Chapter 2

Morphology and number of sensilla on the antennae and maxillary palps of different sized houseflies, *Musca domestica* L.

Summary

Antennae and maxillary palps of both sexes of the housefly *Musca domestica* L. were investigated using scanning and transmission electron microscopy to determine types, morphology and distribution of olfactory sensory structures. Non-innervated microtrichia were found on all segments of the antennae and on the palps. Mechanosensory bristles were present on the scape, pedicel and on the palp. Several types of olfactory sensilla were present on the funiculus. Trichoid, basiconic, grooved and clavate sensilla are described and counted. In two of the three olfactory pits grooved, striated and conical sensilla were found, in the most proximal pit only clavate sensilla were present. On the palp, only basiconic olfactory sensilla were found. Comparing small and large flies of the same strain, it appeared that the size of the sensilla remained constant, but that the number of sensilla in small flies was lower than that in large flies by a factor larger than the size ratio.
Chapter 2

Introduction

The morphology and distribution of the various types of sensilla present on the antennae and palps have been studied in different species of flies, e.g., face fly (Bay and Pitts, 1976), fruitfly (Venkatesh and Singh, 1984), blowfly (Kuhbandner, 1985), sheep head fly (Been et al., 1988) and cabbage root fly (Ross, 1992). One study compared the external morphology of the sensilla on the antennae of the housefly, *Musca domestica*, and the lesser housefly, *Fannia canicularis* (Bellingham, 1994), but up till now a detailed study of the morphology and distribution of sensilla on both the antennae and the palps of the housefly, *Musca domestica*, has not been reported.

In the present paper we present an inventory of the antennal and palpal sensilla of both sexes of *Musca domestica*. In addition, we compare the size and numbers of these sensilla on flies of different size. Depending on the conditions at which the larvae grow up, last instar larvae and, consequently, the pupae and flies may differ considerably in size. When little food is available or the density of larvae at a food source is very high, the flies are much smaller than those originating from larvae which have grown up under optimum conditions. The latter flies weigh about 3 times more and are about 1.5 times longer than the former. We have investigated which consequences these differences in size may have on the size and numbers of the antennal and palpal sensilla.

Materials and methods

Insects

*Musca domestica* pupae of the WHO strain Ij2 were obtained from the Danish Pest Infestation Laboratory (Lyngby, Denmark). Cultures of the strain were kept in the laboratory at 25°C and 75% RH. Larvae were reared in an aqueous jelly of agar, yeast and skim milk powder (1:5:5 by weight), and allowed to pupate in wood curls on top of the jelly. Two cultures were maintained. In one culture the jelly contained a high density of larvae, from which relatively small flies (6-9 mg wet weight, 4.2-5.5 mm from forehead to abdomen tip) were obtained. In the other culture a low density of larvae was present, from which relatively large flies were reared (16-27 mg wet weight, 6.7-7.8 mm in length). Seven to ten flies of each culture were investigated separately. We preferably used newly emerged flies to minimize damage or contamination of the antennae and palps.

Scanning Electron Microscopy

Flies were immersed in hexane and shaken for several minutes to remove the cuticular
wax layer. Then the antennae and palps were cut and attached to brass holders, using two-component glue. The preparations were coated with gold in a high-vacuum sputtering device and stored in a desiccator until use. The preparations were studied with a Jeol-36C scanning electron microscope. Photographs of dorsal, ventral, lateral and medial sides of the antennae and palps of males and females of each of the cultures were made at 470x magnification. The lengths of the funiculi were measured from the proximal rim to the tip and the lengths of the palps from the basal attachment to the tip. Sensillum density was determined by covering the photographs with a grid, each compartment representing 1000 µm², and counting the number of sensilla in each compartment. Higher magnifications were used to study the morphology of single sensilla in more detail.

Transmission Electron Microscopy
Antennae and palps of hexane-washed flies were cut and fixed overnight at 4°C in 2.5% glutaraldehyde containing 0.1% teepol soap. After 4 times rinsing with cacodylate buffer (pH = 7.2), and postfixation for several hours in a solution of 0.7% osmium tetroxide and 2% potassium bichromate, the specimens were contrasted overnight in 1% uranyl acetate. After dehydration in a graded ethanol series, each specimen was separately embedded in Epon. Sections (about 80 nm thick) were cut with an LKB ultramicrotome, transferred onto single-hole film-coated grids and studied in a Philips 201 or a CM 10 transmission electron microscope.

Results
In rest, the antennae are situated in a cephalic depression (antennal fossa) between the eyes, and consist of a scape, pedicel, funiculus and arista (Fig. 1A). During flight and when probing for food, the antennae are extended, their tip pointing obliquely forward. In this position, the whole surface of the antennae is exposed to the environment. Several structures are distributed over the antennae: microtrichia and grooved bristles are present on the scape and pedicel; microtrichia, trichoid sensilla, basiconic sensilla, grooved sensilla and clavate sensilla cover the funiculus. The arista bears hairlike spines (Fig. 1B).

The palps (Fig. 1A, D) are attached rostrally to the proximal part of the proboscis. In rest, the proboscis is withdrawn in the proboscal cavity, covering the palps except for their tip. The proboscis is extended during probing and feeding. Only then the whole surface of the palps is exposed to the environment. Three types of structures are present on the palps: microtrichia, grooved bristles and basiconic sensilla.
Table 1. Length (± SD) of bodies, funiculi and palps from small- and large-sized houseflies. Differences in body, funiculus and palp length are all significant between small and large flies for both sexes (t-test, P < 0.001, n = 3-6).

<table>
<thead>
<tr>
<th></th>
<th>small</th>
<th></th>
<th>large</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>males</td>
<td>females</td>
<td>males</td>
<td>females</td>
</tr>
<tr>
<td>body (mm)</td>
<td>4.5 ± 0.2 *</td>
<td>4.9 ± 0.4 *</td>
<td>7.1 ± 0.3</td>
<td>7.4 ± 0.3</td>
</tr>
<tr>
<td>funiculi (µm)</td>
<td>356 ± 36 *</td>
<td>403 ± 19 *</td>
<td>479 ± 22</td>
<td>495 ± 41</td>
</tr>
<tr>
<td>palps (µm)</td>
<td>479 ± 46</td>
<td>511 ± 12</td>
<td>605 ± 27 *</td>
<td>766 ± 47 *</td>
</tr>
</tbody>
</table>

* Indicates significant difference between sexes (P < 0.05, n = 3-6).

Houseflies differ in size, depending on the conditions in the larval stage. We reared houseflies from one and the same strain in high larval density to obtain small flies or in low larval density to obtain large flies. In both cultures males were somewhat smaller than females, and so were their funiculi and palps (Table 1). Comparing small with large flies, both the funiculi and the palps were significantly smaller in the former than in the latter for each sex (Fig 1B, C; Table 1). Sensillar densities were determined in both small and large flies. Both sizes of flies bearing the same types of sensilla, we studied the ultrastructure of the sensilla in large flies only.

Surface structures

Microtrichia

The palps and the scape, pedicel and funiculus are covered with microtrichia. They are present in a density of about 0.02 µm² on the palps and 0.05 µm² on the funiculus in males as well as females of both small and large flies. The length of these hairs is 15-26 µm on the palps, 4-40 µm on the pedicel, and varies from 5-12 µm on the top of the funiculus to 9-20 µm on the base of the funiculus. They taper from a 0.6-2.5 µm base to a sharp tip. Two longitudinal grooves run from base to tip (Fig. 2F). Microtrichia are not innervated. They seem to have a channel, the internal opening of which is located above cells with numerous microvilli (Fig. 3A).

Figure 1. A) Frontal view of a female housefly. B) Medial side of the left funiculus from a small fly of about 4.5 mm. C) medial side of the right antenna of a large fly of about 7 mm. D) Medial side of the left palp of a small fly. Sc = scape, Pe = pedicel, F = funiculus, A = arista, af = antennal fossa, Pr = proboscis, P = palp, br = grooved bristle. Bars indicate 100 µm.
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**Grooved bristles**
On the scape and pedicel are longitudinally grooved bristles (10-230 µm in length), arising from a presumably flexible socket (Fig. 1C). Similar grooved bristles (50-450 µm in length) with a base diameter of 3.7-9.4 µm in 4.5-17 µm wide sockets are present in a density of about 6·10^4 µm⁻² on the palps, the longer bristles pointing downwards from the ventral surface (Fig. 1D). The total number per palp is about 30 in small flies to 50 in large flies. 8-12 grooves originate near the base, some of these melting together on their way to the tip. The bristles have a central channel, the diameter of which is less than 1/3 of the thick, unperforated walls.

**Trichoid sensilla**
The density of trichoid sensilla is high at the distal end of the funiculus (up to 3.5·10⁻² µm⁻²) and decreases towards proximal and ventral regions, trichoid sensilla being absent on the most proximal ventral 1/4 of the funiculus. Trichoid sensilla vary in length from about 13 µm at the distal end to about 25 µm at the proximal end of the funiculus in large flies (Fig. 2D, E) and from about 15 to 27 µm from tip to base of the funiculus in small flies. They are curved, their tip pointing to the tip of the funiculus. The curvature of the sensilla at the distal end of the funiculus is more or less constant, but the sensilla at proximal regions show a sharp bend halfway. The trichoid sensilla taper, having a base diameter of 2.5 to 4.5 µm and a blunt tip about 1 µm wide. The cuticle is perforated with pores in a density of about 3 µm⁻² (Fig. 2F). Their walls are relatively thick (about 500 nm at the base and 50 nm at the tip) with 7 nm pores that widen into large 90 nm kettles (Fig. 3D). Cross-sections at the base of the sensillum show 2 or 3 dendrites that branch in the lumen of the sensillum hair, because near the tip up to 11 circular-shaped dendrite-branches are found (Fig. 3B).

**Basiconic sensilla**
These sensilla are slightly tapered in shape. On the funiculus the length of basiconic sensilla varies from 4.5 to 11 µm and their base diameter from 1.3 to 2.7 µm. The shorter ones have a blunt tip (Fig. 2B) and the longer ones a pointed tip (Fig. 2A). Intermediate forms also exist. All these types are present all over the funiculus in both small and large flies. In the lower-magnification photographs, used for determining the density and total number of sensilla, we could not recognize differences in shape of the basiconic sensilla, and therefore we took them together. Basiconic sensilla are most abundant ventrally (19-25·10⁻³ µm⁻²), where they can occur in groups of 2-4 sensilla, whereas on the rest of the funicular surface they occur intermixed with other hairs in a density of about 3·10⁻³ µm⁻².
Figure 3. A) Section through a trichoid sensillum (t), microtrichium (m) and basiconic sensillum (b). Note the difference in thickness of the cuticular wall. B) Cross-sections through the base (bottom) and tip (top) of trichoid sensilla, showing 3 dendrites and 11 dendritic branches, respectively. C) Basiconic sensillum of antenna, showing 2 branching dendrites. Note the many pores in the cuticular wall. D) Longitudinal section through a trichoid sensillum. Arrowheads (<) indicate pores, k = pore kettle, d = dendrite. E) Longitudinal section through a basiconic sensillum. Arrowheads (<) indicate pores, pt = pore tubules, k = pore kettle, d = dendrite. Bars indicate 1 µm in A-C and 100 nm in D and E.
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Figure 4. A) Low section through a grooved sensillum, showing the cuticular sheat (cs) and 3 sections of dendrites (d). B) Grooved sensillum at a higher cross-section showing 2 dendrites in a cuticular sheat (cs). C) Cross-section through the grooved part of a grooved sensillum. D) Cross-section through the top of a clavate sensillum, showing lamellated dendrites and a perforated cuticular wall. Bars indicate 1 µm.

Table 2. Average density of sensilla ($10^3 \text{ µm}^{-2} \pm \text{SD}$) on the funiculi (lateral sides) and palps (distal tip) and estimated total number of each sensillum type on an antenna or a palp.

<table>
<thead>
<tr>
<th></th>
<th>funiculus</th>
<th>palp</th>
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<tbody>
<tr>
<td></td>
<td>Trichoid</td>
<td>basiconic</td>
</tr>
<tr>
<td><strong>small flies</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sensillum density</td>
<td>males</td>
<td>7.2 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>females</td>
<td>7.4 ± 2.4</td>
</tr>
<tr>
<td>total number of sensilla</td>
<td>1000-1200</td>
<td>350-500</td>
</tr>
<tr>
<td><strong>large flies</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sensillum density</td>
<td>Males</td>
<td>9.4 ± 3.6</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>10.0 ± 1.0</td>
</tr>
<tr>
<td>total number of sensilla</td>
<td>1500-2000</td>
<td>530-700</td>
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</table>

* Indicates significant difference between sizes (t-test, P < 0.05, n = 3-5).
# Indicates significant difference between sexes (t-test, P < 0.05; 5 males, 4 females).
Table 3. Types and ultrastructural characteristics of sensilla on funiculi and palps.

<table>
<thead>
<tr>
<th></th>
<th>funiculus</th>
<th>palp</th>
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<tbody>
<tr>
<td>trichoid</td>
<td>12-20</td>
<td>4.5-7.5</td>
</tr>
<tr>
<td>basiconic</td>
<td>4.5-11</td>
<td>1.7-2.6</td>
</tr>
<tr>
<td>grooved</td>
<td>1.5-3</td>
<td>10-14</td>
</tr>
<tr>
<td>clavate</td>
<td>9-11</td>
<td>14</td>
</tr>
<tr>
<td>basiconic</td>
<td>4.5-7.5</td>
<td>1.7-2.6</td>
</tr>
<tr>
<td>length (µm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>basal diameter (µm)</td>
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<tr>
<td>wall thickness (nm)</td>
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<tr>
<td>pore diameter (nm)</td>
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<td></td>
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<tr>
<td>pore kettle diameter (nm)</td>
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<td></td>
</tr>
<tr>
<td>pore density (µm⁻²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>number of dendrites</td>
<td></td>
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</tr>
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</table>

Their cuticular wall is about 70 nm thick at the base of the sensillum and 35 nm at the tip. Figure 3E shows pores 10 nm in diameter, widening into a 22 nm kettle with many pore tubules at the bottom of the pore kettle. The 2 or 3 dendrites that enter the sensillum extensively branch to many irregular forms (Fig. 3C).

The basiconic sensilla on the palps are 4.5-7.5 µm in length and 1.7-2.6 µm in diameter and have a lightly pointed tip (Fig. 2C). They are concentrated on the extreme tip (about 6·10⁻³ µm⁻²) and in a lower density (0.5-3·10⁻³ µm⁻²) below the tip on the distal 1/3 of the palp, the greater part on its ventral side. The pore density in basiconic sensilla on the palp is higher (14 µm⁻²) than in antennal basiconic sensilla (10 µm⁻²). The cuticular thickness is 80 nm, the pores being 22 nm in diameter and the pore kettle 50 nm wide (Table 3).

*Grooved sensilla*

These sensilla are distributed over the whole funicular surface in a low density of about 0.3-2·10⁻³ µm⁻². These small sensilla (1.5-3 µm long, 0.6-1 µm diameter at the base) are characterized by deep, longitudinal grooves in their walls over the distal 2/3 of the sensillum, where they form about 7 finger-shaped ridges (Fig. 2G). TEM-studies show that these sensilla are double-walled. The double wall consists of the cuticular sheath that surrounds three dendrites from deep under the cuticle and the cuticular peg (Fig. 4A). At 1/3 of the peg, the sheath and outer cuticle fuse to hollow, finger-like processions, leaving openings towards the outer environment in the grooves between the “fingers”. Cross-sections of the basal part of the sensillum show two dendrites that are tightly fit in the
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inner lumen (Fig. 4B). In the upper 1/3 of the sensillum the ridges form a stellate configuration (Fig. 4C).

Clavate sensilla
A few sensilla with a club-like shape were found on the proximal part of the funiculus (Fig. 2H). They are about 11 µm in length, characterized by a distal swelling, circa 2.5 µm in diameter, while halfway the sensillum the diameter is about 1.2 µm. Only one cross-section was encountered which showed a wall thickness of 95 nm and pore and pore-kettle diameter of 35 nm and 90 nm, respectively (Table 3). The pore density is comparable to that of the basiconic sensilla. The dendrites are highly lamellated (Fig. 4D).

Olfactory pits
Three so-called olfactory pits are present in the antennae of the housefly (Fig. 5A). Only the olfactory pits of large flies were examined, but the presence of pit-openings also proves their presence in small flies. Two olfactory pits (type I) have their opening near the base of the funiculus, one in the lateral side and one in the ventral side opposite to the point of attachment of the arista. These olfactory pits are 28-35 µm in diameter, consisting of several chambers that contain grooved, striated and conical sensilla. The third olfactory pit (type II) is located ventrally, most proximally inside the funiculus, and its entrance is at the inside of the funnel-like base of the funiculus, near the joint between pedicel and funiculus (Fig. 5A). It has one chamber, 25-50 µm in diameter, and is densely filled with clavate sensilla.

Table 4. Types and ultrastructural characteristics of sensilla located in the olfactory pits of the antennae.

<table>
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<th>olfactory pit</th>
<th>type I</th>
<th>type II</th>
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</thead>
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<tr>
<td></td>
<td>grooved</td>
<td>striated</td>
</tr>
<tr>
<td>length (µm)</td>
<td>2.7-4</td>
<td>3-5</td>
</tr>
<tr>
<td>basal diameter (µm)</td>
<td>0.9</td>
<td>0.9-1.8</td>
</tr>
<tr>
<td>wall thickness (nm)</td>
<td>32</td>
<td>80-?</td>
</tr>
<tr>
<td>pore diameter (nm)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>pore kettle diameter (nm)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>number of dendrites</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>
Figure 5. Olfactory pits and their sensilla. A) Longitudinal section through an antenna showing its inner medial side. Two type I olfactory pits (p.I) are seen, the lower with its entrance. The entrance (e) of the type II olfactory pit (p.II) is located inside the bulge where the funiculus is connected to the pedicel. B) Olfactory pit type I with conical (c) and grooved sensillum (g). C) Olfactory pit type I with striated (s) and grooved sensilla (g). Sensilla the tips of which have been cut off during sectioning, are marked with x. D) Olfactory pit type II, with many clavate sensilla. E) Cross-sections through grooved sensilla, the left one of which has 2 dendrites. F) Cross-section through a striated sensillum with 2 dendrites. G) and H) Cross and longitudinal sections through sensilla clavícula with highly lamellated dendrites. Arrowheads indicate pores in the cuticular wall. Bars indicate 100 µm in A, 10 µm in D and 1 µm in the other graphs.
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**Grooved pit sensilla**

Some grooved pit sensilla resemble the grooved sensilla from the funicular surface in shape and size (2.7 µm length, 0.9 µm diameter, Fig. 5B). Others are longer (4 µm) and the finger-shaped projections are arranged irregularly (Fig. 5C). In cross-section, a stellate form with up to 11 ridges can be found. Two dendrites are present in the lumen (Fig. 5E, Table 4).

**Striated pit sensilla**

These conical structures are 3-5 µm in length, tapering from a base 0.9-1.8 µm in diameter. Fine striations run along the length of the sensillum (Fig. 5C). Two dendrites are tightly fit in the lumen. No pores in the cuticular wall were found (Fig. 5F, Table 4).

**Conical pit sensilla**

Some conical structures with smooth walls were found, tapering from a 1.6 µm base to 2-3.5 µm height (Fig. 5B, Table 4). As no cross-sections were encountered, ultrastructural data cannot be presented.

**Clavate pit sensilla**

These 17 µm long sensilla are present in high density in the type II olfactory pit, their number being about 50 (Fig. 5D). Their distal swelling (3.3 µm diameter) is more pronounced than that of the clavate sensilla on the funicular surface. Sections show a highly lamellated dendrite in the lumen (Fig. 5G, H). The cuticular wall is 150 nm thick at the base and 50 nm at the distal swelling and has many cuticular pores, 36 nm in diameter, widening to a 90 nm pore kettle with pore tubules (Table 4).

Numbers of sensilla in small and large houseflies

The sensillum density of basiconic and trichoid sensilla varies over the funicular surface from rostro-dorsal to proximo-ventral regions. The sensillum density on the lateral side of the funiculus can be assumed to represent an intermediate funicular density, and we used this density to investigate differences between sexes and sizes. We found no significant differences in presence and density of sensilla between sexes of one size, except for a lower density of grooved sensilla in small male vs. female flies (Table 2). Comparing differences in small and large flies, the lateral density of the sensilla on the funiculi of smaller flies was lower than that on the funiculi of large flies, although this difference was not statistically significant for all sensillum types (Table 2). Thus, as small flies had significantly smaller funiculi than large flies, the total number of funicular sensilla was considerably lower in small flies than in large flies. The density of basiconic
sensilla on the tip of the palp was similar in flies of both sizes and sexes. We estimated
the total number of the sensilla for each size of flies from the average number of sensilla
counted on each side (dorsal, lateral, ventral and medial when available) of antenna and
palp, combining results from both sexes (Table 2). Small flies may possess half the
number of sensilla present in large flies.

Discussion

We have classified a variety of sensilla on the antennae and palps of houseflies, the
function of which will be discussed below.

On the scape and pedicel of the antennae only microtrichia and grooved bristles
were found. These structures have no cuticular pores, and therefore they seem to have no
olfactory function. This is supported by the finding that coating the pedicels did not alter
the olfactory responses of Musca domestica (Greenberg and Ash, 1972). We were unable
to confirm the presence of setiferous plaques (with an as yet unknown function), observed
on the pedicel of Musca domestica by Greenberg and Ash (1972). Grooved bristles are
considered to have a mechanosensory function (Been et al., 1988) and are commonly
present on the first two segments of the antennae and on the palps in Diptera.

The funiculus is covered with sensilla, but the arista is devoid of sensory organs
and innervation (Wiesmann, 1960; Lewis, 1971). Liebermann (1926) suggested that the
arista has a protective function to keep dirt from the sensilla on the funiculus, but
Burkhardt (1960) showed that the arista acts like a lever arm, that turns the funiculus
outwards in a stream of air. In this way the Johnston’s Organ in the pedicel is activated,
giving information on airflow dynamics. At the same time the olfactory sensilla on all
sides of the funiculus are exposed to the airflow.

Except for the microtrichia, all hairs on the funiculus are innervated. The trichoid,
basiconic and clavate sensilla have wall-pores and the grooved sensilla have openings in
the grooves. All these sensilla may have an olfactory function, the odours diffusing
towards the dendrites through these pores (Steinbrecht, 1997).

The distribution of receptors found on the funiculus of Musca domestica resembles
what is found in many other flies, e.g. Phormia regina (Dethier et al., 1963), Stomoxys
calcitrans (Lewis, 1971), Musca autumnalis (Bay and Pitts, 1976), Hydrotaea irritans
(Been et al., 1988), Ceratitis capitata (Mayo et al., 1987), Drosophila melanogaster
(Venkatesh and Singh, 1984), Delia spp. (Ross and Anderson, 1987; Ross, 1992), and
Pseudoperichaeta nigrolineata (Rahal et al., 1996). The trichoid sensilla are the most
robust in construction and are present on the most exposed surfaces. The more fragile
sensilla are protected by the larger trichoid sensilla or present at less exposed places of the funiculus (Lewis, 1971). In contrast to other Diptera, in *Musca domestica* no basiconic sensilla were found in the olfactory pits. The type II pit containing clavate sensilla has only been found in *Fannia canicularis* (Bellingham, 1994).

**Trichoid sensilla**

Trichoid sensilla represent the highest number of olfactory sensilla in the housefly and many other Diptera. In moths, trichoid sensilla respond to sex pheromones (Den Otter *et al.*, 1978; Grant *et al.*, 1998), but in mosquitoes these sensilla respond to various odours (Van den Broek and Den Otter, 1999). It is likely that in houseflies trichoid sensilla are also sensitive to various types of substances, because only a few olfactory cells appear to respond to the housefly sex pheromone muscalure and only very few specialist cells were found (see Chapter 3).

**Basiconic sensilla**

Basiconic sensilla are present in different shapes and sizes on the antennae and palps of the housefly. In other flies, several subtypes of basiconic sensilla were described; for instance, 8 types in *Hydrotaea irritans* (Been *et al.*, 1988), 3 types in *Ceratitis capitata* (Mayo *et al.*, 1987), a large and a small type in *Musca autumnalis* (Bay and Pitts, 1976), a blunt and a pointed type in *Delia* spp. (Ross, 1992) and in *Pseudoperichaeta nigrolineata* (Rahal *et al.*, 1996). We also found large and small, blunt and pointed basiconic sensilla (see Fig. 2D, E), but intermediate shapes and sizes were also found, making a clear distinction difficult. In the TEM studies, no differences in basiconic sensilla were found.

The maxillary palps of the housefly only bear one type of olfactory sensillum, the basiconic sensillum. This was also found on palps of *Calliphora vicina* (Van der Starre and Tempelaar, 1976), *Drosophila melanogaster* (Singh and Nayak, 1985) and *Hydrotaea irritans* (Been *et al.*, 1988). These are all Diptera, bearing maxillary palps that do not contact the substrate while the fly is examining the food with the proboscis extended. Therefore, absence of contact-chemoreceptors on the palps is understandable. Odours emanating from the substrate may stimulate the olfactory receptors of palp (and antenna) for on site examining of the food. When the proboscis is retracted, it covers most of the palps, except for the tip. This may explain that the highest density of sensilla is on the tip of the palps. The presence of mechanoreceptive bristles remains unclear as the palps do not handle the food and will only be stimulated by airflow or during the infolding of the proboscis.
Chapter 2

Clavate sensilla
A few sensilla with club-like shape were found. Some authors classified them as a subtype basiconic sensillum (Rahal et al., 1996; Been et al., 1988), but we prefer the name clavate sensilla, in accordance with other authors (Lewis, 1971; Mayo et al., 1987; Ross, 1992). These sensilla house highly lamellated dendrites, as was also found for clavate sensilla in Stomoxys calcitrans (Lewis, 1971) and Delia radicum (Ross and Anderson, 1991). Lamellated dendrites also occur in the knob sensillum of the terminal organ of housefly larvae (Chu and Axtell, 1972) and in coeloconic thermoreceptive sensilla of mosquitoes (McIver, 1982). Some cold receptors seem to be characterized by a highly lamellated dendritic end structure (Altner and Loftus, 1985), and, therefore, clavate sensilla could have a thermosensitive function, as was suggested by Ross and Anderson (1991). Having numerous cuticular pores with pore tubules, an additional olfactory function seems obvious for the clavate sensilla of the housefly.

Grooved sensilla
Grooved pegs were found in many insect species and were called stellate sensilla (Dethier et al., 1963), sensilla styloconica (Been et al., 1988), sensilla coeloconica (Venkatesh and Singh, 1984; Hunger and Steinbrecht, 1998) or double-walled sensilla (Kuhbandner, 1985). Hunger and Steinbrecht (1998) describe spoke channels connecting the central lumen with the grooves through which odour molecules may be transported. We could not confirm the presence of these spoke channels, but we saw some electron-dense material between the “fingers”, as found in the grooved sensilla of Calliphora erythrocephala (Kuhbandner, 1985). In the olfactory pits we found two types of grooved sensilla, small ones with regular “fingers” and longer ones with irregularly set “fingers”. In the olfactory pit of Drosophila, also two types of grooved sensilla were found (Shanbhag et al., 1995), but these differed only in diameter. A combined chemoreception and thermoreception function was proposed for grooved sensilla in Periplaneta americana and Locusta migratoria (Altner and Loftus, 1985). This may also be the case in Musca domestica.

No-pore sensilla
The type I olfactory pits have two types of sensilla without wall pores, the striated and conical sensilla. These also exist in the olfactory pits of Delia radicum (Ross and Anderson, 1991). Unfortunately, no cross-section of the conical sensillum was obtained, so we cannot elucidate its inner structure. The striated sensilla contain two dendrites that fill the lumen almost completely. The ultrastructure resembles that of the no-pore sensillum with inflexible socket that usually contains a triad of a moist air, a dry air and a cold receptor (Altner and Loftus, 1985). The dendrite of the cold cell usually ends
beneath the peg, displaying membrane invaginations (Altner et al. 1978, 1983). Although we did not find sections at this below-peg level, and thus cannot confirm the presence of a triad of hygro- and cold receptors we may assume that the no-pore sensilla have a hygroreceptive function. Hygroreceptors may be stimulated mechanically by swelling of the cuticular wall, as is suggested by the results of Yokohari (1978), who showed that inadequate mechanical stimulation of hygroreceptors affects the firing rate. As in known hygroreceptors (Altner et al., 1983) we find in no-pore sensilla a tight contact of the dendrites with the sensillum wall, inflexibility of the wall by its thickness and lack of socket structures, and a protected position (in pits or covered by other hairs) to prevent mechanical deformation.

Distribution of sensilla

There were only minor differences between males and females in the presence and distribution of the sensilla on the antennae and palps. This might indicate that both sexes of houseflies are sensitive to the same odours (Chapman, 1982).

The number of sensilla differs considerably between large and small flies of the same strain. Chapman (1982) has shown that species size and number of antennal sensilla are correlated, but no studies exist concerning differences in size within one species. One might expect that the total number of sensilla within one species is constant to keep the olfactory sensitivity and possibility of discrimination of different odours at a desired level. This study shows that when larvae are reared at inferior conditions, small adults emerge that have significantly less sensilla. Surprisingly, the density on the antennae of small flies was lower than the density on large flies, which enhanced the difference in total sensillum number. The size of the sensilla shows some variation, but seems to be bound to a certain, genetically determined range, presumably depending on the mechanism of ontogeny of functional sensilla. Within the variation of sensillum size, we found that trichoid sensilla in small flies were even somewhat larger than in large flies. As a small fly has small antennae, less sensilla fit on the surface.

Dethier et al. (1963) claim that axonal fusion is a common feature of the insect sensory system. When this is true, in smaller flies less axons could fuse to keep the total number of axons, projecting to the olfactory lobe the same. However, Strausfeld (1976) counted about 7300 axons in the antennal nerve of the housefly. This fits with our counts of between 5100 and 7500 dendrites in large flies, derived from about 1750 trichoid sensilla with 2-3 dendrites, plus about 650 basiconic sensilla with 2-3 dendrites, plus 100 grooved sensilla with 3 dendrites. The number of dendrites from clavate sensilla and the sensilla from the olfactory pits must be added to get the total number of sensillar dendrites. This total number then is the number of sensory neurons, each of which sends
one axon to the olfactory lobe. Therefore, axonal fusion does not seem to take place in the antennal olfactory system.

We have to conclude that small houseflies are olfactory less equipped, but as houseflies also orient on visual cues and are not dependent on very selective food sources, they may survive and give rise to next generations. When ample food is present for their larvae, the size of the next generation of flies is large again.

References


