ONTOGENY OF THE LARVAL STAGE OF *SABETHES CHLOROPTERUS*, WITH SPECIAL REFERENCE TO SETAL DEVELOPMENT AND PHYLOGENETIC IMPLICATIONS FOR THE FAMILY CULICIDAE (DIPTERA)[1]

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ABSTRACT. The four larval instars of *Sabethes chloropterus* are illustrated and the salient features of each are described and discussed in relation to species of other genera. Eight specific criteria for determining setal homologies are stated and used to establish homologies for the ventral abdominal setae of first instar larvae. The facts of development of setae 7-P, 8-M, 7-T, 9,12-I-VII, and 4-X are reviewed and discussed in terms of heterochrony. Setae retain their relative positions during development, and the importance of this phenomenon in recognizing phylogenetic relationships is noted.

INTRODUCTION

Over the years since Ronald Ross and Walter Reed demonstrated respectively that malaria and yellow fever were carried by mosquitoes, a concern of increasing importance to entomologists and paramedical personnel has been the accurate and rapid identification of mosquito vectors of human pathogens. Obviously, accurate identification depends upon a sound system of classification. The classification of any animal group inherently reflects the evolutionary history of that group. Since systematists primarily use the data of comparative morphology to establish natural systems of classification, it is important to learn how far homology agrees with morphological evidence for taxonomic relationships. The precise determination of homologous characters is necessary for working out the differences and relationships between species which form the basis for identification and classification, respectively.

There is considerable disorder in the classification of sabethine mosquitoes, and despite numerous taxonomic revisions and other studies many problems still remain to be clarified in the classification of non-sabethine mosquitoes. In the case of sabethines, the existing classifications of several genera are largely artificial and phylogenetic interpretations are based almost completely on adult morphology. From recent studies (Zavortink 1979; Harbach and Peyton 1990, 1991; Harbach 1991), it is obvious that the immature stages hold the key to understanding the phylogenetic relationships and classification of these mosquitoes. This leads to the purpose of the present study. Although initiated as part of a revisionary study of the genus *Sabethes* Robineau-Desvoidy, particular impetus was provided in a statement made by Zavortink (1979): "It will also be necessary to study the younger instar larvae of the sabethines before a natural classification of the tribe can be achieved. There are often remarkable shifts in position and changes in development of setae from one instar to the next in a particular species. It is clear in groups like *Shannoniana*, where the fourth instar larvae of most species differ conspicuously in many setal characteristics, that many of the specific differences of the mature larvae result from only differing degrees of neoteny in the various species." As the study

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progressed, it became apparent that a great degree of quantitative continuity exists in the characteristics of the different instars of *Sabethes chloropterus* (von Humboldt). When compared with information on the larval development of other mosquito species, the analysis yielded ideas pertinent to mosquitoes in general. A synthesis of these ideas and the traditional criteria of similarity, ontogeny, and position as means of recognizing homologous structures (Remane 1956) resulted in a number of conclusions which are expressed below as eight specific criteria for homologizing individual elements of the larval and pupal chaetotaxy. Consequently, the objective of this study evolved from a morphological assessment of the larval instars of *Sa. chloropterus* to include an elucidation of morphological data and principles with phylogenetic implications for the family Culicidae.

MATERIALS AND METHODS

Specimens used in this study came from a colony maintained by Woodbridge Foster at Ohio State University. The colony was started from biting females which he collected at the Isla Maje Scientific Reserve in Panama in December, 1988.

Instars were determined by rearing in the laboratory and confirmed by the presence of an egg-burster in the first instar, absence of setae 8-M and 7-T in the second instar, and differences in the comb, maxilla, and size between the third and fourth instars. Specimens were cleared in cellosolve and mounted in euparal. Observations and drawings are based on 5-24 specimens of each instar. More specimens were used to study the first and second instars.

Morphological terminology and abbreviations are taken from Harbach and Knight (1980). Except for the ventral abdominal setae of the first instar, setae are numbered according to Belkin (1962).

OBSERVATIONS

General. Growth of the larva of *Sabethes chloropterus*, like that of all mosquito larvae, is punctuated by a series of three molts, one between each of the four instars. Development from one instar to the next is marked by conspicuous discontinuous changes (increases) in body size, setal branching, number of fixed cuticular processes (e.g., comb scales), and extent of sclerotization (e.g., siphon, saddle). In general, the form of features which first appear in the newly emerged larva become increasingly elaborate in structural details in subsequent instars, with the most striking changes occurring between the first and second instars. Except for the maxilla and the siphon, the definitive form of the body parts and the relative positions of the setae are already evident in the first instar, except that certain setae of the thorax and abdomen are not yet present. The occipital foramen (OF) with its slit-like dorsolateral extensions is already distinct, and the structure of the head remains more or less uniform during subsequent development. There are certain characters, however, that are specific to each instar.

First instar larva (Fig. 1). With few exceptions the setae present in the first instar are either single or double. The majority are single. The head of the larva bears the same complement of setae found in later instars, and differs significantly only in its smaller size and in the presence of an egg-burster (EBu) on the dorsal surface. The thorax and abdomen, however, are missing setae which are present in the fourth instar. Setae 7-P, 8-M, and 7-T are absent from the thorax, and two ventral setae are absent from abdominal segments I-VII. The number of setae on abdominal segments VIII and X is the same as in the mature larva. Seta 4-X is present. The proximal one-third or so of the siphon is unsclerotized, and the distal sclerotized portion possesses a posterolateral row of pecten spines.

Second instar larva (Fig. 2). The second instar is similar to the first, but more closely resembles later instars in overall development. Characteristic features of this instar include the addition of seta 7-P and the appearance of an additional ventral seta on abdominal segments II-VII. The positional relationships of the ventral abdominal setae seem to be modified or confused by the acquisition of another seta, and the homologies of these setae with those present in

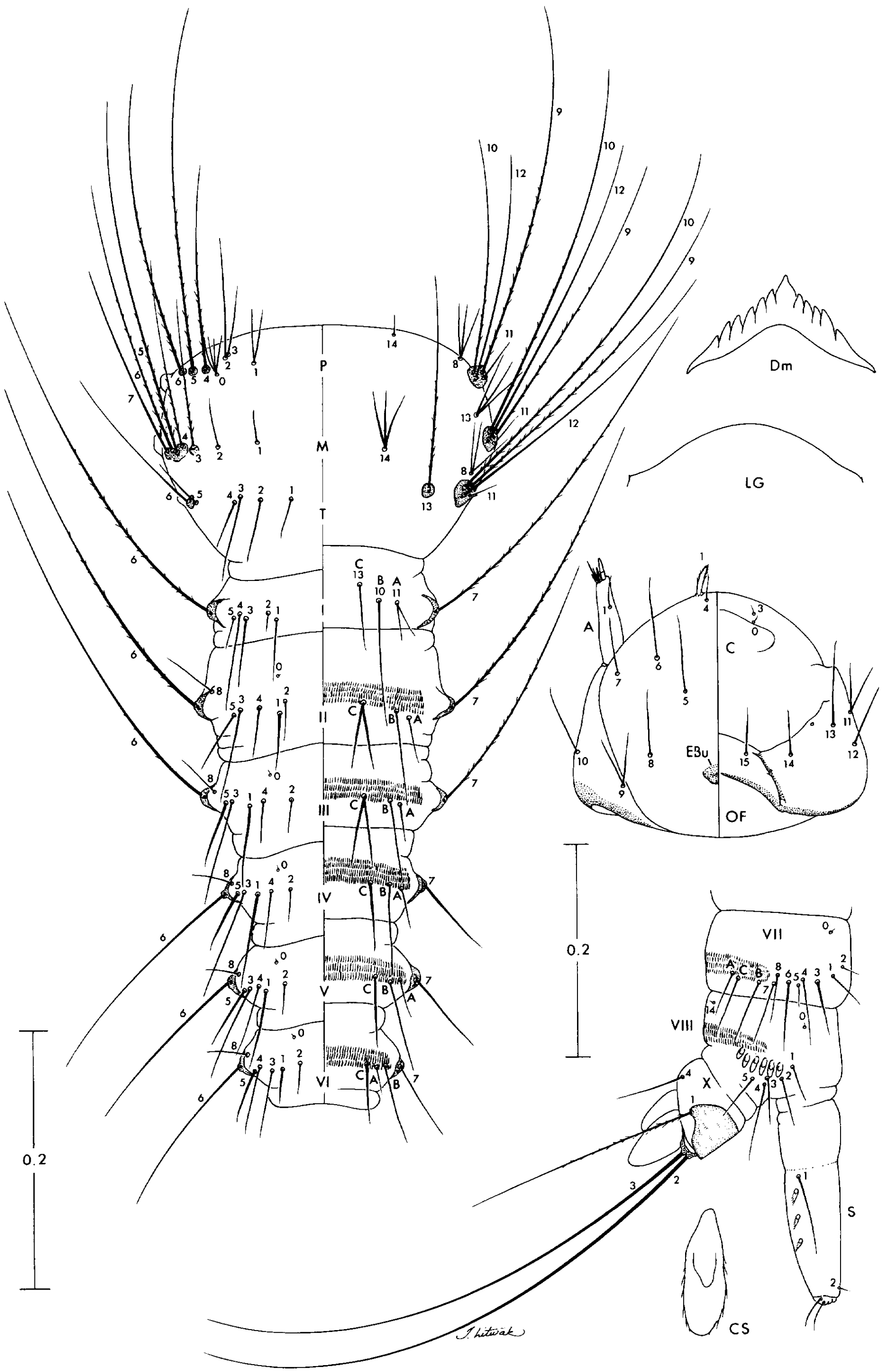

Fig. 1. First instar larva of *Sabethes chloropterus*. Letter designations of ventral abdominal setae reflect serial homologies. Except for abdominal segment I of sabethines and certain aedines, the ontogenetic homologies of these setae have not been definitely established. Seta 4-X is present and pecten spines occur on the siphon.

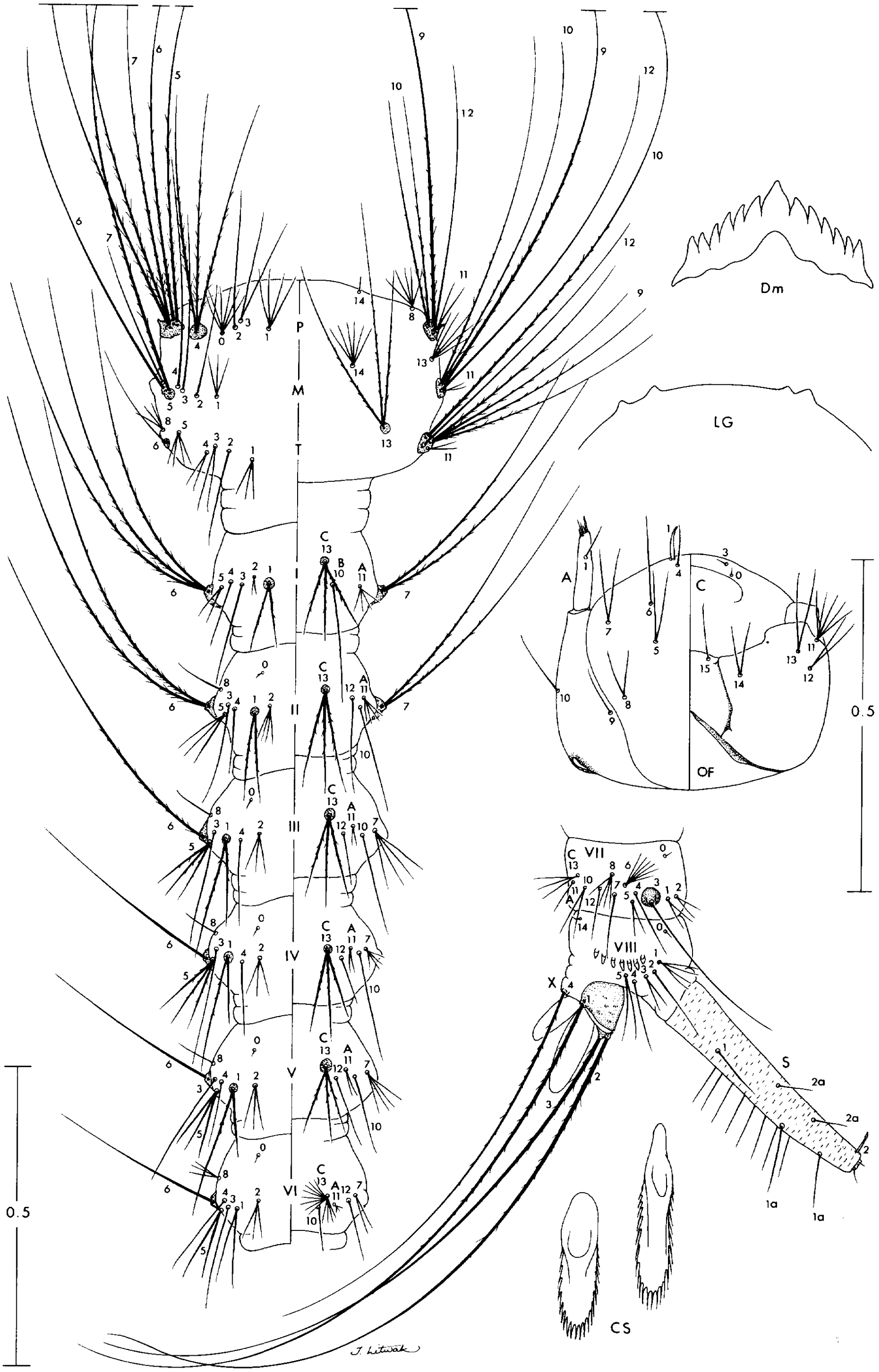

Fig 2. Second instar larva of *Sabethes chloropterus*. Setae 7-P and 12-II-VII (see discussion) appear for the first time. Letter designations for ventral abdominal setae reflect obvious homologies based on the ontogeny of segment I. Siphon lacks pecten spines, but posterior filaments and additional setae are present.

the first instar are not readily apparent. The identities of the other abdominal setae, as well as those on the head and thorax, are obvious because they occupy the same relative positions as in the first instar. The definitive form of the siphon is evident at this stage of development, differing conspicuously from its previous condition by the absence of pecten spines, presence of a posterior row of filaments, and the presence of two or three setae located distally on the dorsolateral and ventrolateral margins (setae 2a and 1a, respectively). The siphon is completely sclerotized and considerably longer than it was in the first instar.

Third instar larva (Fig. 3). Besides the obvious increase in size, the third instar is characterized by the appearance of setae 8-M and 7-T, and seta 9 appears for the first time on abdominal segments I-VII. Development is marked by further increase in the branching of setae, but their relative positions remain unchanged from the second instar. The minor differences in setal positions apparent in the illustrations (compare, for example, Figs. 2 and 3) reflect individual variation of the specific setal pattern rather than absolute shifts in position during the lifetime of an individual larva, although minor changes in position from instar to instar are expected as a result of unequal growth of neighboring tissues and structures.

Fourth instar larva (Fig. 4). The fourth instar very closely resembles the third. Growth includes a noticeable difference in the number of sclerotized structures such as comb scales. The numbers, form, and positions of the setae on the head, thorax, and abdomen are the same as for the third instar. Although the setae generally have more branches in the fourth instar, some may have the same number or fewer branches than the third instar. Seta 1-II-VI almost always changes from a double (sometimes triple) seta in the third instar into a single seta in the fourth instar.

Maxilla (Fig. 5). The development of the maxilla reflects the same trends that are apparent in the development of the other parts of the larva. Tremendous increase in size is accompanied by an increase in the numbers of substructures (cuticular processes). Greatest change occurs in the transition from the first to the second instar, where the definitive form of the maxilla is evident in the character of the terminal clawlike process and the lateral teeth (laciniarastrum). The form of the maxilla in the first instar closely resembles the form of its homolog in fourth instars of a number of species of *Malaya* Leicester (Old World) and *Wyeomyia* Theobald (New World), except that the palpus is not fused with the maxillary body in species of *Wyeomyia*.

DISCUSSION

As the development of the setal pattern of *Sabethes chloropterus* was studied and contrasted with data for other species, it became apparent that the traditional criteria for recognizing homologous structures (Remane 1956) should be modified and expanded to include eight distinct criteria for specific use in determining setal homologies. These specific criteria are expressed in the following statements. Criteria 2-5 have been previously implied or recognized in different ways by mosquito workers. Criterion 6 was first discovered and applied by Belkin (1960, 1962).

(1) Serially homologous setae make their appearance at the same time.

(2) Serially homologous setae generally occupy the same relative positions on different segments.

(3) Serially homologous setae are developed in a similar manner.

(4) Ontogenetically homologous setae generally increase in complexity from instar to instar, usually first appearing single or double.

(5) Ontogenetically homologous setae usually retain their relative positions from instar to instar.

(6) Nerve connections between the external setae of one instar and the internal developing setae of the next instar or pupa provide absolute proof of ontogenetic homology.

(7) Phylogenetically homologous setae are more uniform in appearance and position on first instar larvae. First instars also have fewer setae, thus phylogenetic homologies are more readily apparent in first than in later instars.

(8) Phylogenetically homologous setae appear (or fail to appear) as new acquisitions in

later instars. Setae which make their first appearance in later instars may be evolutionary novelties or the result of retarded morphogenesis.

For the most part, application of these criteria confirm previous conclusions regarding setal homologies, but in some cases existing notions of homology implied by identical numbers are not concordant with other setae. In determining the homologies of the chaetotaxy of the first and fourth instars, serious difficulties arise only on the ventral surface of abdominal segments I-VII. Beginning with Martini (1923) and culminating with Belkin (1962), the system of nomenclature developed for the fourth instar includes designations for two ventral abdominal setae which are absent in the first instar. Noting that the first instar larva and the pupa possess the same number of abdominal setae on segments II-VII, Baisas and Ubaldo-Pagayon (1952) and Belkin (1952) surmised that the two ventral setae absent in the first instar are those absent in the pupa. This idea led Baisas and Ubaldo-Pagayon (1952) and Belkin (1953) to interpret the missing setae as 9 and 13, and this interpretation was accepted until Belkin (1962) changed the designations for pupal setae 7, 10 and 12 to reflect their correct ontogenetic homologies (criterion 6) with larval setae 9, 7 and 10, respectively. Concomitant with this change, Belkin (1962) renumbered the ventral setae of the first instar larva to show the presence of setae 9-11 and the absence of 12 and 13. Although Belkin never provided an explanation for this action, it likely was based on the idea that setae 12 and 13 must be absent in the first instar larva because they are absent in the pupa. Studies of shared nerve connections in prepupal fourth instar larvae (criterion 6) unequivocally demonstrate that these setae are not carried over from the fourth instar larva to the pupa (Belkin 1962, Harbach 1991). Unfortunately, the absence of setae 12 and 13 on the abdominal segments of the pupa is not proof in itself for the absence of these setae in the first instar larva.

A review of the literature shows that all first instar mosquito larvae have three ventral abdominal setae arranged in a similar pattern. This similarity strongly indicates phylogenetic homology throughout the Culicidae (criterion 7). Since abdominal segment I of *Sabethes chloropterus* (as well as all other sabethines and some aedines) bears only three obviously ontogenetically homologous ventral setae in all instars (Figs. 1-4), this segment was chosen as a starting point for determining the homologies of the ventral setae. For ease of discussion, these setae are designated A, B, and C in sequence from the more lateral to the more mesal seta in figure 1. The serial homologies of these setae (relative to segment I) are easily established by applying criteria 1-3. Looking down the row of segments, it is obvious that their relative positions are the same (criterion 2) and each is similarly developed (criterion 3) on each segment. Criterion 2, however, does not hold for setae A and B on segment VI where their positions appear to be reversed in agreement with criterion 3. Application of criterion 3 further indicates that setae A and C on segment VII occupy positions opposite those on segment VI.

The constancy in position and number of the three ventral setae on segment I allows their ontogenetic homologies to be determined without difficulty. Comparison of this segment in the first and second instars (Figs. 1,2) shows that setae A and C increase in complexity (criterion 4) while seta B remains single. Looking down the row of segments in the second instar (Fig. 2), the serial homologs of setae A and C are relatively easy to identify on the basis of shared similarity of development (criterion 3). It is not readily apparent, however, which of the two single setae on segments II-VII is seta B and which is the new acquisition. Based on the degree of development (length), it would appear that the more lateral of the two is homologous with seta B. Further support for this interpretation is found when the letter designations for this seta (B) and seta A are converted to their numerical equivalents (10 and 11, respectively). When this is done the identities of these setae are easily traced from the second instar to the pupa. By carefully comparing their positions on corresponding segments in the three larval instars and the pupa (Figs. 2-4, venter of segments III,IV of pupa shown for comparison in Fig. 4), it is immediately clear that the relative

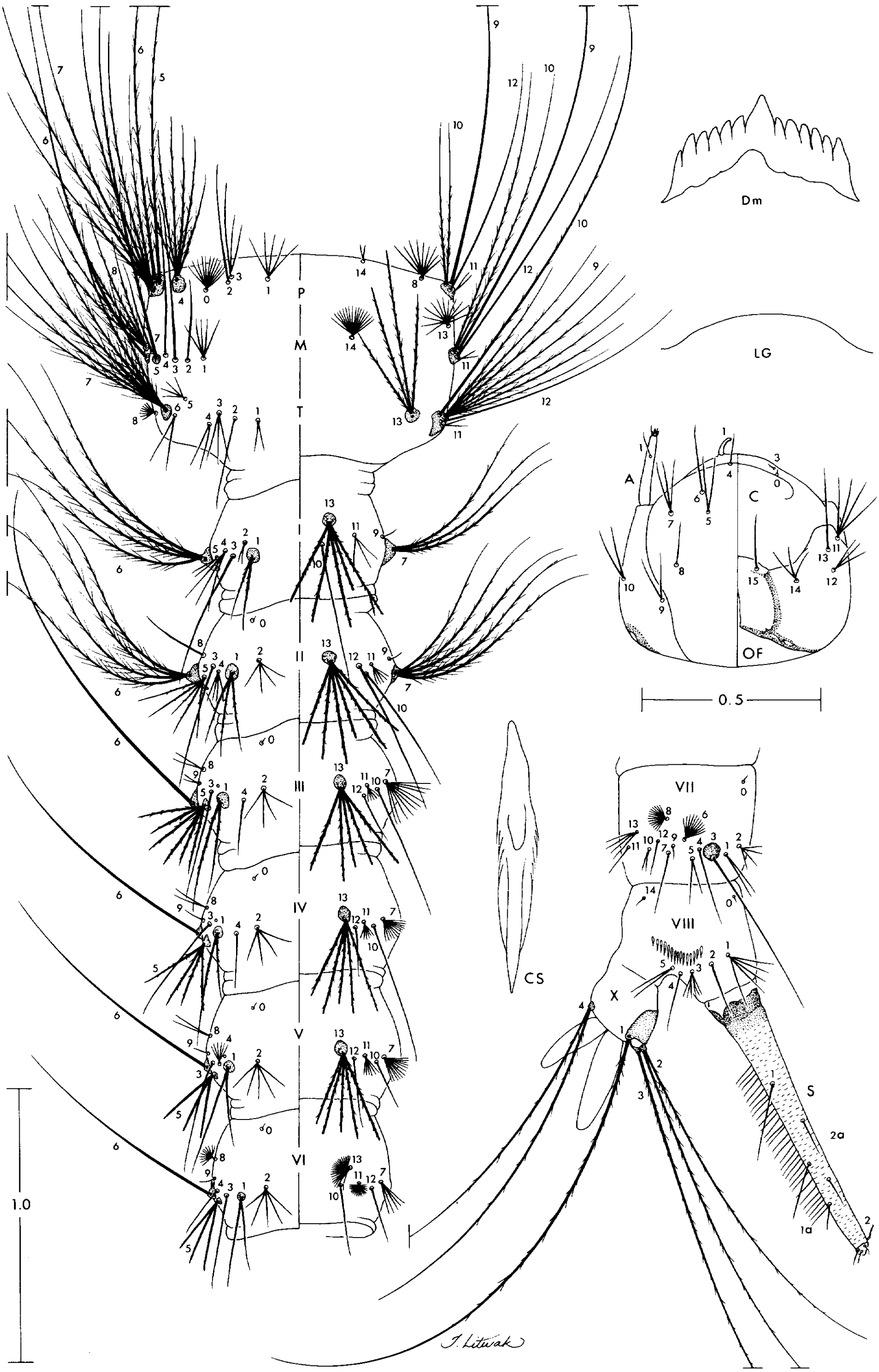

Fig. 3. Third instar larva of *Sabethes chloropterus*. Setae 8-M, 7-T, and 9-I-VII appear for the first time. The setae are easily homologized with those of the second instar.

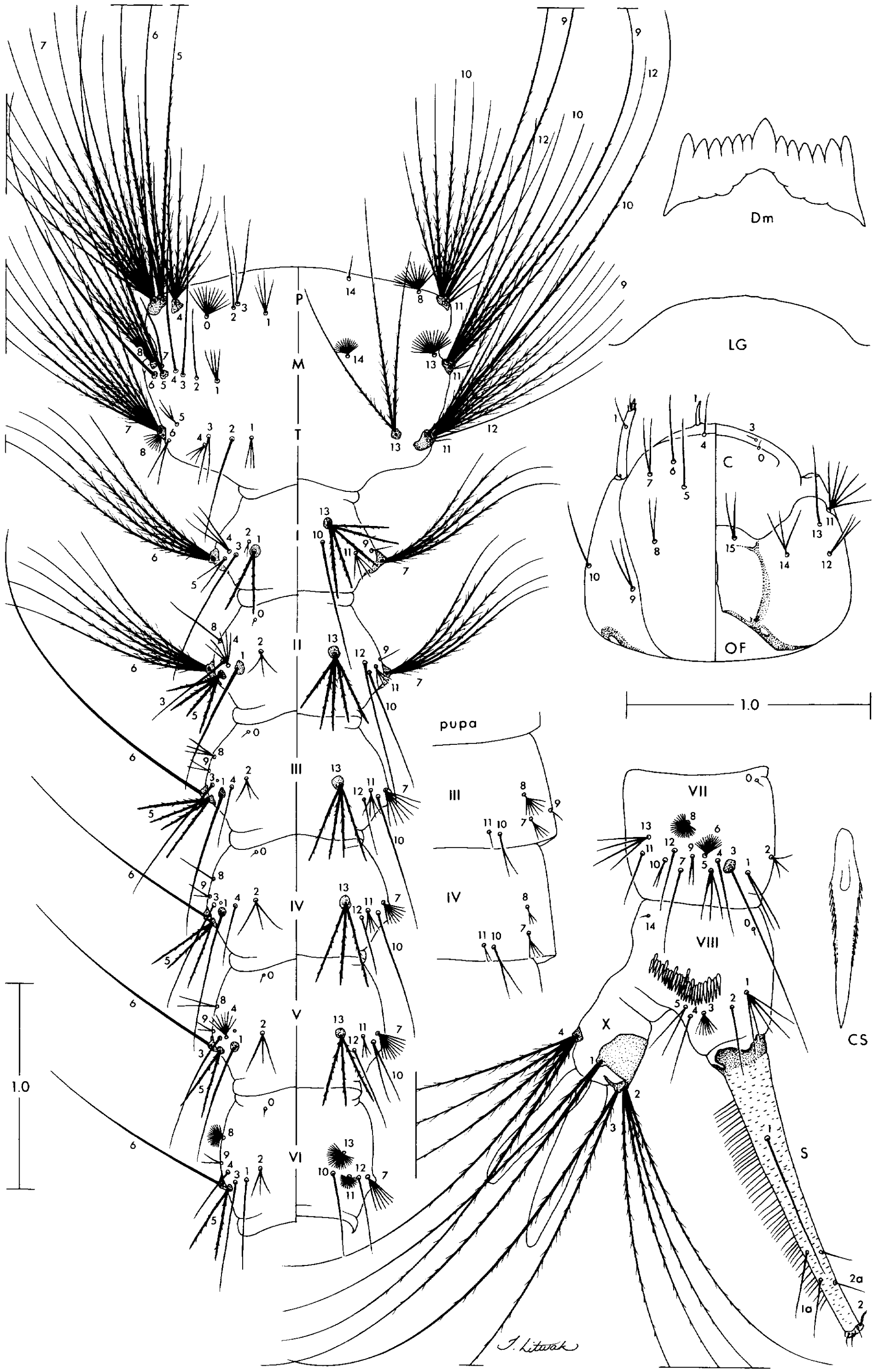

Fig. 4. Fourth instar (mature) larva of *Sabethes chloropterus*. This instar very closely resembles the third instar. Comparison of the ventral surface of segments III and IV of the larva and pupa (center) shows that the relative positions of setae 10 and 11 are the same in both stages, and setae 12 and 13 do not develop in the pupa.

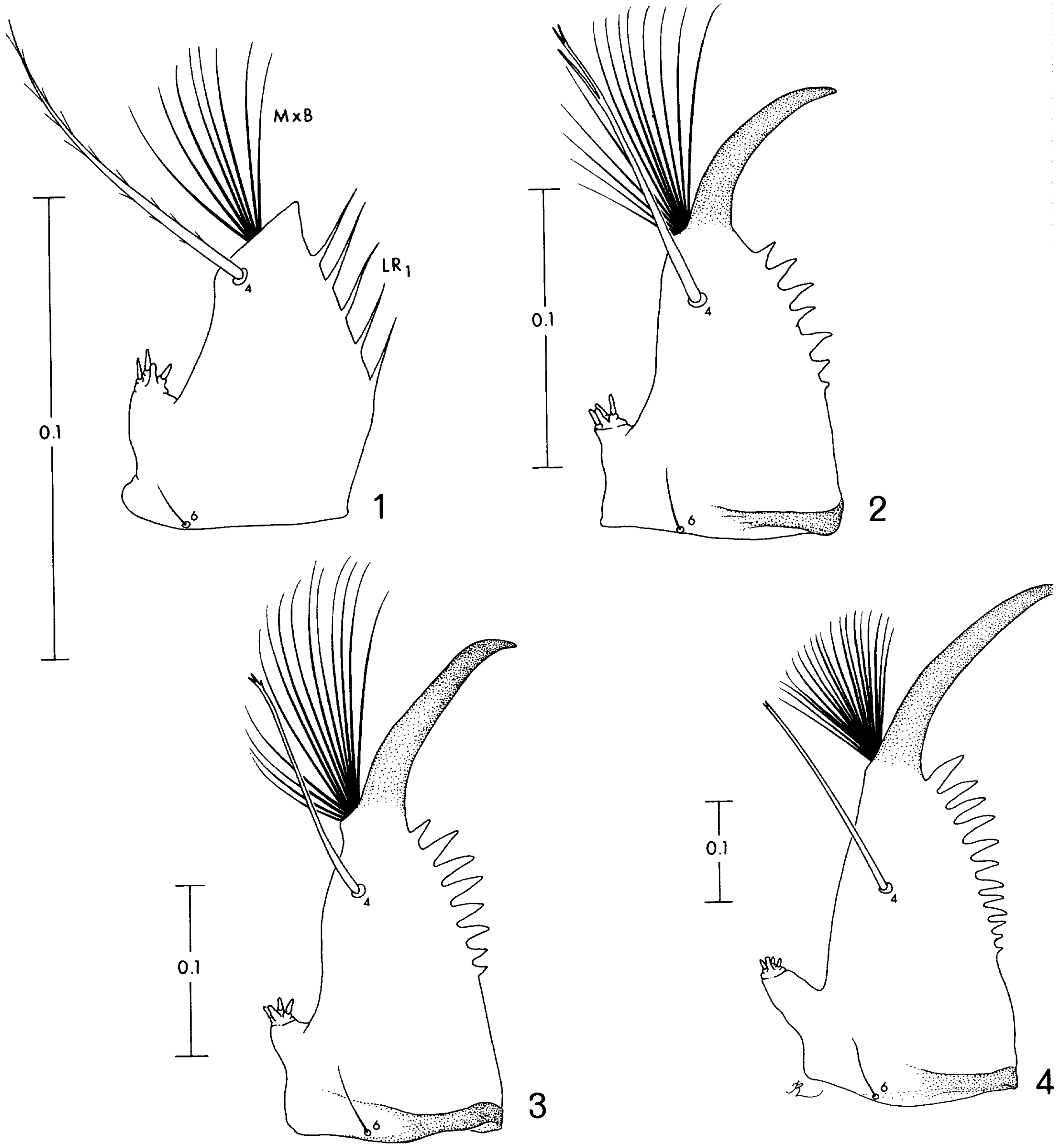

Fig. 5. Form of the maxilla in each of the four larval instars (1-4) of *Sabethes chloropterus*. Fusion of the palpus, cardo, and maxillary body is a generic trait which is already fixed in the first instar.

positions of these setae are exactly the same in both stages (criterion 5). This comparison also indicates that setae 12 and 13 (C) do not develop beyond the larval stage. It appears, therefore, that seta B in the first instar is the same as seta 10 in later instars and the pupa. If this is true, then setae A and B (10 and 11) must reverse their positions on segments III-VI during development from the first to the second instar. A closer examination of segment II in the second instar (Fig. 2) adds support to this idea. In this instar, seta 10-II is located more or less posterior to seta 11, a positional relationship which is more or less intermediate between the positional relationships of these setae on segments I and III. In certain other sabethines, species of *Tripteroides* Giles for example, setae 10 and 11 occupy the same positions on segments I and II (retention of the first instar condition), but occupy opposite positions on segments III-VI (reversal of the first instar condition).

From the foregoing analysis, it seems likely that the ventral setae on abdominal segments I-VII of the first instar larva are ontogenetically homologous with setae 10, 11, and 13 of later instars. This interpretation differs at least in part from all previous interpretations (Table 1), but is otherwise in perfect agreement with the serial and ontogenetic homologies established by Belkin (1962). The nomenclature previously applied to these setae in first instars is easily reconciled with the new designations by reference to Table 1. After serial homologies are established by comparison with abdominal segment I (criteria 2 and 3), ontogenetic and phylogenetic homologies can be determined by applying criteria 4, 5, 7, and 8. To date, criterion 6 has only been used to demonstrate ontogenetic homologies between the fourth instar larva and the pupa, but it should be possible to use this criterion to trace setal homologies from instar to instar, thus eliminating the need to rely on criteria 4 and 5 for this purpose.

A number of workers have examined the thoracic chaetotaxy in the different instars of various species. Table 2 provides a summary of previous observations. These studies show that setae 7-P, 8-M (13-M in *Toxorhynchites*), and 7-T are absent in the first instar. Seta 7-P first appears in the second instar, while setae 8-M and 7-T first appear in the third. Seta 8-M fails to appear at all in species of *Trichoprosopon* Theobald (Zavortink 1979), several species of *Tripteroides* (Mattingly 1981), and at least one species of *Sabethes* (Harbach, unpublished observation). Since these setae, with the exception of 7-P, are absent in the first and second instars, application of criteria 1 and 8 above would indicate that these setae are both serially and phylogenetically homologous. Although seta 7-P shows up one instar earlier and 8-M bears a different numerical designation, this does not necessarily deny the possibility of serial homology or invalidate criterion 1. There is no doubt that much work needs to be done before the homologies of the thoracic setae are definitely known. In this connection, it is noted that the seta missing from the mesothorax in *Toxorhynchites rutilus septentrionalis* (Dyar and Knab) appears to be 13-M as currently interpreted (Dodge 1964, his seta 7-M).

In the majority of species studied, seta 9 first appears on abdominal segments I-VII in the third instar larva (Table 3). In *Tripteroides* this seta makes its first appearance along with seta 7-P in the second instar. Is this coincidence or is there a genetic basis for the late appearance and differential development of seta 9 and the three thoracic setae in different taxa? Considered in terms of heterochrony (p. 22), it is possible that these setae are serially homologous with different times of appearance due to differing degrees of retardation in their morphogenesis. Regardless of their true homologies, the facts of development of these setae show that they form at different times during development, or fail to develop at all. The meaning of these ontogenetic differences in the phylogeny and classification of mosquitoes is problematic and requires much additional study.

The presence of pecten spines and seta 4-X in the first instar of *Sabethes chloropterus* warrants consideration. Based on circumstantial evidence, it is assumed that the pecten spines are homologous with the ventral row of filaments which appears on the siphon of the second instar. Since at least two species of *Wyeomyia* (Harbach and Peyton 1990) are known to bear a ventral row of pecten spines in the fourth

Table 1. Comparison of designations for ventral setae on abdominal segment I of first instar larvae.

Species	Seta A	Seta B	Seta C	Authors
Sa. chloropterus	11	10	13	by convention
Bi. hollandi	9	10	11	Belkin 1962
*An. punctulatus**	9	10	11	Belkin 1962
An. crucians/bradleyi	10	11	12	Floore et al. 1976
An. freeborni	10	11	12	Belkin 1953
An. baezai (as *gateri*)	10	11	12	Baisas and Ubaldo-Pagayon 1952
An. walkeri	11	12	13	Hurlbut 1938
An. flavirostris/peditaeniatus (as *nigerrimus*)	9	11	13	Baisas 1947
Ur. anhydor	10	11	12	Belkin & McDonald 1956
Tp. microcala/nepenthicola	10	11	12	Baisas and Ubaldo-Pagayon 1952

*Same designations used for *An. farauti*, *koliensis*, *solomonis*, and *lungae*.

Table 2. Pairs of setae occurring on thoracic segments of larval instars of Culicidae.

	Prothorax[a]		Mesothorax[b]		Metathorax[c]		
Genus	1st	2nd-4th	1st/2nd	3rd/4th	1st/2nd	3rd/4th	Authors*
Anopheles	14[d]	15[d]	13	14	12	13	(1)(2)(4)(9)(12)
Bironella	14	15	13	14	12	13	(4)
Uranotaenia	13	14	13	14	12	13	(3)
Aedes	13	14	13	14	12	13	(6)(7)(8)(12)
Culex	13	14	13	14	12	13	(10)(12)
Culiseta		14	13	14	12	13	(12)
Johnbelkinia		14	13	14	12	13	(11)
Trichoprosopon		14		13		13	(11)
Runchomyia		14	13	14	12	13	(11)
Tripteroides	13	14	13	14	12	13	(2)
Sabethes	13	14	13	14	12	13	(13)
Wyeomyia		14	13	14	12	13	(12)
Toxoryhnchites	13	14	12?	14	10?	13	(5)

[a] Seta 7-P appears in 2nd instar.

[b] Seta 8-M appears in 3rd instar, except *Trichoprosopon*, some *Tripteroides*, and one species of *Sabethes* which never develop this seta.

[c] Seta 7-T appears in 3rd instar.

[d] Seta 13-P not present in all species.

*Authors: (1) = Hurlbut 1938; (2) = Baisas and Ubaldo-Pagayon 1952; (3) = Belkin and McDonald 1956; (4) = Belkin 1962; (5) = Dodge 1964; (6) Smith 1969; (7) = MacKenzie 1971; (8) = Harrison and Rattanarithikul 1973; (9) = Floore et al. 1976; (10) = Yan 1977; (11) = Zavortink 1979; (12) = Savignac and Maire 1981; (13) = present study.

Table 3. Pairs of primary setae (excluding 0 and 14) occurring on abdominal segments I-VII of larval instars of Culicidae.

	1st instar[a]		2nd instar[b]		3rd/4th instars[c]		
Genus	I	II-VII	I	II-VII	I	II-VII	Authors*
Anopheles	10	11	11	12	12	13	(1)(2)(5)(6)(7)
Bironella	10	11			12	13	(6)
Uranotaenia	11[d]	11	12	12	12[d]	13	(4)
Tripteroides	10	11	11	13	11	13	(3)
Sabethes	10	11	10	12	11	13	(8)

[a] Includes 3 ventral setae per segment.

[b] One ventral seta appears, except on segment I of *Sabethes* and *Tripteroides*; seta 9 appears in *Tripteroides*.

[c] Seta 9 appears in 3rd instar, except in *Tripteroides* where it appears in the second instar.

[d] Seta 8-I present, substituted for 9-I in 3rd instar.

*Authors: (1) = Hurlbut 1938; (2) = Baisas 1947; (3) = Baisas and Ubaldo-Pagayon 1952; (4) = Belkin and McDonald 1956; (5) = Belkin 1953; (6) = Belkin 1962; (7) = Floore et al. 1976; (8) = present study.

instar larva, a row that is anatomically in the same position as the filaments of *Sabethes*, and noting that some sabethine larvae, for example *Wyeomyia leucostigma* Lutz, possess a "false pecten" which is intermediate in structure and position between the pecten and the filaments, it is not too difficult to imagine that the pecten spines are transformed into filaments in the second instar.

Seta 4-X (ventral brush) has been reported previously in first instar larvae of species of *Wyeomyia* (Dodge 1964, 1966) and *Tripteroides* (Baisas and Ubaldo-Pagayon 1952), but is absent in first instars of all non-sabethine genera studied to date (10 genera, see Dodge 1966 for examples from North America). Anophelines, however, have a well developed cluster of spicules which are believed to be the first instar equivalent of the ventral brush. The presence of seta 4-X in first instar larvae of sabethines appears to be a unique development within the Culicidae. The precocious appearance of this seta with respect to its later appearance in the second instar of non-sabethine mosquitoes sheds some doubt on its homology with seta 4-X (ventral brush) in other taxa. The seta in question could be homologous with seta z-X which occurs in a ventrolateral position either on or off the saddle (usually on) in members of the genus *Corethrella* Coquillett (family Corethrellidae) and certain species of *Uranotaenia* Lynch Arribalzaga and *Coquillettidia* Dyar (Belkin 1962). Although "seta 4-X" usually occurs on the membranous part of segment X in sabethines, it is known to occur on the ventral margin of the saddle in some species, e.g., *Phoniomyia diabolica* Lane and Forattini, *Tripteroides coheni* Belkin, and *Wyeomyia bicornis* (Root). Until further study can resolve the identity of this seta in sabethines, its homology with seta 4-X (ventral brush) in non-sabethine mosquitoes must remain uncertain.

Although generic characters among mosquitoes appear to be fixed in first instar larvae, larvae of different genera more closely resemble one another in the earliest stage of development. This resemblance progressively diminishes as the larvae approach their definitive forms. Setae generally become more complex in form during development from one instar to the next, but they do not seem to exhibit the "remarkable shifts in position" noted by Zavortink (1979). On the contrary, from an examination of all previous works on different instars of individual species, including the second (incomplete), third, and fourth instars of *Johnbelkinia ulopus* (Dyar and Knab) illustrated by Zavortink, it is apparent that setae generally retain their relative positions to one another during development and individual variation in position is slight. For this reason, the relative positions of setae are considered to be of more importance in the identification and classification of mosquitoes than the structure of setae. Paraphrasing Belkin (1951), structural differences in setae represent specific characters while positional differences reflect supraspecific relationships.

Zavortink (1979) attributed specific differences in setal characteristics of fourth instar larvae in groups like *Shannoniana* to "differing degrees of neoteny in various species." By all accounts, neoteny applies to cases where larval characters are retained in adults by the retardation of somatic development (see, for example, de Beer 1958, Matsuda 1976, and Gould 1977). Neoteny is a case of heterochrony. Heterochrony refers to the acceleration or retardation of morphogenesis (development) during ontogeny so that homologous structures appear earlier or later, respectively, relative to their appearance in the ontogeny of an ancestor. This phenomenon applies to the development (appearance) of setae 7-P, 8-M, 7-T, 9,12-I-VII, and 4-X, but not to differences in the characteristics of phylogenetically homologous setae of mature larvae. Zavortink's statement seems to refer to specific phenotypic differences in the larval chaetotaxy of various species. These differences probably have a genetic basis, but may be influenced by environmental factors as well.

SUMMARY

This study included an analysis and comparison of published data on the development of the larval chaetotaxy, with special emphasis on the determination of homologous setae in the first instar. The main points of discussion may be summarized as follows:

First instar larvae should be used as a starting point for determining setal homologies, especially phylogenetic homologies.

Setae 10,11-I-VII are present in all larval instars and the pupa.

Seta 13-I-VII is present in all larval instars, but is lost in the pupa.

Seta 12-I-VII (12-I is absent in sabethines and some aedines) makes its first appearance in the second instar larva and is lost in the pupa.

Seta 9-I-VII first appears in the second or third instar larva and is retained in the pupa.

Seta 7-P first appears in the second instar larva.

Setae 8-M and 7-T first appear in the third instar larva, except in certain sabethines where 8-M fails to appear at any time during larval development.

Although seta 7-P develops earlier than 8-M and 7-T, it is possible that these setae are serially homologous. It is also possible that these setae are serially homologous with seta 9-I-VII.

The early appearance of seta 4-X in sabethine larvae sheds some doubt on its homology with the ventral brush (seta 4-X) of other taxa. It could be homologous with seta z-X.

The appearance of setae 7-P, 8-M, 7-T, 9,12-I-VII, and 4-X at different times in development may be explained in terms of heterochrony.

The relative positions of setae remain constant during development. Therefore, absolute differences in setal positions are generally supraspecific in nature, and groups containing larvae with quantitative differences in the placement of setae probably are not monophyletic.

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