

Carmine cochineal killers: the flower fly genus *Eosalpingogaster* Hull (Diptera: Syrphidae) revised

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Abstract. The flower fly genus *Eosalpingogaster* Hull, predator of the carminic acid producer cochineal (Dactylopiidae), is revised. Two new species are described (*knutsoni* sp.n. and *umbra* sp.n.) and an identification key is provided for all known species. Diagnoses, illustrations, synonymies and distributional and biological data are given. Three new synonyms are proposed [*texana* Curran as **jun.syn.** of *cochenillivora* (Guérin-Méneville); *liposeta* Fluke and *dactylopianus* Blanchard as **jun.syn.** of *nigriventris* (Bigot)] and two lectotypes are designated for *cochenillivora* (Guérin-Méneville) and *nigriventris* (Bigot). *Eosalpingogaster* is elevated to full generic status based on adult morphological characters, biological data and a new phylogenetic analysis of molecular characters with genes 28S, 18S and cytochrome *c* oxidase subunit I. All data, images and drawings are available online as an example of the utility of international standards for biodiversity informatics.

Introduction

The carmine cochineal or grana fina, *Dactylopius coccus* Costa (Hemiptera: Stenorrhyncha: Dactylopiidae), lives on cacti of the genus *Opuntia*, commonly known as prickly pear, nopal or tuna. Nymphs and adult males are crawlers, whereas adult females are sessile parasites sucking plant sap, but they can be also found on roots and fruits (Marín & Cisneros, 1977; Flores-Flores & Tekelenburg, 1995).

The cochineal scale produces carminic acid in different concentrations, from 18 to 30% expressed in dry weight, that deters predation by other arthropods (Eisner & Nowicki, 1980). All *Dactylopius* can produce cochineal, but domesticated cochineal (*D. coccus*), the largest species, produces the most carminic acid, of a better quality than that obtained from the other forms (Mann, 1969; Donkin, 1977; Portillo, 2005). The cactus used most commonly for rearing cochineal is *O. ficus-indica* (L.) Mill. (Donkin, 1977; Portillo, 2008a), although all *Opuntia* species and certain other cactus can be parasitized by scale insects (Zimmermann *et al.*, 1979; Moran & Zimmermann, 1991a; Portillo, 2008a).

Carmine was used in the dyeing of cloth and in medicine in the highlands of Central and South America before the Spanish

conquest (Humboldt, 1966; Donkin, 1977; Piña, 1977). Production peaked in the 1850s and 1870s, but diminished during the 1880s as new synthetic dyes rapidly superseded it (Mann, 1969; Donkin, 1977; Eisner & Nowicki, 1980). Carmine is now used in foods, pharmaceuticals, textiles and cosmetics and is known as colorant E-120 based on the European code (Flores-Flores & Tekelenburg, 1995; Dickens, 2010).

Dactylopius species can be considered either pests or biological control agents in their interaction with the genus *Opuntia* depending of the use of cacti by humans. On one hand, *Opuntia* species are used as fodder for cattle, for prickly pear production, or to produce raw material for medical preparations, cosmetic products, bio-gas or ethanol; some *Opuntia* species are consumed as vegetables and other species are used for cochineal cultivation (Chávez-Moreno *et al.*, 2009). In these cases, *D. opunitae* Cockerell, also known as wild cochineal, is considered a severe infestation in Brazil and Spain that provokes very important economic losses due to the damage on the *Opuntia* plants and the mix with domesticated cochineal (Esparza-Gómez *et al.*, 2008; Portillo, 2008b; Suassuna *et al.*, 2008). On the other hand, the same *Dactylopius* species and others play a positive role when they act as biological control agents in South Africa, Mauritius and Australia against weedy cacti, including *Opuntia* species (Haseler, 1966; Moran & Zimmermann, 1991a,b; Zimmermann & Moran, 1991; Hosking *et al.*, 1994; Volchansky *et al.*, 1999; Fowler *et al.*, 2000). Thus, the study of natural enemies of cochineal species and their host affinities is crucial.

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Natural enemies of *D. coccus* have been known since the 16th century (Gómez de Cervantes, 1599). Among them are immature stages of Lepidoptera, Coleoptera, Diptera and Neuroptera. Two dipteran families have been reported to feed on carmine cochineal: Chamaemyiidae (*Leucopis bellula* Williston) and Syrphidae (Mann, 1969; Gilreath & Smith, 1988; Portillo & Viguera, 1998). The first flower fly reported as a predator of carmine cochineal was due to Guérin-Méneville (1848a,b) who described a new fly species from Guatemala, *Baccha cochenillivora* Guérin-Méneville, whose larvae fed actively on domesticated cochineal. In reviewing the literature about syrphid flies as predators of cochineal, Esparza *et al.* (2008) concluded that the specimens identified as *Baccha Fabricius* (Mann, 1969; Piña, 1977) or as *Allograpta* Osten Sacken (Marín & Cisneros, 1983; Flores-Flores & Tekelburg, 1995) belong to *Eosalpingogaster* Hull, also known as gusano tambor ('drum worm') (Portillo, 2005; Esparza *et al.*, 2008; Portillo, 2008b).

Few studies exist on cochineal natural enemies (Gilreath & Smith, 1988; Portillo & Viguera, 1998, 2006; Esparza-Gómez *et al.*, 2008), and new host relationships might be expected (Grissell, 2004). Here we review the species of *Eosalpingogaster*, a natural enemy of cochineal species in the American continent, and present new biological data of the cochineal-syrphid relationship based on specimen information. Two new species are described (*E. knutsoni* and *E. umbra*), new synonyms are established and a diagnostic key for all known species is also provided, together with a complete catalogue of the species with full references to all critical literature. Bibliographical references for nomenclatural information not directly related to *Eosalpingogaster* are listed in Table S1 and are available from Systema Dipterorum (Pape & Thompson, 2010). We discuss the systematic rank of *Eosalpingogaster* and elevate to genus based on molecular evidence, adult morphology and biological data.

Systematics

Eosalpingogaster species are only found in the New World and mainly in the neotropics. *Eosalpingogaster* flower flies visit flowers for pollen and nectar and are presumably common pollinators, as are all the adults of the subfamily Syrphinae (Syrphidae). The larval biology of a few species is known: all are predators of sternorrhynchans, including of some pests (Rojo *et al.*, 2003).

Eosalpingogaster was proposed by Hull (1949: 299) as a new subgenus of *Salpingogaster* Schiner for *S. conopida* Philippi. Originally, it included also the species *S. nepenthe* Hull and *S. dactylopianus* Blanchard (= *nigriventris* Bigot). Hull based his decision on the absence of a sharp hook on anterior corners of the first abdominal segment and on the slight curvature of vein R_{4+5} (see Figs 3, 6). In contrast, the species of the genus *Salpingogaster* s.s. have the first abdominal tergum produced laterally into a strong spur and vein R_{4+5} strongly sinuate (see Figs 1, 2). In the last published catalogue of the Diptera of the Americas South of the U.S.A.,

Thompson *et al.* (1976) included another species, *S. liposeta* Fluke, and placed *S. macula* Schiner and *S. nigriventris* Bigot as synonyms of *S. conopida*.

The species of both groups, *Salpingogaster* and *Eosalpingogaster*, all share four characters: (i) vein M_1 very abruptly and strongly sinuated (Figs 2, 3); (ii) abdomen distinctly and strongly petiolate (Figs 1, 6, 7); (iii) postmetacoxal bridge complete; and (iv) femora with ventral spinose bristles (Figs 9, 13, 21). However, these taxa appear to have different natural histories as they attack different larval prey. *Eosalpingogaster* species feed mainly on scale insects (Coccoidea), but in contrast *Salpingogaster* species have been reported only as predators of spittlebugs (family Cercopidae) (Rojo *et al.*, 2003).

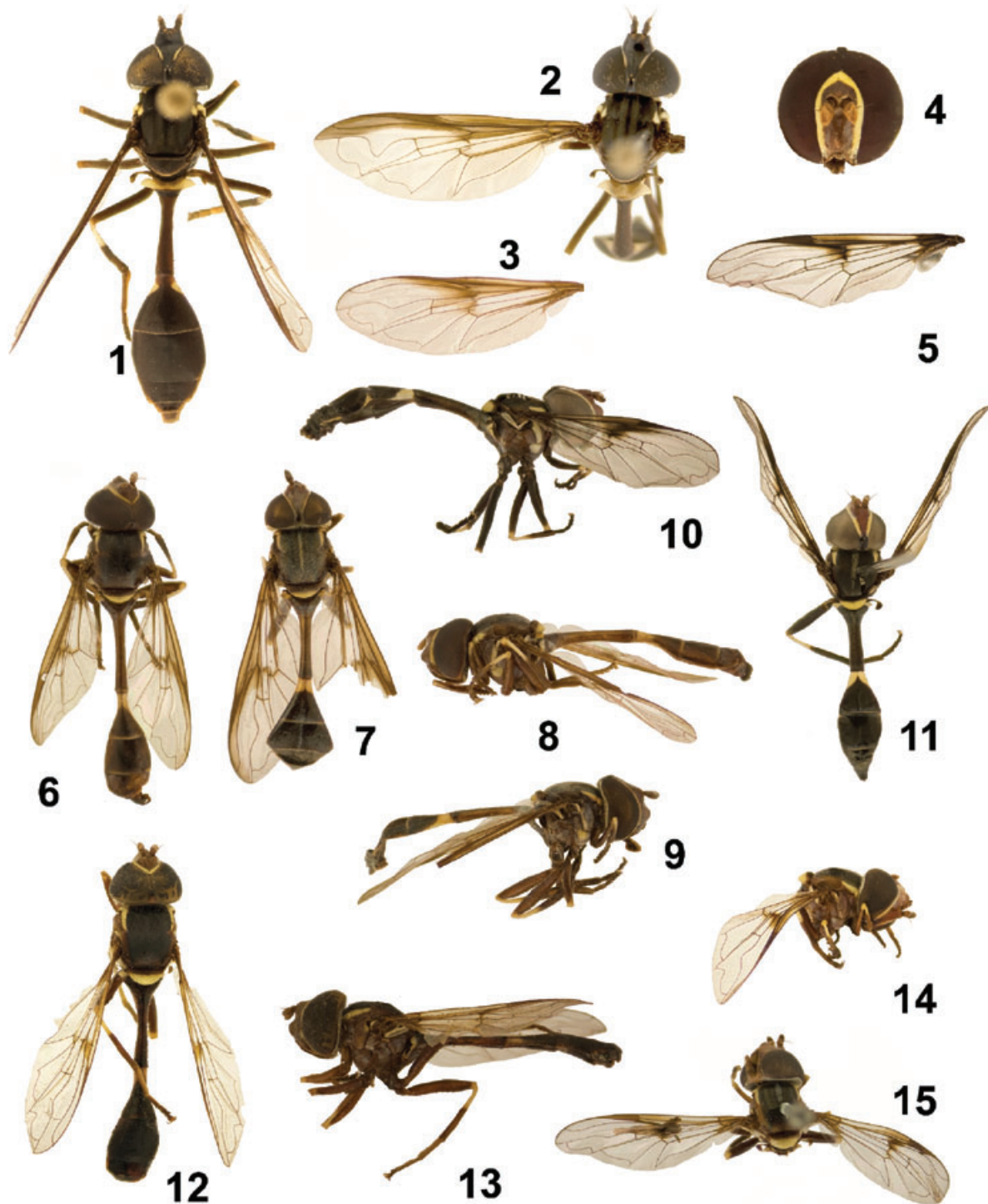
Materials and methods

Taxonomic revision

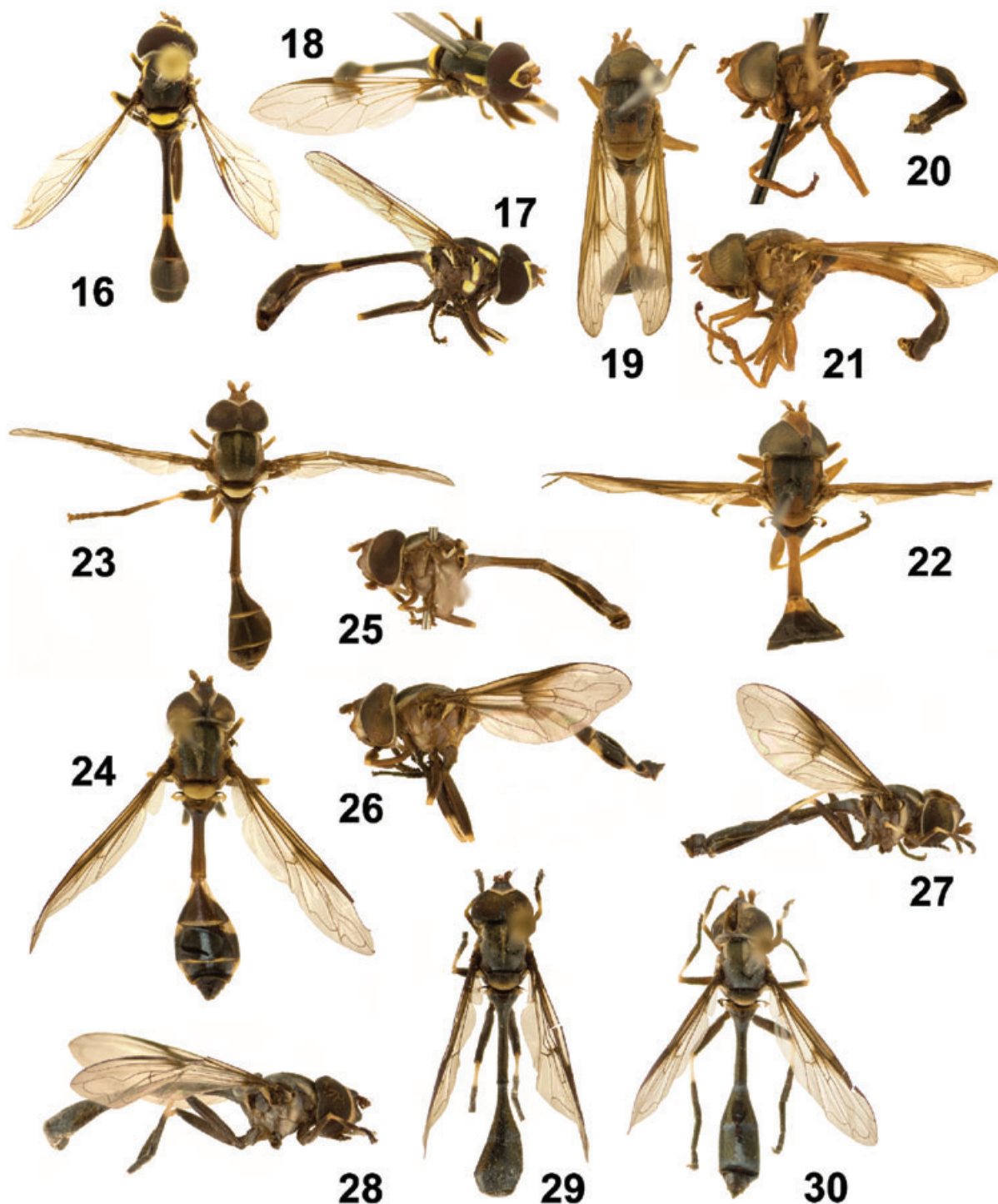
Diagnoses, complete synonymies, illustrations and distributions are given for all species of *Eosalpingogaster*. New species are described in full, with terminology following Thompson (1999). An asterisk (*) in the distribution statement signifies unverified records: the responsible is given in square brackets. In the material examined section, the use of ellipses follows standard English practice and merely indicates that the missing information is the same as that in the preceding record. The acronyms used for collections follow the standard of the *Systema Dipterorum* (Thompson, 2010), and their equivalents are given in the acknowledgements. In the description of type labels, the contents of each label is enclosed within quote marks (‘’) and the individual lines of data are separated by two forward slashes (//). Complete specimen data are given in Table S2. In the ‘Type locality’ paragraph, current country names and new data, such as province or district, are given, as well as geographical coordinates. Most of the specimens lack information about geographical coordinates on their labels, but we consider these data important to locate sampling points on a map. Google Earth was used to locate the type localities easily and to get the geographical coordinates used in this work. Distribution records can be viewed interactively in Google Earth (<http://earth.google.com/>) (Map S1).

All measurements are in millimetres and were taken using a reticule in a Wild M5A microscope. Illustrations of male genitalia were drawn using a camera lucida mounted on an Olympus BX51 compound microscope with the help of a Nikon SMZ1500 microscope. Manual drawings were redrawn as a vectorial image using Adobe Illustrator (version CS3). Illustrations of male and female abdomens were composed using the software COMBINEZP based on images of pinned specimens taken with a Canon EOS40D mounted on a Microptics Camlift and the help of Adobe Lightroom (version 2).

All images included in this publication have been deposited in MorphBank (<http://www.morphbank.net>). The direct hyperlink for each taxon is given and colour pictures of the species can be found in the online collections. New taxonomic names



Figs 1–15. 1, *Salpingogaster nigra*, female habitus [USNM ENT00037200]. 2, *S. nigra*, detail of thorax and wing [USNM ENT00037201]. 3, *Eosalpingogaster nigriventris*, wing [USNM ENT00036844]. 4, *E. knutsoni*, male head [USNM ENT00036811]. 5, *E. knutsoni*, female wing [USNM ENT00036889]. 6, *E. cochenillivora*, male habitus [USNM ENT00036835]. 7, *E. cochenillivora*, female habitus [USNM ENT00036825]. 8, *E. cochenillivora*, male lateral view [USNM ENT00036835]. 9, *E. cochenillivora*, female lateral view [USNM ENT00036825]. 10, *E. knutsoni*, female lateral view [USNM ENT00036889]. 11, *E. knutsoni*, female habitus [USNM ENT00036889]. 12, *E. conopida*, male habitus [USNM ENT00036807]. 13, *E. conopida*, male lateral view [USNM ENT00036807]. 14, *E. conopida*, female lateral view [USNM ENT00036809]. 15, *E. conopida*, female habitus [USNM ENT00036809].



Figs 16–30. 16, *Eosalpingogaster knutsoni*, male habitus [USNM ENT00036811]. 17, *E. knutsoni*, male lateral view [USNM ENT00036811]. 18, *E. knutsoni*, detail of thorax and wing [USNM ENT00036811]. 19, *E. nepenthe*, male habitus [USNM ENT00036803]. 20, *E. nepenthe*, female lateral view [USNM ENT00036804]. 21, *E. nepenthe*, male lateral view [USNM ENT00036803]. 22, *E. nepenthe*, female habitus [USNM ENT00036804]. 23, *E. nigriventris*, male habitus [USNM ENT00036849]. 24, *E. nigriventris*, female habitus [USNM ENT00036844]. 25, *E. nigriventris*, male lateral view [USNM ENT00036849]. 26, *E. nigriventris*, female lateral view [USNM ENT00036844]. 27, *E. umbra*, female lateral view [USNM ENT00036794]. 28, *E. umbra*, female habitus [USNM ENT00036793]. 29, *E. umbra*, male habitus [USNM ENT00036793]. 30, *E. umbra*, male lateral view [USNM ENT00036794].

proposed in this paper have been registered with ZooBank (<http://www.zoobank.org/>) as part of this cybertaxonomic publication and all taxon names have a Life Science Identifiers number (LSID) following each name. The information here-with will be converted to species pages for Encyclopedia of Life (www.eol.org) upon publication.

Molecular analysis

Taxon sampling covered as much taxonomic diversity as possible, particularly of the genera *Salpingogaster* and *Eosalpingogaster*, based on results from previous molecular analyses (Mengual *et al.*, 2008a,b). Four specimens of three *Eosalpingogaster* species and four different species of *Salpingogaster* were included in the analyses. *Syrphus vitripennis* Meigen was chosen as the outgroup, and we included multiple representatives of the genera *Allobaccha* Curran, *Allograpta*, *Asarkina* Macquart, *Episyrphus* Matsumura & Adachi, *Meliscaeva* Frey, *Ocyptamus* Macquart, *Paragus* Latreille, *Sphaerophoria* Lepelletier & Serville and *Toxomerus* Macquart. Unnamed taxa, referred to as sp. 1, sp. 2, etc., with high probability are species new to science. Species new to science identified by F.C. Thompson from Costa Rica are denoted as, e.g. CR-9, CR-29. Entomological collections where DNA voucher specimens are deposited are indicated in Table 1.

Phylogenetic relationships between *Salpingogaster* and *Eosalpingogaster* were explored with the mitochondrial protein-coding gene cytochrome *c* oxidase subunit I (COI) and the region D2-3 of the nuclear 28S rRNA gene, in addition to a fragment of 18S rRNA gene. Laboratory procedures follow the protocols explained in Mengual *et al.* (2008b). In some cases, we used a different primer combination to obtain the 'Folmer fragment', a 648 bp region of the COI gene proposed as a DNA barcode (Hebert *et al.*, 2003). These degenerated primers are called jgHCO_2198 (forward primer: TAIACYTCIGGRTGIC CRAARAAYCA) and jgLCO_1490 (reverse primer: TITCIA CIAAYCAYAARGAYATTGG).

The protein-coding COI gene was aligned manually with no gaps needed to align. Ribosomal gene alignments were less straightforward as the protein-coding genes, thus 28S and 18S genes were aligned using the E-INS-I strategy implemented in MAFFT (Kato *et al.*, 2005, 2009).

Maximum parsimony and maximum likelihood (ML) analyses were performed for the dataset as well as Bayesian inference. For the parsimony analysis, the combined dataset of the three genes was analysed using PAUP* version 4.0b10 (Swofford, 2002) performing a heuristic search with 10 000 random addition sequence searches using tree bisection and reconnection branch swapping, holding ten trees at each step and swapping on all the trees. Bootstrap support values (BP) for the most parsimonious tree(s) were estimated from 1000 replicates. All trees were drawn with the aid of FIGTREE v.1.3.1 (Rambaut, 2009).

For ML analyses, the dataset was divided into five partitions: 28S gen, 18S gen, position 1 of COI, position 2 of COI and position 3 of COI. We determined the best choice of model for each partition and for the entire concatenated

dataset using JMODELTEST 0.1.1 (Posada, 2008, 2009) under the Akaike Information Criterion, as recommended by Posada & Buckley (2004). The model chosen for 28S was GTR + G, TPM3uf + G for 18S, TrN + G for position1, TIM2 + G for position 2 and TPM1uf + G for position 3 of COI gen. Data were analysed under the recommended models using GARLI-PART v0.97 (Zwickl, 2006, 2010) and conducted with 100 independent runs using default settings (scorethreshforterm = 0.05; significanttopchange = 0.01) and the automated stopping criterion, terminating the search when the ln score remained constant for 20 000 consecutive generations. The tree with the highest likelihood was retained and is presented here. Bootstrap support values (BL) were estimated from 1000 replicates using the same independent models in GARLI-PART v0.97.

Phylogenetic estimation using the Markov Chain Monte Carlo algorithm as implemented in MRBAYES 3.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) was performed using a parallelized version of the software using MPICH2 1.2.1p1 (<http://www.mcs.anl.gov/research/projects/mpich2>). Data were divided into the above five partitions and the analysis run specifying a separate GTR + I + G model for each partition, where each partition has its own set of parameters. Eight runs with four chains each (one 'cold' chain and three heated chains; default values) were performed simultaneously for 25 000 000 generations, which were sufficient to bring the convergence (also called the average standard deviation) to a value <0.006 (Ronquist *et al.*, 2005), sampling trees every 1000 generations. The initial 6250 trees (25%) were discarded as burn-in and clade support was calculated using Bayesian posterior probabilities (PP).

Eosalpingogaster Hull

Eosalpingogaster Hull, 1949: 299 (proposed as a subgenus).

Type species, *Baccha conopida* Philippi by original designation.

Description

Head. Face with tubercle, not produced greatly anteriorly nor ventrally, yellow with medial broad dark vitta; oral opening slightly longer than broad (Figs 4, 8, 9); gena linear; frons normal, slightly produced anteriorly antennae base; eye bare; male holoptic (Fig. 4), ommatidia uniform; antenna short, less than head width (Figs 8, 9); scape and pedicel about as long as broad, together about as long as basoflagellomere; basoflagellomere oval to slightly elongate, not more than 1.6 times as long as broad; arista basal, bare; occiput with three to four rows of cilia dorsally.

Thorax. Postpronotum bare (Figs 6, 7); scutum black dorsally, with very short appressed pile; scutellum yellow, black basally, without ventral pile fringe (Figs 6, 7); anepisternum bare on anterior flatten portion; katepisternum bare or with only short appressed pile posteriorly; metasternum bare (Fig. 10); metathoracic pleuron bare; plumula absent; calypter bare, reduced, with short fringe. *Legs:* simple except metafemora with short black spinose bristles apically; metacoxa with pile

Table 1. Taxon sampling used in the molecular analysis, including GenBank accession numbers.

Taxon	Laboratory code – holding institution	Label information	Accession no. COI	Accession no. 28S	Accession no. 18S
<i>Allobaccha sapphirina</i> (Wiedemann, 1830)	S87 – MZH	Thailand, Chiang Mae, IV-2001. Leg.: D. Quicke & N. Laurence. Det.: F.C. Thompson.	EF127349	EF127430	EU409230
<i>Allobaccha</i> sp.	XP177 – MZH	East Timor, Maliana, road verge in town. S8°58'51"E125°13'08". 200 m. 11-XII-2005. Leg.: M.P. van Zijjen. Det.: M.P. van Zijjen.	EU409120	EU409175	EU409229
<i>Allograpta (Allograpta) obliqua</i> (Say, 1823)	XP38 – MZH	U.S.A., Utah, Garfield Co., Alvoy Wash. 7 km S Escalante. 37°42.5'N 111°37.8'W. 1990 m. 29-VI-2002. Leg.: M.E. Irwin & F. Parker. Det.: F.C. Thompson.	EF127310	EF127389	EU241833
<i>Allograpta (Facia) micrura</i> (Osten Sacken, 1877)	XP183 – MZH	Venezuela, Edo. Aragua. P.N. Henri Pittier, Portachuelo, 1152 m. 26-I-2007. N10°20.828'W067°41.309'. Leg.: X. Mengual. Det.: X. Mengual.	EU241723	EU241771	EU241821
<i>Asarkina (Asarkina) ericetorum</i> (Fabricius, 1781)	S222 – MZH	Kenya, Kakamega forest, 5-XII-1995, 0°17.13'N34°56.32'E. Leg.: Earthwatch Team 6. Det.: F.C. Thompson.	EF127353	EF127434	EU241837
<i>Asarkina (Asarkina) fitva</i> Hull, 1941	XP100 – MZH	Madagascar, Fianarantsoa Prov. Ranomafana N.P., Talatakely region. 22-XI-2004. Leg.: X. Mengual. Det. X. Mengual.	EU241738	EU241785	EU241838
<i>Asarkina (Asarkina)</i> sp.	XP99 – MZH	Madagascar, Fianarantsoa Prov. Ranomafana N.P., Talatakely region. 27-XI-2004. Leg.: X. Mengual.	EU241739	EU241786	EU241839
<i>Episyrrhus (Episyrrhus) balteatus</i> (De Geer, 1776)	XP153 – MZH	Spain, Alicante. P.N. Marjal Pego-Oliva, Muntanyeta Verda. 19-V-2007. Leg.: X. Mengual. Det.: X. Mengual.	EU241740	EU241788	EU241840
<i>Eosalpingogaster conopida</i> (Philippi, 1865)	Y214 – MZH	Chile, Region IV, Limari prov., Fundo Agua Amarilla, 7 km N Los Vilos; malaise in stable dunes, 58 m., 31°50.96'S71°29.60'W. 28-XII-2003/8-I-2004. Leg.: M.E. Irwin. Det.: F.C. Thompson.	EF127359	EF127440	EU241850
<i>Eosalpingogaster knutsoni</i>	MS2 – USNM	Argentina, Salta Prov., 4 km W Cafayate. 1760 m. Malaise on steep sandy hillside, 26°04.550'S 66°00.332'W. 1–2.x.2009. Leg.: M.E. Irwin.	HQ845755	—	HQ845763
<i>Eosalpingogaster knutsoni</i>	MS4 – USNM	Argentina, Salta Prov., 4 km W Cafayate. 1760 m. Malaise on steep sandy hillside, 26°04.550'S 66°00.332'W. 4–5.x.2009. Leg.: M.E. Irwin.	HQ845756	—	HQ845764
<i>Eosalpingogaster umbra</i>	Y1035 – MZH	Venezuela, Lara, P.N. Cerro Saroche, Sector Batatal. 700 m. 15-19/vii/2008. Trampa amarilla. Leg.: E. Arcaya.	HQ845759	HQ845762	HQ845767
<i>Meliscaeva auricollis</i> (Meigen, 1822)	S123 – MZH	Greece, Lesbos island, IV-2001. Leg.: S. Rojo & C. Pérez.	EF127341	EF127423	EU241844
<i>Meliscaeva cinctella</i> (Zetterstedt, 1843)	S557 – MZH	Czech Republic, Bohemia PLA Jezerske mountains, Korenov, 12-VI-2005. Leg.: L. Mazanek. Det.: L. Mazanek.	EU241743	EU241791	EU241845
<i>Ocyptamus (Hermesomyia) wulpianus</i> (Lynch Arribalzaga, 1891)	Y121 – MZH	Argentina, Jujuy prov., 36 km S Jujuy, Arroyo Las Lanzas; malaise trap in wooded, damp wash; 24°27.25'S 65°17.83'W. 1278 m., 27-X/14-XI-2003. Leg.: M.E. Irwin & F.D. Parker. Det.: F.C. Thompson.	EF127356	EF127437	EU241849
<i>Ocyptamus antiphates</i> (Walker, 1849)	XP29 – MZH	U.S.A., Florida: Monroe Co. Everglades NP; Mtazek Pond. 25°08.4'N 080°55.5'W. 1-I-2004. Leg.: W. van Steenis. Det.: W. van Steenis.	EF127304	EF127383	EU241847

Table 1. Continued.

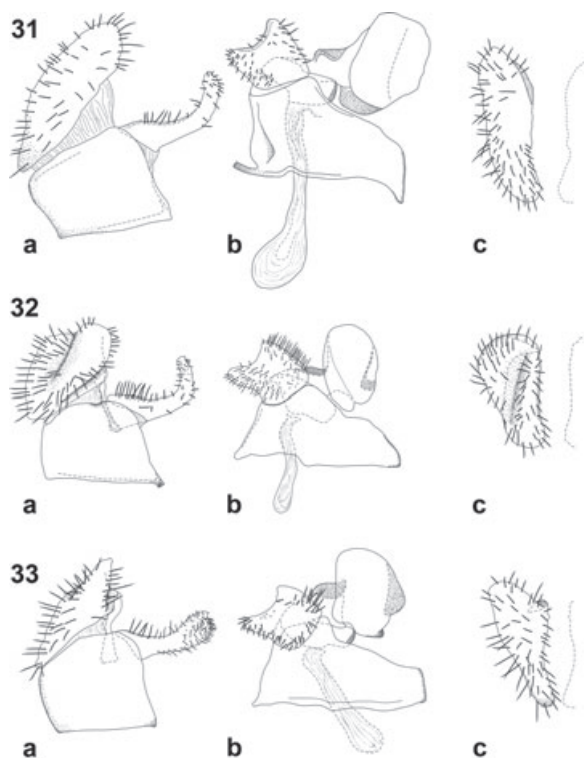
Taxon	Laboratory code – holding institution	Label information	Accession no. COI	Accession no. 28S	Accession no. 18S
<i>Ocyptamus CR-29</i> Thompson, <i>in litt.</i>	XP174 – MZH	Venezuela, Edo. Aragua. P. N. Henri Pittier, Estación Biológica Rancho Grande, 1183 m. 25-I-2007. N10° 20.994'W067° 41.059'. Leg.: E. Arcaya. Det.: X. Mengual.	EU409125	EU409180	EU409235
<i>Ocyptamus fascipennis</i> (Wiedemann, 1830)	XP222 – MZH	Canada, QC: Manicouag. Les Bergeronnes, Paradis Marin camping. N48° 16'20"W69° 28'11". Alt. 30 m. 21-VIII-2007. Leg. W. van Steenis. Det.: W. van Steenis.	EU409131	EU409186	EU409241
<i>Ocyptamus funebris</i> Macquart, 1834	S487 – MZH	Costa Rica, Heredia, INBiotparque, 15/21-I-2005, malaise trap. Leg.: G. Ståhlis. Det.: F.C. Thompson.	EF127364	EF127443	EU409242
<i>Ocyptamus lineatus</i> (Macquart, 1846).	XP30 – MZH	U.S.A., Florida, Monroe. Big Pink Key: Long Beach. N 24° 38.503'W 081° 19.953'. 04-I-2004. Leg. Stuke. Det.: F.C. Thompson.	EF127305	EF127384	EU409245
<i>Ocyptamus melanorrhinus</i> (Philippi, 1865)	Y215 – MZH	Chile, Region IV, Limari prov., Fundo Agua Amarilla, 7 km N Los Vilos; malaise in stable dunes, 28-XII-2003/8-I-2004; 58 m; 31° 50.96'S, 71° 29.60'W. Leg.: M.E. Irwin. Det.: F.C. Thompson.	EF127360	EF127441	EU409248
<i>Paragus (Pandasyopthalmus) haemorrhous</i> Meigen, 1822	S48 – MZH	Spain, Alicante, 2000. Leg.: S. Rojo & C. Pérez. Det.: S. Rojo.	AY174470	AY476866	EU409259
<i>Paragus (Paragus) bicolor</i> (Fabricius, 1794)	S108 – MZH	Greece, Lesbos island, IV-2001. Leg.: S. Rojo & C. Pérez. Det.: S. Rojo.	AY476857	AY476873	—
<i>Salpingogaster cornuta</i> Hull, 1944	XP78 – MZH	Colombia, Dpto. Cauca, Corr. El Tambo, 20 De Julio. 2900 m. 6/8-III-2006. Leg.: C. Prieto.	EU241746	EU241794	EU241851
<i>Salpingogaster CR-9</i> Thompson, <i>in litt.</i>	XP74 – MZH	Colombia, Dpto. Cauca, Corr. El Tambo, 20 De Julio. 2900 m. 6/8-III-2006. Leg.: C. Prieto.	EU241747	EU241795	EU241852
<i>Salpingogaster nigra</i> Schiner, 1868	XP77 – MZH	Colombia, Dpto Meta, PNN Sumapaz, Cabaña Las Mirilas. 3° 48'N 73° 52'W. 29-V/19-VI-2004. 710 m. Leg.: H. Vargas. Det.: F.C. Thompson.	EU241748	EU241796	EU241853
<i>Salpingogaster pygophora</i> Schiner, 1868	XP169 – MZH	Venezuela, Edo. Aragua. P.N. Henri Pittier, Portachuelo, 1152 m. 26-I-2007. N10° 20.828'W067° 41.309'. Leg.: G. Ståhlis. Det.: X. Mengual.	EU241749	EU241797	EU241854
<i>Sphaerophoria (Sphaerophoria) scripta</i> (Linnaeus, 1758)	XP142 – MZH	Spain, Alicante, Aspe. Partida Tolomó.07-II-2006. Leg.: P. Hurtado. Det.: X. Mengual.	EU241752	EU241800	EU241860
<i>Toxomerus flaviplurus</i> (Hall, 1927)	XP94 – MZH	Colombia, Dpto Valle del Cauca. Palmira, Corr. La Buitrera. Nirvana. 14-II-2006. 1440–1530 m. Leg.: X. Mengual.	EU241753	EU241801	EU241861
<i>Toxomerus mutuus</i> (Say, 1829)	XP92 – MZH	Colombia, Dpto Caldas, Manizales. Corr. Las Palomas, Reserva Natural Río Blanco. 18-II-2006. 2200–2500 m. 5° 04'N75° 26.2'W. Leg.: X. Mengual.	EU241754	EU241802	EU241862
<i>Toxomerus politus</i> (Say, 1823)	XP82 – MZH	Costa Rica, P.N. Tapanfí. 12-I-2005. 1600 m. Leg.: S. Rojo.	EU241755	EU241803	EU241863
<i>Toxomerus virgulatus</i> (Macquart, 1850)	S79 – MZH	Brazil, 2000. Det.: F.C. Thompson.	EF127330	EF127411	EU409291
Outgroup					
<i>Syrphus vitripennis</i> Meigen	S53 – MZH	Greece, Lesbos Island, April 2001. Leg.: S. Rojo & C. Pérez.	AY212797	AY261728	HQ845768

COI, cytochrome *c* oxidase subunit I; MZH, Zoological Museum of the University of Helsinki, Finnish Museum of Natural History, Helsinki, Finland; USNM, National Museum of Natural History, Washington DC, U.S.A.

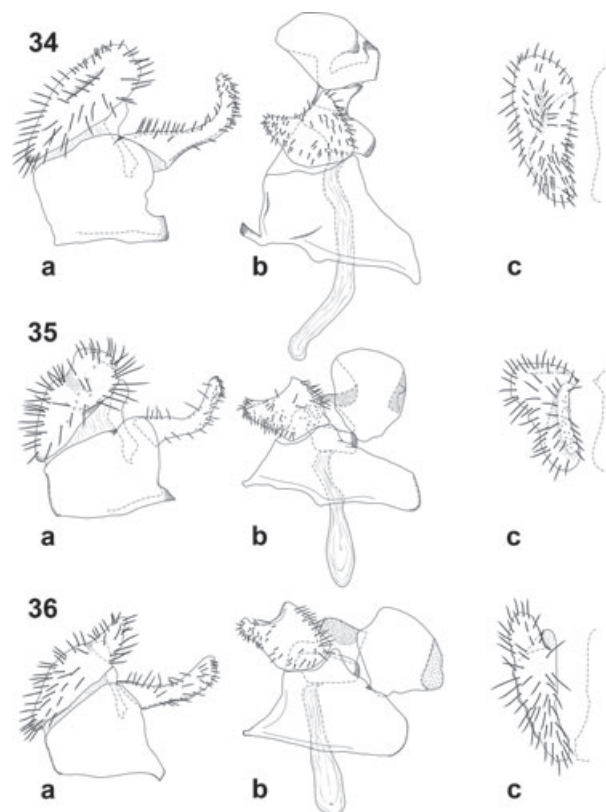
tuft on posteroventral apical angle (Figs 10, 13). *Wing*: coloration variable, from hyaline to with dark anterior margin and with medial macula, from microtrichose to partially bare basally; vein R_{4+5} only slightly sinuate; vein M_1 (apical crossvein) slightly recessive, strongly sinuate; posterior margin without black sclerotized puncta; alula normal, broad, partly bare (Fig. 5).

Abdomen. First tergum not produced laterally into a spur, strongly petiolate, second tergum four to six times as long as wide, flatten dorsoventrally, without marginal sulcus (Figs 6–13). *Male genitalia*: globular, enlarged, fifth and sixth sterna modified to accommodate it; cercus enlarge; surstylus elongate; without lingua; aedeagus two-segmented; superior lobe free, articulate (Figs 31–36).

Diagnosis. *Eosalpingogaster* and *Salpingogaster* are readily distinguished from all other syrphine groups by the presence of distinct black spinose bristles on the metafemur combined with the petiolate abdomen and sinuate vein R_{4+5} . Both genera have petiolate abdomens, but *Salpingogaster* is distinguished from *Eosalpingogaster* by the much more greatly sinuate vein R_{4+5} (Fig. 2); other syrphines with sinuate vein R_{4+5} have oval abdomens. *Eosalpingogaster* has first tergum not produced into a spur (Figs 6, 7), vein R_{4+5} only slightly sinuate (Fig. 5) and occipital cilia in three to four rows dorsally. In



Figs 31–33. Male genitalia: (a) epandrium, cercus and surstylus, lateral view; (b) hypandrium, superior lobe and aedeagus, lateral view; (c) right cercus, dorsal view. 31, *Eosalpingogaster cochenillivora* [USNM ENT00036835]. 32, *E. conopida* [USNM ENT00036808]. 33, *E. knutseni* [USNM ENT00036812].



Figs 34–36. 34, *Eosalpingogaster nepenthe* [USNM ENT00036803]. 35, *E. nigriventris* [USNM ENT00036833]. 36, *E. umbra* [USNM ENT00036792].

contrast, *Salpingogaster* has first tergum produced laterally into a strong spur (Figs 1, 2) and occipital cilia reduced to a single row dorsally.

Distribution. From south of U.S.A. (Texas, Florida) to Argentina and Chile.

Biology. The larvae of the *Eosalpingogaster* species have been reported as predators of scale insects (Coccoidea), feeding mainly on cochineals (family Dactylopiidae), but also on soft scales (Coccidae) and armoured scales (Diaspididae) (Rojo *et al.*, 2003).

Etymology. The name is probably derived from the prefix *eo-*, from the Greek *eu-*, *ēōs-*, meaning 'original, primitive, earliest' (Brown, 1956: 135) and the name *Salpingogaster*, clearly referring to the similar adult habitus in both genera. *Salpingogaster* is a combination of *salpingo-* [from Greek *salpinx*, *-ingos* meaning trumpet, tube (Brown, 1956: 422)] and *-gaster* [from Greek *gaster* meaning stomach, belly, womb (Brown, 1956: 754)]. The name alludes to the greatly petiolate abdomen of these species.

Schiner (1868) did not state the gender when he described the genus, but he included three new species (*macula*,

niger and *pygophora*). Some subsequent authors treated it as feminine (Williston, 1886; Austen, 1893; Sack, 1920, 1941; Curran, 1932, 1941) others as masculine (Bigot, 1883) and some (Schiner, 1868; Hull, 1943, 1949) treated it both ways. Article 30.1.2 (ICZN, 1999) declares that: 'A genus-group name that is or ends in a Greek word transliterated into Latin without other changes takes the gender given for that word in standard Greek dictionaries'. The word *gaster* is feminine in Greek (Brown, 1956). Moreover, Article 30.1.2 states 'Names ending in *-gaster* are feminine'. Thus, *Salpingogaster* and *Eosalpingogaster* are to be treated as feminine.

Keys to genera and species

1. Vein R_{4+5} strongly sinuate (Fig. 2); first tergum produced laterally into a strong spur (Figs 1, 2); occipital cilia reduced to a single row dorsally *Salpingogaster*
 – Vein R_{4+5} only slightly sinuate (Fig. 3); first tergum not produced into a spur (Figs 6, 7); occipital cilia in three to four rows dorsally *Eosalpingogaster*

Eosalpingogaster

1. Abdomen black, without yellow maculae; costal cell dark in female, pale in male (Figs 29, 30) (Venezuela)
 *umbra* **sp.n.**
 – Abdomen with yellow maculae, at least with basolateral yellow maculae on third tergum and posteromedial narrow yellow fascia on posterior margin on third and fourth terga (Figs 6, 7) 2
 2. Legs and second tergum reddish orange, much lighter than fourth tergum; costal cell dark (Figs 19, 20) (Florida, U.S.A.)
 *nepenthe* (Hull)
 – Legs brownish to black except for yellow basal one third of tibiae; second tergum dark, dark brown to black except may be pale along lateral margin (Figs 11, 12) 3
 3. Pleuron entirely reddish brown, with slight bluish metallic luster (Figs 14, 15) (Chile)
 *conopida* (Philippi)
 – Pleuron with large yellow macula on anepisternum and katepisternum (Figs 8, 10) 4
 4. Second costal cell bare on basal one third or more. Males: second costal cell mostly bare, microtrichose only apically, hyaline in contrast with stigma. Females: second costal cell bare on basal half, hyaline in bare area, brown apically (Figs 5, 17, 18) (Paraguay, northern Argentina)
 *knutsoni* **sp.n.**
 – Second costal cell entirely microtrichose, sometimes bare on basal one fifth or less, brown to black in females, almost hyaline in males (Figs 6, 7) 5
 5. Scutum broadly reddish brown anterior to scutellum and laterally; fourth tergum dark laterally; femora only very narrowly yellow apically; scutum without or with a very narrow medial pollinose vitta (Figs 6, 7) (Texas to Guatemala, Argentina)
 *cochenillivora* (Guérin-Méneville)
 – Scutum only reddish laterally, black anterior to scutellum; fourth tergum with yellow basolateral triangular macula,

larger in females (Figs 25, 26); femora with apical one sixth to one fifth; scutum with broad yellow pollinose medial vitta, usually broader than ocellar triangle (Figs 23, 24) (Ecuador, Peru, Venezuela, Trinidad, Brazil, Uruguay, Argentina)
 *nigriventris* (Bigot)

Eosalpingogaster cochenillivora (Guérin-Méneville)

Figs 6–9, 31; MorphBank [http://www.morphbank.net/?id=578690].

Baccha cochenillivora Guérin-Méneville, 1848a: lxxxi (1848b: 350). Guatemala: Sacatepéquez, La Antigua (LT, MNHN, here designated); Aldrich, 1905: 355 (cat. cit.); Kertész, 1910: 158 (cat. cit.); Fluke, 1957: 240 (cat. cit.).

Salpingogaster cochenillivorus: Ramírez-García & Sarmiento-Cordero, 2004: 184 (Mexico).

Salpingogaster texana Curran, 1932: 6. U.S.A.: Texas, Brownsville (HT, ♀, AMNH). Curran, 1932: 6 (prey: *Dactylopius confusus*), 1941: 284 (key ref.); Wirth *et al.*, 1965: 574 (catalogue cit.); Knutson, 1971: 32 (descr. pupa, prey: *Dactylopius tomentosus*; figs 1–6); Arnaud & Owen, 1981: 125 (type data). **Syn.n.**

Differential diagnosis. Very common species with pleuron reddish brown with anepisternum yellow on posterior one third and katepisternum with a dorsal large yellow macula; scutum black medially with a narrow, sometime indistinct, medial pollinose vitta; abdomen black except first tergum yellow basolaterally, second tergum black, third tergum with a basal broad yellow fascia and a narrow yellow fascia on posterior margin, fourth tergum black with a narrow yellow fascia on posterior margin. *Eosalpingogaster cochenillivora* is similar to *E. nigriventris*, but the last has fourth tergum with two basolateral triangular yellow maculae and scutum with a medial broad pollinose vitta. Male genitalia are also different (see Figs 31 and 35). *Length* (2): body, 12.2–13.2 (12.7) mm; wing, 8.3–9.0 (8.7) mm.

Types. *Baccha cochenillivora* Guérin-Méneville was based on unknown number of specimens collected by M. Sallé. In the MNHN, Paris, in the general Diptera collection, box #41, there is a pin with a wing and the following label 'Baccha, cochenillivora, Guer., sp. nov., Lt. Guatemala, Antigua, D. Sallé'. We accept this fragment as a valid syntype and herewith designate the specimen lectotype to assure that this name is and will be in future interpreted consistently.

Salpingogaster texana Curran was described from Brownsville, Texas where P. H. Timberlake reared the specimen from larva feeding on *Dactylopius confusus* and emerged on 11 February 1915. Holotype female in the AMNH, New York City, and labelled: '*Salpingogaster*//TYPE//*texana*//Curran. ♀' (red, handwritten except line 2) 'C. H. Curran//Collection//Acc. 31144' 'Timberlake//Coll.' (handwritten) 'Brownsville//Tex 11 February, 1915' (italics = handwritten) 'On *Dactylopius*//*confusus*' (handwritten).

Type localities. For *cochenillivora*: Guatemala, Sacatopéquez, La Antigua, 14°34'N 90°44' W. For *texana*: U.S.A., Texas, Cameron County, Brownsville, 25°56' N 97°29' W.

Distribution. U.S.A. (Texas), south to Argentina (Salta). This species is very wide spread in Mexico and other countries with carmine dye production because it has a very close relationship with its preys. This is probably the reason *E. cochenillivora* was found in Argentina on a farm dedicated to the production of carminic acid and we expect new records will appear in more countries.

Material examined. Lectotype + 14♂ 15♀.

Biology. As the name implies, *E. cochenillivora* is a predator of the cochineal scale, *D. coccus* Costa (Guérin-Méneville, 1848a,b). It is also found feeding on the California cochineal scale, *D. confusus* (Cockerell) (Gilreath & Smith, 1988) and on the tomentose cochineal scale, *D. tomentosus* (Lamarck) (Knutson, 1971). In the collection of the USNM, there is a vial with a pupa of *E. cochenillivora* and seven larvae of *Laetilia* sp. (Lepidoptera: Pyralidae), another predator of *D. confusus* (Gilreath & Smith, 1988), from *Opuntia* sp. [U.S.A.: Texas, Hidalgo Co., Santa Ana NWR, 22.x.1984, F.D. Fee]. In the same collection, there is a vial with two pupae of *E. cochenillivora* parasited by *Pachyneuron* sp. (Hymenoptera: Pteromalidae) (U.S.A.: Texas, Hidalgo Co., Santa Ana NWR, Ex pupa 19.x.1984, emerged 24.x.1984, F.D. Fee). In the CNC collection, there is a male reared from a larva preying on *Dactylopius* (CNC Accession # 1047613).

Remarks. *Eosalpingogaster cochenillivora* is easily recognized in Mesoamerica as it is the only species of *Eosalpingogaster* in the area.

Eosalpingogaster conopida (Philippi)

Figs 12–15, 32; MorphBank [http://www.morphbank.net/?id=578696].

Baccha conopida Philippi, 1865: 750. Chile, Santiago [HT, MNHN, (lost)].

Baccha conopida: Williston, 1886: 314 (cat. cit.); Kertész, 1910: 158 (cat. cit.); Shannon, 1927: 30 (key ref., Chile); Porter, 1927: 122 (Chile), 1932: 190 (Chile).

Salpingogaster conopida: Williston, 1886: 315 (cat. cit.); Porter, 1923: 117, 1924: 98; Shannon & Aubertin, 1933: 135 (in part, Chile records; comb., descr. notes, syn.); Curran, 1941: 283 (key ref.); Stuardo, 1946: 124 (Chile, cat. cit.); Hull, 1949: 299 (comb.); Fluke, 1957: 4 (cat. cit.); Etcheverry, 1963: 72 (Chile, syn., distr.); Thompson *et al.*, 1976: 32 (cat. cit.).

Salpingogaster macula Schiner, 1868: 345. Chile (ST, 2 ♂, NMW); Williston, 1886: 315 (cat. cit.); Kertész, 1910: 168 (cat. cit.); Sack, 1920: 244 (descr.), 1941: 106, 1951: 102 (Peru); Porter, 1923: 117 (Chile), 1924: 98 (Chile); Curran, 1932: 5 (key ref.), 1934: 396 (key ref.); Soukup, 1959: 204 (Peru and Chile). Syn. by Shannon & Aubertin 1933: 135.

Salpingogaster macula (missp.): Reed, 1888: 25 (separate), 299 (journal) (Chile).

Salpingogaster conopida (misidentification): Sauer, 1946 (prey, Brazil); Silva *et al.*, 1968 (prey, Brazil); Knutson, 1971: 34 (descr. of puparium, prey and parasitoids), figs 3, 5 (puparium); Rojo *et al.*, 2003 (prey, Argentina), refer to *E. nigriventris*.

Salpingogaster conopida (misidentification): Shannon & Aubertin, 1933: 135 (in part, Argentina record) refers to *E. knutsoni*.

Differential diagnosis. Species only known from the Andean region, very distinct with no yellow maculae on pleuron. *Eosalpingogaster conopida* has black abdomen with third abdominal tergum with two basolateral yellow maculae that can join medially forming a broad fascia. Similar to *E. cochenillivora* but this species has posterior anepisternum yellow on posterior one third and katepisternum with dorsal broad yellow macula. *Length* (2): body, 11.3–13.4 (12.4) mm; wing, 7.8–8.8 (8.3) mm.

Types. *Baccha conopida* Philippi was described from a specimen collected in the province of Santiago by Ferd. Paulsen ('Specimen ab orn. Ferd. Paulsen captum in prov. Santiago'). As previously noted (Thompson & Thompson, 2007: 329) no syrphid types remain in the Philippi collection now housed in Santiago. Within the context of the known Chilean flower fly fauna, the original description clearly applies only to the current species.

Salpingogaster macula Schiner was based on a pair from Chile, without more precise locality. There are two syntype male specimens in Vienna today with the following labels: 'Novara-R./Chili' 'macula//Alte Sammlung'.

Type localities. For *conopida*: Chile, Santiago Prov., Santiago, 33°26'S 70°39'W. We here restrict the type locality to Santiago, the capital of the province in which the type was collected. For *macula*: Chile, Valparaíso Prov., Valparaíso, 33°03'S 71°37'W. The label data provide no precise information on where in Chile the material was collected. As the material was collected as part of the Novara expedition (Papavero, 1973: 286–288), which stopped in Valparaíso and collected just in that province, we here restricted the type locality to the port of Valparaíso.

Distribution. Chile [*Mancera (Porter, 1927), *Quilpué (Porter, 1932), Valparaíso, Santiago, *San José de Maipo (Porter, 1924), *Bio-Bio (Porter, 1923), *Atacama: Candelaria, *Antofagasta: Llepe].

Material examined. 5♂ 3♀.

Biology. Porter (1924) obtained an adult of *S. macula* from a pupa collected on *Foeniculum dulce* Mill. infested with aphids. Mann (1969) cited *E. conopida* as an important predator of *Dactylopius* species in Argentina, but he did not indicate the location or any reference for those records. Silva *et al.* (1968)

recorded *E. conopida* as a predator of *Cephus siccifolius* (Walker) (Cercopidae) in Rio de Janeiro and Rio Grande do Sul states (Brazil), but we think this record might refer to a species of *Salpingogaster* sensu stricto because the prey is a spittlebug. More recently, Zimmermann *et al.* (1979) reported this syrphid species feeding on *Dactylopius* sp. (Dactylopiidae) in South America with no more details.

Remarks. Shannon & Aubertin (1933) were the first to recognize the current placement of *Baccha conopida* Philippi and included *macula* Schiner and *nigriventris* Bigot as synonyms based only on the original descriptions of Philippi and Schiner. Shannon and Aubertin mentioned three syntypes of *nigriventris* in the BMNH collection, but only one female was found in a recent visit to the BMNH collection (February 2010). This female is here designated as *nigriventris* lectotype (see below). We think that the other two females were not *nigriventris* syntypes, but they belong to *E. conopida* and *E. knutsoni* as explained below.

Shannon & Aubertin (1933) studied four specimens from Santiago and Valparaíso (Chile) and Mendoza (Argentina); thus they studied a specimen from each locality if the *nigriventris* lectotype (from Uruguay) is also included. The first author (XM) found a male from Chile (no other location's details mentioned) and two females (from Valparaíso and Mendoza) in the BMNH collection that belong to *E. conopida* (a male from Chile and a female from Valparaíso, Chile) and *E. knutsoni* (a female from Potrerillos, Mendoza, Argentina). These specimens are most probably the material Shannon & Aubertin (1933) studied in the BMNH collection.

Knutson (1971: 30) questioned this synonymy as material in the USNM suggested that multiple species may be involved. We follow his view and recognize the Chilean populations (*conopida*) separate from those of northeastern Argentina to southern Brazil to Venezuela (*nigriventris*). Knutson (1971) studied three males from Brazil in the USNM collection that he used to make the pupal description of *conopida* and gave some biological data. However, after our study, specimens used by Knutson (1971) are identified as *E. nigriventris*. Specimens identified as *S. macula* by Sack (1951) and Soukup (1959) based on Peruvian records are most probably *E. nigriventris*. Thus, *E. conopida* is only known from Chile.

***Eosalpingogaster knutsoni* Mengual & Thompson sp.n.**

urn:lsid:zoobank.org:act:9D8AFC43-9119-47D2-96C9-C592153C3E39

Figs 4–5, 10–11, 16–18, 33; MorphBank [http://www.morphbank.net/?id=578736].

Salpingogaster conopida (misidentification): Shannon & Aubertin, 1933: 135 (in part, Argentina record) refers to *E. knutsoni* (see remarks under *E. conopida*).

Description

Male. Head. Face with facial tubercle, yellow with medial broad dark vitta, yellow pilose; gena dark brown; lunule dark

brown; frontal triangle yellow with a medial dark brown joining facial vitta ventrally; vertical triangle black; antenna brown, basoflagellomere orange; occiput black, silver pollinose, whitish-yellow pilose.

Thorax. Scutum black with dorsomedial broad white pollinose vitta, reddish anterior to scutellum; postpronotum yellow; notopleuron mostly yellow, brown laterally. Pleuron mostly reddish-brown, except posterior anepisternum with yellow vitta and katepisternum with dorsal yellow macula. **Wing.** Wing membrane mostly hyaline, dark brown in basal costal cell, subcostal cell (sc), stigma and area around furcation of RS; apically microtrichose, cells CuP, CuA₁, DM, R₄₊₅, R₂₊₃ and anal lobe bare basally, cell R₁ bare except apically and medially in the brown area, cells BM and R entirely bare. Alula bare. **Legs.** Entirely black except tibiae yellow on basal two fifths and femora yellow very apically.

Abdomen. Strongly petiolate, dorsum mainly black, yellow pilose; first tergum black, yellow basolaterally; third tergum black with basal broad yellow fascia (about one quarter of tergum length); second, third and fourth terga black with medial thin yellow vitta on posterior margin; sterna black; male genitalia as in Fig. 33.

Female. Similar to male except for normal sexual dimorphism and as follows: second costal cell bare on basal half, microtrichose on apical half, hyaline on bare area, brown apically; fourth tergum black with two basolateral triangular yellow macula; fifth tergum black, yellow on lateral margins.

Differential diagnosis. Species with yellow maculae on abdomen and pleuron and second costal cell bare basally, microtrichose only on apical half or less. Similar to *E. cochenillivora* and *E. nigriventris*, but differs by microtrichia wing pattern and male genitalia (see Figs 31, 33 and 35). **Length (2):** body, 11.8–12.2 (12.0) mm; wing, 8.0–9.1 (8.6) mm.

Type. Holotype male deposited in the USNM (Washington DC, U.S.A.) and labelled: 'PARAGUAY//Depto. Nueva Asuncion//Parq. Nac. Tte. Enciso//21°13'S 61°39'W//26–28 March 1986//M. Pogue & M. Solis' 'HOLOTYPE//*Eosalpingogaster knutsoni*//Mengual & Thompson' (red, handwritten) 'USNM ENT00036811'.

Type locality. Paraguay, Boquerón Dept, Parque Nacional Teniente Agripino Enciso, 21°13'S 61°39'W.

Distribution. Paraguay (Boquerón), Argentina (Salta, Tucumán, Mendoza).

Etymology. This species is named after Lloyd V. Knutson in recognition of his work on these flies. He was the first to recognize this species based on the male from Tucumán.

Material examined. Holotype: as above. **Paratypes:** ARGENTINA: Salta, Moldes, Finca Las Tipas, 26.iv.1999, A.L.

Vigueras Guzmán, 'reared from *Dactylopius*' USNM ENT00036812 (1♂, USNM); Salta, 4 km W Cafayate, 1760 m. Malaise on steep sandy hillside, 26°04.550' S 66° 00.332'W, 26–27.ix.2009, M.E. Irwin USNM ENT00036886 (1♀, USNM); ... 4–5.x.2009 ... 036887 (1♂, USNM); ... 1–2.x.2009 ... 036888 (1♀, USNM); ... 26.ix.2009 ... 036889 (1♀, USNM); ... 30.ix–1.x.2009 036890 (1♀, USNM); Tucumán, ii. 1932, 'bred from larvae preying on cochineal' USNM ENT00036813 (1♂, USNM); Mendoza, Potrerillos, 6.i.1927, F. & M. Edwards. B.M. 1927-63 USNM ENT00036962 (1♀, BMNH).

Biology. Paratypes from Salta and Tucumán were reared from material collected feeding on cochineal.

Eosalpingogaster nepenthe (Hull)

Figs 19–22, 34; MorphBank [http://www.morphbank.net/?id=578735].

Baccha nepenthe Hull, 1943: 40. Florida, Bonita (HT, ♂, USNM); Hull, 1943: 40 (prey: *Dactylopius tomentosus*); Weems, 1951: 95 (cat. cit., Fla.).

Baccha (Mimocalla) nepenthe: Wirth *et al.*, 1965: 574 (cat. cit.).

Salpingogaster nepenthe: Knutson, 1971: 35 (prey).

Differential diagnosis. Very light species with pleuron, legs and second abdominal tergum reddish brown instead of black, as the rest of species. It has third tegum also distinct with yellow fascia on basal one third extending apically on lateral margins, and wing veins bordered with brown except apically. *Length* (3): body, 11.9–12.2 (12.1) mm; wing, 8.7–9.2 (8.8) mm.

Type. *Baccha nepenthe* was described from a series of adults, two males and a female, reared from larvae preying on *D. tomentosus* in Bonita, Florida. The holotype male in the USNM (Washington DC, U.S.A.) is labelled: 'Bonita//Fla.//v.20.32' 'A.R. Taylor//Collector' 'F2//Ex. Dactyl.//tomentosus' 'Holotype' [red] 'Type//56423//U.S.N.M.' [red] 'USNM ENT 00036803'.

Type locality. U.S.A.: Florida, Lee County, Bonita Springs, 26°21'N 81°47'W. Bonita Springs was established in 1999, so it is assumed that the locality on the label is the same as the later named town.

Distribution. U.S.A. (Florida).

Material examined. Holotype + paratypes (1♂1♀) + 2♂1♀.

Biology. Type material was reared from larvae found feeding on *D. tomentosus* (Lamarck) and the male specimen from Big Pine Key was reared from a larva preying on *Dactylopius*.

Eosalpingogaster nigriventris (bigot)

Figs 23–26, 35; MorphBank [http://www.morphbank.net/?id=578733].

Salpingogaster nigriventris Bigot, 1883: 329. Uruguay, Montevideo (LT, ♀, BMNH, here designated); Brèthes, 1907: 292 (cat. cit. Argentina, missid., see below); Lahille, 1907: 119 (descr., Argentina), fig. 27 (wing), fig. 28 (antenna), plate VII figs 1, 2, 3 (male, female, puparium); Kertész, 1910: 169 (cat. cit.); Sack, 1920: 249 (descr., figs. J, K, L head, mesonotum, puparium), 1921: 135 figs 7, 8 (mesonotum, puparium); Curran, 1932: 5 (key ref.), 1934: 396 (key ref.), 1941: 283 (key ref.); Shannon & Aubertin, 1933: 135 (in part, as a syn. of *conopida*, types in BMNH); Thompson *et al.*, 1976: 33 (cat. cit. as a syn. of *conopida*).

Salpingogaster nigriventris (missp.): Lynch Arribalzaga, 1892: 248 (comments on original description).

Salpingogaster nigroventris (missp.): Williston, 1886: 315 (cat. cit.).

Baccha mimetica Brèthes, 1907: 292 (*nomen nudum*, attributed to Lahille, and refers to *nigriventris*)

Salpingogaster liposeta Fluke, 1937: 10. Ecuador, Isla Puná, Puerto Grande (HT, ♀, AMNH); Fluke, 1937: 5, fig. 12 (wing), 13 (thorax), 1957: 5 (cat. cit., Argentina); Curran, 1941: 284 (key ref.); Thompson *et al.*, 1976: 33 (cat. cit.). **syn.n.**

Salpingogaster dactylopianus Blanchard, 1938: 348. Argentina: Entre Rios and Catamarca (ST, author's collection, MACN), fig. 2 (head, mesonotum, abdomen, puparium), fig. 8f (wing); Hull, 1949: 299 [placed in subgenus *Eosalpingogaster*, fig. 11H (wing)]; Fluke, 1957: 4 (cat. cit.). **syn.n.**

Salpingogaster (Eosalpingogaster) dactylopiana: Thompson *et al.*, 1976: 33 (cat. cit.).

Salpingogaster macula (misidentification): Sack, 1920: 224 (in part, Peru records), 1941: 106, 1951: 102 (Peru); Soukup, 1959: 204 (Peru).

Salpingogaster conopida (misidentification): Sauer, 1946 (prey, Brazil); Silva *et al.*, 1968 (prey, Brazil); Knutson, 1971: 34 (descr. of puparium, prey and parasitoids), figs 3, 5 (puparium); Rojo *et al.*, 2003 (prey, Argentina). 'Sifideo predando cochonilha-verde': Postali Parra *et al.*, 2003: 112 (colour figs. larva, puparium, adult; Brazil).

Salpingogaster nigriventris (misidentification): Brèthes (1907: 292), Sack (1920: 240; 1921: 135) and Bruch (1923) refer to *Ocyptamus (Mimocalla) bonariensis* (Brèthes) (Thompson & Zumbado, 2000: 777).

Differential diagnosis. Species very similar to *E. cochenillivora*, but *E. nigriventris* has fourth tergum with two basolateral triangular yellow maculae, scutum with a medial broad pollinose vitta, and femora with yellow apical area broader. *Eosalpingogaster nigriventris* has a larger distribution than *E. conopida*, which is known only from the Andean region. *Length* (5): body, 12.1–12.7 (12.4) mm; wing, 8.7–9.4 (9.1) mm.

Types. *Salpingogaster nigriventris* Bigot was based on three females from Montevideo. In BMNH, London, there is a female labelled: 'BMNH(E) #/230624' 'SYN-//TYPE' (round and light blue border) 'Uruguay' 'ex coll. Bigot.//B. 7.94.234' 'Salpingogaster//nigriventris//Cotype. Big'.. This specimen is here designated as lectotype to ensure that this name will be consistently interpreted.

Salpingogaster dactylopianus Blanchard was described from an unspecified number of male specimens reared by K. J. Hayward from *D. indicus* (Green) from two localities in Argentina (Catamarca and Entre Ríos). The 'cotipos' were held in the author's collection with the following information: 'Amadores, Catamarca, 17/III/1938' (*Los Armadores* in original publication) and 'Entre Ríos, 26/IV/1937' (1397 in original publication). Dr Roig Alsina found a microscope slide preparation with two wings in the MACN, Buenos Aires. This slide has a Blanchard's manuscript note saying '*Salpingogaster dactylopianus*' and a posterior added label with the word 'sintipo'. Based on the microtrichia pattern of the wing, the original description and the distribution, there is no doubt that *S. dactylopianus* is a junior synonym of *E. nigriventris*.

Salpingogaster liposeta Fluke was described from three females collected in Ecuador, Isla Puná, Puerto Grande by Campos, Santiago and Navarro. The holotype in the AMNH is labelled: 'HOLOTYPE//Salpingogaster//♀ liposeta//Fluke' (red, handwritten) 'PuertoGrande//Isla Puna//Ecuador' 'F. Campos R.//Santiago A.//Navarro'.

Type localities. For *nigriventris*: Uruguay: Montevideo Dept, Montevideo, 36°26' 47"S 55°21'11"W. For *dactylopianus*, no type locality restriction has been made as no lectotype has been designated. For *liposeta*: Ecuador: Quayas, Isla Puná, Puerto Grande, 02°56'50"S 80°05'59"W.

Distribution. Argentina, Uruguay, Peru, Ecuador, Venezuela, Trinidad Island, Brazil.

Material examined. Lectotype + 11♂ 17♀.

Biology. Lynch Arribálzaga (1892) included *S. nigriventris* in his 'Dipterología Argentina' without seeing any specimen and citing the original description of Bigot (1883) based on specimens from Montevideo (Uruguay). He stated that this species could be in Argentina as a reason to include it in his work. Later, Lahille (1907) reported several specimens of *S. nigriventris* from Villa Elisa (Entre Ríos Prov., northeast Argentina) reared from pupae located in branches with *Pseudaulacaspis pentagona* (Targioni Tozzetti) (Diaspididae). Blanchard (1938) reported this species from *D. indicus* (Green), now a junior synonym of *D. ceylonicus* (Green) (Ben-Dov, 2006).

Sauer (1946) cited *E. conopida* as predator of *Saissetia* sp. (Coccidae) from Ituverava (Sao Paulo, Brazil, 07.xi.1939), but *E. conopida* is not known from Brazil and it must be a misidentification of *E. nigriventris*.

In 1962, da Costa Lima stated that Brèthes (1909) described *Euperilampus cesarinus* (= *Prosaspicera cesarina*) as a parasitoid of *S. nigriventris*, but Brèthes (1909) gave no detail about the biology of this figitid in the original description. Thus, we do not consider this relationship as valid. Concerning *Pachyneuron syrphiphagum*, da Costa Lima (1962) said that it was a parasitoid of *S. nigriventris* and *Allograpta exotica*. These references were based on Brèthes (1913) and De Santis (1942), respectively, but as mentioned above, *S. nigriventris* of Brèthes is *Ocyptamus bonariensis*. Thus, there is no evidence of *Pachyneuron syrphiphagum* as a parasitoid of *E. conopida*.

Silva *et al.* (1968) mentioned *Ethelurgus rufipes* (Brèthes) (Ichneumonidae), *Prosaspicera cesarina* (Brèthes) (Figitidae), *Trichomalus polviventris* Brèthes and *Pachyneuron syrphiphagum* Brèthes (Pteromalidae) as parasitoids of *E. conopida*. Brèthes (1909), in his original work, said that *Alegina ruficeps* (= *Ethelurgus rufipes*) and *Trichomalus polviventris* were parasitoids of *Baccha nigriventris*. *Baccha nigriventris* of Brèthes is *Ocyptamus (Mimocalla) bonariensis* (Brèthes) (Thompson & Zumbado, 2000: 777), thus these species should be referred as parasitoids of *O. bonariensis*.

Knutson (1971) described the puparium of *E. nigriventris* (misidentified as *E. conopida*) based on material in the USNM collection and reported this species as a predator of a cotton scale and *Coccus viridis* (Green) (Coccidae). In this collection there are three males and four females from Brazil reared from the coconut scale, *Aspidiotus destructor* Signoret (Diaspididae). Another male from Brazil at USNM was reared from *Diaspis echinocacti* Bouché (= *Diaspis calyptroides* Costa). At BMNH, there is a female reared from a larva preying on *Ceroplastes* sp. (Coccidae) from Brazil and another female from Trinidad Island reared from larva feeding on *Aspidiotus destructor* (Diaspididae). Rojo *et al.* (2003) cited *E. conopida* feeding on *Pulvinaria convexa* from Argentina, but the original work (Lizer y Trelles, 1939) states that the predator is *S. nigriventris* identified by Hayward.

Remarks. The confusion between *conopida* and *nigriventris* originated in the suggested synonymy due to their morphological overall similarity (Shannon & Aubertin, 1933). They placed two species (*S. nigriventris* and *S. macula*) under *S. conopida* based only on the original descriptions (see comments on *E. conopida*).

Eosalpingogaster umbra Mengual & Thompson sp.n.

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Figs 27–30, 36; MorphBank [http://www.morphbank.net/?id=578750].

Description

Male. *Head.* Face with facial tubercle, yellow with medial broad dark vitta, yellow pilose, white pollinose laterally; gena dark brown; lunule dark brown; holoptic; frontal triangle

yellow with a medial dark brown joining facial vitta ventrally; vertical triangle black; antenna light brown; occiput black, silver pollinose, withish-yellow pilose on ventral two third, golden pilose dorsally with some black pile dorsolaterally.

Thorax. Scutum black with dorsomedial broad white pollinose vitta; postpronotum yellow; notopleuron mostly yellow, brown laterally. Pleuron mostly brown, except posterior anepisternum with yellow vitta and katapisternum with dorsal yellow macula. **Wing.** Wing membrane mostly hyaline, dark brown in basal costal cell, subcostal cell (sc), stigma and area around furcation of RS; apically microtrichose, cells CuP, CuA₁, DM, R₄₊₅ and R₂₊₃ bare basally, cell R₁ bare except apically and medially in the brown area, cells BM and R entirely bare; second costal cell mostly bare, microtrichose on apical quarter. Alula bare. **Legs.** Entirely black except tibiae yellow on basal two fifths and femora yellow very apically.

Abdomen. Strongly petiolate, dorsum black, except first tergum yellow basolaterally, black pilose; sterna black; male genitalia as in Fig. 36.

Female. Similar to male except for normal sexual dimorphism and as follows: abdomen black with bluish metallic iridescence; second costal cell dark, entirely microtrichose; cell R₁ medially dark.

Differential diagnosis. Species only known from Venezuela, very distinct without any yellow marking on abdomen, except first tergum yellow on very basolateral corners. Male and female with different wing pattern as described. **Length** (5): body, 10.9–13.0 (12.1) mm; wing, 8.0–9.5 (8.7) mm.

Type. Holotype male deposited in the National USNM (Washington DC, U.S.A.) and labelled: ‘Timotes//Venezuela-Meri-//da. 2050 m.//12-x-1971’ ‘Ex. larva pred.//Dactylopius Costa/en Opuntia’ ‘col.//A. Briceño’ ‘Ver Ficha//REGISTRO’ (orange) ‘Venezuela Inst.//Zool. Agrícola//Fac. Agronomía//Univ. Central’ (green) ‘HOLOTYPE//Eosalpingogaster//umbra//Mengual & Thompson’ (red, handwritten) ‘USNM ENT00036792’.

Type locality. Venezuela, Mérida, Timotes, 2050 m., 08°58'N 70°44'W.

Distribution. Venezuela (Mérida, Falcón, Lara).

Etymology. The specific epithet is derived from the Latin *umbra*, meaning ‘shade, shadow’ (Brown, 1956: 701), and refers to the absence of yellow markings on the abdomen. Species epithet is an adjective.

Material examined. **Holotype:** as above. **Paratypes:** VENEZUELA: Mérida, Timotes, 2050 m., 12.x.1971, A. Briceño ‘Ex. larva pred. *Dactylopius* Costa en *Opuntia*’ USNM ENT00036793, ...036794, ...036795, ...036796, ...036797, ...036798, ...037122 (1♂ 5♀, USNM; 1♀, MIZA); Distrito Federal, cumbre de Boquerón frente a Bajo Seco,

1700 m., 7.iii.1970, F. Fernandez & C.J. Rosales, ‘ex. larva predadora de *Coccus viridis* sobre naranjo’ ENT00037123 (1♂, MIZA); Falcón, El Supi, 29.xii.1971, V. Vargas ‘ex. larva pred. *Aspidiotus destructor* en *Cocos nucifera*’ USNM ENT00036799, ...036800 (2♂, USNM); Lara, P.N. Cerro Saroche, Sector Batatal 700 m. 15–19/vii/2008, E. Arcaya USNM ENT00036801, ...036802 (1♂ 1♀, MJMO).

Biology. Holotype and paratypes were found preying on *Dactylopius* sp. Paratype from Falcón was found feeding on *Aspidiotus destructor* Signoret on *Cocos nucifera* L., and the male paratype from Boquerón was reared from a larva feeding on *Coccus viridis* on *Citrus sinensis* (L.) Osbeck.

Results

Phylogeny

The results resolve *Eosalpingogaster* and *Salpingogaster* in two different clades, independent of the method used to infer the phylogeny (BP = 100; BL = 100; PP = 1). In ML and Bayesian analyses, the species of *Eosalpingogaster* were clustered together with the species of *Ocyptamus* and *Toxomerus* with very high support values (BL = 100; PP = 1). On the other hand, the genus *Salpingogaster* was resolved as monophyletic with high support values (BP = 100; BL = 100; PP = 1), but it is not clearly resolved as to what genus or clade is its sister group.

The strict consensus tree (Fig. S1) of 18 equally most parsimonious trees (Fig. S2) of length 2614 steps is a poorly resolved cladogram, but with high support bootstrap values for the genera *Asarkina*, *Eosalpingoaster*, *Toxomerus*, *Salpingogaster* and *Allobaccha*, as well as for the clade (*Allograpta* + *Sphaerophoria*). The genera *Salpingogaster* and *Eosalpingogaster* were never resolved in the same clade or closely related in any of the equally most parsimonious trees and *Eosalpingogaster* was always placed with species of *Ocyptamus*. A possible reason for the many equally parsimonious trees might be the problematic placement for the *Ocyptamus* species, which might require an independent analysis to study their relationships, and the complex interrelationships of the genera *Episyrrhus*, *Meliscaeva*, *Asarkina* and *Salpingogaster*.

The likelihood score for the best ML tree (Fig. 37) was –13746.751794. The topology of the most likely tree compares favourably with the majority rule consensus tree resulting from Bayesian inference (Fig. 38). In both cases, *Salpingogaster* and *Eosalpingogaster* were resolved as monophyletic genera, but distantly related. Although the resolution of the deep nodes in the Bayesian inference is poor, the clade grouping *Ocyptamus*, *Toxomerus* and *Eosalpingogaster* is very well supported and clearly resolved.

Taxonomic rank of *Eosalpingogaster*

Salpingogaster and *Eosalpingogaster* have always been considered subgenera in the literature (Hull, 1949; Thompson

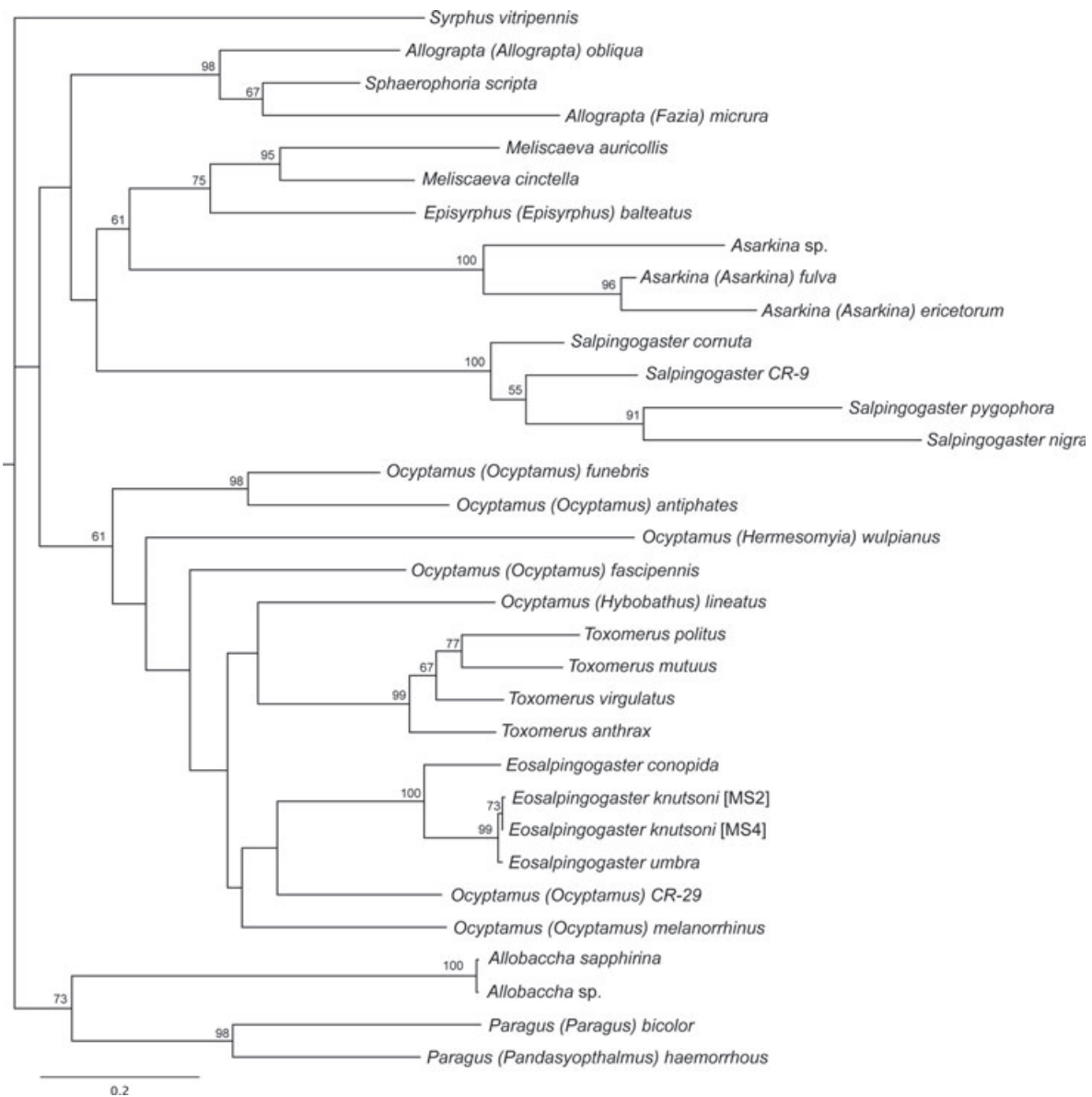


Fig. 37. Phylogram of the best tree from a maximum likelihood search of the combined dataset using GARLI-PART v0.97 ($\ln L = -13746.751794$). Numbers above nodes are maximum likelihood bootstrap support values (>50%).

et al., 1976; Thompson, 1981, 1999; Vockeroth & Thompson, 1987; Mengual *et al.*, 2008a). The genus *Salpingogaster* was considered to be a member of the tribe Bacchini until Thompson *et al.* (1976) placed it under Syrphini. No phylogenetic placement or sister group have been suggested for *Salpingogaster*. The molecular analyses by Mengual *et al.* (2008b) resolved the species of the subgenus *Salpingogaster* as sister group of the genus of a clade with the genera *Asarkina*, *Meliscaeva*, *Episyrphus*, *Allograpta*, *Sphaerophoria* and *Exallandra* in the analysis with equal weights (gap cost = 1; indels cost = 1), but as sister group of the cluster *Allograpta*, *Sphaerophoria* and *Exallandra* using different weights (gap cost = 2; indels cost = 1). In both cases, the

single *Eosalpingogaster* species included in the analyses was resolved in a completely different placement, within the clade of the genus *Ocyptamus*. Our results agree with this phylogenetic placement and resolve *Eosalpingogaster* as related with *Toxomerus* and *Ocyptamus*.

Based on our molecular studies and the morphological and ecological differences between the two taxa, we conclude that *Eosalpingogaster* is only distantly related to *Salpingogaster* and that *Eosalpingogaster* must be considered a distinct valid genus.

As mentioned above, *Eosalpingogaster* larvae are predators of scale insects (Coccoidea), in contrast with the larvae of *Salpingogaster*, which feed on spittlebugs (family Cercopidae)

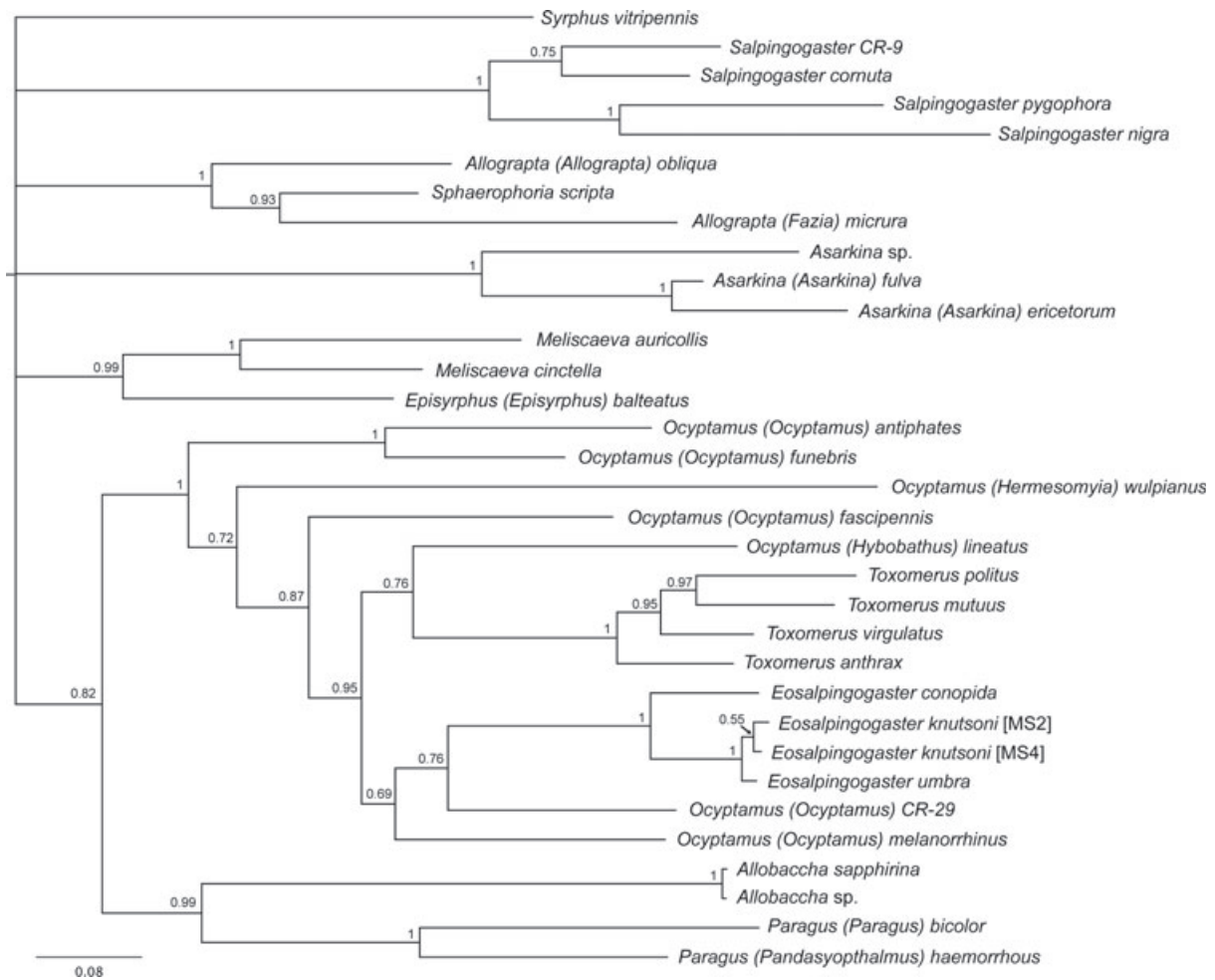


Fig. 38. Phylogenetic relationships of the studied taxa based on the majority-rule consensus from the Bayesian analysis of the full dataset. The Bayesian posterior probability values (>50%) are given above the nodes.

(see Rojo *et al.*, 2003 for a review). This difference in the prey preference makes the genus *Eosalpingogaster* an important factor in the international trade of the cochineal for producing carminic acid. In countries where cochineal scales are used to produce carminic acid, such as Mexico, Guatemala or Argentina, or in countries where cochineal scales are used as biological control agents of cactus weeds (e.g. South Africa, Australia and Mauritius), *Eosalpingogaster* might be considered a pest and it could decrease populations of *Dactylopius*.

On the other hand, in countries where *Dactylopius* may be considered a pest because cacti are cultivated for fodder, for prickly pear production or to obtain raw materials for medicaments and cosmetics, the genus *Eosalpingogaster* might be considered a biological control agent because its larvae feed on *Dactylopius* species.

Due to this ambivalence, the taxonomy of the genus *Eosalpingogaster* and its relationship with the genus *Salpingogaster* has become an important issue for pest control and biodiversity programmes. With this revisionary work, we clarify the taxonomic situation of *Eosalpingogaster* and compile

biological information about the relationship between this genus and the cochineal scales.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2011.00588.x

Table S1. Additional references cited in the text for all nomenclatural information not directly related to *Eosalpingogaster* (doc file).

Table S2. Examined material of *Eosalpingogaster*. For each specimen, data of locality, altitude, collecting date, collector and gender are provided. Additionally, the holding institution, the USNM collection number, the type material and the link to MorphBank images are also included (xls file).

Map S1. World distribution for examined specimens of *Eosalpingogaster* (kml file). Solid dots indicate examined specimens and empty stars specimens known from the literature.

Fig. S1. Strict consensus tree of 18 equally parsimonious trees (S5) based on COI, 28S and 18S genes using PAUP*. Bootstrap support values are indicated above nodes for values >50%.

Fig. S2. The 18 equally most parsimonious trees with a length of 2614 steps reported from the parsimony analysis of the combined dataset using PAUP* are provided (pdf file).

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