A Revised Nomenclature for the Chaetotaxy of the Mosquito Larva

(Diptera: Culicidae)

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The recent recognition of species complexes within populations formerly believed to represent a single species has focused the attention of students of mosquitoes to a reexamination of characters previously used in the separation of species and to a search for new morphological features useful in diagnosis. The immature stages of mosquitoes offer a greater variety of morphological characters which can be studied quantitatively, analyzed, and used for recognition of species than do the adults. Until recently almost all the attention was paid to the head, a few thoracic and abdominal hairs and the terminal abdominal segments of the larva, and the trumpets, paddles and a few abdominal hairs of the pupa. The larval characters used have not been entirely satisfactory and in the last few years the pupal stage has attracted more attention in the search for additional diagnostic characters. This interest in the pupa has culminated in the work of Knight and Chamberlain (1948) who made a comparative study, devised a new nomenclature, and illustrated the complete chaetotaxy of representatives of practically all the genera. The study of the larva has not progressed as rapidly, perhaps because of the greater complexity of the chaetotaxy, since the larva has upward of 200 pairs of hairs while the pupa appears to have about 105 pairs. The complete larval chaetotaxy for the majority of the genera is still unknown. In the course of a study on the genus *Uranotaenia* from the Solomon Islands, the complete larval chaetotaxy of seven species was described and figured by the author. In the preparation of descriptions it became evident that the existing nomenclatures were not entirely satisfactory as various combinations of numerical, alphabetical and nominal terminologies have been used by different workers according to their individual preferences and no system used all the elements of the larval chaetotaxy known at the present time. It seemed advisable, therefore, to prepare a uniform nomenclature which would (1) take into account all the established elements of the chaetotaxy of the fourth instar mosquito larva, (2) allow for the later inclusion of certain elements now poorly known, (3) show homologies where they have been established, (4) be equally suitable for anophelines and culicines, and (5) be easy to use in descriptions.

The chaetotaxy of mosquito larvae has been thoroughly studied by a large number of workers, notably Martini, Christophers, Puri, Root, Edwards, Barraud, Baisas, and Hurlbut. With the exception of the mouthparts it is believed that all the hairs have been described. The system of nomenclature devised originally by Martini and greatly modified and improved by various workers is based on the homology of hairs of anopheline and culicine larvae with those of the subfamily Dixinae. Since it shows so clearly the common pattern of chaetotaxy in the entire family and provides us with means of determining relationships and evolutionary lines, this system seems to be ideal and it would appear foolhardy and unwise to discard it. Therefore, it is retained almost entirely in the revised nomenclature proposed here and is modified extensively only on the head by renumbering certain hairs to allow for an orderly numbering of appendicular hairs in separate sequences, and on the terminal abdominal segments where a completely artificial nomenclature is introduced. The other changes suggested are minor ones on the thorax and abdominal segments. It may be argued that a revised nomenclature should not be attempted until a comparative study of all the genera has been made. Such a study, undoubtedly, would be desirable. On the other hand the general pattern of chaetotaxy is already known so that it is unlikely that any new elements will be added to the basic pattern for which no provision has been made in this system. Furthermore it is impossible for one individual to study an adequate number of forms since it appears that, at least in some genera, there are several different plans of chaetotaxy and all these would have to be taken into account. It is the intent of the author to review the chaetotaxy of mosquito larvae, to discuss the criteria of homologies, and to provide in one paper a basis for other workers in the field so that eventually such a comparative study may be accomplished cooperatively.

BASIC PATTERN OF CHAETOTAXY

The basic plan of chaetotaxy of a mosquito larva consists of 15 pairs of hairs per segment arranged in an orderly linear bilateral manner from middorsal to midventral lines. This complete number of hairs is retained in at least a few abdominal segments of apparently the majority of species of mosquitoes. Two pairs are usually poorly developed and one or both may be entirely absent. They were originally overlooked in the nomenclature. If one considers only the 13 pairs of hairs normally well developed, then all mosquitoes have them on abdominal segments II through VII, without any exceptions known to me. In all mosquitoes, certain of these abdominal hairs always have a characteristic position corresponding from species to species in anophelines and culicines and furthermore show a corresponding degree of development as far as length and branching are concerned. The first abdominal segment usually lacks one or more additional pairs of hairs. The terminal abdominal segments are greatly modified, differently in the anophelines from other mosquitoes, but even here there is a complete correspondence in all the forms.

On the thorax there are three groups of hairs corresponding to the three segments forming this tagma. The primitive number of 15 pairs of hairs is retained on the prothorax of at least some anophelines and sabethines. The mesothoracic group has 14 pairs of hairs in all mosquitoes and the metathoracic 13. As on the abdomen, certain hairs or groups of hairs show a similar position, degree of development, and association in species of widely divergent lines.

As the head consists of a number of segments completely fused together and is a highly specialized tagma its chaetotaxy is greatly modified. The head capsule appears to have 16 pairs of hairs primitively. One or two pairs of these are frequently absent but the remainder occur in definite positions in all mosquitoes. Of the head appendages, only the antenna has been adequately studied and it too has a uniform pattern of chaetotaxy, bearing 6 hairs in the same relative position in all species of mosquitoes.

It seems obvious, therefore, that the chaetotaxy of mosquito larvae is generally homologous (from species to species) in all forms and that furthermore it is serially homologous in each species except for the head and its appendages and the anal segment. That general and serial homologies extend to individual hairs seems unquestionable also, since at least certain corresponding hairs are developed in a similar manner and furthermore it seems likely that such uniformity in the general pattern could arise in the entire group only if homologous units were involved.

CRITERIA FOR HOMOLOGY

When it comes to actually determining the general homology of individual hairs in different forms, the greatest difficulties have arisen in the more generalized tagma of the body, the abdomen. The chaetotaxy of the head, and perhaps its appendages, is so set that no difficulties are usually encountered in general homologies. The criterion used is that of position of the hair—not its absolute position but its relative position to certain constant morphological features of the exoskeleton and its relation to other hairs. The degree of development, length, and branching are of no particular value, neither is the absolute position since it is affected by differential development of the head capsule. Individual variation in position is not great on the head of the larva. The same criterion is applied to the anal segment where the chaetotaxy is greatly reduced and very uniform.

Homologies on the thorax are relatively easy to determine. Although no sclerites are present and other morphological features are lacking, hairs 9 to 12 uniformly occur as a group which serves as a land mark for general homologies as well as serial homologies. Except for hair 0 on the prothorax, hair 14 (old terminology) on the prothorax and mesothorax, and hairs 3 and 4 of the metathorax of anophelines, all the hairs retain their relative position to each other in regular numerical sequence but may show shifts in cephalic or caudal direction. Individual variation in position is slight. A great deal of variation in the development of the various hairs occurs in different groups and between the three segments within a particular group of species. Several homologies within the thorax are dependent almost entirely on position of a hair in relation to another hair of definite position and of characteristic development, branching or basal tubercle. It is probable that, as interpreted in the past, the thoracic chaetotaxy is serially homologous with that of abdominal segments with the possible exception of the prothoracic hair 0 in all forms and median dorsal hairs of the anopheline metathorax. To determine this more definitely would require the examination of a large number of species from many different groups. Furthermore it cannot be done satisfactorily until a better understanding of abdominal chaetotaxy is at hand.

The chaetotaxy of the proximal abdominal segments has been studied to a limited degree in anophelines but has been almost entirely neglected in other mosquitoes. Most investigators, even in the case of anophelines, have been determining homologies largely on the basis of direct comparison of individual species, segment for segment, with previously published figures and basing their homologies primarily on the degree of development of the hairs rather than their relative position. This has led to a multitude of different interpretations. It would appear from an examination of these interpretations that every hair changes position but that it generally tends to retain its characteristic branching and degree of development. To follow such a procedure is to disregard completely the criteria which have been found workable on the head and thorax, which have been investigated much more thoroughly. It is undoubtedly true that the chaetotaxy of abdominal segments is much more plastic than that of the head and thorax. Nevertheless it would appear that the same criteria should be used with the same relative weight as on the other regions of the body. It is also evident that the degree of development of a hair is a specific character while changes in position are supraspecific in nature.

In determining homologies in forms which exhibit serial as well as general homologies, it is essential that a basic segment be chosen as a starting point. Such a segment should show as closely as possible the primitive condition and be least modified in all the forms considered. It is well known that different segments of a segmented animal may specialize in different ways even in closely related forms and, therefore, direct comparison, segment for segment, is dangerous. Such a basic primitive segment for the chaetotaxy of mosquito larvae is unquestionably the second abdominal segment. It shows, in all the forms examined, a remarkable constancy in position of hairs and a full complement of hairs which can be easily homologized from species to species. Almost invariably all the hairs are present in a regular linear numerical sequence from middorsal to midventral line and any departure from this can be easily determined. Thus general homologies are usually very simply made. In cases where the hairs are arranged in two rows on the dorsal and ventral surfaces or there has been a shift in position, the criteria outlined below for serial homologies are used. After the homologies are established for the basic second abdominal segment, serial homologies are determined for all the other segments. There is a considerable amount of shifting of hairs in different ways on different segments in various groups of species. It appears evident nevertheless that certain hairs always retain the same position, and that the extensive shifting is apparently largely confined to hairs 2 and 3 on the dorsal surface and to hairs 11 and 12 on the ventral surface. For homologies on the abdomen, the same criteria are used as for the cephalic and thoracic areas and in the same order of importance. It should be stressed again that it is the relative and not always the absolute position of a hair that is important. Most hairs, with the exceptions noted, tend to retain a definite relationship to each other. This is particularly important to remember when dealing with segments in which part or all of the hairs have been moved from their normal position through differential growth. In such cases, it appears that hairs now occurring in a new area have a tendency to develop in a different manner resembling hairs normally present in that area. This may seem to completely contradict the entire system. It is quite evident, nevertheless, from the relative position of other hairs that this actually occurs, for this reason little weight is placed on the length and branching of hairs which do not occur normally in a definite position on the segment.

The eighth abdominal segment and the spiracular lobe or siphon present a special problem which is discussed below. For reasons outlined there, it appears best to drop homologies with the proximal abdominal segments and adopt for the eighth segment proper, the spiracular lobe or siphon, as well as the anal segment, completely independent numerical terminologies which do not imply homologies with the rest of the abdomen.

The pupal chaetotaxy appears to bear a direct relationship to that of the larva, at least on the generalized abdominal segments. It may seem far-fetched to homologize them but striking similarities are evident: (1) the position of hair 13 of the pupa corresponds to hair 14 of the larva, (2) hair 1 of pupa occupies the same position as hair 0 of the larva, (3) hair 2 of the pupa occupies the same position as hair 1 of the larva, (4) hair 5 corresponds in both stages as does hair 8, (5) on the ventral surface hairs 9 and 10 exhibit the same relationship as they do in the larva. Furthermore corresponding hairs show shifts in position, for example pupal 3 and 4 equivalent to larval 2 and 3, and larval and pupal 11 and 12. Abdominal larval hair 13, which is usually well developed and stellate, is absent in the pupa, in line with the general reduction of the ventral hairs in this stage. It appears also that the arrangement of hairs on the dorsum of the second abdominal segment is more uniform and more easily homologized from species to species than on any other segment, in the pupa as well as in the larva. For these reasons, it might be advisable to re-examine the pupal nomenclature in the future and homologize it with the larval chaetotaxy.

GENERAL CONSIDERATIONS

The general plan of this revised nomenclature is the same as in the original Martini system, i.e. the designation of hairs by arabic numerals in sequence from middorsal to midventral line, and in cephalo-caudal sequence if more than one row of hairs is present. In several cases, in order to minimize confusion, hair 0 has been utilized to designate certain hairs which were originally overlooked and actually probably belong at the head of the sequence, but not always. The plan used for appendages is a numerical sequence starting at the proximal end and running to the apex, and on the latter extending from mesal to ectal surfaces. The same plan is utilized for the spiracular lobe or siphon and the anal segment, except that at the apex of these structures, the sequence is from dorsal to ventral externally, and mesal to ectal internally on the valves. Where a duplication of hairs occurs, as on the thorax of *Toxorhynchites* (=*Megarhinus*), or when a single number is given to a hair group, the individual elements are designated as 1a, 1b, 1c—etc. . . . as indicated in the discussions below.

One hundred and ninety-three pairs or groups of hairs are numbered in the present system. This number does not include the mouthparts, which have not been adequately studied, nor the dorsal, lateral, and ventral hairs of the sabethine siphon which are of restricted occurrence. The complete larval chaetotaxy of *Uranotaenia atra* Theo. is illustrated as no member of this genus has been previously figured. Figures of the head and terminal abdominal segments of *Anopheles walkeri* Theo. are labeled to indicate the principal changes in nomenclature proposed here.

In order to establish homologies for *Uranotaenia* it was necessary to study representatives of the majority of genera. Observations on these indicate that there is a multitude of specific and supraspecific characters in the abdominal as well as the thoracic chaetotaxy of culicine and sabethine larvae. The larval hairs are subject in most cases to less individual variation, particularly in position and to a lesser extent in branching, than those of the pupa. Since there appear to be several different chaetotaxy patterns in the larger genera, a great deal of work needs to be done before the various homologies are definitely established. It is hoped that more attention will be paid in the future to the abdominal and thoracic chaetotaxy of culicine and sabethine larvae. The study of species with well developed stellate hairs is particularly illuminating since the hairs are easily recognized by their characteristic development, and their migration or constant position can be readily determined. Such species occur in the majority of genera and particular emphasis should be placed on them.

In determining the homologies of lateral abdominal hairs it is necessary to examine unmounted whole larvae in which the relative positions are easily seen. Details of branching and the presence of abdominal hairs 0 and 14 are more easily determined from cast skins. Following this, drawings are best made from mounted whole larvae.

THE HEAD CAPSULE

Twenty-one pairs of head hairs have been given numbers in the modified Martini system. In addition to the hairs of the head capsule, these included two hairs on the antenna and three on the maxilla. Both the antenna and the maxilla have additional hairs which are constant in occurrence and show specific differences. Furthermore, other head appendages may prove, upon investigation, to have a constant chaetotaxy and will have to be recognized. It is proposed, therefore, to treat the head capsule separately from the appendages. This requires a renumbering of the head hairs since the 5 appendicular hairs were mixed in the previous terminology. Fortunately the proposed changes affect hairs which have seldom been used in descriptions, although they show good characters in some forms and should be studied more. It is believed that the renumbering, as here proposed, will facilitate descriptions since the hairs are located in a regular numerical sequence which is easy to follow.

TABLE 1.—Chaetotaxy of the head.

·Proposed System	Descriptive Terminology	Present Terminology	
		Numerical	Alphabetical
Head Capsule			
0*	Outer preclypeal	1a*	
1	Inner preclypeal, clypeal or labral spine	1	
2	Inner clypeal, inner anterior clypeal	2	
3	Outer clypeal, outer anterior clypeal	3	
4	Post clypeal, posterior clypeal, preantennal	4	d*
5	Inner frontal, inner postantennal, upper head hair	5	C*
6	Midfrontal, midpostantennal, lower head hair	6	B*
7	Outer frontal, outer postantennal, preantennal	7	A*
8	Sutural, inner occipital, vertical	8	e*
9	Transsutural, outer occipital	9	f*
10*	Supraorbital, orbital, dorsal eye hair	14*	
11*	Basal, subantennal	12*	
12*	Infraorbital, ventral eye hair	15*	
13	Subbasal, postmandibular	13	
14*	Post maxillary	18*	
15*	Submental	20*	
Antenna			
1*	Antennal, shaft hair	11*	
2*	Inner subapical, dorasl sabre		
3*	Outer subapical, ventral sabre		
4*	Terminal antennal	10*	
5*	Hyaline process, papilla		
6*	Finger process		

* Indicates a proposed change in nomenclature.

A maximum of 16 pairs of hairs occurs on the head capsule proper as follows: (* indicates a change in nomenclature)

*0. The outer preclypeal or outer labral hair was not recognized in the original system. It is usually a minute hair situated laterad of hair 1, either at the lateral extremity of the labral flap (preclypeus) or on its underside. It is generally flattened and translucent but may be elongate. In *Uranotaenia* it is well developed and shows good specific differences.

1. The inner preclypeal hair or clypeal spine is the most anterior and median hair on the labral flap (preclypeus). It is well developed in most species and shows good specific characters in many culicines. In predaceous species with the labrum reduced in the center and the anterolateral angles of the head capsule produced forward, it is caudad of hairs 0 and 3, and possibly 2.

2. The inner clypeal hair is well developed in anophelines and has been much used in descriptions. In the culicines it is usually absent but may be represented by a minute peg in a setal ring in certain *Aedes* or by a minute spine in some species of the subgenus *Culiciomyia.* No trace of it could be found in *Uranotaenia.* This hair is the median of the two pairs of hairs situated at the anterior border of the clypeus on the portion of this sclerite elevated above the labrum.

3. The outer clypeal hair is well developed in anophelines and shows excellent characters. In the culicines it is small but distinct, situated near the lateral anterior border of the clypeus. In sabethines and certain species of *Aedes,*

which have the head capsule rounded in front, what appears to be this hair is carried on the underside of the head capsule, above the base of the mouthparts where it joins hair 0. It is possible that the two hairs present in this position are 2 and 3, but since hair 0 is of more general occurrence than 2 in culicines and no trace of hair 0 could be found anywhere else on the "preclypeus" of these species, it appears that the first interpretation is correct.

4. The postclypeal hair is sometimes well developed in culicines and sabethines but is usually small in most mosquitoes. It is generally the most anterior and median of the "fronto-clypeal" hairs.

5 to 7. The inner (upper), median (lower), and outer (preantennal) frontal head hairs respectively are the three conspicuous dorsal head hairs, located in variable position on the "fronto-clypeus." They retain the above sequence in most cases.

8. The sutural head hair is located posteriorly (usually) near the lateral border of the "fronto-clypeus."

9. The transsutural hair is located laterad of the "fronto-clypeal" suture at the level of hair 8.

*10. The orbital hair is located laterally above the larval eye.

*11. The subantennal hair is located ventro-laterad near the base of the antenna.

*12. The infraorbital hair has a characteristic position laterally below the eye. It may migrate mesad but is always laterad of hair 13.

13. The subbasal or postmandibular hair is located mesad and usually caudad of hair 11 in anophelines. Depending on the shape of the head capsule it changes its position considerably in culicines, usually becoming associated with hair 12.

*14. The postmaxillary hair is ventral in position at the base of the maxilla. It shifts its position considerably in different forms and should not be confused with the basal maxillary hair with which it may be associated. The latter is located on a small triangular basal sclerite of the maxilla which may appear to belong to the head capsule but is actually separated from it by a suture.

*15. The submental hair is usually the most mesal of the ventral head hairs. It is located on the "submentum" when the latter is indicated by the "gular" sutures. When the latter are absent it is distinctly the most mesal of the ventral hairs.

THE ANTENNA

The six hairs which regularly occur on each antenna show excellent characters for the separation of species. Two of these hairs were formerly numbered along with the hairs of the head capsule, while the others were not considered in any numerical or alphabetical system. These hairs show considerable variation in position in different species but are easily homologized both in anophelines and culicines on the basis of the characters given below. They are numbered in a separate numerical sequence starting at the proximal end of the antenna as follows:

*1. The antennal shaft hair is variable in position and development but is nearly always proximal to the remaining hairs and easily identified.

*2. The inner subapical hair of the culicines arises subapically on the internal ventral surface but may be carried dorsad on the internal surface. The corresponding hair in anophelines is the dorsal sabre located near the internal angle of the ventral surface.

*3. The outer subapical hair of the culicines arises subapically on the external ventral surface but may accompany hair 3 to the internal surface of the antenna where it is then ventral to hair 3. The corresponding hair in anophelines is the ventral saber located near the external angle of the ventral surface.

*4. The terminal antennal hair is dorsal and terminal and usually median in position in culicines. In anophelines it appears to arise externally but actually has the same relative position because of the rotation of the antenna on its axis which brings the ventral surface mesad and slightly dorsad.

*5. The hyaline process arises in the center of the apex in a small depression or slightly before the apex in some culicines. It is easily recognized in both anophelines and culicines by its translucent outer portion.

*6. The finger process is terminal, dorsal and external. It is easily recognized by its blunt apex and the presence of a transverse transparent portion near its base.

THE MOUTHPARTS

The mouthparts of mosquito larvae have not been adequately studied as yet and homologies are not clear. Therefore their chaetotaxy is not taken into account at this time but it can be easily added in the future using the same system of nomenclature as for the antenna above. The maxillary palpus, in particular, shows a great number of specific differences in some groups. It is interesting to note that the palpus of dixines, and to a lesser extent of the anophelines, shows striking similarity in chaetotaxy to the antenna in these forms. There is a need for homologizing the hairs of the culicine palpus with those of the anophelines and dixines as there is a reduction in the number of hairs in the former. The basal maxillary hair is present in all groups but the culicines appear to lack the palpal hair and the terminal hairs are reduced from 7 to 4 in number. The body of the maxilla appears to have more than the single hair described and numbered to date. The mandible has several hairs which may be of general occurrence. Finally, the labial complex has not been studied and may reveal elements of chaetotaxy which should be included in a complete nomenclature.

THE THORAX

The thoracic chaetotaxy of anophelines has been extensively studied by Puri and has been adapted by Barraud and others for culicines. Certain discrepancies in their individual interpretations of the thoracic chaetotaxy and differences in both interpretations from the chaetotaxy of the abdomen are evident. It is believed that the changes proposed here to correct these reflect more the true condition. The renumbering of these hairs does not necessitate the renumbering of the entire series.

THE PROTHORAX

The prothorax has a full complement of 15 pairs of hairs, numbered 0 to 14. In general these follow a regular sequence starting at the middorsal line. There is a considerable variation from group to group in the relative length, branching, and development of basal tubercles in these hairs, but they appear to retain their relative position in all groups with the exceptions noted below.

0. Hair 0 in culicines is placed caudad of 4; in anophelines when present it is mesad and caudad of 1. It appears improbable that it is homologous with hair 0 of the abdomen, since in the latter it is always cephalad of 1. No change is proposed at the present time since the homology is not clear to me.

1, 2 & 3. These hairs, the *submedian prothoracic* group, are closely associated and often occur on a common tubercle. It is probable that one of these is homologous with hair 0 of the abdomen.

4 to 7. These hairs are dorsal in position, in regular sequence and variously developed.

8. Hair 8 is lateral or ventrolateral in position.

9 to 12. The *prothoracic pleural* group is the conspicuous landmark on the ventral or ventrolateral surface. The hairs occur in two series on a common tubercle. Hair 9 is the external anterior hair, 10 the internal anterior, 11 the external posterior, and 12 the internal posterior. Hair 10 has a tendency to be longer than the others, 9 to be slightly shorter and branched, 11 to be reduced, and 12 to be medium sized.

*13. It is evident from comparison with a large number of species of sabethines and culicines that the hair formerly known as 14 is more probably homologous with hair 13 of the abdomen. In sabethines both this and the following hair are well developed and their relationships are clear. Hair 13 is associated on all thoracic segments with the pleural group. On the prothorax it is placed cephalad of this group and sometimes slightly laterad. It is absent in all culicines examined, the hair formerly known as 13 in these forms is actually hair 14.

*14. This hair has been called 13 in the past. It is the hair closest to the midventral line of segment. As indicated above both 13 and 14 are well developed in sabethines and it appears more probable that 14 would retain its usual position near the median line.

TABLE 2.—Chaetotaxy of the thorax.

Proposed System	Descriptive Terminology or Position	Present numerical system	
		Anophelines	Others
Prothorax			
0	Accessory dorsal	0	0
1 to 3	Submedian group, shoulder hairs	1 to 3	1 to 3
4 to 7	Dorsal	4 to 7	4 to 7
8	Dorsolateral	8	8
9 to 12	Prothoracic pleural group	9 to 12	9 to 12
*13	Ventrolateral	*14	not recognized
*14	Median ventral	*13	*13
Mesothorax			
1 to 7	Dorsal	1 to 7	1 to 7
8	Dorsolateral	8	8
9 to 12	Mesothoracic pleural group	9 to 12	9 to 12
*13	Ventrolateral	*14	*14
*14	Median ventral	*13	*13
Metathorax			
*1	Dorsal	*3	1
*2	Dorsal	*4	2
*3	Dorsal (palmate in anophelines)	*1	3
*4	Dorsal	*2	4
5 to 7	Dorsal	5 to 7	5 to 7
8	Dorsolateral	8	8
9 to 12	Metathoracic pleural group	9 to 12	9 to 12
13	Median ventral	13	13

* Indicates a proposed change in nomenclature.

MESOTHORAX

The mesothorax carries a maximum of 14 pairs of hairs numbered 1 to 14, hair 0 being apparently absent. All 14 pairs of hairs are usually present. They normally follow a regular numerical sequence as on the prothorax but corresponding hairs on the two segments show entirely different development. In anophelines hairs 1 and 2 are usually placed considerably caudad of the others on the dorsal surface. The same changes in hairs 13 and 14 are proposed here as they are just as clearly shown on this segment in sabethines and in some culicines.

1. This hair has a tendency to be stellate or branched in culicines and is characteristically developed in anophelines.

2 to 7. These are dorsal in position and variously developed.

8. Hair 8 is lateral or ventrolateral in position.

9 to 12. The mesothorax pleural group, with the same arrangement of individual hairs as on the prothorax, is ventrolateral in position, mesad of 8.

*13. This hair is cephalad and sometimes laterad of 9 to 12. It was formerly known as 14.

*14. This is the most mesal hair and is characteristically developed.

METATHORAX

The metathorax has a complement of 13 pairs of hairs, 0 and 14 not having been recognized. It appears to me that in both anophelines and culicines the primitive sequence of the hairs is retained and the numbering used by Puri is incorrect for the following reasons. In culicines both hairs 1 and 3 are frequently stellate, a condition comparable to a palmate hair in anophelines, and hair 3 is often better developed than 1. In first instar anopheline larvae, hairs 1 and 3 are both developed as lanceolate hairs similar to hair 1, the future palmate of the abdominal segments. The palmate or branched hair of the metathorax of the fourth instar anopheline larva has been interpreted as hair 1 principally because of its resemblance to the palmates of the abdomen and to the characteristic branched hair of the mesothorax. This hair can be interpreted on the basis of position as corresponding to hair 3 of culicines, an interpretation consistent with the potentiality of hair 3 to develop into a palmate or stellate hair as shown by the first instar anopheline and also by the characteristic development in culicines. Furthermore, no wholesale migration of hairs occurs anywhere else on the thorax. Therefore the anopheline hairs are renumbered and brought in line with those of the culicines.

*1. Renumbered in anophelines only—formerly hair 3. This is the most mesal of the metathoracic hairs.

*2. Renumbered in anophelines only—formerly hair 4. This hair is slightly external and caudal to 1.

*3. Renumbered in anophelines only—formerly hair 1. This is the palmate hair of the metathorax. It is removed some distance cephalad and lateral of the preceding two hairs in anophelines, culicines, and sabethines.

*4. This hair is renumbered in anophelines only—formerly hair 2. The position of this hair is somewhat variable but usually it is laterad and caudad of 3.

5 to 7. These hairs are dorsal or dorsolateral in position and variously developed.

8. Hair 8 is ventrolateral in position, usually cephalad of 7.

9 to 12. The *metathoracic pleural* group is ventrolateral in position and has the same arrangement of hairs as the prothoracic group.

13. Hair 13 is mesad of 9 to 12 and usually quite close to this group.

THE ABDOMEN

The abdominal chaetotaxy has not been used extensively except for the terminal segments, the subdorsal and lateral hairs in the culicines, and a few additional hairs in anophelines. No real attempt at homologies in culicines has been made to date. From observations made in the course of this study, it appears that, in addition to specific differences, valuable supraspecific characters are to be found in the position of hairs on various abdominal segments but since no special effort was made to study these, no generalizations can be made at this time.

A maximum of 15 pairs of hairs are found on segments II to VII; apparently 12 pairs on segment I, although all 15 are known to occur but not in any one species; 7 pairs on segment VIII (as restricted in this study); 13 pairs on the spiracular lobe or siphon; and 4 pairs or groups on the anal segment.

The basic segment for serial homologies appears to be segment II on which, in all forms examined, all the hairs are present in consecutive numerical sequence or departures from this are simply determined. Homologies on segments I and III to VIII are easily determined by working out the constant relative position of certain diagnostic hairs. Segment VIII, the spiracular lobe or siphon, and the anal segment have a specialized chaetotaxy which is not homologized with the preceding abdominal segments as indicated below.

ABDOMINAL SEGMENTS II TO VII

Each of these segments may carry a full complement of 15 pairs of hairs but generally only 13 pairs are well developed in culicines, 14 pairs in anophelines, and the full 15 pairs in some sabethines.

The second abdominal segment is taken as a basic segment from which serial homologies are determined for the other segments. The usual position and development of hairs on this segment is as follows. Hairs 0 to 5 are dorsal, 6 to 8 lateral, 9 to 14 ventral in position.

0. This hair is usually placed far forward on the segment. It is of general occurrence in anophelines, is present in some sabethines, but apparently is greatly reduced in most culicines. Usually it is poorly developed but may be very conspicuous as in some sabethines.

1. Hair 1 is constant in position, being the most caudal and mesal hair on the dorsal surface of the segment. It is usually well developed and has a tendency to become stellate or palmate.

2, 3. These hairs are subject to much change in position but are usually present in the proper sequence on this segment. When they shift their position cephalad or mesad, the more cephalic hair is arbitrarily called hair 2.

4. Hair 4 may change its position but usually does not migrate as much as 2 or 3 and remains close to hair 5.

TABLE 3.—Chaetotaxy of the abdomen.

Proposed System	Description Terminology or Position	Present numerical system	
		Anophelines	Others
Segment I	As in segment II, usually only 12 pairs present, with following hairs present or absent:		
0*	Accessory dorsal	not rec.*	not rec.*
2	Dorsal	2	2
8*	Anterior dorsolateral	not rec.*	not rec.*
9	Posterior ventrolateral	9	9
11	Ventral	11	11
14*	Ventral intersegmental	not rec.*	not rec.*
Segment II	Usually 0 and 14 missing or undeveloped		
0*	Accessory dorsal	0	not rec.*
1 to 5	Dorsal	1 to 5	1 to 5
6 & 7	Upper and lower lateral	6 & 7	6 & 7
8	Anterior dorsolateral	8	8
9	Posterior ventrolateral	9	9
10 to 13	Ventral	10 to 13	10 to 13
14*	Ventral intersegmental	0*	not rec.*
Segments III to VII	As on segment II with the following exceptions:		
7*	Lower lateral	9*	7
9*	Posterior ventrolateral	7*	9
Segment VIII	No homologies with other segments		
0*	Accessory dorsal	0	not rec.*
1*	First pentad	α,7,8*	A,α*
2*	Second pentad	β,6,7*	β*
3*	Third pentad	γ,9*	B,γ*
4*	Fourth pentad	δ,10,11*	δ*
5*	Fifth pentad	ϵ,13*	C,ϵ*
14*	Ventral intersegmental	$0'$*	not rec.*
Spiracular Lobe or Siphon	No homologies with other segments		
1*	Postspiracular or siphonal tuft	g*	g*
2*	Dorsal preapical or basal of pecten	6,h*	h*
3*	Inner fossate	3*	3*
4*	Median fossate	2*	2*
5*	Outer fossate	1*	1*
6*	Proximal dorsal valve hair	5*	5*
7*	Distal dorsal valve hair	4*	4*
8*	Proximal ventral valve hair	f*	f*
9*	Distal ventral valve hair	e*	e*
10*	Inner basal ventral valve hair	a*	a*
11*	Inner apical ventral valve hair	b*	b*
12*	Inner apical ventral valve hair	c*	c*
13*	Median ventral valve hair	d*	d*
Anal Segment	No homologies with other segments		
1*	Lateral hair of saddle		
2*	Inner or dorsal of dorsal brush		
3*	Outer or ventral of dorsal brush		
4*	Ventral brush		

* Indicates a proposed change in nomenclature.

5\. Hair 5 has a very characteristic position on the posterolateral angle of the segment, dorsal and slightly caudad of hair 6.

6\. Hair 6 is the upper pleural hair and is well developed on segments I and II. It may become variously reduced on the following segments but not to the extent of being difficult to identify by its characteristic lateral position.

*7. Hair 7 is the lower pleural hair situated directly ventrad of hair 6 but sometimes slightly caudad as well. When it becomes reduced, as is frequently the case on segments III to VII, it can be identified by its position in relation to hair 6. It appears to me that it has been incorrectly interpreted in anophelines. From an examination of a large number of species it is evident that it always retains its relationship to hair 6 and does not move cephalad and mesad of 9 as interpreted in anophelines.

8\. Hair 8 is always lateral and placed far forward on the segment.

*9. Hair 9 is ventrolateral in position. In anophelines it has been confused with hair 7 on segments III to VII as indicated above. It is normally slightly cephalad of hair 6 and does not move caudad of it.

10\. Hair 10 always retains its relation to hair 9. It is usually mesad and caudad of this hair although in some forms it may move cephalad of 9.

11 & 12. Hairs 11 and 12 are subject to much change in position. When they move cephalad or mesad, the more cephalic hair is arbitrarily called hair 11.

13\. Hair 13 is usually easily recognized as it has a tendency to become stellate or multibranched and is the most median and caudal of the ventral hairs. On segment VI it has a tendency to move forward, become reduced in size and in most culicines develop a dendroid branching.

14\. Hair 14 is minute in anophelines and placed in the intersegmental membrane in front of the segment. It is also minute in culicines but is very well developed in some sabethines. The two members of a pair are usually very closely associated on the midventral line.

In *general homologies* the hairs are first selected on segment II using the characteristic positions described above and taking into account the usual migrations. On the dorsal surface it is easiest to select hair 1 first then 6, 5 and 8. Hair 4 then becomes obvious and it remains to decide on hairs 2 and 3. Hair 7 can be determined in its relation to 6. On the ventral surface hair 13 is first decided on and then hairs 9 and 10. Following that hairs 11 and 12 present no difficulties. Hairs 0 and 14 are left for the last step. It should be emphasized that only after the pattern for segment II has been established is it advisable to attempt *serial homologies*. These are carried out in the same steps from segment to segment, additional help is derived from the characteristic development and branching of hairs which have a characteristic position.

Although segment VII has the same number of hairs as the 5 preceding segments the chaetotaxy is considerably modified in culicines and homologies are more difficult to determine. The situation is complicated by the movement of most hairs into a compact lateral group. The chaetotaxy of this segment provides valuable diagnostic characters so that it becomes necessary to homologize it carefully. It appears that in the past this has been done largely by direct comparison with anopheline chaetotaxy of this segment and this has led to misinterpretations. The same procedure should be followed as outlined above but the following additional notes may prove to be of help. Hairs 1 and 13 are usually strongly developed and easily determined since they retain their usual position. Hair 8 is placed forward of all the other hairs and is usually a small multibranched tuft. Hair 3 is well developed and is the third hair from the middorsal line. Hair 5 is usually small in culicines and apparently is subject to migration on this segment towards the midventral line. Hair 4 is strongly developed. Hair 6 is greatly reduced in most cases but usually retains its branched condition. Hair 7 retains its relation to 6, being ventrad and caudad of 6. Hair 9 is cephalad and ventral of 6 as on the other segments. The hair nearest to 9 ventrally is hair 10. Hairs 11 and 12 show the usual migration.

ABDOMINAL SEGMENT I

The first abdominal segment usually carries 12 pairs of hairs. It was formerly generally accepted that hairs 0, 14, and 8 were absent from this segment. This appears to be the condition in anophelines but undoubtedly is not always so in culicines and sabethines. The latter show particularly interesting developments which throw some light on the entire problem of larval chaetotaxy. On the dorsal surface of the abdominal segments certain species of *Tripteroides* have an extremely well developed hair 0. A hair in exactly the same position occurs on segment I of these species and hair 2, which on segment II and following also has a characteristic position, is absent. In other species of *Tripteroides* hair 0 is lacking on segment II and may be absent or present on the more distal segments, in such species hair 2 is present on the first segment and occurs in almost exactly the same position as on segment II. On the ventral surface hair 14 may be extremely well developed in the intersegmental membrane. In at least one species of *Tripteroides* it is present on segment I in exactly the same position. The most convincing evidence that different hairs are present on this segment is to be deduced from the fact that in this particular group of *Tripteroides* the above mentioned species with hair 14 is the only one which has 4 pairs of ventral hairs on segment I, the others all have 3 pairs only, one less than the usual condition in most mosquitoes. It is also probable that the hair which has been interpreted as hair 9 on this segment may be actually hair 8. Such is the case in other species of *Tripteroides* in which hair 8 is characteristically developed on all the segments and is present in exactly the same dorsolateral position on segment I as on all others. Hair 9 as mentioned in the general discussion above is ventrolateral in position always. Hair 8 has a characteristic lateral or dorsolateral position in all forms examined. In *Uranotaenia,* members of the typical subgenus appear to have retained hair 8 on the first abdominal segment, while in *U. quadrimaculata* of the subgenus *Pseudoficalbia* it is obviously hair 9 that is retained and 8 lost. It appears, therefore, that potentially every one of the 15 pairs of hairs may appear on this segment and homologies on this segment may be of considerable phylogenetic interest and should be done very carefully. Homologies are complicated by the fact that hairs 0 and 14 may be either well developed or so small and inconspicuous that they are overlooked in related species and particular attention should be paid to them. The author is fully aware that his present interpretations of the chaetotaxy of this segment are not entirely clear and considerable revision will be needed after more work is done.

ABDOMINAL SEGMENT VIII

The eighth abdominal segment, the spiracular lobe of anophelines and the siphon of the culicines present a special problem in nomenclature. It appears quite evident, as shown by Christophers and Martini, that the siphon of the culicines with its valves and the spiracular lobe with the perispiracular apparatus are homologous structures and are derived from part of the eighth and from the ninth abdominal segments and that the hairs located on these two structures belong to different segments. What is usually called the eighth segment has the chaetotaxy greatly reduced as a result. On the other hand the homologies of these hairs with those of the preceding abdominal segments are not clear by any means nor does it seem probable that they can ever be determined with any degree of certainty, as can be seen by examining the great variety of interpretations which have appeared in print. Martini used numbers to designate the hairs belonging to the eighth segment and letters for those of the ninth segment. When one attempts to use this mixed terminology on the siphon and valve hairs of the culicines, which show good specific and perhaps generic characters, a great deal of confusion results. It seems advisable, therefore, to treat the eighth abdominal segment proper separately from the spiracular lobe and the siphon and to use an arbitrary numerical designation for the hairs on these structures which does not imply homologies with the seventh or more proximal segments. The homologies of these hairs between anophelines and culicines are quite obvious and the proposed system would reflect this condition. No confusion should result from the use of this system in anophelines since the spiracular lobe is quite distinct from the eighth segment and the two groups of hairs could not be mixed.

The eighth abdominal segment proper bears five pairs of conspicuous hairs and in addition has two pairs of minute hairs. The latter are obviously homologous with hairs 0 and 14 of the preceding segments. The homologies of the other hairs are not clear, at least at the present time. For this reason these hairs are arbitrarily numbered 1 to 5 in a dorsoventral sequence. Should homologies be definitely established in the future, they could be renumbered.

*0. This hair is minute, placed anteriorly on the dorsal surface of the segment in the same relative position as the corresponding hair on the preceding segment.

*1. Hair 1 is the most dorsal of the well developed hairs of the eighth abdominal segment proper.

*2. Hair 2 is ventrad and caudad of 1 in culicines, while in anophelines it is ventrad and cephalad of 1.

*3. Hair 3 is the middle of the 5 lateral hairs and is usually conspicuously branched in anophelines as well as culicines.

*4. Hair 4 is ventrad of 3.

*5. Hair 5 is the most ventral of the conspicuous hairs.

*14. The ventral intersegmental hair occurs in the same position as on the other abdominal segments. It is usually minute.

SPIRACULAR LOBE AND SIPHON

Thirteen pairs of hairs are of uniform occurrence on the spiracular lobe and perispiracular apparatus of the anophelines and the siphon and valves of culicines. In sabethines additional median ventral, median dorsal and lateral siphonal tufts are present but they do not occur in other forms and are, therefore, left out of consideration in the proposed nomenclature.

The pecten of anophelines is undoubtedly homologous with the pecten of culicines. Two hairs are associated with the pecten of anophelines. The dorsal of these, situated on the basal plate of the pecten, has been homologized with the dorsal preapical siphonal hair of culicines. The postspiracular hair of anophelines undoubtedly corresponds to the ventrolateral hair tuft of the culicine siphon. The siphon of culicines is considered to have been formed by the expansion and fusion of a structure corresponding to the basal plates of the two pectines over the dorsal surface and the expansion ventrally of their connecting ventral sclerotized bar. In the process the valves have been carried out away from the eighth abdominal and anal segments.

The hairs on these structures are numbered from the proximal end distad and from the base of the valves distad as follows. No homologies are implied with any hairs on the other portions of the abdomen.

*1. Hair 1 is the siphonal tuft of culicines and the post spiracular hair of anophelines. In culicines where more than one pair is present they are designated as 1a, 1b, 1c from the base outward.

*2. Hair 2 is the dorsal preapical siphonal hair of culicines and is located either in that position on the siphon or in a membrane just beyond its apex in some sabethines. In anophelines it is the basal pectinal hair.

*3. Hair 3 is the proximal fossate hair of the middorsal valve on its lateral surface.

*4. Hair 4 is the middle fossate of the middorsal valve and is usually better developed than either 3 or 5.

*5. Hair 5 is the distal fossate hair of the middorsal valve.

*6. Hair 6 is the proximal dorsal valve hair and is located on the lateral surface at the base of the dorsolateral valve.

*7. Hair 7 is the distal dorsal valve hair and is located at the apex of the distal part of the dorsolateral valve.

*8. Hair 8 is the proximal ventral valve hair and is located on the lateral surface at the base of the ventral valve.

*9. Hair 9 is the distal ventral valve hair and is located preapically on the lateral surface of the ventral valve. It is often developed into a curved spine in culicines.

*10. Hair 10 is the inner basal valve hair. Because of its position on the inner surface at the base of the ventral valve it is seldom seen.

*11 & 12. Hairs 11 and 12 are the inner apical ventral valve hairs and are located near the apex of the lower inner surface of the ventral valve. They are seldom well developed.

*13. Hair 13 is the median ventral valve hair, located on the upper inner surface of the ventral valve. In culicines it is frequently well developed and has an expanded base and a conspicuous proximal curvature in *Uranotaenia.*

THE ANAL SEGMENT

Four pairs or groups of hairs are of uniform occurrence on the 10th abdominal segment. No homologies with other abdominal hairs are implied on this segment.

*1. The lateral saddle hair arises laterally from the saddle.

*2. The inner dorsal hair of the dorsal brush is the dorsal, upper, or inner component of the dorsal brush.

*3. The outer dorsal hair of the dorsal brush is the ventral, lower, or outer component of the dorsal brush.

*4. The ventral brush is composed of a variable number of paired or unpaired hairs. The most distal component of the brush is designated as 4a, the next proximad 4b, etc. . . . for ease of reference.

SUMMARY

A revised uniform numerical nomenclature for the chaetotaxy of the fourth instar mosquito larva is proposed. It can be applied uniformly to all members of the subfamily *Culicinae.* One hundred and ninety-three pairs or groups of hairs are included. Only the hairs of the mouthparts and the midventral, dorsal and lateral hairs of the culicine siphon are not taken into consideration. All the established homologies are retained in this nomenclature and a minimum of changes are introduced in the modified Martini system on which it is based. To allow for separate numerical sequence for the head appendages, the lateral and ventral head capsule hairs are renumbered. All the antennal hairs are given a separate numerical sequence. Prothoracic and mesothoracic hairs 13 and 14 are interchanged. Metathoracic hairs 1, 2, 3, 4 of anophelines are renumbered. No modifications are introduced into the proximal abdominal nomenclature except for the interchanging of hairs 7 and 9 in anophelines on segments III to VII and the possible occurrence of hairs 0, 8 and 14 on segment II. Separate numerical sequences not serially homologous with the remainder of the abdomen are introduced for the eighth abdominal segment proper, the spiracular lobe of anophelines and its homologue, the siphon of the culicines, and the anal segment. Criteria for general and serial homologies are discussed with the relative position of hairs considered to be of more importance than the development of hairs. A table indicating the changes and synonymy of the nomenclature is appended and drawings of *Anopheles walkeri* Theo. and *Uranotaenia atra* Theo., labelled with the revised nomenclature are given.

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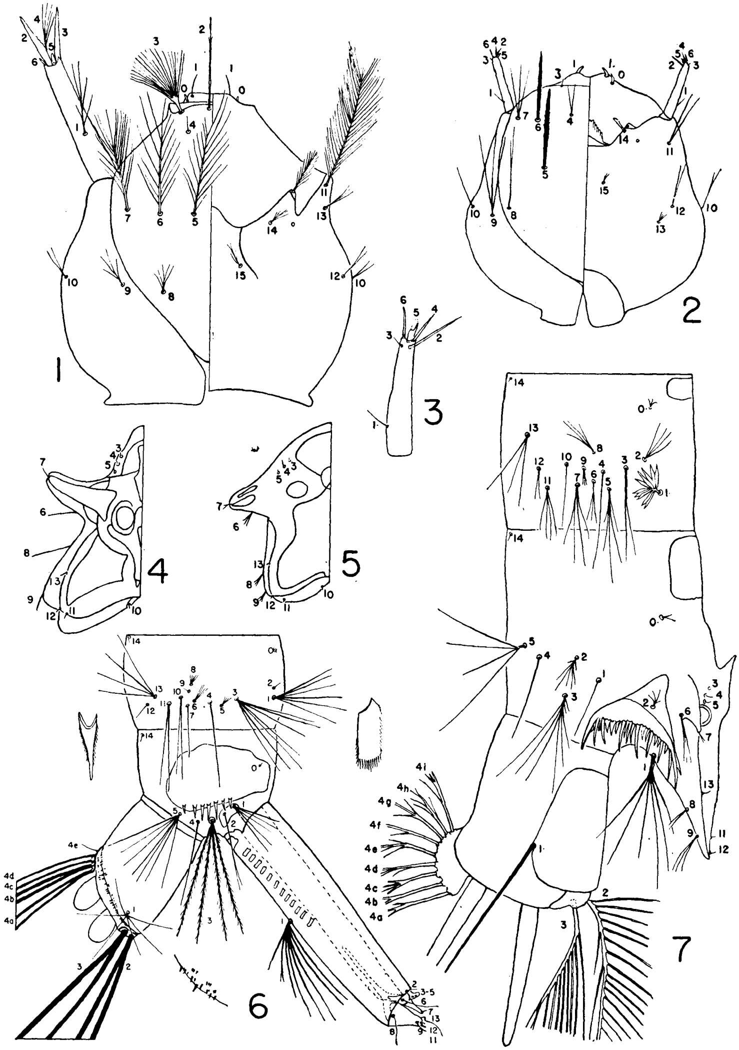

Figs. 1-7.—1. *Anopheles walkeri* Theo. Dorsal and ventral aspects of head (After Hurlbut); 2. *Uranotaenia atra* Theo. Dorsal and ventral aspects of head; 3. *Uranotaenia atra* Theo. Dorsal aspect of left antenna; 4. Caudal aspect of left side of generalized culicine siphon with valves open (After Marshall); 5. Caudal aspect of left side of generalized anopheline perispiracular apparatus (After Marshall); 6. *Uranotaenia atra* Theo. Left lateral aspect of terminal abdominal segments; 7. *Anopheles walkeri* Theo. Left lateral aspect of terminal abdominal segments (Modified from Hurlbut).

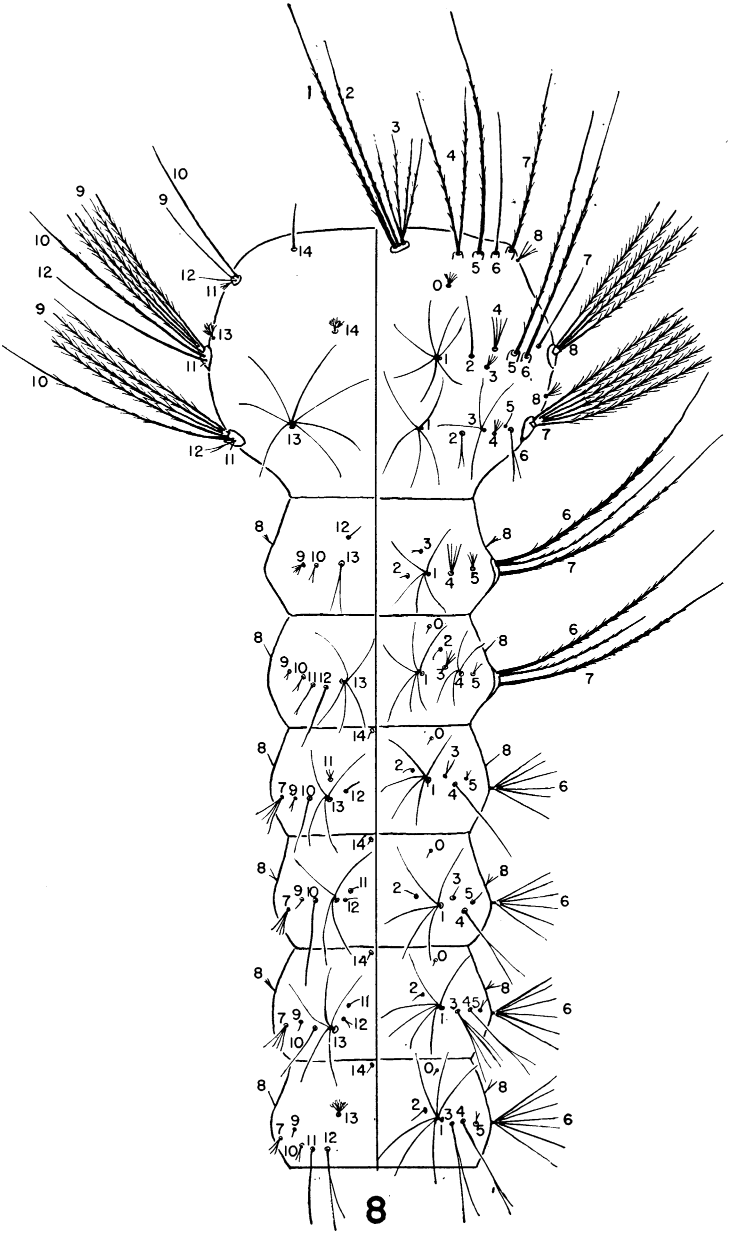

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Fig. 8.—*Uranotaenia atra* Theo. Dorsal and ventral aspects of thorax and abdominal segments I to VI.