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Heterobathmia pseuderiocrania (Heterobathmiina): mouthparts, mouthpart sensilla, and comparison with other non-glossatan suborders (Insecta, Lepidoptera)

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Abstract: The mouthparts of *Heterobathmia pseuderiocrania* are primitive and well adapted for collecting and grinding pollen of *Nothofagus.* The five- segmented maxillary palps show specialized structures for collecting pollen: spatula-shaped sensilla chaetica. The epipharynx and the teeth on the mandibles grind the pollen to powder before ingestion. Mechanoreceptive aporous sensilla chaetica are located on the labrum, the galeae, the maxillary and labial palps. Proprioceptive sensilla campaniformia are observed only on the maxillary palps. Two types of gustative uniporous sensilla basiconica are observed on the galeae and one type at the apex of the maxillary palps. The apical segment of the labial palps shows uniporous sensilla chaetica and multiporous sensilla basiconica. Compared to the suborder Zeugloptera, the species of which are also pollen-grinders, the suborder Heterobathmiina, as exemplified by *H. pseuderiocrania*, is less specialized: presence of one type of pollen-collecting structures; absence of large sensilla placodea (perforated heart-shaped organ and perforated oval area) on the labial and maxillary palps, sensilla present in *Micropterix calthella*. In view of these differ-ences, the Heterobathmiina are closer to the suborder Glossata. *H. pseuderiocrania* reveals several autapomorphies: absence of linking legulae on the galeae, which are clearly outlined structures in the Zeugloptera and very developed in the Glossata; presence of long uniporous sensilla basiconica on the apex of the galeae, and uniporous sensilla chaetica on the labial palps.

Key words: Lepidoptera, *Heterobathmia*, mouthparts, maxillary palp, sensilla, evolution.

Within the lower Lepidoptera, the suborder Heterobathmiina follows the two previous suborders Zeugloptera and Aglossata and is the sister group of the suborder Glossata, which comprises all higher Lepidoptera. Relatively few studies concern the single family of Heterobathmiina, the Heterobathmiidae, which contains only the genus *Heterobathmia* which occurs in temperate South America. The phylogenetic position of Heterobathmiidae has already been discussed. First considered as a subfamily of Micropterigidae, because of numerous characteristics in common as regards the adults (Kristensen & Nielsen, 1979), the Heterobathmiidae have now been placed in a new suborder, the Heterobathmiina, by the same authors who show that immature stages contradict the assignment of *Heterobathmia* to the suborder Zeugloptera (Kristensen & Nielsen, 1983). With Microp-terigidae and Agathiphagidae, the Heterobathmiidae are one of the three extant families in the non-glossatan grade within the Lepi-doptera, and as the putative sister group of Glossata, the family is of exceptional phyloge-netic interest (Kristensen, 1984).

In the genus *Heterobathmia*, *H. pseuderio-crania* Kristensen & Nielsen, 1979 is the most com-mon and widespread moth. If the antennal sen-silla have already been studied (Faucheux, 2004a), those of the mouthparts are little known. The gross morphology of mouthparts is described by Kristensen & Nielsen (1979) but, apart from the existence of presumed chemoreceptive sensilla on the epipharynx and of a "von Rath's organ" on the third segment of the labial palp, no other men-tion of sensory organs is made. As regards the feeding behaviour, *H. pseuderiocrania* has only been observed feeding in the flowers of the de-ciduous *Nothofagus obliqua* (Mirb.) Oerst., and Kristensen & Nielsen (1983) assume that the moth is a pollen-feeder. However, in nature and under laboratory conditions, adults have been seen drinking from a drop of water. Likewise, adults were never observed on flowering grasses or on mosses and ferns with sporangia.

The suborder Zeugloptera has been more carefully studied: the morphology of adult grinding mouthparts in several species of Microp-terigidae has been described by Tillyard (1923), Issiki (1931), Hannemann (1956) and the sensilla by

Le Cerf (1926) and Chauvin & Faucheux (1981). They are characteristically endowed with functional mandibles and long maxillary palps equipped with pollen-collecting structures and peculiar sensilla. Concerning the Aglossata, with the single genus *Agathiphaga*, we have very little information. According to Kristensen (1984), the examination of the few adult specimens found in nature has so far yielded no evidence as to whether the moths feed at all. However, although the mandibles are rather large and have a distal lobe articulation, they are devoid of genuine incisor cusps and are probably incapable of biting. The galeae of Zeugloptera and Aglossata are not joined so as to form a proboscis; they resemble one another but the distal lobe in Aglossata is larger than in Zeugloptera. The maxillary palps show an identical development in the two suborders. The only information related to the sen-silla of the Aglossata is to be found in articles by Kristensen (1984) and Faucheux (1999). Our intention is to describe the mouthpart sensilla of *H. pseuderiocrania* so as to compare them with the other suborders.

MATERIAL AND METHODS

The moths *Heterobathmia pseuderiocrania* Kristensen & Nielsen 1979 were provided by the Australian National Insect Collection (A.N.I.C.), Division of Entomology, CSIRO, Canberra, Australia, thanks to Dr E. S. Nielsen. They were collected in San Martín de los Andes, altitude 640 m, Province of Neuquén, Argentine Patagonia, 29-9-1981, by E. S. Nielsen and O. Karsholt. For the study with scanning electron microscopy (SEM), the female mouthparts were mounted *in toto* or dissected, 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 Zacharuk (1985) is used in naming the types of sensilla.

RESULTS

The mouthparts of *H. pseuderiocrania* comprise the labrum-epipharynx, two mandibles, and two maxillae, each composed of a galea, a lacinia and a maxillary palp, and the labium with the labial palps (Figs. 1 y 2).

The labrum-epipharynx

The labrum -epipharynx, which is entirely visible from an anterior view of the head, is a well-developed piece, pentagonal, measuring 300 µm in its widest section (Fig. 3). Its ante-rior (inner) surface, or labrum *sensu stricto*, is sclerotized and bears lamellar scales and microtrichia, uniformly distributed over the whole surface of the piece. Aporous sensilla chaetica, 24 µm long, are scattered on the distal part (Fig. 4) and are more numerous and strong near the lateral corners of the labrum. The distalmost region is membranous and bears about ten aporous sensilla chaetica some of which are the longest (35 µm) and the thickest of the labrum (Fig. 4).

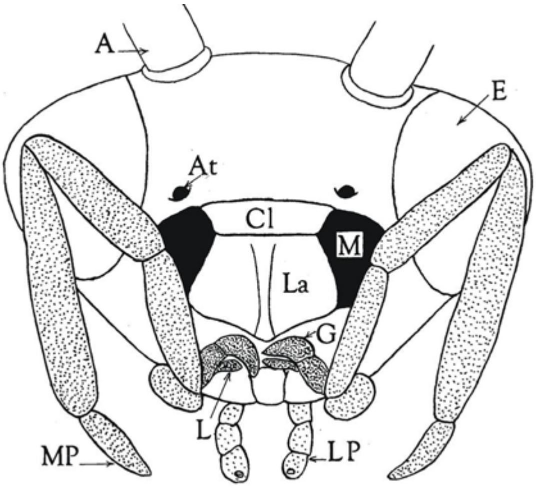


Fig. 1. *Heterobathmia pseuderiocrania*: diagram of anterior view of the head. A, antenna; At, anterior tentorial pit; Cl, clypeus; E, compound eye; G, galea; L, lacinia; La, labrum-epipharynx; LP, labial palp; M, mandible; MP, maxillary palp.

The mandibles

In situ , the mandibles are covered by the labrum and only their base is visible (Fig. 3). The right mandible is not quite identical with the left mandible: its teeth are more numerous and more pointed than those of the left mandible. Each mandible measures 160 µm in length and 125 µm in width (Fig. 5). The two mandibles possess a *pars incisoris* and a *pars molaris*: together they constitute the mandibular plate. The *pars incisoris* can be divided into two distinct parts. The first region, located distally, is characterized by three prominent teeth which clearly exceed the surface of the mandibular plate. The second region is proximal and comprises some ten smaller teeth. The *pars molaris,* or molar area, reveals at least two distinct regions. The lateral region bears close-set hair-like cuticular processes (Fig. 6) and most of the mandibular plate is covered by scale-like cuticular processes (Fig. 7). No sensillum has been observed dorsally or ventrally on the mandibles.

The maxillae

Each maxilla is constituted by a cardo and a basal stipes, invisible on the mouthparts *in situ* (Fig. 4), a galea, a lacinia (Fig. 4) and a five-seg-mented maxillary palp (Fig. 2). The two galeae, separated from one another, do not form a pro-boscis. The galea is a moderately sclerotized lobe, not forming a groove, measuring 80 µm in length and barely stretching to half of the first maxil-lary palp segment. Its dorsal surface, entirely covered by microtrichia, possesses aporous sen-silla chaetica, longitudinally striated, and of vari-able length. The largest of these, 40 µm long, extend beyond the galea and are visible on Fig. 8. Three regions are observed on the ventral face of the galea. A median region is covered by close-set microtrichia and devoid of sensilla. A second region, more internal and close to the lacinia, is scantily provided with microtrichia but possesses at least four short uniporous sensilla basiconica (B1) which are regularly spaced out and more or less lined up lengthwise on the galea. The third region, situated on the external edge of the galea, is proximally smooth but becomes distally squa-mous and bears distally five uniporous smooth-walled sensilla basiconica B2, of variable length, but from two to four times longer than the pre-ceding sensilla (Fig. 8).

The maxillary lacinia is barely sclerotized, slightly hollowed out like a spoon and tapering towards the apex. It has for the most part a smooth surface and is devoid of sensilla (Fig. 8).

The five-segmented maxillary palp is the most striking mouthpart (Fig. 9). It measures 0.95 mm in length. Very mobile (the principal points of flexion are located between segments 1/2 and 3/4), it can project well beyond the head. From base to tip, the lengths of the segments 1-5 are respectively 115, 170, 230, 340 and 95 µm. The segments 1- 4 have a vestiture of microtrichia and lamellar or piliform scales. As with *M. calthella* (Chauvin & Faucheux, 1981), the fourth segment has annulate cuticular striae. The distal segment is unscaled but the microtrichia are long and close-set (Fig. 10). The first four segments bear aporous sensilla chaetica which are regularly distributed (Figs. 9, 10) . At the level of their articulation, the segments 4 and 5 each present one aporous sen-sillum campaniformium (Fig. 10).

Five or six uniporous sensilla basiconica, of intermediary length between the two types of sensilla basiconica present on the galea, are situated on the palp apex (Fig. 11). The 5th segment reveals as well a particular structure which we have called spatula–shaped aporous sensilla chaetica (Fig. 11, S). These sensilla, 20 -45 µm long, have a circular base but flatten subsequently and widen out towards the apex to form a kind of spatula. Their dorsal face is slightly convex and shows two fine longitudinal ridges, whereas the ventral face is furrowed with two deep grooves reaching the apex of the sensillum (inset, Fig. 11). The sensilla are inserted in a dome-shaped alveolus with a wide aperture permitting ample hair displacement. Contrary to the typical sensilla chaetica, the interior of the alveoli does not possess the characteristic inter-nal ring limiting hair movement (Fig. 13, aster-isk). Frequently, the dome of the alveoli possesses one or two minute holes which are not seen on the alveoli of the other sensilla chaetica (Fig. 14, asterisk). Broken hairs show a straight internal lumen which is characteristic of mechanoreceptive sensilla (Fig. 14, arrow). The distribution of spatula-shaped sensilla chaetica makes the apical segment of the palp resemble a pincushion. Twenty five to thirty sensilla are situated on the two faces of the palp, inserted perpendicularly in relation to the integumental surface, and equidistant from one another (Fig. 12). Fern spores are often observed, attached to these sensilla alone (Fig. 12, inset).

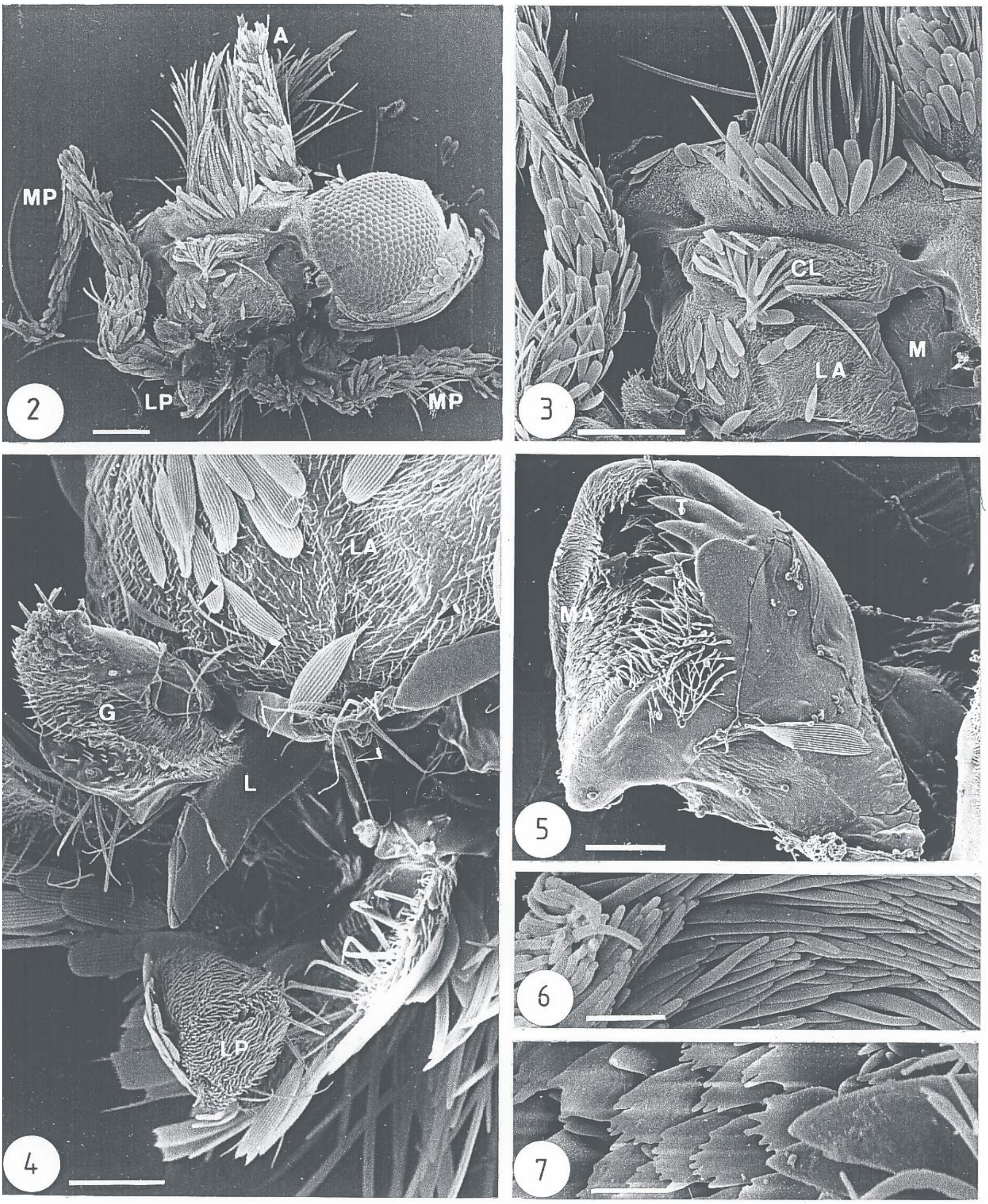
The labium

The labium comprises a postlabium, a proximal prelabium and a distal prelabium bearing two three-segmented labial palps (Kristensen & Nielsen, 1979). The two basal palp segments are covered by a vestiture of appressed lamellar scales and they bear thorny and pointed aporous sensilla chaetica C1 (Fig. 15). The third segment possesses none of the preceding sensilla but blunt-tipped and smooth sensilla chaetica C2 (Fig. 15). By analogy to other sensilla of the same type, a terminal pore, which is always difficult to observe in scanning electron microscope, is presumed to exist at the apex of these sensilla. Six grooved multiporous sensilla basiconica are located in an apical pit (Figs. 15, 16).

DISCUSSION

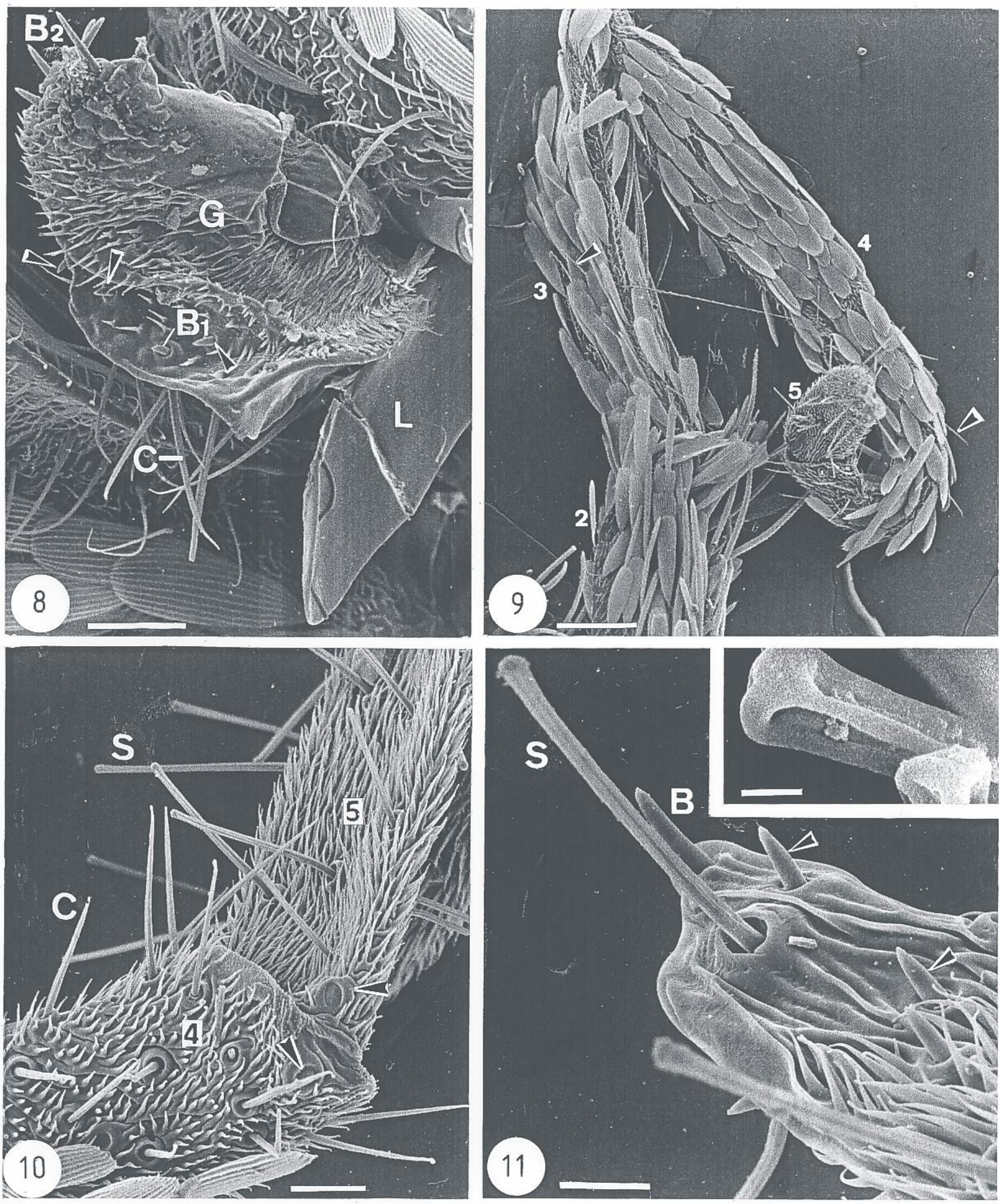
The structure of the mouthparts of *H. pseuderiocrania* reveals that this moth belongs to the pre-glossatan grade.

The shape and considerable development of the labrum are comparable in the Micropterigidae and the Heterobathmiidae, in contrast with the Glossata, in which the labrum is always small.



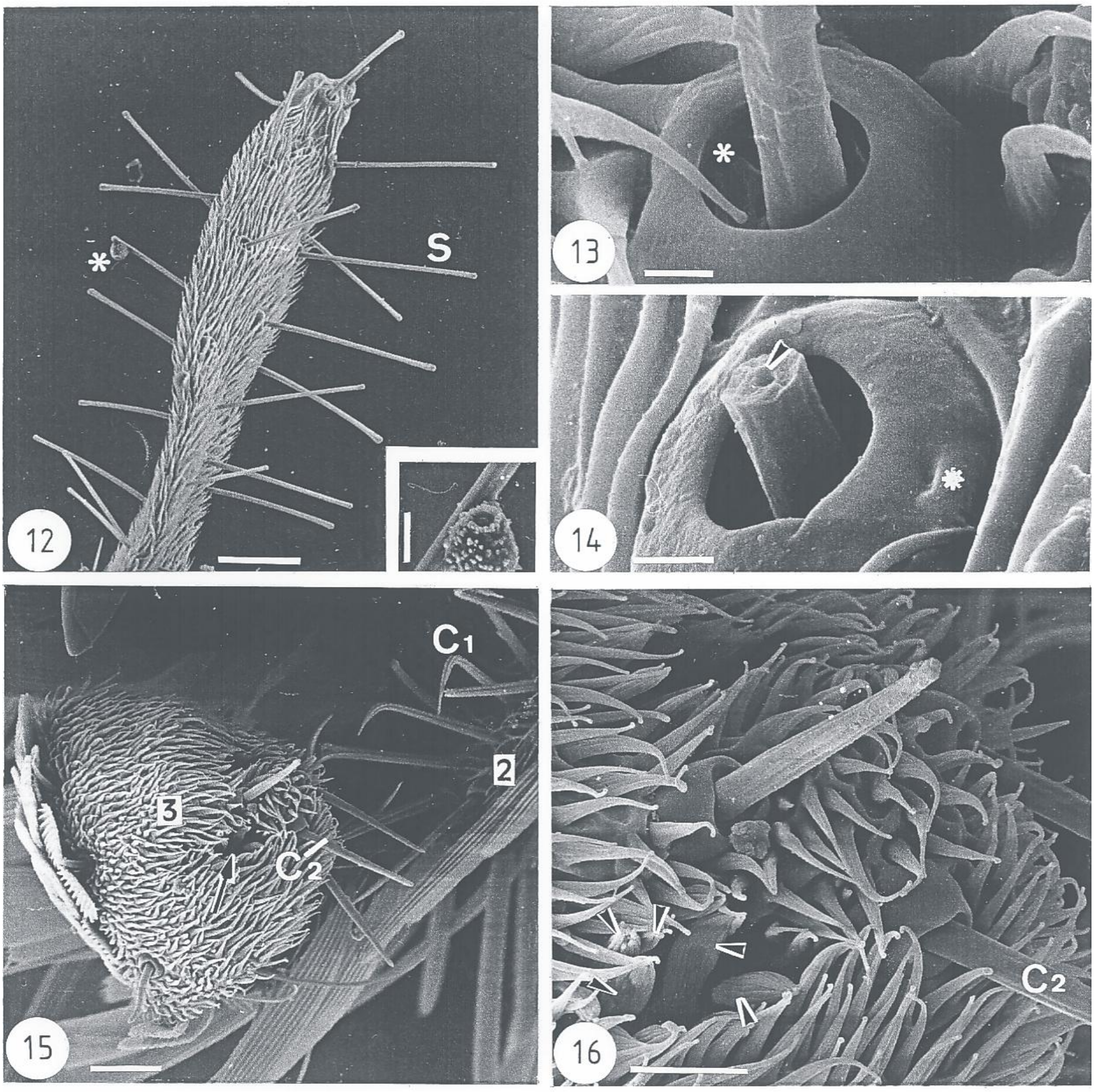
Figs. 2-7. Mouthparts of *Heterobathmia pseuderiocrania*, female. 2, Anterior view of head showing max-illary palp (MP), labial palp (LP) and base of antenna (A). Bar = 100 µm. 3, Clypeus (CL), labrum (LA) and base of mandible (M). Bar = 100 µm. 4, Labrum (LA) with sensilla chaetica (arrows), galea (G), lacinia (L), labial palp (LP). Bar = 30 µm. 5, Right mandible with teeth (T) and molar area (MA). Bar = 30 µm. 6, Detail of lateral part of molar area. Bar = 2 µm. 7, Median part of molar area. Bar = 3 µm.

However, only the apex of the labrum is unsclerotized in *H. pseuderiocrania* whereas the corresponding unsclerotized region in the Micropterigidae such as *Micropterix* (Hannemann, 1956), *Paramartyria* and *Paleomi-croides* (Issiki, 1931), extends into the central region of the labrum. As concerns the labral sensilla, an essential difference is the presence in *M. calthella* of



Figs. 8-11. 8, Lacinia (L) and galea (G) of *H. pseuderiocrania*, female, with sensilla chaetica (C), short sensilla basiconica (B1, arrows) and long sensilla basiconica (B2). Bar = 20 µm. 9-11. Maxillary palp of *H. pseuderiocrania*, female. 9, View of scaled segments 2-5 with sensilla chaetica (arrows). Bar = 50 µm. 10, Joint between segments 4-5 showing sensilla: chaetica (C), spatula-shaped chaetica (S), campaniformia (arrows). Bar = 10 µm. 11, Apex of 5th segment with sensilla basiconica (B, arrows), spatula-shaped sensilla chaetica (S). Bar = 5 µm. Inset: inner face of two spatula-shaped sensilla chaetica. Bar = 0.5 µm.

two lateral pilifers, each made up of a group of some 15 strong and prominent aporous sensilla chaetica (Chauvin & Faucheux, 1981). On the con-trary, the homologous sensilla of *H. pseuderiocrania*, are much smaller and never laid out in groups and do not constitute pilifers. It is curiously noteworthy that the pilifers are once again well developed in the higher Lepidoptera



Figs. 12- 16. 12-14. Spatula-shaped sensilla chaetica (S) of *H. pseuderiocrania*, female. 12, Apical segment showing distribution of sensilla and spore (asterisk). Bar = 20 µm. Inset: detail of spore. Bar = 2 µm. 13, Base of sensillum showing the interior of alveolus (asterisk). Bar = 1 µm. 14, Broken base of sensillum with lumen of hair (arrow) and hole on alveolus (asterisk). Bar = 1 µm. 15-16. Labial palp of *H. pseuderiocrania*, female. 15, Second (2) and third (3) segments showing thorny sensilla chaetica (C1), smooth sensilla chaetica (C2) and pit organ (arrow) . Bar = 10 µm. 16, Grooved sensilla basiconica of pit organ (arrows) and sensilla chaetica (C2). Bar = 5 µm.

such as the Tineidae (Faucheux & Chauvin, 1979). However, their number is remarkably diverse at lower taxonomic levels and they are absent both in the other non- glossatan Lepidoptera such as Agathiphagidae, and in the Nepticulidae and homoneurous Glossata (Krenn & Kristensen, 2000). According the latter authors, the function of pilifers is proprioceptive and they could registrate proboscis movements via labral dis-placement. If this is verified for all Lepidoptera, it is easier to understand the absence of pilifer bristles in *H. pseuderio-crania* which possesses no proboscis.

The specialized armature of the epipharynx present both in Zeugloptera and Heterobathmiina is a character which does not represent a genuine synapomorphy between the two groups, but perhaps a parallel evolution, and this similarity is at least partly plesiomorphic (Kristensen & Nielsen, 1983).

The mandibles of *H. pseuderiocrania* reveal the same degree of development as that of the Zeugloptera but differ in the disposition of the teeth. In all of the micropterigid genera described, the left mandible is similar in that it possesses incisor teeth near the apex only while the non-concentrated tooth arrangement in Heterobathmiidae represents the plesiomorphous condition (Kristensen & Nielsen, 1979).

The maxillae of *H. pseuderiocrania* resemble in their main aspects those of *M. calthella* but some details are different and need to be taken into account. The galea of *M. calthella* possesses on its dorsal side a dozen lamellar setae which taken together resemble piano keyboards (Chauvin & Faucheux, 1981). These setae prefigure the "legulae" which will make possible the linking structures of the two galeae and constitute the proboscis of nectarivorous Lepidoptera Glossata (Krenn & Kristensen, 2000). Now it so happens that in *H. pseuderiocrania*, situated from the phylogenetic point of view between the Micropterigidae and the basal Glossata such as the Eriocraniidae, the galea is devoid of lamellar setae. The same remark can be said of the separated galeae of the Agathiphagidae (Faucheux, 1999). The lamellar setae may have been lost in the Aglossata and the Heterobathmiina, or else, the lamellar setae and the legulae are not homolo-gous, have independent origins, and the type of galea of Aglossata and Heterobathmiina repre-sents the plesiomorphous condition of the entire order. Thus, as regards the formation of the pro-boscis, the two intermediary groups follow a dif-ferent evolution from the Zeugloptera. This fact is important because the transformation of the adult generalized galeae into a coilable probos-cis is one of the most significant events in the early evolution of the Lepidoptera. As concerns the sensory equipment, sensilla chaetica and short sensilla basiconica exist both on the galeae of the Heterobathmiina and of the three other suborders of Lepidoptera. However, *H. pseu-deriocrania* is distinguished by the presence of apical and grouped long sensilla basiconica, which have been described in no other lepi-dopteran insect; they probably constitute an autapomorphy of Heterobathmiina. It is worth noting that the external face of the galeae pre-sents identical sensilla in the majority of Lepi-doptera but possesses in addition a particular type in Aglossata (aporous grooved sensillum basiconicum) and in Heterobathmiina (uniporous long sensillum basiconicum).

The apical sensilla of *H. pseuderiocrania* have probably a tactile or gustative function because, according to Kristensen & Nielsen (1983), "when an adult is examining a substrate, the yellowish orange galeae palpate the surface".

The maxillary lacinia is present in *Heterobathmia* as in the two other non-glossatan sub-orders. We have observed no sensilla chaetica, whereas these sensilla occur in Micropterigidae (Chauvin & Faucheux, 1981) and Agathiphagidae (Kristensen, 1984).

The maxillary palp of *H. pseuderiocrania* which offers a comparable development to that of *M. calthella* , is moved around very actively when an adult is examining a substrate (Kris-tensen & Nielsen, 1983). The first four segments bear numerous aporous sensilla chaetica and sen-silla campaniformia, in both species. The apical segment of *Heterobathmia* shares common structures with those of the Micropterigidae, whereas others are absent. The sensory organs peculiar to the Micropterigidae are the large paddle-shaped sensilla chaetica present both in *M. calthella* (Chauvin & Faucheux, 1981) and *Saba-tinca sterops* (Faucheux, 2005); the umbel-shaped sensilla chaetica, only in *M. calthella*; and a multiporous oval apical area, developed in *M. calthella* but reduced in *S. sterops*. The first two sensillar types probably have a mechanoreceptive function and are specialized for the collection of pollen, whereas the third structure is a large sensillum placodeum, with a putative olfactive function (Faucheux, 2004b). The absence of these sensilla in *H. pseuderiocrania* indicates that this species is less well adapted than the Micropterigidae for pollen-gathering.

The sensilla common to *Heterobathmia* and to the Micropterigidae are the tactile -chemore-ceptive uniporous sensilla basiconica located at the apex of the palp and the spatula-shaped sen-silla chaetica. Indeed, about 6 of the latter sen-silla have recently been identified in *S. sterops* (Faucheux, 2005) and the majority of the sensilla formerly considered as typical sensilla chaetica (Chauvin & Faucheux, 1981) have the apex abruptly enlarged and must be considered as homologous with the spatula-shaped sensilla chaetica (Faucheux, 1999). However, it does not appear that these sensilla in *S. sterops* are ca-pable of an authentic prehension role. In short, the prehension of pollen grains is carried out by the paddle-shaped and umbel-shaped sensilla chaetica in *M. calthella*, by the paddle-shaped and spatula-shaped sensilla chaetica in *S. sterops*, and only by the spatula-shaped sensilla chaetica in *H. pseuderiocrania*. When the maxillary palps are not cleaned with acetone for their observation in S.E.M., pollen grains or spores frequently re-main attached to the prehensile sensilla (Chauvin & Faucheux, 1981; this paper). These sensilla, and particularly the spatula-shaped sensilla chaetica in *H. pseuderiocrania* could have an-nexed glands the secretion of which flows into the grooves of the sensilla. Such an interpreta-tion would agree with the particular structure presumed to exist in the alveoli of the sensilla. In the primitive families of Lepidoptera Glossata, the maxillary palps are reduced to three segments and possess only uniporous sensilla basiconica and aporous sensilla chaetica (Davis, 1978, 1986).

In Zeugloptera and Heterobathmiina, the labial palps are shortened while they are developed in Aglossata and Glossata. In the first two groups, this character was initially presumed to be apomorphic (Kristensen & Nielsen, 1979) but subsequently considered not to be a genuine synapomorphy, but at most a partly plesiomorphic character (Kristensen & Nielsen, 1983).

Based on analogous structures found in morphologically or physiologically characterized sensilla on the labial palps of other moths, the thorny aporous sensilla chaetica, grooved multiporous sensilla basiconica and presumed uniporous blunt-tipped sensilla chaetica of *H. pseude-riocrania*, are likely to be respectively tactile (Lee, 1987), olfactory or sensitive to carbon di-oxide (Lee *et al*., 1985; Kent *et al*., 1986; Bogner *et al*., 1986), and gustative (Zacharuk, 1985). According to Kristensen & Nielsen (1983), when an adult is examining a substrate, the labial palps of *H. pseuderiocrania* are turned outwards and do not seem to be actively moved. It may be de-duced that the labial palps have no tactile or gustative function. This observation may be re-lated to the absence of tactile sensilla chaetica on the apical segment. From a phylogenetic point of view, an interesting aspect is the absence of aporous sensilla chaetica and the presence of the blunt -tipped sensilla chaetica on the apical segment of *Heterobathmia*, whereas in the same localization, only mechanoreceptive tactile sensilla can be found in Zeugloptera and Glossata. The presence of the above mentioned sensilla might be considered as an autapomorphy of *Heterobathmiina* if this character is found in all other species of *Heterobathmia.* Furthermore, the absence of the perforated heart-shaped organ in *H. pseuderiocrania* (present in *M. calthella*, present but reduced in *S. sterops*), suggests a closer prox-imity of the Glossata than of the Zeugloptera.

A general tendency towards the simplification and reduction of sensillar types already noticed on the antennae of Lepidoptera (Faucheux, 1999) is manifest here as regards the mouthparts. Compared to another pollen-grinding moth such as *M. calthella*, *H. pseuderiocrania* possesses a more limited range of types, in particular on the maxillary and labial palps. Thus, the evolution of the sensilla would appear to precede the evolution of pollen-grinding mouthparts towards the suck-ing mouthparts.

Heterobathmia pseuderiocrania possesses particular sensilla which may be considered as autapomorphies of Heterobathmiina: the uniporous smooth-walled sensilla basiconica of the galeae, and the blunt-tipped sensilla chaetica of labial palps.

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