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Antennal sensilla of the male praying mantid *Oxyothespis maroccana* Bolivar, 1908 (Insecta: Mantodea: Mantidae): distribution and functional implications

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Abstract. The sensory organs of the male antenna of the praying mantid *Oxyothespis maroccana* are studied by means of scanning electron microscopy. The scape and the pedicel bear two sensillum types: aporous sensilla chaetica and sensilla campaniformia. Four sensillum types are present on the flagellum composed of 73 flagellomeres: aporous sensilla filiformia, aporous sensilla chaetica, multiporous sensilla basiconica of two subtypes, multiporous sensilla trichodea. No uniporous sensillum has been observed. The most characteristic sensilla on the antenna of *Oxyothespis* are the sensilla filiformia which make up 48% of the total of the flagellum sensilla. A function receptive of air currents and of low-frequence sounds is assigned to them. The sensilla chaetica of flagellum are tactile mechanoreceptors; those grouped in hair plates on the scape are proprioceptors monitoring the movements of the antenna in conjunction with the head. The pedicel sensilla campaniformia are proprioceptors which detect any bending of the flagellum against the pedicel. An olfactive function, receptive of the airborne pheromone, is assigned to sensilla basiconica of subtype I, present in great numbers on the male antenna. Sensilla basiconica of subtype II and sensilla trichodea are probably responsible for the detection of odours in the insect's environment, i.e. for determining the suitability of foraging sites for oviposition.

Key words: *Oxyothespis*, Mantidae, antenna, sensilla, morphology, filiformium, chaeticum, basiconicum, trichoïdeum, aporous, multiporous.

Les sensilles antennaires du mâle de la mante *Oxyothespis maroccana* Bolivar, 1908 (Insecta: Mantodea: Mantidae): distribution et implications fonctionnelles.

Résumé. Les organes sensoriels de l'antenne du mâle de la mante religieuse *Oxyothespis maroccana* ont été étudiés à l'aide de la microscopie électronique à balayage. Le scape et le pédicelle portent deux types de sensilles: des sensilles chétiformes sans pore et des sensilles campaniformes. Quatre types sensillaires sont présents sur le flagelle de 73 segments: des sensilles filiformes sans pore, des sensilles chétiformes sans pore, des sensilles basiconiques multipores de deux sous-types, des sensilles trichoïdes multipores. Aucune sensille unipore n'a été observée. Les sensilles les plus caractéristiques de l'antenne d'*Oxyothespis* sont les sensilles filiformes qui constituent 48% de l'ensemble des sensilles du flagelle. Une fonction réceptrice des courants d'air et des sons de basse fréquence leur est attribuée. Les sensilles chétiformes du flagelle sont des mécanorécepteurs tactiles; celles du scape groupées en aires pilifères sont des propriocepteurs enregistrant les mouvements de l'antenne par rapport à la tête. Les sensilles campaniformes du pédicelle sont des propriocepteurs qui enregistrent la courbure du flagelle par rapport au pédicelle. Une fonction olfactive, réceptrice de la phéromone sexuelle femelle, est attribuée aux sensilles basiconiques du sous-type I, présentes en grands nombres sur l'antenne mâle. Les sensilles basiconiques du sous-type II et les sensilles trichoïdes sont probablement sensibles aux odeurs dans l'environnement proche de l'insecte, par exemple lors de la recherche de sites convenables pour la ponte.

Mots clés : *Oxyothespis*, Mantidae, antenne, sensilles, morphologie, filiforme, chétiforme, basiconique, trichoïde, sans pore, multipore.

INTRODUCTION

The praying mantids are diurnally active insects whose large eyes and excellent vision dominate their sensory world (Prete & Wolfe 1992, Prete 1999). At least some mantids are active both at night and during the day. Courtship is not simple in these insects and one nonvisual sense, olfaction, certainly plays an important role (Yager 1999). Pheromones, in conjunction with visual and tactile cues, are an important feature of the reproductive biology of many species of mantids (Robinson & Robinson 1979, Maxwell 1999, Hurd *et al*. 2004, Holwell *et al*. 2007). Males respond to pheromones in a number of genera, including *Sphodromantis lineola* (Burmeister, 1758) (Hurd *et al*. 2004), *Mantis religiosa* (Linnaeus, 1758), *Empusa pennata* (Thunberg, 1815) (Gemeno *et al.* 2005), and *Hierodula patellifera* (Serville, 1839) (Perez 2005).

The role of the antennae in the mantids has been evoked by several authors. The tips of the antennae of *M. religiosa* can brush against the prey before it is seized (Roeder 1935, Gurney 1950). With its antennae, the male of the same species touches the wings of female when close to her and, during mating, it intermittently flagellates the head of the female (Roeder 1935, 1963). However, Rau & Rau (1913) declare that the males of *Stagmomantis carolina* Johannson, 1763, with one or both antennae removed, mate normally with females. According to Crane (1952), the antennae of some Trinidad mantids are not needed for normal defensive behaviour but, in the presence of lizards, the antennae quiver in an exaggerated way, which suggests that the mantid reacts to odours.

An early study (Slifer 1968), which does not use the scanning electron microscope, describes four types of chemoreceptive sensilla on the antennal flagellum of the mantid *Tenodera* sp. Recently, the observation of *Sphodromantis viridis occidentalis* (Werner, 1906) (Faucheux 2006) has revealed the existence of one type of mechanoreceptor and three types of chemoreceptor. In two

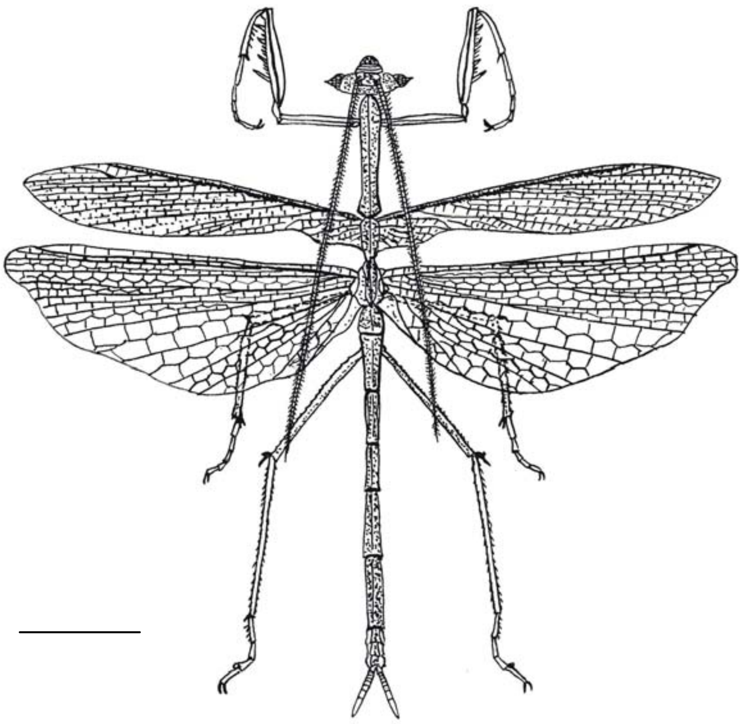


Figure 1. *Oxyothespis maroccana*, male adult. Scale = 5 mm.

Australian species, Holwell *et al.* (2007) described long and medium sensilla trichodea in female, short sensilla trichodea and sensilla basiconica in male *Pseudomantis albofimbriata* (Stal, 1860), long and short sensilla trichodea in both sexes of *Ciulfina biseriata* (Westwood, 1889). The present study concerns the male of a small moroccan mantid, *Oxyothespis maroccana* Bolivar, 1908 (Mantidae), whose sensory antennal structure is compared with that of previously studied species.

MATERIAL AND METHODS

The specimen of *Oxyothespis maroccana* studied, a male adult, was captured by us on 26 June 2001, on the atlantic coast, just behind the Lazari beach between Essaouira and Diabat, in an environment corresponding to a "erme arbustif " according the terminology of Fennane (2006). In such an environment composed of *Tamaris africana* Poiret, *Retama monosperma* (Linné) Boissier and *Suaeda fruticosa* var. *brevifolia* Moq. , whose clay soil is flooded in winter and dry in summer, the mantid was struggling on the ground with a young brown specimen of *M. religiosa* of the same size.

For the study with scanning electron microscopy (SEM), the antennae were dissected, déhydrated in absolute ethanol, mounted in several parts 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 terminologies of Snodgrass (1926) and Zacharuk (1985) are used in naming the types of sensilla.

RESULTS

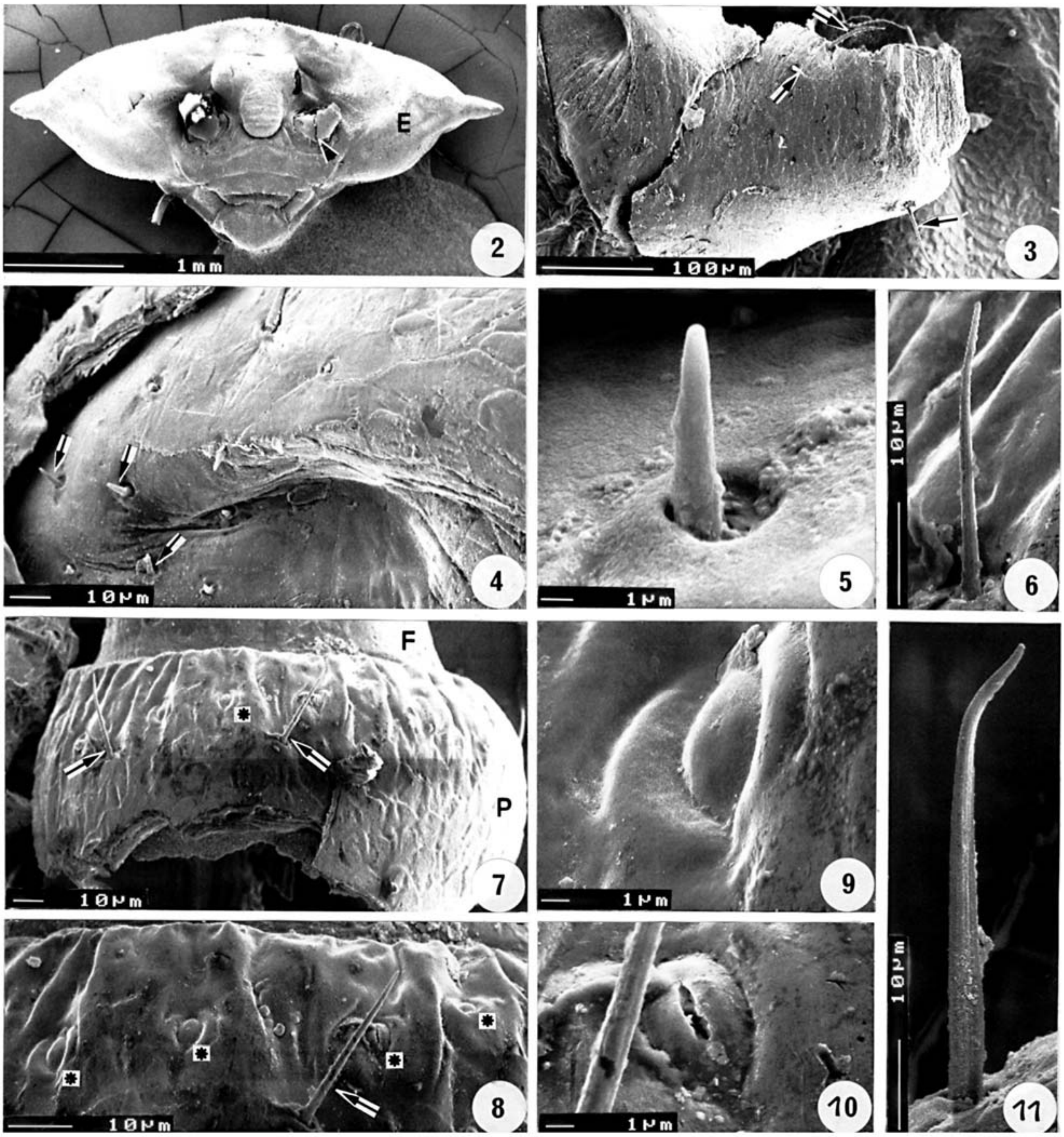
Gross morphology

The antennae of mantids are most often filiform and fine and consist of a large number of segments (Roy 1999). Those of the male adult of *Oxyothespis maroccana* are 22 mm long, filiform and ciliated (Fig. 1). They are composed of a scape, a pedicel and a flagellum of 73 flagellomeres. The scape is a bow-shaped cylinder, 370-380 µm in length and 145-155 µm in cross section. It is slightly concave dorsally; this configuration may facilitate bending of the scape-head joint (Figs. 2, 3). The pedicel is bulbous and measures 90 µm in length and 180 µm in maximum diameter (Fig. 7). The third antennal segment, or 1st flagellomere, is called the meriston and measures 460 µm in length and 130 µm in diameter; it is considered as being composed of several segments whose constrictions separating them are vague or incomplete. The proximal flagellomeres are cylindrical and measure 300 µm in length and 120 µm in diameter (Fig. 12). The distal flagellomeres, 350 µm long and 70 µm wide, (Fig. 15) are five to six times longer than they are wide (Fig. 17).

Sensilla of scape and pedicel

Two types of sensilla (sensilla chaetica and sensilla campaniformia) have been identified on the scape and the pedicel.

Aporous sensilla chaetica of the scape are smooth-surfaced. Some of them, 26-85 µm in length, are distributed over the surface of the scape (Fig. 3, arrows); most are grouped in hair-plates, on the more proximal part of the



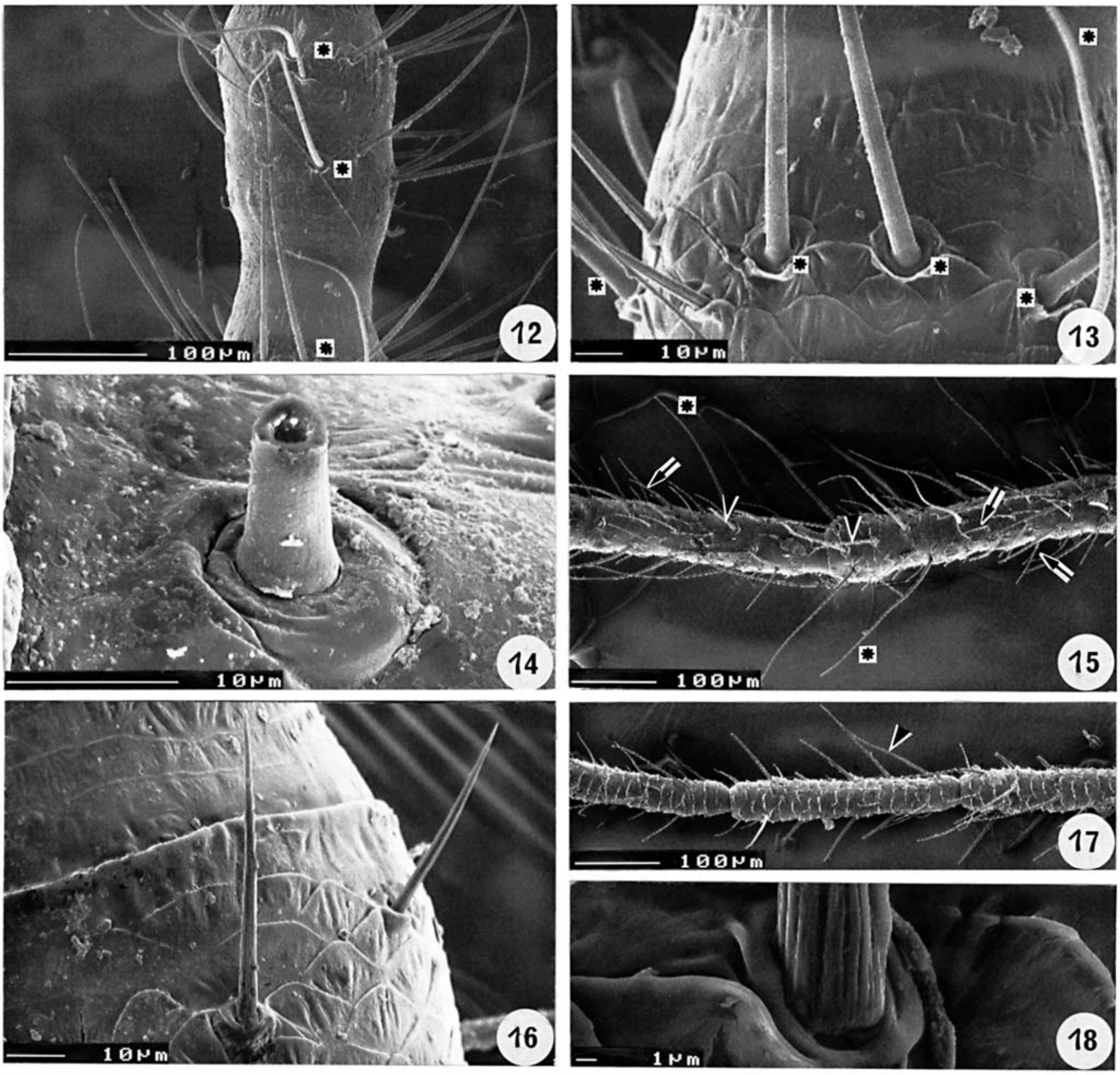
Figures 2-11. *Oxyothespis maroccana*. **2**, frontal view of the head showing the compound eyes (E) and the broken base of antenna (arrowhead); **3**, left scape with scattered aporous sensilla chaetica (arrows); **4**, proximal part of scape showing a hair plate of aporous sensilla chaetica (arrows); **5**, aporous sensillum chaeticum of hair plate; **6**, aporous sensillum chaeticum of pedicel; **7**, pedicel (P) and base of 1st flagellomere (F) showing the sensilla campaniformia (asterisk) and aporous sensilla chaetica (arrows); **8**, detail of Fig. 7, identical captions; **9**, typical sensillum campaniformium; **10**, particular sensillum campaniformium; **11**, aporous sensillum chaeticum of the base of pedicel.

scape, and measure only 6-7 µm in length (Figs. 4, 5). The latter hairs stand erect or incline toward the base of the scape. On the pedicel, there are a median circle of 5-6 aporous sensilla chaetica, 25-30 µm long (Figs. 6, 7, 8) and some sensilla, which are 50 µm long, located at the base of the pedicel (Fig. 11). The hair wall of the pedicel sensilla is longitudinally grooved.

About 20 sensilla campaniformia are circularly arranged in a single row at the distal region of the pedicel (Figs. 7, 8). The majority possess oval domes with the long axis of the dome parallel to the long axis of the pedicel (Fig. 9). Some atypical sensilla have a slit delimiting two lips above the dome (Fig. 10).

Sensilla of flagellum

The flagellum bears four types of sensilla: aporous sensilla filiformia, aporous sensilla chaetica, multiporous sensilla basiconica of subtypes I and II, multiporous sensilla trichodea.



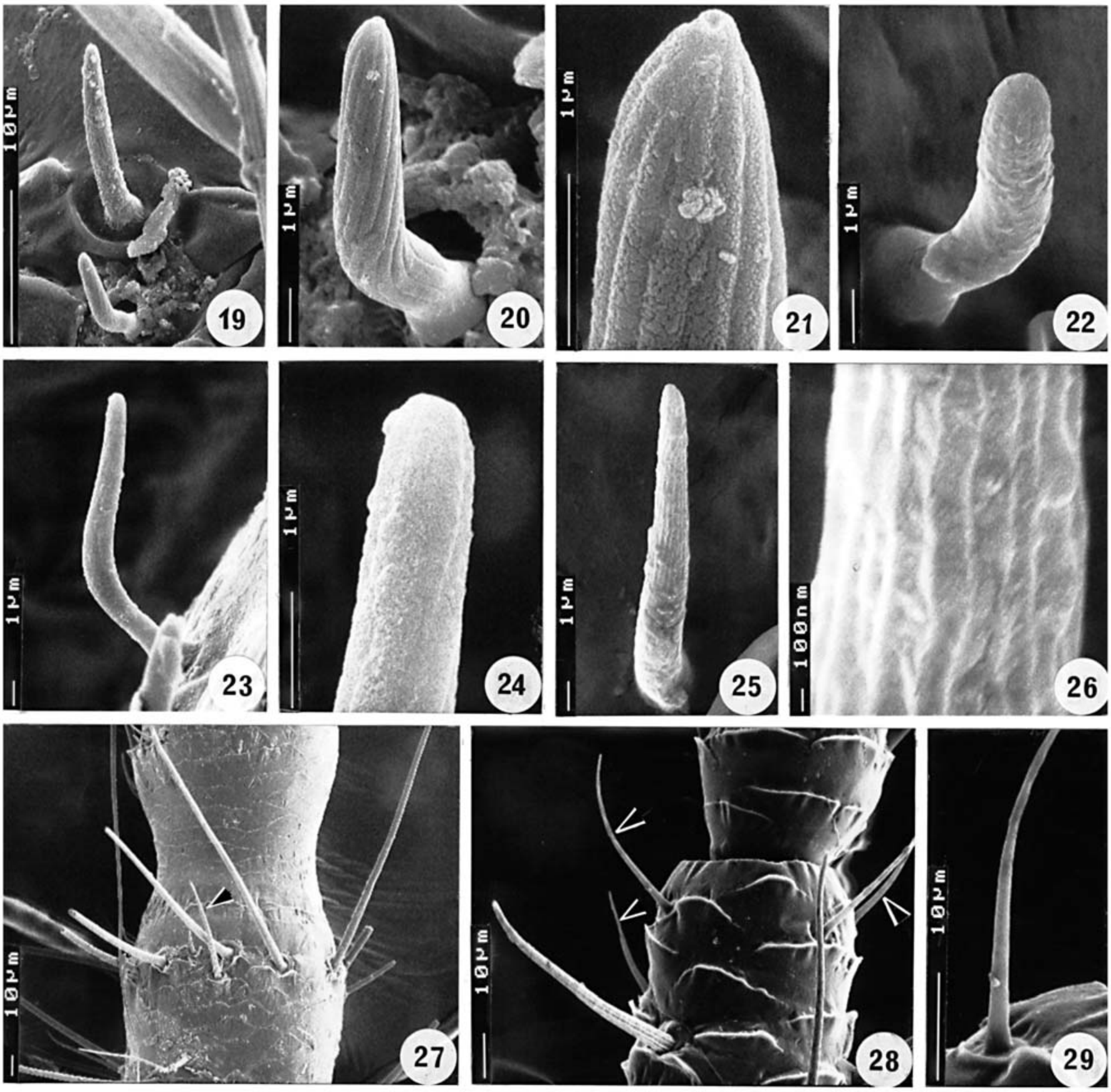
Figures 12-18. *Oxyopthespis maroccana*. **12**, 10th flagellomere showing three circles of aporous sensilla filiformia (asterisks); **13**, a circle of sensilla filiformia (asterisks); **14**, broken base of a sensillum filiformium; **15**, 55th- 56th flagellomeres showing rare sensilla filiformia (asterisks), aporous sensilla chaetica (arrowheads) and numerous multiporous sensilla trichodea (arrows); **16**, two aporous sensilla chaetica of 14th flagellomere; **17**, 68th flagellomere with numerous aporous sensilla chaetica (arrowhead); **18**, base of aporous sensillum chaeticum.

Aporous sensilla filiformia

The aporous sensilla filiformia are the longest and the most slender on the antenna. Their length varies from 200 µm to 300 µm (Fig. 12). On the meriston, they already reach 250 µm and it is only from two thirds along the flagellum that they measure a mere 200 µm (Fig. 15). They possess neither wall pores nor terminal pore. They are fairly flexible and stand erect perpendicularly to the antennal surface on the meriston but inclined at 45° toward the distal part of the following flagellomeres (Fig. 12). The hair wall is thick (Fig. 14) and appears smooth in external surface but it is in reality finely grooved (Figs. 13, 14). The sensilla are inserted into a double cupola, of modest height, which permits ample displacement of the hair (Fig. 13). The sensilla filiformia are present on the proximal three quarters of the flagellum, from the 1st to the 60th flagellomere (Figs. 12, 15). Typically, the sensilla are arranged in two circles from the 2nd to the 7th flagellomere and in three circles (proximal, median, distal) from the 8th to the 60th flagellomere. The number of sensilla per circle is 8-10; the total number is estimated at 1,600 per antenna.

Aporous sensilla chaetica

The aporous sensilla chaetica offer a thorny aspect to the antenna. They are of variable lengths: 38-60 µm on proximal flagellomeres (Fig. 16), 100 µm on distal ones



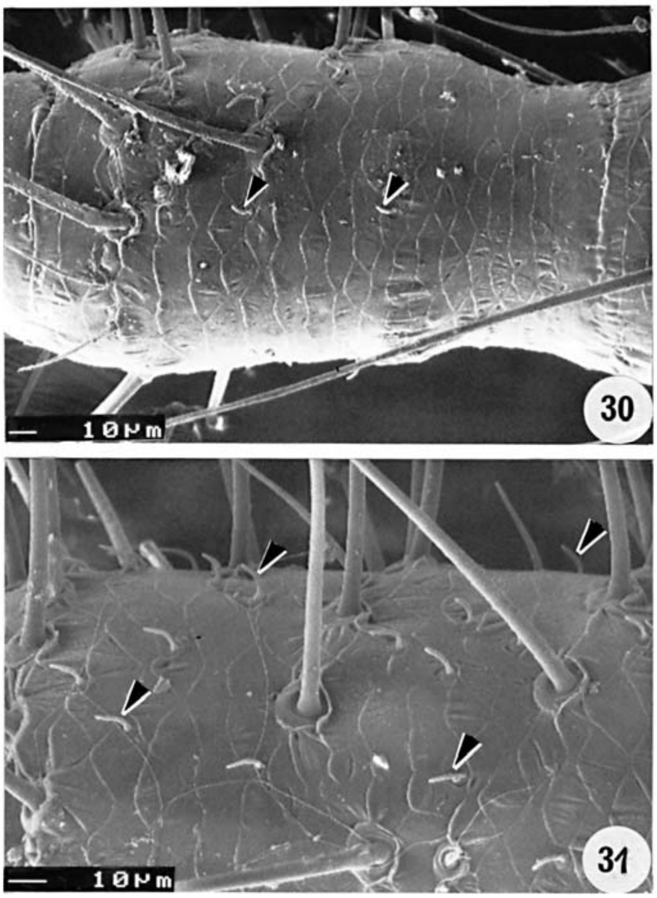
Figures 19-29. *Oxyothespis maroccana*. **19**, Multiporous sensilla basiconica of subtypes I (below) and II (above); **20**, sensillum basiconicum subtype I with apical pore; **21**, detail of the distal part with an ecdysial pore; **22**, sensillum basiconicum subtype I with a rounded tip; **23**, sensillum basiconicum subtype I, slender and curved; **24**, detail of the smooth distal part; **25**, multiporous sensillum basiconicum subtype II; **26**, longitudinal ridges of subtype II; **27-29**, multiporous sensilla trichodea (arrowheads) on 52^{h} flagellomere (27), 68th flagellomere (28), and isolated (29).

(Fig. 15, 17). The hair, deeply grooved, has a sharp tip without any pore (Fig. 16, 18). These sensilla are located on all flagellomeres and are interspersed between the sensilla filiformia of proximal and distal circles, at the rate of 8-10 per flagellomere. The seven distal flagellomeres are better endowed in sensilla chaetica (Fig. 15). Their total number is estimated at 630 sensilla per antenna.

Multiporous sensilla basiconica

The multiporous sensilla basiconica of *O. maroccana* are of two distinct subtypes which differ in size, shape, and distribution.

The subtype I is the more common and appears between the 12th flagellomere and the 65th flagellomere. Some sensilla are straight but many of them are variously curved (Figs. 19, 22, 23). Their length varies from 6 to 11 µm, the tip is more or less rounded and sometimes perforated by an apical pore, probably the ecdysial pore (Fig. 21). The more typical sensilla are grooved pegs (Fig. 20) but some of them are almost smooth (Figs. 23, 24). The wall pores are difficult to observe in SEM but they have been described, using other techniques, in the same sensilla, by Slifer (1968). When they are few in number, the sensilla basiconica subtype I are located among the sensilla



Figures 30-31. *Oxyothespis maroccana*. **30**, dorsal face of 34th flagellomere with rare sensilla basiconica subtype I (arrowheads); **31**, ventral face of the same flagellomere rich in sensilla basiconica subtype I (arrowheads).

filiformia. On the median flagellomeres, the dorsal face bears 4-6 sensilla, the ventral face 16-20 (Figs. 30, 31). The total number of sensilla is 850 per antenna.

The sensilla basiconica of subtype II, with a length of 13 µm, are twice as long as the sensilla of subtype I (Fig. 19, upper sensillum); their diameter at mid height is 1.7 µm. They are pegs adorned by 16 longitudinal grooves (Figs. 24, 25), whose large base is located in an alveolus two or three times larger than that of subtype I (Fig. 19). The wall pores are not visible in SEM. These sensilla are most often located among the sensilla filiformia of the proximal circle. Very rare, their number per antenna does not exceed 45 sensilla.

Multiporous sensilla trichodea

The multiporous sensilla trichodea are situated only on the distal quarter of the antenna, between the 50th and the 73rd flagellomere (Fig. 15). Their form is identical to that of the sensilla chaetica, but is more slender; they measure from 34 to 43 µm (Figs. 28, 29). They are curved slightly and directed towards the apex of the antenna. The pores, observed in another mantid using the crystal violet method by Slifer (1968) are not visible with the SEM. The total number of sensilla trichodea is estimated at 180 per antenna.

DISCUSSION

Comparison with other mantids

The uniporous sensilla, named thick-walled chemoreceptors, described by Slifer (1968) in *T. angustipennis*, have not been observed either in *O. maroccana*, or in *M. religiosa* and *S. viridis occidentalis* (Faucheux 2005 b, 2006). In Insects, the uniporous contact chemoreceptors have a combined taste-and mechanoreceptive function (Zacharuk 1985, Faucheux 1999a); their number is always limited on the flagellomeres. Roeder (1935) notes that *M. religiosa* may touch its prey lightly with its antennae before seizing it but this behaviour was never seen by Slifer (1978) in a large number of observations made on *T. angustipennis* and *Tenodera arififolia sinensis* Saussure 1871. Thus, the role of antenna of Mantids as a taste organ seems unfounded. The aporous sensilla chaetica of *O. maroccana* are identical to the same sensilla in *M. religiosa* (Faucheux 2005 b), *S. viridis occidentalis* (Faucheux 2006), and to the long sensilla trichodea in *C. biseriata* and *P. albofimbriata* (Holwell *et al.* 2007). The sensilla filiformia are not observed in the other studied mantids.

The morphology of multiporous sensilla basiconica I and II and of multiporous sensilla trichodea of *O. maroccana* is similar to that of the short-, medium-, and long thin-walled chemoreceptors described in *T. angustipennis* (Slifer 1968) as well as in the sensilla coeloconica and sensilla trichodea A and B of *S. viridis* (Faucheux 2006). More precisely, the structure of the sensilla basiconica I resembles that of the sensilla basiconica of male *P. albofimbriata*; the sensilla trichodea have been referred to as short sensilla trichodea on the antennae of both sexes *C. biseriata* and of male *P. albofimbriata* (Holwell *et al*. 2007).

Probable function of the sensilla

Aporous sensilla filiformia

In mantids, the long-haired antennae possess aporous sensilla filiformia; this fact observed in *O. maroccana* has been confirmed in the male with long-haired antennae of another small species, *Tropidomantis tenera* (Stal, 1860) (Iridopterygidae) (unpublished observations). It appears that small and generally fragile mantids frequently possess long-haired antennae and consequently sensilla filiformia. On the contrary, the larger species such as *S. viridis occidentalis* (Faucheux 2006), *M. religiosa* (Faucheux 2005 b), *Rivetina baetica tenuidentata* La Greca & Lombardo, 1982 and *Iris oratoria* (Linnaeus, 1758) have glabrous antennae and are unprovided with sensilla filiformia (personal observations).

In Insects, aporous sensilla filiformia are found on the cerci of crickets (Gnatzy & Schmidt 1971), cockroaches (Gnatzy 1976), earwigs (Faucheux 1999 b), embiids (Faucheux 2002), and also on the male genitalia of certain Lepidoptera (Faucheux 2005 a), the antennae of bugs (McIver & Siemicki 1984) and of odonat larvae (Meurgey & Faucheux 2006), and among the arachnids, on the pedipalps of spiders (Christian 1971). In all insects, they are deflected by faint air currents and low-frequency sounds or medium vibrations (Gnatzy & Tautz 1980).

As regards hearing, there are three types of mantids: those that possess tympanal organs, those that are primitively earless, and those whose hearing has been lost. Nothing is known on the subject of hearing in *O. maroccana*. However, the existence of numerous sensilla filiformia may warn the mantid of the approach of a prey or a predator. On the cerci of cockroaches, the sensilla are arranged in a stereotyped pattern in rows; in each row, all hairs can be deflected either parallel, or normal to the circus axis (Keil 1997). The circular location of sensilla filiformia on the antennae of *O. maroccana* may allow a similar function.

Aporous sensilla chaetica

According to their morphological characteristics (Zacharuk 1985, Faucheux 1999 a), the aporous sensilla chaetica of flagellum are tactile mechanoreceptors which allow the mantid to enter into physical contact with environmental obstacles. The abundance of sensilla chaetica at the antennal tip may facilite contact with distant objects.

According to their external morphology and their distribution, the aporous sensilla chaetica of scape and pedicel appear to be mechanoreceptive (Faucheux 1999 a). The scattered sensilla are tactile whereas the sensilla of scape, grouped in hair-plates, are moved by the wall of the head when the scape-head joint bends, and thus act as proprioceptors. The gradations of joint movements may be detected in the central nervous system by a summation of the responses of several displaced hairs (Toh 1981).

Multiporous sensilla basiconica subtype I

Like identical sensilla in other species, the multiporous sensilla basiconica of subtype I must be considered as olfactive chemoreceptors.

The occurrence of relatively large numbers of chemoreceptors on the male antennae of *Oxyothespis* is not surprising because many male mantids can locate females solely using chemoreception from a long distance away. A same result has been observed by Slifer (1968) in *Tenodera* (32,000 multiporous sensilla for one male antenna, 5,000 for a female one). In the absence of female *Oxyothespis*, we have been unable to study sexual dimorphism. It is essentially the multiporous sensilla basiconica of subtype I which are the object of this dimorphism whereas the subtype II exists in approximately equal numbers both in males and females. The great sexual dimorphism described in other mantids suggests that the multiporous sensilla basiconica of subtype I in the male *Oxyothespis* are the sex-pheromone receptor. If one compares the maximum number of sensilla basiconica I per flagellomere (250 in male *M. religiosa*, 50 in female *S. viridis occidentalis* (Faucheux 2005 b, 2006), 25 in male *O. maroccana*), it is clear that the low number in *Oxyothespis* may indicate that sexual pheromone attraction is less developed in that species. It may perhaps be compensated for the presence of sensilla filiformia sensitive to sounds emitted by conspecifics, a hypothesis which of course would require confirmation.

Multiporous sensilla basiconica subtype II and multiporous sensilla trichodea

The multiporous sensilla basiconica subtype II and the multiporous sensilla trichodea, which reveal no notable sexual dimorphism in other species (Slifer 1968) would appear to have similar functions in both sexes and may intervene in the olfactive identification of prey at short distance or in the olfactive detection of predators. Since the antennae are long in *O. maroccana*, monitoring antennal position may facilitate a distant chemoreceptive function.

Sensilla campaniformia

Sensilla campaniformia are thought to be mechanoreceptors which detect stresses applied to the surface of the cuticle. Since these sensilla occur around the distal part of the pedicel, it is thought that they may be proprioceptors which detect bending of the meriston or flagellum against the pedicel.

A specificity of the antennal flagella of mantids is to possess very few sensilla (only chaetica) on the proximal segments: on the first 16 flagellomeres in *T. angustipennis* (Slifer 1968), the first 50 in *S. viridis occidentalis* (Faucheux 2006) and in *M. religiosa*, *R. baetica* (unpublished observations). Curiously, *O. maroccana* already possesses numerous sensilla filiformia on the 1st flagellomere. We may suppose that, even if the antennae are partially amputated, the small mantid possesses enough sensilla filiformia to be warned of the presence of prey or of any kind of danger.

CONCLUSION

Our study revealed the existence of five sensillum types on the antennae of *O. maroccana*: aporous sensilla chaetica, aporous sensilla filiformia, multiporous sensilla basiconica of two subtypes, multiporous sensilla trichodea and sensilla campaniformia. The presence of a great number of sensilla basiconica on the male antenna is in accord with the results obtained by Slifer (1968) in *Tenodera angustipennis* and Holwell *et al*. (2007) in *Pseudomantis albofimbriata.* The latter sensilla are probable pheromone receptors which are found in greater abundance in male than in female mantids of other species. These results based on the observation of a single male antenna need to be completed by the study of other male and female antennae in order to confirm sexual dimorphism of sensilla basiconica.

The most striking fact revealed by our study is the presence of sensilla filiformia in abundance (50% of antennal sensilla) since this sensillum type has so far never been revealed in mantids. The sensilla filiformia which, in all insects, are deflected by faint air-currents and low frequency sounds or medium vibrations, may possess in *O. maroccana* an auditive role warning the small mantid of the approach of a predator or a prey. Observation in nature of an adult male *O. maroccana*, in conflict with a young larva of *M. religiosa*, revealed an unequal struggle in favour of *M. religiosa*.

The results obtained with SEM need to be confirmed by a structural study with the transmission electron microscope.

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