THE HOMOLOGY OF THE CHAETOTAXY OF IMMATURE MOSQUITOES AND A REVISED NOMENCLATURE FOR THE CHAETOTAXY OF THE PUPA

(Diptera, Culicidae)

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There are in use at the present time several systems of nomenclature for the chaetotaxy of the immature stages of mosquitoes. These were developed independently for the larval and pupal stages. Recently Belkin (1951) revised the nomenclatures for the larva in an effort to obtain a more uniform system, equally applicable to anopheline and non-anopheline mosquitoes. Knight and Chamberlain (1948), after a comparative study of all but 2 of the 30 recognized genera, devised a special nomenclature for the pupa. In the work of these authors no attempt was made to homologize the elements of the larval and pupal chaetotaxy, although Belkin (1951) suggested possible homologies. It appears that Baisas and Pagayon (1949) were the first to recognize the evident homologies of the chaetotaxy of the larva and the pupa and to attempt to correlate its individual elements in the two stages. They utilized as a criterion of homology the position of the developing pupal hairs in relation to the position of the overlying hairs of the fourth instar larva shortly before pupation. It is indeed remarkable that this well known condition has been overlooked for so long. The homologies determined by Baisas and Pagayon (1949) do not agree closely with either the system proposed by Belkin (1951) for the larva or Knight and Chamberlain (1949) for the pupa since they were not aware of the work of these authors and the latter were equally ignorant of theirs. More recently Baisas (1951) and Baisas and Pagayon (1951), drawing on unparalleled knowledge of the first-instar larva and the information obtained by Knight and Chamberlain for the pupa pointed out the very remarkable fact of the similarity of the chaetotaxy of the first-instar larva and the pupa. Puri (1931), Hurlbut (1938), Baisas (1948, 1951), and Baisas and Pagayon (1951) have shown that the first-instar larva has two ventral hairs less than the fourth-instar. It can be readily seen from an examination of the figures in Knight and Chamberlain as well as direct comparison of the developing pupal hairs in the mature fourth-instar larva that the pupa also has two hairs less ventrally. Baisas (1951) and Baisas and Pagayon believe that the two hairs that are added in later larval instars are not carried over to the pupa. My own work fully supports this view, as will be seen below. It is of interest to note that the situation clarified by Baisas and Pagayon appears to be an excellent illustration of Berlese's theory as to the nature of the larva in the life history of insects with complete metamorphosis. The specialization of the chaetotaxy of the larva, including the development of characteristic branching as well as the addition of new elements, is lost at pupation and the chaetotaxy of the pupa reverts to the earliest stage of the larva. It is of further interest to note that the pupal chaetotaxy, which apparently originates from pupal discs similar to imaginal discs, appears to be influenced, to some degree at least, by the characteristic development of the homologous elements of the superimposed larval stage as can be seen by the similarity of the branching of some of the mature larval and pupal hairs.

In determining the homologies of the chaetotaxy of the first- and fourth-instar larvae with the pupa difficulties arise only on the venter of the abdominal segments, where the transitory larval hairs are found. The system of nomenclature for the chaetotaxy of the larva, originated by Martini (1923) was developed for the fourth-instar anopheline larva and includes the transitory larval hairs mixed in with the others. This system in its various forms and modifications is at present widely used and it appears best to retain it. Baisas (1948) first suggested that the transitory hairs be put at the end of the numerical sequence but agreed that the necessary changes in nomenclature would lead to confusion and that the original nomenclature should be retained, modified only to conform to the new findings. This necessitates the determination of the homologies of the first-instar hairs with those of the older instars. The transitory abdominal hairs both appear in the second-instar (Baisas. 1951 and Baisas and Pagayon, 1951), in some forms or one in the second- and the other in the third-instar. In the past the chief criterion used in homologizing these hairs in the different instars has been the degree of development of the hairs and to a lesser extent the relative position. Baisas (1951) has used the method of position of developing hairs in relation to the position of the overlying hairs of the preceding instar just before molting. This appears to be very difficult to determine accurately, particularly because of the simplicity of the hairs involved in the earlier instars, but can undoubtedly be accomplished with a great deal of painstaking work, if a large species with characteristically developed hairs is used. As a result of inherent difficulties a variety of different interpretations have arisen in determining the homology of the transitory ventral hairs of the first instar larva. Hurlbut interpreted them in *Anopheles walkeri* Theobald, 1901 as hair 10 on abdominal segments I, II, V, or hair 11 on segments III, IV, VI, VII, appearing in the 2nd instar, and hair 9 on segments I, II, III, IV, V, or hair 6 on segment VI or hair 7 on segment VII, appearing in the third-instar. Baisas (1948) on the other hand considered them to be uniformly hairs 12 and 10 in Oriental species of *Anopheles* and later (Baisas, 1951 and Baisas and Pagayon, 1951) changed them uniformly on all segments to 13 and 9 in both anophelines and *Tripteroides microcala* Dyar, 1929. When one attempts to reconcile these interpretations and to homologize the chaetotaxy of the first- and fourth-instar larvae and the pupa one is faced with an impossible situation where for each species or group and for different segments entirely different hairs are involved. On the other hand it is perfectly obvious from an examination of Knight and Chamberlain's figures that there is a perfect similarity on all unmodified segments and in all species considered. It seems likely that the same hairs are lacking on all abdominal segments or there would be little chance for the uniformity that is so clear in the pupa. Furthermore the fact that a hair appears at a given instar indicates a homology in time as pointed out by Baisas (1951). Belkin (1951) showed that some of the difficulties encountered were due to the incorrect interpretation of hairs 7 and 9 on abdominal segments III-VII in fourth-instar anopheline larvae.

A further complication is introduced into the homology of the larval and pupal chaetotaxy in the form of the pupal abdominal hair 8 of Knight and Chamberlain, an extremely uniformly placed hair but one whose homology can be interpreted in different ways. In order to clarify this puzzling situation I have attempted to reexamine all the previous interpretations, to check them all on the material available to me, and in addition to try all the other possible combinations of larval hairs since even Baisas and Pagayon's latest (1951) interpretation did not appear to fit in with the findings of Knight and Chamberlain. My own interpretation based entirely on evidence from larval chaetotaxy, is almost in perfect agreement with the serial homologies established by Knight and Chamberlain solely on the basis of pupal chaetotaxy. Furthermore, the criteria used by Belkin (1951) for determining general and serial homologies hold equally well for the pupa, at least on the dorsum of the abdomen and with the exceptions noted below. I believe that the abdominal segment II of the larva is the most useful segment for general homologies and as a starting point for serial homologies because on this segment there is no difficulty in determining the important landmark of hairs 6 and 7 in addition to the greater regularity of sequence of all hairs. Baisas (1951) and Baisas and Pagayon (1951) recommend segments III-V for the fourth-instar larva and Knight and Chamberlain (1948) segment VI for the pupa. Superficially these appear to be the least modified segments in the respective stages but the characteristic chaetotaxy of a species or group appears to be best developed on the second segment of both stages.

Following is a discussion of the comparative chaetotaxy of the fourth-instar larva and the pupa with a revised nomenclature for the pupa homologous with the revised nomenclature for the mosquito larva proposed by Belkin (1951). Again as few changes as possible are introduced and where no homologies can be determined an artificial numerical sequence is used or the old nomenclature retained. For the sake of completeness the entire pupal chaetotaxy is reviewed and a few new morphological features which came to light during this work are included. For those who wish to use the revised nomenclature here proposed it will be a simple matter to make the necessary changes on the excellent drawings of Knight and Chamberlain. A pupal drawing (fig. 14)of *Tripteroides mathesoni* Belkin, 1950 is included and labelled with the new terminology to add a member of the subgenus *Rachisoura* to the series presented by the above-mentioned investigators. It is of interest to note that the pupal chaetotaxy can be of considerable help in solving problems in the homology of larval chaetotaxy. For this reason it is highly advisable to study the two stages together and not treat them as two entirely different animals as has often been done in the past.

I wish to acknowledge my indebtedness to F. E. Baisas, without whose meticulous work in all fields of chaetotaxy of immature stages of mosquitoes this study would not have been possible, and who further contributed by sharing his views in personal communications.

MATERIAL AND METHODS

Pupal hairs *in situ* in full-grown fourth-instar larvae were studied in the following species, representing the chief groups of mosquitoes: *Anopheles* (*Nyssorhynchus*) *albimanus* Wiedemann, 1821; *Trichoprosopon* (*T.*) *digitatum* (Rondani), 1848; *Tripteroides* (*T.*) *lipovskyi* Belkin, 1950; *Uranotaenia* (*U.*) *geometrica* Lutz, 1901; *Culiseta* (*C.*) *incidens* (Thomson), 1868; *Aedes* (*Mucidus*) *aurantius nigrescens* (Edwards), 1929; and *Culex* (*Lutzia*) *halifaxii* Theobald, 1903. No such material was available for the genus *Toxorhynchites* (= *Megarhinus*) and only larvae and pupal skins of *T. rutilus septentrionalis* (Dyar and Knab), 1907 were examined.

The homologies were determined according to the following criteria, used in this order: (1) relative position of developing pupal hairs to one another, (2) comparison of these relative positions to the relative positions of the overlying larval hairs, allowing for mass movement of hairs, (3) similarity in degree of development and branching with larval hairs, (4) local shifting of hairs due to differential growth influenced by adjoining structure, such as the appendage and wing cases on the first two abdominal segments, (5) comparison with the chaetotaxy of the first instar larva in case of the ventral abdominal hairs.

A word of caution is needed regarding the examination of material. First of all, large species with characteristic stable larval chaetotaxy make observations easier. Second, the proper stage of pupal development must be secured or the correspondence of the hairs is difficult to determine as a great deal of shifting takes place at later stages. Duplications and omissions of pupal hairs occur occasionally and may lead to misinterpretations,. It appears best to figure the pupal hairs *in situ* along with the larval hairs and then to check them independently against immature fourth-instar larvae as well as free pupae.

HEAD AND THORAX

In the pupa the head capsule, the prothorax, and the mesothorax are closely united into the *cephalothorax,* while the metathorax is reduced almost entirely to a dorsal plate known as the *metanotum.* There are four groups of hairs corresponding to these regions. Baisas and Pagayon (1949) have demonstrated the homologies of these hairs with those of the pupa in the genus *Tripteroides.* The homologies of the cephalic hairs appear quite clear but the thoracic hairs may be interpreted in several ways. Since the larval thoracic chaetotaxy of the majority of culicines is not known at present and several glaring discrepancies are apparent in the present serial homologies within the thorax it seems best to retain the pupal nomenclature in use at the present time. Furthermore since the cephalothorax is usually mounted, studied and figured as a unit, the introduction of larval homologies would lead to confusion because of the repetition of identical numbers.

It should be pointed out that the pupal cephalothorax, in addition to trumpets, possesses several anatomical features that have not been studied, namely the various sclerites and appendage cases. Its chaetotaxy too, despite statements to the contrary, is quite varied. Both of these features appear to offer more possibilities for generic differentations than have been found on the pupal abdomen. Similarly the larval thoracic chaetotaxy is extremely varied and appears to show supraspecific as well as specific differences. It, too, has been largely neglected to the present.

Head Capsule (fig. 1).—The three pairs of cephalic pupal hairs are borne on the two ocular plates overlying the imaginal eyes. These plates appear to correspond to the ''ocular lobes'' of the larva. In the method of mounting the cephalothorax currently in vogue the pupal ocular lobes are folded in such a manner that the hair 1, the most dorsal of the three becomes the most mesal and caudal while hair 3 becomes the most lateral and anterior. The anatomical positions and homologies of these hairs are as follows:

1—the most dorsal pupal cephalic hair; homologous with larval cephalic hair 10;

2—the median pupal cephalic hair; homologous with larval cephalic hair 12;

3—the ventral pupal cephalic hair; homologous with larval cephalic hair 13.

Prothorax (fig. 2).—The four pairs of pupal prothoracic hairs are developed dorsally mesad of the trumpets and are borne on a distinct prothoracic lobe. They are arranged in two distinct groups of two hairs on each side. In the fourth-instar larva they appear to develop in the region of larval prothoracic hairs 0 to 4 but since this area is greatly altered through the development of the pupal trumpet this relationship may be misleading. Several interpretations of homologies can be made but none appear conclusive at this time. Superficially it appears that in *Trichoprosopon* the more lateral group (hairs 6 and 7) may be homologous with larval prothoracic hairs 4 and 0. Hair 0 is a transitory one, appearing, if at all developed, in the second- or third-instar. It is not clear at present whether this hair is homologous with the transitory ventral abdominal hairs and the transitory ventral meso- and metathoracic hairs (8 and 7 respectively) or whether it is homologous with the dorsal abdominal hair 0 which is frequently poorly developed or entirely lacking in the larva while it is always conspicuous although small in the pupa. Furthermore in anophelines hair 0 has a different, more mesal, position. For these reasons it would appear that none of the pupal prothoracic hairs are likely to be homologous with larval prothoracic 0. Going back to the first-instar larva it is noted that the most median prothoracic hairs are generally found in two groups, 1-3 and 4-5 respectively. In subsequent instars hairs 4 and 5 usually become widely separated and 5 becomes associated with 6 and 7. The third alternative is to disregard the grouping of the pupal hairs and to homologize them with larval hairs 1 to 4. At the present time there appears to be little to choose among the alternatives. To summarize:

4 and 5—the more dorsal or mesal group; probably homologous with larval hairs 1 and 2, 1 and 3 or 2 and 3 respectively;

6 and 7—the more ventral or lateral group; homologous with 3 and 4, 4 and 0 or 4 and 5 respectively.

Mesothorax (fig. 2).—The mesonotal plate of the pupa bears two pairs of hairs. They develop close to the middorsal line of the larva. Their position and homologies are as follows:

8—the more dorsal hair appears to be homologous with larval mesothoracic 1 both on position and degree of development;

9—the more ventral hair, because of the space separating it from 8, does not appear to be larval hair 2; it could be homologized with any of the other larval dorsal mesothoracic hairs; Baisas homologizes it with larval hair 5 but in *Trichoprosopon* its branching suggests hair 4.

Metathorax (figs. 2 and 6).—The three pairs of pupal metathoracic hairs are borne on the metanotal plate which is more closely associated with the abdomen than with the cephalothorax and is ordinarily mounted with the former. In *Trichoprosopon* (fig. 2) their relative position and branching make it easy to homologize them with larval metathoracic hairs 1, 2, and 3. It will be noted that their position and relation to the larval hairs is almost identical in *Anopheles albimanus* (fig. 6). This appears to support the change made by Belkin (1951) in the terminology of the larval metathoracic hairs 1 to 4 in anophelines to conform to the condition found in non-anophelines. To summarize:

10, 11 and 12—the dorsal, median, and ventral (or lateral) pupal metanotal hairs are homologous with larval metathoracic hairs 1, 2, and 3 respectively.

ABDOMEN

As mentioned above there is no difficulty in homologizing the dorsal abdominal chaetotaxy of the pupa with that of the larva utilizing the criteria mentioned above in that order. As can be seen on fig. 9-12, the developing pupal hairs generally shift mesad of the corresponding overlying larval hairs but normally retain their relative position mesolaterad and cephalocaudad and frequently preserve the corresponding relative development and branching of the individual hairs. The latter may be misleading however for certain pupal hairs may have a characteristic development of their own on the majority of the abdominal segments independent of the different development of the corresponding larval hairs on these segments. On abdominal segments VI and VII the shift of the pupal hairs is laterad but again the relative positions are preserved.

The homology of the dorsolateral and ventral hairs involves disregarding two pairs of fourth-instar larval hairs, which are absent from the first instar larva. After trying various combinations previously suggested it became obvious that none of these would fit the known facts in all cases without extreme migration of hairs, unexplainable by differential growth of the pupal discs, and that none of these would fit all the forms studied both in the larva and the pupa. It was thought that possibly those hairs which were missing on the venter of the first instar larva behaved in the same manner as dorsal hair 0 which is apparently absent in some larvae but is always present in the pupa. This again introduced unsurmountable difficulties. All the other possible combinations of larval hairs 6 to 13 were also tried and of these only one appears to meet the test. I believe that larval hairs 9 and 11 are absent in the first instar larva and that they are also absent in the pupa. At least in the forms I have studied such an interpretation makes possible a uniform homology of pupal hairs, fits all the known facts, and furthermore explains certain discrepancies formerly noted in the larval chaetotaxy.

In the larva hairs 9 and 11 may appear in different positions in different species and at different stages of development, or either one or perhaps even both may not be developed at all. From examination of the available material it seems to me that hair 9 always appears ventrolaterally in association with hairs 7 and 8 and usually between them. Hair 8 is always the most anterior lateral hair on segment II and, as far as I am aware, always retains its relationship to the *rudimentary spiracle* which is cephalad of it and usually slightly dorsad. The *rudimentary spiracles* occur on all seven proximal abdominal segments of the larva. They have generally been overlooked by culicidologists, although Dodge (1945) noted them in several species of mosquitoes. It appears that these *rudimentary spiracles* may be developed into special sense organs in the larva. Work is now in progress to determine their histological nature. In the pupa the rudimentary spiracles become larger and more anteriorly placed. Their structure and function in the pupa are also being investigated. It is of interest to note that these *rudimentary spiracles* appear to be embryonic features retained by the larva and carried through the pupa to the adult stage where they become functional—again supporting Berlese's theory. The functional spiracles of the larva, those of segment VIII, are vestigial in the pupa and disappear completely in the adult. Whatever the nature of these structures is, hair 8 is associated with them on all seven proximal abdominal segments and hair 9 is always caudad of hair 8. Hair 11 usually appears in its numerical sequence on segment II but is subject to considerable migration or even disappearance on other segments. In sabethines it frequently appears laterad of hair 10 in association with hair 9 on segments II-VI, and is frequently entirely absent on segment I.

In the pupa the lateral hairs 6 and 7 (new terminology) are developed slightly mesad (or dorsad) of the corresponding larval hairs. Hair 6 is often well developed on the proximal abdominal segments and its homology is evident. Hair 7 becomes greatly reduced and usually occurs on the extreme lateral margin of each segment but may move dorsad or ventrad in some species or some segments. It is interesting to note that the homology of this hair with pupal hair 8 of Knight and Chamberlain supports the change proposed by Belkin (1951) for the nomenclature of hairs 7 and 9 in anopheline larvae. Hair 8 moves ventrad and frequently caudad of its larval homologue. The three ventral hairs 10, 12 and 13 on the other hand move laterad as a group. Their homologies are somewhat obscured by the extensive shifting of larval hairs in this region and to a larger degree by the presence of transient larval hair 11. On the other hand the uniform occurrence of a considerable space

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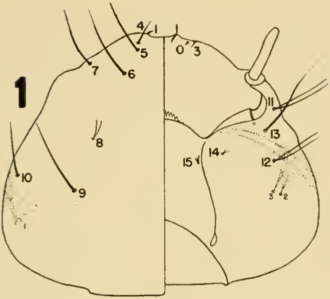
PLATE I. FOURTH-INSTAR MOSQUITO LARVAE.

(Pupal hairs and structures are represented *in situ* by broken lines.)

Fig. 1, *Trichoprosopon digitatum,* dorsal and ventral aspects of head; fig. 2, same, dorsal aspect of left side of thorax; fig. 3, *Anopheles albimanus*, caudal aspect of spiracular lobe; fig. 4, *Aedes aurantius nigrescens,* left lateral aspect of siphon; fig. 5, *Anopheles albimanus,* left lateral aspect of abdominal segment VII; fig. 6, same, dorsal aspect of metathorax; fig. 7 and 8, same, dorsal and ventral aspects of abdominal segment II.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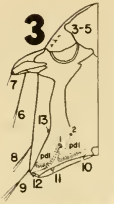
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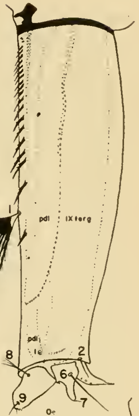
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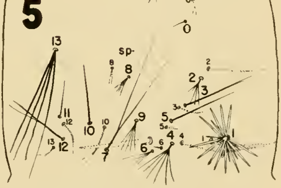
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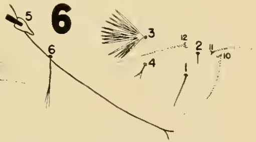
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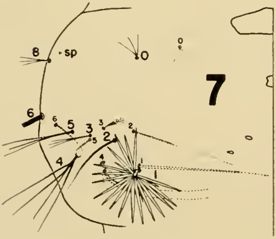
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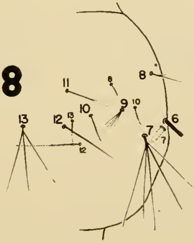
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between pupal hairs 10 and 12 supports the interpretation that the more mesal hairs are 12 and 13 since that appears to be the more common occurrence also in the larval hairs. Hair 14 is generally developed on the anterior margin of each segment in the same position as the corresponding larval hair, except on segment VIII where it moves caudad and laterad for a considerable distance. In *Trichoprosopon* hair 14 apparently also moves far caudad to the point where it confuses the homologies of hairs 12 and 13. To further complicate the situation larval hair 14 is apparently undeveloped in the species I have examined.

The homologies determined in this investigation are based on the revised larval terminology of Belkin (1951) and are indicated below. In parentheses following the homologous terminology is a reference to the nomenclature of Knight and Chamberlain (1949). The new terminology applies to abdominal segments I through VII and it appears that on these segments the serial as well as the general homologies determined by Knight and Chamberlain hold perfectly so that in order to use the new terminology all that is needed is to relabel the excellent figures already available. On segments VIII-XII the homologies are not as evident, although the pupal chaetotaxy appears to clarify the larval chaetotaxy somewhat. Therefore for the present the terminology proposed is partially homologous and partially arbitrary.

Segments I through VII (figs. 5, 7-13).—There is essentially no difference in the chaetotaxy of these segments except that on segment I and frequently on segment II hairs 6, 7 and 10 move dorsad, the ventral hairs are entirely absent on I and frequently reduced in number on II, and hair 0 is absent on segment I. The homologies have been determined as follows:

0 (1)—always the most anterior dorsal hair; absent on I; its characteristic position in the pupa clarifies the larval chaetotaxy of species of sabethines with hair 0 and 2 both developed as large stellate tufts, in such situations hair 2 is mesad of 0 in the larva and is placed considerably more cephalad in the pupa than normally;

1 (2)—usually the most mesal and caudal hair on segment II; on other segments hair 2 (3) usually moves mesad of it and may rarely do so on segment II, in which case this hair is usually small and more cephalic; often as well developed as 5;

2 (3)—generally poorly developed and bearing the relationship to 1 as outlined above;

PLATE II. FOURTH-INSTAR MOSQUITO LARVAE AND PUPA

(Pupal hairs are represented *in situ* by broken lines in figs. 9-13.)

Figs. 9-12, *Trichoprosopon digitatum*, dorsal and ventral aspects of abdominal segments I, II, III, VI respectively; fig. 13, same, left lateral aspect of abdominal segment VII; fig. 14, *Tripteroides* (*Rachisoura*) *mathesoni*, dorsal and ventral aspects of pupal abdomen and metanotum.


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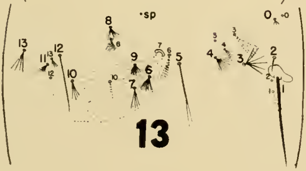
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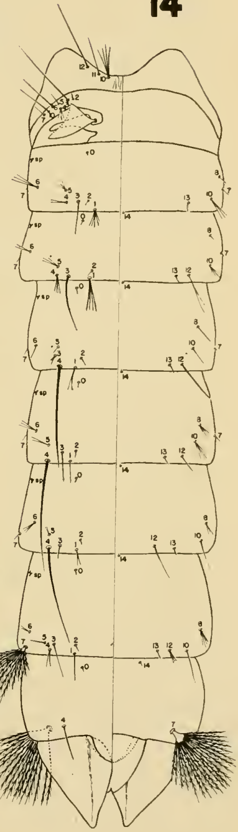
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3 (4)—generally well developed on segments I, II and III and variously on other segments, and subject to considerable shift in position;

4 (5)—generally the most conspicuous hair on segments IV-VII and placed on caudal margin;

5 (6)—associated with the "hairless setal ring" on segments III through V and subject to much shifting of position in relation to 4;

6 (7)—dorsolateral in position; frequently well developed; may move to lateral margin on caudal segments;

7 (8)—generally lateral in position; often well developed on I, reduced on II and becoming progressively larger on following segments; in sabethines greatly developed as a tuft on VII and subject to migration ventrad; the "lateral spine" of anophelines, (fig. 5, 7, 8), placed on extreme caudolateral margin of segments much as the corresponding larval hair; in non-anophelines generally placed more cephalad on each segment except on caudal segments and subject to migration ventrad;

8 (9)—ventral or ventrolateral; always the nearest hair ventrally to the rudimentary spiracle; absent on I and often on II;

10 (10)—ventral in position and caudad of 8 except on I and usually on II; generally ventrad of 7 and laterad of 8; on I and II often moves caudad and dorsad of 7 as the venter of these segments appears to be affected by the development of the leg and wing cases;

12 & 13 (11, 12)—ventral in position; subject to considerable change in position in relation to each other as in the larva; generally 13 is more cephalic and smaller than 12;

14 (13)—ventral in position; placed far forward near midventral line, except in *Trichoprosopon* in which it is associated with hairs 12 and 13; may be entirely absent, developed on all segments except I, or absent from the more anterior segments.

Segment VIII.—The pupal chaetotaxy of segment VIII is even further reduced than its larval chaetotaxy. It is evident that hairs 0 and 14 are serially homologous with those of the proximal segments as in the larva. It appears further that in the pupa Knight and Chamberlain have demonstrated that the posterolateral hair is hair 7 and that possibly the remaining hair is 4. It was not possible to homologize these hairs *in situ* in the mature larva in the material available to me and the first-instar larva was again of no help. It seems nevertheless that with the proper type of larva this can be sucessfully accomplished in the future and by working back through the pupa it will be possible to determine the serial homology of the hairs of the segment VIII in the larva. For the present time the following partially homologous nomenclature is suggested:

0 (1)—anterior dorsal hair;
4 (5)—inner dorsal hair;
7 (8)—lateral caudal hair;
14 (13)—Anterior ventral hair.

Caudal Segments (figs. 3 and 4).—The "anal flap" medially produced from the posterior margin of segment VIII of the pupa has been shown by Christophers (1922a, b) to be tergite IX. *In situ* in the fourth-instar larva (fig. 4) it extends as a lobe to the tip of the siphon in the region of the dorsal valves. It has been impossible to see in my material the pair of usually minute hairs found laterally on this lobe. It appears that any number of the larval siphonal hairs belonging to segment IX, outside of those associated with the ventral valves, could be homologous with this hair. Study of adequate material will resolve this problem undoubtedly, but for the present I suggest that this hair be called arbitrarily hair 1. Christophers has indicated that at pupation this median flap is withdrawn into the body so that only a short piece remains exposed. In the pupa vestigial spiracles of segment VIII are sometimes found near its junction with this segment.

Ventrad of tergite IX are the two paddles and below them two superimposed lobes, more evidently separated in the male. The dorsal lobe is the anal lobe or proctiger and will be considered below. The ventral lobe is the "genital lobe" and is much better developed in the male. Tergite IX, the paddles, the genital lobe and connecting lateral areas, as well as a distinct basal sternal sclerotization in the female (greatly reduced or apparently entirely absent in the male) represent segment IX. The paddles develop in the ventral part of the spiracular lobe of anopheline larvae (fig. 3) and in the ventral part of the siphon of non-anopheline larvae (fig. 4). At the apex of each paddle one or two pairs of hairs may be developed. They appear to correspond to the two outer hairs of the ventral valve but could be homologized equally well with some of the inner ventral valve hairs. For this reason it appears best to use an artificial terminology for these hairs at present. The genital lobe develops in the ventral proximal part of the anal segment of the larva. It bears no hairs. The paddles are transitory pupal structures as is the great development of tergite IX, while the genital lobe, the remainder of segment IX and the proctiger are developed into the genitalia or terminalia of the imago.

The anal lobe or proctiger is a composite structure, being composed of segments X, XI with its cerci, and the telson or segment XII. It develops in the lateral, dorsal, and apicoventral portions of the anal segment of the larva. In *Toxorhynchites*, and to a lesser extent in other genera, it shows a pair of lateral sclerotizations which appear to overlie the area where, according to Christophers (1922a, b), the cerci develop. In this genus a hair arises from each of the lateral sclerotizations. I have not been able to observe this hair *in situ* because of absence of material in the proper stage of development but it appears very likely that this hair is homologous with hair 1 of the anal segment of the larva.

The homologies and changes in nomenclature proposed for the caudal abdominal segments are as follows:

1 (1)—lateral hair of abdominal tergite IX; may be absent, poorly developed, or conspicuous as in *Uranotaenia;*

1 (8)—terminal or outer hair of paddle; usually present;
2 (7)—subterminal or inner hair of paddle; often absent;
1 (8)—lateral hair of proctiger; observed only in *Toxorhynchites*.

Addendum

Anomalies, particularly those produced through developmental arrest or excess, furnish some of the most convincing evidence for the homology of structures and are widely used in the field of comparative anatomy. Several authors have reported the presence of ''extra'' hairs in the mosquito pupa as well as the absence of other hairs normally present. As far as I am aware, no attempt has been made to identify these hairs or to utilize their presence or absence to determine or support the homology of other hairs. Since the main body of this paper was completed I have studied several such anomalies in the pupa of *Uranotaenia quadrimaculata* Edwards, 1929 and they appear to support the interpretation of the homology of larval and pupal hairs outlined above and also require a modification in the interpretation of hair 14 in the pupa of *Trichoprosopon digitatum* (Rondani), 1848. On abdominal segments III-V (and occasionally on others as well) of the pupa of *U. quadrimaculata* an extra hair associated with hairs 12 and 13 is frequently present. This extra hair is evidently homologous with larval hair 11 as it shows the same relationship in position to these hairs in the pupa as hair 11 does in the larva. It may be present on both sides or on only one side of the segments. In this species hair 14 has the normal anterior intersegmental position but is frequently absent. In view of this evidence it appears that the hair I interpreted as hair 14 on abdominal segments III-VI of *Trichoprosopon* is actually hair 11, that the true hair 14 is absent in this species, and that, in all probability, hair 14 does not shift caudad on these segments in other mosquitoes. It is well known that anomalies, ordinarily sporadic, may become established in certain lines as hereditary characteristics. It appears that this is the case with hair 11 in *Trichoprosopon*. In addition to the sporadic presence of hair 11 in *U. quadrimaculata* it is not uncommon to find duplications of hairs 12 or 13. These duplications occur either cephalocaudad or mesolaterad and may be distinguished from the ''extra'' hairs by their symmetrical relationship as well as the identical degree of development of the ''twins.''

U. quadrimaculata also furnished evidence for the interpretation that hair 9 is normally absent on the abdominal segments of the mosquito pupa. I have a single pupal skin which shows an extra hair in the region of hairs 7, 8, and 10 on the left side of abdominal segment V. This hair is entirely different in appearance from any other pupal hair, bears a very strong resemblance in degree of development to hair 9 of the larva, and shows the same relationship in position to hairs 7, 8, and 10 in the pupa as in the case of the larva.

It is of interest to note that one or two ''extra'' hairs are occasionally present on the metanotum of this species. One of these is associated with hair 12 in the same relationship as larval hair 4 bears to larval 3, while the second more lateral hair cannot be homologized directly. All the anomalous pupal hairs and their alveoli in particular are generally weaker than the normal ones. It appears that such anomalies may have taken part in the evolution and differentiation of some groups of mosquitoes through their hereditary retention, as in the case of duplication of some of the thoracic hairs of *Toxorhynchites* larvae.

Summary

The homologies of the pupal and larval hairs and the criteria used to determine them are reviewed. It is shown that the first-instar larva and the pupa lack abdominal hairs 9 and 11. A revised terminology for the pupa is proposed to indicate the homology with the larval nomenclature of Belkin (1951). It is shown that some of the difficulties encountered in homologizing the larval chaetotaxy may be resolved by studying the pupal stage. The morphological relationships of the caudal abdominal segments of the larva, pupa, and imago are reviewed.

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LARVACARUS, A NEW GENUS OF FALSE SPIDER MITES

(ACARINA, PHYTOPTIPALPIDAE)

By EDWARD W. BAKER[1] and A. EARL PRITCHARD[2]

Two species of false spider mites are remarkable in that the adults retain nearly all the characters of the larval stage. One species, *Phytoptipalpus paradoxus* Trägårdh (1905) forms cortical galls on the gum arabic tree (*Acacia nilotica* Willd.) in Egypt. The other species, *P. transitans* Ewing (1922), forms galls on the jujube tree (*Zizyphus jujuba* Lam.) in India.

P. paradoxus, the type of the genus *Phytoptipalpus*, was redescribed and illustrated by Sayed (1942). A new genus is here proposed for *transitans*, and this species is illustrated for the first time and redescribed.

Larvacarus, new genus

Type.—*Phytoptipalpus transitans* Ewing.

Adults.—Body subelliptical, the integument finely striate. Palpus one segmented, proximally fused to rostrum. Legs six in number; coxa III without seta. Rostral shield absent. Propodosoma with 3 pairs of dorsal setae; hysterosoma with 3 pairs of setae mediodorsally, six setae on each lateral margin, and one seta between the first dorsocentral and first lateral. Podosoma with 1 pair of medioventral setae. Female opisthosoma with 1 pair of medioventral setae, the ventral plate absent; 2 pairs of genital setae, the genital plate absent; 2 pairs of anal setae, the anal plates absent. Male opisthosoma with 1 pair of medioventral setae and 3 pairs of genito-anal setae.

Nymph.—Similar to female except with only 1 pair of genital setae and vulva absent.

Larva.—Similar to female except genua of legs I and II without dorsal setae, and opisthosoma with medioventral and genital setae absent.

In addition to differing from Sayed's drawings (1942) of *Phytoptipalpus* by the strongly reduced number of palpal segments, *Larvacarus* further differs by having only 1 pair of setae between the dorsolaterals and laterals on the hysterosoma, by having only a single pair of medioventrals on the podosoma, and by lacking a seta on coxa III.

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