

## EPHEMEROPTERA

GEORGE F. EDMUNDS, JR.

Mayflies, an order of paleopterous Insecta. Adults have inconspicuous, setiform antennae. The compound eyes are sexually dimorphic in most species. The eyes of the male are large and relatively close together, usually with larger facets on the upper part, while the eyes of the female are small and widely separated; in some small mayflies the eyes of the male are like those of the female. The mouthparts are vestigial. The prothorax and metathorax are reduced;

the mesothorax is large. The forewings are more or less triangular, and their surface is usually strongly fluted. There are usually many longitudinal veins and crossveins; convex and concave veins may be paired; in small mayflies there are usually few crossveins. Hindwings are absent or present; their size ranges from minute to 60% as long as the forewings. The forelegs of the male are elongated and specialized for grasping the female in flight; in some short-

lived adults the middle and hind legs of the male and all legs of the female may be obsolescent or vestigial. The abdomen is 10-segmented and bears two long cerci and a median terminal filament which is vestigial in many species. The male genitalia consist of paired forceps or styli of one to seven segments and a pair of penes that may be partially or completely fused.

The larvae, also called nymphs or naiads, usually have chewing mouthparts; some carnivores lack a molar area on the mandibles. The labial and maxillary palpi usually have three segments (sometimes two, rarely many). The tarsi consist of a single segment. The claws are single, rarely absent. The forelegs may be adapted for burrowing, filter feeding, or grooming. The abdomen is usually cylindrical but is sometimes strongly depressed. Gills arise from the pleural region of abdominal segments I-VII on the primitive extant genera, but may be present only on I-V, I-VI, II-VII, III-VII, or IV-VII; gill positions range from lateral to dorsal or ventral. There are two or three caudal filaments.

The eggs are laid in the water. They may hatch in a few minutes or lie dormant for as long as 11 months. In temperate regions most species have an annual cycle and take 3 to 11 months for larval development. In colder waters development is longer, and *Hexagenia* larvae may take 2 years in Canada; larval development in some temperate species may take as little as 10 days to 2 weeks. In the tropics only a small percentage of the species appear to have an annual cycle, and the average development times are probably shorter. Larvae are reported to pass through up to 55 instars; recent studies show 12 to 14 instars, and this may be more typical for the order. The emergence of the subimago may occur after the larva crawls out of the water, or from

the water surface, or underwater.

Mayflies are the only insects with two winged stages; the winged subimago molts and becomes the imago. In some genera the female does not molt to the imago, and in the Oligoneuriidae the subimaginal molt does not occur on the wing surfaces. The subimago stage lasts from a few minutes to 2 days. The imagos may live only for about 2 hr in a number of specialized forms, but many live 2 or 3 days; in the tropics most mayflies live less than 1 day. Adult mayflies do not feed, but they are capable of imbibing water.

Most mayflies mate in the air, although a few individuals may copulate on a substrate; at least some Palingeniidae mate on the surface of the water. Mass nuptial flights occur in some species. The males typically form swarms and fly up and down or hover; a few specialized genera have rapid, level flight. A female that enters the swarm is grasped by a male, and copulation ensues. Males or females may mate more than once.

Most mayfly larvae feed on detritus. Others scrape diatoms and other microscopic life from rocks, decaying leaves, and the surfaces of higher plants. Several independent lineages filter their food from the passing water column. A few genera are primarily carnivores. Mayflies are widespread in a great variety of fresh (rarely brackish) water over most of the earth; they tend to be absent from most true oceanic islands.

The extant species of Ephemeroptera (=Ephemerida) are divided into 2 suborders (Schistonota and Pannota), 6 superfamilies, and 19 families. There are about 2100 described species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

### SCHISTONOTA

Adults usually lack a mesoscutellum extending over the metanotum. The metanotum is relatively large and mostly exposed. The mesoscutellum is usually not highly tapered; however, when it is tapered, more than half of the metanotum is exposed.

Mature larvae usually have wing pads which are free from each other at the midline for more than half their length; in primitive *Anaetris* the wing pads are free nearly to the base. The gills of the Schistonota may be dorsal, ventral, or lateral but are rarely on a shelflike area of the abdomen. When dorsal, the gills tend to project upward from the abdomen and are usually placed more laterally than those of Pannota.

Schistonota are variously swimmers, sprawlers, burrowers, crawlers, or clingers. Strong swimming habits are characteristic of most subfamilies of the Siphonuridae, most Baetidae, the Metretopodidae, the primitive Oligoneuriidae (Isonychiinae), and the Ametropodidae. Some Oligoneuriinae have slow movements which strongly parallel the Pannota. The Heptageniidae and many Leptophlebiidae are flattened and adapted for clinging to stones; they are generally poor swimmers. Specializations for burrowing have evolved several times in the Schistonota.

The larvae are detritivores, scrapers of algae from stones, feeders on filamentous algae, omnivores, and predators. The predatory habit has evolved no fewer than eight times in these largely active larvae.

Schistonota are widely distributed, the 2 included families Baetidae and Leptophlebiidae being the most widespread in the world. The suborder is divided into 3 superfamilies (Baetoidea, Leptophlebiioidea, and Ephe-

meroidea); it contains more than 85% of the genera and more than 80% of the extant species of mayflies.

**References.** W. P. McCafferty and G. F. Edmunds, Jr., The higher classification of the Ephemeroptera and its evolutionary basis, *Ann. Entomol. Soc. Amer.*, 72:5-12, 1979.

### Baetoidea

This group includes the most primitive families, but some genera are specialized as adults, larvae, or both. Morphological characterization thus would be tedious and have many exceptions. The adults are variable. The larvae are usually streamlined, minnowlike, and active or flatheaded with the mouthparts totally hidden beneath the head. The gills usually consist of a simple flat plate or of a plate and fibrilliform tuft; they usually occur on segments I-VII.

This superfamily (often called Heptagenioidea) is extremely widespread; there are 6 families.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Siphonuridae.** In adults the eyes are sexually dimorphic; the upper portion has larger facets than the lower portion in the male. The forewings are relatively narrow and triangular, with numerous crossveins; the hindwings are relatively large. The anterior cubitus (CuA) vein is attached to the hind margin by a series of veinlets; the fork of the posterior medius (MP) vein is relatively symmetrical. The posterior medius (MP) of the hindwing is forked near the base or is unforked. The larvae are streamlined and minnowlike. The head is hypognathous; the eyes are lateral; and the antennae are usually short. The glossae and paraglossae of the labium are short and broad. The gills usually occur

on segments I–VII. The posterolateral corners of the abdominal segments usually have well-developed projections.

This family includes the most primitive of the extant mayflies. The larvae of the subfamilies Siphonurinae and Oniscigastrinae appear to be omnivores, while other larvae feed on detritus, plants, or other insects. Acanthametro-pinae and Ameletopsinae are carnivores. Most Siphonuridae are found in streams, but some live in standing waters. Siphonuridae contain 22 genera and 123 species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Ametropodidae.** Family containing the single genus *Ametropus*. The forewings of adults have unique venation. There are two pairs of cubital intercalary veins, the anterior pair longer and attached to the posterior cubitus (CuP) basally; the first anal vein is attached to the margin by six or more veinlets. The larvae are flattened. The forelegs are short; the claws have four or five long spines. The middle and hind pairs of legs are twice as long as the forelegs, with the tibiae only half as long as the tarsi; the claws are long, without spines.

The family is found in the Holarctic Region, primarily in large rivers where the larvae burrow into the sand, leaving only the gills and dorsal surface exposed. Larval development appears to take about 1 year.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Baetidae.** These are mostly small species (less than 8 mm). The forewings have the long intercalary (IMA) and the second branch of the anterior medius (MA<sub>2</sub>) vein detached basally. Short, single or paired veins lie between most of the long veins of the forewing (absent in *Siphlaenigma*). The intercalary (IMP) and the second branch of the posterior medius (MP<sub>2</sub>) vein are also detached basally (except in *Siphlaenigma*). The cubital area has two long, free intercalaries (attached at the base with obsolescent crossveins in *Siphlaenigma*). The eyes of the male are divided, with the upper portion in the form of a turban (except in *Siphlaenigma*). The hindwings are absent or reduced with one, two, or three longitudinal veins; the veins are numerous in *Siphlaenigma*. The penes of the male are greatly reduced; there are two caudal filaments. The larvae are streamlined and minnowlike [see illustration page 335]. The antennae are usually two or more times as long as the head is wide (rarely shorter). The labium has glossae and paraglossae which are usually about twice as long as wide. The gills are found on segments I–VII, II–VII, or I–VI; they are usually simple oval plates but are sometimes folded into two or three plates. The posterolateral corners of the abdominal segments are usually without projections.

*Siphlaenigma* (Siphlaenigmatinae, New Zealand) larvae are externally like other baetids, but the glossae and paraglossae are intermediate between those of the Baetinae and of the Siphonuridae; the Malpighian tubules are like those of Siphonuridae.

Baetid larvae usually mature, from egg to emergence, in 10 days to 3 months; at cooler temperatures most develop more slowly. Adult stages last 1–3 days, with females of ovoviparous species living for extended periods.

Baetidae are the most widespread mayfly family, extending to higher latitudes and altitudes than any other mayflies. They also reach a large number of islands. There are 20 described genera and 520 species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Metretopodidae.** The forewings of the adults have one or two pairs of cubital intercalaries. The fore tarsi of the male are about three times as long as the tibiae; the hind tarsi have the basal segment partially fused to the tibia and are longer than the hind tibiae. There are two caudal filaments. The larvae are minnowlike. The claws of the foreleg are uniquely bifid; the claws of the middle and hind pairs of legs are long and slender, longer than the tibiae.

The life cycle takes less than 1 year. Most of the larval development is completed in the first year; adults emerge in the spring. The larvae appear to feed on detritus. They are usually found in vegetated areas of streams, in stream margins, or in lakes.

The family includes 2 genera (*Metretopus* and *Siphloplecton*), with 8 species of Holarctic distribution.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Oligoneuriidae.** The eyes of the male have ommatidia of uniform size. Wing venation varies according to subfamily. In Isonychiinae the anterior cubitus (CuA) of the forewing is attached to the margin by crossveins, and the fork of the posterior medius (MP) vein of the hindwing is less than one-fourth as long as the base. In Coloburiscinae the anterior cubitus (CuA) of the forewing is attached to the margin by crossveins, and the costal projection of the hindwing is acute. In Chromarcyinae two forked intercalaries and one single cubital intercalary connect the anterior cubitus (CuA) to the margin, and the fork of the posterior medius (MP) of the hindwing is less than one-fourth as long as the base. Oligoneuriinae have the major veins behind the first radius paired together; the pair appears single. The forelegs of the male are longer than the other legs in Isonychiinae and Coloburiscinae, shorter in Chromarcyinae and Oligoneuriinae. The larvae are unique in having a double row of long setae on the leading edge of the femur and the tibia; the maxillae have blood gills. The long setae of the legs and mouthparts are used in filter feeding. The larvae are variable in body form: the primitive *Isonychia* is an active minnowlike form; the Coloburiscinae are slow-moving with robust bodies.

*Chromarcys* (Chromarcyinae) is active and minnowlike. Oligoneuriinae are either minnowlike, slow-moving clingers, or slender sand burrowers.

Oligoneuriids are widespread; they are in New Zealand but not New Caledonia. There are 13 genera and 89 species.

**References.** W. P. McCafferty and G. F. Edmunds, Jr., The higher classification of the Ephemeroptera and its evolutionary basis, *Ann. Entomol. Soc. Amer.*, 72:5–12, 1979.

**Heptageniidae.** In the adult the forewings have two pairs of intercalaries in the cubital region, the posterior pair longer; the fork of the posterior median (MP) vein is symmetrical. There are two caudal filaments. The larvae are depressed. The eyes and antennae are dorsal, and the head capsule forms the entire dorsal surface of the head; the mandibles are not visible in the dorsal view. The gills are found on abdominal segments I–VII (rarely I–V). The maxillary and labial palpi are usually two-segmented.

Most Heptageniidae are found in running streams, usually on rocks or submerged wood. They are highly active,

shifting their flattened bodies backward, forward, or to the side with equal facility. Most of the larvae scrape algae from rocks or feed on detritus; *Spinadis*, *Anepeorus*, and *Pseudiron* are carnivorous.

This widespread family is found in North and Central America (doubtfully in South America), Eurasia, Madagascar, and Africa. There are 30 genera and 380 species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

### Leptophlebiioidea

Superfamily containing the single family Leptophlebiidae. Formerly, it frequently included the families Ephemerellidae and Tricorythidae.

In the adult male the eyes are usually divided into an upper portion, with large facets, and a lower portion, with smaller facets; in small forms the eyes may be divided, or small and undivided. The forewings lack short, free marginal intercalaries between the longer veins; there are two to four long intercalaries in the cubital area; the posterior cubitus (CuP) vein is strongly recurved. The hindwings may be absent, minute, or relatively large. There are three caudal filaments. The larvae have extremely diverse body shapes. If the head is strongly flattened, the mandibles form part of the upper surface. The maxillary and labial palpi are three-segmented; the crown of each maxilla has a dense brush of setae. The gills are extremely variable. [See illustration pages 335 and 336.]

Leptophlebiid larvae are primarily found in streams and rivers, although some occur in lakes and ponds. The larvae are detritus feeders.

Leptophlebiidae are widely distributed, reaching only slightly lower latitudes and altitudes than Baetidae. In the Southern Hemisphere the species are often extremely diverse and occupy many niches. There are 68 described genera and 380 species, and numerous undescribed genera are known to occur, primarily in the tropics and in the Southern Hemisphere.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976; W. P. McCafferty and G. F. Edmunds, Jr., The higher classification of the Ephemeroptera and its evolutionary basis, *Ann. Entomol. Soc. Amer.*, 72:5-12, 1979; W. L. Peters and G. F. Edmunds, A generic revision of the Leptophlebiidae of the Eastern Hemisphere, *Pac. Insects*, 12:111-180, 1970.

### Ephemeroidea

Burrowing mayflies. Adults have the second posterior medius (MP<sub>2</sub>) and the anterior cubitus strongly divergent from the first medius posterior (MP<sub>1</sub>) vein, and the costal projection of the hindwing is at right angles, and obtuse or rounded. In the larvae the gills occur on abdominal segments II-VI (present or absent on I, variable); they may be forked or bilamellate, with fringed margins. All larvae burrow in substrates when young, but in the Potamanthidae and Euthyplociidae many older larvae are found on the undersides of rocks.

The superfamily is widespread but absent from Australia and most small islands; there are 6 families.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Behningiidae.** Adults and larvae are very distinctive. The adults are relatively large (12-18 mm). The legs of both

sexes are feeble and twisted. The cubital area of the forewing has four long intercalaries in *Dolania* and one in *Behningia*. The longitudinal veins of the forewing are normally spaced in *Dolania*; they occur in distinct pairs in *Behningia*; their spacing in *Protobehningia* is unknown. The costal projection of the wing is prominent. The penes of the male extend beyond the forceps. The larvae have small mandibles without projecting tusks; the anterolateral corners of the head and the pronotum are armed with unique patches of coarse setae. In *Protobehningia* of eastern Siberia, the gills are dorsal in position and the legs have claws; in *Dolania* (southeastern United States) and *Behningia* (Poland, European Soviet Union, and Siberia) the gills are ventral and the claws are absent.

The life cycle is approximately 1 year. The larvae burrow in coarse sand in moderately large rivers. They feed primarily on Chironomidae. Adults live only about 2 hr. Emergence and mating occur before dawn.

This small family includes only 3 genera with 5 species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Potamanthidae.** Moderate to large insects; the body is 8-25 mm long. Adults are usually pale, and many are marked with reddish pigments. The eyes may or may not be sexually dimorphic. Venation is ephemeroid; the first anal vein is forked near the wing margin. The costal projection of the hindwing is slightly rounded, at approximately a right angle. The forelegs of the male are shorter than the body; the claws on the forelegs are similar, and both are blunt; on the other legs of the male, and on all legs of the female, one is blunt and one is rounded. The larvae have mandibular tusks varying from short (extending to the front of the head) to long (much longer than the head); the tusks have only scattered short setae in the apical half. The forelegs are not modified for burrowing. The tibiae are cylindrical. The caudal filaments have a row of long setae on each side.

Young larvae of Potamanthidae burrow in the substrate of rivers and streams; as the larvae grow, most live on the undersides of rocks. Mature *Potamanthodes* larvae burrow under boulders at the silt-rock interface.

The family is distributed in the Holarctic and Oriental regions. There are 7 genera and 27 species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Euthyplociidae.** Adults are medium to large, sexually dimorphic in size, with females 1½ to 2 times as large as males. In adults the eyes are not sexually dimorphic. The forewings are nearly half as broad as long. Venation is ephemeroid. The radial sector (Rs) vein is forked less than one-sixth of the distance from the base; the anterior medius (MA) vein is forked near or beyond the fork of the radial sector (Rs) vein; the anterior cubitus (CuA) or a parallel intercalary is connected to the hind margin by six or more veins. The legs are well developed. The larvae have tusks longer than the head, with numerous long setae. The forelegs are not modified for burrowing. The tibiae are cylindrical. The caudal filaments have only short setae.

The larvae probably burrow in the substrate when young, but well-developed larvae of most species are found on large smooth rocks. Some may burrow in rubble substrates until mature. Adults emerge after dark and have an extremely short life.

Distribution of the family is pantropical, in South and

Central America, Africa, Madagascar, and the Oriental Region. There are 7 genera and 12 species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Polymitarcyidae.** Moderate to large mayflies with both the adult and the larval body 12–35 mm long. Adults have wings which are somewhat translucent, milky white, often with purplish to brownish shading along the costal margin or near the wing base. The wings have ephemeroid venation. The middle and hind legs of the male and all legs of the female are poorly developed, often vestigial. In the larvae the maxillary and labial palpi are two-segmented. The labial palpi lie beneath and at right angles to the glossae and paraglossae. The mandibular tusks curve downward apically; this is not obvious in the short tusks of the Asthenopodiinae. The tibiae and tarsi of the forelegs are fused, and the claw is in an apical cleft in Campsurinae and Asthenopodiinae; the tibiae of Polymitarcyinae have numerous tubercles and are not fused to the tarsi.

Polymitarcyinae larvae burrow in firm clay or in sand-clay-rock mixtures. Campsurinae burrow principally in the clay banks of rivers. Asthenopodiinae are reported to burrow in wood, freshwater sponges, or papyrus stems, or to live in the cavities of clamshells.

The family includes 6 genera and 70 species; they are widespread on the continents but absent in Australia and New Zealand.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Ephemeridae.** Large mayflies, with the body 10–32 mm long. Adults usually have distinctive dark markings on a pale body. Venation is ephemeroid; the first anal vein is attached to the hind margin by two to many veinlets. The legs are well developed. The pronotum of the male is no more than twice as wide as long. The caudal filaments of the female are longer than the body. The eyes are sexually dimorphic. The larvae have mandibular tusks projecting in front of the head; the tusks curve upward apically without a spuriferous dorsolateral keel [see illustration page 335]. The galea-lacinia of each maxilla is two or more times as long as wide. The maxillary palpi are slender; the second and third segments are more than four times as long as broad. The forelegs are modified for burrowing, and the tibiae are flattened.

The larvae are burrowers in silt, sandy silt, or sand. Most feed on detritus, but a few are carnivores. Development from egg to emergence takes 4 months to 2 years.

Ephemeridae are found over most of the major continents and in New Zealand but not in Australia. The family includes 8 genera and 99 species.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Palingeniidae.** The body is 15–35 mm long. Adults have ephemeroid venation; the first anal vein is not forked. Pentageniinae (North America) have longitudinal veins regularly distributed in the wing; the first anal vein is attached to the hind margin by two or three crossveins; the tibiae and tarsi of the forelegs are not bowed in the male; the pronotum of the male is one-third as long as wide; the caudal filaments of the female are shorter than the body. In Palingeniinae of the Old World, the longitudinal veins of the

radial and medial areas tend to converge in pairs at the wing margin; the first anal vein is not attached to the wing margin; the tibiae and tarsi of the forelegs are bowed in the male. The larvae have tusks with a spur-bearing dorsolateral keel; in derived forms, spurs are large and prominent. The frontal projection is broad, the lateral margins terminating in projecting points; it is emarginate medially, the emarginate edge rough or spuriferous. The galea-lacinia of each maxilla is about as long as broad. The maxillary palpi are broad and rounded apically, with the second and third segments less than three times as long as broad. The middle abdomen has lateral projections bearing long setae; on segments III–V these projections are as long as their width at the base.

Palingeniid larvae form U-shaped burrows in clay and silt, and occasionally burrow in soft rotting wood in medium to large rivers; some occur in larger lakes. They feed on detritus. The primitive genus *Pentagenia* occurs in North America. The Palingeniinae are found in the Old World, with 1 genus in Madagascar and 1 in New Guinea, with most of the subfamily in Eurasia. There are 6 genera and 31 species.

**References.** G. Demoulin, Contribution à l'étude des Palingeniidae (Insecta, Ephemeroptera), *Nova Guinea*, 33: 305–344, 1965.

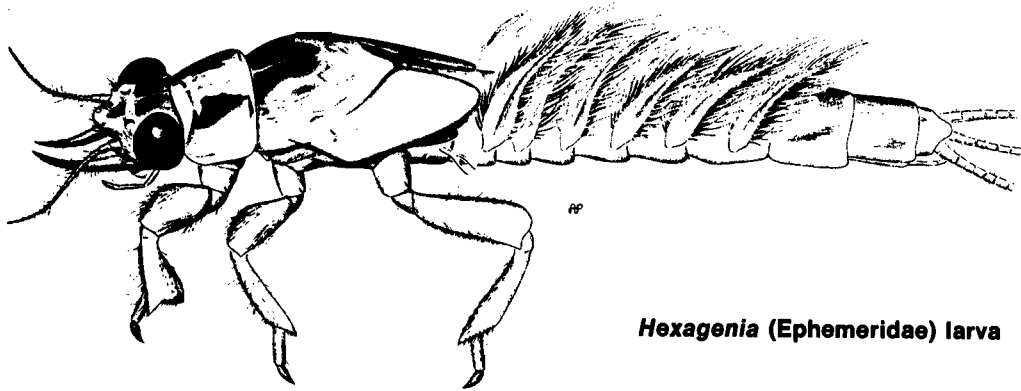
#### PANNOTATA

Adults generally have a well-developed mesoscutellum which extends posteriorly for over half the length of the metanotum and tends to overlap the relatively short metanotum; the margins of the metanotum are always highly tapered. The characters of the adults do not delineate the Pannotata as clearly as do the larval characters. The schistonote genus *Traverella* has a generally pannotelike thorax, and other cases of convergence may be found. The pannote genus *Neoephemera* has a somewhat schistonote thorax. It is probable that internal anatomical characters will be less subject to convergent evolution.

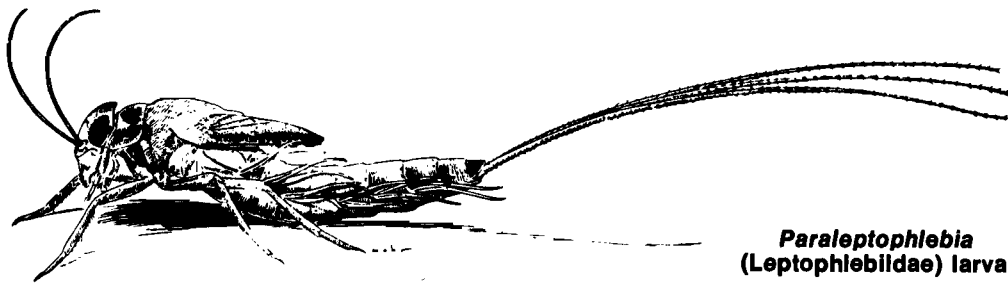
The larvae have the mesothoracic wing pads fused along the midline, and the mesonotum is overthrust in relation to the metanotum. The maximum expression of the fusion is seen in the "carapace" of the Prosopistomatoidea. The gills tend to be reduced in the number of segments on which they occur, and they are generally more protected than those of the Schistonota. The gills usually lie along the lateral shelves of the abdomen; they are protected either by the dorsal plates of the same gill and by the overlapping of gills (many Ephemerellidae and some Tricorythidae), by specialized operculate gills (some Ephemerellidae and Tricorythidae, and Caenoidea), by the legs (Tricorythidae: Diceromyzinae), or by the fused metathorax (Prosopistomatoidea). Pannote larvae are generally slow-moving, relatively inactive crawlers or clingers; many have dorsal setae on which debris clings and provides camouflage. They are generally secretive and inconspicuous. They tend to swim only if disturbed or dislodged from their normal microhabitats; they are generally ineffective swimmers. The Prosopistomatoidea have retained or secondarily acquired swimming ability, but they rarely swim.

Most pannote larvae are detritivores, although some larger species of *Ephemerella* are omnivores or carnivores; the relative lack of predators in the group is probably related to their slow movement and small average size.

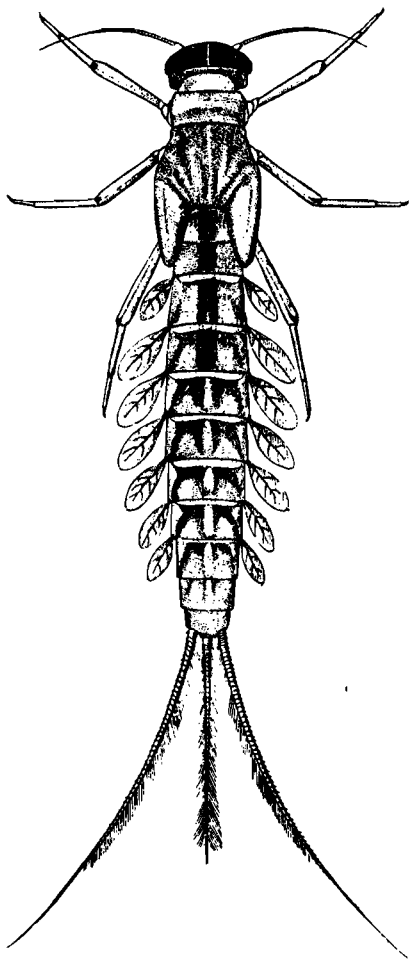
Pannotata are widely distributed but are absent from New Zealand and poorly represented in Australia and Chile. The suborder is divided into 3 superfamilies (Ephemerelloidea, Caenoidea, and Prosopistomatoidea); it



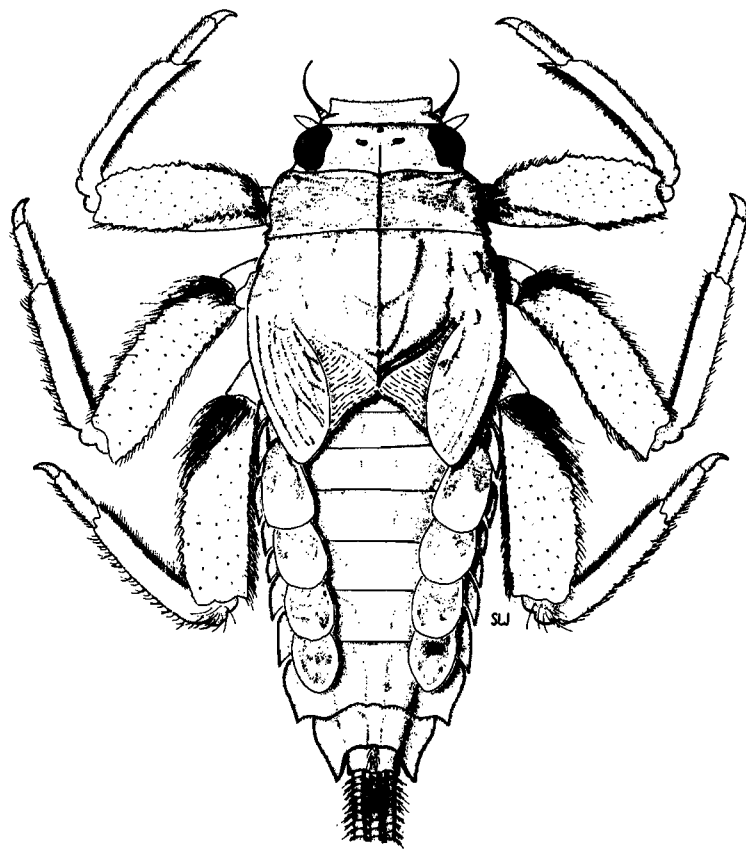
*Hexagenia* (Ephemera) larva



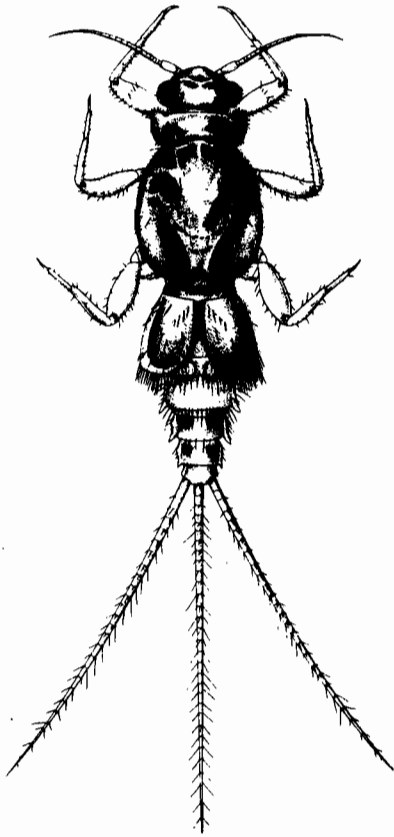
*Paraleptophlebia*  
(Leptophlebiidae) larva



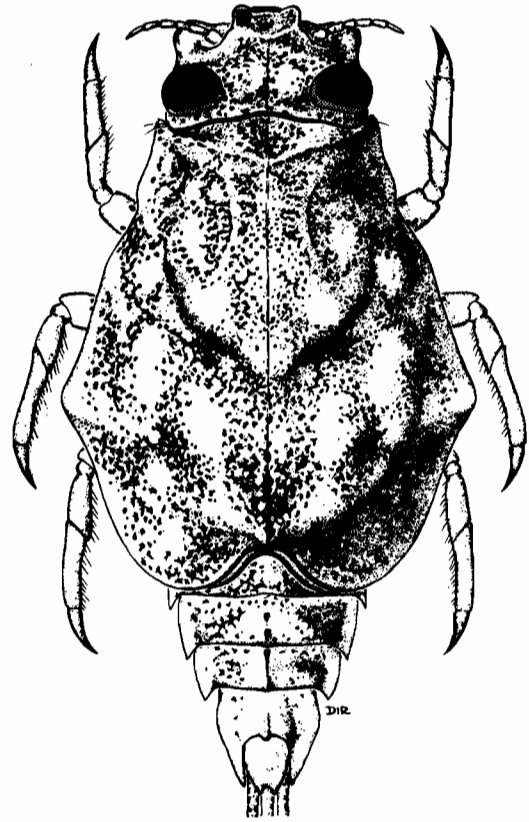
*Baetis* (Baetidae) larva



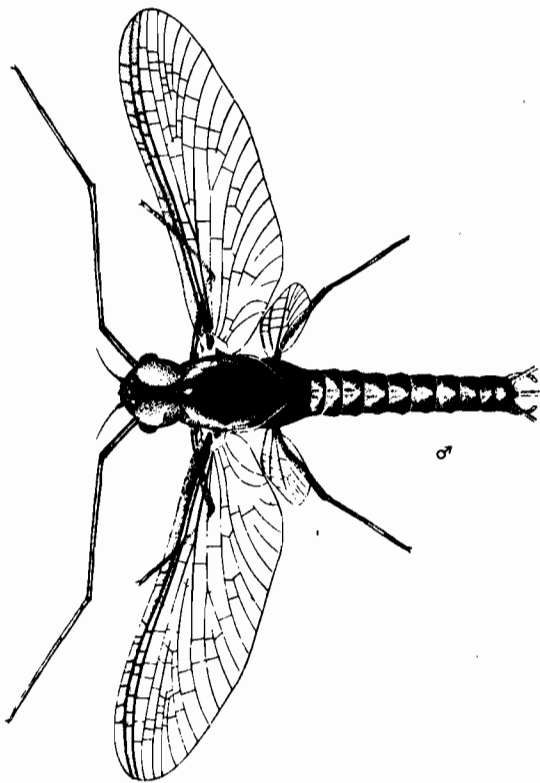
*Drunella* (Ephemerellidae) larva



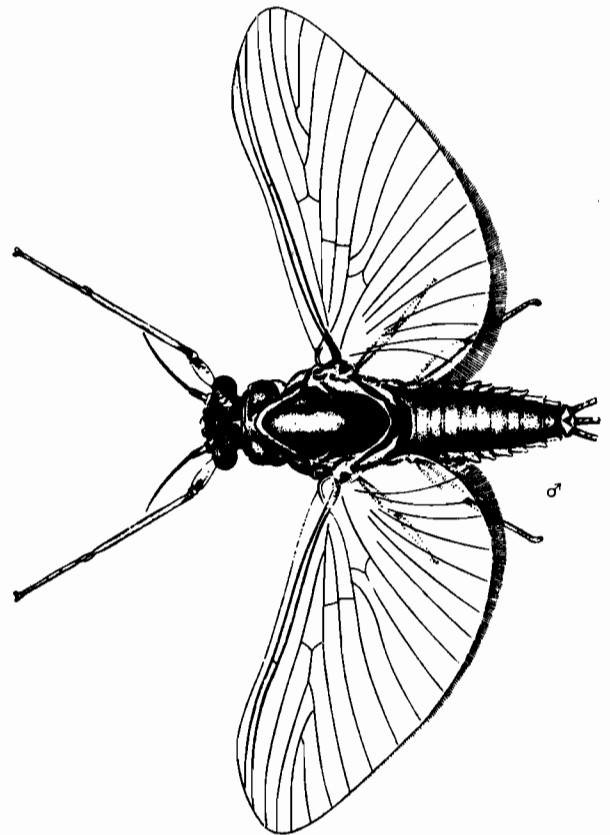
**Caenis (Caenidae) larva**



**Baetisca (Baetiscidae) larva**



**Choroterpes (Leptophlebiidae) imago**



**Caenis (Caenidae) imago**

contains less than 15% of the genera and less than 20% of the extant species in the Ephemeroptera.

**References.** W. P. McCafferty and G. F. Edmunds, Jr., The higher classification of the Ephemeroptera and its evolutionary basis. *Ann. Entomol. Soc. Amer.*, 72:5–12, 1979.

### Ephemerelloidea

Because of the great reduction of venation and genitalia, the superfamily is difficult to characterize in the adult stage.

In the larvae the gills are absent or vestigial and finger-like on segment I; the second gill may be absent or present and operculate, semioperculate, or overlapping the next pair of gills like shingles. The gills usually consist of two lamellae, with the ventral lamella subdivided; they are never covered by an enlarged mesonotum or a quadrate plate-like second gill; they may rarely have fringed margins, in which case the gills are protected by enlarged femora. Spinellike setae are usually present on the margin or the surface of the femora. The labial glossae and paraglossae usually consist of short lobes, but they are completely fused into a single plate in some genera.

Ephemerelloidea are extremely diverse both as adults and as larvae. None of the larvae has the gills protected as do the Caenoidea or the Prosopistomatoidea.

The superfamily contains 2 families (Ephemerellidae and Tricorythidae); V. Landa divides the group into 3, splitting the Tricorythidae of most authors into Tricorythidae and Leptohiphidae.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Ephemerellidae.** In the forewings of adults the cubitus posterior (CuP) vein is strongly recurved and connected to the cubitus anterior (CuA) near the base by a crossvein; short, free intercalary veins run along the wing margin between the longitudinal veins. The hindwings are relatively large, with numerous longitudinal veins and crossveins. There are two or three caudal filaments. The genital forceps of the male has one or two apical segments beyond the long segment. The larvae are diverse, slender and elongate to broad and robust; some are depressed [see illustration page 335]. Hindwing pads are present and well developed. Gills are absent or rudimentary and fingerlike on segment I; they are present on segments II–V or II–VI in the subfamily Teloganodinae and on segments III–VII or IV–VII in Ephemerellinae (Melanemerellinae are unknown). The gills are composed of two plates, with the ventral plate usually divided into two parts, each part with many lobes overlapping like shingles or divided into three to eight fingerlike lobes.

These insects are inhabitants of rivers and creeks, except that the subgenus *Eurylophella* (of *Ephemerella*) is found equally in lakes. Most are detritus feeders, but the larger species of the subgenus *Drunella* (of *Ephemerella*) may be omnivorous or carnivorous. Ephemerellidae are widespread, but absent from New Zealand and rare in South America.

The family currently includes 7 genera and 163 species recognized by North American mayfly specialists. However, the genus *Ephemerella* is divided into 13 subgenera; most workers in Europe give generic status to each of the subgenera. It seems almost certain that with further clarification of the limits and relationships of these groups, more genera will be recognized. It is also clear that some changes in family classification are probable, and classifications other than the one proposed here have been suggested.

**Tricorythidae.** Adults are small, with the wing usually less than 10 mm long. The eyes of both sexes are usually small and widely separated; the males of a few species have large eyes. The thorax is robust. The forewings are more or less broad, with the cubitoanal area expanded and the posterior cubitus (CuP) vein strongly recurved; there are usually no short, free intercalaries along the margin, but these are present in *Ephemerythus* (Africa). The hindwings are absent or greatly reduced; usually only one or two veins occur behind the subcosta. There are usually three caudal filaments, rarely two. The larvae are diverse, but all are relatively robust, with gills on segments II–V, II–VI, or II–VII. The gill structure is diverse, but distinct in each subfamily. Leptohiphinae (Americas) usually have double gills; on segment II the gills are triangular to oval and cover the gills behind. The gills of Dicercomyzinae are single, have fringed margins, and are hidden beneath the huge femora. Machadorythinae have enlarged gills on segment II, with the gills further protected by the edges of the abdomen. Ephemerythinae and Tricorythinae have the gills arranged in a shinglelike manner from segments II to VI.

Tricorythidae are found in a wide variety of streams. They appear to be primarily detritus feeders.

The family contains 13 genera and 122 species. The relationships between the subfamilies are not well understood, and the relationship of the family to the subfamily Teloganodinae of Ephemerellidae is not clear. The family occurs in Africa, Madagascar, the Oriental Region, and the Americas.

### Caenoidea

Adults are difficult to define. The posterior medius (MP) vein is forked at the wing base. The penes of the male are fused nearly to the apex. The larvae have quadrate operculate gills on segment II, covering the other gills; the gills on segments III–VI have fringed margins.

The superfamily is widespread, but absent in New Zealand and most oceanic islands. There are 2 families, Neophemeridae and Caenidae.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Neophemeridae.** In adults the eyes are sexually dimorphic: those of males are relatively large; those of females are small and widely separated. In the forewing the second posterior medius (MP<sub>2</sub>) and anterior cubitus (CuA) veins diverge from the first medius anterior (MA). The hindwings have an acute costal projection. There are three caudal filaments. Mature larvae are 8 to 17 mm long. The legs are long and slender. The gills on the second abdominal segment are operculate, quadrate, and fused at the midline; the gills on segments III–VI have fringed margins and a small tuft of fibrillae near the base. The larvae are found in streams, where most live in roots and in tangles of plant debris.

Neophemeridae have a spotty distribution pattern: they are found in eastern North America, Europe, the Soviet Union (Republic of Turkmen and Uzbek Republic), and the Oriental Region from India to Java. There are 3 genera and 10 species.

**Caenidae.** Family of ephemeropterans of small size (wings 2–8 mm long). Adults have only one pair of wings. The wings are very broad; the intercalary and second posterior medius (MP) veins extend nearly to the wing base. The eyes are small and widely separated in both sexes; the eyes of the



male are large in *Caenopsella*. The male genital forceps are one-segmented. The larvae have a robust thorax and a moderately to strongly flattened abdomen; they lack hindwing pads [see illustration page 336]. Abdominal segments III–VI are shortened relative to segments VII–IX. The operculate gills on segment II are quadrate and not fused together at the midline; the gills on segments III–VI have fringed margins, with no basal fibrilliform tuft.

Caenidae are widespread; they are absent only in New Zealand and on most oceanic islands. They are frequently abundant. They are short-lived as adults, usually living 1½ to 2 hr.

The larvae are most commonly found in the slowly flowing waters of rivers, but in cooler climates most of the species of *Caenis* live in ponds and lakes. They feed on detritus.

Currently there are 9 described genera and 85 species. The taxonomy of the family has been largely based on the adults, but recent emphasis on the larvae has led to the recognition of more genera.

### Prosopistomatoidea

This superfamily is difficult to characterize as adults but has a number of shared derived characters in the larvae. The adults have an extremely robust thorax and a short abdomen. Wing venation is variable, but there is no forked vein in the cubital area. In the larvae the pronotum and the mesonotum are fused and extended posteriorly to the sixth abdominal tergum to form a shield that covers the gills. The gills have fringed margins. The most posterior ventral ganglion is in the metathorax.

The superfamily as recognized here contains only the families Baetiscidae and Prosopistomatidae. The distribution is somewhat erratic, but it is of interest that the superfamily is not known in Mexico or South and Central America and is also absent from New Zealand and Australia; it is present in New Guinea and the Solomon Islands.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Baetiscidae.** Family represented by the single genus *Baetisca*. Adults are distinctive. The thorax is robust. The first anal vein of the forewing terminates in the outer margin. The hindwings have numerous long, free marginal inter-

calaries. There are two caudal filaments. The larvae have a large mesonotal shield or carapace. The head is distinct from the thorax and does not fit into a notch so as to form an oval outline with the thorax [see illustration page 336]. The gills are enclosed in a chamber. There are three short caudal filaments.

The larvae live principally in small or medium-sized streams, occasionally in larger rivers; some live in lakes where there is some current from wave action. The larvae of *Baetisca rogersi* develop in approximately 4 months; there are 12 larval instars. The larvae are detritivores.

There are 12 included species. They are found chiefly in eastern North America.

**References.** G. F. Edmunds et al., *The Mayflies of North and Central America*, University of Minnesota Press, Minneapolis, 1976.

**Prosopistomatidae.** Family represented by the single Old World genus *Prosopistoma*. The body is usually less than 5 mm long, rarely as long as 9 mm. Adults have a robust thorax and a short abdomen. The eyes of both sexes are small and widely separated. The caudal filaments of males are about three-fifths as long as the forewing, and those of females are about one-tenth as long as the forewing. The forelegs of the male are only slightly longer than the other pairs, and the legs of the female are vestigial. The forewings are without crossveins. In the larvae the head is set into the emargination of the thorax so as to form a smooth oval outline. The pronotum and the mesonotum are fused into a shield that extends to abdominal segment VI, covering the gills. The legs are short, not visible dorsally. The caudal filaments are short.

The larvae are found primarily clinging to the undersides of large rocks. The adults are known to fly from 5:00 to 7:15 A.M.

The family includes 11 species. Distribution is in Europe, Africa, Madagascar, and from the Oriental Region to New Guinea and the Solomon Islands.

**References.** M. T. Gillies, The adult stages of *Prosopistoma* Latreille (Ephemeroptera) with description of two new species from Africa, *Trans. Roy. Entomol. Soc. London*, 105: 355–372, 1954; W. L. Peters, New species of *Prosopistoma* from the Oriental Region (Prosopistomatoidea: Ephemeroptera), *Tijdschr. Entomol.*, 110:207–222, 1967.