Sensory Functions of the Palps and First Tarsi of *Macrocheles muscaedomesticae* (Acarina: Macrochelidae), a Predator of the House Fly¹

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ABSTRACT

The effect of amputations of the palps and tarsi I on the sensory behavior of *Macrocheles muscaedomesticae* (Scopoli), a mite which is predaceous on house fly, *Musca domestica* L., eggs and phoretic on adult house flies, was determined. With tarsi I removed, the mites did not attach to house flies and were not attracted to the adults, eggs, or pupae of house flies. With the palps

removed, the mites were less mobile than normal, but responded normally to a repellent. It was demonstrated that the palps touch the substrate alternately when the mite is walking. It was concluded that receptors of olfactory stimuli are on tarsi I and receptors of contact stimuli are on the palps.

Macrocheles muscaedomesticae (Scopoli) is a mature-inhabiting mesostigmatid mite, predaceous on the eggs and first-instar larvae of the house fly, *Musca domestica* L. The rate of predation was investigated by Axtell (1961, 1963) and Rodriguez et al. (1962), nutrition by Rodriguez and Wade (1961), and life history by Wade and Rodriguez (1961).

The adult female *M. muscaedomesticae* are transported to new areas of manure by attaching to house flies. The stable fly, *Stomoxys calcitrans* (L.), and the little house fly, *Fannia canicularis* (L.), also transport macrochelid mites (Filipponi 1960, Axtell 1964). Since there is no apparent feeding by the mite during this period of attachment, this is a case of phoresy, rather than parasitism (Filipponi 1955).

The factors affecting the rate of phoresy are now under investigation in this laboratory. One aspect is an investigation of the means by which the mites locate the flies. It has generally been assumed that the first pair of legs of Macrochelidae perform sensory functions (Hughes 1959, p. 154), but neither the function of the legs nor of the palps has been established experimentally. The effects of amputation of the palps and the first pair of tarsi on the behavior of female *M. muscaedomesticae* are presented in this report.

MATERIALS AND METHODS

M. muscaedomesticae were reared in plastic dishes

on a substrate of fresh cow manure, CSMA³ medium previously used to raise house fly larvae, and vermiculite in a 3:2:1 ratio. The mites were fed house fly eggs which were previously frozen to prevent hatching.

The palps and tarsi I were removed with scalpels of fine (0.20 mm-diam.) tungsten wire imbedded in glass. To prepare the cutting edge, the free end of the wire was heated, plunged into sodium nitrite, and further sharpened with a fine carborundum block. Operations were performed at first with a Leitz[®] micromanipulator, and later by hand.

The mites were anesthetized with ether prior to surgery. (Preliminary studies showed that ether had no apparent effect on the phoretic rate.) Amputations were performed on a polystyrene base to prevent unnecessary dulling of the knife edge. Amputee mites were held 1 day or more before being tested. Samples of the amputated structures were slide-mounted and examined microscopically to verify the degree of amputation. The mites were examined before and after tests to ensure that the structures were totally removed. The tarsus of leg I, the tarsus of leg III (a normal walking leg), and a palp are illustrated in Fig. 1.

The emergence container (Fig. 2) used to compare the phoretic response of amputee and intact mites consisted of 2 polystyrene containers (52×36 mm).⁴ The eccentric positioning of the connective tubing facilitated fly emergence and discouraged their return to the lower container. In tests, 10 amputee mites, 10 intact mites, and 10 house flies were placed together in the lower chamber of the emergence con-

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³ Chemical Specialties Manufacturers' Association medium, obtained from Ralston-Purina Co., St. Louis, Mo.

⁴ Obtained from Tri-State Plastic Molding Co., Henderson, Ky.

FIG. 1.—*Macrocheles muscaedomesticae*. A, Tarsus of leg I. B, Tarsus of leg II (a walking leg). C, Tibia and tarsus of palp.

tainer. The flies were placed in a freezer (-14°C) for 4 min, rendering them immobile for 5 min after transfer to the emergence container, during which time the mites could attach. After 10 min, the flies began emerging into the upper container, and after 30–60 min both containers were placed into the freezer. Counts were made of the amputee and the intact mites attached to flies after all were frozen. Except where otherwise noted, each experiment involved 5 replications.

Two types of olfactometers were used to compare the reactions of amputee mites and intact mites to candidate materials. Both were constructed primarily of polystyrene containers. The first (Fig. 3) consisted of a container (26×9 cm) with plastic boxes (2 cm square) placed below each of 4 screened ports (1 cm diam.) equally spaced around the perimeter of the base. In tests, 2 boxes held 5 flies each, and the other 2 were empty. After the flies were inside 30 min, 25 mites were added singly through the hole in the top of the container. Counts were made of the numbers of mites at each port at 4 or 5 successive 1-hr intervals. The boxes were interchanged during the test. Since 2 of the boxes were empty, water was tested to assess the possibility of a positive hygrotaxis. Other tests utilized treated pupae and adult flies. The response to house fly eggs was tested in an olfactometer of the same design but having a diameter of 9 cm.

The second olfactometer (Fig. 4) was used to compare the reactions of amputee and intact mites to a repellent. A side-arm (25 cm long) of polyethylene tubing (1 cm diam.) was attached to a 52×36-mm polystyrene container with the inside bottom covered with blotting paper. In each test, 25 mites were added

to the distal end of the tubing and shaken to the proximal end. At the end of 30 min the mites in the distal centimeter of tubing were counted. Tests were conducted with 20 drops of the repellent MGK 5780⁵ and 15 drops of water added to the blotting paper and with only the water added.

To substantiate the observation that mites normally touch their palps to the substrate as they move, mites were allowed to walk on kymograph paper blackened with kerosene soot.

RESULTS

The rates of phoretic attachment by *M. muscaedomesticae* at 1- to 5-day intervals after removal of the first tarsi were consistent indicating no temporary change in phoretic behavior owing to postoperative shock (Table 1A). The rate of intact mite attachment ranged from 70% to 90%, whereas the rate of the amputee mites was never higher than 10%. As a further test for the effects of shock, the tarsi of legs III (walking legs) were removed instead of the tarsi of legs I, the assumption being that a roughly equivalent injury would be produced. However, the mites were not able to move normally with this degree of injury to their walking legs and this test was rejected. As a third means of assessing the effect of shock, the first tarsi were removed from a total of 40 deutonymphs on 3 different days. Of the mites which survived the operation, 34 molted to adults. The phoretic rate of these adults was very low in comparison with intact mites (Table 1B), and similar to the rate of

⁵ Courtesy McLaughlin-Gormley-King Co. MGK 5780 consists of 75% ethyl hexanediol, 4% *N*-octyl bicycloheptene dicarboximide (MGK 264), 1% 2,3,4,5-bis (Δ^2 -butylene)-tetrahydrofurfural (MGK 11), 1% di-*n*-propyl isocinchomeronate (MGK 326), and 19% isopropanol.

FIG. 2.—Emergence container used to compare the rate of phoretic attachment of mites. Mites and flies were placed at position A.

other tarsiless mites (Table 1A). The phoretic rate of 50 mites with only a single tarsus I removed was 8%.

In a similar experiment with mites which were depalped (Table 1C), the rate of phoresy for the palpless mites was 0. In this case the mites were held only 2-3 days after the amputation, since the depalped mites did not feed and began to die after 5 days. This lack of feeding was confirmed by placing 40 house fly eggs in each of 3 containers and adding 10 tarsiless mites to the first, 10 palpless mites to the second, and leaving the third without mites as a control. In the presence of palpless mites and in the control, there were 1-7 collapsed chorions on each of the 2 test days, whereas in the presence of tarsiless mites, there were 39 the first day, and 40 the second day.

In the olfactometer tests, the intact mites were attracted to house fly eggs and adults whereas the tarsiless mites were not attracted (Tables 2, 3). Intact mites were attracted to living pupae and adults, pupae and adults frozen overnight, pupae placed in acetone

for 15 min, and mashed adults, but were not attracted to pupae or adults dried overnight in an oven (135°C) and only slightly to water (Table 4). Palpless mites did not move when placed in the same type olfactometer with flies and fly eggs, but did react to the repellent in the side-arm type of olfactometer. Both intact and palpless mites moved immediately from the repellent whereas the tarsiless mites did not respond (Table 5).

The mite trail in kerosene soot (Fig. 5) demonstrated that the palps are touched alternately to the substrate as the mite walks. In the linear representation of the photograph, the solid black dots represent the places where the palp mark is clearly seen.

DISCUSSION

The waving of the first pair of legs as *M. muscae-domesticae* moved suggested a sensory function. (Similar behavior was reported by Lees (1948), who termed it "questing" in the tick *Ixodes ricinus* L., and by Rapp (1959), who called it "wittern" (scenting) in *Parasitus coleoptratorum* L.) Morphologically, the first tarsi are distinct from the walking legs since they bear many very long setae and have neither claws nor caruncles. No structure appearing morphologically to be a specialized light receptor was found on tarsi I. Positive reaction by intact mites to live flies, frozen flies, mashed flies, living fly pupae, frozen

FIG. 3.—(Top) Olfactometer used to determine reactions of mites to attractants. A, Area where mites were first placed. B, Port covered with 100-mesh screen, allowing diffusion of odors from lower box. C, Position of attractant (only 2 boxes contained the attractant).

FIG. 4.—(Bottom) Repellent chamber. A, Screened cap, and area where mites were first placed. B, Screened cap, and area where mites were counted after ½ hr. C, Location of repellent.

Table 1.—Numbers of adult female *Macrocheles muscaedomesticae* attaching to house flies after mutilation by removal of tarsi I or of palps.

Days after surgery	Replicate no.	No. mites/ test	No. attached to flies	No. controls ^a attached
<i>A. Tarsi I removed from mites when adults</i>				
1	b	50	0	42
2	b	50	5	37
3	b	50	2	45
4	b	50	1	45
5	b	50	2	38
<i>B. Tarsi I removed from mites when deutonymphs</i>				
—	—	9	0	9
—	—	15	0	12
—	—	10	2	8
<i>C. Palpi removed from mites when adults</i>				
—	1	10	0	8
—	2	10	0	6
—	3	10	0	7
—	4	10	0	9
—	5	10	0	10

^a Equal numbers of intact mites were used as controls in the several experiments.

^b Total of 5 replicates (50 mites)/day.

fly pupae, and pupae killed in acetone, but no such reaction to pupae and adults dried in an oven indicated that visual stimuli were not important in determining the mites' responses. All experiments indicated that the first tarsi were involved in odor reception. On the basis of 250 mites having both tarsi I amputated, there was a phoretic rate of only 2.3% as compared with 83% for the same number of intact mites. Mites with a single tarsus I removed were 8% phoretic, a rate closer to that of tarsiless mites than intact mites. The mites lacking a single tarsus I apparently were able to detect odors but were less able than intact mites to locate the source of the odors. Perhaps the differences in the intensities of the stimuli received by the right and by the left tarsus orient the mite toward the odor source.

The abundance of setae on the palps implicated them in sensory reception. The mites were observed to drape their palps over a fly egg when feeding, suggesting the reception of contact stimuli. However, the palps did not move in the olfactometer containing flies. This suggested that either the palps were needed for the reception of olfactory stimuli or

Table 2.—Number of *Macrocheles muscaedomesticae* occurring at ports (with and without flies) of olfactometer after 1 hr. 25 mites per treatment per experiment.

Exp. no.	Tarsi I intact		Tarsi I removed	
	Ports with flies	Ports without flies	Ports with flies	Ports without flies
1	24	0	1	1
2	21	0	1	0
3	21	0	1	1
4	21	3	1	0

Table 3.—Number of *Macrocheles muscaedomesticae* occurring at ports (with and without fly eggs) of olfactometer after 15 minutes.^a 25 mites per treatment per experiment.

Exp. no.	Tarsi I intact		Tarsi I removed	
	Ports with eggs	Ports without eggs	Ports with eggs	Ports without eggs
1	25	0	8	12
2	23	1	15	8
3	20	1	8	1
4	15	4	7	3

^a Since a smaller olfactometer (9 cm diam) was used with these tests, although the port diameter remained 1 cm, the numbers are somewhat higher than in Table 2. As a result of the reduced area, the mites were often located near a port when counts were made even though they were not necessarily attracted to the port.

some other sensory reception was removed by palpal amputation. The fact that palpsless mites reacted in the same way as intact mites in the presence of a repellent, whereas the tarsiless mites did not respond, demonstrated that the palps were not apparently necessary for olfactory reception. (It is not known if repellent and attractant reception involves the same sensory routes in *M. muscaedomesticae*.) In addition, we observed that intact mites touched their palps to the substrate as they walked. This contact was further substantiated by the palpal prints in the mite's trail. Thus, with no palps, the mites were unable to detect the substrate, and hence became immobile. On the basis of this evidence, we concluded that the palps of *M. muscaedomesticae* possess the receptors for contact stimuli. It is not known whether these "contact stimuli" involve mechanoreception (touch) or chemoreception (taste), or a combination of the two.

Amputations have been used to determine the locations of sensory receptors in other Acarina with similar results. Hindle and Merriman (1913) were able to pinpoint the olfactory sense of the tick *Argas persicus* (Oken) in Haller's organ. Lees (1948) reported that in *Ixodes ricinus* one-half of Haller's organ is responsible for the perception of olfactory stimuli, and, finding no tick attachment when the palps were removed, concluded that warmth and chemotactile reactions caused the ticks to attach. Camin (1953) im-

Table 4.—Number of *Macrocheles muscaedomesticae* occurring at ports (with and without test materials) of olfactometer after 45 min. 50 mites per treatment per experiment.

Test material	Ports with materials	Ports without materials
Untreated house fly pupae	32	3
Frozen house fly pupae	28	0
Acetone-dipped house fly pupae	20	1
Dried house fly pupae	2	10
Live house fly adults	32	0
Frozen house fly adults	27	1
Mashed house fly adults	28	1
Dried house fly adults	1	9
Water	10	4

Table 5.—Number of adult female intact, tarsiless, and palpless *Macrocheles muscaedomesticae* located, after 30 minutes exposure, in the distal centimeter of the sidearm of a chamber alternately containing water and a repellent (MGK 5780). 25 mites per treatment per replicate.

Rep. no.	Intact		Tarsi I removed		Palps removed	
	Water	Repell.	Water	Repell.	Water	Repell.
1	0	21	4	3	0	17
2	3	18	7	4	3	14
3	2	15	2	6	1	16

plicated club-shaped setae at the tip of tarsi I in olfactory reception by *Ophionyssus natricus* (Ger-vais) (Macronyssidae). In several oribatid mites, Pauly (1956) determined that the pseudostigmatic organs of the dorsal shield (which are not present in

M. muscaedomesticae) were mechanoreceptors, and the first legs olfactory receptors. Rapp (1959) reported olfactory reception in *P. coleoptratorum* (Parasitidae) by the first tarsi, and to a lesser extent by the palps.

Of the species cited, only *P. coleoptratorum* is phoretic and lacks claws and caruncles on the first legs. However, the deutonymphs are phoretic; not the adults, as in *M. muscaedomesticae*. Rapp did not investigate the phoretic behavior of amputee mites. His conclusion that the palps function as secondary olfactory receptors could not be substantiated in *M. muscaedomesticae*. Nevertheless, a consistency holds throughout the Acarina regarding the function of the palps and particularly the first tarsi.

Although Sychevskaya (1964) cites 16 species of flies in 14 genera to which *M. muscaedomesticae* has

FIG. 5.—Photograph of mite trail on kymograph paper, with line-drawing tracing. Circles and hollow oblongs represent tracks of walking legs; black dots represent tracks of palps.

been found attached, it has been found most frequently attached to *M. domestica* (Filipponi 1960). This relationship may exist simply because of similar ecological niches or there may be some selection by the mites since they utilize olfactory and contact stimuli to locate food and transport hosts. Moreover, the mite finds its host and attaches in manure yet will detach upon being carried to fresh manure, indicating a balance between the relative attractiveness of the fly and the manure. These relationships deserve further investigation.

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