

# A Revision of the Generic Classification of Certain Leptophlebiidae from Southern South America (Ephemeroptera)<sup>1</sup>

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## ABSTRACT

Southern South American genera of Leptophlebiidae are described in this paper from reared nymphs and adults. The genera *Massartella*, *Atalonella*, and *Massartellopsis* are redescribed. A type-species, *A. ophis* Needham & Murphy, is designated for *Atalonella*. Three new genera, *PENAPHLEBIA*, *HAPSIPHLEBIA*, and *MERIDIALARIS* are established for species previously placed in Australian genera. The status of *Nousia* and the possible synonymy of *Atalonella* with *Nousia* are discussed. The following new combinations are included: *Penaphlebia*

*chilensis* (Eaton), *P. fulvipes* (Needham & Murphy), *P. sepi* (Thew), *P. vinosa* (Demoulin), *Hapsiphlebia anastomosis* (Demoulin), *Meridialaris biobionica* (Ulmer), *M. chiloeense* (Demoulin), *M. diguillina* (Demoulin), *M. illapelii* (Demoulin), *M. laminata* (Ulmer), *M. patagonica* (Lestage), and *M. penai* (Demoulin). Illustrated keys to the nymphs and adults of the genera are given. Preliminary studies on the relationships and phylogeny of these genera are presented.

For years the placement to genus of certain species of Leptophlebiidae from southern South America has been doubtful, and nymphs of none of these species have been known with certainty. Some of these species were placed into the predominantly Australian genera *Atalophlebia* and *Deleatidium*. Lestage (1930) established *Massartella* for one species originally placed in *Atalophlebia*, while Demoulin (1955c) established *Massartellopsis* for a new species from Chile. Navas (1918) established *Nousia* for the Chilean species *N. delicata* which he described from a male subimago. Needham and Murphy (1924) established *Atalonella* for 2 species from Chile and Australia, but Navas (1925) placed *Atalonella* as a synonym of *Nousia*. While it is apparent these temperate South American species are similar to representatives in the Australian region, the relationships and generic classification of the South American species remained questionable because reared adults and nymphs were not available.

We have made large collections and reared many of these species from temperate South America. This report is based on these and other collections; it revises the generic classification of these species and gives preliminary results of phylogenetic studies.

The following terms and procedures used in the generic descriptions of the imagos and nymphs 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. Venational terminology used is as given in Peters and Edmunds (1964, 1970). Each segment of the fore legs of the male imagos is compared to the length of the fore tibiae and expressed as a ratio, while the average length in millimeters of the fore tibiae is given in parentheses. The generic descriptions are consistent with those given by Peters and Edmunds (1964, 1970) except several additional morphological characters are used to further delineate the genera described herein.

The following keys will serve to distinguish the imagos and nymphs of genera discussed herein. All references in the keys to wing characters are for the fore wings unless otherwise stated.

## IMAGOS

1. Cross vein in apical  $\frac{1}{3}$  of cell C anastomosed (Fig. 4); female with a well-developed ovipositor or egg guide extended to just past anterior margin of segment 8 (Fig. 32) ..... *Hapsiphlebia*, n. gen.  
Cross veins in cell C not as above (Fig. 2, 6, 8, 10, 12); female without an ovipositor or egg guide.. 2
2. Vein  $MP_2$  strongly recurved (Fig. 2, 6) ..... 3  
Vein  $MP_2$  moderately recurved (Fig. 8, 10, 12) ... 4
3. Vein  $ICu_1$  attached at base to vein  $CuA$  (Fig. 2); distal portion of vein MA not sagged posteriorly (Fig. 2) ..... *Penaphlebia*, n. gen.  
Vein  $ICu_1$  attached at base by a cross vein to veins  $CuA$  and  $CuP$  (Fig. 6); distal portion of vein MA sagged posteriorly (Fig. 6) .....  
..... *Massartella* Lestage
4. Vein  $MP_2$  attached at base to vein  $MP_1$  with a cross vein more than  $\frac{1}{3}$  distance from base to margin (Fig. 12); distal portion of vein MA strongly sagged posteriorly (Fig. 12) .....  
..... *Atalonella* Needham & Murphy  
Vein  $MP_2$  attached at base to vein  $MP_1$  with a cross vein  $\frac{1}{3}$  distance from base to margin (Fig. 8, 10); distal portion of vein MA moderately sagged posteriorly (Fig. 8, 10) ..... 5
5. Claws of a pair alike, each apically hooked and with an opposing hook (Fig. 18); penes of male genitalia divided, tubular (Fig. 28) .....  
..... *Massartellopsis* Demoulin  
Claws of a pair dissimilar, one apically hooked with an opposing hook, other obtuse, pad-like (Fig. 17); penis lobes of male genitalia fused except at apical cleft (Fig. 25, 26) .....  
..... *Meridialaris*, n. gen.

## MATURE NYMPHS

1. Middle abdominal gills plate-like (Fig. 1, 75, 76, 78); glossae curved over ventrally (Fig. 69-71) .. 2  
Middle abdominal gills slender (Fig. 79-81); glossae straight, not curved over ventrally (Fig. 72-74) ..... 4
2. Main trunk of tracheae of gills along medium line of lamellae (Fig. 75); gills alike on abdominal segments 1-7; posterolateral spines on abdominal segments 7-9 ..... *Penaphlebia*  
Main trunk of tracheae of gills strongly curved towards inner margin of lamellae (Fig. 76, 78); gills not as above; posterolateral spines on abdominal segments 1 or 2-9 ..... 3
3. Gills present on abdominal segments 1-6 only, gills

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- plate-like (Fig. 78); denticles on claws progressively larger apically, except apical denticle larger (Fig. 90) ..... *Massartella*
- Gills present on abdominal segments 1-7, those on segments 1-5 plate-like (Fig. 76), those on segments 6 and 7 extremely reduced (Fig. 77); denticles on claws subequal (Fig. 89) . . . *Hapsiphlebia*
- 4. Abdominal gills terminated in a slender tapering process (Fig. 81); 5 denticles on anteromedian emargination of labrum (Fig. 50); posterolateral spines on abdominal segments 6-9 ..... *Atalonella*
- Abdominal gills slightly tapered at apex (Fig. 79, 80); no denticles on anteromedian emargination of labrum (Fig. 46, 48); posterolateral spines on abdominal segments 2-9 ..... 5
- 5. Anteromedian margin of labrum deeply incised ventrally (Fig. 46); denticles on claws long, progressively larger apically (Fig. 91); tracheae of abdominal gills pigmented, branches much lighter (Fig. 79) ..... *Meridialaris*
- Anteromedian margin of labrum deeply incised (Fig. 48); denticles on claws long (Fig. 92); tracheae of abdominal gills pigmented (Fig. 80) ..... *Massartellopsis*

***Penaphebia* Peters & Edmunds, n. gen.**

(Fig. 2, 3, 14, 20, 21, 33, 39, 40, 51, 57, 63, 69, 75, 82, 88)

*Type-species.*—*Atalophlebia chilensis* Eaton.

*Species Included* (All new combinations).—*P. chilensis* (Eaton, 1884: 91) (*Atalophlebia*); *P. fulvipes* (Needham and Murphy, 1924: 34) (*Atalophlebia*); *P. scypha* (Thew, 1960: 130) (*Atalophlebia*); *P. vinosa* (Demoulin, 1955c: 7) (*Atalophlebia*).

*Species Examined.*—*P. chilensis*, male and female imagos and nymphs; *P. scypha*, male imago; *Penaphebia* spp., numerous male and female imagos and nymphs from southern Chile, Argentina, and southern Brazil.

*Distribution.*—Magallanes Province, Chile (ca. 53° S) north along Coast Range and along Andes, with northernmost record on east slope in Tucumán area of Argentina (ca. 26° S); also southeastern Brazilian States of Santa Catarina and Rio Grande do Sul.

*Etymology.*—The genus is named for Sr. Luis E. Peña, distinguished naturalist of Santiago, Chile, who greatly helped one of us (G.F.E.) obtain reared specimens of the genera described in this paper.

**IMAGO.**—Length of ♂: body 10.0-15.0; fore wings 12.0-17.0 mm. Length of ♀: body 9.0-14.0; fore wings 10.0-15.0 mm. Eyes of ♂ meet on meson of head, lower portion of eyes 2/3 length of upper portion; eyes of ♀ separated on meson of head by a length 4 times as great as maximum width of an eye. Wings (Fig. 2, 3): vein R<sub>s</sub> of fore wings forked 1/5-1/4 distance from base to margin; vein MA forked 1/2 distance from base to margin, fork symmetrical; vein MP<sub>2</sub> attached at base to vein MP<sub>1</sub> with cross vein less than 1/3 distance from base to margin, vein MP<sub>2</sub> strongly recurved (Fig. 2); vein ICu<sub>1</sub> attached at base to vein CuA (Fig. 2); cross veins numerous. Costal margin of hind wings convex, apex of convexity located 1/3-1/2 distance from base (Fig. 3); cross veins numerous. Legs: ratios of segments in male fore legs, 0.74:1.00 (2.6 mm):0.03:0.34:0.37:0.26:0.11. Claws of a pair alike, apically hooked, each with an opposing hook (Fig. 14). Male

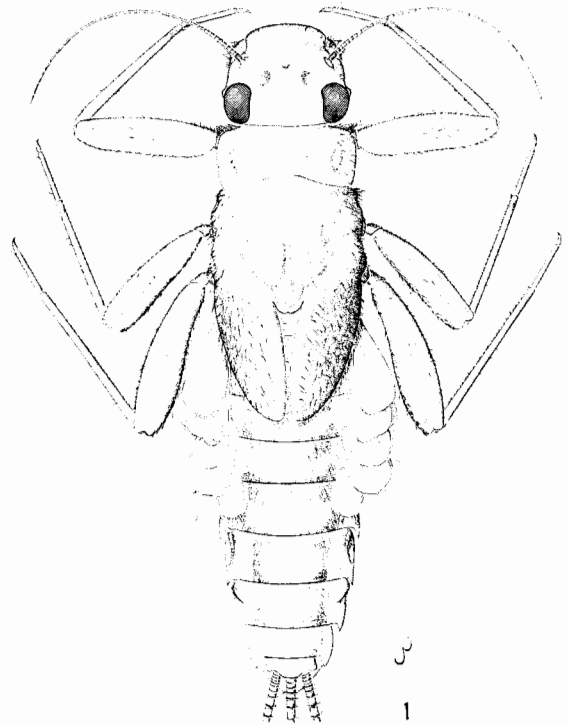


FIG. 1.—Mature female nymph of *H. anastomosis*.

genitalia (Fig. 20, 21); segments 2 and 3 of forceps about equal sized, either segment 1/3 length of segment 1, base of forceps broad, its inner margin forming an extreme angular bend; length of styliger plate along median line 1/3 maximum width; penes divided, tubular, broader at base, a subapical, ventral, well-developed spine arising from each penis lobe (Fig. 20, 21). Ninth sternum of ♀ deeply cleft apically (Fig. 33). Terminal filament longer than cerci.

**MATURE NYMPH.**—Head prognathous. Antennae 2 times as long as maximum length of head. Mouthparts (Fig. 39, 40, 51, 57, 63, 69): dorsal hair on labrum as in Fig. 39; submedian and anteromedian areas of hair ventrally; 3-5 irregular teeth on anteromedian emargination (Fig. 40). Clypeus as in Fig. 39. Left mandible as in Fig. 51. Lingua of hypopharynx with well-developed lateral processes (Fig. 63), anterior margin shallowly cleft; superlingua of hypopharynx as in Fig. 63, with a row of hair along anterior margin. Segment 2 of maxillary palpi a little longer to 1 1/4 length of segment 1; segment 3 of palpi 3/4 length of segment 2, triangular; a V-shaped ridge near the ventral, inner anterolateral margin of maxillae; hair on maxillae as in Fig. 57. Labium as in Fig. 69; segment 2 of palpi a little shorter to a little longer than segment 1; segment 3 of palpi 3/4 to a little longer than 3/4 length of segment 2, triangular; glossae ventral to paraglossae, glossae curved over ventrally. Short hair on entire body. Legs (Fig. 82, 88): apex of claws hooked and narrow, denticles on claws progressively larger apically. Gills (Fig. 75): gills 1-7

alike; dorsal and ventral portions of lamellae plate-like, terminated in one slender process, gill 7 smaller; main trunk of tracheae along median line of lamellae, tracheae on both sides of main trunk branched, tra-

cheae pigmented. Posterolateral spines on abdominal segments 7-9, those on segment 7 small, those on segments 8 and 9 large and projected outwardly. Terminal filament longer than cerci.

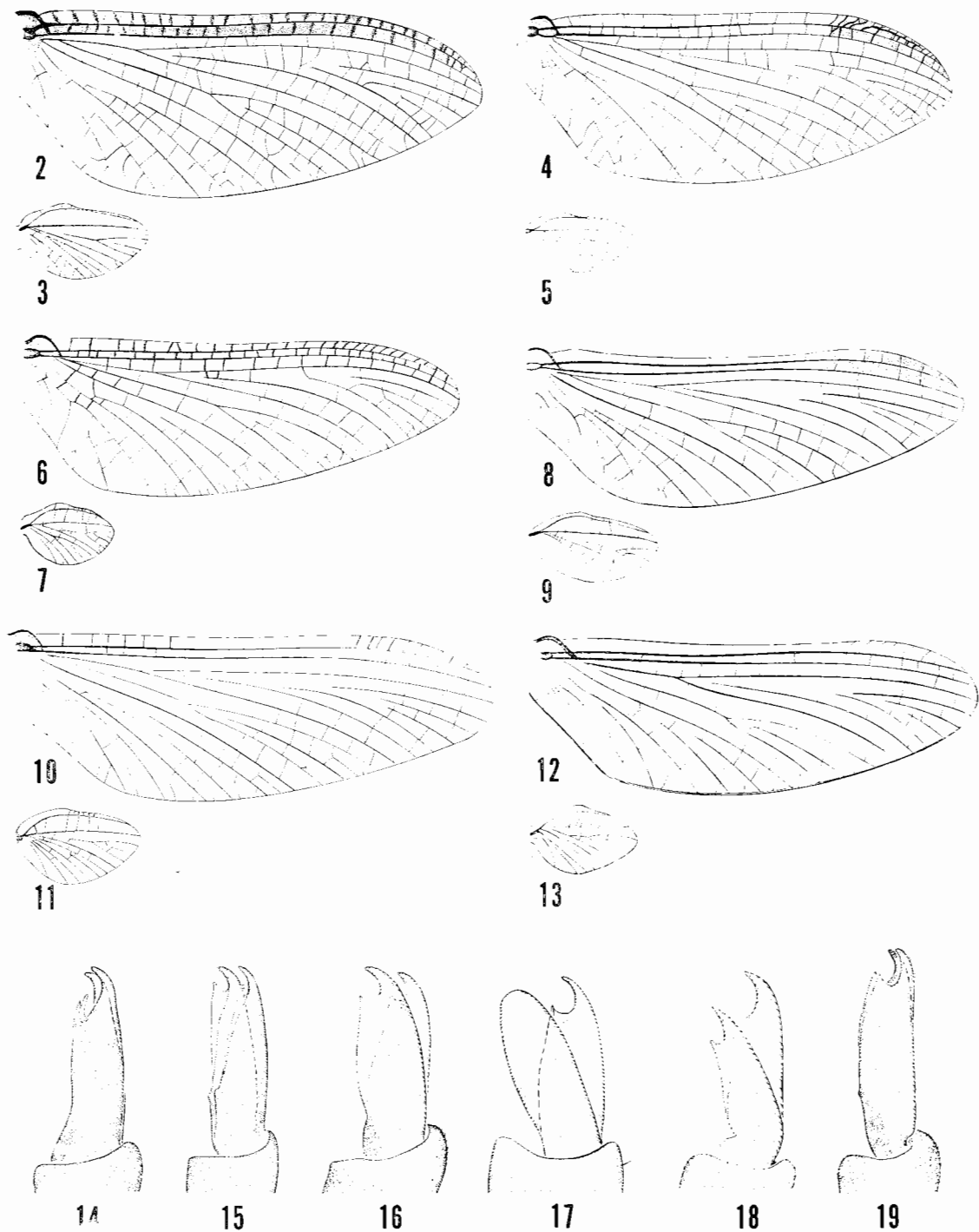


FIG. 2-13.—Wings of male imago. 2, 3, *Penaphlebia* sp. (2, forewing; 3, hind wing); 4, 5, *H. anastomosis*; 6, 7, *Massartella* sp.; 8, 9, *Meridialaris* sp.; 10, 11, *M. irrazavali*; 12, 13, *Atalonella* sp.

FIG. 14-19.—Fore claw of male imago. 14, *Penaphlebia* sp.; 15, *H. anastomosis*; 16, *Massartella* sp.; 17, *Meridialaris* sp.; 18, *M. irrazavali*; 19, *Atalonella* sp.

*History and Discussion.*—Eaton (1881) established *Atalophlebia* with *A. australis* (Walker) from Tasmania as the type-species. *Atalophlebia* has included species from Australia, New Zealand, Tasmania, Chile, and various localities in the Eastern Hemisphere. All species described from the Eastern Hemisphere have now been transferred to other genera except *A. femoralis* (Hagen). Based on examination of the type-series, this species appears to represent an undescribed genus. Penniket (1961) transferred all species occurring in New Zealand to *Zephlebia*. After study of reared material from Chile, Australia, and New Zealand, we herein place 4 species originally described as *Atalophlebia* from Chile in *Penaphlebia*. The nymphs described as *Atalophlebia* sp.? by Needham and Murphy (1924) are nymphs of *Penaphlebia*.

In addition, Navas (1928, 1930, 1934a, b) described 7 other species of *Atalophlebia* from Chile: *A. anastasis*, *A. athanasii*, *A. discolor*, *A. fenestrata*, *A. hyalina*, *A. rofucensis*, and *A. valdiviae*. We retain all 7 of these species in *Atalophlebia* until the type-series of each species can be studied.

*Penaphlebia* can be distinguished from *Atalophlebia* by the following combination of characters. In the imago a subapical, ventral, well-developed spine arises from each penis lobe of the male genitalia (Fig. 20, 21). In the nymphs, (1) abdominal gills 1-7 are alike; each portion of lamellae is plate-like and terminated in one slender process (Fig. 75), and (2) posterolateral spines occur on abdominal segments 7-9. *Penaphlebia* can be distinguished from all genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) vein  $MP_2$  of the fore wings is strongly recurved (Fig. 2), (2) vein  $ICu_1$  of the fore wings is attached at base to vein  $CuA$  (Fig. 2), (3) the claws of a pair are alike; each is apically hooked with an opposing hook (Fig. 14), and (4) the penes of the male genitalia are divided and tubular; a subapical, ventral, well-developed spine arises from each penis lobe (Fig. 20, 21). In the nymphs, (1) 3-5 irregular teeth occur on the anteromedian emargination of the labrum (Fig. 40), (2) glossae of the labium are curved over ventrally (Fig. 69), (3) abdominal gills 1-7 are alike; each portion of the lamellae is terminated in one slender process (Fig. 75), and (4) posterolateral spines occur on abdominal segments 7-9.

Illustrations of *Penaphlebia* sp. were made from specimens collected at the following localities in Chile: Fig. 2, 3, 14, 20, 21, 39, 40, 51, 57, 63, 69, 75, and 88 from Prov. Valparaiso, Colliguay (near La Retna), 5-XI-1963, G. F. Edmunds, Jr. (G.F.E.); Fig. 82 from Prov. Coquimbo, Rio Illapel, Huintil, Hacienda Illapel, 500 m, 12-XI-1963, G.F.E.; and Fig. 33 from a stream on Puyehue Lake, 17-XII-1957, J. Illies.

*Biology.*—The genus *Penaphlebia* has a rather wide ecological tolerance and is common in most parts of its range. The nymphs are found in permanent streams of a wide variety of sizes from rivulets

to all but the largest rivers. The flattened nymphs are found primarily on rocks, but they are also frequently found on the surfaces of submerged wood and other objects. The nymphs behave much as do the Heptageniidae, being equally able to move to either side, forward, or backward.

The various species have a wide variety of emergence dates, ranging from mid-September to mid-April. The males of some species form small swarms only over the "slicks" or flat water surfaces of streams. Other species form large conspicuous swarms 8-10 m above the stream. When the wind becomes moderately gusty, the swarms drop in unison to 2-3 m above the stream.

### *Hapsiphlebia* Peters & Edmunds, n. gen.

(Fig. 1, 4, 5, 15, 22, 23, 32, 34, 41, 42, 52, 58, 64, 70, 76, 77, 83, 89)

*Type-species.*—*Atalophlebia anastomosis* Demoulin.

*Species Included.*—*H. anastomosis* (Demoulin, 1955: 10). New combination (*Atalophlebia*).

*Species Examined.*—*H. anastomosis*, male and female imagos and nymphs; *Hapsiphlebia* sp., numerous male and female imagos and nymphs from southern Chile.

*Distribution.*—Chilean-Argentine Lakes District; also Llanquihue Province of Chile (ca. 41° S) north to Curico Province (ca. 35° S).

*Etymology.*—Hapsis, Gr., meaning mesh; phlebo, Gr., meaning vein.

*Imago.*—Length of ♂: body 13.0-14.0; fore wings 14.0-16.0 mm. Length of ♀: body 13.0-14.0; fore wings 15.0-16.0 mm. Eyes of ♂ meet on meson of head, lower portion of eyes  $\frac{2}{3}$  length of upper portion; eyes of ♀ separated on meson of head by a length 3 times as great as maximum width of an eye. Wings (Fig. 4, 5): vein  $R_4$  of fore wings forked less than  $\frac{1}{2}$  distance from base to margin; vein  $MA$  forked less than  $\frac{1}{2}$  distance from base to margin, fork symmetrical; vein  $MP_2$  attached at base to vein  $MP_1$  with a cross vein less than  $\frac{1}{2}$  distance from base to margin, vein  $MP_2$  strongly recurved (Fig. 4); vein  $ICu_1$  attached at base to vein  $CuA$  (Fig. 4); cross veins numerous; cross veins in apical  $\frac{1}{2}$  of cell  $C$  anastomosed (Fig. 4). Costal margin of hind wings convex, apex of convexity located  $\frac{1}{4}$ - $\frac{1}{2}$  distance from base (Fig. 5); cross veins numerous. Legs: ratios of segments in male fore legs, 0.51:1.00 (5.8 mm):0.04:0.47:0.47:0.39:0.12. Claws of a pair alike, apically hooked, each with an opposing hook (Fig. 15). Male genitalia (Fig. 22, 23): segment 3 of forceps  $\frac{1}{2}$  length of segment 2, segment 2 of forceps  $\frac{3}{4}$  length of segment 1, base of forceps broad, its inner margin forming an extreme angular bend; length of styliger plate along median line more than  $\frac{1}{2}$  maximum width; penes divided, tubular, broader at base, a small, subapical spinelike projection on or near outer margin of penis lobes (Fig. 22, 23). Ninth sternum of ♀ deeply cleft apically (Fig. 34). Female with a well-developed ovipositor or egg guide extended to just past the anterior margin of segment 8 (Fig. 32). Terminal filament longer than cerci.

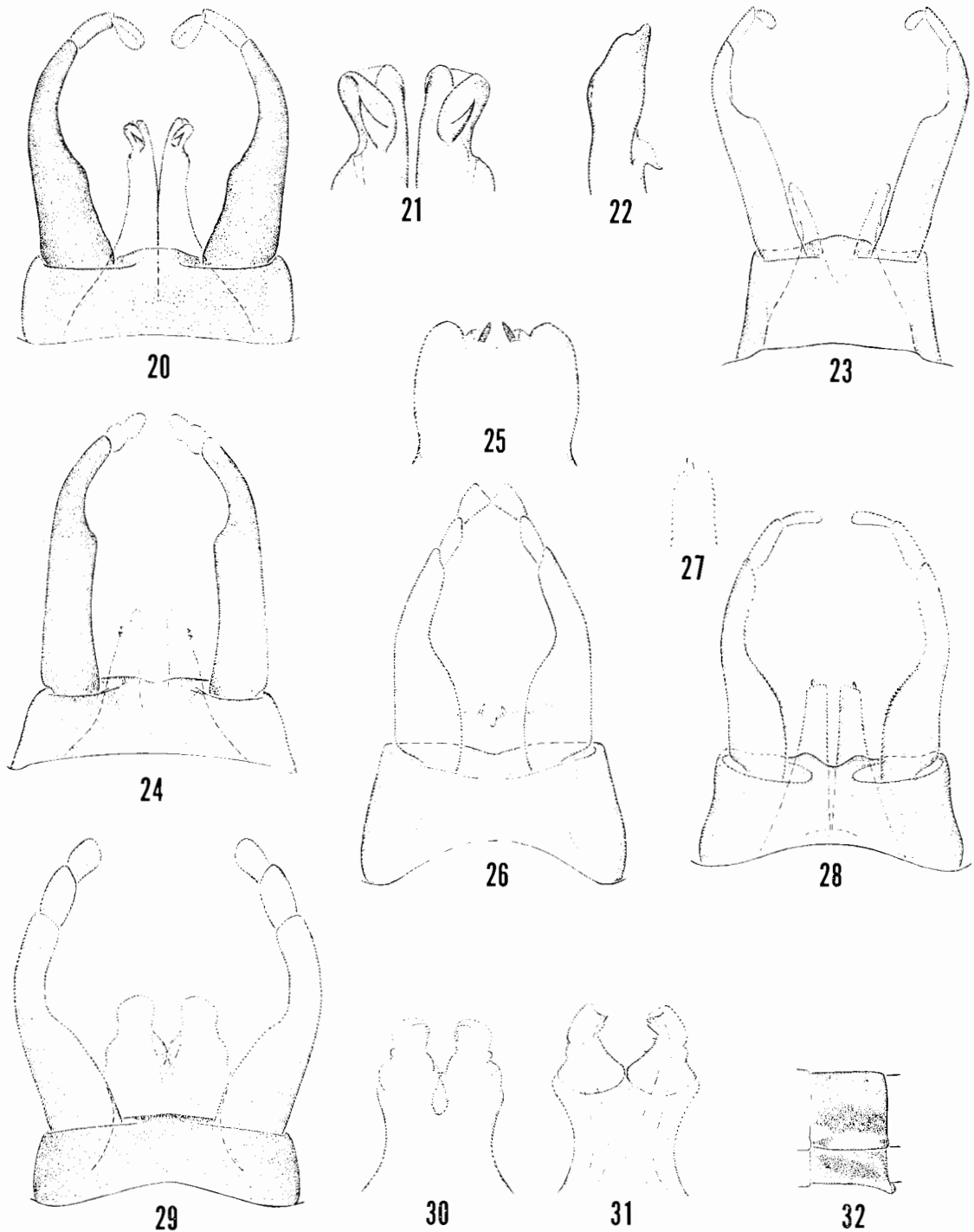


FIG. 20-31.—Genitalia of male imago. 20, 21, *Penaphlebia* sp. (20, ventral view; 21, apex of penis lobes enlarged); 22, 23, *H. anastomosis* (22, dorsal view of apex of penis lobe enlarged; 23, ventral view); 24, *Massartella* sp., ventral view; 25, 26, *Meridialaris* sp. (25, dorsal view of penes; 26, ventral view); 27, 28, *M. irrazavali* (27, dorsal view of apex of penis lobe enlarged; 28, ventral view); 29-31, *Atalonella* sp. (29, ventral view; 30, 31, dorsal view of penes showing variation).

FIG. 32.—*H. anastomosis*, lateral view of female abdominal segment 7.

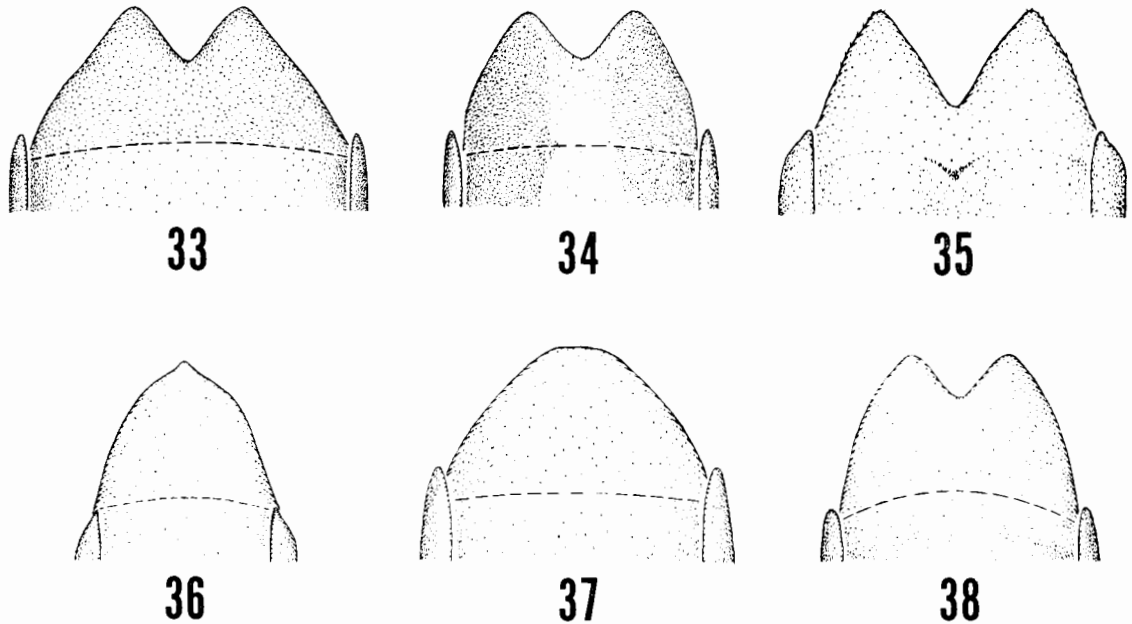


FIG. 33-38.—Ventral view of 9th sternum of female imago. 33, *Penaphlebia* sp.; 34, *H. anastomosis*; 35, *M. brieni*; 36, *Meridialaris* sp.; 37, *M. irarrazavali*; 38, *Atalonella* sp.

**MATURE NYMPH.**—Head prognathous. Antennae 2 times as long as maximum length of head. Mouthparts (Fig. 41, 42, 52, 58, 64, 70): dorsal hair on labrum as in Fig. 41; submedian and anterior bands of hair ventrally, 5 small, equal sized denticles on anteromedian emargination (Fig. 42). Clypeus as in Fig. 41. Left mandible as in Fig. 52. Lingua of hypopharynx with well-developed lateral processes (Fig. 64), anterior margin shallowly cleft; superlingua of hypopharynx as in Fig. 64, with a row of hair along anterior margin. Segment 2 of maxillary palpi  $\frac{3}{4}$  to a little more than  $\frac{3}{4}$  length of segment 1; segment 3 of palpi a little longer than length of segment 2, triangular; a V-shaped ridge near the ventral, inner anterolateral margin of maxillae; hair on maxillae as in Fig. 58. Labium as in Fig. 70; segment 2 of palpi  $\frac{3}{4}$  length of segment 1; segment 3 of palpi equal to length of segment 2, triangular; glossae ventral to paraglossae, glossae curved over ventrally. Long hair on entire body. Legs (Fig. 83, 89): apex of claws hooked and narrow, denticles on claws subequal. Gills (Fig. 76, 77): gills on segments 1-7; gills 1-5 alike, dorsal and ventral portions of lamellae plate-like, ventral portion smaller, apex of dorsal portion fringed with long hair, dorsal portion terminated in one slender process fringed with long hair, gills progressively smaller posteriorly; main trunk of tracheae strongly curved towards inner margin of lamellae, tracheae on both sides of main trunk branched, tracheae unpigmented. Gills 6 and 7 consist of one slender filament, fringed with long hair, no tracheae present (Fig. 77). Posterolateral spines on abdominal segments 1-9, spines progressively larger posteriorly. Terminal filament longer than cerci.

**History and Discussion.**—Upon obtaining reared material from Chile, we herein place *Atalophlebia anastomosis* Demoulin from Chile in a new monotypic genus *Hapsiphlebia*. *Hapsiphlebia* can be distinguished from *Atalophlebia* and *Penaphlebia* by the following combination of characters. In the imago, (1) a small, subapical spinelike projection arises on or near outer margin of penis lobes of the male genitalia (Fig. 2, 23), and (2) the ♀ possesses a well-developed ovipositor or egg guide extending to just past the anterior margin of abdominal segment 8 (Fig. 32). In the nymphs, (1) abdominal gills 1-7 are dissimilar; each portion of lamellae of gills 1-5 is plate-like and only the dorsal portion is terminated in one slender process (Fig. 76), and (2) posterolateral spines occur on abdominal segments 1-9. *Hapsiphlebia* can be distinguished from all genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) vein  $MP_2$  of the fore wings is strongly recurved (Fig. 4), (2) cross veins in apical  $\frac{1}{2}$  of cell C of fore wings are anastomosed (Fig. 4), (3) the claws of a pair are alike; each is apically hooked and with an opposing hook (Fig. 15), and (4) a small, subapical spinelike projection arises on or near outer margin of penis lobes of the male genitalia (Fig. 22, 23). In the nymphs, (1) 5 small, equal sized denticles occur on anteromedian emargination of labrum (Fig. 41, 42), (2) glossae of the labium are curved over ventrally (Fig. 70), (3) abdominal gills 1-7 are dissimilar; gills 1-5 are plate-like with 2 well-developed portions (Fig. 76); gills 6 and 7 consist of one slender filament (Fig. 77), and (4) posterolateral spines occur on abdominal segments 1-9.

Illustrations of *H. anastomosis* were made from

specimens collected at the following localities in Chile: Fig. 4, 5, 32, and 34 from Prov. Valdivia, stream near Fundo Walper, near Valdivia, 16-II-1968, J. Illies; Fig. 15, 22, and 23 from Prov. Curico, Buchem, III-1956, L. Peña (no. IG-20-998 of the Musée royale des Sciences naturelles de Belgique); Fig. 1, 76, 77, 83, and 89 from Prov. Curico, El Coigual, 20-26-I-1964, L. Peña; and Fig. 41, 42, 52, 58, 64, and 70 from Prov. Talca, Alto de Vilches, 23-30-I-1964, L. Peña.

*Biology.*—The genus *Hapsiphlebia* is rather narrowly limited ecologically and geographically. It seems to be confined to small to medium streams where the current is of moderate velocity. The nymphs are soft bodied and fragile. They have the habit of twisting the body to the left or right, somewhat like many stoneflies, apparently an adaptation for crawling into crevices and for crawling in gravel and debris. The nymphs mature in late January and February with the adult records ranging from mid-September to mid-June.

### *Massartella* Lestage, 1930

(Fig. 6, 7, 16, 24, 35, 43, 44, 53, 59, 65, 71, 78, 84, 90)

*Massartella* Lestage, 1930: 249; Traver 1946: 422; Ulmer 1943: 14.

*Type-species.*—*Atalophlebia brieni* Lestage, original designation.

*Species Included.*—*M. alegrettac* Ulmer, 1943: 21; *M. brieni* (Lestage, 1924: 21) (*Atalophlebia*); *M. fruhstorfferi* Ulmer, 1943: 20.

*Species Examined.*—*M. brieni*, male and female imago and nymphs; *Massartella* spp., numerous male and female imago and nymphs from Brazil.

*Distribution.*—Rio Grande do Sul State, Brazil (ca. 30° S), along Serra do Mar to Minas Gerais State (ca. 18° S).

*IMAGO.*—Length of ♂: body 10.0–15.0; fore wings 12.5–19.0 mm. Length of ♀: body 12.0–19.0; fore wings 15.0–18.0 mm. Eyes of ♂ meet on meson of head, lower portion of eyes  $\frac{3}{4}$  length of upper portion; eyes of ♀ separated on meson of head by a

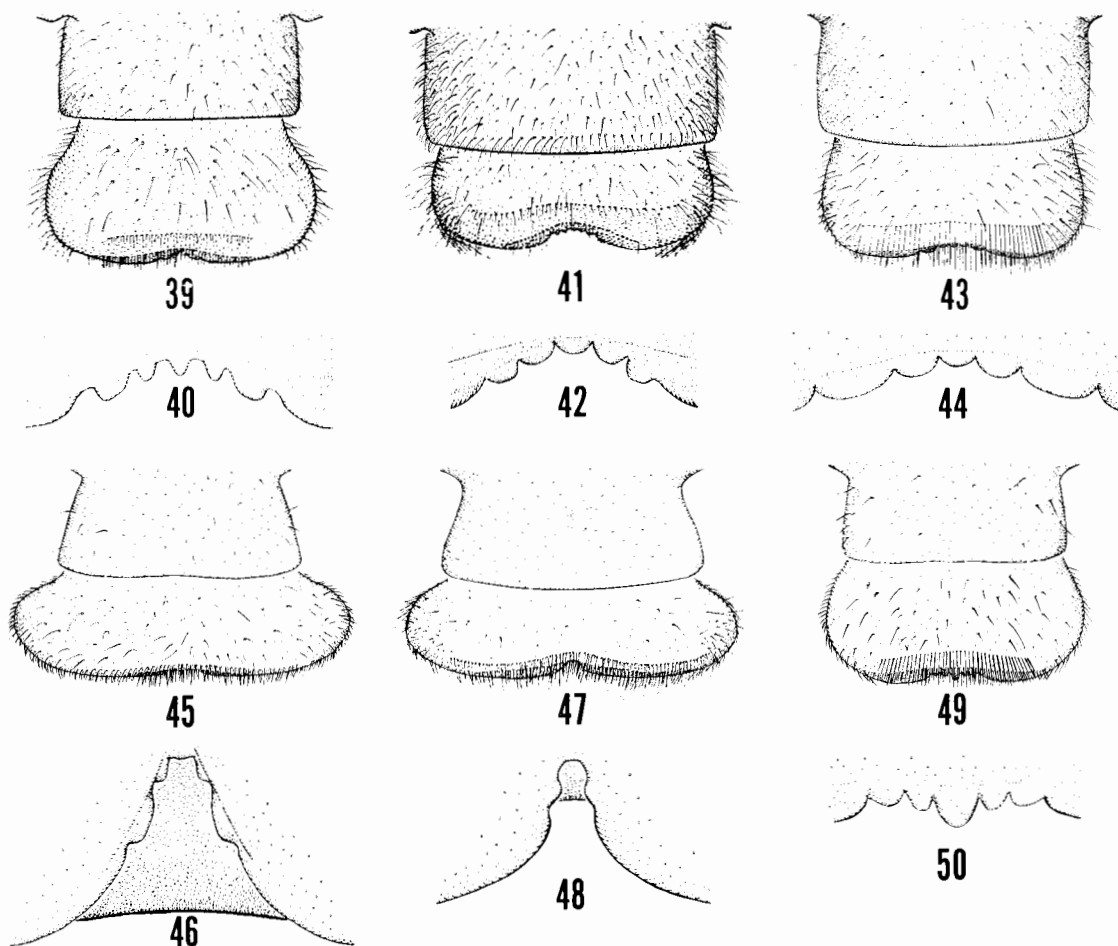


FIG. 39-50.—Clypeus and labrum of nymph. 39, 40, *Penaphlebia* sp. (39, dorsal view; 40 anteromedian emargination of labrum, enlarged); 41, 42, *H. anastomosis*, same; 43, 44, *Massartella* sp., same; 45, 46, *Meridialaris* sp. (45, dorsal view; 46, ventral view of anteromedian emargination of labrum, enlarged); 47, 48, *M. irarrazavali*, same; 49, 50, *Atalonella* sp. (49, dorsal view; 50, anteromedian emargination of labrum, enlarged).

length 4 times as great as maximum width of an eye. Wings (Fig. 6, 7): vein  $R_s$  of fore wings forked  $\frac{1}{4}$  distance from base to margin; vein MA forked a little more than  $\frac{1}{2}$  distance from base to margin, fork symmetrical, distal portion of vein MA a little sagged posteriorly; vein  $MP_2$  attached at base to vein  $MP_1$  with cross vein  $\frac{1}{5}$  distance from base to margin, vein  $MP_2$  strongly recurved (Fig. 6); vein  $ICu_1$  attached at base by a cross vein to veins CuA and CuP (Fig. 6); cross veins numerous. Costal margin of hind wings a little convex, apex of convexity located  $\frac{1}{3}$  to a little more than  $\frac{1}{2}$  distance from base (Fig. 7); cross veins numerous. Legs: ratios of segments in male fore legs, 0.64:1.00(5.3 mm):0.05:0.30:0.30:0.18:0.11. Claws of a pair alike, apically hooked, each with an opposing hook (Fig. 16). Male genitalia (Fig. 24): segments 2 and 3 of forceps equal length, either segment  $\frac{1}{2}$  length of segment 1, base of forceps broad, its inner margin forming an extreme angular bend; length of styliar plate along median line  $\frac{1}{4}$  maximum width; penes divided, tubular, one or 2 small, subapical, lateral spines or projections on outer margin of each penis lobe (Fig. 24). Ninth sternum of ♀ deeply cleft apically (Fig. 35). Terminal filament a little longer than cerci.

**MATURE NYMPH.**—Head prognathous. Antennae 2 times as long as maximum length of head. Mouthparts (Fig. 43, 44, 53, 59, 65, 71): dorsal hair on labrum as in Fig. 43; submedian and anterolateral bands of hair ventrally, 5 small, blunt, unequal sized denticles on anteromedian emargination (Fig. 44). Clypeus as in Fig. 43. Left mandible as in Fig. 53. Lingua of hypopharynx with well-developed lateral processes (Fig. 65), anterior margin shallowly cleft; superlingua of hypopharynx as in Fig. 65, with a row of hair along anterior margin. Segment 2 of maxillary palpi a little shorter to a little longer than segment 1; segment 3 of palpi  $\frac{3}{4}$  to equal to length of segment 2, triangular; a V-shaped ridge near the ventral, inner anterolateral margin of maxillae; hair on maxillae as in Fig. 59. Labium as in Fig. 71; segment 2 of palpi  $\frac{3}{4}$  length of segment 1; segment 3 of palpi a little shorter to equal to length of segment 2, triangular; glossae ventral to paraglossae, glossae curved over ventrally. Short hair on entire body, hair a little longer on lateral margins of abdominal segments. Legs (Fig. 84, 90): apex of claws hooked and narrow, denticles on claws progressively larger apically, except apical denticle larger. Gills (Fig. 78): gills 1-6 alike; dorsal and ventral portions of lamellae plate-like, dorsal lamella terminated in one slender process, gills progressively smaller posteriorly; main trunk of tracheae strongly curved towards inner margin of lamellae, tracheae on both sides of main trunk branched, tracheae unpigmented. Posterolateral spines on abdominal segments 2-9, spines progressively larger posteriorly. Terminal filament longer than cerci.

**History and Discussion.**—Lestage (1930) established *Massartella* for the species *brieni* which he earlier (1924) had placed in *Atalophlebia*. The species was known from adults only. Ulmer (1943)

described 2 new species from adults collected in Brazil. Demoulin (1955a) questionably described the nymph of *Massartella*. Herein the generic descriptions are based on reared material and confirm Demoulin's association.

*Massartella* can be distinguished from all genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) vein  $MP_2$  of the fore wings is strongly recurved (Fig. 6), (2) vein  $ICu_1$  of forewings is attached at base by a cross vein to veins CuA and CuP (Fig. 6), (3) the claws of a pair are alike; each is apically hooked and with an opposing hook (Fig. 16), and (4) the penes of the male genitalia are divided, tubular; 1 or 2 small, subapical, lateral spines or projections occur on each penis lobe (Fig. 24). In the nymphs, (1) 5 small, blunt, unequal sized denticles occur on the anteromedian emargination of the labrum (Fig. 43, 44), (2) glossae of the labium are curved over ventrally (Fig. 71), (3) abdominal gills occur on segments 1-6 only and are similar (Fig. 78), and (4) posterolateral spines occur on abdominal segments 2-9.

Illustrations of *Massartella* sp. and *M. brieni* were made from specimens collected at the following localities in Brazil: Fig. 6, 7, 16, and 24 from São Paulo St., corrigo da pedreira, 23-30-IX-1966, C. Froehlich; Fig. 43, 44, 53, 65, 71, and 90 from São Paulo St., Caverna do Diablo, near Eldorado, 23-X-1966, M. T. Veta; and Fig. 35, 78, and 84 from Paraná St., Ipiranga, Estrada do Itupava, 21-23-II-1969, W. L. and J. Peters.

**Biology.**—Biological notes given here are based on *M. brieni* observed at the type-locality and other localities in Paraná State, Brazil. Nymphs occur on rocks in the faster portions of large rivers to small mountain streams. Last-stage nymphs migrate to sidepools without current and climb out of the water onto dry rocks in or around the stream to emerge. Imagos mate in midmorning in small companies ca. 10 m above the river. The various species emerge from mid-September through mid-July.

#### *Meridialaris* Peters & Edmunds, n. gen.

(Fig. 8, 9, 17, 25, 26, 36, 45, 46, 54, 60, 66, 72, 79, 85, 91)

**Types-species.**—*Deleatidium laminata* Ulmer.

Species included (All new combinations).—*M. biobionica* (Ulmer, 1938: 85) (*Deleatidium*); *M. chiloscense* (Demoulin, 1955b: 13) (*Deleatidium*); *M. diguillina* (Demoulin, 1955c: 23) (*Deleatidium*); *M. illapeli* (Demoulin, 1955c: 26) (*Deleatidium*); *M. laminata* (Ulmer, 1919: 23) (*Deleatidium*); *M. patagonica* (Lestage, 1931: 52) (*Atalophlebia*); *M. penai* (Demoulin, 1955c: 27) (*Deleatidium*).

**Species Examined.**—*M. biobionica*, female wings; *Meridialaris* spp., numerous male and female imagos and nymphs from Chile and Argentina.

**Distribution.**—Chile and on eastern slope of Andes in Argentina from Magallanes Province (ca. 53° S) north to Tucumán region (ca. 26° S).

**Etymology.**—Meridies, L., meaning south; alaris, L., meaning wing.

**IMAGO.**—Length of ♂: body 6.5-8.5; fore wings



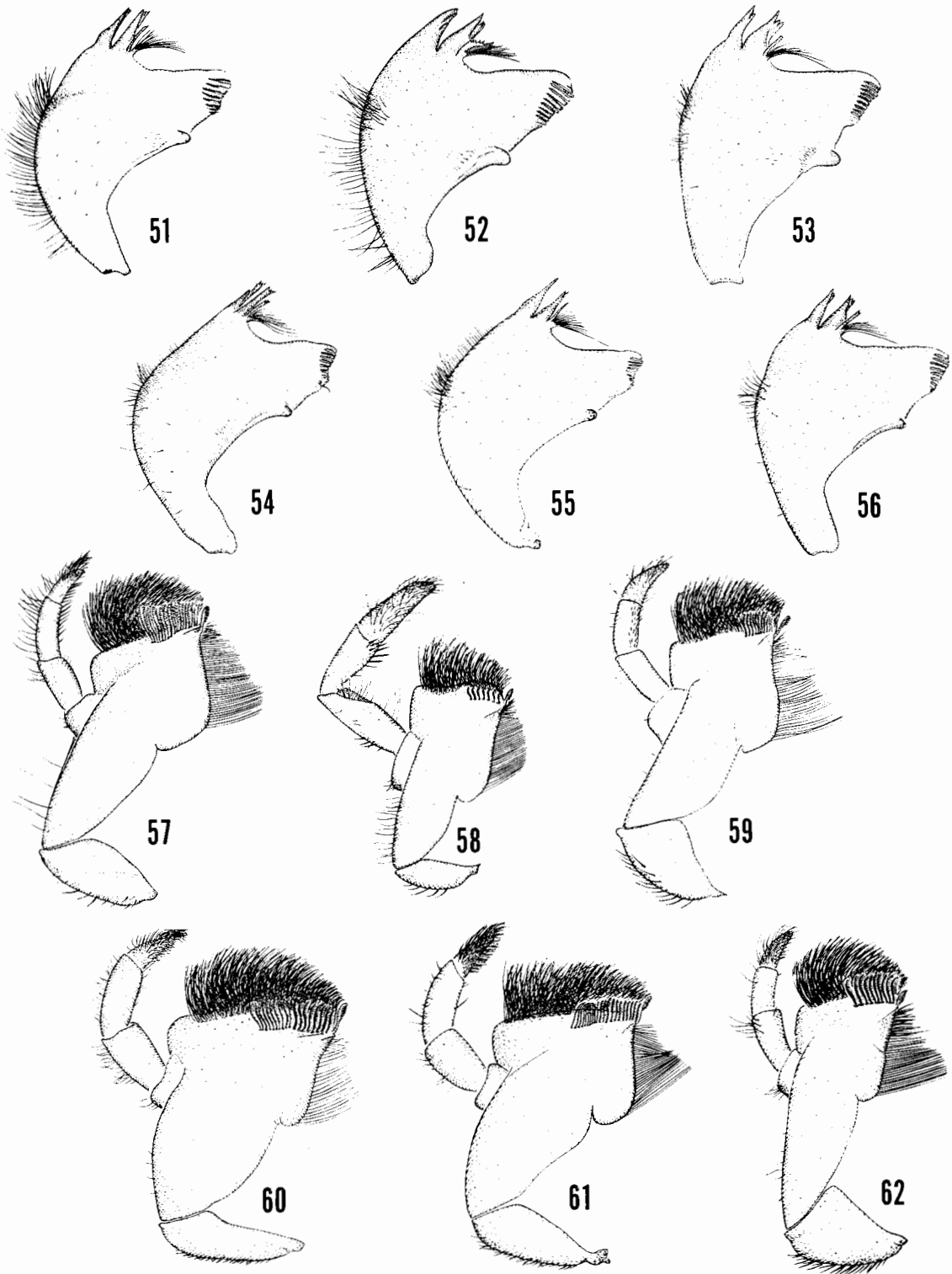


FIG. 51-56.—Left mandible of nymph. 51, *Penaphlebia* sp.; 52, *H. anastomosis*; 53, *Massartella* sp.; 54, *Meridialaris* sp.; 55, *M. irrazavali*; 56, *Atalonella* sp.

FIG. 57-62.—Ventral view of maxilla of nymph. 57, *Penaphlebia* sp.; 58, *H. anastomosis*; 59, *Massartella* sp.; 60, *Meridialaris* sp.; 61, *M. irrazavali*; 62, *Atalonella* sp.

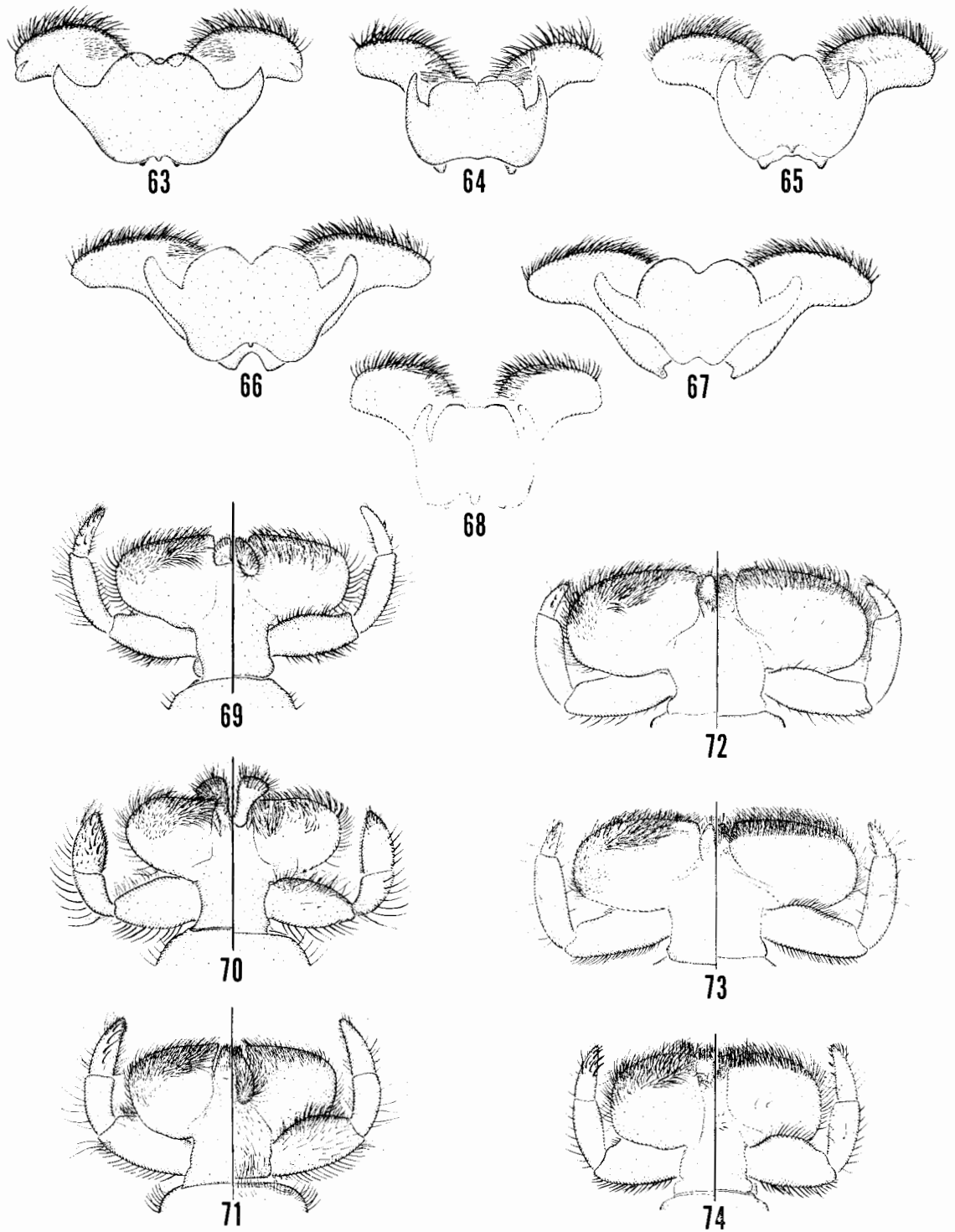


FIG. 63-68.—Hypopharynx of nymph. 63, *Penaphlebia* sp.; 64, *H. anastomosis*; 65, *Massartella* sp.; 66, *Meridialaris* sp.; 67, *M. irrazavali*; 68, *Atalonella* sp.

FIG. 69-74.—Labium of nymph (ventral surface on right side of drawing, dorsal surface on left side). 69, *Penaphlebia* sp.; 70, *H. anastomosis*; 71, *Massartella* sp.; 72, *Meridialaris* sp.; 73, *M. irrazavali*; 74, *Atalonella* sp.

6.5–10.0 mm. Length of ♀: body 7.0–9.0; fore wings 7.5–10.5 mm. Eyes of ♂ meet on meson of head, lower portion of eyes  $\frac{3}{4}$  length of upper portion; eyes of ♀ separated on meson of head by a length 5 times as great as maximum width of an eye. Wings (Fig. 8, 9): vein  $R_5$  of fore wings forked  $\frac{1}{5}$  to a little more than  $\frac{1}{4}$  distance from base to margin; vein MA forked a little more than  $\frac{1}{2}$  distance from base to margin, fork symmetrical; vein  $MP_2$  attached at base to vein  $MP_1$  with a cross vein more than  $\frac{1}{5}$  distance from base to margin, vein  $MP_2$  moderately recurved (Fig. 8); vein  $ICu_1$  attached at base by a cross vein to vein CuA or to veins CuA and CuP (Fig. 8); cross veins numerous. Costal margin of hind wings convex, apex of convexity located  $\frac{1}{8}$ – $\frac{1}{2}$  distance from base (Fig. 9); cross veins numerous. Legs: ratios of segments in male fore legs, 0.75:1.00 (2.7 mm)0.06:0.31:0.34:0.28:0.13. Claws of a pair dissimilar, one apically hooked with an opposing hook, other obtuse, pad-like (Fig. 17). Male genitalia (Fig. 25, 26): segments 2 and 3 of forceps about equal sized, either segment  $\frac{1}{5}$  length of segment 1, base of forceps broad, its inner margin forming an extreme angular bend; length of styliger plate along median line  $\frac{1}{3}$  maximum width; penes fused except for apical cleft, sometimes each side of penes with a large apical spine or many smaller apical spines (Fig. 25, 26). Ninth sternum of ♀ entire (Fig. 36). Terminal filament longer than cerci.

**MATURE NYMPH.**—Head prognathous. Antennae  $1\frac{1}{2}$  times as long as maximum length of head. Mouthparts (Fig. 45, 46, 54, 60, 66, 72): dorsal hair on labrum as in Fig. 45; submedian and anteromarginal areas of hair ventrally; anteromedian margin deeply incised ventrally (Fig. 46). Clypeus as in Fig. 45. Left mandible as in Fig. 45. Lingua of hypopharynx with well-developed lateral processes (Fig. 66), anterior margin deeply cleft; superlingua of hypopharynx as in Fig. 66, with a row of hair along anterior margin. Segment 2 of maxillary palpi  $1\frac{1}{4}$  length of segment 1; segment 3 of palpi a little longer than  $\frac{1}{2}$  length of segment 2, triangular; hair on maxillae as in Fig. 60; a large V-shaped ridge on inner anterior margin of galea-lacinia. Labium as in Fig. 72; segment 2 of palpi equal to a little longer than segment 1; segment 3 of palpi a little less than  $\frac{1}{2}$  to  $\frac{1}{3}$  length of segment 2, triangular; paraglossae ventral to glossae. Short hair on thorax, longer hair on lateral margins of abdominal segments. Legs (Fig. 85, 91): apex of claws hooked and narrow, denticles on claws long, progressively large apically. Gills (Fig. 79): gills 1–7 alike; dorsal and ventral portions of lamellae slender, each portion tapered at apex, gills progressively smaller posteriorly; main trunk of tracheae along median line of lamellae, tracheae on both sides of main trunk branched, tracheae pigmented, branches much lighter. Posterolateral spines on abdominal segments 2–9, spines progressively larger posteriorly. Terminal filament a little longer than cerci.

**History and Discussion.**—Eaton (1899) established *Deleatidium* with *D. lillii* Eaton from New Zealand

as the type species. *Deleatidium* has included species from Australia, New Zealand, Chile, and Brazil. Upon obtaining reared material from Chile, we herein place the species originally described as *Deleatidium* from Chile in *Meridialaris*. The Chilean nymphs described as (?) *Deleatidium* by Needham and Murphy (1924) have not been studied by us, and we do not know if they are nymphs of *Meridialaris*.

Thew (1960) described from female imagos the Brazilian species *D. vittatum*. One of us (W.L.P.) has examined the holotype of this species and finds it does not represent *Meridialaris* as the fork of vein MP of the fore wings is symmetrical, the cubital area of the fore wings is expanded, and the 9th sternum is apically cleft. Until reared material of this species is available, we tentatively retain the species in *Deleatidium*, although it obviously does not belong there.

*Meridialaris* can be distinguished from *Deleatidium* by the following combination of characters. In the imago, (1) the claws of a pair are dissimilar, one is apically hooked and with an opposing hook, while the other is obtuse and pad-like (Fig. 17), and (2) the distal portion of vein MA is not greatly sagged posteriorly (Fig. 8). In the nymphs, abdominal gills are alike on segments 1–7; dorsal and ventral portions of lamellae are slender and each portion is tapered at apex (Fig. 79).

*Meridialaris* can be distinguished from all genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) vein  $MP_2$  of the fore wings is moderately recurved (Fig. 8), (2) the distal portion of vein MA is not greatly sagged posteriorly (Fig. 8), (3) the claws of a pair are dissimilar, one is apically hooked and with an opposing hook, while the other is obtuse and pad-like (Fig. 17), and (4) the penes of the male genitalia are fused except for the apical cleft (Fig. 25, 26). In the nymphs, (1) the anteromedian margin of the labrum is deeply incised ventrally (Fig. 46), (2) the denticles on the claws are long and are progressively larger apically (Fig. 91), (3) abdominal gills occur on segments 1–7 and are alike; dorsal and ventral portions of lamellae are slender, each portion is tapered apically (Fig. 79), and (4) posterolateral spines occur on abdominal segments 2–9.

Illustrations of *Meridialaris* sp. were made from specimens collected at the following localities: Fig. 8, 9, 17, 25, and 26 from Argentina, Neuquén Prov., Nireco, near Bariloche, 5-XII-1957, J. Illies; Fig. 36 from Chile, Prov. Cautin, Lago Villarica, 26-II-1958, Besch; Fig. 45, 46, 54, 60, 66, 72, and 91 from Chile, Prov. Osorno, Rio Chanlefu, Puyehue, 22-XI-1963, G.F.E.; and Fig. 79 and 85 from Chile, Prov. Coquimbo, Rio Illapel, Huintil, Hacienda Illapel, 500 m, 12-XI-1963, G.F.E.

**Biology.**—The genus *Meridialaris* is rather broadly distributed ecologically and geographically. The nymphs occupy a wide variety of permanent streams from small rivulets to large rivers (e.g. Bio Bio, Golgol, and Rahue). The ability to live in a relatively wide variety of streams, including large and warmer

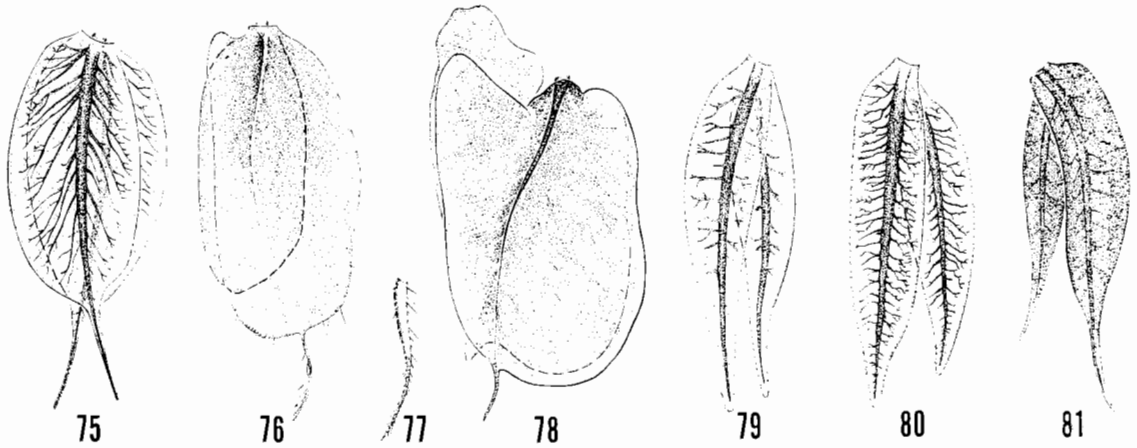


FIG. 75-81.—Gills of nymph. 75, *Penaphlebia* sp., gill 4; 76, 77, *H. anastomosis* (76, gill 3; 77, gill 7); 78, *M. brieni*, gill 4; 79, *Meridialaris* sp., gill 4; 80, *M. irarrazavali*, gill 4; 80, *M. irarrazavali*, gill 4; 81, *Atalaphella* sp., gill 4.

rivers, gives the genus a great ability to disperse. The nymphs of *Meridialaris* are flattened. They occupy a variety of microhabitats, but are found primarily on the surfaces of stones and other flat objects. The nymphs have the ability to move freely in any direction in much the same way as do the Heptageniidae.

Adults of *Meridialaris* were observed on numerous occasions swarming in the evening over rivers and streams most commonly swarming 3-5 m above the stream. The adults tend to be scattered widely above the water, not responding to specific water surfaces. The nymphs of the various species mature at various times throughout the summer. Adult records have a seasonal range from mid-October to mid-May.

#### *Massartellopsis* Demoulin, 1955

(Fig. 10, 11, 18, 27, 28, 37, 47, 48, 55, 61, 67, 73, 80, 86, 92)

*Massartellopsis* Demoulin, 1955c: 9.

*Type-species*.—*M. irarrazavali* Demoulin, original designation.

*Species Included*.—*M. irarrazavali* Demoulin, 1955c: 9.

*Species Examined*.—*M. irarrazavali* male imagos, female imagos, and nymphs.

*Distribution*.—Andes of Argentina and Chile, from Malleco Province (ca. 39° S) north to Coquimbo Province (ca. 30° S).

*IMAGO*.—Length of ♂: body 8.5; fore wings 11.0 mm. Length of ♀: body 9.0; fore wings 10.0 mm. Eyes of ♂ meet on meson of head, lower portion of eyes  $\frac{3}{4}$  length of upper portion; eyes of ♀ separated on meson of head by a length 4 times as great as maximum width of an eye. Wings (Fig. 10, 11): vein  $R_5$  of fore wings forked a little more than  $\frac{1}{4}$  distance from base to margin; vein MA forked a little more than  $\frac{1}{2}$  distance from base to margin, fork symmetrical, distal portion of vein MA moderately sagged posteriorly; vein  $MP_2$  attached at base to vein  $MP_1$  with a cross vein more than  $\frac{1}{2}$

distance from base to margin; vein  $MP_2$  moderately recurved (Fig. 10); vein  $ICu_1$  attached at base by a cross vein to veins  $CuA$  and  $CuP$  (Fig. 10); cross veins numerous. Costal margin of hind wings convex, apex of convexity located  $\frac{1}{2}$  distance from base (Fig. 11); cross veins numerous. Legs: ratios of segments in male fore legs, 0.75:1.00(3.3 mm):0.05:0.26:0.21:0.21:0.16. Claws of a pair alike, apically hooked, each with an opposing hook (Fig. 18). Male genitalia (Fig. 27, 28): segments 2 and 3 of forceps subequal in length, either segment a little shorter than  $\frac{1}{4}$  length of segment 1, base of forceps broad, its inner margin forming an extreme angular bend; length of styliger plate along median line a little longer than  $\frac{1}{2}$ ; maximum width; penes divided, tubular, an apical, dorsal projection on each penis lobe (Fig. 27, 28). Ninth sternum of ♂ entire (Fig. 37). Terminal filament a little longer than cerci.

*MATURE NYMPH*.—Head prognathous. Antennae  $1\frac{1}{2}$  times as long as maximum length of head. Mouthparts (Fig. 47, 48, 55, 61, 67, 73): dorsal hair on labrum as in Fig. 47; submedian band of hair extended along anterior margin ventrally; anteromedian margin deeply incised (Fig. 48). Clypeus as in Fig. 47. Left mandible as in Fig. 55. Lingua of hypopharynx with well-developed lateral processes (Fig. 67), anterior margin deeply cleft; superlingua of hypopharynx as in Fig. 67, with a row of hair along anterior margin. Segment 2 of maxillary palpi  $\frac{3}{4}$  length of segment 1; segment 3 of palpi a little longer than  $\frac{1}{2}$  length of segment 2, triangular; hair on maxillae as in Fig. 61; a V-shaped ridge on inner anterior margin of galea-lacinia. Labium as in Fig. 73; segment 2 of palpi  $\frac{3}{4}$  to equal in length to segment 1; segment 3 of palpi a little more than  $\frac{1}{2}$  length of segment 2, triangular; paraglossae ventral to glossae. Short hair on dorsum of body, longer hair on lateral margins of abdominal segments. Legs (Fig. 86, 92): apex of claws hooked and narrow, denticles on claws long. Gills (Fig. 80): gills 1-7

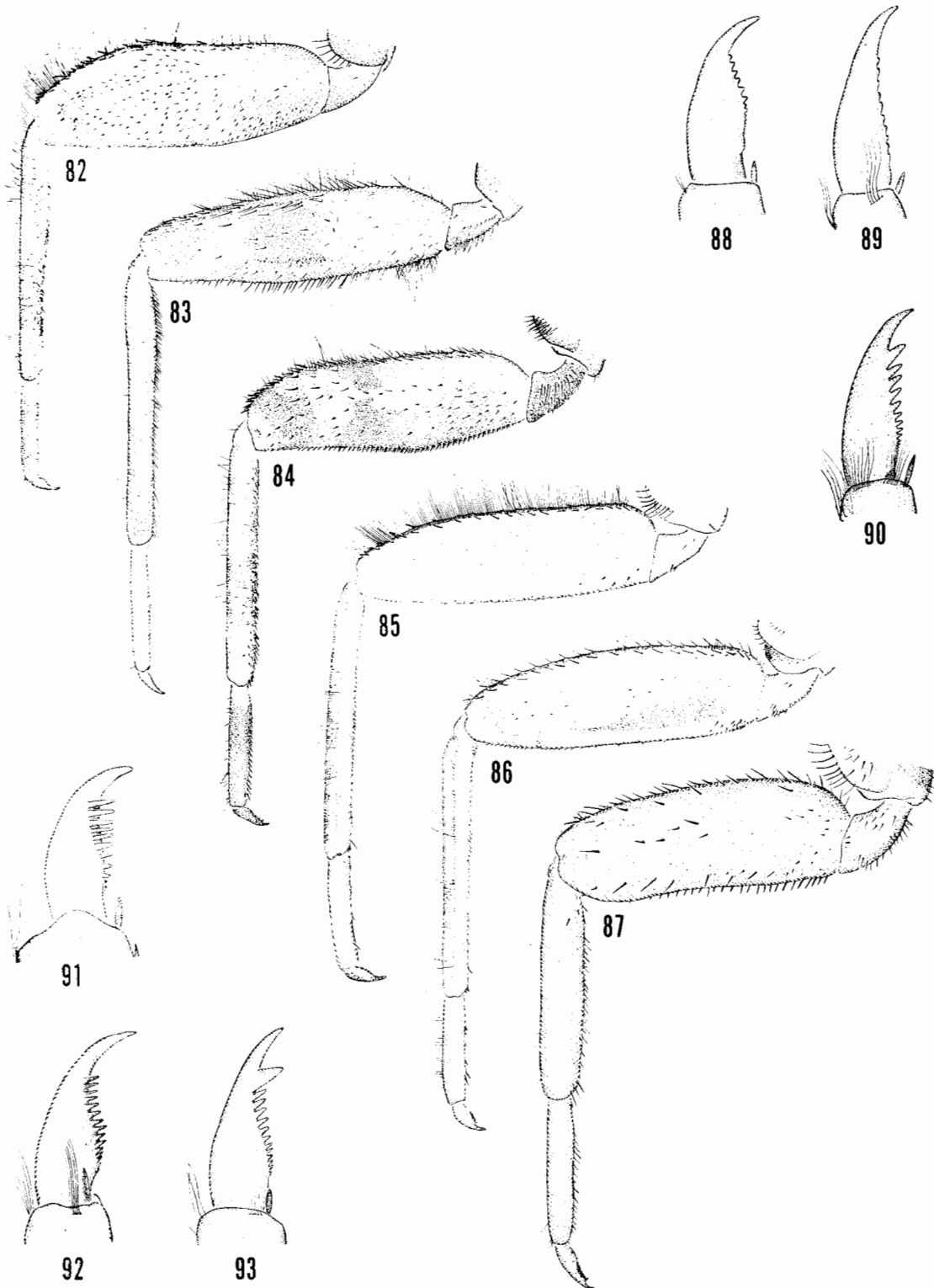


FIG. 82-87.—Fore leg of nymph. 82, *Penaphlebia* sp.; 83, *H. anastomosis*; 84, *M. brieni*; 85, *Meridialaris* sp.; 86, *M. irrazazali*; 87, *Atalonella* sp.

FIG. 88-93.—Fore claw of nymph. 88, *Penaphlebia* sp.; 89, *H. anastomosis*; 90, *Massartella* sp.; 91, *Meridialaris* sp.; 92, *M. irrazazali*; 93, *Atalonella* sp.

alike; dorsal and ventral portions of lamellae slender, each portion tapered at apex, gills progressively smaller posteriorly; main trunk of tracheae along median line of lamellae, tracheae on both sides of main trunk branched, tracheae pigmented. Posterolateral spines on abdominal segments 2-9, spines progressively larger posteriorly. Terminal filament longer than cerci.

*History and Discussion.*—Demoulin (1955c) established the monotypic genus *Massartellopsis* for *M. irarrazavali* occurring in Chile. The species was described from male and female subimagos. Herein the generic description is based on male and female imagos and mature nymphs. The nymphs and adults of *Massartellopsis* are reared.

Scholes (1961) placed the Tasmanian species *ida* in *Massartellopsis*. The male imago and nymph of this species are undescribed. Scholes (1961) commented that the undescribed nymph of *ida* resembles that of *Atalophlebia*. The female imago of *ida* as described by Tillyard (1935) has a 9th sternum which is deeply incised posteriorly.

*Massartellopsis* can be distinguished from all genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) vein  $MP_2$  of the fore wings is moderately recurved (Fig. 10), (2) vein  $MP_2$  of the fore wings is attached at base to vein  $MP_1$  with a cross vein  $\frac{1}{2}$  the distance from base to margin (Fig. 10), (3) the claws of a pair are alike; each is apically hooked, and with an opposing hook (Fig. 18), and (4) the penes of the male genitalia are divided and tubular; an apical dorsal projection occurs on each penis lobe (Fig. 27, 28). In the nymphs, (1) the anteromedian margin of the labrum is deeply incised (Fig. 47, 48), (2) the denticles on the claws are long (Fig. 92), (3) abdominal gills occur on segments 1-7 and are alike; dorsal and ventral portions of lamellae are slender, each portion is tapered at apex (Fig. 80), and (4) posterolateral spines occur on abdominal segments 2-9.

Illustrations of *M. irarrazavali* were made from specimens collected at the following localities in Chile: Fig. 10, 11, 18, 27 and 28 from Prov. Aconcagua, trib. Rio Blanco, 1600 m, 10-XI-1963, G.F.E.; Fig. 37, 47, 48, 55, 61, 67, 73, 80, and 86 from Prov. Aconcagua, Rio Blanco, 2200 m, 10-XI-1963, G.F.E.; and Fig. 92 from Prov. Coquimbo, Rio Illapel, Caren, Hacienda Illapel, 800 m, 13-XI-1963, G.F.E.

*Biology.*—The genus *Massartellopsis* is a moderately narrow ranging genus both ecologically and geographically. The genus is found primarily in medium to large streams. In the Rio Blanco (Aconcagua) at 2200 m elevation, the nymphs were very abundant and the mayfly fauna was otherwise limited to Baetidae. At this date (early November) the water was very cold with snow still present on nearby shaded slopes. The nymphs are flattened and well adapted for fast water. The nymphs mature in November or December with known adult emergence ranging from mid-September to late March. Swarming of adults has not been observed.

### *Atalonella* Needham & Murphy, 1924

(Fig. 12, 13, 19, 29-31, 38, 49, 50, 56, 62, 68, 74, 81, 87, 93)  
*Atalonella* Needham and Murphy, 1924: 34; Traver 1946: 420.

*Type-species.*—*A. ophis* Needham & Murphy, present designation.

*Species Included in South America.*—*A. grandis* Demoulin, 1955c: 21; *A. maculata* Demoulin, 1955c: 18; *A. minor* Demoulin, 1955c: 16; *A. ophis* Needham and Murphy, 1924: 34.

*Species Examined.*—*A. ophis* male and female imagos and nymphs; *Atalonella* spp., numerous male and female imagos and nymphs from Chile.

*Distribution.*—Magallanes Province (ca. 53° S) north along Coast Range in Chile and along Andes in Chile and Argentina to Coquimbo Province, Chile (ca. 30° S).

*IMAGO.*—Length of ♂: body 6.0-8.0; fore wings 7.0-9.0 mm. Length of ♀: body 6.0-10.0; fore wings 7.0-12.5 mm. Eyes of ♂ separated on meson of head by a length of little less than maximum width of a lateral ocellus, lower portion of eyes  $\frac{3}{4}$  length of upper portion; eyes of ♀ separated on meson of head by a length 4 times as great as maximum width of an eye. Wings (Fig. 12, 13): vein  $R_s$  of fore wings forked  $\frac{1}{2}$  to a little more than  $\frac{1}{4}$  distance from base to margin; vein MA forked a little more than  $\frac{1}{2}$  distance from base to margin, fork symmetrical, distal portion of vein MA sagged posteriorly; vein  $MP_2$  attached at base to vein  $MP_1$  with a cross vein more than  $\frac{1}{3}$  distance from base to margin, vein  $MP_2$  moderately recurved (Fig. 12); vein  $ICu_1$  attached, attached by a cross vein, or not attached at base to vein  $CuA$  (Fig. 12); cross veins numerous. Costal margin of hind wings convex, apex of convexity located  $\frac{1}{2}$  distance from base (Fig. 13); cross veins numerous. Legs: ratios of segments in male fore legs, 0.77:1.00(2.2 mm):0.12:0.35:0.35:0.27:0.15. Claws of a pair alike, apically hooked, each with an opposing hook (Fig. 19). Male genitalia (Fig. 29-31): segment 3 of forceps a little shorter than segment 2, segment 2 of forceps  $\frac{1}{4}$  length of segment 1, base of forceps broad, its inner margin forming an extreme angular bend; length of styliiger plate along median line  $\frac{1}{4}$  maximum width; basal half of penes fused, apical half divided, tubular, apex blunt, shape as in Fig. 29-31. Ninth sternum of ♀ deeply cleft apically (Fig. 38). Terminal filament longer than cerci.

*MATURE NYMPH.*—Head prognathous. Antennae 2 times as long as maximum length of head. Mouthparts (Fig. 49, 50, 56, 62, 68, 74): dorsal hair on labrum as in Fig. 49; submedian and anterolateral bands of hair ventrally, 5 denticles on anteromedian emargination, lateral 2 denticles on each side small, equal sized, median denticle larger (Fig. 50). Clypeus as in Fig. 49. Left mandible as in Fig. 56. Lingua of hypopharynx with well-developed lateral processes (Fig. 68), anterior margin shallowly cleft; superlingua of hypopharynx as in Fig. 68, with a row of hair along anterior margin. Segment 2 of maxillary

palpi a little longer than  $\frac{3}{4}$  length of segment 1; segment 3 of palpi a little shorter to equal length of segment 2, triangular: a V-shaped ridge near the ventral, inner anterolateral margin of maxillae; hair on maxillae as in Fig. 62. Labium as in Fig. 74; segment 2 of palpi a little shorter in length than segment 1; segment 3 of palpi a little more than  $\frac{3}{4}$  length of segment 2, triangular; paraglossae ventral to glossae. Short hair on thorax. Legs (Fig. 87, 93): apex of claws hooked and narrow, denticles on claws progressively larger apically, except apical denticle much larger. Gills (Fig. 81): gills 1-7 alike: dorsal and ventral portions of lamellae slender, terminating in a slender tapered process at apex, ventral portion smaller, gills progressively smaller posteriorly: main trunk of tracheae nearer to inner margin of lamellae, more so in dorsal portion, tracheae on both sides of main trunk branched, tracheae pigmented but just a little darker than pigment of lamellae. Posterolateral spines on abdominal segments 6-9, spines progressively larger posteriorly. Terminal filament a little longer than cerci.

*History and Discussion.*—Needham and Murphy (1924) established *Atalonella* for the new species *A. ophis* and for *A. fusca* (Ulmer, 1919). *Atalonella* has included species from Australia, Tasmania, and Chile. Upon obtaining reared material from Chile, we herein redescribe the adults and nymphs of the Chilean representatives. Needham and Murphy (1924) described the supposed nymph of *Atalonella* and our research confirms this association.

Needham and Murphy (1924) stated both species, *A. ophis* and *A. fusca*, occur in Chile, but did not state which species was to be the type-species. Lesage (1931) and Traver (1946) pointed out that *A. fusca* occurs in Australia and not Chile, but neither designated a type-species of *Atalonella*. We herein designate *A. ophis* as the type-species of *Atalonella*.

Navas (1918) established *Nousia* for the Chilean species *N. delicata* and, in 1925, placed *Atalonella* as a synonym of *Nousia*. The question of whether or not *Atalonella* is a junior synonym of *Nousia* is complicated. Traver (1946) did not accept *N. delicata* as a congener of *Atalonella* because the drawing of the hind wings of *Nousia* by Navas does not correspond to that of the hindwings of known species of *Atalonella*. One of us (G.F.E.) spent 2½ months collecting and rearing Ephemeroptera in Chile and visited the type locality of *Nousia*, Los Perales, a hacienda on the Marga-Marga River ca. 30 km ESE of Valparaiso. The mayflies of the area are thus moderately well known and *Atalonella* was collected from the Marga-Marga, both upstream and downstream from Los Perales. The only recognized leptophlebiid genus in Chile agreeing with *N. delicata* in hind wing shape, genitalia shape, and fore wings as short as 7 mm is *Atalonella*. However, Navas' figure of the male genitalia of *Nousia* is so featureless that it could apply to almost any species of *Atalonella*. The fact that the figure of the hind wings does not agree with the wing venation of the known species of *Atalonella* is not surprising. Navas was notori-

ously inept. The type has not been located, so one must depend on the description and the probably inaccurate drawings. *N. delicata* is almost certainly congeneric with *Atalonella*, but there is no way at present to determine the identity of the species. Except where the types can still be found the application of the names given by Navas to Neotropical mayflies is virtually impossible. If one applied the name *Nousia* to *delicata* and the species now assigned to *Atalonella*, one would not know the identity of the type-species and hence would not be able to apply the name *Nousia* in case the group was divided into 2 or more genera or subgenera. It therefore seems advisable to regard *N. delicata* as a name of dubious application.

*Atalonella* can be distinguished from all genera of the Leptophlebiidae by the following combination of characters. In the imago, (1) vein  $MP_2$  of the fore wings is moderately recurved (Fig. 12), (2) vein  $MP_2$  of the fore wings is attached at base to vein  $MP_1$  with a cross vein more than  $\frac{1}{3}$  the distance from base to margin (Fig. 12), (3) the claws of a pair are alike; each is apically hooked and with an opposing hook (Fig. 19), and (4) the basal half of penes of the male genitalia is fused, while the apical half is divided, tubular, and apex blunt as in Fig. 29-31. In the nymphs, (1) 5 denticles occur on the anteromedian emargination of the labrum; lateral 2 denticles on each side are small and equal sized while median denticle is larger (Fig. 49, 50), (2) denticles on the claws are progressively larger apically, except apical denticle is much larger (Fig. 93), (3) abdominal gills occur on segments 1-7 and are alike; dorsal and ventral portions of lamellae are slender and terminated in a slender tapered apical process (Fig. 81), and (4) posterolateral spines occur on abdominal segments 6-9.

Illustrations of *Atalonella* sp. were made from specimens collected at the following locality in Chile: Prov. Malleco, Arroyo Pehuenco, Trib. Rio Bio Bio, near Marimenuco, 12-XII-1963, G.F.E.

*Biology.*—The genus *Atalonella* is quite wide ranging ecologically and geographically. It is found in the Andes in numerous arroyo streams that dry up in middle to late summer. Streams whose vernal runoff is quite brief has no Leptophlebiidae, being populated principally by Chironomidae and Simuliidae. The nymphs are not found in the larger rivers, but they are common in a wide variety of streams up to ca. 10 m wide. The nymphs are moderately flattened and occur on a wide variety of objects in the streams.

The males of various species swarm from mid- to late morning. Some of the small dark species have the flights of males widely scattered over places clear of vegetation near the streams; these males swarm in full sunshine from midmorning until early afternoon. Males of other species swarm over and near streams in the evening. The various species have a wide range of emergence dates with adult records ranging from mid-September to mid-June.

## PHYLOGENY AND RELATIONSHIPS OF THE GENERA

A review of the literature concerning the genera discussed herein reveals the morphological similarities between these southern South American genera and genera occurring in the Ethiopian and Australian regions. Peters and Edmunds (1964, 1970) discussed the relationships of certain Ethiopian representatives to genera occurring in the Neotropical and Australian regions and indicated that further studies would clarify the possibility of a Paleantarctic dispersal route. While we have not yet completed a detailed study of the genera occurring in the Australian region, some preliminary conclusions can be made concerning the South American representatives.

*Penaphlebia*, *Hapsiphlebia*, and *Massartella* all appear to be closely related, and all possess several similar morphological traits. In the imagos, (1) vein  $MP_2$  of the fore wings is strongly recurved (Fig. 2, 4, 6), (2) the claws of a pair are alike: each is apically hooked with an opposing hook (Fig. 14-16), and (3) the penes of the male imagos are divided and tubular, and each lobe possesses at least one subapical spine or projection (Fig. 20-24). In the nymphs, (1) the glossae of the labium are curved over ventrally (Fig. 69-71), and (2) the middle abdominal gills are plate-like (Fig. 75, 76, 78).

*Penaphlebia* appears to be the most primitive of these 3 genera. No specializations of the wings or external female genitalia appear to occur in the adults. The abdominal gills are plate-like and with no apparent specialized modifications in the nymphs.

*Hapsiphlebia* appears to be more specialized than *Penaphlebia* and probably arose from a *Penaphlebia*-type ancestor in continental South America. In the imagos, (1) the cross veins in the apical  $\frac{1}{3}$  of cell C of the fore wings are anastomosed (Fig. 4), (2) the male forelegs are much longer in relation to body length than those of *Penaphlebia*, and (3) the ♀ possesses a well-developed ovipositor or egg guide extending to just past the anterior margin of abdominal segment 8 (Fig. 32). In the nymphs, the abdominal gills occur on segments 1-7; gills on segments 1-5 are alike and plate-like while gills on segments 6 and 7 are slender (Fig. 76, 77).

*Massartella* appears to be more specialized than *Penaphlebia* and probably arose from a *Penaphlebia*-type ancestor in continental South America. In the imagos, (1) distal portion of vein MA of fore wings is a little sagged posteriorly (Fig. 6), (2) vein  $ICu_1$  of the fore wings is attached at base by a cross vein to vein CuA and CuP (Fig. 6), and (3) segments 2 and 3 of forceps of male genitalia are each  $\frac{1}{3}$  length of segment 1 (Fig. 24). In the nymphs, (1) the denticles on the claws are progressively larger apically, except the apical denticle is larger (Fig. 90), and (2) abdominal gills occur on only segments 1-6.

No known representatives from the Ethiopian region appear to be closely related to these 3 genera; however, *Atalophlebia* and related genera from the Australian region appear to be closely related. As pointed out in the discussion of *Penaphlebia*, prelimi-

nary studies indicate the adults of *Atalophlebia*, *Penaphlebia*, *Hapsiphlebia*, and *Massartella* are morphologically very similar, while the nymphs of all these genera are distinct. Based on the generic criteria discussed by Peters and Edmunds (1970) the 3 temperate South American groups should be recognized as genera distinct from *Atalophlebia*.

*Meridialaris* and *Massartellopsis* appear to be closely related. The 2 genera possess several similar morphological traits. In the imagos, (1) vein  $MP_2$  of the fore wings is moderately recurved (Fig. 8, 10), (2) spines or projections, when present, are located at the apex of the penes of male genitalia (Fig. 25-28), (3) the eyes of the ♂ meet on meson of head, and (4) the 9th sternum of the ♀ is entire (Fig. 36, 37). In the nymphs, (1) the anteromedian emargination of the labrum is deeply incised as in Fig. 46, 48, (2) the glossae of the labium are straight and not curved over ventrally (Fig. 72, 73), (3) dorsal and ventral portions of lamellae of the abdominal gills are slender and each portion is tapered at apex; the main trunk of tracheae runs along the median line of lamellae of the abdominal gills (Fig. 79, 80), and (4) posterolateral spines occur on abdominal segments 2-9.

*Massartellopsis* appears to be more specialized than *Meridialaris* and probably arose from a *Meridialaris*-type ancestor in continental South America. The adults of the 2 genera are morphologically very similar, and it is conceivable that the divided, tubular penes of the male genitalia (Fig. 28) of *Massartellopsis* arose from the primitive fused penes (Fig. 25, 26) of *Meridialaris*. In fact, on first examination the penes of *Massartellopsis* superficially resemble those of *Meridialaris* as the 2 penis lobes usually lie close together. The nymphs of these 2 genera are morphologically very similar.

No known representatives from the Ethiopian and Australian regions appear to be closely related to *Massartellopsis*. However, *Deleatidium* from the Australian region appears to be closely related to *Meridialaris* and the 2 genera can be distinguished in the adults and nymphs by the characters given in the discussion on *Meridialaris*. Also, *Meridialaris* and *Deleatidium* appear closely related to *Aprionyx* and *Adenophlebia* in the Ethiopian region as the wing venation and fused penes of the male genitalia are similar for all the genera. Peters and Edmunds (1970) noted adults from Madagascar that are very similar to *Deleatidium* (comparison made to Chilean species now placed in *Meridialaris*).

*Atalonella* appears to represent a separate line of evolution. While the genus does belong to the same complex as the other genera discussed herein, its relationships to these genera and other southern hemisphere genera is unclear. No known representatives from the Ethiopian region appear to be closely related to *Atalonella*. Several species from the Australian region are at present placed in *Atalonella* and preliminary examination indicates these species to be morphologically very similar to the South American species.



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