EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz
Eur. J. Entomol. **120**: 26–34, 2023
doi: 10.14411/eje.2023.004
REVIEW

Distribution, host range and host preferences of *Dinocampus coccinellae* (Hymenoptera: Braconidae): A worldwide database*

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Key words. Coleoptera, Coccinellidae, parasitoid, biogeography, host spectrum

Abstract. *Dinocampus coccinellae* (Schrank) is a braconid parasitoid of ladybird beetles (Coleoptera: Coccinellidae) and has exceptionally wide geographical and host ranges. Based on published and unpublished sources *Dinocampus coccinellae* probably occurs throughout the temperate, subtropical and tropical climatic zones, but some regions, such as sub-Saharan Africa (except its southernmost part) and the Malay Archipelago, have not so far been surveyed for this wasp. In most of its extensive range *D. coccinellae* was present before the widespread use of classical biological control. It is likely, however, to have reached some oceanic islands and archipelagos at a later date, along with ladybirds used as biocontrol agents. At least 72 species of Coccinellidae are hosts of *D. coccinellae*. Three of them, *Vibidia duodecimguttata* (Poda), *Calvia decemguttata* (L.) and *Coccinella miranda* Wollaston, are reported here for the first time as hosts of this parasitoid. The most often reported host of *D. coccinellae* worldwide is *Coccinella septempunctata* L. followed by *Harmonia axyridis* (Pallas), *Coleomegilla maculata* (De Geer) and *Hippodamia convergens* Guerin.

INTRODUCTION

Dinocampus coccinellae (Schrank) is a parasitic wasp that reproduces by thelytoky and is a parasitoid of ladybird beetles (Coleoptera: Coccinellidae). For several reasons, it can be regarded as an unusual parasitoid. It is nearly cosmopolitan and has an exceptionally wide host range. Unlike most parasitoids, it is not host stage-specific; oviposition into ladybirds at various developmental stages (adults, larvae, pupae) can lead to successful parasitism, although fully grown parasitoid larvae always emerge from their hosts when they are in the adult stage (Ceryngier et al., 2012).

Due to indirect larval feeding mediated by so-called teratocytes (Okuda & Kadono-Okuda, 1995), the development of *D. coccinellae* causes relatively little harm to its ladybird host. As a result, the host usually survives the emergence of the parasitoid and, in some cases, can completely recover and even resume its reproductive functions (Triltsch, 1996; Maure et al., 2014). This feature makes *D. coccinellae* similar to true parasites, i.e. organisms that, in contrast to parasitoids, do not directly kill their hosts (Haelewaters et al., 2017). Although the rate of recovery of ladybirds following *D. coccinellae* emergence is not high, it would probably be considerably higher were it not for the symbiotic relationship between the parasitoid and a specific virus called *D. coccinellae* paralysis virus (DcPV). This recently discovered relationship, which involves manipulation of host behaviour (Dheilly et al., 2015), is one of the most sophisticated strategies used by parasitoids. During the process of parasitism, DcPV is transmitted from the parasitoid larva to the ladybird nervous system, where it replicates and subsequently paralyses the ladybird. The host is paralyzed shortly before the emergence of the parasitoid larva, which enables the larva to spin a cocoon between the host's legs. As a consequence, the cocoon is protected against natural enemies beneath the aposematically coloured and chemically defended host body. Although the virus-induced paralysis may recede when adult *D. coccinellae* leaves the cocoon, most hosts die, probably of starvation (Balduf, 1926). The association between *D. coccinellae* and DcPV seems to occur worldwide, as this virus is reported in this wasp in several countries (Canada, Poland, Japan, the Netherlands) (Dheilly et al., 2015).

Morphologically, *D. coccinellae* varies very little. Timberlake (1918) notes that it is "extremely constant throughout its vast range, and although there is a slight variation in color this seems to be independent of its geographic distribution". This species is quite uniform in some other

* This paper was contributed to a virtual special issue in memory of Ivo Hodek, a long-time editor of the *European Journal of Entomology*, who died on June 11, 2021, shortly after his ninetieth birthday.

respects as well. As mentioned above, it appears to have a symbiotic relationship with DcPV throughout its range, and another feature is also probably shared by all extant strains of this wasp, reproduction by thelytokous parthenogenesis. The feature of *D. coccinellae* that seems almost universal is a strong preference for parasitizing ladybirds of the tribe Coccinellini (Ceryngier et al., 2012), although there is at least one exception to this. Maqbool et al. (2018) report this wasps in Kashmir (India) readily attacking Coccinellini (*Oenopia conglobata* (L.), *Coccinella undecimpunctata* L.) and Chilocorini (*Priscibrumus uropygialis* (Mulsant)) and developing successfully in both kinds of host. This finding suggests that local strains of *D. coccinellae* may adapt to atypical or less suitable hosts. Another example indicating such adaptability is the exploitation by *D. coccinellae* of the invasive ladybird *Harmonia axyridis* (Pallas), which is generally considered a marginal host of this parasitoid with a low suitability for its development (Hoogendoorn & Heimpel, 2002; Firlej et al., 2005, 2007, 2010; Koyama & Majerus, 2008; Minnaar et al., 2014; Romero et al., 2020). In central Europe, however, *D. coccinellae* has rapidly adapted to successfully developing in *H. axyridis* (Ceryngier et al., 2018; Knapp et al., 2019).

Dinocampus coccinellae is frequently reported in the field, which may indicate its high abundance and ease of detection (an immobilized ladybird 'sitting' on a parasitoid cocoon attracts attention). The fact that its hosts are economically important and intensively studied members of the family Coccinellidae certainly also has a role. Over the past 220 years, since the description of this species by Schrank (1802), an extensive literature on the occurrence and hosts of *D. coccinellae* worldwide has accumulated. The aim of this paper is to compile this large body of information, including available PhD and MSc theses and our unpublished data, and then analyse the known host spectrum, host preferences and distribution of this parasitoid.

MATERIAL AND METHODS

The first step was the gathering of data on the occurrence of *D. coccinellae* and its hosts worldwide and the creation of a database containing this information (Supplement S1). The objective was to collect as complete a set of published and unpublished information on *D. coccinellae* as possible. In order to achieve this various methods were used. Firstly, papers on the enemies of Coccinellidae were collected, which were systematically accumulated over about three decades. Secondly, databases and web browsers were searched, such as Web of Science and Google Scholar, entering the valid name of the wasp ('Dinocampus coccinellae', 'Dinocampus') or its synonyms ('Ichneumon coccinellae', 'Bracon terminatus', 'Perilitus terminatus', 'Microctonus terminatus', 'Dinocampus terminatus', 'Euphorus sculptus', 'Perilitus americanus', 'Centistes americana') as keywords. Thirdly, the sources cited in the papers on *D. coccinellae* previously accessed were searched. However, in several cases we could not examine the original papers and relied on quotations by other authors or abstracts/summaries available on the internet. In a few cases, certain publications were thought to contain data on *D. coccinellae*, but they were not available either directly or indirectly, and hence not included in the database.

The database consists a series of records each containing information on the host species and/or the geographical location of *D. coccinellae*. However, as reports on *D. coccinellae* found in different sources are very diverse in terms of the accuracy of the distributional information, date on collection, abundance or percentage parasitism by the parasitoid, methods of collecting or ascertaining the parasitism, etc., rigid criteria were used for defining a single record. In a given paper (or another source of information), each of the reported localities is considered a single record. If more than one host species is reported from the same locality, each host species represents a separate record. When distinguishing individual records, quantitative data (number of specimens, percentage parasitism) were not included. Even if a given publication reports that *D. coccinellae* parasitized the same host species at the same locality for several years, this is considered a single record. Furthermore, attempts were made to identify instances where the same data was reported more than once (in different publications). Such redundant data was treated as a single record. A complete list of bibliographic items used to create the *D. coccinellae* database can be found in Supplement S1.

Based on the records included in this database, the worldwide distribution of *D. coccinellae*, its host spectrum and host preferences are discussed. However, while discussing host preferences, experimental data on host selectivity by *D. coccinellae* or suitability of individual host species for the wasp's development are not considered, but only the frequency of records of individual ladybird species as hosts of *D. coccinellae*. After this part of the paper, details of previously unpublished data on the distribution and host species of *D. coccinellae* that were included in the database are discussed.

To discuss issues of distribution of *D. coccinellae* and its hosts, the traditional biogeographical division of the world proposed by Udvardy (1975) was used. This division does not differ much from the classical Wallace's (1876) division, with the main difference being the addition of the Antarctic realm. More recent classifications (e.g. Cox, 2001; Kreft & Jetz, 2010; Holt et al., 2013; Rueda et al., 2013) are often constructed on the basis of distributional data of specific vertebrate or plant groups, and the accompanying maps are not always precise enough to unambiguously assign certain records to a particular biogeographical region.

RESULTS

Worldwide distribution

Altogether, 810 single records of the occurrence of *D. coccinellae* were distinguished and based on these records, the worldwide distribution of the wasp was mapped (Fig. 1). The majority of records are from the temperate zone of the northern hemisphere (the Palaearctic and Nearctic), while in the analogous zone in the southern hemisphere there are few records of *D. coccinellae*. However, the records are relatively numerous in the belt around the equator (tropics and subtropics), especially in the Americas. Very few records are from higher latitudes, but one of them (from Greenland) is even slightly north of the Arctic Circle.

Host spectrum

Of the 810 records of *D. coccinellae* in the database, 654 are linked to particular host species. These host-linked records include data on parasitism by *D. coccinellae* of 72 species of Coccinellidae. Of these, one belongs to the tribe

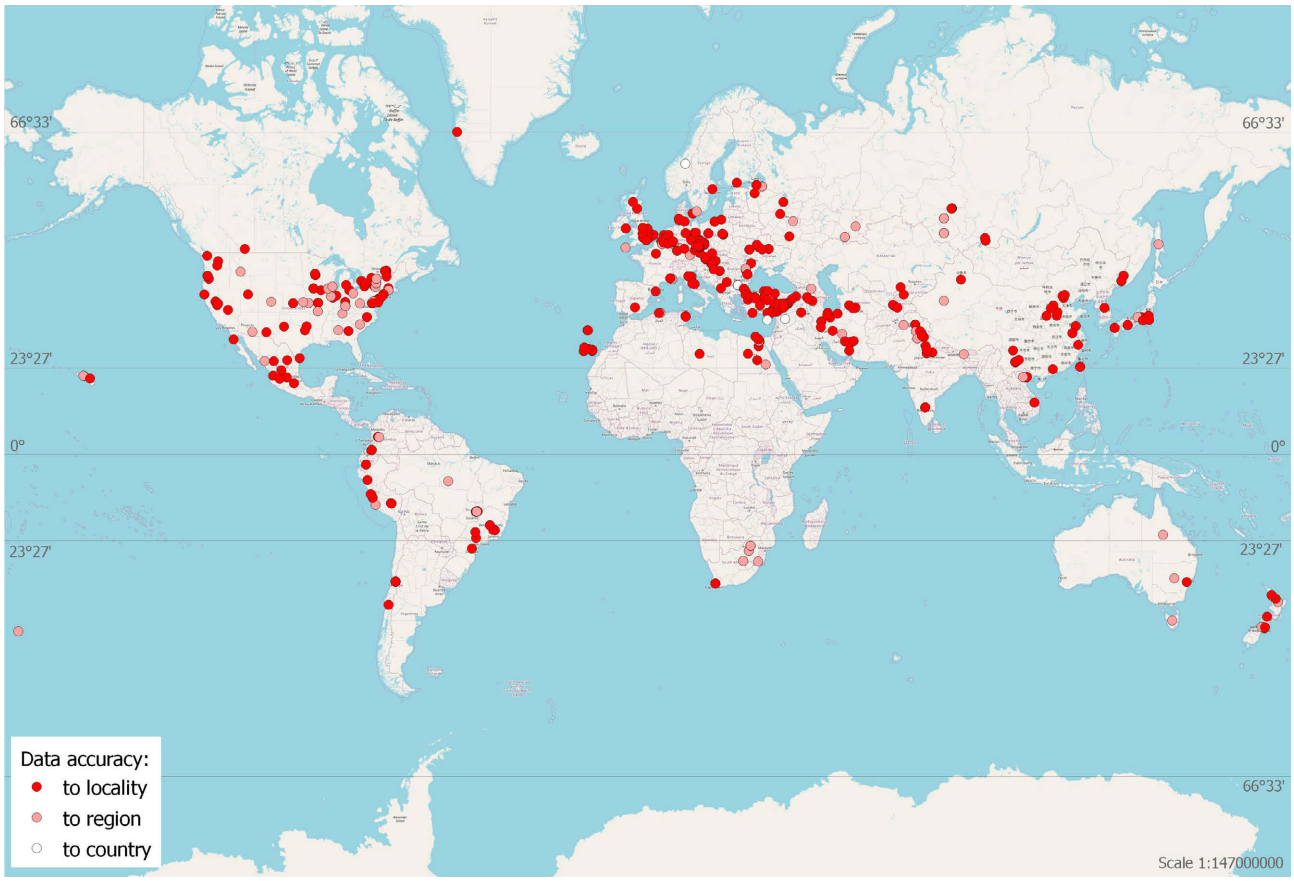

Fig. 1. Map showing the distribution of the records of *Dinocampus coccinellae*. The records are categorized according to their degree of geographical accuracy. Accuracy to locality means that a specific locality or its vicinity is cited, accuracy to a specific region, a state or province, and accuracy to country means a specific country. For records with lower accuracy, a marker on the map is placed in the middle of a region or country. If there are both more and less accurate records from the same region or country, the low accuracy records are not included on the map.

Brachiacanthini, six to Chilocorini and the remaining 65 species to Coccinellini (Table 1). The records are for all of the eight biogeographical realms distinguished by Udvardy (1975), but the majority are for the Palaearctic and Nearctic: the total number of records for these two realms is 548 (84% of all host-linked records) and the number of host species is 53 (74% of all host species).

Frequency of records for individual host species

Considering the entire database, the most frequently reported host of *D. coccinellae* is *Coccinella septempunctata* L. The total number of records for this species (including the subspecies *C. s. brucki* Mulsant and *C. s. algerica* Kovář) is 189, which accounts for 29% of all the host records. The next most frequently recorded hosts are *Harmonia axyridis* (65 records, 10%), *Coleomegilla maculata* (De Geer) (52 records, 8%), *Hippodamia convergens* Guerin (44 records, 7%), *H. variegata* (37 records, 5.5%) and *Coccinella undecimpunctata* L. (22 records, 3%).

In the Palaearctic, the most common host of *D. coccinellae* is *C. septempunctata* (166 records, 46% of all Palaearctic records), followed by *H. axyridis* (50 records, 14%) and *H. variegata* (30 records, 8%). The hosts most frequently recorded in the Nearctic are *C. maculata* (49 records, 29%) and *H. convergens* (36 records, 21%), and in the Neotropical realm, *Cycloneda sanguinea* (L.) (14 records, 32%) and *H. convergens* (8 records, 18%). In the remaining biogeographical realms, data on the hosts of *D. coccinellae* are too few to discuss their frequencies.

New distribution and host records

POLAND

***Vibidia duodecimguttata* (Poda).** A specimen of this species with a *D. coccinellae* cocoon was collected on 16 June 2018 in Warsaw, Poland (52.2122, 21.0554). On 18 June 2018, an adult female wasp emerged from the cocoon. Another specimen of *V. duodecimguttata* was collected on 24 May 2019 on the northwestern outskirts of Warsaw (52.3122, 20.9309). Between 25 and 27 May, a *D. coccinellae* larva emerged from the host and spun a cocoon under its ventral side. On 6 June, an adult wasp emerged from the cocoon.

***Calvia decemguttata* (L.).** Of 42 *C. decemguttata* specimens caught by light traps in 2018 in Las Bielański nature reserve in Warsaw (52.2972, 20.9580) (Kamiński et al., 2020), two were parasitized by *D. coccinellae*. Both were found in traps that operated on the night of 20–21 September 2018 and each had a dead *D. coccinellae* larva protruding from the dorsal part of its abdomen. The larvae could not complete their exit from the host beetles because the trapped insects were killed by tetrachloroethylene vapour.

Both, *V. duodecimguttata* and *C. decemguttata* have not previously been reported as hosts of *D. coccinellae*.

Table 1. Hosts of *Dinocampus coccinellae* recorded in different biogeographical realms. The Palaearctic realm is additionally divided into its Asiatic, European and North African parts. Numbers indicate number of records.

Host	Palaearctic			Nearctic	Afro-tropical	Indo-malayan	Oceanian	Australian	Antarctic	Neo-tropical
	Asia	Europe	North Africa							
Brachiacanthini										
Brachiacantha ursina (Fabricius)				1						
Chilocorini										
Exochomus octosignatus (Gebler)	1									
Exochomus quadripustulatus (L.)		2								
Parexochomus flavipes (Thunberg)					2					
Parexochomus troberti concavus Fürsch					1					
Priscibrumus lituratus (Gorham)	1									
Priscibrumus uropygialis (Mulsant)	2									
Coccinellini										
Adalia bipunctata (L.)	1	8		4						
Adalia decempunctata (L.)		1								
Adalia deficiens Mulsant										1
Anatis ocellata (L.)		1								
Anisosticta sibirica Bielawski	1									
Calvia decemguttata (L.)		1								
Calvia muiri (Timberlake)	1									
Calvia quatuordecimguttata (L.)	1	2		1						
Cheilomenes lunata (Fabricius)					6					
Cheilomenes propinqua (Mulsant)			1		1					
Cheilomenes sexmaculata (Fabricius)	2					6				
Cleobora mellyi (Mulsant)								1		
Coccinella californica Mannerheim				2						
Coccinella hieroglyphica L.		1								
Coccinella leonina transversalis Fabricius						3		2		
Coccinella longifasciata Liu	1									
Coccinella magnifica Redtenbacher		2								
Coccinella miranda Wollaston			5							
Coccinella novemnotata Herbst				8						
Coccinella quinquepunctata L.	4	13								
Coccinella septempunctata L.	61*	100*	8	14		8				
Coccinella trifasciata L.	4			3						
Coccinella undecimpunctata L.	1	4	8	2					7	
Coccinula quatuordecimpustulata (L.)	3	2								
Coccinula sinensis (Weise)	2									
Coelophora biplagiata (Swartz)						1				
Coelophora inaequalis (Fabricius)							3	1		
Coleomegilla maculata (De Geer)				49						3
Coleomegilla quadrifasciata (Schöenherr)										1
Cycloneda munda (Say)				9						
Cycloneda polita Casey				1						
Cycloneda sanguinea (L.)				2						14
Eriopis chilensis Hofmann										2
Eriopis connexa (Germar)										5
Eriopis peruviana Hofmann										2
Halyzia sedecimguttata (L.)		1								
Harmonia antipoda (Mulsant)									1	
Harmonia axyridis (Pallas)	13	38	1	8	1					4
Harmonia conformis (Boisduval)								1		
Harmonia dimidiata (Fabricius)						1				
Harmonia expalliata Sicard	1									
Harmonia octomaculata (Fabricius)						3				
Harmonia quadripunctata (Pontoppidan)	3	3								
Hippodamia arctica (Schneider)	2									
Hippodamia convergens Guerin				36						8
Hippodamia parenthesis (Say)				12						
Hippodamia quinquesignata (Kirby)				2						
Hippodamia sinuata Mulsant				2						
Hippodamia tredecimpunctata (L.)	4	3		7						
Hippodamia undecimnotata (Schneider)	1	4								
Hippodamia variegata (Goeze)	14*	14*	4		2					3
Illeis cincta (Fabricius)						1				
Lioadalia flavomaculata (De Geer)					4					
Macronaemia hauseri Weise	1									
Micraspis discolor (Fabricius)						4				
Mulsantina picta (Randall)				1						
Myrrha octodecimguttata (L.)		1								
Myzia oblongoguttata (L.)		1								
Oenopia conglobata (L.)	2	4								
Olla v-nigrum (Mulsant)			1	4			2			1
Propylea japonica (Thunberg)	3									
Propylea quatuordecimpunctata (L.)	7	8								
Psyllobora vigintiduopunctata (L.)		1								
Tytthaspis sedecimpunctata (L.)		1								
Vibidia duodecimguttata (Poda)		2								
No. records	137	218	28	168	17	27	5	5	8	44
No. species	26	24	6	20	7	8	2	4	2	11

* Two records of *C. septempunctata* and one record of *H. variegata* as hosts of *D. coccinellae* are reported from the Asia-Europe border. These records are here counted twice, as both European and Asian.

Table 2. First records of *Dinocampus coccinellae* on the mainland and islands of each biogeographical realm. The notation "before + year of publication" is used when the date of the record is not mentioned in the paper.

Realm/region	Locality	Year	Reference
Palaearctic			
continental Asia	Yunnan, China	1939	Liu (1944)
continental Europe	Bavaria, Germany	before 1802	Schrank (1802)
	Bruxelles, Belgium	1781	König (1972)
continental North Africa	Egypt	before 1951	Kamal (1951)
Japan		before 1918	Timberlake (1918)
Taiwan		before 1939	Sonan (1939) [ref. in Maeta (1969)]
Sakhalin Island		before 1983	Kuznetsov & Semyanov (1983)
Great Britain	Shere, Surrey	1921	Lyle (1927)
Ireland	Dublin	1973	Blackith (1973)
Madeira	Machico	1973	Graham (1986)
Canary Islands	El Hierro	before 2010	Báez & Oromí (2010)
Nearctic			
North America	Illinois, USA	before 1872	Cresson (1872)
Greenland	Itilleq	2003	van Achterberg (2006)
Afrotropical			
South Africa		1912–1913	Moore (1914)
Indomalayan			
India	Bangalore	before 1977	Ghorpade (1977)
Oceanian			
Hawaii		before 1906	Kotinsky (1906)
Fiji		before 1918	Timberlake (1918)
Australian			
Australia		1892	Coquillett (1893)
Tasmania		before 1980	Alma (1980)
Antarctic			
New Zealand	Paeroa	before 1918	Timberlake (1918)
Neotropical			
South America	Chile	before 1936	Muesebeck (1936)

CANARY ISLANDS (SPAIN)

The data on *D. coccinellae* and its hosts in the Canary Islands were collected while surveying the fauna of Coccinellidae on the islands of Lanzarote (Romanowski et al., 2020a), Gran Canaria (Romanowski et al., 2020b), El Hierro (Romanowski et al., 2020c), Tenerife, La Palma and La Gomera (Romanowski & Ceryngier, unpubl.).

***Coccinella septempunctata algerica* Kovář.** Lanzarote: three *D. coccinellae* bred from this host collected on 11 February (one individual) and 13 February 2018 (two individuals); Gran Canaria: two *D. coccinellae* bred from this host collected on 3 and 4 April 2019; El Hierro: two *D. coccinellae* from this host collected on 10 April 2019.

***Coccinella miranda* Wollaston.** Gran Canaria: *D. coccinellae* emerged from 11 of 65 adults of *C. miranda* collected between 31 March and 6 April 2019.

***Cheilomenes propinqua* (Mulsant).** Gran Canaria: Two *D. coccinellae* individuals were bred from this host collected in Maspalomas on 5 April 2019.

***Harmonia axyridis* (Pallas).** Tenerife: *D. coccinellae* specimen was bred from this host collected on 23 February 2022 in Santa Cruz de Tenerife (1 March – cocoon, 11 March – adult wasp).

***Hippodamia variegata* (Goeze)**: La Palma: from a host collected on 20 June 2021 (7 July – cocoon, 17 July – adult wasp).

***Olla v-nigrum* (Mulsant).** La Gomera: the parasitoid wasp was bred from *O. v-nigrum* collected as pupa on 24 February 2022 in San Sebastian (before 18 March – cocoon, 25 March – adult emergence).

These findings are the first detailed reports on the occurrence of *D. coccinellae* in the Canary Islands and the first records of *C. miranda* as a host of this parasitoid. Previously, *D. coccinellae* was mentioned in the checklist of the Canarian Hymenoptera (Báez & Oromí, 2010) as occurring on the island of El Hierro.

MADEIRA (PORTUGAL)

***Hippodamia variegata* (Goeze).** From a specimen of this species, collected on 8 February 2020 at Pico Areeiro, a larva of *D. coccinellae* emerged and spun a cocoon on 29 February, and on 10 March an adult wasp emerged from the cocoon.

Before this report, *D. coccinellae* was reported without a host association from Machico in Madeira by Graham (1986).

ARMENIA

***Hippodamia undecimnotata* (Schneider).** From a host collected on 7 June 2022 near Tigranashen (14 June – cocoon, adult wasp did not emerge).

***Hippodamia variegata* (Goeze).** From a host collected on 8 June 2022 at Nzhdeh (16 June – cocoon, 26 June – wasp emergence).

***Propylea quatuordecimpunctata* (L.).** From a host collected on 7 June 2022 at Khor Virap (24 June – cocoon, about 3 July – wasp emergence).

Previously, *D. coccinellae* was reported from Armenia only once; Tobias (1971) recorded it in Yerevan as a parasitoid of *Exochomus octosignatus* (Gebler).

DISCUSSION

Distribution of *Dinocampus coccinellae* and the problem of its native range

Although the general pattern of the occurrence of *D. coccinellae* worldwide (Fig. 1) confirms its almost cosmopolitan distribution, there are vast areas on most continents for which there is no information. Almost complete lack of records from high latitudes (northern North America and Eurasia and the southern portion of South America) may indicate that the occurrence of *D. coccinellae* is limited by cold climatic conditions. On the other hand, the relatively many records from the tropical and subtropical regions indicate that neither hot humid nor hot dry climates preclude the occurrence of *D. coccinellae*.

There are also no records for some parts of the world in temperate and warm climatic zones, in particular the Afro-

tropical realm except its southernmost part (South Africa) and the Malay Archipelago [the insular part of the Indomalayan realm (islands of Indonesia, Malaysia and the Philippines) plus the neighbouring island of New Guinea (Oceanian realm)]. Other record-poor regions include Australia, especially its central and western parts, and most of the Palaearctic part of Asia. The most likely reason for these gaps in distribution is that the regions mentioned have not yet been surveyed for *D. coccinellae*. It is, therefore, concluded that *D. coccinellae* is presumably common at middle and low latitudes throughout the World, but rare or absent at high latitudes and probably also at high altitudes.

The current state of knowledge makes it difficult to determine which parts of the huge present range of *D. coccinellae* can be considered native (occurrence in a given area as a result of natural processes) and which was colonized by this species due to human activity. The latter has mainly been connected with the use of Coccinellidae in so-called classical biological control (introductions of species outside of their native ranges in order to limit the numbers of unwanted organisms). The first known long-distance movement of ladybirds for biocontrol purposes took place in 1874 and involved the release of *Coccinella undecimpunctata* L. of English origin in New Zealand (Doutt, 1964). This early introduction is believed to have resulted in the establishment of *D. coccinellae* in that country (Gourlay, 1930). The massive use of Coccinellidae in classical biological control, however, began later, in 1888, with the well-known campaign against the cottony cushion scale (*Icerya purchasi* Maskell) devastating Californian citrus groves (Doutt, 1964). The ladybird species that was then imported from Australia and subsequently established in California to efficiently control *I. purchasi*, *Novius* (=*Rodolia*) *cardinalis* (Mulsant), is not known to be a host of *D. coccinellae*. However, the impressive success of that project launched a period of frequent intercontinental translocations of various Coccinellidae, also generally suitable for the development of this wasp: members of the tribe Coccinellini. Soon after the introduction of *N. cardinalis* in California, between 1893 and 1897, many ladybirds, including about 30 species of Coccinellini, were introduced in the Hawaiian Islands (Leeper, 2015). One of them, *O. v-nigrum*, was according to Timberlake (1918) the source of the Hawaiian population of *D. coccinellae*. That this parasitoid cannot be native to Hawaii is also indicated by the fact that there are no native Hawaiian ladybirds (Leeper, 2015).

New Zealand and the Hawaiian Islands are the only regions where *D. coccinellae* is suspected to occur non-natively and where a means of its introduction there has been proposed. The parasitoid may also have been introduced with its ladybird hosts to other islands and archipelagos, but data on this are lacking. As regards the origin of *D. coccinellae* on continents, already Balduf (1926) wondered whether it was brought to North America from Europe or was native to both. *Dinocampus coccinellae* was taxonomically described four times: twice based on specimens from Europe (as *Ichneumon coccinellae* Schrank, 1802 and *Bracon terminatus* Nees, 1811) and twice from the United States (as *Euphorus sculptus* Cresson, 1872 and *Perilitus americanus* Riley, 1889). Although the American descriptions are much younger than the European ones, they are all based on specimens collected before classical biological control became more widely used. The first historical records of *D. coccinellae* in some other parts of the world are also quite old (Table 2). Especially interesting in this respect is the first Australian record. Two wasps of *D. coccinellae* were bred by Coquillett (1893) from specimens of "the yellow ladybirds with six elytral black spots" sent to him by Albert Koebele from Australia in 1892. The host ladybirds were later identified as *Coccinella repanda* (= *C. leonina transversalis* Fabricius) (Chittenden, 1898). This record indicates that *D. coccinellae* was present in Australia prior to the widespread use of classical biological control, and therefore its status there as a native species cannot be ruled out.

Hosts of *Dinocampus coccinellae*

In their review of the hosts of *D. coccinellae*, Ceryngier et al. (2012) list 56 species of Coccinellidae and one species of Curculionidae. The present survey of literature and unpublished records has increased this number to 72 species of Coccinellidae. The weevil *Sitona discoideus* Gyllenhal was removed from this updated host list, because successful parasitoid development in such an untypical host seems highly unlikely. As an occasional host of *D. coccinellae*, *S. discoideus* is reported from New Zealand only on the basis of dissections of adult beetles (Wightman, 1986). On the other hand, a record was added of another untypical host, *Brachiacantha ursina* (Fabricius), a member of the coccinellid tribe Brachiacanthini. Richerson & DeLoach (1973) revealed by dissection of field-collected adults of this species a small fraction (1.8%) of which contained *D. coccinellae* larvae. In their other paper, Richerson & DeLoach (1972) report the successful development of *D. coccinellae* in laboratory parasitized *B. ursina*. Other untypical hosts of this parasitoid include several members of the tribe Chilocorini. Although questioned by Ceryngier & Hodek (1996), it is now proven that they are suitable hosts of *D. coccinellae* in some regions (Minnaar et al., 2014; Maqbool et al., 2018).

The present study revealed that the most frequently reported *D. coccinellae* host is *C. septempunctata*, which is not surprising considering its relatively high suitability for the parasitoid (Cartwright et al., 1982; Sloggett et al., 2004; Koyama & Majerus, 2008), wide distribution, both in its native Palaearctic range and invasive Nearctic range, and abundant occurrence in various habitats (Hodek & Michaud, 2008). The second position in terms of frequency of records is occupied by *H. axyridis*, which, however, is not so obvious. *Harmonia axyridis* is considered a host of low suitability for *D. coccinellae* (e.g. Firlej et al., 2007; Koyama & Majerus, 2008; Romero et al., 2020), although central European populations of the latter have adapted to its exploitation (Knapp et al., 2019). The reason for such a high number of records is certainly the popularity of *H. axyridis* as a subject of research, due to its invasiveness

and global spread. Studying natural enemies of *H. axyridis* fits in well with this research trend. Of 65 records of *H. axyridis* as a host of *D. coccinellae*, 52 relatively recent ones (between 1994 and 2022) come from the areas where this ladybird is non-indigenous, and only 13 records (usually much older) are from its native range.

Richerson & DeLoach (1972) show experimentally that large ladybird species are preferred by *D. coccinellae* over small ones and that in large ladybirds the parasitoid larvae develop more successfully than in small ones. The species most frequently recorded as hosts of *D. coccinellae* in nature, such as *C. septempunctata* and *H. axyridis* in the Palaearctic, *C. maculata* (Nearctic), *H. convergens* (Nearctic and Neotropical) and *C. sanguinea* (Neotropical), are medium-sized to large ladybirds. Interestingly, very large ladybirds seem to be avoided by and/or unsuitable for the wasp. There are no reports that giant ladybirds, such as members of the genera *Aiolocaria, Megalocaria, Synonycha* or *Neda*, are hosts of *D. coccinellae*. The largest European ladybirds, *Anatis ocellata* (L.) and *Myzia oblongoguttata* (L.) are only reported once (Majerus, 1997) as occasional hosts of *D. coccinellae* in Britain.

Research prospects

Although the number of records of *D. coccinellae* and number of its host species recorded may seem very high, they are also very unevenly distributed, with the vast majority coming from the Palaearctic (mainly its European part) and Nearctic (mainly the USA). Surveys in regions such as sub-Saharan Africa or the Malay Archipelago are likely to considerably extend the host list of *D. coccinellae* and fill in the gaps in its recorded distribution. It is also worth checking how far towards the poles the range of this species extends and which ladybirds serve as its hosts in the northern and southern extremes of its range. Furthermore, it would be interesting to compare robust quantitative field data on the host preferences of *D. coccinellae* in different parts of its range. This can be done by assessing percentage parasitism or parasitoid emergence from many different potential hosts within a given area, region or country. So far, the only paper providing such data is that of Majerus (1997), which compares the percentage emergence of *D. coccinellae* from over 20 species of British Coccinellidae. The results of these comparisons are not obvious; the highest percentages were recorded for *Coccinella undecimpunctata* (22.1%) and *Harmonia quadripunctata* (19.4%), while the species most frequently recorded worldwide as a host of *D. coccinellae*, *C. septempunctata*, ranked only third with a percentage emergence of 17.4%. The question of the origin of *D. coccinellae* can presumably be clarified using molecular methods. Phylogeographic analyses would perhaps help to determine which areas fall within the native range of *D. coccinellae* and the routes of its worldwide spread.

ACKNOWLEDGEMENTS. This paper is dedicated to the memory of Ivo Hodek. For the first author (PC) Ivo was a unique person. He introduced PC to ladybird research and encouraged him to focus on their natural enemies.

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Received October 2, 2022; revised and accepted January 20, 2023
Published online February 2, 2023

Online supplementary file:
Supplement S1 (http://www.eje.cz/2023/004/S01.xlsx). Database of *Dinocampus coccinellae* (Schrank, 1802) (Hymenoptera: Braconidae) distribution and host records.