. 269–274.
- Ogden, T.H., Gattolliat, J.L., Sartori, M., Staniczek, A.H., Soldán, T., Whiting, M.F., 2009. Towards a new paradigm in mayfly phylogeny (Ephemeroptera): combined analysis of morphological and molecular data. *Syst. Entomol.* 34, 616–634.
- Ogden, T.H., Whiting, M.F., 2005. Phylogeny of Ephemeroptera (mayflies) based on molecular evidence. *Mol. Phylogenet. Evol.* 37, 625–643.
- Peckarsky, B.L., 1996. Alternative predator avoidance syndromes of stream-dwelling mayfly larvae. *Ecology* 77, 1888–1905.
- Peckarsky, B.L., Cowan, C.A., Penton, M.A., Anderson, C., 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* 74, 1836–1846.
- Peckarsky, B.L., Hughes, J.M., Mather, P.B., Hillyer, M., Encalada, A.C., 2005. Are populations of mayflies living in adjacent fish and fishless streams genetically differentiated? *Freshw. Biol.* 50, 42–51.
- Peters, J.G., Peters, W.L., 1995. Evidence for a dispersal morph in females of *Dolania americana*. In: Corkum, L.D., Ciborowski, J.J.H. (Eds.), *Current Directions in Research on Ephemeroptera*. Canadian Scholars' Press Inc., Toronto, pp. 253–262.
- Ramirez, A., Pringle, C.M., Wantzen, K.M., 2008. Tropical stream conservation. In: Dudgeon, D. (Ed.), *Tropical Stream Ecology*. Academic Press, London, pp. 285–304.
- Ruffieux, L., Elouard, J.-M., Sartori, M., 1998. Flightlessness in mayflies and its relevance to hypotheses on the origin of insect flight. *Proc. Roy. Soc. B Biol. Sci.* 265, 2135–2140.
- Ruffieux, L., Sartori, M., L'Eplattenier, G., 1996. Palmen body: a reliable structure to estimate the number of instars in *Siphonurus aestivalis* (Eaton) (Ephemeroptera: Siphonuridae). *Int. J. Insect Morphol. Embryol.* 25, 341–344.
- Salles, F.F., Gattolliat, J.-L., Angeli, K.B., De-Souza, M.R., Goncalves, I.C., Nessimian, J.L., Sartori, M., 2014. Discovery of an alien species of mayfly in South America (Ephemeroptera). *ZooKeys* 399, 1–16.
- Sand, K., Brittain, J.E., 2009. Life cycle shifts in *Baetis rhodani* (Ephemeroptera) in the Norwegian mountains. *Aquat. Insects* 31, 283–291.
- Sartori, M., Keller, L., Thomas, A.G.B., Passera, L., 1992. Flight energetics in relation to sexual differences in the mating behaviour of a mayfly, *Siphonurus aestivalis*. *Oecologia* 92, 172–176.
- Schloesser, D.W., Nalepa, T.F., 2001. Changing abundance of *Hexagenia* mayfly nymphs in western Lake Erie of the Laurentian Great Lakes: impediments to assessment of lake recovery? *Int. Rev. Hydrobiol.* 86, 87–103.
- Smith, G.C., 2000. Rediscovery of the introduced mayfly *Caenis nigropunctata* (Ephemeroptera: Caenidae) in Waimānalo stream, O'ahu. *Bish. Mus. Occas. Pap.* 64, 30–31.
- Staniczek, A.H., Bechly, G., Godunko, R.J., 2011. Coxoplectoptera, a new fossil order of Palaeoptera (Arthropoda: Insecta), with comments on the phylogeny of the stem group of mayflies (Ephemeroptera). *Insect Syst. Evol.* 42, 101–138.
- Studemann, D., Landolt, P., Sartori, M., Hefti, D., Tomka, I., 1992. Ephemeroptera. *Insecta Helvetica Fauna* 9. Neuchâtel. 175 pp.
- Sweeney, B.W., Vannote, R.L., 1978. Variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* 200, 444–446.
- Sweeney, B.W., Vannote, R.L., 1982. Population synchrony in mayflies: a predator satiation hypothesis. *Evolution* 36, 810–821.
- Thomas, J.A., Trueman, J.W.H., Rambaut, A., Welch, J.J., 2013. Relaxed phylogenetics and the Palaeoptera problem: resolving deep ancestral splits in the insect phylogeny. *Syst. Biol.* 62, 285–297.
- Tikkanen, P., Muotka, T., Huhta, A., 1994. Predator detection and avoidance by lotic mayfly nymphs of different size. *Oecologia* 99, 252–259.
- Tojo, K., Sekine, K., Matsumoto, A., 2006. Reproductive mode of the geographic parthenogenetic mayfly *Ephoron shigae*, with findings from some new localities (Insecta: Ephemeroptera, Polymitarcyidae). *Limnology* 7, 31–39.
- Tokeshi, M., 1985. Life-cycle and production of the burrowing mayfly, *Ephemera danica*: a new method for estimating degree-days required for growth. *J. Anim. Ecol.* 54, 919–930.
- Usseglio-Polatera, P., 1997. Long-term changes in the Ephemeroptera of the River Rhone at Lyon, France, assessed using a fuzzy coding approach. In: Landolt, P., Sartori, M. (Eds.), *Ephemeroptera & Plecoptera Biology–Ecology–Systematics*. Mauron+Tinguely & Lachat SA, Fribourg, pp. 227–234.

- Vance, S.A., 1996. Morphological and behavioural sex reversal in mermithid- infected mayflies. *Proc. Roy. Soc. B Biol. Sci.* 263, 907–912.
- Vance, S.A., Peckarsky, B.L., 1997. The effect of mermithid parasitism on predation of nymphal *Baetis bicaudatus* (Ephemeroptera) by invertebrates. *Oecologia* 110, 147–152.
- Vasquez, D., Flowers, R.W., Springer, M., 2009. Life history of five small minnow mayflies (Ephemeroptera: Baetidae) in a small tropical stream on the Caribbean slope of Costa Rica. *Aquat. Insects* 31, 319–332.
- Watanabe, N.C., Ohkita, A., 2000. Life cycle and synchronization of nymphal development of the mayfly *Ephoron shigae* in Japan (Ephemeroptera: Polymitarcyidae). *Aquat. Insects* 22, 108–121.
- Williams, J.K., Townsend, C.R., Poulin, R.G., 2001. Mermithid nematode infections and drift in the mayfly *Deleatidium* spp. (Ephemeroptera). *J. Parasitol.* 87, 1227–1229.
- Zhou, C.F., Peters, J.G., 2003. The nymph of *Siphuriscus chinensis* and additional imaginal description: a living mayfly with Jurassic origins (Siphuriscidae new family: Ephemeroptera). *Fla. Entomol.* 86, 345–352.