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Research Article

Comparative Study of the Morphology of the Ovipositor of *Platygaster diplosisae* (Hymenoptera: Platygasteridae) and *Aprostocetus procerae* (Hymenoptera: Eulophidae) Two Parasitoids Associated with the African Rice Gall Midge, *Orseolia oryzivora* (Diptera: Cecidomyiidae)

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We studied the morphology of the ovipositor of *Platygaster diplosisae* (Hymenoptera: Platygasteridae) and *Aprostocetus procerae* (= *Tetrastichus pachydiplosisae*) (Hymenoptera: Eulophidae), two parasitoids associated with the African rice gall midge (AFRGM), and *Orseolia oryzivora* (Diptera: Cecidomyiidae). Scanning electron microscope techniques were used for this study. The ovipositor of *P. diplosisae* was short (40 μm), and most of the sensillae found on it were mechanoreceptors and located on the distal portion of the 3rd valvulae. These sensillae may be involved in selection of an egg or larval host. The shortness of this ovipositor may be an adaptation to a host whose egg envelope thickness is not more than 0.7 μm. The ovipositor of *A. procerae* was 30 times (1.2 mm) the length of the *P. diplosisae* ovipositor. It was not only well equipped with mechanoreceptive sensillae, but these sensillae were very diverse and distributed along the length of the valvulae. The 10 denticulations of the lancet of this ovipositor allow this parasitoid to exploit hosts that are not otherwise readily accesible. These two parasitoids share the same resource by infesting different life stages of the host. The ovipositor of each species of parasitoid enhanced resource sharing, due to its length and its sensillae type and distribution.

1. Introduction

The African rice gall midge (AfRGM), *Orseolia oryzivora* Harris & Gagné (Diptera: Cecidomyiidae), is an insect pest indigenous to Africa. It was considered a minor pest prior to the 1970s but has since caused increasingly severe damage to rice crops [1].

The young larva feeds on tillers at the growing point of the rice plant and induces the plant to form an oval, hollow gall. Each gall prevents production of a panicle. The amount of yield loss caused by the gall midge larva varies among rice varieties. Nacro et al. [2], and Williams et al. [3] showed that an increase in 1% in the percentage of tillers with galls at the stem-elongation stage reduced yield by 2 to 3%.

It has been reported that early and synchronized plantings of rice reduce the damage by the AfRGM [1]. Unfortunately, these cultural control methods are very often insufficient because of problems with water management and the conflicting management of both upland cereal crops and irrigated rice. The use of insecticides to control AfRGM is not ideal because of the cost, the risk to human health and the environment, and the destruction of natural enemies [4]. Furthermore, only systemic insecticides are likely to be effective in the control of the midge because of its feeding

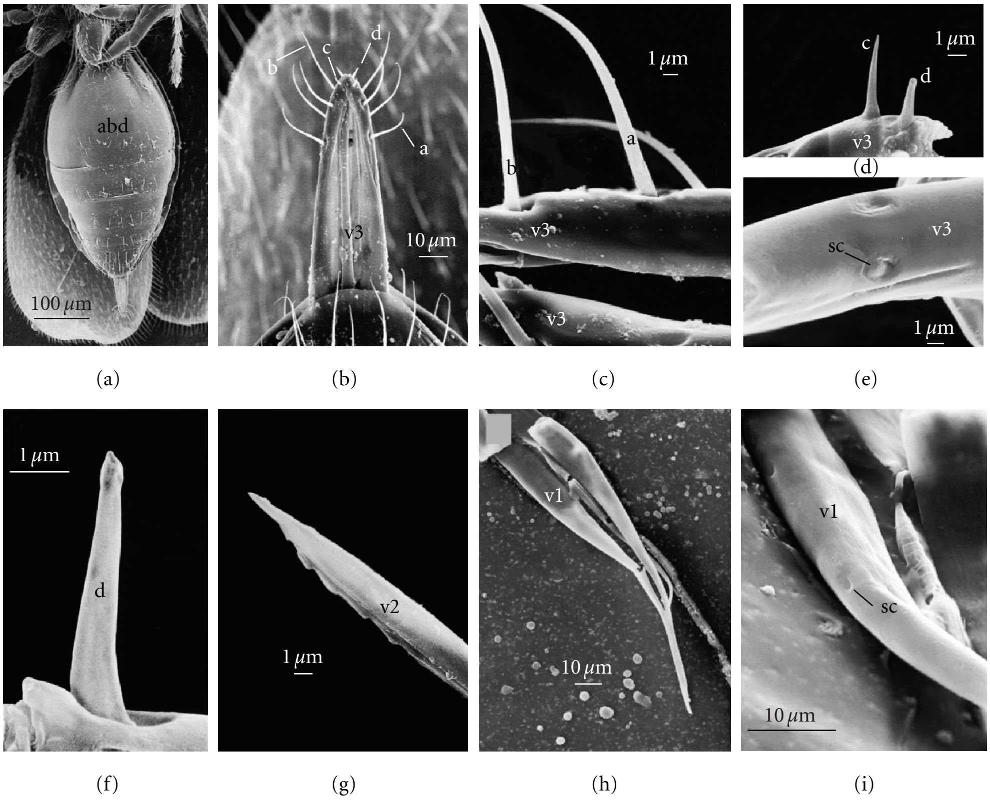

Figure 1: Ovipositor of *P. diplosisae*. (a) View of the abdomen showing the ovipositor at its distal end. abd: abdomen. (b) Front view of the ovipositor of *P. diplosisae*. Several sensillae are seen on the 3rd valvulae. a: trichoid sensillum of type a; b: trichoid sensillum of type b; c: sensillum of type c; d: sensillum of type d. (c) Valves 3 showing 2 types of trichoid sensillae. a: sensillum of type a; b: sensillum of type b. (d) Distal end of the 3rd valvulae with 2 types of trichoid sensillae. c: sensillae of type c; d: sensillae of type d. (e) Two campaniform sensillae located at the proximal portion of the 3rd valvulae. v3: 3rd valvula; sc: campaniform sensillum. (f) Sensillum of type d observed on the distal end of the 3rd valvula. d: sensillum of type d. (g) Distal end of the ventral part of a 2nd valvula viewed in profile. Five denticles are seen on this valvula. v2: 2nd valvula. (h) 1st valvula of the ovipositor. They appear large in their proximal portion and more and more slender near their distal end. v1: 1st valvula. (i) Two campaniform sensillae on the proximal portion of a 1st valvula. v1: 1st valvula.

habit inside plant tissue. The conservation of natural enemies of the AfRGM may be a good alternative to insecticidal control.

So far, little is known about the predators of AfRGM. Some egg predators have been reported [1]. These include tiny predatory mites (*Neoseiulus* sp., Phytoseiidae), the bug *Cyrtorhinus viridis* Linnavuori (Miridae), and the sword-tailed crickets *Anexipha longipennis* Serville, and *Trigonidium cicindeloides* Rambur (Gryllidae). Ladybird beetles (Coccinellidae) and the long-horned grasshopper *Conocephalus* (Tettigoniidae) are also egg predators. Two common parasitoids are known to be associated with the AfRGM. These are *Platygaster diplosisae* Risbec (Hymenoptera: Platygastridae) and *Aprostocetus procerae* Risbec (=*Tetrastichus pachydiplosisae*) (Hymenoptera: Eulophidae). These two parasitoids are the primary biological control agents. *P. diplosisae* is a gregarious larval parasitoid whereas *A. procerae* is a solitary pupal parasitoid of the AfRGM [5]. *P. diplosisae* oviposits inside the eggs or the larvae of AfRGM. The parasitoid's larvae hatch inside the young AfRGM larva. They feed inside the larva and kill it when it is fully grown. They then pupate inside the corpse, from which the adults emerge. The adults cut one or more very small exit holes in the gall and disperse. The adult *A. procerae* lays its eggs onto AfRGM pupae, or occasionally onto large larvae. It does this by piercing through the wall of the gall with the tip of its abdomen. The host is stung and paralyzed by the female parasitoid as the egg is laid. *A. procerae* feeds on, rather than inside, the host, and only one larva develops on each host. After it has finished feeding, the parasitoid larva changes into a pupa inside the gall. The adult that emerges cuts an exit hole in the gall to escape. Cumulative parasitism due to these two hymenopterans has been reported to reach 77% [6–9]. However, sometimes, such a high level of parasitism occurs too late to prevent damage by the pest.

The ovipositor of parasitic hymenopterans is primarily used to deposit an egg into or onto a host [9]. The structure of the ovipositor in different species of parasitic hymenoptera varies both in length and in its arrangement on the terminal metasomal segments. The general organization of the ovipositor includes 3-paired valvulae (1, 2, and 3), one paired valvifers. The paired 1st valvulae and the 2nd paired valvulae are fused in their distal portion to form the lancet, which is the piercing organ.

This study compares the ovipositor of *A. procerae* and *P. diplosisae* in terms of morphology and function of the associated sensillae. Furthermore, we hypothesize about the possible effect of the sensillae richness and diversity on the parasitism rate of *A. procerae* and *P. diplosisae.*

2. Material and Methods

Adult parasitoids were captured from irrigated rice fields in Burkina Faso and kept in a 90% alcohol solution and sent to France where all the laboratory work was completed. The average age of the specimen was 7. We used about 100 individuals of each parasitoid species in 5 replicates. Unfortunately, due to the smallness of the ovipositor of *P. diplosisae* only a few samples were observed under electron microscope. Ovipositors of *A. procerae* and *P. diplosisae* were dehydrated in successive alcohol solutions (70%, 80%, 95%, and 100%) and acetone solutions (50%, 70%, 90%, and 100%). Ovipositors were then mounted on a lead object-holder. Samples were critical point dried in a Balzers CPD 010 apparatus with liquid CO_2 gas and then gold palladium coated with a JEOL JFC-100 sputter. These samples were observed under a JSM 6400 electron-scanning microscope (JEOL Ltd, Japan).

3. Results

3.1. Description of the Ovipositor of Platygaster diplosisae. The ovipositor of *P. diplosisae* measures 40 μm in length (Figure 1(a)).

3.1.1. 3rd Valvulae. The paired 3rd valvulae are 40 μm in length and protect the 1st and 2nd valvulae when the ovipositor is at rest (Figure 1(a); see arrow). 3rd valvulae are connected distally, which causes a cone that has a slightly flat peak (Figure 1(b)).

3.1.2. 1st and 2nd Valvulae. The two pairs of 1st and 2nd valvulae are fused and form the ovipositor stylet (Figure 1(g)).

At rest, this ovipositor stylet is entirely embedded in the cavity of the 3rd valvulae (Figure 1(b)). The paired valvulae are larger in their proximal portion and come to a sharp point distally (Figure 1(h)). The extremity of the paired 2nd valvulae, also called the lancet, is equipped with five denticles (Figure 1(g); see arrow).

3.2. Sensillae on the Ovipositor of P. diplosisae. The sensillae on the ovipositor are relatively simple.

3.2.1. 3rd Valvulae. Two-thirds of these sensillae are campaniform sensillae whose external process is a dome embedded in a cuticular depression (Figure 1(e)). The distal 1/3 of the 3rd valvulae possesses four types of sensillae (Figures 1(b), 1(f)). Following is a list and description of the four sensillae types:

(i) 3 trichoid sensillae of type a, nonaligned. They are slightly curved and measure 12 μm in length.

(ii) 1 trichoid sensillum of type b, slightly straighter than the other three but as long as them (13 μm length) (Figures 1(b), 1(c)).

(iii) 1 unique sensillum of type c, 3 μm in length, so 4 times shorter than the trichoid sensillae described early (Figures 1(b), 1(d)). Unlike the trichoid sensillae, the base of the type c sensillum is not embedded in a cuticular depression. Its diameter is more continuous and its extremity is less sharp.

(iv) 1 unique sensillum of type d, located near the sensillum of the type c (Figures 1(b), 1(d), 1(f)). It measures 2.5 μm. The base is embedded in a depression similar to the trichoid sensillum. It is grooved and its extremity ends with a bludgeon. It measures 2.5 μm in length. This type of sensillum resembles the chaetica of type 1 observed by Van Baaren [10], on the antenna of *Epidinocarsis lopezi* (de Santis) (Hymenoptera: Encyrtidae) a solitary endoparasitoid of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae). The extremity of this sensillum which was not explored by scanning electron microscopy could bear a pore. The trichoid sensillae, the campaniform sensillae and the sensillum of type c may be mechanoreceptors.

3.2.2. 1st and 2nd Valvulae. The 1st paired valvulae are equipped with campaniform sensillae aligned on a line that runs the length of the valvulae (Figure 1(i)). These sensillae are the same type as those observed on the distal two thirds of the 3rd valvulae. These are mechanoreceptive sensillae similar to those described on the ovipositor valvulae of several hymenopteran parasitoids [11].

The size and the low number of ovipositors examined did not allow us to determine whether the 2nd valvulae are equipped with sensillae.

Table 1 summarizes the different types of sensillae and their possible function.

3.3. Description of the Ovipositor of A. procerae. The ovipositor of *A. procerae* consists of a stylet surrounded by the paired 3rd valvulae (Figure 2(a)).

3.3.1. 3rd Valvulae. These valvulae are largest proximally, but slightly sharp distally (Figure 2(b)). The internal surface of the 3rd valvulae has many cuticular spines (Figure 2(d); see arrow).

3.3.2. 1st and 2nd Valvulae. The ovipositor stylet of *A. procerae* is 1.2 mm in length, surrounded by the paired 3rd valvulae. The paired 2nd valvulae are coupled by the 1st valvulae. A sliding system allows the lancet formed by the fusion of the paired 2nd valvulae to move backward and forward. The lancet bears a notch that limits the movements of the paired 2nd and 1st valvulae. This lancet is 92 μm long and bears 10 denticles on its external surface (Figures 2(e), 2(f)). These denticles are increasingly smaller from proximal to distal, which gives the perforating system of the ovipositor its sharp form.

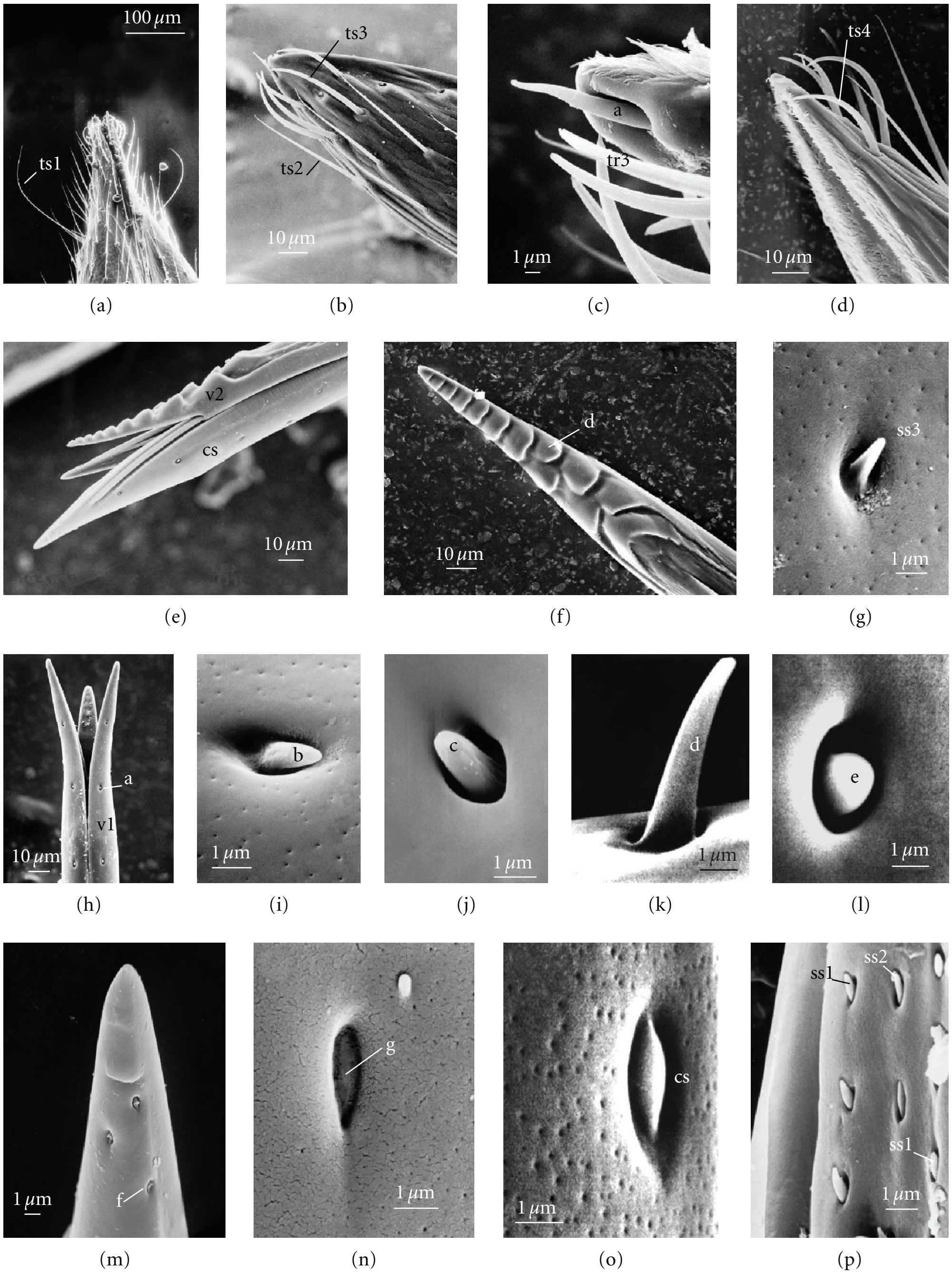

Figure 2: Ovipositor of *A. procerae*. (a) Extremity of the abdomen of *A. procerae* showing the valvulae at the distal end of the stylet. ts1: trichoid sensillum of type 1. (b) External surface of the distal end of a 3rd valvula bearing several types of trichoid sensillae; ts2: trichoid sensillum of type 2; ts3: trichoid sensillum of type 3. (c) Extremity of a 3rd valvula showing 3 sensillae of type 3. a: sensillum of type a. (d) Internal surface of the distal end of a 3rd valvula, viewed in profile. The interior of the valvula is empty. A trichoid sensillum of type 4 is seen. ts4: trichoid sensillum of type 4. (e) Distal extremity of the stylet of the ovipositor viewed in profile. The 2nd valvulae are carried by the 1st valvulae. v2: 2nd valvula; cs: campaniform sensillum. (f) Distal end of the dorsal surface of a 2nd valvula showing 10 denticulations making a united lancet. d: denticulation. (g) Styloconic sensillum of type 3 on the external surface of the proximal part of a valve 2. ss3: styloconic sensillum of type 3. (h) Distal extremity of the ventral part of the stylet of the ovipositor viewed in front. v1: valve 1; a: campaniform sensillum of type a. (i) Sensillum of type b located on the half proximal part of the external surface of a valve 1. b: sensillum of type b. (j) Sensillum of type c located on the half proximal part of the external surface of a valve 1. c: sensillum of type c. (k) Sensillum of type d, observed on the external surface of the proximal part of a valve 1. d: sensillum of type d. (l) Sensillum of type e, located at 120 μm of the distal extremity of a valve 1. e: sensillum of type e. (m) External surface of the distal extremity of a valve 1. The three sensillae of type f are distributed in triangle. f: sensillum of type f. (n) Sensillum of type g located at the half proximal part on the external surface of a valve 1. g: sensillum of type g. (o) Campaniform sensillum located at the 2/3 proximal of the a valve 1. cs: campaniform sensillum. (p) Three rows of styloconic sensillae of type 1 and 2 on the external surface of the distal extremity of a valve 3. ss1: styloconic sensillum of type 1; ss2: styloconic sensillum of type 2.

Table 1: Distribution of the sensillae on the ovipositor of *P. diplosisae*.

Type	Localization	Number	Length(μm)	Existence of an apical pore	Possible function
Campaniform mechanoreceptors	2/3 proximal of 3rd valvulae	—	—	—	—
Mechanoreceptors	Entire length of 1st valvulae 3rd valvulae	—	—	—	—
Trichoid a	1/3 distal	3	12	No	Mechanoreceptors
Trichoid b	Distal extremity of 3rd valvulae	1	13	No	Mechanoreceptors
c	Distal extremity of 3rd valvulae	1	3	No	Mechanoreceptors
d	Distal extremity of 3rd valvulae	1	2.5	Not sure	Chemoreceptors

Table 2: Distribution of the sensillae on the ovipositor of *A. procerae*.

Type	Localization (μm)	Number	Extremity	Length	Existence of an apical pore	Probable function
Trichoid 1	Proximal portion of 3rd valvula	1	Sharp	104	No	Mechanoreceptor
Trichoid 2	58 μm from distal extremity of 3rd valvula	The most common of the trichoid type	Slightly sharp	51	No	Mechanoreceptor
Trichoid 3	42 μm from the distal extremity of 3rd valvula	—	Slightly rounded	38	No	Mechanoreceptor
Type a	Distal extremity of 3rd valvula	1	Rounded	5.3	No	Mechanoreceptor
Type b	Distal of 1st valvula	Few	Rounded	0.9	No	Mechanoreceptor
Type c	Half proximal of 1st valvula	Few	Rounded	0.8	No	Mechanoreceptor
Type d	Proximal portion of 1st valvula	1	Rounded	0.47	No	Mechanoreceptor
Type e	120 μm from the distal extrimity of 1st valvula					
Type f	5 μm from the distal extremity of 1st valvula 3	3	Slightly rounded	0.4	Probable	Chemoreceptor
Type g	Half proximal of 1st valvula	—	—	—	—	—
Campaniform	2/3 proximal of 1st valvula	—	Rounded	2	—	Mechanoreceptor
Styloconic 1	Proximal portion of 1st valvula	—	Rounded	0.7	No	Mechanoreceptor
Styloconic 2	Proximal portion of 1st valvula	—	Rounded	0.7	No	Mechanoreceptor
Styloconic 3	Proximal part, interior surface of 2nd valvulae	3	Slightly sharp	0.7	No	Mechanoreceptor

Table 3: Main biological features of *O. oryzivora* (host), *Platygaster diplosisae*, and *Aprostocetus procerae* (parasitoids). (According to Nacro and Nénon, 2006.)

	Nature	Average potential fecundity	Average fertility	Eggs' envelopes thickness	Length of the ovipositor	Distribution of the sensorial organs on the ovipositor	Nature of the parasitism
O. oryzivora	host	High (300 eggs)	Medium (35.6)	Thin (0.7 μm)	—	—	—
P. diplosisae	parasitoid	Very high	Not assessed	Very thin	40 μm	Mainly distributed on the distal portion of valve 3 Mechanoreceptors and chemioreceptors	Gregarious endoparasitism of the egg or L1 of the host
A. procerae	parasitoid	Low	Not assessed	Thin	1.2 μm	well distributed on the different parts of the ovipositor Mechanoreceptors and chemioreceptors	Solitary ectoparasitism of the pupae of the host

3.4. Sensillae on the Ovipositor of A. procerae. The paired 3rd valvulae bear four types of sensillae, three of which are trichoid sensillae.

(i) Type 1: a long trichoid sensillum, 104 μm in length. It is located proximally (Figure 2(a)).

(ii) Type 2: this type of trichoid sensillum is the most common on the paired 3rd valvulae. These sensillae are nearly straight, 51 μm in length and distributed on the 3rd paired valvulae up to 58 μm from the base. They appear smooth when observed under the scanning electron microscope (Figure 2(b)).

(iii) Type 3: these are trichoid sensillae, 38 μm in length, curved and observed from 42 μm distally on the 3rd paired valvulae where 6 sensillae of this type are observed. They are channeled and slightly rounded distally (Figures 2(b), 2(c)).

(iv) Type A: this unique sensillum is observed at the proximal end of the 3rd paired valvulae. It is 5.3 μm in length and originates from a depression. It is slightly curved and half of its proximal part is sharper than its basal part. This styloconic sensillum is the shortest sensillum of all sensillae observed on the 3rd paired valvulae (Figure 2(c)).

3.4.1. 1st Paired Valvulae. The 1st paired valvulae are very rich in sensillae. Eight types of sensillae were observed on these valvulae.

(i) Type b: the external process is located in a large groove. This type of sensillum is located in the proximal half of the 1st paired valvulae. It is basiconic (Figure 2(i)).

(ii) Type c: basiconic sensillum has a large groove. The external process is prominent, almost perpendicular to the axis of the valvula (Figure 2(j)).

(iii) Type d: styloconic sensillum, unique, with an appearance similar to a trichoid sensillum. It is located basally and is 4.7 μm in length (Figure 2(k)).

(iv) Type e: a basiconic sensillum. Five sensillae of this type are arranged randomly, and the last one is located at 120 μm distally from the base of the valvula (Figure 2(l)).

(v) Type f: 3 sensillae arranged in a triangle at the distal portion of the valvulae (Figure 2(m)). The external process is short. In their morphology and distribution, these sensillae look like the sensilla observed by Le Ralec [11] on the 1st paired valvulae of *Encarsia formosa* Gahen (Hymenoptera: Aphilinidae), larval parasitoid of the greenhouse Aleyrodid *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrididae).

(vi) Type g: the process is stretched and embedded in a depression (Figure 2(n)).

(vii) Campaniform sensillum: the external process is a dome. This sensillum is located on the basal 2/3 of the valvulae. Its diameter is 2 μm (Figure 2(o)).

(viii) Styloconic sensillae of type 1 and type 2: one row of type 2 is enclosed by two rows of type 1. Type one has an external process that is entirely embedded in a depression. Three rows of styloconic sensillae are distributed on the external surface of the basic portion of the valvulae. They are 0.7 μm in length (Figure 2(p)).

3.4.2. 2nd Paired Valvulae. The sensillae on the paired 2nd valvulae are less abundant than those of the paired 1st valvulae.

They include

(i) styloconic sensillae of type 3. Three of these sensillae are observed on the basal external surface of the valvulae. Their external process is more developed than that observed on the other types of styloconic sensillae. This process appears erect and oblique as compared to the axis of the valvula. The sensillum is embedded in a narrow depression. Its external process is 0.7 μm in length (Figure 2(g));

(ii) sensillae of type g: they are located on the distal half of the valvula but are not illustrated.

The distribution of the sensillae on the valvulae of the ovipositor of *A. procerae* and their possible functions are summarized in the Table 2. The sensillae of the ovipositor of this eulophid are as abundant as diverse and probably mainly function as mechanoreceptors. The main biological features of the host (*O. oryzivora*) and its two parasitoids are presented in Table 3.

4. Discussion

Table 3 explains the main biological features of the host and its associated parasitoids. The reproductive biology of hymenopterans has been used to explain the nature of their parasitism. Price [12] showed that larval parasitoids of the wood fly, *Neodiprion swainei*, had a high fecundity and were gregarious. Their hosts were relatively abundant and easy to find. In contrast, the pupal parasitoids of the fly were ectoparasitoids with low fecundity. We are in a similar situation, where *P. diplosisae* and *A. procerae* share the same host at its different developmental stages due to the adaptations of their reproductive biology.

The ovipositor plays an essential role in the success of parasitism in Hymenoptera. Le Ralec [11], showed adaptive morphological features, according to the type of hosts, in 22 parasitoid hymenopteran species. These features are related not only to the morphology of the ovipositor (length and width of the diameter) but also to the quantity, the quality, and the way the sensillae are distributed on it. Thus, the species that easily access their hosts have ovipositors well equipped with mechanoreceptive sensillae spread along the length of the valvulae. The species that have difficulty accessing their hosts have poorly equipped ovipositors with mechanoreceptive sensillae that are generally grouped at the distal end of the valvulae. The case of these two parasitoid species associated with *O. oryzivora* is consistent with what was stated above.

Indeed, we have already observed that most of the sensillae found on the ovipositor of *P. diplosisae* are mechanoreceptors located essentially at the extremity of the 3rd valvulae. These sensillae may be important for host selection, which for this parasitoid is either an egg or a larva. So, these sensillae could "inform" the parasitoid on the status of the surface of the host. The sensillae of type B, observed at the extremity of the 3rd valvulae, probably of chemoreceptor type, could "inform" the parasitoid on the interior status (parasitized or unparasitized) of the host. Lastly, the short length of the ovipositor (40 μm) seems an adaptation to this type of host where the thickness of the egg envelope is not more than 0.7 μm.

The ovipositor of *A. procerae* is not only well equipped with mechanoreceptive sensillae, but these sensillae are diverse and distributed along the length of the valvulae. In addition to these features, the length of the stylet of the ovipositor (1.2 mm) is 30 times the length of the ovipositor of *P. diplosisae*, and the 10 denticulations of the lancet meet the conditions of a parasitoid that exploits a host that is less accessible. As for *P. diplosisae*, the very abundant mechanoreceptive sensillae observed at the distal end of the paired 3rd valvulae could be used by *A. procerae* to detect the substrate within which the host is located and to determine the depth at which it is located. The three chemoreceptive sensillae of type F observed at the distal end of the paired 1st valvulae could "inform" the parasitoid on the depth and the condition of the host. The length of the ovipositor has already been recognized as an adaptive feature for several parasitoids that exploit the same host, *Tryporyza incertulas* Walker, a lepidoperan rice stemborer whose egg masses have different layers [13]. The two parasitoid species examined share the same resource by infesting different stages of the host and by the ovipositor of each species differing in length and associated sensillae. In fact, the parasitic action of the two parasitoids may be complimentary.

The role of the two examined parasitoids in the natural regulation of the AfRGM has already been investigated by several authors [1, 4–7]. These parasitoids parasitize the midge simultaneously, and they can find and kill up to 70% of the immature populations of the pest. However, sometimes, such a high level of parasitism occurs too late in the season to prevent large AfRGM populations from building up and causing serious yield losses. The role of these parasitoids could be integrated into an Integrated Pest Management (IPM) strategy that could include also cultural control (early and synchronized planting, management of alternative hosts and fertilizer), host plant resistance, and chemical control.

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