

New records and a voucher collection of parasitoid wasps (Hymenoptera) inhabiting agroforestry systems in the colombian amazon basin

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Abstract. Cacao (*Theobroma cacao*) and copoazú (*T. grandiflorum*) agroecosystems represent a common source of income or many small-scale farmers in the Colombian Amazon basin. Most of these systems are set in low disturbance environments; they are considered biodiversity-friendly ecosystems inhabited by several groups of insects. In this study, we carried out a preliminary taxonomic inventory of the microhymenopteran parasitoids present in these agroforestry systems. Twenty-six localities of the Amazonian basin of Colombia were sampled using several insect collecting methods (Malaise trap, sweep net, pitfall, and rearing boxes). Collected specimens were curated and cataloged, establishing the first taxonomic voucher collection of parasitoids from the Colombian Amazon basin. We identified 767 specimens representing 64 species, 274 morphospecies, 143 genera and 20 families, 34 genera and 16 species of these being recorded for the first time in the country. The genus *Gbelcia* is reported for the first time from the Neotropical region. A new parasitoid-host relationship was found for *Horismenus cupreus* (Eulophidae) attacking larvae of *Phyllocoptis* sp. (Lepidoptera, Gracillariidae), which feeds on *Annona montana* (Annonaceae) leaves.

Keywords. Plant hosts; Insect inventory; Insect taxonomy; Biological control; Insect biodiversity; Insect curatorship; Insect decline; *Theobroma*.

INTRODUCTION

Museum collections based on insect collecting are among the most valuable resources for recognizing taxa from both simple and complex ecosystems, being important also in tracing historical data concerning local and widespread species and populations (Shaffer *et al.*, 1998; Turney *et al.*, 2015; Wagner, 2020). Even in agriculture, an activity in which pest management is a permanent activity, species inventories and reference collections of natural controllers, such as parasitoid wasps, still need to be carried out (Fernandez, 2000; Sääksjärvi *et al.*, 2004; Lopez *et al.*, 2009), since the proper identification of insects is the first step toward designing effective control strategies.

Cacao (*Theobroma cacao* L.) is one of the world's most important perennial crops (Almeida & Valle, 2010), both socially and economically, mainly for 5 to 6 million farmers worldwide that depend on cocoa farming for their livelihood (WCF, 2014). Copoazu (*T. grandiflorum* (Willd. ex Spreng.)), an Amazonian species related to cacao, is a promising tree crop whose pulp and seeds may be used for a variety of food and cosmetic products, which contribute to the household income of family businesses in Colombia (Chaparro-Orozco & Lopez-Rodriguez, 2018). Both species are important crops in rural areas of Colombian, where they can be found being cultivated in agroecological systems, especially in small-scale, family-based economies that have preserved cacaos within



mixed cropping systems (Espinal *et al.*, 2005). These agroforestry systems have arisen as important alternatives for forest conservation and substitution of illicit crops for the country (Ortiz, 1993; Pineda-Jaimes, 2018).

Taxonomic inventories of beneficial insects such as parasitoid wasps are scarce in agroforestry systems. Most studies in agroecosystems have been carried out on insects of economic importance, *e.g.*, pests (Miller, 1941; Conway, 1971; Entwistle, 1972; Keane & Putter, 1992; Ramirez-Cortés *et al.*, 2008; Posada *et al.*, 2011; Castillo, 2013; Srikumar & Shivarama, 2013), and pollinators (Winder, 1978; Adjalo & Oduro, 2013; Mavisoy *et al.*, 2013). This situation is similar for megadiverse countries such as Colombia, where taxonomic groups such as ants (Vergara & Serna, 2013; Fernandez *et al.*, 2019) and bees (González *et al.*, 2005; Parra & Londoño, 2013; Londoño-Carvajal *et al.*, 2020) have been the focus of research efforts, but most other hymenopteran taxa remain poorly investigated. This is especially noticeable for parasitic wasps, in which only around 800 species have been recorded (Fernandez, 1995; Campos, 2001; Arias-Penna, 2004; Arias & Delvare, 2003; MBD, 2021; Noyes, 2021; SIB Colombia, 2021), representing about 0.8% of the total species predicted to occur in Colombia.

Parasitoid wasps constitute the most species-rich group of Hymenoptera, and the most common and abundant natural enemies of insect pests (Sharkey, 2007; Price *et al.*, 2011). Nonetheless, the identification of microhymenopteran parasitoids often represents a challenging task due to their small size, high level of intraspecific variation of some taxa, the convergence of morphological traits, scarcity of taxonomic tools for their identification (Townes & Townes, 1966; Gebiola *et al.*, 2012; Konstantinov & Namyatova, 2019), and the lack of representativeness of these species in voucher collections.

Given the lack of information regarding the identity of insects associated with cacao and copoazu crops in agroforestry systems of the Colombian Amazon basin and the scarce taxonomic records of parasitic wasps in Colombia, our primary aim was to carry out an inventory of the hymenopteran parasitoids inhabiting the above-mentioned crops. Our work consists of an initial alpha taxonomic effort in the cacao and copoazu farms located in the Amazon basin of Colombia. It was carried out by collecting, preserving, and curating parasitoid specimens from several farms. Identifications were based on the observation of morphological characters using available taxonomic identification tools. Thereby, we also managed to establish a catalogued voucher collection of the parasitoid wasps from the Colombian Amazon basin based on the collected specimens.

MATERIAL AND METHODS

Sampling localities and fieldwork

Adult specimens were collected in the departments (states) of Caquetá, Putumayo, and Amazonas (Fig. 1, Table 1), which are part of the Amazon basin region of Colombia. Between 2014 and 2018, we sampled 24 ca-

Table 1. Locations of the cacao agroforestry systems which were sampled.

Departament (State)	Locality code	Latitude	Longitude	Altitude (m)
AMAZONAS	AM01	S 03°29'	W 70°12'	100
	AM02	S 04°08'47"	W 69°54'49"	70
	AM03	S 04°11'35"	W 69°56'23"	102
	AM04	S 04°11'38"	W 69°56'18"	96
	AM05	S 04°12'55"	W 69°56'26"	82
CAQUETÁ	CA01	N 01°22'03"	W 74°49'04"	278
	CA02	N 01°25'35"	W 75°30'57"	266
	CA03	N 01°29'59"	W 75°39'46"	300
	CA04	N 01°30'04"	W 75°36'22"	250
	CA05	N 01°30'06"	W 75°39'47"	263
	CA06	N 01°30'37"	W 75°40'21"	233
	CA07	N 01°40'02"	W 75°16'57"	337
	CA08	N 01°40'55"	W 75°18'30"	618
	CA09	N 02°07'11"	W 74°45'01"	270
	CA10	N 02°50'04"	W 74°46'08"	255
PUTUMAYO	PU01	N 00°28'01"	W 76°49'23"	316
	PU02	N 00°28'50"	W 76°30'18"	270
	PU03	N 00°39'27"	W 76°47'24"	325
	PU04	N 00°47'41"	W 76°38'49"	317
	PU05	N 00°47'42"	W 76°35'08"	317
	PU06	N 00°50'14"	W 76°38'06"	352
	PU07	N 01°07'06"	W 76°37'59"	584
	PU08	N 01°07'49"	W 76°39'56"	700
	PU09	N 01°11'28"	W 76°38'48"	352

cao and copoazu agroforestry farms. Overall, farm areas ranged from 1 to 5 ha and had a low level of technical crop production, with a mixture of different crops and a few timber trees or native forest. Each agroforestry farm was sampled using one Malaise and 10 pitfall traps for 60 days. The insects collected in Malaise traps were retrieved every 15 days (4 times). Pitfall traps were left operating for 24 hours every 15 days.

Additionally, in every farm, we performed two active sampling efforts (once a month) using sweep nets and manual sampling during the two-month sampling period, between 10:00 and 15:00 hours. Manual sampling included a search for potential hosts of parasitoid wasps, including pupae, larvae, nymphs, and galls with signs of parasitism. The material found was placed inside insect breeding boxes (dimensions 20 × 10 × 5 cm), where a 5 × 5 cm hole was made in the lid of each box and covered with a muslin cloth. To avoid excess moisture, a piece of paper towel was placed inside each box. All collected and reared specimens were preserved in 76% ethanol.

Additional material

In addition to the previously described samples, we included in our collection other identified and curated parasitoid wasps (UNAB 5021, UNAB 1868, UNAB 3559, UNAB 3547, and UNAB 5562) housed at the Museo entomológico UNAB Facultad de Ciencias Agrarias, Bogotá, Universidad Nacional de Colombia, Bogotá, Colombia (UNAB), which were collected in cacao or copoazu crops in the Amazon region of Colombia, according to their label information.

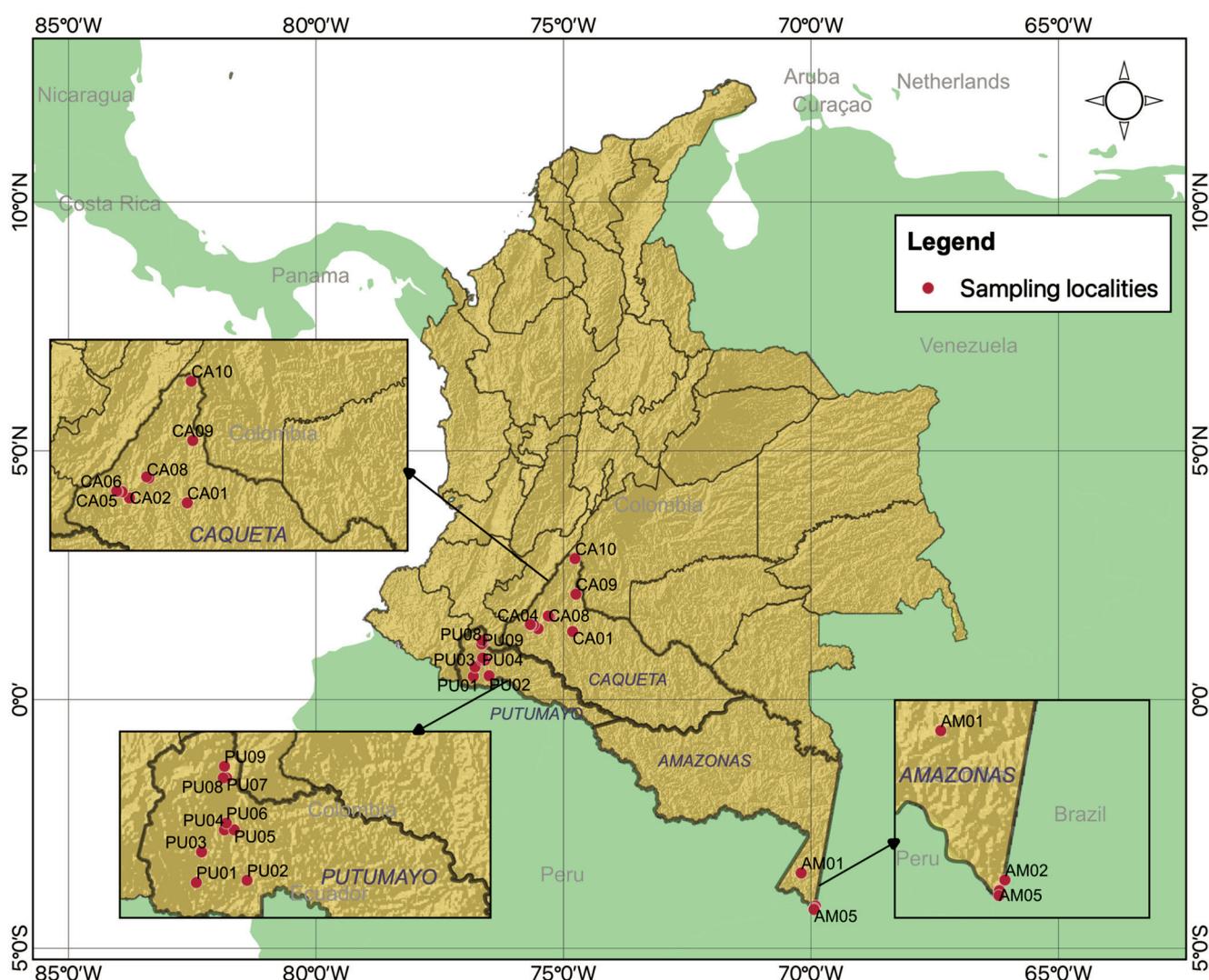


Figure 1. Sampling localities in the Amazonian basin of Colombia.

Voucher collection and Imaging

Specimens were point-mounted, identified, cataloged (Excel database with location and biology information), and deposited in the Central Taxonomic Collection (CTC) of the UNAB museum (Martínez & Serna, 2015). Habitus (lateral view) photographs of pinned specimens were taken using a Canon 5D Mk II camera with an EF 100 mm f2.8, macro lens, and extension tubes.

Taxonomic identification

In this study we included the following families: Scelionidae, Platygastriidae, Braconidae, Chalcididae, Pteromalidae, Eulophidae, Eurytomidae, Eucharitidae, Mymaridae, Encyrtidae, Eupelmidae, Perilampidae, Signiphoridae, Torymidae, Diapriidae, Figitidae, Evaniidae, Ceraphronidae, Bethylidae, Chrysidae, and Dryinidae. We employed the following identification keys, diagnoses, and descriptions: Chrysidae: Morgan (1984); Dryinidae: Olmi & Virla (2014); Bethylidae: Evans (1965), Terayama (2003), Azevedo (2014), Barbosa & Azevedo (2018), and Alencar & Azevedo (2020); Evaniidae: Deans (2006);

Braconidae: Wharton *et al.* (1997); Figitidae: Forshage & Nordlander (2008), Buffington (2009), and Van-Noort *et al.* (2015); Platygastroidea: Masner (1980) and Chen *et al.* (2018); Diapriidae: Nixon (1980) and Masner & Garcia (2002); Chalcidoidea: Gibson *et al.* (1997) and Hanson & Gauld (2006); Chalcididae: Burks (1960) and Delvare (1992); Encyrtidae: Noyes (1980, 2010) and Trjapitzin *et al.* (2008); Eulophidae: Hansson (2009); Eucharitidae: Burks *et al.* (2015, 2018); Eupelmidae: Gibson (1995, 2004) and Pérez-Benavides *et al.* (2016); Eurytomidae: Gates (2008); Mymaridae: Huber (2015); Pteromalidae: Strand (1911).

To verify species distributions, we consulted Fernandez (1995), the NSF (National Science Foundation) database (2006), MBD (Biological Diversity database) (2021), Hansson (2019), and Noyes (2021). When a species determination was not possible using the available taxonomic tools, specimens were identified as morphospecies. For Platygastroidea, we followed the proposed classification of Chen *et al.* (2021), in which the superfamily is classified into eight families. Specimens of Ichneumonidae and Proctotrupidae (> 1,000 specimens) were not identified due to a lack of experience in these groups. We examined the specimens using a Nikon stereomicroscope using 60-120× magnification and direct lighting of 150 W.

RESULTS

We curated 767 parasitoid wasp specimens (Table 2). The greatest number of collected specimens were in the families Scelionidae (148 specimens), Braconidae (140), Chalcididae (97), and Pteromalidae (75) (Fig. 2A), while families with the least number of individuals were Chrysidiidae (5), Signiphoridae (3), Dryinidae (1), and Torymidae (1). Chalcidoidea and Platygastroidea contained over 37% of the total parasitoid wasps collected and curated (Table 2, Fig. 2A). We identified a total of 64 species and 274 morphospecies from 147 different genera, 20 families, and eight superfamilies (Table 2): Diaprioidae (16 species/morphospecies; 11 genera; 1 family) (Fig. 3A-C), Cynipoidea (30; 14; 1) (Fig. 3D-F), Chalcidoidea (159; 66; 11) (Fig. 4), Chrysoidea (20; 11; 3), Ceraphronoidea (8; 2; 1), Evanioidea (10; 4; 1), Ichneumonoidea (39; 16; 1), and Platygastroidea (60; 24; 2) (Fig. 5). The largest number of genera happened in the families Scelionidae (18), Pteromalidae (17), Braconidae (16), and Figitidae (14) (Fig. 2B). On the other hand, the most species-rich superfamilies were Chalcidoidea (159 species) and Platygastroidea (60 species) (Table 2), while the most species-rich families comprised Chalcididae (50), Scelionidae (42), Braconidae (39), and Figitidae (30) (Fig. 2B).

A total of 20 genera and 23 species are new records for Colombia (Table 2). These belong to the families Braconidae, Bethylidae, Diapriidae, Figitidae, Encyrtidae, Eucharitidae, Eulophidae, Eurytomidae, Pteromalidae, and Scelionidae.

New ecological observations

From the insect-rearing boxes, we obtained several individuals of *Horismenus cupreus* (Eulophidae) emerging from larvae of *Phylloclnistis* sp. (Gracillariidae), which in turn were feeding on leaves of *Annona montana* (Annonaceae) (Table 2). We also observed *Elachertus* sp.

(Eulophidae) emerging from larvae of Gracillariinae (Lepidoptera: Gracillariidae), which were feeding on leaves of *Chrysophyllum cainito* Griseb. ex Pierre (Sapotaceae). Lastly, we obtained *Brachymeria mnestor* Walker, 1841 (Chalcididae), parasitoids of a pupa of Pieridae (Lepidoptera) found on leaves of *Duranta* sp. (Verbenaceae).

DISCUSSION

Our results provide the first taxonomic list of parasitoid wasps from the Colombian Amazon region inhabiting agroecosystems of cacao and copoazu identified to genus and species levels. In addition, the list includes an important number of new records for the country. These findings supplement relevant information provided in different datasets such as those in Noyes (2021) (Chalcidoidea), Biological Diversity database (MBD) of Ohio State University (Platygastroidea), Biological information system (SiB) of Colombia, and the study of Fernandez (1995).

Parasitoid wasps in cacao agroecosystems

We recorded here 20 parasitoid wasp families. This number is similar to that observed in cacao agroecosystems areas in Brazil, where 31 families were reported from Bahia (Sperber et al., 2004), then 30 from Itabuna (Nakayama et al., 2008), and 30 from Ilhéus (Sperber et al., 2012). The taxonomic composition of the families was almost the same in these studies and in ours. When we compare the taxa recorded from Bahia with those from the Colombian Amazon region, they are the same, except for Liopteridae, Megaspilidae, Agaonidae, Aphelinidae, Sclerogibbidae, Gasteruptiidae, Ichneumonidae, Monomachidae, and Proctotrupidae. The above-mentioned results of Sperber et al. (2004, 2012) and Nakayama et al. (2008) showed a high oc-

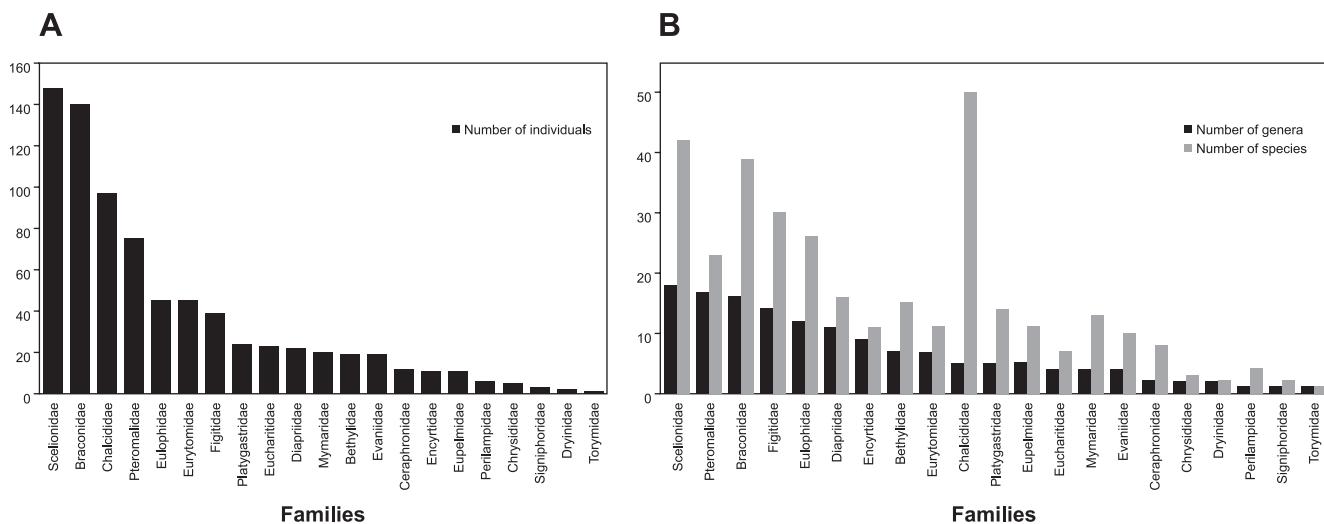


Figure 2. Bar charts of parasitoid wasp families and genera of collected individuals inhabiting agroforestry systems of cacao (*Theobroma cacao*) and copoazu (*T. grandiflorum*) from the Colombian Amazon basin. (A) number of individuals per family, (B) number of genera and species per family.

Table 2. List of the parasitic wasps associated with cacao species in the Colombian Amazon basin*.

UNAB Catal	Sampling methods	Taxon	Number of specimens	Sampling localities	Host	Previous records
ICHNEUMONOIDEA						
BRACONIDAE						
5010	SW	<i>Aleiodes</i> sp.	7	PU04, PU05, PU06, PU08		
5553	SW	<i>Apanteles carpatus</i> (Say, 1836)	3	PU07		
1477	MN	<i>Apanteles</i> sp.	9	CA06	Reared from larva of Notodontidae on leaf of <i>Cedrela</i> sp. (Meliaceae)	
1365	SW	<i>Aphaereta</i> sp.	1	CA03		
1364	SW	<i>Bracon</i> sp.	1	CA03		
3427-3428	MT	<i>Chelonus</i> sp.1-sp.2	3	CA06, PU06		
1042	MN	<i>Cotesia</i> sp.	7	CA03	Reared from larva of <i>Manduca sexta</i> (Sphingidae) on Solanaceae	
3440	MT	<i>Cyclaularidea</i> sp.	1	CA06		
3416-3420	SW	<i>Digonogastra</i> sp.1-sp.5	7	PU03, PU05, PU06, PU07, PU08		
1476	SW	<i>Heterospilus achi</i> Marsh, 2013	7	CA01		
3430	SW	<i>Heterospilus levitergum</i> Marsh, 2013	2	CA01		
3431	SW	<i>Heterospilus tres</i> Marsh, 2013	2	CA03		
3432-3239, 3822	SW	<i>Heterospilus</i> sp.1-sp.9	17	CA01, CA03, PU01, PU07	sp.9: Reared from root galls on <i>Ficus</i> sp. associated with species of Eurytomidae, Braconidae and Ichneumonidae	
1474	MN	<i>Hypomicrogaster</i> sp.	19	CA01	Reared from larva of Sphingidae on <i>Jussiaea linifolia</i> (Onagraceae)	
3823	MN	<i>Labania ficophaga</i> Belokobylskij & Zaldívar-Riverón, 2015**	6	PU07	Reared from root galls on <i>Ficus</i> sp. associated with species of Eurytomidae, Braconidae, and Ichneumonidae. The biology is similar to that found by Belokobylskij et al., 2015	Costa Rica (Belokobylskij et al., 2015)
3441	SW	<i>Lasiphorus</i> sp.	1	PU06		
1367	MN	<i>Lysiphlebus</i> sp.	12	CA08		
1366	MN	<i>Lysiphlebus testaceipes</i> Cresson, 1880	26	CA07, CA08	Reared from <i>Toxoptera</i> sp. on <i>Citrus</i> sp.	
3421-3426	MT	<i>Lytopylus</i> sp.1-sp.6	6	CA06, PU05, PU06, PU07, PU09		
5552	SW	<i>Notiospathius</i> sp.	2	PU03, PU07		
1363	SW	<i>Praon</i> sp.	1	CA03		
CHRYSIDOIDEA						
BETHYLIDAE						
5125	MN	<i>Anisepyrus angulatus</i> Santos & Azevedo, 2000*	1	AM02		Brazil (Barbosa & Azevedo, 2018)
5124	MT	<i>Anisepyrus borladi</i> Barbosa & Azevedo, 2018*	2	CA04		Brazil, Bolivia, Paraguay (Barbosa & Azevedo, 2018)
1193	SW	<i>Anisepyrus fortunatus</i> Evans, 1965*	1	PU07		Costa Rica, Ecuador, Guiana (Barbosa & Azevedo, 2018)
3925-3928	SW, MT	<i>Apenesia</i> sp.1-sp.4	6	CA06, PU07		
3923, 5132	MT	<i>Bakeriella lata</i> Kawada & Azevedo, 2003*	2	CA04		Brazil (Azevedo, 2014)
3224	MT	<i>Bakeriella reclusa</i> (Evans, 1969)*	1	CA06		El Salvador, Costa Rica, Ecuador, Bolivia (Azevedo, 2014)
5127-5128	MT, SW	<i>Dissomphalus</i> sp.1-sp.2	2	CA04, PU09		
5126	MT	<i>Epyris</i> sp.	1	AM04		
5129-5130	MN, MT	<i>Pristocera</i> sp.1-sp.2	2	AM03, AM04		
5123	SW	<i>Rhabdepyris</i> (<i>Trichotepyris</i>) sp.	1	CA04		
CHRYSIDIDAE						
3931	MT	<i>Adelphe paradoxa</i> (Ducke, 1902)	3	CA06		
3617-3618	MT	<i>Caenochrysis</i> sp.1-sp.2	2	CA06, CA07		
DRYINIDAE						
5131	SW	<i>Gonadryinus hansonii</i> Olmi, 1991	1	PU05		
662	MT	<i>Gonatopus</i> sp.	1	CA06		
CERAPHRONOIDEA						
CERAPHRONIDAE						
5011-5012	SW	<i>Aphanogmus</i> sp.1-sp.2	2	CA03		

Table 2. Continued.

UNAB Catal	Sampling methods	Taxon	Number of specimens	Sampling localities	Host	Previous records
1448-1449, 4136-4139	SW, MT, MN	<i>Ceraphron</i> sp.1-sp.6	10	CA03, CA06, CA07		
		CHALCIDOIDEA				
		CHALCIDIDAE	100			
5025	SW	<i>Brachymeria annulata</i> (Fabricius, 1793)	2	CA04, PU08		
3525	MN	<i>Brachymeria mnestor</i> Walker, 1841	2	CA06	Rearred from pupa of Pieridae on <i>Duranta</i> sp. (Verbenaceae)	
1041, 1345, 1348	SW, MT	<i>Brachymeria</i> sp.1-sp.3	9	CA03, CA04, CA06, CA07, PU06		
1865	SW	<i>Conura albomaculata</i> (Ashmead, 1904)	1	CA09		
1872	MT	<i>Conura apicalis</i> (Ashmead, 1904)	1	PU09		
1886	SW	<i>Conura decis</i> (Walker, 1862)	4	PU05, PU06, PU07, PU08		
1032	MN, SW	<i>Conura dimidiata</i> (Fabricius, 1804)	4	CA04, PU02, PU05		
1866	SW	<i>Conura enocki</i> (Ashmead, 1904)	1	PU06		
3527	SW	<i>Conura marginata</i> Ashmead, 1904	1	PU03		
3465	SW	<i>Conura mesomelas</i> Walker, 1862	1	PU07		
3429	MT	<i>Conura nigrita</i> (Howard, 1894)	1	PU09		
5021	SW	<i>Conura nigropetiolata</i> Ashmead, 1904	1	AM05		
1868	SW	<i>Conura quadripunctata</i> (Fabricius, 1804)	1	AM01		
1033, 1036, 1350-1354, 3531-3549, 3559, 5022, 5024	MN, MT, SW, PT	<i>Conura</i> sp.1-sp.29	58	AM04-05, CA03-04, CA07-09, PU03, PU05, PU07-09	sp.11: Rearred from pupa of Pieridae on <i>Duranta</i> sp. (Verbenaceae)	
1190	SW	<i>Haltichella hydara</i> (Walker, 1842)	1	CA03		
2530	SW	<i>Haltichella ornaticornis</i> Cameron, 1884	2	CA03, CA04		
2531-2532	SW	<i>Haltichella</i> sp.1-sp.2	2	CA03		
1189	SW	<i>Notaspidium</i> sp.	2	CA03		
1356	SW, MT	<i>Stypiura</i> sp.	3	CA03, CA06		
		ENCYRTIDAE	11			
663, 3821	MT	<i>Aenasius</i> sp.1-sp.2	2	CA06, CA07		
2537	SW	<i>Anagyrus</i> sp.	1	CA03		
1473	MT	<i>Caenohomalopoda</i> sp.**	1	CA06		Algeria, Cayman Islands, China, India, Indonesia, Japan, Guam, North Korea, Puerto Rico, South Africa, South Korea, United States of America, Vietnam (Noyes, 2021)
1433	MT	<i>Cerchysiella</i> sp.	1	CA06		
1463	MT	<i>Cercobelus</i> sp.**	1	CA06		Armenia, Azerbaijan, Belgium, Costa Rica, Czechoslovakia, Denmark, Finland, France, Germany, Hungary, India, Lithuania, Moldova, Montenegro, Netherlands, Norway, Russia, Sweden, United Kingdom (Noyes, 2021)
2538	MT	<i>Coelopencyrtus</i> sp.	1	CA06		
2536	MT	<i>Encyrtus infelix</i> (Embleton, 1902)	1	CA06		
3820, 3919	MT, SW	<i>Ooencyrtus</i> sp.1-sp.2	2	CA06, PU01		
1436	MT	<i>Tetracnemoidea</i> sp.	1	CA06		
		EUCHARITIDAE	23			
4133	MN	<i>Dicoelothorax</i> sp.	1	CA05		
1820	MN, MT, SW	<i>Kapala</i> sp.	14	CA03, CA04, CA06, PU09		
5027	MN	<i>Lirata luteogaster</i> Cameron, 1884**	1	CA06		Brazil, Costa Rica, Ecuador, Mexico, Panama, Venezuela (Noyes, 2021)
1460, 3783	MT, SW	<i>Orasema</i> sp.	2	CA03, CA06		
5110	SW	<i>Orasema erwini</i> Burks, Mottern & Heraty, 2015*	1	CA04		Brazil, Ecuador, Peru (Burks et al., 2015)
5111	SW	<i>Orasema evansi</i> Burks, Heraty & Dominguez, 2018*	1	CA04		Costa Rica, Dominican Republic, Honduras, Nicaragua, Panama, St Vincent & Grenadines, Trinidad & Tobago, United States of America (Burks et al., 2018)

Table 2. Continued.

UNAB Catal	Sampling methods	Taxon	Number of specimens	Sampling localities	Host	Previous records
5112	SW	<i>Orasema susanae</i> species group	3	PU02, PU06, PU09		
		EULOPHIDAE	45			
5039	MT	<i>Ametallon</i> sp.	1	CA06		
1197	SW	<i>Aprostocetus (Aprostocetus)</i> sp.	1	CA03		
3817	MN	<i>Aprostocetus gala</i> (Walker, 1847) pos.	2	CA03	Reared from Cecidomyiidae on leaf galls of <i>Manihot esculenta</i> (Euphorbiaceae)*	
3832-3835	MT, SW	<i>Aprostocetus</i> sp.1-sp.4	4	CA06, CA08, CA09, PU09		
5040	SW	<i>Chrysonotomyia</i> sp.	1	PU03		
3818	SW	<i>Deutereulophus</i> sp.**	1	CA03		Australasia, Nearctic, Neotropics, Palearctic (Noyes, 2021)
4091	MN	<i>Elachertus</i> sp.	6	CA01	Reared from Gracillariinae on <i>Chrysophyllum cainito</i> (Sapotaceae)	
5043	SW	<i>Entedon</i> sp.	2	CA03		
3826-3837	SW	<i>Euderus</i> sp.1-sp.2	2	CA01, CA03		
5042	SW	<i>Hadrotrichodes</i> sp.	3	CA03		
3830	MT	<i>Horismenus bennetti</i> Schauf, 1987*	1	CA06		Costa Rica, Trinidad & Tobago (Noyes, 2021)
5037	SW	<i>Horismenus chydaeus</i> Hansson, 2009*	2	CA03		Belize, Costa Rica, Dominican Republic, Ecuador, Honduras, Peru (Noyes, 2021)
4093	MN	<i>Horismenus cupreus</i> (Ashmead, 1894)*	2	CA07	Reared from <i>Phyllocoptis</i> sp. (Gracillariidae) on <i>Annona montana</i> (Annonaceae)*	
1467	MT	<i>Horismenus elachurus</i> Hansson, 2009*	1	CA06		Costa Rica (Noyes, 2021)
3831	SW	<i>Horismenus eumantis</i> Hansson, 2009*	2	CA03		Costa Rica, Ecuador, Panama, Peru, Trinidad & Tobago (Noyes, 2021)
1465	MT	<i>Horismenus lacticoxa</i> Hansson, 2009*	1	CA06		Costa Rica (Noyes, 2021)
1466	MT	<i>Horismenus nr. selvensis</i> Hansson, 2009	1	CA06		
3828	SW, MT	<i>Horismenus orbicularis</i> Hansson, 2009	2	CA03, CA06		
1196	SW	<i>Horismenus striatus</i> Hansson, 2009*	2	CA03		Costa Rica, Ecuador, El Salvador; Honduras, Trinidad & Tobago (Noyes, 2021)
3829	MN	<i>Horismenus</i> sp.	1	CA06		
5041	SW, MT	<i>Phymasticus</i> sp.	6	CA03, CA06		
3469	MT	<i>Tetrastichus</i> sp.	1	CA06		
		EUPELMIDAE	11			
1192, 1360, 1821, 3778, 5016, 5554	MT, MN, SW	<i>Anastatus</i> sp.1-sp.6	6	CA03, CA04, CA06, CA07, PU09		
1359	MT	<i>Brasema</i> sp.	1	CA03		
1358	MT	<i>Brasema</i> sp.	1	CA06		
2535	MT	<i>Merostenus (Merostenus)</i> sp.	1	CA06		
3777	MN	<i>Phlebopenes longicollis</i> (Westwood, 1874)	1	PU05		
3776	SW	<i>Zaischnopsis</i> sp.	1	CA03		
		EURYTOMIDAE	45			
1450	MT	<i>Aximopsis</i> sp.	1	CA06		
1429-1431, 4090	SW, MN	<i>Eurytoma</i> sp.	18	CA01, CA07, CA10, PU07	sp.4: Reared from root galls on <i>Ficus</i> sp. associated with species of Eurytomidae, Braconidae and Ichneumonidae	
5046	SW	<i>Isosomodes monteria</i> Hanson & Gates, 2013	1	PU09		
3779	SW	<i>Neorileya meridionalis</i> Gahan, 1927*	1	PU03		Argentina, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Panama, Peru, Trinidad & Tobago (Noyes, 2021)
1432	MN	<i>Noerileya flavipes</i> Ashmead, 1904*	1	CA10	Reared from Ascomycota fungus on <i>Zygia longifolia</i> (Fabaceae). Note: The fungus supplies food resources to different parasitoids (Observed in field)	Argentina, Brazil, Costa Rica, El Salvador, Nicaragua, Panama, Peru, Venezuela (Noyes, 2021)
3824	MN	<i>Phylloxerexenus</i> sp.	7	PU07		

Table 2. Continued.

UNAB Catal	Sampling methods	Taxon	Number of specimens	Sampling localities	Host	Previous records
3825-3827, 5120	MT, MN, SW	<i>Prodecatoma</i> sp.1-sp.4	14	CA06, PU01, PU02		
5047	SW	<i>Rileya antennata</i> Gates, 2008*	2	CA04, PU06		Brazil, Ecuador, Honduras, Peru, Surinam, Trinidad & Tobago
		MYMARIDAE	20			
1451-1455, 3841-3843	MN, MT, SW	<i>Gonatocerus</i> sp.1-sp.8	15	CA01, CA03, CA06, CA08		
3415	SW	<i>Neomyrmar</i> sp.	1	CA03		
3838-3840	MT	<i>Polynema</i> sp.1-sp.3	3	CA06		
1471	MT	<i>Stephanodes</i> sp.	1	CA06		
		PERILAMPIDAE	6			
5562	SW	<i>Perilampus</i> nr. <i>hyalinus</i> Say, 1829	1	AM05		
4128, 4129, 1361	MT, SW	<i>Perilampus</i> sp.1-sp.3	5	PU03, PU06, CA04, CA06		
		PTEROMALIDAE	75			
3463	SW	<i>Anisopteromalus</i> sp.	1	PU09		
3464	SW	<i>Bubekia tricarinata</i> (Ashmead, 1888)**	1	PU09		Argentina, United States of America (Noyes, 2021)
3467	SW	<i>Chrysoglyphe apicalis</i> Ashmead, 1894**	1	CA03		Nicaragua, St. Vincent & Grenadines, Venezuela (Noyes, 2021)
5119	MT, SW	<i>Critogaster</i> sp.	4	CA04, PU09		
1534	MT	<i>Epistenia</i> (<i>Epistenia</i>) sp.	2	CA04, CA06		
661	MT	<i>Erotolepsia</i> sp.**	1	CA06		Brazil, Grenada, St. Vincent & Grenadines
3844	SW	<i>Gbelcia</i> sp.**	1	PU07		Canada, Czechoslovakia, Hungary, Kazakhstan, Moldova, Romania, Sweden, Kazakhstan, United Kingdom, United States of America (Noyes, 2021)
3459	MT	<i>Hadroepistenia erwini</i> Gibson, 2003	1	CA06		
5207	MN, SW	<i>Halticopterooides exemae</i> Bouček, 1993**	1	AM03, CA04		Canada, United States of America, Argentina, Paraguay
1437	MN	<i>Heteroschema rugosopunctata</i> (Ashmead, 1894)	42	CA03, PU06	Reared from <i>Melanagromyza obtusa</i> (Agromyzidae) in pods of <i>Flemingia macrophylla</i> (Fabaceae)	
1347, 4134	MT, SW	<i>Heteroschema</i> sp.1-sp.2	5	CA03, CA06, CA09		
659	MT	<i>Lelaps aeneiceps</i> Ashmead, 1904*	1	CA07		Brazil (Noyes, 2021)
658	MN	<i>Lelaps affinis</i> Ashmead, 1904*	1	CA07		Brazil (Noyes, 2021)
3461	SW	<i>Lelaps bimaculata</i> Ashmead, 1904*	1	PU05		Argentina, Brazil (Noyes, 2021)
3462	MN, SW	<i>Lelaps</i> nr. <i>striaticeps</i> Strand, 1911	4	AM02, CA06, PU08, PU09		
5205	MN, SW	<i>Lelaps setifrons</i> Strand, 1911*	2	CA04		Peru (Noyes, 2021)
3466	SW	<i>Neocatolaccus</i> sp.**	1	PU01		Australasia, Africa, Nearctic, Neotropics (Noyes, 2021)
660	SW	<i>Netomocera</i> sp.**	1	CA09		Australasia, Africa, Asia, Neotropical, Nearctic, Palearctic (Noyes, 2021)
3468	SW	<i>Propodeia complexa</i> Bouček, 1993**	1	CA03		United States of America, Trinidad & Tobago (Noyes, 2021)
3460	MT	<i>Prashizonotus</i> sp.	1	CA03		
5122	MT	<i>Psilocera</i> sp.	1	CA04		
5121	MT	<i>Tomocerodes</i> sp.**	1	CA06		United States of America, Mexico (Noyes, 2021)
		SIGNIPHORIDAE	3			
4132	MN	<i>Signiphora merceti</i> Malenotti, 1917	1	CA05		
1434	MT	<i>Signiphora</i> sp.	2	CA06		
		TORYMIDAE	1			
1425	MT	<i>Podagrion</i> sp.	1	CA06		
		CYNOPOIDEA				
		FIGITIDAE	39			
4095	MT, SW	<i>Acantheucoela</i> sp.**	2	CA03, PU05		Belize
1464,	MT, SW	<i>Aganaspis</i> sp.1-sp.6	8	CA03, CA06, PU08		
4111-4115						

Table 2. Continued.

UNAB Catal	Sampling methods	Taxon	Number of specimens	Sampling localities	Host	Previous records
1424	SW	<i>Agrostocynips</i> sp.**	1	CA03		Argentina, Canada, Chile, Mexico, United States of America (Buffington & Scheffer, 2008)
4094	MN	<i>Caleucoela</i> sp.	1	PU08		
4102	SW	<i>Dieucoila</i> sp.	1	CA03		
1426-1428, 4105-4110	MT, SW	<i>Ganaspis</i> sp.1-sp.9	11	CA03, CA06, CA08, PU09		
4100, 4101	SW	<i>Hexacola</i> sp.1-sp.2	2	CA07, PU09		
4116-4118	MT	<i>Leptopilina</i> sp.1-sp.3	3	CA06		
4096	SW	<i>Neralsia</i> sp.	1	PU04		
4104	SW	<i>Odonteucoila</i> sp.	1	PU07		
1423	SW	<i>Trichoplasta</i> sp.	1	CA03		
1422	SW, MT	<i>Tropideucoila</i> sp.	3	CA03, CA06, CA07		
2533, 2534, 4103	SW	<i>Trybliographa</i> sp.	3	CA03		
3784	SW	<i>Zaeucoila</i> sp.	1	PU01		
DIAPRIOIDEA						
DIAPRIIDAE						
3452	SW	<i>Acanthropia</i> sp.	1	CA03		
3447, 3448	MT	<i>Aclista</i> sp.1-sp.2	3	CA06		
1198-1201	MN, SW	<i>Basalys</i> sp.1-sp.4	9	CA03, CA07		
3446	SW	<i>Doliopria</i> sp.	1	CA03		
3449	SW	<i>Hansonia</i> sp.**	1	PU09		Brazil, Costa Rica, Ecuador, Panama, Trinidad, Venezuela (Masner & García, 2002)
3453	SW	<i>Idiotypa</i> sp.**	1	CA03		Australia, Belize, Brazil, Canada, Jamaica, Mexico, United State of America, Venezuela (Masner & García, 2002)
3456	SW	<i>Megalastopia</i> sp.**	1	CA03		Antilles, Brazil, Mexico (Masner & García, 2002)
1459	MN	<i>Monelata</i> sp.	1	CA07		
1194	SW	<i>Paramesius</i> sp.**	1	CA03		Australia, Brazil, Brunei, India, Jamaica, Mexico, Pakistan, United States of America, Venezuela (Masner & García, 2002)
1816	SW	<i>Spilomicrus integer</i> Thomson, 1858**	1	PU01		Australia, Belize, Brazil, British Virgin Islands, Brunei, Costa Rica, Dominican Republic, Guatemala, India, Jamaica, Japan, New Caledonia, Mexico, Trinidad & Tobago, Venezuela (Masner & García, 2002)
3450	SW	<i>Spilomicrus</i> sp.	1	CA03		
1357	MT	<i>Trichopria</i> sp.	1	CA06		
EVANIOIDEA						
EVANIIDAE						
4125	SW	<i>Evania</i> sp.	1	PU09		
4121, 4126-4127	MN	<i>Evaniella</i> sp.1-sp.3	10	CA04, PU03, PU05, PU06, PU07, PU09		
4124	SW	<i>Hyptia</i> sp.	1	PU06		
3780-3782, 4122-4123	MT	<i>Semaeomyia</i> sp.1-sp.5	7	CA06, PU01, PU05, PU07, PU08		
PLATYGASTROIDEA						
PLATYGASTRIDAE						
1435	SW	<i>Inostemma</i> sp.	1	CA07		
3457, 3767-3769, 4130	MN, MT, SW	<i>Leptacis</i> sp.1-sp.5	11	CA03, CA05, CA06, CA07	sp.5: Reared from galls of Cecidomyiidae	
1469	MT	<i>Leptoteleia</i> sp.	1	CA06		
3773-3775	MN, SW	<i>Platygaster</i> sp.	3	CA03, CA08, PU09		
3458, 3770-3772, 4131, 5015	MN, MT, SW	<i>Synopeas</i> sp.1-sp.6	8	CA01, CA03, CA05, CA06, PU09	sp.5: Reared from galls of Cecidomyiidae	

Table 2. Continued.

UNAB Catal	Sampling methods	TAXON	Number of specimens	Sampling localities	Host	Previous records
		SCELIONIDAE	148			
5117	MT	<i>Acanthoscelio acutus</i> Dotseth & Johnson, 2001	1	CA04		
1445	SW	<i>Apegus</i> sp.	1	CA03		
3756-5118	MT, PT	<i>Baeus</i> sp.	2	CA04, CA06		
3761-3762	SW, MT	<i>Baryconus</i> sp.	6	CA03, CA04, CA06		
1439-1440	MT, SW	<i>Calliscelio</i> sp.	2	CA03, CA06		
1441	MT	<i>Calliscelio suni</i> Chen & Johnson, 2017	1	AM02		
1472, 1446-1447, 3454-3455	MT, SW	<i>Ceratobaeus</i> sp.1-sp.5	8	CA03, CA04, CA06		
5114	MT	<i>Chromoteleia copiosa</i> Chen & Johnson, 2018*	3	CA06		Belize, Brazil, Costa Rica, Guatemala, Honduras, Mexico, Panama, Trinidad & Tobago, Venezuela (MBD, 2021)
5116	MT	<i>Chromoteleia cuneus</i> Chen & Johnson, 2018*	4	AM02		Costa Rica, Ecuador, Panama (MBD, 2021)
5115	MT	<i>Chromoteleia fuscicornis</i> Kieffer, 1910	2	CA04, CA06		
1470	SW	<i>Duta</i> sp.	1	CA07		
1442, 3816	MT, SW	<i>Gryon</i> sp.1-sp.2	6	CA03, CA06		
1475	MT	<i>Macroteleia</i> sp.	1	CA06		
3760	SW	<i>Opisthacantha</i> sp.	1	PU09		
3766	MT	<i>Probaryconus</i> sp.	1	CA06		
3815	SW, PT	<i>Scelio luteus</i> (Cameron, 1888)	2	CA02, CA06		
1438, 3757-3759	MT	<i>Scelio</i> sp.1-sp.5	9	CA06, PU09		
1456-1458, 3804-3813	MN, MT, SW	<i>Telenomus</i> sp.1-sp.13	74	AM04, CA01, CA03, CA04, CA06, CA07, CA09, PU02, PU07, PU08		
3765	SW	<i>Thoron</i> sp.	1	CA06		Azerbaijan, Brazil, Mexico, Sweden, Paraguay, United States, Ukraine (MBD, 2021)
1195, 1462	MN	<i>Trissolcus</i> sp.1-sp.2	18	CA03, CA09	sp.1: Reared from eggs of <i>Antiteuchus</i> sp. (Pentatomidae) on leaves of <i>Theobroma cacao</i>	
3763-3764, 1468	MN, MT, SW	<i>Triteleia</i> sp.1-sp.3	3	CA06, CA07, CA09		
1443	SW	<i>Xenomerus</i> sp.	1	CA03		

* Record for species, ** Record for genus, SW = Sweep net, MT = Malaise trap, MN = Manually, PT = Pitfall.

currence of Scelionidae and Braconidae. This is similar to our results, in which these families were mainly represented by the genera *Telenomus* and *Lysiphlebus*, respectively.

In cacao agroecosystems from Merida (Venezuela), Mazón (2015) and Mazón *et al.* (2018) reported 33 and 23 families of parasitoid wasps, respectively. Again, the richest families were similar to what we obtained in this study: Braconidae, Ichneumonidae, Scelionidae, Pteromalidae, Figitidae, Encyrtidae, and Mymaridae. However, our results for Chalcidoidea showed a higher richness of Chalcididae, Pteromalidae, and Eulophidae. Taxonomic identifications of the parasitoids in those investigations were carried out to the family level, whereas we achieved genus and species level identifications, which offer far greater information about the biology (Lenat & Resh, 2001). This is particularly true for parasitoid wasps, where the biology varies widely between species (Branca *et al.*, 2019). For example, many of the hymenopteran genera we found in the current survey, such as *Telenomus* (Eberhard, 1975; Pardede, 1986), *Brachymeria* (Entwistle, 1963), *Conura* (García & Montilla,

2010), *Aenasius*, *Anagyrus* (Ackonor, 2002), *Aprostocetus* (Kerrich, 1963; LaSalle, 1994), *Perilampus*, and *Heterospilus* (García & Montilla, 2010), have been previously recorded as parasitoids of phytophagous species that feed on cacao.

Richness and number of curated parasitoids

Chalcididae accounted for 50 identified species and five genera, which makes it the richest family within the cacao and copoazu agroecosystems. Despite the lack of studies investigating the diversity of Chalcididae in cacao or copoazu, members of this family have been reported as parasitoids in pupae of phytophagous species such as *Carmenta* sp. (Sesiidae), an insect that feeds on cacao pods (García & Montilla, 2010). Chalcidid wasps have a cosmopolitan distribution, with a greater diversity in the Neotropical lowlands (Delvare, 1995). In Colombia, 17 genera and 115 species have been reported, many of them occurring in the Amazon basin (Pérez-Benavides & Serna, 2019).

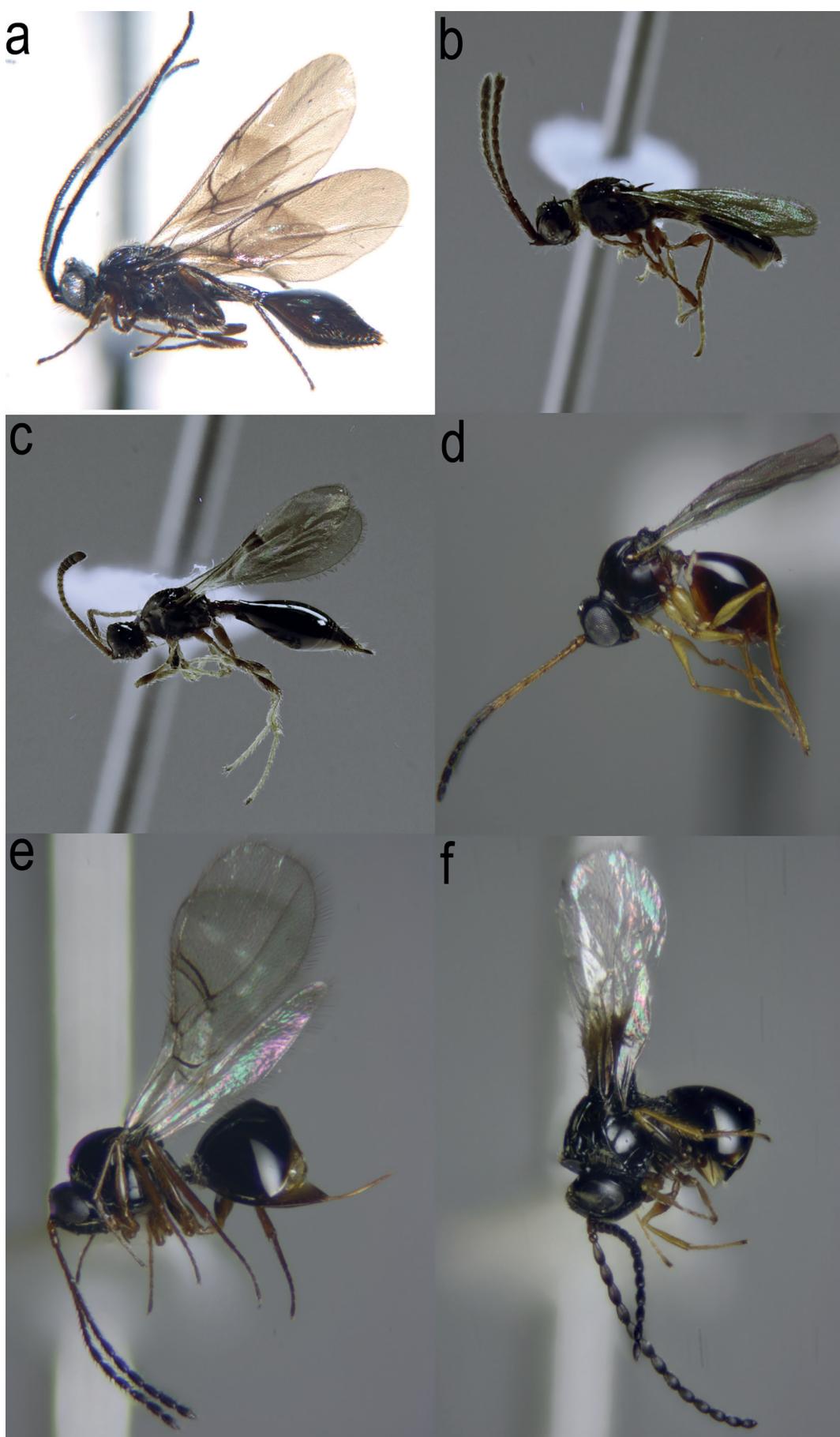


Figure 3. Habitus of parasitoid wasps collected in agroforestry systems of cacao (*Theobroma cacao*) and copoazu (*T. grandiflorum*). (A) *Aclista* sp. (Diapriidae) [UNAB 3747], (B) *Basalys* sp. (Diapriidae) [UNAB 1198], (C) *Paramesius* sp. (Diapriidae) [UNAB 1194], (D) *Trichoplasta* sp. (Figitidae) [UNAB 1423], (E) *Aganaspis* sp. (Figitidae) [UNAB 1464], (F) *Tropideucoila* sp. (Figitidae) [UNAB 1422].

Scelionidae constituted the second richest family we found in the cacao and copoazu agroforestry systems. Comparable results were found by García & Montilla

(2005) in cacao, who reported 33 genera with the genera *Idris*, *Trimorus*, and *Gryon* as the most diverse. Although we recovered a lower number of genera, *Apegeus*,

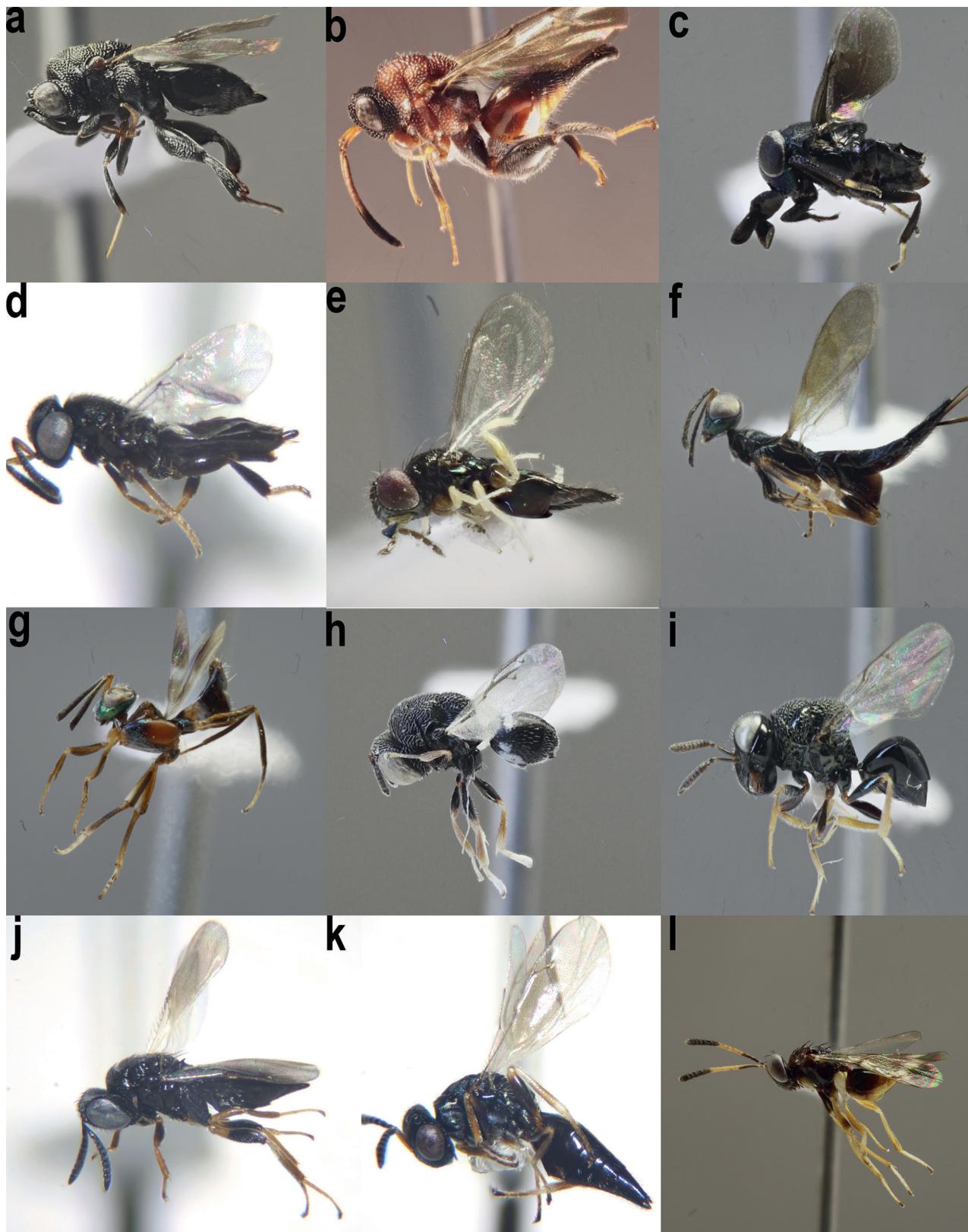


Figure 4. Habitus of Chalcidoidea collected in agroforestry systems of cacao (*Theobroma cacao*) and copoazu (*T. grandiflorum*). (A) *Haltichella hydara* (Walker, 1842) [UNAB 1190], (B) *Stypiura* sp. [UNAB 1356], (C) *Aenasius* sp. (Encyrtidae) [UNAB 663], (D) *Coelopencyrus* sp. [UNAB 2538], (E) *Horismenus striatus* Hansson, 2009 (Eulophidae) [UNAB 1196], (F) *Brasema* sp. (Eupelmidae) [UNAB 1358], (G) *Anastatus* sp. (Eupelmidae) [UNAB 1192], (H) *Neorileya flavipes* Ashmead, 1904 (Eurytomidae) [UNAB 1432], (I) *Perilampus* sp. (Perilampidae) [UNAB 1361], (J) *Erotolepsia* sp. (Pteromalidae) [UNAB 661], (K) *Bubekia tricarinata* (Ashmead, 1888) (Pteromalidae) [UNAB 3464], (L) *Lelaps affinis* Ashmead, 1904 (Pteromalidae) [UNAB 658].

Ceratobaeus, *Thoron*, and *Xenomerus* constitute additional reports observed for the family in these agroecosystems. Scelionidae is a highly diverse family in tropical

forests, with 57 genera and 342 species reported from the Neotropics (Arias-Penna, 2002), out of 176 genera (extant and fossil) (Chen et al., 2021) and approximately

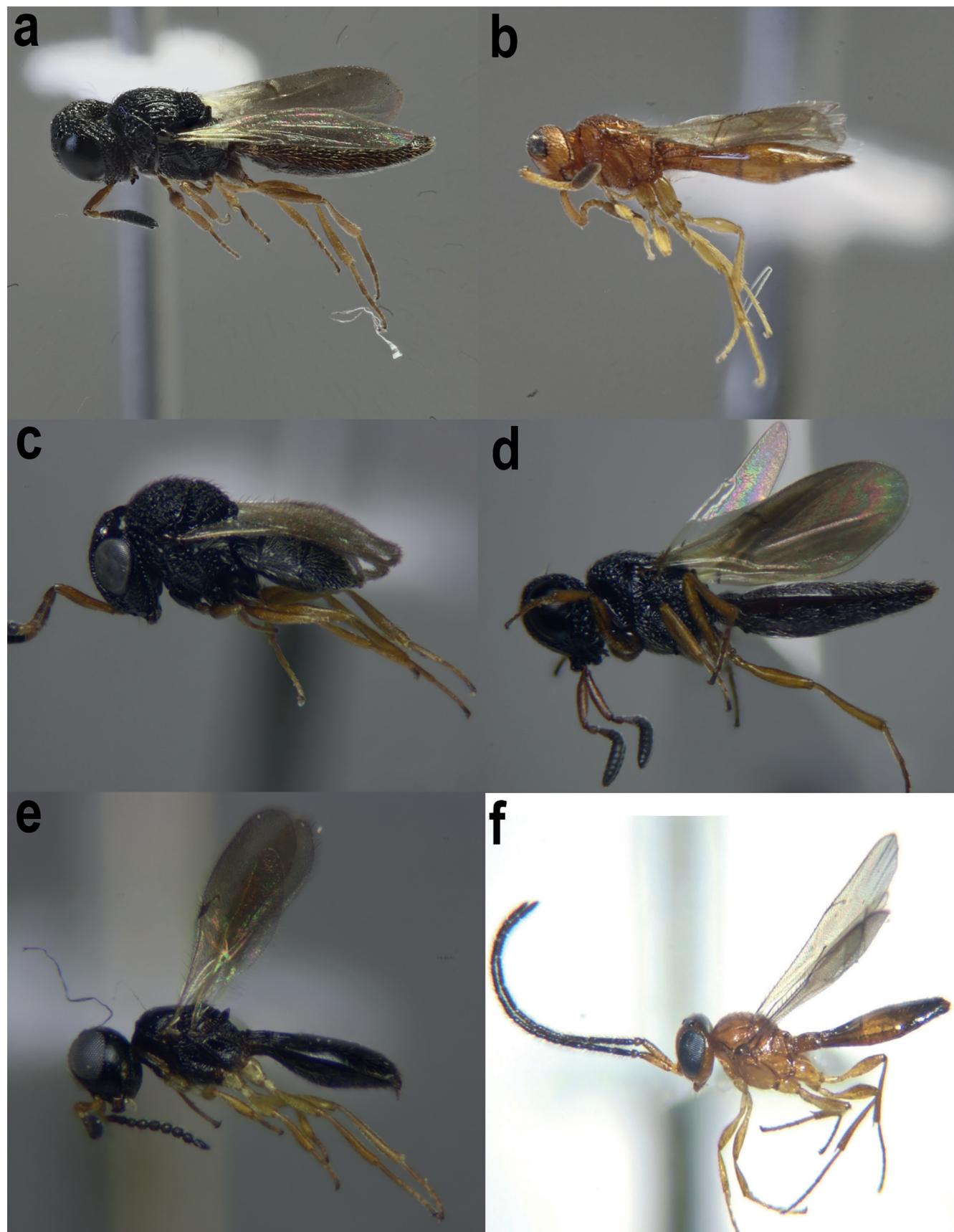


Figure 5. Habitus of Platygastroidea (Scelionidae) collected in agroforestry systems of cacao (*Theobroma cacao*) and copoazu (*T. grandiflorum*). (A) *Apegenus* sp. [UNAB 1445], (B) *Calliscelio* sp. [UNAB 1439], (C) *Gryon* sp. [UNAB 1442], (D) *Scelio* sp. [UNAB 1438], (E) *Xenomerus* sp. [UNAB 1443], (F) *Thoron* sp. [UNAB 3765].

3,000 described species worldwide. According to Masner & Arias-Penna (2006), mixed agroecosystems can have a source-sink dynamics between forest and crop areas, where adults of Scelionidae are abundant in the surrounding forest, especially in the forest canopy where many of them search for hosts, which could also explain in part its high diversity in our work.

A high number of individuals of Braconidae (the third richest family within the agroecosystems) was chiefly reached due to *Hypomicrogaster* sp., reared from larvae of Sphingidae on *Ludwigia hyssopifolia* (G. Don) Exell (Onagraceae), as well as by the species *Lysiphlebus testaceipes* (Cresson) reared from *Aphis* sp. on *Citrus* sp. (Rutaceae). *Hypomicrogaster* is a large genus, mainly distributed in the Neotropical region, with 45 described species, nine of which have been recorded from Colombia and the Amazon basin (Fernandez, 2000). Species of *Hypomicrogaster* act as parasitoids of microlepidopteran leaf-mining and other cryptic or endophytic hosts (Valerio & Whitfield, 2015). *Lysiphlebus testaceipes* is widely distributed in the Nearctic region, and to a lesser degree in the Neotropics (Stary, 1976). It has also been reported from the Palearctic region as an introduced species. *Lysiphlebus testaceipes* attacks more than 100 aphid species, often suppressing their populations below economic injury levels (Jones et al., 2007).

New taxa and occurrence records

Even though most of our new records of genera and species have a Neotropical distribution, one of those found in our study, *Gbelcia* (Pteromalidae), has an atypical occurrence, given that its natural distribution is Holartic (Noyes, 2021). *Gbelcia* is recognized by the following combination of diagnostic features, observed in the specimens examined in this study: transverse and stout head, depressed thoracic dorsum, rugose-reticulate propodeum with distinct though slightly irregular median carina and plicae, pronotal collar with a high carina, and forewings with 1 to 6 hairs on the basal fold (Bouček, 1993; Gibson et al., 1997). *Gbelcia* comprises two described species: *G. cordilurae* Bouček, whose adults are parasitoids of the pupae of *Cordilura varipes* (Walker) and *C. praeusta* Loew (Diptera: Scathophagidae: Scathophaginae) (Bouček, 1993); and *G. crassiceps* Bouček, which are associated with *Phragmites* sp. (Poaceae) (Mitroiu, 2013).

New host records

Our new record of *Phyllocoptis* sp. (Gracillariidae) as a host of *Horismenus cupreus* is congruent with previous observations by Hansson (2009), who reported *H. cupreus* as a species that primarily attacks leaf-miners, mainly from the families Buprestidae, Curculionidae, Agromyzidae, Tischeriidae, and several unidentified microlepidopterans, as well as two records from spider eggs, probably as primary parasitoids (Hansson, 2009).

CONCLUSION

The collection of wasp parasitoids obtained in the present work constitutes an important contribution to our knowledge of natural biological controllers in agroforestry systems of the Colombian Amazon basin. It also provides a basic alpha taxonomic input for new studies. Agroforestry systems of cacao and copoazu provide a refuge for a high number of parasitoid wasps and allow multiple ecological interactions with their hosts. The life histories of most of the taxa found here remain unknown, as well as their functional role in agricultural ecosystems as potential natural enemies of phytophagous insects. Therefore, much work remains to be done on this topic. We also accumulated the first catalogued voucher collection of parasitoid wasps in Colombia, which in times of the Anthropocene insect decline, will be a continuing source of data and information to be used by future scientists, especially applied entomologists.

AUTHORS' CONTRIBUTIONS: **ALPB, FS, LMA:** Conceptualization; **ALPB, LMA, PH, FS:** Methodology; **ALPB:** Data curation, Investigation, Writing – original draft; **LMA, PH, FS:** Supervision, Writing – review & editing; **FS:** Project administration, Funding acquisition; **LMA, PH:** Validation. All authors actively participated in the discussion of the results; they reviewed and approved the final version of the paper.

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