RESEARCH ARTICLE



A new species of Stenoloba Staudinger, 1892 from China (Lepidoptera, Noctuidae, Bryophilinae)

Oleg Pekarsky^{1,†}, Aidas Saldaitis^{2,‡}

l H-1068 Budapest, Felsőerdősor u. 16-18, Hungary **2** Nature Research Centre, Akademijos str. 2, LT–08412 Vilnius-21, Lithuania

t urn:lsid:zoobank.org:author:40DC027F-FCF3-4953-AC60-C071E814A768 *urn:lsid:zoobank.org:author:1C168900-4B0F-4999-895D-FAB0B16B14C1*

Corresponding author: Oleg Pekarsky (opbp@t-online.hu)

Academic editor: D. Lafontaine Received 13 March 2013 Accepted 12 June 2013 I	Published 17 June 2013
urn:lsid:zoobank.org:pub:0E571669-1249-486C-853A-6232012767A9	

Citation: Pekarsky O, Saldaitis A (2013) A new species of *Stenoloba* Staudinger, 1892 from China (Lepidoptera, Noctuidae, Bryophilinae). ZooKeys 310: 1–6. doi: 10.3897/zookeys.310.5125

Abstract

A new species of *Stenoloba* from the *olivacea* species group, *S. solaris*, **sp. n.** (Lepidoptera, Noctuidae), is described from Yunnan, China. Illustrations of the male holotype and its genitalia are provided. A diagnostic comparison is made with *Stenoloba albistriata* Kononenko & Ronkay, 2000, *Stenoloba olivacea* (Wileman, 1914), and *Stenoloba benedeki* Ronkay, 2001 (Fig. 4).

Keywords

Lepidoptera, Noctuidae, Stenoloba, new species, China

Introduction

Stenoloba Staudinger, 1892 is an East Asian genus of the subfamily Bryophilinae. The first comprehensive revisions of the genus were published by Kononenko and Ronkay (2000, 2001) and Ronkay (2001) based on the East Palaearctic and northern Oriental species.

Subsequently, several articles have increased taxonomic knowledge of this large and very diverse genus including most notably a 2010 publication by Behounek & Kononenko which listed 75 species arranged into 14 species-groups. Recently an additional three new species were described from the Oriental region (Pekarsky 2011), (Sohn and Tzuoo 2012), (Pekarsky et al. in press).

Descriptions of Chinese *Stenoloba* have rapidly increased in the last two decades. Chen (1999) listed only seven species from China, whereas a more comprehensive review of the Chinese *Stenoloba*, published by Han and Kononenko (2009), contained 37 species. This paper describes one more new species and found with the recent and intensive exploration of the Chinese insect fauna and further future discoveries are predicted.

During a spring expedition to north-west Yunnan, a striking specimen of an undescribed *Stenoloba* was collected. The new species, described below, resembles members of the *S. olivacea* species-group, especially *S. albistriata* Kononenko & Ronkay, 2000, *S. olivacea* (Wileman, 1914) and *S. benedeki* Ronkay, 2001, but displays clearly recognisable external and genital differences.

Abbreviations of material depositories: GBG/ZSM = Gottfried Behounek (Grafing, Germany)/Zoologische Staatssammlung, München (Germany); HNHM = Hungarian Natural History Museum, Budapest (Hungary); ZFMK = Zoologische Forschungsistitut und Museum Alexander Koenig (Bonn, Germany).

Systematic accounts

Stenoloba solaris, sp. n.

urn:lsid:zoobank.org:act:80CD3AD9-74EC-411B-8ECD-BF069AF612A3 http://species-id.net/wiki/Stenoloba_solaris Figs 1, 6, 7

Type material. Holotype Male (Fig. 1). China, NW Yunnan, Lijiang/Zhongdian near Tuguancum, N27°29'700", E99°53'700", 24–25.V.2012, 3200 m, leg. A. Floriani; slide No.: OP1780m (coll. GBG/ZSM).

Etymology. The name "*solaris*" refers to the orange circular patch at the reniform stigma resembling the rising sun.

Diagnosis. The new species belongs to the *olivacea* species-group and externally resembles *S. albistriata* (Fig. 2) and *S. olivacea* (Fig. 3), but is clearly separable from them by both wing pattern and genitalia. The most prominent distinguishing feature, unique within the genus, is the presence of circular orange patches in the forewing basal area and in the reniform stigma. *S. solaris* differs from all related species by its forewing's bright lettuce-green colour, as opposed to the olive ground colour and dark grey hindwings of the other species. The specific features of the male genitalia can be found in the shape of the uncus, juxta, and valvae, and in the structure of the vesica. The male genitalia of *S. solaris* (Figs 6, 7) differ from those of *S. albistriata* (Figs 8, 9) by the wider base of the uncus, the wider, shorter and less curved valvae, and by the rounded juxta with straight lateral margins. The uncus of *S. albistriata* is constricted at the base and dilated medially, the longer and narrower valvae have more curved costal margins, and the juxta has concave lateral margins. The other somewhat similar species, *S. olivacea* (Figs 10, 11) and



Figures 1–5. Stenoloba spp. adults and biotope. I S. solaris, sp. n., male, holotypus, Yunnan, China (GBG/ZSM) 2 S. albistriata, male, paratypus, N. Vietnam (ZFMK) 3 S. olivacea, male, Taiwan (HNHM)
4 S. benedeki, male, paratypus, N. Vietnam (HNHM) 5 Type locality of Stenoloba solaris, sp. n. China, NW Yunnan, Lijiang/Zhongdian near Tuguancum, N27°29'700", E99°53'700".



Figures 6–13. *Stenoloba* spp. male genitalia. 6 *S. solaris*, sp. n., male, China, capsule, prep. OP1780m 7 *S. solaris*, sp. n., male, China, aedeagus, prep. OP1780m 8 *S. albistriata*, male, Vietnam, capsule, prep. LR10566m 9 *S. albistriata*, male, Vietnam, aedeagus, prep. LR10566m 10 *S. olivacea*, male, Taiwan, capsule, prep. LR7131m 11 *S. olivacea*, male, Taiwan, aedeagus, prep. LR7131m 12 *S. benedeki*, male, Vietnam, aedeagus, prep. LR7127m 13 *S. benedeki*, male, Vietnam, aedeagus, prep. LR7127m.

S. benedeki (Figs 12, 13) each have a longer uncus, rounded juxta, and a large, medially positioned cornuti field consisting of fine spiculi and the terminal cornutus is either small and nail-like (*S. olivacea*) or large and thorn-like (*S. benedeki*). In addition, the clasping apparatus of the latter two species is significantly larger than in the new species, but the size of the aedeagus and vesica is practically the same.

Description. Male (Fig. 1). Wingspan 34 mm. Head and thorax lettuce green; collar with a row of black scales at base forming black line; tegulae edged by black line; abdomen blackish grey; forewing relatively elongated, with costa remarkably arched, apex finely pointed, outer margin oblique, ground colour lettuce green with dark-grey area medially; wing pattern well marked with well-developed cross-lines; basal field with circular orange patch bordered with white fascia distally; cross-lines black, basal line strongly marked; subbasal line strong, curved, bordered by white fascia proximally; antemedial line waved, oblique with wide white fascia; lower part of medial area dark grey; medial line nearly straight, slightly bent in middle; postmedial line undulate with white fascia; subterminal and terminal lines formed by large black arrowheads. Noctuid maculation typical and well developed; large orange reniform patch, rounded, defined by black scales; inner edge of stigma forming prominent semilunar arch; orbicular stigma black, dot-like; claviform stigma present as diffuse dark streak; cilia dark grey checkered with white. Hindwing grey, discal spot dark grey, terminal line heavy black. Female unknown. Male genitalia (Figs 6, 7). Uncus short and strong, wide at base and tapering towards apex; tegumen somewhat shorter than vinculum; transtilla relatively wide; juxta wide, rounded quadrangular with triangular cleft on posterior margin; vinculum strong, V-shaped; valva simple, elongate, evenly tapering distally and apex rounded, with a few short spine-like setae at apical margin; sacculus elongate, broad; costa slightly concave; clasper forming long, narrow, dorsally dentate plate. Aedeagus short and straight; vesica bulb-like, everted posteriorly, recurved ventrally; medial part of vesica with three diverticula, one with large, stout cornutus.

Biology and distribution. The single male was collected at ultraviolet light on 24–25 May 2012 near Zhongdian in northwest China's Yunnan province in the remote Baima Xue mountain range (Fig. 5). The new species was collected at an elevation of 3200 meters in a wide river valley near mountain mixed forests dominated by various conifer trees, bushes and rhododendron. Many other spring Noctuidae species were collected there at that time including *Panolis pinicortex* Draudt, 1950, *Orthosia reserva* Ronkay, Ronkay, Gyulai & Hacker, 2010 and *Hada antonraui* Gyulai, Ronkay & Saldaitis, 2011.

Acknowledgements

We would like to express our gratitude to László Ronkay (HNHM, Budapest) for critical comments on the manuscript, and help with photos of the adults and genitalia slides of *S. albistriata, S. olivacea* and *S. benedeki*, and to Gábor Ronkay (Budapest, Hungary) for access of his extensive private collection. The authors are grateful to Tomas Zubacikas (Vilnius, Lithuania) for assistance with imago pictures.

References

- Behounek G, Kononenko VS (2010) Fourteen new species of the genus *Stenoloba* Staudinger, 1892 from South East Asia (Lepidoptera: Noctuidae, Bryophilinae). Zootaxa 2679: 1–31.
- Chen YX (1999) Lepidoptera, Noctuidae. In: Zhu HF et al. (Ed) Fauna Sinica Insect, Vol. 16. Science Press, Beijing, 1596 pp.
- Han HL, Kononenko VS (2009) A review of the genus *Stenoloba* Staudinger, 1892 from China, with description of 6 new species and 7 new records for China (Lepidoptera: Noctuidae, Bryophilinae). Zootaxa 2268: 1–22.
- Kononenko VS, Ronkay L (2000) A revision of the genus Stenoloba Staudinger, 1892 (Lepidoptera, Noctuidae, Bryophilinae) with description of 25 new species and 3 new subspecies from East Asia (I). Insecta Koreana, 17(3): 137–174.
- Kononenko VS, Ronkay L (2001) A revision of the genus Stenoloba Staudinger, 1892 (Lepidoptera, Noctuidae, Bryophilinae) with description of 15 new species and 3 new subspecies from East Asia (II). Insecta Koreana, 18(2): 95–121.
- Pekarsky O (2011) A new Stenoloba Staudinger species from China (Lepidoptera, Noctuidae, Bryophilinae). ZooKeys 108: 67–72. doi: 10.3897/zookeys.108.1208
- Pekarsky O, Dvořák M, Ronkay G (in press) Three new species of *Stenoloba* Staudinger, 1892 from Southeast Asia (Lepidoptera, Noctuidae, Bryophilinae). Fibigeriana Supplement Vol. I. Heterocera Press, Budapest.
- Ronkay L (2001) New Stenoloba Staudinger, 1892 species from Taiwan and Vietnam (Lepidoptera: Noctuidae, Bryophilinae). Annales Historico-Naturales Musei Nationalis Hungarici, Vol. 93, Budapest 2001, 219–229.
- Sohn JC, Tzuoo HR (2012) Two new species of *Stenoloba* (Lepidoptera: Noctuidae) from East Asia with the first description of *S. nora* female genitalia. Journal of Asia-Pacific Entomology 15: 241–244. doi: 10.1016/j.aspen.2011.11.005



A neotype designation for the bone-skipper Centrophlebomyia anthropophaga (Diptera, Piophilidae, Thyreophorina), with a review of the Palaearctic species of Centrophlebomyia

Maurizio Mei¹, Daniel Whitmore², Giuseppe Lo Giudice^{1,3}, Pierfilippo Cerretti^{1,3}

I Dipartimento di Biologia e Biotecnologie "Charles Darwin", Università di Roma "La Sapienza", Piazzale A. Moro 5, I 00185 Rome, Italy 2 Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK 3 Centro Nazionale Biodiversità Forestale (CNBFVR) – Corpo Forestale dello Stato, via Carlo Ederle 16/a, 37100 Verona, Italy

Corresponding author: Pierfilippo Cerretti (pierfilippo.cerretti@uniroma1.it)

Academic editor: Rudolf Meier 1	Received 26 February 2013	Accepted 13 June 2013	Published 17 June 2013
-----------------------------------	---------------------------	-----------------------	------------------------

Citation: Mei M, Whitmore D, Lo Giudice G, Cerretti P (2013) A neotype designation for the bone-skipper *Centrophlebomyia anthropophaga* (Diptera, Piophilidae, Thyreophorina), with a review of the Palaearctic species of *Centrophlebomyia*. ZooKeys 310: 7–28. doi: 10.3897/zookeys.310.4914

Abstract

The European bone-skippers (Diptera: Piophilidae: Thyreophorina), long considered extinct, have recently been the object of much interest by dipterists after their unexpected rediscovery. Considerable faunistic work has been done on these flies in recent years. However, some nomenclatural and taxonomic issues still require attention. A neotype is designated for *Thyreophora anthropophaga* Robineau-Desvoidy, 1830 (now in the genus *Centrophlebomyia* Hendel, 1903) to fix the identity of this nominal species. *Centrophlebomyia anthropophaga* is recognized as a valid species. It is described and illustrated in detail, and information on its preimaginal instars is provided for the first time. Four Palaearctic species of *Centrophlebomyia* are recognized and reviewed and a key is provided for their identification. *Centrophlebomyia orientalis* Hendel, 1907 from northern India, is removed from synonymy with *C. anthropophaga* and recognized as a valid species of *Centrophlebomyia*, **stat. r.** The nominal genus *Protothyreophora* Ozerov, 1984 is considered a junior synonym of *Centrophlebomyia*, **syn. n.**

Keywords

Neotype designation, new synonymy, Protothyreophora, preimaginal instars, life history, systematics

Introduction

It is undeniable that some organisms are able to provoke great curiosity, which may last through generations of students. There are several, often interrelated reasons for this: rarity for example, true or apparent, but also a certain aesthetic appeal or unusual biology. All of these factors have contributed to the long-term popularity of thyreophorine Piophilidae, particularly that of the European species. These unusual-looking flies, commonly known as bone-skippers, appear to be associated as necrophages with large vertebrate carrion, including human corpses, and have always been considered rare, almost legendary (cf. Pape, 2009). The three European thyreophorines, Centrophlebomyia furcata (Fabricius, 1794), C. anthropophaga (Robineau-Desvoidy, 1830) and Thyreophora cynophila (Panzer, 1798), were even considered extinct for over a century. All three were rediscovered in the last 30 years, during which almost every record of a thyreophorine was published (Freidberg 1981; Michelsen 1983; Contini and Rivosecchi 1993; Gòmez-Gòmez et al. 2008; Martín-Vega and Baz 2011; Martín-Vega et al. 2010; Carles-Tolrá 2011; Carles-Tolrá et al. 2010, 2011, 2012; Zaldivar Ezquerro et al. 2011), sometimes with a certain media emphasis (Appendix 1). Despite the aura of exceptionality surrounding these flies, and the excitement their rediscovery has recently raised among dipterists, there is still some confusion concerning their taxonomy and nomenclature.

The present work was triggered by the finding of several specimens of a species of *Centrophlebomyia* Hendel, 1903 in central Italy (Monte Velino, Central Apennines), during a study on the necrophilous insect fauna associated with carrion (Lo Giudice, 2007). These specimens are conspecific with those recorded 25 years ago from Sardinia as *C. anthropophaga* (Contini and Rivosecchi 1993; Martín-Vega et al. 2010). However, their identification turned out to be trickier than expected and had to rely on the study of all known Palaearctic thyreophorines, including genus *Protothyreophora* Ozerov, 1984. This allowed us to review the taxonomy and nomenclature of the Palaearctic Thyreophorina, modifying the arrangement proposed for this group by Martín-Vega et al. (2010), and designating a neotype for *C. anthropophaga*. We also provide the first ever information on preimaginal instars of *C. anthropophaga* and an updated key to all Palaearctic species of the group.

Material and methods

Specimens

Male terminalia, pinned specimens and larvae were examined, uncoated, with a Hitachi TM1000 environmental scanning electron microscope (ESEM). Male terminalia were also slide mounted. Line drawings were made using a drawing tube. Figure 38 was prepared from composites of images captured using a DS-L1 digital camera (Nikon, Tokyo) mounted on a MZ 12.5 stereoscopic microscope (Leica, Wetzlar, Germany) and processed with Helicon Focus Pro software (Kharkov, Ukraine). Male terminalia were dissected following the method described by Cerretti & Pape (2012) and, after examination, were preserved in glycerine in a plastic microvial pinned beneath the specimen.

The material examined is deposited in the following collections (acronyms as used in the text):

MZUR	Museum of Zoology, Sapienza Università di Roma, Italy;
NHMW	Naturhistorische Museum, Wien, Austria;
TAU	Department of Zoology, Tel Aviv University, Tel Aviv, Israel;
ZMUC	Natural History Museum of Denmark, Zoological Museum, University of
	Copenhagen, Denmark.

Label data of type specimens are given verbatim using the following symbols:

/ end of a line and beginning of the next;// end of a label and beginning of the next (from top to bottom on the same pin).

Terminology

Morphological terminology essentially follows Merz and Haenni (2000) except for the antenna, for which we follow Stuckenberg (1999). Measurements and ratios of the head follow Cerretti (2010).

Results

Taxonomy

Genus *Centrophlebomyia* Hendel, 1903 http://species-id.net/wiki/Centrophlebomyia

Figs 1–38

- *Centrophlebomyia* Hendel 1903: 216. [original description] type species: *Musca fur-cata* Fabricius, 1794: 343, by original designation.
- *Thyreolepida* Sack 1939: 4. [original description] type species: *Thyreolepida cinerea* Sack, 1939:4, by original designation.
- Protothyreophora Ozerov 1984a: 465. [original description] type species: Protothyreophora grunini Ozerov 1984a, by original designation; syn. n. (see below).

References. Hendel 1903; McAlpine 1977; Ozerov 1984a; Ozerov 1984b; Ozerov 2000.
 Recognition. Brownish, scathophagid-like flies, body length 4–8 mm. Body densely to moderately microtomentose and covered with long, fine setulae, especially

in males. Frons with one or two upper reclinate orbital setae. Ocellar seta, medial and lateral vertical setae, and postvertical seta long and robust. Two to ten frontal setae usually arranged more or less regularly around lunula. Face with a strong, flattened median carina, antennal grooves deep. Parafacial with a patch of microtomentum at mid length (Fig. 15). Compound eye almost round in lateral view. Two pairs of strong vibrissae present, subequal in length and strength. Thoracic chaetotaxy as follows: 0-2 postpronotal setae (postpronotal setae usually absent in male of *C. furcata*); 1 + 1 intraalar, 1-2 + 3 strong dorsocentral setae, 1 postalar, 2 notopleural setae, 0-1 prescutellar acrostichal setae. Scutellum long, dorsally flattened, much more developed in male than in female, with two pairs of setae, apical pair very long and strong, almost spiniform in larger males. Dorsal surface of scutellum bare. Development of scutellum in male related to body size. Propleural seta strong. Katepisternum densely setulose, with one strong katepisternal seta at upper posterior margin. Anepisternum with a row of setae along posterior margin, one of them strong. Thorax (except scutellum) very finely setulose throughout, besides the strong setae.

Wing membrane hyaline. Costa more or less spinose (i.e., with a regular row of stronger setulae interspersed with the general costal setulae), spine-like setae stronger in male than in female. Anal vein fading out well before wing margin. Legs thickly setulose in both sexes (almost woolly in male). Fore femur with 5–6 weak posteroventral setae near apex, scarcely differentiated in male. Hind femur with 2–3 anteroventral setae near apex. Mid tibia with five apical setae on ventral side: middle and lateral ones strongest. Hind tibia with one short, curved apical seta on posteroventral surface. Tarsi unmodified.

Preimaginal instars. Described by Freidberg (1981) and below.

Distribution. Europe, North Africa, Middle East, Russian Far East, northern India (Kashmir and Darjeeling).

Remarks. The generic diagnosis incorporates the characters given by McAlpine (1977) based only on the type species *C. furcata*.

Included species

Centrophlebomyia anthropophaga (Robineau-Desvoidy, 1830)

http://species-id.net/wiki/Centrophlebomyia_anthropophaga Figs 1-4, 11, 12, 15-18, 22, 24-38

Thyreophora anthropophaga Robineau-Desvoidy 1830: 623 – type locality: Paris (France).

Type material examined. Neotype (designated below). Male (ZMUC), here designated, from Sardinia, Italy and bearing the following labels: SARDEGNA / Belvì (NU) / 10.X.'84 [39°57.889'N, 9°11.111'E] // Neotype & / *Thyreophora | anthropophaga |* Robineau-Desvoidy, 1830 / M. Mei & P. Cerretti des. 2013 // *Centrophlebomyia | anthropophaga |* (Robineau-Desvoidy, 1830) / M. Mei & P. Cerretti det. 2013).



Figures 1–10. Males of *Centrophlebomyia* spp. **1**, **3**, **5**, **7**, **9** head and thorax in dorsal view **2**, **4**, **6**, **8**, **10** head in lateral view **1–4** *C. anthropophaga* (Italy) **5–6** *C. furcata* (Italy) **7–8** *C. grunini* (Russian Far East) **9–10** *C. orientalis* (India). In red the microtomentum pattern of head; in yellow the shiny, non microtomentose, pattern of thorax.

Other material examined. 5 $\Diamond \Diamond$, 5 $\bigcirc \Diamond$, same data as neotype. 35 $\Diamond \Diamond$, 3 $\bigcirc \Diamond$, Italy, Abruzzo, L'Aquila province, Riserva Naturale Orientata Monte Velino, Man-

dridi, 42°7.696'N, 13°22.247'E, 1270 m, 11.XI.2005, G. Lo Giudice, M. Mini, A. Vigna Taglianti legit. 20 \Im \Im , 13 \Im \Im , same data but 9.XII.2005; 13 \Im \Im , 4 \Im \Im , same data but 25.I.2006; 7 \Im \Im , 1 \Im \Im , same data but 25.X.2006; 2 \Im \Im , same data but 9.XI.2006; 3 \Im \Im , 5 \Im \Im , same data but 16.XI.2006; 6 \Im \Im , 4 \Im \Im , same data but 30.XI.2006; 2 \Im \Im , same data but XI.2006 reared from larvae, (see below); 13 \Im \Im , 2 \Im \Im , same data but 14.X.2007; 2 \Im \Im , same data but 18.XI.2008.

References. Michelsen 1983; Contini and Rivosecchi 1993; Martin-Vega et al. 2010.

Remarks. Specimens from Sardinia were collected from a bag of dead, decaying snails (Contini and Rivosecchi, 1993). Specimens from central Italy were collected with hand net (adults) and pitfall traps (adults, larvae) filled with a saturated solution of water and salt (NaCl), in a large fenced area where a feeding station ("vulture restaurant") was kept for a population of griffon vultures living in the Nature Reserve. Twenty pitfall traps were placed around dead and dismembered sheep (front and rear quarters without skin and guts).

Distribution. ?France (Paris), Italy (Sardinia, Central Apennines).

Redescription. Colouration. Head, including antenna and palpus, usually reddish yellow; sometimes dorsal half of occiput black. Occiput, ocellar triangle, genal dilation, and parafacial covered with microtomentum. When seen in dorsal view, the microtomentum that covers the occiput anteriorly outlines a three-pointed crown on the frons between the medial posterior margin of eyes (Figs 1, 3, 11, 12); middle tip of crown corresponds to anterior ocellus; lateral tips, laterally confined by eyes, end about level with posterior ocelli or slightly anteriorly. Prementum black. Postpronotum at least partly reddish laterally (reddish colour usually not visible in dorsal view). Scutum black in ground colour, covered with thin microtomentum except around base of dorsocentral setae and two lateral, longitudinal shiny vittae, widely interrupted at level of transverse suture (Figs 1, 27) (suture well developed laterally up to level of dorsocentral row). Scutellum at least apically yellow. Legs usually entirely yellow, rarely tarsi darkened. Abdomen usually entirely yellow or light brown, but can vary from dark brown to shiny black dorsally in some females. Setae of whole body black. Wing hyaline.

Head (Figs 1–4, 11–12, 15, 27). Head about as wide as thorax. Eye almost round. Frons 2.0–2.5 times as wide as an eye in dorsal view. Parafacial 1/2–2/3 as wide as first flagellomere, both measured at mid length. Gena, in profile, 0.33–0.65 times as high as eye. Medial vertical seta well developed, reclinate. Lateral vertical seta well developed, about 4/5 of medial vertical seta, lateroclinate. One or (usually) two upper reclinate orbital setae; when two are present, then anterior one at most 1/3 as long as posterior seta, and distinctly thinner. Postocellar seta strong and reclinate, subequal in size to ocellar and medial vertical setae. Ocellar seta proclinate. Anterior margin of frons with 2–3 pairs of pro- and medioclinate, strong frontal setae. Fronto-orbital plate with scattered, short, proclinate or medioclinate setae, between posteriormost upper reclinate orbital seta and distal margin of pedicel. Vibrissa double, very strong. Antenna shorter than height of facial ridge; first flagellomere 1.3–2.0 times as long as pedicel. Occiput and genal dilation covered



Figures 11–15. *Centrophlebomyia* spp. **11–14** head in dorsolateral view [dotted line indicates the border of microtomentum] **11–12** *C. anthropophaga* (Italy) **13–14** *C. orientalis* (India) **15** *C. anthropophaga* (Italy), detail of head in anterodorsal view [arrow indicates microtomentum on parafacial].

with scattered black setae. Palpus well developed, apically clavate, covered with fine black setae.

Thorax (Figs 1, 3, 16, 17, 27). Thorax covered with fine black setulae, those on scutum distinctly shorter than those on pleurae. Postpronotum with or without 1–2 very fine setae in male (Fig. 16), usually with 2, relatively strong setae in female (Fig. 17). One strong presutural and 2 postsutural supra-alar setae; posterior postsutural supra-alar seta short and thin. One presutural and 3 postsutural dorso-



Figures 16–21. *Centrophlebomyia* spp. **16–17** *C. anthropophaga* (Italy), anterior part of thorax in dorsolateral view [red circles indicate postpronotal setae] **16** male **17** female **18–21** Wing **18** *C. anthropophaga* (Italy), detail of third costal sector (Cs₃) [in red the costal spine-like setae] **19–20** *C. grunini* (Russian Far East) **21** *C. orientalis* (India), detail of third costal sector (Cs₃).

central setae (Figs 1, 27) (2 postsutural dorsocentral setae may occur in smaller sized male specimens (Fig. 3)). One, short and weak, prescutellar acrostichal seta. Scutellum dorsally flat to slightly concave (ground plan trait of the Thyreophorina, McAlpine, 1977), more or less elongated posteriorly, with one lateral seta and one apical seta (Figs 1, 3); lateral seta usually much smaller than apical seta. Shape and size of scutellum strongly variable (Figs 1, 3, 27) between sexes and between males



Figures 22–26. Male terminalia of *Centrophlebomyia* spp. [**Ae** = ejaculatory apodeme; **Ap** = phallapodeme; **C** = cerci; **Ep** = epandrium; **Ph** = phallus; **S** = surstylus] **22** *C. anthropophaga* (Italy) **23** *C. orientalis* (India) **24–26** *C. anthropophaga* (Italy), phallus.

of different sizes (Figs 1, 3). Two notopleural setae. One anepisternal seta. One katepisternal seta. Legs robust, covered with long and fine setulae. Mid tibia with 3–5 robust ventral preapical setae. Claws well developed in both sexes, about as



Figures 27–29. Female of *Centrophlebomyia anthropophaga* (Italy) **27** head and thorax in dorsal view **28** ovipositor in dorsal view **29** spermatheca.

long as fifth tarsal segment in male, varying in length between 0.5 and 0.7 times as long as fifth tarsal segment in female. Ventral row of costal setae (specifically CS_3) characterized by the presence of some longer and stouter setae placed at more or less regular intervals (Fig. 18).

Abdomen. Male: more or less elongated; tergite 1 laterodorsally covered with short erect hair-like setae, medially bare; tergites 2 and 3 laterodorsally and ventrally covered with long, hair-like setae that become shorter toward the midline of tergites. Tergites 4 and 5 evenly covered with long, erect hair-like setae. Female: abdominal setae distinctly shorter.

Male terminalia (Figs 22, 24–26). Epandrium short and convex. Surstyli massive, almost touching each other posteromedially; distal margin of surstylus slightly bent pos-



Figures 30–34. Third instar of *Centrophlebomyia anthropophaga* (Italy) **30** habitus in dorsal view **31** habitus in lateral view **32** head in frontal view **33** cephalopharyngeal skeleton in lateral view **34** aQnterior spiracle in lateral view.

teriorly. Cerci very small, bearing long setae. Phallapodeme, in lateral view, very large with an evenly convex dorsal margin (Fig. 22). Pregonite well sclerotized, relatively narrow and slightly bent posteriorly; basally fused to hypandrium; pregonite with 1–2 fine setae distally. Postgonite very long, well sclerotized and evenly bent anteriorly. Pregonite and postgonite pincer-like in relative position, almost touching each other distally. Epiphallus attached basally and well developed. Basiphallus very long, tubular, covered with fine pubescence and membranous. Distiphallus massive, slightly sclerotized, covered with fine pubescence as in basiphallus; distiphallus with two large laterodistal lobes.

Female terminalia (Figs 28–29). Ovipositor long and telescopically retracted within fifth segment. Tergites 6 and 7 relatively wide and more or less flattened. Tergite 8 longitudinally divided into two halves. Cerci not differentiated. Two rounded and well sclerotized spermathecae.

Description of third instar and puparium. Both the larva and puparium of *C. anthropophaga* (Figs 30-38) correspond well to features given by McAlpine



Figures 35–38. Third instar and puparium of *Centrophlebomyia anthropophaga* (Italy) **35** last segment bearing posterior spiracle in posterior view **36** last segment bearing posterior spiracle in lateral view **37** posterior spiracles in posterior view **38** puparium in dorsal view.

(1977), Ozerov (2000) and Ozerov and Norrbom (2010) for other piophilids and by Freidberg (1981) for *C. furcata*. Here we provide additional information not given in previous descriptions. Nearly all the segments of the third instars have a lateral "dotted" line composed of microscopic, concave structures which may be sensory organs (Fig. 31). Their shape and position suggest that they may be mechanoreceptors of pressure or stretching. These structures have not been noted in previous descriptions of piophilid larvae; they were either overlooked or are unique to *C. anthropophaga*.

Notes on larval development. On April 5th (n=15) and May 3rd (n=7), 2006, several mature larvae were collected from the soil a few centimetres below the sheep quarters used as bait for the pitfall traps set in the "vulture restaurant" (see above under "Remarks"). The larvae were then transferred into two petri dishes (12 cm diameter): one filled with potting soil, the other with natural soil collected with the larvae from under the carcass. Moisture was provided each week until midsummer. All larvae remained active, though only slightly so, during this time. By June 1st, five out of 22 larvae had died. The loss of larvae continued steadily and by the beginning of September only six

larvae were left, three in the potting soil and three in the natural soil. In early October 2006, two puparia were found in each dish and all the remaining larvae were dead. The four puparia and small amounts of soil were isolated in smaller dishes. An adult male emerged in November from one of the puparia in the natural soil, and another adult (possibly a male) was found dead in its puparium in the potting soil. The remaining two puparia failed to produce adults.

Our observations are consistent with those of Freidberg (1981; 2010 pers. comm.) on *C. furcata* larvae reared in Israel. Mature *C. furcata* larvae remained buried in the soil through spring and summer, estivating in this stage or as prepupae, and pupariated at the beginning of autumn. The larvae did not feed but were still more or less active. Most of the larvae died during the summer months and only very few adults emerged in October.

Centrophlebomyia furcata (Fabricius, 1794)

http://species-id.net/wiki/Centrophlebomyia_furcata Figs 5–6

Musca furcata Fabricius, 1794: 343 – type locality: "habitat in Gallia". *Thyreolepida cinerea* Sack, 1939: 4 – type locality: "Rehoboth [Rehovot] bei Jaffa" (Israel).

Material examined. 1 \bigcirc , 1 \bigcirc , 1 \bigcirc , 1srael, Tel Aviv, 17.XII.1977, A. Freiberg legit (MZUR); several males and females, same data (TAU). 16 $\bigcirc \bigcirc$, 9 $\bigcirc \bigcirc$, Italy, Latium, Monti della Tolfa, Mount S. Ansino, 332 m, 42°03'51.85"N, 11°59'47.05"E, 28.XII.2011, M. Mei legit, on dead sheep (MZUR).

References. Hendel 1903; McAlpine 1977; Freidberg 1981; Ozerov 2000; Martìn-Vega et al. 2010.

Distribution. Europe: Austria, Cyprus, France, Germany, Greece, Italy, Spain, United Kingdom; North Africa: Algeria; Middle East: Turkey, Israel.

Centrophlebomyia grunini (Ozerov, 1984), comb. n.

http://species-id.net/wiki/Centrophlebomyia_grunini Figs 7–8, 19–20

Protothyreophora grunini Ozerov 1984a: 466 – type locality: "Амурская област, Г. ЗеЯ" [= Amur region, near Zeya].

Material examined. 1 ♂,1 ♀, each bearing the following labels: [Russia] Амурская обл[аст] / Г. ЗеЯ [= Amur region, Zeya.] 1.VIII.1981 /А. Ozerov / PARATYPE (ZMUC). **References.** Ozerov 1984a, 2000.

Distribution. Russian Far East.

Centrophlebomyia orientalis (Hendel, 1907), stat. r.

Figs 9-10, 13-14, 21, 23

- *Centrophlebomyia orientalis* Hendel 1907: 243 type locality: "Indien, Darjeeling, am Himalaya".
- Treated as junior synonym of *anthropophaga* Robineau-Desvoidy, 1830 by Martin-Vega et al. (2010: 611).

Type material examined. Holotype male, bearing the following labels: [INDIA] Darjeeling / Juni / Frusthofer leg. // *Centrophlebomyia* / *orientalis* / Hendel [handwritten] // Type [red label] // Holotypus [red label] // *Pseudotyreo-* / *phora orientalis* / Hendel / A. Ozerov det., 1984 (NHMW).

Other material examined. INDIA (Kashmir) Gulmarg, 2600–3000 m, 17.VIII 5.IX.1978: 2 승승, 1 ♀ (ZMUC).

References. Hendel 1907; Michelsen 1983; Ozerov 2000.

Distribution. Northern India (Darjeeling, Kashmir).

Key to species of Centrophlebomyia

1 Scutum mostly shiny black with two large, longitudinal, silver stripes of microtomentum aligned with, and along the entire length of, dorsocentral setae (Fig. 7 [where the three shiny black vittae are yellow highlighted]). Head almost entirely smooth, katepisternum without microtomentum. Costal vein without spine-like setae (Figs 19-20). [Gena 0.44-0.47 times as high as eye in lateral view (Fig. 8)]..... C. grunini (Ozerov) comb. n. Scutum usually more extensively covered with microtomentum, and not showing the pattern described above (Figs 1, 3, 5, 9, 27). Head microtomentose at least on medial dorsal portion of postcranium, katepisternum at least partly microtomentose (e.g., dorsal and posterior to base of katepisternal seta). Ventral row of costal setae characterized by some longer and stouter (spine-like) setae placed at more or less regular intervals, especially on Cs_a 2 Gena 0.68–0.95 times as high as eye in lateral view (Fig. 6). One upper reclinate orbital seta (Figs 5, 6). Genal dilation and occiput entirely covered with microtometum. Occipital microtomentum extends anteriorly on fronto-orbital plate as shown in Fig. 5 [in red]. One presutural dorsocentral seta (Fig. 5). Katepisternum entirely covered with microtomentum. Male: Gena 0.33–0.65 times as high as eye in lateral view (Figs 2, 4, 10). Two upper reclinate orbital setae (exceptionally only one in *C. anthropophaga*) (Figs 2, 4, 10). Occipital microtomentum never extending anteriorly on fronto-orbital plate (Figs 1, 3, 9 [in red]). Occipital microtomentum extends anteriorly on frons as shown in Figs 1, 3, 9, 11-14 [in red]. One or two presutural dorsocentral setae. Katepisternum varying from entirely covered with microtomen-Genal dilation and occiput entirely covered with microtometum (Figs 1, 3, 11, 12 [in red]). Occipital microtomentum extends anteriorly on frons as shown in Figs 1, 3, 11, 12 [in red]. One presutural dorsocentral seta (Figs 1, 3, 27). Katepisternum entirely covered with thick microtomentum. Usually two upper reclinate orbital setae, the anterior one very short and weak (Figs 2, 4) (only one upper reclinate orbital seta present in a few specimens from Sardinia). Male: phallapodeme, in lateral view, with an evenly convex dorsal margin and posterior tip lobe-like (Fig. 22); one or rarely two hair-like postpronotal setae......anthropophaga (Robineau-Desvoidy) Genal dilation entirely smooth, occiput largely without microtomentum laterally (Figs 9, 13, 14 [where microtomentum is red highlighted]). Occipital microtomentum extends anteriorly on frons as shown in Figs 9, 13, 14 [in red]. Two presutural dorsocentral setae (Fig. 9). Katepisternum almost entirely smooth. Two upper reclinate orbital setae, the anterior one distinctly shorter but somewhat stout (Fig. 10). Male: phallapodeme, in lateral view, with an almost straight dorsal margin, posterior tip narrow and hook-like (Fig. 23); two strong postpronotal setaeorientalis (Hendel)

Discussion and conclusion

The neotype designation of "anthropophaga"

Martín-Vega et al. (2010) recognised two species in the genus *Centrophlebomyia: Centrophlebomyia furcata* (Fabricius, 1794), found in Europe, North Africa and the Near East, and *C. anthropophaga* (Robineau-Desvoidy, 1830) (with *Centrophlebomyia orientalis* Hendel, 1907 in synonymy), known from Paris (France), Sardinia (Italy) and northern India.

Centrophlebomyia anthropophaga was described by Robineau-Desvoidy (1830, in *Thyreophora*) "based solely on his memory of specimens he had observed in large numbers destroying preparations of human muscles, ligaments and bones in the Paris School of Medicine in August 1821" (Martín-Vega et al. 2010: 611). The original description is too general and inadequate to properly characterize the species and, as usual for Robineau-Desvoidy, there are no illustrations. No type material exists because no specimens were collected at the time the observations were made. Hence, the true identity of this nominal species has remained uncertain. It was treated as an "invalid" (in the sense of "unavailable") name in the Catalogue of Palaearctic Diptera (Papp, 1984), but was correctly interpreted as an available name according to the present *Code* (ICZN 1999) by Martìn-Vega et al. (2010). Just prior to the appearance of the Catalogue, the name *anthropophaga* was resurrected by Michelsen (1983)

("with a rather bold assumption", see Martín-Vega et al. 2010: 611) for specimens of a thyreophorine species collected in Kashmir. This name was used also by Contini and Rivosecchi (1993) for specimens of Centrophlebomyia collected in Sardinia that were considered conspecific with those of Michelsen (see also Rivosecchi, 2008). The existence of *C. orientalis*, a nominal species briefly described by Hendel (1907) from Darjeeling (West Bengal, India), appears to have escaped the attention of these authors also because not listed in the catalogues. Ozerov (2000), in his review of the Palaearctic Piophilidae, treated the specimens from Kashmir (Michelsen, 1983) and Sardinia (Contini & Rivosecchi, 1993) as C. orientalis. Ozerov (2004) later recognized only C. furcata in Europe and recorded it from Sardinia and Czech Republic. In the most recent treatment of Centrophlebomyia, Martín-Vega et al. (2010) considered Centrophlebomyia from Sardinia and India as conspecific under the name C. anthropophaga and formally placed C. orientalis in synonymy. It is noteworthy that Contini & Rivosecchi (1993) never studied the material of Michelsen (1983), only his drawings and descriptions, and neither Ozerov (2000) nor Martín-Vega et al. (2010) studied the Sardinian specimens.

Our study shows that specimens of *Centrophlebomyia* from Sardinia and central Italy are conspecific and are different from both *C. orientalis* and *C. furcata*, so we here propose to remove *orientalis* Hendel from synonymy with *anthropophaga* Robineau-Desvoidy.

Furthermore, considering the confused taxonomic and nomenclatural situation described above, created by Michelsen's (1983) resurrection of the name *anthropopha-ga* and by the subsequent repeated use of this name (Contini and Rivosecchi,1993; Martìn-Vega et al., 2010), we see a need to designate a neotype to fix once and for all the identity of this nominal species.

Considering that:

- *Centrophlebomyia anthropophaga*'s original description is vague and insufficient, and no type specimens ever existed in collections as no actual specimen was ever collected;
- ii) The name *anthropophaga* is nomenclaturally available according to the *International Code of Zoological Nomenclature* (1999);
- Michelsen (1983) convincingly showed that Robineau-Desvoidy's original description of *C. anthropophaga* is a poor match with *C. furcata* (the only other european species known at the time) but provides a reasonable fit with his Kashmir material (i.e., with *C. orientalis*);
- iv) Robineau-Desvoidy's original description of *C. anthropophaga* is not inconsistent also with characters shown by the Italian specimens;
- v) The *Centrophlebomyia* from Italy is not conspecific with *C. orientalis*, the species dealt with by Michelsen (1983), nor with *C. furcata*, and is actually an unnamed species;
- vi) The specimens from Sardinia were already referred to under the name *an-thropophaga* by Contini and Rivosecchi (1993) and Martin-Vega et al. (2010);

we select as neotype a male specimen from Sardinia chosen among those studied by Contini and Rivosecchi (1993). As no French or European material of *C. anthropophaga* (*sensu* this paper) is known to exist, our choice of a Sardinian specimen is essentially as near as practicable to the original type locality, thereby fulfilling Article 75.3.6 of the *Code* (ICZN 1999). We refrain from proposing a new name for the Italian species because it would not resolve the problem of the name *anthropophaga*, that would remain available and valid, though not associated with type specimens nor unambiguously attributable to a known species.

Protothyreophora as a junior synonym of Centrophlebomyia

The thyreophorine genus *Protothyreophora* was proposed by Ozerov (1984a) for the single species P. grunini, stressing that it is distinct from Centrophlebomyia in having two upper reclinate orbital setae instead of only one, two presutural dorsocentral setae instead of one, a distinctive pattern of thoracic microtomentum and the costal vein without any spine-like setae distally. This shows that Ozerov based his definition of Centrophlebomyia exclusively on characters of the type species C. furcata. Our examination of specimens of C. orientalis shows that this species has 2 upper reclinate orbital setae and 2 presutural dorsocentral setae, as in C. grunini. Moreover, the spine-like setae on the costa in thyreophorines may vary also between males and females of the same species (C. furcata), and be present or absent in different species of the same genus (Piophilosoma Hendel). The characteristic pattern on the thorax of C. grunini (Fig. 7), with two longitudinal bands of grey microtomentum along the line of the dorsocentral setae, contrasting with the remaining smooth surface, can be interpreted as having evolved from the pattern found in other species of Centrophlebomyia (small smooth areas lacking microtomentum, feebly developed in C. furcata and C. anthropophaga but much more extensive in C. orientalis) (Figs 1, 5, 9).

For these reasons, we consider the monotypic genus *Protothyreophora* as a junior synonym of *Centrophlebomyia*.

Concluding remarks

The European thyreophorine species have always been considered very rare insects and have famously also been considered as locally or even globally extinct (Cogan and Dear 1975; Fontaine et al. 2007; Pape 2009). We still know almost nothing about the biology, ecology and distribution of these flies, due both to their apparent rarity and the lack of targeted research. It was known for a long time (e.g., Robineau-Desvoidy 1842, 1849) that thyreophorine species have a winter phenology and are preferentially associated with large carcasses in an advanced state of decay, but for many decades there was no attempt to use this information to launch determined searches for these insects. The first detailed study was that of Freidberg (1981) on the biology of *C. furcata* in

Israel. Additional data were published on *C. grunini* in the Russian Far East by Ozerov (1984b), and only in the last few years are we beginning to understand the ecology of *Thyreophora cynophila* after its rediscovery in Spain (Carles-Tolrá et al. 2010; Martín-Vega and Baz 2011). Further studies are necessary to increase our knowledge of the ecology of these flies and to assess their conservation status.

It would seem that these flies may also be relatively abundant in sites where they are present (Freidberg 1981; Carles-Tolrá et al. 2010; and authors pers. obs.), but in general they seem to be very localized and living at low population densities. Martín-Vega and Baz (2011) noted the role of "vulture restaurants" and protected areas in maintaining populations of bone-skippers, but they considered other measures to be necessary as well, such as different management practices of livestock and wild ungulates aimed at naturally generating a constant availability of large carcasses. As mentioned above, *C. anthropophaga* was also collected by us in a "vulture restaurant", where it was present in abundance, but we have no further information on the presence of this species elsewhere in central Italy. *Centrophlebomyia furcata* was collected by one of us (MM) in a rather remote area characterized by a considerable and continuous presence of wild cattle, sheep and horses, and where carcasses of such large animals that died naturally are regularly present.

It would also be interesting to assess the role of food sources other than large mammal carcasses in maintaining natural populations of these flies. Other studies have shown that thyreophorine species have also been collected from a bag of dead decaying snails (*C. anthropophaga*: Contini & Rivosecchi, 1993), dead rodents (*C. grunini*: Ozerov, 1984a), traps baited with dead squids (*T. cynophila*: Martín-Vega et al., 2010), and a dead bird (Carles-Tolrá 2011). This would seem to indicate that these alternative food sources may play some role in maintaining populations of these insects.

We hope that the interest generated by the recent rediscovery of these flies will result in further studies on their reproductive biology and ethology, as combining the results of such studies with the already available morphological data may help explain the great polymorphism observed in adult males.

Acknowledgements

Most sincere thanks are due to J.E. O'Hara (Canadian National Collection of Insects, Ottawa, Canada) and two anonymous reviewers for their constructive comments on earlier drafts of this manuscript, to A. Minelli (Padova University, Italy), T. Pape and V. Michelsen (ZMUC) for their very useful and appreciated advice during the course of this study. Many thanks also to T. Pape (ZMUC), P. Sehnal (NHMW), A. Freidberg (TAU) and L. Rivosecchi (Rome, Italy), who allowed us to study the material under their care; to Tiziana Altea, Luciano Sammarone, Mario Posillico, Rosario Bartolo and Vincenzo Cofini (Riserva Nazionale Orientata Monte Velino, Abruzzo, Italy) who facilitated access and field work in the Reserve; to M. Mini (Rome, Italy) for help collecting the material; to Angela Cerasoli (Vienna) for assistance in examining the

holotype of *C. orientalis*. The authors also thank F. Mason (Italian National Forestry Service, Verona, Italy) and A. Vigna Taglianti (MZUR) for their constant support of our research activities in the Central Apennines.

References

- Carles-Tolrá M (2011) Primera cita de *Thyreophora cynophila* (Panzer) sobre cadáveres de aves (Diptera: Piophilidae: Thyreophorina). Boletín de la Sociedad Entomologica Aragonesa, 49: 355–356.
- Carles-Tolrá M, Cañete Saiz FJ (2012) Primera cita de *Thyreophora cynophila* (Panzer) para la provincia de Cuenca (España) (Diptera: Piophilidae: Thyreophorina). Boletín de la Sociedad Entomologica Aragonesa, 50: 254.
- Carles-Tolrá M, Compaired F, Vlasco J (2011) Thyreophora cynophila (Panzer), Centrophlebomyia furcata (fabricius) and other dipterans associated to winter carcasses (Insecta: Diptera). Boletín de la Sociedad Entomologica Aragonesa, 48: 217–220.
- Carles-Tolrá M, Rodriguez PC, Verdù J (2010) *Thyreophora cynophila* (Panzer, 1794): collected in Spain 160 years after it was thought to be extinct (Diptera: Piophilidae: Thyreophorini). Boletín de la Sociedad Entomologica Aragonesa, 46: 1–7.
- Cerretti P (2010) I tachinidi della fauna italiana (Diptera Tachinidae), con chiave interattiva dei generi ovest-paleartici. Volume I, 573 pp., Volume II, 339 pp. + CD-ROM. Cierre Edizioni, Verona.
- Cerretti P, Pape T (2012) Phylogenetics and taxonomy of *Ventrops* the largest genus of Afrotropical Rhinophoridae (Diptera). Invertebrate Systematics, 26(3): 274–292. doi: 10.1071/IS12001
- Cogan BH, Dear JP (1975) Additions and corrections to the list of British Acalypterate Diptera. Entomologist's Monthly Magazine, 110: 173–180.
- Contini C, Rivosecchi L (1993) Sulla presenza in Sardegna di *Centrophlebomyia anthropophaga* (Rob. Desv., 1830) (*sensu* Michelsen, 1983) (Diptera Thyreophoridae). Fragmenta entomologica, 25: 275–280.
- Fabricius JC (1794) Entomologia Systematica emendata et aucta. Vol. 4. Hafniae [= Copenhagen], 472 + i-vi + 1 pp.
- Fontaine B, Bouchet P, van Achterberg K (2007) The European union's 2010 target: putting rare species in focus. Biological Conservation, 139: 167–185. doi: 10.1016/j.biocon.2007.06.012
- Freidberg A (1981) Taxonomy, natural history and immature stages of the bone-skipper, Centrophlebomyia furcata (Fabricius) (Diptera: Piophilidae, Thyreophorina). Entomologica Scandinavica, 12: 320–326. doi: 10.1163/187631281794709728
- Gomez-Gomez A, Diaz-Aranda LM, Michelsen V (2008) Rediscovery of *Centrophle-bomyia furcata* (Fabricius, 1794) (Diptera: Piophilidae) in Europe. Studia dipterologica, 15(1/2): 231–237.
- Hendel F (1903) *Centrophlebomyia* nov. gen. Thyreophorinae. Zeitschrift für systematische Hymenopterologie und Dipterologie, 3: 215–216.

- Hendel F (1907) Neue und interessante Dipteren aus der kaiserl. Museum in Wien. Wiener Entomologische Zeitung 26(7–9): 245.
- International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature. Fourth edition adopted by the International Union of Biological Sciences. International Trust for Zoological Nomenclature, London. xxix + 306 pp.
- Lo Giudice G (2007) Studio di una comunità di Ditteri necrofagi nel Massiccio del Velino-Sirente (Appennino Centrale). Degree thesis (not published), supervisor A. Vigna Taglianti, Facoltà di Scienze Matematiche, Fisiche e Naturali, Università degli Studi di Roma "La Sapienza", 114 pp.
- Martín-Vega D, Baz A, Michelsen V (2010) Back from the dead: *Thyreophora cynophila* (Panzer, 1798) (Diptera: Piophilidae) "globally extinct" fugitive in Spain. Systematic Entomology, 35(4): 607–613. doi: 10.1111/j.1365-3113.2010.00541.x
- Martín-Vega D, Baz A (2011) Could the "vulture restaurants" be a lifeboat for the recently rediscovered bone-skippers (Diptera, Piophilidae). Journal of Insect Conservation, 15(5): 747–753. doi: 10.1007/s10841-011-9429-0
- McAlpine JF (1977) A revised classification of the Piophilidae, including "Neottiophilidae" and "Thyreophoridae" (Diptera: Schizophora). Memoirs of the Entomological Society of Canada, 103: i–vi, 1–66.
- Merz B, Haenni JP (2000) 1. 1. Morphology and terminology of adult Diptera (other than terminalia). In: Papp L, Darvas B (Eds) Contribution to a Manual of Palaearctic Diptera (with special reference to flies of economic importance). Vol. 1. General and Applied Dipterology. Science Herald, Budapest: 21–51.
- Michelsen V (1983) Thyreophora anthropophaga Robineau-Desvoidy, an "extinct" bone-skipper rediscovered in Kashmir (Diptera: Piophilidae, Thyreophorina). Entomologica Scandinavica, 14: 411–414. doi: 10.1163/187631283X00173
- Ozerov AL (1984a) A new Palearctic genus of the family Thyreophoridae (Diptera) from the Soviet Far East [in Russian]. Zoologicheskii Zhurnal, 63(3): 464–466.
- Ozerov AL (1984b) К биологин *Protothyreophora grunini* Ozerov (Diptera, Thyreophoridae). Доклады высшей школы. Биологические науки. № 4, С. 39–41. [The biology of *Proto-thyreophora grunini* Ozerov (Diptera, Thyreophoridae). Reports of the High School. Biological sciences, 4: 39–41.]
- Ozerov AL (2000) A.9. Family Piophilidae. In: Papp L, Darvas B (Eds) Contributions to a manual of Palearctic Diptera. Appendix. Science Herald, Budapest: 355–365.
- Ozerov AL (2004) Fauna Europaea: Piophilidae. In: Pape T (Ed) Fauna Europaea: Diptera Brachycera. Fauna Europaea version 2.4, http://www.faunaeur.org [accessed 23 January 2013]
- Ozerov AL, Norrbom AL (2010) Piophilidae. In: Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE, Zumbado M (Eds). Manual of Central American Diptera. Ottawa, Canada: National Research Council Press: 865–869.
- Pape T (2009) Chapter 5. Palaearctic Diptera from tundra to desert. In: Pape T, Bickel D, Meier R (Eds) Diptera Diversity: Status, Challenges and Tools. Brill, Leiden – Boston: 121–154. doi: 10.1163/ej.9789004148970.I-459.27

- Papp L (1984) Family Thyreophoridae. Vol. 9. In: Soós Á, Papp L (Eds) Catalogue of Palearctic Diptera. Micropezidae-Agromyzidae. Akadémiai Kiadó, Budapest: 241–242.
- Rivosecchi L (2008) Aggiunte e correzioni alle checklist di alcune famiglie di Ditteri della fauna italiana (Diptera). Bollettino della Società entomologica italiana 140 (2): 95–103
- Robineau-Desvoidy JB (1830) Essai sur les myodaires. Mémoires présentés par divers Savans à l'Académie Royal des Sciences de l'Institut de France (Sciences Mathématiques et Physiques), (2) 2: 813 pp.
- Robineau-Desvoidy JB (1842) Note sur le *Thyreophora cynophila*. Annales de la Société Entomologique de France 10, (1841): 273.
- Robineau-Desvoidy JB (1849) Communication (Séance du 10 Janvier 1849). Annales de la Société Entomologique de France 7: iv–vi.
- Sack P (1939) 62b. Thyreophoridae. In: Lindner E (Ed) Die Fliegen der palearktischen Region. Stuttgart: 1–7.
- Stuckenberg BR (1999) Antennal evolution in the Brachycera (Diptera) with a reassessment of terminology relating to the flagellum. Studia dipterologica 6: 33–48.
- Zaldivar Ezquerro C, Rodrìguez PC, Gòmez Vargas J (2011) *Thyreophora cynophila* (Panzer, 1798) (Diptera: Piophilidae: Thyreophorini): distribution area in La Rioja (Spain). Boletín de la Sociedad Entomologica Aragonesa 48: 403–405.

Appendix I

Online media coverage of recent findings of Thyreophorina in Europe: http://www.youtube.com/watch?v=gwqL02RstAw http://www.youtube.com/watch?v=QW-tOF0WtXA http://www.youtube.com/watch?v=zXgIrfwwRvg http://www.youtube.com/watch?v=Bmqgf-TaJsQ http://www.youtube.com/watch?v=eCm9I G7HI http://www.youtube.com/watch?v=p1QcpliZm3g http://www.youtube.com/watch?v=gGqGAEUDFUU http://www.youtube.com/watch?v=NnECVsursMs http://www.diptera.info/forum/viewthread.php?forum_id=5&thread_id=46137 http://www.diptera.info/forum/viewthread.php?forum_id=5&thread_id=26429 http://www.diptera.info/forum/viewthread.php?forum_id=22&thread_id=12704 http://www.diptera.info/forum/viewthread.php?forum_id=5&thread_id=11348 http://www.diptera.info/forum/viewthread.php?forum_id=5&thread_id=32315 http://www.diptera.info/forum/viewthread.php?forum_id=12&thread_id=32317 http://www.diptera.info/forum/viewthread.php?forum id=5&thread id=26429 http://news.bbc.co.uk/earth/hi/earth_news/newsid_9008000/9008585.stm

RESEARCH ARTICLE



First records of the genera Histeromerus Wesmael (Hymenoptera, Braconidae, Histeromerinae) and Ecclitura Kokujev (Hymenoptera, Braconidae, Euphorinae) in Italy

Sergey A. Belokobylskij¹, Augusto Loni², Andrea Lucchi², Umberto Bernardo³

I Zoological Institute Russian Academy of Sciences, St. Petersburg, 199034, Russia; Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, Warszawa 00–679, Poland 2 Department of Agriculture, Food and Environment, Pisa University, Via del Borghetto, 80 56124 Pisa, Italys 3 Istituto per la Protezione delle Piante, Consiglio Nazionale delle Ricerche, Sezione di Portici, Via Università, 133, Portici 80055, NA, Italy

Corresponding author: Sergey A. Belokobylskij (doryctes@gmail.com)

Academic editor: K. van Achterberg | Received 15 March 2013 | Accepted 13 June 2013 | Published 19 June 2013

Citation: Belokobylskij SA, Loni A, Lucchi A, Bernardo U (2013) First records of the genera *Histeromerus* Wesmael (Hymenoptera, Braconidae, Histeromerinae) and *Ecclitura* Kokujev (Hymenoptera, Braconidae, Euphorinae) in Italy. ZooKeys 310: 29–40. doi: 10.3897/zookeys.310.5136

Abstract

Braconid genera *Histeromerus* Wesmael, 1838 from subfamily Histeromerinae and *Ecclitura* Kokujev, 1902 from subfamily Euphorinae are recorded in the fauna of Italy for the first time. The discussions about taxonomic position, morphological characters and composition of these genera as well as the redescriptions of the genus and species of *E. primoris* Kokujev are given.

Keywords

Braconidae, Histeromerus, Ecclitura, parasitoids, new records, redescriptions

Introduction

Family Braconidae represents one of the largest and diversified families of parasitic Hymenoptera, including, with a few exceptions, mainly primary parasitoids. These occur in very diverse habitats and result linked to a wide range of hosts. As a fact, braconids can represent an interesting ecological resource as sensitive indicators of environmental richness and stability and of local diversity. The regulatory effect which they exert on host insects population derives from a very wide diversity of physiological and behavioural adaptations (Wharton 1993). On the other hand, the ecological information about many species of this family is scarce, so that any information regarding new findings in new areas is very welcome, as well as any information related to the habitat context where recordings are made. This paper deals with the first Italian record of Histeromerus mystacinus Wesmael and Ecclitura primoris Kokujev. Italian peninsula extends over a wide range of latitudes with numerous mountain ranges along its length. Such a geomorphological configuration results in many different environments suited to host a large insect biodiversity. Particularly interesting is the finding of E. primoris both in central (Tuscany) than southern (Campania) Italy, in two different environmental contexts. Nowadays, this species was considered very rare on the base of its reduced world distribution (Shaw 1997). Discovery of H. mystacinus in Italy is also very interesting because this is first record of this taxon on the real Mediterranean territory.

Terminology adopted for morphological features and measurements follows Belokobylskij and Maetô (2009). Wing venation nomenclature follows Belokobylskij and Tobias (1998) and Belokobylskij and Maetô (2009). The studied materials are kept in the collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia) and Department of Agriculture, Food and Environment, Pisa University (Pisa, Italy).

Taxonomic part

Genus Histeromerus Wesmael, 1838

http://species-id.net/wiki/Histeromerus

Type species. Histeromerus mystacinus Wesmael, 1838

Comments. *Histeromerus* Wesmael is a type genus of the monotypic subfamily Histeromerinae. The systematic position of this peculiar genus changed many times during its study. For a long time *Histeromerus* was considered as a member of subfamily Doryctinae and included in the tribe Doryctini or Histeromerini (Shenefelt and Marsh 1976, Yu et al. 2012), but other authors treated it inside the subfamily Braconinae (Achterberg 1976, Quicke 1987) or as a member of the separated subfamily Histeromerinae (Achterberg 1984, Quicke and Achterberg 1990, Belokobylskij 1998). According to the more recent molecular phylogenetic study on the cyclostome subfamilies (Zaldivar et al. 2006, Sharanowski et al. 2011), this genus was put inside subfamily Rhyssalinae. On the other side, numerous apomorphic characters of this taxon (prepectal carina and metapleural flange absent, fore and middle tibiae with clusters of spines, hind basitarsus about twice longer than remainder of hind tarsus, first



Figures 1–9. *Histeromerus mystacinus* Wesmael (female) 1 habitus, dorsal view 2 head, lateral view 3 head, front view 4 head and antenna, dorsal view 5 fore tibia and tarsus 6 tip of ovipositor 7 mesosoma and first metasomal tergite, dorsal view 8 mesosoma, lateral view 9 fore and hind wings.

metasomal tergite without sublateral grooves, dorsope absent, ovipositor compressed and without apical notch or teeth, etc.) did not show a close relation of *Histeromerus* with any rhyssaline taxa so seems better to keep this genus in the separate subfamily Histeromerinae until receiving of additional and more robust information about its taxonomic position.

Hitherto, four species of *Histeromerus* are known. Type species *H. mystacinus* was recorded only in the Western Palaearctic (including Iran). *H. canadensis* Ashmead, 1891, mainly known from U.S.A. and Canada, was also found in the Netherlands. *H. orientalis* Chou & Chou, 1991 was described from Taiwan and later was additionally recorded in Japan (Ogasawara Islands). Finally a fourth species, *H. clavatus* Austin & Wharton, 1992, was described from Australia (Queensland) (Yu et al. 2012).

Histeromerus mystacinus Wesmael is widely distributed in several European countries and also in Caucasus and Central Asia (North Iran). On the other hand, this species practically resulted unknown for the south part of Europe (Mediterranean coast). First discovery of *H. mystacinus* in Italy is very interesting, because expands the geographical distribution of this taxon in dry territories. Members of *Histeromerus* are gregarious ectoparasitoids of concealed living beetles' larvae from subfamilies Anobiidae, Buprestidae, Cerambycidae, Cisidae, Elateridae, Lucanidae, Lyctidae, and Ptinidae (Yu et al. 2012).

Histeromerus mystacinus Wesmael, 1838

http://species-id.net/wiki/Histeromerus_mystacinus Figures 1–9

Material examined. Italy: 1 female, Campania, Torre del Greco, (NA), Parco del Vesuvio, 3–18.VII.2007, Guerrieri leg.

Distribution. Ireland, U.K., Belgium, Netherland, Denmark, France, Germany, Czech Republic, Hungary, Italy (first record), Sweden, Poland, Slovakia, Ukraine, Bulgaria, Russia (European part), Georgia, Iran.

Genus Ecclitura Kokujev, 1902

http://species-id.net/wiki/Ecclitura

Type species. Ecclitura primoris Kokujev, 1902.

Comments. *Ecclitura* Kokujev is until recently monotypic genus originally described from Turkmenistan in the beginning of 20th century (Kokujev 1902).

Taxonomic position of *Ecclitura* was discussed in several publications. Muesebeck (1936) defined this genus as the most similar to *Perilitus* Nees, 1819 and *Rhopalo-phorus* Curtis, 1837 on the base of the wings venation and the long exerted ovipositor. Tobias (1966) in his paper about generic groupings and evolution of subfamily Euphorinae included *Ecclitura* in the *Perilitus* group together with the genera *Perili*

tus, Microctonus Wesmael, 1835, *Dinocampus* Foerster, 1862, *Streblocera* Westwood, 1833, *Ropalophorus* and *Centistina* Enderlein, 1912. Shaw (1985) in his phylogenetic study of subfamily Euphorinae, concluded that *Ecclitura* is a sister group of *Streblocera* focusing the synapomorphies on the lack of the first medial abscissa in the fore wing, the long and slender scape and the presence of dorsope on the first metasomal tergite. He included this genus in the tribe Microctonini (section 3) together with *Microctonus, Proclithrophorus* Tobias & Belokobylskij, 1981, and *Streblocera* and separated the tribes Perilitini (only with *Perilitus*) and Dinocampini (with *Centistina, Dinocampus* and *Rhopalophorus*). However, Tobias (1986) in his key to European species of Euphorinae retained the previous position of this genus in the tribe, but separated *Proclithrophorus* in the new tribe Proclithrophorini. Belokobylskij (2000), in the new key to Palaearctic euphorine genera, synonymized with *Perilitini* also tribes Cryptoxilonini and Townesilitini. *Ecclitura* here was related with *Streblocera* and *Heia* Chen & Achterberg.

Knowledge on molecular phylogeny and its implication for classification of subfamily Euphorinae are very limited. A specific publication for this task (Li et al. 2003) studied only a few taxa and a single gene (ribosomal 28S). This investigation included in the same group the genera *Microctonus* and *Streblocera* (and possibly related *Ecclitura*), but monophyly of the tribe Microctonini was not resolved. New preliminary information about Euphorinae phylogeny on the base of combined morphological (37 characters) and molecular (4 markers: 18S, 28S, CAD, COI) data was suggested by Stigenberg and Boring (Internet, unpublished data). One of the result of this work was the arrangement of *Ecclitura* in the tribe Dinocampini. A final and more comprehensive published information about this topic should help to better understand the real results of this vast and diverse investigation.

The single described species of this genus, *E. primoris*, was recorded in the Western Palaearctic Region. Two other undescribed species of this genus were reported also from U.S.A. (Shaw 1985), India and Vietnam (Belokobylskij 2000). The discovery of these genus and species in Italy makes it likely the finding of *Ecclitura* also in other climatically similar localities of South Europe and North Africa. No data are available about *Ecclitura* hosts. However, being phylogenetically related with the genus *Streblocera* (associated with Chrysomelidae) and sharing with this genus distinctive morphological features (structure of antenna, first metasomal tergite and ovipositor shapes: Shaw 1985, 2004) *Ecclitura* could be also imagobiont and parasitoid of the adults of some beetles (Chrysomelidae or Curculionidae).

Four females of *Ecclitura* were collected by Malaise traps closely to Napoli in the Campania Province. Fourteen females were captured in 2012 in three vineyards in the surroundings of Pisa (Tuscany), by using Malaise traps. These traps worked from the half of May to the half of October. *Ecclitura* specimens were captured from July 12 to October 4. Hitherto, no males of this species have never been recorded over area of his distribution, and it is possible *E. primoris* reproduces by thelytokous modality as already observed for several other species of Euphorinae (Shaw 2004, Reumer et

al. 2012). We have redescribed below the genus *Ecclitura* as well as its type species, because their original descriptions were incomplete and because variability of morphological characters of these taxa were investigated on the base of additional material from different localities.

Redescription of the genus. *Head* strongly transverse (Figs 10, 21). Vertex at least in anterior half densely rugose-reticulate with granulation. Eye with very short and rather dense setae. Ocelli arranged in obtuse triangle with base 1.1–1.3 times its sides. Occipital carina complete dorsally, archedly fused below with hypostomal carina weakly upper base of mandible. Frons with more or less distinct median carina in anterior half. Face weakly convex. Eye distinctly convergent below (Figs 14, 17). Tentorial pits deep, situated upper lower level of eyes. Malar suture distinct. Clypeal suture complete, but shallow. Mandible medium sized, almost not twisted. Palpi short, maxillary palpus 3-segmented, labial palpus 2-segmented. Antennae (Figs 11, 19, 20) weakly claviform, stable 17-segmented. Scape (Figs 12, 14, 17, 22) long, weakly curved, almost as long as maximum diameter of eye. Pedicel rather long, oval. First flagellar segment as long as or weakly longer than second segment. Segments in apical half of antenna weakly thickened. Apical segment pointed, but without spine.

Mesosoma (Figs 13, 16, 21, 23, 24). Pronope absent. Notauli complete, shallow and wide, densely rugulose-reticulate. Mesoscutum rugose-striate and setose on wide medioposterior half, smooth and glabrous on anterior and sublateral areas. Prescutellar depression deep and long. Scutellum convex, with lateral carinae, at least partly rugose. Sternaulus (precoxal sulcus) shallow, wide, long, densely rugulose. Prepectal carina distinct. Postpectal carina absent. Metapleural lobe long, wide, rounded apically. Propodeum strongly and abruptly rounded from median part (lateral view), weakly and widely longitudinally concave in medioposterior half (dorsal view), entirely ruguloseareolate, with lateral carinae.

Wings (Fig. 11, 15). Radial vein arising behind middle of pterostigma. Radial cell distinctly shortened. Second radial abscissa evenly and distinctly curved. First medial abscissa absent; as result, discoidal and first radiomedial cells fused. Mediocubital vein entirely sclerotised. Basal and recurrent veins distinctly convergent. Brachial cell short, widely open distally. Basal part of parallel vein weakly curved. In hind wing, first abscissa of mediocubital vein 4.0–5.0 times longer than second abscissa. Third abscissa of costal vein long; fourth abscissa almost straight.

Legs long and slender. Segments of median tarsus long. Fifth tarsal segments slender. Hind femur slender. Tarsal claws long, slender and weakly curved (Fig. 25).

Metasoma (Figs 11, 18). First tergite long, distinctly widened towards apex, its latero-ventral sides not fused, widely separated and with distinct split; dorsope small and very shallow; laterope indistinct. Second suture very shallow and fine. Only second tergite with separated laterotergites. Ovipositor (Figs 26, 27) long, straight, compressed laterally.

Distribution. Western Palaearctic, Nearctic, Oriental Regions.

Ecclitura primoris Kokujev, 1902

http://species-id.net/wiki/Ecclitura_primoris Figures 10–27

Material examined. Turkmenistan: female (holotype), "K.S. Anger", "Askhabad, 8. VI. 98, on lamp", "*Ecclitura Megaura primoris* ♀ Kok." (ZISP). Italy: 4 females, Campania, Torre del Greco, (NA), MT, 18–30.VII.2007 (Guerrieri leg.); 7 females, Pisa, Ceppaiano Crespina, MT, 28.VI–12.VII, 12–24.VII, 24.VII–09.VIII, 04–20. IX, 20.IX–04.X.2012 (A. Loni leg.); 7 females, Pisa, Poggio a Casone Crespina, MT, 12–24.VII, 24.VII–09.VIII, 09.VIII–04.IX, 20.IX–04.X.2012 (A. Loni leg.). Turkey: 1 female, "TR Edirne, Trakya, Univ. Biyoloji Bol. (Noct.) 16.9.1999"

Redescription. Female. Body length 2.3–2.5 mm; fore wing length 1.9–2.2 mm. *Head*. Width of head 2.1–2.3 times its median length, 1.4–1.5 times width of mesoscutum. Head behind eye strongly and weakly-curvedly narrowed. Length of eye (dorsal view) 1.8–2.0 times longer than temple. POL 1.0–1.5 times Od, 0.3–0.4 times OOL. Minimum width of face 0.70–0.75 times its height, 0.5–0.6 times its maximum width at level of antennal toruli or level of upper margins of eyes, almost equal to width of clypeus, about 0.9 times minimum (transverse) diameter of eye. Maximum diameter of eye 1.5–1.6 times its minimum diameter. Malar space very short, 0.10–0.13 times maximum diameter of eye, 0.4–0.5 times basal width of mandible. Distance between tentorial pits 2.5–3.0 times distance from pit to eye. Width of clypeus 1.9–2.0 times its median height.

Antennae 17-segmented, weakly claviform. Scape 1.0–1.2 times as long as height of face, 5.5–6.5 times longer than maximum width anteriorly, 4.0–5.0 times longer than maximum width laterally. Pedicel 1.3–1.5 times longer than wide. First flagellar segment 4.0–5.0 times longer than its maximum apical width, about as long as second segment. Penultimate segment 1.5–1.8 times longer than wide, 0.50–0.55 times as long as first segment, 0.5–0.8 times as long as apical segment.

Mesosoma. Length 1.4–1.5 times its median width. Mesoscutum highly and subvertically elevated above pronotum. Scutellum distinctly convex. Prescutellar depression long, with high median and often two to four lateral carinae, finely rugulose between carinae, depression about 0.3 times as long as scutellum. Scutellum 1.1–1.3 times longer than its anterior width. Subalar depression shallow, rather wide, densely rugulose-reticulate. Sternaulus complete, shallow, curved, coarsely rugulose-reticulate. Posterior mesopleural furrow (along mesopleural suture) coarsely crenulate.

Wings. Length of fore wing 2.7–2.8 times its width. Metacarp (inside radial cell) 0.7–0.9 times as long as pterostigma, 2.0–2.4 times longer than distance between apex of radial cell and apex of wing. Radial cell 2.4–2.5 times longer than maximum width. First radial abscissa about 0.5 times as long as maximum width of pterostigma. First radiomedial vein weakly sinuate or straight, 2.5–3.0 times longer than first radial abscissa, 0.3–0.4 times as long as second radial abscissa, 0.7–0.9 times as long as recurrent and second abscissa of medial veins combined. Distance between nervulus and basal vein



Figures 10–16. *Ecclitura primoris* Kokujev (holotype, female, Turkmenistan) 10 head, dorsal view 11 habitus, dorsal view 12 head and scape of antenna, lateral view 13 mesosoma and first metasomal tergite, dorsal view 14 head and scape of antenna, front view 15 fore wing 16 mesosoma, lateral view.

0.5–0.8 times nervulus length. Parallel vein basally sclerotised and weakly curved, unsclerotised its most apical part. Hind wing 3.8–4.1 times longer than maximum width.

Legs. Hind femur 4.9–5.5 times longer than maximum width. Hind tarsus almost as long as hind tibia. Hind basitarsus 0.6–0.7 times as long as second-fifth segments combined. Second segment of hind tarsus 0.45–0.50 times as long as basitarsus, 1.15–1.25 times longer than fifth segment.

Metasoma. First tergite almost regularly and distinctly widened from base to apex, with fine spiracular tubercle in basal third. Apical width of first tergite 2.3–2.8 times its mini-


Figures 17–27. *Ecclitura primoris* Kokujev (female, Italy) 17 head and scape of antenna, front view 18 first metasomal tergite, dorsal view 19 antenna, lateral view 20 basal part of antenna 21 head and mesosoma, dorsal view 22 scape of antenna, dorso-lateral view 23 mesosoma, lateral view 24 head, mesosoma and first metasomal tergite, dorso-lateral view 25 fore tarsus 26 tip of ovipositor, lateral view 27 tip of ovipositor, dorsal view.

mum width; length of tergite 1.8–2.0 times its apical width. Length of second and third tergites combined 1.1–1.3 times basal width of second tergite, 0.9 times their maximum width. Ovipositor sheath 0.6–0.7 times as long as metasoma, 1.4–1.5 times longer than first tergite, 0.7–0.8 times as long as mesosoma, and 0.30–0.35 times as long as fore wing.

Sculpture and pubescence. Head mainly and densely rugose-reticulate with granulation, vertex sometimes almost smooth posteriorly. Mesoscutum smooth in anterior half of median lobe and on wide median areas of lateral lobes, rugose-reticulate wide along notauli and rugose-striate on wide area in medioposterior half. Scutellum almost entirely distinctly rugose-reticulate, partly with granulation, sometimes smooth or almost smooth on medio-anterior third or anterior half. Mesopleuron mainly reticulaterugulose, smooth or almost smooth medially on rather small area. Propodeum without areas, coarsely and rather densely reticulate-areolate, with fine rugulosity. Hind femur densely and rather distinctly rugulose-granulate. First metasomal tergite densely striate in basal 0.6–0.8, smooth in apical 0.2–0.4. Remaining tergites entirely smooth. Mesoscutum glabrous on smooth areas, coved by short setae on sculptured areas. Face densely and very shortly setose.

Colour. Body mainly brownish yellow or yellow, metasoma often almost entirely yellow. Antennae yellow, infuscate in apical half. Palpi yellow. Legs yellow, all legs brownish. Ovipositor sheath almost black. Wings hyaline. Pterostigma entirely yellow.

Male. Unknown.

Distribution. Tajikistan, Turkmenistan, Iran, Azerbaijan, Russia (Dagestan), Turkey (first record), Albania, Italy (first record).

Acknowledgements

This work was partly supported by the grant of the research project within the framework of the Scientific Cooperation Agreement between CNR (Italy) and RAS (Russia) for first and fourth authors, grant of the Russian Foundation for Basic Research (No. 13-04-00026) for the first author and by Fondi di Ateneo 2012 (Pisa University) for the second and third authors. We are very thankful to Dr Emilio Guerrieri (Portici) for his interesting material collected in Campania and to Dr. Piergiorgio Castellani for hosting our surveys in his farm of Crespina (Pisa).

References

- Achterberg C van (1976) A preliminary key to the subfamilies of the Braconidae (Hymenoptera). Tijdschrift voor Entomologie 119(3): 33–78.
- Achterberg C van (1984) Essay on the phylogeny of Braconidae (Hymenoptera: Ichneumonoidea). Entomologisk Tidskrift 105(1/2): 41–58.
- Achterberg C van (1992) Revision of the genus Histeromerus Wesmael (Hymenoptera: Braconidae). Zoologische Mededelingen 66(9): 189–196.

- Belokobylskij SA (1998) Subfam. Histeromerinae. In: Lehr PA (Ed) Keys to insects of the Russian Far East. Neuroptera, Mecoptera, Hymenoptera 4(3): 109–111. Dal'nauka, Vladivostok. [In Russian].
- Belokobylskij SA (2000) Subfam. Euphorinae. In: Lehr PA (Ed) Keys to insects of the Russian Far East. Neuroptera, Mecoptera, Hymenoptera 4(4): 192–399. Dal'nauka, Vladivostok. [In Russian].
- Belokobylskij SA, Maeto K (2009) Doryctinae (Hymenoptera, Braconidae) of Japan. (Fauna mundi. Vol. 1). Warshawska Drukarnia Naukowa, Warszawa. 806 pp.
- Belokobylskij SA, Tobias VI (1998) Fam. Braconidae. Introduction. In: Lehr PA (Ed) Keys to insects of the Russian Far East. Neuroptera, Mecoptera, Hymenoptera 4(3): 8–25. Dal'nauka, Vladivostok. [In Russian].
- Li FF, Chen XX, Piao MH, He JH, Ma Y (2003) Phylogenetic relationships of the Euphorinae (Hymenoptera: Braconidae) based on the D2 variable region of 28S ribosomal RNA. Entomotaxonomia 25(3): 217–226.
- Kokujev NR (1902) Matériaux pour la faune hyménoptèrologique de la Russie. Entomologicheskoe Obozrenie 2: 4–12.
- Muesebeck CFW (1936) The genera of parasitic wasps of the braconid subfamily Euphorinae, with a review of the Nearctic species. United States Department of Agriculture, Miscellaneous Publications 241: 1–38.
- Quicke DLJ (1987) The Old World genera of braconine wasps (Hymenoptera: Braconidae). Journal of Natural History 21(1): 43–157. doi: 10.1080/00222938700770031
- Quicke DLJ, Achterberg C van (1990) Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 258: 1–95.
- Reumer BM, van Alphen JJM, Kraaijeveld K (2012) Occasional males in parthenogenetic populations of *Asobara japonica* (Hymenoptera: Braconidae): low *Wolbachia* titer or incomplete coadaptation? Heredity 108(3): 341–346. doi: 10.1038/hdy.2011.82
- Sharanowski BL, Dowling APG, Sharkey MJ (2011) Molecular phylogenetics of Braconidae (Hymenoptera: Ichneumonoidea), based on multiple nuclear genes, and implications for classification. Systematic Entomology 36: 549–572. doi: 10.1111/j.1365-3113.2011.00580.x
- Shaw SR (1985) A phylogenetic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). Entomography 3: 277–370.
- Shaw SR (1997) Subfamily Euphorinae. In: Wharton RA, Marsh PM, Sharkey MJ, (Eds) Manual of New World genera of the family Braconidae (Hymenoptera). The International Society of Hymenopterist, Washington, DC: 235–254
- Shaw SR (2004) Essay on the evolution of adult-parasitism in the subfamily Euphorinae (Hymenoptera: Braconidae). Proceedings of the Russian Entomological Society 75(1): 82–95.
- Shenefelt RD, Marsh PM (1976) Hymenopterorum Catalogus. Pars 13. Braconidae 9. Doryctinae. Dr W. Junk, 's-Gravenhage: 1263–1424.
- Tobias VI (1966) Genera groupings and evolution of the subfamily Euphorinae (Hymenoptera: Braconidae). Part II. Entomologicheskoe Obozrenie 45(3): 612–633 [In Russian]
- Tobias VI (1986) Subfam. Euphorinae. In: Medvedev GS (Ed) Keys to insects of the European part of the USSR. Hymenoptera. Braconidae. 3(4): 181–250. Nauka, Leningrad [In Russian]

- Wharton RA (1993) Bionomics of Braconidae. Annual Review of Entomology 38: 121–143. doi: 10.1146/annurev.en.38.010193.001005
- Yu DS, Achterberg C van, Horstman K (2012) World Ichneumonoidea 2011. Taxonomy, biology, morphology and distribution. CD/DVD. Taxapad, Vancouver, Canada. www.taxapad.com
- Zaldivar-Riveron A, Mori M, Quicke DLJ (2006) Systematics of the cyclostome subfamilies of braconid parasitic wasps (Hymenoptera: Ichenumonoidea): a simultaneous molecular and morphological Bayesian approach. Molecular Phylogenetics and Evolution 38: 130–145. doi: 10.1016/j.ympev.2005.08.006

RESEARCH ARTICLE



Review of the genus Agria (Diptera, Sarcophagidae) from China

Ming Zhang¹, Yi-ou Chen¹, Thomas Pape², Dong Zhang¹

1 College of Nature Conservation, Beijing Forestry University, Beijing 100083, China **2** Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK–2100 Copenhagen, Denmark

Corresponding author: Dong Zhang (ernest8445@163.com)

Academic editor: P. Cerretti | Received 17 April 2013 | Accepted 12 June 2013 | Published 19 June 2013

Citation: Zhang M, Chen YO, Pape T, Zhang D (2013) Review of the genus *Agria* (Diptera, Sarcophagidae) from China. ZooKeys 310: 41–55. doi: 10.3897/zookeys.310.5346

Abstract

Agria mihalyii (Rohdendorf and Verves, 1978) is recorded from China for the first time, and both sexes are thoroughly documented using a combination of illustrations, photographs and scanning electron microscopy images. The generic affiliation is corroborated from an expanded definition of genus *Agria* Robineau-Desvoidy, 1830, and a key to males of the two known species from China is provided. The distribution of coeloconic sensilla on the male pre- and postgonite are shown to possess significant diagnostic and phylogenetic information in this genus.

Keywords

Paramacronychiinae, Agria, coeloconic sensilla, new record, China

Introduction

The genus *Agria* Robineau-Desvoidy is a small genus of the subfamily Paramacronychiinae (Sarcophagidae), occurring in the Holarctic region and comprising eight species worldwide (Pape 1987, 1996, 1998, Fan and Pape 1996). The larvae are parasitoids of last instar larvae and pupae of Lepidoptera, occasionally also attacking sawflies (Roback 1954, Pape 1987, Kuhlmann 1995). Pape (1987, 1992, 1998) published a series of comprehensive taxonomic studies including this genus, which formed the basis for further research on this genus.

Copyright Ming Zhang et al. This is an open access article distributed under the terms of the Creative Commons Attribution License 3.0 (CC-BY), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Before the present contribution, only *A. affinis* (Fallén, 1817) was known from China (Fan and Pape 1996). Chao and Zhang (1988) described *Agria xiangchengensis* from Xiangcheng, Sichuan, but the species does not possess any of the features usually considered diagnostic for species of *Agria*, which led Pape (1996) to catalogue it under "Unplaced species-group taxa of Paramacronychiinae", and it was subsequently made the type species of a monotypic genus *Mimagria* by Verves (2001). While checking a series of *Agria* specimens from Beijing and Shanxi, we found one additional Chinese species, *A. mihalyii* (Rohdendorf and Verves, 1978). The primary aims of this article are to review the genus *Agria* from China; to redescribe the newly recorded species; to provide detailed documentation through illustrations, photographs and scanning electron microscopy images of *A. affinis* and *A. mihalyii*; and to refine the scientific definition of the genus. A key to the known species of *Agria* from China is also provided.

Materials and methods

The specimens examined were collected by sweeping from brushwood in mountainous regions and are deposited in the Museum of Beijing Forestry University, Beijing, China.

Methods for the preparation of terminalia, illustrations, photographs and scanning electron microscopy images follow Zhang et al. (2013).

Terminology of male morphology and terminalia follows McAlpine (1981) and Giroux et al. (2010), except for the term 'lateral sclerotization', which follows Pape (1992). Distributional data is taken from Pape (1996).

Taxonomic account

Agria affinis (Fallén, 1817)

http://species-id.net/wiki/Agria_affinis Figs 1 and 7

Musca affinis Fallén, 1817: 237.

Agria punctata: Robineau-Desvoidy 1830: 377; Pape 1987: 85; Fan et al. 1992: 613. *Agria affinis*: Verves 1982: 273; Pape 1996: 158; Fan and Pape 1996: 244.

Material examined. China: Beijing: 1 ♂, Xiaolongmen, 39°57'50"N, 115°28'26"E, 1100 m, 6.VII.2009, Coll. R. Bi and F. Li; 1 ♂, Mt. Songshan, 40°30'00"N, 115°49'12"E, 800–1000 m, 30.V.2012, Coll. Y.O. Chen; 1 ♂, Mt. Songshan, 40°30'00"N, 115°49'12"E, 800–1000 m, 30.V.2012, [collector unknown].

Distribution. China (Beijing, Qinghai, Xinjiang); Mongolia; Kazakhstan; Kyrgyzstan; common throughout Europe.



Figure I. Light micrographs of the male *Agria affinis* (Fallén, 1817). **A** Habitus, lateral view **B** Head, anterolateral view **C** Terminalia, epandrium, surstylus and cercus, lateral view **D** Surstylus and cerci, dorsal view **E** Sternite 5, ventral view **F** Genitalia, lateral view. Scale bars: **A**= 2.00 mm, **B**= 1.00 mm, **C**-**F**= 0.25 mm.

Agria mihalyii (Rohdendorf & Verves, 1978)

http://species-id.net/wiki/Agria_mihalyii Figs 2–6, 8 and 9

Angiometopa mihalyii Rohdendorf & Verves, 1978: 247. *Angiometopa mihalyii:* Verves 1981: 198, 1982: 279. *Agria mihalyii:* Pape 1992: 309, 1996: 159

Redescription. MALE. Body length 7.8-10.4 mm. Eyes bare. Fronto-orbital and parafacial plates black with grey pollinosity; postocular strip bare and with silvery grey pollinosity; parafacial plate and fronto-orbital plate with rows of fine bristles. Frontal vitta black, 2.10 × as broad as fronto-orbital plate at the narrowest point; frons at vertex $0.30 \times$ head width; frontal row of 9–12 strong bristles; outer vertical bristle not differentiated from postocular bristles, upper orbital bristle one. One pair of strong ocellar bristles. Gena ground color black, with sparse and short black bristles and silvery grey pollinosity, height $0.47 \times$ eye height in lateral view. Antenna slightly reddish basally, otherwise blackish, not reaching the level of vibrissal insertion, first flagellomere $1.70 \times$ as long as pedicel; arista black brown, short plumose in basal 3/5-2/3. Palpus orange. Thorax ground color black; scutum with three black dorsal vittae. Chaetotaxy: acrostichals 0+1, dorsocentrals 2(3)+3, intra-alars 1(0)+2(3), supra-alars 2, postpronotals 3, postalars 3 or 4, notopleurals 2, scutellum with 1 apical, 1 subapical, 1 basal and 1 discal bristles, with or without prebasal bristle. Pleuron with meropleurals 8–10, katepisternal bristles 2(3)+1, prosternum and metasternum bare, proepisternum bare, proepimeron in lower part with fine bristles, postalar wall bare or with fine bristles. Wing hyaline; subcostal sclerite and basicosta yellow, bare; tegula dark yellow, with black setulae; costal spine not differentiated, several dorsal black bristles at node of $R_{4,5}$ - $R_{2,3}$. Legs dark; fore femur with one strong row of posterior bristles, and with long and dense bristles along anteroventral, ventral and posteroventral margins, fore tibia with four anterodorsal and one posterior bristles; mid femur with two anterior and two posterior bristles, and distal 1/3 with short ventral comb-like posteroventral bristles, mid tibia with two or three anterior and one or two hair-like posterior bristles; hind femur with one row of anterodorsal bristles, and with long and dense bristles along anteroventral, ventral and posteroventral margins, hind tibia with one posterodorsal bristle, one row of anteroventral bristles (7 or 8) and one row of anterodorsal bristles (3 or 4). Abdomen long oval with densely grey pollinosity; tergites each with three distinct black spots; tergite 3 without median marginal bristles, tergite 4 with one pair of median marginal bristles, tergite 5 with strong marginal bristles, tergites 7+8 form a hump-shaped structure, epandrium brownish black, sternites 1-4 with long and dense bristles. Terminalia: Cercus tapering and pointed distally, basal 1/3 with long dense bristles; surstylus long and with oval rounded tip in lateral view (Fig. 5A). Ejaculatory apodeme large (Figs 4 and 8B). Pregonite broad, longer than postgonite, with some fine bristles on the basal part (Fig. 8C), and distal half perpendicular to basal half (Figs 4, 8A, 8C, 9A and 9D); postgonite broad with curved tip and a strong bristle proximally on anterior margin, six



Figure 2. *Agria mihalyii* (Rohdendorf and Verves, 1978). **A** Male habitus, lateral view **B** Female habitus, lateral view. Scale bars: A and B= 2.00 mm.

coeloconic sensilla (2.10 μ m in height, 1.68 μ m in width at the base and 1.20 μ m at the middle, and originating from a cuticular ring inside a shallow depression) distributed on distal half (Figs 8E and 8F); juxta very large and shell-shaped, apically with a pair



Figure 3. *Agria mihalyii* (Rohdendorf and Verves, 1978). **A** Male head, left anterolateral view **B** Female head, left anterolateral view **C** Male abdomen, dorsal view **D** Female abdomen, dorsal view. Scale bars: **A**-**D**= 1.00 mm.

of slanting processes covering most of the acrophallus in lateral view (Figs 4, 8A and 9A–C); phallic tube broad, with the dorsal part dark; acrophallus very broad basally, the distal part strongly tapering and recurving between the juxta (Figs 4, 9B and 9C); lateral sclerotizations short, with a serrated distal margin (Figs 4 and 9C).

FEMALE. Body length 7.0–9.0 mm. Frons at vertex $0.40 \times$ as broad as head width; frontal row of 9 or 10 bristles; outer vertical bristle differentiated from postocular bristles, proclinate orbital bristles two . Gena height $0.40 \times$ eye height in lateral view.



ejaculatory apodeme

Figure 4. Agria mihalyii (Rohdendorf and Verves, 1978). Male, genitalia, lateral view. Scale bar = 0.50 mm.



Figure 5. *Agria mihalyii* (Rohdendorf and Verves, 1978). Male, terminalia. **A** Cercus and surstylus, lateral view **B** Cerci, dorsal view **C** Sternite 5, ventral view. Scale bars: **A**-**C** = 0.50 mm.



Figure 6. Light micrographs of the female terminalia of *Agria mihalyii* (Rohdendorf and Verves, 1978). **A** Sternites 1–6, ventral view **B** Tergite 6, dorsal view **C** Terminalia, posterior view **D** Spermathecae **E** Terminalia, ventral view. Scale bars: **A**–**C** and **E**= 0.50 mm, **D**= 0.25 mm. Abbreviations: cercus (cerc); epiproct (epiprct); hypoproct (hyprct); sternite (st); tergite (tg).

First flagellomere length $1.40 \times as$ long as pedicel. Thorax chaetotaxy: acrostichals 0+2, intra-alars 1+2. Fore femur with one posterior, one posterodorsal and one posteroventral rows of bristles; mid femur with short and sparse ventral bristles, without apical comb-like posteroventral bristles, mid tibia with two posterodorsal and two posterior bristles, one strong ventral bristle; hind tibia with two or three posterodorsal bristles, one anteroventral bristle. Abdomen oval; tergites 5 and 6 entire, tergite 7 membranous like with several bristles on the anterior margin, tergite 8 divided into two plates and each with two strong bristles (Fig. 6E); sternites 1–6 without long and dense bristles (Fig. 6A); epiproct as a single setose plate, hypoproct and sternite 8 sclerotized (Fig. 6E). Other morphological characteristics are the same as for the male.

Material examined. China: Shanxi: 3 ♂♂, Tianzhen county, 40°24'00"N, 114°6'00"E, 1600–1700 m, 24.V.1987, Coll. M.F. Wang; 1 ♂, Yuxian county, Mt. Zangshan, 38°6'00"N, 113°24'00"E, 900–1000 m, 23.VI.1999, Coll. M.F. Wang. Beijing: 1 ♂, Mt. Songshan, 40°30'00"N 115°49'12"E, 800–1000 m, 5.VII.2008, [collector unknown]; 1 ♂, Mt. Songshan, 40°30'00"N, 115°49'12"E, 800–1000 m, 5.VI.2009, [collector unknown]; 1 ♂, Mt. Songshan, Daxigou, 40°31'30"N,



Figure 7. Scanning electron micrographs of the male genitalia of *Agria affinis* (Fallén, 1817). **A** Lateral view of the genitalia **B** Ventral view of distiphallus, arrows show the dividing line between phallic tube and juxta **C** Surstylus, lateral view **D** Cercus, lateral view **E** Pregonite and base of postgonite enlarged view, with inset showing highly enlarged view of one of the sockets from a coeloconic sensilla. Abbreviations: acrophallus (acr); cercus (cerc); juxta (j); lateral sclerotization (ls); phallic tube (ph); postgonite (pog); pregonite (prg); surstylus (sur).

115°46'19"E, 1200 m, 25.VII.2009, Coll. D. Zhang; 1 ♀, Mt. Songshan, Changyugou, 40°30'00"N, 115°48'57"E, 800 m, 28.VII.2009, Coll. D. Zhang; 2 ♂♂, Mt. Songshan, 40°30'00"N, 115°49'12"E, 800-1000 m, 29.VII.2010, [collector unknown]; 1 ♂, Mt. Songshan, 40°30'00"N, 115°49'12"E, 800-1000 m, 30.V.2012, Coll. Y.O. Chen.

Distribution. China (Beijing, Shanxi); Mongolia; North Korea; Russia (East Siberia, Far East, West Siberia); Ukraine.



Figure 8. Scanning electron micrographs of the male genitalia of *Agria mihalyii* (Rohdendorf and Verves, 1978). **A** Lateral view of the entire genitalia **B** Ejaculatory apodeme **C** Pregonite and postgonite, the former with some fine bristles at the dorso-basal edge (arrow) **D** Postgonite, with one well developed bristle (arrow) near base of anterior margin **E** Distal half of postgonite (extreme tip broken), arrows show the distribution of coeloconic sensilla **F** Coeloconic sensilla on the postgonite. Abbreviations: aedeagal apodeme (aea); coeloconic sensillum (Co); ejaculatory apodeme (eja); hypandrium (hyp); juxta (j); phallic tube (ph); postgonite (pog); pregonite (prg).



Figure 9. Scanning electron micrographs of the male genitalia of *Agria mihalyii* (Rohdendorf and Verves, 1978). **A** Lateral view of the genitalia **B** Lateral view of distiphallus **C** Acrophallus in anterior view, apex of the lateral sclerotizations with serrated margin (arrows) **D** Pregonite, enlarged view. Abbreviations: acrophallus (acr); hypandrium (hyp); juxta (j); phallic tube (ph); postgonite (pog); pregonite (prg).

Key to known Chinese species of genus Agria Robineau-Desvoidy [males only]

Discussion

Pape (1998) investigated the phylogenetic relationships of the world genera of Paramacronychiinae but his analysis gave very little phylogenetic resolution among the genera. More novel morphological characters should be added; especially the structures of the male paramacronychiine genitalia need a much more detailed comparative study. The scanning electron microscopy was here utilized to achieve more morphological details of the male genitalia of *Agria*. Two features seem to be particularly valuable in corroborating the monophyly of *Agria*: (1) the shape of the acrophallus, which from a broad base curves back strongly between the juxta, and (2) the pair of lateral sclerotizations originating just distal to the acrophallus and slanting antero-ventrally partly covering the latter.

The present SEM documentation has revealed the presence of coeloconic sensilla on the distal half of the A. mihalyii postgonite (Figs 8E and 8F) and on both pre- and postgonite in A. affinis. This type of sensilla has been proposed to be sensitive to chemo-, thermo-, or hygro-stimulation (Altner et al. 1981, Zacharuk 1985, Blackwell et al. 1992, Cribb 1997), and is usually found on the insect antenna, for example: in Diptera (Sukontason et al. 2004, Wang et al. 2012a, Zhang et al. 2012), Lepidoptera (Hunger and Steinbrecht 1998, Binyameen et al. 2012), Hemiptera (Silva et al. 2010, Wang et al. 2012b), and Hymenoptera (Onagbola and Fadamiro 2008). Only few authors have found sensilla on Diptera terminalia (Hooper et al. 1972, Rossignol and McIver 2005, Ngern-Klun et al. 2007, Chaiwong et al. 2007, 2008), and this is the first explicit record of the presence and distribution of coeloconic sensilla on the gonites in the subfamily Paramacronychiinae. These sensilla may aid in copulation (Rossignol and McIver 2005, Chaiwong et al. 2008), and their distribution may therefore be highly species-specific, as indicated by the marked differences between A. affinis and A. mihalyii. Pape (1992) proposed A. mihalyii to be the sister taxon of the remaining species of Agria, with the latter clade supported by two character states: (1) costal spine reduced, and (2) male lower calypter at least partly brownish. The material examined for our study has led us to reinterpret A. mihalvii as having a reduced costal spine, which leaves this character state as phylogenetically uninformative for species-level relationships within Agria. However, two other character states appear to support a basal split between A. mihalyii and the remaining species of *Agria*, which all share the following: (a) antero-basal bristle of postgonite reduced; and (b) pregonite with numerous coeloconic sensilla scattered across its surface. The latter character state is documented in Fig. 7E for A. affinis and in Kurahashi (1972, figs 2, 3b, 3f) for A. monachae, A. hikosana and A. shinonagai. The distribution of sensilla and other ultrastructural details of male terminalia in Sarcophagidae obviously is a potentially rich source of phylogenetic data, that still remains to be fully explored.

Acknowledgments

We wish to extend our sincerest thanks to Prof. M.F. Wang (Institute of Entomology, Shenyang Normal University, Shenyang), for donating specimens, and we are thankful

to two anonymous reviewers for their constructive comments on the manuscript. This study was supported by the Program for New Century Excellent Talents in University (No. NCET-12-0783), National Science Foundation of China (No. 31201741), and the Chinese Postdoctoral Science Foundation (No. 20100470009, No. SFG-201104059).

References

- Altner H, Routil C, Loftus R (1981) The structure of bimodal chemo-, thermo-, and hygroreceptive sensilla on the antenna of *Locusta migratoria*. Cell and Tissue Research 215: 289–308. doi: 10.1007/BF00239116
- Binyameen M, Anderson P, Ignell R, Seada MA, Hansson BS, Schlyter F (2012) Spatial organization of antennal olfactory sensory neurons in the female *Spodoptera littoralis* moth: Differences in sensitivity and temporal characteristics. Chemical Senses 37: 613–629. doi: 10.1093/chemse/bjs043
- Blackwell A, Mordue AJ, Mordue W (1992) Morphology of the antennae of two species of biting midge: *Culicoides impunctatus* (Goetghebuer) and *Culicoides nubeculosus* (Meigen) (Diptera: Ceratopogonidae). Journal of Morphology 213: 85–103. doi: 10.1002/ jmor.1052130107
- Chaiwong T, Sukontason KL, Chaithong U, Olson JK, Kurahashi H, Sukontason K (2007) Male genitalia of flesh fly *Parasarcophaga (Liosarcophaga) dux* (Diptera: Sarcophagidae) revealed by scanning electron microscopy. Journal of the American Mosquito Control Association 23: 80–83. doi: 10.2987/8756-971X(2007)23[80:MGOFFP]2.0.CO;2
- Chaiwong T, Sukontason K, Olson JK, Kurahashi H, Chaithong U, Sukontason KL (2008) Fine structure of the reproductive system of *Chrysomya megacephala* (Diptera: Calliphoridae): the external sexual organ. Parasitology Research 102: 973–980. doi: 10.1007/ s00436-007-0863-6
- Chao JM, Zhang XZ (1988) New species of Agriinae, Miltogrammatinae and Macronychiinae from China (Diptera: Sarcophagidae). Sinozoologia 6: 273–288.
- Cribb BW (1997) Antennal sensilla of the female biting midge: Forcipomyia (Lasiohelea) townsvillensis (Taylor) (Diptera: Ceratopogonidae). International Journal of Insect Morphology 25: 405–425. doi: 10.1016/S0020-7322(96)00013-X
- Fallén CF (1817) Beskrifning öfver de i Sverige funna fluge arter, som kunna föras till slägtet Musca. Första afdelningen. Kungliga Svenska Vetenskaps-Akademiens Handlingar (3) 1816: 226–257.
- Fan ZD, Pape T (1996) Checklist of Sarcophagidae (Diptera) recorded from China. Studia dipterologica 3: 237–258.
- Fan ZD, Zhao JM, Zhang XZ (1992) Paramacronychiinae. In Fan ZD (Ed) Key to the Common Flies of China, Second Edition. Science Press, Beijing, 611–613.
- Giroux M, Pape T, Wheeler TA (2010) Towards a phylogeny of the flesh flies (Diptera: Sarcophagidae): morphology and phylogenetic implications of the acrophallus in the subfamily Sarcophaginae. Zoological Journal of the Linnean Society 158: 740–778. doi: 10.1111/j.1096-3642.2009.00561.x

- Hooper RL, Pitts CW, Westfall JA (1972) Sense organs on the ovipositor of the face fly, *Musca autumnalis*. Annals of the Entomological Society of America 65: 577–586.
- Hunger T, Steinbrecht RA (1998) Functional morphology of a double-walled multiporous olfactory sensillum: the sensillum coeloconicum of *Bombyx mori* (Insecta, Lepidoptera). Tissue and Cell 30: 14–29. doi: 10.1016/S0040-8166(98)80003-7
- Kuhlmann U (1995) Biology and predation rate of the sarcophagid fly, Agria mamillata, a predator of European small ermine moths. International Journal of Pest Management 41: 67–73. doi: 10.1080/09670879509371925
- Kurahashi H (1972) Studies of the calypterate muscoid flies from Japan XI. Subfamily Agriinae (Diptera, Sarcophagidae). Kontyû 43: 202–213.
- McAlpine JF (1981) Morphology and terminology adults. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (Eds) Manual of Nearctic Diptera, Vol. 1. Research Branch, Agriculture Canada Monograph, 27, Ottawa, 9–63.
- Ngern-Klun R, Sukontason K, Methanitikorn R, Vogtsberger RC, Sukontason KL (2007) Fine structure of *Chrysomya nigripes* (Diptera: Calliphoridae), a fly species of medical importance. Parasitology Research 100: 993–1002. doi: 10.1007/s00436-006-0426-2
- Onagbola EO, Fadamiro HY (2008) Scanning electron microscopy studies of antennal sensilla of *Pteromalus cerealellae* (Hymenoptera: Pteromalidae). Micron 39: 526–535. doi: 10.1016/j.micron.2007.08.001
- Pape T (1987) The Sarcophagidae (Diptera) of Fennoscandia and Denmark. Leiden & Copenhagen: Fauna Entomologica scandinavica, 19, 203 pp.
- Pape T (1992) Redefinition of Agria Robineau-Desvoidy, Angiometopa Brauer & Bergenstamm and Toxonagria Shewell, with the description of a new species (Diptera: Sarcophagidae). Entomologica scandinavica 23: 307–317. doi: 10.1163/187631292X00137
- Pape T (1996) Catalogue of the Sarcophagidae of the World (Insecta: Diptera). Memoirs on Entomology, International 8: 1–558.
- Pape T (1998) A new genus of Paramacronychiinae (Diptera: Sarcophagidae), argued from a genus-level cladistic analysis. Systematic Entomology 23: 187–200. doi: 10.1046/j.1365-3113.1998.00047.x
- Roback SS (1954) The evolution and taxonomy of the Sarcophaginae (Diptera: Sarcophagidae). Illinois Biological Monograph 23: 1–181.
- Robineau-Desvoidy JB (1830) Essai sur les myodaires. Mémoires présentés par divers savans. Academie des Sciences, France 2: 1–813.
- Rohdendorf BB, Verves YuG (1978) Sarcophaginae (Diptera, Sarcophagidae) from Mongolia. Annales historico-naturales Musei nationalis hungarici 70: 241–258.
- Rossignol PA, McIver SB (2005) Fine structure and role in behavior of sensilla on the terminalia of *Aedes aegypti* (L.) (Diptera: Culicidae). Journal of Morphology 151: 419–437. doi: 10.1002/jmor.1051510307
- Silva CCA, de Capdeville G, Moraes MCB, Falcao R, Solino LF, Laumann RA, Silva JP, Borges M (2010) Morphology, distribution and abundance of antennal sensilla in three stink bug species (Hemiptera: Pentatomidae). Micron 41: 289–300. doi: 10.1016/j.micron.2009.11.009
- Sukontason K, Sukontason KL, Piangjai S, Boonchu N, Chaiwong T, Ngern-Klun R, Sripakdee D, Vogtsberger RC, Olson JK (2004) Antennal sensilla of some forensically important

flies in families Calliphoridae, Sarcophagidae and Muscidae. Micron 35: 671–679. doi: 10.1016/j.micron.2004.05.005

- Verves YuG (1981) Sarcophagidae (Diptera) from Korea. Folia entomologica Hungrica 42: 197–201.
- Verves YuG (1982) 64h. Sarcophaginae. In: Lindner (Ed) Die Fliegen der palaearktischen Region, 11: 235–296.
- Verves YuG (2001) The composition of Paramacronychiinae (Sarcophagidae, Diptera) with the descriptions of two new genera. International Journal of Dipterological Research 12: 145–149.
- Wang QK, Zhang M, Li K, Zhang D (2012a) Olfactory sensilla on antennae and maxillary palps of *Fannia hirticeps* (Stein, 1892) (Diptera: Fanniidae). Microscopy Research and Technique 75: 1313–1320. doi: 10.1002/jemt.22066
- Wang RR, Wan XY, Liang AP, Bourgoin T (2012b) Ultrastructure of sensory equipments on the heads of *Kallitaxila granulata* (Stal) (Hemiptera: Fulgoromorpha: Tropiduchidae). Microscopy Research and Technique 75: 1659–1665. doi: 10.1002/jemt.22113
- Zacharuk RY (1985) Antennal sensilla. In: Kerkut GA, Gilbert LI (Eds) Comprehensive insect physiology, biochemistry and pharmacology, Vol. 6. Pergamon Press. Oxford, 1–69.
- Zhang D, Wang QK, Hu DF, Li K (2012) Cuticular structures on antennae of the bot fly, *Portschinskia magnifica* (Diptera: Oestridae). Parasitology Research 111: 1651–1659. doi: 10.1007/s00436-012-3004-9
- Zhang D, Zhang M, Pape T, Gu CW, Wu W (2013) *Sarcophaga (Hoa) flexuosa* Ho (Diptera: Sarcophagidae): association of sexes using morphological and molecular approaches, and a re-definition of *Hoa* Rohdendorf. Zootaxa 3670: 71–79.

RESEARCH ARTICLE



Two common and problematic leucochrysine species-Leucochrysa (Leucochrysa) varia (Schneider) and L. (L.) pretiosa (Banks) (Neuroptera, Chrysopidae): redescriptions and synonymies

Catherine A. Tauber¹, Francisco Sosa², Gilberto S. Albuquerque³

I Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY 14853-2601 and Department of Entomology, University of California, Davis, CA, USA 2 Museo Entomológico "Dr. José Manuel Osorio" (UCOB), Universidad Centroccidental "Lisandro Alvarado", Venezuela 3 Laboratório de Entomologia e Fitopatologia, CCTA, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes, RJ, Brazil 28013-602

Corresponding author: Catherine A. Tauber (cat6@cornell.edu)

Academic editor: A. Contreras-Ramos | Received 7 March 2013 | Accepted 23 May 2013 | Published 19 June 2013

Citation: Tauber CA, Sosa F, Albuquerque GS (2013) Two common and problematic leucochrysine species–*Leucochrysa* (*Leucochrysa*) varia (Schneider) and *L. (L.) pretiosa* (Banks) (Neuroptera, Chrysopidae): redescriptions and synonymies. ZooKeys 310: 57–101. doi: 10.3897/zooKeys.310.5071

We dedicate this article to the memory of Sergio de Freitas, FCAV-UNESP, Jaboticabal, São Paulo, Brazil (deceased, 2012). He was an active and enthusiastic Neuropterist and the cherished mentor and friend of Francisco Sosa.

Abstract

Leucochrysa McLachlan is the largest genus in the Chrysopidae, yet it has received relatively little taxonomic attention. We treat two problematic and common Leucochrysa species–Leucochrysa (Leucochrysa) varia (Schneider, 1851) and Leucochrysa (Leucochrysa) pretiosa (Banks, 1910). Both are highly variable in coloration and were described before the systematic importance of chrysopid genitalia was recognized. Recent studies show that these species occur within a large complex of cryptic species and that they have accumulated a number of taxonomic problems. We identify new synonymies for each of the species–for L. (L.) varia: Leucochrysa (Leucochrysa) ampla (Walker, 1853), Leucochrysa internata (Walker, 1853), and Leucochrysa (Leucochrysa) walkerina Navás, 1913; for L. (L.) pretiosa: Leucochrysa (Leucochrysa) erminea Banks, 1946. The synonymy of Leucochrysa delicata Navás, 1925 with L. (L.) pretiosa is stabilized by the designation of a neotype. The following species, which were previously synonymized with L. (L.) varia or L. (L.) pretiosa, are reinstated as valid: Leucochrysa (Leucochrysa) phaeocephala Navás, 1929, Leucochrysa

Copyright Catherine A. Tauber et al. This is an open access article distributed under the terms of the Creative Commons Attribution License 3.0 (CC-BY), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

(Leucochrysa) angrandi (Navás, 1911), and Leucochrysa (Leucochrysa) variata (Navás, 1913). To help stabilize Leucochrysa taxonomy, lectotypes are designated for Allochrysa pretiosa and A. variata. Finally, Leucochrysa vegana Navás, 1917 is considered a nomen dubium.

Resumen

Leucochrysa McLachlan es el género más grande de Chrysopidae, sin embargo, ha recibido poca atención taxonómica. Dos de las especies más comunes y problemáticas de *Leucochrysa* son estudiadas– *Leucochrysa* (*Leucochrysa*) varia (Schneider, 1851) y *Leucochrysa* (*Leucochrysa*) pretiosa (Banks, 1910). Ambas son altamente variables en coloración y fueron descritas antes de que se reconociera la importancia de la genitalia en la sistemática de Chrysopidae. Estudios recientes demuestran que estas especies pertenecen a un complejo de especies crípticas, razón por la cual han acumulado numerosos problemas taxonómicos. En este estudio se identificaron las siguientes sinonimias; para *L. (L.) varia: Leucochrysa (Leucochrysa) ampla* (Walker, 1853), *Leucochrysa internata* (Walker, 1853), y *Leucochrysa (Leucochrysa (Leucochrysa) ampla* (Walker, 1853), *Leucochrysa (teucochrysa) erminea* Banks, 1946. La sinonimia de *Leucochrysa delicata* Navás, 1925 con *L. (L.) pretiosa* es estabilizada por la designación de un neotipo. Las especies *Leucochrysa (Leucochrysa) phaeocephala* Navás, 1929, *Leucochrysa (Leucochrysa) angrandi* (Navás, 1911) y *Leucochrysa (Leucochrysa) variata* (Navás, 1913) las cuales fueron previamente sinonimizadas con *L. (L.) varia* o *L. (L.) pretiosa*, son reestablecidas como válidas. Para ayudar a estabilizar la taxonomía de *Leucochrysa*, se designaron lectotipos para *Allochrysa pretiosa* y *A. variata*. Finalmente, *Leucochrysa vegana* Navás, 1917 es considerada como un *nomen dubium*.

Resumo

Leucochrysa McLachlan é o maior gênero de Chrysopidae; no entanto, ele tem recebido relativamente pouca atenção taxonômica. Nesse trabalho, duas espécies de *Leucochrysa* problemáticas e comuns são analisadas - *Leucochrysa (Leucochrysa) varia* (Schneider, 1851) e *Leucochrysa (Leucochrysa) pretiosa* (Banks, 1910). Ambas foram descritas antes da importância sistemática da genitália de crisopídeos ter sido reconhecida e são altamente variáveis na coloração. Estudos recentes têm demonstrado que essas espécies ocorrem dentro de um grande complexo de espécies crípticas e que elas têm acumulado diversos problemas taxonômicos. Foram identificadas novas sinonímias para cada uma das espécies - para *L. (L.) varia: Leucochrysa (Leucochrysa) ampla* (Walker, 1853), *Leucochrysa internata* (Walker, 1853) e *Leucochrysa (Leucochrysa) walkerina* Navás, 1913; para *L. (L.) pretiosa: Leucochrysa (Leucochrysa) erminea* Banks, 1946. A sinonímia de *Leucochrysa delicata* Navás, 1925 com *L. (L.) pretiosa* é estabilizada pela designação de um neótipo. As seguintes espécies, que eram previamente sinonimizadas com *L. (L.) varia* ou *L. (L.) pretiosa*, são reintegradas como válidas: *Leucochrysa (Leucochrysa) variata* (Navás, 1913). Para auxiliar na estabilização da taxonomia de *Leucochrysa*, lectótipos são designados para *Allochrysa pretiosa* e *A. variata*. Finalmente, *Leucochrysa vegana* Navás, 1917 é considerada *nomen dubium*.

Keywords

Chrysopinae, Leucochrysini, Leucochrysa, ampla, angrandi, delicata, erminea, internata, phaeocephala, variata, vegana, walkerina

Introduction

Leucochrysa McLachlan is the largest genus in the family Chrysopidae; it is restricted to the New World, and it is most diverse and abundant in the Neotropics (Adams and Penny 1986). Currently, *Leucochrysa* includes two subgenera, *Leucochrysa* (*Leu*-

cochrysa), with ca 46 species, and *Leucochrysa* (*Nodita*), with ca 150 species (Brooks and Barnard 1990, Penny 1998, 2001, Freitas and Penny 2001, Freitas 2005, Tauber et al. 2008, 2011a, 2011b). The genus has numerous taxonomic complications, many stemming from the poor status of its descriptive systematics. Most *Leucochrysa* species were described without reference to their internal anatomy (e.g., genitalia), and in many cases, these structures continue to remain unknown. As a result, identifications are difficult and a large number of cryptic species have gone unrecognized. In addition, polymorphisms and other forms of intraspecific variation are often interpreted as species differences; in some cases, males and females of the same species are described under different names. Moreover, systematic study of the group has been slow because types are sometimes difficult to locate or access; many are in poor condition. As a result, synonymies are numerous; species are difficult to identify with accuracy; a significant number of species remain undescribed; and the genus is a taxonomic enigma for systematists and ecologists who are interested in chrysopids.

Efforts to improve the descriptive systematics of *Leucochrysa* began in the late 1970s with work by Adams (1977, 1979); his studies were the first to include the genitalia (male and female), and his findings were strongly rooted in careful examination of type specimens. Subsequently, in the last ca 10 years, interest in the descriptive systematics of *Leucochrysa* has increased. Regional treatments of *Leucochrysa* have been published; new species have been described; polymorphisms have been elucidated; and, larval morphology has been explored (Freitas and Penny 2001, Penny 2002, Tauber 2004, Freitas 2005, Mantoanelli et al. 2006, 2011, Tauber et al. 2008, 2011a, 2011b). Unfortunately, in some of these studies, type specimens do not appear to have received appropriate attention. As a result, errors continue to creep into the literature on the taxonomy of the group.

Recently we examined specimens of *Leucochrysa* (*Leucochrysa*) that resemble the relatively common species, *Leucochrysa* (*L.*) varia (Schneider). We were surprised to find that our specimens included numerous cryptic species. Among them was *Leucochrysa* (*L.*) pretiosa (Banks); most, if not all, of the other species appear to be undescribed. To help provide a sound morphological and systematic basis for future comparative study and description of the newly discovered species, we examine the taxonomy and morphology of the two previously named species. In doing so, we (a) redescribe and provide images of the two species, including the genitalia of both males and females, (b) identify new synonymies for each of the species, (c) help stabilize the nomenclature of the group by designating a neotype and two lectotypes, (d) reinstate to valid status three species that had previously been synonymized with one or the other of the species, and (e) designate one species as a nomen dubium. All of these taxonomic actions are verified with images of the appropriate types.

Materials and methods

We searched for specimens in a large number of entomological collections. Below are the institutions (with acronyms) where we found and used specimens. Tauber: AMNH, American Museum of Natural History, New York, NY; CAS, California Academy of Sciences, San Francisco, CA; FMNH, Field Museum of Natural History, Chicago, IL; SEM, Snow Entomological Museum, University of Kansas, Lawrence, KS; LACM, Los Angeles County Museum of Natural History, Los Angeles, CA; ROM, Royal Ontario Museum, Toronto, ON, Canada; UCB, Essig Museum, University of California, Berkeley, CA; UID, W. F. Barr Entomological Collection, University of Idaho, Moscow, ID; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.; USU, Entomological Museum, Utah State University, Logan, UT.

Tauber and Albuquerque: BMNH, The Natural History Museum (formerly British Museum of Natural History), London, England; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MNHN, Muséum national d'Histoire naturelle, Paris, France.

Sosa: UCOB, Museo Entomológico "Dr. José Manuel Osorio", Universidad Centroccidental "Lisandro Alvarado", Barquisimeto, Lara, Venezuela; MIZA, Museum of the Institute of Agricultural Zoology, Universidad Central de Venezuela, Maracay, Aragua, Venezuela; FCAV-UNESP, Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista "Júlio de Mesquita Filho", Jaboticabal, São Paulo, Brazil (Sergio de Freitas Collection).

Albuquerque: UENF, Insect Collection, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes, Rio de Janeiro, Brazil.

For the genitalia studies, the entire abdomen or the apical region of the abdomen was removed and cleared in 10% KOH, tinged with Clorazol Black E, and transferred to glycerine. Subsequently, the structures were stored in plastic microvials attached to the corresponding specimens. Measurements were made with the aid of Image J 1.46 (NIH, public domain) (Tauber) and Motic Image Plus (version 2.0) (Sosa). All measurements were made as previously described (Tauber 2010); the numbers of specimens measured ranged from four (internal structures) to ten (external structures). We made frequent use of the Neuropterida website: http://lacewing.tamu.edu/index.html (Oswald 2006, 2007) and the images of *Leucochrysa* types in the MCZ On-line Type Database: http://insects.oeb.harvard.edu/MCZ/index.htm (all of which were captured for the MCZ by CAT, GSA and MJT in 2010).

Shared characteristics of Leucochrysa (L.) varia-like species

The two species that we are considering here are among a relatively large number of mostly undescribed *Leucochrysa* (*Leucochrysa*) species–all of which resemble each other very closely. We refer loosely to these species as "*varia*-like". The species in this group generally express the following suite of external features: (1) head yellow to cream-colored, tinged slightly to extensively with red to red-wine coloration; (2) occiput tinged with red; (3) vertex raised, tinged with red laterally, with reddish brown transverse, V-shaped bar above antennae; (4) antenna with basal membrane variably tinged with red; (5) scape with red to red-wine coloration throughout; (6) pedicel generally cream-colored, with inner margin shaded brown; (7) flagellum cream-colored to yellow, covered with pale bristles, basal three to five flagellomeres generally with inner margin streaked with black; (8) frons and clypeus white to cream-colored or variably red suffused; (9) gena tinged with pink, red or reddish brown; (10) labrum yellowish, generally not marked; (11) maxillary and labial palpi yellowish; (12) cervix with small, red, lateral mark; (13) pronotum greenish to yellowish, unmarked; (14) mesonotum, metanotum variably pigmented with red, reddish brown or black (pigmentation with wide range of intraspecific and interspecific variation); (15) abdominal tergites 5-6 with dark brown oval spot, bordered with red and yellow.

Internal features, including any genital characters that may characterize this group will be considered in a later publication.

Leucochrysa (Leucochrysa) varia (Schneider, 1851)

http://species-id.net/wiki/Leucochrysa_varia Figs 1–14

- Chrysopa varia Schneider [1851] (1851: 154, Plate 58) original description: "Brasilia, ubi a Dr. Clausen inventa; (collect. E. de Selys-Longchamps!)". Walker (1853: 268) brief redescription, collection records; McLachlan (1868a: 270) taxonomic note; Brooks and Barnard (1990: 247) confirmed type species of genus Leucochrysa. Leucochrysa varia (Schneider). McLachlan (1868b: 208) first reference to combination, L. varia designated as type species of genus; Navás (1917: 279) species list; Navás (1922a: 392) collection record; Navás (1922b: 89) collection record; Navás (1924: 28) collection record; Navás (1926: 12) collection record; Navás (1928a: 131) collection record (probably in error); Navás (1928b: 111) collection record; Navás (1928c: 35) collection record; Navás (1929: 862) collection records; Navás (1932: 57) collection record; Banks (1944: 31) note on type, species distribution records (probably in error); Banks (1945: 168) note on geographic distribution, comparison with L. pretiosa; Penny (1977: 23) species list; Adams (1979: 97) probable occurrence in Mexico. Allochrysa varia (Schneider). Banks (1910: 150) first reference to combination; Navás (1912-1913: 313) species list, collection record; Navás (1913: 156) brief redescription; Navás (1917: 279) genus synonymized with Leucochrysa.
- Leucochrysa (Leucochrysa) varia (Schneider). Brooks and Barnard (1990: 248, 277, figs. 498-507) subgeneric determination, species list, figures; Freitas and Penny (2001: 282, 354, fig. 43) brief redescription, collection records, figures -- based on misidentified specimens in the FCAV-UNESP, not L. (L.) varia; Mantoanelli et al. (2006: 7) description of larvae, developmental data, analysis of color polymorphism; Mantoanelli and Albuquerque (2007: 302) behavioral and developmental data; Oswald (2007) catalog listing.
- *Chrysopa internata* Walker [1853] (1853: 252) original description: "*a*. Brazil. *b*. -----? From Mr. Children's collection". McLachlan (1868a: 269) synonymy with *Chrysopa ampla* Walker.

- Leucochrysa internata (Walker). Navás (1912-1913: 303) first reference to combination, species list; Navás (1913: 102) brief redescription, reversal of McLachlan's 1868a synonymy with *L. ampla*; Kimmins (1940: 444) identification of Walker's specimen *b*, without locality data, as primary type; Penny (1977: 23) species list; Brooks and Barnard (1990: 277) apparently listed in error as a synonym of *Leucochrysa (Leucochrysa) walkerina* Navás; Oswald (2007) catalog listing as a synonym of *L. (L.) walkerina* as per Brooks and Barnard (1990). Syn. n.
- Allochrysa internata (Walker). Banks (1914-1915: 625) first reference to combination; Navás (1917: 279, internata not specifically mentioned) genus synonymized with Leucochrysa; Oswald (2007) catalog listing as synonym of L. (L.) walkerina, apparently in error.
- Nodita internata (Walker). Navás (1917: 280) first reference to combination, species list (probably an error); Oswald (2007) catalog listing as synonym of *L*. (*L*.) walkerina.
- Chrysopa ampla Walker [1853] (1853: 268) original description: "a. Georgia. From Mr. Abbot's collection. b. -----? From Mr. Children's collection". McLachlan (1868a: 270) taxonomic note and mention of close relationship with C. varia. Kimmins (1940: 444) identification of Walker's specimen b, without locality data, as primary type. Penny (1977: 23) listing as a synonym of Leucochrysa internata (Walker), without comment.
- *Leucochrysa (Leucochrysa) ampla* (Walker). Brooks and Barnard (1990: 276) first reference to generic, subgeneric combinations, species list; Freitas and Penny (2001: 280, 351, fig. 40) brief redescription, collection records, figures; Oswald (2007) catalog listing. **Syn. n.**
- Leucochrysa vegana Navás [1917] (1917: 278) (not Nodita vegana Navás, 1925) original description: "Colombia: La Vega, Juni 1915 (Coll. Br. Apolinar Maria)". Banks (1944: 30) synonymy with L. varia.; Penny (1977: 23) listing as a synonym; Brooks and Barnard (1990: 277) listing as a synonym; Oswald (2007) catalog listing as a synonym. Nom. d.
- *Leucochrysa phaeocephala* Navás [1929] (1929b: 21) original description: "America: «Niederl. Guayan. Obere Commaryne, 28. 11. 1908». Mus. Hamburg". Banks (1944: 30) synonymy with *L. varia*. Penny (1977: 23) listing as a synonym; Brooks and Barnard (1990: 277) listing as a synonym; Oswald (2007) catalog listing as a synonym.
- Leucochrysa (Leucochrysa) phaeocephala Navás. Valid status reinstated. See below.
- Leucochrysa walkerina Navás [1913] (1913: 102) original description: "Brazil". Penny (1977: 23), as "Leucochrysa walkerina Navás (1917)", listing as a synonym of L. internata, without comment.
- *Leucochrysa (Leucochrysa) walkerina* Navás. Brooks and Barnard (1990: 277) subgeneric determination, species list; Freitas and Penny (2001: 283, 355, fig. 44) brief redescription, collection records, figures -- based on misidentified specimens in the FCAV-UNESP; Oswald (2007) catalog listing. **Syn. n.**

Known geographical distribution. Our findings [based on confirmed published records and specimens examined] indicate that *L. (L.) varia* occurs from the western, lowland regions of the Amazonian drainage basin of Brazil, Ecuador and Peru, through-

out much of forested Brazil (coastal and inland), and in northeastern, mid-elevation regions of Argentina. The specific areas that we have confirmed include: **Argentina:** Province of Salta. **Brazil:** States of Bahia, Distrito Federal, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro, Rondônia, São Paulo. **Ecuador:** Provinces of Napo, Orellana. **Peru:** District of Madre de Dios. Confirmed published records include: Freitas and Penny (2001: 280, as *L. (L.) ampla*), and Mantoanelli et al. (2006: 8).

Unconfirmed, published records from South America include --- Brazil: Espírito Santo (Navás 1922b: 89), Mato Grosso (Navás 1932: 57); Pará (Navás 1912-1913: 314), Rio de Janeiro (Navás 1922a: 392; Navás 1926: 12; Navás 1929a: 862), Paraguay: San Bernardino [Cordillera] (Navás 1913: 157), and Bolivia: Buenavista [Santa Cruz] (Navás 1928b: 111). The Brazilian records of *L. (L.) varia* and *L. (L.) walkerina* by Freitas and Penny (2001: 282) were based on misidentified specimens; thus, only their records for *L. (L.) ampla* [= *L. (L.) varia*] are included here.

Leucochrysa (*L.*) *varia* was reported from British Guiana, Suriname, Central America, and Mexico; however we have not confirmed any of these records. Banks (1945: 168) questioned the Navás (1928a: 131) record for Central America (Guatemala). Based on our study here, we also question this record. We confirmed that the Banks (1944: 31) record for British Guiana was in error; a specimen in the AMNH with the data he reported is probably an undescribed species; its abdomen is missing. The specimen(s) that he identified as *L.* (*L.*) *varia* from Suriname (Banks 1944: 31) were not found in the MCZ (P. Perkins, personal communication), nor in the AMNH. This record probably applies to *L.* (*L.*) *varia* from norther, undescribed species. In summary, we have not seen specimens of *L.* (*L.*) *varia* from northern South America, the Caribbean region, Central America, or Mexico.

Type specimens and rationale for taxonomic changes.

Chrysopa varia. Holotype, by original designation, MCZ, male (examined).

The type is in fairly good condition. Its primary label is hand-written, apparently in Schneider's hand; it reads: "varia nov. sp. / Schneider / Brasilia". The exact collection site is unknown. In addition to Fig. 1 here, images of the external and male features are in the MCZ Type Database (website: http://insects.oeb.harvard.edu/MCZ/ index.htm).

Chrysopa internata. Holotype by monotypy, BMNH, male (examined).

Walker originally referenced two specimens under the name *Chrysopa internata* ("*a*" from Brazil and "*b*" without locality data); he also stated that *C. internata* had two varieties. Because one of the specimens must represent Walker's lettered variety ("var. β "), that specimen must be excluded from the type series of *C. internata* under Art. 72.4.1 (see Oswald 2007). Kimmins (1940: 444) identified the specimen without locality data (specimen "*b*") as the primary *C. internata* type (a lectotype). Because the actual type series of *C. internata* consists of only a single specimen, his lectotype designation was unnecessary; we recognize Kimmins' action as identification of the holotype.

The excluded "var. β " specimen (specimen "*a*" from Brazil), was subsequently designated the type of *Leucochrysa walkerina* Navás (see below).



Figure I. Holotype, *Chrysopa varia* [= *Leucochrysa* (*L.*) *varia*], male, MCZ, gonarcal complex. A Frontal
B Posterior C Ventral D Dorsal E Lateral. Scale applies to all images. *Abbreviations:* bk beak-like tip of mediuncus gc gonocornu gsa gonosaccus g.a. gonarcal apodeme g.b. gonarcal bridge hy.i. hypandrium internum mu mediuncus rod mediuncal rod.



Figure 2. Holotype, *Chrysopa internata* [= *L.* (*L.*) *varia*], male, BMNH, external features. **A** Habitus **B** Labels **C** Head, frontal **D** Thorax, base of wings, dorsal **E**, **F** Forewing and hindwing; scale applies to both wings.

The *C. internata* holotype is in fairly good condition; the head is separated from the body and the dissected abdomen is in glycerin, in a vial attached to the pinned specimen. The labels are hand-written and printed (Fig. 2B). The specimen carries no locality data; its collection site is unknown. All of its features, including the male terminalia, correspond to those of the *L*. (*L*.) *varia* type (see Figs 2–3).



Figure 3. Holotype, *Chrysopa internata* [= *L*. (*L*.) *varia*], male, BMNH, terminalia. **A** Abdominal segments 5–9, lateral **B** Terminal segments, lateral **C** Gonarcal complex, frontal **D** Gonarcal complex, lateral **E** Gonarcal complex, frontoventral **F** Gonarcal complex, ventral; same scale applies to **C**–**F**.



Figure 4. Holotype, *Chrysopa ampla* [= *L.* (*L.*) *varia*], female, BMNH, external features. A Labels
B Head, frontal C, D Forewing and hindwing; scale applies to both wings E Head and prothorax, dorsal
F Mesonotum, metanotum, base of wings.



Figure 5. Holotype, *Chrysopa ampla* [= *L.* (*L.*) *varia*], female, BMNH, abdomen (teneral). A Abdominal segments 6–9, lateral B Genitalia. *Abbreviations:* b.d. bursal duct sg subgenitale sp spermatheca sp.d. spermathecal duct.

Chrysopa ampla. Holotype by monotypy, BMNH, female (examined).

Walker originally referenced two specimens ("*a*" and "*b*") under the name *Chrysopa ampla*; he also stated that *C. ampla* had two varieties. Because one of the specimens must represent Walker's lettered variety ("var. β "), that specimen must be excluded from the type series of *C. ampla* under Art. 72.4.1 (see Oswald 2007). Thus, the actual type series of *C. ampla* consists of only a single specimen, the one that was listed by Walker as "var. α " and that carries no locality data. Therefore, this specimen constitutes the holotype by monotypy. This designation is consistent, nomenclaturally, with the action by Kimmins (1940: 444), who considered the specimen as the name-bearing type when he designated it as the "lectotype".

The excluded "var. β " specimen was reported from "Georgia". Tauber (2004: 1132) identified it as *Leucochrysa* (*L*.) *insularis* Walker, and it bears her label with that name.

The *C. ampla* holotype is in fairly good condition; the dissected abdomen is in glycerin, in a vial attached to the pinned specimen. The labels are hand-written (not by Navás) and printed (Fig. 4A). The specimen carries no locality data; its collection site is unknown. All of the features (external and genitalic) of this type correspond to those of female *L.* (*L.*) varia (see Figs 4–5).

Leucochrysa vegana. Type(s) by original designation, probably missing.

Navás (1917: 278), in his original description, did not indicate the depository or sex of the type; he reported that it was from the "Coll. Br. [Brother] Apolinar Maria [María]" (not examined). It was not found in the Navás collection (Monserrat 1985: 240), the BMNH, the MNHN, or the MCZ. And despite searches by colleagues (see acknowledgements) in Colombia where Br. Apolinar María lived, it was not found. Apparently, the Br. Apolinar María collection was housed in the Museo de la Universidad de la Salle and was destroyed during a political upheaval in 1948.

Navás mentioned the similarity between *L. vegana* and *L. varia* ("variae Schn."), but he did not point out why he considered that *L. vegana* was different. Most of the



Figure 6. Holotype, *Leucochrysa walkerina* [= *L.* (*L.*) *varia*], female, BMNH, external features. **A** Labels **B** Habitus **C** Head, frontal **D** Head, lateral **E** Head, dorsal **F** Head, thorax, dorsal **G & H** Forewing and hindwing; scale applies to both wings.

features that he described for *L. vegana* are found on *L. (L.) varia* specimens, including the markings at the base of the *L. vegana* forewing that he illustrated. Thus, although it is unlikely that Banks actually saw the *L. vegana* type, his synonymy (based on Navás' description) made sense at the time.

The type locality of *L. vegana* (La Vega, which is in the Cordillera Oriental of Colombia), is considerably north of the currently known northern limit of *L. (L.) varia* [the western regions of the Amazon drainage basin of Ecuador and Peru (e.g., the Yasuní Reserve in the Province of Napo, Ecuador and the Tambopata district of Peru)], but well within the ranges of other, undescribed *Leucochrysa (L.) varia*-like species. At this time, we suspect that *L. vegana* is not synonymous with *L. (L.) varia*. However, the region remains very poorly collected, so it is possible that our suspicion is in error. Thus, while we await the collection of *L. (L.) varia* from La Vega or nearby, to confirm Banks' synonymy, we consider the species name to be a nomen dubium.



Figure 7. Holotype, *Leucochrysa walkerina* [= *L.* (*L.*) *varia*], female, BMNH, abdomen and genitalia. **A** Terminal segments, genitalia visible within abdominal cavity **B** Enlargement of genital structures [Note the spermathecal duct and subgenitale.]. *Abbreviations:* **sg** subgenitale **sp.d.** spermathecal duct.

Leucochrysa phaeocephala. Type(s), by original designation, Hamburg, probably destroyed during W.W. II, sex unknown (not examined).

Banks' (1944: 30) synonymy was made on the basis of the description; it does not appear that he saw the type. Navás (1929b: 21) reported that the specimen was collected in Dutch Guiana in 1908 (now, Suriname). Because we have found no records of *L*. (*L*.) varia from the northern regions of South America, we reverse Bank's synonymy; we will deal with the species in a later publication.

Leucochrysa walkerina. Holotype by monotypy, BMNH, female (examined).

Navás (1913: 102) considered that Walker's *internata* variety β represented a distinct species; he explicitly applied the species name "*walkerina*" in honor of Walker. Kimmins (1940: 444) designated Walker's specimen "*a*" of *internata* (labeled from Brazil) as the type of *C. internata* variety β ; thus it became the holotype of *L. walkerina* (see Oswald 2007).

The *walkerina* type is slightly teneral, but in good condition; the cleared abdomen is in glycerine, in a vial attached to the specimen. The pin carries four labels below the specimen (including a locality label, "Brazil") (Fig. 6A); it also has a "Paralectotype" label above the specimen (Fig. 6B). The external characteristics (Fig. 6) are consistent with those of *L*. (*L*.) *varia*, and the elongate, coiled, spermathecal duct is that of *L*. (*L*.) *varia* (Fig. 7).

Diagnosis. As the name *varia* implies, adults of *L*. (*L*.) *varia* exhibit a wide range of color variation; there are black and red morphs, with and without coloration on the mesoscutellum (See Fig. 8 here, Fig. 7 in Mantoanelli et al. 2006). In addition, preserved specimens of *varia*-like species tend to loose their natural coloration very quickly; old specimens are especially discolored. Thus, it is important to emphasize that accurate identification of the *varia*-like species can only be made by careful examination of the male or female genital characters.



Figure 8. Variation in *Leucochrysa (L.) varia* head and thoracic markings. **A**, **B** Head, thorax, dorsal **C–D** head, frontal (all, state of Minas Gerais, Brazil).

Externally, L. (L.) varia and L. (L.) pretiosa adults usually (but not always) can be separated by differences in the darkness of certain veins and the degree of suffusion around the veins. Both species have black to dark brown suffusion surrounding the second m-cu crossvein, but the marking generally is less prominent in L. (L.) varia than in L. (L.) pretiosa. Moreover, in both species the distal two to four Psm–Psc crossveins and at least the three basal outer gradates are darkened and the membranes surrounding these veins are shaded to some degree. In L. (L.) varia, the degree of



Figure 9A. Forewings from three specimens each of *Leucochrysa (L.) varia* and *Leucochrysa (L.) pretiosa,* illustrating interspecific and intraspecific variation in markings, size, and shape **Left** *L. (L.) varia* (V1. Salta, Argentina; V2. Rio de Janeiro, Brazil; V3 Napo, Ecuador) **Right** *L. (L.) pretiosa* (P1. Capital District, Venezuela; P2. Carabobo, Venezuela; P3. Trinidad Island, Trinidad & Tobago). *Abbreviations:* **b'**-**d** distal cell in lower Banksian series **cv** distal Psm-Psc crossvein **ma** median arculus (= basal vein of im1) **m-cu2** distal (= second) m-cu crossvein **o.g.** basal three outer gradates.

darkening and suffusion around these veins is generally uniform, whereas in *L*. (*L*.) *pretiosa*, the distal Psm-Psc crossvein is usually darker and more prominent than the other Psm-Psc crossveins or the outer gradates.

In *L*. (*L*.) varia males, the sclerotized mediuncal plate is elongate; its rods are narrow and parallel; its membranous connection to the gonarcal bridge does not extend laterally beyond the gonocornua and is soft [not broad, leathery and stiff, as in *L*. (*L*.) *pretiosa*]. The *L*. (*L*.) varia female is distinguished by a very long, strongly coiled spermathecal duct and a spermatheca that is scoop-shaped distally and has a convoluted, tubular, basal section leading to a broad, fluted bursal duct.

Redescription. *Head* (Fig. 8): 1.8–1.9 mm wide (including eyes). Frons, clypeus cream to red, with anterior clypeal margin dark red; gena red to reddish brown; maxillary, labial palp yellowish to cream-colored. Vertex with central area raised, yellowish to cream-colored, with prominent, dark red-wine-colored, V-shaped mark along anterior margin; lateral margin, midline sometimes also with red-wine-colored marks. Antenna: dorsum of scape lightly to darkly tinged with red-wine color; pedicel dark



Figure 9B. Hindwings from three specimens each of *Leucochrysa* (*L*.) *varia* and *Leucochrysa* (*L*.) *pretiosa*. Same information as Fig. 9A.

red to ivory-colored, with inner margin darkened; flagellum cream-colored, with amber bristles; inner margin of basal ca 3 flagellomeres tinged with red to black; antennal fossa marked with red laterally.

Thorax (Fig. 8): Cervix lightly tinged with red laterally. Pronotum 1.2–1.5 mm long, 1.2–1.5 mm wide, yellowish to greenish, unmarked except for small posteromesal red to black mark. Mesonotum, metanotum mostly dark, variable, with four types of color morphs (black entire, black open, red entire, red open) [see Fig. 8 and Mantoanelli et al. 2006].

Wings (Fig. 9A–B): Forewing 17.3–20.5 mm long, 6.5–7.8 mm wide (at widest point); ratio of length : maximum width = 2.6–2.7:1. Costal area moderately broad; tallest costal cell (#9–10) 1.5–1.9 mm tall, 2.6–3.3 times width, 0.3 times width of wing (midwing). First intramedian (im1) cell quadrangular, width (anterior margin) 1.4–1.6 times width (anterior margin) of third median cell (m3), 2.3–3.2 times length of posterior margin of m3, length of basal vein (= ma, median arculus) 1.0–1.1 times greater than length of distal vein. First radial crossvein distal to origin of radial sector (Rs); radial area (between R and Rs) with single row of 16–18 closed cells; tallest cell (#6–8) 2.16–2.58 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; 6–11 inner gradates, 7–9 outer gradates. Height of fourth gradate cell 3.6–5.4 times width. Eight to nine b' cells (cells beneath Pseudomedia after im2). Three intracubital cells (two closed). Membrane mostly clear except basal area with small, reddish brown patch, stigma opaque to light brown, with large very dark brown mark basally, small, light



Figure 10. *Leucochrysa* (*L.*) *varia* male abdominal structures. **A, B, C** Terminal segments, lateral, demonstrating intraspecific variation in the shape, expansion and sclerotization of the abdomen **D** Tergite 9+ectoproct **E** Abdominal segments 8 & 9, dorsal **F** Callus cerci. (A–D State of Rio de Janeiro, Brazil; E–F Province of Orellana, Ecuador). *Abbreviations:* **c.c.** callus cerci **d.a.** dorsal apodeme of ninth tergite+ectoproct **ev.p.** eversible membranous pouch **gs** gonarcus **memb** membrane **S8+9** fused eighth and ninth sternites **tr** trichobothria **T8** eighth tergite **T9+ect** fused ninth tergite and ectoproct.

brown clouding around second m-cu crossvein and around distal Psm–Psc crossveins, sometimes with clouding around distal leg of im1 and around crossveins between distal b' cells. Veins mostly green, except anterior tips of most costal crossveins, base of Radius, bases of ca three to five radial crossveins, distal three to four Psm–Psc cross-
veins, outer gradates, and forks of posterior marginal veins darkened to black; inner gradates, posterior veins of distal three to four b' cells slightly darkened. Hindwing 16.2–18.3 mm long, 5.3–6.0 mm wide. Two series of gradate veins; 6–10 inner, 6–8 outer; 14–17 radial cells (counted from origin of R, not false origin). Four to six b cells (including small b1 cell); six to eight b' cells beyond im2; two intracubital cells (one closed). Membrane clear; stigma with pronounced dark brown mark basally. Veins mostly light green; middle costal crossveins, outer gradates, bases of marginal forks, black.

Abdomen (Figs 1, 10–14): Sternites, tergites with long, slender setae throughout, microsetae moderately dense; pleural region with setae small, very sparse, microsetae very small. Rim around each sternite heavily sclerotized, especially anteriorly, fading posteriorly. Tergites narrow, roughly rectangular, with rounded margins. Spiracles oval externally; atria not enlarged. Sternites S2–3 longer than tall; S5–7 more square-shaped; distal segments (beyond A4) expanded, height of pleural region greater than height of sternites. Coloration: mostly green, with yellow mesally. Tergites T5, T6 with large black spots, bordered by red; callus cerci white; setae, trichobothria golden.

Male: S6 height and length approximately equal, S7 height ca 1.1–1.2 times length (lateral view); S4–S8 with dense microtholi, S3 with microtholi laterally, sometimes also across entire posterior region, absent or sparse anteriorly, mesally; S1-2, S9 without microtholi. Callus cerci round to slightly oval (ca 1.1–1.2× taller than wide), diameter ca 0.16–0.28 mm, with ca 30–35 trichobothria of variable length. T9+ectoproct rounded posterodorsally, truncate to rounded distally, broadly fused mesally, midline with small distal cleft, with long setae; ventral section tapering, rounded proximally, extending above S8+9 only to suture between S8 and S9; dorsal apodeme substantial, but not thick, straight basally, forking midway on anterior margin of callus cerci; dorsal branch extending around dorsal margin of callus cerci to midway on posterior margin, ventral branch curving ventrally well below callus cerci, then bending posteriorly, extending along ventral margin of ectoproct. S8+9 fused, with trace of suture dorsally, with clear intersegmental demarcation throughout; S8 tall (1.5–2.0× taller than long), ca one-half (0.44–0.47×) length of S8+9 along ventral margin; S8+9 (lateral view) with proximal margin slightly convex, dorsal surface of S8 rounded, of S9 curved distally, steeply sloped at terminus; terminus without knob or gonocristae; membranous region above terminus of S9 with pair of large, eversible, lateral pouches. Gonarcus well sclerotized, widely arcuate (total span, 0.67-0.84 mm); bridge broad (0.38-0.62 mm long), dorsoventrally flattened, gently curved throughout; lateral apodeme rounded dorsally, more acute ventrally (0.21-0.24 mm wide; 0.29-0.33 mm tall); gonocornua extending forward from anterior edge of gonarcal bridge, basally stout, with ventral, straight projection, tapering to narrow, rounded apex (length, 0.09-0.15 mm); distance between inner bases of gonocornua 0.15-0.25 mm, distance between tips 0.20-0.26 mm. Mediuncus located beneath, and well separated from gonarcus, with mesal, recurved beak, lateral, well-sclerotized, stiff membranous, curved arms; mediuncus attached to gonarcal bridge via robust membrane that extends along width of gonarcal bridge between outside margins of gonocornua, folds beneath gonarcal bridge



Figure 11. *Leucochrysa (L.) varia* male genitalia. **A** Gonarcal complex, dorsal **B** Gonarcus, ventral **C** Gonarcus, lateral **D** Mediuncus, ventral **E** Hypandrium internum **F** Gonosetae inside gonosaccus. (A, C–F State of Rio de Janeiro, Brazil; B Province of Orellana, Ecuador). *Abbreviations:* **bk** beak-like tip of mediuncus **co** comes **gc** gonocornu **gsa** gonosaccus **gsa-i** interior of gonosaccus **gse** gonosetae **g.a.** gonarcal apodeme **g.b.** gonarcal bridge **mu-m** mediuncal membrane **mu-s** sclerotized section of mediuncus (mediuncal rod).

and beneath mediuncal beak to form deep gonosaccus; gonosaccus with two fields of five to seven short gonosetae on chalazae. Hypandrium internum: arm 0.25–0.37 mm long, distal span between arms 0.24–0.32 mm.

Female. Height of S6 ca 0.75 times length, S7 height ca 0.60 times length. Callus cerci round, diameter 0.17–18 mm, with 30–35 trichobothria. T8 roughly quadrate

(lateral view) with rounded corners, similar in depth to T6. T9+ectoproct elongate, slanting anteriorly; ventral margin slightly convex, extending slightly below level of gonapophyses laterales. Dorsal margin of S7 with slight taper basally, becoming more pronounced distally; terminus unmodified, with terminal (posteroventral) setae slightly more dense than in other areas. Gonapophysis lateralis rounded to slightly acute dorsally, rounded distally, ventrally, ca 0.53–0.60 height of T9+ectoproct; inner membranous surface not expandable, with ca two vertical rows of short setae. Colleterial complex consisting of membranous gland connected to colleterial reservoir via broad duct, and elongate ribbon-like accessory gland; colleterial gland elongate, delicate, transparent; colleterial reservoir smaller, delicate, transparent, tapering to narrow, granulose, spiny duct; accessory gland narrow, elongate, forked distally, with spiny surface; accessory gland and colleterial duct connected to lightly sclerotized, widened, flattened platform extending from below transverse sclerite; transverse sclerite curved, lightly sclerotized, slender throughout, with long teeth (setae?). Spermatheca with initial (posterior) section scoop-shaped, broad, thick, tapering slightly at base (ca 0.25 mm wide along distal margin x ca 0.20 mm height from tip of distal margin to base of scoop), with elongate, broad, smooth, convoluted tube extending down one side, looping in U-shaped turn, then twisting through several loops before joining bursal duct [tube ca 1.1 mm in total length, ca 0.05 mm in width throughout]; spermathecal invagination not specifically identified. Spermathecal duct extremely long, well sclerotized throughout, densely, tightly coiled, arising from side of scoop-shaped section of spermatheca; coiled length ca 3-5 mm, including membranous, brushy, less coiled distal section, uncoiled length much greater. Bursal duct extending from tip of tubular spermathecal velum, basal section membranous, broad, curved, fluted; surface with striated folds, lateral margins of major folds heavily granulose. Bursa copulatrix small, saccular, extended over spermatheca, slightly into section of S7; ventral surface with small striated folds; dorsal surface smooth; pair of clear, elongate, tubular bursal glands attached dorsally to base of bursa via clear, pipe-fitting-like bases; bursal glands very long, unbranched; surface lightly granulose. Subgenitale with smooth (unfolded), rounded surface, broad, rectangular, robust, bilobed projection extending distally at ca 90° angle to subgenitale surface, lobes large, with minute setae on surface, region between lobes extending distally as smaller, acute lobe; base of bilobed projection with dense transverse folding, with sclerotized, knob-like mesal lobe projecting from pair of scalloped, sclerotized arms.

Larva. All instars described (Mantoanelli et al. 2006).

Biology. Developmental and survival rates of immature stages under five constant temperatures and larval trash-carrying behavior studied by Mantoanelli et al. (2006) and Mantoanelli and Albuquerque (2007).

Variation. The coloration of the head, mesonotum and metanotum is the most obvious variation expressed by *L*. (*L*.) *varia* [see above]. However, color is not the only feature that varies among *L*. (*L*.) *varia* specimens. For example, the expansion of abdominal segments 4–9 and the degree of sclerotization of the integument varies greatly among both male and female specimens (see Figs 10, 12). Differences in sclerotization are particularly noticeable in the ventral apodemes of the male T9+ectoproct (Fig. 10).



Figure 12. *Leucochrysa* (*L.*) *varia* female abdominal structures. **A, B, C** Terminal segments, lateral, demonstrating intraspecific variation in the shape and expansion of the abdomen **D** Genitalia, lateral **E** Callus cerci and trichobothria. (A–B, D District of Madre de Dios, Peru; C, E State of Rio de Janeiro, Brazil). *Abbreviations:* **b.c.** bursa copulatrix **b.d.** bursal duct **b.g.** bursal gland **g.l.** gonapophysis lateralis **sg** subgenitale **sp** spermatheca **sp.d.** spermathecal duct **S7** seventh sternite **tr** trichobothria **T8** eighth tergite **T9+ect** fused ninth tergite and ectoproct.

We suspect that these features (abdominal expansion and integumental sclerotization) are at least partially a function of age and developmental or reproductive maturation.

Two features, specific to males, also show considerable variation. First, the breadth of the elongate mediuncal "rods" varies. For example, the *C. internata* type [= L. (L.)

varia] has very broad mediuncal rods (Fig. 3), whereas the *C. varia* type [= L. (L.) *varia*] has considerably narrower ones (Fig. 1). Other specimens express a range in size between these two specimens (Fig. 11). Finally, the pattern of microtholi on the third abdominal sternite varies among males. In one specimen from Ecuador, the microtholi were restricted to a relatively small lateral patch; they were absent from the mesal region of the sternite. In another specimen, this one from Brazil, microtholi were present along the entire lateral region of the sternite and also in a strip along the posterior margin. Whether this variation has a geographical component is unknown.

Material examined (in addition to the types listed above). ARGENTINA. Salta: Cafayate, ii-iv.1968, Hayward (23, 39, USNM). BRAZIL. Mato Grosso: Itiquira [17°12'S, 54°09'W], 522 m, 17.i.1996, 2Å, V. Cruz; idem, 26.viii.1996, 2Å, V. Cruz; idem, 5.x.1996, 1∂, V. Cruz; 18.x.1996, 1∂, 3♀, V. Cruz; idem, 31.xii.1996, 2∂, V. Cruz; idem, 13.i.1997, 1^o, S. Freitas (all FCAV-UNESP). *Minas Gerais*: Caratinga, 19.ix.2011, S. Freitas & F. Sosa (2³, 2², UCOB). *Pará*: Rio Xingu Camp, ca 60 km S. Altamira [3°39'S, 52°22'W], 2-8.x.1986, malaise trap, night collection, P. Spangler & O. Flint (1^Q, USNM). Babia: Camacan, Reserva Serra Bonita, Fazenda Paris, 200 m, 6.x.2005, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, Oct. 2005 (15d), 11^Q, UCB). Distrito Federal: CENARGEN Farm nr. Núcleo Bandeirante, 20.iii.1999, M. J. & C. A. Tauber (23, 39, UCB); idem, 9.v.2002 (23, UCB). Rio de Janeiro: Parque Estadual do Desengano, Santa Maria Madalena, Terras Frias, 30.iii.1999, M. J., C. A. & P. J. Tauber, G. S. Albuquerque (3∂, 2♀, UCB); idem, 15.v.2002, M. J., C. A., P. J. & A. J. Tauber, G. S. Albuquerque, E. A. Silva (9♂, 6♀, UCB); idem, 28.x.2003, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, Oct-Nov 2003 (1^Q, UCB); idem, 22.iv.2004, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, April 2004 (16∂, 10^Q, UCB); Parque Estadual do Desengano, Campos dos Goytacazes, Babilônia, 26.iii.1999, M. J., C. A. & P. J. Tauber, G. S. Albuquerque (9∂, 6♀, UCB); idem, 21 & 27.iii.2001, M. J., C. A. & P. J. Tauber, G. S. Albuquerque (5♂, 3♀, UCB); idem, 20.v.2002, M. J., C. A., P. J. & A. J. Tauber, G. S. Albuquerque, E. A. Silva (6d, UCB); Parque Estadual do Desengano, Campos dos Goytacazes, Santo Antônio do Imbé, 24 & 31.iii.1999, M. J., C. A. & P. J. Tauber, G. S. Albuquerque (8, 2, 2, UCB); idem, 27.iii.2001, M. J., C. A. & P. J. Tauber, G. S. Albuquerque (1∂, 1♀, UCB); idem, 1 & 5.v.2003, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, April-May 2003 (2⁽²⁾, UCB); Parque Estadual do Desengano, Campos dos Goytacazes, Sossego, 25.iii.1999, M. J., C. A. & P. J. Tauber, G. S. Albuquerque (13, 19, UCB); Parque Estadual do Desengano, Campos dos Goytacazes, Fazenda Pedrinho, 3.v.2003, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, Apr.-May 2003 (13, UCB); near Parque Estadual do Desengano, Campos dos Goytacazes, Fazenda Boa Vista, M. J., C. A. & P. J. Tauber, G. S. Albuquerque (8∂, 6♀, 1 teneral, UCB); Campos dos Goytacazes, Dist. de Morangaba, Fazenda São Julião, 18.x.2005, M. J. & C. A. Tauber, G. S. Albuquerque (23, 1[♀], UCB); Campos dos Goytacazes, Conceição de Macabu, Santo Agostinho, 21.v.2002, M. J., C. A., P. J. & A. J. Tauber, G. S. Albuquerque, E. A. Silva (1³, UCB); Campos dos Goytacazes, Conceição de Macabu, Fazenda Carrapeta, 29.iv-6.v.2003, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, Apr.-May 2003 (1⁽²⁾, UCB); idem, 23.



Figure 13. *Leucochrysa (L.) varia* female genitalia. **A–E** Spermatheca complex with a variety of views and magnifications **F** Subgenitale (all, State of Rio de Janeiro, Brazil). *Abbreviations:* **b.c.** bursa copulatrix **b.d.** bursal duct **knob** protruding knob on surface of subgenitale **lobe** distal lobe of subgenitale **sg** subgenitale **sp** spermatheca **sp/bd** connection between spermatheca and bursal duct **sp.c.** spermathecal connection to spermathecal duct **sp.d.** brush terminus of spermathecal duct in subgenitale.

iv.2004, G. S. Albuquerque, M. J. Tauber, C. A. Tauber Expedition, April 2004 (11∂, 4♀, UCB); Ilha Grande, 01.vi.2002, G. S. Albuquerque (1∂, UCB). *São Paulo*: São Vicente [23°57'S, 46°23'W], 916 m, 21.x.2009, S. Freitas (1♀, FCAV-UNESP). *Rondônia*: 62 km s. Ariquemes, 8–20.xi.1994, W. J. Hanson (1♀, USU); idem, 22–31.x.1997 (1♀, USU). **ECUADOR.** *Orellana* [*Napo**]: Yasuní Res. Sta. [0°38'S, 6°36'W [Sic!, probably



Figure 14. *Leucochrysa (L.) varia* female genitalia. **A** Colleterial and accessory glands [Arrow 1 indicates the connection of the duct from the colleterial reservoir to the shelf of the transverse sclerite. Arrow 2 indicates the connection of the duct from the accessory gland to the shelf of the transverse sclerite.] **B** Transverse sclerite **C** Genitalia, including bursal glands **D** Tip of bursa copulatrix with pipe-fitting-like connection to bursal gland (all, State of Rio de Janeiro, Brazil). *Abbreviations:* **acc.gl.** bifurcated accessory gland **b.c.** bursa copulatrix (tip) **b.d.** bursal duct **b.gl.** bursal gland **b.gl.c.** connection between bursal gland and bursa copulatrix **col.gl.** colleterial gland **col.r.** colleterial reservoir **sp/bd** connection between spermatheca and bursal duct **tr.s.** transverse sclerite.

76°36'], 250 m, 19–30.x.1996, W. J. Hanson (1 \bigcirc , USU); idem, 18–30.x.1998, W. J. Hanson (1 \bigcirc , USU); Misahualli nr. Tena, 3–8.x.1999, S. R. Keller (1 \bigcirc , USU); idem, 26.viii-2.ix.2000, S. & P. Keller (1 \bigcirc , USU); idem, 6–19.x.2001, C. Branimer (1 \bigcirc , USU); Yasuni Biol. Res. Sta. [ca 0°40'S, 76°24'W] 1–7.xi.2002, E. M. Fisher (1 \bigcirc , 1 \bigcirc , CAS); Coca [= Puerto Francisco de Orellana] [0°03'S, 79°40'W], v.1965, L. C. Peña (1 \bigcirc , CAS). **PERU.** *Madre de Dios:* Tambopata, 15 km NE Pto. Maldonado, 200 m, 25.vi.1989, R. A. Leschen #177, ex malaise trap (1 \bigcirc , SEM); Río Tambopata Res., 30 km (air) sw Pto. Maldonado [12°50'S, 69°20'W], 290 m, 08.xi.1984, T. L. Erwin, canopy fogging 04/01 (1 \bigcirc alcohol, USNM); idem, 02.v.1984, T. L. Erwin et al., canopy fogging project 02/03 (1 \bigcirc alcohol, USNM); Pakitza, Zone 02 [11°55'48"S, 71°35'18"W], 9.ix.1988, insecticidal fog, canopy/pouteria, BIOLAT 02180413, T. L. Erwin (1 \bigcirc alcohol, USNM).

[Note: *The Yasuní Research Station is located in Orellana (a province that was separated from Napo province in 1998). Ecuador's entire Yasuní Biosphere Reserve (established by UNESCO in 1989) encompasses a large area between the Napo River in the north and west and the Curaray River in the south and east; in terms of biological diversity, it is an extremely rich area.]

Leucochrysa (Leucochrysa) pretiosa (Banks, 1910)

http://species-id.net/wiki/Leucochrysa_pretiosa Figs 9A–B, 15–26

- Allochrysa pretiosa Banks [1910] (1910: 150) original description: [Colombia] "Inmba, Cauca, 1,000 meters, January (Fassl)". Navás (1913: 157) comparison with Allochrysa colombia Banks and A. varia.
- Leucochrysa pretiosa (Banks). Navás (1917: 279) first reference to combination; Banks (1944: 31) collection records; Banks (1945: 167-168) comparison with *L. varia* and *Leucochrysa vulnerata* (Navás), synonymy of *Leucochrysa variata* (Navás), *Leucochrysa delicata* Navás, *Leucochrysa angrandi* (Navás) with *L. pretiosa*, collection records; Banks (1948: 169) collection record; Penny (1977: 23) species list; Adams (1979: 97) species list, record from Mexico considered doubtful.
- *Leucochrysa (Leucochrysa) pretiosa* (Banks). Brooks and Barnard (1990: 276) subgeneric determination, species list; Freitas and Penny (2001: 281, 353, fig. 42) brief redescription, collection records, figures -- based on misidentified specimens in the FCAV-U-NESP, not *L. (L.) pretiosa*; Penny (2002: 194, figs 60-62) brief diagnosis, collection records in Costa Rica, drawings of head, wings; Valencia Luna et al. (2006: 48) collection records, image -- species identification unconfirmed; Oswald (2007) catalog listing.
- Allochrysa angrandi Navás [1911] (1911: 278) original description: "Guatemala. Angrand leg.". Navás (1917: 279, angrandi not specifically mentioned) genus synonymized with Leucochrysa; Penny (1977: 23, as A. angrandi and A. angradi) listing as synonyms of L. pretiosa; Legrand et al. (2008: 113) lectotype designation, taxonomic notes.
- *Leucochrysa angrandi* (Navás). Banks (1945: 167) first reference to combination, synonymy with *L. pretiosa*; Penny (1977: 23, as *L. angradi*) listing as a synonym of *L. pretiosa*; Adams (1979: 97) listing as a valid species, without comment, probable occurrence in Mexico; Brooks and Barnard (1990: 276) listing as a synonym of *L. (L.) pretiosa*, without comment; Oswald (2007) catalog listing, as a synonym of *L. (L.) pretiosa*.

Leucochrysa (Leucochrysa) angrandi (Navás). Valid status reinstated. See below.

- Allochrysa variata Navás [1913] (1912-1913: 315) original description: "Panamá: V. de Chiriqui, 25-400 ft., Champion; Mexique: Cuesta de Misantla, M. Trujillo".
 Penny (1977: 23, as A. varieta) listing as a synonym of L. pretiosa.
- Leucochrysa variata (Navás). Navás (1917: 279) first reference to combination; Banks (1945: 167) synonymy with *L. pretiosa*; Penny (1977: 23, as *L. varieta*) listing as a synonym of *L. pretiosa*; Brooks and Barnard (1990: 276) listing as a synonym of *L. (L.) pretiosa*.

Leucochrysa (Leucochrysa) variata (Navás). Valid status reinstated. See below.

- *Leucochrysa delicata* Navás [1925] (1925: 190, fig. 18) original description: "Costa Rica: Reventazón, 15 de Marzo de 1923. Janson et Sons. Col. m.". Banks (1945: 167) synonymy with *L. pretiosa*; Adams (1979: 97) species list, note regarding absence of type; Brooks and Barnard (1990; 276) listing as a synonym of *L. (L.) pretiosa*; Oswald (2007) catalog listing of *L. delicata* and *L. (L.) delicata* as synonyms of *L. (L.) pretiosa*. Neotype designation below.
- *Leucochrysa erminea* Banks [1946] (1945: 169) original description: "Barro Colorado, Canal Zone, August (F. H. Hull) Type M.C.Z. no. 25657". Penny (1977: 22) species list; Adams (1979: 97) species list.
- Leucochrysa (Leucochrysa) erminea Banks. Brooks and Barnard (1990: 276) subgeneric determination, species list; Oswald (2007) catalog listing. Syn. n.

Known geographical distribution. Southern Mexico, northern to southern Central America, the Caribbean region, and northern region of South America (Venezuela, central Ecuador, and western Colombia) [based on confirmed published records and specimens examined]. Mexico: Chiapas. Belize: Cayo District. Costa Rica: Provinces of Cartago, Puntarenas. Panama: Canal Zone. Trinidad & Tobago: Trinidad Island. Venezuela: States of Amazonas, Aragua, Carabobo, Falcón, Lara, Mérida, Miranda, Portuguesa, Táchira, Yaracuy, Capital District. Colombia: Department of Valle del Cauca. Ecuador: Provinces of Esmeraldas, Napo, Pichincha. Paraguay: Department of Caaguazú. The treatment of *L. (L.) pretiosa* by Freitas and Penny (2001: 281) was based on misidentified specimens in the FCAV-UNESP; thus, their distribution records were not included here.

Banks' (1945: 168) records from Central America (Barro Colorado, Canal Zone; El Cermeno and La Campana, Panama; Cayuga, Volcan [prob. Volcán] Sta. Marta, and Alta Vera Paz, Guatemala; Limon [prob. Limón], Costa Rica) and his records from Colombia (Banks 1944: 31) are all well within the confirmed range of *L. (L.) pretiosa.* We have seen specimens from most of the areas he reported; however, we have not examined his specimens. The northern-most specimen of *L. (L.) pretiosa* that we have seen is from Chiapas, Mexico. Valencia Luna et al. (2006: 48) also reported the species from Morelos, Mexico; however, we have not seen specimens to confirm the report. The southern-most record is based on a single specimen, with somewhat obscure data that we interpreted as referring to the Mennonite Colony of Sommerfeld, ca 210 km east of Asunción, Paraguay. This locality is far south of the second southern-most record for the species (north-central Ecuador).

Type specimens and rationale for taxonomic changes.

Allochrysa pretiosa. Two syntypes from "Inmbo", Cauca, Colombia, MCZ (one female, one with abdomen missing, examined).

Here, to stabilize the nomenclature of this taxonomically difficult group of lacewings, we recognize the specimen with an abdomen (female) as the **Lectotype** [present designation].



Figure 15. Lectotype, *Allochrysa pretiosa* [= *L.* (*L.*) *pretiosa*], female, MCZ, abdomen and genitalia. **A** Abdominal segments 4–9, lateral **B** Genitalia within terminal segments [Note the bursal glands that extruded from a tear on the right side.] **C** Spermathecal complex and subgenitale, ventral **D** Internal genitalia and subgenitale, lateral **E** Callus cerci **F** Gonapophysis lateralis, lateral **G** Spermathecal duct [The sclerotized section of the duct is brownish; the brushy, membranous section is longer; it extends to the right, bends abruptly to the left, and then ends at the arrow.]. *Abbreviations:* **b.d.** bursal duct **b.gl.** bursal gland **g.l.** gonapophysis lateralis **knob** protruding knob on surface of subgenitale **lobe** distal lobe of subgenitale **pegs** small and large pegs on bursal duct **sg** subgenitale **sp** spermatheca **S7** seventh sternite **T8** eighth tergite **T9+ect** fused ninth tergite and ectoproct.

Its labels read: (1) "Inmbo Cauca / Colombia S. Am." [Banks' hand]; (2) "1000 m / Jan" [Banks' hand]; (3) "Collection / N. Banks"; (4) "Type" [red, Banks' hand]; (5) "Type / 12005"; (6) "Allochrysa / pretiosa / type / Bks" [white, red border, Banks' hand]; (7) "LECTOTYPE / *Allochrysa pretiosa* / Banks, 1910 des. / C. A. Tauber 2013"

[red]. The specimen is in fairly good condition; the terminalia are in a vial with glycerine. Images, in addition to Fig. 15 here, are in the MCZ Type Database (http://insects.oeb. harvard.edu/MCZ/index.htm). The remaining type is now labelled as a paralectotype.

"Cauca" probably refers to the Valle del Cauca, which is in southwestern Colombia. We could not locate an "Inmba" (spelling in original description), "Inmbo" (spelling on lectotype label and by Banks 1944: 31), or "Jumba" (spelling by Navás 1913: 158); we suspect that these names are all misspellings of Yumbo, a town near Cali, Valle del Cauca Department.

Allochrysa angrandi. Lectotype, designated by Legrand et al. (2008: 113), MNHN (female, examined).

From his discussion, it appears that Banks (1945: 167) did not see the type of *A. an-grandi*; even so, he suggested that the species was synonymous with *L. pretiosa* and, with one exception (Adams 1979: 97), it has been treated as synonymous. Our comparison of the lectotypes of the two species (both females) indicates that they are distinct [compare Fig. 15 with Figs 17–18]. Indeed, the *A. angrandi* lectotype lacks some characteristics of the *varia*-like species that we have examined. For example, it appears to have red lateral stripes on the prothorax (Figs 16C–E), no suffusion on the forewing crossveins, and the base of the forewing lacks dark markings (Fig. 16I). In addition, the fifth and sixth tergites of the cleared abdomen (Fig. 17) lack the large spots that are typical of *varia*-like species. This characteristic sometimes is not visible in cleared *varia*-like specimens, especially teneral ones, and thus its absence from the *A. angrandi* type is not definitive for excluding the species from the group. This species will be re-described elsewhere.

Allochrysa variata. Lectotype by present designation, BMNH (male, examined).

In his original description, Navás (1912-1913: 315) mentioned two localities; thus, it is clear that he had more than one specimen of this species. We have found only one-the one from Panama (a male in the BMNH). To stabilize the nomenclature of this taxonomically difficult group of lacewings, we designate this specimen as the **Lectotype** [**present designation**]. Its labels read: (1) "V. De Chiriqui, / 25–1000 ft. / Champion."; (2) "Godman-Salvin / Collection / 1911–24."; (3) "Typus" [pink, hand-written, Navás]; (4) "Allochrysa / variata Nav. / Navás S.J. det." [hand-written, Navás & printed]; (5) "Type / H.T." [round, with red border]; (6) "LECTOTYPE / *Allochrysa variata* / Navás, 1913 des. / C.A. Tauber 2013" [red]. The specimen is discolored with age, but otherwise in reasonably good condition; the terminalia are in a vial with glycerine.

Banks (1945: 167) suggested that *A. variata* was synonymous with *L. pretiosa*, and it was subsequently treated as such. However, our comparison of the *A. variata* male lecto-type with specimens of *L. (L.) pretiosa* indicates that the two are distinct [compare Figs 19–21 (*variata*) with Figs 22–24 (*pretiosa*)]. This species will be re-described elsewhere.

Leucochrysa delicata. Type apparently missing, sex unknown (not examined).

In the original description, Navás stated that he retained the type in his personal collection; it is not there now (Monserrat 1985: 240), nor was it found at the MNHN



Figure 16. Lectotype, *Allochrysa angrandi*, female, MNHN, external features. A Labels B Body, lateral C Head, thorax, base of wings, dorsal D Pronotal, mesonotal markings E Head markings, dorsal (slightly obscured)
 F Head, frontal G Head, frontolateral H Scapes, dorsal I, J Forewing and hindwing; scale applies to both wings.

or the BMNH. Presumably, it is lost (see Adams 1979: 97). Given the collection site of the type (Costa Rica), it is possible that it was either *L. (L.) angrandi* or *L. (L.) pretiosa*. Because *L. (L.) pretiosa* is the more common and therefore most likely of the two, we have no basis for altering Banks' synonymy; thus it pertains. To help stabilize the taxonomy of this taxonomically difficult group of *Leucochrysa*, we designate a female specimen in the William F. Barr Entomological Collection (UID), University of Idaho, as the Neotype. This specimen is from Turrialba, a locality in the Reventazón River basin of Costa Rica; its labels read: (1) "COSTA RICA. Cart. / Turrialba, CATIE / 26-29 Jun 1986 / Nadeer Youssef", (2) "NEOTYPE" / *Leucochrysa delicata* / Navás, 1925 des. / Tauber et al. 2013"; (3) "*Leucochrysa (L.) / pretiosa* Banks / det. C. A. Tauber 2013".

Leucochrysa erminea Banks. Holotype by original designation, MCZ (sex unknown, abdomen missing, examined). No other type material was found in the MCZ (P. D. Perkins, personal communication).

Banks (1945: 169) did not compare his type of *L. erminea* with the *L. pretiosa* specimens that he had described many years earlier. He was probably unaware of the variation in body color expressed by this species. We make the synonymy on the basis of external features, notably the wings, which are almost identical on the *A. pretiosa* and *L. erminea* types [See images in MCZ Type Database (http://insects.oeb.harvard. edu/MCZ/index.htm)]. In addition, *L. (L.) pretiosa* is the most common species of *L. (L.) varia*-like lacewings in Panama [the type locality of *L. (L.) erminea*].

Diagnosis. Leucochrysa (L.) pretiosa expresses the external features listed above for the "varia-like" species. In addition, both L. (L.) pretiosa and L. (L.) varia have notable variation in head and thoracic coloration, black shading around the second m-cu crossvein and the distal Psm-Psc crossveins. Although examination of the genitalia is essential for accurate identification of the varia-like species, these two species often can be separated externally on the basis of wing characteristics. L. (L.) pretiosa generally has a lighter brown mark on the stigma, a larger, rounded patch of shading around the distal leg of the im1, and slightly more shading around the basal outer gradate veins, second m-cu crossvein, and distal Psm-Psc crossvein than does L. (L.) varia. In general, the distal gradate veins and shaded veins of L. (L.) varia are darker (brown or black) than those of L. (L.) pretiosa.

The males of *L*. (*L*.) *pretiosa* are distinguished by: (i) sternite S3 with microtholi usually present only posterolaterally, rarely anterolaterally or posteromesally [both of which occur in *L*. (*L*.) *varia*]; (ii) much smaller genital structures [gonarcal span of 0.40–0.65 mm; cf., 0.67–0.84 mm in *L*. (*L*.) *varia*]; (iii) gonarcal bridge straight between gonocornua and bent at the interior margin of the gonocornua [not gently curved throughout as in *L*. (*L*.) *varia*]; (iv) basal section of mediuncus broad [extending laterally well beyond gonocornua], leathery, rigid membrane, not a light, flexible membrane as in *L*. (*L*.) *varia*; (v) gonarcus with a pair of slender ventral processes between the lateral apodemes and gonocornua [absent from *L*. (*L*.) *varia*]. Female *L*. (*L*.) *pretiosa* have a very distinctive, bowl-shaped spermatheca, with a relatively short spermathecal duct.

Redescription. *Head* (Fig. 22): 1.7–1.9 mm wide (including eyes). Frons, clypeus white, red suffused, or entirely red; gena pink to dark red; maxillary and labial palpi yellowish. Vertex with central area raised, yellowish to green, with prominent, dark red to dark brown, V-shaped mark along anterior margin; lateral margins with narrow to wide stripes; post-ocular area with red spot. Antenna: scape tinged with red-wine coloration, especially mesally; pedicel yellowish green, inner margin with dark mark; flagellum cream-colored, with amber bristles; inner margin of basal ca three flagellomeres tinged with black; dorsal antennal fossae marked with red laterally.

Thorax (Fig. 22): Cervix with red mark laterally. Pronotum 1.1–1.5 mm long, 1.2–1.4 mm wide, yellowish green, unmarked. Mesonotum, metanotum variable,



Figure 17. Lectotype, *Allochrysa angrandi*, female, MNHN, external abdomen. **A** Abdominal segments 6–9, lateral (with dorsal tear) **B** callus cerci **C** Subgenitale, ventral. *Abbreviations:* **b.gl.** bursal gland **g.l.** gonapophysis lateralis **knob** protruding knob on surface of subgenitale **lobe** distal lobe of subgenitale **sg** subgenitale **sg-b** broad base of subgenitale **sp.d.** spermathecal duct **S7** seventh sternite.

entirely dark brown to yellow with brown marks of various sizes. Posterior margin of mesoscutum with prominent dark brown, transverse stripe; metascutum with small or large brown marks; mesoscutellum, metascutellum yellow to light green, without marks.

Wings (Fig. 9A-B) Forewing 18.5-21.8 mm long, 7.2-7.9 mm wide (at widest point); ratio of length : maximum width = 2.51-2.75:1. Costal area moderately broad; tallest costal cell (#8-10) 1.6-1.9 mm tall, 2.4-2.8 times width, 0.2-0.3 times width of wing (midwing). First intramedian cell quadrangular, width (anterior margin) 1.5–2.0 times width (anterior margin) of m3, 1.0–1.2 times length of posterior margin of m3, length of basal vein (= ma, median arculus) 2.0–3.8 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 15-19 closed cells; tallest cell (#7-10) 1.72-2.80 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; 8-10 inner gradates, 8–10 outer gradates. Height of fourth gradate cell 3.5–5.5 times width. Seven to eight b' cells (cells beneath pseudomedia after im2). Three intracubital cells (two closed). Membrane mostly clear except basal area marked with reddish brown, stigma opaque, with large dark brown mark basally, dark clouding around second m-cu crossvein and around distal Psm-Psc crossveins, sometimes with clouding around distal leg of im1 and around crossveins between distal b' cells. Veins mostly green, except basal costal crossveins, base of Radius, ca three radial crossveins, distal Psm-Psc crossveins, outer gradates, and forks of marginal veins usually entirely black; costal crossveins with black tips; inner gradates, posterior crossveins of distal b' cells mostly black. Hindwing 16.4-19.4 mm long, 5.5-6.7 mm wide. Two series of gradate veins; 7–10 inner, 7–9 outer; 15–17 radial cells (counted from origin of Radius, not false origin). Five to six b cells (including small b1 cell); seven b' cells beyond im2; two intracubital cells (one closed). Membrane clear; stigma with pronounced brown mark basally. Veins mostly light green; outer gradates, tips of costal crossveins brown to black.



Figure 18. Lectotype, *Allochrysa angrandi*, female, MNHN, genitalia. **A** Bursal and spermathecal complexes [Note the C-shaped spermatheca.] **B** Paired bursal glands with accessory glands **C** Spermatheca at attachment of spermathecal duct **D** Tip of spermatheca at attachment of bursal duct **E** Spermathecal duct with brushy tip **F** Tip of spermatheca, with slit-like opening to setose bursal duct. *Abbreviations:* **acc.gl.** accessory gland of bursal gland **b.c.** bursa copulatrix **b.d.** bursal duct **b.gl.** bursal gland **sp** spermatheca **sp.d.** spermathecal duct.

Abdomen (Figs 15, 23–26): 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 S2–3 longer



Figure 19. Lectotype, *Allochrysa variata*, male, BMNH, external features. **A** Labels **B** Habitus, dorsal **C** Forewing and hindwing, left.

than wide; S5–7 more square-shaped (lateral view); distal segments (beyond A4) expanded, height of pleural region greater than height of sternites [integument of cleared specimens soft, floppy, easily damaged]. Coloration: mostly green, with yellow mesally. Tergites T5, T6 with large black spots, bordered by red; callus cerci white; setae, trichobothria golden.

Male. Height and length of S6 ca equal, S7 height ca 1.1–1.2 times length (lateral view). Microtholi dense on S4–S8, usually sparse, only present distolaterally on S3 (rarely, a few microtholi along posteromesal edge), absent from S1–2, S9.



Figure 20. Lectotype, *Allochrysa variata*, male, BMNH, external features. **A** Head, frontal **B** Head, dorsal **C** Scapes, dorsal **D** Pronotum, mesonotum **E** Metanotum **F** Head, thorax, left lateral **G** Head, prothorax, mesothorax, right lateral.

Callus cerci slightly oval (ca 1.2–1.3× taller than wide), diameter 0.16–0.23 mm, with 28–38 trichobothria of variable length. T9+ectoproct soft, lightly sclerotized, rounded posterodorsally, truncate to rounded distally, broadly fused mesally, midline with small distal cleft; ventral section rounded, tapering proximally, extending proximally only to suture line between fused S8 and S9 (dorsal margin); dorsal apodeme lightly to moderately sclerotized, straight, with two dorsal forks before callus cerci, curving along ventral margin of ectoproct to terminus; first branch of dorsal apodeme extending posterodorsally to level midway up callus cerci; second branch extending around proximal, dorsal and posterodistal margins of callus cerci. S8+9 fused, with trace of suture dorsally, with clear intersegmental demarcation through-



Figure 21. Lectotype, *Allochrysa variata*, male, BMNH, genitalia. A Tip of abdomen, lateral (damaged)B Gonarcus, lateral C Gonarcus, ventral. *Abbreviations:* bk beak-like tip of mediuncus c.c. callus cercigc gonocornu gsa gonosaccus g.a. gonarcal apodeme.

out; S8 1.6–2.0× taller than long, less than one-half (0.36–0.45×) length of S8+9; S8+9 (lateral view) with proximal margin slightly convex, dorsal surface gradually curving ventrally over 3/4ths distance from proximal margin, then curving steeply to terminus; terminus without knob or gonocristae; membrane above terminus with pair of large, eversible, membranous pouches. Gonarcus well sclerotized, arcuate,



Figure 22. *Leucochrysa* (*L*.) *pretiosa* variation in head and thoracic markings. **A, B** Head, thorax, dorsal **C–F** head, frontal (A Locality unknown; B, D, F State of Portuguesa, Venezuela; C, E State of Mérida, Venezuela). Scale in **C** applies to **C–F**.



Figure 23. Leucochrysa (L.) pretiosa male abdominal structures. **A**, **B** Terminal segments, lateral, demonstrating intraspecific variation in the shape and expansion of the abdomen **C**, **D** Tergite 9+ectoproct, lateral, illustrating variation in the sclerotization of the dorsal apodeme **E** Abdominal tergite 8 and fused tergite 9+ectoproct, dorsal, slightly tilted to one side **F** Callus cerci (A Province of Esmeraldas, Ecuador B, D, F Trinidad Island, Trinidad & Tobago; C State of Chiapas, Mexico; E Province of Puntarenas, Costa Rica). *Abbreviations:* **c.c.** callus cerci **d.a.** dorsal apodeme of ninth tergite+ectoproct **d.a.-d1**, **d.a.d2** first and second dorsal arms of dorsal apodeme **d.a.-v** ventral arm of dorsal apodeme **ev.p.** eversible membranous pouch **gs** gonarcus **s.a.m.** subanal membrane **S8+9** fused eighth and ninth sternites **tr** trichobothria **T8** eighth tergite **T9+ect** fused ninth tergite and ectoproct.

total span: 0.40–0.65 mm; bridge broad, straight mesally, curved abruptly at interior margin of gonocornua, dorsoventrally flattened, distance between apodemes 0.30–0.36 mm; lateral apodeme bell-shaped, broader ventrally than dorsally (0.32–0.36

mm wide, 0.18–0.19 mm tall); gonocornua extending from lateral edge of gonarcal bridge, basally stout, tapering to narrow, rounded apex, length 0.08–0.13 mm; distance between inner bases of gonocornua 0.08–0.13 mm, distance between tips 0.11–0.16 mm. Gonarcus, between lateral apodeme and gonocornu, with moderately sclerotized, elongate posteroventral processus with membrane attached. Mediuncus with basal section consisting of broad, leathery, membranous plate extending from distal margin of gonarcal bridge, recurving below gonarcal bridge; distal section of mediuncus consisting of heavily sclerotized, flat, broadly V-shaped plate, below and well separated from gonarcus; distal plate with mesal beak extending ventrally, deep mesal trough dorsally, between rounded, lateral ridges that extend above beak; membrane below gonarcus forming deep pouch with two fields of three to six stout gonosetae on chalazae; fields of gonosetae on surface of membrane facing mediuncus. Hypandrium internum: arm 0.20–0.24 mm long, distal span between arms 0.17–0.24 mm.

Female. Height of S6 ca 0.62-0.70 times length, S7 height ca 0.51-0.57 times length. Callus cerci round, diameter ca 0.15 mm, with 24-28 trichobothria. Tergite T8 roughly quadrate (lateral view) with rounded corners, similar in depth to T6. T9+ectoproct elongate, slanting anteriorly; ventral margin convex, extending slightly below level of gonapophyses laterales. Dorsal margin of S7 straight, tapering abruptly distally; terminus unmodified, with terminal (posteroventral) setae slightly more numerous, longer than in other areas. Gonapophysis lateralis rounded throughout, ca 0.53-0.58 times 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 elongate, ribbon-like accessory gland, both opening to exterior via narrow ducts above transverse sclerite; colleterial gland elongate, robust; colleterial reservoir shorter, robust; accessory gland narrow, elongate, granular, forked distally; transverse sclerite broad, flat to slightly convex, with broad, robust teeth. Spermatheca bowl-shaped basally (0.3-0.4 mm width x 0.2 mm height), with invagination tubular, extending around wall of spermathecal bowl; distal, tubular section of spermatheca broad, convoluted with ca 10 complete loops; spermathecal duct short, ca 0.8 mm including membranous, brushy, distal section, with single short, well sclerotized loop basally, longer, lightly sclerotized, brushy loop distally. Bursa copulatrix saccular, with heavily textured surface near bursal duct, becoming smoother posteriorly; bursal duct membranous, broad, flat, folded, spinose basally (near spermathecal velum), becoming broader, granulose, with patches of small, then large, robust pegs distally (near base of bursa); pair of elongate, tubular bursal glands attached to base of each side of bursa via enlarged, granular, conical bases. Subgenitale with smooth (unfolded), rounded surface, with bilobed projection dorsally, ca two times wider distally than at base, midsection with prominent lobe extending outward at ca 90° angle to subgenitale surface.

Larvae. Unknown. Biology. Unknown.



Figure 24. *Leucochrysa (L.) pretiosa* male genitalia. **A** Gonarcal complex, dorsal, gonosaccus removed **B** Gonarcus, ventral **C** Gonarcus, lateral, enhanced slightly to increase contrast **D** Mediuncus, ventral **E** Hypandrium internum, illustrating the variation in the shape of the arms and density of connecting membrane **F** Gonarcus and mediuncus, frontal [Note the gonosetae on the inside of the gonosaccus] [A, B, D State of Carabobo, Venezuela; C, E (right), F Trinidad Island, Trinidad & Tobago; E (left) State of Chiapas, Mexico]. *Abbreviations:* **bk** beak-like tip of mediuncus **co** comes **gc** gonocornu **gsa** gonosaccus **gsa-i** interior of gonosaccus **gse** gonosetae **g.a.** gonarcal apodeme **g.b.** gonarcal bridge **mu** mediuncus **mu-m** mediuncal membrane **rod** sclerotized mediuncal rod.

Variation. *Leucochrysa* (*L.*) *pretiosa* expresses considerable variation in head, mesothoracic and metathoracic coloration, as well as wing size, shape and degree of suffusion on various veins. The range of variation in several of these traits is shown on Figs 9



Figure 25. *Leucochrysa* (*L.*) *pretiosa* female. **A–B** Abdominal structures **C–D** Colleterial complex. **A** Terminal segments, lateral **B** Callus cerci **C** Transverse sclerite **D** Colleterial and accessory glands [The arrow indicates the junction of the duct from the colleterial reservoir with the accessory gland immediately before the structures attach to the shelf of the transverse sclerite.] (A State of Carabobo, Venezuela; B–D Cayo District, Belize). *Abbreviations:* **acc.gl.** bifurcated, granulose accessory gland **b.c.** bursa copulatrix **col.gl.** colleterial gland **col.r.** colleterial reservoir **g.l.** gonapophysis lateralis **sg** subgenitale **S7** seventh sternite **tr** trichobothria **tr.s.** transverse sclerite **T8** eighth tergite **T9+ect** fused ninth tergite and ectoproct.

and 22. As in *L*. (*L*.) *varia*, the expansion of abdominal segments 4–9 and the degree of sclerotization of the apodemes and sclerites varies considerably among specimens (see Figs 23, 25). This variation may be related in part to age and/or maturation; however, both male and female specimens with large, expanded (apparently mature) abdomens often had very soft and delicate integuments that tore easily during dissection. Thus, a delicate integument may not necessarily be associated with a teneral status.



Figure 26. *Leucochrysa (L.) pretiosa* female genitalia. **A** Internal genital complex, including bursal glands **B** Bursal and spermathecal complexes, with subgenitale [Note the small pegs at the base of the bursal duct and the larger ones distally.] **C** Bursal and spermathecal complexes **D** Spermathecal complex [Note the large spermathecal invagination that tapers to a narrow tubule in the upper part of the bowl.] **E** Tip of bursa copulatrix with granulose, conical connection with bursal gland (A–D Cayo District, Belize; E State of Carabobo, Venezuela). *Abbreviations:* **b.c.** bursa copulatrix **b.d.** bursal duct **b.gl.** bursal gland **b.gl.c.** connection between bursal gland and bursa copulatrix **inv** spermathecal invagination **lpeg** large peg on distal part of bursal duct **sg** subgenitale **sp** spermatheca **speg** small peg on basal part of bursal duct **sp.d.** -t brushy terminus of spermathecal duct.

Material examined (in addition to the types listed above). MEXICO. *Chiapas*: San Jerónimo, Tacaná, 6.ix.1970, T. W. Taylow Colln. (1⁽²⁾, LACM). BELIZE. *Belize*: 1 mi. N. Sibun R., 14 mi. N. Belize City, in cork forest, 5.vii.1973, Y. Sedman

(13, CAS); Cayo: 5 mi. N. San Ignacio, 12–13.xii.1988, F. D. Parker (1 \mathcal{Q} , USU). COSTA RICA. Puntarenas: Golfito, 23.vii.1957, Truxel & Menke (1^o, LACM); Golfito-United Fruit Co., 2.vii. 1976, Malaise trap 8A-5P, M. Wasbauer (1°_{\circ} , SDCM). NICARAGUA. No department: Eden [14°0'N, 84°26'W] (locality not confirmed), Th. W. Bouchelle (13, PNAS, det. by N. Banks). PANAMA. Canal Zone: Pipeline Road, 22.iii.1982, W. J. Hanson (19, USU); Barro Colorado Island, 14.ii.1955, C. W. Rettenmeyer (1 \bigcirc , SEM); idem, 9.i.1929, C. H. Curran (1 \bigcirc , AMNH). **TRINI**-DAD & TOBAGO. Trinidad Island: St Andrew Parish, Brigand Hill, 21.vii.1979, L. Sorkin (1^Q, AMNH); Arima Valley, 800–1200 ft, 5–15.ii.1965, J. G. Rozen (1^Q, AMNH); Arima Valley, 4.ii.1953, J. G. Rozen (1♀, AMNH); "Naracas" [= "Maracas"] Valley, 18.v–10.vi.1957, ROM party (1^Q, ROM); Simla Res. Sta., 2–15.vi.1961, Hanson, Clemons (30, 19, USU). VENEZUELA. Amazonas: Cerro de la Neblina Basecamp, 140 m, 0°50'N, 66°9'44"W, 13-20.ii.1984, D. Davis & T. McCabe (1°) , USNM); idem, 3.ii.1985, on low foilage, rainforest trail, W. E. Steiner (1°) , USNM); Aragua: Parque Nacional Henri Pittier (formerly Parque Nacional Rancho Grande), 1100 m, 7.iii.1959, C. J. Rosales (1^Q, MIZA); idem, 1–5.i.1966, S. S. & W. D. Duckworth (1 \bigcirc , USNM); idem, 11–15.i.1966, S. S. & W. D. Duckworth (1 \bigcirc , USNM); 1 km S. Rancho Grande, 5.ii.1976, C. M. & O. S. Flint, Jr. (13, USNM); Ocumare [1123099N - 0547148W], 100 m, 20.ii.2008, F. Sosa, F. Díaz & R. Zúñiga (1⁽¹), UCOB); *Capital District*: Caracas, R. M. Bartleman (1⁽²⁾, USNM); *Carabobo*: San Esteban, Las Quiguas, 185 m, 5-8.x.1974, J. Salcedo, R. Dietz & J. L. García (1♂, 1♀, MIZA); Yuma, 13.v.1980, F. Fernández Y & A. Chacón (without abdomen, MIZA); nr Canoabo, 850 m, 24.i.1983, O. S. Flint, Jr. (53, 62, USNM); *Falcón*: Sierra de San Luis, Valle de Acarite, 980 m, 15.vii.1983, J. Lattke (13, MIZA); *Lara*: Parque Nacional Yacambú, El Blanquito, 1100 m, 19.i.2011, F. Sosa & J. Torres (2, UCOB); Santa Rosa de la Fila, Finca Dos Aguas, 1300 m, 5-8.iii.2011, H. Chavez & A. Chavez (1^Q, UCOB); Parque Nacional Terepaima, 1100 m, 12.i.2012, F. Sosa & D. R. R. Fernandes (1^Q, UCOB); *Mérida*: El Pedregal, 200 m, 22.i.2009, F. Sosa & F. Díaz (2♀, UCOB); idem, 25.i.2009, F. Sosa & F. Díaz (1♂, 3♀, UCOB); *Miran*da: Parque Nacional Guatopo, km 24 N. Altagracia de Orituco, 640 m, 5-9.v.1975, malaise trap, J. Salcedo & R. Dietz (13, 2 without abdomen, MIZA); Portuguesa: Araure, Finca Barra de Oro [9°36'N, 69°19W], 310 m, 11.i.2008, F. Sosa & A. López (1∂, 1♀, UCOB); La Estación, Los Borbollones [9°22'N, 69°28'W], 310 m, 26.xii.2007, F. Sosa (1^Q, UCOB); *Táchira*: Paramillo, UNET, 1050 m, 23.vii.2007, F. Sosa & F. Díaz (1⁽²⁾, UCOB); *Yaracuy:* San Felipe, Hacienda Guaquira [10°17'N, 68°39 W], 100 m, 14.ii. 2010, F. Sosa & J. Torres (2∂, 2♀, UCOB); idem, 13.i.2012, F. Sosa & D.R.R Fernandes (2∂, 1♀, UCOB). ECUADOR. Esmeraldas: Parr. San Mateo, 4.v.1956 (13, CAS, bought from F. H. Walz, PAA); Napo: Misahualli nr. Tena, 26.viii–2.ix.2000, S. & P. Keller (13, USU). Pichincha: E. Sto. Domingo, 8-16.v.1988, Hanson & Bohart (1^Q, USU). PARAGUAY. No district: Summerfield, 7.x.1965, rec MAZ, A. C. Allyn, Acc. 1969–20 (19, FMNH). [The locality in Paraguay probably is the Sommerfeld (Mennonite) Colony in Caaguazú Department.]

Acknowledgements

It is a pleasure to acknowledge the following people for making specimens and/or images available for study: D. A. Grimaldi and T. Nguyen (AMNH), D. Goodger and S. Brooks (BMNH), N. D. Penny and D. H. Kavanaugh (CAS), M. K. Thayer and J. H. Boone (FMNH), J. S. Ashe and Z. H. Falin (SEM), B. V. Brown and W. Xie (LACM), P. Perkins, S. P. Cover and B. D. Farrell (MCZ), J. Legrand (MNHN), D. C. Darling (ROM), C. B. Barr and P. Oboyski (UCB), J. B. Johnson (UID), O. S. Flint, D. G. Furth and T. Erwin (USNM), C. D. von Dohlen (USU), A. M. Muscari and S. de Freitas (FCAV-UNESP), F. Díaz and E. Arcaya (UCOB), J. Demarmels and J. Clavijo (MIZA). We thank the following who assisted with collecting specimens: V. Becker, E. M. G. Fontes, F. Franca, J. S. Multani, C. S. S. Pires, E. A. Silva, E. R. Sujii, A. J. Tauber, and P. J. Tauber, and the following who helped find missing specimens, information, or references: D. T. Kondo, A. E. Díaz Montilla, G. Mendoza, C. E. Sarmiento Monroy, S. J. Brooks, and J. D. Oswald.

We greatly appreciate the help of the librarians at the Peter J. Shields Library (University of California, Davis) and the Albert R. Mann Library (Cornell University, Ithaca); we acknowledge J. D. Oswald (Texas A & M University) for access to the "Lacewing Digital Library" that he developed. Finally, we thank M. J. Tauber (MJT) (Cornell University and UCD) for his help, encouragement, discussions, and careful reading of the manuscript. This research received support from the National Science Foundation (Grants INT-9817231, DEB-0542373, MJT, CAT), the National Geographic Society (MJT, CAT, GSA), the USDA/NRI (Competitive Grant 9802447, MJT, CAT), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil–Grants 300504/96-9, 466439/00-8, 475848/04-7, 484497/07-3, GSA), Regional Project W-1385, Cornell University, and the Universidade Estadual do Norte Fluminense.

References

- Adams PA (1977) Taxonomy of United States *Leucochrysa* (Neuroptera: Chrysopidae). Psyche 84: 92–102. doi: 10.1155/1977/56815
- Adams PA (1979) A new species of *Leucochrysa* from Mexico (Neuroptera, Chrysopidae). Folia Entomologica Mexicana 41: 95–101.
- Adams PA, Penny ND (1986) Faunal relations of Amazonian Chrysopidae. In: Gepp J, Aspöck H, Hölzel H (Eds) Recent Research in Neuropterology. Proceedings of the 2nd International Symposium on Neuropterology (21–23 August 1984, Hamburg, Germany; held in association with the XVII International Congress of Entomology), Graz, Austria, 119–124.
- Banks N (1910) New South American neuropteroid insects. Proceedings of the Entomological Society of Washington 12: 146–160.
- Banks N (1914–1915) New neuropteroid insects, native and exotic. Proceedings of the Academy of Natural Sciences of Philadelphia 66: 608–632.

- Banks N (1944) Neuroptera of northern South America. Part III. Chrysopidae. Boletín de Entomología Venezolana 3: 1–34.
- Banks N (1945) [1946] A review of the Chrysopidae (Nothochrysidae) of Central America. Psyche 52: 139–174. doi: 10.1155/1945/39092
- Banks N (1948) [1949] Chrysopidae (Nothochrysidae) collected in Mexico by Dr. A. Dampf (Neuroptera). Psyche 55: 151–177. doi: 10.1155/1948/36576
- Brooks SJ, Barnard PC (1990) The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). Bulletin of the British Museum of Natural History, Entomology 59: 117–286.
- Freitas S de (2005) [2007] New species of Brazilian green lacewings genus *Leucochrysa* McLachlan, 1868 (Neuroptera Chrysopidae). In: Pantaleoni RA, Letardi A, Corazza C (Eds) Proceedings of the Ninth International Symposium on Neuropterology (20–23 June 2005, Ferrara, Italy). Annali del Museo Civico di Storia Naturale di Ferrara 8: 49–54.
- Freitas S de, Penny ND (2001) The green lacewings (Neuroptera: Chrysopidae) of Brazilian agro-ecosystems. Proceedings of the California Academy of Sciences 52: 245–395.
- Kimmins DE (1940) Notes on some types of Chrysopidae (Neuroptera) in the British Museum Collections. Annals and Magazine of Natural History 5: 442–449. doi: 10.1080/00222934008527058
- Legrand J, Tauber CA, Albuquerque GS, Tauber MJ (2008) [2009] Navás' type and non-type specimens of Chrysopidae in the MNHN, Paris [Neuroptera]. Revue Française d'Entomologie (NS) 30: 103–183.
- Mantoanelli E, Albuquerque GS (2007) Desenvolvimento e comportamento larval de Leucochrysa (Leucochrysa) varia (Schneider) (Neuroptera, Chrysopidae) em laboratório [=Development and larval behavior of Leucochrysa (Leucochrysa) varia (Schneider) (Neuroptera, Chrysopidae) in the laboratory]. Revista Brasileira de Zoologia 24: 302–311. doi: 10.1590/S0101-81752007000200006
- Mantoanelli E, Albuquerque GS, Tauber CA, Tauber MJ (2006) Leucochrysa (Leucochrysa) varia (Neuroptera: Chrysopidae): larval descriptions, developmental rates, and adult color variation. Annals of the Entomological Society of America 99: 7–18. doi: 10.1603/0013-8746(2006)099[0007:LLVNCL]2.0.CO;2
- Mantoanelli E, Tauber CA, Albuquerque GS, Tauber MJ (2011) Larvae of four *Leucochrysa* (*Nodita*) species (Neuroptera: Chrysopidae: Leucochrysini) from Brazil's Atlantic coast. Annals of the Entomological Society of America 104: 1233–1259. doi: 10.1603/AN11070
- McLachlan R (1868a) [1867] New genera and species, &c., of neuropterous insects; and a revision of Mr. F. Walker's British Museum Catalogue of Neuroptera, part ii. (1853), as far as the end of the genus *Myrmeleon*. Journal of the Linnean Society of London, Zoology 9: 230–281.
- McLachlan R (1868b) A monograph of the British Neuroptera-Planipennia. Transactions of the [Royal] Entomological Society of London 16: 145–224. doi: 10.1111/j.1365-2311.1868.tb00622.x
- Monserrat VJ (1985) Lista de los tipos de Mecoptera y Neuroptera (Insecta) de la colección L. Navás, depositados en el Museo de Zoología de Barcelona. Miscellània Zoològica 9: 233–243.
- Navás L (1911) Chrysopides nouveaux (Ins Neur). Annales de la Société Scientifique de Bruxelles 35: 266–282.

- Navás L (1912–1913) [1913] Les Chrysopides (Ins Névr) du Musée de Londres [Ia]. Annales de la Société Scientifique de Bruxelles 37: 292–330.
- Navás L (1913) Crisópidos sudamericanos. Brotéria (Zoológica) 11: 73-104, 149-168.
- Navás L (1917) Neue Neuropteren. Dritte [III] serie. Entomologische Mitteilungen 6: 274–282.
- Navás L (1922a) Insectos nuevos o poco conocidos [I]. Memorias de la Real Academia de Ciencias y Artes de Barcelona 17: 383–400.
- Navás L (1922b) Algunos insectos del Museo Entomológico de Berlín "Deutsches Entomologisches Museum". Brotéria (Zoológica) 20: 87–92.
- Navás L (1924) [1925] Comunicaciones entomológicas. 7. Neurópteros del Museo de Berlín. Revista de la [Real] Academia de Ciencias Exactas Físico-Químicas y Naturales de Zaragoza 9: 20–34.
- Navás L (1925) Insectos exóticos nuevos o poco conocidos. Segunda [II] serie. Memorias de la Real Academia de Ciencias y Artes de Barcelona 19: 181–200.
- Navás L (1926) Algunos insectos del Brasil (3.a serie) [IIIb]. Brotéria (Zoológica) 23: 5-15.
- Navás L (1928a) Insectos del Museo de Hamburgo. Primera [I] serie. Boletín de la Sociedad Entomológica de España 11: 59–67, 90–100, 121–138.
- Navás L (1928b) [1929]. Insectos neotropicos. 4.a serie. Revista Chilena de Historia Natural 32: 106–128.
- Navás L (1928c) Insectos del Museo de Estocolmo. Revista de la Real Academia de Ciencias Exactas Físicas y Naturales de Madrid 24: 28–39.
- Navás L (1929a) Insectos del Brasil. 3.a serie [IIIa]. Revista do Museu Paulista, São Paulo 16: 857–864.
- Navás L (1929b) Insecta nova. Series XIII. Memorie dell'Accademia Pontifica dei Nuovi Lincei, Rome 12: 15–23.
- Navás L (1932) Insectos suramericanos. Quinta [V] serie. Revista de la Real Academia de Ciencias Exactas Físicas y Naturales de Madrid 29: 53–66.
- Oswald JD (2006) Bibliography of the Neuropterida: a working bibliography of the literature on extant and fossil Neuroptera, Megaloptera and Raphidioptera (Insecta: Neuropterida) of the World. Version 7.06. http://lacewing.tamu.edu/Bibliography/index.html [Last access: 01/01/2013]
- Oswald JD (2007) Neuropterida Species of the World. Version 2.0. http://lacewing.tamu.edu/ species-catalogue/ [Last access: 01/01/2013]
- Penny ND (1977) [1978] Lista de Megaloptera, Neuroptera e Raphidioptera do México, América Central, ilhas Caraíbas e América do Sul. Acta Amazonica 7(4)(Suplemento): 1–61.
- Penny ND (1998) New Chrysopinae from Costa Rica (Neuroptera: Chrysopidae). Journal of Neuropterology 1: 55–78.
- Penny ND (2001) New species of Chrysopinae (Neuroptera: Chrysopidae) from Costa Rica, with selected taxonomic notes and a neotype designation. Entomological News 112: 1–14.
- Penny ND (2002) Family Chrysopidae. In: Penny ND (Ed.) A Guide to the Lacewings (Neuroptera) of Costa Rica. Proceedings of the California Academy of Sciences 53: 187–227.
- Schneider WG (1851) Die in Schlesien einheimischen Arten der Gattung *Chrysopa*. Zeitschrift für Entomologie, Breslau 5: 16.

- Tauber CA (2004) A systematic review of the genus *Leucochrysa* (Neuroptera: Chrysopidae) in the United States. Annals of the Entomological Society of America 97: 1129–1158. doi: 10.1603/0013-8746(2004)097[1129:ASROTG]2.0.CO;2
- Tauber CA (2010) Revision of *Neosuarius*, a subgenus of *Chrysopodes* (Neuroptera, Chrysopidae). ZooKeys 44: 1–104. doi: 10.3897/zookeys.44.387
- Tauber CA, Albuquerque GS, Tauber MJ (2008) A new species of *Leucochrysa* and a redescription of *Leucochrysa* (*Nodita*) *clepsydra* Banks (Neuroptera: Chrysopidae). Zootaxa 1781: 1–19. http://www.mapress.com/zootaxa/2008/f/z01781p019f.pdf
- Tauber CA, Albuquerque GS, Tauber MJ (2011a) Nomenclatorial changes and redescriptions of three of Navás' *Leucochrysa (Nodita)* species (Neuroptera, Chrysopidae). ZooKeys 92: 9–33. doi: 10.3897/zookeys.92.828
- Tauber CA, Mantoanelli E, Albuquerque GS, Reguilón C, González Olazo E, Tauber MJ (2011b) A taxonomically significant polymorphism in *Leucochrysa* (Neuroptera: Chrysopidae): nomenclature, larval and adult descriptions, and biological notes. Zootaxa 3130: 1–29. http://www.mapress.com/zootaxa/2011/f/zt03130p029.pdf
- Valencia Luna LA, Romero Nápoles J, Valdez Carrasco J, Carrillo Sánchez JL, López Martínez V (2006) Taxonomía y registros de Chrysopidae (Insecta: Neuroptera) en el Estado de Morelos, México [=Taxonomy and records of Chrysopidae (Insecta: Neuroptera) in the state of Morelos, Mexico]. Acta Zoológica Mexicana (NS) 22: 17–61.
- Walker F (1853) List of the specimens of neuropterous insects in the collection of the British Museum. Part II. (Sialides Nemopterides). British Museum, London, 193–476.