# A taxonomically significant polymorphism in Leucochrysa (Neuroptera: Chrysopidae): Nomenclature, larval and adult descriptions, and biological notes 

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#### Abstract

Leucochrysa (Leucochrysa) loretana Navás, 1935, a species described from Argentina, was discovered to have a geographically variable polymorphism, with two forms of adult coloration. One of the morphs (the "brown-spotted" morph) is indistiguishable from the widespread species Leucochrysa (Leucochrysa) longicornis (G. Gray in Cuvier, 1832) and the second morph (the "white-spotted" morph) is identical to another Argentinian species, Leucochrysa (Leucochrysa) boxi Navás, 1930. These observations generated a number of nomenclatural changes: (1) The oldest of the three names, $L$. (L.) longicornis (= Hemerobius longicornis), is a secondary homonym of a Linnaean species described in 1764 and therefore is unavailable for Gray's species. (2) Thus, by priority, $L$. (L.) boxi becomes the valid name for the polymorphic species. (3) Leucochrysa (L.) loretana becomes a synonym of $L$. (L.) boxi. (4) The above three names are stabilized by the designation of primary types for each of the species, and by other nomenclatural actions. Specifically, (a) a lectotype is designated for Hemerobius longicornis G. Gray and, as First Revisers, we selected the species name from among two that were published in the original description; (b) a lectotype is designated for Leucochrysa boxi Navás; and (c) a neotype is designated for Leucochrysa loretana Navás. Finally, the $L$. (L.) boxi adult is redescribed (both morphs, as well as the male and female genitalia); the larvae (all instars) are described; and aspects of the biology of the species (geographic variation in the polymorphism and a new record of ectoparasitism) are presented.


## Resumo

Descobriu-se que Leucochrysa (Leucochrysa) loretana Navás, 1935, espécie descrita da Argentina, apresenta polimorfismo geograficamente variável, com duas formas de coloração dos adultos. Um dos morfotipos ("mancha marrom") é indistinguível da espécie de ampla distribuição Leucochrysa (Leucochrysa) longicornis (G. Gray, em Cuvier, 1832) e o segundo morfotipo ("mancha branca") é idêntico à outra espécie argentina, Leucochrysa (Leucochrysa) boxi Navás, 1930. Essas observações e uma informação da literatura originaram uma série de mudanças nomenclaturais: (1) O nome mais antigo dos três, L. (L.) longicornis (= Hemerobius longicornis), é um homônimo secundário de uma espécie que Lineu descreveu em 1764, e, portanto, é indisponível para a espécie de Gray. (2) Assim, pela prioridade, L. (L.) boxi é o nome válido da espécie polimórfica. (3) Leucochrysa (L.) loretana torna-se sinônimo de L. (L.) boxi. (4) Os três nomes acima são estabilizados pela designação de tipos primários para cada uma das espécies e por outras ações nomenclaturais. Especificamente, (a) um lectótipo é designado para Hemerobius longicornis G. Gray e, como Primeiros Revisores, selecionamos o nome da espécie dentre os dois que foram publicados na descrição original; (b) um lectótipo é designado para Leucochrysa boxi Navás, e (c) um neótipo é designado para Leucochrysa loretana Navás. Finalmente, o adulto de L. (L.) boxi é redescrito (ambos os morfotipos, bem como a genitália masculina e feminina); as larvas (todos os instares) são descritas; e aspectos da biologia da espécie (variação geográfica no polimorfismo e um novo registro de ectoparasitismo) são apresentados.

Key words: Leucochrysinae, Leucochrysa (L.) boxi Navás, Leucochrysa (L.) loretana Navás, Leucochrysa (L.) longicornis (Gray), synonymy, comparative morphology, ectoparasitoid

## Introduction

The green lacewing genus Leucochrysa expresses considerable intraspecific variation in adult color and morphology; this variability has resulted in numerous synonymies and other taxonomic problems (Adams 1977, 1987; Tauber 2004; Mantoanelli et al. 2006; Tauber et al. 2008, 2011). The expression of the variability throughout the genus is itself variable and includes subtle, continuous developmental and individual variation within populations, geographic clines, and genetically based polymorphisms (Tauber 2004, Mantoanelli et al. 2006; Tauber et al. 2008, 2011). Here, we elucidate another genetically based polymorphism in the group and, as a result, we contracted three species names into one. The discovery of this polymorphism illustrates the taxonomic value of (1) rearing and characterizing offspring from individual females and (2) studying larval and biological characteristics, along with adult morphology.

The polymorphic species on which we focus-Leucochrysa (Leucochrysa) boxi Navás-is relatively common in forested areas of coastal Brazil and northern Argentina. Our rearings of this species led us to conclude that the adult color pattern is polymorphic, and that two other species [Leucochrysa (Leucochrysa) longicornis (Gray) and Leucochrysa (Leucochrysa) loretana Navás] are conspecific with L. (L.) boxi. Sorting out the polymorphism required a number of steps that we present. Specifically, we (a) clarify the nomenclature related to the polymorphic species, (b) identify the synonymies, (c) redescribe the adults, and (d) describe the larval stages. Finally, we (e) present biological notes from our collections and rearings that we hope will stimulate future studies on the species' polymorphism, larval biology, and ectoparasitism.

## Materials and Methods

To prepare our descriptions, we used both field-collected and laboratory-reared adult specimens; eggs and larval specimens were obtained from field-collected females. For our methods of rearing, preserving, preparing and measuring larval specimens, see Mantoanelli et al. (2011); for adult specimens see Tauber et al. (2008) and Tauber (2010).

We examined specimens from the following institutions: Natural History Museum (NHM, London), Museo de La Plata (MLPA, La Plata), Museo Argentino de Ciencias Naturales (MACN, Buenos Aires), Museum of Comparative Zoology (MCZ, Cambridge), California Academy of Sciences (CAS, San Francisco), Instituto Fundación Miguel Lillo (IFML, San Miguel de Tucumán), the Universidade Estadual do Norte Fluminense (UENF, Campos dos Goytacazes), and the Institut royal des Sciences naturelles de Belgique (IRSNB, Brussels; images). Adult specimens from our rearings are deposited in the insect collections at UENF, Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, and the Essig Entomological Museum, University of California, Berkeley. Larval specimens are in the research collections of MJT \& CAT (in Davis, CA), GSA (at UENF), and the collection at IFML.

## Leucochrysa (Leucochrysa) boxi Navás

Hemerobius longicornis G. Gray in Cuvier, 1832: 331, pl. 72, fig. 3 [original description, text as "Hemerobius longicornis", figure labeled "Hemerobius longicollis"]; Guérin-Méneville 1829-38: 389 [catalog listing, as "Hemerobius longicornis", no mention of "Hemerobius longicollis"].

When G. Gray proposed the name Hemerobius longicornis, it was preoccupied by an ascalaphid species described by Linnaeus (1764: 402) (also see Oswald 2007). Subsequently, the unavailability of G. Gray's name was not recognized, and the name continued to be in use for the chrysopid, as follows:

Chrysopa longicornis, Schneider 1851: 156, tab. 59 [first combination in Chrysopa, redescription, text as "Chrysopa longicornis", illustration as "Chrysopa longicollis"; no selection of correct spelling]; Walker 1853: 270 [catalog listing, brief redescription, as Chrysopa longicollis; reference to "Hemerobius longicollis, G. R. Gray..."; no mention of species name "longicornis"].

Allochrysa longicornis, Navás 1912-13: 22 [first combination in Allochrysa, comment on Schneider's (1851) use of the names "longicornis" and "longicollis", erroneous record from Guatemala] (see "Known Distribution", below).

Leucochrysa longicornis Navás 1929: 863 [first combination in Leucochrysa (as longicollis), records from Brazil: Santa Cruz (Rio Grande do Sul) and Colonia Hansa (misspelled as "Hausa"), then a district of Joinville (now a city, Corupá) (Santa Catarina) (all specimens in the museum at Hamburg, destroyed)]; Navás 1930: 128 [notation of similarity with Leucochrysa boxi; notation of Schneider's, but not Gray's use of two spellings for the species name (longicornis in the text and longicollis on the illustration)]; Navás 1932: 57 [record from Espírito Santo, Brazil, specimen in the Natural History Museum Berlin-Dahlem]; Penny 1977: 23 [species list].

Leucochrysa (Leucochrysa) longicornis, Brooks and Barnard 1990: 276 [first combination in Leucochrysa (subgenus Leucochrysa), species list]; Oswald 2007 [catalog listing]. Not Leucochrysa longicornis Walker of Banks 1907: 26, Adams 1977: 100.

Type material: G. Gray did not mention a type specimen or type locality for H. longicornis, and neither did Guérin-Méneville nor Schneider (see above). Because G. Gray was Assistant Keeper of the Zoology Branch of the (now) Natural History Museum, London, when he prepared his description for Cuvier's Animal Kingdom, it is likely that, if a type had been designated, it would have been deposited in the collection in London. However, McLachlan (1868: 271) did not report Hemerobius longicornis, Hemerobius longicollis, or Chrysopa longicornis from the collection. Our search of the collection in 2010 did not yield a specimen that showed any clear indication that Gray had seen it.

At the NHM there are eight chrysopid specimens categorized as " $L$. longicornis", including seven in the McLachlan collection (from Brazil and Peru). The eighth is a Leucochrysa (Leucochrysa) specimen from Panama that Navás identified incorrectly (see "Known Distribution", below). One of the L. (L.) boxi specimens, the one from Rio de Janeiro, bears a hand-written label reading: "longicollis Gray"; none of the others bear identification labels.

In addition, a Schneider specimen is in the Institut royal des Sciences naturelles de Belgique, Brussels; it bears labels that read as follows:(1) "B--" [writing not clear]; (2) "Latr" [light orange]; (3) "164" [light green]; (4) "Collection / Ede Sélys-Longchamps"; (5) "31"; (6) "C. longicollis Gray Schn.*"; (7) "LECTOTYPE / Hemerobius longicornis / G. Gray 1832, desig. / C. A. Tauber, 2011" [red]. It is generally considered that Schneider's specimens that are marked with an asterisk are type specimens. Thus, given that the original description does not indicate how many specimens G. Gray examined, to promote taxonomic stability we designate this specimen as the lectotype. This specimen is very delicate and the abdomen is damaged; it could not be sent via mail, and we did not determine the sex. Images of the specimen and its labels are on the project page at the Morphobank website: http://www.morphobank.org/index.php?g=search\&s=browse\&ss=overview\&project id=505

Leucochrysa boxi Navás, 1930: 127 [original description]. Type: MACN \#5639; Lectotype, male examined; "Argentina: Tucumán, 29.VII.1929. H. E. Box (Coll. Bruch)"; Stange 1967: 39 [catalog listing, type location, as $L$. boxii]; Penny 1977: 22 [species list]; González Olazo 1996: 382 [catalog listing, type location, as L. boxii].

Leucochrysa (Leucochrysa) boxi, Brooks and Barnard 1990: 276 [first combination in Leucochrysa (subgenus Leucochrysa), species list]; Freitas and Penny 2001:281, fig. 41 [redescription, illustrations]; Oswald 2007 [catalog listing].

Type material: No L. boxi types are reported from the Muséum national d'Histoire naturelle, Paris (Legrand et al. 2008) or from the Navás collection in the Museo de Ciencias Naturales de Barcelona (MCNB) (Monserrat 1985: 241), and none were found in the NHM, London. Navás (1930) did not mention how many specimens he used in preparing his description of $L$. boxi. Thus, although the specimen in the MACN, a male, is probably the sole type, it is designated here as the lectotype. Its labels read: (1) "TUCUMAN / 29.VII.1927"; (2) "H. E. Box / Collector"; (3) "Leucochrysa Boxi ô Nav. / P. Navás S.J. det." [Navás label, Navás handwriting]; (4) "Leucochrysa Boxi Nav." [white, black border]; (5) "HOLOTYPUS" [red, black border]; (6) "Genit. Prep. por / P. Adams 1985"; (7) "LECTOTYPE / Leucochrysa boxi / Navás 1930; desig. / C. A. Tauber 2011" [red]. Images are on the project page at the Morphobank website: http://www.morphobank.org/index.php?g=search\&s=browse\&ss=overview\&project id=505

Leucochrysa loretana Navás 1935: 365, fig. 60 [original description, figure caption with the genus name misspelled as "Lencochrysa" in some versions of the publication]. Type: Holotype, "República Argentina: 'Est. Exp. Loreto (Misiones-Arg.), Dr. A. A. Oglobin, 12-IX-1934. Citrus"; Stange 1967: 39 [catalog listing, type location]; Penny 1977: 23 [species list]; González Olazo 1996: 382 [catalog listing, type location]; Brooks and Barnard 1990: 276 [first combination in Leucochrysa (subgenus Leucochrysa), species list]; Oswald 2007 [catalog listing]. New Synonymy.

Type material: In his original description of $L$. loretana, Navás explicitly mentioned having one specimen that was collected by Dr. Oglobin and sent to him by Dr. Bruch; his description provides collection data that apparently was from the labels associated with this specimen; they are in quotation marks. Navás also stated that this specimen, which would be considered the holotype, was spread and attached to a cardboard. No such specimen currently exists in the Navás collection in Barcelona (Monserrat 1985: 240); thus, we assume that Navás' name-bearing type is missing.

However, there are two specimens in the MLPA that are from the type locality and that were collected by Oglobin; both of the specimens carry "Paratypus" labels, probably in Bruch's hand-writing [MLPA \#3404]. We suspect that Dr. Bruch provided Navás with a single specimen (which served as the holotype) and that he retained two specimens in his personal collection that he considered paratypes. Whether Navás actually saw these two specimens and considered them to be paratypes, is not known.

Given the absence of Navás' holotype and the presence of the polymorphism, to promote taxonomic stability, we designate as a neotype one of Bruch's specimens in the MLPA. We chose the specimen, a female, that P. A. Adams had labelled in 1985 as the one he intended to designate as the lectotype, but never published. Its labels read: (1) "Est. Exp. Loreto / (Misiones Arg.) / Dr. A. A. Oglobin"; (2) "Leucochrysa / loretana / Paratypus - Nav. / C. BRUCH DETERM." [white, black border]; (3) "Paratypus" [green]; (4) "3404"; (5) "Leucochrysa / loretana / ô Navás / LECTOTYPE / Prep/det Adams '85"; (6) "NEOTYPE / Leucochrysa loretana / Navás 1935; desig. / C. A. Tauber 2011" [red]. Note: Adams' label stating that the specimen is a male is in error; it is a female.

The second specimen, with the terminus of the abdomen missing, has labels that read: (1) "Loreto, Misiones / Rep. Argentina / Dr. A. A. Ogloblin [misspelling of Oglobin]"; (2) "Paratypus" [green]; (3) "Leucochrysa / loretana / Paratypus -- Nav. / C. BRUCH DETERM."; (4) "3404". Images are on the project page at the Morphobank website: http://www.morphobank.org/index.php?g=search\&s=browse\&ss=overview\&project id=505

Actions and Justification Our goal in this paper is to stabilize the nomenclature pertaining to the species; in doing so, we faced several issues:

Two names and publication dates. In his original description of $H$. longicornis, which was published in Cuvier's "Animal Kingdom", G. Gray used two names to refer to this species (H. longicornis and H. longicollis). Because Cuvier's "Animal Kingdom" was published over a broad span of years, it was necessary to determine the publication dates for each of the names: longicornis which occurs on page 331 in the text of Volume 15 (Part 2 of Insecta), and longicollis which occurs on Plate 72 of the same volume. According to Cowan (1969), the most recent published work concerning the dates of publication for the Griffith edition of Cuvier's "Animal Kingdom", the plate in question was probably included in the bound publication, and the part of the volume containing Gray's brief description and figure probably were issued simultaneously around June 1832. Thus, for nomenclatural purposes, the names in the text and on the figure are assumed to have the same publication date, and thus both are considered to be available.

First Reviser action. Given the above, it was necessary to determine whether a previous author had taken a valid First Reviser action in choosing between longicornis and longicollis. Our determination is that such an action has not been taken previously. None of the early authors who dealt with the species (see above: Guérin-Méneville, Schneider, Walker, Navás) addressed the issue of Gray's use of two names [Navás (1930: 128) mentioned Schneider's use of the two names, but did not deal with the problem caused by Gray's error.]. Thus both names continued to be available. To resolve the issue and stabilize the nomenclature surrounding this species, we are acting as First Revisers here; we have chosen Hemerobius longicornis G. Gray in Cuvier as the name for Gray's species; $H$. longicollis is thus considered a misspelling.

Selection of name. Our reasons for choosing longicornis rather than longicollis as the available name are twofold. First, retention of longicornis conforms with common usage in recent literature (see references above). Second, this action restricts the resulting nomenclatural changes to a single species, and thus causes the least disruption of currently accepted nomenclature. If Hemerobius longicollis G. Gray were chosen, the action would necessitate the proposal of a replacement name for Lomamyia longicollis (Walker, 1853) (a berothid that has no junior synonyms). By choosing $H$. longicornis, which is a preoccupied name, only the chrysopid in question would undergo a name change.

Justification for synonymizations. Navás (1930) noted that $L$. boxi resembled $L$. longicornis, but he also presented some compelling reasons for recognizing the two as separate species. His specimens of $L$. boxi had large white spots on the mesothorax and metathorax; he considered this variation in markings to represent species-level
differences. Later, Freitas and Penny (2001) also retained the two species based on differences in pronotal markings and wing venation. Initially, we agreed with the above authors, until we (a) examined the types of the two species side-by-side, (b) studied the genitalia of both color-forms, and (c) reared offspring of both color-forms from individual field-collected females. It then became apparent that the color forms belong to a single polymorphic species, with Leucochrysa (L.) boxi Navás as its valid name.

Navás (1935) did not mention that L. loretana resembled either L. longicornis or L. boxi. However, as a result of our rearings and examination of the types in the MLPA, it was clear that this species should be synonymized with $L$. boxi. The specimens that we collected in the field and reared from field-collected females are consistent in external coloration, morphology and female genitalia with those of $L$. (L.) boxi (see images on http://www.morphobank.org/index.php?g=search\&s=browse\&ss=overview\&project id=505.

Diagnosis (adults) Externally, L. (L.) boxi adults resemble those of the closely related species, Leucochrysa (L.) magnifica (Banks). Both species have similar body size, wing venation, diffuse cloudy streak across the posterolateral section of the wings, and large, dark brown to black markings on the pterostigma of the fore and hind wings. They also share an extended series of inner gradate veins that parallels the pseudomedius, a feature that Freitas and Penny (2001) considered to be characteristic of $L$. (L.) boxi. The "white-spotted" morph of $L$. (L.) boxi is remarkably similar to $L$. (L.) magnifica because the mesal sections of the mesothoracic prescutum and scutellum are pure white, and the metanotum has white markings. [Note: these white markings are absent from the "brown-spotted" morph of $L$. (L.) boxi.]

The two species can be differentiated by their head and prothoracic markings, the shape of the scape, and their terminalia [Fig. 1 here and images on the MCZ Type Database online]. In $L$. (L.) boxi adults, the vertex is green and sometimes has small brown marks (Figs 1A-C); whereas in L. (L.) magnifica, the vertex is white with large red marks lateral to the eyes (Fig. 1D). The L. (L.) boxi scape is elongate, and it has a reddish brown stripe that runs the full length of the lateral margin. In contrast, the $L$. (L.) magnifica scape is swollen, and it lacks a lateral stripe, but it has a dark, mesal spot. In $L$. (L.) boxi males, the terminus of the final abdominal sternite is laterally constricted and appears apically up-turned in lateral view; in $L$. (L.) magnifica, the abdominal tip is blunt and not up-turned. The gonarcus and gonocornua of the two species also differ in shape. Females of $L$. (L.) boxi are distinguished by their small genitalia, that do not extend proximally much beyond the posterior margin of segment 7 , a relatively large, divided subgenitale with two ventral projections, and a compact, funnel-shaped spermatheca with a Ushaped, mesal bend.

Description (adults). [Measurements: head, thorax $(n=9)$, abdomen ( $n=7$ males; $n=6$ females), wings $(n=5)$ ]. Head: 1.8-2.2 mm wide (including eyes); ratio of head width to eye width $=1.6-2.2: 1$. Vertex raised, with slightly rough, pitted surface, prominent, rounded posterior fold, surface with small setae. Antenna 31.7-35.8 mm long (1.3-1.5 times length of forewing); scape longer than broad, ( $0.44-0.57 \mathrm{~mm}$ long, $0.36-0.41 \mathrm{~mm}$ wide); lateral margin of scapes fairly straight, mesal margin straight basally, curved outward distally; proximal flagellomeres short (segments $1,2,3$ : length $=0.8-1.3$ times width), with irregularly placed setae; middle and distal segments becoming longer (segments 9-11: length $=1.4-1.8$ times width; distal segments, midlength on antenna: length $=$ $2.5-2.8$ times width) with four concentric rings of setae. Distance between scapes $0.07-0.11 \mathrm{~mm}$; distance between tentorial pits $0.58-0.69 \mathrm{~mm}$; length of frons (midway between scapes-midway between tentorial pits) 0.49-0.64 mm . Frons relatively flat mesally, with shallow, scalloped fold below toruli; surface smooth to slightly textured, with short setae. Clypeal margins straight; surface slightly textured, not horizontally striated. Labrum with distal margin indented mesally; dorsal surface smooth, rounded, setose distally. Ratio of genal length to distance between tentorial pits $=0.39-0.45: 1$.

Head coloration (Figs 1A-C): Antennae: scape creamy white with diffuse reddish brown lateral stripe extending full length of scape, but not onto vertex; pedicel creamy with reddish brown, lateral stripe; flagellum cream with thin, black setae, basal antennomeres with dark brown to black mark ventrolaterally, fading on antennomeres $\sim 11-22$; marks forming prominent dark ventrolateral stripe. Vertex, toruli bright green, sometimes speckled with small brown spots; area lateral to eyes creamy, sometimes with light tinge of rose. Frons, clypeus, frontal torulus white, sometimes with tinge of green near antennae, usually unmarked, sometimes with small brown stripe above gena, rosy spot in middle of frons. Labrum cream; gena white, usually unmarked, sometimes with reddish brown or brown stripe immediately below tentorial pit or fully dark brown. Maxilla, maxillary palpi, labium, labial palpi white to cream, sometimes with brown marks on terminal segment.


FIGURE 1. Head and thorax, dorsal. A. Leucochrysa (L.) boxi "brown-spotted" morph (Tucumán, Argentina); B. L. (L.) boxi "white-spotted" morph (Tucumán, Argentina) ; C. L. (L.) boxi, "brown-spotted" morph (Babilônia, Campos dos Goytacazes, RJ, Brazil), specimen slightly faded; D. For comparison, Leucochrysa (L.) magnifica (Terras Frias, Santa Maria Madalena, RJ, Brazil). Scale applies to all images.

Thorax (Figs 1A-C): Cervix small, largely withdrawn below prothorax, light green, with pair of small reddish brown lateral marks. Prothorax (sclerotized region) $1.3-2.0 \mathrm{~mm}$ long; $1.4-1.9 \mathrm{~mm}$ wide; ratio of length to width $=$ 0.93-1.04: 1; setae thin, long, light golden; pronotum bright green, with pair of elongate, red to reddish brown marks anterolaterally, one to two pairs of small (sometimes diffuse) brown marks submesally, reddish brown mesal mark of variable size on posterior margin. Mesonotum variable; "brown-spotted" morph: prescutum brown mesally, light green to brownish green laterally, scutum light green with brownish mesal bridge, scutellum dark brown, with light green to brownish green laterally; "white-spotted" morph: prescutum white mesally, dark brown to brownish green laterally, scutum light green, with scattered brown marks submesally, scutellum white mesally, dark brown laterally. Metanotum variable; "brown-spotted" morph: mostly brown throughout; "white-spotted" morph: light green laterally, dark brown submesally, white and yellow hour-glass shaped spot mesally. Legs white to cream colored, unmarked, with golden setae; coxae, femora cream to white; tibiae light green, tarsi golden. Tarsal claws broadly extended, elongate, narrow, with basal cleft; quadrate base, with broad spur mesally.

Wings (Fig. 2): Forewing 21.9-27.3 mm long, 7.4-9.5 mm wide (at widest point); ratio of length : maximum width $=2.81-2.96: 1$. Costal area moderately broad; tallest costal cell (\#10-13) $2.0-2.2 \mathrm{~mm}$ tall, $3.2-4.3$ times width, $0.26-0.29$ times width of wing (midwing). First intramedian cell usually quadrangular, occasionally triangular, 0.9-1.6 times width of third median cell. First radial crossvein distal to origin of radial sector (Rs); radial area (between Radius and Rs) with single row of 23-29 closed cells; tallest cell (\#10-15) 2.2-3.2 times taller than wide. No crassate veins; 5-7 b cells (= cells beneath Rs, not including an inner gradate vein). Two series of gradate veins; 17-20 inner gradates, 10-14 outer gradates. Thirteen to 14 b cells (cells beneath pseudomedia after second intramedian cell). Three intracubital cells (two closed). Membrane clear; stigma opaque, usually with large dark brown mark. Veins mostly green; costal veinlets with black tips; outer gradates, posterior sections of distal b' cells mostly black; posterodistal region of wing with dark brown to black streak from midposterior margin through distal b' cells and outer gradate veins, almost to distal margin of wing.


FIGURE 2. Leucochrysa (L.) boxi forewing (upper), hindwing (lower), Tucumán, Argentina ("white-spotted" morph).

Hindwing 17.8-24.5 mm long, 5.8-7.5 mm wide. Two series of gradate veins; 11-16 inner, 8-10 outer; 19-25 radial cells (counted from origin of Radius, not false origin). Five to six b cells (including small b1 cell); ten to thirteen $\mathrm{b}^{\prime}$ cells beyond second intramedian cell; two intracubital cells (one closed). Membrane clear, with dark brown markings to black streak from midposterior margin through base of forked terminal veinlets, behind distal b' cells; stigma pronounced, marked with brown basally. Veins mostly light green; tips of costal veinlets dark brown to black.

Abdomen (Fig. 3): Distal segments (beyond A4) not largely expanded; height of pleural region smaller than height of sternites. Sternites, tergites with microsetae moderately dense; pleural region with very dense microsetae. Male: S6 approx. 1.2 times longer than tall, S7 approx. 1.0-1.1 times longer than tall (lateral view); female: S6 approx 1.3-1.6 times longer than tall, S7 approx. 1.7 times longer than tall. Tergites narrow, roughly rectangular, with shorter setae and longer microsetae than on sternites. Spiracles oval externally; atria not enlarged. Coloration: often discolored. Tergites green, with small reddish brown markings at base of T 1 , T 2 , larger ones on $\mathrm{T} 3-\mathrm{T} 7$; sternites white to amber, without markings; T9+ectoproct white, callus cerci white; setae, trichobothria golden.


FIGURE 3. Leucochrysa (L.) boxi terminal segments of abdomen (A6-A9), lateral, Terras Frias, Santa Maria Madalena, RJ, Brazil. Upper: Female. Lower: Male. Scale applies to both figures. Abbreviations: c.c., callus cercus; d.a., dorsal apodeme; g.l., gonapophysis lateralis; sg, subgenitale; sp+b, spermathecal-bursal complex; S 7 , seventh sternite; $\mathrm{S} 8+9$, fused sternites eight and nine; T8, eighth tergite; T9+ect, fused ninth tergite and ectoproct; v.a., ventral apodeme.

Male (Figs 3-8): Callus cerci rectangular with curved edges, $0.23-0.27 \mathrm{~mm}$ length, $0.17-0.21 \mathrm{~mm}$ width, with 29-43 trichobothria of various lengths. Sternites 3-8 (not S1 or S2) with microtholi. T9+ectoproct truncate distally, broadly fused mesally, midline without deep cleft, setae robust throughout, shorter proximally than distally; ventral section of T9+ectoproct extending broadly below full length of T8; proximal section well sclerotized, with apodeme substantial, but not thick, extending posteroventrally beyond callus cercus, with two branches; dorsal branch extending around anterior margin of callus cercus, ventral branch extending ventrally below callus cercus. S8+9 fused, without suture, but with clear intersegmental demarcation; S9 without microtholi; length of S8 approximately one-half ( $0.44-0.55 x$ ) length of $\mathrm{S} 8+9$; S8+9 (lateral view) with proximal margin straight, rounded dorsally, acute ventrally; tip elongate distally, with rounded, up-turned, terminal knob. Setae on S9 slightly longer than those on S5-S8; terminus of S9 with field of robust, well-sclerotized gonocristae that may or may not extend along mar-
gin of S9. Upper margin of S9, near midregion, sometimes with separate patch of gonosetae (see "Variation" below). Subanal region large, perhaps slightly sclerotized, with patch of elongate setae ventrally, near connection to gonarcus. Gonarcal complex connected to terminus of ectoproct by moderately long, clear, smooth membrane that attaches to top of gonarcus, behind base of gonocornua, membrane extending around sides of gonarcus, becoming confluent with distal base of gonosaccus, holding hypandrium internum. Gonarcus robust, narrowly arcuate, with lateral apodemes extending perpendicularly from gonarcal bridge; gonarcal apodemes enlarged distally. Gonocornua broadly attached to top of gonarcal bridge, lateral to mediuncus, extending upward, outward, away from mediuncus, broad, rounded basally, with inner, outer margins curving inward, tapering distally to blunt rounded tip. Mediuncus broad, dome-like; basal half with smooth, lightly sclerotized surface, well sclerotized mesal arm; distal half (arcessus of Freitas \& Penny 2001) with mesal arm becoming heavy (triangular in lateral view), projecting downward, with elongate, sharp beak at tip, pair of inflated lateral lobes on either side of beak; tops of lobes with rough-textured crest. Gonosaccus below mediuncus, smooth to folded, without gonosetae. Entoprocessus, tignum, gonapsis, pseudopenis, spinellae, gonocristae absent. Hypandrium internum arrow-shaped, slender arms with acute apex, approx. 2/3rd length of shaft (including comes), sometimes lightly sclerotized; comes extending beyond arms, bulging basally, tapering distally, with upward bend in center (lateral view).


FIGURE 4. Terminal segments (A8+9) of males from four populations of Leucochrysa (L.) boxi . Left: Tucumán, Argentina; A. "brown-spotted" morph; B. "white-spotted" morph. Right: C. Terras Frias, Santa Maria Madalena, RJ, Brazil ("brown-spotted" morph); D. Babilônia, Campos dos Goytacazes, RJ, Brazil ("brown-spotted" morph). Note the elongate S9 and the raised area with gonocristae (arrow) on the specimens from Tucumán. Abbreviation: S9, ninth sternite. Scale applies to all images.


FIGURE 5. Tip of male Leucochrysa (L.) boxi abdomen, lateral. A. Tucumán, Argentina ("brown-spotted" morph); B. Terras Frias, Santa Maria Madalena, RJ, Brazil ("brown-spotted" morph). Note (arrows): (A) the raised area with gonocristae anterior to the tip of the segment and the small patch of terminal gonocristae on the specimen from Tucumán; (B) the absence of the spiney raised area and the presence of a larger terminal patch of gonocristae on the specimen from Terras Frias. Scale applies to both images.


FIGURE 6. Gonarcus of male Leucochrysa (L.) boxi (Terras Frias, Santa Maria Madalena, RJ, Brazil). A. Lateral; B. dorsal. Abbreviations: fl, flange of mediuncus; gc, gonocornu; g.a., gonarcal apodeme; memb, membranous attachment to tergite nine; mu , mediuncus.

Female (Figs 3, 9-13): Callus cerci approximately round, $0.25-0.27 \mathrm{~mm}$ maximum diameter, with $36-45$ trichobothria of mixed length. Tergite 8 roughly quadrate (lateral view) with rounded corners, similar in depth to T6. Tergite $9+$ ectoproct elongate; posterior margin: dorsal half straight, almost perpendicular to dorsal margin of tergite, ventral half angled posteriorly, straight; ventral margin slightly convex, extending approximately one-third distance below gonapophyses laterales. Sternite 7 without transverse weakness, dorsal margin straight, not tapering distally; terminus unmodified, with terminal (posteroventral) setae slightly more dense, robust, and longer than other setae. Gonapophysis lateralis angled dorsally, rounded distally, ventrally, $\sim 0.54-0.61$ height of T9+ect; inner membranous surface not expandable, with $\sim$ two vertical rows of short setae. Colleterial gland smooth-walled, delicate, with elongate, ribbon-like accessory glands distally, extending into S7, with fluted, globate reservoir attached via a narrow duct immediately before transverse sclerification. Transverse sclerification very broadly V-shaped, platformlike, with straight lateral margins, elongate longitudinal striations. Bursa copulatrix delicate, folded membrane, extending anteriorly over spermatheca, approximately $3 / 4$ length of T9+ectoproct; pair of delicate, elongate, unbranched, tubular bursal glands, connected to dorsolateral surface. Spermatheca funnel-like, bent, tapering abruptly from mouth ( $0.24-0.25 \mathrm{~mm}$ diameter at mouth) to bend at midsection ( $0.10-0.11 \mathrm{~mm}$ diameter at midsec-


FIGURE 7. Mediuncus and gonocornua (frontal view) of male Leucochrysa (L.) boxi (Tucumán, Argentina, "brown-spotted" morph). Abbreviations: bk, beak of mediuncus; fl, flange of mediuncus; gc, gonocornu. Note: The terminus of the beak extends downward, below the paired flanges.


FIGURE 8. Male Leucochrysa (L.) boxi (Tucumán, Argentina, "brown-spotted" morph). A. Callus cercus. Note the quadrate shape. B. Hypandrium internum. Abbreviation: co, comes.


FIGURE 9. Diagram of female Leucochrysa (L.) boxi genital structures, lateral. Abbreviations: acc.gl., colleterial accessory gland; b.c., bursa copulatrix; b.p., basal process of subgenitale; b.gl., bursal gland; col.gl., colleterial gland; col.r., colleterial reservoir; d.p., distal process of subgenitale; g.1., gonapophysis lateralis; s.d., spermathecal duct; sp, spermatheca; S7, seventh sternite; tr.sc., transverse sclerite at base of duct from colleterial reservoir; vel, vellum at tip of spermatheca.


FIGURE 10. Leucochrysa (L.) boxi spermathecal complex and subgenitale, lateral (Tucumán, Argentina, "brown-spotted" morph). Abbreviations: b.p., basal process of subgenitale; d.p., distal process of subgenitale; g.l., gonapophysis lateralis; s.d., spermathecal duct; sp, spermatheca; S 7 , seventh sternite.
tion）， $0.35-0.41 \mathrm{~mm}$ long，with V－shaped invagination（ 0.11 mm diameter at mouth， $0.07-0.08 \mathrm{~mm}$ deep）；slit along entire side of spermatheca opening to bursa．Terminus of spermatheca attached laterally to dome－like vellum with dense covering of spines（gonocristae）．Spermathecal duct attached to anterior，right margin of spermatheca； basal section thick，with 3－4 curves before entering subgenitale，forming U－shaped curve at distal margin of sub－ genitale，becoming brushy after leaving subgenitale；basal $\sim 5 / 6$ ths to $6 / 7$ ths of duct well sclerotized；distal $1 / 6$ th to 1／7th clear，brushy．Subgenitale large，composed of two sections：basal section（extending from membrane folded within tip of S7）heavily fluted basally with numerous，small，longitudinal folds，distally with ventral，triangular， probably invaginated，projection，extending posteriorly below distal section of subgenitale；distal section of sub－ genitale with fluted，transverse folds basally，smooth，fairly rigid surface distally，terminus broad，bilobed，with deep，flat depression between lobes（heart shaped in posterior view），without ventral projection．

Adult specimens examined．In addition to the types listed above：ARGENTINA．Corrientes：Corrientes，1971， Porter，col．（1 ${ }^{\top}$ ，IFML）．Jujuy，Calilegua，1999，M．Dode，col．（1q，IFML）．Tucumán：Alpapuyo，1998，S．Nuñez
 Reguilón，S．R．Nuñez Campero，Collectors［2q， 5 laboratory－reared（3§， 2 q）IFML］；San Javier，1978，R．Gol－ bach col．（ $10^{\lambda}$ ，IFML）；Villa Nougues， $26^{\circ} 51^{\prime} \mathrm{S}, 65^{\circ} 23^{\prime}$ W，III－15－2011，G．S．Albuquerque，M．J．Tauber，C．A．Tau－
 2007，M．Oviedo Collector［1q， 7 laboratory－reared（ 5 §， 2 q）IFML］；locality unknown，1989，Brizuela col．（ $1 q$ ， IFML）．BOLIVIA．Cochabamba：Cochabamba，Porter，Stange y Demorest cols．（1 $\uparrow$ ，IFML；genitalia not exam－ ined）．BRAZIL．Espírito Santo：McLachlan Coll．B．M．1938－674［1o（prob．）， 1 q（prob．），NHM］．Rio de Janeiro：Rio Janeiro，McLachlan Coll．B．M．1938－674（1 ？sex NHM），1969，M．Alvarenga col．（1 §̂，IFML）； Santa Maria Madalena，Terras Frias，X－28－2003，G．S．Albuquerque，M．T．Tauber，C．A．Tauber Expedition，Oct－ Nov 2003 （1 ${ }^{\lambda}$ ，TRC），IV－22－2004，G．S．Albuquerque，M．T．Tauber，C．A．Tauber Expedition，April $2004\left(2{ }^{\wedge}, 1 q\right.$ ， TRC）；Conceição de Macabu，Faz．Carrapeta，IV－23－04，G．S．Albuquerque，M．T．Tauber，C．A．Tauber Expedition， April 2004 （2q，TRC）；Conceição de Macabu，VII－22－1998，D．Cavan（1 ${ }^{\lambda}$ ，UENF）；Campos dos Goytacazes， Parque Estadual Desengano，Babilônia，III－26－1999，M．J．\＆C．A．Tauber，P．J．Tauber，G．S．Albuquerque（1q ten－ eral，TRC），III－27－2001，M．J．\＆C．A．Tauber，P．J．Tauber，G．S．Albuquerque（1q，TRC），II－26－2002，G．S．Albu－ querque（ 1 q，UENF），V－20－2002，M．J．\＆C．A．Tauber，G．S．Albuquerque，E．S．Silva，Collectors，（ $1 \delta^{\lambda}$, TRC），X－ 02－2003，G．S．Albuquerque（3q，UENF），X－26－2003，G．S．Albuquerque，M．T．Tauber，C．A．Tauber Expedition， Oct－Nov 2003 （5才，9q，TRC），XI－22－2003，G．S．Albuquerque（3才， 2 q，UENF），IV－24－04，G．S．Albuquerque，M． T．Tauber，C．A．Tauber Expedition，April 2004 （ $6{ }^{\wedge}$ ，5q，TRC；1q，UENF），II－16－2005，G．S．Albuquerque（ $2 q$ ， UENF）．Rio Grande do Sul：McLachlan Coll．B．M．1938－674（1q， 1 ？sex，NHM）；Cachoeira do Sul，Faz．São Nicolau，I－16 \＆17－2007，G．S．Albuquerque，M．J．Tauber，C．A．Tauber，Collectors（3才，2q，TRC）；Candelária， Morro Botucaraí，XII－31－2006，G．S．Albuquerque，Collector（ $1 \delta^{\wedge}, \mathrm{TRC}$ ）；Maquiné，Garapiá Falls， $29^{\circ} 30^{\prime} 08^{\prime} \mathrm{S}$ ， $50^{\circ} 14^{\prime} 11^{\prime \prime}$ W，I－10－2007，G．S．Albuquerque，M．J．Tauber，C．A．Tauber，Collectors（ $3{ }^{\wedge}, 1 q$ ，TRC）．Santa Cata－ rina：Nova Teutonia，1930，F．Plaumann，col．（1q，IFML；1q，CAS）．PERU．Lima：Callanga，McLachlan Coll． B．M．1938－674［1 ，NHM；genitalia not examined］．

Variation（adult）．In addition to the color polymorphism described above，the male terminalia also shows geo－ graphic variation（Figs 4，5）．In specimens from Tucumán，Argentina and Rio Grande do Sul，Brazil，the ninth ster－ nite is more elongate and slightly more up－turned than that of specimens from more northern Brazil（Rio de Janeiro and Espírito Santo）．Furthermore，they have a relatively small patch of gonocristae at the tip of the sternite and another，separate，well－defined，slightly enlarged，patch of well sclerotized，robust gonocristae midway on the dor－ sal margin of the sclerite．In males from more northern populations，（a）the ninth sternite is less elongate，and（b） the patch of gonocristae is large and dense at the posterior tip of the sternite；it extends along the distal half of the upper margin of S9．

There is also considerable variation in the gonarcal complex，probably largely related to the degree of scleroti－ zation that occurs with maturation．The variation is expressed in the width and robustness of the gonarcal bridge，as well as the heaviness of the gonarcal bases．Images of the extremes are on the project page website at Morphobank website：http：／／www．morphobank．org／index．php？g＝search\＆s＝browse\＆ss＝overview\＆project id＝505．


FIGURE 11. Leucochrysa (L.) boxi female genital structures, ventral (Tucumán, Argentina, "brown-spotted" morph). A. Spermathecal complex and subgenitale. B. Spermathecal complex. Abbreviations: b.p., basal process of subgenitale; d.p., distal process of subgenitale; s.d., spermathecal duct; sg, subgenitale; sp, spermatheca; tr.sc., transverse sclerite; vel, vellum at tip of spermatheca.


FIGURE 12. Ventral surface of Leucochrysa (L.) boxi subgenitale (Tucumán, Argentina, "brown-spotted" morph). Abbreviations: b.p., basal process; d.p., distal process.
FIGURE 13. Callus cercus, female Leucochrysa (L.) boxi (Tucumán, Argentina, "brown-spotted" morph). Note the circular shape.

Larval diagnosis. Larvae of $L$. (L.) boxi express all of the eleven features previously proposed to distinguish the genus Leucochrysa (for details, see Tauber 2004; Mantoanelli et al. 2006, 2011). Here we propose a twelfth feature (\#7):

1. Thoracic lateral tubercles long: prothoracic tubercles extending at least to the middle of the head and meso-and metathoracic tubercles longer than half the width of the corresponding segment (all instars),
2. Thoracic tubercles with very long setae, extending in a fan-shape from the apical and lateral surfaces (all instars),
3. Anterior segments of the abdomen thicker than those of the thorax, giving the larva a humpback appearance in lateral view (all instars),
4. Abdominal segments A7 to A10 small, curved ventrally and partially retracted into one another (all instars),
5. Terminal seta of the antenna at least half the length of the flagellum (all instars),
6. Prothorax with primary setae $\mathrm{S} 1, \mathrm{~S} 3, \mathrm{~S} 4$, and S 5 present, S 2 absent (all instars),
7. Mesonotum and metanotum each with two transverse rows of long, smooth, hooked (rarely straight) setae arising from chalazae [all instars of all species, except Leucochrysa (L.) varia (Schneider) where the anterior row is absent on all instars],
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 a pointed microseta (all instars),
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 three (L3, L2) or two (L1) rows of smooth, hooked submedian setae, the posterior row between the laterodorsal tubercles (L1: four setae in anterior row, two in posterior row; L2, L3: number of setae variable).

A number of unique features distinguish L. (L.) boxi larvae from the other Leucochrysa species that have been described to date (c.f., Tauber 2004, Mantoanelli et al., 2006, 2011). First, the larvae (all instars) of $L$. (L.) boxi are much larger and have longer lateral tubercles on the thorax than the other species. The semaphoront B (second and third instar) of $L$. (L.) boxi also tends to have a larger number of dorsal setae than the other species, except Leucochrysa ( $N$.) digitiformis Tauber \& Albuquerque, which has similar numbers (Mantoanelli et al. 2011). Unlike any of the other species studied to date, the $L$. (L.) boxi semaphoront B has four to six long, hooked setae on the posterior region of the prothorax, between S 3 and S 4 , and it has a larger number of setae in the mesothoracic and metathoracic rows of setae. Also, there are more setae on the lateral tubercles and on the abdominal dorsum between the laterodorsal tubercles of the $L$. (L.) boxi semaphoront B , than on the other species [except $L .(N$.$) digitiformis, where the numbers of setae are similar to those on L$. (L.) boxi]. Like many Leucochrysa species, all of the L. (L.) boxi larval setae are smooth (not serrated), and most are hooked apically.

Second, the spiracles (on the mesothorax and the abdomen) have a sclerotized ring that rests above the surface of the integument, and below the opening is a bulbous chamber (L1, L2, and immature L3) (see Fig. 16C). These features are shared only with the single other species of the subgenus that has been studied-L. (L.) varia.

Third, unique markings distinguish $L$. (L.) boxi larvae. For example, the epicranial marking is divided, with the mesal section elongate and roughly rectangular in shape, and with the lateral section of approximately the same length as the mesal section. The postfrontal marking is simple and free from the other markings (L2, L3); the paired frontal marking (L3) is broadly T-shaped and separated from the intermandibular marking by a small, cream-colored, tentorial pit. The intermandibular marking is thick laterally and tapers to a distinct constriction at the midline. The jaws and labial palpi are brown to dark brown; the labial palpi have a white to cream-colored band basally. The prothoracic markings also are distinctive; below a prominent pair of brown lateral sclerites is a pair of transverse, laterally tapering, dark brown, pigmented markings. Also, there is a pair of brown, pigmented markings mesal to the paired sclerites on the prothorax. Finally, a series of irregularly shaped, light brown marks form a pair of longitudinal, sublateral bands on the dorsum of the abdomen.

Descriptions. Semaphoront B (Third Instar). Body. $9.0-10.5 \mathrm{~mm}$ long; cream-colored, with light to dark brown dorsal markings on thorax and abdomen, light brown ventral markings on abdomen. Spiracles brown; setae golden to dark brown, all smooth.

Head (Figs 14A, 17). 1.25-1.47 mm wide; mandibles 1.77-2.15 mm long. Dorsum cream-colored, with brown to dark brown markings. Epicranial marking brown, divided into two well-defined sections: lateral, mesal, both in contact with posterior margin of head; lateral section irregularly shaped, with distal margin appearing to end well before eye, but with a small, diffuse, separate section immediately lateral to eye; mesal section longitudinally elongate, rectangular shape. Postfrontal marking dark brown, not confluent with epicranial or frontal markings, extending from middle of head to near base of antenna. Frontal marking dark brown, contiguous mesally, broadly Tshaped, with small, pale, tentorial pit at anterolateral tip. Intermandibular marking dark brown, lightly contiguous with anterior margin of frontal marking, extending broadly between bases of mandibles, becoming narrow at midline. Clypeolabral region mostly covered by intermandibular marking, distal section (distal to intermandibular marking) cream-colored, unmarked. Integument surrounding eyes cream-colored. Gena cream-colored, with irregularly shaped, dark brown marking throughout length of ventral surface, not visible in dorsal view. Mandible, maxilla dark brown. Labial palpus: basal segment brown basally, cream-colored distally; terminal segment brown. Antenna with scape dark brown; pedicel light brown basally, becoming cream-colored mesally, brown distally; flagellum brown.

Venter cream-colored, with margin of cranium dark brown. Cardo dark brown anteriorly, with small, dark brown marking at base; stipes brown basally, with anterior margin darker. Mentum white to cream-colored, with pair of light brown marks basally; palpiger cream-colored, with brown mark at base. Cervix cream-colored, with light brown lateral patch.

Anterior margin of head with slightly enlarged, rough, obtuse lateral edges, with three pairs of relatively short setae. Labial palpus: midsegment with distal annulation bearing four medium length setae (one basal, three distal), remaining annulations with six medium-length setae; basal segment with three setae (one medium-length, lateral; one long, ventral; one short, dorsal). Mentum with two ventral setae.

Primary cephalic setae present: S2-10, S12 of medium length, S11 long, S1 intermediate, S5 shortest; Vx setae robust, beneath cervical membrane.

Thorax (Figs 14A, B, D, 18). White to cream-colored, with mostly light brown markings. LTs white to creamcolored, with LS smooth, brown to light brown, mostly hooked, except several distal setae straight; setae on nota mostly hooked, as noted below. Venter cream-colored, unmarked or with a few light brown sublateral marks, tip of A10 with brown, triangular mark. Legs cream-colored, with markings on each segment; coxa with brown marking on basolateral surface, dark brown band mesally; trochanter with small brown anterior, posterior marks; femur brown distally; tibia, tarsus light brown throughout; claws curved, brown; empodia brown.

T1: Anterior margin with pair of small, diffuse, transverse, dark brown markings. Sc1 large, obtuse, light to dark brown, with pair of diffuse brown, obtuse markings mesally; pair of dark brown, transversely elongate, tapering or scalloped, markings below Sc1. Row of short setae (R1) mesal to base of lateral tubercles. S1Sc1 long, thin, hooked; S2Sc1 short, anterior to S1Sc1; 5-6 pairs of associated secondary setae mesal to anterior margin of Sc1. Sc2 transparent (only visible with transmitted light), slightly less than one-half length of Sc1, approximately three times longer than wide. LT elongate, extending beyond middle of mandibles, with 72-75 LS (27-28 apical, 45-47 lateral, dorsal). Primary setae S1, S3, S4, S5 long, arising from chalazae; three to five pairs of associated long to intermediate-length secondary setae.


FIGURE 14. Leucochrysa (L.) boxi third instar (Tucumán, Argentina). A. Head, prothorax, mesothorax (dorsal). B. Thorax and abdominal segments A1-A6 (dorsal). C. Abdominal segments A4-A10 (dorsal). D. Body (lateral).

T2: Anterior subsegment short, unmarked, with row of eight to ten intermediate-length secondary setae between spiracles. Anterior sclerite (Sc1) with three associated setae (S1Sc1, S2Sc1, S3Sc1). Spiracles prominently raised (young specimens) or flat with integumental surface (mature specimens), circular, brown to dark brown. Posterior subsegment with irregularly shaped, elongate, paired, submesal, brown markings mesal to LTs; sclerite on anterior margin (Sc2) with two, very small, associated setae (S1Sc2, S2Sc2); mesolateral
sclerites (Sc3) with one small associated seta (S1Sc3); patch of three to six intermediate-length setae between Sc2 and anteromesal base of LT; anterior row with ~12-16 long setae; posterior row with 56-60 long setae. LT bearing 77-81 LS (24-26 apical, 53-55 lateral).

T3: Dorsum with light brown markings similar to those on posterior subsegment of T2, but slightly larger. LT bearing ~57-62 LS (21-23 apical, 36-39 lateral). Anterior row with 12-14 intermediate-length setae; posterior row with $\sim 48$ setae (10-12 long, $36-38$ intermediate-length); area between Sc 1 and base of LT with patch of four-five intermediate-length setae. Anterior sclerite ( Sc 1 ), mesolateral sclerite ( Sc 2 ), each with one associated seta ( S 1 Sc 1 , S1Sc2).

Abdomen (Figs 14B-D, 19). Dorsum, venter white to cream-colored, with brown to dark brown markings (often faded on preserved specimens). Spiracles brown, prominent. Dorsal markings: A1-A7 with submesal band of irregular brown to light brown markings, series of scattered, smaller, lighter dorsolateral markings. LTs creamcolored with light to faint brown basal marks. A8 with vertical row of light brown dorsal marks; A9 cream-colored to slightly tinged with light brown; A10 with pair of brown lateral marks, single dorsal mark. Venter creamcolored, with mesal, submesal, lateral pairs of very light brown spots on A1-A7.

Setae golden to brown, many dark brown, robust, prominent. A1-A6: most LS, all SMS hooked; some short setae at base of LTs, most spiracular setae unhooked, straight; setae on A7-A10 unhooked. LTs well sclerotized; those on A2, A3, papiliform, with setae arsing mainly from anterior surface; those on A4-A7 more elongate to digitiform, with LS arising mostly from distal and anterior surfaces. A1 with two transverse rows of long to intermedi-ate-length, submesal setae (SMS): A2-A7 with three transverse rows of long SMS; posterior row of each segment with pair of tubercles (LDTs) at lateral edge. LDTs small, lightly sclerotized, each with two long, hooked LDS, microseta between; posterior rows with no SMS lateral to LDTs. Spiracles circular, flat with surface of integument, with one or two associated setae ( SSp ), except on A1 where SSp absent.

A1: Dorsum with one pair of small, straight setae on anterior margin, two transverse rows of SMS; anterior row with five to six intermediate-length SMS; posterior row with $\sim 18$ SMS ( $\sim 6$ long, $\sim 12$ intermediate-length).

A2-A3: LT with ~23 LS (17-20 apical, lateral: long, hooked; ~3-7 basal: short, straight). Dorsum with three rows of SMS: anterior row with $\sim$ twelve SMS (A2, A3), mesal row with ~eight (A2, A3), posterior row with $\sim 22$ (A2) or $\sim 26$ (A3). Each spiracle with two SSp.

A4: LT with $\sim 32$ LS (apical, anterior: $\sim 23$ long, robust and intermediate length, thinner; basal: $\sim$ nine short, straight). Anterior row with $\sim 12$ SMS, mesal row with $\sim$ eight, posterior row with $\sim 27$. Each spiracle with two SSp .

A5-A6: LT apex and sides with $\sim$ six long, robust, hooked LS, $\sim$ twelve (A5) to seven (A6) intermediate-length, hooked LS, base with seven to eight, short, straight LS. LDT on A5 with two long, hooked LDS; LDT on A6 with one long, one short, hooked LDS. Dorsum with three rows of long, hooked SMS: anterior row with $\sim$ ten; mesal row with ~eight; posterior row with $\sim 24$. Each spiracle with one SSp.

A7: LT with $\sim$ six long, robust, straight LS apically, laterally; ~nine short, straight LS basally. LDT with one long, hooked LDS, one short, straight LDS. Dorsum with two transverse rows of straight SMS; anterior row with four, posterior row with ten to 14 , small. Each spiracle with one SSp.

A8: LT small, with two straight LS (anterior one short, posterior one longer). Two transverse rows of short, straight SMS: anterior row with four, posterior row with 12. Each spiracle with one SSp.

A9: Dorsum with three transverse rows of short, straight setae (four anterior, four to seven mesal, 12-16 posterior).

A10: Dorsum with ~eight short, straight setae, most lateral.
Semaphoront B (Second Instar). Similar to third instar with following exceptions. Body. $5.02-6.90 \mathrm{~mm}$ long.
Head (Fig. 15A). $0.88-0.93 \mathrm{~mm}$ wide; mandibles: $1.07-1.19 \mathrm{~mm}$ long. Second segment of labial palpus with nine setae: distal annulation with four (one long, three intermediate-length); remaining annulations with five setae; basal segment with two intermediate-length setae.


FIGURE 15. Leucochrysa (L.) boxi second instar (Tucumán, Argentina). A. Head, prothorax, mesothorax (dorsal). B. Abdominal segments A4-A10 (dorsal).

Thorax (Fig 15A). T1: LT with ~38 LS ( $\sim 17$ apical, 21 lateral, dorsal); Sc1 with three pairs of associated secondary setae. T2: LTs with $\sim 37$ LS ( $\sim 18$ apical, $\sim 19$ lateral, dorsal); anterior subsegment with row of four to six intermediate-length setae; posterior subsegment with anterior row of $\sim$ six intermediate-length setae, posterior row of 18-20 intermediate-length setae. T3: LT with $\sim 32$ LS ( $\sim 17$ apical, $\sim 15$ lateral, dorsal); anterior row with $\sim$ six setae, posterior row with $\sim 16-18$ setae.

Abdomen (Fig. 15B). A1: Only one transverse row of eight to ten SMS setae between LDTs. A2-A3: LT with $\sim$ ten to twelve LS; anterior row with six to eight long SMS; mesal row with four; posterior row with ten to twelve. A4, A5: LT with $\sim 10-13 \mathrm{LS}$; anterior row with six to eight long SMS, mesal row with four, posterior row with ten to twelve. A6, A7: LT with ~ eight to ten LS (A6: ~eight straight, two hooked; A7: ~eight straight); anterior row with six SMS, mesal row with four, posterior row with six to eight (A6) or six (A7). A8: LT with one long, straight LS, one short, straight LS. Dorsum with two rows of short, straight setae (six anterior, four posterior). A9: Dorsum with two rows of short, straight setae (four anterior, six posterior).

Semaphoront A (First Instar). Body. $3.90-4.06 \mathrm{~mm}$ long, predominantly white to cream-colored; abdomen with light to dark brown markings (Figs 16A, B). LS light amber to dark brown; dorsal setae light brown to cream-colored; all setae smooth.

Head (Figs 16A, B, 20A). $0.53-0.59 \mathrm{~mm}$ wide; mandibles $0.61-0.74 \mathrm{~mm}$ long. Epicranial, postfrontal, frontal markings light to dark brown, with pattern resembling that of third instar (e.g., divided epicranial marking, intermandibular marking constricted mesally); postfrontal marking simple, sometimes connected to mesal section of epicranial marking; frontal marking roughly Y-shaped, separated from intermandibular marking by small, pale, tentorial pit. Labial palpus mostly light brown; middle segment with cream-colored to white band basally, dark brown band distally; terminal segment brown to dark brown. Mandibles brown to dark brown. Antenna light brown. Venter white to cream-colored, with brown mark on lateral edge of stipes.

Thorax (Fig. 16A, B, C, 20B). Legs mostly white to cream colored, with brown as follows: brown to dark brown marks at base of coxae, anterior, posterior surfaces of trochanters, tip of tibiae; brown subapical bands on coxae, femora; tibiae, claws, empodia entirely brown.

T1: LT with two long, straight, amber to dark brown LS, with microseta between. Sc1 brown, large; S1Sc1 long, straight, arising from small chalaza; S2Sc1 short, anterior to S1Sc1. S1 long; S3, S4, S5 intermediate-length, straight; S2 absent.

T2: Spiracles prominent, tubercle-shaped, with apex sclerotized, dome-shaped, amber-colored. LT with three amber to dark brown LS; anterior LS intermediate-length, hooked; mesal, posterior LS long, straight. Sc1, Sc2 small; associated setae (S1Sc1, S2Sc1 and S1Sc2) very small; Sc3 intermediate-sized, transparent, with associated
seta (S1Sc3) small. Posterior subsegment with pair of hooked intermediate-length setae anterior to Sc3, row of four hooked setae posterior to Sc 3 (mesal pair intermediate-length, lateral pair long, arising from large chalazae).

T3: LT with three amber to dark brown LS; anterior one intermediate-length, hooked; mesal, posterior ones long, straight. Sc1 small, with S1Sc1 very small; Sc2 distinguishable, with S1Sc2 small. Anterior region with pair of hooked setae; posterior region with four long, hooked setae arising from chalazae.


FIGURE 16. Leucochrysa (L.) boxi first instar (Tucumán, Argentina). A. Head, prothorax (dorsal). B. Body (dorsal). C. Mesothoracic spiracle; note (arrow): enlarged, sclerotized ring at tip of spiracle, lateral tubercle below.

Abdomen (Figs 16B, 20C). Dorsum with subapical band of light brown marks; dorsum of A8, A10 with large, darker brown markings (often faded on preserved specimens). A2-A5: LS hooked, both amber (A2, A3), one amber, one dark brown (A4, A5). A6, A7: LS straight, dark brown. A1-A5: LDS amber to light amber. A6: one LDS long, hooked, one short, hooked. A7: LDS amber to light amber, one long, straight; one short, straight. A2A8: Spiracles each with an associated seta (SSp). A1-A5: SMS long. A6: SMS long to medium-length. A7: SMS short, straight. A8: LT with one short LS, one of medium-length, straight; SMS short, straight. A9: Dorsum with three rows of short, straight SMS (anterior with two, posterior, each with four); two pairs of lateral setae (one short, one long). A10: Two to three pairs of short, straight setae on sides.

Larval specimens examined (see full locality data on adult specimens). ARGENTINA. Tucumán: Villa Nougues (Tauber Lots 2011:03, 2011:04A, 2011:04B, TRC); Yerba Buena (Reguilón Lot 2007:01, IFML); Horco Molle (Reguilón Lots 2009:02, 2009:03, IFML). BRAZIL. Rio de Janeiro: Santa Maria Madalena, Terras Frias (Tauber Lot 2004:13, TRC); Conceição de Macabu, Faz. Carrapeta (Tauber Lot 2004:03, TRC); Campos dos Goytacazes, Parque Estadual Desengano, Babilônia (Tauber Lots 2001:06, 2003: 41, TRC; Albuquerque Lot 2003:8, UENF). Rio Grande do Sul: Cachoeira do Sul, Faz. São Nicolau (Tauber Lots 2007:15, 2007:16, TRC).

Variation (larval). The color of our specimens varied considerably—perhaps related to the age of the preserved specimens. The individuals that we studied from Tucumán, Argentina, had been preserved for only a few months; their markings were bold-brown to dark brown against a white to light cream-colored background. Our specimens from Brazil had been preserved for three to ten years when we studied them; their brown markings were distinct but appeared slightly faded and less apparent against a somewhat discolored, cream to tan, background.

Specimens also varied in the setal numbers as indicated in the descriptions. Many showed asymmetry in setal numbers between the left and right sides of the body; such a pattern of asymmetry appears very common among chrysopid species (see Mantoanelli et al. 2006). We did not determine if one side or the other consistently had the higher number.

Our specimens also showed some asymmetry in mandible length, with ratios (right mandible length : left mandible length) as follows: L3, $0.96-1.06: 1.00$; L2, $0.94-1.05: 1.00$; L1, $0.99-1.06: 1.00$. Unlike in $L$. (L.) varia, neither the left nor the right mandible tended to be consistently longer.


FIGURE 17. Leucochrysa (L.) boxi third instar. A. Head, dorsal. B. Head, ventral. Abbreviations: co, cardo; cr, ventral margin of cranium; epi-l, epi-m, lateral and mesal sections of the epicranial marking; fr, frontal marking; gen, gena; int, intermandibular marking; lp, labial palpus; mb, mandible; mx, maxilla; pg, palpiger; post, postfrontal marking; stp, stipes; S1-S12, primary cephalic setae 1-12; Vx, three short posterior setae surrounding a pore.


FIGURE 18. Leucochrysa (L.) boxi third instar. Thorax, dorsal. Abbreviations: LS, setae on lateral tubercle; LT, lateral tubercle; R1, row of three small anterior setae; $\mathrm{Sc} 1, \mathrm{Sc} 2$, Sc 3 , first, second and third primary dorsal thoracic sclerites; Sp , spiracle; S1, S3-5, primary thoracic setae; S1Sc1, S2Sc1, S3Sc1, S1Sc2, S2Sc2, S1Sc3, setae associated with primary sclerites; T1, T2, T3, first, second and third thoracic segments.


FIGURE 19. Leucochrysa (L.) boxi third instar. Abdominal segments, dorsal. Abbreviations: A1, A2, A4, A6, A7, A10, first, second, third, sixth, seventh, and tenth abdominal segments; LDS, setae on laterodorsal tubercle; LDT, laterodorsal tubercle; LS, setae on lateral tubercle; LT, lateral tubercle; SMS, submesal setae; Sp , spiracle; SSp , seta associated with spiracle.

Egg. Ovoid, 1.13-1.25 mm long; 0.62-0.67 mm wide; deposited separately, with isolated stalks, in no particular pattern. Stalk hyaline, $6.8-10.0 \mathrm{~mm}$ long; stalk and egg sticky, but without droplets. Color: initially green with white micropyle, becoming bluish green with cream-colored longitudinal stripe, to grey with dark, developing embryo visible beneath chorion.

Biology. This species has been collected on trees in forested areas in both northwestern Argentina and coastal southeastern Brazil. In some cases, we encountered them in relatively substantial numbers, especially in moist habitats near streams.


FIGURE 20. Leucochrysa (L.) boxi first instar. A. Head, dorsal, B. Thorax, dorsal, C. Abdomen, dorsal. Abbreviations, Head: epi-l, epi-m, lateral and mesal sections of the epicranial marking; fr, frontal marking; int, intermandibular marking; post, postfrontal marking; S1-S7, S11, S12, primary cephalic setae; Vx, three short posterior setae surrounding a pore. Thorax: LS, setae on lateral tubercle; LT, lateral tubercle; R1, row of three small anterior setae; S1, S3-5, primary thoracic setae; S1Sc1, S2Sc1, S1Sc2, S1Sc3, setae associated with primary sclerites; Sc1, Sc2, Sc3, first, second and third primary dorsal thoracic sclerites; Sp, spiracle; T1, T2, T3, first, second and third thoracic segments. Abdomen: A1, A5, A10, abdominal segments; LDS, setae on laterodorsal tubercle; LDT, laterodorsal tubercle; LS, setae on lateral tubercle; LT, lateral tubercle; SMS, submesal setae; Sp, spiracle; SSp, seta associated with spiracle.


FIGURE 21. Ectoparasitic flies [Forcipomyia (Trichohelea) sp.] on the forewings of Leucochrysa (L.) boxi [Tucumán, Argentina].

In the laboratory, gravid, field-collected females oviposited two to 25 stalked eggs per day. At room temperature ( $\sim 20 \pm 3^{\circ} \mathrm{C}$ ), hatching occurred within five to six days. Larval development took approximately 20 to 28 days, after which a robust cocoon was spun.

Ectoparasitoids. Four of the specimens that we collected in Tucumán, Argentina, had adult ectoparasitic flies (Diptera: Ceratopogonidae) on the veins of their forewings (Fig. 21). In one case there were four flies on the wing; in the others there were one to three. The flies appeared to be attached or feeding at the veins. They were identified as an undescribed species of Forcipomyia (Trichohelea) (det. Art Borkent, 2011, Royal British Columbia Museum). Another species of ectoparasitic, ceratopogonid flies [Forcipomyia (Trichohelea) eques Johannsen] has been reported for the European lacewing species Nineta flava (Scopoli) and Chrysopa perla (L.) (Greve 1968, 1969, Gepp 1982). But, this is the first record of a neotropical member of this subgenus feeding on the wings of Neuroptera (personal communication, Art Borkent, 2011). Three of these flies will be deposited in the Canadian National Collection, Ottawa, Ontario, Canada, and another is in the TRC.

Polymorphism. As described above, L. (L.) boxi adults express a notable, geographically variable, polymorphism in their thoracic color pattern. Specimens from Tucumán, Argentina, and from several localities in Rio Grande do Sul and Santa Catarina, Brazil, have two morphs: one in which the meso and metanota are dark brown throughout (= "brown-spotted" morph) and another in which the meso and metanota have bright, white regions (= "white-spotted" morph) (Figs 1A-C).

We confirmed the existence of the polymorphism through separate rearings of F1 offspring from each of four individual females from Tucumán. Two of the mothers were field-collected "brown-spotted" morphs; the color patterns of their mates are unknown. One of these females produced twelve offspring, nine of which were "brownspotted" morphs $\left(4 q, 5 \delta^{\lambda}\right)$, and three were "white-spotted" morphs $\left(1 q, 2 \delta^{\lambda}\right)$. The other produced seven offspring, three of which were "brown-spotted" morphs $\left(1 q, 2 \delta^{\lambda}\right)$ and four were "white-spotted" morphs $\left(1 q, 3 \delta^{\lambda}\right)$. The other two mothers from Tucumán were "white-spotted"; all of their offspring were also "white-spotted" $(2 Q, 3 \AA$ from one female; $2 q, 5 \delta$ from the second female). In addition, we reared offspring from four "brown-spotted" morph females collected in Rio Grande do Sul $(\mathrm{n}=1)$ and Rio de Janeiro States $(\mathrm{n}=3)$; all of their offspring were "brownspotted" morphs (Rio Grande do Sul: $\mathrm{n}=4$; Rio de Janeiro ( $\mathrm{n}=3,5,7$ ).

Mode of inheritance. The total number of offspring that we reared is small. Thus, conclusions concerning the genetic basis for the polymorphism are limited to the following:
(1) Both males and females exhibit the two color phenotypes; thus the expression of the polymorphism is not sexlimited.
(2) The ratios of "brown-spotted" to "white-spotted" morphs (3:1, $\sim 1: 1,1: 0,0: 1)$ that we reared from the eight individual females do not exclude any of a range of possibilities-from simple Mendelian inheritance of autosomal dominant ("brown-spotted") / recessive ("white-spotted") alleles, to polygenic inheritance.
(3) The expression of the polymorphism appears to be geographically variable. We have seen "white-spotted" morphs in $L$. (L.) boxi populations from Tucumán in Argentina and from Brazil's southern-most states of Rio Grande do Sul and Santa Catarina, but we have not seen them in populations from the more northern Brazilian states of Rio de Janeiro or Espírito Santo.

Ecology. The role of the polymorphism (if any) is not apparent. Leucochrysa adults are not known to be predaceous; thus the polymorphism is unlikely to camouflage adults from prey. However, it is possible that the polymorphism offers the adults a degree of protection from predators with acute search images.

An interesting consideration is that the monomorphic "brown-spotted" populations that we sampled in Brazil occur sympatrically with Leucochrysa (L.) magnifica (Banks)—a species that has white meso and metanotal color patterns closely resembling those of the $L$. (L.) boxi "white-spotted" morphs (cf. Fig. 1B with 1D). Although $L$. ( $L$.) magnifica was reported from Misiones, Argentina (det. P. A. Adams; González Olazo et al. 1999), a locality where "white-spotted" and "brown-spotted" morphs of $L$. (L.) boxi occur, we have not confirmed the identification.

Known distribution. South America. We have confirmed records for L. (L.) boxi only from Argentina (Corrientes, Misiones, Tucumán) and Brazil (Espírito Santo, Rio de Janeiro, Rio Grande do Sul, Santa Catarina). The records from Bolivia (Cochabamba) and Peru (Lima) are tentative; although our examination of the specimens indicate that the wings and external body features are those of $L$. (L.) boxi, we have not examined the genitalia of the specimens.

At this time, only the "brown-spotted" morph is known from the Brazilian states of Espírito Santo and Rio de Janeiro; both morphs were collected in the southernmost Brazilian states (Rio Grande do Sul, Santa Catarina) and from northern Argentina (Tucumán, Misiones).

Navás' (1912-13: 22) record of this species from Central America (Guatemala) was erroneous. The specimen that formed the basis for his report was collected by Champion; Navás identified it as "Allochrysa longicornis" and attributed it to "Guatemala: Buyaba". We examined the specimen, a male bearing Navás' identification label in the Godman-Salvin collection (NHM); it is from "Bugaba", which is in Panama, not Guatemala, and it is a specimen of L. (L.) magnifica.

Etymology. Navás named the species after the collector of the type specimen, H. E. Box.

## Keys to the larvae of South American Leucochrysa spp.

The keys below include the six Leucochrysa species from South America whose larvae have been described in detail (Mantoanelli et al. 2006, Mantoanelli et al. 2011, and L. (L.) boxi). Although the number of species included is very small relative to the diversity of Leucochrysa spp. in the region, the key serves to identify some of the most commonly found species in orchards and in the Atlantic forest. Furthermore, it provides a framework for developing more comprehensive keys, as descriptions of larvae from other species become available.

The following keys are modified after Mantoanelli et al. (2011); see that publication and Mantoanelli et al. 2006 for illustrations.

## Key to semaphoront B (2nd and 3rd instars)

[^0]
## Key to semaphoront A (1st instar)

1. Epicranial marking with only a mesal section, no lateral section ..... 2
1 '. Epicranial marking with two sections (mesal and lateral) ..... 3
2. Thorax without dorsal markings ..... vás
2'. Thorax with brown markings ..... azevedoi Navás
3. Thoracic spiracles small, not elevated above the integument, with narrow chamber ..... 4
3 '. Thoracic spiracles large, raised above the integument, with bulbous chamber ..... 5
4. Dorsal setae on mesothorax and metathorax hooked; abdominal segments with brown markingsdigitiformis Tauber \& Albuquerque
4 '. Dorsal setae on mesothorax and metathorax with straight tips; abdominal segments without markings ..... . marquezi Navás
5. Setae (LS) on mesothoracic and metathoracic tubercles of similar size, all with straight tips; submesal setae of mesothorax andmetathorax with straight tips varia (Schneider)5 '. Setae (LS) on mesothoracic and metathoracic tubercles with anterior seta hooked and shorter than the other two; submesalsetae of mesothorax and metathorax with hooked tips.boxi Navás

## Consideration of the current subgeneric division of Leucochrysa

Do larval morphological characteristics support the division of Leucochrysa into the two subgenera Nodita and Leucochrysa? Currently, the division of Leucochrysa into two subgenera is largely based on size differences and two morphological characters of the adult stage, i.e., the shape of the intramedian cell in the forewing (triangular vs. quadrangular) and the shape of the radial sector (straight or sinuous) (Adams 1977, Brooks \& Barnard 1990). This division has been questioned because the range of variation in these adult characteristics overlaps between the two subgenera, and because no distinguishing differences have been identified in the male or female genitalia of the two groups (Adams 1977, Freitas \& Penny 2001, Tauber 2004). All of the above authors have recommended that more species and more characters be examined, and that alternate subdivisions of the genus be considered.

Several larval features have been proposed as potentially useful in classifying the genus (Mantoanelli et al. 2006). These features were identified on the basis of eight species of Leucochrysa (Nodita) and a single species of Leucochrysa (Leucochrysa). In the current study of the larvae of a second Leucochrysa (Leucochrysa) species, only two structural features of the thoracic and abdominal spiracles continue to support the subdivision of the genus into the two current subgenera. In Leucochrysa (Leucochrysa), the spiracles have well sclerotized rings that are elevated above the surface of the integument, and in most specimens (L1, L2 and immature L3) they are located on prominent, tubercle-like swellings (see Fig. 16C). In contrast, the spiracles of Leucochrysa (Nodita) larvae are not on swellings and they have lightly sclerotized, unmodified openings that are level with the surface of the integument.

The large size of the larval mandibles was also proposed as a character that distinguishes Leucochrysa (Leucochrysa) from Leucochrysa (Nodita); however, we question its value. Although the ratio of mandible length to head width is greater for the two Leucochrysa (Leucochrysa) species than for the eight species of Leucochrysa (Nodita) species studied to date, this feature varies considerably among the Leucochrysa (Nodita) species, and it may be correlated with body size. Thus, conclusions concerning the usefulness of this character must wait until the larvae of additional large Leucochrysa (Nodita) species are studied.

Other characteristics, especially those related to the chaetotaxy, also do not support the subgeneric division. For example, $L$. (L.) varia has much lower numbers of setae on the thoracic and abdominal segments than those of all species in the subgenus Nodita that have been studied; thus, a small setal number was proposed as a possible feature of the subgenus Leucochrysa (Mantoanelli et al. 2006). However, this character fails because L. (L.) boxi has the highest number of setae on the thoracic and abdominal segments among all the species.

At this time, for convenience, we retain the current subdivision of Leucochrysa, based on the adult characters that have been used traditionally to distinguish the subgenera, as well as the larval spiracular differences. However, further study is required to elucidate these subgeneric affinities.

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[^0]:    1. Epicranial marking with only a mesal section, no lateral section2
    1 . Epicranial marking with two sections (mesal and lateral) ..... 3
    2. Thoracic lateral tubercles with setae smooth, all hooked. ..... rodriguezi Navás
    2 '. Thoracic lateral tubercles with setae serrated, setal tips straight or hooked ..... azevedoi Navás
    3. Thoracic spiracles small, round, not elevated above surface of integument, with chamber narrow. ..... 4
    $3^{\prime}$. Thoracic spiracles large, tuberculiform and raised above surface of integument, with chamber bulbous ..... 5
    Prothorax with dorsal setae smooth, hooked; mesothorax and metathorax without markingsdigitiformis Tauber \& Albuquerque
    $4^{\prime}$. Prothorax with dorsal setae smooth, setal tips pointed; mesothorax and metathorax with dark brown markingsmarquezi Navás5. Thoracic lateral tubercles with less than 25 (2nd instar) or 30 (3rd instar) setae (LS); mesothorax and metathorax withoutmarkings . varia (Schneider)
    5 '. Thoracic lateral tubercles with more than 35 (2nd instar) or 70 ( 3 rd instar) setae (LS); mesothorax and metathorax with mark-ings light brown.boxi Navás
