Mouthparts and associated sensilla of a South American moth, *Synempora andesae* (Lepidoptera: Neopseustidae)

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Piezas bucales y sensilios asociados de *Synempora andesae*, una polilla de Sudamérica (Lepidoptera: Neopseustidae)

**RESUMEN.** Las piezas bucales de *Synempora andesae* Davis & Nielsen fueron estudiadas con un microscopio electrónico de barrido. Se demuestra, por segunda vez, la existencia de sensilios estilocónicos gustativos uniporosos en la proboscis de Neopseustidae. Es en esta familia, y no en un estadio posterior dentro de Incurvaroidea, que aparecen estos sensilios durante la evolución de Lepidoptera. Contrario a lo que se cree, el órgano sensitivo labial u órgano de Von Rath, se encuentra en la extremidad distal del palpo labial de *S. andesae*. Está conformado por una docena de sensilios celocónicos multiporosos estriados, cuya función es percibir el dióxido de carbono. Por lo tanto, su supuesta ausencia ya no puede considerarse una autapomorfía de Neopseustidae. *S. andesae* posee otras características originales: sensilios tricodeos aporosos tanto cortos como largos en el labro, numerosos sensilios campaniformes en el primer segmento del palpo labial; así como también aquellas previamente descritas: la configuración en doble tubo de la proboscis y los sensilios basiconicos compuestos y polimórficos sobre las antenas. Además, se describen otros sensilios cefálicos: sensilios tricodeos aporosos bifurcados en el clípeo, sensilios aporosos campaniformes por encima de las mandíbulas y sobre la chaetosemata.


**ABSTRACT.** The mouthparts of *Synempora andesae* Davis & Nielsen were studied by means of scanning electron microscope. The existence of gustative uniporous sensilla styloconica is demonstrated for the second time on the proboscis of Neopseustidae. It is with this family, and not at a later stage within the Incurvaroidea, that these sensilla appear during the evolution of Lepidoptera. Contrary to common belief, the labial-palp-pit organ, or organ of vom Rath, is present at the distal extremity of the labial palpi of *S. andesae*. It is made up of a dozen of grooved multiporous sensilla coeloconica whose function is carbon dioxide sensitive. Thus, its presumed absence can no longer be considered as an autapomorphy of Neopseustidae. *S. andesae* possesses other original characteristics: both short and long bifurcate aporous sensilla chaetica on the labrum, numerous sensilla campaniformia on the first segment of labial palpi, as well as those previously described: the double-tube configuration of the proboscis and the composite and polymorphic multiporous sensilla basiconica on the antennae. Other cephalic sensilla are also described: aporous bifurcate sensilla chaetica on the clypeus, aporous sensilla campaniformia above the mandibles, and on the chaetosemata.
INTRODUCTION

The primitive Lepidopteran family Neopseustidae, which belongs to the basal Glossata, comprises four genera which are rare, both in nature and in collections. Kristensen (1968) considers the general morphology of the head of Neopseustidae to show a mixture of primitive and specialized features. The most primitive features are the five-segmented maxillary palpi, the large labrum and a well-developed chaetosemata. The characteristics of the head that may be considered as modified or derived are in particular the reduction of the mandibles, the specialization of the maxillary galeae forming the proboscis, and the loss of the labial-palp-pit organ (Davis, 1975). Whereas adults Lepidoptera-Glossata possess a proboscis with a single food canal, the proboscis of Neopseustidae is made up of two independent and functional sucking tubes (Kristensen & Nielsen, 1981). That configuration is unique among the Lepidoptera and permits the assignment to the neopseustid ground plan (Krenn & Kristensen, 2000).

As regards the mouthpart sensilla, the latter authors mention only «short and blunt sensilla basiconica situated on low sockets on the dorsal galea zone, numerous bristle-like sensilla trichodea on the external wall of the galea base, no sensilla in the food canals». Furthermore, they consider that sensilla styloconica, uniporous sensilla characteristic of the proboscis of lepidopterans, appear for the first time in the Incurvarioida (Adelidae, Incurvariidae, Prodoxidae), i.e. several clades after the Neopseustidae. However, we have shown the existence of uniporous sensilla styloconica on the proboscis of the South American neopseustid moth *Apoplania valdiviana* Davis & Nielsen (Faucheux, 2007), which means that these sensilla appear for the first time in the Neopseustidae. The aim of the present study is to verify the presence of sensilla styloconica and the absence of the labial-palp-pit organ in another neopseustid, *Synempora andesae*, and to discover the sensory organs on all the mouthparts.

MATERIAL AND METHODS

Specimens of *Synempora andesae* were obtained from the collections of the Zoological Museum, University of Copenhagen, Denmark and the Australian National Insect Collection (CSIRO, Canberra); the specimens studied (two males, two females) were collected in Puerto El Sagrario between the western end of Brazo Norte (Lago Menéndez) and Lago Cisne in Parque Nacional Los Alerces, west of Esquel, Argentina.

For the scanning electron microscopic (SEM) study, the heads were cleaned in acetone, dehydrated into pure alcohol and mounted on specimen holders. After coating with gold and palladium, preparations were examined in a Jeol J.S.M. 6400F SEM at 7 kV. Sensillum terminology follows Zacharuk (1985) and Faucheux (1999).

RESULTS

The mouthparts of *S. andesae* comprise the labrum, the mandibles, the maxillae (two galeae or proboscis, and two maxillary palpi) and two labial palpi (Figs. 1-2).

1 - The labrum

The labrum is relatively large and triangular; it bears numerous microtrichia and 10 aportal sensilla chaetica (Fig. 3). These sensilla may be classified under four subtypes (Fig. 4): a) long and slender; b) long and thick; c) long, thick and bifurcate (Fig. 5); d) short and bifurcate. They are more or less symmetrically arranged on each side of the labrum.

2 - The mandibles

The mandibles are enlarged but only weakly sclerotized, nonarticulated and non-functional. They possess no sensilla (Fig. 6).
3 - The maxillary galeae

The galeae are relatively short, their length not exceeding that of the labial palpi and approximately half the length of the maxillary palpi. Whereas the proboscis of all other adult Lepidoptera Glossata is formed by a sucking tube with a single food canal, that of Neopseustidae has two independent sucking tubes (Fig. 7) whose dorsal and ventral margins come very close together; but each tube possesses its own food canal (Kristensen & Nielsen 1981). Scattered scales cover the galeae on the basal third, the two distal thirds being unscaled. The external wall is densely covered with non-innervated microtrichia on the ventral and lateral surfaces whereas, dorsally, the wall texture lacks microtrichia and becomes tuberculate (Fig. 8). The dorsal legulae are close-set, broad and flat processes which are pressed against the galea wall bordering the lower margin of the food canal; these dorsal legulae are non-functional in the coupling of galeae in Neopseustidae. The ventral margin of each galea is bordered by a longitudinal row of ventral legulae or «zip-scales» which are oriented towards the inside (Fig. 8). The two galeae are apparently linked together by zip-scales. The external wall of each galea bears four sensillum types:

- Aporous sensilla chaetica are from 10
Figs. 2-8. Head and mouthparts of *Synempora andesae*. 2, frontal view showing the antennae (A), the maxillary palpi (MP) and the labial palpi (LP); 3, labrum with aporous sensilla chaetica (arrowheads); 4, detail of left upper part of labrum showing aporous sensilla chaetica of various types a, b, c, d; 5, long and bifurcate sensillum chaeticum of labrum; 6, right mandible (arrowheads); 7, the two galeae; 8, external wall of a galea showing tuberculate scales (T), zip-scales (Z) and lateral microtrichia (M).
to 14 μm in length and possess a base of 1 μm in diameter. Their broad cupola allows ample movement of the hair (Fig. 10). They are few in number, no more than seven sensilla per galea (Fig. 9). They are located at the base of the galea, at the level of the zone with scales and microtrichia, as well as at the base of the tuberculate zone. The sensilla located on the external edge of the galea are bristly and form an angle of 45° with the integument, the dorsal sensilla are pressed against the galea.

- Uniporous sensilla chaetica, 8-10 μm long, have a basal diameter of 1.7 μm and a blunt distal extremity. The narrow cupola limits the movement of the hair (Fig. 11). These sensilla are located at the base of the galea like the previous ones; they are flattened against the galea and oriented towards its distal part. Their number is estimated at 2 per galea.

- Uniporous sensilla basiconica are made up of a cone of between 3.3 to 4 μm long, with smooth walls surrounded by a ring 3.3 μm in height whose aperture is restricted by an internal membrane (Fig. 12). The terminal pore is difficult to see with the SEM. They form three longitudinal rows the whole length of the galea (Fig. 9). They number about 24 sensilla per galea.

- Uniporous sensilla styloconica appear in the distal half of the galea (Fig. 13) and are only truly characteristic at the apex of the galea (Fig. 15). The stylus, 10 μm long and 7.5 μm in basal diameter, bears 4-6 ribs (Fig. 15). The cone, 3.5 μm long, is stocky and depressed at the apex. No cavity or membrane analogous to those of sensilla basiconica can be observed at the apex of the stylus (Fig. 14). I have counted 2 apical sensilla and 3 or 4 subapical sensilla per galea.

I have been unable to describe the uniporous sensilla basiconica which might be present in the two food canals for their diameter is too small for SEM observation. According to Kristensen (1968), basing his observations on histological sections, the internal wall of the food canal consists of transverse bars, possibly subdivided into densely packed lamellae similar to the condition in higher Lepidoptera.

4 - The maxillary palpi

The maxillary palpi are 1.5 mm long, 5-segmented, folded against the head in rest (Fig. 2); the fourth and fifth segments are the longest and of equal lengths. They possess five types of sensilla. Long uniporous sensilla chaetica, 65 μm long, and blunt-tipped, are located on the 4th and 5th segments (Figs. 16, 17), exclusively on the face in contact with the galea.

They number about 40 on the 4th segment and 30 on the 5th segment. Short uniporous sensilla chaetica, 10 μm long, are much shorter and more difficult to identify than the preceding ones. They are irregularly and more conspicuously striated (Fig. 19). They are spread out among the aporous sensilla chaetica and they number no more than 5 on segments 4 or 5. Aporous sensilla chaetica, 30 μm long, are slender sensilla located on the external edge of the segments and few in number: 10 for the 4th segment, 8 for the 5th segment (Fig. 18). They are the only sensilla present on the 3rd segment where they follow a regular arrangement (Fig. 20). From 6 to 8 aporous sensilla campaniformia are lined up along the 2nd palpal segment which does not bear any other sensillum type (Fig. 21). The short 1st segment only bears non-innervated microtrichia (Fig. 23). Three uniporous sensilla styloconica are present at the distal end of the maxillary palp: two apical and one subapical (Fig. 22).

5 - The labial palpi

The labial palpi are 3-segmented and 0.8 mm long; the terminal segment is elongated, about equalling the length of the second (Fig. 2). The 2nd and 3rd segments are entirely covered by scales and microtrichia. Some twenty aporous sensilla chaetica are spread out over the terminal segment (Fig. 25). This segment, at the tip, has sensilla located in a ventral pit with a restricted oval opening, a length of about 18 μm and a width of 10 μm. This labial-palp-pit-organ contains a cluster of 7-10 multiporous elongated and grooved sensilla coeloconica (Fig. 25). They are about 20 μm long, with a basal diameter of 1.4 μm, tapering to about 1 μm. The surface of the pegs is furrowed, with numerous irregular...
longitudinal ridges. Pores in the furrows between the ridges are difficult to observe (Fig. 26). The first segment, deprived of scales, bears from 16 to 20 aporous sensilla campaniformia spread out over its whole surface (Fig. 24). Three of them are concentrated in the proximal region, and seven sensilla are aligned transversally at the distal extremity of the segment.

6 - Other sensory structures

Besides the anteninal sensilla, we have observed a few sensory structures near the mouthparts: the chaetosemata and isolated sensilla.

- The chaetosemata are cuticular elevated
Figs. 16-23. Maxillary palpus of *Synempora andesae*. 16, 4th segment with numerous long uniporous sensilla chaetica (arrowhead). 17, detail showing long uniporous sensilla chaetica (arrowhead); 18, 5th segment with aporous sensillum chaeticum (C) and long uniporous sensilla chaetica (arrowhead); 19, short uniporous sensillum chaeticum on the 5th segment; 20, 3rd segment with aporous sensilla chaetica (arrowhead); 21, 2nd segment with sensilla campaniformia (arrowheads); 22, apical and sub-apical sensilla styloconica of 5th segment (arrowheads); 23, base of palpus with microtrichia.
clusters or patches of piliform scales on the head and generally posterior to the antennae on some adult Lepidoptera. *S. andesae* possesses well developed frontal chaetosemata composed of a pair of swollen areas on the frons beneath the antennal sockets (upper chaetosemata) with another smaller pair situated above the antennae across the vertex (lower chaetosemata) (Fig. 1). Each upper chaetosema is comprised of
about 120 piliform scales (Fig. 27). Each lower chaetosema has a triangular shape and bears 95-100 piliform scales (Fig. 28). A few thinner piliform scales are spread out among the others. On the study heads that were preserved in alcohol, the piliform scales dehisce easily and only their alveoli remain in situ. The piliform scales possess the structure characteristic for long scales (Figs. 29, 30). A single sensillum campaniformium is present on each upper (Figs. 28) or lower chaetosema (Figs. 31, 32).

- Scattered cephalic sensilla: An aporous bifurcate sensillum chaeticum is found on each side of the clypeus (Figs. 1, 33). One or two sensilla campaniformia are situated between the compound eyes and the mandibles (Figs. 1, 34).

Figs. 30-34. *Synempora andesae*. 30, two piliform scales of a chaetosema; 31, right lower chaetosema of another individual with a single sensillum campaniformium (arrow); 32, detail of sensillum campaniformium; 33, aporous bifurcate sensillum chaeticum of the clypeus; 34, sensillum campaniformium (arrow) located between the compound eye (E) and the mandible (see Fig. 1).
DISCUSSION

Morphological and functional considerations

The sensory equipment of the labrum of *S. andesae* recalls that of *Micropterix calthella* Linnaeus (Chauvin & Faucheux, 1981; Faucheux, 1999) However, the aporous bifurcate sensilla chaetica (long and short) are identified here for the first time on the labrum of Lepidoptera (see Faucheux, 1999).

We have not been able to study the sensilla of the epipharynx which constitutes the internal face of the labrum because the dissection of the labrum of this small moth is very delicate and we have too few specimens at our disposal. According to the results obtained for the Micropterigidae, the Tineidae and Rhopalocera (Chauvin & Faucheux, 1981; Faucheux, 1981; Faucheux & Lebrun, 1981; Faucheux, 1999), uniporous gustative sensilla basiconica are frequent on the epipharynx of Lepidoptera and therefore, they may be present in *S. andesae*. The mandibles of *S. andesae* are reduced and non functional.

The uniporous smooth sensilla basiconica on the galeae of *S. andesae* are frequent in the lower Lepidoptera and with the aporous sensilla chaetica, they are the only sensilla on the proboscis of Neopseustidae that have been identified by previous authors (Kristensen & Nielsen, 1981; Krenn & Kristensen, 2000). The gustative function of uniporous sensilla basiconica and styloconica on the proboscis of Lepidoptera has been demonstrated before (Walters et al., 1998).

Kristensen & Nielsen (1981), carrying out histological sections of the proboscis of *S. andesae* observe a large gustatory sensillum basiconicum which projects into each groove only in the most basal part of the proboscis where it is roofed over by the labrum, whereas the closed tubular portion of the food canal is devoid of sensilla. The absence of uniporous sensilla basiconica in each food canal, repeated by Krenn & Kristensen (2000) is questionable for it is not demonstrated by a figure. In any case, the presence or absence of sensilla in the food canals cannot be proved because the latter have a very small diameter in Neopseustidae and it seems impossible to separate the two edges of the galeae.

The sensory equipment on the maxillary palpi of a neopseustid moth is described for the second time. It is comparable to that of *Apoplania valdiviana* (see Faucheux, 2007) and rather similar to that of other primitive moths (Faucheux, 1999). A mechanical function has been suggested by Davis & Nielsen (1984): «In the resting position, the fourth and longest segments of each maxillary palpus are kept in a parallel position and close together, and it seems plausible that the strong spines (in fact, the aporous sensilla chaetica) on the medial surface of this segment, could have a locking function, keeping the long maxillary palpi fixed during rest». The developed and varied sensory equipment of the maxillary palpi is related to their functional importance. In particular, the large number of sensilla campaniformia with a proprioceptive function on the basal segment suggests considerable mobility in the palpus. However, nothing is known of the biology, ecological tolerance and requirements of the Neopseustidae. The preferred habitat for *S. andesae* is characterized by a dominance of *Nothofagus dombeyi*, with a very dense understorey of *Chusquea culeou*. It appears to be possible that the bamboo *C. culeou* could be the food plant for the South American Neopseustidae (Davis & Nielsen, 1980). The palpi probably play a prehensile role in *S. andesae*.

The abundance of sensilla campaniformia in the proximity of the basal area of the labial palpi of *S. andesae* also testifies to their functional importance. Such a large number of sensilla in this area has so far never been mentioned in Lepidoptera (Faucheux, 1999). Bogner et al. (1986) clearly demonstrated electrophysiologically, for the first time, that the sensilla of the labial-palp-pit-organ are primarily tuned to the detection of carbon dioxide.

The chaetosemata of Lepidoptera were first described by Jordan (1923) and further studied by Eltringham (1925), who demonstrated their nerve supply. In the Neopseustidae, the chaetosemata have been
referred to as Eltringham’s organ by Kristensen (1968) and Mutuura (1971). They also occur in Zygaenidae, Tortricidae and all Rhopalocera (Bourgogne, 1951).

In our opinion, the bristles with their alveoli observed on the two pairs of chaetosemata of *S. andesae* do not correspond to sensilla. Most of the hairs have left their alveolus, which is characteristic of non-innervated lamellar scales and piliform scales. In a broken sensillum, the base always remains within its alveolus. Consequently in *S. andesae*, the sensory role of each chaetosoma is performed exclusively by the sensillum campaniformium.

The sensilla campaniformia in insects are stimulated by passive mechanical deformations of the cuticle which can either be brought about by external forces or by self-produced movements (Keil, 1997). Two groups of six or seven sensilla campaniformia described on the frons of the adult primitive moth *Heterobathmia pseudoeriodactyla* Kristensen & Nielsen are supposed to be an aerodynamic organ capable of apprehending air movements in front of the head (Faucheux, 1999). Day (1995) described a paired sense organ found in the head of adult mosquitoes, whose structure prompts the suggestion that it might be involved in the detection of changes in pressure. The sensilla campaniformia of the chaetosemata of *S. andesae* may play a similar role to that of the sense organ of mosquitoes.

**Phylogenetic considerations**

A very large labrum such the one in *S. andesae* can only be observed in Lower Lepidoptera (Chauvin & Faucheux, 1981; Faucheux, 2005c). The aperous bifurcate sensilla chaetica could constitute an autapomorphy for the Neopseustididae but would need to be described further in other species of that family.

The five-segmented maxillary palpi are primitive features which exist in Micropterigidae (Chauvin & Faucheux, 1981), Agathiphagidae (Kristensen, 1984), Heterobathmiidae (Faucheux, 2005c), Lophocoronidae (Faucheux, 2006), most Monotrysia and many Tineidae (Bourgogne, 1951). In some studied groups such as the Micropterigidae and the Heterobathmiidae which are spore/pollen feeders, the long maxillary palpi possess sensilla which are supposed to have both a prehensile and a mechanoreceptive role. However in *S. andesae*, they do not possess specialized sensilla for collecting pollen or spores.

Typical sensilla styloconica are present on the proboscis of *S. andesae* (this paper) and *Apoplania valdiviana* (Faucheux, 2007). Now, Krenn & Kristensen (2000) claim that the appearance of sensilla styloconica on the proboscis of Lepidoptera begins with the Adelidae, which are more advanced in the classification than the Neopseustidae. They consider that the presence of ribbed sensilla styloconica is a groundplan autapomorphy of non-nepticuloid Heteroneura. In support of their view, they mention only the sensilla basiconica and bristle-like sensilla trichodea in Neopseustidae. In our view, the «ribbed» character of sensilla styloconica is too variable, whether in the sensilla of the proboscis or in that of the antennae (Faucheux, 1999) to possess any phylogenetic signal. In fact, it is the appearance of sensilla styloconica, whether ribbed or not, which is of phylogenetic interest. Sensilla styloconica of the proboscis are the most conspicuous sensilla: they are characterized by a big stylus and differ from sensilla basiconica which possess only a basal collar. The stylus is a protrusion of the cuticle of the proboscis or the antenna (Faucheux, 1982, 1999) and thus, the ornamentation of its smooth, ribbed or spiky wall reflects the cuticle of these appendages. For example, the smooth styli and more or less ribbed styli coexist in the higher Lepidoptera and Rhopalocera (Sellier, 1975). This author has admirably described the successive stages of the passage from the sensilla basiconica with collars to the sensilla styloconica on the proboscis tip of the papilionid *Parnassius apollo* Linnaeus. Furthermore, if the Adelidae and the Yponomeutidae (basal Ditrysia) possess long and ribbed styli, more advanced lepidopterans, in terms of classification (higher Lepidoptera), such as the satyrid...
Melanargia galathaea Linnaeus, the pierid Gonepteryx cleopatra Linnaeus and the lycaenid Polygonne coridon Poda, also possess the same sensillum type. On the contrary, Nymphalidae such as Vanessa atalanta Linnaeus and Pandoriana pandora Denis & Schiffermüller have long styli which are flattened and smooth. The sensilla styloconica with a short and smooth stylus, present in Parnassius apollo and the hesperiid Thymelicus sylvestris Poda (Sellier, 1975), are identical to those of the neopseustids A. valdiviana (Faucheux, 2007) and S. andesae (this paper). Consequently, the sensilla styloconica must appear on the proboscis of basal Glossata with the Neopseustidae. The results of Krenn & Kristensen (2000), which mention these sensilla only in more recent clades, from the Incurvarioidea onwards (Adelidae, Incurvaridae, Prodoxidae) are therefore not supported. It would be interesting to study the existence of sensilla styloconica in the families intermediary between the Neopseustidae and the Incurvarioidea.

The presence of sensilla styloconica on the proboscis is therefore a characteristic of the Neopseustidae to be added to the previously mentioned autapomorphies such as the double-tube configuration of the proboscis (Kristensen & Nielsen, 1981) and the presence of antennal composite sensilla basiconica with concentrated pores (Faucheux, 2005 a, b; submitted).

Contrary to widespread opinion (Kristensen, 1968; Davis, 1975; Krenn & Kristensen, 2000), the presence of the labial-palp-pit-organ (or organ of Vom Rath) is verified on the eight palpi studied (2 males and 2 females) in S. andesae. The absence of this sensory organ has been hitherto considered as an autapomorphy of Neopseustidae (Davis, 1975). In studying the mouthparts of A. valdiviana (Faucheux, 2007), the labial palpi of the specimens examined were incomplete, and I was unable to observe their apices. Nevertheless, it must be accepted that this organ is at least present in a neopseustid moth. The fact that this organ was not recognized by the above-mentioned authors is probably due to confusion between the concentration of very long sensilla and the nearby sensilla chaetica or the non-innervated microtrichia. In our synthesis (Faucheux, 1999) of the results obtained with the Lepidoptera, we concluded that the labial-palp-pit-organ was present in most insects, but that the number of sensilla could vary greatly. Thus, the keratophagous Tineidae Tineinae are a good example of the reduction of the number of sensilla, which drops from 70 in Monopis crocicapitella Clemens to a single sensillum in Tineola bisselliella Hummel (Faucheux & Chauvin, 1980).

In summary, the presence of uniporous sensilla styloconica on the proboscis, and of the labial-palp-pit organ is demonstrated in S. andesae. These unique characteristics are to be added to those already described for the Neopseustidae such as the double-tube configuration of the proboscis and the composite and polymorphic multiporous sensilla basiconica on the antennae (Faucheux et al., 2006).

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LITERATURE CITED


