

Antennal sensilla in the endemic New Zealand moth family Mnesarchaeidae: morphology and phylogenetic implications (Lepidoptera: Mnesarchaeoidea)

By Michel J. FAUCHEUX, and George W. GIBBS

Abstract

A scanning electron microscope study of the antennal sensilla in five species of *Mnesarchaea*, sole genus in the endemic New Zealand moth family Mnesarchaeidae was made to elucidate their potential phylogenetic significance. Twelve sensillum types are described. Eight are common to all the species: multiporous long sensilla basiconica, multiporous sensilla trichodea, multiporous sensilla coeloconica, uniporous sensilla chaetica, aporous sensilla chaetica, aporous long-haired sensilla styloconica, aporous Böhm's sensilla and sensilla campaniformia.

Some sensillum types occur only in members of one of the two species groups currently recognized. The multiporous multibranching sensilla basiconica are present only in the *fallax*-group (*paracosma*, undescribed species 1), while the multiporous sensilla auricillica and the atypical short-styled sensilla styloconica appear restricted to the *acuta*-group (*acuta*, *fusilella*, undescribed species 2).

The Mnesarchaeidae share with some other homoneurous moth families the presence of long-haired sensilla styloconica, and with the Neopseustidae also the aggregation of pores on some subtypes of sensilla basiconica (viz, the multibranching type and sensilla auricillica). The multibranching sensilla basiconica in the *fallax*-group are in some aspects different from the sensilla ascoidea present in Micropterigidae and Opostegidae; they may be considered as a good autapomorphy of this species group. The aporous short-styled sensilla auricillica recorded from the *Mnesarchaea acuta*-group seem so far to have been described elsewhere only from a hepialid among the homoneurous moths.

Key words: Lepidoptera, *Mnesarchaea*, *acuta*-group, *fallax*-group, antenna, sensilla, phylogeny.

Résumé

Une étude au microscope électronique à balayage des sensilles antennaires dans cinq espèces de *Mnesarchaea*, unique genre de la famille des Mnesarchaeidae, endémique de Nouvelle-Zélande, a été réalisée pour élucider leur éventuelle signification phylogénétique. Douze types sensillaires ont été décrits. Huit sont communs à toutes les espèces: les longues sensilles basiconiques multipores, les sensilles trichoides multipores, les sensilles coeloconiques multipores, les sensilles chétiformes unipores, les sensilles chétiformes sans pore, les sensilles styloconiques sans pore à long poil, les sensilles de Böhm et les sensilles campaniformes.

Quatre types sensillaires existent seulement chez les membres

de l'un des deux groupes d'espèces couramment reconnus. Les sensilles basiconiques ramifiées multipores sont présentes seulement dans le groupe *fallax* (*paracosma*, espèce 1 non décrite) tandis que les sensilles auricilliformes multipores et les sensilles styloconiques atypiques à style court sont restreintes au groupe *acuta* (*acuta*, *fusilella*, espèce 2 non décrite).

Les Mnesarchaeidae partagent avec quelques autres familles de Lépidoptères homoneures la présence de sensilles styloconiques à long poil, et avec les Neopseustidae le groupement des pores chez quelques sous-types de sensilles basiconiques (ex. le type ramifié et les sensilles auricilliformes). Les sensilles basiconiques ramifiées du groupe *fallax* sont par plusieurs aspects différentes des sensilles ascoïdes présentes chez les Micropterigidae et les Opostegidae; elles peuvent être considérées comme étant une bonne autapomorphie de ce groupe d'espèces. Les sensilles styloconiques à style court identifiées dans le groupe *acuta* semblent avoir été décrites seulement chez un Hepialidae parmi les Lépidoptères homoneures.

Mots-clés: Lépidoptère, *Mnesarchaea*, groupe *acuta*, groupe *fallax*, antenne, sensilles, phylogénèse.

Introduction

For some time now, the study of antennal sensilla has been known to contribute useful data for the understanding of the phylogeny of lower (homoneurous) Lepidoptera: Micropterigidae (FAUCHEUX, 1997; 2004b), Agathiphagidae (FAUCHEUX, 1990; 2004a), Heterobathmiidae (FAUCHEUX, 2004c), Lophocoronidae (FAUCHEUX, 2006b) and Neopseustidae (FAUCHEUX, 2005a, b; FAUCHEUX, *et al.*, 2006). The Mnesarchaeidae, which pertain to the Exoporia (one of the two lineages arising in the basal splitting event recognizable in the Neolepidoptera), have never been studied in this respect.

The Mnesarchaeidae are a small family of the Lepidoptera, which is endemic to New Zealand. Its single genus, *Mnesarchaea* Meyrick, 1885, comprises small moths with wingspans between 8 and 12 mm. The family Mnesarchaeidae is of particular interest

for being among the most overall generalized Neolepidoptera. MUTUURA (1972) noted the similarity of their external female genitalia to those of the Hepialoidea, and the exoporian nature of the female genital apparatus was convincingly demonstrated by DUGDALE (1974). A position of the Mnesarchaeidae as a sister-group of Hepialoidea and constituting with the latter the high-rank taxon Exoporia (which in turn is the sister-group of the Heteroneura) has been the consensus phylogeny adapted in subsequent work (GIBBS, 1979; KRISTENSEN, 1997; KRISTENSEN *et al.*, 2007).

As noted already by PHILPOTT (1927), members of the genus *Mnesarchaea* present a very striking diversity in male genitalia and colour pattern features. Subsequent work (GIBBS, WIEGMANN & KRISTENSEN, in preparation) has led to the recognition of two species groups: 1° - the *fallax*-group species comprising *M. fallax* PHILPOTT, 1927; *M. fusca* PHILPOTT, 1922; *M. paracosma* MEYRICK, 1885 and an undescribed taxon *Mnesarchaea* species 1 (*M. fallax* being outside a clade comprising the other three and likely in most characters being closest to the morphological ground plan of the group). 2° - the *acuta*-group species comprising *M. acuta* PHILPOTT, 1930; *M. fusilella* WALKER, 1864; *M. hamadelpha* MEYRICK, 1888; *M. loxoscia* MEYRICK, 1888; and six undescribed species (*Mnesarchaea* species 2-7). The Mnesarchaeidae are represented only in relatively few collections and several species are rare and/or have very restricted ranges. The present study is based on a sample of taxa from each species-group, but omits *M. fallax*.

Material and methods

The examined material, all collected by G.W. Gibbs, comprises from the *fallax*-group: *M. paracosma* male, female, *M. undescribed* species 1; from the *acuta*-group: *M. fusilella* male, female, *M. acuta*, *M. undescribed* species 2. For S.E.M. study, the antennae were cleaned in acetone, dehydrated into pure alcohol and mounted, both on the ventral and the dorsal face, on specimen holders. After coating with gold and palladium, preparations were examined in a Jeol J.S.M. 6400F SEM at 10 kV. The mean number of each sensillum type was calculated from the counts of every fifth flagellomere with SEM. Sensillum terminology follows ZACHARUK (1985), FAUCHEUX (1999), HALLBERG *et al.* (2003).

Results

A – Gross morphology of antennae

The antennae of *Mnesarchaea* spp. are about 2.0-2.7 mm long, depending on size of the moth. They comprise an enlarged scape, a pedicel and a flagellum with 31-43 (male) and 28-37 (female) cylindrical flagellomeres, of which the two basal ones may be incompletely or not at all separated. The gross morphology of the flagellum is constant throughout the family, and all segments are more or less uniform (Figs 1, 2).

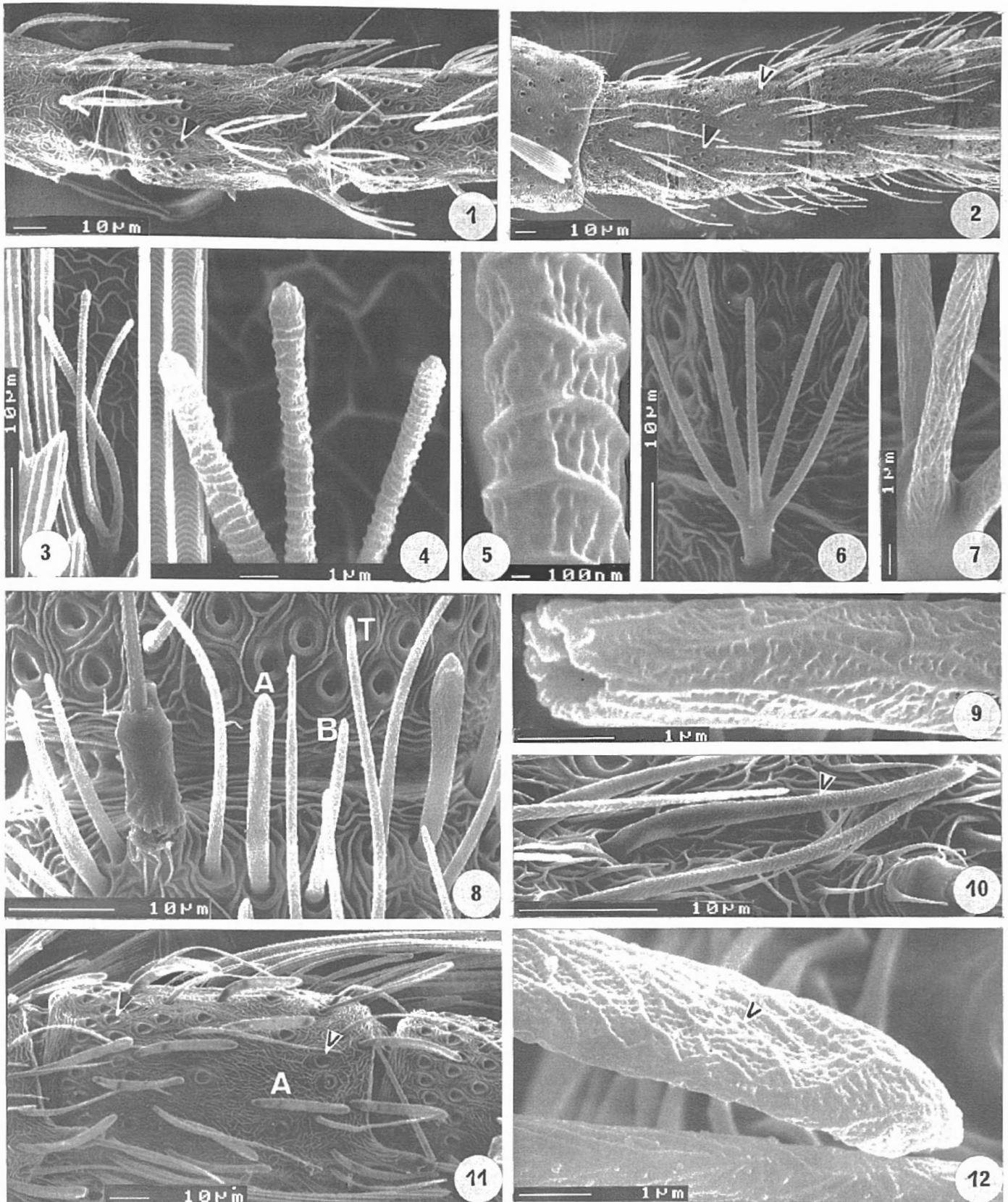
The flagellomeres have elongate arrowhead-like lamellar scales with a forked apex; they overlap each other and cover the flagellum surface almost entirely; thus there is no scaleless areas. In *M. paracosma* and *M. species 1*, the scale sockets are concentrated in the proximal third of each flagellomere and thus constitute a single band (Fig. 1). In the examined *acuta*-group species (*M. acuta*, *M. fusilella*, *M. species 2*) there are, in addition to the proximal scale-band, scattered scales on the remaining surface of the flagellomere (Figs 2, 11).

There is little differentiation between dorsal and ventral surfaces which is not surprising in view of the erect position of antennae (GIBBS, 1979). The flagellum cuticle is wrinkled in a reticulate pattern and microtrichia are absent.

B – The different types of sensilla

In *Mnesarchaea*, a total of twelve types of antennal sensilla have so far been identified, but a few are restricted to just one of the two species groups. These sensillum types are: multiporous multibranching sensilla basiconica, multiporous long sensilla basiconica, multiporous sensilla auricillica, multiporous sensilla trichodea, multiporous sensilla coeloconica, uniporous sensilla chaetica, aporous sensilla chaetica, aporous long-haired sensilla styloconica, aporous long-styled sensilla styloconica, aporous short-styled sensilla styloconica, aporous Böhm's sensilla and aporous sensilla campaniformia. The morphological characters of these sensilla and their occurrence in all taxa are given in Tables 1 and 2. No sexual dimorphism in sensillum complement was observed. As in many lower Lepidoptera, for example the Neopseustidae (FAUCHEUX, 2005b), most sensillum types (s. styloconica excepted) occur all around the flagellomeres, but are frequently more numerous on the ventral face.

1 - The multiporous multibranching sensilla basiconica (MMSB) have been found only in the *fallax*-group where they are present from the 1st flagellomere to



Figs 1-12 — Antennal sensilla of *Mnesarchaea* sp. 1. *M. paracosma*, 4-6th descaled flagellomeres showing sensilla and alveola of proximal scales (arrow); 2. *M. species 2*, basal flagellomeres showing proximal (black arrow) and distal (white arrow) scale alveola; 3-5. *M. species 1* male, multibranching sensillum basiconicum; 6-7. *M. paracosma*, multibranching sensillum basiconicum; 8. *M. species 2*, sensillum auricullicum (A), basiconicum (B) and trichodeum (T); 9. *M. species 2*, broken sensillum basiconicum; 10. *M. fusilella* female, sensillum basiconicum (arrow); 11. *M. acuta*, sensilla auricullica (A), proximal (black arrow) and distal (white arrow) scale alveola; 12. *M. acuta*, pores (arrow) of sensillum auricullicum.

Table 1 – Length and basal width of antennal sensilla of *Mnesarchaea* sp.

Sensilla	Length (μm)	Basal width (μm)
Multiporous multibranch sensilla basiconica (MMSB)	25.7 +/- 3.8	3.3 +/- 0.4
Multiporous long sensilla basiconica (MLSB)	23.8 +/- 4.2	1.7 +/- 0.2
Multiporous sensilla auricillica (MSA)	24.9 +/- 4.5	2.2 +/- 0.4
Multiporous sensilla trichodea (MST)	42.1 +/- 5.3	1.3 +/- 0.2
Multiporous sensilla coeloconica (MSC)	4.8 +/- 1.9	1.6 +/- 0.3
Uniporous sensilla chaetica (USC)	32.5 +/- 3.6	1.1 +/- 0.2
Aporous sensilla chaetica (ASC)	28.5 +/- 3.2	1.1 +/- 0.1
Aporous long-haired sensilla styloconica (ALHSS)	49.4 +/- 4.8	5.2 +/- 0.3
Aporous long-styled sensilla styloconica (ALSSS)	6.9 +/- 1.3	3.6 +/- 0.4
Aporous short-styled sensilla styloconica (ASSSS)	3.7 +/- 0.9	1.5 +/- 0.2
Aporous Böhm's sensilla (ABS)	10.5 +/- 2.4	0.8 +/- 0.1
Aporous sensilla campaniformia (ASC)	2.5 +/- 0.5	7.5 +/- 0.2

the apical flagellomere. They consist of 2-6 branches of slightly different lengths (Fig. 3) originating from a common base which usually has the form of a short (3-4 μm) stem. The number of branches varies between flagellomeres and for a given flagellomere it varies from one specimen to another (of the same sex). Also occasionally, sensilla on the same flagellomere may have different branch numbers: thus in one male *M. paracosma* examined, the basal flagellomere has one sensillum with 2 branches on one face and one with 6 on another. There seems to be a general trend towards higher branch number from the antennal base to a region around mid-length, while in the distal part, the dominant branch number is 3. The basal diameter of the sensillum is 3 or 4 times larger than that of a sensillum

basiconicum or trichodeum, which suggests that the MMSB corresponds to several combined sensilla (Table 1). The diameter of each branch is similar to that of a trichoïd sensillum. The sensillum wall possesses oblique ribs at the base which become annular towards the tip (Figs 4, 7). The wall structure of the MMSB thus resembles that of a typical sensillum trichodeum of Lepidoptera. In *M. paracosma*, the ribs at the base constitute a reticular pattern. The pores are located in the depressions delimited by the ribs (Fig. 5). On each flagellomere of both two species, the sensilla are located in 2 circles of 4 sensilla each: a median circle and a distal circle. Thus, in *M. paracosma* and *M. hudsoni*, the MMSB is the most frequent sensillum type.

Table 2 – Distribution of antennal sensilla in five species of *Mnesarchaea* sp.

Sensilla	<i>fallax</i> -group species		<i>acuta</i> -group species		
	<i>paracosma</i>	species 1	<i>acuta</i>	<i>fusilella</i>	species 2
MMSB	+	+	-	-	-
MLSB	-	-	+	+	+
MSA	-	-	+	+	+
MST	-	+	+	+	+
MSC	+	+	+	+	+
USC	+	+	+	+	+
ASC	+	+	+	+	+
ALHSS	+	+	+	+	+
ALSSS	+	+	-	-	-
ASSSS	-	-	+	+	+
ABS	+	+	+	+	+
ASC	+	+	+	+	+

2 - The multiporous long sensilla basiconica (MLSB) are present only in *M. acuta*, *M. fusilella* and *M. species 2*. In the latter species, their size is equivalent to that of the sensilla auriculica and, like them, they are situated in a distal circle (Fig. 8). Their thin wall possesses an irregular network of ribs between which are located the pores (Fig. 9). In *M. acuta* and *M. fusilella*, they are much longer than the sensilla auriculica and they are always dispersed (Fig. 10). The number of MLSB varies from 2 to 6 per flagellomere.

3 - The multiporous sensilla auriculica (MSA) have similarly been observed in the *acuta*-group species only. They are flattened, in the shape of an elongated tongue and their width can measure two or three times that of a sensillum basiconicum (Fig. 8). The MSA are perforated by pores placed between the branches of an irregular network of ribs (Fig. 12). Present from the 1st flagellomere onwards, they continue up to the apex of the antenna. In *M. species 2*, they are all grouped in a circle of from 8 to 10 sensilla at the distal end of each flagellomere (Fig. 8). In *M. fusilella*, they are less frequent and dispersed over the flagellomere to the extent of 2 to 3 per antennal face. In *M. acuta*, the MSA are spread out regularly over the total surface of the flagellomere except for the distal end where they form a circle (Fig. 11); the maximum number of sensilla observed in this species is 24 on the flagellomeres near mid-length.

4 - The multiporous sensilla trichodea (MST), observed in all species, are the longest sensilla and are recognisable by their curvature (Fig. 13). They can be identified by their oblique striae at the base which become annular on the remainder of the hair (Figs 14, 15). In the *acuta*-group, they are numerous on each flagellomere: 16 (*acuta*), 18 (*fusilella*) and 12 (*M. species 2*). Only two sensilla per flagellomere were observed in *M. hudsoni* male or female, and no sensillum was observed in *M. paracosma*. Thus, in the *fallax*-group which possesses multibranching sensilla basiconica, the MST are rare or absent.

5 - The multiporous sensilla coeloconica (MSC) without a fringe of microtrichia are present in the five species to the extent of 1-2 per flagellomere (Fig. 16). They are always located towards the distal edge of the flagellomere.

6 - The uniporous sensilla chaetica (USC) are characterised by their basal cupola, their stiff hair being

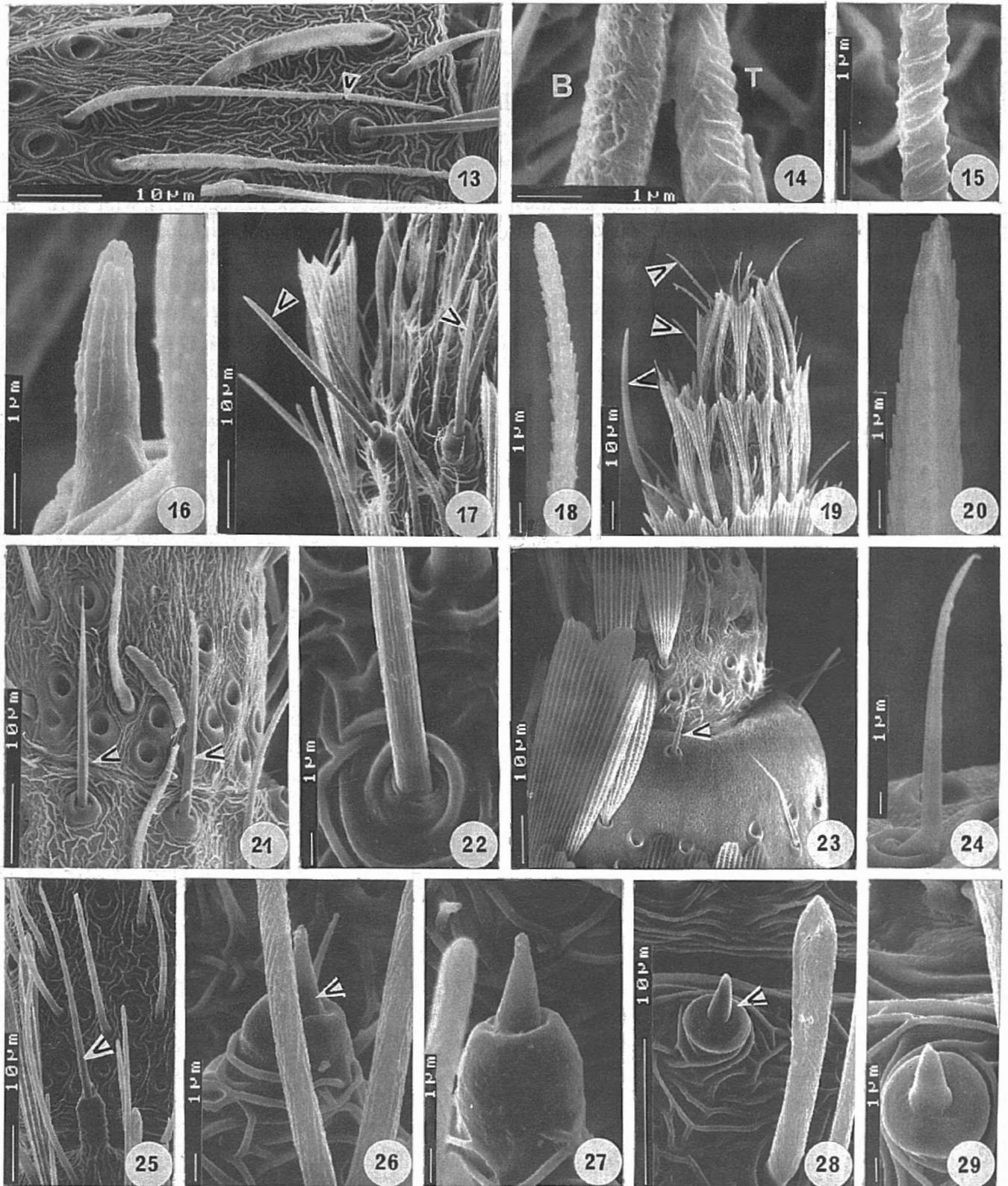
inclined about 45° relative to the antennal surface (Fig. 17), their blunt apex pierced by a terminal pore, and the longitudinal ribs (Fig. 18). Present in all species, they are relatively infrequent: 2-3 per flagellomere. However, in *M. fusilella*, they are arranged in a circle of 9-10 sensilla on many of the flagellomeres. The apical flagellomere in all the species bears two circles (near mid-length and apex respectively) with 8-10 sensilla (Fig. 19). The subapical flagellomere of the male *M. species 1* possesses a particular USC; it is 80-100 µm in length and its diameter is three times that of a normal sensillum (Figs 19, 20). This sensillum has not been observed in any species of *Mnesarchaea* or even of any other Lepidoptera (FAUCHEUX, 1999).

7 - The aporous sensilla chaetica (ASC) possess a wall which is ornamented like that of uniporous sensilla chaetica. They clearly differ by their double basal cupola of limited height, their slender, pointed apex and the absence of a terminal pore (Figs 21, 22). Their number does not exceed 2 to 4 sensilla per flagellomere. Similar sensilla inclined at an angle of 45° are also present on the scape and the pedicel (Figs 23, 24).

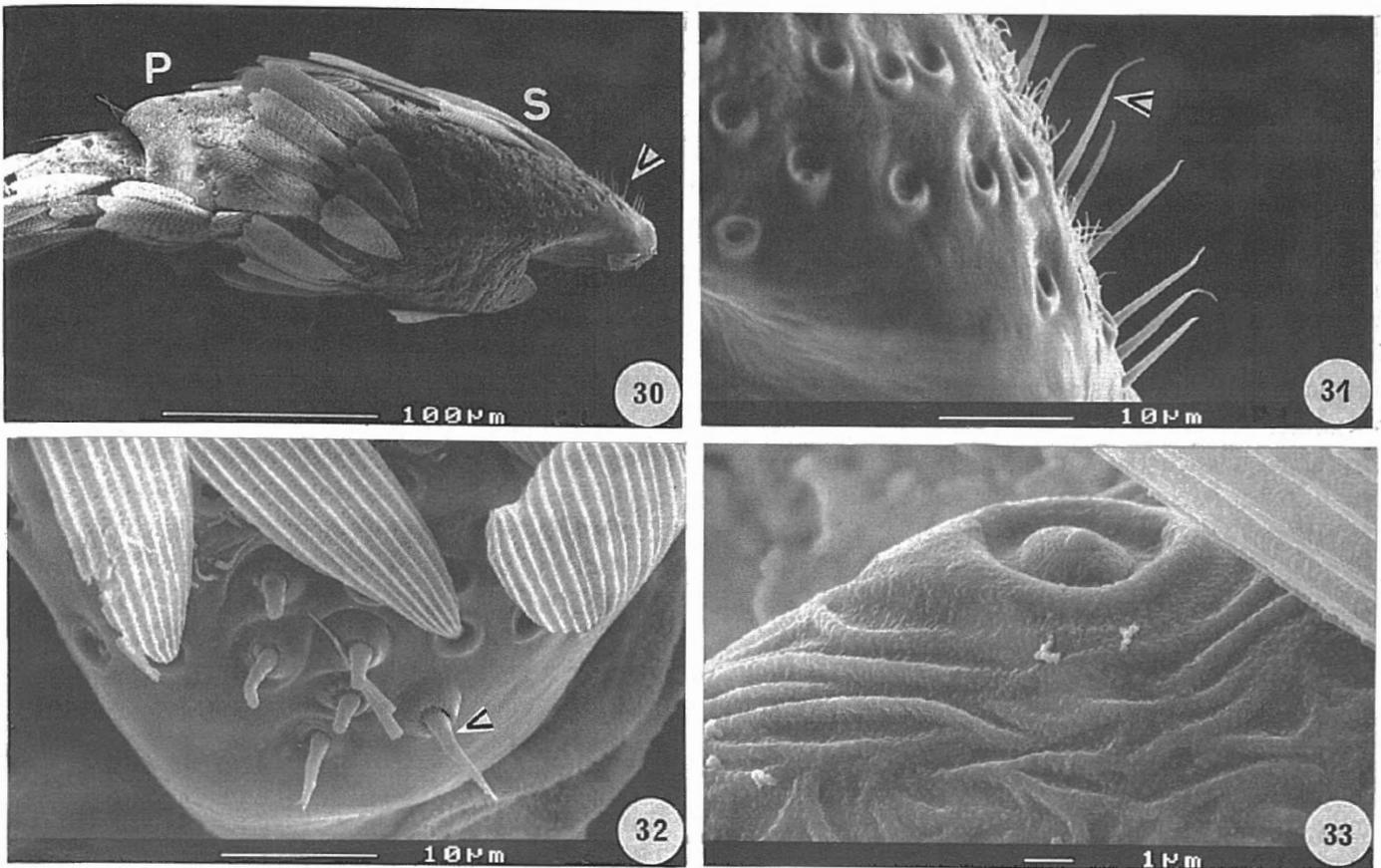
8 - The aporous long-haired sensilla styloconica (ALHSS) resemble uniporous sensilla chaetica whose cupola is transformed into a prominent stylus of a height three times that of a typical sensillum styloconicum (Fig. 25). The proximal half of the stylus often reveals the same reticulate pattern as the antennal cuticle whereas the distal half is smooth. The sensillum is ventral, always located at the distal end of the flagellomere, and is present on only about 1/5th of the flagellomeres.

9 - The aporous long-styled sensilla styloconica (ALSSS) possess the typical morphology of the antennal sensilla styloconica of Lepidoptera. They are only present in *M. paracosma* (Fig. 26) and *M. hudsoni* (Fig. 27). As in all other Lepidoptera, one sensillum is situated ventrally in the middle of the distal edge of flagellomere. It is absent on about a third of flagellomeres.

10 - The aporous short-styled sensilla styloconica (ASSSS) are present in *M. fusilella* (Fig. 28), *M. falcata* (Fig. 29) and *M. acuta* in which the typical sensilla styloconica are absent. They occupy the same position in the middle of the distal edge of the flagellomere. They resemble blunt-tipped sensilla basiconica inserted in a very broad socket.



Figs 13-29 — Antennal sensilla of *Mnesarchaea* sp. **13.** *M. acuta*, sensillum trichodeum (arrow); **14.** *M. fusilella*, detail of sensillum basiconicum (B) and trichodeum (T); **15.** *M. species 1*, male, distal part of sensillum trichodeum; **16.** *M. paracosma*, sensillum coeloconicum; **17.** *M. fusilella* female, uniporous sensilla chaetica (arrows); **18.** *M. species 1*, male, detail of uniporous sensillum chaeticum; **19.** apical flagellomere of *M. species 1*, male, typical uniporous sensilla chaetica (white arrows) and long uniporous sensillum chaeticum (black arrow); **20.** detail of long uniporous sensillum chaeticum; **21-22.** *M. fusilella* male, aporous sensilla chaetica of flagellomere (arrows) and detail; **23-24.** *M. fusilella* male, aporous sensilla chaetica of pedicel (arrow) and detail; **25.** *M. species 2*, long-haired sensillum styloconicum; **26.** *M. paracosma*, long-styled sensillum styloconicum (arrow); **27.** idem in *M. hudsoni*; **28.** *M. fusilella*, short-styled sensillum styloconicum (arrow); **29.** idem in *M. species 2*.



Figs 30-33 — Antennal sensilla of *Mnesarchaea* sp. 30. *M. fusilella* male, scape (S), pedicel (P) and Bohm's sensilla (arrow); 31. *M. fusilella*, Bohm's sensilla of scape (arrow); 32. *M.* species 1, male, Bohm's sensilla of pedicel (arrow); 33. *M. paracosma*, sensillum campaniformium at the apex of pedicel.

11 - The aporous Böhm's sensilla (ABS) are grouped at the base of the scape (Figs 30, 31) and the pedicel (Fig. 32). As we have only a few specimens of moths in our possession, we have been unable to specify the exact number of sensillum groups.

12 - The aporous sensilla campaniformium (ASC) is located at the apex of the pedicel (Fig. 33).

Discussion

Morphological and functional aspects

A probably olfactory function of the sensilla trichodea, basiconica, auriculica and coeloconica in *Mnesarchaea* can be inferred by analogy with morphologically similar and physiologically characterized multiporous sensilla of other moths (ZACHARUK, 1985; FAUCHEUX, 1999).

The multiporous sensilla trichodea are specialized for perception of female sex-produced pheromones (HANSSON *et al.*, 1989). In Lepidoptera, they are always more numerous in the male than in the female but in *M. paracosma* and *M. fusilella*, we have no observed a

sexual difference in sensillum numbers. The behaviour of adult moths suggests sex pheromones are involved, but attempts to confirm this have not met with success to date.

The multiporous multibranch sensilla basiconica of *Mnesarchaea* bear some resemblance to the sensilla ascoidea of Micropterigidae (FAUCHEUX, 1997; 2004b) and Opostegidae (NIEUKERKEN & DOP, 1987; DAVIS, 1989; DAVIS & STONIS, 2007), but in these, the branches always originate from the sensillum base itself, never with a common "stem", and the branch numbers always exceed four on all but the most basal flagellomeres. Moreover, the ascoids of Micropterigidae and Opostegidae occur in small numbers and in fixed positions on each typical flagellomere: in the former, there are two, located on opposite lateral faces of the proximal part of the flagellomere and one on the mid-dorsal distal part.

In Micropterigidae, the sensillum branches have a thin, flattened wall surface which is perforated only on the upper surface whereas the sensilla of Opostegidae have a cuticular wall surface which is circular, thick and entirely perforated. We have observed no notable sexual

dimorphism in the number of multibranched sensilla basiconica in *M. paracosma*.

While sensilla auricillica have been stated to be absent in Lophocoronidae, Neopseustidae and Mnesarchaeidae (NIELSEN & KRISTENSEN, 1996), their presence in these families of lower Lepidoptera has subsequently been revealed (FAUCHEUX, 2006b; FAUCHEUX, *et al.*, 2006; present paper). Since sensilla auricillica were first described by CALLAHAN (1975), subsequent research has demonstrated considerable polymorphism in their structure; the only trait which unites them is their flatness: they are simply flattened sensilla basiconica (FAUCHEUX, 1999). The wall pores of multiporous sensilla basiconica and s. auricillica of lepidopteran antennae are either aligned longitudinally, or without apparent order (review in FAUCHEUX, 1999). The clustered arrangement of the pores observed in long sensilla basiconica and sensilla auricillica of Mnesarchaeidae is a character shared with the family of Neopseustidae (FAUCHEUX *et al.*, 2006). The sensilla auricillica in Noctuidae are sensitive to plant odours (ANDERSON *et al.*, 2000), but in the basal glossatan family Eriocraniidae, they are also known to respond to sex pheromone compounds (LARSSON *et al.*, 2002). Thus, the sensilla auricillica in the *acuta*-group (and also perhaps the multibranched sensilla basiconica in the *fallax*-group) of *Mnesarchaea* may be the principal receptors of sex pheromones. The long sensilla basiconica and sensilla coeloconica in lepidopterans are sensitive to plant odours (KAFKA, 1987; POPHOFF, 1997).

The uniporous sensilla chaetica have a gustative function which probably is significant in the choice of egg-laying site. The aporous sensilla chaetica are rare on the antennae of Lepidoptera and are only present in the basal lineages in the order (FAUCHEUX, 1999). Those of the flagellum are located under the scales and therefore probably mechanoreceptors and sensitive to pressure from the scales. According to NIEUKERKEN & DOP (1987), they may have a function in registration of air pressure and thus direction and velocity of flight. The isolated erect sensilla of the scape and pedicel are probably tactile mechanoreceptors.

Long-haired sensilla styloconica are described from basal clades in the Lepidoptera, viz., Micropterigidae (FAUCHEUX, 1997), Lophocoronidae (NIELSEN & KRISTENSEN, 1996), Neopseustidae (FAUCHEUX, 2005b; FAUCHEUX *et al.*, 2006; here they have been termed "aporous stylus-shaped sensilla chaetica"), and Mnesarchaeidae. In mnesarchaeids, these sensilla are probably tactile mechanoreceptors, because no membrane is clearly visible at the distal end of the stylus. Moreover, in known tactile sensilla, the

dendrite of the bipolar neuron is very short, forming a tubular body which, in the sensillum styloconicum of *Mnesarchaea*, would expectedly be located in the distal end of the stylus, and also the pericaryon would be situated in the stylus (FAUCHEUX, 1999), this appears improbable. Consequently, it is possible that the long-haired sensilla styloconica are thermo- and hygroreceptors, as are the antennal cone-shaped sensilla styloconica of Lepidoptera examined by STEINBRECHT (1998). In some insects, poreless sensilla with inflexible sockets and apical hairs are known to be thermo- and hygroreceptors (ALTNER *et al.*, 1983). Moreover, in certain Tineidae such as *Trichophaga tapetzella* LINNAEUS, the cone of sensilla styloconica is very long (FAUCHEUX, 1989) and transient forms between sensilla chaetica and sensilla styloconica have been described in Lepidoptera (FAUCHEUX, 2006a).

Aporous long-styled and aporous short-styled sensilla styloconica are thermo-hygroreceptors in moths (STEINBRECHT & MÜLLER, 1991). Böhm's sensilla monitor the position of the FAUCHEUX, 1999).

Sensillum homology and phylogenetic implications

The multiporous multibranched sensilla basiconica differ from multiporous sensilla auricillica in the arrangement of their pores and their distribution on the flagellomere. In no species of the *fallax*-group, have we observed unbranched multiporous sensilla basiconica on the first flagellomeres, while this modification of the "sensilla ascoidea" (multibranched sensilla basiconica) is frequent in Micropterigidae (FAUCHEUX, 1997) and Opostegidae (DAVIS, 1989). It remains very uncertain whether the aporous short-styled and the aporous long-styled sensilla styloconica may be considered homologous.

The two species groups (*fallax*- and *acuta*-groups) recognized in ongoing phylogenetic analyses of *Mnesarchaea* appear strongly supported by both morphological and molecular data (GIBBS, WIEGMANN & KRISTENSEN, in preparation) and the results here obtained on the antennal sensilla underscore the phenetic distinctness of these groups: only the examined *acuta*-group (*M. acuta*, *M. fusilella*, *M. species 2*) possesses multiporous sensilla auricillica and aporous short-styled sensilla styloconica, whereas only the *fallax*-group members species possesses multiporous multibranched sensillum basiconica. Such diversity in antennal sensillum-type complement between species assigned to the same genus may be previously unrecorded from Lepidoptera. The uniqueness of the multibranched sensilla basiconica arguably makes this sensillum type a strong autapomorphic character for this group. In

contrast, the sensilla auricillica and the short-styled sensilla styloconica may pertain to the ground plan of the Exoporia hence their presence in the studied species of the *acuta*-group do not *per se* support the monophyly of this group. The other sensilla, being overall uniform in all species of *Mnesarchaea* do not give new data on phylogeny.

The aporous long-haired sensilla styloconica, present in Mnesarchaeidae, have counterparts in micropterigids, lophocoronids and neopseustids (FAUCHEUX, 1997; NIELSEN & KRISTENSEN, 1996; FAUCHEUX, 2005b; FAUCHEUX *et al.*, 2006); is this type indeed restricted to the homoneurous grade within the order? – and has it been independently lost in more lineages? Perhaps the most surprising character shared by members of the Mnesarchaeidae and Neopseustidae is the grouping of the pores of the sensilla basiconica: multiporous large sensilla basiconica and multiporous sensilla basiconica in Neopseustidae (FAUCHEUX, 2005a; 2005b; FAUCHEUX, *et al.*, 2006) and on the multiporous multibranching sensilla basiconica and multiporous sensilla auricillica in Mnesarchaeidae. This resemblance also indicates that a number of distinctive sensillum types (large s. basiconicum, multibranching s. basiconicum, and s. auricillicum) are variants of a single type, viz. the multiporous sensillum basiconicum (FAUCHEUX, 1999). What is more, the sensilla auricillica of the *acuta*-group are morphologically very close to the “multiporous large sensilla basiconica” of certain Neopseustidae.

As mentioned, the Mnesarchaeidae (sole family in the formally redundant superfamily Mnesarchaeoidea) are presently grouped with the Hepialoidea (Neotheoridae, Palaeosetidae, Prototheoridae, Hepialidae *s. lat.*) in the Exoporia (review in KRISTENSEN, 1998). Comparisons between the antennal sensillum complements in the sister-superfamilies Mnesarchaeoidea and Hepialoidea await more in-depth examinations of a broad taxon sample across the latter. Suffice it here to say that while in the hepialid *s. str.* *Triodia sylvina* (Linnaeus, 1761), sensilla auricillica, multibranching basiconica and typical sensilla styloconica are absent (FAUCHEUX, 1999; 2008), sensilla auricillica do occur in some Hepialidae from New Zealand (FLOWER & HELSON, 1976), while the sensilla styloconica described by these previous authors are in fact sensilla coeloconica (FAUCHEUX, 1999). The African *Afrotheora thermodes* (Meyrick) belonging to the informal genus group “primitive Hepialidae” (see KRISTENSEN, 1998) has a sensillum styloconicum (NIELSEN & SCOBLE, 1986; fig. 24, p. 35) which, by its form and position on the flagellomere, resembles the aporous short-styled sensillum styloconicum in the *Mnesarchaea acuta*-group; this type may then

straightforwardly be ascribed to the exoporian ground plan.

Acknowledgements

We are indebted to M. Pierre Watelet, Director of Museum of Natural History of Nantes, France, for facilitating use of SEM; M. Nicolas Stephant (Centre of SEM, University of Nantes); M. Vittorio Ballardini for technical assistance and in particular to Niels P. Kristensen for critically reviewing an earlier draft and offering his comments and advice.

References

- 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 probably comprising thermo- and hygroreceptors. *Cell and Tissue Research*, 234: 279-307.
- ANDERSON, P., HALLBERG, E. & SUBCHEV, M., 2000. Morphology of antennal sensilla auricillica and their detection of plant volatiles in the Herald moth, *Scoliopteryx libatrix* L. (Lepidoptera: Noctuidae). *Arthropod Structure and Development*, 29: 33-41.
- CALLHAN, P.S., 1975. Insect antennae, with special reference to the mechanism of scent detection and the evolution of the sensilla. *International Journal of Insect Morphology and Embryology*, 4: 381-430.
- DAVIS, D.R., 1989. Generic revision of the Opostegidae, with a synoptic catalog of the world's species (Lepidoptera: Nepticuloidea). *Smithsonian Contributions to Zoology*, 478: 1-97.
- DAVIS, D.R. & STONIS, J.R., 2007. A revision of the New World plant-mining moths of the family Opostegidae (Lepidoptera: Nepticuloidea). *Smithsonian Contributions to Zoology*, 625: 1-212.
- DUGDALE, J.S., 1974. Female genital configuration in the classification of Lepidoptera. *New Zealand Journal of Zoology*, 1: 127-146.
- FAUCHEUX, M.J., 1989. Antennal sensilla in male and female carpet moth, *Trichophaga tapetzella* L. (Lepidoptera: Tineidae): a scanning electron microscopic study. *Annales de la Société entomologique de France (n.s.)*, 25: 83-93.
- FAUCHEUX, M.J., 1990. Antennal sensilla in adult *Agathiphaga vitiensis* Duml. and *A. queenslandensis* Duml. (Lepidoptera: Agathiphagidae). *International Journal of Insect Morphology and Embryology*, 19: 257-268.
- FAUCHEUX, M.J., 1997. Sensory organs on the antennae of *Micropterix calthella* L. (Lepidoptera: Micropterigidae). *Acta Zoologica (Stockholm)*, 78: 1-8.

- FAUCHEUX, M.J., 1999. *Biodiversity and Unity of Sensory Organs in the Lepidopteran Insects*. Société des Sciences Naturelles de l'Ouest de la France (Editor), Nantes, 296 pp. (in French; full English summaries of all chapters, legend figures translated).
- FAUCHEUX, M.J., 2004a. Polymorphisme des sensilles basiconiques bifurquées de l'antenne de l'Agathiphage du Queensland, *Agathiphaga queenslandensis* Dumbleton, 1952 (Lepidoptera: Aglossata: Agathiphagidae). *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (n.s.)*, 26: 138-139.
- FAUCHEUX, M.J., 2004b. Antennal sensilla of *Sabatinca sterops* Turner (Lepidoptera: Micropterigidae). *Transactions of the Royal Society of South Australia*, 128: 187-194.
- FAUCHEUX, M.J., 2004c. Antennal sensilla in female *Heterobathmia pseuderiocrania* (Insecta, Lepidoptera, Heterobathmiina). *Revista del Museo Argentino de Ciencias Naturales, nueva serie*, 6: 167-175.
- FAUCHEUX, M.J., 2005a. Les sensilles basiconiques gaufrées à base double ou triple de l'antenne du papillon sud-américain *Apoplania valdiviana* Davis & Nielsen 1984 (Lepidoptera: Neopseustidae): distribution et importance numérique. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (n.s.)*, 27: 1-18.
- FAUCHEUX, M.J., 2005b. The antennae of *Neopseustis meyricki*: morphology and phylogenetic implications with special reference to the sensilla basiconica and styloconica (Lepidoptera: Neopseustidae). *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Entomologie*, 75: 71-78.
- FAUCHEUX, M.J., 2006a. De la sensille chétiforme tactile à la sensille tactile thermo-hygro-réceptrice des antennes de Lépidoptères. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (n.s.)*, 28: 35-42.
- FAUCHEUX, M.J., 2006b. Antennal sensilla of male *Lophocorona pediasa* Common 1973 and their phylogenetic implications (Lepidoptera: Lophocoronidae). *Annales de la Société entomologique de France (n.s.)*, 42: 113-118.
- FAUCHEUX, M.J., 2008. Considérations morphologiques et implications phylogénétiques relatives aux organes sensoriels antennaires de la Sylvine, *Triodia sylvina* (Linnaeus, 1761). *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (n.s.)*, 30: in press.
- FAUCHEUX, M.J., KRISTENSEN, N.P. & YEN, S. H., 2006. The antennae of neopseustid moths: Morphology and phylogenetic implications, with special reference to the sensilla (Insecta, Lepidoptera, Neopseustidae). *Zoologischer Anzeiger*, 245: 131-142.
- FLOWER, N.E. & HELSON, G.A.H., 1976. Variation in antennal sensilla of some hepialid moths: a scanning electron microscope study. *New Zealand Journal of Zoology*, 3: 327-331.
- GIBBS, G.W., 1979. Some notes on the biology and status of the Mnesarchaeidae (Lepidoptera). *New Zealand Entomologist*, 7: 2-9.
- HALLBERG, E., HANSSON, B.S. & LÖFSTEDT, C., 2003. Sensilla and proprioceptors. In: KRISTENSEN, N.P. (Editor), *Lepidoptera: Moths and Butterflies. Vol. 2: Morphology, Physiology and Development*. Walter de Gruyter, Berlin & New York, pp. 267-288.
- HANSSON, E., VAN DER PERS, J.N.C. & LÖFQVIST, J., 1989. Comparison of male and female olfactory cell responses to pheromone compounds and plant volatiles in the turnip moth, *Agrotis segetum*. *Physiological Entomology*, 14: 147-155.
- KAFKA, W.A., 1987. Similarity of reaction spectra and odor discrimination single receptor cell recordings in *Antheraea polyphemus* (Saturniidae). *Journal of Comparative physiology (A)*, 161: 867-880.
- KRISTENSEN, N.P., 1997. Early evolution of the Lepidoptera + Trichoptera lineage: phylogeny and the ecological scenario. In: GRANDCOLAS, P. (Editor), *The Origin of Biodiversity in Insects: Phylogenetic tests of evolutionary scenarios*. Mém. Mus. Natn. Hist. nat. 173, Paris, pp. 253-271.
- KRISTENSEN, N.P., 1998. The homoneurous Glossata. In: KRISTENSEN, N.P. (Editor), *Lepidoptera: Moths and Butterflies 1. Handbuch der Zoologie/Handbook of Zoology IV/35*. Walter de Gruyter, Berlin & New York, pp. 51-63.
- KRISTENSEN, N.P., SCOBLE, M.J. & KARSHOLT, O., 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa*, 1668: 699-747. [Open access: <http://www.mapress.com/zootaxa/list/2007/Linnaeus.html>]
- LARSSON, M.C., HALLBERG, E., KOSLOV, M.V., FRANCKE W., HANSSON, B.S. & LÖFSTEDT, C., 2002. Specialized olfactory receptor neurons mediating intra- and interspecific chemical communication in leafminer moths *Eriocrania* spp. (Lepidoptera: Eriocraniidae). *Journal of Experimental Biology*, 205: 989-998.
- MUTUURA, A., 1972. Morphology of the female terminalia in Lepidoptera, and its taxonomic significance. *Canadian Entomologist*, 104: 1055-1071.
- NIELSEN, E.S. & KRISTENSEN, N.P., 1996. The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera Glossata. *Invertebrate Taxonomy*, 10: 1199-1302.
- NIELSEN, E.S. & SCOBLE, M.J., 1986. *Afrotheora*, a new genus of primitive Hepialidae from Africa (Lepidoptera: Hepialoidea). *Entomologica scandinavica*, 17: 29-54.
- NIEUKERKEN, E.J. & DOP, H., 1987. Antennal sensory structures in Nepticulidae (Lepidoptera) and their phylogenetic implications. *Zeitschrift für Zoologie, Systematik und Evolution-Forschung*, 25: 104-126.
- PHILPOTT, A., 1927. The genitalia of the Mnesarchaeidae.

Transactions and Proceedings of the Royal Society of the New Zealand (1968-1961), 57: 710-715.

POPHOF, B., 1997. Olfactory responses recorded from sensilla coeloconica of the silkmoth *Bombyx mori*. *Physiological Entomology*, 22: 239-248.

SELLIER, R., 1975. Étude morphologique et topographique en microscopie électronique à balayage des sensilles de Böhm chez les Lépidoptères: essai d'interprétation de leur mode de fonctionnement. *Comptes rendus de l'Académie des Sciences*, Paris, série D, 280: 1869-1872.

STEINBRECHT, R.A., 1998. Bimodal thermo- and hygrosensitive sensilla. In: HARRISON, F.W. & LOCKE, M. (Editors), *Microscopic Anatomy of Invertebrates*, vol. 11 B, Insecta, pp. 405-422.

STEINBRECHT, R.A. & MÜLLER, B., 1991. The thermo-/hygrosensitive sensilla in the silkmoth *Bombyx mori*: morphological changes after dry- and moist-adaptation. *Cell and Tissue Research*, 266: 441-456.

ZACHARUK, R.Y., 1985. Antennae and sensilla. In: KERKUT, G.A. & GILBERT, L.I. (Editors), *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 6, Pergamon Press, London, pp. 1-70.

Michel J. FAUCHEUX

Laboratoire d'Endocrinologie des Insectes Sociaux
Université de Nantes, 2 rue de la Houssinière
B.P. 92208, F-44322 Nantes Cedex 3, France
Muséum d'Histoire Naturelle de Nantes
12 rue Voltaire, F-44000 Nantes, France
e-mail: faucheux.michel@free.fr

George W. GIBBS

School of Biological Sciences
Victoria University of Wellington
Wellington, New Zealand
e-mail: George.Gibbs@VUW.AC.NZ

