

Annotated Catalog of Vespid Hosts (Hymenoptera: Vespidae) of Tachinidae (Diptera), with Description of a New Species of *Ophirion* Townsend from Brazil

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Although tachinids parasitize a wide variety of insects, vespid wasps are not commonly recorded as hosts. Three lineages of Tachinidae are parasitoids of larvae of eusocial Vespidae, namely the Old World tribe Anacamptomyiini and some Neotropical species of the Blondeliini genera *Ophirion* Townsend and *Lixophaga* Townsend. The taxonomy of anacamptomyiine species has been improved and clarified in the last decades, but Neotropical species of *Ophirion* and *Lixophaga* are still difficult to identify, preventing further studies in the group. I present here an annotated catalog of vespid hosts of Tachinidae, with an overview of host use and oviposition strategies of their parasitoid species. Moreover, I describe a new host record for *O. lenkoi* sp. nov. Gudin and *L. punctata* (Townsend), reared from a nest of *Polybia* (*Myrapetra*) *scutellaris* (White) in Nova Europa, São Paulo, Brazil. *Ophirion lenkoi* sp. nov. is described and *L. punctata* is redescribed, with two new junior synonyms proposed: *L. fitzgeraldi* (Curran), syn. nov., and *L. dubiosa* (Thompson), syn. nov. I also include illustrations of type material and discuss the most relevant diagnostic characters for species of both genera. Lastly, I argue that the biology of *Lixophaga* species may be a suitable model to understand how tachinids were able to explore eusocial vespid hosts.

Key words: Parasitoid flies, Oviposition strategy, Meconium, Eusociality, New synonym.

BACKGROUND

Tachinid flies constitute the largest group of endoparasitoid Diptera, using several species of insects and other arthropods as hosts (Stireman et al. 2006). Tachinidae consists of four subfamilies: Dexiinae, Exoristinae, Phasiinae and Tachininae (O'Hara et al. 2020). Of the host records from Hymenoptera, most are in immature sawflies (Crosskey 1973 1976; Guimarães 1977; Arnaud 1978; Tschorsnig 2017), which have an ecological role similar to that of caterpillars (Eggleton and Belshaw 1992). In Apocrita, however, parasitism records by tachinids are scarce, occurring mostly on larvae of eusocial Vespidae, an unexpected association

due to the aggressiveness, complex nest architecture and parental care found in many species in the family (Prezoto et al. 2021).

Vespidae consists of nine subfamilies and includes solitary, subsocial and eusocial species (Piekarski et al. 2018). Eusociality evolved twice in the family: in Stenogastrinae, sister group of all remaining vespids, and in the clade nesting Vespinae and Polistinae. Nest architecture in eusocial Vespidae is very diverse, showing different types of materials, forms of attachment to the substrate, and arrangement and covering of combs (Wenzel 1998; Noll et al. 2021), which add more barriers to parasitoids (Jeane 2021).

In Tachinidae, only a few Exoristinae species

parasitize larvae of eusocial Vespidae, namely the Old World tribe Anacamptomyiini and some Neotropical species of the Blondeliini genera *Ophirion* Townsend and *Lixophaga* Townsend (Roubaud and Villeneuve 1914; Curran 1937). Knowledge about the oviposition strategy of these flies is restricted to a few observations in species of Afrotropical *Anacamptomyia* Bischof (Roubaud and Villeneuve 1914): females are ovoviviparous and lay their eggs on the external wall of the nest with well-developed first instar larvae. The larvae then enter the nest and search for wasp larvae nested in their comb cells. There are 21 valid species within six genera in Anacamptomyiini (O'Hara et al. 2020), whose taxonomy has been developed and clarified with identification keys to genera and species (Crosskey 1973 1976 1984; Zeegers 2014).

The taxonomy of Neotropical *Ophirion* and *Lixophaga*, however, is still complex and challenging, with no identification keys to species and no taxonomic revisions, precluding further studies in both groups. The most recent comparative work on both genera is that of Wood (1985), who proposed several synonyms and provided important diagnostic characters for each genus. *Ophirion* includes seven species restricted to the Neotropical Region (O'Hara et al. 2020) and *Lixophaga* includes 79 valid species distributed worldwide, except in the Afrotropical Region (Gudin et al. 2022). *Lixophaga* species usually attack borers of fruit or stems of the host plant, mainly caterpillars and beetle larvae (Guimarães 1977; Arnaud 1978). Only the Neotropical species *L. fitzgeraldi* (Curran) was reared from a vespid host, *Polybia* (*Myrapetra*) *occidentalis* (Olivier) in Trinidad and Tobago (Curran 1937). In *Ophirion*, there is only one host record: *O. polybia* (Curran) from *Polybia* (*Formicicola*) *rejecta* (Fabr.) in Trinidad and Tobago (Curran 1937).

When examining the Tachinidae collection of MZSP, I found unidentified specimens of *Ophirion* and *Lixophaga* reared from a nest of *P. (M.) scutellaris* (White) in 1964, in São Paulo, Brazil. In order to record this new host and to clarify the associations between tachinids and their vespid hosts, I provide here an annotated catalog of vespid hosts of Tachinidae and discuss the evolution of host transition and oviposition strategies of their respective parasitoids. Moreover, *Ophirion lenkoi* sp. nov. Gudin is described and *Lixophaga punctata* (Townsend) is redescribed with two new junior synonyms: *L. fitzgeraldi* (Curran), syn. nov., and *L. dubiosa* (Thompson), syn. nov. I also include illustrations of type material and discuss the most relevant diagnostic characters for species of both genera.

MATERIALS AND METHODS

Ophirion and *Lixophaga* specimens deposited at MZSP were identified using the key to New World genera of Blondeliini (Wood 1985). I verified the original descriptions of the seven species of *Ophirion* and all 15 Nearctic and 53 Neotropical valid species of *Lixophaga*. I also examined the following type material: *Polybiophila fitzgeraldi* Curran and *Telothyriosoma polybia* Curran, deposited at AMNH; *Santacruzia dubiosa* Thompson, deposited at CNC; and *Ophirionopsis brasiliensis* Townsend, *Oxyophirion punctigerum* Townsend and *Paranetia punctata* Townsend, deposited at USNM. Nigel Wyatt provided additional descriptions of the holotypes of *L. trichosoma* (van der Wulp) and *L. umbripennis* (van der Wulp) deposited at NHMUK. Label data are quoted within double quotation marks, with different lines separated by a forward slash.

For the study of terminalia, the abdomens of pinned specimens were detached, placed in a 10% KOH solution, and heated to 60°C for 10 minutes to soften the membranes and clear the tissues. The terminalia were then dissected and heated for 10 more minutes to lighten the structures. After being neutralized in a 5% acetic acid solution and rinsed with water, the abdomens were dried and glued back to the specimens, and the terminalia were placed in glycerin in plastic microvials, pinned with their respective specimens. Photographs were taken with a Leica MC170 HD digital camera attached to a Leica MZ16 stereomicroscope, using the software Leica Application Suite 4.12.0, stacked with the software Helicon Focus 6.7.1 and edited in Gimp 2.10. Illustrations of terminalia were made using a Leica MZ16 stereomicroscope with camera lucida and edited in Inkscape 1.1. Morphological terminology follows Cumming and Wood (2017).

The annotated host catalog follows an adapted format presented by Guimarães (1977) and Arnaud (1978). Species of vespid hosts are listed alphabetically according to biogeographical regions, followed by records with author, year of publication, page number, locality, respective tachinid parasitoid and notes about the record. When necessary, I included in square brackets comments and amendments regarding taxonomic nomenclature. Only published records were considered, not including dissertations and theses. References merely citing previous records were also not included in the catalog. All references were checked to ensure the accuracy of dates, titles, pagination, names, and localities. The classification of Tachinidae follows O'Hara et al. (2020) and the classification of Vespidae follows Vecht and Carpenter (1990), Carpenter (1996), Kojima and Carpenter (1997) and Nguyen et al. (2014).

RESULTS

Record of *Ophirion lenkoi* sp. nov. and *Lixophaga punctata* in *Polybia (Myrapetra) scutellaris*

On 23 December 1964, one male of *O. lenkoi* sp. nov. and thirteen specimens of *L. punctata* were reared from a nest of *P. (M.) scutellaris* in Itaquerê Farm, Nova Europa, São Paulo, Brazil (Figs. 1, 4). There is no further information on the parasitism record other than that on the label, but some hypotheses regarding the oviposition strategy of both species are discussed below. This is the first record of two species of different genera of Tachinidae in the same nest of Vespidae.

Annotated catalog of vespid hosts of Tachinidae

At least 15 species of Tachinidae in six genera, four in Anacamptomyiini and two in Blondeliini, are currently recorded as parasitoids of at least 47 eusocial species of Vespidae in the subfamilies Polistinae, Stenogastrinae and Vespinae (Table 1). Records were found in all biogeographical regions, except the Nearctic Region. Only one tachinid larva was reared per host, found at the bottom of the comb cell.

Tachinids were also recorded in Eumeninae, but these records must be treated carefully. Most eumenine wasps are mass provisioners, *i.e.*, adults provide their nests with high amounts of prey, usually immature of Lepidoptera and Coleoptera (Carpenter and Cumming 1985). The parasitism, therefore, may not have occurred in the wasp larva, but in a preyed specimen that was already parasitized when captured. For instance, tachinids were recorded in preys of *Abispa* Mitchell in Australia (Matthews and Matthews 2004), *Katamenes* Meade-Waldo in Ukraine (Fateryga and Ivanov 2009), *Odynerus* Latreille in Russia (Fateryga 2013), *Rhynchium* Spinola in India, Thailand and Vietnam (Iwata 1964; Dang and Nguyen 2019; Udayakumar et al. 2022), and *Symmorphus* Wesmael in Japan (Hamanishi 1996). The following records of parasitism in Eumeninae by tachinids are therefore probably unreliable: *Alastor* Lepelletier in Ukraine (Fateryga and Podunay 2018), *Brachymenes* Giordani Soika in Brazil (Camillo 1999), *Delta* Saussure in Malaysia (Crosskey 1976, as *Eumenes campaniformis* (Fabr.)), and *Monobia* Saussure in Brazil (Camillo et al. 1997; Oliveira and Gonçalves 2017).

Records of parasitism by unidentified dipterous flies were also not included in the catalog, as the larvae of some species of Phoridae and Sarcophagidae are parasitoids or kleptoparasites in nests of Vespidae (Nelson 1968; Makino 1985; Lutz and Brown 2013). The following records are therefore pending review:

Agelaia lobipleura melanogaster (Richards) in Peru (Richards 1978a), *A. yepocapa* (Richards) in Costa Rica (Hunt et al. 2001), *Belonogaster discifera* Hensen and Blommers in Africa (Wenzel 1991), *Liostenogaster tutua* Turillazzi in Malaysia (Turillazzi 1999), *Mischocyttarus (Haplometrobium) surinamensis occidentalis* Richards and *Polistes (Epicnemius) pacificus* Fabr. in Trinidad and Tobago (Vesey-FitzGerald 1938), *Polybia (Myrapetra) erythrothorax* Richards and *P. (M.) platycephala sylvestris* Richards in Brazil (Richards 1978a), *P. (M.) ruficeps ruficeps* Schrottky, locality not given (Richards 1978a), *Ropalidia kurandae* Richards and *R. turneri* Richards in Australia (Richards 1978b), and *R. tomentosa* (Gerstaecker) in Tanzania (Vesey-FitzGerald 1940).

The classifications of Vespidae and Tachinidae used in the Australasian, Neotropical and Oriental catalogs are out of date, whereas the records presented in the Palaearctic catalog were recently reviewed: Tschorsnig (2017) lists five species of *Polistes* Latreille and two species of *Vespa* L. for the anacamptomyiine *Euvespivora decipiens* (Walker) in Japan (Table 1). The reader is referred to Tschorsnig (2017) to check further details regarding localities, references and notes about these records. An updated and annotated host catalog of Afrotropical, Australasian, Neotropical and Oriental vespid hosts of Tachinidae is provided below.

Afrotropical Region

POLISTINAE

Belonogaster dubia Kohl

Roubaud and Villeneuve (1914: 128, record from Republic of the Congo [as Congo], as *B. dubius*, parasitoid as *Anacamptomyia rufescens* (Villeneuve)); Cuthbertson (1939: 146, record from Harare [as Salisbury], Zimbabwe [as Southern Rhodesia], as *Belanogaster* [misspelling] *dubius*, parasitoid as *Anacamptomyia bisetosa* (Roubaud and Villeneuve)).

Belonogaster grisea (Fabr.)

Cuthbertson and Munro (1941: 91, locality not given, as *Belanogaster* [misspelling] *griseus*, parasitoid as *Anacamptomyia africana* Bischof); Roubaud and Villeneuve (1914: 128, record from Republic of the Congo [as Congo], as *B. griseus*, parasitoids as *Anacamptomyia pallida* (Roubaud and Villeneuve) and *A. rufescens* (Villeneuve)).

Belonogaster juncea (Fabr.)

Roubaud and Villeneuve (1914: 125, record from Western Africa [origin not specified], as *B. junceus*, parasitoid as *Anacamptomyia bisetosa* (Roubaud and Villeneuve)); Richards (1969: 91, record from Legon, Accra, Ghana, as *B. junceus*, parasitoid as *Anacamptomyia bisetosa* (Roubaud

and Villeneuve)); Keeping and Crewe (1983: 311, record from Makapansgat, Limpopo [as Northern Transvaal], South Africa, parasitoid as unidentified *Anacamptomyia* Bischof).

Belonogaster juncea colonialis Kohl Keeping (1997: 363, record from KwaZulu-Natal, South Africa, parasitoid as unidentified Tachinidae, probably *Anacamptomyia* Bischof).

A

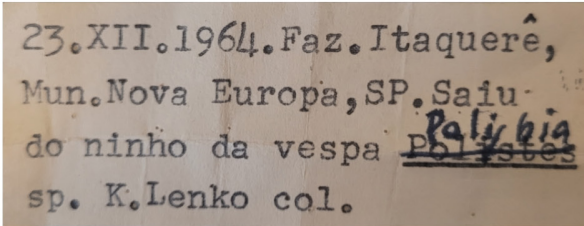


Fig. 1. Record of *Ophirion lenkoi* sp. nov. in *Polybia* (*Myrapetra*) *scutellaris* (White). A, Label; B, D, F: Head in frontal view, lateral habitus and dorsal habitus of holotype male of *O. lenkoi* sp. nov. (MZSP), respectively; C, E: Lateral habitus and dorsal habitus of worker female of *P. (M.) scutellaris*, respectively. Scale bars = 2 mm.

Belonogaster petiolata (DeGeer)

Keeping and Crewe (1983: 311, record from Witwatersrand, South Africa, parasitoid as unidentified *Anacamptomyia* Bischof).

Belonogaster sp.

Roubaud and Villeneuve (1914: 125, record from Western Africa [origin not specified], parasitoid as *Anacamptomyia bisetosa* (Roubaud and Villeneuve)).

Polistes africanus Palisot de Beauvois

Roubaud and Villeneuve (1914: 124, record from Satadougou [as Haute-Gambie], Senegal, as *P. marginalis africanus*, parasitoid as *Anacamptomyia pallida* (Roubaud and Villeneuve)); Vesey-FitzGerald (1940: 33, record from Dar es Salaam, Dar es Salaam, Tanzania, as *P. marginalis africanus*, parasitoid as *Anacamptomyia africana* Bischof); Richards (1969: 81, record from Legon, Accra, Ghana, as *Polistes spilophorus* Schletterer, parasitoid as unidentified Tachinidae, probably

Anacamptomyia Bischof).

Polistes dominulus (Christ)

Benadé et al. (2014: 222, record from Stellenbosch, Western Cape, South Africa, as *P. dominula*, parasitoid as unidentified *Anacamptomyia* Bischof); Roets et al. (2019: 927, same locality, as *P. dominula*, parasitoid as unidentified *Anacamptomyia* Bischof).

Polistes marginalis (Fabr.)

Roubaud and Villeneuve (1914: 123, record from Austral Africa and Casamance [as Haute-Gambie], Senegal, parasitoid as *Anacamptomyia africana* Bischof; 128, record from Republic of the Congo [as Congo], parasitoid as *Anacamptomyia rufescens* (Villeneuve)); Cuthbertson and Munro (1941: 91, record from Pretoria, Transvaal, South Africa, parasitoid as *Anacamptomyia pallida* (Roubaud and Villeneuve)); Benadé et al. (2014: 222, record from Stellenbosch, Western Cape, South Africa, parasitoid as unidentified *Anacamptomyia*

Table 1. List of vespid hosts and their respective tachinid parasitoids according to biogeographical regions. Details about records, localities and respective references can be found in Tschorsnig (2017) and in the host catalog in the main text

Vespid hosts	Species of Tachinidae
Afrotropical Region	
POLISTINAE	
<i>Belonogaster dubia</i>	<i>Anacamptomyia bisetosa</i>
<i>Belonogaster grisea</i>	<i>Anacamptomyia rufescens</i> <i>Anacamptomyia africana</i> <i>Anacamptomyia pallida</i> <i>Anacamptomyia rufescens</i>
<i>Belonogaster juncea</i>	<i>Anacamptomyia bisetosa</i> <i>Anacamptomyia</i> sp.
<i>Belonogaster juncea colonialis</i>	Unidentified species
<i>Belonogaster petiolata</i>	<i>Anacamptomyia</i> sp.
<i>Belonogaster</i> sp.	<i>Anacamptomyia bisetosa</i>
<i>Polistes africanus</i>	<i>Anacamptomyia africana</i> <i>Anacamptomyia pallida</i> Unidentified species
<i>Polistes dominulus</i>	<i>Anacamptomyia</i> sp.
<i>Polistes marginalis</i>	<i>Anacamptomyia africana</i> <i>Anacamptomyia pallida</i> <i>Anacamptomyia</i> sp.
<i>Polistes rubidus</i> [unrecognized species]	<i>Anacamptomyia africana</i>
<i>Polistes</i> sp.	<i>Anacamptomyia africana</i>
<i>Polybia</i> sp.	<i>Anacamptomyia africana</i> <i>Anacamptomyia pallida</i>
<i>Ropalidia carinata</i>	<i>Parapales</i> aff. <i>micronychia</i>
<i>Ropalidia cincta</i>	<i>Anacamptomyia pallida</i>
<i>Ropalidia cocoscicola</i>	Unidentified species
<i>Ropalidia flavoviridis</i>	<i>Parapales pallidula</i>
<i>Ropalidia formosa</i>	<i>Anacamptomyia</i> sp.
<i>Ropalidia galimatia</i>	<i>Anacamptomyia blommersi</i>

Table 1. (Continued)

Vespid hosts	Species of Tachinidae
<i>Ropalidia grandidieri</i>	<i>Anacamptomyia aurifrons</i>
<i>Ropalidia guttatipennis</i>	<i>Anacamptomyia pallida</i>
<i>Ropalidia merina</i>	<i>Anacamptomyia blommersi</i>
<i>Ropalidia rosae</i>	Unidentified species
<i>Ropalidia shestakowi</i>	<i>Anacamptomyia blommersi</i>
<i>Ropalidia variabilis</i>	<i>Anacamptomyia aurifrons</i>
Australasian Region	
STENOGASTRINAE	
<i>Anischnogaster iridipennis</i>	<i>Euvespivora decipiens</i>
<i>Anischnogaster laticeps</i>	Unidentified species
<i>Anischnogaster</i> sp.	Unidentified species
<i>Stenogaster concinna</i>	Unidentified species
POLISTINAE	
<i>Polistes humilis humilis</i>	<i>Anacamptomyia nigriventris</i>
<i>Polistes stigma maculipennis</i>	<i>Euvespivora decipiens</i>
<i>Polistes</i> sp.	<i>Anacamptomyia nigriventris</i>
	<i>Euvespivora decipiens</i>
	<i>Koralliomysia</i> sp.
<i>Ropalidia marginata jucunda</i>	<i>Koralliomysia</i> sp.
<i>Ropalidia socialistica</i>	<i>Anacamptomyia</i> sp.
<i>Ropalidia</i> sp.	<i>Euvespivora</i> sp.
Unidentified species [probably <i>Polistes</i>]	<i>Anacamptomyia nigriventris</i>
Neotropical Region	
POLISTINAE	
<i>Mischocyttarus (Haplometrobis) iheringi</i>	Unidentified species
<i>Mischocyttarus (Monocyttarus) declaratus</i>	Unidentified species
<i>Mischocyttarus (Monocyttarus) flavicornis nigricornis</i>	<i>Lixophaga</i> sp.
<i>Polistes myersi</i>	Unidentified species
<i>Polybia (Formicicola) rejecta</i>	<i>Ophirion polybia</i>
<i>Polybia (Myrapetra) juruana</i>	<i>Ophirion</i> sp.
<i>Polybia (Myrapetra) occidentalis</i>	<i>Lixophaga punctata</i>
<i>Polybia (Myrapetra) scutellaris</i>	<i>Lixophaga punctata</i>
	<i>Ophirion lenkoi</i>
<i>Polybia</i> sp.	Unidentified species
Oriental Region	
STENOGASTRINAE	
<i>Parischnogaster mellyi</i>	Unidentified species
POLISTINAE	
<i>Ropalidia marginata</i>	<i>Koralliomysia portentosa</i>
	<i>Koralliomysia</i> sp.
<i>Ropalidia</i> sp.	<i>Euvespivora decipiens</i>
VESPINAE	
<i>Vespa analis</i>	<i>Euvespivora orientalis</i>
<i>Vespa ducalis</i>	Unidentified species
<i>Vespa velutina</i>	Unidentified species
Palearctic Region	
POLISTINAE	
<i>Polistes chinensis</i>	<i>Euvespivora decipiens</i>
<i>Polistes jadvigae</i>	<i>Euvespivora decipiens</i>
<i>Polistes nipponensis</i>	<i>Euvespivora decipiens</i>
<i>Polistes rothney</i>	<i>Euvespivora decipiens</i>
<i>Polistes snelleni</i>	<i>Euvespivora decipiens</i>
VESPINAE	
<i>Vespa mandarinia</i>	<i>Euvespivora decipiens</i>
<i>Vespa simillima</i>	<i>Euvespivora decipiens</i>

- Bischof); Roets et al. (2019: 927, same locality as Benadé et al. (2014), parasitoid as unidentified *Anacamptomyia* Bischof).
- Polistes rubidus* Lepeletier [unrecognized species]
Cuthbertson and Munro (1941: 91, locality not specified, parasitoid as *Anacamptomyia africana* Bischof).
- Polistes* sp.
Bischof (1904: 81, record from Algoa Bay, Eastern Cape, South Africa, parasitoid as *Anacamptomyia africana* Bischof).
- Polybia* spp.
Roubaud and Villeneuve (1914: 124, record from Republic of the Congo [as Congo belge], Nigeria and Zimbabwe [as Rhodesia], parasitoid as *Anacamptomyia pallida* (Roubaud and Villeneuve)); Cuthbertson (1935: 20, record from Bulawayo [as Southern Rhodesia], Zimbabwe, parasitoid as *Anacamptomyia africana* Bischof); Cuthbertson and Munro (1941: 91, record from Bulawayo [as Southern Rhodesia], Zimbabwe, parasitoid as *Anacamptomyia pallida* (Roubaud and Villeneuve)).
- Ropalidia carinata* (de Saussure)
Blommers (2012: 170, record from Mananjary, Vatovavy, Madagascar, parasitoid as unidentified Tachinidae); Zeegers (2014: 102, same locality, parasitoid in Blommers (2012) as *Parapales* aff. *micronychia* Mesnil).
- Ropalidia cincta* (Lepelletier)
Roubaud and Villeneuve (1914: 124, record from Senegal [as Haute-Gambie], as *Icaria* de Saussure, parasitoid as *Anacamptomyia pallida* (Roubaud and Villeneuve)).
- Ropalidia cocoscola* Blommers
Blommers (2012: 146, record from Toliara, Atsimo-Andrefana, Madagascar, parasitoid as unidentified Tachinidae).
- Ropalidia flavoviridis* Kojima
Blommers (2012: 176, record from Akarafantsika Forest Station, Ampijoroa, Tsaramandroso, Boeny, Madagascar, parasitoid as unidentified Tachinidae); Zeegers (2014: 101, same locality, parasitoid in Blommers (2012) as *Parapales pallidula* (Mesnil)).
- Ropalidia formosa* (de Saussure)
Brooks and Wahl (1987: 548, record from Parc Tsimbazaza, Antananarivo [as Tananarive], Analamanga, Madagascar, parasitoid as unidentified *Anacamptomyia* Bischof).
- Ropalidia galimatia* (de Saussure)
Blommers (2012: 187, record from Toliara, Atsimo-Andrefana, Madagascar, parasitoid as unidentified *Anacamptomyia* Bischof); Zeegers (2014: 99, same locality, parasitoid in Blommers (2012) as *Anacamptomyia blommersi* Zeegers).
- Ropalidia grandidieri* (de Saussure)
Blommers (2012: 143, record from Parc Tsimbazaza, Antananarivo [as Tananarive], Analamanga, Madagascar, parasitoid as unidentified *Anacamptomyia* Bischof); Zeegers (2014: 97, same locality, parasitoid in Blommers (2012) as *Anacamptomyia aurifrons* Zeegers).
- Ropalidia guttatipennis* (de Saussure)
Roubaud and Villeneuve (1914: 124, record from Senegal [as Haute-Gambie], as *Icaria* de Saussure, parasitoid as *Anacamptomyia pallida* (Roubaud and Villeneuve)).
- Ropalidia merina* Blommers
Blommers (2012: 156, record from Parc Tsimbazaza, Antananarivo [as Tananarive], Analamanga, Madagascar, parasitoid as unidentified *Anacamptomyia* Bischof); Zeegers (2014: 99, same locality, parasitoid in Blommers (2012) as *Anacamptomyia blommersi* Zeegers).
- Ropalidia rosae* Blommers
Blommers (2012: 170, record from Ampijoroa, Tsaramandroso, Boeny, Madagascar, parasitoid as unidentified Tachinidae).
- Ropalidia shestakowi* (von Schulthess)
Blommers (2012: 141, record from Parc Tsimbazaza, Antananarivo [as Tananarive], Analamanga, Madagascar and Angorombalo, Nosy Be, Diana, Madagascar, parasitoid as unidentified *Anacamptomyia* Bischof); Zeegers (2014: 99–100, same localities, parasitoids in Blommers (2012) as *Anacamptomyia blommersi* Zeegers).
- Ropalidia variabilis* (de Saussure)
Blommers (2012: 150, record from Manjakatropo, Ankaratra Mountains, Ambatolampy, Vakinankaratra, Madagascar, parasitoid as unidentified *Anacamptomyia* Bischof); Zeegers (2014: 97, same locality, parasitoid in Blommers (2012) as *Anacamptomyia aurifrons* Zeegers).

Australasian Region

STENOGASTRINAE

- Anischnogaster iridipennis* (Smith)
Spradbery (1989: 227, record from Central Province [as Central District], Papua New Guinea [several localities, origin not specified], parasitoid as *Euvespivora decipiens* (Walker)).
- Anischnogaster laticeps* Van der Vecht
Turillazzi and Hansell (1991: 429, record from Madang, Madang, Papua New Guinea, parasitoid as unidentified Tachinidae); Hansell and Turillazzi (1995: 212, same locality, parasitoid as unidentified Tachinidae).
- Anischnogaster* spp.
Turillazzi and Hansell (1991: 429, record from

Madang, Madang, Papua New Guinea, parasitoid as unidentified Tachinidae); Hansell and Turillazzi (1995: 213, same locality, parasitoid as unidentified Tachinidae).

Stenogaster concinna van der Vecht

Spradbery (1975: 313, record from Baruanumu Hill, Central Province [as Central District], Papua New Guinea, parasitoid as unidentified Tachinidae).

POLISTINAE

Polistes humilis humilis (Fabr.)

Crosskey (1973: 173, locality not specified, as *Polistes tasmaniensis* de Saussure, parasitoid as *Anacamptomyia nigriventris* (Malloch)); Chadwick and Nikitin (1985: 588, record from Ryde, New South Wales, Australia, as *Polistes tasmaniensis* de Saussure, parasitoid as *Anacamptomyia nigriventris* (Malloch)).

Polistes stigma maculipennis de Saussure

Richards (1978b: 33, record from Wau, Morobe, Papua New Guinea, as *P. bernardii comis* Cheesman, parasitoid as *Euvespivora decipiens* (Walker)).

Polistes spp.

Crosskey (1973: 173, locality not specified, parasitoids as *Anacamptomyia nigriventris* (Malloch), *Euvespivora decipiens* (Walker), and unidentified *Koralliomyia* Mesnil); Chadwick and Nikitin (1985: 588, record from Canyon Camp, Warrumbungle National Park, Australia, parasitoid as *Anacamptomyia nigriventris* (Malloch)).

Ropalidia marginata jucunda (Cameron)

Crosskey (1973: 173, locality not specified, parasitoid as unidentified *Koralliomyia* Mesnil).

Ropalidia socialistica (de Saussure)

Hook and Evans (1982: 271, record from Tamborine Village, Queensland, Australia, parasitoid as unidentified *Anacamptomyia* Bischof).

Ropalidia sp.

Cantrell (1986: 256, record from Australia [origin not specified], parasitoid as unidentified *Euvespivora* Baranov).

Unidentified species [probably *Polistes* Latreille, see Crosskey (1973): 173]

Malloch (1930: 347, record from Eidsvold, Queensland, Australia, parasitoid as *Vespivora nigriventris* Malloch [= *Anacamptomyia nigriventris* (Malloch)]).

Neotropical Region

POLISTINAE

Mischocyttarus (Haplometrobis) iheringi Zikán

Zikán (1935: 180, record from Itatiaia, Rio de Janeiro, Brazil, as *M. iheringi*, parasitoid as

unidentified Tachinidae).

Mischocyttarus (Monocyttarus) declaratus Zikán

Zikán (1935: 164, record from Itatiaia, Rio de Janeiro, Brazil, as *M. declaratus*, parasitoid as unidentified Tachinidae).

Mischocyttarus (Monocyttarus) flavicornis nigricornis Zikán

Richards (1978a: 342, record from Tingo María, Huánuco, Peru, parasitoid as unidentified *Polybiaphila* [misspelling, *Polybiophila* Curran, senior synonym of *Lixophaga* Townsend]).

Polistes myersi Bequaert

Mayorga-Ch. and Sarmiento (2020: 474, record from Fusagasugá, Condinamarca, Colombia, parasitoid as unidentified Blondeliini).

Polybia (Formicicola) rejecta (Fabr.)

Curran (1937: 2, record from Maine Club, Trinidad and Tobago, as *P. rejecta*, parasitoid as *Telothyriosoma polybia* Curran, 1937 [= *Ophirion polybia* (Curran)]).

Polybia (Myrapetra) juruana (Ihering)

Richards (1978a: 80, record from Lake Yarinacocha, Pucallpa, Ucayali, Peru, parasitoid as unidentified *Ophirion* Townsend).

Polybia (Myrapetra) occidentalis (Olivier)

Curran (1937: 3, record from Mt. Saint Benedict, Trinidad and Tobago, as *P. occidentalis*, parasitoid as *Polybiophila fitzgeraldi* Curran [junior synonym of *Lixophaga punctata* (Townsend)]).

Polybia (Myrapetra) scutellaris (White)

Gudin, present record from Nova Europa, São Paulo, Brazil, parasitoids as *Lixophaga punctata* (Townsend) and *Ophirion lenkoi* sp. nov. Gudin.

Polybia sp.

Lima et al. (2000: 74, record from Juiz de Fora, Minas Gerais, Brazil, parasitoid as unidentified Tachinidae).

Oriental Region

STENOGASTRINAE

Parischnogaster mellyi (de Saussure)

Turillazzi (1991: 95, locality not given, parasitoid as unidentified Tachinidae).

POLISTINAE

Ropalidia marginata (Lepelletier)

Crosskey (1976: 296, record from India, parasitoid as unidentified *Koralliomyia* Mesnil, probably *K. portentosa* Mesnil); Belavadi and Govindan (1981: 100, record from Bangalore, Karnataka, India, as *R. (Icariola) marginata*, parasitoid as *Koralliomyia portentosa* Mesnil).

Ropalidia sp.

Crosskey (1976: 296, record from Malaysia [as

Malaya], parasitoid as *Euvespivora decipiens* (Walker)).

VESPINAE

Vespa analis Fabr.

Baranov (1942: 162, record from Jawa, Indonesia, parasitoid as *Euvespivora orientalis* Baranov).

Vespa ducalis Smith

Dazhi and Yunzhen (1989: 160, record from Guangnan County, as *V. tropica ducalis*, Yunnan, China, parasitoid as unidentified Tachinidae).

Vespa velutina Lepeletier

Dazhi and Yunzhen (1989: 160, record from Guangnan County, as *V. v. auraria*, Yunnan, China, parasitoid as unidentified Tachinidae).

TAXONOMY

Family Tachinidae Robineau-Desvoidy, 1830 Subfamily Exoristinae Robineau-Desvoidy, 1830 Tribe Blondeliini Robineau-Desvoidy, 1863

As *Ophirion* and *Lixophaga* include parasitoids of Neotropical Vespidae, the following characters can be used to identify males and females of both genera:

1. Eyes bare or with short hairs (Fig. 2E); ocellar setae absent; frontal setae above pedicel reclinate and continuous to reclinate orbital setae (Fig. 1B); 2 katepisternal setae; wing with strong costal spine (Fig. 2C); abdomen without discal setae on intermediate abdominal tergites *Ophirion*
- Eyes bare; ocellar setae present; frontal setae inclinate (Fig. 4E); 2–3 katepisternal setae; wing with weak costal spine (Fig. 4C); abdomen with or without discal setae on intermediate abdominal tergites *Lixophaga*

Genus *Ophirion* Townsend, 1911

Ophirion comprises eight valid species, including *O. lenkoi* sp. nov.; five genera were synonymized with *Ophirion* by Wood (1985). The complete list of species and synonyms can be checked in O'Hara et al. (2020).

Ophirion lenkoi sp. nov. Gudin

(Fig. 1B, D, F)

urn:lsid:zoobank.org:act:5F859590-3E87-4066-AC66-6FFBABE3197D

Material examined: Holotype ♂: “Brasil, SP, Nova Europa/ Faz. Itaquerê, 23.xii.1964/ Lenko col., emergido de ninho/ de vespa *Polybia scutellaris*”/ “Holótipo” (MZSP). Holotype in good condition and not dissected.

Diagnosis: *Ophirion lenkoi* can be distinguished from other *Ophirion* species by having: pale golden pruinosity on head and dorsal surface of thorax and

abdomen; abdomen yellowish at base and with brown dorsal vitta from base to apex, faint in syntergite 1+2, narrow in tergite 3 and covering the dorsal surface of tergites 4 and 5; antennal axis about two-thirds head height; eyes with sparse minute inconspicuous hairs; one very short anepimeral seta; and wings hyaline. A comprehensive comparison of the main diagnostic characters of *Ophirion* species is covered in the Remarks section below.

Description: Body length: 6.30 mm. Wing length: 5.96 mm.

Coloration: Head with pale golden pruinosity, except face, gena and postgena, with silver pruinosity. Frontal vitta and lunule dark brown. Pedicel and arista yellow, with first flagellomere brown. Clypeus, palpi and labella yellow. Occiput dark brown, covered with silver pruinosity. Thorax with pale golden pruinosity, except lower region of pleural sclerites, with faint silvery pruinosity. Scutum with four weak, brown vittae; outer vittae interrupted by transverse suture and not reaching last postsutural dorsocentral seta, and inner vittae continuous and extending to first postsutural acrostichal seta. Lateral surface of thorax and spiracles yellow. Scutellum and subscutellum yellow, entirely covered with pale golden pruinosity. Wing hyaline. Tegula, basicosta and veins yellow. Halter light yellow. Calypteres yellowish, with yellow border. Legs yellow, with silver pruinosity. Tarsal claws brown. Pulvilli light brown. Abdomen with faint silvery pruinosity. Syntergite 1+2, tergite 3 and lateral surface of tergite 4 yellow. Tergites with brown vitta from base to apex, faint in syntergite 1+2, narrow in tergite 3 and covering the dorsal surface of tergites 4 and 5.

Head (Fig. 1B): Ratio of head height/ head width in frontal view 0.86. Ratio of frontal vitta width/ fronto-orbital plate width in dorsal view 0.92. Ratio of vertex width/ head width in dorsal view 0.26. Ratio of first flagellomere length/ pedicel length 2.83. Ratio genal height/ head height in lateral view 0.17. Dichoptic. Eye with sparse minute inconspicuous hairs. Antennal axis about two-thirds head height. Antenna inserted at middle level of eye, almost reaching lower facial margin. Scape short, about one-quarter length of pedicel. Pedicel setose dorsally. First flagellomere subrectangular, with outer surface bearing one minute sensory pit closer to posterior margin. Arista long, pubescent and thickened at base, arising in basal dorsal surface of first flagellomere. Three inclinate and four reclinate frontal setae from level of pedicel to level of upper quarter of eye, with upper setae longer and stronger than lower ones. Proclinate orbital setae absent. Two reclinate orbital setae, continuous with frontal setae, with posterior setae about three-quarters length of anterior seta. Ocellar triangle setulose, without ocellar

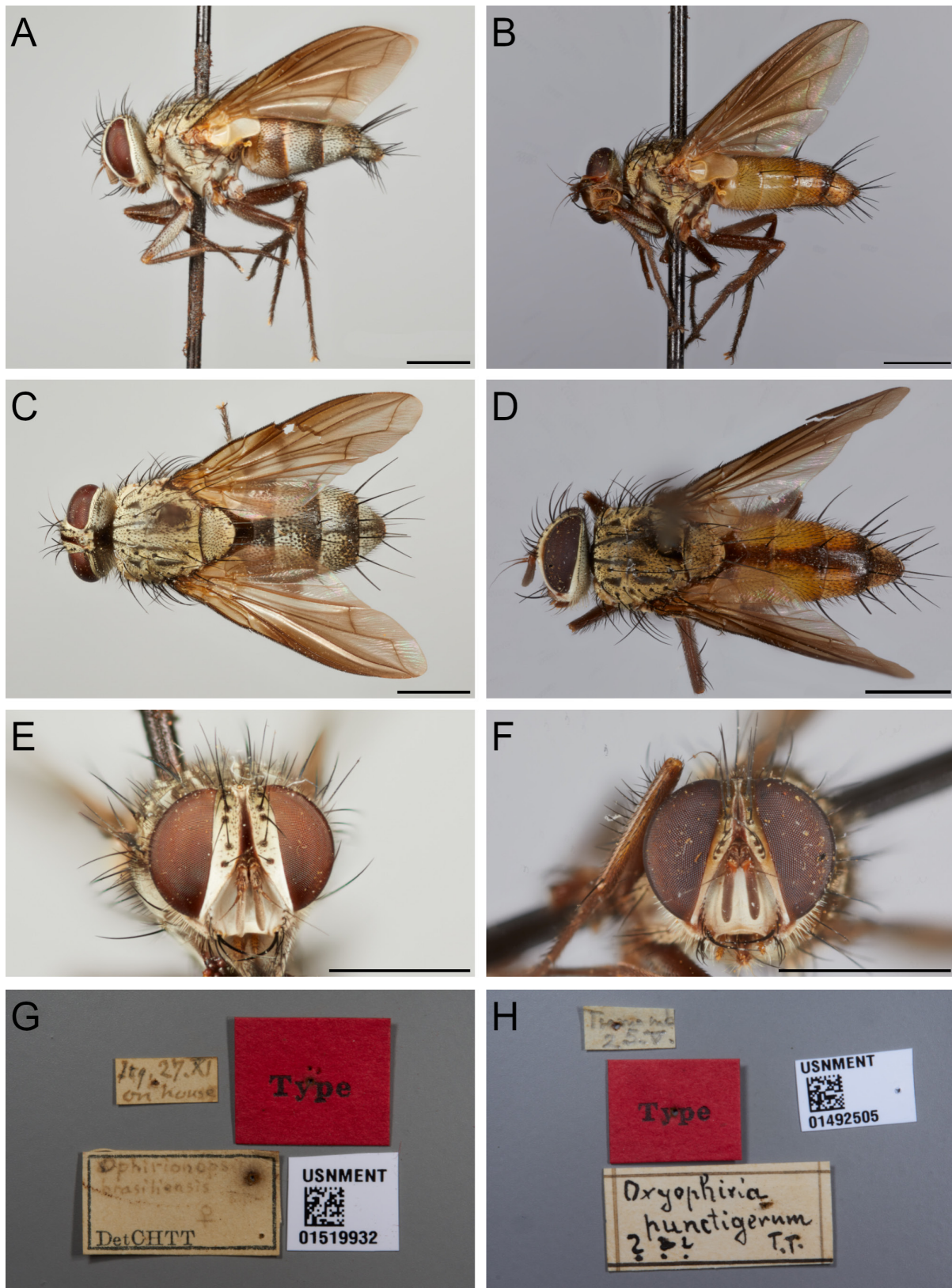


Fig. 2. Type material of *Ophirion* Townsend. A, C, E, G: Lateral habitus, dorsal habitus, head in frontal view and labels of holotype female of *Ophirionopsis brasiliensis* Townsend (USNM), respectively; B, D, F, H: Lateral habitus, dorsal habitus, head in frontal view and labels of holotype male of *Oxyophiria punctigerum* Townsend (USNM), respectively. Scale bars = 2 mm.

setae; all ocelli with similar size. Two short postocellar setae. Inner vertical setae reclinate, subparallel. Outer vertical setae weak, about one-fifth length of inner vertical. Fronto-orbital plate with fine setulae. Parafacial bare, about two-thirds width of fronto-orbital plate. Facial ridge bare, except on lowest quarter, with three or four weak supravibrissal setae. Vibrissa strong and crossed, arising at level of lower facial margin, with two or three subvibrissal setae. Face flat and not visible in lateral view, with facial carina. Gena with four setae on ventral margin. Genal dilation and postgena setulose, with patches of long, white setulae. Clypeus U-shaped. Palpi clavate and setose. Prementum short, setulose. Labella padlike.

Thorax (Fig. 1D, F): Prosternum setose. Proepisternum bare. Two proepimeral setae, strong, upcurved, with setulae at base. Anterior spiracle with both lappets well-developed, covering almost entire opening. Posterior spiracle with posterior lappet shaped as an operculum. Three postpronotal setae, arranged as an arc. Scutum with 3+? [postsutural area damaged by pin] acrostichal setae; 2+2 dorsocentral setae; 2+3 intralar setae; 1+2 supra-alar setae, with first postsutural seta absent, and second postsutural seta strong and subequal to median postalar seta. One well-developed intrapostalar seta. Two notopleural setae. Three postalar setae, with median seta stronger than other two. Two katapisternal setae. Anepisternum anterodorsal corner with one seta, about half length of notopleural setae; posterior margin with row of six setae. One short anepimeral seta, with patch of setulae at base. Six meral setae. Anatergite bare. Scutellum with one pair of basal setae, convergent and long, about two-thirds length of subapical setae; one pair of lateral setae, subparallel and about two-thirds length of basal setae; one pair of subapical setae, divergent; apical setae absent; one pair of discal setae arising at level of subapical setae. Wing: Vein C ending right after R_{4+5} , just before wing apex, with strong costal spine. Vein R_{4+5} setose only at base. Bend of M obtuse, with distal part straight to wing margin. Cell r_{4+5} almost closed, reaching wing margin close to vein R_{4+5} . Legs: Fore coxa with two longitudinal rows of setae on anterior surface. Fore femur with dorsal, posterodorsal and posteroventral rows of setae from base to apex. Fore tibia with one strong apical seta on dorsal surface, one strong median seta and one apical seta on posterior surface. Mid coxa with row of setae on anterior surface. Mid femur with one median seta on anterior surface and one basal seta on posteroventral surface. Mid tibia with one strong median seta and one apical seta on anterodorsal surface, one apical seta on anteroventral surface, two median setae on posterior surface, one median seta and one apical seta on posteroventral surface. Hind coxa with row of setae

on apical and outer lateral margin. Hind femur with anterodorsal and anteroventral rows of setae from base to apex, and one incomplete row of posteroventral setae. Hind tibia with anterodorsal row of setae from base to apex, with median seta strong, one strong apical seta on dorsal surface, two strong median setae and one apical seta on anteroventral surface, two strong median setae and one apical seta on posterodorsal surface. Basal tarsomeres long, subequal to combined length of remaining tarsomeres. Tarsal claws long, almost as long as last tarsomeres.

Abdomen (Fig. 1D, F): Subtriangular, tapering towards posterior end. Syntergite 1+2 with mid-dorsal depression extending half way to hind margin. Syntergite 1+2 and tergite 3 with one pair of median marginal setae and one pair of lateral marginal setae. Tergite 4 with row of marginal setae. Tergite 5 with row of marginal setae. Sexual patches of setae absent. Sternites completely overlapped by tergites.

Etymology: This species is named for the Polish entomologist Karol Lenko, former curator of Hymenoptera of MZSP who collected the specimen.

Distribution: Brazil (São Paulo).

Remarks: The chaetotaxy of species of *Ophirion* show little variation, which may cause confusion in species identification. The main informative characters are variations of pruinosity color on each tagma, presence and color of abdominal dorsal vitta, presence and shape of infuscation on wings, presence of eye hairs, length of antennal axis and presence of anepimeral setae. *Ophirion flava* (Townsend, 1919), *O. mirabile* (Townsend, 1911, adult description provided in Townsend (1912)) and *O. punctigerum* (Townsend, 1927) also have eyes apparently bare, with sparse minute inconspicuous hairs (Fig. 2F); *O. flava* and *O. mirabile*, however, have abdomen entirely yellow or brownish-yellow, without a marked dorsal vitta and wings faintly infuscated on distal half of the costal margin, and *O. punctigerum* has abdomen with dark brown vitta covering only the posterior margin of tergite 4, wings strongly infuscated distally, legs dark brown and antennal axis about half head height (Fig. 2B, D). *Ophirion atlixcoensis* (Reinhard, 1975), *O. brasiliensis* (Townsend, 1927), *O. polybia* (Curran, 1937) and *O. tersum* (Townsend, 1919) have eyes conspicuously haired and abdomen with marked dark brown vitta (Fig. 3), except *O. brasiliensis*, with abdomen without vitta and with silver pruinose bands (Fig. 2A, C). Characters of male and female terminalia of *Ophirion* species remain unknown.

Ophirion lenkoi is not the only species in the genus parasitoid of *Polybia*, as *O. polybia* (Fig. 3) was reared from *P. (M.) occidentalis* in Trinidad and Tobago and other record for *Ophirion* is listed in the

catalog above. Therefore, *Ophirion* species appear to be specialized parasitoids of vespid larvae. *Ophirion brasiliensis* and *O. punctigerum* were also collected in the Atlantic Forest of São Paulo, just a few kilometers away from the municipality of Nova Europa, but they are easily separated from *O. lenkoi* based on characters listed above. As *P. (M.) scutellaris* is distributed throughout the Brazilian Atlantic Forest, Argentina, Paraguay and Uruguay (Richards 1978a), *O. lenkoi*

could have a wider distribution in South America.

Genus *Lixophaga* Townsend, 1908

Lixophaga comprises 77 valid species, including the nomenclatural acts proposed here; thirty-one genera have been synonymized with *Lixophaga*, most of them by Wood (1985). The complete list of species and synonyms can be checked in O’Hara et al. (2020).

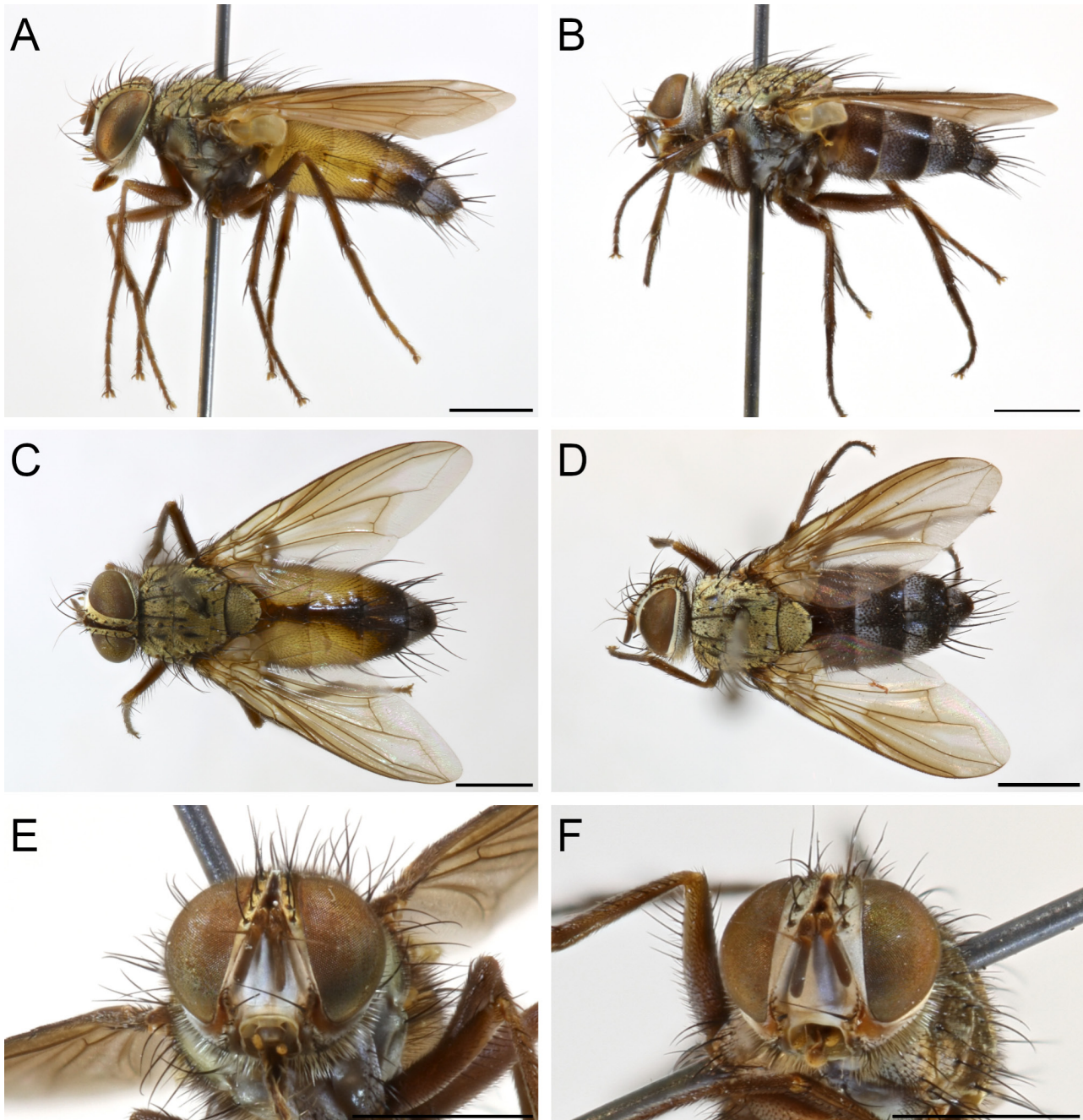


Fig. 3. Type material of *Telothyriosoma polybia* Curran. A, C, E: Lateral habitus, dorsal habitus and head in frontal view of holotype male (AMNH), respectively; B, D, F: Lateral habitus, dorsal habitus and head in frontal view of paratype female (AMNH), respectively. Scale bars = 2 mm.

***Lixophaga punctata* (Townsend, 1927)**

(Figs. 4, 8, 9)

Paranetia punctata Townsend, 1927: 344. Holotype male (USNM), examined (Fig. 5). Type locality: Brazil, São Paulo, Itaquaquecetuba.

Polybiophila fitzgeraldi Curran, 1937: 3. Holotype male (AMNH), examined (Fig. 6). Type locality: Trinidad and Tobago, Mount Saint Benedict. syn. nov.

Santacruzia dubiosa Thompson, 1968: 125. Holotype female (CNC), examined (Fig. 7). Type locality: Trinidad and Tobago, Santa Cruz Valley. syn. nov.

Material examined: 10 ♂ (one dissected), 3 ♀ (two dissected): same data as *O. lenkoi* (MZSP).

Diagnosis: *Lixophaga punctata* can be distinguished from other Nearctic and Neotropical *Lixophaga* species by having: pale golden pruinosity on head and dorsal surface of thorax and abdomen; abdominal tergites 3 and 4 with pruinose bands on basal two-thirds and apical third dark brown; abdominal tergite 5 completely covered with pruinosity; palpi yellow; two katepisternal setae; anatergite bare; pair of apical scutellar setae subparallel or divergent; wings hyaline; one or two pairs of median discal setae on intermediate abdominal tergites; and males with terminalia bearing epiphallus very short, completely covered by postgonites, pregonites narrow and long, and surstyli and cerci arched in posterior view, with apical parts of cerci bent towards posterior region in lateral view. A comprehensive comparison of the main diagnostic characters of *Lixophaga* species similar to *L. punctata* is covered in the Remarks section below.

Redescription of males: Body length: 5.17–5.58 mm (mean = 5.44 mm). Wing length: 4.49–5.74 mm (mean = 5.25 mm).

Coloration: Head with pale golden pruinosity, including face, gena and postgena. Frontal vitta, lunule, antenna and arista dark brown. Clypeus black. Palpi and labella yellow. Occiput black, covered with silver pruinosity. Thorax with pale golden pruinosity, except lower region of pleural sclerites, with faint silvery pruinosity. Scutum with four marked, black vittae; outer vittae interrupted by transverse suture and extending to last postsutural dorsocentral seta, and inner vittae continuous and extending to median postsutural acrostichal seta. Lateral surface of thorax dark brown. Basal area of scutellum dark brown, with posterior half covered with pale golden pruinosity. Wing hyaline. Tegula and basicosta dark brown. Veins and halter light yellow. Calypteres yellowish, with yellow border. Legs dark brown, with silver pruinosity. Tarsal claws brown. Pulvilli light brown. Abdomen with pale golden pruinosity, except ventral surface of tergites, with silvery pruinosity; basal lateral surface of intermediate

tergites yellowish in background. Syntergite 1+2 dark brown, becoming lighter towards ventral surface. Tergites 3 and 4 with pruinose bands on basal two-thirds, with apical third dark brown. Tergite 5 dark brown, completely covered with pruinosity.

Head (Fig. 4E): Ratio of head height/ head width in frontal view 0.86–0.89 (mean = 0.87). Ratio of frontal vitta width/ fronto-orbital plate width in dorsal view 0.58–0.82 (mean = 0.73). Ratio of vertex width/ head width in dorsal view 0.21–0.23 (mean = 0.22). Ratio of first flagellomere length/ pedicel length 2.93–3.16 (mean = 3.05). Ratio genal height/ head height in lateral view 0.21–0.23 (mean = 0.22). Dichoptic. Eye bare. Antenna inserted at middle level of eye, almost reaching lower facial margin. Scape short, about one-third length of pedicel. Pedicel setose dorsally, with one apical erect seta. First flagellomere subrectangular, with outer surface bearing one minute sensory pit closer to posterior margin. Arista long, pubescent and thickened at base, arising in basal dorsal surface of first flagellomere. Seven or eight subequal inclinate frontal setae from level of pedicel to level of upper quarter of eye. Proclinate orbital setae absent. Two or three reclinate orbital setae, with posterior setae about two-thirds length of anterior seta. Ocellar triangle densely setulose, with one pair of proclinate ocellar setae, about half length of anterior reclinate orbital seta; all ocelli with similar size. Two postocellar setae, about half length of ocellar setae. Inner vertical setae reclinate, subparallel. Outer vertical setae weak, about one-fifth length of inner vertical. Fronto-orbital plate setulose to second anterior frontal seta. Parafacial bare, about two-thirds width of fronto-orbital plate. Facial ridge bare, except on lowest quarter, with three or four weak supravibrissal setae. Vibrissa strong and crossed, arising at level of lower facial margin, with two or three subvibrissal setae. Face flat and not visible in lateral view, with slight facial carina on upper half. Gena with two or three setae on ventral margin. Genal dilation and postgena setulose, with patches of long, white setulae. Clypeus U-shaped. Palpi clavate and setose. Prementum short, setulose. Labella padlike.

Thorax (Fig. 4A, C): Prosternum setose. Proepisternum bare. Two proepimeral setae, strong, upcurved, with setulae at base. Anterior spiracle with both lappets well-developed, covering almost entire opening. Posterior spiracle with posterior lappet shaped as an operculum. Three postpronotal setae, arranged as triangle. Scutum with 3+3 acrostichal setae; 2+2–3 dorsocentral setae; 2+3 intra-alar setae; 1+3 supra-alar setae, with first postsutural seta shorter than second, and second postsutural seta strong and subequal to median postalar seta. One weak intrapostalar seta. Two notopleural setae. Three postalar setae, with median

seta stronger than other two. Two katepisternal setae. Anepisternum anterodorsal corner with one seta, about half length of notopleural setae; posterior margin with row of six setae. One anepimeral seta, with patch of setulae at base. Six or seven meral setae. Anatergite

bare. Scutellum with one pair of basal setae, convergent and long, subequal to subapical setae; one pair of lateral setae, subparallel and about two-thirds length of basal setae; one pair of subapical setae, divergent; one pair of apical setae, subparallel or divergent, about one-fifth

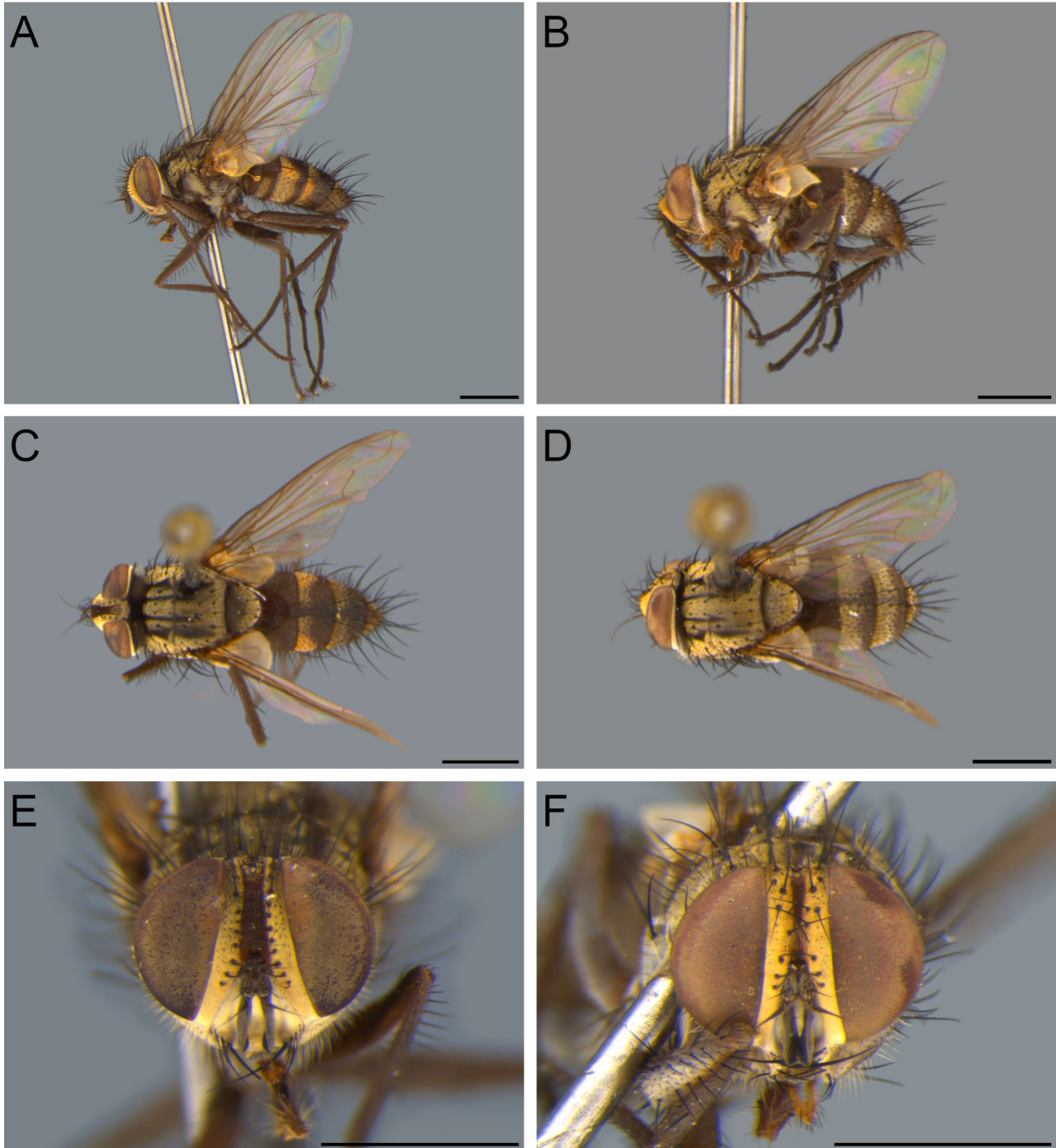


Fig. 4. Record of *Lixophaga punctata* (Townsend) in *Polybia* (*Myrapetra*) *scutellaris* (White). A, C, E: Lateral habitus, dorsal habitus and head in frontal view of male (MZSP), respectively; B, D, F: Lateral habitus, dorsal habitus and head in frontal view of female (MZSP), respectively. Scale bars = 2 mm.

length of subapical setae; one pair of discal setae arising at level of subapical setae. Wing: Vein C ending right after R_{4+5} , just before wing apex, with short costal spine. Vein R_{4+5} setose only at base. Bend of M obtuse, with distal part straight to wing margin. Cell r_{4+5} open, with length shorter than crossvein r-m. Legs: Fore coxa with two longitudinal rows of setae on anterior surface. Fore femur with dorsal, posterodorsal and posteroventral rows of setae from base to apex. Fore tibia with one strong apical seta on dorsal surface, one strong median seta and one apical seta on posterior surface. Mid coxa with row of setae on anterior surface. Mid femur with two median setae on anterior surface and an incomplete row of setae on posteroventral surface. Mid tibia with one strong median seta on anterodorsal surface, one strong apical seta on anterior surface, two median setae on posterior surface, one median seta and one apical seta on posteroventral surface. Hind coxa with row of setae on apical and outer lateral margin. Hind femur with anterodorsal and anteroventral rows of setae from base to apex, and one incomplete row of posteroventral

setae. Hind tibia with anterodorsal row of setae from base to apex, with median seta strong, one strong apical seta on dorsal surface, two strong median setae and one apical seta on anteroventral surface, two strong setae on posterodorsal surface. Basal tarsomeres long, but shorter than combined length of remaining tarsomeres; second and third tarsomeres long, about half length of basal tarsomeres. Tarsal claws long, almost as long as last tarsomeres.

Abdomen (Fig. 4A, C): Subtriangular, tapering towards posterior end. Syntergite 1+2 with mid-dorsal depression extending more than half way to hind margin, but not reaching hind margin. Syntergite 1+2 and tergite 3 with one pair of median marginal setae and one pair of lateral marginal setae. Tergite 4 with row of marginal setae. One or two pairs of median discal setae on intermediate tergites. Tergite 5 with row of discal and marginal setae. Sexual patches of setae absent. Sternites completely overlapped by tergites. Sternite 5 short, wider than long and subrectangular, with posterior margin with pair of lobes delimiting U-shaped notch;



Fig. 5. Holotype male of *Paranetia punctata* Townsend (USNM). A, Habitus, lateral view; B, Head, frontal view; C, Habitus, dorsal view; D, Labels. Scale bars = 2 mm.

lobes covered with setulae and bearing single long seta on each one.

Terminalia (Fig. 8): Tergite 6 divided into two hemitergites with pair of spiracles on membrane; left hemitergite well-developed and right hemitergite reduced to narrow strip. Sternite 6 asymmetrical, connected to left hemitergite of tergite 6 by wide area, tapering towards middle and ending right after connection to sternite 5, not reaching right hemitergite

of tergite 6. Syntergite 7 + 8 with anterior half bearing pair of spiracles, and posterior half setulose. Anterior epandrial process well projected beyond ventral epandrial margin. Epandrium setulose, with dorsal surface about half length of ventral surface in lateral view; posterior margin forming pointed, projected lobe at middle and rounded, lower lobe in lateral view. Surstylus not fused with epandrium or bacilliform sclerite, same width as cercus in lateral view, with

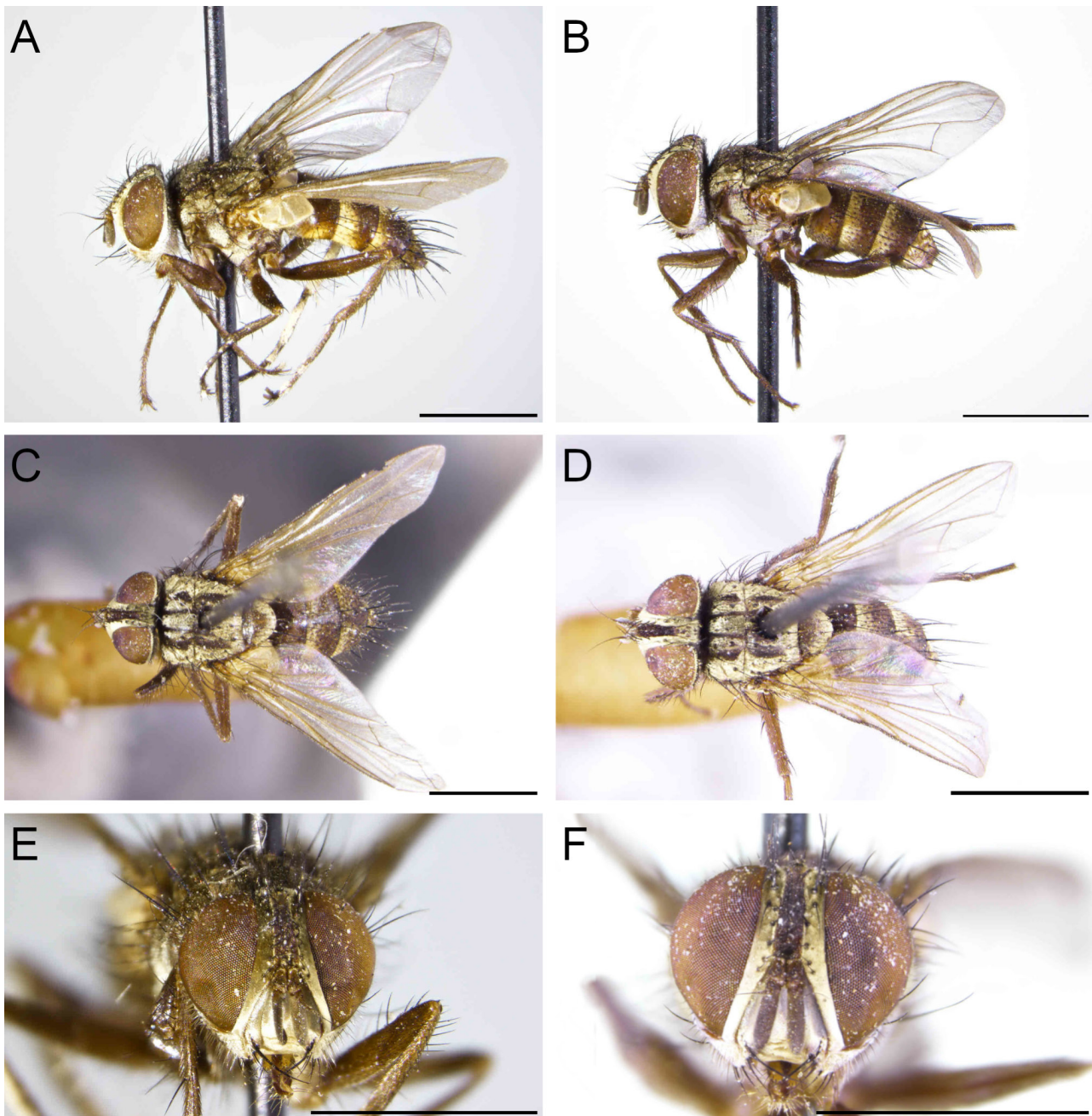


Fig. 6. Type material of *Polybiophila fitzgeraldi* Curran. A, C, E: Lateral habitus, dorsal habitus and head in frontal view of holotype male (AMNH), respectively; B, D, F: Lateral habitus, dorsal habitus and head in frontal view paratype female (AMNH), respectively. Scale bars = 2 mm.

apex slightly curved towards anterior region; arched in posterior view, with apex clavate, with inner and outer surface covered with short, erect setulae. Bacilliform sclerite slender, connected to middle part of hypandrial arm. Hypandrium with hypandrial apodeme concave, with narrow and rounded apex in ventral view, almost as long as central plate of hypandrium; hypandrial plate concave, with posterior margin fused with pregonites; hypandrial arms not fused with each other. Phallic guide long. Ejaculatory apodeme small, with upper part flattened and lower part broad. Phallus with epiphallus attached to base of distiphallus and very short, completely covered by postgonites; basiphallus

without basal process, stout and about half length of distiphallus, with apex wider than base; dorsal sclerite of distiphallus fused with basiphallus, with long median process extending to apex of distiphallus; distiphallus slightly curved towards anterior region, forming an obtuse angle with basiphallus, with pair of lateroventral sclerites strongly sclerotized, without apparent granules and lobed apically; median groove short and sclerotized, located between lateroventral sclerites and distad on ventral surface of distiphallus. Pregonite with anterior base fused with central plate of hypandrium, narrow and long, with apex rounded and slightly curved towards anterior region; lower posterior margin bearing minute fine setae. Postgonite bare and bacilliform, same width

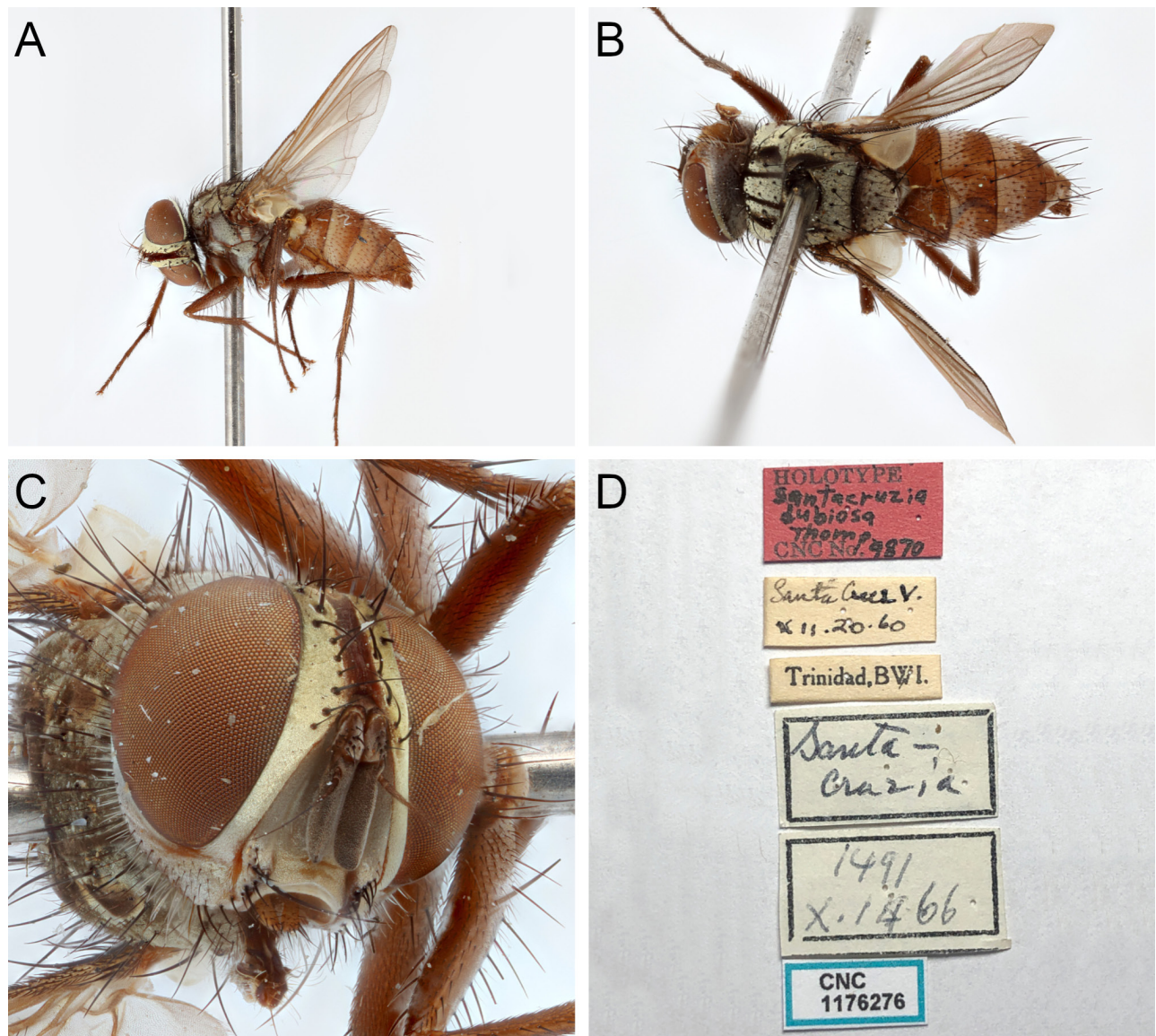


Fig. 7. Holotype male of *Santacruzia dubiosa* Thompson (CNC). A, Habitus, lateral view; B, Habitus, dorsal view; C, Head, frontal view; D, Labels. Images originally lacking scales.

as pregonite, with rounded apex. Cerci entirely setose, not fused with each other and with narrow median cleft on basal third; apex extending to level of apical part of surstyli, slightly arched in posterior view and with apical part bent towards posterior region in lateral view.

Redescription of females (Fig. 4B, D, F): Differ from male as follows: Body length: 5.21–5.36 mm (mean = 5.29 mm). Wing length: 5.07–5.14 mm (mean = 5.10 mm).

Coloration: Parafacial with silver pruinosity.

Head: Ratio of head height/ head width in frontal view 0.86–0.88 (mean = 0.87). Ratio of frontal vitta width/ fronto-orbital plate width in dorsal view 0.57–0.94 (mean = 0.75). Ratio of vertex width/ head width in dorsal view 0.25–0.25 (mean = 0.25). Ratio of first flagellomere length/ pedicel length 3.39–4.13 (mean = 3.76). Ratio genal height/ head height in lateral view 0.24–0.25 (mean = 0.24). Five or six inclinate

frontal setae. Two proclinate orbital setae, with anterior seta arising at level of last posterior frontal seta and posterior seta arising between reclinate orbital setae. Basal tarsomeres almost as long as combined length of remaining tarsomeres.

Abdomen: Ellipsoidal, tapering towards posterior end.

Terminalia (Fig. 9): Ovipositor long, with membranous area between segment 6 and 7 as long as tergite 6. Spermathecae lost during dissection. Tergites 6 and 7 divided into two hemitergites, with posterior margin with few fine setae; hemitergites of tergite 6 with posterior margin wider than anterior margin; hemitergites of tergite 7 subrectangular. Sixth pair of spiracles located in membrane, before hemitergites of tergite 6; seventh pair of spiracles on anterolateral margin of hemitergites of tergite 6. Sternite 6 subtriangular, with posterior margin setose and wider

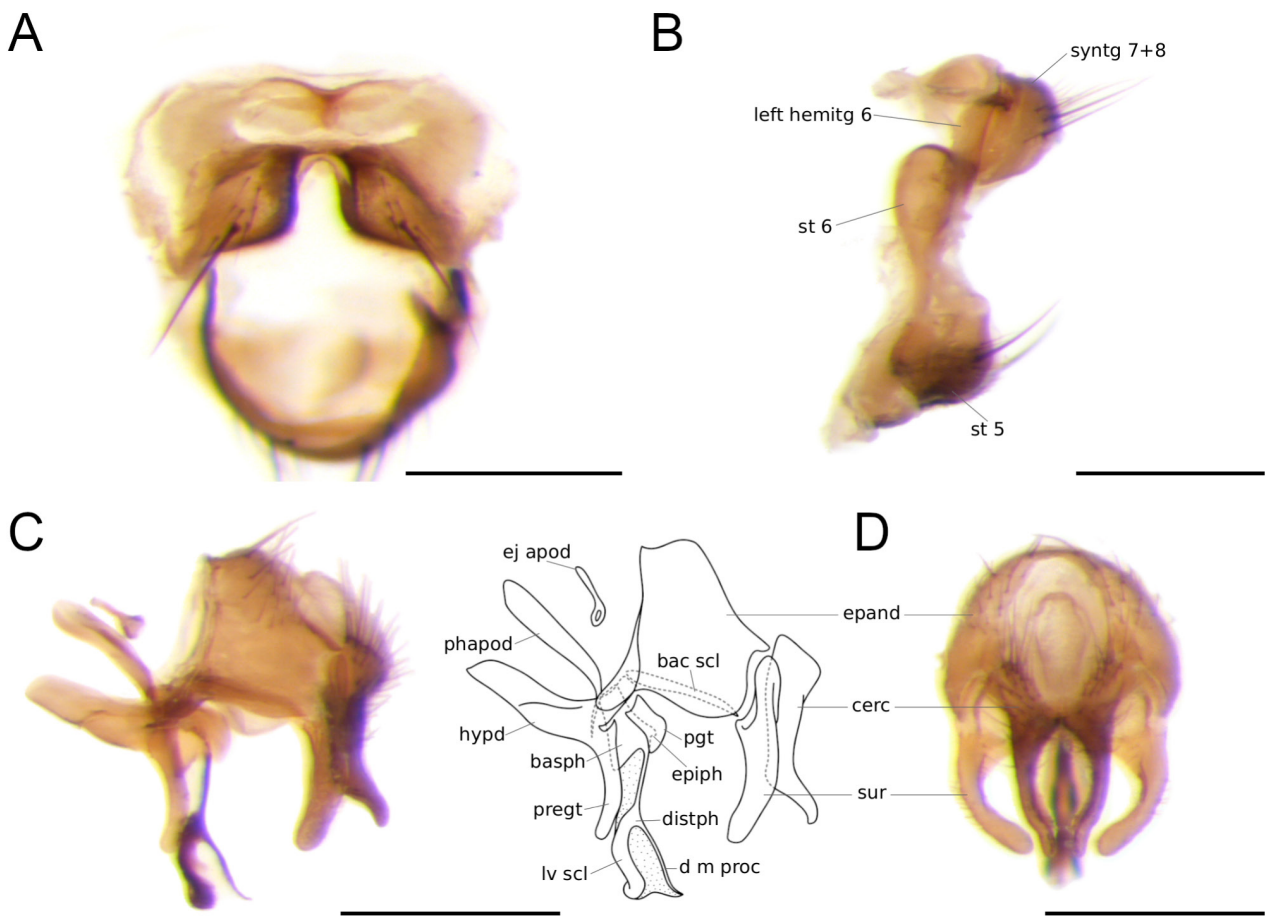


Fig. 8. Male terminalia of *Lixophaga punctata* (Townsend). A, Sternite five; B, Lateral view of postabdomen, showing sclerites of segments 5–8; C, Lateral view of genitalia and line drawing highlighting outer and inner structures (gray dashed lines) and membranous surfaces (dotted areas); D, Posterior view of genitalia. Scale bars = 0.5 mm. Abbreviations: bac scl = bacilliform sclerite, basph = basiphallus, epand = epandrium, cerc = cercus, d m proc = dorsal median process, distph = distiphallus, ej apod = ejaculatory apodeme, epiph = epiphallus, hemitg = hemitergite, hypd = hypandrium, lv scl = lateroventral sclerite, pgt = postgonite, phapod = phallapodeme, pregt = pregonite, st = sternite, sur = surstylus, syntg = syntergite.

than anterior margin. Sternite 7 longer than wide, with narrow and setose posterior margin. Tergite 8 very small, reduced to pair of lateral narrow sclerites, close to hypoproct. Sternite 8 setose, short and convex in ventral view. Epiproct absent. Hypoproct evenly setose, wide and subrectangular in ventral view and compressed in lateral view, with pair of well-developed lateral arms arising on anterolateral margin and directed downwards. Cerci not fused, setose on posterior half.

Distribution: Trinidad and Tobago (San Juan-Laventille and Tunapuna-Piarco) and Brazil (São Paulo).

Remarks: The presence of median discal setae on abdominal tergites is also found in seven *Lixophaga* species, namely *L. aristalis* (Townsend, 1927), *L. leucophaea* (van der Wulp, 1890a), *L. neglecta* (van der Wulp, 1890b), *L. solitaria* (Curran, 1926), *L. trichosoma* (van der Wulp, 1890c), *L. umbripennis*

A



B

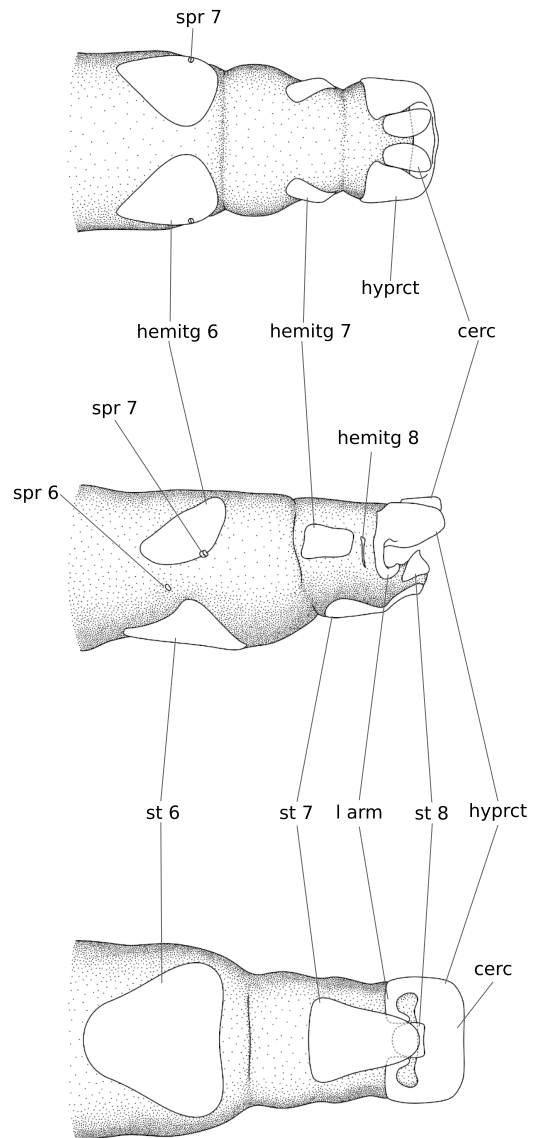


Fig. 9. Female terminalia of *Lixophaga punctata* (Townsend). A, Dorsal, lateral, and ventral views, respectively; B, Line drawings of dorsal, lateral, and ventral views, respectively, highlighting outer and inner structures (gray dashed lines) and membranous surfaces (dotted areas). Scale bar = 0.5 mm. Abbreviations: cerc = cercus, hemitg = hemitergite, hyp = hypoproct, l arm = lateral arm; spr = spiracle, st = sternite, tg = tergite.

(van der Wulp, 1890a) and *L. unicolor* (Smith, 1917). *Lixophaga leucophaea*, *L. solitaria* and *L. unicolor* were described from Mexico, Jamaica and United States of America, respectively, showing silvery pruinosity covering the entire body; furthermore, *L. leucophaea* has palpi black and *L. solitaria* does not have apical scutellar setae. *Lixophaga aristalis* and *L. neglecta* were described based on a single specimen from Brazil and Mexico, respectively, showing pale golden pruinosity covering the entire body; they differ from *L. punctata* by having three katepisternal setae and wings infuscated along costal margin. The holotype female of *L. trichosoma* and the holotype male of *L. umbripennis* are from Mexico and both show pale golden pruinosity covering the entire body; *L. trichosoma* also has wings hyaline, differing from *L. punctata* by having three katepisternal setae and apical scutellar setae crossed; *L. umbripennis* also has two katepisternal setae and apical scutellar setae divergent, but differs from *L. punctata* in having wings infuscated along costal margin, especially around the veins R₁ and R₂₊₃. Other two *Lixophaga* species present only two katepisternal setae: *L. charapensis* (Townsend, 1927) and *L. parva* Townsend, 1908 (Townsend 1940 1941). *Lixophaga charapensis* was described based on one female from Peru with pale golden pruinosity covering the entire body, but has apical scutellar setae crossed and no discal setae on intermediate abdominal tergites. *Lixophaga parva* was described based on one male from United States of America with silvery pruinosity covering the entire body and no discal setae on intermediate abdominal tergites.

On examining the type material of *Paranetia punctata*, *Polybiophila fitzgeraldi* and *Santacruzia dubiosa* (Figs. 5–7), I conclude that these species are synonyms, showing the same diagnostic characters provided above. *Paranetia punctata* was collected in the Atlantic Forest in Itaquaquacetuba, just a few kilometers away from the municipality of Nova Europa. Besides having a similar morphology with *P. punctata*, *P. fitzgeraldi* was also reared from *Polybia*, an additional evidence that both species are synonyms. Although the host of *S. dubiosa* is unknown, it was collected near the type locality of *P. fitzgeraldi* in Trinidad and Tobago, and shares the same characters; the abdomen color is lighter than usual due to the dissection made by Thompson. These synonyms expand the distribution of *L. punctata* in South America, which has a large gap between records. This fragmented distribution actually reflects the lack of specimen collection and taxonomic studies in Neotropical Tachinidae. As New World *Polybia* species are distributed from Mexico to Argentina (Richards 1978a), *L. punctata* could have a wider distribution in the Neotropical Region.

DISCUSSION

Only eusocial species of Vespidae are parasitized by tachinids, but most of the data and discussion about parasitoid-host interactions are based in studies of polistine wasps, as there are very few records in Stenogastrinae and Vespinae. The evolution of parasitism of eusocial Vespidae in Tachinidae seems to have occurred independently at least three times, only in Exoristinae: in the tribe Anacamptomyiini, in *L. punctata* and in the genus *Ophirion*. Wood (1985) suggested that *Ophirion* may be a subgroup of *Lixophaga*, but both genera have clear diagnostic characters. Anacamptomyiini has been considered close to genera of the former tribe Carceliini, now classified in the tribes Eryciini and Goniini (Crosskey 1973 1976). These taxa, however, were not sampled in the most comprehensive phylogenetic studies in the family (Cerretti et al. 2014; Stireman et al. 2019), hampering a better understanding on the evolution of host use in vespid larvae by tachinids.

The oviposition strategy of *Lixophaga* species, however, sheds some light on this subject, suggesting that a key factor in host transition is present in the way tachinid females detect cues to locate their hosts. *Lixophaga* females usually attack hosts that are not exposed, locating them through olfactory cues present in the host's frass and laying their eggs at the entrance of tunnels or cavities made by plant or fungi boring insects (Waggy and Beardsley 1974; Roth et al. 1978). Since borers are found in several lineages of insects, it is not surprising to see that different species of *Lixophaga* explore a varied set of hosts in different orders (Table 2). Although eusocial vespids are not borers, their larvae are reared within comb cells that have varied degrees of exposition and length (Turillazzi 1991; Wenzel 1998). As *Lixophaga* females lay eggs with well-developed first instar larvae that actively seek out the host within its cavity, it is expected that they can perform the same oviposition behavior in search of eusocial wasp larvae nested in comb cells. *Lixophaga punctata* is the only species in the genus parasitizing Vespidae larvae, but its oviposition strategy has not yet been recorded. Roubaud and Villeneuve (1914) and Townsend (1936) described the morphology of first instar larvae of species of *Anacamptomyia* and *Ophirion*, respectively, suggesting that they are active in locomotion, similarly to those of *Lixophaga*. The biology of *Lixophaga* species, therefore, may serve as a model to understand the host transition in *Ophirion* and Anacamptomyiini as well.

As the olfactory cues used by species of *Lixophaga* are present in the host's frass, the main cue used by tachinids to locate vespid hosts should be present in the meconia, *i.e.*, the fecal waste that vespid

Table 2. List of species of *Lixophaga* Townsend and their respective hosts. Host species that are borers of plants or fungi are highlighted in bold. Details about records, localities and respective references can be found in Guimarães (1977), Arnaud (1978), Carrejo et al. (2013), Tschorsnig (2017) and Gudin et al. (2022)

Species of <i>Lixophaga</i>	Hosts
<i>Lixophaga cinctella</i> (Mesnil)	Mesalcidodes trifidus Pascoe (COL: Curculionidae)
<i>Lixophaga diatraeae</i> (Townsend)	<i>Calpodes ethlius</i> (Stoll) (LEP: Hesperidae)
	Diatraea spp. (LEP: Crambidae)
	<i>Spodoptera frugiperda</i> (Smith) (LEP: Noctuidae)
	<i>Utetheisa ornatrix</i> (L.) (LEP: Erebidae)
<i>Lixophaga grisea</i> (Curran)	Diatraea saccharalis (Fabr.) (LEP: Crambidae)
<i>Lixophaga jennei</i> Aldrich	Cydia pomonella (L.) (LEP: Tortricidae)
<i>Lixophaga latigena</i> Shima	Curculio spp. (COL: Curculionidae)
<i>Lixophaga limonina</i> Richter	Metalimnobia quadrimaculata L. (DIP: Limoniidae)
<i>Lixophaga mediocris</i> Aldrich	<i>Cnidocampa flavescens</i> (Walker) (LEP: Limacodidae)
	Cydia caryana (Fitch) (LEP: Tortricidae)
	<i>Frumenta nundinella</i> (Zeller) (LEP: Gelechiidae)
	Grapholita molesta (Busck) (LEP: Tortricidae)
	Rhyacionia spp. (LEP: Tortricidae)
	Suleima helianthana (Riley) (LEP: Tortricidae)
<i>Lixophaga orbitalis</i> Aldrich	Cydia pomonella (L.) (LEP: Tortricidae)
<i>Lixophaga parva</i> Townsend	Grapholita molesta (Busck) (LEP: Tortricidae)
	Lixus scrobicollis Boheman (COL: Curculionidae)
<i>Lixophaga plumbea</i> Aldrich	<i>Cochylina oenotherana</i> (Riley) (LEP: Tortricidae)
	Grapholita molesta (Busck) (LEP: Tortricidae)
	Rhyacionia frustrana (Comstock) (LEP: Tortricidae)
	<i>Saucrobotys futilalis</i> (Lederer) (LEP: Crambidae)
	<i>Xenotemna pallorana</i> (Robinson) (LEP: Tortricidae)
<i>Lixophaga punctata</i> (Townsend)	<i>Polybia occidentalis</i> (Olivier) (HYM: Vespidae)
	<i>Polybia scutellaris</i> (White) (HYM: Vespidae)
<i>Lixophaga puscolulo</i> Carrejo and Woodley	Neoleucinodes elegantalis (Guenée) (LEP: Crambidae)
<i>Lixophaga stratiophaga</i> Gudin	Ptecticus testaceus (Fabr.) (DIP: Stratiomyidae)
<i>Lixophaga sphenophori</i> (Villeneuve)	Diatraea crambidoides (Grote) (LEP: Crambidae)
	Rhabdoscelus obscurus (Boisduval) (COL: Curculionidae)
<i>Lixophaga stenomae</i> Curran	Stenoma spp. (LEP: Elachistidae)
<i>Lixophaga tenuis</i> (Blanchard)	<i>Hypercompe indecisa</i> (Walker) (LEP: Erebidae)
<i>Lixophaga variabilis</i> (Coquillett)	Amphicerus bicaudatus (Say) (COL: Bostrichidae)
	<i>Ancylis comptana</i> (Frölich) (LEP: Tortricidae)
	<i>Anomis erosa</i> Hübner (LEP: Noctuidae)
	Cydia spp. (LEP: Tortricidae)
	<i>Desmia funeralis</i> (Hübner) (LEP: Crambidae)
	Epiblema spp. (LEP: Tortricidae)
	<i>Eumaroza malachitana</i> (Zeller) (LEP: Tortricidae)
	Grapholita molesta (Busck) (LEP: Tortricidae)
	<i>Homoeosoma electellum</i> (Hulst) (LEP: Pyralidae)
	Lixus scrobicollis Boheman (COL: Curculionidae)
	<i>Loxostege similalis</i> (Guenée) (LEP: Crambidae)
	Oberea bimaculata (Olivier) (COL: Cerambicidae)
	Ostrinia spp. (LEP: Crambidae)
	Papaipema spp. (LEP: Noctuidae)
	<i>Plagiomimicus spumosum</i> (Grote) (LEP: Noctuidae)
	Rhyacionia rigidana (Fernald) (LEP: Tortricidae)
	Suleima helianthana (Riley) (LEP: Tortricidae)
	Sphenophorus pontederiae Chittenden (COL: Curculionidae)
	<i>Trichoplusia ni</i> (Hübner) (LEP: Noctuidae)

Abbreviations: COL = Coleoptera, DIP = Diptera, LEP = Lepidoptera, HYM = Hymenoptera.

larvae eject only in the prepupal stage (Bağrıaçık 2020). Wenzel (1991) hypothesized that tachinid parasitoids of Vespidae may use olfactory cues present in the larvae's meconia, which have a strong smell. The end of the digestive system of a wasp larva is closed, finishing its development only in the fifth instar, also known as prepupal stage; the larva then ejects the meconium at the bottom of its comb cell before pupation (Bağrıaçık 2020). If tachinid females can detect cues present in the meconium, it is expected that their first instar larvae would preferably search for prepupal wasp larvae. In fact, in several records in Polistinae listed in the host catalog, larvae or pupae of tachinids were found within a silken covered cell with remnants of prepupal wasp larvae (Curran 1937; Richards 1969; Hook and Evans 1982; Keeping and Crewe 1983; Keeping 1997). Species of *Belonogaster* and *Ropalidia* and other Old World genera of Polistinae have the habit of cutting the bottom of old cells to remove the meconium, which may be a result of selection pressure caused by parasitoids, mainly anacamptomyiine flies (Wenzel 1991). The use of olfactory cues in the meconium can also explain why some lineages of Tachinidae have adapted only to eusocial species, as the density of olfactory cues in a colony must be much higher than in a single solitary wasp nest, which facilitates detection by tachinid females.

In *Anacamptomyia*, the oviposition strategy of *A. bisetosa* in nests of *Belonogaster* was described by Roubaud and Villeneuve (1914): female flies rest in the vicinity of wasp nests, waiting for an opportunity to lay their eggs on the nest external wall. The wasps usually react to the presence of the fly, demonstrating some aggressiveness. The authors mentioned that female flies may lay their eggs when wasps are less active during nightfall or when they are foraging outside the nest, but it is not clear if these behaviors were direct observations or hypotheses. Colonies of *Belonogaster*, *Mischocyttarus*, *Polistes* and *Ropalidia* are usually started by a single foundress, a process known as independent foundation, whereas in epiponine wasps, such as *Polybia*, the nest is started by a queen accompanied by several workers, a process known as swarm foundation (Noll et al. 2021). Although in independent-founding wasps the parasitism may be facilitated, since the nest is left alone by the single foundress and the first workers more often, the aggressiveness and defense of swarm-founding wasps usually decreases after the first days of colony initiation (Kudô et al. 2003), which should create more opportunities for the oviposition of tachinid females.

The architecture of the nest may also play an important role in the effectiveness of parasitism by tachinids. Species of Anacamptomyiini usually have

high rates of parasitism, commonly reaching more than 40 %, and sometimes up to 80%, of silken covered cells parasitized (Hook and Evans 1982; Keeping and Crewe 1983; Spradbery 1989). In *Lixophaga* and *Ophirion*, however, the parasitism rates seem to be much smaller, as only a few specimens are reared per nest (Curran 1937; Richards 1978a). The combs of *Mischocyttarus*, many Old World Polistinae and Stenogastrinae are usually naked, not having an envelope covering the nest (Wenzel 1998), which can facilitate the access of tachinid females and their larvae to comb cells. In most Epiponini and Vespinae, the nest has only a single entrance and is covered with an envelope that protects the combs (Noll et al. 2021). The envelope morphology is varied, having a smooth surface or apophyses shaped as spiny processes that may be useful to regulate the nest temperature and to protect it against rain, insulation and predators (Richards and Richards 1951; Richards 1978a). Jeane (2021) argued that the envelope and its shape should act as additional barriers to parasitoids as well, which explains the low parasitism rate of species of *Lixophaga* and *Ophirion*.

CONCLUSIONS

The evolution of host-parasitoid associations between tachinids and eusocial Vespidae still have much to be clarified, but some hypotheses discussed here can guide future studies. The biology of *Lixophaga* species provide a suitable model to explain how tachinids were able to explore eusocial vespid hosts, since *L. punctata* is the only species adapted to vespid hosts in a genus characterized by species parasitoids of plant or fungi boring insects. The adaptation to ovoviviparity with first instar larvae that seek out hosts inside a cavity is probably the key factor that enabled tachinids to explore eusocial vespid hosts. The main cue used by tachinid females may be present in the meconia of wasp larvae, but further tests and observations of oviposition strategies of tachinid females are required. The taxonomy of Neotropical tachinid parasitoids of eusocial Vespidae is improved, providing a valuable resource for identification of species. These results are a clear example of how valuable natural history collections are, which hold timeless and precious pieces of information that help us understand important questions in nature.

List of abbreviations

AMNH, American Museum of Natural History, New York, United States of America.
CNC, Canadian National Collection of Insects, Ottawa, Canada.

MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

NHMUK, Natural History Museum, London, United Kingdom.

USNM, National Museum of Natural History, Washington DC., United States of America.

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Authors' contributions: The author designed the study and wrote the manuscript.

Competing interests: The author declares that he has no competing interests.

Availability of data and materials: Holotype of *Ophirion lenkoi* and males and females of *Lixophaga punctata* are deposited at Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

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Ethics approval consent to participate: Not applicable.

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