

# The composition of the egg-parasitoid guild of the golden egg bug, *Phyllomorpha laciniata* (Heteroptera: Coreidae), in Spain

David Carrasco & Gergely Várkonyi\*

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The golden egg bug (*Phyllomorpha laciniata* (Villers)) is a phytophagous insect with an unusual reproductive system. Females use the bodies of conspecifics, both males and females, as oviposition substrates. In addition, a varying fraction of the eggs is laid on the food plant. Egg carrying on conspecifics increases offspring survival. Predators and, especially, hymenopteran parasitoids are the main cause of egg mortality. So far, only the wasp *Gryon bolivari* (Giard) (Hymenoptera: Scelionidae) has been reported as an egg parasitoid of *P. laciniata* in several Mediterranean populations. In this study, three new egg-parasitoid species are recorded from *P. laciniata*: the primary solitary parasitoids *Gryon monspeliense* (Picard) and *Telenomus* sp. (Hymenoptera: Scelionidae), and the facultative hyperparasitoid *Ooencyrtus telenomicida* (Vassiliev) (Hymenoptera: Encyrtidae). All of these parasitoids have been reared from host eggs being carried by conspecific bugs. We discuss the taxonomy and biology of the individual parasitoid species, as well as ecological and evolutionary aspects of the interactions in this host-parasitoid system.

*D. Carrasco, Department of Plant Protection Biology, Division of Chemical Ecology, Swedish University of Agricultural Sciences, P.O. Box 102, SE-23053, Alnarp, Sweden; E-mail: dvd.crrasco@gmail.com*

*G. Várkonyi (\*corresponding author), Finnish Environment Institute, Natural Environment Centre, Friendship Park Research Centre, Lentiirantie 342 B, FI-88900 Kuhmo, Finland; E-mail: gergely.varkonyi@ymparisto.fi*

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## 1. Introduction

The golden egg bug, *Phyllomorpha laciniata* (Villers, 1789) (Heteroptera: Coreidae) is a phytophagous insect distributed throughout the Mediterranean area (Moulet 1995). In Spanish populations, females mainly use their conspecifics, both males and other females, as oviposition substrates (Kaitala 1996, Kaitala & Smith 2002, Reguera & Gomendio 2002). Yet, some eggs can also be found on the food plant *Paronychia ar-*

*gentea* Lam. (Caryophyllaceae). In the laboratory, females oviposit for over two months, laying clutches of 1–3 eggs every second day (Kaitala & Miettinen 1997). Individuals are commonly found carrying eggs of different developmental stages in the field. Eggshell colouration covaries with the stage of larval development. Recently laid eggs are white, then they gradually turn yellow and eventually shiny golden. Nymphs leave the carrier directly after eclosion, whereas eggshells remain attached to the body of the bug.

In the wild, eggs laid on plants suffer from higher mortality than those carried on bugs due to predators and, especially, parasitoid wasps (Kaitala 1996, Reguera & Gomendio 2002, Gomendio *et al.* 2008). Thus far, only the scelionid wasp *Gryon bolivari* (Giard, 1895) has been reported as an egg parasitoid of the golden egg bug in different populations in Spain, France and Italy (Giard 1895, Mineo 1984, Kaitala 1996, Carrasco *et al.* 2007, Gomendio *et al.* 2008).

In this study, we report on a further three egg parasitoid species associated with the golden egg bug in different Spanish populations of *P. laciniata*, and discuss their taxonomy and biology as well as ecological and evolutionary aspects of the interactions in this host-parasitoid system.

## 2. Materials and methods

Adult *P. laciniata* individuals were collected from five locations within Spain during 2004–2008 (Table 1). One sampling site was situated in the Southwest near the locality of El Puerto de Santa María (Cádiz). The remaining sites were situated in the Northeast near the localities of Viladecans (Barcelona), El Prat de Llobregat (Barcelona), Llançà (Girona) and Portbou (Girona). The sites shared similar habitat characteristics. They were open areas surrounded by either maquis (shrub land) or beach dune habitat, with sandy gravel ground, low and patchy vegetation structure and abundant food plant *P. argentea*. Collection dates were selected according to the reproductive period of bugs in each place.

All parasitoid specimens were obtained from the eggs carried on *P. laciniata* individuals. Parasitized eggs are easily determined by their black colouration. We carefully removed parasitized eggs from the bugs using a small lab spoon. Parasitized eggs were stored inside small vials for incubation in laboratory conditions ( $26 \pm 2$  °C, L17:D7). After eclosion, parasitoids were preserved in 70% alcohol.

A batch of reared parasitoids obtained in 2005 was sent to Giovanni Mineo (Palermo, Italy) and Martti Koponen (Mikkeli, Finland) for identification of scelionid and encyrtid wasps, respectively. This material, together with the wasps reared dur-

ing 2004–2008, was carefully re-examined by one of us (GV).

The identification literature employed in this study included (i) original descriptions of individual species: Giard (1895) for *Gryon bolivari*, Picard (1924) for *G. monspeliense*, Mineo & Szabó (1978) for *G. bosellii* and Mineo (1979a) for *Gryon laraichii*; (ii) keys with detailed descriptions of species: Mineo (1981) to separate *G. bolivari* from *G. bosellii*, and Mineo (1979a) to distinguish between *G. laraichii* and *G. monspeliense*; (iii) revisions of Palaearctic species of *Gryon* Haliday (Kononova & Petrov 2002, Kononova & Kozlov 2008); (iv) a revision of the telenomine wasps (Hymenoptera: Scelionidae: Telenominae) of the USSR (Kozlov & Kononova 1983); and (v) a key to the Palaearctic species of *Ooencyrtus* Ashmead (Trjapitzin 1978).

Morphological terminology follows Mineo (1980, 1981) and Masner (1980, 1983).

## 3. Parasitoid species pool

Insect rearing conducted in 2004–2008 yielded altogether four egg parasitoid species of *P. laciniata*. Next we provide sampling data for each species and discuss their taxonomy and biology.

### 3.1. *Gryon bolivari* (Giard, 1895) (Hymenoptera: Scelionidae: Scelioninae)

Material examined:

- 1♀ El Puerto 10.V.2005, 2♀ Cap de Ras 5.VI.2005 (det. G. Mineo)
- 10♂ + 6♀ El Puerto 1.–10.V.2004, 17♂ + 11♀ El Puerto 2.–15.V.2005, 2♂ + 4♀ El Puerto 10.V.2005, 1♂ Cap de Ras 1.–5.VI.2005, 1♂ + 1♀ Cap de Ras 5.VI.2005, 1♀ Remolar 23.V.2007, 4♂ + 3♀ Remolar 2008, 8♂ + 10♀ Carrabiners 2008 (det. GV)
- 1♂ + 4♀ Coll del Frare 26.V.2006 (det. DC)

We found a greater variation in this species than reported earlier (cf. Mineo 1981, Kononova & Kozlov 2008), in particular in the length ratio of postmarginal (*pm*) and stigmal (*st*) veins as well as in the length of the longitudinal striae on metasomal tergite 2 (T2). In fact, the range of

Table 1. Localities, sampling years of *Phyllomorpha laciniata* individuals, and parasitoid species reared in each sampling site.

Sampling site	Coordinates	Locality	Years	Parasitoid species
El Puerto	36°36'N, 6°15'W	El Puerto de Santa María	2004, 2005	<i>G. bolivari</i> <i>O. telenomicida</i>
Remolar	41°16'N, 2°03'E	Viladecans	2007, 2008	<i>G. bolivari</i> <i>G. monspeliense</i>
Carrabiners	41°17'N, 2°07'E	El Prat de Llobregat	2007, 2008	<i>G. bolivari</i> <i>G. monspeliense</i> <i>O. telenomicida</i>
Cap de Ras	42°23'N, 3°09'E	Llançà	2005, 2006, 2007, 2008	<i>G. bolivari</i> <i>G. monspeliense</i> <i>O. telenomicida</i>
Coll del Frare	42°25'N, 3°09'E	Portbou	2006	<i>G. bolivari</i> <i>Telenomus</i> sp.

variation in our material partially overlapped with that found in *G. bosellii* Mineo and Szabó, 1978 (see Mineo 1981, Kononova & Kozlov 2008). However, all our individuals shared the character of possessing short rows of minute teeth on the mesoscutum along the lines of notauli (referred to as “abbreviate sulci” in Mineo (1981); see his Fig. II on p. 121 (*ibid.*) and Fig. 4 on p. 237 in Mineo (1979b)), which is a unique character of *G. bolivari* (Mineo 1979b, 1981).

Based on (i) the possession of this unique character; (ii) the fact that variability in the above mentioned characters occurred as continua rather than distinct character states; and (iii) that host eggs producing morphologically variable *G. bolivari* individuals were sampled from the same carrier bug specimens on the same days, we concluded that it is not justified to divide our reared material into two species, i.e. *G. bolivari* and *G. bosellii*.

In the remarks of a description of *G. bosellii*, Mineo (1981, p. 126) provides the following character states to separate these closely related species: “*G. bosellii* is the only species which has in the female the postmarginalis as long as stigmalis. This character and the coarse striae running only in the middle of T2 for about ¼ of its length easily distinguish this species from *G. bolivari*. Further it appears rather than constantly black in the body colour.” We found the following pattern in our material: specimens with dark mesosoma and metasoma were on average more

coarsely sculptured, and the longitudinal striae on T2 were longer, than in light-coloured specimens. The colour of the mesosoma and metasoma varied from almost uniformly red-brown to fully black. A large proportion of specimens had a dark mesosoma but the colour of the metasoma ranged from red-brown to black. Females had on average a slightly shorter *pm* than *st*, but in a few specimens *pm* was equal to or even slightly longer than *st*. In males, *pm* was usually somewhat longer than *st*, but we have also seen a single specimen with *pm* < *st*. Owing to the considerable variation of these character states found in *G. bosellii*, the most useful character to reliably separate this species from *G. bolivari* seems to be the absence of the short rows of minute teeth on the mesoscutum along the lines of notauli (see above).

The known hosts of *G. bolivari* include *Phyllomorpha laciniata* (e.g. Giard 1895, Mineo 1979b, Mineo 1984, Kaitala 1996, Carrasco *et al.* 2007), *Coreus marginatus* (Linnaeus, 1758) (Heteroptera: Coreidae) and an unidentified species of Rhopalidae (Heteroptera) (Mineo 1979b). Moreover, Mineo (1979b) postulated that, since *G. bolivari* is also distributed in areas where its known hosts fail to occur, *G. bolivari* would parasitize other coreid species. *Gryon bolivari* was fairly abundant and strongly associated with *P. laciniata* in all our study sites (Table 1). However, being an idiobiont parasitoid of heteropteran eggs, *G. bolivari* may also attack alternative hosts even in the presence of *P. laciniata*.

### 3.2. *Gryon monspeliense* (Picard, 1924) (Hymenoptera: Scelionidae: Scelioninae)

Material examined:

- 1♀ Cap de Ras 1.–5.VI.2005 (det. G. Mineo as *G. laraichii*)
- 1♀ Cap de Ras 11.V.2006, 1♀ Remolar 29.V.2007, 1♂ Carrabiners 26.VI.2008 (det. GV)

*Gryon laraichii* Mineo, 1979 was originally described in a key couplet (Mineo 1979a) along with *G. monspeliense*. In the same year, Mineo (1979b) gave a description of this new species, in which he addresses the problem of failing to find strong morphological differences to separate *G. laraichii* from *G. monspeliense*. In their recent monograph of Palaearctic Scelionidae, Kononova and Kozlov (2008) considered the name *G. laraichii* Mineo to be a junior synonym of *G. monspeliense* (Picard). Hence, we refer to this species as *G. monspeliense*.

The known host range of *G. monspeliense* includes *Aelia rostrata* Boheman, 1852, *A. germari* Küster, 1852 (Pentatomidae), *Eurygaster integriceps* Puton, 1881 (Scutelleridae), *Gonocerus acuteangulatus* (Goeze, 1778) (Coreidae) (Mineo 1979a,b, Kononova & Kozlov 2008) and *P. laciniata* (Coreidae) (new host record added here). *Gryon monspeliense* seems to be a fairly rare but constant member of the egg-parasitoid guild of *P. laciniata* in northeastern Spanish study sites (Table 1). *Phyllomorpha laciniata* is probably not the main host of this species.

### 3.3. *Telenomus* (*Telenomus*) sp. (Hymenoptera: Scelionidae: Telenominae)

Material examined:

- 1♂ + 1♀ Coll del Frare 26.V.2006

We used the revision of the subfamily Telenominae by Kozlov and Kononova (1983) in our attempt to identify this species. Although it is evident that it belongs to the species-rich subgenus *Telenomus* of the genus *Telenomus* Haliday, 1833, this species did not fit the description of any

species in the revision used. Hence, for the time being, we refer to it as an unidentified species in the genus *Telenomus*. In any case, and in spite of the vagueness of our identification, we note that this is the first record of this subfamily as parasitoids of *P. laciniata*.

### 3.4. *Ooencyrtus telenomicida* (Vassiliev, 1904) (Hymenoptera: Encyrtidae)

Material examined:

- 1♂ + 1♀ without label data (det. M. Koponen; the remaining material: det. GV)
- 5♂ + 5♀ El Puerto 1.–10.V.2004
- 1♂ + 1♀ El Puerto 20.V.2004
- 1♂ El Puerto 2.–15.V.2005
- 1♂ + 1♀ hatched from a single host egg, Cap de Ras 28.V.2005
- 1♂ + 3♀ (hatched) + 1 pharate ♀ inside host egg, Cap de Ras 11.V.2006
- 7♀ + 1 pupa Cap de Ras 25.V.2007
- 1♂ Cap de Ras 01.VI.2007
- 1♂ Cap de Ras 08.VI.2007
- 2♂ + 2♀ Cap de Ras 15.VI.2008
- 1♀ + 2♂ (hatched) + 1♂ inside host egg + 1 pharate adult inside host egg, Carrabiners 2008
- 4♂ + 16♀, (specimens without label data) 2008

This species has a vast distribution area from Germany in the north to Syria and Iran in the south, and from Spain, Portugal and Morocco in the west to eastern China in the east (Noyes 2001, Zhang *et al.* 2005). *Ooencyrtus telenomicida* has a very wide host range composed of many species in mainly heteropteran (Coreidae: 6 spp., Pentatomidae: 18 spp., Pyrrhocoridae: 1 sp., Reduviidae: 1 sp., Scutelleridae: 3 spp.) and lepidopteran (1 sp. in each: Lasiocampidae, Lymantriidae, Noctuidae, Papilionidae and Sphingidae) families (Noyes 2010). *Phyllomorpha laciniata* is a new coreid host for this species. There are also a few records of primary egg-parasitoid hosts of *O. telenomicida* in the hymenopteran genera *Trisolcus* Ashmead and *Telenomus* Haliday (Scelionidae: Telenominae: Telenomini) (Noyes 2001).

#### 4. Interaction between parasitoids

According to the literature (see Noyes 2001 and references therein), *O. telenomicida* is a primary egg parasitoid or a (facultative) hyperparasitoid. This species was abundant in both the southern and the northeastern study areas and it frequently coexisted with *G. bolivari* (Table 1). As we have no direct observations of parasitism of *G. bolivari* by *O. telenomicida*, the nature of their interaction might be competition over eggs of *P. laciniata*, hyperparasitism, or both.

Unlike the scelionid parasitoids of *P. laciniata* eggs, which developed as solitary parasitoids, eggs attacked by *O. telenomicida* sometimes produced two adult parasitoids (see section 3.4.) that were smaller than their solitary conspecifics. Moreover, all *P. laciniata* eggs hosting *O. telenomicida* contained numerous undeveloped eggs. A potential explanation for this phenomenon is superparasitism by (different female individuals of) *O. telenomicida*. An alternative mechanism, i.e. oviposition of several eggs by a single female parasitoid, is known from several koinobiont larval endoparasitoids (see Godfray 1994 for a review). Such behaviour might be favoured by selection as it may exhaust the cellular immune response of the host. However, in idiobiont parasitoids such as *O. telenomicida*, laying several eggs in a single host egg probably would not be similarly beneficial. Nonetheless, at present we have no means to validate either of the two alternative hypotheses.

Gregarious development is widely known to occur in *Ooencyrtus* species. For instance, *O. nezarae* Ishii, 1928 has been reported to parasitize four species of phytophagous bugs in Japan and to develop as a gregarious parasitoid in one of them (Mizutani *et al.* 1996). This parasitoid is usually solitary in a small host but gregarious in a large host (Takasu & Hirose 1991), suggesting that the size of progeny depends on both host size and the outcome of competition following superparasitism. Superparasitism is in fact very common in *O. nezarae* (e.g. Takasu & Hirose 1991). In a similar host-parasitoid system found in Venezuela (Conde & Rabinovich 1979), consisting of eggs of the reduviid bug *Rhodnius prolixus* Stål, 1859 and their parasitoids *Teleonomus costalimai* Ortiz & Alvarez, 1959 and

*Ooencyrtus venatorius* De Santis & Vidal Sarmiento, 1976, *O. venatorius* was a generally more successful competitor than *T. costalimai* after nearly simultaneous oviposition by the two parasitoid species. Another example of a host-multiparasitoid community engaging *Ooencyrtus* was studied in California (e.g. Amarasekare 2003). In that system, *Trissolcus murgantiae* Ashmead, 1893 and *Ooencyrtus johnstonii* (Howard, 1898) both attack the eggs of the pentatomid harlequin bug *Murgantia histrionica* (Hahn, 1834). *Ooencyrtus johnstonii* is a gregarious and superparasitic species competing with the solitary *T. murgantiae* for host eggs, and the latter parasitoid is superior in this exploitative competition. It has also been shown that interaction between these coexisting parasitoid species dampens host population fluctuations (Amarasekare 2003).

#### 5. Interaction between *P. laciniata* and its egg parasitoids

It is important to underline the evolutionary-ecological significance of our new rearing records from the viewpoints of both the host and the parasitoid species. Parasitoids act as selective pressure on their hosts. As a result, new adaptations may arise in the host species in order to minimize the risk of parasitism. It has been suggested that oviposition on conspecifics in *P. laciniata* may represent a strategy to reduce predation and parasitism of the eggs (Kaitala 1996, Reguera & Gomendio 2002, Carrasco *et al.* 2007, Gomendio *et al.* 2008, Carrasco & Kaitala 2009, Carrasco & Kaitala 2010). The new parasitoid records reported in this study increase markedly the diversity of parasitoid species found to be associated with *P. laciniata* eggs. These results give further support to the hypothesis that egg parasitoids play an important role in the oviposition strategy of *P. laciniata* females, and may help to explain the evolution of such unusual behaviour. Nevertheless, additional investigations should be conducted to test this hypothesis. For instance, there is a need to assess the incidence of individual parasitoid species in *P. laciniata* eggs in various populations. It may be interesting to study further (see Gomendio *et al.* 2008) the relationship be-

tween the incidence of egg-parasitism and the oviposition strategy of *P. laciniata* among populations, especially those in which female egg-laying behaviour differs from ovipositing primarily on conspecifics (e.g. Kaitala 1996, Reguera & Gomendio 2002, D. Carrasco, S. Kivelä & A. Kaitala unpubl.) by ovipositing mostly on plants and other substrates (e.g. Mineo 1984, D. Carrasco, L. Härkönen & A. Kaitala unpubl.).

A previous study shows that *P. laciniata* individuals counteract most of the attempts of *G. bolivari* to approach the eggs they carry (Carrasco & Kaitala 2010). The authors suggest that the mere fact of egg carrying and the behavioural responses bugs display against parasitoids may considerably decrease the rate of successful egg parasitization and increase the length of the parasitoid's host location process. Thus, as the time cost in parasitizing the eggs carried by bugs may be higher compared to eggs deposited on plants (or eggs of other species), the benefit to the idiobiont parasitoid species reported in this study (particularly *G. bolivari*, *G. monspeliense* and *O. telenomicida*) that parasitize eggs carried on *P. laciniata* remains unclear. Further studies on this host-multiparasitoid system should investigate: (i) the host location mechanism of each parasitoid species; (ii) the interaction between coexisting parasitoid species; and (iii) whether these parasitoids gain some fitness benefit, such as reduced predation or reduced superparasitism and/or hyperparasitism, by exploiting the egg-carrying and defensive behaviour of adult *P. laciniata*.

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