# Sensory and glandular structures on the antennae of *Mantis religiosa*, *Iris oratoria* and *Rivetina baetica*: sexual dimorphism, physiological implications (Mantodea: Mantidae)

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## Abstract

The sexual dimorphism of antennal sensilla in three species of Mantodea Mantidae (*Mantis religiosa religiosa, Iris oratoria, Rivetina baetica tenuidentata*) has been studied with scanning electron microscope. Six sensillum types exist on the flagellum in both sexes of all species: multiporous sensilla coeloconica subtype I, multiporous sensilla coeloconica subtype II, multiporous sensilla trichodea subtype I, multiporous sensilla trichodea subtype II, aporous sensilla chaetica and uniporous sensilla chaetica. Two types are present only in one or two species: multiporous sensilla basiconica in *I. oratoria*, multiporous sensilla coeloconica subtype III in *M. religiosa* and *I. oratoria*. Aporous sensilla chaetica and aporous Böhm's sensilla are borne by the scape and the pedicel. Two distal circles of sensilla campaniformia are present on the pedicel. The sexual dimorphism concerns mainly the sensilla coeloconica subtype I which are present in large numbers in males (73-89%), unlike the females ( 12-51%), and the sensilla trichodea I and II, more numerous in females (39-83%) than in males (7-20%). An olfactive function, receptive of the sex pheromones is assigned to sensilla coeloconica I. Sensilla trichodea I, II and sensilla basiconica are olfactory receptors. Aporous sensilla chaetica are tactile. A terminal vesicle, unique among the Insects, is present in both sexes of the three species; it is probably a glandular structure capable of secreting a substance identifying sexual partners of the same species. Uniporous sensilla chaetica, with a gustative function, could react to this presumed substance.

**Key words**: Mantodea, Praying mantids, *Mantis, Iris, Rivetina*, antenna, sensilla, sexual dimorphism, terminal vesicle.

## Résumé

Le dimorphisme sexuel des sensilles antennaires chez trois espèces de Mantoptera Mantidae (*Mantis religiosa religiosa, Iris oratoria, Rivetina baetica tenuidentata)* a été étudié à l'aide du microscope électronique à balayage. Six types sensillaires existent sur le flagellum des deux sexes de toutes les espèces: les sensilles coeloconiques multipores de sous-type I, les sensilles coeloconiques multipores de sous-type II, les sensilles trichoïdes multipores de sous-type I, les sensilles trichoïdes multipores de sous-type II, les sensilles chétiformes sans pore, les sensilles chétiformes unipores. Deux types sont présents seulement dans une ou deux espèces : les sensilles basiconiques multipores chez *I. oratoria*, les sensilles coeloconiques multipores de sous-type III chez *M. religiosa* et *I. oratoria*. Les sensilles chétiformes sans pore et les sensilles de Böhm sont portées par le scape et le pédicelle. Deux cercles distaux de sensilles campaniformes sont présents sur le pédicelle. Le dimorphisme sexuel concerne essentiellement les sensilles coeloconiques I présentes en grands nombres chez les mâles (73-89%) contrairement aux femelles (12-51%) et les sensilles trichoïdes I et II plus nombreuses chez les femelles (39-83%) que chez les mâles (7-20%). Une fonction olfactive, réceptrice des phéromones sexuelles, est attribuée aux sensilles coeloconiques I. Les sensilles trichoïdes I, II et les sensilles basiconiques sont olfactives. Les sensilles chétiformes sans pore sont tactiles.

Une vésicule terminale, unique parmi les Insectes, est présente dans les deux sexes des trois espèces ; c'est probablement une structure glandulaire susceptible de sécréter une substance de marquage des partenaires sexuels d'une même espèce. Les sensilles chétiformes unipores, à fonction gustative, pourraient percevoir cette substance.

**Mots-clefs**: Mantodea, mantes, *Mantis, Iris, Rivetina*, antenne, sensilles, dimorphisme sexuel, vésicule terminale.

## Introduction

The antennal sensilla of Mantids have so far mainly been referred to in relation to their role in the reception of sex pheromones. Indeed, ROBINSON & ROBINSON's experiments (1979) demonstrated that males of *Acanthops falcata* STÅL, 1877 will fly toward virgin females in the pheromone-release posture even if visual cues are eliminated by a cloth partition between the males and the females. Similarly, males respond to pheromones in *Sphodromantis lineola* (BURMEISTER, 1838) (HURD *et al.*, 2004).

The first morphological study related to the antennae of Mantids was carried out by SLIFER (1968) in *Tenodera angustipennis* SAUSSURE, 1871 using light microscopy.

The more recent scanning electron microscopic studies concerned antennal sensilla of the female of a Mantidae Mantinae, *Sphodromantis viridis occidentalis* (WERNER, 1906), a species common in Morocco (FAUCHEUX, 2006b) and of the male of a

Mantidae Oxyothespinae, *Oxyothespis maroccana* BOLIVAR, 1908, a species present in the Essaouira and Souss region (FAUCHEUX, 2008). A brief paper revealed the abundance of a sensillum type, the "grooved pegs" in the male of *Mantis religiosa religiosa* (LINNÉ, 1758) (FAUCHEUX, 2005). A few sensilla types have been noted in two Australian species (HOLWELL *et al.*, 2007). No study dealt both with the male and female of the same species. The present paper proposes to compare the sensory equipment of antennae in both sexes of the two species of Mantidae Mantinae: *M. religiosa religiosa* and *Rivetina baetica tenuidentata* LA GRECA & LOMBARDO, 1982, and one species of Mantidae Tarachodinae: *Iris oratoria* (LINNÉ, 1758), all of which being common in Morocco.

## Material and methods

The mantids (3 male and 3 female adults of *M. religiosa*, 2 male and 2 female adults of *I. oratoria* and *R. baetica*) were captured in July and August 2003 and 2004 in the region of Essaouira (South West Morocco). For scanning electron microscope study (SEM), the heads were separated, dehydrated in absolute ethanol, mounted either on the ventral face or on the dorsal on specimen holders and coated with a thin layer of gold and palladium in a JFC 1100 sputter coater. Preparations were examined in a Jeol JSM 6400 SEM at different magnifications. The mean number of each sensillum type was calculated with SEM from the counts on every 5th flagellomere, and expressed as mean +/- SD. The terminologies of SCHNEIDER (1964), ZACHARUK (1985) and FAUCHEUX (1999, 2008) are used in naming the types of sensilla.

## Results

### A – Gross morphology of antennae
The antennae in both sexes of the three adult species are long and filiform. The antennal length and the number of segments attain, for the male and the female respectively, in *M. religiosa*: 23 mm, 79 segments; 22 mm, 74 segments; in *I. oratoria*: 16 mm, 81 segments; 16 mm, 79 segments; and in *R. baetica*: 28 mm, 125 segments; 21 mm, 113 segments. Each antenna comprises a scape, a pedicel, and flagellomeres (Fig.1). In all species, the scape is very long in comparison to the other segments (0.59 X 0.42 mm in *M. religiosa*) and is cylindrical (Figs. 1, 32). The pedicel is bulbous and slightly longer than it is wide (0.28 X 0.25 mm)

and it articulates distally with the flagellum (Figs 1, 33). The first flagellomere is distinguished by its length (325 μm) almost twice as long as the 10th flagellomere (Fig. 1); present in all mantids and cockroaches and principal growth centre in larval antennae, it is called the meriston (CAMPBELL & PRIESTLEY, 1970). The meristal flagellomeres are approximately flagellomeres 2-5 which are the new segments which emerge from the meriston at each ecdysis (Fig. 1). They are easily recognized at the base of the antennal flagellum because they are shorter than the more distal flagellomeres and carry fewer sensilla. It is only from the 10th flagellomere on that the segments acquire regular dimensions (325 X 265 μm) which they maintain over two thirds of the antenna. On the other hand, the distal flagellomeres, 325 μm long and 100 μm wide, are three times as long as they are wide.

### B – The different types of sensilla
The flagellum of all species bears 6 types and subtypes of sensilla: multiporous sensilla coeloconica subtypes I, II and III, multiporous sensilla basiconica, multiporous sensilla trichodea subtypes I and II, uniporous sensilla chaetica, aporous sensilla chaetica.

These sensillar types were observed in both sexes. Multiporous sensilla coeloconica subtype III and multiporous sensilla basiconica are present exclusively in one or two species.

The scape and the pedicel possess aporous "Böhm" sensilla and aporous sensilla campaniformia.

Approximately the first flagellomeres (the first ten in *M.religiosa*, for example) are poorly equipped in sensilla and especially in sensilla chaetica. A few morphological characteristics in the sensilla of *M. religiosa* are offered as examples in Table 1. The numerical data concerning the three species are in Table 2.

*1 – The multiporous sensilla coeloconica subtype I (MSC I)* are grooved or fluted pegs with a thick wall located in a depression of the cuticle which measures from 8 to 10 μm in diameter (Fig. 9). Some sensilla are straight and others are variously curved; the tip is blunt and sometimes bulbous (Figs. 9-13). These variations exist both over the length of a single antenna and in different species. Their fairly constant length (Table 1) can vary in the same species (Fig. 9). An ecdysial pore may sometimes be observed at the apex of the sensillum. The wall pores placed between the grooves are invisible in SEM.

Apart from a few aporous sensilla chaetica present on the first flagellomeres, it is the MSC I which appear first in large numbers on the male flagella. For example,
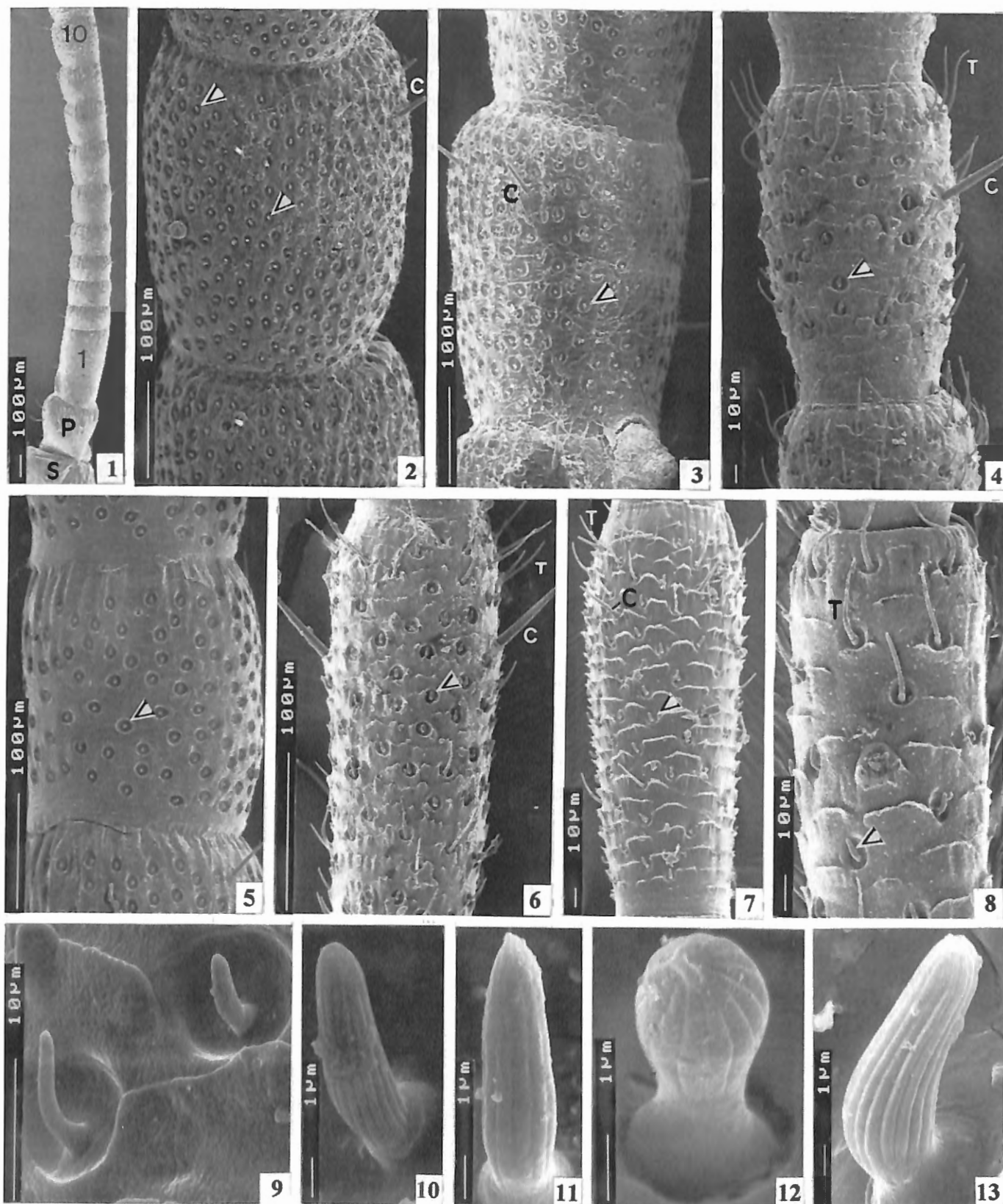
Figs 1-13. – Antennal sensilla of Mantids. **1-4.** *Mantis religiosa*; **1.** base of male antenna showing scape (S), pedicel (P), flagellomeres 1-10; **2.** ventral view of 11th male flagellomere with a majority of sensilla coeloconica I (arrows) and sensilla chaetica (C); **3.** dorsal view of the same flagellomere; **4.** ventral view of 16th female flagellomere with sensilla coeloconica I (arrows), trichodea (T) and chaetica (C); **5-6.** *Rivetina baetica*; **5.** ventral view of 19th male flagellomere; **6.** ventral view of 19th female flagellomere; **7-8.** *Iris oratoria*; **7.** ventral view of 23rd male flagellomere; **8.** ventral view of 23rd female flagellomere; **9-13.** sensilla coeloconica I; **9-10.** *M. religiosa* female; **11-12.** *R. baetica* male; **13.** *I. oratoria* female.

| Sensilla | Length | Basal width |
|---|---|---|
| Coeloconica I | 6.4 ± 1.5 | 1.4 ± 0.3 |
| Coeloconica II | 1.1 ±0.3 | 1.2 ±0.1 |
| Coeloconica III | 3.0 ± 0.2 | 2.4 ± 0.3 |
| Basiconica | 5.5 ± 0.4 | 2.1 ± 0.1 |
| Trichodea I | 36.7 ± 5.6 | 1.7 ± 0.2 |
| Trichodea II | 21.4 ± 2.3 | 1.6 ± 0.4 |
| Aporous chaetica | 108.7 ± 9.5 | 4.5 ± 1.6 |
| Uniporous chaetica | 32.4 ± 4.1 | 5.3 ± 0.9 |

Table 1 – Length and basal width (in μm) of sensilla on an antennal flagellum in *Mantis religiosa* (mean +/- S.D.)

in *M. religiosa*, they are absent on the 8th flagellomere, but take up the distal half of the 9th flagellomere, the distal two thirds of the 10th and the whole of the 11th flagellomere on which we counted 240 sensilla on the ventral face and 110 on the dorsal face (Figs. 2, 3). The number of sensilla is still considerable on 3/5ths of the flagellum but diminishes on the most distal segments (Fig. 19).

In males of all species, the MSC I are the most numerous sensilla (Table 2), and represent 89.3% (*M. religiosa*), 85.7% (*R. baetica*) and 73.4% (*I. oratoria*) of the total number of antennal sensilla (Figs. 2, 5, 7). In females, their number which is reducedt in *M. religiosa* (12%), is much less so in *R. baetica* (51%) and *I. oratoria* (46%) (Figs. 4, 6, 8).

**2 – The multiporous sensilla coeloconica subtype II (MSC II)** are dome-shaped pegs arising from the floor of a pit whose diameter of 5-6.6 μm is smaller than that of the MSC I (Fig. 14). The dome possesses an apical ecdysial pore and some grooves (Fig. 15). The wall pores are invisible in SEM. The sensilla which can easily be mistaken for MSC I, differ by their smaller but deeper pit; the sensillum dome does not rise above the surface of the antenna. They are present only on the distal half of the antenna, between 0 and 2 per flagellomere. They are mixed with the other sensilla on the distal part of the flagellmomere. Present in both sexes in the three species, the MSC II make up between 0.3 and 2.4% of the total number of sensilla.

**3 – The multiporous sensilla coeloconica subtype III (MSC III)** are absent in *R. baetica*. In the two other species, they are situated in a pit whose diameter is 4.1- 4.3 μm. They are the most difficult to identify:

they possess the form of a roughly conic structure with a wall showing finger-like expansions (Fig. 16). They appear from the 32nd flagellomere onwards in the male of *Mantis religiosa*, and from the 25th on in the female; from the 52nd and the 68th respectively in the male and the female of *I. oratoria*. The MSC III are situated in the distal half of the flagellomeres and in zones largely free of sensilla; their distribution is very irregular. Their number is less than 1% (Table 2).

**4 – The multiporous sensilla basiconica (MSB)** have only been observed in both sexes of *I. oratoria* which makes them difficult to distinguish from the sensilla coeloconica I. Their number is always limited, varying from 1 to 3% according to sex. In their form, they resemble on the whole the MSC I but they differ by the absence of grooves and by the presence of a few irregular striae towards the apex of the peg (Fig. 17). The whole of the wall is perforated by pores regularly spread out but more or less lined up near the apex. The pore density reaches about 56 pores/μm² (Fig. 18). The MSB are located in the distal half of the flagellomeres.

**5 – The multiporous sensilla trichodea subtype I (MST I)**
Two subtypes of sensilla trichodea can be distinguished in terms of length. The MST I are both more numerous and longer. They possess the form of a slightly curved hair whose length varies from 30 to 45 μm (Fig. 19). The wall is relatively thin (Fig. 21) and perforated with pores whose mean density is 26 pores/μm² (Fig. 20). They appear only from the 2nd quarter of the antenna onwards and are present up to the apex (Fig. 10) in all the species. They are always more numerous in the apical quarter of each flagellomere. In *R. baetica* and *M. religiosa*, the MST I are two or three times more numerous in the females than in the males whereas the numbers are equivalent in *I. oratoria* (table 2). In the females of the three species, they make up from 26 to 55% of the total number of antennal sensilla.

**6 – The multiporous sensilla trichodea subtype II (MST II)** are half the length of the MST I and are curved at the base; their apex is blunt (Fig. 22). The wall pores are spread out with no apparent order at the sensillum base (Fig. 23) but are subsequently lined up along the rest of the sensilla (Fig. 24). The pore density which reaches 60 pores/μm² is identical to that of the sensilla basiconica. The MST II are spread out among the preceding sensilla over the whole of the flagellomeres. As for the subtype I, the subtype II of sensilla trichodea is numerically better represented in the females of *M.*

| | Mantis religiosa | | Rivetina baetica | | Iris oratoria | |
|---|---|---|---|---|---|---|
| | Male | Female | Male | Female | Male | Female |
| Coeloconica I | 20360 (89.3) | 730 (12.5) | 15800 (85.7) | 5200 (51.1) | 3550 (73.4) | 840 (46.1) |
| Coeloconica II | 65 (0.3) | 59 (1.0) | 80 (0.4) | 73 (0.8) | 55 (1.2) | 45 (2.4) |
| Coeloconica III | 32 (0.1) | 25 (0.3) | 0 | 0 | 21 (0.4) | 14 (0.8) |
| Basiconica | 0 | 0 | 0 | 0 | 64 (1.3) | 57 (3.2) |
| Trichodea I | 990 (4.4) | 3200 (55.2) | 1580 (8.6) | 3410 (33.5) | 540 (11.2) | 464 (25.7) |
| Trichodea II | 530 (2.3) | 1630 (28.1) | 475 (2.6) | 1080 (10.6) | 452 (9.3) | 238 (12.9) |
| Aporous chaetica | 435 (1.9) | 120 (2.6) | 330 (1.8) | 280 (2.7) | 113 (2.3) | 106 (5.8) |
| Uniporous chaetica | 390 (1.7) | 22 (0.3) | 170 (0.9) | 130 (1.3) | 48 (0.9) | 56 (3.1) |
| Total | 22802 | 5786 | 18435 | 10173 | 4843 | 1820 |

Table 2. – Average numbers and percentages ( ) of sensilla on a male and female antennal flagellum of *Mantis religiosa*, *Rivetina baetica* and *Iris oratoria*.

*religiosa* and *R. baetica* whereas the contrary is the case in *I. oratoria*. The numbers of sensilla trichodea I and II are limited in males (7-20%) but very large in females (38-83%). With sensilla coeloconica I, the sensilla trichodea I and II constitute the majority of the antennal sensilla, respectively up to 96.0% and 95.8% (*M. religiosa*), 96.9% and 95.2% (*R. baetica*), 93.9% and 84.7% (*I. oratoria*) in the males and females.

**7 – The aporous sensilla chaetica (ASC)** are the most easily identifiable sensilla, as well as the thickest and the longest of the antennae to which they give a bristly aspect. They have the shape of a sharp, rigid thorn with some twenty grooves but without pores, and articulated at the base (Figs. 25, 26). Their wall is thick and the sensillar channel is narrow (Fig. 26). Their maximum length varies according the species and sex: for the male and female respectively, it reaches 95μm and 140 μm (*M. religiosa*), 50 μm and 65 μm (*R. baetica*), 25 μm and 28 μm (*I. oratoria*). They are arranged perpendicularly with regard to the antenna in level with the first flagellomeres but subsequently they form an angle of 45° (Figs. 4, 6, 19). The ASC appear from the meriston, first one sensillum then two on the flagellomeres 2-9. In *M. religiosa*, it is only from the 10th

flagellomere that they form a distal circle of 6-8 sensilla which persists over most of the antenna (Fig. 25). Their distribution is less evident on the distal flagellomeres (Fig. 19). The number of sensilla is greater in the male than in the female of *M. religiosa* and *R. baetica* but is almost identical in both sexes of *I. oratoria* (Table 2).

**8 – The uniporous sensilla chaetica (USC)** are difficult to distinguish from aporous sensilla chaetica. They do however differ by their position on the flagellomere, outside the circle of ASC (Fig. 27); by their shorter length (Fig. 28, Table 2); by a larger number of grooves (about thirty) and by the arrangement in herring-bone pattern of these grooves at the base of the sensillum (Fig. 29). A break at the base of the sensillum reveals a narrow circular cavity surrounded by the dendritic sheath, and a second, arc-shaped cavity partly obscured on the photo by cuticular material belonging to the wall (Fig. 30). Such a hair comprising two internal channels is characteristic of uniporous sensilla (ZACHARUK, 1980). The terminal pore is situated at the base of a semi-circular swelling of the cuticle (Fig. 31). The USC were identified in both sexes of the three mantids; they are rarer than the ASC and slightly more numerous in the males (Table 2).

## 9 – The aporous Böhm's sensilla (ABS)

Aporous sensilla chaetica and sensilla campaniformia are the only sensilla on the scape and the pedicel. The most characteristic aporous sensilla chaetica are the Böhm's sensilla which form groups in hair plates, located on the proximal parts of the scape (Fig. 32) and of the pedicel (Fig. 33, arrows). A hair plate is made up of 15-20 aporous sensilla chaetica, 17-33 μm long, and smooth-surfaced. Other longer aporous sensilla chaetica, 45-80 μm long, are scattered over both two segments. Some of them form a distal circle of about ten sensilla on the pedicel (Fig. 33).
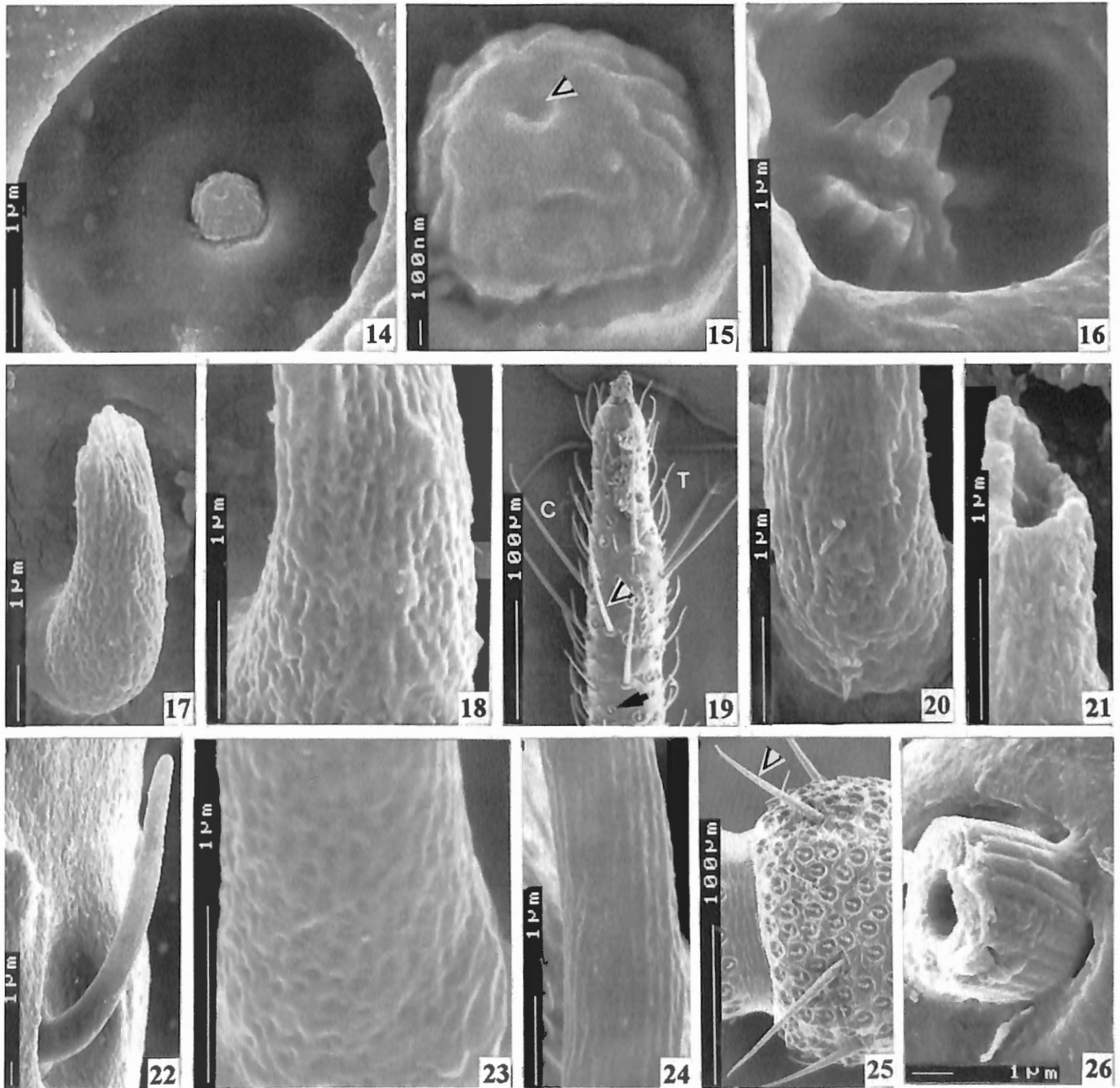


Figs 14-26. – Antennal sensilla of Mantids. **14-16.** *Mantis religiosa* female; **14-15.** sensillum coeloconicum II with ecdysial pore (arrow); **16.** sensillum coeloconicum III ; **17-18.** *Iris oratoria* male, sensillum basiconicum; **19.** *M. religiosa* female, apical flagellomere showing aporous sensilla chaetica (C), uniporous sensilla chaetica (white arrow), sensilla trichodea (T) and rare sensilla coeloconica I (black arrow); **20-21.** *I. oratoria* male, base and broken hair of sensillum trichodeum I; **22-24.** *Rivetina baetica* male, sensillum trichodeum II, base, median part; **25.** *M. religiosa* male, aporous sensilla chaetica (arrow); **26.** *I. oratoria* female, broken base of aporous sensillum chaeticum.
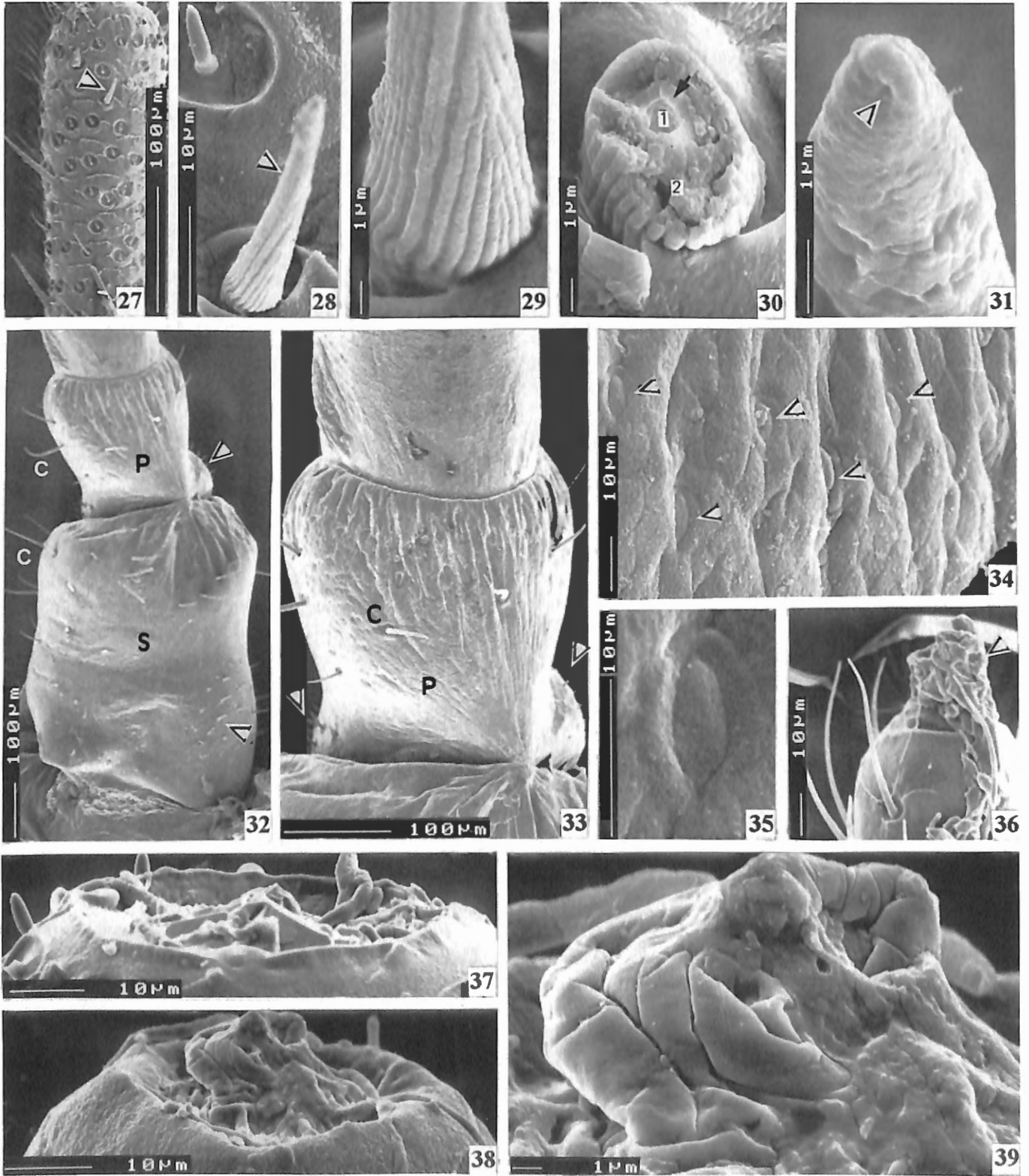
Figs 27-39. – Sensory and glandular structures of Mantids. **27-31**. *Rivetina baetica* male; **27**. uniporous sensillum chaeticum (arrow) on the 72$^{nd}$ flagellomere; **28**. uniporous sensillum chaeticum; **29**. base; **30**. break through the base showing cavities 1 and 2, and dendritic sheath (arrow); **31**. terminal pore (arrow); **32-35**. *Mantis religiosa* male; **32-33**. Böhm's sensilla (arrows) and aporous sensilla chaetica (C) on the dorsal face of scape (S) and pedicel (P); **34-35**. sensilla campaniformia on the distal part of pedicel (arrows), detail; **36-37**. terminal vesicle of *M. religiosa* female; **38-39**. terminal vesicle of *M. religiosa* male.

*10 – The sensilla campaniformia (SC)* are arranged in two close-set circles of about 20 sensilla each at the distal part of the pedicel (Fig. 34). Each sensillum, 11.4 μm long and 7.4 μm wide, forms an oval dome whose principal axe is parallel to the longitudinal axe of the pedicel (Fig. 35).

## C – The vesicular apical structure

A vesicular structure is present at the tip of the terminal flagellomere in antennae of both sexes of the three mantids (Figs. 36-39). Its crumpled appearance, probably due to the dehydration of the antenna, suggests that the vesicle has a thin wall that is very little sclerotized and that it normally contains a liquid. It is more or less extended on the preparations with SEM. When it is clearly retracted, it can be seen that it derives from a considerable depression in the apex of the antenna (Fig. 38). Contrary to the antennal cuticle which is formed of smooth scales, the cuticle of this vesicle is made up of papilla and finger-like expansions, and is sometimes pierced by pores 0.6 μm in diameter (Fig. 39). The basal diameter of the vesicle is of about 50 μm in the female (Fig. 36) and 25 μm in the male of *M. religiosa* (Fig. 38).

## Discussion

### A - Comparison with other Mantids

Ten sensillar types or subtypes have been described in the three Mantidae; this is two types more compared with *O. maroccana* (FAUCHEUX, 2008). Two types, the multiporous sensilla coeloconica II and III, have never been mentioned in other mantids (SLIFER, 1968; FAUCHEUX , 2006b) and only rarely in other insects; they are always found in reduced numbers in the three species. Another essential difference is the presence of uniporous sensilla chaetica in the three Mantidae and their absence in *O. maroccana*. These sensilla had been revealed by SLIFER (1968) in *Tenodera* sp.

The number of sensillar types (6-8) described on the flagellum of the three Mantidae is significantly larger than that indicated by HOLWELL *et al.* (2007) in two other Mantodea. These authors mention only short and long « trichoid sensilla » (= sensilla chaetica according to SCHNEIDER, 1964 and FAUCHEUX, 1999) with a presumed mechanosensory or gustatory function in both sexes of *Ciulfina biseriata* (WESTWOOD, 1889) (Liturgusidae Liturgusinae) and females of *Pseudomantis albofimbriata* (STÅL, 1860) (Mantinae). Only the males of *P. albofimbriata* possess in addition numerous « sensilla basiconica » analogous to the MSC I. The presence of these sensilla in the latter species belonging to the family of Mantidae, like our three species, shows that the MSC I are common to Mantidae Mantinae. Their absence in *C. biseriata* is perhaps related to its classification in another family. In our opinion, these mantids probably possess other sensillar types which have gone unnoticed because of their rarity. What is more, the absence of multiporous sensilla trichodea is surprising but the authors were not looking for pores on the sensilla of *C. biseriata* and *P. albofimbriata.*

The essential characteristic opposing *Oxyothespis* (Oxyothespinae) to Mantinae and Tarachodinae is the presence in that species of aporous sensilla filiformia (48% of antennal sensilla).These sensilla, which are vibration receptors, are useful in the small, vulnerable mantis to warn it of the arrival of a prey or a predator. They can also functionally replace the ears which are absent in *Oxyothespis*. On the other hand, the three Mantidae are provided with functional well developped ears and, being large species, are capable of defending themselves. In Essaouira (Morocco), we have had the occasion of observing an adult male of *O. maroccana* struggling with a juvenile of *M. religiosa* of the same length but twice as robust; the advantage was clearly in favour of the juvenile mantid. Thus, the antennal and the cercal sensilla filiformia (FAUCHEUX, 2009b) warn *O. maroccana* of a danger, both from frontal and from behind. In the three Mantidae, only the cerci bear sensilla filiformia (pers. obs.).

In the chapter « Results », we have frequently underlined the resemblances between *M. religiosa* and *R. baetica* (large number of sensilla, notable sexual dimorphism as regards the number of sensilla coeloconica subtype I, presence of sensilla basiconica) in contrast to *I. oratoria* (smaller number of sensilla), less visible sexual dimorphism of sensilla trichodea I and II). These differences could be justified by a recent classification of the Mantodea (EHRMANN, 2002) which leaves *M. religiosa* and *R. baetica* in the family of the Mantidae but isolates *I. oratoria* in that of the Tarachodidae.

### B – Morphological and physiological implications

The MSC I have been called "multiporous sensilla basiconica subtype I" in *O. maroccana* (FAUCHEUX, 2008) and "sensilla coeloconica" in *M. religiosa* and *S. viridis* (FAUCHEUX, 2005, 2006b). They would be better classified in the coeloconic type. Indeed, according to

SCHNEIDER (1964), sensilla coeloconica or « sensory pit pegs » are cones on the floor of depressions in the antennal cuticle and the cone's wall appears fluted in cross section. Sensilla morphologically similar to MSC I, referred to as sensilla coeloconica, exist in the orthopterans *Locusta migratoria* (LINNAEUS, 1758) (ALTNER *et al.* 1981) and *Schistocerca gregaria* (FORSKÅL, 1775) (OCHIENG *et al.*, 1998).

Certain MSC I of *M. religiosa* resemble antennal grooved pegs described in culicine mosquitoes which are thick-walled, non-articulated pegs with 12 grooves in the wall and bearing one terminal pore. According to McIVER (1974), although these grooved pegs have the structure commonly associated with contact chemo-receptors, they function exclusively in the reception of air-borne stimuli and therefore are olfactory receptors. ALTNER & PRILLINGER (1980) consider the grooved sensilla as double-walled sensilla to which a chemoreceptive function is assigned. The pores are not visible in SEM but slit-like pores forming redial channels are located in grooves and are visible in transmission electron microscopy (HALLBERG, 1982).

The abundance of the MSC I and the strong sexual dimorphism in the three species suggest that these sensilla are the major pheromone receptors in Mantidae. This fact is uncommon for, in insects, it is usually the sensilla trichodea which are the receptors of sexual pheromones. However, receptors of female odours are short basiconic sensilla in male cockroaches, which are closely related to mantids (BOECKH, 1984).

For many mantids, it seems reasonable to assume that the majority of copulations begin during the day because finding, approaching, and mounting a female may involve a number of visual cues (MAXWELL, 1999). However, LAWRENCE (1992) reported that male *M. religiosa* arrive at cages of females during the night; in this case, the males fly in search of females guided, presumably, by the pheromones. The first mantid sex pheromone has been identified by HURD *et al.* (2004) who prepared a synthetic mixture of the pheromone compounds and found that males were both attracted to this mixture and stimulated to exhibit typical precopulatory behaviour.

The interest for the males to possess a very large number of MSC I from the 10th flagellomere on, is to offer them possibilities to encounter females, even if their antennae are partially amputated. The predominance of these sensilla, to the exclusion of other types in the proximal region of the antennae, may mean that their function is essential.

One may ask what is the function of the MSC I in females, a function whose importance is limited in *M.*

*religiosa* (12%) but considerable in *R. baetica* (51%) and *I. oratoria* (46%). In Lepidoptera, whose sensilla trichodea possess the sex pheromone receptors, the trichoïd sensilla of females responded to the female sex pheromone (DEN OTTER *et al.*, 1978) but were 10-100 times less sensitive to sex attractants than those of males. The same situation is likely for the MSC I of mantids.

The MSC II resemble "pit organs" present on the flagellum of a lamellicorn beetle, which are thick-walled with a supposed dendritic shaft (ÅGREN, 1985), as well as the "sensilla coeloconica without grooves" of *L. migratoria* (ALTNER *et al.*, 1981) and "type II coeloconic" of *Gryllus bimaculatus* (ITOH *et al.*, 1984) which are thermo-hygroreceptive sensilla. They are also close to the sensilla coeloconica types I and II of the imagines of odonats (SLIFER & SEKHON, 1972; FAUCHEUX, 2009a). A hygroreceptive function is attributed to the latter sensilla (REBORA *et al.*, 2006). The limited number of these sensilla in the three mantids is identical to the number of hygroreceptive sensilla in other insects (FAUCHEUX, 1999).

The MSC III are rare in the Higher Insecta only a few sensilla having been found on the antennae of the tineid moth *Monopis crocicapitella* (CLEMENS, 1859) (FAUCHEUX, 2006a). They are present in the odonat *Brachythemis leucosticta* (FAUCHEUX, 2009a). A hygroreceptive function has been suggested for this type of sensillum coeloconicum (REBORA *et al.*, 2006). However, the coexistence in *M. religiosa* of MSC II and MSC III, which have a very different aspect and, nevertheless, an identical function, does little to support this interpretation.

The MSB resemble the "sensilla basiconica" of *S. gregaria* (OCHIENG *et al.* 1998). Their pore density is superior to that observed on the sensilla basiconica of Lepidoptera where it varies from 30 to 40 pores/$\mu m^2$ (FAUCHEUX, 1999). In many insects, the sensilla basiconica are involved in the search for food and oviposition sites (FAUCHEUX, 1999). According to HARMER & SHIPLEY (1922) AND PRETE *et al.* (1992), when sufficiently deprived, at least two species of mantids (*T. sinensis* and *S. lineola*) will eat fruit which apparently they identify by olfaction, and locate by olfaction, taste and vision. The sensilla basiconica of *I. oratoria* may be involved in this unusual search for food.

The MST I and MST II are analogous to "sensilla trichodea" of *S. gregaria* (OCHIENG *et al.*, 1998). In accordance with their structure, multiporous sensilla trichodea are olfactory receptors (ZACHARUK, 1985; FAUCHEUX, 1999). According to species, these sensilla can be from two to twelve times more numerous in

females than in males; they must presumably be involved in other behaviour besides sexual behaviour. Thus, in field studies concerning *M. religiosa*, females were found to move as far as males during a given period of time, it was probably the search for prey and oviposition sites – not for males – that influenced movement by the females (LAWRENCE, 1992). If the MSC I perceive odours at a great distance, the other multiporous sensilla are involved in short distance perception. They can be sensitive to odours emitted by male or female glands (see below the role of the terminal vesicle).

The ASC are mechanoreceptors conferring a tactile function to antennae (ZACHARUK, 1985; FAUCHEUX, 1999). The presence of these sensilla along the whole length of the long antennae of the mantids up to the apex allows the latter to enter into physical contact from a long distance with their environment. It is possible that the antennal drumming that sometimes precedes prey capture conveys mechanosensory and/or olfactory cues to mantids (PRETE, 1999). Previous to prey capture, the antennae, thanks to the sensilla chaetica, could help to determine the optimum mantid-prey distance for hitting and, consequently, to establish the relationship between this maximum distance and the length of the raptorial forelegs.

The USC are gustative receptors (ZACHARUK, 1985), which can intervene during sexual behaviour. When the partners are in contact with one another, the male of *Tenedora sinensis* SAUSSURE, 1871 approaches the female, slowly and with vigorous antennal movements (LISKE & DAVIS, 1987). When a male and a female of *M. religiosa* meet to, it sometimes happens that the male's antennae touch the one of the female and the latter responds in its turn with antennal contacts (pers. obs.). When the male mounts the female, it palps the female's abdomen with its cerci and, simultaneously, the male's antennae lash about the female's head (DAVIS & LISKE, 1988). During this behaviour, the aporous sensilla chaetica and also the uniporous sensilla chaetica present on each flagellomere are stimulated. The latter thus receive gustatory information from the terminal vesicle.

The ABS in insects functions as proprioceptors for the cephalic-scape and scape-pedicel joints. When the antennal position is changed, the sensilla are bent by the cuticle of the neighbouring segment and the head or by the joint membranes. The ASC are proprioceptors which detect stresses applied to the surface of the cuticle. Since the sensilla occur on the distal part of the pedicel, it is thought that they detect bending of the flagellum against the pedicel.

**C – Putative function of the terminal vesicle:**

The vesicular apical structure was pointed out by SLIFER (1968) in both sexes of *T. angustipennis*; it is a soft, transparent, thin-walled bladder from 40 to 50 µm in length. When the antenna is placed in a dye, such as methylene blue or crystal violet, stain enters through the bladder. But the author has been unable to determine whether the vesicle is truly permeable or whether the dye has entered through abraded spots in the thin wall. Our observations show that this vesicle is perforated and that it can release the secretion it contains.

Earlier observations by ROEDER (1935) show that the tips of the antennae in both sexes of *M. religiosa* may touch lightly the prey before it is seized and that the male touches the female's wings with his antennae when close to her. GURNEY (1950) also says that the prey may be touched by the antennae of mantids before seizure. During mating, the male intermittently flagellates the female's head with his antennae (ROEDER, 1963). Thus, when predation and pre-copulatory behaviour take place, the vesicle enters into contact with the prey or the partner. The aspect of the vesicle in SEM reveals that it may be distorted by contact. In certain hymenopteran insects, marking pheromones allow males to mark the females and to reduce the attractiveness of the latter by other males (VELTHUIS & CAMARGO, 1975). The antennal terminal vesicle of mantids may contain a marking substance which during contact could be secreted by the pores of the vesicle. This substance could mark the prey, which would prevent the covetousness of a con-specific, or impregnate the sexual partner, which would repulse other suitors (the other males may be repelled by secretion deposited by a first male). Indeed, males of other insects are known to release pheromone repellent to intrasexuals during close range intra- or intersexual encounters (PROKOPY *et al.*, 1984). Thus, a male armyworm moth, when courting a female, releases a pheromone which not only has an aphrodisiac effect upon the female, but may inhibit the approach and courtship activity of other con-specific males (HIRAI, 1982).

The existence of a terminal vesicle in females is more difficult to explain. However, LISKE & DAVIS (1987) reported in the mantid, *T. sinensis*, a behaviour that has not been described in other species. A few females approached males and touched them with their antennae before the males attempted to mount them. SLIFER (1968), who has also studied this species, makes it clear that no important differences were found between the antennae of *T. angustipennis* and that of *T. sinensis*. One may therefore suppose that the latter also

possesses the terminal vesicle whose secretion marks the male. If such behaviour exists in our three species, the secretion would allow two con-specific partners to recognise each other. The impregnated male would be recognised by the other females of the same species or of a different one and would not be accepted by them.

According to SLIFER (1968), the vesicle may serve as part of a mechanoreceptor system. Our present understanding of the mechano-receptive organs in insects does not allow us to retain this hypothesis. Besides, this author finds a resemblance between the vesicle of the mantid *T. angustipennis* and a two-parted structure present at the distal end of the antenna of the mosquito *Aedes aegypti* (LINNAEUS, 1762) (SLIFER & SEKHON, 1962). In fact, this latter structure is composed of two sensilla coeloconica borne by a terminal extension of the antenna which hardly resembles the vesicle of mantids (MCIVER, 1973). The presence of the terminal vesicle in several genera of Mantids (*Tenodera, Mantis, Iris, Rivetina*) leads one to suppose that this is frequent in the Mantodea.

## Acknowledgements

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