



Review of the genus *Chagasia* (Diptera: Culicidae: Anophelinae)

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Abstract

Genus *Chagasia* Cruz of subfamily Anophelinae (Diptera: Culicidae) is comprised of five species in the Neotropical Region: *Ch. ablusa* Harbach, **n. sp.**, *Ch. bathana* (Dyar), *Ch. bonneae* Root, *Ch. fajardi* (Lutz) and *Ch. rozeboomi* Causey, Deane & Deane. The genus is described in detail and diagnoses, keys and illustrations are provided for the identification of the adult, pupal and larval stages of each species. The larval and pupal stages of a *Chagasia* species (*Ch. bonneae*) are fully illustrated for the first time. A neotype specimen is designated for *Ch. fajardi* to fix its identity and distinguish it from *Ch. ablusa*. The species treatments also include a synonymy (where applicable), a discussion, information on distribution, a synopsis of material examined and a summary of previous literature. The work is considered to be a review rather than a revision of the genus because too few link-reared specimens were available for detailed comparative study of all life stages, and it was not possible to determine the total range of morphological variation and the actual distributions of the species.

Key words: *ablusa* new species, *bathana*, *bonneae*, *fajardi*, mosquito, *rozeboomi*, taxonomy

Introduction

Mosquitoes, family Culicidae, comprise two principal phyletic lineages that are recognised as subfamilies, the Anophelinae and Culicinae (Harbach & Kitching, 1998, Mitchell *et al.*, 2002). The traditional classification of subfamily Anophelinae includes three genera: *Anopheles* Meigen (cosmopolitan), *Bironella* Theobald (Australasian) and *Chagasia* Cruz (Neotropical). Cladistic analyses of morphological data and DNA sequences of various ribosomal, mitochondrial and nuclear genes strongly support the monophyly of the subfamily and the placement of *Chagasia* in an ancestral relationship to all other anophelines (Harbach & Kitching, 1998, 2005; Besansky & Fahey, 1997; Foley *et al.*, 1998; Krzywinski *et al.*, 2001a, b; Sallum *et al.*, 2000, 2002).

Anopheline mosquitoes are traditionally regarded as the most primitive group of Culicidae. However, Belkin (1962) argued that this was not necessarily so and cited morphological traits that could be interpreted to contradict this notion. When and where anophelines evolved could not be definitely determined but he hypothesised that initial differentiation of the group took place in the American Mediterranean Region, probably at the same time that the other major groups of mosquitoes evolved. The basal placement of Anophelinae relative to Culicinae (Pawłowski *et al.*, 1996; Miller *et al.*, 1997; Besansky & Fahey, 1997; Harbach & Kitching, 1998; Mitchell *et al.*, 2002; Shepard *et al.*, 2006) supports the traditional view, and the fact that *Chagasia*, which is confined to the Neotropical Region, is placed basal to the other anophelines suggests a possible New World origin for Anophelinae (Harbach & Kitching, 1998; Krzywinski *et al.*, 2001b). *Chagasia* show several characters reminiscent of non-anopheline mosquitoes, including the strongly arched scutum, trilobed scutellum and setae on the postpronotum. Based on these similarities, *Chagasia* has been considered an ancient group showing affinities with non-anophelines.

Chromosomal karyotypes have been observed in more than 200 mosquito species representing approximately half of the traditionally recognised genera (White, 1980; Rao & Rai, 1987, 1990). With the exception of *Chagasia bathana* (Dyar), which has three pairs of autosomes and a pair of sex chromosomes ($2n = 8$) (Kreutzer, 1978), the basic number of chromosomes in all mosquito species examined to date is $2n = 6$. Based on chromosome studies of Culicidae, Dixidae, Chaoboridae and Tipulidae, Rao & Rai (1987) concluded that mosquitoes evolved from a *Mochlonyx*-like chaoborid ancestor and the subfamilies Anophelinae and Culicinae diverged from a common lineage. These authors considered the karyotype of *Chagasia*, which is similar to that of *Mochlonyx velutinus* (Ruthe) ($2n = 8$), to be primitive for Anophelinae before this notion was supported by the cladistic analyses mentioned above.

Compared with other anopheline taxa, the taxonomy of genus *Chagasia* has received little attention since it was treated by Lane (1953). While collecting anatomical data for a phylogenetic analysis of mosquito genera (Harbach & Kitching, 1998), it was noted that the larval and pupal stages of *Chagasia* were incompletely known and only partially illustrated. To complete the data matrix for the phylogenetic study, we undertook a review of the genus and prepared illustrations of the larval and pupal stages of *Ch. bonneae* Root for comparative study. The present review is the culmination of those earlier studies.

Materials and methods

The study is based on specimens deposited in the collections of the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC, and the Natural History Museum (NHM), London. Pinned adults were examined under simulated natural light. Dissected genitalia, larvae and larval and pupal exuviae were studied with differential interference contrast optics. Anatomical terminology and abbreviations used in the descriptions and illustrations, respectively, follow Harbach & Knight (1980, 1982). The symbols ♀, ♂, ♂G, E, Le, Pe, L and P used in the literature summaries and material examined sections represent female(s), male(s), male genitalia, egg(s), larval exuviae, pupal exuviae, fourth-instar larvae and pupae, respectively. An asterisk (*) following these symbols in literature citations indicates that at least part of the life stage is illustrated in the publication.

Taxonomy

Genus *Chagasia* Cruz

Type species: *Chagasia neivae* Cruz (monotypy).

Chagasia Cruz, 1906: 199 (new genus), haplotype: *neivae* Cruz (1906: 199). Edwards, 1911: 141 (to subgeneric status in *Anopheles*, but later abandoned); Christophers, 1924: 5, 7 (to subgeneric status in *Anopheles*); Root, 1923: 267, Root, 1927: 471 (generic status reinstated).

Pyrethophorus in part of Lutz, 1904, in Bourroul, 1904: 64; Blanchard, 1905: 623.

Chagasia of Peryassú, 1908: 33, 41, 61, 121–125; Theobald, 1907: 122–124; Theobald, 1910: 3, 75, 77, 79; Surcouf & Gonzalez-Rincones, 1911: 37, 41–44; Brunetti, 1914: 22, 33, 34, 57; Peryassú, 1921a: 71; Peryassú, 1923: 63; Root, 1923: 267, 270; Root, 1927: 471–474; Shannon & del Ponte, 1928: 36, 38, 61; Edwards, 1930: 287; Shannon, 1931: 131, 135, 136, 152–153; Edwards, 1932: 29, 31–32; Martini, 1935: 4, 11, 14; Pinto, 1939: 304; Gabaldon *et al.*, 1940: 57; Kumm *et al.*, 1940: 413, 414, 419; Vargas, 1940: 191; Komp, 1941: 89, 90, 91, 92, 94, 96; Floch & Abonnenc, 1942: 1; Simmons & Aitkin, 1942: 38, 39, 40, 41, 46, 47, 54; Gast Galvis, 1943: 6, 7, 8–9, 19; Komp, 1942: 38, 79, 131, 166, 177, 180; Russell *et al.*, 1943: 6, 7, 24, 30, 35, 39, 42; Leví-Castillo, 1945: 2, 13, 15–16. pl. XI; Pelaez, 1945: 70, 71; Causey *et al.*, 1946: 25; Deane, L.M. *et al.*, 1946: 8; Deane, M.P. *et al.*, 1946a: 40; Deane, M.P. *et al.*, 1946b: 360; Deane, L.M. *et al.*, 1948: 831; Rachou, 1948: 13; Vargas & Martinez Palacios 1950: 2, 17, 42, 43, 47, 50, 54, 61; Floch & Abonnenc, 1951: 8, 9, 10, 21, 22, 23, 27; Ross, 1951: 129; Levi-Castillo, 1951: 77, 79; Lane, 1953: 138–147; Horsfall, 1955: 41; Vargas & Martinez Palacios, 1956: 10, 16, 20, 41, 44, 45, 48, 52, 55; Senevet, 1958: 6, 7–9; Stone *et al.*, 1959: 6, 10; Cova-Garcia, 1961: 167, 168, 173–174, 178; Rodriguez, 1961: 217, 218, 222; Belkin, 1962: 117, 123, 124, 125, 126, Fig. 37; Forattini, 1962: 180, 285, 303, 304, 305, 306, 467, 468;

García & Ronderos, 1962: 124, 125, 139; Forattini *et al.*, 1970: 20; Mattingly, 1971: 4, 9, 15, 21, 29; Cova Garcia & Sutil O., 1976: 15–16; Cova Garcia & Sutil O., 1977: 7–8; Knight & Stone, 1977: 2, 67–68; Harbach & Knight 1980: 114, 131, 140; Darsie, 1985: 158, 172, 193, 221, 237; Clark-Gil & Darsie, 1990: 167, 183, 206, 218; Forattini, 1996: 232, 233; Guimarães, 1997: 1, 2, 29–30; Harbach & Sandlant, 1997; Harbach & Kitching, 1998: 335, 336, 342, 343, 346, 349, 350, 352, 353, 359, 360, 367; Rueda *et al.*, 1998; Reinert, 1999: 77, 81; Sallum *et al.*, 2000: 745, 748, 769, 770, 771, 774; Krzywinski *et al.*, 2001a: 479, 480, 484, 486; Krzywinski *et al.*, 2001b: 540, 542, 552, 553; Forattini, 2002: 36, 191, 192, 193–195, 236–241, 802; Huang, 2002: 2, 25; Sallum *et al.*, 2002: 361, 362, 367, 369, 370, 374, 375, 376; Krzywinski & Besansky, 2003: 115, 116, 117; Harbach & Kitching, 2005: 345, 346, 347, 351, 352, 355, 362, 364; González & Carrejo, 2007: 11, 32, 35, 36; Harbach, 2007: 594, 596, 600, 601, 606, 608, 609, 610, 611, 612, 628.

Anopheles (Chagasia) of Edwards, 1911: 141; Dyar, 1918: 142, 149; Root, 1922: 388; Christophers, 1924: 15, 77, 78; Bonne & Bonne-Wepster, 1925: 497, 543–546; Dyar, 1928: 431–433; Komp, 1936: 66.

Diagnosis. The adults of *Chagasia* are similar to those of *Anopheles*, but the resting posture is like culicine mosquitoes with the head and abdomen at angles to the thorax and the scutellum is tri-lobed with setae in three distinct groups. The wings are principally dark-scaled or have a mixture of dark and pale scales. Eggs have a circumferential covering of longitudinal floats and the micropylar apparatus is borne dorsally at the anterior end. Larvae have three pairs of exceptionally long broom-like dorsal cranial setae (setae 2,4,6-C) that project forward from the anterior margin of the head, they bear uniquely shaped palmate setae (seta 1) on abdominal segments III–V and the spiracular apparatus has a long filamentous anterior median process and a fringe-like row of setae on either side. Pupae have a strong dorsal spine (seta 2) on segments III to VII in addition to the strong lateral spine (seta 9-V–VIII) that is usually present in anopheline mosquitoes. The apical seta of the pupal paddle (seta 1-Pa) is also stout and spine-like.

Females. In general as in *Anopheles* except for the following striking differences. *Head*: Eyes narrowly separated above antennae; dorsum with narrow elongate forked scales and broad falcate scales from posterior margin (occiput) confluent with dorsolateral line and a wide median band of similar scales on vertex, ocular line and interocular space, space between median band and dorsolateral line without scales; postgena with scales anteriorly; clypeus bare. Antenna slightly shorter than proboscis; pedicel with scales dorsally; flagellum bare ventrally, flagellar whorls reduced to relatively few short setae at apex of flagellomeres, flagellomere 2 short, about half length of other flagellomeres, apices of flagellomeres 1–9 with dorsal patch of dark scales. Proboscis about same length as forefemur, dorsal surface narrowly without scales, sides and venter entirely dark-scaled, scales semi-erect to near labella. Maxillary palpus slightly longer than proboscis, comprised of 5 palpomeres, ventral surface narrowly without scales, sides and dorsum with semi-erect dark scales (very shaggy) and few pale scales dorsally at apices of palpomeres 2–4. Cibarial armature formed of 3 large teeth between the lateral flanges (Romeo Viamonte & Castro, 1951). *Thorax*: Scutum with distinct lines of decumbent generally white spatulate scales along acrostichal and anterior dorsocentral setae [posterior acrostichal scales dark in *Ch. ablusa* Harbach, **n. sp.**, *Ch. fajardi* (Lutz) and *Ch. rozeboomi* Causey, Deane & Deane] and margins of scutal fossa and prescutellar area; posterior dorsocentral area with decumbent to semi-erect dark spatulate scales; antealar and supraalar areas with long outstanding dark truncate spatulate scales. Scutellum trilobed with median and lateral clusters of setae and narrow white spatulate scales on median lobe extending on either side to setae of lateral lobes. Mesopostnotum bare; anteprepronotum, postpronotum, anterior area of paratergite, upper proepisternum, upper and lower areas of mesokatepisternum and upper area of mesepimeron with narrow pale spatulate scales; setae present on these areas, except paratergite, as well as on prespiracular and prealar areas; lower mesepimeron, mesomeron and metameron bare; prealar area not separated by suture from mesokatepisternum; mesomeron relatively large, its upper edge above base of hindcoxa. *Wing*: Membrane with distinct microtrichia; spatulate scales of veins relatively narrow to broad, scales all dark, almost entirely dark or mixture of pale and dark scales; cell R_2 longer than vein R_{2+3} ; vein R_s (contrary to Harbach & Kitching, 1998) apparently without basal spur; vein 1A ending well beyond furcation of mcu and CuA; vein R without dorsal remigial setae; subcosta without distinct setae ventrally at base; alula bare; upper calypter with complete row of marginal setae. *Legs*: Very long and slender; femora with speckles and blotches or spots of pale scales and narrow apical pale fringe, sometimes with ill-defined preapical pale

patch on anterior surface; tibiae with dorsoanterior blotches or spots of pale scales, without tibial setae; tarsi with pale bands, hindtarsomere 1 usually with 5 or 6 pale bands (range = 4–7); all ungues simple, fore- and midungues noticeably larger than hindungues; pulvilli not developed. *Abdomen*: Terga and sterna without scales, densely setose; laterotergite bare. *Genitalia*: Not studied; one spermathecal capsule.

Males. Similar to females except for obvious sexual differences; other differences include the following. *Head*: Antennal pedicel strongly swollen and much larger than in females; flagellum strongly verticillate. Maxillary palpus slightly longer than proboscis, with 5 palpomeres, palpomeres 4 and 5 not conspicuously swollen. *Legs*: Ungues of fore- and midlegs large, anterior unguis slightly larger, with 2 teeth, one at base and one at midlength, posterior unguis with single tooth at base; hindungues as in females. *Genitalia*: In general as in *Anopheles* except for the following distinctive differences, which are shown in Fig. 1C. Segment IX reduced, tergum and sternum fused, tergum IX bi-lobed, densely spiculate, with prominent setae, sternum IX without setae; gonocoxite simple, without scales, with dorsomesal prominence bearing specialised stout spine-like setae; gonostylus long, slender, with row of minute setae along sternomesal margin and short apical flattened claw; claspette simple, lobe-like, densely spiculate, with or without setae; aedeagus long, more or less cylindrical, without apical leaflets; proctiger membranous, paraprocts weakly sclerotised; cercal setae absent.

Pupae. In general as in *Anopheles*; known in detail only for *Ch. bonneae* (Fig. 1A,B). *Cephalothorax*: Dorsal apotome evenly sclerotised, undivided; middorsal ridge well developed; all setae present, rather short. *Trumpet*: Laticorn, strongly flared and deeply divided to near base, without tragus; tracheoid area present; placed on basal tubercle. *Abdomen*: Segments III–VII with ventral fold lines; tergum IX distinct, not fused with tergum VIII; seta 1-I strongly developed, dendritic; setae 1-II–VII and 5-II–VII similarly developed, branched; seta 2-III–VII single, stout, spine-like, 2-III–V inserted mesad of seta 1, 2-VI,VII inserted lateral of seta 1; seta 6-II–V inserted anterodorsal and mesal to seta 9, 6-VI,VII inserted posteroventral to seta 9; seta 9-I shorter than seta 6-I; seta 9-II–VIII single, stout, spine-like, 9-VI,VII inserted slightly anterior to caudolateral angle of segment, 9-VIII inserted at caudolateral angle; seta 0-VII inserted on anterior 0.5 of tergum (as in culicine mosquitoes); seta 4-VIII inserted mesad of seta 9; seta 14-VIII usually absent, very weak and inserted near midline when present; seta 1-IX present; 1-X absent. *Genital lobe*: Cercus well developed in female, projecting beyond apex of genital lobe; genital lobe of male slightly tapered distally, apex broadly rounded. *Paddle*: Longer than broad; external buttress more or less distinct; midrib long, distinct to near tip of paddle; outer part broader than inner part; outer margin and distal part of inner margin with minute spines; setae 1,2-Pa present, 1-Pa stout, spine-like, inserted at apex; 2-Pa removed cephalad from apical margin on ventral surface.

Larvae, fourth-instars. In general as in *Anopheles*; as exemplified by *Ch. bonneae* (Fig. 2). *Head*: Width slightly greater than length; collar wider than distance between antennae; posterior tentorial pit (PTP) at considerable distance from caudal border; hypostomal suture complete, extending slightly caudad of PTP; cephalic border of labiogula produced in front; hypostomal sclerite (“cardo”) triangular, width greater than length; seta 1-C small, arising ventrally immediately mesad of seta 0-C; setae 2,4,6-C strongly developed, inserted far forward with 4-C more posterior than 6-C; broom-like with long stem and long distal branches, about 0.75 length of head capsule; seta 3-C stout, spine-like, inserted at margin of cranium laterad of 6-C; setae 5,7-C rather weakly plumose, 5-C inserted more or less on level of base of antenna, 7-C inserted posterior to this level; seta 13-C strongly plumose, large, inserted more or less on level with seta 11-C. *Antenna*: Shorter than head capsule, ventral surface spiculate; seta 1-A small, inserted dorsomesally in basal half; seta 2-A inserted subapically; seta 4-A short, single. *Thorax*: Lateral and ventral surfaces densely spiculate; seta 0-P apparently absent; seta 1-P asymmetrically branched, lanceolate branches arise on one side of main stem; seta 2-P with 2 stout divergent branches; seta 4-P inserted anterior to 2,3-P; Nuttal and Shipley’s organ caudad of setae 5,6-P; setae 7,8-P and 5,7,8-T long, strongly plumose; seta 9-P on tubercle with setae 10–12-P (contrary to Belkin, 1962: 124, Sallum *et al.*, 2000 and Harbach & Kitching, 2005); seta 14-P absent; seta 1-M usually with lanceolate branches; setae 3–5-M on common tubercle; seta 8-T inserted posterolaterad of setae 9–12-T. *Abdomen*: Lateral and ventral surfaces densely spiculate; single tergal plate anteriorly on segments I–VII; seta 0-II–VII more mesal than other dorsal setae; seta 1-I,II,VI,VII not palmate,

1-I,II usually with lanceolate branches, 1-VI,VII with normal branches; seta 1-III-V uniquely palmate, branches with distally expanded blade and hair-like apical filament; seta 2-I,II,VI inserted anterolateral and 2-III-V inserted anteromesal to seta 1; setae 6,7-I,II long and strongly plumose (as in other anophelines); setae 2,5,6,7,9-III-VI short and plumose. *Spiracular apparatus* (see Harbach & Knight, 1980: Fig. 64d): Anterior median process very long, filamentous; posterolateral spiracular lobe with fringe of setae on outer margins (as in dixid larvae). *Segment X*: Saddle a small dorsal sclerite; seta 1-X inserted on integument adjacent to margin of saddle, single; setae 2,3-X strongly developed, 2-X distinctly asymmetrically branched, shorter than 3-X, 3-X hooked at apex; seta 4-X (ventral brush) very strongly developed, with 9 pairs of setae.

Eggs. Surface almost entirely covered by multiple longitudinal floats with numerous transverse ridges; without large areas of outer chorionic cells, however limited areas between floats at anterior and posterior ends of eggs of *Ch. fajardi* bear cells with floors perforated by pores (Linley & Milstrey, 1995); anterior end abruptly tapered, apex with small area bound by collar and bearing variable number of lobed tubercles; posterior end more gradually tapered, apex with larger area bound by collar, area with variable number of lobed tubercles around periphery, floor of area with few chorionic cells; lobed tubercles widely separated, generally thin and not swollen apically, less compact than those of *Anopheles* eggs; micropylar apparatus borne dorsally near collar at anterior end, bound by narrow ridge-like collar, surface of collar nodular, tending to be flat posteriorly and elevated anteriorly, disk fairly smooth with central radial depressions surrounding inconspicuous micropyle.

Discussion. Genus *Chagasia* is a small homogenous group of species that exhibit characteristics of both subfamilies Anophelinae and Culicinae, but are obviously more closely allied with anopheline taxa based on overall morphology of the immature stages. Certain features of the adults, especially the scaling of the scutum and wings, bear a resemblance to the adults of genus *Aedeomyia*, which based on morphology and distribution appears to be a primitive group of subfamily Culicinae (Belkin, 1962; Harbach & Kitching, 1998). The male proctiger of *Aedeomyia* species, like that of *Chagasia* and other anophelines, as well as *Uranotaenia* and a few aedines, is largely unsclerotized and lacks cercal setae. Whereas *Chagasia* are mainly found in tropical areas of the Neotropical Region, species of *Aedeomyia* principally occur in tropical areas of the Southern Hemisphere. In as much as the analysis of Harbach & Kitching (1998) indicated that *Aedeomyia* is a cladistically basal group of subfamily Culicinae, it is possible that *Chagasia* and *Aedeomyia* could have been early offshoots of an ancestral lineage in the Southern Hemisphere. It is also interesting to note that *Chagasia* are the only species of Culicidae that bear a fringe of setae on the posterolateral lobes of the larval spiracular apparatus in common with species of family Dixidae.

Bionomics. *Chagasia* larvae are usually found in shaded streams among the roots of trees and in grassy margins or dead leaves and other debris. They sometimes occur in clear rock-pools along shaded streams. Adults remain in vegetation near the larval habitats or enter nearby forest canopy. Females bite during the day and night, but seldom feed on humans. Species of *Chagasia* are not known to transmit pathogens of human diseases.

Distribution. *Chagasia* are Neotropical mosquitoes. The distribution of *Ch. bathana* extends from Peru, Colombia and Venezuela through Central America into southern Mexico. The other species are restricted to South America. Country records for each species are listed below.

Species of genus *Chagasia*

Chagasia ablusa Harbach, new species

Chagasia fajardoi of Komp, 1936: 66 (Colombia, ♀ L P, bionomics); Gast Galvis, 1943: 5, 8, 9, 19 (Colombia, ♂ ♀ L); ?Romeo Viamonte & Castro, 1951: 319, 324, Fig. 12 (♀*); Gabaldon & Cova-Garcia, 1952: 179, 197, 198, Fig. 8H (in part, ?Bolivia, Colombia); Lane, 1953: 139–144 (in part, Colombia, ♂* ♀ E* L* P*); Horsfall, 1955: 41 (distribution, L, bionomics); Stone *et al.*, 1959: 10 (in part, catalogue, Colombia); Cova-Garcia, 1961: 181–183 (?Venezuela, A, identification).

Chagasia fajardi of Russell *et al.*, 1943: 35, 39, 42 (♀ L, bionomics, distribution); Knight & Stone, 1977: 68 (in part, catalogue, Colombia); Guimarães, 1997: 30 (in part, catalogue, Colombia).

Diagnosis. The adults of *Ch. ablusa* are distinguished from those of other species of *Chagasia* as follows: front of anterior promontory with yellow scales contiguous and well-contrasted with white dorsocentral scales (distinction from *Ch. fajardi*); acrostichal scales pale anteriorly, dark posteriorly (as in Fig. 3B) (distinction from *Ch. bathana* and *Ch. bonneae*); without pale scales on mesal margin of supraalar scales (distinction from *Ch. fajardi*); wing dark-scaled with speckling of pale scales on proximal half of costa (distinction from *Ch. bathana* and *Ch. bonneae*), vein R_{4+5} with distinct cluster of darker scales at base; hindtibia with distinct semi-erect clusters of dark scales (Fig. 4A) (distinction from *Ch. fajardi* and *Ch. rozeboomi*); hindtarsomeres 2–5 without postbasal dark bands (distinction from *Ch. bathana*), basal pale band of hindtarsomere 2 usually very long, 3.17–10.33 (mean = 5.89) length of apical dark band (Fig. 5D) (92% distinction from *Ch. fajardi*), hindtarsomere 5 with apical dark band (distinction from *Ch. bonneae*). Males are distinguished by the presence of a single stout specialised seta on the dorsomesal prominence of the gonocoxite (unique) and fine setae on the claspette (distinction from *Ch. bathana* and *Ch. bonneae*). Larvae are distinguished by the development of certain setae: setae 5- and 7-C are long (distinction from *Ch. rozeboomi*); seta 5-C is inserted anterior to the base of the antenna on a line midway between the insertions of setae 4- and 7-C, the rachis (main stem) of 5-C reaches the base of seta 4-C and the distance between the insertions of the 2 seta 5-C is less than the distance between the insertions of setae 4- and 7-C (distinctions from *Ch. bathana*, *Ch. bonneae* and *Ch. rozeboomi*); setae 11- and 13-C are about the same length and shorter than the antenna, about two-thirds as long (distinction from *Ch. bathana*, *Ch. bonneae* and *Ch. rozeboomi*); seta 15-C is single and long (distinction from *Ch. bonneae*); and seta 1-P has long aciculae that arise near the middle of each primary branch (distinction from *Ch. rozeboomi*). Pupae have no diagnostic features but they differ from pupae of *Ch. bonneae* in lacking a ligulate process on the rim of the trumpet.

Etymology. The specific name *ablusa* is the feminine form of the Latin adjective *ablusus*, which means ‘different’.

Discussion. *Chagasia ablusa* has been misidentified as *Ch. fajardi* in the past based on superficial similarities of the adults. Whether or not these similarities indicate that *Ch. ablusa* is more closely related to *Ch. fajardi* than to the other species of *Chagasia* is a moot question. The structure of the male genitalia and the darkly scaled wings and posterior dorsocentral area suggest that *Ch. ablusa*, *Ch. fajardi* and *Ch. rozeboomi* are more closely related to one another than either is to *Ch. bathana* and *Ch. bonneae*. Until the larva of *Ch. fajardi* is known with certainty (see below), it is pointless to speculate on relationships based on larval morphology. Because *Chagasia* is a small homogeneous assemblage of species that exhibit a paucity of anatomical distinctions, molecular data will probably be needed to resolve phylogenetic relationships within the genus.

Distribution. Colombia, Peru and ?Venezuela. Published reports of *Ch. fajardi* in Venezuela (see above) probably refer to *Ch. ablusa* based on its proximity and topographic similarity to Colombia, but this requires confirmation as specimens from Venezuela were not available for study. *Chagasia ablusa* surely occurs in Ecuador and is likely to be present in western Bolivia. In fact, reports of *Ch. fajardi* in the latter country (see below) may refer to this species.

Material examined. Type series: Twenty specimens (10♀, 1♂, 1♂G, 3Le, 3Pe, 2L). HOLOTYPE, female (PE 288-1), with LePe on microscope slide, PERU: *Junín*, Satipo, Mission Cutivireni (12 S 74 W), 400 m, 10 March 1985 (*Calderone*), WRBU ACC 1131. *Paratypes*, 1♀LePe (PE288-4), 1♂ with dissected genitalia (PE 288-105), 1L (PE 288), same data as holotype; 5♀ (PE 359), same as holotype except 22 March 1985 (*Hayes, Harrison & Savage*); 1♀ (PE 357), same as holotype except 21 March 1985 (*Victor Lugo & others*); PE 467-16 (1♀LePe), 1L (PE 467a) *Madre de Dios*, Rio Manu, Pakitza (11° 55' 48" S 71° 15' 18" W), 250 m, 31 October 1990 (*Wilkerson, Gaffigan & Mallampalli*), WRBU ACC 1445. The type series is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Other material examined: Sixty-one specimens, COLOMBIA, *Meta*, Restrepo (1♀, 2♂, 1♂G), Villavicencio (15♀, 5♂, 1♂G, 13Le, 14Pe, 4L); unknown locality (1♀).

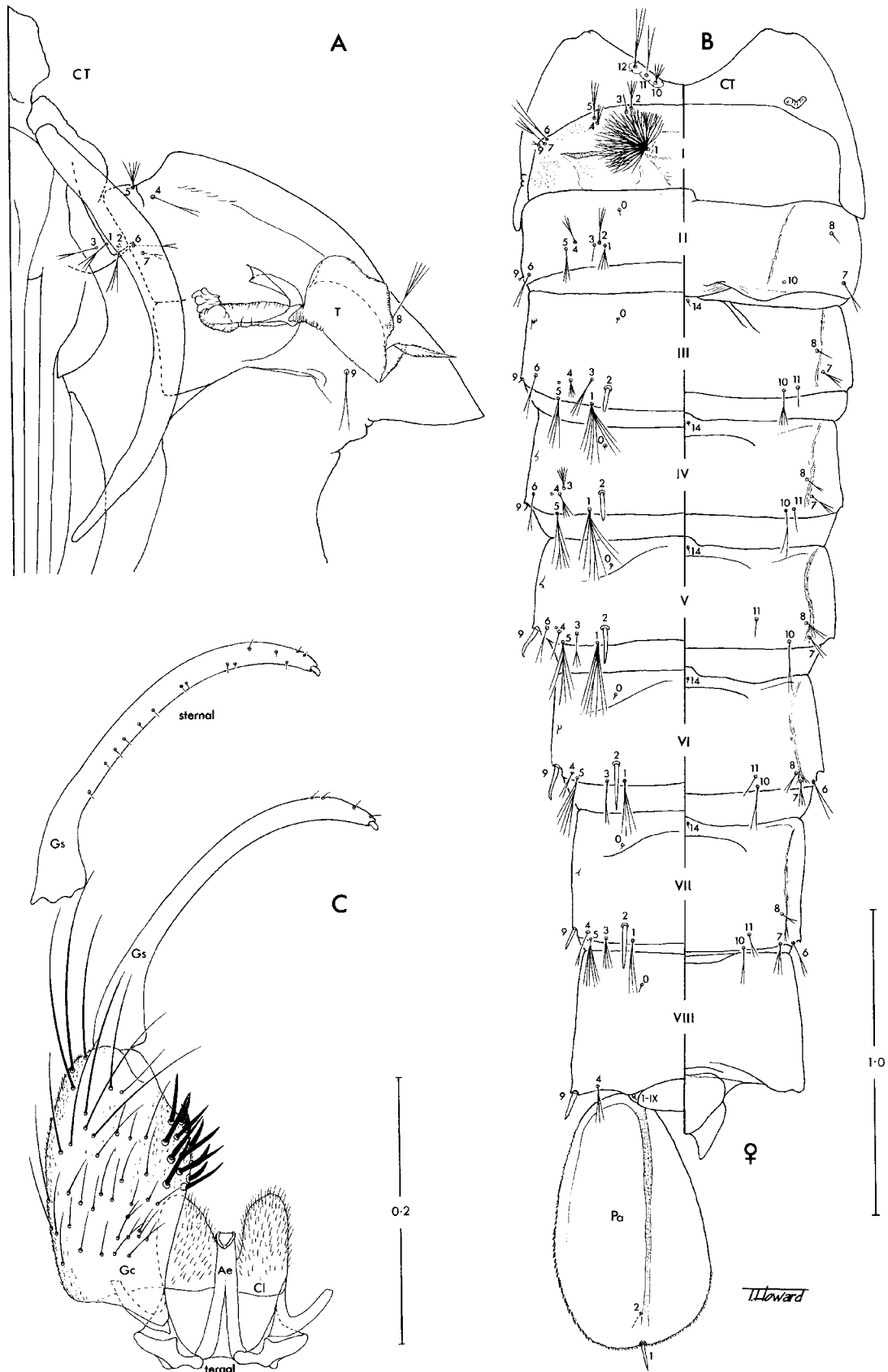


FIGURE 1. Pupa and male genitalia of *Chagasia bonneae*: A, pupa, left side of cephalothorax, dorsal to right; B, pupa, dorsal (left) and ventral (right) aspects of metathorax and abdomen; C, male genitalia, aspects as indicated. Ae, aedeagus; Cl, claspette; CT, cephalothorax; Gc, gonocoxite; Gs, gonostylus; Pa, paddle; T, trumpet; I–IX = abdominal segments I–IX; 1–14 = setal numbers for specified areas, e.g., seta 3-I. Scales in mm.

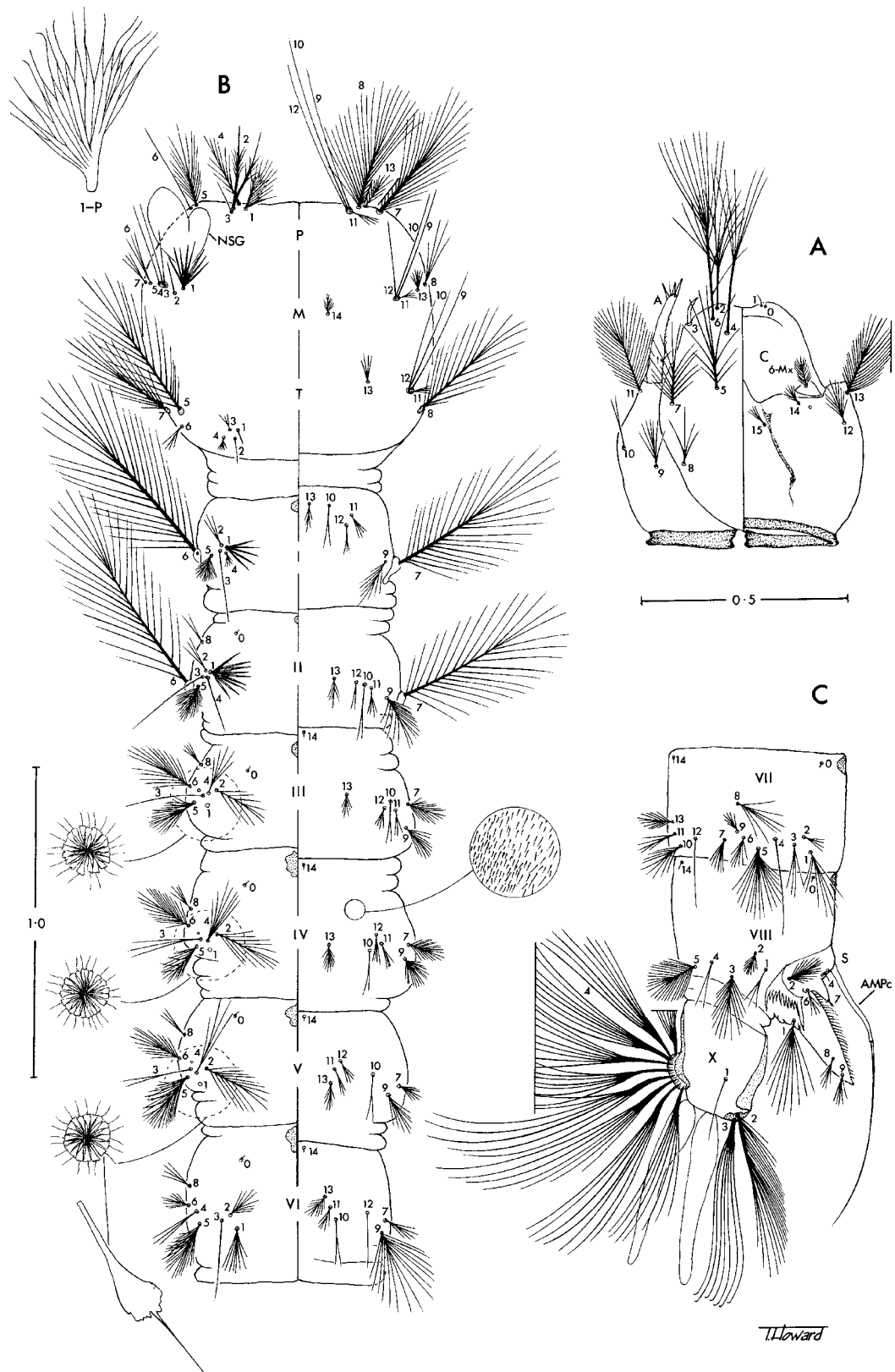


FIGURE 2. Fourth-instar larva of *Chagasia bonnae*: A, head, dorsal (left) and ventral (right) aspects of left side; B, thorax and abdominal segments I–VI, dorsal (left) and ventral (right) aspects of left side; C, abdominal segments VII–X, left side. A, antenna; AMPc, anterior median process; C, cranium; P, prothorax; M, mesothorax; NSG, Nuttall and Shipley's organ; S, spiracular lobe; T, metathorax; TP, tergal plate; I–VIII, X = abdominal segments I–VIII and X; 1–15 = setal numbers for specified areas, e.g., seta 5-C. Scales in mm.

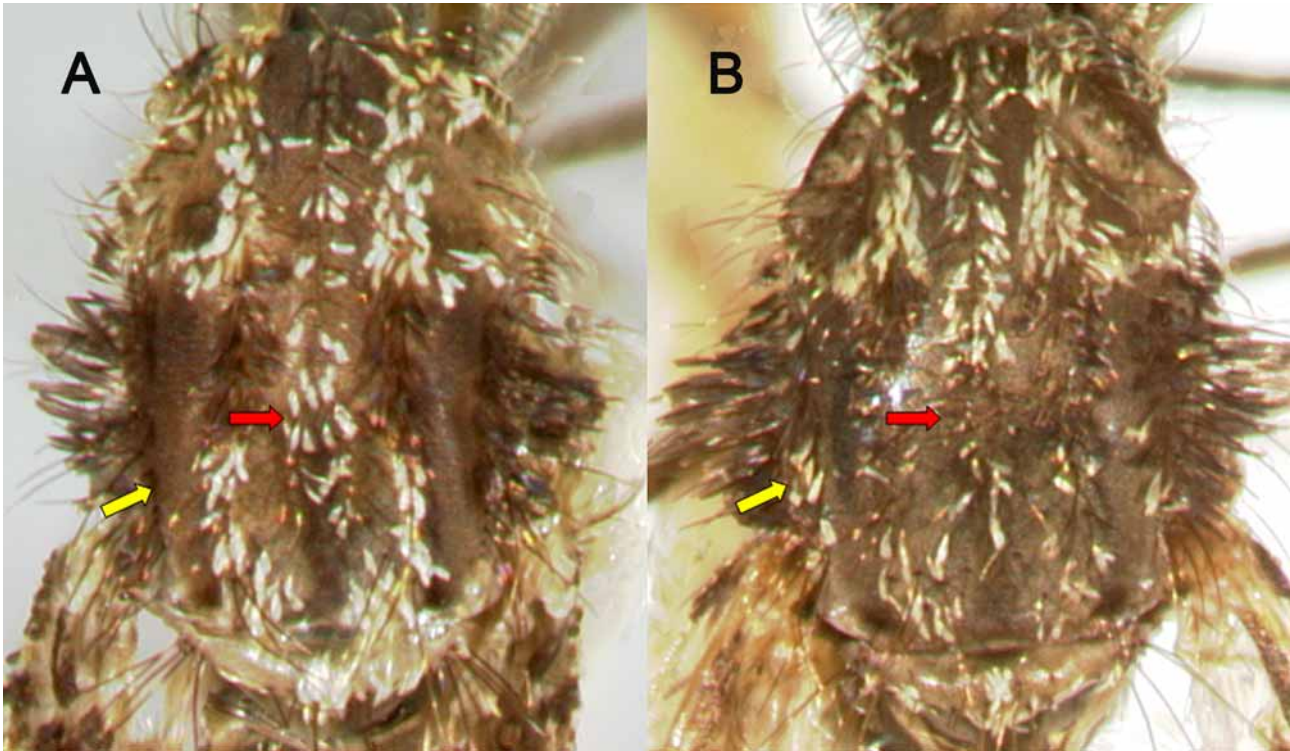


FIGURE 3. Scutum (dorsal view) of (A) *Chagasia bonneae* and (B) *Ch. fajardi*. The acrostichal scales (red arrows) are entirely pale in *Ch. bonneae* and dark posteriorly in *Ch. fajardi* (some scales have been lost in specimen shown); pale para-supraalar scales (yellow arrows), absent in the former species, are often present in the latter species. Note that the dorsocentral scales on the anterior promontory are distinctly yellow in *Ch. bonneae* but more or less unicolorous with the other dorsocentral scales in *Ch. fajardi*.

Chagasia bathana (Dyar, 1928)

bathana (Dyar, 1928), in Curry, 1928: 244 (♀ L P, *Anopheles*), holotype ♀ LePe (USNM): Gatun, Canal Zone, Panama.

Diagnosis. The adults of *Ch. bathana* are distinguished from those of other species of *Chagasia* as follows: scales on front of anterior promontory usually concolorous with dorsocentral scales, usually yellow sometimes white; acrostichal scales all pale (Fig. 3A) (distinction from *Ch. abluca*, *Ch. fajardi* and *Ch. rozeboomi*); without short line of pale scales on mesal margin of supraalar scales (distinction from *Ch. fajardi*); veins of wing with mixture of dark and pale scales (distinction from *Ch. abluca*, *Ch. fajardi* and *Ch. rozeboomi*); hindtibia with distinct semi-erect clusters of dark scales (as in Fig. 4A) (distinction from *Ch. fajardi* and *Ch. rozeboomi*); hindtarsomeres 2–5 with postbasal dark bands (unique) (Fig. 5A), postbasal band of tarsomere 5 sometimes (and that of tarsomere 4 occasionally) obsolescent or absent, basal pale band of hindtarsomere 2 moderately long, hindtarsomere 5 with apical dark band (distinction from *Ch. bonneae*), sometimes extended proximally on ventral surface (as in *Ch. bonneae*). Males have many stout specialised setae on the dorsomesal prominence of the gonocoxite and setae are absent from the claspette (as in Fig. 1C) (distinctions from *Ch. abluca*, *Ch. fajardi* and *Ch. rozeboomi*). Larvae have long setae 5- and 7-C (distinction from *Ch. rozeboomi*); seta 5-C is inserted more or less in line with base of antenna, its rachis extends forward to a point less than halfway to the insertion of seta 4-C and the distance between the insertions of the 2 seta 5-C is greater than the distance between the insertions of setae 5- and 7-C (distinctions from *Ch. abluca*); seta 11-C is shorter than seta 13-C and the antenna, about three-quarters as long (distinction from *Ch. abluca*, *Ch. bonneae* and *Ch. rozeboomi*); seta 15-C is long, single or split distally and extends to seta 14-C (distinction from *Ch. bonneae*); and seta 1-P has long aciculae that arise near the middle of each primary branch

(distinction from *Ch. rozeboomi*). Pupae have no diagnostic features but they differ from pupae of *Ch. bonneae* in lacking a ligulate process on the rim of the trumpet.

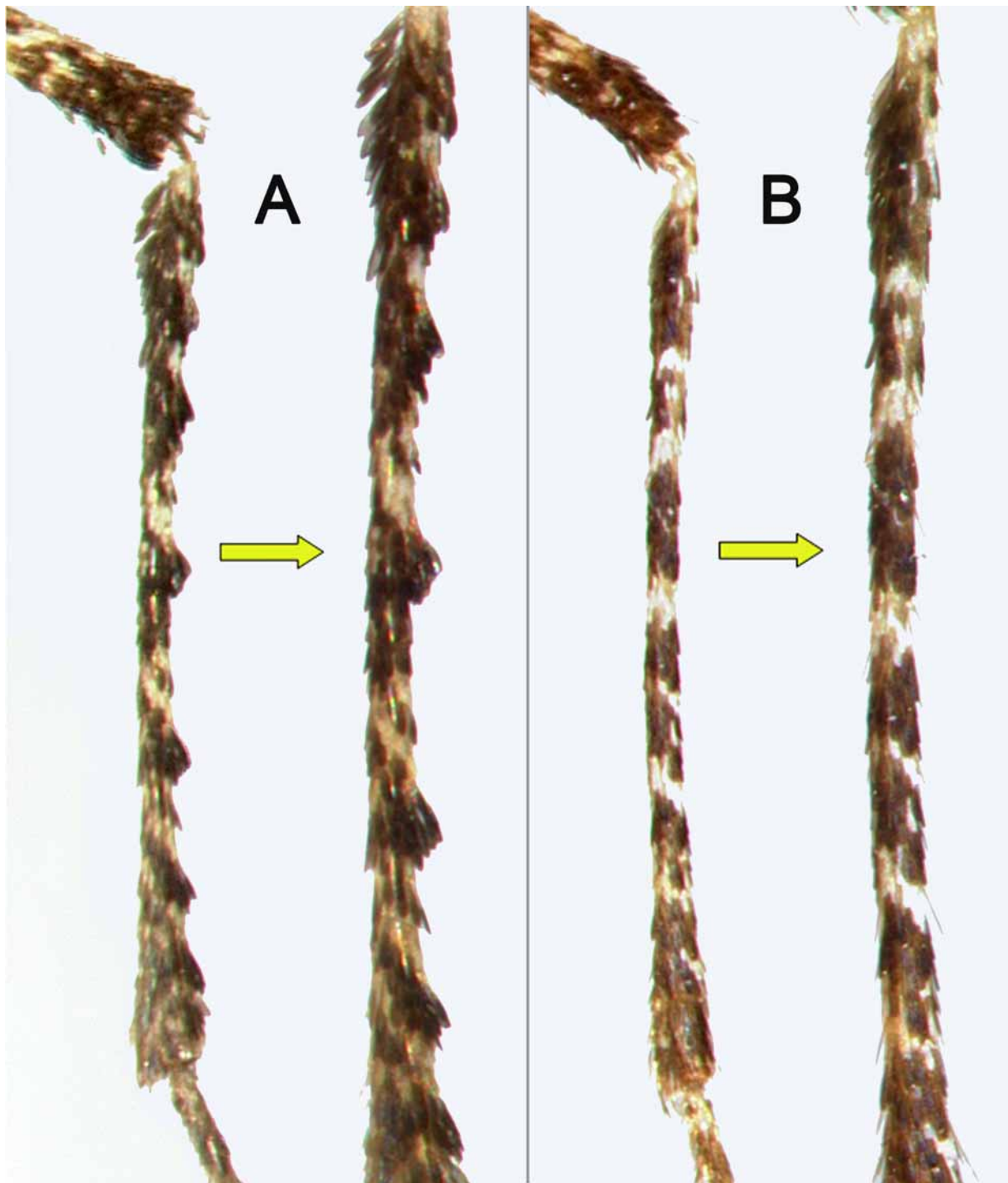


FIGURE 4. Hindtibia (anterior view) of (A) *Chagasia ablusa* and (B) *Ch. fajardi* showing the presence and absence of semi-erect clusters of dark scales, respectively.

Etymology. This species was originally described as *Anopheles (Chagasia) bathanus*. According to Kitzmiller (1982), the species was named in honour of Mr C.H. Bath, a sanitary inspector for the Panama Canal Zone Company. Mr Bath obtained the type female bred from a larva collected near Gatun, Canal Zone (Curry, 1928: 245).

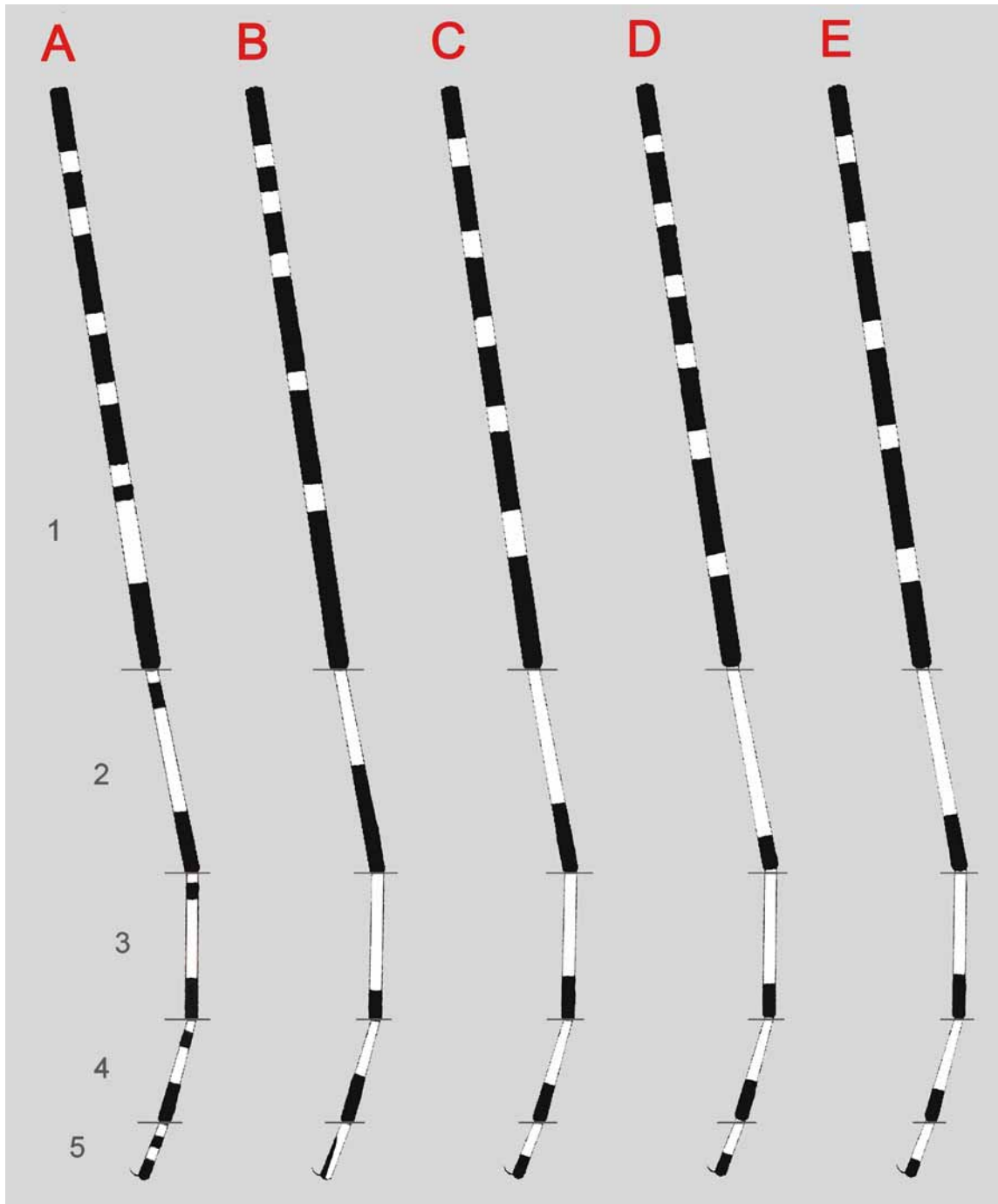


FIGURE 5. Hindtarsus (anterior view) of (A) *Chagasia bathana*, (B) *Ch. bonneae*, (C) *Ch. fajardi*, (D) *Ch. ablusa* and (E) *Ch. rozeboomi*.

Discussion. As far as is currently known, the distribution of *Ch. bathana* only overlaps with the distributions of *Ch. ablusa* and *Ch. bonneae* in northwestern areas of South America (Ecuador to Venezuela). The adults of *Ch. bathana* are easily distinguished from the adults of the other two species by the presence of postbasal dark bands on tarsomeres 4–5 of the hindleg. Damaged specimens and rare specimens that lack the postbasal bands are easily distinguished from *Ch. ablusa* by the mixture of dark and pale scales on the wings, but it would not be possible to distinguish them from *Ch. bonneae*.

Distribution. Belize, Colombia, Costa Rica, Ecuador, Honduras, French Guiana, Guatemala, Mexico, Nicaragua, Panama and Venezuela. Records of *Ch. bathana* in Peru (Villanueva Rodriguez, 1961; Forattini *et*

al., 1970) refer to *Ch. bonneae*. The distribution of *Ch. bathana* appears to extend no further south than Ecuador (Lev-Castillo, 1945; present observations).

Material examined. Three hundred and eleven specimens: BELIZE, *Cayo*, Caves Branch (1♀), Chiquibul National Park (4♀), Hummingbird Highway (2♀); *Stann Creek* (7♀). COSTA RICA, *Guanacaste*, Arado (2L); *Heredia*, Lagunilla (1L); *Limon*, Barra de Cobrado (2♀), Puerto Viejo (6L); *Puntarenas*, Aguirre (1♀), Rio Seco (4L). ECUADOR, *Pichincha*, Santo Domingo (21♀, 5♂). GUATAMALA, *Petén*, Santa Teresa (1♀). HONDURAS, *Colón*, Trujillo (5♀, 1♂, 1L). MEXICO, *Chiapas*, Palenque (2L). NICARAGUA, *Zelaya*, Bluefields (14♀). PANAMA, *Bocas del Toro*, Almirante (3♀, 3♂, 2♂G, 1Le, 7L), Isla Colon (4L); Canal Zone (34♀, 21♂, 3♂G, 46Le, 44Pe, 5L); *Darien*, Purco (2♀, 1Pe); *Tocumen*, Cerro Azul (1LePe); unknown localities (1♀, 8♂, 5♂G, 7Le, 3Pe, 23L). VENEZUELA, unknown locality (2L).

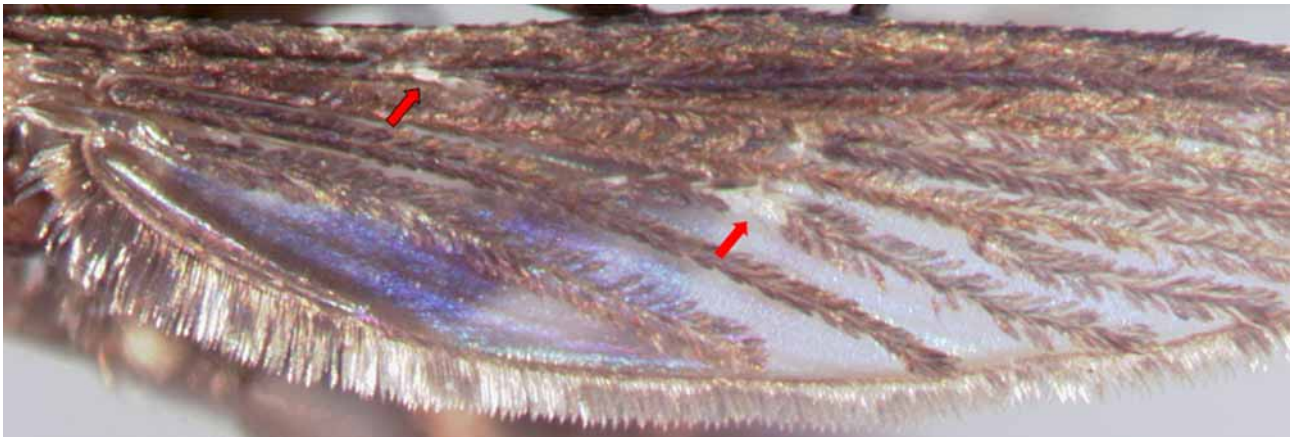


FIGURE 6. Wing of *Ch. fajardi* showing the pale spots that are usually present on the radius (upper arrow) and at the base of media-two (lower arrow).

Literature. Dyar, 1928: 428, 433 (as *bathanus*, Costa Rica, Panama, ♂ ♀ L); Shannon, 1931: 152, 153 (as *bathanus*, taxonomy); Curry, 1932: 369 (as *bathanus*, Panama, L, bionomics); Edwards, 1932: 32 (as *bathanus*, type data); Senevet, 1934: 29–33, 59, 67 (as *bathanus*, Panama, P*); Martini, 1935: 25–26 (as *bathanus*, Mexico); Gabaldon *et al.*, 1940: 58–62 (as *bathanus*, Venezuela, A L* P*); Kumm *et al.*, 1940: 388, 389, 391, 392, 412–413, 419 (as *bathanus*, Costa Rica, bionomics, identification); Komp, 1941: 89, 92, 94, 96 (as *bathanus*, ♀ L ♂G keys); Rozeboom, 1941: 98 (as *bathanus*, Belize, Costa Rica, Mexico, Panama, Venezuela, bionomics); Floch & Abonnenc, 1942: 1 (as *bathanus*, distribution); Komp, 1942: 5, 38, 41, 43, 46–47, 79, 82–86, 131, 133–134, 166, 177, 180 (as *bathanus*, Belize [as British Honduras], Colombia, Costa Rica, Mexico, Panama, Venezuela, ♂* ♀* L* P*); Simmons & Aitkin, 1942: 39, 41, 48, 54, 62–63 (as *bathanus*, ♂ ♀ L keys, distribution, bionomics); Gast Galvis, 1943: 9 (as *bathanus*, ♂ ♀ L); Russell *et al.*, 1943: 24, 30, 35, 39 (as *bathanus*, ♀ L, bionomics, distribution); Causey *et al.*, 1945: 341, 344–346 (as *bathanus*, ♂ ♀ L*); Leví-Castillo, 1945: 17–29, 143, 145, 148, 149, 163, pls I, XIII–XV, map (as *bathanus*, Ecuador, ♂* ♀* L* P*, L bionomics, keys, distribution); Pelaez, 1945: 71, 72, 77 (as *bathanus*, Mexico, ♀* in key); Arnett, 1947: 187–188 (as *bathanus*, Panama, bionomics); Knight & Chamberlain, 1948: 9, 11 (as *bathanus*, P*); Rachou, 1948: 715–717 (as *bathanus*, L, identification); Vargas, 1949: 231, 234, 235 (as *bathanus*, P); Galindo *et al.*, 1950: 549, 552, 555, 566, 568, 569 (as *bathanus*, Panama, ♀, bionomics); Vargas & Martinez Palacios, 1950: 2, 5, 8, 42, 43, 47, 50, 54, 61–64 (as *bathanus*, Mexico, ♂* ♀ L* P, bionomics, identification); Levi-Castillo, 1951: 79 (as *bathanus*, list); Gabaldon & Cova-Garcia, 1952: 178, 185, 186, 197, Fig. 8F (as *bathanus*, Costa Rica, Guatemala, Honduras, Mexico, Panama); Lane, 1953: 139, 140, 146–147 (as *bathanus*, Belize, Costa Rica, Guatemala, Mexico, Panama, Venezuela, ♂* ♀ L*); Horsfall, 1955: 41, 179 (as *bathanus*, distribution, L, bionomics); Trapido *et al.*, 1955: 533, 536, 537, 538, 539 (as *bathanus*, Panama, ♀, bionomics); Vargas & Martinez Palacios, 1956: 10, 11, 12, 44, 45, 48, 52, 55, 58, 62–63, 137, 140, 145, 157, 163, 171 (as *bathanus*, Mexico, ♂* ♀* E L* P, bionomics, distribution); Galindo & Trapido,

1957: 146 (as *bathanus*, Nicaragua, A); Trapido & Galindo, 1957: 123, 124, 125, 129, 130 (as *bathanus*, Panama, ♀, bionomics); Senevet, 1958: 8 (as *bathanus*, catalogue); Stone *et al.*, 1959: 10 (catalogue); Cova-Garcia, 1961: 62–64, 108–109, 148–149, 163, 164, 178, 181, 182, 183, Tables 1, 2, 3 (as *bathanus*, Venezuela, ♂* ♀* L*); Villanueva Rodriguez, 1961: 217, 218 (as *bathanus*, in part, distribution other than Peru); Forattini, 1962: 306, 469 (as *bathanus*, distribution, A,L keys); García & Ronderos, 1962: Fig. 58 (as *bathanus*, L*); Forattini *et al.*, 1970: 20 (as *bathanus*, in part, Panama, collection); Bertram, 1971: 745, 747, 748, 749, 750, 752, 753, 754 (Belize [as British Honduras], A, bionomics); Knight, 1971: 192 (L*); Mattingly, 1971: Figs 21c, 43a (L* P*); Baerg & Boreham, 1974: 631 (Panama, E*); Fauran & Pajot, 1974: 100 (French Guiana); Cova Garcia & Sutil O., 1975a: 8 (as *bathanus*, Venezuela, L*, identification); Cova Garcia & Sutil O., 1975b: 202 (as *bathanus*, Venezuela, ♀*, identification); Cova Garcia & Sutil O., 1976: 16 (as *bathanus*, Venezuela, ♂*, identification); Cova Garcia & Sutil O., 1977: 32, 53, 73 (as *bathanus*, Venezuela, ♂* ♀* L*, identification); Heinemann & Belkin, 1977a: 261, 282 (Costa Rica, collection record); Heinemann & Belkin, 1977b: 410, 411, 414, 449, 452 (Belize, Nicaragua, collection records); Knight & Harbach, 1977: 460 (L*); Knight & Stone, 1977: 67 (catalogue, excluding Peru); Harbach, 1978: 311 (L*); Heinemann & Belkin, 1978a: 124, 151, 152, 153, 168, 170, 175, 183, 191, 192, 194 (Panama, collection records); Kreutzer, 1978: 554–558 (Panama, karyotype*); Harbach & Knight, 1980: 244, 245 (Fig. 64d); Sutil O., 1980: 11, 24 (Venezuela, list); White, 1980: 245, 252 (karyotype); Rao & Rai, 1987: 321, 329, 330, 331 (karyotype, chromosome evolution); Clark-Gil & Darsie, 1990: 155, 167, 183, 206, 218, 241, 246 (Guatemala, A, L, identification, bionomics); Wilkerson & Strickman, 1990: 8, 10, 14, 32 (Belize, Costa Rica, Guatemala, Mexico, Nicaragua, Panama, ♀*, identification); Mora *et al.*, 1994: 159 (as *bathanus*, Venezuela); Guimarães, 1997: 29–30 (catalogue, excluding Peru); Berti *et al.*, 1998: 23 (Venezuela); Harbach & Kitching, 1998: 367; Reinert, 1999: 77 (P); Moreno *et al.*, 2000: 24, 25, 28 (Venezuela, L, bionomics); Krzywinski *et al.*, 2001a: 480, 483 (molecular phylogenetics); Krzywinski *et al.*, 2001b: 542, 543, 545, 546, 548 (molecular phylogenetics); Forattini, 2002: 194, 195, 241 (A, L, distribution); Pecor *et al.*, 2002: 244, 272, 373 (Belize, L, bionomics); Sallum *et al.*, 2002: 363, 369, 370, 372, 373, 374, 375 (molecular phylogenetics); Harbach & Kitching, 2005: 364 (cladistic analysis); Rubio-Palis, 2005: 1, 2 (Venezuela, list).

Chagasia bonneae Root, 1927

bonneae Root, 1927: 474 (♂ ♀ L* P*), holotype ♂LePe: Dam, Suriname (USNM).

Diagnosis. The adults of *Ch. bonneae* are distinguished from those of other species of *Chagasia* as follows: front of anterior promontory with yellow scales contiguous and well contrasted with dorsocentral scales (distinction from *Ch. fajardi*); acrostichal scales all pale (Fig. 3A) (distinction from *Ch. ablusa*, *Ch. fajardi* and *Ch. rozeboomi*); without short line of pale scales on mesal margin of supraalar scales (distinction from *Ch. fajardi*); veins of wing with mixture of dark and pale scales (distinction from *Ch. ablusa*, *Ch. fajardi* and *Ch. rozeboomi*); hindtibia with distinct semi-erect clusters of dark scales (as in Fig. 4A) (distinction from *Ch. fajardi* and *Ch. rozeboomi*); hindtarsomeres 2–5 without postbasal dark band (distinction from *Ch. bathana*), basal pale band of hindtarsomere 2 relatively short, 0.90–1.53 (mean = 1.24) length of apical dark band, hindtarsomere 5 with line of dark scales on distal 0.7 of ventral surface (unique) (Fig. 5B). Males have many stout specialised setae on the dorsomesal prominence of the gonocoxite and setae are absent from the claspette (Fig. 1C) (distinctions from *Ch. ablusa*, *Ch. fajardi* and *Ch. rozeboomi*). Larvae have long setae 5- and 7-C (distinction from *Ch. rozeboomi*); seta 5-C is inserted more or less in line with base of antenna, its rachis extends forward to a point about halfway to the insertion of seta 4-C and the distance between the insertions of the 2 seta 5-C is greater than the distance between the insertions of setae 5- and 7-C (distinctions from *Ch. ablusa*); seta 11-C is about as long as seta 13-C and the antenna (distinction from *Ch. ablusa*, *Ch. bathana* and *Ch. rozeboomi*); seta 15-C is short and multiple branched and extends only about halfway to seta 14-C (distinction from *Ch. ablusa*, *Ch. bathana* and *Ch. rozeboomi*); and seta 1-P has long aciculae that arise near

the middle of each primary branch (distinction from *Ch. rozeboomi*). Pupae are easily recognised by the presence of a unique ligulate process that emanates from the rim of the trumpet.

Etymology. Although there is no specific dedication to Johanna Bonne-Wepster, there is no doubt that this species was named in her honour (Kitzmilller, 1982). Mrs Bonne-Wepster and her husband Prof. Cornelis Bonne, both Dutch, jointly and separately published the results of fieldwork they conducted in Suriname and the East Indies.

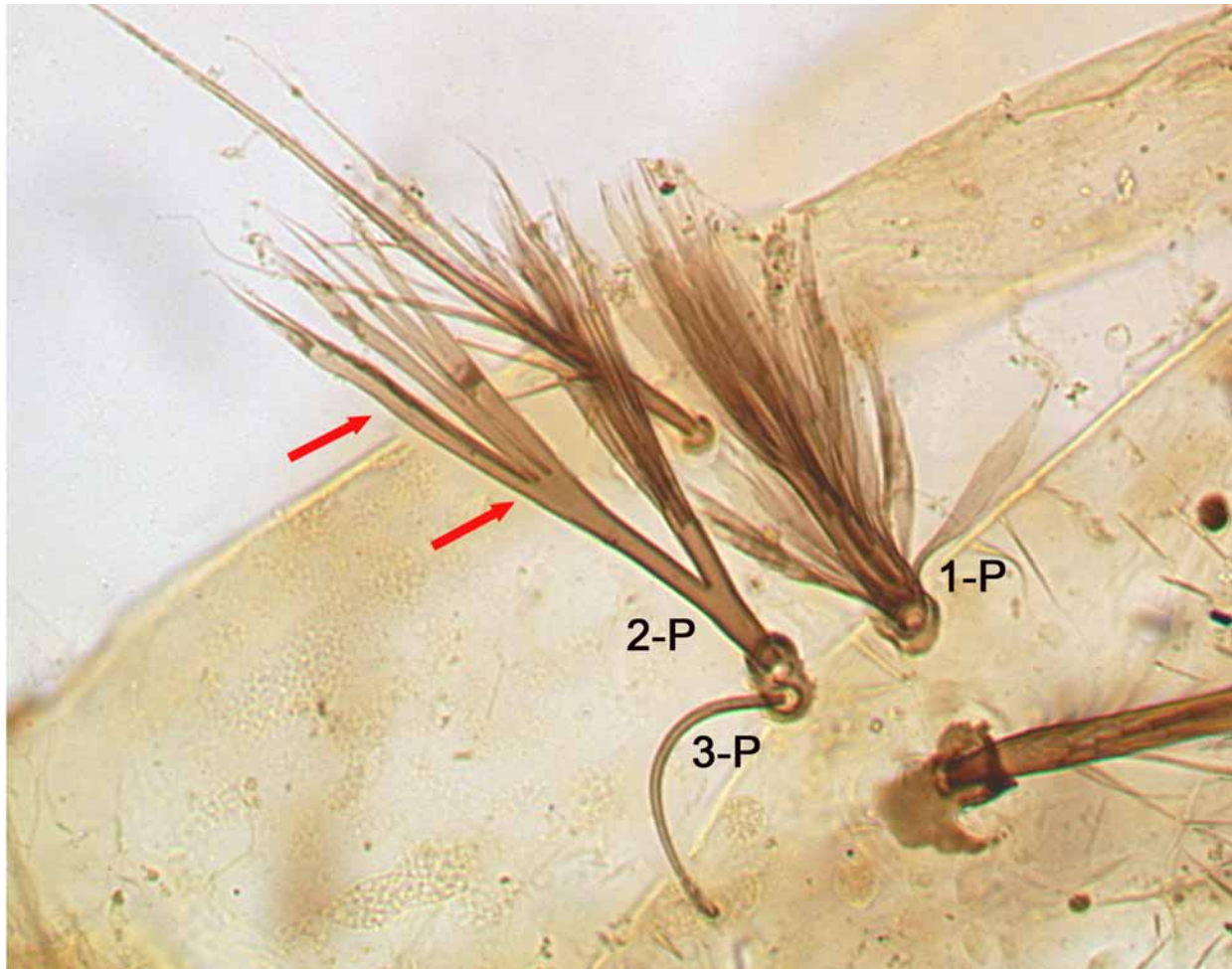


FIGURE 7. Seta 2-P of the larva of *Ch. rozeboomi*. The thickened secondary branches (upper arrow) borne at the ends of the primary branches (lower arrow) is a unique feature of the species (compare with seta 2-P in Figure 2B).

Discussion. Based on overall similarity, *Ch. bonneae* appears to be more closely related to *Ch. bathana* than to the other species of *Chagasia*. They appear to be sister species. The adults are only distinguished by features of the hindtarsi (postbasal dark bands in *Ch. bathana*; a ventral line of dark scales on tarsomere 5 in *Ch. bonneae*) and larvae are difficult to distinguish despite the differences noted in the keys below. Pupae of *Ch. bonneae* are easily recognised by the presence of the ligulate process that projects from the rim of the trumpet.

Distribution. Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname and Venezuela.

Material examined. Three hundred and twenty-two specimens: BRAZIL, *Mato Grosso*, Aripuan (1♀); *Pará*, Marabá (1♀), Gnanía (1♀); *Rondonia*, Costa Marques (15♀, 7♂, 14Le, 19Pe, 8L). COLOMBIA, *Meta*, Villavicencio (9♀, 6♂, 6♂G, 12Le, 11Pe, 4L); unknown locality (10♀). ECUADOR, *Nepo*, Coca (1♀), Tena (3♀); *Pastaza*, Santa Ana (1♀). FRENCH GUIANA, *Guyane*, Cayenne (1♀). GUYANA, unknown locality (1Le, 1Pe). PERU, *Huánuco*, Cochicote (6♀), Tingo María (4♀, 2♂); *Junín*, Satipo (94♀, 8♂, 4♂G, 10Le, 18Pe, 1L, 1P); *Madre de Dios*, Pakitza (12♀, 7♂, 2♂G, 10Le, 10Pe, 1L).

Literature. Bonne, 1923: 112–114 (as *farjardi*, ♂*); Root, 1922: 382, 384, 387–89, 392 (as *fajardoi*, L*); Root, 1923: 266, 270, 271 (as *fajardoi*, ♂*); Bonne & Bonne-Wepster, 1925: 544–546 (as *farjardi*, Suriname, ♂* ♀ L*); Dyar, 1928: 428, 432–433 (Suriname, ♂* ♀ L*); Shannon, 1931: 152, 153 (taxonomy); Edwards, 1932: 32 (type data); Senevet, 1934: 67 (P key); Antunes, 1937: 79, 84 (Colombia, ♀); Pinto, 1939: 305 (♂*); Gabaldon *et al.*, 1940: 58, 60, 61 (A L P*); Floch & Abonnenc, 1942: 1–3 (French Guiana, ♀*); Simmons & Aitkin, 1942: 39, 41, 48, 54, 62–63 (♂ ♀ L keys, distribution, bionomics); Cerqueira, 1943: 16 (Bolivia, collection record); Gast Galvis, 1943: 5, 8, 9, 19 (Colombia, ♂ ♀ L); Russell *et al.*, 1943: 35, 39, 42 (♀ L, bionomics, distribution); Causey *et al.*, 1945: 341, 344–346, 348 (Brazil, ♂ ♀ L*); Causey *et al.*, 1946: 25, Fig. 4 (Brazil, ♂*); Deane, L.M. *et al.*, 1946: 9, 16, Figs 59, 62, 62a (Brazil, ♀*); Deane, M.P. *et al.*, 1946a: 40, 44, Figs 17, 19, 22 (Brazil, L*); Deane, M.P. *et al.*, 1946b: 360, 366, Figs 17, 19, 22 (Brazil, L*, identification); Deane, L.M. *et al.*, 1948: 831, 832, 930–931, 933, 937, 945, 946, 949, 951 (Brazil, bionomics); Rachou, 1948: 715–717 (Brazil, distribution, L identification); Floch & Abonnenc, 1951: 5, 22, 23–27, 78, 81, 85 (French Guiana, ♂* ♀* L*, distribution, keys); Levi-Castillo, 1951: 79 (list); Gabaldon & Cova-Garcia, 1952: 179, 197, Fig. 8G (Bolivia, Brazil, Colombia, Guyana); Lane, 1953: 140, 144–146 (Colombia, Peru, Suriname, ♂* ♀ L* P*); Horsfall, 1955: 41 (distribution, L, bionomics); Senevet, 1958: 8 (catalogue); Stone *et al.*, 1959: 10 (catalogue); Cova-Garcia, 1961: 181–183 (Venezuela, A, identification); Villanueva Rodriguez, 1961: 219–223 (as *bathanus*, Peru, L, collections, bionomics); Forattini, 1962: 306, 469 (distribution, A L keys); Deane, L.M. *et al.*, 1968: 338, 339, 340 (Brazil, ♀, bionomics); Ferreira Neto *et al.*, 1970: 171, 172, 174 (Brazil, ♀, bionomics); Forattini *et al.*, 1970: 20 (Brazil, Colombia, collection); Deane, L.M. *et al.*, 1971: 316, 317 (Brazil, ♀, bionomics); Knight & Stone, 1977: 68 (catalogue); Heinemann & Belkin, 1978b: 412, 437 (French Guiana, collection record); Heinemann & Belkin, 1978c: 532, 537 (Colombia, collection record); Heinemann & Belkin, 1979: 65, 80, 97, 107 (Brazil, Ecuador, collection records); Wilkes & Charlwood, 1979: 137, 138 (Brazil, ♀, gonotrophic cycle); Wilke *et al.*, 1980: 587 (Bolivia, Brazil, collection data); Roberts *et al.*, 1981: 383, 384, 385 (Brazil, A, bionomics); Hayes *et al.*, 1987: 420, 421 (Peru, ♀, bionomics); Lourenço de Oliveira, 1989: 394, 395, 396 (Brazil, A, bionomics); Guimarães, 1997: 30 (catalogue); Harbach & Kitching, 1998: 343, 367; Ianelli *et al.*, 1998: 199, 200 (Brazil, ♀, bionomics); Lourenço-de-Oliveira & Luz, 1998: 690, 691, 692 (Brazil, A, bionomics); Reinert, 1999: 77 (P); Forattini, 2002: 194, 195, 241 (A, L, distribution).

Chagasia fajardi (Lutz, 1904)

fajardi (Lutz, 1904), in Bourroul, 1904: 64 (♀, *Pyrethophorus*), types ♀ (location unknown): Cantareira, São Paulo, Brazil.

neivae Cruz, 1906: 199 (♀), syntypes ♀ (location unknown): Juiz de Fóra, Minas Gerais, Brazil; synonymy by Theobald (1907: 123). Belkin *et al.*, 1971: 2 (type data).

maculata Peryassú, 1921b: 141 (A, as *fajardi* variety), type(s) A (location unknown): Parque em Cambuquira, Minas Gerais, Brazil. Peryassú, 1923: 63 (as *Chagasia maculata*, catalogue); Belkin *et al.*, 1971: 2 (type data).

stigmopteryx Martini, 1932: 276–277 (♀, as *fajardi* variety), holotype ♀ (IP): Butantan, São Paulo, Brazil. Belkin *et al.*, 1971: 2 (type data).

Diagnosis. The adults of *Ch. fajardi* are distinguished from those of other species of *Chagasia* as follows: front of anterior promontory with white (usually) or slightly yellowish scales contiguous but not contrasting with white dorsocentral scales (distinction from *Ch. ablusa*, *Ch. bathana* and *Ch. bonneae*); acrostichal scales pale anteriorly, dark posteriorly (Fig. 3B) (distinction from *Ch. bathana* and *Ch. bonneae*); usually with short line of pale scales (easily lost) on mesal margin of supraalar scales (unique) (Fig. 3B); wing dark-scaled with speckling of pale scales on proximal half of costa and spots of pale scales (unique) (Fig. 6) on radius (R) before furcation of radius-one (R₁) and radial sector (R_s), junction of radiomedial crossvein (rm) and media-two (M₂) and sometimes at base of rm (rm occasionally completely pale-scaled), pale scaling and spots weak or absent in males making them indistinguishable from males of *Ch. rozeboomi*; hindtibia without semi-erect

clusters of dark scales (Fig. 4B) (distinction from *Ch. ablusus*, *Ch. bathana* and *Ch. bonneae*); hindtarsomeres 2–5 without postbasal dark band (distinction from *Ch. bathana*), basal pale band of hindtarsomere 2 moderately long, 1.67–3.71 (mean = 2.16) length of apical dark band (Fig. 5C) (distinction from *Ch. ablusus*), hindtarsomere 5 with apical dark band (distinction from *Ch. bonneae*). Males are distinguished by the presence of two stout specialised seta on the dorsomesal prominence of the gonocoxite (distinction from *Ch. ablusus*) and fine setae on the claspette (distinctions from *Ch. bathana* and *Ch. bonneae*). The larva and pupa of *Ch. fajardi* are not known with certainty and they cannot be distinguished from other species of *Chagasia* based on currently available information (see **Discussion** below).

Neotype designation. Lane (1953) indicated that the “types of *Ch. fajardi* were in the collection of the Instituto Oswaldo Cruz (IOC), Rio de Janeiro, Brazil, but they were not found when the collection was examined by Belkin *et al.* (1971). The location has since been regarded as unknown (Knight & Stone, 1977), but insofar as the specimens have never been found and are not listed among the type specimens deposited in the IOC (Marchon-Silva *et al.*, 1996), it must be assumed that they no longer exist. Consequently, in the interest of taxonomic stability, a neotype is designated here to fix the identity of *Ch. fajardi* and distinguish the species from *Ch. ablusus*. NEOTYPE, hereby designated, adult female bearing the following labels: “Brasil / S. Paulo / Coqueiros [geographical location: Jardinopolis, São Paulo State, 21 0' 0" S, 47 50' 0" W] / Col. Duret / 18.ix.54” // “*Chagasia* / fajardoi [*sic*] (Lutz, 1904) / J. P. Duret-Det. 1968”. The neotype is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Etymology. Adolfo Lutz dedicated this species to his friend Francisco Fajardo, but apparently inadvertently dropped the last letter of his surname (Kitzmilller, 1982) when he described it as *Pyretophorus fajardi*. The name was subsequently amended to *fajardoi* and commonly used in the mosquito taxonomic literature until the original spelling gradually became accepted following publication of the world catalogues of Culicidae by Stone *et al.* (1959) and Knight & Stone (1977). As indicated above, the names of three nominal forms are junior synonyms of *Ch. fajardi*. *Anopheles neivae* was described by Oswaldo Cruz in honour of Dr Arthur Neiva (Cruz, 1906: 200), a medical doctor who devoted his career to medical entomology and malaria (Kitzmilller, 1982). *Chagasia fajardi* variety *maculata* Peryassú, 1921 and *Ch. fajardi* variety *stigmopteryx* Martini, 1932 were named for the two pale spots borne on the wing (see above). It is obvious that neither Peryassú (1921) nor Martini (1932) were aware that the pale spots are normally present in the species.

Discussion. The larva and pupa of *Ch. fajardi* are to all intents and purposes unknown. Specimens of these life stages were not available during the present study and published descriptions and illustrations (see literature listed below) are too superficial and incomplete to provide diagnostic and differential characters for their identification and separation from *Ch. ablusus*, *Ch. bathana* and *Ch. bonneae*.

Root (1927: 475) stated that the shape of the genital lobe distinguished the pupa of *Ch. fajardi* from the pupa of *Ch. bonneae*, but this is not the case. Root apparently did not realise that the genital lobe is differently formed in males and females, and actually compared the female pupa of *Ch. fajardi* with the male pupa of *Ch. bonneae*.

The historical perception that *Ch. fajardi* is principally a dark-winged form is not supported by the specimens available for the present study. The two pale spots on the wing, although variable in size and distinctness, are almost always present. In the few specimens where the spots appear to be indistinct or absent, scattered pale scales are generally clearly visible on the proximal portion of the costa. However, it is possible, perhaps probable, that another species is involved. This possibility is based on six specimens (four females; 2 males) from Água Limpa, Minas Gerais? (or Goiás?), Brazil, with entirely dark wings that one of us (REH) had identified as *Ch. rozeboomi* until it was noted that the larval exuviae of two specimens could not be that species. Extensive collection and comparative study, and perhaps the application of molecular methods, are needed to determine whether these are melanic specimens of *Ch. fajardi* or an undescribed species.

Distribution. Argentina, Bolivia, Brazil and ?Guyana. The occurrence of *Ch. fajardi* in Bolivia requires confirmation as reports of the species in that country may refer to *Ch. ablusus*. Based on the credible

distribution of *Ch. fajardi* in southern Brazil and northern Argentina (Forattini, 2002: 241), the occurrence of *Ch. fajardi* in Guyana seems unlikely. Specimens of *Chagasia* from Bolivia and Guyana were not available for the present study.

Material examined. One hundred and thirty-six specimens: ARGENTINA, *Misiones*, Eldorado (3♀), Iguazú Falls (1♀), Montecarto (1♀), Puerto Rico (4♀), uncertain localities (4♀). BRAZIL, *Bahia*, Bomfim (4♀); *Mato Grosso do Sul*, Maracaju (82♀, 1♂); *Minas Gerais*, Abadia dos Dourados (1♀); *Rio de Janeiro*, District Federal (1♀), Macieira (1♀); *São Paulo*, Avaré (1♀), Coqueiros (15♀, 2♂, 2♂G), Guaratinoveta (1♀), Ribeirão Preto (6♀); unknown localities (5♀).

Literature. Blanchard, 1905: 623 (unjustified emendation to *fajardoi*); Theobald, 1907: 123–124 (♀); Peryassú, 1908: 41, 61, 122–125, 334–336, 361–362 (as *fajardoi*, Brazil, ♀* E* L*); Theobald, 1910: 75–76 (as *fajardoi*, Brazil, ♀* E* L*); Surcouf & Gonzalez-Rincones, 1911: 42–44 (as *fajardoi*, Brazil, ♀); Howard *et al.*, 1913: 143 (as *fajardoi*, E); Howard *et al.*, 1917: 992 (as *fajardoi*, E L); Dyar, 1918: 149 (Brazil, synonymy); Peryassú, 1921a: 71 (as *fajardoi*, ♀*); Peryassú, 1923: 63 (as *fajardoi*, catalogue); Christophers, 1924: 10, 15, 78 (catalogue); Root, 1927: 476–479 (as *fajardoi*, Brazil, ♂* ♀* L* P*); Dyar, 1928: 428, 431–432 (as *fajardi*, Argentina, Brazil, ♂ ♀ L); Shannon & del Ponte, 1928: 61–64 (as *fajardoi*, Argentina, ♂* ♀ E* L*); Shannon, 1931: 152, 153 (as *fajardoi*, taxonomy); Edwards, 1932: 32, Pl. 1 Figs 1, 2, 4, Pl. 5 Fig. 8 (as *fajardoi*, type data, A* ♂* E L*, bionomics); Pinto, 1932: 293 (Brazil, bionomics); Senevet, 1934: 67 (P key); Galvão & Barretto, 1938: 110, 114, 115, Fig. 10 (as *fajardoi*, Brazil, E*); Galvão & Barretto, 1939: 114–115, Pls XXIII, XXIV (as *fajardoi*, Brazil, E* L*); Pinto, 1939: 305 (Guyana [as Guiana], ♂); Gabaldon *et al.*, 1940: 58–61 (as *fajardoi*, A L* P); Corrêa & Ramos, 1942: 38, 39, 43, 44 (as *fajardoi*, Brazil, L); Floch & Abonnenc, 1942: 1–3 (as *fajardoi*, ♀); Simmons & Aitkin, 1942: 39, 41, 48, 54, 62–63 (♂ ♀ L keys, distribution, bionomics); Coutinho *et al.*, 1944: 8, 11, 18 (as *fajardoi*, Brazil, L, bionomics); Causey *et al.*, 1945: 341, 342, 344–346, 348 (as *fajardoi*, Brazil, ♂ ♀ E* L*); Rachou, 1948: 715–717 (Brazil, distribution, L identification); Levi-Castillo, 1951: 79 (as *fajardoi*, list); ?Romeo Viamonte & Castro, 1951: 319, 324, Fig. 12 (as *fajardoi*, ♀*); Gabaldon & Cova-Garcia, 1952: 179, 197, 198, Fig. 8H (as *fajardoi*, in part, Argentina, ?Bolivia, Brazil); Lane, 1953: 139–144 (as *fajardoi*, in part, Argentina, Brazil, ?Guyana, ♂* ♀ E* L* P*); Senevet, 1958: 8 (catalogue); Stone *et al.*, 1959: 10 (as *fajardoi*, in part, catalogue, Argentina, Brazil, ?Guyana [as British Guiana]); Villanueva Rodriguez, 1961: 217, 218 (as *fajardoi*, distribution); Forattini, 1962: 306, 468 (L*, distribution, A L keys); García & Ronderos, 1962: 139, 141, Figs 54, 59, 60–63, Map 1 (as *fajardoi*, Argentina, ♂* ♀ L* P, distribution); Forattini *et al.*, 1970: 20 (as *fajardoi*, Brazil, collection); Belkin *et al.*, 1971: 2 (type data); Deane, L.M. *et al.*, 1971: 312, 314, 315, 317 (as *fajardoi*, Brazil, ♀, bionomics); Mattingly, 1971: Fig. 3a (as *fajardoi*, ♀*); Neves & da Silva, 1973: 289, 291, 292 (as *fajardoi*, Brazil, A, bionomics); Neves & Pedersoli, 1976: 551 (as *fajardoi*, Brazil, ♀, bionomics); Knight & Stone, 1977: 68 (in part, catalogue, Argentina, Brazil, ?Guyana); Wilke *et al.*, 1980: 587–588 (as *fajardoi*, Brazil, collection data); Darsie, 1985: 1158, 172, 193, 221, 237 (Argentina, ♀, L, identification); Linley & Milstrey, 1995: 27, 32–38 (Brazil, E*); Lopes & Lozovei, 1995: 186, 187 (Brazil, L, bionomics); Guimarães, 1997: 30 (in part, catalogue, Argentina, Brazil, ?Guyana); Harbach & Howard, 1997: 102 (♀); Harbach & Kitching, 1998: 367; Reinert, 1999: 77 (as *fajardoi*, P); Sallum *et al.*, 2000: 746, 749–754, 755, 757, 758, 759, 760, 763, 768, 769, 770 (♂ ♀ L P, cladistic analysis); Guimarães *et al.*, 2001: 395, 396, 397 (as *fajardoi*, Brazil, ♀, bionomics); Forattini, 2002: 193, 194, 195, 238, 239, 241, 802 (A, L, E*, distribution); Guimarães *et al.*, 2003: 1110, 1111, 1113, 1114 (as *fajardoi*, Brazil, ♀, bionomics); Alencar *et al.*, 2005: 182–184 (Brazil, ♀, bionomics); Harbach & Kitching, 2005: 348, 351, 355, 356, 357, 358, 367–374 (♂ ♀ L P, cladistic analysis).

***Chagasia rozeboomi* Causey, Deane & Deane, 1944**

rozeboomi Causey, Deane & Deane, 1944: 3 (E*), syntypes E (non-existent): Loando, near Crato, Ceará, Brazil (see Causey *et al.*, 1945: 341; invalid restriction to vicinity of São Benedito by Belkin *et al.*, 1971: 2, 31).

Diagnosis. The adults of *Ch. rozeboomi* are distinguished from those of other species of *Chagasia* as follows: front of anterior promontory with white or yellowish scales contiguous with white dorsocentral scales (distinction from *Ch. ablusa*, *Ch. bathana* and *Ch. bonneae*); acrostichal scales pale anteriorly, dark posteriorly (as in Fig. 3B) (distinction from *Ch. bathana* and *Ch. bonneae*); without pale scales on mesal margin of supraalar scales; wing entirely dark-scaled (unique); hindtibia without semi-erect clusters of dark scales (as in Fig. 4B) (distinction from *Ch. ablusa*, *Ch. bathana* and *Ch. bonneae*); hindtarsomeres 2–5 without postbasal dark band (distinction from *Ch. bathana*), basal pale band of hindtarsomere 2 moderately long, 2.50–2.63 length of apical dark band (mean = 2.57), hindtarsomere 5 with apical dark band (Fig. 5E) (distinction from *Ch. bonneae*). Males have two stout specialised seta on the dorsomesal prominence of the gonocoxite (distinction from *Ch. ablusa*) and fine setae on the claspette (distinctions from *Ch. bathana* and *Ch. bonneae*). The development of setae 5-, 7- and 11-C and seta 2-P readily distinguish larvae of *Ch. rozeboomi* from larvae of the other *Chagasia* species. These setae are noticeably shorter, seta 5-C is shorter than half the distance between its insertion and the insertion of seta 4-C, seta 2-P has uniquely thickened and truncated secondary branches that arise from the ends of the primary branches and seta 11-C is less than half as long as seta 13-C and the antenna. Pupae have no diagnostic features but they differ from pupae of *Ch. bonneae* in lacking a ligulate process on the rim of the trumpet.

Etymology. The derivation of the specific name is not mentioned in the publication in which this species was originally described based on eggs (Causey *et al.*, 1944), but the authors clearly state in a second paper (Causey *et al.*, 1945) that the species was named in honour of Lloyd E. Rozeboom. The late Prof. Rozeboom was a renowned medical entomologist at Johns Hopkins University School of Hygiene and Public Health in Baltimore, Maryland, USA.

Discussion. The affinity of this species with *Ch. ablusa* and *Ch. fajardi* is indicated by the ornamentation of the adults and the structure of male genitalia. It is immediately distinguished from the other species of *Chagasia* by the reduced cranial setae of the larva.

Distribution. Brazil. The occurrence of *Ch. rozeboomi* in Bolivia indicated on the map reproduced as figure 8I in Gabaldon & Cova-Garcia (1952) is unsubstantiated.

Material examined. Fourteen specimens: BRAZIL, Bahia, Bomfim (2♂); Ceará, Crato (2♀, 1♂, 2Le, 1Pe, 1L), unknown locality (1♀); Minas Gerais, Rio Doce (2♀, 2♂).

Literature. Causey *et al.*, 1945: 341–349 (Brazil, ♂* ♀* E* L* P*); Causey *et al.*, 1946: 25, Fig. 3 (Brazil, ♂*); Deane, L.M. *et al.*, 1946: 9, 16, Figs 58, 60, 63, 63a (Brazil, ♀*); Deane, M.P. *et al.*, 1946a: 40, 44, Figs 18, 20, 23 (Brazil, L*); Deane, M.P. *et al.*, 1946b: 360, 366, Figs 18, 20, 23 (Brazil, L*, identification); Deane, L.M. *et al.*, 1948: 831, 832, 931–932, 933, 937, 945, 946, 947, 949, 951, 953 (Brazil, bionomics); Rachou, 1948: 715–717 (Brazil, distribution, L identification); Levi-Castillo, 1951: 79 (list); Gabaldon & Cova-Garcia, 1952: 179, 198, 199, Fig. 8I (Brazil, not Bolivia); Lane, 1953: 140, 143–144 (Brazil, ♂ ♀ E* L* P); Horsfall, 1955: 41 (distribution, L, bionomics); Senevet, 1958: 9 (catalogue); Stone *et al.*, 1959: 10 (catalogue); Villanueva Rodriguez, 1961: 217, 218 (distribution); Forattini, 1962: 306, 468 (distribution, A,L keys); Forattini *et al.*, 1970: 20 (Brazil, collection); Belkin *et al.*, 1971: 2 31 (type data); Knight & Stone, 1977: 68 (catalogue); Neves & Pedersoli, 1976: 551 (Brazil, ♀, bionomics); Peyton, 1993 (mention); Guimarães, 1997: 30 (catalogue); Forattini, 2002: 194, 195, 241 (A, L, distribution).

Keys to the species of *Chagasia*

Adults

1. Wing with mixture of dark and pale scales; acrostichal area with pale scales only (Fig. 3A) 2
- Wing mainly or entirely dark-scaled; acrostichal area with dark scales posteriorly (Fig. 3B) 3
2. Hindtarsomeres 2–5 with postbasal and apical dark bands (Fig. 5A); hindtarsomere 5 usually without distal line of dark scales on ventral surface *bathana*

- Hindtarsomeres 2–5 without postbasal dark bands, hindtarsomere 5 with line of dark scales on distal 0.7 of ventral surface (Fig. 5B) *bonneae*
- 3. Hindtibia with semi-erect clusters of black scales on dorsoanterior surface (Fig. 4A); hindtarsomeres 2–4 with relatively narrow apical dark bands, basal pale band of tarsomere 2 normally more than 4.0 length of apical dark band (Fig. 5D); radius (R), mediocubital crossvein (mcu) and/or base of media-two (M_2) of wing without spots of pale scales *ablusa*
- Hindtibia without semi-erect clusters of black scales, dark scales brown and decumbent (Fig. 4B); hindtarsomeres 2–4 with relatively broad apical dark bands, basal pale band of tarsomere 2 less than 4.0 length of apical dark band (Fig. 5C); wing with or without spots of pale scales on R, mcu and M_2 4
- 4. Wing usually with spots of pale scales on R, mcu and/or base of M_2 (Fig. 6), proximal portion of costa speckled with pale scales, anal vein with narrow generally truncate spatulate scales; scutum often with short line of pale scales on mesal side of supraalar scales (Fig. 3B) *fajardi*
- Wing entirely dark-scaled, scales of anal vein generally narrower, longer and more acute at tip; scutum without pale scales on mesal side of supraalar scales *rozeboomi*

Male genitalia

- 1. Gonocoxite with many stout specialised setae on dorsomesal prominence; claspette without setae, only spicules present (Fig. 1C) *bathana, bonneae*
- Gonocoxite with 1 or 2 stout specialised setae on dorsomesal prominence; claspette with fine setae in addition to covering of spicules 2
- 2. Gonocoxite with 1 stout specialised seta on the dorsomesal prominence *ablusa*
- Gonocoxite with 2 stout specialised setae on dorsomesal prominence *fajardi, rozeboomi*

Pupae

(The pupa of *Ch. fajardi* is not included for reasons noted above.)

- 1. Rim of trumpet with a narrow ligulate process arising from posterior margin (Fig. 1A) *bonneae*
- Rim of trumpet without ligulate process *ablusa, bathana, rozeboomi*

Larvae

(The larva of *Ch. fajardi* is not included for reasons noted above.)

- 1. Setae 5,7-C small, usually with 5–8 branches, 5-C projects forward to point less than 0.5 distance to insertion of seta 4-C; seta 2-P slightly longer than 1-P, with thickened secondary branches arising at end of each primary branch (Fig. 7); seta 11-C short, less than 0.5 length of seta 13-C (13-C about as long as antenna) *rozeboomi*
- Setae 5,7-C large, usually with 10–24 branches, 5-C projects forward to or beyond insertion of seta 4-C (Fig. 2A); seta 2-P about twice as long as 1-P, with long aciculae arising near mid-length of each primary branch (Fig. 2B); seta 11-C long or short 2
- 2. Seta 5-C inserted anterior to base of antenna on line midway between level of insertions of setae 4- and 7-C, rachis (main stem) extends forward to point near base of seta 4-C, distance between insertions of 2 seta 5-C less than distance between insertions of setae 5- and 7-C *ablusa*
- Seta 5-C inserted in line with base of antenna on level closer to level of seta 7-C, rachis extends forward to point \leq 0.6 distance between its insertion and insertion of seta 4-C, distance between insertions of 2 seta 5-C greater than distance between insertions of setae 5- and 7-C (Fig. 2A) 3
- 3. Setae 11-C shorter than 13-C, about 0.75 length of antenna (13-C about as long as antenna); seta 15-C long, single or split distally, extending to seta 14-C *bathana*
- Seta 11-C about as long as 13-C, both about as long as antenna (Fig. 2A); seta 15-C short, multiple branched, extending about halfway to seta 14-C (Fig. 2A) *bonneae*

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