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## Adults and larvae of two *Leucochrysa* (*Leucochrysa*) species (Neuroptera: Chrysopidae): descriptions, biological notes, and relationships

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### Abstract

This taxonomic study includes: (i) a redescription of *Leucochrysa* (*Leucochrysa*) *nigrilabris* (Banks) (♂ and ♀), based on the type specimen and new material and (ii) images of the *Leucochrysa* (*L.*) *insularis* (Walker) type, adult color polymorphism, and genital characters (♂ and ♀). For both species, it provides: (iii) descriptions of the larvae, (iv) biological notes, and (v) geographic records. Using the above information, we compare the two species with each other and with other *Leucochrysa* (*Leucochrysa*) species that purportedly are closely related. We conclude: First, the larval features of *L.* (*L.*) *nigrilabris* and *L.* (*L.*) *insularis* coincide with those previously described as characteristic of the genus *Leucochrysa* and its subgenus *Leucochrysa*. Second, based on their genitalia (♂ and ♀), larval morphology, and biology (e.g., deposition of eggs in clusters), the two species are distinct, but very closely related. And, third, *L.* (*L.*) *nigrilabris* and *L.* (*L.*) *insularis* share several characteristics with the *Leucochrysa* (*L.*) “*varia*-like” species; these include similar adult color polymorphisms and aspects of their larval morphology. However, their genitalia (♂ and ♀) differ significantly from those of the described *L.* (*L.*) “*varia*-like” species, and thus we consider the two sets of species to be distinct.

**Key words:** Chrysopinae, *Leucochrysa* (*L.*) *nigrilabris*, *Leucochrysa* (*L.*) *insularis*, *Leucochrysa* (*L.*) *varia*, oviposition, color morphs

### Resumo

O presente estudo taxonômico inclui: (i) redescricao de *Leucochrysa* (*Leucochrysa*) *nigrilabris* (Banks) (♂ e ♀), com base no espécime-tipo e novo material, e (ii) imagens do tipo, polimorfismo de coloração dos adultos e genitália (♂ e ♀) de *Leucochrysa* (*L.*) *insularis* (Walker). Para ambas as espécies, apresentam-se ainda: (iii) descrições das larvas, (iv) informações biológicas e (v) registros geográficos. Tais informações são usadas para comparar as duas espécies entre si e com outras espécies de *Leucochrysa* (*Leucochrysa*) que supostamente são proximamente relacionadas. A partir dessas comparações, conclui-se que (1) as características das larvas de *L.* (*L.*) *nigrilabris* e de *L.* (*L.*) *insularis* coincidem com aquelas previamente descritas como típicas do gênero *Leucochrysa* e de seu subgênero *Leucochrysa*; (2) com base nas características da genitália (♂ e ♀), morfologia larval e biologia (por exemplo, deposição de ovos em cachos), as duas espécies são distintas, mas muito proximamente relacionadas, e (3) *L.* (*L.*) *nigrilabris* e *L.* (*L.*) *insularis* compartilham várias características com *Leucochrysa* (*L.*) *varia* e espécies afins, as quais incluem polimorfismo de coloração no estágio adulto e aspectos da morfologia larval semelhantes. Entretanto, suas genitálias (♂ e ♀) diferem significativamente das de *L.* (*L.*) *varia* e espécies afins descritas, de forma que esses dois conjuntos de espécies são considerados como distintos.

### Resumen

El presente estudio taxonómico incluye: (i) redescrición de *Leucochrysa* (*Leucochrysa*) *nigrilabris* (Banks) (♂ y ♀), con base en el espécimen tipo y nuevo material y (ii) imágenes del tipo, polimorfismo de coloración de adultos y genitália (♂

y ♀) de *Leucochrysa (L.) insularis* (Walker). Para ambas especies se presenta: (iii) descripciones de las larvas, (iv) informaciones biológicas y (v) registros geográficos. Tales informaciones son usadas para comparar las dos especies entre sí y con otras especies de *Leucochrysa (Leucochrysa)* que supuestamente están estrechamente relacionadas. A partir de las comparaciones, se concluye que: primero, las características de las larvas de *L. (L.) nigrilabris* y de *L. (L.) insularis* coinciden con aquellas previamente descritas como típicas del género *Leucochrysa* y del subgénero *Leucochrysa*; segundo, con base en las características de la genitalia (♂ y ♀), morfología larval y biología (por ejemplo, deposición de huevos en racimos) las dos especies son distintas, pero están estrechamente relacionadas y tercero, *L. (L.) nigrilabris* y *L. (L.) insularis* comparten varias características con *Leucochrysa (L.) varia* y especies relacionadas, las cuales incluyen polimorfismo de coloración en la fase adulta y aspectos de la morfología larval. Sin embargo, las genitalias (♂ y ♀) difieren significativamente de las de *L. (L.) varia* y las especies relacionadas descritas, de forma que los dos conjuntos de especies son considerados distintos.

## Introduction

Our study provides a taxonomic treatment of two species -- *Leucochrysa (Leucochrysa) nigrilabris* (Banks) and *Leucochrysa (Leucochrysa) insularis* (Walker). It is part of a series dealing with the systematics of the leucochry sine subgenus *Leucochrysa (Leucochrysa)* (Tauber 2004, Mantoanelli et al. 2006, Tauber et al. 2011, 2013).

Previously, *L. (L.) nigrilabris* was known from a single male specimen (the type, from Colombia), whose original description (Banks 1914-1915) included only external features of the body and wings. Subsequently, the species received no additional descriptive work. Given the large diversity of similarly colored *Leucochrysa (Leucochrysa)* species, and given the variability in adult coloration and markings, current information is insufficient for secure identifications.

In contrast, the adults of *L. (L.) insularis*, a species reported from eastern USA and the Caribbean region, have had modern taxonomic treatment (Adams 1977, Tauber 2004) and identifications are possible. Also, the larvae have received some attention and the unusual biology of this species has been described (Jones 1929, 1941), but there are insufficient data to make larval identifications or meaningful comparisons with other *Leucochrysa* species.

In the past, systematic relationships were proposed for these two *Leucochrysa* species, but the corroborating evidence was meagre. Some authors noted that the external features of *L. (L.) nigrilabris* and *L. (L.) insularis* adults resemble those of the South American *Leucochrysa (L.) varia* (Schneider) [= *L. (L.) varia*-like species] (Banks 1914-1915; also see Tauber et al. 2013). In addition, the two species themselves were considered either very closely related or synonymous (Tauber 2004).

To help clarify the systematics of the subgenus *Leucochrysa (Leucochrysa)*, we redescribe the *L. (L.) nigrilabris* adults (male & female) on the basis of the type and newer material from Venezuela and Brazil, and we provide images of the *L. (L.) insularis* type, as well as comparative information on the species' color polymorphism and genitalia. Also, we describe the larvae of *L. (L.) nigrilabris* (all instars) and *L. (L.) insularis* (first and third instars), and provide new biological notes on both species. Finally, to elucidate the systematic relationships of the two species with each other and within the subgenus, we consider three questions: (1) Are the larval features of *L. (L.) nigrilabris* and *L. (L.) insularis* consistent with those of other species in the subgenus *Leucochrysa (Leucochrysa)*? (2) Do adult and larval features support the synonymy and/or proposed close relationship between the two species? (3) Should the two species be aligned with the *L. (L.) varia*-like species?

## Materials and methods

All terminology and methods are identical to those used previously (Mantoanelli et al. 2011, Tauber et al. 2013). The specimens are from the following museums: American Museum of Natural History, New York, NY (**AMNH**); The Natural History Museum (formerly British Museum of Natural History), London, England (**BMNH**); Bernice P. Bishop Museum, Honolulu, HI (**BPBM**); Carnegie Museum of Natural History, Pittsburgh, PA (**CMNH**); C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Boulder, CO (**COSU**); Cornell University Insect Collection, Ithaca, NY (**CUIC**); University of Guelph Insect Collection, Guelph, Ontario, Canada (**DEBU**);

Los Angeles County Museum, Los Angeles, CA (**LACM**); Museum of Comparative Zoology, Harvard University, Cambridge, MA (**MCZ**); Museum of the Institute of Agricultural Zoology, Universidad Central de Venezuela, Maracay, Aragua, Venezuela (**MIZA**); Royal Ontario Museum, Toronto, Ontario, Canada (**ROM**); Essig Museum, University of California, Berkeley, CA (**UCB**); Bohart Entomological Museum, University of California, Davis, CA (**UCD**); Museo Entomológico “Dr. José Manuel Osorio”, Universidad Centroccidental “Lisandro Alvarado”, Barquisimeto, Lara, Venezuela (**UCOB**); National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C. (**USNM**).

### ***Leucochrysa (Leucochrysa) nigrilabris* (Banks, 1915)**

Figs 1–12, 19

*Allochrysa nigrilabris* Banks, [1915] (Banks 1914–1915: 623) original description: [Colombia] “St. Antonio, Colombia, 1,800 m., December (Fassl)”.

*Leucochrysa nigrilabris* (Banks). Banks (1944: 32) first reference to combination; Penny (1977: 23) species list.

*Leucochrysa (Leucochrysa) nigrilabris* (Banks). Brooks & Barnard (1990: 276) subgeneric designation, species list; Tauber (2004: 1140) possible synonymy with *Leucochrysa (Leucochrysa) insularis* (Walker); Oswald (2007) catalog listing.

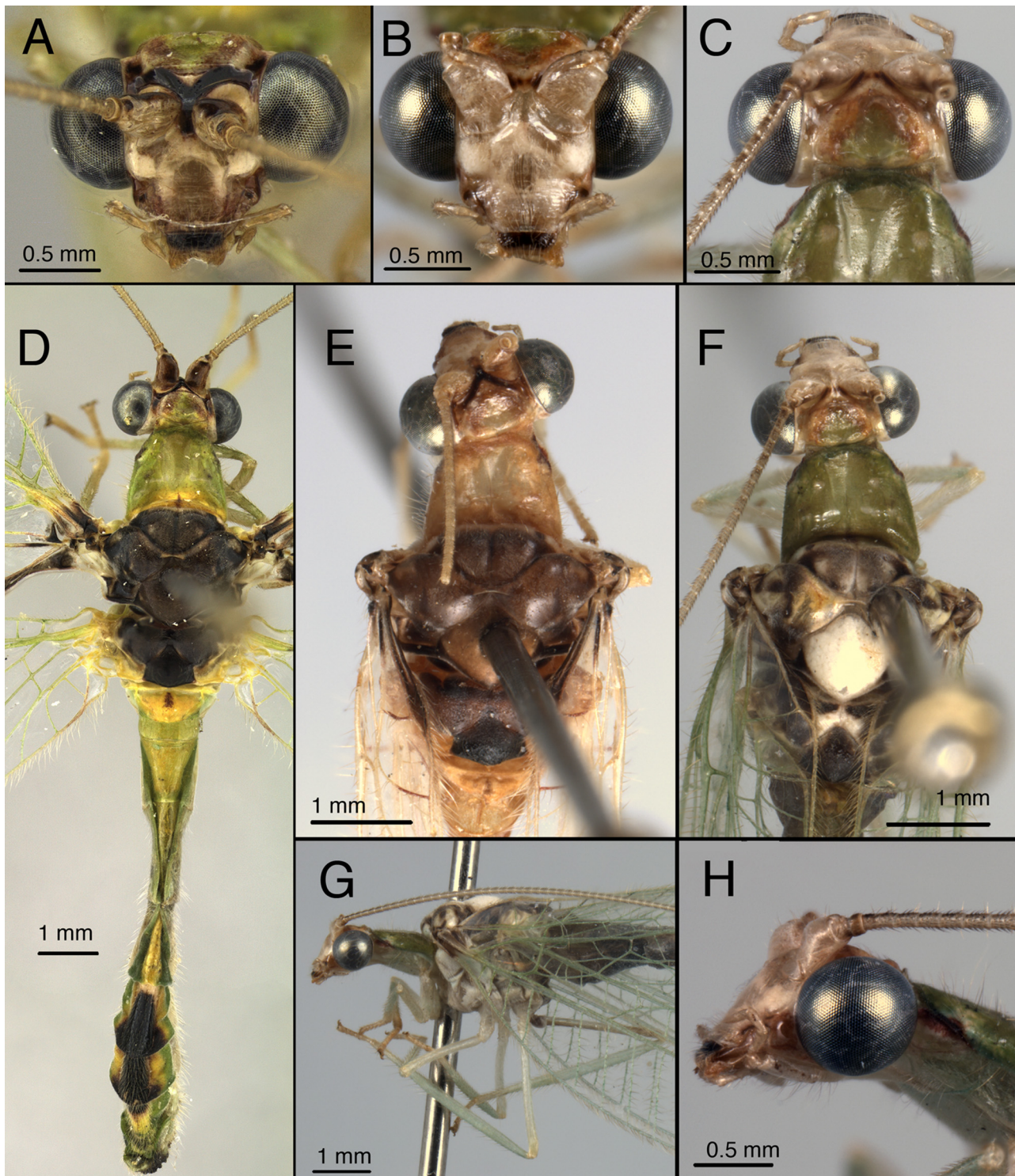
**Type specimen.** One type, from San Antonio, Colombia, MCZ (male, examined). We assume that the locality “St. Antonio” refers to the city of San Antonio in the Department of Tolima. Banks (1914–1915) did not state how many specimens he used to write his description; it is likely that he had only one. There is only one type in the MCZ and none in the AMNH, USNM, or the Academy of Natural Sciences of Philadelphia, where Banks occasionally deposited types. Thus, we consider the specimen in the MCZ to be the holotype, by monotypy. Its labels read: (1) “St Antonio / Colombia S. Am” [Banks’ hand]; (2) “1800 m / Dec” [Banks’ hand]; (3) “Collection / N. Banks”; (4) “Type” [red, Banks’ hand]; (5) “Type / 12004”; (6) “Allochrysa / nigrilabris / type / Bks” [white, red border, Banks’ hand]; (7) “Genitalia / prep P. Adams / 1982”.

The specimen is in fairly good condition; the body (thorax and head) are somewhat flattened, the forewings and one hindwing are missing, and the terminalia are in a vial with glycerine. We took images that are now placed in the MCZ Type Database (<http://insects.oeb.harvard.edu/MCZ/index.htm>).

**Known geographical distribution.** **Colombia:** Department of Tolima. **Venezuela:** States of Aragua, Mérida, Portuguesa, Yaracuy. **Brazil:** State of Rio de Janeiro.

**Diagnosis (adult).** Externally, *L. (L.) nigrilabris* adults are distinguished from many *Leucochrysa (Leucochrysa)* species by a dark brown to black labrum, white frons, a single, small spot on the forewing (brown suffusion on the membrane around the distal Psm-Pcu crossvein), and all veins mostly green except inner and outer gradates dark brown to black. However, these features are shared with other *Leucochrysa (Leucochrysa)* species, including some *L. (L.) “varia-like species”* and *L. (L.) insularis*. Thus, a reliable identification requires examination of the genitalia. The males of *L. (L.) nigrilabris* are distinguished by: (i) dense microtholi on sternites 3–8; (ii) small genital structures [gonarcal span of 0.40–0.65 mm; cf., 0.67–0.84 mm in *L. (L.) varia*]; (iii) a narrow, elongate mediuncus that is well separated from the gonarcal bridge, and terminates in a long, slender hook and a pair of large, inflated flanges; and (iv) terminus of S8+9 with an attached pair of flat, sclerotized, plate-like projections with toothed mesal margins. Female *L. (L.) nigrilabris* have a doughnut-shaped spermatheca with a broad, bent velum, a deep, relatively narrow invagination, a relatively long, robust spermathecal duct, and apparently no bursal duct; the subgenitale has a well-sclerotized ventral process that extends perpendicularly from the distal margin of the base.

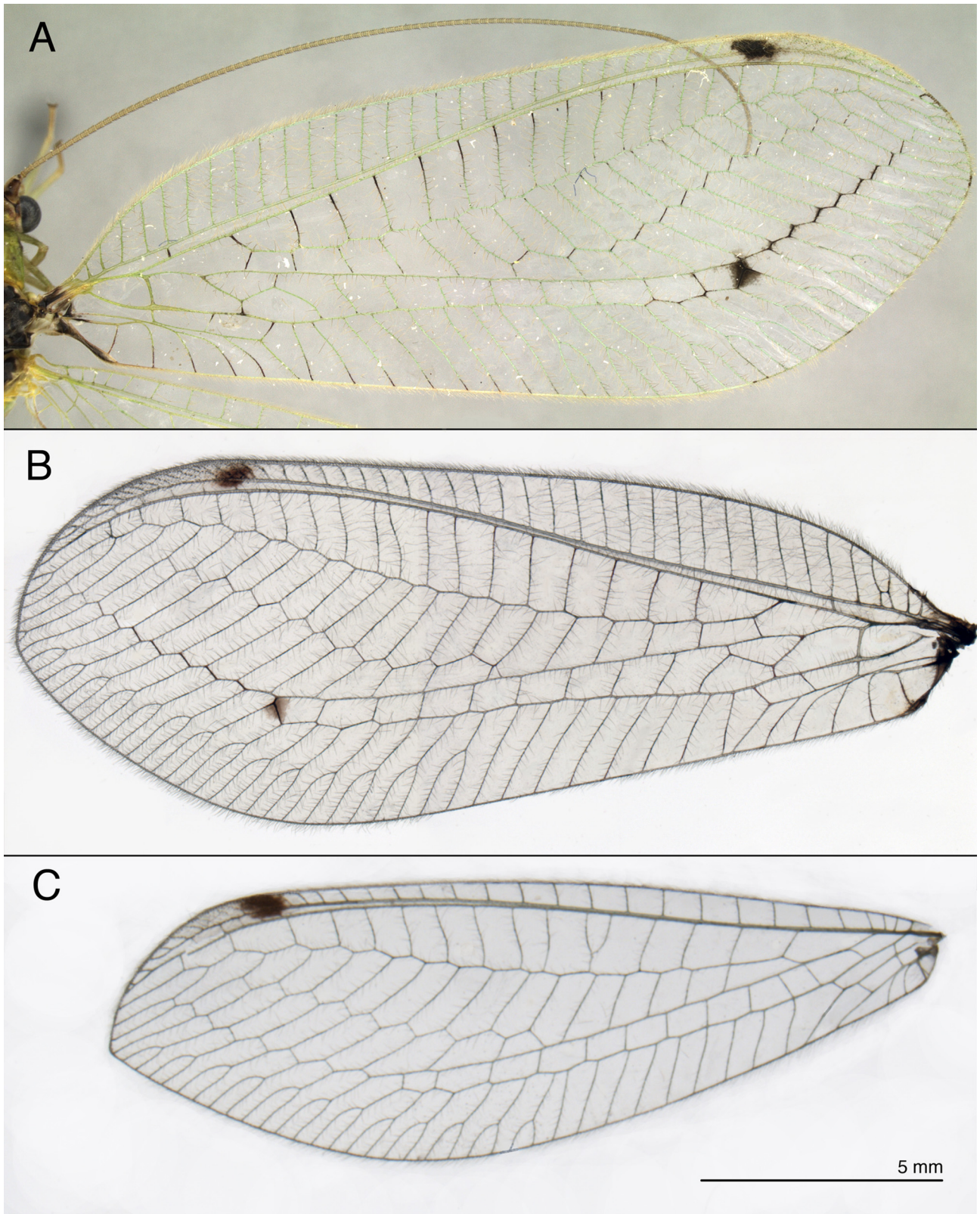
**Redescription (adult).** *Head* (Fig. 1): 1.7–1.9 mm wide (including eyes). Frons, clypeus white to cream-colored, frons without red or pink suffusion, clypeus with or without tinge of pink; genae reddish brown; labrum black throughout; maxillary, labial palpi yellowish to cream-colored. Vertex with central area raised, green mesally, golden brown to reddish brown laterally; lateral, frontal areas cream-colored, with prominent, dark red to dark brown, scalloped to V-shaped mark along anterior margin, extending anteriorly to or between mesal margins of scapes, extending laterally to eyes; post-ocular area cream-colored, without spots. Antenna: scape cream-colored ventrally, with reddish brown mark of various sizes on distal, dorsolateral surface; pedicel cream-colored basally, with brown band distally; flagellum cream-colored, with brown bristles; mesal-ventral surface of basal one to seven flagellomeres lightly tinged with brown (variable); dorsal antennal fossae cream-colored.



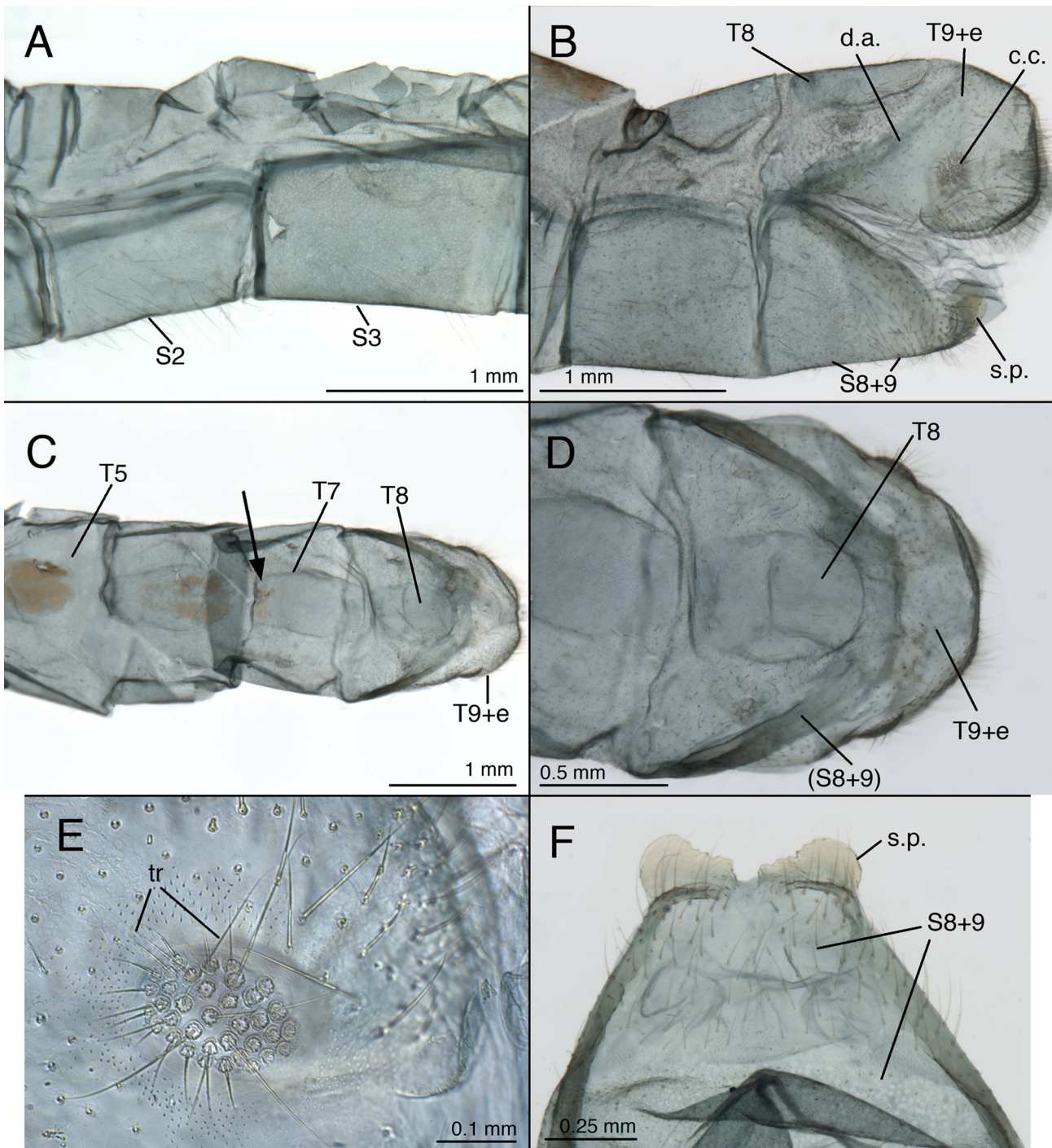
**FIGURE 1.** *Leucochrysa (L.) nigrilabris* external features. A, B. Head, frontal; C. Head, dorsal; D. Body, dorsal E, F. Head and thorax, dorsal [note the variation in the coloration of the mesoprescutum and mesoscutellum]; G. Head, thorax, lateral; H. Head, prothorax, lateral [A, D, State of Yaracuy, Venezuela, female; B, C, F–H, State of Rio de Janeiro, Brazil, female; E, State of Aragua, Venezuela, female].

*Thorax* (Figs 1D–H): Cervical sclerite with large, red mark laterally. Pronotum 0.92–0.98 mm long, 1.41–1.44 mm wide, light green, with elongate, dark red stripe on anterolateral margin, diffuse, light brown, sublateral spots anteriorly, posteriorly. Mesonotum, metanotum variable, with two distinct morphs [Figs 1D, E (brown), 1F (white)]. Brown morph: mesonotum, metanotum dark brown throughout, except anterior margin of prescutum cream-colored, with pair of sublateral, dark brown spots; mesoscutellum slightly lighter brown than remainder of

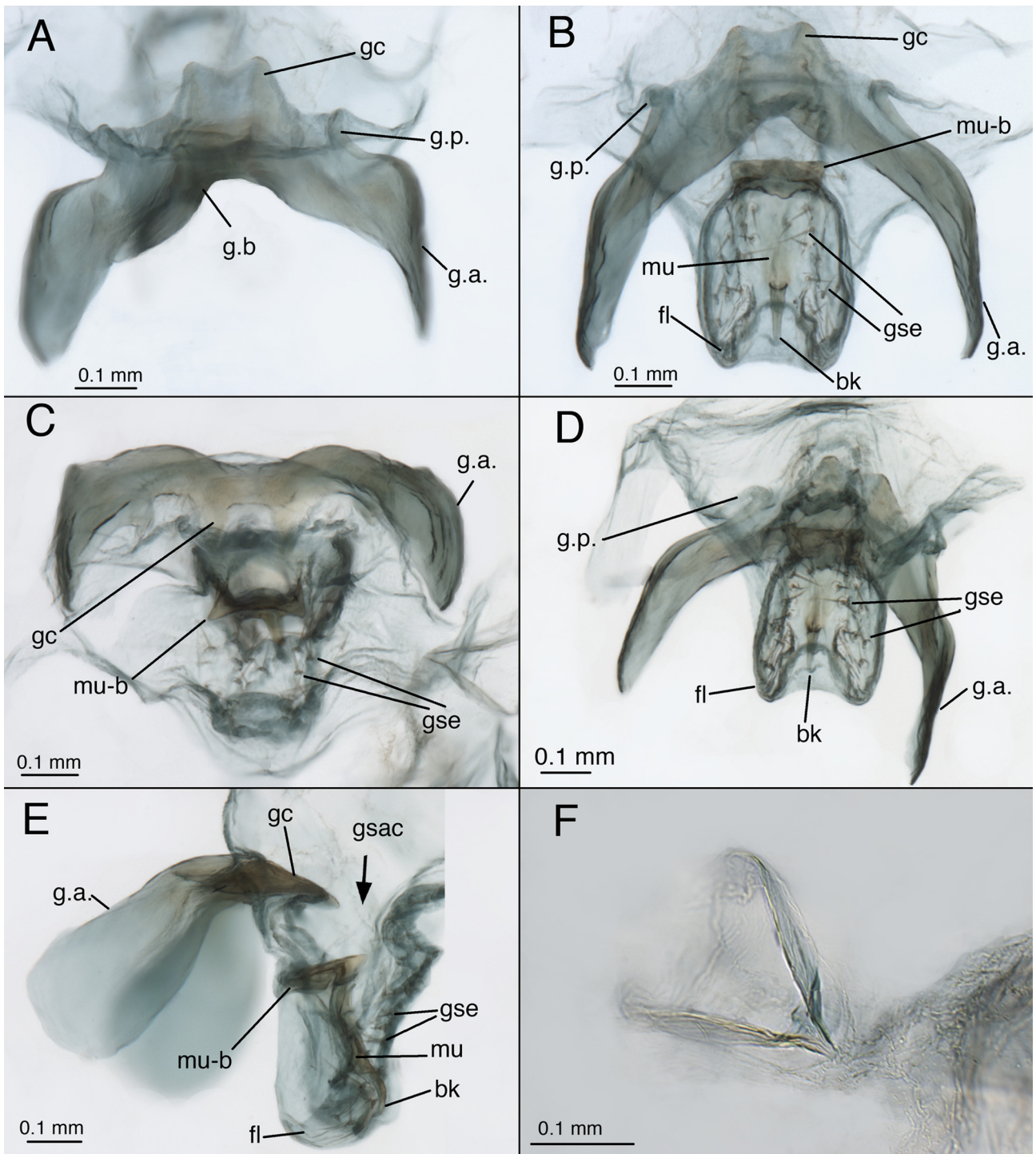
notum; metascutellum black throughout. White morph: mesonotum mottled black to brownish black, anterior margin of prescutum cream-colored, with pair of sublateral, dark brown spots, posterior margin with cream-colored areas, mesoscutellum entirely white; metanotum largely dark brown to black, metascutum with large, white posteromesal patch; metascutellum black throughout.



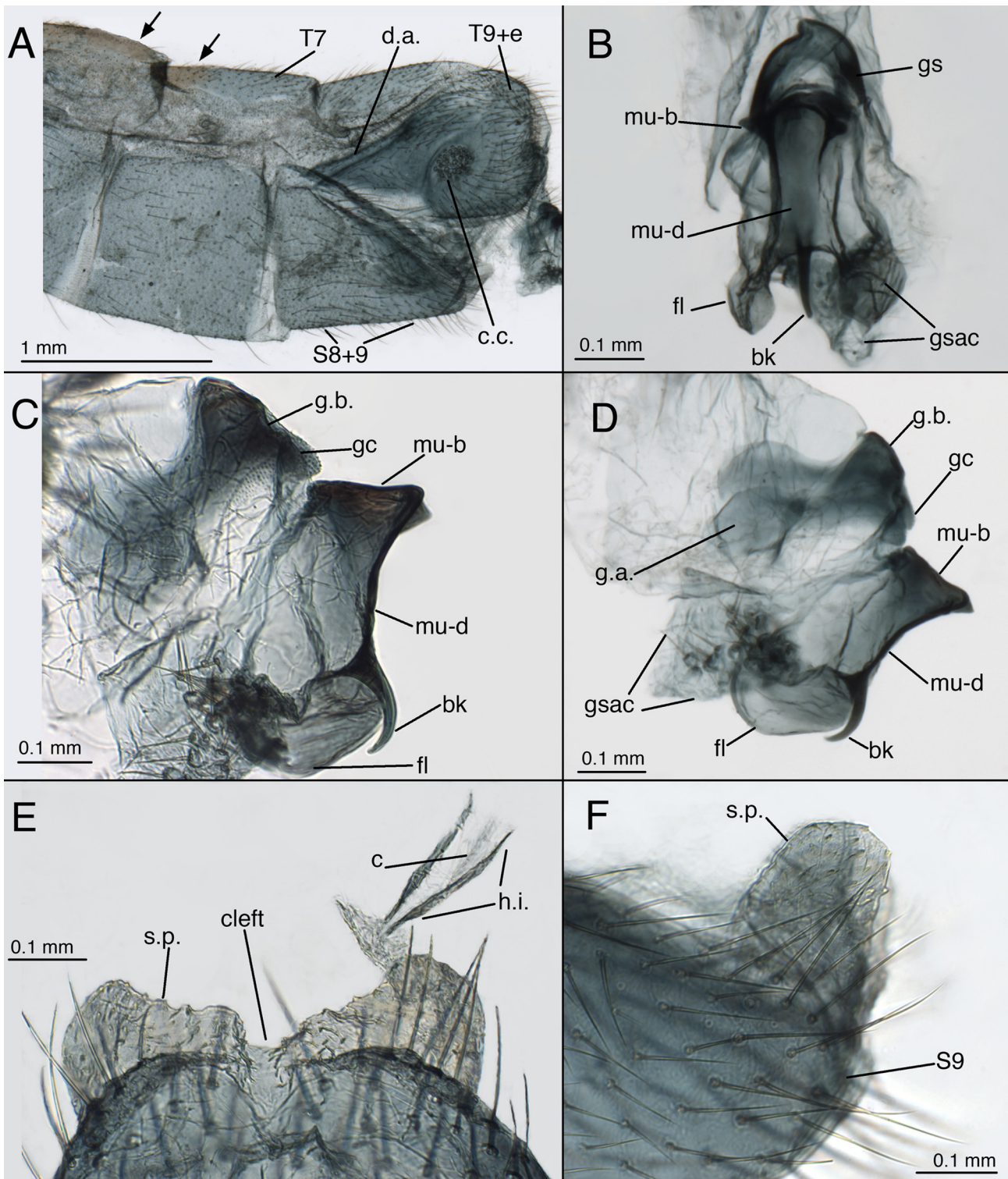
**FIGURE 2.** *Leucochrysa (L.) nigrilabris* wings. A, B. Forewing, two specimens to illustrate relatively minor variation; C. Hindwing [A, State of Yaracuy, Venezuela; B, C, State of Aragua, Venezuela, all female]. Scale applies to all three images.



**FIGURE 3.** *Leucochrysa (L.) nigrilabris* male abdomen, mature specimen. A. Second and third abdominal segments, lateral [note absence of microtholi from S2, dense microtholi on S3]; B. Terminal segments, lateral; C. Terminal segments, dorsal [note large brown spots on T5, T6, base of T7 (arrow)]; D. Terminal segments, dorsal [note dorsally fused T9+ectoproct, without suture or distal cleft. The U-shaped darkening is the distal margin of S8+9 below]; E. Callus cerci; F. Fused sternite 8+9, ventral, with sclerotized terminal plates extended distally [all, Aragua, Venezuela]. *Abbreviations:* c.c., callus cerci; d.a., dorsal apodeme of ninth tergite+ectoproct; s.p., sclerotized plate at tip of S8+9; S2, S3, second and third sternites; S8+9, fused eighth and ninth sternites (in parentheses, out of focus through dorsal surface); tr, trichobothria; T5, T7, T8, fifth to eighth tergites; T9+ect, fused ninth tergite and ectoproct.

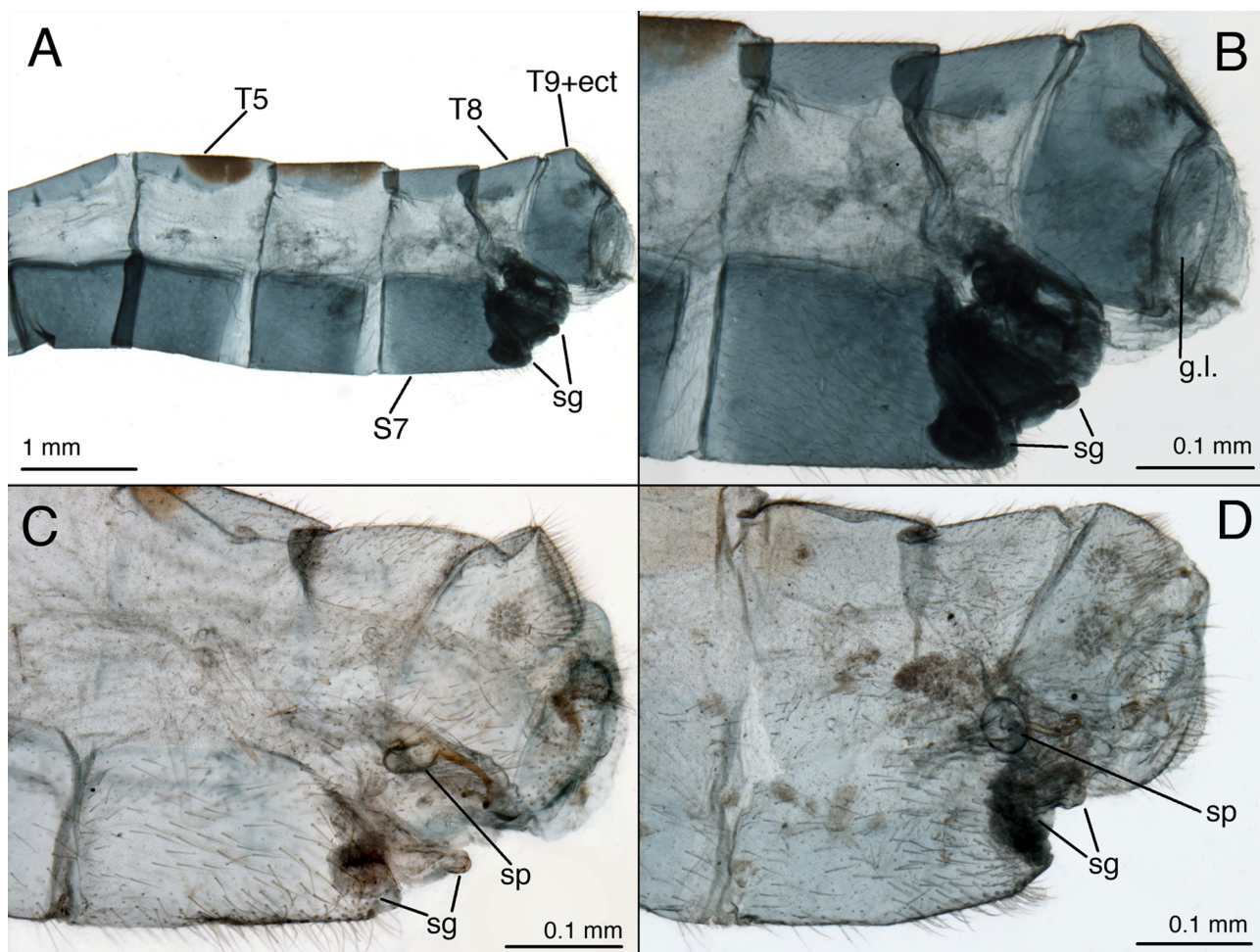


**FIGURE 4.** *Leucochrysa (L.) nigrilabris* male genitalia, mature specimen. A. Gonarcus, posterodorsal (mediuncus removed); B. Gonarcus, posterior (view into gonosaccus from behind, through membrane) [note the mediuncal beak and flanges extend forward (away) and downward]; C. Gonarcus, dorsal [view into gonosaccus from above, unobscured by membrane, base of mediuncus in focus, mediuncal beak present (extending forward), but out of focus]; D. Gonarcus, frontal [note the gonosaccus is below the mediuncal flanges; the gonosetae are within the gonosaccus]; E. Gonarcus, lateral; F. Hyandrium internum (comes very reduced or absent) [all, Aragua, Venezuela]. *Abbreviations:* bk, beak-like tip of mediuncus; fl, mediuncal flange; gc, gonocornu, encased in membrane; g.a., gonarcus apodeme; g.b., gonarcus bridge; g.p., gonarcus process (membrane attachment); gsac, gonosaccus; gse, gonosetae (within gonosaccus); mu, mediuncus (fused rods and beak); mu-b, sclerotized base of mediuncus.



**FIGURE 5.** *Leucochrysa (L.) nigrilabris* male abdomen, teneral specimen. A. Terminal segments, lateral (arrows mark the large brown spots on T6, base of T7); B. Gonarcal complex, frontal; C. Gonarcal complex, lateral [note thorny membrane over gonarcal bridge and gonocornua]; D. Gonarcal complex, lateral (thorny membrane above gonarcus partially removed); E. Tip of sternite 8+9, dorsal, with sclerotized terminal plates extended distally, hypandrium internum (attached to small membrane that had been everted beneath the sclerotized plate); F. Sclerotized plate at tip of S8+9, lateral (all, Aragua, Venezuela). *Abbreviations:* bk, beak-like tip of mediuncus; c, comes; cleft, cleft separating distal margins of T9+ect; c.c., callus cerci; d.a., dorsal apodeme of T9+ect; fl, mediuncal flange; gc, gonocornu; gs, gonarcus; gsac, gonosaccus with robust gonosetae on bulbous chalazae; g.a., gonarcal apodeme; g.b., gonarcal bridge; h.i., hypandrium internum; mu-b, sclerotized base of mediuncus; mu-d, elongate distal section of mediuncus; s.p., sclerotized plate at tip of S8+9; S8+9, fused eighth and ninth sternites; S9, ninth sternite (tip); T7, seventh tergite; T9+ect, fused ninth tergite and ectoproct..



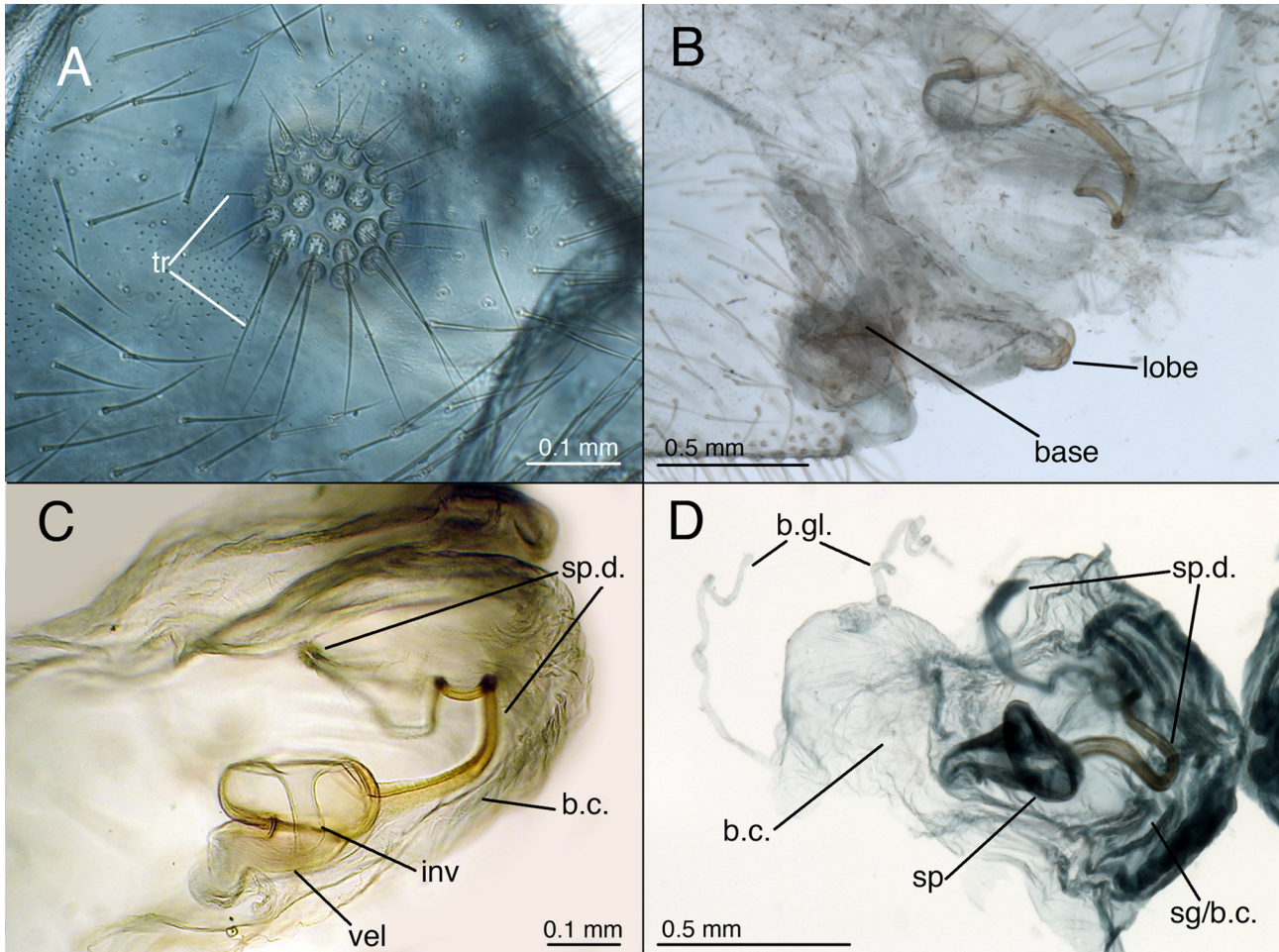


**FIGURE 6.** *Leucochrysa (L.) nigrilabris* female abdomen. A. Fifth to terminal segments, lateral; B-D. Seventh to terminal segment, lateral [A, B, mature specimens, State of Rio de Janeiro, Brazil; C, D, teneral specimens, State of Aragua, Venezuela]. Abbreviations: g.l., gonapophysis lateralis; sg, subgenitale; sp, spermatheca; S7, seventh sternite; T5, T8, fifth and eighth tergites; T9+ect, fused ninth tergite and ectoproct.

*Wings* (Fig. 2) Forewing 18.8–19.9 mm long, 6.5–6.9 mm wide (at widest point); ratio of length: maximum width = 2.6–2.7:1. Costal area moderately broad; tallest costal cell (#9–10) 1.6–1.7 mm tall, 3.0–3.1 times width, 0.2–0.3 times width of wing (midwing). First intramedian cell quadrangular, width (anterior margin) 1.4–1.7 times width (anterior margin) of third median cell, 0.9–1.1 times length of posterior margin of m3; length of basal vein (= ma, median arculus) 2.1–6.2 times greater than length of distal vein. First radial crossvein distal to origin of radial sector (Rs); radial area (between Radius and Rs) with single row of 17–18 closed cells; tallest cell (#8) 2.3–2.4 times taller than wide. No crassate veins; 5–6 b cells (= cells beneath Rs, not including an inner gradate vein). Two series of gradate veins; 10–12 inner gradates, 8–10 outer gradates. Height of fourth gradate cell 4.3–5.3 times width. Eight to nine b' cells (cells beneath pseudomedia after second intramedian cell). Three intracubital cells (two closed). Membrane clear except stigma opaque, with dark brown mark basally, distal two crossveins of last b' cell (distal Psm-Pcu crossveins) surrounded by dark brown suffusion, and (some specimens) small amount of brown suffusion basally. Veins green, except distal two crossveins of last b' cell, inner and outer gradates dark brown to black, sometimes anterior tips of basal R-Rs crossveins, base of Rs, basal Rs-m, basal medial crossveins, tips of posterobasal marginal veins lightly darkened.

Hindwing 16.7–17.7 mm long, 5.5–5.8 mm wide. Two series of gradate veins; 9–10 inner, 8–9 outer; 15–16 radial cells (counted from origin of Radius, not false origin). Five to six b cells (including small b1 cell); seven to nine b' cells beyond second intramedian cell; two intracubital cells (one closed). Membrane clear; stigma with pronounced brown mark basally. Veins light green.

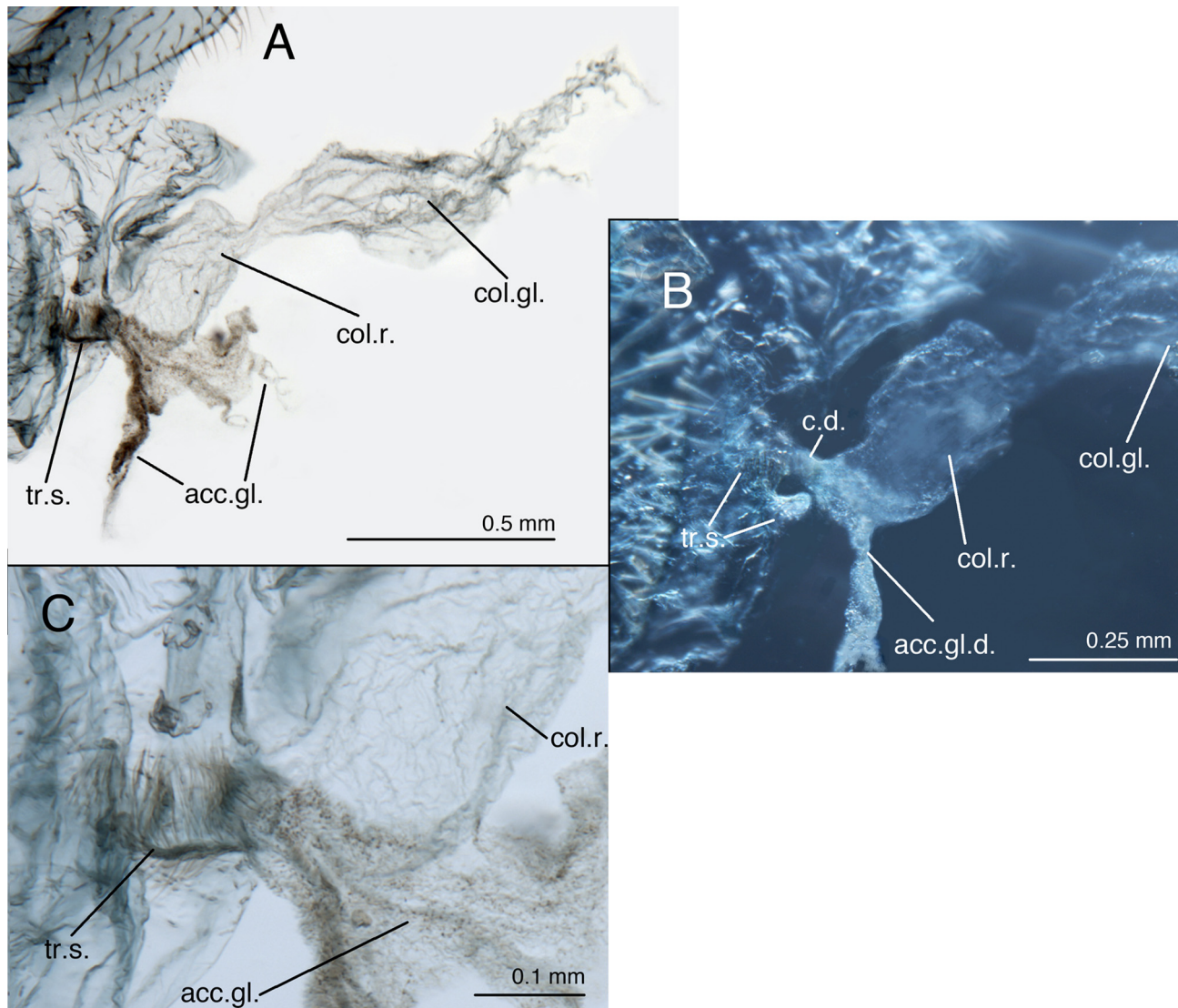
*Abdomen* (Figs 3–8): Tergites with mostly short, slender setae throughout, sternites with longer, slender setae; microsetae dense; pleural region with setae small, very sparse, microsetae very small. Tergites narrow, roughly rectangular, with rounded or irregular margins. Spiracles oval externally; atria not enlarged. Sternites S2–S5 longer than wide (lateral view). Coloration: mostly green, with diffuse yellow dorsal stripe; tergites T5, T6, base of T7 each with large dark brown to black spot, bordered with yellow and patches of red; callus cerci white; setae, trichobothria golden.



**FIGURE 7.** *Leucochrysa* (*L.*) *nigrilabris* female abdominal and genitalic structures. A. Callus cerci; B. Subgenitale, posterior; C. Spermatheca, lateral; D. Genitalia, ventral [A, B, D, State of Rio de Janeiro, Brazil, mature specimen; C, State of Aragua, Venezuela]. *Abbreviations:* base, sclerotized base of subgenitale; b.c., bursa copulatrix; b.gl., bursal gland; inv, spermathecal invagination; lobe, rounded lobe of subgenitale; sg/b.c., heavy folded membrane [distally (right): dorsum of subgenitale, proximally (left): venter of bursa copulatrix]; sp, spermatheca; sp.d., spermathecal duct; tr, trichobothria; vel, velum.

*Male.* S6, S7 height *ca* 1.1–1.2 times length (lateral view). Microtholi dense on S3–S8, absent from S1–S2, S9. Callus cerci oval (*ca* 1.3–1.5x taller than wide), greatest diameter 0.22–0.26 mm, with 26–35 trichobothria of variable length. T9+ectoproct soft, lightly sclerotized, rounded posterodorsally, truncate distally, broadly fused mesally, midline without distal cleft (mature specimen; cleft present in teneral specimen); ventral section tapering proximally, extending beyond midline of S9; dorsal apodeme lightly to moderately sclerotized, straight, extending *ca* half distance along dorsal margin of ectoproct; small, lightly sclerotized apodeme around proximal margin of callus cerci. S8+9 fused, without suture, with clear intersegmental demarcation throughout; dorsal margin with lightly sclerotized, straight apodeme; S8 1.7x taller than long, *ca* one-half (0.47–0.51x) length of S8+9; S8+9 (lateral view) with proximal margin relatively straight, dorsal surface straight, sloping ventrally to distal margin; terminus rounded; tip with pair of flat, sclerotized, plate-like projections with mesal edge toothed, lateral edge rounded. Gonarcus arcuate; bridge straight, narrow mesally (0.19 mm), curved abruptly at exterior margin of gonocornua; gonarcus covered with robust membrane bearing dense gonocristae; gonocornua short (length, 0.07 mm), extending forward from edge of gonarcus, stout basally, tapering to rounded apex;

distance between inner bases of gonocornua 0.07 mm basally, distance between tips 0.12 mm; gonarcial lateral apodeme long, relatively narrow (0.60 mm long, 0.20 mm wide), not extending above bridge, curved distally (lateral view); distance between apodemes distally 0.72 mm. Gonarcus, between lateral apodeme and gonocornu, with moderately sclerotized, elongate posteroventral projection holding membrane that extends beneath mediuncus. Mediuncus well separated from gonarcus, with basal membranous connection stout; basal section of mediuncus consisting of heavily sclerotized platform with distal projections laterally, distal section consisting of well sclerotized, ventrally-projecting, smooth plate terminating in sharp, curved, elongate, mesal beak, pair of large lateral lobes; heavy membrane from gonarcus extending beneath mediuncus, recurving above beak to form gonosaccus with pair of elongate, lateral fields of robust gonosetae on bulbous chalazae; fields of gonosetae on surface of membrane facing mediuncus; each field with *ca* 15–20 gonosetae. Hypandrium internum broadly V-shaped, with comes not visible (mature specimen); arm 0.20–0.22 mm long, distal span between arms 0.19 mm.



**FIGURE 8.** *Leucochrysa (L.) nigrilabris* colleterial complex. A. Colleterial complex, lateral; B. Base of colleterial complex, lateral (pulled posteriorly); C. Transverse sclerite, posterior. [all, State of Rio de Janeiro, Brazil, mature specimen]. *Abbreviations:* acc. gl., colleterial accessory gland; acc.gl.d., duct of colleterial accessory gland; c.d., common duct (colleterial reservoir and accessory gland to transverse sclerite); col.gl., colleterial gland; col.r., colleterial reservoir; tr.s., transverse sclerite.

*Female.* S6 height *ca* 0.67–0.92 times length, S7 height *ca* 0.55–0.65 times length. Callus cerci round, diameter *ca* 0.17–0.19 mm, with 29–34 trichobothria. T8 roughly elliptical (lateral view) with rounded corners, similar in depth to T6. T9+ectoproct elongate, vertically erect; ventral margin slightly rounded, extending below level of gonapophyses laterales. S7 with dorsal margin straight, distal end tapering abruptly; terminus truncate,

unmodified, with terminal (posteroventral) setae slightly more numerous, longer than in other areas. Gonapophysis lateralis rounded throughout, ~0.48–0.52 height of T9+ectoproct; inner membranous surface slightly expandable, with vertical patch of small, delicate setae arising from slightly swollen membrane. Colleterial complex consisting of membranous gland, connected to colleterial reservoir via broad duct, and large accessory gland, both opening to exterior via narrow common duct above transverse sclerite; colleterial gland elongate, delicate; colleterial reservoir shorter, robust; accessory gland probably bulbous (torn in our specimens), elongate, granular, with multiple forks distally; transverse sclerite broad, flat, bent distally, with relatively dense, elongate, hair-like setae. Spermatheca simple, doughnut-shaped, with broad, flat, L-shaped velum, maximum diameter 0.26–0.31 mm, total length (spermatheca + velum) *ca* 0.35 mm; spermathecal invagination deep, narrow, with rounded terminus; velum with elongate slit opening to bursa copulatrix; tip of velum bending slightly into bursa copulatrix; bursal duct very small or absent; spermathecal duct relatively long, *ca* 1.13–1.51 mm, originating from side of spermatheca distal to slit in velum, basal half well sclerotized, tapering throughout, with lateral bend, then U-shaped loop; distal *ca* half narrow, brushy throughout, with curve, followed by distinct swelling mesally, with densely hirsute, swollen terminus. Bursa copulatrix saccular, with heavily textured surface distally (below subgenitale), becoming smoother anteriorly, with pair of elongate, tubular bursal glands attached to distal end, connections appearing unremarkable. Subgenitale with sclerotized surface smooth (unfolded), attached basally to heavy, transversely folded basal membrane (base of subgenitale then top of bursa copulatrix), with two projections, bilobed one on dorsodistal margin, unilobed one on anteroventral margin base withdrawn above tip of S7 [with pressure, the withdrawn lobe can be extruded].

**Intraspecific variation (adult).** *Leucochrysa (L.) nigrilabris* expresses considerable variation in head and mesothoracic coloration, as well as wing size, shape and degree of brown suffusion surrounding various veins. The most striking aspect of the variation is the polymorphism in mesothoracic coloration (Figs 1D–F). Among the specimens we examined, eight (4♀, 4♂) had brown mesoscutella, and five (2♀, 3♂) had white; both color forms occurred among the Venezuelan specimens.

The male genitalia show considerable developmental variation (Compare Fig. 5 with Figs 3, 4). In the teneral male, the gonarcus is weakly sclerotized and narrow; the mediuncal bridge appears wide (in lateral view) and is tightly encased by the gonocristae-bearing membrane; the mediuncus is very narrow; and the hypandrium internum is unexpanded [length of arms, 0.20 mm—as in mature specimens; distal span between arms, 0.06 mm—*ca* 3x narrower than mature specimens]. Females, too, show considerable variation with age and maturation. For example, in the teneral female, the subgenitale is small, weakly sclerotized, and withdrawn, and the spermatheca is shifted anteriorly from the distal wall; whereas in mature specimens, the subgenitale is large, robust, heavily sclerotized and expanded, so that the spermatheca appears surrounded by the distal wall (Figs 6, 7B).

**Description (First Instar, Semaphoront A).** *Body* (Fig. 10). 2.8–3.0 mm long. All setae smooth.

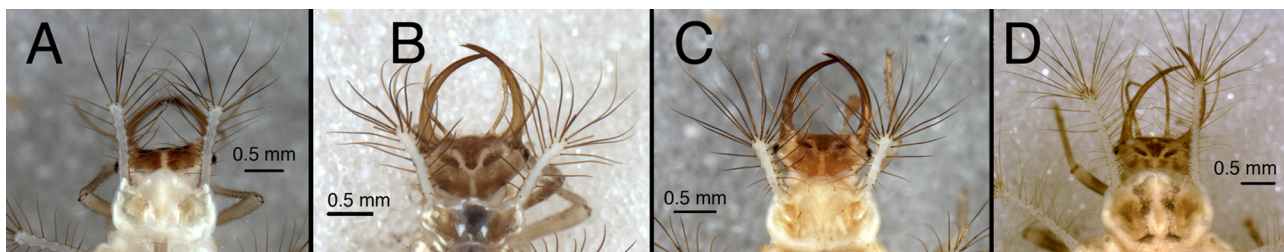
*Head* (Figs 10A–C). 0.55–0.56 mm wide, 0.38–0.39 mm long; mandibles 0.59–0.61 mm long; ratio, mandible length : head width, ~1.09:1. Epicranial marking brown, paired, extending along entire basal margin of cranium, laterally extending to eye, mesally becoming confluent with base of postfrontal marking. Postfrontal marking slightly darker brown than epicranial marking, elongate, extending to base of antenna. Frontal marking V-shaped, arms extending forward through dark tentorial pits becoming confluent with intermandibular marking. Intermandibular marking broken mesally, extending laterally from tentorial pits to base of mandibles, anteriorly to tip of clypeus. Gena with single, elongate, brown stripe extending from base of eye to posterior edge of cranium. Labial palpus cream-colored basally, light brown distally. Mandibles amber to brown. Antenna light brown to cream-colored. Venter cream-colored to white mesally, light brown laterally, with brown transverse stripe distally; cardo, stipes brown.

All cephalic setae straight, with pointed terminus. Primary setae S1–S12 present; S1, S11 long; S2, S3, S5 short. Labial palpus: basal segment with two setae—one lateral, one ventral; midsegment with two distal setae—one lateral, one mesal. Mandible with one basolateral seta; maxillae with basal seta. Palpiger with two basal setae. Scape without setae; pedicel with one small distal seta; flagellar seta slightly longer than one-half length of segment.

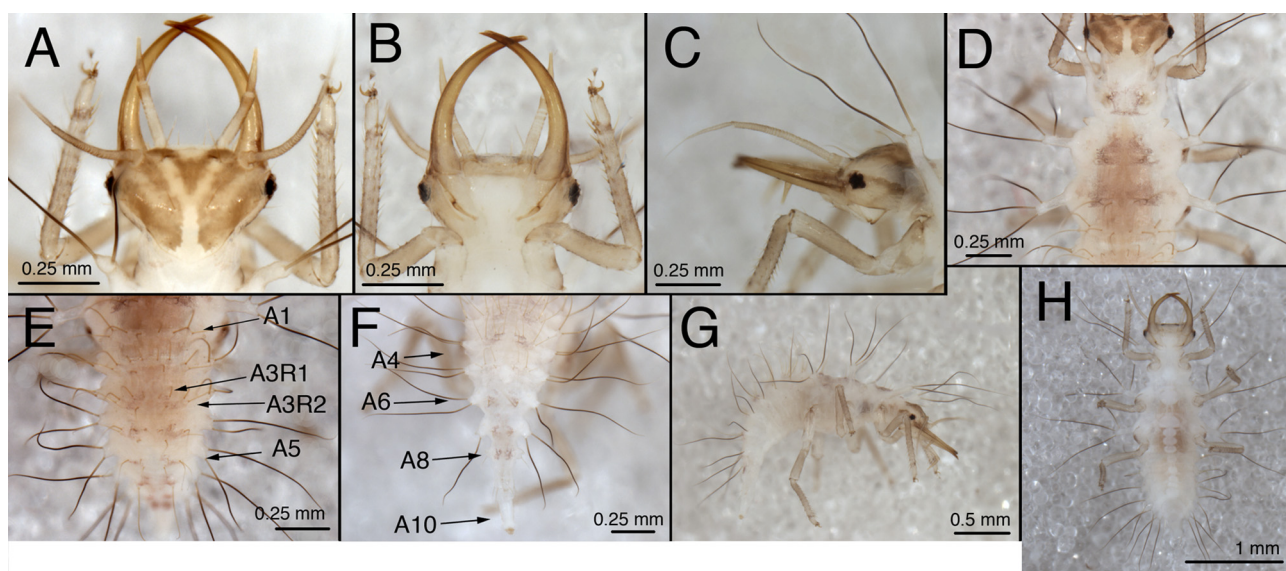
*Thorax* (Figs 10D, G, H). Notum with diffuse, reddish brown, submesal markings; Setae (LS) on lateral tubercles (LTs) dark brown; dorsal setae light brown. Legs mostly light brown to brown; trochanters, tarsi white to cream-colored; claws, empodia brown. LS gently curved throughout, with tips pointed, fine; all other setae straight to gently curved, with terminus pointed.

T1: LT with two long LS, without microseta between. First primary sclerite (Sc1) light brown, large, with associated seta (S1Sc1) long, arising from small chalaza; S2Sc1 short, anterior to S1Sc1. S1 long, arising from small chalaza; S2 absent; S3, S4, S5 short.

T2: Spiracles prominent, tubercle-shaped, apex sclerotized, dome-shaped, amber-colored. LT with three long LS. Sc1, Sc2 small; associated setae (S1Sc1, S2Sc1 and S1Sc2) very small; Sc3 intermediate-sized, light brown, with associated seta (S1Sc3) small. Posterior subsegment with pair of short setae mesal to Sc3, row of four setae posterior to Sc3 (mesal pair short, lateral pair long, arising from robust chalazae).



**FIGURE 9.** Prothorax of third instar of four *Leucochrysa* (*Leucochrysa*) species. A. *L. (L.) nigrilabris*; B. *L. (L.) insularis*; C. *L. (L.) varia*; D. *L. (L.) boxi* [A, C, D, State of Rio de Janeiro, Brazil; B, North Carolina, United States].



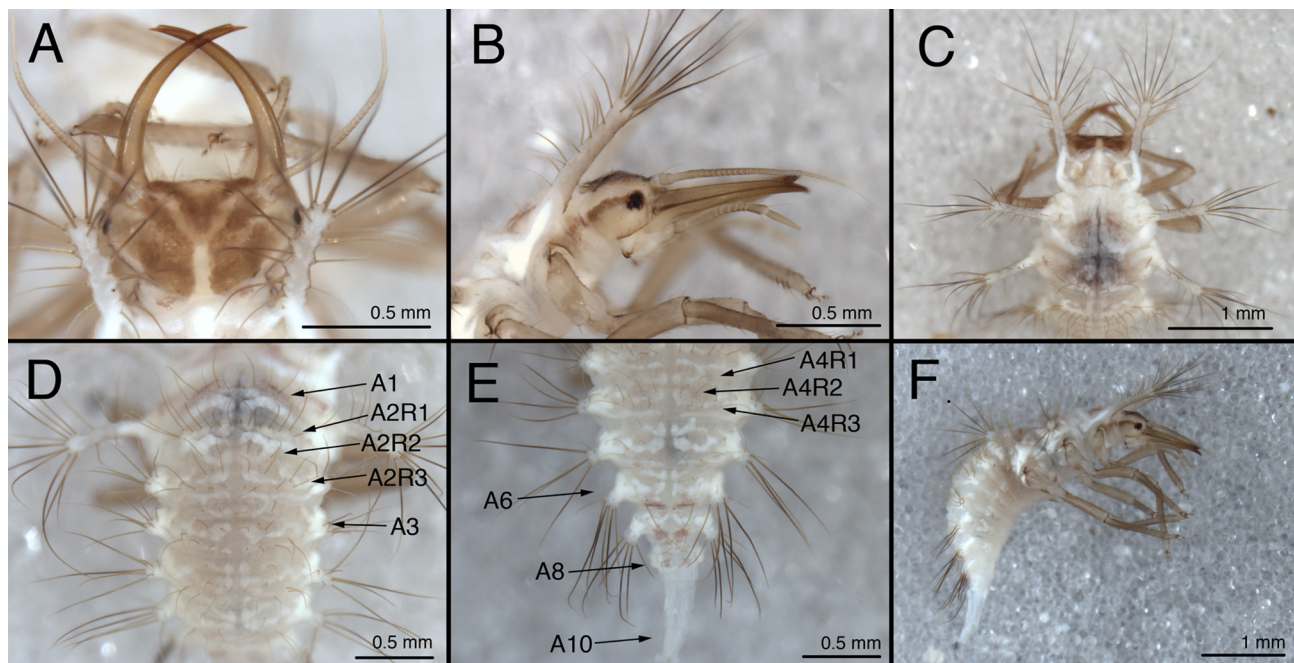
**FIGURE 10.** *Leucochrysa* (*L.*) *nigrilabris* first instar. A. Head, dorsal; B. Head, ventral; C. Head, lateral; D. Thorax, dorsal; E. Abdominal segments 1 to 5, dorsal; F. Abdominal segments 4–10, dorsal; G. Body, lateral; H. Body, ventral [all, State of Rio de Janeiro, Brazil]. *Abbreviations:* Ax, abdominal segment number; AxRx, setal row number.

T3: LT with three long LS. Sc1 small, with S1Sc1 very small; Sc2 light brown, with S1Sc2 small. Anterior region with pair of short setae; posterior region with four long setae arising from robust, fleshy chalazae.

*Abdomen* (Figs 10E–H). White to cream-colored; dorsum of A1–A3 with diffuse, submesal, reddish brown band; dorsum of A4, A6–A8 each with pair of reddish brown submesal spots. LTs each with two long LS (A2–A7), without microseta between; LS straight, with pointed tip, dark brown; submedian setae (SMS), setae (LDS) on laterodorsal tubercles (A1–A5) hooked, light brown. A1, A6–A8: Spiracle without associated seta (SSp); A2–A5: each spiracle with small to minute SSp. A1–A5: Laterodorsal tubercles (LDTs) each with two long, hooked LDS, one microseta between LDS. A1: Single row of four SMS between LDTs. A2–A4: Anterior row of four SMS, posterior row of two SMS, both between LDTs. A5: Anterior row of two to three SMS, posterior row of two SMS, both between LDTs. A6: Two short, straight setae anteriorly, two intermediate-length, hooked setae posteriorly; LDT with one long, hooked LDS, one short, straight LDS. A7: LDT with one intermediate-length, straight LDS, two very short LDS; dorsum with pair of minute setae anteriorly. A8: LT with one short, straight LS, two to three small setae, base of LT with spiracular tubercle projecting from anterior surface; spiracular base and sclerotized ring elongate, projecting posteriorly; dorsum with three to four short, straight setae between LTs. A9: Dorsum with

three rows of short, straight setae (anterior two minute, middle four short, posterior four slightly longer). A10: Apparently without setae; terminus light brown, with small eversible pouch.

**Description (Second & Third Instars, Semaphoront B).** *Body* (Figs 9, 11–12). L2: 4.7–4.9 mm; L3: 8.6–9.0 mm long. Dorsum cream-colored, with dark brown markings.



**FIGURE 11.** *Leucochrysa* (*L.*) *nigrilabris* second instar. A. Head, dorsal; B. Head, lateral; C. Thorax, dorsal; D. Abdominal segments 1 to 4, dorsal; E. Abdominal segments 4–10, dorsal; F. Body, lateral [all, State of Rio de Janeiro, Brazil]. Abbreviations: Ax, abdominal segment number; AxRx, setal row number.

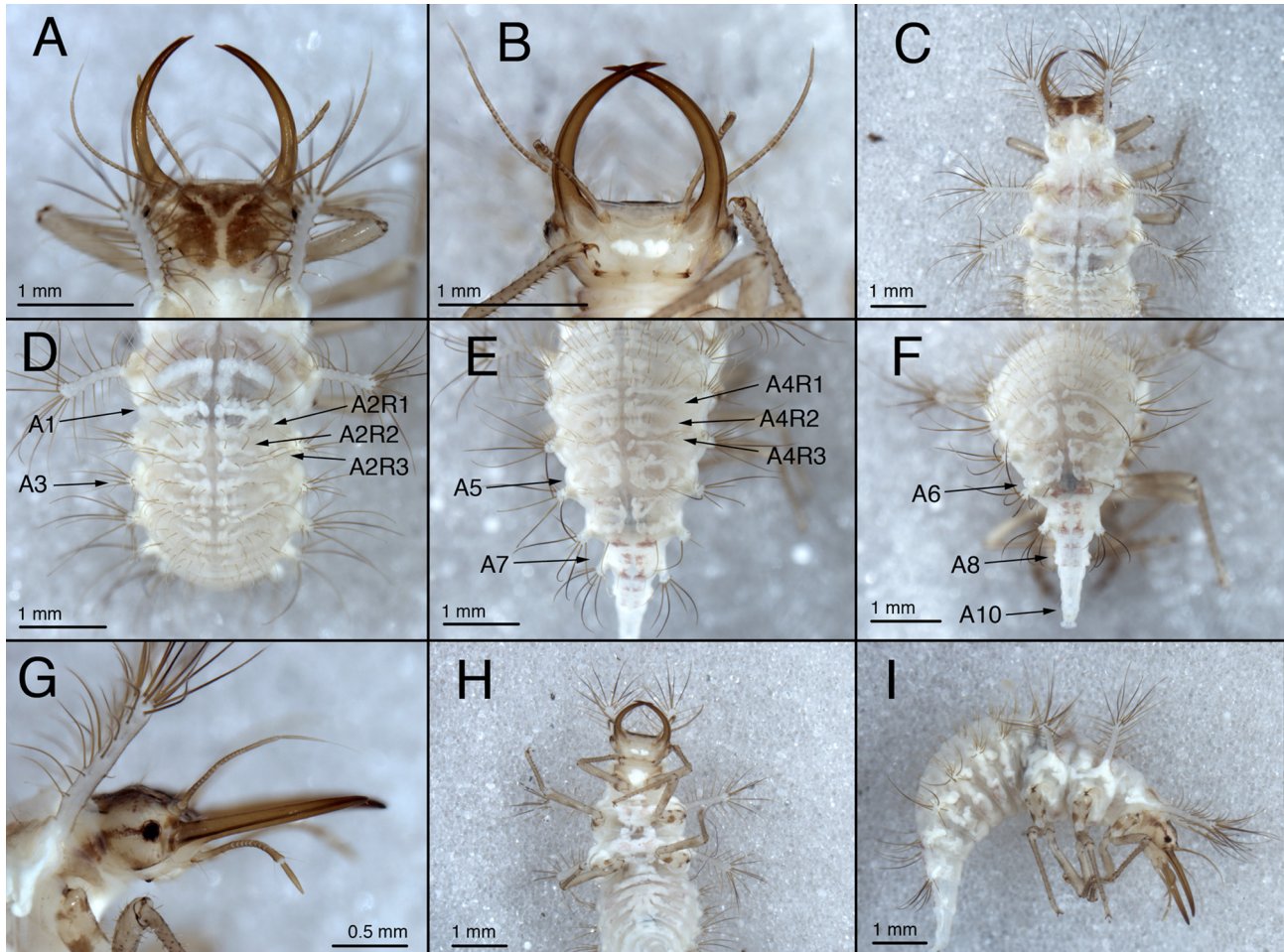
*Head* (Figs 11A, B, 12A, B, G, H). L2: 0.81–0.83 mm wide, 0.53–0.58 mm long; mandibles 0.93–0.96 mm long; ratio mandible length : head width 1.14–1.17:1. L3: 1.3–1.4 mm wide, 0.86–0.91 mm long, mandibles 1.5–1.7 mm long; ratio mandible length : head width, 1.19–1.23:1. Epicranial marking paired, brown to dark brown, covering entire basal portion of cranium, laterally becoming lighter brown, extending to eye, mesally becoming confluent with base of postfrontal marking. Postfrontal marking slightly darker brown than epicranial marking, elongate, extending to base of antenna. Frontal marking V-shaped, arms extending forward through dark tentorial pits, then curving to base of mandibles becoming confluent with intermandibular marking. Intermandibular marking brown, divided into three sections—two lateral sections at mesal base of mandibles, mesal section between, but separated from two lateral sections; clypeolabral region partially covered by intermandibular marking. Gena with single, elongate, brown stripe extending from base of eye to posterior edge of cranium; region around eyes cream-colored; stemmata, except posteroventral margin, surrounded by brown. Labial palpus: basal segment light brown; mesal segment light brown basally, darker distally, with well defined annulations; terminal segment dark brown. Mandibles brown basally to dark brown at tip. Antenna light brown to brown. Ventrolateral cranial surface light brown. Cardio with light brown mark basally, dark brown mark distally, narrow; stipes light brown to tan, narrow, elongate. Mentum white to cream-colored, with tinge of light brown anteriorly; palpiger light brown. Cervix cream-colored, with prominent lateral patches of brown.

Anterior margin of head with slightly rough, obtuse lateral edges; posterior section of cranium spiculate. All cephalic setae smooth, straight, with acute tip; S1–S12 present; S1, S11 long; S2, S3, S5 short. Labial palpus: basal segment with three setae, midsegment with distal annulation bearing four setae, remaining annulations with *ca* six (L2) or seven (L3). Mandible with one basolateral seta; maxillae with basal seta. Palpiger with two basal setae. Scape with one distolateral seta; pedicel with one small distal seta; flagellar seta *ca* one-half length of segment.

*Thorax* (Figs 9, 11C, F, 12C, H, I). LTs white to cream-colored, with diffuse to very pale, reddish brown markings at dorsal base submesally; LS mostly dark brown; large sclerites Sc1 (prothorax), Sc3 (mesothorax), Sc2 (metathorax) light amber, shiny. Venter white to cream-colored, with small, diffuse, rosy, submesal patches on each segment. Spiracles amber to light amber; setae mostly brown or light brown. Legs: coxa with dark brown marking

on dorsal connection to base, pair of brown marks, one anterior, one posterior; trochanter with pair of dark brown marks, one anterior, one posterior; femur brown dorsobasally, light brown distally; tibia brown throughout; tarsus light brown; claws curved, large, dark brown; empodia dark brown.

LTs smooth; LS smooth, except very fine tips sometimes slightly salebrose, seldom sparsely and finely barbed, slender, gently curved throughout, tips tapering to very fine terminus; tips of distal LS mostly pointed, tips of lateral LS mostly with small hook. All dorsal, ventral setae smooth.



**FIGURE 12.** *Leucochrysa (L.) nigrilabris* third instar. A. Head, dorsal; B. Head, ventral; C. Thorax, dorsal; D. Abdominal segments 1 to 3, dorsal; E. Abdominal segments 3–7, dorsal; F. Abdominal segments 6–10, dorsal; G. Head, lateral; H. Body, ventral; I. Body, lateral [all, State of Rio de Janeiro, Brazil]. *Abbreviations:* Ax, abdominal segment number; AxRx, setal row number.

T1: All dorsal, ventral setae straight; Sc1 large, extending laterally to dorsal surface of LT, with S1Sc1 long, slender, S2Sc1 very short, slender. Sc2 transparent, oval-shaped, *ca* one-third length of Sc1. LT (L2) with 19–21 LS (*ca* 10 apical, *ca* 9–11 lateral); LT (L3) with *ca* 27–30 LS (*ca* 10 apical, *ca* 17–20 lateral). Primary setae S1 medium-length, S2, S3, S4, S5 short, slender; no secondary setae.

T2: Anterior subsegment without secondary setae between spiracles; anterior sclerite (Sc1) with three associated setae (S1Sc1, S2Sc1, S3Sc1); spiracles prominent, with opening sclerotized, dome-shaped, amber-colored ring on small tubercle; walls of chamber parallel, not bulbous; SSp absent. Posterior subsegment with anterior sclerite (Sc2) bearing two very small associated setae (S1Sc2, S2Sc2); Sc3 with small associated seta (S1Sc3); anterior row with two intermediate-length, slender, straight setae; posterior row (L2) with *ca* 5–6 setae (3–4 long, robust, 1–2 slender, hooked or straight), arising from large, plump chalazae; posterior row (L3) with *ca* 11–14 setae (6–8 long, robust, 5–7 slender, hooked or straight), arising from large, plump chalazae. LT (L2) bearing *ca* 17–19 LS (*ca* 8–9 apical, *ca* 9–10 lateral, mostly straight); LT (L3) bearing *ca* 26 LS (*ca* 10 apical, *ca* 15–17 lateral).

T3: Sclerites (Sc1, Sc2) each with one associated setae (S1Sc1, S1Sc2); sometimes small seta on anterior fold, lateral to Sc1. Anterior row with one to two short (L2) or two to four intermediate-length (L3), slender, straight setae; posterior row (L2) with *ca* 12 long, robust, straight or hooked setae arising from large, plump chalazae; posterior row (L3) with *ca* 15–16 setae (*ca* ~12–14 long, robust, 2–4 intermediate-length, slender, straight or hooked), arising from large, plump chalazae. LT (L2) bearing *ca* 19–20 LS (*ca* 9 apical, 10–11 lateral, mostly straight). LT (L3) bearing *ca* 21–25 LS (*ca* 9 apical, 12–16 lateral).

*Abdomen* (Figs 11D–F, 12D–F, H, I). Dorsum, venter white to cream-colored; anterior segments without dorsal markings; A6–A8 with diffuse, reddish dorsal marks; A10 with small, brownish mesal spot distally. Venter of A2–A4 with diffuse, light reddish sublateral patches; A10 with pair of brown, submesal spots. LS on A2–A3 light brown, A4–A7 dark brown; SMS light brown to dark amber.

All setae smooth. SMS of A1–A6 hooked, slender, arising from plump chalazae; SMS longest, chalazae largest on A1, A2, becoming smaller posteriorly. A1–A5: LDT plump, with two long, slender, hooked LDS, one microseta between LDS. A1–A8: Spiracle small, slightly raised, dome-like, with minute to very small associated seta (SSp?) anteriorly or mesally.

A1: Single transverse row of eight (L2) or *ca* nine to ten (L3) SMS mesal to LDTs.

A2–A3: LT broad, plump, fleshy, with seven (L2) or eight (L3) long, robust LS arranged transversely along dorsal surface, *ca* two (L2) or four (L3) shorter, straight setae basally. L2: Dorsum with anterior row of four SMS, mesal row of four, posterior row of four (A2) or six (A3) between LDTs. L3: Dorsum with anterior row of *ca* ten (A2) or ~12 (A3) SMS, mesal row of four (A2, A3), posterior row of *ca* 12 (A2, A3) between LDTs.

A4–A5: LT tuberculiform, with *ca* five (L2) or 12 (A4, L3), 9–10 (A5, L3) robust, hooked or straight LS apically, dorsally, *ca* four (L2, L3) short, straight LS basally. LDS intermediate length, hooked. L2: Dorsum with anterior row of four (L2) intermediate-length SMS, mesal row of four, posterior row of four between LDTs. L3: Dorsum with anterior row of *ca* 12 (A4) or *ca* nine (A5) intermediate-length SMS, mesal row of four, posterior row of *ca* ten between LDTs.

A6: LT tuberculiform, with *ca* five (L2) or six (L3) robust, straight LS apically, *ca* three short, straight LS basally. LDT with one long, hooked LDS, two to three short, straight LDS. Anterior row of three (L2) or five (L3) intermediate-length SMS, no other SMS.

A7: LT tuberculiform with posterior projection, with *ca* five (L2) or six (L3) robust, straight LS apically, *ca* three short, straight LS basally. LDT with one intermediate-length, straight LDS, one to two short, straight LDS. Two pairs of very small setae between spiracles.

A8: LT with four to five short, straight LS (two short, two to three very short). Row of four to five very short setae between spiracles. Posterior margin with *ca* four (L2) or seven to eight (L3) very short setae.

A9: Two transverse rows of *ca* four to six short setae.

A10: Dorsum with *ca* four to five very short setae.

**Intraspecific variation (larva).** Three variable features warrant notation. (i) As with the larvae of all chrysopids we have studied, *L. (L.) nigrilabris* larvae exhibit considerable bilateral asymmetry in the numbers and size of setae across the dorsum of body. Odd numbers of setae are common. (ii) The left side of the first abdominal segment (A1) of one L3 specimen has a fleshy, lateral protuberance (LT?) bearing an elongate, robust, hooked seta. This feature is unusual because LTs rarely occur on the A1 (e.g., in some *Chrysopa* spp., see Principi 1940, Tsukaguchi 1978), and they have not been reported for leucochrysine larvae. Moreover, LTs almost always bear more than one elongate seta. Thus, we do not know whether this structure is homologous to those on the larva's subsequent segments (A2–A7) and/or to those on the *Chrysopa* A1. (iii) Among the first instars, the elongate setae (LS) on the apex of the lateral tubercles are mostly very long, straight, and tapering to pointed tips; occasionally some are hooked.

**Biological notes.** Adults were collected in disturbed habitats (e.g., coffee plantation, roadside, along trail) at the edges of mature forests. One female specimen, collected in the State of Rio de Janeiro, was maintained in the laboratory for *ca* two weeks. During that time she laid two batches of eggs. Each batch consisted of a hanging cluster of *ca* 15–20 eggs attached to the ends of a series of long intertwined stalks.

The *L. (L.) nigrilabris* eggs were maintained at room temperature; hatching occurred within *ca* ten days. The larvae applied and carried dense packets of trash [in this case, frozen & thawed eggs of *Ephestia kuehniella* (Zeller)] on their dorsa. The first moult occurred *ca* six days after hatching, and the second moult *ca* seven days after the first; cocoons were spun *ca* 10 days later. Four pharate adults emerged from their cocoons; only one completed ecdysis to the adult stage.



**Specimens examined (adults and larvae, in addition to the type listed above).** VENEZUELA. *Aragua*: Parque Nacional Henri Pittier (formerly Parque Nacional Rancho Grande), 1100 m, 11–13.ii.1969, J. Salcedo (1♂, MIZA); idem, 22.v.1967, L. Rodriguez V. (1♀, MIZA, determined by Adams 1979); idem, 9.xi.1990, V. Savini, trampa de luz (1♂, MIZA); idem, 5.vi.1958, F. Fernández Y. (MIZA, determined by Adams 1979); idem, 16–31.x.1966, S. S. & W. D. Duckworth (5♀, USNM); idem, 10–21.x.1969, Duckworth & Dietz (1♂, 1♀, USNM); idem, 8.vi.1967, R. W. Poole (2♀, CUIC); idem, 5.viii.1967, R. W. Poole (1♂, CUIC); idem, 20.ix.1973, B. Villegas (1♂, UCD); idem, 24–25.i.1996, white light, J. & A. Skevington (2♂, 2♀, DEBU); idem, 1150 m, at lights on bldg, 24.ii–12.iii.1996, S. Marshall (1♂, 1♀, DEBU); El Limón, 450 m, 20.iv.1964, E. Osuna (MIZA, determined by Adams 1979); *Mérida*: Mérida, el. ca 4500 ft., 8.5942°N / 71.1429°W, 22–23.ii.1994, J. P. Donahue (1♀, LACM); *Portuguesa*: Córdoba 800 m, 24–29.xi.2008, R. Páz, Malaise Trap (1♀, UCOB); *Yaracuy*: La Cumbre, Chivacoa Council, 1075 m, 10°14'N / 68°58'W, 22.vii.2012, in *Coffea arabica*, F. Sosa, manual net (1♀, UCOB); idem, 1200 m, 10°16'N / 68°56'W, 11.ii.2013, in *Coffea arabica*, F. Sosa, manual net (1♂, UCOB); idem, 18.iv.2013, in *Coffea arabica*, F. Sosa, C. Martins and F. Díaz, manual net (2♂, 1♀, UCOB); El Canelo, Cocorote Council, 1309 m, 10°20'N / 68°49'W, 18.iv.2013, in forest, F. Sosa, C. Martins and F. Díaz, manual net (1♂, UCOB). BRAZIL. *Rio de Janeiro*: Sta. M. Madalena, Terras Frias, 28.x.2003, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, Oct.–Nov. 2003 [1♀, 3?sex (lab-reared, pharate adults, incompletely emerged), 9 larvae (Tauber Lot 2003:067, UCB); 15 larvae (Albuquerque Lot 2003:021, UENF)].

### *Leucochrysa (Leucochrysa) insularis* (Walker, 1853)

Figs 9, 13–22

***L. (L.) insularis* taxonomic history & geographic distribution.** Adams (1977) and Tauber (2004) provided the taxonomic history of the species and redescribed the adults based on the type specimen and other material. The type of *L. (L.) insularis* (male, BMNH) is in relatively poor condition; it appears to be teneral, and its body was damaged by dermestids. See images (Fig. 13).

Adams (1977) and Tauber (2004) also illustrated the male and female genitalia and documented significant geographic variation in the species' adult coloration. To help facilitate comparisons, here we provide images of the *L. (L.) insularis* adult color polymorphism (Fig. 14), wing markings (Fig. 15), and genitalia (♂: Fig. 16; ♀: Figs 17, 18).

*Leucochrysa (L.) insularis* occurs throughout the eastern and central states of the United States (north to Massachusetts and Nebraska, south to Texas and Florida), eastern Mexico [Hidalgo, San Luis Potosí, Tamaulipas, Veracruz (new state record)], and the West Indies (Cuba, Dominican Republic and Jamaica). Thus, *L. (L.) insularis* and *L. (L.) nigrilabris* appear to have adjacent, allopatric distributions.

Jones (1929) provided a well-illustrated larval description of *L. (L.) insularis* [as *Nodita virginica* (Fitch)]. Although it does not specify which instar (2<sup>nd</sup> or 3<sup>rd</sup>) is described, it contains fascinating information on both the morphology and biology of the larvae. The descriptions below are based on new material. The first instars were teneral and somewhat shriveled; their structures were not measured; many small setae were not visible. The third instar was teneral and not measured. For both instars, characteristics are as described above for *L. (L.) nigrilabris*, except where noted.

#### **Description (First Instar, Semaphoront A).**

*Head.* 0.54 mm wide, 0.40 mm long; mandibles 0.56 mm long; ratio, mandible length : head width, ~1.02:1.

*Thorax.* T1: S1 long, arising from large chalaza; S3, S4, S5 very short.

*Abdomen.* A6: Two short, straight setae anteriorly, no setae posteriorly.

#### **Description (Third Instar, Semaphoront B).**

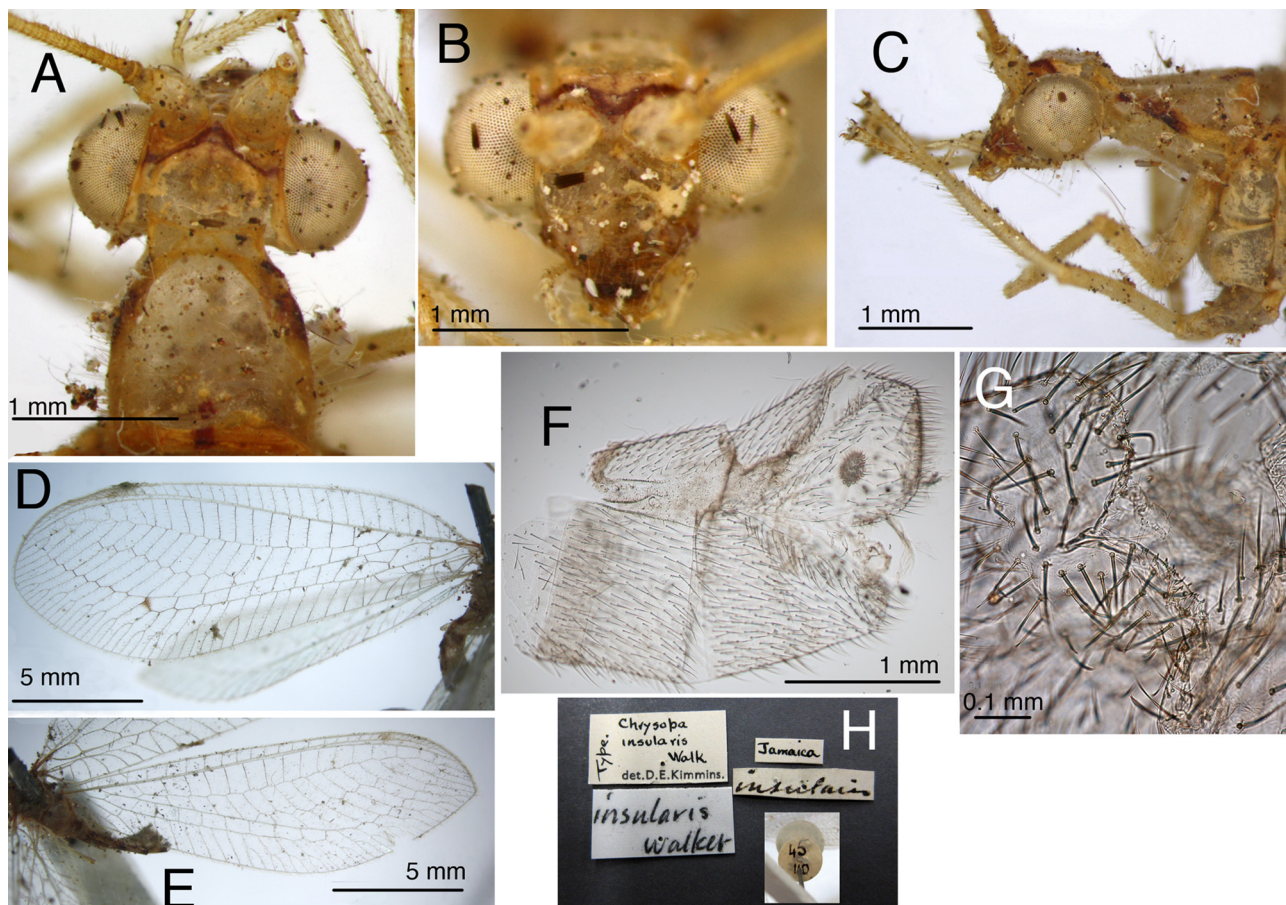
*Body.* Dorsum cream-colored to brown, with brown sclerites.

*Head* (Figs 20A–D). 1.32 mm wide, 0.76 mm long, mandibles 1.48–1.53 mm (right-left) long; ratio mandible length : head width, 1.12:1.0. Genal marking light brown, diffuse, extending broadly toward eye and ventral margin of cranium. All stemmata, including posteroventral one, surrounded by brown outline. Posterior section of cranium densely spiculate.

*Thorax* (Figs 20D, E). Large sclerites Sc1 (prothorax), Sc3 (mesothorax), Sc2 (metathorax) brown, shiny; markings on venter not visible. Setae associated with small sclerites between segments and subsegments not

readily observed. LTs spiculate; LS smooth basally becoming slightly scabrous distally, with tips mostly curly, sometimes with small hook.

T1: Sc1 large, extending laterally to base of LT; S1Sc1 long, robust, S2Sc1 very short. LT with *ca* 22 LS (*ca* 10 apical, *ca* 12 lateral). Primary setae S1 long, robust; S2 short; S3, S4, S5 very short. T2: Posterior row with 6 setae – 4 long, robust, straight to curvey, arising from 2 pairs of large, plump, juxtaposed chalazae, and 2 short, straight, arising from mesal margin of mesal chalazae. LT bearing 20–24 LS (8 apical, 14–16 lateral). T3: Anterior row with two intermediate-length, robust setae; posterior row with 12 long, robust, hooked setae arising from large, plump chalazae. LT bearing *ca* 20–23 LS (8–9 apical, 11–15 lateral). [Note: The ranges in setal counts are derived from paired tubercles.]



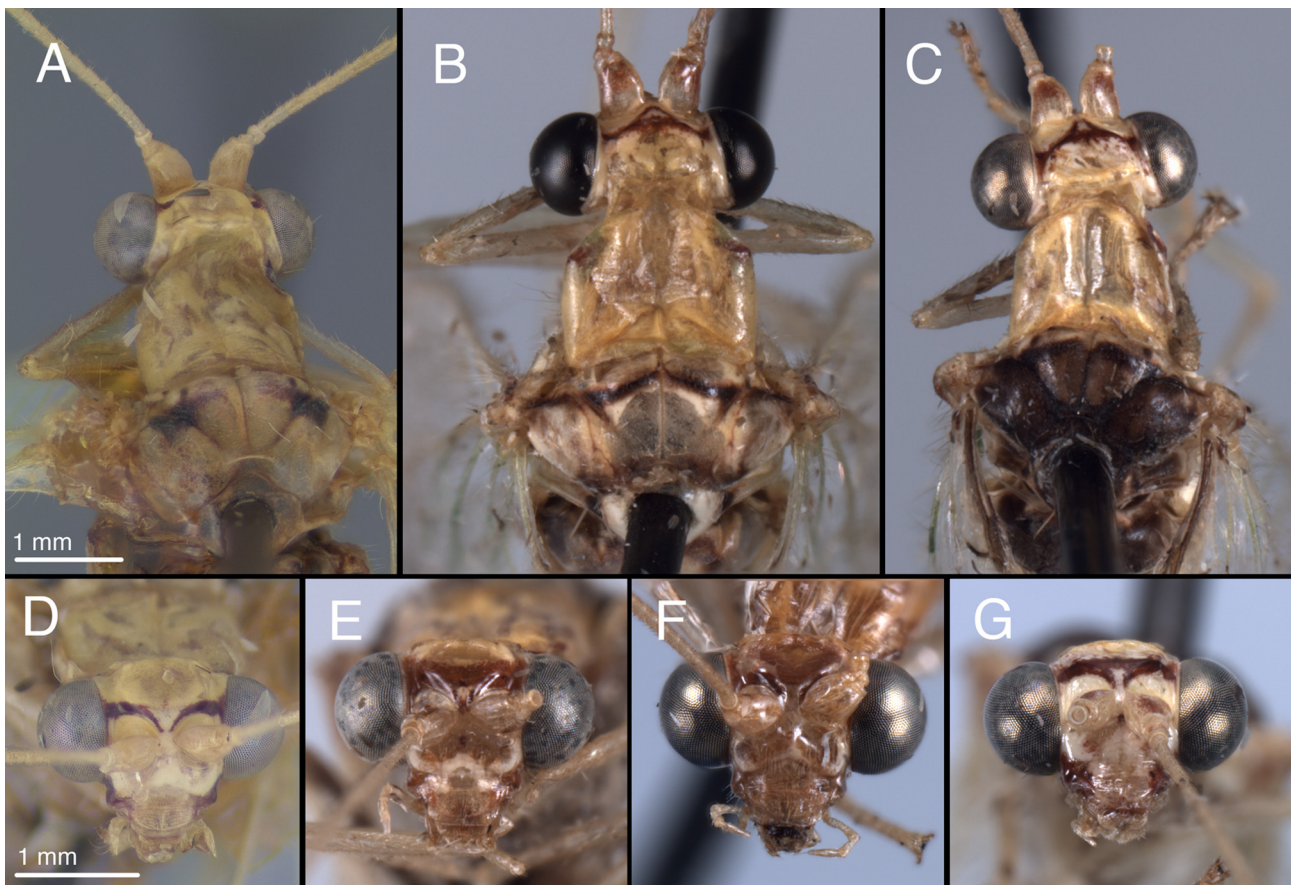
**FIGURE 13.** *Leucochrysa (L.) insularis* holotype (male), Jamaica, BMNH. A. Head, prothorax, dorsal; B. Head, frontal; C. Head, prothorax, lateral; D. Forewing; E. Hindwing; F. Terminal segments of abdomen, lateral; G. Terminus of ninth abdominal sternite, ventral; H. Labels.

*Abdomen* (Figs 20E, F). SMS of A1–A6 robust, hooked, arising from plump chalazae; A1–A5: LDT plump, with two long, hooked, robust LDS, one microseta between LDS. [Note: The right LDT bore 3 full-sized LDS.]

A2–A3: LT with seven to eight long, robust LS, four shorter, straight setae basally. Dorsum with anterior row of seven to ten (A2, A3) SMS, mesal row of four (A2, A3), posterior row of eight (A2, A3) between LDTs. A4–A5: LT with nine to ten (A4), six (A5) robust, hooked or straight LS apically, dorsally, one to four short, straight LS basally. LDS long, robust, hooked. Dorsum with anterior row of eight (A4, A5) long SMS, mesal row of four SMS, posterior row of eleven to eight SMS (A4, A5) between LDTs. A6: Anterior row of three intermediate-length SMS, no other SMS. A7: LDT with one long, robust, straight LDS, two short, straight LDS. Two to three pairs of very small setae between spiracles. A8: Row of four short, robust setae between spiracles. Posterior margin with four short, robust setae.

**Biological notes.** Like *L. (L.) nigrilabris* females, *L. (L.) insularis* females lay their eggs in clusters at the ends of long, intertwined stalks [Mark S. Fox, personal communication; his photos here (Fig. 21) and on <http://bugguide.net/node/view/350432>].

*L. (L.) insularis* larvae have been found in leaf litter, and their debris packets consist largely of small snail shells, and sometimes live snails. Jones (1929, 1941) reported the following snail species from specimens collected in Vinton and Washington Counties, Ohio: *Punctum vitreum* (H. B. Baker) [as *Punctum pygmaeum* (Drap.)], *Euconulus fulvus* (Müller), *Striatura milium* (Morse), *Carychium exiguum* (Say), *Strobilops labyrinthica* (Say), *Cochlicopa lubrica* (Müller). Archer (1938) reported the following snail species from larvae that are almost certainly *L. (L.) insularis*, in North Carolina and Alabama: *Glyphyalinia indentata* (Say) [as *Retinella indentata paucilirata*], *Glyphyalinia carolinensis* (Cockerell) [as *R. carolinensis wetherbyi*], juveniles of *Inflectarius rugeli* (Shuttleworth) [as *Polygyra rugeli*], *Hawaiiia minuscula* (A. Binney), *Guppya sterkii* (Dall) [as *Euconulus sterkii*], *Euconulus chersinus* (Say), and *Vertigo gouldii* (A. Binney). The third instar (described here, collected in Swain County, North Carolina) also carried mainly small snail shells in its packet (Fig. 22); D. C. Dourson (personal communication, 2005) identified them as *Carychium clappi* Hubricht, *Gastrocopta contracta* (Say), *G. pentadon* (Say), *Punctum blandianum* Pilsbry, *P. minutissimum* (I. Lea), and *P. vitreum*. For systematic and biological information on many of the snails listed above, see Dourson & Dourson (2006).

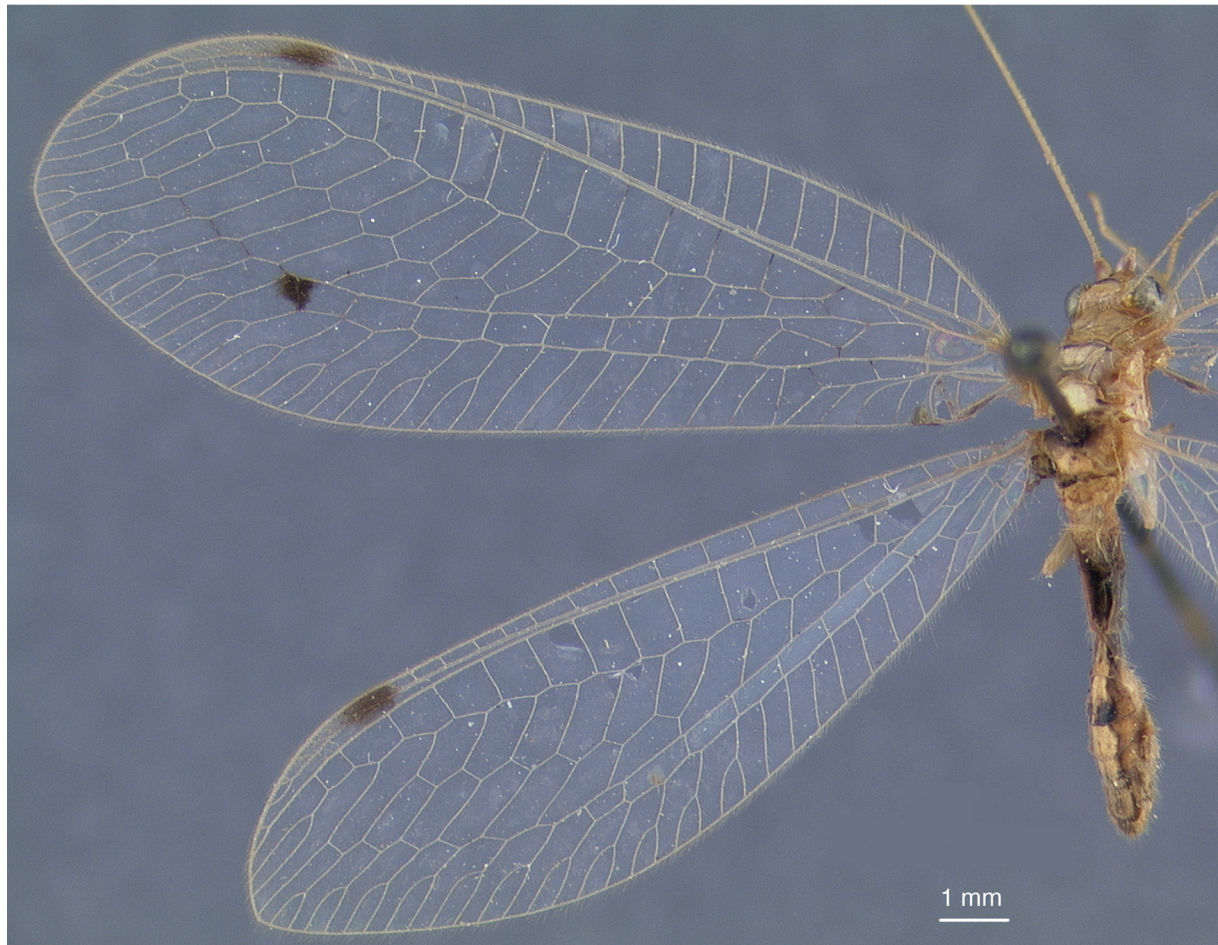


**FIGURE 14.** *Leucochrysa (L.) insularis*, variation in head and thoracic coloration. A-C. Head, thorax, dorsal; D-G. Head, frontal [note the polymorphic coloration of the mesoscutellum (Figs A-C, partially obscured by pins).] [A, D. Jefferson County, FL, female (prob); B, C, E, G. Dominican Republic (B, E, G, females; C, male); F. State of Veracruz, Mexico, female].

In addition to snail shells, body parts from a diverse array of insects also are reported from the packets. Jones (1941) described the behavior involved in applying the snail shells to the larval dorsum. He observed that the shells were held to the larval setae via silken strands; he suggested that the strands originate from a fluid that the tip of the abdomen applies to the shell and that hardens on the snail shell. He also stated that larvae feed on snails and that sometimes larvae carry living snails in the packet which are later removed and eaten. Finally, Jones (1941) mentioned that *L. (L.) insularis* larvae overwinter hidden within coiled leaves.

**Specimens examined (adults and larvae, in addition to the type).** **UNITED STATES.** **GA:** Richmond Co., Augusta, 24.v.1968 (1♂, AMNH); **KY:** Carter Co., along Little Sandy River below Grayson Dam (US-CI), 10.viii.1995, B. C. Kondratieff & R. F. Kirchner (1♀, COSU); **LA:** St. Tammany Parish, Honey Island Swamp, M. Fox, 26.x.2009 (♀) (1♀, cluster of hatched eggs laid in lab, 6 neonates, unfed; UCB); **MI:** Hinds Co., Jackson,

24.viii.1968, B. Mather (1♂, prob., AMNH); **NC**: Swain Co., Great Smoky Mountains National Park, Purchase Knob Survey / Site #28, Sap Tree 00ZING 9-6-05, D. Dourson (1L3, UCB, on loan from Great Smoky Mountains National Park); **VA**: Frederick Co. Rt. 50, Back Cr., 16.vii.1980, Kondratieff (1♂, COSU). **MEXICO. Veracruz**: Córdoba, 11.x.1966, A. & B. Lan (1♀, ROM). **DOMINICAN REPUBLIC. Azua**: East side of crest, Sierra Martin Garcia, 7 km WNW Barrero, k18-21N, 70–50W, 860m, 25–26.vii.1992, cloud forest adjacent to disturbed forest, C. Young, R. Davidson, S. Thompson, J. Rawlins (6♂, 8♀, CMNH); **La Vega**: Jarabacoá, 4000', ex vegetation, J. Doyen (1♂, prob., UCB); **San Juan**: Estrelleta, Rio Limpio, 650 m, 15.viii.1980, A. Norrbom (1♂, CMNH); **Santiago**: Cordillera Septentrional, Pico Diego de Ocampo, 1.1 km E. summit, 19.35.06N, 70.44.23M, 958 m, 31.v.2004, J. Rawlins, C. Young, C. Nunez, J. Fetzner (1♂, CMNH); **Santiago Rodriguez**: 7 km from Moncion, nr. Mao River, 23.x.1986, R. Greenfield (1?, BPBM); **Province unknown**: 20.ii.1978, S. A. Marshall (1♀, DEBU). **UNKNOWN**. Sanchez, xii.1915, ac. 4806 (1♂, 1♀, AMNH).

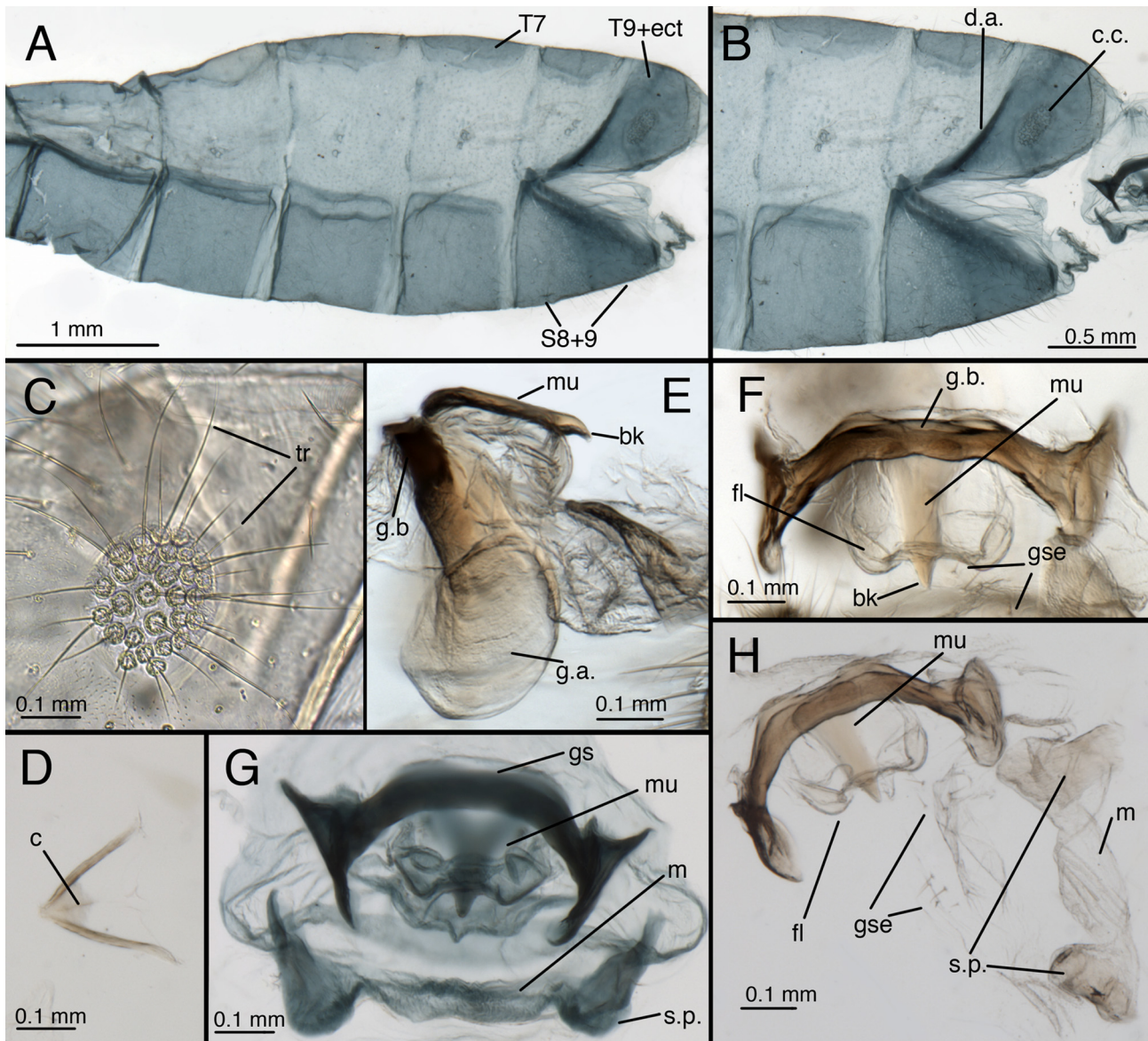


**FIGURE 15.** *Leucochrysa (L.) insularis*, wings, body, dorsal [Santiago, Cuba, male].

## Discussion

### 1. Are the larval features of *L. (L.) nigrilabris* and *L. (L.) insularis* consistent with those of other species in the subgenus *Leucochrysa (Leucochrysa)*?

Larvae of *L. (L.) nigrilabris* and *L. (L.) insularis* express all of the twelve features previously proposed to characterize the genus *Leucochrysa*, except two (# 6 and # 7 below, marked with asterisks). This list, which initially was derived from two *Leucochrysa (Leucochrysa)* species and nine *Leucochrysa (Nodita)* species (see Adams 1987, Tauber 2004, Mantoanelli *et al.* 2006, 2011, Tauber *et al.* 2011), now is generally supported by a broader diversity of *Leucochrysa (Leucochrysa)* species. We suspect that these two exceptions, especially # 6 are the result of reversals; thus, we temporarily retain the two features (# 6 and # 7) on the list of *Leucochrysa* characteristics until larvae from more species have been studied.

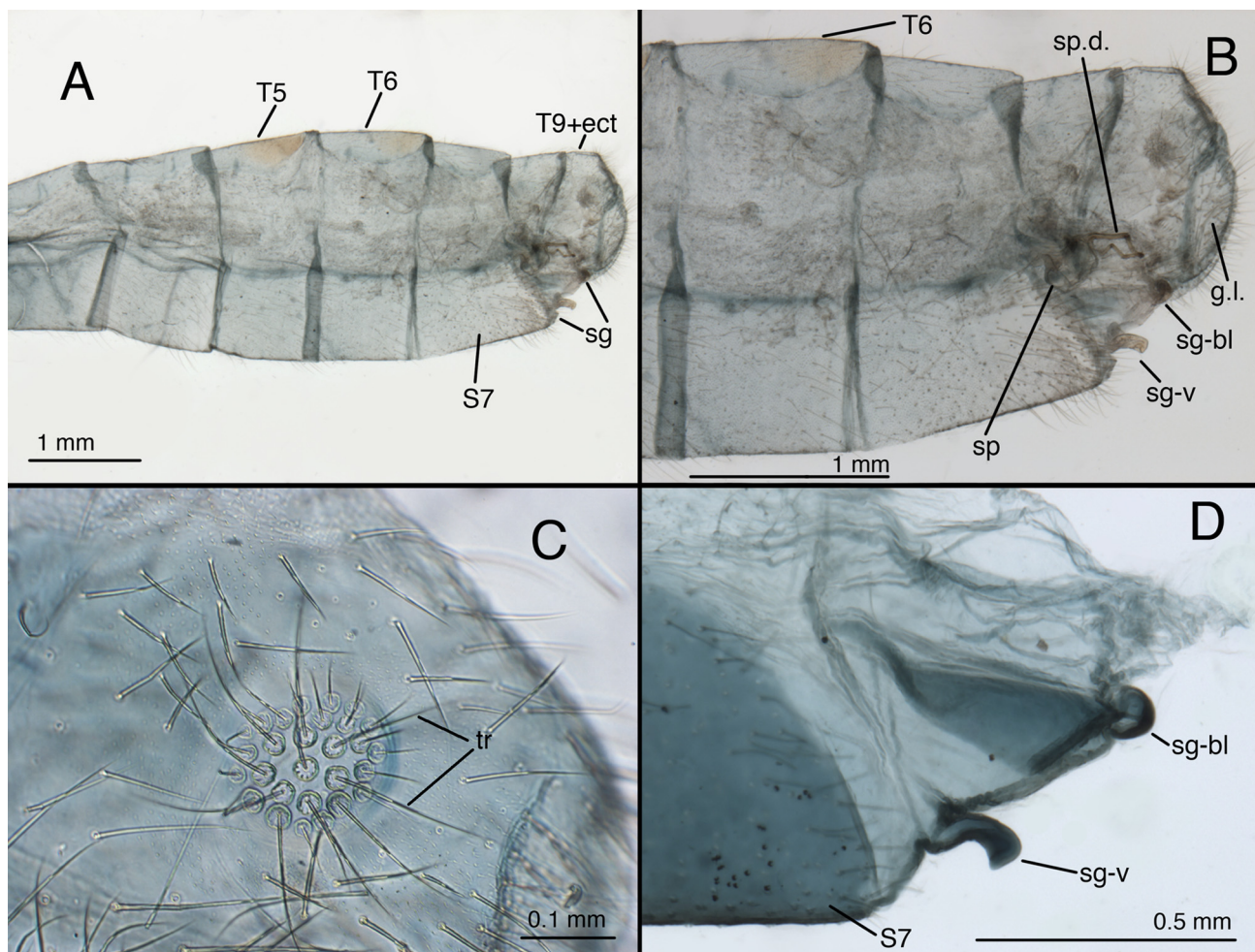


**FIGURE 16.** *Leucochrysa (L.) insularis*, male abdomen and genitalia. A. Abdomen, lateral; B. Terminal abdominal segments, lateral; C. Callus cerci; D. Hypandrium internum; E. Gonarcus, lateral; F. Gonarcus, dorsal; G. Gonarcus, dorsofrontal, with sclerotized plates and connecting semi-sclerotized membrane bearing gonocristae; H. Gonarcus, dorsal, with sclerotized plates and connecting semi-sclerotized membrane bearing gonocristae [note two patches of gonosetae on membrane below mediuncus] [A, B, G, Cuba; C-F, H, Dominican Republic]. *Abbreviations:* bk, beak-like tip of mediuncus; c, comes; c.c., callus cerci; d.a., dorsal apodeme of T9+ect; fl, mediuncal flange; gs, gonarcus; gse, gonosetae on small chalazae; g.a., gonarcus apodeme; g.b., gonarcus bridge; m, membranous connection between sclerotized plates, with gonocristae; mu, mediuncus (fused rods and beak); s.p., sclerotized plate on membrane above tip of S8+9; S8+9, fused eighth and ninth sternites; tr, trichobothria; T7, seventh tergite; T9+ect, fused ninth tergite and ectoproct.

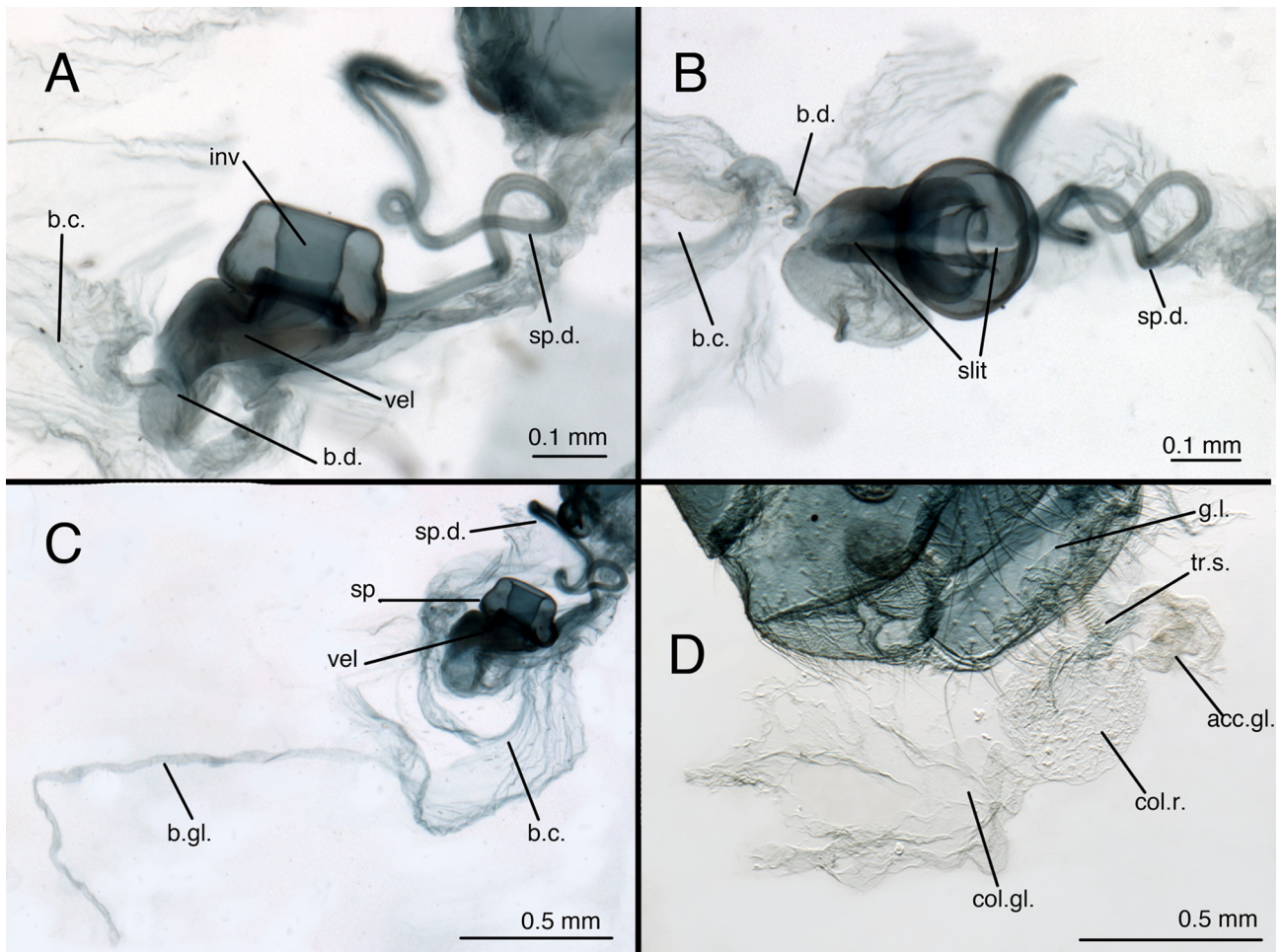
#### Larval characteristics of the genus *Leucochrysa*

- 1 Thoracic lateral tubercles long: prothoracic tubercles extending at least to mid-head, and meso- and metathoracic tubercles longer than half the width of the corresponding segment (all instars),
- 2 Thoracic tubercles with very long setae (all instars), extending in a fan-shape from the apical and lateral surfaces (L2, L3),
- 3 Anterior segments of the abdomen thicker than those of the thorax, giving the abdomen a humped appearance in lateral view (all instars),
- 4 Abdominal segments A7 to A10 small, curved ventrally, and partially telescoped into the anterior segment (all instars),

- 5 Terminal seta of the antenna at least half the length of the flagellum (all instars),
- 6 \*Prothorax with primary setae S1, S3, S4, and S5 present, S2 absent [all instars, except L2 and L3 of *L. (L.) nigrilabris* and *L. (L.) insularis*],
- 7 \*Mesonotum and metanotum each with two transverse rows of long, smooth, usually hooked setae arising from chalazae [all instars, except *L. (L.) varia*, *L. (L.) nigrilabris* and *L. (L.) insularis* (see Mantoanelli *et al.* 2006, descriptions above)],
- 8 Lateral tubercles on abdominal segments A2 and A3 papilliform, with long setae extending from the anterior, dorsal and apical surfaces (L2, L3),
- 9 Lateral tubercles on abdominal segments A4 to A7 slightly elongated, bearing long setae mainly on the apical surface (L2, L3),
- 10 Abdominal segments A1 to A5 each with a pair of laterodorsal tubercles, each tubercle with two long, smooth, hooked setae, separated by microseta [all instars, except microseta sometimes absent from L1: e.g. *Leucochrysa (Nodita) azevedoi* Navás (Mantoanelli *et al.* 2011)],
- 11 Abdominal segment A1 with a single row of smooth, hooked submedian setae, between the laterodorsal tubercles (all instars; L1: four setae in row; L2, L3: number of setae variable),
- 12 Abdominal segments A2 to A5 with two (L1) or three (L2, L3) rows of smooth, hooked submedian setae, the posterior row between the laterodorsal tubercles (L1: four setae in anterior row, two in posterior row, all between LDTs; L2, L3: number of setae variable).



**FIGURE 17.** *Leucochrysa (L.) insularis* female abdomen. A. Fourth to terminal segments, lateral; B. Sixth to terminal segments, lateral; C. Callus cerci; D. Subgenitale, lateral, with genitalia removed [A, B. Dominican Republic, mature specimens; C. Dominican Republic, slightly teneral specimen; D. Veracruz, Mexico, teneral specimen]. *Abbreviations:* g.l., gonapophysis lateralis; sg, subgenitale; sg-bl, bilobed, dorsal process of subgenitale; sg-v, protruding ventral process of subgenitale; sp, spermatheca; sp.d., spermathecal duct; S7, seventh sternite; tr, trichobothria; T5, T6, fifth and sixth tergites; T9+ect, fused ninth tergite and ectoproct.



**FIGURE 18.** *Leucochrysa (L.) insularis* female genitalia. A. Spermatheca, lateral; B. Spermatheca, dorsal; C. Dissected genitalia, bursa copulatrix (torn); D. Colleterial complex, lateral [all, Veracruz, Mexico]. *Abbreviations:* acc.gl., colleterial accessory gland; b.c., bursa copulatrix; b.d., bursal duct; b.gl., bursal gland; col.gl., colleterial gland; col. r., colleterial reservoir; g.l., gonapophysis lateralis; inv, spermathecal invagination; slit, dorsal slit in spermathecal vellum that opens to bursa copulatrix; sp, spermatheca; sp.d., spermathecal duct; tr.s., transverse sclerite; vel, velum.

#### Larval characteristics of the subgenus *Leucochrysa*

Only two larval features are known to differentiate the larvae of subgenus *Leucochrysa* from those in subgenus *Nodita*; both are derived from the spiracles (Mantoanelli *et al.* 2006, Tauber *et al.* 2011). For subgenus *Leucochrysa* the character states are: (i) spiracles borne on top of plump protuberances (swellings), especially on the mesothorax and A1, and (ii) spiracular openings surrounded by well-sclerotized rings that project substantially above the surface of the integument. As with the two species in the subgenus that were previously described in detail, *L. (L.) nigrilabris* and *L. (L.) insularis* larvae express the above attributes.

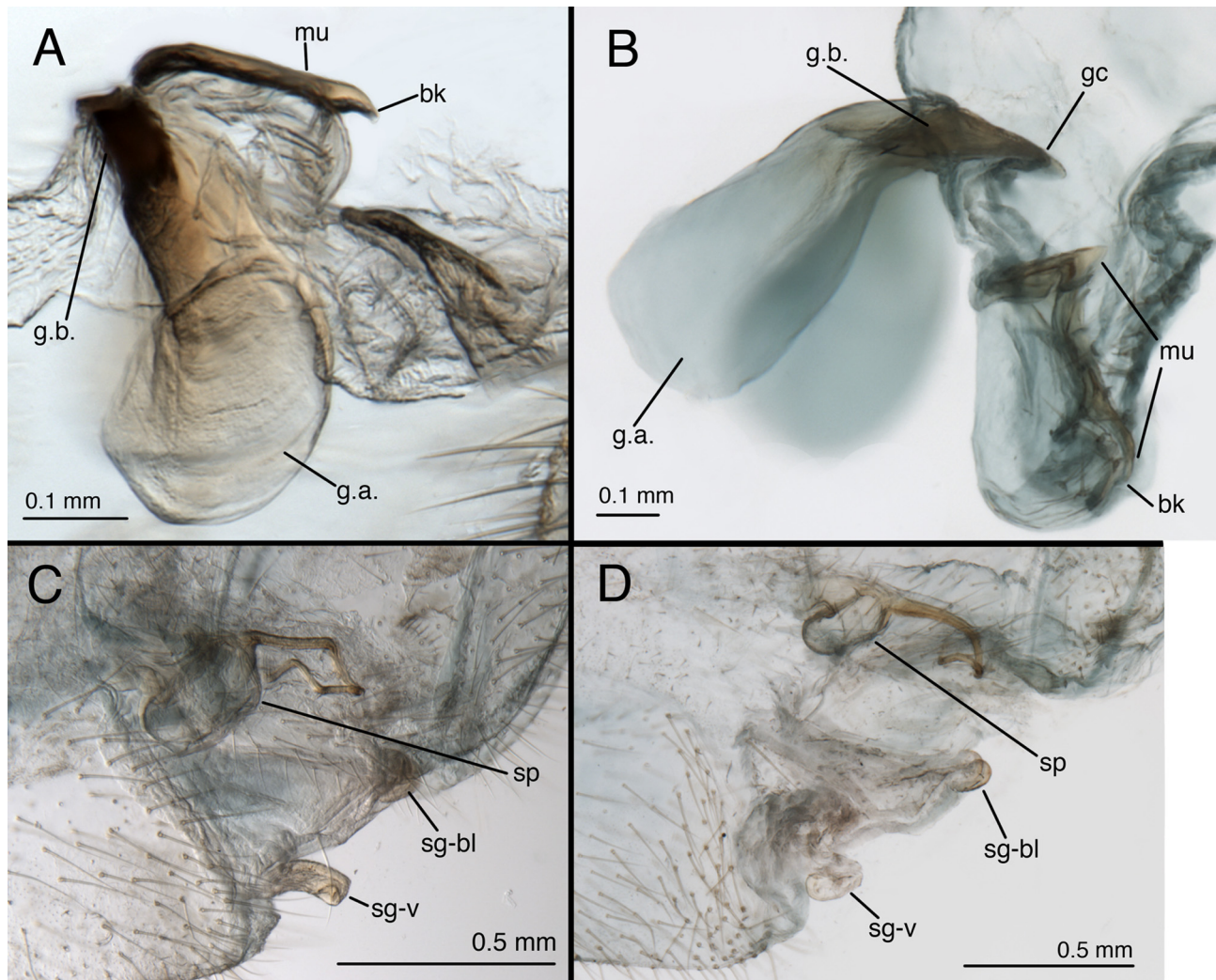
#### (2) Do adult and larval features support the synonymy and/or proposed close relationship between the two species?

A. The findings of this study do not support Tauber's (2004) suggestion that *L. (L.) nigrilabris* might be synonymous with *L. (L.) insularis*. Rather, they provide morphological evidence from both adults and larvae that clearly indicates the two species are distinct.

#### Differences between *L. (L.) nigrilabris* and *L. (L.) insularis*

*Male:* (i) The gonarcus of *L. (L.) nigrilabris*, but not *L. (L.) insularis*, has a pair of gonocornua (Compare Figs 19A and B; also Figs 4A–C, E and 16E–H). (ii) The gonosetae of *L. (L.) nigrilabris* are located on a stiff membrane above the mediuncus, whereas in *L. (L.) insularis* the gonosetae are on a loosely attached membrane below the

mediuncus (Figs 3B–E, 16H). (iii) The sclerotized genital plates are attached to the S9 in *L. (L.) nigrilabris*, whereas in *L. (L.) insularis* they are attached to each other, but not to S9, by a lightly sclerotized membranous connection bearing gonocristae (Figs 3B, F, 16G).

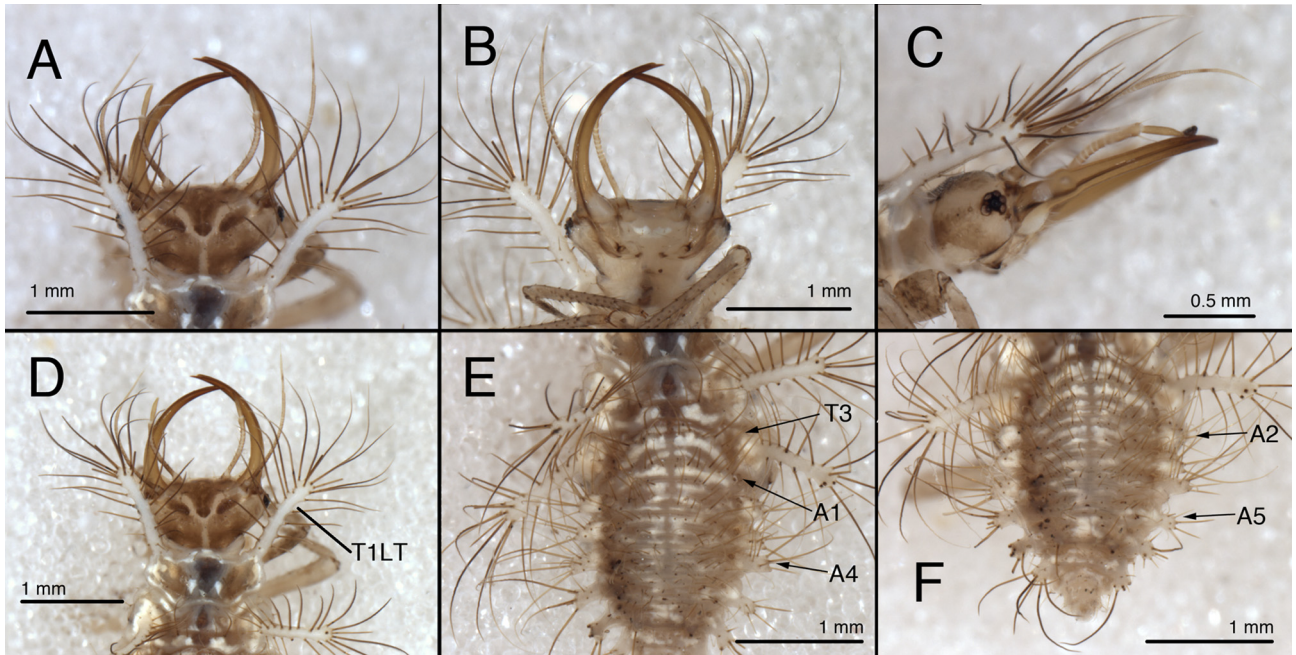


**FIGURE 19.** Species-specific genital characteristics of *Leucochrysa (L.) insularis* (left column) and *L. (L.) nigrilabris* (right column). A, B. Gonarcal complex; C, D. Subgenitale [A, C. Dominican Republic; B, D. Aragua, Venezuela]. *Abbreviations:* bk, beak-like tip of mediuncus; gc, gonocornu; g.a., gonarcal apodeme; g.b., gonarcal bridge; mu, mediuncus (fused rods and beak); sg-bl, bilobed, dorsal process of subgenitale; sg-v, protruding ventral process of subgenitale; sp, spermatheca.

*Female:* (i) Both species have subgenitale with two posterior processes (“lobe” of Tauber 2004), the ventral one is knob-like and withdrawn in *L. (L.) nigrilabris*, whereas in *L. (L.) insularis*, it is cylindrical and protruding posteriorly (Compare Figs 19C and D; also Figs 7B and 17A, B, D) (the dorsal process is bilobed and protruding in both species). (ii) The *L. (L.) nigrilabris* spermatheca has rounded lateral walls and a deep, narrow invagination (Figs 7B, C, 19D); in contrast, the *L. (L.) insularis* spermatheca has straight, steep lateral walls and a deep, broad invagination (Figs 18A, B, 19C). (iii). The *L. (L.) insularis* callus cerci is round as in *L. (L.) nigrilabris*, but its trichobothria are larger and fewer (Figs 7, 16, 17).

*Larvae:* *Leucochrysa (L.) nigrilabris* and *L. (L.) insularis* differ in their (i) genal markings (Figs 12G, 20C), (ii) the robustness of their primary setae, and (iii) the number of thoracic and abdominal setae (e.g., Table 1).

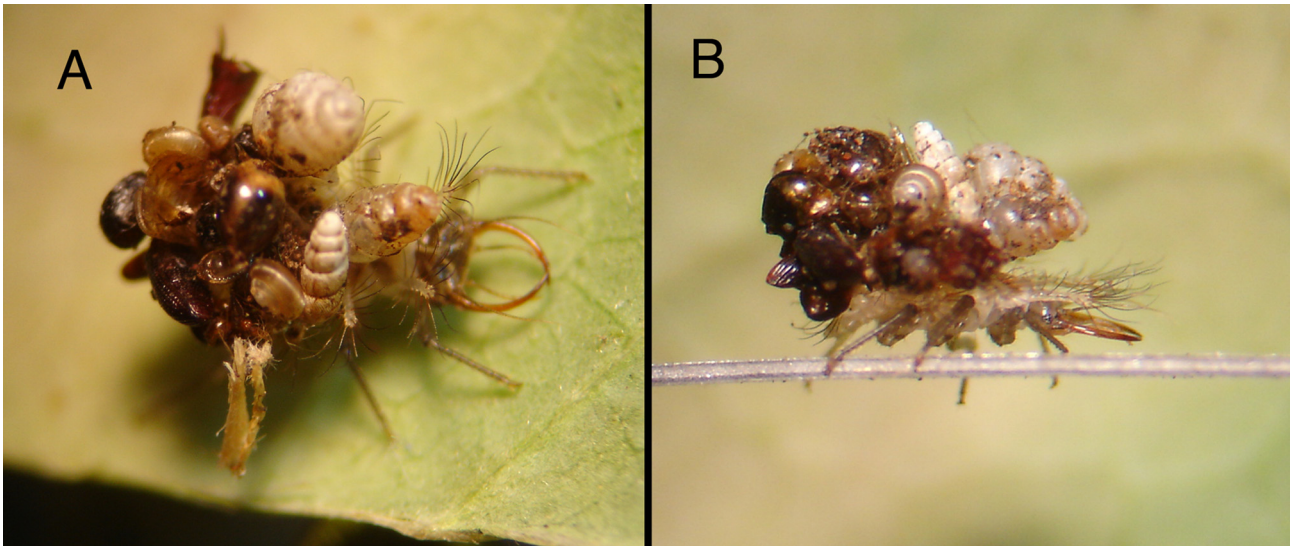




**FIGURE 20.** *Leucochrysa (L.) insularis* third instar. A. Head, dorsal; B. Head, ventral; C. Head, lateral; D. Head and prothorax; E. Mesothorax, metathorax, and abdominal segments A1–A5; F. Abdominal segments 1–10, dorsal [all, North Carolina, USA]. *Abbreviations:* Ax, abdominal segment number; T1LT, prothoracic lateral tubercle; T3, metathorax.



**FIGURE 21.** *Leucochrysa (L.) insularis* cluster of hatched eggs; stalk length ~1 cm [Honey Island Swamp, St. Tammany Parish, LA]. Photo by Mark S. Fox.



**FIGURE 22.** *Leucochrysa (L.) insularis* third instar with debris packet containing snails. A. Dorsal; B. Lateral. [Great Smoky Mountains National Park, Swain Co., NC]. Photo by Daniel C. Dourson.

**TABLE 1.** Comparisons of selected larval features among four *Leucochrysa (Leucochrysa)* species.

	<i>L. (L.) varia</i>	<i>L. (L.) nigrilabris</i>	<i>L. (L.) insularis</i>	<i>L. (L.) boxi</i>
<b>Third Instars</b>				
<b>Ratio</b>				
Mandible length : head width	1.1–1.2	1.2	1.1	1.4
TILT length : width	7.0–7.6	9.5–10.9	8.3	13.2–13.5
TILT length : mandible length	0.5–0.6	0.7	0.6	0.9
TILT length : prothoracic length	0.8	1.2–1.3	--	1.2
<b>Number of setae</b>				
Mesothorax, posterior row	6	11–14	4	56–60
Metathorax, posterior row	8	15–16	12	48
Dorsum, A1 row of SMS	9	10	10	5+18 (2 rows)
A2, posterior row of SMS	6–7	10	8	12
A3, posterior row of SMS	8	10	8	12
<b>Second Instars</b>				
<b>Number of setae</b>				
Mesothorax, posterior row	6	5	--	16–18
Metathorax, posterior row	8	11	--	16–18
Dorsum, A1 row of SMS	5	8	--	8–10 (1 row)
A2, posterior row of SMS	2–4	4	--	6–8
A3, posterior row of SMS	2–4	4	--	6–8

Note: The values are approximations, based on two to three sets of measurements per value for each species except *L. (L.) insularis* for which only one third instar (teneral) was available. The SMS lie between the laterodorsal tubercles and do not include the LDS.

B. Adult and larval morphology support the hypothesis that *L. (L.) nigrilabris* and *L. (L.) insularis* are very closely related.

Similarities between *L. (L.) nigrilabris* and *L. (L.) insularis*

*Adult coloration:* (i) Southern Caribbean populations of *L. (L.) insularis* are similar to those of *L. (L.) nigrilabris* in the depth of their coloration and body markings, as well as in the pattern of their markings, including,

in some specimens, the darkened surface of the labrum (compare Figs 1 and 14). (ii) Populations of both species exhibit a similar type of polymorphism (intrapopulation variation) in the coloration of the mesoscutellum; in both species, the sclerite can be entirely dark brown, tan or white [*L. (L.) nigrilabris*: Figs 1D–F; *L. (L.) insularis*: Figs 14A–C]. (iii) *L. (L.) nigrilabris* and *L. (L.) insularis* both exhibit large dark spots on the fifth and sixth abdominal tergites.

*Abdomen*: Both species have round callus cerci (Figs 3B, E, 5A, 6A–D, 16A, B, 17A–C); in many leucochrysin species they are oval-shaped.

*Male*: Some characteristics of the male genitalia that are shared by the two species appear to be unique among members of the subgenus. They are: (i) a narrow, elongate mediuncus that terminates in a relatively large, narrow, deeply curved hook (Figs 4B, E, 16E, F, H), (ii) gonosaccus with relatively robust gonosetae arising from chalazae (Figs 4B–E, 16F, H), and (iii) terminus of S9 with a pair of flat, sclerotized lobes. The lobes are well developed and attached to S9 in *L. (L.) nigrilabris* (Figs 3B, F); they are less developed and located on a partially sclerotized membranous fold in *L. (L.) insularis* (Figs 16G, H).

*Female*: Both species have (i) a simple, doughnut-shaped, invaginated spermatheca, and (ii) either a very small, simple bursal duct or none at all (Figs 7B–D, 18A, B, 19C, D). The spermatheca opens to the bursa copulatrix via a slit in the spermathecal velum (Figs 7D, 18B), and the bursal glands are elongate, tubular and unbranched (Fig. 7D, 18C). The above two features are not unique among females of the subgenus [e.g., the spermathecal characteristics occur in *Leucochrysa (L.) colombia* Banks (Adams 1977) and *L. (L.) boxi* (Tauber *et al.* 2011)]; nevertheless, they separate *L. (L.) nigrilabris* and *L. (L.) insularis* from the *Leucochrysa (Leucochrysa)* “*varia*-like” species, all of which have elongate, tubular, often coiled spermathecae, well developed bursal ducts, and bulbous bursal glands.

On the basis of the above shared, distinguishing male and female features, we consider that *L. (L.) nigrilabris* and *L. (L.) insularis* are very closely related to each other, but not to the “*varia*-like” species.

*Larvae*: *Leucochrysa (L.) nigrilabris* and *L. (L.) insularis* share some features not yet reported for other *Leucochrysa (Leucochrysa)* species (Table 1). Both have: (i) similar ratios of prothoracic lateral tubercle length : width (= 8.7–10.9, slightly longer than that of *L. (L.) varia*, but shorter than that of *L. (L.) boxi*), and (ii) S2 present on the prothorax of L2 and L3.

*Biology*: Both *L. (L.) nigrilabris* and *L. (L.) insularis* females lay their eggs in clusters at the ends of long, intertwined stalks (Fig. 21). This type of oviposition behavior has been reported for a few species in the chrysopine genera *Pseudomallada*, *Nineta*, and *Ungla* (Withycombe 1922, Principi 1940, 1956, Duelli 1984, Gepp 1988, Díaz-Aranda & Monserrat 1991, Tsukaguchi 1995, Freitas 2003), but *L. (L.) nigrilabris* and *L. (L.) insularis* have the only records for the Leucochrysinini.

It is noteworthy that *L. (L.) insularis* larvae are found in the leaf litter, and that they prey on small snails, whose shells they place and carry on their dorsa. We have not observed *L. (L.) nigrilabris* larvae in the field and thus do not know whether they resemble those of *L. (L.) insularis* in their habitat association, feeding habits, or trash packets.

### (3) Should the two species be aligned with the *L. (L.) varia*-like species?

Although *L. (L.) nigrilabris* and *L. (L.) insularis* adults share a number of external features with the *L. (L.) varia*-like” species, the results from our studies here and elsewhere (Tauber *et al.* 2013) do not provide support for a particularly close relationship among these taxa.

*Adults*: The most obvious shared adult characteristics of the three species include (i) a conspicuous polymorphism in mesothoracic markings, (ii) red to reddish brown scapes, (iii) vertex with red to reddish brown lateral marks, and (iv) dark shading around the distal Psm and Psc crossveins of the forewing (Figs 1, 2, 14, 15).

In contrast, the *L. (L.) nigrilabris* and *L. (L.) insularis* adults lack many other external features of the “*varia*-like” species (see Tauber *et al.* 2013); i.e., they do not have the (i) red coloration on the frons, gena and scapes or (ii) shading around the second m-cu<sub>2</sub> crossvein of the forewing that the “*varia*-like” species usually express. More importantly, their genital characteristics are distinct from those of the *varia*-like species. For example, in *L. (L.) nigrilabris* and *L. (L.) insularis* females, (iii) the spermatheca is simple, and it lacks a coiled, tubular bursal duct that typifies the “*varia*-like” species. In the males, (iv) the mediuncus is narrow and elongate, and it terminates in a slender, elongate and deeply curved mediuncal beak (c.f. Tauber *et al.* 2013). Thus, on the basis of adult features, it appears that the *L. (L.) nigrilabris* and *L. (L.) insularis* should not be grouped with the “*varia*-like” species.

*Larvae:* The situation is less clear for the larvae. Of the four *Leucochrysa* (*Leucochrysa*) species that have detailed larval descriptions, *L. (L.) nigrilabris*, *L. (L.) insularis*, and *L. (L.) varia* share a number of features that distinguish them from *L. (L.) boxi* (Mantoanelli *et al.* 2006, Tauber *et al.* 2011). For example, (i) their head markings, which are very similar, differ from those of *L. (L.) boxi*; (ii) they have similar ratios of mandible length : head width that are shorter than those of *L. (L.) boxi*, (iii) their mesothorax and metathorax have only one transverse row of hooked setae [not two rows as in *L. (L.) boxi*], and (iv) they have fewer setae overall than does *L. (L.) boxi* (Figs 12A, 21A, Table 1).

However, *L. (L.) nigrilabris* and *L. (L.) insularis* (L2, L3) differ markedly from *L. (L.) varia* in a number of other important traits: (i) their thoracic lateral tubercles are longer (relative to their width and relative to the length of the prothorax) (See Fig. 9, Table 1); (ii) the head markings, mandibles and setae are darker brown; (iii) the dorsal setae are larger, more robust, and, on some segments, more numerous (Table 1); and (iv) the posterior sections of the mesothorax and metathorax have more setae than those of *L. (L.) varia*.

The first instars of *L. (L.) nigrilabris*, *L. (L.) insularis*, and *L. (L.) varia* have very similar setal patterns; however, there are some important exceptions. For example, in *L. (L.) nigrilabris* and *L. (L.) insularis*, the prothoracic lateral tubercle (LT) and the abdominal LDTs lack a microseta between the two long setae (LS, LDS) on the tubercles, whereas in the *L. (L.) varia* first instars, those microsetae are present on both types of tubercles.

## Conclusion

On the basis of both adult and larval characters, it appears that *L. (L.) nigrilabris* and *L. (L.) insularis* are very closely related to each other. In turn, these two species express several adult (external) and larval features that are consistent with those of *L. (L.) varia*; these similarities may indicate a relationship between the two sets of species. However, the genitalia (male & female) of *L. (L.) nigrilabris* and *L. (L.) insularis* differ significantly from those of the *L. (L.) varia*-like species. Thus, at this time, we refrain from grouping the two sets of species together.

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