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Antennal sensory structures and their ecological-behavioural meaning in Cecidomyiidae (Diptera) larvae***

ABSTRACT

Cecidomyiidae larval antennae, so far considered to be biarticulate (rarely triarticulate), are here indicated as uniarticulate on the basis of anatomical evidence. Each of these monomerous antennae rises on a dome-shaped prominence (former «first antennomere») and bears 5 kinds of sensilla: one large placoid sensillum (multiporous placoid sensillum), covering most of the antennal surface, a dorsal one (basal sensillum), and an apical sensillum; an intermediate dorsal one (sensillum microampullaceum) and a basal, completely internal proprioceptor, both very difficult to detect with a light microscope. Functional morphology of the mentioned sensilla, carried out in scanning and transmission electron microscopy, revealed that: the large placoid sensillum is a multiporous chemoreceptor, most probably olfactory; the basal s. is a mechanoreceptor, probably hygro- and thermoreceptor; the apical s. is a uniporous chemoreceptor, most probably gustative; the s. microampullaceum is very difficult to interpret on a mere morphological basis; the proprioceptor may be interpreted as a Johnston's organ reduced to a single scolopidium. Some considerations about ecological-behavioural involvement of these antennal structures are here given.

Key words: anatomy, chemoreceptors, convergent adaptation, functional morphology, hygrothermoreceptor, scolopidium, ultrastructure.

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1. INTRODUCTION

The antennae of Cecidomyiidae larvae are, as a rule, well developed appendages of a minute head which, in the resting position, is retracted in the prothorax from which it extends out when the larva moves for exploration, deambulation, and taking in food. In this way, antennae, together with all the numerous head sensilla (OTTER, 1938; PRINCIPI, 1958. SOLINAS, 1968), are also kept safe and clean.

So far, morphological knowledge of these antennae has usually been restricted to in-outline descriptions reporting them as biarticulate (or triarticulate: KIEFFER, 1900), and having the first antennomere quite short and dome-shaped, and the second (or third) one roughly cylindrical or conical, more or less elongate according to the taxonomic group the larva belongs to (MÖHN, 1955). Also, papers reporting relatively detailed illustrations of these antennae do not deal with antennal sensilla. To our knowledge, the most detailed description of a Cecidomyiidae larval antenna, given so far, is that of *Aphidoletes aphidimyza* Rond. (SOLINAS, 1968), of which three sensilla have been indicated, all on the «second» antennomere, namely, one «placoid sensillum» covering most of the article surface, and two other very small ones, situated at the antennomere base and tip, respectively. Only the said features are detectable with the highest magnification in light-microscopy and, as far as we know, no electron microscopy investigation has yet been carried out on this subject.

Our aim was to study the functional morphology of the said antennal sensilla through scanning and transmission electron microscopy, in order to contribute new information to the knowledge of the ecological-behavioural role of these antennae and relative sensory structures.

2. MATERIAL AND METHODS

Mature larvae of *Aphidoletes aphidimyza* (Rond.) feeding on *Brachycaudus schwartzi* (Börner) on *Prunus avium* L. (Perugia 10th/07/1987), *Dasineura odoratae* Stelter on *Viola odorata* L. (Perugia, 20th/10/1987), and *Mycodiplosis coniophaga* Winn. feeding on *Puccinia* sp. spores on *Cirsium arvense* (L.) Scop. (Perugia 20th/05/87) were collected in the field and then comparatively investigated in scanning (SEM) and transmission (TEM) electron microscopy. Mature larvae of the species reported in Fig. 1, purposely chosen from M. SOLINAS personal collection, were used for light microscopy observations: specimens were fixed, cleared and mounted on slides according to Gisin's method (1960). For all other purposes, specimens were fixed in Karnowsky's fixative (1965) with 2% Acrolein for 3 hours, washed overnight in cacodylate buffer, postifixed in 1% Osmium tetroxide for 1h 30' and rinsed in the same buffer. Then: for S.E.M. observations, specimens were dehydrated in graded ethanol series, critical point dried, gold coated in a Balzers Union SCD 040 sputter unit, and viewed in a Philips 501B; for T.E.M. observations, specimens were dehydrated in graded ethanol series, block stained with 1% uranil acetate in 95% ethanol solution for 1h (during dehydration process), embedded through propylene oxide in Epon-Araldite. Thin sections obtained by a «Nova» L.K.B. ultramicrotome, sequentially stained with uranyl acetate and lead citrate were examined in a Zeiss EM 109 and/or in a Philips EM 400T.

Behavioural observations were carried out in nature using a stereo microscope.

Explanation of symbols used in the Figs:

AD,	apical end of dendritic sheath
AM,	sensillum «microampullaceum»
AS,	apical sensillum
BS,	basal sensillum
C,	cap of scolopidium (or dendritic cap)
CC,	cap (or attachment) cell of scolopidium
CL,	collar
CR,	ciliary rootlets
CS,	ciliary arrangement of microtubules ($9 \times 2 + 0$ configuration)
CU,	cuticle
D,	dendrite
DB,	dendritic branches
DC,	antennal «dorsal column»
DS,	dendritic sheath
HP,	hypopharinx
MP,	multiporous placoid sensillum
MT,	microtubules
NU,	neuronal units
P,	apical pore
PH,	pharinx
PP,	plate pores
SC,	sheath cell
SL,	scolopale cell
SLS,	scolopale space (i.e. ciliary sinus of scolopidium)
SO,	antennal socket and/or relative supporting prominence
SP,	scolopales
SS,	sensillar sinus
TB,	tubular body

3. RESULTS AND DISCUSSION

3.1 ANTENNAL TOPOGRAPHIC ANATOMY

Most specialists consider the antennae of Cecidomyiidae larvae to be formed by two (exceptionally three: KIEFFER, 1900; and personal observation of M. SOLINAS on a Lestremiinae species from Ecuador kindly sent to him by R. GAGNÉ from Washington) antennomeres (Fig. 1), the first of which is very simple, consisting of a membranous, dome-shaped, more or less swollen prominence (usually reinforced by a light sclerotized, dorso lateral, narrow band sometimes forming a complete ring) not bearing any external sensillum but containing the cellular parts of the sensilla of the second (or third) antennomere, and without any muscular structure. Therefore, the «first antennomere», not having any typical antennal structure, cannot be considered a true antennomere but rather a membranous prominence supporting the antennal socket (torulus).

Consequently, the said antennae consist, as a rule, of a single antennomere that is roughly conical or cylindrical, rising on a more or less considerable prominence, made of a solid part including the base and a sort of column (Figs: DC) dorsally or dorsolaterally embedded and running up to the antennal tip, and a soft part occupying most of the antennal volume and looking like a large multipo-

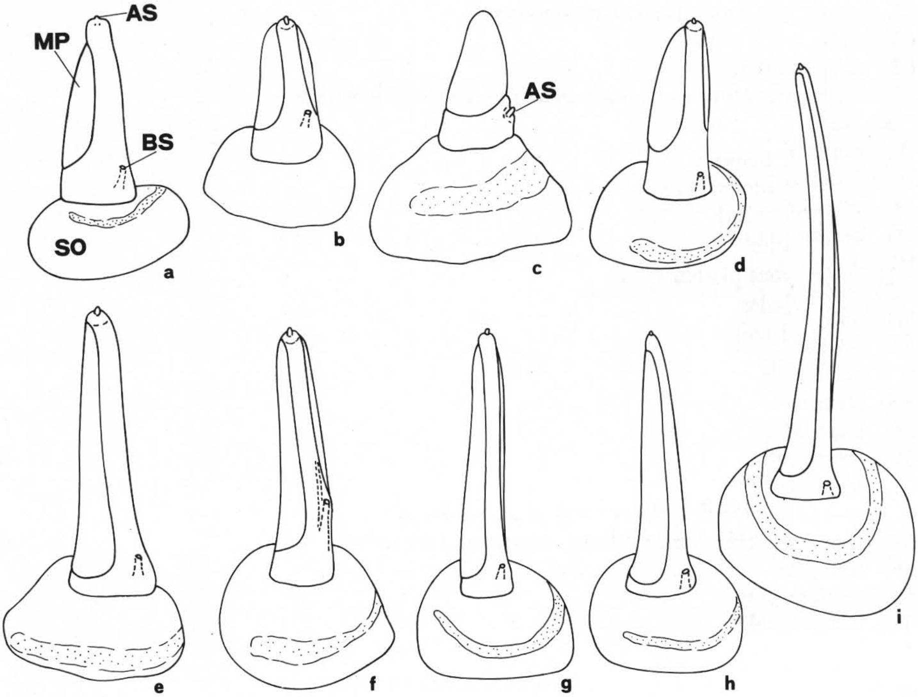

Fig. 1 - «Camera lucida» diagrams of mature larva antennae of: a) *Neolasioptera martelli* Nijvelt; b) *Jaapiella medicaginis* Rübs.; c) *Monarthropalpus buxi* (Laboulb.); d) *Prolasioptera berlesiana* Paoli; e) *Mycodiplosis erysiphes* Rübs.; f) *M. tremulae* Kieff.; g) *Dicrodiplosis pseudococci* (Felt); h) *Aphidoletes aphidimyza* (Rond.); i) *Therodiplosis persicae* Kieff. (a-e, at same magnification; f, g, i, at 80% of ditto, and h at 90% of ditto).

rous placoid sensillum (Figs: MP), as already interpreted (Solinas, l.c.). So far, two other much smaller sensilla have been indicated: a dorsobasal sensillum (BS, Figs 1, 2, 10) looking like a round areola, in light microscopy (Solinas, l.c., Fig. 5), and an apical one (AS, Figs 1, 2, 10) resembling a very minute papilla rising on the antennal tip. In addition, there are two other sensory structures, very difficult (if not impossible) to detect with a light microscope, thus not indicated yet, viz. a dorsointermediate exteroceptor (Fig. 10, AM) and an internal basal proprioceptor, a scolopidium (Fig. 10, CC-SL).

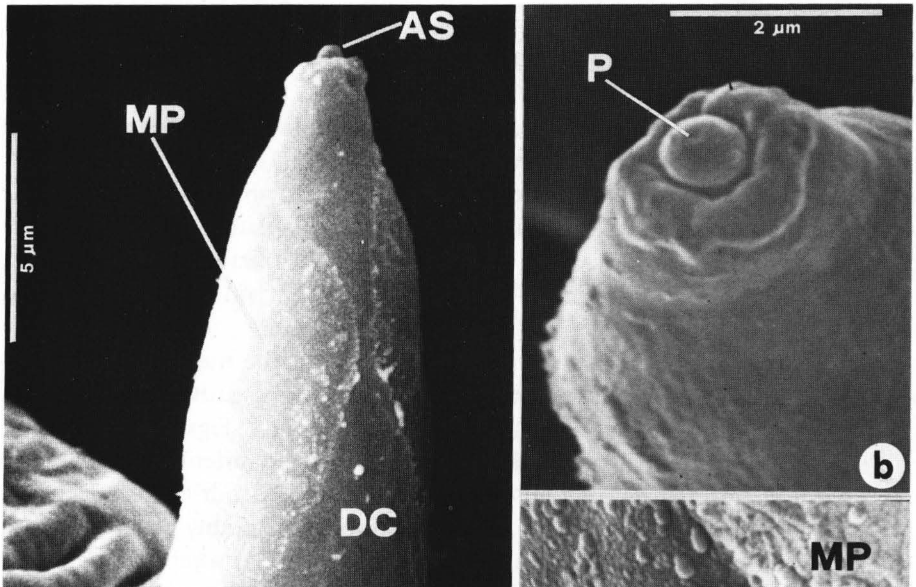

Fig. 2 - S.E.M. micrographs from *Dasineura odoratae* Stelter mature larva: a) whole antenna, dorsal aspect; b) apical view of ditto; c) dorsal, subbasal detail of ditto.

3.2 - ANTENNAL SENSILLA FINE MORPHOLOGY

It is very difficult to obtain good SEM pictures of Cecidomyiidae larval antennae for they almost always collapse, no matter how they have been prepared. Therefore, our SEM observations did not give much more information than light microscopy has given. Our results, essentially reported in Fig. 2 as an example, contribute useful information to topographic anatomy but very little to fine morphology: the antennal structures displayed are almost the same as already known, viz. «dorsal column» (DC), «multiporous placoid sensillum» (MP), «apical sensillum» (AS) and «basal sensillum (BS). Most of our investigation has been carried out through TEM observations and the results are reported below.

Multiporous placoid sensillum (MP)

The cuticular part consists of a relatively large multiporous thin wall (plate) covering most of the antennal surface (MP: Figs. 1, 2, 10). The plate-pores are simple and so minute as to be undectable through SEM observations but, as the single pores remarkably widen inwards like funnels, the plate-porosity can be detected with a phase contrast, high magnification light microscope (cf. SOLINAS, l.c., Fig. 5). However, only TEM observations allow the said pores to be viewed clearly (PP: Figs. 3, 4).

The cellular components are represented by: a) a large number (several dozens) of sensory neurons whose outer dendritic segments, gathered into 9 bundles, or «neuronal units» (*sensu* JEZ e MC IVER, 1980; NU: Figs 3, 7, 8, 9, 10), run through the antennal supporting prominence up to antennal socket. Each neuronal unit, formed by a variable number (3 to 9) of dendrites, is encased in a common dendritic sheath which is relatively thick, remarkably plicate (Figs 3a, 7b, 8, 9a) and terminates at the antennal base (Figs 3c, 7a) where the dendrites singly (D: Figs 3c, 10) enter the antennal shaft and start branching (DB: Figs 3c, 7a, 10). These dendritic branches are almost always moniliform (Fig. 3), each containing one or more microtubules, and, as a whole, almost completely filling the antennal shaft lumen (DB: Figs 3, 4, 5, 10); and b) numerous accessory (sheath) cells (SC: Figs 3a, 7, 8b, 9a) enclosing a single common sensillar sinus (SS: Figs 3, 7, 8) into which they extend long, sparse microvilli and release abundant secretion (sensillar lymph: Fig. 7b). Sensillar sinus and relative sheat cells fill the antennal supporting prominence almost completely (Figs 3, 7, 8).

This kind of sensillum looks very much like the cephalic «dorsal organs» of some brachycerous larvae (R. NARESH SINGH & KUSUM SINGH, 1984), interpreted as (I. HONDA & Y. ISHIKAWA, 1987a) and proven to be (I. HONDA & Y. ISHIKAWA, 1987b) olfactory organs by electrophysiological investigation.

Apical sensillum (AS)

The outer cuticular part is represented by a uniporous minute papilla whose pore lies at the bottom of a tiny apical depression (Fig. 2b) and consists of three short incisions converging in the center (P, Fig. 4: a, b) so as to form a special valve. This sensillum may be proximally shifted in relation to a dorsal column shortening (e.g. in *Asphondylia* spp. and *Monarthropalpus buxi* (Laboulb): Fig. 1c).

There are four sensory neurons whose outer dendritic segments arise at the antennal base (as ciliary arrangement of microtubules denotes in AS, Fig. 7b) and run up together within the dorsal column, being almost entirely encased in a common thick sheath (Figs 3-6) which sometimes also surrounds the single dendrites proximally (AS, Fig. 6: b, c.). Three of the dendrites end free just be-

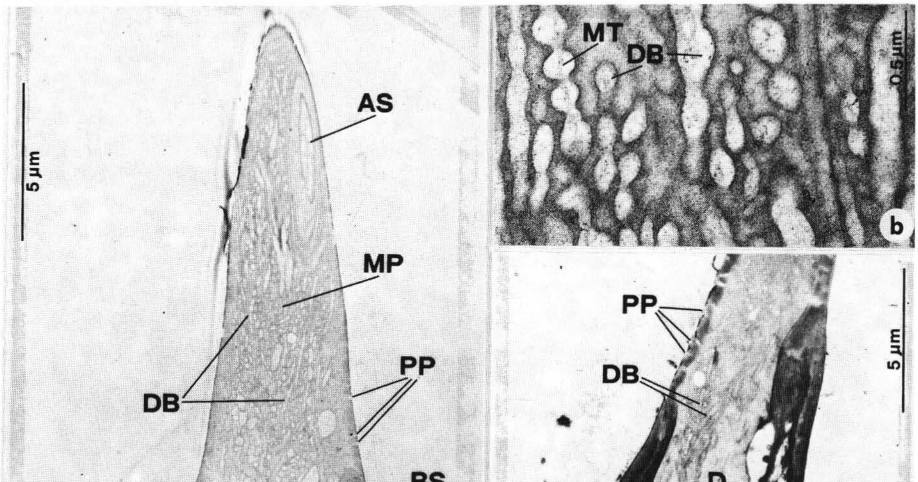

Fig. 3 - Antennal oblique sections from: a) *Aphidoletes aphidimyza*; b) detail of ditto; c) *Mycodiplosis coniophaga* Winn.

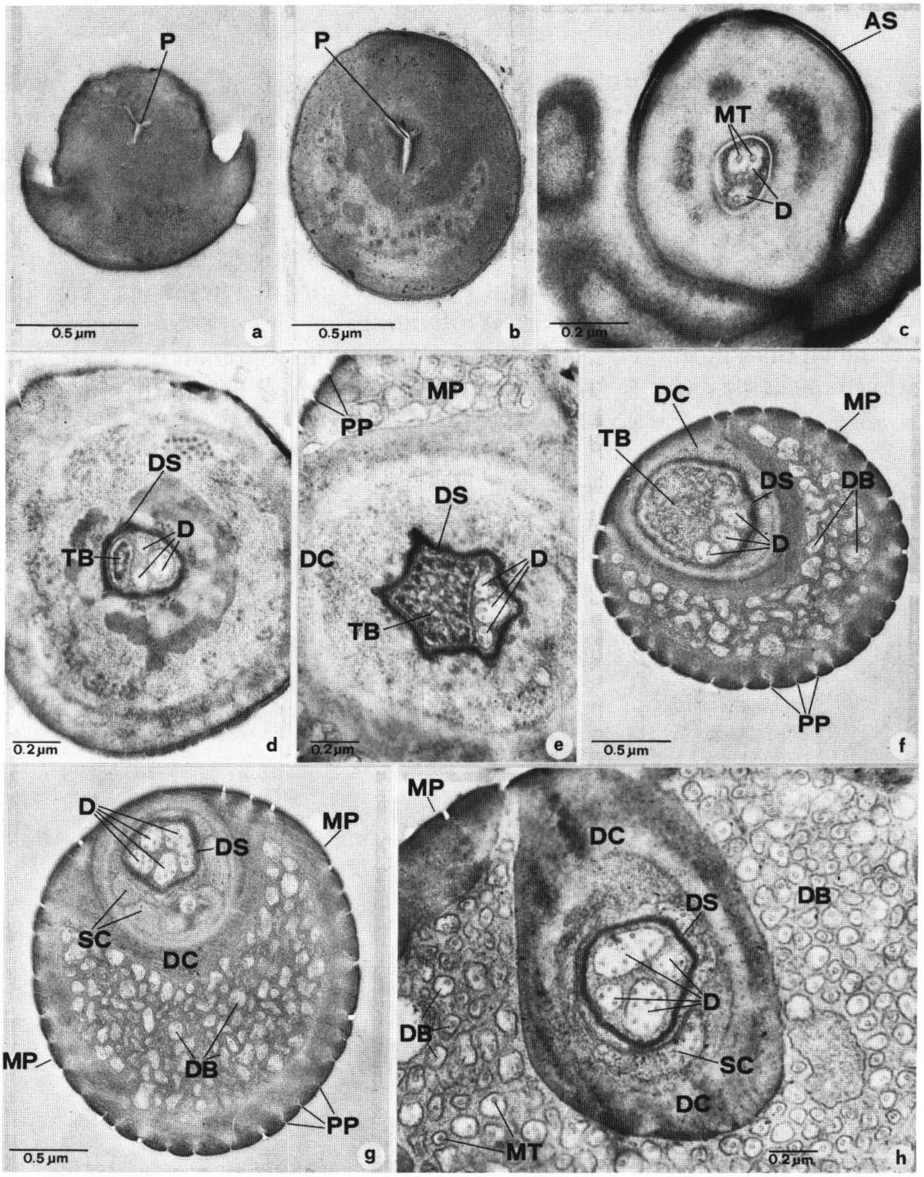

Fig. 4 - Antennal cross sections from: a) *A. aphidimyza* showing the apical sensillum at level A (Fig. 10); b) ditto, a little proximal; c) *M. coniophaga* at level B; d) ditto, at level C; e) ditto at level D; f) *A. aphidimyza* at same level as in (e); g) ditto at level E; h) *M. coniophaga* (a detail) at same level as in (g).

neath the apical pore (Figs 4c, 10), whereas the fourth one terminates first, within the common dendritic sheath, with a relatively big tubular body (TB, Figs 4: d, e, f, 10). The outer accessory cells extend into the dorsal column, accompanying the said dendritic segments up to near the mentioned tubular body (SC: Figs 4, 5, 6) and displaying numerous cystoskeletal elements.

Morphologically speaking, this is a typical gustatory sensillum.

Sensillum microampullaceum (MA)

We have called «microampullaceum» this sensory structure as its cuticular part resembles the flask-like pit of sensilla ampullacea (*sensu* SCHNEIDER, 1964) and because of the exceptionally minute dimensions of the same (AM: Figs 5, 10): having a free aperture about 0.1 μm wide, maximum diameter of the lumen of about 2.5 μm, and length of about 5 μm; but it is relatively thick walled (Fig. 5: b, c, d, h) and obliquely embedded in the dorsal column. At the bottom it tapers to a second opening (about 0.1 μm wide) closed by the distal termination of the single dendrite sheath (AD, Fig. 5: d, e) whose material sometimes partially invades the sensillum lumen (Fig. 5c). In fact, there is a single sensory neuron lying quite deep in the head and whose outer dendritic segment, starting at the antennal base (Fig. 7b) and entirely encased in a very thick dendritic sheath (Figs 5-9), runs within the dorsal column, gradually tapering, up to the cuticular «flask», as above described. It is remarkable that microtubules are usually few (Figs 6d, 7) or become fewer as they approach the dendrite tip (cf Figs 5f with 6b-c). The outer sheath cells are very much like those of the apical sensillum above described and, within the dorsal column, they are frequently connected with them by septate junctions (Figs 5f, 6d).

To our knowledge, this kind of sensillum is a novelty in the fine morphological typology of insect sensilla. In fact, there is a sensory dendrite ending without any known mechanoreceptive (e.g. tubular body) or chemoreceptive (dendritic tip unsheathed) structure at the base of a cuticular hollow structure.

Basal sensillum (BS)

The outer cuticular part consists of an elongate (2-2.5 μm long), inflexible, poreless peg (Fig. 6) having the distal third solid and the rest hollow, set in a pit well fit to prevent any deflection of the peg while allowing air circulation around it.

There are three sensory neurons whose outer dendritic segments start from

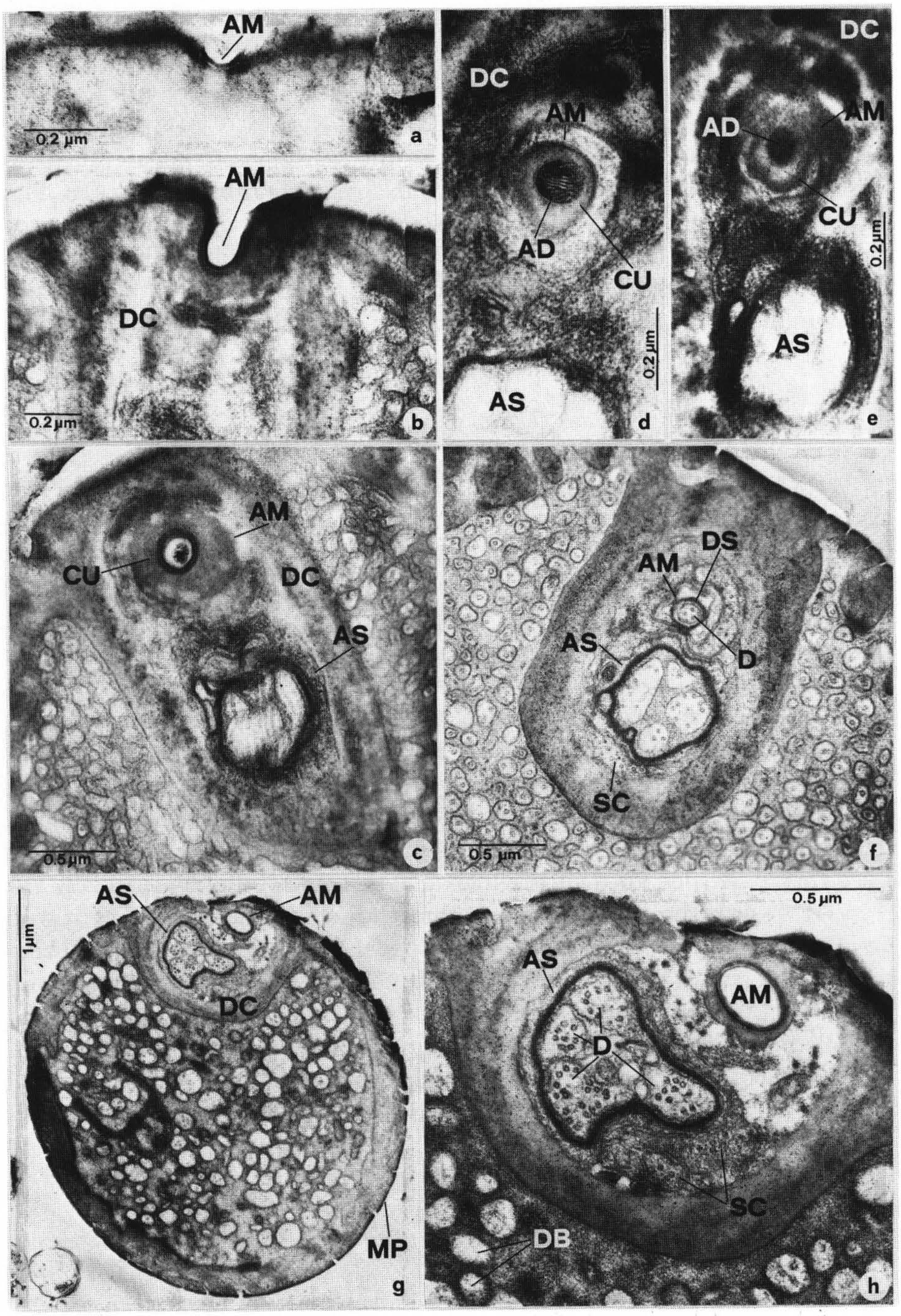

Fig. 5 - Details of antennal cross sections through the sensillum microampullaceum from *M. coniophaga* (a-f): a) at level F (fig. 10), showing sensillum aperture; b) ditto, a little proximal; c) at level G: maximum diameter of sensillum lumen; d) at level H: bottom of sensillum lumen; e) ditto, a little proximal; f) ditto, at level I; g) antennal cross section from *A. aphidimyza* at level G; h) detail of ditto.

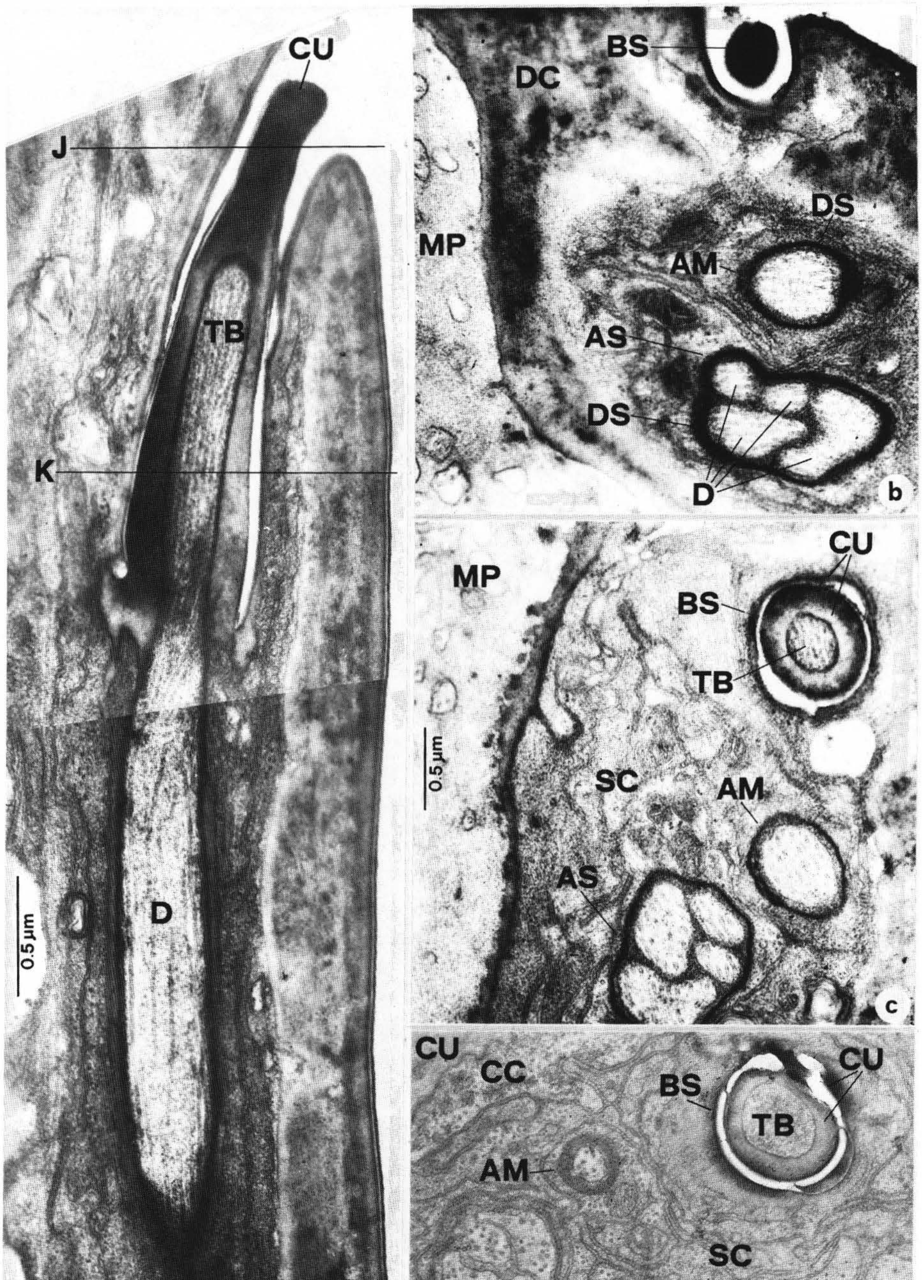

Fig. 6 - Details of antennal sections showing: a) longitudinal aspect of the basal sensillum distal portion, from *M. coniophaga* Winn.; b) cross section of ditto at level **J** (Figs 10, 6a); c) ditto at level **K**; d) ditto from *A. aphidimyza* (b, c, d at same magnification).

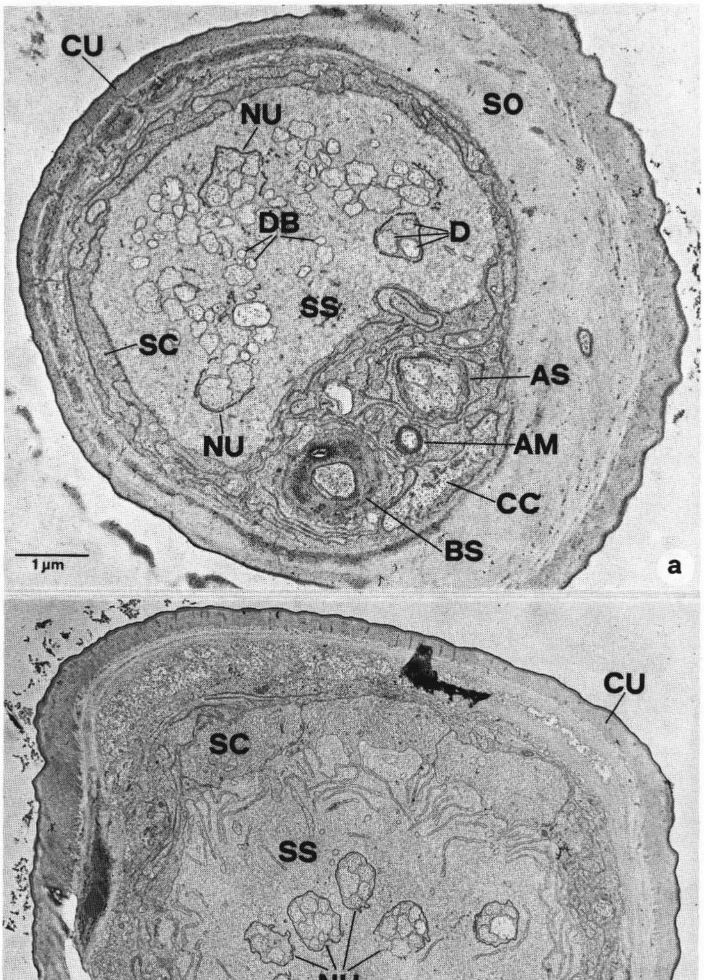

Fig. 7 - *A. aphidimyza*: a) cross section of antennal base (Fig. 10, level L); b) oblique section of antennal socket and relative supporting prominence.

the antennal base (Fig. 9a) and, encased in a common thick sheath (Fig. 7b), run within the solid antennal part to the peg base where two of them terminate at slightly different levels (cf. Figs 7b, 8b) while the third enters the peg lumen, filling it completely and forming a tubular body (Fig. 6a, c, d). The outer sheath cells are very similar to those of the preceding sensillum.

This kind of sensillum corresponds very much, both in cuticular and cellular components, to ALTNER and LOFTUS' (1985) description of «poreless sensilla with inflexible socket», interpreted as hygroreceptors combined with thermoreceptors.

Scolopidium

It is a typical mononematic scolopidium (MC IVER, 1985) distally attached to the inner dorsal wall of the antennal base (Fig. 7a, CC), running almost parallel to the antennal axis through the antennal supporting prominence (Fig. 10), starting from within the head capsule (Fig. 9d-e).

The sensillar components are represented by: a) a single sensory neuron whose outer dendritic segment displays a ciliary arrangement of microtubules (9 × 2 + 0, Fig. 9b-c) for almost full length, while ciliary rootlets run backwards almost to the perikaryon (CR: Figs 9d-e, 10); b) a relatively large scolopal cell (SL: Figs 9, 10) typically rich in longitudinally oriented cytoskeletal elements, most of them running together in bundles called scolopales (SP: Figs 9b-e, 10) which usually meet all together around the wide scolopale space (SLS, Fig. 9b-c); c) an attachment cell (CC: Figs 6d, 7, 9a, 10), also called cap-cell because it produces the cuticular cap (C, Fig. 9a-b), or dendritic cap, to encase the dendritic tip; the said cell displays numerous cytoskeletal elements running radially from cap to attachment area (CC: Figs 6d, 7a, 9b), and also covering the scolopale cell distal portion (Figs 9b, 10).

This scolopophorous sensillum, given its location and attachment above described, strongly reminds us of the Johnston's organ of adult Nematocera antennae, which is a multi-scolopidial structure lying within the pedicellus and serving insect detection of antennal dynamic position. Therefore, we interpret our scolopidium as a Johnston's larval organ reduced to a single functional element.

3.3 - ECOLOGICAL-BEHAVIOURAL INFERENCES

Cecidomyiidae larvae, not only gall makers and inquilines but also free living species like saprophagous, mycophagous and predacious ones, dwell in relatively narrow habitats previously and appropriately selected (though not always to the

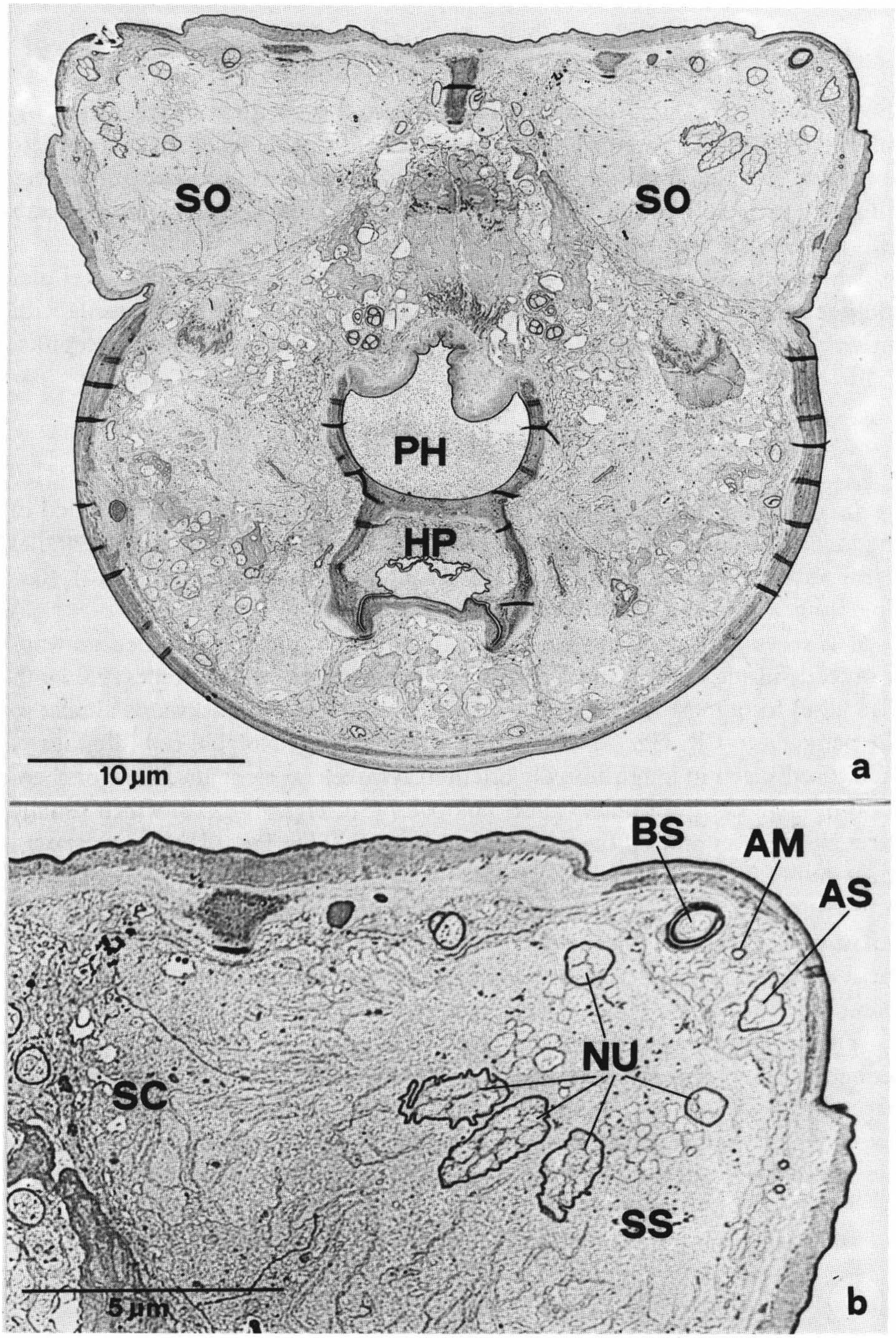

Fig. 8 - *A. aphidimyza*: a) head cross section at antennal socket level; b) detail of ditto.

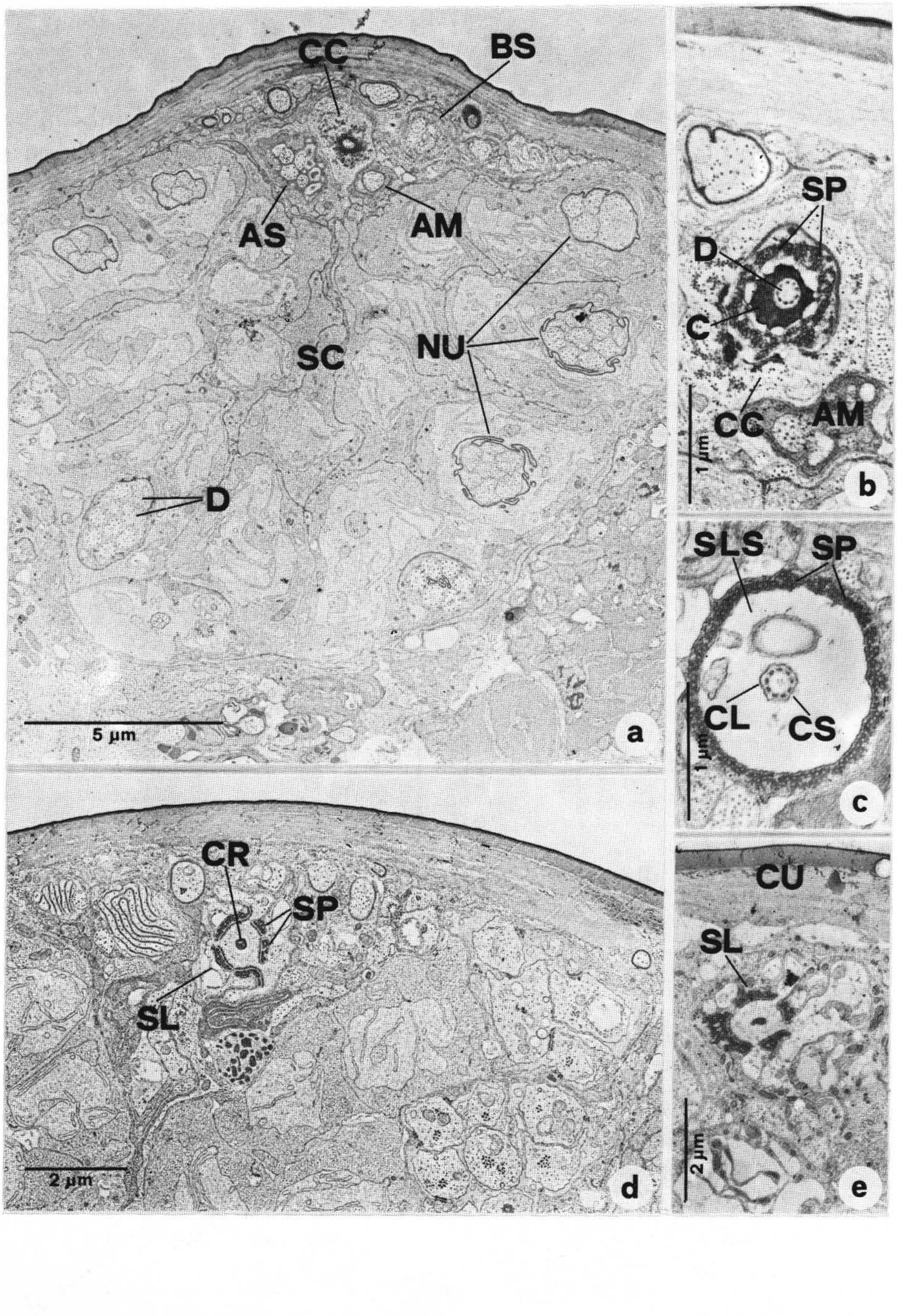

Fig. 9 - Details of antennal supporting prominence successive oblique sections showing: a) a general view of sensilla cross sections at level M (Fig. 10) from *A. aphidimyza*; b), c) successive cross sections of the scolopidium at about level N from *A. aphidimyza*; d) ditto at level O; e) same view as in (d) but from *D. odoratae*.

full extent) by adult females at the respective oviposition times. Furthermore, although the habitats may be very different from one another, the physical environmental conditions needed by the larvae are rather similar; notably common is the need for a high degree of relative humidity throughout the larval life. The

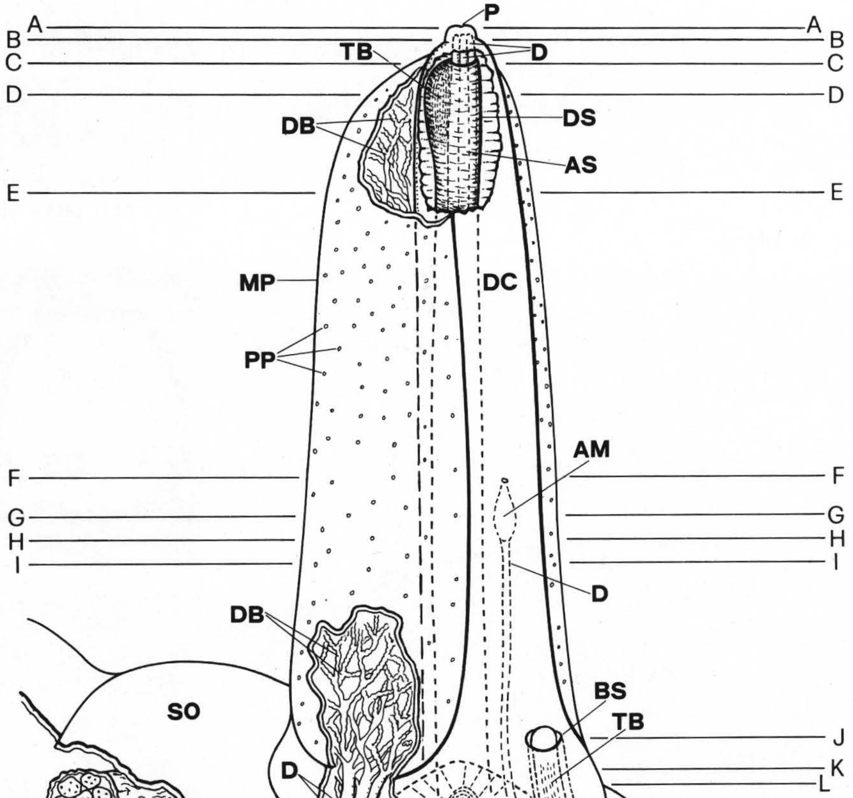

Fig. 10 - Tridimensional diagram of a larval antenna reconstructed through TEM serial sections from *A. aphidimyza, D. odoratae* and *M. coniophaga* (Sheat cells omitted).

kinds of behaviour displayed by the larvae may be also very different in general but, concerning antennal monitoring of the external environment, the larvae behave in almost the same way especially in:

a) keeping themselves within the spatial boundaries of their habitat;

b) moving to a proper place in the ground (when needed) for pupation and/or to overwinter;

c) searching for food.

In performing (a) and (b) the larvae obviously need the same kind of environmental information; also for (c) they require the same type of information but the olfactory structures are expected to be more or less powerful, in proportion to the average distance between larva and food and/or between larva and pupation place.

In fact, the above reported results evidence a wide structural homogeneity among the antennae of Cecidomyiidae larvae with only one important difference between the various ecological-behavioural groups: a different antennal length, that essentially means a more or less large and powerful olfactory organ (Fig. 1).

On the other hand it is well known that:

a) predaceous gall midge larvae like *Aphidoletes, Arthrocnodax, Dicrodiplosis, Lestodiplosis*, etc., and myco-sporophagous ones like *Mycodiplosis*, all of which must search around for food, have much longer antennae than gall dwellers and saprophagous species which usually find food at an obvious, much shorter distance from their mouths.

b) gall forming species whose larvae live very confined and almost immovable, like *Mayetiola* (ROBERTI, 1953) and *Allocontarina sorghicola* (Coq.) (SOLINAS, 1986), display least developed antennae;

c) newly hatched larvae, as a rule, possess relatively longer antennae than the respective successive instars, but, within gall makers, this is true only with species ovipositing and hatching outside the host plant (e.g. *Diplosiola bursaria* SOLINAS, 1965b; *Dryomyia lichtensteini* (F. Lw.) and *Mikiola fagi* Hartig: our personal, unpublished observations) whereas with species ovipositing inside the host plant (e.g. *Monarthropalpus buxi* Laboulb.), as well as with species whose larvae hatch in the same environment where the respective successive larval instars live (e.g. *Contarinia medicaginis* Kff., SOLINAS 1965a; *Dasineura odorata* Stelter and *Gephyraulus diplotaxis* (Solinas): our personal, unpublished observations), newly hatched larvae display antennae relatively as long as the respective successive larval instars;

d) MÖHN (1961) reports that all Cecidomyiinae gall maker larvae have antennae («2. Fühlerglied») secondarily shortened, and in particular, that Asphondyliidi larval antennae are always shorter in the species pupating in the gall than in those pupating in the soil. It is remarkable that MÖHN (1961, 1966) considers both larval antennal lengthening (in zoophagous species) and shortening (in gall makers) as apomorphic characters.

4. CONCLUSIONS

Our aim was essentially to supply a morpho-functional explanation of the ecological-behavioural meaning of Cecidomyiidae larval antennae.

Our results from morphological investigations through light microscopy and scanning and transmission electron microscopy, and from ecological-behavioural observations, all discussed together with published reports on the topics, allow the following conclusions to be made:

a) larval antennae are structurally rather homogeneous among the various, numerous Cecidomyiidae species, especially concerning the single antennomere (formerly, «second» or exceptionally «third»), particularly representing the flagellum;

b) each antenna displays 5 sensilla belonging to as many different kinds:

1 - *multiporous placoid sensillum* (MP), multineuronal, typically olfactory, more or less extended depending on the larva species, in close relation to the antennal length;

2 - *apical sensillum* (AS), papilliform, uniporous, tetraneuronal, typically gustatory;

3 - *sensillum microampullaceum* (AM), very minute, peculiarly shaped, unineuronal, unknown type, unconceivable function;

4 - *basal sensillum* (BS), aporous, inflexible, immovable peg, trineuronal, typical hygro-thermoreceptor;

5 - *scolopidium*, mononematic, unineuronal, interpreted as a Johnston's larval organ reduced to a single functional element.

c) the well known apomorphies consisting both in antennal lengthening (in zoophagous larvae) and shortening (in gall markers) are here explained as convergent adaptations of the range of the antennal olfactory organ to the larval ecological-behavioural needs.

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RIASSUNTO

STRUTTURE SENSORIALI ANTENNALI E RELATIVE INTERPRETAZIONI ECO-ETOLOGICHE NELLE LARVE DEI DITTERI CECIDOMIIDI

Le larve dei Cecidomiidi (Cecidomyiidae) hanno la testa minuscola ma bene strutturata, anoftalma, provvista di antenne relativamente ben sviluppate, in posizione di riposo completamente invaginata nel protorace, donde fuoriesce per esplorare l'ambiente circostante, per gli spostamenti della larva e per l'assunzione del cibo. La morfologia antennale è molto caratteristica, notevolmente omogenea nell'ambito della famiglia e piuttosto semplice, trattandosi di antenne sostanzialmente uniarticolate, apparentemente biarticolate (eccezionalmente triarticolate) per essere il torulo posto alla sommità di una vistosa prominenza membranosa, spesso interpretata, erroneamente, come «primo antennomero». Nonostante le ridotte o ridottissime dimensioni e l'apparente limitazione d'uso, dette antenne risultano sorprendentemente dotate di organi di senso tra i più complessi finora conosciuti: una «placca olfattiva» (Figs: MP) che ricopre in massima parte la superficie antennale; un chemiorecettore apicale di tipo gustativo (AS); un recettore dorsale con apparato esterno assai minuto, di tipo ampullaceo (MA) ma difficilmente interpretabile su base esclusivamente morfologica; un meccanorecettore basale (BS) con probabili funzioni igrorecettiva e termorecettiva; un propriorecettore basale interno, interpretabile come organo di JOHNSTON ridotto ad un singolo scolopidio. Dette strutture sensoriali appaiono nell'insieme idonee ad assicurare alla larva le informazioni ecologiche essenziali per vivere nel suo microambiente. In particolare, lo sviluppo della placca olfattiva risulta strettamente correlato con la maggiore o minore difficoltà per le larve nel reperire il cibo e/o il rifugio idoneo per impuparsi e per svernare.

BIBLIOGRAFIA

ALTNER H., LOFTUS R., 1985 - Ultrastructure and function of insect thermo-and hygroreceptors. *Ann. Rev. Entomol.*, 30: 273-295.

GISIN H., 1960 - Collembolenfauna Europas. Naturwiss. Museum, Geneve.

HONDA I., ISHIKAWA Y., 1987a - Ultrastructures of the larval cephalic sensory organs of the onion and seed-corn flies, *Hylemya antiqua* Meigen and *H. planura* Meigen (Diptera: Anthomyiidae). *Appl. Ent. Zool.*, 22 (3): 325-334.

HONDA I., ISHIKAWA Y., 1987b - Electrophysiological studies on the dorsal and anterior organs of the onion fly larva, *Hylemya antiqua* Meigen (Diptera: Anthomyiidae). *Appl. Ent. Zool.* 22 (4): 410-416.

HOWSE P.E., 1968 - The fine structure and functional organization of chordotonal organs. *Symp. zool. Soc. Lond.* 23: 167-198.

JEZ D.H., MCIVER S.B., 1980 - Fine structure of antennal sensilla of larval *Toxorhynchites brevipalpis* Theobald (Diptera: Culicidae). *J. Insect Morphol. & Embryol.*, 9: 147-159.

KARNOVSKY M.J., 1965 - A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. *J. Cell. Biol.*, 27: 137 A-8.

KIEFFER J.J., 1900 - Monographie des Cecidomyides d'Europe et d'Algerie. *Ann. Soc. Entomol. France*, LXIX: 181-472.

MAMAEV B.M., 1968 - Evolyutsiya galloobrazuyushchikh nasekomykh gallits. «Nauka», Leningrad, 1-237.

MCIVER S.B., 1985 - Mechanoreception. In KERKUT G.A., GILBERT L.I., Eds., Comprehensive insect physiology, biochemistry and pharmacology, 6: 71-132, Pergamon Press.

MÖHN E., 1955 - Beiträge zur Systematik der larven der Itonididae. Zoologica, Stuttgart, 38 (105): 1-247.

MÖHN E., 1961 - Gallmücken (Diptera, Itonididae) aus El Salvador. 4. Zur Phylogenie der Asphondyliidi der neotropischen und holarktischen Region. *Senckenbergiana biologica*, Frankfurt am Main, 42: 131-330.

MÖHN E., 1966 - Cecidomyiidae (= Itonididae). In Lindner E.: Die Fliegen der palaearktischen Region, Stuttgart, Lief. 269.

OTTER G.W., 1938 - On the morphology of the larvae of three species of Cecidomyiidae (Diptera) from Knapweed (Centaurea) flowers. *Trans. R. Ent. Soc. London*, 87, 2: 39-68.

PANELIUS S., 1965 - A revision of European gall midges of the subfamily Porricondylinae (Diptera: Itonididae). *Acta Zool. Fennica*, 113, Helsinki-Helsingfors.

PRINCIPI M.M., 1958 - Ricerche di morfologia e di etologia su di un Dittero Cecidomiide galligeno, la *Putoniella marsupialis* F. Loew, vivente su piante del genere «Prunus». *Boll. Ist. di Entomologia*, Bologna, XXII: 35-68.

ROBERTI D., 1953 - Contributo alla conoscenza delle specie italiane di *Mayetiola* Kieffer (Diptera, Cecidomyiidae). *Boll. Lab. Entom. Agr. «Filippo Silvestri»*, Portici, XII: 98-153.

ROSKAM J.C., 1979 - Biosystematics of insects living in female birch catkins. II. Inquiline and predaceous gall midges beloging to various genera. *Netherland Journ. Zool.*, 29: 283-351.

RÜBSAAMEN E.H., EEDICKE H., 1925-39 - Die Cecidomyiden un ihre Cecidien, *Zoologica*, Stuttgart, XXIX: 1-350.

SCHNEIDER D., 1964 - Insect antennae. *Ann. Rev. Entomol.*, Vol. 9: 103-122.

SINGH R.N., SINGH K., 1984 - Fine structure of the sensory organs of *Drosophila melanogaster* Meigen larva (Diptera: Drosophilidae). *J. Insect Morphol. & Embryol.*, 13 (4): 255-273.

SOLINAS M., 1965a - Studi sui ditteri Cecidomiidi. I. *Contarinia medicaginis* Kieffer. *Boll. Ist. Ent. Bologna*, XXVII: 249-300.

SOLINAS M., 1965b - Studi sui ditteri Cecidomiidi. III. *Diplosiola bursaria* n.g., n.sp. *Entomologica*, II: 55-92.

SOLINAS M., 1968 - Morfologia, anatomia e organizzazione funzionale del capo della larva matura di *Phaenobremia aphidimyza* (Rondani). *Entomologica*, IV: 7-44.

SOLINAS M., 1986 - *Allocontarinia* n.g., *A. sorghicola* (Coq.) n. comb. (Diptera: Cecidomyiidae). *Entomologica*, XXI: 23-35.

SOLINAS M., BUCCI M., 1982 - An ecological investigation into flower galls on *Diplotaxis muralis* D.C. caused by the gall midge *Paragephyraulus diplotaxis* Solinas. *Entomologica*, XVII: 5-22.

WYATT I.J., 1964 - Immature stages of Lestremiinae (Diptera: Cecidomyiidae) infesting cultivated mushrooms. *Trans. R. ent. Soc. Lond.*, 116: 15-28.

ZACHARUK R.V., 1985 - Antennae and sensilla. In KERKUT G.A., GILBERT L.I.; Eds., Comprehensive insect physiology, biochemistry and pharmacology, 6: 1-69, Pergamon Press.