# 12. Ephemeroptera of Sri Lanka: an introduction to their ecology and biogeography

M. D. Hubbard & W. L. Peters

#### Introduction

The Ephemeroptera fauna of Sri Lanka is not well known. Treatment of the mayflies of Sri Lanka has been sparse and sporadic since Walker with Caenis perpusilla and Baetis taprobanes in 1853 was the first to describe any mayflies from the island. Hagen (1858) then described 8 new Sri Lankan species, upon which he elaborated in additional works in 1859 and 1873. Eaton (1871, 1883-1888) included some Sri Lankan species in his work, although they comprised only a minor portion in his cosmopolitan taxonomic treatments. A few other authors (e.g. Banks, Chopra, Kimmins, Navás, Lestage, Ulmer; see Hubbard & Peters 1978, for references) dealt briefly or indirectly with mayflies of Sri Lanka.

It was not until the 1960's and 1970's that there emerged even a basic picture of the mayfly fauna of Sri Lanka. Peters (1967) and Peters & Edmunds (1970) published on the taxonomy of the Leptophlebiidae and Prosopistomatidae of Sri Lanka. Fernando (1965) compiled a list of all reported Sri Lankan mayflies; this was followed by inclusion of Sri Lanka in the more comprehensive catalog of the Ephemeroptera of the Indian Subregion by Hubbard & Peters (1978), which gives the most complete account to date of the extent of the Sri Lanka mayfly fauna. Both of these last publications suffered from dependence on inadequate studies of the Sri Lankan fauna.

The taxonomic understanding of the Sri Lankan mayflies still is sketchy, as most of the published papers were based on only a few specimens encountered in collections or supplied by general collectors. The ecological and biogeographical understanding of the Sri Lankan mayflies obviously lags far behind the taxonomic knowledge.

However, several major efforts concentrating on the aquatic fauna, beginning with the Lund University Expedition in 1962 and the Austrian-Ceylonese Hydrobiological Mission of the University of Vienna and the Vidyalankara University in 1970, and continuing with several investigators (including the senior author) associated with the Smithsonian Institution's 'Biosystematic Studies of the Insects of Ceylon' project, have now yielded a large number of specimens which allows us

to start toward an understanding of the Ephemeroptera fauna of Sri Lanka.

We are still in the process of studying these specimens and it will be some time before the work is completed. It must therefore be borne in mind that many of the data reported here are preliminary in nature and will change somewhat as our research progresses and the results are published. Several of these papers should be forthcoming shortly, but others will not appear for some time. It is quite clear to us that there is a need for much more collecting and rearing of mayflies in Sri Lanka if we are to understand fully the taxonomic situation there. Ecological research on Sri Lankan Ephemeroptera has been almost non-existent, and much could be learned from such urgently needed research in the future.

# **Ecology**

The island of Sri Lanka is roughly ovate, with an area of approximately 65,600 square kilometres. The south central portion is occupied by the hill country (Fig. 1-4), reaching from about 300 m to an altitude of 2,524 m. Surrounding the hill country below about 300 m altitude, and especially extensive to the north, are the lowlands (Fig. 5-8). The lowland area to the east and north of the mountains of the hill country, known as the dry zone, receives much less rainfall than the hill country



Fig. 1. Hill country stream south of Kandy at 750 m altitude.

and the southern and western lowlands, which together are known as the 'wet zone'.

The principal river systems radiate out from the hill country like the spokes of a wheel. The streams usually are quite rapid in their upper reaches, due to the steepness of the drop in elevation as they leave the hill country. Upon reaching the low country, the rivers slow and broaden.

Water temperatures in the hill country streams range from about  $14\,^{\circ}\mathrm{C}$  to over  $25\,^{\circ}\mathrm{C}$ . Fig. 8 illustrates representative water temperatures in relation to altitude (taken from September through April). Temperatures at lower elevations can vary greatly depending on the steepness of the drop from the higher elevations; those streams with a rapid descent are cooler than those with a slower rate of descent. Water temperatures near the river mouths can reach almost  $30\,^{\circ}\mathrm{C}$ .

The hill country contains myriads of streams and rivers. These streams usually have a substrate of rock, or stones and gravel. The species richness of Ephemeroptera is much greater in this region than in the lowlands. Except for *Chromarcys*, *Povilla*, and to some extent *Ephoron*, the Sri Lankan mayflies are found throughout the streams of the hill country (Fig. 9), with no obvious vertical zonation. Much of the hill country aquatic fauna also extends deep into the lowlands in the streams at the bottom of their steep drop from the hill country highlands, especially in the southern and western wet zone lowlands. The hill country can be considered to be much more extensive for the mayfly fauna than for terrestrial organisms.



Fig. 2. Belihul Oya at about 650 m altitude after its steep fall from the Horton Plains.

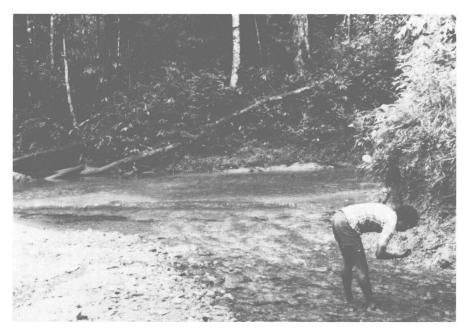


Fig. 3. Stream in the Sinharaja rain forest.



Fig. 4. Waterfall in a hill country stream at about 600 m altitude.



Fig. 5. Tributary of the Kelani Ganga, a typical Prosopistoma habitat.

The northern and eastern dry zones have been little collected for mayflies, although the few localities which have been collected point to a reduced fauna in most areas in comparison with the upland wet zone fauna. *Povilla* and *Chromarcys* are typical low country genera. *Choroterpes* is known from marshes and streams in the northern dry zone, as are the Caenidae.

There are almost no natural lakes in Sri Lanka, but there are a tremendous number of tanks and reservoirs, both large and small. Most of these standing waters have only a moderate mayfly fauna, mainly Baetidae and Caenidae. The mainfly fauna of paddy fields appears somewhat limited, probably because of the fluctuating water regime, although Fernando (1980) found Ephemeroptera to be not uncommon in paddy field samples.

Many of Sri Lanka's aquatic habitats remain in a semi-natural state; others show vivid evidence of the influence of man. These differences often are reflected in the mayfly fauna. It was readily apparent, for instance, after collecting a number of localities in the hill country, that those streams which periodically carried a silt load from rainfall runoff were distinguished by a dearth of mayflies. This was especially common in many of the streams which ran through tea plantations. There is no ground cover among the tea bushes and the red soil readily runs off into nearby streams after heavy rains. Similar streams close by which did not receive the silty runoff had a healthy mayfly fauna. This same phenomenon also was evident in



Fig. 6. A slow-moving lowland river.

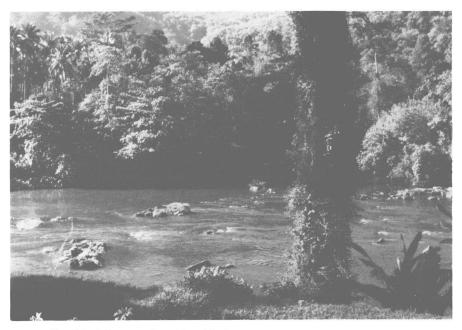


Fig. 7. The Kelani Ganga at about 60 m altitude.

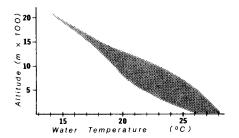


Fig. 8. Representative water temperatures in Sri Lankan streams (data from Costa & Stamühlner 1972 and Hubbard unpublished).

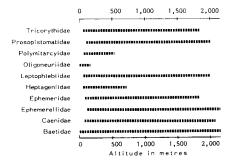


Fig. 9. Altitudinal distribution of the families of Ephemeroptera in Sri Lanka.

streams at lower elevations. In several localities, where buffalo were watered in the stream, periodic heavy silt loads reduced the mayfly population greatly compared to nearby areas.

Edmunds & Edmunds (1980) indicate that the most common pattern for tropical mayflies is emergence just after dark and transformation to imagos before dawn. Swarming then takes place from before dawn through the early morning hours. Light trapping and observations by the senior author in Sri Lanka indicate that most of the mayfly subimagos emerge in the first hours of darkness. The only emergence of subimagos observed in the field took place at or shortly after dusk. Subimagos placed in rearing cages generally had transformed to imagos by the next morning. Early morning light trapping was generally quite unproductive; most of the mayflies have stopped coming to the light by about three hours after sunset, regardless of the altitude. Swarming (other than at light traps) was never observed in two months in the field. This may be because of remote swarming (either in height or distance) or because swarming took place only in darkness. Little is known of emergence patterns of the mayflies of the low country, although

light trapping suggests that the mayflies of the wet lowlands follow the same pattern as those of the hill country.

There is no obvious pattern of seasonal development yet evident in the mayflies of Sri Lanka. Although most of the specimens we have examined were collected from November through April, this time period coincides with the major aquatic collecting effort in Sri Lanka. Examination of specimens collected at various times throughout the year reveal no obvious pattern of development of mayfly nymphs. We also were unable to discern any altitudinal, seasonal or temporal differences in development, although the sporadic collecting that has been done seems unlikely to reveal such patterns as lunar periodicity if they are present. It appears from what data we do have that the Ephemeroptera in Sri Lanka emerge, as a general rule, throughout the year in an aseasonal pattern.

# Biogeography

As is apparent in this chapter, few taxonomic studies have been completed on any group of the Ephemeroptera from Sri Lanka or the Indian Peninsula. Detailed phylogenetic studies of Ephemeroptera occurring in this area of the world have been completed only for the Leptophlebiidae and these studies are only at the generic level (Peters & Edmunds 1970). Therefore, it is impossible at this time to discuss the biogeographical elements within Sri Lanka and the probable more recent relationships of these elements to the fauna of the Indian Peninsula. However, we can discuss in some detail the origins of the mayfly fauna of Sri Lanka at the generic level.

The fauna of any area, especially such a small area as Sri Lanka, can only be examined in the context of being part of a larger geographic distribution. The presence or absence of a genus or species in Sri Lanka, or how a species arrived there, depends on its place in a much larger pattern. One must examine the phylogeny of a group to determine the history of its dispersal. Consequently the biogeography of the mayflies of Sri Lanka can be no better than their phylogeny.

Mani (1974) discussed in detail the biogeography of the Indian Peninsula. He concluded that the biogeographical elements of the present day fauna of the Peninsula could be divided into two groups. One group is composed of the derivatives of older faunas which differentiated in a southern landmass (Gondwanaland) and the other group is composed of the derivatives of a relatively younger fauna, which differentiated mainly in Asia and comprises essentially the Tertiary mountain faunas. The mayfly fauna of Sri Lanka and the Indian Peninsula indicates similar biogeographical patterns.

Few references exist on the biogeography of mayfly genera occurring in Sri Lanka. The phylogeny and biogeography of various genera of the Leptophlebiidae are discussed by Peters & Edmunds (1970), Sivaramakrishnan & Peters (in press a, in press b) and Sivaramakrishnan (in press). Edmunds (1979) discussed the bio-

geographical relationships of the Oriental and Ethiopian mayflies. He concluded that faunal interchange between the two areas occurred by the northern movement of the Indian Peninsula at an early time, and by dispersal through the Middle East. Additional comments on biogeographical relationships of various families and genera are given by Edmunds (1972, 1975).

The following comments summarize our knowledge of the biogeography of the Sri Lankan mayflies.

# A. Leptophlebiidae

- 1. Kimminsula-Kimminsula and several related, but undescribed, genera from Sri Lanka and southern India are true Gondwanian derivatives (Peters & Edmunds 1970). Phylogenetic studies indicate a common ancestor between the Kimminsula group and undescribed genera in Madagascar. The ancestor of these modern genera must have been present during the time that Madagascar and the Indian Peninsula were connected. At present, these genera are the only confirmed Gondwanian derivatives in Sri Lanka.
- 2. Choroterpes-Choroterpes appears to be northern in origin and Choroterpes s.s. gave rise to C. (Euthraulus) which is now widespread throughout the Oriental and Ethiopian Regions. Sri Lankan species of C. (Euthraulus) probably are closely related to those of the Indian Peninsula.
- 3. Megaglena-Megaglena is a member of the Thraulus lineage and presently is endemic to Sri Lanka.
- 4. Isca-Isca is a highly specialized member of the Atalophlebiinae and is known throughout the mainland of the Oriental Region and probably evolved within the region. The subgenus I. (Tanycola) is presently endemic to Sri Lanka.

#### B. Raetidae

- 1. Baetis-The Baetidae probably had their principal evolutionary development in Gondwanaland with South America as the prime centre of evolution, and Africa as a secondary evolutionary centre (Edmunds 1979). The exact dispersals of the baetid groupings between the Ethiopian and Oriental Regions are not known. The species of Baetis in Sri Lanka probably are closely related to other species in the Indian Peninsula.
- 2 Cloeon -The Sri Lankan species probably are related to other species in the Indian Peninsula.
- 3. Indobaetis -At present Indobaetis is endemic to Sri Lanka and appears to be most closely related to the Baetis muticus group in Europe (Müller-Liebenau & Morihara 1982). This is the first recorded influence of the Palearctic Region on the mayfly fauna in the Indian Peninsula and Sri Lanka.
- 4. Indocloeon -This genus is endemic to Sri Lanka and is thought to be most closely related to Procloeon and Centroptilum

- 5. *Procloeon*-The Sri Lankan species of *Procloeon* probably are closely related to other species in the Indian Peninsula.
- 6. Pseudocloeon-Several distinct phylogenetic lineages from various areas of the world have been assigned to Pseudocloeon (Müller-Liebenau 1981). Four species of true Pseudocloeon have now been described from Sri Lanka. This phyletic lineage is known only from the Oriental Region.

#### C. Caenidae

- 1. Caenis-The Caenidae probably have spread from the Oriental Region to much of the rest of the world (Edmunds 1979). Caenis is widespread in the Indian Peninsula and Sri Lanka, as in many areas of the world, and the Sri Lankan species of Caenis probably are closely related to those in the Peninsula.
- 2. Clypeocaenis-Clypeocaenis presently is thought to be endemic to the Indian Peninsula and Sri Lanka.

# D. Ephemerellidae

Teloganodes-Teloganodes occurs throughout the Oriental Region and apparently evolved within the region. Its closest relatives occur in Africa (Edmunds 1972, 1975) and its ancestor probably spread to Asia via the Asia Minor land bridge.

# E. Ephemeridae

1. Ephemera-Ephemera s.s. probably dispersed from the Oriental to the Ethiopian Region (Edmunds 1979). At least four species of Ephemera s.s. occur in and apparently are endemic to Sri Lanka (Hubbard in press a). These species probably are closely related to those living in the Indian Peninsula.

## F. Heptageniidae

 Compsoneuriella-Compsoneuriella is widespread in Africa, some areas of the Malagasy Republic, and southeast Asia. It is possible that Compsoneuriella is present in Sri Lanka and southeast Asia due to transport by the drift of the Indian Peninsula (Edmunds 1979).

### G. Oligoneuriidae

1. Chromarcys-Chromarcys, known from Sumatra, China and Thailand, in addition to Sri Lanka, is closely related to the African and Madagascan Elassoneuria. They probably evolved in Africa from an Isonychia-like ancestor (Edmunds 1975, 1979). Chromarcys was carried to Asia with drifting India and then spread east from the Indian Peninsula on its union with Asia.

# H. Polymitarcyidae

- 1. Povilla-Povilla evolved in Africa as a sister group of Asthenopus when South America separated from Africa. It then spread through the Middle East land bridge to Sri Lanka and the rest of Asia where the genus radiated into the present species (Hubbard unpublished).
- 2. Ephoron-Ephoron probably dispersed from the Oriental Region to the Ethiopian Region (Edmunds 1979). The species of Ephoron occurring in Sri Lanka is either E. indicus, which is widespread throughout the Oriental Region or, if it is not E. indicus, then this is indicative of a closely evolved species group.

# I. Prosopistomatidae

1. Prosopistoma-Prosopistoma is fairly diverse in Africa and the Malagasy Republic, and occurs also from Sri Lanka to the Philippines and Australia with one species in Europe. The Asian species appear to be closely related and may have arisen from the speciation of the original ancestor that arrived in Asia from Gondwanaland via the Indian Peninsula (Edmunds 1975, 1979).

## J. Tricorythidae

1. Neurocaenis -The Tricorythidae appear to have evolved primarily in Gondwanaland (Edmunds 1979). The ancestor of Neurocaenis probably spread northward via the Middle East (Edmunds 1972, 1975). Neurocaenis is widespread throughout the Oriental Region.

### Systematic accounts

### Baetidae

Six genera of Baetidae, Baetis, Cloeon, Indobaetis, Indocloeon, Procloeon and Pseudocloeon have been reported from Sri Lanka, and twelve Sri Lankan baetid species have been described up to this time. Hagen (1858) described Cloe consuetus and Cloe solidus, both now placed in Baetis. These two species, known only from the adults, are endemic to Sri Lanka. A third endemic species of Baetis, B. feminalis, also known only from the adults, was described by Eaton in 1885. Cloeon marginale was described from the female by Hagen in 1858 (as Cloe marginalis). This species, whose type locality is in Sri Lanka, has since been reported from as far east as Taiwan and the Philippines. Procloeon bimaculatum, described in Cloeon by Eaton from Sri Lankan adults in 1885, has since also been reported from as far east as Taiwan and the Philippines. Müller-Liebenau & Morihara (1982) described two species of the endemic genus Indobaetis, viz., I.

costata and I. starmuehlneri from nymphs. The monotypic endemic Indocloeon primum was described by Müller-Liebenau (1982a). Müller-Liebenau (1982b) described four species of true Pseudocloeon which are endemic to Sri Lanka (P. ambiguum, P. difficilum, P. klapaleki and P. orientale).

Examination of the specimens of Sri Lankan Baetidae available to us indicates the presence of at least a few more species in the genera *Baetis*, *Cloeon* and *Procloeon*, and of two distinct '*Pseudocloeon*-type' genera.

The Baetidae are common in every sized stream throughout Sri Lanka. They have been collected at altitudes of over 2,000 m in the Horton Plains, to almost sea level, from a known temperature range from about 14 °C to >27 °C. They occur in tanks and reservoirs as well as the lotic habitats of streams and rivers. They probably are the most ubiquitous family of Ephemeroptera on the island, also the most diverse, occurring in the hill country, the wet lowlands, and throughout the dry zone lowlands.

#### Caenidae

Caenis perpusilla was described from Sri Lanka by Walker in 1853. This species has since been reported from Bangladesh and India. In addition to this species, we have specimens of an undescribed species in our collection. The genus Clypeocaenis also is present in our collections from Sri Lanka.

The Caenidae have been collected from streams and rivers from over 2,000 m in the hill country down to about 60 m in the wet lowlands. They also have been found in streams and tanks in the dry lowlands almost to sea level.

Nymphs of the Caenidae have been collected in Sri Lanka in February, March, April, June, October and December, and adults are known from January, February, March, April, June and November.

### **Ephemerellidae**

Only the subfamily Teloganodinae of the Ephemerellidae is known from Sri Lanka. Two species of the genus *Teloganodes, T. tristis* (originally described as *Cloe*) and *T. major*, have been described from the island. Both species were based only on females. *Teloganodes tristis* has since been reported from Java, Sumatra and the Philippines.

A luminous male imago, identified by the Rev. A.E. Eaton as *Teloganodes* was captured at Kitulgalle, at 1,500 ft. This specimen was said to be luminous, 'sufficiently to serve for its capture on a very dark night' (Ent. Soc. Lond. 1882). The senior author was unable to find any luminous mayflies in Sri Lanka, even though a special search was made.

We have seen specimens of Teloganodes from about 2,100 m in the Horton

Plains down to about 90 m. The water temperatures ranged from about 14 °C to about 26 °C. Always occurring on rock in swiftly flowing waters from large rivers to small streams, the nymphs of *Teloganodes* have been collected by the senior author even on vertical rock faces in waterfalls.

Nymphs of *Teloganodes* have been collected in Sri Lanka in February, March, April, September and December, and adults have been collected in March.

## **Ephemeridae**

The genus *Ephemera* is the only genus of Ephemeridae found in Sri Lanka. There are at least four endemic species of *Ephemera* on the island, all apparently belonging to the subgenus *Ephemera s.s.* (Hubbard in press a). Two of these species, *E. supposita* and *E. postica* (originally described as a *Rhoenanthus*), previously were known. We also have specimens of at least two undescribed species. Reports of *E. supposita* from Taiwan were based on misidentifications.

Ephemera is found in flowing waters where sandy substrates predominate and stable, moderately cool water temperatures occur (16 °C to 25 °C). It has been collected from about 1,800 m in the hill country to about 60 m in the wet lowlands. Adults have been collected in February, March, April and October, and nymphs have been collected in February, March, April and November.

# Heptageniidae

We have specimens of adults and nymphs of an undescribed species of *Compsoneuriella* from Sri Lanka. The Heptageniidae previously have been unreported from the island. *Compsoneuriella* has been collected in Sri Lanka from habitats ranging from medium sized streams to large rivers. The localities ranged from about 700 m altitude in the hill country to about 50 m in the wet zone and the northern edge of the hill country, temperature range about 20 °C to 25 °C. Both nymphs and adults have been collected in March.

## Leptophlebiidae

The Leptophlebiidae probably are the most diverse family of mayflies in Sri Lanka, rivalled only by the Baetidae. The genera *Choroterpes, Isca* and *Kimminsula*, along with several related but undescribed genera, are known from Sri Lanka. All the known Sri Lankan species are endemic and belong to the subfamily Atalophlebiinae.

There appear to be several species of Choroterpes in Sri Lanka. All belong to the subgenus Euthraulus. Only one species, Choroterpes (Euthraulus) signata (origi-

nally described in Cloe), has yet been described.

Choroterpes has been collected from streams at altitudes over 1,800 m in the hill country to about 60 m in the wet lowlands, temperature range of about 14 °C to 26 °C. Choroterpes also has been taken from streams in the dry lowlands of the Eastern Province, and from a marsh in the Northwestern Province at an altitude of 2-5 m.

The adults of *Choroterpes* are known from January, February, March, April, June and September, and the nymphs have been collected in February, March, April, June, September, October, November and December.

Megaglena brincki has been described from Sri Lanka. At least one additional species probably is present on the island. Nymphs are known from February, March, November and December, and adults have been collected in January, February, March and April. Megaglena is known from stream habitats with a

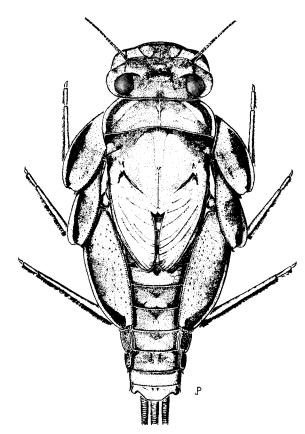


Fig. 10. Nymph of Kimminsula sp., a representative of the only confirmed Gondwanian derivatives (after Peters & Edmunds 1970).

temperature range of about 14 °C to about 26 °C, from about 2,000 m in the hill country, down to about 60 m in the wet lowlands.

Isca (Tanycola) serendiba has been described from Sri Lanka. Further study may reveal at least one more species of Isca on the island. Isca has been collected in streams from about 2,000 m altitude in hill country to 60 m in the wet lowlands, temperature range of about 14 °C to 26 °C. Adults have been collected also at a paddy field, although it is probable that they emerged from streams nearby and not from the paddy field itself.

The adults have been collected in January, February and March, and the nymphs are known from January, February, March, April, November and December.

Kimminsula (Fig. 10), and several related but undescribed genera, contain four described and several undescribed species from Sri Lanka. The species described originally as Potamanthus femoralis, Potamanthus fasciatus, Potamanthus annulatus and Baetis taprobanes were last placed in either Atalophlebia or Kimminsula, but definitely do not belong to the former genus, which does not occur in southern Asia. Some generic rearrangement in regard to the species currently placed in Kimminsula will also be forthcoming as our research progresses.

Species of the 'Kimminsula-group' have been collected from small to mediumsized streams from an altitude of about 1,800 m in the hill country to about 60 m in the wet lowlands, temperature range about 16 °C to 26 °C. Adults are known from February, March, April, September, October and December, and nymphs have been collected in January, February, March, April, August, September, October, November and December.

# Oligoneuriidae

The subfamily Chromarcyinae of the Oligoneuriidae is represented in Sri Lanka by an undescribed species of the genus *Chromarcys*. *Chromarcys* has been collected in both the wet lowlands and the dry lowlands in moderately sized streams below about 150 m in Sri Lanka, although Peters (unpublished) found it only in torrential mountain streams in Thailand. Adults have been collected in March, October, November and December, and nymphs have been collected in April.

# Polymitarcyidae

The Polymitarcyidae are represented in Sri Lanka by one species of the asthenopodine genus *Povilla* and one species of the polymitarcyine genus *Ephoron. Povilla* are burrowers in mud, vegetable matter, and even wood. Nymphs of this undescribed endemic species of *Povilla* have been collected burrowing into teak lock gates and at 120 m altitude in the wet country from a medium sized stream

(Hubbard in press b). The nymphs have been collected in April and October.

The species of *Ephoron*, originally described as *Anagenesia greeni* by Banks (1914), has since been thought to be synonymous with *Ephoron indicus*. Further study is needed to confirm this synonymy. Adults have been collected from reservoirs, and large rivers to medium sized streams in March, April and October from 500 m altitude to 60 m in the wet zone, and from about 60 m in the northern dry zone.

#### Potamanthidae

Banks (1914) described *Rhoenanthus posticus* from Sri Lanka. However, examination of the types reveals that *R. posticus* is in fact and *Ephemera*, and that the Potamanthidae are not known to occur in Sri Lanka.

## Prosopistomatidae

One species of *Prosopistoma*, the endemic *P. lieftincki*, has been described from Sri Lanka. The somewhat cryptic nymph of *Prosopistoma* is found on flat rock surfaces in small swiftly flowing streams in the hill country and wet lowlands. We have seen specimens collected from 2,000 m to 90 m, at temperatures of 14 °C to 26 °C. The nymphs have been collected in February through April and August through October.

#### Tricorythidae

The tricorythid species *Neurocaenis jacobsoni* (originally described in *Tricorythus*) has been reported from Sri Lanka (Ulmer 1924). Further study of speciments may reveal two species of *Neurocaenis* in Sri Lanka. The assignment of Sri Lankan specimens to *N. jacobsoni*, whose type locality is Java, needs re-evaluation.

Neurocaenis has been collected in the hill country at about 1,800 m to 50 m in the wet lowlands. It has been collected from large rivers to moderately sized streams, in a temperature range of about 16-25 °C.

The adults often fly in great numbers at dusk, usually the earliest of the crepuscular flyers to arrive at light traps. Adults of *Neurocaenis* have been collected in Sri Lanka in January, February, March, April and November, and nymphs have been collected in September, October and December.

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#### References

Banks, N. 1914. New neuropteroid insects, native and exotic. Proc. Acad. Nat. Sci. Phil. 66:608-618.
Costa, H.H. & F. Starmühlner. 1972. Results of the Austrian-Ceylonese Hydrobiological Mission 1970 of the 1st Zoological Institute of the University of Vienna (Austria) and the Department of Zoology of the Vidyalankara University of Ceylon, Kelaniya. Part I. Preliminary Report: Introduction and description of the stations. Bull. Fish. Res. Stn Sri Lanka (Ceylon) 23:43-76.

Eaton, A.E. 1871. A monograph on the Ephemeridae. Trans. Ent. Soc. Lond. 1871:1-164.

Eaton, A.E. 1883-1888. A revisional monograph of Recent Ephemeridae or mayflies. Trans. Linn. Soc. Lond. 2nd Ser. Zool. 3:1-352.

Edmunds, G.F. Jr. 1972. Biogeography and evolution of Ephemeroptera. Ann. Rev. Ent. 17:21-42.

Edmunds, G.F. Jr. 1975. Phylogenetic biogeography of mayflies. Ann. Miss. Bot. Gardens 62:251-263.

Edmunds, G.F. Jr. 1979. Biogeographical relationships of the Oriental and Ethiopian mayflies. pp. 11-14 ln: K. Pasternak & R. Sowa (Eds.) Proc. 2nd. Int. Conf. Ephem. Państowowe Wydawnictwo Naukowe, Warzawa-Kraców.

Edmunds, G.F. Jr. & C.H. Edmunds. 1980. Predation, climate, and emergence and mating of mayflies. pp. 277-285 In. J.F. Flannagan & K.E. Marshall (Eds.) Advances in Ephemeroptera Biology. Plenum Press, N.Y.

Entomological Society of London. 1882. [Report of meeting]. Trans. Ent. Soc. Lond. 1882: xii.

Fernando, C.H. 1965. A guide to the freshwater fauna of Ceylon. Suppl. 2. Bull. Fish. Res. Stn Ceylon 17:177-211.

Fernando, C.H. 1980. The freshwater zooplankton of Sri Lanka, with a discussion of tropical freshwater zooplankton composition. Int. Rev. ges. Hydrobiol. 65:85-125.

Hagen, H.A. 1858. Synopsis der Neuroptera Ceylons. Verh. Zool. Bot. Ges. Wien 8:471-488.

Hagen, H.A. 1859. Synopsis der Neuroptera Ceylons.II. Verh. Zool. Bot. Gess. Wien 9:199-212.

Hagen, H.A. 1873. Notes on the Ephemeridae, by Dr H.A. Hagen; compiled (with remarks) by the Rev. A.E. Eaton, M.A. Trans. Ent. Soc. Lond. 1873:381-406.

Hubbard, M.D. in press a. Ephemeroptera of Sri Lanka: Ephemeridae. Syst. Entomol.

Hubbard, M.D. in press b. A revision of the genus *Povilla* (Ephemeroptera:Polymitarcyidae). Aq. Insects.

Hubbard, M.D. & Peters, W.L. 1978. A catalogue of the Ephemeroptera of the Indian Subregion.
 Orient. Insects, Suppl. 9:1-43.Mani, M.S. 1974. Biogeography of the Peninsula. pp. 614-647 In:
 M.S. Mali (Ed.) Ecology and biogeography in India. Monogr. Biol. 23. Dr W. Junk. The Hague.

- Müller-Liebenau, I. 1982a. A new genus and species of Baetidae from Sri Lanka (Ceylon): *Indocloeon primum* gen.n., sp.n. (Insecta, Ephemeroptera). Aq. Insects 4:125-129.
- Müller-Liebenau, I. 1982b. Five new species of *Pseudocloeon* Klapalek, 1905, (Fam. Baetidae) from the Oriental Region (Insecta, Ephemeroptera) with some general remarks on *Pseudocloeon*. Arch. Hydrobiol. 95:283-298.
- Müller-Liebenau, I. & D.K. Morihara. 1982. *Indobaetis*: a new genus of Baetidae from Sri Lanka (Insecta: Ephemeroptera) with two new species. Gewäss. Abwäss. 68/69:26-34.
- Peters, W.L. 1967. New species of *Prosopistoma* from the Oriental Region (Prosopistomatoidea: Ephemeroptera). Tijdschr. Entomol. 110:207-222.
- Peters, W.L. & G.F. Edmunds Jr. 1970. Revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera). Pac. Insects 12:157-240.
- Pictet, F.J. 1843-1845. Histoire naturelle générale et particuliere des Insectes Névroptères. Famille des Ephémérines. J. Kessman & Ab. Cherbuliez, Geneva. 300 pp.
- Sivaramakrishnan, K.G. in press. A new genus and two new species of Leptophlebiidae from southern India (Ephemeroptera).
- Sivaramakrishnan, K.G. & W.L. Peters. in press a. *Notophlebia*: one new species and reassignment of the nymph of *Nathanella* (Ephemeroptera:Leptophlebiidae).
- Sivaramakrishnan, K.G. & W.L. Peters. in press b. A new genus and species of Atalophlebiinae (Ephemeroptera: Leptophlebiidae) from southern India.
- Ułmer, G. 1913. Note V. Ephemeriden aus Java, gesammelt von Edw. Jacobson. Notes Leyden Mus. 35:102-120.
- Ulmer, G. 1924. Ephemeropteren von den Sunda-Inseln und den Philippinen. Treubia 6:28-91.
- Walker, F. 1853. Ephermeridae. pp. 533-585 ln: List of the specimens of neuropterous insects in the collection of the British Museum. Part III. (Termitidae-Ephemeridae).