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Distribution, host range, and climatic constraints on *Centistes gasseni* (Hymenoptera: Braconidae), a South American parasitoid of cucumber beetles, *Diabrotica* spp. (Coleoptera: Chrysomelidae)

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Abstract

The genus *Diabrotica* includes a large number of pest species, including some of the most important crop pests of the Americas. The parasitoid *Centistes gasseni* Shaw is the first braconid to be described parasitizing *Diabrotica* in South America, and high natural infestations are reported. Field and experimental observations on the host range, distribution and biology of this parasitoid are described. *Centistes gasseni* was collected in southern Brazil, eastern Paraguay and northeastern Argentina, in a region comprising humid lowlands and highlands, and cool temperate to warm subtropical climates, with regular rainfall in excess of 1300 mm. Three *Diabrotica* species, *D. limitata* (Sahlberg), *D. speciosa* (Germar) and *D. viridula* (Fabricius) were found to host the parasitoid, with mean percent parasitism of 5.4, 2.0 and 1.0%, respectively. *Diabrotica speciosa* and *D. viridula* are the two most important pest *Diabrotica* species in South America. Laboratory experiments with field-collected beetles and parasitoid cocoons indicated that *C. gasseni* overwinters in adult host beetles, remaining dormant in its live host below developmental temperatures. A potential distribution of *C. gasseni* in North America is proposed based on its known climatic range and the distribution of the main pest species of adult overwintering North American *Diabrotica*.

Introduction

The tribe Luperini, subtribe Diabroticina (Coleoptera: Chrysomelidae) comprises many polyphagous and oligophagous species of beetles. The genus *Diabrotica*, includes the majority of pest species, including some of the most important crop pests of the Americas: *Diabrotica speciosa* (Germar) and *D. viridula* (Fabricius) in South America (Christensen, 1943; Link & Costa, 1978; Olalquiaga, 1980; Sarasola *et al.*, 1980; Krysan, 1986; Reyes & Castillo, 1988); and the North American *D. balteata* LeConte, *D. undecimpunctata howardi* Barber, *D. undecimpunctata undecimpunctata* Mannerheim, *D. barberi* Smith & Lawrence,

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D. virgifera virgifera LeConte, and *D. virgifera zeae* Krysan & Smith (Krysan, 1986; Metcalf, 1986). Despite being a large genus, well represented throughout the Americas, and often very abundant, a surprisingly low number of parasitoids of *Diabrotica* have been recorded: four species in the genus *Celatoria* (Diptera: Tachinidae), and *Centistes gasseni* Shaw (Hymenoptera: Braconidae) (Sell, 1915; D'Araujo e Silva *et al.*, 1968; Elsey, 1988; Eben & Barbercheck, 1996; Heineck-Leonel & Salles, 1997; Kuhlmann & van der Burgt, 1998).

Attempts at biocontrol have so far involved mainly pathogens isolated from *Diabrotica* spp. (Creighton & Fassuliotis, 1985; Tallamy *et al.*, 1998), or from other beetle species (Wright *et al.*, 1993; Jackson & Brooks, 1995; Jackson, 1996; Ellers-Kirk *et al.*, 2000). Parasitoids, on the other hand, have not been applied in the field. The reasons for this are probably that pest *Diabrotica* are mostly native to their distribution areas, and natural infestations of their parasitoids are low and irregular. Consequently, the practicality and chances of success of an augmentative or introduction release plan have never been seriously considered.

However, the reduced success of traditional management alternatives (Metcalf, 1986; Levine & Oloumi-Sadeghi, 1996), and the accidental release of *D. v. virgifera* in Europe (Baca, 1994; Kuhlmann & van der Burgt, 1998), has spurred interest in parasitoids as alternative biocontrol agents (Zhang *et al.*, 2003). Furthermore, both known South American parasitoids of *Diabrotica*, *Celatoria bosqi* Blanchard (Diptera: Tachinidae) and *C. gasseni*, and the Mexican species, *Celatoria compressa* Wulp (Diptera: Tachinidae), have shown high and regular natural infestations (Blanchard, 1937; Eben & Barbercheck, 1996; Heineck-Leonel & Salles, 1997; Eben, 2002; Schroder & Athanas, 2002), suggesting they exert a certain level of control on their host populations.

The parasitoid *C. gasseni* was the first braconid to be described parasitizing diabroticine beetles in South America, and large natural infestations have been reported (Shaw, 1995; Heineck-Leonel & Salles, 1997; Schroder & Athanas, 2002). The objectives of this work were to report field observations, and results of experiments performed at the ARS-USDA South American Biological Control Laboratory (SABCL), Hurlingham, Argentina, on the reproductive biology and ecology of *C. gasseni*, as a step to comply with the requirements for release of this species into the USA, including host range, distribution, and analysis of its potential distribution and hosts in North America.

Materials and methods

Host and parasitoid collection and handling

Host beetles were collected between April 1994 and June 2002 during a total of 22 trips to southern Brazil, southern Bolivia, Argentina, Paraguay and Uruguay, during late spring/summer, autumn and winter. At each collection site all the available chrysomelid beetles were collected with standard entomological tools, or baits (Cabrera Walsh, 2001). The beetles were transported to one of the laboratories involved (USDA/ARS-South American Biological Control Laboratory (SABCL), Argentina, and Centro de Pesquisa Agropecuária de Clima Temperado (CPACT), EMBRAPA, Pelotas, RS, Brazil) in 2-l plastic cages with sleeves (up to 500 beetles per cage), and provided with slices of squash for food and water. In the laboratory the beetles were identified and separated into species, and maintained in cages at 25 ± 1°C, 14:10 L:D photoperiod. The cages had a size 12 plastic mesh attached to the bottom through which emerging parasitoid larvae could fall onto a moist sand bed below. Adults were fed a diet based on that developed by Campbell & Jackson (1987) for North American *Diabrotica*, and provided with water from 45 ml plastic cups with cotton wool wicks through the lids (Cabrera Walsh, 2001).

Rearing of C. gasseni

Centistes gasseni cocoons were incubated at 23 ± 1°C or 26 ± 1°C, 65 ± 10% rh, 14:10 L:D photoperiod, in plastic containers with a plaster of Paris bottom covered with a layer of peat moss. This combination maintained moisture efficiently, and provided crevices where the parasitoids could hide to spin cocoons. Emerged parasitoids were chilled on a cryolizer, identified under a dissecting microscope, and the hyperparasitoids accounted for and discarded. Then one female together with 6–8 males were aspirated into 0.25-l glass tubes with sleeves at the ends, in order to encourage mating (Schroder & Athanas, 2002). They were provided with cotton rolls saturated with diluted raw sugar. Following mating, 6–8 *D. speciosa* beetles were introduced into each tube. They were observed closely so they could be removed immediately after being attacked to prevent multiple ovipositions.

Overwintering tests

Five groups of five *C. gasseni* cocoons were kept in ventilated plastic containers with moist peat moss, in rearing chambers at 8 ± 2°C, 14:10 L:D photoperiod, in order to evaluate their capacity to remain quiescent in cool conditions. Every five days one group was transferred to a 25°C chamber, and the number of adult wasps emerged was recorded.

Large samples of field-collected beetles were divided into two subsamples in order to investigate how the parasitoid overwinters: one group was kept in a rearing chamber (25 ± 1°C, 14:10 L:D photoperiod). The other subsample was reared under 'garden' conditions, under a thatched roof without walls, during autumn and winter at the USDA/ARS–South American Biological Control Laboratory (mean annual and mean minimum temperature 16.5°C, and 11.1°C, respectively, altitude 22 masl). The number and timing of emergence of parasitoids from cocoons in each subsample was recorded, to obtain data on the dynamics of overwintering and host re-colonization of *C. gasseni*. Also, small groups of outdoor-reared beetles and parasitoid cocoons were transferred every month to the rearing chamber in order to detect delays in the appearance of new cocoons, or in their emergence.

Geographic and climatic boundaries

The distribution and physico-climatic boundaries of *C. gasseni* were defined by comparison with climate diagrams (Atlas climático de la República Argentina, 1960; Estadística climatológica, 1985; Cartas de precipitação e temperatura mensais, 1990) and altitudinal data (Trimble Scout GPS, Trimble Navigation Limited, California, USA). The variables taken into account and compared, were altitude, mean annual, mean winter minimum, and mean summer maximum average temperatures, average rainfall and rainfall seasonality. These data, together with known data on the biology of the parasitoid hosts were extrapolated to infer the potential distribution of *C. gasseni* in areas of North America where the parasitoid could be released. For this, climatic data on minimum average temperatures and monthly rainfall (Climatic Atlas of the United States, 1977; Servicio Meteorológico Nacional, 2001), were matched with distribution data on North American pest *Diabrotica* species (i.e. potential North American hosts) (Krysan, 1986; Meinke & Gould, 1987).

Results

Collection results

A total of 106458 Diabroticina, principally *D. speciosa*, were collected between April 1994 and June 2002, from Argentina, Bolivia, Brazil, Paraguay and Uruguay (table 1; fig. 1, area enclosed within the dotted line). Three species of *Diabrotica* were found to be common natural hosts of *C. gasseni*: *D. speciosa*, *D. viridula* and *D. limitata* (Sahlberg). Average parasitism was 2.0, 0.98 and 5.4%, respectively (range 0–45%). The highest parasitism rates, of 3.9 ± 4.63%, were observed during autumn, in April and May, in the regions of Passo Fundo, Caxias do Sul, and Pelotas, in the state of Rio Grande do Sul, southeast Brazil (28°15′ S, 52°24′ W; 29°,10′ S, 51°12′ W; 31°45′ S, 52°20′ W, respectively) (table 2). Over 6800 individuals of other Chrysomelidae were also collected, including species in the subfamilies Galerucinae, Alticinae, Eumolpinae and Megascelinae, but they were not found to host the parasitoid (table 1). One *C. gasseni* was collected from the South American striped cucumber beetle, *Acalymma bivittula* (Kirsch) (Chrysomelidae) from a total of 3690 individuals collected in the known distribution area of the parasitoid.

Table 1. Host range of *Centistes gasseni* from samples collected within its geographical range from 1995 to 2002.

Beetle species	No. collected	Host
Diabrotica speciosa	91510	+
D. viridula	2483	+
D. limitata	117	+
D. amoena Dalman	22	–
D. marginata Harold	12	–
D. emorsitans Baly	186	–
D. panchroma Bechyné	23	–
Acalymma bivittula	3690	–*
A. bruchii (Bowditch)	192	–
A. albidovittata (Baly)	690	–
A. vittigera (Boheman)	25	–
Paranapiacaba significata (Gahan)	405	–
P. duodecimmaculata (Klug)	240	–
Paranapiacaba sp.	8	–
Cochabamba rufolimbata (Baly)	50	–
Cerotoma arcuata Olivier	232	–
Cerotoma sp.	32	–
Platybrotica misionensis Cabrera & Cabrera Walsh	118	–
Amphelasma spp.	45	–
Disonycha sp.	41	–
Caeporis sp.	36	–
Epitrix sp.	26	–
Colaspis sp.	33	–
Maecolaspis spp.	72	–
Megascelis sp.	36	–

*See discussion.

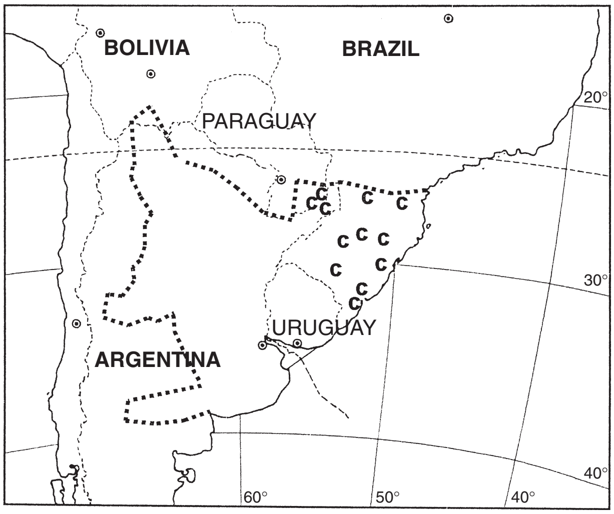

Fig. 1. Map of southern South America showing the distribution of *Centistes gasseni* (bold capital **C**s), and its host Diabroticina (area enclosed within the dotted line).

The hyperparasitoid *Mesochorus* sp. (Hymenoptera: Ichneumonidae), was found in up to 11% of *C. gasseni* cocoons.

Laboratory rearing of C. gasseni

Mating in the glass tubes was observed at 10 to 120 min after the female and males were confined together. After that period, no further mating occurred. Oviposition attempts on the beetles offered began immediately after mating, although unmated females also attacked the beetles. Females continued to oviposit for 4–5 days, but the highest numbers of cocoons reared per female were obtained from those ovipositing within 48 h of mating. Almost no offspring emerged from beetles attacked by 4- to 5-day-old parasites (table 3). Males lived 4–5 days, and the females 7–9 days. The parasitoid larva took 16–20 days to exit a host, depending on the temperature (table 3), usually from the anal opening, or by opening a hole in the sides of the abdominal terga. They immediately sought a crevice in which to spin a cocoon. Adults emerged in 14–23 days (table 3). An average of 40 parasitoids was obtained per female. Results suggested that pupal survival was higher at 23°C than 26°C (table 3), but female emergence was delayed by two to three days compared to males, which could produce a shortage of males when females were available. This delay was shortened to one day at 26°C, for which this temperature was preferred.

Parasitoid and host overwintering

The laboratory experiments on overwintering populations of *D. speciosa*, and its parasitoid *C. gasseni*, provided evidence that neither species showed overwintering adaptations involving diapause. *Diabrotica speciosa* fed whenever temperatures allowed (*c.* 12°C), and oviposited after approximately one week of warm daytime temperatures (> 18°C). Also, colonies of laboratory-reared

Table 2. Percent incidence of *Centistes gasseni* in its temperate and subtropical ranges according to season.

Season	Temperate[a]		Subtropical[b]	
	No. of beetles	% *C. gasseni*	No. of beetles	% *C. gasseni*
Spring/Summer	17997	0.67 ± 0.34	4282	0.02 ± 0.02
Autumn	26654	3.80 ± 0.67	4617	0.82 ± 0.4
Winter	320	0.30 ± 0.00	4821	0.07 ± 0.07
Total	44971	1.60	13720	0.30

[a] Average percent incidence ± SE of *C. gasseni* within its temperate distribution range (approx. 28–32°S; 49–55°W).
[b] Average percent incidence ± SE of *C. gasseni* within its subtropical distribution range (approx. 25–27°S; 49–56°W).

Table 3. Duration in days of the life cycle of *Centistes gasseni* (mean ± SE), and number of successful attacks according to female age (resulting mean no. of cocoons ± SE).

	23°C	26°C
Egg + larva (days)	21.4 ± 0.3	16.3 ± 0.3
Cocoon (days)	19.7 ± 1.7	15.0 ± 0.6
Cocoon % survival	66%	58%

No. cocoons per female[a]	<24 h	48 h	72 h	>96 h
	7.2 ± 2.9	3.5 ± 1.5	0.5 ± 0.2	0.2 ± 0.03

Total no. of cocoons reared = 928.
[a] No. of cocoons obtained per female from attacks occurring <24, 48, 72, and >96 h after mating at 25 ± 2°C.

D. speciosa kept under outdoor insectary conditions through autumn and winter, lived up to six months.

Similarly, *C. gasseni* immatures lived as larvae in the host, and emergence of pupating larvae depended on the exposure to warm temperatures, as did the emergence of the adult parasitoid. In the temperate winter conditions of Buenos Aires, the emergence of pupating larvae of *C. gasseni* from field-collected *D. speciosa* took up to 110 days ($\bar{x} = 51.3 \pm \mathrm{SD} = 41$), whereas at 26°C, development was completed in 29 ± 2 days. Development of *C. gasseni* resumed when overwintering host beetles were transferred to rearing chambers at 25°C, as emergence of pupating larvae occurred in 3–4 days. Furthermore, chilling was not required for emergence, indicating a full diapause was not involved in the overwintering strategy of *C. gasseni*, but rather, a capacity to remain quiescent in its host below development temperatures. On the other hand, no chilled cocoons survived more than 25 days, and only 20% survived 20 days, indicating the pupa was not capable of remaining dormant for very long in cold conditions.

Actual and inferred distribution of C. gasseni

The known distribution of *C. gasseni* currently includes the three southernmost states of Brazil: Rio Grande do Sul, Santa Catarina and Paraná; eastern Paraguay, and northeast Argentina (fig. 1, bold capital letter Cs). *Centistes gasseni* was collected throughout the year at altitudes ranging from 4 to 1135 masl, with mean minimum, maximum and annual temperatures ranging from 7.2–11°C, 16.2 – 32.6°C and 11.9–21.1°C, respectively (temperate to subtropical climates). Most collection sites can have sub-zero temperatures during winter, and the cooler areas of the known distribution of *C. gasseni* (Passo Fundo and Vacaría, state of Rio Grande do Sul; and Caçador, state of Santa Catarina), have occasional snowfalls. The sole common climatic trait of the area enveloped by these collection sites is annual rainfall over 1300 mm, devoid of any marked seasonality. However, within this distribution area, the cooler, temperate areas, and/or higher altitudes, tended to support larger and more regular populations of *C. gasseni* (table 2).

Based on the apparent climatic constraints of *C. gasseni*, a map of its potential distribution in North America was prepared, based on monthly rainfall over 100 mm, and minimum average temperatures in excess of 7°C. The areas of similar climate were found to be practically limited to the southernmost eastern portion of the United States, from the states of Florida to eastern Texas, and an eastern coastal and southern portion of Mexico (fig. 2, hatched areas).

Discussion

Despite the large sampling area covered in South America, and the number of potential host species of Chrysomelidae collected, no new parasitoids were found. This confirms the pattern observed in North America, where the Diabroticina are also a large, abundant, and widespread group showing a very low number of specific natural enemies. The reasons for this may be related to the extensive adaptation within the Galerucinae of storing toxic glucosides (cucurbitacins) from their host plants in their fat bodies. There is evidence that these compounds have a

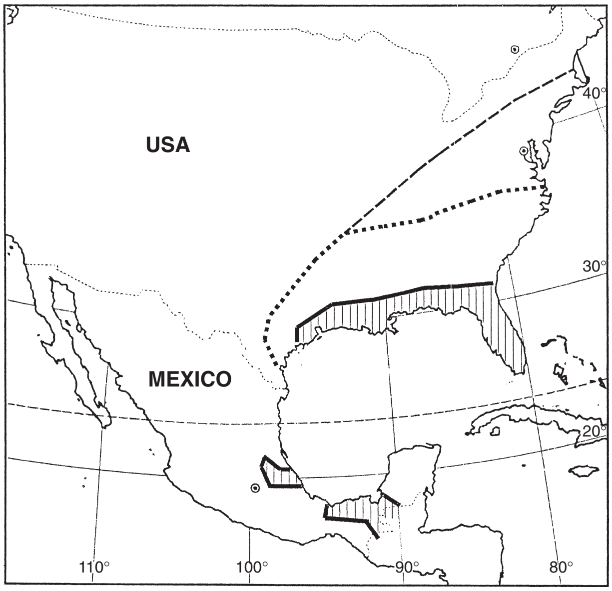

Fig. 2. Partial map of North America depicting hypothetical distribution range of *Centistes gasseni*: ▥, climatic conditions similar to its homeland in South America; ...., permanent (overwintering) range of potential hosts with regular annual rainfall in excess of 1100 mm; — — — —, extended (migratory) range of potential hosts with regular annual rainfall in excess of 1100 mm.

deterrent effect on predators, parasitoids and pathogens alike (Metcalf & Lampman, 1989; Nishida & Fukami, 1989; Brust & Barbercheck, 1992; Tallamy *et al.*, 1997, 1998), which may explain why only two parasitoid genera have adapted to the Diabroticites. Furthermore, of all the potential hosts sampled, only three *Diabrotica* species hosted *C. gasseni*. The host with the highest parasitism rates was *D. limitata*, an infrequent, non-pest species normally associated with Cucurbitaceae (Cabrera Walsh, 2003). The other two host species, *D. speciosa* and *D. viridula*, are the two most common rootworm species in South America, and important agricultural pests throughout the continent (Krysan, 1986; Cabrera Walsh, 2003). The three species hosted the parasitoid consistently throughout the sampling period, and its distribution area. The single record of *C. gasseni* from *A. bivittula* indicates it is an extremely rare, or perhaps accidental, event, suggesting this species should not be considered a natural host of the parasitoid.

The known hosts of *C. gasseni* overwinter as adults (Krysan, 1986; Cabrera Walsh, 2001, 2003). The experiments show *C. gasseni* overwinters as a larva inside its host, and thus depends on the survival of adult host beetles during this period. The results also suggest the parasitoid has no mechanism of overwintering outside its hosts. This implies that any programme to release *C. gasseni* in North America or Europe as a biocontrol agent against pest *Diabrotica*, must assume the existence of a species that will host the parasitoid through the winter, or implement massive releases of laboratory-reared parasitoids every spring. In North America, the 'backup' hosts of choice in suitable climatic areas, would be the pest species that overwinter as adults, namely *D. balteata* and *D. u. howardi*. In this way, there would be a bank of parasitoids available by the time *Diabrotica* species that overwinter as eggs (*D. barberi*, *D. v. virgifera* and *D. v. zeae*) appear in the field during the warm season. As *D. u. howardi* migrates as far north as Canada during spring (Krysan, 1986; Elsey, 1989) it may be expected to vector the parasitoid throughout a large part of the distribution areas of both *D. v. virgifera* and *D. barberi*.

Extensive collections in temperate to tropical climates, and humid to dry highlands and plains (fig. 1), indicate *C. gasseni* has a limited area of distribution, restricted to a humid, temperate to subtropical climatic zone. The correspondence between the distribution of *C. gasseni* and areas of high, regular precipitation, suggests the parasitoid pupa and/or adult may be sensitive to desiccation, and require high, permanent soil moisture levels for survival. The few existing publications reporting on collections of *D. speciosa* or *D. viridula* in tropical areas of South America do not mention the presence of *C. gasseni* (D'Araujo e Silva *et al.*, 1968; Harries, 1975; Krysan *et al.*, 1984; Reyes & Castillo, 1988). This might be simply because the parasitoid is difficult to detect and may have been overlooked in the past. However, the abundance of *C. gasseni* declined drastically toward its northern, more tropical ranges, where it was limited to higher, cooler altitudes (table 2), suggesting it is sensitive to high temperatures, radiation balances, and/or water balance. Furthermore, in the subtropical distribution areas where *C. gasseni* occurs the densities of host *Diabrotica* are higher and more regular throughout the year than in temperate areas (Cabrera Walsh, 2003). This apparent contradiction further supports the idea that the physiological optimum of the species is closer to a temperate climate.

By contrast, relatively harsh winters can occur in some of the more elevated areas of its distribution, coincidentally the sites with higher parasitism rates, with snowfalls and frequent freezing temperatures. This suggests that the survival of *C. gasseni* may not be limited at low temperatures, providing they allow the survival of its overwintering hosts.

Based on the biological constraints described above, two additional hypothetical distribution areas in North America are proposed (fig. 2), enveloping the range of the potential overwintering host *Diabrotica*, matched with regular annual rainfall in excess of 1100 mm. One area is determined by the permanent range of *D. u. howardi* (dotted line), and the other by its spring/summer range (dashed line). If the assumptions behind this hypothetical distribution could be experimentally substantiated, namely: (i) low winter temperatures are not limiting to the survival of *C. gasseni*, providing its host is not killed; and (ii) the overwintering species of North American pest *Diabrotica* can host *C. gasseni* in the field, the parasitoid could cover a large part of the areas affected by pest *Diabrotica* in North America. In fact, in host range cage experiments, *C. gasseni* oviposited and developed in three species of North American pest *Diabrotica*, including *D. u. howardi*, and one species of *Acalymma*, but none of the beetles in other genera exposed to the parasitoid (Schroder & Athanas, 2002).

The evidence presented here suggests *C. gasseni* is specific to a few species of *Diabrotica* in its native habitat in South America, in spite of having a rich array of potential chrysomelid hosts. Also, it displays a limited potential range, limited only to part of the area of North America where *Diabrotica* spp. are pests. Thus, it is considered to be a sound biocontrol candidate for quarantine studies leading to release in the field.

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