Ovipositor sensilla of the Yellow longicorn beetle
Phoracantha recurva Newman, 1840 (Coleoptera: Cerambycidae)

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Abstract. The sensilla of the post-abdomen of *Phoracantha recurva* are studied with scanning electron microscopy in order to understand their role in the oviposition behaviour. Aporous sensilla chaetica (subtype I) entirely cover the 7th abdominal segment. The telescoping ovipositor (segments 8 and 9) bears numerous aporous sensilla basiconica (subtype I) exclusively located on the 9th segment. Three types, aporous sensilla chaetica (subtype II), aporous sensilla basiconica (subtypes II and III) and multiporous sensilla basiconica, are located in the distal region of each coxite. Three types, aporous sensilla chaetica II, uniporous sensilla basiconica and sensilla coeloconica, are situated on the apex of each stylus. Sensilla chaetica I and II and sensilla basiconica I are tactile mechanoreceptors. A gustative function is probable for uniporous sensilla basiconica and an olfactive function for multiporous sensilla basiconica. Aporous sensilla basiconica (II and III) and sensilla coeloconica are thought to have a hygroreceptive function. The existence of olfactive sensilla on the ovipositor of *P. recurva* is surprising because it conflicts the behaviourial observations carried out in *P. semipunctata*.

Key words: *Phoracantha recurva*, Cerambycidae, ovipositor, sensilla, mechanoreceptors, chemoreceptors, hygroreceptors.

Les sensilles de l'ovipositeur du Longicorne jaune de l'Eucalyptus *Phoracantha recurva* Newman, 1840 (Coleoptera: Cerambycidae).

Résumé. Les sensilles du post-abdomen de *Phoracantha recurva* sont étudiées à l'aide de la microscopie électronique à balayage afin de comprendre leur rôle dans le comportement de ponte. Des sensilles chétiformes sans pore (subtype I) couvrent entièrement le $7^{ème}$ segment abdominal. L'ovipositeur télescopique (segments 8 et 9) porte de nombreuses sensilles basiconiques sans pore (sous-type I) localisées uniquement sur le $9^{ème}$ segment. Trois types, des sensilles chétiformes sans pore (sous-type II), des sensilles basiconiques sans pore (sous-types II et III) et des sensilles basiconiques multipores sont localisés dans la région distale de chaque coxite. Trois types, des sensilles chétiformes sans pore du sous-type II, des sensilles basiconiques à pore terminal, et des sensilles coeloconiques sont situés à l'apex de chaque style. Les sensilles chétiformes I et II et les sensilles basiconiques I sont des mécanorécepteurs tactiles. Une fonction gustative est probable pour les sensilles basiconiques à pore terminal et une fonction olfactive pour les sensilles basiconiques multipores. Les sensilles basiconiques sans pore (II et III) et les sensilles coeloconiques sont supposées avoir une fonction hygroréceptrice. L'existence de sensilles olfactives sur l'ovipositeur de *P. recurva* est surprenante car elle est en désaccord avec les observations comportementales réalisées chez *P. semipunctata*.

Mots clés : *Phoracantha recurva*, Cerambycidae, ovipositeur, sensilles, mécanorécepteurs, chimiorécepteurs, hygrorécepteurs.

INTRODUCTION

Phoracantha semipunctata Fabricius, 1775 and *Phoracantha recurva* Newman 1940 are two Eucalyptus pests originating from Australia which have been introduced into other parts of the world. *P. recurva* was first reported in 1998 in Sebta and subsequently in other regions of Morocco (Haddan & Lieutier 2002). In fact, we discovered its existence in Essaouira in 1997 and observed it in Oualidia in 2006 (Faucheux 2009). Most of what we know about the oviposition in the two longicorn beetles of Eucalyptus is essentially related to *P. semipunctata*. In this species, the eggs are laid in batches of 10 to 110 eggs (average: 43) on the lower parts of the bark on the trunks of *Eucalyptus* sp., in superficial crevices of the branches or on the underside of felled trees (Balachowsky 1962, Haddan 1987). On contact with the substrate, females choose the site for laying their eggs by probing with their ovipositor (Fraval & Haddan 1989). According to Hanks *et al*. (1996), females moved haltingly as they probed for oviposition sites, and their progress was governed primarily by the sensory organs of the ovipositor. The hygrometry of the environment plays an important role. Indeed, Chararas (1979) indicates that the females deposit their eggs on bark with a humidity range of 35 to 40%, which corresponds to a humidity of the underlying phloem of 60 to 68%. In arid regions, the longicorns lay their eggs preferably on the wettest parts of the trees. The topography of the substrate is also important. According to Chararas (1979), the odour of the bark has no effect on egg-laying. In ideal conditions, immediately after their emergence, the neonate larvae groove irregular galleries directly beneath the bark and devour the sub-cortical cambium.

Thus, egg-laying behaviour involves contact stimuli, whether tactile or gustative, as well as hygrometric stimuli, which implies the presence of tactile mechanoreceptors, contact chemoreceptors, and hygroreceptors on the ovipositor. Olfactive stimuli are not involved, which *a priori* excludes the intervention of olfactive chemoreceptors.
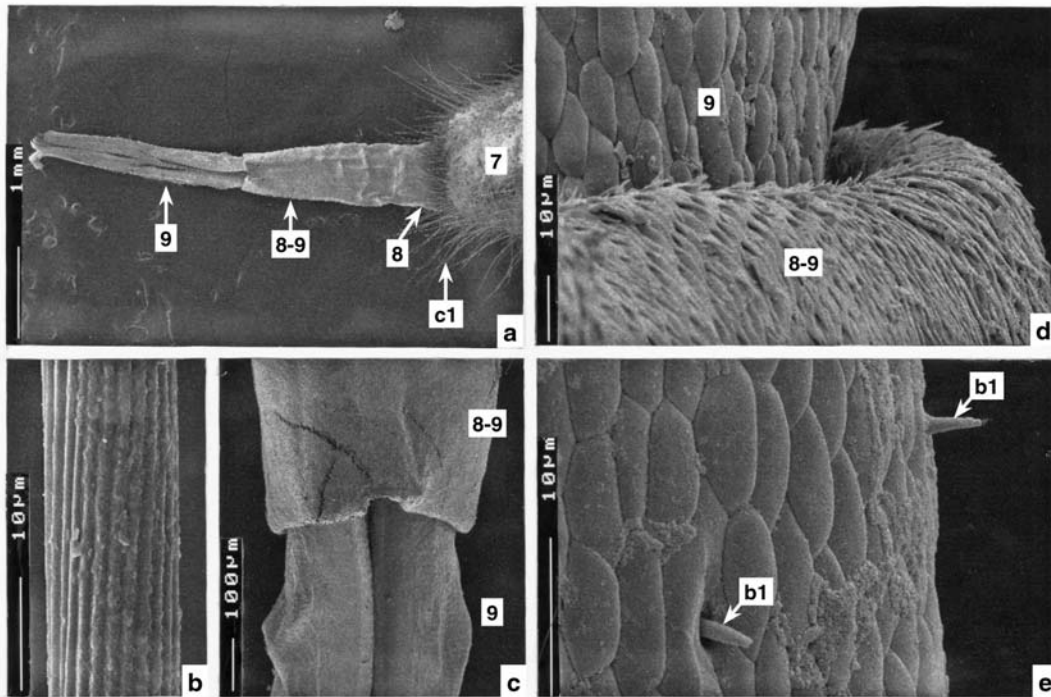
Figure 1. *Phoracantha recurva*, dorsal view of the partially extended ovipositor. **a**, segments 7, 8 and 9, intersegmental membrane (8-9), aporous sensilla chaetica subtype I on 7th segment (c 1); **b**, detail of sensillum chaeticum; **c**, joint between 9th segment and intersegmental membrane (8-9); **d**, detail of cuticular structures of 9th segment (9) and intersegmental membrane (8-9); **e**, two aporous sensilla basiconica subtype I on 9th segment (b 1).

It is tempting to suppose that the egg-laying behaviour of *P. recurva* is analogous to that which we have just described in *P. semipunctata*. The aim of the present study is to identify the sensilla of the ovipositor of *P. recurva* and to discuss the importance of their function in this longicorn.

MATERIAL AND METHODS

The beetles were captured on the Atlantic coast of Morocco, in the forest of Essaouira (June, September 2003, 2004) and at Oualidia (September 2006, April 2008) where the adults infested *Eucalyptus camaldulensis* Dehn. and *Eucalyptus gomphocephalus* DC. For the study with scanning electron microscopy (SEM), the ovipositors were dissected, dehydrated in a graded ethanol series, mounted 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 different magnifications.

To allow a better detection of the wall pores of sensilla, some ovipositors were treated with a lipid solvent, tetrachloromethane, before dehydratation, following the technique of Cuperus (1985). The ovipositors were transferred to a vial containing tetrachloromethane which then was brought to boil. After some 30 sec, the fluid was renewed and boiled again. This was repeated 4-5 times, after which ovipositors 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.

RESULTS

Gross morphology of the ovipositor

The last visible abdominal segment of the Cerambycidae, which is in the form of a small tongue, is the seventh. In the female, the following segments (8th and 9th) are invisible outside the oviposition behaviour because they are retracted within the abdomen, but during the act of oviposition they are protracted and appear as a telescoping ovipositor forming a very long egg-laying organ. The length of the ovipositor in *P. recurva* resembles other Cerambycidae (Faucheux 2001b), the 8th segment is very elongated and the intersegmental membrane between the 8th and 9th segments is well developed (Figs. 1a, 2a). The great length of the ovipositor when in action allows the female to deposit its eggs deeply into the bark crevices. The 9th segment is the real genital segment which comprises a simple tergite and a sternite divided into two sclerotized parts called hemisternites (Bitsch 1979). Each hemisternite bears an articulated appendage comprising a proximal coxite and a distal stylus (Fig. 2b).

Sensilla on the 7th abdominal segment

The entire surface of the 7th abdominal segment is covered with aporous sensilla chaetica (subtype I) on the tergite (Fig. 1a) as on the sternite (Fig. 2a). These sensilla are non-porous, slender and flexible hairs, arising from a raised base with an articulatory socket. They are from 0.8 to 1.0 mm in length and 10-12 µm in width at the base. The wall possesses about 24 furrows (Fig. 1b).
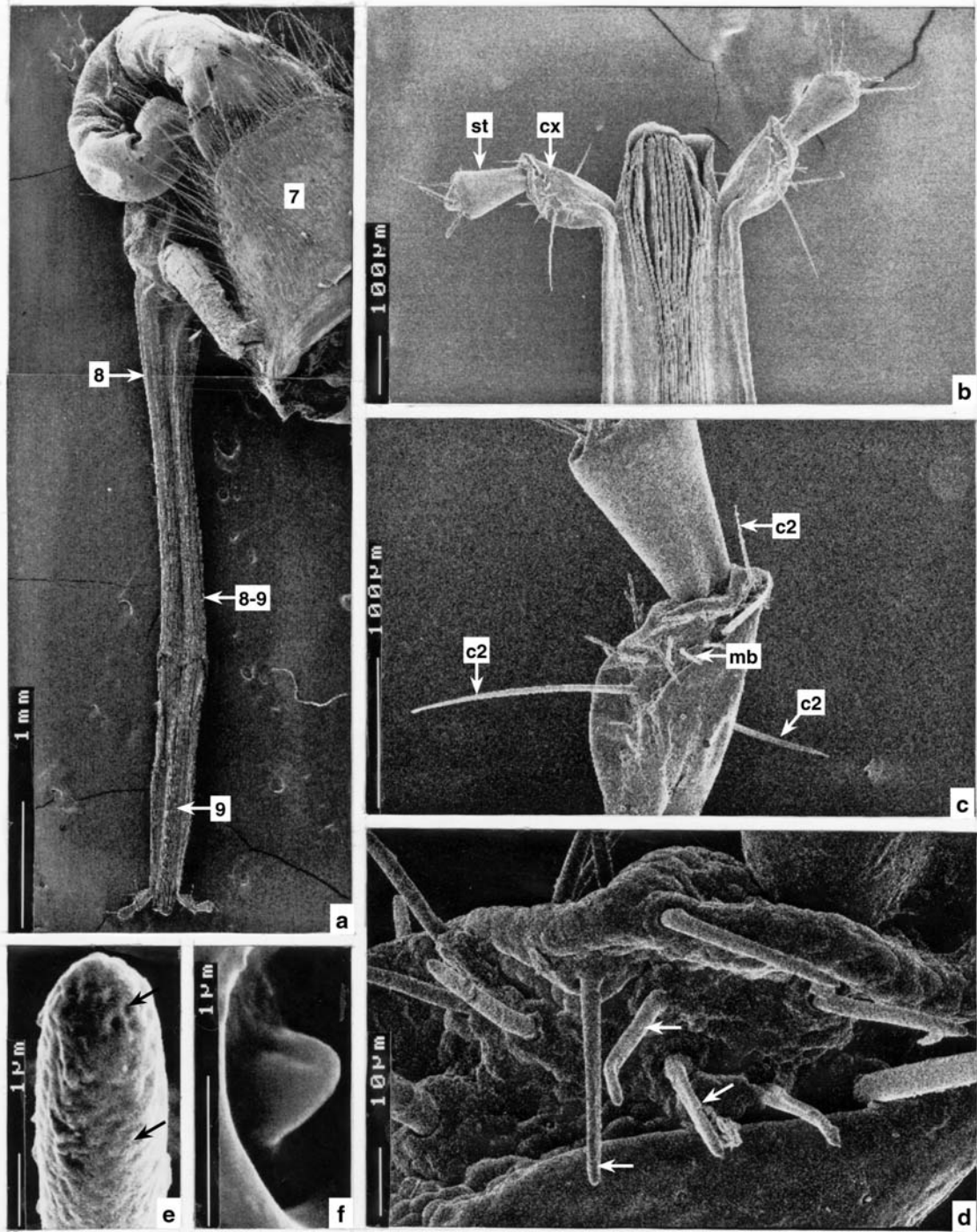
Figure 2. *Phoracantha recurva*, ventral view of the fully extended ovipositor. **a**, segments 7, 8 and 9, intersegmental membrane (8-9); **b**, tip of ovipositor showing the coxites (cx) and the styli (st); **c**, detail of the coxite with the aporous sensilla chaetica subtype II (c 2) and multiporous sensilla basiconica (mb); **d**, multiporous sensilla basiconica (arrows); **e**, apex of a multiporous sensillum basiconicum showing wall pores (arrows); **f**, aporous sensillum basiconicum subtype II.

Sensilla on the 9th abdominal segment

Whereas the intersegmental membrane 8-9 is covered with spine-like structures without sensilla (Fig. 1d), the 9th segment bears cuticular scales and small sensilla regularly distributed over the whole length of the segment. These sensilla are aporous sensilla basiconica (subtype I) the pegs of which measure 3-4 µm in length and 1.2 µm in width at the base (Fig. 1e).

Sensilla of the proximal coxites

Three types of sensilla (aporous chaetica, multiporous basiconica and aporous basiconica) have been identified in
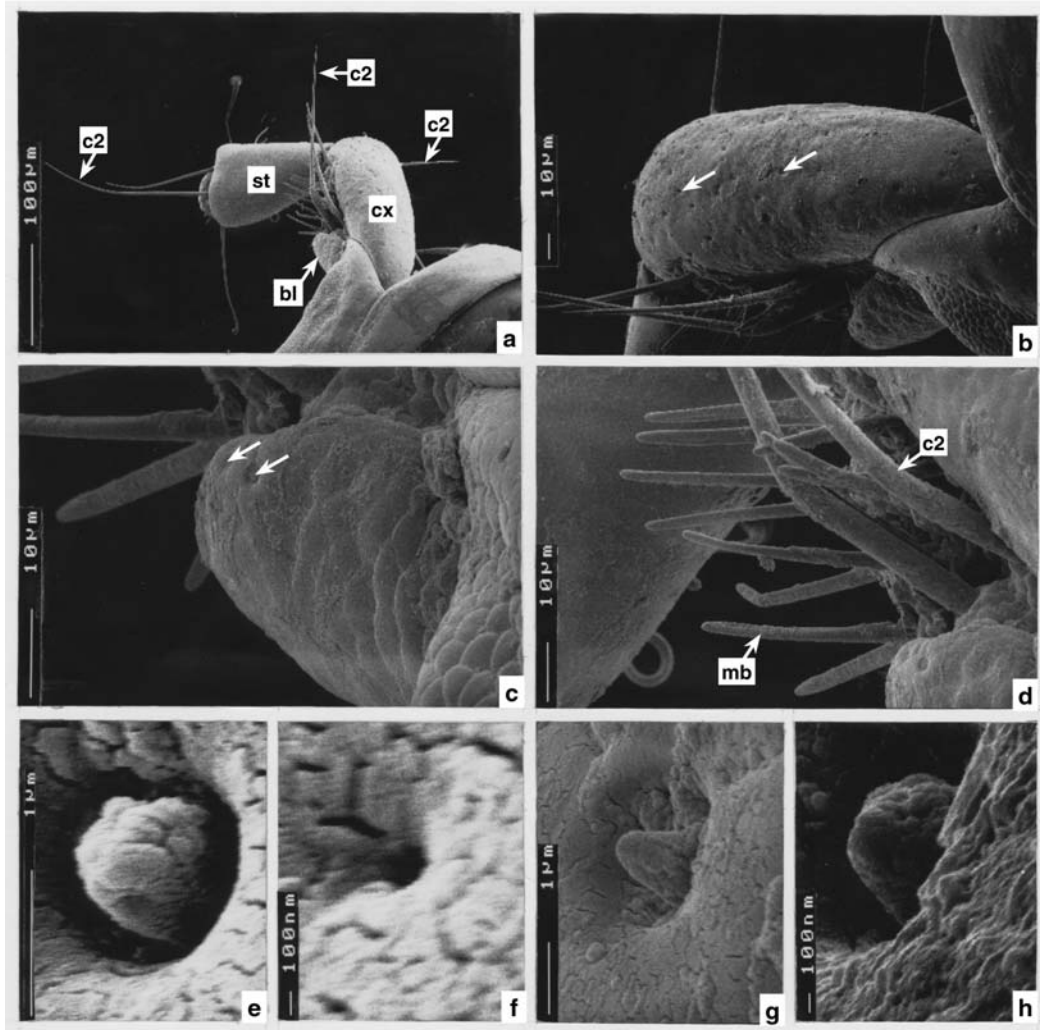
Figure 3. *Phoracantha recurva*, dorsal view of the tip of ovipositor. **a**, coxite (cx), stylus (st) and basal lobe (bl), aporous sensilla chaetica subtype II (c 2); **b**, coxite with aporous sensilla basiconica subtype III (arrows); **c**, basal lobe with apical aporous sensilla basiconica subtype III (arrows); **d**, aporous sensilla chaetica subtype II (c 2) and multiporous sensilla basiconica (mb) on the coxite; **e**, aporous sensillum basiconicum subtype III on the coxite; **f**, glandular pore on the coxite; **g, h**, two forms of aporous sensilla basiconica subtype III on the basal lobe.

a distal position on the ventral surface of each coxite (Fig. 2 b, c). The longest ones are aporous sensilla chaetica (subtype II), 80-135 µm long, with 10 furrows. Each sensillum is a rigid hair, raised perpendicularly from the surface of the coxite. There are: a long sensillum on the external edge and three shorter sensilla on the internal edge of the coxite (Fig. 2c). From eight to ten multiporous sensilla basiconica are found on the apical plate of the coxite. They are blunt-tipped smooth-walled pegs, rising from a discrete base (Fig. 2d). They are 17-40 µm in length and 3 µm in width at the base. The cuticular wall is pierced by numerous pores regularly distributed along its length. The pore density is 9 pores/µm^2 (Fig. 2e). These sensilla are also visible dorsally on the external edge of the coxite (Fig. 3d). Some aporous sensilla basiconica (subtype II), measuring 0.8 µm in length and 0.7 µm in width at the base, are situated near the sensilla chaetica (Fig. 2f). These sensilla resemble small smooth-walled pegs which are found in slight depressions on the cuticular surface.

The dorsal surface of the coxite is provided with aporous sensilla basiconica (subtype III) regularly distributed over the entire length (Fig. 3b). These small spherical pegs are 1.1-1.3 µm in length and 1.0 µm in width at the base and are found in deep depressions on the cuticular surface (Fig. 3e).

Sensilla on the basal lobes

The basal lobes are visible dorsally near the proximal part of each coxite (Fig. 3 a, b). From three to four aporous sensilla basiconica of subtype III are found on the distal part of the lobe. Two forms are present: a conical form and a spherical form (Fig. 3 g, h).

Sensilla of the distal styli

Three types of sensilla (chaetica, basiconica, and coeloconica) have been identified on the distal part of each
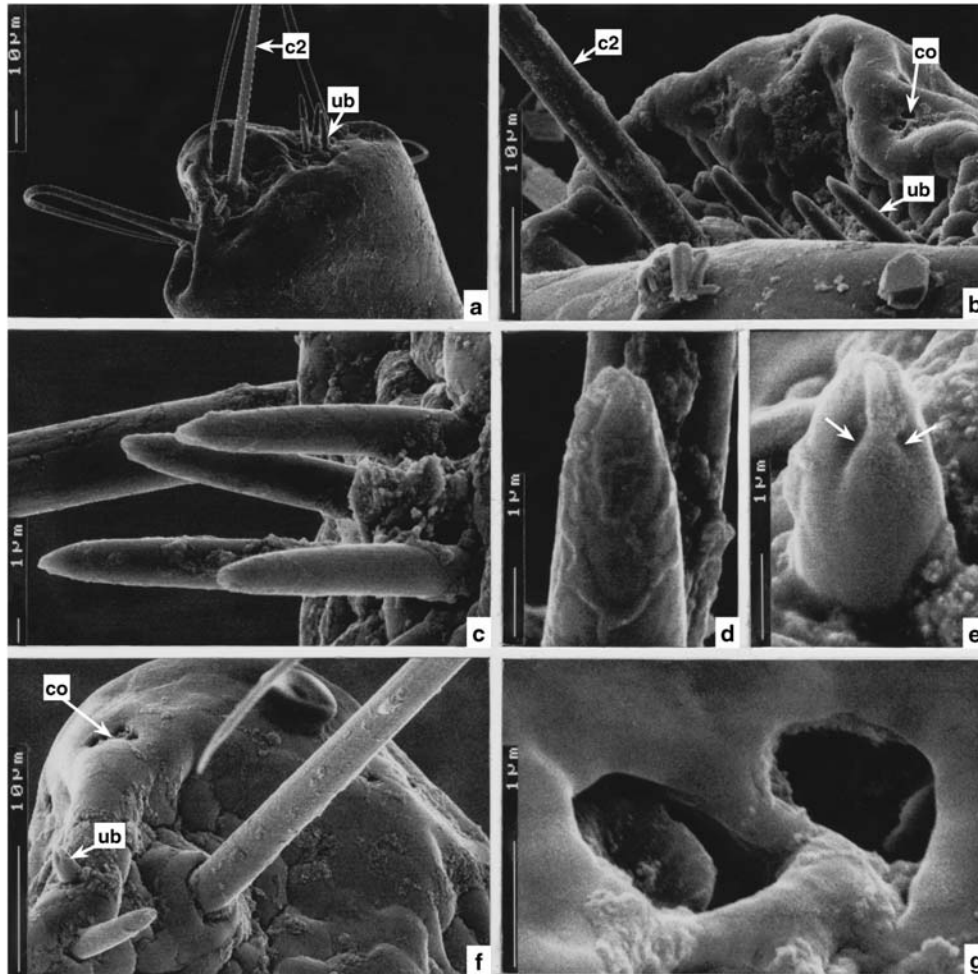
Figure 4. *Phoracantha recurva*, ventral view of stylus. **a**, tip of stylus showing aporous sensilla chaetica subtype II (c 2) and uniporous sensilla basiconica (ub); **b**, detail with the same sensilla and sensilla coeloconica (co); **c**, four long uniporous sensilla basiconica; **d**, apex of long uniporous sensillum basiconicum; **e**, short uniporous sensillum basiconicum with pores (arrow); **f**, location of the short sensillum basiconicum (ub) and sensilla coeloconica (co); **g**, two sensilla coeloconica.

stylus (Fig. 4a). The aporous sensilla chaetica of subtype II of the stylus resemble the same sensilla of the coxite but they are longer (100-175 µm) with a basal width of 4 µm; there are 4 sensilla for each stylus (Figs. 3a, 4a). The sensilla basiconica end distally in three finger-like excrescences which reveal three presumed pores (Fig. 4 d, e). They are to be considered as uniporous sensilla according to Zacharuk (1980). There are two groups: a group of 4 sensilla (Fig. 4 b, c) and a group of 2 sensilla (Fig. 4f). Among these sensilla can be distinguished 5 long sensilla basiconica, of 19-12 µm in length and with a basal width of 2.5 µm, and one short sensillum basiconicum 3 µm in length and with a basal width of 1.8 µm (Fig. 4f). Sensilla coeloconica are found in deep pits of 1.6 µm in diameter (Fig. 4g). They are grouped by 2, 3 or 4 lined-up sensilla (Fig. 4 b, f). Some 12 sensilla occur on each stylus.

Glandular pores

Glandular pores are located on the coxites and the styli (Fig. 3f).

DISCUSSION

Comparison with other Coleoptera

Curiously, the sensory equipment of the ovipositor in *P. recurva* is closer to that of the anobiid *Anobium punctatum* (De Geer, 1774) (Faucheux 2001a) and of the clerid *Thanasimus dubius* (Fabricius, 1777) (Baker & Nebeker 1986) than to that of the cerambycid *Cerambyx cerdo* Linnaeus, 1758 (Faucheux 2001b). The three first species possess in common aporous sensilla chaetica, multiporous sensilla basiconica (in identical numbers in *Phoracantha* and *Thanasimus*, but are fewer in *Anobium*), and 6-8 uniporous sensilla basiconica. Indeed, the sensilla basiconica present on the styli of *P. recurva* resemble sensilla basiconica on the styli of *Thanasimus*: like the latter, the grooves on the peg surface do not extend to the apex of each sensillum, and the apex of these sensilla consists of a tripartite projection. Using the crystal violet method of Slifer (1960) to detect porous sensilla, these authors declare that these sensilla basiconica are porous but do not make clear whether there are wall pores or a terminal

pore. We believe that the uniporous sensilla basiconica of *P. recurva* – which possess a terminal pore – are contact chemoreceptors.

The two Cerambycidae *P. recurva* and *C. cerdo* possess in common aporous sensilla chaetica in almost equivalent numbers on the stylus, but five times greater on the coxite of *C. cerdo*. The uniporous sensilla are absent in *C. cerdo*. The multiporous sensilla consist of 12 sensilla basiconica in *P. recurva* but some fifty papilliform sensilla in *C. cerdo*. The sensilla campaniformia which are present in *C. cerdo* and *A. punctatum* are absent from *P. recurva*.

Probable function of the sensilla

In *P. recurva*, the ovipositor is repeatedly touched on the substrate prior to egg-laying (Fraval & Haddan 1989). Even after egg-laying has commenced, the substrate is probed with the sensilla for a few seconds before each egg is added to the batch. Prior to and sometimes during egg-laying, the ovipositor is extended backwards and forwards, and moved from one side to another. Thus, in insects, it is probable that the ovipositor sensilla are assessing the most suitable site for egg deposition in terms of egg-hatching and larval well-being (Merritt & Rice 1984). Aporous sensilla chaetica, trichodea and long basiconica on the ovipositors of insects have been shown to function as tactile mechanoreceptors (Hooper *et al*. 1972, Behan & Ryan 1977, Zacharuk *et al*. 1986, Stoffolano & Yin 1987, Faucheux 2001a, b). Thus, one can readily postulate that the function of the sensilla basiconica subtype 1 on the 9th segment of *Phoracantha* is to transmit positional information to the beetle through deformation of the sensilla as the ovipositor is inserted into the bark crevices. Similarly, the sensilla chaetica of subtype II on the coxites and styli would be presumed to be mechanoreceptors in the close vicinity of egg release. As in other insects, according to Hooper *et al*. (1972), Rice (1976) Rossignol & McIver (1977), the mechanosensilla of *P. recurva* monitor the surface texture of the bark; they guide the egg-laying apparatus when being inserted into the holes and crevices; they monitor the physical stress on the ovipositor as the eggs are being laid; they monitor the depth of ovipositor penetration. They are also presumably involved in evaluating distances from the substrate and other spatial relationships of oviposition and in monitoring contact with the male during copulation.

The uniporous sensilla basiconica are taste hairs specialized to monitor the chemical nature of liquids (Zacharuk 1985). A certain number of electron microscope studies concerning the sensilla of ovipositor appendages (ovipositor lobes, valves, styli) have been undertaken in several insect orders: Hymenoptera such as *Pseudocoila bochei* Weld (van Lenteren 1972), *Biosteres longicaudatus* Ashmead, 1905 (Greany *et al*. 1977); Lepidoptera such as *Chilo partellus* (Swinhoe, 1884) and *Spodoptera littoralis* Boisduval, 1833 (Chadha & Roome 1980), *Phthorimaea operculella* (Zeller, 1873) (Valencia & Rice 1982), *Monopis crocicapitella* (Clemens, 1859) and *Tineola bisselliella* (Hummel, 1823) (Faucheux 1987); Coleoptera such as *Acanthoscelides obtectus* Say, 1831 (Szentesi 1976);

Diptera such as *Lucinia cuprina* (Wiedemann, 1830) (Rice 1976, Merritt & Rice 1984), *Metasyrphus venablesi* (Curran, 1929) and *Eupeodes volucris* Osten Sacken, 1877 (Hood Henderson 1982). The ovipositors of these species possess both contact chemoreceptors and mechanoreceptors. The gustatory function of the contact chemoreceptors present on the ovipositors has been confirmed by electrophysiological recording in Diptera and Lepidoptera (Rice 1976, Hood Henderson 1982, Waladde 1983, Girolami *et al*. 1986, Crnjar *et al*. 1989, Banga 1997, Maher *et al*. 2006). The presence of taste hairs may easily be associated with oviposition in fresh plants: indeed, the uniporous sensilla are known to respond to chemicals such as salts, water, and amino acids (Rice 1976, Chadha & Roome 1980). The occurrence of uniporous sensilla basiconica in *P. recurva* is more difficult to explain because the longicorn lays its eggs only on the bark of Eucalyptus.

The aporous sensilla basiconica subtypes I, II and III as well as the sensilla coeloconica of *P. recurva* are pegs that possess no pores and are connected to the surrounding cuticle by a rigid, nondeformable socket and are defined as no-pore (NP) sensilla by Altner (1977). Such pegs are found standing on the surface and have the appearance of basiconic sensilla or are sunken into pits and named sensilla coeloconica. These sensilla possess sensory cells sensitive to temperature (cold) and humidity (dry or moist air). Some of the previously mentioned sensilla in *P. recurva* could be the thermo-hygroreceptors which are predictable according to the observations of Chararas (1979) in *P. semipunctata* quoted in the introduction. In other wood borers such as the cerambycid *Monochamus* sp., non-olfactory causes such as a reduced resin pressure combined with the presence of a favourable phloem moisture could be effective signals of the physiolagial state of a tree over the necessary time-span (Dyer & Seabrook 1978).

The multiporous sensilla basiconica on the coxites of the ovipositor of *P. recurva* share structural features typical of insect olfactory sensilla such as a non-flexible base, a multiporous cuticular wall (Zacharuk 1980). Sensilla basiconica on the antennae play a major role to attract from a distance the beetles towards the host-trees (Faucheux 2011). Contrary to *P. semipunctata* in which it has been shown that the odour of the bark had no effect on egg-laying behaviour, the presence of multiporous sensilla on the ovipositor of *P. recurva* seems to prove that the odour of Eucalyptus barks is likely to influence oviposition in the latter species. It is known that the flagellar multiporous sensilla basiconica of type I and II in *P. semipunctata* are structurally adapted to play a functional role in olfactory recognition of plant odours (monoterpenes, sesquiterpenes) (Lopes *et al*. 2002). Although the ovipositional behaviour is not necessarily mediated by the same signals as host attraction, it is reasonable to think that the sensilla basiconica on the ovipositor of *P. recurva* play a similar role to that of antennal sensilla basiconica. Evidence has been presented for several insects that multiporous sensilla located on the ovipositor respond to volatile compounds (Barton Browne 1960, Wallis 1962, Hooper *et al*. 1972, Rice 1976, Behan & Ryan 1977, Merritt & Rice 1984, Crnjar *et al*. 1989). In *P. recurva*, the multiporous sensilla

basiconica may possibly identify the odour of Eucalyptus bark, but also detect conspecifics. Indeed, certain species of insects avoid laying eggs on the normal oviposition media because of the presence of other species (Bradley & Sheppard 1984). Moreover, in the mating behaviour of *P. semipunctata*, within seconds of mounting a female, the male curled his abdomen and extracted the ovipositor by raising his body and pulling back. The ovipositor remained extended during copulation (Hanks *et al.* 1996). If this behaviour also exists in *P. recurva*, which is likely, the olfactive sensilla basiconica of the ovipositor, sensitive to the odour of the male, can favour copulation on the part of the female.

Glandular pores are also recognized on the ovipositors of diverse Coleoptera such as the cerambycid *Cerambyx cerdo* (Faucheux 2001b), the anobiid *Anobium punctatum* (Faucheux 2001a), the languriid *Languria mozardi* Latreille, 1807 (Ellsbury & Baker 1988). They have been described on the antennae of *P. recurva* (Faucheux 2011). As for the antennae, these glandular pores are the apertures of glands which can secrete a kind of lubricant for the telescoping ovipositor. A similar function has been proposed for the integumental glands on the ovipositor of tephritid flies which may lubricate the ovipositor during eversion and retraction (Berube & Zacharuk 1984).

CONCLUSION

Contrary to *P. semipunctata* in which it has been shown that the odour of the Eucalyptus bark had no effect on egg-laying, the presence of multiporous sensilla on the coxites of the ovipositor of *P. recurva* seems to prove that the olfactive stimuli from the barks are likely to influence oviposition in that species. The presence of numerous types of sensilla thought to be hygroreceptive (three types of sensilla basiconica, one type of sensilla coeloconica) on the coxites and the styli of the ovipositor tend to confirm the importance of humidity in egg-laying behaviour.

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