

**TRITROPHIC ASSOCIATIONS AND TAXONOMIC NOTES ON *LYSIPHLEBUS FABARUM*
(MARSHALL) (HYMENOPTERA: BRACONIDAE: APHIDIINAE),
A KEYSTONE APHID PARASITOID IN IRAN**

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Abstract - An investigation of host associations, distribution and types of reproduction (sexual, asexual) of *Lysiphlebus fabarum* (Marshall) across 20 provinces of Iran during 2006-2011 was undertaken. The parasitoid was reared from three groups of host aphids belonging to genera *Aphis* and *Brachycaudus*, and occasional host aphid genera. *Aphis craccivora* Koch was the most frequent host aphid for *L. fabarum* on various host plants, including economically important crops. The field sex ratio generally favored females, but in some cases, only thelytokous (uniparental) populations were found. In those cases, the host was always an *Aphis* species. Specimens reared from *Brachycaudus* aphids were all biparental, indicating the presence of a sibling biological species. Overall analysis of diagnostic morphological characters in the forewing indicated intra-specific variability in forewing marginal setae as well as variations in length of the R1 vein.

Key words: Host associations, *Aphis*, *Brachycaudus*, intra-specific variation, sex ratio

INTRODUCTION

Hymenopterous parasitoids are one of the most important groups acting as biological control agents. This is due to the high level of diversity and specificity of their hosts (LaSalle and Gauld, 1993). The subfamily Aphidiinae (Ichneumonoidea, Braconidae) is a group of solitary endoparasitoids of aphid that has a significant impact on populations of these insects (Starý, 1970, 2006). The genus *Lysiphlebus* Förster is a moderately diverse group of aphidiines with about 20 described species (excluding *Adialytus*) attacking different host aphids in various habitats (Mescheloff and Rosen, 1990; Starý, 1961a, b, 1970, 1971, 1975, 1979, Starý and Juchnevič, 1978; Starý et al., 2000, 2010).

Lysiphlebus fabarum (Marshall) is an aphid parasitoid that has been known to manifest numerous taxonomic problems. It may represent a group of taxa with specific host associations or even a single taxon with a wide range of host aphids (Belshaw et al., 1999; Carver and Franzmann, 2001; Sandrock et al., 2007, 2011; Starý, 1999, 2006). *Lysiphlebus fabarum* is also a specialized parasitoid of ant-defended aphid colonies, avoiding aggression from ants through mimicry of aphid cuticular hydrocarbons (Völkl and Mackauer, 1993; Rasekh et al., 2010b). The females tend to parasitize aphids from the same colonies from which they themselves emerged (Rasekh et al., 2011).

Like some other members of the genus, *L. fabarum* represents an interesting system of natu-

rally occurring sexual-asexual shifts in a population (Starý, 1999; Belshaw et al., 1999), suggesting that the phenomenon is determined by genetic characteristics (Sandrock and Vorburger, 2011). Many other studies have been done on different aspects of the biology, ecology and biosystematics of *L. fabarum* in Iran (Bagheri Matin et al., 2005, 2009; Barahoei et al., 2011; Rasekh et al., 2010a, b, 2011; Takaloozadeh et al., 2003).

L. fabarum is the most abundant parasitoid of some economically important aphids such as *Aphis fabae* Scopoli (Starý, 1986b; Starý et al., 2000) and *Aphis craccivora* Koch (Rakhshani et al., 2005a,b) on various different crops. Such parasitoid species need to be classified as “key-stone species” within an overall evaluation of parasitoids in agro-ecosystems (LaSalle and Gauld 1993; Starý et al., 2002). Knowledge about host range patterns and consequent relationships with type of reproduction within different populations of *L. fabarum* in Iran has remained insufficient; it has therefore been necessary to compile a summary and to cover the fundamental work on different aspects of host associations as well as to provide a background for further studies on the biological complexities of the diversity and distribution of the species. Host associations and distribution of the aphid parasitoid reflect the importance of the biosystematics and biodiversity of these parasitoids as potentially promising bio control agents.

MATERIALS AND METHODS

These studies were carried out across 20 provinces of Iran, extending from its eastern to its western borders, to represent the whole country. Sampling was done from 2006-2011. Colonies of different host aphids collected from fields were transferred to a laboratory where they were kept inside mesh-covered plastic boxes, together with parts from the host plants. A number of healthy adult aphids was simultaneously collected and preserved in 55% ethanol for later identification. The rearing boxes were kept at room temperature for 2-3 weeks and the emerged parasitoids were clipped daily using an aspirator, and dropped into ethanol (75%) for later examination.

A few specimens from each sample were dissected and slide-mounted in Hoyer media. The external morphology of the parasitoids was studied using a NIKON SMZ645 stereomicroscope and a NIKON Eclipse E200 microscope. Total numbers of emerged wasps (males and females) were counted for each sample to determine the sex ratio and the relationship with host associations. For evaluation of the field sex ratio and type of reproduction, those samples with fewer than ten specimens were removed from the analysis. In addition, host aphids that were found only in a single sample were not included in comparisons. The ant-attended colonies were recorded in the case of each aphid species with regards to presence of the parasitoids. Aphid nomenclature and classification follows that of Remaudière and Remaudière (1997). The specimens were deposited in the collection of the first author.

RESULTS

Host associations

Tritrophic parasitoid-aphid-plant associations for *L. fabarum* including 47 aphid hosts belong to 12 genera and over 99 host plant species were presented from 20 provinces (Table 1). Most of the host aphids belonged to the genus *Aphis* L. (78.84%) followed by *Brachycaudus* van der Goot (11.54%) and other genera (09.61%). *Aphis craccivora* Koch and *Aphis fabae* Scopoli were the most frequently encountered host aphids from the first group. The colonies of *A. craccivora* on its primary host plants were evidently heavily parasitized early in the season. The same situation was evident at the end of spring as well as on colonies of some other aphids, such as *Aphis idaei* van der Goot and *A. fabae*. The third most commonly encountered host aphid was *Aphis gossypii* Glover on a wide variety of host plants including vegetables and ornamentals. No association between *L. fabarum* and *Brachycaudus* spp., was evident in lowland regions such as northern Sistan and Baluchistan province (altitude less than 475m A.M.S.L), but *Brachycaudus* aphids occurred on respective host plants in the same area. Instead, some other species of aphid parasitoids, including *Aphidius colemani* Viereck and

Table 1. Host associations and distributional data for *Lysiphlebus fabarum* at different provinces of Iran

Host aphids	Host plants	Localities (Provinces)
<i>Acyrtosiphon gossypii</i> Mordvilko	<i>Sophora alopecuroides</i>	KERMAN
<i>Aphis acetosae</i> L.	<i>Rumex</i> sp.	KERMAN
<i>Aphis affinis</i> del Guercio	<i>Mentha longifolia</i> (L.)	ISFAHAN, KERMAN, KERMANSHAH, NORTH KHORASAN, TEHRAN
<i>Aphis</i> (<i>Protaphis</i>) <i>alexandrae</i> (Nevsky)	<i>Carthamus oxyacantha</i>	NORTH KHORASAN
<i>Aphis</i> (<i>Protaphis</i>) <i>anthemidis</i> (Börner)	<i>Anthemis nobilis</i>	SANANDAJ
	<i>Achillea</i> sp.	KERMAN
	<i>Alcea rosea</i>	FARS, KHUZISTAN, SISTAN and BALUCHISTAN
	<i>Alhagi maurorum</i>	FARS, GOLESTAN, ISFAHAN, MARKAZI, NORTH KHORASAN, SISTAN and BALUCHISTAN, TEHRAN
	<i>Amaranthus albus</i>	GOLESTAN
	<i>Amaranthus blitoides</i>	KERMANSHAH
	<i>Amaranthus caudatus</i>	ARDEBIL, ISFAHAN
	<i>Anagallis arvensis</i>	KERMAN
	<i>Astragalus</i> sp.	KERMAN, TEHRAN
	<i>Atriplex</i> sp.	KERMAN
	<i>Capsella bursa-pastoris</i>	GOLESTAN, FARS
	<i>Cardaria draba</i>	FARS, ISFAHAN
	<i>Celosia cristata</i>	KERMANSHAH
	<i>Chenopodium</i> sp.	ARDEBIL, KERMAN
	<i>Elaeagnus angustifoliae</i>	KERMAN
	<i>Erodium deserti</i>	KERMAN
<i>Aphis craccivora</i> Koch	<i>Glycyrrhiza aspera</i>	FARS, ISFAHAN, SISTAN and BALUCHISTAN
	<i>Glycyrrhiza glabra</i>	HAMADAN, KERMAN, KERMANSHAH, NORTH KHORASAN, QUAZVIN
	<i>Gundelia tournefortii</i>	KERMAN
	<i>Kochia scoparia</i>	KERMAN, KERMANSHAH, NORTH KHORASAN
	<i>Medicago sativa</i>	GOLESTAN, FARS, ISFAHAN, KERMAN, NORTH KHORASAN, KERMANSHAH
	<i>Melilothus officinalis</i>	EAST AZARBAIJAN, KERMANSHAH
	<i>Peganum harmala</i>	KERMAN, SEMNAN
	<i>Portulaca oleracea</i>	GOLESTAN, NORTH KHORASAN
	<i>Robinia pseudoacacia</i>	EAST AZARBAIJAN, FARS, ISFAHAN, KERMANSHAH, MARKAZI,
	<i>Sophora alopecuroides</i>	GOLESTAN, KERMAN, SISTAN and BALUCHISTAN
	<i>Sophora mollis</i>	ISFAHAN
	<i>Tragopogon graminifolius</i>	KERMAN
	<i>Torilis arvensis</i>	GOLESTAN
	<i>Trigonella foenum-graecum</i>	ISFAHAN
	<i>Vicia villosa</i>	KERMANSHAH
<i>Aphis davletshinae</i> Hille Ris Lambers	<i>Malva parviflora</i>	NORTH KHORASAN
	<i>Alcea</i> sp.	GOLESTAN
<i>Aphis</i> (<i>Protaphis</i>) <i>elongata</i> (Nevsky)	<i>Artemisia absinthium</i>	GUILAN
<i>Aphis</i> (<i>Bursaphis</i>) <i>epilobii</i> Kaltenbach	<i>Epilobium angustifolium</i> L.	KERMANSHAH

Table 1. Continued

Host aphids	Host plants	Localities (Provinces)
<i>Aphis euonymi</i> Fabricius	<i>Arctium lappa</i>	TEHRAN
<i>Aphis euphorbiae</i> Kaltenbach	<i>Euphorbia aucheri</i>	ISFAHAN
<i>Aphis euphorbicola</i> Rezwani and Lampel	<i>Euphorbia aelleni</i>	NORTH KHORASAN
	<i>Carduus onopordiodes</i>	FARS
<i>Aphis fabae cirsiacanthoidis</i> (Schrank)	<i>Carduus arabicus</i>	KERMANSHAH
	<i>Centaurea iberica</i>	KERMAN
	<i>Cirsium arvense</i>	ISFAHAN, KERMANSHAH, NORTH KHORASAN
	<i>Cirsium hygrophilum</i>	KERMAN
	<i>Cirsium vulgare</i>	ISFAHAN, EAST AZARBAIJAN
	<i>Cousinia</i> sp.	KERMAN
	<i>Amaranthus retroflexus</i>	KERMANSHAH, KORDIATAN
	<i>Arctium lappa</i>	ISFAHAN
	<i>Beta vulgaris</i>	ISFAHAN
	<i>Brassica rapa</i>	KERMAN
<i>Aphis fabae fabae</i> Scopoli	<i>Chenopodium album</i>	FARS, GOLESTAN, ISFAHAN
	<i>Citrus aurantiifolia</i>	FARS
	<i>Glycyrrhiza glabra</i>	FARS
	<i>Hibiscus trionum</i>	TEHRAN
	<i>Lawsonia inermis</i>	SISTAN and BALUCHISTAN
	<i>Ligustrum vulgare</i>	FARS
	<i>Phaseolus vulgaris</i>	ISFAHAN
	<i>Raphanus sativus</i>	KERMAN
	<i>Rosa damascena</i>	HAMADAN
	<i>Rumex acetosa</i>	HAMADAN, ISFAHAN
	<i>Rumex crispus</i>	GOLESTAN, GUILAN, QUAZVIN, KERMAN, SEMNAN, TEHRAN
	<i>Salsola canescens</i>	KERMAN
	<i>Silybum marianum</i>	GOLESTAN
<i>Aphis fabae solanella</i> Theobald	<i>Sinapis arvensis</i>	KOHKYLOYE and BOYERAHMAD
	<i>Spinacia oleracea</i>	ISFAHAN
	<i>Vicia faba</i>	KERMANSHAH, KHUZISTAN
<i>Aphis gerardiana</i> Mordvilko	<i>Solanum nigrum</i>	NORTH KHORASAN, TEHRAN
	<i>Euphorbia aelleni</i>	NORTH KHORASAN

Table 1. Continued

Host aphids	Host plants	Localities (Provinces)
	<i>Calendula persica</i>	KERMAN
	<i>Chrysanthemum sp.</i>	KERMAN
	<i>Cucumis sativus</i>	GOLESTAN, ISFAHAN, KERMANSHAH
	<i>Cucurbita pepo</i>	ISFAHAN KERMAN
	<i>Lamium sp.</i>	GOLESTAN
	<i>Malva neglecta</i>	FARS
	<i>Mirabilis jalapa</i>	KERMANSHAH, NORTH KHORASAN
<i>Aphis gossypii</i> Glover	<i>Nonea sp.</i>	KERMAN
	<i>Picnomon acarna</i>	FARS
	<i>Rosa damascena</i>	HAMADAN, SEMNAN
	<i>Tecoma stans</i>	GOLESTAN
	<i>Salsola sp.</i>	KERMAN
	<i>Urtica orens</i>	GOLESTAN
	<i>Veronica persica</i>	KERMAN
	<i>Zinia elegans</i>	KERMANSHAH
<i>Aphis idaei</i> van der Goot	<i>Rubus idaeus</i>	TEHRAN, GOLESTAN
	<i>Rubus persicus</i>	FARS
<i>Aphis intybi</i> Koch	<i>Cichorium intybus</i>	HAMADAN, NORTH KHORASAN
<i>Aphis nasturtii</i> Kaltenbach	<i>Marrubium sp.</i>	KERMAN
	<i>Plantago lanceolata</i>	KERMANSHAH
<i>Aphis nerii</i> Boyer de Fonscolombe	<i>Nerium oleander</i>	GOLESTAN, KERMAN, SISAN and BALUCHISTAN, TEHRAN
<i>Aphis origani</i> Passerini	<i>Mentha longifolia</i>	ISFAHAN
<i>Aphis plantaginis</i> Goeze	<i>Plantago lanceolata</i>	KERMAN
<i>Aphis punicae</i> Passerini	<i>Punica granatum</i>	FARS, GOLESTAN, KERMANSHAH, SISTAN and BALUCHISTAN, TEHRAN
<i>Aphis ruborum</i> (Börner)	<i>Rubus idaeus</i>	GOLESTAN
<i>Aphis rumicis</i> L.	<i>Rumex crispus</i>	KERMANSHAH, SEMNAN, TEHRAN
<i>Aphis spiraecola</i> Patch	<i>Crataegus monogyna</i>	GOLESTAN
	<i>Cydonia oblonga</i>	GOLESTAN
<i>Aphis (Protaphis) terricola</i> Rondani	<i>Anthemis arvensis</i>	KERMAN
	<i>Malva neglecta</i>	KERMANSHAH, KHUZISTAN, TEHRAN
<i>Aphis umbrella</i> (Börner)	<i>Malva sylvestris</i>	ARDEBIL, HAMADAN, ISFAHAN
<i>Aphis urticata</i> Gmelin	<i>Urtica dioica</i>	GOLESTAN
	<i>Carduus arabicus</i>	KERMANSHAH
<i>Brachycaudus (Prunaphis) cardui</i> (L.)	<i>Cirsium arvense</i>	ISFAHAN, NORTH KHORASAN, SEMNAN
	<i>Carduus onopordioides</i>	FARS, KORDIATAN
	<i>Calendula officinalis</i>	ARDEBIL, FARS
<i>Brachycaudus helichrysi</i> (Kaltenbach)	<i>Chrysanthemum morifolium</i>	KERMANSHAH
	<i>Prunus sp.</i>	ISFAHAN
	<i>Tanacetum vulgare</i>	KERMANSHAH

Table 1. Continued

Host aphids	Host plants	Localities (Provinces)
<i>Brachycaudus (Appelia) tragopogonis</i> (Kaltenbach)	<i>Scorzonera isphahanica</i> <i>Tragopogon graminifolius</i>	ISFAHAN ISFAHAN, KERMAN, NORTH KHORASAN, TEHRAN, ZANJAN, KORDIATAN
<i>Brachyunguis harmalae</i> Das	<i>Peganum harmala</i>	NORTH KHORASAN, SISTAN and BALUCHISTAN
<i>Brachyunguis</i> sp.	<i>Cynanchum acutum</i>	ISFAHAN
<i>Brachyunguis zygophylli</i> (Nevsky)	<i>Zygophyllum fabago</i>	KERMAN
<i>Dysaphis (Pomaphis) plantaginea</i> (Passerini)	<i>Malus domestica</i>	ISFAHAN
<i>Dysaphis radicola</i> (Mordvilko)	<i>Rheum palmatum</i>	SISTAN and BALUCHISTAN
<i>Hayhurstia atriplicis</i> (L.)	<i>Chenopodium album</i>	KERMANSHAH, KORDIATAN
<i>Hyadaphis coriandri</i> (Das)	<i>Coriandrum sativum</i>	SISTAN and BALUCHISTAN
<i>Lipaphis erysimi</i> (Kaltenbach)	<i>Capsella bursa pasturis</i>	ISFAHAN
<i>Lipaphis (Lipaphidiella) lepidii</i> (Nevsky)	<i>Cardaria draba</i>	SISTAN and BALUCHISTAN, TEHRAN
<i>Macrosiphoniella (Papillomyzus) papilata</i> Holman	<i>Artemisia biennis</i>	KERMAN
<i>Melanaphis sacchari</i> (Zehntner)	<i>Sorghum halepense</i>	KERMAN
<i>Metopolophium dirhodum</i> (Walker)	<i>Rosa damascena</i>	KERMAN
<i>Myzus (Nectarosiphon) beybienkoi</i> (Narzikulov)	<i>Fraxinus oxycarpa</i>	TEHRAN
	<i>Lycopersicum esculentum</i>	KERMAN
<i>Myzus (Nectarosiphon) persicae</i> (Sulzer)	<i>Malva neglecta</i>	FARS, ISFAHAN, SISTAN and BALUCHISTAN
	<i>Trigonella foenum-graecum</i>	FARS
	<i>Solanum melongena</i>	TEHRAN
<i>Rhopalosiphum padi</i> (L.)	<i>Triticum aestivum</i>	KERMANSHAH
<i>Toxoptera aurantii</i> (Boyer de Fonscolombe)	<i>Citrus sinensis</i>	GOLESTAN, GUILAN

Aphidius matricariae Haliday replaced *L. fabarum* in this area. However, the association of *Brachycaudus* species on the creeping thistles, *Cirsium arvense*, and goatsbeard, *Tragopogon* spp., were quite common in sub-mountainous areas of the various different provinces.

The association of *L. fabarum* with aphids on the collar regions of host plants was found in the case of *Aphis (Protaphis) elongata* (Nevsky) on *Artemisia absinthium* and *Dysaphis radicola* (Mordvilko) on *Rheum palmatum*. In both cases, aphids were protected by ants, but parasitism occurred in considerable numbers. The same relationship with ants was commonly evident in cases of many other aphid species that had colonized stems and leaves (Table 2).

Sex ratio and type of reproduction

The relationship between host aphid and sex ratio of *L. fabarum* is indicated in Table 3. There was an equal male:female ratio in association with *Brachyunguis zygophylli* (Nevsky) in only a few cases, but in the rest of samples there was a great bias toward females in the range of zero to 0.94. The occurrence of these completely uniparental specimens within the sampled material was evident in the case of *Aphis (Protaphis) elongata* (Nevsky) and *Aphis euphorbicola* Rezwani and Lampel. In both samples it can be assumed that males are rare because they were found on only two occasions, while the occurrence of uniparental populations ranged from zero to 50% in other host aphids. The populations of *L. fabarum* reared from *Brachycaudus* spp. were almost completely biparental, with

Table 2. The host aphids belonging to the genera *Aphis* and *Brachycaudus* on their host plants, which were commonly found in association with ants

Host aphid	Host plant
<i>Aphis affinis</i>	<i>Mentha longifolia</i>
<i>Aphis craccivora</i>	<i>Achillea</i> sp., <i>Alhagi maurorum</i> , <i>Glycyrrhiza aspera</i> , <i>Glycyrrhiza glabra</i> , <i>Gundelia tournefortii</i> , <i>Medicago sativa</i> , <i>Melilothus officinalis</i> , <i>Robinia pseudoacacia</i> , <i>Sophora alopecuroides</i> , <i>Vicia villosa</i>
<i>Aphis (Protaphis) elongata</i>	<i>Artemisia absinthium</i>
<i>Aphis euonymi</i>	<i>Arctium lappa</i>
<i>Aphis fabae cirsiacanthoidis</i>	<i>Carduus arabicus</i> , <i>Cirsium arvense</i> , <i>Cirsium vulgare</i>
<i>Aphis fabae fabae</i>	<i>Phaseolus vulgaris</i> , <i>Vicia faba</i>
<i>Aphis fabae solanella</i>	<i>Solanum nigrum</i>
<i>Aphis gossypii</i>	<i>Mirabilis jalapa</i>
<i>Aphis intybi</i>	<i>Cichorium intybus</i>
<i>Aphis rumicis</i>	<i>Rumex crispus</i>
<i>Aphis (Protaphis) terricola</i>	<i>Anthemis arvensis</i>
<i>Aphis umbrella</i>	<i>Malva neglecta</i> , <i>Malva sylvestris</i>
<i>Brachycaudus (Prunaphis) cardui</i>	<i>Carduus arabicus</i> , <i>Cirsium arvense</i>
<i>Brachycaudus (Appelia) tragopogonis</i>	<i>Tragopogon graminifolius</i>
<i>Toxoptera aurantii</i>	<i>Citrus sinensis</i>

a sex ratio of 0.49-0.71:1 (M:F). An exceptional sample was identified with only female specimens, reared from *Brachycaudus (Appelia) tragopogonis*. The host aphids that were only sampled on a single occasion were ignored, but it is noteworthy that for some of them, there was an insufficient number of specimens per sample to explain the overall type of reproduction. For example, all specimens of *L. fabarum* from *Aphis epilobii* were females.

Morphological variability

A few specimens from each sample were slide-mounted and diagnostic characters were compared with descriptions and keys. There was a great variation in morphological characters, excluding color pattern, among different populations of *L. fabarum*. The most important diagnostic character for separation of *L. fabarum* from allied species (*Lysiphlebus confusus* Tremblay and Eady and *Lysiphlebus maris-*

mortui Mescheloff and Rosen) was the absence of long forewing marginal setae. Several specimens of *L. fabarum* were identified from various host aphids or even from a single sample with different patterns of forewing marginal setae (Figs. 8-10). Furthermore, the length of the forewing R1 vein was variable in different populations (Figs. 1-10). Geographically, there were different populations of *L. fabarum* in association with *Aphis affinis* del Guercio. These specimens from high southeastern mountains (2500-3000 m A.M.S.L) always had a set of forewing marginal setae and a medium-sized R1 vein (Fig. 9), but in specimens from central and western provinces the forewing marginal setae were absent and the R1 vein was commonly elongated. The number of antennal segments in all specimens ranged from 12-13 as a normal variability among the individuals even from the same sample. The hind femora in female wasps were always covered with short depressed setae, which were slightly erect toward the tip of the femur,

Table 3. Sex ratio and Frequency of the asexual population of *Lysiphlebus fabarum* on different host aphids

Host aphid	Number of samples	Number of specimens	Sex ratio (M: F)		Frequency of asexual population (%)
<i>Aphis (Protaphis) elongata</i>	2	47	0.00	1	100
<i>Aphis affinis</i>	15	528	0.64	1	13.33
<i>Aphis craccivora</i>	84	5925	0.55	1	04.76
<i>Aphis davletshinae</i>	2	27	0.17	1	50.00
<i>Aphis euphorbiae</i>	3	65	0.00	1	100
<i>Aphis euphorbicola</i>	2	32	0.03	1	50.00
<i>Aphis fabae cirsiacanthoidis</i>	9	858	0.58	1	0.00
<i>Aphis fabae fabae</i>	29	898	0.40	1	05.26
<i>Aphis gossypii</i>	13	612	0.41	1	07.69
<i>Aphis idaei</i>	7	449	0.48	1	0.00
<i>Aphis intybi</i>	3	74	0.94	1	0.00
<i>Aphis nasturtii</i>	2	46	0.31	1	0.00
<i>Aphis punicae</i>	4	101	0.77	1	0.00
<i>Aphis rumicis</i>	5	159	0.47	1	40.00
<i>Aphis fabae solanella</i>	12	278	0.07	1	25.00
<i>Aphis umbrella</i>	6	165	0.41	1	16.66
<i>Aphis urticata</i>	3	36	0.56	1	00.00
<i>Brachycaudus cardui</i>	9	188	0.71	1	0.00
<i>Brachycaudus helichrysi</i>	4	112	0.49	1	0.00
<i>Brachycaudus tragopogonis</i>	17	864	0.56	1	05.88
<i>Brachyunguis harmalae</i>	5	115	0.69	1	0.00
<i>Brachyunguis zygophylli</i>	2	119	1	1	0.00
<i>Myzus persicae</i>	5	133	0.40	1	40.00

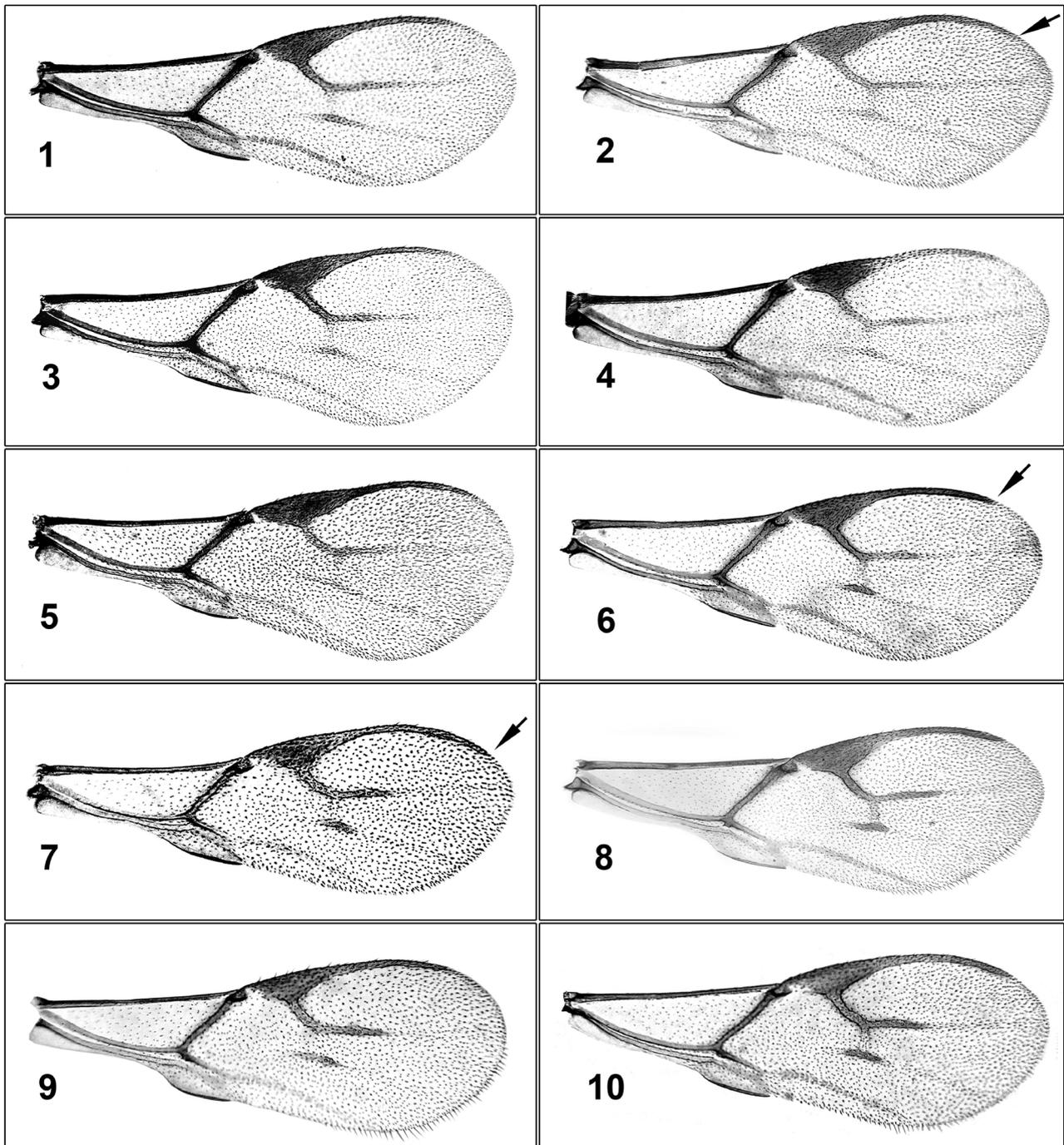
except on the few occasions where there were a few erect setae on the hind femurs.

DISCUSSION

Biocontrol significance

Generally, host aphids could be divided into three groups, 1. *Aphis* spp., 2. *Brachycaudus* spp., 3. Oc-

casional various aphids. *L. fabarum* showed a great tendency toward the genus *Aphis* that includes many important pest species. The more frequently occurring samples of host aphids were *A. craccivora* and *A. fabae*, followed by *A. gossypii*, which are the most common and important aphid pests on various cultivated plants. Starý (1981) indicated that the genus *Lysiphlebus* is prevalently in association with the phylogenetically youngest group of aphids, the Aphidi-



Figs. 1-10. Morphological variability in forewing of *Lysiphlebus fabarum* reared from different host aphids: 1. *Aphis craccivora* on *Medicago sativa*, 2. *Aphis fabae solanella* on *Solanum lycopersicum*, 3. *Brachycaudus tragopogonis* on *Tragopogon graminifolius*, 4. *Brachycaudus cardui* on *Cirsium arvense*, 5. *Myzus persicae* on *Malva neglecta*, 6. *Aphis (Protaphis) elongata* on *Artemisia absinthium*, 7. *Toxoptera aurantii* on *Citrus sinensis*, 8. *Aphis fabae* on *Vicia fabae*, 9. *Aphis affinis* on *Mentha longifolia*, 10. *Aphis euphorbicola* on *Euphorbia aelleni*. Black arrows indicating the ultimate tip of R1 vein.

nae. The common association of *L. fabarum* with *Aphis* species as a large genus of aphids with a fast process of diversification (Coeur d'acier et al., 2007), has been clearly confirmed. Furthermore, the establishment of this parasitoid on aphids with economically indifferent importance can act as a reservoir or a refugium (Starý, 1986a; Kavallieratos et al., 2002, 2004; Havelka et al., 2012) from which the parasitoid can migrate short distances onto neighboring crops.

Both *Aphis* and *Brachycaudus* aphids are categorized as myrmecophilous aphids based on their poorly developed cornicles, reduced cauda, and a thin coating of wax filaments (Holldobler and Wilson, 1990). *Lysiphlebus fabarum* is known to have highly evolved adaptations to forage undisturbed within ant-attended aphid colonies (Rasekh et al., 2010a, b). The same behavior has also been recorded and investigated in some other *Lysiphlebus* species (Völkl and Mackauer, 1993; Kaneko, 2003; Vinson and Scarborough, 1991). While, ant-attendance is thought to protect aphid colonies against natural enemies (Kaneko, 2002; Vinson and Scarborough, 1991; Völkl, 1997), *L. fabarum* may benefit from ant-attendance and parasitize the host aphids even at higher rates compared to the ant-unattended aphid colonies (Rasekh et al., 2010b). Therefore, it can be concluded that in the case of the above-mentioned, of those aphids that are protected by ants, *L. fabarum* is the most important natural biological control agent.

Host range pattern, type of reproduction and biological species

Like other aphidiine parasitoids, *L. fabarum* also manifests a more or less definable oligophagy (Starý, 1988) that enables it to alternate between various host aphid species in the course of a season. This feature will increase its resistance to changes in population densities of the host aphid, that has been subjected as a significant reason for the speciation within this group (Starý, 1970). *Lysiphlebus fabarum* seems to be a complex species that includes several biological species. The correlation between the host range pattern, i.e. *Aphis* vs *Brachycaudus*, and shifting to asexual reproduction in the first group of host

aphids (*Aphis* spp.) suggests a young group that is undergoing biological evolution that enables them to readily become specific to their host aphids. However, shifting to another host is a hypothesis that has already been discussed, as the thelytokous populations of *L. fabarum* were not affected by host alternation, as well as generation number (Starý, 1999; Sandrock et al., 2011). In cases where there is the presence of both thelytokous and biparental populations on the same host group (*Aphis* spp.), it can be an indication of sibling species that co-exist in the same area. Additionally, it is possible to elaborate a new species, *Lysiphlebus brachycaudi* (MS name), based on its specific host range which is restricted to *Brachycaudus* spp., with a biparental type of reproduction (Starý, 1999). An absence of any association between *L. fabarum* and *Brachycaudus* species in lowland areas may also be an indication of habitate preference for *L. brachycaudi*. *Lysiphlebus melandriicola* Starý is a very close taxon to *L. fabarum*, strictly attacking *Brachycaudus lychnidis* (L.) in Europe (Starý, 1961b). It can be a good example of sympatric speciation after selection of a specific host by an aphid parasitoid.

Generally, there was a great bias toward females, even in those cases in which the host aphids were *Brachycaudus* spp. Mackauer and Völkl (2002) has also analyzed seasonal variations in brood size and sex ratio in three aphid parasitoids and reported that the sex ratio at eclosion was biased toward females for all three species. The biased sex ratio in parasitoids can result either from the female's control of fertilization at oviposition or from the differential pre-imaginal mortalities (Charnov et al., 1981; Jarošík et al., 2003). In addition, mated females are able to regulate the sex ratio of their offspring in relation to the size of the host they attack (Godfray, 1994). Sex ratios of progeny emerging from small hosts tend to be male-biased and those from large hosts tend to be female-biased. Pandey and Singh (1999) reported that females of *Lysiphlebia mirzai* Shuja-Uddin could adjust the progeny sex ratio according to the host size as host size affected the fitness of the females more than that of male progenies. However, the biased sex ratio may not be attributed to manipulation of the primary

sex ratio at the time of oviposition, but on the contrary, arises directly from the higher mortality of female progenies in aphids with smaller size compared to males (Jarošík et al., 2003; Wellings et al., 1986). Generally, it can be a naturally selected trait, as the males of *L. fabarum* are polygamous (Bagheri Matin et al., 2005) and in this condition, fewer males manage larger numbers of females. However, if females oviposit without copulation, the progenies will all be males (Starý, 1988) to compensate for the deficiency of the male:female balance. The sex ratio of the aphid parasitoids naturally fluctuates along the life span of a reproductive female (Srivastava and Singh, 1995) and it is affected by environmental and genetic factors (Starý, 1988).

Specimens of *L. fabarum* were collected mostly in early and mid spring, which is the normal time for reproduction and population growth. Temperature is assumed to be an important factor affecting the sex ratio (Bagheri Matin et al., 2005). These authors have recently found a positive correlation between temperature and percentage of males in *L. fabarum*. Generally, this phenomenon was attributed to a decline in the activity of parasitoids, including mating, that increases the number of male progenies (Tremblay, 1964). However, hot temperatures (in territories like Iran) are known to have an inhibitory effect on the activities of the microbes in association (*Wolbachia*) with sex determination (Bordenstein and Bordenstein, 2011; Stouthamer and Werren, 1993) that could account for the common occurrence of males in different populations. However, no evidence of bacterial symbiont *Wolbachia* was found in thelytokous populations of *L. fabarum* (Belshaw and Quicke, 2003); instead, they found the central fusion automixis as the mechanism and asexuality. Further evidence has demonstrated that thelytokous reproduction in *L. fabarum* manifests from only a simple genetic basis, which is consistently inherited as a single-locus recessive trait. This contagious system allows closely related individuals to reproduce with different modes (Sandrock and Vorburger, 2011). The occurrence of both thelytokous and biparental (arrhenotokous) populations of *L. fabarum* on the same host aphids (Table 3) was quite common when

the host aphid was an *Aphis* species or even in the case of *Myzus persicae* (Sulzer).

Lysiphlebus cardui (Marshall), a closely related species to *L. fabarum*, is also a questionable taxon. Its host range is limited to species of *Aphis*, as the major host group for *L. fabarum*. Morphological separation of these two species is rather difficult. This species is a specialized parasitoid of *Aphis fabae cirsiacanthoidis* (Schrank) on *Cirsium arvense* (Starý, 1986a, b), but often co-exists with *L. fabarum* on the same host (Starý, 1999). Molecular studies have mostly failed to separate these two species (Belshaw et al., 1999); sometimes *L. cardui* was classified as a sister taxon of *L. fabarum* (Kambhampathi et al., 2000).

Until now, the results of molecular studies have largely not elucidated species' boundaries and sibling species/biotypes in the case of *L. fabarum*. The important issue here is relations between molecular and morphological variability affected by asexuality. Molecular markers can help to detect some species but they create new problems that sometimes contradict morphological and biological approaches (Belshaw et al., 1999). One of the major reasons for the incomplete or controversial results of molecular studies is the aim of those specific researches that often target higher-level phylogeny (Smith et al., 1999; Kambhampathi et al., 2000; Sanchis et al., 2000).

Variability of the morphological characters

Lysiphlebus fabarum can typically be separated from the other congeneric species, *L. confusus*, by the absence of long marginal setae of the forewing (females). But there were various patterns of marginal hairs in position and length within the population of *L. fabarum* from different host aphids and localities. *Lysiphlebus marismortui* is a recently described species with marginal setae of different and irregular lengths together with an arch on the 3RSb vein (Mescheloff and Rosen, 1990). But even the latter character seems to be an intraspecific variation irregularly shifting in different individuals. Furthermore, this species was described from *A. craccivora* as the most common host aphid for *L. fabarum*. Thus, there is still

not enough evidence to validate *L. marismortui* as a separate species. The number of maxillary and labial palpomers was constant in all specimens. However, measuring the length of the palpomers, as well as the characters of the flagellar segments (number of placods) as the major sensorial organs associated with host selection (Quicke, 1997), should be considered in future research.

A recent morphometric analysis of populations of *L. fabarum* from different host aphids (Barahoei et al., 2011) surprisingly clarified significant differences among so called "biotypes". However, this study was carried out on a restricted number of biotypes. They found that the major variable characters were on the forewing venations, as well as in the lengths of the ovipositors and hind legs. In spite of limitations on the scope of this essay to the local host aphids, which evolutionarily says nothing, it throws the significance of the traditional means of species identification into a big controversy. The same procedure should be effective on more justified biological species reared from phylogenetically distant aphids with different biology and type of reproduction. Limitations in the numbers of diagnostic characters, together with intra-specific variations cannot be justified for populations of *L. fabarum* and presents a complicated question both for known members of the *L. fabarum*-complex and for the more recently identified groups (Starý, 1999).

The exact identification of a species or sibling species, sometimes termed as "biotypes" has created some problems not only in taxonomy, but also in terms of biological control (Carver and Franzmann, 2001). Consequently, a detailed morphological and biological investigation is needed to confirm the presence of some reliable differences between representative taxa and the relation between morphological studies with biological data. At the same time, selection of suitable molecular markers is also required as proof.

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