

Antennal sensilla of the yellow longicorn beetle *Phoracantha recurva* Newman, 1840: distribution and comparison with *Phoracantha semipunctata* (Fabricius, 1775) (Coleoptera: Cerambycidae)

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Abstract. The male and female antennal sensilla of the yellow longicorn *Phoracantha recurva* are here studied with scanning electron microscopy in order to compare them with those of *Phoracantha semipunctata* and to appreciate the similarities and differences between the two species. Twelve types of sensilla have been observed: aporous Böhm's sensilla with a proprioceptive function; multiporous sensilla basiconica types I, II, III, IV which are all presumably olfactory; uniporous sensilla chaetica with a contact-chemoreceptive function; aporous sensilla chaetica of types I, II, III with a tactile mechanoreceptive function, and aporous sensilla filiformia of types I, II, III with a putative vibroreceptive function. Most of the sensilla basiconica I are concentrated in numerous clusters disposed at regular intervals on each flagellomere, which may constitute an enlarged odor-sensing area on the antennae. Unlike *P. semipunctata*, a sexual dimorphism was found in the numbers of sensilla basiconica I in favour of the male antennae, one and a half times greater in the male than in the female. Sensilla basiconica III and IV have not been described in *P. semipunctata*. The most striking difference is the presence in *P. recurva* of sensilla filiformia in great numbers in both sexes and their rarity or absence in *P. semipunctata*. These results seem to indicate that *P. recurva* is more sensitive to air currents in its environment. Sensilla present in other cerambycids, such as the dome-shaped organs, conical pegs, male peg sensilla, have not been observed.

Key words: Cerambycidae, *Phoracantha recurva*, antenna, sensilla, scanning electron microscope.

Les sensilles antennaires du Longicorne jaune *Phoracantha recurva* Newman, 1840: distribution et comparaison avec *P. semipunctata* (Fabricius, 1775) (Coleoptera: Cerambycidae).

Résumé. Les sensilles antennaires du mâle et de la femelle du longicorne jaune *Phoracantha recurva* ont été étudiées en microscopie électronique à balayage dans le but de les comparer à celles de *Phoracantha semipunctata* et d'apprécier les ressemblances et les différences entre les deux espèces. Douze types de sensilles ont été observés : des sensilles de Böhm sans pore à fonction proprioceptive ; des sensilles basiconiques multipores de types I, II, III, IV qui sont probablement olfactives ; des sensilles chétiformes unipores qui sont des chimiorécepteurs de contact ; des sensilles chétiformes sans pore de types I, II, III qui sont des mécanorécepteurs tactiles et des sensilles filiformes de types I, II, III à fonction vibroréceptrice présumée. La majorité des sensilles basiconiques I sont concentrées en de nombreux groupes disposés à intervalles réguliers, ce qui peut constituer sur l'antenne une large surface sensible aux odeurs. Contrairement à *P. semipunctata*, un dimorphisme sexuel en faveur des mâles concerne les sensilles basiconiques I ; il est dû essentiellement à la longueur une fois et demie plus grande de l'antenne mâle par rapport à l'antenne femelle. Les sensilles basiconiques III et IV n'ont pas été décrites chez *P. semipunctata*. La différence la plus surprenante est la présence chez *P. recurva* de sensilles filiformes en grand nombre dans les deux sexes et leur rareté ou leur absence chez *P. semipunctata*. Ces résultats semblent indiquer que *P. recurva* est plus sensible aux courants d'air de son environnement.

Mots clés : Cerambycidae, *Phoracantha recurva*, antenne, sensilles, microscope électronique à balayage.

INTRODUCTION

Two species of eucalyptus woodborers are present in Morocco: *Phoracantha semipunctata* (Fabricius, 1775) and *Phoracantha recurva* Newman, 1840. Both are found in many areas of mainland Australia, their original habitat, and were introduced to Morocco with the *Eucalyptus* sp. trees (Myrtaceae). Adults of the Eucalyptus longicorns are nocturnal; they hide during the day under loose bark or in crevices and emerge at night to feed. Their larvae bore into the trunks and branches of dead or dying *Eucalyptus* species. Both the adults and larvae are known to attack many *Eucalyptus* sp. and they can cause damage when large numbers of individuals occur in single trees.

Most existing studies concern *P. semipunctata*. The role of olfaction in host plant recognition and location by

P. semipunctata is well established. Males and females are similarly attracted to host-tree odor (Barata *et al.* 1992, Barata 1997, Barata & Araújo 2001). Males oriented to and attempted copulation with live conspecifics but only after antennal contact with their bodies (Lopes *et al.* 2005). The structure and distribution of two types of antennal sensilla basiconica have been described by Lopes *et al.* (2002) who correlated their results with responses of single olfactory receptor cells to host and non-host plant volatiles from a previous study (Barata *et al.* 2002).

The rare studies related to *P. recurva* concern their biological cycle and egg-laying preferences (Haddan & Lieutier 2002), their fecundity and longevity (Millar *et al.* 2003, Bybee *et al.* 2004a), and their seasonal development (Bybee *et al.* 2004b). In the present study, we have

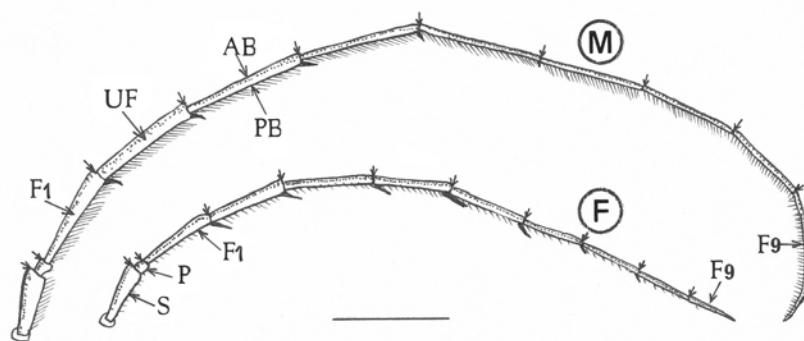


Figure 1. *Phoracantha recurva*. Right antenna of a male (M) and a female (F) view of the upper face (UF). S, scape; P, pedicel; F1, first flagellomere; F9, ninth flagellomere; AB, anterior border; PB, posterior border. The segments are delimited by small arrows. Scale bar = 4 mm.

examined the antennal sensory equipment of *P. recurva* and compare it with that of *P. semipunctata* of which only the sensilla basiconica have been described in detail (Lopes *et al.* 2002). A more exhaustive study should allow a fuller understanding of the role of the antennae in the particular behaviours of this longhorned beetle.

MATERIAL AND METHODS

Beetles were captured on the Moroccan Atlantic coast, in the forest of Essaouira (June, September 2003, 2004) and Oualidia (September 2006, April 2008) where the adults infested *Eucalyptus camaldulensis* Dehn. and *Eucalyptus gomphocephalus* D C. For the study with scanning electron microscopy (SEM), the antennae of both sexes were dissected, dehydrated in a graded ethanol series, mounted in several parts on specimen holders, either on the upper or the lower face, 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 10 kV, at different magnifications.

To allow a better detection of wall pores of sensilla, some antennae were treated with a lipid solvent, tetrachloromethane, before dehydration, according the technique of Cuperus (1985). The antennae are transferred to a vial containing tetrachloromethane which then was brought to a boil. After some 30 sec, the fluid was renewed and boiled again. This was repeated 4-5 times, after which antennae were air dried, mounted on specimen holders and coated with gold-palladium. The terminologies of Zacharuk (1985) and Faucheux (1999) are used in naming the types of sensilla.

Counts of the sensilla were made in 10 males and 10 females by using the SEM at different magnifications. The total number of pores on the surface of each sensillum was measured directly from SEM micrographs. To determine whether pore density is even all around the circumference of sensilla, 10 measurements were taken: 5 on the outer surface and 5 on the surface facing the antenna.

RESULTS

Gross morphology

As in most longicorn beetles, the antennae of *P. recurva* are longer (males) or as long as their body (females). The results concerning the length of the antennae and corresponding to the most frequently observed individuals are as follows: males, body measuring 23, 25, 26 mm (24.7 ± 1.5); antennae 36, 39, 43 mm (39.2 ± 2.7); females, body measuring 23, 24 mm (23.6 ± 0.8); antennae 22, 26 mm (25.1 ± 1.2).

In the Essaouira population, we captured males of very varied sizes, their bodies measuring between 16 and 26 mm (20.8 ± 3.6), and the antennae between 22 and 44 mm (30.9 ± 4.3). In both sexes, the antennae are composed of 11 segments or antennomeres comprising the scape, the pedicel and the flagellum of 9 flagellomeres (F1-F9) (Fig. 1). The scape is thick-set and articulated to the head by means of a ball-joint (Fig. 2d,e). The pedicel, which is the shortest antennomere, is composed of a hairy distal half and an apparently smooth, convex proximal half, articulated in the hollowed cavity of the scape (Fig. 2d,i). These two basal antennomeres present very considerable mobility. The first flagellomere is fixed tight to the pedicel (Fig. 2i). It is the largest of all the other flagellomeres, which from the 2nd to the 9th tend to be longer and narrower. Except for flagellomeres 1 and 8-9, the others have a bulbous base without sensilla which is articulated in a distal cavity of the previous segment. Flagellomeres 1-6 are cylindrical in cross section but the distal 7-9 are flattened. At rest, the antennae are bent backwards along the body and flagellomeres 7-9 are bent outwards. When the beetle is active, the antennae are stretched forwards. On most antennae, flagellomeres 1-5 in both sexes possess a distal spine located on the posterior border (Fig. 1). Spines 1-3 are strong and identical, the 4th is smaller and the 5th is very limited. Variations between individuals concern the length of the spines. The posterior border of the flagellum is ciliated over its full length in both sexes (Fig. 1). The integumental surface has a structure of scales which is perfectly visible in the zones

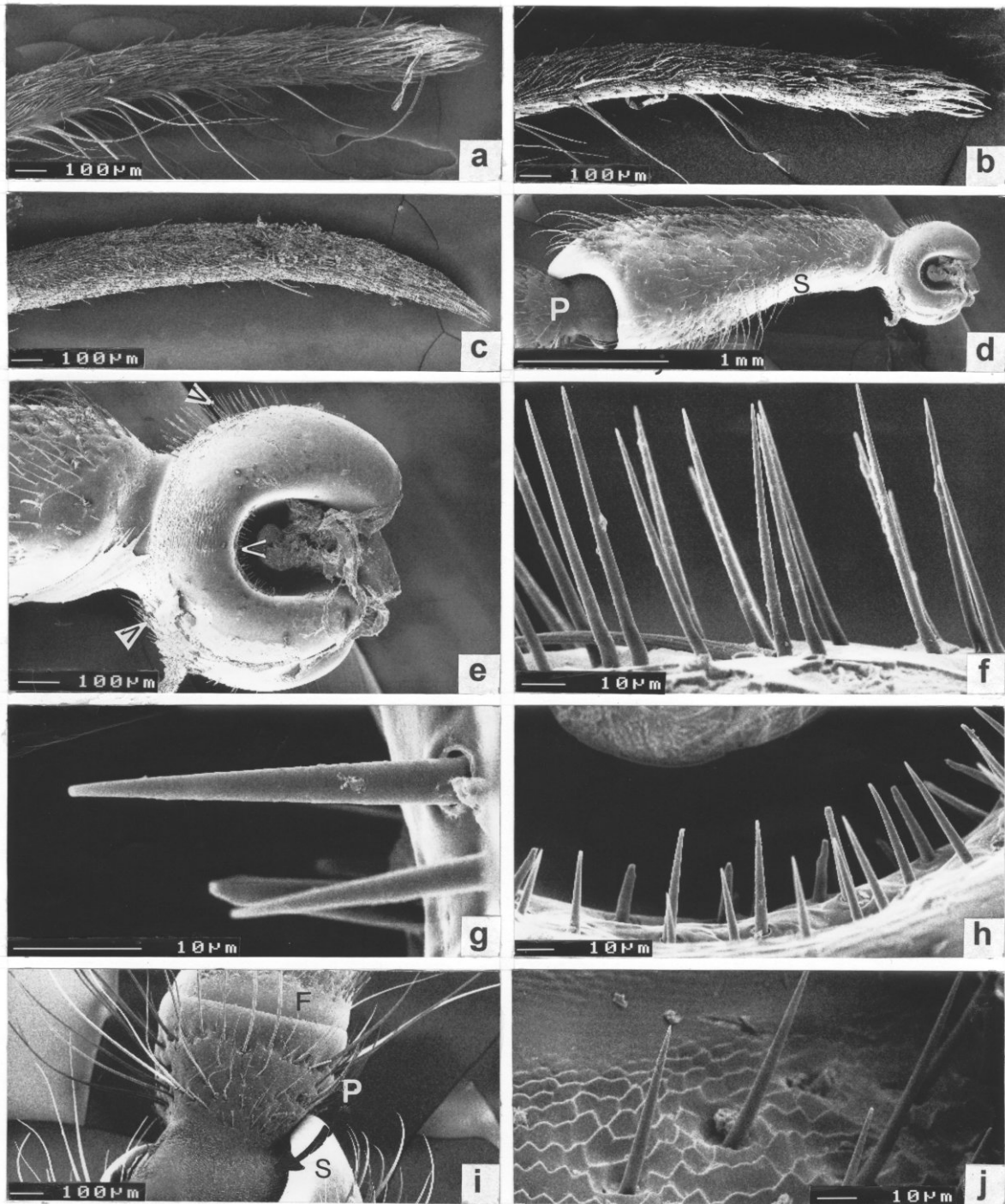


Figure 2. *Phoracantha recurva*. **a**, 9th flagellomere of the left male antenna showing the lower face; **b**, 9th flagellomere of the right male antenna showing the upper face; **c**, 9th flagellomere of the right female antenna showing the lower face; **d**, lower face of scape (S) and pedicel (P); **e**, ball-joint of the scape view of the lower face showing the Böhm's sensilla on the anterior and posterior borders (white arrows) and on the internal border (black arrow); **f**, Böhm's sensilla of the anterior border; **g**, detail of the latter sensilla showing the articulated base; **h**, Böhm's sensilla of the internal border; **i**, lower face of pedicel (P), the arrow shows the location of Böhm's sensilla; S, scape; F, 1st flagellomere; **j**, detail of these sensilla.

where sensilla are rare (Figs. 2j, 4f). A glandular pore is located in the hollow of each scale.

Antennal sensilla

The antenna of *P. recurva* is densely covered by sensilla which are more numerous in both sexes on the lower than

on the upper face (Figs. 2a-c). The upper face bears almost exclusively aporous sensilla chaetica type I. Twelve sensillum types have been observed in both sexes: aporous Böhm's sensilla, four types of multiporous sensilla basiconica, uniporous sensilla chaetica, three types of aporous sensilla chaetica, three types of aporous sensilla filiformia.

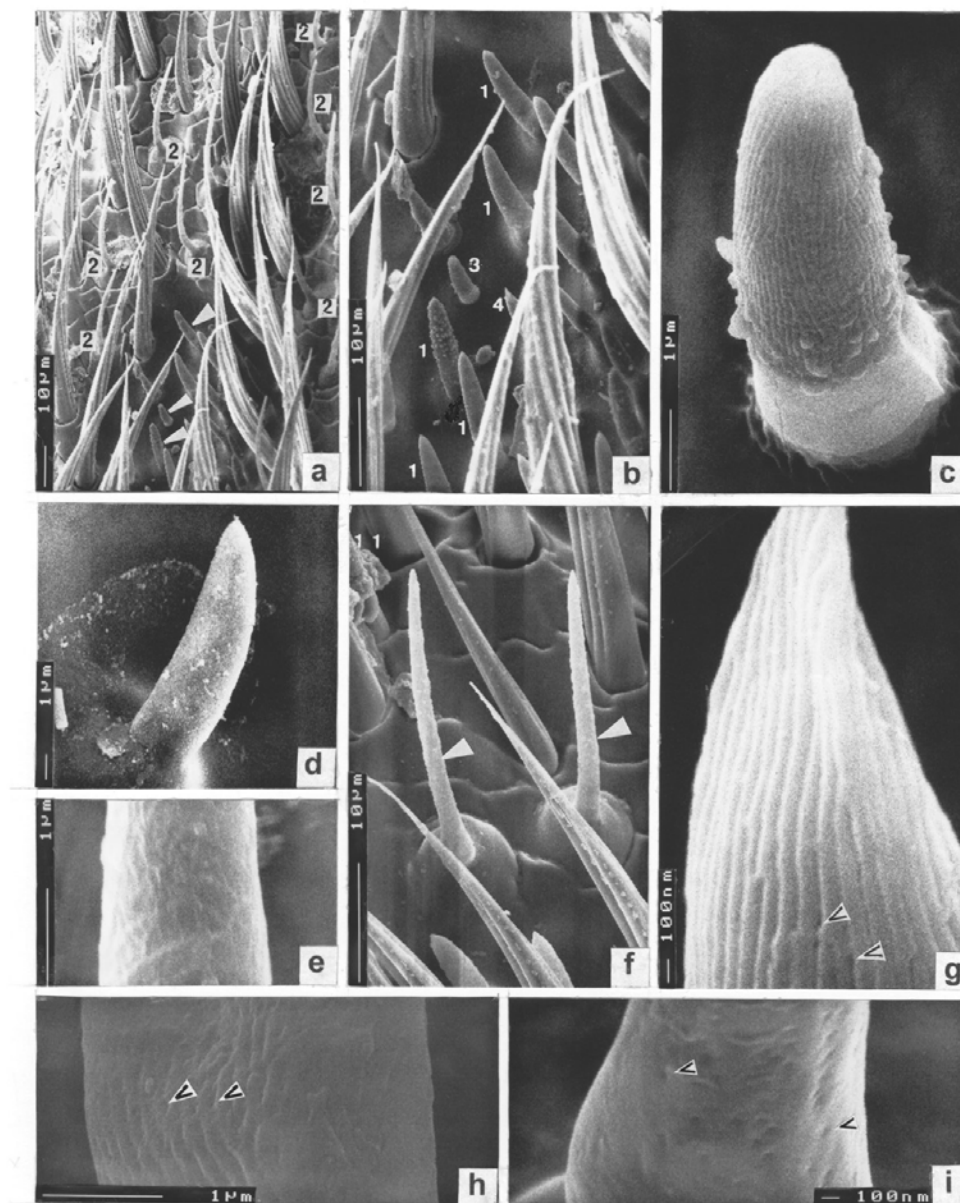


Figure 3. *Phoracantha recurva*. **a**, detail of 5th male flagellomere showing sensilla basiconica type II (2) and cluster of sensilla basiconica types I, III, IV (white arrows); **b**, cluster of sensilla basiconica type I (1), III (3) and IV (4); **c**, sensillum basiconicum type III showing ridges; **d**, sensillum basiconicum type I; **e**, detail of sensillum basiconicum type I; **f**, two sensilla basiconica type II (arrows); **g**, detail of sensillum basiconicum type IV showing ridges and pores (arrows); **h**, detail of sensillum basiconicum type I showing pores (arrows); **i**, detail of sensillum basiconicum type II showing pores (arrows).

Aporous Böhm's sensilla

The aporous Böhm's sensilla are only located on the ball-joint of the scape and at the base of the pedicel. On the scape, they are distributed in three regions: the anterior border, the posterior border and the internal border (Fig. 2e). They are sharp-tipped, smooth-walled hairs, arising from a raised base with articulatory socket and pointed laterally, for the external sensilla, and internally for the sensilla on the internal border (Figs. 2 f-h). The external sensilla are 35-71 μm in length and 3.6-4.3 μm in width at the base, whereas the internal sensilla are 13.4-33.5 μm in length. The Böhm's sensilla also exist on the anterior border of the pedicel next to the ball-joint (Figs. 2i, j).

Multiporous sensilla basiconica

Four types of multiporous sensilla basiconica are interspersed among the sensilla chaetica and are found on all flagellomeres.

Sensilla basiconica type I are generally located in clusters lined up on both sides of the lower face where the latter meets the upper face of each flagellomere (Fig. 3b). On the 5th flagellomere, taken as an example in the male, 9 clusters/mm are situated at equal distance from one another. Since this flagellomere has an average length of 4.00 mm, the number of clusters amounts to 36 on each side, which means a total of 72 clusters per segment. On the female 5th flagellomere measuring an average of 2.50 mm, there are

10 clusters/mm, that is 25 on each side of the lower face and 50 clusters for the whole of the segment. The number of sensilla basiconica I is estimated at about 28 sensilla/cluster in males, and 30 sensilla/cluster in females. Then, using the same 5th flagellomere as an example, we estimated a total of 2,000 sensilla in males and 1,500 in females. As the male antenna is longer than the female antenna, the sexual dimorphism relative to the number of sensilla basiconica is in favour of the males.

These sensilla are blunt-tipped and smooth-walled pegs, slightly curved near the base, without an articulatory socket (Fig. 3d). They pointed externally and distally. They are 11.8-12.6 μm in length and 2.9-3.2 μm in width at the base. The cuticular wall is pierced by numerous pores lined up between slight longitudinal and more or less curved ridges over the whole length of the sensillum. With the usual technique for the preparation of samples, the pores are invisible (Fig. 3e) but, using the Cuperus technique (1985), they become more visible (Fig. 3h). The pore density is estimated at 42-49 pores/ μm^2 .

Sensilla basiconica type II are located outside the clusters of basiconica I but nearby, and they sometimes appear to surround them. They are disposed in longitudinal rows and at regular intervals of ca. 40 μm (Fig. 3a). In this figure, we have counted six lines with a total of 14 sensilla. Very widespread and rare on the posterior border of the flagellum, they are regularly scattered on the lower face. They are less numerous than the sensilla type I but their number is difficult to estimate for they are often hidden by the dense cover of the aporous sensilla chaetica type I. For example, the total number of sensilla on the 5th flagellomere is ca. 480 in males and 420 in females. They resemble type I but they are straight and more elongated than this type. They are curved at their base like the sensilla chaetica nearby and are disposed on a characteristic dome (Fig. 3f). They are 23.4-25.8 μm in length and 2.3-2.7 μm in width at the base. The pore density is estimated at 22-25 pores/ μm^2 (Fig. 3i).

Sensilla basiconica type III are found among the clusters of basiconica I and their number in both sexes is of 1-2 sensilla per cluster (Fig. 3b). They have the form of a cylindrical, thick-set and blunt-tipped peg. Their wall is densely grooved, with 50 furrows, in which the pores are located. They are 5.2-5.4 μm in length and 2.1-2.3 μm in width at the base (Fig. 3c). The pore density is of 50-60 pores/ μm^2 .

Sensilla basiconica type IV are located among the sensilla basiconica I, at the rate of 1 or 2 sensilla per cluster (Fig. 3b). They have the same size as type I: 11.5-12.8 μm in length and 2.9-3.3 μm in diameter near the base. They are sharp-tipped and longitudinally grooved on the whole length, totalling about 30-35 grooves in which the pores are located (Fig. 3g). The pore density reaches 78-90 pores/ μm^2 .

Uniporous sensilla chaetica

Uniporous sensilla chaetica exist on all flagellomeres. Unlike aporous sensilla chaetica and sensilla basiconica

which lie flat against the antennal integument, they stand aside from the integument forming an angle of 45° and their tip protrudes from all other sensilla (Fig. 4b). They are therefore clearly recognizable on the sides of the antenna on which they are regularly spaced at intervals of approximately 100 μm (Fig. 4a). They are long, blunt-tipped hairs, with a fluted wall and an articulatory and prominent socket; they measure 38.4-85.7 μm in length and 2.0-2.2 μm in diameter at the base but 3.5-3.8 μm in the median region. The longest sensilla are lateral, the shortest are dorsal or ventral (Fig. 4c). They possess two curves, a basal and an apical one (Fig. 4b). Near the latter, the apex is truncated and reveals a terminal pore that is frequently obturated in S.E.M. (Fig. 4d). No sexual dimorphism is distinguished in the number and distribution of sensilla. Thus, 28-30 sensilla were counted on the anterior border of the 3rd flagellomere; on the 9th flagellomere, they are spread out over the whole of the lower face, but we counted 26-28 sensilla on the anterior border and 30-36 on the posterior border.

Aporous sensilla chaetica

Three types of aporous sensilla chaetica are distinguished according their length, number and distribution on the antenna.

Aporous sensilla chaetica of type I are present on the scape, the pedicel and the flagellum. They are the most numerous antennal sensilla and they cover the integument in a uniform and dense manner (Fig. 4e). They are denser on the lower face than on the upper one (Figs. 4e, 4f). On the male 5th flagellomere, there are 2,400 sensilla/ mm^2 on the lower face and 650 sensilla/ mm^2 on the upper one and consequently, this segment bears about 2,880 sensilla (lower face) and 780 (upper face), that is a total of 3,660 sensilla. On the female 5th flagellomere, there are 2,400 sensilla/ mm^2 on the lower face and 600 sensilla/ mm^2 on the upper one, hence a total of 1,800 sensilla (lower face) and 450 sensilla (upper face), that is a total of 2,250 sensilla. The scarcity of sensilla on the upper face reveals the scaled integument, which is impossible on the lower face. Sensilla chaetica type I are curved hairs, 71.4-85.7 μm in length and with a basal diameter of 7.0-8.5 μm which diminishes regularly from the base to the sharp-pointed apex (Fig. 4f). On the lower face, the sensilla are larger, more curved and shorter. The antennal apical sensilla are the longest and can reach 150 μm in length (Fig. 4a). They possess 5-6 oblique grooves which join towards the apex, and are adorned by a multitude of fine striae in a herring-bone pattern (Fig. 4g).

Aporous sensilla chaetica of type II are among the longest sensilla chaetica of the antenna. They are disposed in a circle of 4-5 sensilla in the distal region of each flagellomere (Fig. 4h). They are fluted-walled (14 grooves), blunt-tipped hairs with an articulatory socket, 380-410 μm in length and 2.1-2.4 μm in diameter at the base.

Aporous sensilla chaetica of type III are scattered among the type I. They resemble the latter but they are only half as long and measure from 28.4 to 30.6 μm in length with a basal diameter of 2.1-2.4 μm (Fig. 4i). They are

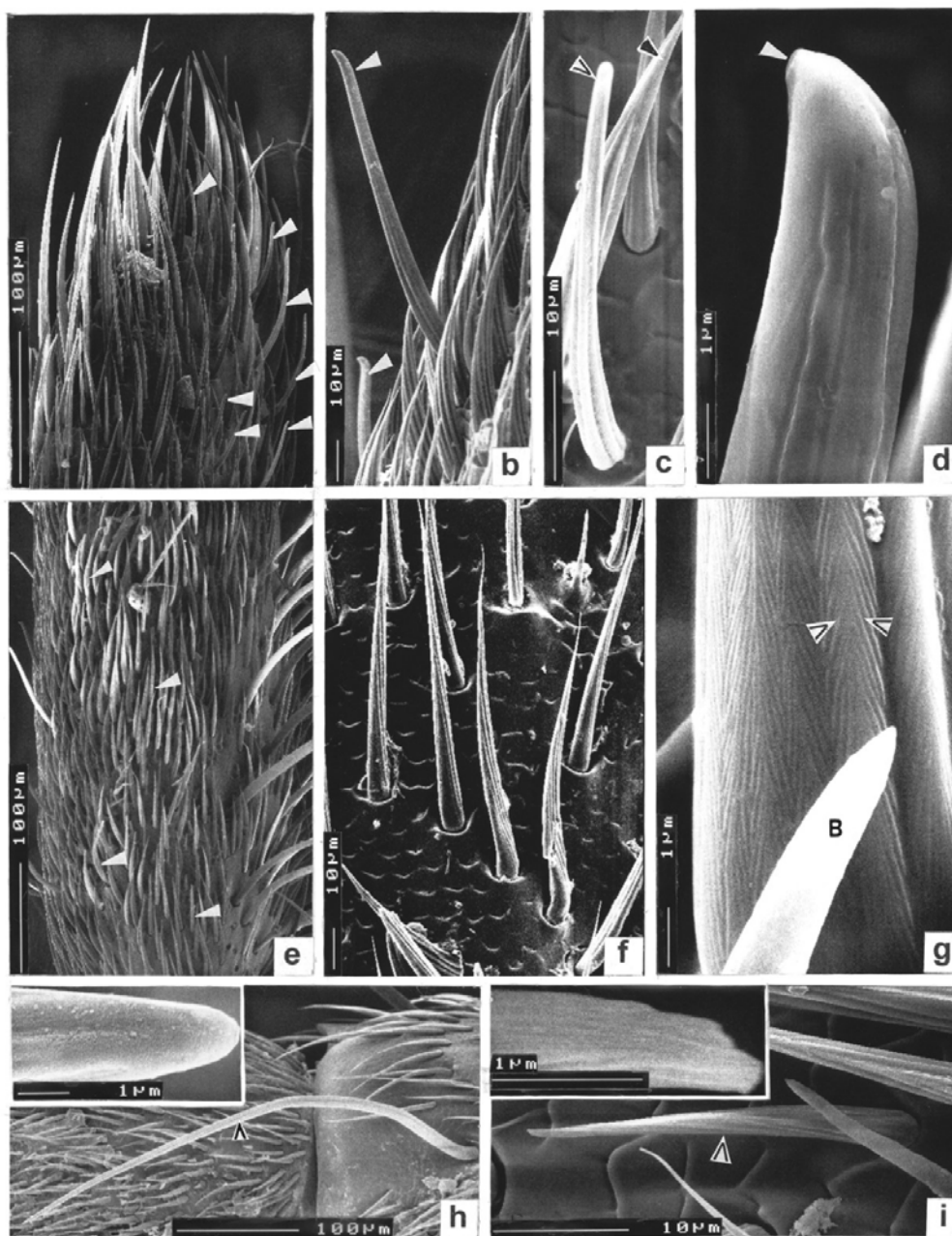


Figure 4. *Phoracantha recurva*. **a**, uniporous sensilla chaetica (arrows) on the lower face of the apex of the 9th flagellomere in the male; **b**, detail of two uniporous sensilla chaetica (arrows); **c**, uniporous sensillum chaeticum (white arrow) and aporous sensillum chaeticum (black arrow); **d**, apex of uniporous sensillum chaeticum showing the location of terminal pore (arrow); **e**, lower face of 8th flagellomere of male showing its wealth of aporous sensilla chaetica type I (arrows); **f**, upper face of 8th flagellomere of male showing aporous sensilla chaetica type I more spaced out; **g**, detail of the wall of aporous sensilla chaeticum type I showing slender striae disposed in herring-bone pattern (arrows), **h**, sensillum basiconicum; **h**, aporous sensillum chaeticum type II (arrow), inset; distal region; **i**, aporous sensillum chaeticum type III (arrow), inset; distal region.

longitudinally grooved and also provided with striae herring-bone formation. Their distal tip is narrowed but not pointed and very irregular (inset, Fig. 4i). They are difficult to identify among the type I sensilla and seem to be few in number.

Aporous sensilla filiformia

Aporous sensilla filiformia are principally located on the posterior border and give a ciliated appearance to the

antenna in both sexes (Figs. 1, 5a-c). Most are curved or undulated as befits their considerable flexibility. Three types are recognizable from their length and the appearance of their cuticular wall. The scape and the pedicel bear sensilla filiformia II and III on the posterior border and sensilla I on the anterior border.

The aporous sensilla filiformia of type I with 1.08-1.25 mm in length measure 4 times the width of the flagellomeres (Fig. 5a,b). Their diameter, which is about 9.3 μm at the base, widens to reach 13.8-14.1 μm over the

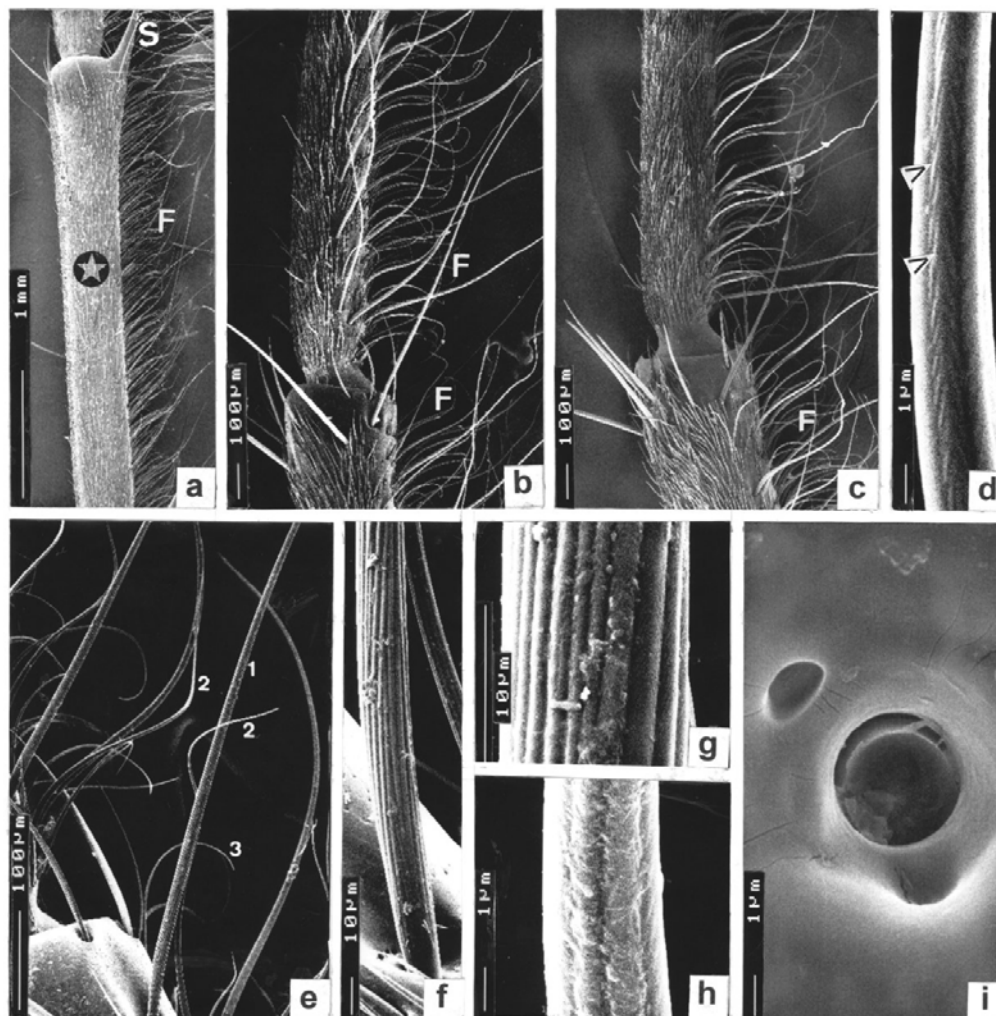


Figure 5. *Phoracantha recurva*. **a**, upper face with rare sensilla (star) of the female 4th flagellomere showing numerous aporous sensilla filiformia on the posterior boarder (F); S, spine; **b**, upper face of the male left antenna of 8th and 9th flagellomeres showing aporous sensilla filiformia of different lengths (F); **c**, lower face of the male right antenna of 8th and 9th flagellomeres; **d**, detail of aporous sensillum filiformium type III showing striae in herring-bone pattern (arrows); **e**, the three types I, II, III of aporous sensilla filiformia (1, 2, 3); **f**, detail of the base of aporous sensillum filiformium type I; **g**, grooves of aporous sensillum filiformium type I; **h**, grooves of aporous sensillum filiformium type II; **i**, base of a broken aporous sensillum filiformium type II with two lateral holes.

whole length of the hair before diminishing towards the tip (Fig. 5f). The cuticular wall, without pores, possesses from 22 to 25 grooves adorned with fine striae in herring-bone pattern (Fig. 5g).

The aporous sensilla filiformia of type II measure from 291 to 315 μm in length with a basal diameter of 2.6-3.1 μm (Fig. 5e). Frequently curved, these sensilla possess 7-9 smooth grooves (Fig. 5h).

The aporous sensilla filiformia of type III are the shortest of sensilla filiformia with 98-112 μm in length and 2.1-2.3 in basal diameter (Fig. 5e). The grooves are few in number (3-4), barely marked, with striae in herring-bone pattern (Fig. 5d). The hair of all the sensilla filiformia shows no internal lumen; it is inserted in a cupola which permits a slight displacement and is often accompanied at its base by two semi-circular and diametrically opposed holes (Fig. 5i).

Unlike the flagella of the males, the two female flagellomeres 8 and 9 are devoid of sensilla filiformia (Figs. 2a-c). The density of the sensilla filiformia is considerable: for example, we have calculated as many as 210 sensilla on the posterior border of the male 1st flagellomere.

DISCUSSION

Comparison with other cerambycids

The general antennal morphology is similar in the two *Phoracantha* species but *P. recurva* differs by the presence of long sensilla filiformia on the posterior border of the antenna and of two supplementary types of multiporous sensilla basiconica. We have looked in vain for the “flattened area devoid of sensilla on the posterior surface of the F9 of the males” described by Lopes (2000) in *P. semipunctata*. In this respect, this glabrous region (Fig. 2A

in Lopes *et al.* 2002) seem to us to be rather an artefact due to the preparation of the sample (secretion, gold coating) than to any real existence and this is for the two following reasons: (a) curiously, the long sensilla chaetica are the only ones to emerge from that glabrous surface, and (b) the limit between the glabrous region and the haired region being far too clear-cut.

The number of sensilla types in *P. recurva* is generally similar to that of other cerambycids (Dyer & Seabrook 1975, Dai & Honda 1990, Lopes 2000). However, we have not found the « dome shaped organs », considered as being sensilla campaniformia, and the « conical pegs » present in *Psacotha hilaris* (Pascoe, 1857) (Dai & Honda 1990) or the « male peg sensilla chaetica » described in *Monochamus* sp. (Dyer & Seabrook 1975) and *Acalolepta luxuriosa* (Bates, 1873) (Akutsu 1985).

Probable function of the antennal sensilla

Aporous Böhm's sensilla

During displacements of the antenna, external Böhm's sensilla of the scape enter into contact with the external edges of the articular cavity of the antenna whereas the internal sensilla touch the internal apodeme of that cavity. The greater length of the external sensilla is related to the greater displacements of the antenna; the shortest length of the internal sensilla indicates a closer contact with the internal apodeme. Similarly, the Böhm's sensilla of the pedicel are stimulated by their contact with the distal edge of the scape during the displacement of the pedicel. All these aporous sensilla are mechanoreceptors involved in the proprioception. Their localisation over a considerable length of the scape testifies to the great mobility of the antennae of the longicorn beetle.

Multiporous sensilla basiconica

Types I and II of sensilla basiconica of *P. recurva* are similar to the same types described in *P. semipunctata* by Lopes *et al.* (2002) whereas the types III and IV we have observed have not been mentioned by these authors. Type I is also present in other longicorn beetles: « thin sensilla basiconica » of *Monochamus* sp. (Dyer & Seabrook 1975), « sensilla basiconica type I » of *P. hilaris* (Dai & Honda 1990), « sensille basiconique B 1 » of *Hylotrupes bajulus* (Linnaeus, 1758) (Faucheux 2001a). Type II is named « stout sensilla basiconica » in *Monochamus* sp. (Dyer & Seabrook 1975), « sensilla basiconica type II » in *P. hilaris* (Dai & Honda 1990), « sensille basiconique B 2 » in *H. bajulus* (Faucheux 2001a).

The concentration of sensilla basiconica in sensory clusters of variable size on each flagellomere appears to be common in Coleoptera: *Monochamus* sp. (Dyer & Seabrook 1975), *H. bajulus*, *Cerambyx cerdo* Linnaeus, 1758 (Faucheux 2001a,c), *Xestobium rufovillosum* (De Geer, 1774) (Faucheux 2001b). In *P. recurva*, the number of clusters is large.

The ultrastructure of sensilla basiconica type I and type II, described by Lopes *et al.* (2002) in *P. semipunctata*, has revealed the existence of a single bipolar neuron in type I and two bipolar neurons in type II. Both types reveal structural characteristics of insect olfactory sensilla (Zacharuk 1985). No sexual dimorphism was found in the fine structure and distribution pattern of types I and II sensilla basiconica in *P. semipunctata* (Lopes *et al.* 2002).

The adult beetles of *P. semipunctata* detect a large number of plant volatiles including terpenoid and non-terpenoid compounds (Barata *et al.* 2000). According to electrophysiological recordings obtained by Lopes *et al.* (2002), most cells associated with each sensillum type were narrowly tuned, each being specialized for the detection of one or two chemically related compounds. However, no clear functional distinction between the two types was found, although the few cells that respond specifically to non-host plant volatiles were associated with sensilla basiconica type II. Since both *P. semipunctata* and *P. recurva* attack trees of *Eucalyptus* sp., it is likely that its sensilla basiconica I and II possess the same functional properties. Contrary to our results, Lopes (2000) found no sexual dimorphism concerning the number of sensilla in *P. semipunctata*. The large number of sensilla basiconica I in *P. recurva* seems to indicate a higher degree of activity of these sensilla in males. The concentration in sensilla clusters allows the latter to function as sensory fields which constitute an enlarged odor-sensing area that would be advantageous for locating food at long distance and would explain their keen olfactory sense for eucalyptus-specific odours (Inouchi *et al.* 1987). In *P. semipunctata*, neither sex depends on the presence of the other to locate the tree host, and females and males are independently attracted to the eucalyptus (Hanks *et al.* 1996b).

Generally, two types of sensilla basiconica, which are present in large numbers, are described in Cerambycids but other types are sometimes present in smaller numbers. Thus, a third type with longitudinal grooves and wall pores, called « sensilla basiconica type III », similar to type IV of *P. recurva*, exists in *Monochamus* sp., at the rate of one to four sensilla on each flagellomere (Dyer & Seabrook 1975) and in *P. hilaris* (Dai & Honda 1990). Based on analogous structures found in the morphologically or physiologically characterized multiporous basiconic sensilla of other insects, sensilla basiconica IV are likely to be olfactory.

Uniporous sensilla chaetica

Uniporous sensilla chaetica are similar in morphology to those described on the antennal flagellum of the cerambycid species: « sensilla trichodea » of *Monochamus* sp. (Dyer & Seabrook 1975) and of *P. hilaris* (Dai & Honda 1990) as well as the « sensilles chétiformes à pore apical » of *C. cerdo* (Faucheux 2001c).

The uniporous sensilla chaetica seemed to possess a gustative function as they have several features in common with the contact chemoreceptors of many other insects,

such as a terminal pore at the blunt tip, and a reverse curvature and because they protrude above all other sensilla (Zacharuk 1985, Faucheux 1999). The absence of sexual dimorphism and their large number at the distal extremity of the antenna also testify in favour of that function. Lopes *et al.* (2005) observed that males of *P. semipunctata* attempted copulation with live conspecifics only upon antennal contact with their bodies and showed similar responses to intact dead females and males but failed to respond to washed bodies. This constitutes behavioral evidence that unidentified chemical(s) on the body surface play a major role in mate recognition, and they can only be perceived after antennal contact. Uniporous sensilla chaetica of *P. recurva*, named “sensilla trichodea” in *P. semipunctata* by Lopes *et al.* (2005), are candidates for this contact chemoreception.

Aporous sensilla chaetica

Aporous sensilla chaetica type I of *P. recurva* correspond to “stout sensilla chaetica” of *Monochamus notatus* (Drury, 1773) (Dyer & Seabrook 1975), “sensilla chaetica type III” of *P. hilaris* (Dai & Honda 1990), “courtes sensilles chétiformes” of *H. bajulus* (Faucheux 2001a), “sensilles trichoïdes” of *C. cerdo* (Faucheux 2001c). They are also present in the Anobiidae (Faucheux 2001b). Like the latter, they are the most abundant of all receptors on the antennae and are distributed uniformly over the surface of the flagellum, with however a higher density on the ventral side than on the dorsal side. They are considered as tactile mechanoreceptors which function only when the antenna is in close contact with the substratum and surrounding objects. Moreover, they protect underlying sensilla basiconica. The behavioral role of antennal contact to locate and identify females necessitates the intervention of aporous sensilla chaetica I, with a tactile function, since in the absence of this antennal contact, males passed within centimeters of females without responding (Hanks *et al.* 1996b). Subsequently, immediately after copulation, the male violently swung his antennae to strike those of the female, which resulted in her beginning to proceed to search for oviposition sites. While walking, the male constantly tapped with his antennae the dorsal surface of the female’s antennae. During this behaviour, the sensilla chaetica I in both sexes are of course stimulated. The selective advantage of elongate antennae is illustrated by the greater mating success of *P. semipunctata* males that have longer antennae and, as a result, a larger number of sensilla chaetica (Hanks *et al.* 1996a). A similar explanation may be valid for *P. recurva*.

Seeing their articulated socket and the absence of pore, sensilla chaetica types II and III are probably also mechanoreceptors. Sensilla chaetica II resemble “sensilla chaetica type II” of *P. hilaris* (Dai & Honda 1990), “longues sensilles chétiformes” of *H. bajulus* (Faucheux 2001a) and occupy the same position on the distal edge of each flagellomere. Like this species, they may function as proprioceptors because the tips of the sensilla enter into contact with the succeeding flagellomere and they would then be stimulated by a positional change in the latter. A

similar function has been shown for the same type of sensilla disposed in a circle (“curved sensilla chaetica”) on the antennal larvae of odonates (Faucheux 2006, Meurgey & Faucheux 2006).

Type III of *P. recurva* is similar to the “sensilla squamiformia” present in very small numbers on male flagellomeres of *P. hilaris* (Dai & Honda 1990). The name of “squamiformia” cannot be attributed to this type of sensillum in coleopteran insects because the sensillum squamiformium, defined in Lepidoptera, is essentially an innervated lamellar scale, with longitudinal ridges which bear overlapping lamellae and crossribs which join the ridges to one another (Faucheux 1999). At most, one can consider these type III sensilla as a variant of type I. However, their constant presence both in *P. hilaris* and *P. recurva* suggest a particular role for this sensillum type in longicorn beetles.

Aporous sensilla filiformia

The two species of *Phoracantha* differ by the presence in *P. recurva* of long and dense golden hairs (sensilla filiformia) on the posterior border of each antennomere and their rarity or total absence in *P. semipunctata*. This difference must influence the behaviour of the two insects.

Sensilla filiformia particularly resemble the «long sensilla chaetica» of *M. notatus* (Dyer & Seabrook 1975). Like these sensilla, they are the only sensilla on the *Phoracantha* antennae which fit the description of hairs known to respond to sound or to air currents, being aporous, long, thin, and set in a wide socket. Several longicorn beetles possess a stridulatory organ of mesonotal-pronotal type (Wessel 2006) but this organ is unknown in *Phoracantha* sp. Thus the sensilla filiformia of *P. recurva* are likely to function as wind receptors.

Glands

The two holes associated with aporous sensilla filiformia in *P. recurva* resemble the openings of hypodermal glands described in scolytids (Moeck 1968) and the flask-shaped glands associated with the sensilla chaetica of cerambycids (Dyer & Seabrook 1975). According to the latter, the association with sensilla affords protected locations for the openings, which may reduce the likelihood of obstruction. It is possible that the dermal glands secrete a substance used in species recognition. Indeed in *P. recurva*, when two individuals are close to each other, neither shows any noticeable awareness of the presence of the other until the antennae contact the antennae of the other insect. The contact with the cuticle of another individual can convey information about its sex.

Generally speaking, depending on their distribution among females and males, and the general life habits of the studied insects, these glands have been thought to represent either a kind of lubricant for the antennae and their sensilla or appeasement glands, pheromone glands, or kairomone

glands (Dahms 1984, Bin *et al.* 1989, Skilbeck and Anderson 1994, Weis *et al.* 1999).

CONCLUSION

Twelve types of sensilla have been described on the antennae of male and female *P. recurva*: multiporous sensilla basiconica of four types, uniporous sensilla chaetica, aporous sensilla chaetica of three types, aporous sensilla filiformia of three types and aporous Böhm's sensilla. The multiporous sensilla trichodea were not observed. Two types of sensilla basiconica (I and II) are common to the sensilla of *P. semipunctata* and probably possess the same functions but *P. recurva* possess two other types (basiconica III and IV). The existence of sensilla basiconica III and IV suppose supplementary olfactive potentialities in *P. recurva* as compared to *P. semipunctata*. The differences between the numbers of sensilla basiconica I and sensilla chaetica I in the two sexes are attributable to the differences in the size of the antennae.

Sensilla filiformia have not been recognized in *P. semipunctata*. Their presence in *P. recurva* shows that this species is very sensitive to air displacements because in insects, these sensilla are deflected by faint air-currents and low frequency sounds or medium vibrations. The absence of multiporous sensilla trichodea (usually involved in the detection of sex pheromones) is to be related to the fact that both sexes are equally attracted by the host-tree.

The results obtained with SEM need to be confirmed by both an ultrastructural study with the transmission electron microscope and electrophysiological research.

Acknowledgements

My acknowledgements to Mr M'Barek Agnas (Oualidia, Morocco) for his help in finding and capturing the longicorn beetles, to Mr Nicolas Stephant, Centre of Scanning Electron Microscopy and Microanalyse X, University of Nantes, and Mrs Catherine Cerclé for their help with the photography, and Mr. Vittorio Ballardini for help with the translation. I also thank Greg Holwell (University of Auckland, New Zealand) for fruitful review of the manuscript.

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Manuscript received 13 December 2010

Revised version accepted 9 June 2011