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W. L. PETERS AND G. F. EDMUNDS, JNR.

A revision of the generic classification of the Ethiopian
Leptophlebiidae (Ephemeroptera)

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A revision of the generic classification of the Ethiopian Leptophlebiidae (Ephemeroptera)*

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With 141 Text-figures

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SYNOPSIS

Descriptions are given of 12 genera (including one new genus) and two subgenera of Leptophlebiidae from the Ethiopian region, with notes on their distribution and biology. A key to the genera is included, and their relationships are discussed. One new species, for which the new genus is established, is described from a male specimen taken in Madagascar. *Atalophlebioides cromwelli* is designated as the type species of *Atalophlebioides*.

I. INTRODUCTION

THE family Leptophlebiidae is the largest family of mayflies, being composed of numerous species that are currently assigned to 46 genera. It 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 the Leptophlebiidae are so poorly defined that it is sometimes impossible to place a species in the proper genus. A modern revision of the genera of the entire family Leptophlebiidae has never been attempted, although small groups of related genera have been reworked at various times. The purpose of the present study is to revise the genera of the Leptophlebiidae that occur in the Ethiopian region.

Of the 12 genera of Leptophlebiidae known from the Ethiopian area, the genera *Adenophlebia*, *Adenophlebiodes*, *Aprionyx*, *Castanophlebia*, *Fulleta*, *Fulletomimus*, *Hagenulodes*, *Maheathraulius*, and *Nesophlebia* are endemic. The genus *Masharikella* is known from the Ethiopian, Oriental and Australian regions. The genus *Choroterpes* is nearly world-wide: the subgenus *Choroterpes* s.s. is known from the Ethiopian, Oriental, Palaearctic, Nearctic and Neotropical regions, and the subgenus *Euthraulius* is known from the Ethiopian, Oriental and Palaearctic regions. In characterising the genera, we have considered all species included in *Masharikella* and *Choroterpes*. The genus *Atalophlebioides* is known from the Australian, Neotropical and Ethiopian regions. The one Ethiopian species assigned to it is retained in this genus until it and related genera can be studied, and this species only has been considered in keying and characterising the genus in this paper.

*The research on which this report is based was supported by grants from the National Science Foundation, U.S.A., George F. Edmunds, Jr., Principal Investigator.

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The following terms and procedures used in the descriptions of the imago and nymph require further explanation. The lengths of the body and fore wing 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 figures 2 and 3. 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 millimetres 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.

II. RELATIONSHIPS OF THE ETHIOPIAN GENERA

The relationships of the Ethiopian genera of Leptophlebiidae cannot be fully understood unless they are compared with other genera in Europe, Asia, South America, Australia and New Zealand. At present, many of the genera occurring outside the Ethiopian region need revision. Until these genera are studied, an adequate phylogenetic interpretation is not possible; however, at present some phylogenetic conclusions can be drawn relative to the Ethiopian genera.

The genera *Adenophlebia* and *Aprionyx* seem to be most closely related to a complex of genera occurring in South America, Australia and New Zealand. All these genera have primitive venation of the fore and hind wings (figs. 4-5, 9-10), except that the hind wings are reduced in *Adenophlebia* (fig. 5). The penes are fused in all genera (figs. 31, 33-34). The abdominal gills of the mature nymphs are plate-like (figs. 123, 126-7), and the mouthparts of the genera are similar in structure (figs. 64, 66, 73, 75, 82, 84, 91, 93, 100, 102). The distribution of this complex indicates a possible palaeantarctic dispersal. Support for this hypothesis 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. Also in our collections are imagos from Madagascar that resemble those of *Deleatidium*: the wing venation and male genitalia are similar to those of *Deleatidium* which occur in Chile. Further studies of mayflies from southern Africa, Madagascar and southern South America will undoubtedly clarify the possibility of a palaeantarctic dispersal route.

The remaining Ethiopian genera are all closely related to one another, and together with a number of European and Asiatic genera form a single complex centring around the types of *Choroterpes*, *Thraulius* and *Habrophlebiodes*. All these genera have fore and hind wings with reduced venation (figs. 13-14), and in some genera the hind wings are small (fig. 30) or absent. The penes are tubular and divided (figs. 36, 43). The mature nymphs have many specialisations, but all show distinct similarity in many characters.

Adenophlebiodes, *Castanophlebia* and *Fulleta* are the most specialised genera of this group in the Ethiopian region. The penis lobes of *Adenophlebiodes* and *Castanophlebia*, although tubular and divided, are specialised; those of *Adenophlebiodes* are apically bent inwardly (fig. 32) and those of *Castanophlebia* are divergent outwardly, with ventral spines (fig. 35). Although the tubular and divided penis lobes of *Fulleta* (fig. 38) are unmodified, the fore wings are specialised (fig. 18) and the hind wings are secondarily lost. The nymphs of *Adenophlebiodes* are specialised for slow running and silted streams, the abdominal gills on segment one being operculiform (figs. 1, 124), and the femora of the fore legs greatly enlarged to protect the abdominal gills (fig. 1). Nymphs of *Castanophlebia* have abdominal gills that are long and slender (fig. 129). The nymphs of *Fulleta* are unknown. The relationships of these three genera are doubtful, although the nymphs of *Adenophlebiodes* and *Castanophlebia* are clearly allied to the *Choroterpes-Thraulius-Habrophlebiodes* complex.

The Ethiopian genera *Choroterpes* and *Fullemimus* and the Oriental genus *Cryptopenella* are closely related. The venation of the wings of all three genera is similar (figs. 13-17, 19-21). The tubular and divided penes of *Choroterpes* and

Fullemimus are unmodified (figs. 36–37, 39), whereas the tubular and divided penes of *Cryptopenella* are small and almost entirely hidden behind the male subgenital plate. Abdominal gill 1 of the nymphs of *Choroterpes* is of a single, long and slender lamella (figs. 132–3, 135), whereas abdominal gills 2–7 are plate-like (figs. 136–7). Nymphs of *Fullemimus* and *Cryptopenella* are unknown.

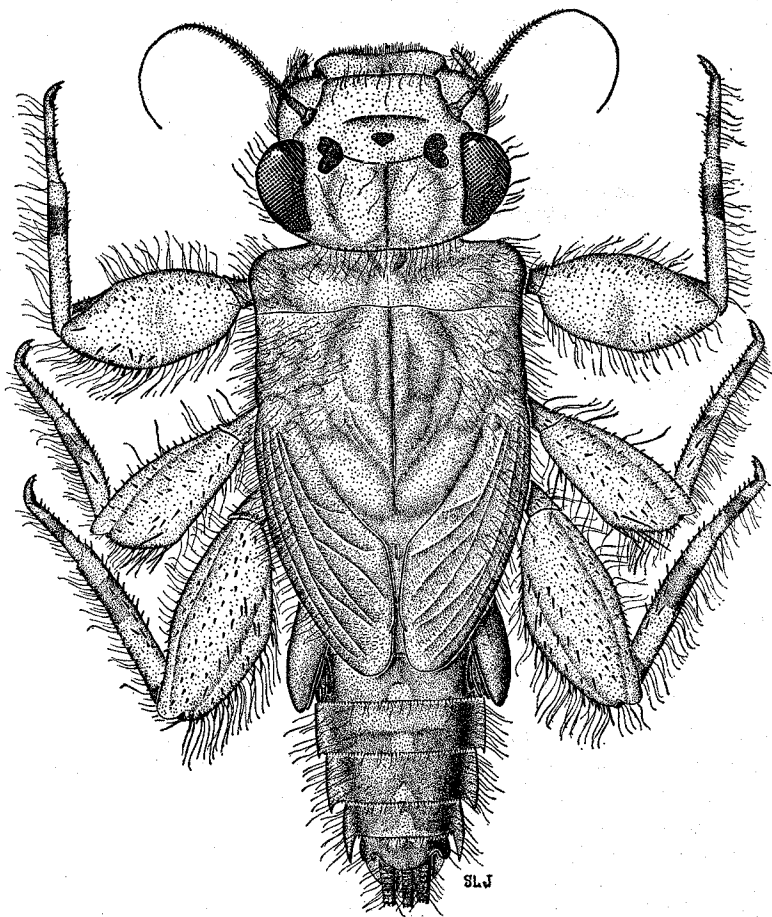


FIG. 1.—*Adenophlebiodes* sp., dorsal view of mature male nymph.

The Ethiopian genera *Masharikella*, *Hagenulodes* and *Nesophlebia*, the Palaearctic and Oriental genus *Thraulius*, and the Oriental genus *Simothraulius* are closely related. All genera have similar venation of the fore wings (figs. 22, 26, 28) and the tubular and divided penes are unmodified (figs. 40, 41, 43). *Hagenulodes* has secondarily lost the hind wings, and the hind wings of *Nesophlebia* are small (fig. 30). The nymphs of *Masharikella* and *Thraulius* are the only ones known. The abdominal gills on segments 2–7 of these two genera are plate-like with fringed margins (fig. 141), and the mouthparts of the genera are similar (figs. 72, 81, 90, 99, 108).

The Ethiopian genus *Maheathraulius*, the Oriental genera *Dipterophlebiodes* and *Nathanella*, and the Nearctic and Oriental genus *Habrophlebiodes* are closely related. All four genera have similar venation of the fore wings (fig. 23). The hind wings of *Maheathraulius* and *Habrophlebiodes* are well developed (fig. 25); those of *Dipterophlebiodes* and *Nathanella*, however, are secondarily lost. The tubular and divided penes of *Maheathraulius* and *Nathanella* are unmodified (fig. 42), whereas those of *Dipter-*
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rophlebiodes are bent outwardly at their apices. The penes of *Habrophlebiodes* are partially or entirely fused and possess elongated ventral appendages. Female imagos of *Maheathraulius* and *Habrophlebiodes* have long egg guides or ovipositors (fig. 61); the female imagos of *Dipterophlebiodes* and *Nathanella* are unknown. The mouth-parts of *Habrophlebiodes* and *Maheathraulius* are similar (figs. 71, 80, 89, 98, 107) and the middle abdominal gills of both are long, slender and bifurcated (fig. 139). Nymphs of *Dipterophlebiodes* and *Nathanella* are unknown.

III. SYSTEMATICS

(1) Family Leptophlebiidae Banks, 1900

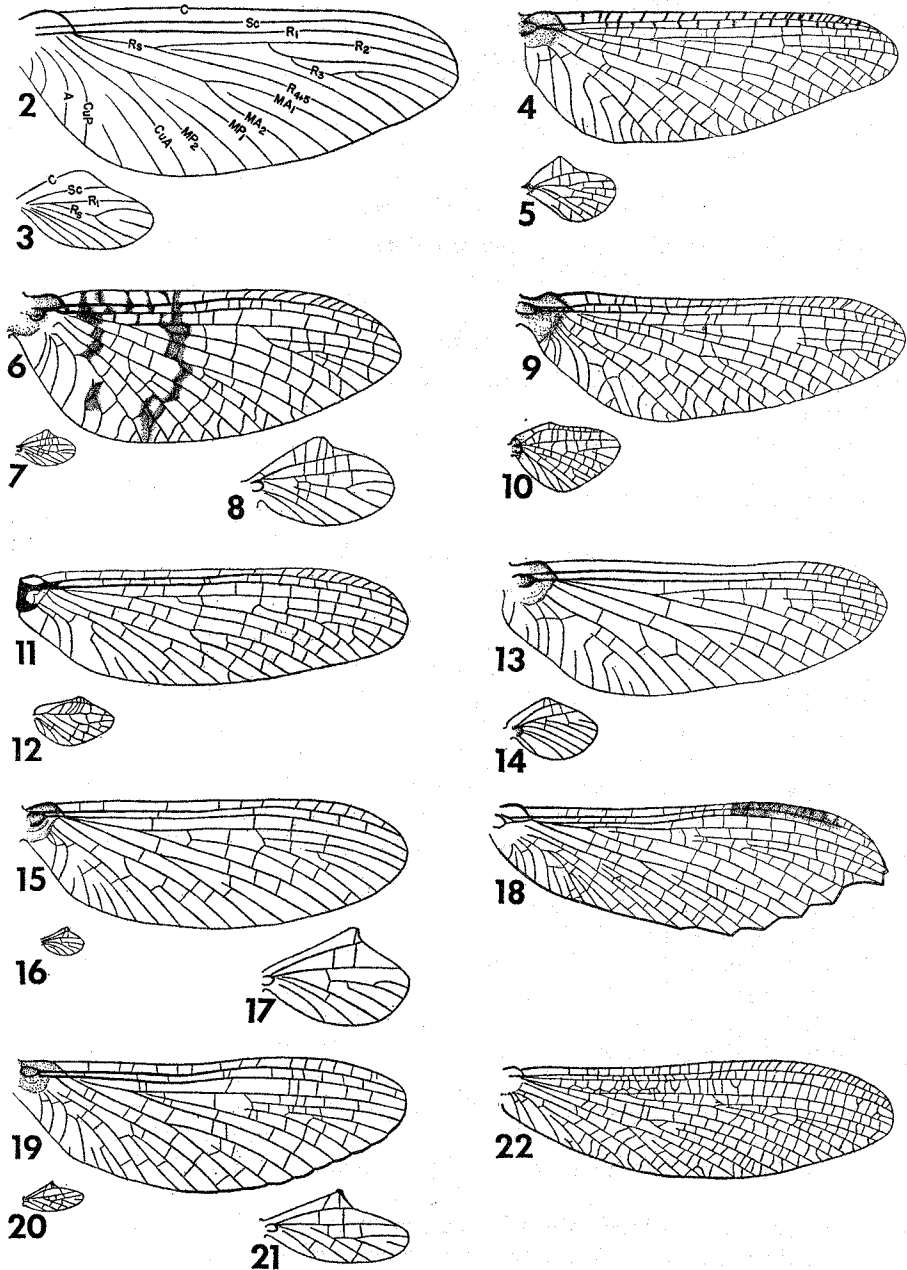
- Eaton, 1884 (1883–88), *Trans. Linn. Soc. Lond. (Zool.)* 3 : 82. (Section 5 of *Leptophlebia*.)
 Banks, 1900, *Trans. Amer. ent. Soc.* 26 : 246–7. (Leptophlebiini.)
 Jacobson & Bianchi, 1905, *Orthoptera and Pseudoneuroptera of the Russian Empire*, pp. 873–4. (Leptophlebiinae.)
 Klapálek, 1909, *Süsswasserfauna Deutschl.* 8 : 10.
 Lestage, 1919, *Ann. Biol. lacust.* 9 : 112. (Leptophlebiinae.)
 Ulmer, 1920, *Stettin ent. Ztg.* 81 : 112.
 Phillips, 1930, *Trans. N.Z. Inst.* 61 : 335–6.
 Barnard, 1932, *Trans. roy. Soc. S. Afr.* 20 : 233.
 Ulmer, 1932a, *Stettin ent. Ztg.* 93 : 112–4.
 Ulmer, 1932b, *Peking nat. Hist. Bull.* 7 : 201–4.
 Spieth, 1933, *J. N. Y. ent. Soc.* 41 : 342–5.
 Traver, 1935, *The Biology of Mayflies*, pp. 504–5. (Leptophlebiinae.)
 Burks, 1953, *Bull. Ill. nat. Hist. Surv.* 26 (Art. 1) : 81.
 Edmunds & Traver, 1954, *Proc. ent. Soc. Wash.* 56 : 238.
 Bogoescu, 1958, *Fauna Rep. Pop. Romine, Insects* 7 (3) : 71–72.
 Demoulin, 1958, *Bull. Inst. roy. Sci. nat. Belg.* 34 : 10.
 Grandi, 1960, *Fauna d'Italia* 3 : 212, 396.

The Leptophlebiidae were first recognised 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 are all so alike in 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; no reasons were given, however, for this decision. Landa (1959), in his study of the internal systems of the mayflies, confirmed Edmunds' & Traver's placing of this family. 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 specialisations, in doubtful cases of classification the adult characters were used to make the final decisions. However, he justifies the placing of the Leptophlebiidae in the Heptagenioidea almost entirely upon nymphal characteristics.

The imagos and the mature nymphs of the family Leptophlebiidae are characterised as follows.

Imago.—Eyes of male divided into large upper portion with large facets and smaller lower portion with smaller facets, or composed entirely of small facets; female eyes not divided into upper and lower portion, similar to lower portion of eyes of male. Median and lateral ocelli well developed. Wings: veins *C* and *Sc* of fore wings well developed (fig. 4); vein *MA*₂ attached at base to *MA*₁, one intercalary present between veins *MA*₁ and *MA*₂ (fig. 4); vein *MP*₂ attached at base to *MP*₁ (fig. 4) or vein *MP*₂ independent of vein *MP*₁ (fig. 23), one intercalary between veins *MP*₁ and *MP*₂; no intercalaries between veins *MP*₂ and *CuA*; several varied intercalaries between veins *CuA* and *CuP* (figs. 4, 13); vein *CuP* strongly recurved (fig. 4); 2–3 anal veins present, all strongly recurved (fig. 4); cross veins few to numerous. Hind wings present or absent; if present, well developed, sometimes small; costal projection well developed (fig. 27) to absent (fig. 10); venation highly varied; cross veins few to numerous. Tarsi of male fore legs five-segmented, segment one reduced; tarsi of male middle and hind legs four-segmented; tarsi of all 3 pairs of female legs four-segmented; claws alike (fig. 44) or dissimilar (fig. 47). External ovipositor present (fig. 61) or absent on abdomen of female. Male



FIGS. 2-22.—(2-3) Schematic wings, showing abbreviations of venational terminology used in paper: (2) fore wing; (3) hind wing. (4-5) *Adenophlebia auriculata*: (4) fore wing; (5) hind wing. (6-8) *Adenophlebiodes ornata*: (6) fore wing; (7) hind wing; (8) hind wing enlarged. (9-10) *Aprionyx intermedius*: (9) fore wing; (10) hind wing. (11-12) *Castanophlebia calida*: (11) fore wing (after Barnard, 1932); (12) hind wing (after Barnard, 1932). (13-14) *Choroterpes* (*Choroterpes*) *nigrescens*: (13) fore wing; (14) hind wing. (15-17) *Choroterpes* (*Euthraulius*) *elegans*: (15) fore wing; (16) hind wing; (17) hind wing enlarged. (18) *Fullea dentata*, fore wing. (19-21) *Fulletonimus marlieri*: (19) fore wing; (20) hind wing; (21) hind wing enlarged. (22) *Hagenulodes braueri*, fore wing (after Ulmer, 1919).

genitalia: forceps two- or three-segmented, segments two and three (when present) shorter than segment one (fig. 31); elongated penis lobes partly to entirely fused on mesal margins (figs. 31, 36). Caudal filaments well developed.

Mature nymph.—Nymph depressed; head hypognathous, semi-hypognathous or prognathous in position. Maxillary palpi three-segmented; a rake-like spine usually present on inner apical angle of galea-lacinia (fig. 82). Hypopharynx well developed, usually with well developed lateral processes (fig. 91). Labial palpi three-segmented; glossae and paraglossae well developed (fig. 64). Gills on abdominal segments 1-7, 2-7 or 1-6, ventral lamellae absent (fig. 124) or present (fig. 123). Caudal filaments well developed.

(2) Keys to the Genera

The following keys will serve to distinguish the imagos and nymphs of the Ethiopian genera and subgenera of Leptophlebiidae.

Imagos

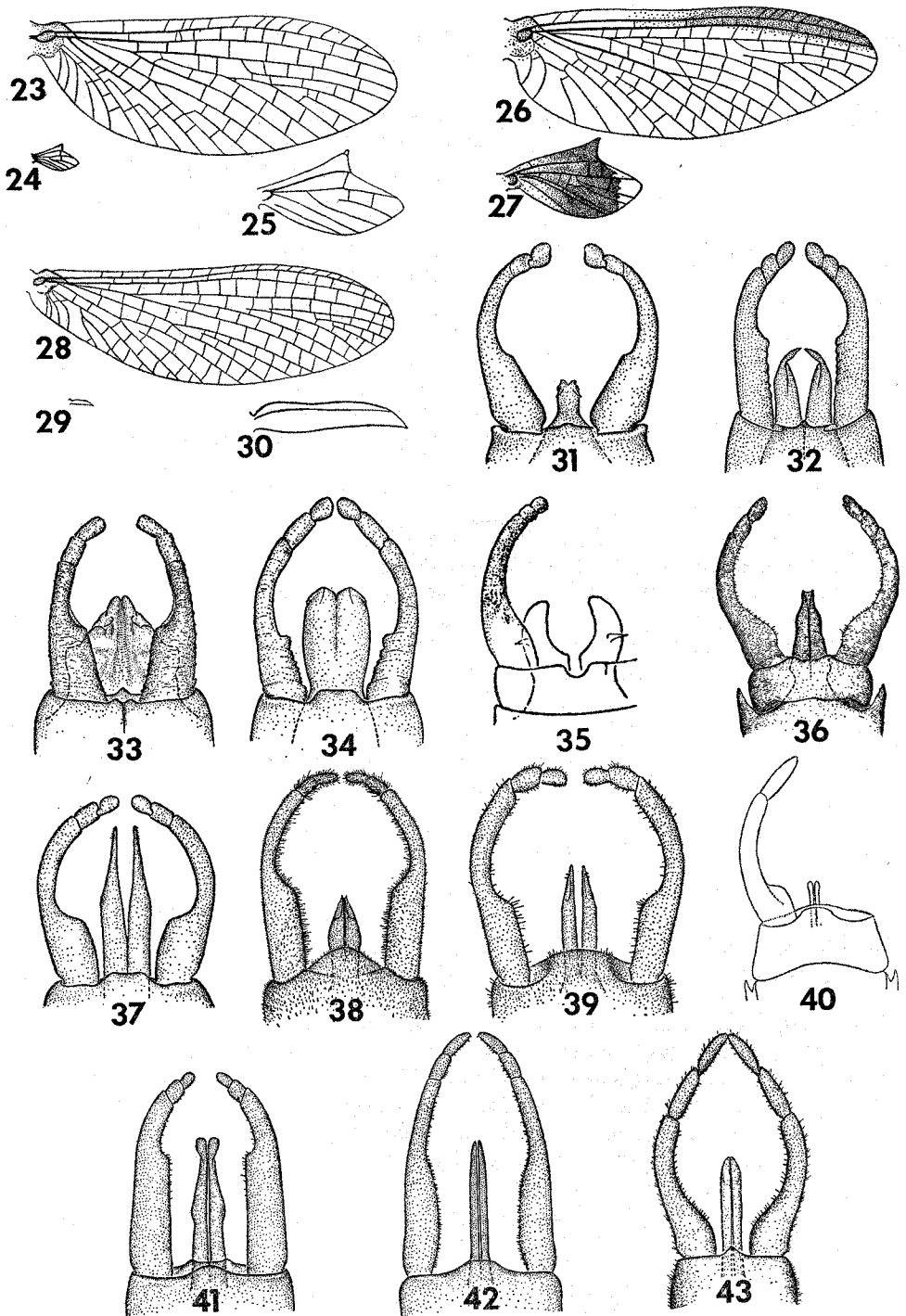
- | | | |
|---|---|--|
| 1 | Hind wings present (figs. 10, 21), although sometimes small (fig. 30) | 3 |
| - | Hind wings absent | 2 |
| 2 | Genital forceps three-segmented (fig. 38); outer margin of fore wings serrate (fig. 18) | <i>Fullea</i> Navás (p. 244) |
| - | Genital forceps two-segmented (fig. 40); outer margin of fore wings entire (fig. 22) | <i>Hagenulodes</i> Ulmer (p. 245) |
| 3 | Hind wings small with only one longitudinal vein (fig. 30); segments two and three of genital forceps each one-third length of segment one (fig. 43) | <i>Nesophlebia</i> gen. n. (p. 248) |
| - | Hind wings well developed (figs. 10, 21); segment two and three of genital forceps each less than one-third length of segment one (figs. 33, 39) | 4 |
| 4 | Penis lobes of male genitalia fused except for apical cleft (figs. 31, 33-34); vein MP_2 attached to vein MP_1 and strongly bowed (figs. 4, 9) | 5 |
| - | Penis lobes of male genitalia divided, only partly fused at base (figs. 32, 43); vein MP_2 attached to vein MP_1 and smoothly curved (fig. 13), or vein MP_2 independent of vein MP_1 (fig. 23) | 6 |
| 5 | Costal projection of hind wings acute and well developed (fig. 5); a ventral spine on each penis lobe (fig. 31) | <i>Adenophlebia</i> Eaton (p. 233) |
| - | Costal margin of hind wings convex (fig. 10); a recurved flap near each orifice of penes (figs. 33-34) | <i>Aprionyx</i> Barnard (p. 237) |
| 6 | Eyes of male divided into upper portion with large facets and lower portion with smaller facets; outer margin of fore wings entire (figs. 13, 26) | 7 |
| - | Eyes of male not divided into upper and lower portion, eyes composed entirely of small facets; outer margin of fore wings serrate (fig. 19) | <i>Fulletomimus</i> Demoulin (p. 245) |
| 7 | Claws of pretarsi ¹ alike, apically hooked, each claw with an opposing hook (fig. 45) | <i>Adenophlebiodes</i> Ulmer (p. 234) |
| - | Claws of pretarsi dissimilar, one apically hooked, the other obtuse, pad-like (figs. 51-52) | 8 |
| 8 | Veins R_s and MP of fore wings forked equidistant from base (figs. 11, 13); costal projection of hind wings rounded and well developed (fig. 14), or costal margin convex (fig. 12) | 10 |
| - | Veins R_s and MP of fore wings not forked equidistant from base (figs. 23, 26); costal projection of hind wings acute and well developed (figs. 25, 27) | 9 |
| 9 | Vein MP_2 attached to MP_1 as a symmetrical fork (fig. 26); female without an egg guide or ovipositor | <i>Masharikella</i> Peters, Gillies & Edmunds (p. 248) |

¹ Called tarsal claws by most authors. Snodgrass (1935) points out that the claws are part of the pretarsus.

- Vein MP_2 independent of vein MP_1 (fig. 23); female with an egg guide or ovipositor extending to posterior margin of abdominal segment 10 (fig. 61) *Maheathraulius* Peters, Gillies & Edmunds (p. 246)
- 10 Costal projection of hind wings rounded and well developed (figs. 14, 17); penes divided and tubular, without appendages (figs. 36-37) . (*Choroterpes*) 11
- Costal margin of hind wings convex (fig. 12); penes divided, lobes divergent outwardly, a ventral spine on each lobe (fig. 35) *Castanophlebia* Barnard (p. 239)
- 11 Vein MA of fore wings forked one-half of the distance from base to the margin; fork of vein MP of fore wings asymmetrical (fig. 15); proximal base of costal projection of hind wings smoothly curved, distal base angular (fig. 17) *Choroterpes (Euthraulius)* Barnard (p. 244)
- Vein MA of fore wings forked over one-half of the distance from base to the margin; fork of vein MP of fore wings symmetrical (fig. 13); bases of costal projection of hind wings both smoothly curved (fig. 14) *Choroterpes (Choroterpes s.s.)* Eaton (p. 241)

Mature Nymphs

- 1 Abdominal gill 1 similar to middle abdominal gills (figs. 127, 129) 2
- Abdominal gill 1 not similar to middle abdominal gills (figs. 124, 132, 138) 5
- 2 Middle abdominal gills slender, tracheae unbranched (fig. 129), ventral lamellae present or absent, when present similar to dorsal lamellae; lingua of hypopharynx cordate (fig. 95) *Castanophlebia* Barnard (p. 239)
- Middle abdominal gills plate-like, tracheae branched (figs. 123, 126); lingua of hypopharynx with well developed lateral processes (figs. 91, 93) 3
- 3 Claws hooked and narrow, denticles present (figs. 109, 114); single posterolateral spines on abdominal segments 8 and 9 (fig. 1) 4
- Claws long and tapered, no denticles present (fig. 112); double posterolateral spines on abdominal segments 8 and 9 (fig. 121) *Aprionyx* Barnard (p. 237)
- 4 Ventral lamellae of abdominal gills terminated in one slender, filamentous process (fig. 123); posterolateral spines on abdominal segments 3-9 *Adenophlebia* Eaton (p. 233)
- Ventral lamellae of abdominal gills rounded apically (fig. 128); posterolateral spines on abdominal segments 4-9 *Atalophlebioides* Phillips (p. 238)
- 5 Middle abdominal gills long, slender and bifurcate (fig. 139); egg guide or ovipositor present on female nymphs (fig. 122) *Maheathraulius* Peters, Gillies & Edmund (p. 246)
- Middle abdominal gills plate-like (figs. 125, 134, 141); egg guide or ovipositor not present on female nymphs 6
- 6 Middle abdominal gills with fringed margins (fig. 141); abdominal gill 1 consisting of two lamellae (fig. 140) *Masharikella* Peters, Gillies & Edmunds (p. 248)
- Middle abdominal gills without fringed margins, gills forked (fig. 125) or terminated in one to three slender, filamentous processes (figs. 134, 136); abdominal gill 1 consisting of one lamella (figs. 124, 132) 7
- 7 Abdominal gill 1 operculiform (fig. 1); abdominal segments 1-5 shortened and compacted (fig. 1) *Adenophlebiodes* Ulmer (p. 235)
- Abdominal gill 1 long and slender (figs. 132-3, 135); all abdominal segments of about equal length (*Choroterpes*) 8



FIGS. 23-43.—(23-25) *Maheathraulius scotti*: (23) fore wing; (24) hind wing; (25) hind wing enlarged. (26-27) *Masharikella torrentis*: (26) fore wing; (27) hind wing. (28-30) *Nesophlebia adusta* sp. n.: (28) fore wing; (29) hind wing; (30) hind wing enlarged. (31-43) Ventral views of genitalia of male imago: (31) *Adenophlebia auriculata*; (32) *Adenophlebiodes discolor*; (33) *Aprionyx intermedius*; (34) *Aprionyx natalicus*; (35) *Castanophlebia calida* (after Barnard, 1932); (36) *Choroterpes (Choroterpes) picteti*; (37) *Choroterpes (Euthraulius) elegans*; (38) *Fullela dentata*; (39) *Fulletomimus marlieri*; (40) *Hagenulodes braueri* (after Ulmer, 1919); (41) *Masharikella torrentis*; (42) *Maheathraulius scotti*; (43) *Nesophlebia adusta* sp. n.

- 8 Abdominal gills 2-7 terminated in three, slender, subequal processes (fig. 136) *Choroterpes (Euthraulius)* Barnard (p. 244)
 - Abdominal gills 2-7 terminated in three processes, with median projection longer than laterals (fig. 134) *Choroterpes (Choroterpes s.s.)* Eaton (p. 242)

(3) Descriptions of and Notes on the Genera

Genus *Adenophlebia* Eaton, 1881

(figs. 4-5, 31, 44, 53, 64, 73, 82, 91, 100, 109, 123)

- Walker, 1860, *Trans. ent. Soc. Lond.* 5 : 198 (*Ephemera* partim).
 Eaton, 1871, *Trans. ent. Soc. Lond.* 1871 : 83 (*Leptophlebia* partim).
 Eaton, 1881, *Ent. mon. Mag.* 17 : 194.
 Eaton, 1884 (1883-88), *Trans. Linn. Soc. Lond. (Zool.)* 3 : 111.
 Ulmer, 1920, *Stettin ent. Ztg.* 81 : 112, 115.
 Lestage, 1924, *Rev. zool. afr.* 12 : 332 (*Esbenophlebia*).
 Ulmer, 1924, *Konowia* 3 : 35.
 Barnard, 1932, *Trans. roy. Soc. S. Afr.* 20 : 240 (*Esbenophlebia* = *Adenophlebia*).
 Ulmer, 1932a, *Stettin ent. Ztg.* 93 : 212-3.
 Ulmer, 1932b, *Peking nat. Hist. Bull.* 7 : 202.

Type species, *A. dislocans* (Walker) (originally placed in *Ephemera*), by original designation.

Species included.—*A. auriculata* (Eaton, 1871 : 83) (*Leptophlebia*); *A. burgeoni* Navás, 1929 : 110 (= *A. elegantula* Navás, 1931a : 272); *A. collarti* Navás, 1930 : 316; *A. dislocans* (Walker, 1860 : 198) (*Ephemera*); *A. infuscata* Navás, 1936 : 365; *A. peringueyella* Lestage, 1924 : 333; *A. sinuosa* Navás, 1931c : 109; *A. sylvatica* Crass, 1947 : 102; *A. westermanni* Esben-Petersen, 1913 : 180.

Species examined.—*A. auriculata*, male and female imagos, nymph; *A. dislocans*, male imago; *A. peringueyella*, female imago, nymph; *Adenophlebia* spp., numerous nymphs from the Belgian Congo.

Distribution.—Africa, south of equator.

Imago.—Length of male: body, 6.0-10.5 mm.; fore wings, 6.5-10.5 mm. Length of female: body, 8.0-12.0 mm.; fore wings, 8.0-13.0 mm. Eyes of male separated on meson of head by a narrow space, lower portion of eyes three-fourths length of upper portion; eyes of female separated on meson of head by a length 3 times as great as maximum width of an eye. Wings (figs. 4-5): vein *Rs* of fore wings forked one-third of distance from base to the margin; vein *MA* forked one-half of distance from base to margin, fork asymmetrical; vein *MP* forked near base, fork asymmetrical (fig. 4); cubital area as in figure 4; cross veins numerous. Costal projection of hind wings acute and well developed, apex of projection located about one-third distance from base (fig. 5); cross veins numerous. Legs: ratios of segments in male fore legs, 1.00 : 1.00 (2.15 mm.) : 0.10 : 0.33 : 0.28 : 0.19 : 0.11. Claws alike, apically hooked, each with an opposing hook (fig. 44). Male genitalia (fig. 31): segments two and three of forceps short, second segment not clearly demarcated from segment three, base of forceps broad; penes fused except for apical cleft, each lobe with a ventral spine. Ninth sternum of female slightly cleft apically (fig. 53). Terminal filament longer than cerci.

Mature nymph.—Antennae two and one-fourth times as long as maximum length of head. Mouthparts (figs. 64, 73, 82, 91, 100): dorsal hair on labrum as in figure 73; submedian areas of hair ventrally, 2-5 denticles on anteromedian emargination. Left mandible as in figure 100. Lingua of hypopharynx with well developed lateral processes (fig. 91), anterior margin shallowly cleft; superlingua of hypopharynx as in figure 91, with a row of hair along anterior margin. Segment two of maxillary palpi one and one-third as long as segment one; segment three one-half length of segment two, triangular; hair on maxillae as in figure 82. Labium as in figure 64; segment two of palpi a little longer than segment one; segment three a little longer than one-half length of segment two, triangular; paraglossae ventral to glossae. Hair on anterolateral margins of prothorax only. Legs (fig. 109): apex of claws hooked and narrow, denticles on claws progressively larger apically, except apical denticle much larger. Gills (fig. 123): gills on segments 1-7 alike; both lamellae plate-like, ventral lamellae smaller. Posterolateral spines on abdominal segments 3-7, larger posterolateral spines on segments 8 and 9. Terminal filament longer than cerci.

History and Discussion

Eaton (1881) erected the genus *Adenophlebia* for Walker's species *Ephemera dislocans* on the basis of relative lengths of the leg segments and of the genitalia. Lesage (1924) created the genus *Esbenophlebia* for the species *A. westermanni* on the basis of the shape of the fore wings and minor venational characters; however, Barnard (1932) synonymised *Esbenophlebia* and placed *E. westermanni* in *Adenophlebia*. He stated that the shape and venation of the fore wings of *E. westermanni* are typical of *Adenophlebia*.

Adenophlebia is a distinctive genus; however, it is doubtful if *A. collarti* and *A. sinuosa*, named by Navás, are representatives of this genus, as Navás' figures of the wings of these two species show little resemblance to wings of *Adenophlebia*. Demoulin (1955*b*), in his revisions of Navás' African species, was unable to study the types of these two species.

Biology

The biology of several species of *Adenophlebia* is summarised in Barnard (1932) and in A.C. Harrison (1949*a*). The nymphs are abundant in upland rivers and are found under large rocks.

Genus *Adenophlebiodes* Ulmer, 1924

(figs. 1, 6-8, 32, 45, 54, 65, 74, 83, 92, 101, 110-111, 119-120, 124-5)

Ulmer, 1915, *Arch. Naturgesch.* 81 : 13, figs. 12-14 (*Adenophlebia* partim).

Ulmer, 1924, *Konowia* 3 : 33.

Ulmer, 1932*b*, *Peking nat. Hist. Bull.* 7 : 202.

Crass, 1947, *Ann. Natal Mus.* 11 : 104 (*Euphlebia*).

Edmunds, 1953, *Rev. Zool. Bot. afr.* 48 : 79 (*Euphlebia* = *Adenophlebiodes*).

Demoulin, 1955*b*, *Bull. (Ann.) Soc. ent. Belg.* 91 : 285. (Subgenera *Adenophlebiodes* s.s. and *Hyalophlebia*.)

Agnew, 1961, *Novos Taxa ent.* 26 : 6.

Agnew, 1962, *Arch. Hydrobiol.* 58 : 361.

Type species, *A. ornata* (Ulmer) (originally placed in *Adenophlebia*) by original designation.

Species included. *A. bicolor* (Crass, 1947:104) (*Euphlebia*); *A. decorata* (Navás, 1931*b*:137) (*Adenophlebia*); *A. demoulini* Kimmins, 1960:354 (= *A. decoratus* Kimmins, 1956 nec Navás, 1931*b*); *A. dentifera* (Navás, 1930:314) (*Atalophlebia*); *A. masonella* Agnew, 1961:3; *A. ornata* (Ulmer, 1915:13) (*Adenophlebia*) (= *A. delamarei* Verrier, 1951 : 45) (*Habrophlebia*); *A. patriciae* Agnew, 1962 : 358; *A. seydeli* (Navás, 1930 : 315) (*Adenophlebia*).

Species examined.—*A. bicolor*, male and female imagos; *A. ornata*, male and female imagos; *A. patriciae*, male and female imagos, nymph; *Adenophlebiodes* spp., numerous nymphs from the Belgian Congo and Gold Coast (Ghana).

Distribution.—Africa, south of Sahara Desert.

Imago.—Length of male: body, 7.0-8.5 mm.; fore wings, 7.0-9.0 mm. Length of female: body, 5.0-11.0 mm.; fore wings, 7.5-15.0 mm. Eyes of male separated on meson of head by a length as great as maximum width of a lateral ocellus or eyes meet on meson of head, lower portion of eyes one-half length of upper portion; eyes of female separated on meson of head by a length three and one-half times the maximum width of an eye. Wings (figs. 6-8): vein *Rs* of fore wings forked one-fifth of distance from base to margin; vein *MA* forked one-half of distance from base to margin, fork symmetrical; veins *Rs* and *MP* forked equidistant from base, fork of vein *MP* asymmetrical; cubital area as in figure 6; cross veins numerous. Costal projection of hind wings rounded and well developed, apex of projection rounded, and located one-half distance from base (fig. 8); cross veins numerous. Legs: ratios of segments in male fore leg, 0.60 : 1.00 (1.60 mm.) : 0.70 : 0.33 : 0.33 : 0.20 : 0.10. Claws alike, apically hooked, each with an opposing hook (fig. 45). Male genitalia (fig. 32): segments two and three of forceps short, base of forceps broad, its inner margin forming an angular bend; penes divided, each lobe apically tapered, apex of lobe bent inwardly (fig. 32). Ninth sternum of female entire (fig. 54) or apically cleft. Terminal filament slightly longer than cerci.

Mature nymph.—Antennae one and one-half times as long as maximum length of head. Mouthparts (figs. 65, 74, 83, 92, 101): dorsal hair on labrum as in figure 74; submedian areas and anterolateral areas of hair ventrally, anteromedian margin shallowly emarginated (fig. 74). Left mandible as in figure 101. Lingua of hypopharynx with well developed lateral processes (fig. 92), anterior margin shallowly cleft; superlingua of hypopharynx as in figure 92, with a row of hair along anterior margin. Segment two of maxillary palpi equal in length to segment one; segment three slightly shorter than segment two, triangular; hair on maxillae as in figure 83. Labium as in figure 65; segment two of palpi slightly shorter than segment one; segment three slightly shorter than segment two, triangular; paraglossae dorsal to glossae. Hair on body varies from small hair on anterolateral margins of prothorax only, to entire body covered. Legs (figs. 1, 110–11): claws apically hooked, denticles on claws progressively larger apically (fig. 110), or denticles uniform, except apical denticle larger, basal to large denticle a long thin denticle (fig. 111). Gills (figs. 1, 124–5): gills on segments 1–6 or 1–7; gill 1 of single lamella, operculiform (figs. 1, 124); gills 2–6 or 2–7 with dorsal and ventral lamellae present (figs. 1, 125), ventral lamellae larger, gills deeply cleft apically, an elongated lobe on anterior inner margin of ventral lamellae, gills 2–6 progressively smaller posteriorly. Abdominal segments 1–5 shortened and compacted (fig. 1), a small posterolateral spine on segment 5; larger posterolateral spines on segments 6–9, spines progressively larger posteriorly or posterolateral spines on segments 6–9 similar to small spine of segment 5. Terminal filament slightly longer than cerci; posterior margin of each segment with a whorl of sparse hair (fig. 119), or with a whorl of sparse hair and spines (fig. 120).

History and discussion

The genus *Adenophlebiodes* was erected by Ulmer (1924) for the single species *A. ornata*, which he had placed earlier in *Adenophlebia*. Crass (1947) created the genus *Euphlebia* for *bicolor* from Natal; however, Edmunds (1953) synonymised this genus with *Adenophlebiodes*. Subsequently, Demoulin (1955b) divided *Adenophlebiodes* into two subgenera, *Adenophlebiodes* s.s. and *Hyalophlebia*, on the following characters:

In *Adenophlebiodes* s.s., (1) the length of vein *Sc* of the hind wings is four-fifths the length of the wings, (2) four intercalaries occur within the fork of vein *Rs* of the hind wings and (3) the membrane of the wings is pigmented. In *Hyalophlebia*, (1) the length of vein *Sc* of the hind wings is five-sevenths to five-eighths the length of the wings, (2) one intercalary occurs within the fork of vein *Rs* of the hind wings and (3) the membrane of the wings is unpigmented, except that the anterior border of the fore wings may be tinted.

Our study has shown that the length of vein *Sc* of the hind wings and the number of intercalaries within the fork of vein *Rs* of the hind wings varies within each nominal subgenus. Thus, the only character that can be used in distinguishing the two subgenera is that the members of *Adenophlebiodes* s.s. have pigmented wings, whereas those of *Hyalophlebia* have clear wings. This character is usually not reliable for the characterisation of genera or subgenera of the Ephemeroptera.

The nymphs of *Adenophlebiodes* fall into two distinctive groups separable by the following characters:

In group I, (1) abdominal gills occur on segments 1–7, (2) the denticles of the claws are uniform in size, except that the apical denticle is larger, and basal to the large denticle is a long thin denticle (fig. 111), (3) the posterior margin of each segment of the caudal filaments possesses a whorl of sparse hair and spines (fig. 120) and (4) the spines on abdominal segments 6–9 are similar to the small spine on segment 5.

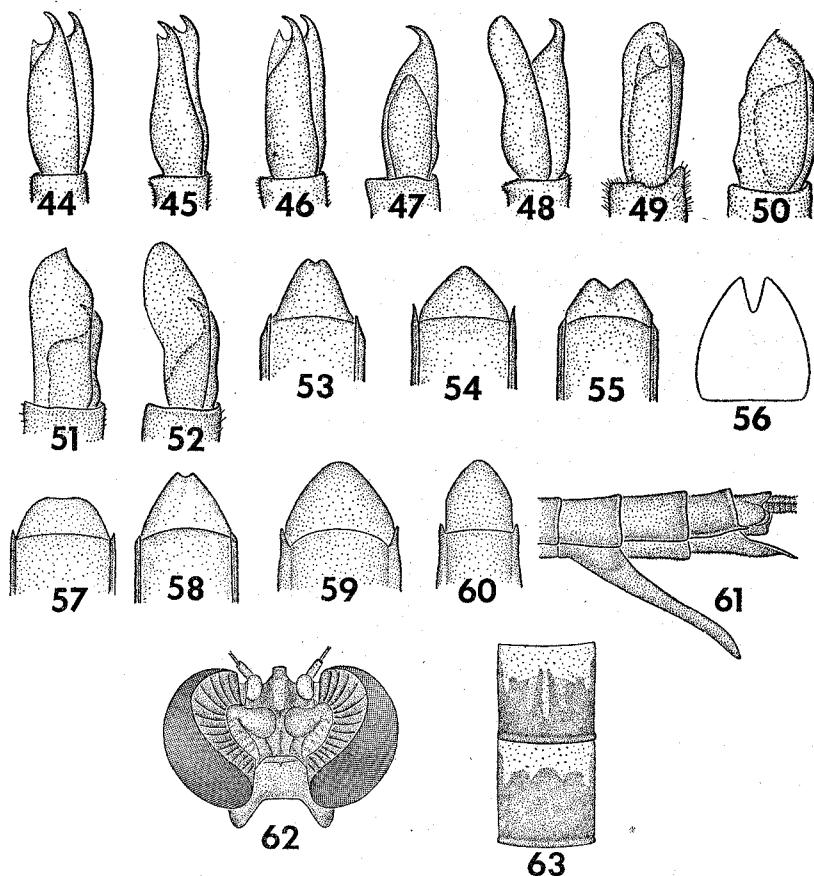
In group II, (1) abdominal gills occur on segments 1–6 (fig. 1), (2) the denticles of the claws are progressively larger towards apex of claws (fig. 110), (3) the posterior margin of each segment of the caudal filaments has a whorl of hair (fig. 119) and (4) the spines on abdominal segments 6–9 are well developed, with the spine on segment 5 small.

In other genera of the Leptophlebiidae, such characters of the gills, claws and caudal filaments have been found to be constant within a genus. Agnew (1961, 1962) has noted the characters of the gill and claw in these two groups of nymphs. Agnew (1962) has also associated the adult and nymph of *A. patriciae*; the nymph of this

species belongs to group I. The nymph of *A. bicolor*, associated by Crass (1947), and the nymph of *A. masonella*, associated by Agnew (1961), belong to group II. On wing pigmentation, *A. bicolor* and *A. masonella* would belong to *Adenophlebiodes* s.s., whereas *A. patriciae* would belong to *Hyalophlebia*. Thus there is evidence that the two groups of nymphs correlate with the subgenera proposed by Demoulin. Perhaps the two subgenera are weakly differentiated in the adults, although the nymphs are well differentiated. We have not segregated the named species into subgenera, but if additional rearing or association of species confirms that the two nymphal types conform to groupings of the adults based on wing pigmentation, the two subgeneric names should be applied.

Biology

Little is known about the biology of this genus. Tjønneland (1960) recorded data concerning the flight activity of *A. demoulini*. Crass (1947) reported that nymphs



FIGS. 44-63.—(44-52) Claws of fore leg of male imago: (44) *Adenophlebia auriculata*; (45) *Adenophlebiodes ornata*; (46) *Aprionyx intermedius*; (47) *Choroterpes (Choroterpes) picteti*; (48) *Choroterpes (Euthraulius) elegans*; (49) *Fullella dentata*; (50) *Fullemimimus marlieri*; (51) *Maheathraulius scotti*; (52) *Masharikella torrentis*. (53-60) Ninth sternum of female imago: (53) *Adenophlebia auriculata*; (54) *Adenophlebiodes ornata*; (55) *Aprionyx natalicus*; (56) *Castanophlebia calida* (after Barnard, 1932); (57) *Choroterpes (Choroterpes) picteti*; (58) *Choroterpes (Euthraulius) elegans*; (59) *Maheathraulius scotti*; (60) *Masharikella torrentis*. (61) *Maheathraulius scotti*, lateral view of egg guide or ovipositor of female imago. (62) *Nesophlebia adusta* sp. n., dorsal view of head of male imago. (63) *Nesophlebia adusta* sp. n., terga 5-6 of male imago.

of *A. bicolor* live in still, deep stretches of water in which there is cover in the form of trailing herbage and vegetable detritus. He also stated that the imagos were swarming at midday and that they are swift and powerful fliers.

Genus *Aprionyx* Barnard, 1932

(figs. 9–10, 33–34, 46, 55, 66, 75, 84, 93, 102, 112, 121, 126–127)

Eaton, 1884 (1883–88), *Trans. Linn. Soc. Lond. (Zool.)* 3 : 83 (*Atalophlebia* partim).

Ulmer, 1920, *Stettin ent. Ztg.* 81 : 115 (*Atalophlebia* partim).

Barnard, 1932, *Trans. roy. Soc. S. Afr.* 20 : 233–4.

Ulmer, 1932a, *Stettin ent. Ztg.* 93 : 212–13.

Tillyard, 1934, *Pap. roy. Soc. Tasm.* 1933 : 5–6.

Barnard, 1940, *Ann. S. Afr. Mus.* 32 : 616.

Crass, 1947, *Ann. Natal Mus.* 11 : 95–96.

Harrison, 1949b, *Piscator* 3 : 83.

Type species, *A. tabularis* (Eaton) (originally placed in *Atalophlebia*), designated by Barnard (1940).

Species included.—*A. argus* Barnard, 1940 : 628; *A. intermedius* Barnard, 1932 : 238; *A. natalicus* (Lestage, 1924 : 325) (*Atalophlebia*); *A. pellucidulus* (Esben-Petersen, 1920 : 499) (*Atalophlebia*); *A. peterseni* (Lestage, 1924 : 328) (*Atalophlebia*); *A. rubicundus* Barnard, 1932 : 239; *A. tabularis* (Eaton, 1884 : 91) (*Atalophlebia*) (= *Atalophlebia phoeocera* Lestage, 1924 : 325); *A. tricuspidatus* Crass, 1947 : 97.

Species examined.—*A. intermedius*, male imago, nymph; *A. natalicus*, male and female imagos; *A. peterseni*, male and female imagos, nymph; *A. tabularis*, nymph; *A. tricuspidatus*, male imago, nymph.

Distribution.—Africa, extreme southern portion.

Imago.—Length of male: body, 7.0–12.5 mm.; fore wings, 7.0–13.0 mm. Length of female: body, 10.5–14.0 mm.; fore wings, 10.0–15.0 mm. Eyes of male meeting on meson of head or separated by up to two and one-half times maximum width of a lateral ocellus, lower portion of eyes three-fourths to equal length of upper portion; eyes of female separated on meson of head by a length three and one-half times maximum width of an eye. Wings (figs. 9–10): vein *Rs* of fore wings forked one-third of distance from base to margin; vein *MA* forked one-half of distance from base to margin, fork asymmetrical; vein *MP* forked near base, vein *MP*₂ strongly recurved (fig. 9); cubital area as in figure 9; cross veins numerous. Costal margin of hind wings convex, apex of convexity located one-third distance from base (fig. 10); cross veins numerous. Legs: ratios of segments in male fore legs, 0.83 : 1.00 (3.80 mm.) : 0.05 : 0.34 : 0.36 : 0.30 : 0.13. Claws alike, apically hooked, each with an opposing hook (fig. 46). Male genitalia (figs. 33–34): segments two and three of forceps short; base of forceps broad, its inner margin forming an angular bend; penes fused except for apical cleft, flattened dorsoventrally, broad basally, tapering towards apex (fig. 33), or rectangular shaped (fig. 34); a recurved flap near each orifice (figs. 33–34). Ninth sternum of female imago deeply incised apically (fig. 55). Terminal filament longer than cerci.

Mature nymph.—Antennae four times as long as maximum length of head, a row of long hair at apex of each flagellar segment. Mouthparts (figs. 66, 75, 84, 93, 102): dorsal hair on labrum as in figure 75; submedian areas and an area of hair on anterolateral margins of ventral surface; five to six denticles on anteromedian emargination. Left mandible as in figure 102. Lingua of hypopharynx with well developed lateral processes (fig. 93), anterior margin deeply cleft; superlingua of hypopharynx as in figure 93, with a row of hair along anterior margin. Segment two of maxillary palpi one and one-fourth as long as segment one; segment three three-fourths length of segment two, triangular; hair on maxillae as in figure 84. Labium as in figure 66; segment two of palpi equal to length of segment one; segment three short and truncate (fig. 66); glossae ventral to paraglossae. Fine hair present on dorsum of thorax only. Legs (fig. 112): claws long and tapered, no denticles present. Gills (figs. 126–7): gills on segments 1–7 alike; both lamellae plate like, ventral lamellae smaller; each gill terminated in one slender, filamentous process (fig. 126) or terminated in three slender, filamentous processes (fig. 127). Single posterolateral spines on abdominal segments 6 and 7, double posterolateral spines on abdominal segments 8 and 9 (fig. 121). Terminal filament longer than cerci.

History and discussion

Eaton (1883–88) described *Atalophlebia tabularis* from specimens from the Cape of Good Hope. Barnard (1932), upon obtaining reared specimens of *A. tabularis*,

created the genus *Aprionyx* to include this and five other related species. Since that time, two other species have been placed in this genus.

Many of the nymphal specimens of *Aprionyx* from Natal have gills that terminate in three long, slender, filamentous processes (fig. 127). According to Crass (1947), and from our own observations, specimens of one species may have gills with one or three processes. We have also observed both types of gills on a single specimen.

Biology

A. C. Harrison (1949b) summarised the biology of *Aprionyx*. The nymphs are abundant in upland rivers, where they occur under large rocks.

Genus *Atalophlebioides* Phillips, 1930

(figs. 67, 76, 85, 94, 103, 113, 128)

Phillips, 1930, *Trans. N.Z. Inst.* 61 : 336.

Ulmer, 1932a, *Stettin ent. Ztg.* 93 : 214.

Ulmer, 1938, *Arb. morph. taxon. Ent.* 5 : 104.

Traver, 1946, *Rev. de Ent.* 17 : 423-4.

Harker, 1954, *Trans. R. ent. Soc. Lond.* 105 : 253.

Type species, *A. cromwelli* (Phillips), present designation.

Species occurring in the Ethiopian region.—*A. inequalis* Demoulin, 1955a : 1.

Species examined.—*A. inequalis*, nymph.

Distribution.—New Zealand, Australia, Chile and Madagascar.

Imago.—Unknown from the Ethiopian region.

Mature nymph.—Mouthparts (figs. 67, 76, 85, 94, 103): dorsal hair on labrum as in figure 76; submedian and lateral areas of hair ventrally, anteromedian margin shallowly emarginated. Left mandible as in figure 103. Lingua of hypopharynx with well developed lateral processes (fig. 94), anterior margin deeply cleft; superlingua of hypopharynx as in figure 94, with a row of hairs along anterior margin. Segment two of maxillary palpi about equal in length to segment one; segment three a little longer than two-thirds length of segment two, triangular; hair on maxillae as in figure 85. Labium as in figure 67; segment two of palpi equal in length to segment one; segment three one-half length of segment two, triangular; paraglossae ventral to glossae. Hair on anterolateral margins of prothorax only. Legs (fig. 113): apex of claws hooked and narrow, denticles on claws all of about equal length. Gills (fig. 128): gills on segments 1-7 alike; both lamellae plate-like, ventral lamellae smaller, dorsal lamellae terminated in one slender, filamentous process, gills smaller posteriorly. Posterolateral spines on abdominal segments 4-9, spines progressively larger posteriorly.

History and discussion

The genus *Atalophlebioides* was described by Phillips (1930) from New Zealand as a subgenus of *Deleatidium*. Phillips placed all species in which the gills had double lamellae in the subgenus *Atalophlebioides*, and those in which the gills had a single lamella in the subgenus *Deleatidium* s.s. Ulmer (1938) and Traver (1946) have both considered *Atalophlebioides* worthy of generic rank, whereas Harker (1954) agreed with Phillips (1930).

Atalophlebioides and related genera from New Zealand, Australia and southern South America are a complex of genera with ill-defined limits. Since the nymph of *A. inequalis* generally resembles the nymphs of the New Zealand *Atalophlebioides* described by Phillips, the nymphs from Madagascar should remain in *Atalophlebioides* until this genus and related genera can be revised, and reared material of *A. inequalis* is available. The above nymphal description is based only on *A. inequalis*.

Until now no type species has been designated for the genus *Atalophlebioides*. Penniket (*personal communication*) has suggested that *A. cromwelli* be placed as the type species, since it was more fully figured than *A. sepia* by Phillips (1930). Therefore, we are designating herein *A. cromwelli* as the type species of *Atalophlebioides*.

Biology

Phillips (1930) noted the habitat of the nymph of *A. cromwelli*. Nothing is known about the biology of the representative from Madagascar.

Genus *Castanophlebia* Barnard, 1932

(figs. 11–12, 35, 56, 68, 77, 86, 95, 104, 114, 129–131)

Barnard, 1932, *Trans. roy. Soc. S. Afr.* 20 : 244–6.

Ulmer, 1932a, *Stettin ent. Ztg.* 93 : 214.

Barnard, 1940, *Ann. S. Afr. Mus.* 32 : 631.

Type species, *C. calida* Barnard, monobasic.

Species included.—*C. albicauda* Barnard, 1940 : 631; *C. calida* Barnard, 1932 : 246.

Species examined.—*C. calida*, nymph.

Distribution.—Extreme southern Africa.

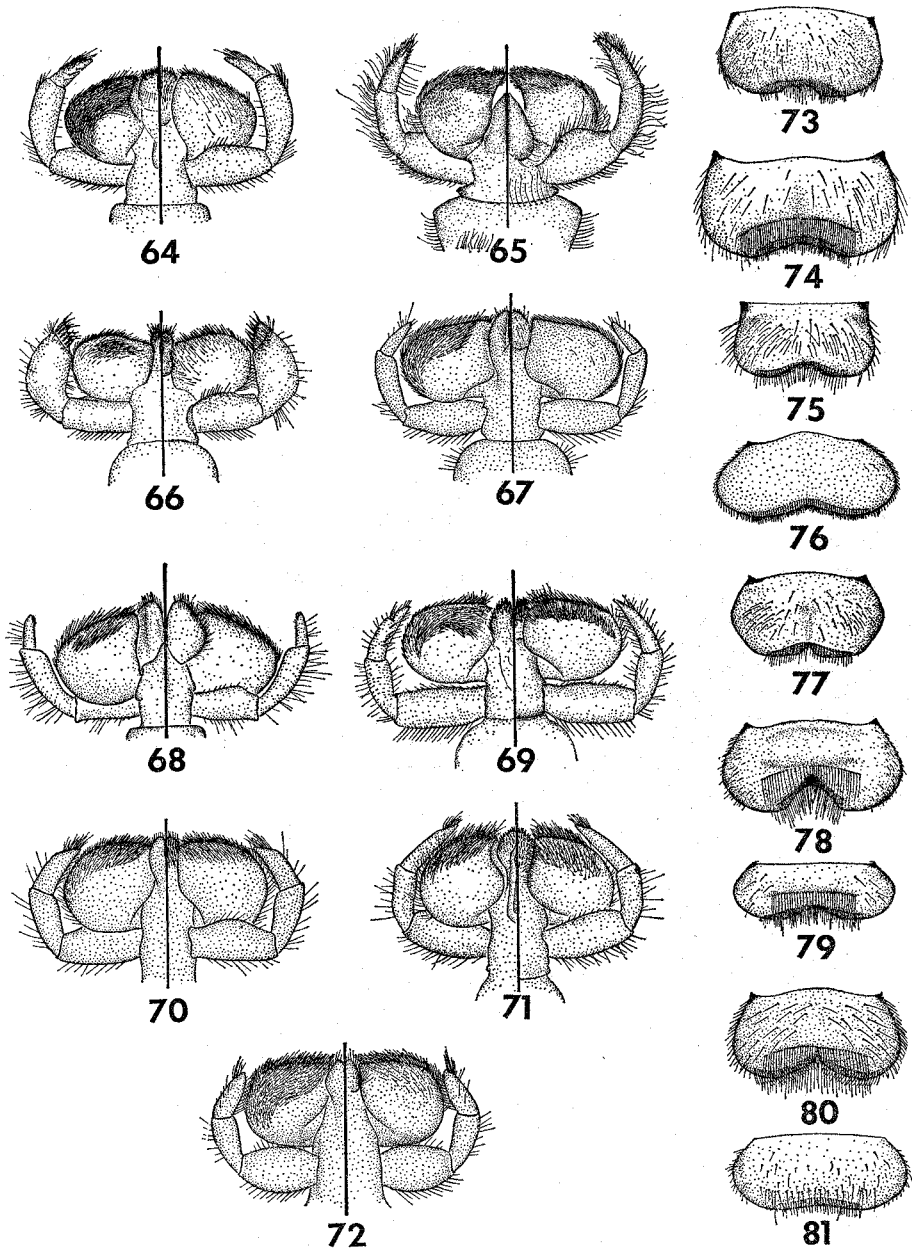
Imago.—Length of male: body, 6.5 mm.; fore wings, 7.0–9.0 mm. Length of female: body, 6.0–9.0 mm.; fore wings, 6.5–11.0 mm. Wings (figs. 11–12): fore wings long and narrow; vein *Rs* of fore wings forked one-third of distance from base to margin; vein *MA* forked one-half of distance from base to margin, fork asymmetrical; veins *Rs* and *MP* forked equidistant from base (fig. 11), fork of vein *MP* symmetrical; cubital area as in figure 11; cross veins few. Costal margin of hind wings convex, apex of convexity located beyond middle (fig. 12); cross veins few. Legs: claws dissimilar, one apically hooked, the other obtuse, pad like. Male genitalia (fig. 35): segments two and three of forceps short, base of forceps broad, its inner margin forming a gradual angular bend; penes broad, divided, lobes divergent outwardly, ventral spine on each. Ninth sternum of female deeply incised apically (fig. 56). Terminal filament slightly longer than cerci. (Description from Barnard, 1932.)

Mature nymph.—Antennae two times as long as maximum length of head. Mouthparts (figs. 68, 77, 86, 95, 104): dorsal hair on labrum as in figure 77; small, submedian areas of hair ventrally; anteromedian margin incised (fig. 77); shape as in figure 77 or more angular laterally. Left mandible as in figure 104. Lingua of hypopharynx cordate (fig. 95) with a row of hair along anterior margin; superlingua of hypopharynx as in figure 95, with a row of hair along anterior margin. Segment two of maxillary palpi one and one-half to two times as long as segment one; segment three one-half to equal length of second segment; hair on third segment as in figure 86 or a dense row along inner margin; hair on remainder of maxillae as in figure 86; joint between segments two and three transverse as in figure 86 or strongly oblique. Labium as in figure 68; segment two of labial palpi more than one and one-half times length of segment one; segment three a little less than one-half length of segment two, slender as in figure 68 or as broad as segment two; glossae ventral to paraglossae. Fine hair on posterolateral margins of prothorax only. Legs (fig. 114): claws moderately hooked, slender; a large denticle in middle of inner margin; basal to large denticle several anterior denticles, apical to large denticle four posterior denticles. Gills (figs. 129–31): gills on segments 1–7; gills on segments 1–6 alike, slender, tracheae unbranched (fig. 129), ventral lamellae present or absent, when present similar to dorsal lamellae, gill 7 similar in structure to gills 1–6, ventral lamella present (fig. 130) or absent (fig. 131), even in specimens with ventral lamellae on gills 1–6, gills on latter segments reduced in length. Small posterolateral spines on abdominal segments 8 and 9. Terminal filament slightly longer than cerci.

History and discussion

Barnard (1932) erected the genus *Castanophlebia* for the species *C. calida* and in 1940 described an additional species in this genus.

The imagos of both species of *Castanophlebia* are quite similar; however, some differences are apparent in the nymphs. The labrum is more angular laterally in *C. albicauda* than in *C. calida* (fig. 77). Segment one of the maxillary palpi of *C. calida* is less than two-thirds as long as segment two (fig. 86), whereas segment one of the maxillary palpi of *C. albicauda* is one-half as long as segment two. In *C. calida* the joint between segments two and three of the maxillary palpi is transverse (fig. 86), but in *C. albicauda* the joint is strongly oblique. Abdominal gills 1 to 6 of specimens of *C. calida* have both dorsal and ventral lamellae present (fig. 129), whereas in *C. albicauda* the ventral lamellae are absent from gills 1 to 6. The ventral lamellae of gill 7 may be present or absent in either species.



FIGS. 64-81.—(64-72) Labium of mature nymph: (64) *Adenophlebia auriculata*; (65) *Adenophlebioides* sp.; (66) *Aprionyx intermedius*; (67) *Atalophlebioides inequalis*; (68) *Castanophlebia calida*; (69) *Choroterpes (Choroterpes) nigrescens*; (70) *Choroterpes (Euthraulius)* sp.; (71) *Maheathraulius scotti*; (72) *Masharikella torrentis*. (73-81) Labrum of mature nymph: (73) *Adenophlebia auriculata*; (74) *Adenophlebioides* sp.; (75) *Aprionyx intermedius*; (76) *Atalophlebioides inequalis*; (77) *Castanophlebia calida*; (78) *Choroterpes (Choroterpes) nigrescens*; (79) *Choroterpes (Euthraulius)* sp.; (80) *Maheathraulius scotti*; (81) *Masharikella torrentis*.

Each of the two species of *Castanophlebia* may represent a distinct subgenus; however, we postpone such consideration until additional specimens are available for study.

Biology

The biology of both species of *Castanophlebia* is summarised by A. C. Harrison (1949c). The nymphs of *C. calida* are found in torrential streams and are often found at the tops of waterfalls in mountain streams. Nymphs of *C. albicauda* are confined to mountain streams at higher elevations than *C. calida*. Barnard (1940) reported nymphs of *C. albicauda* at altitudes from 4,000 feet to 5,000 feet. A. D. Harrison *et al.* (1958) has given additional ecological notes concerning *C. calida*.

Genus *Choroterpes* Eaton, 1881

(figs. 13–17, 36–37, 47–48, 57–58, 69–70, 78–79, 87–88, 96–97, 105–106, 115–116, 132–137)

Eaton, 1881, *Ent. mon. Mag.* 17 : 194.

Eaton, 1884 (1883–88), *Trans. Linn. Soc. Lond. (Zool.)* 3 : 104.

Ulmer, 1920, *Stettin ent. Ztg.* 81 : 114, 116–7.

Lestage, 1921, *Ephemeroptera*, in Rousseau, *Les Larves et Nymphes Aquatiques des Insectes d'Europe*, pp. 228–9.

Barnard, 1932, *Trans. roy. Soc. S. Afr.* 20 : 247–8 (*Choroterpes*); 249 (*Euthraululus*).

Ulmer, 1932a, *Stettin ent. Ztg.* 93 : 212, 214 (*Euthraululus*).

Ulmer, 1932b, *Peking nat. Hist. Bull.* 7 : 204.

Ulmer, 1939, *Arch. Hydrobiol., Supp.* 16 : 499–500 (*Thraululus*).

Gillies, 1957, *Proc. R. ent. Soc. Lond. (B)* 26 : 43 (*Thraululus* = *Euthraululus*).

Grandi, 1960, *Fauna d'Italia* 3 : 248–9, 412.

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

Species occurring in the Ethiopian and Oriental regions.—*C. (E.) bugandensis* (Kimmins, 1956 : 79) (*Euthraululus*); *C. (E.) curta* (Kimmins, 1956 : 80) (*Euthraululus*); *C. (E.) elegans* (Barnard, 1932 : 249) (*Euthraululus*); *C. (E.) marginata* (Ulmer, 1913 : 103) (*Thraululus*); *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. (C.) proba* Ulmer, 1939 : 495; *C. (E.) trifurcata* Ueno, 1928 : 40; *C. (E.) tropicalis* (Gillies, 1957 : 44) (*Euthraululus*); *C. (E.) usambarae* (Gillies, 1957 : 46) (*Euthraululus*); *Choroterpes (E.)* sp. A. (Gillies, 1957 : 48) (*Euthraululus*); *Choroterpes (E.)* sp. B. (Gillies, 1957 : 48) (*Euthraululus*).

Species examined.—*C. (E.) bugandensis*, male and female imagos, nymph; *C. (E.) curta*, male and female imagos; *C. (E.) elegans*, male and female imagos, nymph; *C. (C.) ndebele*, male and female imagos, nymph; *C. (C.) nigrescens*, male imago, nymph; *C. (C.) picteti*, male imago, nymph; *Choroterpes (E.)* sp. A., male and female imagos; *C. (E.) tropicalis*, female imago; *C. (E.) usambarae*, female imago, nymph; *Choroterpes (E.)* sp., numerous nymphs from Africa and Nepal.

Distribution.—Africa south of Sahara Desert, Zanzibar, Asia, Southwest Arabia (Gillies, *personal communication*), Europe, Formosa, Java and North and South America.

Imago.—Length of male: body, 4.0–8.0 mm.; fore wings, 4.0–8.0 mm. Length of female: body, 4.0–10.0 mm.; fore wings, 4.0–10.5 mm. Eyes of male separated on meson of head by a length three-fourths maximum width of median ocellus or eyes meet on meson of head, lower portion of eyes one-half to two-thirds maximum length of upper portion, upper portion on short stalk; eyes of female separated on meson of head by a length three to six and one-half times as great as maximum width of an eye. Wings (figs. 13–17): vein *Rs* of fore wings forked one-fourth of the distance from base to the margin; vein *MA* forked one-half to over one-half of distance from base to margin, fork symmetrical; veins *Rs* and *MP* forked equidistant from base, fork symmetrical (fig. 13) or asymmetrical (fig. 15); cubital area as in figures 13 and 15; cross veins few. Costal projection of hind wings rounded and well developed (figs. 14, 17), apex located one-half distance from base; cross veins

few. Legs: ratios of segments in male fore legs, 0.63 : 1.00 (1.60 mm.) : 0.08 : 0.25 : 0.24 : 0.16 : 0.09. Claws dissimilar, one apically hooked (figs. 47–48), other obtuse, pad-like. Male genitalia (figs. 36–37): segments two and three of forceps short, base of forceps broad, its inner margin forming an extreme angular bend (figs. 36–37) or base of forceps bulbous, base of segment one may be indented giving appearance of a basal fourth segment; penes divided, tubular, each lobe tapered to an apical point (figs. 36–37). Ninth sternum of female shallowly cleft apically (figs. 57–58). Terminal filament slightly longer than cerci.

Mature nymph.—Antennae one and one-half times to equal maximum length of head. Mouthparts (figs. 69–70, 78–79, 87–88, 96–97, 105–106): dorsal hair on labrum as in figures 78–79; submedian areas and anterolateral areas of hair ventrally; anteromedian margin shallowly emarginated (fig. 79) to deeply incised (fig. 78). Left mandible as in figures 105 and 106. Lingua of hypopharynx with well developed lateral processes (figs. 96–97), anterior margin shallowly cleft; superlingua of hypopharynx as in figures 96–97, with a row of hair along anterior margin. Segment two of maxillary palpi slightly longer than segment one; segment three slightly longer than one-half length of segment two, triangular; a large tooth-like process on inner anterior margin of galea-lacinia; hair on maxillae as in figures 87–88. Labium as in figures 69–70; segment two of palpi three-fourths to a little longer than segment one; segment three over one-half length to as long as segment two, triangular; paraglossae ventral to glossae. Fine hair on anterolateral margins of prothorax only. Legs (figs. 115–16): claws apically hooked, denticles on claws progressively larger apically. Gills (figs. 132–7): gills on segments 1–7; gill 1 slender, lanceolate (figs. 132, 135) or similar to dorsal lamellae on gills 2–6 (fig. 133); gills 2–7 alike, dorsal and ventral lamellae plate-like and terminated in three, slender, subequal processes (fig. 136), gills 6 and 7 may be rather small (fig. 137), or dorsal and ventral lamellae plate-like and terminated in three processes, with median projection longer than laterals, ventral lamellae smaller (fig. 134). Posterolateral spines on abdominal segments 4 or 5–9, spines progressively larger posteriorly. Terminal filament slightly longer than cerci.

History and discussion

Eaton (1881) erected the genus *Choroterpes* for the European species *C. picteti*. Since that time nineteen species have been placed in the genus. Barnard (1932) erected the genus *Euthraulius* for the African species *E. elegans*. Ulmer in 1939 erected the genus *Thraululus* for the Oriental species *marginatus*, and later Gillies (1951) added a second species to *Thraululus*. Gillies (1957) placed *Thraululus* as a synonym of *Euthraulius*, thus recognising *Euthraulius* as a wide ranging genus.

We have examined specimens of both *Choroterpes* and *Euthraulius* and have found them identical except for minor characters in the length of the body and wings, fork of veins *MA* and *MP*, and costal projection of the hind wings of the imagos, and the form of the abdominal gills of the nymphs. Although *Euthraulius* is a group distinct from *Choroterpes*, these two genera are so similar in both the imago and nymphal stages that we place *Euthraulius* as a subgenus of *Choroterpes*.

Subgenus *Choroterpes* s.s. Eaton, 1881

(figs. 13–14, 36, 47, 57, 69, 78, 87, 96, 105, 115, 132–134)

Imago.—Length of male: body, 7.0–8.0 mm.; fore wings, 7.0–8.0 mm. Length of female: body, 7.0–10.0 mm.; fore wings, 7.5–10.5 mm. Vein *MA* of fore wings forked over one-half of distance from base to margin (fig. 13); fork of vein *MP* of fore wings symmetrical (fig. 13); bases of costal projection of hind wings both smoothly curved (fig. 14).

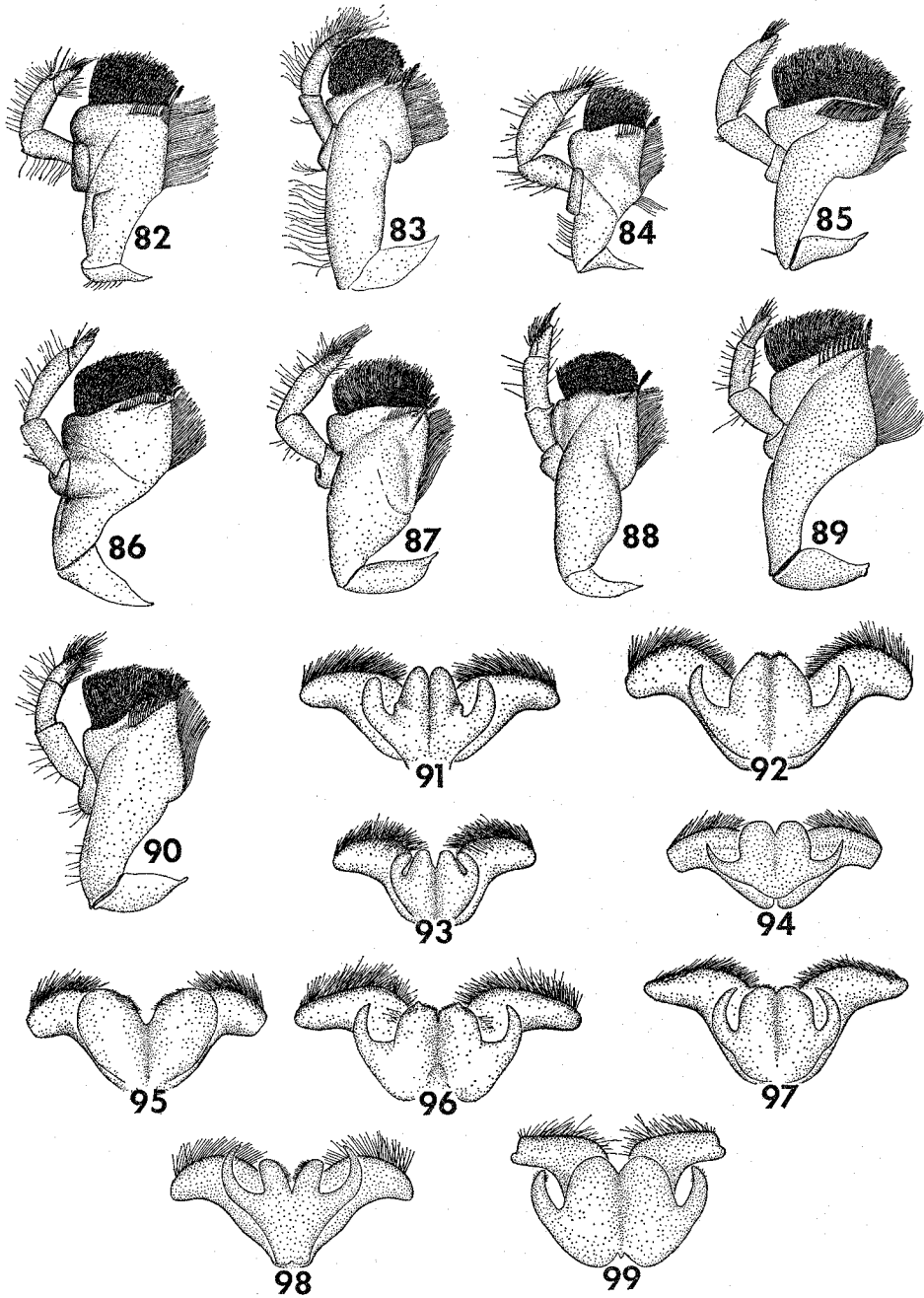
Mature nymph.—Gills 2–7 alike, dorsal and ventral lamellae plate-like and terminated in three processes, with median projection longer than laterals (fig. 134), ventral lamellae smaller.

Discussion

The subgenus *Choroterpes* s.s. is widely distributed, occurring in most parts of the world. The characters above will distinguish it from the subgenus *Euthraulius*.

Biology

The biology of *C. (C.) nigrescens* is summarised in A. C. Harrison (1949c). The nymphs are found in still water. Additional ecological notes concerning this species are given by A. D. Harrison *et al.* (1958).



FIGS. 82-99.—(82-90) Left maxilla of mature nymph: (82) *Adenophlebia auriculata*; (83) *Adenophlebioides* sp.; (84) *Aprionyx intermedius*; (85) *Atalophlebioides inequalis*; (86) *Castanophlebia calida*; (87) *Choroterpes (Choroterpes) nigrescens*; (88) *Choroterpes (Euthraulius)* sp.; (89) *Maheathraulius scotti*; (90) *Masharikella torrentis*. (91-99) Hypopharynx of mature nymph: (91) *Adenophlebia auriculata*; (92) *Adenophlebioides* sp.; (93) *Aprionyx intermedius*; (94) *Atalophlebioides inequalis*; (95) *Castanophlebia calida*; (96) *Choroterpes (Choroterpes) nigrescens*; (97) *Choroterpes (Euthraulius)* sp.; (98) *Maheathraulius scotti*; (99) *Masharikella torrentis*.

Subgenus *Euthraulius* Barnard, 1932

(figs. 15–17, 37, 48, 58, 70, 79, 88, 97, 106, 116, 135–137)

Imago.—Length of male: body, 4.0–5.0 mm.; fore wings, 4.0–8.0 mm. Length of female: body, 4.0–6.0 mm.; fore wings, 4.0–8.0 mm. Vein *MA* of fore wings forked one-half of distance from base to margin (fig. 15); fork of vein *MP* of fore wings asymmetrical (fig. 15); proximal base of costal projection of hind wings smoothly curved, distal base angular (fig. 17).

Mature nymph.—Gills 2–7 alike, dorsal and ventral lamellae plate-like and terminated in three slender subequal processes (fig. 136), gills 6 and 7 may be rather small (fig. 137).

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

Discussion

The drawings by Ulmer (1939) of the fore wings of *C. (E.) marginata* and by Gillies (1957) of the fore wings of *C. (E.) tropicalis* show that the vein MP_2 is not attached. In specimens of *C. (E.) tropicalis* sent to us by Dr. Gillies, vein MP_2 is definitely attached, although the base of MP_2 is unpigmented, and probably this is the case with *C. (E.) marginata*.

The above characters will distinguish the subgenus *Choroaterpes* s.s. from the subgenus *Euthraulius*.

Biology

A. C. Harrison (1949c) has given general habitat notes for *C. (E.) elegans*. The nymphs are found in stony stream beds and are tolerant of still water conditions. Ecological information about this species is given by A. D. Harrison *et al.* (1960). Tjønneland (1960) has recorded data on flight activity for *C. (E.) bugandensis* and *C. (E.) curta*.

Genus *Fulleta* Navás, 1930

(figs. 18, 38, 49)

Navás, 1930, *Rev. Zool. Bot. afr.* 19 : 318–9.

Ulmer, 1932a, *Stettin ent. Ztg.* 93 : 212–3.

Demoulin, 1954, *Ann. Mus. Congo belge Tervuren, Zool.* 1 : 342–5.

Type species, *F. dentata* Navás, by original designation.

Species included.—*F. dentata* Navás, 1930 : 318.

Species examined.—*F. dentata*, male imago.

Distribution.—Africa, Lake Tanganyika area.

Imago.—Length of male: body, 3.5 mm.; fore wings, 3.7 mm. Eyes of male not divided into upper and lower portions, eyes composed entirely of small facets; eyes separated on meson of head by a length four times as great as maximum width of an eye. Wings (fig. 18): vein *Rs* of fore wings forked one-eighth of distance from base to margin; vein *MA* forked less than one-half of distance from base to margin, fork symmetrical; vein MP_2 not attached at base to MP_1 , veins MP_1 and MP_2 independent of each other; cubital area as in figure 18; cross veins numerous; outer margin of fore wings serrate (fig. 18). Hind wings absent. Legs: ratios of segments in male fore leg, 0.56 : 1.00 (0.98 mm.): 0.11 : 0.13 : 0.17 : 0.10 : 0.20. Claws dissimilar, one claw apically hooked and with an opposing hook, other claw obtuse, pad-like (fig. 49). Male genitalia (fig. 38): segments two and three of forceps short; base of forceps broad, its inner margin forming an angular bend; penes divided, tubular, each lobe apically tapered to a point (fig. 38). Terminal filament slightly longer than cerci.

Mature nymph.—Unknown.

History and discussion

Navás (1930) erected *Fulleta* for a peculiar species, *F. dentata*, from the Belgian

Congo. Since that time Demoulin (1954) has redescribed the species from the type material. The nymph is unknown.

Biology

Unknown.

Genus *Fullemimus* Demoulin, 1956a

(figs. 19–21, 39, 50)

Demoulin, 1956a, *Bull. (Ann.) Soc. Roy. ent. Belg.* 92 : 280–2.

Demoulin, 1956b, *Inst. roy. Sci. nat. Belg.* 3 (7) : 14–16.

Type species, *F. marlieri* Demoulin, by original designation.

Species included.—*F. marlieri* Demoulin, 1956a : 280.

Species examined.—*F. marlieri*, male imago.

Distribution.—Africa, Lake Kivu area.

Imago.—Female unknown. Length of male: body, 4.0 mm.; fore wings, 4.4 mm. Eyes not divided into upper and lower portions, eyes composed entirely of small facets; eyes separated on meson of head by a length three times as great as maximum width of an eye. Pedicel of antennae one-third maximum length of flagellum. Wings (figs. 19–21): vein *Rs* of fore wings forked one-third of distance from base to margin; vein *MA* forked beyond one-half of distance from base to margin, fork symmetrical; vein *MP*₂ not attached at base to *MP*₁, veins *MP*₁ and *MP*₂ independent of each other (fig. 19); cubital area as in figure 19; cross veins few; outer margin of fore wings serrate (fig. 19). Costal projection of hind wings acute and well developed, apex of projection located one-half distance from base (figs. 20–21); cross veins few. Legs: ratios of segments in male fore legs, 0.71 : 1.00 (1.15 mm.) : 0.06 : 0.22 : 0.23 : 0.17 : 0.14 (from Demoulin, 1956a). Claws dissimilar, one apically hooked, the other obtuse, pad-like (fig. 50). Male genitalia (fig. 39): segments two and three of forceps short, base of forceps broad, its inner margin forming an angular bend; penes divided, tubular, each lobe tapered to a point (fig. 39), two small, subapical spines on each penis lobe.

Mature nymph.—Unknown.

History and discussion

Demoulin (1956a) erected *Fullemimus* for the species *F. marlieri* from the Lake Kivu area. Since that time Demoulin (1956b) has questionably named a nymph from Lake Tanganyika as *Fullemimus*. In our opinion, however, this is a typical nymph of *Choroterpes* (*Euthraulius*), except for the number of spines on the posterolateral margins of the abdomen. The nymph from Lake Kivu is described by Demoulin as having well developed posterolateral spines on segments 3–9, which become progressively larger posteriorly, and double posterolateral spines on segments 8 and 9, as in figure 121. Nymphs of *Choroterpes* (*Euthraulius*) have posterolateral spines on abdominal segments 6–9, progressively larger posteriorly. There is no proof that the nymph from Lake Tanganyika belongs to *F. marlieri*, and we therefore defer assigning this nymph to genus until specimens can be examined and preferably associated with the adult stage.

Biology

Unknown.

Genus *Hagenulodes* Ulmer, 1919

(figs. 22, 40)

Ulmer, 1919, *Arch. Naturgesch.* 85 : 37.

Ulmer, 1920, *Stettin ent. Ztg.* 81 : 114, 117.

Ulmer, 1932b, *Peking nat. Hist. Bull.* 7 : 204.

Type species, *H. braueri* Ulmer, by original designation.

Species included.—*H. braueri* Ulmer, 1919 : 38.

Species examined.—None.

Distribution.—Mahé Island, Seychelles.

Imago.—Female unknown. Length of male: body, 7.0–8.0 mm.; fore wings, 7.5–8.5 mm. Wings (fig. 22): vein *Rs* of fore wings forked one-fifth of distance from base to margin; vein *MA* forked one-half of distance from base to margin; vein *MP* forked one-half of distance from base to margin; cubital area as in figure 22; cross veins numerous. Hind wings absent. Legs: claws dissimilar, one apically hooked, the other obtuse, pad-like. Male genitalia (fig. 40): forceps two-segmented, segment two one-third as long as segment one, base of forceps broad, inner margin of forceps forming an angular bend; penes divided, tubular. Caudal filaments of about equal length. (Description from Ulmer, 1919).

Mature nymph.—Unknown.

History and discussion

Ulmer (1919) erected *Hagenulodes* for a peculiar species, *H. braueri*, from the Seychelles. The genital forceps of *H. braueri* are two-segmented, a condition that does not occur in any other known Leptophlebiid.

Biology

Unknown.

Genus *Maheathraulus* Peters, Gillies & Edmunds, 1964

(figs. 23–25, 42, 51, 59, 61, 71, 80, 89, 98, 107,
117, 138–139, 122)

Peters, Gillies & Edmunds, 1964, *Proc. R. ent. Soc. Lond.* (B) 33 : 122.

Type species, *M. scotti* (Eaton) (originally placed in *Hagenulus*), by original designation.

Species included.—*M. scotti* (Eaton, 1913 : 433) (*Hagenulus*).

Species examined.—*M. scotti*, male and female imagos, nymph.

Distribution.—Mahé Island, Seychelles.

Imago.—Length of male: body, 2.7 mm.; fore wings, 2.7 mm. Length of female: body, 2.1 mm.; fore wings, 2.7 mm. Eyes of male meet on meson of head, lower portion of eyes less than one-half length of upper portion, upper portion on short stock; eyes of female separated on meson of head by a space two times as great as maximum width of an eye. Wings (figs. 23–25): vein *Rs* of fore wings forked one-sixth of distance from base to margin; vein *MA* forked over one-half of distance from base to margin, fork symmetrical; vein *MP*₂ independent of vein *MP*₁ (fig. 23); cubital area as in figure 23; cross veins numerous. Costal projection of hind wings acute and well developed, projection located one-half distance from base to margin; cross veins few (figs. 24–25). Legs: ratio of segments in male fore leg, 0.50 : 1.00 (1.30 mm.) : 0.04 : 0.54 : 0.46 : 0.23 : 0.15. Claws dissimilar, one apically hooked, the other obtuse, pad-like (fig. 51). Male genitalia (fig. 42): segments two and three of forceps short, segment one long and slender; penes tubular, divided and slender. Egg guide or ovipositor of female extends to posterior margin of abdominal segment ten (fig. 61). Ninth sternum of female entire (fig. 59). Terminal filament slightly longer than cerci.

Mature nymph.—Antennae two times as long as maximum length of head. Mouthparts (figs. 71, 80, 89, 98, 107): dorsal hair on labrum as in figure 80; a band of hair along anterior margin and submedian areas of hair ventrally. Left mandible as in figure 107. Lingua of hypopharynx with well developed lateral processes (fig. 98), hair on apex of lateral processes short, anterior margin deeply cleft; superlingua of hypopharynx as in figure 98, with a row of hair along anterior margin. Segment two of maxillary palpi equal to length of segment one; segment three one-half length of segment two, triangular in shape; hair on maxillae as in figure 89. Labium as in figure 71; segment two of labial palpi four-fifths length of segment one; segment three three-fourths length of segment two, triangular in shape; paraglossae ventral to glossae. Legs (fig. 117): denticles on claws progressively larger apically, apex of claws hooked and narrow. Gills (figs. 138–9): gills on segments 1–7; gill 1 long, slender, consisting of one filament (fig. 138), gills 2–7 long, slender and bifurcate (fig. 139). Egg guide or ovipositor present on female nymphs (fig. 122). Posterolateral spines on abdominal segments 6–9, those on segments 8 and 9 larger. Terminal filament slightly longer than cerci.

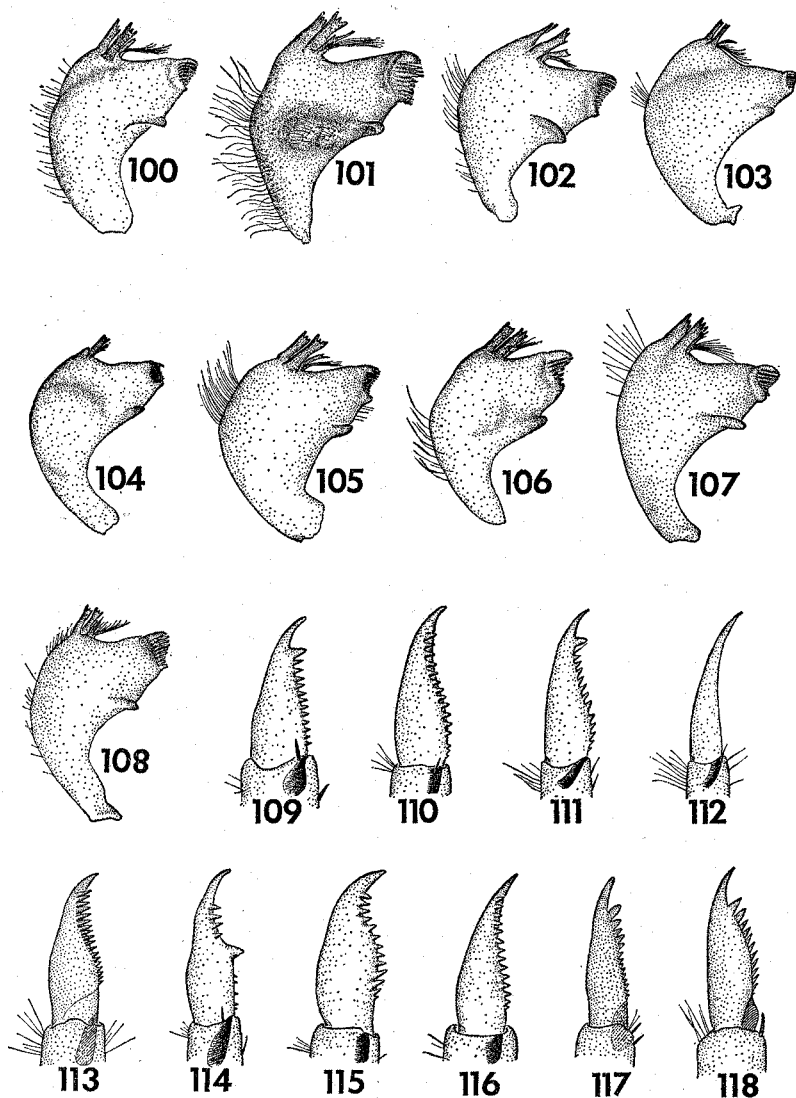
History and discussion

Eaton (1913) described *Hagenulus scotti* from male and female imagos collected on

Mahé Island. Peters, Gillies and Edmunds (1964), upon obtaining associated adult and nymphal material, erected the genus *Maheathraulus* for this species.

Biology

Peters, Gillies and Edmunds (1964) have reported on the habits of the nymphs and swarming behaviour of the adults of *M. scotti*.



FIGS. 100-118.—(100-108) Left mandible of mature nymph: (100) *Adenophlebia auriculata*; (101) *Adenophlebiodes* sp.; (102) *Aprionyx intermedius*; (103) *Atalophlebioides inequalis*; (104) *Castanophlebia calida*; (105) *Choroterpes (Choroterpes) nigrescens*; (106) *Choroterpes (Euthraulus)* sp.; (107) *Maheathraulus scotti*; (108) *Masharikella torrentis*. (109-118) Fore nymphal claw: (109) *Adenophlebia auriculata*; (110) *Adenophlebiodes* sp.; (111) *Adenophlebiodes* sp.; (112) *Aprionyx intermedius*; (113) *Atalophlebioides inequalis*; (114) *Castanophlebia calida*; (115) *Choroterpes (Choroterpes) nigrescens*; (116) *Choroterpes (Euthraulus)* sp.; (117) *Maheathraulus scotti*; (118) *Masharikella torrentis*.

Genus *Masharikella* Peters, Gillies & Edmunds, 1964(figs. 26–27, 41, 52, 60, 72, 81, 90, 99, 108,
118, 140–141)Peters, Gillies & Edmunds, 1964, *Proc. R. ent. Soc. Lond.* (B) 33 : 118.

Type species, *M. fasciata* (Kimmins) (originally placed in *Hagenulus*), by original designation.

Species occurring in the Ethiopian region.—*M. fasciata* (Kimmins, 1956 : 81) (*Hagenulus*); *M. torrentis* (Gillies in Peters, Gillies & Edmunds, 1964 : 120); *M. turbinata* (Ulmer, 1909 : 367) (*Hagenulus*).

Species examined.—*M. duliti*, male imago; *M. fasciata*, male and female imagos; *M. torrentis*, male and female imagos, nymph.

Distribution.—Tanganyika, Uganda, Comoro Islands, India, Borneo, New Guinea and New Ireland.

Imago.—Length of male: body, 5.0–7.0 mm.; fore wings, 5.5–10.0 mm. Length of female: body, 8.0–9.0 mm.; fore wings, 8.5–10.0 mm. Eyes of male meet on meson of head, lower portion of eyes over one-half length of upper portion; eyes of female separated on meson of head by a space four times as great as maximum width of an eye. Wings (figs. 26–27): vein *Rs* of fore wings forked less than one-fourth of distance from base to margin; vein *MA* forked over one-half of distance from base to margin, fork symmetrical; vein *MP* forked nearer to base than vein *Rs* (fig. 26), fork asymmetrical; cubital area as in figure 26; cross veins numerous. Costal projection of hind wings acute and well developed (fig. 27); cross veins few. Legs: ratio of segments in male fore leg, 0.63 : 1.00 (2.20 mm.) : 0.05 : 0.36 : 0.27 : 0.18 : 0.14. Claws dissimilar, one apically hooked, the other obtuse, pad-like (fig. 52). Male genitalia (fig. 41): segments two and three of forceps each one-sixth or less length of segment one, segment one broad, its inner margin forming an angular bend; penes tubular, divided and simple. Ninth sternum of female entire (fig. 60). Terminal filament slightly longer than cerci.

Mature nymph.—Antennae one and one-half times as long as maximum length of head. Mouthparts (figs. 72, 81, 90, 99, 108): dorsal hair on labrum as in figure 81; a band of short spines along anterior margin ventrally. Left mandible as in figure 108. Lingua of hypopharynx with well developed lateral processes (fig. 99), hair on apex of lateral processes short, anterior margin deeply cleft; superlingua of hypopharynx as in figure 99, with a row of hair along anterior margin, lateral tips emarginate. Segment two of maxillary palpi two-thirds length of segment one; segment three equal in length to segment two, triangular in shape; hair on maxillae as in figure 90. Labium as in figure 72; segment two of labial palpi three-fourths length of segment one; segment three slightly longer than segment two, pointed at apex; paraglossae ventral to glossae. Legs (fig. 118): denticles on claws progressively larger apically, apex of claws hooked and narrow. Gills (figs. 140–1): gills on segment 1–7; ventral lamella of gill 1 ovate with fringed margins (fig. 140), dorsal lamella slender, lanceolate (fig. 140), gills 2–7 alike (fig. 141), both lamellae ovate with fringed margins. Small posterolateral spines on abdominal segments 8 and 9. Terminal filament slightly longer than cerci.

History and discussion

Peters, Gillies and Edmunds (1964), upon obtaining the nymph of an Ethiopian representative, placed all but three of the Ethiopian and Oriental species of *Hagenulus* in their new genus *Masharikella*. Two species, *H. karnyi* and *H. monstratus*, from the Oriental region were retained in *Hagenulus*, and the third species from the Ethiopian region was placed in the genus *Maheathraulius*.

Biology

Peters, Gillies and Edmunds (1964) have noted the habitat of the two African species.

Genus *Nesophlebia* gen. n.

(figs. 28–30, 43, 62–63)

Male imago.—Length: body, 7.6 mm.; fore wings, 8.3 mm.; hind wings, 0.3 mm. Eyes separated on meson of head by a space three times as great as maximum width of a lateral ocellus (fig. 62), lower portion of eyes one-half length of upper portion, upper portion of eyes reniform (fig. 62).

Wings (figs. 28–30): vein *Rs* of fore wings forked one-fourth of distance from base to margin; vein *MA* forked one-half of distance from base to margin, fork asymmetrical; veins *MP* and *Rs* forked equidistant from base to margin, fork symmetrical; cubital area as in figure 28; cross veins numerous. Hind wings very small; one longitudinal vein present (figs. 29–30). Male genitalia (fig. 43): segments two and three of forceps about equal in length, each one-third length of segment one; base of forceps broad, its inner margin forming an angular bend; penes divided and tubular. Terminal filament slightly longer than cerci.

Female imago.—Unknown.

Mature nymph.—Unknown.

Etymology.—*nesos*, Gr., meaning island; *phlebos*, Gr., meaning vein.

Type species, *Nesophlebia adusta* sp. n.

Nesophlebia adusta sp. n.

Male imago (in alcohol).—Upper portion of eyes brownish-orange, lower portion black. Ocelli white. Head and thorax light brown, sutures lighter. Coxae and trochanters of legs light chestnut brown. Wings (figs. 28–30): venation of fore wings brown, membrane light amber brown, paler basally and darker anterior to subcosta, especially in apical half (fig. 28); venation and membrane of hind wings chestnut brown. Abdomen: posterior half of terga 1–9 fuscous, markings as in figure 63, but less extensive on terga 1 and 2, remainder of segments 1–7 hyaline, remainder of segments 8 and 9 light chestnut brown, tergum 10 uniformly fuscous; sterna pale, except sterna 1 to 3 and 8 to 10 faintly suffused with light brown. Genitalia (fig. 43): forceps chestnut brown, penes lighter. Caudal filaments light brown.

Female imago and *nymph* unknown.

Holotype ♂ imago, MADAGASCAR: Perinet, xii.1955 (*Brian R. Stuckenberg*). Holotype in alcohol and deposited in the collections of the Paris Museum.

Discussion

The only other known Leptophlebiid with very small hind wings is *Borinquena carmencita*, described from Puerto Rico by Traver (1938). *Nesophlebia* differs from *Borinquena* in the genital structures, venation of the fore wings and the number of longitudinal veins in the hind wings.

The genus *Nesophlebia* can be differentiated from all other genera of the Leptophlebiidae by the following combination of characters: (1) the hind wings are small, with only one longitudinal vein (figs. 29–30); (2) segments two and three of the genital forceps are each one-third the length of segment one (fig. 43); (3) the upper portion of eyes of the male are reniform (fig. 62); and (4) the penes are divided and tubular (fig. 43).

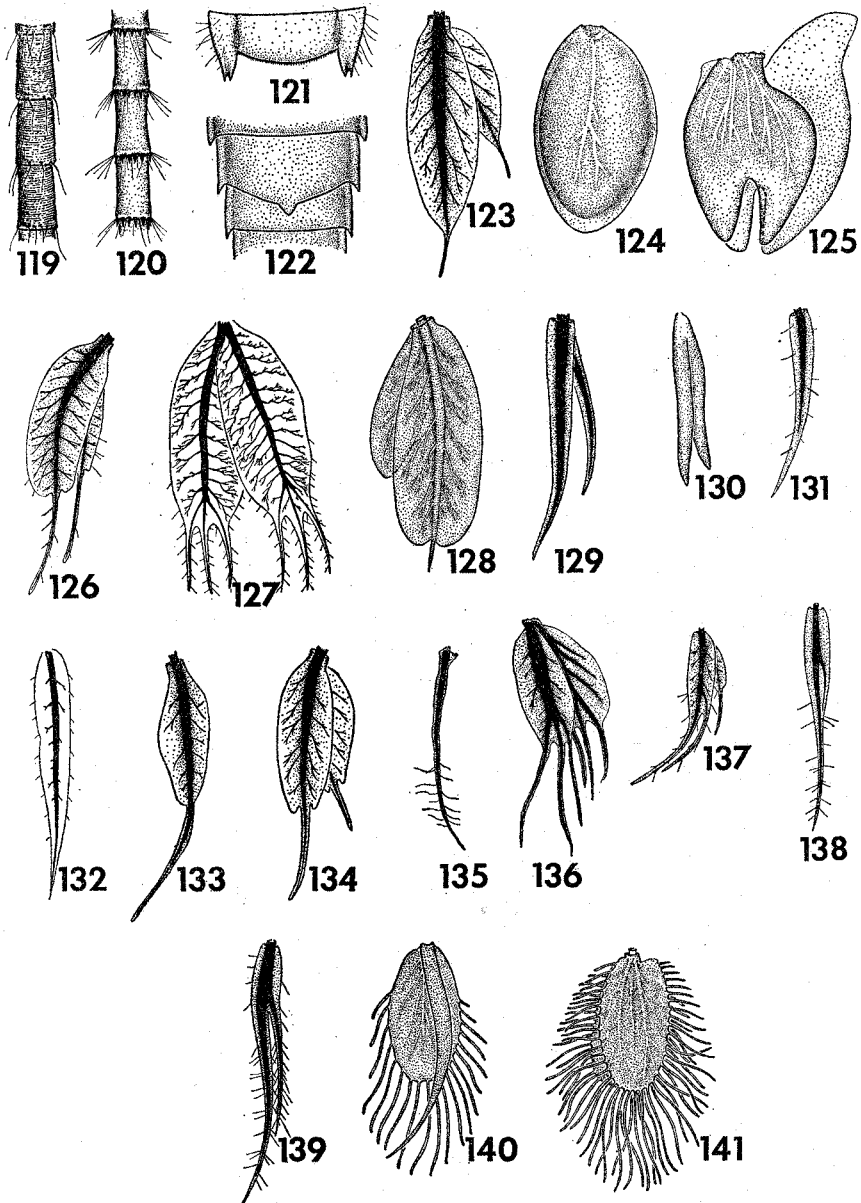
Biology

Unknown.

IV. SUMMARY

Twelve valid genera of the Leptophlebiidae are known to occur in the Ethiopian region. They are *Adenophlebia*, *Adenophlebiodes*, *Aprionyx*, *Atalophlebioides*, *Castanophlebia*, *Choroterpes*, *Fulleta*, *Fullemimus*, *Hagenulodes*, *Maheathraulus*, *Masharikella* and *Nesophlebia*. Keys to the genera and subgenera, and new uniform generic and subgeneric descriptions are presented for all known adults and nymphs. In characterising the genera *Choroterpes* and *Masharikella*, we have included all known species regardless of geographic occurrence.

Demoulin (1955b) divided the genus *Adenophlebiodes* into two subgenera, *Adenophlebiodes* s.s. and *Hyalophlebia*. Our study has shown that all the characters, except differences in wing colour, used by Demoulin in separating these two subgenera vary within each subgenus. No other characters were found that successfully separate



FIGS. 119-141.—(119-120) Segments of terminal filaments of nymph: (119) *Adenophlebiodes* sp.; (120) *Adenophlebiodes* sp. (121) *Aprionyx intermedius*, abdominal tergum 9 of mature nymph. (122) *Maheathraulus scotti*, abdominal sterna 7-8 of mature nymph. (123) *Adenophlebia auriculata*, abdominal gill 4. (124-125) *Adenophlebiodes* sp.: (124) abdominal gill 1; (125) abdominal gill 4. (126) *Aprionyx intermedius*, abdominal gill 4. (127) *Aprionyx tricuspoidatus*, abdominal gill 4 (after Crass, 1947). (128) *Atalophlebioides inequalis*, abdominal gill 4. (129-131) *Castanophlebia calida*: (129) abdominal gill 4; (130) abdominal gill 7; (131) abdominal gill 7. (132-134) *Choroterpes (Choroterpes) nigrescens*: (132) abdominal gill 1 (after Barnard, 1932); (133) abdominal gill 1; (134) abdominal gill 4. (135-137) *Choroterpes (Euthraulus)* sp.: (135) abdominal gill 1; (136) abdominal gill 4; (137) abdominal gill 7. (138-139) *Maheathraulus scotti*: (138) abdominal gill 1; (139) abdominal gill 4. (140-141) *Masharikella torrentis*: (140) abdominal gill 1; (141) abdominal gill 4.

them. The unassociated nymphs of *Adenophlebiodes* fall into two distinctive groups. Agnew (1961, 1962) has presented some evidence that these two groups of nymphs correlate with the subgenera proposed by Demoulin. Perhaps the two subgenera are weakly differentiated in the adults, although the nymphs are well differentiated. However, we have not applied these subgeneric names, but suggest that they should be applied if additional evidence is discovered to show that the nymphal and adult groupings are congruent.

Atalophlebioides inequalis Demoulin from Madagascar is retained in *Atalophlebioides* until typical members of this genus and related genera are revised, and reared material of *A. inequalis* is available. Until now no type species has been designated for *Atalophlebioides*, and we are therefore designating *A. cromwelli* as the type species.

The imagos of both species of *Castanophlebia* are quite similar, whereas some morphological differences are apparent in the labra, maxillae and abdominal gills of the nymphs. It is hypothesised that each species of *Castanophlebia* may represent a distinct subgenus.

We have examined specimens of *Choroterpes* and *Euthraulius* and have found them morphologically identical except for minor characters in the length of the body and wings, fork of veins *MA* and *MP*, and costal projection of the hind wings of the imagos, and the form of the abdominal gills of the nymphs. Although *Euthraulius* is distinguishable from *Choroterpes*, these two groups of species are so similar in both the imaginal and nymphal stages that we place *Euthraulius* as a subgenus of *Choroterpes*.

Demoulin (1956b) has questionably named a nymph from Lake Tanganyika as *Fulletomimus*. This, in our opinion, is a typical nymph of *Choroterpes* (*Euthraulius*), except for the number of spines on the posterolateral margins of the abdomen, and there is no proof that it belongs to *F. marlieri*. We therefore defer assigning this nymph to genus until specimens can be examined and preferably associated with the adult stage.

A new genus, *Nesophlebia*, is established for a new species from Madagascar. *Nesophlebia* can be differentiated from all other genera of the Leptophlebiidae by the small hind wings, with only one longitudinal vein, and by the length of segments two and three of the forceps.

Adenophlebia, *Aprionyx* and the Madagascar representative of *Atalophlebioides* appear to be related to a complex of genera occurring in South America, Australia and New Zealand, indicating a possible palaeantarctic dispersal. The remaining Ethiopian genera are all closely related to one another and together with a number of European and Asiatic genera form a single complex centring around the types of *Choroterpes*, *Thraulius* and *Habrophlebiodes*. Analyses of generic relationships are presented, with pertinent comments on related genera from other geographic regions.

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