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Comparative Study of Sense Organs in the Antennae of Culicine and Anopheline Female Mosquitoes.*

By I. A. H. ISMAIL.

Introduction.

Sense organs in the antennae of female mosquitoes have received much attention because of their importance in the attraction of mosquitoes to man.

In our previous paper (ISMAIL, 1962), we studied thoroughly the sense organs in the antenna of the female mosquito *Anopheles maculipennis atroparvus*; morpho-histology, number, distribution on the different flagellar segments, and possible function were discussed. Several types of sense organs have been found. If we compare our findings with the studies of SMITH (1919) and ROTH & WILLIS (1952), on the sense organs in the antennae of *Culex pipiens* and *Aedes aegypti* respectively, variations in the types of sense organs are apparent. *Anopheles maculipennis* carries coeloconic and campaniform sensilla, while in no case is mention made of these two types in the antennae of the other two species. This prompted us to carry out the present work, in which we endeavoured to ascertain the types of sense organs; their number and distribution on the antennal segments in several species of mosquitoes (*Culex pipiens* [Linné], *Culex fatigans* [Wiedemann], *Aedes aegypti* [Linné], *Anopheles gambiae* [Giles], *Anopheles stephensi* [Liston]). Our findings reveal new morphological variations between the two tribes of Culicini and Anophelini mosquitoes. Hence, these variations might explain the differences in their behaviour.

The writer would like to express his gratitude to Prof. Dr. R. Geigy for suggesting the subject of this paper. Thanks are also due to Mr. I. Bigland for his help during the preparation of the manuscript and to the Swiss Tropical Institute for providing the material.

Material and Technique.

To prepare the antennae for the studies of their sense organs, we followed the same technique we employed (ISMAIL, 1962) for the antenna of *Anopheles maculipennis*. The findings with this species were also used in the present work, to provide more specimens for comparison purposes.

All given numbers of sense organs represent their averages in five antennae.

Antennae of Female Mosquitoes.

The antennae in both *Culicini* and *Anophelini* mosquitoes are made up of 15 segments, comprising a scape, a pedicel, and

Dedicated to Prof. Dr. R. Geigy, Rector of the University of Basle and Director of the Swiss Tropical Institute, on the occasion of his 60th birthday (December, 1962).



Fig. 1. Antennae of female mosquitoes with the sense organs distributed on their walls. A: *Aedes aegypti*. B: *Anopheles maculipennis*. (Drawn from ISMAIL, 1962.) C: *Culex pipiens*. Magnification 700 \times .

13 flagellar segments. The scape is an irregular chitinous ring, connected with a rounded pedicel which carries a few scales and short articulated thick-walled sensilla. Some of these sensilla are branched (plumose hairs).

The length ¹ of the antennae (Fig. 1), as well as the number of sense organs (sensilla) in the form of hairs distributed on the flagellum, differs in the various species. In *C. pipiens* and *C. fatigans*, the antenna measures about 2.30 mm and 2.25 mm, and carries about 1,300 and 1,350 sense organs respectively. In each case, there are about 150 organs with thick walls, while the rest are thin-walled sensilla. In *Aedes aegypti*, the antenna is shorter. It measures about 2.00 mm and at the same time the flagellum carries fewer sense organs, about 1,000. This number includes 150 organs, the same as in *C. pipiens* and *C. fatigans*, with thick walls.

The antennae in the anophelines are smaller than in the culicines. Their lengths are about 1.45 mm, 1.35 mm and 1.60 mm in *A. gambiae*, *A. stephensi*, and *A. maculipennis* respectively. At the same time the flagellum carries fewer sense organs—about 950 in *A. gambiae*, 1,000 in *A. stephensi*, and 900 in *A. maculipennis*. The anophelines, in spite of having fewer sense organs, possess more organs with thick walls. *A. gambiae* and *A. maculipennis* each carries about 200 and *A. stephensi* 275. Consequently the important thin-walled sensilla are better protected in the anophelines.

In culicine and anopheline mosquitoes, there are special areas in the antennal wall where the cuticle is very thin. They are almost rounded in shape and measure about $3\ \mu$ in diameter. From the lateral side and through the cuticle, we were able to see a structure (presumably a cell) (Fig. 2 H) attached to every specific area. No sections or histological examinations were done, and therefore the nature of this structure is not known. There are from 4 to 8 of these areas on the first basal flagellar segment and one on the second segment.

Types of Sensilla ².

According to their external structure, the sensilla are classified into several types (Fig. 2): thick-walled sensilla, long and short bristles; thin-walled sensilla, trichodea, basiconica, coeloconica; and campaniform sensilla. All these types are distributed on the flagellum of the species of mosquitoes investigated except coeloconic sensilla, which were found to be missing from the culicines.

¹ Lengths of the antennae are represented by the average of 12.

² Attention is drawn to the additional note at the end of the paper.

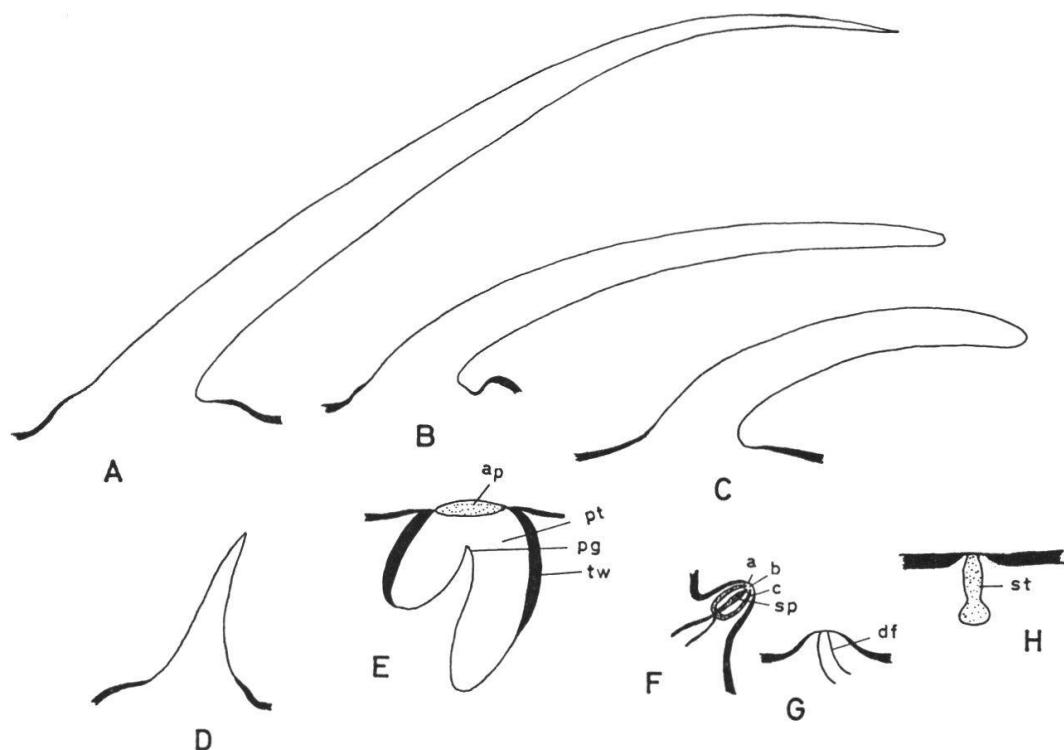


Fig. 2. Diagrams showing the different types of sensilla. A: Trichoid sensillum with pointed tip. B: Trichoid sensillum with blunt tip. C: Short, very thin-walled trichoid sensillum. D: Basiconic sensillum. E: Coeloconic sensillum. ap: aperture; pg: peg-like structure; pt: pit; tw: thick chitinous wall. F: Campaniform sensillum in Anopheline (drawn from ISMAIL, 1962). a: outer lamella; b: inner layer; c: cuticular cylinder; sp: scolopale. G: Campaniform sensillum in Culicine. df: distal filament of presumably one or more sense cells. H: An almost rounded area in the antennal wall with thin cuticle. st: structure, presumably a cell.

The distribution of these types on the different segments of the flagellum in the various species is shown in Tables 1 and 2.

I. Long bristles.

Long, rigid thick-walled bristles, arising from a socket and ending at the apex in a sharp point. They project from a sub-basal area on segments 2 to 13.

Culicines.

The number in the culicines is always constant, being 6 on each segment with 4 bristles just below the apical end of the last one.

Anophelines.

The number varies on the different segments; it lies between 10 and 7 in *A. gambiae*, 9 and 6 in *A. stephensi*, and 8 and 6 in *A. maculipennis*. Below the apical end in the first and second

TABLE 1.

Distribution and number of long and short bristles* and sensilla trichodea on the antennae** of female mosquitoes, *C. fatigans*, *Aedes aegypti*, *A. gambiae*, *A. stephensi*, and *A. maculipennis*.

Flagellar Segments	Type I Long bristles		Type II Short bristles		Type III Sensilla trichodea		A. maculipennis	
	Ae. aegypti	A. gambiae	Ae. aegypti	A. gambiae	Ae. aegypti	A. gambiae		
1 (base)	undifferentiated		5	14	2	25	34	
2	6	6	6	9	7	8	27	
3	6	6	6	10	8	6	21	
4	6	6	6	9	7	5	17	
5	6	6	6	10	8	4	15	
6	6	6	6	9	7	3	11	
7	6	6	6	9	8	2	4	
8	6	6	6	9	8	2	1	
9	6	6	6	9	7	1	1	
10	6	6	6	8	7	6	1	
11	6	6	6	8	7	6	1	
12	6	6	6	7	6	1	1	
13 (tip)	6+4	6+4	6+4	7+1	6+2	6+4	0	
Total	76	76	76	105	92	86	34	
	27	36	56	135	80	424	479	
						477	500	
						507	529	
						573	573	
						618		

* Total numbers of long and short bristles are recorded without the undifferentiated sensilla on the basal segment.

** Average of five antennae.

TABLE 2.

Distribution and number of sensilla basiconica, coeloconica and campaniformia on the antennae* of female mosquitoes *C. pipiens*, *C. fatigans*, *Aedes aegypti*, *A. gambiae*, *A. stephensi*, and *A. maculipennis*.

Flagellar Segments	Type IV Sensilla basiconica						Type V Sensilla coeloconica						Type VI Sensilla campaniformia						
	<i>C. pipiens</i>	<i>C. fatigans</i>	<i>Ae. aegypti</i>	<i>A. gambiae</i>	<i>A. stephensi</i>	<i>A. maculipennis</i>	<i>C. pipiens</i>	<i>C. fatigans</i>	<i>Ae. aegypti</i>	<i>A. gambiae</i>	<i>A. stephensi</i>	<i>A. maculipennis</i>	<i>C. pipiens</i>	<i>C. fatigans</i>	<i>Ae. aegypti</i>	<i>A. gambiae</i>	<i>A. stephensi</i>	<i>A. maculipennis</i>	
1 (base)	13	11	0	0	0	0	—	—	2	1	2	2	3	3	3	2	0	0	0
2	22	14	4	0	6	0	—	—	—	5	3	0	0	0	0	0	0	0	0
3	21	17	6	0	7	0	—	—	—	6	5	4	0	0	0	0	0	0	0
4	20	14	7	2	8	1	—	—	—	4	5	4	0	0	0	0	0	0	0
5	19	17	8	4	8	2	—	—	—	4	5	4	0	0	0	0	0	0	0
6	18	16	9	5	8	3	—	—	—	4	4	3	0	0	0	0	0	0	0
7	20	16	8	5	8	4	—	—	—	4	3	2	0	0	0	0	0	0	0
8	19	15	9	7	8	6	—	—	—	2	0	2	0	0	0	0	0	0	0
9	18	20	9	7	7	8	—	—	—	2	0	1	0	0	0	0	0	0	0
10	22	12	10	7	8	—	—	—	—	0	0	1	1	1	0	0	0	0	0
11	21	21	10	13	11	9	—	—	—	0	0	1	0	0	0	0	0	0	0
12	25	24	11	15	13	11	—	—	—	0	0	1	1	1	1	1	1	1	1
13 (tip)	27	26	12	16	16	10	—	—	0	0	1	2	2	2	3	3	3	3	3
Total	265	233	105	84	107	62	—	—	33	31	28	6	6	6	7	7	7	6	6

* Average of five antennae.

there are only 1 or 2 bristles projecting out, while in *A. maculipennis* there is always a constant number of 4 bristles, the same as in the culicines.

The first basal flagellar segment in the culicines and anophelines carries many undifferentiated bristles which fall between the two categories of long and short bristles.

II. Short bristles.

These are like the first type, but smaller and distributed particularly near the top of each segment. In all species, as shown in Table 1, these bristles have their maximum numbers on the basal flagellar segments, and decrease gradually towards the apex. The anophelines carry more of this type than culicines.

III. *Sensilla trichodea*.

This type of sensillum has thin walls, and is not articulated at the base. The length varies greatly. The tip is either pointed or blunt and accordingly we divided this type into two forms:

- a) *Sensilla trichodea* with pointed tips (Fig. 2 A);
- b) *Sensilla trichodea* with blunt tips (Fig. 2 B).

The difference between these two forms is very clear in the culicines, and therefore their numbers and distributions were examined separately, but in the anophelines all the trichoid sensilla look more or less the same, with pointed tips, and therefore they were counted together.

Culicines.

In *C. pipiens* the antenna carries about 424 pointed and 477 blunt trichoid sensilla. The difference in number between the two forms is not great, but the distribution varies considerably. The pointed sensilla have their lowest number of 5 on the basal segment and then they increase, fluctuating between 29 and 45 on the following segments. The highest number is carried on the last terminal segment. In the case of the blunt form on the other hand, 25 sensilla are located on the basal segment, and the maximum of 62 and 61 on segments 2 and 3 respectively, while the number then decreases gradually on the following segments till it reaches the minimum of 17 on the last one.

In *C. fatigans*, the pointed and blunt trichoid sensilla are more or less equal in number, 479 and 500, and in their distribution they follow the same pattern as in *C. pipiens*.

In *Aedes aegypti*, the number of pointed sensilla is about half that of the blunt ones, i.e. 245 and 507 respectively. These blunt sensilla are similar to those in *C. pipiens* and *C. fatigans*, in number as well as in distribution patterns, while the pointed sensilla are less and their distribution is different. Their numbers on the basal segments are much lower.

Anophelines.

The basal segment in *A. gambiae* carries few trichoid sensilla, 6, and the second carries the comparatively high number of 26; the number then increases and fluctuates on the following segments between 40 and 67, the highest being found on the last segment.

In both *A. stephensi* and *A. maculipennis*, the basal segment does not carry any of this type of sensillum, and the second carries only a few, 5 and 10 respectively. The third segment in *A. stephensi* still carries the small number of 17, and the fourth, 32. On the following segments, 5 to 12, the number increases and fluctuates between 42 and 62. The last segment carries the highest number of sensilla, 84.

While the third segment in *A. stephensi* carries few trichoid sensilla, we find that this segment in *A. maculipennis* carries the high number of 39, the number then increasing and fluctuating between 42 and 64 on the following segments.

The number of trichoid sensilla carried on the whole flagellum is about the same in *A. gambiae* and *A. maculipennis* (629 and 618 respectively), and slightly less in *A. stephensi* (573).

During our studies, we were able to detect a special form of trichoid sensillum (Fig. 2 C), found occasionally on the various segments in small numbers. They are shorter than the normal trichoid sensilla. The tips are blunt, their walls are thinner than the walls in any other form or type of sensilla, and they lie very close to the surface of the antennae.

In *C. pipiens* and *C. fatigans*, there are from 2 to 6 sensilla of this form on each of the three basal segments, and from 0 to 2 on the following ones. In *Aedes aegypti*, the number varies between 0 and 3 on the various segments, and in *A. gambiae*, there is none on the basal segment, and from 0 to 6 on each of the rest. Usually the few terminal segments (2 to 6), are free from such a form of sensillum.

In our preparations, we were able to see through the thin walls of these sensilla a large number of very small droplets distributed on the inner surface. This would be a proof that this form of sensillum is permeable through the whole surface of the sensillum, and thus strongly supports the conclusions of authors such as SLIFER (1954), working with other insects, that such structures may serve as chemoreceptors, hygroreceptors, or both. On the sensory pegs on the antenna of the grasshopper, SLIFER (1956) was able to detect a small specialised region through which water and dyes in aqueous solution pass readily. This specialised area is at the tip in a few types, while in others it is located at the base. Therefore, it is of interest to show that the permeability of our type of short trichoid sensillum extends through the whole surface, as stated in the literature, and not through specialised areas as stated by SLIFER in connection with the sense organs in the antennae of the grasshopper.

IV. *Sensilla basiconica*.

Short peg-like sense organs (Fig. 2 D). The thickness of their walls lies between that of the normal and the short trichoid sensilla. The number of pegs, as well as their distribution, is quite different in the various species, but on the whole, their numbers are more or less higher on the terminal segments than on the basal ones.

The flagellum in *C. pipiens* and *C. fatigans* carries a high number of this type, 265 and 233 respectively, while in *Aedes aegypti* and *A. stephensi*, it carries less, 105 and 107, and in *A. gambiae* and *A. maculipennis* even much less, 84 and 62 respectively.

Culicines.

On the basal segment in *C. pipiens*, there are 13 pegs, and on the following segments the number fluctuates between 18 and 27. In *C. fatigans*, the distribution differs to some extent. The basal segment carries 11 pegs, and each of the following ones carries a number of between 14 and 26.

In *Aedes aegypti*, the total number of pegs carried on the flagellum is less than that in *C. pipiens* and *C. fatigans* being 105, and at the same time no pegs were found on the basal segment. The second segment carries 4 pegs, and on the following segments the number increases more or less till it reaches the maximum of 12 on the last one.

Anophelines.

In *A. gambiae* and *A. maculipennis*, no pegs exist on the first three basal segments, and 2 and 1 are present on segment 4. The number increases gradually towards the apex of the antenna, with variations of 1, 2 or 3, and reaches the maximum of 16 on the last segment in *A. gambiae*, and the maximum of 11 and 10 on segments 12 and 13 in *A. maculipennis*.

In *A. stephensi*, the basal segment is usually free from pegs; in rare cases it carries one. In contrast to *A. gambiae* and *A. maculipennis*, the second and the third basal segments each carries several pegs. The number of pegs on segments 2 to 10 varies between 6 and 8, while on the last three segments the number increases considerably to 11, 13 and 16.

On the basal segments in *A. stephensi*, unlike all the other species of mosquitoes studied, the peg organs exist in groups, each group consisting of 2, 3 and sometimes 4 pegs. This arrangement differs in a few antennae, where the pegs exist singly and their numbers on each of the second and third basal segments are reduced to 2 to 4.

V. Sensilla coeloconica.

The coeloconic sensillum consists of one single, thin-walled peg sunk into a depression of the antennal wall (Fig. 2 E). The sensillum is seen on the surface of the antennae as a dark chitinous ring with a nearly rounded aperture inside.

Culicines.

The antennae in the culicines are entirely free from this type of sense organs, since we did not see any pits on their walls.

Anophelines.

The anophelines carry sense organs of this type. Their numbers on the whole flagellum are more or less the same; 33 in *A. gambiae*, 31 in *A. stephensi*, and 28 in *A. maculipennis*.

The organs are concentrated on the basal segments; in *A. gambiae* there are 2 on segment 1, and 5 and 6 on segments 2 and 3, the number then decreasing to 4 on segments 4, 5, 6 and 7, and to 2 on segments 8 and 9. No organs exist on segments 10 to 13.

In *A. stephensi*, segment 1 carries 4 organs, segments 2 to 5 carry 5 each, and on segments 6 and 7 the number decreases to 4 and 3. Segments 8 to 13 do not carry any of this type.

A. maculipennis has 1, rarely 2, on segment 1, the highest

number, 3 or 4 being on segments 2, 3, 4, 5, and 6; it then decreases to 2 on segment 7 and 8 and to one on the remaining segments.

The main difference in the distribution of this type of sense organs between the various members of the anophelines is as follows: *A. maculipennis* carries one and rarely two organs on each segment from 9 to 13, while *A. gambiae* and *A. stephensi* carry no organs on segments 10 to 13 and 8 to 13 respectively.

VI. *Sensilla campaniformia.*

This type was mentioned for the first time in connection with the sense organs in the antennae of mosquitoes in our previous paper (ISMAIL, 1962). The organs appear externally at the top of the segments as very small swellings which measure about $4\ \mu$ in length and $3\ \mu$ in diameter. They were found in the antennae of the anophelines, but another form, much simpler, as shown in Fig. 2 G, was found in the culicines. Its external swelling is about $2\ \mu$ in length and $3\ \mu$ in diameter, and the internal construction, which could be partly seen through the antennal wall, is quite different. The internal construction of this form in the anophelines was described by us (ISMAIL, 1962) (Fig. 2 F) in the following terms: "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." In the culicines the internal construction is quite different, as only the distal filament of one sense cell (or may be more) is clear.

Culicines.

There are 1, 2, and rarely 3 organs on the first basal segment, and always one on segment 10 and 12. Both tips in segment 13 end with one, while segments 2 to 9, and 11 are completely free from this type.

Anophelines.

The basal segment always carries 3 organs in *A. gambiae*, 2 in *A. maculipennis*, and between 2 and 4 in *A. stephensi*; segments 2 to 11 carry none, while segment 12 carries one. In segment 13, both tips end with one and a third is found just below the long bristles.

Note by the Editor.

In agreement with the author we should like to point out that, while the present paper was in press, C. C. STEWARD & C. E. ATWOOD published their

work "The Sensory Organs of Mosquito Antenna" in the Canadian Journal of Zoology, 41, 1963, 577-594.

In order to make it easier to compare the two papers, a list of the respective terms follows:

Steward & Atwood		Ismail
Large bristles	Sensilla chaetica	Type I Long bristles
A_1	S. tricho(i) dea	Type IIIa (with pointed tip)
A_2	S. tricho(i) dea	Type IIIb (with blunt tip)
A_3	S. basiconica	Type IV
A_4	S. coeloconica	Type V
B—Small bristles	S. chaetica	Type II Short bristles
C—	S. campaniformia	Type VI

Furthermore, the lists giving the numbers of sensilla found on the antenna of female *Aedes aegypti* are reproduced in part hereafter. The reader will note that the numbers mentioned by ISMAIL are somewhat higher than the ones of STEWARD & ATWOOD.

Segment No.	Steward & Atwood			Ismail		
	A_1	A_2	A_3	Type IIIa	Type IIIb	Type IV
1	1	24	0	2	29	0
2	2	40	3	6	49	4
3	4	50	3	8	52	6
4	5	43	5	10	56	7
5	5	40	6	11	48	8
6	6	38	7	15	51	9
7	7	32	7	16	45	8
8	10	28	7	16	45	9
9	13	25	7	23	32	9
10	20	22	8	28	34	12
11	22	16	8	31	25	10
12	25	14	11	34	22	11
13	28	12	11	45	19	12
totals	148	384	83	245	507	105

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Zusammenfassung.

1. Es wurde eine vergleichende Untersuchung über die Morphologie, die Anzahl und Verteilung der Sinnesorgane (Sensillen) auf den Antennen weiblicher Culicinen (*C. pipiens*, *C. fatigans*, *Aedes aegypti*) und Anophelin (A. *gambiae*, *A. stephensi*, *A. maculipennis*) durchgeführt.
2. Es werden folgende Typen von Sensillen unterschieden: dickwandige Sensillen; lange und kurze Borsten; dünnwandige Sensillen; s. trichodea, s. basiconica und s. campaniformia.
3. Die Anzahl von Sensillen beträgt pro Antenne bei *C. pipiens* ungefähr 1300, bei *C. fatigans* 1350, bei *Aedes aegypti* 1000, bei *A. gambiae* 950, bei *A. stephensi* 1000 und bei *A. maculipennis* 900.
4. Die Sensilla trichodea der Culicinen haben zum Teil spitze, zum Teil stumpfe Enden, während bei den Anophelin alle ziemlich gleich spitz enden. Bei allen Arten werden gelegentlich auf den verschiedenen Segmenten kurze, sehr dünnwandige Sensilla trichodea mit stumpfen Enden gefunden. Bei diesen Sensillen können auf der Innenseite der Oberfläche viele winzige Tröpfchen beobachtet werden, was darauf hinweist, daß ihre gesamte Oberfläche durchlässig ist.
5. Die Sensilla basiconica sind bei *C. pipiens* und bei *C. fatigans* in viel größerer Anzahl vorhanden als bei *Aedes aegypti* und bei den Anophelin. Ihre Verteilung auf den Antennen variiert stark je nach den Arten.
6. Die Sensilla coeloconica fehlen bei den Culicinen, während sie für die Anophelin characteristisch sind. Sie sind auf die basalen Flagellar-Segmente konzentriert, auf den Terminalsegmenten findet man höchstens eine solche Sensille.
7. Die Sensilla campaniformia der Culicinen unterscheiden sich von denjenigen der Anophelin durch ihre einfache Struktur.
8. Die Anzahl und Verteilung der verschiedenen Typen von Sensillen auf den Antennen werden auf zwei Tabellen dargestellt.

Résumé.

1^o L'auteur s'est livré à une étude comparée de la morphologie, du nombre et de la répartition des organes sensoriels sur l'antenne de Culicinés et d'Anophelinés femelles (*C. pipiens*, *C. fatigans* et *Aedes aegypti* d'une part, *A. gambiae*, *A. stephensi* et *A. maculipennis* d'autre part).

2^o Les organes sensoriels peuvent être classifiés comme suit : sensilla à cuticule épaisse ; soies longues et courtes ; sensilla à cuticule mince ; s. trichodea, s. basiconica et s. campaniformia.

3^o Chaque antenne porte environ 1300 organes sensoriels chez *C. pipiens*, 1350 chez *C. fatigans*, 1000 chez *Aedes aegypti*, 950 chez *A. gambiae*, 1000 chez *A. stephensi* et 900 chez *A. maculipennis*.

4^o Les Sensilla trichodea des Culicinés ont des terminaisons soit pointues, soit émoussées, alors que chez les Anophelinés les organes sont plus ou moins les mêmes avec des terminaisons pointues. Dans toutes les espèces les divers segments portaient occasionnellement de courts organes sensoriels, s. trichodea, à pointes émoussées et cuticule très mince. Leur surface interne était couverte

d'un grand nombre de très petites gouttes. Ceci démontre que la perméabilité de ce type de sensille s'étend à toute la surface.

5^o Les organes sensoriels du type basiconica sont beaucoup plus nombreux chez *C. pipiens* et *C. fatigans* que chez *Aedes aegypti* et les Anophélinés. Leur répartition varie grandement selon les espèces.

6^o Les organes sensoriels du type coeloconica n'existent pas chez les Culicinés alors qu'ils sont le caractéristique des antennes d'Anophélinés. Ils sont concentrés sur les segments flagellaires basaux. Les segments terminaux, s'ils en possèdent, n'en possède qu'un seul.

7^o Les Sensilla campaniformia des Culicinés ont une structure différente de celle des Anophélinés en ce sens qu'elle est plus simple chez les Culicinés.

8^o Deux tables donnent le nombre et la répartition des différents types de sensilles.