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Sense Organs in the Antennae of *Anopheles Maculipennis Atroparvus* (V. THIEL), and their Possible Function in Relation to the Attraction of Female Mosquito to Man.

By I. A. H. ISMAIL.

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I. Introduction.

Mosquitoes are responsible for the transmission of several human diseases. Intensive investigations have been undertaken in many countries on mosquito repellents capable of protecting mankind against these vectors. The repellent substance must not only possess intrinsic repellency; it must be able to offset the attractive stimuli of man. This explains the revival of interest in the nature of the stimuli that attract mosquitoes to their hosts. Research workers in this field have shown that body odour, moisture, temperature and carbon dioxide emanating from the host are the main responsible factors.

For several years the Swiss Tropical Institute has been working on this problem. RAHM (1956-1958) conducted experiments which determined the effect of these factors on the attraction of the female mosquito *Aedes aegypti*.

Once it had been established that these factors did actually have the power of attracting the mosquito, other types of experiments were made with the aim of discovering the sense organs in the insect which receive these stimuli from a considerable distance and guide the mosquito to its host. ROTH (1951), ROTH and

WILLIS (1952) and RAHM (1958) proved that the antennae are the sites of these sense organs.

In order to continue this work and in view of the importance of female anopheline mosquitoes for the transmission of malaria, a study of the morphology, distribution and quantitative record of the sense organs in the antennae of *Anopheles maculipennis atroparvus* (v. THIEL), has been carried out by the author and will be described in the present paper. The study was followed by experiments designed to identify the possible chemo-, hygro- and thermoreceptors by cutting the antennae at different levels and exposing the operated mosquitoes to an air stream loaded with the different factors. The behaviour of the amputated mosquitoes was recorded quantitatively and compared with the distribution and number of the different types of sense organs in the antennal segments.

The author was also anxious to study the sense organs, as well as their distribution and number, in the antenna of the male mosquito in order to obtain a clear picture of the differences in both sexes.

II. Previous Investigations of the Role Played by the Host and the Female Mosquito in the Attraction.

In discussing the attraction of the female mosquito to the host we must remember that the process is twofold. On the one hand, the host emits from his body the necessary stimuli, and on the other, the mosquito receives these stimuli through its sense organs and is directed by the latter towards their source.

A. The host.

It is a known fact that the female mosquito does not approach and attack the host as an act of volition—in a search for food, for example—but because it responds to a number of factors introduced by the host into the environment, each of which might be a stimulus that the mosquito makes use of. These factors can be divided into: 1. Optical factors. 2. Physical factors (heat, moisture, etc.). 3. Chemical factors (carbon dioxide and other volatile substances which we may call “odours”).

1. Optical factors.

As regards guiding the mosquito to the host, optical factors are not of primary importance either in *Anopheles*, which is a nocturnal insect, or even in *Aedes*, which is active in the daytime. It has been proved that mosquitoes are capable of finding man in total darkness. ROTH (1951), by covering the eyes of female *Aedes aegypti* with a layer of shellac rendered opaque with carbon dioxide, found that the eyes are not necessary for locating the host. The experiments of WILLIS (1947) showed that female *Aedes aegypti* and *Anopheles quadrimaculatus* will orient themselves towards an air stream loaded with human body odour in the dark chamber of an olfactometer.

2. Physical factors.

Heat: Attempts have long been made to find the causes which excite the insects to attack. HOWLETT (1910) was one of the first workers in this field. He found that if a test tube filled with hot water is put close to a cage containing

female *Aedes*, it attracts them and incites them to probe the gauze of their cage. HOWLETT believed that temperature was the dominant factor in provoking the attacks of mosquitoes.

Differences in temperature have a considerable effect on the behaviour of mosquitoes. RUDOLFS (1922), by raising the temperature of a tube containing female *Aedes*, noticed that this caused a considerable change in their behaviour. They were most active at about human body temperature and became less active with each degree of additional heat until death resulted at 45-46°C. When an actual blood supplier was used, BROWN (1958) found that warm-skinned Caucasian males attracted on the average 30% more than cool-skinned Caucasian males. Even when one of the hands of an individual was artificially cooled to 22°C and compared to the other hand at its normal temperature of 30°C, the cooled hand was found to be much less attractive than the normal one.

Heat was thoroughly investigated by PETERSON and BROWN (1951). They found that the mosquitoes are attracted when they are reached by a convective heat stream but do not respond to heat radiation.

Moisture: REUTER (1936) studied the part played by this factor on *Aedes aegypti* and *Anopheles atroparvus*. He found that a warm moist strip of filter-paper is attractive, while a moist paper at room temperature attracts no mosquitoes at all. On the other hand, PARKER (1953) mentioned that a moist surface (i.e. moisture alone) exerts a quite definite attraction on female *Aedes*. His findings contradict those of REUTER, as well as CHRISTOPHERS (1947), who also observed that a moist surface alone (at room temperature) exerted no influence on *Aedes*.

Nevertheless, PARKER explained that the difference in results between his experiments and CHRISTOPHERS' lies in the fact that whereas CHRISTOPHERS' experiments were carried out at an ambient temperature of 25°C and a relative humidity of 80-90%, his experiments were done at 28°C and a relative humidity of 50-70%. He suggested that behaviour reactions of this type depend on the precise climatic conditions to which the insect is subjected. Beside the part played by the temperature and humidity of the milieu on the behaviour of mosquitoes, HAUFÉ (1955) showed that the atmospheric pressure takes a part as well in the process (see page 34).

BROWN and co-workers (1951) showed that a slightly heated, moist current of air (85% R.H.), introduced in an olfactometer, attracted 3-5 times as many *Aedes* mosquitoes as a dry one (15% R. H.) at the same temperature, and that a moistened billiard ball was approximately five times as attractive as one with a dry surface. These results were obtained in an experimental room with a relative humidity of 36-65%. But when the relative humidity was raised, the attractivity was reduced, even being reversed at very high room humidities.

BROWN (1951) also noted the importance of the part played by the temperature of the milieu in his field experiments on the effect of moisture. Moisture increased the attractiveness of a warm body two to four times when the air temperature exceeded 15.5°C, while at cooler temperatures, surface moisture decreased in attractiveness.

Water vapour is not attractive at all concentrations. ROTH and WILLIS (1952), working on the hygroreceptors in *Aedes aegypti*, noticed that when the females were given a choice between 0% and 100% R. H., their behaviour was very erratic; the insects were almost continually in flight. This erratic behaviour was thought to be due to the fact that the mosquitoes were attempting to avoid both 0% and 100% R. H. When presented with a choice between 75% and 100% R. H., they chose dry conditions, and when presented with a choice between 0% and 75% R. H., they chose wet conditions.

3. Chemical factors.

The volatile chemical emanations of which the body odour is made up play the chief part in orienting the mosquito from far away to the source of stimuli, while temperature and moisture are no longer of any importance. Flying mosquitoes normally travel upwind, but they take off very much more readily when the wind carries human emanations than when no such stimuli are present. Important observations had been reported by HADDOW (1942). Washed and unwashed native children were placed in similar huts, with all their clothes and personal belongings removed; the boys slept naked in clean blankets. Records of the number of mosquitoes caught both during the day and at night indicated that the unwashed children were more attractive to *Anopheles gambiae*, *Anopheles funestus* and *Anopheles pharoensis*. HADDOW also found that when dirty native clothes were put alternately on successive nights in 1 of 2 empty huts, they were attractive to *Anopheles gambiae* and *Anopheles funestus*.

WILLIS (1954) succeeded in constructing an insect olfactometer for testing the behaviour of mosquitoes. By means of this apparatus he reached the conclusion that it was only the odour in the "arm air" which attracted *Aedes aegypti* and *Anopheles quadrimaculatus*. His experiments were made by passing an air current over a human arm, held inside a cylinder, and then led to a cage containing the mosquitoes. The degree of attraction was expressed quantitatively as compared to that of control currents of air which had not been passed over the skin. The test and control air currents were similar in temperature, humidity, light, sound and velocity. WILLIS also added that carbon dioxide which is excreted in small quantities through the skin, is not the chemical factor that attracts mosquitoes. In addition, the results obtained by RAHM (1956-57) using a different kind of technique on *Aedes aegypti* parallel those of WILLIS concerning the importance of the host odour in the attraction of mosquitoes and the unimportance of carbon dioxide in the process.

The results of these two authors are supported by LAARMAN's experiments (1955) on *Anopheles maculipennis atroparvus*. LAARMAN concluded that the diffusion of odour from epithelia of the lung, skin and mouth is an important element in the attractiveness of the host. But with his type of technique, LAARMAN, unlike WILLIS and RAHM, found that carbon dioxide plays a part in the attractiveness.

We are not going to discuss here in detail the possible effect of carbon dioxide alone as in our experiments no attempts have been made to distinguish between the effect of body odour and that of carbon dioxide on the attractiveness.

Some years ago SCHAEERFENBERG and KUPKA (1951), working together with O. BALLAUS, reported that they had succeeded in separating, from ox blood, a substance called "Blutduftstoff", which is very volatile and exercises a strong attraction on *Culex pipiens* and *Stomoxys calcitrans*. This substance, when diluted 1/2,000 times in water, was 5 times more attractive than pure water. Later SCHAEERFENBERG and KUPKA (1959) demonstrated the chemical nature of this volatile substance. It is a mixture of cysteine, cystine, alanine, glutamic acid, lactic acid, methylamine, dimethylamine, trimethylamine and ammonia. They concluded that the attraction of the insects to the host increases with rises in temperature and in the concentration of the substance from 0.05 to 0.1%. From this they inferred that flying blood-sucking insects would follow a trace of the host smell, carried by the air, until they reach the host itself, where the concentration of the volatile odour is at its maximum.

Recently BROWN and CARMICHAEL (1961) have shown that lysine present in the blood plasma is the most attractive component for culicine mosquitoes; alanine also exerts attraction, but not so strongly.

B. The female mosquito.

The sense organs in the female mosquito which receive the different host stimuli and direct the female mosquito to the source of these stimuli are located in the antennae. ROTH (1951) found that bilaterally antennectomized *Aedes aegypti* and *Anopheles quadrimaculatus* do not react with any sense of direction to an arm placed in their cage. Similar results were obtained when he used temperature as the only stimulus. ROTH added that since in using the arm as a stimulus one is dealing not only with chemical but thermal stimuli as well, it is not possible to conclude that the antennae function as "distance chemoreceptors", although this is highly probable. RAHM (1958), working with *Aedes aegypti*, showed by the type of select experiments that the antennae are the directional chemoreceptors. His female mosquitoes with different antennal segments missing, could not differentiate between a human hand and a moistened warm bottle (artificial arm).

Finally, the experiments of ROTH and WILLIS (1952) on the behaviour of *Aedes* mosquitoes towards airborne vapour have shown that the antennae are also the sites of the water-vapour sense.

There is still one point which we should mention, and which plays an important part in the attraction of mosquitoes to the stimuli—viz., the physiological condition of the individual mosquito. This factor can lead to differences in results between experiments of the same type. On this point VAN THIEL (1937) remarked that it was not strange that out of 100 unselected *Aedes* only a few reacted to carbon dioxide, while in experiments, where mosquitoes were caught on the arm and therefore were in a state of "reaction-preparedness", they reacted more violently.

LAARMAN (1955) wrote about the importance of the physiological condition of the mosquito: "This question may become particularly important when it is found that, at a given moment, certain stimuli do, and at another moment, do not lead to responses".

The writer himself has noticed that female *Anopheles maculipennis atroparvus*, though reared in the same cage and being approximately of the same age, do not all react in the same way. When the hand was put into the cage, it was found that the time required for the mosquitoes to start reacting varied from one individual to another in spite of the fact that they were all in the same state of hunger.

The above discussion can be summarized as follows:

1. Temperature, moisture and the volatile substances (odours) emanating from the body are important factors in the attraction of mosquitoes.
2. The degree of temperature and humidity, to which the mosquitoes are exposed, has a considerable effect on the intensity of their reaction.
3. The attraction of heat and moisture depends on the ambient temperature and relative humidity.
4. The physiological condition of the female mosquito has an effect on its behaviour towards the attracting factors.
5. The antennae of the female mosquito are the sites of the chemo-, hygro- and thermo-receptors which receive the various factors from a distance and guide the mosquito to the host.

III. Material and Technique.

The mosquitoes used in the present studies were exclusively *Anopheles maculipennis atroparvus* (V. THIEL), obtained from the laboratory colonies of the Swiss Tropical Institute.

A. Technique used in the morphological and histological work.

For studies on the morphology and distribution of the sense organs in the antennae, adult *Anopheles* of both sexes were killed with ether and their heads cleared in 10% potassium hydroxide for 24 hours. Then the antennae were separated, washed in distilled water and mounted in Puri solution. They were mounted in between two cover slides in order to be able to examine the antennae from both sides.

For histological examinations the mosquitoes were fixed in Duboscq fluid for 6 hours, dehydrated in alcohol and butyl alcohol, then the antennae were cut off and sectioned 3 to 5 μ thick in paraffin wax (melting point 58°C). Two staining methods were used; Delafield's haematoxylin, counterstained with Erythrosin; and Heidenhain haematoxylin.

All the drawings were made with the help of a drawing mirror, projecting the segments with their sense organs or the sections from the microscope on to the paper in darkness with magnifications of 700 \times and 3,500 \times .

B. Technique used in the experimental work.

Physiological condition of female mosquitoes used in the experiments:

THOMSON (1938), working on *Culex fatigans*, found that in many cases the type and intensity of reactions towards temperature and humidity vary according to whether the mosquitoes are newly emerged, starved or blood-fed. We could confirm this for *Anopheles*. It is thus essential, in order to obtain more or less accurate results in such experiments, to use mosquitoes which are in the same physiological condition. The following precautions were taken to ensure this.

Immediately after the adults emerged, they were fed on honey solution, and about 5 to 8 days later they had one blood meal, which was found to be necessary in order to obtain continuously and regularly the large amount of mosquitoes needed for the experiments. RAHM (1956-58) in his experiments on the attraction of female *Aedes aegypti* employed individuals which had had one blood meal, and they were also quite active towards the attractive stimuli used for test purposes.

The honey solution was removed from the breeding cage for one day. Then, a hand was inserted into the cage and the most active females which landed on the hand and tried to feed were taken away by means of an aspirator. Amputation of the antennal segments followed. The mosquitoes were left to recover from the operation until the next day, when they were used in experiments. On that day, the mosquitoes, aged between 15 and 20 days, had all been starved for two days, and moreover they were in a state of "reaction preparedness"—although the reactions of one group of mosquitoes sometimes showed considerable differences in successive tests (see page 34).

Anaesthetizing and dissecting method:

To immobilize the mosquitoes before amputating various segments of their antennae, we tried at the beginning to use low temperature which had proved effective with *Tenebrio molitor* (PIELOU, 1940), *Drosophila melanogaster* (PERTUNEN and SYRJÄMÄKI, 1958) and *Aedes aegypti* (RAHM, 1958). With our *Anopheles* species, however, it was unsuccessful. The mosquitoes used to recover very quickly before amputation could be completed, and even in the few seconds during which they were immobilized their antennae were not motionless¹. For this reason, we adopted the technique, formerly used by ROTH (1948) on *Aedes aegypti*, of anaesthetizing our *Anopheles* females with carbon dioxide.

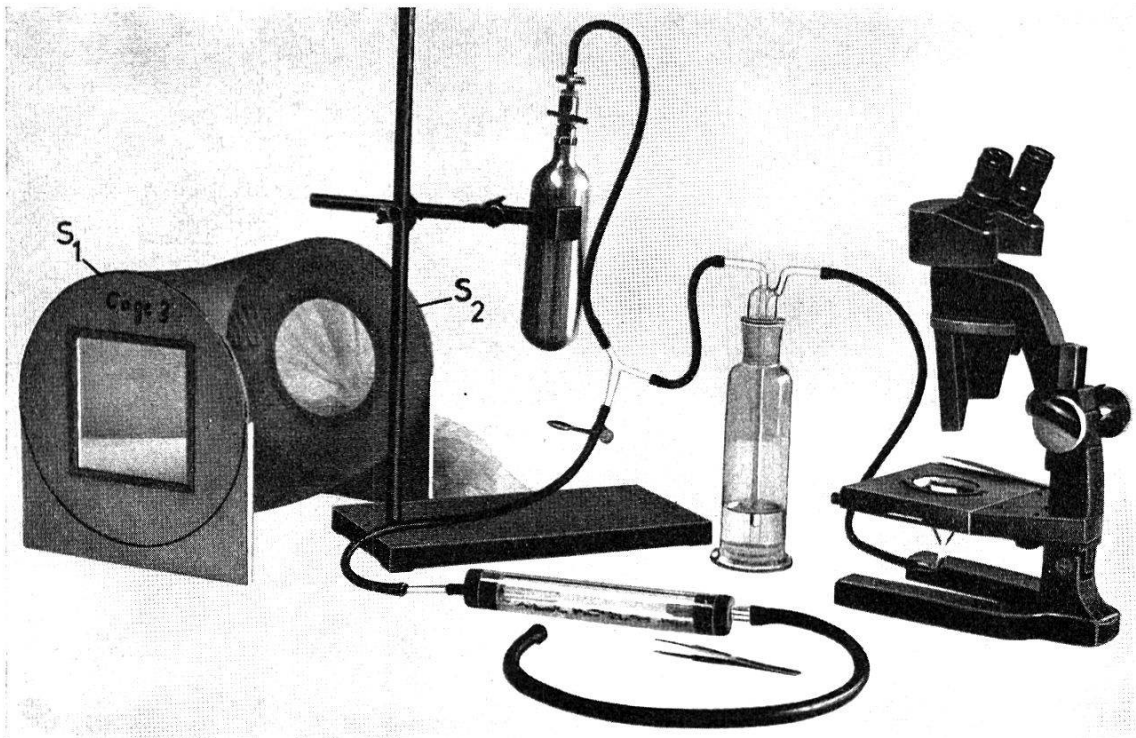


Fig. 1. The anaesthetizing and dissecting apparatus. From the gas cylinder (left) carbon dioxide flows through a rubber tube divided into two lines. One line (at the bottom) leads to the aspirator which contains the mosquitoes, and the second line (at the top) passes through a gas washing bottle (containing water) to the binocular dissecting microscope (right) where the mosquitoes were operated on under continuous anaesthesia. An experimental cage is shown on the left side. S_1 = front base; S_2 = rear base.

The anaesthetizing and dissecting apparatus was made as follows (Fig. 1): The stage of a binocular dissecting microscope was removed and replaced by a wooden plate with a circular opening in the middle. A piece of wire screen was fixed in the opening on which a small square filter paper was laid; a conical funnel was attached underneath the opening. Carbon dioxide obtained from a compressed gas cylinder passed through a rubber tube divided by a "Y" tube into two lines. One line led to the conical funnel after passing through a gas washing bottle which indicated the speed of the gas flow by bubbles in the water, and the other line led to an aspirator containing the mosquitoes. To

¹ Own experiments on immobilizing female *Aedes aegypti* with low temperature gave positive results.

anaesthetize the mosquitoes a pinchcock clamp on the second line was opened to permit a slow flow of carbon dioxide. The anaesthetized mosquitoes were then transferred to the wire screen and the pinchcock clamp was closed. The gas flow was diverted to the other line so that the anaesthetized mosquitoes were completely surrounded by the gas and were under continuous anaesthesia. 30 to 35 mosquitoes were used each time; with a larger number the wire screen would have been overcrowded, and some mosquitoes had to stay longer under anaesthesia, which could have had a fatal effect.

To amputate the different antennal segments, 5 mosquitoes were removed at a time from the wire screen and placed on the white square filter paper. The operation was carried out on them, one by one, with the help of two sharply pointed forceps, used by watch makers. It took only a few seconds to operate on one single mosquito, and when the five had been finished, they were removed and placed in the experimental cage. At the same time, another 5 mosquitoes were taken away from the wire screen without being operated on and put in another similar cage to be used as controls. By treating the control mosquitoes as well with carbon dioxide, we avoid differences in behaviour (if any) due to the effect of the gas. Amputated and control mosquitoes were transferred in their cages to the breeding room where they were kept overnight to recover before being used in the experiments on the next day.

The experimental apparatus:

Our apparatus is in principle the same as the olfactometer described by WIETING and HOSKINS (1939), in which the stimulating factors are carried in an air stream. We also incorporated the modifications of WILLIS (1947) and LAARMAN (1955) for passing the air stream over a part of the host and testing its effect on the behaviour of female mosquitoes. Certain further modifications and simplifications were devised for the purpose of this work.

The apparatus (Fig. 2A) consists of an electric pump (P) drawing outdoor air into the circuit of the apparatus. The air was passed through a cotton filter pad in a flask (FL₁) to eliminate all droplets of oil used for the lubrication of the pump, and its flow was regulated by means of a valve (V) before passing over the palm of the hand (H) in the glass cylinder (C). The hand was fixed by means of a plastic membrane (PM), and the glass cylinder was added only when the chemical stimuli emitted from the hand were needed². The velocity of the air stream was checked by means of a flow-meter (FM) before and during the running of every test. After the air had been checked, it passed through glass helices (GH) in a water bath (WB) with a thermostat, for heating the air stream, and finally it was discharged through a widened glass outlet tube (OT), with an opening of 1.7 cm in diameter into the experimental cylindrical cage (CC) which contained the mosquitoes. When the air had to be moistened, a humidifying flask (FL₂) was inserted in the line; when it had to be dried, a flask with silica gel was inserted. In both cases, the flask was inserted before the flow-meter (FM).

The experimental cage as seen on the left side of Fig. 1 is cylindrical in shape with a length of 30 cm, diameter of 22 cm, and is made mainly out of wire-gauze screen, except for the two bases. The front base (S₁) facing the observer is made of wood with a square glass window measuring 11 × 11 cm in the middle to allow visual recording of the mosquito reactions, while the rear base (S₂), where the air stream enters, is also made of wood, except that the port consists of a

² The hand was washed about 15 minutes before the beginning of each experiment with pure water to avoid any possible external odour.

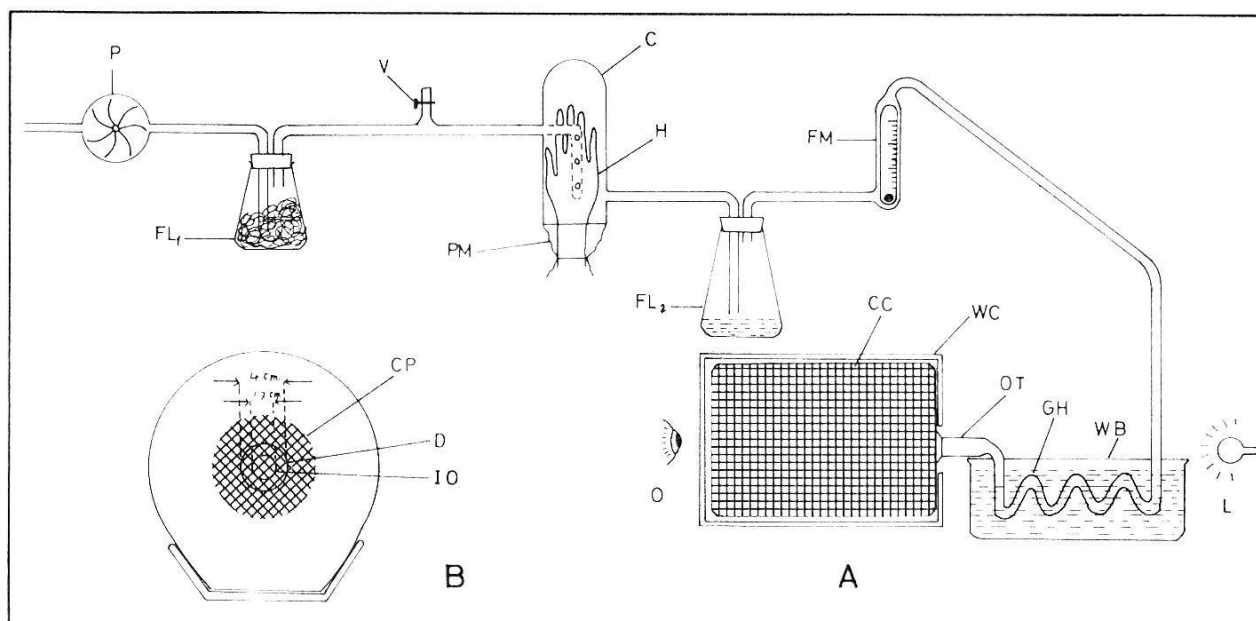


Fig. 2. A. The experimental apparatus. P = electric pump; FL₁ = flask containing a cotton pad; V = valve for regulating the rate of flow; C = glass cylinder; H = hand inserted in the glass cylinder; PM = plastic membrane; FL₂ = flask containing either water for humidifying or silica gel for drying; FM = air current flowmeter; WB = water bath; GH = glass helices; OT = outlet tube; WC = wooden cover enclosing the cage with a glass side facing the observer; CC = cylindrical cage; O = observer; L = lamp of 25 W. B. The aspect of the experimental cage before the outlet as seen by the observer. CP = cage port; D = diaphragm (diameter of 4 cm); IO = air inlet opening (diameter of 1.7 cm).

wire-gauze screen with a diameter of 12 cm. As viewed by the observer (Fig. 2B), the cage's port (CP) has a diaphragm (D) of 4 cm in the centre on which the opening of the outer tube (OT) was fixed (IO) by means of a plastic screw-cap.

During the experiments, the cage with the amputated or control mosquitoes was closed by a well-fitted wooden cover (WC), to eliminate the influence of the observer (O) on the mosquitoes, so that their reactions would be due only to the effect of the experimental factors used. The side of the cover facing the observer was, like the cage, made out of glass for the same purpose of permitting visual recording. A small lamp of 25 W. (L) was placed behind the water bath to illuminate the port and diaphragm.

Our apparatus was constructed for only one line of air stream, instead of two (as used by other authors), in order to enable a single person, who was at the same time using one hand to perform the experiments, to make a more or less accurate record of the mosquito reactions.

As recommended by LAARMAN (1955), a short time was allowed to elapse after the air current had been started and before any observations were recorded; this was done to ensure a steady air current. The air flow was discharged from the outlet against the gauze of the mosquitoes' cage at a constant rate of 3 litres per minute, and the exhausted air escaped through an opening in the top of the wooden cover. The temperature and relative humidity of the air stream were checked at the air outlet before and after the beginning of each test. In all our experiments only two temperature degrees were used: 33.5-34.5°C, which closely approximates to the temperature of the human hand (WILLIS, 1947), and 25-26°C which is equal to the experimental room temperature. To achieve these two degrees at the air outlet, we had to regulate the temperature of the water bath. We invariably found a difference in temperature between the air stream and

the water bath. For this reason the thermostat was constantly regulated. As for the relative humidity, the humidifying flask was set to load the air current with a relative humidity of 75-85%, while the silica gel was used to dry it to 15-25%.

The experiments with certain airborne factors were performed on several groups of mosquitoes, each with a different number of antennal segments missing. The reactions of one single group were studied in a series of 8 experiments which were carried out during the daytime in darkness, using only the small lamp (L) to give the necessary illumination. An interval of one hour was allowed to elapse between every two successive experiments. A single experiment with amputated mosquitoes lasted for 10 minutes and it was always preceded by a control experiment (unoperated mosquitoes) of the same duration. Hence the test consisted of a series of 8 experiments with control mosquitoes and 8 with amputated mosquitoes. Cages containing control and amputated mosquitoes were fixed, each in its turn, in the apparatus at the air outlet.

Sometimes, when many mosquitoes were available, experiments were done by using one control followed by two groups of mosquitoes with different numbers of antennal segments amputated. The number of amputated mosquitoes in every cage varied between 35 and 40, depending on the mortality rate, but the control group always consisted of 40 mosquitoes, those that died being replaced by new ones.

In all our experiments we tested about: 600 mosquitoes in a normal state, 1,600 mosquitoes after amputation and 1,400 mosquitoes as controls. All experiments were carried out in a small room maintained at a temperature of 25-26°C and a relative humidity of 50-60%.

Quantitative recording of the mosquito reactions:

In describing the way we recorded the reactions of the mosquitoes during their attraction to the different stimuli, we should point out that the meaning of the word "attraction" can vary. Since attraction is the result of a number of different reactions, we must bear in mind the difficulty of comparing the respective test results of different authors. But for our type of experiments designed to investigate the attractive function of sense organs receiving the stimuli from a distance, we found that the following two kinds of reactions, used also by LAARMAN (1955), were the most satisfactory:

1. Hovering

Mosquitoes flying towards the air stream outlet, and hovering immediately in front of the outlet.

2. Alighting

Mosquitoes settling on the gauze of the diaphragm, in and around the outlet of the air stream. In most cases, this reaction was followed by typical probing movements.

These two kinds of reaction were measured quantitatively by means of two counters in the hand of the observer. It must be remarked here that this counted number of reactions does not correspond to the number of mosquitoes used, but to the number of hovering and alighting movements of the attracted mosquitoes. In many cases the same individual mosquito was counted more than once, because every mosquito disappearing from the air current in front of the outlet or from the diaphragm and then repeatedly reacting again was counted accordingly.

Mosquitoes which walked from the outside to the inside of the diaphragm were not counted, so as to eliminate the reaction due to the perception of non-directional receptors existing on other parts of the insect body which receive the stimuli when the insect is on or near the source of stimuli (ROTH, 1951 & RAHM, 1958).

IV. The Antennae of *Anopheles Maculipennis*.

It is a well-known fact that the antennae of males and females differ markedly in *Anopheles*. They can be distinguished with the naked eye by the very long fibrillae which exist on the different segments of the male antennae. The flagellar segments in the females are loosely articulated, while they are more closely attached to each other in the males. In both sexes the antenna is made up of 15 segments, comprising a scape, a pedicel and 13 flagellar segments.

1. *The antenna of the female.*

The antenna of the female (Fig. 3) is about 1.6 mm long (average of twelve antennae, minimum of 1.4 mm and maximum of 1.7 mm). The scape is an irregular chitinous ring, connected with a rounded pedicel which measures about $125\ \mu$ in diameter and carries a few scales and short articulated thick-walled sensilla (bristles or spines). Both the scape and the pedicel are darkly pigmented and carry many small, slender microtrichia. These are merely cuticular outgrowths and no innervation to them was seen in the histological preparations.

The first flagellar segment fits into the hollow of the pedicel. It is the longest segment of the antenna, measuring about $200\ \mu$ in length and $43\ \mu$ at its greatest diameter³. It bears scales and various lengths of articulated thick-walled sensilla (bristles or spines) on the whole segment except for a small portion at the base. Like the scape and the pedicel it is darkly pigmented and carries many microtrichia.

The second flagellar segment is the shortest of the flagellum, measuring about $80\ \mu$ in length and $40\ \mu$ in diameter. It carries several short bristles or spines, few thin-walled sensilla and very few microtrichia. It is also darkly pigmented except for a sub-basal colourless ring where long bristles are inserted.

Flagellar segments 3 to 12 are more or less similar to each other, with the segments decreasing slightly in diameter towards

³ Measurements of all diameters were taken at the widest part of the segments.

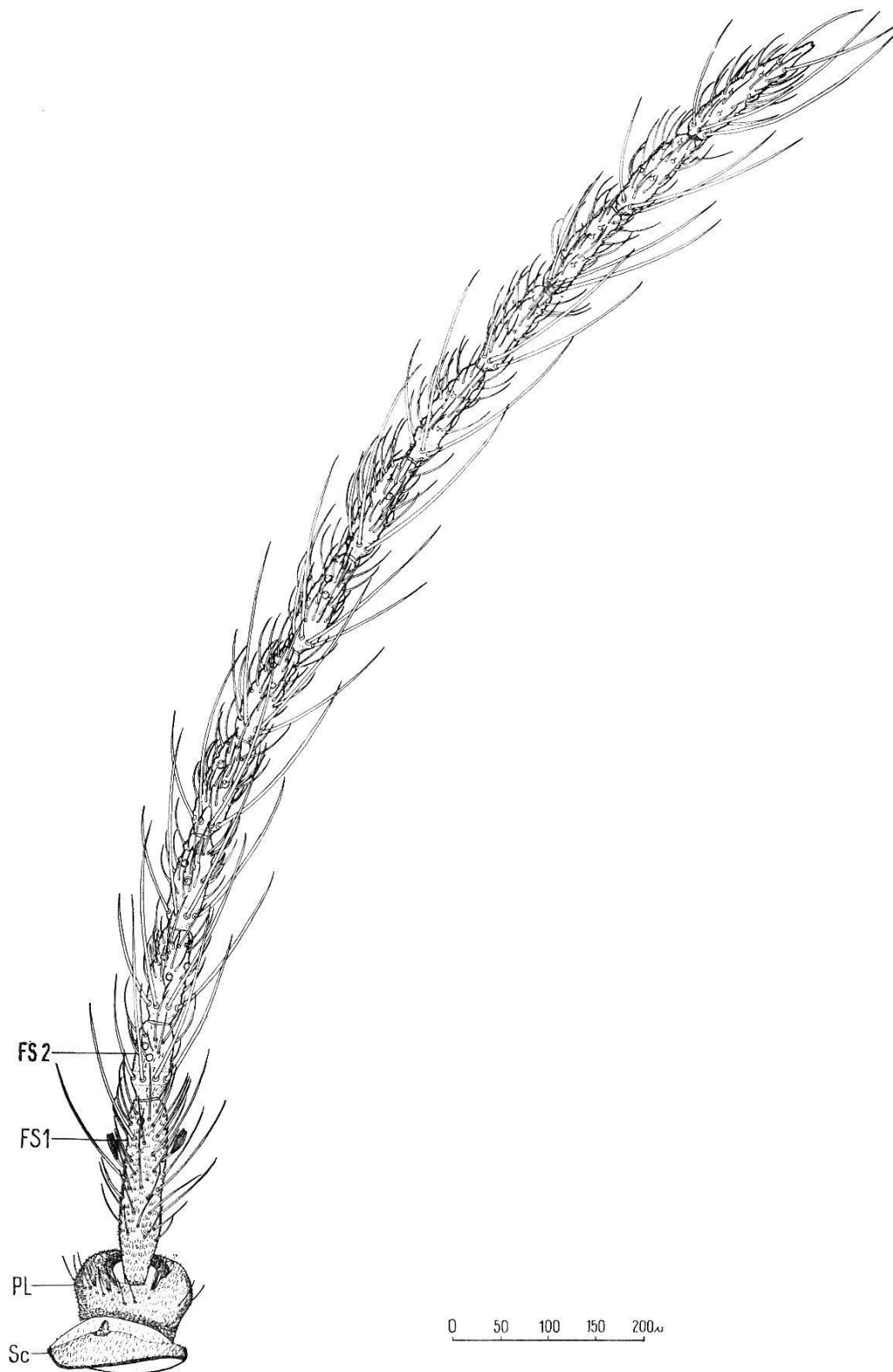


Fig. 3. Antenna of the female *Anopheles maculipennis*. FS1 = first flagellar segment; FS2 = second flagellar segment; PL = pedicel; Sc = scape.

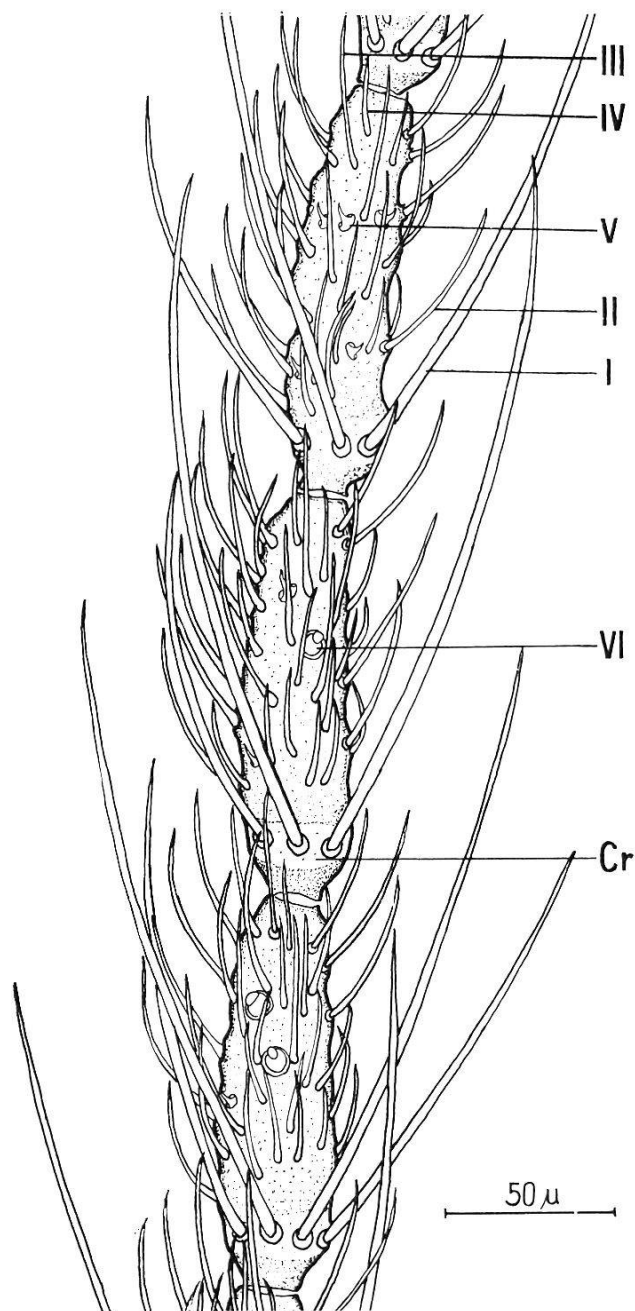


Fig. 4 A. Female flagellar segments 7-9, with the different types of sensilla. I = long bristles (or spines); II = short bristles (or spines); III & IV = trichoid sensilla; V = basiconic sensilla; VI = coeloconic sensilla; Cr = sub-basal colourless ring.

the apex of the antenna, measuring from $40\ \mu$ to $30\ \mu$; their lengths vary between $100\ \mu$ and $120\ \mu$. They carry few small bristles and many thin-walled sensilla.

The last segment is shorter than the first flagellar segment, but longer than any other, measuring about $165\ \mu$ in length and $30\ \mu$ in diameter. It also carries few small bristles and many thin-walled sensilla. The apical end of the segment is branched into two small tips (Fig. 4 C). Near the apex there is a subapical circle of four large bristles.

Each of the segments 3 to 13 (Fig. 4 A) has a sub-basal colourless ring carrying large bristles; their pigmentation is lighter to-

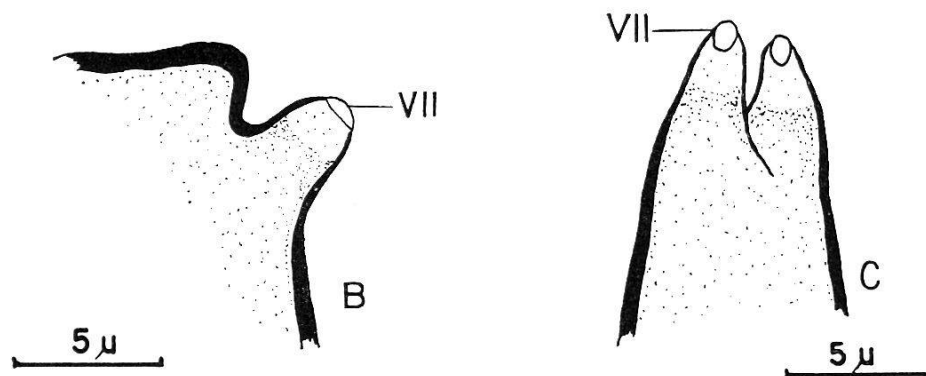


Fig. 4 B & C. B. Lateral view of sensillum type VII at the top of the female flagellar segment 12. C. The apex of the female antenna branches in two tips. Each tip ends with a sensillum type VII.

wards the apex. Occasionally there are articulated feathered bristles on the different antennal segments.

2. The antenna of the male.

The antenna of the male (Fig. 5) is longer than that of the female, measuring about 2 mm (average of twelve antennae, minimum of 1.8 mm and maximum of 2.1 mm). The scape is a narrow irregular ring attached to a greatly enlarged pedicel which measures about 240 μ in diameter. The scape and the pedicel are darkly pigmented and bear many minute microtrichia.

The large size of the pedicel of the male is due to the presence of a very well developed Johnston's organ. ROTH (1948) described this organ in the large pedicel of male *Aedes aegypti*. It is supposed that this well-developed organ in male culicids has an auditory function.

Each of the first 11 flagellar segments has a subapical or nearly medial whorl of numerous very long fibrillae. They differ in length and become shorter towards the apex of the antenna. The part of the segment where the whorl is inserted is somewhat enlarged. The fibrillae extend in all directions; they form a nearly complete ring with two gaps on both surfaces of the antenna. On the first five segments one gap is much wider than the other; both are very small on the subsequent segments. The function of the fibrillae has been investigated in the male mosquito *Aedes aegypti* by ROTH (1948). He says that the induction of male mating behaviour apparently is dependent upon the condition of the fibrillae. The male attempts to copulate when a sufficient number of its antennal fibrillae are extended, making possible the perception of the sound of the flying female.

The first flagellar segment is somewhat longer than the other

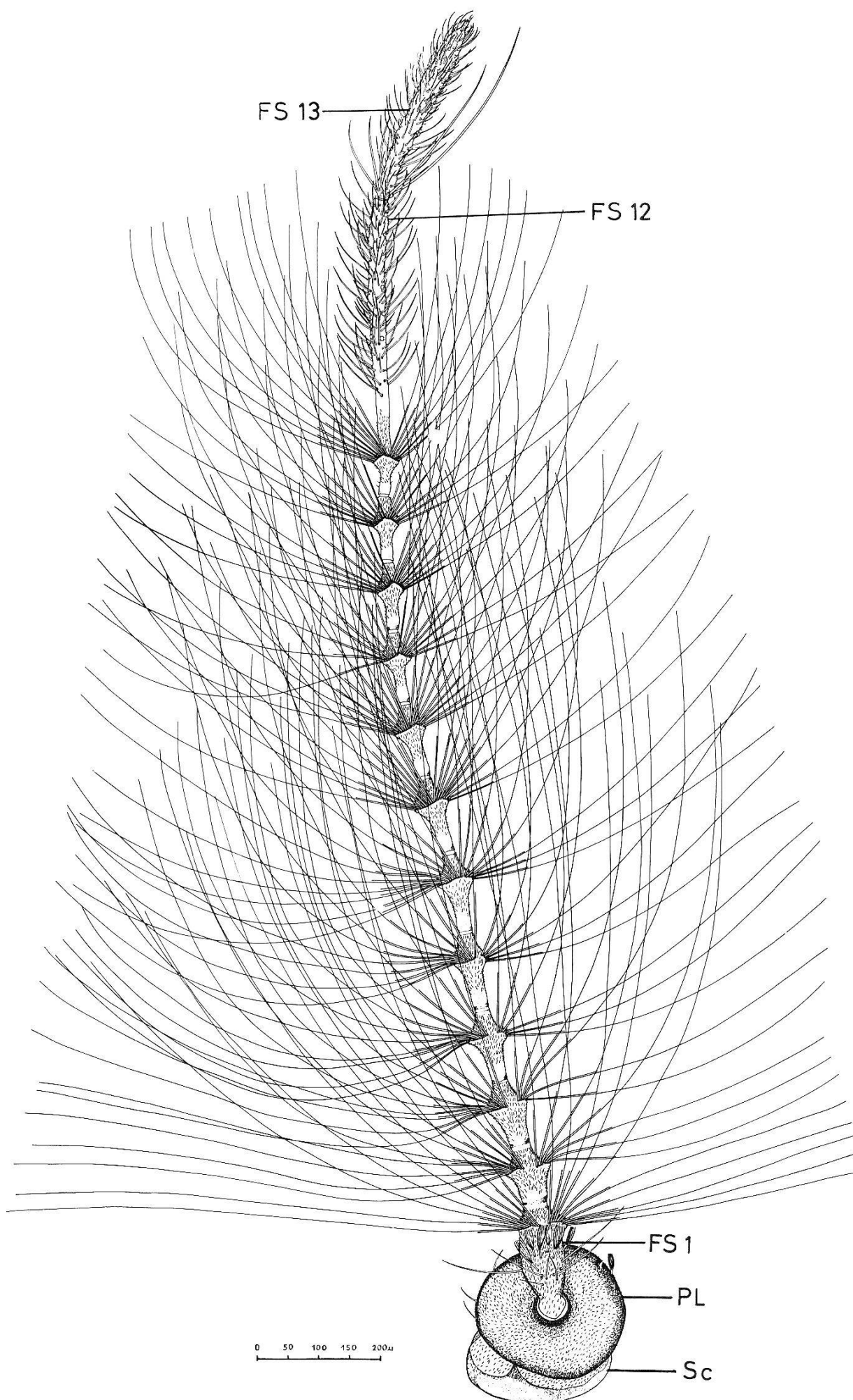


Fig. 5. Antenna of the male *Anopheles maculipennis*. Flagellar segments 1-12 with their whorls of fibrillae. The fibrillae show the same thickness (indicated at their bases in the figure) throughout their whole length. FS 1 = first flagellar segment; FS 12 = flagellar segment 12; FS 13 = flagellar segment 13; PL =

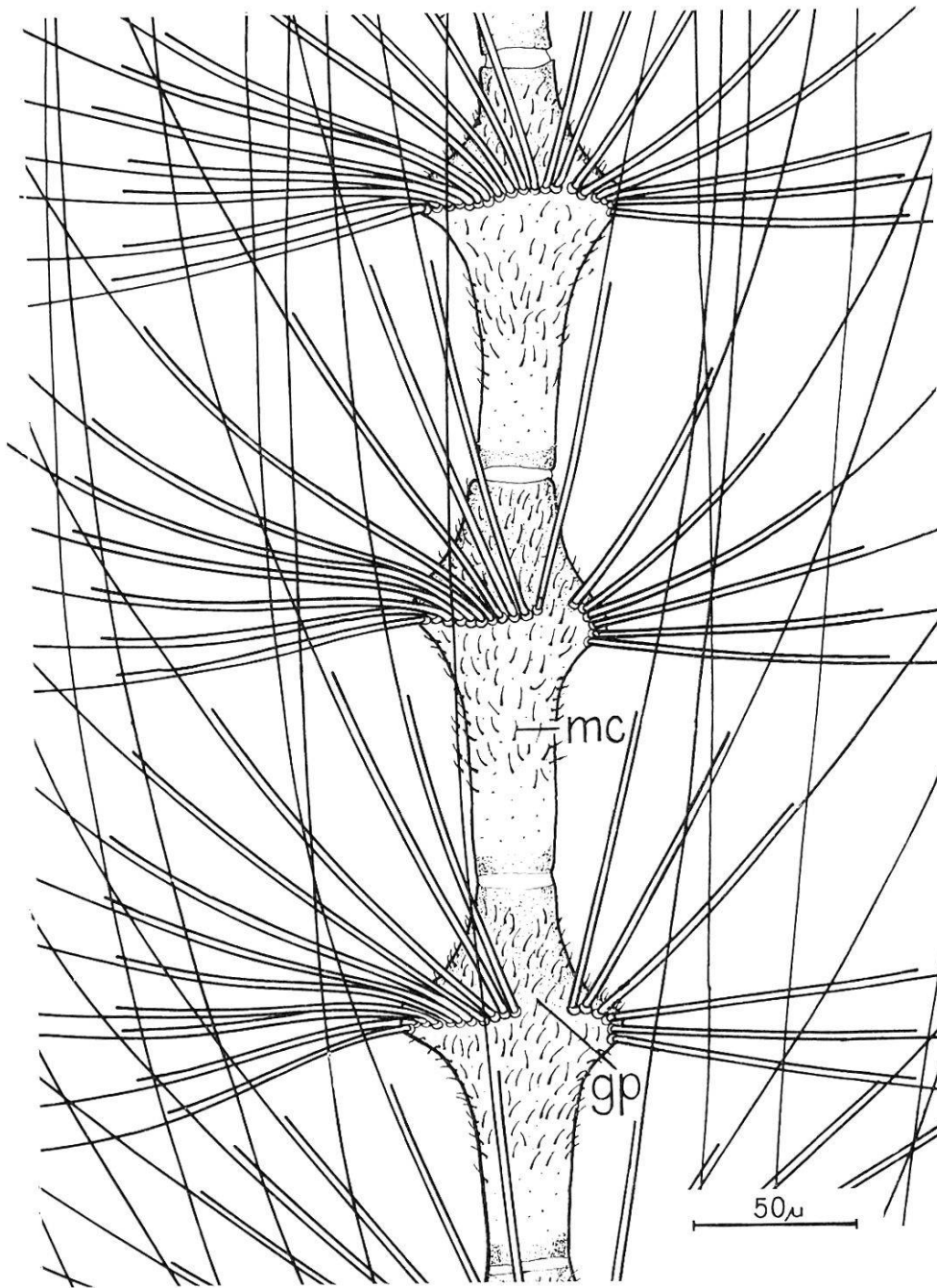


Fig. 6 A. Male flagellar segments 4-6 with their whorls of fibrillae. gp = large gap; mc = microtrichia.

following ten. It is nearly as long as the first of the female and twice as large in diameter. It fits into the hollow of the pedicel and is darkly pigmented except for a small irregular colourless area below the subapical whorl. The pigmented region below this area carries scales and several small and large bristles. The whole segment bears minute microtrichia.

Flagellar segments 2 to 11 (Fig. 6A) are more or less similar, measuring from $95\ \mu$ to $125\ \mu$ in length and decreasing slightly in diameter from $75\ \mu$ to $45\ \mu$ towards the apex of the antenna. They have a pigmented basal ring (very narrow compared with that of

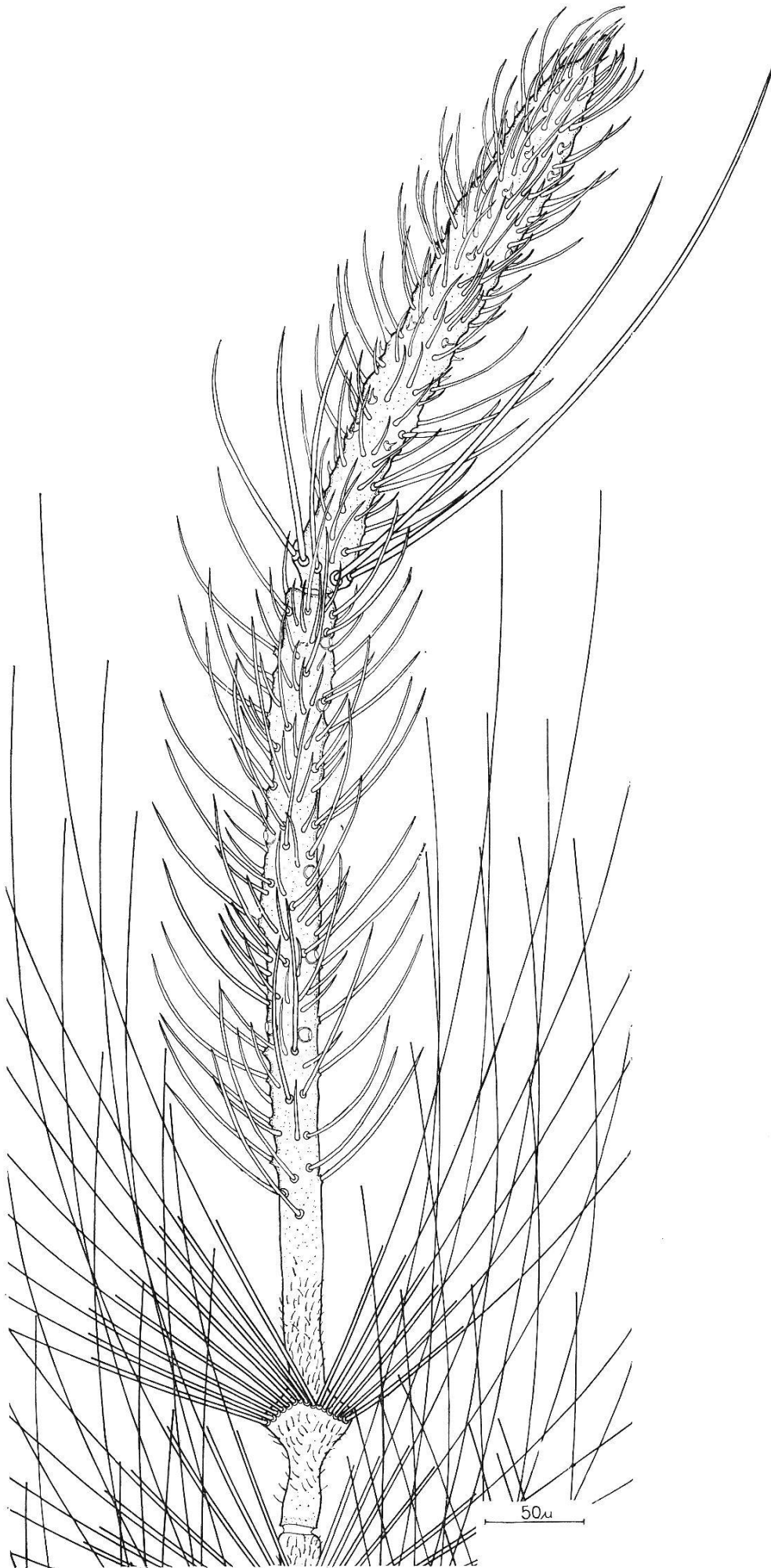


Fig. 6 B. Last two segments in the male antenna with their different types of sensilla.

the first segment), a colourless area below the whorl and a pigmented region above the whorl. Each segment is covered with microtrichia except for a small portion at the base.

The flagellar segments 12 and 13 (Fig. 6 B) differ markedly from the rest. They are comparatively long, about $470\ \mu$ and $315\ \mu$ in length and $30\ \mu$ and $40\ \mu$ in diameter, respectively. Segment 12 has a whorl of fibrillae like segments 2 to 11, but as the apical part is greatly prolonged, the position of the whorl is much nearer to the base of the segment instead of being subapical or nearly medial as in the others. There is a narrow pigmented ring at the base of the segment; between it and the whorl is an unpigmented area with microtrichia. The prolonged region above the whorl is darkly pigmented; it carries many thin-walled sensilla, except for the portion immediately after the whorl which is bare of any kind of sensilla and carries only slender microtrichia. The terminal segment carries few small bristles and many thin-walled sensilla. Similar to the terminal segment of the antenna of the female, it is loosely articulated, darkly pigmented except for the irregular colourless ring near the base which carries large bristles, and ends in two small tips.

V. Morphology and Histology of the Different Types of Sensilla.

Insects possess many different kinds of sense organs. They are defined by SNODGRASS (1935) as being literally "places on the periphery of the animal where forms of energy existing in the environment may activate the form of energy latent in the nerve tissue of the animal". IMMS (1942) wrote, in this connection, that the various and often minute forces acting on the organism need special mechanisms in order to differentiate between them. Such mechanisms are of various kinds and differ according to the nature of the stimuli which they are capable of appreciating. These structures are the sense organs or receptor organs. The simplest types of sense organs are the sensilla.

We found seven different types of sensilla distributed on the 13 flagellar segments of the female antenna (Figs 4 A and B, C). All these types are also found on the male antenna, where, however, they are restricted to the last two segments, except for one type (Type VII) which has two organs on the first segment. Since both sexes possess the same types of sensilla, sections were made only in the female antennae. The morphology and histology of each type are described below and a further chapter is devoted to their number and distribution.

Type I (Long bristles or spines).

Consist of large, rigid thick-walled bristles from 110 to 230 μ long, arising from a distinct socket and ending at the apex in a sharp point. Figs 7 A & B show two cells lying at the base of the bristle; one of these is large, nearly rounded and vacuolated; the other is smaller with no vacuole. They are presumably the trichogen and the tormogen cells respectively. A filament comes from the base of the bristle, swells somewhat and leads to a presumably bipolar sense cell, then the cell narrows again to form the proximal process which runs to the main nerve.

Type II (Short bristles or spines).

Like Type I in structure, having a thick wall, a sharp tip and the same cellular elements. But they differ in being smaller, about 60 μ long, more curved and articulated in a small socket.

Type III (Sensilla trichodea).

Vary in length from 45 to 55 μ , not articulated at the base, curved, having a sharp tip and relatively thin-walled sensilla. At the base (Fig. 8) there is one large cell (presumably the trichogen cell) which extends into the cavity of the seta. This latter is connected by two sense cells through their distal processes which run through the trichogen cell into the cavity. In this type no tormogen cell could be detected at the base.

Type IV (Sensilla trichodea).

They are smaller than the previous type (from 20 to 30 μ long). They are thin-walled structures and lie close to the surface of the antenna. Fig. 9 shows a large cell (trichogen cell), extending in the same manner as in the previous type into the cavity of the seta. A fusiform of about five sense cells gives off very delicate filaments in the form of a cylindrical bundle running into the cavity.

Type V (Sensilla basiconica).

Exceedingly thin-walled, transparent sensilla, small and peg-like (peg organs), about 7 μ long. At the attachment of the peg to the surface of the antenna there is a clear, colourless area in the shape of a ring surrounding the peg. Figs 10 A & B show two large cells at the base of the peg. The tormogen cell appears to embrace the distal end of the trichogen cell. A group of about 7 sense cells is seen to have distal processes as in the last type, forming a cylindrical bundle ending in the cavity of the peg.

At about the middle of the bundle a group of minute, dark-stained bodies (e) is seen. Only two of these bodies were observed in Types III and IV. These bodies have been studied in the wasp by VOGEL (1923), who calls them "olfactory rods" (Riechstäbchen). But SNODGRASS (1935) says that they are so extremely minute that nothing satisfactory can be determined as to their nature or structure. He adds that while they appear to belong to the sense cell processes, it is perhaps possible that the terminal filaments beyond them are cuticular processes to which the cell processes are attached, and that the bodies in question might therefore be cuticular structures themselves.

Type VI (Sensilla coeloconica).

Peg organs sunken into depressions of the antennal wall. The coeloconic sensilla are seen on the surface of the antennae as dark chitinous rings with a nearly rounded aperture inside. Figs 11 A & B show this type of sensilla which has very short pegs, about 5.5μ long with very thin walls. The pit measures about 5μ (without the thickness of the walls) and contains only one peg organ. A thick chitinous wall surrounds the pit from the lateral sides and appears on the surface of the antenna as a dark ring; a thin wall forms the floor of the pit. The abrupt change from the thick to the thin wall is very clearly marked. The wall forming the floor is not on one level parallel to the surface of the antenna, as one half lies deeper than the other; the peg projects between them. There are two cells; one is very large at the base of the pit and darkly stained; the other is smaller, not stained so dark and ending at the base of the peg. These two cells are presumably the tormogen and the trichogen cells respectively. A compact group of about six relatively large cells is seen, their distal processes forming a cylindrical bundle thicker than that of the last type, ending in a terminal strand attached distally by a scolopale to the apex of the peg (Pg). A group of minute bodies (e) lies in about the middle of the distal processes.

This type of sensilla is found on the antennae of many dipterous insects, usually as groups of pegs lying in large pits. SMITH (1919) described a typical sense-pit in the antennae of some dipterous insects: "There is first a somewhat large opening in the chitin leading down into the pit itself; in *Sarcophaga carnaria* this opening is wide and leads abruptly to the sensory processes, but in some species, e.g. certain Muscidae, this opening leads into a long channel lined by chitin which sometimes exhibits spiral or convoluted folds or even a series of communicating ridges like basket-work (*Musca domestica*). The floor of the pit consists of a very thin

chitinous membrane which is produced into the sensory processes much in the same fashion that fingers arise from a glove". SMITH found a mass of radiating cells beneath the floor of the pit; each one is connected with a sense process. In agreement with many scientists, he says that these cells are themselves nervous elements, although BERLESE and others assert that this is a mistaken view and that they are glandular, while the nerve fibres run between them and the cells secrete a fluid which fills the sensory processes; passes through the chitin to the exterior and bathes the whole surface of the pit. PACHARD also says that these sensory processes are filled with a serous fluid and are definitely olfactory in function, but SMITH has never been able to find any trace of this fluid. HSÜ (1938) also found pits in the antennae of the fly *Calliphora erythrocephala*, either in the form of simple cavities or divided into several compartments. In each cavity or compartment there are numerous sensory processes, concentrated in the centre. He says that the number of sense cells seems to be variable as he sometimes found three and at other times five, but four was the usual number.

Type VII (Sensilla campaniformia).

The sense organs of this type are similar to sensilla campaniformia described by SNODGRASS (1926, 1935), which were also called organs of Hicks, papillae, cupola organs, dome organs, umbrella organs, bell organs, and sense pores. Externally (Fig. 4 B), they appear (laterally) as very small swellings on the surface, which measure about $4\ \mu$ in length and $3\ \mu$ in diameter. Great care was needed to find these organs as at the beginning it was difficult to distinguish them from the bristle sockets. MCINDOO (1918) faced the same difficulty when he searched for these organs, which he called "olfactory pores", in the tibiae of various species of Diptera.

The basal half of the external part of the organ is pigmented in the same manner as the surface of the antenna, while the upper half is less pigmented. The apex has the shape of a bell and lies totally above the surrounding chitin. It consists (Fig. 12 B) of a very thin outer lamella of the cuticula (a) and of an inner layer of clear, soft chitin (b). A cuticular structure in the form of a cylinder (c) is present in the middle of the organ, with a small aperture at the top and closed at the bottom except for a small portion, penetrated by a scolopale. The scolopale (Sp) is darkly stained, cylindrical, somewhat expanded towards the distal end and tapering to an acute point which lies within the opening of the cylinder in the layer (b) of the bell. The sense process (Fig. 12 A) runs out from the cylinder through the distal end of a very long, large cell; it is

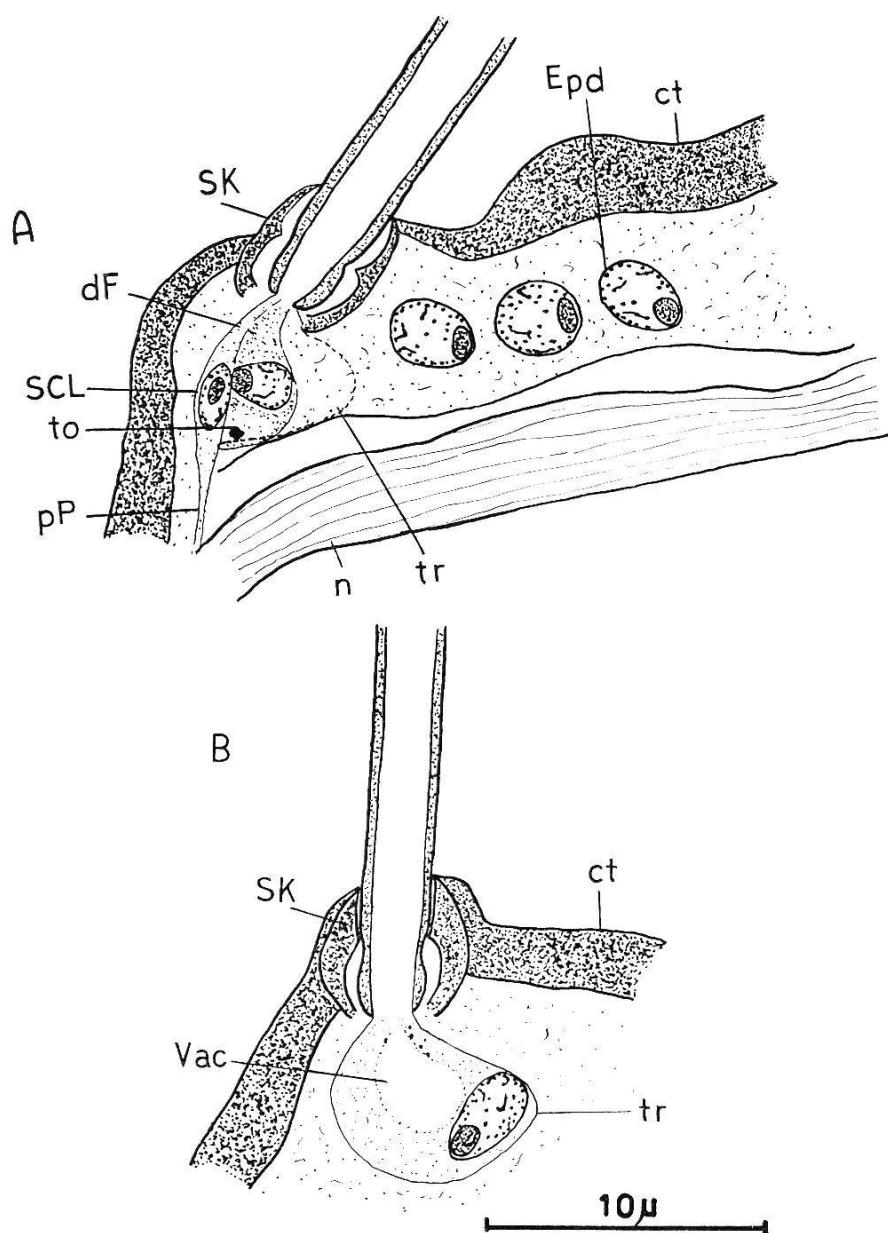


Fig. 7. Sensillum type I (long bristles or spines). A. Section of a sensillum with the sense, tormogen and trichogen cells, the latter drawn in dots to show the tormogen cell below. B. Section with only the trichogen cell.

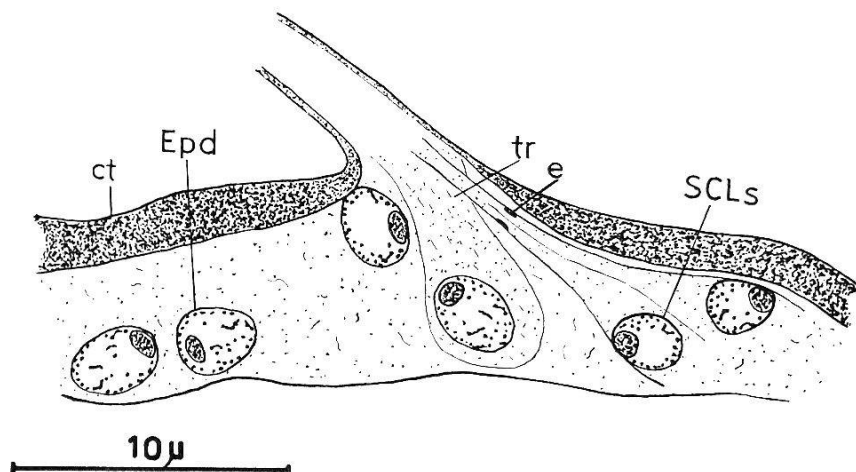


Fig. 8. Section of a sensillum type III (trichodea).

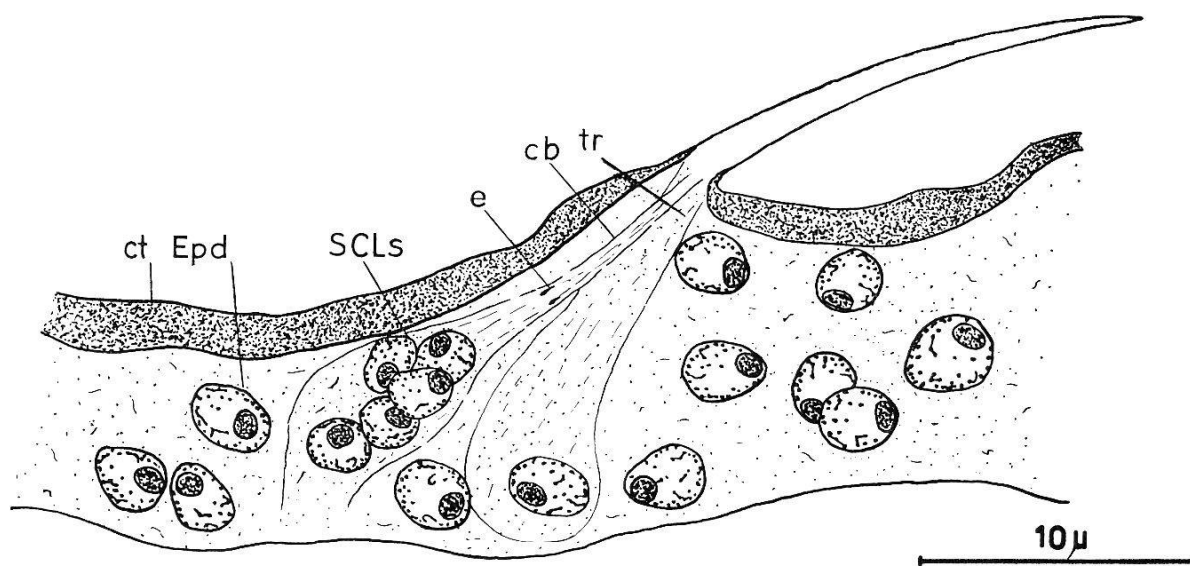


Fig. 9. Section of a sensillum type IV (trichodea).

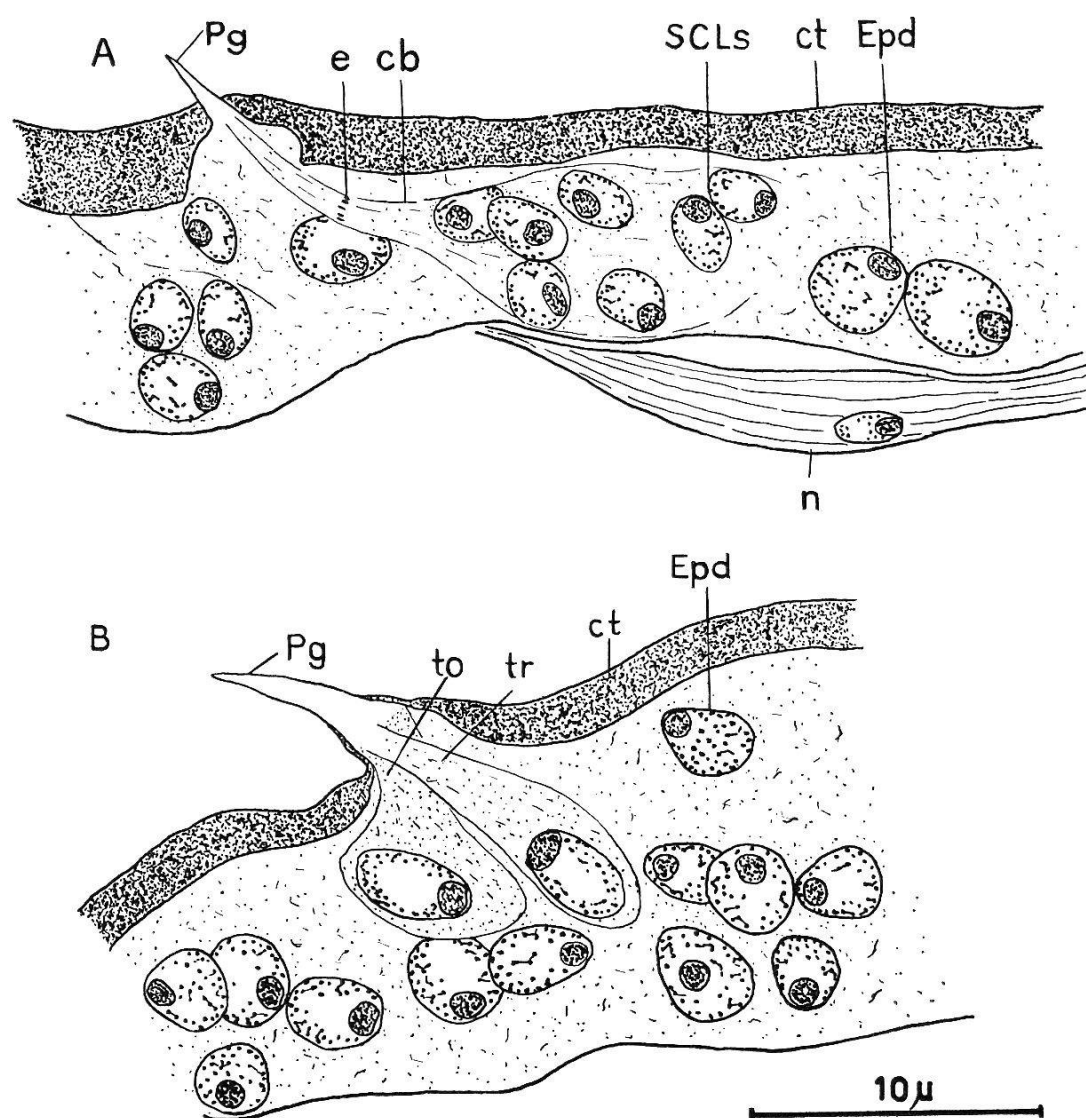


Fig. 10. Sensillum type V (basiconica). A. Section with the sense cells and a part of the peg. B. Section with the tormogen and trichogen cells.

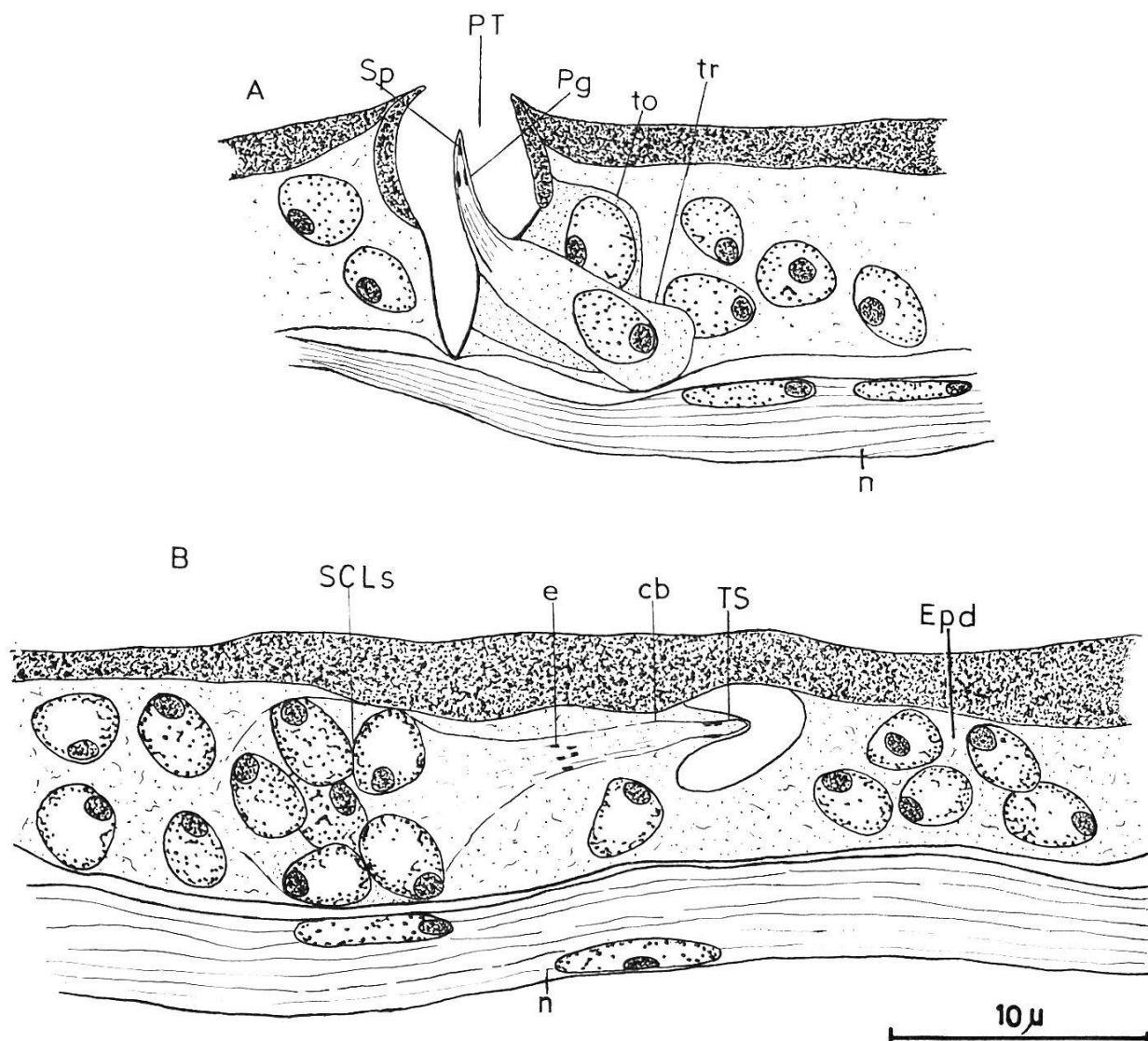


Fig. 11. Sensillum type VI (coeloconica). A. Section showing the pit, tormogen, trichogen cells and the terminal strand of the sense processes with the scolopale. B. Section with the sense cells.

not clear where it leads to. Minute bodies (e) are seen in two places on the sense process and a large body apparently of the same structure (ee) is found beyond the second group. Traces of three cells comparatively larger than the surrounding epidermal cells are seen close to the large cell. Whether one or more of these three cells, or the large cell, is the reception cell, was not possible to determine. In spite of the numerous sections which were made, they could not show clearly the cellular elements of this type. These cellular elements were seen in the organs which lie in the tips of the antenna but it was even impossible to see such parts in organs which lie in the other parts of the antenna.

NEWTON (1931) suggested that the large cell in such a type of sensilla is chitinogenous and receptive in function, although according to SNODGRASS (1926, 1935) various investigators have

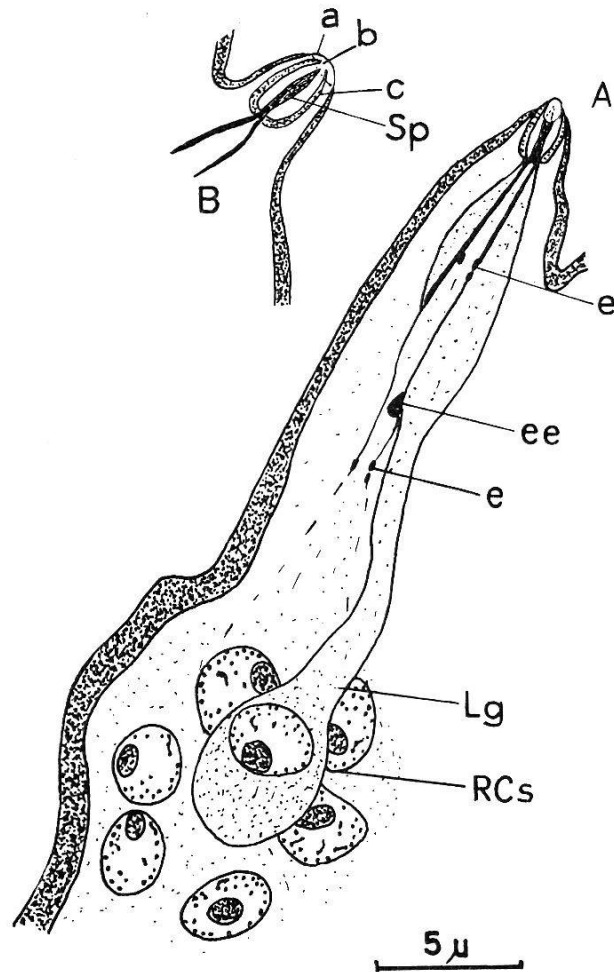


Fig. 12 A & B. A = Section of a sensillum type VII (campaniformia) in one of the tips of the female antenna. B = Section of the external part of type VII in the female flagellar segment 12. a = outer lamella; b = inner layer; c = cuticular cylinder; ee = large body apparently of the same structure as the minute bodies; Lg = large long cell; RCs = three large cells.

Abbreviations: cb = cylindrical bundle; ct = cuticula; dF = distal filament; e = minute bodies; Epd = epidermis; n = antennal nerve; Pg = peg-like structure; pP = proximal process; PT = pit; SCL = sense cell; SCLs = sense cells; SK = socket; Sp = scolopale; to = tormogen cell; tr = trichogen cell; TS = terminal strand; Vac = vacuole.

found traces of other cells. He mentioned SIHLER, who describes in *Periplaneta* a large cell ending in the canal of the cuticula, which is transversed by the distal process of the sense cell. HSÜ (1938) mentions one sense cell in this type and a large vacuolated cell; he calls it a membranous cell. A third cell lies between the first two and envelops the distal process of the nerve cell and the scolopale which he calls the accessory cell. SNODGRASS (1926) says that the other cells beside the sense cell have not been definitely identified with those of the hair-bearing sensilla.

VI. Distribution and Number of Sensilla Types.

The distribution and number of the different types of sensilla were studied thoroughly in the antennae of both sexes. This knowledge served as a basis for the experimental studies on the possible function of each type of sensilla in the female antenna in relation to the attraction of mosquitoes to the host.

1. Antenna of the female.

Tables 1, 2 and Fig. 13⁴ give the detailed number and distribution of each type of sensilla on the various segments of the female mosquito's flagellum. The number was counted on the two sides of five antennae. The counting is more reliable in types of sensilla I, V, VI, and VII than in types II and III + IV, as the possibility of some error exists when counting the sensilla on the sides of the

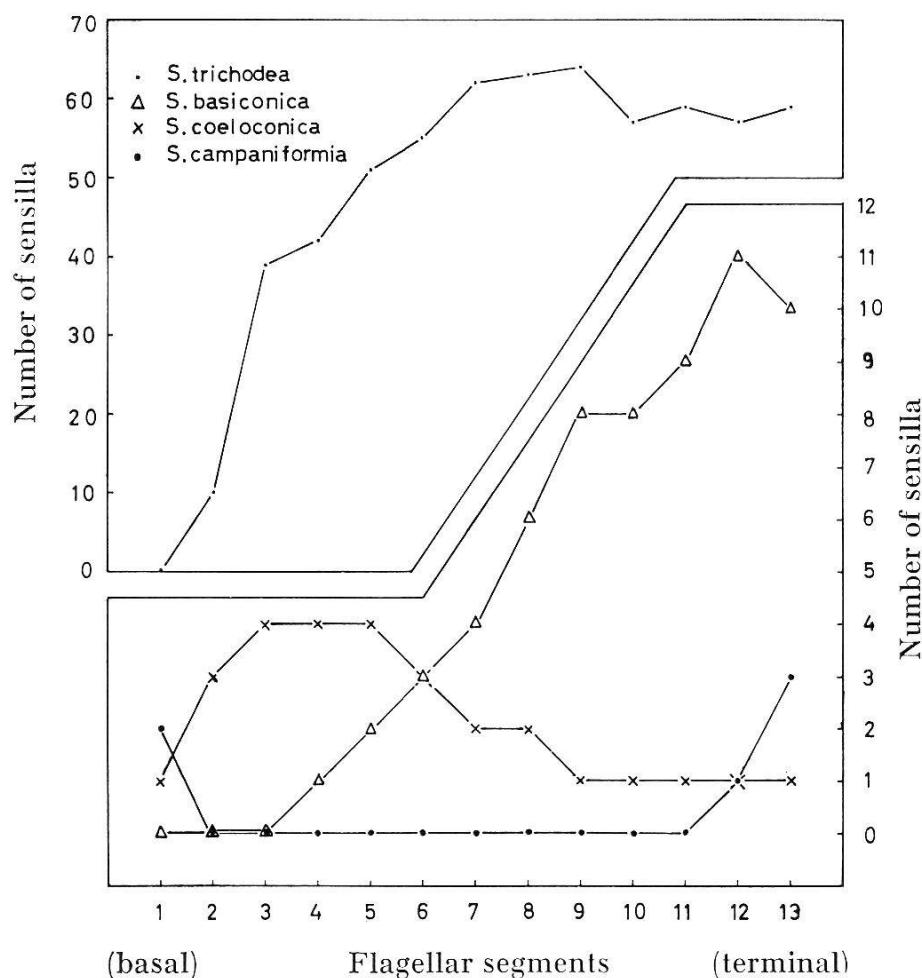


Fig. 13. Number of each type of sensilla trichodea, basiconica, coeloconica and campaniformia on the thirteen flagellar segments of the antenna of female mosquito *Anopheles maculipennis* (average of five flagella).

⁴ Includes only types of sensilla III + IV, V, VI and VII.

TABLE 1.

Distribution and number of long and short bristles or spines and sensilla trichodea in five female antennae.

Flagellar segments	Type I Long bristles or spines						Type II Short bristles or spines						Types III+IV Sensilla trichodea					
	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Aver- age	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Aver- age	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Aver- age
1 (base)	undifferentiated																	
2	8	8	8	8	8	8	13	13	11	12	12	13	12	11	10	8	11	10
3	8	8	8	8	8	8	6	10	11	8	10	9	44	40	37	35	41	39
4	7	7	7	8	7	7	8	10	12	8	8	9	48	45	38	40	39	42
5	7	7	8	7	7	7	7	12	8	10	6	9	56	51	47	49	51	51
6	7	7	8	7	7	7	5	8	8	8	6	7	57	60	57	52	48	55
7	7	7	8	7	7	7	5	8	6	7	5	6	63	65	61	63	58	62
8	7	7	7	7	7	7	4	9	5	5	6	6	66	65	61	60	63	63
9	7	7	6	6	7	7	5	7	5	5	4	5	66	65	53	67	68	64
10	6	6	6	6	6	6	4	7	5	4	6	5	59	52	52	63	59	57
11	6	6	6	6	6	6	3	5	6	4	3	4	62	66	55	57	56	59
12	6	6	6	6	6	6	4	6	6	3	3	4	58	59	52	61	56	57
13 (tip)	6+4	6+4	6+4	6+4	6+4	6+4	2	2	4	2	4	3	67	52	57	58	60	59
Total							66	97	87	76	74	80	658	631	580	613	610	618

TABLE 2.

Distribution and number of sensilla basiconica, coeloconica and campaniformia in five female antennae.

Flagellar segments	Type V Sensilla basiconica						Type VI Sensilla coeloconica						Type VII Sensilla campaniformia					
	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Aver- age	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Aver- age	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Aver- age
1 (base)	0	0	0	0	0	0	1	1	2	2	1	1	2	2	2	2	2	2
2	0	0	0	0	0	0	3	3	3	3	3	3	0	0	0	0	0	0
3	0	0	0	0	0	0	3	4	4	3	4	4	0	0	0	0	0	0
4	1	1	1	1	1	1	3	4	3	4	4	4	0	0	0	0	0	0
5	1	2	2	2	2	2	4	4	3	4	4	4	0	0	0	0	0	0
6	2	3	3	2	3	3	3	3	3	3	3	3	0	0	0	0	0	0
7	4	4	3	3	4	4	2	2	2	2	2	2	0	0	0	0	0	0
8	7	7	5	5	7	6	2	2	2	2	2	2	0	0	0	0	0	0
9	9	7	9	8	8	8	1	2	1	1	2	1	0	0	0	0	0	0
10	8	8	9	8	8	8	2	1	1	1	1	1	0	0	0	0	0	0
11	11	8	10	10	9	9	1	1	1	2	1	1	0	0	0	0	0	0
12	11	11	11	10	10	11	2	1	2	1	1	1	1	1	1	1	1	1
13 (tip)	11	9	10	11	11	10	1	1	1	1	1	1	3	3	3	3	3	3
Total	65	60	63	60	63	60/62	28	29	28	29	29	29/28	6	6	6	6	6	6

In calculating the average, fractions were approximated to the next round figures.

segments. Some sensilla were broken; they were classified according to the form of the base.

Type I (Long bristles or spines).

It is found projecting in all directions from the colourless sub-basal area on segments 2 to 13 and near the apex of the last segment. The number is constant on the basal segments 2 and 3 (8 bristles), then it decreases towards the apex with 6 bristles on each of the last four segments 10, 11, 12 and 13; on the segments between, the number varies from 8 to 6. There are always 4 bristles just below the apical end of the last segment in a circle.

The longest bristles are usually seen on the outer side of the antennae and the smaller ones on the inner side⁵. The first segment possesses many undifferentiated bristles of between Type I and II, except for a small area at the base.

Type II (Short bristles).

It is distributed on segments 2 to 13, with the maximum number of bristles (average number 13) on segment 2; the number decreases towards the apex of the antennae with a minimum average of 3 bristles on segment 13. This type of sensilla is seen in different places on the segments and, particularly, near the top of each.

Types III and IV (S. trichodea).

They have the greatest number of sensilla on the antennae. These two types are distributed in such a way that it was difficult to count them separately. On the whole antenna there are from 580 to 658 sensilla with an average of 618 (in five antennae). Segment 1 lacks this type and segment 2 possesses a relatively small number (average 10 sensilla). The number rises to an average of 39 on segment 3 and remains at about this level with 42 on segment 4. On segments 5 to 13 the number varies between a minimum of 51 and a maximum of 64.

Type V (S. basiconica).

It is not found on the first three flagellar segments and one only is present on segment 4. The number increases gradually towards the apex of the antenna with usual variations of 1 or 2, and rarely 3 or 4, and reaches a maximum of 11 on the average on segment 12, and 10 on segment 13.

ROTH & WILLIS (1952) found in the female *Aedes aegypti* on

⁵ Observed in preparations of the whole head.

each of the 13 flagellar segments many thin-walled trichoid sensilla (Types III and IV) and occasional small peg organs (Type V).

Type VI (S. coeloconica).

This type is rarer than the previous one. It has one or two sensilla on segment 1, the highest number, 3 to 4, being on segments 2, 3, 4, 5 and 6; then it decreases to 2 on segments 7 and 8 and to an average of 1 on the remaining segments.

According to McINDOO (1918), NAGEL did not find any pits in the antennae of *Culex pipiens*, and SMITH (1919) obtained the same negative results on the same species. ROTH (1948) described the antenna of the male *Aedes aegypti*, and ROTH & WILLIS (1952) describe that of the female with their different types of sensilla; in no case is mention made of any pits.

It seems, according to these results, that pits are characteristic in the antennae of Anophelini and not so in Culicini.

Type VII (S. campaniformia).

It contains the smallest and most constant number of sensilla. Segment 1 carries two, segment 2 to 11 none, while segment 12 carries only one and segment 13 three. This organ is very near to the top in segments 1 and 12. In segment 13 both tips end with one and the third is found just below the circle of the four Type I sensilla.

The campaniform sensilla have been found by HOCHREUTHER (1912) in the antenna of *Dytiscus*, and by McINDOO (1918 a) distributed over the head, antennae, mouth parts, thorax and legs of the larva of *Allorhina* (Scarabaeidae).

2. Antenna of the male.

The flagellar segments 2 to 11 carry no sensilla, except for the whorls of fibrillae which project in all directions. No attention was paid to the number of fibrillae on the different segments.

Table 3 shows the distribution and number of the types of sensilla basiconica, coeloconica and campaniformia on segments 1, 12 and 13 in the flagellum of five antennae.

Segment 1.

It carries very few sensilla of between Types I and II, undifferentiated in size, length and thickness, as well as a constant number (2) of campaniform sensilla which are seen near the top of the segment, and the whorl of fibrillae.

TABLE 3.
Distribution and number of sensilla basiconica, coeloconica and campaniformia in five male antennae.

Flagellar segments	Type V Sensilla basiconica					Type VI Sensilla coeloconica					Type VII Sensilla campaniformia				
	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5	Ant. 1	Ant. 2	Ant. 3	Ant. 4	Ant. 5
1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2
12	0	0	0	0	0	8	8	8	8	10	1	1	1	1	1
13	24	26	28	24	32	3	2	3	4	5	3	3	3	3	3
Total	24	26	28	24	32	11	10	11	12	15	6	6	6	6	6

Segment 12.

The sensilla are on the last two-thirds, whereas the basal third lacks any type except for the whorl of fibrillae. The short bristles number about 80; they are curved and stretched out in such a way as to cover the other, more delicate sensilla. Trichoid have the maximum number of sensilla, about 100, being found close to the surface of the segment. Coeloconic sensilla are usually constant, with 8 organs in the upper half of the segment. Segment 12 also possesses one campaniform organ near the top and none of basiconic sensilla.

Segment 13.

Comparing the number and distribution of the various types of sensilla in this segment with the previous one, we find that it carries fewer small bristles, about 12, and twice as many trichoid sensilla (about 200). It bears between 24 and 32 basiconic sensilla, which are rare at the base and increase towards the apex. There are less coeloconic sensilla, between 2 and 5, with an average of three, and more campaniform sensilla with a constant number of three, two in the tips and one in the last fourth of the segment. Eight large bristles project from the colourless sub-basal area.

From the number of the different types of sensilla on the different antennal flagellar segments (Tables 1, 2 and 3), we can see that the number of each type varies in a small range in each segment.

When comparing the total number of sensilla of each type in the whole antenna of females and males we find that there are nearly twice as many trichoid, basiconic and coeloconic sensilla in the female as in the male; of campaniform sensilla there is the same constant number (6) in both sexes.

VII. Reactivity of the Normal Female Mosquitoes towards the Attracting Factors.

Before testing the behaviour of mosquitoes with certain sense organs missing towards the attracting factors, it was important at the beginning to test the behaviour of normal unoperated mosquitoes towards these factors and to ascertain the degree to which the factors differed in attractiveness.

In preliminary experiments the behaviour of the unoperated mosquitoes was tested towards an air stream carrying the following combinations of factors:

1) Low moisture content of 15-25% R.H. and temperature of 34°C.

2) Moisture content of 75-85% R.H. and temperature the same as that of the experimental room (25-26°C).

3) Body odour, associated with a low moisture content of 15-25% R.H. and a temperature of 25-26°C.

These combinations proved to have very little effect on the attraction of mosquitoes, as shown in Table 4.

TABLE 4.

Preliminary experiments on the behaviour of unoperated mosquitoes towards an air stream of 3 L/min. loaded with different combinations and degrees of the three factors⁶, body odour, moisture and temperature, only one of these factors being used in each experiment, and this according to previous investigations, in its highest attractive effect.

No.	Number of experiments	Factors	Mean reactions of 40 mosquitoes	
			Alighting	Hovering
1	16	Low moisture content of 15-25 % R.H. and temperature of 34° C.	1	16
2	10	Moisture content of 75-85 % R.H. and temperature of 25-26° C.	0	8
3	10	Body odour, low moisture content of 15-25 % R.H. and temperature of 25-26° C.	0	11

The number of mosquito reactions to these combinations of factors was low and not high enough for us to be able to use such combinations on amputated mosquitoes. It is obvious that the results are more reliable when a high number of reactions is obtained in the control experiments, because there would then be a gradual decrease in reactions along with the progressive elimination of the antennal sense organs. For this reason, we abandoned those combinations in which only one factor was at its highest attractive effect and turned to using combinations with more than one factor at their highest attractive effects. Four combinations were tried:

⁶ Of the attracting factors only temperature and moisture content varied in degree. Body odour was always taken from the left hand of the same test subject.

- 1) Body odour, accompanied by moisture content of 75-85% R.H. and temperature of 34°C.
- 2) Moisture content of 75-85% R.H., accompanied by temperature of 34°C.
- 3) Body odour, accompanied by moisture content of 75-85% R. H. and temperature of 25-26°C.
- 4) Body odour, accompanied by low moisture content of 15-25% R.H. and temperature of 34°C.

The result with the first three combinations showed high reactivity (see Tables 5 to 7), while the last combination gave a comparatively low reactivity with a mean number of 7 alightings and 22 hoverings in 17 experiments. This last result was still not high enough to make us use such a combination on amputated mosquitoes, and, therefore, only the first three types of combinations were adopted and used in the following experiments with amputated mosquitoes. But before we discuss the results with these combinations we should point out that in spite of all the precautions we took in our experimental technique—using mosquitoes of nearly the same age and physiological condition and carrying out all the experiments in an air-conditioned room with a constant temperature and humidity—the reactivity of mosquitoes towards the same attracting factors differed from one day to another and sometimes from one experiment to the next on the same day. On some days the mosquitoes reacted very well towards the attracting factors, while on others they reacted less and occasionally even they showed a low level of reactivity either throughout the day or just in some of the experiments carried out on a given day .

The reasons or factors which might account for variations in the results of the same experiments are:

- 1) The final record of the reactions of flying insects in a limited time of 10 minutes could change to a certain extent owing to the behaviour of the individual mosquito. As also noticed by LAARMAN (1955) a mosquito might stay on the gauze in front of the air outlet for a very long time, and so it is counted once, or else it stays for a short time, then it flies away and might return to be counted again for the second time. The same thing happens with the hovering reactions of mosquitoes. Some used to fly in front of the air outlet for a long time and others for a short time, then disappear and might appear afterwards again.

⁷ No experiments were made on the days when mosquito reactivity was very low. The results of single experiments during which mosquitoes were not active enough were excluded from the final record of the day's experiments and were replaced by those of other experiments made on the same day.

2) The condition of the testing person could change from one day or from one time to another and this might affect the reactivity of mosquitoes in experiments with odour (FREYVOGEL, 1961).

3) Nevertheless, RAHM (1956) has noticed that the mosquito reactivity (*Aedes aegypti*) differs as well with the "artificial arm". This fact indicates that the mosquito reactivity might also be affected by climatic and weather factors. As we worked in a climatized room, temperature and humidity were kept constant and there would thus be no variation in the effect of these two factors on mosquito reactivity. As to the air pressure: HAUFE (1955) with his laboratory experiments on female *Aedes aegypti* found that the atmospheric pressure has a sufficiently significant effect on the flight activity of this species. The effect of decreasing pressure was more stimulating than that of increasing pressure for pressures above 735 mm, while below 735 mm the opposite relation was obtained. However, in his discussion, FREYVOGEL (1961) points out that changes in air pressure as applied by HAUFE in his experiments are unlikely to occur in nature and this author reached the conclusion that the changes in the reactivity of mosquitoes cannot be ascribed to one single weather element, whereas he definitely thinks that the mosquito reactivity is affected by changes of the weather as a whole.

It is not possible for us to say whether FREYVOGEL or HAUFE is right, since we did not ascertain the effect of atmospheric pressure alone on mosquito reactivity. What we can say, however, is that despite our climatized room (constant temperature and humidity) we still found a marked fluctuation in mosquito reactivity.

4) One must be aware that to carry on the experiments during the day, the *Anopheles* mosquitoes, being nocturnal insects, were placed under fairly abnormal conditions.

Owing to these and possibly other factors the results of the same experiments could change. We shall call them henceforth the "uncontrollable interfering factors".

Because of the uncontrollable interfering factors which would affect the behaviour of mosquitoes, many experiments were necessary in order to obtain a representative sample of the whole population. For this reason all the results of control experiments (carried out prior to those with amputated mosquitoes) were included together to provide an exact picture for a more or less homogeneous population. In this way we can reduce the variability due to those factors and minimise observational experimental errors.

For measuring the mosquito reactivity, the arithmetical mean obtained from 7 series of experiments (each series consisting of

8 individual experiments) was calculated. And as an appropriate measure of a mean value, we used the arithmetical mean as given by the formula

$$\bar{x} = \frac{\sum x}{N}.$$

This procedure was carried out in each type of experiment (or, in other words, in each type of factor combination), and the results are given in Tables 5, 6 and 7.

TABLE 5.

Reactivity of normal mosquitoes in control experiments towards an air stream of 3 L/min. loaded with body odour, moisture content of 75-85% R.H. and temperature of 34°C.

Series	Reactivity of 40 mosquitoes in 8 experiments								Total reactivity	Mean
	1	2	3	4	5	6	7	8		
1	185	190	168	155	119	157	178	188	1340	168
2	118	135	138	154	174	157	162	156	1194	149
3	126	138	139	119	151	165	144	131	1113	139
4	209	175	189	202	183	177	156	151	1442	180
5	176	151	131	137	144	125	118	120	1102	138
6	190	206	185	169	192	173	152	155	1422	178
7	132	138	167	159	128	148	138	157	1167	146

Mean reactivity (\bar{x}) of normal mosquitoes in 7 series of experiments = 157.

TABLE 6.

Reactivity of normal mosquitoes in control experiments towards an air stream of 3 L/min. loaded with moisture content of 75-85% R.H. and temperature of 34°C.

Series	Reactivity of 40 mosquitoes in 8 experiments								Total reactivity	Mean
	1	2	3	4	5	6	7	8		
1	72	111	89	88	58	113	87	95	713	89
2	162	151	148	125	137	113	139	135	1110	139
3	88	91	80	106	113	81	95	108	762	95
4	128	92	98	119	96	78	83	97	791	99
5	133	123	141	105	113	131	137	142	1025	128
6	89	97	119	115	101	138	140	126	925	116
7	75	115	124	112	125	132	92	108	883	110

Mean reactivity (\bar{x}) of normal mosquitoes in 7 series of experiments = 111.

TABLE 7.

Reactivity of normal mosquitoes in control experiments towards an air stream of 3 L/min. loaded with body odour, moisture content of 75-85% R.H. and temperature of 25-26°C.

Series	Reactivity of 40 mosquitoes in 8 experiments								Total reactivity	Mean
	1	2	3	4	5	6	7	8		
1	59	52	66	75	39	59	46	45	441	55
2	117	100	62	85	79	68	83	68	662	83
3	90	80	68	66	38	72	61	45	520	65
4	84	75	74	87	65	49	58	42	534	67
5	72	74	64	92	47	60	53	32	494	62
6	97	81	89	77	60	51	54	59	568	71
7	62	49	73	68	53	59	49	57	470	59

Mean reactivity (\bar{x}) of normal mosquitoes in 7 series of experiments = 66.

As a measure of dispersion, the standard deviation was calculated according to the following formula

$$s = \sqrt{\frac{\sum (x - \bar{x})^2}{N - 1}} \quad (\text{Documenta Geigy, 1960})$$

where N denotes the number of series of experiments, s the standard deviation of the numbers observed, x the mean reactivity of one single series of experiments, and \bar{x} the mean reactivity of 7 series of experiments.

After calculating the standard deviation for each type of experiments, the relative standard deviation ($s_{\text{rel.}}$)⁸ expressed as a percentage of the mean reactivity (\bar{x}) was reduced. Like the standard deviation, the relative standard deviation measures the distribution of the individual values around the mean; in addition, it facilitates in our case comparison of the range of variation in each type of experiments.

In order to study the effect of the different types of factor combination on attraction, the mean reactivity, standard deviation and relative standard deviation were calculated for each type. The results are given in Table 8.

From Table 8, we see that the statistical variation within each type of experiments, as shown by the relative standard deviation, lies within a range of 11.2 and 16.4%. This range of variation within each type of experiments could be attributed to the pre-

⁸ This relative standard deviation is usually called coefficient of variation.

viously mentioned factors. However, this range of variation is rather narrow and at the same time it is practically common to all types of experiments; which permits comparison of the mean reactivity values.

TABLE 8.

Mean reactivity, standard deviation and relative standard deviation for the three types of attracting factor combinations.

No.	Type of attracting factor combinations	Mean reactivity (\bar{x})	Standard deviation s	Relative standard deviation $s_{rel.}$
1	Body odour, moisture content of 75–85 % R.H. and temperature of 34° C.	157	17.6	11.2 %
2	Moisture content of 75–85 % R.H. and temperature of 34° C.	111	18.2	16.4 %
3	Body odour, moisture content of 75–85 % R.H. and temperature of 25–26° C.	66	9.0	13.6 %

The last table reveals a significant difference in the mean reactivity value (\bar{x}) between each type of experiments (as proved by the t test). In the first type, for instance, the mean reactivity value is 157 with a relative standard deviation of 11.2%, while in the second it is 111 with a relative standard deviation of 16.4% and in the third 66 with a relative standard deviation of 13.6%.

From these results we can conclude that in a constant room humidity of 50–60% R.H. and temperature of 25–26°C. the effect of human body odour combined with moisture content of 75–85% R.H. and temperature of 34°C would result in a high reactivity value (157), but when the temperature is reduced and becomes equal to the room temperature, the reactivity value decreases considerably (66). When body odour is excluded and temperature increased again to 34°C with the same moisture content of 75–85% R.H., the reactivity value increases considerably (111), although it is still much less than in the first combination. This would show that heat has a great effect on mosquito reactivity, even more than body odour (over the limited distance used in our experiments).

If we compare the two kinds of reaction—i.e. alighting, which was usually followed by probing movements, and hovering—in the different types of combination, we find, as shown in Table 9, that

when the temperature was 34°C in the first and second types, the alighting reactions were more numerous than the hovering ones. The addition of body odour, as in the first combination, raised the alighting reactions from 76% to 89.3%, while in spite of the presence of body odour but with a decrease of temperature to 25-26°C, as in the third combination, the alighting reactions declined considerably to 24.5%.

In the three combinations of factors mentioned the moisture content was always constant at 75-85% R.H. But in some experiments we made (20 experiments), when the moisture content decreased to 40-50% R.H. and was combined with the temperature of 34°C, the alighting reactions were about 60% (alighting reactions 30, hovering 19). This result, compared with the result obtained from the second combination in the last table, shows that the number of alighting reactions has decreased.

From these findings we can conclude that the change of tem-

TABLE 9.

Reactions of normal mosquitoes in the control experiments towards the three types of attracting factor combinations.

No. of experimental series	Body odour, moisture content of 75-85 % R.H. and temperature of 34° C.		Moisture content of 75-85 % R.H. and temperature of 34° C.		Body odour, moisture content of 75-85 % R.H. and temperature of 25-26° C.	
	Kind of reaction		Kind of reaction		Kind of reaction	
	Alighting	Hovering	Alighting	Hovering	Alighting	Hovering
1	1222	118	532	181	85	356
2	1072	122	915	195	142	520
3	1032	81	560	202	148	372
4	1036	131	564	227	118	416
5	1338	104	786	239	132	338
6	978	124	665	260	123	371
7	1166	256	634	249	150	418
Total reactions	7844	936	4656	1553	903	2791
Total reactions in per cent	89.3	10.7	76	24	24.5	75.5

Reactions are calculated in 7 series of experiments with each type of combination, and each series is composed of 8 experiments. 40 mosquitoes were used in each experiment.

perature, in combination with body odour and humidity, has more effect on the alighting reactions than changes in the other two factors. This explains what happens in nature: at a distance odour alone is the factor reaching the mosquito and guiding it to its host, in the vicinity of the host the effect of odour is increased by the addition of body moisture. Warmth, then, is the factor responsible for the actual alighting, followed usually by the probing action.

VIII. Reactivity of Female Mosquitoes with Progressive Amputation of their Antennal Flagellar Segments towards the Attracting Factors.

The three combinations of factors which showed the high attractive effect with the normal unoperated mosquitoes were tested against groups of mosquitoes with progressive symmetrical amputation of their antennal flagellar segments. In each operation an equal number of segments from both antennae were eliminated. It was hoped that the study of the change in reaction intensity with different amputated groups of mosquitoes, would reveal the possible function of the sense organs distributed on the antennae.

In order to estimate the change in reaction caused by progressive amputation, each group of operated mosquitoes was tested with a parallel control group of unoperated mosquitoes. In each group of operated mosquitoes the number of mosquitoes involved was between 35 and 40, whereas the number of accompanying controls was fixed at 40.

When comparing the corresponding reactions we were restricted by the following facts:

- 1) Owing to mortality, the number of operated mosquitoes used finally in the reaction experiments was not always the same.
- 2) Variations due to the uncontrollable interfering factors from one experiment to another or one day to the next (see p. 34).

Hence a standard basis was necessary, in which the influence of these factors was eliminated and consequently direct comparison possible. So in each series of experiments the reactions of the operated mosquitoes were corrected to give a value corresponding to the number of control mosquitoes (40).

To exclude as far as possible the influence of the other uncontrollable interfering factors, the reactions of the operated mosquitoes were corrected with reference to a constant reactivity value (100). This procedure would allow us to compare the influence of progressive amputation on reactivity.

To illustrate this, we would give the following example for body odour, moisture content of 75-85% R.H. and temperature of 34°C.:

Mean reactivity of amputated mosquitoes (8 exp.)	3
Mean reactivity of accompanying controls (8 exp.)	168
A constant reactivity value	100

Accordingly, the theoretical reactivity of the amputated mosquitoes (both flagella completely eliminated) under these testing factors would be $\frac{100 \times 3}{168} = 1.8$. From now on this value will be referred to as "Index of Reaction Intensity (I.R.I.)" and will be adopted in investigating the effect of progressive amputation on reactivity, and later on to find a correlation between the sense organs and the possible functions.

Results of the three combinations of factors are given in Tables 10, 11 and 12 and graphically represented in Figs 14, 15, 16 respectively.

Combination of body odour, moisture content of 75-85% R.H. and temperature of 34°C.

TABLE 10.

The reaction intensity of female mosquitoes towards body odour, moisture content of 75-75% R.H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments.

Number of flagellar segments remaining in each antenna	Mean reactivity of amputated mosquitoes and accompanying controls (8 exp.)		Index of Reaction Intensity (I.R.I.) %
	Amputated	Controls	
12	130	138	94.2
10	150	180	83.3
8	120	178	67.4
6	85	180	47.2
5	52	146	35.6
3	20	139	14.4
1	10	149	6.7
0	3	168	1.8

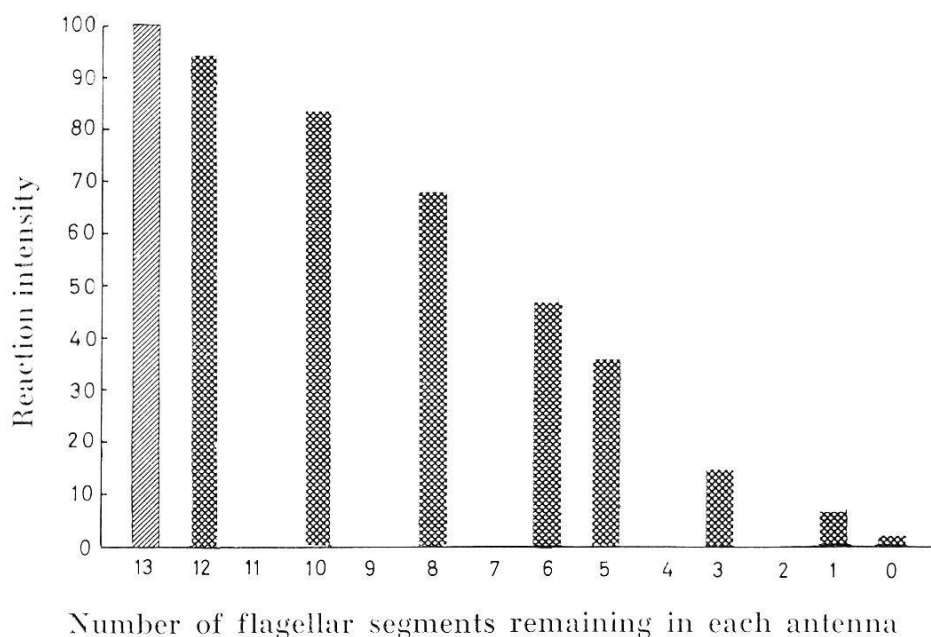


Fig. 14. The reaction intensity of female mosquitoes towards body odour, moisture content of 75-85% R.H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments. The reaction intensity with 13 flagellar segments represents the mean reactivity of control mosquitoes (56 exp.).

When female mosquitoes were tested against this combination of factors, the control experiments showed a mean reactivity (\bar{x}) of 157 (100%) (cf. Table 5). Table 10 shows that with the gradual elimination of the flagellar segments the reaction intensity decreased gradually and no considerable change occurred between any successive eliminations of segments. When one segment was eliminated, the I.R.I. fell to 94.2%, and then decreased gradually with the progressive elimination of the flagellar segments to 83.3% when 10 segments remained in each antenna and to 67.4% with 8 segments remaining; when 6 segments (about half of the total number) were left, the reaction intensity was also about one half (47.2%). With the elimination of the whole flagellum there was a reaction intensity of 1.8%.

In *Anopheles maculipennis* the flagellectomized females are practically not able to respond any more to the combination of body odour, moisture content of 75-85% R.H. and temperature of 34°C. This proves that the antennae are the organs responsible for directing the female mosquito to the source of attraction from a distance; these results agree with the findings of ROTH (1951) and RAHM (1958) on *Aedes aegypti* and *Anopheles quadrimaculatus*.

The gradual decrease in the reaction intensity with the progressive elimination of the flagellar segments shows that the sense organs which locate the source of the stimuli—body odour, hu-

midity and temperature—are distributed on the flagellar segments in such a way that their combined effectiveness at perceiving the different stimuli seems also to be distributed equally on the different segments.

Since the scape and pedicel do not carry sense organs (as seen in the morphological and histological studies) which could be responsible for the location of the tested stimuli, the small value of response with the flagellectomized mosquitoes (1.8%) is probably due to other sense organs existing on other parts of the insect's body.

*Combination of moisture content of 75-85% R.H.
and temperature of 34°C.*

TABLE 11.

The reaction intensity of female mosquitoes towards moisture content of 75 to 85% R.H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments.

Number of flagellar segments remaining in each antenna	Mean reactivity of amputated mosquitoes and accompanying controls (8 exp.)		Index of Reaction Intensity (I.R.I.) %
	Amputated	Controls	
12	75	99	75.8
10	65	110	59
8	58	128	45.4
7	43	116	37
6	17	116	14.7
4	12	99	12
3	11	95	11.6
2	9	139	6.5
1	4	89	4.5

When the moisture content of 75-85% R.H. combined with the temperature of 34°C was used without the body odour, the reaction intensity of amputated mosquitoes did not decrease in the same gradual manner as in the first combination (with body odour). In this combination the mean reactivity of control mosquitoes (\bar{x}) was 111 (100%) (Table 6). Table 11 shows that when one segment was eliminated and 12 segments remained in each antenna, the reaction intensity decreased considerably to 75.8%. By the progressive elimination of the next flagellar segments the intensity decreased gradually to 59% with 10 segments remaining

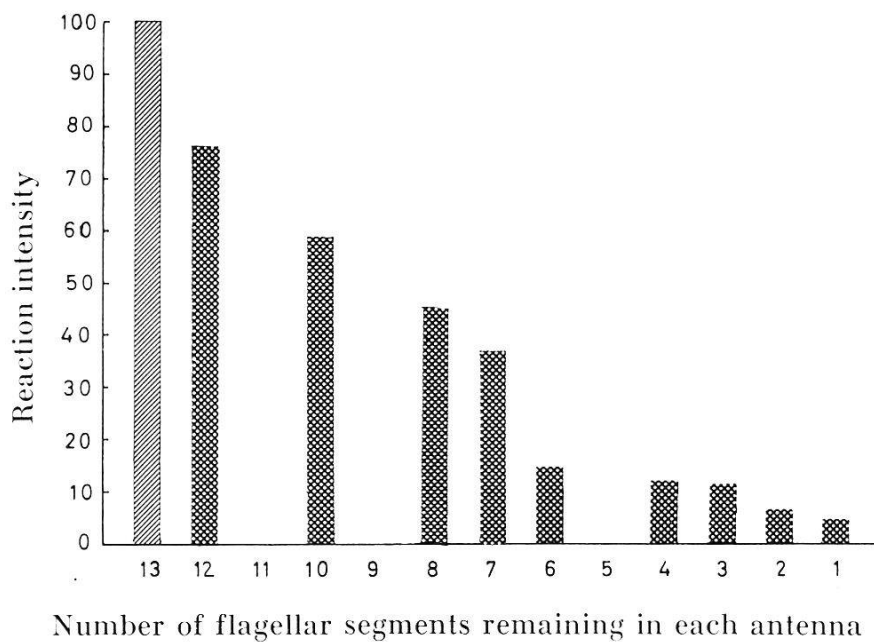


Fig. 15. The reaction intensity of female mosquitoes towards moisture content of 75-85% R. H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments. The reaction intensity with 13 flagellar segments represents the mean reactivity of control mosquitoes (56 exp.).

in each antenna, 45.4% with 8 segments and 37% with 7 segments; then when one more segment was eliminated and 6 remained, the intensity decreased again considerably from 37 to 14.7%. The intensity with 4 and 3 segments remaining gave nearly the same value as that with 6 segments, i.e. 12% and 11.6 respectively, and then decreased to 6.5 with 2 segments remaining and 4.5% with one segment.

The considerable change in reactivity with the elimination of the last flagellar segment (terminal) from each antenna suggests that this segment plays an important role in the location of humidity and/or temperature.

With the elimination of 3, 5 and 6 segments (10, 8 and 7 remaining), the mosquitoes showed a clear response to the source of stimuli, which suggests that there are sufficient receptors on the remaining segments to mediate the stimuli. Also the gradual decrease in reaction intensity with the elimination of those segments shows that the responsible hygromoreceptors and/or thermoreceptors are distributed quantitatively on the terminal segments.

The big decrease in reaction intensity with the elimination of 7 segments (6 remaining) and the persistence of this low intensity with gradual elimination of the basal segments suggests that the hygromoreceptors and/or thermoreceptors on these basal segments cannot mediate and consequently cannot show a significant response to the source of humidity and/or temperature.

Combination of body odour, moisture content of 75-85% R.H. and temperature of 25-26°C.

TABLE 12.

The reaction intensity of female mosquitoes towards body odour, moisture content of 75-85% R.H. and temperature of 25-26°C with the progressive symmetrical amputation of the antennal flagellar segments.

Number of flagellar segments remaining in each antenna	Mean reactivity of amputated mosquitoes and accompanying controls (8 exp.)		Index of Reaction Intensity (I.R.I.) %
	Amputated	Controls	
12	78	62	126.3
10	76	67	113.4
8	69	71	97.2
7	55	62	88.7
6	32	59	54.3
4	23	65	35.4
2	19	83	22.8
0	4	55	7.3

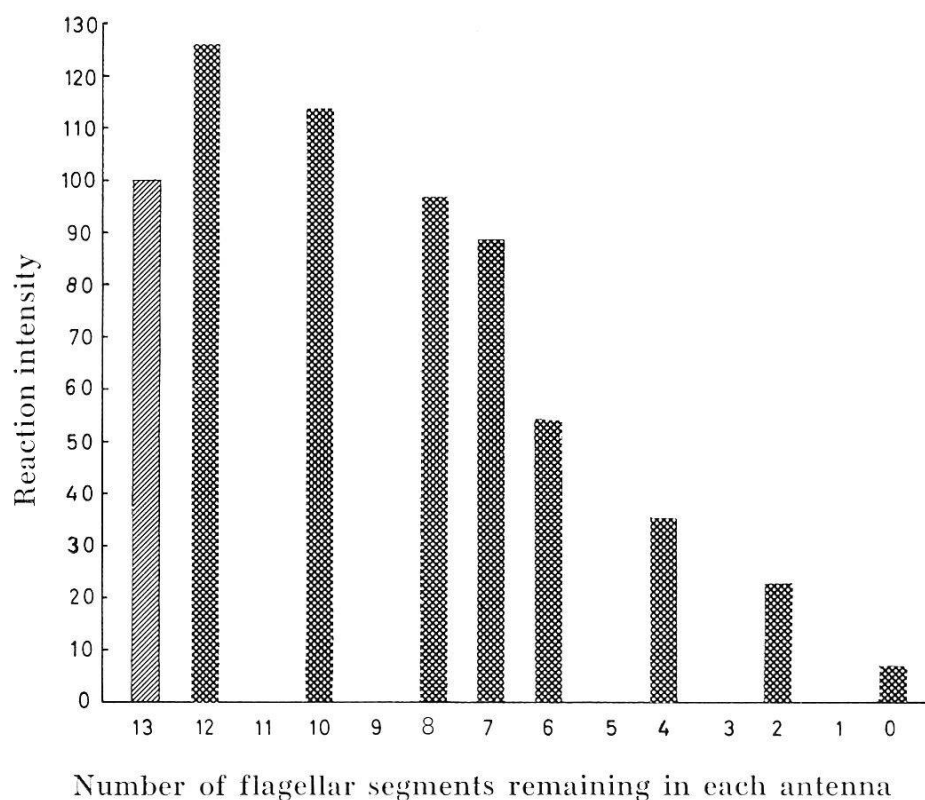


Fig. 16. The reaction intensity of female mosquitoes towards body odour, moisture content of 75-85% R. H. and temperature of 25-26°C with the progressive symmetrical amputation of the antennal flagellar segments. The reaction intensity with 13 flagellar segments represents the mean reactivity of control mosquitoes (56 exp.).

When body odour was used with a moisture content of 75-85% R.H. and a temperature of 25-26° C, the reactivity of the amputated mosquitoes unexpectedly changed in a different way. By comparing the values of the reaction intensity with the gradual elimination of the flagellar segments we find that with the elimination of one segment, the reaction intensity, instead of being decreased, increased from 100% (equivalent to 66, the mean reactivity of the controls) to 126.3%, and then gradually decreased with the progressive elimination of the flagellar segments to 113.4% with 10 segments remaining in each antenna, 97.2 with 8 segments and 88.7 with 7 segments. When only 6 segments were left in each antenna, the reaction intensity decreased considerably from 88.7% to 54.3%, and then the decrease became gradual again with the progressive elimination of the rest of the segments. When the whole flagellum was eliminated a considerable intensity was still obtained (7.3%).

The possible explanation for the increase of reaction intensity with the elimination of the terminal segments is that there might exist a type of sense organ on the last flagellar segment which has an inhibiting function, preventing the female mosquitoes from showing a high response to such a combination of factors. Since the body odour and this moisture content (75-85% R.H.) proved very attractive in the other combinations, it would be expected that the lower degree of temperature was the factor responsible for such a change.

With the elimination of 7 segments, the sense organs left on the remaining 6 segments which are responsible for mediating one or more of these factors show a considerable decrease in function.

In contrast to the second combination of factors, the responsible sense organs still showed a sufficient response in spite of the fact that the intensity of reaction was considerably decreased with the elimination of 7 segments. Also with the progressive elimination of the basal segments, the reaction intensity decreased gradually.

The response obtained with the elimination of the whole flagellum from each antenna demonstrates the existence of sense organs on other parts of the insect's body which play a role in the attraction.

IX. Possible Function of the Sense Organs.

The specific function of the sense organs would have been clearly demonstrated if each type was limited to special segments. But they are scattered over the flagellar segments in a way that makes

it quite impossible to test one single type alone towards the attracting stimulus or stimuli, in order to know its proper function. This distribution forces us to combine the morphological and histological findings, the distribution and number of sense organs on the different flagellar segments and the reaction changing with the progressive elimination of the flagellar segments. By such combinations only indirect evidence of the possible function of each type of sense organ can be suggested.

According to the structure of the different types of sensilla, in the form of hairs, we can classify them into two groups. In the first group, each organ has an external thick-walled cuticular process, one sense cell (long and short bristles, Types I and II respectively), and is articulated in a distinct socket. The second group has thin walls, innervated through more than one sense cell and possesses no sockets: sensilla trichodea (Types III and IV); sensilla basiconica (Type V) and sensilla coeloconica (Type VI).

The first group has been classified (WIGGLESWORTH, 1953) as tactile receptors, and from their structure and distribution there seems to be no doubt that these sensilla are responsible for perceiving contact. They stand out in all directions, beyond the other types of sensilla in two circles, the long bristles in the outer circle projecting from the base of the segments and the short bristles in the inner circle, so as to prevent any object from coming in contact with the more delicate sensilla with which the antennae are richly equipped. Possibly these two types are also responsible for the perception of air movements as proposed by WIGGLESWORTH & GILLET (1934) in *Rhodnius prolixus*.

The perception of body odour, moisture and heat mostly concerns the second group of sensilla, and Table 13 includes the number of these sense organs⁹ remaining on each antenna with the progressive elimination of the flagellar segments as well as the corresponding reaction intensity of female mosquitoes towards the three combinations of factors. The number of sense organs (in per cent) remaining on the antennae with the progressive elimination of the flagellar segments is illustrated in Fig. 17.

Sensilla coeloconica and basiconica.

These two types of sense organs are distributed on the flagellar segments in a special manner; sensilla coeloconica is concentrated on the basal segments and sensilla basiconica on the terminal ones. The following findings and results would reveal in an in-

⁹ Sensilla campaniformia is also included in the table.

TABLE 13.

The number of sensilla¹ coeloconica, basiconica, trichodea, and campaniformia remaining on the antennae of the amputated mosquitoes and the corresponding index of reaction intensity with the three combinations of factors.

Number of flagellar segments remaining in each antenna	Sensilla								Index of reaction intensity (I.R.I.)		
	Average of sensilla coeloconica		Average of sensilla basiconica		Average of sensilla trichodea		Average of sensilla campaniformia		Body odour, 75-85 % R. H. and 34° C.	75-85 % R. H. and 34° C.	Body odour, 75-85 % R. H. and 25-26° C.
	in number	in per cent	in number	in per cent	in number	in per cent	in number	in per cent			
13	28	100	62	100	618	100	6	100	100	100	100
12	27	96.43	52	83.87	559	90.45	3	50	94.2	75.8	126.3
10	25	89.29	32	51.61	443	71.68	2	33.33	83.3	59.	113.4
8	23	82.14	16	25.81	322	52.10	2	33.33	67.4	45.4	97.2
7	21	75.00	10	16.13	259	41.91	2	33.33	—	37.	88.7
6	19	67.86	6	9.68	197	31.88	2	33.33	47.2	14.7	54.3
5	16	57.14	3	4.84	142	22.98	2	33.33	35.6	—	—
4	12	42.86	1	1.61	91	14.72	2	33.33	—	12.	35.4
3	8	28.57	0	0	49	7.93	2	33.33	14.4	11.6	—
2	4	14.29	0	0	10	1.62	2	33.33	—	6.5	22.8
1	1	3.57	0	0	0	0	2	33.33	6.7	4.5	—
0	0	0	0	0	0	0	0	0	1.8	—	7.3

¹ Average of 5 antennae.

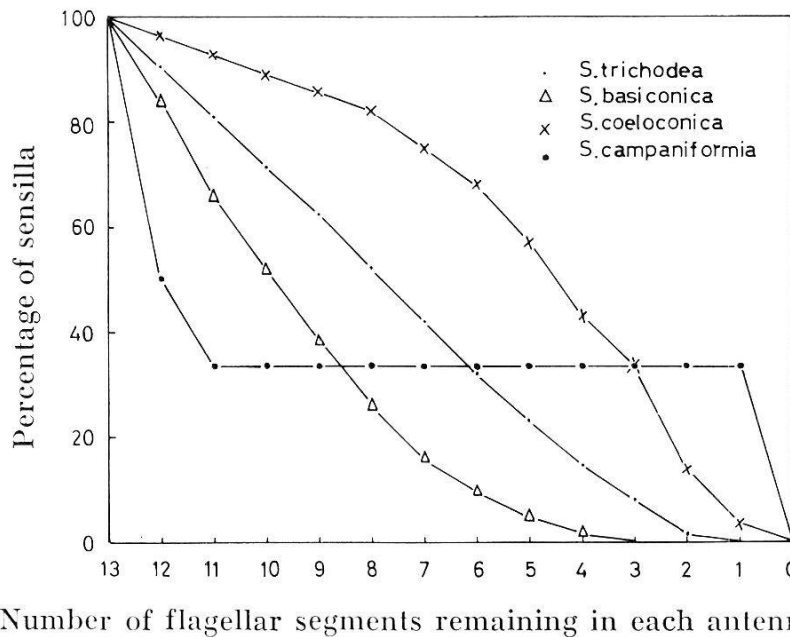


Fig. 17. Proportion of each type of sensilla trichodea, basiconica, coeloconica and campaniformia remaining as the flagellar segments of *Anopheles maculipennis* are progressively amputated symmetrically.

direct way the possible function of each. We repeat first the results obtained in the combinations used in our experiments.

1) The reaction intensity decreased considerably with six segments left in each antenna when mosquitoes were tested towards:

- a) Moisture content of 75-85% R.H. and temperature of 34°C.
- b) Body odour combined with moisture content of 75-85% R.H. and temperature of 25-26°C.

2) When body odour was added to the moisture content of 75-85% R.H. and temperature of 34°C, the reaction intensity decreased gradually with the progressive elimination of flagellar segments, even the six basal ones.

3) On the six basal segments there are averages of: 197 trichoid sensilla from the total of 618 on the whole antenna (about one-third) and 6 basiconic sensilla from the total of 62 (one-tenth) and 19 coeloconic sensilla from the total of 28 (about two-thirds).

These results enable us to draw the following conclusions:

- a) For the *Sensilla coeloconica*.

If the mainly basal coeloconic sensilla were responsible for the perception of heat and/or humidity (result 1 a), the perception of such factor or factors would be more likely not to decrease con-

siderably when the flagellar six basal segments are still present, because these contain about two-thirds of the total number of sensilla coeloconica. In adding body odour, as shown in result 2, progressive amputation provoked gradual decreasing reaction. This seems to indicate that the sensilla coeloconica are the sense organs responsible for the perception of odour.

The morphological and histological structure of this type also provides further evidence to support this idea. They are peg organs with very thin walls, and they are protected by being sunken into pits. The floor of the pit being thin increases the surface of perception. Every sensillum innervates through about six sense cells, relatively larger than the sense cells of the other types of sensilla.

b) For the *Sensilla basiconica*.

The reaction intensity decreased considerably (result 1 a) when only 6 segments were left. It seems that the number of receptors for heat and/or humidity on the six basal segments is less than that required to mediate a clear response (PIELOU 1940, ROTH & WILLIS 1951 b, 1952). It is more reasonable to consider that sensilla basiconica, which have about one-tenth of their total number left on the six basal segments, are responsible for the big decrease rather than trichoid sensilla which still have a considerable number, about one-third¹⁰. The results with the addition of body odour and the decrease of temperature to 25-26°C (result 1 b), also showed a considerable decrease when 6 segments remained in the antenna. Heat in this case would not have a great influence on the responses of mosquitoes as long as it is equal to the degree of ambient temperature. LAARMAN (1955) wrote about the influence of the milieu on the responses of mosquitoes: "... one should always bear in mind the possibility that Weber's Law may here be applicable: if the stimulus is to be perceived by the insect, there must be a certain relationship between it and already existing, similar stimuli." Moreover, BATES (1949) mentioned that the critical temperature below which attraction of mosquitoes does not occur seems to be 28°C. From this we can conclude that the basiconic sensilla are possible hygroreceptors.

c) For the *Sensilla trichodea*: (Types III and IV).

This kind of sensilla is different from the coeloconic and basiconic sensilla in being distributed on all the flagellar segments with no special concentration on any. For this reason it is quite

¹⁰ Trichoid sensilla, Types III and IV on the six basal segments are nearly equal in number.

difficult to correlate any considerable change in reaction intensity with the number of sense organs present on the antenna. But their great number, combined with the sensitivity of the antenna to warmth, suggests that they may act as thermoreceptors; but we have no other experimental evidence for this, nor for stating which one of these two types of trichoid sensilla is responsible, or if both are. The last probability, however, is not likely owing to the big difference in structure and cellular elements.

d) For the *Sensilla campaniformia*.

This type of sensilla is not included either in the first or in the second group of sensilla, as it possesses no external process in the form of hair. It has the fewest number of sensilla: two in the basal flagellar segment, one in segment 12 and 3 in the terminal one. For the possible function of this type there are two probabilities:

1) According to WIGGLESWORTH (1953), almost all authors agree that the campaniform sensilla are sensitive to mechanical stimuli. The distribution of the sense organs in the female and male antenna may fit in with this idea, and the following explanation would support it. It is known that the female mosquitoes normally travel upwind, but they take off much more readily when the wind carries host stimuli and, according to the same principle, the males would be expected to react as well in order to reach their source of nutrition such as nectar and plant juices. In this case females and males are almost in equal need of receptor organs for detecting air movements.

The presence of two campaniform sensilla in the terminal end of the antenna with a third one just beneath (one-half of the total number) would be highly satisfactory for such a function. On the basis of the histological studies, if only one of the cells is receptive in function, this would give further support for this possible function.

2) The experimental results when the temperature decreased to 25-26°C and was combined with the body odour and moisture content of 75-85% R.H. showed that the reaction intensity with one segment missing was considerably higher than in the controls. This leads us to think that there could exist a kind of inhibiting sense organ which prevents the mosquitoes from responding to such a lower degree of temperature. The campaniform sensilla having half of its total number on the last segment could be responsible for such changes, but there is no further evidence to support this idea.

X. Discussion.

In relation to the sense organs and their distribution on the antennae, the female mosquito differs in behaviour from the male. Females possess many thin-walled sensilla on the flagellar segments which undoubtedly are the organs responsible for their attraction to man. Males carry less sensilla of these types (only on the last two antennal segments) and a whorl of rigid, thick-walled fibrillae on all flagellar segments except the terminal one.

Since the male mosquito is harmless to man and the thin-walled sensilla are restricted to the last two flagellar segments, little attention was paid to their function in males by workers in this field. The long fibrillae play an important role in the mating process during flight. ROTH (1948) wrote that when the males of *Anopheles quadrimaculatus* are sexually active, their antennal fibrillae are extended away from the shaft to receive the sound stimuli of the females while they are flying.

The sense organs in female mosquitoes have received much attention from scientists for their importance in the attraction to man and analytical investigations of the nature of the attracting stimuli have shown that body odour, temperature and moisture are the main stimuli involved (see second chapter). When one of these factors was tested against the normal unoperated mosquitoes it had a very low effect on the activity of mosquitoes. DETHIER (1947) recognized the fact that no one attractant alone performs the service of guiding an animal to its proper habitat or mate or food. On this basis, LAARMAN (1955) says that there seems to be not the slightest reason to assume that one single factor would be capable of leading an *Anopheles* specimen to its host and causing it to suck blood. It is far more probable that the insect's need of a blood meal leads to an "appetitive behaviour" and that finally the animal, at the end of a chain of reactions, each released by a particular stimulus, satisfies its appetite.

By the technique we followed, cutting the antennae at different levels and testing the behaviour of the amputated mosquitoes towards the different stimuli in an olfactometer, it has been shown that the antennae are the main sites of the distance chemo-, hygro- and thermoreceptors. WIGGLESWORTH (1953) reviewed that the sense of smell in insects is located chiefly in the antennae, as is the sense of temperature in insects which suck the blood of mammals, such as the mosquito *Anopheles*, the lice *Pediculus* and *Haematopinus*. Also BATES (1949) stated that the ability of orientation to the source of food by the chemoreceptor organs in the paired antennae is shared by so many different insects that it

can safely be assumed to exist in mosquitoes in spite of the lack of direct experimental evidence. WIGGLESWORTH & GILLET (1934) and WIESMANN (1960) have shown that the antennae are the main sites for smell, temperature and humidity in *Rhodnius prolixus* and *Musca domestica* respectively. The antennae in female *Aedes aegypti* do function as directional distance thermoreceptors (ROTH, 1951; RAHM, 1958), as well as hygromoreceptors (ROTH & WILLIS, 1952; RAHM, 1958; BAR-ZEEV, 1960).

By combining the studies of morphology, histology and distribution of sense organs with the reaction intensity of mosquitoes with different numbers of these sense organs missing towards the testing stimuli, it was possible to reach indirect conclusions as to the possible functions of the types of sense organs. According to this:

1) Sensilla coeloconica are the possible chemoreceptors. The reviews of SNODGRASS (1935) and WIGGLESWORTH (1953) support such a conclusion. Every pit in each sensillum contains only one single seta, but in other dipterous insects several setae were found in each pit (ROEHLER, 1906; SMITH, 1919; Hsü, 1938; BEGG & HOGBEN, 1946; WIESMANN, 1960), whereas the pit is either in the form of simple or compound cavities. Although this type is present in the antennae of *Anopheles maculipennis* and several dipterous insects, they do not exist in Culicini mosquitoes. NAGEL, according to MCINDOO (1918) and SMITH (1919), did not find pits in the antennae of *Culex pipiens*, nor did ROTH (1949) and ROTH & WILLIS (1952) in *Aedes aegypti*.

2. Sensilla basiconica are the possible hygromoreceptors. They are concentrated mostly on the terminal segments in contrast to the coeloconic sensilla which are concentrated on the basal flagellar segments. These sense organs are receptors for mediating wet reactions because we used only 75-85% R.H. and since our experiments did not deal with the effect of dryness on the behaviour of the mosquitoes, we cannot conclude that these receptors serve as well to mediate dry reactions. In some insects it has been shown that there exist two types of receptors which mediate a wet and a dry reaction. These two types of receptors may exist on different parts of the body (BEGG & HOGBEN, 1946; ROTH & WILLIS, 1951 b) or on the same appendage (ROTH & WILLIS, 1951 a, b, 1952; BAR-ZEEV, 1960).

3) Concerning sensilla campaniformia, there are two probabilities for its possible function. Each one has its supporting evidence. From the fact that they are present in the antennae of both males and females it can be assumed, as many authors have found, that this type is for perceiving mechanical stimuli.

The second probability is based on the experimental results. The avoidance of relatively low temperature ($25-26^{\circ}\text{C}$), in combination with other factors, by female mosquitoes is upset if the last terminal segment is removed, and as long as half of the campaniform sensilla exist on this segment and few of the other types, it is strongly possible that it possesses an inhibiting character for relatively low temperature. With regard to our experiments, this leads us to think that temperature under 28°C is not only unattractive to mosquitoes (BATES, 1949) but even inhibits them. But we are not in a position to decide whether the campaniform sensilla possibly perform one of these two functions (and if so, which) or both together.

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Résumé.

1^o L'auteur a étudié la morphologie, l'histologie, la répartition et le nombre d'organes sensoriels (sensilles) sur les antennes d'*Anopheles maculipennis* des deux sexes.

2^o Les antennes des mâles et des femelles se composent de 15 articles : un scape, un pédicelle et 13 articles du flagelle. Les antennes diffèrent sensiblement selon le sexe. Celle de la femelle est plus courte et possède de nombreux sensilles à cuticule mince sur tous les articles du flagelle, excepté sur l'article basal 1. Sur l'antenne mâle, par contre, les sensilles à cuticule mince sont limités aux deux derniers articles. Les autres articles du flagelle, ainsi que la base de l'article 12 portent des touffes de longues soies à cuticule épaisse, connues pour enregistrer le son du vol des femelles.

3^o On trouve 7 types différents de sensilles sur les antennes. Type I et II sont des soies raides à cuticule épaisse. Types III et IV sont des sensilla trichodea à cuticule mince. Type V sont des sensilla basiconica à cuticule mince. Type VI sont des sensilla coeloconica formés d'une cavité de laquelle s'élève une seule pointe à cuticule mince. Ce dernier type ne se trouve pas chez *Culex pipiens* ou chez *Aedes aegypti*. Le type VII est semblable aux sensilla campaniformia et n'a pas été mentionné auparavant dans la description d'antennes de moustiques.

4^o On a construit un appareil spécial afin d'examiner l'attraction qu'exercent sur les moustiques femelles des facteurs transmis par air tel que l'odeur corporelle, l'humidité et la chaleur.

5^o Un saut de température de 26° à 34° C active davantage les réactions des moustiques que l'odeur du corps ou le degré d'humidité. C'est le facteur le plus

important pour inciter les moustiques à se poser sur la source d'attraction et à y puiser du sang.

6° La combinaison de l'odeur corporelle avec un degré d'humidité de 75-85 % RH et une température de 25° à 26° C (condition de la chambre d'expérimentation) n'a provoqué qu'une réaction relativement faible. Cette réaction a considérablement augmenté avec une autre combinaison dont l'odeur corporelle était exclue et la température élevée à 34° C (équivalent à la température de la main). La plus forte réaction a été enregistrée lorsque l'odeur corporelle a été ajoutée à cette dernière combinaison.

7° On a étudié les fonctions possibles des organes sensoriels des antennes de moustiques femelles en amputant progressivement les articles du flagelle. Les résultats des tests d'attraction des moustiques après amputation ont été examinés en relation avec la morphologie, l'histologie, la répartition et le nombre des organes sensoriels du flagelle.

8° Chez les moustiques femelles, les sensilla coeloconica sont concentrés pour la plupart sur les articles basaux et semblent jouer un rôle chimioréceptif, alors qu'au contraire, les sensilla basiconica se trouvent sur les articles terminaux et conditionneraient l'hygrotropisme. Les sensilla trichodea sont répartis sur tout le flagelle et servent probablement au thermotropisme (type III et IV).

9° Lors du test d'attraction des moustiques par une combinaison d'odeur corporelle, de degré d'humidité de 75-85 % RH et de température de 25° à 26° C (température de la chambre d'expérimentation) l'attraction augmente après l'amputation du dernier article. Cela laisse supposer que dans le dernier article se trouvent des organes sensoriels (probablement les sensilla campaniformia) qui ont un effet inhibitif à une température relativement basse. Il semble, en effet, qu'à une température inférieure à 28° C les réactions de moustiques non opérés seraient inhibées vis-à-vis de leur hôte.

Zusammenfassung.

1. Es wurden die Morphologie, die Histologie, die Verteilung und Anzahl der Sinnesorgane (Sensillen) auf den Antennen männlicher und weiblicher *Anopheles maculipennis* studiert.

2. Bei beiden Geschlechtern bestehen die Antennen aus 15 Segmenten, nämlich aus Scapus, Pedicellus und 13 Flagellar-Segmenten. Sie sind nach dem Geschlecht deutlich unterscheidbar. Die Antennen des Weibchens sind kürzer und weisen zahlreiche dünnhäutige Sensillen auf allen Flagellar-Segmenten auf, außer auf dem Basal-Segment 1. Bei denjenigen des Männchens sind solche dünnhäutige Sensillen auf die äußersten zwei Segmente beschränkt; die übrigen Flagellar-Segmente und die Basis von Segment 12 tragen Kränze sehr langer, dickhäutiger Fibrillen, von denen bekannt ist, daß sie als Rezeptoren für das Summen fliegender Weibchen dienen.

3. Es werden 7 Typen von Antennen-Sensillen unterschieden. Die Typen I und II sind steife, dickwandige Borsten, Typen III und IV sind dünnhäutige Sensilla trichodea. Typus V sind dünnwandige Sensilla basiconica. Bei Typus VI handelt es sich um Sensilla coeloconica, bei denen in der Vertiefung je ein zartwandiger Stift steht. Dieser Typus kommt weder bei *Culex pipiens* noch bei *Aedes aegypti* vor. Typus VII gleicht den Sensilla campaniformia und wurde bisher noch nie in Beschreibungen von Mücken-Antennen erwähnt.

4. Um die Reaktion der Mückenweibchen gegenüber den durch einen Luftstrom übertragenen Reizen wie Duftstoffe des Körpers, Feuchtigkeit und Wärme zu untersuchen, wurde eine spezielle Apparatur erbaut.

5. Einer Erhöhung der Temperatur von 26° C auf 34° C kommt für das Absitzen der Mücken eine größere Bedeutung zu als den Duftstoffen oder der

Feuchtigkeit. Der Wärme-Unterschied bildet den ausschlaggebenden Reiz, der das Absitzen und die Stechversuche der Mücke an der Attraktionsquelle auslöst.

6. Bei der Kombination von Duftstoffen mit einer relativen Luftfeuchtigkeit von 78-85% und einer Temperatur von 25—26° C (entsprechend der Raumtemperatur) blieb die Reaktion verhältnismäßig schwach. Dagegen bewirkte die Kombination von 34° C (entsprechend der Temperatur einer menschlichen Hand) mit demselben Feuchtigkeits-Grad, aber ohne Duftstoffe, eine wesentlich verstärkte Reaktion. Diese erreichte ihr Maximum, wenn derselben Kombination noch Duftstoffe beigelegt wurden.

7. Die Funktionen der Sinnesorgane auf den Antennen der weiblichen Mücken wurden durch progressives Amputieren der Flagellar-Segmente ermittelt. Es wurde die Reaktionsfähigkeit der solchermaßen amputierten Tiere auf die anziehenden Faktoren geprüft und diese Resultate mit den Befunden der Morphologie, Histologie, Verteilung und Anzahl der Sensillen verglichen.

8. Bei den weiblichen *Anopheles* sind die *Sensilla coelonica* größtenteils auf dem Basal-Segment konzentriert und wirken wahrscheinlich als Chemorezeptoren. Die *Sensilla basiconica* finden sich im Gegenteil auf den terminalen Segmenten und dürften Hygrorezeptoren sein. Die *Sensilla trichodea* (Typus III u. IV) sind auf alle Segmente verteilt und dienen vermutlich der Wärme-Empfindung.

9. Die Anzahl der angelockten Mücken steigt nach Amputation des Endgliedes bei der Kombination von Duftstoffen mit einer relativen Luftfeuchtigkeit von 75-85%, bei einer Temperatur von 25-26° C (Zimmertemperatur), an. Dies deutet darauf hin, daß auf dem terminalen Segment Sinnesorgane sitzen (möglicherweise die *Sensilla campaniformia*), welchen bei verhältnismäßig tiefer Temperatur eine Hemmwirkung zukäme. Es scheint, daß nicht-amputierte Mücken bei Temperaturen unter 28° C in ihrer Reaktion gegenüber dem Wirt gehindert werden.