THE HYPOPUS OF *HEMISARCOPTES COCCOPHAGUS* MEYER (ACARI : ASTIGMATA : HEMISARCOPTIDAE)

BY U. GERSON * & R. SCHNEIDER *

HYPOPUS

ABSTRACT : Development of *Hemisarcoptes coccophagus* Meyer was uninterrupted by a hypopodial stage upon being reared on its prey, healthy armored scale insects (Homoptera : Diaspididae). However, when mite eggs were placed on moribund scales, hypopodes were formed. Over 500 field-collected male and female *Chilocorus bipustulatus* (L.) (Coleoptera : Coccinellidae), the vector of *H. coccophagus*, were examined, and an equal load of hypopodes was found on both sexes. Hypopodes were significantly attracted to *Chilocorus* in choice tests, both beetle sexes evoking a simiiar response. Very few hypopodes molted at low or high relative humidities. Mechanism of hypopus induction in *H. coccophagus* thus resembles that known from some stored food mites, but the factors causing hypopus molting appear to be different.

HYPOPE

RÉSUMÉ : Le développement de *Hemisarcoptes coccophagus* Meyer ne fut pas interrompu par un stade hypope lorsqu'il était élevé sur de saines cochenilles à bouclier (Homoptera : Diaspididae). Cependant, quand les œufs des Acariens étaient placés sur des cochenilles moribondes, des hypopes furent formés. Prélevés dans les champs, plus de 500 mâles et femelles de *Chilocorus bipustulatus* (L.) (Coleoptera : Coccinellidae), le vecteur de *H. coccophagus*, furent examinés. Une quantité égale d'hypopes fut trouvée dans les deux sexes. Lors du test de choix, les hypopes furent attirés de manière significative vers *Chilocorus*. Les Coléoptères des deux sexes évoquent une réponse similaire.

Très peu d'hypopes muèrent à faible et fort taux d'humidité relative. Le mécanisme d'induction de l'hypope chez *H. coccophagus* ressemble donc à celui connu chez certains acariens des nourritures entreposées, mais le facteur produisant la mue de l'hypope semble être différent.

INTRODUCTION

Approximately 100 years have passed since MICHAEL (1884) opened new vistas in acarological research with his publication on " The hypopus question ". MICHAEL established that certain mites in the order Astigmata pass through a heteromorphic stadium, the hypopus, between their first and third nymphal instars. The hypopus is usually invested in a yellow-to-brown, hard cuticle (in contrast to the whitish, soft derm of all other instars) and lacks functional mouth parts. On the other hand, it is equipped with ventral suckers or claspers, with which it may attach itself to pas-

* The Hebrew University of Jerusalem, Faculty of Agriculture, Rehovot 76100, Israel.

sing animals. The organs of attachment and the darkish strong cuticle suggest that the hypopus serves to disseminate these mites. Hypopodes occur in the life cycle of free-living as well as parasitic species, and may or may not be formed in any given generation (HUGHES, 1976 ; KRANTZ, 1978 and citations therein).

Hypopus formation appears to be induced by several quite disparate groups of factors. One group comprises environmental conditions which slow down the rate of larval and protonymphal development (CHMIELEWSKI, 1971 ; GRIFFITHS, 1966, 1969 ; MATSUMOTO, 1978 ; WALLACE, 1969). Another group appears to be associated with phenological events, hypopodes being produced only in concert with the appearance of their specific vectors (FASHING, 1976 ; ROBINSON, 1953). The discovery of hypopodes which are parasitic during their hypopodial stage(s) (FAIN, 1969) indicates that hypopus formation can also be an obligatory phase in the life of some species, independent of any environmental or phenological events. No theory capable of accommodating all observed phenomena related to hypopus formation has yet been formulated.

Hypopus behavior in regard to insects which transport them has seldom been studied, being mainly confined to lists of hypopodes and their vectors (i.e., ZAKHVATKIN, 1959). GREENBERG (1961), GREENBERG and CARPENTER (1960) and THOMAȘ (1961) provided some suggestive data concerning the orientation of hypopodes towards, and their preference for, specific vectors.

Hypopodial molt (apolysis) has been attributed to addition of fresh food to the culture, to higher ambient relative humidities or to changes in the osmotic pressure (CUTCHER and WOODRING, 1969, and papers cited therein). FAIN (1977) and KUO and NESBITT (1970) regularly obtained tritonymphs upon transferring hypopodes of parasitic and stored-food mites, respectively, to very humid (close to saturation) conditions.

The species whose hypopodes have so far been studied live in stored food, in seewage, in water-filled tree holes or in vertebrate hosts. No comparative data were available for Astigmata parasitic on invertebrates, like *Hemisarcoptes*, which feeds on armored scale insects (Homoptera : Diaspididae). In a former paper (GERSON and SCHNEIDER, 1981) we reported on the biology of *H. coccophagus* Meyer and on its relationships with its host scales. The present essay deals with the hypopus of *H. coccophagus* (Figs 1-2).

HYPOPUS FORMATION

■ *Methods :* Mite culture, described in detail in the former paper, will herein be recapitulated. Armored scale insects (usually the California red scale, *Aonidiella aurantii* (Maskell) were reared on green lemons. The shield of young females was removed and replaced by an artificial, transparent cover made from collodion. *Hemisarcoptes* eggs were then introduced beneath the artificial shield and their subsequent development (at 28°C) observed through the transparent cover.

A total of 120 such scales, each with three mite eggs, were divided into four groups : A, in which the scales were not touched and remained healthy ; B, in which only moribund scales were used, most dying during the mites' larval or protonymphal instars ; C, in which only freshly-killed scales were utilized, and D, in which scales were pricked (subsequently causing their death) as soon as mite larvae were observed to feed on them.

■ *Results :* All mites in Group A developed to tritonymphs directly from protonymphs, no hypopodes occurring amongst them. In Group B, about 80 % of the protonymphs molted to hypopodes. Those of Group C left the dead scales shortly after hatching, and most of the Group D mites did likewise, except for a few which, having remained, molted to hypopodes. The hypopodial instar is thus not obligatory for the development of *H. coccophagus*. Live, healthy hosts ensured an uninterrupted cycle, whereas inadequate food during the early active stages promoted hypopus formation.

Hemisarcoptes — *Chilocorus* INTERACTIONS

The hypopodes of *Hemisarcoptes* have a world-wide, close association with lady-beetles (Cocci-

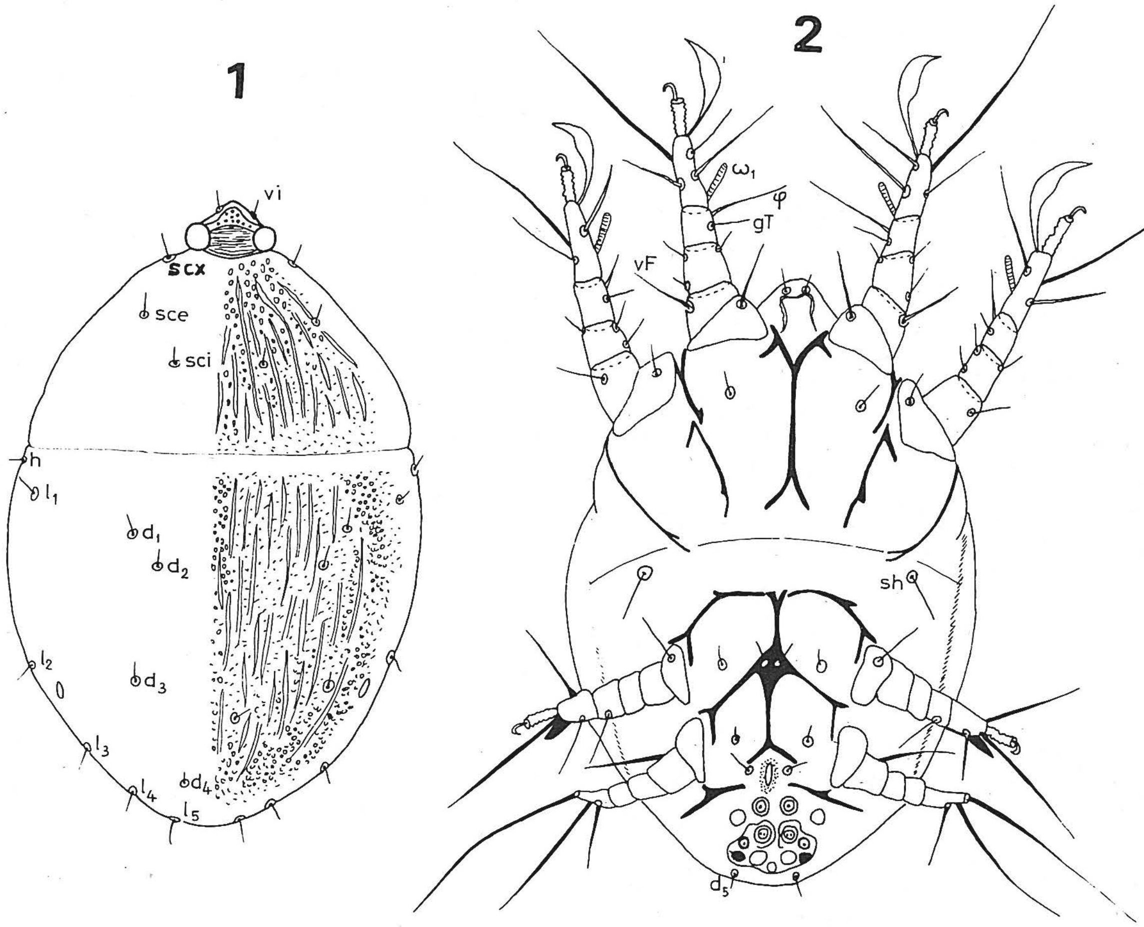

FIG. 1-2. : *Hemisarcoptes coccophagus* Meyer. Hypopus, dorsum (1), venter (2).

nellidae) of the genus *Chilocorus*, different species of the former being disseminated by various species of the latter (GERSON, 1967). The hypopodes of *H. coccophagus* occur under the elytra of *C. bipustulatus* (L.) (Figs 3-4) in Israel, being especially abundant in late summer (GERSON, 1967). During the present study we made field observations to assay the occurrence of hypopodes on either sex of the beetle, and laboratory tests to observe the pattern of *Hemisarcoptes* attraction to *Chilocorus*.

■ : *Field studies* : A total of 510 beetles were collected from eight citrus groves, sexed and then examined for presence of *Hemisarcoptes* hypopodes. Female beetles predominated at all sites (Table 1), but mite colonization was even on both sexes. Furthermore, at sites 3 and 5, whence most beetles carried hypopodes, female as well as male

TABLE 1 : Presence of hypopodes of *Hemisarcoptes coccophagus* on field-collected *Chilocorus bipustulatus* beetles.

Sample	Beetles		Beetles (%) with hypopodes		Hypopodes (No.) /beetle	
Site	Total	females %	Females	Males	Females	Males
1	70	60.0	52	53	8	7
2	78	53.8	33	50	4	4
3	42	66.7	100	100	34	29
4	58	79.3	11	33	3	5
5	67	70.1	63	64	16	22
6	70	68.6	21	18	5	3
7	60	81.7	58	55	11	8
8	65	73.8	42	38	9	7
Total/ Average	510	69.2	47.5	51.4	11.2	10.6

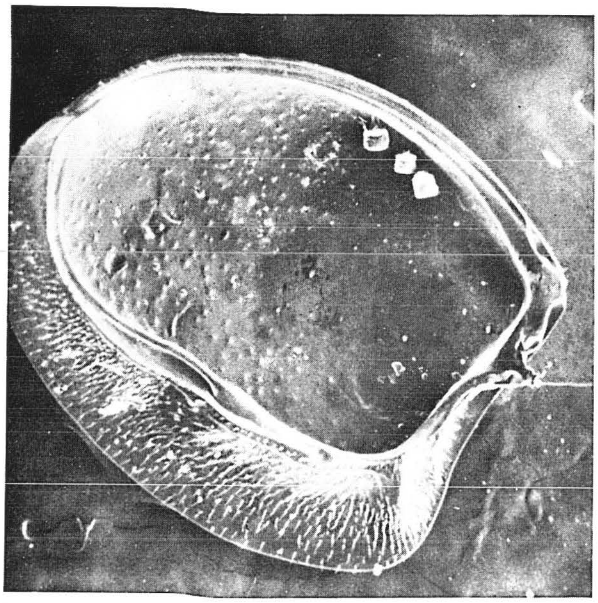

FIG. 3 : The venter of an elytron of *Chilocorus bipustulatus* (L.), with hypopodes of *Hemisarcoptes coccophagus* Meyer *in situ*.

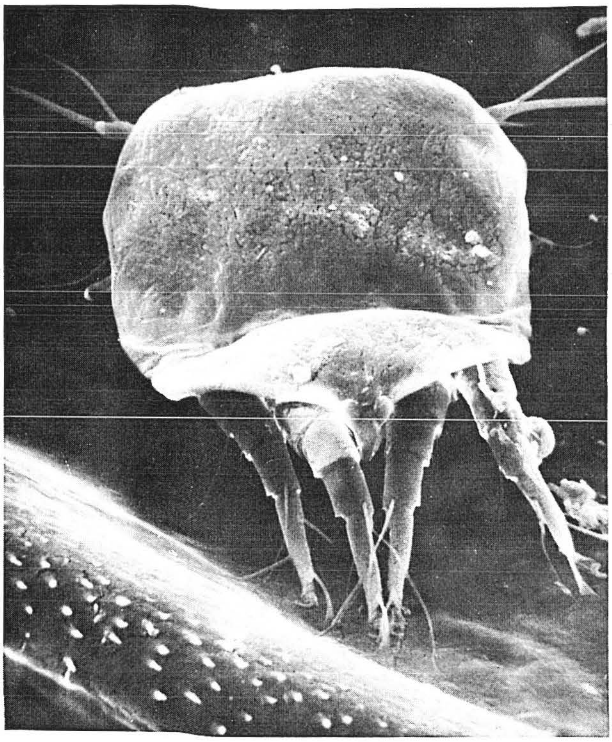

FIG. 4 : A single hypopus of *Hemisarcoptes coccophagus* Meyer on the ventral side of an elytron of *Chilocorus bipustulatus* (L.).

Chilocorus were heavily infested. These data suggest that the hypopodes of *H. coccophagus* are equally attracted to both sexes of *C. bipustulatus*, colonizing all available beetles in their habitat.

■ *Laboratory studies :* Preliminary observations indicated that hypopodes of *Hemisarcoptes* tended to move towards adult *Chilocorus* upon being placed together in a closed petri dish. A series of preference experiments was therefore run using a specially-constructed choice unit. This device was made from three plastic containers (1^3 inch each) originally used for storing microscope glass covers, and now utilized as three cells placed in tandem. Two holes were bored on either side of the middle cell, flush with its bottom, and glass tubes (5 cm long, inner diameter 0.5 cm) glued there. These tubes were connected to holes bored in the appropriate side of each of the flanking cells. Hypopodes, obtained from the cultures, were placed in the middle cell and beetles in the side ones. The beetles used were individually reared (on *A. aurantii*, in a culture totally free of *Hemisarcoptes*) so as to prevent the sexes from coming in contact and thus contaminating each other. Containers were then covered and the unit placed parallel to a light source, at approximately 24°C. Mite movement was recorded for three days ; hypopodes observed moving in the connecting glass tubes towards either of the side cells or which had already reached them were considered as positives.

Experiment 1 : A total of 141 hypopodes (in eight groups or replicates) were placed in the middle cell, the side ones being left empty. Seventy (49 %) were seen in motion towards one or another of the cells during the experimental period. Hypopus movement is thus not totally dependent on vector presence.

Experiment 2 : Two beetles were closed in one side cell, the other being left empty. Number of hypopodes (out of 150 used, in eight replicates) which were moving towards, or had reached, the inhabited cell was compared with those recorded in motion during Experiment 1. A total of 127 (84.7 %) had moved, all to the *Chilocorus*-containing cells. Results of a chi-square test (corrected for continuity) were $\chi_1^2 = 39.18$, $\alpha < 0.01$. In other words, the hypopodes of *H. coccophagus* have a direct movement towards *C. bipustulatus*.

Experiment 3 was conducted to examine the possibility that either of the sexes of *Chilocorus* is differentially attractive to *Hemisarcoptes*. Two female beetles were placed in one side cell, and two males in the other. Great care was taken to use the same cells for either gender in all (10) replicates (with 200 hypopodes). An almost equal number of hypopodes (98 : 97) moved to each side (sex), so that female and male beetles may be said to be equally attractive to *Hemisarcoptes*.

During experiments 2 and 3 it was observed that most motion took place within the initial two days, 53 % of the hypopodes moving in the first, 41 % in the second. This indicates the celerity with which hypopodes of *Hemisarcoptes* sense and move towards their vector in the field.

Hypopus molting

■ *Methods :* Hypopodes (of indeterminate age) were obtained from the cultures or collected off elytra of *Chilocorus*. They were placed in small plexiglass cages (4.0 × 2.5 cm) which were padded with dark filter paper, covered with microscope glass slides and held in place by metal clips. The hypopodes were exposed (at 22 ± 1°C) to the following treatments : A. Ambient relative humidities (ca. 40-50 %) ; B. Saturation ; C. As in B, but with lives bodies of the California red scale ; D. Submerged in distilled water. In addition, irregular observations were made of hypopodes kept with live scales at 80 % r.h. and 28°C.

■ *Results :* Hypopus survival was quite different under the various humidity conditions, but all induced only very little molting (Table 2). The low, similar rates of apolysis obtained in Treatments A and B suggest that humidity levels by themselves do not promote molting, nor does the addition of host scales (Treatment C). Very little (ca. 6 %) apolysis was also recorded in regard to the hypopodes under irregular observations. All molts took place during the experiments' first three days. The prolonged survival while submerged (Treatment D) is difficult to interprete, as neither mites nor beetles are aquatic.

TABLE 2 : Survival and molting of hypopodes of *Hemisarcoptes coccophagus* under various experimental conditions (see text), all at 22 ± 1°C.

Treatment	N	Days to 50 %death	Days to 100 %death	Molt (%)
A	44	2	4	6.8
B	50	5	16	6.0
C	32	4	19	3.1
D	34	14	27	—

Discussion

GERSON and SCHNEIDER (1981) have already shown that *H. coccophagus* may complete its development on live California red scales without forming a hypopus. However, as noted above, when pre-hypopodial stages were forced to subsist on moribund scales, hypopodes (deutonymphs) emerged from molting protonymphs. Hypopus formation in this species is thus facultative, its induction conforming to the model proposed by GRIFFITHS (1966, 1969) for some stored food mites. No data were hitherto available on factors inducing hypopus formation in a parasitic mite with a facultative hypopodial stage.

THOMAS (1961) reported that females of *Chilocorus cacti* (L.) carried significantly more hypopodes of *Hemisarcoptes cooremani* (Thomas) than its males. Our field data (Table 1) and experiments do not agree with this pattern, as the females and males of *C. bipustulatus* were equally attractive to *H. coccophagus*. The choice unit experiments further indicate the importance of olfaction for the navigation of this hypopus.

Molting of free-living and of parasitic hypopodes at very high relative humidities was obtained by KUO and NESBITT (1970) and by FAIN (1977), respectively. Thus we cannot explain why the hypopodes of *Hemisarcoptes* failed to molt under similar conditions (Table 2). GERSON (1967) obtained colonies of this mite after placing hypopodes-bearing elytra of *Chilocorus* on scale-infested potatoes at 80 % r.h. These hypopodes thus appear to require some special, humidity plus host plus an unknown factor(s) stimulus for molting. The need for such stimuli may be warranted by the special life style of *Hemisarcoptes*, displaying, as it does, two features uncommon to astigmatid mites. It feeds, predator-like, on living insects and their eggs, and it is specifically associated with two quite different insects orders (Homoptera and Coleoptera). *Hemisarcoptes* can thus be expected to have evolved the ability to react to a rich and diverse array of environmental signals. The cues triggering hypopus molting may well be among them.

ACKNOWLEDGEMENT

This study was partially supported by a grant from the Hebrew University Center for Integrated Pest Control, and constitutes a contribution from that Center.

REFERENCES

CHMIELEWSKI (W.), 1971. — Morfologia, Biologia I Ekologia *Carpoglyphus lactis* (L., 1758) (Glycyphagidae, Acarina). — Trace naukowe Inst. Ochr. Roslin, **13** : 63-166.

CUTCHER (J. J.) and WOODRING (J. P.), 1969. — Environmental regulation of hypopial apolysis of the mite *Caloglyphus boharti*. — J. Insect. Physiol., **15** : 2045-2057.

FAIN (A.), 1969. — Adaptation of parasitism in mites. — Acarologia, **11** : 429-449.

FAIN (A.), 1977. — Une méthode simple pour provoquer l'éclosion des hypopes pilicoles et endofolliculaires en mettre en évidence les acariens parasites endocutanés. — Acarologia, **19** : 298-301.

FASHING (N. J.), 1976. — The evolutionary modification of dispersal in *Naiadacarus arboricola* Fashing, a mite resticted to water-filled treeholes (Acarina : Acaridae). — Amer. Mid. Natur., **95** : 337-346.

GERSON (U.), 1967. — Observations on *Hemisarcoptes coccophagus* Meyer (Astigmata : Hemisarcoptidae), with a new synonym. — Acarologia, **9** : 632-638.

GERSON (U.) and SCHNEIDER (R.), 1981. — Laboratory and field studies on the mite *Hemisarcoptes coccophagus* Meyer (Astigmata : Hemisarcoptidae), a natural enemy of armored scale insects. — Acarologia, **22** : 199-208.

GREENBERG (B.), 1961. — Mite orientation and survival on flies. — Nature, **190** : 107-108.

GREENBERG (B.) and CARPENTER (P. D.), 1960. — Factors in phoretic association of a mite and fly. — Science, **132** : 738-739.

GRIFFITHS (D. A.), 1966. — Nutrition as a factor influencing hypopus formation in the *Acarus siro* species complex (Acarina, Acaridae). — J. Stored Prod. Res., **1** : 325-340.

GRIFFITHS (D. A.), 1969. — The influence of dietary factors on hypopus formation in *Acarus immobilis* Griffiths (Acari, Acaridae). — Proc 2nd Inter. Cong. Acarology, 419-432.

HUGHES (A. M.), 1976. — The Mites of Stored Food and Houses. — Her Majesty's Stationary Office, 2nd Edition.

KRANTZ (G. W.), 1978. — A Manual of Acarology. — Oregon State University Book Stores, 2nd Edition.

KUO (J. S.) and NESBITT (H. H. J.), 1970. — Termination of the hypopial stage in *Caloglyphus mycophagus* (Mégnin) (Acarina : Acaridae). — Can. J. Zool., **48** : 529-537.

MATSUMOTO (K.), 1978. — Studies on the environmental factors for the breeding of grain mites. XII. Observations on the mode of breeding and of hypopus appearance of *Lardoglyphus konoi* (Sasa and Asanuma, 1951) in various kinds of diet. — Jap. J. Sanit. Zool., **29** : 287-294 (in Japanese with English summary).

MICHAEL (A. D.), 1884. — The hypopus question, or the life-history of certain Acarina. — Jour. Linn. Soc. Zool., **17** : 371-394.

ROBINSON (I.), 1953. — The hypopus of *Hericia hericia* (Kramer), Acarina, Tyroglyphidae. — Proc. Zool. Soc. London, **123** : 267-272.

THOMAS (H. A.), 1961. — *Vidia (Coleovidia) cooremani*, new subgenus and new species, and notes on the life history (Acarina : Saproglyphidae). — Ann. Ent. Soc. America, **54** : 461-463.

WALLACE (D. R. J.), 1960. — Observations on hypopus development in the Acarina. — J. Insect Physiol., **5** : 216-229.

ZAKHVATKIN (A. A.), 1959. — Fauna of U.S.S.R., Arachnoidea. Vol. VI, No. 1, Tyroglyphoidea (Acari). — American Institue of Biological Sciences.

Paru en juillet 1982.