

Redescription of *Apanteles mimoristae* (Hymenoptera, Braconidae), a parasitoid of the native pyralid cactus moth *Melitara* cf. *nephelepasa* in central Mexico

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Abstract

Novel trophic associations have sometimes resulted in fortuitous and significant biological control. After the invasion of North America by the South American cactus moth, *Cactoblastis cactorum* (Berg) (Pyralidae: Phycitinae), it is pertinent to characterize the assemblage of local natural enemies that could utilize this moth in new host-parasitoid associations. Herein we report on *Apanteles mimoristae* Muesebeck (Braconidae: Microgastrinae), a North American gregarious endoparasitoid wasp attacking the caterpillar of the phycitine cactus moth *Melitara* cf. *nephelepasa* (Dyar) (Pyralidae: Phycitinae, also known as zebra worm), also native to North America; both collected in *Opuntia ficus-indica* (L.) Mill. (Cactaceae) cultivated fields at rural areas of Mexico City. We provide an updated morphological account for *A. mimoristae* visualized with light microscopy and scanning electron microscope (SEM); a fragment of its cytochrome oxidase subunit I (COI) gene sequence data is reported for the first time. Additionally, we analyze its taxonomical position relative to other *Apanteles* species from the Americas including those attacking cactus-feeding moths. Our analyses place *A. mimoristae* (from Mexico) in a clade with *A. esthercentenoae* Fernández-Triana (from Costa Rica), a parasitoid of both *Cromarcha stroudagnesia* Solis (Pyralidae) and *Palpita venatalis* (Schaus) (Crambidae) (non cactus-feeding), and in a sister clade to *A. opuntiarum* Martínez &

Berta (from Argentina) and *A. alexanderi* Brèthes (from Argentina and Uruguay), parasitoids of the cactus-feeding phycitines *Cactoblastis* and *Tucumania* respectively. Finally, we provide an updated key for the identification of *Apanteles* species recorded parasitizing cactus moth caterpillars in the American continent.

Keywords

Agriculture, biological control, ecosystem, invasive insect, North America, *Opuntia*, South America

Introduction

Novel trophic associations can result after dispersal and expansion of the geographical distribution of organisms. Some novel associations (e.g., infection, parasitism, parasitoidism, predation) sometimes bring about significant levels of mortality of phytophagous insects (Torres-Acosta et al. 1916; Felipe-Victoriano et al. 1917; Durocher-Granger et al. 2021) resulting (in the case of pests) in fortuitous or “new association” biological control (Sterling 1978; Hokkanen and Pimentel 1989). The South American cactus moth *Cactoblastis cactorum* (Berg) (Pyralidae: Phycitinae) is one of the most important herbivores of *Opuntia* Miller and related genera (prickly pears, Cactaceae) (Morrison et al. 2021). It poses a serious threat to *Opuntia* cacti in North America, both in their native natural communities and in commercial plantations (Starmer et al. 1988; Hight and Carpenter 2009). *Opuntia* (called nopal in Mexico) is widely consumed by the Mexican people since prehispanic times. The areas involved are of a continental scale and this implies that intensive measures like chemical control and physical destruction of *C. cactorum* are not feasible, making biological control by permanently established natural enemies (classical biological control) the most viable option (Habeck and Bennet 1990; Viguera and Portillo 2001).

North American *Opuntia* species are attacked by caterpillars of native cactus moths in the Pyralidae. Among these, the genus *Melitara* Walker is widespread in the deserts of northern Mexico and the southern and western United States; these insects usually bore into pads, are solitary and occasionally cause economic damage or plant dieback (Mann 1969; personal observations).

The study of local natural enemies is a key aspect in biocontrol of native and exotic insects (Morales-Galvez et al. 2022). Several species of Microgastrinae (Braconidae) are among the potential natural enemies considered for biological control of *C. cactorum*. Some species of *Apanteles* Foerster have been reported as parasitoids of pyralid cactus feeding moths, such as *Cactoblastis* Ragonot in South America, and the closely related genus *Melitara* in North America as well as *Loxomorpha* Amsel (= *Mimorista*) in the related family Crambidae (Muesebeck 1921). This family and the Pyralidae form the superfamily Pyraloidea. About half of described species of *Apanteles* are gregarious endoparasitoids of the host larval stage (Fernández-Triana et al. 2014; Varone et al. 2015; Figueroa et al. 2021). *Apanteles alexanderi* Brèthes,

A. mimoristae Muesebeck, *A. opuntiarum* Martínez & Bertha, and *Iconella etiellae* Viereck (a genus closely related to *Apanteles*) are among native Microgastrinae species parasitizing pyralid *Opuntia*-feeding moths in the American continent (Muesebeck 1921; Martínez et al. 2012; Fernández-Triana et al. 2013). Of those, only *A. opuntiarum* from Argentina has been studied as biological control agent of *C. cactorum* (Martínez et al. 2012). The most frequent reported hosts of another related wasp, *Apanteles megathymi* Riley, are butterfly larvae in the HesperIIDae (giant skippers like *Megathymus* spp.), but it has also been reported attacking the cactus zebra worm, *Melitara nephelapasa* (Dyar) and *Laniifera cyclades* (Druce) (Crambidae) in *Opuntia* spp (Mann 1969).

Apanteles mimoristae was described in the early 1900s based on four females and one male (Muesebeck 1921). However, the taxon is not well defined taxonomically: the original description is very short and incomplete, and it lacks illustrations and molecular information. Another important aspect in the Microgastrinae, as in other parasitoid wasp families, is the existence of cryptic species (Whitfield 1997; Hoy et al. 2000) making accurate species identification difficult even for specialists.

Indigenous parasitoids and other natural enemies may associate to invasive species (cactus moth in this context) to create new trophic relationships, exemplifying the so-called “new association biological control” (Hokkanen and Pimentel 1989). It is possible that indigenous *Apanteles* species parasitizing *Melitara*, like *A. mimoristae*, might exploit the invasive moth *C. cactorum* as a host. Our objective is to clarify and refine the description of *A. mimoristae* to better characterize the species and support its identification. DNA barcode sequences complemented by morphological comparison were used to investigate species boundaries. A key is provided to highlight the differences between *Apanteles* species reported to attack phycitine cactus moths in the American continent. The information presented here will serve as a foundation for investigations on the possible interactions of *A. mimoristae* in the zones invaded by *C. cactorum* in North America as an element in a biological control approach.

Materials and methods

Rearing material. Seventy caterpillars (larval stage) of zebra worm, *Melitara* cf. *nephelapasa* ranging from half-grown to fully grown were collected from prickly pear pads (*Opuntia ficus-indica* L. var. Milpa Alta) at commercial plots in Mexico City, central Mexico (19.191444, -99.003810) (Fig. 1) in the summer and fall of 2019 and 2020. These caterpillars were transported to the laboratory of the Universidad Autónoma Agraria Antonio Narro, and were placed individually in plastic containers, on a layer of moist filter paper at room temperature ($25^{\circ}\pm 2^{\circ}\text{C}$), 100% RH, and 12:12 h L:D, and fed daily fresh fragments of *O. ficus-indica* pads until they reached the adult stage or parasitoid emergence.



Figure 1. Collection site of *Apanteles mimoristae* from *Melitara cf. nephelipasa* in cultivated fields of *Opuntia ficus-indica* (Cactaceae) in San Jerónimo Miactalán (SJM), in the municipality of Milpa Alta, Mexico City, MX (left). The cactus fields are partially surrounded by houses and other agricultural areas (right).

Morphological analysis

Parasitoid wasp. After emergence, adult wasps were preserved in 70% ethanol (for mounting and photographing) and 96% ethanol (for DNA analysis). Morphological terms and diagnostic structures followed Wharton (1997) and Wharton et al. (1997). Features were compared with the original description of *A. mimoristae* (Muesebeck 1921), and also Martínez et al. (2012) and Fernández-Triana et al. (2013, 2014).

Due to costs and travel limitations, it was not possible for the first author to examine the holotype of *A. mimoristae*. The Mexican material listed was examined by author JFT and compared to paratypes of *A. mimoristae* in the Canadian National Collection of Insects (CNC). They were also compared to the brief but valid description of the species by Muesebeck (1921). The geographical distribution of *Apanteles* species was obtained from Fernández-Triana et al. (2020). Morphological analysis and imaging used a microscope eye-piece Dino-Lite AM7025x camera (Dino-Lite, Los Angeles, USA) adapted on an Olympus SZ51stereoscope plus an Olympus 110 AL2X-2WD38 magnifying lens (Olympus, Fukuoka, Japan). Images were also obtained with a Hitachi TM-3000 scanning electron microscope (SEM) (Hitachi High-Tech Corp., Fukuoka, Japan). For measurements, the DinoXcope software version 2.3 (Dino-Lite) was used. Images were edited on ImageJ (National Institutes of Health, USA). All measurements are expressed in mm. Morphological terms and their abbreviations used are: SV = surface of the vertex, T1 = mediotergite 1, and T2 = mediotergite 2. Abbreviations of depositories are:

- UNAM** Colección Nacional de Insectos, Instituto de Biología, UNAM, Ciudad de México, México
- CNC** Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada
- NMNH** National Museum of Natural History, Washington D.C., United States
- UT** University of Texas at Austin, United States

Melitara cf. *nephelepasa* caterpillars were identified following the description and geographical range reported in Mann (1969), collected in the host plant *O. ficus-indica*.

DNA extraction and PCR

Extraction, PCR conditions, and sequencing for the cytochrome oxidase subunit 1 (COI) were performed following Lopez-Monzon et al. (2019). Barcode sequences were obtained both at Brackenridge Field Laboratory, University of Texas (UT) at Austin, US (5 specimens) and at Facultad de Agronomía, Universidad Autónoma de Zacatecas (UAZ) at Zacatecas, MX (1 specimen).

Phylogenetic analysis

There were no known *A. mimoristae* sequences available before this work. A fragment of 628 base pairs (bp) of the cytochrome oxidase subunit I (COI) gene was obtained from all specimens at UT. The raw sequences were edited in Codon Code ver. 5.0.1 (Codon Code Corporation, Dedham, MA, US). The obtained sequences were aligned using ClustalW within the Molecular Evolutionary Genetics Analysis (MEGA) Version X software (Kumar et al. 2018), alongside a total of 152 sequences from *Apanteles* (Smith et al. 2008), supplemented with sequences from other *Apanteles* and related genera and species in the Braconidae retrieved through the Basic Local Alignment Search Tool (BLAST). Utilizing various exploratory phylogenetic trees derived from the Neighbor-Joining (NJ) and Maximum Likelihood (ML) algorithms, the alignment was refined to a subset of 33 sequences to ascertain the taxonomic and phylogenetic placement of *A. mimoristae* (Table 1). The phylogenetic relationship for the *Apanteles* species attacking cactus-feeding moths was then constructed by Maximum Likelihood (ML) algorithm using MEGA version X (Kumar et al. 2018) and parameter as GTR+I+G (General Time Reversible with invariant sites and a gamma distribution) an evolutionary model with 1,000 replicates. Model selection was performed using statistical and evolutionary analysis of multiple sequence alignments TOPALi v2 (Milne et al. 2009). In MrBayes ver.3.2.5 5 (Ronquist et al. 2012) we set partitions, first, second and third positions of COI, and models as selected by Partition Finder v1.1.1 (Lanfear et al. 2012) under the Bayesian information criterion (BIC) and the “all” search algorithm. For the first partition and second position the best model was GTR+I+G, and for the third partition the best model was HKY+I+G (Hasegawa-Kishino-Yano with invariant sites and a gamma distribution). We conducted the Bayesian phylogenetic analysis with nucmodel = 4by4, nruns = 2, nchains = 4, and sampled freq = 1000 (Sanchez-Peña et al. 2017), for one billion generations. We assessed convergence and stationarity in the Bayesian analysis using the “sump” command to examine log marginal likelihood plots, average standard deviation of split frequencies among runs, and the potential scale reduction factor for all parameters. Nodes that had posterior probabilities greater than 0.95, were considered well supported.

Table 1. Dataset of selected COI sequences of 33 species of Microgastrinae (*Apanteles* Förster, *Dolichogenidea* Viereck, *Glyptapanteles* Ashmead, *Iconella* Mason, and *Parapanteles* Ashmead) and their GenBank accession numbers utilized in the phylogenetic analysis. DNA voucher numbers [DHJPAR = Daniel H. Janzen and Winnie Hallwachs database at University of Pennsylvania; CNIN = Colección Nacional de Insectos, Universidad Nacional Autónoma de México (UNAM); USNM, National Museum of Natural History] * = *Apanteles* species parasitizing cactus moths in the Phycitinae on the American continent. A recent revision of the genus *Parapanteles* (Parks et al. 2020) indicated that it is not monophyletic, with species interspersed among *Apanteles* and closely related genera of Braconidae.

Microgastrinae species with COI sequence	Collection and voucher code	GenBank Accession number
<i>Apanteles</i> sp. Rodriguez48	DHJPAR0002317	KF462163
<i>Apanteles</i> sp. Rodriguez48	DHJPAR0047068	KF462208
<i>Apanteles</i> sp. Rodriguez106	DHJPAR0049396	KF462061
<i>Apanteles</i> sp. Rodriguez12	DHJPAR0047067	KF462166
<i>Apanteles</i> sp. Rodriguez169	DHJPAR0041984	JQ575692
<i>Apanteles</i> sp. Rodriguez69(3)	DHJPAR0039707	HQ926377
<i>Apanteles</i> sp. Rodriguez47	DHJPAR0002260	MT469770
<i>Apanteles</i> sp. Rodriguez47	DHJPAR0045169	KF462233
<i>Apanteles</i> sp. Rodriguez107	DHJPAR0034228	JQ853633
<i>Apanteles</i> sp. Rodriguez32	DHJPAR0048151	KF462206
<i>Apanteles</i> sp. Rodriguez158	DHJPAR0049161	KF461918
<i>Apanteles</i> sp. Rodriguez168	DHJPAR0045255	KF462252
<i>Apanteles</i> sp. Rodriguez68(2)	DHJPAR0004091	EU397563
<i>Apanteles</i> sp. Rodriguez33	DHJPAR0048132	KF462068
<i>Apanteles</i> sp. Rodriguez67	DHJPAR0049140	KF462152
* <i>Apanteles alexanderi</i>	CNIN1122	JX566790
* <i>Apanteles opuntiarum</i>	CNIN1113	JX566778
<i>Apanteles</i> sp. Rodriguez105 (<i>A. esthercentenoae</i>)	DHJPAR0005185	EU396687
* <i>Apanteles</i> Milpa Alta DF (<i>A. mimoristae</i>)		OQ676887
<i>Parapanteles</i> sp. Whitfield133	DHJPAR0020673	JQ850314
<i>Parapanteles</i> sp. Whitfield44	DHJPAR0030780	JQ854565
<i>Parapanteles</i> sp. Whitfield45(2)	DHJPAR0020128	EU397378
<i>Apanteles</i> sp. Rodriguez110	DHJPAR0005168	EU396741
<i>Parapanteles</i> sp. Whitfield102	DHJPAR0041787	MN645414
<i>Parapanteles</i> sp. Whitfield303	DHJPAR0012759	EU396804
<i>Parapanteles</i> sp. Whitfield302	DHJPAR0012793	EU396799
<i>Parapanteles</i> sp. Whitfield70	DHJPAR0020653	JQ853731
<i>Apanteles</i> sp. Rodriguez167	DHJPAR0045315	KF462011
<i>Apanteles</i> sp. Rodriguez169	DHJPAR0041984	JQ575692
<i>Iconella</i> sp. Whitfield05	DHJPAR0045362	KC685306
<i>Dolichogenidea</i> sp. Whitfield11	USNM00496786	JQ852381
<i>Glyptapanteles</i> sp. Whitfield175	DHJPAR0040014	JQ574612

Results

Material examined

Mexico, 15♀, 15♂ of *A. mimoristae*; Mexico City, Milpa Alta, San Jerónimo Mia-catlán; 19.191444, -99.003810, 2384 masl; 21.xi.2020; Renato Villegas leg.; zebra worm, *Melitara* cf. *nephelepasa* in commercial plots of *Opuntia ficus-indica* (Cactaceae) (prickly pear or nopal); GenBank: [OQ676887.1](https://www.ncbi.nlm.nih.gov/nuclot/OQ676887.1) and [OQ561741.1](https://www.ncbi.nlm.nih.gov/nuclot/OQ561741.1).

Redescription

Apanteles mimoristae Muesebeck, 1921

Note. Measurements from reared specimens in this work.

Female. Body length of $\bar{x}=2.94$ (2.805–3.097) (Figs 2–4).

Head. Transverse; antennae shorter than body, $\bar{x}=2.45$ (2.282–2.605), face smooth and eyes moderately setose in frontal view (Fig. 3A). SV finely wrinkled around the ocelli, but smooth and opaque between the ocelli (Figs 3B, 3C). Ocular–ocellar line/posterior ocellus diameter: 2.13–2.32. Intercellular distance/posterior ocellar diameter: 2.15–2.33. Antennal flagellomere 2 length/width: 2.06–2.46. Antennal flagellomere 14 length/width: 1.06–1.40. Length of antennal flagellomere 2/length of antennal flagellomere 14: 2.08–2.18.

Mesosoma. Dull black. Mesoscutum: indistinctly/irregularly punctate, profusely setose and markedly rugose, the roughness does not cover its surface in dorsal view (Fig. 3D). Scutellum: flat, dull, smooth, and setose. Pits in the scutoscutellar sulcus: 10. Mesopleura: anterior half punctate and pilose; posterior half smooth and polished. Propodeum: with rugae; with a well-defined broad median areola, inside of areola with marked wrinkles, and a transversal carina which does not reach the spiracle (Fig. 3D, E).



Figure 2. *Apanteles mimoristae* Muesebeck (Braconidae: Microgastrinae) female. Habitus.

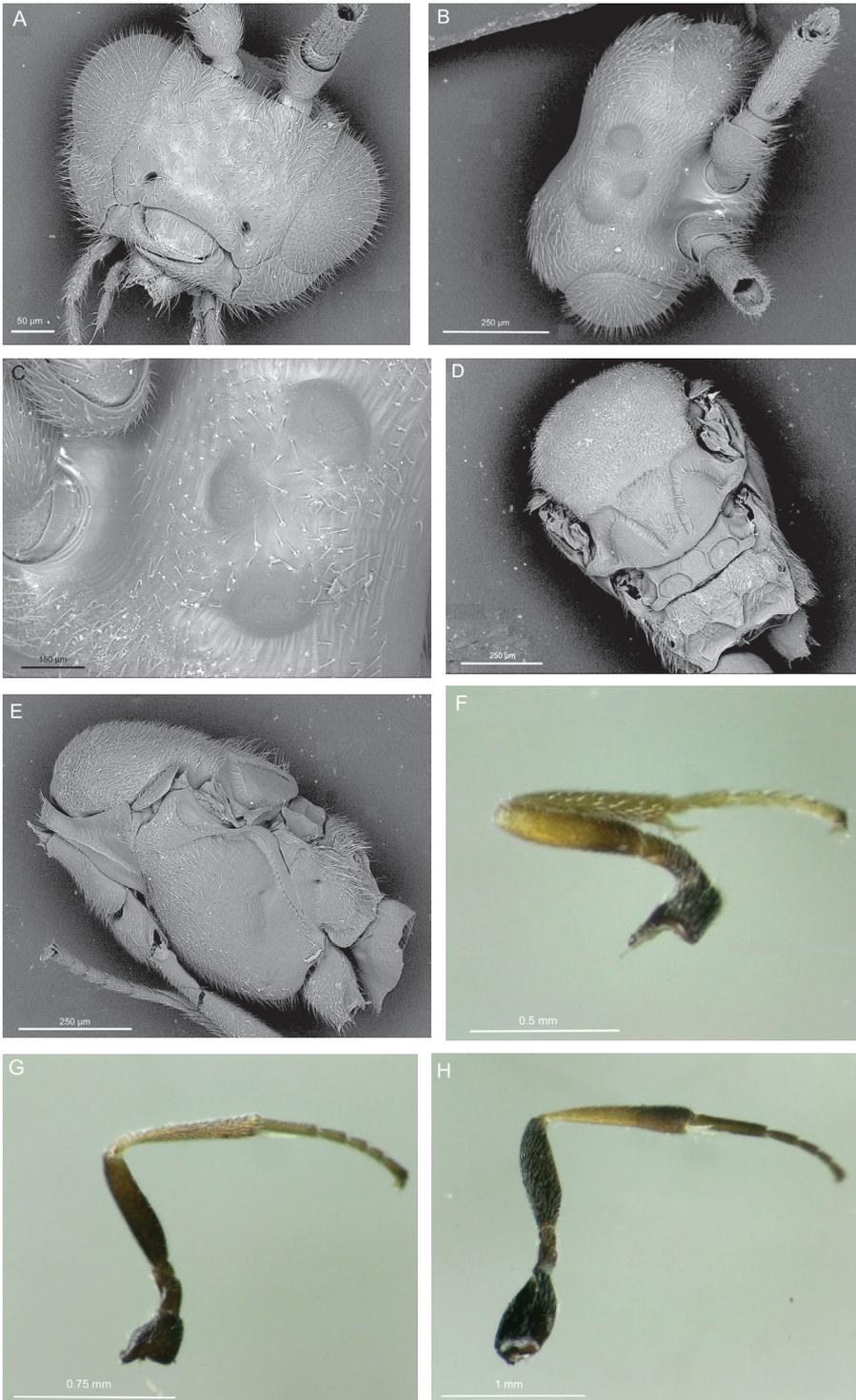


Figure 3. *Apanteles mimoristae* Muesebeck **A–C** head **A** frontal view **B** dorsal view **C** ocelli **D, E** mesosoma **D** dorsal view **E** lateral view **F–H** legs **F** anterior **G** medium **H** posterior.

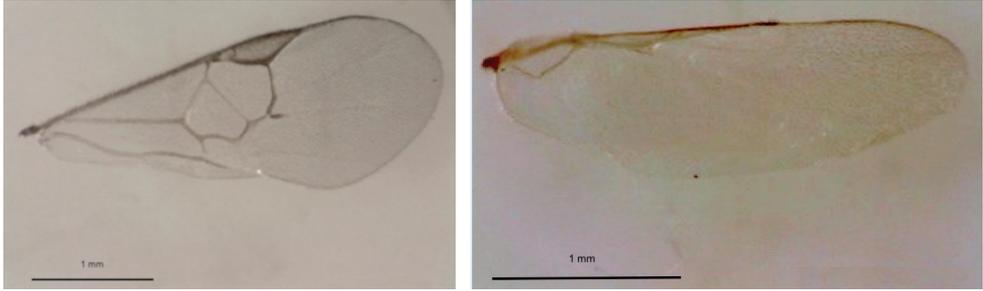


Figure 4. *Apanteles mimoristae* Muesebeck, female wings: forewing (left) and hindwing (right)

Legs: all coxae blackish; profemur: with less of the basal half dark brown and the rest dark yellow or light brown; mesofemur: more than half blackish and the rest dark brown; metafemur: entirely black; protibia: evenly light yellowish; mesotibia: basally yellowish and mostly light brown towards the apex; metatibia: color pattern varies from dark brown fading to light yellow from the base to the apex (Fig. 3E, H). Metatibia inner spur length slightly longer than half of metatarsus (Fig. 3H). Metafemur length/width: 2.92–3.16. Metatibia inner spur length/metatarsus length: 0.48–0.50. Wings: hyaline; translucent pterostigma with dark brown margins; veins transparent to dark brown (Fig. 4). Fore wing length: 3.61–3.65 mm. Fore wing veins length: r/2RS: 1.56–1.62, 2RS: 1.11–1.19, 2M/(RS+M)b: 0.78–0.85. Pterostigma length/width: 3.19–3.66. Anterior half of humeral complex whitish yellow, posterior half is light to dark brown; tegula pale to dark.

Metasoma. T1: elongated from above, wider at the base than at the apex, with marked wrinkles across all surface, mainly in the median area; barely setose, with two depressions on the posterior margin, more or less of the same size (Fig. 5A). T1 length/width at posterior margin: 2.42–2.50. T2: wider than long, smooth, without rugosities, with little setae in dorsal view and two groups of setae in lateral view (Fig. 5B, C). Width at posterior margin/length: 2.90–3.05. Ovipositor: mean length of sheaths = 0.895 mm (0.863–0.935); black, slightly wider at the base than at the apex, almost as long as the abdomen, smooth, opaque, moderately setose, and covering all the ovipositor (Fig. 5D). Ovipositor sheaths length/metatibial length: 0.833–1.02. Pleats in the hypopygium: at least 4.

Male. Very similar to female (Fig. 6), excepting smaller body size, \bar{x} = 2.696 (2.599–2.785); antennae longer than body, 3.008 (2.752–3.187).

Distribution. Mexico (Mexico City), United States (Texas and Florida).

Biology. Gregarious larva-prepupa koinobiont endoparasitoid.

Hosts. *Melitara* cf. *nephelepasa* (Pyralidae) feeding on *Opuntia ficus-indica* (Cactaceae); *Melitara junctolineella* Hulst (Pyralidae); *Loxomorpha flavidissimalis* (Grote) (Crambidae).

A list of selected morphological differences between *A. mimoristae* and four other *Apanteles* species parasitic on Pyralidae: Phycitine stem- and cladode borer larvae are summarized in Table 2. The dichotomous key provided below includes selected *Apanteles* species parasitizing phycitine cactus moths in North and South America.

Table 2. List of morphological features with measurements (mm) and rates in female specimens of known *Apanteles* species parasitizing pyraloid moths that mostly feed on cacti (*Opuntia*) in the Americas. NR = Not Reported.

Features / <i>Apanteles</i> species	<i>A. minoristae</i> Muesebeck (Muesebeck 1921, and this work)	<i>A. esthercentenoae</i> Fernández-Triana (Fernández-Triana et al. 2014) (not from <i>Opuntia</i> caterpillars)	<i>A. opuntiarum</i> Martínez & Berta (Martínez et al. 2012)	<i>A. alexanderi</i> Brèthes (Martínez et al. 2012)	<i>A. megathymyi</i> Riley (Fernández-Triana et al. 2014)
Body length	2.80–3.09	3.50–3.80	2.40–3.70	2.90–3.70	3.50–3.60
Ocular-ocellar line/ posterior ocellar diameter	2.13–2.32	2.00–2.20	NR	NR	1.40–1.60
Interocellar distance/posterior ocellar diameter	2.15–2.33	1.40–1.60	NR	NR	1.70–1.90
Antennal flagellomere 2 length/ width	2.06–2.46	2.60–2.80	NR	NR	2.60–2.80
Antennal flagellomere 14 length/ width	1.06–1.40	1.40–1.60	NR	NR	2.00–2.20
Length of antennal flagellomere 2/14	2.08–2.18	2.00–2.20	NR	NR	1.70–1.90
Metafemur length/width	2.92–3.16	3.00–3.10	NR	NR	3.20–3.30
Metatibia inner spur length / metabasisarsus length	0.48–0.5	0.40–0.50	-0.40	0.40–0.50	0.40–0.50
Fore wing length	3.61–3.65	3.90–4.00	2.30–3.70	2.90–3.80	3.70–3.80
Length of fore wing veins:	1.56–1.62	2.00–2.30 or more	1.70–1.80	1.30–1.40	1.00 or less
r/2RS	1.11–1.19	1.70–1.80	NR	NR	1.40–1.60
2RS/2M	0.78–0.85	0.50–0.60	NR	NR	0.70–0.80
2M/(RS+M) b					
Pterostigma length/width	3.19–3.66	3.10–3.50	2.50	2.50–2.60	2.60–3.00
Pits in scutrocellular sulcus	10	11 or 12	9 or 10	9 or 10	7 or 8
T1 length/width at posterior margin	2.42–2.50	1.10–1.30	1.00	1.00	2.3–2.8
T2 width at posterior margin/ length	2.90–3.05/ 4.00 or more	3.60–3.90	3.20	3.10–3.20	2.80–3.10
Ovipositor sheaths length/ metatibial length	0.83–1.02	1.20–1.30	NR	1.40–1.50	1.40–1.50
Pleats in the hypopygium	4 or more	4 or more	NR	NR	4 or more

Key to *Apanteles* species parasitoids of Pyralidae: Phycitine stem- and cladode (*Opuntia*) borer larvae in the Western hemisphere

(After Muesebeck 1921; Martínez et al. 2012; Fernández-Triana et al. 2014, and this work).

- 1 Ovipositor sheaths shorter than metasoma..... **2**
 – Ovipositor sheaths as long as metasoma..... **4**
 2 Body length more than 3.50 mm; T1 sculptured, centrally with excavated area and transverse striation inside and/or a polished knob centrally on posterior margin of mediotergite. From North America, reported mainly parasitizing caterpillars of large-sized desert Hesperidae (giant skippers) in *Yucca* plants; also from Crambidae and Pyralidae infesting Cactaceae ***A. megathymi* Riley**
 – Body length 2.9–3.0 mm; T1 smooth or with partial faint punctae or small rugae. Parasitoids of stem-boring Pyraloids including *Opuntia*-feeding caterpillars (Pyralidae: Phycitinae) **3**
 3 T1 elongated, with two similar-sized depressions on the posterior margin, one at each corner (Fig. 5A, B); posterior half with a longitudinal fovea medially; sculpturing on T1 variable, smooth or closely and finely ruguloso-punctate or with faint wrinkles across the surface, mainly in the median area; T1 barely setose; T2 with short setae in dorsal view (Fig. 5B) and two groups of setae in lateral view (Fig. 5C). North American parasitoid of *Opuntia*-feeding caterpillars: *Loxomorpha* (Crambidae) and *Melitara* spp. (Pyralidae: Phycitinae) ***A. mimoristae* Muesebeck**
 – T1 approximately square, or only slightly longer than wide, with two apicolateral transverse depressions (fig. 13, Martínez et al. 2012, pp. 441); T1 punctate and occasionally rugulose medially. From temperate South America, parasitoid of *Opuntia*-feeding caterpillars (*Cactoblastis cactorum*, Pyralidae: Phycitinae) ***A. opuntiarum* Martínez & Berta**
 4 Body length more than 3.60 mm, T1 mostly sculptured, excavated area centrally with transverse striation inside and/or a polished knob centrally on posterior margin of mediotergite; T2 with some sculpture, mostly near posterior margin (fig. 150G, Fernández-Triana et al. 2014, pp. 482). From tropical forests in Central America; parasitoid of stem-boring Crambidae and Pyralidae (not in *Opuntia*) ***A. esthercentenoae* Fernández-Triana**
 – Body length less than 3.00 mm, T1 anteriorly smooth and rugose to rugulose (figs 6, 7, Martínez et al. 2012, pp. 438), T2 with faint but distinguishable rugosities (figs 6, 7, Martínez et al. 2012, pp. 438). From semiarid temperate South America; parasitoid of *Opuntia*-feeding caterpillars (*Tucumania* sp.; Pyralidae: Phycitinae) ***A. alexanderi* Brèthes**

Phylogenetic analysis

Five barcode sequences (COI) were obtained at UT; these were all were identical and differed by only one base pair from the single sequence obtained at UAZ (0.16%); such

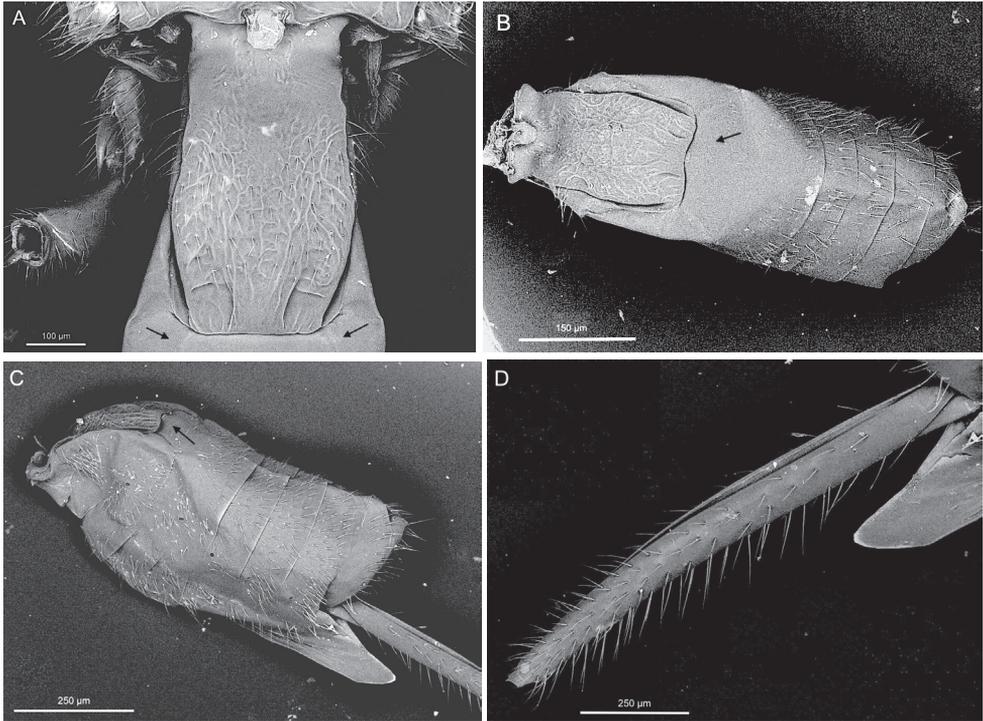


Figure 5. *Apanteles mimoristae* Muesebeck, female **A** T1, dorsal view, rough surface and posterior margin with two lateral depressions **B** metasoma dorsal view **C** metasoma lateral view, lateral setae on second and third tergite **D** ovipositor sheaths. Arrows in **A–C** indicate smooth surface of T2.

a low percentage of divergence should be considered intraspecific polymorphism. The Genbank accession numbers are [OQ676887](#) (UT) and [OQ561741](#) (UAZ). These are the first COI gene sequences reported for *A. mimoristae*.

BLAST searches of the UT sequence indicated highest similarity to *A. esthercentenoae* Fernández-Triana (2014) (Genbank sequences [EU396681](#) and [EU396684](#)) (both as *Apanteles* sp. Rodríguez 105) with 92.33 and 92.32% identity respectively and 99% cover.

Phylogenetic trees were constructed using Bayesian and maximum likelihood analyses (Figs 7, 8 respectively) of previously published *Apanteles* sequences and sequences of *A. mimoristae* obtained in this work. In both trees, *A. mimoristae* and *A. esthercentenoae* (a parasitoid of the non cactus-feeding moths *Palpita venatalis* (Schaus) (Crambidae) and *Cromarcha stroudagnesia* Solis (Pylalidae) in Costa Rica) belong in a sister group to *A. alexanderi* and *A. opuntiarum*, parasitoids of cactus-feeding phycitine Pylalidae in temperate South America. These relationships are expected considering the geographical distribution of these species pairs (North-Central America and South America respectively).

Field observations

In a collection, wasp larvae had already emerged from a dead zebra worm, preparing to pupate in the worm's gallery in a split-opened *O. ficus-indica* pad. The transparent



Figure 6. *Apanteles mimoristae* Muesebeck, male. Habitus.

cuticle of these wasp larvae reveals their striking blue or turquoise hemolymph indicating they were feeding on the hemolymph of the caterpillar host, which has the same characteristic color (Fig. 9).

Cocoons

In a field collection, a cluster of parasitic wasp cocoons was already formed and attached to the cuticle of the dead *M. cf. nephelypasa* caterpillar, inside a cactus pad; this cocoon mass was collected and incubated in the laboratory until adult emergence (Fig. 10). Cocoons were white/beige, elongated-oval, made of silk fibers, smooth. An irregular mass of cocoons was tightly packed (Fig. 10) and the cocoons were separated from each other. Some cocoons were adhered to the caterpillar cuticle, while other cocoons were inside the worm's gallery in a split-opened *O. ficus-indica* pad.

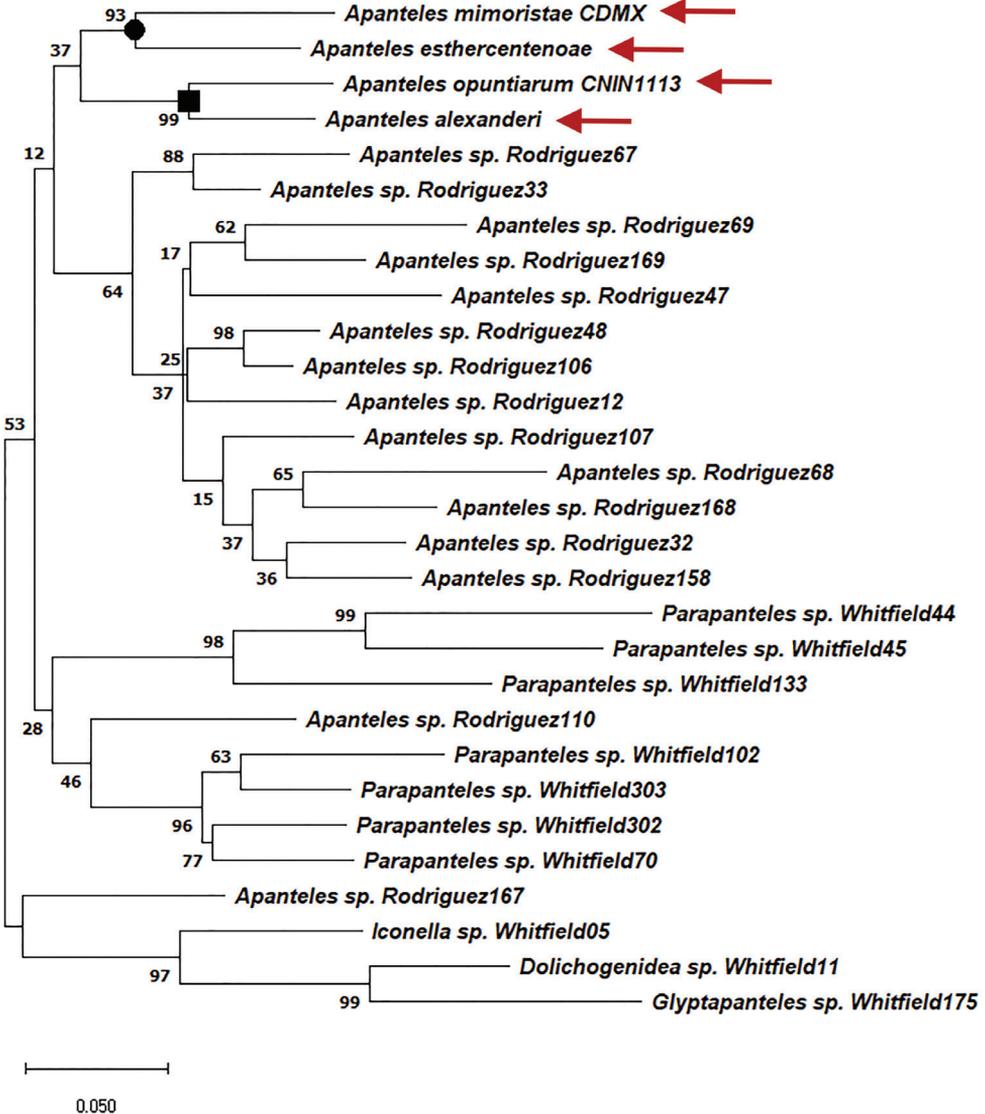


Figure 7. Bayesian tree for *Apanteles mimoristae* and related species. Arrows indicate *Apanteles mimoristae*, *A. esthercentenoae*, *A. alexanderi* and *A. opuntiarum*.

Discussion

Morphological analysis and diagnosis

Apanteles mimoristae can be distinguished from other *Apanteles* species, such as *A. alexanderi* and *A. opuntiarum*, which also attack phycitine moths feeding on *Opuntia*. They can be separated by the faint, but distinguishable rugosity on the second metasomal tergite (present in *A. alexanderi*, absent in *A. mimoristae* and *A. opuntiarum*), and the length of the ovipositor sheaths in relation to the metasoma (shorter in

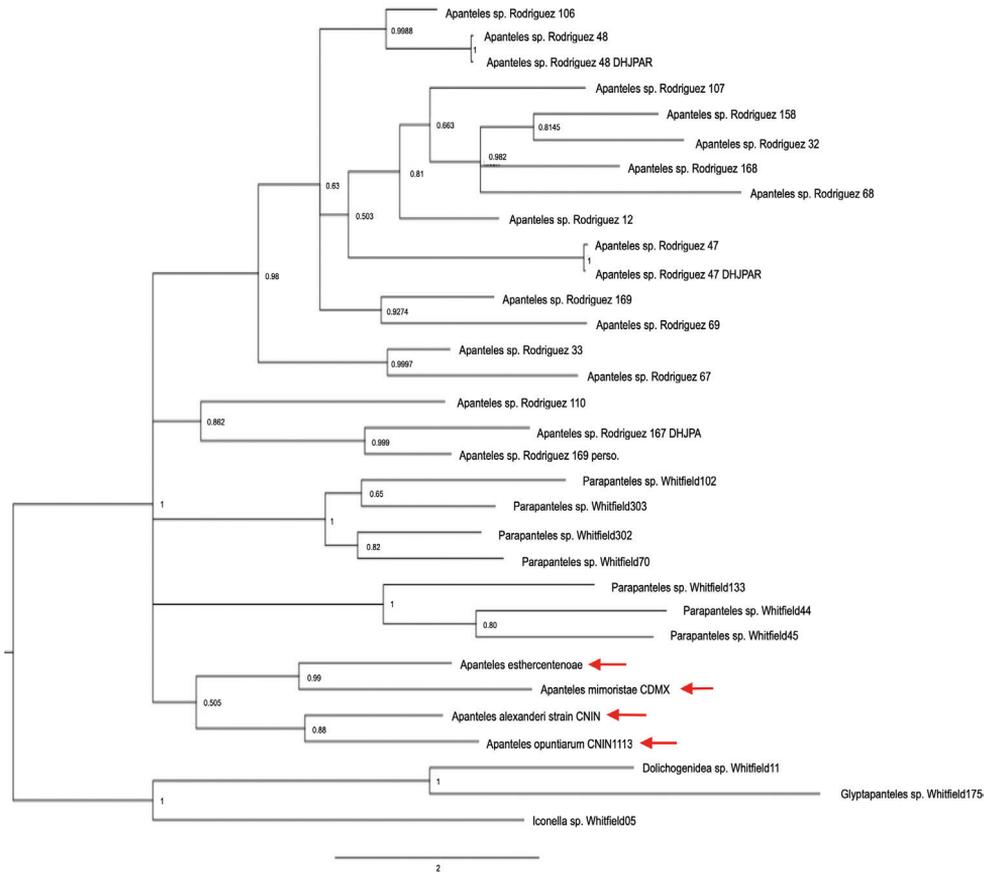


Figure 8. Maximum likelihood (1000 reps) tree for *Apanteles mimoristae* and related species. Arrows indicate *Apanteles mimoristae*, *A. esthercentenoae*, *A. alexanderi* and *A. opuntiarum*.



Figure 9. Turquoise-colored larvae of *Apanteles mimoristae* Muesebeck (Braconidae: Microgastrinae) next to a dead caterpillar of *Melitara cf. nephelepasa* (Pyrilidae) (zebra worm), inside an opened *Opuntia ficus-indica* (Cactaceae) pad. The blue-turquoise color of the wasp larvae indicates feeding on caterpillar hemolymph, which has a similar color. The arrow indicates the caterpillar's characteristic whitish stripes.



Figure 10. Adults of *Apanteles mimoristae* Muesebeck recently emerged from the irregular mass of cocoons (center). Both sexes emerged from a single caterpillar of the zebra worm, *Melitara* cf. *nephelepasa* (Pyralidae) feeding on *Opuntia ficus-indica* (Cactaceae) commercial plots from Milpa Alta, Mexico City, MX. The mass of cocoons in the center of the Petri dish shows compact, oval cocoons made up of tightly arranged silk threads.

A. opuntiarum and *A. alexanderi*, and longer in *A. mimoristae*). Also, their geographic distribution is distinctly different: *A. mimoristae* has been reported from Mexico and the United States, *A. alexanderi* from Argentina and Uruguay, and *A. opuntiarum* from Argentina (Fernández-Triana et al. 2020). Regarding related species like *A. esthercentenoae* (Costa Rica) and *A. megathymi* (Mexico and the United States), the following features present in *A. mimoristae* are diagnostic: the vertex is finely wrinkled around the ocelli but smooth between them; segment T1 has prominent and irregular roughness, and the posterior margin has two depressions of similar size, one at each corner; the second and third tergites are smooth and shiny (See key for additional features).

Molecular and phylogenetic analysis

Percent identity is a quantitative measure of the similarity between two sequences. Closely related species are expected to have a higher percentage of identity for a given sequence than distantly related species. The BLAST analysis indicated that the UT COI sequence has the highest similarity to *A. esthercentenoae* (Fernández-Triana 2014) (Genbank sequences [EU396681](#) and [EU396684](#)) with 7.67% and 7.66% difference respectively and 99% cover. The identity percentages are quite low to be considered the same species. A threshold of around 2–3% difference is commonly considered to discriminate hymenopteran species using barcode sequences ((Martinez et al. 2012; Fernández-Triana et al. 2014; Sanchez-Peña et al. 2017). The difference in sequence identity between *A. mimoristae* and the Argentinian species *A. alexanderi* and *A. opuntiarum* is more than 12%. The interspecific variation between Argentinian species is 6.8–8.1%, whereas variation among these two species and species of the similar *A. leucostigmus* complex is 9.6–12.6% (Martinez et al. 2012).

The estimated number of undescribed *Apanteles* species parasitizing Pyraloids (Pyralidae and Crambidae) in the New World is exceedingly high (Fernández-Triana et al. 2014). There are very few DNA sequences available for *Apanteles* species currently described that attack cactus moths; thus, we consider that the sampling of *Apanteles* species related to *A. mimoristae* is very incomplete; as a result, the molecular analysis presented here is eminently alpha-taxonomical, while only preliminarily phylogenetic (Fernández-Triana et al. 2014).

Both phylogenetic trees (Figs 9, 10) show that *A. mimoristae* and *A. esthercentenoae* form a clade which is the sister group of the clade containing *A. alexanderi* and *A. opuntiarum*. This could be expected from geographical separation: the first two species live north of South America (Costa Rica, United States and Mexico), while the last two species are sympatric in temperate South America (Martínez et al. 2012; Fernández-Triana et al. 2014). The genera *Dolichogenidea*, *Glyptapanteles* and *Iconella* were placed in branches separated from *Apanteles* spp. including *Apanteles mimoristae* and related species.

Geographical distribution

The species *A. mimoristae* is clearly allopatric regarding *A. alexanderi* and *A. opuntiarum*: *A. mimoristae* inhabits warm North American deserts, while *A. alexanderi* and *A. opuntiarum* are found in similar areas of temperate South America. The type specimens of *A. mimoristae* were collected at Uvalde, Texas, US (Muesebeck 1921), where the dominant vegetation is microphyllous scrub, with cactus, oaks (*Quercus* L., Fagaceae), and mesquite (*Prosopis* L., Fabaceae). It has also been reported from Florida (Fernández-Triana et al. 2020). Here, *A. mimoristae* is confirmed in detail for the first time in central Mexico (Milpa Alta), specifically from commercial *Opuntia* farms. Original vegetation there is or was a semiarid grassy steppe and open forest of pine and oak trees. This finding expands the known distribution of the species, mak-

ing it the southernmost record to date. Regarding *A. esthercentenoae*, it has been found in Costa Rica (Área de Conservación Guanacaste, ACG) from natural vegetation in tropical seasonal dry forest. *Apanteles megathymi* has been reported from Mexico and the United States (several states) where the main vegetation is thorn scrub and cactus (Muesebeck 1921; Mann 1969; and Fernández-Triana et al. 2014).

Notes on *Melitara* spp., *A. mimoristae* and related species, and biological control of invasive cactus moth

Apanteles mimoristae is a gregarious endoparasitoid of caterpillars. The herbivore host reported here is *Melitara* cf. *nephelepasa*. It should be mentioned that the taxonomy of this *Melitara* species and related North American phycitines from *Opuntia* remained unsettled until recently. One recent online review (Simonsen and Brown 2015) synonymized *M. nephelepasa* (in part) with *Melitara subumbrella* (Dyar) and declared this and *M. junctolineella* “most similar species”. However, a substantial part of the literature traditionally refers to the central Mexico zebra worm populations as *M. nephelepasa* (Mann 1968; Arnaud 1978; Badii and Flores 2001) although the correct identity of these populations is probably not *M. nephelepasa* but perhaps *M. subumbrella* or *M. junctolineella* (Simonsen and Brown 2008; Moth Photographers Group 2023).

Muesebeck (1921) did not report whether the *A. mimoristae* specimens were solitary or gregarious. They emerged from a very similar or identical zebra worm species, *M. junctolineella* and from the *Opuntia* webworm *Loxomorpha flavidissimalis* (Grote) (Crambidae). The genus *Loxomorpha* was formerly known as *Mimorista*, hence the etymology of this wasp species, *A. mimoristae*. As for the parasitoids *A. alexanderi* and *A. opuntiarum*, each has a strong preference for the phycitines *Tucumania* and *Cactoblastis* respectively, in arid temperate South America (Martinez et al. 2012). *Apanteles esthercentenoae* has been reared from *Palpita venatalis* (Crambidae) and *Cromarcha stroudagnesia* (Pyrilidae), a stem borer. *Apanteles megathymi* mainly parasitizes borer larvae of some of the largest-sized known Hesperiiidae, the “giant skippers”: *Agathymus stephensi* (Skinner) and species of *Megathymus* like *M. coloradensis* (Fernández-Triana et al. 2014); it has also been reported from *M. nephelepasa* at San Luis Potosí state, central Mexico (Mann 1969). These five *Apanteles* species form a biologically heterogeneous assemblage of species with dissimilar environments and hosts. This suggests that many undescribed species might belong in this assemblage, and that our taxonomical sampling remains quite incomplete.

Regarding biological control of the invasive *C. cactorum*, it should be considered that *A. mimoristae* is very similar to *A. opuntiarum*, whose release in North America is being explored. Therefore, accurate identification of these wasps is essential. Future work should consider experiments exposing *C. cactorum* caterpillars to *A. mimoristae*, to determine their suitability as hosts of these wasps. The role of this and other possible new associations in biological control of *C. cactorum*, in areas where protection of susceptible species of Cactaceae is a concern should be investigated.

Author contribution statement

RVL: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Validation; Visualization; Writing – original draft. RP: Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Visualization; LEG: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing – review and editing. JCR: Investigation; Methodology; Resources; Validation. GGM: Investigation; Methodology; Resources. RCC: Data curation; Investigation; Methodology; Resources; Validation. MPEL: Methodology; Resources. JFT: Investigation; Resources; Validation. SRSP: Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Validation; Visualization; Writing – original draft; Writing – review & editing.

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