SENSORY RECEPTORS OF THE OVIPOSITOR OF TRICHOGRAMMA MAIDIS [HYM.: TRICHOGRAMMATIDAE]

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Sensory receptors of the ovipositor of *Trichogramma maidis* are described. Sense organs are found on the 2^{nd} valvifers (1 type), on the tip of the 3^{rd} valvulae (2 types) and on the 1^{st} valvulae (4 types). The nature and possible functions of these sensilla are discussed.

KEY-WORDS : Trichogramma, ovipositor, sensory receptors.

The ability to discriminate between unparasitized and parasitized hosts is a very common feature among hymenopterous parasitoids. Such a discrimination ability implicates that the wasp is able to obtain informations from the external and/or internal part of the host. In the latter case, this is done with some sensory receptors used during a probing of the host with the ovipositor (King & Rafai, 1970; Wylie, 1971; Greany & Oatman, 1972; Van Lenteren, 1972; Ganesalingam, 1974; Hofsvang, 1988).

Trichogramma species are known to recognize healthy hosts this way (Strand, 1986), and this observation has led some authors to suggest the existence of sensilla on the ovipositor (Salt, 1937; Klomp et al., 1980). Nevertheless, such sensory receptors have never been observed.

The present work has been done to know if such receptors could be found in *Trichogramma maidis* Pintureau & Voegelé.

MATERIALS AND METHODS

The *T. maidis* strain used originated from Antibes (Biological Control Station, I.N.R.A., France) where it has been reared for many generations on *Ephestia kuehniella* Zeller (*Lep.*: *Pyralidae*) eggs at 25 °C.

Scanning electron microscopy: Freshly emerged females were fixed in 2.5 % glutaraldehyde buffered to pH 7.4 for 2 h, washed in 0.1 M sodium cacodylate buffer, gradually dehydrated in alcohol and critical point dried. After dissection, samples were sputtercoated with fine gold and observed in a JEOL J.S.M.35 microscope.

RESULTS

The basic organization of female genitalia shows a remarkable uniformity among *Hymenoptera* (Smith, 1970; Matsuda, 1976). It consists of 2 pairs of valvifers and 3 pairs

of valvulae derived from the 8^{th} and the 9^{th} abdominal segments. The 1^{st} valvifers (gonocoxites VIII) are continuous with the rami of the 1^{st} valvulae (gonapophyses VIII). The 2^{nd} valvifers (gonocoxites IX) extend as the 3^{rd} valvulae (gonostyli) and ventrally bear the fused 2^{nd} valvulae (gonapophyses IX). The interlocked 1^{st} and 2^{nd} valvulae, surrounded with the 3^{rd} , form the shaft of the ovipositor.

T. maidis female's genitalia follow this basic organization (fig. 1). The shaft of the ovipositor is on average 160 μ m long (about a third of the whole adult body length) and 6 μ m thick. It is a rigid structure that ends in a pointed tip. The 2nd valvula is showing its double origin in a dorsal membraneous fold and ends in series of teeth that form a perforating lancet (fig. 3); there are 4 cuticular spines on each side of the lancet (fig. 2). A





- Fig. 1. Diagram of the ovipositor of T. maidis. (V1, V2 & V3 : 1st, 2nd and 3rd valvulae; Vf1 & Vf2 : 1st and 2nd valvifers).
- Fig. 2. Tip of the ovipositor showing the 4 types (A, B, C, D) of sensilla on a 1st valvula (f : dorsal fold of the 2nd valvula; n : notch of the 1st valvula; sp : cuticular spine; t : tooth of the perforating lancet; V1 : 1st valvula; V2 : 2nd valvula).

Scale bars in micrometers

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- Fig. 3. Tip of the 2^{nd} valvula (f: dorsal fold; sp: cuticular spine; t: tooth of the perforating lancet). Fig. 4. Ventral view of the ovipositor: distal part of the 1^{st} valvulae (C: type C sensilla; n: notch; V3: 3^{rd}
- valvulae).
- Fig. 5. Rows of cuticular spines in the egg canal. Inner surface of the 1st valvula (sp : cuticular spine). Fig. 6. Sensilla of one 2nd valvifer (s : sensilla ; r : ramus of the 1st valvula ; Vfl & Vf2 : 1st and 2nd valvifers). Fig. 7. Tips of the 3rd valvulae showing the 2 types of sensilla (lt : long trichoid sensilla ; d : digitation ; ds : digitated sensilla. Note the different aspects of the digitations).

Scale bars in micrometers

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ventral notch can be seen on the 1^{st} valvulae. It marks the beginning of the distal narrowing (fig. 4). The 1^{st} valvulae end with 2 small denticulations. The inner surface of the 1^{st} and 2^{nd} valvulae, which forms the egg canal, is lined with rows of backwards pointed cuticular spines (fig. 5). They probably help the advance of the egg along the ovipositor during the back and forth movements of the 1^{st} and $the 2^{nd}$ valvulae (Austin & Browning, 1981).

Three parts of the *T. maidis* ovipositor bear sense organs : the 2^{nd} valvifers, the 3^{rd} and the 1^{st} valvulae.

Sensilla on the second valvifers : there are 5 styloconic sensilla : 4 on the posterior edge and 1 under the 1st valvifer (fig. 6). Such sensilla, which can be found in all *Chalcidoidea* in a variable number, are probably mechanoreceptors and are likely stimulated by movements of the 1st valvifers and the 1st valvulae during oviposition.

Sensilla on the third valvulae : the extremity of each 3rd valvula bears 5 sensory hairs : 2 long trichoid sensilla located on the dorsal and ventral edges and 3 shorter digitate setae located at the tip (fig. 7). The 4 distal digitations on each of those sensilla have been observed either open or closed.

Sensilla on the first valuale : 12 to 13 sensilla belonging to 4 different types (here labelled A, B, C & D) were observed on each 1^{st} valual (fig. 2) :

- Type A: These sensilla show a rigid hook-shaped cuticular process in an ovoid cupule (fig. 8); a pore can be found at the root of this process (fig. 9). Two type A sensilla are located on the distal extremity of each valvula, before the terminal denticulations.

— Type B : Forward to type A sensilla, and in a more ventral position, there is a unique, yet undescribed wrinkled and lightly-depressed cuticular structure (fig. 8 & 9). Its sensory function remains to be proved.

— Type C: On each valvula, there are 7 to 8 processes which are flexible styloconic sensilla (fig. 10). The 1^{st} one is always in a distal position from the cuticular notch, the others are regularly arranged on the distal 3^{rd} of the valvula (fig. 4).

— Type D: These are not very prominent campaniform sensilla which are $1.4 \,\mu\text{m}$ in diameter (fig. 11). Two such sensilla can be found, 1 between the 2 distal styloconic sensilla, the other just after the proximal styloconic sensilla.

DISCUSSION

The existence of sensory receptors on hymenopterous parasitoids ovipositor has already been pointed out by several authors (King & Fordy, 1970; Ganesalingam, 1972; Hermann & Douglas, 1976; Domenichini, 1977-1978; Van Veen & Van Wijk, 1985). Ultrastructural studies have shown that such sense organs could be mechanoreceptors, contact-chemoreceptors or both (Hawke *et al.*, 1973; Greany *et al.*, 1977; Le Ralec & Rabasse, 1988).

In T. maidis, such sensory receptors are numerous and diversified.

The trichoid hairs and digitated setae found on the 3^{rd} valvulae may have a functional implication in the host selection process or in the location of the probing site during egg examination.

Up to now, no information is available concerning the nature of the sensilla located on the ovipositor. However, the fact that there are a pore and a well-developed process on the type A sensilla leads to the supposition that they could be both contact-chemoreceptors and mechanoreceptors.

Types C & D are probably mechanoreceptors. Their arrangement on the valvula may enable the female to quantify the insertion level of the ovipositor inside the host.

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Fig. 8. Types A & B sensilla on the tip of one 1st valvula (V1 : 1st valvula ; V2 : 2nd valvula).
Fig. 9. Type A sensilla, with a basal pore and type B sensilla (p : pore).
Fig. 10. Type C sensilla.
Fig. 11. Types C and D sensilla.

Scale bars in micrometers

A study of the fine internal structure of these sensory receptors is necessary in order to verify these hypotheses, in particular to better understand the functional nature of the type B organs, which are particularly original.

These ovipositor sensilla probably have an important function in the whole host selection process, both for the recognition of already parasitized host from unparasitized

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one, and for the perception of kairomonal cues that stimulate the egg-laying decision (Wu & Qin, 1982; Tilden & Ferkovitch, 1988; Kainoh & Tatsuki, 1988).

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RÉSUMÉ

Les récepteurs sensoriels de l'ovipositeur de Trichogramma maidis [Hym. : Trichogrammatidae]

Des récepteurs sensoriels ont été mis en évidence sur l'ovipositeur de *T. maidis*. Il existe des sensilles sur les valvifères 2 (1 type), l'extrémité des valves 3 (2 types) et les valves 1 (4 types). La nature et le rôle possibles de ces organes sont discutés.

MOTS CLÉS : Trichogramma, ovipositeur, organes sensoriels.

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REFERENCES

- Austin, A. D. & Browning, T. O. 1981. A mechanism for movement of eggs along insect ovipositors. J. Insect Morphol. & Embryol., 10, 93-108.
- Domenichini, G. 1977-1978. Some structures of various Hymenoptera Chalcidoidea and their functions. Bull. Zool. Agr. Bachic. Ser. II, 14, 29-93.
- Ganesalingam, V. K. 1972. Anatomy and histology of the sense organs of the ovipositor of the Ichneumonid wasp, *Devorgilla canescens.* J. Insect Physiol., 18, 1857-1867.
- Ganesalingam, V. K. 1974. Mechanism of host discrimination between parasitized and unparasitized hosts by Venturia canescens [Hym. : Ichneumonidae]. — Entomol. Exp. & Appl., 17, 36-44.
- Greany, P. D. & Oatman, E. R. 1972. Analysis of host discrimination in the parasite Orgilus lepidus [Hym. : Braconidae]. Ann. Entomol. Soc. Am., 65, 377-383.
- Greany, P. D., Hawke, S. D., Carlyse, T. C. & Anthony, D. W. 1977. Sense organs in the ovipositor of *Biosteres (Opius) longicaudatus*, a parasite of the Caribbean fruit fly *Anastrepha suspensa*. *Ann. Entomol. Soc. Am.*, 70, 319-321.
- Hawke, S. D., Farley, R. D. & Greany, P. D. 1973. The fine structure of sense organs in the ovipositor of the parasitic wasp Orgilus lepidus Muesbeck. Tissue Cell, 5, 171-184.
- Hermann, H. R. & Douglas, M. E. 1976. Comparative survey of the sensory structures on the sting and the ovipositor of hymenopterous insects. — J. Georgia Entomol. Soc., 11, 223-239.
- Hofsvang, T. 1988. Mechanisms of host discrimination and intraspecific competition in the aphid parasitoid *Ephedrus cerasicola*. *Entomol. Exp. & Appl.*, 48, 233-239.
- Kainoh, Y. & Tatsuki, S. 1988. Host egg kairomones essential for the egg-larval parasitoid, Ascogaster reticulatus Watanabe [Hym.: Braconidae] I. Internal and external kairomones. — J. Chem. Ecol., 14, 1475-1484.
- King, P. E. & Fordy, M. R. 1970. The external morphology of the "pore" structures on the tip of the ovipositor in Hymenoptera. — Entomol. mon. Mag., 106, 245-254.
- King, P. E. & Rafai, J. 1970. Host discrimination in a gregarious parasitoid Nasonia vitripennis (Walker) [Hym. : Pteromalidae]. J. Exp. Biol., 53, 245-254.

- Klomp, K., Teerink, B. J. & Wei Chun Ma. 1980. Discrimination between parasitized and unparasitized hosts in the egg parasite *Trichogramma embryophagum* [Hym. : *Trichogrammatidae*]: a matter of learning and forgetting. *Neth. J. Zool.*, 30, 254-277.
- Lenteren, J. C. Van 1972. Contact-chemoreceptors on the ovipositor of *Pseudeucoila bochei* Weld [*Cynipidae*]. *Neth. J. Zool.*, 22, 347-350.
- Le Ralec, A. & Rabasse J. M. 1988. Structure, sensory receptors and operation of the ovipositor of three *Aphidiidae*. In : Ecology and effectiveness of *Aphidophaga* (E. Niemczyk & A. F. G. Dixon, eds.). SPB Academic Publishing, The Hague, 83-88.
- Matsuda, R. 1976. The Hymenoptera. In : Morphology and Evolution of the Insect Abdomen. Pergamon Press, New York, 373-396.
- Salt, G. 1937. The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts. *Proc. R. Soc. Lond.*, 122, 57-75.
- Smith, E. L. 1970. Evolutionary Morphology of the External Insect Genitalia. 2. Hymenoptera. — Ann. Entomol. Soc. Am., 63, 1-27.
- Strand, M. R. 1986. The physiological interactions of parasitoids with their hosts and their influence on reproductive strategies. In : Insect Parasitoids (J. Waage & D. Greathead, eds.). Academic Press, 97-138.
- Tilden, R. L. & Ferkovitch, S. M. 1988. Kairomonal stimulation of oviposition in an artificial substrate by the endoparasitoid *Microplitis croceipes* [Hym. : Braconidae]. Ann. Entomol. Soc. Am., 81, 152-156.
- Veen, J. C. Van & Wijk, M. L. E. Van 1985. The unique structure and functions of the ovipositor of the non-paralyzing ectoparasitoid *Colpoclypeus florus* Walk. [Hym. : Eulophidae] with special reference to antennal sensilla and immature stages. — J. Appl. Entomol., 99, 511-531.
- Wu, Z. X. & Qin, J. 1982. Ovipositional response of Trichogramma dendrolimi to the chemical contents of artificial eggs. Acta Entomol. Sin., 25, 363-372.
- Wylie, H. G. 1971. Oviposition restraint of *Muscidifurax zaraptor* [Hym.: Pteromalidae] on the parasitized housefly pupae. Can. Entomol., 103, 1537-1544.