

Mouthpart sensilla of the adult Yellow longicorn beetle *Phoracantha recurva* Newman, 1840 (Coleoptera, Cerambycidae, Cerambycinae)

Les sensilles des pièces buccales du Longicorne jaune de l'Eucalyptus Phoracantha recurva Newman, 1840 (Coleoptera, Cerambycidae, Cerambycinae)

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Abstract. The mouthparts of *Phoracantha recurva* were studied in order to better understand their involvement in feeding. The mandibles without mola have no chewing function. The laciniae and galeae maxillaries, as well as the labium are equipped with specialized bristles, which form brushes to gather pollen grains. These structures are related to the type of nutrition composed of nectar or pollen consumed by adults. Aporous sensilla chaetica are distributed on labrum, mandibles, galeae and laciniae maxillaries, maxillary and labial palps and labium. The terminal segment of maxillary and labial palps bears 6 or 5 sensillum types respectively : uniporous sensilla basiconica, multiporous sensilla basiconica, aporous sensilla styloconica, aporous sensilla basiconica subtypes 1 and 2, and aporous sensilla digitiformia. Sensilla styloconica are absent on the labial palps. The number of apical sensilla is very large in *P. recurva* compared to those observed in other coleopteran families e.g. Passalidae, Scolytidae, Curculionidae; which implies a greater sensory function of the palps in the yellow longicorn beetle. Sensilla digitiformia are congregated on a ventral oval surface of terminal segment of the palps, comprising 50 sensilla on the maxillary palp and 30 sensilla on the labial palp. Sensilla chaetica monitor movements of the food in direction to the oral cavity. Uniporous sensilla basiconica are contact-chemoreceptors, and detect the gustatory quality of *Eucalyptus*'s nectar. An olfactory function is attributed to the multiporous sensilla basiconica. Sensilla styloconica and sensilla basiconica of subtype 2 may serve as thermo- and hygro-receptors. Sensilla basiconica of subtype 1 have the morphological characteristics of the proprioceptors. Sensilla digitiformia may detect tension-forces exerted on the surface of terminal segments of the palps.

Keywords : *Phoracantha recurva*, Cerambycidae, woodborer, mouthparts, sensilla.

Résumé. Les pièces buccales de *Phoracantha recurva* ont été étudiées pour comprendre leur implication dans la prise de nourriture. Les mandibules sans mola n'ont pas de fonction masticatrice. Les laciniae et galeae maxillaires ainsi que le labium sont équipés de poils spécialisés qui constituent des brosses rassemblant les grains de pollen. Ces structures sont en rapport avec le type de nourriture des adultes, constituée à la fois de nectar et de pollen. Les sensilles chétiformes sans pore sont réparties sur le labre, les mandibules, les galeae et laciniae maxillaires, les palpes maxillaires et labiaux et le labium. Le segment terminal des palpes maxillaires et labiaux porte respectivement 6 ou 5 types sensillaires: des sensilles basiconiques unipores, des sensilles basiconiques multipores, des sensilles styloconiques sans pore, des sensilles basiconiques sans pore des sous-types 1 et 2, et des sensilles digitiformes sans pore. Les sensilles styloconiques sont absentes sur les palpes labiaux. Le nombre des sensilles apicales est très élevé chez *P. recurva*, comparé à celui observé chez les autres familles de coléoptères telles que les Passalidae, Scolytidae et Curculionidae, ce qui implique une fonction sensorielle des palpes plus grande chez le longicorne jaune de l'*Eucalyptus*. Les sensilles digitiformes sont groupées sur une surface ovale ventrale du segment terminal des palpes comprenant 50 sensilles sur le palpe maxillaire et 30 sensilles sur le palpe labial. Les sensilles chétiformes contrôlent les déplacements de la nourriture en direction de la cavité buccale. Les sensilles basiconiques unipores sont des chimiorécepteurs de contact qui détectent les qualités gustatives du nectar d'*Eucalyptus*. Une fonction olfactive est attribuée aux sensilles basiconiques multipores. Les sensilles styloconiques et les sensilles basiconiques du sous-type 2 peuvent être des thermo- et hygro-récepteurs. Les sensilles basiconiques du sous-type 1 ont les caractéristiques morphologiques des propriocepteurs. Les sensilles digitiformes peuvent détecter les forces de tension exercées à la surface des segments terminaux des palpes.

Mots-clés : *Phoracantha recurva*, Cerambycidae, xylophage, pièces buccales, sensilles.

INTRODUCTION

The adults of the yellow longicorn, *Phoracantha recurva* Newman 1840, are nocturnal, hiding during the day under loose bark or in crevices and emerging at night to feed.

According to Drinkwater (1973, in Gil Sotres & Mansilla Vazquez 1983), a closely related species, *Phoracantha semipunctata* (Fabricius, 1775) sucks the sap of trees having lost their bark. Helal & El Sebay (1980) observed that the adult did not feed of them but merely bit them in order to choose its egg-laying site. Chararas (1969, 1979) pointed out that the adults feed at night on the pollen and nectar of various flowers. According to Hanks *et al.* (1996),

they ate the nectar and pollen of *Eucalyptus*. As *P. recurva* is relatively similar in his biology, it may be presumed that, it also feeds in the same way (Bosmans 2006). Indeed, Fraval & Haddan (1989) found *Eucalyptus* pollen in the faeces of imagos.

According to Chararas (1979), the extracts of nectar are very attractive for *P. semipunctata*, whose feeding activity is stimulated by numerous sugars. Roovers & Yana (1967) have pointed out, the greater attractiveness of *Eucalyptus* honey of its fresh flowers and the mixture after decoction of flowers and honey compared to that of numerous other preparations based on *Eucalyptus* organs such as its wood, bark or leaves. According to Millar *et al.* (2003), females

P. recurva fed on a diet of *Eucalyptus* pollen and sucrose solution lived 34-56% longer than females which fed on diets containing other types of pollen, such as ground dog chow, or sucrose solution alone. The females which fed on the *Eucalyptus* pollen diet lay 4-8 times more eggs than females on the other diets. These results imply the involvement of gustatory and olfactory stimuli during feeding.

MATERIAL AND METHODS

Beetles were captured on the Moroccan Atlantic coast, in the forest of Essaouira (June, September 2003, 2004) and at Oualidia (September 2006, April 2008) where the adults infested *Eucalyptus camaldulensis* and *Eucalyptus gomphocephalus* (Faucheux 2009b). For the study with scanning electron microscopy (SEM), the heads of both sexes were dissected, dehydrated in a graded ethanol series, mounted 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 10 kV, at different magnifications. The terminologies of Zacharuk (1985) and Faucheux (1999) are used in naming the types of sensilla.

RESULTS

General morphology

The mouthparts, of the grinding type, are formed by the labrum, the mandibles, the maxillae and the labial parts (Figs. 1a, b).

Labrum

The labrum is a mobile part of quadrangular shape. It is located on the upper surface of the head and is articulated with the clypeus; it hides the mandibles partially (Figs. 1b, d).

Mandibles

The mandibles protrude beyond the lateral and anterior labral margins. The dorsal and ventral surfaces are flattened. The right and left mandibles are symmetrical bilaterally. The ventral surface is slightly concave and bears a ball joint-like ventral condyle (Figs. 2d, e). The dorsal surface bears a socket to accommodate a condyle from the head, named acetabulum (Figs. 2a, b). These two structures are on the outer edge of the mandible. The inner margin is extended to a blunt and smooth surface over the lower half of the mandible. Above this area, there occurs a mesal tooth and a light subapical protrusion which can appear broadened into a blade. The apex of the mandible bears one

biting tooth termed incisor. It should be remembered that this tooth is subject to wear and breakage by the chewing action of the beetle or by grinding during food processing (Kvenberg 1977). The outer edge of the mandible, termed lateral margin, is broadened and bordered by a dorsal rib. The external half of each mandible is covered dorsally with hairs. The ventral surface also has a raised area called ventral rib (Figs. 2d, e). This rib serves as a point of attachment for a ventral fringe of hairs or brush, which stretches from the base of the mandible to the distal cutting edge.

Maxillae

The basal segment, or cardo, of the maxilla is housed in a deep maxillary cavity of the skull; it is here connected to this part of the skull by means of a maxillary joint, or cardo process, (Figs. 3 e, f). The two following segments constitute the stipe of the maxilla and are not separated from each other. The eustipes, or coxa, is extended on the inner side by a mobile slat, called the lacinia, or internal lobe, which is well developed in *Phoracantha* sp. and all other Cerambycinae (Figs. 3 a, b). The costipes, or palpiger, is connected to the outside of the eustipes and bears the galea, or external lobe, and the maxillary palp (Jeannel 1949) (Figs. 3a, b). The lacinia is a ciliate piece bearing an apical and a lateral fringes of hairs (Fig. 3c). The galea is unarticulated and extended by two fringes of hairs (apical and lateral) (Fig. 3d). The maxillary palp is 4-segmented and its terminal segment is ovoid, blunt apically, flat on the ventral surface, and convex on the dorsal surface.

Labium

The labium is made up of two parts: a proximal part, which constitutes the postlabium or mentum and a distal part which forms the prelabium or prementum (Fig. 6a). The prementum is represented by soft elements, hidden behind the mentum, which bear two lateral and membranous lobes, named paraglossa, and labial palps (Figs. 6a, 7a). The labial palps are 3-segmented and attached to the prementum by the intervening of a palpiger (Figs. 6b, 7f). Like the maxillary palp, the terminal segment of the labial palp is flat on its ventral surface, and convex on its dorsal surface.

The ventral surface (Fig. 6a) and the dorsal surface (Figs. 7b, c) of the prementum possess non innervated hairs, which constitute a system of filters. The ventral surface is almost entirely covered with hairs (Fig. 6a); whereas the dorsal surface possesses an apical fringe of hairs and an internal fringe of hairs on each paraglossum (Fig. 7c).

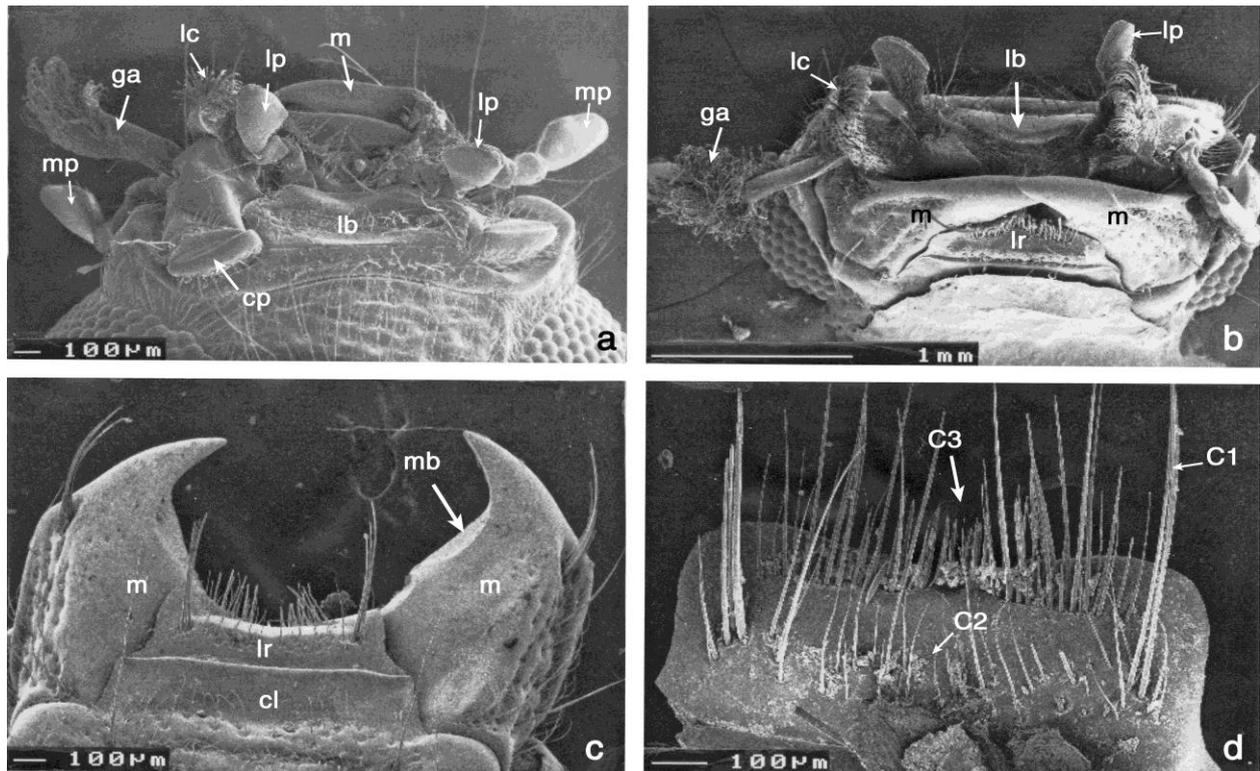


Figure 1. *Phoracantha recurva*. **a**, ventral view of head; **b**, frontal view of head; **c**, dorsal view of mandibles; **d**, dorsal view of labrum. cp, cardo process; cl, clypeus; ga, galea; lb, labium; lc, lacinia; lp, labial palp; lr, labrum; m, mandible; mb, mesal blade; mp, maxillary palp; C1, long aporous sensilla chaetica; C2, short aporous sensilla chaetica; C3, thick-set aporous sensilla chaetica.

Sensilla of labrum

The labrum bears only aporous sensilla chaetica (Fig. 1d). Three subtypes are distinguished in terms of their length and shape. The sensilla C 1 are long and slender sensilla (440-640 μm) whose basal diameter of 12 μm , diminishes regularly up to the apex. The sensilla C 2 are short and slender with 120-200 μm in length and 4 μm in basal diameter. The sensilla C 3 are thickest and have 120 μm in length and 12 μm in basal diameter. All these sensilla are arranged in two transversal rows: a proximal row of 8 sensilla C 1, arranged in two lateral groups, and 32 sensilla C 2 and a distal row of 48 sensilla, as follows: 10 sensilla C 1, 30 sensilla C 2 and 8 sensilla C 3 which are median.

Sensilla of mandibles

The lateral margin of the right and left mandibles is covered with large hairs which are all aporous sensilla chaetica; they extend along more than half the dorsal surface (Figs. 2a, b, c). Some sensilla are also present on the ventral surface (Figs. 2d, e). Two types of sensilla are recognized on the dorsal surface of the left mandible (Fig. 2a): long sensilla C 1 of 380-590 μm in length and 10-11 μm in width at the base; short sensilla C 2 of 60-120 μm in length and 3.5 μm in basal diameter (Fig. 2c). Both types are longitudinally striated and possess 18 striae for C 1 and 10 for C 2. There are 4 sensilla C 1 and 48-50 sensilla C 2 on the left mandible (Fig. 2a), while 3 sensilla C 1 (one of which is 1 mm long) and 35 sensilla C 2 occur on the right mandible (Fig. 2b). On both mandibles, the sensilla C 1 are situated laterally and distally; the sensilla C 2 are scattered

over the whole of the lateral margin, except for certain sensilla, which form two groups: a proximal one of 9 sensilla located near the acetabulum and a distal one of 5 sensilla (Figs. 2a, b). The ventral surfaces of the mandibles bear only 6-8 sensilla C 2 at the base of the lateral margin (Figs. 2d, e).

Sensilla of maxillae

The basal segments (cardo and stipes), the galea and the lacinia possess only aporous sensilla chaetica. The cardo process is equipped on its ventral surface with sensilla of 79-160 μm in length, composed of 45 proximal and 20 distal sensilla (Figs. 3e, f). The sensilla of the cardo, is of identical length and are lined up on the outer edge and number from 20 to 22 sensilla (Fig. 3a). The dorsal surface of the galea is glabrous. Its ventral surface bears sensilla of 160-180 μm in length, comprising 15 distal (Fig. 3d) and 20 proximal sensilla (Fig. 3e). All these sensilla are stiff and slightly curved towards the internal margin of the galea. They cannot be confused with the fringes of hairs for these non-innervated hairs which are three times longer are clearly wavy and packed close together. The lacinia bears 15 sensilla close to the fringes of hairs, dorsally and 25 sensilla 30-100 μm long, curved towards the inner edge, ventrally.

The maxillary palp possesses aporous sensilla chaetica 25-40 μm long over the whole extent of its segments. The dorsal sensilla number 4, 4, 3, 0 (segments 1-4), (Fig. 3b) and the ventral sensilla: 0, 14, 12, 32 (segments 1-4), (Figs. 3a, 4a, 5a).



Figure 2. *Phoracantha recurva*. **a**, left mandible, dorsal view; **b**, right mandible, dorsal view; **c**, lateral margin of left mandible showing the two types of sensilla C1 and C2; **d**, right mandible, ventral view; **e**, left mandible, ventral view; **f**, detail of the ventral fringe of hairs. ac, acetabulum; ai, apical incisor; cue, cutting edge; fh, fringe of hairs; lm, lateral margin; mb, mesal blade; mr, margin ridge; mt, mesal tooth; vc, ventral condyle; vr, ventral rib; C1, long aporous sensilla chaetica; C2, short aporous sensillum chaeticum. The two arrows show two groups of sensilla C2.

The 4th maxillary palpal segment, in addition to the sensilla chaetica, is equipped with an apical sensory slit (Fig. 4), and an oval sensory area located on the ventral surface (Fig. 5), as well as short sensilla scattered around. The sensory slit comprises uniporous sensilla basiconica UBs, multiporous sensilla basiconica MBs, aporous sensilla styloconica ASs, and aporous sensilla basiconica of subtype 1, AB1s (Figs. 4a, b).

The UBs are cylindrical pegs 4.9-5.4 μm in length and 2.1 μm in basal diameter inserted in a socket. The apex of each peg presents an oblique section pierced by a longitudinal pore 1.7 μm in length and 0.3 μm in medial width (Fig. 4c). The MBs are pegs 4.9-8.4 μm in length and

1.8 μm in basal diameter (Figs 4b, e). The wall pores are difficult to observe in SEM (Fig. 4f). The ASs are made up of a terminal sensory cone of 0.6 μm in height supported by a stylus 8.0-8.4 μm in length, which is higher on the inner surface than the outer, where it has a long notch (Fig. 4e). The AB1s are short sensilla 1.2 μm in length and 1.0 μm in basal width, whose cone is prolonged by a narrow process and surrounded basally by a collar (Figs. 4b, d). The different types of sensilla are mixed except for the ASs which are situated on the periphery of the sensory field. The average number of the 4 sensillum types (UBs, MBs, ASs, AB1s) in each maxillary palp are 80, 76, 54 and 42, respectively.

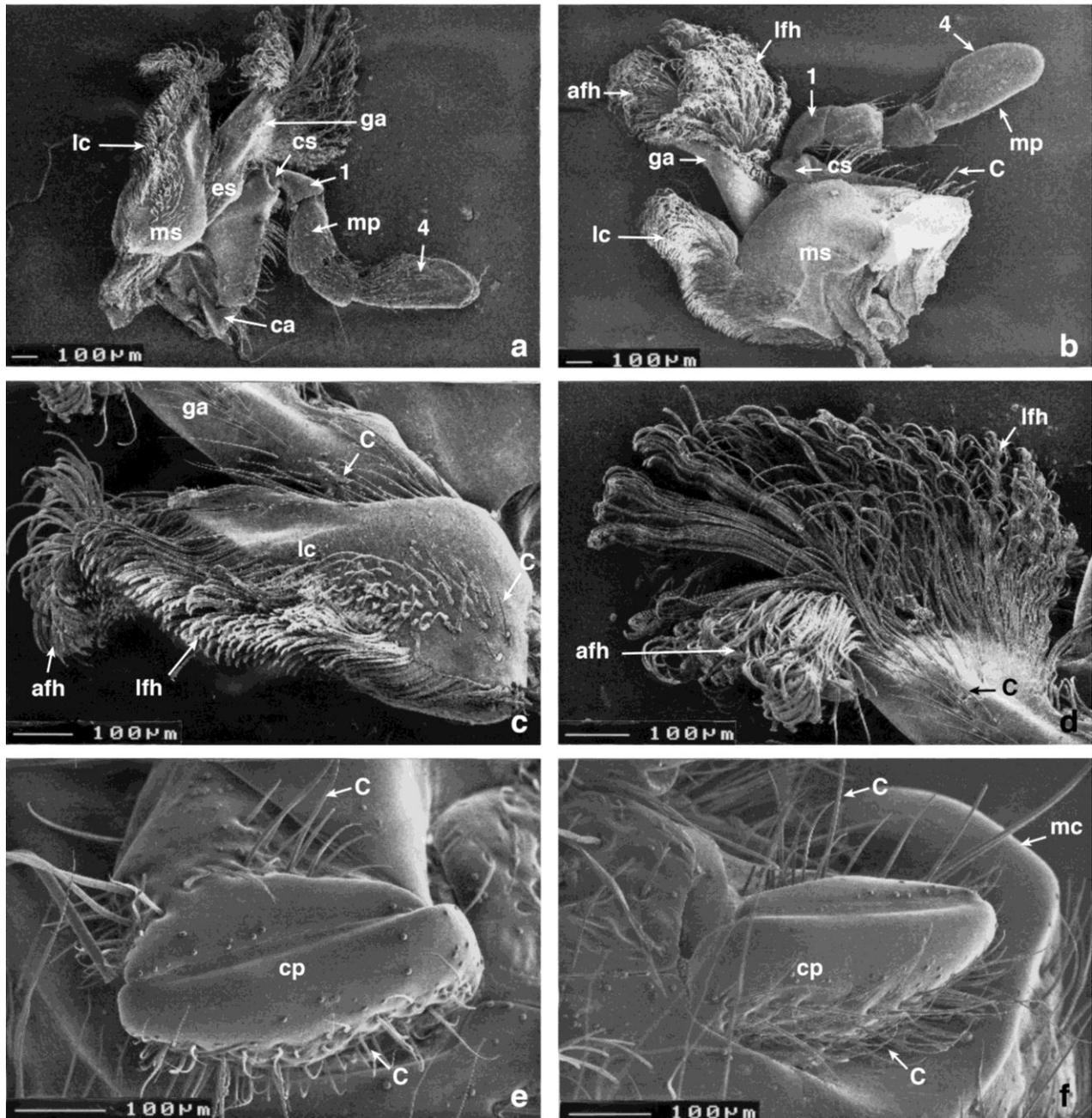


Figure 3. *Phoracantha recurva*. **a**, left maxilla, ventral view; **b**, right mandible, dorsal view; **c**, lacinia, ventral view; **d**, fringe of hairs of lacinia; **e**, **f**, two views of cardo process. afh, apical fringe of hairs; C, sensilla chaetica; ca, cardo; cp, cardo process; cs, costipes; es, eustipes; ga, galea; lc, lacinia; lfth, lateral fringe of hairs; mc, maxillary cavity; mp, maxillary palp; ms, mediostipes; 1-4, palpal segments.

Short aporous sensilla basiconica of subtype 2, (AB2s), are regularly scattered over the total dorsal and ventral surfaces of the 4th palpal segment. The sensillum cone measures 0.5 µm in length and 1.0 µm in basal diameter (Fig. 4g). Their number is of approximately 30 ventral sensilla and 70 dorsal sensilla.

The oval sensory area located on the ventral surface is a cluster of aporous sensilla digitiformia, which measures 160 µm in length for a median width of 40 µm (Figs. 5a, b). Each sensillum digitiformium measures 20-23 µm in length (Fig. 5c). It is made up of a peg inserted in a cuticular crevice (Fig. 5d). The sensilla are arranged in the form of a large fish-bone, the distal parts are directed towards the axis of the fish-bone (Fig. 5c). Each digitiformia complex comprises 50 sensilla.

Sensilla of labium and labial palps

The mentum is equipped with aporous sensilla chaetica 100-400 µm long, located in six groups: two proximal groups of 20 sensilla, in each of which the hairs are directed towards the medial part of the mentum; two latero-distal groups of 8 sensilla, each group is oriented backwards, and two distal groups of 6 sensilla, each of which is turned towards the prementum (Figs. 6a, b). The prementum bears no sensilla.

The labial palps have the same sensilla spread as the maxillary palps. Aporous sensilla chaetica are spread over both surfaces of the first two segments (Figs. 6b, 7d, e), measuring about 40 µm, except for a single sensillum of

230 μm on the external margin of the 2nd segment (Fig. 7d). On the terminal segment, they are both proximal and rare (5-6) on the dorsal surface, whereas they are more numerous and spread out uniformly on the ventral surface (Figs. 6b, f, 7d, f). The sensory slit comprises 90 uniporous sensilla basiconica (UBs), 33 multiporous sensilla basiconica MBs and 3-5 aporous sensilla basiconica of subtype 1, AB1s and no aporous sensilla styloconica (Figs. 6c, d). The oval sensory area measures 90 μm in length and 36 μm in width (Figs. 7f, g); it comprises 30 aporous

sensilla digitiformia 24 μm long (Figs. 7g, h). Aporous sensilla basiconica of subtype 2, (AB2s), are distributed on the dorsal and ventral surfaces of the terminal segment (Fig. 6e).

Glandular pores

Glandular pores are located on the maxillary and labial palps (Figs. 4g, 6e).

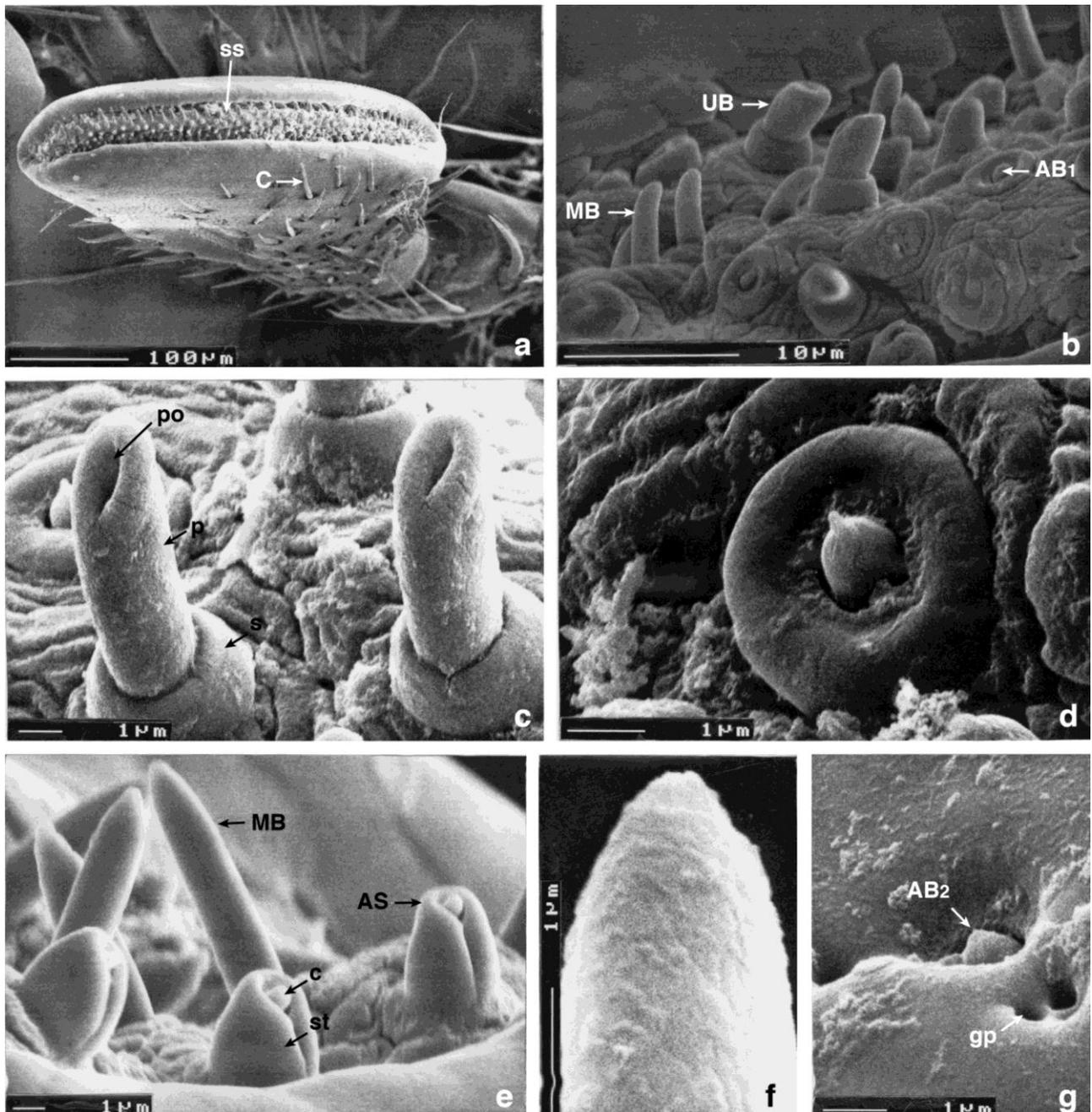


Figure 4. *Phoracantha recurva*, maxillary palp. **a**, apical view of 4th segment; ss, sensory slit; C, aporous sensillum chaeticum; **b**, uniporous sensillum basiconicum UB, multiporous sensillum basiconicum MB, aporous short sensillum basiconicum subtype 1 AB1; **c**, two uniporous sensilla basiconica showing the socket s, the peg p, the terminal pore po; **d**, detail of aporous short sensillum basiconicum subtype 1; **e**, three aporous sensilla styloconica AS with the stylus st and the sensory cone c, and sensilla MB; **f**, detail of sensillum MB; **g**, glandular pores gp and aporous short sensillum basiconicum subtype 2 AB2.

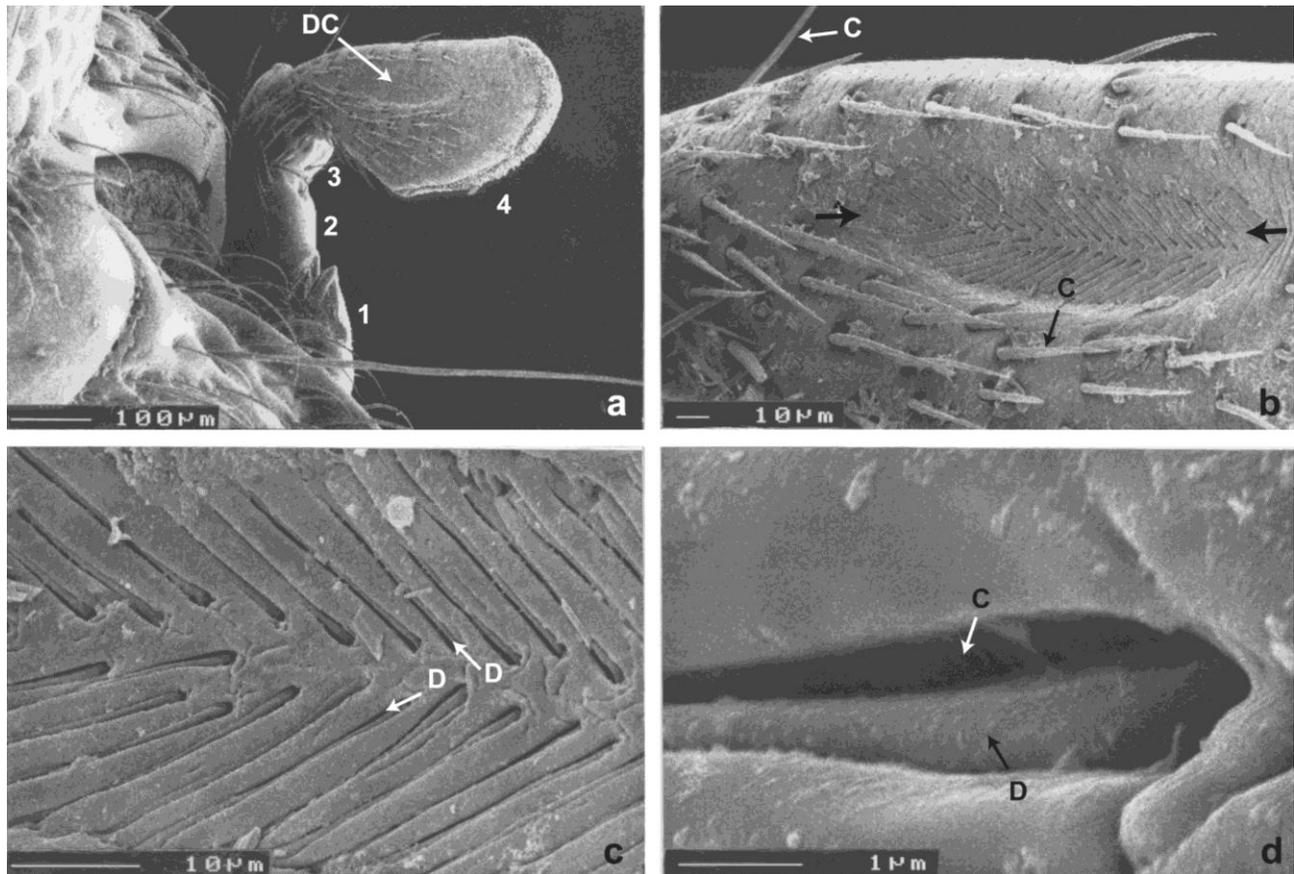


Figure 5. *Phoracantha recurva*, ventral view of maxillary palp. **a**, the 4 segments 1-4 and the digitiformia complex DC; **b**, the digitiformia complex limited by two arrows, and aporous sensilla chaetica C; **c**, detail of sensilla digitiformia D; **d**, distal part of a sensillum digitiformium D in its cuticular crevice c.

DISCUSSION

Comparison with other Coleoptera

The mouthparts of adult Coleoptera offer considerable similarities between different families (Jeannel 1949) and those of *Phoracantha recurva* are not exception. The same can be said concerning their sensory equipment.

The multiporous sensilla basiconica, uniporous sensilla basiconica and the aporous sensilla styloconica are present on the terminal segment of maxillary and labial palps in *Odontotaenius disjunctus* (Illiger, 1800), Passalidae (Baker 1987), *Ips typographus* (Linnaeus, 1758), Scolytidae (Hallberg 1982, Faucheux 2001a), *Pissodes* sp., Curculionidae (Faucheux 2001b). The aporous sensilla styloconica of *P. recurva* are similar to those of *O. disjunctus* (called "coronal sensilla" because of their ring-shaped arrangement), but differ greatly from the other coronal sensilla of other beetles, which have a collar of uniform length and no frontal notch (Doane & Klinger 1978, Whitehead 1981, Hallberg 1982). The total numbers of terminal sensilla are different within the species. Concerning the maxillary palp and the labial palp, their number is 250 and 130 respectively (*Phoracantha*),

35 and 30 (*Odontotaenius*), 21 and 14 (*Ips*), and 8 and 6 (*Pissodes*).

The sensilla digitiformia, generally exist on the terminal palpal segment of beetles. When the palps possess a circular section, they number from 4 to 6 and are arranged in parallel rows as it is the case of the Scolytidae and Curculionidae (Faucheux 2001a, b). When the terminal palpal segment is flattened as in *P. recurva*, the sensilla digitiformia are arranged in compact groups, which can be regarded as sensory organs, (Alekseev *et al.* 2005). These groups occur in the cerambycids *Callidium violaceum* (Linnaeus, 1758), *Spondylis buprestoides* (Linnaeus, 1758; Schmitt, 1994). Honomichl (1980) investigated in detail the topography of the sensilla digitiformia of 35 beetle species from 23 families. Mann & Crowson (1984) gave detailed information about the sensilla patterns of 58 leaf beetle species (Chrysomelidae). Schmitt (1994) which studied 9 families (Chrysomelidae, Bruchidae, Cerambycidae, Nemonychidae, Curculionidae, Urodontidae, Coccinellidae and Silphidae) showed that all beetles have sensilla digitiformia on the terminal segment of either maxillary or labial palps or both. The studied cerambycids possess numbers of sensilla digitiformia close to those of *P. recurva*.

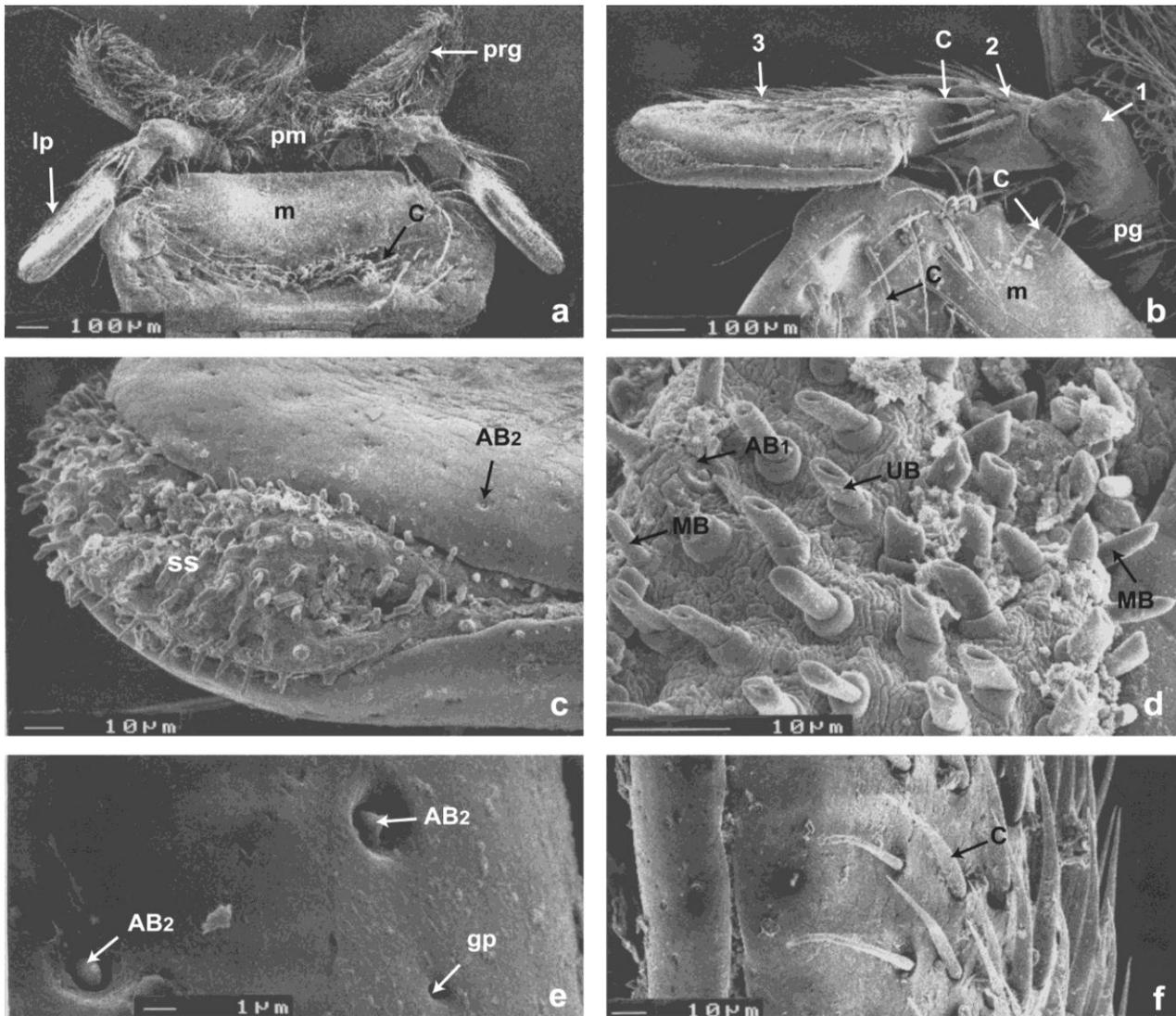


Figure 6. *Phoracantha recurva*, ventral views of labium. **a**, mentum m and prementum pm bearing paraglossa prg and labial palps lp; **b**, segments 1, 2, 3 of labial palp and part of mentum m; pg, palpiger; C, aporous sensilla chaetica; **c**, sensory slit ss of labial palp; AB2, aporous sensilla basiconica subtype 2; **d**, detail of aporous sensilla basiconica subtype 1 AB1, multiporous sensilla basiconica MB and uniporous sensilla basiconica UB; **e**, aporous sensilla basiconica subtype 2 AB2 and glandular pore gp; **f**, aporous sensilla chaetica C on the dorsal surface of labial palp.

Functions of mouthparts

Mechanical role

Contrary to many beetle mandibles (Kvenberg 1977, Dressler & Beutel 2010), the mandibles of *P. recurva* are not bilaterally asymmetrical; they bear only apical incisors without subapical incisors and they don't possess chewing molar surfaces. Their morphology is identical to those of small Coleoptera such as the Ptinidae and the Dermestidae (Kvenberg 1977). They are capable of cutting and tearing vegetable matter, but incapable of crushing it. These results are in accordance with the pollen-eating diet of adults. Mandibular movements serve to convey pollen to the mouth where pollen grains are ingested. The symmetrical mandibles of *P. recurva* may be used to crush pollen grains but this assumption has not been substantiated in many Coleoptera (Roulston & Cane 2000). Pollen grains are probably enzymatically broken down in the gut (Johnson &

Nicolson 2001). However, the mandibles have other functions beside feeding. Indeed, when matured, the females of *Monochamus* sp. (Coleoptera, Cerambycidae) use their mandibles to excavate slits in the bark of recently killed or weakened pine trees and lay one or two eggs in each wound (Tomminen 1993). Similarly, the females of *Phoracantha semipunctata* bite the *Eucalyptus* bark in order to choose their egg-laying sites (Helal & El Sebay 1980).

The maxillae are a masticatory organ in Coleoptera. In *P. recurva*, this role is performed by the laciniae and the galeae which are used to manoeuvre food particles into, or away from, the functional mouth. The abundant fringes of hairs on the maxillary laciniae and galeae and on the labium of *P. recurva* make it possible to gather and fix the *Eucalyptus* pollens and to direct them towards the mouth. Mouthparts of *P. recurva* serve well for both nectar and pollen-feeding. Undoubtedly, the contact chemosensilla on the maxillae taste the grains and nectar for their suitability as food.

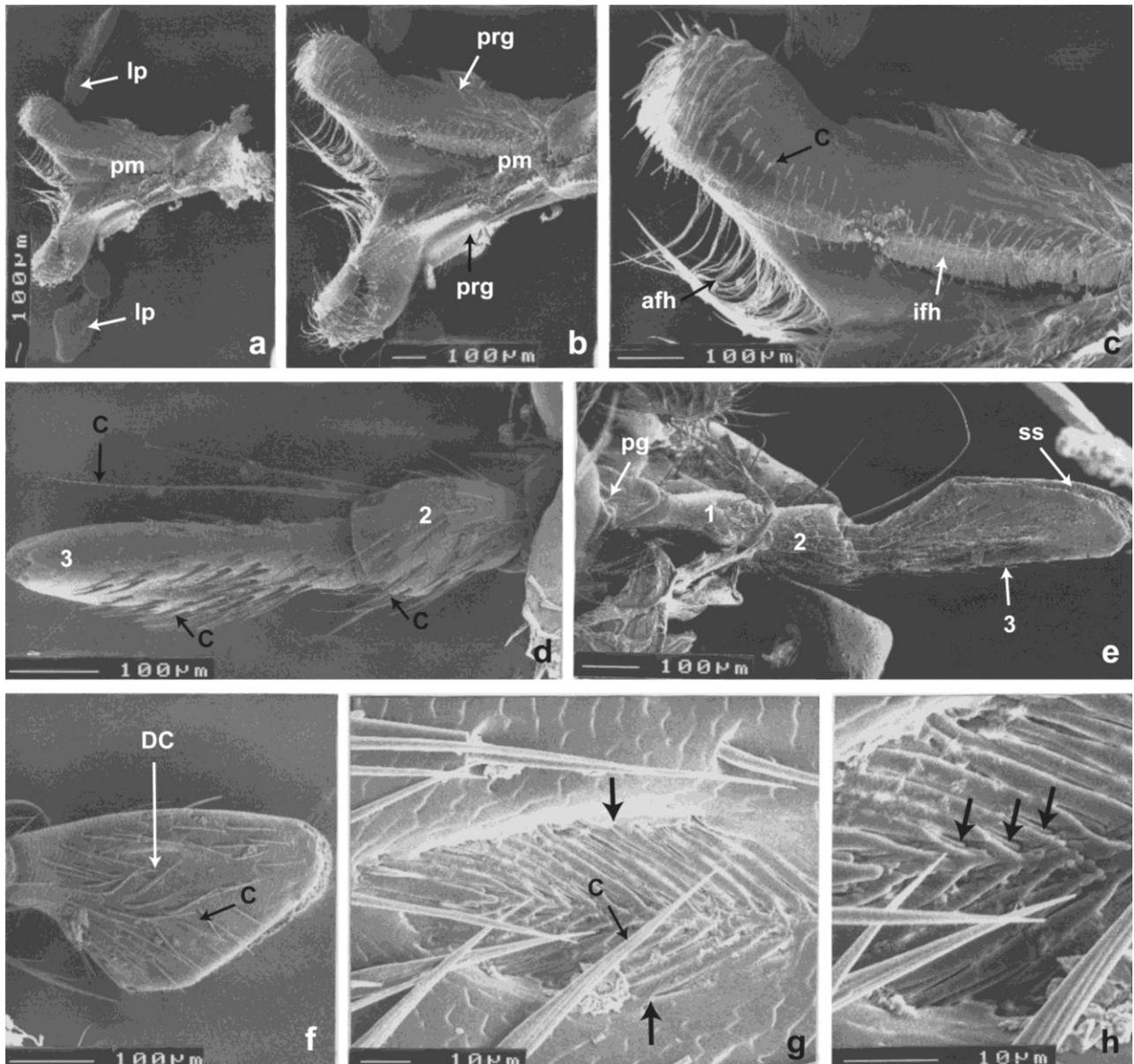


Figure 7. *Phoracantha recurva*, **a-e**, dorsal view of labium; **a**, prementum pm and labial palps lp; **b**, the two paraglossa prg of prementum; **c**, anterior and internal fringe of hairs afh, ifh of paraglossa; **d**, segments 2 and 3 of labial palp seen on their lateral surface; **e**, dorsal view of the three segments 1-3 of labial palp with sensory slit ss and palpiger pg; **f**, ventral view of 3rd palp segment showing the location of the digitiformia complex DC; **g**, digitiformia complex limited by arrows; C, aporous sensilla chaetica; **h**, detail of sensilla digitiformia (arrows).

Sensory role

According to Altner (1977), Altner *et al.* (1983) et Zacharuk (1980, 1985), the aporous sensilla chaetica with a flexible socket are contact mechanoreceptors (tactile sensilla), the aporous sensilla chaetica with an inflexible socket are thermo- and hygrometers, the uniporous sensilla are contact chemoreceptors (gustative sensilla), and the multiporous sensilla are olfactory chemoreceptors.

1. Aporous sensilla chaetica

The tactile sensilla chaetica of the mandibles probably have a limited function during feeding. They are stimulated when the females bite the *Eucalyptus* bark to choose their egg-laying site: the long sensilla C 1 intervene first during contact with the bark, the short sensilla C 2 intervene subsequently after estimating the depth of the bite.

All the other mouthparts possess numerous tactile sensilla chaetica. Previous results have shown that they were more numerous on the ventral face of these different pieces which are in contact with the food. All these tactile sensilla probably monitor movements of the food particles in order to direct them towards the mouth.

2. Uniporous sensilla basiconica (Ubs)

The ultra-structure of the UBs studied in *Dendroctonus ponderosae* Hopkins 1902 (Whitehead 1981) and *I. typographus* (Hallberg 1982) indicates that this sensillum type is probably a mechano- and contact chemoreceptor. This has been confirmed by electrophysiological data obtained on galeal sensilla of *Entomoscelis americana* Brown 1942 (Sutcliffe & Mitchell 1980). In the adults of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say,

1824), the uniporous pegs present on the maxillary galeae described by Sen & Mitchell (1987) are sensitive to sucrose, L-alanine and gamma amino butyric acid (GABA) (Mitchell 1974, Mitchell & Schoonhoven 1974, Mitchell & Harrison 1984). Now, the nectar of *Eucalyptus* absorbed by *P. recurva* contains water, sugars (sucrose, fructose, glucose, raffinose), amino acids and GABA which is known to be accumulated in nectar (Nicolson & Thornburg 2007). It can be surmised that the UBs of the yellow longicorn are likewise sensitive to the different aforementioned constituents.

The large numbers of the uniporous sensilla in *P. recurva*, compared to those of other beetles, show that the sensilla on the terminal palpal slits perform a crucial gustative role in the choice of food.

3. Multiporous sensilla basiconica (MBs)

The multiporous pegs of *O. disjunctus* stain with the crystal violet method of Slifer (1960) and the reduced silver nitrate technique of Schafer and Sanchez (1976). This demonstrates their porosity and is an indication of a presumed chemoreceptor. The ultrastructural results obtained on this sensillum type from other beetles, reveal that it is an olfactory receptor (Whitehead 1981, Hallberg 1982). The same sensilla on the apex of maxillary and labial palps of other beetles respond to a wide variety of olfactory stimuli (White *et al.* 1974, Doane & Klinger 1978). Because of the large number of MBs on the palps of *P. recurva*, the latter are extremely sensitive to odours of *Eucalyptus*; this sensitivity is greater on the maxillary palps than on the labial palps.

4. Aporous sensilla styloconica (ASs)

From ultrastructural observations in other Coleoptera (Whitehead 1981, Hallberg 1882) and because of their non-porosity as indicated by the lack of staining with crystal violet and reduced silver nitrate (Baker 1987), the ASs of maxillary palps are considered to be contact mechanoreceptors. Their absence on the labial palps is not really surprising, because these sensilla are not found on beetle larvae and adults of *Lyctus brunneus* (Stephens 1830) (Iwata and Nishimoto 1981) and *Sitophilus oryzae* (Linnaeus 1763) (Speirs *et al.* 1986). This seems to indicate the absence of tactile sensitivity on the labial palps of *P. recurva*.

However, no electrophysiological study has been carried out on this sensillum type, which does not possess the typical morphology of a tactile sensillum. The ASs of *P. recurva* bear great resemblance to the aporous sensilla styloconica, present on the antennae of Lepidoptera in which a thermo- hygroreceptrice function has been demonstrated (see Faucheux 1999).

5. Aporous sensilla basiconica of subtype 1 (AB1s)

The AB1s are not mentioned in any other Coleoptera. They resemble sensilla campaniformia and may respond to the pressures exerted on them when the maxillary and labial palps enter into contact with the food.

6. Aporous sensilla basiconica of subtype 2 (AB2s)

The AB2s spread out on the surfaces of the palpal

terminal segment are not mentioned either in other beetles. Their possible porosity has not been demonstrated. They may be classified among the «no-pore sensilla with an inflexible socket» and may therefore be thermo-hygroreceptrice (Altner *et al.* 1978, 1983).

7. Aporous sensilla digitiformia

A pore system was not found in the sensory hairs of sensilla digitiformia, which excludes an olfactory or gustative chemosensory function (Altner 1977, Zacharuk 1985). Indeed, in the coleopteran *Ctenicera destructor* (Brown, 1853), the sensilla digitiformia on the larval labial palps do not respond electrophysiologically to amino-acids, sugars, salts and water tested (Zacharuk *et al.* 1977). The sensilla digitiformia on the larval maxillary palps of the lepidopteran *Euxoa messoria* (Harris, 1842) and the coleopteran *Stegobium paniceum* (Linnaeus, 1758) are innervated by a single sensory neuron, whose the distal part of the dendrite is divided into several lamellated branches (Devitt & Smith 1982, Romani *et al.* 2011). Now, physiological investigations have provided some evidence that the sensory cells bearing a lamellated outer segment are thermoreceptive (Altner *et al.* 1978, Loftus & Corbière-Tichané 1981). However, Zacharuk *et al.* (1977) have shown that the sensilla of *C. destructor* were sensitive to contact and to vibratory stimuli. The sensilla digitiformia on the antennae of the cockroach *Periplaneta americana* (Linnaeus, 1758) and the cricket *Acheta domestica* Linnaeus 1758, are considered as mechanoreceptors with a proprioceptive function (Toh 1977, Faucheux 2009a). Mann & Crowson (1984) also suppose that the sensilla digitiformia of adult beetles, function as proprioceptive vibration detectors. On the basis of the position and the alignment of the sensilla in ca. 130 analysed species, Schmitt (1994) suspected that the primary biological role of these sensory organs is the detection of stretching forces acting upon the cuticular surface of the terminal maxillary or labial palpal segment.

The groups of sensilla digitiformia of *P. recurva* can be compared to the “compound slit organs” or “lyriform organs” of Arachnids. In the lyriform organs, several innervated cuticular slits are closely arranged in parallel lines. According to Barth & Pickelmann (1975), deformation of slits is measured in terms of compression and dilatation, respectively. The peripheral slits of a group, take up much more load than the intermediate slits. In large groups they are deformed even more than a single, isolated slit. Compression is the adequate deformation of the slit leading to nervous activity. The main physiological consequence deduced from model studies for a close parallel arrangement of slits is a considerable enlargement of the stimuli range accessible for a sensory analysis at a specific site.

The digitiformia compounds of the maxillary and labial palps of *P. recurva* could play an important role in testing the consistence of the food.

8. Glandular pores and glands

The pores distributed over much of the palpal surfaces are associated with glandular complexes. The function of these glands is not known. Glands almost anywhere on an

insect's body are common (Noirot & Quennedey 1974) and this instance cannot be considered unusual. Glandular pores have been described on the antennae and the ovipositor of *P. recurva* (Faucheux 2011, 2012). They are present on the galeae of the chrysomelid *E. americana* (Sutcliffe & Mitchell 1980). Now, these authors have noted that when the beetle is disturbed it egests a fluid, which on drying, forms a clot around the mouthparts. However this material never sticks to the mouthparts, thereby encumbering them. It may be that the glands of the galeae secrete a substance that coats the mouthparts and prevents such sticking. The glands in *P. recurva* could have this function.

CONCLUSION

The large numbers of sensilla on the terminal segment of the maxillary and labial palps of *Phoracantha recurva*, compared to those of other species in different families, show that palps play an important sensory role in feeding. The abundance of filtering devices on the maxillary laciniae and galeae as well as on the labium is related to the type of food (pollen grains) absorbed by the insect.

ACKNOWLEDGEMENTS

My acknowledgements to Mr M'Barek Agnas, (Oualidia, Morocco) for his help in finding and capturing the longicorn beetles; Mr Nicolas Stephant, Centre of Scanning Electron Microscopy and Microanalyse X, University of Nantes, for his help with the photography; Mrs Catherine Cerclé for preparing the plates, and Mr. Vittorio Ballardini for help with the translation. I also thanks the anonymous reviewers for fruitful reviews of the manuscript.

REFERENCES

- Alekseev M.A., Sinitsina E.E. & Chaika S.Y. 2005. Digitiform sensilla in beetles (Coleoptera). *Ent. Rev.* 85, 1045-1054.
- Altner H. 1977. Insect sensillum specificity and structure: an approach to a new typology. In LeMagen J. and MacLeod P. (eds.). *Olfaction and Taste*, Vol. VI, Information Retrieval, London, 295-303.
- Altner H., Tichy H. & Altner I. 1978. Lamellated outer dendritic segments of a sensory cell within a poreless thermo- and hygroreceptive sensillum of the insect *Carausius morosus*. *Cell Tissue Res.* 191, 287-304.
- Altner H., Schaller-Selzer L., Stetter H. & Wohlrab I. 1983. Poreless sensilla with inflexible sockets: a comparative study of a fundamental type of insect sensilla comprising thermo and hygroreceptors. *Cell Tissue Res.* 234, 279-307.
- Baker G.T. 1987. Apical sensilla on the adult and larval labial and maxillary palpi of *Odontotaenius disjunctus* (Illiger) (Coleoptera: Passalidae). *Proc. Entomol. Soc. Wash.* 89, 682-686.
- Baker G.T. & Monroe W.A. 1995. Sensory receptors on the adult labial and maxillary palpi and galea of *Cicindela sexguttata* (Coleoptera: Cicindelidae). *J. Morph.* 226, 25-31.
- Barth F.G. & Pickelmann P. 1975. Lyriform slit sense organs. *J. comp. Physiol.* 103, 39-54.
- Bland R.G. 1984. Mouthpart sensilla and mandibles of the adult alfalfa weevil *Hypera postica* and the Egyptian alfalfa weevil *H. brunneipennis* (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* 77, 720-724.
- Bosmans B. 2006. *Phoracantha recurva* (Coleoptera: Cerambycidae) found in a cluster of bananas. *Phegea* 34, 105-106.
- Chararas C. 1969. Biologie et écologie de *Phoracantha semipunctata* F. (Coléoptère Cerambycidae xylophage) ravageur des *Eucalyptus* en Tunisie, et méthodes de protection des peuplements. *Ann. Inst. Nat. Rech. For. Tunisie* 2, 1-37.
- Chararas C. 1979. *Ecophysiologie des insectes parasites des forêts*. Chararas (éd.), Paris, 297 p.
- Devitt B.D. & Smith J.J.B. 1982. Morphology and fine structure of mouthpart sensilla in the dark-sided cutworm *Euxoa messoria* (Harris) (Lepidoptera: Noctuidae). *Int. J. Insect Morphol. & Embryol.* 11, 255-270.
- Doane J. & Klinger J. 1978. Location of CO₂-receptive sensilla on the larvae of the wireworms *Agriotes lineatus-obscurus* and *Limonijs californicus*. *Ann. Entomol. Soc. Am.* 71, 357-363.
- Dressler C. & Beutel R.G. 2010. The morphology and evolution of the adult head of Adephaga (Insecta: Coleoptera). *Arthropod Syst. & Phylog.* 68, 239-287.
- Faucheux M.J. 1999. *Biodiversité et unité des organes sensoriels chez les Insectes Lépidoptères*. Ed. Soc. Sci. nat. Ouest Fr., Nantes, 296 p.
- Faucheux M.J. 2001a. Les Scolytes. In: Faucheux M.J., Lebrun D. & Sadorge A. (eds.). *Les Insectes du bois: Capricornes, Vrillettes, Termites et autres xylophages*, Ed. Soc. Sci. nat. Ouest Fr., Nantes, 179-228.
- Faucheux M.J. 2001b. Les Pissodes ou Charançons du pin et du sapin. In: Faucheux M.J., Lebrun D. & Sadorge A. (eds.). *Les Insectes du bois: Capricornes, Vrillettes, Termites et autres xylophages*, Ed. Soc. Sci. nat. Ouest Fr., Nantes, 229-251.
- Faucheux M.J. 2009a. Une nouvelle sensille sur les antennes des imagos d'Insectes: la sensille digitiforme du Grillon domestique, *Acheta domesticus* Linnaeus, 1758 (Orthoptera: Ensifera: Gryllidae). *Bull. Soc. Sci. nat. Ouest Fr.*, n.s. 31, p. 48.
- Faucheux M.J. 2009b. *Phoracantha recurva* Newman, 1840 (Coleoptera: Cerambycidae) au Maroc atlantique. *Bull. Soc. Sci. nat. Ouest Fr.*, n.s., 31, p. 70.
- Faucheux M.J. 2011. Antennal sensilla of the Yellow longicorn beetle *Phoracantha recurva* Newman, 1840: distribution and comparison with *Phoracantha semipunctata* (Fabricius, 1775) (Coleoptera: Cerambycidae). *Bull. Inst. Sci.*, Rabat, 33, 19-29.
- Faucheux M.J. 2012. Ovipositor sensilla of the Yellow longicorn beetle *Phoracantha recurva* Newman, 1840 (Coleoptera: Cerambycidae). *Bull. Inst. Sci.*, Rabat, 34, 11-18.
- Fraval A. & Haddan M. 1989. *Phoracantha*. Actes Ed., Rabat. Coll. Doc. Sci. techn., 38 p.
- Gil Sotres M. & Mansilla Vazquez J.P. 1983. Detection en España de *Phoracantha semipunctata* Fb. sobre *Eucalyptus globulus* Labill. *Ann. INIA, serie Forstal*, 7, 171-192.
- Hallberg E. 1982. Sensory organs in *Ips typographus* (Insecta: Coleoptera). Fine structure of the sensilla of the maxillary and labial palps. *Acta Zool.* 63, 191-198.
- Hanks L.M., Millar J.G. & Paine T.D. 1996. Mating behavior of the *Eucalyptus* longhorned borer (Coleoptera: Cerambycidae) and the adaptive significance of long "horns". *J. Insect Behav.* 9, 383-393.
- Helal H. & El Sebay Y. 1980. The *Eucalyptus* borer *Phoracantha semipunctata* (F.), behaviour, nature of the damage, and its parasites and predators in Egypt (Cerambycidae: Coleoptera). *Agric. Res. Review* 58, 31-37.
- Honmichl K. 1980. Die digitiform sensillen auf dem Maxillarpalpus von Coleoptera. I. Vergleichend-topographische Untersuchung des Kutikulären Apparates. *Zool. Anz.*, 20, 1-12.
- Iwata R. & Nishimoto K. 1981. Observations on the external

- morphology and the surface structure of *Lyctus brunneus* (Stephens) (Coleoptera: Lyctidae) by scanning electron microscopy. *Kontyu* (Tokyo), 49, 542-557.
- Jeannel R. 1949. Ordre des Coléoptères, partie générale. In: Grassé P.-P. (éd.). *Traité de Zoologie, tome IX, Insectes*. Masson et C^{ie}, Paris, 771-891.
- Johnson S.A. & Nicolson S.W. 2001. Pollen digestion by flower-feeding Scarabaeidae: protea beetles (Cetoniini) and monkey beetles (Hopliini). *J. Insect Physiol.* 47, 725-733.
- Kvenberg J. E. 1977. Scanning electron microscopic study of adult stored product beetle mandibles. *Journal of the AOAC*, 60, 5, 1185-2009.
- Loftus R. & Corbière-Tichané G. 1981. Antennal warm and cold receptors of the cave beetle, *Speophyes lucidulus* Delar., in sensilla with a lamellated dendrite. I. Response to sudden temperature change. *J. Comp. Physiol.* 143, 443-452.
- Mann J.S. & Crowson R.A. 1984. On the digitiform sensilla of adult leaf beetles (Coleoptera: Chrysomelidae). *Ent. Gener.* 9, 121-133.
- Millar J.G., Paine T.D., Joyce A.L. & Hanks L.M. 2003. The effects of *Eucalyptus* pollen on longevity and fecundity of *Eucalyptus* longhorned borers (Coleoptera: Cerambycidae). *J. Econ. Entomol.* 96, 370-376.
- Mitchell B.K. 1974. Behavioral and electrophysiological investigations on the responses of larvae of the Colorado potato beetle (*Leptinotarsa decemlineata*) to amino acids. *Entomol. exp. appl.* 17, 255-264.
- Mitchell B. K. & Harrison G. D. 1984. Characterization of galeal chemosensilla in the adult Colorado beetle, *Leptinotarsa decemlineata*. *Physiol. Entomol.* 9, 49-56.
- Mitchell B.K. & Schoonhoven L.M. 1974. Taste receptors in Colorado beetle larva. *J. Insect Physiol.* 20, 255-264.
- Nicolson S.W. & Thornburg R.W. 2007. Nectar chemistry. In: Nicolson S.W. et al. (eds.), *Nectaries and Nectar*, Springer, 215-263.
- Noirot C. & Quennedey A. 1974. Fine structure of insect epidermal glands. *Ann. Rev. Entomol.* 19, 61-80.
- Romani R., Rossi Stacconi M.V. & Chiappini E. 2011. Preliminary data on *Segobium paniceum* (L.) larval head sensilla. *J. Ent. Acarol. Res.* ser 2, 43, 77-82.
- Roovers M. & Yana A. 1967. Premiers essais d'attraction de *Phoracantha semipunctata* F. par quelques substances naturelles. *Bull. Ec. Nation. Sup. Tunisie* 14, 51-64.
- Roulston T.H. & Cane J.H. 2000. Pollen nutritional content and digestibility for animals. *Plant Syst. Evol.* 222, 187-209.
- Schafer R. & Sanchez T. 1976. The nature and development of sex attractant specificity in cockroaches of the genus *Periplaneta*. I, Sexual dimorphism in the distribution of antennal sense organs in five species. *J. Morphol.* 149, 139-158.
- Schmitt M. 1994. The position of the Megalopodinae and Zeugophorinae in a phylogenetic system of the Chrysomeloidea (Insecta: Coleoptera). In: Furth D.G. (ed.). *Proceedings of the Third International Symposium on the Chrysomelidae*. Beijing 1992, Backhuys Pub., Leiden, 38-44.
- Sen A. & Mitchell B.K. 1987. Ultrastructure of the galeal sensory complex in adults of the Colorado potato beetle, *Leptinotarsa decemlineata*. *Physiol. Entomol.* 12, 81-90.
- Slifer E.H. 1960. A rapid and sensitive method for identifying permeable areas in the body wall of insects. *Entomol. News.*, 71, 179-182.
- Speirs R., White G. & Wilson J. 1986. SEM observations of rice weevil larvae, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae). *J. Kans. Entomol. Soc.* 59, 390-394.
- Sutcliffe J.F. & Mitchell B.K. 1980. Structure of galeal sensory complex in adults of the red turnip beetle, *Entomoscelis americana* Brown (Coleoptera, Chrysomelidae). *Zoomorphology* 96, 63-76.
- Toh Y. 1977. Fine structure of antennal sense organs of the male cockroach, *Periplaneta americana*. *J. Ultrastr. Res.* 60, 373-394.
- Tomminen J. 1993. Development of *Monochamus galloprovincialis* (Olivier) (Coleoptera, Cerambycidae) in cut trees of young pines (*Pinus sylvestris* L.) and log bolts in southern Finland. *Entomol. Fennica* 4, 137-142.
- White R., Paim U. & Seabrook W. 1974. Maxillary and labial sites of carbon dioxide sensitive receptors of larval *Orthosoma brunneum*. *J. comp. Physiol.* 88, 235-246.
- Whitehead A. 1981. Ultrastructure of sensilla on the female mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Int. J. Insect Morphol. & Embryol.* 10, 19-28.
- Zacharuk R.Y. 1980. Ultrastructure and function of insect chemosensilla. *Ann. Rev. Entomol.* 25, 27-47.
- Zacharuk R.Y. 1985. Antennae and sensilla. In: Kerkut G.A. & Gilbert L.I. (eds.). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 6. Pergamon Press, London, 1-70.
- Zacharuk R.Y., Albert P.J. & Bellamy F.W. 1977. Ultrastructure and function of digitiform sensilla on the labial palp of a larval elaterid (Coleoptera). *Can. J. Zool.* 55, 569-578.

Manuscrit reçu le 03/4/2013

Version révisée acceptée le 12/12/2013

Version finale reçue le 11/04/2014

Mise en ligne le 28/04/2014