

Antennal sensilla in the female of *Dyseriocrania subpurpurella* (HAWORTH, 1828) (Lepidoptera: Eriocraniidae). Replacement of aporous sensilla chaetica by uniporous sensilla chaetica

By Michel J. FAUCHEUX

Abstract

Seven sensillum types are present on the female antenna of *Dyseriocrania subpurpurella* (Eriocraniidae): multiporous sensilla trichodea, multiporous sensilla auriculica, multiporous sensilla coeloconica, uniporous sensilla basiconica, aporous sensilla chaetica, uniporous sensilla chaetica, and aporous Böhm's sensilla.

Only the sensilla auriculica and sensilla trichodea have been mentioned by previous authors. The fluted sensilla auriculica belong to the same type as the type II sensilla auriculica of the (more "basal") family Heterobathmiidae and the sensilla auriculica of the (more "advanced") family Lophocoronidae. The sensilla trichodea (30 %) are probably sensitive to the sex pheromone. The sensilla auriculica (14 %) are thought to be sensitive to the odours of host-plants and of egg-laying sites.

The aporous sensilla chaetica with a tactile function (13 %), which are present on the proximal flagellomeres, are progressively replaced on the more distal flagellomeres by (more numerous: 34 %) uniporous sensilla chaetica with a gustative function. This modification can be related to the emergence of the proboscis, the gustatory organ by excellence, in the Lepidoptera Glossata. This is the first time that such a development has been described on lepidopteran antennae.

Two ubiquitous types which normally occur in Lepidoptera are absent in *D. subpurpurella*: the aporous sensillum styloconicum and the multiporous sensillum basiconicum.

Key words. Lepidoptera, Eriocraniidae, *Dyseriocrania subpurpurella*, female, antenna, sensilla, phylogeny.

Résumé

Sept types de sensilles sont présents sur l'antenne femelle de *Dyseriocrania subpurpurella*: sensilles trichoïdes multipores, sensilles auricilliformes multipores, sensilles coeloconiques multipores, sensilles basiconiques unipores, sensilles chétiformes sans pore, sensilles chétiformes unipores, sensilles de Böhm. Seules les sensilles auricilliformes et les sensilles trichoïdes avaient été mentionnées par les auteurs précédents. Les sensilles auricilliformes, cannelées, sont du même type que les sensilles auricilliformes de type II de la famille (plus « primitive ») des Heterobathmiidae et des sensilles auricilliformes de la famille (plus « évoluée ») des Lophocoronidae. Les sensilles trichoïdes (30 % du total) sont probablement sensibles à la phéromone sexuelle. Les sensilles auricilliformes (14 %) sont supposées être sensibles aux odeurs des

plantes nourricières et des sites d'oviposition.

Les sensilles chétiformes sans pore à fonction tactile (13 %) présentes sur les flagellomères proximaux sont remplacées progressivement sur les flagellomères les plus distaux par des sensilles chétiformes (plus nombreuses: 34 %) à pore terminal à fonction gustative. Cette modification peut être mise en relation avec l'apparition de la trompe, organe gustatif par excellence, chez les Eriocraniidae (Lepidoptera Glossata). C'est la première fois qu'une telle évolution est décrite sur une même antenne de lépidoptère.

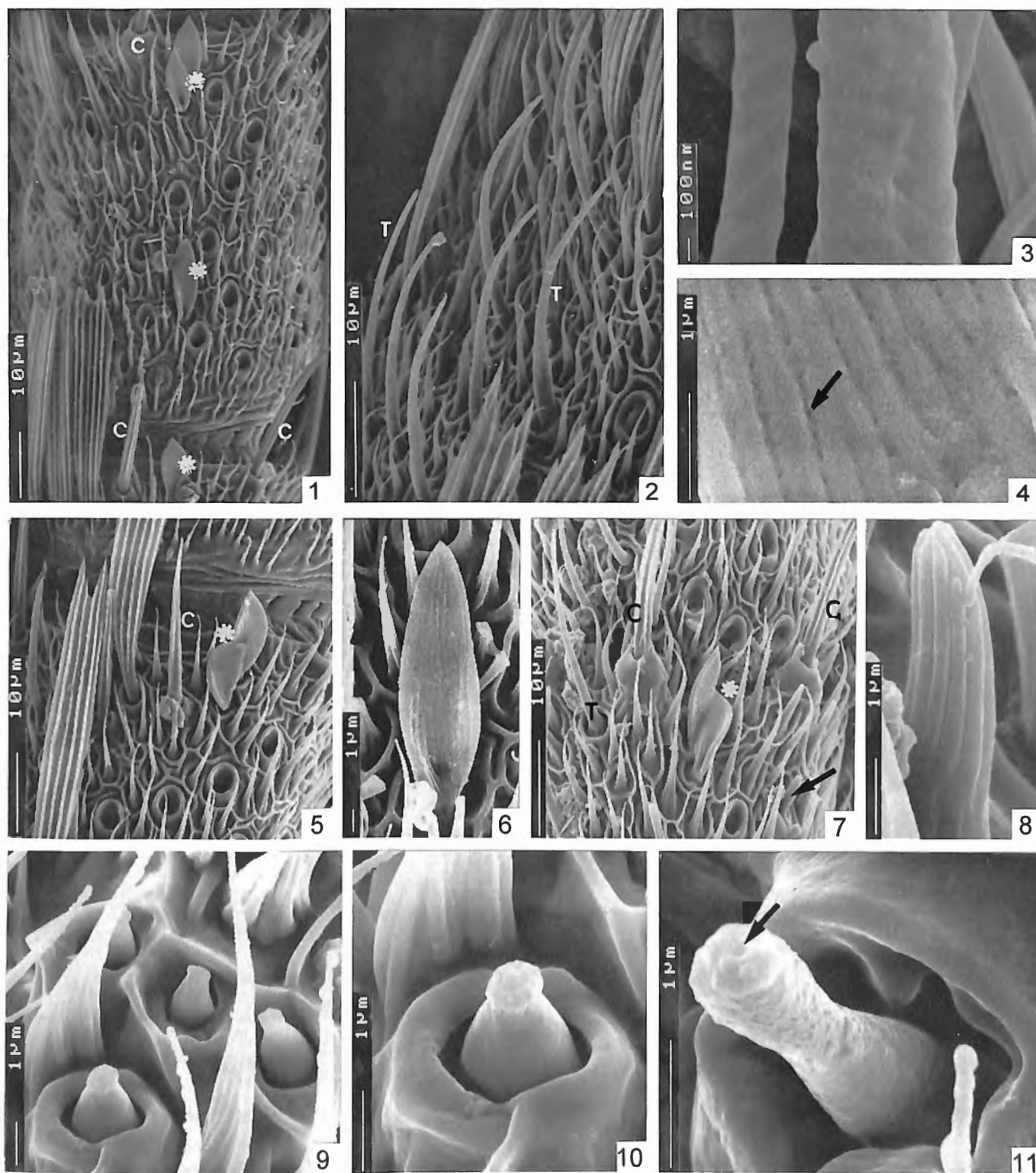
Deux types ubiquistes reconnus chez les Lépidoptères sont absents chez *D. subpurpurella*: la sensille styloconique sans pore et la sensille basiconique multipore.

Mots-clefs. Lépidoptères, Eriocraniidés, *Dyseriocrania subpurpurella*, femelle, antenne, sensilles, phylogénie.

Introduction

The Eriocraniidae are micromoths which are placed after the Heterobathmiidae in a linear arrangement of the lepidopteran families (KRISTENSEN, 1997).

Incomplete studies have been devoted to the antennal sensilla of this family. DAVIS (1978) mentions in *Eriocrania* sp., *Dyseriocrania* sp., and *Eriocraniella* sp., the presence of sensilla auriculica which he calls « sensory scales, sensory structures », whereas other sensilla (chaetica, trichodea), which he does not identify, are visible on his plates. According to NIELSEN & KRISTENSEN (1996), sensilla styloconica with short styles exist in the Eriocraniidae (p. 1261, l. 4). In 1999, in a synthesis of the results obtained so far by DAVIS (1978) and NIELSEN & KRISTENSEN (1996), we mentioned the existence of sensilla auriculica and aporous sensilla chaetica (FAUCHEUX, 1999). In 2002, LARSSON *et al.* indicate in the male of *Eriocrania semipurpurella* (STEPHENS, 1835) the presence of sensilla trichodea and auriculica everywhere on the antenna, and of « stout sensilla chaetica » only on the distal flagellomeres, as well as the absence of sensilla coeloconica and sensilla



Figs 1-11 – Antennal sensilla of female *Dyseriocrania subpurpurella*. 1. 7th flagellomere showing sensilla auricullica (asterisk), sensilla chaetica (C); 2. sensilla trichodea (T); 3. detail of sensillum trichodeum; 4. pores (arrow) of sensillum auricullicum; 5. 4th flagellomere showing an aporous sensillum chaeticum (C) and two sensilla auricullica (asterisk); 6. sensillum auricullicum; 7. 8th flagellomere showing sensillum coeloconicum (arrow), uniporous sensilla chaetica (C), trichodeum (T), auricullica (asterisk); 8. sensillum coeloconicum; 9. cluster of 4 sensilla basiconica on the apical flagellomere; 10. sensillum basiconicum; 11. another shape of sensillum basiconicum showing terminal pore (arrow).

basiconica. Finally HALLBERG *et al.* (2003) mention only sensilla auricillica and trichodea.

These partial results encourage us to carry a full study of female antennal sensilla in *Dyseriocrania subpurpurella* (HAWORTH, 1828) in order to situate the Eriocraniidae in the evolution of the antennal sensory equipment in Lepidoptera.

Material and methods

The female moths provided by the Tiroler Landesmuseum Ferdinandeum, Innsbruck, were lent to Eric Drouet in June 2007. One of them bore the label: Wurttenberg, Boilstein, 11.4.1966, female, det. L. Süßner; the other, as follows: Wurttenber, Grosboitwor, Hasberg, 9.4.1972, det. L. Süßner. For scanning electron microscope study, the antennae were cleaned in acetone, dehydrated into pure alcohol and mounted, both on the dorsal and ventral surfaces, on specimen holders. After coating with gold and palladium, preparations were examined in a Jeol J.S.M. 6 400 F SEM at 7 kV. Sensillum terminology follows FAUCHEUX (1999).

Results

The – relatively short – antenna of the female of *D. subpurpurella* measures 4.1 to 4.3 mm in length; it comprises the scape, the pedicel, and the flagellum composed of 43–46 cylindrical flagellomeres. The cuticular surface of the antenna bears a regular hexagonal reticulum made up of folds, within which each hexagon surrounds either a microtrichium, or a lamellar scale or a sensillum (Fig. 5). The scales are distributed over the whole surface of the antenna but are more numerous on the dorsal surface. The microtrichia are non-innervated “hairs”, 10–12 µm long, and are arranged in a regular fashion. They are sometimes difficult to distinguish from sensilla (Figs 5, 7, 17).

Seven types of sensilla (s.) have been identified: multiporous sensilla trichodea, multiporous sensilla auricillica, multiporous sensilla coeloconica, uniporous short sensilla basiconica, aporous sensilla chaetica, uniporous sensilla chaetica, and aporous Böhm's sensilla. Their size, number and percentage of the total number are indicated in the Table.

Apart from Böhm's sensilla and some aporous sensilla chaetica, all the other sensilla are located on the flagellum where they are more numerous on the ventral surface.

1 – *Multiporous sensilla trichodea*

The sensilla trichodea are of the same length as the sensilla chaetica, and twice as thin; they are smooth and curved towards the surface of the antenna; they are located on the surface of the antenna opposite that which bears the sensilla auricillica (Fig. 2). Their wall is slightly striated but the pores are invisible with S.E.M. (Fig. 3). They appear on the antenna from the 2nd flagellomere onwards and are still present in large numbers on the apical segments (Fig. 14). On, e.g., the 20th flagellomere, 17 sensilla were counted on the whole ventral surface. With the uniporous sensilla chaetica, they form the most numerous group on the antenna (30 %). The sensilla trichodea are more numerous than the sensilla auricillica (Table).

2 – *Multiporous sensilla auricillica*

The sensilla auricillica, 16 µm in length and 4 µm at the widest section, are in the form of a rabbit's ear with a sharp extremity (Fig. 5). Each of the two surfaces has a dozen of longitudinal furrows in which the pores were found (Figs 4, 6). The sensilla possess a relatively constant number and location over the total length of the antenna: two sensilla placed side by side are always located on the distal edge of each flagellomere, between one and three sensilla are isolated on the proximal half of the flagellomere (Figs 1, 5, 7). They appear from the 2nd flagellomere onwards. The percentage of these sensilla is estimated as 14% of the total number of sensilla.

3 – *Multiporous sensilla coeloconica*

The sensilla coeloconica are difficult to spot because they are very rare and smaller than the non-innervated microtrichia. They are distinguished from the latter by their thickset aspect in the form of a peg (Fig. 7). They are 6 µm in length and widen at the base; they are devoid of the fringe of microtrichia characteristic of this type in most lepidopterans: they are « naked sensilla coeloconica » (Fig. 8). They are located on the distal edge of the flagellomere, in the ratio of one sensillum per segment (Fig. 7).

4 – *Uniporous sensilla basiconica*

The sensilla basiconica are the smallest sensilla on the antenna; the cone is extended by a structure resembling the neck of a bottle of variable length, pierced by a terminal pore (Figs 9, 10, 11). Sometimes, on isolated sensilla, the neck is almost as long as the cone itself (Fig. 11). Each sensillum is inserted in a cupola which is surrounded in its turn by a thick fold (Fig. 10). These short sensilla basiconica are located exclusively on the penultimate and apical segments of the antenna (Fig.

15). On the apical flagellomere, four sensilla form a group and a single sensillum is isolated on the proximal half (Figs 9, 15).

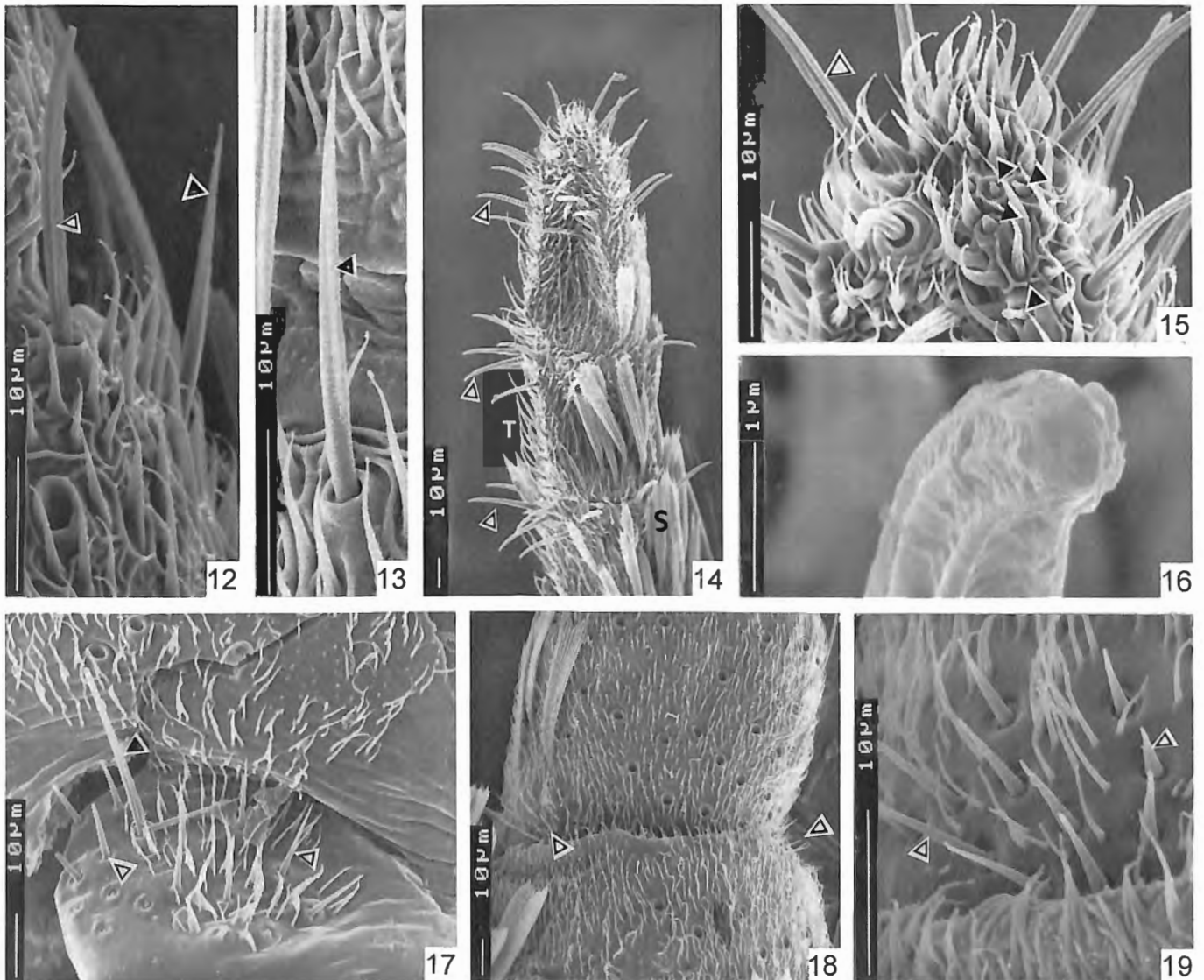
5 - *Aporous sensilla chaetica*

The aporous sensilla chaetica, of identical length to that of the sensilla trichodea, are distinguished from the latter by their stiff form, without curves, and increasingly pointed up to their extremity (Fig. 5). They possess a small number of longitudinal ribs; their base is inserted in a fairly wide cupola which facilitates the movements of the hair (Fig. 13). Apart from Böhm's sensilla, they are the only sensilla present on the scape (Fig. 17). On

each flagellomere, with the exception of the basalmost one from which they are absent, the aporous sensilla chaetica are regularly situated on the edge around the segment, in a ratio of 2 to 6 per segment (Figs 5, 12). Their number tends to diminish from the most proximal flagellomeres on in direction of the most distal ones where they are replaced by uniporous sensilla chaetica. Their number is identical to that of the sensilla auricillica (Table).

6 - *Uniporous sensilla chaetica*

These sensilla are thickset in aspect, which distinguishes them from the aporous sensilla chaetica (Fig. 12). They



Figs 12-19 – Antennal sensilla of female *Dyseriocrania subpurpurella*. 12. uniporous sensillum chaeticum (white arrow) and aporous sensillum chaeticum (black arrow); 13. aporous sensillum chaeticum; 14. lateral view of apical flagellomeres showing numerous uniporous sensilla chaetica (white arrows), sensilla trichodea (T) on the ventral surface, and scales (S) on the dorsal surface; 15. distal part of antenna showing sensilla basiconica (black arrows) and uniporous sensilla chaetica (white arrow); 16. tip of uniporous sensillum chaeticum; 17. cluster of Böhm's sensilla (white arrows) and aporous sensillum chaeticum (black arrow) on the scape; 18. two clusters of Böhm's sensilla on the pedicel (arrows); 19. detail of Böhm's sensilla.

Table – Length, basal width, average numbers and percentages of sensilla on a female antenna *Dyseriocrania subpurpurella* (mean +/- S.D.).

Sensilla	Basal width		Numbers	%
	(μm)	(μm)		
Trichodea	23.6 +/-3.4	1.5+/-0.2	326	30.1
Auricillica	12.8+/-4.1	1.7+/-0.4	148	13.7
Coeloconica	4.7+/-1.1	1.3+/-0.1	35	3.2
Basiconica	2.3+/-0.8	1.6+/-0.3	9	0.8
Aporous chaetica	25.4+/-2.3	1.7+/-0.2	144	13.3
Uniporous chaetica	26.2+/-2.5	1.7+/-0.1	365	33.7
Böhm's sensilla	6.2+/-1.7	1.2+/-0.1	56	5.2
Total			1083	

are deeply fluted and situated in a cupola which is both wide and high but nevertheless limits their movements by the presence of an internal membrane (Figs 7, 12). They possess a blunt tip and the terminal pore is invisible with S.E.M. (Fig. 16). They are arranged in a distal circle of 5 or 6 sensilla on each flagellomere, at the level of the aporous sensilla chaetica. They partly replace the latter from the distal half of the antenna onwards. The uniporous sensilla chaetica are the only sensilla chaetica present on the last ten distal flagellomeres. They number 30 at the tip of the apical flagellomere (Figs 14, 15). They form a ring of erected sensilla on each flagellomere (Fig. 14) and are the most numerous sensilla on the antenna.

7 - Aporous Böhm's sensilla

Two clusters of aporous Böhm's sensilla are present at the base of the scape (Fig. 17) and at the base of the pedicel (Fig. 18). Their length varies from 3.3 to 8.4 μm (Fig. 19). On the scape, they are mixed with microtrichia and one aporous sensilla chaeticum.

Discussion

Morphological and physiological considerations

The Eriocraniidae possess most of the ubiquitous sensilla of Lepidoptera (FAUCHEUX, 1999). Nevertheless, they are devoid of multiporous sensilla basiconica and of aporous sensilla styloconica.

The sensilla styloconica are the only thermo-hygroreceptive sensilla on the antennae of Lepidoptera (FAUCHEUX, 1999). Is one to assume that hygroreception is not available to the Eriocraniidae? In the Rhopalocera, diurnal species, the sensilla styloconica were not identified by SELIER (1976) but they have recently been described in *Ornithoptera* sp. (SCHMITZ & WASSERTHAL, 1993).

The uniporous sensilla basiconica of *Dyseriocrania* have been described by no previous authors. Because of the presence of a terminal pore, they are presumed to be gustatory (ZACHARUK, 1985). Their presence at the apex in important number argues in favour of that function. However a study in transmission electron microscopy and an electrophysiological study could alone prove that this function actually exists. Moreover, these sensilla in *Dyseriocrania* greatly resemble the uniporous pegs that we have described in Noctuidae (FAUCHEUX, 1993); or a previous TEM study reveals ultrastructural details corresponding to hygro- and thermoreceptors (BECKER, 1978). The uniporous sensilla basiconica of *Dyseriocrania* could possess an analogous function which would explain the absence of typical sensilla styloconica.

In spite of the allegations of HALLBERG & HANSSON (1999), repeated later by the same authors (LARSSON *et al.*, 2002), the Eriocraniidae do not possess sensilla placodea; these authors mistakenly call "placodea" the sensilla auricillica (FAUCHEUX, 2004 a, c). This confusion results from a misinterpretation of an article by DENIS (1985) concerning the antennae of Trichoptera; this author manifestly confused sensillum placodeum and « sensille otoïde » [the name given to the sensillum auricillicum by SELIER (1976) but which has not been accepted by later authors and has rapidly fallen into disuse]. Since then, in comparing the sensillum types described by DENIS in the Trichoptera and the known types in the Lepidoptera, we have shown (1) that the two types, placodeum and auricillicum, are present in the two sister-orders, (2) that the sensillum placodeum is not as wide-spread in the Trichoptera as DENIS thought, and (3) that, in the Lepidoptera, it is limited to the primitive family Micropterigidae (FAUCHEUX, 2004d).

According to LARSSON *et al.* (2002), the sensilla

auricillica are sex pheromone receptors in the male of *D. semipurpurella*, but these authors have not studied the sensilla trichodea. In our view, this function attributed to sensilla auricillica, and identified only in the Eriocraniidae, needs to be confirmed. It is a pity that the authors did not undertake the electrophysiological study of sensilla trichodea in this species.

So far, most electrophysiological studies have attributed the olfactive reception of the sex pheromones of the Lepidoptera to the sensilla trichodea of males and, to a lesser degree, to the identical sensilla of the females (FAUCHEUX, 1999). A similar function can be attributed to sensilla trichodea in female *D. subpurpurella*. The sensilla auricillica in females seem to be sensitive to the odours of egg-laying sites, the leaves of Fagaceae (FAUCHEUX, 2010b). In most Lepidoptera, this function belongs essentially to the multiporous sensilla basiconica and, in a lesser measure, to sensilla auricillica (FAUCHEUX, 1999). The absence of multiporous sensilla basiconica in *D. subpurpurella* is largely compensated for by the relatively large number of multiporous sensilla auricillica.

The accompanying presence of uniporous sensilla chaetica and aporous sensilla chaetica shows that gustatory chemoreception and tactile mechanoreception are carried out simultaneously in the Eriocraniidae. The large proportion (34 %) of gustatory sensilla must be pointed out for it is unique in Lepidoptera, in which the percentage of these sensilla varies from 1 to 10 % (review in FAUCHEUX, 1987). This makes of the antenna of *Dyseriocrania* a by no means negligible gustatory organ whose role completes that of the proboscis, which appears for the first time in lepidopteran evolution in the Eriocraniidae.

Phylogenetic considerations

In order to better understand the following interpretations, it should be recalled that the classification of the Lepidoptera, from the basalmost family to the most advanced one, can be established as follows: Agathiphagidae, Micropterigidae, Heterobathmiidae, Eriocraniidae, Acanthopteroctetidae, Lophocoronidae, Neopseustidae, Mnesarchaeidae, etc. (FAUCHEUX, 2010a).

The uniporous sensilla basiconica of *Dyseriocrania* are similar to those of the Agathiphagidae, Micropterigidae, and Heterobathmiidae – which are the only families to possess them – and they can therefore be regarded as a plesiomorphic sensillum type (FAUCHEUX, 1990, 1997, 2004b, e); they are absent from more advanced families (FAUCHEUX, 2005, 2006; FAUCHEUX & GIBBS, 2008; FAUCHEUX *et al.*, 2006).

The presence of sensilla auricillica is a common trait of the «*Dacnonypha* s. l.», which include the Eriocraniidae, Acanthopteroctetidae and Lophocoronidae. If the Eriocraniidae are the first Glossata to possess these sensilla, they are not however the first in the course of the evolution of the Lepidoptera, as has often been claimed; we have discovered two types of «*sensilla auricillica*» in two more primitive families, namely the Heterobathmiidae (FAUCHEUX, 2004b) and the Micropterigidae (FAUCHEUX, 2010a). The fluted type of the Eriocraniidae is similar to the fluted type (sensillum auricillicum type II) of the Heterobathmiidae; this type will persist only in the family Lophocoronidae, which is more advanced in the classification (FAUCHEUX, 2006). The dotted type represented by the «*s. auricillicum* type I» in the Heterobathmiidae will persist in the Acanthopteroctetidae (according to the plates in DAVIS, 1978) and in all the more advanced Lepidoptera which possess sensilla auricillica (FAUCHEUX, 1999; FAUCHEUX & GIBBS, 2008).

The taxon «*Dacnonypha* HINTON, 1946» is not monophyletic (KRISTENSEN, 1997). In 2002, MINET proposed the infraorder «*Acanthoctesia*» for the Acanthopteroctetidae and retained the infraorder «*Lophocoronina* Common, 1990» for the Lophocoronidae, the Eriocraniidae remaining in the infraorder «*Dacnonypha*». With regard to the sensilla auricillica, these three infraorders differ from each other: fluted and numerous sensilla (*Dacnonypha*), fluted and rare (*Lophocoronina*), dotted and numerous (*Acanthoctesia*).

The Eriocraniidae and the Acanthopteroctetidae (DAVIS, 1978) are the only families to possess: (1) a large number of sensilla auricillica; (2) a spread of these sensilla over the whole of the flagellomere. A concentration of these sensilla on the distal part of the flagellomere will only be found later in the evolution of the Lepidoptera, as in the tineid *Tineola bisselliella* (Hummel, 1823) (FAUCHEUX, 1987).

The aporous sensilla chaetica and the uniporous sensilla chaetica are associated for the second time in the course of the evolution of the Lepidoptera. Before this, the two types were present only in the Agathiphagidae (FAUCHEUX, 1990, 1999). In the more advanced species, the aporous sensilla chaetica, with a tactile function, are extremely rare. Thus, it is with the Eriocraniidae that the antennae of the Lepidoptera cease almost entirely to possess a tactile function and adopt a gustatory function. The eriocraniid moth *D. subpurpurella* is the only lepidopteran insect whose antennal uniporous sensilla chaetica represent the highest percentage of sensilla (see review in FAUCHEUX, 1987).

The typical sensilla styloconica are absent from Eriocraniidae, as is the case in Heterobathmiidae (FAUCHEUX, 2004b) and Lophocoronidae (FAUCHEUX, 2006). Our results are in contradiction with the claims of NIELSEN & KRISTENSEN (1996), who declare without accompanying argument or plates (p. 1261, l. 4): « These formations [the sensilla styloconica] are paralleled within the Eriocraniidae (where they are smaller) and in the Exoporia-Mnesarchaeidae ». In fact, it is only in the Neopseustidae that the typical sensilla styloconica, with short cones, appear in the Lepidoptera. Curiously, in that family, sensilla styloconica with a hair and sensilla styloconica with a cone coexist (FAUCHEUX, 2005; FAUCHEUX *et al.*, 2006).

The naked sensilla coeloconica, that is without a fence of microtrichia, are often regarded as a primitive type because the higher Lepidoptera only possess the type with microtrichia. Now, we have shown that the Agathiphagidae, the most primitive lepidopterans, only possess the type with microtrichia (named type 1 coeloconica), excluding the naked type, and this in very great numbers from the first flagellomere (FAUCHEUX, 1990). The following family in the classification, the Micropterigidae, possesses both types of sensilla coeloconica, with and without microtrichia (FAUCHEUX, 1997). The presence of “type 1” sensilla coeloconica in the two basal most lepidopteran families (Agathiphagidae; Micropterigidae) should be regarded as a plesiomorphic (= “primitive”) character corresponding to the ground plan of the order (plesiomorphy maintained in the higher Lepidoptera); the absence of “type 1” sensilla coeloconica in the Eriocraniidae is thus likely to represent a loss, i.e. an apomorphy.

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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