

**REVISION OF THE GENERIC CLASSIFICATION OF
THE EASTERN HEMISPHERE LEPTOPHLEBIIDAE
(Ephemeroptera)¹**

By William L. Peters² and George F. Edmunds, Jr.³

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2. Florida A & M University, Tallahassee, Fla. 32307.
3. University of Utah, Salt Lake City, Ut. 84112.

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Abstract: The generic classification of the Eastern Hemisphere Leptophlebiidae is revised. Because of their clear affinity with Ethiopian and Oriental mayflies, the Leptophlebiidae of New Guinea are included. Those of Australia and New Zealand are excluded because their affinities are with genera occurring in Australia, New Zealand and the temperate Neotropical Region, especially Chile, Argentina and Southern Brazil.

Only those known genera occurring in the Oriental and Palearctic regions are described in this paper. Other genera occurring only in the Ethiopian Region are defined by Peters & Edmunds (1964) with their generic descriptions consistent in style with those given in this revision. Illustration of important morphological features and keys to the imagos and mature nymphs are given for all genera occurring in the Eastern Hemisphere as defined above.

Generic and subgeneric criteria used in this revision are basically similar to those given by Edmunds (1962), but certain generic and subgeneric problems arising in this study are also considered.

Those morphological characteristics used to define and delimit each genus of the Eastern Hemisphere Leptophlebiidae were carefully selected as being those of the most value for these genera. It is recognized that additional or alternate characters may be needed as revisionary studies extend to define all genera of the Leptophlebiidae.

Twenty-nine genera of the Leptophlebiidae are known to occur in the Eastern Hemisphere. Five new genera, *Gilliesia*, *Kimminsula*, *Indialis*, *Megaglana*, and *Notophlebia*, are described in this revision. Two new subgenera, *Minyphlebia* and *Tanycola*, are established in the genus *Isca*. Other genera defined and considered valid in this report are *Calliarcys*, *Choroerpes*, *Choroerterpides*, *Cryptopenella*, *Dipterophlebiodes*, *Habrophlebia*, *Habrophlebiodes*, *Habroleptoides*, *Isca*, *Leptophlebia*, *Nathanella*, *Paraleptophlebia*, *Simothraulius*, and *Thraulius*. Those Ethiopian genera defined by Peters & Edmunds (1964) and considered valid in this revision are *Adenophlebia*, *Adenophlebiodes*, *Aprionyx*, *Atalophlebioides*, *Castanophlebia*, *Fullea*, *Fulletomimus*, *Hagenulodes*, *Maheathraulius*, and *Nesophlebia*.

The mature nymphs of *Cryptopenella*, *Nathanella* and *Isca* and the female imagos of *Choroerterpides* are described for the first time. *Thraulius signatus* Hagen and *Hagenulus karnyi* Ulmer are placed in the subgenus *Euthraulius* of the genus *Choroerpes*. *Habroleptoides* is considered as a separate genus from *Habrophlebia*, and *Masharikella* is placed as a synonym of *Thraulius*.

A hypothesized phylogeny is given for the Eastern Hemisphere genera of Leptophlebiidae. As the fossil record of the Leptophlebiidae is poorly known the phylogeny was formulated and repeatedly tested from comparative external and internal morphological data of recent taxa and further tested for consistency with zoogeographical criteria.

INTRODUCTION

The family Leptophlebiidae is one of the most distinctive families of mayflies. Although members of the family share many similarities, it is a highly successful and diverse family with over 75 described genera. The family is nearly cosmopolitan in

distribution and is represented by several to many genera in most parts of the world. The nymphs live in a variety of habitats and thus have developed many adaptations.

Many genera of Leptophlebiidae are so poorly defined that sometimes it is impossible to place a species into the proper genus. A revision of the generic classification of the entire family Leptophlebiidae has never been attempted, although small groups of geographically related genera have been studied. The purpose of this study is to redefine the genera of the Eastern Hemisphere Leptophlebiidae including those of New Guinea, but not those of Australia and New Zealand. The affinities of the genera occurring in Australia and New Zealand are almost entirely with those of the Chilean subregion of the Neotropical Region and revision of these genera must be undertaken simultaneously with the Neotropical genera. It is planned eventually to study all genera of the family.

In the systematic section of this revision only those genera occurring in the Oriental and Palearctic regions are defined. Other genera occurring only in the Ethiopian Region have been treated previously by Peters & Edmunds (1964, 1966). The style of the generic descriptions of the Ethiopian genera given by Peters & Edmunds (1964) is consistent with those given in this study, and it would be redundant to include them here. However, the keys and phylogeny section of this revision treat all genera of the Eastern Hemisphere (except Australia). In most cases figures of important morphological features of the Ethiopian genera are included in the plates. The sequence of treatment is phylogenetic as given in figure 1 beginning with the plesiomorphic *Paraleptophlebia* and advancing to the apomorphic *Gilliesia*. Then the sequence continues with the plesiomorphic *Aprionyx* and advances to the apomorphic *Isca*.

Although all described species from the Ethiopian, Oriental, and Palearctic regions are considered in this study, 6 species have not been assigned to genus herein. *Hagenulus monstratus* Eaton, 1892, is known only from the adult type series deposited in the British Museum (Natural History). Peters has examined this series and found all the specimens badly broken. Correct assignment of this species is impossible until topotypic material can be collected in the Tenasserim Valley in Burma. Eaton (1892) did not give figures of this species.

Atalophlebia femoralis (Hagen), 1858, is known only from the adult type series deposited in the Museum of Comparative Zoology, Cambridge. We have examined a portion of the type series and found the specimens badly broken. However, the species appears to represent an undescribed genus. Until reared material of this species is available from Ceylon the correct assignment of the species is impossible. Hagen (1858) did not give figures of the species.

Navas (1936) described *Leptophlebia duplex* and *L. simplex* from Kuling, China. The deposition of the types of these 2 species is unknown, but they are probably in the Museum Heude, Shanghai. Based on Navas' descriptions and figures of the cubital area of the fore wings, correct assignment of either species is impossible. If Navas' figure of the cubital area of the fore wings of *L. duplex* is correct, the species could belong to the Ephemerellidae. The description and figure of *L. simplex* given by Navas (1936) suggests that the species belongs to the Leptophlebiidae, but it is not certain.

Demoulin (1966) described *Ulmerophlebia* (?) *succinea* and *U.* (?) *variegata* from Madagascar. Both species were described from female imagos. While it is unlikely that either species belongs to the Australian genus *Ulmerophlebia*, correct assignment of the

species is impossible until the male imagos and nymphs are known.

The following terms and procedures used in the descriptions of the imago and nymph require further explanation. The lengths of the body and fore wings of the male and female imagos are given as the total observed variation within a genus or subgenus. Venational terminology used is as indicated in fig. 7 and 8. Each segment of the fore legs of the male imago is compared to the length of the fore tibiae and expressed as a ratio. The average length in millimeters of the fore tibiae is given in parentheses. In the figures of the labia of the genera, the ventral surface is shown on the right hand side of the drawing, and the dorsal surface is shown on the left.

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GENERIC CRITERIA

Guidelines for recognizing generic and subgeneric groups in this revision are modified from those stated by Edmunds (1962) in order to deal effectively with some of the problems encountered in this study. Our criteria are as follows.

If two or more groups of species are separated by a distinct gap of characters evident in both adults and nymphs, then the groups are considered as separate genera. All

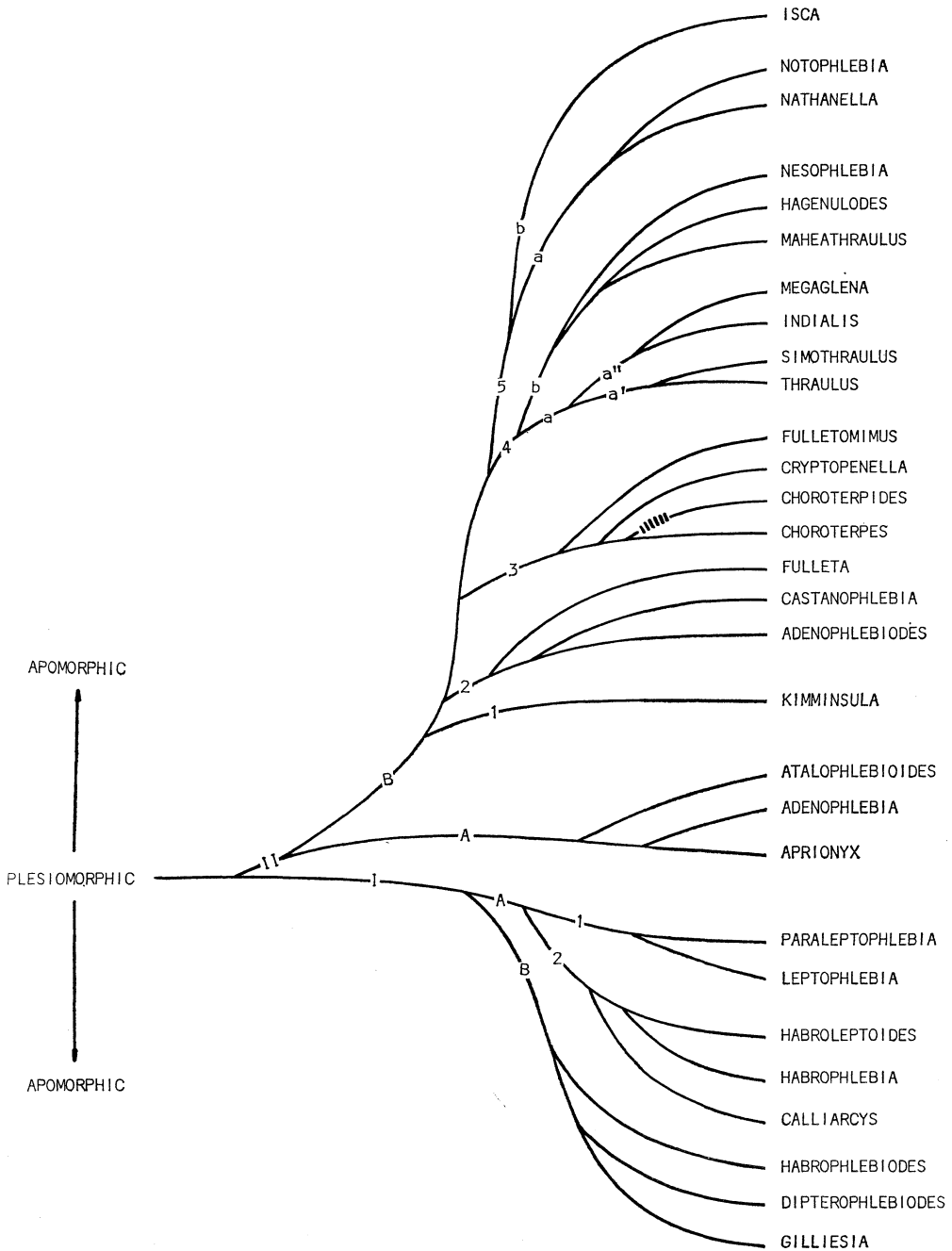


Fig. 1. Phyletic diagram representing the probable phylogeny of the Eastern Hemisphere genera of the Leptophlebiidae. (Designations in fig.1. correspond to those in Table I.)

Table I. List of adult and nymphal exoskeletal characters used in determining furcations of phyletic lines in fig.1. (Designations in table correspond to those in fig. 1.)

Primitive Characters

Adult

- No intercalaries present between veins MP_2 and CuA of the fore wings (fig. 9, 19, 48, 64).
- Vein CuP of the fore wings strongly recurved (fig.9, 19, 48, 64).
- Fore wings triangular in shape (fig. 9, 11, 13, 15, 26).
- Hind wings present, with no well developed costal projection and with numerous longitudinal veins (fig. 10, 12, 14, 16, 27).

Nymph

- Body depressed dorsoventrally (fig. 2-6).
- Labial palpi 3-segmented (fig. 152-173).
- Maxillary palpi 3-segmented (fig. 174-195).
- Head hypognathous.
- Outer margin of mandibles straight (fig. 218-222).
- Lingua of hypopharynx without well developed lateral projections (fig. 196-200).
- Gills similar on segments 1-7, forked (fig. 287-288, 290, 292), lateral in position.

Characters of Recent Genera

- I. Adult
 - 9th sternum of ♂ greatly enlarged posteriorly and deeply cleft (fig. 72-73, 76-80), except enlargement secondarily reduced in *Habroleptoides* and *Habrophlebia* fig. 74-75.
- Nymph
 - Brush on anterior margin of maxillae composed entirely of fine hair (fig. 174-178).
- IA. Adult
 - 4 or 5 intercalaries present in Cu area of fore wings (fig. 9, 11, 13, 15, 17).
- Nymph
 - An even row of hair not present along dorsal, anterior margin of labrum (fig. 240-243).
- IA1. Adult
 - Anterior margin of hind wings convex and with no costal projection (fig. 10, 12).
- Nymph
 - Head hypognathous.
- IA2. Adult
 - Anterior margin of hind wings with a costal projection, often not well developed (fig. 14, 16, 18).
- Nymph
 - Head prognathous.
- IB. Adult
 - 2 intercalaries present in Cu area of fore wings (fig. 19, 22-23).
 - Anal fan of adult fore wings reduced making wings less triangular (fig. 19, 22-23).
- Nymph
 - An even row of hair along dorsal, anterior margin of labrum (fig. 244).

- II. Adult
9th sternum of ♂ not greatly enlarged posteriorly and not deeply cleft (fig. 81-92, 95-106), except 9th sternum of *Cryptopenella* enlarged but not cleft (fig. 93).
- Nymph
Brush on anterior margin of maxillae composed of fine hair and thick spines (fig. 179-186, 188-192, 194-195), except thick spines secondarily lost in *Nathanella* and *Choroterpides* (fig. 187, 193).
Lingua of hypopharynx with well developed lateral projections (fig. 201-205, 207-217), except projections secondarily lost in *Castanophlebia* (fig. 206).
- IIA. Adult
♂ penes fused to near apex (fig. 81-83).
- Nymph
Ventral surface of maxillae without a V-shaped ridge near inner anterolateral margin (fig. 179-181).
- IIB. Adult
♂ penes fused only in basal 1/2 (fig. 85-106).
- Nymph
A V-shaped ridge present on ventral surface of nymphal maxillae near the inner anterolateral margin (fig. 182, 185, 188, 192, 195), except ridge often developed into a large tooth-like projection (fig. 187, 190, 193).
- IIB1. Adult
Anterior margin of hind wings smoothly convex and without a well developed costal projection (fig. 31).
- IIB2. Adult
Cross veins in fore wings numerous (fig. 32, 35, 37).
Intercalaries in Cu area of adult fore wings relatively long (fig. 32, 35, 37).
- IIB3. Adult
In Cu area of fore wings 2 long intercalaries with 2 greatly shortened intercalaries between them; remainder of intercalaries in Cu area greatly shortened (fig. 38, 40, 43, 46, 48).
- Nymph
Middle abdominal gills plate-like with each portion terminated in 3 long processes (fig. 304, 306, 308, 342).
- IIB4. Adult
Hind wings present, except secondarily absent in *Hagenulodes* (fig. 53, 55, 58, 60, 63, 67).
- Nymph
A row of thick spines present on ventral surface of maxillae near inner anterolateral margin (fig. 188-192).
- IIB4a. Adult
Anal fan of fore wings expanded and rounded (fig. 51, 54, 56, 59).
- Nymph
Body flattened dorsoventrally.
- IIB4aa'. Adult
Fork of vein MP of fore wings nearer to base than fork of vein R_s (fig. 51, 54).
- Nymph

- Middle abdominal gills plate-like (fig. 311).
- IIB4aa''. Adult
 Fork of veins MP and R_s of fore wings forked about equidistant from base (fig. 56, 59).
- Nymph
 Middle abdominal gills slender (fig. 312-313).
- IIB4b. Adult
 Anal fan of fore wings reduced (fig. 61, 64, 65).
- Nymph
 Body not as greatly flattened dorsoventrally.
- IIB5. Adult
 Hind wings absent.
- Nymph
 A row of thick spines absent on ventral surface of maxillae near inner anterolateral margin (fig. 193-195, 350).
- IIB5a. Adult
 Cross veins in fore wings spaced evenly throughout wings (fig. 68, 346).
- Nymph
 Abdominal tergites extend to lateral sides of abdomen, all abdominal gills lateral (fig. 6).
- IIB5b. Adult
 Cross veins absent in posterior margin of fore wings (fig. 69-71).
- Nymph
 Abdominal tergites extend around to venter of abdomen, thus producing ventral gills (fig. 332).

characters are considered, whether they are morphological, behavioral, ecological, etc.

We call two or more groups subgenera in the following cases. (a) If two or more groups of species are separable by a distinct gap of characters evident in either the adults or nymphs but this gap of characters is weakly indicated in the other stage. (b) If two or more groups of species are weakly differentiated in characters in both adults and nymphs. An example of this is seen in the subgenera of *Choroterpes*, *Choroterpes* s. s. and *Euthraulius*. The subgenera appear to be weakly differentiated morphologically, ecologically, and behaviorally. (c) When two or more groups of species are separated by a distinct gap of characters evident in either the adult or the nymph but no character gap is detectable in the other stage. We have followed this practice in the subgenera of the genus *Isca* where the adults may be separated into three distinct groups separated by a distinct character gap but no character gap is apparent in the nymphs. The nymphs of the three groups also appear to be similar ecologically.

If two or more groups of species are weakly differentiated in either the adult or the nymphs, but a character gap is lacking in the other stage, we have included all species in a single genus with no subgenera. We have followed this practice in recognizing only a single genus with no subgenera in the genus *Thraulius*, despite the fact that three distinct types of nymphs can be designated on the basis of the form of gills on segment one. This character difference is regarded as weak differentiation because it does not seem to be reinforced by other concordantly occurring differences in either stage.

In general we have been extremely conservative about establishing new generic names for mayflies that are only known in one stage. If a group of species known only from the adults or only from the nymphs can be conveniently placed in a previously named group, even though it seems to us to warrant generic rank, we think that it is best to wait for knowledge of the other stage rather than to chance the unnecessary establishment of a generic synonym. In some cases we have established a new genus for a distinct form on the basis of our knowledge of only one stage, as for example in the genus *Gilliesia*, when it seems unlikely to us that nymphal collections will be available in the near future. Generally speaking, we believe that it is best to delay the application of names when it seems likely that in the near future the systematic relationships are likely to be clarified by new material.

SYSTEMATICS

Family LEPTOPHLEBIIDAE Banks, 1900

Eaton, 1884 (1883-88): 82. (Section 5 of *Leptophlebia*.)

Banks, 1900: 246. (Leptophlebiini.)

Jacobson & Bianchi, 1905: 873. (Leptophlebiinae.)

Klapálek, 1909: 10.

Lestage, 1919: 112. (Leptophlebiinae.)

Ulmer, 1920: 112.—Phillips, 1930: 335.—Schoenemund, 1930: 49.—Barnard, 1932: 233.—
Ulmer, 1932a: 112; 1932b: 201.—Spieth, 1933: 342.

Traver, 1935: 504. (Leptophlebiinae.)

Burks, 1953: 81.—Edmunds & Traver, 1954: 238.—Bogoescu, 1958: 71.—Demoulin, 1958:
10.—Ujhelyi, 1959: 37, 82.—Grandi, 1960: 212, 396.—Edmunds, Allen & Peters, 1963:
14.—Peters & Edmunds, 1964: 228.

The Leptophlebiidae were first recognized by Eaton 1884 (1883-88) as "Section 5 of *Leptophlebia*" and the authorship of the family name was established by Banks (1900) (as Leptophlebiini). The diverse genera share so many fundamental characteristics that no genus once placed in the Leptophlebiidae has ever been transferred to another family.

Edmunds & Traver (1954) placed this family with the Ephemerellidae and Tricorythidae in the superfamily Leptophlebioidea. Landa (1959), in his study of the internal systems of the mayflies, confirmed Edmunds' & Traver's arrangement. Demoulin (1958) placed the Leptophlebiidae, Ametropodidae, and Heptageniidae into the superfamily Heptagenioidea, stating that he used evidence from fossils to arrive at a different classification. He also stated that, since the nymphs of mayflies often show many specializations, in doubtful cases of classification the adult characters were used to make the final decisions. However, he justified the inclusion of Leptophlebiidae in Heptagenioidea almost entirely upon nymphal characteristics. We would also point out that the Leptophlebiidae are similar to the plesiomorphic members of the Ephemeroidea and are closely allied to this superfamily.

Peters & Edmunds (1964) characterized the family Leptophlebiidae in their generic

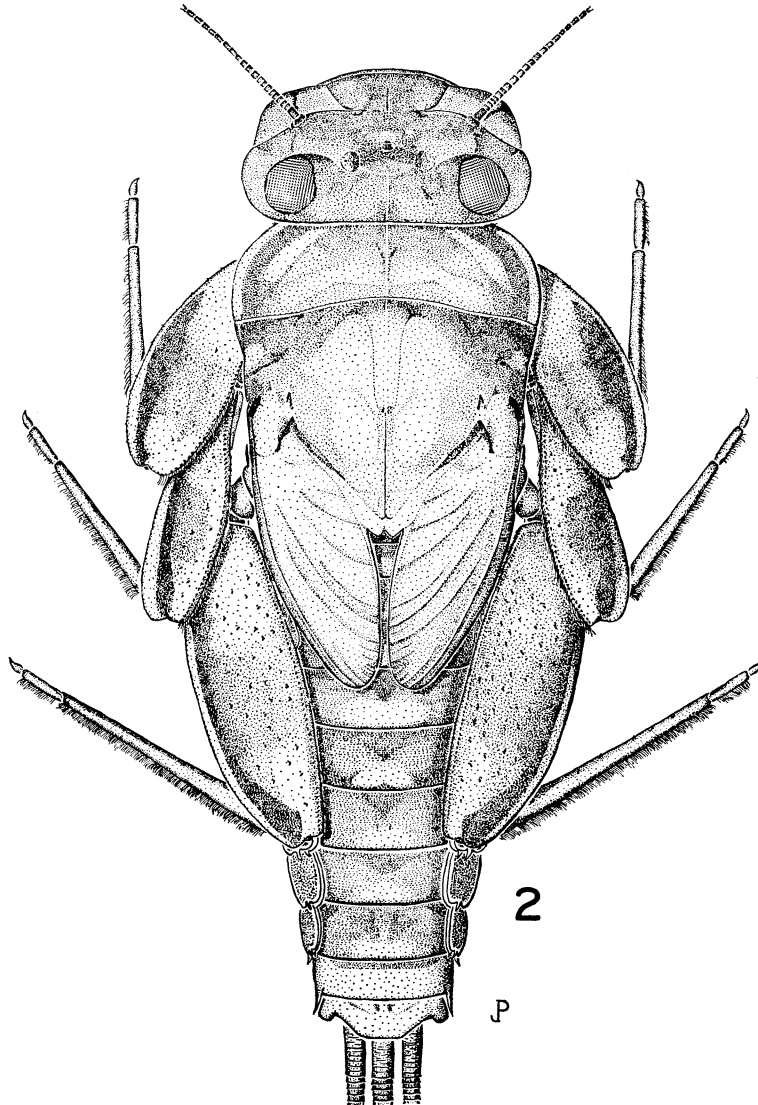


Fig. 2. *Kimminsula* sp., dorsal view of mature ♀ nymph.

revision of the Ethiopian Leptophlebiidae. However, their characterization of the family was based almost entirely on data from the Ethiopian Region. Based on data from the Eastern Hemisphere study and incomplete data from the Western Hemisphere, the imagos and mature nymphs of the family are characterized as follows.

Imago. Eyes of ♂ divided into large upper portion with large facets and smaller lower portion with smaller facets, upper portion contiguous with lower portion to upper portion on long stalk (fig. 326), or eyes of ♂ composed entirely of small facets; eyes of ♀ not divided, com-

posed entirely of small facets. Median and lateral ocelli well developed. Fore wings: veins C and Sc well developed (fig. 9, 38, 71); vein MA₂ attached at base to vein MA₁, 1 intercalary present between veins MA₁ and MA₂ (fig. 9, 38, 71); vein MP₂ attached at base to MP₁ (fig. 9, 15), or vein MP₂ independent of vein MP₁ (fig. 37, 61), 1 intercalary between veins MP₁ and MP₂; no intercalaries present between veins MP₂ and CuA; 2-8 intercalaries between veins CuA and CuP (fig. 9, 38, 71); vein CuP strongly bowed (fig. 11, 32, 69); 2 to 3 anal veins present, all strongly bowed (fig. 9, 43, 64); cross veins few to numerous. Hind wings present or absent; if present, well developed (fig. 12, 52) to very small (fig. 66); costal projection well developed (fig. 39, 50) to absent (fig. 10, 12); venation highly varied; cross veins few to numerous. Tarsi of fore legs of ♂ 5-segmented, segment 1 short; tarsi of middle and hind legs of ♂ 4-segmented; tarsi of all 3 pairs of legs of ♀ 4-segmented; claws of a pair similar (fig. 111, 114, 128) or dissimilar (fig. 119, 124, 129). Well developed external ovipositor or egg guide present (fig. 322-324) or absent on abdomen of ♀. ♂ genitalia: forceps 2 or 3-segmented, segments 2 and 3 (when present) shorter than segment 1 (fig. 72, 88, 103); penis lobes partly (fig. 86, 96, 100) to entirely (fig. 81-83) fused on mesal margins, ventral spines or appendages present (fig. 74, 83, 87) or absent (fig. 89, 100, 103). Ninth sternum of ♀ entire (fig. 142, 146, 149) to deeply cleft apically (fig. 131, 135, 139). Caudal filaments well developed, usually 3, but the median terminal filament sometimes reduced or vestigial.

Mature nymph. Nymph depressed. Head hypognathous or prognathous. Denticles present (fig. 255, 257) or absent (fig. 251, 262) on anterior emargination of labrum. Hypopharynx well developed, usually with well developed lateral processes (fig. 196, 205, 207). Maxillary palpi 3-segmented; a rake-line spine usually present on inner anterior margin of maxillae (fig. 177, 183, 188); a large tooth-like projection present (fig. 187, 189, 190) or absent (fig. 174, 177-178) on inner anterior margin of maxillae. Labial palpi 3-segmented; glossae and paraglossae well developed (fig. 152, 162, 172). A row of denticles present (fig. 264, 274, 285) or absent (fig. 269) on nymphal claws. Gills on abdominal segments 1-7, 1-6, or 2-7, ventral portion of gills present (fig. 289, 308, 311) or absent (fig. 298, 303, 305). 3 well developed caudal filaments present.

KEYS TO GENERA

The following keys will serve to distinguish the imagos and nymphs of genera and subgenera of the Leptophlebiidae from the Eastern Hemisphere. In the key to the imagos all references to veins are to the fore wings unless otherwise stated.

Imagos

1. Hind wings present (fig. 10, 34, 45), although sometimes small (fig. 66-67) 9
Hind wings absent 2
- 2 (1). Outer margin of fore wings serrate (fig. 37); eyes of ♂ not divided into upper and lower portions, composed entirely of small facets **Fulleta** Navas
Outer margin of fore wings entire (fig. 64, 68-69); eyes of ♂ divided into upper portion with large facets and lower portion with smaller facets (fig. 328-330) 3
- 3 (2). Vein MP₂ independent of vein MP₁ (fig. 69-70) 4
Vein MP₂ attached to vein MP₁ to form a fork (fig. 64, 71) or vein MP₂ attached at base to vein MP₁ by a cross vein (fig. 22, 68) 5
- 4 (3). Cilia present on posterior margin of fore wings (fig. 70); penes of ♂ divided, apical 1/2 of each penis lobe slender, tubular, basal 1/2 of each penis lobe greatly ex-

* Described as new.

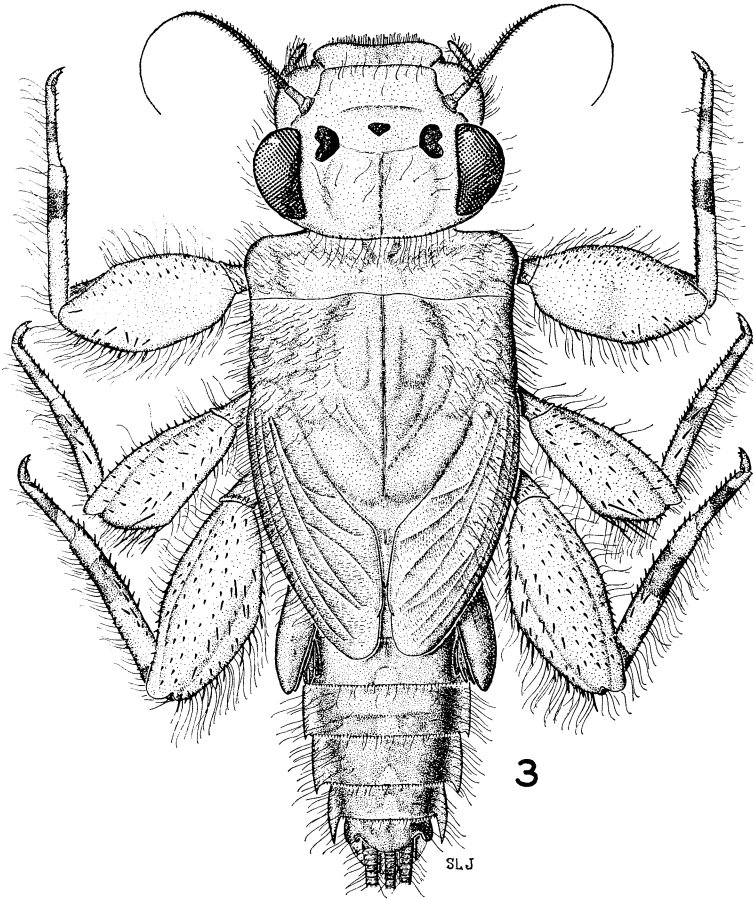


Fig. 3. *Adenophlebiodes* sp., dorsal view of mature ♂ nymph.

- panded laterally (fig. 105) **Isca (Tanycola)***
 Cilia absent on posterior margin of fore wings (fig. 69); penes divided, tubular, broad, the outer margin of each penis lobe curved inwardly forming an apical point (fig. 104) **Isca (Minyphlebia)***
 5 (3). Vein MP_2 attached to vein MP_1 to form a fork (fig. 64, 71) 6
 Vein MP_2 attached at base to vein MP_1 by a cross vein (fig. 22, 68) 7
 6 (5). Cilia present on posterior margin of fore wings (fig. 71); abdominal terga extend around onto venter of abdomen, this most marked on segment 7 but scarcely at all on segment 1 and 2 **Isca (Isca s. s.) Gillies**
 Cilia absent on posterior margin of fore wings (fig. 64); abdominal terga extend to lateral sides of abdomen **Hagenulodes Ulmer**
 7 (5). Claws of a pair alike, each apically hooked, with an opposing subapical hook (fig. 128) **Nathanella Demoulin**
 Claws of a pair dissimilar, one apically hooked, the other obtuse, pad-like (fig. 347) 8
 8 (7). Membrane of anal area of fore wings enlarged posteriorly (fig. 346); fork of vein

- MA symmetrical (fig. 346) **Notophlebia***
 Membrane of anal area of fore wings not enlarged as above (fig. 22); fork of vein
 MA asymmetrical (fig. 22) **Dipterophlebiodes** Demoulin
- 9 (1). Hind wings small with only 1 longitudinal vein (fig. 66-67).....
 **Nesophlebia** Peters & Edmunds
 Hind wings well developed with more than 1 longitudinal vein (fig. 10, 36, 45) 10
- 10 (9). Costal projection of hind wings well developed and rounded with apex of projec-
 tion located nearer apex of wings than middle (fig. 55); dorsal surface of penes
 of ♂ serrate (fig. 97) **Simothraululus** Ulmer
 Costal projection of hind wings not as above, either acute (fig. 50, 52, 63), or absent
 (fig. 10, 12), or if rounded, with apex of projection located nearer middle of wings
 than apex (fig. 34, 42, 60); dorsal surface of penes of ♂ not serrate (fig. 72, 86,
 96) 11
- 11(10). Claws of a pair alike (fig. 111, 114-115, 117) 12
 Claws of a pair dissimilar, one hooked, the other obtuse, pad-like (fig. 119, 123-
 124) 17
- 12(11). Costal margin of hind wings convex (fig. 27, 31) 13
 Costal margin of hind wings with a well developed projection (fig. 34, 52, 60)..... 14
- 13(12). Vein MP₂ attached to vein MP₁ and strongly bowed (fig. 26); penes of ♂ fused ex-
 cept for apical cleft (fig. 81-82) **Aprionyx** Barnard
 Vein MP₂ attached at base to vein MP₁ by a cross vein (fig. 30); penes of ♂ divided
 (fig. 85) **Kimminsula***
- 14(12). Vein R_s and MP forked about equidistant from base of wings to margin (fig. 32);
 no appendages on penes of ♂ (fig. 86) **Adenophlebiodes** Ulmer
 Vein MP forked closer to base of wings than vein R_s (fig. 13, 15, 28); ventral spines
 or appendages on penes of ♂ (fig. 74-75, 83) 15
- 15(14). Penes of ♂ fused except for apical cleft, each lobe with a ventral spine (fig. 83);
 9th sternum of ♀ slightly cleft apically (fig. 138) **Adenophlebia** Eaton
 Penes of ♂ tubular, basal 1/2 of penes fused, a ventral appendage arising from apex
 of each lobe (fig. 74-75); 9th sternum of ♀ deeply cleft apically (fig. 133-134).....16
- 16(15). Base of genital forceps of ♂ broad, its inner margin forming an extreme angular
 bend (fig. 75); ♀ with a well developed ovipositor or egg guide (fig. 322)
 **Habrophlebia** Eaton (in part)
 Base of genital forceps of ♂ broad, its inner margin at base with a pointed or blunt
 projection (fig. 74); ♀ without a well developed ovipositor or egg guide
 **Habroleptoides** Schoenemund (in part)
- 17(11). Vein MP₂ attached at base to vein MP₁ more basally than fork of vein R_s (fig. 9,
 17, 56); vein MP₂ attached to vein MP₁ and smoothly curved (fig. 9, 11, 56), or
 vein MP₂ attached at base to vein MP₁ by a cross vein (fig. 17)..... 18
 Vein R_s and MP forked equidistant from base of wings to margin (fig. 35, 38, 59)
 or vein R_s forked more basally than attachment of vein MP₂ to vein MP₁ (fig.
 46, 48), or vein MP₂ independent of vein MP₁ (fig. 23, 61) 24
- 18(17). Costal margin of hind wings slightly concave near middle (fig. 10, 12) 19
 Costal margin of hind wings with an acute projection (fig. 18, 39, 50) 20
- 19(18). Long slender ventral appendages arising at apex of penis lobes and usually extending
 to base of lobes (fig. 73) **Leptophlebia** Westwood
 Ventral appendages not as above, appendages usually short and stout (fig. 72).....
 **Paraleptophlebia** Lestage
- 20(18). Hooked claw of each pair with an opposing hook (similar to fig. 107); prominent
 projection present on 9th sternum of ♂ at inner basal angles of forceps (fig. 76)
 **Calliarceus** Eaton

- Hooked claw of the pair without an opposing hook (fig. 109, 124-125); 9th sternum of ♂ without projection as above (fig. 74-75) 21
- 21(20). Fork of vein MA symmetrical (fig. 53, 56) 22
- Fork of vein MA asymmetrical (fig. 13, 15) 23
- 22(21). Veins R_s and MP forked almost equidistant from base of wings to margin (fig. 56); 3 cubital intercalaries in fore wings (fig. 56) **Indialis***
- Vein MP forked much nearer to base of wings than vein R_s (fig. 51); 2 intercalaries in cubital area of fore wings (fig. 51) **Thraulius** Eaton
- 23(21). Inner margin of genital forceps of ♂ forming an extreme angular bend (fig. 75); ♀ with a well developed ovipositor or egg guide (fig. 322)

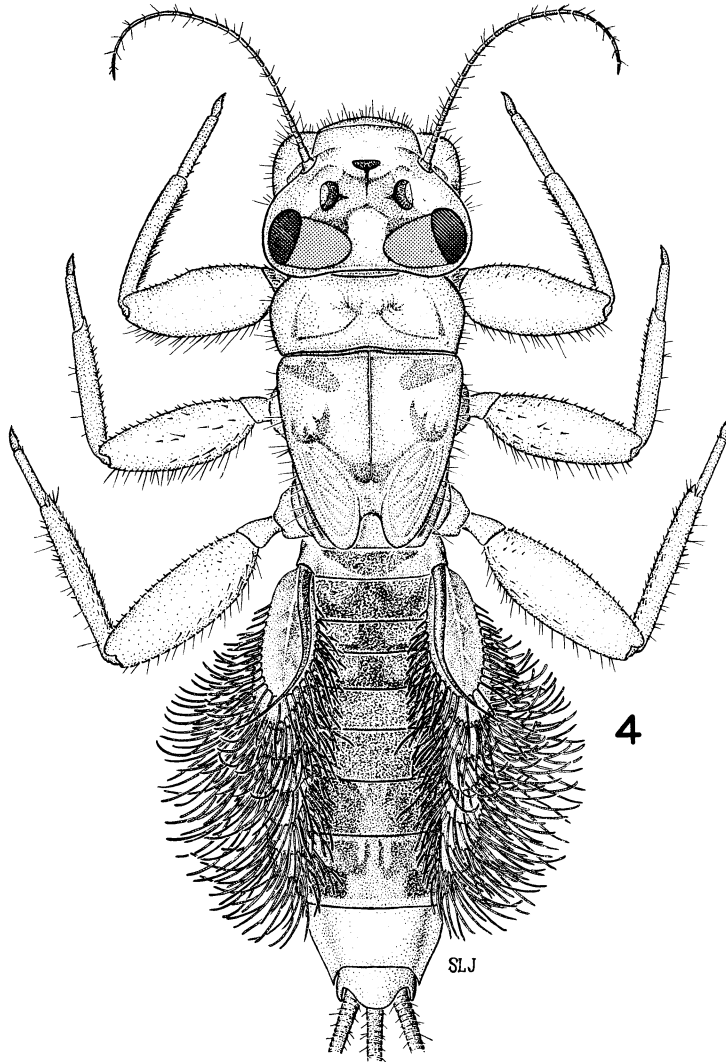


Fig. 4. *Thraulius torrentis* n. comb., dorsal view of ♂ nymph.

- **Habrophlebia** Eaton (in part)
 Inner margin of genital forceps of ♂ at base with a pointed or blunt projection (fig. 74); ♀ without a well developed ovipositor or egg guide
- **Habroleptooides** Schoenemund (in part)
- 24(17). Veins R_s and MP forked equidistant from base of wings to margin (fig. 35, 38, 59) 25
 Vein R_s forked nearer to base of wings than attachment of vein MP_2 to MP_1 (fig. 46, 48), or vein MP_2 independent of vein MP_1 (fig. 23, 61) 28
- 25(24). Fork of vein MA asymmetrical (fig. 35); penes divided, lobes divergent outwardly, a ventral spine on each lobe (fig. 87) **Castanophlebia** Barnard
 Fork of vein MA symmetrical (fig. 40, 43); penes divided, tubular, without appendages (fig. 90, 92)..... 26
- 26(25). Sclerotization on posterior margin of fore and hind wings set in from edge (fig. 43) **Choropterpides** Ulmer
 Sclerotization on posterior margin of fore and hind wings at edge (fig. 38, 40).....
 (**Choroterpes**) 27
- 27(26). Vein MA forked 1/2 of distance from base of wings to margin; fork of vein MP asymmetrical (fig. 40); base of costal projection of hind wings smoothly curved proximally and angular distally (fig. 41) **Choroterpes (Euthraulius)** Barnard
 Vein MA forked over 1/2 of distance from base of wings to margin; fork of vein MP symmetrical (fig. 38); base of costal projection of hind wings smoothly curved proximally and distally (fig. 39) **Choroterpes (Choroterpes s. s.)** Eaton
- 28(24). Costal projection of hind wings rounded (fig. 47, 60) 29
 Costal projection of hind wings acute (fig. 21, 63) 30
- 29(28). Two intercalaries in cubital area of fore wings (fig. 59); upper portion of eyes of ♂ on long stalk (fig. 326); ♀ with a well developed ovipositor or egg guide (fig. 324) **Megaglana***
 More than 2 intercalaries in cubital area of fore wings (fig. 46); upper portion of eyes of ♂ contiguous with lower portion; ♀ without a well developed ovipositor or egg guide
- 30(28). Outer margin of fore wings serrate (fig. 48); eyes of ♂ not divided into upper and lower portion, eyes composed entirely of small facets **Fullemimus** Demoulin
 Outer margin of fore wings entire (fig. 19, 23, 61); eyes of ♂ divided into upper portion with large facets and lower portion with smaller facets 31
- 31(30). Penes of ♂ tubular and slender, without appendages (fig. 100); 9th sternum of ♂ and ♀ entire (fig. 149) **Maheathraulius** Peters et al.
 Penes of ♂ not as above, either with a long ventral appendage on each lobe (fig. 77), or each lobe bent laterally and then ventrally, without appendages (fig. 79-80); 9th sternum of ♂ and ♀ deeply cleft (fig. 135) 32
- 32(31). Penes of ♂ with a long ventral appendage on each lobe (fig. 77); ♀ with a well developed ovipositor or egg guide (fig. 323) **Habrophlebiodes** Ulmer
 Penes of ♂ divided with each lobe bent laterally and then ventrally, without appendages (fig. 79-80); ♀ without an ovipositor or egg guide **Gilliesia***

Mature Nymphs

1. Abdominal terga extending around to venter of abdomen on segments 3-7 as in fig. 332 **Isca** Gillies, **Isca** s. s., **Minyphlebia** and **Tanycola**
 Abdominal terga extending to lateral sides of abdomen, all abdominal gills lateral or dorsal (fig. 2-6) 2

- 2 (1). Maxillary and labial palpi greatly elongated and extending beyond sides of head as in fig. 6 and 331..... 3
 Maxillary and labial palpi not greatly elongated and usually not extending beyond sides of head as in fig. 2-5 4
- 3 (2). Abdominal gills present on segments 1-6; apical denticle of claws greatly enlarged (fig. 284) **Nathanella** Demoulin
 Abdominal gills present on segments 2-7; denticles on claws about equal length (fig. 278) **Choroterpides** Ulmer
- 4 (2). Abdominal gill 1 operculiform (fig. 3); abdominal segments 1-5 shortened (fig. 3) **Adenophlebiodes** Ulmer
 Abdominal gill 1 not covering remaining gills (fig. 2, 4-5); all abdominal segments of about equal length (fig. 2, 4-5) 5
- 5 (4). Middle abdominal gills plate-like with fringed margins (fig. 311) **Thraulius** Eaton
 Middle abdominal gills plate-like, or long, slender and bifurcate (fig. 5, 292, 316), if plate-like not with fringed margins (fig. 2, 293, 296) 6
- 6 (5). Abdominal gill 1 similar to middle abdominal gills (fig. 5) 7
 Abdominal gill 1 differs in structure from middle abdominal gills (fig. 4) 18
- 7 (6). Claws long and tapered, no denticles present (fig. 269); double posterolateral spines on abdominal segments 8 and 9 (fig. 335) **Aprionyx** Barnard
 Claws hooked and narrow, denticles present (fig. 264, 272, 280); single posterolateral spines on abdominal segments 8 and 9 (fig. 2, 5) 8
- 8 (7). Middle abdominal gills plate-like and broad (fig. 291, 295, 297) 9
 Middle abdominal gills long, slender, and bifurcate (fig. 287, 301, 316) 12
- 9 (8). Middle abdominal gills terminated in 3 to 10 slender, filamentous processes (fig. 291); posterolateral spines on abdominal segments 8 and 9 **Habrophlebia** Eaton
 Upper portion of abdominal gills terminated in 1 slender, filamentous process (fig. 295-297); posterolateral spines on abdominal segments 3-9 or 4-9 10
- 10 (9). Apex of ventral portion of middle abdominal gills deeply cleft, a median, slender, filamentous process arising from cleft (fig. 297)..... **Kimminsula***
 Apex of ventral portion of middle abdominal gills tapered and terminated in 1 slender, filamentous process (fig. 295), or rounded (fig. 296) 11
- 11(10). Ventral portion of middle abdominal gills terminated in 1 slender, filamentous process (fig. 295); posterolateral spines on abdominal segments 3-9 **Adenophlebia** Eaton
 Ventral portion of middle abdominal gills rounded apically (fig. 296); posterolateral spines on abdominal segments 4-9 **Atalophlebioides** Phillips
- 12 (8). Labrum greatly expanded laterally beyond attachment with clypeus (fig. 260); outer margin of mandibles extremely angular as in fig. 236 **Hagenulodes** Ulmer
 Labrum not greatly expanded laterally beyond attachment with clypeus (fig. 240, 242, 256); outer margin of mandibles smoothly curved as in fig. 218, 220, 233 13
- 13(12). Head prognathous 14
 Head hypognathous 17
- 14(13). Posterolateral spines on abdominal segments 5-9; large tooth-like projection on inner margin of maxillae (fig. 189-190) 15
 Posterolateral spines on abdominal segments 8-9 or 9; no tooth-like projection on inner margin of maxillae (fig. 176, 184) 16
- 15(14). Apex of claws hooked, denticles on claws progressively larger apically (fig. 280); tracheae of abdominal gills branched (fig. 312) **Indialis***
 Apex of claws hooked and narrow, denticles on claws progressively larger apically, except apical denticle much larger (fig. 281); tracheae of abdominal gills unbranched (fig. 313) **Megaglena***
- 16(14). Apex of claws moderately hooked, narrow, a large denticle in middle of inner mar-

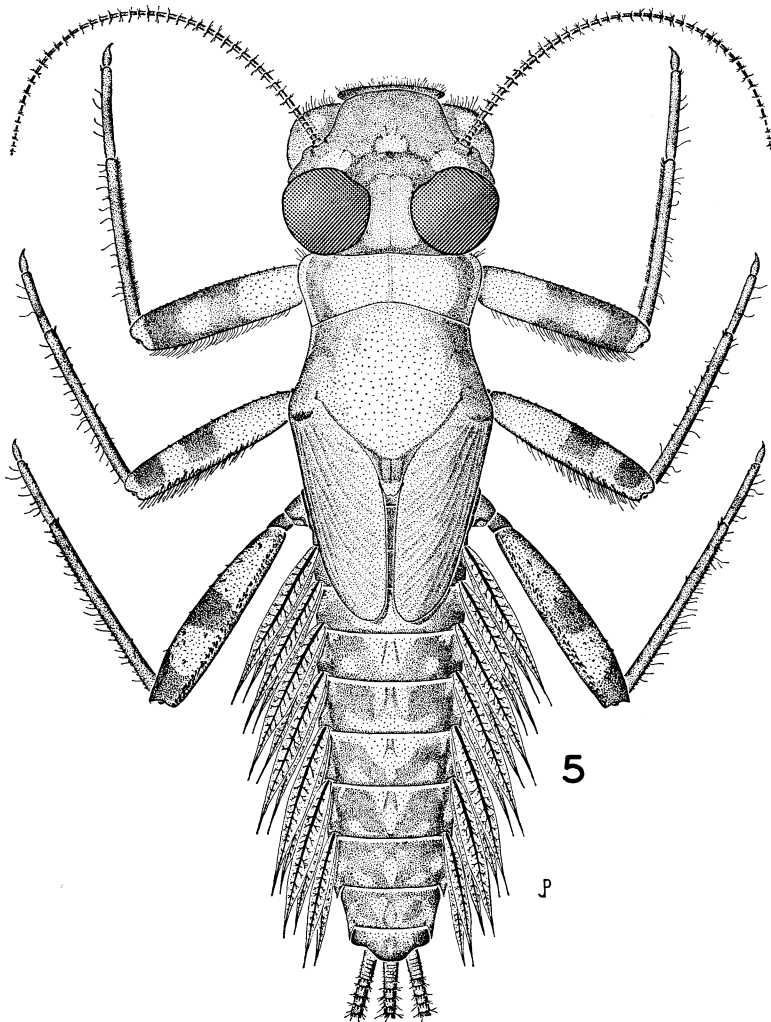


Fig. 5. *Indialis badia* n. sp., dorsal view of mature ♂ nymph.

- gin, basal to large denticle several anterior denticles, apical to large denticle 4 posterior denticles (fig. 275); small posterolateral spines on abdominal segments 8 and 9 **Castanophlebia** Barnard
- Apex of claws hooked, narrow, with a row of equal-sized denticles (fig. 266); small posterolateral spines on abdominal segment 9 **Habroleptoides** Schoenemund
- 17(13). Labrum deeply emarginated on anterior margin (fig. 244); occurring in Oriental Region **Habrophlebiodes** Ulmer
- Labrum shallowly emarginated on anterior margin (fig. 240); occurring in Palearctic Region **Paraleptophlebia** Lestage
- 18 (6). Head hypognathous; middle abdominal gills plate-like, each portion of gills terminated in 1 slender, filamentous process (fig. 289) **Leptophlebia** Westwood
- Head prognathous; middle abdominal gills long, slender, and bifurcate (fig. 315), or

- plate-like, each portion of gills with more than 1 process (fig. 304, 342) 19
- 19(18). Middle abdominal gills long, slender and bifurcate (fig. 315); posterolateral spines on abdominal segments 6-9, those on segments 8 and 9 larger **Maheathraulus** Peters et al.
- Middle gills plate-like (fig. 304, 342); posterolateral spines on abdominal segments 3, or 4, or 5-9 20
- 20(19). Posterolateral spines on abdominal segments 3-9; inner edge of spine on segment 9 curved and producing a 2nd blunt spine (fig. 344-345), or double posterolateral spines on segments 8 and 9; a large tooth-like process on inner anterolateral margin of maxillae (fig. 336) 22
- Posterolateral spines on abdominal segments 4 or 5-9; spine on segments 8 and 9 not as above; no large tooth-like process on maxillae as above (fig. 185-186)

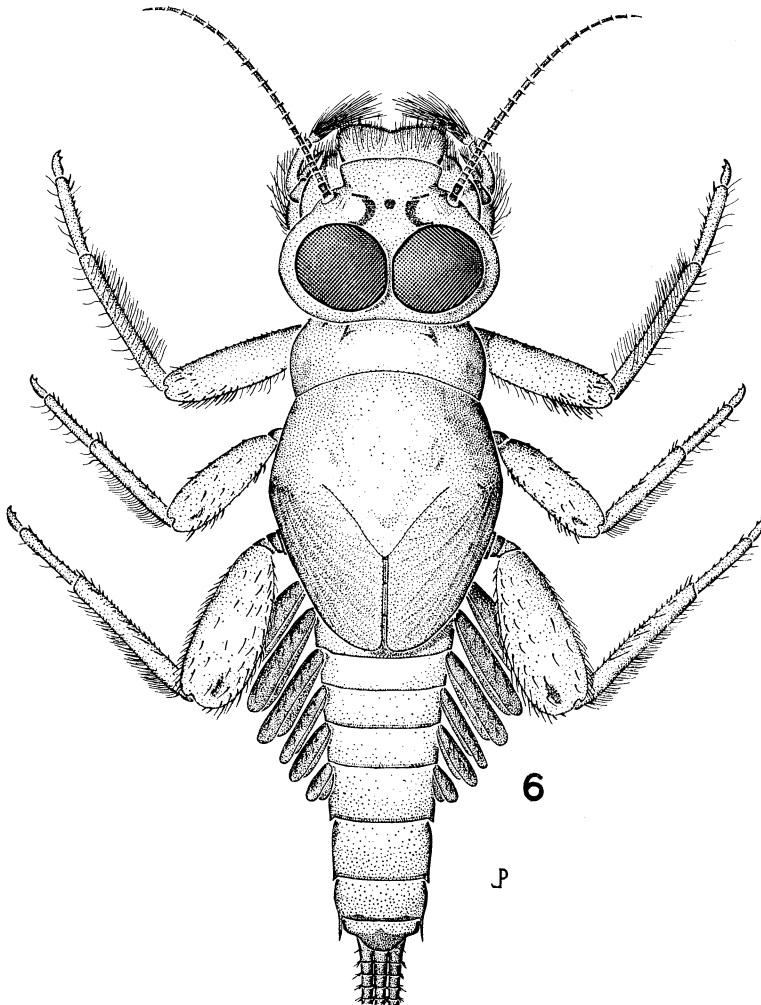


Fig. 6. *Nathanella* sp., dorsal view of mature ♂ nymph.

- (Choroterpes) 21
 21(20). Middle abdominal gills terminated in 3 slender, subequal processes (fig. 306)
 Choroterpes (Euthraulus) Barnard
 Middle abdominal gills terminated in 3 processes, with median projection longer than
 laterals (fig. 304) Choroterpes (Choroterpes s. s.) Eaton
 22(20). Inner edge of spine on abdominal segment 9 curved and producing a 2nd blunt spine
 (fig. 344-345) Cryptopenella Gillies
 Double posterolateral spines on segments 8 and 9 Fulletomimus? Demoulin

Genus **Paraleptophlebia** Lestage, 1917

Fig. 9-10, 72, 107, 131, 152, 174, 196, 218, 240, 264, 287.

Leptophlebia partim Eaton, 1871: 77; 1881: 193; 1884 (1883-88): 91.

Paraleptophlebia Lestage, 1917: 340; 1919: 112.—Ulmer, 1920: 116.—Lestage, 1921: 222; 1924b: 42.
 —Ulmer, 1929: 10.—Schoenemund, 1930: 49.—Ulmer, 1932b: 202.—Traver, 1935: 510.—Ujhelyi,
 1959: 38.—Grandi, 1960: 216

Type species: *P. cincta* (Retzius) (originally placed in *Ephemera*), by subsequent designation, Lestage (1924b).

Species occurring in the Eastern Hemisphere: *P. chocolata* Imanishi, 1937: 330; *P. cincta* (Retzius, 1783: 57) (*Ephemera*) (= *Ephemera nigra* Fourcroy, 1785: 352) (= *Ephemera inanis* Gmelin, 1790: 2629) (= *Ephemera albipennis* Fabricius, 1793: 70) (= *Ephemera hyalinata* Zetterstedt, 1840: 1044) (= *Cloe fuscata* Pictet, 1843-45: 251); *P. cothurnata* Tshernova, 1952: 267; *P. curvata* Ulmer, 1927: 10; *P. lacustris* Ikononov, 1962: 129; *P. longilobata* Tshernova, 1928: 113; *P. lunata* Tshernova, 1952: 269; *P. placita* (Bengtsson, 1917: 176) (*Leptophlebia*); *P. ruffoi* Biancheri, 1956: 191; *P. spinosa* Ueno, 1931: 57; *P. strandii* (Eaton, 1901: 253) (*Leptophlebia*); *P. submarginata* (Stephens, 1835: 58) (*Ephemera*) (= *Ephemera dispar* Stephens, 1835: 58) (= *Ephemera helvipes* Stephens, 1835: 59) (= *Potamanthus geerii* Pictet, 1853-55: 211) (= ? *Baetis reticulata* Burmeister, 1839: 801) (= *Cloeon culiciformis* Walker, 1853: 576) (= *Potamanthus castaneus* Pictet, 1843-45: 215); *P. tumida* Bengtsson, 1930: 8; *P. werneri* Ulmer, 1919: 25; *P. westoni* Imanishi, 1937: 332.

SPECIES EXAMINED. *P. chocolata*, ♂, ♀ imagos, nymph; *P. cincta*, ♂, ♀ imagos, nymph; *P. longilobata*, ♂ imago; *P. spinosa*, ♂ imago, nymph; *P. submarginata*, ♂, ♀ imagos; *P. werneri*, ♂ imago; *Paraleptophlebia* spp., numerous ♂, ♀ imagos, nymphs from N. India and Nepal.

DISTRIBUTION: Palearctic and Nearctic regions.

Imago. Length of ♂: body 4.5-10.0; fore wings 5.0-12.0 mm. Length of ♀: body 4.5-12.0; fore wings 5.0-12.0 mm. Eyes of ♂ meet on meson of head to separated on meson of head by a length equal to maximum width of a lateral ocellus, lower portion of eyes 1/3 to 1/2 length of upper portion; eyes of ♀ separated on meson of head by a length 6-7 × as great as maximum width of an eye. Wings (fig. 9-10): vein R_s of fore wings forked 1/5 of distance from base to margin; vein MA forked slightly more than 1/2 of distance from base to margin, fork asymmetrical; vein MP forked near base, fork asymmetrical (fig. 9); cubital area as in fig. 9; cross veins numerous. Costal margin of hind wings slightly concave near middle of wings (fig. 10); cross veins numerous. Legs: ratios of segments in ♂ fore legs, 0.79: 1.00 (3.2 mm): 0.08: 0.34: 0.34: 0.29: 0.13. Claws dissimilar, one apically hooked, with a small opposing hook, the

other obtuse, pad-like (fig. 107). ♂ genitalia (fig. 72): Segments 2 and 3 of forceps short, base of forceps broad; 9th sternum deeply cleft apically; penes fused except at apex and is divided except at base, a ventral appendage arising near apex of each penis lobe (fig. 72), a well developed lateral projection usually at or near apex of each penis lobe. Ninth sternum of ♀ deeply cleft apically (fig. 131). Terminal filament longer than cerci.

Mature nymph. Head hypognathous. Antennae 2-3 × as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 240; submedian and anterolateral areas of hair ventrally. Left mandible as in fig. 218. Lingua of hypopharynx rectangular (fig. 196); superlingua of hypopharynx as in fig. 196, with a row of hair along anterior margin. Segment 2 of maxillary palpi 3/4 to slightly shorter in length than segment 1; segment 3 a little longer to 1.25 × length of segment 2, triangular; hair on maxillae as in fig. 174. Labium as in fig. 152; segment 2 of palpi 1.75-2.0 × length of segment 1; segment 3 equal to 2 × length of segment 2, triangular; glossae ventral to paraglossae. Hair on anterolateral margins of prothorax only. Legs (fig. 264): apex of claws hooked and narrow, denticles on claws progressively larger apically. Gills on segments 1-7 alike, gills deeply forked, slender (fig. 287), tracheae branched or unbranched. Posterolateral spines on abdominal segments 8-9, those on segment 9 larger. Terminal filament longer than cerci.

History and discussion: *Paraleptophlebia* was established by Lestage (1917) and included *P. cincta* (Retzius), *P. submarginata* (Eaton), and 3 unnamed nymphs. Later Lestage (1924 b) designated *P. cincta* (Retzius) as the type species of *Paraleptophlebia*.

Bengtsson (1912) pointed out after examining the ♂ type that *Ephemera cincta* Retzius was not a leptophlebiid but was *Baetis*, possibly *B. incurvus* Bengtsson. Lestage (1924b) did not accept Bengtsson's synonymy. Either Bengtsson is incorrect or Lestage (1917) misidentified *Ephemera cincta* Retzius. If Lestage (1917) did misidentify the species, the species before him could possibly have been *Leptophlebisa cincta* Eaton 1884 (1883-88) which is indeed *Paraleptophlebia* (but not clearly *cincta* Retzius or *cincta* of Lestage). Until Bengtsson's synonymy and the possibility of Lestage's misidentification of *Ephemera cincta* Retzius are both verified, we have retained *P. cincta* (Retzius) as type-species of *Paraleptophlebia*. For the purpose of stability it may be necessary to get an unequivocal type-species designation, even if arbitrary, for the genus *Paraleptophlebia*.

Only the Palearctic representatives of *Paraleptophlebia* are considered in this revision. The North American species of *Paraleptophlebia* will require additional study as there are some specialized groups within the North American *Paraleptophlebia*.

Biology: The biology of the Palearctic species of *Paraleptophlebia* is given by various authors. Summaries are available in Grandi (1960) and Macan (1961). The biology of various Nearctic species of *Paraleptophlebia* is given in Berner (1950), Burks (1953), and Leonard & Leonard (1962).

Genus *Leptophlebia* Westwood, 1840

Fig. 11-12, 73, 108, 132, 153, 175, 197, 219, 241, 265, 288-289.

Leptophlebia Westwood, 1840: 31.—Lestage, 1917: 119; 1921: 220.—Ulmer, 1929: 9.—Schoenemund, 1930: 51.—Ulmer, 1932b: 202.—Traver, 1935: 507.—Ujhelyi, 1959: 38.—Grandi, 1960: 213.

Leptophlebia partim Eaton, 1871: 77; 1881: 193; 1884 (1883-88): 91.—Bengtsson, 1917: 176.—Lestage, 1917: 327.—Ulmer, 1920: 115.

Blasturus partim Eaton, 1881: 193; 1884 (1883-88): 100.—Ulmer, 1920: 116; 1932b: 202.—Traver, 1935: 531.

Blasturus=*Leptophlebia* Banks, 1900: 245.—Ide, 1935: 124.

Euphyurus Bengtsson, 1909: 4; 1917: 177.

Euphyurus=*Leptophlebia* Lestage, 1917: 327.

Subgenera *Leptophlebia* ss. and *Blasturus* Edmunds & Traver 1954: 238.—Edmunds, Allen & Peters, 1963: 15.

Type-species: *L. marginata* (Linn.) (originally placed in *Ephemera*), monobasic.

Species included in Eastern Hemisphere. *L. marginata* (Linn., 1767: 906) (*Ephemera*) (= *Ephemera viridescens* Fourcroy, 1785: 351) (= *Ephemera procellaria* Schwarz, 1793-1830: 1) (= *Ephemera stigma* Stephens, 1835: 56) (= *Ephemera talcosa* Stephens, 1835: 57); *L. vespertina* (Linn., 1758: 547) (*Ephemera*) [= *L. meyeri* Eaton, 1884 (1883-88): 95] (= *Euphyurus albitarsis* Bengtsson, 1909: 4); *L. wui* Ulmer, 1936: 206.

SPECIES EXAMINED. *L. marginata*, ♂, ♀ imagos, nymph; *L. vespertina*, ♂, ♀ imagos, nymph; *L. wui*, ♂, ♀ imagos.

DISTRIBUTION: Palearctic and Nearctic regions.

Imago. Length of ♂: body 6.0-9.4; fore wings 6.2-9.5 mm. Length of ♀. Body 6.0-9.0; fore wings 6.3-9.6 mm. Eyes of ♂ meet on meson of head to separated on meson of head by a length equal to maximum width of a lateral ocellus, lower portion of eyes 1/3 to more than 1/2 length of upper portion; ♀ eyes separated on meson of head by a length 6 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked 1/5-1/4 of distance from base to margin; vein MA forked a little more than 1/2 of distance from base to margin, fork asymmetrical; vein MP forked near base, fork asymmetrical (fig. 11); cubital area as in fig. 11; cross veins numerous. Costal margin of hind wings slightly concave near middle of wings (fig. 12); cross veins numerous. Legs: ratios of segments in ♂ fore legs, 1.06: 1.00 (1.9 mm): 0.06: 0.21: 0.21; 0.16: 0.13. Claws dissimilar, 1 apically hooked, with a small opposing hook, the other obtuse, pad-like (fig. 108). ♂ genitalia (fig. 73): segments 2 and 3 of forceps short, segment 3 a little shorter than segment 2, base of forceps broad; 9th sternum deeply cleft apically; penes divided, except for base, a ventral appendage arising from apex of each penis lobe (fig. 73). Ninth sternum of ♀ deeply cleft apically (fig. 132). Terminal filament longer than cerci.

Mature nymph. Head hypognathous. Antennae 2-2.5 × as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 241; submedian areas of hair ventrally. Left mandible as in fig. 219. Lingua of hypopharynx rectangular shaped (fig. 197); superlingua of hypopharynx as in fig. 197, with a row of hair along anterior margin. Segment 2 of maxillary palpi equal in length to segment 1; segment 3 of palpi slightly shorter in length than segment 2, triangular; hair on maxillae as in fig. 175. Labium as in fig. 153; segment 2 of palpi 3/4 length of segment 1; segment 3 of palpi equal in length to segment 2, triangular; glossae ventral to paraglossae. Hair on anterolateral margins of prothorax only. Legs (fig. 265): apex of claws hooked and narrow, denticles on claws progressively larger apically. Gills on segments 1-7; gills on segment 1 deeply forked, slender (fig. 288); gills on segments 2-7 plate-like, each lamella terminated in 1 slender, filamentous process (fig. 289), gills smaller posteriorly. Posterolateral spines on abdominal segments 8-9, those on segment 9 larger. Terminal filament longer than cerci.

History and discussion: Westwood (1840) first proposed the name *Leptophlebia* for *Ephemera marginata*. Eaton (1871) divided *Leptophlebia* into 5 series. Later Eaton (1881) restricted the genus to the "series 3" of his 1871 paper. Bengtsson (1909) described the

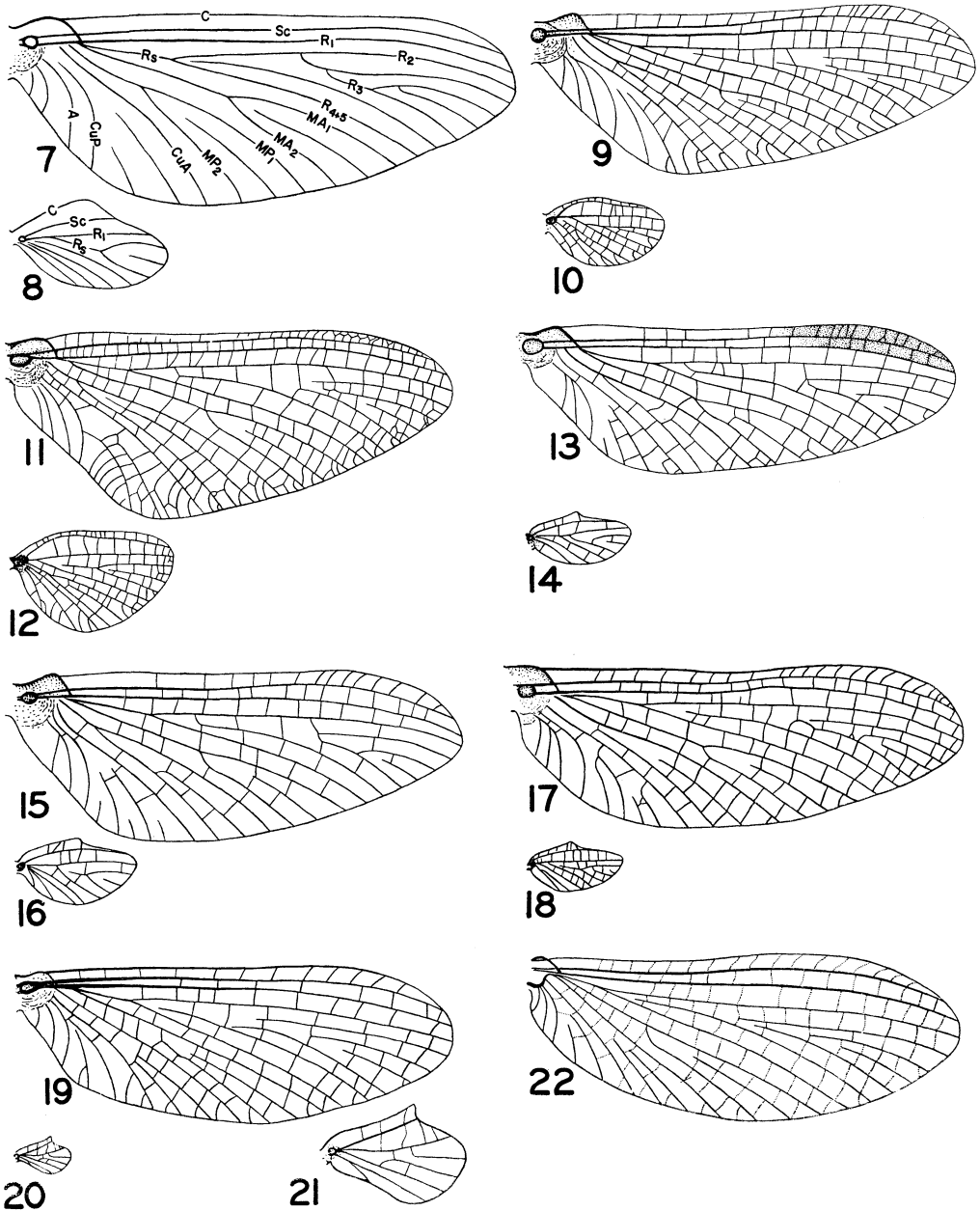


Fig. 7-22. Adult fore and hind wings: Fig. 7-8, schematic wings, showing abbreviations of venational terminology used in text: 7, fore wing; 8, hind wing. Fig. 9-10, *Paraleptophlebia cincta*: 9, fore wing; 10, hind wing. Fig. 11-12, *Leptophlebia marginata*: 11, fore wing; 12, hind wing. Fig. 13-14, *Habroleptoides modesta*: 13, fore wing; 14, hind wing. Fig. 15-16, *Habrophlebia fusca*: 15, fore wing; 16, hind wing. Fig. 17-18, *Calliarcys humilis*: 17, fore wing; 18, hind wing. Fig. 19-21, *Habrophlebiodes gilliesi*: 19, fore wing; 20, hind wing; 21, hind wing enlarged. Fig. 22, *Dipterophlebiodes sarawacensis*, fore wing (after Demoulin, 1954).

genus *Euphyurus* which Lestage (1917) placed as a synonym of *Leptophlebia*.

Eaton (1881) established the genus *Blasturus* for *Leptophlebia* "series 4" which he proposed in 1871 and placed *L. cupida* as the type-species. "Series 4" of Eaton (1881) was composed of 2 North American species. Banks (1900) and Ide (1935) have both considered *Blasturus* as a synonym of *Leptophlebia*. Banks considered the difference between the length of the terminal filament of the 2 genera of no generic importance. Ide considered the nymphs of *L. johnsoni* an intermediate between *Leptophlebia* and *Blasturus*. Berner (1950) retained the genus *Blasturus* while other North American workers consider *Blasturus* as a weak subgenus of *Leptophlebia* (Edmunds & Traver 1954; Edmunds, Allen & Peters 1963).

Only the Palearctic representatives of *Leptophlebia* are considered in this revision. The generic, subgeneric rank or synonymy of *Leptophlebia* and *Blasturus* in North America will be reconsidered when material of the various species is studied. The 1 species of *Leptophlebia* s. s. occurring in North America, *L. johnsoni*, is intermediate between *Blasturus* in North America and *Leptophlebia* in the Palearctic region.

Biology: The biology of the Palearctic species of *Leptophlebia* is given by various authors. Summaries are available in Grandi (1960) and Macan (1961). The biology of various Nearctic species is given in Ide (1935), Berner (1950), Burks (1953), & Leonard & Leonard (1962).

Genus *Habroleptoides* Schoenemund, 1929

Fig. 13-14, 74, 109, 133, 154, 176, 198, 220, 242, 266, 290.

Habrophlebia partim Eaton, 1884 (1883-88): 114.—Grandi, 1960: 224.

Habroleptoides Schoenemund, 1929: 222.—Ulmer, 1929: 11.—Schoenemund, 1930: 53.—Ulmer, 1929a: 212; 1932b: 203.—Ujheyli, 1959: 43.

Subgenus *Habroleptoides* Biancheri, 1953: 54.

Habroleptoides=*Habrophlebia* Grandi, 1955: 1.

Type-species: *H. modesta* (Hagen) (originally placed in *Potamanthus*), monobasic.

Species included: *H. auberti* Biancheri, 1954: 161; *H. budtzi* (Esben-Petersen, 1912: 349) (*Thraululus*); *H. carpathica* Bogoescu and Craşnaru, 1930: 7; *H. caucasica* Tshernova, 1931: 216; *H. modesta* (Hagen, 1864: 39) (*Potamanthus*); *H. pauliana* Grandi, 1957: 233; *H. umbratilis* [Eaton, 1884, (1883-88): 119] (*Habrophlebia*).

SPECIES EXAMINED. *H. modesta*, ♂ and ♀ imagos, nymph,

DISTRIBUTION: Europe, SW Russia.

Imago. Length of ♂: body 5.0-12.0; fore wings 5.2-12.4 mm. Length of ♀: body 5.0-12.0; fore wings 5.3-12.2 mm. Eyes of ♂ separated on meson of head by a length 2 × maximum width of median ocellus, lower portion of eyes 2/3 to slightly shorter than maximum length of upper portion; ♀ eyes separated on meson of head by a length 4 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked less than 1/4 of distance from base to margin; vein MA forked 1/2 of distance from base to margin, fork asymmetrical; vein MP forked near base of wings, fork asymmetrical; cubital area as in fig. 13; cross veins few. Costal projection of hind wings well developed and acute, apex located 1/2 distance from base (fig. 14); cross veins few. Legs: ratios of segments in ♂ fore legs, 0.73: 1.00 (3.00

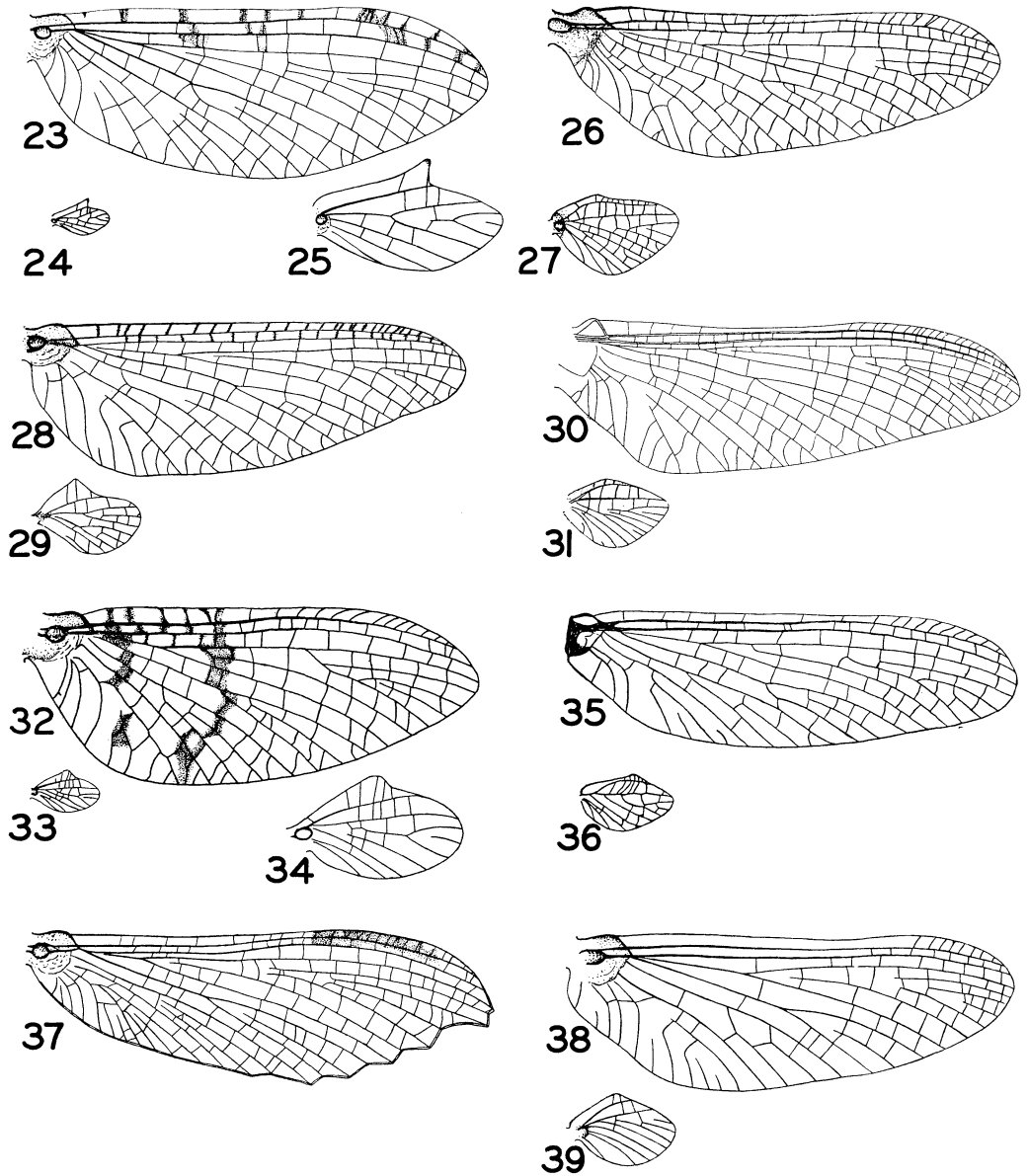


Fig. 23-39. Adult fore and hind wings. Fig. 23-25, *Gilliesia hindustanica* n. comb.: 23, fore wing; 24, hind wing; 25, hind wing enlarged. Fig. 26-27, *Aprionyx intermedius*: 26, fore wing; 27, hind wing. Fig. 28-29, *Adenophlebia auriculata*: 28, fore wing; 29, hind wing. Fig. 30-31, *Kimminsula annulata* n. comb.: 30, fore wing [after Eaton, 1884 (1883-88)]; 31, hind wing [after Eaton, 1884 (1883-88)]. Fig. 32-34, *Adenophlebiodes ornata*: 32, fore wing; 33, hind wing; 34, hind wing enlarged. Fig. 35-36, *Castanophlebia calida*: 35, fore wing (after Barnard, 1932); 36, hind wing (after Barnard, 1932). Fig. 37, *Fulleia dentata*, fore wing. Fig. 38-39, *Choroterpes (Choroterpes) nigrescens*: 38, fore wing; 39, hind wing.

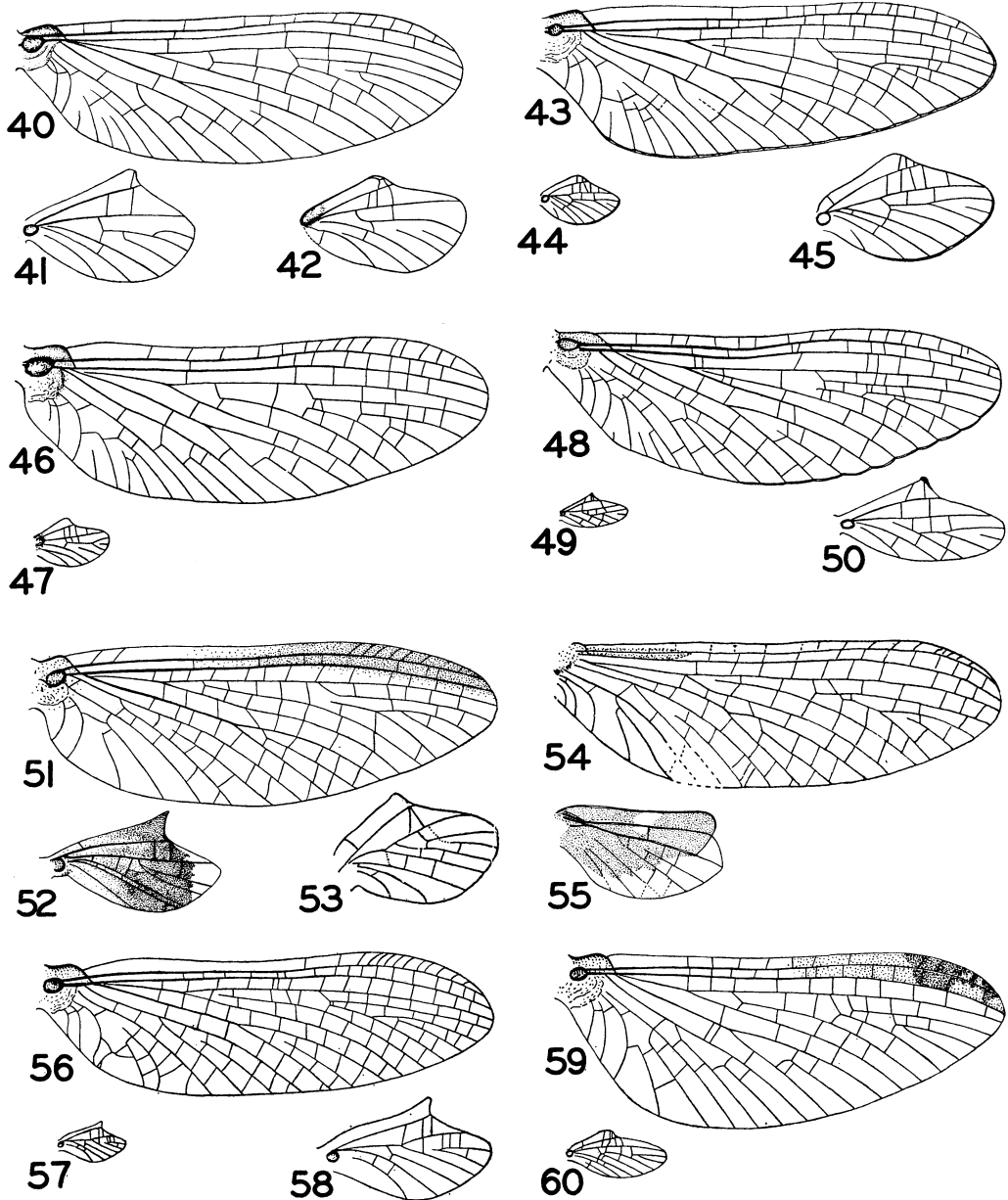


Fig. 40-60. Adult fore and hind wings. Fig. 40-41, *Choroterpes (Euthraulus) elegans*: 40, fore wing; 41, hind wing. Fig. 42, *Choroterpes (Euthraulus) signata* n. comb., hind wing. Fig. 43-45, *Choroterpides* sp.: 43, fore wing; 44, hind wing; 45, hind wing enlarged. Fig. 46-47, *Cryptopenella facialis*: 46, fore wing; 47, hind wing. Fig. 48-50, *Fullemimus marlieri*: 48, fore wing; 49, hind wing; 50, hind wing enlarged. Fig. 51-52, *Thraulius torrentis* n. comb.: 51, fore wing; 52, hind wing. Fig. 53, *Thraulius bellus*, hind wing (after Edmunds, 1950). Fig. 54-55, *Simothraulius seminiger*: 54, fore wing (after Ulmer, 1939); 55, hind wing (after Ulmer, 1939). Fig. 56-58, *Indialis badia* n. sp.: 56, fore wing; 57, hind wing; 58, hind wing enlarged. Fig. 59-60, *Megaglena brincki* n. sp.: 59, fore wing; 60, hind wing.

mm): 0.03: 0.37: 0.37: 0.27: 0.10. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 109), or claws similar, both claws obtuse, pad-like. ♂ genitalia: segments 2 and 3 of forceps long (fig. 74), base of forceps broad, its inner margin at base with a pointed or blunt projection (fig. 74); 9th sternum deeply cleft apically; basal 1/2 of penes fused and tubular, a ventral appendage arising from apex of each penis lobe (fig. 74). Ninth sternum of ♀ deeply cleft apically (fig. 133). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae $2 \times$ maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 242; submedian and anteromarginal areas of hair ventrally. Left mandible as in fig. 220. Lingua of hypopharynx cordate (fig. 198); superlingua of hypopharynx as in fig. 198, with a row of hair along anterior margin. Segment 2 of maxillary palpi 3/4 to equal in length to segment 1; segment 3 of palpi 3/4 to equal in length to segment 2, triangular; hair on maxillae as in fig. 176. Labium as in fig. 154; segment 2 of palpi 3/4 length of segment 1; segment 3 of palpi equal in length to segment 2, triangular; glossae ventral to paraglossae. Fine hair present or absent on dorsum of thorax and abdomen. Legs (fig. 266): apex of claws hooked and narrow, with a row of equal-sized denticles. Gills on segments 1-7 alike; gills 1-7 deeply forked, tracheae unbranched (fig. 290). Small posterolateral spines on abdominal segments 8 and 9, those on segment 9 larger. Terminal filament slightly longer than cerci.

History and discussion: Schoenemund (1929) established the genus *Habroleptoides* for the single species *H. modesta*. Biancheri (1953) considered *Habroleptoides* a subgenus of *Habrophlebia*, while Grandi (1955) considered *Habroleptoides* synonymous with *Habrophlebia*. We consider *Habroleptoides* a separate genus. The adults of *Habroleptoides* can be distinguished from those of *Habrophlebia* by the inner margin of the ♂ genital forceps with a pointed or blunt projection (fig. 74), and the ♀ without a well developed ovipositor or egg guide. The nymphs of *Habroleptoides* can be distinguished from those of *Habrophlebia* by the abdominal gills 1-7 being deeply forked with tracheae unbranched (fig. 290), and the small posterolateral spines on abdominal segments 8-9, those on segment 9 larger.

Biology: The biology of several species of *Habroleptoides* is summarized in Pleskot (1953) and Grandi (1960).

Genus **Habrophlebia** Eaton, 1881

Fig. 15-16, 75, 110-111, 134, 155, 177, 199, 221, 243, 267, 291, 322.

Habrophlebia partim, Eaton, 1881: 195; 1884 (1883-88): 114.—Ulmer, 1920: Lestage, 1921: 225.—Grandi, 1960: 224.

Habrophlebia Ulmer, 1929: 11.—Schoenemund, 1930: 53.—Ulmer, 1932b: 203.—Traver, 1935: 549.—Ujhelyi, 1959: 42.

Type-species: *H. fusca* (Curtis) (originally placed in *Ephemera*), by original designation.

Species included in Eastern Hemisphere. *H. consiglioi* Biancheri, 1959: 35; *H. fusca* (Curtis, 1834: 120) (*Ephemera*) (= *Ephemera minor* Stephens, 1835: 60) (= *Baetis cingulata* Stephens, 1835: 67) (= *Potamanthus brunneus* Pictet, 1843-45: 217); *H. konjarensis* Ikonomov, 1963: 175; *H. lauta* Eaton, 1884 (1883-88): 120 (= *Potamanthus cinctus* Pictet, 1843-45: 219); *H. nervulosa* Eaton, 1884 (1883-88): 117.

SPECIES EXAMINED. *H. fusca*, ♂ and ♀ imagos, nymph.

DISTRIBUTION: Europe, E. North America.

Imago. Length of ♂: body 5.0–8.0; fore wings 5.4–8.5 mm. Length of ♀: body 6.0–7.0; fore wings 6.0–7.0 mm. Eyes of ♂ separated on meson of head by a length equal to maximum width of median ocellus, lower portion of eyes 2/3 to slightly shorter than maximum length of upper portion; ♀ eyes separated on meson of head by a length 4 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked less than 1/4 of distance from base to margin; vein MA forked 1/2 of distance from base to margin, fork asymmetrical; vein MP forked near base of wings, fork asymmetrical; cubital area as in fig. 15; cross veins few. Costal projection of hind wings well developed and acute, apex located 1/2 distance from base (fig. 16); cross veins few. Legs: ratios of segments in ♂ fore legs, 0.66: 1.00 (2.70 mm): 0.04: 0.75: 0.33: 0.29: 0.15. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 110), or claws similar, both claws obtuse, pad-like (fig. 111). ♂ genitalia: segments 2 and 3 of forceps long (fig. 75), base of forceps broad, its inner margin forming an extreme angular bend (fig. 75); 9th sternum deeply cleft apically; basal 1/2 of penes fused and tubular, a ventral appendage arising from apex of each penis lobe (fig. 75). ♀ with a well developed ovipositor or egg guide extending to middle of abdominal segment 8 (fig. 322). Ninth sternum of ♀ deeply cleft apically (fig. 134). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae 2 × maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 243; submedian and anterior areas of hair ventrally. Left mandible as in fig. 221. Lingua of hypopharynx cordate (fig. 199); superlingua of hypopharynx as in fig. 199, with a row of hair along anterior margin. Segment 2 of maxillary palpi 3/4 to equal in length to segment 1; segment 3 of palpi 3/4 to equal in length to segment 2, triangular; hair on maxillae as in fig. 177. Labium as in fig. 155; segment 2 of palpi 3/4 length of segment 1; segment 3 of palpi equal in length to segment 2, triangular; glossae ventral to paraglossae. Fine hair present or absent on dorsum of thorax and abdomen. Legs (fig. 267): apex of claws hooked, narrow, with a row of subequal sized denticles. Gills on segments 1–7 alike; gills plate-like, each portion terminated in 3 to 10 filamentous processes, tracheae branched (fig. 291). Small posterolateral spines on abdominal segment 9. Terminal filament slightly longer than cerci.

History and discussion: Eaton (1881) established the genus *Habrophlebia*. As discussed under *Habroleptoides*, we have included this as a genus separate from *Habroleptoides*. The adults of *Habrophlebia* can be distinguished from those of *Habroleptoides* by the inner margin of the genital forceps of the ♂ forming an extreme angular bend (fig. 75), and the well developed ♀ ovipositor or egg guide (fig. 322). The nymphs of *Habrophlebia* can be distinguished from those of *Habroleptoides* by the abdominal gills 1–7 being plate-like, with each gill portion terminating in 3 to 10 filamentous processes (fig. 291), and the small posterolateral spines on abdominal segment 9.

The Eastern North American representatives of *Habrophlebia* are separable from the Eastern Hemisphere members of *Habrophlebia* in the adult by the small size (length of ♂ fore wings 4.5–5.0 mm), the absence of an acute angulation on the inner margin of the ♂ genital forceps base, and the absence of a ♀ ovipositor or egg guide, but nymphs of the American *Habrophlebia* appear inseparable from those of *Habrophlebia* in the Eastern Hemisphere.

Biology: The biology of several species of *Habrophlebia* is summarized in Pleskot (1953), Landa (1957), and Grandi (1960).

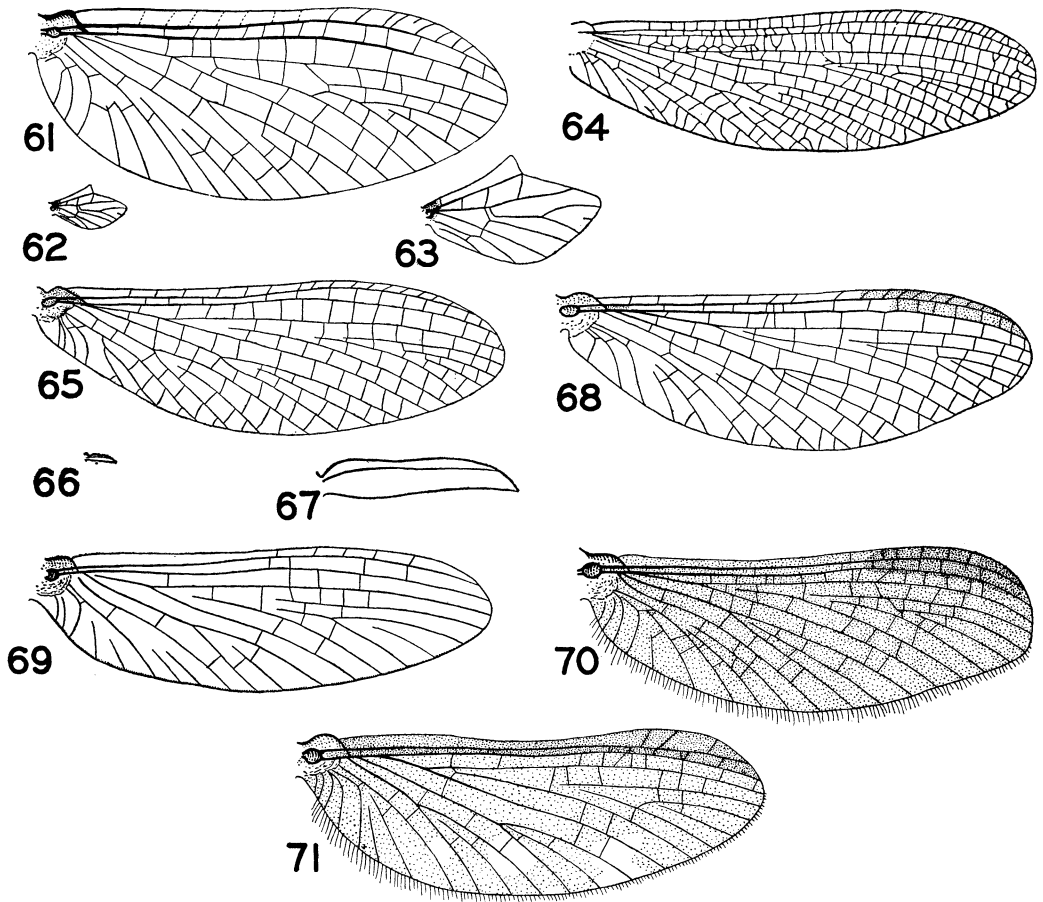


Fig. 61-71. Adult fore and hind wings. Fig. 61-63, *Maheathraulus scotti*: 61, fore wing; 62, hind wing; 63, hind wing enlarged. Fig. 64, *Hagenulodes braueri*, fore wing (after Ulmer, 1919). Fig. 65-67, *Nesophlebia adusta*: 65, fore wing; 66, hind wing; 67, hind wing enlarged. Fig. 68, *Nathanella indica*, fore wing. Fig. 69, *Isca (Minyphlebia) janiceae* n. sp., fore wing. 70, *Isca (Tanycola) serendiba* n. sp., fore wing. Fig. 71, *Isca (Isca s. s.) purpurea*, fore wing.

Genus **Calliarcys** Eaton, 1881

Fig. 17-18, 76.

Calliarcys Eaton, 1881: 21; 1884 (1883-88): 121. — Lestage, 1917: 350. — Kimmins, 1960: 296.

Type-species: *C. humilis* Eaton, by original designation.

Species included: *C. humilis* Eaton, 1881: 21.

SPECIES EXAMINED. *C. humilis*, male imago lectotype and paratype.

DISTRIBUTION: Portugal.

Imago. Length of ♂: body 7.0-9.0; fore wings 7.0-8.5 mm. Length of ♀: body 7.0-9.0; fore wings 9.0 mm. Eyes of ♂ separated on meson of head by a length as great as maximum width of median ocellus. Wings: vein R_s of fore wings forked less than 1/4 of distance from base to margin; vein MA forked a little more than 1/2 of distance from base to margin, fork asymmetrical; vein MP_2 attached at base to vein MP_1 by a cross vein less than 1/5 of distance from base to margin (fig. 17); cubital area as in fig. 17; cross veins numerous. Costal projection of hind wings well developed and acute, apex of projection located less than 1/2 distance from base (fig. 18); cross veins numerous. Legs: ratios of segments in ♂ fore legs, 0.86: 1.00: 0.03: 0.41: 0.41: 0.41: 0.14. Claws dissimilar, 1 with an apical hook and with an opposing hook, other obtuse, pad-like. ♂ genitalia (fig. 76): Segments 2 and 3 of forceps long; 9th sternum deeply cleft, paired submedian projections extending posteriorly; penes tubular, divided, except at base, apex of each penis lobe bent inwardly. Ninth sternum of ♀ deeply cleft apically. Terminal filament slightly longer than cerci.

Mature nymph. Unknown.

History and discussion: Eaton (1881) established the genus *Calliarcys* for a peculiar species from Portugal. Eaton 1884 (1883-88) redescribed the species, and Kimmins (1960) redrew figures of the ♂ genitalia from the lectotype. The genus is known only from the type series.

Biology: Eaton 1884 (1883-88) gives biological notes on *C. humilis*.

Genus *Habrophlebiodes* Ulmer, 1919

Fig. 19-21, 77, 112, 135, 156, 178, 200, 222, 244, 268, 292, 323.

Habrophlebioides Ulmer, 1919: 39; 1920: 118; 1932b: 204.—Traver, 1935: 546.—Ulmer, 1939: 501; 1940: 623.

Type-species: *H. americana* (Banks) (originally placed in *Habrophlebia*), by original designation.

Species occurring in the Eastern Hemisphere: *H. gilliesi* Peters, 1963: 41; *H. prominens* Ulmer, 1939: 502.

SPECIES EXAMINED. *H. gilliesi*, ♂ and ♀ imagos; *H. prominens*, ♂ and ♀ imagos; *Habrophlebiodes* spp., numerous nymphs from Hong Kong.

DISTRIBUTION: Oriental Region and E. North America.

Imago. Length of ♂: body 5.0-8.0; fore wings 4.9-8.0 mm. Length of ♀: body 4.4-6.5; fore wings 5.2-7.6 mm. Eyes of ♂ separated on meson of head by a narrow space, lower portion of eyes slightly shorter in length than upper portion; eyes of ♀ separated on meson of head by a length 3 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked near base; vein MA forked less than 1/2 of distance from base to margin, fork asymmetrical; vein MP_2 attached at base to vein MP_1 by a cross vein more than 1/2 distance from base to margin (fig. 19); cubital area as in fig. 19; cross veins few. Costal projection of hind wings well developed and apex blunt, apex of projection located 1/2 distance from base of wings (fig. 21); cross veins few. Legs: ratios of segments in ♂ fore legs, 0.52: 1.00 (2.20 mm): 0.05: 0.37: 0.28: 0.23: 0.05. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 112). ♂ genitalia (fig. 77): segments 2 and 3 of forceps short, base of forceps broad, its inner

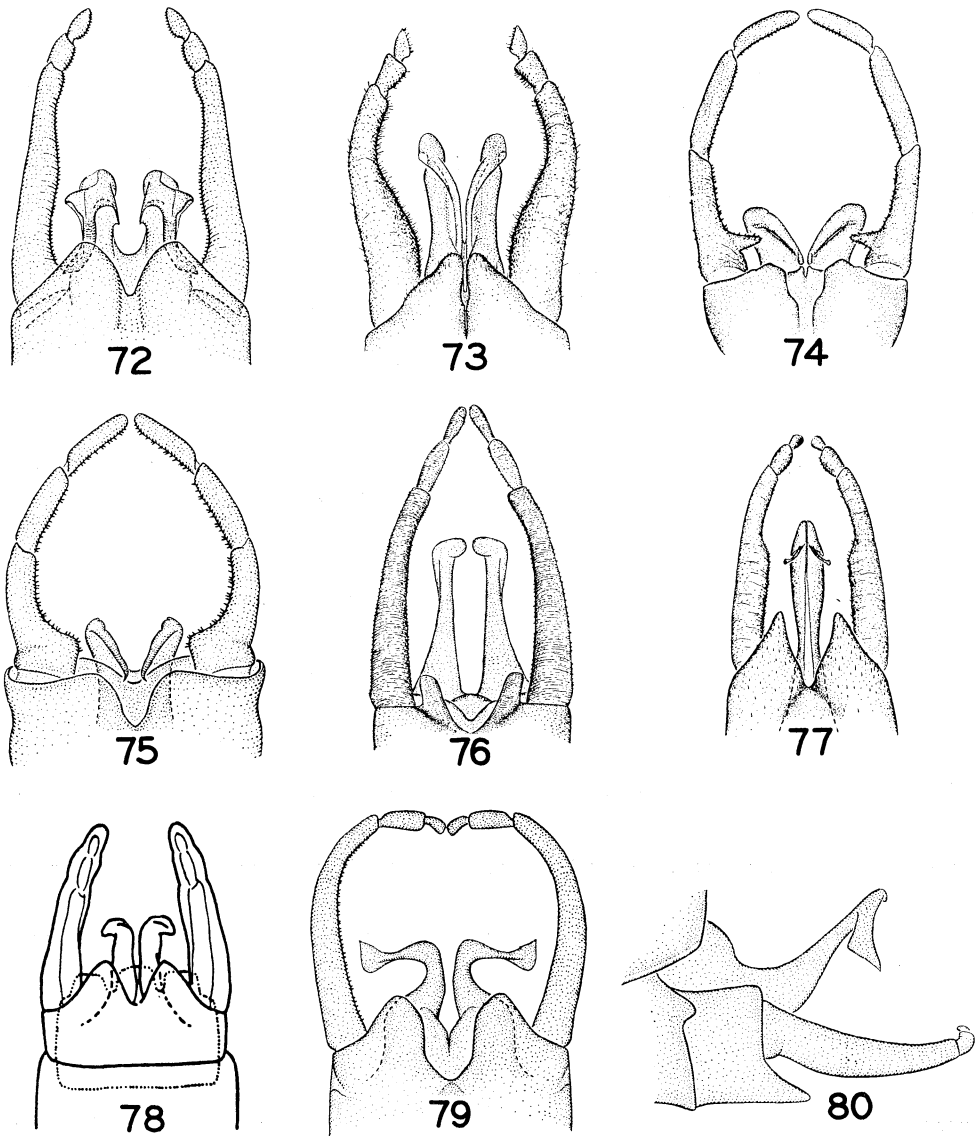


Fig. 72-80. Genitalia of ♂ imago. Fig. 72, *Paraleptophlebia cincta*, ventral view; 73, *Leptophlebia marginata*, ventral view; 74, *Habroleptoides modesta*, ventral view; 75, *Habrophlebia fusca*, ventral view; 76, *Calliarcys humilis*, ventral view; 77, *Habrophlebiodes gilliesi*, ventral view; 78, *Dipterophlebiodes sarawacensis*, ventral view (after Demoulin, 1954); 79, *Gilliesia hindustanica* n. comb., ventral view; 80, *Gilliesia hindustanica* n. comb., lateral view.

margin forming an extreme angular bend; 9th sternum deeply cleft apically; penes fused except at apical tip, a long ventral appendage on each penis lobe. ♀ with a well developed ovipositor or egg guide extending to middle of abdominal segment 8 to posterior margin of segment 9 (fig. 323). Ninth sternum of ♀ deeply cleft apically (fig. 135). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae $1.5 \times$ as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 244; submedian and anterolateral areas of hair ventrally. Left mandible as in fig. 222. Lingua of hypopharynx rectangular or cordate (fig. 200); superlingua of hypopharynx as in fig. 200, with a row of hair along anterior margin. Segment 2 of maxillary palpi a little more than $1/2$ to slightly more than $3/4$ as long as segment 1; segment 3 equal to a little longer than $2 \times$ length of segment 2, triangular; hair on maxillae as in fig. 178. Labium as in fig. 156; segment 2 of palpi $3/4$ to slightly more than $2 \times$ length of segment 1; segment 3 a little shorter than length of segment 2, triangular; glossae ventral to paraglossae. Legs (fig. 268): apex of claws hooked and narrow, denticles on claws progressively larger apically. Gills (fig. 292): gills on segments 1-7 alike; gills long, slender and deeply forked. Posterolateral spines on abdominal segments 8 and 9, those on segment 9 larger. Terminal filament longer than cerci.

History and discussion: Ulmer (1919) established *Habrophlebiodes* for the North American species *H. americana*. Since that time 3 other eastern North American species of *Habrophlebiodes* have been described, although *H. betteni* is now considered to be a synonym of *H. americana*. Ulmer (1939) described the first Oriental species, *H. prominens*, from Java and Sumatra. Peters (1963) described *H. gilliesi* from China. The Oriental species appear to be congeneric with those of eastern North America.

Biology: Biological notes concerning *H. prominens* and *H. gilliesi* appear in Ulmer (1940) and Peters (1963) respectively. The biology of the North American species *H. brunneipennis* is given in Berner (1950).

Genus *Dipterophlebiodes* Demoulin, 1954

Fig. 22, 78.

Dipterophlebiodes Demoulin, 1954: 129.

Type-species: *D. sarawacensis* Demoulin, by original designation.

Species included: *D. sarawacensis* Demoulin, 1954: 129.

SPECIES EXAMINED. None.

DISTRIBUTION: Sarawak.

Imago. ♀ unknown. Length of ♂: body 4.0; fore wings 5.0 mm. Wings: vein R_s of fore wings forked near base; vein MA forked less than $1/2$ of distance from base to margin, fork asymmetrical; vein MP_2 attached at base to vein MP_1 by a cross vein $1/2$ distance from base to margin (fig. 22); cubital area as in fig. 22; cross veins numerous. Hind wings absent. Legs: claws dissimilar, 1 apically hooked, the other obtuse, pad-like. ♂ genitalia (fig. 78): Penes divided, tubular, tip of each penis lobe bent laterally; 9th sternum deeply cleft. (Description from Demoulin, 1954.)

Mature nymph. Unknown.

History and discussion: Demoulin (1954) established *Dipterophlebiodes* for *D. sarawacensis* which is known from 1 ♂ subimago.

Biology: Unknown.

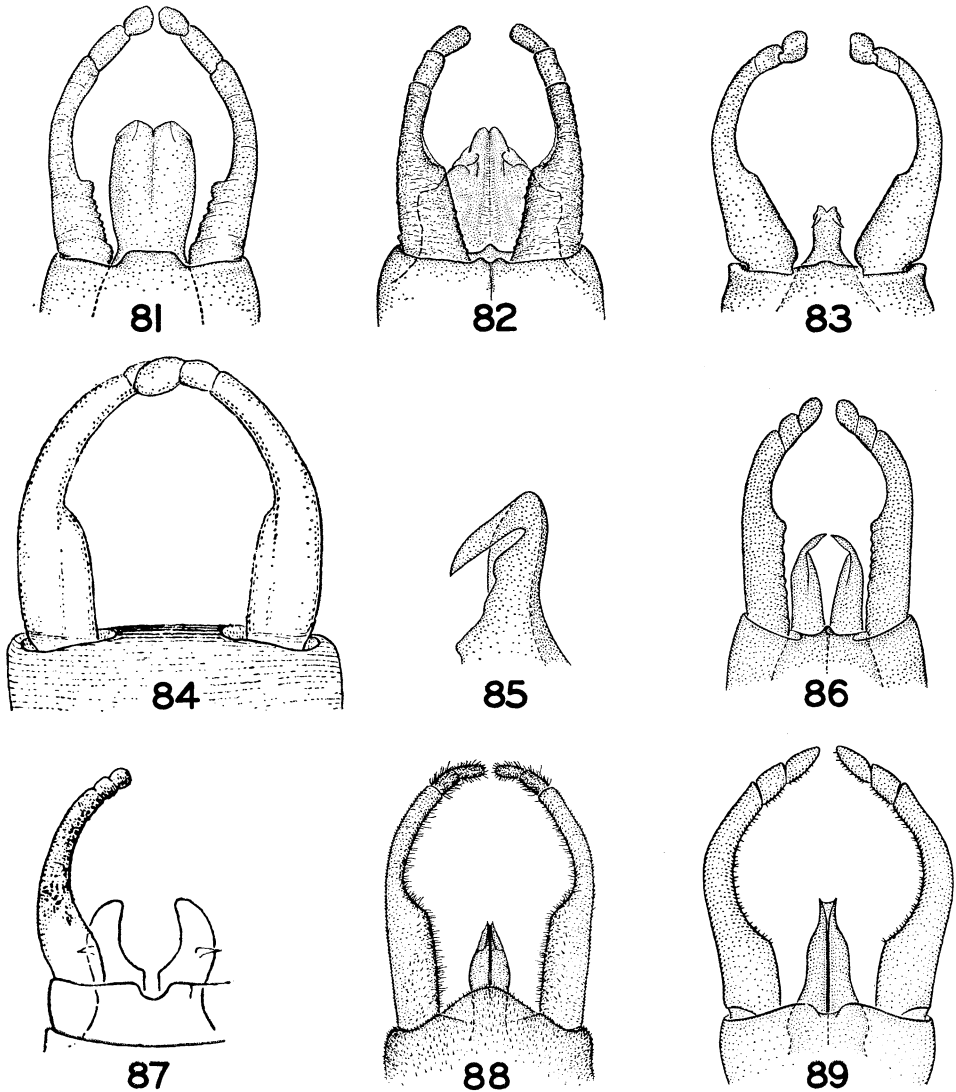


Fig. 81-89. Ventral views of genitalia of ♂ imago. 81, *Aprionyx natalicus*, ventral view; 82, *A. intermedius*, ventral view; 83, *Adenophlebia auriculata*, ventral view; 84, *Kimminsula annulata* n. comb. forceps [after Eaton, 1884 (1883-88)]; 85, *Kimminsula annulata* n. comb., right penis lobe; 86, *Adenophlebiodes* sp.; 87, *Castanophlebia calida* (after Barnard, 1932); 88, *Fullela dentata*; 89, *Choroaterpes (Choroaterpes) picteti*.

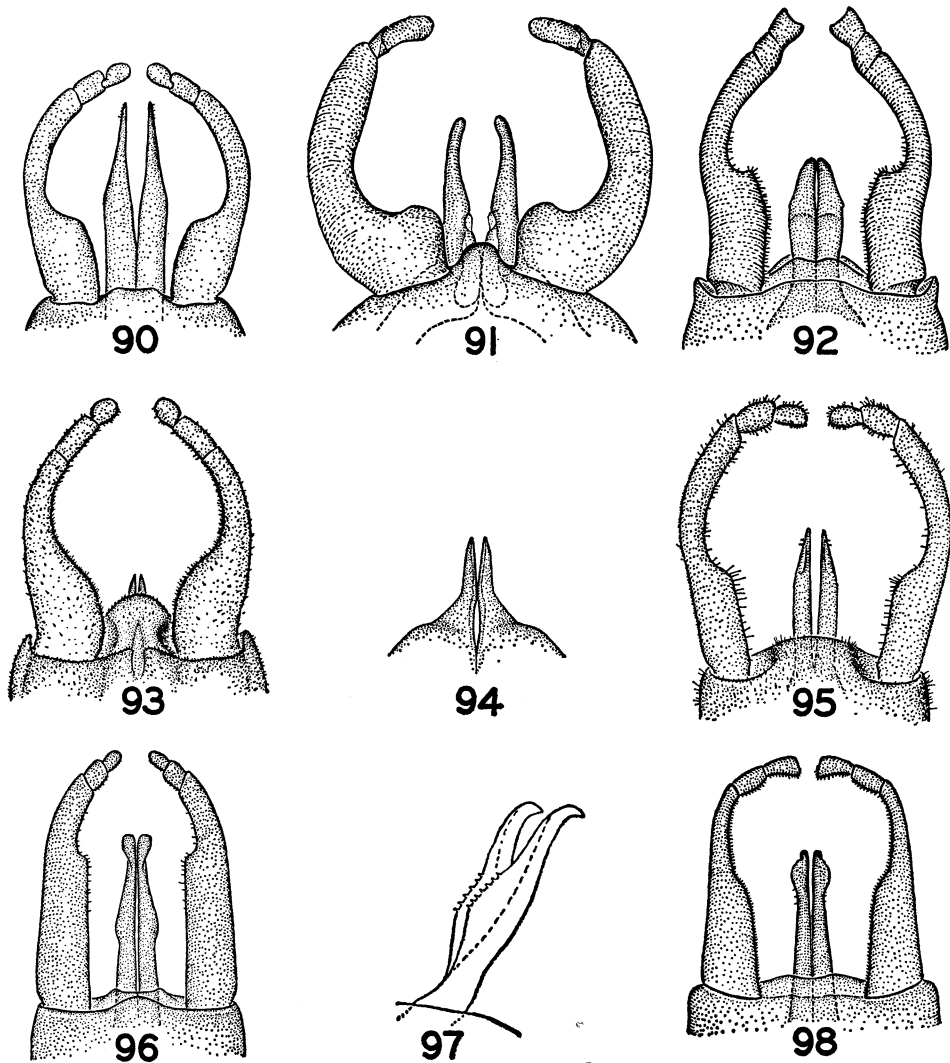


Fig. 90-98. Ventral view of genitalia of ♂ imago. 90, *Choroerpes (Euthraulus) elegans*; 91, *Choroerpes (Euthraulus) signata* n. comb.; 92, *Choroerpedes* sp.; 93, *Cryptopenella facialis*; 94, *Cryptopenella facialis*, penes; 95, *Fulletomimus marlieri*. Fig. 96-98. Genitalia of ♂ imago. 96, *Thraulius torrentis* n. comb., ventral view; 97, *Simothraulus seminiger*, lateral view of penes (after Ulmer, 1939), 98, *Indialis badia* n. sp., ventral view.

Genus *Gilliesia* Peters and Edmunds, new genus

Fig. 23-25, 79-80, 113, 136.

Imago. Length ♂ imago: body 5.5-6.5; fore wings 6.5-7.0 mm. Length ♀ imago: body 6.0-8.0; fore wings 8.0-8.5 mm. Eyes of ♂ imago meet on meson of head, lower portion of eyes

less than 1/2 length of upper portion; ♀ eyes separated on meson of head by a length 5 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked 1/7 of distance from base to margin; vein MA forked less than 1/2 of distance from base to margin, fork asymmetrical; vein MP_2 independent of vein MP_1 (fig. 23); cubital area as in fig. 23; cross veins numerous. Costal projection of hind wings well developed and acute, apex of projection located about 1/2 distance from base (fig. 25); cross veins few. Legs: ratios of ♂ fore leg segments, 0.48: 1.00 (3.30 mm): 0.03: 0.36: 0.33: 0.21: 0.06. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 113). ♂ genitalia: forceps segments 2 and 3 short; base of forceps narrow; penes divided except at base, apical 1/3 of each lobe bent laterally and then ventrally (fig. 79-80); 9th sternum deeply cleft apically (fig. 79). Ninth sternum of ♀ deeply cleft apically (fig. 136). Terminal filament a little longer than cerci.

Mature nymph. Unknown.

Etymology: Genus is named for Dr M. T. Gillies, Lewes, Sussex, England, who has contributed greatly to the knowledge of African and Asian Ephemeroptera and who has encouraged and aided the present study.

Type-species: *Gilliesia hindustanica* (Gillies) n. comb., originally placed in *Thraulius*.

DISTRIBUTION: Northern India.

Gilliesia hindustanica (Gillies), n. comb. Fig. 23-25, 79-80, 113, 136.

Thraulius hindustanicus Gillies, 1951: 122.

This species is represented from the following new localities.

INDIA, ASSAM, NORTH EAST FRONTIER AGENCY, KAMENG FRONTIER DIVISION: 2 ♂ and 2 ♀ imagos pinned, 15 ♂ imagos, 10 ♀ imagos, 5 ♂ subimagos and 4 ♀ subimagos in alcohol, Lifakpo, 930 m, 15.V. 1961; 1 ♂ imago, 1 ♀ imago in alcohol, Ankaling, 630 m, 26.V. 1961; 1 ♂ imago pinned, 5 ♂ subimagos in alcohol, Bhairabkunda, 210-300m, 5-6.III. 1961; 1 ♂ imago pinned, 1 ♂ imago and 1 ♂ subimago in alcohol, Bokhar, 660-750 m, 27-28.V. 1961; 1 ♂ imago pinned, Amatulla, 390-600 m, 23-25.V. 1961; 3 ♂ imagos, 1 ♀ imago pinned, Rupa, 1650-1800 m, 11-12.VI. 1961; 1 ♂ imago, 2 ♀ imagos pinned, Kujjalong, 1350 m, 28-30.VI. 1961; 1 ♂ imago pinned, Dirang Dzong, 1590-1800 m, 18-22.VII. 1961. All specimens were collected by F. Schmid and are deposited in the collections of the University of Utah and Florida A & M University.

Discussion: Gillies (1951) described *Thraulius hindustanicus* from adults collected at Mirik, Darjeeling District, India. The species does not belong in *Thraulius* or any other genus, and we therefore have established the new genus *Gilliesia*. The nymphs are unknown.

Gilliesia is most similar to *Habrophlebiodes* and *Dipterophlebiodes*. However adults of *Gilliesia* can be distinguished from those of *Habrophlebiodes* by the unique structure of the ♂ penes (fig. 79-80), and the absence of a ♀ ovipositor or egg guide. Adults of *Gilliesia* can be distinguished from those of *Dipterophlebiodes* by the presence of well developed hind wings (fig. 24-25), and the unique structure of the ♂ penes (fig. 79-80).

Gilliesia can be differentiated in the imago from all other genera of the Leptophlebiidae by the following combination of characters: (1) the hind wings are present and well

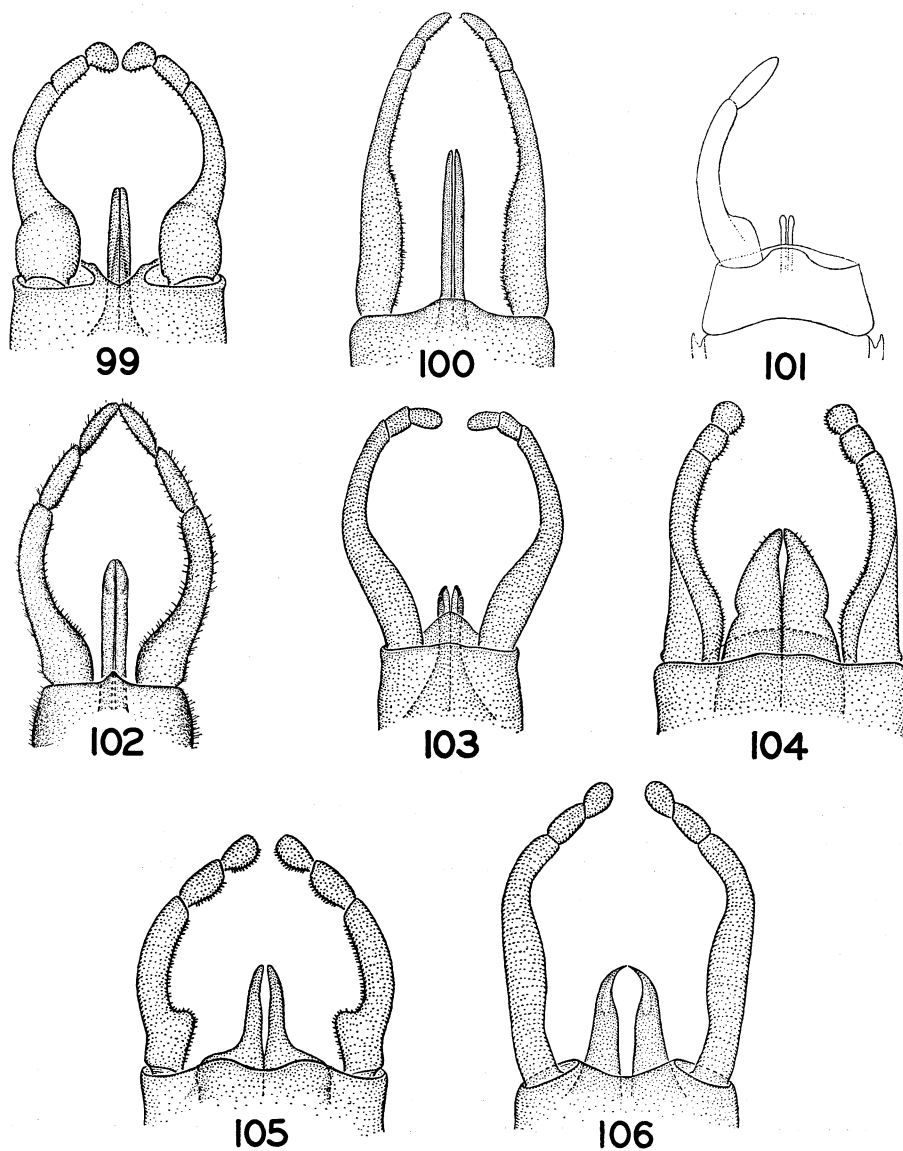


Fig. 99-106. Genitalia of male imago: 99, *Megaglena brincki* n. sp., ventral view; 100, *Maheathraulius scotti*, ventral view; 101, *Hagenulodes braueri*, ventral view (after Ulmer, 1919); 102, *Nesophlebia adusta*, ventral view; 103, *Nathanella indica*, ventral view; 104, *Isca (Minyphlebia) janiceae* n. sp., ventral view; 105, *Isca (Tanycola) serendiba* n. sp., ventral view; 106, *Isca (Isca s. s.) purpurea*, ventral view.

developed (fig. 24-25); (2) vein MP_2 of the fore wings is independent of vein MP_1 (fig. 23); (3) the ♀ possesses no ovipositor or egg guide; and (4) the 9th sternum of the ♂ is deeply cleft apically (fig. 136).

Biology: Gillies (1951) gives biological notes concerning *G. hindustanica*.

Genus **Kimminsula** Peters and Edmunds, new genus

Fig. 2, 30-31, 84-85, 116, 139, 160, 182, 204, 226, 248, 272, 297.

Type-species: *K. annulata* (Hagen) n. comb., originally placed in *Potamanthus*.

Species included: *K. annulata* n. comb. (Hagen, 1858: 476) (*Potamanthus*); *K. fasciata* n. comb. (Hagen, 1858: 476) (*Potamanthus*); *K. taprobanes* n. comb. (Walker, 1853: 567) (*Baetis*).

SPECIES EXAMINED. *K. annulata*, male imago; *K. fasciata*, male imago; *Kimminsula* spp., numerous male imagos and nymphs from Ceylon.

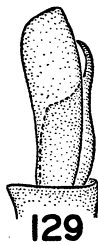
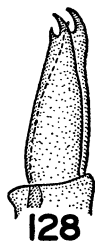
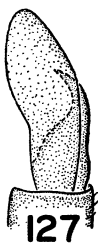
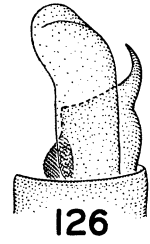
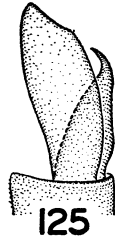
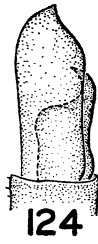
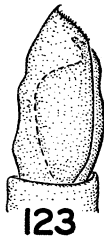
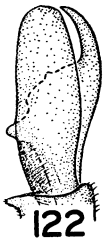
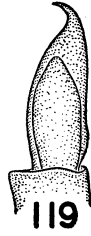
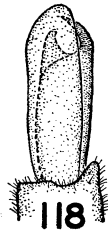
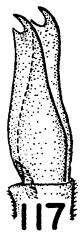
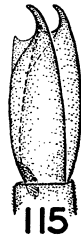
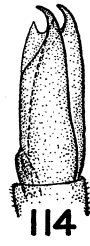
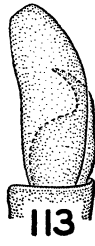
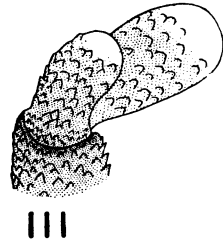
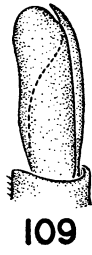
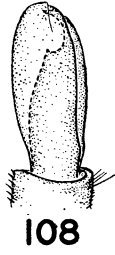
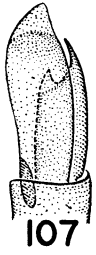
DISTRIBUTION: Ceylon.

Etymology: Genus is named for Mr D. E. Kimmins, British Museum (Nat. Hist.), London, who has contributed greatly to the knowledge of Ephemeroptera.

Imago. Length of ♂: body 9.0-11.0; fore wings 12.5-15.0 mm. Length of ♀: body 10.0; fore wings 12.5 mm. Eyes of ♂ separated on meson of head by a length $1.5 \times$ as long as maximum width of a lateral ocellus, lower portion of eyes a little shorter in length than upper portion; ♀ eyes separated on meson of head by a length $4.5 \times$ as great as maximum width of an eye. Wings (fig. 30-31): vein R_s of fore wings forked $1/4$ of distance from base to margin; vein MA forked $1/2$ of distance from base to margin, fork symmetrical; vein MP_2 attached at base to vein MP_1 with cross vein less than $1/4$ of distance from base to margin (fig. 30), vein MP_2 strongly recurved (fig. 30); cubital area as in fig. 30; cross veins numerous. Costal margin of hind wings convex, apex of convexity located less than $1/2$ distance from base (fig. 31); cross veins numerous. Legs: ratios of segments in ♂ fore legs, 0.61:1.00 (3.20 mm): 0.05:0.30:0.27:0.16:0.10. Claws alike, apically hooked, each with an opposing hook (fig. 116). ♂ genitalia (84-85): segments 2 and 3 of forceps short, base of forceps broad, its inner margin forming an extreme angular bend; penes divided, tubular, broader at base, a ventral spine-like projection arising from tip of each penis lobe (fig. 85). Ninth sternum of ♀ shallowly cleft apically (fig. 139). Terminal filament slightly longer than cerci.

Mature nymph: Head prognathous. Antennae $2-2.5 \times$ as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 248; submedian and anteromarginal areas of hair ventrally. Left mandible as in fig. 226. Lingua of hypopharynx with well developed lateral processes (fig. 204), anterior margin deeply cleft; superlingua of hypopharynx as in fig. 204, with a row of hair along anterior margin, lateral tips emarginate. Segment 2 of maxillary palpi a little shorter in length than segment 1; segment 3 of palpi $1/2$ to over $1/2$ length of segment 2, triangular; hair on maxillae as in fig. 182. Labium as in fig. 160; segment 2 of palpi equal to length of segment 1; segment 3 of palpi $3/4$ to equal in length to segment 2,

Fig. 107-130. Claws of fore leg of ♂ imago: 107, *Paraleptophlebia cincta*; 108, *Leptophlebia marginata*; 109, *Habroleptoides modesta*; 110, *Habrophlebia fusca*; 111, *Habrophlebia fusca* (after Grandi, 1960); 112, *Habrophlebiodes gilliesi*; 113, *Gilliesia hindustanica* n. comb.; 114, *Aprionyx intermedius*; 115, *Adenophlebia auriculata*; 116, *Kimminsula* sp.; 117, *Adenophlebiodes ornata*; 118, *Fullela dentata*; 119, *Choroterpes (Choroterpes) picteti*; 120, *Choroterpes (Euthraulius) elegans*; 121, *Choroterpides* sp.; 122, *Cryptopenella facialis*; 123, *Fulletomimus marlieri*; 124, *Thraulius torrentis* n. comb.; 125, *Indialis badia* n. sp.; 126, *Megaglena brincki* n. sp.; 127, *Maethraulius scotti*; 128, *Nathanella indica*; 129, *Isca (Minyphlebia) janiceae* n. sp.; 130, *Isca (Tanycola) serendiba* n. sp.



triangular; paraglossae ventral to glossae. Hair on anterolateral margins of prothorax only. Legs (fig. 272): apex of claws hooked and narrow, denticles on claws progressively larger apically. Gills 1-7 alike; dorsal and ventral portions of lamellae plate-like, apically cleft, a median, slender process arising from cleft (fig. 297), posterior gills smaller. Posterolateral spines on abdominal segments 3-9, progressively larger posteriorly. Terminal filament longer than cerci.

History and discussion: Walker (1853) described *Baetis taprobanes* from Ceylon, and Hagen (1858) described *Potamanthus annulatus* and *P. fasciatus* from Ceylon, Eaton [1884 (1883-88)] placed all 3 species in *Atalophlebia*. Upon obtaining the associated nymphs and adults from the same locality of these species, we herein place the 3 species in a new genus *Kimminsula*.

Kimminsula is most closely related to *Leptophlebia* and related genera in the Palearctic Region and *Adenophlebia* and *Aprionyx* in the Ethiopian Region. However the adults of *Kimminsula* can be differentiated from the adults of these genera by the spear-like penes of the ♂ (fig. 85). The nymphs of *Kimminsula* can be differentiated from the nymphs of these genera by the plate-like abdominal gills (fig. 297) and the shape of the labrum (fig. 248).

Kimminsula can be differentiated from all other genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) vein MP_2 of fore wings is attached to vein MP_1 with a cross vein less than 1/4 of distance from base to margin of wings (fig. 30); (2) costal projection of hind wings is convex (fig. 31); (3) tarsal claws are alike, and each is apically hooked with an opposing hook (fig. 116); and (4) ♂ penes are spear-like (fig. 85). In the nymphs, (1) abdominal gills 1-7 are alike; each portion of gills is plate-like and apically cleft; a median slender process arises from cleft (fig. 297); (2) lingua of hypopharynx with well developed lateral processes (fig. 204); (3) denticles on claws progressively larger apically (fig. 272); and (4) posterolateral spines are present on abdominal segments 3-9.

Biology: Eaton 1884 (1883-88) briefly noted the habitats of *K. annulata* and *K. fasciata*.

Genus *Choroterpes* Eaton, 1881

Fig. 38-42, 89-91, 119-120, 142-143, 163-164, 185-186, 207-208,
229-230, 251-252, 276-277, 303-307.

Choroterpes Eaton, 1881: 194; 1884 (1883-88): 104.—Ulmer, 1920: 114, 116.—Lestage, 1921: 228.—Ulmer, 1929: 10.—Schoenemund, 1930: 52.—Barnard, 1932: 247.—Ulmer, 1932b: 204.—Traver, 1935: 540.—Ujhelyi, 1959: 41.—Grandi, 1960: 248-49, 412.

Euthraululus Barnard, 1932: 240.—Ulmer, 1932a: 212, 214.

Thraululus Ulmer, 1939: 499.

Thraululus=*Euthraululus* Gillies, 1957: 43.

Subgenera *Choroterpes* s. s. and *Euthraululus* Peters & Edmunds, 1964: 241.

Type-species: *C. (C.) picteti* (Eaton) (originally placed in *Leptophlebia*), by original designation.

Species occurring in the Eastern Hemisphere: *C. (Euthraululus) balcanica* (Ikonomov, 1961: 1) (*Euthraululus*); *C. (E.) bugandensis* (Kimmins, 1956: 79) (*Euthraululus*); *C. (E.) curta*

(Kimmins, 1956: 80) (*Euthraulius*); *C. (E.) elegans* (Barnard, 1932: 249) (*Euthraulius*); *C. (E.) exigua* Eaton, 1892: 189; *C. (E.) karnyi* (Ulmer, 1939: 505) (*Hagenulus*) n. comb.; *C. (E.) marginata* (Ulmer, 1913: 103) (*Thraulius*); *C. (C.) ndebele* Agnew, 1962: 363; *C. (C.) nigrescens* Barnard, 1932: 248; *C. (E.) parvula* (Gillies, 1951: 124) (*Thraululus*); *C. (C.) picteti* (Eaton, 1871: 87) (*Leptophlebia*) (= *C. lusitanica* Eaton, 1881: 194); *C. (C.) proba* Ulmer, 1939: 495; *C. (E.) signata* (Hagen, 1858: 477) (*Cloe?*) n. comb. *C. (E.) trifurcata* Ueno, 1928: 40; *C. (E.) tropicalis* (Gillies, 1957: 44) (*Euthraulius*); *C. (E.) usambarae* (Gillies, 1957: 46) (*Euthraulius*); *Choroerpes (E.)* sp. A. (Gillies, 1957: 48) (*Euthraulius*); *Choroerpes (E.)* sp. B (Gillies, 1957: 48) (*Euthraulius*).

SPECIES EXAMINED. *C. (E.) bugandensis*, ♂ and ♀ imagos, nymph; *C. (E.) curta*, ♂ and ♀ imagos; *C. (E.) elegans*, ♂ and ♀ imagos, nymph; *C. (C.) ndebele*, ♂ and ♀ imagos, nymph; *C. (C.) nigrescens*, ♂ imago, nymph; *C. (C.) picteti*, ♂ imago, nymph; *Choroerpes (E.)* sp. A., ♂ and ♀ imagos; *C. (E.) tropicalis*, ♀ imago; *C. (E.) usambarae*, ♀ imago, nymph; *Choroerpes (E.)* spp., numerous ♂ and ♀ imagos and nymphs from Africa, India, Nepal, Thailand, Hong Kong, Korea, Borneo, and Malaya; *Choroerpes (C.)* spp., numerous ♂ and ♀ imagos and nymphs from India and Nepal.

DISTRIBUTION: Ethiopian, Oriental, Palearctic, Nearctic, and Neotropical regions.

Imago. Length of ♂: body 4.0-8.0; fore wings 4.0-8.0 mm. Length of ♀: body 4.0-10.0; fore wings 4.0-10.5 mm. Eyes of ♂ separated on meson of head by a length 3/4 maximum width of median ocellus or eyes meet on meson of head, lower portion of eyes 1/2 to 2/3 maximum length of upper portion, upper portion on short stalk; eyes of female separated on meson of head by a length 3-6.5 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked 1/4 of distance from base to margin; vein MA forked 1/2 to over 1/2 of distance from base to margin, fork symmetrical; veins R_s and MP forked equidistant from base, fork asymmetrical (fig. 40); cubital area as in fig. 38 and 40; cross veins few. Costal projection of hindwings rounded and well developed (fig. 39, 41), apex located 1/2 distance from base; cross veins few. Legs: ratios of segments in ♂ fore legs, 0.63: 1.00 (1.60 mm): 0.08: 0.25: 0.24: 0.16: 0.09. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 119-120). ♂ genitalia: segments 2 and 3 of forceps short, base of forceps broad, its inner margin forming an extreme angular bend (fig. 89-90) or base of forceps bulbous (fig. 91), base of segment 1 may be indented giving appearance of a basal 4th segment; penes divided, tubular, each lobe tapered to an apical point (fig. 89-91). Ninth sternum of ♀ shallowly cleft apically (fig. 142-143). Terminal filament slightly longer than cerci.

Mature nymph. Head prognathous. Antennae 1.5× to equal maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 251 and 252; submedian areas and anterolateral areas of hair ventrally; anteromedian margin shallowly emarginated (fig. 252) to deeply incised (fig. 251). Left mandible as in fig. 229 and 230. Lingua of hypopharynx with well developed lateral processes (fig. 207-208), anterior margin shallowly cleft; superlingua of hypopharynx as in fig. 207 and 208, with a row of hair along anterior margin. Segment 2 of maxillary palpi a little longer than segment 1; segment 3 of palpi a little longer than 1/2 length of segment 2, triangular; hair on maxillae as in fig. 185 and 186. Labium as in fig. 163 and 164; segment 2 of palpi 3/4 to a little longer than segment 1; segment 3 of palpi over 1/2 length to as long as segment 2, triangular; paraglossae ventral to glossae. Fine hair on anterolateral margins of prothorax only. Legs (fig. 276-277): claws apically hooked, denticles on claws progressively larger apically. Gills on segments 1-7; gill 1 slender, lanceolate (fig. 303, 305) or similar to dorsal lamellae on gills 2-6; gills 2-7 alike, dorsal and ventral lamellae plate-like and terminated in 3 slender, subequal processes (fig. 306), gills 6 and 7 may be rather small (fig. 307), or dorsal and ventral lamellae plate-like and terminated in 3 processes, with median projection longer than laterals,

ventral lamellae smaller (fig. 304). Posterolateral spines on abdominal segments 4 or 5-9, spines progressively larger posteriorly. Terminal filament slightly longer than cerci.

History and discussion. Eaton (1881) described the genus *Choroterpes* for the European species *C. picteti*. Barnard (1932) described the genus *Euthraululus* for the African species *E. elegans*. Ulmer (1939) established the genus *Thraululus* for the Oriental species *T. marginatus*, and later Gillies (1951) added a second species to *Thraululus*. Gillies (1957) placed *Thraululus* as a synonym of *Euthraululus*. Peters & Edmunds (1964) placed *Euthraululus* as a subgenus of *Choroterpes*, thus recognizing *Choroterpes* as a wide-ranging genus. Both subgenera are widely distributed in the Eastern Hemisphere, but *Euthraululus* is of rare occurrence in Europe.

The North American species of *Choroterpes* appear to be congeneric with the Eastern Hemisphere representatives. However, preliminary study indicates that members of *Choroterpes* occur throughout Central America and Northern South America. These Neotropical species appear to form a group distinct from those of the Eastern Hemisphere. This Neotropical group will be considered when sufficient reared material is available.

Subgenus *Choroterpes* s. s. Eaton, 1881

Fig. 38-39, 89, 119, 142, 163, 185, 207, 229, 251, 276, 303-304.

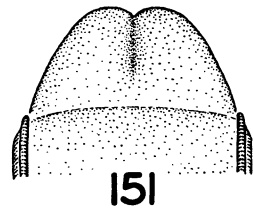
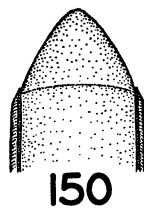
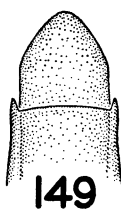
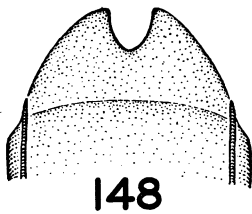
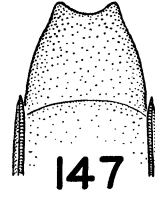
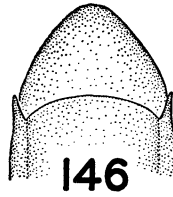
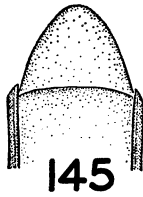
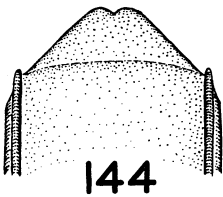
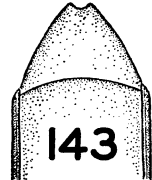
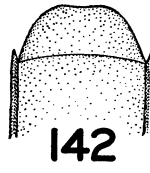
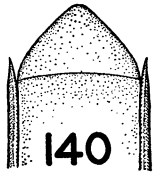
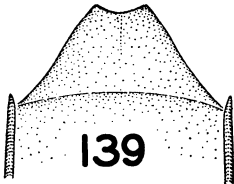
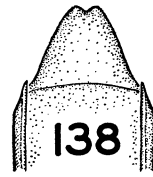
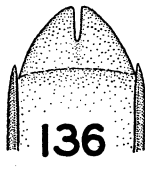
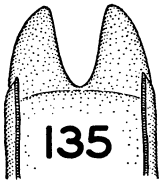
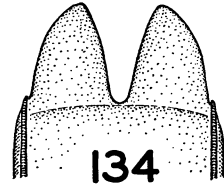
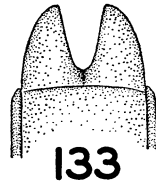
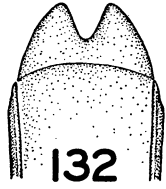
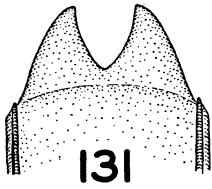
Imago. Length of ♂: body 7.0-9.0; fore wings 7.0-8.0 mm. Length of ♀: body 7.0-10.0; fore wings 7.5-10.5 mm. Vein MA of fore wings forked over 1/2 of distance from base to margin (fig. 38); bases of costal projection of hind wings both smoothly curved (fig. 39).

Mature nymph. Gills 2-7 alike, dorsal and ventral lamellae plate-like and terminated in 3 processes, with median projection longer than laterals (fig. 304), ventral lamellae smaller.

Discussion: The subgenus *Choroterpes* s. s. is widely distributed, occurring in every major zoogeographical region in the world except the Australian Region. The characters above will distinguish it from the subgenus *Euthraululus*.

Biology: The biology of the African species *C. (C.) nigrescens* is summarized in A. C. Harrison (1949c) and A. D. Harrison et al. (1958). Grandi (1960) summarized the biology of the European species *C. (C.) picteti*. Nymphs of several undescribed species are common in a variety of habitats from torrential, rocky bottom streams to quiet, silt bottom pools of large streams. Subimagos emerge at dusk and mating appears to occur at dusk the following day. The biology of several North American species has been reported by Needham (1905) and Berner (1950).

Fig. 131-151. 9th sternum of ♀ imago: 131, *Paraleptophlebia cincta*; 132, *Leptophlebia marginata*; 133, *Habroleptoides modesta*; 134, *Habrophlebia fusca*; 135, *Habrophlebiodes gilliesi*; 136, *Gilliesia hindustanica* n. comb.; 137, *Aprionyx natalicus*; 138, *Adenophlebia auriculata*; 139, *Kimminsula* sp.; 140, *Adenophlebiodes ornata*; 141, *Castanophlebia calida* (after Barnard, 1932); 142, *Choroterpes (Choroterpes) picteti*; 143, *Choroterpes (Euthraululus) elegans*; 144, *Choroterpides* sp.; 145, *Cryptopenella facialis*; 146, *Thraululus torrentis* n. comb.; 147, *Thraululus* sp.; 148, *Megaglena brincki* n. sp.; 149, *Maheathraululus scotti*; 150, *Isca (Minyphlebia) janiceae* n. sp.; 151, *Isca (Tanycola) serendiba* n. sp.



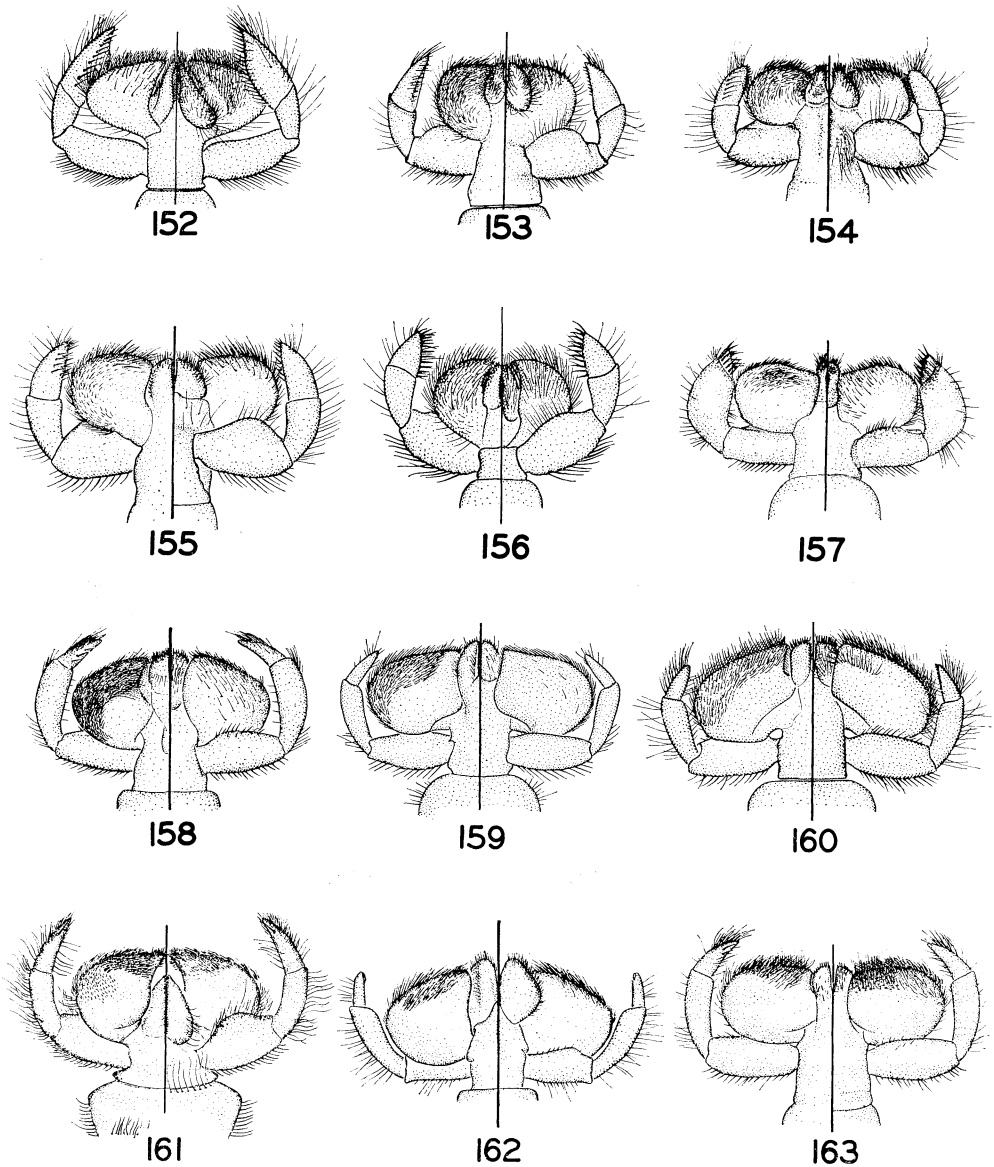


Fig. 152-163. Labium of mature nymph: 152, *Paraleptophlebia cincta*; 153, *Leptophlebia marginata*; 154, *Habroleptoides modesta*; 155, *Habrophlebia fusca*; 156, *Habrophlebiodes prominens*; 157, *Aprionyx intermedius*; 158, *Adenophlebia auriculata*; 159, *Atalophlebioides inequalis*; 160, *Kimminsula* sp.; 161, *Adenophlebiodes* sp.; 162, *Castanophlebia calida*; 163, *Choroterpes* (*Choroterpes*) *picteti*.

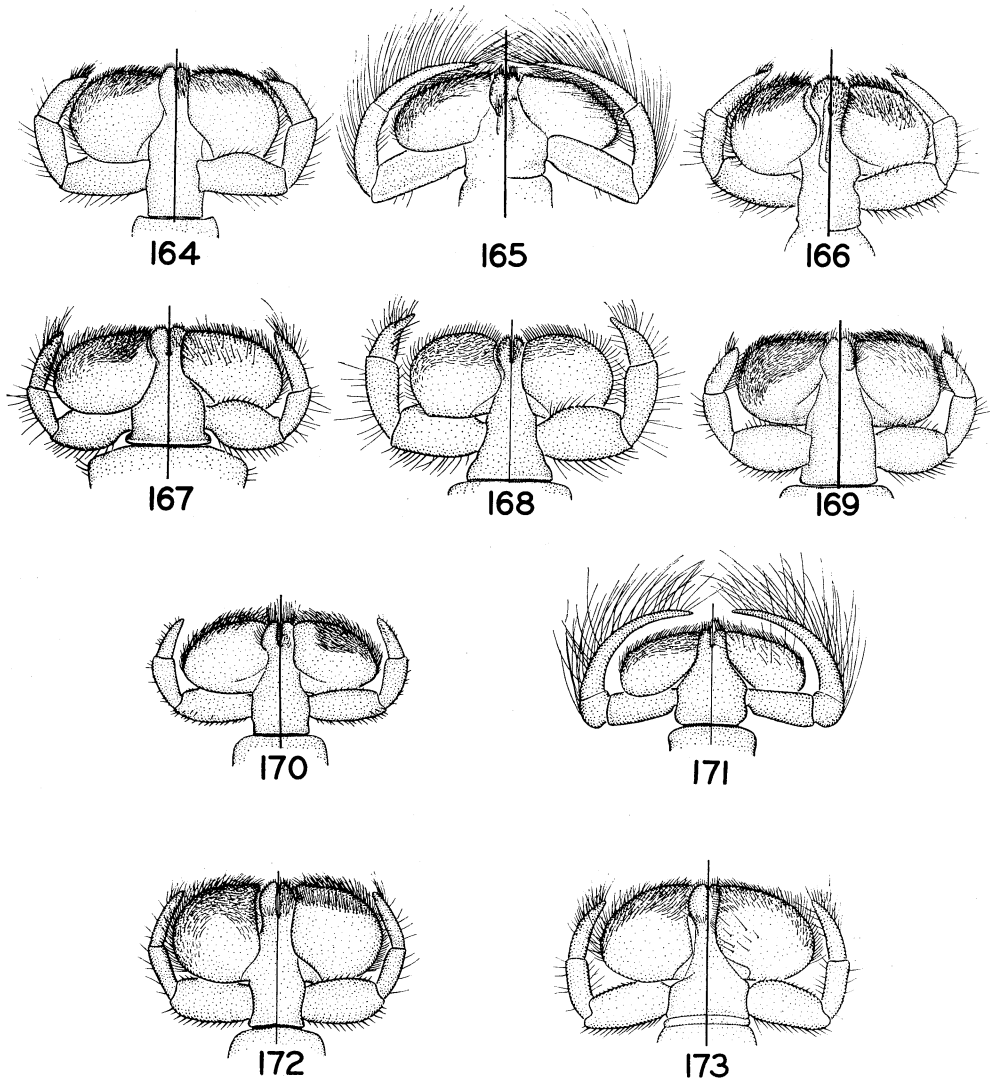


Fig. 164-173. Labium of mature nymph: 164, *Choro-terpes (Euthraulus)* sp.; 165, *Choro-terpides* sp.; 166, *Thraulius torrentis* n. comb; 167, *Indialis badia* n. sp.; 168, *Megaglena brincki* n. sp.; 169, *Maheathraulius scotti*; 170, *Hagenulodes braueri*; 171, *Nathanella* sp.; 172, *Isca (Minyphlebia) janiceae* n. sp.; 173, *Isca (Tanycola) serendiba* n. sp.

Subgenus *Euthraulus* Barnard, 1932

Fig. 40-42, 90-91, 120, 143, 164, 186, 208, 230, 252, 277, 305-307.

Imago. Length of ♂: body 4.0-5.0; fore wings 4.0-8.0 mm. Length of ♀: body 4.0-6.0; fore wings 4.0-8.0 mm. Vein MA of fore wings forked 1/2 of distance from base to margin (fig. 40); proximal base of costal projection of hind wings smoothly curved, distal base angular (fig. 41).

Mature nymph. Gills 2-7 alike, dorsal and ventral lamellae plate-like and terminated in 3 slender subequal processes (fig. 306), gills 6 and 7 may be rather small (fig. 307).

Type-species: *C. (E.) elegans* (Barnard) (originally described in *Euthraulius*), monobasic.

Discussion: The subgenus *Euthraulius* is known to occur throughout the Ethiopian and Oriental regions and the Palearctic region of Asia. The above characters will distinguish the subgenus *Euthraulius* from the subgenus *Choroterpes* s. s.

G. F. Edmunds, Jr. has examined the types of *Thraulius signatus* in the Museum of Comparative Zoology, Cambridge. The shape and venation of the hind wings (fig. 42) and the ♂ genitalia (fig. 91) are similar to those of the species of *Choroterpes (Euthraulius)*. For this reason, the species *signatus* is placed in the subgenus *Euthraulius*.

According to the figures drawn by Ulmer (1939), the wings, ♂ genitalia, ♂ tarsal claws and the ♀ 9th sternum of *Hagenulus karnyi* are similar to those structures of *Choroterpes (Euthraulius)*. For this reason, the species *karnyi* is placed in the subgenus *Euthraulius*.

Biology: A. C. Harrison (1949c) and A. D. Harrison et al. (1960) have published biological data on the African species *C. (E.) elegans*. Tjønneland (1960) has recorded data on the flight activity for the African species *C. (E.) bugandensis* and *C. (E.) curta*. Immature nymphs of several species of *Choroterpes (Euthraulius)* from India are found in the torrential areas of streams and rivers, while the mature nymphs are found in quiet sidepools. Subimagos emerge at dusk and mating appears to occur at dusk the following day.

Genus *Choroterpides* Ulmer, 1939

Fig. 43-45, 92, 121, 144, 165, 187, 209, 231, 253, 278, 308, 331.

Thraulius Ulmer, 1924: 39

Choroterpides Ulmer, 1939: 494; 1940: 613.

Type-species: *C. exigua* (Eaton) (originally placed in *Thraulius*) by original designation.

Species included: *C. exigua* [Eaton, 1884 (1883-88)]; *C. major* Ulmer, 1939: 497.

SPECIES EXAMINED: *C. exigua*, ♂ and ♀ imagos and nymph; *Choroterpides* spp., numerous ♂ and ♀ imagos and nymphs from Thailand and Nepal.

DISTRIBUTION: Nepal, Thailand, Java, and Sumatra.

Imago. Length of ♂: body 6.0-8.5; fore wings 6.5-9.0 mm. Length of ♀: body 5.8; fore wings 6.3 mm. Eyes of ♂ separated on meson of head by a narrow space, lower portion of eyes 1/2 length of upper portion; ♀ eyes separated on meson of head by a length 3 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked 1/4 of distance from base to margin; vein MA forked over 1/2 of distance from base to margin, fork symmetrical; vein MP forked less than 1/2 of distance from base to margin, fork asymmetrical; cubital area as in fig. 43; cross veins few; sclerotization on posterior margin set in from edge (fig. 43). Costal projection of hind wings well developed and rounded, apex of projection located about 1/2

distance from base (fig. 44), cross veins few; sclerotization on posterior margins set in from edge (fig. 45). Legs: ratios of segments in ♂ fore legs, 0.58: 1.00 (2.40 mm): 0.04: 0.33: 0.33: 0.17: 0.08. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 121). ♂ genitalia (fig. 92): segments 2 and 3 of forceps short, base of forceps broad, its inner margin forming an extreme angular bend; penes divided, tubular. Ninth sternum of ♀ shallowly cleft apically (fig. 144). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae $2.25 \times$ as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 253; submedian, anterior and lateral areas of hair ventrally; anterior emargination present (fig. 231) to absent (fig. 253). Left mandible as in fig. 231. Lingua of hypopharynx with well developed lateral processes (fig. 209), anterior margin deeply cleft; superlingua of hypopharynx as in fig. 209, with a row of hair along anterior margin. Maxillary palpi greatly elongated (fig. 187, 331); segment 2 of maxillary palpi equal to length of segment 1; segment 3 of palpi 1.25 length of segment 2, triangular; a large projection on inner anterior margin of maxillae (fig. 187); hair on maxillae as in fig. 187. Labium as in fig. 165; labial palpi greatly elongated; segment 2 of palpi a little shorter in length than segment 1; segment 3 of palpi equal to length of segment 2, triangular; paraglossae ventral to glossae. Hair on anterolateral margins of prothorax only. Legs (fig. 278): apex of claws hooked and narrow, a row of subequal sized denticles on claws. Gills on segments 2-7 alike; dorsal and ventral portions of lamellae plate-like and terminated in 3 processes, with median projection equal to or longer than laterals. Posterolateral spines on abdominal segments 8 and 9, those on segment 9 larger. Terminal filament longer than cerci.

History and discussion: Eaton 1884 (1883-88) described *Thraulius exiguus* from Lahat, Palenburg (misspelling for Palembang in Southern Sumatra). Ulmer (1924) redescribed the species from specimens in Java. Later Ulmer (1939) established the genus *Choroterpides* for *T. exiguus* and another species *C. major* Ulmer (1939) from Java and Sumatra.

The ♀ imago of *Choroterpides* was previously unknown. Characters of the ♀ imago listed in the generic description were described from specimens collected in Northern Thailand.

Biology: Ulmer (1940) stated that adults of *C. exigua* and *C. major* were collected in Java sporadically throughout the year, and the nymphs were found in running water. Nymphs of this genus in Northern Thailand are found in torrential rivers with rock bottoms. Subimagos emerge at dusk and the adults appear to mate at dusk the following day.

Genus *Cryptopenella* Gillies, 1951

Fig. 46-47, 93-94, 122, 145, 336-345.

Cryptopenella Gillies, 1951: 125.

Type-species: *C. facialis* Gillies, by original designation.

Species included: *C. facialis* Gillies, 1951: 127.

SPECIES EXAMINED. *C. facialis*, ♂ and ♀ imagos, nymph; *Cryptopenella* sp., numerous ♂ and ♀ imagos from Thailand.

DISTRIBUTION. Hong Kong and Thailand.

Imago. Length of ♂: body 5.0; fore wings 5.5 mm. Length of ♀: body 5.0; fore wings 5.5

mm. Eyes of ♂ separated on meson of head by a narrow space, lower portion of eyes slightly more than 1/2 length of upper portion; ♀ eyes separated on meson of head by a length $3 \times$ as great as maximum width of an eye. Nasal carina of head well developed and ridge-like, lower margin of face everted and projected directly forwards to form an irregular shelf. Wings: vein R_s of fore wings forked less than 1/4 of distance from base to margin; vein MA forked more than 1/2 of distance from base to margin, fork symmetrical; vein MP forked 1/2 of distance from base to margin, fork asymmetrical; cubital area as in fig. 46; cross veins few. Costal projection of hind wings well developed and rounded, apex of projection located less than 1/2 distance from base (fig. 47); cross veins few. Legs: ratios of segments in ♂ fore legs, 0.75 : 1.00 (1.60 mm) : 0.06 : 0.38 : 0.25 : 0.19 : 0.09. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 122). ♂ genitalia (fig. 93-94): segments 2 and 3 of forceps short, base of forceps broad, its inner margin forming an angular bend; penes divided, tubular, short, apical 1/2 of each penis lobe acute; 9th sternum extends posteriorly and covers penes except for apical tip (fig. 93). Ninth sternum of ♀ entire (fig. 145). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae $2 \times$ maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 338; submedian areas and anterolateral areas of hair ventrally; anteromedian margin deeply incised (fig. 338). Left mandible as in fig. 337. Lingua of hypopharynx with well developed lateral processes (fig. 339), anterior margin cleft; superlingua of hypopharynx as in fig. 339, with a row of hair along anterior margin. Segment 2 of maxillary palpi a little longer than segment 1; segment 3, 1/2 length of segment 2, triangular; hair on maxillae as in fig. 336; a large tooth-like projection on inner anterolateral margin of maxillae (fig. 336). Labium as in fig. 340; segment 2 of palpi a little longer than segment 1; segment 3 of palpi 1/2 length of segment 2, triangular; paraglossae ventral to glossae. Fine hair on anterolateral margins of prothorax only. Legs (fig. 343): claws apically hooked, denticles on claws all about equal sized. Gills on segments 1-7; gill 1 slender (fig. 341); gills 2-7 alike, dorsal and ventral lamellae plate-like and terminated in 3, slender, subequal processes (fig. 342). Posterolateral spines on abdominal segments 3-9, spines progressively larger posteriorly; inner edge of spine on segment 9 curved and producing a 2nd blunt spine (fig. 344-345). Terminal filament longer than cerci.

History and discussion: Gillies (1951) established *Cryptopenella* for the single species *C. facialis* which he collected in Hong Kong. The species was originally described from the adults only. Herein the reared nymphs of *Cryptopenella* are described. The nymphs of *Cryptopenella* are most similar to those of *Choroterpes* and the nymphs of *Fulletomimus* (?) described by Demoulin; however, they can be distinguished from the above genera by the large tooth-like projection on the inner anterolateral margin of the maxillae (fig. 336), and the shape of the posterolateral spine on abdominal segment 9 (fig. 344-345).

Cryptopenella can be differentiated in the nymphs from all other genera of the Lep-tophlebiidae by the following combination of characters: (1) the dorsal and ventral lamellae of abdominal gills 2-7 are plate-like and terminated in 3, slender, subequal processes (fig. 342); (2) a large tooth-like projection occurs on the inner anterolateral margin of the maxillae (fig. 336), (3) posterolateral spines occur on abdominal segments 3-9, and (4) inner edge of spine on abdominal segment 9 is curved and producing a 2nd blunt spine (fig. 344-345).

Biology: Gillies (1951) included biological notes on *C. facialis*.

Genus *Thraululus* Eaton, 1881

Fig. 4, 51-53, 96, 124, 146-147, 166, 188, 210, 232, 254-255, 279, 309-311, 333-334.

Thraululus Eaton, 1881: 195, 1884 (1883-88): 106.—Ulmer, 1920: 117.—Lestage, 1921: 230.—Ulmer, 1932b: 204.

Masharikella Peters, Gillies & Edmunds, 1964: 118.—Peters & Edmunds, 1964: 248.

Type-species: *T. bellus* Eaton, by original designation.

Species included: *T. bellus* Eaton, 1881: 195; *T. duliti* (Demoulin, 1954: 124) [*Hagenulus* (?)] n. comb.; *T. fasciatus* (Kimmins, 1956: 81) (*Hagenulus*) n. comb.; *T. semicastanea* (Gillies, 1951: 125) (*Habrophlebiodes*) n. comb.; *T. torrentis* (Gillies In Peters, Gillies & Edmunds, 1964: 120) (*Masharikella*) n. comb.; *T. turbinatus* (Ulmer, 1909: 267) (*Hagenulus*) n. comb.

SPECIES EXAMINED. *T. bellus*, ♂ and ♀ imagos, nymph; *T. duliti*, ♂ imago; *T. fasciatus*, ♂ and ♀ imagos; *T. torrentis*, ♂ and ♀ imagos, nymph; *Thraululus* sp., numerous ♂ and ♀ imagos, nymphs from Comoro Islands, India, Nepal, Thailand, Malaya, Hong Kong, Philippine Is., Borneo, New Guinea, and New Ireland.

DISTRIBUTION: Ethiopian, Oriental, and Palearctic regions.

Imago. Length of ♂: body 5.0-7.2; fore wings 5.5-10.0 mm. Length of ♀: body 8.9-9.0; fore wings 8.5-10.0 mm. Eyes of ♂ meet on meson of head, lower portion of eyes 2/3 length of upper portion; ♀ eyes separated on meson of head by a space 4 × as great as maximum width of an eye. Wings: vein R_s of fore wings forked 1/4 or less distance from base to margin; vein MA forked 1/2 or more distance from base to margin, fork symmetrical; vein MP forked less than 1/3 to less than 1/4 of distance from base to margin, fork asymmetrical; cubital area as in fig. 51; cross veins numerous. Costal projection of hind wings well developed and acute (fig. 52) to blunt (fig. 53), apex of projection located about 1/2 of distance from base (fig. 52-53); cross veins few. Legs: ratios of segments in ♂ fore leg, 0.63: 1.00 (2.40 mm): 0.05: 0.36: 0.27: 0.18: 0.14. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 124). ♂ genitalia (fig. 96): segments 2 and 3 of forceps short; base of forceps broad, its inner margin forming an angular bend; penes tubular, divided. Ninth sternum of ♀ entire (fig. 146) or shallowly cleft (fig. 147). Terminal filament slightly longer than cerci.

Mature nymph. Head prognathous. Antennae 1.5-2 × as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 254 and 255; submedian and anteromarginal areas of hair ventrally; 5 denticles may (fig. 254) or may not (fig. 255) be present on anteromedian emargination. Left mandible as in fig. 232. Lingua of hypopharynx with well developed lateral processes (fig. 210), short hair on apex of lateral processes, anterior margin deeply cleft; superlingua of hypopharynx as in fig. 210, with a row of hair along anterior margin, lateral tips emarginate. Segment 2 of maxillary palpi 2/3 to equal in length to segment 1; segment 3 of palpi 3/4 to equal in length to segment 2, triangular; hair on maxillae as in fig. 188. Labium as in fig. 166; segment 2 of labial palpi 3/4 length of segment 1; segment 3 of palpi slightly shorter to slightly longer in length than segment 2, triangular; paraglossae ventral to glossae. Legs (fig. 279): apex of claws hooked and narrow, denticles on claws progressively larger apically. Gills on segments 1-7; dorsal and ventral portions of gill 1 slender, lanceolate (fig. 309), or dorsal portion of gill 1 slender, lanceolate, ventral portion ovate with fringed margins (fig. 310) or dorsal and ventral portions of gill 1 ovate with fringed margins (fig. 311); dorsal and ventral portions of gills 2-7 ovate with fringed margins (fig. 311). Small posterolateral spines on abdominal segments 8-9 or 7-9, spines progressively larger posteriorly. Terminal

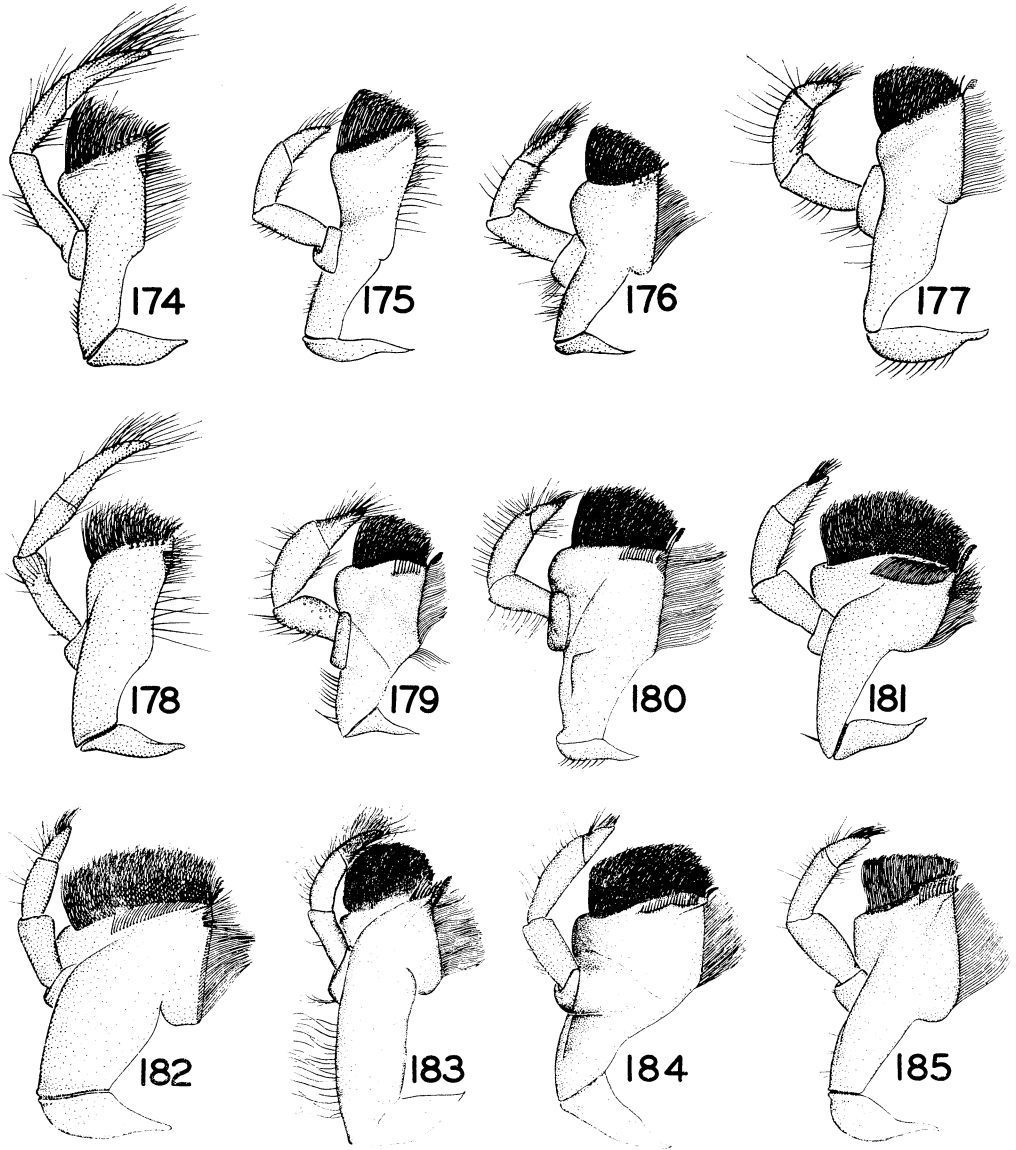


Fig. 174-185. Maxilla of mature nymph : 174, *Paraleptophlebia cincta*; 175, *Leptophlebia marginata*; 176, *Habroleptoides modesta*; 177, *Habrophlebia fusca*; 178, *Habrophlebiodes prominens*; 179, *Aprionyx intermedius*; 180, *Adenophlebia auriculata*; 181, *Atalophlebioides inequalis*; 182, *Kimminsula* sp.; 183, *Adenophlebiodes* sp.; 184, *Castanophlebia calida*; 185, *Choroerpes (Choroerpes) picteti*.

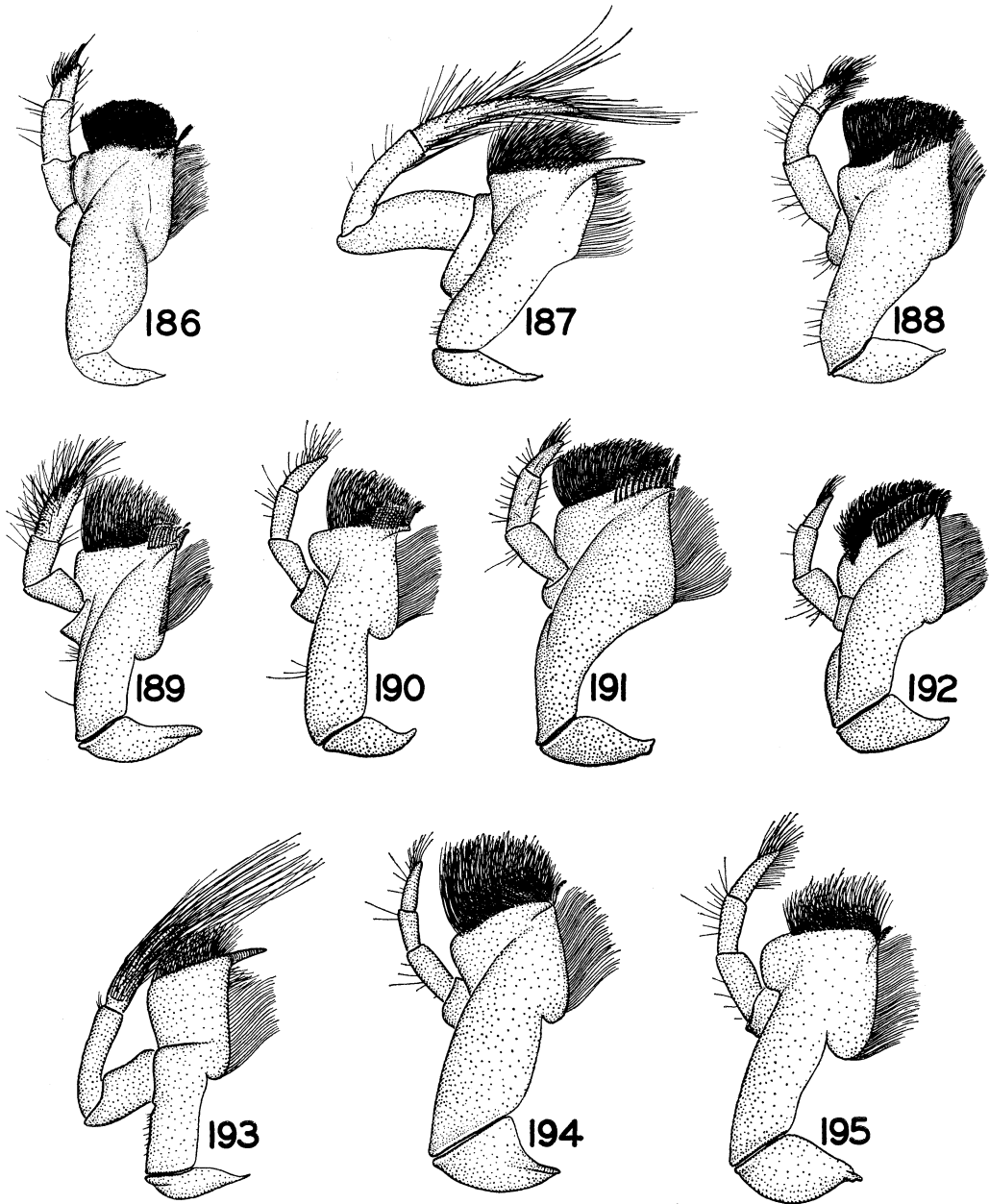


Fig. 186-195. Maxilla of mature nymph: 186, *Choroterpes (Euthraulius)* sp.; 187, *Choroterpides* sp.; 188, *Thraulius torrentis* n. comb.; 189, *Indialis badia* n. sp.; 190, *Megaglena brincki* n. sp.; 191, *Maheathraulius scotti*; 192, *Hagenulodes braueri*; 193, *Nathanella* sp.; 194, *Isca (Minyphlebia) janiceae* n. sp.; 195, *Isca (Tanycola) serendiba* n. sp.

filament slightly longer than cerci.

History and discussion: Eaton (1881) established the genus *Thraululus* for the European species *T. bellus*. Peters, Gillies & Edmunds (1964) described the genus *Masharikella* upon obtaining reared material of a new species from Africa. They indicated that *Masharikella* is closely related to the monotypic genus *Thraululus* and distinguished it from *Thraululus* in the adults by the shape of the costal projection of the hind wings (fig. 52) and the form of the tarsal claws (fig. 279), and in the nymphs by the form of the 1st abdominal gills (fig. 310). The dorsal and ventral portions of gill 1 of *Thraululus* are slender and lanceolate (fig. 309), while the dorsal portion of gill 1 of *Masharikella* is slender and lanceolate and the ventral portion is ovate and fringed (fig. 310). Also Peters, Gillies & Edmunds (1964) placed 2 Ethiopian species previously described in *Hagenulus*, 1 Oriental species provisionally described in *Hagenulus*, and 1 Oriental species previously described in *Habrophlebiodes* in the genus *Masharikella*. The nymphs of these 4 species are not known, and assignment of the species was based on the similarity of the fore and hind wings and ♂ genitalia.

Recently considerable reared and unreared material of this complex from the Ethiopian and Oriental regions and New Guinea has been made available to us. This material contains a 3rd group of species from New Guinea closely related to the nominal *Thraululus* and *Masharikella*. The 1st abdominal gills of the species of this group are similar to the middle abdominal gills; both the dorsal and ventral portions are ovate with fringed margins (fig. 311). Also the anterior margin of the labrum is deeply emarginated, and 5 denticles are present on this emargination (fig. 255), but those of *Thraululus* and *Masharikella* are not (fig. 254). The 9th sternum of the ♀ adults of this group is shallowly cleft (fig. 147), while those of *Thraululus* and *Masharikella* are entire (fig. 146). Van Bruggen (1957) pointed out that Ulmer had seen nymphs of this group from New Guinea.

The new material contains several reared species from Northern Thailand, India, and New Guinea. The fore and hind wings, claws and ♂ genitalia of the adults of these species are similar to those adult structures of *Masharikella* and the unnamed group in New Guinea. But the nymphal 1st gills of these species are similar to those of true *Thraululus*.

Additional adults, similar to adults from Thailand, India, and New Guinea and the unnamed group in New Guinea, are represented from Nepal, Malaya, Borneo, and the Philippine Islands. Imanishi (1940) illustrated a nymph similar to *Thraululus* from Japan, and nymphs of *Thraululus* are known from the Comoro Islands in the Ethiopian Region.

Peters, Gillies & Edmunds (1964) described the egg of *Masharikella* as terminating at each pole in 4-8 long, stout, curved spinous processes (fig. 334). Degrange (1960) described the egg of *Thraululus bellus* with no such terminating processes (fig. 333). However, no correlation seems to exist between egg types and the 3 groups of species. A Northern Thailand species of *Thraululus* possesses an egg similar to that described by Peters, Gillies & Edmunds (1964) for an Ethiopian species of *Masharikella*. Species of both the unnamed group and *Thraululus* in New Guinea possess eggs similar to the egg of *Thraululus bellus* described by Degrange (1960).

Although 3 natural groups apparently occur within this complex, separable in the nymphs only by the shape of the first abdominal gills, no concordant character separates

the adults of these same 3 groups. Apparently the 1st abdominal gill types present among species in the Ethiopian Region and New Guinea have evolved from the primitive slender, lanceolate gill condition existing in *Thraululus*. Therefore, we herein place *Masharikella* as a synonym of *Thraululus* and include the unnamed group of species in New Guinea in *Thraululus*, thus recognizing the genus as wide-ranging throughout the Eastern Hemisphere. As the 3 groups of *Thraululus* can be recognized only on the shape of the nymphal first gills, we have not recognized the three groups as subgenera. The shape of the costal projection and the tarsal claws of the type species, *T. bellus*, are not similar, however, to the corresponding structures of other species of *Thraululus*.

Previously 22 species from South America have been placed in *Thraululus*. However, all except *T. caribbeanus* Traver, *T. costalis* Navas, *T. demarara* Traver, and *T. larensis* Navas have now been assigned to other genera. Undoubtedly these 4 remaining species are not congeneric with the Eastern Hemisphere genus *Thraululus*.

Thraululus is most similar to *Simothraululus*. However, the costal projection of the hind wings of the adults of *Thraululus* is more acute and well developed (fig. 52), while that of *Simothraululus* is rounded and well developed (fig. 55). The penes of the adult ♂ of *Simothraululus* are serrated dorsally (fig. 97) but those of *Thraululus* are not (fig. 96).

Thraululus can be differentiated from all other genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) fork of vein MP of fore wings is closer to base of wings than fork of vein R_s (fig. 51); (2) 2 intercalaries occur in cubital area of fore wings (fig. 51); (3) ♂ penes are tubular, divided and simple (fig. 96); and (4) costal projection of hind wings acute and well developed (fig. 52), except for the costal projection of *T. bellus* which is more rounded (fig. 53). In the nymph, (1) dorsal and ventral portions of abdominal gills 2-7 ovate with fringed margins (fig. 311); (2) dorsal and ventral portions of abdominal gills 1 slender, lanceolate (fig. 309), or ovate with fringed margins (fig. 311), or dorsal portion slender, lanceolate and ventral portion ovate with fringed margins (fig. 310); (3) lateral tips of superlingua of hypopharynx emarginated (fig. 210); and (4) tarsal claws hooked and narrow and with a row of denticles that are progressively larger apically (fig. 279).

Biology: Eaton 1884 (1883-88), Réal (1947), and Verrier (1948) give biological information on *T. bellus*. Peters, Gillies & Edmunds (1964) included biological notes on *T. fasciatus* and *T. torrentis* from Africa and Tjønneland (1960) discussed the flight activity of *T. fasciatus* from Africa.

The nymphs of 1 species in New Guinea with the 1st abdominal gills similar to *T. bellus* occur in torrential, rock bottom areas of rivers. The subimagos emerge at dusk and the adults appear to mate in early morning in full sunlight.

The immature nymphs of another species in New Guinea with abdominal gills 1-7 alike occur in torrential, rock bottom areas of rivers. The mature nymphs occur in still and silted side pools. The subimagos emerge after dusk. Mating was not observed.

Genus *Simothraululus* Ulmer, 1939

Fig. 54-55, 97.

Simothraululus Ulmer, 1939: 508.

Type-species: *S. seminiger* Ulmer, by original designation.

Species included: *S. seminiger* Ulmer, 1939: 509.

SPECIES EXAMINED. None.

DISTRIBUTION: North Borneo.

Imago. ♀ unknown. Length of ♂: body 7.5; fore wings 8.0 mm. Eyes of ♂ meet on meson of head. Wings: vein R_s of fore wings forked more than 1/4 of distance from base to margin; vein MA forked more than 1/2 of distance from base to margin, fork symmetrical; vein MP forked more than 1/4 of distance from base to margin, fork symmetrical; cubital area as in fig. 54; cross veins few. Costal projection of hind wings well developed and rounded (fig. 55), apex of projection located near apex of wing (fig. 55). Male genitalia (fig. 97): Segments 2 and 3 of forceps short; penes tubular, divided, tip of each penis lobe pointed and curved ventrally, dorso-median area of each lobe serrated. (Description from Ulmer, 1939).

Mature nymph. Unknown.

History and discussion: Ulmer (1939) established *Simothraulius* for *S. seminiger* which is known from 1 ♂ imago.

Biology: The ♂ imago was collected in August.

Genus *Indialis* Peters and Edmunds, new genus

Fig. 5, 56-58, 98, 125, 167, 189, 211, 233, 256-257, 280, 312.

Imago. ♀ unknown. Length of ♂: body 4.5; fore wings 5.8 mm. Eyes of ♂ meet on meson of head, lower portion of eyes slightly shorter in length than upper portion. Wings vein R_s of fore wings forked less than 1/4 of distance from base to margin; vein MA forked over 1/2 of distance from base to margin, fork symmetrical; vein MP forked less than 1/2 of distance from base to margin, fork symmetrical; cubital area as in fig. 56; cross veins few. Costal projection of hind wings well developed and acute, apex of projection located 1/2 distance from base (fig. 58); cross veins few. Legs: claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 125). Male genitalia (fig. 98): segments 2 and 3 of forceps short, segment 1 broad, its inner margin forming an angular bend; penes tubular, divided and slender (fig. 98). Terminal filament slightly longer than cerci.

Mature nymph. Head prognathous. Antennae $2 \times$ as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 256; submedian areas of hair ventrally; 5 denticles on anteromedian emargination (fig. 257). Left mandible as in fig. 233. Lingua of hypopharynx with well developed lateral processes (fig. 211), anterior margin deeply cleft; superlingua of hypopharynx as in fig. 211, with a row of hair along anterior margin. Segment 2 of maxillary palpi equal in length to segment 1; segment 3 of palpi slightly longer than segment 2, triangular; dense long hair on segment 3, hair on remainder of maxillae as in fig. 189; a large tooth-like projection on inner anterior margin of maxillae (fig. 189). Labium as in fig. 167; segment 2 of palpi 3/4 length of segment 1; segment 3 of palpi a little longer in length than segment 2, triangular; paraglossae ventral to glossae. Fine hair present on posterolateral margins of prothorax only. Legs (fig. 280): apex of claws hooked, denticles on claws progressively larger apically. Gills on segments 1-7 alike, dorsal and ventral portions of lamellae slender, tracheae branched (fig. 312). Posterolateral spines on abdominal segments 5-9, spines progressively larger posteriorly. Terminal filament slightly longer than cerci.

Etymology: Indicus, L., meaning of India; alis, L., meaning pertaining to.

Type-species: *Indialis badia* Peters and Edmunds, n. sp.

Indialis badia Peters and Edmunds, new species Fig. 5, 56-58, 98, 125, 167, 189, 211,
233, 256-257, 280, 312.

♂ *subimago* (in alcohol). Upper portion of eyes dark brown, lower portion black. Ocelli light brown, head darker. Thorax dark brown, sutures lighter. Coxae of legs dark brown, trochanters lighter; remainder of legs hyaline, washed with light brown; a wide, transverse, dark brown band on apex of femora, a dark brown macula near middle of fore and middle femora, a wide, transverse, dark brown band near middle of hind femora. Wings (fig. 56-58): venation of wings light brown, darker near base; membranes hyaline, brown at base. Abdomen: terga 1-8 dark brown, posterior 1/2 of each tergum darker, a wide, lighter, median, longitudinal band on anterior 1/2 of each tergum; sterna 1-8 brown, posterior 1/2 of each sternum darker; segments 9 and 10 dark brown. Genitalia (fig. 98): forceps white, washed with light brown; penes brown. Caudal filaments hyaline.

♂ *imago*, ♀ *imago and subimago*. Unknown.

Mature nymph (in alcohol). Body dark brown, sutures and sterna paler, markings on abdomen as in imago. Legs and caudal filaments pale, markings on legs as in imago. Gills hyaline, tracheae black.

Holotype ♂ *subimago*, India: Kerala State, Koratty Riv., Erumeli, 56 km E. of Kottayam, 105 m, 6. II., W.L. & J.G. Peters; paratopotypes, 46 nymphs, same data as for holotype; paratypes, 3 nymphs, Andhra Pradesh State, Thannirpandal Riv., Kambakkam, 15 km W. of Tada, 12 m, 11. XII., W.L. & J.G. Peters. (Preserved in alcohol). Holotype, 16 paratopotypes, and 1 paratype deposited in the collections of Florida A & M University; 15 paratopotypes and 1 paratype each deposited in the collections of the University of Utah and B.P. Bishop Museum, Honolulu.

Etymology: badius, L., meaning dark brown.

Discussion: Although it is not our regular practice to place a ♂ *subimago* as the holotype, it is the only adult specimen of a new genus. However, the holotype specimen died during subimaginal moult and the genitalia and abdomen were fully out of the subimaginal skin before death. As the *subimago* ♂ specimen is associated with nymphal material from the same locality, it is considered best to describe the subimaginal specimen along with the nymphs of the genus *Indialis*.

The adults of *Indialis* are most similar to those of *Thraulius* and related genera. However, the adults of *Indialis* can be distinguished from those of *Thraulius* and related genera by veins R_s and MP of the fore wings being forked about equidistant from the base of the wings to the margin (fig. 56), the symmetrical fork of vein MP of the fore wings (fig. 56), and the well developed costal projection of the hind wings (fig. 57-58). Although the nymphs of *Indialis* are most similar to those of *Thraulius* and related genera, the labrum of *Indialis* has 5 denticles on the anteromedian emargination similar to those on the labrum of *Adenophlebia* and related genera in Africa. The nymphs of *Indialis* can be distinguished from those of *Thraulius* and related genera by the presence of abdominal gills 1-7 being alike and slender with tracheae branched (fig. 312). The nymphs of *Indialis* can be distinguished from those of *Adenophlebia* and related genera by the presence of a large tooth-like projection on the anterior margin of the maxillae (fig. 189), and by the slender abdominal gills (fig. 312).

Indialis can be differentiated from all other Leptophlebiid genera by the following combination of characters. In the imago, (1) ♂ penes are tubular, divided and slender

(fig. 98); (2) 2 intercalaries are present in cubital area of fore wings (fig. 56); (3) veins R_s and MP of fore wings are forked about equidistant from base to margin; fork of vein MP is symmetrical (fig. 56); and (4) costal projection of hind wings are well developed and acute (fig. 57-58). In the nymph, (1) abdominal gills 1-7 are alike and slender with tracheae branched (fig. 312); (2) a large tooth-like projection is present on inner anterior margin of the maxillae (fig. 189); (3) tarsal claws are hooked, with a row of denticles that are progressively larger apically (fig. 280); and (4) 5 denticles are present on anteromedian emargination of labrum (fig. 257).

Biology: Nymphs of *Indialis* are found in torrential areas of small streams to large rivers. Subimagos emerge after sunset.

Genus *Megaglana* Peters and Edmunds, new genus

Fig. 59-60, 99, 126, 148, 168, 190, 212, 234, 258, 281, 313, 324, 326.

Imago. Length of ♂: body 4.2-5.5; fore wings 4.0-5.5 mm. Length of ♀: body 4.4-5.2; fore wings 4.5-5.0 mm. Eyes of ♂ separated on meson of head by a narrow space; lower portion of eyes slightly shorter in length than upper portion; upper portion on long stalk (fig. 326), facets of upper portion large; ♀ eyes separated on meson of head by a length $3 \times$ as great as maximum width of an eye. Lateral ocelli of ♂ greatly enlarged (fig. 326). Wings (fig. 59-60): vein R_s of fore wings forked less than $1/4$ of distance from base to margin; vein MA forked more than $1/2$ of distance from base to margin, fork symmetrical; vein MP forked more than $1/3$ of distance from base to margin, fork symmetrical; cubital area as in fig. 59; cross veins few. Costal projection of hind wings well developed and rounded; apex of projection located less than $1/3$ distance from base (fig. 60); cross veins few. Legs: ratios of segments in ♂ fore legs, 0.43: 1.00 (2.80 mm): 0.04: 0.43: 0.36: 0.21: 0.07. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 126). ♂ genitalia (fig. 99): segments 2 and 3 of forceps short, base of forceps bulbous; penes divided, tubular (fig. 99). ♀ with well developed ovipositor or egg guide extending to posterior margin of abdominal segment 8 (fig. 324). Ninth sternum of ♀ deeply cleft apically (fig. 148). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae $3 \times$ as long as maximum length of head. Mouthparts (fig. 168, 190, 212, 234, 258): dorsal hair on labrum as in fig. 258; submedian and anterior areas of hair ventrally. Left mandible as in fig. 234. Lingua of hypopharynx with well developed lateral processes (fig. 212), anterior margin shallowly cleft; superlingua of hypopharynx as in fig. 212, with a row of hair along anterior margin. Segment 2 of maxillary palpi a little longer than segment 1; segment 3 equal in length to segment 2, triangular; hair on maxillae as in fig. 190; a large tooth-like projection on inner anterior margin of maxillae (fig. 190). Labium as in fig. 168; segment 2 of palpi a little shorter in length than segment 1; segment 3 of palpi $3/4$ length of segment 2, triangular; paraglossae ventral to glossae. Hair on anterolateral margins of prothorax only. Legs (fig. 281): apex of claws hooked and narrow, denticles on claws progressively larger apically, except apical denticle much larger. Gills on segments 1-7 alike, dorsal and ventral portions of lamellae slender, tracheae unbranched (fig. 313). Posterolateral spines on abdominal segments 5-9, spines progressively larger posteriorly. Terminal filament longer than cerci.

Etymology: mega, Gr., meaning large, great; glene, Gr., meaning eyeball.

Type-species: *Megaglana brincki* Peters and Edmunds, n. sp.

Megaglena brincki Peters and Edmunds, new species

Fig. 59-60, 99, 126, 148, 168, 190, 212, 234, 258, 281, 313, 324, 326.

♂ *Imago* (in alcohol). Upper portion of eyes and stalks light brownish orange, lower portion black. Ocelli light brown. Head, thorax and coxae of legs brown, sutures paler. Femora of prothoracic legs brown, remainder of legs pale except tip of tibiae brown; mesothoracic legs pale, except tip of tibiae washed lightly with brown; metathoracic legs pale except subapical portion of femora with a wide, brown, transverse band. Wings (fig. 59-60): longitudinal veins of fore and hind wings light brown, cross veins paler; membrane of fore and hind wings hyaline, except apical 1/3 of cells C and Sc translucent. Abdomen: terga 1-10 brown, a narrow, pale, longitudinal, median line on terga 1-9, a large, pale anteromedian and smaller, pale anterolateral maculae on terga 2-7, posterior margin of terga 1-9 darker brown; sterna light brown, posterior margin of terga 1-8 darker. Genitalia (fig. 99): brown. Caudal filaments light brown, annulations at articulations dark brown.

♀ *Imago* (in alcohol). Eyes black. Color of head, thorax, and coxae of legs as in ♂ imago. Color and markings of legs as in ♂ imago, except mesothoracic legs entirely pale. Color of fore and hind wings as in ♂ imago. Color and markings on abdominal terga as in ♂, except terga 2-7 each with narrow, pale, transverse, anterior and posterior bands, and narrow, pale, longitudinal bars; color and markings on abdominal sterna as in male, except sterna 2-7 with large, dark brown anterolateral spots. Well developed ovipositor or egg guide extending to posterior margin of abdominal segment 8 (fig. 324), ovipositor dark brown. Color and markings of caudal filaments as in male imago.

Mature nymph (in alcohol). Abdominal terga dark brown except lateral areas paler; color and markings of sterna as in imago. Color and markings of legs as in imago. Caudal filaments pale. Gills grayish blue, tracheae black.

Holotype ♂ imago, Ceylon: Sabaragamuwa Prov., Maratenna, 11 km N. Balangoda, 1350 m, 22. II. 1962. Allotype ♀ imago, Ceylon: West Prov., Labugama, 29 km. ESE Colombo, 21. I. 1962. Paratypes, CEYLON: 3 ♂ imagos, same data as for holotype; 1 ♂ imago, 1 ♀ imago, 1 nymph, same data as for allotype; 1 ♂ imago, Central Prov., Hakgala, 8 km SE Nuwara-Eliya, 3. III. 1962.; 2 nymphs, West Prov., Alawala, 31 km, NE Colombo, 17. I. 1962; 4 nymphs, Sabaragamuwa Prov., Deerwood Kuruwita, 10 km. NNE Ratnapura, 18-21. II. 62; 1 nymph, Sabaragamuwa Prov., Malwala, 5 km, NE Ratnapura, 20. II. 1962; 1 nymph, Sabaragamuwa Prov., Carney, 13 km, NE Ratnapura, 20. II. 1962; 1 nymph, Sabaragamuwa Prov., Lankaberiya, 10 km SE Rakwana, 28. II. 1962; 2 nymphs, Prov. of Uva, stream 3km, NW Haldummulla, 1080 m 2. III. 1962; 1 nymph, Central Prov., Muddok, 8 km, NW Nuwara-Eliya, 1650 m, 4. III. 1962; 5 nymphs, Central Prov., small stream in foothills of Knuckle Mountains, 16 km ENE Kandy, 11. III. 1962; 2 nymphs, Prov. of Uva, Yalakumbura, 8 km SSW Bibile, 390 m, 13. III. 1962; 4 nymphs, Central Prov., Harasbedda, 14 km NE Nuwara - Eliya, 15. III. 1962; 1 nymph, Central Prov., small stream on Horton Plains, 18 km. SSE Nuwara-Eliya, 2010 m, 19-20. III. 1962. All types are collected by P. Brinck, H. Andersson, and L. Cederholm and are in alcohol. Holotype, allotype, 1 ♂ imaginal paratype, and 9 nymphal paratypes are deposited in the collections of the Zoological Institute, Lund, Sweden. Two ♂ imaginal paratypes and 8 nymphal paratypes are deposited in the collections of the University of Utah. Two ♂, 1 ♀ imaginal paratype, and 8 nymphal paratypes are deposited in the collections of Florida A & M University.

Etymology: The species *M. brincki* is named for Prof. Dr Per Brinck, Zoological Institute, Lund, Sweden, who collected the specimens in Ceylon.

Discussion: *Megaglena* is most closely related to *Indialis* and related genera. However the adults of *Megaglena* can be distinguished from these genera by the well developed ♂ eyes (fig. 326), the well developed and rounded costal projection of the hind wings (fig. 60), and the bulbous base of the ♂ genital forceps (fig. 99). The nymphs of *Megaglena* can be distinguished from nymphs of these genera by similar slender abdominal gills on segments 1-7, with the tracheae unbranched (fig. 313), and the greatly enlarged apical denticle on the claws (fig. 281). The nymphs and adults of *Megaglena brincki* are associated from the same locality by the color markings on the legs and abdomen.

Megaglena can be differentiated from all other genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) upper portion of eyes of ♂ well developed and on a long stalk (fig. 326); (2) veins R_s and MP of fore wings forked about equidistant from base to margin (fig. 59); (3) penes of ♂ divided and tubular (fig. 99); and (4) costal projection of hind wings well developed and rounded (fig. 60). In the nymph, (1) abdominal gills 1-7 are alike and slender, with tracheae unbranched (fig. 313); (2) a large tooth-like projection present on inner anterior margin of the maxillae (fig. 190); (3) the tarsal claws are hooked, with a row of denticles that are progressively larger apically, apical denticle much larger (fig. 281); and (4) denticles are not present on the anterior emargination of the labrum (fig. 258).

Biology: The nymphs of *M. brincki* are found in small mountain streams.

Genus *Nathanella* Demoulin, 1955

Fig. 6, 68, 103, 128, 171, 193, 215, 237, 261, 284, 317.

Nathanella Demoulin, 1955: 1.

Type-species: *N. indica* Demoulin, by original designation.

Species included: *N. indica* Demoulin, 1955: 2.

SPECIES EXAMINED. *N. indica*, ♂ imago; *Nathanella* spp., nymphs from Southern India.

DISTRIBUTION: Southern India.

Imago. ♀ unknown. Length of ♂: body 7.5; fore wings 8.0 mm. Eyes of ♂ separated on meson of head by a narrow space, lower portion of eyes 3/4 length of upper portion. Wings (fig. 68): vein R_s of fore wings forked about 1/4 of distance from base to margin; vein MA forked slightly more than 1/2 of distance from base to margin, fork symmetrical; vein MP_2 attached at base to vein MP_1 by a cross vein more than 1/4 distance from base to margin (fig. 68); cubital area as in fig. 68; cross veins few. Hind wings absent. Legs: Ratios of segments in ♂ fore leg, 0.67: 1.00 (3.60 mm): 0.03: 0.33: 0.19: 0.11: 0.09. Claws alike, apically hooked, each with an opposing hook (fig. 128). ♂ genitalia (fig. 103): segments 2 and 3 of forceps short, base of forceps narrow; penes divided, tubular, base of penes moderately expanded laterally (fig. 103). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae $2 \times$ as long as maximum length of head. Mouthparts (fig. 171, 193, 215, 237, 261): dorsal hair on labrum as in fig. 261; submedian, anterior and lateral areas of hair ventrally. Left mandible as in fig. 237. Lingua of hypopharynx with well developed lateral processes (fig. 215), anterior margin shallowly cleft; superlingua

of hypopharynx as in fig. 215, with a row of hair along anterior margin. Maxillary palpi greatly elongated (fig. 193); segment 2 of maxillary palpi slightly longer in length than segment 1; segment 3 of palpi equal in length to segment 2, triangular; a large projection on inner anterior margin of maxillae (fig. 193); hair on maxillae as in fig. 193. Labium as in fig. 171; labial palpi greatly elongated (fig. 171); segment 2 of palpi a little shorter than 1/2 length of segment 1; segment 3 of palpi $4 \times$ length of segment 2, triangular; paraglossae ventral to glossae. Hair on dorsum of thorax and abdomen. Legs (fig. 284): Apex of claws hooked and narrow, a row of denticles on claw, apical denticle much larger. Gills (fig. 317) on segments 1-6 alike, both portions of lamellae plate-like, tracheae branched. Posterolateral spines on abdominal segments 7-9, those on segment 9 larger. Abdominal segments 7-9 greatly elongated. Terminal filament longer than cerci.

History and discussion: Demoulin (1955) established *Nathanella* for a distinctive species, *N. indica* Demoulin, known only from adults collected in Southern India. Herein the nymphs of *Nathanella* are described. They are associated by the developing wing pads and genitalia of the nymphs. The nymphs of *Nathanella* are most similar to those of *Choroterpides*; however, they can be distinguished from *Choroterpides* by the shape of the outer margin and presence of hair on the mandibles (fig. 237), and the large apical denticle on the nymphal claws (fig. 284).

Nathanella can be differentiated in the nymphs from all other genera of the Leptophlebiidae by the following combination of characters: (1) abdominal gills present on segments 1-6 (fig. 6); (2) maxillary palpi elongated and extend beyond lateral sides of head (fig. 6); (3) apical denticle on nymphal claws greatly enlarged (fig. 284); and (4) posterolateral spines present on abdominal segments 7-9.

Biology: The nymphs of *Nathanella* occur in mountain steams.

Genus *Notophlebia* Peters and Edmunds, new genus

Fig. 346-349.

Imago. ♀ unknown. Length of ♂: body 7.5; fore wings 8.0 mm. Eyes of ♂ meet on meson of head; lower portion of eyes 3/4 length of upper portion; upper portion on short stalk. Wings (fig. 346): vein R_s of fore wings forked less than 1/6 of distance from base to margin; vein MA forked more than 1/2 of distance from base to margin, fork symmetrical; vein MP_2 attached to vein MP_1 by a cross vein more than 1/4 of distance from base to margin; cubital area as in fig. 346; cross veins few, membrane of anal area enlarged posteriorly (fig. 346); cilia present on posterior margin of wings. Hind wings absent. Legs: ratios of segments in ♂ fore legs, 0.50: 1.00 (3.1 mm): 0.03: 0.29: 0.19: 0.10: 0.06. Claws dissimilar, 1 apically hooked, the other obtuse, pad-like (fig. 347). ♂ genitalia (fig. 348-349): segments 2 and 3 of forceps short, basal 1/2 of forceps segment 1 broad, its inner margin forming an extreme angular bend (fig. 348); penes divided, tubular, slender, apex of each penis lobe pointed and finely serrated (fig. 348-349). Terminal filament longer than cerci.

Mature nymph: Unknown.

Etymology: notos, Gr., meaning south; phlebos, Gr., meaning vein.

Type-species: *Notophlebia hyalina* Peters and Edmunds, n. sp.

Notophlebia hyalina Peters and Edmunds, new species Fig. 346-349.

♂ **Imago** (in alcohol). Upper portion of eyes chestnut brown, lower portion black. Ocelli

pale, base of ocelli darker. Head chestnut brown. Thorax chestnut brown, carinae darker, sutures pale. Coxae, trochanters, femora and base of tibiae of prothoracic legs chestnut brown, remainder of legs pale; mesothoracic and metathoracic legs chestnut brown, tarsi and claws pale. Wings (fig. 346): cross veins in basal portion of fore wings, cubital and anal veins and basal portion of remaining longitudinal veins chestnut brown, remainder of veins hyaline; membrane of fore wings hyaline, except basal 1/2 of cell Sc chestnut brown. Abdomen: Segments 1-7 hyaline, segments 8-10 chestnut brown; terga 2-7 with a narrow posterior, chestnut brown band, faded laterally. Genitalia (fig. 348-349): forceps pale, penes chestnut brown. Basal 5 segments of each caudal filament dark chestnut brown, remainder of filaments pale.

♀ *Imago*. Unknown.

Mature nymph. Unknown.

Holotype ♂ imago, India: Madras State, Kunjankhuzi, 120 m, 2. I. 1962, F. Schmid. Holotype in alcohol and deposited in the collections of Florida A & M University.

Etymology: *hyalinus*, L., meaning transparent.

Discussion: *Notophlebia* is most closely related to *Isca* and *Nathanella*. However the ♂ imagos of *Notophlebia* can be distinguished from these genera by the membrane of the anal area of the fore wings being enlarged posteriorly (fig. 346), and the penes being tubular, straight, and pointed (fig. 348-349).

Notophlebia can be differentiated from all other genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) hind wings absent; (2) cilia occur on posterior margin of fore wings (fig. 346); (3) membrane of anal area of fore wings enlarged posteriorly (fig. 346); and (4) penes of ♂ genitalia tubular, straight, and pointed (fig. 348-349).

Biology: Unknown.

Genus *Isca* Gillies, 1951

Fig. 69-71, 104-106, 129-130, 150-151, 172-173, 194-195, 216-217,
238-239, 262-263, 285-286, 318-321, 328-330, 332, 350-357.

Isca Gillies, 1951: 127.

Type-species: *I. (I.) purpurea* Gillies, by original designation.

Species included: *I. (M.) janiceae* Peters & Edmunds, n. sp. *I. (I.) purpurea* Gillies, 1951: 128; *I. (T.) serendiba* Peters & Edmunds, n. sp.

SPECIES EXAMINED. *I. (M.) janiceae*, ♂ and ♀ imagos, nymph; *I. (I.) purpurea*, ♂ imago, nymph; *I. (T.) serendiba*, ♂ and ♀ imagos, nymph.

DISTRIBUTION: Hong Kong, India, Ceylon, Thailand.

Imago. Length of ♂: body 2.2-5.0; fore wings 2.4-4.5 mm. Length of ♀: body 2.2-5.0; fore wings 2.6-4.5 mm. Eyes (fig. 328-330): ♂ eyes variable; ♀ eyes separated on meson of head by a length 3.5-4 × maximum width of an eye. Wings: vein R_s of fore wings forked 1/6 of distance from base to margin; vein MA forked from less to more than 1/2 of distance from base to margin (fig. 69-71); fork symmetrical (fig. 70) or asymmetrical (fig. 69, 71); vein MP_2 independent of vein MP_1 (fig. 69-70) or vein MP forked less than 1/2 of distance from

base to margin (fig. 71); cubital area as in fig. 69, 70, or 71; cross veins few; cilia on posterior margin of fore wings present (fig. 70-71) or absent (fig. 69). Hind wings absent. Legs: ratios of segments in ♂ fore legs variable. Claws dissimilar, 1 apically hooked (fig. 129) or apically hooked with a small opposing hook (fig. 130), the other obtuse, pad-like (fig. 129-130). Abdominal terga extend around onto venter of abdomen, this most marked on segment 7 but scarcely at all on segments 1 and 2, or abdominal terga extend only to lateral sides. ♂ genitalia (fig. 104-106): forceps and penes variable. Ninth sternum of ♀ entire (fig. 150), or shallowly cleft (fig. 151). Terminal filament longer than cerci.

Mature nymph. Head prognathous. Antennae $2.5 \times$ as long as maximum length of head. Mouthparts: dorsal hair on labrum as in fig. 262, 263 and 352; submedian and anterolateral areas of hair ventrally. Left mandible as in fig. 238, 239 and 351. Lingua of hypopharynx with well developed lateral processes (fig. 216-217, 353), anterior margin cleft; superlingua of hypopharynx as in fig. 216, 217 and 353, with a row of hair along anterior margin. Segment 2 of maxillary palpi equal in length to slightly longer than $3/4$ of segment 1; segment 3 equal in length to slightly longer than segment 2, triangular; hair on maxillae as in fig. 194, 195 and 350. Labium as in fig. 172, 173 and 354; segment 2 of palpi $3/4$ as long as segment 1; segment 3 slightly shorter to slightly longer in length than segment 2, triangular; paraglossae ventral to glossae. Legs (fig. 285-286, 355): claws apically hooked, a row of denticles on claws, apical denticle larger. Gills on segments 2-7; dorsal and ventral portions of gills 2-6 slender, tracheae unbranched (fig. 318, 320, 356); gill 7 consists of 1 lamella, slender, tracheae unbranched (fig. 319, 321, 357). Abdominal terga extend around to venter of abdomen as in fig. 332, abdominal gills ventral. Small posterolateral spines on abdominal segments 7-9, spines progressively larger posteriorly. Terminal filament slightly longer than cerci.

History and discussion: Gillies (1951) established *Isca* from ♂ and ♀ imagos of *I. purpurea* that he collected in Hong Kong and India. Herein the nymphs of *Isca* are described. Two new species of *Isca* are also described. Nymphs of these 2 species are congeneric with those of *I. purpurea*; however, the adults are so morphologically distinct from *I. purpurea* and each other that 2 new subgenera are established for these species herein.

Isca is most closely related to *Nathanella*. However, the adults of *Isca* can be distinguished from those of *Nathanella* by the dissimilar claws (fig. 129-130), and the absence of cross veins in the basal $1/2$ of cell C in the fore wings (fig. 69-71). The nymphs of *Isca* can be distinguished by the ventral slender gills (fig. 318-321, 332, 356-357.)

Isca can be differentiated from all other leptophlebiid genera by the following combination of characters. In the imago, (1) hind wings absent; (2) cross veins absent in basal $1/2$ of cell C in fore wings (fig. 69-71); (3) tarsal claws dissimilar (fig. 129-130); and (4) segments 2 and 3 of ♂ genital forceps short (fig. 104-106). In the nymph, (1) abdominal segments extend around to venter of abdomen as in fig. 332; (2) dorsal and ventral portion of abdominal gills 2-6 slender and tracheae unbranched (fig. 318, 320, 356); gill 7 consists of 1 slender lamella and tracheae unbranched (fig. 319, 321, 357); (3) claws apically hooked, and with a row of denticles; apical denticle larger (fig. 285-286, 355); and (4) small posterolateral spines present on abdominal segments 7-9, and spines progressively larger posteriorly.

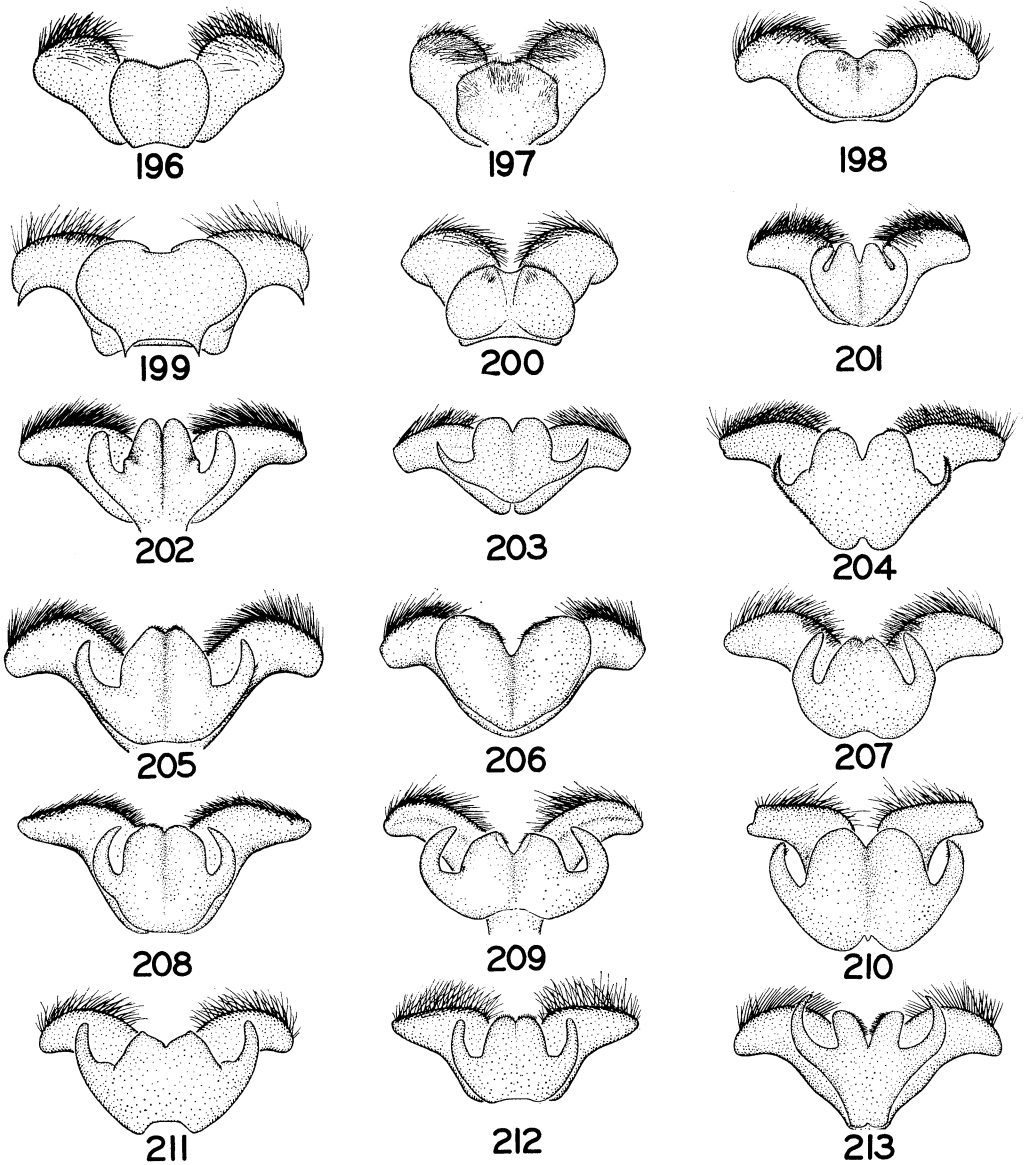


Fig. 196-213. Hypopharynx of mature nymph: 196, *Paraleptophlebia cincta*; 197, *Leptophlebia marginata*; 198, *Habroleptoides modesta*; 199, *Habrophlebia fusca*; 200, *Habrophlebiodes prominens*; 201, *Aprionyx intermedius*; 202, *Adenophlebia auriculata*; 203, *Atalophlebioides inequalis*; 204, *Kimminsula* sp.; 205, *Adenophlebiodes* sp.; 206, *Castanophlebia calida*; 207, *Choroterpes (Choroterpes) picteti*; 208, *Choroterpes (Euthraulius)* sp.; 209, *Choroterpides* sp.; 210, *Thraulius torrentis* n. comb.; 211, *Indialis badia* n. sp.; 212, *Megaglena brincki* n. sp.; 213, *Maheathraulius scotti*.

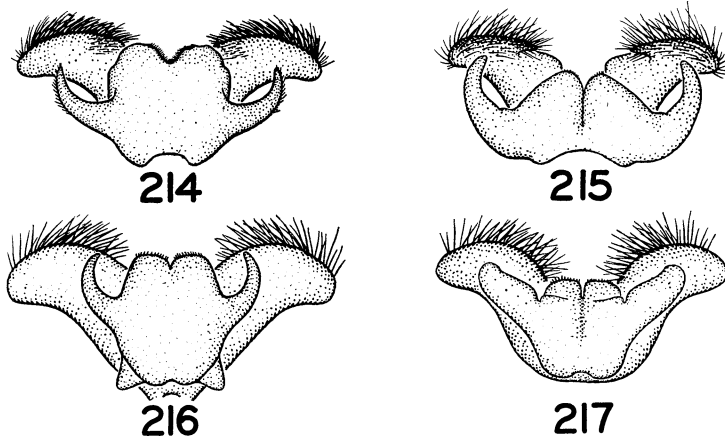


Fig. 214-217. Hypopharynx of mature nymph: 214, *Hagenulodes braueri*; 215, *Nathanella* sp.; 216, *Isca (Minyphlebia) janiceae* n. sp.; 217, *Isca (Tanycola) serendiba* n. sp.

Subgenus *Isca* s. s. Gillies, 1951

Fig. 71, 106, 330, 350-357.

Imago. Length of ♂: body 5.0; fore wings 4.5 mm. Length of ♀: body 4.5-5.0; fore wings 4.0-4.5 mm. Eyes (fig. 330): ♂ eyes separated on meson of head by a length $1.5 \times$ maximum width of median ocellus, upper portion of eyes on long stalk (fig. 330), dorsal aspect of upper portion circular shaped, facets of upper portion large, position of facets as in fig. 330. Wings: vein MA forked a little more than $1/2$ of distance from base to margin, fork asymmetrical; cilia present along posterior margin of wings (fig. 71). Legs: ratios of segments in ♂ fore legs, 0.33: 1.00 (2.40 mm): 0.02: 0.33: 0.29: 0.17: 0.04. Abdominal terga extend around onto venter of abdomen, this most marked on segment 7 but scarcely at all on segments 1 and 2. Genitalia (fig. 106): penes divided, tubular, broad, apex of each penis lobe curved inwardly and ventrally (fig. 106). Ninth sternum of ♀ apically cleft.

Discussion: The characters above will distinguish the adults of *Isca* s. s. from those of *Minyphlebia* and *Tanycola*. The nymphs of *Isca* s. s. are indistinguishable from those of *Minyphlebia* and *Tanycola*. Nymphs and adults of *Isca (I.) purpurea* are associated by rearing.

Biology: Gillies (1951) included biological notes on *I. (I.) purpurea*.

Subgenus *Minyphlebia* Peters and Edmunds, new subgenus

Fig. 69, 104, 129, 150, 172, 194, 216, 238, 262, 285, 318-319, 328, 332.

Imago. Length of ♂: body 2.2-2.8; fore wings 2.4-2.8 mm. Length of ♀: body 2.7; fore wings 2.6 mm. Eyes: ♂ eyes separated on meson of head by a length as great as maximum width of median ocellus, lower portion of eyes $3/4$ length of upper portion, upper portion on short stalk, dorsal aspect of upper portion kidney shaped, facets of upper portion large, position of facets as in fig. 328. Wings (fig. 69): vein MA forked more than $1/2$ of distance from

base of wings to margin, fork asymmetrical; cilia absent on posterior margin of fore wings (fig. 69). Legs: ratios of segments in ♂ fore legs, 0.50: 1.00 (0.40 mm.): 0.06: 0.38: 0.25: 0.25: 0.19. Abdominal terga extend only to lateral sides. Genitalia (fig. 104): Penes divided, tubular, broad, the outer margin of each penis lobe curved inwardly forming an apical point (fig. 104). Ninth sternum of ♀ entire (fig. 150).

Etymology: minys, Gr., meaning little; phlebos, Gr., meaning vein.

Type-species: *Isca (M.) janiceae* Peters and Edmunds, n. sp.

***Isca (Minyphlebia) janiceae* Peters and Edmunds, new species**

Fig. 69, 104, 129, 150, 172, 194, 216, 238, 262, 285, 318-319, 328, 332.

♂ *Imago* (in alcohol). Upper portion of eyes brown, lower portion black. Ocelli light brown. Head and antennae dark brown, flagella of antennae lighter. Thorax dark brown, sutures paler. Coxae of legs dark brown, remainder of legs lighter. Wings (fig. 69): Venation of fore wings light brown, membrane dark brown at wing bases, remainder of membrane hyaline. Hind wings absent. Abdomen: Terga generally dark brown, posterior margin of terga 1-8 paler, a median longitudinal dark stripe on terga 2-8; sternum 1 dark brown, sterna 2-8 light brown, lateral margins darker, sterna 9 and 10 dark brown. Genitalia (fig. 104): Genital forceps light brown, penes darker. Caudal filaments light brown.

♀ *Imago* (in alcohol). Eyes black. Head and antennae brown, ocelli paler. Thorax brown, sutures lighter. Wings: colored as in ♂ imago. Coxae of legs brown, remainder of legs lighter. Abdomen: terga uniformly brown, sterna paler. Caudal filaments light brown.

Mature nymph (in alcohol). Body brown, sutures and sterna paler, posterior margin of abdominal segments darker. Legs and caudal filaments light brown. Gills grayish blue, tracheae black.

Holotype ♂ imago, Thailand: Chiangmai Prov., Mae Ping, Chiangmai, 300 m, 13. XI. 1964, W. L. & J. G. Peters. Allotopotype ♀ imago, same data as type. Paratypes: THAILAND: 10 male imagos, same data as for holotype; 1 nymph, Chiangmai Prov., E fork Mae Ping at junc. with small stream, 59 km N Chiangmai, 405 m, 30. XI. 1964, W. L. & J. G. Peters; 4 nymphs, Chiangmai Prov., small stream and waterfalls, Doi Sutep, W of Chiangmai, 345 m, 8. XI. 1964, W. L. & J. G. Peters; 7 nymphs, 2. XII. 1964; 7 nymphs, 435 m, 11-19. XI. 1964; 7 nymphs, 480 m, 28. XI. 1964. All types are in alcohol. Holotype, allotype, 3 ♂ imaginal paratypes, and 7 nymphal paratypes are deposited in the collections of Florida A & M University. Four ♂ imaginal paratypes and 6 nymphal paratypes are deposited in the collections of the University of Utah. Three ♂ imaginal paratypes and 6 nymphal paratypes are deposited in the collections of the B. P. Bishop Museum, Honolulu.

Etymology: *Isca (M.) janiceae* is named in honor of the senior author's wife, Janice G. Peters, who collected the majority of the specimens of the species and who has contributed greatly to the present study.

Discussion: The characters above will distinguish the adults of *Minyphlebia* from those of the subgenera *Isca* s. s. and *Tanycola*. The nymphs of *Minyphlebia* are indistinguishable from those of *Isca* s. s. and *Tanycola*. Nymphs and adults of *Isca (M.) janiceae* are associated from developing wing pads and genitalia of mature nymphs and matching color patterns on the legs and abdomen.

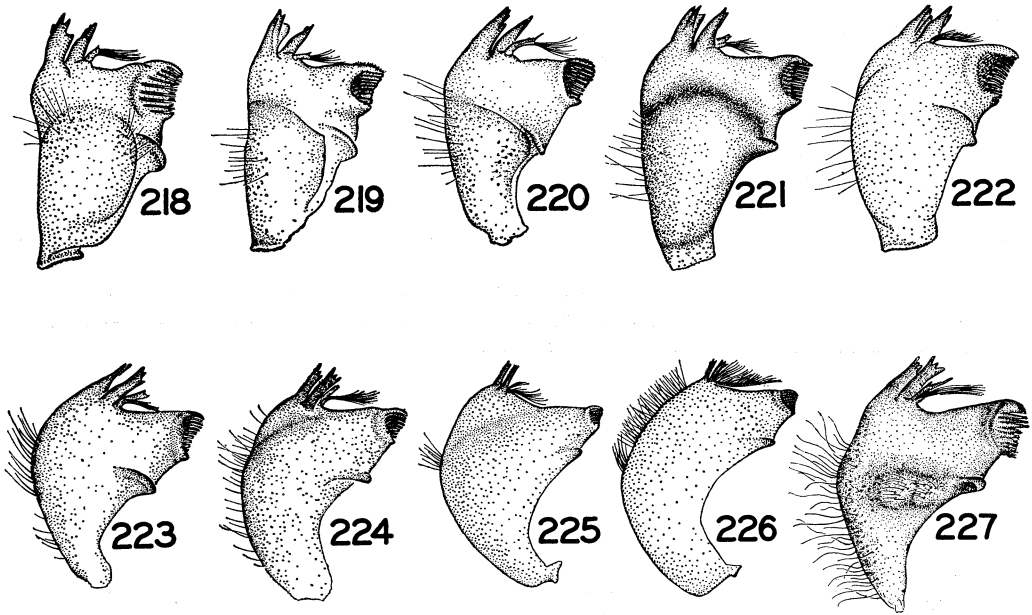


Fig. 218-227. Left mandible of mature nymph: 218, *Paraleptophlebia cincta*; 219, *Leptophlebia marginata*; 220, *Habroleptoides modesta*; 221, *Habrophlebia fusca*; 222, *Habrophlebiodes prominens*; 223, *Aprionyx intermedius*; 224, *Adenophlebia auriculata*; 225, *Atalophlebioides inequalis*; 226, *Kimminsula* sp.; 227, *Adenophlebiodes* sp.

Biology: Nymphs are found underneath stones and rocks in the quiet portions of mountain streams and lowland large rivers. Adults swarm in the late afternoon before sunset.

Subgenus *Tanycola* Peters and Edmunds, new subgenus

Fig. 70, 105, 130, 151, 173, 195, 217, 239, 263, 286, 320-321, 329.

Imago. Length of ♂: body 2.8-4.2; fore wings 2.8-4.0 mm. Length of ♀: body 2.2; fore wings 2.8 mm. Eyes (fig. 329): ♂ eyes separated on meson of head by a length $3 \times$ as great as maximum width of a lateral ocellus, lower portion of eyes $1/2$ length of upper portion, upper portion contiguous with lower portion, dorsal aspect of upper portion half circle in shape, facets of upper portion small, position of facets as in fig. 329. Wings: vein MA forked less than $1/2$ of distance from base to margin, fork symmetrical; cilia present on posterior margin of fore wings (fig. 70). Legs: ratios of segments in ♂ fore legs, 0.34: 1.00 (1.90 mm): 0.03: 0.32: 0.24: 0.24: 0.11. Abdominal terga extend only to lateral sides. Genitalia (fig. 105): Penes divided, apical $1/2$ of each penis lobe slender, tubular, basal $1/2$ of each penis lobe greatly expanded laterally (fig. 105). Ninth sternum of ♀ shallowly cleft (fig. 151).

Etymology: tany, Gr., meaning long; kolon, Gr., meaning leg.

Type-species: *Isca* (*T.*) *serendiba* Peters and Edmunds, n. sp.

***Isca (Tanycola) serendiba* Peters and Edmunds, new species**

Fig. 70, 105, 130, 151, 173, 195, 217, 239, 263, 286, 320-321, 329.

♂ *Imago* (in alcohol). Upper portion of eyes orangish brown, lower portion black. Head and thorax dark brown; ocelli, antennae, and sutures of thorax paler. Coxae of legs dark brown; femora of prothoracic legs brown, apical 1/3 of outer surface dark brown, remainder of legs paler except apical and distal tips of tibiae dark brown; remainder of mesothoracic and metathoracic legs brown. Wings (fig. 70): venation of fore wings brown; membrane brown, translucent; cilia present on posterior margin of fore wings. Hind wings absent. Abdomen: Abdominal terga and sterna brown, anterior margin of segments 2-7 hyaline and washed lightly with brown; posterior margin of segments 1-9 dark brown. Genitalia (fig. 105): penes brown, genital forceps pale. Caudal filaments pale.

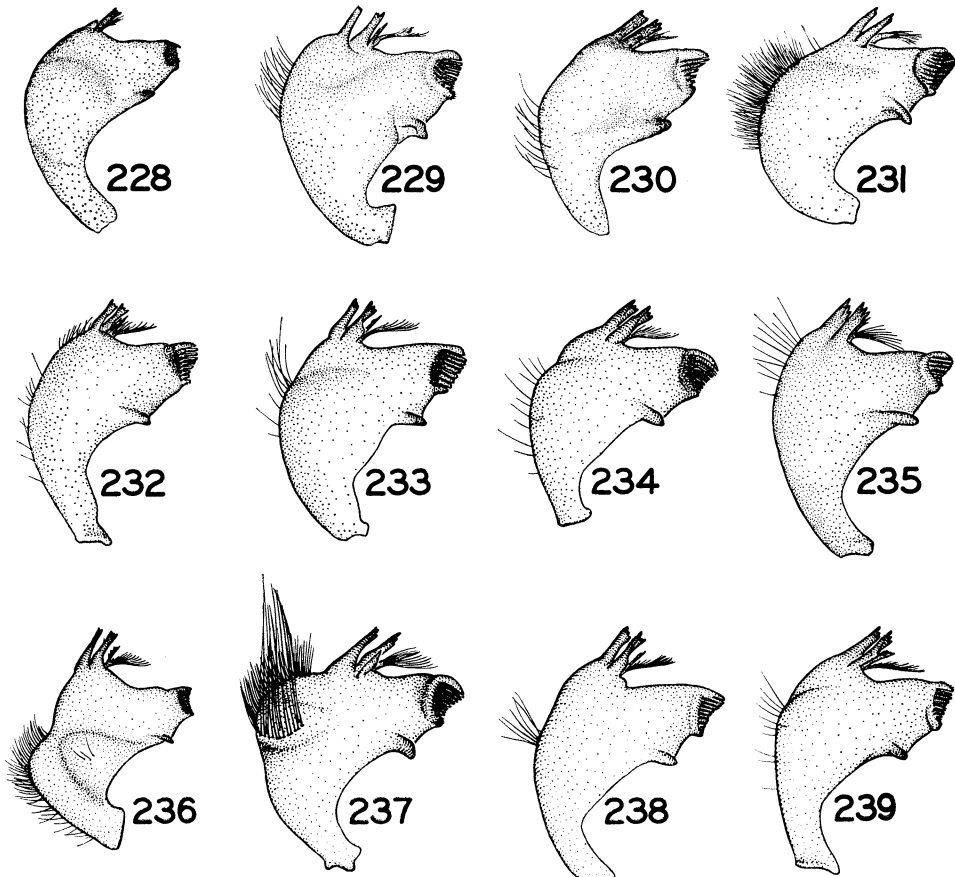


Fig. 228-239. Left mandible of mature nymph: 228, *Castanophlebia calida*; 229, *Choroterpes (Choroterpes) picteti*; 230, *Choroterpes (Euthraulus)* sp.; 231, *Choroterpides* sp.; 232, *Thraululus torrentis* n. comb.; 233, *Indialis badia* n. sp.; 234, *Megaglena brincki* n. sp.; 235, *Maheathraululus scotti*; 236, *Hagenulodes braueri*; 237, *Nathanella* sp.; 238, *Isca (Minyphlebia) janiceae* n. sp.; 239, *Isca (Tanycola) serendiba* n. sp.

♀ *Imago* (in alcohol). Eyes black. Head, antennae, and thorax brown; ocelli and sutures of thorax paler. Wings: colored as in ♂ imago. Legs brown (prothoracic legs broken off and missing). Abdomen: brown, posterior margin of segments 1-9 darker. Caudal filaments brown.

Mature nymph (in alcohol). Dorsum of head, thorax and abdomen brown, posterior margin of terga 2-9 with a wide, transverse, dark brown band. Venter of head, thorax and abdomen pale. Gills grayish blue, tracheae black. Caudal filaments pale.

Holotype ♂ imago, Ceylon: West Prov., Paddy field, Yakkala, 29 km NE Colombo, 16-28. II. 62. Allotype ♀ imago, Ceylon: Central Prov., stream, Rambukpath Oya, 16 km NW Hatton, 18. III. 1962. Paratypes: CEYLON: 4 ♂ imagos, same data as for holotype; 31 ♂ imagos, same data as for allotype; 2 ♂ imagos, Sabaragamuwa Prov., Gillmale, 9.6 km NE Ratnapura, 90 m, 20. II. 1962; 11 ♂ imagos, 2 nymphs, Sabaragamuwa Prov., stream, Hatherleigh, 1.6 km S Rakwana, 510 m, 28. II. 1962; 2 ♂ imagos, Sabaragamuwa Prov., stream, Allerton, 1.6 km SW Rakwana, 28. II. 1962; 4 nymphs, West Prov., stream, Alawala, 42 km NE Colombo, 17-18. I. 1962; 4 nymphs, South Prov., stream, Haycock, 34 km NNE Galle, 28. I. 1962; 1 nymph, Northwest Prov., stream, Andapolakanda, 5 km NE Melsiripura, 7. II. 1962; 4 nymphs, Sabaragamuwa Prov., stream, Malwala, 5 km NE Ratnapura, 20. II. 1962; 1 nymph, Sabaragamuwa Prov., mountain river, Carney, 10 km NE Ratnapura, 300 m, 20. II. 1962; 4 nymphs, Sabaragamuwa Prov., stream, 8 km NNW Balangoda, 1050 m, 22. II. 1962; 3 nymphs, Sabaragamuwa Prov., Maratenna, 11 km N Balangoda, 1350 m., 22. II. 1962; 1 nymph, Sabaragamuwa Prov., stream from Mantalawa Mountain, 14 km NNE Belihul-Oya, 1610 m, 1. III. 1962; 1 nymph, Sabaragamuwa Prov., Belihul-Oya, 540 m, 1-2. III. 1962; 1 nymph, Prov. of Uva, Beauvais, 8 km WNW Haputale, 1350 m, 3. III. 1962; 1 nymph, Central Prov., small stream, Hakgala, 8 km SE Nuwara-Eliya, 3. III. 1962; 8 nymphs, Central Prov., Udawela near Teldeniya, 13 km E. Kandy, 450 m, 11. III. 1962; 16 nymphs, Central Prov., stream, foothills of Knuckle Mountains, 16 km ENE Kandy, 11. III. 1962; 3 nymphs, Central Prov., Horton Plains, 18 km SSE Nuwara-Eliya, 2010 m, 19-20. III. 1962. All types are collected by P. Brinck, H. Andersson, and L. Cederholm and are in alcohol. Holotype, allotype, 14 ♂ imaginal paratypes, and 15 nymphal paratypes are deposited in the collections of the Zoological Institute, Lund, Sweden. Twelve ♂ imaginal paratypes and 13 nymphal paratypes each are deposited in the collections of the University of Utah, Florida A & M University and the Bernice P. Bishop Museum.

Etymology: Serendib, Arab., meaning Ceylon.

Discussion: The characters above will distinguish the adults of *Tanycola* from those of the subgenera *Isca* s. s. and *Minyphlebia*. The nymphs of *Tanycola* are indistinguishable from those of *Isca* s. s. and *Minyphlebia*. Nymphs and adults of *Isca* (*T.*) *serendiba* were associated from the same locality. Adults of a 2nd undescribed species of *Tanycola* are in our collections; this species has been collected from several localities in Assam, India.

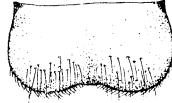
Biology: Nymphs are found in mountain streams and rivers.

PHYLOGENY AND RELATIONSHIPS OF THE EASTERN HEMISPHERE GENERA

The phylogeny and relationships of the Eastern Hemisphere genera of Leptophlebiidae will be more fully understood when the study is extended to include all the genera. At



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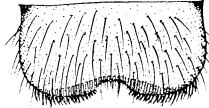
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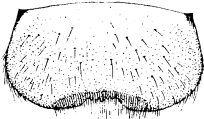
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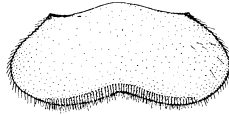
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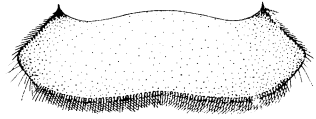
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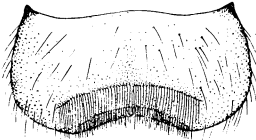
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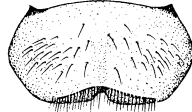
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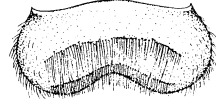
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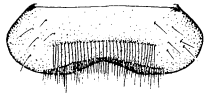
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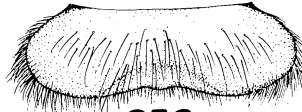
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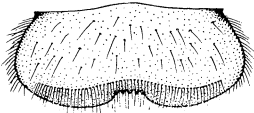
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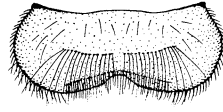
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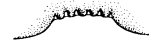
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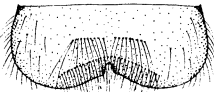
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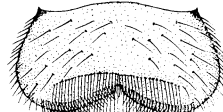
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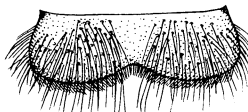
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present, the numerous leptophlebiid genera occurring in South America, Australia, and New Zealand are particularly in need of comparative study. However, there are enough genera whose evolution appears to have occurred primarily in the Eastern Hemisphere that many conclusions can be drawn relative to the phylogeny of these genera.

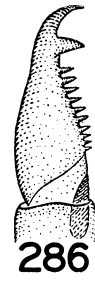
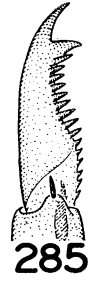
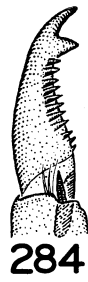
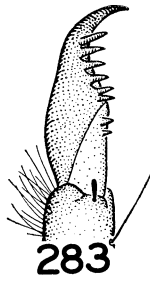
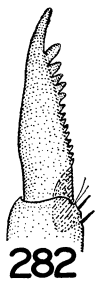
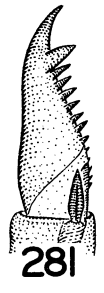
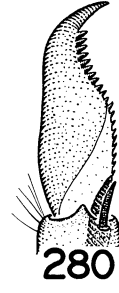
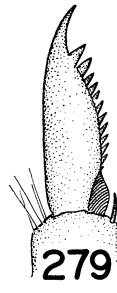
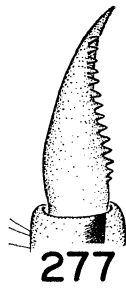
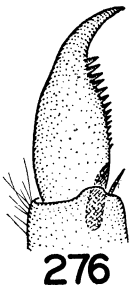
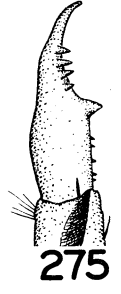
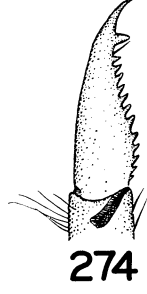
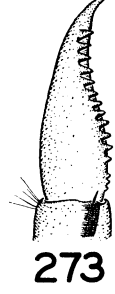
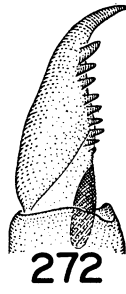
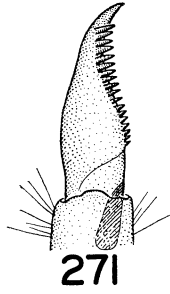
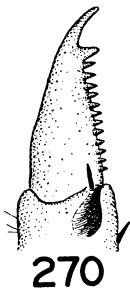
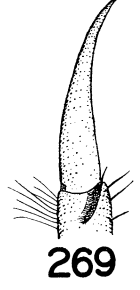
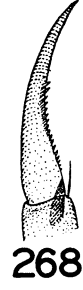
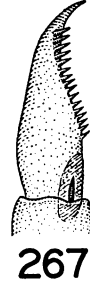
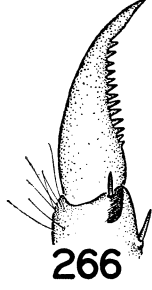
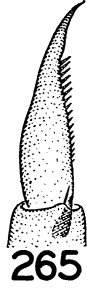
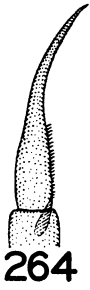
Little has been written concerning the phylogeny and relationships of the Eastern Hemisphere genera of the Leptophlebiidae, except for the discussion by Peters & Edmunds (1964) on the relationships of the African genera. They noted that *Adenophlebia* and *Aprionyx* are apparently closely related to genera occurring in southern South America, New Zealand, and Australia. The remaining African genera are all closely related to one another and together with a number of European and Asiatic genera form a single complex centering around the *Choroterpes* and *Thraululus* types.

Listed in Table 1 are a few hypothetical characters of the ancestral leptophlebiid type, based on data from recent taxa. The fossil record gives little or no aid in establishing these criteria. Tshernova (1962) reported only 4 records of fossil Leptophlebiidae and Demoulin (1965, 1968) has recently established 3 genera for 4 species. The extinct genus *Mesobaetis* Brauer, Redtenbacher & Gangebauer is known from the Lower Jurassic in Siberia and North America. The genus is known only from nymphs which have a broad abdomen, 3 caudal filaments, and thin unclear gills. There are no characteristics evident that would allow the genus to be placed to family with confidence. One fossil species of *Atalophlebia* is known from the adults from the Miocene of Australia. One fossil species of *Paraleptophlebia*, 1 undescribed fossil species of *Choroterpes*?, 1 fossil species of *Xenophlebia* Demoulin, 1 fossil species of *Blasturophlebia* Demoulin, and 2 fossil species of *Oligophlebia* Demoulin are known from the adults from Baltic amber in Europe. *Oligophlebia* resembles the recent genus *Calliarceus*, while *Blasturophlebia* resembles to a certain extent the recent genus *Deleatidium*. *Xenophlebia* is known only from 1 male subimaginal skin, but Demoulin (1968) believes the genus resembles *Leptophlebia* (*Blasturus*).

The most primitive furcation in the evolution of the Eastern Hemisphere Leptophlebiidae is hypothesized in fig. 1 by daughter line I. Daughter line I represents an ancient Northern Hemisphere dispersal. The adult males of all recent genera of this line possess a 9th sternum which is greatly enlarged posteriorly and deeply cleft (fig. 72-73, 76-79), except that the enlargement is secondarily reduced in *Habroleptoides* and *Habrophlebia* (fig. 74-75). The brush on the anterior margin of the maxillae of these genera is composed entirely of fine hair (fig. 174-178). Also the linguae of the hypopharynx do not have lateral projections (fig. 196-200).

Daughter line IA (fig. 1) represents the recent genera *Paraleptophlebia*, *Leptophlebia*,

Fig. 240-263. Labrum of mature nymph: 240, *Paraleptophlebia cincta*; 241, *Leptophlebia marginata*; 242, *Habroleptoides modesta*; 243, *Habrophlebia fusca*; 244, *Habrophlebiodes prominens*; 245, *Aprionyx intermedius*; 246, *Adenophlebia auriculata*; 247, *Atalophlebioides inequalis*; 248, *Kimminsula* sp.; 249, *Adenophlebiodes* sp.; 250, *Castanophlebia calida*; 251, *Choroterpes* (*Choroterpes*) *picteti*; 252, *Choroterpes* (*Euthraululus*) sp.; 253, *Choroterpides* sp.; 254, *Thraululus torrentis* n. comb.; 255, *Thraululus* sp.; 256, *Indialis badia* n. sp.; 257, *Indialis badia* n. sp., detail of denticles on anterior emargination; 258, *Megaglena brincki* n. sp.; 259, *Maheathraululus scotti*; 260, *Hagenulodes braueri*; 261, *Nathanella* sp.; 262, *Isca* (*Minyphlebia*) *janiceae* n. sp.; 263, *Isca* (*Tanycola*) *serendiba* n. sp.



Habroleptoides, *Habrophlebia*, and *Calliarcys*. Four or 5 intercalaries are present in the Cu area of the fore wings of these genera (fig. 9, 11, 13, 15, 17). An even row of hair is not present along the dorsal anterior margin of the labrum (fig. 240-243).

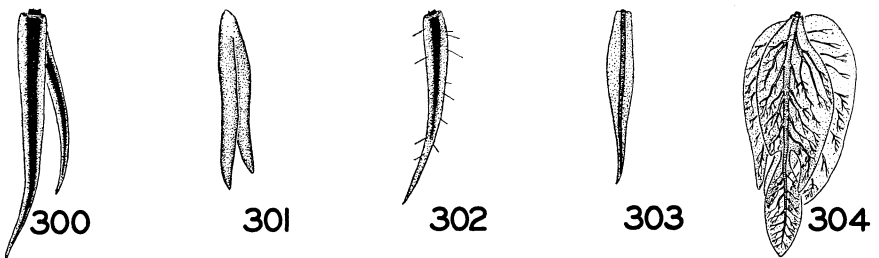
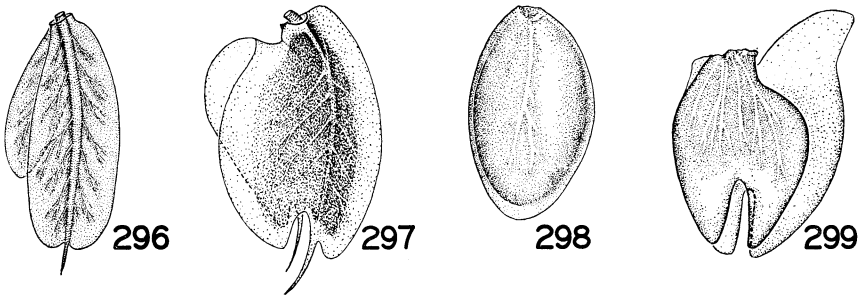
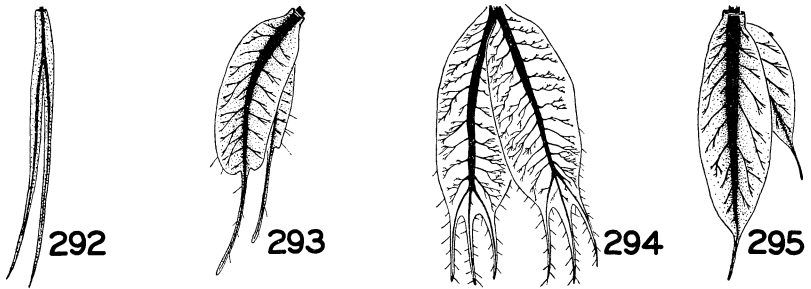
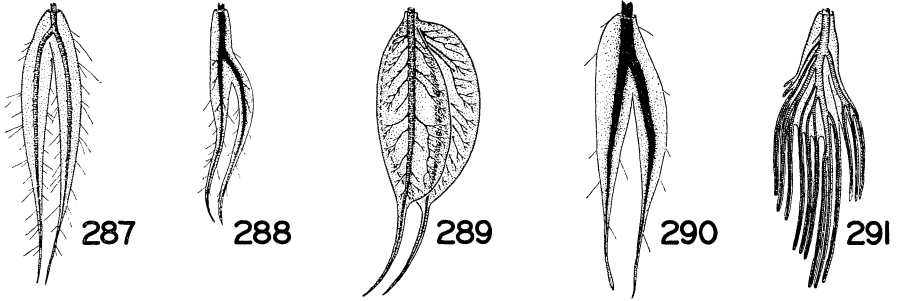
Daughter line IA1 (fig. 1) represents the line of evolution to the most primitive existing genera of the Leptophlebiidae, *Leptophlebia* and *Paraleptophlebia*. The fore wings are distinctly triangular and the cubital area is well developed (fig. 9, 11), which herein is considered to be a primitive condition. The hind wings of these 2 genera are large with numerous veins and cross veins (fig. 10, 12) and the anterior margin of the hind wings is smoothly convex and without a costal projection. Well developed hind wings are a primitive characteristic of the Leptophlebiidae. The penis lobes of the male genitalia of these 2 genera are partially fused (fig. 72-73). Fused penis lobes are normally considered to be a specialized condition. However the evidence is not conclusive as to whether the penis lobes of the ancestral leptophlebiid type were fused or divided. The heads of the nymphs of *Leptophlebia* and *Paraleptophlebia* are hypognathous which is assumed to be primitive as it is the condition in most mayfly families. *Leptophlebia* and *Paraleptophlebia* both occur in the Palearctic and Nearctic regions.

Daughter line IA2 (fig. 1) represents the recent genera *Habroleptoides*, *Habrophlebia*, and *Calliarcys*. The anterior margin of the hind wings of these genera have a costal projection, but it is often not developed (fig. 14, 16, 18). The nymphal heads are prognathous. *Habroleptoides* and *Calliarcys* occur in the Palearctic Region, while *Habrophlebia* occurs in both the Palearctic and Nearctic regions.

Daughter line IB (fig. 1) represents the recent genera *Habrophlebiodes*, *Dipterophlebiodes*, and *Gilliesia*. Two intercalaries are present in the Cu area of the fore wings of these genera (fig. 19, 22-23). The anal fan of the fore wings is reduced thus making the wings less triangular (fig. 19, 22-23). Without question the reduction in wing structure and venation is independent of that in line IA2. An even row of hair occurs along the dorsal, anterior margin of the labrum (fig. 244). Unfortunately, the nymphs of *Dipterophlebiodes* and *Gilliesia* are unknown. *Habrophlebiodes* nymphs are so much like those of *Paraleptophlebia* that it is certain that the ancestor of *Habrophlebiodes* was *Paraleptophlebia*-like. Because *Paraleptophlebia* nymphs remain completely plesiomorphic it is impossible to determine whether the line split from *Paraleptophlebia*-like forms early or late. Since the modifications of the adult are principally those of wing reduction it could be that the branching took place at a much later date than indicated on the phylogeny diagram. *Dipterophlebiodes* and *Gilliesia* occur in the Oriental Region, while *Habrophlebiodes* occurs in the Oriental and Nearctic regions.

Apparently, dispersal between the Palearctic and Oriental regions and between the Palearctic and Nearctic regions occurred several times during the evolution of daughter

Fig. 264-286. Fore nymphal claw: 264, *Paraleptophlebia cincta*; 265, *Leptophlebia marginata*; 266, *Habroleptoides modesta*; 267, *Habrophlebia fusca*; 268, *Habrophlebiodes prominens*; 269, *Aprionyx intermedius*; 270, *Adenophlebia auriculata*; 271, *Atalophlebioides inequalis*; 272, *Kimminsula* sp.; 273, *Adenophlebiodes* sp.; 274, *Adenophlebiodes* sp.; 275, *Castanophlebia calida*; 276, *Choroterpes* (*Choroterpes*) *picteti*; 277, *Choroterpes* (*Euthraulius*) sp.; 278, *Choroterpides* sp.; 279, *Thraulius torrentis* n. comb.; 280 *Indialis badia* n. sp.; 281, *Megaglana brincki* n. sp.; 282, *Maheathraulius scotti*; 283, *Hagenulodes braueri*; 284, *Nathanella* sp.; 285, *Isca* (*Minyphlebia*) *janiceae* n. sp.; 286, *Isca* (*Tanycola*) *serendiba* n. sp.



line I. Each of the 3 major lines of evolution has at least 1 genus present in both the Eastern and Western Hemispheres. The genera of daughter line IB are most distinct and definable in the Palearctic region, while the genera of daughter line IA are most distinct and definable in the Nearctic region.

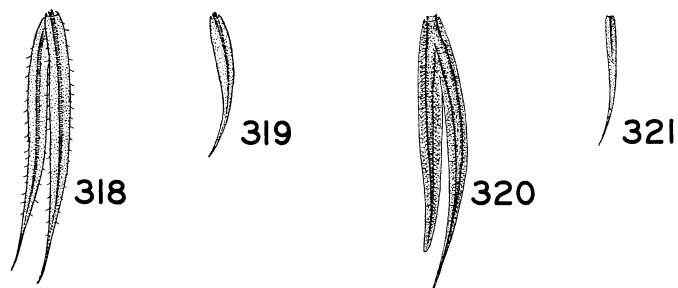
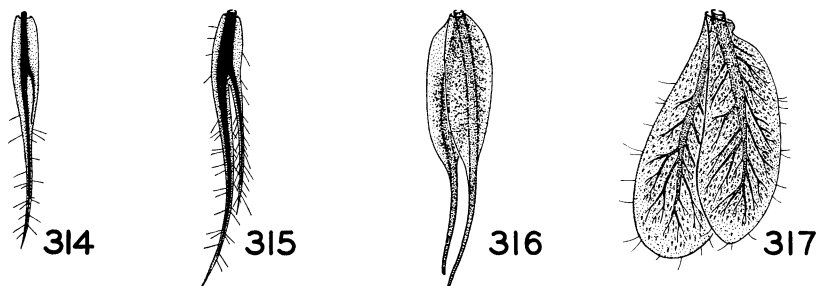
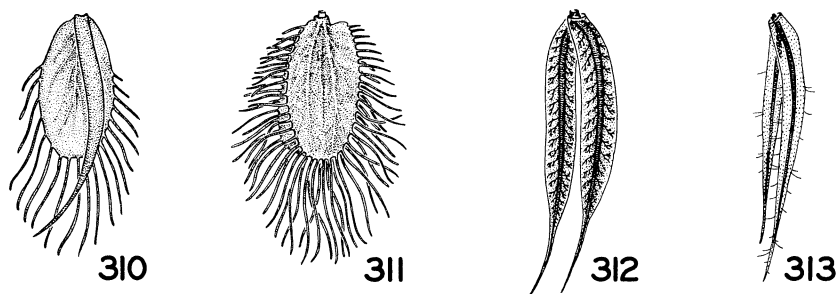
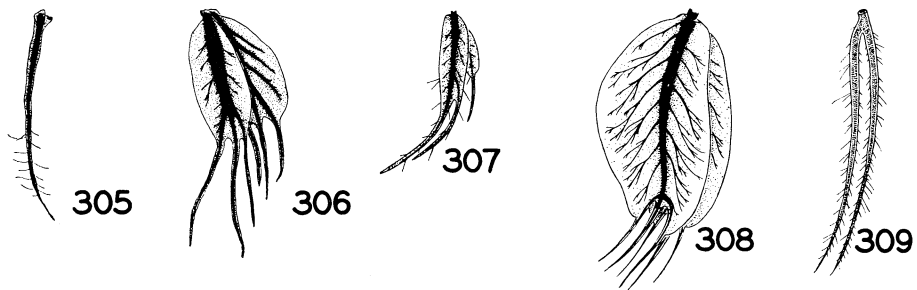
It is not known what affinities the South American, New Zealand, and Australian genera of Leptophlebiidae have with those of daughter line I.

Daughter line II (fig. 1) represents an ancient Southern Hemisphere dispersal which apparently later reinvaded the Northern Hemisphere several times. The adult males of all except 1 of the recent genera of this line possess a 9th sternum which is not greatly enlarged posteriorly and not deeply cleft (fig. 81-106). In males of *Cryptopenella* the 9th sternum is greatly enlarged and almost completely covers the penes (fig. 93), but it is formed differently than the enlargement of the 9th sternum of the recent genera of daughter line I and is presumed to have been a parallel evolutionary derivation. The brush on the anterior margin of the maxillae of these genera is composed of fine hairs and thick spines (fig. 179-195). The thick spines on the brush are secondarily lost in the nymphs of *Nathanella* (fig. 193). Also the linguae of the hypopharynx in these genera possess well developed lateral projections (fig. 201-217). The lingual projections on the hypopharynx are secondarily lost in *Castanophlebia* (fig. 206).

Daughter line IIA (fig. 1) represents the line of evolution to the most primitive recent genera of daughter line II, *Aprionyx*, *Adenophlebia*, and *Atalophlebioides*, all of which occur in the Ethiopian region. *Aprionyx* and *Adenophlebia* occur in South Africa. *Atalophlebioides* is known in the Eastern Hemisphere only from nymphs collected in Madagascar. As pointed out by Peters & Edmunds (1964) the nymphs from Madagascar generally resemble nymphs of the New Zealand *Atalophlebioides*. Until *Atalophlebioides* and related genera in South America and Australia can be studied in detail, and reared material of the Madagascar species is available, the Madagascar species should remain provisionally in *Atalophlebioides*. The male penes are fused nearly to the apex (fig. 81-83) in all 3 genera, and there is no V-shaped ridge on the ventral surface of the maxillae near the inner anterolateral margin (fig. 179-181).

As noted previously by Peters & Edmunds (1964) *Aprionyx* and *Adenophlebia* are most closely related to a complex of genera occurring in South America, Australia, and New Zealand. Both genera have primitive venation of the fore and hind wings and the penes are fused. The abdominal gills of the mature nymphs are plate-like and the mouthparts of the genera are similar in structure. This hypothesized relationship is also suggested by the fact that the nymphs of *Atalophlebioides* from Madagascar are very similar to nymphs found in South America, Australia, and New Zealand. We have also examined imagoes from Madagascar that resemble those of *Deleatidium*, a close ally of *Atalophlebioides*; the wing venation and the male genitalia are similar to those of Chilean

Fig. 287-304. Nymphal abdominal gills: 287, *Paraleptohlebia cincta*, gill 4. Fig. 288-289, *Leptophlebia marginata*: 288, gill 1; 289, gill 4. 290, *Habroleptoides modesta*, gill 4; 291, *Habrophlebia fusca*, gill 4. 292, *Habrophlebioides prominens*, gill 4. 293, *Aprionyx intermedius*, gill 4. 294, *Aprionyx tricuspидatus*, gill 4 (after Crass, 1947). 295, *Adenophlebia auriculata*, gill 4. 296, *Atalophlebioides inequalis*, gill 4. 297, *Kimminsula* sp., gill 4. 298-299, *Adenophlebioides* sp.: 298, gill 1; 299, gill 4. 300-302, *Castanophlebia calida*: 300, gill 4; 301, gill 7; 302, gill 7; 303-304, *Choroterpes* (*Choroterpes*) *picteti*: 303, gill 1; 304, gill 4.



adults presently referred to *Deleatidium*. Further studies of mayflies from Southern Africa, Madagascar, Southern South America, Australia, and New Zealand are needed to clarify the phylogeny and dispersal.

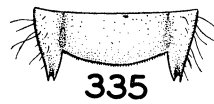
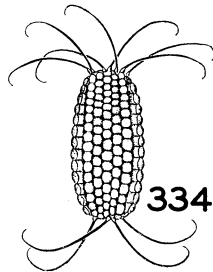
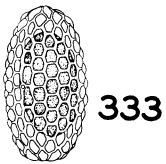
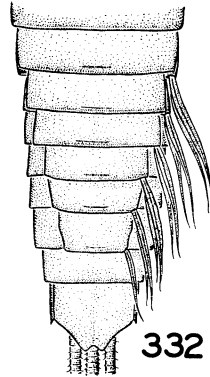
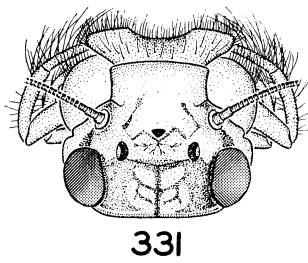
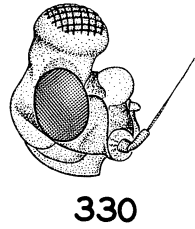
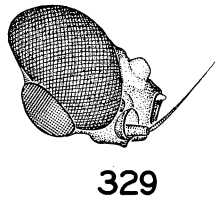
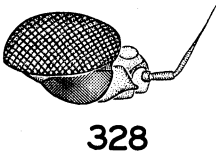
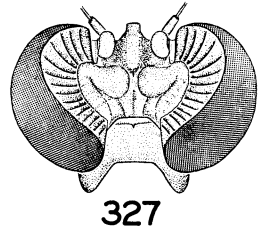
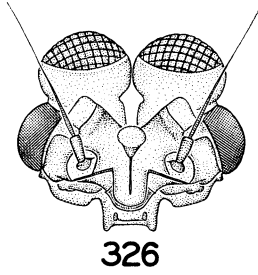
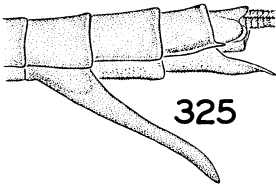
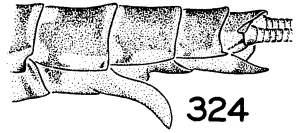
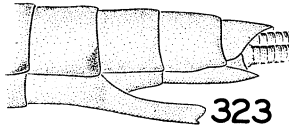
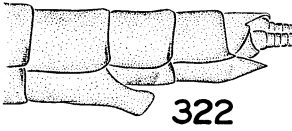
Daughter line IIB (fig. 1) represents a more specialized line of evolution from the primitive daughter line IIA. The penes of the males are fused only in the basal half (fig. 85-106). A V-shaped ridge is present on the ventral surface of the maxillae near the inner anterolateral margin (fig. 182, 185, 188, 192, 195), but in some genera the ridge is developed into a large tooth-like projection (fig. 187, 190, 193).

Daughter line IIB (fig. 1) represents the recent genus *Kimminsula*. Also collections recently made available to us contain 5 undescribed genera belonging to daughter line IIB1. Unfortunately the material of these undescribed genera includes only nymphs and subimago males. Until reared adult material is available these new genera will not be described. The anterior margin of the hind wings of all genera is smoothly convex and without a well developed costal projection (fig. 31). Present data are inadequate to characterize the nymphs of this group. However they generally resemble those nymphs of daughter line IIB. *Kimminsula* occurs in Ceylon while the undescribed genera occur in Ceylon and extreme Southern India.

Daughter line IIB2 represents the recent genera *Adenophlebiodes*, *Castanophlebia*, and *Fulleta*. The cross veins in the fore wings of all 3 genera are numerous (fig. 32, 35, 37) and the intercalaries in the Cu area are relatively long. Nymphs of *Fulleta* are unknown, while nymphs of *Adenophlebiodes* are highly specialized for living in silted habitats (fig. 3). No character successfully separates the nymphs of this daughter line. The penes of the males of *Fulleta* are basically similar to those in recent genera of daughter lines IIB3 and IIB4. However, the fore wing venation is more similar to that of *Adenophlebiodes* and *Castanophlebia*. Until the nymphs of *Fulleta* are known, its phylogeny is questionable. All three genera occur in the Ethiopian region.

Daughter line IIB3 (fig. 1) represents the recent genera *Choroterpes*, *Choroterpides*, *Cryptopenella*, and *Fulletomimus*. In the Cu area of the fore wings of these genera, 2 long intercalaries occur with 2 greatly shortened intercalaries between them; remainder of intercalaries in the Cu area are greatly shortened (fig. 38, 40, 43, 46, 48). The middle abdominal gills are plate-like and each portion is terminated in 3 long processes (fig. 304, 306, 308, 342). However the nymphs of *Fulletomimus* are questionably described. The nymphs of *Choroterpides* have highly specialized mouthparts, but all the changes seem to be in a probable shift from feeding on attached periphyton to straining food from the current. The adults are similar to *Choroterpes* as are the nymphs except for the head. *Cryptopenella* and *Choroterpides* occur in the Oriental region, while *Fulletomimus* occurs in the Ethiopian region. *Choroterpes* occurs in the Ethiopian, Oriental, Palearctic, and Nearctic regions. Also species have been described in *Choroterpes* from the Neotropical region. All of these species are known only from the adults but are similar to adults of typical *Choroterpes*. Packer (1966) has reported the occurrence of true *Choroterpes* nymphs from Honduras.

Fig. 305-321. Nymphal abdominal gills. 305-307, *Choroterpes (Euthraulius)* sp.: 305, gill 1; 306, gill 4; 307, gill 7; 308, *Choroterpides* sp., gill 4. 309, *Thraulius bellus*, gill 1. 310-311, *Thraulius torrentis* n. comb.: 310, gill 1; 311, gill 4. 312, *Indialis badia* n. sp., gill 4. 313, *Megaglana brincki* n. sp., gill 4. 314-315, *Maheathraulius scotti*: 314, gill 1; 315, gill 4. 316, *Hagenulodes braueri*, gill 4. 317, *Nathanella* sp., gill 4. 318-319, *Isca (Minyphlebia) janiceae* n. sp.: 318, gill 4; 319, gill 7. 320-321, *Isca (Tanycola) serendiba* n. sp.: 320, gill 4; 321, gill 7.



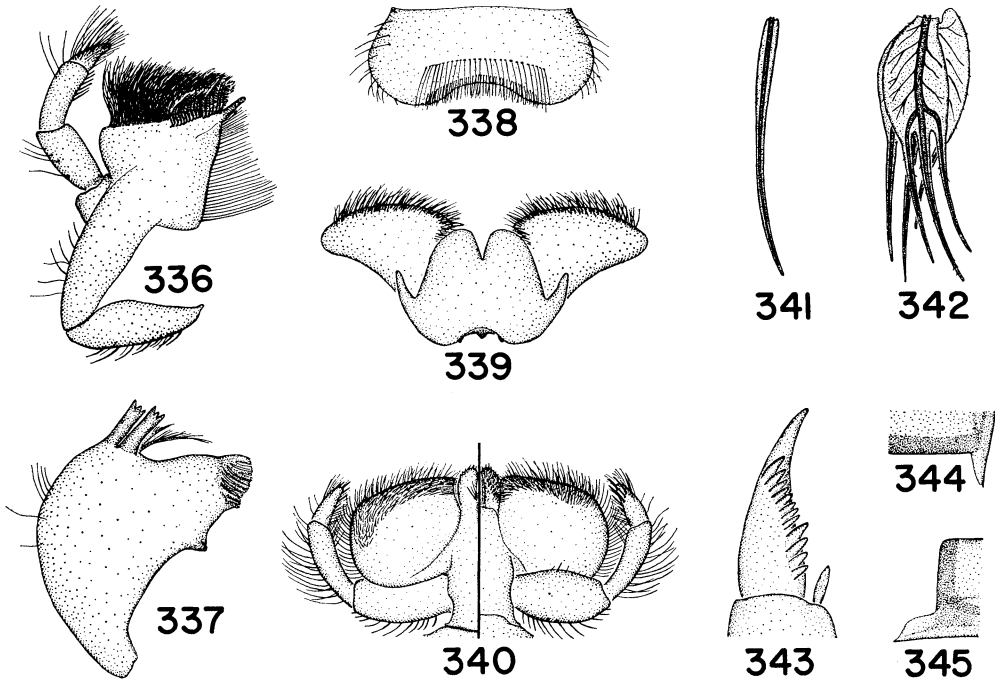


Fig. 336-345. *Cryptopenella facialis*: 336, maxilla; 337, left mandible; 338, labrum; 339, hypopharynx; 340, labium; 341, abdominal gill 1; 342, abdominal gill 4; 343, nymphal claw; 344, dorsal view of posterolateral spine on segment 9; 345, lateral view of posterolateral spine on segment 9.

Daughter line IIB4 (fig. 1) represents the recent genera *Thraululus*, *Simothraululus Indialis*, *Megaglena*, *Maheathraululus*, *Hagenulodes*, and *Nesophlebia*. The hind wings of these genera are present, except they are secondarily absent in *Hagenulodes* (fig. 53, 55, 58, 60, 63, 67). A row of thick spines are present on the ventral surface of the maxillae near the inner anterolateral margin (fig. 188-192).

Daughter line IIB4a (fig. 1) represents the recent genera *Thraululus*, *Simothraululus*, *Indialis*, and *Megaglena*. The anal fan of the fore wings of these genera is expanded and rounded (fig. 51, 54, 56, 59). The nymphal body is flattened dorsoventrally.

Daughter line IIB4aa' (fig. 1) represents the recent genera *Thraululus* and *Simothraululus*. The fork of vein MP of the fore wings of both genera is nearer to the base than the

Fig. 322-335. 322-25, Lateral view of ovipositor of ♀ imago: 322, *Habrophlebia fusca*; 323, *Habrophlebioides gilliesi*; 324, *Megaglena brincki* n. sp., 325, *Maheathraululus scotti*. 326, *Megaglena brincki* n. sp., frontal view of head of ♂ imago; 327, *Nesophlebia adusta*, dorsal view of head of ♂ imago; 328, *Isca (Minyphlebia) janiceae* n. sp., lateral view of head of ♂ imago; 329, *Isca (Tanycola) serendiba* n. sp., lateral view of head of ♂ imago; 330, *Isca (Isca s.s.) purpurea*, lateral view of head of male imago; 331, *Choroterpides* sp., dorsal view of head of mature nymph; 332, *Isca (Minyphlebia) janiceae* n. sp., ventral view of nymphal abdomen; 333, *Thraululus bellus*, egg (after Degrange, 1960); 334, *Thraululus torrentis* n. comb., egg; 335, *Aprionyx intermedius*, abdominal tergum 9 of mature nymph.

fork of vein R_s (fig. 51, 54). The middle abdominal gills are plate-like (fig. 310-311). *Thraulius* occurs in the Ethiopian, Oriental, and Palearctic regions, while *Simothraulius* occurs in the Oriental region.

Daughter line IIB4aa" (fig. 1) represents the recent genera *Indialis* and *Megaglana*. The fork of veins MP and R_s of the fore wings of both genera are forked about equidistant from the base (fig. 56-57). The middle abdominal gills are slender (fig. 312-313). *Indialis* and *Megaglana* occur in the Oriental region.

Daughter line IIB4b (fig. 1) represents the recent genera *Maheathraulius*, *Hagenulodes*, and *Nesophlebia*. The anal fan of the fore wings of all 3 genera is reduced (fig. 61, 64-65). The nymphal body is not as flattened dorsoventrally. All 3 genera occur in the Ethiopian region.

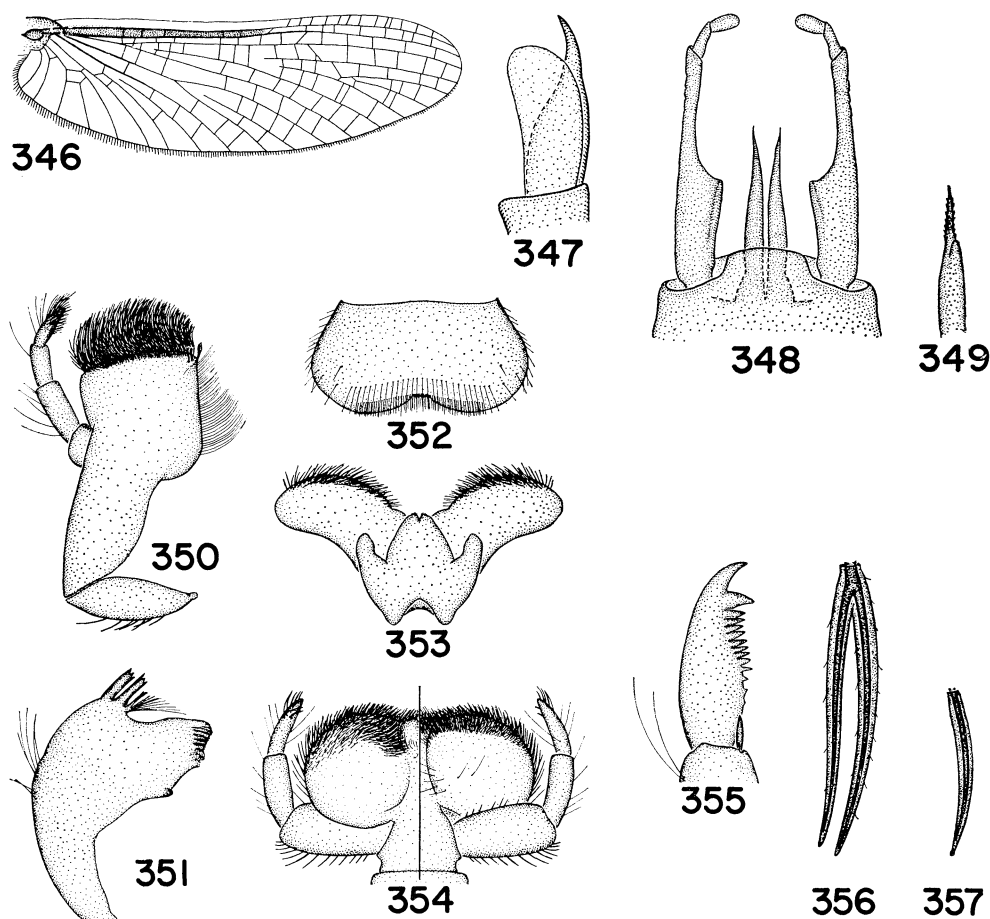


Fig. 346-349, *Notophlebia hyalina* n. sp.: 346, fore wing; 347, adult fore claw; 348, ventral view of genitalia of ♂ imago; 349, lateral view of penes enlarged. 350-357, *Isca* (*Isca* s. s.) *purpurea*: 350, maxilla; 351, left mandible; 352, labrum; 353, hypopharynx; 354, labium; 355, nymphal claw; 356, abdominal gill 4; 357, abdominal gill 7.

Daughter line IIB5 in fig. 1 represents the recent genera *Nathanella*, *Notophlebia*, and *Isca*. The hind wings of all 3 genera are absent. A row of thick spines is absent on the ventral surface of the maxillae near the inner anterolateral margin (fig. 193-195, 350). The nymphs of *Notophlebia* are unknown.

Daughter line IIB5a (fig. 1) represents the recent genera *Nathanella* and *Notophlebia*. Also recent adult collections made available to us indicate 2 undescribed genera closely related to *Nathanella* and *Notophlebia*. Until reared nymphal material is available, these 2 genera will not be described. The cross veins in the fore wings of all 4 genera are evenly spaced throughout the wings (fig. 68). The nymphal abdominal tergites extend to the lateral sides of the abdomen; all gills are lateral (fig. 6). *Notophlebia*, *Nathanella* and the 2 undescribed genera occur in the Oriental region.

Daughter line IIB5b (fig. 1) represents the recent genus *Isca*. The cross veins are absent in the posterior margin of the fore wings (fig. 69-71). The nymphal abdominal tergites extend around to the venter of the abdomen, thus producing ventral gills (fig. 332). *Isca* occurs in the Oriental region.

SUMMARY

This revision of the generic classification of the Eastern Hemisphere Leptophlebiidae includes those genera of New Guinea, but not those of Australia and New Zealand. The affinities of the genera occurring in Australia and New Zealand are almost entirely with those of the Neotropical region while those from New Guinea are clearly of Oriental affinity.

Only those genera known to occur in the Oriental and Palearctic regions are defined in this report. Other genera occurring only in the Ethiopian region have been recently defined and discussed by Peters & Edmunds (1964). Their generic descriptions of the Ethiopian genera are consistent in style with those used herein and their inclusion is not necessary. Ethiopian genera, however, are considered in the keys and phylogenetic study.

Although all described species from the Eastern Hemisphere are considered in this study, it has been impossible to assign 6 of the species to their proper genus. These are *Hagenulus monstratus* Eaton, *Atalophlebia femoralis* (Hagen), *Leptophlebia duplex* Navas, *L. simplex* Navas, *Ulmerophlebia* (?) *succinea* Demoulin, and *Ulmerophlebia* (?) *variegata* Demoulin. The fragmentary adult type series and the original descriptions are inadequate for *Hagenulus monstratus* and *Atalophlebia femoralis*, but *A. femoralis* appears to require a new generic name. The types of *Leptophlebia duplex* and *L. simplex* are unavailable for study, and the original descriptions and illustrations are inadequate. Both species of *Ulmerophlebia* (?) from Madagascar were described from female imagos. While it is unlikely that either species belongs to the Australian genus *Ulmerophlebia*, correct assignment of the species is impossible until the male imagos and nymphs are known.

Twenty-nine valid genera of the Leptophlebiidae were found to occur in the Eastern Hemisphere. Of these, 5 genera and 2 subgenera are described as new. Illustrations of important morphological features and keys to the imagos and mature nymphs are given for all genera defined herein and for those genera occurring only in the Ethiopian region but not defined in this work.

The imaginal and nymphal descriptions of *Choroterpes* are based only on species occurring in the Eastern Hemisphere. Two subgenera, *Choroterpes* s. s. and *Euthraulius*, are considered valid. The North American species of *Choroterpes* appear to be congeneric with the Eastern Hemisphere representatives. One group of species occurring in Central America and Northern South America appears to be distinct from those of the Eastern Hemisphere and is in need of further study. *Thraulius signatus* Hagen and *Hagenulus karnyi* Ulmer herein are placed in the subgenus *Euthraulius* of the genus *Choroterpes*.

The female imagos of *Choroterpides* are described here for the first time. *Choroterpides exigua* (Eaton), the type species, was described from specimens from "Lahat, Palenburg". Palenburg is obviously a misspelling for Palembang in Southern Sumatra.

The nymphs of *Cryptopenella* are described here for the first time. Nymphs of the monotypic genus are morphologically similar to those of *Choroterpes* (*Euthraulius*).

Gilliesia new genus is established for *Thraulius hindustanicus* Gillies. The genus is known only from the male and female imagos from Northern India. *Gilliesia* is most closely related to *Habrophlebiodes* and *Dipterophlebiodes*.

Biancheri (1953) considered the genus *Habroleptoides* described by Schoenemund (1929) as a subgenus of *Habrophlebia*, while Grandi (1955) considered *Habroleptoides* to be synonymous with *Habrophlebia*. We consider *Habroleptoides* as a valid genus. The adults of *Habrophlebia* and *Habroleptoides* can be distinguished by the shape of the genital forceps of the male and the presence of a well developed female ovipositor or egg guide. The nymphs of *Habrophlebia* and *Habroleptoides* can be distinguished by the abdominal gills and hypopharynx, and by the number of posterolateral spines on the abdominal segments. The Eastern North American representatives of *Habrophlebia* are separable in the adult stage from those from the Eastern Hemisphere by small size, absence of an acute angulation on the inner margin of the base of the male genital forceps, and the absence of a female ovipositor or egg guide. The nymphs of the Eastern North American *Habrophlebia* are not separable from those of the Eastern Hemisphere.

Indialis new genus is established for *Indialis badia* new species. The genus is known from the male subimagos and mature nymphs from Southern India. *Indialis* is most closely related to *Megaglana* new genus and to *Thraulius* and related genera.

Kimminsula new genus is established for *Atalophlebia annulatus* (Hagen), *A. fasciatus* (Hagen), and *A. taprobanes* (Walker). The type species is *Kimminsula annulata* n. comb. The genus is known from the male imagos and mature nymphs from Ceylon. *Kimminsula* is most closely related to *Aprionyx*, *Adenophlebia*, and *Atalophlebioides* of the Ethiopian region.

Only the Palearctic representatives of *Leptophlebia* are considered in this revision. The Palearctic species of *Leptophlebia* are distinct from the Palearctic species of *Paraleptophlebia*. The definition of *Leptophlebia* and the rank to be accorded *Blasturus* in North America will be reconsidered when all of the American species are studied.

Megaglana new genus is established for *Megaglana brincki* new species. The genus is known from the male and female imagos and mature nymphs and occurs in Ceylon. *Megaglana* is most closely related to *Indialis* new genus and *Thraulius* and related genera.

Two monotypic subgenera, *Minyphlebia* new subgenus, for *Isca* (*M.*) *janiceae* new species, and *Tanycola* new subgenus, for *Isca* (*T.*) *serendiba* new species, are established within *Isca*. Both subgenera are known from the male and female imagos and mature

nymphs. *Minyphlebia* is known to occur in Thailand while the subgenus *Tanycola* is known to occur in Ceylon. *Isca* is most closely related to *Nathanella* and *Notophlebia* new genus.

The mature nymphs of *Nathanella* are described for the first time. This genus occurs in Southern India and probably is most closely related to *Notophlebia* new genus. Although the nymphs of *Nathanella* resemble superficially those of *Choroterpides*, it is hypothesized that the specialized mouthparts of *Nathanella* evolved independently. The adults of *Nathanella* and *Notophlebia* new genus are basically similar in structure.

Notophlebia new genus is established for *Notophlebia hyalina* new species. The monotypic genus occurs in Southern India and is known only from the adults.

Only the Palearctic representatives of *Paraleptophlebia* are considered in this revision. The Palearctic species of *Paraleptophlebia* are distinct from the Palearctic species of *Leptophlebia*. The definition of *Paraleptophlebia* may need to be revised when all of the American species are studied. Preliminary work indicates that more than 1 natural group occurs within the North American *Paraleptophlebia*.

Herein, *Masharikella* Peters, Gillies & Edmunds is placed as a synonym of *Thraululus*, thus making *Thraululus* a wide-ranging genus in the Eastern Hemisphere. Apparently there are 3 natural groups within *Thraululus*, which are separable in the nymphs only by the shape of the first abdominal gills. No character successfully separates the adults.

The monotypic Oriental genera, *Dipterophlebiodes* and *Simothraululus*, and the monotypic Palearctic genus *Calliarcys* are considered valid in this revision. The Oriental species of *Habrophlebiodes* are considered congeneric with the North American species assigned to the genus.

The Ethiopian genera *Adenophlebia*, *Adenophlebiodes*, *Aprionyx*, *Atalophlebioides*, *Castanophlebia*, *Fullea*, *Fulletomimus*, *Hagenulodes*, *Maheathraululus*, and *Nesophlebia* are considered valid. Descriptions of all these genera are given in Peters & Edmunds (1964).

In fig. 1, the hypothesized phylogeny of the Eastern Hemisphere genera of Leptophlebiidae is presented. As the fossil record of Leptophlebiidae is almost unknown, the phylogeny is hypothesized from comparative external and internal morphological data from recent taxa and from zoogeographical data. It is recognized that the phylogeny and relationships of Leptophlebiidae can be more fully understood when a study is made of those genera occurring in the Western Hemisphere, Australia, and New Zealand.

Daughter line I represents an ancient dispersal in the Northern Hemisphere and includes the most primitive existing genera of the Leptophlebiidae, *Paraleptophlebia* and *Leptophlebia*. Apparently, dispersal between the Palearctic and Oriental regions and the Palearctic and Nearctic regions occurred several times during the evolution of daughter line I. Each of the 3 major lines of evolution has at least 1 genus present in both the Eastern and Western Hemisphere.

Daughter line II represents an ancient dispersal in the Southern Hemisphere which apparently later reinvaded the Northern Hemisphere several times. Daughter line IIA represents the line of evolution to the most primitive recent genera of daughter line II. All 3 genera, *Aprionyx*, *Adenophlebia*, and *Atalophlebioides*, seem to be most closely related to a complex of genera occurring in South America, Australia, and New Zealand. Daughter line IIB represents the line of evolution to a variety of recent genera occur-

ring in the Ethiopian, Oriental, Palearctic, and Neotropical regions.

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