

The Insects of Australia

*A textbook for students
and research workers*

SECOND EDITION

Volume I

DIVISION OF ENTOMOLOGY
COMMONWEALTH SCIENTIFIC AND
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16

Ephemeroptera

(*Mayflies*)

W. L. PETERS *and* I. C. CAMPBELL

Palaeoptera with mouth-parts mandibulate in the nymph, but vestigial and nonfunctional in the adult; abdomen of both nymph and adult with 2 or 3 long caudal filaments (cerci and terminal filament). Nymph with abdominal gills; adult with subimaginal and imaginal winged stages.

This is the most primitive order of living, winged insects and, though small, it is nearly cosmopolitan. Nymphs (Figs 16.11–14A) of all species are aquatic and occur in relatively unpolluted, standing and running freshwaters. The adults (both subimagos and imagos) (Fig. 16.1) are short lived (a few minutes to several days) and usually do not move far from water. Adults take no food and the alimentary canal of the male is inflated with air. Imagos of most species have a characteristic, aerial mating flight either over water or over nearby landmarks. A few species reproduce parthenogenetically.

Anatomy of Adult

Head (Fig. 16.1B). Usually appears triangular when viewed dorsally, with well developed posterolateral eyes. Eyes of female more or less rounded and widely separated dorsally. Eyes of male usually large, often meeting dorsally and usually divided transversely into an upper part with large facets and a lower part with smaller and usually darker facets. Males of baetids and some leptophlebiids have eyes divided into a lower rounded portion and a stalked upper portion. The exceptional development of the male eye is correlated with mating behaviour. Three ocelli present, the laterals often large. Antennae shorter to longer than head; flagellum filiform and sometimes multisegmented; scape and pedicel shorter and thicker. Mouth-parts vestigial, asymmetrical, lacking

sclerotisation and shrunken closely together in a single, externally visible, pale mass beneath the clypeus.

Thorax. Highly developed for flight. Prothorax reduced, notum shield-like. Meso- and metathorax fused together and large. Mesothorax greatly developed, its notum longitudinally grooved and strongly convex dorsally. Metathorax quadrangular and transversely ridged, sometimes produced posteriorly. Spiracles on meso- and metathorax.

Legs. Tarsi with 4 or 5 segments (rarely fewer), basal segment sometimes fused in varying degrees to tibia (Figs 16.9C, D). Pretarsal claws (Figs 16.9A, B) usually paired, both sharply hooked, or 1 hooked and 1 blunt, or both blunt. Fore legs of most males elongate (Fig. 16.1A), often as long as body, used for seizing female during mating flight. In several families the mid and hind legs of the male and all legs of the female are poorly sclerotised and probably non-functional and in the extralimital *Campsurus* (Polymitarciidae) they appear broken off distal to the trochanter. In the North American *Dolania* (Behningiidae), the distal segments of the mid and hind legs of males break during the subimaginal moult and remain in the cast exuviae.

Wings (Figs 16.1A, 6–8). Somewhat triangular, both pairs held rigidly upright when at rest. Hind wings smaller than fore wings and with reduced venation; hind wings greatly reduced in size or absent as in Caenidae, Baetidae,

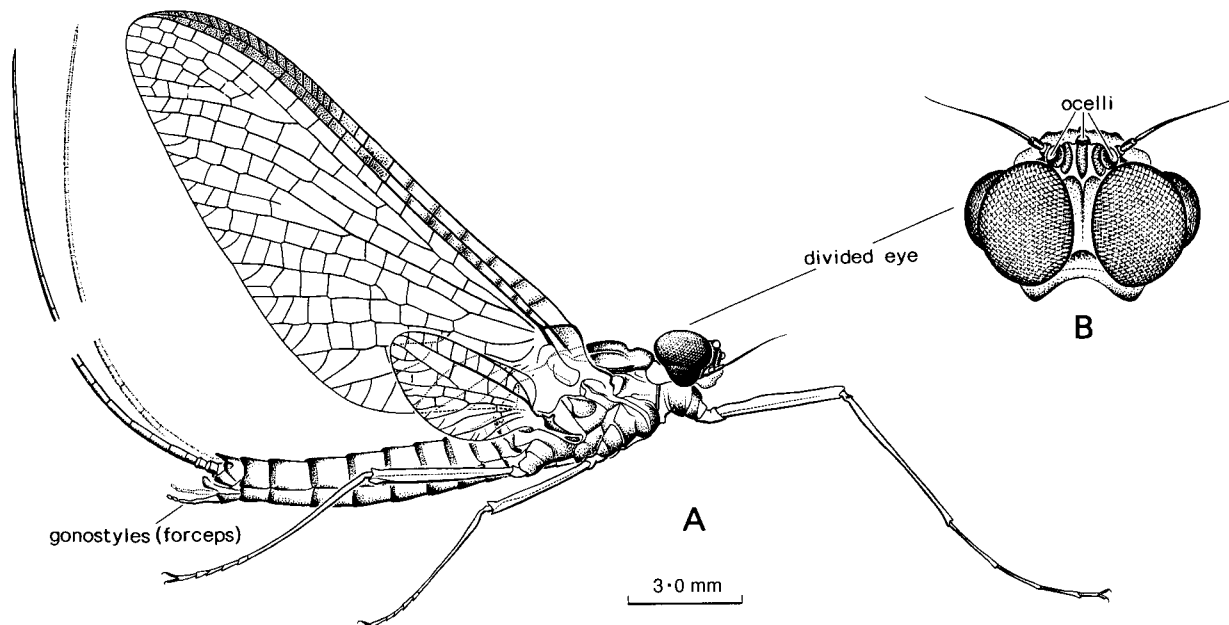


Fig. 16.1 *Atalophlebia* sp., ♂, Leptophlebiidae: A, lateral view; B, head, dorsal.

[T. Binder]

some Leptophlebiidae and the extralimital Tricorythidae. Venational nomenclature used in this chapter is as proposed by Tillyard (1932) and discussed by Edmunds and Traver (1954). Venation of fore wings sometimes reduced, e.g. in Caenidae. Wing surfaces fluted with regular alternation of convex and concave veins. In subimagos, wing membranes translucent to opaque, usually with uniform colour, sometimes with colour patterns. In imagos, membranes hyaline or translucent, sometimes with colour patterns, especially along costal margin. Anterior margin of each hind wing convex, variable, sometimes with a well developed costal projection used to couple hind wing to fore wing during flight. In *Mirawara* the veins of the posterior edge of each fore wing and the corresponding costal veinlets of the hind wing are weaker just before the margin, allowing the edge of the fore wing to roll downwards and forwards and couple with the upwardly rolled edge of the hind wing.

Abdomen. Ten-segmented, segment 1 broadly joined to metathorax. Segments 1–9 ring-like, with tergum and sternum; some species with posterolateral spines on some segments, spines occasionally pronounced. Apex of abdomen with multisegmented caudal filaments consisting of 2 lateral cerci and median, terminal filament; terminal filament sometimes reduced or absent; length of caudal filaments variable, but mostly 2 to 3 times as long as body. Spiracles on segments 1–8.

Male genitalia well developed externally (Figs 1.25D, 16.2B, D). Posterior portion of S9 enlarged into subgenital plate (styliiger plate), enlargement and shape variable. Posterior margin of subgenital plate with paired, lateral forceps (gonostyles); length and shape of forceps variable, usually basal segment long with 2 or more small apical segments, Caenidae with only 1 segment. Paired penes located dorsomedially to subgenital plate; penes

often partially to completely fused, length and shape variable, membranous and extrudable in Baetidae and Oligoneuriinae; each penis with various lobes, spines and processes.

Posterior portion of S9 of female enlarged into subanal plate, enlargement and shape variable (Figs 16.2A, C). Oviducts opening by a pair of gonopores or joined at unpaired vestibulum with common opening between S7 and S8. Duct openings of the European *Caenis robusta* are non-functional and oviposition occurs by rupture of intersegmental membranes between S7 and S8. Posterior margin of S7 (sometimes also anterior margin of S8) prolonged into a genital extension and forming a long egg guide in some Leptophlebiidae; this structure may break the surface tension of the water during egg laying.

Internal Anatomy. Alimentary tract modified for aerostatic purposes, no digestive function. Musculature well developed in thoracic cavity and male genital area. Central nervous system consists of brain, suboesophageal ganglion and usually 3 thoracic ganglia with 7 or 8 distinct abdominal ganglia. Male reproductive system with paired testes (testicular follicles numerous), each joined to separate vas deferens, seminal vesicles and separate ejaculatory ducts. Female reproductive system with numerous panoistic ovarioles joined to paired oviducts, no accessory glands.

Immature Stages

Egg (Fig. 16.4). Small (average length 0.22 mm, 0.82–0.94 mm in the Holarctic Behningiidae), of varied shape, chorionic sculpturing and colour; with 1 to several micropyles and suprachorionic sperm guides; many species with various types of attachment structures and polar cap, suprachorionic layer often adhesive.

Nymph. Morphologically different from adult, particu-

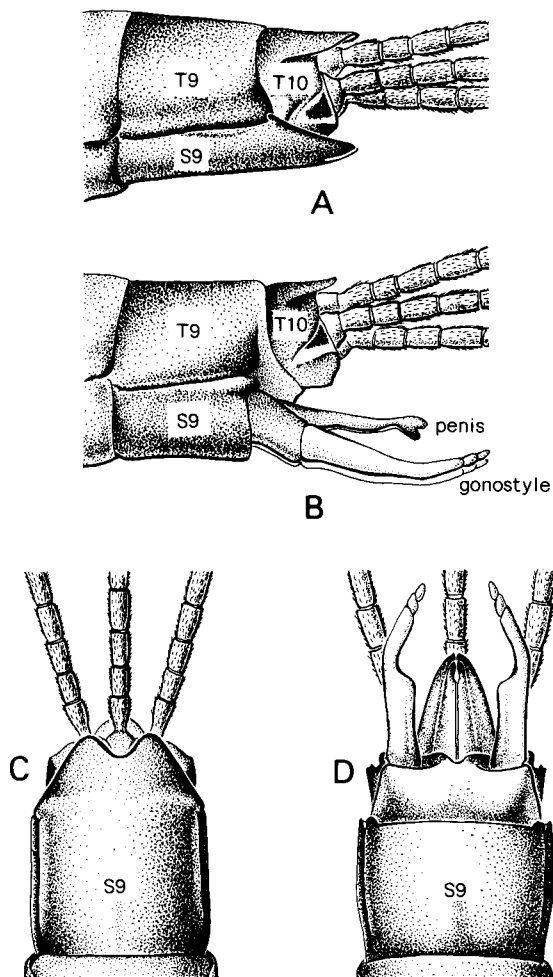


Fig. 16.2 Terminalia of *Atalophlebia* sp., Leptophlebiidae: A, ♀, lateral; B, ♂, lateral; C, ♀, ventral; D, ♂, ventral. [R. Ewins]

larly in having fully developed mouth-parts and abdominal gills (except the South American *Murphyella*); body form variable (Figs 16.11–14A).

Head (Figs 16.3A, B, 10) hypognathous to prognathous with head capsule well developed; sometimes with processes and projections. Eyes large, sexually dimorphic. Three ocelli present. Antennae shorter to longer than head; flagellum filiform and multisegmented; scape and pedicel shorter and thicker. Mouth-parts mandibulate. Labrum and clypeus well developed (Fig. 16.3D); labrum sometimes wider than head. Hypopharynx with well developed lingua (Fig. 16.3E); superlinguae well developed to absent. Mandibles with 3 condyles (Fig. 16.3C); apex of each with inner and outer incisors (usually), protheca (usually), and molar lobe (usually), molar lobes of left and right mandibles asymmetrical so that surfaces mesh. Distal portion of each maxilla fused into galealacinia (Fig. 16.3F) bearing various hairs and spines; palps 1–multisegmented, sometimes reduced or absent; maxillae usually with distinct stipes and cardo; gills present at base of each maxilla in Oligoneuriidae, Coloburiscidae, some Baetidae and *Ameletoides*, and the extralimital

Isonychia, *Metamonius*, *Nesameletus* and *Rallidens*. Labium with small mentum and larger submentum (Fig. 16.3G), submentum sometimes greatly enlarged; glossae and paraglossae well developed, palps 2–multisegmented; paired gills present on venter of mentum near base of palps in *Coloburiscoides* and *Murphyella*. Mouth-parts highly modified in predacious species.

Thorax with 3 distinct segments, fore and hind wing pads developing on meso- and metanotum; sometimes a variety of projections on 1 to all 3 thoracic nota, well developed ridges or spines on thoracic sterna in a few genera, and thoracic sternal gills present in *Murphyella*. In *Prosopistoma* and the North American *Baetisca*, the mesonotum forms a shield-like carapace extending to abdominal segment 6 or 7 (Fig. 16.14A).

Legs shorter and stouter than in adult, hind legs usually longer than fore legs; femora more or less flattened; tarsi usually unsegmented; claw single, rarely absent, usually with denticles, shape and length of claw and denticles variable; legs with a variety of spines, tubercles and/or setae; gills present at or near base of coxae in *Isonychia*, *Murphyella* and some Baetidae; legs of some genera modified for burrowing, filtering food, grooming or gill protection.

Abdomen 10-segmented, S1 broadly fused to metathorax; terga sometimes with paired or unpaired spines and/or tubercles; posterolateral tergal spines usually present, spines often small but sometimes greatly expanded.

Abdominal gills (Figs 16.14B, c, 15) present on abdominal segments 1–7 (rarely 8), or absent from 1 or more segments in various combinations; gill position variable, either ventral, lateral or dorsal; gill structure highly variable, the first gill pair often dissimilar to remaining gill pairs. Abdominal gills absent in *Murphyella*.

Apex of abdomen with multisegmented caudal filaments consisting of 2 lateral cerci and a terminal filament; terminal filament sometimes reduced or absent; length of caudal filaments varies from shorter than to several times longer than body; caudal filaments with various (sometimes dense) setae, spines and denticles. The caudal filaments of *Prosopistoma* can be retracted into the abdomen.

Biology

Imagos. Most imagos live no more than 24 hours. Some live only a few minutes while others, especially in colder climates, live for several days. Reproduction and dispersal are the sole functions of mayfly imagos. Adults usually do not move far from water, but some species may be found several kilometres from their emergence site. Mated females of some species of Holarctic burrowing mayflies are known to make long upstream flights before oviposition.

Imagos usually swarm, mate and oviposit at a specific time of the day. The time of swarming is characteristic for a species and is influenced by cloud cover, light intensity, temperature and other weather factors. In temperate areas imagos generally swarm during the warmer period of midday to dark while species living in more tropical areas

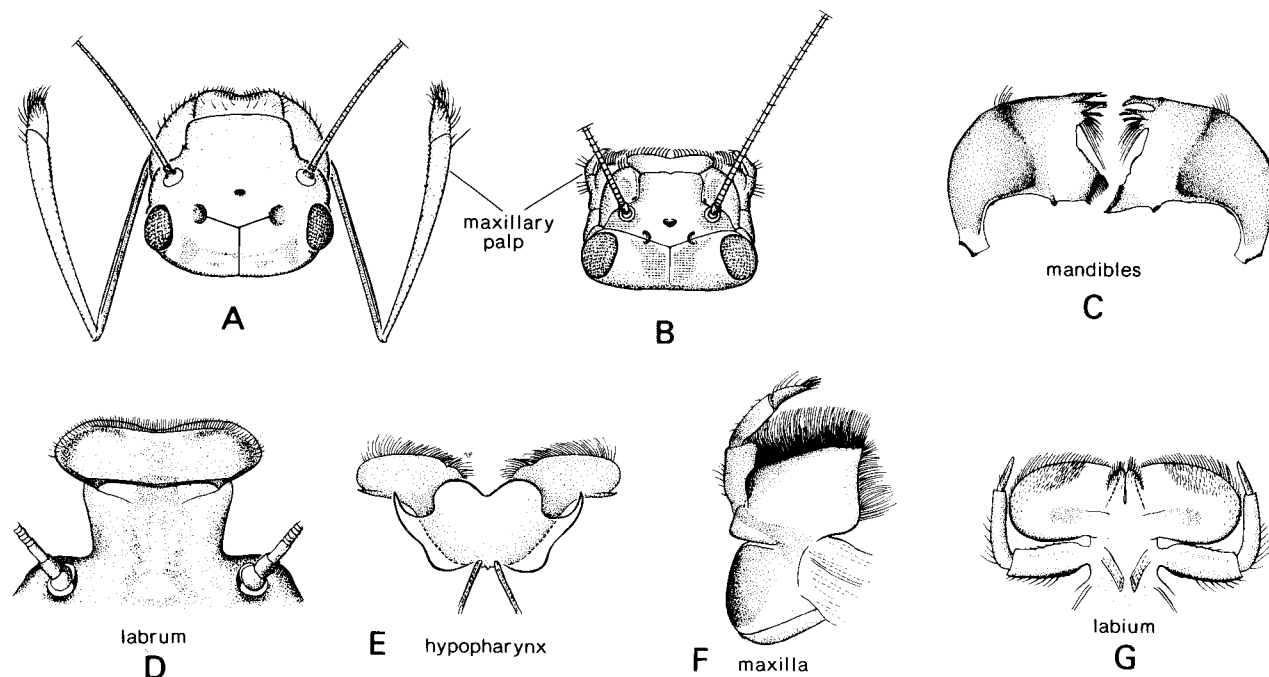


Fig. 16.3 Nymphs of Leptophlebiidae: A, *Atalophlebia yugana*, head, dorsal; B–G, *Atalophlebioides* sp., head and mouth-parts.

[A by J. Peters; B–G by M. Quick, R. Ewins]

may swarm from before dawn to mid-morning. In genera such as *Prosopistoma* where the adult is very short-lived or the female is mature as a subimago, factors determining emergence of subimagos necessarily are those which also determine swarming.

Swarms of mayflies characteristically consist of several to many thousands of males flying in an up and down pattern over water or nearby land objects. When the companies of males are small, swarming occurs over a specific swarm marker, such as a rock, bush, tree, light-coloured object, bridge or shore line. The type of marker and whether the swarm is found over land or water are different for each species (Savolainen 1978). Large swarms of some burrowing mayflies may cover an entire body of water. When imaginal emergence is synchronised over a short period, swarms are much larger than when emergence extends over many months.

In a few species males fly in a horizontal pattern as they search for females. According to Riek (1970), males of some Caenidae and *Atalophlebia* patrol stretches of streams. Swarming is usually a male activity with females entering the swarm, but males and females of Caenidae and Tricorythidae both participate in such flights.

Reproduction. Copulation (Fig. 1.26) normally takes place in flight. For the Holarctic *Parameletus* the male generally approaches the female from below, his long fore legs extend upward and his tarsi curve around the female wing bases while his abdomen recurves up and back so the genital forceps grasp the apex of the female abdomen (the female curves her abdomen so the penis can be inserted easily into the opening of her S7) (Brinck 1957). However, the external genitalia of some mayflies are highly modified and the details of copulation vary.

Mating may last from a few seconds to several minutes, but usually less than a minute.

Mayfly eggs are deposited in water. Most females oviposit by descending to the water, dipping the abdomen into the water and releasing a few eggs at a time; such behaviour is displayed by many Australian Leptophlebiidae. Some species, such as *Coloburiscoides haleuticus*, release all their eggs in a single batch that separates immediately on contact with water. In other species, the female enters the water for oviposition, either placing the apex of the abdomen below the surface (some Australian species of *Atalophlebia*) (Riek 1970) or crawling beneath the surface to deposit eggs on stones or other substrates on the bottom (some Northern Hemisphere species of *Baetis*). Oviposition by Caenidae is effected by rupture of the abdominal wall upon contact with water (Soldán, pers. comm.).

Fecundity varies from about 100 eggs in *Prosopistoma* and Behningiidae to 12 000 eggs in the extralimital *Palingenia*; however, most species range from 500 to 3000 eggs. Parthenogenesis is known for about 50 species, although obligatory in only a few. Some species of *Cloeon* and the extralimital *Callibaetis* are ovo-viviparous; female imagos oviposit up to 3 weeks after mating and as soon as the eggs contact the water young nymphs hatch.

Immature Stages. The period of egg development varies from a week to a year, depending on species and temperature. For some European species without diapause, egg development takes 2–3 weeks at optimum temperatures, but much longer at colder temperatures (Humpesch 1984). Australian species have a wide range of developmental times (Campbell 1986). Winter dia-

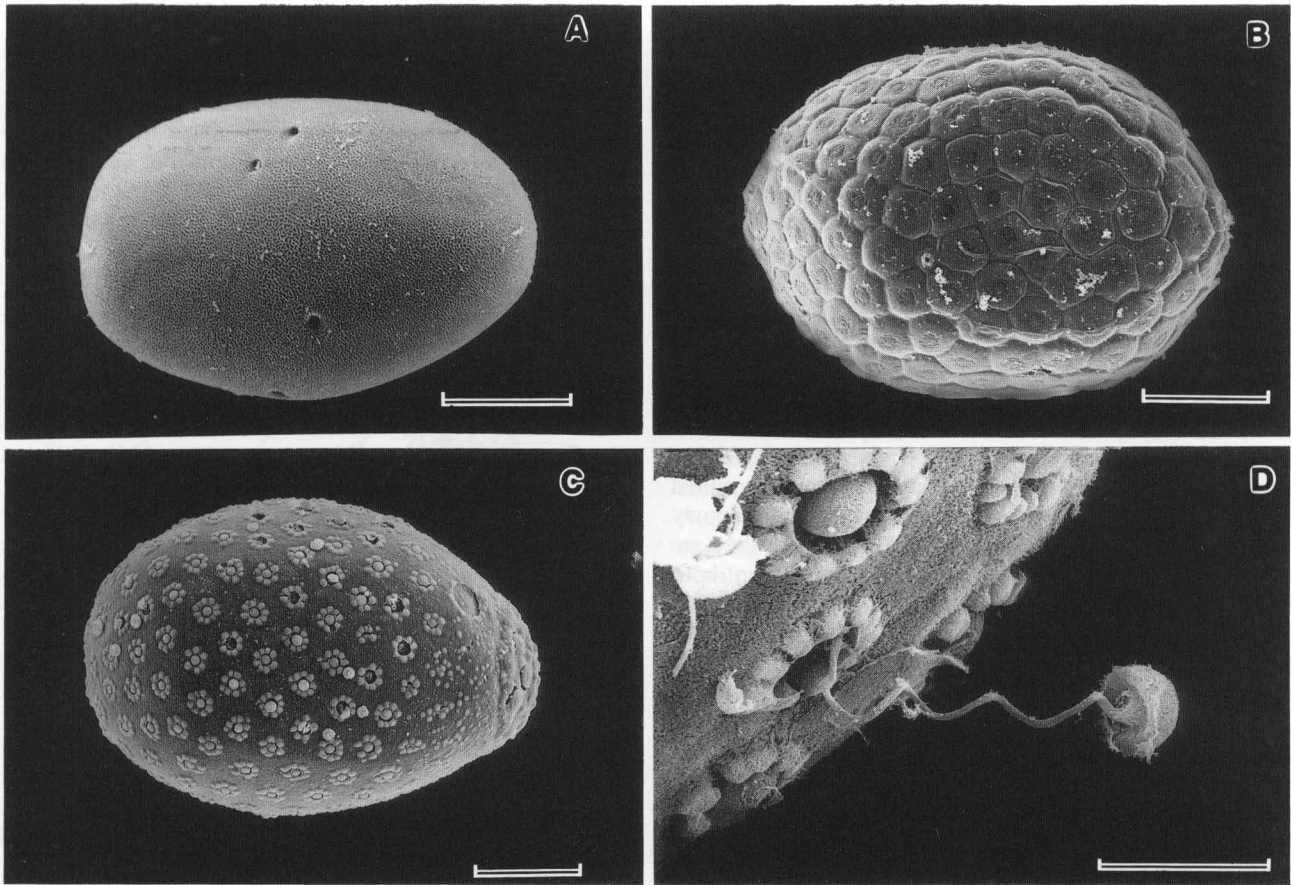


Fig. 16.4 Eggs: A, *Tasmanophlebia lacuscoerulei*, Oniscigastridae; B, *Kirrara procera*, Leptophlebiidae; C, D, *Coloburiscoides haleuticus*, Coloburiscidae, with detail of adhesive structure. Scales: A–C = 50 μm ; D = 10 μm .

pause, which is known for a few Holarctic species, appears to occur in *Coloburiscoides giganteus* and *Baetis soror* in Australia. Summer egg diapause is also likely for several species including *Atalophlebia australasica* which occurs in temporary streams. Eggs of some species demonstrate asynchronous development, or delayed hatching, which possibly involves diapause (Hynes 1970). *Kirrara procera* has a short oviposition period but young nymphs are found every month (Campbell and Holt 1984). Eggs developing parthenogenetically develop more slowly than fertilised eggs.

The duration of nymphal development varies from 3 weeks in the North American *Parameletus columbiae* to 3 years in some temperate, burrowing mayflies. Mayflies have 10–50 nymphal instars depending on species, diet and temperature, but 15–30 is most common. Diet and water temperature determine rate of growth, and light appears to play only an indirect role (as it affects water temperature and algal growth). Life cycles are either uni-, bi- or multivoltine, depending on species. In the tropics, non-seasonal, multivoltine cycles predominate, and towards the Arctic, seasonal, univoltine cycles (Brittain 1982). In New Zealand (Towns 1981, 1983a) and Australia (Riek 1970; Campbell 1986), most species are univoltine but life cycles range from 6 months to 3 years. Many Australian species have overlapping broods and

unsynchronised development, and their life cycles are less seasonal than is the case in univoltine species of the Northern Hemisphere. A few, such as *Kirrara procera*, do show a seasonal, univoltine pattern with a single cohort of nymphs (Campbell and Holt 1984).

In Swedish ponds, *Cloeon inscriptum* overwinters without oxygen under ice in an anaerobic diapause induced by decreasing water temperatures (Nagell 1980). Nymphal diapause, frequently suggested, is as yet unconfirmed for other species. Temperature limits for growth may vary by species, population or developmental stage, and cold winters or hot dry summers may induce strong seasonal patterns without a true diapause.

Nymphs of each species are normally restricted to a particular type of habitat, ranging from lakes and large rivers to temporary ponds and streams. A very few species occur in stagnant, lowland, weed-choked backwaters and bogs, while many occur on stones and rocks (i.e. are *epilithic*) in high, cold, snow-melt streams. In Australia, the mayflies inhabiting lowland, standing or slowly flowing waters include the small, swimming nymphs of *Cloeon*, the large, flattened, clinging nymphs of the *Atalophlebia australasica* group of species, and *Tasmanocoenis*. Swimming nymphs often have enlarged, overlapping rows of hairs on the inner surfaces of the cerci and lateral surfaces of the terminal filament, these

together forming a paddle. In one species from New Caledonia the swimming paddles are formed by enlarged femora. Nymphs of *Prosopistoma* resemble small, well-camouflaged crustaceans and are found underneath large rocks in the fastest parts of rivers or small streams.

The sprawling nymphs of *Austrophlebioides* are the most commonly encountered mayflies in upland Australian streams. They occur on surfaces of stones in moderate currents. In areas of rapid current, nymphs of *Kirrara*, with greatly enlarged abdominal gills forming an adhesion disc, occur on the tops of stones and *Coloburiscoides*, with gills modified to provide anchorage, occur beneath stones. *Neboissophlebia* nymphs are also abundant in these streams, where they are often associated with accumulations of leaves.

Tasmanophlebia and several species of *Atalophlebia* may be found on stones in upland lakes. The streamlined nymphs of *Ameletoides* also occur in lakes of the Snowy Mountains, but not in Tasmanian lakes, although they are characteristic of small, cool, upland streams in both regions.

Burrowing mayflies (superfamily Ephemeroidea) in other countries are morphologically remarkable with the legs, frontal processes of the head and mandibular tusks all modified; feathery gills well-supplied with tracheae constantly pump water through the burrow. Wood-boring, South American *Asthenopus* (Polymitarcyidae) line burrows with wood chips and secretions from the Malpighian tubules. Some non-Ephemeroidea in Australia show degrees of burrowing behaviour. Nymphs of *Jappa* burrow under stones in silty sections of sluggish streams, and have long setae on the gill margins. *Tasmanophlebia* and *Tasmanocoenis* settle into sand or silt until they are almost completely hidden; in both genera, the anterior gill is modified into a protective cover for the remaining gills.

Legs and mouth-parts are also modified for feeding. Most mayflies scrape or graze detritus, diatoms and algae from rocks and leaves. Some, such as *Coloburiscoides*, are filter feeders and a few, such as *Mirawara*, are carnivores. Feeding ceases some time during the last nymphal instars as the digestive system degenerates and adult structures complete development. Nymphs often move to another habitat during this period, frequently toward the sides of rivers where they will eventually emerge.

Subimago. Mayflies emerge as winged subimagos, which usually moult to imagos, or true adults (Edmunds and McCafferty 1988). They are the only insects that undergo an ecdysis after having acquired functional wings. Some nymphs emerge to subimagos in a few seconds on the surface film of water, while others crawl out on rocks and sticks and emerge slowly, taking up to five minutes. Emergence appears to require a minimum water temperature and some seasonal cue such as a temperature change or a full moon, emergence occurring several hours to days after a particular cue. Different species emerge at different times during the diel cycle. *Tasmanocoenis* normally emerge shortly after dawn whereas those leptophlebiids that emerge on the surface film of lakes prefer the warmer midday. The nymphs of *Ameletoides* and *Tasmanophlebia* crawl out of the water onto rocks at

dusk to emerge. Subimagos of some species cling to rocks overnight and are ready to fly with the first light, while others fly away immediately after emergence.

Subimagos usually rest with little movement in bushes and trees and for most species the stage lasts about 24 hours. Cooler temperatures can extend the subimaginal stage up to several days. Some Caenidae moult to imagos in five minutes or less. In *Tasmanocoenis*, moulting usually takes from 10–20 seconds, measured from the time the subimagos alight on an object to the time the imagos fly off to join the swarm; imagos often take flight before the caudal filaments are free of the subimaginal exuvia.

In *Prosopistoma*, in the Papuan *Plethogenesia* and other Palingeniidae, and in some Northern Hemisphere families, the female subimagos mate and die without moulting.

Subimagos (and imagos) may be strictly seasonal or present nearly all year. The latter pattern is common in warm, tropical areas, while in colder, temperate areas subimaginal emergence tends to occur during the warmest periods. However, non-seasonal life cycles predominate in New Zealand (Towns 1981, 1983a) where the potential emergence period is long and the entire mayfly fauna in New Caledonia (all Leptophlebiidae) is highly seasonal (Peters unpubl.). In Australia, the subimaginal emergence of mayflies is not strongly seasonal (Campbell and Holt 1984, 1986). One species of *Austrophlebioides* emerges over 4–5 months during the summer (Duncan 1972) and *Koornonga inconspicua* emerges over 10 months during autumn-spring (Suter 1980). *Tasmanocoenis tillyardi* emerges over 6 months during spring-autumn with two distinct generations (Suter and Bishop 1980).

Natural Enemies. Mayfly nymphs and adults are important food items for many freshwater fish. Nymphs may be eaten on the stream bottom, as they drift in the current or swim to the surface, or on the surface as they emerge to the subimago. Many nymphs are also eaten by the carnivorous nymphs and larvae of other aquatic insects (Odonata, Plecoptera, Coleoptera and some Ephemeroptera). Adults are ensnared in spider webs spun over or beside streams and others are eaten by insectivorous birds and Odonata. Emerging mayflies are food for streamside amphibians, mammals and man. Szent-Ivany and Ujházy (1973) described cakes made of adult mayflies (probably the large burrower *Plethogenesia*) by natives of the Sepik River region in Papua New Guinea.

Fungi (Trichomycetes), algae, Protozoa (Peritrichidae), some tube-dwelling Chironomidae and some Simuliidae (DIPT) are phoretic commensals on nymphs but *Symbiocladius* (Fig. 16.5) is ectoparasitic (Riek 1970, 1974a; Hynes 1976a; Arvy and Peters 1976). Nymphs are intermediate hosts for certain Trematoda which parasitise fish, and both nymphs and adults are sometimes parasitised by Nematoda.

Economic Significance. Mayflies are important in the trophic structure of aquatic environments. Nymphs are mostly collector-gatherers or scrapers although some are predator-engulfers (Merritt and Cummins 1984; Edmunds 1984). Nymphs and adults, in turn, are preyed on by

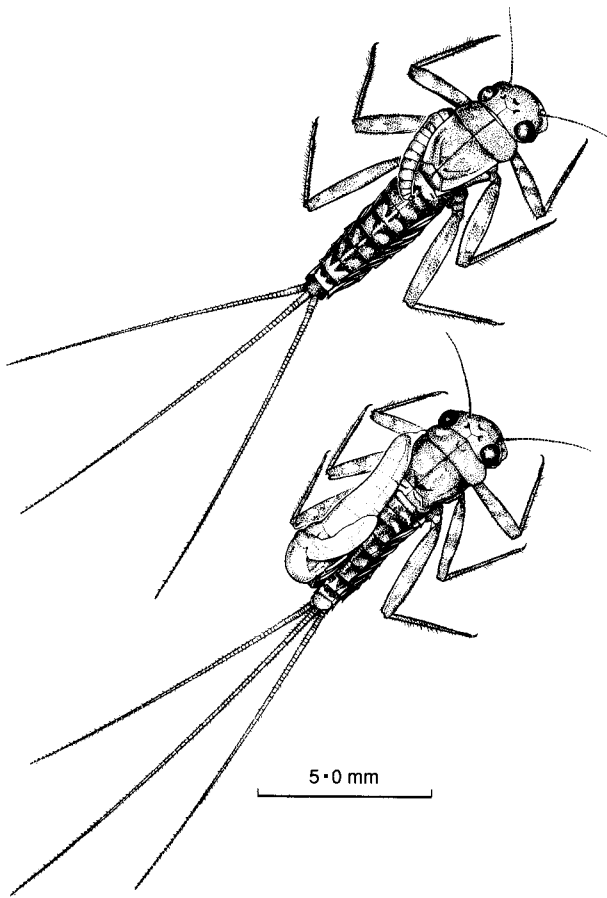


Fig. 16.5 Parasitic larva and pupa of *Symbiocladius* sp., Chironomidae, on nymphs of *Austrophlebioides* sp., Leptophlebiidae. Young larvae face in the same direction as the nymph, but older larvae and pupae always face posteriorly. [S. Monteith]

many aquatic predators, including sport fish. The particular species, overall diversity and abundance of mayflies can indicate water quality. Mayflies help to purify freshwaters; filter feeders especially remove large amounts of particulate nutrients. Adults of a few species may swarm to lights and become a nuisance in towns near lakes, and great swarms may provoke allergies in sensitised individuals. Nymphs of Asthenopodinae, such as the South-East Asian *Povilla corporaali*, excavate wood and wooden structures in water, including boats and irrigation gates (Vejabhongse 1937).

Special Features of the Australian Fauna

Australia has representatives of nine of the 23 extant mayfly families. Of the superfamilies, only the Ephemeroidea are not represented. The mayfly faunas of Australia, New Zealand and temperate South America are strikingly similar. This is evident in the Leptophlebiidae, Siphonuridae, Oniscigastridae, Ameletopsidae and Coloburiscidae, and the presence of these families in Australia is the result of Gondwanan dispersals. Certain elements of the Australian mayfly fauna are northern in origin, e.g. the Ephemerellidae, a few Leptophlebiidae, Prosopistomatidae, Caenidae and probably most Baetidae. Ephemeridae are known from New Zealand and Palingeniidae from New Guinea. Heptageniidae, Tricorythidae and Neophemeridae are widespread through the Sunda Is.

Mayflies are most abundant in the highlands of south-eastern Australia and in Tas., but there are numerous species in the colder sections of east coast streams as far north as Cape York Peninsula. There are several species in the wet south-western corner of W.A. and a few, widely distributed species in the slow-flowing, inland streams of the eastern states.

CLASSIFICATION

Order EPHEMEROPTERA (84 Australian spp.)

Suborder SCHISTONOTA (77)

BAETOIDEA (20)

1. Siphonuridae (1)
2. Baetidae (13)
3. Oniscigastridae (3)
4. Ameletopsidae (3)
- Ametropodidae (0)

HEPTAGENIOIDEA (3)

5. Coloburiscidae (3)
- Oligoneuriidae (0)
- Isonychiidae (0)
- Heptageniidae (0)

EPHEMEROIDEA (0)

- Behningiidae (0)
- Potamanthidae (0)
- Euthyplociidae (0)
- Polymitarciidae (0)
- Ephemeridae (0)
- Palingeniidae (0)

LEPTOPHLEBIOIDEA (54)

6. Leptophlebiidae (54)

Suborder PANNOTA (7)

EPHEMERELLOIDEA (1)

7. Ephemerellidae (1)
- Leptohyphidae (0)
- Tricorythidae (0)

CAENOIDEA (6)

- Neophemeridae (0)
- Baetiscidae (0)

8. Caenidae (5)
9. Prosopistomatidae (1)

There has been little agreement concerning the classification of this order (Ulmer 1920; Handlirsch 1922; Needham *et al.* 1935; Burks 1953; Edmunds and Traver 1954; Demoulin 1958; Edmunds 1962; Landa 1969; Chernova 1970; Riek 1973d; McCafferty and Edmunds 1979; Landa and Soldán 1985). The classification used

here and in Campbell (1988) is that of Landa and Soldán (1985), except that the Coloburiscinae of the Oligoneuriidae are treated as a separate family—Coloburiscidae. Further, the fossil taxa and extant subfamilies given in Landa and Soldán (1985) are not included here.

The suborders and superfamilies are evolutionary con-

cepts which have never been defined morphologically in both nymphs and adults and present definitions of the families Siphonuridae, Oniscigastridae, Ameletopsidae and Coloburiscidae are based on nymphs only. The classification of Landa and Soldán (1985) is based upon comparative internal anatomy. In the keys below, we use

external morphological characters of the Australian representatives of the families rather than the family characteristics given by Landa and Soldán.

The Heptageniidae were mistakenly recorded in the Australian fauna by Harker (1950, 1954). Campbell (1988) has catalogued the Australian species.

Keys to the Families of Ephemeroptera Known in Australia

ADULTS

1. Vein MA₂ of fore wings entirely detached basally from stem of vein MA (Fig. 16.7A), or vein MA apparently unforked (Fig. 16.8A) 2
 Vein MA of fore wings forked (Figs 16.6A–D, 7B, D, 8B, C) or vein MA₂ attached at base to vein MA₁ by a cross-vein (Fig. 16.7C) 3
- 2(1). Short, basally detached, single or double, marginal intercalaries present in centre of each interspace of fore wings (Fig. 16.7A); hind wings present or absent (if present with no more than 3 longitudinal veins) **Baetidae**
 Long, basally detached, double, marginal intercalaries present near longitudinal veins of fore wings of males (Fig. 16.8A), or intercalaries absent in fore wings of females; hind wings present (with more than 3 longitudinal veins as in Fig. 16.8A) **Prosopistomatidae**
- 3(1). Vein MA₂ of fore wings attached at base to vein MA₁ by a cross-vein (Fig. 16.7C); genital forceps of male 1-segmented; hind wings absent **Caenidae**
 Vein MA of fore wings forked (Figs 16.6A–D, 7B, D, 8B, C); genital forceps of male with 2 or more segments (Figs 16.2B, D); hind wings present 4
- 4(3). Cubital intercalaries in fore wings usually detached basally from a longitudinal vein, or 1 or more intercalaries attached to vein CuA or CuP by a cross-vein (cross-vein sometimes appears as a fork) (Figs 16.6B–D, 7D) 5
 Cubital intercalaries in fore wings consist of a series of veinlets, often forking, and attaching vein CuA to hind margin (Figs 16.6A, 7B, 8B, C) 6
- 5(4). Two short, basally detached, marginal intercalaries present in interspace between veins MP₂ and CuA of the fore wings (Fig. 16.7D); genital forceps of male with 1 short terminal segment **Ephemerellidae**
 No marginal intercalaries present in interspace between veins MP₂ and CuA of the fore wings (Figs 16.6B–D); genital forceps of male with 2 short, terminal segments, segmentation often indistinct (Figs 16.2B, D) **Leptophlebiidae**
- 6(4). Fore wing margin between veins CuA and CuP smoothly curved, tornus midway between veins CuA and CuP (Fig. 16.8B); 2 or more cubital intercalaries forked in fore wings (Fig. 16.8B); fore claw appears single (hypertrophied in male), one of the pair reduced (Fig. 16.9A) **Coloburiscidae**
 Fore wing margin between veins CuA and CuP straight to slightly curved, tornus close to vein CuA; cubital intercalaries of fore wings unforked, or sometimes with one fork (Figs 16.6A, 7B, 8C); fore claw paired (Fig. 16.9B) 7
- 7(6). Vein MP₂ of fore wings attached at base to vein CuA (Fig. 16.8C); terminal filament multisegmented, nearly equal in length to cerci **Siphonuridae**
 Vein MP₂ of fore wings attached at base to vein MP₁, directly or by cross-vein or intercalary (Figs 16.6A, 7B); terminal filament much shorter than cerci, with 1 to a few segments 8
- 8(7). First tarsal segment of hind legs (partially fused to tibia) less than half as long as tibia (Fig. 16.9C); base of vein MP₂ of fore wings attached to intercalary of vein MP, intercalary attached to vein MP₁ (Fig. 16.7B); vein MP of hind wings forked in basal half of wings **Ameletopsidae**
 First tarsal segment of hind legs (partially fused to tibia) a little shorter than tibia (Fig. 16.9D); base of vein MP₂ of fore wings attached to vein MP₁ (Fig. 16.6A); vein MP of hind wings forked in apical half of wings **Oniscigastridae**

NYMPHS

1. Mesonotum forms a shield-like carapace extending to abdominal segment 7 (Fig. 16.14A); caudal filaments retractable into abdomen **Prosopistomatidae**
 Mesonotum without a shield-like carapace (Figs 16.11–13); caudal filaments not retractable 2
- 2(1). Abdominal gills on segment 1 operculate, covering remaining gills; gills on abdominal segments 1–4 (Fig. 16.13F) **Oniscigastridae**
 Abdominal gills on segment 1 not operculate, not covering remaining gills; gills on abdominal segments 1–5, 1–6, 1–7, 2–6 or 2–7 (Figs 16.11A, B, 12A, B, 13A–E) 3
- 3(2). Abdominal gills on segment 2 operculate and quadrate (Fig. 16.12B) **Caenidae**
 Abdominal gills on segment 2 neither operculate nor quadrate, although other gills sometimes semi-operculate (Figs 16.11A, B, 12A, 13A–E) 4
- 4(3). Abdominal gills on segments 2–6 (Fig. 16.13E); ventral lamella of each gill subdivided into 2 series of small, overlapping lobes **Ephemerellidae**
 Abdominal gills on segments 1–5, 1–6, 1–7 or 2–7 (Figs 16.11A, B, 12A, 13A–D); ventral lamella of each gill plate-like (Fig. 16.15), fibrilliform (Figs 16.14B, C) or absent 5
- 5(4). Dorsal lamella of each abdominal gill sclerotised, bifid and with heavy spines (Figs 16.11B, 14B); ventral lamella unsclerotised, fibrilliform **Coloburiscidae**

- Dorsal lamella of each abdominal gill usually plate-like, neither sclerotised, bifid nor spinose (Figs 16.11A, 12A, 13A–D, 14C) ventral lamella plate-like (Fig. 16.15), fibrilliform (Fig. 16.14C) or absent 6
- 6(5). Clypeus apparently fused to frons (Figs 16.3A, B, 10B) 7
- Clypeus distinctly separated from frons by epistomal suture (Figs 16.10A, C) 8
- 7(6). Dorsal portion of each abdominal gill plate-like and ventral portion fibrilliform (Figs 16.11A, 14C); maxillary and labial palps multisegmented **Ameletopsidae**
- Gills variable, but dorsal and ventral portions similar in shape and structure (ventral portion occasionally lost) (Fig. 16.15); maxillary and labial palps 3-segmented, although segmentation often indistinct (Figs 16.3A, B, F, G) **Leptophlebiidae**
- 8(6). Antennae short, length less than length of head (Fig. 16.10C); posterolateral projections present and usually well developed on abdominal segments 8–9 **Siphonuridae**
- Antennae long, length more than twice length of head (Figs 16.10A, 12A); posterolateral projections weakly developed or absent **Baetidae**

Suborder SCHISTONOTA

Superfamily BAETOIDEA

1. Siphonuridae. The family is represented in Australia by *Ameletoides lacusalbinae*. Nymphs, with their streamlined shape and single, plate-like, abdominal gills, resemble large baetids (Fig. 16.10C); in addition to the abdominal gills nymphs have single gills on each maxilla.

A. lacusalbinae is widespread in high altitude streams in south-eastern, mainland Australia and Tas. (Tillyard 1933; Campbell 1981, 1986) and near Mt Kosciusko also occurs in lakes. Nymphs are algal scrapers (Campbell 1985) and, on the mainland at least, nymphal development ranges from less than 1 year to 2 years. Adults emerge from September to January, each female producing about 11 000 eggs.

2. Baetidae. Baetids are extremely widespread and abundant in Australia. *Baetis* (4 spp.), *Cloeon* (5 spp.), *Centroptilum* (2 spp.) and *Pseudocloeon* (1 sp.) are cosmopolitan while *Bungona* (1 sp.) is endemic. The family has received comparatively little study in Australia and undoubtedly there are undescribed species.

Nymphs are small (less than 1 cm long), slender and streamlined, with plate-like gills. They differ from nymphs of siphonurids by their smaller size and longer antennae (Fig. 16.10A), and in the structure of the labrum. Adults have transparent wings with reduced venation. *Bungona*, *Cloeon* and *Pseudocloeon* all lack hind wings.

In males the compound eyes are divided completely with the dorsal part developed into a large, turbinate structure. The eyes of females are small and comparatively simple. The penes of the male are membranous and extrudable.

Baetis occurs only in permanent, flowing water and are most common in the clear water of cold streams. The genus is widespread in Tas., the eastern mainland (including S.A.) and the south-west of W.A. (Bunn *et al.* 1986). Nymphs appear to feed mostly by scraping algae and fine particulate detritus from solid surfaces (Chessman 1986). One species of *Baetis* in a Victorian high mountain stream is univoltine with a summer emergence period (November–March) (Duncan 1972). *Baetis soror* is univoltine in one S.A. stream and bivoltine in another; both populations have multiple cohorts, with emergence over at least 9 months of the year (Suter 1980; Suter and Bishop 1980).

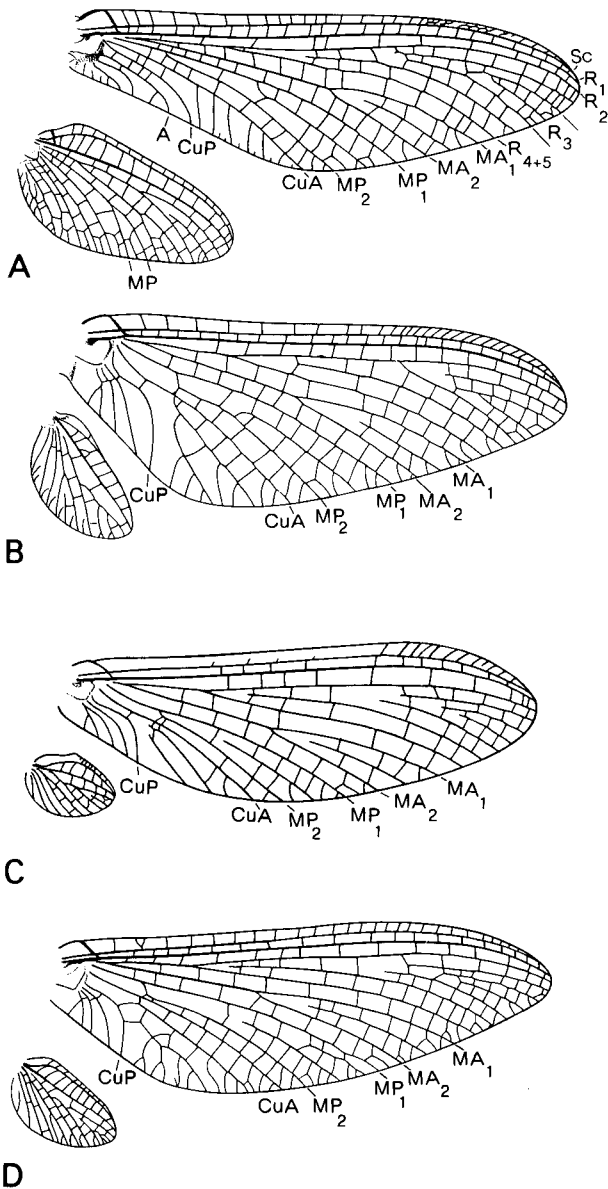


Fig. 16.6 Wing venation: A, *Tasmanophlebia* sp., Oniscigastriidae; B–D, Leptophlebiidae: B, *Atalophlebia* sp.; C, *Nousia* sp.; D, *Jappa* sp.

[M. Quick]

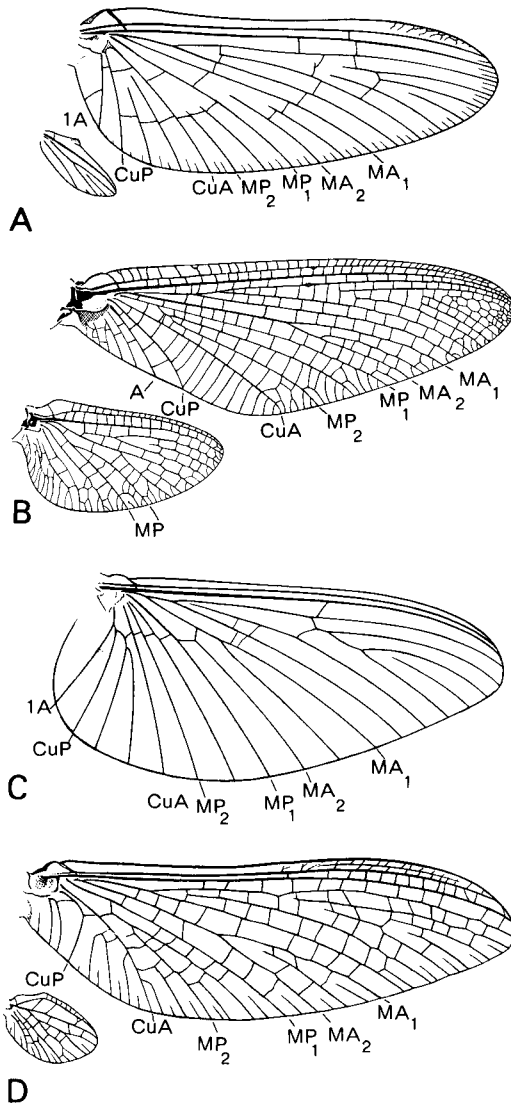


Fig. 16.7 Wing venation: A, *Baetis* sp., Baetidae; B, *Mirawara* sp., Ameletopsidae; C, *Tasmanocoenis* sp., Caenidae; D, *Ephemerellina* (*Austremarella*) sp., Ephemerellidae. [M. Quick]

Centroptilum and *Baetis* occur in similar habitats and sometimes together, but generally *Centroptilum* is absent from north-eastern Australia. Nymphs are generally larger than those of *Baetis* and have greatly elongated tarsal claws but apparently they feed in a similar fashion.

Cloeon is widespread in eastern Australia from Tas. to the tropics. Nymphs are most common in standing waters such as billabongs and farm dams and are also found in slowly flowing reaches of rivers. Nymphs of at least one species feed mostly on filamentous algae (Chessman 1986). In a seasonal creek in the N.T., nymphs of *Cloeon fluviatile* develop rapidly (about 4 weeks) and eggs can resist desiccation during dry months (Marchant 1982).

Bungona narilla was collected from a small coastal stream near Sydney but nothing more is known of its biology. *Pseudocloeon* is very small and occurs in the mountain streams of coastal Qld and N.S.W. (Riek 1970).

3. Oniscigastridae. The family is represented in

Australia by *Tasmanophlebia*. Nymphs are large with the first abdominal gills covering the other gill pairs (Fig. 16.13F). Adults have transparent wings with the wing bases washed with intense orange or dark brown.

T. lacustris is recorded from Tas., and *T. lacuscoerulei* and *T. nigrescens* from the south-eastern mainland. The genus occurs on the mainland from Barrington Tops, N.S.W., to the Fleurieu Peninsula, S.A. and is also present on Flinders I. in Bass Strait. Nymphs occur in upland lakes and the sandy, silty, slowly flowing reaches of usually small streams (where they sometimes burrow), and

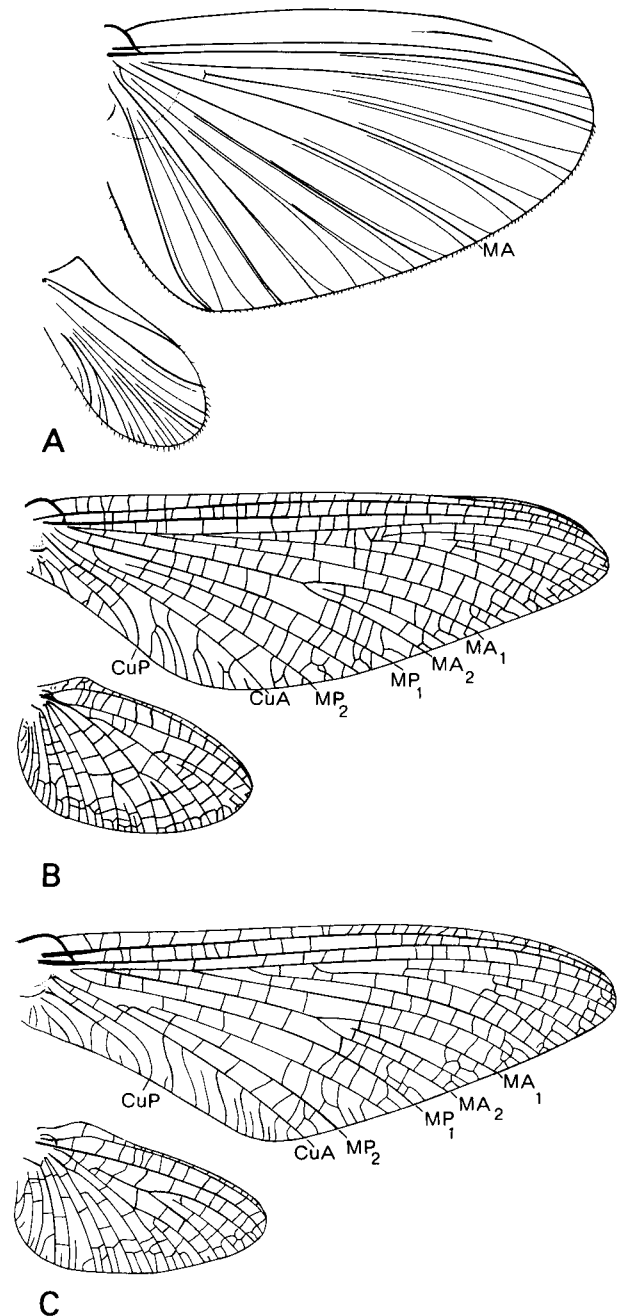


Fig. 16.8 Wing venation: A, *Prosopistoma* sp., Prosopistomatidae (drawn from Malaysian subimago); B, *Coloburiscoides* sp., Coloburiscidae; C, *Ameletoides* sp., Siphonuridae. [J. Peters]

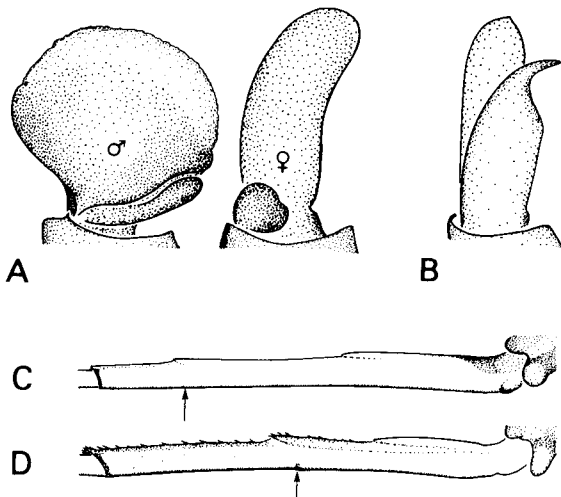


Fig. 16.9 Adults. Fore claw of: A, Coloburiscidae; B, Oniscigastridae. Fused patello-tibia and first tarsal segment of hind leg of: C, Ameletopsidae; D, Oniscigastridae; arrow indicates point of partial fusion of tibia and first tarsal segment. [J. Peters]

over altitudes from near the summit of Mt Kosciusko (about 2000 m) to almost sea-level in small, coastal streams. Nymphs feed on fine particulate detritus (Campbell 1985).

An undescribed species of *Tasmanophlebia* in a small, sub-alpine stream was found to be basically univoltine, but with some early emerging individuals giving rise to a second summer generation (Campbell 1986). Nymphs leave the water prior to ecdysis, and emergence occurs at dusk during November–March. Each female produces about 1500 eggs. Males of *T. lacuscoerulei* have been observed swarming near the edges of a lake in the middle of a hot, summer day, while males of *T. lacustris* swarm some distance from the water. No species of *Tasmanophlebia* appear to be attracted to lights.

4. Ameletopsidae. Nymphs of *Mirawara* (3 spp.) are large with prognathous heads (Figs 16.10B, 11A) and gills bearing both a plate-like lamella and a tuft (Fig. 16.14C). Adults are unique among Australian mayflies in often having red or purple wings. The genus is widespread on the mainland from Cairns to near Melbourne (Campbell 1981).

Nymphs are nocturnal and carnivorous, feeding mainly on other mayflies and chironomids which they engulf whole (Campbell 1980, 1985). They occur in stony, upland streams where they appear to require large cobbles for shelter. The life history of *M. aapta* is quite variable, occupying 10–18 months (Campbell 1986). Nymphs undergo their final ecdysis on the stream bed and subimagos rise through the water to emerge directly from the water surface. Adults are present from October to April, and females may be seen during the day depositing eggs in small groups on the surface of river pools. Each female produces about 8000 eggs.

Superfamily HEPTAGENIOIDEA

5. Coloburiscidae. *Coloburiscoides* (5 spp.) are known from the south-eastern mainland (Lestage 1935; Riek

1955e, though Riek's redefinition of *Coloburiscoides* is incorrect and applies to the New Zealand genus *Coloburiscus*). *Coloburiscoides* nymphs have mouth-parts modified for filter feeding (Fig. 16.11B) and 2 pairs of finger-like, oral gills as well as abdominal gills. Each of the latter consists of a bifid, spinose lamella and a basal tuft of filaments (Fig. 16.14B). Both the oral gills and the tufts of the abdominal gills have large numbers of chloride cells and appear to be both osmoregulatory and respiratory (Filshie and Campbell 1984). The spinose structures of the gills appear to anchor nymphs beneath rocks in stony, upland streams.

Nymphs trap fine, particulate, organic material and algae with their mouth-parts and fore legs (Campbell 1985). Nymphal development takes from 6 months to 2 years with emergence in most species occurring directly from the water surface (Campbell 1986). The emergence period is variable ranging from 4 months (November–March) for *C. giganteus* to 9 months (August–April) for *C. haleuticus* (Campbell 1986). Adults of *C. haleuticus* and at least one other undescribed species from the Snowy Mountains swarm above streams at dusk, often using bridges as markers. Females of *C. munionga* pro-

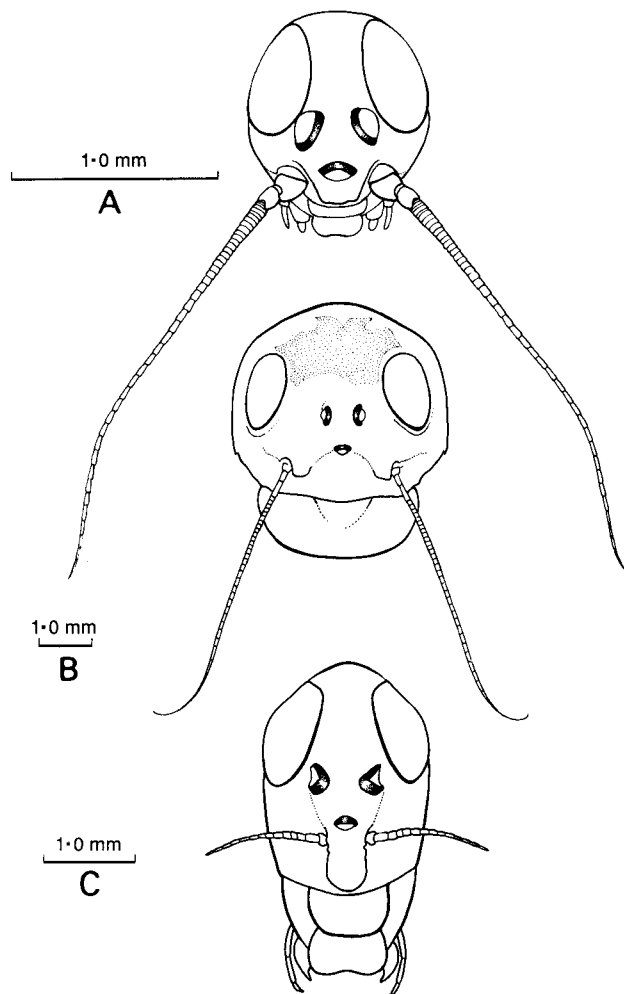


Fig. 16.10 Heads of nymphs: A, *Baetis* sp., Baetidae; B, *Mirawara* sp., Ameletopsidae; C, *Ameletoides* sp., Siphonuridae. [A. Hastings]

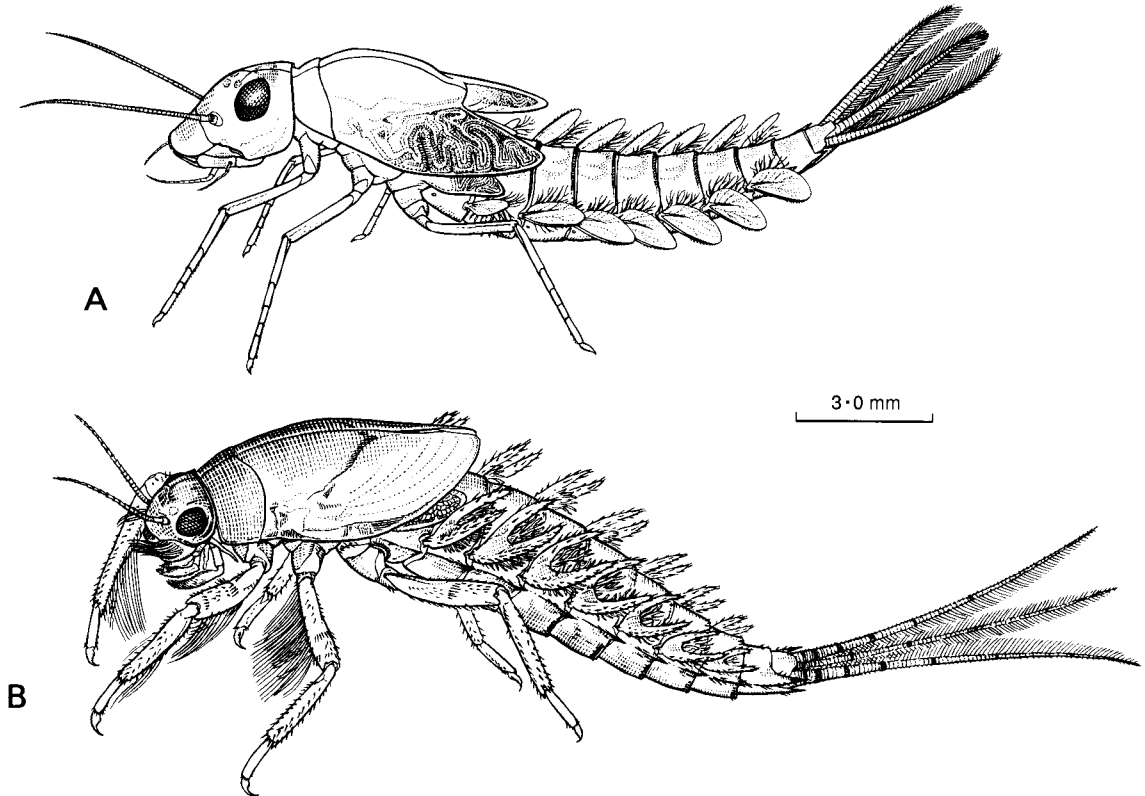


Fig. 16.11 Nymphs: A, *Mirawara* sp., Ameletopsidae; B, *Coloburiscoides* sp., Coloburiscidae.

[M. Quick]

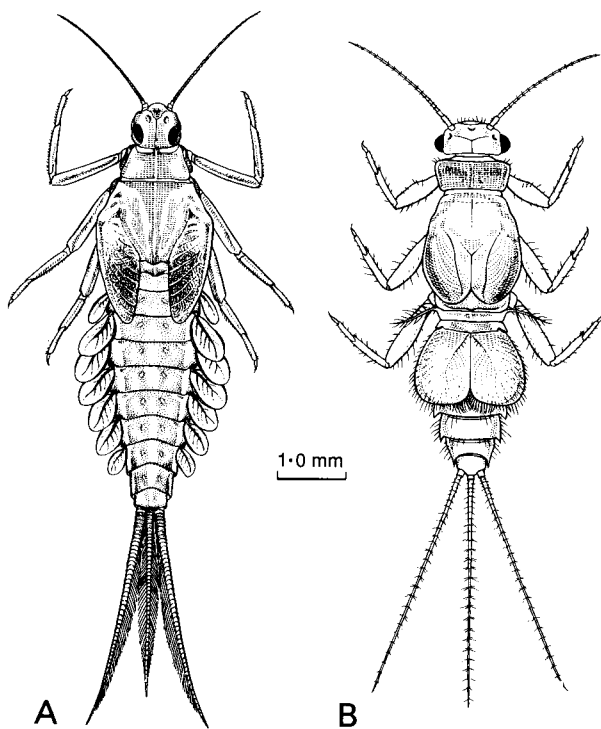


Fig. 16.12 Nymphs: A, *Centropitulum* sp., Baetidae; B, *Tasmanocoenis* sp., Caenidae.

[M. Quick]

duce between 2000 and 12 000 eggs. Eggs of all species have unusual adhesive structures (Figs 16.4C, D), and in at least one species there appears to be an 11 month egg stage or early nymphal diapause.

Superfamily LEPTOPHLEBIOIDEA

6. Leptophlebiidae. This is the dominant family of Australian mayflies, comprising more than 50% of the described genera and about 70% of the described species; numerous genera and species remain to be described. Only the subfamily ATALOPHLEBIINAE occurs in Australia. Nymphs are dorso-ventrally flattened with prognathous heads (Fig. 16.13A–D) and variously shaped gills, usually with double lamellae, on abdominal segments 1–7 (Fig. 16.15). Adult males have their eyes divided into a large upper portion with large facets and a smaller, lower portion with smaller facets (Fig. 16.1) (Horridge and McLean 1978). In the fore wings, vein CuP is strongly recurved. The hind wings are relatively small (Figs 16.6B–D) and are absent in some exotic genera. The two tarsal claws may be similar or dissimilar.

Atalophlebia is the largest Australian leptophlebiid genus at present with 18 described species, some of which are certain to be transferred to other genera in the future. Nymphs of many species with multidigitate abdominal gills tend to be found in standing or slowly flowing waters. Several species inhabit the crevices of logs. Nymphs of many species crawl from the water before ecdysis, and although some species have adults

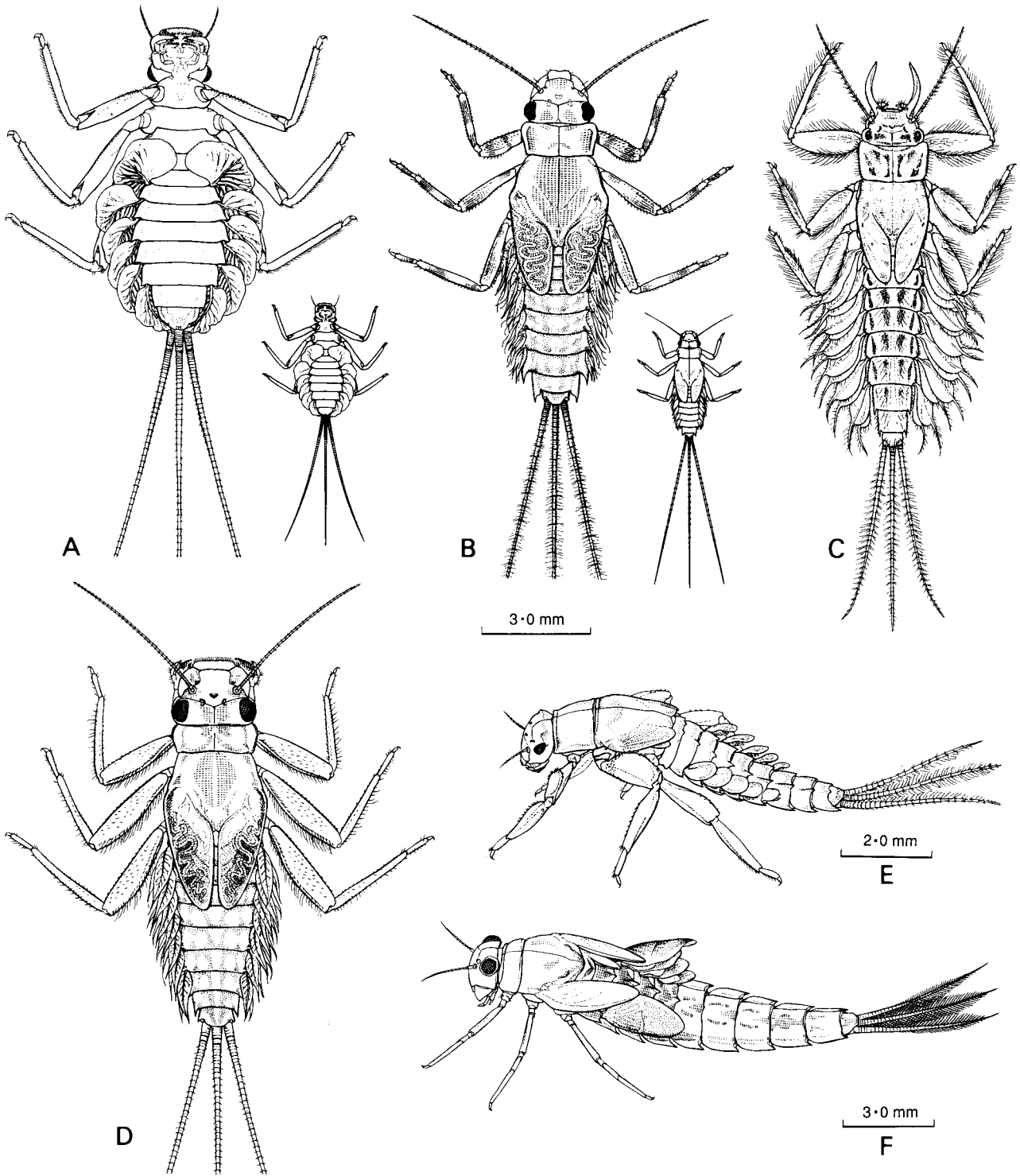


Fig. 16.13 Nymphs: A, *Kirrara* sp., Leptophlebiidae; B, *Atalophlebia* sp., Leptophlebiidae; C, *Jappa* sp., Leptophlebiidae; D, *Austrophlebioides* sp., Leptophlebiidae; E, *Ephemerellina* (*Austremerella*) *picta*, Ephemerellidae; F, *Tasmanophlebia* sp., Oniscigastridae. [M. Quick]

which swarm above the stream, it is more common for the males to patrol stretches of stream.

Atalophlebia is a widespread genus with species occurring in a range of habitats from stony upland streams and lakes, such as those in the Mt Kosciusko area, to permanent and intermittent lowland and inland streams, bill-

abongs, lakes and reservoirs. Nymphs appear to be shredders, consuming wood and leaf material (Chessman 1986). *A. australasica*, common in small, temporary and permanent streams in the Murray-Darling Basin, presumably has some mechanism for withstanding drought conditions since some of the streams in which it is abundant

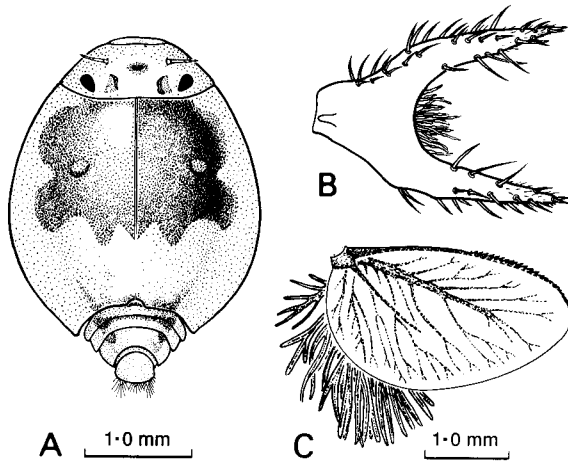


Fig. 16.14 Nymphs. A, *Prosopistoma* sp., Prosopistomatidae, dorsal aspect. Abdominal gill 4 of: B, *Coloburiscoides* sp., Coloburiscidae; C, *Mirawara* sp., Ameletopsidae. [A. Hastings]

are completely dry for more than half the year; the species is univoltine but with multiple cohorts present and adults emerge intermittently throughout the year (Suter 1980).

Austrophlebioides (Campbell and Suter 1988) includes most of the Australian species previously ascribed to *Atalophlebioides* and *Deleatidium*. Nymphs are of the sprawling type and are abundant on rocks in moderate current areas of upland streams. Adults are medium sized mayflies with completely transparent wings, and often form large swarms above streams around dusk. The genus occurs in Tas. and in streams along the eastern coast of the mainland.

Nymphs appear to be epilithic browsers (Chessman 1986) feeding on the upper surfaces of stones, mainly at night (Bailey 1981b); they are commonly collected drifting in the water (Bailey 1981a,b). Two species in a cool mountain stream near Mt Buller, Vic., are univoltine with adult emergence November–March (Duncan 1972). In the warmer La Trobe R. another species is bivoltine with a long winter and a shorter summer generation; the emergence period is February–April (Marchant *et al.* 1984).

Jappa and *Ulmerophlebia* have burrowing nymphs which are somewhat similar in appearance except that nymphs of *Jappa* possess prominent protuberances on the head. Nymphs of *Jappa* burrow in gravel and sand in stony streams (Riek 1970; Skedros and Polhemus 1986). Nymphs of *Ulmerophlebia* occur in sandy and silty areas of upland streams and in lakes (Suter 1986). Both genera appear to be absent from large, silty rivers. They feed on detritus and can also skeletonise leaves (Chessman 1986).

The 3 species currently included in *Kirrara* are not congeneric (Campbell and Peters 1986). Nymphs have greatly expanded abdominal gills forming an adhesion disc by which they anchor themselves to the tops of boulders in areas of rapid current. Adults are conspicuous because the costal and subcostal areas of the fore wings are bright orange-brown. Eggs are faceted and each facet appears to bear an adhesive structure (Fig. 16.4B).

Kirrara nymphs occur mostly in fairly warm, medium to large, upland streams on the south-eastern mainland where they browse the epilithic layers and consume both plant and animal material (Chessman 1986). The life cycle is univoltine with an adult emergence period of 3 months in early to mid-summer (Campbell and Holt 1984).

Australian *Nousia* (2 spp.) are placed in the endemic subgenus *Australonousia* (Campbell and Suter 1988); both species occur in Tasmania and *Nousia fuscata* also occurs on the mainland.

Nymphs of *Koornonga* (Campbell and Suter 1988) occur in a variety of habitats including riffles, pools and logs, and mostly feed on detritus and possibly also on coarse, particulate, organic material such as leaves. The genus is present in Tas. and over the whole of the eastern mainland. In a S.A. stream *K. inconspicua* is univoltine with a poorly synchronised life cycle, and adult emergence is spread over 10 months (Suter 1980). Of 2 species studied in Vic., one is univoltine, the other bivoltine with a short summer generation (Marchant *et al.* 1984). Emergence periods for both species are relatively short in spring and summer.

Garinjuga (Campbell and Suter 1988) occurs in upland streams of the south-eastern mainland, where the nymphs, with their characteristic broad gills (Fig. 16.15E) occur under stones in areas of rapid current. *Neboissoflebia* (Dean 1988) is distributed in both the south-eastern main-

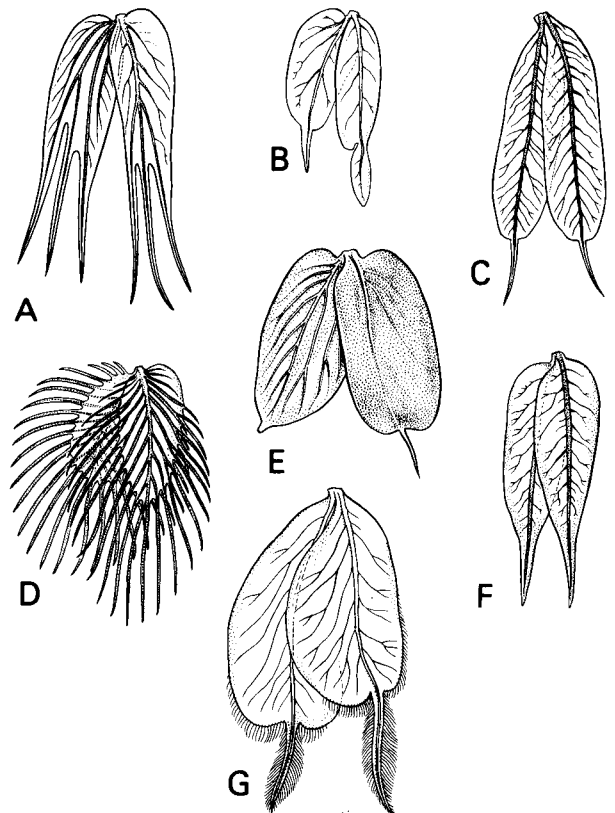


Fig. 16.15 Abdominal gills of leptophlebiid nymphs: A, *Atalophlebia australis*; B, *Choroterpes* sp.; C, *Atalophlebia yugana*; D, *A. australasica*; E, *Garinjuga maryannae*; F, *Austrophlebioides* sp.; G, *Jappa* sp. [M. Quick]

land and south-western W.A. with the nymphs feeding on leaf accumulations.

Nyungara (2 spp.) and *Bibulmena* (1 sp.) appear to be restricted to south-western W.A. where they occur in small streams in jarrah forests of the Darling Range. Nymphs of *Nyungara* resemble those of *Nousia*, while nymphs of *Bibulmena* resemble those of *Penaphlebia* from South America (Dean 1987).

Nymphs of *Atalomicria* and *Thraulophlebia* are unknown. *Thraululus* occurs in northern Australia (Grant pers. comm.) although no Australian species have yet been described.

Suborder PANNOTA

Superfamily EPHEMERELLOIDEA

7. Ephemerellidae. The single Australian species, *Ephemerellina* (*Austremerella*) *picta*, was described from a small, stony stream in southern Qld (Riek 1963; Allen 1965). Nymphs are less flattened than those of lepto-phlebiids, and bear a prominent, double row of spines dorsally on the abdomen (Fig. 16.13E). They possess gills on abdominal segments 2–6; the dorsal portion of each gill is plate-like and the ventral portion consists of 2 rows of overlapping lobes. Adults have detached marginal intercalary veins and 1 or 2 long intercalaries between veins MP_2 and CuA in the fore wings (Fig. 16.7D).

The family is widespread in the Holarctic with genera also occurring in South America, Asia and South Africa. The subfamily in which the Australian species has been placed, *TELOGANODINAE*, is primarily Ethiopian and Oriental in distribution, and *Ephemerellina s.str.* is limited in distribution to 2 provinces in China and South Africa.

Superfamily CAENOIDEA

8. Caenidae. In Australia this family is represented by *Tasmanocoenis* (5 spp.) (Suter 1984). Like the nymphs of *Tasmanophlebia*, nymphs of *Tasmanocoenis* have an operculate abdominal gill covering the other gills, but in *Tasmanocoenis* it is the second gill rather than the first, and the operculate gills are fringed with fine hairs (Fig. 16.12B). Nymphs of *Tasmanocoenis* are also considerably smaller than those of *Tasmanophlebia*. Adults of *Tasmanocoenis* are small but distinctive; the sexes are alike, with eyes of similar size, and the hind wings are absent. The fore wings are broad (Fig. 16.7C) and fringed with fine hair (not shown in Fig. 16.7C).

Nymphs are widespread in Tas. and the mainland, occurring especially in silty areas of stony streams or

rivers, and also in standing waters. Their diet seems to consist mainly of fine detritus (Chessman 1986) and they are among the more pollution-tolerant of Australian mayflies. *T. tillyardi* in S.A. streams has 1 or 2 generations per year with multiple cohorts continuously present (Suter 1980; Suter and Bishop 1980). *T. tonnoiri* is bivoltine in the La Trobe R. while another unnamed species is univoltine (Marchant *et al.* 1984). For all 3 species the emergence period is spring-summer, and for the first 2, adults emerge for 5 months or more. In the tropical Magela Ck system, a species of *Tasmanocoenis* similar to *T. tillyardi* has a nymphal development time of about 4 weeks on average and as short as 2 weeks (Marchant 1982), with adults emerging year round.

Adults of *Tasmanocoenis* frequently swarm along the margins of streams in the early morning in temperate Australia. In tropical species swarming may occur at night at sites remote from water (Marchant 1982).

9. Prosopistomatidae. Nymphs from tropical rivers in far northern Qld (Pearson and Penridge 1980) represent an undescribed species of *Prosopistoma*. Prosopistomatid nymphs are unusual in having the mesonotum forming a carapace over the thorax and abdomen as far as segment 7 so that they superficially resemble notostracan Crustacea (Fig. 16.14A). Adults are morphologically unusual. The eyes of both sexes are small and widely separated. The fore wings have no cross-veins and the longitudinal veins in males are bordered by deep intercalaries (Fig. 16.8A); the venation of females is similar but there are no intercalaries. The fore legs of the male are barely longer than the mid and hind legs, while the legs of the female are vestigial. Females do not moult to the imaginal stage.

The family contains a single genus with a wide distribution (Africa, Madagascar, Europe, southern Asia, the Philippines, Sunda I., Sulawesi, New Guinea, Solomon Is and Australia). Adults are rarely collected because they fly before dawn for a short period only, and the taxonomy of the genus is based almost solely on the nymphs (Peters 1967). Nymphs inhabit large rivers or small streams with rubble or boulder substrata. Pearson and Penridge (1980) collected the North Qld nymphs in drift samples.

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