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Taxonomy and systematics

Integrative taxonomy to assess the species richness of chalcidoid parasitoids (Hymenoptera) associated to Bruchinae (Coleoptera: Chrysomelidae) from Mexico

Taxonomía integrativa para investigar la riqueza de especies de parasitoides calcidoideos (Hymenoptera:) asociados con Bruchinae (Coleoptera: Chrysomelidae) de México

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Abstract

Chalcidoidea are a highly diverse group of Hymenoptera and the most common parasitoids, being associated to more than 15 hexapod orders. The identification of species in this superfamily is considerably difficult due to their small size, lack of comprehensive taxonomic studies for many groups and convergence of morphological features. In this study, we aimed to identify the chalcidoid species that are associated to bruchine beetles (Chrysomelidae) from central and southern Mexico, using morphological and molecular (mitochondrial COI gene) evidence. We report a total of 39 bruchine species associated to 8 plant taxa. The gathered morphological and molecular evidence allowed to delimit 29 chalcidoid species, 6 of which are new records for Mexico. We found inconsistencies in the species delimitation between the morphological and molecular data in species of *Eupelmus* (Eupelmidae) and *Horismenus* (Eulophidae). This study highlights the considerable species richness of chalcidoid taxa that are associated to bruchine beetles, and the need to provide reliable host records for members of this group of parasitoids.

Keywords: Host-parasitoid association; Neotropics; Bean weevils; COI; Taxonomy

Resumen

Chalcidoidea es un grupo extremadamente diverso de Hymenoptera y los parasitoides más comunes, encontrándose asociados con más de 15 órdenes de hexápodos. La identificación de especies en esta superfamilia tiende a ser difícil debido a su tamaño pequeño, falta de estudios taxonómicos exhaustivos para muchos grupos y convergencia de caracteres morfológicos. El presente estudio tuvo como objetivo identificar las especies de parasitoides (Hymenoptera: Chalcidoidea) asociados con escarabajos Bruchinae (Coleoptera: Chrysomelidae) del centro y sur de México utilizando evidencia morfológica y molecular (gen mitocondrial COI). Se reportan 39 especies de bruchinos asociadas con 8 taxones vegetales. La evidencia morfológica y molecular examinada permitió delimitar 29 especies de chalcidoideos, de las cuales 6 son nuevos registros para el territorio mexicano. Se encontraron inconsistencias en la delimitación de especies entre los datos morfológicos y moleculares en los géneros *Eupelmus* (Eupelmidae) y *Horismenus* (Eulophidae). Este estudio destaca la considerable riqueza de especies de Chalcidoidea que está asociada a los Bruchinae, así como la necesidad de proporcionar registros confiables de hospedantes para los miembros de este grupo de parasitoides.

Palabras clave: Relación parasitoide-hospedero; Neotrópico; Gorgojo del frijol; COI; Taxonomía

Introduction

Parasitoid wasps are one of the most preferred model systems in evolutionary biology, behavioral and community ecology and biological control due to their high complexity of trophic interactions (Godfray & Shimada, 1999). Like other parasitoid wasps, chalcidoids are among the most difficult insects to identify and classify due to their small size, lack of comprehensive taxonomic studies for many groups and convergence of morphological features (Gebiola et al., 2012).

With over 25,000 described species, the superfamily Chalcidoidea (Hymenoptera) is an extremely diverse group of hymenopterans characterized by having high morphological variation and considerable size range (0.13 to 20 mm) (Heraty et al., 2013). This morphological diversity has resulted in a large number of currently described supraspecific taxa, with 19 families, more than 90 subfamilies and around 300 genera (Heraty et al., 2013; Noyes, 2020). Chalcidoidea contain one-third of all hymenopteran parasitoid species and is the second most speciose group of parasitoids after Ichneumonoidea (LaSalle & Gauld, 1991). Ecologically and economically, they are one of the most important taxa used to regulate or manage insect populations (Heraty, 2004; LaSalle, 1993; Noyes, 1978), having the highest success rate in biological control programs for the establishment and control of pest populations. Moreover, their high degree of specificity to their hosts clearly reduces the possibility of attacking non-target organisms (Greathead, 1986; Heraty, 2004; Noyes, 1978; Noyes & Hayat, 1994).

Chalcidoidea parasitize a great diversity of taxonomic groups (approximately 19 insects orders) (Noyes, 2020), including Bruchinae (Coleoptera: Chrysomelidae), commonly known as bean weevils (Romero, 2002). About 30 species of bruchines around the world are considered as serious pests, and at least 9 are cosmopolitan as a result of

commercial activities (Kingsolver, 2004). Bruchine larvae feed inside seeds, which makes their detection and control extremely difficult (Southgate, 1979).

Currently, a total of 334 bruchine species grouped in 27 genera have been reported for the Mexican territory, representing 43.5% of the total genera for this subfamily (De la Cruz, 2013; Johnson & Kingsolver, 1981; Luna et al., 2002; Romero, 2009; Romero & Johnson, 2004). To date, 139 Chalcidoidea species belonging to 9 families are known as primary parasitoids of 242 species of bruchines around the world, of which 42 have been recorded for Mexico (Pérez-Benavides et al., 2019). Factors such as subtle morphological differences, sexual dimorphism, and lack of host records and taxonomic keys have traditionally impeded the accurate identification of species. Therefore, it is necessary to include other approaches for species delimitation in the group.

The use of molecular markers in systematics has proven to be essential for delimiting cryptic hymenopteran parasitoid species (Heraty, 2009; Santos et al., 2011). Mitochondrial (mt) genes have served as a practical, efficient markers for studies on molecular evolution and populations genetics in Chalcidoidea since they are characterized by high rates of evolution and genome reorganization (Dowton & Austin, 1995; Oliveira et al., 2008; Xiao et al., 2011). In particular, a fragment of the cytochrome oxidase subunit 1 (COI) mt gene known as the DNA Barcode (Hebert et al., 2004) has proved to be a very useful tool for species identification in many groups of animals, including insects (Jeffery et al., 2011; Rivera & Currie, 2009; Robinson et al., 2009). However, there is controversy about the exclusive dependence of species delimitation on mtDNA without inclusion of morphological or ecological data (Cognato, 2006; Meier et al., 2006). Accordingly, it is necessary to include an integrative taxonomic approach using multiple data sources to avoid dependence on just one

key character to test species hypotheses in problematic groups (Dayrat, 2005; Padial et al., 2010; Will et al., 2005). In hymenopteran parasitoids, the DNA barcode locus has helped to determine the identity of a number of poorly known taxa in combination with morphological and ecological evidence, and also has served to evaluate the geographic variation and specificity of their hosts (e.g., Ács et al., 2010; Gebiola et al., 2012; Kaartinen et al., 2010; Sheffield et al., 2009; Smith et al., 2008; Sun et al., 2011).

In this work, we employ an integrative taxonomy approach to identify chalcidoid parasitoid species associated to Bruchinae that were collected in several localities along central and southeast Mexico. For this, we use morphological evidence and generate COI sequences for most of the reared chalcidoid morphospecies to delineate species using the 2% divergence criterion (Ratnasingham & Hebert, 2013) and a coalescent approach (General Mixed Yules Coalescent model; GMYC) (Fujisawa & Barraclough, 2013). This faunistic study highlights the considerable but mostly neglected species richness of Chalcidoidea associated to bruchines in the Mexican territory

Materials and methods

Mature pods of the following 8 legume species were collected between 2014–2017 in 53 localities from 10 Mexican states (Fig. 1): *Acacia pennatula* (Schltdl. & Cham.) Benth., *Ac. farnesiana* (L.) Willd., *Leucaena leucocephala* (Lam.) de Wit, *L. pulverulenta* (Schltdl.) Benth., *Lysiloma microphyllum* Benth., *Phaseolus lunatus* L., *P. vulgaris* L. and *Senna polyantha* (Colladon) Irwin & Barneby. Once collected, pods were placed in plastic bags for insect rearing at the Instituto de Biología, Universidad Nacional Autónoma de México (IB-UNAM). All pods were examined every 1 to 4 days for both parasitoids and bruchines. All the emerged insects were sacrificed, placed in 96% ethanol and stored at -20 °C until they were processed for DNA extraction. A list with the examined taxa and their localities of provenance and GenBank accession numbers is given in the discussion section.

All emerged chalcidoid specimens were mounted on a card-point according to Triplehorn and Johnson (2005). Taxonomic identifications were carried out with a Leica® MZ16 stereomicroscope. Photographs were taken with an AxioCam MRc5 camera with MTB extension tubes adapted to Zeiss Discovery V12 stereomicroscope. The literature employed for identification included keys and descriptions by Burks (1956), Gibson (1995, 2011, 2013), Gibson et al. (1997), Grissell (1976), Hansson (2002, 2009) and Hansson et al. (2004). Each description was reviewed to corroborate identification and the material was also



Figure 1. Sampling points of plants collected in Mexico.

compared with specimens deposited at the Entomological Collection of the Zoology Museum in the University of Costa Rica (MZUCR).

DNA was extracted from each specimen using the EZ-10 spin Column Genomic DNA Minipreps extraction Kit (Biobasic Canada, Ontario, Canada). The entire body of each specimen was used for DNA extraction using the following non-destructive method. Specimens stored in 96% EtOH were air-dried and then placed in a mix of 180 µl of ACL buffer (Biobasic Canada INC) and proteinase K (20 µl). Specimens were subsequently incubated for 4 hours at 56 °C. We then carefully removed the supernatant and washed and returned the specimens to 96% ethanol until they were mounted. The supernatant was treated as lysate for DNA extraction following the manufacturer's protocol. The DNA template was eluted in a final volume of 30 µl of dd water.

We generated sequences belonging to a fragment of the COI mt DNA gene, which represents most of the standard locus used for DNA barcoding in animals (Hebert et al., 2003). The following primers were used to amplify the selected COI fragment: LCO1490 (5' -GGT CAA CAA ATC ATA AAG ATA TTG G-3'), HCO2198 (5' -TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al., 1994), LCO1490puc 5' -TTT CAA CWA ATC ATA AAG ATA TTG G-3' and HCO2198puc 5' -TAA ACT TCW GGR TGW CCA AAR AAT CA-3' (Cruaud et al., 2010). PCRs were performed in a final volume of 15 µl, which consisted of 1.5 µl PCR buffer, 0.2 µl of each primer (2 µM), 0.2 µl of Taq polymerase (Invitrogen, Grand Island, NY, USA, 1 unit/25 µl), 2 µl of DNA extract, and 10.9 of H₂O. Unpurified PCR products were sent for sequencing to the laboratory of Genomic Sequencing of Biodiversity and Health at IB-UNAM. Sequences were edited and aligned with ClustalW implemented in the program BioEdit version 7.0.5 (Hall, 2005).

Two DNA sequence-based species delimitation approaches were employed, a 2% sequence divergence criterion and the GMYC model (Hebert et al., 2003; Pons et al., 2006). For the first approach, we estimated corrected COI pairwise distances with the program Mega6 using the Kimura 2-parameter model (Kimura, 1980) (Supplementary material 1). Substitution-rate variation among sites was modeled with a gamma distribution (shape parameter = 1). COI distances were visualized reconstructing a Neighbor-Joining (NJ) tree (Supplementary material 2). We also compared the sequences that were generated for specimens assigned to *Eupelmus* sp. aff. *annulatus* and *E. sp. aff. pulchripes* with sequences of *E. annulatus* Nees and *E. pulchripes* Cameron retrieved from GenBank from the western Palaearctic and USA and Canada, respectively (GenBank accession numbers: KJ018333, 363, 379, 395, 401, 403, 438, 439, 471 and KF444812, KR996137, MG485752; respectively).

For the GMYC model, we generated an ultrametric tree using the Bayesian inference method with the program BEAST version 2.4.6 (Bouckaert et al., 2014). We ran the analysis for 10 million generations, with samples retained every 1000 generations, using “uncorrelated lognormal relaxed clock” and a coalescing “tree prior”. The first 25% of sampled trees from all runs were discarded as burn-in and the remaining trees were used to build a maximum clade credibility consensus tree with the program TreeAnnotator version 2.4.6 (part of the BEAST package; Bouckaert et al., 2014) using the “mean heights” option. We used the GMYC web server (<https://species.h-its.org/gmyc/>) to carry out the GMYC analysis.

Results

We examined 603 chalcidoid specimens. Of these specimens, 6 belong to the genus *Elachertus* (Eulophidae)

associated to legumes of *Senna polyantha*. Members of *Elachertus* are mainly parasitoids of concealed larvae of Lepidoptera (Schauff, 1985), and therefore they are not directly associated to Bruchinae. We morphologically assigned the remaining 597 chalcidoid specimens that probably are parasitoids of Bruchinae to 5 families, 10 genera and 29 species (Table 1). Below we treat these taxa by family in alphabetical order.

We generated a total of 74 COI sequences, which ranged from 400 to 630 bp in length. These sequences were assigned to 19 species that were identified based on morphology, which belong to the following 9 chalcidoid genera: *Horismenus*, *Elachertus*, *Paracrias*, *Eupelmus*, *Brasema*, *Eurydinoitoides*, *Lariophagus*, *Monoksa* and *Chryseida*. We could not generate sequences for members of *Eurytoma*, *Phylloxeroxenus* and *Torymus*.

Use of 2% sequence divergence approach recovered a total of 32 ‘molecular operational taxonomic units’ (MOTUs) (Fig. 2, Supplementary material 1), whereas the GMYC model recovered 22 species (Supplementary material 2). A higher number of MOTUs was found among the examined specimens of *Horismenus* (19 MOTUs) and *E. sp. aff. pulchripes* (5 MOTUs) with respect to the morphological identification (8 and 3 morphospecies, respectively). In contrast, the GMYC model and our morphological discrimination of species were concordant for the latter 2 taxa (Supplementary material 2). All MOTUs assigned to *E. aff. sp. annulatus* and *E. aff. sp. pulchriceps* had considerably high genetic distances compared to sequences of specimens assigned to *E. annulatus* and *E. pulchriceps* from the western Palaearctic and the Nearctic, respectively (12.13%-13.73% and 10.66%-13.95%, respectively).

Table 1

List of parasitoid species (Chalcidoidea) with their associated host plant species and probable bruchine hosts. * = New host records.

Taxa	Associated host plant taxon	Associated Bruchinae taxon
<i>Elachertus</i> sp.	<i>Senna polyantha</i> (Colladon) Irwin & Barneby	
<i>Horismenus bruchophagus</i> Burks, 1971	<i>Acacia pennatula</i> (Schltdl. & Cham.) Benth. *	<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907) *
	<i>Acacia farnesiana</i> (L.) Willd. *	<i>Acanthoscelides mankinsi</i> Johnson, 1983 *
		<i>Mimosestes nubigens</i> (Motschulsky, 1874) Bruchinae sp.
<i>Horismenus butcheri</i> Hansson et al., 2004	<i>Leucaena leucocephala</i> (Lam.) * <i>Phaseolus vulgaris</i> L.	Bruchinae sp. <i>Acanthoscelides obvelatus</i> Bridwell, 1942 <i>Acanthoscelides obtectus</i> (Say, 1831)

Table 1
Continued

Taxa	Associated host plant taxon	Associated Bruchinae taxon
		<i>Zabrotes</i> spp.*
	-	<i>Merobruchus insolitus</i> (Sharp, 1885) *
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980 *
	-	<i>Stator limbatus</i> (Horn, 1873) *
<i>Horismenus depressus</i> Gahan, 1930	<i>Senna polyantha</i> (Colladon) Irwin & Barneby *	Bruchinae sp.
	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obvelatus</i> Bridwell, 1942
		<i>Acanthoscelides obtectus</i> (Say, 1831)
		<i>Zabrotes</i> spp.
	-	<i>Merobruchus insolitus</i> (Sharp, 1885) *
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980*
	-	<i>Stator limbatus</i> (Horn, 1873) *
<i>Horismenus missouriensis</i> (Ashmead, 1888)	<i>Leucaena leucocephala</i> (Lam.)	Bruchinae sp.
		<i>Merobruchus sonorensis</i> Kingsolver, 1980*
		<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907)
		<i>Acanthoscelides mankinsi</i> Johnson, 1983
	-	<i>Acanthoscelides</i> sp. 1
	<i>Leucaena pulverulenta</i> (Schltdl.) Benth. *	Bruchinae sp.
	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obtectus</i> (Say, 1831)
		<i>Acanthoscelides obvelatus</i> Bridwell, 1942
		<i>Zabrotes</i> spp.
	<i>Phaseolus lunatus</i> L.*	<i>Mimosestes nubigens</i> (Motschulsky, 1874)
	-	<i>Merobruchus insolitus</i> (Sharp, 1885)
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980*
	-	<i>Stator limbatus</i> (Horn, 1873)
<i>Horismenus nigrocyanus</i> Ashmead, 1894*	-	Bruchinae sp.
<i>Horismenus</i> sp.1	-	<i>Merobruchus insolitus</i> (Sharp, 1885)
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980
	-	<i>Stator limbatus</i> (Horn, 1873)
<i>Horismenus</i> sp. 2	<i>Leucaena leucocephala</i> (Lam.)	<i>Merobruchus sonorensis</i> Kingsolver, 1980
		<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907)
		<i>Acanthoscelides mankinsi</i> Johnson, 1983
		Bruchinae sp.
	<i>Leucaena pulverulenta</i> (Schltdl.) Benth.	Bruchinae sp.
	<i>Lysiloma microphyllum</i> Benth.	Bruchinae sp.
	<i>Senna polyantha</i> (Colladon) Irwin & Barneby	-
	-	<i>Acanthoscelides</i> sp. 1
	-	<i>Merobruchus insolitus</i> (Sharp, 1885)
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980
	-	<i>Stator limbatus</i> (Horn, 1873)
<i>Horismenus</i> sp. 3	-	<i>Merobruchus insolitus</i> (Sharp, 1885)

Table 1
Continued

Taxa	Associated host plant taxon	Associated Bruchinae taxon
<i>Horismenus</i> sp. 4	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obtectus</i> (Say, 1831) <i>Acanthoscelides obvelatus</i> Bridwell, 1942 <i>Zabrotes</i> spp.
	<i>Lysiloma microphyllum</i>	-
	-	<i>Merobruchus insolitus</i> (Sharp, 1885)
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980
	-	<i>Stator limbatus</i> (Horn, 1873)
	-	<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907)
<i>Paracrias pluteus</i> Hansson, 2002*	-	<i>Merobruchus insolitus</i> (Sharp, 1885) *
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980 *
	-	<i>Stator limbatus</i> (Horn, 1873) *
	<i>Leucaena pulverulenta</i> (Schltdl.) Benth. *	Bruchinae sp.
	<i>Lysiloma microphyllum</i> Benth. *	Bruchinae sp.
<i>Brasema bruchivora</i> Crawford, 1908 *	<i>Lysiloma microphyllum</i> Benth. *	Bruchinae sp.
<i>Brasema neococcidis</i> (Peck, 1951) *	<i>Phaseolus vulgaris</i> L. *	<i>Acanthoscelides obtectus</i> (Say, 1831) *
		<i>Acanthoscelides obvelatus</i> Bridwell, 1942*
		<i>Zabrotes</i> spp. *
	<i>Lysiloma microphyllum</i> Benth. *	Bruchinae sp.
<i>Eupelmus</i> sp. aff. <i>annulatus</i>	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obtectus</i> (Say, 1831) <i>Acanthoscelides obvelatus</i> Bridwell, 1942 <i>Zabrotes</i> spp.
<i>Eupelmus</i> sp. aff. <i>pulchriceps</i>	<i>Leucaena leucocephala</i> (Lam.)	Bruchinae sp.
	<i>Lysiloma microphyllum</i> Benth.	Bruchinae sp.
	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obtectus</i> (Say, 1831) <i>Acanthoscelides obvelatus</i> Bridwell, 1942 <i>Zabrotes</i> spp.
	<i>Phaseolus lunatus</i> L.	<i>Acanthoscelides argillaceus</i> (Sharp, 1885) <i>Acanthoscelides taboga</i> Johnson, 1983 <i>Acanthoscelides obtectus</i> (Say, 1831) <i>Acanthoscelides obvelatus</i> Bridwell, 1942 <i>Mimosestes mimosae</i> (Fabricius, 1781) <i>Acanthoscelides</i> sp. <i>Zabrotes</i> spp.
	<i>Senna polyantha</i> (Colladon) Irwin & Barneby	Bruchinae sp.
	-	<i>Merobruchus insolitus</i> (Sharp, 1885)
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980
	-	<i>Mimosestes nubigens</i> (Motschulsky, 1874)
	-	<i>Stator limbatus</i> (Horn, 1873)
<i>Chryseida bennetti</i> Burks, 1956	<i>Leucaena leucocephala</i> (Lam.) *	<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907)* <i>Merobruchus sonorensis</i> Kingsolver, 1980*
		<i>Acanthoscelides mankinsi</i> Johnson, 1983 *
	<i>Phaseolus lunatus</i> L *	<i>Acanthoscelides obtectus</i> (Say) <i>Acanthoscelides obvelatus</i> Bridwell*

Table 1
Continued

Taxa	Associated host plant taxon	Associated Bruchinae taxon
		<i>Acanthoscelides taboga</i> Johnson, 1983 *
		<i>Acanthoscelides</i> sp.
		<i>Mimosestes mimosae</i> (Fabricius, 1781) *
		<i>Zabrotes</i> spp. *
	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obtectus</i> (Say)
		<i>Acanthoscelides obvelatus</i> Bridwell *
		<i>Zabrotes</i> spp. *
	-	<i>Acanthoscelides</i> sp. 1
	-	<i>Acanthoscelides</i> sp. 2
<i>Eurytoma</i> sp. 1	-	<i>Acanthoscelides</i> sp.
<i>Phylloxeroxenus</i> sp. 1	<i>Acacia farnesiana</i> (L.) Willd.	<i>Mimosestes nubigens</i> (Motschulsky, 1874)
	<i>Phaseolus lunatus</i> L	<i>Acanthoscelides argillaceus</i> (Sharp, 1885)
	-	<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907)
	-	<i>Merobruchus insolitus</i> (Sharp, 1885)
	-	<i>Merobruchus santarosae</i> Kingsolver, 1980
	-	<i>Stator limbatus</i> (Horn, 1873)
<i>Phylloxeroxenus</i> sp. 2	-	Bruchinae sp.
<i>Eurydinoteloides incerta</i> Ashmead, 1893	<i>Phaseolus vulgaris</i> L. *	<i>Acanthoscelides obtectus</i> (Say, 1831) *
		<i>Acanthoscelides obvelatus</i> Bridwell, 1942 *
		<i>Zabrotes</i> spp. *
<i>Eurydinoteloides</i> sp.1, sp. 2	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obtectus</i> (Say, 1831)
		<i>Acanthoscelides obvelatus</i> Bridwell, 1942
		<i>Zabrotes</i> spp.
<i>Lariophagus distinguendus</i> (Förster, 1841)	<i>Phaseolus lunatus</i> L. *	<i>Acanthoscelides argillaceus</i> (Sharp, 1885) *
<i>Lariophagus texanus</i> Crawford, 1909	<i>Leucaena leucocephala</i> (Lam.) *	<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907)
		<i>Acanthoscelides mankinsi</i> Johnson, 1983 *
		<i>Merobruchus sonorensis</i> Kingsolver, 1980 *
<i>Lariophagus</i> sp.	-	-
<i>Monoksa dorsiplana</i> Boucek, 1991 *	<i>Acacia farnesiana</i> (L.)	<i>Mimosestes nubigens</i> (Motschulsky, 1874) *
		Bruchinae sp.
<i>Pteromalus fuscipennis</i> (Walker, 1834) *	<i>Phaseolus vulgaris</i> L. *	<i>Acanthoscelides obtectus</i> (Say, 1831) *
		<i>Acanthoscelides obvelatus</i> Bridwell, 1942 *
		<i>Zabrotes</i> spp. *
<i>Pteromalus</i> sp.	<i>Leucaena leucocephala</i> (Lam.)*	<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907) *
		<i>Acanthoscelides mankinsi</i> Johnson, 1983 *
		<i>Merobruchus sonorensis</i> Kingsolver, 1980 *
<i>Torymus moazopi</i> Pérez-Benavides 2020	<i>Phaseolus vulgaris</i> L.	<i>Acanthoscelides obtectus</i> (Say, 1831)
		<i>Acanthoscelides obvelatus</i> Bridwell, 1942
		<i>Zabrotes</i> spp.
	<i>Phaseolus lunatus</i> L.	<i>Acanthoscelides obtectus</i> (Say, 1831)
		<i>Acanthoscelides obvelatus</i> Bridwell, 1942
		<i>Zabrotes</i> spp.

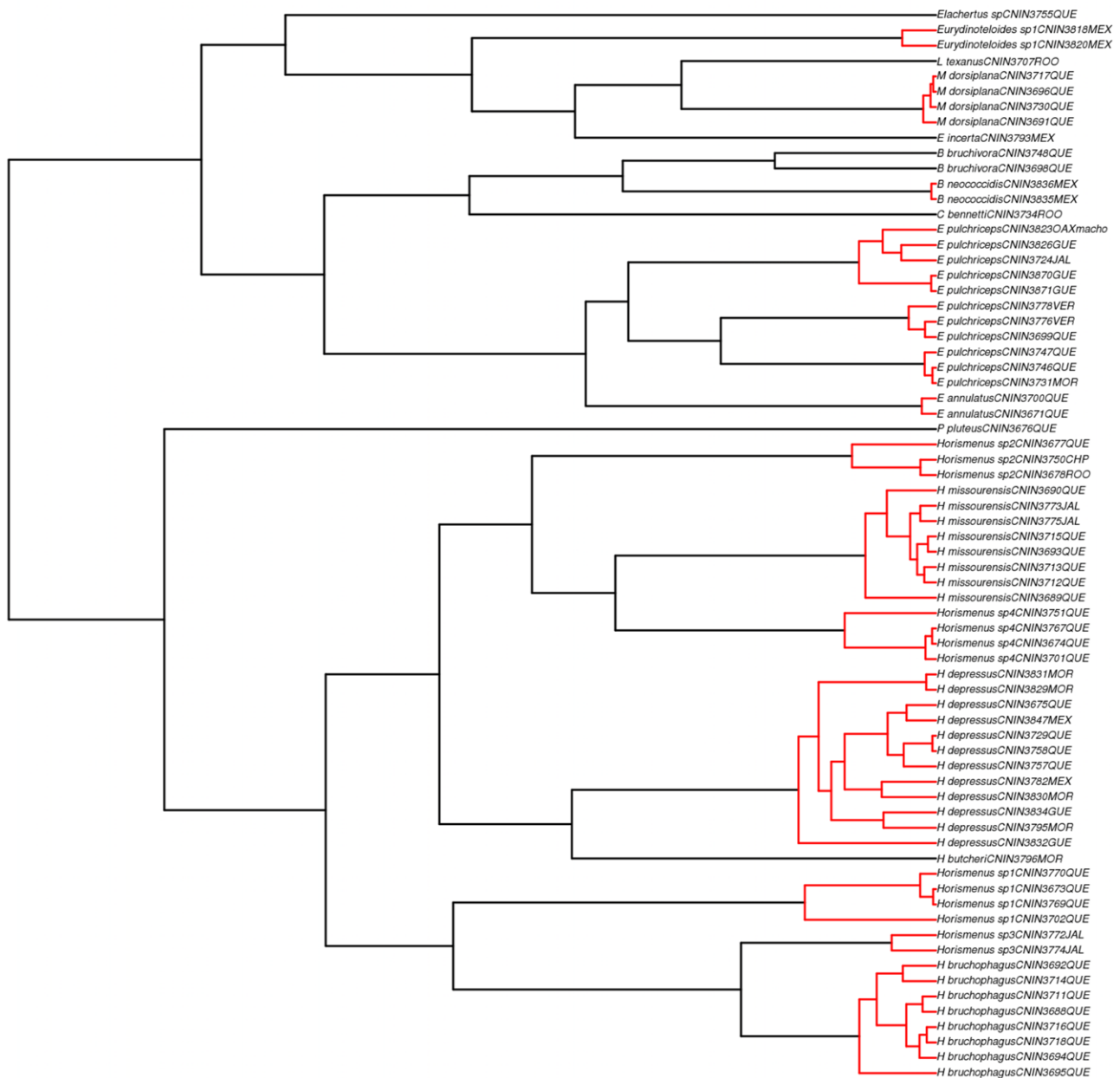


Figure 2. Ultrametric tree obtained with the program BEAST showing the species delimited by the GMYC model using the COI haplotypes. Red branches are GMYC species represented by various haplotypes. Black terminal branches represent singletons. Names of terminal taxa include their voucher numbers, and their three-letter-code refer to the Mexican state where the specimen was collected (CHP = Chiapas, GUE = Guerrero, JAL = Jalisco, MEX = Estado de México, MOR = Morelos, OAX = Oaxaca, QUE = Querétaro, ROO = Quintana Roo, VER= Veracruz).

Eulophidae

Elachertus sp. (Fig. 3a)

Material examined: 4 specimens; Mexico, Querétaro, Chichidho, 20°45'14.93" N, 99°56'59.99" W, 2,044 m alt. N. Delgado & J. Gutiérrez CNIN 3670. 2 specimens;

Mexico, Querétaro, Chichidho, 20°45'40.85" N, 99°56'44.28" W, 2,009 m alt. N. Delgado & J. Gutiérrez CNIN 3755, 3756 ex *Senna polyantha* (Colladon) Irwin & Barneby.

Horismenus bruchophagus Burks, 1971 (Fig. 3b)

Material examined: 2 specimens; Mexico, Querétaro, Landa de Matamoros, 21°11'7.28" N, 99°19'2.82" W, 1,011 m alt. N. Delgado & J. Gutiérrez ex *Acanthoscelides macrophthalmus* (Schaeffer, 1907), *Acanthoscelides mankinsi* Johnson, 1983 in pods of *Acacia pennatula* (Schltdl. & Cham.) Benth. 5 specimens; Mexico, Querétaro, Chichidho, 20°45'14.99" N, 99°57'1.51" W, 2,071 m alt. N. Delgado & J. Gutiérrez ex *Mimosestes nubigens* (Motschulsky, 1874) in pods of *Acacia farnesiana* (L.) Willd. 5 specimens; Mexico, Querétaro, 20°36'23.89" N, 100°9'55.08" W, 1,913 m alt. N. Delgado & J. Gutiérrez CNIN 3714, 3692 ex Bruchinae in pods of *Acacia farnesiana* (L.) Willd. 3 specimens; Mexico, Querétaro, Chichido, 20°45'14.99" N, 99°57'1.51" W, 2,071 m alt. N. Delgado & J. Gutiérrez CNIN 3716, 3694, 3695 ex Bruchinae in pods of *Acacia farnesiana* (L.) Willd. 10 specimens; Mexico, Querétaro, Chichidho-Bernal, 20°44'33.63" N, 99°56'21.11" W, 2,089 m alt. N. Delgado & J. Gutiérrez CNIN 3697, 3718 ex Bruchinae in pods of *Acacia farnesiana* (L.) Willd. 7 specimens; Mexico, Querétaro, 6 Chichido-Bernal, 20°45'16.82" N, 99°57'4.12" W, 2,059 m alt. N. Delgado & J. Gutiérrez CNIN 3688, 3711.

Horismenus butcheri Hansson et al., 2004 (Fig. 3c)

Material examined: 1 specimen; Mexico, Chiapas, Chiapa de Corzo, Colonia Emiliano Zapata, 16°9' N, 93°15' W, 599 m alt. A. Zaldivar ex Bruchinae in pods of *Leucaena leucocephala* (Lam.). 2 specimens; Mexico, Estado de México, 18°58'46.265" N, 99°12'53.171" W, 1,858 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Estado de México, 19°1'1.06" N, 100°1'48.165" W, 1,964 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Estado de México, Cuernavaca - Tepoztlán road, 18°58'33.387" N, 99°10'12.252" W, 1,676 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Morelos, Morelos Cuernavaca - Yautepec de Zaragoza 4b, Ixcatepec, 18°58'35.321" N, 99°7'1.358" W, 1,743 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Querétaro, Jalpan-puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980) and *Stator limbatus* (Horn, 1873).

Horismenus depressus Gahan, 1930 (Fig. 3d)

Material examined: 1 specimen; Mexico, Estado de México, Cerca de la carretera, La Joya, 19°10'59.679" N, 100°7'17.475" W, 1,851 m alt. D. Schneider ex

Acanthoscelides obtectus (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Estado de México, Mex 7 road, 18°51'38.574" N, 99°46'40.598" W, 1,888 m alt. D. Schneider CNIN 3848, 3849 ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Guerrero, Mexico 200, Cuquita Massieu, Tres Palos, Gro., Mexico, 16°46'28.614" N, 99°37'19.891" W, 59 m alt. D. Schneider CNIN 3833, 3834, BAS282 ex *Acanthoscelides argillaceus* (Sharp, 1885) in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Guerrero, Acapulco-Zihuatanejo road, 17°9'43.974" N, 100°25'23.725" W, 27 m alt. D. Schneider CNIN 3847, 3856 ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 2 specimens; Mexico, Morelos, Tepoztlán- Cuernavaca road, 18°58'35.321" N, 99°7'1.358" W, 1,743 m alt. D. Schneider TECO, CNIN 3795 ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Morelos, Morelos Oaxtepec - Yautepec de Zaragoza 124, Jacarandas, 62731 Yautepec de Zaragoza, 18°54'58.626" N, 99°2'29.457" W, 1,226 m alt. D. Schneider CNIN 3829, 3830, 3831 ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Morelos, Cuernavaca-Tepoztlán 662 road, 18°58'33.387" N, 99°10'12.252" W, 1,676 m alt. D. Schneider CNIN 3782 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Oaxaca, Mexico 175 road, 15°40'17.613" N, 96°33'32.36" W, 75 m alt. D. Schneider CNIN 3832 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 9 specimens; Mexico, Querétaro, Jalpan Puente- Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez CNIN 3675 ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873). 4 specimens; Mexico, Querétaro, Chichidho, 20°45'15.51" N, 99°56'54.30" W, 2,042 m alt. N. Delgado & J. Gutiérrez CNIN 3728 ex Bruchinae. 3 specimens; Mexico, Querétaro, Chichidho, 20°45'40.85" N, 99°56'44.28" W, 2,009 m alt. N. Delgado & J. Gutiérrez 2CHI ex Bruchinae in pods of *Senna polyantha* (Colladon) Irwin & Barneby.

Horismenus missouriensis (Ashmead, 1888)

Material examined: 2 specimens; Mexico, Chiapas, Chiapa de Corzo, Colonia Emiliano Zapata, 16°9' N, 93°15' W, 599 m alt. A. Zaldivar ex Bruchinae en *Leucaena leucocephala* (Lam.). 2 specimens; Mexico, Chiapas, 15°47'54.34" N, 93°23'21.83" W, 53 m alt. N. Delgado ex *Acanthoscelides* sp. 1 specimen; Mexico,

Estado de México, 19°1'1.06" N, 100°1'48.165" W, 1,964 m alt. D. Schneider CNIN 3798 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Jalisco, Chamela Biological Station, 19°29'40.80" N, 105°02'46.12" W, 90 m alt. N. Delgado CNIN 3773, 3775 ex *Merobruchus insolitus* (Sharp, 1885). 12 specimens; Mexico, Jalisco, Chamela Biological Station, 19°35'39.49" N, 105°05'03.40" W, 21 m alt. N. Delgado ex Bruchinae. 2 specimens; Mexico, Jalisco, Chamela Biological Station, 19°38'50" N, 104°49'39" W, 536 m alt. N. Delgado ex *Mimosestes nubigens* (Motschulsky, 1874) in pods of *Phaseolus lunatus* L. 1 specimen; Mexico, Michoacan, El Guayabo, 18°58'40" N, 102°9'54" W, 330 m alt. N. Delgado ex Bruchinae. 7 specimens; Mexico, Morelos, Paraje Alarcón 49, Ocotepéc, 62220 Cuernavaca, 18°58'50.025" N, 99°12'47.966" W, 1,871 m alt. D. Schneider CNIN 3803,3804, 3805 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Morelos, Dolores 1, Ocotepéc, 62220 Cuernavaca, 18°58'44.285" N, 99°12'58.588" W, 1,843 m alt. D. Schneider CNIN 3799, 3800 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. en *Phaseolus vulgaris* L. 2 specimens; Mexico, Morelos, Cuernavaca-Tepoztlán 662 road, 18°58'33.387" N, 99°10'12.252" W, 1,676 m alt. D. Schneider CNIN 3783 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Morelos, Tepoztlán- Cuernavaca road, 18°58'35.321" N, 99°7'1.358" W, 1,743 m alt. D. Schneider CNIN 3797 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 11 specimens; Mexico, Querétaro, way Chichidho to Bernal, way Chichidho to Bernal, 20°45'16.82" N, 99°57'4.12" W, 2,059 m alt. N. Delgado & J. Gutiérrez CNIN 3689, 3690, 3712, 3713 ex Bruchinae. 5 specimens; Mexico, Querétaro, airport, 20°36'23.89" N, 100°9'55.08" W, 1,913 m alt. N. Delgado & J. Gutiérrez CNIN 3693, 3715 ex Bruchinae. 1 specimen; Mexico, Querétaro, Jalpan -puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873). 2 specimens; Mexico, Querétaro, 21°14'26.75" N, 99°15'59.87" W, 1,088 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 3 specimens; Mexico, Querétaro, Ayutla-Jalpan km18, 21°17'17.53" N, 99°30'28.43" W, 801 m alt. N. Delgado & J. Gutiérrez ex *Acanthoscelides macrophthalmus* (Schaeffer, 1907). 2 specimens; Mexico, Querétaro, Jalpan -Bernal, 21°12'3.50" N, 99°34'3.21" W, 1,160 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 1 specimen; Mexico,

Querétaro, Jalpan, 21°13'15.08" N, 99°28'37.28" W, 773 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Leucaena pulverulenta* (Schltdl.) Benth. 1 specimen; Mexico, Querétaro, Bernal- Chichidho, 20°44'35.83" N, 99°56'20.95" W, 2,070 m alt. N. Delgado & J. Gutiérrez CNIN 3704 ex Bruchinae. 4 specimens; Mexico, Quintana Roo, Chetumal, outside of archaeological site Oxtankah, 18°36'37" N, 88°13'54" W, 12 m alt. A. Zaldívar & M. Elias CNIN 3705 ex *Merobruchus sonorensis* Kingsolver, 1980, *Acanthoscelides macrophthalmus* (Schaeffer, 1907), *A. mankinsi* Johnson, 1983, in pods of *Leucaena leucocephala* (Lam.)

Horismenus nigrocyaneus Ashmead, 1894 (Fig. 3e)

Material examined: 2 specimens; Mexico, Querétaro, Chichidho, 20°45'40.85" N, 99°56'44.28" W, 2,009 m alt. N. Delgado & J. Gutiérrez ex Bruchinae.

Horismenus sp. 1

Material examined: 6 specimens; Mexico, Querétaro, Jalpan-puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez CNIN 3702, 3673 ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873).

Horismenus sp. 2

Material examined: 12 specimens; Mexico, Querétaro, Jalpan -puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873). 1 specimen; Mexico, Quintana Roo, Chetumal, outside of archaeological site Oxtankah, 18°36'37" N, 88°13'54" W, 12 m alt. A. Zaldívar & M. Elias CNIN 3678 ex *Merobruchus sonorensis* Kingsolver, 1980, *Acanthoscelides macrophthalmus* (Schaeffer, 1907), *A. mankinsi* Johnson, 1983 in pods of *Leucaena leucocephala* (Lam.). 6 specimens; Mexico, Querétaro, 7 Entrando a Bernal desde Chichidho, 20°44'35.83" N, 99°56'20.95" W, 2,070 m alt. N. Delgado & J. Gutiérrez CNIN3677, 3704 ex Bruchinae in pods of *Leucaena pulverulenta* (Schltdl.) Benth. 1 specimen; Mexico, Querétaro, 21°11'14.9" N, 99°26'33.6" W, 837 m alt. N. Delgado & J. Gutiérrez ex Bruchinae en *Leucaena pulverulenta* (Schltdl.) Benth. 2 specimens; Mexico, Querétaro, Jalpan -Bernal, 21°12'3.50" N, 99°34'3.21" W, 1,160 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Lysiloma microphyllum* Benth. 1 specimen; Mexico, Querétaro, Chichidho, 20°45'40.85" N, 99°56'44.28" W, 2,009 m alt. N. Delgado & J. Gutiérrez ex Bruchinae en *Senna polyantha* (Colladon) Irwin & Barneby. 1 specimen; Mexico, Querétaro, 21°14'26.75" N, 99°15'59.87" W, 1,088 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 2 specimens; Mexico, Querétaro, Jalpan, 21°13'15.08" N, 99°28'37.28" W, 773 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Leucaena*

pulverulenta (Schltdl.) Benth. 2 specimens; Mexico, Chiapas, Chiapas de corzo, Colonia Emiliano Zapata, 16°9' N, 93°15' W, 599 m alt. A. Zaldívar ex Bruchinae in pods of *Leucaena leucocephala* (Lam.). 1 specimen; Mexico, Chiapas 15°47'54.34" N, 93°23'21.83" W, 53 m alt. N. Delgado ex *Acanthoscelides* sp. 1 specimen; Mexico, Querétaro, Jalpan -Xilitla, 21°12'35.21" N, 99°27'15.88" W, 781 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Leucaena pulverulenta* (Schltdl.) Benth. 1 specimen; Mexico, Querétaro, Jalpan, 21°13'15.08" N, 99°28'37.28" W, 773 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Leucaena pulverulenta* (Schltdl.) Benth.

Horismenus sp. 3

Material examined: 2 specimens; Mexico, Jalisco, Chamela Biological Station, 19°29'40.80" N, 105°02'46.12" W, 90 m alt. N. Delgado CNIN 3772, 3774 ex *Merobruchus insolitus* (Sharp, 1885).

Horismenus sp. 4

Material examined: 4 specimens; Mexico, Estado de México, 18°58'50.025" N, 99°12'47.966" W, 1,871 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. en *Phaseolus vulgaris* L. 7 specimens; Mexico, Querétaro, Jalpan-Puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez CNIN 3701 ex *Merobruchus insolitus*

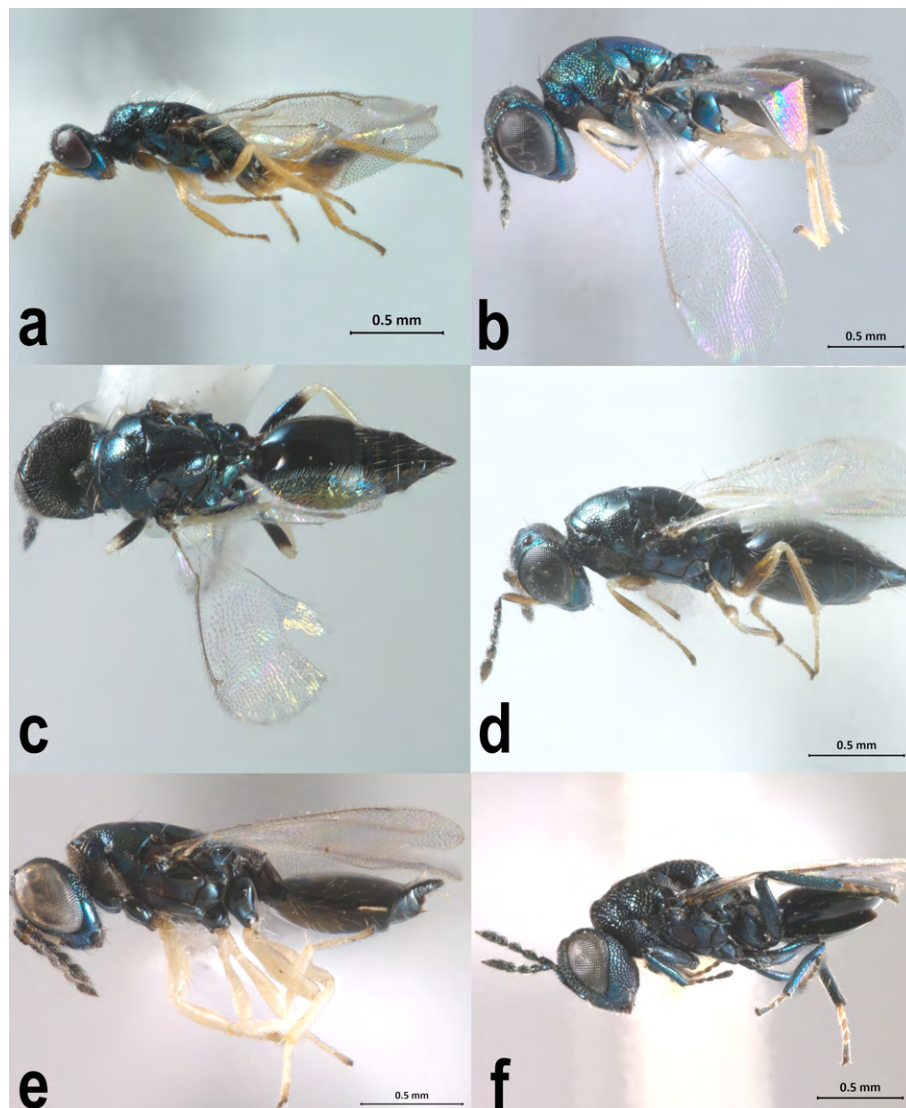


Figure 3. a-f, Eulophidae habitus. a, *Elachertus* sp. b, *Horismenus bruchophagus* Burks, 1971. c, *Horismenus butcheri* Hansson et al., 2004. d, *Horismenus depressus* Gahan, 1930. e, *Horismenus nigrocyaneus* Ashmead, 1894. f, *Paracrias pluteus* Hansson, 2002.

(Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873). 1 specimen; Mexico, Querétaro, Jalpan-Bernal, 21°12'3.50" N, 99°34'3.21" W, 1,160 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Lysiloma microphyllum* Benth. 1 specimen; Mexico, Querétaro, 21°12'50.51" N, 99°29'28.20" W, 974 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 1 specimen; Mexico, Querétaro, Ayutla-Jalpan km 18, 21°17'17.53" N, 99°30'28.43" W, 801 m alt. N. Delgado & J. Gutiérrez ex *Acanthoscelides macrophthalmus* (Schaeffer, 1907). 1 specimen; Mexico, Querétaro, 21°17'17.55" N, 99°15'59.87" W, 1,146 m alt. N. Delgado & J. Gutiérrez ex Bruchinae.

Paracrias pluteus Hansson, 2002 (Fig. 3f)

Material examined: 52 specimens; Mexico, Querétaro, Jalpan- puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez CNIN 3763, 3764, 3765 ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873). 5 specimens; Mexico, Querétaro, 20°44'35.83" N, 99°56'20.95" W, 2,070 m alt. N. Delgado & J. Gutiérrez CNIN 3676, 3703 ex Bruchinae in pods of *Leucaena pulverulenta* (Schltdl.) Benth. 1 specimen; Mexico, Querétaro, La Ceiba. 21°10'30.45" N, 99°25'22.03" W, 896 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Lysiloma microphyllum* Benth.

Eupelmidae

Eupelmus sp. aff. *annulatus* Nees, 1834 (Fig. 4a)

Material examined: 2 specimens; Mexico, Michoacán, El Guayabo, 18°58'40" N 102°9'54" W, 330 m alt. N. Delgado ex Bruchinae. 2 specimens; Mexico, Querétaro, 20°45'14.93" N, 99°56'59.99" W, 2,044 m alt. N. Delgado & J. Gutiérrez CNIN 3671, 3700 ex Bruchinae. 2 specimens; Mexico, Estado de México, Mex 7 road, 18°51'38.574" N, 99°46'40.598" W, 1,888 m alt. D. Schneider CNIN 3789, 3790 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L.

Eupelmus sp. aff. *pulchriceps* Cameron, 1904 (Figs 4b-c)

Material examined: 1 specimen; Mexico, Chiapas, Chiapas de corzo, Colonia Emiliano Zapata, 16°9'N 93°15'W, 599 m alt. A. Zaldivar ex Bruchinae in pods of *Leucaena leucocephala* (Lam.). 2 specimens; Mexico, Estado de México, Mex 7 road, 18°51'38.574" N, 99°46'40.598" W, 1,888 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Guerrero, Mexico 200, Cuquita Massieu, Tres Palos, 16°46'28.614" N, 99°37'19.891" W, 59 m alt. D. Schneider CNIN3871, 3869 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 2 specimens; Mexico,

Guerrero, Tecpan De Galena - San Jerónimo De Juárez 207, 17°7'33.542" N, 100°21'39.542" W, 21 m alt. D. Schneider CNIN3826, 3827. 3 specimens; Mexico, Guerrero, Acapulco-Zihuatanejo road, 17°9'43.974" N, 100°25'23.725" W, 27 m alt. D. Schneider CNIN 3853, 3854, 3855 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 4 specimens; Mexico, Jalisco, Chamela Biological Station, 19°35'20" N, 105°5'24" W, 20 m alt. N. Delgado ex *Mimosestes mimosae* (Fabricius, 1781), *Acanthoscelides taboga* Johnson, 1983, *A. sp.* in pods of *Phaseolus lunatus* L. 4 specimens; Mexico, Jalisco, Chamela biological station, 19°38'50" N 104°49'39" W, 536 m alt. N. Delgado CNIN 3724 ex *Mimosestes nubigens* (Motschulsky, 1874). 2 specimens; Mexico, Morelos, Cuautla - Tepoztlán, 18°58'14.656" N, 99°4'35.822" W, 1,612 m alt. D. Schneider VUL3, CNIN 3788 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 4 specimens; Mexico, Oaxaca, Mexico 175 road, 15°40'17.613" N, 96°33'32.36" W, 75 m alt. D. Schneider CNIN 3821, 3822, 3823, 3872 ex *Acanthoscelides obtectus* (Say), *Acanthoscelides obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 3 specimens; Mexico, Oaxaca, Aguaje del Zapote, San Pedro Mixtepec, 15°55'19.783" N 97°9'7.942" W, 17 m alt. D. Schneider CNIN 3838, 3839, 3840 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 1 specimen; Mexico, Querétaro, 21°14'26.75" N, 99°15'59.87" W, 1,088 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 3 specimens; Mexico, Querétaro, Jalpan - puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez CNIN 3699, 3719 ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873). 2 specimens; Mexico, Querétaro, Jalpan -Bernal, 21°12'50.51" N, 99°29'28.20" W, 974 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Lysiloma microphyllum* Benth. 4 specimens; Mexico, Querétaro, 20°45'14.93" N, 99°56'59.99" W, 2,044 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 1 specimen; Mexico, Querétaro, 20°45'40.85" N, 99°56'44.28" W, 2,009 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Senna polyantha* (Colladon) Irwin & Barneby. 1 specimen; Mexico, Querétaro, La Ceiba, 21°10'30.45" N, 99°25'22.03" W, 896 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 15 specimens; Mexico, Veracruz, 18°35.839" N 95°27.312" W, 25 m alt. N. Delgado CNIN 3778 ex *Acanthoscelides argillaceus* (Sharp, 1885) in pods of *Phaseolus lunatus* L.

Brasema bruchivora Crawford, 1908

Material examined: 1 specimen; Mexico, Querétaro, 21°12'50.51" N, 99°29'28.20" W, 974 m alt. N. Delgado & J. Gutiérrez ex bruchinae in pods of *Lysiloma*

microphyllum Benth. 1 specimen; Mexico, Querétaro, Jalpan - Xilitla, 21°12'35.21" N, 99°27'15.88" W, 781 m alt. N. Delgado & J. Gutiérrez ex bruchinae in pods of *Lysiloma microphyllum* Benth. 1 specimen; Mexico, Querétaro, 21°14'26.75" N, 99°15'59.87" W, 1,088 m alt. N. Delgado & J. Gutiérrez CNIN3698 ex Bruchinae in pods of Leguminosae.

Brasema neococcidis (Peck, 1951) (Fig. 4d)

Material examined: 2 specimens; Mexico, Estado de México, Mex 7 road, 18°51'38.574" N, 99°46'40.598" W, 1,888 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Querétaro, 21°12'35.21" N, 99°27'15.88" W, 781 m alt. N. Delgado & J. Gutiérrez ex Bruchinae in pods of *Lysiloma microphyllum* Benth.

Eurytomidae

Chryseida bennetti Burks, 1956 (Fig. 5a)

Material examined: 1 specimen; Mexico, Chiapas, approximately 7 km from Mapastepec. Direc. SE., 15°25'53.29" N, 92°51'57.11" W, 50 m alt. N. Delgado CNIN 3727 ex *Acanthoscelides taboga* Johnson, 1983,

Acanthoscelides sp. 1 specimen; Mexico, Chiapas, nr. Pijijiapan, 15°42'9.51" N, 93°13'5.81" W, 53 m alt. N. Delgado CNIN 3733 ex *Acanthoscelides* sp. 2 specimens; Mexico, Estado de México, Sultepec-Amatepec road, 18°50'46.441" N, 99°58'5.272" W, 2,200 m alt. D. Schneider CNIN 3801, 3802 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Estado de México, Mex 7 road, 18°51'38.574" N, 99°46'40.598" W, 1,888 m alt. D. Schneider CNIN 3850, 3851, 3852 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Guerrero, Mexico 200, Cuquita Massieu, Tres Palos, 16°46'28.614" N, 99°37'19.891" W, 59 m alt. D. Schneider CNIN 3862, 3863, 3864 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Guerrero, Tecpan De Galena - San Jerónimo De Juárez 207, El Papayo, Guerrero, 17°7'33.542" N, 100°21'39.542" W, 21 m. D. Schneider CNIN 3873 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 1 specimen; Mexico, Jalisco, Chamela Biological Station, 19°35'20" N, 105°5'24" W,

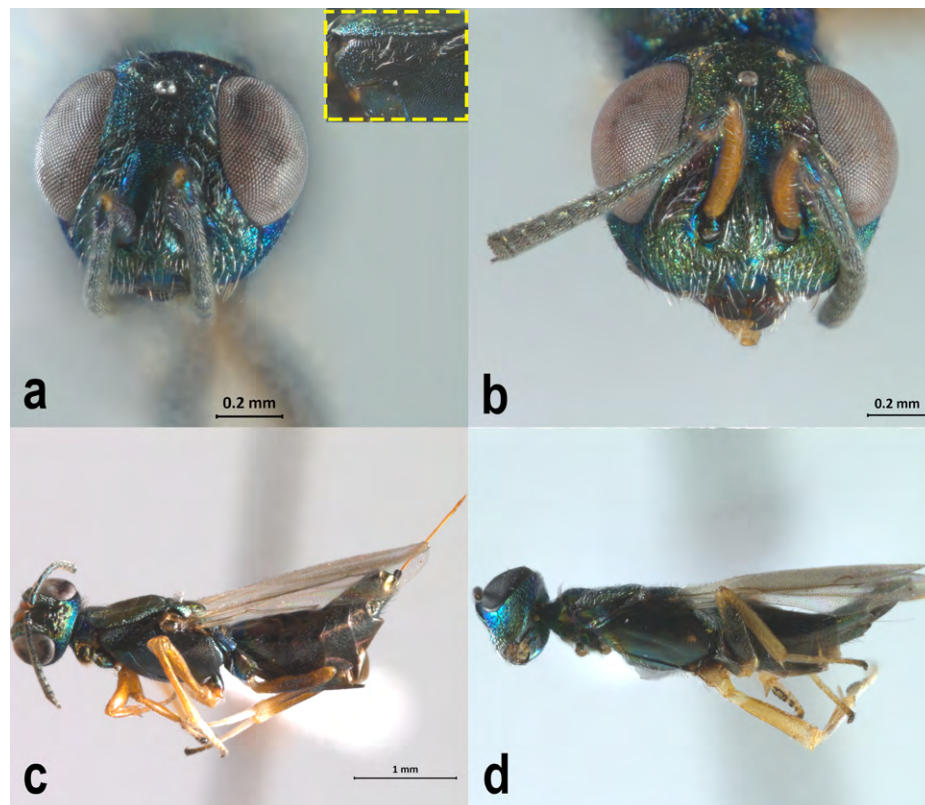


Figure 4. a-f, Eupelmidae habitus. a, *Eupelmus* sp. aff. *annulatus* Nees, 1834. b-c, *Eupelmus* sp. aff. *pulchriceps* Cameron, 1904. b, Head, frontal view. c, mesosoma, pleural view. d, *Brasema neococcidis* (Peck, 1951).

20 m. N. Delgado CNIN 3734 ex *Mimosestes mimosae* (Fabricius, 1781), *Acanthoscelides taboga* Johnson, 1983, *Acanthoscelides* sp. in pods of *Phaseolus lunatus* L. 1 specimen; Mexico, Oaxaca, Mexico 175 road, Oaxaca, 15°40'17.613" N, 96°33'32.36" W, 75 m alt. D. Schneider CNIN 3824, 3825 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 1 specimen; Mexico, Oaxaca, Santiago Pinotepa Nacional - Salina Cruz, Garita, 15°48'43.063" N, 96°3'59.576" W, 35 m alt. D. Schneider CNIN 3878 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 3 specimens; Mexico, Oaxaca, Aguaje del Zapote, San Pedro Mixtepec, 15°55'19.783" N, 97°9'7.942" W, 17 m alt. D. Schneider CNIN 3844, 3845, 3846 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L. 1 specimen; Mexico, Querétaro, Chichidho, 20°45'40.85" N, 99°56'44.28" W, 2,009 m alt. N. Delgado & J. Gutiérrez CNIN 3726 ex Bruchinae. 2 specimen; Mexico, Quintana Roo, Chetumal, outside of archaeological site Oxtankah, 18°36'37" N, 88°13'54" W, 12 m alt. A. Zaldívar & M. Elías CNIN 3706 ex *Merobruchus sonorensis* Kingsolver, 1980, *Acanthoscelides*

macrophthalmus (Schaeffer, 1907), *A. mankinsi* Johnson, 1983 in pods of *Leucaena leucocephala* (Lam.).

Eurytoma sp. (Fig. 5b)

Material examined: 3 specimens; Mexico, Chiapas, 15°42'9.51" N, 93°13'5.81" W, 53 m alt. N. Delgado ex *Acanthoscelides* sp.

Phylloxeroxenus sp. 1 (Fig. 5c)

Material examined: 9 specimens; Mexico, Veracruz, 18°35.839' N, 95°27.312' W, 25 m alt. N. Delgado CNIN 3779, 3780, 3781 ex *Acanthoscelides argillaceus* (Sharp, 1885) in pods of *Phaseolus lunatus* L. 2 specimens; Mexico, Querétaro, 20°45'14.93" N, 99°56'59.99" W, 2,044 m alt. N. Delgado & J. Gutiérrez ex Bruchinae. 1 specimen; Mexico, Querétaro, Jalpan -puente Ayutla, 21°23'43.35" N, 99°34'53.13" W, 532 m alt. N. Delgado & J. Gutiérrez CNIN 3672 ex *Merobruchus insolitus* (Sharp, 1885), *M. santarosae* (Kingsolver, 1980), *Stator limbatus* (Horn, 1873). 5 specimens; Mexico, Querétaro, Chichidho, 20°45'14.99" N, 99°57'1.51" W, 2,071 m alt. N. Delgado & J. Gutiérrez ex *Mimosestes nubigens* (Motschulsky, 1874) in pods of *Acacia farnesiana* (L.) Willd. 3 specimens; Mexico, Querétaro, Chichidho, 20°45'40.85" N, 99°56'44.28" W, 2,009 m alt. N. Delgado

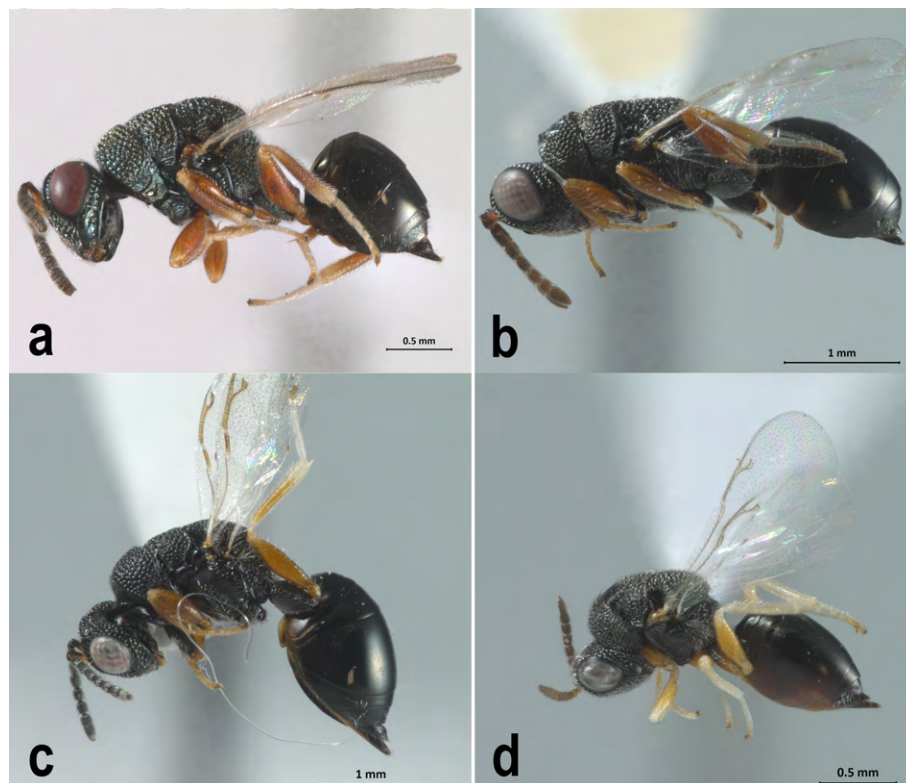


Figure 5. a-d, Eurytomidae habitus. a, *Chryseida bennetti* Burks, 1956. b, *Eurytoma* sp. c, *Phylloxeroxenus* sp.1. d, *Phylloxeroxenus* sp.2.

& J. Gutiérrez ex Bruchinae. 1 specimen; Mexico, Querétaro, Ayutla-Jalpan km18 road, 21°17'17.53" N, 99°30'28.43" W, 801 m alt. N. Delgado & J. Gutiérrez ex *Acanthoscelides macrophthalmus* (Schaeffer, 1907). *Phylloxeroxenus* sp. 2 (Fig. 5d)

Material examined: 1 specimen; Mexico, Querétaro, 21°14'26.75" N, 99°15'59.87" W, 1,088 m alt. N. Delgado & J. Gutiérrez ex Bruchinae.

Pteromalidae

Eurydinoteloides incerta Ashmead, 1893 (Fig. 6a, b)

Material examined: 2 specimens; Mexico, Morelos, Zopilote river, Santa Monica, 18°57'10.508" N, 99°30'17.737" W, 1,834 m alt. D. Schneider CNIN 3811, 3812 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Estado de México, Tenancingo - Chalma 360 road, 18°57'57.153" N, 99°30'25.354"

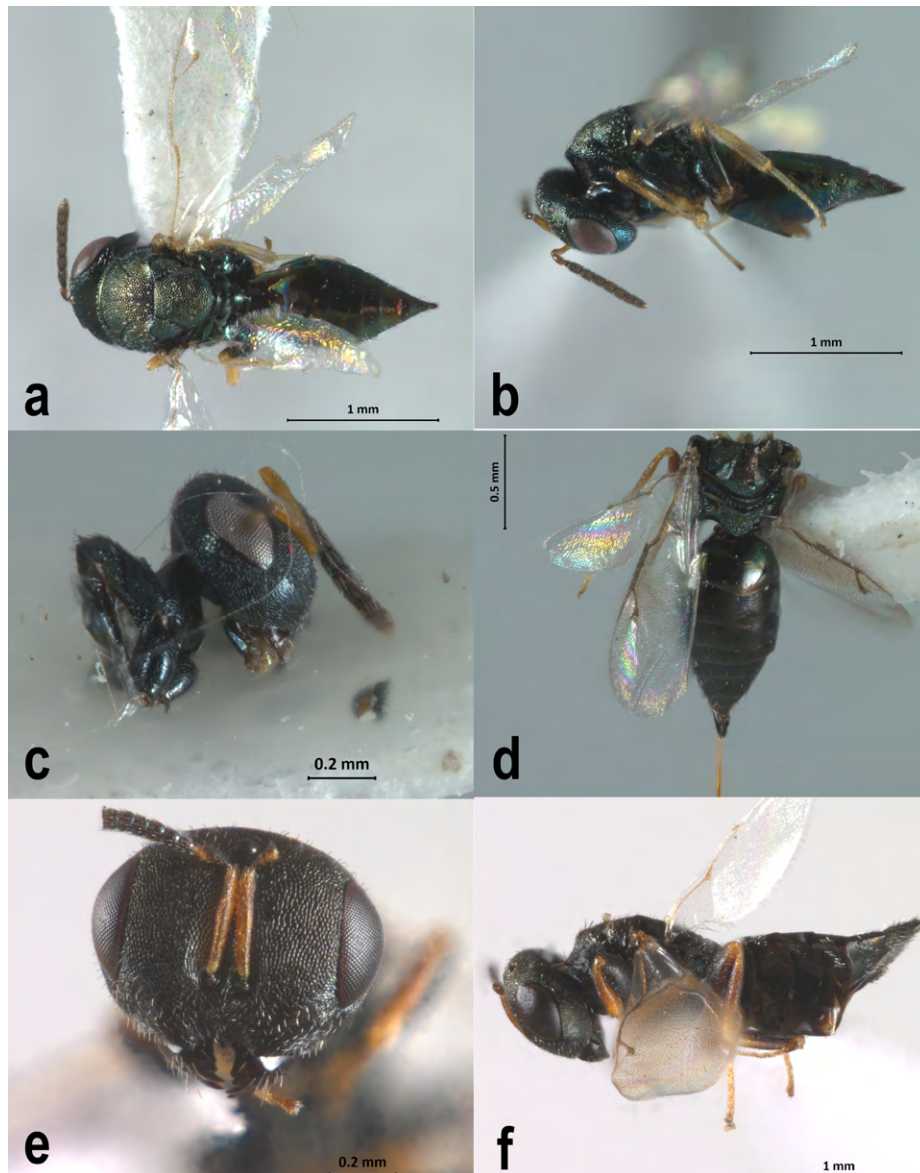


Figure 6. a-f, Pteromalidae habitus. a-b, *Eurydinoteloides incerta* Ashmead, 1893. a, dorsal view. b, habitus. c-d, *Lariophagus distinguendus* (Förster, 1841). c, head, lateral view. d, mesosoma and metasoma, dorsal view. e-f, *Monoksia dorsiplana* Boucek, 1991. e, head, frontal view. f, habitus, lateral view.

W, 2,108 m alt. D. Schneider CNIN 3814, 3815, 3816 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 5 specimens; Mexico, Morelos, Cuautla - Tepoztlán, Tepoztlán, 18°58'14.656" N, 99°4'35.822" W, 1,612 m alt. D. Schneider CNIN 3841, 3842, 3874, 3875, 3876 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 7 specimens; Mexico, Morelos, Cuernavaca-Tepoztlán 662 road, 18°58'33.387" N, 99°10'12.252" W, 1,676 m alt. D. Schneider CNIN 3786, 3787, 3793 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L.

Eurydinoteloides sp. 1

Material examined: 1 specimen; Mexico, Estado de México, Texcaltitlán - Zacualpan, 18°51'6.699" N, 99°50'37.283" W, 1,847 m alt. D. Schneider CNIN 3868 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Morelos, Tepoztlán, 18°58'14.656" N, 99°4'35.822" W, 1,612 m alt. D. Schneider CNIN 3843 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Estado de México, San Pablo Guelatao, Tejupilco de Hidalgo, 18°55'52.464" N, 100°9'4.246" W, 1,468 m alt. D. Schneider CNIN 3819, 3820 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 1 specimen; Mexico, Morelos, Zopilote river, Santa Mónica, 18°57'10.508" N, 99°30'17.737" W, 1,834 m alt. D. Schneider CNIN 3813 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L.

Eurydinoteloides sp. 2

Material examined: 1 specimen; Mexico, Morelos, 18°58'54.103" N, 99°0'17.348" W, 1,863 m alt. D. Schneider ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. *Lariophagus distinguendus* (Förster, 1841) (Figs 6c-d)

Material examined: 1 specimen; Mexico, Veracruz, 18°35.839' N, 95°27.312' W, 25 m alt. N. Delgado ex *Acanthoscelides argillaceus* (Sharp, 1885) in pods of *Phaseolus lunatus* L.

Lariophagus texanus Crawford, 1909

Material examined: 3 specimens; Mexico, Quintana Roo, Chetumal, outside of archaeological site Oxtankah, 18°36'37" N 88°13'54" W, 12 m alt. A. Zaldivar & M. Elias CNIN 3680, 3707 ex *Merobruchus sonorensis* Kingsolver, 1980, *Acanthoscelides macrophthalmus* (Schaeffer, 1907), *A. mankinsi* Johnson, 1983 in pods of *Leucaena leucocephala* (Lam.) 2 specimens; Mexico, Michoacan, El Guayabo, 18°58'40" N 102°9'54" W, 330 m alt. N. Delgado ex Bruchinae.

Lariophagus sp.

Material examined: 1 specimen; Mexico, Jalisco, Chamelabiological station, 19°35'39.49" N, 105°05'03.40" W, 21 m alt. N. Delgado ex Bruchinae.

Monoxsa dorsiplana Boucek, 1991 (Figs 6e-f)

Material examined: 9 specimens; Mexico, Querétaro, Chichidho, 20°45'14.99" N, 99°57'1.51" W, 2,071 m alt. N. Delgado & J. Gutiérrez CNIN 3730 ex *Mimosestes nubigens* (Motschulsky, 1874) in pods of *Acacia farnesiana* (L.) Willd. 8 specimens; Mexico, Querétaro, Chichido-Bernal, 20°44'33.63" N, 99°56'21.11" W, 2,089 m alt. N. Delgado y J. Gutiérrez CNIN 3696, 3717 ex Bruchinae in pods of *Acacia farnesiana* (L.) Willd. 1 specimen; Mexico, Querétaro, Chichidho -Bernal, 20°45'16.82" N, 99°57'4.12" W, 2,059 m alt., N. Delgado & J. Gutiérrez CNIN 3691 ex Bruchinae

Pteromalus fuscipennis (Walker, 1834)

Material examined: 1 specimen; Mexico, Estado de México, Sultepec-Amatepec road, 18°50'46.441" N, 99°58'5.272" W, 2,200 m alt. D. Schneider CNIN 3817 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L.

Pteromalus sp.

Material examined: 7 specimens; Mexico, Quintana Roo, Chetumal, outside of archaeological site Oxtankah, 18°36'37" N, 88°13'54" W, 12 m alt. A. Zaldivar & M. Elias ex *Merobruchus sonorensis* Kingsolver, 1980, *Acanthoscelides macrophthalmus* (Schaeffer, 1907), *A. mankinsi* Johnson, 1983 in pods of *Leucaena leucocephala* (Lam.).

Torymidae

Torymus moazopi Perez-Benavides, 2020

Material examined: 3 specimens; Mexico, Estado de México, Toluca - Cd Altamirano 29, Temascaltepec de González, 19°2'5.021" N, 100°2'31.736" W, 1,968 m alt. D. Schneider CNIN 3784, 3785, 3794 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Estado de México, El Fresno - Temascaltepec de González, 19°3'27.292" N, 100°3'6.155" W, 1,817 m alt. D. Schneider CNIN 3791, 3792 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Estado de México, San Simón de Guerrero, 19°1'37.607" N, 99°59'28.528" W, 2,121 m alt. D. Schneider CNIN 3809, 3810 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Estado de México, Mex 7 road, 18°51'38.574" N, 99°46'40.598" W, 1,888 m alt. D. Schneider CNIN 3859, 3860, 3861 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in

Pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Guerrero, 16°46'28.614" N, 99°37'19.891" W, 59 m alt. D. Schneider CNIN 3865, 3866, 3867 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 3 specimens; Mexico, Morelos, Zopilote river, Santa Monica, 18°57'10.508" N, 99°30'17.737" W, 1,834 m alt. D. Schneider CNIN 3806, 3807, 3808 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus vulgaris* L. 2 specimens; Mexico, Oaxaca, Aguaje del Zapote, San Pedro Mixtepec, 15°55'19.783" N, 97°9'7.942" W, 17 m alt. D. Schneider CNIN 3857, 3858 ex *Acanthoscelides obtectus* (Say), *A. obvelatus* Bridwell, *Zabrotes* spp. in pods of *Phaseolus lunatus* L.

Discussion

Eulophidae

Three genera and 20 eulophid species were reared from various host plants excluding *H. nigrocyanus* Ashmead, where the plant and the bruchine species associated could not be identified (Table 1). *Paracrias pluteus* Hanson represents a new distribution record for the state of Querétaro with a new host record. *Horismenus bruchophagus* Burks was previously reported in Texas (USA) by Burks (1979), and in Mexico by Hetz and Johnson (1988) as parasitoid of 6 Bruchinae species: *Acanthoscelides derifieldi* Johnson, *Mimosestes nubigens* (Motschulsky), *Merobruchus* sp., *M. insolitus* (Sharp), *Stator limbatus* (Horn), and *S. pruininus* (Horn). *Acanthoscelides macrophthalmus* (Schaeffer, 1907) infesting seeds of *Acacia pennatula* (Schltdl. & Cham.) Benth., *A. mankinsi* Johnson, 1983 infesting seeds of *A. pennatula* (Schltdl. & Cham.) Benth. and *Acacia farnesiana* (L.) Willd. are new bruchine records for *H. bruchophagus* (Table 1). *Paracrias pluteus* Hansson was previously registered in Costa Rica and Brazil as a parasitoid of *S. spodiogaster* Kingsolver and *S. cupreatus* Kingsolver in seeds of *Melanoxylon brauna* Schott (Pikart et al., 2011). We report *P. pluteus* for the first time for Mexico with a new host record (Table 1). We also report new host records for *H. butcheri*, *H. depressus*, and *H. missouriensis* (Table 1).

Eupelmidae

Two genera and 4 species of Eupelmidae were reared: *Eupelmus* sp. aff. *pulchriceps*, *Eupelmus* sp. aff. *annulatus*, *Brasema bruchivora* Crawford and *B. neococcidis* Peck. These genera have not been revised for Mexico. Three species of *Brasema* Cameron and 8 species of *Eupelmus* Dalman were previously reported for the country (Noyes, 2020). Gibson's (2011) revision of *Eupelmus* is the best approximation to the Neotropical fauna, but the species

key provided there is only for the Nearctic region, and thus the taxonomy of the genus in the Neotropics is still largely unknown. There are no usable keys for *Brasema*.

The Hymenoptera catalog of DeSantis (1979) reports the presence of *Eupelmus pulchriceps* in Mexico. It is an extremely polyphagous species that has been reported as parasitoid of 76 species belonging to 6 insect orders (Burks, 1979; De Santis, 1967; Forister & Johnson, 1971; Gibson, 2011; Herting, 1973; Peck, 1963; Pérez & Bonet, 1985). This species, however, was originally described from Nicaragua, and thus our specimens assigned to *Eupelmus* sp. aff. *pulchriceps* could represent an undescribed species that is associated to various bruchines and host plants (Gibson, 2016) (Table 1).

Eupelmus annulatus is mainly distributed along the Nearctic and Palearctic regions. Its hosts range includes 26 species of insects belonging to 3 orders, though it mainly attacks species of the hymenopteran family Cynipidae (Boucek, 1977; Gibson, 2011; Gómez et al., 2006; Matošević & Melika, 2013; Melika et al., 2002; Stojanova, 2006; Thompson, 1955). Previous host records of this species did not include members of Bruchinae. In our study, the specimens assigned to *Eupelmus* sp. aff. *annulatus* were associated to 3 bruchine species (Table 1).

The collected specimens of *Brasema bruchivora* Crawford and *B. neococcidis* Peck are new distribution records for Querétaro and the Estado de México, whereas *A. obtectus* (Say, 1831), *A. obvelatus* Bridwell, 1942 and *Zabrotes* spp. represent new host records for *B. neococcidis* Peck (Table 1). *Brasema bruchivora* Crawford has been reported as parasitoid of 3 Bruchinae (*Acanthoscelides submuticus* (Sharp), *Bruchus* sp. (L.) and *Mimosestes nubigens* (Motschulsky)); however, we did not rear Bruchinae associated to *B. bruchivora*. *Lysiloma microphyllum* Benth is a new host plant record. The morphological features for the examined specimens of *B. bruchivora* Crawford are similar to those mentioned in the original description of the species (Crawford, 1908): head and thorax green, with purple tinges, face mostly purplish; antenna dark, scape metallic; pubescent eyes; long, distinct; abdomen bronzy, with bluish reflections, the first segment basally blue; legs dark, tibia with reddish, tarsi basally whitish.

Brasema neococcidis Peck has been found as parasitoid on 6 insect species belonging to 3 families: Coccidae (1 species), Hymenopodidae (1 species) and Mantidae (4 species) (Burks, 1979; DeSantis, 1979; Peck, 1963). The host records mentioned here for this species are therefore new (Table 1). The morphological features are similar to those described by Gahan (1910): head somewhat coarsely and densely punctate with silvery-white pubescence on the gena and face below antenna; body-color brassy-green;

antennal scape cupreous-green, flagellum subclavate, obliquely truncate at the tip; fore and hind coxa metallic-green, median coxae darker; trochanters yellowish; fore and middle femora and tibia brownish-yellow, hind femora dark brown and apical half-light yellow; all tarsi with first joint whitish, following joints brown; ovipositor sheath short, black, except apex, which is yellowish; and ovipositor slightly exerted and yellowish.

Eurytomidae

Three genera and 4 eurytomid species were reared from different host plants and Bruchinae (Table 1). Species of *Phylloxeroxenus* and *Eurytoma* were not identified due to the lack of taxonomic keys. There are speculations about of the vast number of *Eurytoma* species that have been incorrectly identified in the Neotropical region (P. Hanson, pers. comm.). Species of *Eurytoma* are mainly distributed in the Nearctic region, whereas *Phylloxeroxenus* is more common in the Neotropics (Hanson, pers. comm., 2018). *Chryseida bennetti* Burks was the predominant species. It has been previously reported as parasitoid of *Acanthoscelides obtectus*, *Bruchus* sp. and *Merobruchus* sp. associated with *Cajanus cajan* (L.), *Havardia brevifolia* (A.Gray), *Phaseolus vulgaris*, and *Rhynchosia* sp. In this work, we report 7 species of bruchines as possible hosts of *C. bennetti* Burks with 2 plant associations (Table 1).

Chryseida Spinola is a small genus with only 10 species (Noyes, 2020). Burks (1956) provided a taxonomic key for 9 of these species, with the exception of *C. burksi* Zerova that was later described from Costa Rica (Zerova, 1980). *Chryseida bennetti* Burks has been previously reported from Mexico, Trinidad and Tobago, Caribbean, and USA (Burks, 1979; Peck, 1963), *C. inopinata* Brues and *C. bennetti* Burks, both species are the only ones reported for the Country (DeSantis, 1979).

Pteromalidae

Three species of *Eurydinoteloides*, 3 of *Lariophagus*, 2 of *Pteromalus* and 1 of *Monoksa* were reared. *Eurydinoteloides* is distributed in the Nearctic and Neotropical regions (Gibson, 2013). It contains 15 described species, though it probably has many undescribed species. Currently, 5 species have been reported from Mexico: *E. incerta* (Ashmead), *E. orontas* (Walker), *E. syrphidis* (Girault), *E. tepicensis* (Ashmead) and *E. tortricis* (Crawford) (Cross & Mitchell, 1968; DeSantis, 1979, 1989). *Eurydinoteloides incerta* is a parasitoid of 39 Bruchinae species, *Abutiloneus* (1 sp.), *Acanthoscelides* (27 spp.), *Bruchus* (1 sp.), *Merobruchus* (1 sp.), *Mimosestes* (2 spp.), *Sennius* (5 spp.) and *Stator* (1 sp.) (Pérez-Benavides et al., 2019). Three species of

Bruchinae and 1 associated plant are reported here as new hosts for the latter species (Table 1). Two morphospecies that appear to be morphologically different from *E. incerta* emerged from the reared material. The morphological features of the reared species of this genus did not match with any previously described species.

DeSantis and Fidalgo (1994) reported *L. distinguendus* (Forster) in Mexico for the first time. This parasitoid species has been reported to attack the following Bruchinae: *B. brachialis* (Fahraeus), *C. chinensis* (Linnaeus) and *C. maculatus* (Fabricius) (Pérez-Benavides et al., 2019). Here we report *A. argillaceus* (Sharp, 1885) on pods of *Phaseolus lunatus* L. as new host for *L. distinguendus* (Table 1). *Lariophagus texanus* Crawford has also been reported as parasitoid on 15 species: *Acanthoscelides* (3 spp.), *Algorobius* (2 spp.), *Callosobruchus* (1 sp.), *Merobruchus* (1 sp.), *Mimosestes* (3 spp.) and *Stator* (5 spp.) (Pérez-Benavides et al., 2019). In this study, we report new hosts associations for *L. texanus* Crawford: *M. sonorensis* Kingsolver, and *A. mankinsi* Johnson in pods of *Leucaena leucocephala* (Lam.) (Table 1).

Monoksa dorsiplana Boucek is the only described species of its genus. It has been reported in Israel, USA, Argentina, Chile and Uruguay as parasitoid of *Bruchidius* sp., *Pseudopachymerina spinipes* (Erichson) and *Callosobruchus maculatus* (Fabricius) on 2 plants species: *Acacia farnesiana* (L.) and *A. caven* Mol (Boucek, 1991; Burks, 2009; Gates & Burks, 2003; Rojas-Rouisse et al., 2007). Here we report a new distribution record of *M. dorsiplana* for the state of Querétaro in Mexico with *M. nubigena* (Motschulsky) as new hosts record. Boucek (1991) described and illustrated both sexes of *M. dorsiplana*.

One specimen of *Pteromalus fuscipennis* was found associated to 3 Bruchinae species: *A. obtectus* (Say), *A. obvelatus* Bridwell, and *Zabrotes* spp., in pods of *Ph. vulgaris* L. (Table 1). No previous host records had been reported for this species. Graham (1984) reported 2 species of Euphorbiaceae (*Euphorbia amygdaloides* and *E. characias*) as host plants for *P. fuscipennis*, but he did not mention any host insect associated to it. The morphological features of the examined specimen are similar to those mentioned in the description of the species provided by Graham (1984). Also, we report 3 new host records for *Pteromalus*: *A. macrophthalmus* (Schaeffer), *A. mankinsi* Johnson and *M. sonorensis* Kingsolver in *Leucaena leucocephala* (Lam.).

Torymidae

One species was found in this study, *Torymus moazopi*. This species was recently described by Pérez-Benavides et al. (2020).

Host relationships

This study revealed a higher species richness of Chalcidoidea associated to Bruchinae from plant material collected in central and southern Mexico than our previously published records (Pérez-Benavides et al., 2019). *Paracrias pluteus* Hansson, *H. nigrocyaneus* Ashmead, *B. bruchivora* Crawford, *B. neococcidis* Peck, *M. dorsiplana* Boucek and *Pteromalus fuscipennis* (Walker) are new records for Mexico, whereas a number of bruchine species represent new probable host associations (Table 1).

Eupelmus pulchriceps is a relatively common species that has been found in almost all reared bruchine taxa, and thus it is regarded as polyphagous, being registered as parasitoid of more than 21 insect families (Noyes, 2020). *Eupelmus annulatus*, on the other hand, was recently confirmed as a secondary parasitoid through Braconidae and Ichneumonidae (Gibson & Fusu, 2016). Here, we emphasize the importance of including integrative taxonomic studies to investigate the number of actual species among the examined specimens assigned to *E. sp. aff. pulchriceps* and *E. sp. aff. annulatus*. Other species of Chalcidoidea cataloged as highly generalists have been shown to have high levels of cryptic diversity (Al khatib et al., 2016; Deng et al., 2013; Derocles et al., 2016; Fusu, 2017; Gebiola et al., 2012).

Brasema neococcidis and *P. fuscipennis* have new host records, though these only are incidental parasitoids, and thus it was not possible to establish a direct association with any Bruchinae species. It is therefore necessary to evaluate whether these 2 species are hyperparasitoids rather than primary parasitoids, since Bruchinae species have not been reported as their associated hosts (Pérez-Benavides et al., 2019). *Brasema bruchivora*, *M. dorsiplana* and *C. bennetti* (with new hosts records and new distribution records) probably are a primary parasitoids on the species reported here (Table 1), because they have been reported as parasitoids of closely related Bruchinae species (Boucek, 1991; Burks, 1956, 1979; DeSantis & Fidalgo, 1994; Gates & Burks, 2003; Herting, 1973; Peck, 1963; Pérez-Benavides et al., 2019).

The information obtained in this study will not only contribute to a better understanding of the diversity of tropical parasitoids, but will also serve as a basis for their potential use as biocontrol agents. We recognize that the material studied here only represents a small fraction of the actual species diversity of chalcidoids parasitizing Bruchines in the Mexican territory, and thus this number will considerably increase after further taxonomic efforts are conducted for this group.

COI species delimitation

The high rates of evolution of the mt genome within Chalcidoidea are closely correlated with their parasitoid mode of life (Castro et al., 2002; Dowton & Austin, 1995). The GMYC model using the COI data set helped to confirm the 4 undescribed species of *Horismenus* that were discriminated based on external morphology (*Horismenus* spp. 1-4; Fig. 2, Supplementary materials 1, 2). The 2% sequence divergence approach, however, suggested that there is a considerably higher, cryptic species richness in the latter genus. Moreover, the GMYC analysis, which was mostly congruent with our morphological identifications, divided *E. sp. aff. pulchriceps* into 3 MOTUs. The high intraspecific divergence in the latter 2 genera strongly suggests that these actually represent species complexes.

Our results suggests that the potential cryptic diversity in the chalcidoid taxa associated to bruchines in Mexico could have occurred both by sympatric and allopatric speciation events. Based on morphological and mt and nuclear markers, Kenyon et al. (2015) assessed the species diversity *Horismenus* associated to *Phaseolus* in central Mexico and Arizona. These authors found that the putative *H. butcheri* actually represents a complex of species that appear to have diverged by both allopatric and sympatric speciation events, where the involved taxa do not appear to be associated with a specific host plant but with a Bruchinae species. In our study, it was not possible to establish a direct association between a chalcidoid species and a species of Bruchinae, since more than 1 beetle species, and even genera, were found in most of the examined plants. Further studies including additional genetic markers and specimens will therefore help to confirm the species delineation of these taxa.

Through the COI markers, we confirm the utility for species delimitation in Chalcidoidea, including its usefulness to detect considerable high levels of intraspecific variation in *E. sp. aff. pulchriceps*, *H. missourensis* and *H. bruchophagus*. This highlights the necessity to investigate the actual number of species in these taxa, supporting the hypothesis of high levels of cryptic diversity within Chalcidoidea.

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