ENTOMOLOGIE, 75: 71-78, 2005

The antennae of *Neopseustis meyricki*: morphology and phylogenetic implications, with special reference to the sensilla basiconica and styloconica (Lepidoptera: Neopseustidae)

by Michel J. FAUCHEUX

Abstract

The antennal flagellum of both sexes of *Neopseustis meyricki* Hering, 1925 possesses seven types of sensilla: multiporous sensilla trichodea, multiporous large swollen sensilla basiconica, multiporous thin sensilla basiconica, multiporous sensilla coeloconica, two types of aporous sensilla styloconica, and aporous sensilla chaetica. The sexual dimorphism concerns only the number of sensilla for each of these types. The two types of sensilla basiconica are probably a specific structure of Neopseustidae. The two types of sensilla styloconica are an archaic type, the long-haired sensilla, and an evolved type, the typical cone-shaped sensilla. The great length of the sensilla styloconica, their great number, their particular localization, and the coexistence of two both types are specific characteristics of *N. meyricki*.

Key words: Lepidoptera, Neopseustidae, *Neopseustis*, antenna, sensilla, basiconicum, styloconicum, phylogeny.

Résumé

Le flagelle antennaire des deux sexes de *Neopseustis meyricki* Hering, 1925 possède sept types de sensilles: des sensilles trichoïdes multipores, des sensilles basiconiques multipores larges et enflées, des sensilles basiconiques multipores minces, des sensilles coeloconiques multipores, deux types de sensilles styloconiques sans pore, des sensilles chétiformes sans pore. Le dimorphisme sexuel concerne uniquement le nombre de sensilles de chacun des types. Les deux types de sensilles basiconiques sont probablement une structure spécifique des Neopseustidae. Les deux types de sensilles styloconiques correspondent à un type archaïque, les sensilles à long poil, et un type évolué, les sensilles typiques à cône. La grande longueur des sensilles styloconiques, leur nombre élevé, leur localisation particulière et la coexistence de deux types sont des caractéristiques particulières de *N. meyricki*.

Mots-clefs: Lépidoptères, Neopseustidae, *Neopseustis*, antenne, sensilles, basiconique, styloconique, phylogenèse.

Introduction

In Lepidoptera, four primary clades are recognized: the families Micropterigidae, Agathiphagidae, Heterobathmiidae, and the high-rank taxon Glossata. The Glossata comprise six major clades: the families Eriocraniidae, Acanthopteroctetidae, Lophocoronidae, Neopseustidae, and the high-rank taxa Exoporia and Heteroneura (KRISTENSEN, 1997). Indeed, since 1978 (DAVIS, 1978), the Neopseustidae have been regarded as representing a grade above the level of «Dacnonypha» (comprised of the families Eriocraniidae, Acanthopteroctetidae and Lophocoronidae) and thus in cladistic terms representing the possible sister-group of Neolepidoptera (Exoporia + Heteroneura).

The family of Neopseustidae reveals a particular innovation: the formation of a double-tube proboscis (KRISTENSEN & NIELSEN, 1981). However, the antennal sensory organs have been little studied. In a recent review article on sensilla and proprioceptors of Lepidoptera, this family was not even mentioned (HALLBERG *et al.*, 2003). Nevertheless, a preliminary study of the neopseustid *Apoplania valdiviana* DAVIS & NIELSEN, 1984 revealed the presence of 7 antennal sensillum types, including a particular type of sensilla basiconica, the «wafer-like sensillum basiconicum» (FAUCHEUX, 1999). Since then, a more exhaustive study of the species has raised the problem of interpreting «the goffered sensillum basiconicum with a double or triple base» which is an unique type among the Lepidoptera (FAUCHEUX, 2005a). A study is presently being undertaken to ascertain the existence of a similar type of sensilla basiconica in the other species of the same family. We offer here the results obtained from *Neopseustis meyricki* HERING, 1925, a species considered as being less evolved than *A. valdiviana* (DAVIS, 1975).

Material and methods

The microlepidoptera come from Dr Shen-Horn Yen's collection. They were captured in Taiwan, I-Lan Co., Yuan-Shan, Fu-Shan Botanic Garden, altitude 800 m, on 18-IV-1996 for the male and 29-V-1995 for the female. For the study with scanning electron microscopy (S.E.M.), the antennae were descaled, dehydrated in absolute ethanol, 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 different magnifications. The terminology of SCHNEIDER (1964) and ZACHARUK (1985) is used in naming the types of sensilla. The mean number of each sensillar type was calculated with S.E.M. from the counts on every 5th flagellomere, and expressed as mean +/- SD.

Results

The moths are relatively small, with the following wing expanse: male, 20 mm; female, 20-22 mm. The antennae are long, equaling the length of forewing. The scape is large and swollen; the pedicel is four times shorter and only half the width of the scape.

The flagellomeres (male, 65; female, 63) are strongly cupuliform, slightly depressed and asymmetrical (Fig. 1). All flagellomeres possess narrow lamellar scales arranged in longitudinal rows of 2-5 contiguous raised sockets, and noninnervated microtrichia evenly scattered over the enlarged part of each segment (Fig. 3).

Seven types of sensilla were discovered on the antennal flagellum of both sexes of *N. meyricki*. No sexual dimorphism concerning the types of sensilla was observed. The sensilla are located all around the flagellomeres but are twice as numerous on the ventral face. The sensillum types are the following: multiporous sensilla trichodea, multiporous large swollen sensilla basiconica, multiporous thin sensilla basiconica, multiporous sensilla coeloconica, aporous sensilla chaetica, aporous long-haired sensilla styloconica, and aporous cone-shaped sensilla styloconica.

1 – The multiporous sensilla trichodea are spread evenly over both faces of the flagellomeres (Fig. 2) from the proximal edge to the distal edge (Fig. 4). They can be identified by their oblique striae at the base (Fig. 5) which become annular on the remainder of the hair (Fig. 3). The wall pores are difficult to distinguish with scanning electron microscope (Fig. 5). The sensilla trichodea constitute 32% of all the sensilla and are more numerous in the male (Table).

2 – The multiporous large swollen sensilla basiconica (type I) are disseminated among the sensilla trichodea (Fig. 2). They are evenly curved from their base, swollen and flattened in their proximal part but thereafter retain a regular diameter up to their tip (Fig. 6). Their wall offers an irregular network of ridges with in which are located the pores thus concentrated (Figs. 7, 8). The thickness of the wall amounts to 0.13 µm and represents 1/10 of the diameter of the sensillum (Fig. 8). The enlarged base of the sensilla is sometimes deformed by S.E.M. (Figs. 9, 10). The sensilla basiconica B1 are the most numerous of the antennal sensilla (40 to 41% of the total), with a very slight advantage for the male (Table).

3 – The multiporous thin sensilla basiconica (type II) are easily identifiable thanks to their straight aspect and differ from the sensilla basiconica B1 by their circular base, which is never deformed (Fig. 10). Like the latter, they offer a goffered aspect and possess numerous pores in groups (Fig. 12). The wall, 0.15 µm in width, is sometimes thinner than in type I and represents 1/18 of the sensillum diameter (Fig. 13). What is more, they possess a specificity which has been observed neither in sensilla B1, nor in any other lepidopteran antennal sensilla basiconica. At their base, they either narrow (Fig. 16) or reveal a slender bulge followed by a thickening of the hair, the whole resembling a cupola (Figs. 14, 15). This detail will be discussed below. The sensilla B2 are for the most part located at the distal edge of flagellomeres, but they represent a more 6% of the total of sensilla.

4 – The multiporous sensilla coeloconica are small fluted cones; they number 1 or 2 per flagellomere (Fig. 17). Though always visible on the antenna, they only number 3% of the antennal sensilla.

5 – The aporous long-haired sensilla styloconica are the longest and the most surprising of all the antennal sensilla of *N. meyricki* (Fig. 1). The stylus alone is almost as long as another sensillum. The hair is longitudinally ridged like that of a sensillum chaeticum (Fig. 11). They are arranged obliquely on the antennal surface and always at the distal edge of the flagellomeres. According to estimation based on eight successive flagellomeres, their number is as follows: 1, 4, 1, 4, 2, 2, 4, 3. When they attain the maximum number of 4, they are either equidistant from one another and arranged in the middle of the four faces, dorsal, ventral and two lateral (Fig. 1), or grouped two by two in the middle of the dorsal and ventral faces (Fig. 18).

6 – The aporous cone-shaped sensilla styloconica are almost as long as the previous type (Fig. 19). The extraordinarily long stylus is absolutely smooth and

Table — Length, basal width, average numbers and percentages of sensilla on a male and female antennal flagellum of *Neopseustis meyricki* (mean +/- S.D.)

Sensilla	Length (µm)	Basal width (µm)	Numbers (male)	%	Numbers (female)	%
Trichodea	26.7 +/- 4.5	1.8 +/- 0.3	1062	32.3	949	32.1
Basiconica I	28.3 +/- 3.9	2.0 +/- 0.4	1358	41.3	1176	39.8
Basiconica II	30.5 +/- 5.8	2.7 +/- 0.2	195	5.9	183	6.2
Coeloconica	7.5 +/- 1.4	1.7 +/- 0.3	96	3.0	87	2.9
Long-haired styloconica	59.3 +/- 5.2	2.7 +/- 0.2	168	5.1	159	5.4
Cone-shaped styloconica	37.5 +/- 2.7	1.4 +/- 0.2	17	0.5	15	0.5
Aporous chaetica	28.6 +/- 4.3	1.8 +/- 0.4	391	11.9	383	13.1
Total of sensilla			3287		2952	

surmounted by a small sensory cone (Fig. 20). They are present on the antennae of both sexes but absent from many flagellomeres; their frequence is of 1 for 4 flagellomeres. These sensilla are always situated next to a long-haired sensillum styloconicum.

7 – The aporous sensilla chaetica are always straight, of the same length as the sensilla trichodea (Table) and possess a basal alveola (Fig. 21). Their apical end is pointed and without any pore. The wall is marked by 8 longitudinal ridges; between them are arranged thin transversal striae similar to those of a scale (Figs. 22, 23). The sensilla are located towards the distal edge of each flagellomere; they are often grouped together and oriented away from the antenna (Fig. 21). Their number reaches 12% of the antennal sensilla.

Discussion

The sensilla common to two species, *A. valdiviana* et *N. meyricki* are: the sensilla trichodea, the sensilla basiconica I and II, the sensilla coeloconica, the long-haired sensilla styloconica, and the aporous sensilla chaetica. Those present in only one species are the cone-shaped sensilla styloconica, which were observed only in *N. meyricki* and the cupuliform organs, present in *A. valdiviana*. The cupuliform organs are rarely been observed (FAUCHEUX, 1999); they are in fact difficult to identify and probably more frequent than is believed.

The aporous sensilla chaetica are not an ubiquitous type on the antennae of Lepidoptera. They have been described with certainty only in a few families: in the lower Lepidoptera such as the Agathiphagidae (FAUCHEUX, 1990), as well as the Ditrysia such as the Nepticulidae (NIEUKERKEN & DOP, 1987), the Yponomeutidae (CUPERUS, 1983), the Lasiocampidae and the Saturniidae (FAUCHEUX, 1978), and even in the Rhopalocera such as the Pieridae (FAUCHEUX, 1996). Their presence in the Neopseustidae provides their antennae with a particular tactile sensitivity which no doubt shows in their behaviour for most Lepidoptera are deprived of this sensillum type. In particular, the sensilla chaetica of *N.meyricki* are on an average one and a half times larger than those of *A. valdiviana* (FAUCHEUX, 2005a) and four times larger than those of *Synempora andesae* (unpublished observations).

The sensilla trichodea are pheromone receptors (KAISLING *et al.*, 1978; (STEINBRECHT, 1987)). The sensilla basiconica respond to host plant odours in all other moths (SCHNEIDER & STEINBRECHT, 1968; VAN DER PERS, 1981). The sensilla coeloconica are olfactive and respond to short-chain organic acids (POPHOF, 1997). The cone-shaped sensilla styloconica are thermo-hygroreceptors (ALTNER *et al.*, 1983; STEINBRECHT & MÜLLER, 1991). Nothing is known about the function of the hair-shaped sensilla styloconica. We believe they are tactile and represent a transient form between the aporous sensillum chaeticum and the cone-shaped sensillum styloconicum (FAUCHEUX, in press).

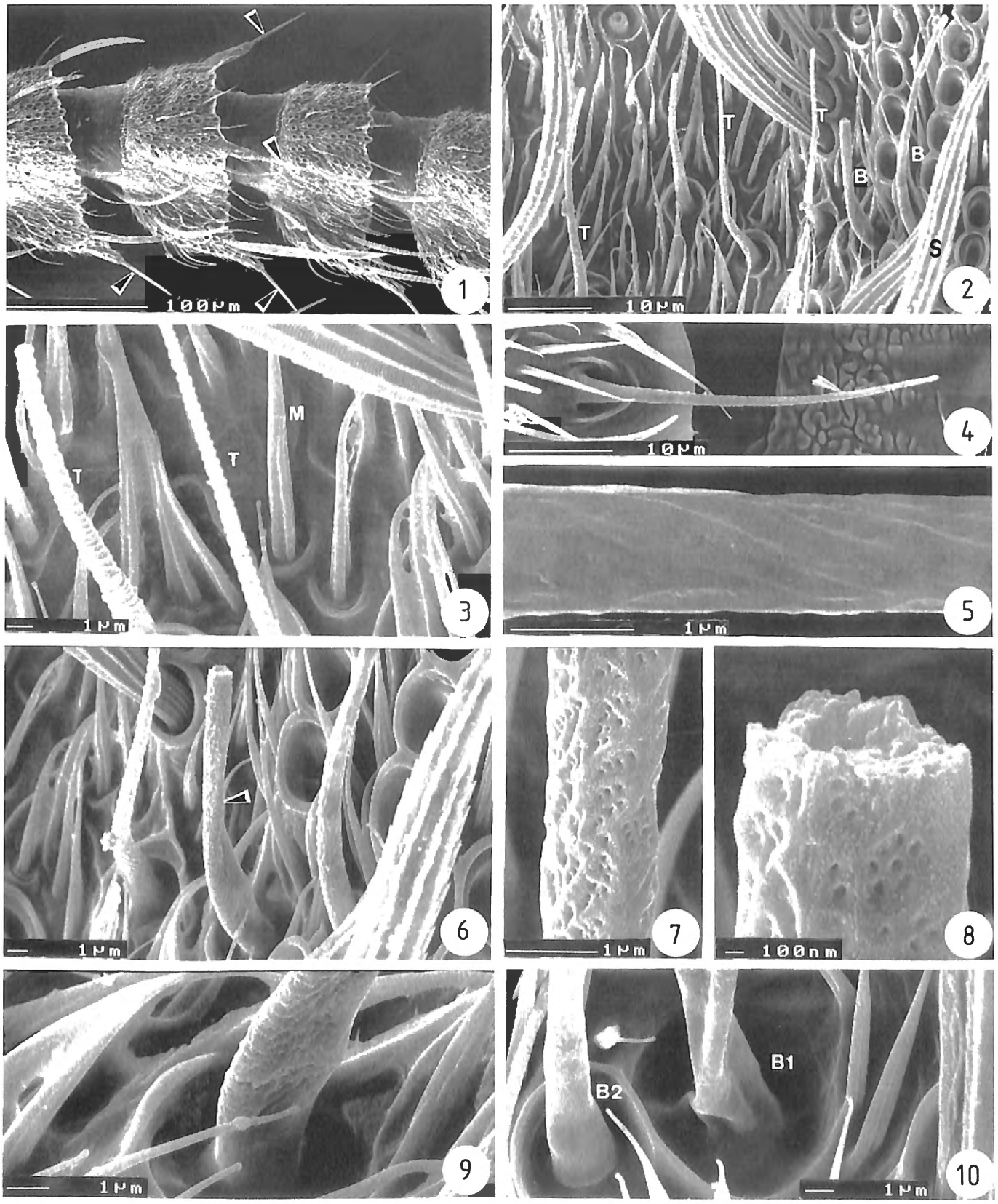
Among the ubiquitous sensilla identified on the antenna of Lepidoptera, the absent sensilla are the multiporous sensilla auricillica and the uniporous sensilla chaetica. Although the lepidopteran sensilla auricillica possess very diverse forms (FAUCHEUX, 2004a), it has not been possible to identify them, either in *N. meyricki*, or in *A. valdiviana*. They exist in families less evolved than the Neopseustidae as in the Heterobathmiidae (FAUCHEUX, 2004c), the Eriocraniidae (DAVIS, 1978) and the Lophocoronidae (FAUCHEUX, in press). Since their appearance in the Heterobathmiidae, the Neopseustidae are the first family deprived of this sensillum type considered as ubiquitous (FAUCHEUX, 1999; HALLBERG *et al.*, 2003). The sensilla auricillica are unevenly represented among the families of Lepidoptera. In the Exoporia (Hepialidae) which follow the Neopseustidae, the distribution of the sensilla is likewise variable: they are present in *Aenetus virescens* and *Wiseana umbraculata* (FLOWER & HELSON, 1976) but absent in *Afrotheora thermodes* (NIELSEN & SCOBLE, 1986) and *Triodia sylvina* (personal observations).Thus, among the higher Lepidoptera, the Rhopalocera may have them, like *Pieris rapae* Linné (FAUCHEUX, 1996).

It may however be thought that the large swollen sensilla basiconica type 1 of *N. meyricki* are close to the sensilla auricillica. Indeed, they closely resemble the sensilla auricillica of the tineid *Monopis crocicapitella* Clemens. We have shown that in the keratophagous Tineidae, these sensilla could possess the shape of an ear or that of a long, flattened hair (FAUCHEUX, 1987).

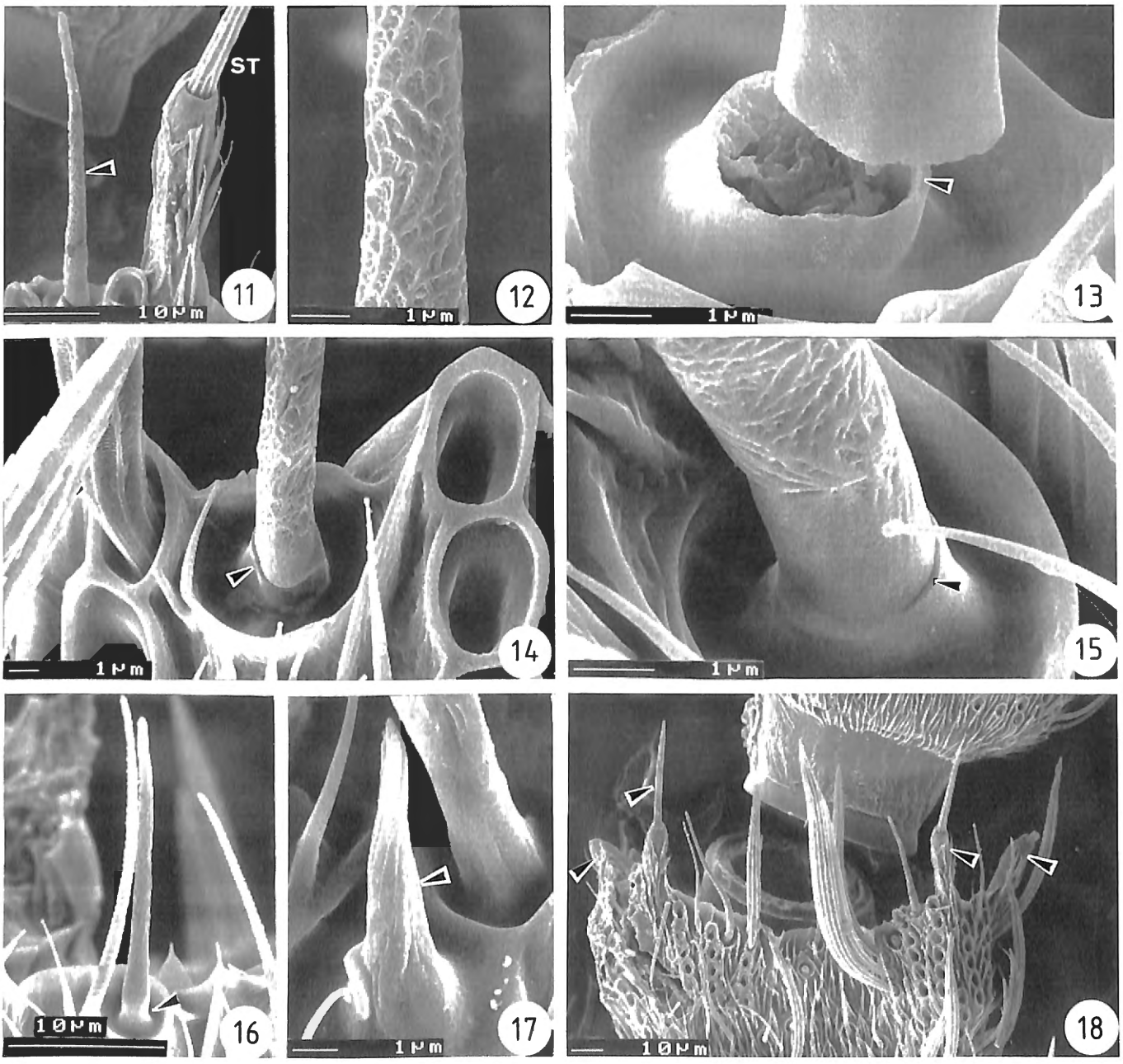
The uniporous sensilla chaetica are a ubiquitous type present in families less evolved than the Neopseustidae. Nevertheless, the Lophocoronidae which directly precede the Neopseustidae are also deprived of such sensilla. They assure a taste function in the antenna, used by certain moths in the choice of site for egg-laying. The antennae of *N. meyricki* do not consequently perform this function.

Phylogenetic considerations

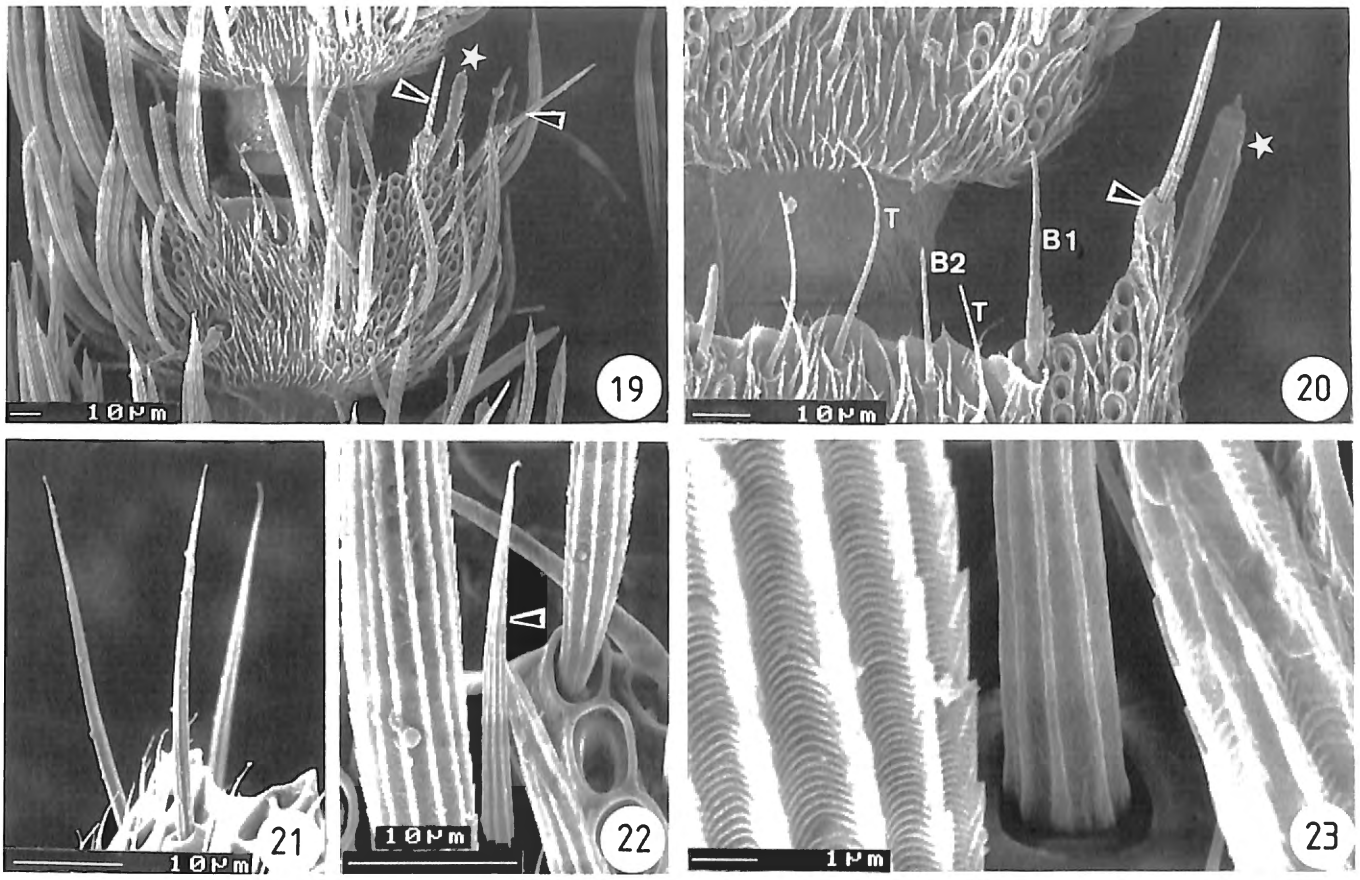
We have not observed in *N. meyricki* the double or triple-based sensilla basiconica present in *A. valdiviana* but this latter type and the sensilla basiconica of type 1 and type 2 of *N. meyricki* have points in common because the three types possess grouped pores. This pore-pattern is unique among the antennal sensilla of Lepidoptera for in all other families, the sensilla basiconica belong to two types, with, either with longitudinally lined pores or with scattered pores (FAUCHEUX, 1999; HALLBERG *et al.* 2003). If this pore-pattern is confirmed in the other genera of Neopseustidae, the grouped-pores sensilla basiconica may be considered as being an autapomorphy of the Neopseustidae. Furthermore, it is reasonable to believe that the single-based sensilla basiconica of *N. meyricki* and the double or triple-based sensilla basiconica of *A. valdiviana* are similar sensilla which evolved differently. The morphology of the type 2 sensilla basiconica of *N. meyricki* furnish no particular information. On the contrary, certain sensilla basiconica of type 1 have a



Figs. 1-10 — Antennal sensilla of *Neopseustis meyricki*. **1**. 24-27th descaled male flagellomeres showing long-haired sensilla styloconica (arrows); **2**. sensilla trichodea (T) and type I basiconica (B), scale (S); **3**. female sensilla trichodea (T), microtriches (M); **4**. male sensillum trichodeum; **5**. oblique ridges of the wall sensillum; **6-10**. type I sensillum basiconicum; **6**. broken sensillum; **7**. detail of pores; **8**. break showing the width of the wall; **9**. base of sensillum; **10**. bases of type I (B1) and type II (B2) sensilla basiconica.



Figs. 11-18 — Antennal sensilla of *Neopseustis meyricki*. **11-16**. sensilla basiconica type II; **11**. the whole sensillum (arrow) and base of a long-haired sensillum styloconicum (ST); **12**. detail of pores; **13**. broken base showing the thin wall (arrow); **14**. kind of alveola at the base (arrow); **15**. idem in other sensillum; **16**. basal narrowing (arrow); **17**. sensillum coeloconicum; **18**. 42th female flagellomere showing the distal location of four long-haired sensilla styloconica whose two are broken (arrows).



Figs. 19-23 — Antennal sensilla of *Neopseustis meyricki*. **19**. 33th male flagellomere with numerous scales, two long-haired sensilla styloconica (arrows) and one cone-shaped sensillum styloconicum (star); **20**. distal edge of the 53th female flagellomere with a cone-shaped sensillum styloconicum (star), a long-haired sensillum styloconicum (arrow), sensilla basiconica type I and II (B1, B2), sensilla trichodea (T); **21**. three sensilla chaetica on the latero-distal part of the 18th female flagellomere; **22**. sensillum chaeticum in the middle of the distal edge of the 57th male flagellomere; **23**. detail of the wall.

particular basal structure which has not so far been observed in any multiporous olfactive sensillum: a narrowing followed by a widening or the presence of a bulge simulating the formation of a cupola or of a stylus, marking a discontinuity between the base and the hair. We propose the hypothesis that, starting from this discontinuity, the base of certain sensilla basiconica has spread out before dividing into two or three bases, resulting in the particular sensillum observed in *A. valdiviana*, a more evolved species than *N. meyricki*.

The presence of two types of sensilla basiconica, thin and large swollen, is common to *N. meyricki* and the family of Lophocoronidae which directly precedes the Neopseustidae (FAUCHEUX, in press). The same is true of the Hepialidae (FLOWER & HELSON, 1976). This diversity of sensilla basiconica which appears with the Lophocoronidae and is confirmed by the Neopseustidae (*N. meyricki* and *A. valdiviana*) will continue in the higher Lepidoptera (FAUCHEUX, 1999).

The sensilla styloconica of *N. meyricki* also raise an interesting problem. They belong to two types, one being considered as archaic (the long-haired type) and the other as evolved (the cone-shaped type). The latter is the most frequently met type in most Lepidoptera. The long-haired type exists only in the Micropterigidae, *Micropterix calthella* Linné (FAUCHEUX, 1997). The cone-shaped type appears in the sister-group, as in *Sabatinca sterops* Turner (Micropterigidae) (FAUCHEUX, 2004b), where in fact it coexists with the long-haired type (FAUCHEUX, in press). In the following families, the Agathiphagidae, Heterobathmiidae, Eriocraniidae, Acanthopteroctetidae, and Lophocoronidae, the two types of sensilla styloconica are absent, except in the last family which possesses a unique type, the long-haired type. It is in the Neopseustidae that the sensilla styloconica reappear in force. *A. valdiviana* possesses only the long-haired type. On the contrary, *N. meyricki* is provided with both types. The long-haired type is the most numerous on the same antenna but the cone-shaped type regularly appears on the flagellomeres. In themselves, the long-haired sensilla styloconica, which are of exceptional length, are enough to identify the species *N. meyricki*. They are twice as long as in *A. valdiviana*. It is also the first time that such a large number of sensilla styloconica has appeared per flagellomere, 4 in *N meyricki*. The most common number is one sensillum per flagellomere in the Lepidoptera. The

Saturniidae, among the higher Lepidoptera, are the only ones known sometimes to possess six (FAUCHEUX, 1978). In families more evolved than the Neopseustidae, the long-haired type of sensilla styloconica disappears completely and only the cone-shaped type remains. Nevertheless, the cone-shaped type may offer a few variants such as a longer cone in the tineid *Trichophaga tapetzella* Linné (FAUCHEUX, 1989) but the latter is different from the hair of a long-haired sensillum styloconicum.

The coexistence of both types of sensilla styloconica, primitive and evolved, in *N. meyricki* accords with the claims by DAVIS (1975): «The general morphology of the head (of Neopseustidae), as reviewed by KRISTENSEN (1968), displays a mixture of primitive and specialized features». In conclusion, in accordance to the results obtained in *A. valdiviana* and *N. meyricki*, the neopseustid antennal sensillum and scale features that may eventually prove phylogenetically significant, perhaps as family autapomorphies, include the following:

- the incomplete covering of the flagellomeres, due to the narrowness of scales. This character is paralleled in the Lophocoronidae (NIELSEN & KRISTENSEN, 1996).
- the absence of sensilla auricillica,
- the presence of two types of sensilla styloconica,
- the presence of a particular type of sensilla basiconica with groups of pores.

The above results, obtained in *A. valdiviana* and *N. meyricki*, need to be confirmed by a comparative study of *Synempora andesae*, a South-American neopseustid.

Acknowledgments

We wish to acknowledge the courtesy of Dr Shen-Horn Yen for providing the specimens of *Neopseustis meyricki*. We are indebted to Dr Yves Gruet (University of Nantes, France), for faciliting use of SEM, A. Barreau (Centre of SEM, University of Nantes), Dr Joseph Baudet and Vittorio Ballardini for technical assistance.

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.

CUPERUS, P.L., 1983. Distribution of antennal sense organs in male and female ermine moths, *Yponomeuta vigintipunctatus* (Retzius) (Lepidoptera: Yponomeutidae). *International Journal of Insect Morphology and Embryology*, 12: 59-66.

DAVIS, D.R., 1975. Systematics and zoogeography of the family Neopseustidae with the proposal of a new superfamily (Lepidoptera: Neopseustoidea). *Smithsonian Contributions to Zoology*, 282: 1-39.

DAVIS, D.R., 1978. A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae (Lepidoptera). *Smithsonian Contributions to Zoology*, 251: 1-131.

DAVIS, D.R., 1986. A search for the type series of *Nematocentropus omeiensis* Huang. *Proceedings of the Entomological Society of Washington*, 88: 391-392.

FAUCHEUX, M.J., 1978. Les récepteurs sensoriels antennaires des Lépidoptères: structure, fonction, dimorphisme sexuel. *L'Information Scientifique (Paris)*, 1: 7-39.

FAUCHEUX, M.J., 1987. Recherches sur les organes sensoriels impliqués dans le comportement de ponte chez deux lépidoptères à larves kératinophages: *Tineola bisselliella* Humm. et *Monopis crocicapitella* Clem. (Tineidae). *Thèse de Doctorat es sciences,* Univ. Nantes, 511 pp.

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* Dumbl. and *A. queenslandensis* Dumbl. (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 (éditeur). 296 pp. [in French, full English summaries of all chapters, figure legends translated].

FAUCHEUX, M.J., 2004a. Antennal sensilla of Trichoptera and Lepidoptera: phylogenetic considerations. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Entomologie*, 74: 69-71.

FAUCHEUX, M.J., 2004b. Antennal sensillla 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, Heterobathmiidae). *Revista del Museo Argentino de Ciencias Naturales (n.s.),* 6: 165-173.

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. Évolution d'un type sensillaire antennaire dans la famille des Neopseustidae (Lepidoptera: Glossata): la sensille basiconique large et enflée. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (n.s.)*, 27: p. 45.

FAUCHEUX, M.J., in press. Antennal sensilla of male *Lophocorona pediasa* Common, 1973 and their phylogenetic implications (Lepidoptera: Lophocoronidae). *Annales de la Société entomologique de France (n.s.),*

FAUCHEUX, M.J., in press. De la sensille chétiforme tactile à la sensille styloconique thermo-hygroréceptrice des antennes de Lépidoptères. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France (n.s.),*

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.

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.

KAISSLING, K.E., KASANG, G., BESTMANN, H.J., STRANSKY, W. & VOSTROWSKY, O., 1978. A new pheromone of the silkworm moth *Bombyx mori*. Sensory pathway and behavioral effect. *Naturwieesenschaften*, 65: 382-384.

KRENN, H.W. & KRISTENSEN, N.P., 2000. Early evolution of the proboscis of Lepidoptera (Insecta): external morphology of the galea in basal glossatan moths lineages, with remarks on the origin of the pilifers. *Zoologischer Anzeiger*, 239: 179-196.

KRISTENSEN, N.P., 1968. The skeletal anatomy of the heads of adult Mnesarchaeidae and Neopseustidae (Lep., Dacnonypha). *Entomologiske Meddelelser*, 36: 137-151.

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: phylogeny tests of evolutionary scenarios. Mémoires du Muséum national d'Histoire naturelle, Paris, 173: 253-271.

KRISTENSEN, N.P. & NIELSEN, E.S., 1981. Double-tube proboscis configuration in Neopseustid moths (Lepidoptera: Neopseustidae). *International Journal of Insect Morphology and Embryology*, 10: 483-486.

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 Evolutionforschung*, 25: 104-126.

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

SCHNEIDER, D., 1964. Insect antennae. *Annual Review of Entomology*, 9: 103-122.

SCHNEIDER, D. & STEINBRECHT, R.A., 1968. Checklist of insect olfactory sensilla. *Symposium of the Zoological Society of London*. n° 23: 279-297.

STEINBRECHT, R.A., 1987. Functional morphology of pheromone-sensitive sensilla. *In*: PRESTWICH, G.D. & BLOMQUIST, G.J. (Editors), Pheromone Biochemistry. Orlando, Academic Press, pp. 353-384.

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

VAN DER PERS, J.N.C., 1981. Comparison of electroantennogram response spectra to plant volatiles in seven species of *Yponomeuta* and in the tortricid *Adoxophyes orana*. *Entomological Experimental and Applied*, 30:181-192.

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, Oxford, pp. 1-69.

Michel J. FAUCHEUX
Laboratoire d'Endocrinologie des Insectes Sociaux
Université de Nantes, 2 rue de la Houssinière
B.P. 92208, F-44322 Nantes Cedex 03, France