



Description of the immature stages of *Wyeomyia (Spilonympha) howardi* Lane & Cerqueira (Diptera: Culicidae) with a redescription of the adults

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Abstract

The immature stages of *Wyeomyia (Spilonympha) howardi* Lane & Cerqueira are described and illustrated for the first time. The morphology characters of adult male, including genitalia, and female are redescribed and illustrated. The systematic treatment includes the geographical distribution of *Spilonympha* species and bionomics data for *Wyeomyia howardi* based on recent field collections as well as the literature.

Key words: systematics, Sabethini, bromeliads, phytotelmata

Introduction

The genus *Wyeomyia* Theobald is predominantly Neotropical and the immature forms develop in natural containers, or phytotelmata. This genus has been investigated to establish a better taxonomic organization and provide a secure identification of species (Judd 1996, 1998, Motta *et al.* 2007). There are about 30 *Wyeomyia* species without subgeneric placement (Motta & Lourenço-de-Oliveira 2000). In addition, morphological characters of all developmental stages of many species are not entirely known, such is the case of *Wyeomyia howardi* Lane & Cerqueira, (1942). *Wyeomyia howardi* was originally described from adult males and females collected in Bahia State, Brazil, during extensive country survey for the natural vectors of sylvatic yellow, which resulted in the review of American sabethines by Lane and Cerqueira in 1942. Since its original description, the larva and pupa of this species have been unknown, despite the value of larval characters in the taxonomy and classification. *Wyeomyia howardi* was originally placed in the subgenus *Dendromyia* (Lane & Cerqueira 1942). It was transferred to the subgenus *Spilonympha* by Motta and Lourenço-de-Oliveira (2005) together with six other species, namely *Wy. aningae* Motta & Lourenço-de-Oliveira, *Wy. mystes* (Dyar), *Wy. bourrouli* (Lutz), *Wy. forcipenis* Lourenço-de-Oliveira & Silva, *Wy. finlayi* Lane & Cerqueira and *Wy. airosai* Lane & Cerqueira. The description of subgenus *Spilonympha* was based on morphological characters of all developmental stages (Motta & Lourenço-de-Oliveira 2005). The subgenus *Spilonympha* was also supported by a phylogenetic study based on molecular and morphological characters that showed this group to be a monophyletic assemblage (Motta *et al.* 2007).

Wyeomyia howardi was the only *Spilonympha* species whose immature forms were unknown. The immature stages provide significant morphological characteristics that allow the distinction of species as well as a better taxonomic grouping of the species, especially in the genus *Wyeomyia* where adult females are very similar, as noted by Judd (1996, 1998) in her studies on Sabethini and *Wyeomyia* phylogeny. Therefore the description of the larval and pupal stages is essential. In this paper we describe and illustrate the immature stages of *Wy. howardi* for the first time, and to conclude the characterization of *Spilonympha* species, we provide herein a redescription of the adult females and males, including the male genitalia.

Materials and methods

Morphological characters of the male, male genitalia, female pupal and fourth-instar larva were examined. Pupal and larval chaetotaxy was studied and the range with modal number of branches is shown in tables. Illustrations are provided based on direct observation of morphological characters of the specimens. The morphological terminology follows Harbach & Knight (1980) and Belkin *et al.* (1970). The specimens examined are listed in the specific sections. All examined specimens are deposited in the collection of - Culicídeos do Laboratório de Transmissores de Hematozoários-, Instituto Oswaldo Cruz (IOC), Rio de Janeiro, Brazil. The geographic distribution of *Spilonympha* species is based on published data as well as new data collected for the present study.

Wyeomyia (Spilonympha) howardi Lane & Cerqueira, 1942

Wyeomyia (Dendromyia) howardi Lane & Cerqueira, 1942: 595 (F, M*)

Lane, 1953: 958 (F, M*)

Hutchings *et al.* 2005:18 (paratype info)

Motta & Lourenço-de-Oliveira, 1995: 384 (to subgenus uncertain)

Wyeomyia (Spilonympha) howardi Motta & Lourenço-de-Oliveira, 2005: 838 (tax.)

Female. *Head:* vertex and occiput covered with broad scales with dull greenish blue iridescence; ocular line with conspicuous line of white scales, setae dark; 2 long, dark interocular setae; postgena with broad white scales. Antenna dark, pedicel pubescent, flagellum weakly verticillate, slightly shorter than proboscis, with 14 flagellomeres. Clypeus, darkish, pubescent, without scales and setae. Proboscis short, length 1.5–1.6 mm (mean 1.58 mm), about 0.8 of forefemur length, slightly expanded distally, covered with dark scales, basal labial setae long, brown. Maxillary palpus short, length 0.2 mm, covered with dark scales. *Thorax:* integument brown, pleural sclerites slightly brown. Scutum and scutellum covered with dark scales with greenish blue iridescence, scutellum with long (3,5) and short (3,4) setae alternating posteriorly. Anterior promontory with dark scales and brown setae; supraalar setae strong and dark brown (17–19). Mesopostnotum with brown integument, weakly pubescent, with brown setae (6,7). Antepronota moderately large, covered with darkish scales with blue reflections (Fig. 1A, B), one row of strong dark setae (8–12) dorsally, small ventral area with whitish scales; 4 brown prealar setae; postpronotum covered with whitish scales. Pleural sclerites covered with whitish scales; 3 or 4 brown prespiracular setae, 2 yellowish upper proepisternal setae, 5 yellowish lower mesokatepisternal setae, inserted above and below upper margin of mesomeron, 8 yellowish upper mesepimeral setae. *Wing:* length 2.7–3.0 mm (mean 2.7 mm). Upper calypter nude. Scales of dorsal surface of wing veins brownish distal third of all veins with elongate anterolateral scales. Veins M and R_s with ligulate scales, vein Cu with elongate anterolateral scales, CuA with narrow appressed scales. Veins of ventral surface similar to those on dorsal surface, veins Cu, CuA and M_{3+4} with ligulate scales; cell R_2 similar in size to cell M_1 . *Halter:* capitellum with dark scales, pedicel with dark scales mesally, scabellum yellowish, without scales. *Legs:* coxae and trochanters with brown integument, covered with whitish scales, brown setae; femora and tibiae dark scaled; mid- and hindfemora and -tibiae with light scales ventrally; tarsomeres entirely dark-scaled, ungues small, simple, black. *Abdomen:* covered with brown scales, similar to scutum. Sternum with whitish scales; line of demarcation between dark and pale scaling nearly straight, sometimes pale scales invade the dark-scaled area on base of terga, mainly on segments VI and VII; tergum VIII with numerous brown setae.

Male: Similar to female except for sexual characters. Antenna slightly more verticillate than female, with 14 flagellomeres. Proboscis length 1.29–1.30 mm, about 0.99 of forefemur length. Maxillary palpus dark, length 0.11 mm. Wing length 1.88–1.94 mm. *Genitalia* (Fig. 2): tergum VIII covered with broad scales intermixed with minute setae on distal half, long setae on distal margin; sternum VIII covered with broad scales and minute setae on the distal half, long setae in one row on the distal margin. Tergum IX with large interlobar space, 2 dorsolateral lobes, each lobe with 2 foliform setae expanded apically, strongly sclerotized.

Gonocoxite elongate, inner surface with minute setae, outer surface with setae and scales; tergal surface with 2 long, strong setae; basal mesal lobe rectangular in shape, slightly sclerotized with minute setae and 2 strong, short setae apically. Gonostylus consisting of basal stem apically divided into 4 lobes: lobe A, digitiform with strong apical tooth and adjacent hyaline seta; lobe E, arising from lobe A, with nearly flat, distal margin bearing one row of short setae; lobe M elongate and curved at apex, median margin with a row of six short setae, apex narrower, fringed at apex; bearing 2 appendages: one at middle, short and filiform, and other basal, straight and long, shorter than lobe M, with 4 weakly sclerotized spicules from middle to apex and a continuous row of 7 setae distally; lobe C curved, ladle-like, membranous rugose. Aedeagus longer than wide; apical tergal arms joined, anterior margin slightly serrated; submedian tergal arms fused; median sternal plate with lateral pointed expansions. Proctiger sclerotized, paraproct with 3 or 4 small cercal setae and 3 apical teeth.

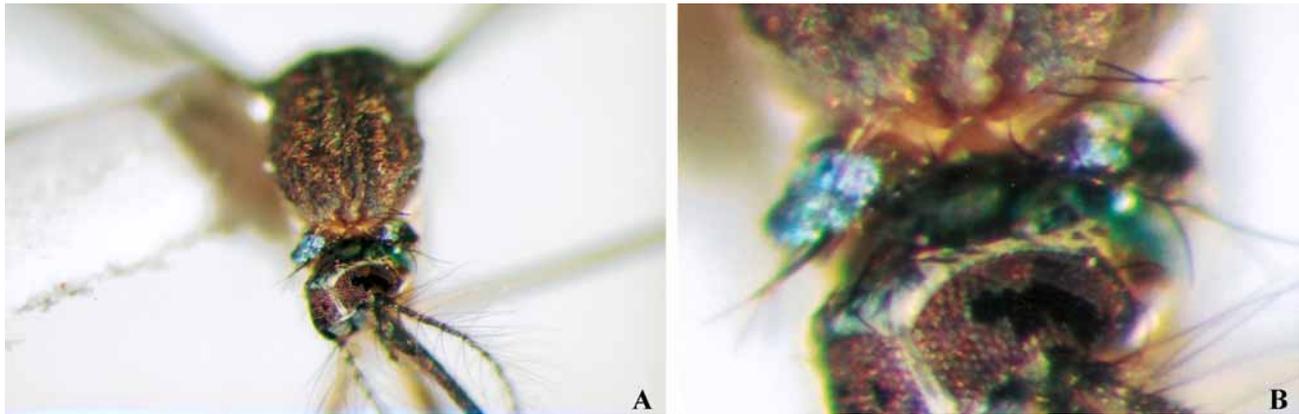


FIGURE 1. *Wyeomyia howardi*, adult. (A, B) General aspects of antepnota, showing the blue reflections of the scales.

TABLE 1. Range of number of branches for pupal setae of *Wyeomyia howardi* (mode in parentheses).

Setae n	Cephalothorax	Abdominal segments							
		I	II	III	IV	V	VI	VII	VIII
0	–	–	1	1	1	1	1	1	1
1	2	n.c.	2–4 (2,3)	2,3 (2)	2,3 (2)	1,2 (2)	1,2 (1,2)	1–2 (2)	–
2	2,3 (2)	1,2 (1)	1	1	1	1	1	1	–
3	2,3 (2)	1	1	1	3,4 (3)	2,3 (2)	1,2 (2)	1,2 (1)	–
4	2,3	2–4 (4)	2–4 (3)	1,2 (1)	1,2 (1)	2–4 (3)	1–3 (2)	1,2 (1)	1
5	4–6 (5)	1,2 (1)	1,2 (1)	1	2	2	2	1,2 (1)	–
6	1,2 (2)	1,2 (1)	1	1	1,2 (1)	1	1,2 (1)	1,2 (1)	–
7	2,3 (2)	2,3 (3)	2,3 (2,3)	1	1,2 (1)	2,3 (2)	1,2 (1,2)	1,2 (1)	–
8	1,2 (1)	–	–	1,2 (2)	1,2 (1)	1,2 (2)	2,3 (2)	3–5 (4)	–
9	2	1	1	1	1	1	1	9–14	12–16
10	1	–	1,2 (1)	1,2 (1,2)	1,2 (2)	1,2 (2)	1,2 (2)	1,2 (2)	–
11	1	–	1	1	1	1	1	1,2 (1)	–
12	1,2 (2)	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	1

Pupa (Fig. 3). Character and positions of setae as figured; range and modal number of branches in Table 1. *Cephalothorax*: pale, mesothoracic wing more pigmented than dorsal region; seta 1-CT strongly developed, long, sigmoid, double with hooked tip, 2,3-CT with similar length, normally double, 4-CT usually with 2,3 fine branches, 5-CT almost as long as at 1-CT, usually with 5 aciculate branches, 6-CT slightly shorter than 7-

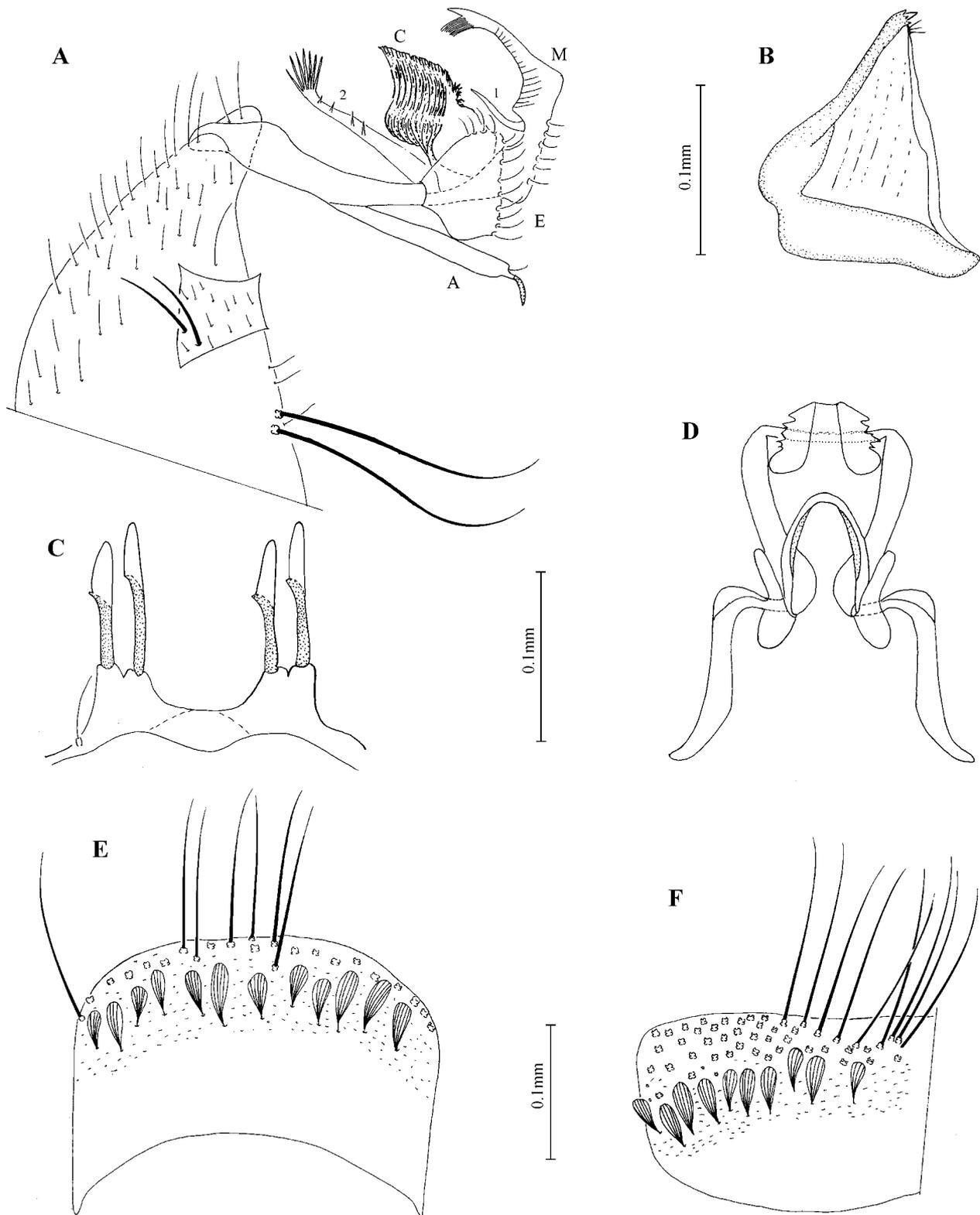


FIGURE 2. Male genitalia of *Wyeomyia howardi*. (A) Gonocoxite and gonostylus (lobes C, A, E, M and appendages 1, 2). (B) Proctiger. (C). Tergum IX. (D) Aedeagus. (E). Sternum VIII. (F) Tergum VIII.

CT, normally double, 8-CT usually single and slightly aciculate, 9-CT double, sometimes aciculate, 10-CT single, 11-CT and 12-CT similar in length, 12-CT usually double. *Trumpet*: slightly more pigmented than mesothoracic wing area, long, narrow, index 5.57–7.80 (mean 6.79). *Abdomen*: pale, integument of metanotum and abdominal terga I–IV darker, forming a pattern of pigmentation, (see figure 1D on page 841 in

Motta & Lourenço-de-Oliveira, 2005). Seta 1-I dendritic, well developed, 1-II-VII inserted on posterior margin of tergum, usually double, 2-I-VII with similar development, 2-II between and nearly in line with seta 1-II and 3-II long, almost the same length as following tergum, 3-IV multiple, noticeably anterior to seta 4-IV, 3-V-VII near posterior margin of tergum, 4-I,II multiple and short, 4-III,IV,VII usually single and short, 4-V,VI usually triple and double respectively, 4-VIII single and long, 5-I usually single, very short, 5-II,III,VII usually single and short, 5-IV-VI, longer than length of following tergum, double, aciculate, 6-I,II single and long, 6-I sometimes double, 6-III-VII usually single, shorter than 6-I,II, 6-VII dorsal; 7-I,II usually triple, 7-II lateral, 7-III,IV single, 7-IV sometimes double near to seta 8-III,IV; 8-III,V,VI normally double, 8-IV usually single, 8-VII usually 4-branched; 9-I-VI single and short, 9-VII,VIII strongly developed, branches aciculate; 10-II,VI almost in line with seta 11-II,VI; 10-III,V,VII posterior to seta 11-III,V,VII; 11-II-VII single, 11-VII sometimes double. *Genital lobe*: slightly darker than abdomen. *Paddle*: index 2.10–2.45 (mean 2.27), tanned, long, almost twice length of tergum VII, minute serrations on margin.

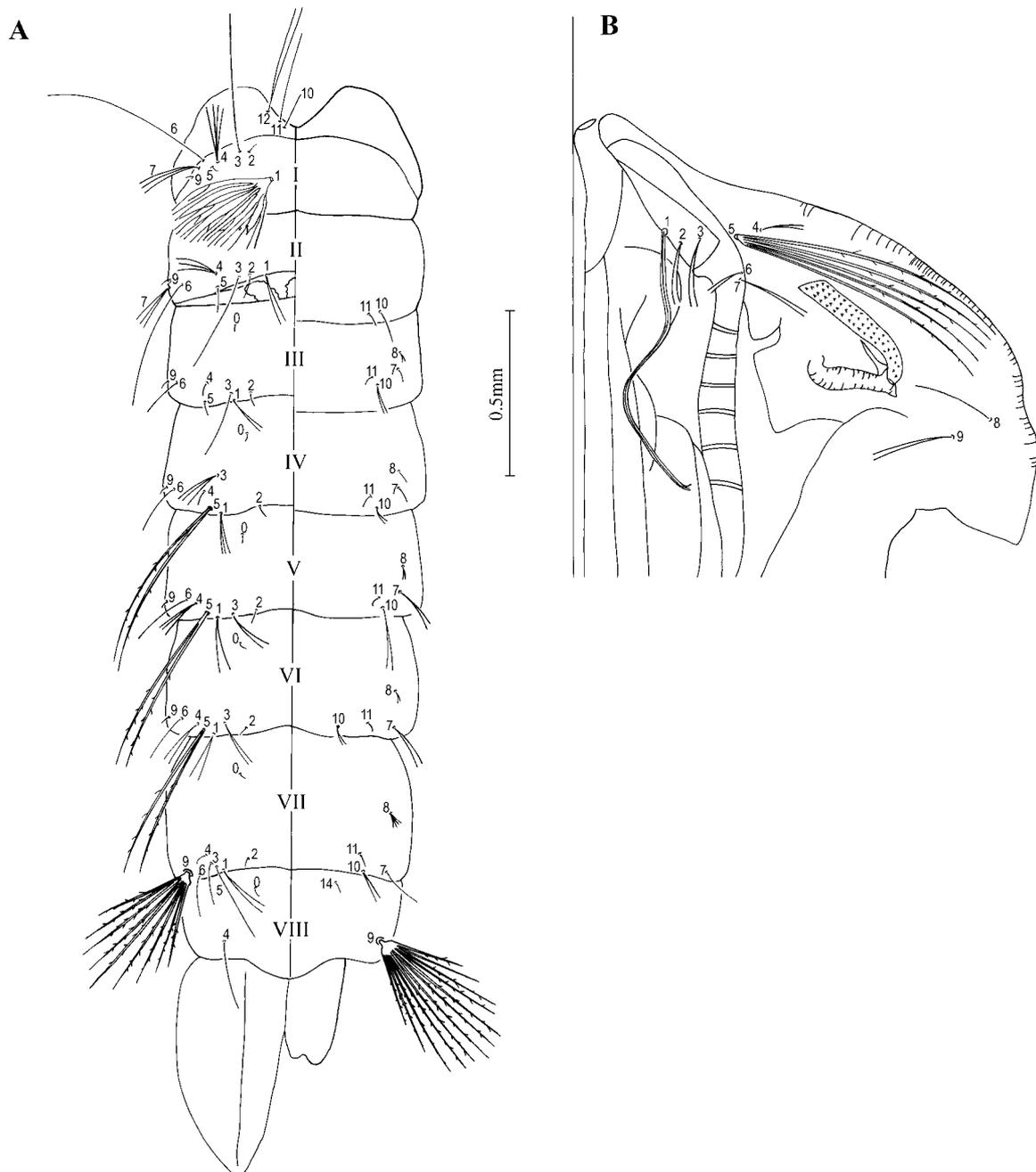


FIGURE 3. Pupa of *Wyeomyia howardi*. (A) Dorsal and ventral aspects of the metanotum and abdomen (I-VIII abdominal segments). (B) Cephalothorax.

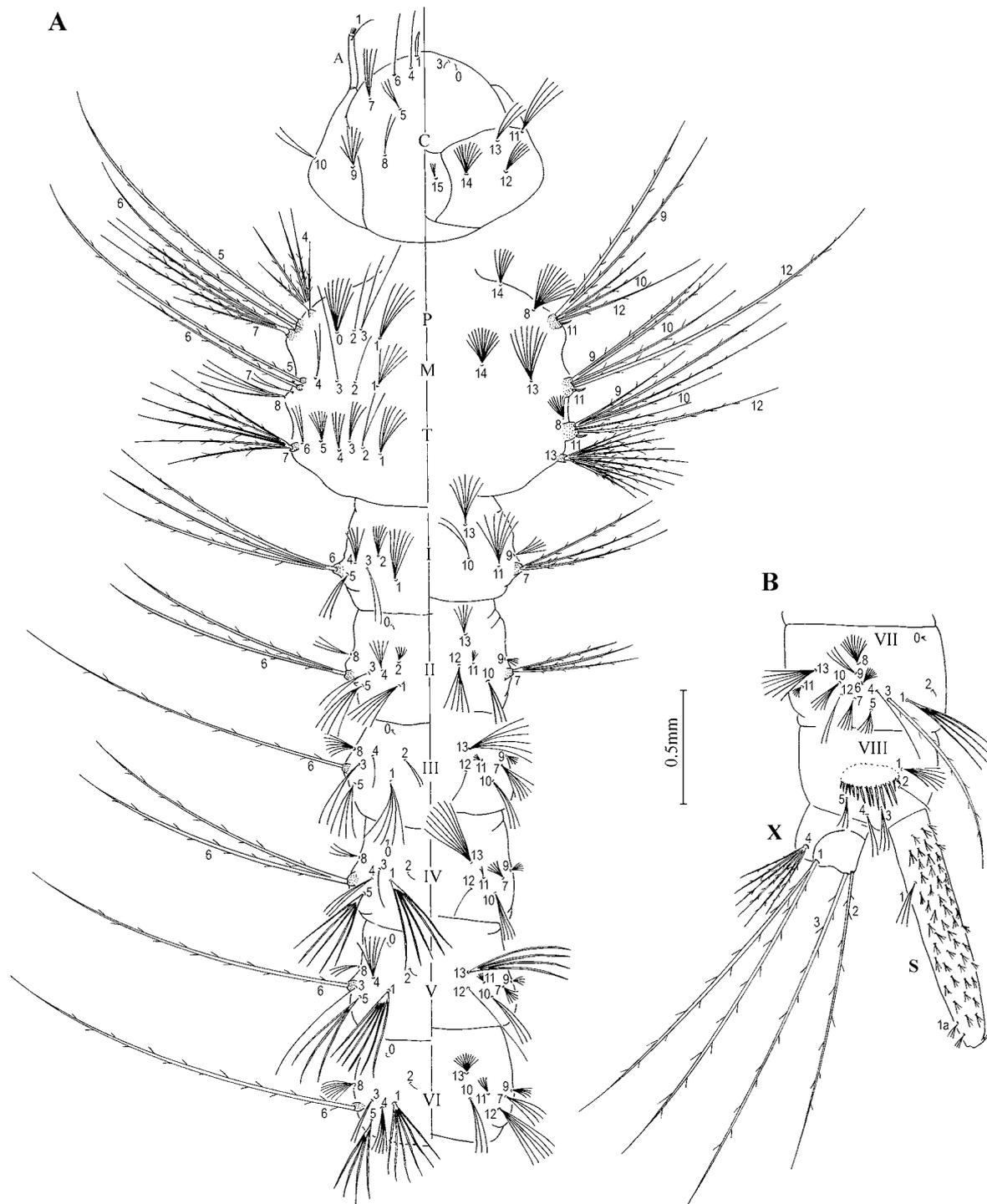


FIGURE 4. Fourth-instar larva of *Wyeomyia howardi*. (A) Head, thorax and abdominal segments I–VI, dorsal and ventral aspects. (B) Abdominal segments VII–X. A: antenna; C: cranium; M: mesothorax; P: prothorax; S: siphon; T: metathorax.

Fourth-instar larva (Figs. 4, 5). Character and positions of setae as figured, range and modal number of branches in Table 2. *Head*: slightly wider than long, rounded, pale. Occipital foramen slit-like; hypostomal suture complete, slightly curved; dorsomentum with 17 (16–18) teeth and a prominent median tooth; maxilla body (MxBo) slightly rounded, apical tooth (AT) forming almost 90° angle with maxillary body; laciniarastrium (LR) with 12 teeth, median tooth slightly more developed, dorsal surface with numerous long setae, median area with short setae, maxillary brush (MxB) with numerous long setae, seta 2,4-Mx single, 6-

Mx double, filiform, inserted on cardo, seta 1-Mx thick, bifid at apex, maxillary palpus (MPlp) not fused to maxillary body with 3 setae apically. Mandible short, mandibular sweeper in groups of 4 pectinate setae (MnS₂) and 2 setae apically serrated (MnS₁). Mandibular rake (MnR) with 2 bifid, hyaline, short setae. Seta 2b-Mn present, shorter than seta 2a-Mn. Seta 0, 3-C single and short, 1-C strong, slightly curved, 4-C single, inserted anterior to seta 6-C, 5-C usually triple, 6-C usually single, as long as seta 4-C, 7-C usually 4-branched, 8-C normally double, 9-C multiple, 10-C lateral, 11,12-C usually 4,5-branched respectively, 13-C usually triple, 14-C multiple, 15-C double or triple, short. *Antenna*: short, seta 1-A single, very close to apex. *Thorax*: integument smooth. Seta 0-P multiple, 1-P,M,T multiple, mesad of setae 2,3-P, 3-P usually double, near seta 2-P, 4-P, inserted on individual plate, very aciculate mostly in mid-length, 5,6-P,M single, long, aciculate, inserted on individual basal plates, 5,6-T multiple, 7-P,T multiple, strongly aciculate, 7,13-T inserted on individual basal plates, 7-M double, 8-P lateral, 8-M multiple, longer than seta 8-T, 9–12-P, M, T inserted on common basal plates, 11-P, M, T single, spine-like, 13-T, multiple, 9,10,12-P,M,T, 13-T aciculate. *Abdomen*: integument smooth. Seta 1-II–III multiple, shorter than 1-IV–VII, sometimes slightly aciculate; 2-I,II multiple, 2-III usually double, 2-IV–VII usually single and short; 3-I mesad and posterior to seta 4-I, 3-II,III,V,VI near and anterior to seta 5, 3-III slightly aciculate, 3-V single and long, 3-IV inserted between setae 1 and 4, anterior to seta 4, 3-VII single, long, aciculate; 4-I,II,V,VI multiple, 4-III,VII single, 4-IV often triple, near to seta 5; 5-I–III usually with 3 or 4 branches, 5-IV–VI more strongly developed on other segments, sometimes slightly aciculate, 5-VII multiple, relatively short; 6-I–VI inserted on individual basal plate, long, aciculate, 6-VII multiple; 7-I, II inserted on individual basal plate, usually triple, aciculate, 7-III,VI,VII normally with 4–6 branches, 7-IV, V multiple and short; 8-II–VI multiple and lateral, 8-VII multiple; 9-I usually with 5 branches, 9-II–VI multiple and short; 10-I usually double, mesad of seta 11, 10-II–VII multiple; 11-I multiple, long, 11-II–VII usually with 2–5 branched, short; 12-II,VI multiple, 12-III,IV,V single, simple, 12-V similar in length to seta 13-V, 12-VII double; 13-I,III,V,VII multiple, moderately long, 13-II, VI multiple and short, 13-V sometimes slightly aciculate, 13-III,IV anterior to seta 12. *Segment VIII*: seta 1-VIII multiple, 2-VIII usually single, moderately long; 3-VIII normally triple; 3,4-VIII similar in development; 4-VIII usually double; 5-VIII inserted near comb plate, usually triple, relatively short; comb normally with 17 (14–21) spine-like scales inserted on a slightly sclerotized plate, scales with variable sizes. *Siphon*: long, index 4.75–5.55 (mean 5.30), (width measured at midlength), parallel-sided; pigmentation same as head; numerous accessory setae unevenly distributed; seta 1-S inserted 0.33 above the base of siphon, usually double or triple; 2 pairs of triple seta 1a-S. *Segment X*: Saddle incomplete, pale; setae 1–4-X aciculate; 1-X double, long, 2,3-X single, long; 4-X multiple, 0.33 length of 1–X.

Material examined. Five females, 4 males, 4 male genitalia, 5 larval exuviae, 6 pupal exuviae. **Holotype**: adult male with dissected male genitalia on microscope slide, number 2299, BRAZIL: Bahia State, Muriqueira, Jun 1929, det. Lane and Cerqueira, 1941, col. R.C. Shannon (IOC); **Allotype**: female, without number, same data, Apr 1929, det. Lane and Cerqueira, 1941, col. Lab. Shannon (IOC); 1 male genitalia, Bahia, Muriqueira, number 2538, det. Lane and Cerqueira, 1940 (CPRR); 2 females with larval and pupal exuviae (specimen numbers 1689, 1698), 1 male, number 1692 with larval and pupal exuviae and dissected genitalia, 1 male, number 1690 with pupal exuviae and dissected genitalia, from larvae collected in bromeliads, Bahia, Goes Calmon (current name of Muriqueira), Oct 2001, det. M. Motta, col. M. Motta; 1 female, number 1693 with the same data except Ilhéus municipality; 1 female number 1691 with larval and pupal exuviae, from eggs laid at the laboratory by wild-caught female, Bahia, Ilhéus, Oct 2001, det. M. Motta, col. M. Motta.

Distribution and bionomics. Little is known about the geographical distribution and biology of the adults and immature stages of *Wyeomyia howardi*, probably because it is difficult to distinguish the females from other *Spilonympha* females, and due to the absence of a morphological characterization of its immature forms. *Wyeomyia howardi* is known only from Bahia State, the type locality, Goes Calmon (= Muriqueira), Simões Filho municipality, and Ilhéus, northeastern Brazil. Species of *Spilonympha* occur in most Brazilian states. *Wyeomyia bourrouli* and *Wy. mystes* seem to be the most widespread species, whereas the majority of *Spilonympha* species such as *Wy. howardi*, *Wy. finlayi* and *Wy. aningae* have been found in only one or two localities in the same Brazilian state or even only at the type locality. (Fig. 6). *Wyeomyia howardi* was

TABLE 2. Range of number of branches for setae of the fourth-instar larva of *Wyeomyia howardi* (mode in parentheses).

Setae n°	Abdominal segments												
	Head	Thorax			I	II	III	IV	V	VI	VII	VIII	X
0	1	7-10 (8)	-	-	1	1	1	1	1	1	1	-	-
1	1	4,5 (5)	5-7 (6)	4-6 (5,6)	4-8 (6)	5,6 (5)	5-10 (5)	3-7 (4,5)	6-9 (6)	6-10 (6,7)	4-8 (4)	6-10 (7)	2
2	-	1	1,2 (1)	1,2 (2)	4-6 (6)	3-5 (5)	1,2 (1,2)	1,2 (1)	1,2 (1)	1	1,2	1,2 (1)	1
3	1	2,3 (2)	1	4-6 (4)	2-4 (2,3)	2,3 (2,3)	2,3 (2)	1	1	2-4 (2)	1	2,3 (3)	1
4	1	4-6 (4,5)	2,3 (2)	4,5 (4)	4-6 (5)	5-7 (5)	1	2-4 (3,4)	4-6 (6)	3-5 (5)	1	1,2 (2)	6-8 (6,8)
5	2-5 (3)	1	1	6-9 (7)	3-5 (3)	3-5 (4)	3-4 (3,4)	3-5 (3,4)	3,4 (3,4)	3,4 (4)	5-7 (5)	3-5 (3)	-
6	1,2 (1)	1	1	1-3 (2,3)	2-4 (3)	2,3 (2)	1,2 (1)	2	1-3 (1)	1,2 (1)	6-9 (7)	-	-
7	3-5 (4)	4,5 (4)	2	5-7 (7)	3,4 (3)	2-4 (3)	3-6 (6)	4-5 (5)	6-8 (6,7)	4-7 (4,5,6)	4,5 (5)	-	-
8	2,3 (2)	10-13 (11)	2-4 (3,4)	5-8 (8)	-	2-5 (2,3,4)	7-12 (7)	2,3 (3)	3,4 (3,4)	8-15 (9,10)	10-13 (10)	-	-
9	6-8 (7,8)	1-3 (2)	2,3 (2)	4-7 (4)	3-6 (5)	3-5 (4)	5-7 (5,6)	4-6 (5)	3-5 (4,5)	4-7 (5)	3	1-S 2-5 (2,3)	-
10	2,3 (2)	1,2 (1,2)	1,2 (1,2)	1	2,3 (2)	2-4 (3)	2,3 (3)	2-4 (4)	3-6 (3,4)	3,4 (3)	3-5 (5)	-	-
11	3-6 (4)	1	1	1	7-11 (7,11)	3-5 (4)	2-4 (4)	2-4 (2)	3-5 (4,5)	3-5 (4)	4-6 (5,6)	1a-S 3	-
12	3-6 (5)	1	1	1	-	4-7 (5)	1	1	1	3-6 (5)	2	-	-
13	3,4 (3)	-	6-9 (8)	8-13 (10)	5-8 (7)	5-8 (5,6)	5-6 (6)	4-8 (8)	4-6	11-14 (12,13)	7-10	-	-
14	8-10 (10)	5-9 (6)	10-14 (12,13)	-	-	-	-	-	-	-	-	-	-
15	2,3 (2,3)	-	-	-	-	-	-	-	-	-	-	-	-

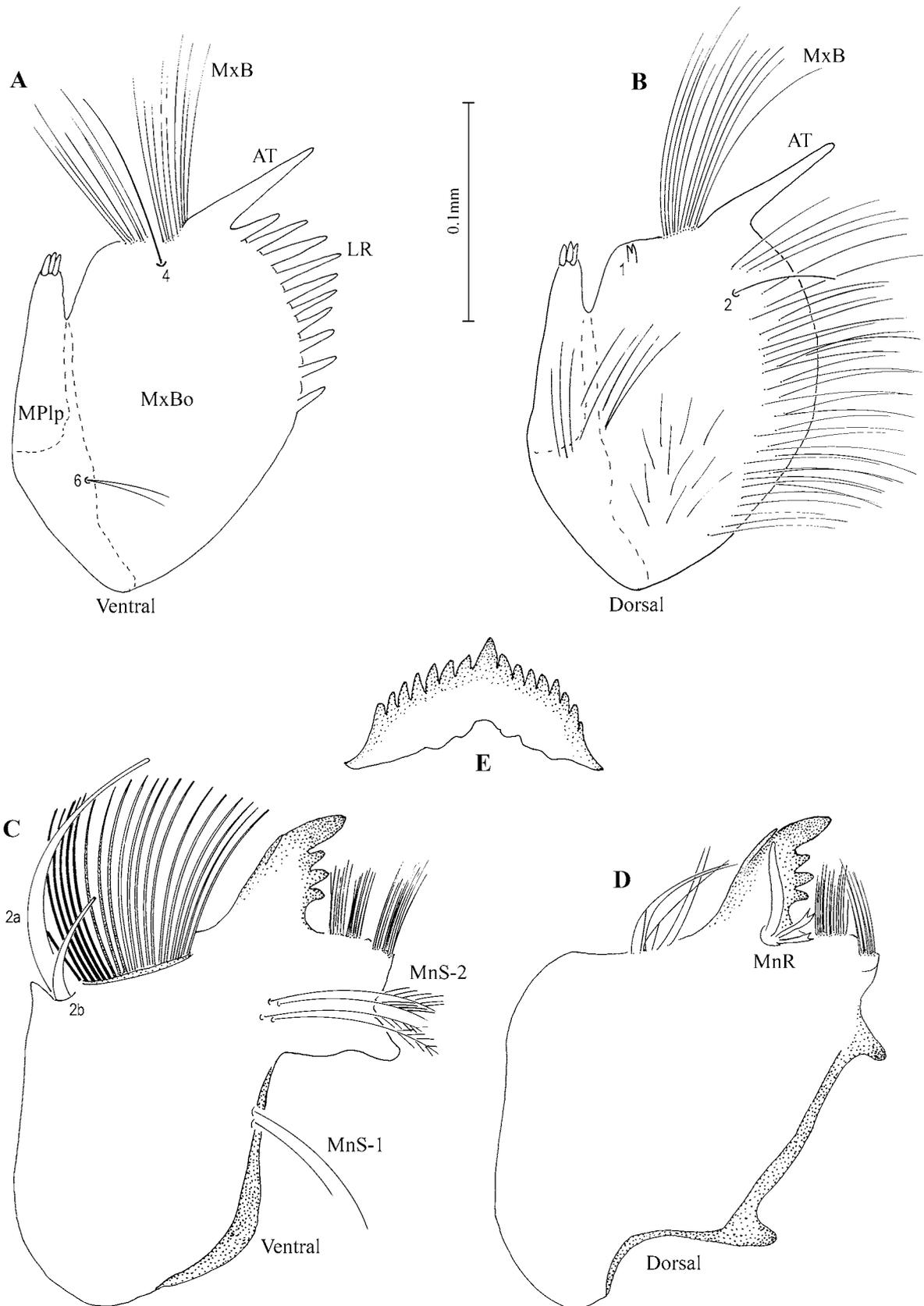


FIGURE 5. Larval mouthparts of *Wyeomyia howardi*. (A and B) Maxilla. (C and D) Mandible. (E) Dorsosentum.

collected on human bait during the day time. Immature forms of *Wy. howardi* were collected only from sunbathed terrestrial bromeliads holding little water (Fig. 7). Similar observations were made in a study in the Atlantic Forest, southeastern of Brazil, where the immature stages of *Wy. airosai* and *Wy. finlayi* were collected only in bromeliads holding about 40 ml of water (Cardoso 2009).

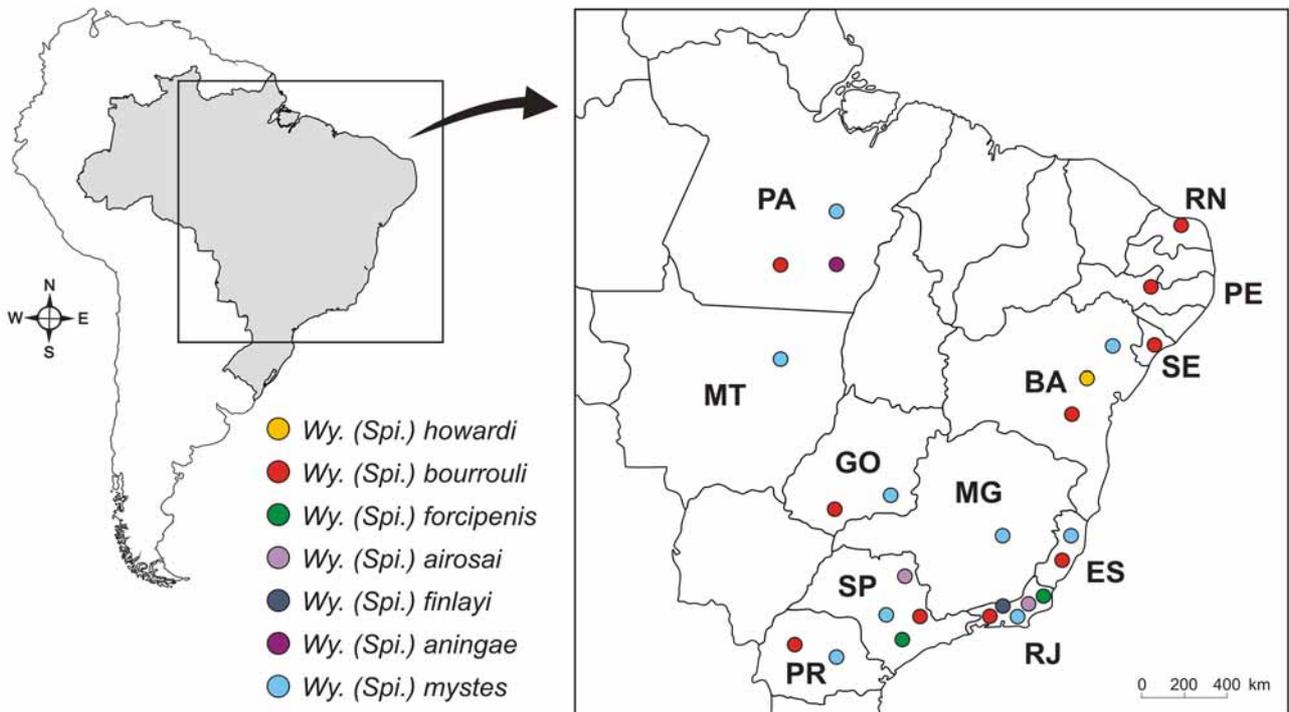


FIGURE 6. Geographical distribution of *Spilomyia* species in Brazil.



FIGURE 7. Bromeliad from which the immature stages of *Wyeomyia howardi* were collected.

Discussion

Wyeomyia howardi is very similar to other *Spilonympha* species in all life stages and bears the characters that distinguish the subgenus, as: male genitalia with elongate gonocoxite bearing two long tergal setae, gonostylus with a stem apically divided into four lobes; larva with a comb plate, siphon with numerous accessory setae and seta 1-S inserted far basal; pupa with a pattern of darkish pigmentation on the cephalothorax and abdomen. Although *Spilonympha* females are very similar, *Wy. howardi* can be distinguished from the other species by the general appearance of the antepnота, which are covered with darkish scales with blue reflections. The male genitalia and immature stages of *Wy. howardi* bear morphological characters that easily differentiate them from other *Spilonympha* species, as follows: 1) the foliiform structure of the tergum IX setae, expanded at the apex; 2) aedeagus with the median sternal plate with lateral pointed expansions; 3) the presence on lobe M of a straight and long basal appendage with an apical row of 7 setae; 4) pupal seta 5-CT nearly as long as 1-CT, with 4-6 branches; 5) trumpet long, index about 7; 6) terga II–V darker, forming a pattern of pigmentation (see figure 1D on page 841 in Motta & Lourenço-de-Oliveira, 2005); 7) pupal seta 5-IV–VI double, longer than the following tergum; 8) larval maxilla with a distinct apical tooth (AT) forming almost a 90° angle with the maxillary body; 9) presence of mandibular seta 2b-Mn; and 10) comb plate normally with 17 spiniform scales. For a detailed account of characters that differentiate *Spilonympha* species see Motta & Lourenço-de-Oliveira (2005).

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