

# A Revision of *Hermanella* and Related Genera (Ephemeroptera: Leptophlebiidae; Atalophlebiinae) from Subtropical South America

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**ABSTRACT** The genus *Hermanella* Needham and Murphy is redescribed and two related genera, *Hylister* and *Needhamella*, are established. *Hermanella* is divided into two subgenera, *Hermanella* s.s. and *Guayakia*, n. subgen. Adults of *Hermanella* (*G.*) *maculipennis* (Ulmer), n. comb., and *Needhamella ehrhardti* (Ulmer), n. comb., and the nymph of *Hermanella* (*H.*) *thelma* Needham and Murphy are redescribed. The subimago of *H. (H.) thelma* and the nymphs of *H. (G.) maculipennis* and *N. ehrhardti* are described for the first time. Three new species, *Hermanella (H.) guttata*, *Hermanella (G.) grandis*, and *Hylister plaumanni*, are described. *Hermanella (H.) guttata* is described from the nymph and male and female imagines, *Hermanella (G.) grandis* from the nymph and female imago, and *Hylister plaumanni* from the nymph and male and female imagines. Eggs of these genera are described and illustrated, and keys to the nymphs and imagines and biological notes are presented.

**KEY WORDS** Insecta, taxonomy, Leptophlebiidae, *Hermanella*

THE *Hermanella* GENERIC COMPLEX is a large group of distinctive leptophlebiid mayflies distributed throughout most of the Neotropics and north into southern Canada. The nymphs have strikingly modified mouthparts; the labrum is greatly enlarged, and it and the maxillae and labium bear rows of long setae. Similar modifications also occur in certain leptophlebiid nymphs of the West Indies and the Old World but, as Sivaramakrishnan & Peters (1984) have pointed out, the *Hermanella* complex is distinct and not related to these other leptophlebiids. In the *Hermanella* complex, the long setae of the mouthparts are aligned in distinct rows; in other genera these setae, if present, are unaligned.

Three genera are currently recognized in the *Hermanella* complex: *Hermanella* Needham and Murphy 1924; *Traverella* Edmunds 1948; and *Leentvaaria* Demoulin 1966. Individuals of *Traverella*, distributed from Argentina to Canada, have been reared, and adults and nymphs have been described (Edmunds 1948). *Leentvaaria*, with greatly elongated labial palpi, is known only from nymphs from the Guyana Highlands (Demoulin 1966). *Hermanella* was described from nymphs (Needham & Murphy 1924) from northeastern Argentina.

Many other undescribed nymphs of this group have since been collected throughout South and Central America; southern Brazil appears to be a center of diversity. These *Hermanella*-like nymphs differ from Needham and Murphy's genotype prin-

cipally in the structure of the gills. William L. and Janice G. Peters collected these forms extensively in southern Brazil and reared two, neither of which was *Hermanella*. Edmunds et al. (1976) figured a presumed *Hermanella* but, as shown below, they portrayed a related genus. In fact, a major stumbling block to the study of this interesting and important generic complex is the lack of information about adult stages, in particular those of true *Hermanella*.

Recently one of us (E.D.) collected and reared mayflies in the type locality of *Hermanella* and in nearby streams in Argentina. This fresh material, added to the Peters's collections at Florida A&M University, Tallahassee, gives the most complete picture yet of the *Hermanella* complex in southern Brazil. In this paper we describe adults of *Hermanella*, including the probable adult of the type species, *H. thelma* Needham and Murphy, establish a new subgenus of *Hermanella*, and describe all stages of two new genera closely related to *Hermanella*.

Although feeding has not been studied, the nymphs of the *Hermanella* complex are assumed to be filter feeders because of the numerous long setae on their mouthparts. This hypothesis is supported by some of our mouthpart slides, which show diatoms trapped in the dorsal setae of the labra of some specimens. Also, one of us (R.W.F.) has collected *Traverella* nymphs which, when preserved, have all the long setae erect and forming a sievelike apparatus around the oral opening. However, we have dissected foreguts of all the taxa discussed in this paper as well as several others and have found only fine detritus, as is common in the guts of many other mayflies.

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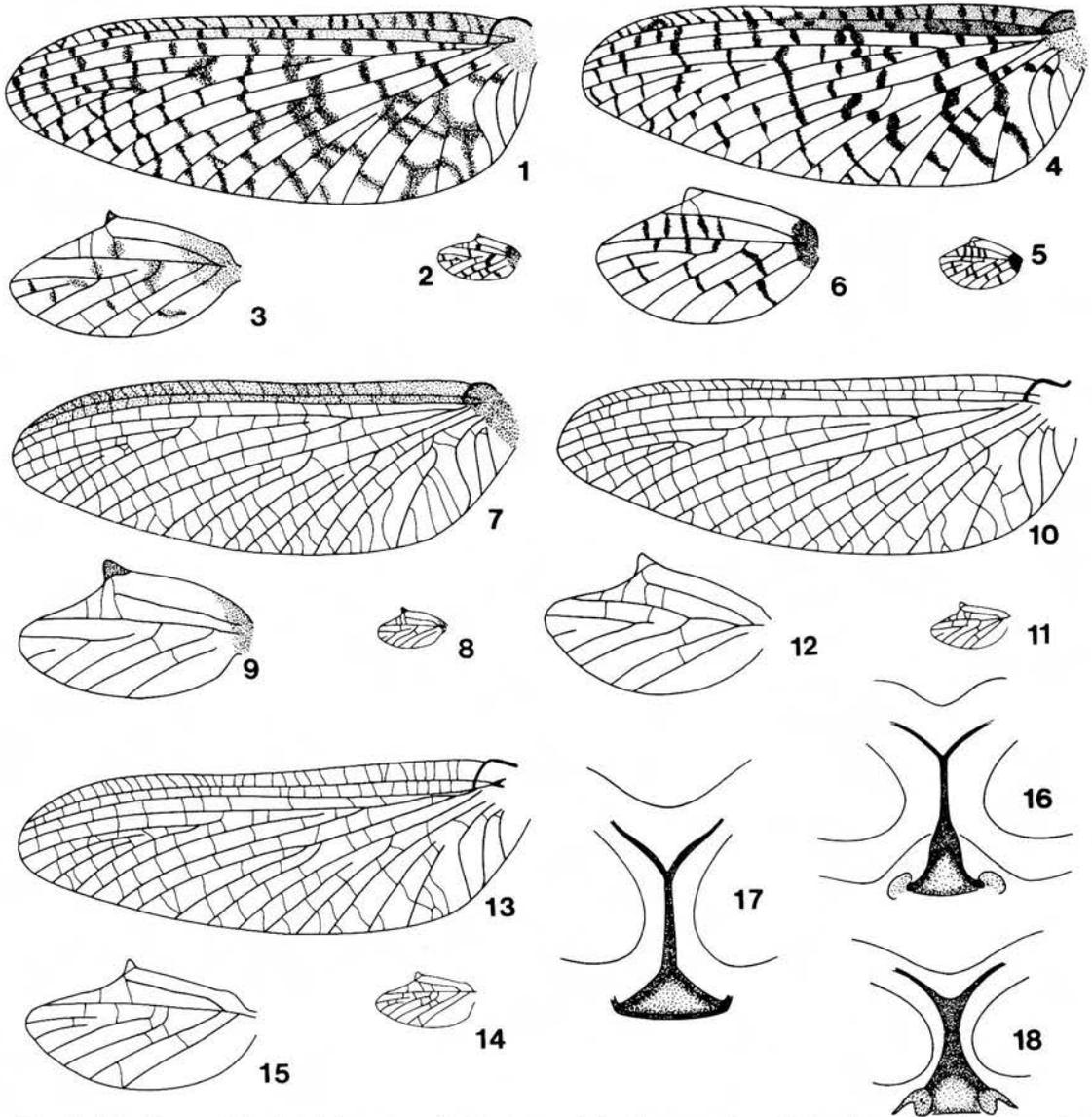


Fig. 1-18. Imago. Fig. 1-14, forewing, hind wing, and hind wing enlarged. (1-3) *Hermanella (Guayakia) maculipennis*. (4-6) *H. (H.) guttata*. (7-9) *H. (G.) grandis*. (10-12) *Hylister plaumanni*. (13-15) *Needhamella ehrhardti*. Fig. 16-18, prosternum. (16) *Hermanella (G.) maculipennis*. (17) *Hylister plaumanni*. (18) *N. ehrhardti*.

In addition to the taxa described in this paper, there are many other members of the *Hermanella* complex in subtropical South America that are still too poorly known to describe. Most are known only from either the adult or nymph. They include several more taxa from Iguazú Falls, Salto in Argentina, and other southern Brazilian streams. A number of unique taxa has been collected from Sete Quedas in Brazil, an especially productive locality that unfortunately now lies submerged at the bottom of the reservoir of Presa Itaipú.

Abbreviations for collections in which specimens are deposited are CU, Cornell University, Ithaca, N.Y.; FAMU, Florida A&M University, Tallahassee; IFML, Instituto-Fundación Miguel Lillo, Tu-

cumán, Argentina; MH, Museum of Hamburg, Federal Republic of Germany; USP, Universidade de São Paulo, São Paulo, Brazil. Also used are N, nymph; S, subimago; I, imago. All measurements are in millimeters.

The following keys will separate the species discussed in this paper.

#### Keys to the Treated Genera and Species

##### Imagines

1. Prosternum relatively wide (Fig. 18), narrowed at middle; ventral projections of

- penes narrow, spinelike and divergent apically (Fig. 26); subgenital plate with a spinelike projection median to the base of each of the forceps .....  
*Needhamella ehrhardti* (Ulmer), n. comb.
- Prosternum with a narrow straight carina medially (Fig. 16 and 17); ventral projections of penes variable, if pointed and divergent apically, no projections on subgenital plate ..... 2
2. Subgenital plate lacking projections; apical  $\frac{1}{4}$  of penes divided; ventral projections spinelike and divergent apically (Fig. 23) .....  
*Hylister plaumanni* Dominguez and Flowers, n. sp.
- Subgenital plate with projections; apical  $\frac{1}{2}$  of penes divided; ventral projections variable, generally short and stout (Fig. 19–21) ...  
*Hermanella* Needham and Murphy ... 3
3. Subgenital plate (Fig. 20 and 21) with broad projections at base of penes; penes with ventral projections broad, lobelike .....  
*Hermanella* (*Hermanella*) ... 4
- Subgenital plate (Fig. 19) with slender projections at base of penes; penes with ventral projections curved, spinelike .....  
*Hermanella* (*Guayakia*) Dominguez and Flowers, n. subgen. ... 5
4. Wings without spots, general coloration of abdomen blackish brown .....  
*H. (H.) thelma* Needham and Murphy
- Wings with spots (Fig. 4 and 5), general coloration of abdomen orange-brown .....  
*H. (H.) guttata* Dominguez and Flowers, n. sp.
5. Wing membrane hyaline, costal and subcostal area orange-brown (Fig. 7); forewing length 12–12.5 .....  
*H. (G.) grandis* Dominguez and Flowers, n. sp.
- Wing membrane with brown spots (Figs. 1–3), forewing length 9.5–10 .....  
*H. (G.) maculipennis* (Ulmer), n. comb.

### Mature Nymphs

1. Gills (Fig. 71 and 72) on segments 1–6, platelike, truncated apically with 8–10 fringes; posterolateral spines on abdominal segments 7–9 .....  
*Hylister plaumanni* Dominguez and Flowers, n. sp.
- Gills on segments 1–7, shape variable (Fig. 49, 50, 60, 61, 83, 84); posterolateral spines on abdominal segments 8 and 9 ..... 2
2. Gills (Fig. 83 and 84) platelike, ending in a single fingerlike process; medial projection on clypeus (Fig. 77) present .....  
*Needhamella ehrhardti* (Ulmer), n. comb.
- Gills (Fig. 49, 50, 60, 61) platelike, ending in two lateral lobes and a medial fingerlike projection; medial projection on clypeus absent .....  
*Hermanella* Needham and Murphy ... 3
3. Tibiae with relatively short dorsal setae and outer margin glabrous (Fig. 51); body length >9 mm .....  
*H. (Guayakia)* ... 5
- Tibiae with longer dorsal setae and outer margin with scattered setae (Fig. 62 and 63); body length <8 mm .....  
*H. (Hermanella)* ... 4
4. Abdominal terga almost completely blackish, with no pattern apparent .....  
*H. (H.) thelma* Needham and Murphy
- Abdominal terga orange-brown, with pattern as in male imago (Fig. 31) .....  
*H. (H.) guttata* Dominguez and Flowers, n. sp.
5. Wing pads showing traces of spotted imaginal wings .....  
*H. (G.) maculipennis* (Ulmer), n. comb.
- Wing pads without traces of spots, outer margins dark .....  
*H. (G.) grandis* Dominguez and Flowers, n. sp.

### Genus *Hermanella* Needham and Murphy

(Fig. 1–9, 16, 19–22, 29–34, 41–52, 53–64, 87)

*Hermanella* Needham and Murphy 1924: 39; Ulmer 1939: 490; Spieth 1943: 8; Demoulin 1955: 7; Traver 1947: 158; Traver 1960: 19; Edmunds et al. 1976: 221.

**Imago.** Length of male: body, 7.8–8.5; forewings, 8.3–9.0, hind wings, 1.2–1.5. Length of female: body, 6.7–9.6; forewings, 8.2–12.5, hind wings, 1.4–1.75. **Head:** Eyes of male separated on meson of head by width of lateral ocellus, lower portion of eyes  $\frac{1}{3}$  length of upper portion; eyes of female separated on meson of head by 5 times maximal width of lateral ocellus. Prosternum with narrow, straight median carina (Fig. 16). **Wings** (Fig. 1–9): maximal width of forewings slightly less to slightly more than  $\frac{1}{2}$  their maximal length; maximal width of hind wings slightly more than  $\frac{1}{2}$  their maximal length; maximal length of hind wings  $\frac{1}{5}$ – $\frac{1}{6}$  maximal length of forewings. Vein Rs of forewing forked at  $\frac{1}{5}$  distance from base of vein to margin (Fig. 1, 4, 7); vein MA forked slightly less than  $\frac{1}{2}$  distance from base of vein to margin, fork asymmetrical; crossvein above fork in MA slanted; vein MA<sub>2</sub> strongly sagged; vein MP forked  $\frac{2}{5}$  distance from base to margin, fork slightly asymmetrical; vein ICu<sub>1</sub> attached at base to vein CuA by a crossvein or free basally; vein ICu<sub>2</sub> free basally or attached to ICu<sub>1</sub>. Hind wings (Fig. 2, 3, 5, 6, 8, 9) with costal projection well developed, acute, rounded at apex, located slightly more than  $\frac{1}{2}$  distance from base to apex; vein MP unforked; apex of wings acutely rounded; vein Sc slightly more than  $\frac{1}{2}$  maximum length of hind wings, ending in a crossvein (except in the holotype of *H. guttata*,

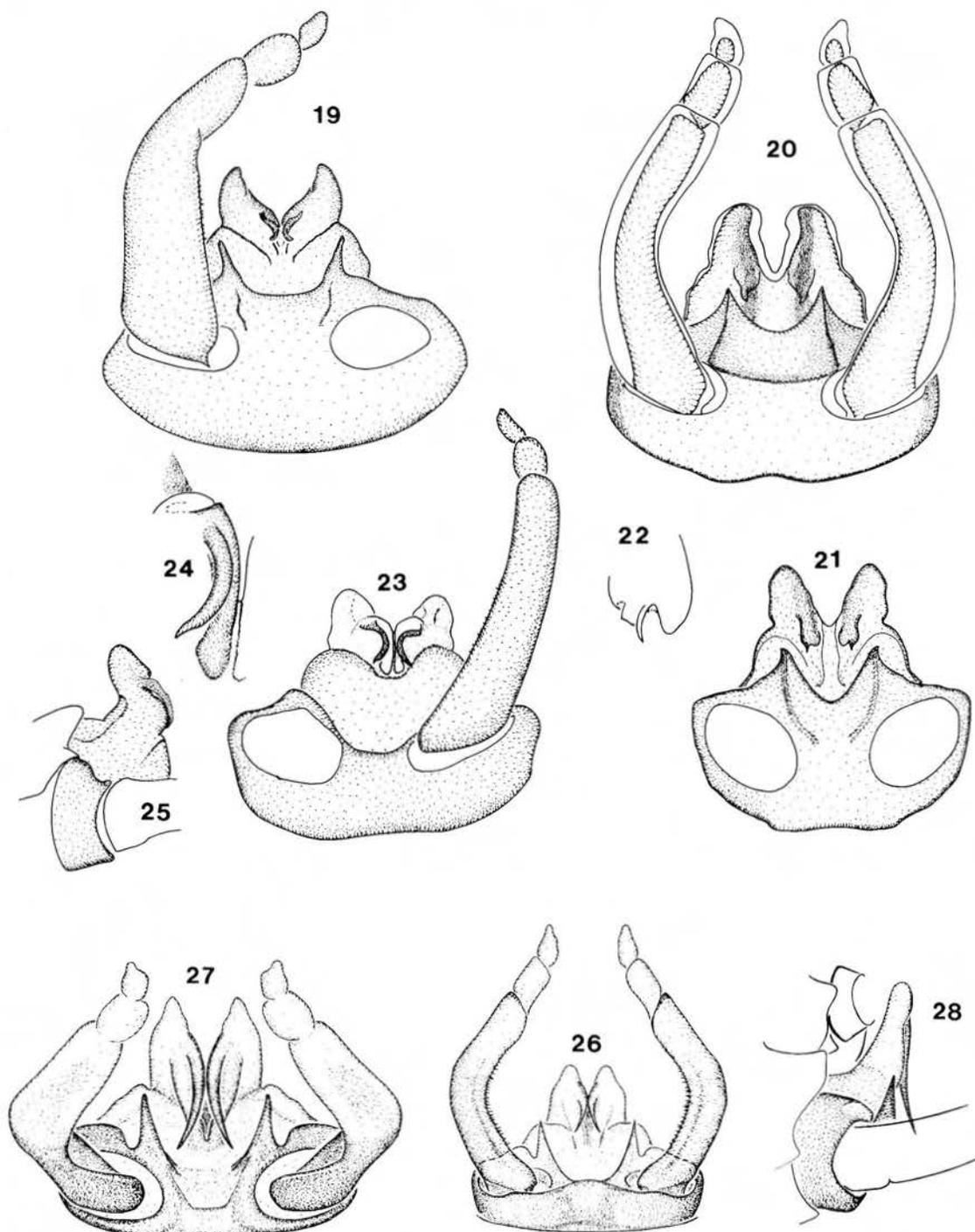


Fig. 19-28. Male genitalia. (19) *Hermanella* (*G.*) *maculipennis*. (20) *H.* (*H.*) *thelma* (subimago). (21-22) *H.* (*H.*) *guttata*. (23-25) *Hylister plaumanni*. (26-28) *Needhamella ehrhardti*. Ventral views except: 22, 24, ventral detail of penis lobe; 25, 28, lateral view; 27, apical view.

where it reaches the costal margin); 6-18 crossveins present. *Legs*: ratios of segments in male forelegs, 0.60:1.00 (2.5 mm):0.9:0.31:0.26:0.16:0.09. Claws of a pair dissimilar, one apically hooked, the other blunt, padlike (as in Fig. 39). *Male genitalia* (Fig.

19-21): subgenital plate with pair of narrow or broad spinelike projections close to base of forceps, segment 2 of forceps  $\frac{1}{6}$ - $\frac{1}{4}$  length of segment 1, 1.5 times length of segment 3; segment 1 strongly curved and narrowed gradually from base to apex.

Basal  $\frac{1}{3}$  of penes lobes each with swollen lateral margin; penes divided in apical  $\frac{1}{2}$ , each lobe with variable ventral projection. Ninth sternum of female cleft apically as in Fig. 40. Terminal filament longer than cerci.

**Mature Nymph.** *Head* prognathous. *Antennae* 2.5–3 times length of head. *Mouthparts* (Fig. 41–48, 53–59): clypeus widened at apex, maximal width of labrum 1.2–1.3 times maximal width of clypeus; length of labrum approximately  $\frac{1}{3}$  maximal width, lateral margins rounded (Fig. 41, 53); anteromedian emargination broad and V-shaped to narrow and slitlike dorsally, deep and U-shaped ventrally (Fig. 42, 54); divided row of long dorsal setae on basal  $\frac{1}{4}$  of labrum with 30–38 setae on each side, numerous short setae scattered on apical  $\frac{3}{4}$  of labrum, lateral and anterolateral margins lined with short setae. *Left mandibles* (Fig. 43, 55, 56): outer margins angularly curved, lacking setae, angles rounded. *Maxillae* (Fig. 44, 57): galealacinia with one long thick seta on venter close to ventral inner margin; subapical pectinate setae lacking; a prominent tusk on inner apical angle. Segments 1 and 3 of maxillary palpi subequal and approximately  $\frac{1}{2}$  length of segment 2; segment 1 with thick blunt setae on outer margin, segment 2 with two long setae on inner apical margin, segment 3 with long setae in ordered rows. *Lingua* of hypopharynx with well-developed lateral processes, anterior margin with a median V-shaped cleft; superlinguae as in Fig. 45, 58. *Labium* (Fig. 46, 47, 59): segment 1 of palpi  $\frac{1}{10}$  length of segment 2, segment 3 approximately  $\frac{2}{3}$  length of segment 2; segment 3 (Fig. 48) curved, with long setae on ventral surface and external margin and short spines on inner margin; segment 2 elbowed with a dorsal row of setae as in Fig. 47; glossae straight, flat, with short setae along anterior margin; paraglossae with subapical row of long setae on ventral surface; submentum with thick setae laterally (Fig. 46, 59). *Anterolateral margins* of pronotum with three stout setae. *Wing pads* pilose. *Legs* (Fig. 51, 62, 63): trochanters with row of spines on apicodorsal surface; anterior femora with long blunt or spatulate setae along posterior (dorsal) margin and subapical area, short blunt setae along inner margin; metathoracic femora (Fig. 62) with long setae along posterior margin only, remainder of dorsal (anterior) surface evenly covered with small blunt setae; tibiae with rows of setae on inner and dorsal surfaces, metathoracic tibiae with short and long blunt setae along outer margins; tarsi with spinelike setae along inner margins, outer margins with a few fine setae or glabrous; claws hooked and narrow, denticles small on basal third, larger in middle, subapical denticle very large (Fig. 52, 64). *Gills* (Fig. 49, 50, 60, 61): gills on segments 1–7, platelike, biramous, progressively smaller posteriorly; each gill ending in a narrow central fingerlike process and wide lateral lobes, dorsal and ventral portions similar, main trachea along median line. Posterolateral projections on abdominal segments 8 and 9. Posterior margins

of terga with alternating spines and setae. Terminal filament longer than cerci, caudal filaments with small spines on posterior margins of each segment.

**Egg.** Chorion with knob-terminated coiled threads (KTCs of Koss & Edmunds [1974]) evenly distributed (Fig. 87). The eggs of this and all other studied genera of the *Hermanella* complex are ridged and are more-or-less hexagonal. These eggs were all dissected from rather old females and the shape may be an artifact of preservation; however, eggs of other families and genera prepared for SEM in a similar manner usually have the customary oval shape.

**Type species.** *Hermanella thelma* Needham and Murphy.

**Species Included.** *H. thelma* Needham and Murphy; *H. maculipennis* (Ulmer); *H. guttata*, n. sp.; and *H. grandis*, n. sp.

**Distribution.** A small area at the junction of Brazil, Paraguay, and Argentina and an adjacent area in southeastern Brazil.

**Discussion.** The genus *Hermanella* was established by Needham & Murphy (1924) for *H. thelma* from the Iguazú Falls in northeastern Argentina. Spieth (1943) described some adults as *Hermanella incertans* Spieth, based on Ulmer's (1939) claim that the nymphs of *Hermanella* and *Choroerterpides* were related despite their differences. Traver (1947) considered the adult described by Spieth as the true *Hermanella* adult and questioned the placement of the two nymphs described by Needham and Murphy in the same genus. Demoulin (1955) separated the species of *Hermanella* into two different subgenera, *H. (Hermanella)* and *H. (Hermanellopsis)*. Traver (1960) questioned the characters used by Demoulin and proposed the elimination of the subgenera. Savage & Peters (1983) established that *Hermanellopsis* is a valid genus quite unrelated to *Hermanella*. Edmunds et al. (1976) correctly described *Hermanella* gills as ending in two lateral lobes and a fingerlike medial projection, but their illustrations are of the genus *Needhamella* (q.v.).

*Hermanella* can be separated from the other genera of Leptophlebiidae by the following combination of characters. In the imago: forks of veins MA and MP of forewings asymmetrical with a slanted crossvein at MA fork (Fig. 1, 4, 7); vein MP of hind wings unforked; costal projection of hind wings (Fig. 2, 3, 5, 6, 8, 9) acute; vein Sc of hind wings ending in a crossvein near base of costal projection, or slightly exceeding projection; penes divided in apical  $\frac{1}{2}$ , projections of penes variable (Fig. 19–21), an external swelling present on basal  $\frac{1}{3}$  of each penis lobe; subgenital plate bearing projections dorsal to the base of forceps (Fig. 19–21); and prosternum bearing a narrow straight median carina (Fig. 16). In the nymph: labrum as wide as head, bearing long setae (Fig. 41–53); long setae on maxillary palpi ordered in rows (Fig. 44–57); tarsal claws bearing a large subapical denticle (Fig. 52, 64); gills (Fig. 49, 50, 60, 61) present on seg-

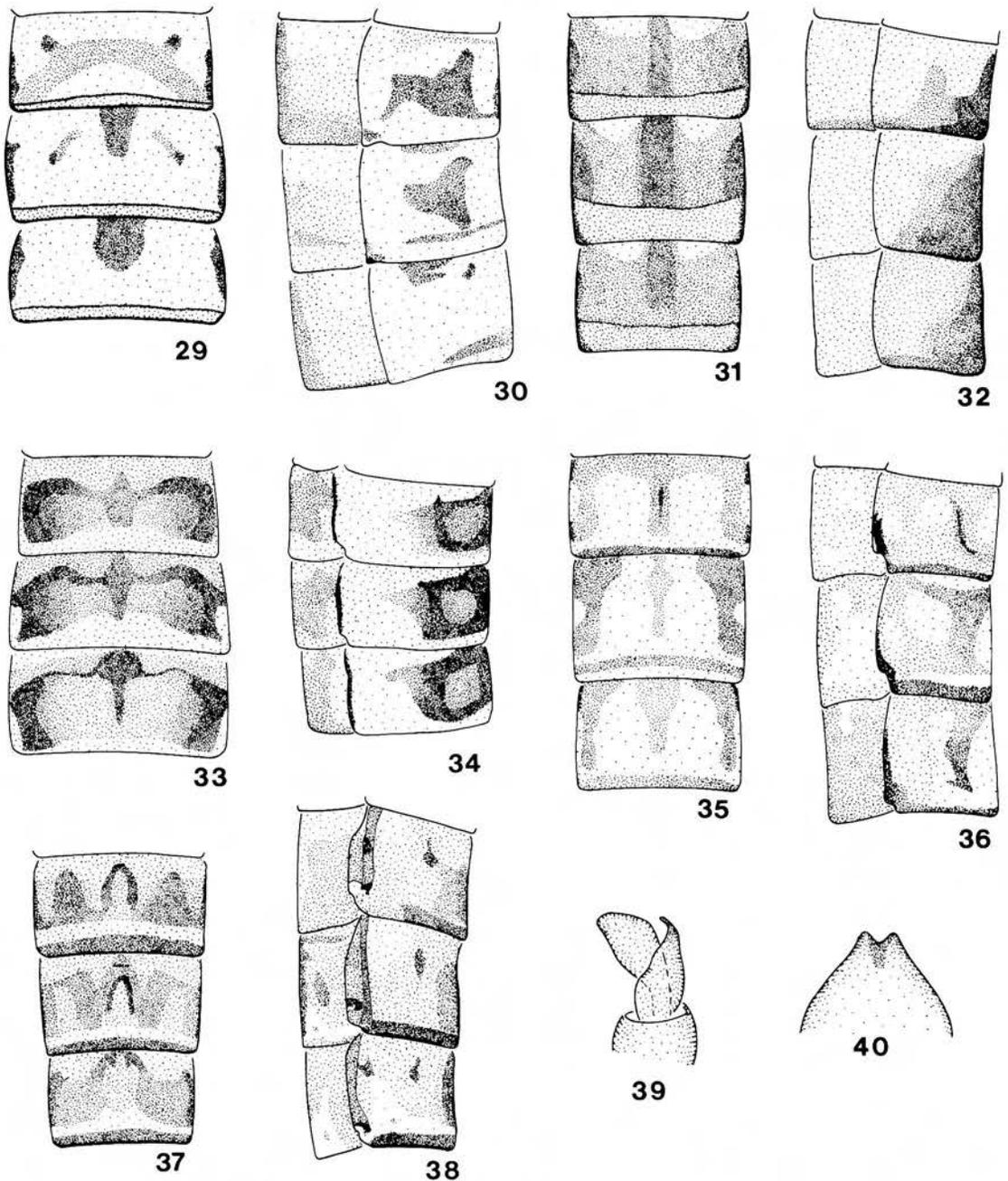


Fig. 29-40. Imago. Fig. 29-38, terga and lateral view of segments 5-7. (29-30) *Hermanella* (*G.*) *maculipennis*. (31-32) *H. (H.) guttata*. (33-34) *H. (G.) grandis*. (35-36) *Hylister plaumanni*. (37-38) *N. ehrhardti*. Fig. 39-40, *Hylister plaumanni*. (39) tarsal claw of male imago; (40) ninth female sternite.

ments 1-7; dorsal and ventral portions platelike, with two lateral lobes and a median fingerlike projection apically; and posterolateral spines present on abdominal segments 8 and 9.

This genus is closely related to *Hylister*, from which it can be distinguished by the spines of the male imaginal subgenital plate and by the shape of the nymphal gills. *Hermanella* can be distin-

guished from *Needhamella* by the shape of the adult prosternum and, in the nymph, by the shape of the gills, the lack of a median projection on the clypeus, and the presence of setae on the apical  $\frac{3}{4}$  of the labrum.

Based on the structure of the male genitalia and body size, two distinct subgenera can be distinguished within *Hermanella*. The nymphs of these

subgenera exhibit less marked differences in body size and width of emargination of the labrum.

***Hermanella (Hermanella)*  
Needham and Murphy, 1924**

**Imago.** Length: male body 5.4–8; forewings 6.25–8.5; female body 6.7–6.9; forewings 8.2–8.5. Male subgenital plate with broad projections at base of forceps (Fig. 20, 21); penes with ventral projections broad, lobelike. Femora lacking distinct black band in basal third.

**Mature Nymph.** Length: <8. Labrum with broad V-shaped median emargination (Fig. 54). Legs with dorsal setae of tibiae long, outer margins of tibiae with scattered setae. Femora lacking black spot on basal third.

**Egg.** Unknown.

**Type Species.** *Hermanella thelma* Needham and Murphy 1924.

**Species Included.** *H. (H.) thelma* Needham and Murphy; *H. (H.) guttata*, n. sp.

**Discussion.** *Hermanella* (s.s.) has been collected only in a limited area of the rios Paraná and Uruguay in the vicinity of Iguazú. Characters given above will distinguish *Hermanella* (s.s.) from the subgenus *Guayakia*.

***Hermanella (Hermanella) thelma*  
Needham and Murphy  
(Fig. 20, 53–64)**

*Hermanella thelma* Needham and Murphy 1924: 40; Lestage 1931: 57; Traver 1947: 158; Edmunds et al. 1976: 221; Hubbard 1982: 264.  
*Hermanella velma* Spieth 1943: 8 (error).

**Mature Nymph.** Body length: 3.4–4.0. General coloration blackish brown. **Head:** dark brown, with triangular whitish spots over ocelli. Ocelli white with inner margins black. Eyes of male with upper portion reddish brown, lower portion black. Eyes of female black. **Antennae** dark brown, paler toward apex. **Mouthparts** (Fig. 53–59): clypeus, labrum, basal ½ and apex of mandibles, and segment 1 of labial palpi dark brown, remaining parts lighter. **Thorax:** nota and pleura dark brown, diffusely washed with black, sterna lighter. **Legs** (Fig. 62, 63): coxae, trochanters and femora blackish with basal light spot ventrally on femora, tibiae and tarsi light brown with black basal and subapical band on tibiae and in basal ½ of tarsi. Dorsal spines on prothoracic tibia long (Fig. 63). Claws blackish brown, lighter at base. **Abdomen:** terga almost uniformly black, sterna blackish on lateral margins, lighter on median line. **Gills** (Fig. 60 and 61): grayish at base, projections whitish. Caudal filaments light brown.

**Male Subimago.** In alcohol. Length: body, 5.4–5.8; forewings, 6.25–6.4; hind wings, 1.0–1.1. General coloration blackish brown. **Head:** yellowish, washed with black around base of antennae and

anterior margin. Upper portion of eyes brownish gray, lower portion blackish. **Antennae:** scape and pedicel blackish, flagellum light brown. **Thorax:** pronotum and metanotum light brown, heavily washed with black, especially on lateral and posterior margins; metanotum dark brown with sutures blackish; pleura and sternites yellowish, with coxal membrane and median area of sternites blackish. **Wings:** membrane translucent with costal and subcostal area grayish brown, lighter apically. Costa, Sc, and R<sub>1</sub> light brown, remaining veins grayish. **Legs:** coxae, trochanters, femora, and anterior tibiae blackish, lighter spots at base of femora and anterior tibiae; meso- and metathoracic tibiae and tarsi light yellow. **Claws** grayish. **Abdomen** blackish except median line of sternites lighter. **Genitalia** (Fig. 20): subgenital plate blackish, forceps and penes grayish brown with black stripe on each penis lobe. Spines of penes shaped as in Fig. 20. Caudal filaments yellowish white.

**Type Material.** HOLOTYPE: nymph; Iguazú Falls, Argentina, 25-I-20, J. C. Bradley, C. U. No. 636 (mounted on slide).

**Other Material Examined.** ARGENTINA: Misiones, 7 N, Río Iguazú, Cataratas, 23-IX-82, J. A. Bechara (3 in FAMU, 4 in IFML); 9 N, Río Iguazú, Arroyo Central, 23-IX-82, J. A. Bechara; 1 ♂ S, Bonpland, 15-II-85, E. Dominguez (IFML).

**Variations.** The younger nymphs are a little lighter with traces of an abdominal pattern and with pale areas along the median line of the terga.

**Discussion.** The redescription of this species is based on the holotype and some new material from the type locality. The description of the male subimago is based on the genitalia of our specimen, which clearly belongs to *Hermanella* (s.s.) and has an abdominal color pattern very similar to that of nymphal *H. (H.) thelma*. The nymphs of *H. thelma* can be distinguished from the nymphs of other species of the genus by the following combination of characters: legs lacking spots; dorsal spines on prothoracic tibiae relatively long (Fig. 63); abdominal terga almost completely blackish, with no apparent pattern; gills grayish at base with whitish projections. *Hermanella (H.) thelma* is most closely related to *Hermanella (H.) guttata* but can be distinguished from it by a darker body color and, in the adult, by a lack of spots on the wings.

**Biology.** The nymphs were collected under rocks in the shallow margins of the Río Iguazú.

***Hermanella (Hermanella) guttata*  
Dominguez and Flowers, new species  
(Fig. 4–6, 21, 22, 31, 32)**

**Male Imago.** In alcohol, one pair of wings and genitalia on slides. Length: body, 7.8–8; forewings, 8.3–8.5; hind wings, 1.2–1.3. General coloration orange-brown, wings spotted with brown. **Head:** light brown with median black line. Upper portion of eyes brownish gray, lower portion blackish. **Antennae:** scape and pedicel orange-brown, flagellum

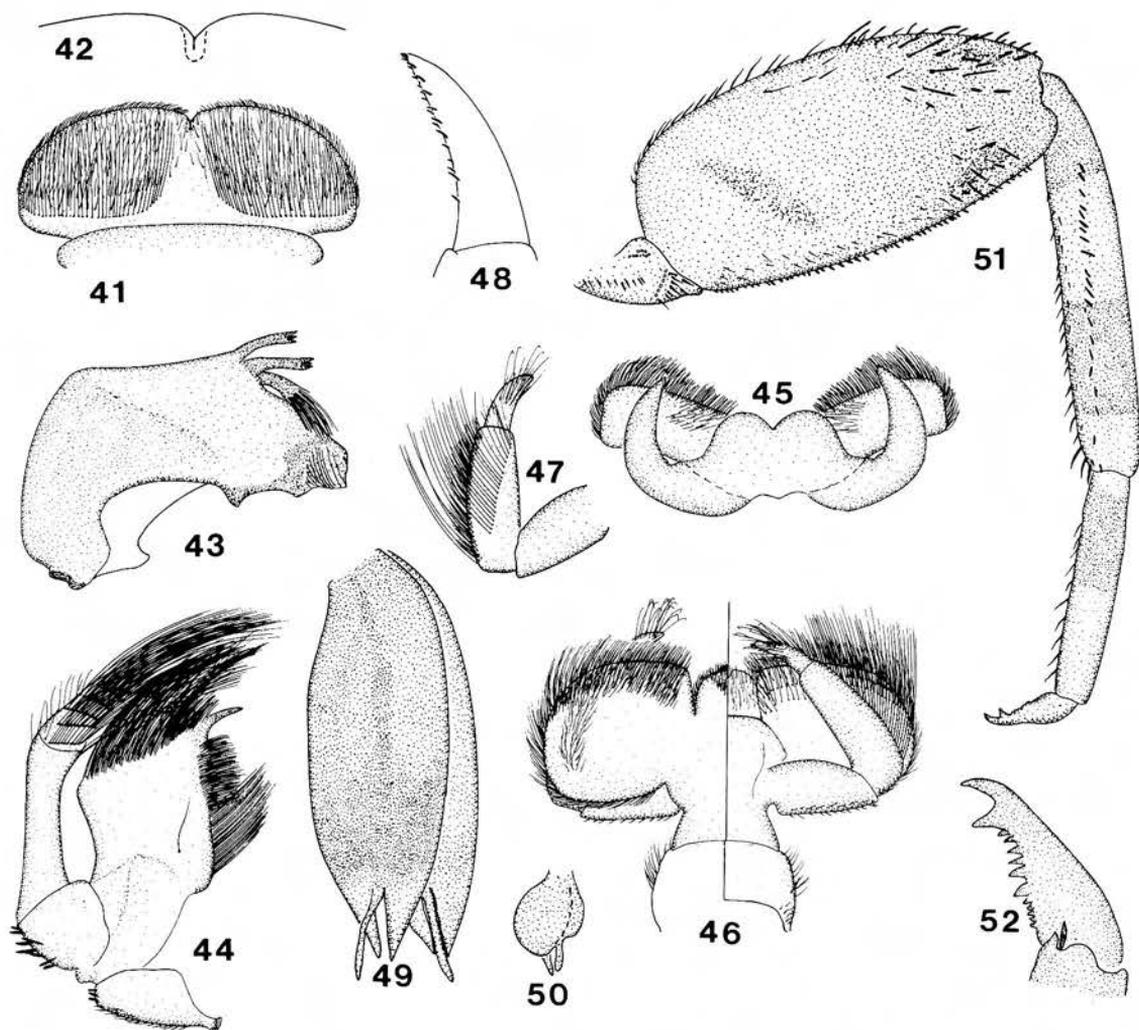


Fig. 41-52. *Hermanella* (G.) *maculipennis*, mature nymph. (41) Labrum. (42) Detail of anteromedian emargination. (43) Left mandible. (44) Maxilla. (45) Hypopharynx. (46) Labium (right, ventral view; left, dorsal view). (47) Detail, dorsal view of labial palpus. (48) Detail of third segment of labial palpus. (49) Gill 1. (50) Gill 7. (51) Foreleg. (52) Tarsal claw.

lighter. *Thorax*: pronotum light brown, median and paramedian lines and posterior margin black; mesonotum, pleurae, and sternites orange-brown, carinae darker; metanotum light brown, washed with black. *Wings* (Fig. 4-6): membrane hyaline, except costal and subcostal areas brown, lighter apically, wing bases brown. Longitudinal veins brown, lighter posteriorly; crossveins black, clouded with dark brown. *Legs*: forelegs light brown, lighter apically; coxae, lower margin of femora, and basal  $\frac{1}{4}$  of tibiae washed with black, black band at apex of tibiae and on tarsomeres 2 and 3, tarsomere 5 brown; tarsal claws grayish brown. Other legs broken off and lost. *Abdomen* (Fig. 31 and 32): all segments yellowish brown, terga 1, 2, 8-10 heavily washed with black, terga 3-7 with black markings as in Fig. 31. Sterna yellow-orange. *Genitalia* (Fig. 21, 22): subgenital plate yellow-orange

with broad spines, penes yellowish with ventral projections orange, shaped as in Fig. 22 (caudal filaments broken off and lost).

**Female Imago.** In alcohol. Length: body, 6.7-6.9; forewings, 8.2-8.5; hind wings, 1.4-1.6. Similar to male imago except as follows—*Head* whitish, spots between ocelli and posterior margin of head brownish; eyes black; mesonotum with yellow and black markings more extensive; *Wings* with basal  $\frac{1}{2}$  yellowish, brown clouds around crossveins more extensive; vein Sc of hind wings ending in a crossvein; coxae, trochanters and anterior tibiae yellow-orange, remainder of foreleg and meso- and metathoracic legs yellowish, black bands at apex of all femora and anterior tibiae; claws brownish; abdominal terga with markings darker, sterna yellowish with apical  $\frac{2}{3}$  of each segment and ganglial areas blackish. Caudal filaments yellowish white.

**Mature Nymph.** In alcohol, mouthparts on slide. Body length 7–7.5. General coloration orange-brown. *Head* orange-brown. Eyes of female black. *Antennae* yellowish, lighter apically. *Mouthparts*: clypeus and labrum orange-brown, other mouthparts light orange, except basal  $\frac{1}{2}$  darker. Thorax, legs, and abdomen as in male imago, but more orange. Dorsal spines on prothoracic tibiae long (but not so long as in *H. thelma*). Claws as in Fig. 64. *Gills* whitish with median area washed with grayish black. Caudal filaments orange.

**Etymology.** *guttatus*, L., meaning spot.

**Type Materials.** HOLOTYPE: ♂ imago, Argentina, Misiones, Panambi, 20-XI-80, E. Dominguez (IFML). ALLOTYPE: ♀ imago, Argentina, Misiones, confluencia Alegre–Piray Guazú, 3–4-XI-86, E. Dominguez (IFML). PARATYPES: ARGENTINA: 1 ♀ I, same data as allotype (FAMU). URUGUAY: Paysandú, 1 ♀ I, Santa Rita, Río Uruguay, 8-XI-55, C. S. Carbonell (URU). BRAZIL: Paraná, 2 ♀♀ I, Guairá (650'), 10-III-69, W. L. & J. G. Peters (1 in FAMU, 1 in USP); 1 N, Rio Paraná, Sete Quedas, 5 km S Guairá (650'), 11-III-69, W. L. & J. G. Peters (FAMU). PARAGUAY: 1 ♂ S, Salto de Guairá, 30-XI-71, L. E. Peña G. (NMNH).

The association of the adults and nymphs is based on the abdominal color pattern and wing pattern (wing extracted from the nymphal wing pad).

**Variations.** The female paratypes are lighter in color and the clouds around the crossveins are less extensive than in the allotype.

**Discussion.** *H. guttata* can be separated from the other species of *Hermanella* by the following combination of characters. In the imago: wings with brown spots as in Fig. 4–6; legs lacking spots on bases of femora; abdominal color pattern as in Fig. 31, 32; ventral projections on penes as in Fig. 22. In the nymph: legs lacking a prominent spot on femora; labrum bearing a broad V-shaped median emargination. *Hermanella (H.) guttata* is most closely related to *H. (H.) thelma* but can be distinguished from it by its spotted wings and lighter body color in the adults and nymphs.

**Biology.** Unknown.

### *Hermanella (Guayakia)*

#### Dominguez and Flowers, new subgenus

**Imago.** Length: male body, 7.9–8.8; forewings, 8.5–9.0; female body, 7.5–10.8; forewings, 10.0–12.5. Male subgenital plate with slender projections at base of penes; penes with ventral projections curved, spinelike (Fig. 19). Femora with distinct black band in basal third.

**Mature Nymph.** Labrum with narrow slitlike median emargination (Fig. 42). Length exceeding 9.0. Legs with dorsal setae of tibiae shorter than in *Hermanella* (s.s.), outer margins of tibiae glabrous. Femora with black spot in basal third.

**Egg.** Chorion with KTCs distributed evenly (Fig. 57).

**Etymology.** Guayakí; Indian tribe in Misiones region.

**Type Species.** *Thraulius maculipennis* Ulmer.

**Species Included.** *H. (G.) maculipennis* (Ulmer); *H. (G.) grandis*, n. sp.

**Discussion.** This subgenus appears to be distributed in the upper reaches of the Iguazú and Uruguay rivers.

### *Hermanella (Guayakia) maculipennis (Ulmer)*, new combination

(Fig. 1–3, 16, 19, 41–52, 87)

*Thraulius maculipennis* Ulmer 1920a: 30; Needham & Murphy 1924: 44; Ulmer 1943: 28.

*Traverella maculipennis* Edmunds 1950: 551; Hubbard 1982: 267.

**Male Imago.** In alcohol. Length: body, 7.9–8.75; forewings, 8.5–9.0; hind wings, 1.15–1.35. General coloration orange-brown, washed with black; wings (Fig. 13) spotted with brown. *Head*: yellowish gray, anterior margins black. Upper portion of eyes light brown, lower portion black. *Antennae*: scape and pedicel orange-yellow, flagellum light brown. *Thorax*: pronotum light brown with median and paramedian lines and lateral margins black; mesonotum yellow-brown, washed with black, carinae and sutures darker; metanotum light brown, washed with black; pleura and sterna yellowish, with membranous parts, basi- and furcasterna washed with black. *Wings* (Fig. 1–3): membrane hyaline; costal and subcostal area light brown, lighter apically. Longitudinal veins yellow-brown, crossveins dark brown clouded with brown. *Legs*: yellowish orange, tarsi yellowish white, coxae washed with black; femora with prominent spots on basal  $\frac{1}{3}$  and apex, tibia with band at apex black. Claws grayish orange. *Abdomen* (Fig. 29, 30): all segments light brown, terga 1–4 almost completely washed with black, tergum 4 with anterior margin and 2 sublateral spots lighter, terga 5–7 as in Fig. 29; terga 8–10 with anterior medial macula and posterior margins blackish; posterior  $\frac{3}{4}$  of sternites washed with black. *Genitalia* (Fig. 19): subgenital plate, segment 1 of forceps, and penis lobes yellow-brown, forceps segments 2 and 3 yellowish white, lateral swellings of penes darker, projections spinelike, orange-brown, narrow as in Fig. 19. Caudal filaments yellowish white, with basal  $\frac{1}{5}$  of each segment black.

**Female Imago.** In alcohol. Length: 7.5–8.3; forewings, 10.0–10.5; hind wings, 1.25–1.5. Similar to male imago except as follows: head grayish white, anterior margin and area at base of antennae washed with black, eyes black, antennae with scape and pedicel light yellow, flagellum grayish; abdomen with black markings more extensive than male; caudal filaments yellowish with narrow black ring at base of each segment.

**Mature Nymph.** In alcohol. Body length: 9.5–10. General coloration orange-brown. *Head*: orange-brown washed with black. Upper portion of

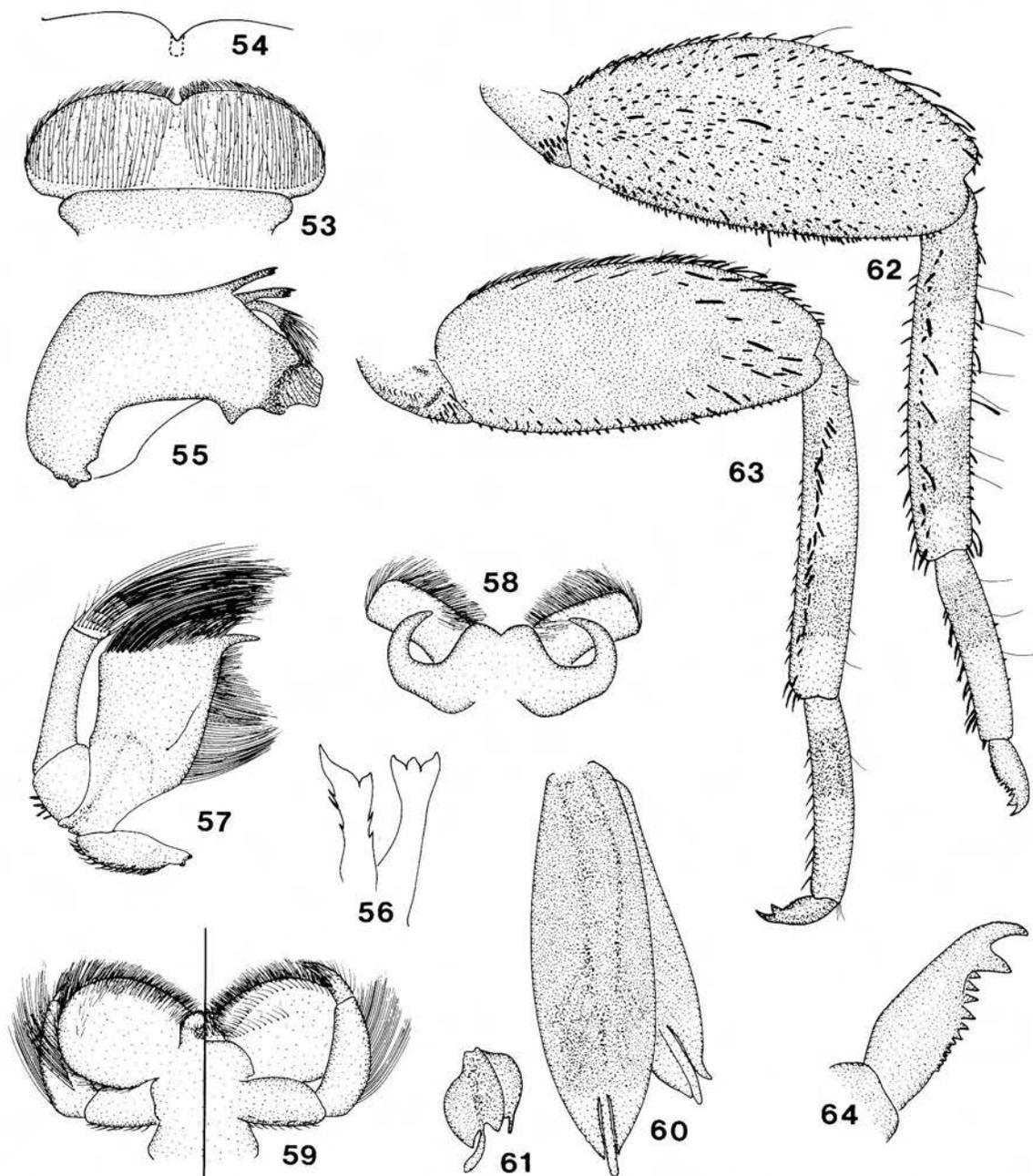


Fig. 53-64. *Hermanella (H.) thelma*, mature nymph. (53) Labrum. (54) Detail of anteromedian emargination. (55) Left mandible. (56) Detail of incisor, right mandible. (57) Maxilla. (58) Hypopharynx. (59) Labium (right, ventral view; left, dorsal view). (60) Gill 1. (61) Gill 7. (62) Metathoracic leg. (63) Foreleg. (64) Tarsal claw. (Fig. 53-55, 57-59 drawn from holotype.)

male eyes reddish brown, lower portion black. Eyes of female black. *Antennae*: scape and pedicel brown, flagellum yellow-orange. *Mouthparts*: clypeus and labrum orange-brown, remaining mouthparts light orange, except basal 1/2 of mandibles darker. Thorax, legs, and abdomen as in male imago, but redder. Dorsal spines on anterior tibiae short. Claws as in Fig. 52. *Gills* blackish, apex grayish. Caudal filaments reddish.

**Type Material.** HOLOTYPE: ♂ imago, Sta. Catarina, Humboldt, Isabela, Brazil, 1-XI-10, W. Ehrhardt (MH).

**Other Material Examined.** BRAZIL: Paraná, 5 ♂♂ I, 19 ♀♀ I, 2 ♂♂ S, Rio dos Patos, 3 km E of Prudentópolis (2,300 m), 2-3-III-69, W. L. & J. G. Peters (3 ♂♂ I, 8 ♀♀ I, 1 ♂ S in FAMU, remainder in USP); 2 N, Guapuava, Rio Coitinho (1,100 m), III-63, F. Plaumann (1 in FAMU, 1 in USP); 8 N,

Guapuava, Rio Jacutinga (500 m), IV-62, F. Plaumann (4 in FAMU, 4 in USP). ARGENTINA: Misiones, 8 ♀♀ I, Bonpland, Arroyo Martires, 26-XI-86, E. Dominguez (IFML); 13 ♀♀ I, Mado, 16-II-1985, E. Dominguez (IFML).

The association of adults and nymphs was based on abdominal and leg markings.

**Variations.** The markings on the abdominal pattern vary in size among individual adults and are very poorly defined in the nymphs.

**Discussion.** Because the holotype was almost completely faded, this species is redescribed based on new material. This species can be separated from the other *Hermanella* species by the following combination of characters. In the imago: wings with brown spots as in Fig. 1-3; legs bearing a black spot on basal 1/2 of femora; abdominal color pattern is as in Fig. 29, 30; spines of penes narrow, curved (Fig. 19). In the nymph: legs bearing a prominent spot on basal 1/2 of femora; spines on anterior tibiae short (Fig. 51); labrum bearing a narrow, slitlike median emargination (Fig. 42).

**Biology.** Adults of *H. (G.) maculipennis* were collected at Rio dos Patos at a light trap just at dark, and adults were seen flying over the river at dusk in rather large swarms.

***Hermanella (Guayakia) grandis*  
Dominguez and Flowers, new species**  
(Fig. 7-9, 33 and 34)

**Female Imago.** In alcohol, one set of wings and legs on slide. Length: body, 10.4-10.8; forewings, 12.0-12.5; hind wings, 1.6-1.8. General coloration yellow-brown. **Head:** light yellow, with whitish areas between ocelli and inner margins of eyes; sutures blackish. Eyes black. **Antennae:** scape and pedicel light brown, flagellum grayish. **Thorax:** pronotum and metanotum light brown, heavily washed with black, especially along median line; metanotum yellow-brown, slightly washed with black; pleura and sterna light brown, heavily washed with black. **Wings** (Fig. 7-9): membrane hyaline, costal and subcostal area orange-brown, lighter apically, base of wings yellowish. Costa, Sc, and R<sub>1</sub> orange-brown, remaining longitudinal and crossveins yellow, lighter posteriorly. Legs orange-brown, coxae and trochanters washed with black, black spots on basal half and apex of femora; anterior tibiae blackish, darker at apex; small black band at apex of mesothoracic tibiae. Claws grayish. **Abdomen** (Fig. 33, 34): yellowish brown, heavily washed with black, especially at median and lateral areas, segments lighter toward apex of abdomen. Caudal filaments blackish brown, lighter toward apex.

**Male Imago.** Unknown.

**Mature Nymph.** In alcohol. Body length: 10.0-12.5. General coloration orange-brown. **Head:** orange-brown with lighter spots around ocelli. Ocelli white with inner margins black. Upper portion of male eyes reddish brown, lower portion black. Eyes

of female black. **Antennae:** scape and pedicel brownish, flagellum yellow-orange. **Mouthparts:** clypeus, labrum, incisors, prosthecae, basal 1/2 of mandibles, and most maxillae light orange-brown, remaining parts lighter. **Thorax:** terga orange-brown, pleura and sterna yellowish brown with ganglial areas blackish. Wing pads of larger nymphs with darkened outer margins. **Legs:** orange-brown, with black spot on basal 1/2 and apex of femora, prothoracic tibiae blackish, small black spot at apex of mesothoracic tibiae; dorsal spines on mesothoracic tibiae short. Claws as in Fig. 52. **Abdomen** orange-brown, with black markings as in female imago. **Gills** black with apex grayish. Caudal filaments brownish orange, lighter apically.

**Etymology.** *grandis*, L., meaning large.

**Type Material.** HOLOTYPE: ♀ imago, Misiones, San Vicente, Inta, Argentina, 30-XII-86, E. Dominguez (IFML). PARATYPES: ARGENTINA: 6 ♀♀ I, same data as holotype (3 in IFML, 3 in FAMU). BRAZIL: Santa Catarina, 1 N, Tupitinga, Rio Santa Cruz (700 m), XII-62, F. Plaumann (3 in IFML, 4 in FAMU, 3 in USP); 15 N, Rio Irani, IV-62, F. Plaumann (8 in FAMU, 7 in USP); 5 N, Rio Irani, XI-62 (3 in FAMU, 2 in USP). Paraná, 1 N, Guapuava, Rio Chalquim (1,200 m), III-63, F. Plaumann (FAMU); 5 N, Guapuava, Rio Coitinho (3 in FAMU, 2 in USP).

The association between nymphs and female imagines was made by legs, abdominal pattern, and wing pattern (subimaginal wing extracted from the nymphal wing pad).

**Discussion.** This species is described because the females are very distinct from those of other known *Hermanella*. The nymphs are similar to those of *H. maculipennis* but can be distinguished when mature by the adult color pattern, which is visible through the nymphal integument, and by the larger body size of *H. grandis*.

*Hermanella grandis* can be separated from the other species of the genus by the following combination of characters. In the female imago: wing length 12.0-12.5; abdominal and wing color patterns as in Fig. 7-9, 33, 34; black spots present on basal 1/2 and apex of femora. In the nymph: abdominal gills blackish; dorsal spines on anterior tibiae short; black spots present on basal 1/2 of femora; wing pads with dark outer margins.

**Biology.** The females were attracted to light.

**Genus *Hyliaster* Dominguez and Flowers,**  
new genus

(Fig. 10-12, 17, 23-25, 35, 36, 39, 40, 65-74, 88)

**Imago.** Length of male: body, 9.5-10.5; forewings, 10.2-10.4; hind wings, 2.0-2.2. Length of female: body 8.7-9.0; forewings, 11.6-12.1; hind wings, 1.5-1.7. **Head:** eyes of male separated on meson of head by a distance equal to lateral ocellus, lower portion of eyes 1/2 length of upper portion; eyes of female separated on meson of head by 5 times maximal width of lateral ocellus. Prosternum

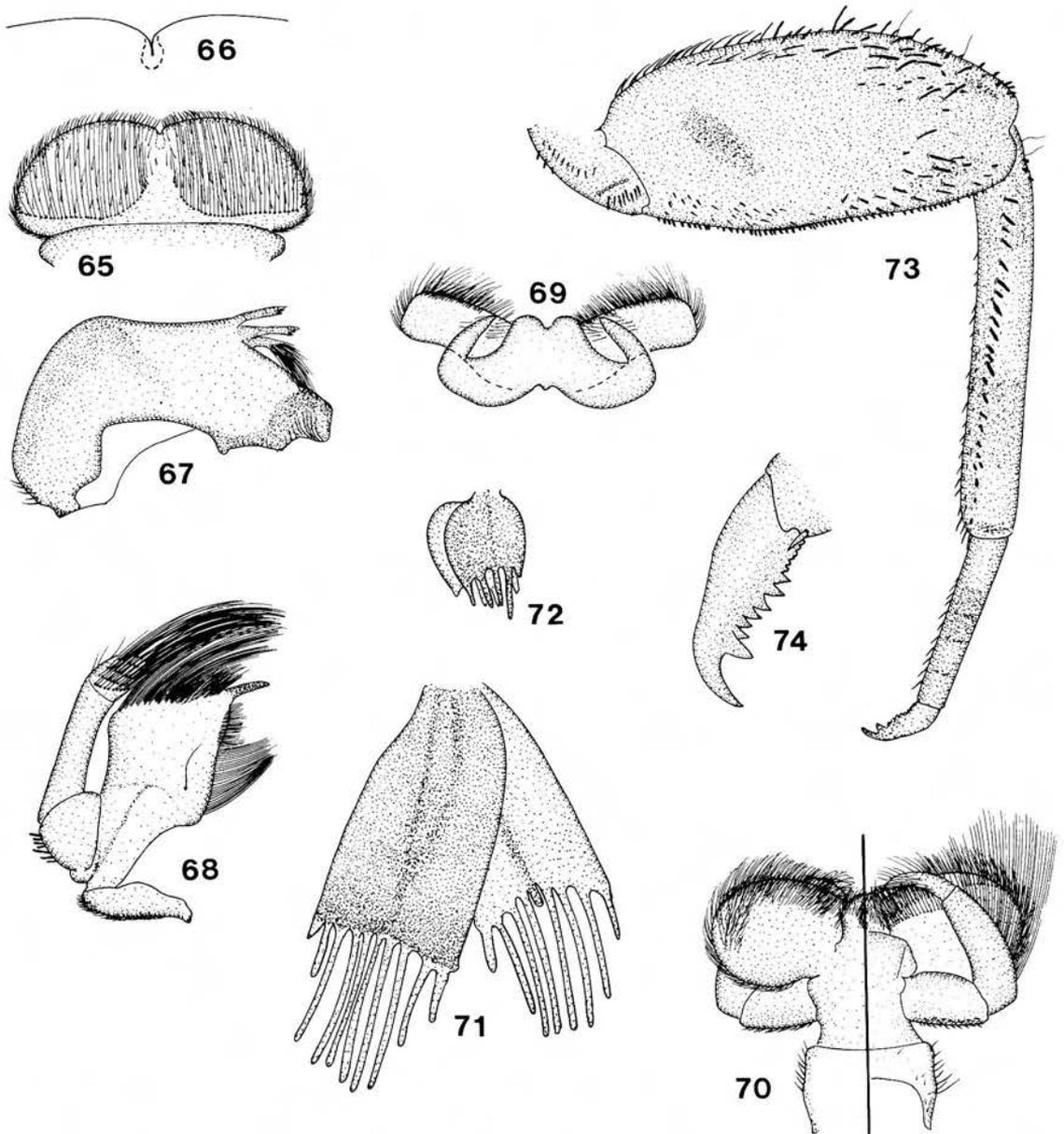


Fig. 65-74. *Hylister plaumanni*, mature nymph. (65) Labrum. (66) Detail of anteromedian emargination. (67) Left mandible. (68) Maxilla. (69) Hypopharynx. (70) Labium (right, ventral view; left, dorsal view). (71) Gill I. (72) Gill 6. (73) Foreleg. (74) Tarsal claw.

with a narrow straight median carina (Fig. 17). *Wings* (Fig. 10-12): maximal width of forewings slightly more than  $\frac{1}{3}$  maximal length; maximal width of hind wings  $\frac{3}{5}$  maximal length; maximal length of hind wings  $\frac{1}{6}$ - $\frac{1}{7}$  maximal length of forewings. Vein Rs of forewing forked slightly more than  $\frac{1}{2}$  distance from base of vein to margin (Fig. 10); vein MA forked slightly less than  $\frac{1}{2}$  distance from base of vein to margin, fork asymmetrical, crossvein above fork in MA slanted, vein MA<sub>2</sub> strongly sagged; vein MP forked slightly more than  $\frac{1}{3}$  distance from base to margin, fork slightly asym-

metrical; vein ICu<sub>1</sub> attached at base to vein CuA or free basally; vein ICu<sub>2</sub> free basally. Hind wings (Fig. 11 and 12) with costal projection well developed, located  $\frac{2}{3}$  distance from base to apex of wing, acute, rounded at apex. Vein MP unforked; apex of wings rounded, rather acute; vein Sc ending slightly more than  $\frac{2}{3}$  distance from base to wing margin, ending in a crossvein; 9 or 10 crossveins present. *Legs*: ratios of segments in male forelegs, 0.65:1.00 (2.25 mm):0.09:0.36:0.29:0.13:0.09. Claws of a pair dissimilar, one apically hooked, the other blunt, padlike, as in Fig. 39. *Male genitalia* (Fig.

23–25): segment 2 of forceps  $\frac{1}{2}$  length of segment 1, subequal to segment 3; segment 1 slightly curved and narrowed gradually from base to apex. Subgenital plate lacking spines. Basal  $\frac{1}{2}$  of penes with swollen lateral margins, penes divided in apical  $\frac{1}{4}$ , each lobe with a curved ventral spine and a groove beneath it (Fig. 24, 25). Ninth sternum of female cleft apically (Fig. 40). Terminal filament longer than cerci.

**Mature Nymph.** *Head* prognathous. *Antennae* 2.5–3 times length of head. *Mouthparts* (Fig. 65–70): lateral margins of clypeus strongly concave; maximal width of labrum 1.2 times wider than maximal width of clypeus; length of labrum little more than  $\frac{1}{2}$  maximal width, lateral margins rounded as in Fig. 65; anteromedian emargination shallow, V-shaped dorsally; deep, U-shaped ventrally (Fig. 66); divided row of long dorsal setae approximately  $\frac{1}{2}$  distance from anterior margin of labrum, 35 or more setae on each side; numerous short setae on apical  $\frac{1}{2}$  of labrum, margins lined with short setae. *Left mandible* (Fig. 67): outer margin curved, angle rounded; a few short, thick setae near basal articulation. *Maxillae* (Fig. 68): galealacinia with one long thick seta on venter close to inner margin; subapical pectinate setae lacking; prominent tusk present on inner apical angle. Segments 1 and 3 of maxillary palpi subequal, each slightly more than  $\frac{1}{2}$  length of segment 2; segment 1 with thick setae on outer margin, segment 2 with two long setae on inner apical angle, segment 3 with long setae in ordered rows. *Lingua* of hypopharynx with well-developed lateral processes, anterior margin with median V-shaped cleft; superlinguae as in Fig. 69. *Labium* (Fig. 70): segment 1 of palpi  $\frac{1}{2}$  length of segment 2, segment 3 approximately  $\frac{1}{10}$  of segment 2; segment 3 curved, with long setae on ventral surface and external margin, and short spines on inner margin; segment 2 elbowed with a dorsal row of setae; glossae straight, flat, with short setae along anterior margin; paraglossae (Fig. 70) with subapical row of long setae on ventral surface; submentum with thick setae laterally, short setae ventrally. Anterolateral margins of pronotum with small stout setae. *Wing pads* pilose. *Legs* (Fig. 73): coxae with some scattered spines, trochanters with row of setae on apicodorsal surface; anterior femora with long blunt or spatulate setae along posterior (dorsal) margin and subapical area, short spines along inner margin, metathoracic femora with long setae along posterior margin only, remainder of dorsal surface evenly covered with small spines; tibiae with rows of short setae on inner and dorsal surfaces, metathoracic tibiae with short and long blunt setae along outer margins; tarsi with spines along inner margins and setae along outer margins; apex of claws hooked, narrow, denticles small on basal third, larger in middle; subapical denticle very large (Fig. 74). *Gills* (Fig. 71, 72): gills on segments 1–6, platelike, biramous; each gill truncated apically in wide V-shaped cleft; 8–10 projections along posterior

margin on gills 1–5, 3 or 4 on gill 6; dorsal and ventral portion of gills similar. Posterolateral projections on abdominal segments 7–9, progressively larger posteriorly. Posterior margins of terga with spines and setae alternating. Terminal filament longer than cerci, caudal filaments with small spines on posterior margin of each segment.

**Egg.** Chorion with KTCs at poles, lacking in central area (Fig. 88).

**Etymology.** *hylister*, Gr., m. Sieve.

**Type Species.** *Hylister plaumanni*, n. sp.

**Species Included.** *Hylister plaumanni*, n. sp.

**Distribution.** Southeastern Brazil.

**Discussion.** *Hylister* can be separated from the other genera of Leptophlebiidae by the following combination of characters. In the imago: forks of veins MA and MP of forewings asymmetrical, a slanted crossvein present at MA fork; vein MP of hind wings not forked; costal projection of hind wings (Fig. 14, 15) acute; vein Sc of hind wings ending in a crossvein at  $\frac{2}{3}$  distance from wing base to margin; penes divided on apical  $\frac{1}{4}$ , each lobe bearing a ventral spine and lying above a groove (Fig. 24, 25), basal  $\frac{1}{2}$  of penes swollen; subgenital plate lacking projections (Fig. 23); a narrow straight median carina present on prosternum (Fig. 17). In the nymph: labrum as wide as head, dorsal setae as in Fig. 65, clypeus lacking dorsal projection; filtering setae on maxillary palpi in ordered rows (Fig. 68); tarsal claws bearing a large subapical denticle (Fig. 74); gills (Fig. 71, 72) on segments 1–6 are platelike, truncated apically with 8–10 fringes; posterolateral spines present on abdominal segments 7–9.

*Hylister* is most closely related to *Hermanella* and can be distinguished from it by the lack of imaginal subgenital plate spines in the male and, in the nymph, by the shape of the gills and the lack of a seventh pair of gills.

***Hylister plaumanni* Dominguez and Flowers,  
new species**

(Fig. 10–12, 17, 23–25, 35, 36, 39, 40, 65–74, 88)

**Male Imago.** In alcohol, one pair of wings and genitalia on slides. Length: body, 9.5–9.8; forewings, 10.2–10.5; hind wings, 2.0–2.2. General coloration: yellow-brown, abdomen stained with black. *Head*: yellowish washed with black on anterior margins close to eyes. Upper portion of eyes yellowish, lower portion blackish. *Antennae*: scape and pedicel yellowish, slightly washed with black (flagellum broken off and lost). *Thorax*: pronotum yellowish with lateral and posterior margins and median and paramedian areas blackish; mesonotum light brown, margins and carinae darker; metanotum yellowish washed with black; pleura light brown, with margins of sclerites darker; sterna light brown, washed with black. *Wings* (Fig. 10–12): membrane of forewings hyaline, costal and subcostal areas light brown, darker at base, stigmatic area translucent, wing base brown. *Costa*

brown, Sc and R<sub>1</sub> light brown, remaining longitudinal veins yellowish; crossveins in costal and subcostal area yellowish, remaining crossveins whitish. Membrane of hind wings hyaline, brown spot at base; costa brownish, remaining longitudinal veins light yellow, crossveins whitish. *Forelegs* brownish yellow, coxae, trochanter, basal ½ and outer margin of femora washed with black; basal and apical black rings on tibiae and basal ¾ of each tarsomere washed with black, darker apically. Claws grayish. All other legs broken off and lost. *Abdomen* (Fig. 35, 36): all segments yellowish, terga 1–2 heavily washed with black, terga 3–5 with median line, posterior margin and lateral third washed with black; terga 6–7 with black markings as in Fig. 35; sterna 1–7 uniformly washed with blackish, ganglial areas darker. *Genitalia* (Fig. 23–25): subgenital plate light yellow-orange, penes and forceps yellowish, spines of penes orange. Caudal filaments yellowish white, basal ½ of each segment black.

**Female Imago.** In alcohol. Length: body 8.75–9; forewings, 11.8–12; hind wings, 1.6–1.7. Similar to male imago except as follows: head with margins anterior to eyes black, base of antennae brownish; eyes blackish; antennae with flagellum light brown at base, whitish apically; meso- and metathoracic legs whitish yellow, with coxae and trochanters lightly washed with black; apices of femora and tibiae and tarsi of mesothoracic legs, and spot on apices of metathoracic femora, black; claws blackish brown; abdominal markings more diffuse than in male (caudal filaments broken off and lost).

**Mature Nymph.** In alcohol. Body length: 10–14. General coloration: orange-brown. *Head*: orange-brown, with black spot between eyes and base of antennae and black area between lateral ocelli and eyes; triangular spot in front of median ocelli whitish. Upper portion of male eyes reddish brown, lower portion black; eyes of female black. *Antennae*: scape and pedicel light brown, flagellum yellowish, paler toward apex. *Mouthparts* (Fig. 65–70): light orange-brown; posterior margin of labrum, segment 1 of maxillary palpi, and basal ¼ of segment 1 of labial palpi darker; central area of mandibles shaded with black. Thorax orange-brown, membranous portions of pleura grayish. *Legs* (Fig. 73): orange-brown with a basal grayish spot on anterior femora, dark bands subapically on tibiae and middle of tarsi. *Abdomen*: terga and sterna orange-brown, darker posteriorly, markings as in male imago. *Gills* (Fig. 71, 72) grayish, fringes whitish. Caudal filaments brown.

**Etymology.** Plaumann, for Fritz Plaumann who collected many mayfly specimens in the *Hermanella* generic complex.

**Type Material.** HOLOTYPE: ♂ imago, Paraná State, Rio Ipiranga, Estrada do Itapua, Brazil, 2,400', 21–23-II-69, W. L. & J. G. Peters (USP). ALLOTYPE: ♀ imago, same data as holotype (USP). PARATYPES: BRAZIL: Paraná, 1 ♀ I, 2 ♂♂ S (FAMU); 46 N, same data as holotype (12 in USP,

20 in FAMU, 12 in IFML). Santa Catarina, 7 N, Nova Teutonia, XI-63, F. Plaumann; 1 N, Rio Iquererim, XI-65, F. Plaumann. Minas Gerais, 14 N, Levantina, Rio Can-Can, IX-63, W. Sattler (UU). Rio de Janeiro, 1 N, Km 44, Cachoeiras de Macacu, 25-IV-77, C. M. & O. S. Flint (NMNH).

The association of the adult and nymph was made from rearings by W. L. Peters and J. G. Peters.

**Variations.** In the nymphs from Paraná, the color varies in different specimens from light brown to dark orange-brown, apparently related to the size. In some specimens the color pattern is less conspicuous than described.

**Discussion.** This species has been collected from both the Iguazú and Uruguay drainages as well as the Atlantic coastal drainage in southeastern Brazil.

**Biology.** Rio Ipiranga is a mountain stream of moderate size with nearly 100% canopy shade. During February 1969, the river was at low level, and boulders and gravel were covered with some algae, although the stream current was strong. Nymphs were collected under medium-sized to large rocks, and subimagines were collected at light traps during complete darkness.

#### Genus *Needhamella* Dominguez and Flowers, new genus

(Fig. 13–15, 18, 26–28, 37, 38, 75–86, 89, 90)

**Imago.** Length of male: body, 8.1–9.2; forewings, 8.2–9.5; hind wings, 1.2–1.8. Length of female: body, 8.5–9.0; forewings, 8.75–10.0; hind wings, 1.3–1.7. *Head*: eyes of male separated on meson of head by distance equal to width of lateral ocellus, lower portion ¾ length of upper portion; eyes of female separated on meson of head by 5 times maximal width of lateral ocellus. Prothorax wider than in *Hermanella* and *Hylister*, narrowed in middle (Fig. 18). *Wings* (Fig. 13–15): maximal width of forewings slightly less than ½ maximal length; maximal width of hind wings ½ maximal length; maximal length of hind wings ⅓–¼ maximal length of forewings. *Forewings* (Fig. 13): vein Rs forked slightly more than ½ distance from base of vein to margin; vein MA forked slightly less than ½ distance from base of vein to margin, fork asymmetrical, crossvein above fork in MA slanted, vein MA<sub>2</sub> strongly sagged; vein MP forked ⅓ distance from base to margin, fork slightly asymmetrical; vein ICu<sub>1</sub> attached at base to vein CuA by a crossvein or free basally; vein ICu<sub>2</sub> free basally. *Hind wings* (Fig. 14, 15) with costal projection well developed, acute, rounded at apex; located ⅓ distance from base to apex of wings. Vein Sc ending slightly more than ½ distance from base to wing margin, ending in crossvein; vein MP unforked; apex of wings rounded, rather acute; 9 or 10 crossveins present. *Legs*: ratios of segments in male forelegs, 0.70:1.00 (2.6 mm):0.10:0.3:0.25:0.14:0.07. Claws of a pair dissimilar, one apically hooked, the other blunt, padlike. *Male genitalia* (Fig. 26–28): subgen-

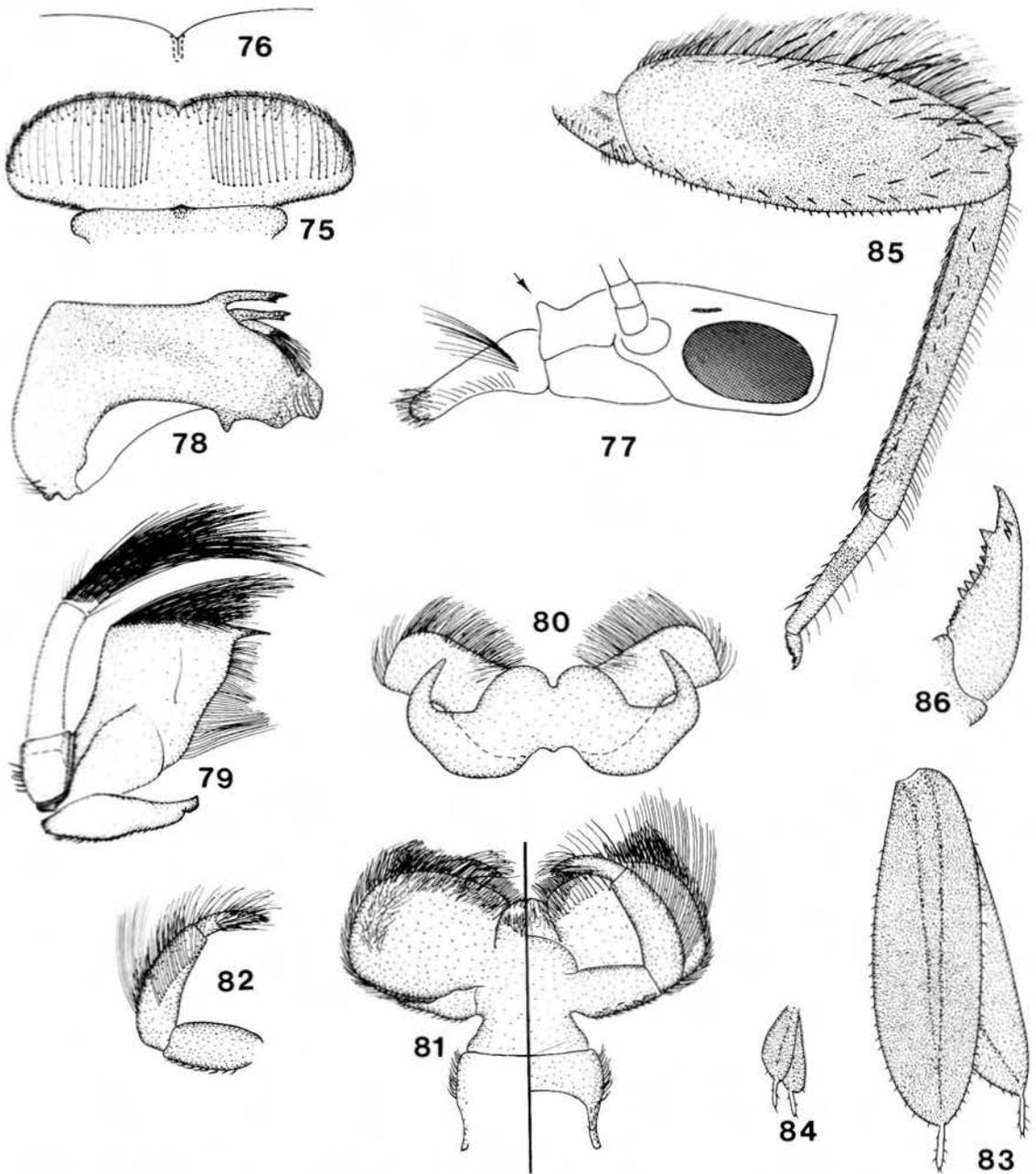


Fig. 75-86. *Needhamella ehrhardti*, mature nymph. (75) Labrum. (76) Detail of anteromedian emargination. (77) Lateral view of head capsule showing clypeal projection. (78) Left mandible. (79) Maxilla. (80) Hypopharynx. (81) Labium (right, ventral view; left, dorsal view). (82) Detail, dorsal view of palpus. (83) Gill 1. (84) Gill 7. (85) Foreleg. (86) Tarsal claw.

ital plate with spines close to base of forceps; segment 2 of forceps  $\frac{1}{2}$  length of segment 1,  $1\frac{1}{4}$  length of segment 3; segment 1 strongly curved and narrowed gradually from base to apex. Basal  $\frac{1}{3}$  of penes with swollen lateral margins; penes divided in apical  $\frac{1}{2}$ , each lobe with a curved median spine. Ninth sternum of female cleft apically (as in Fig. 40). Terminal filament longer than cerci.

**Mature Nymph.** *Head* prognathous. *Antennae* 2-2.5 times length of head. *Mouthparts* (Fig. 75-82): clypeus with lateral margins strongly concave, anterior margin with small dorsal projection (Fig. 77). Maximal width of labrum 1.6-1.7 times maximal width of clypeus; length of labrum less than  $\frac{1}{2}$  maximal width, lateral margins rounded as in Fig. 75 with posterolateral angulation; anterome-

dian emargination narrow, V-shaped dorsally, deep and U-shaped ventrally (Fig. 76); divided row of long dorsal filtering setae about  $\frac{2}{3}$  distance from anterior margin of labrum, 20–25 setae on each side; a few short setae on anterior  $\frac{1}{4}$  of labrum, lateral and anterolateral margins lined with short setae. *Left mandible* (Fig. 78): outer margin angularly curved, angle sharp; a few short, thick setae near basal articulation. *Maxillae* (Fig. 79): galealacinia with one long thick seta on venter close to inner margin; subapical pectinate setae lacking; prominent tusk on inner apical angle. Segment 1 of maxillary palpi  $\frac{2}{3}$  length of segment 2; segment 3 approximately  $\frac{1}{2}$  length of segment 2; segment 1 with thick setae on outer margin, segment 2 with two long setae on inner apical angle, segment 3 with long setae in ordered rows. Lingua of hypopharynx with well-developed lateral processes, anterior margin with median U-shaped cleft; superlinguae (Fig. 80) with long setae along anterior margin. *Labium* (Fig. 81, 82): segment 1 of palpi  $\frac{1}{2}$  of segment 2, segment 3  $\frac{2}{3}$  of segment 2; segment 3 curved, with long setae on ventral surface and external margin, short spines on inner margin; segment 2 elbowed with dorsal row of setae (Fig. 82); glossae straight, flat, with short setae along anterior margin; paraglossae (Fig. 81) with subapical row of long setae on ventral surface; submentum with 10–12 setae laterally. Anterolateral margins of pronotum with 3 large setae. Wing pads glabrous. *Legs* (Fig. 85): trochanters with row of setae on apicodorsal surface; anterior femora with thick, long, pointed setae along posterior margin and subapical area, short spines along inner margin; metathoracic femora with long setae along posterior margin only, remainder of dorsal surface evenly covered with small spines; tibiae with rows of small spinelike setae on inner and dorsal surfaces, tarsi with spinelike setae along inner margins; in addition, dense row of long fine setae on outer margins of all leg segments. Claws hooked, narrow, ventral denticles as in Fig. 86; two small lateral denticles at base of terminal hook. *Gills* (Fig. 83, 84): gills on segments 1–7, platelike, biramous; each gill ending in fingerlike process, fringed with small setae; dorsal and ventral portion of gills similar, main trachea along median line, gills smaller posteriorly. Posterolateral projections on abdominal segments 8–9, larger posteriorly. Posterior margins of terga with alternating spines and setae. Terminal filament longer than cerci, small spines on posterior margin of each segment.

**Egg.** Chorion with KTCs concentrated at poles, evenly distributed elsewhere (Fig. 89, 90).

**Etymology.** Named for James G. Needham, who described the first species of *Hermanella*; and *ella*, a common diminutive ending for mayfly genera.

**Type Species.** *Thraululus ehrhardti* Ulmer.

**Species Included.** *Needhamella ehrhardti* (Ulmer).

**Distribution.** Southern Brazil north to Goias State, Uruguay, northeastern Argentina, and southern

Paraguay. Nymphs in the *Hermanella* complex with gills like those of *Needhamella* occur in Amazonia, the northern Andes, and Central America; however, these nymphs differ in other respects from *Needhamella* and represent undescribed genera.

**Discussion.** The type species of *Needhamella* was described in *Thraululus* by Ulmer (1920a) and later transferred to *Traverella* by Edmunds (1950). Edmunds et al. (1976) included drawings of genitalia and gills of this species (as *Hermanella* sp.). A new genus is established for this species, because both nymphs and adults are distinctly different from *Hermanella*.

*Needhamella* can be separated from the other genera of Leptophlebiidae by the following combination of characters. In the imago: forks of veins MA and MP of forewings asymmetrical, with a slanted crossvein above the fork of MA; vein MP of hind wings unforked; costal projection of hind wings (Fig. 15) acute; vein Sc of hind wings ending in a crossvein slightly  $>\frac{1}{2}$  distance from wing base to margin; penes (Fig. 26–28) divided in apical  $\frac{1}{2}$ , spines of penes narrow and curved, lateral swelling on basal  $\frac{1}{3}$  of each penis lobe; subgenital plate bearing spines (Fig. 26, 27) close to base of forceps; prosternum relatively broad, narrowed at middle (Fig. 18). In the nymph: labrum as wide as head with dorsal setae as in Fig. 75; long setae on maxillary palpi ordered in rows (Fig. 79); apical denticle on tarsal claws much larger than those preceding it, 2 smaller denticles lying beside it (Fig. 86); gills (Fig. 83, 84) on segments 1–7 are platelike, each ending in a single fingerlike process; and posterolateral spines present on abdominal segments 8–9.

*Needhamella* is closely related to *Hermanella* and *Hylister* but can be distinguished from both in the male imago by the shape of the prosternum (Fig. 18) and in the nymph by the presence of a medial projection on the clypeus, the shape of the gills, the lateral apical denticles on the claws (Fig. 86), and the smaller number of setae on the upper surface of the labrum (Fig. 75).

*Needhamella ehrhardti* (Ulmer),

new combination

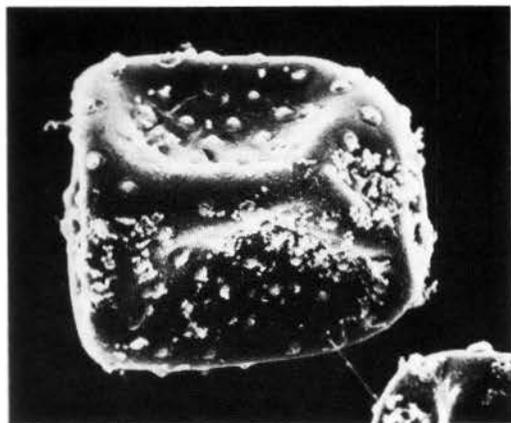
(Fig. 13–15, 18, 26–28, 37, 38, 75–86, 89, 90)

*Thraululus ehrhardti* Ulmer 1920a: 28; Ulmer 1920b: 117; Needham & Murphy 1924: 44; Ulmer 1943: 33.

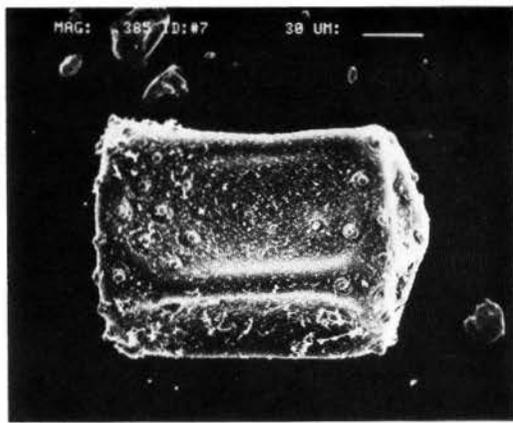
*Traverella ehrhardti* Edmunds 1950: 551; Traver 1959: fig. 15 and 18; Thew 1960: 123; Traver 1963: 28; Hubbard 1982: 267.

*Hermanella* sp. Edmunds et al. 1976: 72.

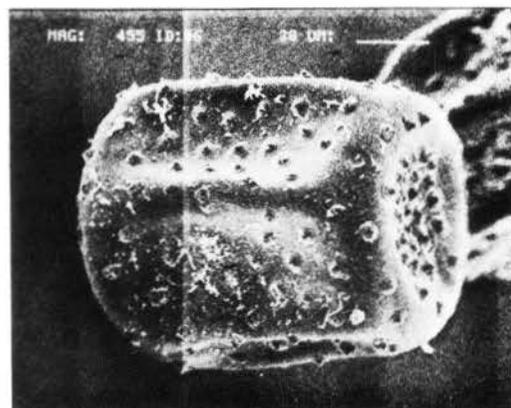
**Male Imago.** In alcohol. Length: body, 7.9–9.2; forewings, 8.2–9.2; hind wings, 1.3–1.8. General coloration brown. **Head:** light brown with black lines around bases of eyes. Upper portions of eyes orange-brown, lower portion grayish black. Antennae with scape and flagellum light brown, pedicel



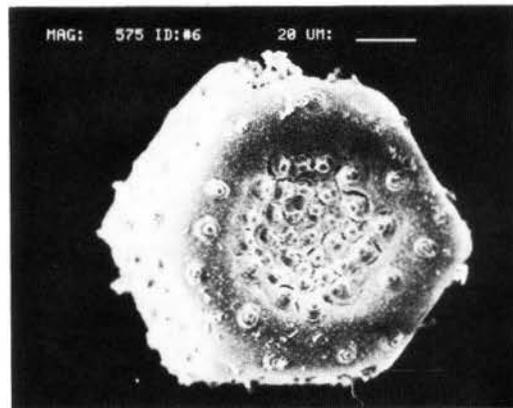
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88



89



90

Fig. 87-90. Eggs. (87) *Hermanella* (*G.*) *maculipennis*, lateral view. (88) *Hylister plaumanni* (lateral view). (89-90) *Needhamella ehrhardti*. (89) Lateral view. (90) Polar view.

dark brown. *Thorax*: pronotum light brown with median line and lateral margins black, mesonotum dark brown with sutures lighter, lateral margins darker; metanotum light brown washed with black; pleura and sterna orange-brown, membranous areas yellowish. *Wings* (Fig. 13-15): membranous hyaline, costal and subcostal areas of forewings light brown, darker at bases; wing bases brown. Longitudinal veins brownish, lighter posteriorly, cross-veins yellowish; in hind wings C and Sc brown, remaining veins yellowish, brown spot at base of wing. *Legs*: coxae, trochanters, femora, and tibiae brown, femora with median and apical black transverse band; tarsi yellowish white, except bases of prothoracic tarsi brown. Claws grayish. *Abdomen* (Fig. 37, 38): tergum 1 blackish, terga 2-7 with anterior  $\frac{1}{3}$  whitish, remainder light orange with median and posterior areas blackish, maculae as in Fig. 37, terga 8-9 almost completely orange with irregular black stripes, tergum 10 black in median area, brownish on margins. Sterna light orange-brown. *Genitalia* (Fig. 26-28): subgenital plate brownish with median area whitish, margins and

lateral swellings black. Segment 1 of forceps and penes light brown, segments 2 and 3 of forceps whitish, spines of penes light orange. Caudal filaments grayish.

**Female Imago.** In alcohol. Length: body, 9-9.5; forewings, 10-10.5; hind wings, 1.5-1.7. Similar to male imago except as follows: general color brownish yellow; head yellowish brown with black markings around antennae; eyes grayish black; antennae yellowish, lighter apically; thorax and wings paler than in male; legs with apical  $\frac{3}{5}$  of femora and anterior tibiae, and basal  $\frac{1}{5}$  of meso- and meta-thoracic tibiae blackish, remaining segments light brown; claws brownish.

**Mature Nymph.** In alcohol. Body length: 7.9-8.75. General coloration orange-brown. *Head*: orange-brown, with white spots external to ocelli. Upper portion of eyes of male reddish brown, lower portion black. Eyes of female blackish. *Antennae*: scape and pedicel brown, paler apically. *Mouthparts* (Fig. 75-82) light orange, molars of mandibles and maxillary palpi darker, basal area of mandibles washed with black. *Thorax*: terga or-

ange-brown, pleura and sterna yellowish. Legs (Fig. 85) yellowish brown, with apical  $\frac{2}{3}$  of anterior femora and all of meso- and metathoracic femora washed with black; basal and subapical bands on tibiae and basal  $\frac{1}{2}$  of tarsi brown. Claws as in Fig. 86. *Abdomen*: terga orange-brown, blackish pattern as in imago; sterna yellowish, darker posteriorly. *Gills* (Fig. 83, 84) grayish black, trachea darker, apical filaments light gray. Caudal filaments orange-brown.

**Type Material.** SYNTYPES: 2 ♂♂ imagines, 1 ♀ imago, Santa Catarina, Humboldt reg. Isabela, Brazil, 1-XI-10, W. H. Ehrhardt (MH).

**Other Material Examined.** BRAZIL: Santa Catarina, 9 N, Rio Jacutinga, V-62, F. Plaumann (UU); 17 N, Nova Teutonia, Ariranha River, XI-61, F. Plaumann (UU); 13 N, Nova Teutonia, XII-61, F. Plaumann (UU); 21 N, Nova Teutonia, II-62, F. Plaumann (UU); 3 N, Nova Teutonia, XI-62, F. Plaumann (UU). Rio Grande do Sul, 67 N, Arroio do Hilario (210 m), XI-64, F. Plaumann (UU); 12 N, Rio Ivay, XI-64, F. Plaumann (UU); 2 N, Cruz Alta (420 m), XI-64, F. Plaumann (UU); 5 N, Arroio Arapua, XI-64, F. Plaumann (UU); 10 N, Arroio Pinguiri, XI-64, F. Plaumann (UU); 4 N, Arroio Inhandui, XI-64, F. Plaumann (UU). Paraná, 9 N, Guapuava, Rio Chalquim (1,200 m), III-63, F. Plaumann (UU); 2 N, Rio Campo-novo, III-63, F. Plaumann (UU); 9 N, Arroio Cui (430 m), III-65, F. Plaumann (UU); 7 N, Rio Jacutinga (900 m), III-65, F. Plaumann (UU); 1 N, Rio das Cobras (775 m), III-63, F. Plaumann (UU); 4 ♂♂ I, 2 ♀♀ I, 4 N, Rio dos Patos, 3 km E Prudentópolis, 2,300', 2-3-III-69, W. L. & J. G. Peters (FAMU); 1 ♂ S, 34 N, Rio Passa Una, 7 km W Curitiba 24-II-69, W. L. & J. G. Peters (FAMU); 1 ♂ S (reared), same locality and collectors, 26-II-69; 1 ♂ S, 1 ♀ S (reared), 7 N, same locality and collectors, 18-II-69; 2 ♀♀ S, 5 N, same locality and collectors, 15-III-69; Rio Paraná, Sete Quedas, 5 km S of Guairá, 11-III-69, W. L. & J. G. Peters (FAMU); 2 N, Goiás, Rio Corumbá, between Anapolis and Brasília, 22-IX-68, C. G. Froehlich (FAMU). ARGENTINA: Misiones, 2 ♂♂ I, 1 ♀ I, Panambi, Río Uruguay, 19-XI-80, E. Dominguez (IFML); 1 ♂ I, 2 ♂♂ S, same locality and collector, 14-II-85; 1 ♂ I, Misiones, Parque Nac. Iguazú, Cataratas, E. Dominguez, 20-XI-80 (IFML); 1 ♂ I, Puerto Canoas, 6-XII-86; 2 ♂♂ I, 1 N, Bonpland, Arroyo Martires, 26-XII-86, E. Dominguez (IFML); 4 N, same locality and collector, 15-II-85; 7 N, Paraiso, Arroyo Fortaleza, 2-XII-86, E. Dominguez (IFML); 10 ♂♂ I, 1 ♀ I, 1 ♂ S (reared), 53 N, Alegre-Piray Guazú, 3-4-XII-86, E. Dominguez (IFML). URUGUAY: 15 ♂♂ I, 8 ♀♀ I, 50 ♂♂ S, 40 ♀♀ S, Salto, Salto Grande, 10-XI-55, C. S. Carbonell (URU); 5 ♂♂ I, 3 ♀♀ I, 8 ♂♂ S, 5 ♀♀ S, Artigas, Frente Isla del Paredón, 21-I-79, L. C. de Zolessi, E. Morelli (URU); 3 ♂♂ S, 5 ♀♀ S, Artigas, Sepulturas, 13-I-52 (URU); 5 ♂♂ I, 10 ♀♀ I, 15 ♂♂ S, 18 ♀♀ S, Paysandú, Santa Rita, Río Uruguay, 8-XI-55, C. S. Carbonell (URU); 1 ♂ I, Cerro Largo, Sarandi del Quebracho, 17-XI-59, C. S. Carbonell

(URU). PARAGUAY: 2 N, Itapua, Río Santa María, 5 km N Encarnación, 25-VII-84, K. Bottger (FAMU).

**Discussion.** One of us (R.W.F.) was able to study the syntypes deposited in the University of Hamburg, which are faded. Ulmer omitted the spines of the subgenital plate in his figure of the genitalia. There is a wide range of intensity of pigmentation among individuals in this species; many specimens are either much paler or much darker than described here. This species has the widest distribution of any species discussed in this paper. Collection records range from northern Uruguay north to the state of Goiás in Brazil.

**Biology.** Collection records indicate the adults emerge from November to March. Most of them were attracted to light. The nymphs were found under rocks along the edges of small streams to medium-sized rivers.

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