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Revising Spider Egg-predating Fly Records (Diptera: Sarcophagidae): New Insights on Prey, Taxonomy, and Distribution of *Sarcophaga* (*Mehria*) *lorosa* Hall in Southern South America

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Flesh flies (Diptera: Sarcophagidae) exhibit a wide range of feeding habits including necrophagy, coprophagy, kleptoparasitism, parasitism, and predation. Among them are species of *Sarcophaga* Meigen belonging to the subgenera *Baranovisca* Lopes and *Mehria* Enderlein that are specialized predators of spider eggs. These flies hover around spider webs and lay their larvae on the spider egg sac. While progress has been made on the taxonomy of *Baranovisca* and *Mehria* in recent decades, our knowledge about their biology, prey selection, and distribution remains limited, restricting our understanding of the evolutionary dynamics of Sarcophagidae-Araneae interactions. Here, we describe and illustrate the first record of *S.* (*M.*) *lorosa* Hall preying on egg sacs of *Metepeira galatheae* (Thorell) (Araneae: Araneidae) in Chile. The taxonomy of *S.* (*M.*) *lorosa* is revised, with two new junior synonyms proposed: *Weyrauchimyia ruficauda* Lopes and Tibana, syn. nov., and *Arachnidomyia travassosi* Tibana and Mello, syn. nov. Furthermore, we present an annotated catalog that comprehensively reviews the existing records of spider egg-predating Sarcophagidae, and provide an overview of the evolution of Sarcophagidae-Araneae interactions. Our catalog includes information on at least four species of *Baranovisca* and 10 species of *Mehria* that have been documented as preying on eggs from species of various spider families, such as Araneidae, Cheiracanthiidae, Clubionidae, Philodromidae, Salticidae, and Tetragnathidae. These records cover all biogeographical regions except the Afrotropical. Our results enhance our understanding of the evolution of Sarcophagidae-Araneae interactions.

Key words: Araneidae, Coevolution, Egg sacs, *Metepeira*, Oviposition strategy

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BACKGROUND

Flesh flies (Diptera: Sarcophagidae) are often considered as necrophagous or coprophagous flies, although there are several lineages with parasitoid or predatory habits (Pape 1996; Pape and Dahlem 2010). The subfamily Miltogramminae contains a large clade of kleptoparasitic species (Piwczyński et al. 2017), while parasitoid and predatory larvae are frequently found in species of the subfamilies Paramacronychiinae and Sarcophaginae, attacking mostly invertebrates such as insects, snails, millipedes, earthworms, and spiders, but even producing myiasis in several species of vertebrates (Aldrich 1914; Pape 1996). For instance, the largest genus of the family, *Sarcophaga* Meigen, includes approximately 890 species classified in several subgenera worldwide (Buenaventura et al. 2017), some of which are adapted to parasitism or predation.

Sarcophaga larvae of the subgenera *Baranovisca* Lopes and *Mehria* Enderlein are specialized predators of spider eggs; the females hover around and fly through the spider web, trying to reach the egg sac, where they lay one larva per attack (Lubin 1974; Hieber and Uetz 1990; Rayor and Uetz 1990; Hieber et al. 2002). The larva then enters the egg sac and eats the eggs, thus completing its development. Some flies of the families Bombyliidae, Chloropidae, Ephydridae, and Phoridae, and wasps of the family Ichneumonidae are also specialized parasitoids or predators of spider eggs (Sobczak et al. 2012; Fritzén and Sääksjärvi 2016; Villanueva-Bonilla et al. 2016; Gillung and Borkent 2017; Riccardi and Pádua 2021; Souza-Santiago et al. 2023). However, in some cases, the incidence of flesh flies is much higher than that of the other parasitoids/predators (Hieber and Uetz 1990).

The subgenus *Baranovisca* includes six species distributed in the Australasian and Oriental regions, while *Mehria* includes 15 species distributed in the Nearctic, Neotropical, and Palaearctic regions (Pape 1996). Although the taxonomy of these species has been improved with detailed descriptions and illustrations during the final decades of the last century (Lopes 1946 1959 1981 1985 1989; Cantrell 1981; Tibana and Mello 1992), information about their biology, prey, and distribution is restricted to a few species, which hinders a deeper understanding of the evolution of Sarcophagidae-Araneae interactions. Most records of flesh flies preying on spider eggs were recently listed (Gillung and Borkent 2017), but not all were included.

Here, we record for the first time the interaction of *Sarcophaga* (*Mehria*) *lorosa* Hall preying on egg sacs of *Metepeira galatheae* (Thorell) (Araneae: Araneidae) during a desert bloom in the Copiapó and Huasco provinces from the Atacama region, Chile (Chávez et al. 2019). The taxonomy and nomenclature of *S.* (*M.*) *lorosa* is revised, including notes on type material and new distribution records. Furthermore, we propose two new junior synonyms: *Weyrauchimyia ruficauda* Lopes and Tibana, syn. nov., and *Arachnidomyia travassosi* Tibana and Mello, syn. nov. Finally, we present an annotated catalog that comprehensively reviews the existing records of spider egg-predating Sarcophagidae and provide an overview of the evolution of Sarcophagidae-Araneae interactions.

MATERIALS AND METHODS

Metepeira galatheae adults (*n* = 20: 5 ♂, 15 ♀) (Fig. 1A, B) and egg sacs (*n* = 21) (Fig. 1C) were manually collected at four localities from two provinces in the Atacama region during a desert bloom (16–17 November 2022): Copiapó Province: Sector Totoral (27°50'14"S, 71°05'05"W); and Huasco Province: Parque Nacional Llanos del Challe (28°08'55"S, 71°09'24"W), Quebrada Honda (27°59'22,30"S, 71°08'14"W), and Parque Eolico Cabo Leones (28°55'14"S, 71°26'38"W) (Fig. 2B). The collected egg sacs and spiders were deposited in Falcon tubes, closed with voile, and transported to the Laboratorio de Ecología de Abejas of the Universidad Católica del Maule (UCM), Talca, Chile. All egg sacs and spiders were kept separately in Falcon tubes at room temperature (27–30°C).

Specimens of *S.* (*M.*) *lorosa* were identified based on examination of the holotype male deposited in the Natural History Museum (NHMUK) in London, United Kingdom. Additional material of *S.* (*M.*) *lorosa* was obtained from the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina. Morphological terminology follows Cumming and Wood (2017). Fly vouchers were deposited in UCM (5 ♂ and 1 ♀), and spider vouchers in UCM (13 ♀) and UNAP (5 ♂ and 2 ♀). *Metepeira galatheae* specimens were identified by Dr. Andres Taucare-Rios de la Universidad Arturo Prat (UNAP), Iquique, Chile.

The catalog follows a format similar to that presented by Guimarães (1977) and Arnaud (1978). Sarcophagidae species are listed alphabetically according to their respective biogeographical regions, with valid names and junior synonyms accompanied by authorship. Published records of egg predation are given with the name of the fly followed by respective spider prey, author, year of publication, page number, locality, and notes on the record. Comments and emendations regarding taxonomy, nomenclature or reliability of the record are included in square brackets. Secondary

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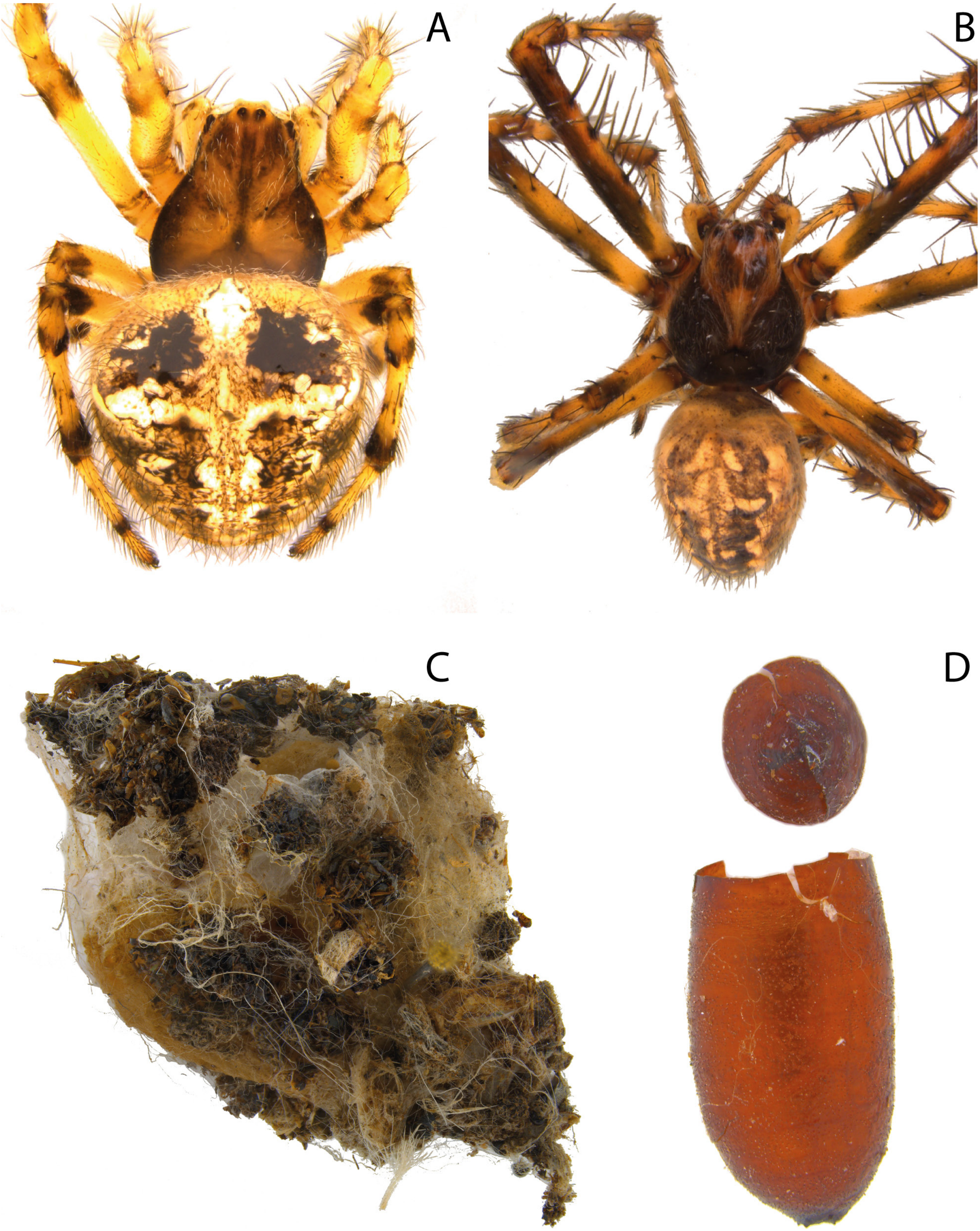

Fig. 1. Record of *Sarcophaga* (*Mehria*) *lorosa* Hall (Diptera: Sarcophagidae) in *Metepeira galatheae* (Thorell) (Araneae: Araneidae). A–C, Female, male, and egg sac of *M. galatheae*, respectively; D, Puparium of *S.* (*M.*) *lorosa*.

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references citing only previous records were not included. The classification of Sarcophagidae follows Pape (1996), and the classification of spiders follows Gloor et al. (2017).

Digital images were taken using a Leica MC170 HD digital camera attached to a Leica S8AP0 stereomicroscope with an LED illumination dome (Kawada and Buffington 2016). Multiple layers were stacked using the software Helicon Focus A8.1.0.0. Distributional data of *S.* (*M.*) *lorosa* were obtained directly from the labels and plotted on a map using SimpleMappr (Shorthouse 2010). When necessary,

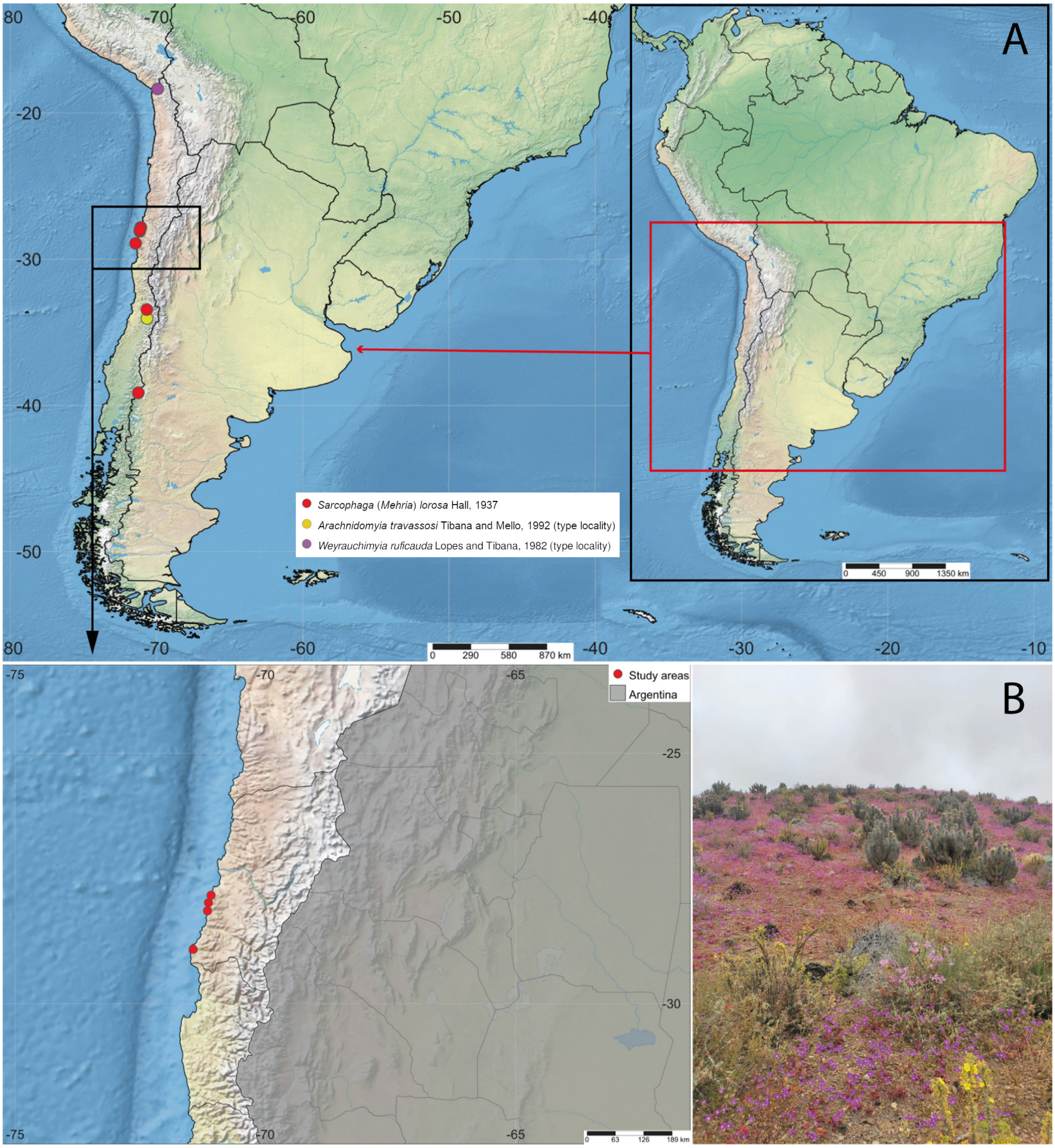

Fig. 2. A, Distribution map of *Sarcophaga* (*Mehria*) *lorosa* Hall, highlighting the type localities of the junior synonyms *Arachnidomyia travassosi* Tibana and Mello, syn. nov., and *Weyrauchimyia ruficauda* Lopes and Tibana, syn. nov.; B, Study areas in the Atacama region, Chile, during a desert bloom. Map created with SimpleMappr (https://www.simplemappr.net/).

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coordinates were estimated using Global Gazetteer Version 2.3.

RESULTS

Records of *Sarcophaga* (*Mehria*) *lorosa* in egg sacs of *Metepeira galatheae*

A total of 21 egg sacs of *M. galatheae* were collected and reared. Six specimens of *S.* (*M.*) *lorosa* emerged from two egg sacs (Fig. 4): four flies (4 ♂) emerged between 27–28 November 2022 from one egg sac collected on 16 November 2022, and two flies (1 ♂ and 1 ♀) emerged on 30 November 2022 from one egg sac collected on 16 November 2022. We verified that no flies emerged from the remaining 19 egg sacs and manually opened them to search for fly puparia. Nineteen hatched puparia were found in seven egg sacs (Fig. 1D): Two egg sacs with one puparium, three egg sacs with two puparia, one egg sac with five puparia, and one egg sac with six puparia. One egg sac had a puparium and a dead specimen of *S.* (*M.*) *lorosa*. Therefore, approximately 42% of the egg sacs had been attacked by *S.* (*M.*) *lorosa*.

TAXONOMY

Sarcophagidae Macquart, 1834
Subfamily Sarcophaginae Macquart, 1835
Genus *Sarcophaga* Meigen, 1824
Subgenus *Mehria* Enderlein, 1928

Sarcophaga (*Mehria*) *lorosa* Hall, 1937

(Figs. 2A, 3, 4)

Sarcophaga lorosa Hall, 1937: 367. Holotype male (NHMUK), examined (Fig. 3A, C, E). Type locality: Chile, Santiago.

Weyrauchimyia ruficauda Lopes and Tibana, 1982: 142. Holotype male (MNRJ, lost). Type locality: Chile, Arica y Parinacota [as Tarapacá], Lluta. [Junior secondary homonym of *Sarcophaga ruficauda* Zetterstedt, 1838.]. Syn. nov.

Arachnidomyia travassosi Tibana and Mello, 1992: 293. Holotype male (CNC), examined (Fig. 3B, D, F). Type locality: Chile, O'Higgins, La Leonera. Syn. nov.

Material examined: **Argentina**: 1 ♂ (MACN): Neuquén, Parque Nacional Lanín, Ñorquinco, S 39°09,073 W 71°15,475, trampa Malaise, 9.i.2013, Olea, Mulieri and Patitucci leg.; **Chile**: 5 ♂, 1 ♀ (UCM): Huasco Province, Parque Nacional Llanos del Challe, 28°08'55"S, 71°09'24"W, reared from *Metepeira galatheae* egg sacs, 27–30.xi.2022, D.G. Pádua et al. leg.

Diagnosis: Distinguished from the other New World species of subgenus *Mehria* by the following morphological features: (1) face with deep golden-yellow pruinosity, (2) wing vein R_1 with setae, (3) abdominal tergite 5 reddish or yellow, and (4) genital segments (syntergosternite 7+8 and epandrium) reddish. Phallic morphology most similar to *S.* (*M.*) *guyanensis* Lopes and *S.* (*M.*) *lindae* Lopes, but separable from *S.* (*M.*) *lindae* by the median stylus of similar length to the lateral styli and its vesica shorter than width of distiphallus; and separable from *S.* (*M.*) *guyanensis* by the shape of juxta slightly folded dorsoapically, not rounded (see Lopes 1946: 125, fig. 15).

Males (Fig. 4A, C, E, G, H): Body length: 7–8 mm. Wing length: 5.5–6 mm (*n* = 6).

Head (Fig. 4E): Parafacial, fronto-orbital plate, and postocular orbits with silvery gray pruinosity; frontal vitta blackish; face with deep golden-yellow pruinosity. Facial ridge setose on lower half; fronto-orbital plate and parafacial with row of setulae close to eye, parafacial with additional row of setulae in lower half. Frons 0.15–0.18 head width at level of ocellar triangle. Antenna black; first flagellomere approximately twice pedicel length; arista short plumose on proximal half. Frontal setae 10–12, well-developed, row reaching level of apex of pedicel; rows of frontal setae parallel for most of their length, diverging at the level of antennal insertion. Two reclinate orbital setae; proclinate orbital setae absent; ocellar setae developed and proclinate; outer vertical seta undifferentiated from postocular setae. Gena with silver pruinosity, covered with black setulae; genal groove blackish; postgena with silver pruinosity, covered with black setulae. Palpus, prementum, and labella blackish.

Thorax (Fig. 4A, C): Black with silvery-gray pruinosity. Acrostichal setae 2+1; dorsocentral setae 2+3; intra-alar setae 1+2; supra-alar setae 2+3; postpronotal setae 3–4; notopleural setae 4. Postalar wall setulose. Postalar callus with 2 setae. Proepisternum bare. Katepisternal setae 3. Scutellum with a pair of basal and subapical setae; apical setae present; discal setae absent. Wing: Tegula black; basicosta yellowish; veins brown. Costal spine not developed; third costal sector setulose ventrally; vein R_1 with setae dorsally; vein R_{4+5} with setulae dorsally from base to crossvein r-m. Cell r_{4+5} open at wing margin. Legs: Black, except for brown tarsi. Mid femur without ctenidium; mid tibia with 1 median anterior seta; posterior femur with anterodorsal row, and anteroventral row with stronger setae on median surface; posterior tibia with three dorsal setae, one anterior row, and three ventral setae. Tarsal claws long, subequal to length of tarsomere 5.

Abdomen (Fig. 4A, C): Syntergite 1+2 to tergite 4 black with silvery-gray pruinosity; tergite 5 reddish.

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Tergites 2 and 3 without median marginal setae; tergite 4 with complete row of marginal setae; tergite 5 with row of marginal setae. Sternite 5 slightly reddish and V-shaped, with fringe of setae along the median margin of each arm.

Terminalia (Fig. 4G, H): Syntergosternite 7+8 and epandrium reddish. Syntergosternite 7+8 with three pairs of setae. Cercus apically curved and pointed.

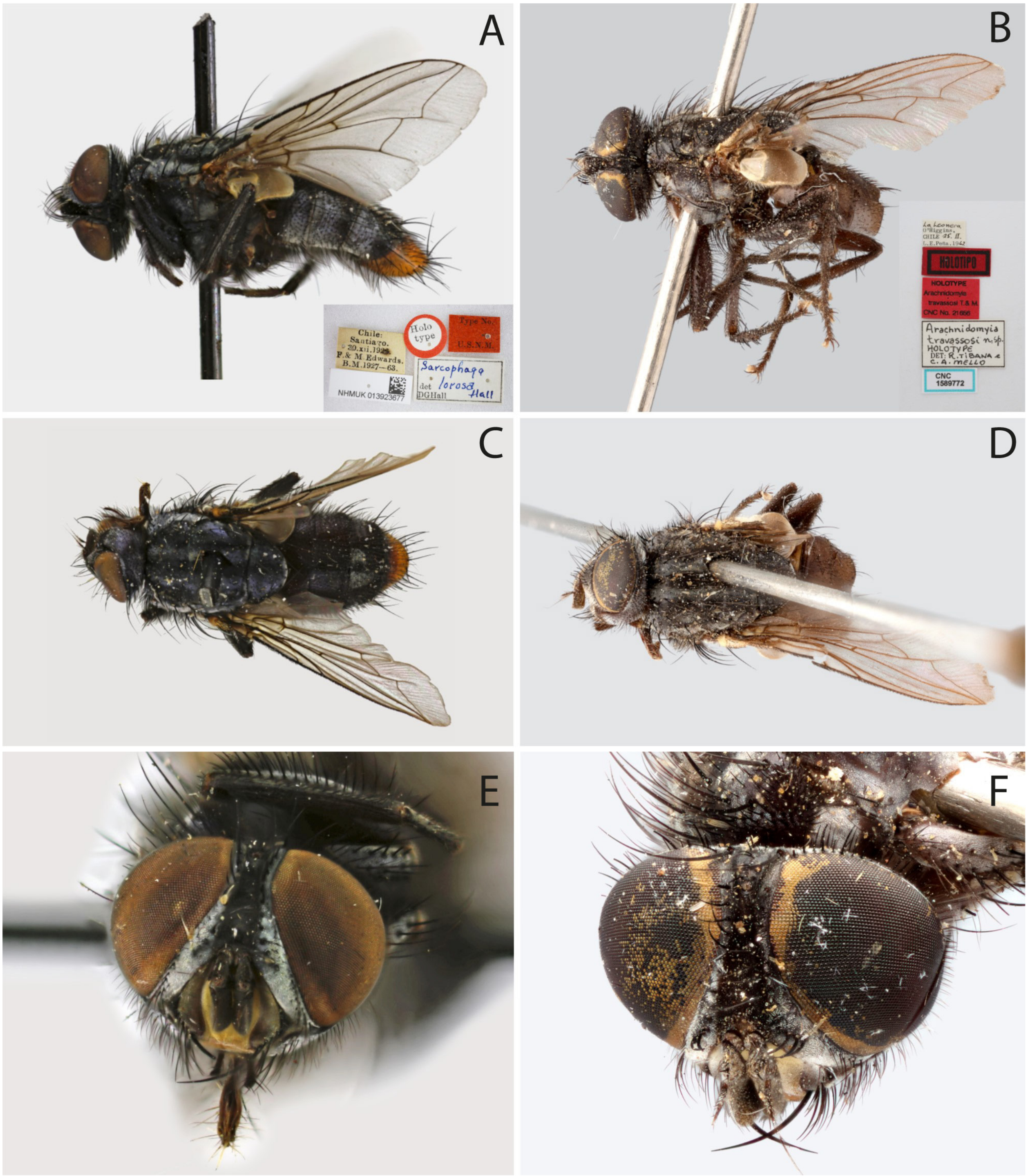

Fig. 3. Holotype male of *Sarcophaga lorosa* Hall (NHMUK) and holotype male of *Arachnidomyia travassosi* Tibana and Mello (CNC), respectively. A, B: Lateral habitus and labels; C, D: Dorsal habitus; E, F: Head in frontal view.

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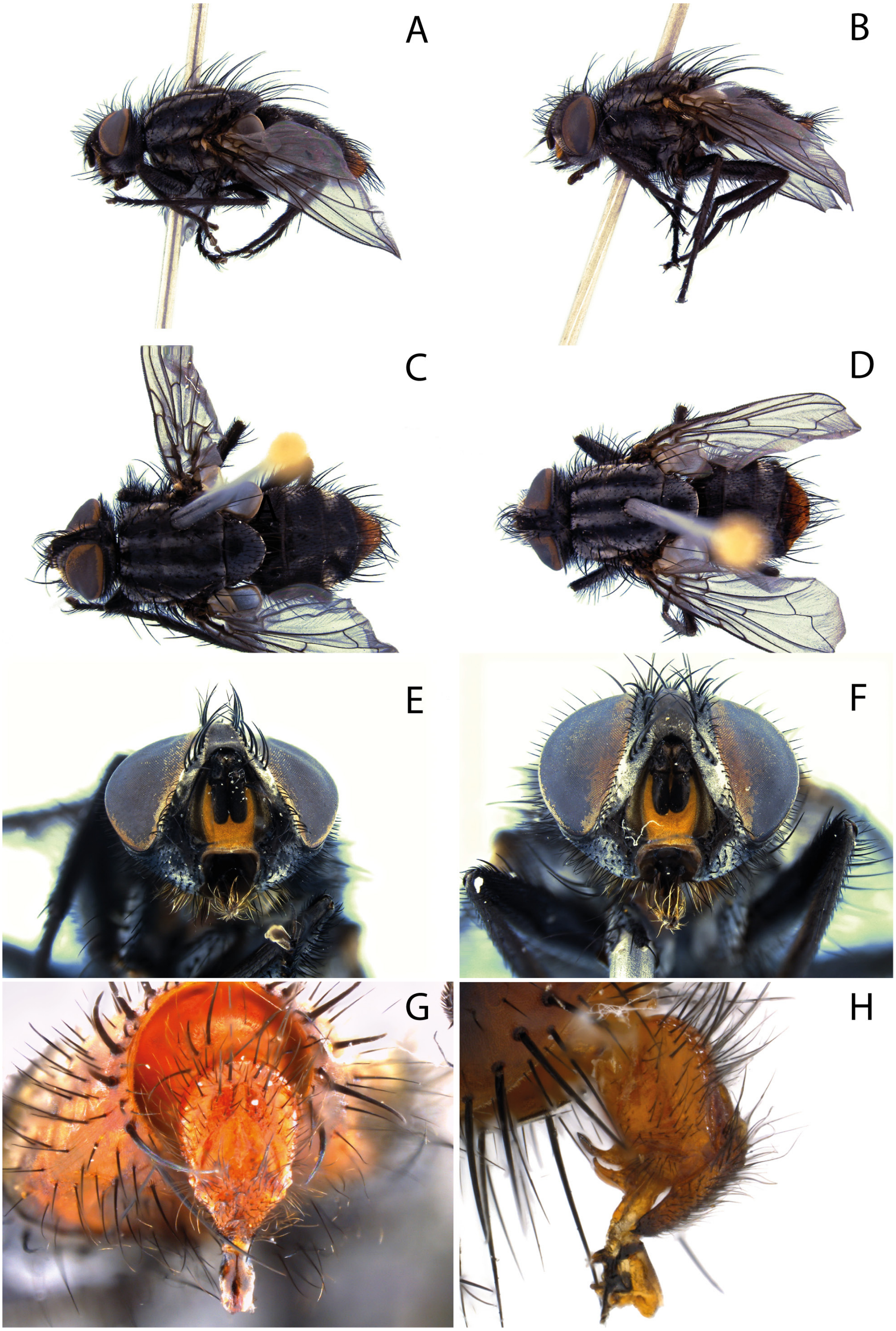

Fig. 4. *Sarcophaga* (*Mehria*) *lorosa* Hall specimens reared from egg sacs of *Metepeira galatheae* (Thorell). A, C, E, G, H: Lateral habitus, dorsal habitus, head in frontal view, terminalia in posterior view, and terminalia in lateral view of male, respectively; B, D, F: Lateral habitus, dorsal habitus, and head in frontal view of female, respectively.

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Pregonite with rounded and well-sclerotized apex, postgonite with short setulae. Phallus with vesica bifid, short; lateral stylus well-sclerotized; juxta rounded apically, slightly folded dorsoapically.

Female (Fig. 4B, D, F): Differs from male as follows: Body length: 8 mm. Wing length: 6.5 mm (n = 1). Frons 0.27 head width at level of ocellar triangle. Frontal setae 8; reclinate setae 2, with posterior seta lateroclinate; proclinate orbital setae 2; inner vertical setae parallel; outer vertical seta about 2/3 inner vertical seta. Tarsal claws shorter than tarsomere 5.

Distribution: Argentina (Neuquén) and Chile (Arica y Parinacota, Atacama, O'Higgins, Región Metropolitana de Santiago) (Fig. 2A).

Remarks: We propose *W. ruficauda* and *A. travassosi* as junior synonyms of *S. lorosa* Hall. Both nominal species share the above enumerated external characters of color of face pruinosity, wing vein R_1, abdominal tergite 5, and genitalia with *S. lorosa*. They also share a short, bifid vesica, and juxta slightly folded dorsoapically, which are here considered to provide a conspecific match. Pape (1996) transferred *W. ruficauda* to *Sarcophaga* and proposed *A. travassosi* as its synonym, keeping *S.* (*M.*) *travassosi* (Tibana and Mello) as the valid name because of the secondary homonymy between *S.* (*M.*) *ruficauda* (Lopes and Tibana) and *Sarcophaga ruficauda* Zetterstedt. Unfortunately, the holotype male of *W. ruficauda* was lost in the fire that consumed most of the MNRJ entomological collection (Cunha 2018; Escobar 2018).

Further clarification is required regarding the type locality of *A. travassosi*. Pape (1996) recorded the city of La Leonera in the Biobío region as the type locality. However, the holotype label explicitly states the city La Leonera in the O'Higgins region (Fig. 3B), which is more than 400 km north of La Leonera in the Biobío region. The exact locality can be verified by consulting the works of the Chilean entomologist Luis Enrique Peña, the collector of the holotype. Peña (1974) listed the type locality of several insects collected by him and included two localities in O'Higgins: La Leonera and Cerro Poqui. Cerro Poqui is a hill located at the border of the regions O'Higgins and Región Metropolitana de Santiago, which shows that Peña used O'Higgins as a reference to the O'Higgins region. Thus, there is no reason to consider that Peña was not accurate when recording La Leonera in the O'Higgins region.

The golden-yellow pruinosity on the face of *S.* (*M.*) *lorosa* is not commonly seen in Sarcophagidae and is not present in Nearctic and Palaearctic species of *Mehria*. In the Neotropical region, only *S.* (*M.*) *insularis* Lopes has the face and frontal vitta slightly golden-yellow (Lopes 1946), but lacks setae on vein R_1.

Based on the specimens examined here, the distribution of *S.* (*M.*) *lorosa* seems to be restricted to southwestern South America, specifically on the western side of the Andes Mountains (Fig. 2A).

Annotated catalog of records of spider egg-predating Sarcophagidae

Four species of the subgenus *Baranovisca* have been recorded as egg predators from at least four species of Araneidae; and 10 species of the subgenus *Mehria* have been recorded from at least 13 species of the families Araneidae, Cheiracanthiidae, Clubionidae, Philodromidae, Salticidae, and Tetragnathidae (Table 1). Records are from all biogeographical regions except the Afrotropical.

Australasian Region

Sarcophaga (*Baranovisca*) *arachnivora* Lopes

From egg sacs of *Ordgarius magnificus* (Rainbow).

Recorded by Lopes (1985: 51, as *B. arachnivora*) as a parasite in egg sacs of *Dicrostichus magnificus* Rainbow [= *O. magnificus* (Rainbow)]) in Hornsby Heights, New South Wales, Australia.

Sarcophaga (*Baranovisca*) *cyrtophorae* Cantrell

From egg sacs of *Cyrtophora moluccensis* (Doleschall).

Recorded by Lubin (1974: 329, as an unidentified Sarcophagidae [identified later by Yefremova and Lubin (2020)]) as preying on eggs of *C. moluccensis* (Doleschall) at Wau Ecology Institute, Wau, Morobe, Papua New Guinea; by Cantrell (1980: 42, as *Parasarcophaga reposita* Lopes [misidentification, see Cantrell (1986)]) as preying on eggs of *C. moluccensis* in Brisbane, Queensland, Australia; by Cantrell (1981: 29, as *P. reposita* Lopes [misidentification, see Cantrell (1986)]) as preying on eggs of *C. moluccensis* in Queensland, Australia, and Papua New Guinea [locality not specified]; by Cantrell (1986: 3, as *Parasarcophaga cyrtophorae*) as preying on eggs of *C. moluccensis* in Brisbane, Queensland, Australia; and by Yefremova and Lubin (2020: 3) as preying on eggs of *C. moluccensis* at Wau Ecology Institute, Wau, Morobe, Papua New Guinea.

Sarcophaga (*Baranovisca*) *reposita* Lopes

From egg sacs of an unidentified spider.

Recorded by Lopes (1959: 65, as *Parasarcophaga* (*Rosellea*) *reposita*) as preying on eggs of an

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unidentified spider in Sidney, New South Wales, Australia.

Nearctic Region

Sarcophaga (*Mehria*) *davidsonii* Coquillett

From egg sacs of *Argiope argentata* (Fabricius) and *Phidippus octopunctatus* (Peckham and Peckham).

Recorded by Coquillett (1892: 24) as preying on eggs of *Phidippus opifex* (McCook) [= *Attus opifex* McCook = *Attus octopunctatus* Peckham and Peckham = *Phidippus octopunctatus* (Peckham and Peckham)] in Los Angeles, Los Angeles County, California, United States of America; and by Davidson (1894: 269) as preying on eggs of *A. argentata* (Fabricius) in Santa Catalina Island and Redondo Beach, Los Angeles County, California, United States of America.

Sarcophaga (*Mehria*) *hinei* Aldrich

From egg sacs of *Larinioides cornutus* (Clerck), *L. sclopetarius* (Clerck), and *Philodromus cespitum* (Walckenaer).

Recorded by Auten (1925: 244) as preying on eggs of *Aranea frondosa* Comstock [as Walckenaer, error] [= *Araneus cornutus* Clerck = *L. cornutus* (Clerck)], *Epeira sclopetaria* (Clerck) [= *Araneus sclopetarius* = *L. sclopetarius*], and *Philodromus canadensis* Emerton [= *Aranea cespitum* Walckenaer = *P. cespitum* (Walckenaer)]) in Put-In-Bay region, Ottawa County, Ohio, United States of America.

Remarks: Gillung and Borkent (2017) listed these records for *S.* (*M.*) *sexpunctata* (Fabricius) as a senior synonym of *S.* (*M.*) *hinei*, following the classification in Systema Dipterorum (Evenhuis and Pape 2022). However, this synonymy has never been published and both nominal species are considered as valid in Pape (1996). They also included *P. aureolus* (Clerck) as prey of *S.* (*M.*) *hinei* as a record made by Auten (1925), but there is no record of this spider species in the original article.

Sarcophaga (*Mehria*) *subaenescens* Aldrich

From egg sacs of an unidentified spider.

Table 1. List of spider egg-predating Sarcophagidae and their respective prey according to biogeographical regions. Details about records, localities, and respective references can be found in the catalog in the main text

Sarcophagidae species	Araneae species
Australasian Region	
Sarcophaga (*Baranovisca*) *arachnivora*	Araneidae: *Ordgarius magnificus*
Sarcophaga (*Baranovisca*) *cyrtophorae*	Araneidae: *Cyrtophora moluccensis*
Sarcophaga (*Baranovisca*) *reposita*	Unidentified spider
Nearctic Region	
Sarcophaga (*Mehria*) *davidsonii*	Araneidae: *Argiope argentata*
	Salticidae: *Phidippus octopunctatus*
Sarcophaga (*Mehria*) *hinei*	Araneidae: *Larinioides cornutus*
	Araneidae: *Larinioides sclopetarius*
	Philodromidae: *Philodromus cespitum*
Sarcophaga (*Mehria*) *subaenescens*	Unidentified spider
Neotropical Region	
Sarcophaga (*Mehria*) *guyanensis*	Araneidae: *Argiope* sp.
Sarcophaga (*Mehria*) *insularis*	Unidentified spider
Sarcophaga (*Mehria*) *lindae*	Araneidae: *Metepeira atascadero*
	Araneidae: *Metepeira incrassata*
Sarcophaga (*Mehria*) *lorosa*	Araneidae: *Metepeira galatheae*
Sarcophaga (*Mehria*) *silbergliedi*	Araneidae: *Argiope argentata*
	Tetragnathidae: *Tetragnatha* sp.
Sarcophaga (*Mehria*) sp.	Araneidae: *Argiope trifasciata*
Oriental Region	
Sarcophaga (*Baranovisca*) *banksi*	Araneidae: *Argiope catenulata*
	Araneidae: *Argiope pulchella*
Palaearctic Region	
Sarcophaga (*Mehria*) *sexpunctata*	Araneidae: *Larinioides cornutus*
	Clubionidae: *Clubiona* sp.
	Cheiracanthiidae: *Cheiracanthium punctorium*

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Recorded by Aldrich (1925: 28) as preying on eggs of an unidentified spider in Somerville, Somerset County, New Jersey, United States of America.

Unidentified *Sarcophaga* Meigen

From egg sacs of *Larinioides cornutus* (Clerck).

Recorded by Kaston and Jenks (1937: 161, as *Sarcophaga* sp. (*hinei*?)) as preying on eggs of *Epeira cornuta* (Clerck) [= *Araneus cornuta* Clerck = *L. cornutus* (Clerck)] in West Haven, New Haven County, Connecticut, United States of America.

Neotropical Region

Sarcophaga (*Mehria*) *guyanensis* Lopes

From egg sacs of unidentified *Argiope* Audouin.

Recorded by Lopes (1946: 126, as *Arachnidomyia guyanensis*) as preying on eggs of unidentified *Argiope* Audouin in Berbice, Guyana.

Sarcophaga (*Mehria*) *insularis* Lopes

From egg sacs of an unidentified spider.

Recorded by Lopes (1946: 125, as *Arachnidomyia insularis*) as preying on eggs of an unidentified spider [as an epeirid spider] in Haiti [locality not specified].

Sarcophaga (*Mehria*) *lindae* Lopes

From egg sacs of *Metepeira atascadero* Piel and *M. incrassata* Pickard-Cambridge.

Recorded by Lopes (1989: 1098, as *Arachnidomyia lindae*) as preying on eggs of *M.* cf. *atascadero* Piel and *M. incrassata* Pickard-Cambridge in Fortin de las Flores, Veracruz, Mexico; and by Hieber and Uetz (1990: 146, as *A. lindae*) as preying on eggs of *M. atascadero* and *M. incrassata* in San Miguel de Allende, Guanajuato, and Fortin de las Flores, Veracruz, Mexico.

Sarcophaga (*Mehria*) *lorosa* Hall

From egg sacs of *Metepeira galatheae* (Thorell).

New record by Gudin et al. as preying on eggs of *M. galatheae* (Thorell) in Copiapó and Huasco, Atacama, Chile.

Sarcophaga (*Mehria*) *silbergliedi* Lopes

From egg sacs of *Argiope argentata* (Fabricius) and unidentified *Tetragnatha* Latreille.

Recorded by Lopes (1981: 310, as *Arachnidomyia silbergliedi*) as preying on eggs of unidentified *Tetragnatha* Latreille in Madden Lake, Canal Zone, Panama; and by Miranda et al. (2020: 10) as preying on eggs of *A. argentata* (Fabricius) in Cerro Azul, Panama City, Panama District, Panama.

Unidentified *Sarcophaga* Meigen

From egg sacs of *Argiope trifasciata* (Forsskål)

Recorded by Armas and Alayón García (1986: 116, as unidentified *Sarcophagula* Wulp [misidentification]) as a parasitoid in egg sacs of *A. trifasciata* (Forsskål) in San Antonio de los Baños, La Habana, Cuba.

Remarks: *Sarcophagula* is a subgenus of *Tricharaea* Thomson including mostly saprophagous and coprophagous species (Pape and Dahlem 2010; Patitucci et al. 2015). Therefore, the specimens recorded in egg sacs of *A. trifasciata* were misidentified and probably belong to *Sarcophaga*, subgenus *Mehria*.

Oriental Region

Sarcophaga (*Baranovisca*) *banksi* Senior-White

From egg sacs of *Argiope catenulata* (Doleschall) and *A. pulchella* Thorell.

Recorded by Prakash and Pandian (1978: 210) as preying on eggs of *A. pulchella* Thorell in Idumban Pond, Ayakudi, Tamil Nadu, India; and by Shinonaga and Barrion (1980: 538, as *Pierretia litsingeri* Shinonaga and Barrion [= *S. banksi* Senior-White]) as preying on eggs of *A. catenulata* (Doleschall) in Laguna, Luzon, Philippines.

Palaearctic Region

Sarcophaga (*Mehria*) *sexpunctata* (Fabricius)

From egg sacs of *Cheiracanthium punctorium* (Villers), unidentified *Clubiona* Latreille, and *Larinioides cornutus* (Clerck).

Recorded by Bertkau (1880: 332, as unidentified *Tachina* Meigen [misidentification; identified later by Mik (1890: 153) as *Sarcophaga clathrata* Meigen = *S.* (*M.*) *sexpunctata*, and confirmed by Herting (2017)]) as preying on eggs of *Epeira cornuta* (Clerck) [= *Araneus cornuta* Clerck = *L. cornutus* (Clerck)] in Bonn, North Rhine-Westphalia, Germany; by Kryger (1910: 267, as unidentified *Sarcophaga* Meigen [identified later by Lundbeck (1927: 181) as *S. clathrata* = *S.* (*M.*) *sexpunctata*]) as preying on eggs of *Epeira cornuta* (Clerck) [= *Araneus cornuta* Clerck = *L. cornutus* (Clerck)] in Gribskov and Hareskoven, Zealand, Denmark; by Grunin (1964: 71, as *Thyrsocnema clathrata* = *S.* (*M.*) *punctata*) as preying on eggs of

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unidentified *Clubiona* Latreille in Ural, Russia; by Finch (2005: 2345) as preying on eggs of *L. cornutus* in Oldenburg, Lower Saxony, Germany; and by Krehenwinkel et al. (2016: 1235) as preying on eggs of *C. punctorium* (Villers) in Italy [locality not specified].

DISCUSSION

Spider egg-predating Sarcophagidae show diverse prey selection. Although the majority of records are from Araneidae, *S.* (*M.*) *davidsonii*, *S.* (*M.*) *hinei*, *S.* (*M.*) *sexpunctata*, and *S.* (*M.*) *silbergliedi* attack prey from different families of Araneomorphae (Table 1). Consequently, prey choice does not seem to be correlated with a particular spider taxon. Previous studies by Lubin (1974) and Hieber and Uetz (1990) demonstrated a positive correlation between the rate of predation and colony size in the social spiders *C. moluccensis* and *M. incrassata*, respectively. However, it is worth noting that prey choice is not exclusively associated with social spiders, as most of the records reviewed here are on solitary species.

Prey choice by predating flies may be determined by the conspicuousness and exposure level of spider egg sacs. The diversity in the shape and structure of egg sacs has been considered a significant adaptation to evade or reduce the success of parasitoids and predators (Austin 1985; Hieber 1992; Cloudsley-Thompson 1995). Hieber (1992) showed that predators that burrow into spider egg sacs, such as fly larvae, achieve higher success rates when attacking loosely woven or flocculated egg sacs than for those with denser coverings. This evidence indicates that egg sacs serve as a protective barrier against parasitoids and predators, requiring them to overcome this barrier to reach the eggs. Furthermore, in the case of the social spider *C. moluccensis*, Lubin (1974) observed that females of *S.* (*B.*) *cyrtophorae* closely inspected only webs with egg sacs within the entire colony, suggesting that these flies are attracted by the presence of conspicuous egg sacs. The egg sacs of spider species attacked by Sarcophagidae are typically conspicuous and are placed in freely exposed areas by the spider: They can be found attached to the spider web, as observed in species such as *A. argentata*, *A. pulchella*, *C. moluccensis*, and *M. incrassata* (Lubin 1974; Prakash and Pandian 1978; Hieber and Uetz 1990; Miranda et al. 2020); hanging from leaves, as in *A. catenulata* and *O. magnificus* (Todd 1988; Brown and Henderson 2019); or found attached to the vegetation, like in *P. octopunctatus* (Edwards 2004).

Although the structure and position of egg sacs provide valuable insights into the prey selection of spider egg-predating flies, the evolutionary pathways that led to this association in the *Sarcophaga* subgenera *Baranovisca* and *Mehria* remain unclear because of the absence of a phylogenetic framework. A few *Mehria* species have been sampled in phylogenetic studies aimed at elucidating the relationships within the subgenera of *Sarcophaga* (Giroux et al. 2010; Piwczyński et al. 2014; Buenaventura et al. 2017; Buenaventura and Pape 2017). However, the monophyly of *Mehria* has not been confirmed. On the other hand, *Baranovisca* species have never been sampled in phylogenetic studies of Sarcophagidae. Buenaventura (2021) proposed the first phylogenetic hypothesis of Sarcophagidae based on protein-encoding ultraconserved elements, revealing that *S.* (*M.*) *sexpunctata* is strongly supported as the basal taxon within a clade that is sister to the subgenus *Pandelleana* Rohdendorf, confirming previous findings (Piwczyński et al. 2014). In this context, larvae of *Mehria* and *Pandelleana* share similar predatory habits, as larvae of *Pandelleana* species are predators of lizard eggs (Pape and Arribas 1999). While this phylogenetic position may indicate a shared predatory habit in the most recent common ancestor of *Mehria* and *Pandelleana*, a larger sampling of both *Mehria* and *Baranovisca* species is required to confirm the robustness of these relationships and to clarify the evolution of Sarcophagidae-Aranae interactions.

Despite this, some evidence indicates that the interactions between spider egg-predating Sarcophagidae and their prey might be a product of coevolution. Hieber et al. (2002) documented a set of stereotyped behaviors exhibited by *S.* (*M.*) *lindae* and *M. incrassata* females as a reaction to each other. As soon as the fly approached the web, the spider started to swing its legs towards the fly and protect the egg sac, grooming it with its chelicerae and pedipalps. In response, the fly tried to lure the spider out of the egg sac by landing on the hub or signal line of the web and mimicking the vibrations of captured prey. Moreover, the spider can distinguish the wing-beat vibrations of *S.* (*M.*) *lindae* from those of other flies. Although these behavioral patterns suggest that the interaction between these two species is a result of coevolution, further studies involving diverse populations and other species of spider egg-predating Sarcophagidae are required to determine the degree of specialization in the relationship between predator and prey.

Lastly, literature records mention spider egg-predating Sarcophagidae either as a parasitoid or as a predator. Hieber et al. (2002) provided an interesting perspective on the nature of this ecological interaction based on observations of the ovi/larviposition behavior of *S.* (*M.*) *lindae* in *M. incrassata.* They argued that the behavior of these flies resembles that of a parasitoid-host system, as the female approaches the egg sac as a suitable host for larval development. However, the fly larvae feed on spider eggs within the sac, which is best described as predatory behavior. Buenaventura (2021) estimated the diversification of larval feeding habits in Sarcophagidae, considering the parasitoid habit as a variation of predation. Although the habits are interconnected, a more precise classification may be necessary to explain the transition between parasitic and predatory habits across the diverse lineages of Sarcophagidae.

CONCLUSIONS

The evolution of Sarcophagidae-Araneae interactions still has much to be clarified, but some hypotheses discussed here can guide future studies. The subgenus *Mehria* includes 14 valid species, with *S.* (*M.*) *lorosa* as the sole species distributed in southwestern South America, specifically on the western side of the Andes Mountains. At least four *Baranovisca* and 10 *Mehria* species have been documented in the families Araneidae, Cheiracanthiidae, Clubionidae, Philodromidae, Salticidae, and Tetragnathidae. Prey selection by spider egg-predating Sarcophagidae does not seem to be correlated with a particular spider taxon; rather, the conspicuousness and exposure level of spider egg sacs may offer a more plausible explanation for prey selection by female flies. Larger sampling of *Baranovisca* and *Mehria* species in phylogenetic studies is required to confirm the validity of both subgenera and to estimate the origin of this predatory behavior in Sarcophagidae.

List of abbreviations

CNC, Canadian National Collection of Insects, Ottawa, Canada.
MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.
MNRJ, Museu Nacional, Rio de Janeiro, Brazil.
NHMUK, Natural History Museum, London, United Kingdom.
UCM, Laboratorio de Ecología de Abejas, Talca, Chile.
UNAP, Universidad Arturo Prat, Iquique, Chile.

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Competing interests: The authors declare that there are no competing interests.

Availability of data and materials: Holotypes of Sarcophaga lorosa Hall and Arachnidomyia travassosi Tibana and Mello are deposited in Natural History Museum, London, United Kingdom, and Canadian National Collection of Insects, Ottawa, Canada, respectively. Additional material examined of S. (Mehria) lorosa is deposited in Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina, and Laboratorio de Ecología de Abejas, Talca, Chile.

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