

Biosystematics of the Genus *Penaphlebia*
(Ephemeroptera: Leptophlebiidae: Atalophlebiinae)
from South America

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ABSTRACT

The systematics of *Penaphlebia* is reviewed, and the genus is redescribed. The egg is described for the first time.

Two subgenera of *Penaphlebia* are established and described. The subgenus *Megalophlebia* is monotypic, represented by *P. vinosa*, and the subgenus *Penaphlebia* s.s. consists of five species: *P. chilensis*, *P. exigua*, *P. fulvipes*, *P. barriai* and *P. flavidula*, the latter two of which are new.

Adults of *P. chilensis*, *P. exigua*, *P. fulvipes* [= *P. sepia* (Thew), NEW SYNONYMY] and *P. vinosa* are redescribed. The nymphs of *P. chilensis*, *P. fulvipes* and *P. vinosa* are described for the first time. *Penaphlebia barriai* and *P. flavidula* are described from the nymphs, imagos and subimagos.

Illustrated keys for the nymphs and imagos, and geographic distribution maps are presented for each species. Notes on the biology of the species are included. A phylogenetic analysis of *Penaphlebia* is presented.

INTRODUCTION

This paper represents Part VI of a series revising the cool-adapted Leptophlebiidae of South America. Part I (Pescador and Peters, 1980b), and Part II (Pescador and Peters, 1982) included descriptions of new genera and species. Part III (Pescador and Peters, 1985) discussed the biosystematics and phylogenetic relationships of the genus *Nousia*, and Parts IV and V revised the genera *Meridialaris* and *Massartellopsis* (Pescador and Peters, 1987), and *Massartella* (Pescador and Peters, 1990).

Methods of gut analysis and descriptive terminology were described in previous parts of the series. Localities, stages (N for nymph, I for imago and S for subimago) and deposition of examined materials are given in the treatments of each species to facilitate access to specimens for future study. Reared specimens are indicated by the abbreviation R following the stages.

For the first time in the series, we are using the recently reorganized geographic limits of the various provinces of Chile for species distributions. Flint (1989) provides a brief background information on Chile's geographic reorganization, and he kindly furnished us the new maps to use for this study.

Locality information listed under "Material Examined Section" however, still follows the old geographic limits of the previous provinces of Chile. Some labels have insufficient locality information but are supplemented with data enclosed in brackets to approximate the location of the collection site. Sources of supplemental data include a gazetteer and Dr. Flint's years of field notes of his collecting trips in the region.

Depositions of specimens are abbreviated as follows: (CAS) California Academy of Sciences; (BMNH) British Museum of Natural History; (CU) Cornell University; (FML) Fundacion Miguel Lillo, Argentina; (FAMU) Florida A&M University; (IRSNB) Institute Royal des Sciences naturelles de Belgique; (INHS) Illinois Natural History Survey; (USNM) National Museum of Natural History, and Smithsonian Institution.

The names of collectors are abbreviated as follows: (BA) B. Akerbergs, (GB) G. Barria, (WB) W. Besch, (TC) T. Cekalovic, (D&MD) D. & M. Davis, (ED) E. Dominguez, (GFE) G. F. Edmunds, Jr., (LE) L. Escobar, (CM & OSF) C. M. & O. S. Flint, Jr. (JI) J. Illies, (EAM) E. A. Michelbacher, (TG) Tom Gonsler, (RG) R. Gomez, (LEP) L. E. Pena, (MLP) M. L. Pescador, (JG & WLP) J. G. & W. L. Peters, (ESR) E. S. Ross, (PJS) P. J. Spangler, (IR) I. Rottman, (SSS) S. S. Schajovskoy, and (WEA) Willink et al.

Genus *Penaphlebia* Peters and Edmunds

Penaphlebia Peters and Edmunds, 1972: 1399; Tsui and Peters, 1975: 548; Pescador and Peters, 1980a: 45.

Atalophlebia Eaton, 1884: 91 (partim), Needham and Murphy, 1924: 34 (partim); Traver, 1946: 419 (partim); 1959: 3; Demoulin, 1955a: 8 (partim); Demoulin, 1955b: 1; Thew, 1960: 130 (partim).

Type species.— *Atalophlebia chilensis* Eaton, by original designation.

Species included.— *P. barriai* new species; *P. chilensis* (Eaton); *P. exigua* Dominguez and Pescador; *P. flavidula* new species; *fulvipes* (Needham and Murphy) [= *P. sepioides* (Thew) NEW SYNONYMY]; *P. vinosa* (Demoulin).

Distribution.— Magallanes Province (ca. 54° S) north to Coquimbo Province (ca. 31° N), CHILE, eastward to Andean range in Chubut, Río Negro, and Neuquen Provinces, Argentina.

Imago.— Length: male body 6.4-16.0 mm, fore wings 6.5-18.0 mm; female body 7.7-18.0 mm, fore wings 8.0-20.0 mm. Eyes of male meet on meson of head, lower portion of eyes 2/3 to 3/4 length of upper portion; eyes of female separated on meson of head by a length 3 to 4 times width of an eye. Wings (Fig. 1-6): vein Rs of fore wings forked approximately 1/4 distance from base to margin; vein MA forked approximately 1/2 distance from base to margin, forked symmetrical; distal portion of vein MA moderately sagged; vein MP₂ strongly recurved, separated or attached at base to vein MP₁ with cross vein approximately 1/4 distance from base to margin; vein ICU₁ attached at base to vein CuA (Fig. 1). Hindwings either elliptic (Fig. 5) or ovate (Fig. 6); costal margin convex with concavity located approximately 1/3 distance from base, apex obtuse (Fig. 5-6); vein Sc_{9/10} maximum length of hindwings (Fig. 5). Legs: ratios of segments in male fore legs, 0.76: 1.00 (4.10 mm); 0.06: 0.35: 0.35: 0.30: 0.14; claws of a pair alike, both apically hooked each with an opposing hook (Fig. 7). Male genitalia (Fig. 9-14): segment 3 of genital forceps equal to 3/5 length of segment 2, segment 2 1/5-1/4 length of segment 1; base of segment 1 broad, inner margin forming an angular bend (Fig. 11, 14). Maximum length of styliger plate along median line slightly less than 1/3 maximum width. Penis lobes divided, tubular, each lobe with subapical spine (Fig. 11). Female ninth sternum deeply cleft apically (Fig. 8). Terminal filament longer

than cerci.

Subimago.—Morphologically similar to imago except fore legs and external genitalia not as fully extended. Wings dull yellow with brown shadings around cross veins; hairs along margins long and branched (Fig. 65-66). Caudal filaments setose.

Egg.—(Fig. 61-64) oblong; polar cap absent, chorion granulate with numerous spongy circular ridges (Fig. 61-63), ridges either hollow (Figs. 62, 64) or with enclosed spongy material (Figs. 61, 63); one sperm guide (Figs. 62-63).

Mature nymph.—Head prognathous. Antennae 2x as long as head, with thick apical hairs and small denticles at joints. Mouthparts (Fig. 29-35). Length of labrum slightly more than 1/2 width, apical 2/3 of margins slightly rounded, dorsal hair as in Fig. 29, apical anteromedian emargination shallow with unequal sized denticles. Clypeus subequal width to labrum, lateral margins parallel (Fig. 29). Outer margin of mandibles slightly curved, basal 1/2 with long thick hair (Fig. 30-31), outer right incisor with pointed denticles (Fig. 32). Galea-lacinia of maxillae apically broad with more than 15 subequal pectinate setae (Fig. 34); segments 1 and 2 of palpi subequal length, segment 3 distinctly shorter (Fig. 34); segment 2 with series of pectinate setae. Lingua of hypopharynx with well developed lateral processes (Fig. 33). Segments 1 and 2 of labial palpi subequal length, segment 3 shorter with a comb of peg-like setae; glossae curved over ventrally (Fig. 35); submentum with long and thick lateral spines (Fig. 35). Pronotum laterally glabrous. Legs (Fig. 36-38): maximum width of tibiae approximately 2x maximum width of tarsi; fore tibiae in cross section rounded; femora dorsally scaly with thick setae of variable shapes (Fig. 54-56); denticles on claws irregular, either middle denticles (Fig. 38) or apical denticles larger than others (Fig. 37). Posterolateral spines on abdominal segments 6-9 (Fig. 43) or 8-9 (Fig. 41-42); lateral margins of terga glabrous, dorsally scaly with fine hairs and short feather-like setae (Fig. 60); posteriorly with spines and hair-like setae (Fig. 57-59). Gills on segments 1-7 alike, lamellae plate-like, apically terminated in one filamentous (Fig. 39); or blade-like (Fig. 40) process; main tracheal trunk along median line of lamellae with several branches on both sides (Fig. 39-40). Terminal filament longer than cerci; segments of filaments with thick spines, and hairs (Fig. 44-45).

Discussion.—Navás (1928, 1930, 1935) described seven species of *Atalophlebia* from Chile other than those now included in *Penaphlebia*: *A. anastasioi*, *A. athanasii*, *A. discolor*, *A. fenestra*, *A. hyalina*, *A. rofucensis* and *A. valdiviae*. Inadequate descriptions and lack of illustrations of these species by Navás make it impossible to identify or compare them with the other species with available specimens. Navás' description of these species were based mainly on color. The illustrations of the genitalia of *A. athanasii*, and the styliger plate and genital forceps of *A. anastasioi* are unclear and could represent any of the species in the genus. There are no descriptions of the nymphs nor female imagos. Attempts to locate the type specimens were unsuccessful. One of us (MLP) visited the church in Santiago, Chile, where the type specimens were known to have been deposited, but was informed by Señor Luis Peña, an eminent Chilean naturalist, that almost all of Navás' collections from Chile that were deposited in this church were destroyed by fire. Presently we know of no mayfly specimens that were saved from the fire. Since the names of the species that Navás described are not certainly applicable to any known taxon, we propose that all seven species be considered *nomen dubium*.

Peters and Edmunds (1972) transferred *A. chilensis* Eaton, *A. fulvipes* Needham and Murphy, *A. sepia* Thew and *A. vinosa* Demoulin to *Penaphlebia*. They listed several characters of the imagos and nymph to distinguish *Penaphlebia* from all the other genera of Leptophlebiidae. Based on this study, we found that *Penaphlebia* can be distinguished from all other genera of Leptophlebiidae by the following combinations of characters. In the

length of hind wings (Fig. 5-6); (2) vein 1Cu₁ of the fore wings is attached at base to vein CuA, and distally parallel to vein CuA and CuP (Fig. 1); (3) claws of a pair are alike, both apically hooked, each with an opposing hook (Fig. 7); (4) penis lobes are divided, long and tubular, and each lobe has one subapical spine (Fig. 9-14); and (5) female 9th abdominal sternite is deeply cleft apically (Fig. 8). In the nymph: (1) maximum width of clypeus is subequal to the maximum width of labrum (Fig. 29); (2) length of labrum is approximately 1/2 maximum width, moderately expanded laterally (Fig. 29) and has long apical hairs (Fig. 52-53); (3) outer margin of mandibles is slightly curved with long hairs on the basal half (Fig. 30-31); (4) glossae are strongly curved over ventrally (Fig. 35), and submentum has long lateral spines (Fig. 35); (5) lateral margins of abdominal terga are glabrous, posterior margin with spines and feather-like setae (Fig. 57-59); and (6) abdominal gills occur on segments 1-7, are platelike, and apically terminated with filamentous (Fig. 39) or blade-like process (Fig. 40). The egg chorion is granulate and has networks of circular ridges (fig.61-64).

Pescador and Peters (1980a, 1990) placed *Penaphlebia* in the same phyletic line with *Massartella* and *Atalophlebia* but it can be distinguished from these genera by any of the following characters. In the imagos: (1) vein Cu₁ of the fore wings is attached at base to vein CuA (Fig. 1); (2) segment 3 of genital forceps is approximately 1/4 length of segment 1 (Fig. 11); and (3) penis lobes are divided, long and tubular, and each lobe has a subapical spine (Fig. 9-14). The eggs have granulate chorion with networks of circular ridges (Fig. 61-64). In the nymph: (1) tarsal claws have irregular denticles with either the middle (Fig. 38) or apical denticles (Fig. 37) much larger than the others; (2) lateral margins of pronotum are glabrous; (3) posterolateral spines occur on abdominal segments 6-9 (Fig. 43) or 8-9 (Fig. 41-42); (4) lateral margins of the abdominal terga are glabrous, and posterior margin has broad spines, and hair-like setae (Fig. 57-59); and (5) abdominal gills occur on segments 1-7, and are plate-like with the main tracheal trunk along median of lamellae (Fig. 39-40).

Key to Species of *Penaphlebia* Imagos

- 1 Hind wings ovate (Fig. 6); segments 3 and 4 of male protarsi equal in length; posterior margin of styliger plate entire (Fig. 14); apical third of penis lobes greatly enlarged, slender subapical spine posteriorly projecting (Fig. 14)
Subgenus *Megalophlebia*, *P. (M.) vinosa* (Demoulin)
- Hind wings elliptic (Fig. 5); segment 3 of male protarsi distinctly longer than segment 4; styliger plate with midposterior emargination (Fig. 11-12); apical third of penis lobes slightly to moderately enlarged, stubby subapical spine posterolaterally projecting (Fig. 9)
Subgenus *Penaphlebia* s. s. 2
- 2(1) Body length of male and female 8.0 mm or less; styliger plate with V-shaped posteromedian emargination (Fig. 12); dark brown maculae on abdominal terga as in Fig. 17; maculae on abdominal sterna absent *P. (P.) exigua* Dominguez & Pescador
- Body length of male and females more than 8 mm; styliger plate with broad U-shaped posteromedian emargination (Fig. 11); dark brown maculae on abdominal terga not as above; abdominal sterna with brown maculae

- 3(2) Abdominal terga 3, 6-7 and 9 with pronounced dark brown to black maculae (Fig. 18);
 membrane flushed with yellow *P. (P.) burruai* new species
- Abdominal terga 1-9 or 1-3, 6-7 and 9 with pronounced dark brown to black maculae;
 penes as in Fig. 9, 10, 13; costal and subcostal membranes of female fore wings flushed
 with brownish yellow 4
- 4(3) Pre-pterostigmatic costal and subcostal veins of male and female fore wings well
 developed and thickly infuscated with dark brown (Fig. 3); penis lobes as in Fig. 9
P. (P.) chilensis (Eaton)
- Pre-pterostigmatic costal and subcostal cross veins of male forewings weakly devel-
 oped (Fig. 4), female fore wings a little more developed, faintly infuscated; penis lobes
 as in Figs. 10, 13 5
- 5(4) Abdominal terga 1-9 with pronounced dark brown to black maculae (Fig. 15); subme-
 dian maculae on terga 8 beyond half length of segment; penis lobes as in Fig. 10
P. (P.) flavidula new species
- Abdominal terga 4-5 and 8 with reduced submedian maculae (figs. 23, 25); submedian
 maculae on terga 8 not extended beyond half length of segment; penis lobes as in Fig.
 13. *P. (P.) fulvipes* (Needham & Murphy)

Mature Nymphs

- 1 Posterolateral spines on abdominal segments 6-9; (Fig. 43); abdominal gills apically
 terminated with a blade-like process (Fig. 40); mandibles with deep dorsal groove
 (Fig. 31) Subgenus *Megalophlebia*, *P. (M.) vinosa* (Demoulin)
- Posterolateral spines on abdominal segments 8-9 (Fig. 41-42); abdominal gills
 apically terminated with a filamentous process (Fig. 39); mandibles without dorsal
 groove, if present shallow (fig. 30) 2
- 2 (1) Mid-denticles of claws larger than apical ones (Fig. 38) 3
- Mid-denticles of claws smaller than apical ones (Fig. 37) 5
- 3 (2) Posterior spines on abdominal terga equal to a little longer than feather-like setae (Fig.
 59); hairs on joints of caudal filaments short (Fig. 44); pronounced dark brown to black
 maculae on abdominal terga 1-9 (Fig. 15, 17) 4
- Posterior spines on abdominal terga distinctly shorter than feather-like setae (Fig. 57);
 hairs on joints of caudal filaments as long or longer than segments (Fig. 45); maculae
 on abdominal terga absent or greatly reduced *P. (P.) barriai* new species
- 4 (3) Body length less than 8 mm; posterolateral spines on abdominal terga 8-9 weakly
 developed (Fig. 41); abdominal gills whitish *P. (P.) exigua* Dominguez & Pescador

- Body length more than 8 mm; posterolateral spines on abdominal terga 8-9 well developed (Fig. 42); abdominal gills greyish-black *P. (P.) flavidula* new species
- 5 (2) Hair-like setae on posterior margin of abdominal terga ~~as long as~~ ^{longer than} spines (Fig. 57); tarsi bicolorous *P. (P.) chilensis* (Eaton)
- Hair-like setae on posterior margin of abdominal terga equal to slightly longer than spines (Fig. 58); tarsi unicolorous *P. (P.) fulvipes* (Needham & Murphy)

Subgenus *Penaphlebia* s. s.

Imago.—Length male body 6.4-14.0 mm, fore wings 6.5-15.0 mm; female body 7.7-15.0 mm; fore wings 8.0-18.0 mm. Hind wings elliptic (Fig. 5). Segment 3 of male protarsi longer than segment 4. Abdominal sterna with dark brown to black abdominal spots. Male genitalia as in Fig. 9-13, apical third of penis lobes slightly to moderately enlarged, stubby subapical spine posterolaterally projected (Fig. 9); styliiger plate with broad U-shaped (Fig. 11) or V-shaped emargination (Fig. 12).

Egg.—Chorion with circular ridges enclosing spongy material (Fig. 61-63).

Mature nymph.—Body length 6.9-14.0 mm. Mandible without dorsal groove (Fig. 31). Dorsum of femora with ovate (Fig. 55) or spatulate setae (Fig. 54). Posterolateral spines occur on abdominal segments 8-9. Abdominal gills apically terminated with a filamentous process (Fig. 39).

Type species.— *Penaphlebia chilensis* (Eaton).

Discussion.— *Penaphlebia* s. s. consists of four species, and occurs in the western and eastern slopes of the southern Andes (Fig. 69). The characters above distinguish it from the subgenus *Megalophlebia*.

Penaphlebia (Penaphlebia) barriai, new species

Male imago.— (in alcohol). Length: body 9.0-12.0 mm, forewings 10.0-12.0 mm. Head yellow. Scape and pedicel of antennae brown, flagellum pale yellow. Ocelli greyish-white, black at base. Upper portion of eyes orange yellow, lower portion black. Thorax: nota yellow, pronotum paler, with anterior and lateral margins black and 2 pairs of dark brown to black median stripes; parapsidal furrows and apex of scutellum washed with dark brown. Pleura pale yellow with broken black markings between procoxae and metacoxae. Sterna yellow, usually washed with brown medially; metasternum with a dark brown to black transverse median band. Wings: membrane of fore and hind wings hyaline, base pale yellow; longitudinal and cross veins of fore and hind wings brown except anal veins and veins C, Sc, and R₁ pale yellow; costal and subcostal cross veins developed and thickly infuscated with dark brown (Fig. 3); hind wings elliptic (fig. 5). Legs: yellow except tibio-tarsal joints black, and apex of segment 5 of tarsi light brown; femora with dark brown median and apical bands; segment 3 of protarsi longer than segment 4. Abdomen (Fig. 18-19): terga pale yellow with pronounced dark brown to black maculae on terga 3, 6-7 and 9 (Fig. 18). Sterna pale yellow with brown maculae on sterna 1-8 (Fig. 19); sterna 2-9 with a prominent dark brown to black spot near anterolateral corners. Genitalia (Fig. 11): genital forceps yellow, segment 3 paler; angular bend of segment 1 of genital forceps moderately developed, denticulate (Fig. 11); segment 3 of forceps approximately 3/4 of segment 2. Penes yellow, inner margins of lobes

washed with reddish-brown; penis lobes as in Fig. 11, subapical spine stubby, posterolaterally projecting. Styliiger plate with broad, shallow U-shaped posteromedian emargination (Fig. 11). Caudal filaments: pale yellow, with alternate broad, and narrow apical dark brown to black bands, banding progressively broader and paler distally; first few basal segments washed with black.

Female imago.—(in alcohol). Length: body 10.0-14.0 mm, fore wings 10.0-14.0 mm. Similar to male imago except as follows: vertex with a pair of narrow dark brown to black median markings; eyes black; prosternum pale yellow; subcostal membrane of fore wings flushed with yellow; margins of fore and hind wings yellowish-brown; tibiae brown; abdominal terga opaque yellow; narrow apical bands of caudal filaments usually inconspicuous.

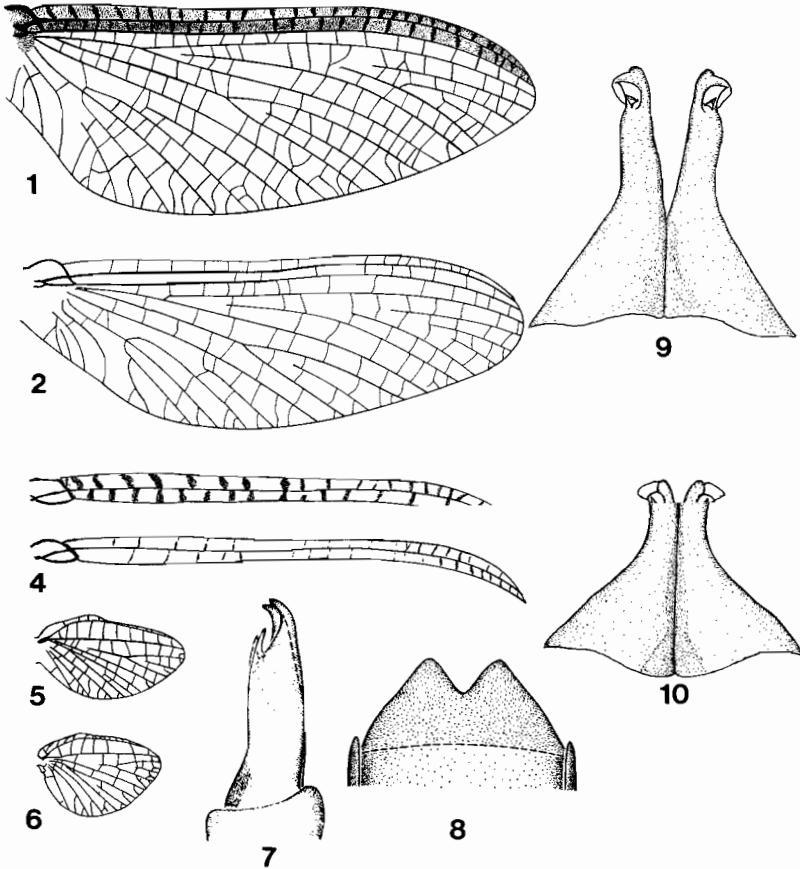
Male subimago.—(in alcohol): Similar to male imago except as follows: head dull yellow; thoracic parapsidal furrows dark brown to black; thoracic sterna brownish yellow with basisterna washed with dark brown; membrane of fore and hind wings cloudy white; cross veins of fore wings lightly shaded with brown; tarsi yellow to brown; genital forceps and penes pale yellow; caudal filaments covered with short hairs.

Female subimago.—(in alcohol): Similar to male subimago except as follows: head pale yellow, color of ocelli, eyes and antennae as in female imago; subcostal membrane of fore wings yellow; fore legs shorter; tarsi light brown.

Mature nymph.—(in alcohol): Body length, 8.0-12.0 mm. Dorsum of head brownish-yellow, venter pale; a small pale yellow marking anterior to median ocellus and lateral to lateral ocelli; ocelli black. Eyes of female black; upper portion of male eyes reddish, lower portion black. Scape and pedicel of antennae brown, flagellum paler. Mouthparts: labrum with a transverse row of widely-set hair near dorsoapical margin (Fig. 52); mandibles lack dorsal groove, or if present, shallow (Fig. 30); maxillary palpi yellow, segment 3 paler. Thorax: nota brownish-yellow, pattern of pale yellow markings similar to Fig. 46. Legs: dorsum yellow, venter pale; tarsi brown; femora with median and apical dark brown to black bands; tibiae with narrow basal and broad apical pale yellow bands; femora dorsally with spatulate setae (Fig. 54); claws with middle denticles larger than apical denticles (Fig. 38). Abdomen: terga yellow with black maculae similar to imagos; terga 1-9 with a pale yellow anterolateral spots, those on tergum 9 elongated; hair-like setae on posterior margin of terga 2x as long as spines (Fig. 57); posterolateral spines on segments 8-9, developed (Fig. 42). Sterna pale yellow, markings similar to imagos but not as pronounced. Gills: membrane greyish-white, trachea dark brown; lamellae apically terminated in a filamentous process (Fig. 39). Caudal filaments: yellow to light brown, darker toward base, a narrow dark brown band on alternate joints; apical hairs thick and long (Fig. 45).

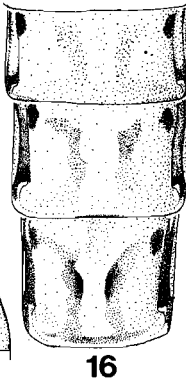
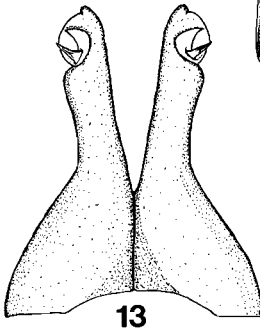
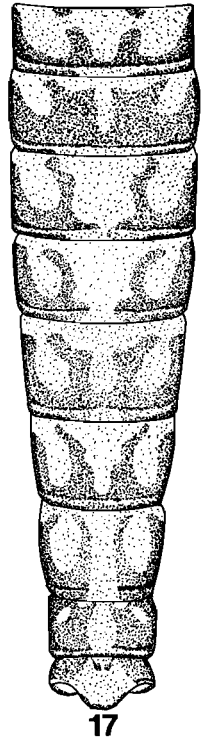
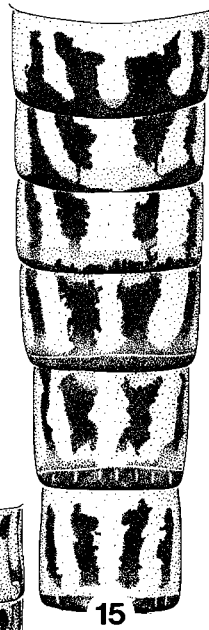
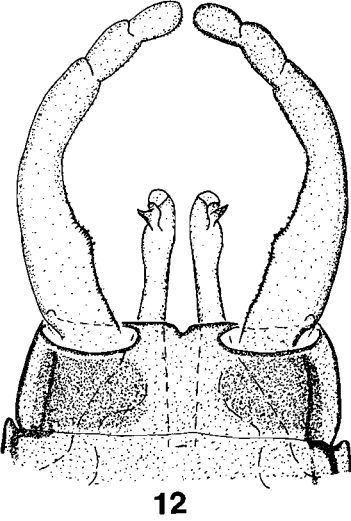
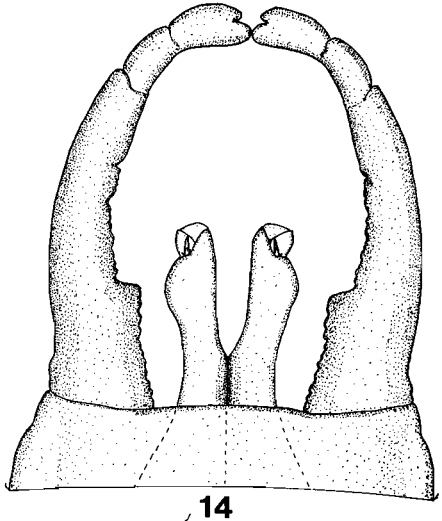
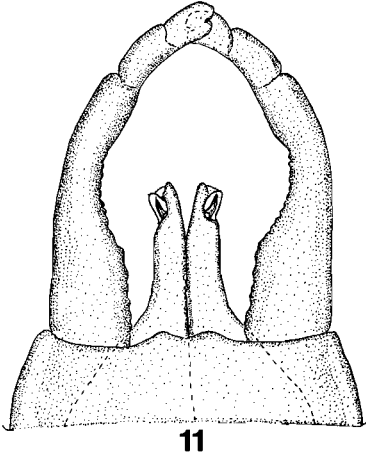
Geographic Distribution.—(Fig. 70). *Penaphlebia barriai* has only been collected from the northern region of Chile, from Valparaiso to Limari Province (Fig. 70).

Specimens examined.—Holotype, male imago, CHILE: *Coquimbo Prov.*, Río Illapel, Sta. Virginia, Hda. Illapel, Illapel, 16.XI.1972, MLP & GB; allotype, female imago, same data as holotype. Paratypes, CHILE: 6 male imagos, 3 female imagos, 2 male subimago, 2 female subimagos, and 200 nymphs, same data as holotype. *Aconcagua Prov.*, 2 nymphs, Pedegua [32°20'P S 71°03'W] 28.XI.1950, ERS & AEM. *Coquimbo Prov.*, 90 nymphs, Río Illapel, "A" 1200 m, 24/31.X.1954, LEP; 50 nymphs, Estero Potrerillos, Hda. Illapel, 800 m, 3.XI.1954, LEP; 8 nymphs, Hda. Illapel, 1000 m, 24.X.1954, LEP; 3 male imagos, Illapel, Huintil, 19.X.1958, LEP; 1 nymph, El Bato Hda. Illapel, Illapel, 22/24.XI.1959 LEP; 2 male imagos, Ovalle, Río Hurtado, 1100 m 6.XI.1962 LEP; 1 female subimago, Illapel, El Bato, 21/22.II.1963, LEP; 40 nymphs, 6 male imagos, 5 female subimagos, 42 nymphs, Río Illapel, Huintil, Hda Illapel, 500 m, 12.XI.1963, GFE; 8 nymphs, Río Illapel, Hda. Illapel, 1,000 m,



Figures 1-10. Structures of *Penaphebia* imagos. Fore wings: 1, *P. (P.) barriai* (female); 2, *P. (P.) exigua* (male). Costal and subcostal cross veins of male fore wings: 3, *P. (P.) chilensis*; 4, *P. (P.) flavidula*. Hind wings: 5, *P. (P.) barriai* (female); 6, *P. (M.) vinosa*. 7, male imaginal fore claw of *P. (P.) barriai*. 8, female 9th abdominal sternum of *P. (P.) barriai*. Ventral view of penes: 9, *P. (P.) chilensis*; 10, *P. (P.) flavidula*.

Figures 11-17. Genitalia and penes, ventral view: 11, *P. (P.) barriai*; 12, *P. (P.) exigua*; 13, *P. (P.) fulvipes*; 14, *P. (M.) vinosa*. Figures 15-17. Abdominal color patterns of abdominal segments of male imagos. *P. (P.) flavidula*: 15, terga 3-8; 16, sterna 5-7. *P. (P.) exigua*: 17, terga 1-9.



13.XI.1963, GFE; 30 male imagos, 2 female subimagos, 17 nymphs, Río Illapel, Hda. Illapel, 800 m, 14.XI.1963, GFE; 8 nymphs, Río Illapel nr. Illapel, 300 m, 16.XI.1963, GFE; 20 nymphs, a trib. of Río Illapel, Illapel, 16.XI.1972, MLP & GB; 4 male, 7 female imagos, 2 female subimagos and 101 nymphs, Río Caren, Sta. Virginia, Hda. Illapel, Illapel, 16/21.1972, MLP & GB; *Santiago Prov.*, 2 female subimagos, El Canelo, 1880 m, 9.XI.1963, GFE; 2 nymphs, El Canelo, 30.XI/2. XII.1972, MLP & GB. *Valparaiso Prov.*, 15 male imagos, Colliguay near La Retuca; 2 nymphs, El Tabon, ca. Valparaiso, 30.XII. 1963, GFE.

The nymphs and adults are associated by rearing. All types are preserved in alcohol. Types are deposited as follows: holotype, allotype, 35 male and 8 female imaginal, 2 male and 5 female subimaginal, and 230 nymphal paratypes, FAMU; 2 nymphal paratypes, CAS; 10 male and 1 female imaginal and 70 nymphal paratypes, USNM.

Etymology.—Species is named for Mr. Gerardo Barria who assisted one of us (MLP) in a collecting trip to Chile.

Discussion.—*Penaphlebia barriai* can be distinguished from the other species of the genus by the following combination of characters. In the imagos: (1) costal and subcostal cross veins of male and female fore wings are well developed and thickly infuscated with dark brown (Fig. 1,3); (2) segment 3 of male protarsi is longer than segment 4; (3) abdominal maculae are greatly reduced and pattern is as in Fig. 18-19; (4) styliiger plate has a broad and shallow U-shaped posteromedian emargination (Fig. 11); (5) angular bend on inner margin of segment 1 of the genital forceps is moderately developed (Fig. 11); and (6) shape of penis lobes is similar to Fig. 11 with the subapical spine posterolaterally projecting. In the nymph: (1) labrum has a transverse row of widely set hair near its dorsoapical margin (Fig. 52); (2) mandibles lack a dorsal groove or if present, it is shallow (Fig. 30); (3) middle denticles on claws are larger than apical ones (Fig. 38); (4) feather-like setae on posterior margin of abdominal terga are at least two times longer than spines (Fig. 57); (5) posterolateral spines occur on abdominal segments 8-9 and well developed (Fig. 39); (6) gill lamellae apically terminate in a filamentous process (Fig. 39); and (7) caudal filaments have long apical and intersegmental hairs (Fig. 45).

Penaphlebia barriai is most closely related to *P. chilensis* but can be distinguished from it by any of the following characters: (1) maculae on the abdominal terga of both the nymphs and adults are greatly reduced (Fig. 18); (2) penis lobes are similar to Fig. 11; and (3) tarsal claws of the nymph have the middle denticles larger than the apical ones (Fig. 38).

Biology.—The nymphs of *P. barriai* were collected in streams and rivers mostly under rocks of various sizes. A few were also found under submerged logs.

The nymphs and adults have been collected in November and December. One of us (MLP) was able to observe the adults emerging in the field early in the morning, between 0700 and 0900 hours. Reared adults mostly emerged in the morning except for 2 male subimagos that emerged later in the afternoon. A small swarm of adults was observed at 0800 hours in Río Illapel, Sta. Virginia, Illapel, Coquimbo Province. The swarm took place approximately three meters above the water in the middle of the river, and the adults flew up and down in a circular fashion then dispersed in every direction. The few specimens collected from the swarm were male imagos. The nymphs were collected from 300 m to 1,100 m above sea level.

Dissected nymphs revealed the dominant gut contents as detritus (66.0%), mineral particles (28.90%), diatoms (3.90%) and filamentous algae (1.20%). Identified diatoms include the genera *Navicula*, *Nitzschia*, *Synedra*, and *Gomphonema*.

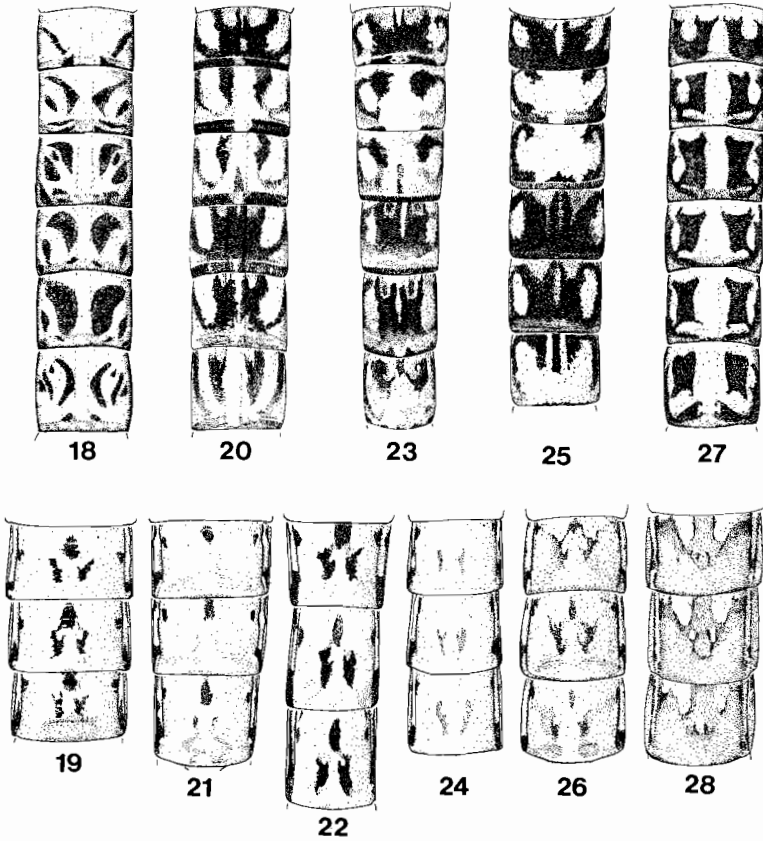
Penaphlebia (Penaphlebia) chilensis (Eaton)

- Atalophlebia chilensis* Eaton, 1883: 91, pl. 10 Fig. 16g (male); nec Ulmer, 1904: Fig. 12-13 (female); Ulmer, 1920: 115; Lestage, 1930: 249; Lestage, 1931: 51; Navás, 1930: 358; Ulmer, 1938: 106; Ulmer, 1942: 124; Fig. 32 (male); Traver, 1946: 419; Demoulin, 1955a: 9; Demoulin, 1955b: 2, Fig. 1a, 2, 5a (male, female); Thew, 1960: 132; Kimmins, 1960: 294.
- Penaphlebia chilensis* Peters & Edmunds, 1972: 1399; Tsui & Peters, 1975: Fig. 58 (male); Hubbard, 1982: 266; Dominguez & Pescador, 1983: 21, Fig. 10 (nymph).

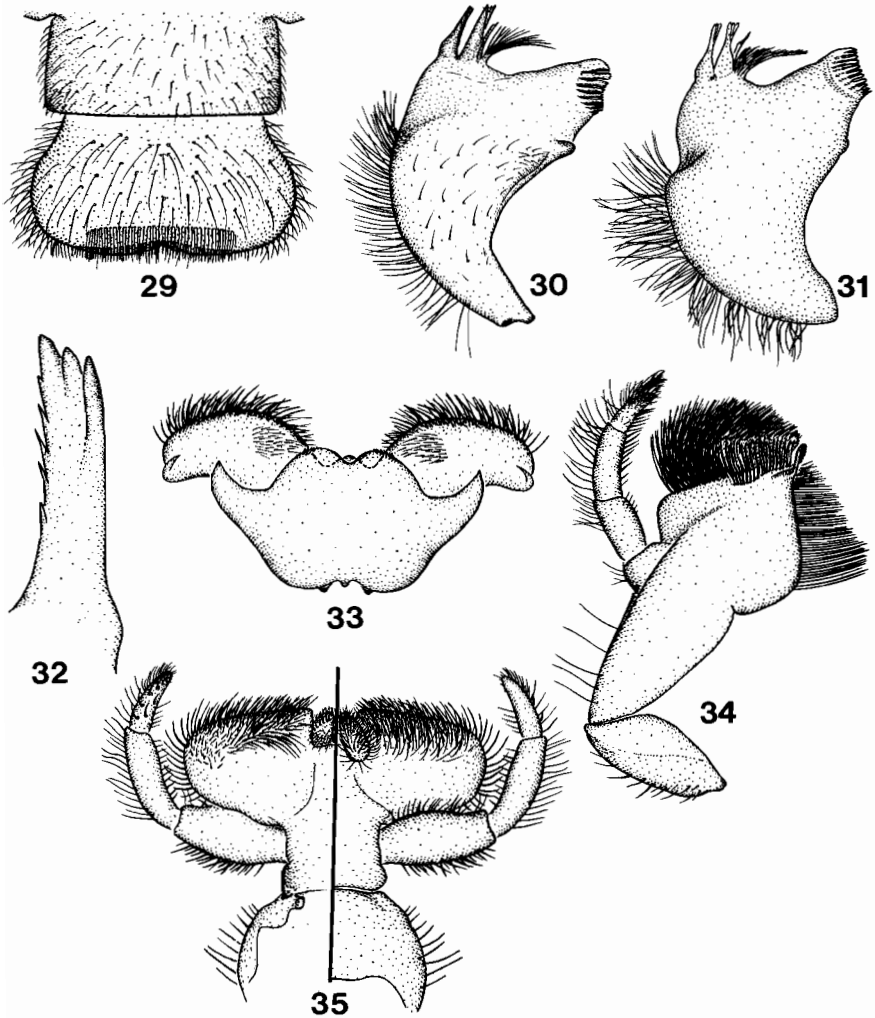
Male imago.—(in alcohol). Length: body 8.0-11.0 mm; fore wings 9.0-12.0 mm. Head yellow. Scape and pedicel of antennae reddish-brown, flagellum yellow to light brown. Ocelli white, black at base. Upper portion of eyes orange-yellow, lower portion black. Thorax: nota yellow, pronotum paler with anterior, lateral and midposterior margins black, and 2 pairs of brown median stripes, outer pair more pronounced and solid; parapsidal furrows and scutellum washed with dark brown to black. Pleura pale yellow with broken dark brown markings between bases of procoxae and metacoxae. Sterna yellow to light brown; metasternum with a dark brown to black transverse median band. Wings: membrane of fore and hind wings hyaline, brownish-yellow at extreme base, costal and subcostal membranes of fore wings translucent, faintly flushed with yellow, pterostigma opaquely whitish; longitudinal and cross veins dark brown, basal 1/2 of veins C, Sc, and R_1 of fore wings yellowish; costal and subcostal cross veins well developed, prominently infuscated with dark brown including humeral veins, and some of radial cross veins; hind wings moderately narrow and elliptic (Fig. 3). Legs: yellow except tibiae dark brown and apical 1/3 of segment 5 of protarsi light brown; femora with a dark brown to black median and apical bands; segment 3 of protarsi longer than segment 4. Abdomen (Fig. 20-22): terga yellow with pronounced dark brown to black maculae on 1-3, 6-7 and 9 (Fig. 20); submedian maculae on terga 8 extend beyond half length of segment but unconnected to posterior margin; sterna translucent pale yellow with dark brown maculae similar to Fig. 21-22; maculae on sterna 1 broad, covering almost entire surface of sterna. Genitalia (Fig. 9): genital forceps yellow; angular bend moderately developed, denticulate (Fig. 3); segment 3 approximately 4/5 length of segment 2. Styliger plate with broad and shallow U-shaped posteromedian emargination. Penes yellow, inner margins washed with reddish-brown; apex of penis lobes as in Fig. 9, subapical spine stubby, postrolaterally projecting (Fig. 9). Caudal filaments: pale yellow with alternate broad and narrow dark brown to black bands, banding gradually broader and paler distally; first few basal segments washed with dark brown.

Female imago.—(in alcohol). Length: body 9.0-11.0 mm; fore wings 9.0-14.0 mm. Similar to male except as follows: vertex with a pair of dark brown to black submedian markings; eyes black; bases of fore and hind wings brownish-yellow; costal and subcostal membranes more intensely flushed with brownish yellow; veins C, Sc, and R_1 of fore wings brownish-yellow; abdominal sterna usually with oblique L-shaped dark brown submedian markings, midposterior margin of sternite 7 often with dark brown band marking base of gonopore.

Male subimago.—(in alcohol). Similar to male imago except as follows: head dusty pale yellow; scape and pedicel of antennae reddish-brown, flagellum light brown; thoracic nota pale yellow, usually with whitish granules near base of wings and scutellum; pro- and mesobasternum washed with greyish-black; membranes of fore and hind wings cloudy white, longitudinal and cross veins brown with anal veins of fore wings and cross veins of fore and hind wings shaded with dark brown; apical and anal margins of wings with hairs; abdominal terga opaque yellow, sterna darker; genital forceps dull yellow faintly washed with brown,



Figures 18-28. Abdominal color patterns of male imagos. *P. (P.) barriai*: 18, terga 3-8; 19, sterna 5-7. *P. (P.) chilensis*: 20, terga 3-8; 21-22, sterna 5-7. *P. (P.) fulvipes*: 23, 25, terga 38; 24, 26, sterna 5-7. *P. (M.) vinosa*: 27, terga 3-8; 28, sterna 5-7.



Figures 29-35. Mouthparts of mature nymph of *P. (P.) barriai* (29-30, 32-35) and *P. (M.) vinosa* (31). 29, clypeus and labrum; 30-31, left mandibles; 32, outer incisor of right mandible, enlarged; 33, hypopharynx; 34, right maxilla, ventral; 35, labium, dorsal (left), ventral (right).

penes yellow with inner margin of lobes washed with brown; caudal filaments covered with short hairs.

Female subimago.—(in alcohol): Similar to male subimago except as follows: head pale yellow, markings as in female imago; color of antennae, ocelli and eyes as in female imago; bases of fore and hind wings light brown; fore legs shorter; abdominal sterna 8-9 whitish, markings as in female imago.

Mature nymph.—(in alcohol): Body length, 9.0-11.0 mm. Dorsum of head yellow to brown, venter pale; a pale yellow marking anterior to median ocellus and lateral to lateral ocelli; vertex with a pale yellow median stripe. Ocelli black. Eyes of female black; upper portion of male eyes reddish-gray, lower portion black. Scape and pedicel of antennae dark brown, flagellum paler. Mouthparts: clypeus with a pair of small submedian pale yellow spots; labrum with a transverse row of widely set hair near dorsoapical margin (Fig. 52); mandibles lack dorsal groove, or if present, shallow (Fig. 30); maxillary palpi unicolorous brown. Thoracic nota brown with pale yellow markings similar to Fig. 47-48; sterna pale yellow. Legs: dorsum brown, venter pale except tibiae and tarsi brown; tibiae with broad transverse median and apical yellow bands; tarsi with a broad basal and apical yellow bands; dorsum of femora with spatulate setae (Fig. 54); tarsal claws with apical denticles larger than others (Fig. 37). Abdomen: terga brownish-yellow with dark brown to black maculae similar to imagos; terga 1-8 with a pair of median pale yellow spots, and a small anterolateral spot; hairlike setae on posterior margin of abdominal terga approximately 2x as long as spines (Fig. 57); posterolateral spines occur on segments 8-9, well developed (Fig. 42). Sterna pale yellow, markings as in imagos but not as pronounced. Gills: membrane grayish white, tracheae black; lamellae apically terminated in a filamentous process (Fig. 39). Caudal filaments: consist of 2 pale yellow segments alternated with brown segment; a narrow reddish-brown to dark brown band on alternate articulations; apical hairs thick and long (Fig. 45).

Geographic Distribution.—(Fig. 69). *Penaphlebia chilensis* is widely distributed and has been collected from Chiloé north to Choapa Province, Chile and east to the Andean Range of southern Argentina (Fig. 69).

Type specimens and deposition.— Holotype male I, Chile (exact locality unknown). Paratype male S, locality same data as in holotype, BMNH.

Additional specimens examined.— CHILE: *Arauco Prov.*, I (male), Pichinahuel, Cord. Nahuelbuta, I. 1959, LEP. *Bío Bío Prov.*, (female), 5 km W Tucapel, 28.XII. 1951, ESR & AEM; N, Río Mulchen, Mulchen, 130 m, 8.XII.1963, GFE; N, I (male, female, R), trib. of Río Bío Bío, Santa Bárbara, 6/8.XII. 1972, MLP & LEP; I (male, female), East. Huequecura, 25 km E. Sta. Bárbara, 24.I.1978, CM & OSF. *Cautín Prov.*, I (female), 10 mi. NE Pucón, 12.I.1951, ESR & AEM; N, 20 km E. Temuco, I.1951, ESR & AEM; N, I (male, female), Río Tolten, Villarica 250 m, 26.XI.1963, GFE; N, a small stream near Villarica, 26.XI.1963, GFE; I (female), Villarica, 25.XI.1963, GFE; N, Río Pedregoso, N Villarica, 235 m, 11.XII.1972, MLP & LEP; N, Río Claro, Pucón, 146 m, 10/11.XII.1972, MLP; N, a stream at Collileufu, 11.XII.1972, MLP. *Chiloe Prov.*, N, Río Butalcura, 16.XII.1972, MLP & LEP; N, Río Quichitúe, 16.XII.1972, MLP & LE. *Curico Prov.*, S (female), El Coigo, Cord. Curico, X.1959 LEP; N, S, I (male, female, R), Río Los Morongos, Bajo Los Morongos, 653 m, 21/22.XI.1972, MLP & GB; N, I (male, female, R), 825 m, 22.XI.1972, MLP. I (male) Cerro Nielol, Temuco, 9.II.1979, D & MD & BA. *Coquimbo Prov.*, N, Río Illapel, Sta. Virginia, El Bato, Hda. Illapel, Illapel, 18.XI.1972, MLP. *Linares Prov.*, N, S, I (male, female, R), Río Longavi, San Pablo, Parral, 425 m, 28.XI.1972, MLP & GB; N, S, I (male, female), Puente Malcho, 600 m, nr. Longavi River, 13/15.I.1979, D & MD & BA; I (male), Río Ancoa, 23.I.1978, PJS; N, near coastal stream 17.5 km S Curanipe, 25.I.1979, D&MD

& BA; *Llanquihue Prov.*, I (male), Los Muermos, 19.I.1951, ESR & AEM; S (male, female), Stream on Lanquihue, 15.XII.1957, JI. N, Río Gomez 6.I.1966, OSF & TC; I (male, R) Lago Llanquihue, Ensenada, 19/21. XII.1972, MLP & LEP; N, I (male, female, R), Río Petrohue nr. Lago Todos Los Santos, 18.XII.1972, MLP; N, I (male, female), Lago Todos Los Santos, Petrohue, 18.XII.1972, MLP, LEP & LE. *Malleco Prov.*, S (female), Angol, 31.XII.1950, ESR & AEM; I (male, female), Angol, 29.I. 1951, ESR & AEM; I (male, female), Angol, 29.I.1951, ESR & AEM; N, I (male), 10 km N Perquenco, 6.I.1951, ESR & AEM; S (female), a stream 15 km W Angol, 500 m, 17.II.1956, LEP; S (male, female) small stream near Victoria, 25.X.57, JI; N, Rucanuco, 3/13.I.1959, LEP; I (female), Lago Laguna, 23/25.I.1959, LEP; (male, female), Curacautin, 18.XII. 1959, LEP; I, S (male, female), Lago Galletue, 22.I.1962, LEP; N, I (male, female), Río Bío Bío ca. Marimenuco, 11.XII.1963, GFE; N, I (male, female), arroyo Pehuenco, trib. Río Bío Bío ca Marimenuco, 12. XII.1963, GFE; N, Río Lonquimay, 9.XII.1963, GFE; I (female), Angol, 22.XI.1964, R; N, S, I (male, female, R), Río Piquiquen, El Manzano, 35 km W Angol 600, 8/9.XII.1972, MLP; N, Río Dumo, 11 km N Victoria, 300 km. 25.I.1978, CM & OSF; N, Nahuelbuta Nat. Park, Cabreria, 12 m, 4.II.1979, D&MD & BA. *Nuble Prov.*, I (female), 40 km E San Carlos, 24.II.1950, ESR & AEM; I (male, female), Atacalco, Río Diguillin, 600 m, 25.I.1955, LEP; I (male, female), Río Niblinto, 35 km E Coihueco, 19.I.1968, LEP; N, I (male, female), Río Niblinto, Niblinto, 230 m, 25/26.XI.1972, MLP & GB; I (male, R), Cascada Las Trancas, Recinto, 1,120 m, 27.XI.1972, MLP; I (male, female), alto. Trequalemu, 500 m ca. 20 km, SE Chovellen, 26/27.I.1979, D&MD & BA. *Osorno Prov.*, I (male), Valley Forest, 18 km. W Purranque, 16.I.1951, ESR & AEM; I (male, female), a stream near Lago Puyehue, 17.XII.1957, JI & LEP; N, Río Rahue, 250 m, 20.XI.1963, GFE; N, Río Pescadero nr. Atilan, Puyehue, 12.XII.1972, MLP. *Santiago Prov.* N, I (male, female), a trib. of Río Mapocho, 1,000 m, 2.XI.1963, GFE; I (male, female), Río Arrayan, El Arrayan, 900 m, 2.XII.1963, GFE; N, El Canelo, 880 m, 4.XII.1963, GFE; N, Río Colorado, Los Maitenes, 4.XII.1963, GFE; N, estero Arrayan, 800-900 m, 12.XI.1972, MLP & LEP; N, I (male, R), El Canelo, 30.XI/2.XII.1972, MLP & GB; N, Melocoton, San Jose de Maipo, 2.XII.1972, MLP & GB; I (male), La Viluma, 350 m, SE Melipilla, 15/17.XII.1987, LEP. *Talca Prov.*, Los Cipreces, 1,000 m, 14.I.1968, LEP; N, I (male, R), Río Lircay, Alto Vilches, 800 m, 22.XI.1972, MLP & GB; N, Estero Vilches, Laguna de los Patos, Altos de Vilches, 1,000 m, 22/24.XI.1972, MLP & GB; N, Río Lircay, 11 km N Talca, 85 m, 23.I.1978, CM & OSF, PJS. *Valdivia Prov.*, I (male), Calle Calle nr. Valdivia, 4.X.1957, JI; S (male, female), Río Calle Calle, 12.X.1958, WB; S (female), stream nr. Valdivia, 11.IX.1958, 1958, WB; I, [Lago] Pillaiifa mountain brook [39°36'; 71°58' W, ~600 m], 20.II.1958, JI. ARGENTINA. *Chubut Prov.*, I (male, female), Río Epuyén, Hoyo de Epuyén, 10.II.1974, OSF; N, Arroyo Golondrinas, 6 km N Lago Puelo 8.II.1974, OSF. *Neuquén Prov.*, N, Lake Lolog, 29.III.1957, SSS. N, Pucara, 1/10.IV.1957, SSS; I (male), a small stream nr. Neuquen, 20.XI.1958, JI; N, I (male, female), Lago Tromen, Lanin, 9.II.1962, IR; N, I (male), Río Quilquihue, Lago Lolog, 22/23.I.1974, OSF; N, Río Totoral, 24 km NW Villa La Angostura, 20.II.1978, CM & OSF; N, Río Alumine, 5km N Aluminé, 27.II.1978, CM & OSF; N, Arroyo del Gato, 8 km 5 Rahue, 2.III.1978, CM & OSF; I (male, female), West shore of Lago Huechulafquen, 3.12.84, TC; I (female), cascada 6 km N Lago Aluminé, 1100 m, 3.II.1987, CM & OSF. *Río Negro Prov.*, N, Lago Nahuel Huapi, San Carlos de Bariloche, 25/27.XII.1972, MLP; N, Cascada Mallin Ahogado, El Bolson, 9.II.1974, OSF.

Discussion.— Eaton (1883) described *P. chilensis* from a male imago and a male subimago collected from an unknown locality in Chile. Demoulin (1955) subsequently redescribed the male imago, and at the same time described the female imago. The species is herein redescribed based on a large series of recently collected and reared specimens from

Chile and Argentina, including the specimens that Demoulin used to describe the imagos. The nymph and female subimago are described for the first time. The nymph and adults of *P. chilensis* collected from Osorno southward to Chiloé Province, Chile, including those from Argentina are generally darker than the specimens from the northern provinces; the abdominal maculae are almost black, and the dark colored legs of the nymphs make the pale yellow markings more pronounced. The sternal abdominal maculae of the adults from the southern provinces appear to have a more elaborate pattern (Fig. 22) than the northern population (Fig. 21).

The nymphs from Lago Todos Los Santos and neighboring streams (Llanquihue Province) have smaller pale spots on the thoracic nota (Fig. 48) than the ones collected from other areas (Fig. 47).

Penaphlebia chilensis can be distinguished from the other species of the genus by the following combinations of characters. In the imagos: (1) costal and subcostal cross veins of male and female fore wings are well developed and thickly infuscated with dark brown (Fig. 1,3); (2) segment 3 of male protarsi is longer than segment 4; (3) maculae on the abdominal terga 1-3, 6-7, and 9 are pronounced, with submedian maculae on terga 8 slightly extended beyond half length of segment (Fig. 20), (4) angular bend on the inner margin of segment 1 of genital forceps is moderately developed (Fig. 11); (5) styliger plate has a broad Ushaped posteromedian emargination (Fig. 11); and (6) shape of apex of penis lobes is similar to Fig. 9, with the subapical spine posterolaterally projecting. In the nymph: (1) labrum has a transverse row of widely set hairs near its dorsoapical margin (Fig. 52); (2) mandibles lack a dorsal groove, or if present, it is shallow (Fig. 30); (3) apical denticles of tarsal claws larger than middle ones (Fig. 37); (4) hair-like setae on the posterior margins of abdominal terga approximately two times as long as the spines (Fig. 57); (5) posterolateral spines occur on abdominal segments 8-9 and well developed (Fig. 42); (6) gill lamellae apically terminated in a filamentous process (Fig. 39); and (7) caudal filaments have thick and long apical hairs (fig 45).

Penaphlebia chilensis appears most closely related to *P. barriai* but can be distinguished from it by any of the following characters: (1) nymphs and adults have pronounced maculae on abdominal terga 1-3, 6-7, and 9; (2) shape of penis lobes is similar to Fig. 9; and (3) apical denticles of nymphal tarsal claws are larger than the middle ones (Fig. 37).

Biology.—The nymphs of *P. chilensis* occur in lake shores, streams and rivers. Most of the nymphs were collected under medium sized rocks exposed to moderately swift current, and some in debris trapped between rocks. Reared nymphs spend the day under stones, and crawl to the surface at night. The nymphs apparently are not good swimmers because upon release into the rearing cages they slowly settled into the bottom, and immediately crawled and attached themselves underneath the stones.

The nymphs have been collected from October to March and the adults from October to March. Adult emergence has never been observed in the field but reared specimens emerged anytime during the day, mostly between 1600 and 1800 hours.

Penaphlebia chilensis has been collected at an altitude ranging from 50 m to 1,100 m above sea level.

Dissected nymphs revealed the major gut contents as detritus (52.90%), mineral particles (42.45%), diatoms (3.38%) and filamentous algae (1.27%). The identified diatoms include the genera *Navicula*, *Nitzschia*, and *Synedra*.

Penaphlebia (Penaphlebia) exigua Dominguez and Pescador

Penaphlebia exigua Dominguez and Pescador, 1983: 21, Fig. 1-11 (male imago, nymph).

Male imago.— (in alcohol). Length: body 6.4-6.9 mm, fore wings 6.5-7.0 mm. Head yellow. Scape and pedicel of antennae pale yellow, flagellum paler. Ocelli greyish-white, black at base. Upper portion of eyes beige, lower portion greyish-black. Thorax: nota light brown, pronotum paler with margins black and 2 pairs of longitudinal submedian black stripes. Pleura and sterna light brown. Wings: membrane of fore and hind wings hyaline, yellowish at extreme base; longitudinal and cross veins yellowish brown, vein C, Sc and R_1 of fore wings darker; vein MP_2 of at least one of fore wings attached at base to vein CuA; pre-pterostigmatic cross veins weakly developed; hind wings moderately narrow and elliptic (Fig. 5). Legs: yellow with coxae, trochanters, tibio-femoral joints, and tarsal joints light brown; femora with faint transverse black median band; segment 3 of protarsi longer than segment 4. Abdomen: terga translucent yellow with pronounced black maculae on terga 1-9 (Fig. 17), submedian maculae on terga 8 extended beyond basal half of segment. Sterna yellow with faint black marking near anterolateral corners. Genitalia (Fig. 12): forceps pale yellow, segment 1 faintly washed with brown, pronounced on inner lateral margin; angular bend moderately developed, slightly denticulate (Fig. 12), segments 2 and 3 subequal length. Styli-ger plate with V-shaped posteromedian emargination (Fig. 12). Penes pale yellow; penis lobes as in Fig. 12, subapical spine stubby, posterolaterally projecting. Caudal filaments: pale yellow, apical 1/3 of basal segments brown, brown portion progressively broader distally until filaments consist of alternating pale yellow, and light brown segments.

Female imago.— (in alcohol). Length: body 7.7 mm, fore wings 8.0 mm. Similar to male imago except as follows: eyes black; longitudinal and cross veins of fore and hind wings brown; costal and subcostal cross veins of fore wings a little more developed.

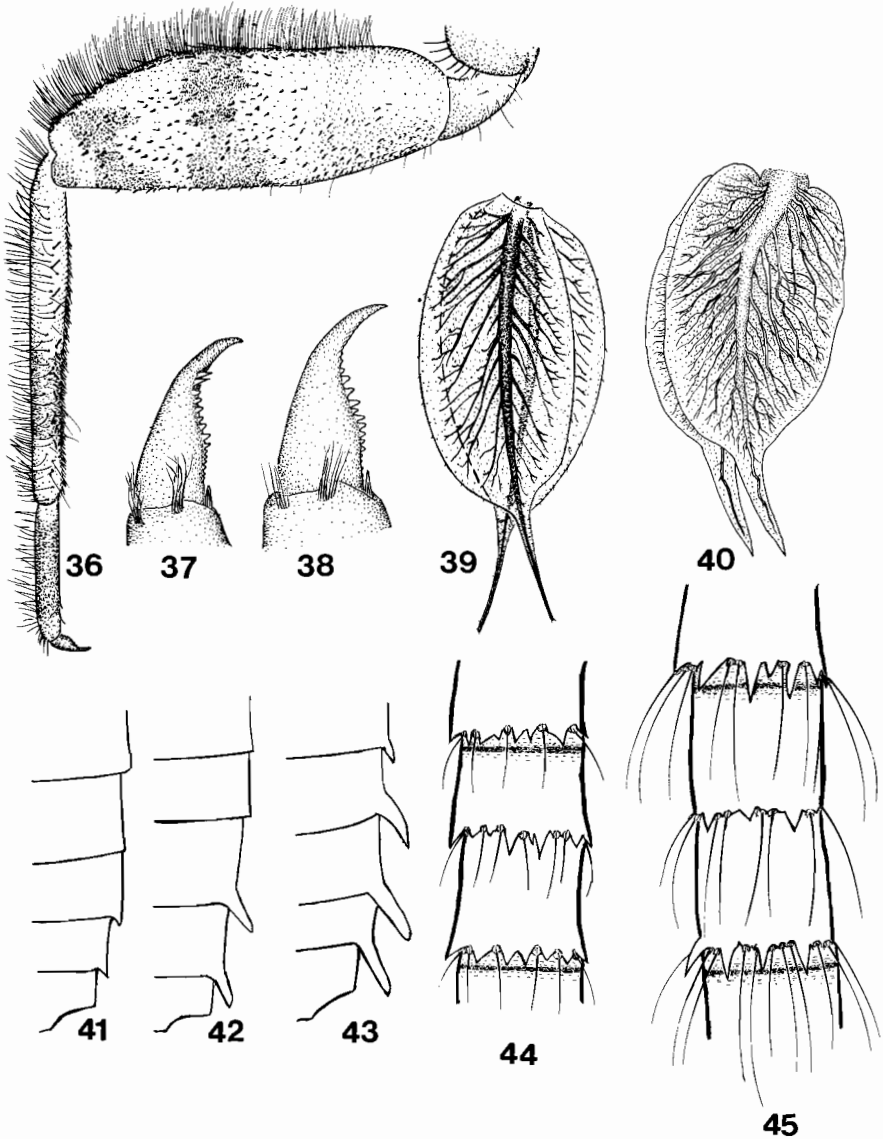
Male subimago.— (in alcohol). Similar to male imago except as follows: head including pronotum dusty yellow; wings pale yellow, margins darker, apical and anal margins with hairs; caudal filaments covered with short hairs.

Female subimago.— Unknown.

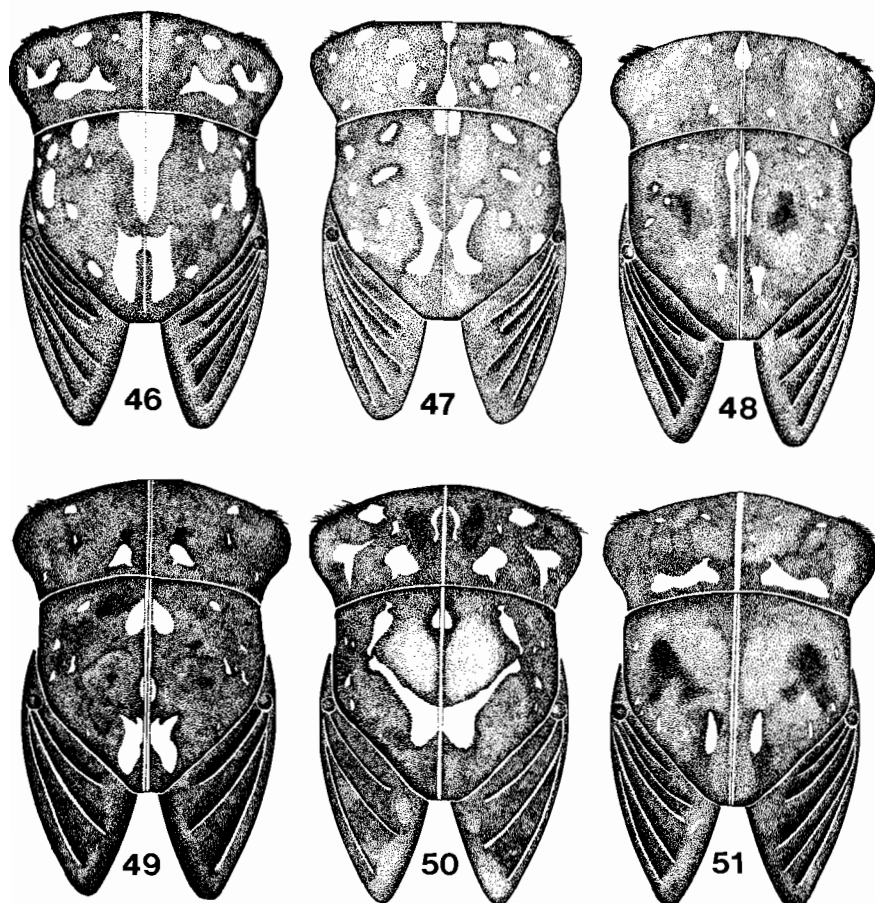
Mature nymph.— (in alcohol). Body length 6.9-7.2 mm. Dorsum of head light brown, venter pale; a pale yellow marking anterior to median ocellus and lateral to lateral ocelli. Ocelli black. Eyes of female black; upper portion of male eyes orange brown, lower portion black. Scape and pedicel of antennae brown, flagellum paler. Mouthparts: clypeus without yellow spots; labrum with a transverse row of closely set hair near dorsoapical margin (Fig. 53); mandibles lack dorsal groove, or if present, shallow (Fig. 30); maxillary palpi unicolourous yellow. Thorax: nota light brown with inconspicuous pale yellow spots, sterna paler. Legs: light brown; femora with transverse median and apical dark brown bands; tarsal claws with middle denticles larger than apical ones (Fig. 38). Abdomen: terga yellowish-brown with black maculae as in imagos; terga 2-7 with mid-sublateral pale yellow spot; spines on posterior margin of terga subequal in length with hair-like setae (Fig. 59); posterolateral spines on segments 8-9, weakly developed (Fig. 41). Sterna pale yellow, anterior margin brownish. Gills: membrane grayish-white; tracheae black; lamellae apically terminated in a filamentous process. Caudal filaments: brownish with dark shiny brown annulation on every other joint; apical hairs thin and short (Fig. 44).

Geographic distribution.— (Fig. 71): *Penaphlebia exigua* has only been collected in Rincon de Asconape, 70 km S Valcheta, Río Negro Prov., Argentina (Fig. 71).

Type specimens and deposition.— Holotype male I, allotype female I, Rincon de Asconape, 70 km S Valcheta, 27.II.1980, WEA, FML. Paratypes, same data as holotype, FML, FAMU.



Figures 36-45. Structures of mature nymph of *Penaphlebia*. **36**, fore leg of *P. (P.) barriai*. Fore claws: **37**, *P. (P.) chilensis*; **38**, *P. (M.) flavidula*. Abdominal gill 4: **39**, *P. (P.) barriai*; **40**, *P. (M.) vinosa*. Abdominal terga 6-10: **41**, *P. (P.) exigua*; **42**, *P. (P.) chilensis*; **43**, *P. (P.) vinosa*. Setation of caudal filaments: **44**, *P. (P.) flavidula*; **45**, *P. (P.) barriai*.



Figures 46-51. Pattern of spots on thoracic nota of mature nymph of *Penaphlebia*. 46, *P. (P.) barriai*; 47-48, *P. (P.) chilensis*; 49, *P. (P.) flavidula*; 50, *P. (P.) fulvipes*; 51, *P. (M.) vinosa*.

Discussion.— Except for the type material, no additional specimens of *P. exigua* have been collected. The description of the species by Dominguez and Pescador (1983) is included herein with minor modifications for purposes of comparative descriptions of all known species of the genus.

Immature nymphs of *P. exigua* have no markings on the abdominal sterna while mature ones have brownish markings on the anterior margin of each sternite. Additionally, male nymphs have more developed posterolateral spines on abdominal segments 8-9 than the female nymphs. Except for three imagos which have the base of vein MP_2 of one of the fore wings attached by a cross vein to vein MP_1 , the rest have vein MP_2 of both fore wings basally attached with vein CUA (Fig. 2).

Penaphlebia exigua can be distinguished from the other species of the genus by the following combination of characters. In the imagos: (1) pre-pterostigmatic costal and subcostal cross veins of male and female fore wings are weakly developed and non-infuscated (Fig. 2,4); (2) segment 3 of male protarsi is longer than segment 4; (3) maculae on the abdominal terga are pronounced on all segments and similar to fig. 17; (4) angular bend on inner margin of segment 1 of genital forceps is moderately developed and weakly denticulate (Fig. 12); (5) styliger plate has a V-shaped posteromedian emargination (Fig. 12); and (6) shape of penis lobes is similar to Fig. 12, with stubby subapical spines posterolaterally projecting (Fig. 12). In the nymph: (1) small body size (body length: male 6.4-6.9 mm, female 7.7 mm); (2) mandibles lack a dorsal groove, or if present, it is shallow (Fig. 30); (3) middle denticles on tarsal claws are larger than the apical ones (Fig. 39); (4) hair-like setae on posterior margin of abdominal terga are shorter or equal to length of spines (Fig. 59); (5) posterolateral spines occur on abdominal segments 8-9, and weakly developed (Fig. 41); and (6) caudal filaments have short and thin apical hairs (Fig. 44).

Biology.— The nymphs of *P. exigua* were collected in a small stream in Somuncura Plateau which supported a thick growth of *Nostoc* and moss. The vegetation along the stream bank of the collection site included thick growths of *Cortaderia speciosa* Nees, *Samolus valerandi* (L.), *Cynodon dactylulum*, *Agrotis* sp., and ferns.

***Penaphlebia* (*Penaphlebia*) *flavidula* new species**

Male imago.—(in alcohol). Length: body 11.0-14.0 mm, fore wings 11.0-15.0 mm. Head yellow. Scape and pedicel of antennae brown, flagellum paler. Ocelli greyish-white, black at base. Upper portion of eyes orange yellow, lower portion greyish-black. Thorax: nota yellow, pronotum paler, margins black with 2 pairs of longitudinal black stripes; parapsidal furrows, and posterior 1/2 of scutellum washed with black. Pleura yellow with broken black markings between procoxae and metacoxae. Sterna yellow to light brown, faintly washed with black; metasternum with transverse dark brown median band. Wings: membrane of fore and hind wings hyaline, base, and costal and subcostal membranes of fore wings flushed with brownish-yellow; longitudinal and cross veins of both wings brown except veins C, Sc, and R_1 pale yellow; pre-pterostigmatic costal and subcostal cross veins of fore wings weakly developed (Fig. 4); hind wings elliptic (Fig. 5). Legs: yellow, femora and tibiae darker; femora with dark brown median and apical bands; segment 3 of protarsi longer than segment 4. Abdomen (Fig. 15-16): terga pale yellow, posterior margins black; dark brown to black maculae pronounced on terga 1-9, pattern similar to Fig. 15; with submedian maculae on tergite 8 extended beyond half length of segment, usually almost to posterior margin of segment (Fig. 15). Sterna yellow with small dark brown maculae on sterna 1-7 similar to Fig. 16. Genitalia (Fig. 10): genital forceps brown; angular bend on inner margin of segment 1 moderately developed, denticulate similar to Fig. 11; segment 3 of forceps approximately 5/

6 length of segment 2. Styliiger plate with broad and shallow U-shaped posteromedian emargination as in Fig. 11. Penes yellow, inner margins usually washed with brown; penis lobes as in Fig. 10, subapical spine stubby, posterolaterally projecting. Caudal filaments: pale yellow, black at base with dark brown to black bands at joints, bands progressively broader and paler distally.

Female imago.—(in alcohol). Length: 11.0-15.0 mm, fore wings 13.0-18.0 mm. Similar to male imago except as follows: head with branched black stripes near anterior base of eyes; eyes black; costal and subcostal membranes of fore wings more intensely flushed with brownish-yellow; costal and subcostal cross veins of fore wings a little more developed and faintly infuscated with dark brown; tarsi dark brown; abdominal terga opaque yellow.

Male subimago.—(in alcohol). Similar to male imago except as follows: head dull yellow; membrane of fore and hind wings whitish, yellowish at base, margins darker; brown shadings around cross veins of fore wings; fore legs slightly longer than meso- and metathoracic legs; abdomen opaque yellow; genital forceps and penes yellow, margins washed with brown; caudal filaments covered with short hairs.

Female subimago.—(in alcohol). Similar to male subimago except as follows: head pale yellow covered with whitish granulations; color of ocelli and eyes as in female imago; costal and subcostal membranes of fore wings brownish-yellow and cross veins faintly shaded.

Mature nymph.—(in alcohol). Body length 10.0-15.0 mm. Dorsum of head dark brown, venter pale yellow; a small pale yellow spot anterior to median ocellus and lateral to lateral ocelli. Ocelli black. Eyes of female black; upper portion of male eyes blackish-red, lower portion black. Scape and pedicel of antennae brown, flagellum paler. Mouthparts: labrum with a transverse row of closely set hairs near dorsoapical margin (Fig. 53); mandibles lack dorsal groove, or if present, shallow (Fig. 30); segments 1 and 2 of maxillary palpi dark brown, segment 3 yellow. Thorax: nota brown with black linings and pale yellow spots (Fig. 49). Sterna pale yellow. Legs: brownish-yellow; venter paler; tarsi brown except extreme base yellow; tibiae brown with basal third paler; femora with median and apical black bands; dorsum of femora with ovate setae (Fig. 55); middle denticles on tarsal claws equal to or larger than apical denticles (Fig. 38). Abdomen: yellowish brown with dark brown to black maculae similar to adults; terga 4-5 and 7-8 with broad pale yellow spot; hairlike setae on posterior margin of abdominal terga subequal length with spines (Fig. 59); posterolateral spines on segments 8-9, and well developed (Fig. 42). Sterna whitish to pale yellow. Gills: membrane greyish-black, tracheae black; lamellae apically terminated in a filamentous process (Fig. 39). Caudal filaments: brown, distal two-thirds with narrow dark brown annulations at joints; apical hairs short and thin (Fig. 44).

Geographical Distribution.—(Fig. 70). Holotype male imago, CHILE: *Llanquihue Prov.*, Río El Canelo, Hornohuino, 22/23.XII.1972, M. L. Pescador and L. E. Peña; allotype, female imago, same data as holotype. Paratypes, CHILE: 2 female imagos and 200 nymphs, same data as holotype. *Aisén Prov.*, 1 male subimago, Pto. Aisen, 24/25.I.1961, LEP; 1 nymph, Pto. Cisnes, II.1961, LEP; 1 female subimago Lago Risopatron, 17 km N Puyuhuapi, 24.I.1987, CM & OSF. *Arauco Prov.*, 1 female subimago, Pichinahuel, Cord. Nahuelbuta, I.1959, LEP; 1 female subimago, Caramavida, 31.I.1967, LEP. *Bío Bío Prov.*; 1 female subimago, 7 nymphs, trib. Río Bío Bío, Santa Barbara, 6/8.XII.1972, MLP & LEP. *Cautín Prov.*, 1 male subimago (R), 4 nymphs, Río Claro, Pucón, 140 m, 10/11.XII.1972, MLP & LEP; 3 nymphs, a stream at Collileufu, 11.XII.1972, MLP; *Chiloé Prov.*, 14 nymphs, small stream in Dalcahue, 16.XII.1972, MLP & LEP; 25 nymphs, Río Butalcura, 16.XII.1972, MLP & LEP; 2 male imagos, 2 male & female subimagos, 30 nymphs, Río Quichitue, 16.XII.1972, MLP & LEP. *Concepción Prov.*, 7 nymphs, Fundo Pinares, [about 10 km E Concepción on southside of Río Bío Bío], 30.XII.1965, OSF & TC. *Linares Prov.*, 1 female

imago, Fundo Malcho, Cord. Parral, X.1956, LEP; 3 nymphs, Romehual, Parral, 5/10.XI.1960, LEP; 5 nymphs, Río Longavi, San Pablo Parral, 425 m, 28.XI.1972, MLP. *Llanquihue Prov.*, 2 nymphs, a small stream near Parga, 15.XII.1972, MLP; 2 male & female imagos, 2 male & female subimagos (R), 66 nymphs, Río Peñon, Maullin, 17.XII.1972, MLP; 7 nymphs, a small stream 1 km E El Jardín, Maullin, 17.XII.1972, MLP; 10 nymphs, a small stream 15 km. SW Las Quemadas, 17.XII.1972, MLP; 2 male & female imagos, 30 nymphs, Río Correntoso, Hornohuínco, Correntoso, 22.XII.1972, LEP; 1 male subimago (R), Estero Hornohuínco, Correntoso, 21.XII.1972, MLP; 33 nymphs, Río Tenio, 3 km W Lago Tenio, 23.XII.1972, MLP; 25, nymphs, an estero 1 km N Río El Canelo on road to Lago Chapo, 23.XII.1972, MLP. *Malleco Prov.*, 1 nymph, Río Lonquimay, Lonquimay, 9.XII.1963, GFE; 2 male imagos, Estero nr. Lonquimay, 8.XII.1963, GFE: nymph, 30 km E. Victoria, 8.XII.1963, GFE; 2 nymphs, Río Manzanares [~ 10 km W Purén], 2.I.1966, OSF & TC; 2 female subimagos (R), 20 nymphs, Río Piquiquén, El Manzano, 35 km W Angol, 600 m, 8/9.XII.1972, MLP; 13 nymphs, Nahuelbuta Nat. Park nr. Los Gringos Camp, 29.I/5.II.1979, D&MD & BA. *Maule Prov.*, 2 nymphs, between Chovellen and Tregualemu, 24.I.1967, LEP. *Nuble Prov.*, 20 nymphs, near coastal stream, 17.5 km 5. Curanipe, 50 m, 25.I.1979, D & MD & BA. *Osorno Prov.*, 2 nymphs, Lago Puyehue, 16.II.1957, LEP; 2 female imago, Río Golgol nr. Puyehue, II.1957, LEP; 5 male imagos, 11 nymphs, a small stream nr. Termas de Puyehue, 22.XI.1963, GFE; 1 nymph, Río Pedregoso, 80 km N Victoria, 28.XI.1963, LEP; 1 female subimago (R), Río Chanlelfú, 300 m, 22.XI.1963, GFE; 4 nymphs, a small stream 1 km SE Río Chanlelfu, Puyehue, 12.XII.1972, MLP & LEP; 7 nymphs, Río Pescadero nr. Antillanca, 12.XII.1972, MLP; 20 nymphs, Río El Gringo Park, Puyehue, 1,075 m, 13.XII.1972, MLP; 2 nymph, Río Golgol, Puyehue, 13.XII.1972, MLP; 7 nymphs, Río Chanlelfú, Puyehue, 11/12.XII.1972, MLP; Chanlelfú, Puyehue, 500m, 11/12.XII.1972, MLP; 1 nymph, Estero El Gringo, 13.II.1976, CM & OSF; 4 nymphs, Pucatrihue, 26.I.1978, PJS; 3 nymphs, Pucatrihue at Puente Hermoso, 20.I.1978, PJS; 20 nymphs, Pucatrihue, 26/30.I.1978, CM & OSF; 14 nymphs, Pulamemo, E. Bahía Mansa, 30.I.1978, CM & OSF; 2 nymphs, P. N. Puyehue, Río Pescadero, 2. II.1978, CM & OSF; 12 nymphs, P. N. Puyehue, Salto del Indio, 1/12.II.1978, CM & OSF; 6 nymphs, P. N. Puyehue, Aguas Calientes, 6.II.1978, CM & OSF; 7 nymphs, Puyehue Nat. Park, Aguas Calientes, 1065 m, 8.II.1978, CM & OSF & PSJ; 1 male subimago, 3 male imagos, P.N. Puyehue, 2 km S Aguas Calientes, 10/22.II.1979, D&MD & BA. *Talca Prov.*, 1 female subimago (R), 13 nymphs, Río Lircay, Alto Vilches, 800 m, 22.XI.1972, MLP. *Valdivia Prov.*, 1 male & female imago, 30 km S Valdivia, 13.I.1951, ESR & AEM; 3 nymph, Fundo Walper, Punucapa, 20.XI.1957, JI; 1 female imago, mountain stream, Lago Pellaifa, 22.I.1958, JI. 1 nymph, Fundo Walper, Punucapa, 3.XI.1957, JI; 1 male imago, 7 male subimago, 5 female subimago, Rincon de Piedra, 30 m, ca. 20 km. SE Valdivia, 24/25 I. 1979, D & MD & BA. ARGENTINA: *Chubut Prov.*, 20 nymphs, Ao. Golondrinas, 6 km N Lago Puelo, 8.II.1974, OSF. *Neuquen Prov.*, 5 nymphs, Pucara, 1/10.IV.1957, SSS; 2 nymphs, 2 km SE Lago Lolog, 22.I.1974, OSF; 1 female imago, 15 nymphs, Ao. Rosales, nr. 5. M. d. 1. Andes, 22.I.1974, OSF; 5 nymphs, 5 km SE Lago Huechulafquén, 26.I.1974, OSF; 15 male imagos, Estacion Forestal, Pucará, 28/29.I.1974, OSF; 9 nymphs, Río Totoral, 24 km NW Villa La Angostura, 20.II.1978, CM & OSF; 42 nymphs, Los Totoros, 23 km NW Villa La Angostura, 20.II.1978, CM & OSF; 6 nymphs, 1 male imago, 2 female imagos, Trib. arroyo Trompul, W S.M. d. 1. Andes, 23. II.1978, CM & OSF; 5 nymphs, Yuco, W S.M. d. 1. Andes, CM & OSF. *Río Negro Prov.*, 20 nymphs, 5 km 5 Río Villegas, 7.II.1974, OSF; 1 female imago, Río Quemquemtrey, El Bolson, 7.II.1974, OSF.

The nymphs and adults are associated by rearing. All types are preserved in alcohol. Types are deposited as follows: holotype, allotype, 16 male and 8 female imaginal, 4 male and 8

female subimaginal, and 480 nymphal paratypes, FAMU; 1 male and 1 female imaginal, and 20 nymphal paratypes, CAS; 20 male and 7 female imaginal, 8 male and 5 female subimaginal and 200 nymphal paratypes, USNM.

Etymology.— *flavidus*, 1. meaning yellow.

Discussion.— The general coloration of *P. flavidula* exhibits a geographic pattern similar to *P. chilensis*. Specimens collected from Malleco Province, Chile, southward, including those from Argentina are generally darker than those from the northern provinces. In fact the abdominal maculae of specimens collected from Llanquihue and Chiloé Provinces are almost black, as is true with the gills. The adults of *P. flavidula* have the abdominal sterna with a typical pattern of markings similar to Fig. 16; but a few specimens have a short midanterior dark stripe on sterna 1-9. This variation sporadically occurs throughout the distributional range of the species. Markings on the nymphal abdominal sterna are quite variable depending on maturity. Black wing pad nymphs basically have similar sternal markings as the adults. Fairly mature nymphs (7.0-9.0 mm, body length) usually have dark brown lines near the lateral margins on abdominal sterna 2-6 which are lacking in younger nymphs, while younger nymphs usually lack sternal markings.

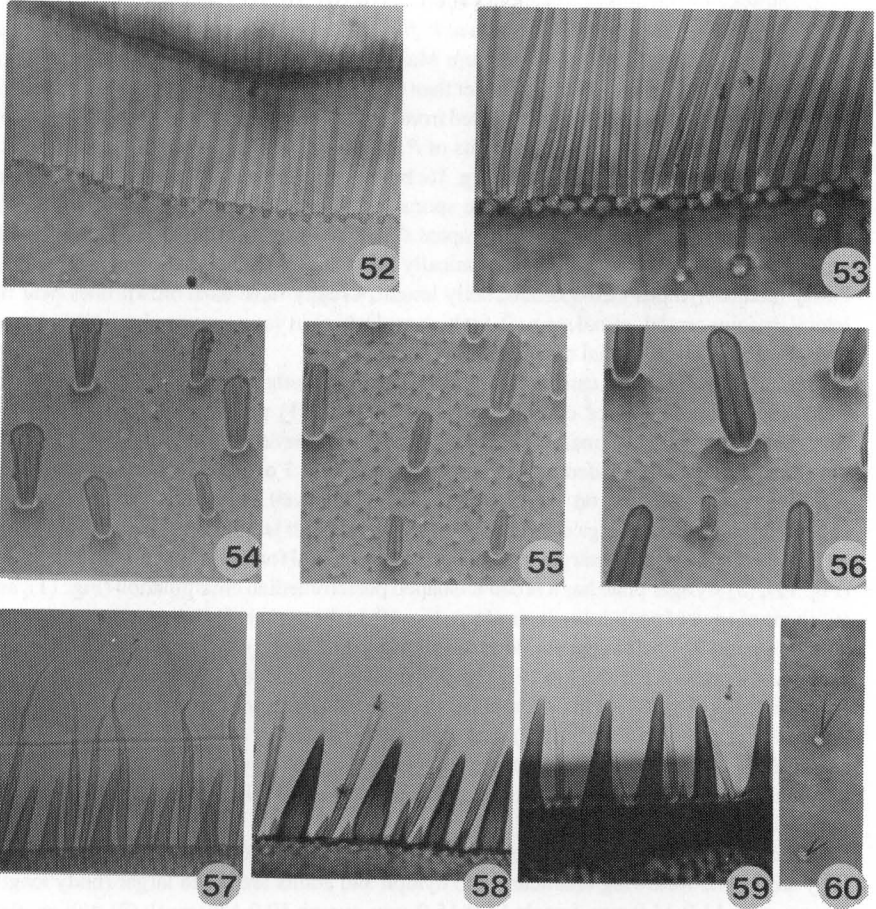
Penaphlebia flavidula can be distinguished from the other species of the genus by the following combinations of characters. In the imagos: (1) pre-pterostigmatic costal and subcostal cross veins of male fore wings are weakly developed (Fig. 4), a little more developed and faintly shaded in the female; (2) segment 3 of male protarsi is longer than segment 4; (3) maculae on the abdominal terga are well developed on all segments, submedian maculae on terga are extended well beyond half length of segment (Fig. 15); (4) angular bend on the inner margin of segment 1 of the genital forceps is moderately developed (Fig. 11); (5) styliger plate has a broad U-shaped posteromedian emargination (Fig. 11); and (6) shape of apex of penis lobes is similar to Fig. 10. In the nymph: (1) labrum has a transverse row of closely set hairs near its dorsoapical margin (Fig. 53); (2) mandibles lack dorsal groove, or if present, it is shallow (Fig. 30); (3) middle denticles of tarsal claws are larger than the apical ones (Fig. 38); (4) hair-like setae and spines on posterior margin of abdominal terga are subequal in length (Fig. 59); (5) posterolateral spines occur on abdominal segments 8-9, and are well developed (Fig. 42); (6) gill lamellae are greyish to black, and apically terminated in a filamentous process (Fig. 39); and (7) caudal filaments have short and thin apical hairs (Fig. 44).

Penaphlebia flavidula appears closely related to *P. exigua* but can be distinguished from it by any of the following characters: (1) nymph and adults are much larger (body length: imago, male 11.0-14.0 mm, female 11.0-15.0 mm; nymph 10.0-15.0 mm); (2) styliger plate has a broad U-shaped posteromedian emargination (Fig. 11); (3) abdominal gills are dark gray to black; and (4) posterolateral spines occur on abdominal terga 8-9 and are well developed (fig.42).

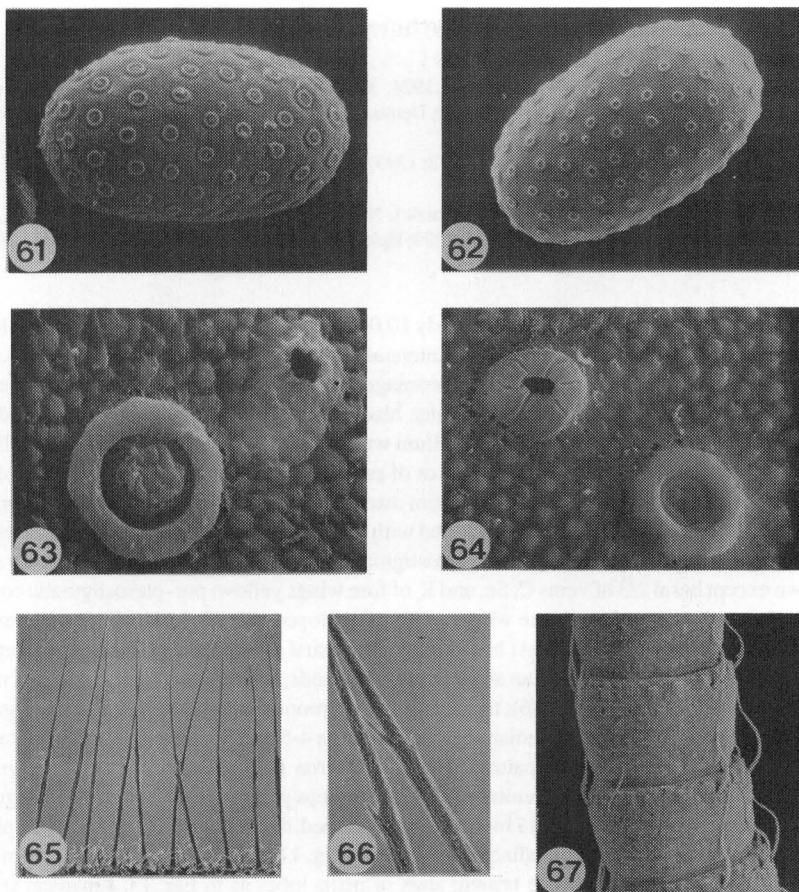
Biology.— The nymphs of *P. flavidula* occur in a wide variety of habitats, from small streams to large rivers and lake shores as well. One of us (MLP) collected nymphs from various types of substrates which include small rocks, debris trapped between rocks, submerged logs and floating roots of vegetation along stream or river banks. The nymphs were collected mostly under small rocks in moderately swift current.

The nymphs and adults of *P. flavidula* have been collected from November to March. The emergence and swarming of adults have never been observed in the field although reared adults emerged between 0700 and 1000 hrs. The nymphs have been collected at altitudes ranging from 50 m to 1,075 m above sea level.

Dissected nymphs revealed the major gut contents as detritus (65.89%), mineral particles (18.70%), diatoms (5.07%) and filamentous algae (10.14%). Identified diatoms include the



Figures 52-60. Photomicrographs of structures of mature nymph of *Penaphlebia*. Setae near apical margin of labrum: 52, *P. (P.) barriai*; 53, *P. (P.) flavidula*. Dorsal setae of femora: 54, *P. (P.) barriai*; 55, *P. (P.) fulvipes*; 56, *P. (M.) vinosa*. Spines and setae of posterior margin of abdominal terga: 57, *P. (P.) barriai*; 58, *P. (P.) fulvipes*; 59, *P. (P.) falvidula*. 60, dorsal setae of abdominal terga, *P. (P.) chilensis*.



Figures 61-67. Scanning electron micrographs of eggs (61-64), hairs on apical and anal margins of subimaginal fore wing (65-66) and nymphal antenna (67). *P. (P.) chilensis*: **61**, egg (600X); **63**, micropyle (6000X). *P. (M.) vinosa*: **62**, egg (540X); **64** micropyle (5600X). **65-66**, subimaginal hairs of *P. (P.) chilensis*. **67**, setae of nymphal antenna of *P. (P.) chilensis*.

genera *Eunotia* and *Navicula*. The filamentous algae include the genus *Oedoqonium*.

Penaphlebia (Penaphlebia) fulvipes (Needham and Murphy)

Atalophlebia fulvipes Needham and Murphy, 1924: 34, pl. 8 Fig. 96, 98; Lestage, 1930: 249; [not Lestage, 1931: 52 (male; Traver, 1946: 420; Demoulin: 1955a: 9, Fig. 3 (male); Demoulin, 1955b: Fig. 1b (male).

Penaphlebia fulvipes Peters and Edmunds, 1972: 1399; Hubbard, 1982: 266; Dominguez and Pescador, 1983: 21.

Atalophlebia sepia Thew, 1960, 130, Fig. 7 (male), NEW SYNONYMY.

Penaphlebia sepia Peters & Edmunds, 1972: 1399; Hubbard, 1982: 266; Dominguez & Pescador, 1983: 21.

Male imago.—(in alcohol). Length: body 10.0-12.0 mm, fore wings, 10.0-14.0 mm. Head brownish-yellow. Scape and pedicel of antennae reddish-brown, flagellum yellow. Ocelli white, black at base. Upper portion of eyes orange yellow, lower portion black. Thorax: nota dark yellow, pronotum paler except margins black, with 2 pairs of anteriorly fused median stripes; furrows and posterior 1/3 of scutellum washed with dark brown. Pleura dark yellow with broken black markings between bases of procoxae and metacoxae. Sterna brownish-yellow with anterior 1/2 of mesobasisternum usually washed with black. Wings: membrane of fore and hind wings hyaline, base washed with brown; costal and subcostal membranes of fore wings faintly flushed with yellow pterostigma cloudy white; longitudinal and cross veins brown except basal 2/3 of veins C, Sc, and R, of fore wings yellow; pre-pterostigmatic costal and subcostal cross veins of fore wings weakly developed (Fig. 4); hind wings moderately narrow and elliptic (Fig. 5). Legs: brownish-yellow, tarsi paler, distal portion of segment 5 brown; femora with broad median and apical black bands; segment 3 of protarsi longer than segment 4. Abdomen (Fig. 23-26): terga yellow with pronounced black maculae on terga 1-3, 6-7 and 9 (Fig. 23, 25); submedian maculae on terga 4-5 and 8 reduced, maculae on terga 1-3 dorsally forming circular pattern (Fig. 23). Sterna pale yellow with faint brownish maculae similar to Fig. 24, 26. Genitalia (Fig. 13): forceps yellow, paler toward apex; angular bend on inner margin of segment 1 moderately developed, denticulate (Fig. 11). Styliiger plate with broad U-shaped posteromedian emargination (Fig. 11). Penes yellow, inner margins of penis lobes faintly washed with brown; apex of penis lobes as in Fig. 13; subapical spine stubby and posterolaterally projecting. Caudal filaments: filaments consist of a unicolorous pale yellow segment alternating with a bicolorous pale yellow and brown segment, brown portion of segments progressively broader and paler distally; first few basal segments washed with brown.

Female imago.—(in alcohol). Length: body 10.0-13.0 mm, fore wings 12.0-14.0 mm. Similar to male imago except as follows: head with black submedian margins on vertex and a branched dark brown stripe near anterior base of compound eyes; eyes black; costal and subcostal membranes of fore wings more intensely flushed with yellow, cross veins a little more developed, faintly infuscated with brown; abdominal terga opaque yellow with maculae on terga 1-3 and 6-7 fused medially covering almost entire segment.

Male subimago.—(in alcohol). Similar to male imago except as follows: head dull yellow; membrane of fore and hind wings whitish, margins yellowish, brown shadings around cross veins particularly pronounced in fore wings; apical and anal margins of wings with hairs; fore legs slightly longer than meso- and metathoracic legs; abdomen opaque yellow; genital forceps and penes pale yellow; caudal filaments covered with hairs.

Female subimago.—(in alcohol). Similar to male subimago except as follows: head pale

yellow with brown submedian markings; color of ocelli and eyes as in female imago; costal and subcostal membranes of fore wings brownish-white, the rest of the membranes of wings including hind wings whitish; brown shadings around cross veins not as pronounced as in male wings.

Mature nymph.—(in alcohol). Body length 9.0-12.0 mm. Dorsum of head dark brown, venter pale yellow; a pale yellow spot anterior to median ocellus, lateral to lateral ocelli, and on vertex. Ocelli black. Eyes of female black; upper portion of eyes of male blackish-red, lower portion black. Scape and pedicel of antennae light brown, flagellum paler. Mouthparts: clypeus brown with a pair of pale yellow submedian spots; labrum with a transverse row of closely set hairs near dorsoapical margin (Fig. 53); mandibles lack dorsal groove, or if present, shallow (Fig. 30); maxillary palpi unicolorous brown. Thorax: nota brown with pale yellow spots, median spot on mesothorax broad, butterfly-like (Fig. 50); Legs: brownish-yellow, venter, and apex of tibiae paler; tarsi unicolorous, dark brown; femora with median and subapical pale yellow spots, particularly prominent on pro- and mesofemora; dorsum of femora with ovate setae (Fig. 55); 2 apical denticles on claws larger than middle denticles (Fig. 37). Abdomen: terga brownish-yellow, posterior margins dark brown to black; pattern of maculae as in adults, terga 4-5 and 8 with pale yellow spot; hair-like setae on posterior margin of abdominal terga equal to or slightly longer than spines (Fig. 58); posterolateral spines on terga 8-9, well developed (Fig. 42). Sterna yellow, markings as in adults. Gills: membrane greyish, tracheae black; lamellae apically terminated in a filamentous process (Fig. 39). Caudal filaments: brownish-yellow with narrow brown rings on alternate articulations; apical hairs thick and long (Fig. 45), subequal to or longer than length of segment.

Geographic Distribution.—(Fig. 72). The specimens of *P. fulvipes* that we have examined were collected from Valdivia southward to Ultima Esperanza Province, Chile, and eastward to the Andean region of Neuquén and Chubut Provinces, Argentina.

Type specimen and deposition.—Holotype, male I, Butalcura, *Chiloé Prov.*, CHILE, coll.

Additional specimens examined.—CHILE: *Aisén Prov.*, N, Río Simpson, Coihaique, 24.I.1958, JI; N, Manihuales, III.1961, LEP. *Chiloé Prov.*, N, Butalcura, 60 m, 27.I.1955, LEP; I (male, female), Dalcahue, II.1961, LEP; N, a small stream in Dalcahue, II.1961, LEP; N, Small stream in Dalcahue, 19.XII.1972, MLP & LEP; N, I (male, R), Río Butalcura, 16.XII.1972, MLP & LEP; I (male, female); N, I (male, female), Río Quichitue, 16.XII.1972, MLP & LEP. *Llanquihue Prov.*, I (male), Frutillar, 15.I.1950, JI; N, I (male, female), Río Maullin, 6.I.1966, OSF; 5 (male), Chamiza, 13.XII.1968, LEP; N, I, S (male, female, R), Río Peñon, Maullin, 17.XII.1972, MLP; N, I (female) a small stream 1 km SW Las Quemadas, 17.XII.1969; N, I (female), a stream 1 km E El Jardín, Maullin, 17.XII.1972; N, Río Petrohue nr. Lago Todos los Santos, 18.XII.1972, MLP. *Magallanes Prov.*, N, I. Mornington, Pto. Alert, 25/27.IX.1969, OSF; N, Pto. Bueno, 51°00'5.74"12'W, 2.X.1969, OSF. *Valdivia Prov.*, N, Estero Chollinco [40°12'72"17'W], 18.VI.1964, TC. ARGENTINA: *Chubut Prov.*, I (male, female) Río Epuyén, Hoyo de Epuyén, 10.II.1974, OSF. *Neuquen Prov.*, N, 5 km SE Lago Huechulafquén, 26.I.1974, OSF; I (male), Río Quilquihue at Lago Lolog, 22/23.I.1974, OSF; N, I, S (male), Lago Lacar, Estacion Forestal Pucara, 29/30.I.1974, OSF.

Discussion.—Needham and Murphy (1924) described *P. fulvipes* from a single male imago collected from Butalcura, Chile. Demoulin (1955a) subsequently redescribed the male imago and delineated it from *P. chilensis* by the degree of development of the angular bend on the inner margin of segment 1 of the genital forceps, body size, and the intensity of shadings of the costal and Sc cross veins of the fore wings. Except for the infuscation of the costal and subcostal cross veins of the fore wings, the two other characters that Demoulin used to distinguish the two species are inapplicable. Thew (1960) described the species, *P. sepi*

based on male imagos from Frutillar, *Llanquihue Prov.*, Chile. Careful examination of the type specimens of *P. sepi* and *P. fulvipes* indicate that the two species are the same. Therefore, we herein synonymize *P. sepi* with *P. fulvipes* and designate the latter as the senior synonym. *Penaphlebia fulvipes* is herein redescribed based on the type materials, and recently collected and reared specimens from Chile and Argentina. The female imago, male and female subimagos, and the nymph are described for the first time. The nymph and adults are associated by rearing.

The nymphs of *P. fulvipes* from Ultima Esperanza Province have smaller and less pronounced pale yellow spots on the abdominal terga 4-5 and 8 than those from the other localities. Female nymphs generally have paler color of the head than the males, and the pale yellow spot on the vertex is confined to the midposterior margin while it extends between the eyes among males. In the imagos, the maculae on the abdominal terga vary from having the maculae on terga 4-5 greatly reduced (Fig. 25) to slightly reduced (Fig. 23). Additionally, the sternal maculation of the abdomen ranges from a simple pair of submedian dark brown marking (Fig. 24) to a little more elaborate pattern (Fig. 26). *Penaphlebia fulvipes* can be distinguished from the other species of the genus by the following combinations of characters. In the imagos: (1) pre-pterostigmatic costal and subcostal cross veins of male fore wings are weakly developed (Fig. 4), a little more developed and faintly infuscated with brown in females; (2) segment 3 of male protarsi is longer than segment 4; (3) maculae on abdominal terga 1-3, 6-7 and 9 are pronounced, submedian maculae on terga 4-5 and 8 are reduced (Fig. 23,25); (4) angular bend on inner margin of segment 1 of genital forceps is moderately developed, denticulate (Fig. 11); (5) styliger plate has a broad U-shaped posteromedian emargination (Fig. 11); and (6) shape of penis lobes is similar to Fig. 13. In the nymph: (1) labrum has a transverse row of closely set hairs near its dorsoapical margin (Fig. 53); (2) mandibles lack a dorsal groove, or if present, it is shallow (Fig. 30); (3) apical denticles of tarsal claws are larger than middle ones (Fig. 37); (4) hair-like setae on posterior margins of abdominal terga are equal to, or slightly longer than the spines (Fig. 58); (5) posterolateral spines occur on abdominal segments 8-9, and are well developed (Fig. 42); (6) gill lamellae apically terminated in a filamentous process (Fig. 39); and (7) caudal filaments have long and thick hairs (Fig. 45).

Penaphlebia fulvipes is most closely related to *P. flavidula* and *P. exigua*, but can be distinguished from them by any of the following characters: (1) maculae on abdominal terga 4-5 and 8 of nymph and adults are reduced (Fig. 23,25); (2) shape of penis lobes is similar to Fig. 13; (3) apical denticles of nymphal tarsal claws are larger than the middle ones (Fig. 37); and (4) caudal filaments have long and thick hairs (fig.45).

Biology.— One of us (MLP) collected the nymphs mostly underneath submerged and decaying logs, and trapped debris in streams and rivers. A submerged log under a bridge in Río Butalcura, Chiloe Province, was literally covered with nymphs. Reared nymphs spent the day underneath twigs provided inside the rearing cages and crawled onto the surface at night. When light was flashed, the nymphs hurriedly scuttled underneath the substrate.

The nymphs of *P. fulvipes* have been collected from September to March and the adults in December to February.

Dissected nymphs revealed the major gut contents as detritus (51.26%), mineral particles (28.60%), diatoms (13.49%) and few filamentous algae (6.83%). Identified diatoms include the genera *Cymbella*, *Gomphonema*, *Navicula* and *Synedra*.

Subgenus **Megalophlebia** Pescador and Peters, new subgenus

Imago.—Length male body 14.0-16.0 mm; fore wings 14.0-18.0 mm; female body 14.0-18.0 mm, fore wings 16.0-20.0 mm. Hind wings ovate (Fig. 6). Segments 3 and 4 of male protarsi equal in length. Abdominal sterna lack anterolateral spots. Male genitalia as in Fig. 14, apical third of penis lobes greatly enlarged, slender subapical spine posteriorly projecting (Fig. 14); posterior margin of styliger plate entire (Fig. 14).

Egg.—Chorion with hollow circular ridges (Fig. 63-64).

Mature Nymph.—Body length 14.0-17.0 mm. Mandibles with deep dorsal groove and thick hair (Fig. 31). Femora with oblong dorsal setae (Fig. 56). Posterolateral spines on abdominal segments 6-9. Abdominal gills apically terminated with blade-like processes (Fig. 40).

Etymology.—megalo, Gr., meaning big; phlebos, Gr. meaning veins.

Type species.—*Penaphlebia vinosa* (Demoulin)

Discussion.—The subgenus *Megalophlebia* is monotypic, and widely distributed throughout the cool regions of southern South America (Fig. 71). The characters given above distinguish it from the subgenus *Penaphlebia* s. s.

Penaphlebia (Megalophlebia) vinosa (Demoulin)

Atalophlebia vinosa Demoulin, 1955b: 7, Fig. 3, 5c

Penaphlebia vinosa Peters and Edmunds, 1972: 1399; Hubbard, 1982a: 266; Dominguez and Pescador, 1983: 21.

Male imago.—(in alcohol). Length: body 14.0-16.0 mm, fore wings 14.0-18.0 mm. Head brownish-yellow. Scape and pedicel of antennae brown, flagellum paler. Ocelli whitish, black at base. Upper portion of eyes orange yellow, lower portion black. Thorax: nota yellow; pronotum with a pair of broad dark brown median stripes, margins black; furrows faintly washed with dark brown to black. Pleura yellow with somewhat broken dark brown longitudinal marking between bases of pro- and metacoxae. Sterna yellow; metasternum with a prominent shiny brown median transverse band. Wings: membrane of fore and hind wings hyaline, faintly flushed with yellow; longitudinal and cross veins dark brown, anal veins paler; pre-pterostigmatic costal and subcostal cross veins of fore wings weakly developed, lightly shaded with brown; hind wings broad and ovate (Fig. 6). Legs: yellow, protarsi paler, except segments 1 and 2 brown, joints of femora and tibiae and tarsal joints dark brown; femora with a broad dark brown median band; segments 3 and 4 of protarsi equal in length. Abdomen: terga yellow, posterior margins dark brown; broad brown maculae on terga 1-9 (Fig. 27); maculae on terga 1-7 broad covering almost entire surface of segments; median maculae on terga 8 extend beyond half length of segment (Fig. 27). Sterna yellow with thin reddish-brown maculae (Fig. 28). Genitalia (Fig. 14): genital forceps brownish yellow, segments 2 and 3 paler; angular bend on inner margin of segment 1 of forceps strongly developed, denticulate (Fig. 14). Posterior margin of styliger plate entire (Fig. 14). Penes brownish-yellow, inner margins of lobes purplish brown; shape of penis lobes as in Fig. 14, subapical spine slender, projecting posteriorly. Caudal filaments: a unicolorous pale yellow segment alternating with a bicolorous pale yellow and brown segment, brown portion progressively paler distally; first few basal segments washed with brown.

Female imago.—(in alcohol). Length: body 14.0-18.0 mm; fore wings 16.0-20.0 mm. Similar to male imago except as follows: vertex with a pair of black submedian markings; eyes black; pronotum with pronounced black markings; costal and subcostal membranes of

fore wings intensely flushed with brownish-yellow.

Male subimago.—(in alcohol). Similar to male imago except as follows: head dull yellow, nota pale yellow to almost white near base of wings; wings cloudy white, brownish at margins, and around cross veins; apical and anal margins of fore and hind wings with hairs; genital forceps and penes brownish-yellow; caudal filaments covered with hairs.

Female subimago.—(in alcohol). Similar to male subimago except as follows: markings of head as in female imago; eyes greyish-black; pronotum whitish, markings as in female imago; costal and subcostal membranes of fore wings brownish, intercalary veins faintly shaded with brown.

Mature nymph.—(in alcohol). Body length, 14.0-17.0 mm. Dorsum of head dark brown, venter pale yellow; small pale yellow spot anterior to median ocellus and lateral to lateral ocelli. Ocelli black. Eyes of female black; upper portion of male eyes reddishorange, lower portion black. Antennae brown. Mouthparts: clypeus brown with no pale yellow spots; labrum with transverse row of widely set hair near dorsoapical margin (Fig. 52); mandibles with deep dorsal groove (Fig. 31); maxillary palpi brown. Thorax: nota brown with pale yellow markings similar to Fig. 51; venter pale yellow. Legs: dorsum brown, venter pale except tarsi dark brown; a broad pale yellow spot near dorso-apical corner of femora; dorsum of femora with oblong setae (Fig. 56); apical denticles on tarsal claws larger than middle ones (Fig. 37). Abdomen: terga brown with dark brown maculae similar to imagos except pattern not as pronounced; hair-like setae on posterior margins of abdominal terga 2x as long as spines (Fig. 57); posterolateral spines occur on segments 6-9, well developed (Fig. 43). Sterna yellow, brownish on sterna 7-9. Gills: membrane whitish, tracheae greyish; lamellae apically terminated in blade-like process (Fig. 40). Caudal filaments: yellowish-brown with narrow dark brown rings on alternate articulations; hairs on articulation as long as or longer than segments (Fig. 45).

Geographic distribution.—(Fig. 71). *Penaphlebia vinosa* is not as common as the other species of the genus but has a wide geographic distribution (Fig. 71). The species has been collected on both the Argentine-Chilean slopes of the Andes Mountain (ca. 33 N) south to Magallanes Province, Chile.

Type specimen and deposition.—Holotype, male I, Atacalco, Río Diguillin, 600 m, Nuble Prov., CHILE, 21.I.1955, LEP. Paratype, 1 male I, same data as holotype except date of collection, 23.IX.1951, ISNB.

Additional specimens examined.—*Bío Bío Prov.*, N, Río Bío Bío, Santa Bárbara, 8.II.1959, LEP; I (male), Santa Barbara, 8.II.1959, LEP; N, I (male, R), a tributary of Río Bío Bío, Santa Bárbara, 6/8.XII.1972, MLP & LEP. *Cautín Prov.*, N, 20 km E Temuco, 8.I.1951, ESR & EAM; N, Río Llancahue, Villarica, 11.II.1958, JI; N, I, (male, female, R), Río Claro, Pucón, 146 m, 10/11.XII.1972, MLP; N, Río Pedregoso, N Villarica, 235 m, 11.XII.1972, MLP & LEP; S (male), Cerro Nielo, Temuco, 200 m, 9.II.1979, D & MD & BA. *Chiloe Prov.*, S (male, R), a small stream in Dalcahue, 16.XII.1972, MLP & LEP. *Curico Prov.*, N, Río Claro, 26.XI.1957, LEP. *Linares Prov.*, Río Longavi, San Pablo, Parral, 425 m, 28.XI.1972, MLP & GB. *Magallanes Prov.*, N, small stream ("tent stream") Ultima Esperanza, 7.III.1958, JI; N, Chorillo Tres Puentes [53°07' S 70°53' W], 15.XI.1960, TC. *Malleco Prov.*, N, Río Bío Bío ca. Marimenuco, 11.XII.1963, GFE; N, Río Manzanares [~10 km W Puren], 2.I.1966, OSF & TC; I (female, R), Río Piquiquen, El Manzano, 35 km W Angol, 600 m, 8/9.XII.1972, MLP; N, Nahuelbuta Nat. Park, Cabreria, 1200 m, 4.II.1979; D&MD & BA. *Nuble Prov.*, N, 40 km E San Carlos, 24.XII.1950, LEP; I (male, female), Río Niblinto, 600 m, 19.I.1968, LEP; N, Río Niblinto, 35 E Coihueco, 650 m, 19.I.1968, LEP; S (female), Río Niblinto, Niblinto, 230 m, 25/26.XI.1972, MLP & GB; S (male, R), Río Renegado at Pte. Marchant, Recinto, 940 m, 26.XI.1972, MLP. *Osorno Prov.*, N, Río Rahue,

31.X.1957, JI; N, Río Golgol, Puyehue, 850 m, 13.XII.1972, MLP. S (male), P. N. Puyehue, Río Golgol, 2.II.1978, CM & OSF. *Santiago Prov.*, N, El Canelo, 30.XI/2.XII.1972, MLP & GB; N, EL Alfalfal, 22.I.1978, CM & OSF. *Talca Prov.*, N, a stream near Alto Vilches, 23/30.I.1964, LEP; N, Estero Vilches Laguna de los Patos, Alto Vilches, 1,030 m, 22/24.XI.1972, MLP & GB; N, Río Lircay, Alto Vilches, 800 m, 22.XI.1972, MLP & GB; N, Piedra de las Tasas, 950 m, 23.XI.1972, MLP. ARGENTINA: *Río Negro Prov.*, N, Lago Nahuel Huapi, San Carlos de Bariloche, 25/27.XII.1972, MLP; N, I (female), a small stream near Bariloche, 15.X.1958, JI. *Neuquen Prov.*, N, Río Limay, 7.IV.1958, LEP; 5 (female), Río Quilquihue at Lago Lolog, 22/23.I.1974, OSF; S (male, female), cascades 6 km N Lago Alumine, 1100 m, 3.II.1987, CM & OSF.

Discussion.—Demoulin (1955c) described *P. vinosa* based on three male imago and one male subimago. The species is herein redescribed based on the type material, and series of recently collected and reared specimens from Chile and Argentina. The nymph, female imago and subimago are described for the first time. The nymph and adults were associated by rearing.

Penaphlebia vinosa is a very distinctive species, and no significant variations were observed among the specimens we have examined. The characters defining the subgenus *Megalophlebia* easily differentiate *P. vinosa* from all the other species of the genus. Some of the characters are as follows: (1) hind wings are large and ovate (Fig. 6); (2) angular bend of inner margin of segment I of genital forceps is strongly developed (Fig. 14); (3) penis lobes have a slender subapical spine that is posteriorly projecting (Fig. 14); (3) posterolateral spines occur on abdominal terga 6-9 (Fig. 43); and (4) abdominal gill lamellae are terminated in blade-like processes (Fig. 40).

Biology.—One of us (MLP) collected the nymphs underneath silt-coated rocks and stones in streams, rivers and lake shores. The nymphs were often covered with silt which made them difficult to recognize, and easy to miss in the field. Briefly exposing the rocks or stones to the sun however, forced the nymphs to move making it easy to detect and collect them.

The nymphs have been collected from October to March, and the adults from October to February.

Dissected nymphs indicate the major gut contents as diatoms (61.71%), detritus (27.50%), mineral particles (8.93%), filamentous algae and desmids (1.86%). The identified diatoms include *Amphora*, *Cymbella*, *Melosira*, *Nitzschia* and *Synedra*. The identified desmid belongs to the genus *Cosmarium*.

Phylogenetic Relationships of the Species of *Penaphlebia*

The phylogenetic relationships of the different species of *Penaphlebia* are herein analyzed based on the external morphological characters of the nymphs and adults. Polarization of the various character states was derived by out-group comparison with the genera *Atalophlebia* and *Massartella*, the sister group of *Penaphlebia* (Pescador and Peters 1980, 1990). The concept of out-group comparison postulates that a character state present in both the proposed monophyletic taxon and the out-group is considered plesiomorphic, and autapomorphic when a character state is present only in the proposed monophyletic taxon.

Figure 68 depicts the probable phylogeny of the species of *Penaphlebia*. Table 1 shows the character states analyzed herein.

Furcation 1 represents the common ancestral derivation of the subgenera *Megalophlebia* (Lineage 1A) and *Penaphlebia* s. s. (Lineage 1B). Lineage 1A, which is represented by the monotypic subgenus *Megalophlebia*, is defined by the following autapomorphic characters:

TABLE 1. Character States of Figure 68. D. derived; P. primitive

Furcation 1	A	B
Mandibles	(D) with deep dorsal groove (Fig. 31)	(P) lack of dorsal groove, if present shallow (Fig. 30)
Abdomen	(P) posterolateral spines on segments 6-9 (Fig. 43)	(D) posterolateral spines on segments 8-9 (Fig. 41-42)
Abdomen gills	(D) apical process blade-like (Fig. 40)	(P) apical process filamentous (Fig. 39)
Hind wings	(P) ovate (Fig. 6)	(D) elliptic (Fig. 5)
Genital forceps weakly	(P) angular bend of inner margin well developed (Fig. 14)	(D) angular bend of inner margin developed (Fig. 11-12)
Stylier plate	(D) posteromedially entire (Fig. 14)	(P) posteromedially emarginated (Fig. 11-12)
Protarsi of male	(D) segment 3 subequal length of segment 4	(P) segment 3 longer than imago segment 4
Furcation 2	A	B
Labrum	(P) hair near dorsoapical margin widely-set (Fig. 52)	(D) hair near dorsoapical margin closely-set (Fig. 53)
Abdominal terga	(P) setae distinctly longer than spines (Fig. 57)	(D) setae subequal to (Fig. 58) or shorter than spines (Fig. 59)
Fore wings	(P) costal and subcostal cross veins well-developed and thickly infuscated (Fig. 3)	(D) costal and subcostal cross veins weakly developed and non-infuscated (Fig. 4)
Furcation 3	A	B
Tarsal claws	(P) apical denticles largest (Fig. 37)	(D) middle denticles largest (Fig. 38)
Caudal filaments shorter	(P) setae thick and subequal in length to segments (Fig. 45)	(D) setae slender and distinctly shorter than segments (Fig. 44)

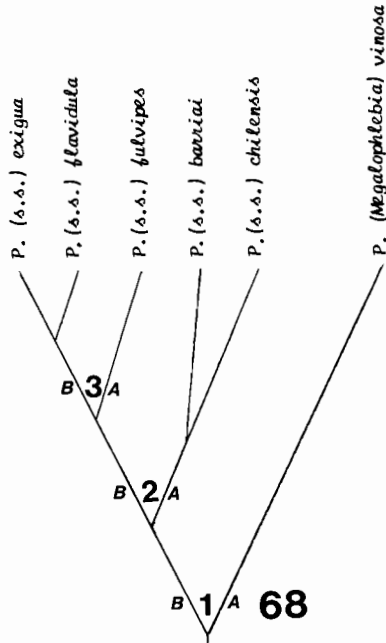
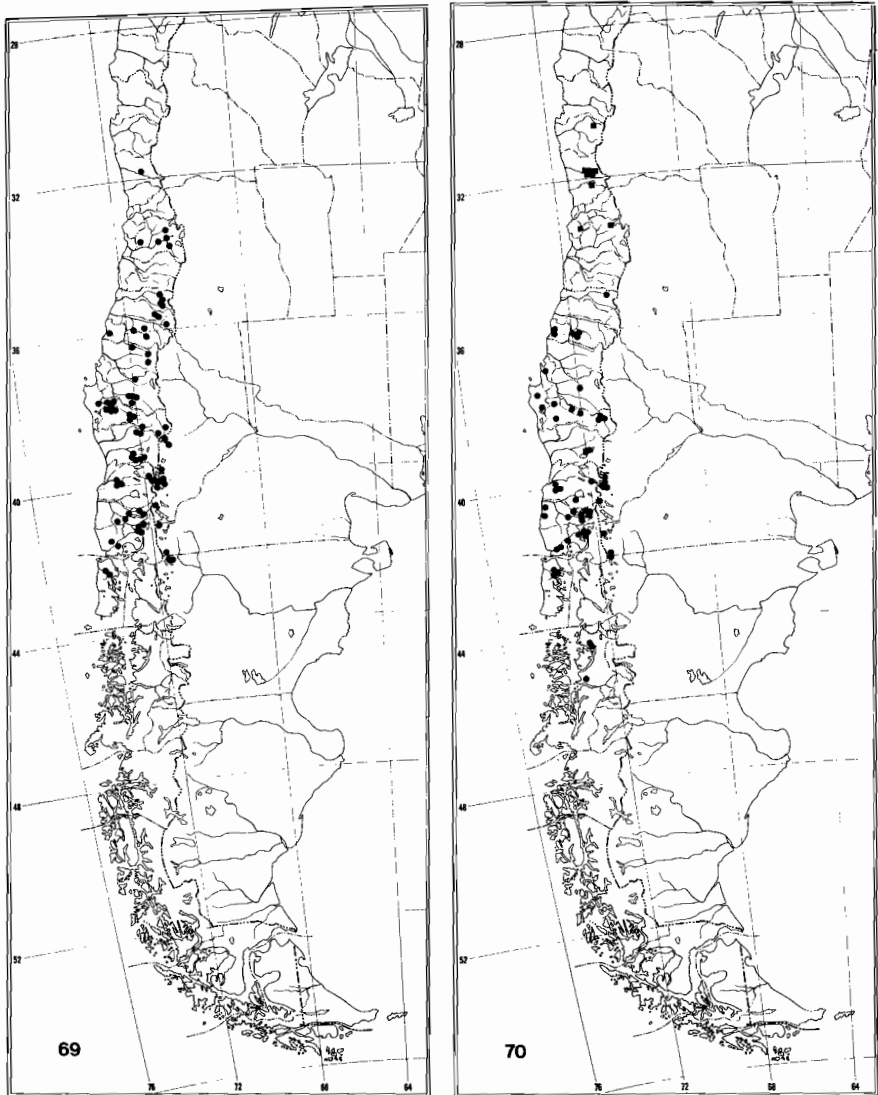
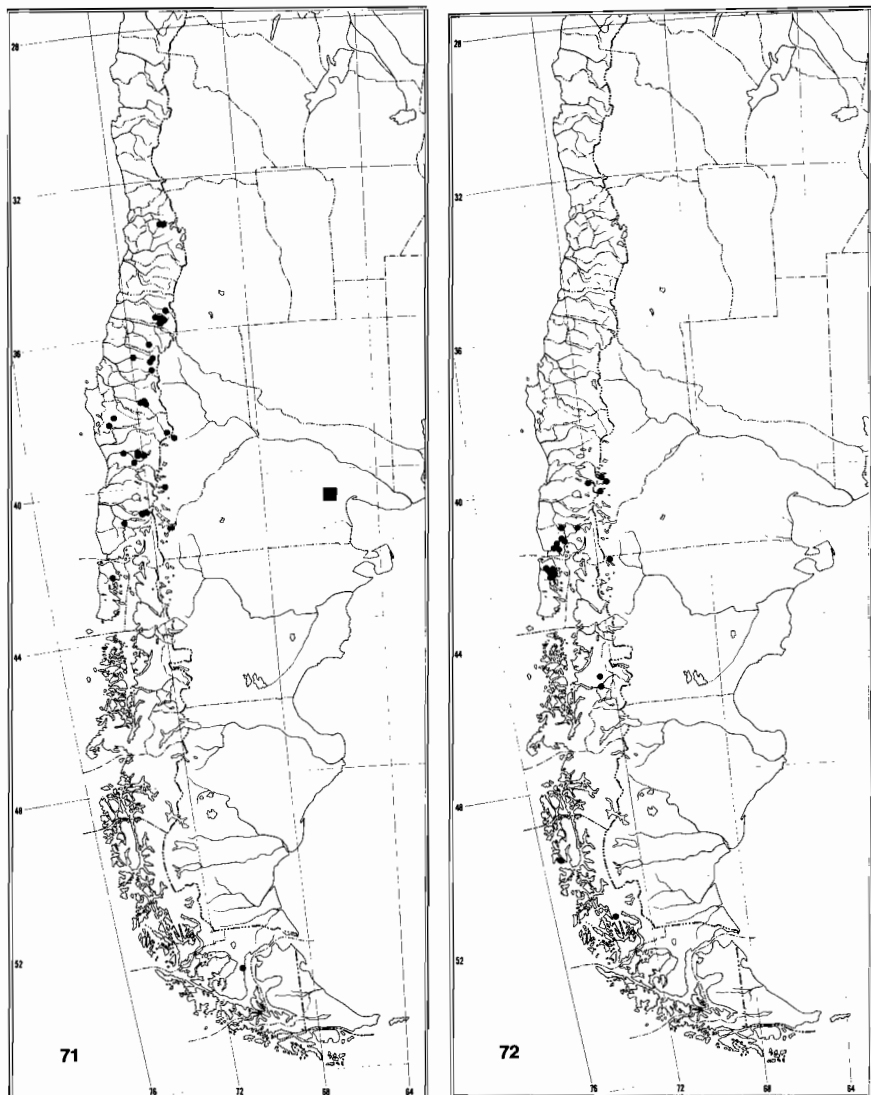


Figure 68. Phylogenetic diagram of *Penaphlebia*.



Figures 69-70. Geographic distribution of *Penaphlebia*. 69, *P. (P.) chilensis* and 70, *P. (P.) flavidula* (solid circles) and *P. (P.) barriai* (solid squares).



Figures 71-72. Geographic distribution of *Penaphlebia*. 71, *P. (M.) vinosa* (solid circles) and *P. (P.) exiqua* (solid squares); 72, *P. (P.) fulvipes*.

deep dorsal groove of the mandibles (Fig. 31) and blade-like apical processes of the abdominal gills of the nymphs (Fig. 40), and the subequal length of segments 3 and 4 of the protarsi and the posteromedially entire styliiger plate of the genitalia of male imagos (Fig. 14). The five species in Lineage 1B (subgenus *Penaphlebia* s.s.) are clustered by the synapomorphic abdominal posterolateral spines of the nymph (Fig. 41-42), and the elliptic hind wings (Fig. 5) and the weakly developed angular bend of the genital forceps (Fig. 12-13).

Lineage 2A includes the sister species *P. barriai* and *P. chilensis* and is defined by the well developed and pronouncedly infuscated costal cross veins of the fore wings of imagos (Fig. 1, 3). *Penaphlebia exigua*, *P. flavidula* and *P. fulvipes* represent Lineage 2B and are defined from Lineage 2A by the synapomorphic closely-set hairs near the dorsoapical margins of the labrum (Fig. 53) and the short setae on the posterior margin of the abdominal terga (Fig. 58). *Penaphlebia fulvipes* and *P. exigua* is defined from Lineage 3A (*P. fulvipes*) by the synapomorphic short setae on the caudal filaments (Fig. 44) and the large middenticles of the tarsal claws (Fig. 38). The latter character state appears however, to be a parallelism because it also occurs in *P. barriai*.

The geographic range of *Penaphlebia* is shown in Figs. 69-71. The disjunctive distribution of *P. exigua* from the rest of the genus could very well be related to past geological events in the region or lack of adequate collections. Savage (1987) recently reviewed the biogeography of the cold-adapted leptophlebiid genera of South America and cited the existence in Argentina of three ancient island shields (the Pampean Ranges Shield, the Patagonian Island Shield and the Deseado Shield), collectively known as the Patagonian Shield, which retained their terrestrial nature when the region was flooded and under water during most of the Cretaceous. The Patagonian Shield presumably served as faunal refugium during this time and later the fauna dispersed after the Cretaceous flood has receded. In late Cretaceous and early Tertiary the Andes Mountains were still not in existence and fauna could have spread freely within the region. Following the formation of the Andes, reportedly in the Upper Tertiary and Quarternary, (Herrero-Ducloux 1963, Sonnenberg 1963, Williams 1963) the once widespread cold adapted fauna presumably became fragmented by the arid climate of the low lying areas between the Andes and the Patagonian Shields which to date appears to be an effective ecological barrier for dispersal. The specimens of *P. exigua* have all been collected in Rincon de Asconape near Valcheta (40.42°S 66.08°W), an area bordering the ancient Patagonian Island Shield. *Penaphlebia exigua* is not the only species among the cold-adapted leptophlebiid genera in South America that exhibits a disjunctive distribution. The species *Meridialaris tintinnabula* which occurs in the high mountain coldstreams of Tucuman Province, Argentina (an area within the Pampean Ranges Shield) is geographically disjunct from the rest of the genus *Meridialaris* (Pescador and Peters, 1987).

The rest of the *Penaphlebia* species are sympatric. *Penaphlebia barriai* the least geographically widespread (Fig. 70) is presently confined in northern Chile (30°-34°S). *Penaphlebia (M.) vinosa* although not as common as the other species of the genus, is the most geographically widespread, occurring from Cordillera Province to Magallanes Province, Chile (Fig. 71).

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