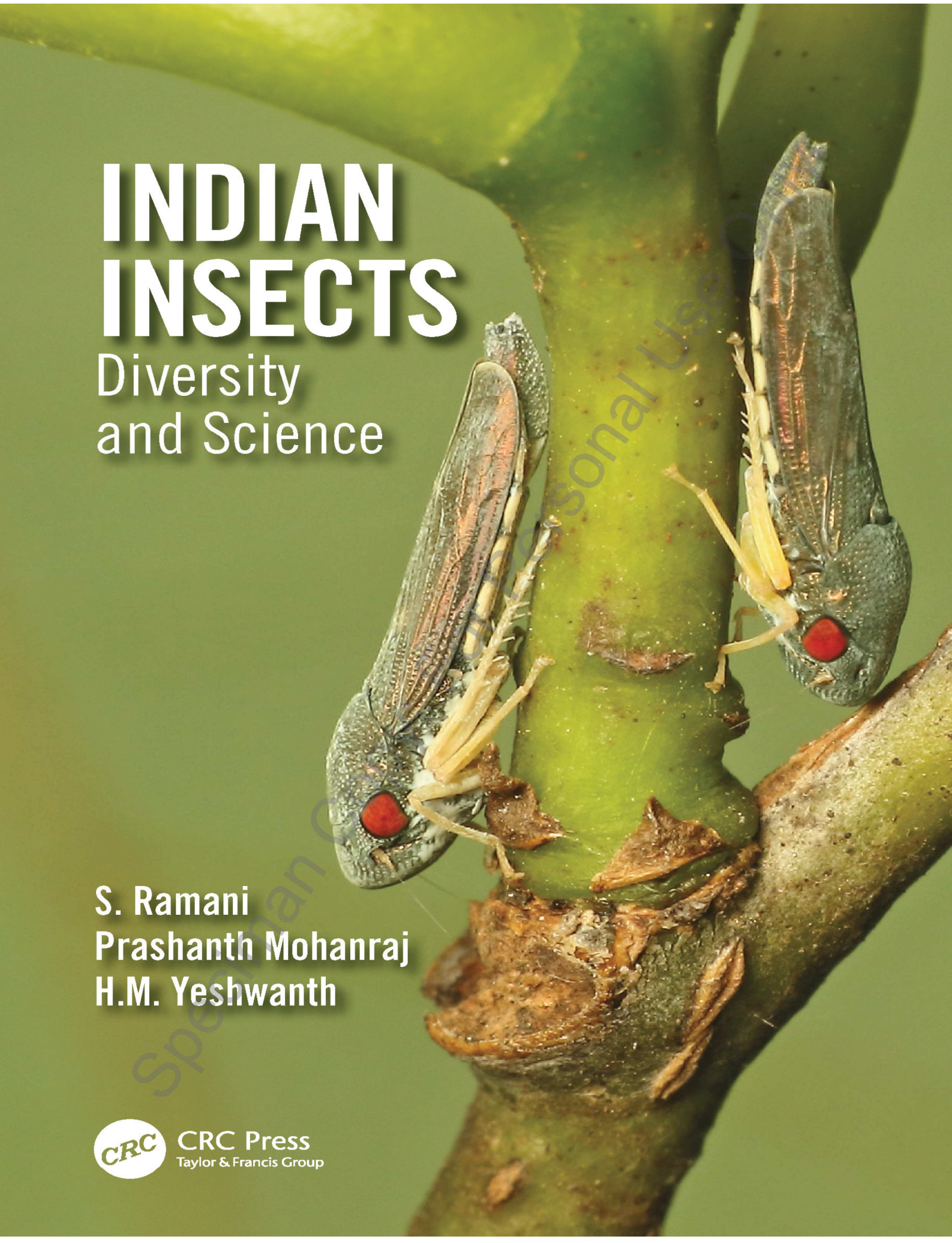

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# Contents

# 2 Mayflies (Insecta: Ephemeroptera) of India

*C. Selvakumar, K. A. Subramanian, and K. G. Sivaramakrishnan*



## CONTENTS



## INTRODUCTION

Ephemeroptera, popularly known as mayflies, are the most primitive and ancient of the extant insect groups. Their evolutionary history dates back to the Carboniferous or Permian period about 290 million years ago, and they attained the highest diversity during the Mesozoic era. Ephemeroptera together with Odonata is traditionally considered as Palaeoptera, i.e., sister group of Neoptera or all other orders of insects. However, recent molecular phylogenetic studies suggest that Ephemeroptera is a sister group to Odonata and other Neopteran insect orders. Ephemeroptera are primarily aquatic insects. The larval stage is the dominant life history stage and is always aquatic. The larvae undergo a series of moults as they grow, the precise number being variable within a species, depending on external factors, such as temperature, food availability and current velocity (Brittain and Sartori 2003) and 10–50 instars have been reported (Ruffieux et al. 1996). Typically, larvae have up to seven pairs of abdominal gills, usually three caudal filaments, and mouthparts generally adapted for collecting/gathering and deposit feeding. A few species are predaceous and some are scrapers. Certain groups are burrowers and have variously developed mandibular tusks and frontal processes to loosen the substrate and flattened legs for digging. Burrowers usually have feathery gills, which are folded over the abdomen and used to create a current through their burrow. Mayfly larvae colonize all types of

freshwaters, but are more diversified in running waters than in lakes or ponds. A couple of species can even be found in brackish waters.

Mayflies undergo hemimetabolous metamorphosis, having a unique maturation stage between the larva and adult, the subimago. Subimagos appear superficially similar to the adults, but are sexually immature. Their wings and abdomens are covered with small water-resistant microtrichia, which help them to leave the water after moulting from the final instar nymph (Edmunds and McCafferty 1988). Except for a few, such as female Polymitarcyidae and Palingeniidae (which are mature as subimagos), most adults have transparent wings and glossy abdomens, having shed the subimaginal cuticle. Males have extended forelegs for grasping the female during mating. Usually, mayfly adults live from a few hours to a few weeks depending on the species. Many species have male mating swarms forming at dawn or dusk. Females have various methods of oviposition, and the number of eggs laid varies according to species and size of female and eggs (Sartori and Sartori-Fausel 1991; Brittain and Sartori 2003). Length and number of life cycles per year depend largely on geographic locality and size of the species, with large burrowers in temperate climates taking over 2 years to mature, while tropical species may have several generations in a year.

## HIGHER CLASSIFICATION

The original suborder classification of McCafferty and Edmunds (1979), based on thoracic morphology and wing pad position, comprised the holophyletic suborder Pannota (larvae with basally fused wingpads) and the paraphyletic suborder Schistonota (larvae with free wingpads) indicating the retention of plesiomorphic traits. Afterwards, McCafferty (1991a) proposed three different suborders viz., Pisciforma, Setisura, and Rectracheata and traced phylogenetic relationships within and among the suborders. Concurrent to McCafferty's work, Kluge (1988, 1998) independently proposed two suborders viz., Furcatergalia and Costatergalia. In contrast to previous hypotheses based on morphological observations by Ogden and Whiting (2005), the relationships inferred from the molecular data were congruent in some cases, but incongruent in others. In their investigation, the groups, Furcatergalia, Pannota, Carapacea, Ephemerelloidea, and Caenoidea, and 15 families were supported as monophyletic. On the other hand, Setisura, Pisciforma, Baetoidea, Siphlonuroidea, Ephemeroidea, Heptagenoidea, and five families were not supported as monophyletic (Sivaramakrishnan et al. 2011). Presently, four suborders are recognized in the order Ephemeroptera viz., Carapacea, Furcatergalia, Setisura, and Pisciforma (Sivaramakrishnan 2016).

**Order Ephemeroptera**
- Suborder: **Carapacea**
  - Superfamily: **Prosopistomatoidea**
    - Family: **PROSOPISTOMATIDAE**
- Suborder: **Furcatergalia**
  - Superfamily: **Leptophlebioidea**
    - Family: **LEPTOPHLEBIIDAE**
      - Subfamily: Atalophlebiinae
      - Subfamily: Leptophlebiinae
  - Superfamily: **Ephemeroidea**
    - Family: **EPHEMERIDAE**
      - Subfamily: Ephemerinae
      - Subfamily: Hexageniinae
      - Subfamily: Palingeniinae
      - Subfamily: Icthybotinae
    - Family: **POLYMITARCYIDAE**
      - Subfamily: Euthyplocynae
      - Subfamily: Asthenopodinae
      - Subfamily: Polymitarcyinae
    - Family: **POTAMANTHIDAE**
  - Superfamily: **Caenoidea**
    - Family: **CAENIDAE**
      - Subfamily: Caeninae
      - Subfamily: Brachycercinae
    - Family: **NEOEPHEMERIDAE**
  - Superfamily: **Ephemerelloidea**
    - Family: **EPHEMERELLIDAE**
      - Subfamily: Ephemerellinae
    - Family: **TELOGANODIDAE**
    - Family: **TRICORYTHIDAE**
- Suborder: **Setisura**
  - Superfamily: **Heptagenioidea**
    - Family: **HEPTAGENIIDAE**
      - Subfamily: Heptageniinae
- Suborder: **Pisciforma**
    - Family: **AMELETIDAE**
    - Family: **BAETIDAE**
      - Subfamily: Baetinae
      - Subfamily: Cloeoninae

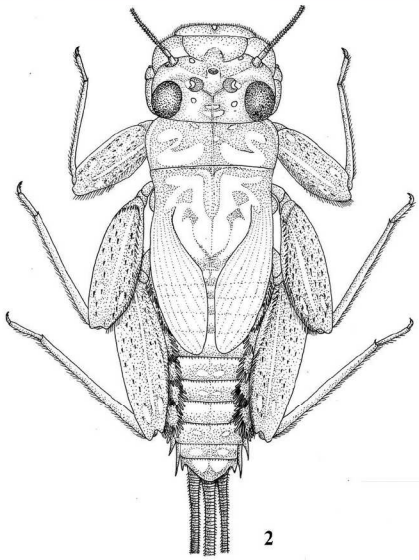
## KEY DIAGNOSTIC CHARACTERS

### Order Ephemeroptera (Figures 2.1 and 2.2)

Mayflies are distinguished from other insect orders by the following characters:

Adult: (i) small-to medium-sized elongate fragile insects; (ii) antennae short and setaceous, mouthparts vestigial, compound eyes large, three ocelli present; (ii) generally two pairs of membranous wings (though hind pair greatly reduced) held vertically over body when at rest, with many cross veins; (iv) abdomen terminated with two very long cerci and frequently a median caudal filament; and (v) with subimaginal and imaginal winged stages.

Larvae: (i) aquatic; (ii) body campodeiform; (iii) antennae short, compound eyes well-developed, biting mouthparts; (iv) abdomen usually with long cerci and a median caudal filament; and (v) four to seven pairs of segmental tracheal gills (Gillott 2005).


**FIGURES 2.1–2.2** **1**. *Klugephlebia kodai* (adult) and **2**. *Petersula courtallensis* (larva).

## Suborder Carapacea

Members of the Carapacea (an allusion to the carapace-like enlargement of the larval mesonotum) are included in a single superfamily Prosopistomatoidea (Gillott 2005).

### Superfamily Prosopistomatoidea

The two small families in this group, the Baetiscidae and Prosopistomatidae, show considerable parallel evolution in the larval stage. Indeed, their larvae are remarkable in having an enormous, posteriorly projecting mesonotal shield that protects the gills so that they superficially resemble notostracan crustacea, into which group *Prosopistoma* was originally placed by the French biologist Latreille in 1833 (Berner and Pescador 1980). Larvae of most species live in moving water, from streams to large rivers, where the bottom has sand, fine gravel, or small stones. Adult baetiscids, which are medium sized insects, have an unusually large mesothorax; the eyes of males are large and almost contiguous, but not divided horizontally. Prosopistomatid adults of both sexes have small, widely separated eyes; males have relatively short forelegs; the legs of females are vestigial; and females do not have an adult moult (Gillott 2005).

Family Prosopistomatidae Lameere, 1917 (Figures 2.3 and 2.4) Prosopistomatidae is a distinct, enigmatic family of mayflies presently confined to the Palaearctic, Afrotropical, Oriental, and Australasian realms and represented by a single genus viz. Prosopistoma Latreille, 1833. The larvae of this family have the following apomorphies: pronotum and mesonotum with rounded lateral margins without protuberances, with strongly derived mouthpart architecture, with symmetric mandibles with complete loss of molar, with first six ventral abdominal segments fused and with gills completely covered by carapace, hidden in a gill chamber (Bauernfeind and Soldán 2012).

## Suborder Furcatergalia

Furcatergalia is the largest suborder of order Ephemeroptera. Its name derives from the forked nature of the larval gills. The group includes five superfamilies: Leptophlebioidea, Behningioidea, Ephemeroidea (burrowing mayflies), Ephemerelloidea, and Caenoidea. The last two superfamilies collectively form the pannote mayflies, so called because of the fused forewing pads of the larvae (Gillott 2005).

### Superfamily Leptophlebioidea

Family Leptophlebiidae Banks, 1900 (Figures 2.5–2.8) Leptophlebiidae is the only family of this primitive lineage. This has maximum diversity in the southern hemisphere (Edmunds 1972). The family is currently defined as monophyletic by the following apomorphies in the larvae: (i) maxilla broadened apically with a special arrangement of filtering setae and (ii) upper part of male compound eyes usually globular (superficially similar to turbinate eyes in Baetidae). In imagines and subimagines: (i) furcasternal protuberances separated; (ii) the metathoracic ganglion situated in between; (iii) cubital field of the forewing usually with two intercalaries or one bifurcate vein; and (iv) paracercus present in larval and imaginal stages (Bauernfeind and Soldán 2012). This represents one of the major stem groups within the Ephemeroptera consisting of relatively ancestral and highly derived components (McCafferty and Edmunds 1979). Leptophlebiidae is a basal lineage and a sister group to a relatively derived clade that includes a pair of sister groups viz., Scapphodonta and Pannota (McCafferty and Wang 2000), in addition to a more basal lineage represented by the Behningiidae (McCafferty 2004). Both the subfamilies of Leptophlebiidae viz., Atalophlebiinae and Leptophlebiinae are known from the Oriental region. Twelve genera of Leptophlebiidae, six of which are endemic to south India are distributed in Western Ghats, all belonging to the subfamily, Atalophlebiinae. The generic limits of Leptophlebiidae, especially those of the eastern hemisphere, are well defined.


**FIGURES 2.3–2.8** Larvae: **3**. *Prosopistoma indicum*; **4**. *Prosopistoma someshwarensis*; **5**. *Edmundsula lotica*; **6**. *Nathanella indica*; **7**. *Notophlebia jobi*; and **8**. *Thraulus gopalani*.

## Superfamily Ephemeroidea

### Family Ephemeridae Latreille, 1810 (Figure 2.9)

Systematic and zoogeographical aspects of Asiatic Ephemeridae were dealt with extensively by McCafferty (1973, 2004). Diagnostic characters of this family are in larvae: mandibular tusks curved, without denticles and round in cross section; abdominal segments 7–9 elongated posteriorly, gills inserted in the middle of the segments; gill 1 vestigial and in imagines forewing with several veins from AA to hind margin of wing. The family is represented in India by the genera *Ephemera* (11 species), *Anagenesia* (3 species), and *Eatonigenia* (2 species). The genus *Ephemera* is the most speciose and widely distributed ephemerid genus, distributed all over the Holarctic, Ethiopian, and Oriental regions. The genus shows a relatively high diversity in the Oriental region from where it probably dispersed to the Holarctic and Afrotropical regions. In India, two subgenera of *Ephemera* viz., *Ephemera* and *Aethephemera* are represented by ten and one species, respectively (Sivaramakrishnan 2016).

### Family Polymitarcyidae Banks, 1900 (Figure 2.10)

Polymitarcyidae is widely distributed, both in tropical and temperate areas with the exception of Australia and New Zealand (Kluge 2004; McCafferty 2004). They are one of the primitive, burrowing mayflies in the larval stage, making tunnels in submerged wood or living in aquatic plants and sponges and also inorganic sediment such as clay, mud, or sand (Hartland-Rowe 1958). Presently, three subfamilies are recognized viz., Polymitarcyinae in the Old World, with a northwestern extension into the Nearctic region, Asthenopodinae in

Afrotropical, Oriental and Nearctic regions, and Campsurinae in Nearctic and Neotropical regions (Needham et al. 1935). Three genera of this family viz., *Ephoron*, *Languidipes,* and *Povilla* are recorded from India.

Family Potamanthidae Albarda, 1888 (Figure 2.11) Potamanthidae is basically a Laurasian family comprising three genera viz., *Rhoenanthus*, *Anthopotamus,* and *Potamanthus*, of which *Anthopotamus* is Nearctic, while others occur in the Oriental region. A revision of the family by Bae and McCafferty (1991) presents a detailed account of the potamanthid phylogeny and biogeography. The larvae of this family are distinguished by somewhat dorsoventrally flattened bodies; small to large, somewhat convergent mandibular tusks projecting in front of the head; outspread legs; and posterolaterally oriented, fringed, and bilobed gills on abdominal segments 2–7. A distinct frontal process on the head and modifications of the legs which are associated with burrowing in other ephemeroids are not present in potamanthids. The adults and subimagos of Potamanthidae are distinguished primarily by wing characters. Besides a strongly arched $MP_2$ and CuA of the forewings, which is typical of all ephemeroids, the $A_1$ is distinctly forked and the hindwings each have an acute costal projection. Depending on the species, adults and subimagos can have three well-developed caudal filaments or the median terminal filament may be partially developed or rudimentary. The genus *Rhoenanthus* (*Rhoenanthus*) occurs in India, Vietnam, Thailand, Malaysia, and Cambodia (but does not reach Sulawesi), while *Rhoenanthus* (*Potamanthindus*) ranges from Korea through China to Vietnam and Thailand.

## Superfamily Caenoidea

Family Caenidae Newman, 1853 (Figures 2.12 and 2.13) The family Caenidae is widespread in tropical and Palaearctic Asia. The family Caenidae is currently defined as monophyletic by the following apomorphies: in larvae second gill operculate, with a row of spiculae (Brachycercinae) or microtrichia (Caeninae) along the ventral outer margin. Imagines with fan-shaped forewings, veins iMP and $MP_2$ in forewings arise independently from one another, hindwings completely missing; forceps without segmentation; paracercus retained in the winged stages; caudal filaments in female imagines distinctly shorter than in male imagines (Bauernfeind and Soldán 2012). Three subfamilies are currently recognized, Brachycercinae, Caeninae and Madecocercinae. Five genera of this family are reported from the Oriental region of which two genera viz., *Caenis* and *Clypeocaenis* are recorded from India (Soldán 1978). Worldwide, about 15 genera including more than 100 species have been recorded. The genus *Caenis* is almost cosmopolitan, excluding Australia. *Caenis* is a large and apparently very old genus, and it could well be of Pangean origin (McCafferty and Wang 2000). The so-called brush-legged *Clypeocaenis* is an Oriental-Ethiopian genus which seems to have its centre of diversity in the Oriental region.

Family Neoephemeridae Traver, 1935 (Figures 2.14 and 2.15) Neoephemeridae is a small group of pannote mayflies presently confined to Holarctic and Oriental regions. The family is a distinct monophyletic group of mayflies (McCafferty and Edmunds 1979), but the taxonomy of its members has been problematic. Neoephemerid larvae are similar to caenid mayflies in that they have a pair of large, subquadrate, operculate




**FIGURES 2.9–2.11** Larvae: **9**. *Ephemera* (*Aethephemera*) *nadinae*; **10**. *Languidipes* sp.; **11**. *Rhoenanthus* (*Potamanthindus*) sp.;


**FIGURES 2.12–2.15** Larvae: **12**. *Caenis* sp.; **13**. *Clypeocaenis bisetosa*; **14**. *Potamanthellus caenoides*; and **15**. *Potamanthellus ganges.*

gills on abdominal segment 2. Adults, on the other hand, are similar to potamanthid mayflies, having similar wing venation (esp., basally arched MP2 and CuA, forked A1 in forewings). Bae and McCafferty (1991) clearly delimited both stages of Neoephemeridae and Potamanthidae. This family is represented by three genera viz., *Potamanthellus* Lestage, 1931 (seven species), *Neoephemera* McDunnough (six species), and *Ochernova* Bae and McCafferty (one species) (Bae and McCafferty 1998; Zhou and Zheng 2000; Nguyen and Bae 2003). Larvae of Neoephemeridae have unique operculate gills on the second abdominal segment that are fused medially. The larvae of *Potamanthellus* are distinguished from those of *Neoephemera* and *Ochernova* by their densely setate mouthparts, by their lack of well developed lateral expansions of the pronotum and mesonotum, and by their possession of rows of long setae on the caudal filaments (Bae and McCafferty 1998).

## Superfamily Ephemerelloidea

**Family Ephemerellidae Klapalek, 1909 (Figures 2.16–2.18)** The family comprises one of the abundant and widespread groups of known pannote mayfly genera mostly inhabiting pristine streams. They are popularly known as 'spiny crawlers'. The family is defined by the apomorphic loss of gills 2 from the larval abdomen (McCafferty and Wang 2000) and male genital forceps segment 1 that has its length much less than its width (Jacobus and McCafferty 2006). This family represents the Laurasian group of a monophyletic ephemerelloid clade differentiated conspicuously from the remaining seven Gondwanian families of Ephemerelloidea (Bauernfeind and Soldán 2012). The family comprises two subfamilies viz., Timpanoginae Allen and Ephemerellinae s.s. (McCafferty and Wang 2000; Jacobus and McCafferty 2006). It is predominantly Holarctic and Oriental, comprising 16–23 genera and 200–400 species globally (Bauernfeind and Soldán 2012). The ephemerelllid larvae like other mayfly larvae constitute vital links in the food chain of several insectivorous fishes and certain birds (Jenkins and Ormerod 1996; Feck and Hall 2004). The concept of Ephemerellidae is broadly outlined in Eaton's monumental monograph (1883–1888). However, Klapalek (1909) formalized it as a family. Traver (1935) recognized this group and Edmunds and Traver (1954), Edmunds et al. (1963), and Allen (1965, 1980, 1984) subsequently revised the concepts of the family. Further refinements in classification and phylogeny of the family reflecting Hennigian phylogenetic hypotheses were made mainly by Kluge (2000), Jacobus and McCafferty (2008), and Ogden et al. (2009a) among others. Though around ten genera of this family inhabit the Oriental region (Soldán 2001), according to Sivaramakrishnan (2016), only three genera viz., *Drunella, Ephemerella,* and *Torleya* are represented so far in India and he has attributed this to lack of extensive survey and investigation of ephemerellids in India, especially from the Himalayas. Five species under three genera have so far been reported from India viz., *Cincticostella indica* (Kapur and Kripalani) from Kulu Valley (N. W. Himalaya), *Drunella submontana* (Brodsky) from Kashmir, *Torleya coheri* (Allen and Edmunds) from Kashmir, *Torleya lacuna* (Jacobus, McCafferty, and Sites) from Kunjankhuzi (Tamil Nadu), and *Torleya nepalica* (Allen and Edmunds) from Karnataka (Kapur and Kripalani 1961; Jacobus and McCafferty 2004a, 2004b; Jacobus et al. 2007).

**Family Teloganodidae Allen, 1965 (Figures 2.19–2.21)** Teloganodidae is an ancient group of mayflies of Gondwanan origin that currently are known from throughout the Oriental region and from the southern tip of Africa (McCafferty and Wang 2000; Jacobus and McCafferty 2006). This family can be separated from other families of Ephemerelloidea in larvae by the presence of gills on abdominal segment II, absence of gills on segment VII, glossae only


**FIGURES 2.16–2.21** Ephemeropteran larvae: **16**. *Drunella submontana*; **17**. *Torleya lacuna*; **18**. *Torleya nepalica*; **19**. *Derlethina tamiraparaniae*; **20**. *Indoganodes jobini*; and **21**. *Teloganella indica*.



partially fused with paraglossae, and male eyes divided in two parts. A unique character shared by all teloganodid nymphs is the presence of stout spatulate setae on margins of coxal projections (Jacobus and McCafferty 2006). The Oriental lineage of Teloganodidae can be separated from the Afrotropical lineage by the absence of gills on abdominal segment I and the reduction of the median caudal filament giving the nymphs a two-tailed appearance (Sartori et al. 2008). Allen (1965) established the subfamily Teloganodinae within the Ephemerellidae. Teloganodinae was raised to family status by McCafferty and Wang (1997), and the composition of the family was refined by McCafferty and Wang (2000). Significant phylogenetic and biogeographic studies of teloganodid, and ephemerelloid mayflies in general, that have contributed to our current understanding of teloganodid systematics include works by McCafferty and Wang (1997, 2000), McCafferty and Benstead (2002), Jacobus and McCafferty (2006), and these works have incorporated various cladistic analyses of both Afrotropical and Oriental Teloganodidae. The recent landmark monograph on Oriental Teloganodidae by Sartori et al. (2008) distinguishes the Oriental lineages of Teloganodidae known at the time from the Afrotropical lineages and contributes to understanding patterns of distribution of the Oriental genera and species. The family currently includes the Afrotropical genera *Ephemerellina* Lestage, *Lestagella* Demoulin, *Lithoglea* Barnard, *Manohyphella* Allen, and *Nadinetella* McCafferty and Wang (Pereira-da-Conceicoa and Barber-James 2013) and the Oriental genera *Derlethina* Sartori, *Dudgeodes* Sartori, and *Teloganodes* Eaton (=*Macafertiella* Wang) (revised by Sartori et al. 2008). Recently, the genus *Indoganodes* Selvakumar, Sivaramakrishnan, and Jacobus was established and five new species were described from South India by Selvakumar et al. (2014a).

Family Tricorythidae Lestage, 1942 (Figure 2.22) The family Tricorythidae is Afrotropical and Oriental. Larval diagnostic characters: labium fused into single semicircular structure, palps with long setae; gills on abdominal segments II–V or

II–VII; gill II may overlay, partially conceal rest of series. All the subfamilies occur in Africa and Malagasy. Only the genus *Sparsorythus* is found in south India, Sri Lanka, and southeast Asia. Sroka and Soldán (2008) have established the genus *Sparsorythus*, based on *S. bifurcatus* from Vietnam. They described *S. gracilis* from northern Western Ghats. This advanced group of Oriental Tricorythidae with many apomorphies have been geographically isolated from African species for more than 100 million years. After splitting of Indian subcontinent from Africa, Indian species evolved further (Sroka and Soldán 2008).

## Suborder Setisura

Included in this suborder are the families listed under the superfamily Heptagenoidea in older classifications. The major family is the Heptageniidae which ranks next to the Baetidae in terms of number of described species. Generally, dark coloured larvae are typically found clinging to the underside (occasionally the exposed face) of stones in fast-flowing streams and on wave-washed shores of large lakes. They are remarkably well adapted for this life. Their body is extremely flattened dorsoventrally; the femora are broad and flat; the tarsal claws have denticles on the lower side; the gills are strengthened on their anterior margin; and in some species the entire body takes on the shape (and function) of a sucking disc. Some larvae have fore tarsi with numerous setae that filter algae etc. from the water. Adults vary in size and colour. The eyes of male are large, but not contiguous (Gillott 2005).

### Superfamily Heptagenoidea

**Family Heptageniidae Needham, 1901 (Figures 2.23–2.25)** Heptageniidae is a family of mayflies with around 509 described species and distributed mainly in the Holarctic, Oriental, and Afrotropical regions (Barber-James et al. 2008). The family is currently defined as monophyletic by the following apomorphies: in larvae, the submentum vestigial, labium highly modified; in imagines, first tarsal segment distinctly articulated with tibia on all legs, cubital field of forewing with four intercalaries forming two pairs, in each pair the first intercalary concave (Bauernfeind and Soldán 2012). The phylogenetic origin of Heptageniidae was studied in detail by McCafferty (1991b), though Edmunds (1979) pioneered to highlight the biogeographic relationships of the Oriental and Ethiopian mayfly fauna. Excellent contributions regarding the understanding of the generic limits of the Heptageniidae were made by Jensen (1974) and Kluge (1988). Biogeography and evolution of the genera of Heptageniidae have been discussed at the global level in the context of a phylogenetic higher classification of the family by Wang and McCafferty (2004). They recognize three subfamilies viz., Ecdyonurinae, Heptageninae, and Rhithrogeninae. The family Heptageniidae is Laurasian in origin and is a conspicuous component of the benthic community in terms of abundance. The subfamily Heptageninae, though recorded from Himalayan streams, essentially as a Palaeactic spillover group, has not penetrated further south into the Western Ghats.




**FIGURES 2.22–2.25** Larvae: **22**. *Sparsorythus gracilis*; **23**. *Afronurus kumbakkaraiensis*; **24**. *Epeorus petersi*; **25**. *Thalerosphyrus flowersi*.


**FIGURES 2.26–2.30** Larvae: **26**. *Ameletus primitives*; **27**. *Baetis michaelohubbardi*; **28**. *Bungona* (*Chopralla*) *pusilla*; **29**. *Labiobaetis jacobusi*; and **30**. *Tenuibaetis frequentus*.



## Suborder Pisciforma

McCafferty (1991) introduced the suborder Pisciforma (the name refers to the minnow-like body and actions of the larvae) for a group of families whose relationships remain unclear. For this reason, no arrangement into superfamilies is undertaken, though in earlier schemes the families were lumped in a single superfamily Baetoidea (Gillott 2005).

### Family Ameletidae McCafferty, 1991 (Figure 2.26)

The family Ameletidae is present worldwide and about 50 species are distributed in the Holarctic, Central American, and Oriental region. The family is currently defined as monophyletic by the following apomorphies: in larvae, mouthparts highly specialized, e.g., maxilla apically broadened with pectinate, comb-shaped bristles; forceps base (styliger) of male imagines with dorsal membranous area (Bauernfeind and Soldán 2012). In India only one genus *Ameletus* Eaton has been recorded with two species.

### Family Baetidae Leech, 1815 (Figures 2.27–2.35)

The homogenous family Baetidae commonly known as minnow mayflies encompasses around 100 genera and 900 species constituting one-quarter of the global Ephemeroptera diversity with a cosmopolitan distribution except for Antarctica and New Zealand (Gattolliat and Nieto 2009). They are one of the major components freshwater zoobenthos less diversified in standing water and mainly diversified in unimpacted lotic water, especially in the tropical belt. They are excellent bioindicators of water quality (Buss and Salles 2007; Kubendran et al. 2017a). Baetidae are distinguished by the presence of turbinate eyes in the male imago, detached $MA_1$ and $MA_2$ forewing veins, the presence of single or double free intercalary vein in the forewing, hind wings reduced or absent, three segmented mid and hind tarsi, and membranous penis (Edmunds et al. 1976). Larvae are pisciform, generally with long antennae and simple or double ovoid gills on segments I–VII or II–VII. They are unique in having the lateral branches of the epicranial suture anterior to the lateral ocellia ventral orientation of the dorsal lobe at the apex of femora (Wang and McCafferty 1996). Kazlauskas (1972) proposed dividing the family into two subfamilies viz., Baetinae and Cloeoninae. This is primarily based on the diversity of the Palaearctic representation of the Baetidae. Furthermore, two conflicting concepts have been proposed, the division of the Baetidae into different subfamilies (Gillies 1991) and the gathering of genera in several complexes (Waltz et al. 1994; Lugo-Ortiz and McCafferty 1996, 1998a, 1998b). Generic delimitation in Baetidae is being fine-tuned by taking into account larval characters rather than only imaginal ones and secondly by the use of phylogenetic methods and the splitting of paraphyletic and polyphyletic genera. Recent molecular studies reveal that the division into subfamilies is too simplistic and most of the complexes are not monophyletic (Gattolliat et al. 2008).


**FIGURES 2.31–2.35** Adults and larvae: **31**. *Cloeon* sp. (larva); **32**. *Cloeon bicolor* (adult); **33**. *Cloeon bimaculatum* (adult); **34**. *Cloeon harveyi* (adult); and **35**. *Procloeon* sp. (larva).

## KEY TO FAMILIES OF EPHEMEROPTERA

### Adults

1. Venation in forewings considerably reduced, cross veins completely missing or missing at least between wing base and vein MA ..... **Prosopistomatidae**
- Venation in forewings not considerably reduced, cross veins present also between wing base and vein MA..... 2
2. Forewings vein $MP_2$ (and CuA) strongly bent near the wing base, diverging from vein $MP_1$ at an angle of almost 80°; hindwings always well developed..... 3
- Forewings vein $MP_2$ (and CuA) not strongly bent near the wing base, almost parallel to vein $MP_1$; hindwings sometimes reduced or absent..... 6
3. Wings dull whitish, unicoloured; hindlegs short, weakly developed; paracercus strongly reduced (to several segments) in male, well developed in female ..... **Polymitarcyidae**
- Wings clear, translucent with or without dark spots; hindlegs normally developed; paracercus either present or absent in both sexes .....4
4. Wings with dark spots; vein AA bifurcate in forewings, costal cross veins distal to bulla simple (forming small quadrangular fields) ..... **Ephemeridae**
- Wings without dark spots; vein AA simple in forewings, costal cross veins distal to bulla forked or branched (forming small polygonal fields)..... 5
5. Paracercus present; forewing length >10 mm; costal cross veins basal to bulla strong and well developed ..... **Potamanthidae**
- Paracercus reduced, missing; forewing length <10 mm; costal cross veins basal to bulla weak, imperfect or atrophied ..... **Neoephemeridae**

6. Paracercus missing (reduced to a few segments) .... 7
- Paracercus present (multisegmented) ..... 9
7. Forewings with short basally detached single or double marginal intercalaries present in each interspace; forewing with $MA_2$ and $MP_2$ detached basally from their respective stems; hindwings small or absent; penes of male membranous; upper portion of eyes of male raised on a stalk-like structure ..... **Baetidae**
- Forewings with marginal intercalaries attached basally to other veins; forewing with $MA_2$ and $MP_2$ attached basally; hindwings relatively large; penes of male well developed; eyes of male not raised on a stalk-like structure ..... 8
8. Cubital field between veins CuA and CuP with two pairs of intercalaries ..... **Heptageniidae**
- Cubital field between veins CuA and CuP with several sinuous intercalaries ..... **Ameletidae**
9. Hindwings present and relatively large, with one or more veins forked; costal projection shorter than wing width ..... 10
- Hindwings absent ..... 12
10. Forewing with short basally detached marginal intercalaries between veins along entire outer margin of wings; genital claspers of male with one short terminal segment ..... 11
- Forewing without short basally detached marginal intercalaries between veins along entire outer margin of wing; genital claspers of male with two or three short terminal segments ..... **Leptophlebiidae**
11. Basal part of forewing vein CuP very near to vein CuA; several free intercalaries present between veins $MP_2$ and CuA; subapical segment of forceps at least 5 times longer than apical segment ..... **Ephemerellidae**
- Basal part of forewing vein CuP very near to vein AA; no free intercalaries present between veins $MP_2$ and CuA; apical and subapical segments of forceps equal or subequal in length ..... **Teloganodidae**
12. Forewing with MA forming a more or less symmetrical fork and with $MP_2$ and 1MP extending less than ¾ distance to base of MP; genital claspers of male 2- or 3-segmented; thorax usually black or gray ..... **Tricorythidae**
- Forewing with MA not forming a more or less symmetrical fork, but with $MP_2$ and 1 MP almost as long as MP, and extending nearly to base; genital claspers of male one segmented; thorax usually brown ..... **Caenidae**

## Larvae

1. Mesonotum forming a carapace; legs and abdominal segments 1–6 covered under carapace, not visible in dorsal view ..... **Prosopistomatidae**
- Mesonotum not forming a carapace; legs and abdominal segments 1–10 visible in dorsal view ..... 2
2. Mandibles with tusk-like projection; gills II–VII double and uniform in structure with fringed margin ..... 3
- Mandibles without tusk-like projection; gills II–VII not as above ..... 5
3. Mandibular tusk long and sickle-shaped, bearing many long setae; maxillary palp more than twice as long as the galea-lacinia (the apical part of the maxilla) ..... 4
- Mandibular tusks, otherwise, bearing short bristles; maxillary palp as long as or slightly longer than the galea-lacinia ..... **Potamanthidae**
4. Tusks curved outwards; abdomen yellowish with conspicuous black pattern ..... **Ephemeridae**
- Tusks curved inwards; abdomen whitish without conspicuous black markings ..... **Polymitarcyidae**
5. Gills on abdominal segment II large, plate-like, touching or overlapping along dorsal midline, covering all or some of the gills arising posteriorly; gills III–VI with fringed margins ..... 6
- Gills on abdominal segment II not as above ..... 7
6. Gills on abdominal segment II meet along midline; terminal filament densely clothed with setae on both margins, lateral filaments with setae on inner margins only; mature larva has small hindwing pads beneath the fore wing pads on meta thorax ..... **Neoephemeridae**
- Gills on abdominal segment II overlap along the midline and covering all of the succeeding gills III–VI; lateral and terminal filament bearing rather short and sparse setae on the inner and outer margins, hind wing pads not present ..... **Caenidae**
7. Head flat, plate-like with dorsal eyes; body dorso-ventrally flattened; gills plate-like, dorsal tuft of tracheae at base of lamellae ..... **Heptageniidae**
- Head not plate-like; body not dorso-ventrally flattened; gill form various shapes without dorsal tracheal tuft at base of lamellae ..... 8
8. Labium fused into single semicircular structure, palps with long setae; gills on abdominal segments II–V or II–VII; gill II may overlay, partially conceal rest of series ..... **Tricorythidae**
- Mouthparts and gills not as above ..... 9
9. Gills on abdominal segment II absent and gills borne dorsally ..... **Ephemerellidae**
- Gills on abdominal segment II present and gills borne laterally ..... 10
10. Lamellate gills on abdominal segment I–V or II–IV or II–V or II–VI ..... **Teloganodidae**
- Lamellate gills on abdominal segment I–VII ..... 11
11. Head rectangular; gills similar, long, slender, and bifurcate form or first pair rudimentary (thread-like) and others plate-like and doubled; terminal filament well-developed and similar to cerci ..... **Leptophlebiidae**
- Head round, antennae long and twice the width of the head; median terminal filament often much reduced and always shorter than the cerci ..... 12

12. Maxilla apically broadened with pectinate, comb-shaped bristles; cerci and terminal filament densely beset with long bristles ..... **Ameletidae**
- Maxilla apically not broadened with pectinate, comb-shaped bristles; cerci and terminal filament not densely beset with long bristles ..... **Baetidae**

## MAJOR WORK ON INDIAN FAUNA

The first mayfly from India was described as early as 1843, when *Palingenia indica* (*Ephoron indicus*) was described by Pictet (1843). Subsequently, Walker (1853) described *Caenis perpusilla* and *Cloeon debilis* (*Procloeon debilis*) based on the specimens at the British Museum and on the collections of W. W. Saunders. During this period, Hagen (1858) worked on baetine mayflies of Sri Lanka. Up to 1900, two species of Ephemeridae and Palingenidae and one species of Heptageniidae were described. Needham (1909), Ulmer (1920), Chopra (1924, 1927), Navas (1931), Hafiz (1937), and Traver (1939) described many species. Needham worked on Ephemeroptera in the collection of the Indian Museum and Ulmer described *Ecdyonurus bengalensis* from Darjeeling, West Bengal. Chopra (1924, 1927) worked on Ephemeroptera of Chilka Lake and described four species. He also worked on Palingeniidae and Ploymitarcyidae. Hafiz (1937) and Traver (1939) worked on Ephemeroptera of the subcontinent.

Workers like Kimmins (1947), Gillies (1949, 1951, 1957), Kapur and Kripalani (1963), Dubey (1970, 1971), Kaul and Dubey (1970), Peters (1967, 1975), Peters and Edmunds (1970), McCafferty (1973), Hubbard and Peters (1978), Sivaramakrishnan (1984, 1985a, 1985b), Sivaramakrishnan and Hubbard (1984), Sivaramakrishnan and Peters (1984), Grant and Sivaramakrishnan (1985), Venkataraman and Sivaramakrishnan (1987, 1989), Sivaramakrishnan et al. (1996b), Dinakaran et al. (2009), Subramanian and Sivaramakrishnan (2009), Selvakumar et al. (2012, 2013, 2014a, 2015a, 2015b, 2016b, 2017b, 2017c, 2017d, 2017e), Sivaruban et al. (2013), Kluge et al. (2013), Kluge (2014), Kluge and Novikova (2014), Kluge et al. (2015), Anbalagan et al. (2014), Kubendran et al. (2014, 2015), Balachandran et al. (2016), and Ramya-Roopa et al. (2017), contributed substantially to the knowledge of Ephemeroptera of India. Significant discoveries of new genera were made during this period: *Petersula* Sivaramakrishnan 1984, *Edmundsula* Sivaramakrishnan 1985, *Indoganodes* Selvakumar, Sivaramakrishnan & Jacobus, 2014 and *Klugephlebia* Selvakumar, Subramanian & Sivaramakrishnan, 2016 from southern Western Ghats which are Gondwanian relicts.

## BIODIVERSITY AND SPECIES RICHNESS

Ephemeroptera constitutes a small order of extant insects, with approximately 40 families, 440 genera, and 3330 species globally, and of these, 561 species in 84 genera and 20 families occur in the Oriental region (Sartori and Brittain 2015). The fauna of the Indian subregion (India, Sri Lanka, Pakistan, Nepal, Bhutan, and Bangladesh) is represented by 4 suborders, 15 families, 60 genera, and 204 species (Sivaramakrishnan et al. 2009). In India, we have 4 suborders, 15 families, 60 genera, and 152 species, and of these, 7 genera and 123 species are endemic (Table 2.1). The present diversity includes two

**TABLE 2.1**
**Diversity and Endemism of Ephemeroptera**

| | | Diversity | | Endemism | |
|---|---|---|---|---|---|
| **Suborder** | **Family** | **No. of Genera** | **No. of Species** | **No. of Genera** | **No. of Species** |
| **Carapacea** | | | | | |
| | Prosopistomatidae | 1 | 3 | 0 | 3 |
| **Furcatergalia** | | | | | |
| | Leptophlebiidae | 12 | 26 | 6 | 22 |
| | Ephemeridae | 4 | 16 | 0 | 15 |
| | Polymitarcyidae | 4 | 5 | 0 | 3 |
| | Potamanthidae | 2 | 2 | 0 | 2 |
| | Caenidae | 2 | 7 | 0 | 7 |
| | Neoephemeridae | 1 | 2 | 0 | 1 |
| | Ephemerellidae | 3 | 5 | 0 | 0 |
| | Teloganodidae | 5 | 8 | 1 | 8 |
| | Tricorythidae | 1 | 1 | 0 | 1 |
| | Vietnamellidae | 1 | 1 | 0 | 0 |
| **Setisura** | | | | | |
| | Heptageniidae | 10 | 26 | 0 | 22 |
| | Isonychiidae | 1 | 1 | 0 | 1 |
| **Pisciforma** | | | | | |
| | Ameletidae | 1 | 2 | 0 | 2 |
| | Baetidae | 12 | 47 | 0 | 36 |
| **Total** | **15** | **60** | **152** | **7** | **123** |

families viz., Vietnamellidae and Isonychiidae which were recently reported from India by Selvakumar et al. (2018) and Vasanth et al. (2019). Species rich families are Leptophlebiidae (12 genera, 26 species), Heptageniidae (10 genera, 26 species), Ephemeriidae (4 genera, 16 species), and Baetidae (12 genera, 47 species). Four families viz., Leptophlebiidae, Ephemeriidae, Heptageniidae, and Baetidae are represented by more than 10 species. Species rich genera with more than ten species each are *Ephemera* (Ephemeriidae), *Baetis,* and *Cloeon* (Baetidae).

## DISTRIBUTION PATTERNS IN THE INDIAN CONTEXT

Mayflies are distributed in diverse inland freshwater habitats. Rich diversity is found in pristine hill streams. The following regions are reasonably well explored in India with regard to species diversity and distribution of Ephemeroptera viz., Western Ghats (76), Central Himalayas (29), and Gangetic plain (21). Going by the number of species in the Deccan peninsula (18), North East (10), Trans Himalaya (9), and Andaman and Nicobar Islands (3), they appear to be less explored. The remaining biogeographical regions (Coast, Desert, Semi-Arid, and Eastern Himalaya) have not been explored, and intensive survey and documentation of mayfly species diversity is needed in these regions.

## IMMATURE TAXONOMY

Till the first half of the twentieth century, Ephemeroptera systematics mainly relied on imaginal characters. However, the crucial importance of ecology and phylogeny of larval stages of mayflies on freshwater ecosystem dynamics led to detailed taxonomic explorations of larval stages and associated adults in addition to the in-depth study of cryptic species complexes. Recently, considerable progress has been made in averting Wallacean shortfall through in-depth study of larval taxonomy in different families of Ephemeroptera in our country (Selvakumar et al. 2012, 2013, 2014a, 2015a, 2015b, 2016b, 2017b, 2017c, 2017d).

A recent publication by Ramya-Roopa et al. (2017) describing a new species and redescribing an already described species of *Prosopistoma* (Prosopistomatidae) from India has highlighted the importance of immature taxonomy in averting Wallacean shortfall besides contributing better understanding of the systematics and phylogeny of this genus especially in the context of the possession of several apomorphic features in the larval stage in contrast to the attenuated morphology of alate stages. This study has global significance in endorsing the hypothesis of Barber-James (2009) in explaining how the two clades of *Prosopistoma* viz., 'variegatum' clade and the 'African' clade were introduced into the Oriental region through drifting India and its collision with Asia some 34 million years back in geological history.

## MOLECULAR CHARACTERIZATION AND PHYLOGENY

The first molecular phylogeny for the order Ephemeroptera was constructed by Ogden and Whiting (2005). Their analyses included 31 of the 37 families, representing more or less 24% of the genera. O'Donnell and Jockusch (2008) investigated the phylogenetic relationships of leptophlebiid mayflies as inferred by histone H3 and 28S ribosomal DNA from six continents. Gattolliat et al. (2008) reconstructed the first comprehensive molecular phylogeny of the Afrotropical Baetidae. The molecular reconstruction indicated the Afrotropical Baetidae require a global revision at a generic as well as suprageneric level. The investigation of Ogden et al. (2009b) represented the combined molecular and morphological analysis for the mayfly family Ephemerellidae, with a focus on the relationships of genera and species groups of the subfamily Ephemerellinae. Gattolliat and Monaghan (2010) have studied DNA-based association of adults and larvae in Baetidae. They used a general mixed Yule-coalescent (GMYC) model to combine population- and species-level sequence variation of mitochondrial deoxyribonucleic acid (mtDNA) to detect species boundaries in Baetidae.

DNA barcoding shows great potential for use by those studying the systematics including cryptic species of many Ephemeroptera species groups (Stahls and Savolainen 2008). A comprehensive DNA barcode library has been established for mayflies from Canada, Mexico, and the United States (Ball et al. 2005; Zhou et al. 2009, 2010; Webb et al. 2012; Gattolliat et al. 2015). Their study has demonstrated that DNA barcoding holds great promise as a tool for a rapid biodiversity assessment of unknown fauna. DNA barcodes of stream mayflies will improve descriptions of community structure and water quality for both ecological and bioassessment purposes (Sweeney et al. 2011). DNA barcodes have also had implications in studying the systematics, diversity, association of adults and larvae, ecology, biogeography, and conservation of aquatic insects (Sivaramakrishnan et al. 2014; Gattolliat et al. 2015). Williams et al. (2006) assessed the molecular diversity of this complex in one of the largest such studies of cryptic species in the order Ephemeroptera.

Molecular techniques have still not been used extensively in mayfly research in India. However, Sivaramakrishnan et al. (2011) reviewed the emerging trends in molecular systematics and molecular phylogeny of mayflies (Ephemeroptera) at the global level, and Selvakumar et al. (2016a) generated DNA barcodes for 40 species belonging to 32 genera under 10 families of Ephemeroptera from South India. Selvakumar et al. (2016a) calculated nucleotide sequence divergence using the Kimura two-parameter distance model and a neighbour-joining analysis was performed to provide a graphic display of the patterns of divergence among the species. Genetic diversity of south Indian endemic mayfly species *Petersula courtallensis* was investigated with wide geographic ranges using mitochondrial cytochrome oxidase gene sequences by Selvakumar et al. (2017a). Their results indicated a general pattern of high genetic diversity between the western and eastern streams and the presence of two genetically distinct populations.

## INTEGRATIVE TAXONOMY

The primitive archaic order of aquatic insects viz., Ephemeroptera has received considerable attention globally in terms of referring species delimitation by incorporating

'integrative taxonomy' that integrates all available data sources and using species tree approaches (Yeates et al. 2011). However, application of integrative taxonomic approach to help in resolving taxonomic riddles vis-a-vis single method has not yet been initiated in studying mayflies of India. Recent integrated taxonomic revision of *Camplocia* belonging to the family Euthyplocidae by GonÇalves et al. (2017) has highlighted the advantages of this approach by including a morphological analysis of type and non-type material of species of *Camplocia* including their junior synonyms, ultrastructural analyses of the egg chorion, and neighbourhood joining based on Kimura 2 Parameter distances and Bayesian inference of 376 bp of the mitochondrial gene cytochrome oxidase (COI) of recently collected specimens to resolve problems in synonymy, fine tuning of species delimitations, precise descriptions of new species, from Amazon forest and Costa Rica, and exploring the possibility of existence of cryptic species.

## TAXONOMIC PROBLEMS

Since most species described earlier were based on the imaginal or the larval stage alone, association of larvae with respective imagos by individual rearing is rather indispensable to arrive at precise taxonomic conclusions. Moreover, many regions of India especially the rivers, streams, and other wetlands of eastern and western Himalaya, central India, and Eastern Ghats are under explored. DNA barcodes were generated for 40 species belonging to 32 genera under 10 families of Ephemeroptera from South India by Selvakumar et al. (2016a), but no other aspects of molecular work were undertaken on mayflies in India so far. Future research should focus on correlating adult and larval stages and exploring under and unexplored regions as well using new tools like generation of DNA barcodes for mayflies (Selvakumar 2018).

## BIOLOGY

**Habitat:** Mayflies inhabit all aquatic habitats except for marine environment, polluted, and underground waters. Some species are found in brackish waters also. Lotic-erosional habitats are more species rich than lotic-depositional and lentic-depositional habitats. In the higher altitudes (>3000 m), species diversity is poor. Species of lentic habitats are found in ponds, lakes, water tanks, paddy fields, etc. In lotic habitats, runs and riffles with bottom substrates such as boulders and cobbles have higher diversity than cascades or waterfalls. Species diversity is also reduced in habitats with bottom substrates such as sand or mud.

### Life Cycle

**Emergence:** In the last larval instar (nymph) food uptake stops, alimentary canal and malpighian tubules degenerate, the former fills up with water first and later with air to develop into an aerostatic organ. Spermatogenesis and oogenesis is already completed before moulting. Haemolymph, mouthparts, visceral muscles, and gonads undergo considerable changes. During this period, oxygen uptake and drift activity increases. Subimago leave the nymphal skin by rupturing the mesonotal cuticle along the midline, which is completed in 10–15 minutes. The subimago, depending upon the species, emerge either from the water surface, above water, or underwater. In some species, more than one type of emergence is observed. Temperature and light intensity influence the metamorphosis. In tropical regions, most of the species emerge within 2 hours after sunset.

**Swarming:** Conspicuous mating swarms of males are typical of mayflies. The mating swarm typically consists of several specimens to thousands of individuals. They swarm over land marks such as vegetation, rock, bush, tree, shore line, bridge, road, etc. The size, timing, height, and time of swarm depends on many factors such as weather, temperature, etc. Typical tropical species swarm during night. However, in the high altitudes of Western Ghats and Himalaya, swarming is also observed in the afternoon.

**Mating:** Mating usually takes place in flight which lasts from a few seconds to several minutes. Males grab the females from below using their forelegs curved around the wing roots. The male abdomen is turned up and the forceps grasps the apex of the female abdomen and the penis is inserted into oviduct opening or copulatory pouches.

**Oviposition:** Eggs are always deposited in water. However, sometimes females are attracted to oviposit in man-made objects such as car roof tops or smooth roads. Depending on species, several types of oviposition are observed: (i) females release a few eggs at a time by dipping the tip of abdomen on the water surface; (ii) releasing all eggs at one time on the water surface; (iii) females fall on the water surface and release the eggs by rupturing the abdominal wall; (iv) females approach the waterline from shore and release eggs; or (v) females crawl beneath the water surface to deposit eggs on stones or logs (Bauernfeind and Soldán 2012). Females typically lay 500–3000 eggs which is influenced by environmental degradation like eutrophication, xenochemicals, and acidification and other environmental variables (Sweeney 1978, 1984).

**Larval stage:** Species are morphologically adapted to current velocity which include hydrodynamic body shape (e.g., *Prosopistoma*), stabilizing and retention structures (e.g., *Epeorus*), friction discs, sclerotized gill margins with microtrichia, or suckers formed by gills. The mayfly larvae require high oxygen content in the water which is generally 3–4 times higher than in other aquatic insect groups such as Diptera. Apart from gills, cutaneous breathing is also important for

mayfly larvae. The larvae are considered 'trophically generalized' or 'selectively omnivorous'. The feeding types are classified as: (i) grazers-scrappers feed on attached algae and mouth parts (maxillae) are scrape-like; (ii) shredders feed on coarse particulate organic matter (CPOM) and mouth parts are not particularly specialized; (iii) gatherers-collectors feed on fine particulate organic matter (FPOM) without specialized mouth parts; (iv) filter feeders use FPOM and seston (plankton, nekton, and detritus); and (v) predators feed on small benthic animals such as nematodes, oligochaetes, etc. Feeding is opportunistic and depends upon availability, substrate composition, and seasonality.

**Adult stage:** Adult mayflies do not feed, and reproduction and dispersal are the sole functions of adults. Adults do not move away from water, but some species are found far away from their emergence site. Females of most species exhibit 'upstream compensatory flight' to minimize downstream drift of eggs and larvae. This flight may vary from several metres to kilometres.

**Longevity:** The lifespan of typical adult mayflies usually lasts for 24 hours. However, depending on species, it varies from few hours to days.

## Ecology

**Diversity profiles/trophic categorization:** Pioneering attempts were made by Sivaramakrishnan and Job (1981) to study the mayfly populations of Courtallam streams. Sivaramakrishnan and Venkataraman (1990) have found that historical immigration, assured perennial flow of a stream, and its pollution-free nature appear to be factors mainly influencing the distribution of a few biogeographically significant genera of Leptophlebiidae in Palani hills, South India. Burton and Sivaramakrishnan (1993) conducted detailed investigations on the insect communities including mayflies and their trophic ecology in the streams of the Silent Valley National Park in Kerala part of the Western Ghats. Composition and zonation of mayfly nymphs were investigated along with other aquatic insects in the entire river basins of Kaveri and Gadananathi by Sivaramakrishnan et al. (1995) and Anbalagan and Dinakaran (2006), respectively.

Anbalagan et al. (2004) studied the diversity profiles and trophic categorization of aquatic insects including mayflies of Courtallam hills of the Western Ghats. There is paucity of information on the diversity of Eastern Ghats mayflies. Notable exceptions include studies on Karandamalai, Sirumalai, and Alagarmalai segments of the Eastern Ghats by Jahir-Hussain et al. (2006), Dinakaran and Anbalagan (2006), and Dinakaran and Krishnan-Kutty (1997), respectively. Kubendran et al. (2017b) have studied diversity and distribution of Baetidae larvae of streams and rivers of the southern Western Ghats. Kubendran et al. (2018) have investigated composition and trophic categorization of aquatic insects including mayflies in the three hill streams and rivers of the Western Ghats.

**Emergence patterns/seasonal abundance:** Sivaramakrishnan and Venkataraman (1990) have observed noon swarming of leptophlebiid and baetid mayflies at a few sites at higher altitudes (above 2000) msl in Palani hills, South India. Seasonal abundance and diet of *Cloeon* sp. were studied in a northeast Indian lake by Gupta et al. (1994). Selvakumar et al. (2016b) have observed noon emergence of *Klugephlebia kodai* in a stream near Pillar Rock of Palani hills, Tamil Nadu.

**Life cycle/voltinism:** Behavioural strategies of emergence, swarming, mating, and oviposition of some mayflies were investigated by Sivaramakrishnan and Venkataraman (1985). They also made observations on feeding propensities, growth rates, and fecundity in two baetine mayflies (Sivaramakrishnan and Venkataraman 1987). Fecundity of mayflies of the Western Ghats was studied by Sridhar and Venkataraman (1989). Sivaramakrishnan et al. (1990) studied life cycle patterns of mayflies of Cardamom hills of the Western Ghats. They found that five species viz., *Baetis frequentus*, *Caenis* sp., *Choroterpes* (*Euthraulus) alagarensis, Notophlebia jobi,* and *Afronurus kumbakkaraiensis* exhibited basically multivoltine pattern with overlapping generations and continuous emergence, whereas one species (*Epeorus* sp.) exhibited more than one univoltine brood. Bioecological studies on the burrowing mayfly, *Ephemera nadinae* (Ephemeridae) in Kurangani streams of the Western Ghats were done by Balasubramanian et al. (1992). Gupta (1993) investigated life histories of two species of *Baetis* in a small Northeast Indian stream. Life cycle and growth of *Cloeon* sp. were studied from Meghalaya by Gupta et al. (1993). Sivaruban et al. (2010) have investigated the life cycle of Heptageniidae in the Kumbbakarai stream of the Western Ghats, Tamil Nadu.

**Biomonitoring tool:** Utility of mayflies of peninsular Indian streams and rivers on biomonitoring water quality has been highlighted based on rapid bioassessment studies on the Kaveri river basin using macroinvertebrate assemblages by Sivaramakrishnan et al. (1996a). Sivaramakrishnan (2000) has generated a refined rapid bioassessment protocol for benthic macroinvertebrates for use in peninsular Indian streams and rivers in which the mayflies form an essential component of the macroinvertebrate assemblage on which the biotic indices are based. Kubendran et al. (2017) investigated Baetidae as biological indicators of environmental degradation in Tamiraparani and Vaigai River basins of southern Western Ghats.

**Anthropogenic/global warming and climate change/ land use impacts:** Impact of riparian land use on stream insects of Kudremukh National Park, Karnataka was investigated by Subramanian et al. (2005). Anthropogenic impacts on aquatic insects including mayflies in six streams of southern Western Ghats were investigated by Dinakaran and Anbalagan (2007). Impact of global warming and climate change on aquatic insects especially mayflies has been reviewed by Sivaramakrishnan et al. (2008). Selvakumar et al. (2014b) studied the impact of riparian land use patterns on Ephemeroptera community structure in river basins of southern Western Ghats.

## ECONOMIC IMPORTANCE

Mayflies are occupying freshwater and brackish water habitats across the world, with the exception of Antarctica. They constitute an important part of the food chain, mainly consuming primary producers such as algae and plants, and as a food source for vertebrate predators like fish. They are excellent biological indicators of water quality and habitat quality (Sivaramakrishnan et al. 1996a; Buffagni 1997; Selvakumar et al. 2014b). They are ideal objects for integrated phylogenetic, biogeographic, and phylogeographic studies, being endowed with several archaic traits in all life stages along with rather weak dispersal powers. Many of the montane mayflies, both nymphs and imagos are equally charismatic. Nymphs are important for freshwater ecological and biomonitoring studies.

## CONSERVATION STATUS

Mayflies along with stoneflies and caddisflies have a significant role in the wetland food chain. Their species assemblages change primarily with levels of human disturbance in freshwaters, both lentic and lotic. Anthropogenic impacts result in habitat fragmentation, global warming, climate change, alien species invasion, as well as major land use changes, especially changes in the riparian zone. Mayfly larvae are microhabitat specialists and inhabit springs, habitats like sandy stretches of streams and rivers, impact-free erosional and depositional zones of pristine, montane headwater streams, as well reasonably clean lentic bodies. Conservation of habitats and microhabitats like leaf packs of leaf litter inhabiting species as well as the fragile microhabitats of phylogenetic relicts and macro and microendemics and pollution intolerant species is highly critical for protecting characteristic Ephemeroptera community assemblages in river catchments is of national importance. Significant Indian publications dealing with habitat diversity and land use impacts include Subramanian and Sivaramakrishnan (2005) on aquatic insects of the river basins of the Western Ghats and Selvakumar et al. (2014b) on Ephemeroptera communities in river basins of the southern Western Ghats. Recently, Sundar and Muralidharan (2017) have briefly reviewed the impact of climatic change on aquatic insects and habitats with particular reference to India. However, specific conservation measures to prioritize habitat and faunal conservation of mayflies within the overall framework of conservation of freshwater biota are yet to gain momentum in India. In this context, Massariol et al. (2014) recommend creation of conservation units of Ephemeroptera using biological information rather than economic, cultural, or political criteria.

## COLLECTION AND PRESERVATION

**Collection:** Mayfly larvae can be collected by a large range of devices viz., kick net, hand screen, dip nets, drift net, etc. Adult mayflies are generally caught using a hand net with a long handle and large opening to catch swarming adults. Beating the vegetation with a stick can also be used to collect resting imagos and subimagos in a hand net. Tent traps, such as the Malaise traps or emergence traps can also be used, but they need to be checked regularly to remove subimagos, preventing them from drowning and enabling rearing to the adult stage. Light traps at dusk and dawn, especially in the tropics, give significant results (Sartori and Brittain 2015).

**Rearing:** Rearing is an important procedure because it allows the association between larval and adult characteristics. Several techniques exist, but the most useful is to select a single mature larva and put it in a rearing cage, either in situ or in a suitably equipped laboratory. Cages should be checked regularly for the emergence of the subimago. Once emerged, the larval skin must be placed in a vial with ethanol, and the subimago placed in another cage without direct sunlight and a relative humidity of more than 50%. Once the imago has moulted, it is necessary to wait for a couple of hours for the teguments to dry and the final colouration to be fixed. The specimen can then be placed in ethanol with its larval and subimaginal exuviae for further study (Sartori and Brittain 2015). Currently, molecular studies particularly DNA barcode are more and more frequently used to associate adult and larval stages (Monaghan and Sartori 2009).

**Specimen preparation:** Their soft cuticle and long appendices make mayflies fragile insects necessitating larvae and adults to be preserved in ethanol. The ethanol concentration should be approximately 80% for long-term preservation, but 100% if molecular studies are planned. If larvae are fixed in 80% ethanol in the field, the medium should be changed when arriving in the laboratory because of the high water and lipid concentration in the body. Preferably, specimens should be kept at low temperatures (<6°C) and definitely never in a warm place, which will rapidly fade the colours. Some small specimens (e.g., *Baetis*) can also be mounted entirely on a slide according to an appropriate protocol for slide preparation. For morphological examination and species identification, slide preparation of larval mouthparts and appendices as well as male genitalia and wings is often necessary (Sartori and Brittain 2015).

**Preparation of slides:** Mayfly parts must frequently be studied from slides. Most of the structures can be easily mounted on slides as outlined below. Some parts such as larval gills are usually best studied in alcohol, but for most of the structures, a better understanding can be achieved by studying both a slide specimen and an alcohol specimen. The wings of adult specimens can be mounted by floating them from clean alcohol onto the slide, arranging them properly in a thin film of alcohol, and covering them with a square cover slip. Narrow strips of white gummed paper are much better than any self-adhesive paper or tape for holding the cover slip tight on the slide. After the wings set in position on the slide, the alcohol is allowed to evaporate. Crumpled wings from dry specimens can be flattened by dropping them gently in boiling water and then quickly floating them onto a slide. Wings are best studied as dry mounts, wings mounted in Canada balsam generally show fewer details.

Male genitalia from dried specimens may need to be softened before mounting. A satisfactory mount results when they are placed for 1 or 2 hours in a solution of 10% potassium hydroxide or sodium hydroxide and then dehydrated and mounted in Canada balsam or Hoyer's medium. For male genitalia or other parts of adults or larvae preserved in alcohol, avoid hydroxide except for very large or dark specimens that otherwise would not clear. Structures can be mounted directly from 95% alcohol or cellosolve (ethylene glycol monoethyl ether) into specially prepared Canada balsam. Commercial neutral Canada balsam in xylene is allowed to dry until it is highly viscous. It is then returned to suitable consistency by replacing the evaporated xylene with cellosolve. Structures placed in this mixture may cloud temporarily, but seldom for more than an hour. The clouding can be reduced by passing the structures through pure cellosolve before mounting.

The cover slip for balsam mounts should be no larger than necessary. For small structures such as male genitalia and claws, use 8 mm round cover slips and larger structures use 12–18 mm round cover slips. An effective method for positioning mounts is to put the structures in a thin film of balsam on the cover slip or the slide. The parts can be repositioned periodically until the balsam has become quite firm. The cover slip can then be transferred to the slide with additional balsam. The structures must be completely covered with balsam and allowed to dry in a dust-free place or in a petri dish. The slides should also be fully labelled with the locality, the date, and the name of the collector or referenced to a specific specimen. When drawings are made for publication, the slide or the specimen used should be labelled (Edmunds et al. 1976).

## USEFUL WEBSITES

**Ephemeroptera of the World** http://www.insecta.bio.spbu.ru/z/Eph-spp/Contents.htm from Russia

**Ephemeroptera Galactica** http://www.ephemeroptera-galactica.com/ from Florida A & M University, currently operating from Germany

**Mayfly Central** http://www.entm.purdue.edu/mayfly/ from Purdue University, U.S.A.

## CONCLUSION

Mayfly fauna of India, a country endowed with two mega diversity hotspots, appears to be an assemblage of ancient Gondwanan derivatives, with a high percentage of endemism, a few Laurasian spillovers, along with some younger faunal elements that might have diversified in several spells at different periods in geological history by vicariant and dispersal events, through 'out of India and towards India' exchanges between Indian subcontinent on the one hand and Afrotropics including Madagascar, Oriental Southeast Asia, and Palearctic North on the other. Due to poor dispersal ability of adults, most of the mayfly species have restricted distribution. To advance our knowledge of Indian Ephemeroptera, the foremost need is a synthesis of the taxonomy of adults and larvae within a global systematic context for each family, precise delimitation of species, an understanding of intraspecific genetic diversity, as well as detection of cryptic species complexes.

## ENDNOTE

After preparation of final manuscript two new families of mayflies*viz*., Vitenamellidae and Isonychidae were reported from India (Selvakumar et al. 2018 & Vasanth et al. 2019) increasing the total number of families reported from Indian region to 17.

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