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Natural enemies of the South American moth, *Tuta absoluta*, in Europe, North Africa and Middle-East, and their potential use in pest control strategies

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1 **Abstract**

2 The South American tomato leaf miner, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), is an
3 invasive Neotropical pest. After its first detection in Europe it rapidly invaded more than 30
4 Western Palaearctic countries becoming a serious agricultural threat to tomato production in both
5 protected and open field crops. Among the pest control tactics against exotic pests, biological
6 control using indigenous natural enemies is one of the most promising. Here, available data on the
7 Afro-Eurasian natural enemies of *T. absoluta* are compiled. Then, their potential for inclusion in
8 sustainable pest control packages is discussed providing relevant examples. Collections were
9 conducted in 12 countries, both in open field and protected susceptible crops, as well as in wild
10 flora and/or using infested sentinel plants. More than seventy arthropod species, 20% predators and
11 80% parasitoids, were recorded attacking the new pest so far. Among the recovered indigenous
12 natural enemies only few parasitoid species, namely some eulophid and braconid wasps, and
13 especially mirid predators have promising potential to be included in effective and environmentally-
14 friendly management strategies of the pest in the newly invaded areas. Finally, a brief outlook of the
15 future researches and applications of indigenous *T. absoluta* biological control agents is provided.

16

17 **Keywords:** Biological control, Generalist predators, Integrated Pest Management, Invasive species,
18 Parasitoid community, Western Palaearctic

19

20 **Introduction**

21 The composition of worldwide biotic communities has greatly changed in recent years due to the
22 collapse of natural barriers to wild species movements mainly in relation to human activities
23 (Liebhold and Tobin 2008). Among the newly-introduced insect species some can become invasive,
24 with subsequent significant economic impacts. The success or failure of a biological invasion may
25 depend on the species' life history parameters, on its response to climatic conditions, on the
26 competition with native species and on the impact of natural enemies (Grabenweger et al. 2010).
27 This last factor may be crucial in the invasion mechanism and the success of an invader, in terms of
28 distribution and abundance, could be related to the absence or low efficacy of natural control in the
29 new territories, as stated by the so called *Enemy Release Hypothesis* (Keane and Crawley 2002).
30 Indeed, it is assumed that natural enemies in the newly invaded areas need time to get adapted and
31 to control the exotic species effectively. This may be due to the fact that native antagonists need to
32 adjust their behaviour and/or physiology to be able to successfully develop on the exotic prey/host.
33 For these reasons natural enemy complexes on invaders may perform initially low percentage
34 predation/parasitism (Cornell and Hawkins 1993). However, several examples of successful
35 biological control using natural enemies that have not coevolved with the pest, the so called *New*
36 *species association*, are also known (Hokkanen and Pimentel 1984; O'Connell et al. 2012).

37 In this framework, gaining knowledge on indigenous natural enemies that get adapted to the
38 new hosts and understanding their role in limiting the alien species is essential for establishing the
39 basis of suitable and sustainable control strategies of exotic pests. This applies also to one of the
40 latest invasive species arrived in the Western Palaearctic region: the South American tomato leaf
41 miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). This moth is a Neotropical species and
42 is considered a key pest of tomato in South America (Guedes and Picanço 2012; Luna et al. 2012)
43 where it remained confined until its first record in Western Palaearctic, in Spain in 2006 (Desneux

44 et al. 2010; Tropea Garzia et al. 2012). Afterwards, it rapidly spread throughout the Mediterranean
45 basin, in Europe, North Africa and Middle East (Desneux et al. 2011). *Tuta absoluta* is considered a
46 typical invasive species because of its capacity to develop very quickly on tomato cultivations and
47 to spread rapidly in new areas causing economically relevant damage (Desneux et al. 2010;
48 Caparros Megido et al. 2012).

49 Although chemical control has been the first strategy adopted in the newly invaded areas,
50 alternative control measures are being investigated (Cagnotti et al. 2012; Cocco et al. 2013) in
51 compliance with the EU Directive on sustainable use of pesticides (Directive 2009/128/EC). In the
52 case of *T. absoluta* the need for alternative control methods is strengthened by the development of
53 resistance to insecticides by the pest (Haddi et al. 2012; Gontijo et al. 2013), as well as to the side
54 effects of pesticides on beneficial arthropods (Arnó and Gabarra 2011; Biondi et al. 2012, 2013a;
55 and see Desneux et al. 2007 for a thorough review).

56 On the other hand, various predators and parasitoids spontaneously attack *T. absoluta* in
57 tomato crops in Europe and in North Africa. Some of these, mainly native Miridae, have been
58 already employed in Integrated Pest Management (IPM) strategies (Castañé et al. 2011; Mollá et al.
59 2011; Cabello et al. 2012; Zappalà et al. 2012b; Chailleux et al. 2013a). However, several
60 screenings for effective natural enemy species in the invaded area are still ongoing (Chailleux et al.
61 2012; Gabarra et al. 2013). More than seventy species of generalist natural enemies have been
62 reported developing on *T. absoluta* in the Western Palaearctic region so far. These have been
63 sampled both on open field and protected susceptible crops as well as on wild flora and/or using
64 infested sentinel plants. Here we take into account all the available data, aiming at giving a
65 comprehensive picture of the composition of the species that spontaneously provide biological
66 control services and their current role in *T. absoluta* control programmes.

67

68

69 **Predators**

70 Fifteen arthropod species were recorded preying on the South American tomato leafminer in the last
71 few years in newly invaded Western Palaearctic countries (Table 1). They mainly belong to the
72 order Hemiptera (ten species) and in particular to the families Miridae, Anthocoridae and Nabidae
73 in descending order of species numbers. These predators include zoophytophagous bugs that
74 usually colonize and establish in organic and IPM crops where they are also able to build up their
75 populations before pest arrival, exploiting alternative preys, such as whiteflies, thrips, aphids, spider
76 mites, leafminers as well as other Lepidoptera, and host plants (e.g. *Dittrichia viscosa* (L.) and
77 *Solanum nigrum* (L.)) as alternative food sources (Perdikis et al. 2007; Desneux and O'Neil 2008;
78 Ingegno et al. 2008).

79 The most widely spread species are mirids belonging to the tribe Dicyphini, with
80 *Nesidiocoris tenuis* (Reuter) spontaneously recovered in eleven countries almost all year round both
81 in protected and open field tomato crops, and *Macrolophus pygmaeus* (Rambur) which was
82 observed preying on *T. absoluta* eggs and young instar larvae in three countries. Guenaoui et al.
83 (2011a) reported *M. caliginosus* Wagner as a predator of *T. absoluta* on tomato in Algeria.
84 However, considering the great number of misconceptions comprised in the classification history of
85 this species [= *M. melanotoma* (Costa)] and in agreement with the most recent taxonomical
86 reconsiderations (Martinez-Cascales et al. 2006; Castañé et al. 2013), also this record is likely to
87 refer to *M. pygmaeus*; therefore, it was included accordingly in table 1. Other four Dicyphini
88 species [*Dicyphus* sp., *D. errans* (Wolff), *D. maroccanus* Wagner and *D. tamanini* Wagner] were
89 sampled from infested tomato plants in Algeria, France, Italy and Spain (Table 1). Anthocorids
90 belonging to the *Orius* genus were found in open field and protected tomato crops infested by *T.*
91 *absoluta* in Jordan. Species of the *Nabis* genus were occasionally found in Iran and Spain. In
92 addition, lacewings belonging to the *Chrysoperla carnea* species group were found feeding on *T.*
93 *absoluta* in open field tomato and two species of predatory mites [*Amblyseius swirskii* Athias-

94 Henriot and *A. cucumeris* (Oudemans)] were also reported from the moth eggs and first instar larvae
95 in Spain. The ant *Tapinoma nigerrimum* (Nylander) (Hymenoptera: Formicidae) was found in
96 Algeria preying on *T. absoluta* larvae. One unidentified species of Hymenoptera Sphecidae was
97 recovered in Spain feeding on larval instars of the moth (Table 1).

98

99

100 **Parasitoids**

101 A quite large number of parasitoid species (more than 50) was recorded developing on all the young
102 instars and eggs of the moth in the newly invaded areas (Table 2). Overall, the most abundant
103 parasitoid family was the Eulophidae one with 28 recovered species. *Neochrysocharis formosa*
104 (Westwood) [= *Closterocerus formosus* (Westwood)] was one of the most widely spread, being
105 found in four countries (Algeria, France, Italy, Spain). So far, this is the only species recorded on
106 *T. absoluta* both in Europe and in South America, where it was mentioned as a potential biocontrol
107 agent based on its wide host range (Noyes 2013) and presence in other crops, with parasitism rates
108 on *T. absoluta* ranging between 1.5 and 11.2% (Luna et al. 2011). *Closterocerus clarus* (Szelenyi)
109 was recovered on *T. absoluta* young larvae in Turkey. Six species belonging to the genus
110 *Necremnus* were found developing on *T. absoluta* in Algeria, Egypt, France, Italy, Spain and
111 Tunisia, including two entities that were identified as *N. sp. near artynes* and *N. sp. near tidius*.
112 *Necremnus artynes* was the most abundant species in Northwestern Algeria (Guenaoui et al.
113 2011b). Urbaneja et al. (2012) found *N. metalarus* (Walker), developing on *T. absoluta*-infested
114 tomato plants in Spain. However, the taxonomy of this genus is currently under revision, therefore
115 most of these records may need to be verified (Ferracini et al. 2012a; Zappalà et al. 2012a). Besides,
116 other aspects of their biology and ecology should be also further investigated. The ectoparasitoids
117 of Diptera, Lepidoptera and Coleoptera leafminer larvae, *Pnigalio incompletus* (Bouček) and *P.*
118 *cristatus* (Ratzeburg), often associated due to their shared hosts (Noyes 2013), emerged from *T.*

119 *absoluta* larvae both in Italy and in Turkey. Wasps identified as *P. soemius* or belonging to *P.*
120 *soemius* species complex were recovered in Italy and in Spain (Table 2). This is a Palaearctic
121 complex of generalist parasitoids, with an intense predatory behaviour both as larva and adult
122 (Bernardo et al. 2006). *Stenomesus* near *japonicus* was recovered in France and in the North East
123 of Spain on *T. absoluta* 2nd and 3rd instar larvae and an unidentified species belonging to the same
124 genus was found in Algeria. Two species belonging to the genus *Elasmus* were recorded on *T.*
125 *absoluta*; one, which was not identified at the species level, was found in Italy while *Elasmus*
126 *phthorimaeae* Ferrière was recorded in Eastern Spain (Table 2). Specimens of *Sympiesis* sp. near
127 *flavopicta* and of *Hemiptarsenus ornatus* (Nees) emerged from larvae collected in open field tomato
128 crops in Israel. Another *Hemiptarsenus* species, *H. zilahisebessi* Erdős, and *Diglyphus isaea*
129 (Walker) were found in association with *T. absoluta* in Algeria. The larval parasitoid *Diglyphus*
130 *crassinervis* Erdős was recorded on *T. absoluta* only in Spain. Specimens classified as belonging to
131 the *Elachertus inunctus* species group emerged from artificially infested sentinel plants in Italy;
132 wasps identified as *Baryscapus bruchophagi* (Gahan) were found in Turkey. Finally, five other
133 eulophid species, not identified at the species level (*Chrysocharis* sp., *Cirrospilus* sp., *Diglyphus*
134 sp., *Elachertus* sp. and *Sympiesis* sp.), were also found parasitizing spontaneously the new host (see
135 Table 2 for details).

136 Almost 30% of the recovered species were Ichneumonoidea, more precisely six species
137 belonged to the family Ichneumonidae and the remaining fourteen to the family Braconidae. Among
138 the six ichneumonids, those belonging to the *Diadegma* genus [*Diadegma* sp., *D. ledicola*
139 Horstmann and *D. pulchripes* (Kokujev)] were found parasitizing *T. absoluta* mature larvae and
140 pupae in Italy. The other three ichneumonid wasps, *Hyposoter didymator* (Thunberg), *Temelucha*
141 *anatolica* (Sedivy) and *Zoophthorus macrops* Bordera & Horstmann, were recorded only in one
142 country, Algeria and Spain respectively, on unspecified host instar stage. Among braconid wasps,
143 some species were found on wild flora, namely *Solanum nigrum*, i.e. *Agathis fuscipennis*

144 Zetterstedt, recovered in Italy, and *Apanteles* sp., *Chelonus* sp., *Choeras semele* (Nixon),
145 *Dolichogenidea litae* (Nixon) and *Diolcogaster* sp., recorded in Spain (Table 2). *Bracon* species
146 were already reported as *T. absoluta* parasitoids in the pest native areas (Desneux et al. 2010) and
147 several species belonging to this genus were found developing on the exotic pest in the newly
148 invaded areas. Some of these were found in various countries, such as *B. hebetor* Say, a worldwide
149 distributed and very polyphagous species (Yu & van Achterberg, 2010), which was recovered on *T.*
150 *absoluta* in Algeria, Israel, Italy and Turkey. The Palaearctic species *B. nigricans* (Szépligeti) was
151 recorded parasitizing *T. absoluta* mature larvae in France, Israel (where it was reported as *B.* near
152 *nigricans*), Italy, Jordan and Spain. Whereas, *B. osculator* (Nees) and *B. didemie* Beyarslan were
153 found only in Italy and in Turkey, respectively. Two braconid wasps, not identified at the species
154 level, *Agathis* sp. and *Bracon* sp., emerged from parasitized larvae collected in Italy and Tunisia.
155 However, some of these records should be verified, evaluating the suitability of *T. absoluta* as host
156 for the reported parasitoids. Indeed, many ichneumonid species are known to develop on noctuid
157 tomato pests, therefore if sampling was not carefully conducted the record can be related to a co-
158 infestation of the crop by *T. absoluta* and noctuids.

159 Two pteromalid species, *Halticoptera aenea* (Walker), *Pteromalus intermedius* (Walker) and
160 *Pteromalus semotus* (Walker), were found developing on the moth larvae in Italy, Turkey and Spain
161 respectively. Moreover, two species of chalcidid wasps, *Brachymeria secundaria* (Ruschka) and
162 *Hockeria unicolor* Walker, were associated with *T. absoluta* in Turkey. *Tuta absoluta* eggs were
163 parasitized spontaneously by *Trichogramma achaeae* Nagaraja & Nagarkatti in France, by
164 *Trichogramma bourarachae* Pintureau & Babault in Tunisia and by various other unidentified
165 *Trichogramma* species in Algeria, Egypt, France, Iran and Spain (Table 2). In South America more
166 than 12 species of Trichogrammatidae, four Encyrtidae and one Eupelmidae gen. sp. were reported
167 as *T. absoluta* egg parasitoids (Desneux et al. 2010). This higher richness may be due to climatic
168 factors as well as to a more intensive monitoring of egg parasitism in *T. absoluta* native region

169 where many biological control programs have been performed using egg parasitoids (Guedes and
170 Picanço 2012; Parra and Zucchi, 2004).

171

172 **Potential for use of indigenous natural enemies**

173 Studies have been carried out under laboratory conditions to assess the suitability of *T. absoluta* for
174 various predator and parasitoid species. The seminal studies of Urbaneja et al. (2009) and Arnó et
175 al. (2009) reported that *N. tenuis* and *M. pygmaeus* adults do actively feed on eggs (up to $\sim 60 \text{ day}^{-1}$)
176 and young larvae ($\sim 2 \text{ day}^{-1}$) of the moth. These results were confirmed in larger scales (greenhouse)
177 experiments (Mollá et al. 2011 and Bompard et al. 2013 for *N. tenuis* and *M. pygmaeus*,
178 respectively). Similar results were obtained in the laboratory by Guenaoui et al. (2011a) with *N.*
179 *tenuis* and *M. caliginosus*, by Cabello et al. (2009) studying *N. pseudoferus ibericus*, by Arnó et al.
180 (unpublished data) for the bugs *D. tamaninii*, *O. majusculus* and *O. laevigatus*, as well as by
181 Ferracini et al. (2012b) for *D. errans*.

182 Other studies were aimed to assess the development of mirid species when feeding on the new
183 prey (Mollá et al. 2014) and the biology and behaviour of parasitoid species on *T. absoluta*. In the
184 case of parasitoids it clearly emerged that under laboratory conditions *N. sp. near artynes*, *N. sp.*
185 *near tidius* and *B. nigricans* were able to reduce significantly *T. absoluta* populations not only
186 owing to the parasitism activity but also thanks to a non reproductive host-killing activity, namely
187 host feeding and host stinging behaviours (Ferracini et al. 2012a; Biondi et al. 2013c).

188 Beside the *environmental resistance* that all the recovered fortuitous natural enemies can
189 spontaneously offer in realistic field conditions, there are several approaches that can be artificially
190 implemented to enhance their role in regulating pest populations. Indeed, these indigenous natural
191 enemies can be *inoculated*, *augmented* and *conserved* in the cultivated environment. Inoculation of
192 mass reared *N. tenuis* has been successfully applied in tomato nurseries for the early installation of
193 the predator population in the young crop (Calvo et al. 2012), or directly in greenhouse with the

194 concomitant application of microbial pesticides (Desneux et al. 2010; Mollá et al. 2011). By
195 contrast, although this generalist predator, as well as *M. pygmaeus*, has been largely employed in
196 biological and integrated *T. absoluta* control programs with contrasting results (Arnó et al. 2009;
197 Abbes and Chermiti 2012; Nannini et al. 2012; Trottin-Caudal et al. 2012), it often prompts
198 insecticide applications at high densities due to damages caused to plants and fruits (e.g. Calvo et al.
199 2009; Arnó et al. 2010; Castañé et al. 2011). On the other hand, *M. pygmaeus* has been recently
200 proved not able to build up its populations when feeding only on this prey (Mollà et al. 2014). Thus,
201 higher levels of prey species diversity, such as the concomitant infestations of whiteflies (Bompard
202 et al. 2013), are required for effective inoculative applications of this predator species.

203 Commercially available *T. acheae* individuals are now used against *T. absoluta* by periodic
204 inundative releases (50 adults/m²) in commercial greenhouse successfully (Cabello et al. 2012;
205 Trottin-Caudal et al. 2012). Whereas, similar control levels can be achieved by combining lower
206 release rate of this egg parasitoid with mirid predators, i.e. *M. pygmaeus* and *N. tenuis* (Calvo et al.
207 2012; Chailleux et al. 2013a; 2013b). Fairly good control was obtained in Southern Spain with
208 multiple releases of *N. artynes*, although the reduction was not enough to limit fruit damage to the
209 level reached by *N. tenuis* when released in the nursery (Calvo et al. 2012; Urbaneja et al., 2012).

210 Finally, the data so far obtained by laboratory bioassays, as well as through various researches
211 conducted in open field and protected tomato crops in the Western Palaearctic area suggest that the
212 potentially effective indigenous antagonist species in *T. absoluta* control are the predators
213 *M. pygmaeus* and *N. tenuis*, as well as the parasitoids *T. acheae*, *N. sp. near artynes*, *N. formosa*, *S.*
214 *cf. japonicus* and *B. nigricans*. The applications of these indigenous organisms, individually and in
215 association, should be further increased via conservation and augmentation strategies.

216

217

218 **Future outlooks**

219 Several entomophagous species recovered on *T. absoluta*, such as *Dicyphus* spp., *Diadegma* spp.,
220 *Bracon* spp., *Necremnus* spp., *N. formosa*, have been recorded in the past as widely spread on
221 tomato crops also in those countries where they were not yet found in association with *T. absoluta*
222 (Kerzhner and Josifov 1999; Yu and Van Achterberg 2010; Noyes 2013). Thus, most likely these
223 species will be found associated to *T. absoluta* in other countries very soon, as expected in Iran
224 (Baniameri and Cheraghian 2012). For this reason, further surveys in areas with still few records of
225 *T. absoluta* natural enemies are encouraged. On the other hand, all the records of *T. absoluta*
226 predator species obtained so far derive from direct field observation and samplings, and from
227 experimental laboratory bioassays, while no studies have been conducted using newly-developed
228 analytical techniques, such as the predator gut content molecular analysis (King et al. 2008; Juen et
229 al. 2012). Indeed, these tools may be very useful to get an exhaustive assessment of the arthropod
230 fauna which actually preys on new invasive pests (Harwood et al. 2007).

231 Further applied aspects of the biology and ecology of the natural enemies species already
232 identified as potential key natural enemies species should be further investigated. These are for
233 example: their potential for mass rearing (Canale and Benelli 2012, Cicero et al. 2012), dispersal
234 capacity (Tabone et al., 2012; Zappalà et al. 2012c), functional response to host densities (Madadi
235 et al. 2011, Savino et al. 2012), foraging and host searching behaviours (Gontijo et al. 2012,
236 Ramirez-Romero et al. 2012). This is particularly needed for those species groups with an uncertain
237 taxonomy (namely *Necremnus*, *Bracon* and *Trichogramma* spp.), since different biological and
238 ecological traits can be highlighted among different parasitoid cryptic species (Heimpel et al. 1997;
239 Desneux et al. 2009b). Furthermore, in order to set up potential commercial mass rearing and/or to
240 commercialize natural enemies throughout different countries, their taxonomy should be
241 definitively clarified (Gordh and Bearsley, 1999; Stouthamer, 2008).

242 In order to reduce the cost of multiple egg parasitoid releases (Cabello et al. 2012) and/or
243 plant damage of the released omnivorous predators (Castañé et al. 2011), further studies aimed at

244 setting economically sound mass rearing protocols of other indigenous natural enemies are to be
245 developed. This should be aimed at rearing entomophagous species having the least secondary
246 effects on the plants (phytophagy) as well as minimum potential for intraguild predation on other
247 beneficials present in the crop.

248 The overall increase of knowledge on the indigenous natural enemy complex would help all
249 habitat management strategies. These should be aimed at increasing the functional biodiversity
250 within the crop and within the farm, such as rational weed management for increasing food and
251 alternative preys/hosts for indigenous predators and parasitoids (Gardiner et al. 2009; Balzan and
252 Wäckers 2013; Tena et al. 2013). The increase in the abundance and diversity of the natural enemy
253 community could be also obtained through the use of the *banker plants* technique (Parolin et al.
254 2012a; 2012b). Actually, the first banker plant system was developed in greenhouse tomatoes using
255 tomato plants both as crop and banker plants (Stacey 1977). However, this made pest control harder
256 and resulted in reduced application of the technique by the growers. Since then this technique has
257 been successfully tested in tomato crops using non-crop banker plants for various pest-natural
258 enemies systems (Lambert et al. 2005; Xiao et al. 2011).

259 To fully exploit this strategy for *T. absoluta* control, increasing knowledge on the prey/host
260 range of its generalist entomophagous species is crucial (Ingegno et al. 2011; Desneux et al. 2009a;
261 2012). Indeed, the potential applications to enhance the natural enemies populations in the crop
262 could be numerous. In our case, an example is the installation or conservation in the tomato crop of
263 *Parietaria officinalis* L. plants infested by *Cosmopterix pulchrimella* Chambers (Lepidoptera:
264 Cosmopterigidae), that is an alternative host of *N. artynes* (Ferracini et al. 2012a). Another source
265 of *T. absoluta* antagonists could be represented by the proximity of potato plants infested by the
266 potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), which is often
267 attacked both by the endoparasitoid *D. pulchripes* and by the ectoparasitoid *B. nigricans* (Yu and
268 Van Actherberg 2010). However, although increasing the “right diversity” (Landis et al. 2000) has

269 been proved to reduce pest pressure effectively and to enhance natural enemy activity,
270 *P. operculella* is a serious potato pest and this application should be carefully evaluated before
271 being implemented. An important role may be played also by *Dittrichia viscosa* which is already
272 reported as a refuge plant for several predatory bugs that do move to tomato crops providing
273 important biological control services (Perdikis et al. 2007; 2011). However, as recently highlighted
274 by Castañé et al. (2013) for *Macrolophus* spp., a clarification in the taxonomy of the species related
275 to tomato is strongly needed for effective applications.

276

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Table 1. Predators observed feeding on *Tuta absoluta* in Western Palaearctic countries.

Order Family	Species	Known distribution ¹	<i>T. absoluta</i> instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Mesostigmata: Phytoseiidae	<i>Amblyseius swirskii</i> Athias - Henriot	Western Palaearctic	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. 2010
	<i>Amblyseius cucumeris</i> (Oudemans)	Cosmopolitan	Eggs and L1	Spain	Protected crop (eggplant) sampling	Summer	Mollá et al. 2010
Hemiptera: Miridae	<i>Dicyphus</i> sp.		Eggs and young larvae	France, Italy	Open field and protected crop sampling	Summer	Biondi et al. 2013b, Zappalà et al. unpublished data
	<i>Dicyphus errans</i> (Wolff)	Western Palaearctic	Eggs and L1	Algeria, Italy	Open field and protected crop sampling	Spring-autumn in the open field; all year round in greenhouses	Boualem et al. 2012, Ferracini et al. 2012b, Ingegno et al. 2013
	<i>Dicyphus maroccanus</i> Wagner	Mediterranean basin	Eggs and young larvae	Spain	Open field and protected crop sampling	Summer	Mollá et al. 2010
	<i>Dicyphus tamaninii</i> Wagner	Western Palaearctic	Eggs and young larvae	Algeria	Not specified	Not specified	Guenaoui et al. 2011a
	<i>Macrolophus pygmaeus</i> (Rambur)	Western Palaearctic	Eggs and young larvae	Algeria, France, Italy, Spain	Open field and protected crop sampling	Spring, summer, autumn	Arnò et al. 2009, Mollá et al. 2010, Guenaoui et al. 2011a, Boualem et al. 2012, Biondi et al. 2013b, Ingegno et al. 2013
	<i>Nesidiocoris tenuis</i> (= <i>Cyrtopeltis tenuis</i>) (Reuter)	Cosmopolitan	Eggs and young larvae	Algeria, Cyprus, Egypt, France, Jordan, Iran, Israel, Italy, Morocco, Spain, Turkey	Open field and protected crop sampling	Spring, summer, autumn, winter	Arnò et al. 2009, Guenaoui et al. 2011a, Karabuyuk, 2011, Rizzo et al. 2011, Al-Jboory et al. 2012, Boualem et al. 2012, El-Arnauty and Kortam 2012, Biondi et al. 2013b, R. Bouharroud pers. comm., Kiliç pers. comm., Martinou and Stavrinides unpublished data, Shaltiel-Harpaz and Gerling unpublished data
Hemiptera: Anthocoridae	<i>Orius</i> sp.		Not specified	Jordan	Open field and protected crop sampling	January-April	Al-Jboory et al. 2012
	<i>Orius albidipennis</i> (Reuter)	South Europe, North Africa and Asia	Not specified	Jordan	Open field and protected crop sampling	January-April	Al-Jboory et al. 2012
Hemiptera: Nabidae	<i>Nabis</i> sp.		Eggs and young larvae	Iran	Open field crop sampling	Summer	H. Madadi pers. comm.
	<i>Nabis pseudoferus ibericus</i>	Western Palaearctic	Not specified	Spain	Not specified	Not specified	Mollá et al. 2010
Neuroptera: Chrysopidae	<i>Chrysoperla carnea</i> species group		Not specified	Egypt	Open field crop sampling	Not specified	El-Arnauty unpublished data
Hymenoptera: Sphecidae	Undetermined species		Larvae	Spain	Not specified	Not specified	Mollá et al. 2008
Hymenoptera: Formicidae	<i>Tapinoma nigerrimum</i> (Nylander)	Western Palaearctic	Larvae	Algeria	Open field and protected crops	Summer	Guenaoui et al. 2011b

570 ¹Kerzhner and Josifov 1999

572 **Table 2.** Parasitoids recovered on *Tuta absoluta* in Western Palaearctic countries.

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Order/Family	Species	Known distribution ²	T. absoluta instars	Country(ies)	Sampling method(s)	Season(s)	Reference(s)
Hymenoptera: Ichneumonidae	<i>Diadegma</i> sp.		Mature larvae-pupae	Italy	Open field crop sampling	Autumn	Zappalà et al. 2012a
	<i>Diadegma ledicola</i> Horstmann	Western Palaearctic	Mature larvae-pupae	Italy	Open field crop sampling	Summer, autumn	Ferracini et al. 2012a
	<i>Diadegma pulchripes</i> (Kokujev)	Palaearctic	Mature larvae-pupae	Italy	Open field (potato) crop sampling, sentinel infested plant	Summer, autumn	Zappalà et al. 2012a
	<i>Hyposoter didymator</i> (Thunberg)	Australasian, Western Palaearctic	Not specified	Algeria	Protected crop sampling	Spring	Boualem et al. 2012
	<i>Temelucha anatolica</i> (Sedivy)	Palaearctic	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
	<i>Zoophthorus macrops</i> Bordera & Horstmann	Spain	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
Hymenoptera: Braconidae	<i>Agathis</i> sp.		Larvae not specified	Italy	Open field crop sampling	Summer	Ferracini et al. 2012a
	<i>Agathis fuscipennis</i> Zetterstedt	Western Palaearctic		Italy	Open field sampling of infested <i>Solanum nigrum</i>	September - October	Loni et al. 2011
	<i>Apanteles</i> sp.		Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Bracon</i> sp.		Mature larvae	Tunisia	Sentinel infested plants exposure	Spring, summer	Abbes et al. 2013
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>didemie</i> Beyarslan	Turkey	Mature larvae	Turkey	Open field and protected crop sampling	Spring	Doganlar and Yigit 2011
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>hebetor</i> Say	Cosmopolitan	Mature larvae	Algeria, Israel, Italy, Turkey	Open field and protected crop sampling	Spring, Summer	Doganlar and Yigit 2011, Ferracini et al. 2012a, Guenaoui and Dahliz unpublished data, Shaltiel-Harpaz and Gerling unpublished data
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>nigricans</i> (= <i>concolorans</i> , <i>concolor</i> , <i>mongolicus</i>) Szépligeti	Palaearctic	Mature larvae	Egypt, France, Italy, Jordan, Spain	Open field and protected crop sampling, sentinel infested plants	Spring, Summer	Al-Jboory et al. 2012, Urbaneja et al. 2012, Zappalà et al. 2012, Biondi et al. 2013b, El-Arnaouty unpublished data
	<i>Bracon</i> (= <i>Habrobracon</i>) sp. near <i>nigricans</i>		Mature larvae	Israel, Spain	Open field crop sampling; sentinel infested plants	Spring, Summer	Gabarra and Arnò 2010, Gabarra et al. 2013, Shaltiel-Harpaz and Gerling unpublished data
	<i>Bracon</i> (= <i>Habrobracon</i>) <i>osculator</i> (Nees)	Palaearctic	Mature larvae	Italy	Open field and protected crop sampling, sentinel infested plants	Summer, autumn	Ferracini et al. 2012a, Zappalà et al. 2012
	<i>Chelonus</i> sp.		Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Choeras semele</i> (Nixon)	Western Palaearctic	Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Cotesia</i> sp.		Not specified	Spain	Open field crop	Not specified	Gabarra et al. 2013
	<i>Diolcogaster</i> sp.		Not specified	Spain	<i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Dolichogenidea litae</i> (Nixon)	Western Palaearctic, Afrotropical	Not specified	Spain	Open field crop, sentinel infested plants	Not specified	Gabarra et al. 2013

Hymenoptera: Chalcididae	<i>Brachymeria secundaria</i> (Ruschka)	Turkey	Larvae not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	<i>Hockeria unicolor</i> (Walker)	Turkey	Larvae not specified	Turkey, Spain	Protected crop sampling, sentinel infested plants	Spring	Doganlar and Yigit 2011, Gabarra et al. 2013
Hymenoptera: Eulophidae	<i>Baryscapus bruchophagi</i> (Gahan)	Turkey	Not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	<i>Chrysocharis</i> sp.		Larvae not specified		Protected crop sampling, sentinel infested plants	Spring, summer, autumn	Zappalà et al. 2012a
	<i>Cirrospilus</i> sp.		Larvae not specified	Algeria	Protected crop sampling	Spring	Guenaoui unpublished data
	<i>Closterocerus clarus</i> (Szelenyi)	Turkey	L1	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	<i>Diglyphus</i> sp.		L2	Algeria	Protected crop sampling	Spring	Guenaoui unpublished data
	<i>Diglyphus crassinervis</i> Erdős	Palearctic	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
	<i>Diglyphus isaea</i> (Walker)	Australasian, Nearctic, Palearctic, Oriental	Larvae not specified	Algeria, Spain	Protected crop sampling; uncultivated tomato; sentinel infested plants	Not specified	Boualem et al. 2012, Gabarra et al. 2013
	<i>Elachertus</i> sp.		Larvae not specified	Italy	Sentinel infested plants	Autumn	Zappalà et al. 2012a
	<i>Elachertus imunctus</i> species group		Larvae not specified	Italy	Sentinel infested plants	Spring	Zappalà et al. 2012a
	<i>Elasmus</i> sp.		Larvae not specified	Italy	Open field crop sampling, sentinel infested plants	Summer	Zappalà et al. 2012a
	<i>Elasmus phthorimaeae</i> Ferriere	Western Palearctic	Not specified	Spain	Uncultivated tomato; <i>Solanum nigrum</i>	Not specified	Gabarra et al. 2013
	<i>Hemiptarsenus ornatus</i> (Nees)	Palearctic, Oriental	Larvae not specified	Israel	Open field crop sampling	Not specified	Shaltiel-Harpaz and Gerling unpublished data
	<i>Hemiptarsenus zilahisebessi</i> Erdős	Palearctic	L2	Algeria	Protected crop sampling	Not specified	Guenaoui et al. 2011b
	<i>Necremnus</i> sp.		Larvae not specified	Italy, Spain	Open field crop sampling; sentinel infested plants	Spring	Zappalà et al. 2012, Gabarra et al. 2013
	<i>Necremnus artynes</i> (Walker)	Palearctic and Nearctic	L2-L3	Algeria, Egypt, Spain, France	Open field and protected crop (tomato, eggplant) sampling, <i>Solanum nigrum</i> , sentinel infested plants	Spring, summer	Gabarra and Arnò 2010, Mollà et al. 2010, Delvare et al. 2011, Guenaoui et al. 2011b, Kolai et al. 2011, Rizzo et al. 2011, Boualem et al. 2012, El-Arnaudy unpublished data
	<i>Necremnus</i> near <i>artynes</i>		L1-L2-L3	Italy, France, Tunisia, Spain	Open field and protected crop (tomato, eggplant) sampling, sentinel infested plants, uncultivated tomato, <i>Solanum nigrum</i>	Spring, summer	Ferracini et al. 2012a, Zappalà et al. 2012a, Abbes et al. 2013, Biondi et al. 2013b, Gabarra et al. 2013
<i>Necremnus metalarius</i> Walker	Western Palearctic and Nearctic	L2-L3	Spain	Open field and protected crop sampling	Not specified	Urbaneja et al. 2012	
<i>Necremnus tidius</i> (Walker)	Palearctic and Nearctic	Not specified	Italy	Not specified	Not specified	Riciputi 2011	

(Hymenoptera: Eulophidae)	<i>Necremnus</i> near <i>tidius</i>		L1-L2	Italy	Open field and protected crop sampling	Spring, summer	Ferracini et al. 2012a, Zappalà et al. 2012
	<i>Neochrysocharis</i> sp.			Algeria	Protected crop sampling	Spring	Boualem et al. 2012
	<i>Neochrysocharis</i> <i>formosa</i> (Westwood) (= <i>Closterocerus</i> <i>formosus</i>)	Cosmopolitan	L1-L2-L3	Algeria, France, Italy, Spain	Open field and protected crop sampling; sentinel infested plants, <i>Solanum nigrum</i>	Spring, summer	Lara et al. 2010, Guenaoui et al. 2011b, Ferracini et al. 2012a, Zappalà et al. 2012, Biondi et al. 2013b, Gabarra et al. 2013
	<i>Pnigalio</i> (= <i>Ratzeburgiola</i>) <i>cristatus</i> (Ratzeburg)	Palaeartic	L1-L2	Italy, Spain, Turkey	Open field and protected crop sampling, sentinel infested plant	Spring, summer, autumn	Doganlar and Yigit 2011, Ferracini et al. 2012a, Zappalà et al. 2012a, Gabarra et al. 2013
	<i>Pnigalio</i> sp. <i>soemius</i> complex		L1-L2	Italy	Open field and protected crop sampling	Summer, autumn	Ferracini et al. 2012a, Zappalà et al. 2012
	<i>Pnigalio soemius</i> (Walker)	Palaeartic, Oriental	Not specified	Spain	Open field crop sampling	Not specified	Gabarra et al. 2013
	<i>Pnigalio incompletus</i> (Boucek) (= <i>Ratzeburgiola</i> <i>incompleta</i>)	Western Palaeartic	Not specified	Italy, Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011, Zappalà et al. 2012a
	<i>Stenomiesius</i> sp.		L2- L3	Algeria	Protected crop sampling	Spring	Guenaoui et al. 2011b
	<i>Stenomiesius</i> sp. near <i>japonicus</i>		L2- L3	France, Spain	Open field and protected crop (tomato, eggplant) sampling, sentinel infested plant, <i>Solanum nigrum</i>	Spring, summer	Gabarra and Arnò 2010, Biondi et al. 2013b, Gabarra et al. 2013
<i>Sympiesis</i> sp.		Not specified	Algeria, Italy	Protected crop sampling, sentinel infested plants	Spring	Boualem et al. 2012, Zappalà et al. 2012a	
<i>Sympiesis</i> sp. near <i>flavopicta</i>		Not specified	Israel	Open field crop sampling	Not specified	Shaltiel-Harpaz and Gerling unpublished data	
Hymenoptera: Pteromalidae	<i>Halticoptera aenea</i> (Walker)	Nearctic, Palaeartic	Larvae not specified	Italy	Sentinel infested plants	Spring	Zappalà et al. 2012a
	<i>Pteromalus</i> <i>intermedius</i> (Walker)	Turkey	Larvae not specified	Turkey	Protected crop sampling	Spring	Doganlar and Yigit 2011
	<i>Pteromalus semotus</i> (Walker)	Palaeartic, Nearctic, Oriental, Australasian	Not specified	Spain	Sentinel infested plants	Not specified	Gabarra et al. 2013
Hymenoptera: Trichogrammatidae	<i>Trichogramma</i> spp.		Eggs	Algeria, Egypt, France, Iran, Spain	Protected crop sampling, sentinel infested plants	Spring, summer, autumn	Gabarra and Arnò 2010, Boualem et al. 2012, Zappalà et al. 2012a, Biondi et al. 2013b, Gabarra et al. 2013, El- Arnaouty unpublished data, H. Madadi pers. comm.,
	<i>Trichogramma</i> <i>achaeae</i> Nagaraja & Nagarkatti	Nearctic, Neotropical, Oriental, Palaeartic	Eggs	France	Protected crop sampling	Summer	Biondi et al. 2013b
	<i>Trichogramma</i> <i>bourarachae</i> Pintureau & Babault	Western Palaeartic	Eggs	Tunisia	Open field crop sampling, sentinel infested plants	Spring	Zouba et al. 2013