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PARASITOIDS OF THE GALL-FORMING APHID *SMYNTHURODES BETAE* [*APHIDOIDEA : FORDINAE*] IN ISRAEL

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In an ecological investigation of the gall-forming aphid, *Smynthurodes betae* Westw., we discovered that more than 20 % of the fundatrix galls were parasitized by *Monoctonia pistaciaecola* Stary (*Aphidiidae*). This is a new host record for this parasitoid. A Pteromalid hyper-parasite was identified as *Pachyneuron ? leucopiscida* Mani. Ecological information on the parasitoid is provided, and the low frequency of parasitoids known from gall-forming aphids, compared with free-living ones, is discussed.

KEY-WORDS : Gall-forming aphid, *Fordinae*, parasitoid, ecology.

The morphological variation and ecology of four species of *Fordinae* (*Homoptera, Aphidoidea*), forming galls on species of *Pistacia* (*Anacardiaceae*) were investigated in our laboratory in the past 20 years (**Wool & Koach,** 1976 ; **Wool,** 1977 ; **Koach & Wool,** 1977 ; **Wool & Manheim,** 1983, 1986, 1988). Occasionally, parasitized fundatrices ("mummies") were discovered in the galls of *Aploneura lentisci, Forda marginata* and *F. riccobonii* (**Wool & Manheim,** 1986, 1988, and unpublished field notes by **D.W.**), but the parasitoids were not identified.

In 1988, we began a detailed ecological study of another gall former, *Smynthurodes betae* Westw., which makes galls on *Pistacia atlantica*. A large proportion of the fundatrix galls were parasitized. In view of the scarcity of published records on parasitoids of gall aphids, our observations are reported below.

MATERIALS AND METHODS

The aphid *Smynthurodes betae* Westw. (*Pemphigidae, Fordinae*) forms 2 types of galls on its primary host, *Pistacia atlantica* (*Anacardiaceae*). The fundatrix makes a small (5-7 mm), red gall on the midrib of the leaflet. [These galls were described as belonging to different aphid species — e.g. by **Houard** (1913) Vol. III, fig. 1479-80 as *Pemphigus*, and by **Mimeur** (1949) p. 92, figs. 98-100 as *Forda follicularia* Pass.]. The second, final gall is spindle-shaped and is formed by the parthenogenetic descendants of the fundatrix, on other leaves, 3-4 weeks later. (See **Koach & Wool,** 1977, and fig. 12 there for the geographic distribution of *S. betae*. Like many gall-forming aphids, *S. betae* has many synonyms, and is listed as *Trifidaphis phaseoli* by **Bodenheimer & Swirski,** 1957, and **Koach & Wool,** 1977).

STUDY SITES

Galls of *S. betae* were collected and studied in 1988 and 1989. The main study sites were : (1) Tel Aviv University Botanical Gardens, (2) Kibbutz Givat Brener, about 35 km south of Tel Aviv, (3) Near Kibbutz Gvar Am, about 70 km south of Tel Aviv (studied only in 1989). Additional samples of galls were collected in 1989 from the Golan heights, the Carmel mountain, and in the Negev desert highlands near Mitzpe Ramon, extending the range of observations to 150, 100, and 200 km north, northeast, and southwest from Tel Aviv respectively.

COLLECTIONS

Fundatrix galls were collected at more-or-less regular intervals in March-June of 1988 and 1989 and brought to the laboratory. The galls were searched for emergence holes, opened, and the "mummified" fundatrices (if any) were removed and held for parasitoid emergence. Empty "mummies", with parasitoid emergence holes, were counted.

In addition, more than 1,000 final, spindle-shaped galls were collected and opened later in the season.

Adult parasitoids were sent for identification to the C.A.B. International Institute of Entomology c/o the British Museum (Natural History), London, and to Dr. **P. Starý**, Czechoslovak Academy of Sciences.

STATISTICAL ANALYSIS

The data were analyzed by G-tests of independence (**Sokal & Rohlf**, 1981).

RESULTS

PARASITOID IDENTIFICATION

Two species of wasps emerged from the "mummies". *Monoctonia pistaciaecola* Starý (*Aphidiidae*), was quite abundant in many samples (see below). Our report on *M. pistaciaecola* from *Smynthurodes betae* is a new host record for this parasitoid. Until now, only doubtful records of parasitoids exist for *S. betae* (**Mackauer & Stary**, 1967). The second species was identified as *Pachyneuron ? leucopiscida* Mani (*Pteromalidae*), which is known as a hyperparasite of Diptera (**Z. Boucek**, pers. comm) but parasitized the aphidiid *Monoctonia* in our *S. betae* fundatrices. Only 4 individuals of this species were collected.

PARASITOID ECOLOGY

The "mummified" fundatrices were located inside the galls. The wasps emerged from the mummies by boring a hole in the aphid skin (fig. 1) and then through the gall wall (fig. 2).

The first fundatrix galls were formed in early March. The first parasitized galls were found in early April. At the Botanical Gardens, samples were taken at bi-weekly intervals in April and early May, 1989, but there was no change in the proportion of parasitized galls. This suggests that the parasitization period was short and occurred around mid- or late March.

The rates of parasitization seem quite similar at different sites (table 1) except that no parasitoids were found in reasonably large gall samples from the Negev desert (last 2 sites

Fig. 1. Above, a parasitic wasp emerging from a "mummified" fundatrix of *Smynthurodes betae*. Below, an empty "mummy" skin with an exit hole.

Fig. 2. Two fundatrix galls of *S. betae* with exit holes drilled by emerging wasps. (The shape of the leaflet was distorted by the photographer in order to bring both exit holes into focus).

in the table). The average proportion of parasitized galls was about 23 % — quite a heavy toll, keeping in mind that when a fundatrix is destroyed an entire aphid clone is lost.

TABLE I

Frequencies of S. betae *galls parasitized by* Monoctonia pistaciaecola *in different collection sites (data from all dates and trees pooled).*

Site	1988			1989		
	galls	parasitized	%	galls	parasitized	%
Tel Aviv						
old Bot. Gardens		no data		64	17	26.6
new Bot. Gardens	248	57	23.0	268	35	13.6
Givat Brener	278	52	21.0	203	69	33.9
Gevat Am		no data		68	14	20.6
Golan heights		no data		105	23	21.9
Carmel		no data		116	32	27.6
Mizpe Ramon		no data		110	none	
Dimona		no data		60	none	

(Mean for all sites excluding Mizpe Ramon and Dimona : 23.5 % ± 2.11 (n = 8)).

A more detailed analysis of the 2 sites for which data have been collected in both years — Tel Aviv and Givat Brener — showed that at the former site, the frequency of parasitized galls was significantly lower in 1989 than in 1988 ; at the latter site the frequency was higher in 1989. ($P < 0.05$ in both cases). The reason seems to be the inclusion in the 1989 sample of trees that were not sampled in 1988, because when tests of independence were carried out on the frequencies of parasitized galls of each tree separately (only trees which were sampled in both years), no significant difference between years was detected. At Tel Aviv and the Carmel, there were significant differences in frequencies of parasitized galls among trees within each site ($P < 0.05$ at least). Data from more years are needed to tell if these differences persist in time and whether they have biological meaning.

Only 9 "mummies" were found in the 1,000 final, spindle-shaped galls, in sharp contrast with the parasitization rate of the fundatrix galls.

DISCUSSION

In their survey of hypotheses on the evolution of insect galls, **Price, Fernandes & Waring** (1987) discussed the value of galls as protective structures of the gallers against parasites. They mention, that although free-living species of aphids have many parasitoid species, gall-forming aphids have no recorded parasitoid species in North America. This is stated more strongly in the introduction to a recent paper by **Price & Pschorn-Walcher** (1988) (p. 196) — "Gall-forming Aphids and Adelgids have no known parasitoids."

This last statement is not justified, because some records of parasitoids in gall aphids (*Pemphigidae*) have been published (see **Starý**, 1970, 1976 ; **Wool & Manheim**, 1986, 1988 ;

and **Aoki & Kurosu,** 1989), (no records are yet known to us from *Adelgidae*). However, the statement that gall-formers have fewer parasitoids than free-living aphids appears to be true.

Aphid parasitoids receive much attention due to their importance as biological control agents (**Starý,** 1970 is an example). In addition, parasitoids may be valuable for the reconstruction of aphid phylogeny (**Mackauer,** 1965). We searched the literature for quantitative information on parasitoids in free-living and gall-forming aphids, and have come up with table 2. (This summary may suffer from ambiguities in definition of galls and other problems of our interpretation of the published lists, but the general pattern is valid). Compared with the numerous parasitoids known from free-living aphids, gall-forming species — in particular, those forming true galls, rather than leaf-curling and other deformities (which are sometimes referred to a simple galls or pseudogalls) — are attacked by very few.

TABLE 2

Summary of the number of parasitoid species recorded from free-living and gall-forming aphids. (Data from 6 different sources)

Source	**Starý,** 1970	**Starý,** 1976	(1) **Bodenheimer & Swirski,** 1957 (2) **Mescheloff & Rosen,** 1988	**Chakrabarti,** 1988	**Koach & Wool,** 1977 and present study
Geographic region :	Holarctic	Mediterranean	Middle East	Himalaya	Israel
A. Free-living and gall-forming aphids :					
Free-living aphids	272	243	168	not listed	not listed
Parasitoids of these species	178	94	(1) 15 (2) 31		
Gall-forming aphids	35	7	39	52	15
Parasitoids of these species	15	4	0	10	1
B. Subdivision of gall-forming aphids					
Leaf-curling aphids	23	not listed	not listed	40	not listed
Parasitoids	13			10	
True-gall formers	12	not listed	39	12	15
Parasitoids.	2		0	0	1

The question why so few parasitoids are known from gall-forming aphids, deserves some discussion. The argument depends on whether the parasitoids in question are « generalists » (polyphagous) or host specific. Aphid "generalists" do not have the tools to attack the aphids through the gall wall, and cannot enter closed galls and, therefore, the gall

provides protection for the aphids from this group of parasitoids (**Starý**, 1970). The parasitoid has a very narrow "time window" when it can get to the aphids, either in the interval between gall initiation and its final closure (which lasts just a few days, e.g. **Wertheim,** 1954) or after the gall opens to release the aphids. The fundatrices of gall-forming aphids are synchronized and appear during a short period in the spring [see **Whitham** (1978) and **Wool & Manheim** (1986) for examples]. In *S. betae*, fundatrix galls are available during about 3 weeks, but all the final galls on any one tree appear during 4-7 days and quickly become tightly closed (our unpublished observations).

Starý (1970, 1976) lists 2 species of parasitoids as specialists, attacking gall-forming aphids: *Monoctonia pistaciaecola* Starý and *Areopraon lebellevi* (Waterston). The latter enters the galls of *Schizoneura ulmi* after they open to release the aphids. *M. pistaciaecola*, however, attacks the fundatrix of *Forda* and of *Pemphigus* before the galls are closed (**Starý,** 1968, 1976).

After emergence from the mummy skin, *M. pistaciaecola* invariably proceeds to drill an exit hole in the gall (fig. 2). In this way, the adult parasitoid solved the problem of emergence from a closed gall, into which it was introduced some weeks earlier as an egg. There are no records of similar behavior in the literature. An unidentified parasitoid attacking *Pemphigus* in Japan is reported to remain inside the closed gall until the following spring, but there is no information on how it gets out (**Aoki & Kurosu,** 1989).

Starý (1968) states that *M. pistaciaecola* has a long diapause in the "mummified" aphids until the reappearance of fundatrices in the following spring. This latter claim does not agree with our observations on *M. pistaciaecola*, as almost all the wasps we collected during the study emerged from the "mummies" 1-2 weeks after collection and no diapause was detected. The discrepancy may be explained when we note that most of the records of *M. pistaciaecola* (on Pemphigus) from Europe (**Starý,** 1968, p. 242) were collected in June and July (three are listed as May-June). *S. betae* in Israel initiates its primary galls as early as mid-March. The parasitoids are then able to complete a full generation and emerge as adults in time to attack the fundatrices of the final, spindle-shaped aphid galls. The second generation of parasitoids may, in fact, diapause in the galls which fall to the ground when the leaves are shed. (We found some "mummies" in such galls).

The rate of parasitization of final galls (less than 1 %) was much lower than in primary galls (average 23 %). One reason may be the short "time window" available to the parasitoid, as mentioned above. But there is another explanation. Experimental work by **M. B.** (to be published elsewhere) indicates that the offspring of a single fundatrix in a primary gall produce, on average, ten successful final galls. But only a single wasp emerges from a parasitized primary gall, and it may be either a male or a female. Therefore, the ratio of parasitoids to parasitizable fundatrices in the final galls should be roughly 1/10 to 1/20 of that in the primary galls. Our observations are within the range.

We still wonder why host-specific parasitoids of gall-forming aphids did not evolve by synchronizing their life cycles with the aphids and/or evolving methods of entering the galls (or ovipositing in them). The presence of hundreds or thousands of aphids in a confined space in the gall could make such an evolutionary shift highly "profitable" for the parasitoid. It is a fact that specialized parasitoids are able to attack other gall-forming insects — Lepidoptera, Diptera and Hymenoptera (e.g. **Price & Pschorn-Walcher,** 1988; **Hawkins,** 1988). We do not have an answer for this intriguing question.

We believe that the continuing study of *S. betae* and its parasitoids may uncover more unknown facts of the host-parasite interactions.

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RÉSUMÉ

Parasitoïdes du puceron gallicole *Smynthurodes betae* [*Aphidoidea : Fordinae*] en Israël

Lors d'une étude écologique du puceron gallicole *Smynthurodes betae* Westw., on a découvert que plus de 20 % des galles dues aux fondatrices étaient parasitées par *Monoctonia pistaciaecola* Starý (*Aphidiidae*). C'est la mention d'un nouvel hôte pour ce parasitoïde. Un hyper-parasite *Pteromalidae* a été identifié comme *Pachyneuron leucopiscida* Mani. Une information écologique sur le parasitoïde est fournie et la faible fréquence de parasitoïdes connus d'aphides gallicoles vis-à-vis de celle des pucerons libres est discutée.

MOTS CLÉS : aphide gallicole, *Fordinae*, parasitoïdes, écologie.

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