

Morphology of the Thoracic Skeleton and Muscles of the Mosquito, *Culiseta inornata* (Williston), (Diptera: Culicidae)

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ABSTRACT The objectives of this research were to investigate the morphology of the thoracic skeleton and muscles of the mosquito, *Culiseta inornata* (Williston). The results are presented in 25 text figures and descriptions of each skeletal part and muscle. Undescribed exoskeletal structures are the postmedio-tergite, intersegmental cleft on the caudal margin of the metapleuron, and the parascutellar process. This process is considered a homologue of the fourth axillary. The acrotergite 2 and subalifer were identified. The prescutum has been called the paratergite by previous authors. The morphological basis for self amputation of legs is described. Undescribed parts of the endoskeleton are: lateral arm of sternal apophysis 1 and its socket on the mesal surface of coxa 1, furcopleural apodeme on sternal apophysis 1, precoxal and postcoxal apodemes arising from the ventral pleural arm, upper and lower laterotergite apodemes on the postnotum, and the pleural and intersegmental apodemes for attachment of halter muscles. Seventy-two muscles are illustrated with their attachments and the origin, insertion, and action of each is described. Ten of the muscles are newly described for the mosquito. There are no muscles inserted on the subalare, second axillary, or third axillary.

Studies on the morphology of the thorax of mosquitoes have been conducted almost entirely by investigators whose primary interests were in taxonomy. Consequently, the exoskeleton is rather well known, but the endoskeleton has been almost completely ignored, and, until recently, little attention was given to the muscles.

The early work of Snodgrass ('12) on the external morphology of *Psorophora ciliata* covered all the large sclerites of the thorax and many of the smaller ones often omitted in later publications. The report of Prashad ('18) on the thorax and wing of *Anopheles* contained the first description of the axillary sclerites of the wing. His terminology for the axillaries was based on the work of Lowne (1890-1895) on the blowfly. Young ('21) depicted the metapostnotum without a label in illustrations of the metathorax of *Anopheles quadrimaculatus* and *Culex canadensis*. Crampton ('25) listed four anatomical features characteristic of the Culicidae, the well-developed posterior pronotum, basalar cleft,

large meron, and the fusion of the posterior anepisternum with the sternopleurite (pre-episternum 2). Snodgrass ('59) used metapostnotum for his earlier term postnotum 3 and described its relationship to the tergum of the first abdominal segment. Christophers ('60) illustrated the thorax of *Aedes aegypti*, but used the terminology of Prashad ('18) for the axillary sclerites of the wing. Belkin ('62) followed Edwards ('41) for terminology of the thorax. Knight and Laffoon ('70a,b) published illustrated taxonomic glossaries for the thorax and legs of mosquitoes.

The external features of some near relatives of mosquitoes were described in the work of Cook ('56) on the Nearctic Chaoborinae and by Peters and Cook ('66) on the Nearctic Dixidae. In both studies the views of Rees and Ferris ('39) and Ferris ('40a,b) were adopted for interpreting the thoracic pleura and sterna.

Information on the thoracic endoskeleton of

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mosquitoes is almost completely lacking except as can be inferred from external observations. The extensive work of Christophers ('60) on *Aedes aegypti* omitted a section on the endothorax. He illustrated only the furcae, first phragma, and parts of the mesosternum.

Investigations have been conducted on certain muscles of the mosquito thorax by Prashad ('18), Hassan ('44), Jones ('54), Tiegs ('55) and Smart ('59). The only attempt to catalogue all the thoracic muscles was by Christophers ('60), who found 64 in *Aedes aegypti*. These were given numbers and assigned to categories, but only a few were named.

The objectives of this research were: (1) to investigate the morphology of the thoracic skeleton of the mosquito *Culiseta inornata*; (2) to determine the origin, insertion, and action of the muscles of the thorax and its appendages; (3) to determine the homologies of certain sclerites and muscles.

MATERIALS AND METHODS

This investigation was conducted primarily on adult females of *Culiseta inornata*. Males of this species and females of other genera were used for limited comparative observations.

Dried and preserved specimens were used for studies on the skeleton. These were treated with 10% KOH at room temperature and inspected at intervals for the desired degree of maceration. The internal organs were removed during this period. After maceration, the specimens were stored in 70% ethanol. For study, the material was placed in water for a few minutes, then transferred to dilute methylene blue vital stain in distilled water. Sutures and lightly sclerotized areas absorbed the stain in about 20 minutes.

Mosquitoes three to four days of age were used for study of muscles. These were preserved and stored in a mixture of 90% ethanol 17 parts, 40% formalin 6 parts, glacial acetic acid 2 parts, and distilled water 28 parts. Prior to dissection, the material was washed in water for 15 minutes, then placed in a mixture of 2 parts 70% ethanol and 1 part glycerine for several days. Following this treatment, the specimens were washed in water and transferred to dilute methylene blue vital stain in distilled water for dissection. The muscles became lightly stained as exposed and the tendons were clearly visible in the solution. The action of muscles was determined by observing their attachments and

also by the use of traction on relaxed preserved specimens.

The skeletal preparations were examined in water under a dissecting microscope at 70 \times , or lower, and the dissection of muscles was performed at 70 \times . Measurements were made with a calibrated ocular micrometer reticule and drawings were done with a free hand. Each figure is a composite based on many specimens. This is especially true of muscles where many dissections were required to locate attachments. The illustrations were designed to demonstrate anatomical relationships. The skeletal parts, with few exceptions, are shown *in situ* and the muscles were drawn with the structures to which they are attached.

The terminology for the skeleton is based on comparative morphology and differs in several instances from that proposed by Knight and Laffoon ('70a,b) for use in mosquito taxonomy. Many of the terms were taken from Crampton ('25, '42), Ferris ('40a), Ferris and Pennebaker ('39), Matsuda ('70), Rees and Ferris ('39) and Snodgrass ('35). Several parts of the endoskeleton are described for the first time and given names. The nomenclature used for the muscles is morphological, the name of each muscle being based on its origin and insertion. This system conforms with that of Schiemenz ('57) for the head muscles of the mosquito *Theobaldia annulata*, with Mickoleit ('62) for the thoracic muscles of *Tipula vernalis*, and it is the style of the Entomologisches Wörterbuch by Kéler ('63). In the text, the name of each muscle is preceded by the number assigned to it in this study and followed by the number of its homologue in *Aedes aegypti* as assigned by Christophers ('60).

OBSERVATIONS

Thoracic skeleton

The neck

The neck is covered with the cervical membrane which has embedded in it on each side a pair of lateral cervical sclerites or laterocervicale of Crampton ('25). Each pair is united by a suture in *Culiseta inornata*, but are separate in *Uranotaenia sapphirina*. These sclerites provide support for the head and points for attachment of muscles (figs. 1-3). The anterior lateral cervicale is heavily sclerotized and somewhat triangular in shape with the mesal surface slightly concave. Anteriorly, the cephaliger of Crampton ('42) articulates with the occipital condyle of the cranium. The

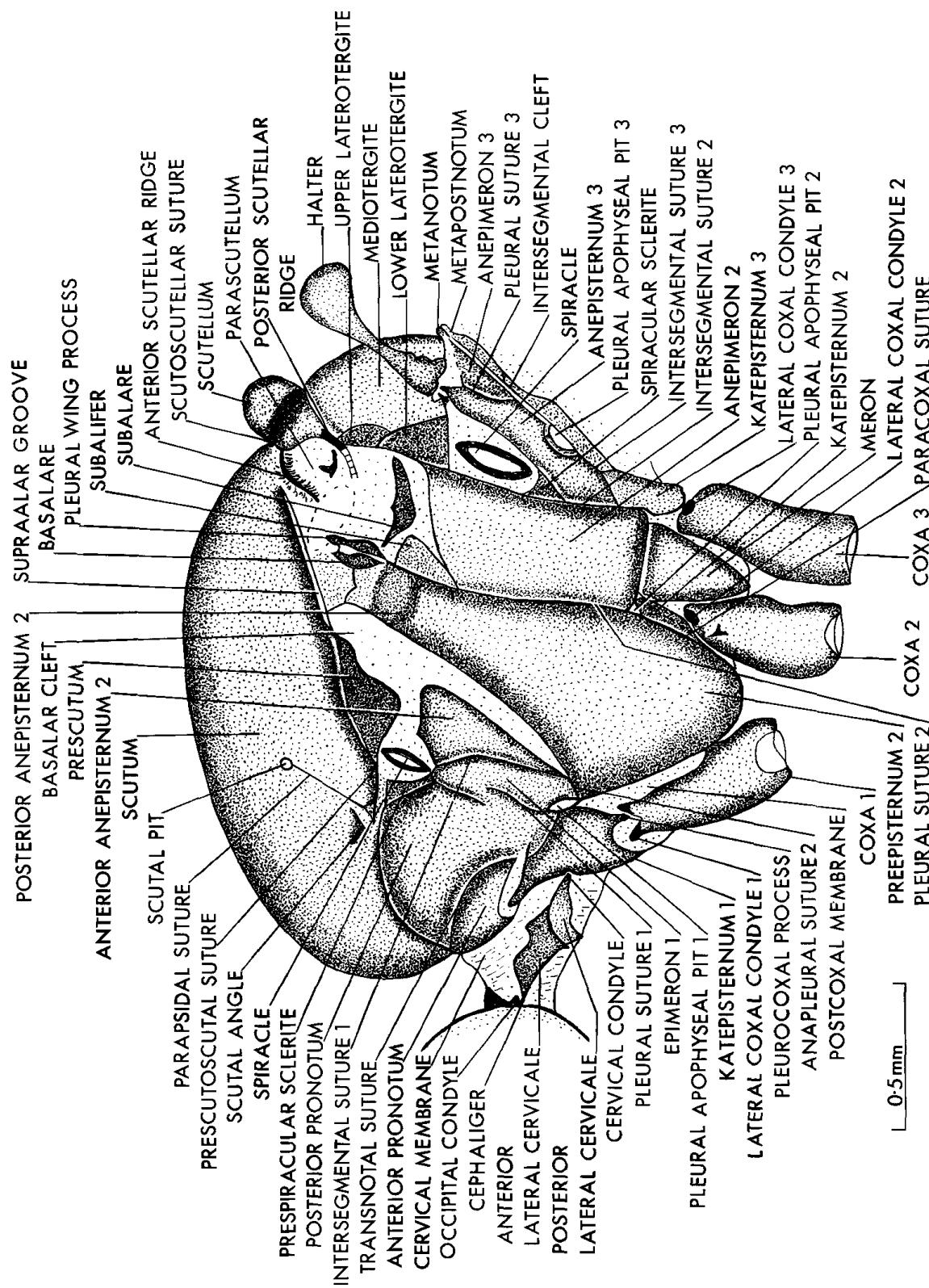


Fig. 1 Lateral view of the thorax in *Culiseta inornata*. Anterior is to the left.

posterior lateral cervicale is lightly sclerotized, somewhat rectangular in shape, and has ventral and caudal arm-like processes. The medioventral arm extends downward beneath the neck to make contact with a similar process from the opposite side (fig. 2). The posterior arm is tapered, forming the cervical condyle that fits into a socket on the anterior surface of the katepisternum 1 to become the cervicoepisternal articulation (fig. 2).

The prothorax

The pronotum is represented by two dorsolateral sclerites on each side, the anterior pronotum and posterior pronotum (fig. 1). The narrow transverse sclerite in the mid-dorsal area that has been considered a part of the pronotum (Belkin, '62) is in reality the acrotergite of the mesonotum (fig. 4). The two pronotal sclerites on a side are separated by the transnotal suture. The anterior pronotum is ovoid in shape, has a cavity within and an elongate aperture on the anterior mesal face (fig. 3). The posterior pronotum is shield-like, and separated from the scutum and the small prespiracular sclerite by a prominent suture. Its posterior margin is demarcated by the pleural suture. The propleuron is composed of the epimeron 1 and katepisternum 1 (fig. 1). Katepisternum 1 is narrow where it joins the anterior pronotum, but the ventral half is enlarged, and anterior to coxa 1 it unites with the precoxale without a suture. On the posterior ventrolateral angle of katepisternum 1 is the small pleurocoxal process of Bonhag ('49) that articulates with the lateral coxal condyle. Internally, on the caudal margin of katepisternum 1 is the episternal apophysis that joins the dorsal limit of the sternal apophysis (figs. 3, 4). Pleural suture 1 arises from the pleural apophyseal pit and extends dorsally to the prespiracular sclerite (fig. 1). This suture is interrupted near the mid-point by a break in continuity in *Culiseta inornata*, *Aedes flavescens*, *Culex tarsalis* and *Psorophora confinis*, but it is continuous in *Anopheles quadrimaculatus*. Internally, the pleural apophysis is formed from pleural suture 1 (fig. 3). Epimeron 1 is an elongate sclerite between pleural suture 1 and intersegmental suture 1 (fig. 1).

The sternal area of the prothorax consists of the paired preepisterna, the two halves of the basisternum, and the unpaired furcasternum 1. The two preepisterna are incompletely separated by the median preepisternal suture

(figs. 2, 4). A lateral arm of each preepisternum 1 extends anterior to the coxal cavity uniting with the katepisternum 1 to form the precoxale or precoxal bridge of Crampton ('42). The preepisterna taper to their caudal limits forming paired ridges and the preepisternal groove ventral to basisternum 1 (fig. 2). The preepisternal suture arises posteriorly from the basisternal suture, describes an arc ventrally, then extends anteriorly on a line beneath the basisternal suture. This relationship is illustrated from a lateral view in figure 3. The only parts of basisternum 1 visible from the ventral aspect are the heavily sclerotized margins of the preepisternal groove at its caudal limits (fig. 2). From the dorsal aspect, the basisternum is triangular, the base uniting with furcasternum 1 and the apex tapering to a point cephalad between the preepisterna (fig. 4). Consequently, the basisternum occupies the space between the coxal cavities except for a narrow strip of preepisternum on the ventral surface.

Furcasternum 1 is somewhat triangular, with extensions from the anterior lateral angles supporting the sternal apophyses (fig. 2). There is an apparent transverse suture in the median area at the level of the apophyseal pits in several genera of Culicini examined, but it is absent in *Anopheles quadrimaculatus*. The sternal apophysis arises from the apophyseal pits and extends dorsally to unite with the episternal and pleural apophyses at the level of the pleural apophyseal pit (figs. 2-4). The sternal apophysis is connected to the posterior margin of the coxal cavity by a thin sheet of sclerotized cuticle that is here named the furcopleural apodeme (figs. 2-4). This apodeme provides surface for the attachment of indirect wing muscles. It is present in *Anopheles quadrimaculatus*, *Aedes flavescens*, *Culex tarsalis*, *Culiseta inornata*, *Psorophora confinis*, *Uranotaenia sapphirina* and *Wyeomyia smithii*. The sternal apophysis has two prominent processes projecting from its central axis. The first is the mesal arm that is slightly curved and extends dorsad (figs. 2-4). This is the mesal arm of the apophysis, as known in many insects, and was illustrated in *Aedes aegypti* by Christophers ('60). Dorsal to the mesal arm there is a lateral process here named the lateral arm of the apophysis. There is no mention of this arm of the sternal apophysis in publications on mosquito morphology. It is present in both sexes. The point of this arm is heavily sclerotized and fits into

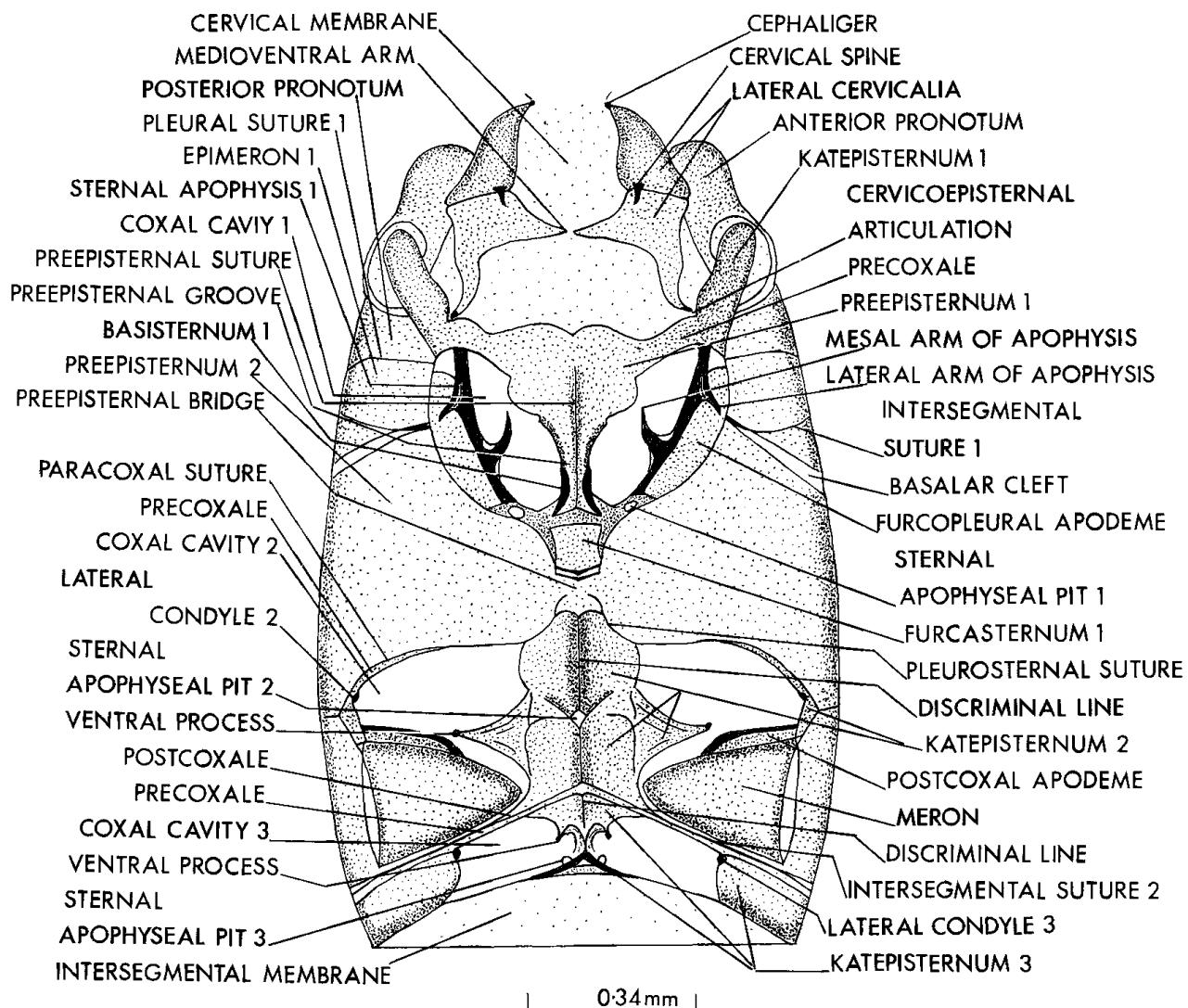


Fig. 2 Ventral view of the thorax in *Culiseta inornata*.

a socket on the mesal surface of coxa 1 near the base (figs. 5A,B). The lateral arm and socket form a type of ball and socket articulation for movements of the coxa.

The mesothorax

The dorsal surface of the mesothorax is covered with acrotergite 2, prescutum, scutum, scutellum, and postnotum. Acrotergite 2 is a small transverse sclerite partly concealed beneath the anterior margin of the scutum (fig. 4). This sclerite has been considered as the dorsal part of the pronotum (Belkin, '62), but it is clearly defined on all sides by sutures, and a comparison with *Tipula reesi*, as depicted by Matsuda ('70), leaves no doubt about its identity. Internally, the first phragma arises from the level of the antecostal su-

ture and projects ventrad (figs. 3, 4). Its shape varies slightly among different mosquito genera. In *Anopheles quadrimaculatus* it is a plain, transverse structure, but in *Aedes*, *Culex*, *Culiseta*, and *Psorophora* paired lateral arms project ventrad from the main body and lateral braces extend to the edge of the scutum. A phragmal thread also extends from the base of the lateral arms to the anterior margin of the scutum (figs. 3, 4). Christophers ('60) recognized the first phragma in *Aedes aegypti* as being mesothoracic in origin, but thought it should be called pronotal apodeme.

The prescutum of the mosquito is lateral to the anterior part of the scutum and has been known for many years as the paratergite (Crampton, '25) (figs. 1, 3). Snodgrass ('12) called it a small lateral lobe and ('59) he used

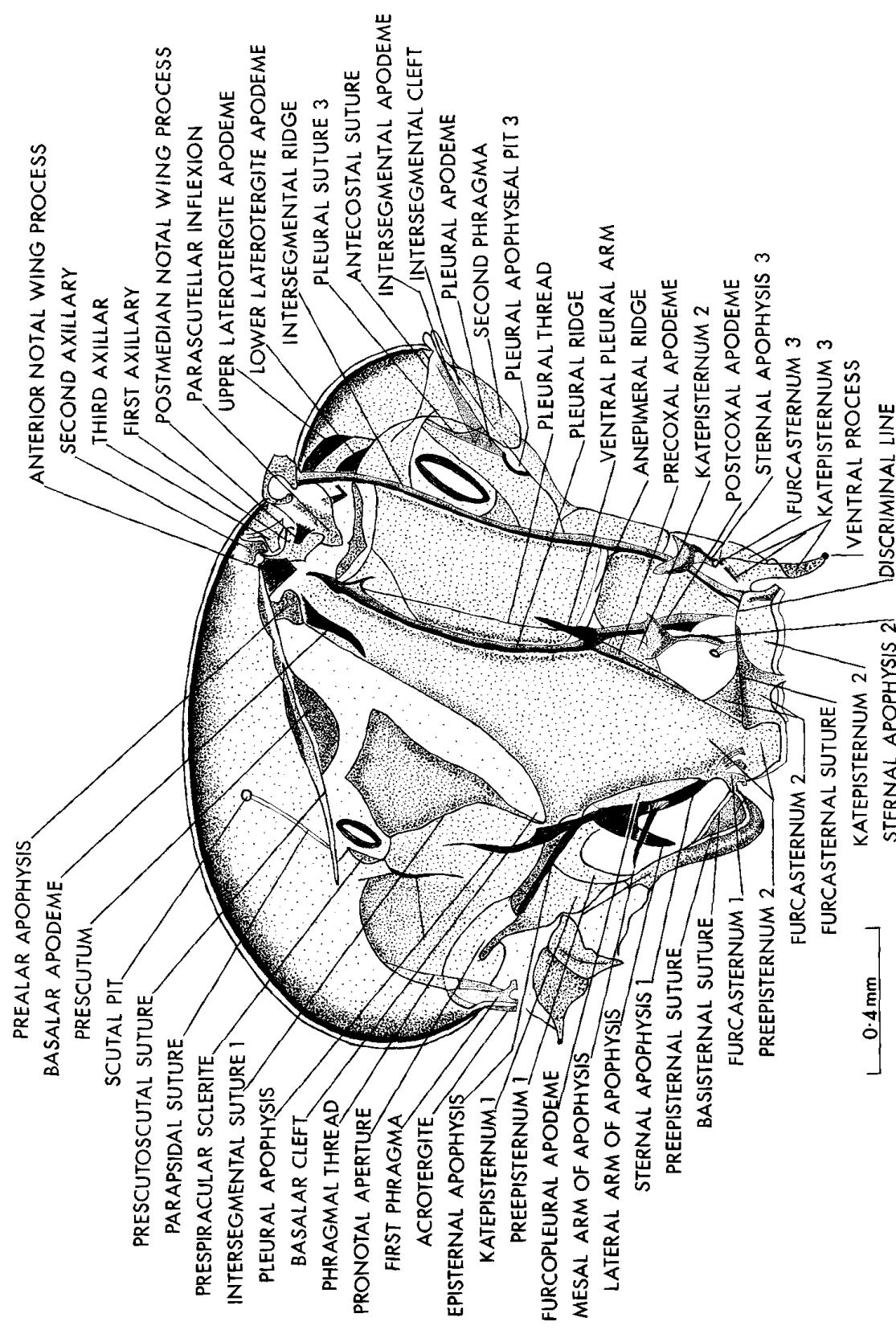


Fig. 3 Lateral internal view of the thorax in *Culiceta inornata* after sagittal section. Anterior is to the left.

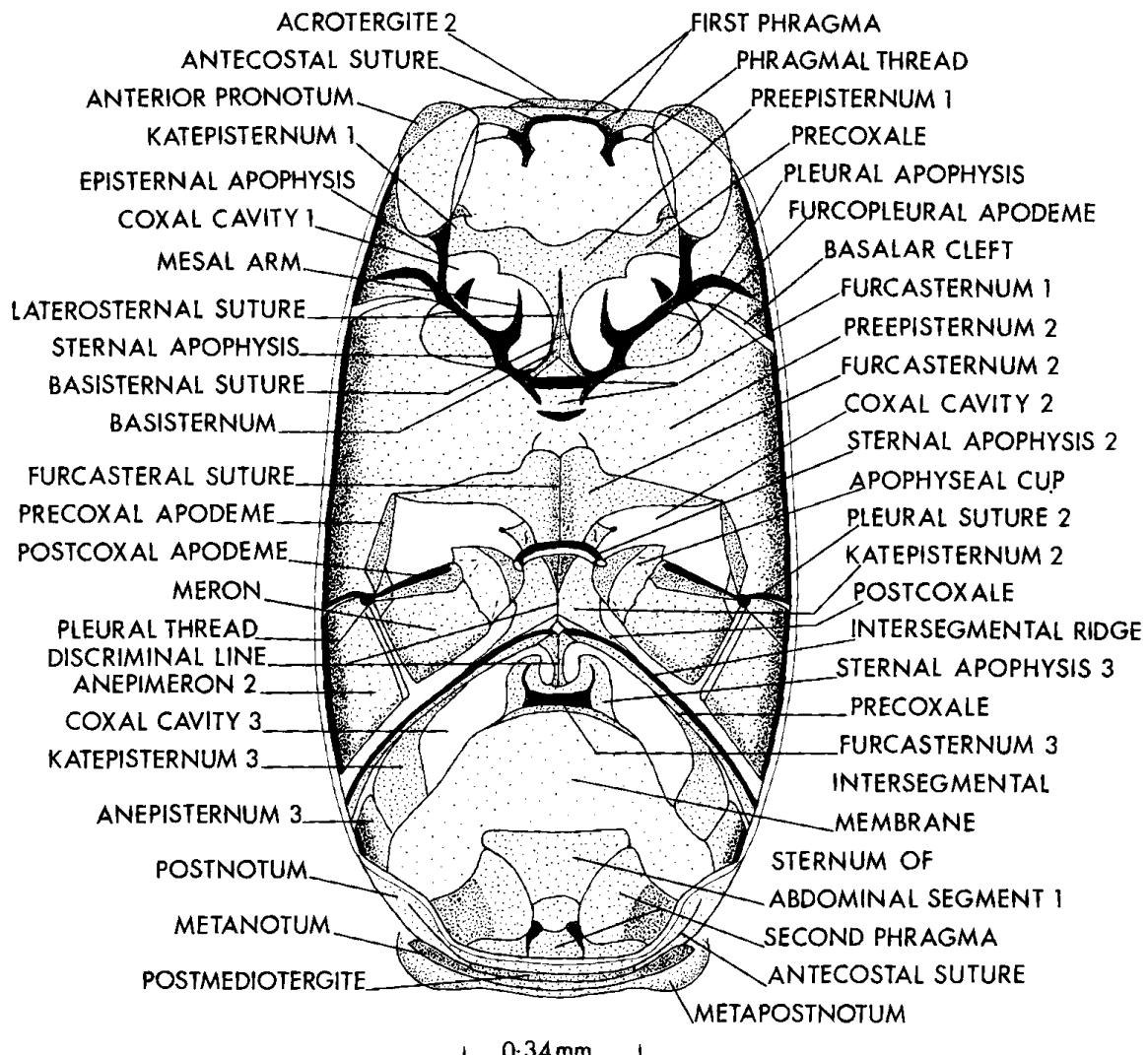


Fig. 4 Dorsal internal view of the sternal area in *Culiseta inornata* after removal of the dorsum.

the term paranotal fold. In *Culiseta inornata* the prescutoscutal suture separates it from the scutum. The scutum is the largest of the mesonotal sclerites extending from the anterior tip of the mesonotum to the scutoscutellar suture (fig. 1). The parapsidal suture of Matsuda ('70) extends from near the scutal angle to the scutal pit. The scutal pit may be the prescutal or humeral pit of Crampton ('42). Internally, the parapsidal suture is represented by a ridge and the pit has a lip. The supraalar groove is lateral to the scutum above the wing base. This groove is marked internally by a prominent ridge on its mesal side (figs. 1, 8, 9).

Posterior to the scutoscutellar suture is the scutellum, a transverse elevated area with paired lateral lobes and an enlarged central

area. The scutellum in *Anopheles* is crescent shaped. Within the scutellum is the scutellar cavity that opens on the ventral side and is filled with muscular tissue (figs. 1, 8, 9). The anterior scutellar ridge extends from the lateroanterior angle of the scutellum to the base of the postmedium notal wing process (figs. 1, 8, 9). The posterior scutellar ridge arises on the laterocaudal angle of the scutellum to divide into a small anterior branch (not illustrated) and a posterior branch that unites with the axillary cord of the wing (figs. 8, 9). The parascutellum of Crampton ('42), also known as postalar callus (Belkin, '62; Knight and Laffoon, '70a), is the area lateroventrad between the anterior and posterior scutellar ridges (figs. 1, 8, 9). The small angular part located near the center of the

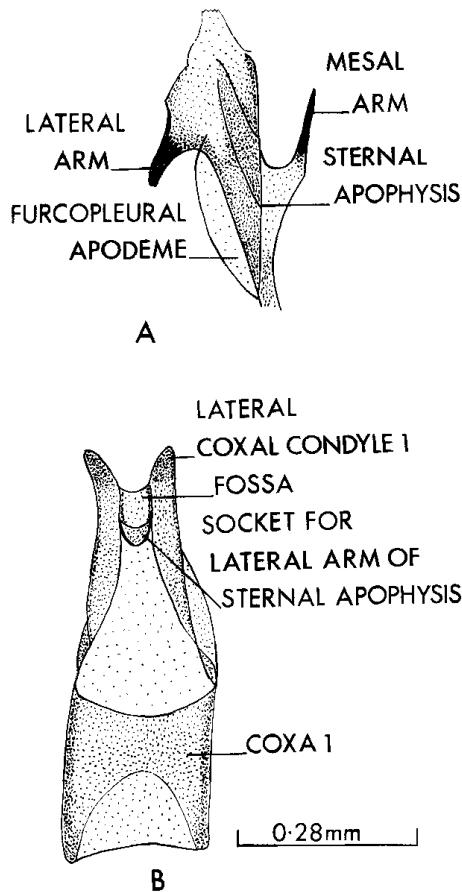


Fig. 5A Part of the sternal apophysis in *Culiseta inornata* illustrating the mesal and lateral arms.

B Mesal surface of apophysis in *Culiseta inornata* illustrating socket for lateral arm of sternal apophysis 1.

parascutellum is here named the parascutellar process. It is represented internally as a ridge or apodeme for insertion of direct wing muscles. The parascutellar process has no connection with either the anterior or posterior scutellar ridges (figs. 8, 9, 23). This process is present in all the mosquito genera examined, i.e., *Aedes*, *Anopheles*, *Culex*, *Culiseta*, *Psorophora*, *Uranotaenia* and *Wyeomyia*. Internally, a blade-like process, here named the parascutellar inflection, projects ventrad from the parascutellum (fig. 3).

The postnotum, also known as postscutellum (Crampton, '42), is oval, shieldlike, and covers the area between the scutellum and metanotum. Its dorsal surface is made up of the large mediotergite and a very small undescribed posterior sclerite, here called the post-mediotorite (fig. 6). On the anterior lateral surfaces are the upper and lower laterotergites that are represented internally by processes here named the upper and lower laterotergite apodemes. These apodemes ap-

pear to give support to the walls of the postnotum (figs. 6, 7). Also internally, the second phragma arises from the posterior lateral margin of the postnotum (figs. 3, 4). It consists of paired oval-shaped flaps projecting ventrally and united at their bases by a narrow median strip. Some longitudinal indirect wing muscles are attached to the second phragma.

The propleuron and mesopleuron are separated by intersegmental suture 1. This suture begins at the posterior ventral angle of epimeron 1 and extends dorsad to the base of the mesothoracic spiracle; here it is interrupted, then reappears to form the anterior border of the prespiracular sclerite (figs. 1, 3). The mesothoracic spiracle is located in lightly sclerotized cuticle posterior to the prespiracular sclerite. The structure of a spiracle in *Anopheles* and *Culiseta* was described by Hassan ('44).

The mesopleuron has a total of ten sclerites as follows: anterior anepisternum 2, posterior anepisternum 2, preepisternum 2, basalare, subalare, pleural wing process, subalifer, anepimeron 2, meron, and katepisternum 2 (fig. 1). Some of these parts are small and not always recognized as separate entities. Crampton ('25) called attention to the peculiar oblique slash-like basalar cleft in the Culicidae. This cleft separates the anterior anepisternum 2 from the posterior anepisternum 2 and preepisternum 2. The dorsal part of anterior anepisternum 2 is known to tax-

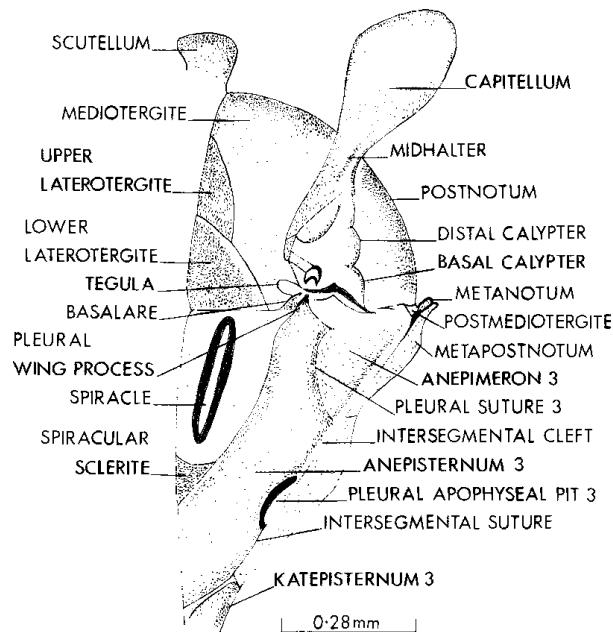


Fig. 6 Lateral view of the postnotum and metathorax in *Culiseta inornata*. Anterior is to the left.

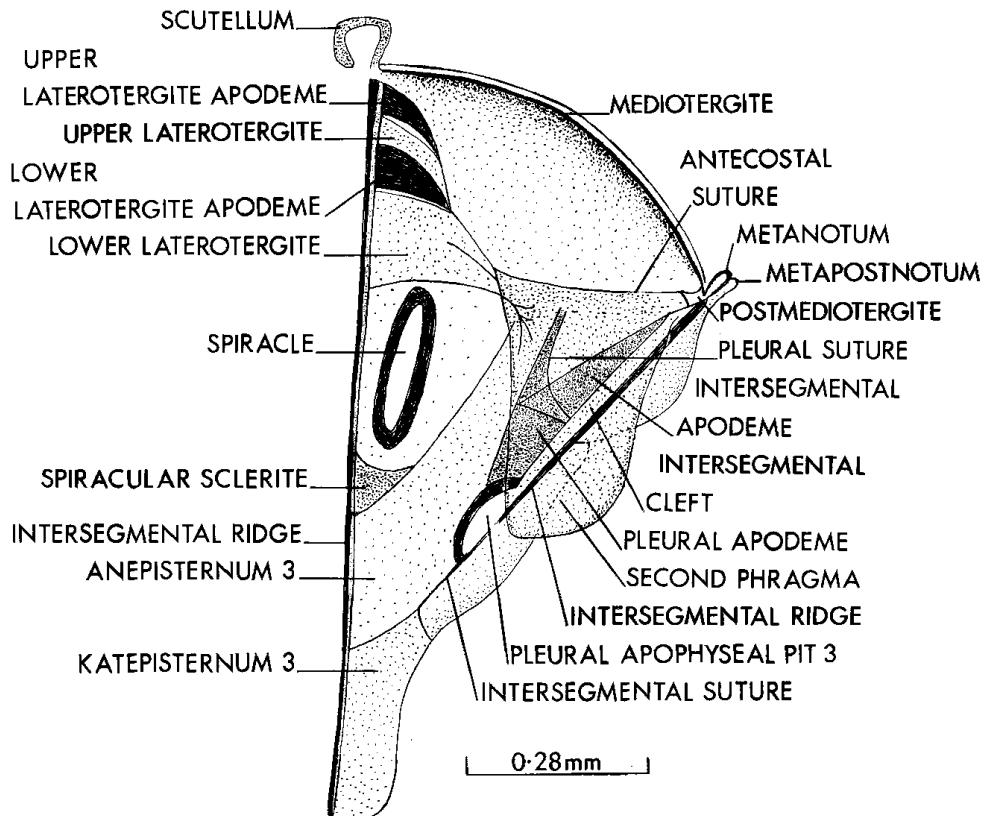


Fig. 7 Lateral internal view of the postnotum and metathorax in *Culiseta inornata* after sagittal section. Anterior is to the left.

onomists as the postspiracular area (Knight and Laffoon, '70a) (fig. 1). The largest mesopleural sclerite is preepisternum 2, also known as sternopleuron (Belkin, '62) and mesepisternum (Knight and Laffoon, '70a). The main body of preepisternum 2 in *Culiseta* is somewhat triangular with an arm-like apical area representing posterior anepisternum 2 (fig. 1). There is no suture in *Culiseta* separating these two sclerites, but in the mosquito *Uranotaenia sapphirina* the anapleural suture is present. In *Anopheles quadrimaculatus* posterior anepisternum 2 is set apart by a lightly sclerotized strip. This sclerite is elevated and known as the prealar knob to taxonomists (Knight and Laffoon, '70a; Belkin, '62). The preepisterna of the two mesopleura are joined ventrally by the preepisternal bridge, a narrow band posterior to furcasternum 1. This is the sternopleural bridge of Christophers ('60) (figs. 2, 4).

The basalar is at the apex of the posterior anepisternum 2 and anterior to the pleural wing process. It is an elevated, arched, shield-like sclerite (figs. 1, 10). Internally, the prominent basalar apodeme arises from the posterior anepisternum 2 slightly below the level of the basalar (figs. 3, 11). It serves for attach-

ment of two mesothoracic muscles. The pleural wing process is posterior to the basalar at the apex of posterior anepisternum 2 (fig. 10). It was called the alifer by Crampton ('42) and hamuloid by Prashad ('18) and Christophers ('60). The prealar bridge of Crampton ('42) extends dorsad from the upper anterior angle of the posterior anepisternum 2 to the supraalar groove (figs. 8, 10). Internally, from the area of the prealar bridge arises the prealar apophysis (figs. 3, 9). An important flight muscle, the prealar apophyso-pleural ridgalis, is attached to this apophysis.

Pleural suture 2 arises from the pleural apophyseal pit 2 at the upper anterior corner of katepisternum 2 and passes dorsad to terminate at the base of the pleural wing process (fig. 1). Internally, the pleural ridge marks the position of pleural suture 2 (fig. 3). Also internally, the pleural thread leads from the ventral pleural arm to unite with a spur at the apex of the pleural ridge. The ventral pleural arm appears to arise from the pleural apophyseal pit 2 (fig. 3). Two prominent apodemes, not previously described, have their origins at the base of the ventral pleural arm. The one extending along the anterior

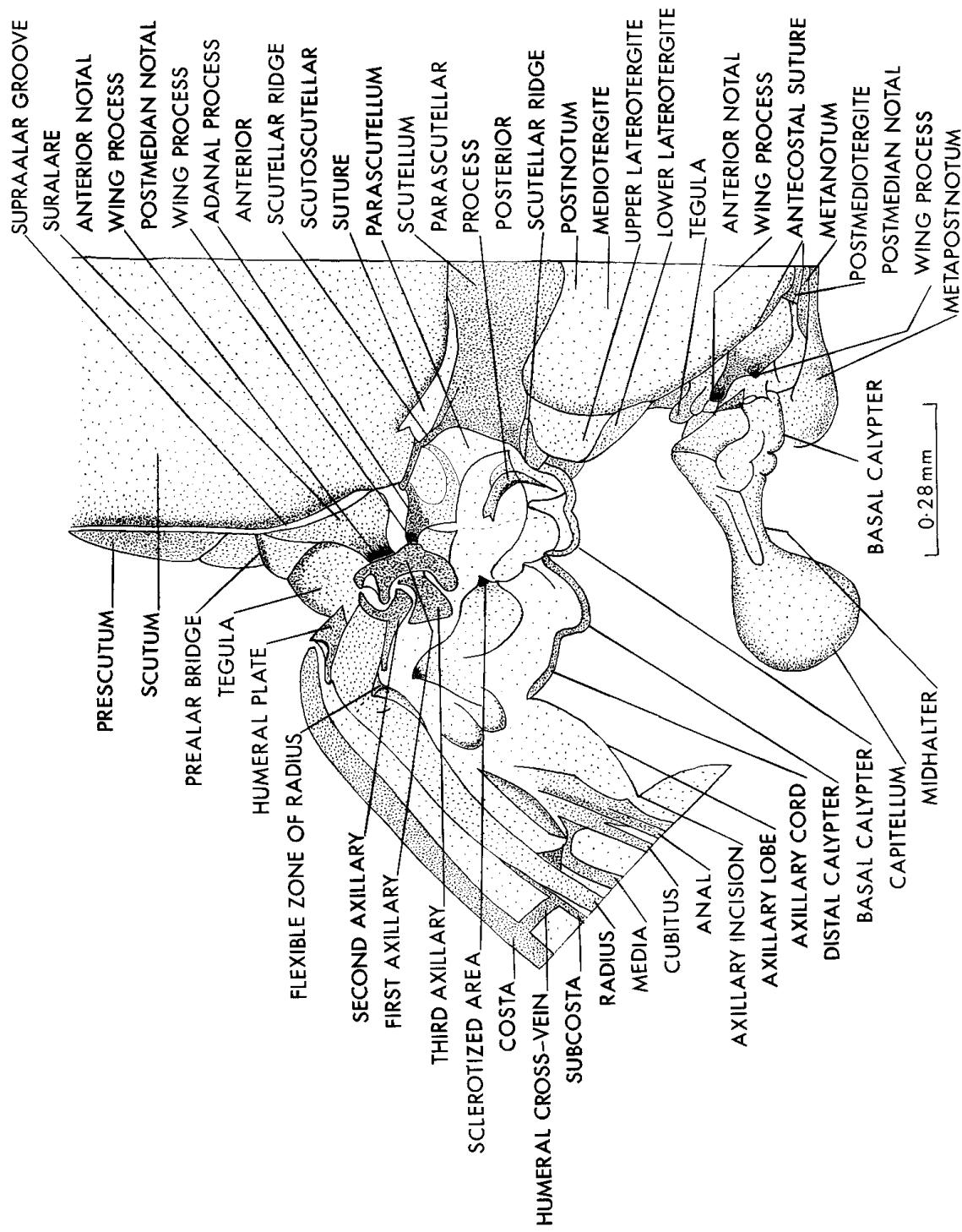


Fig. 8 Dorsal view of the articulation of the wing and halter in *Culiceta inornata*.

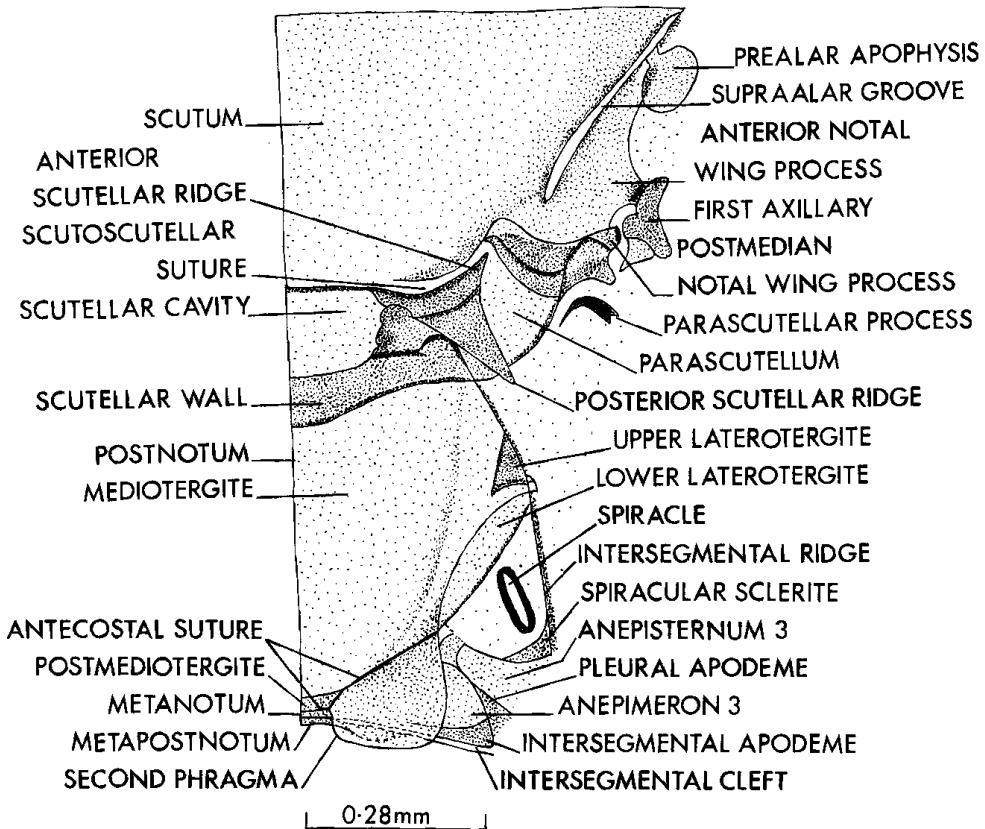


Fig. 9 Ventral view of internal surface of the scutellum, postnotum, metanotum, and associated parts in *Culiseta inornata*.

margin of the coxal cavity is here named the precoxal apodeme and the other, on the posterior margin of the cavity, is named the postcoxal apodeme (figs. 3, 4). Indirect wing muscles are attached to these apodemes.

Anepimeron 2 is posterior to the pleural suture 2 (fig. 1), and is known to taxonomists as the mesepimeron (Belkin, '62; Knight and Laffoon, '70a). Along its ventral margin, on the mesal surface, is the anepimeral ridge for attachment of wing muscles (fig. 3). The small triangular sclerite at the anterodorsal angle of anepimeron 2 was identified as the subalifer of Crampton ('42) (figs. 1, 10). The subalare is in a sclerotized membrane below the wing base (figs. 1, 10). Katepisternum 2, or the pleurotrochantin of Crampton ('42), is ventrad of the anepimeron 2 and anterior to the meron. The site for articulation of lateral coxal condyle 2 is on the ventral margin of katepisternum 2. Ventral to anepimeron 2 is the triangular meron. Intersegmental suture 2 and its ridge internally mark the posterior limits of anepimeron 2 and the meron (figs. 1, 3).

The ventral surface of the mesothorax is covered externally by preepisternum 2, preepisternal bridge, and katepisternum 2. A narrow strip of katepisternum 2 extends ventrad around the anterior margin of coxal cavity 2 to become the precoxale (fig. 2). The paracoxal suture, of Matsuda ('70), separates the precoxale and katepisternum 2 from preepisternum 2 and appears to terminate dorsally at the pleural apophyseal pit (figs. 1, 2). The two halves of the katepisterna are invaginated, forming the discrimin or discrimin line of Ferris ('40a) and, as a result of this infolding, furcasternum 2 is concealed internally (figs. 2-4). The median area of katepisternum 2 is demarcated anteriorly by the pleurosternal suture which joins the paracoxal suture (fig. 2). The lateral margin of each katepisternum 2 is expanded in a wing-like manner, forming the ventral process for articulation with the coxa 2 (fig. 2). The discrimin line is interrupted by the sternal apophyseal pit 2 which marks externally the point of origin of the sternal apophyses (fig. 2). The postcoxale, on the caudal margin of

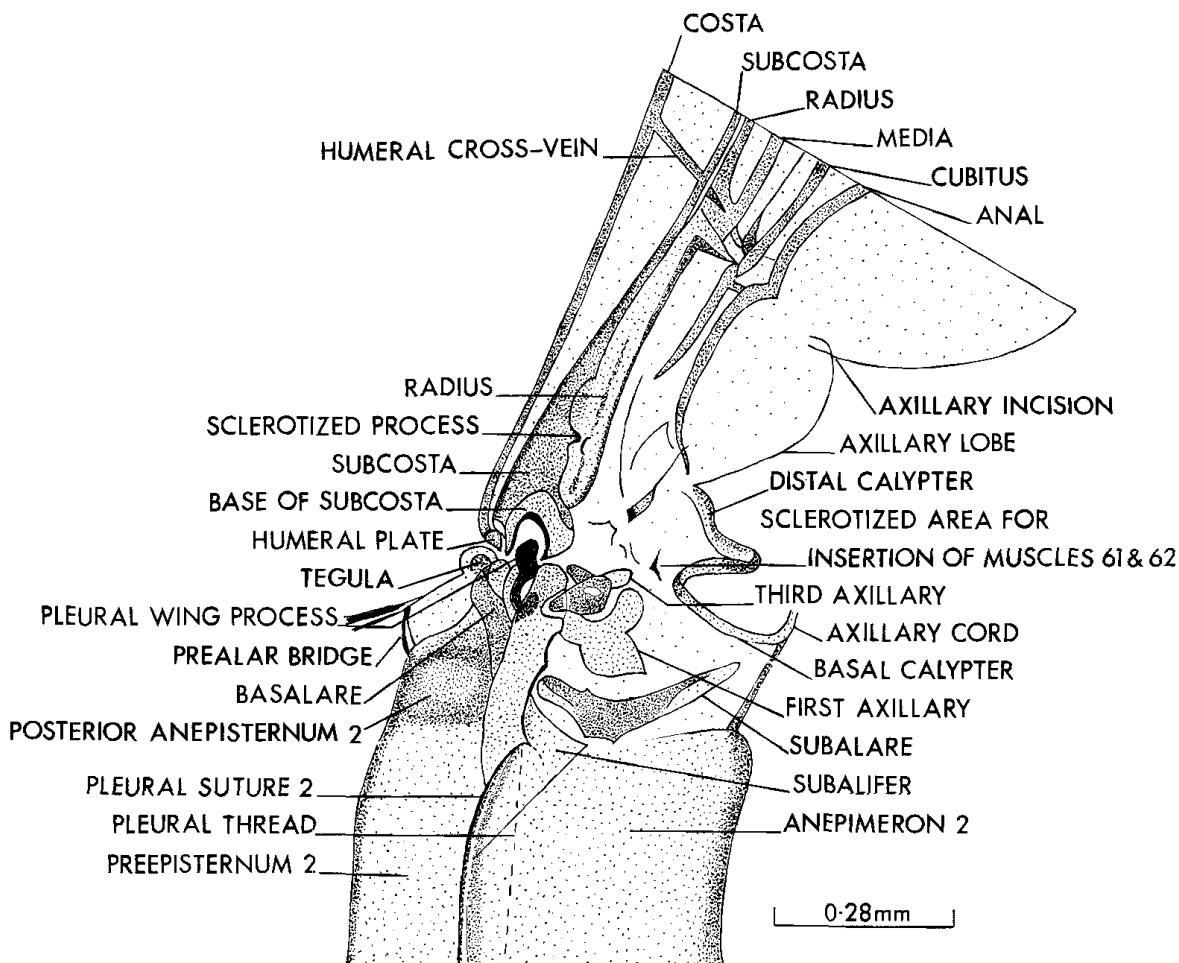


Fig. 10 Ventrolateral view of articulation of the left wing in *Culiseta inornata*. The wing is illustrated in the upstroke position.

coxal cavity 2, is formed by a lateral extension of katepisternum 2 (figs. 2, 4). It is united with the intersegmental ridge, but the two can be separated in specimens treated with a solution of 10% KOH.

Internally, the mesosternal area is composed of furcasternum 2 and the dorsal surface of katepisternum 2. Furcasternum 2 is in the anterior position, having the shape of a pair of wings attached along the median furcasternal suture (figs. 3, 4). Furcasternum 2 is demarcated anteriorly by the pleurosternal and paracoxal sutures. It is clearly dorsal to katepisternum 2 and the furcasternal suture is united with the invaginated katepisternum along the discriminial line (figs. 3, 4). The paired sternal apophyses arise near the posterior limits of furcasternum 2 and extend dorsad, having at their free ends the apophyseal cups (figs. 3, 4).

Intersegmental suture 2 separates the mesothorax and metathorax along their lateral

and ventral surfaces. Externally, it is a suture that arises in the mid-ventral area anterior to katepisternum 3. From this point it extends dorsad, terminating near the base of the scutellum. Internally, this suture is represented by the intersegmental ridge that is evident for its entire length (figs. 1-4). The postnotum is posterior to a vertical line represented by the intersegmental suture and covers almost all the dorsal surface of the metathorax. For this reason, it was considered a part of the metathorax by some early students of the Diptera. Crampton ('42) has reviewed the history of this subject.

The metathorax

The part of the dorsal surface of the metathorax, not concealed by the postnotum, is covered with the metanotum and meta-postnotum (figs. 1, 4, 6, 8). The metanotum is a narrow transverse band caudad of the antecostal suture and limited to the dorsum.

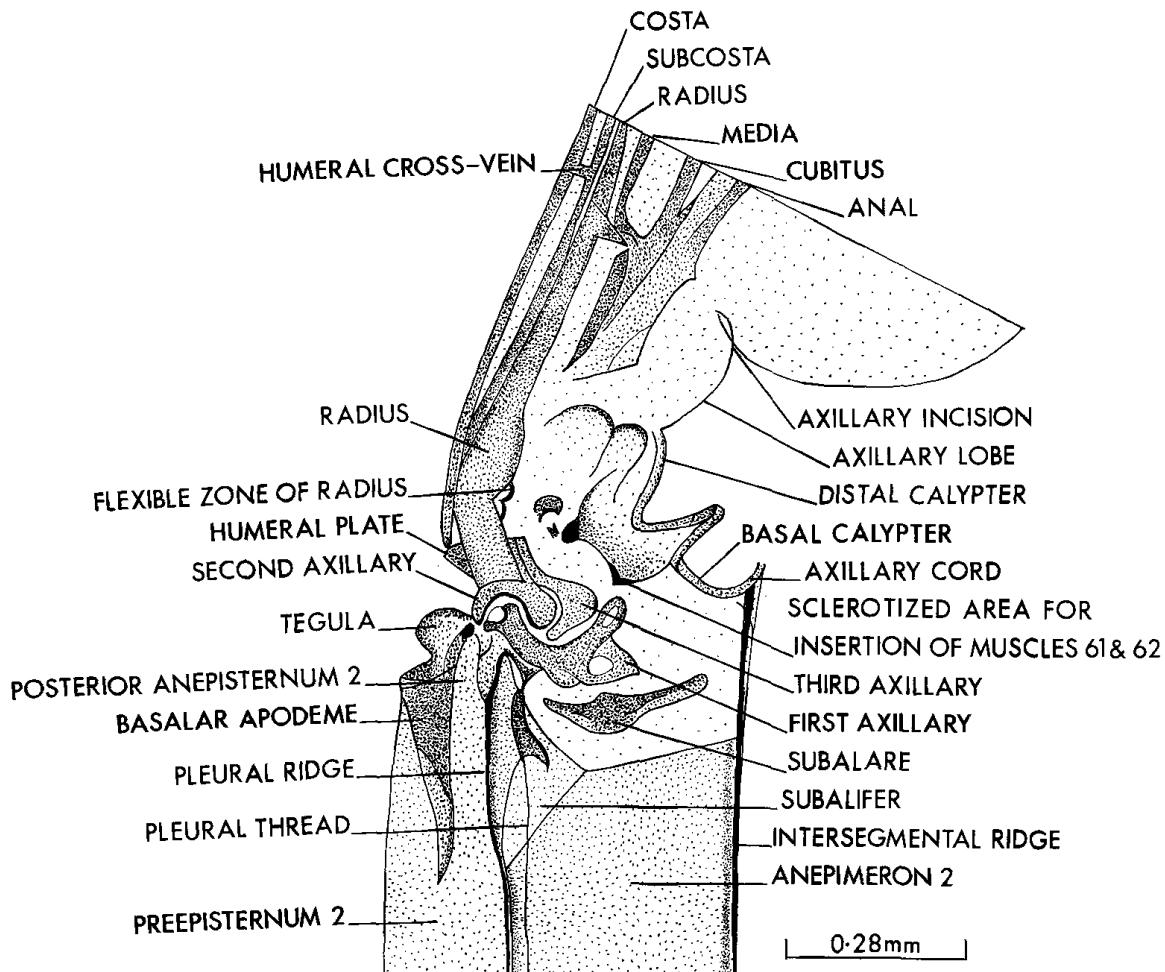


Fig. 11 Dorsomesal internal view of articulation of the right wing in *Culiseta inornata* after removal of dorsum. The wing is illustrated in the initial stage of flexion.

It has a cavity within and an opening on the ventral side (fig. 7). The area posterior to the metanotum is the metapostnotum. In *Culiseta inornata* it is narrow in the median area, extending ventrad on each side to unite with katepisternum 3. The caudal margin is sinuate and there is a transverse suture at the level of pleural suture 3 (figs. 1, 4, 6-8). The longitudinal tergal muscles of the first abdominal segment are attached to the metapostnotum, as depicted by Snodgrass ('59), except that the lateral pair are more ventrad, uniting with the first curvature. The metapostnotum is present in several genera of mosquitoes—*Aedes*, *Anopheles*, *Culex*, *Culiseta*, *Psorophora*, *Uranotaenia*, and *Wyeomyia*.

The metapleuron has five well-defined sclerites: basalare, spiracular, anepimeron 3, anepisternum 3, and katepisternum 3 (fig. 6). The largest of these is anepisternum 3 that is demarcated anteriorly by the metathoracic

spiracle, spiracular sclerite and intersegmental suture 2. On the posterior margin of anepisternum 3 is pleural suture 3, intersegmental cleft, and intersegmental suture 3 (figs. 1, 6). At the apex of anepisternum 3 is the pleural wing process of the halter. The basalare is anterior to this point (fig. 6). The metathoracic spiracle is located in a sclerotized membrane ventrad of the lower laterotergite and caudad of intersegmental suture 2. The spiracular sclerite is small, triangular in shape, and ventrad to the spiracle. Below anepisternum 3 is katepisternum 3. The lateral condyle for articulation of coxa 3 is at the anteroventral angle of katepisternum 3 (figs. 1, 2). Katepisternum 3 continues around the anterior margin of coxal cavity 3 as the precoxale (figs. 2, 4). Ferris ('50) used the name preepisternum 3 for this sclerite in *Drosophila* and Peters and Cook ('66) followed his usage for *Dixella*.

In *Culiseta inornata* the metapostnotum has expanded lateroventrad over the first abdominal segment and appears to be a part of it (fig. 6). Consequently, the anterolateral margin of the metapostnotum represents the level of union between this segment and the metathorax. The intersegmental suture 3 originates at the apex of katepisternum 3 and, after a short distance, joins the pleural apophyseal pit 3, then divides, forming a lightly sclerotized cleft. This cleft is here described for the first time and named the intersegmental cleft (figs. 6, 7). The suture on the anterior margin of the cleft extends dorsad, giving rise at its mid-point to pleural suture 3. The suture on the caudal margin of the cleft is apparently the continuation of the intersegmental suture. These two sutures join at the apex of the cleft and unite with the suture separating the metanotum from the metapostnotum (fig. 6). Internally, the suture on the posterior margin of the cleft gives rise to the intersegmental ridge (fig. 7). This ridge provides a surface for the origin of the intersegmental ridgo-phragmalis muscles. The intersegmental cleft is present in *Aedes canadensis*, *Aedes flavescens*, *Culex tarsalis*, *Culiseta inornata*, *Psorophora confinis*, and *Uranotaenia sapphirina*, but is absent in *Anopheles quadrimaculatus* and *Wyeomyia smithii*.

Two prominent undescribed apodemes are present on the mesal surface of the metapleuron. They provide surface for attachment of halter muscles and are here named the pleural and intersegmental apodemes (fig. 7). The pleural apodeme arises from the anterior margin of the intersegmental cleft, the pleural suture, and the pleural apophyseal pit 3. It projects anteriorly over the posterior half of anepisternum 3 and has its anterior margin free. The intersegmental apodeme arises on the intersegmental cleft dorsad of the pleural suture and projects anteriorly over anepimeron 3, overlapping the pleural apodeme for a short distance (fig. 7). The base of the intersegmental apodeme is attached to anepisternum 3 and the anterior margin is free. In *Anopheles quadrimaculatus*, the pleural apophyseal pit is absent and the pleural suture 3 is almost vertical and straight. Internally, near the apex of pleural suture 3, a short apodeme extends at an angle to the halter base. The pleural suture has a narrow apodeme projecting mesad along its entire

length. This latter apodeme is probably a homologue of the pleural apodeme in *Culiseta inornata*. There is no apodeme attached to the intersegmental ridge in *Anopheles quadrimaculatus*.

The ventral surface of the metathorax is covered with paired katepisterna, separated in the median area by the discriminial line. The anterior part of katepisterna 3 is wing-like, with a ventral process on its posterior margin for articulation with a socket on the mesal surface of coxa 3 (figs. 2, 13). The ventral process projects ventrad and is attached to the coxa by the articular membrane (fig. 13). The posterior part of a katepisternum bears the sternal apophyseal pit 3 and is attached to the articular membrane of the coxa (fig. 2). As a result of invagination of the katepisterna along the discriminial line, furcasternum 3 is internal. In specimens treated with a 10% solution of KOH the katepisterna may be separated, revealing the furcasternal suture (fig. 3). From the dorsal aspect, the furcasternum 3 and its apophyses have the shape of paired wings with a crossbar at the base (fig. 4). Furcasternum 3 consists primarily of the paired sternal apophyses, their basal connection, and the apophyseal cups (figs. 3, 4). Each apophysis arises from a pit and branches into an anterior and posterior arm which support the cup. The intersegmental membrane is united with the posterior border of furcasternum 3 and its two lateral arms (fig. 4). In the median area posterior to the level of the sternal apophyseal pits, katepisternum 3 is ventral to and overlaps the intersegmental membrane (fig. 2).

Thoracic appendages

The wings

The wing venation of the mosquito is so well known that it was omitted in this investigation. Belkin ('62) has given a clear illustration of the wing. Careful attention was given to the union of the wing with the pterothorax and the sclerites at the wing base.

Attachment of the wing. The wing is attached to the pterothorax by a flexible cuticular membrane which remains as evidence of its outgrowth from the body wall. There are four points of articulation between the wing and pterothorax, two on the dorsal side and two on the ventral (figs. 8, 10). The dorsal articulation is with special processes on the margin of the scutum. LaGreca ('47) recog-

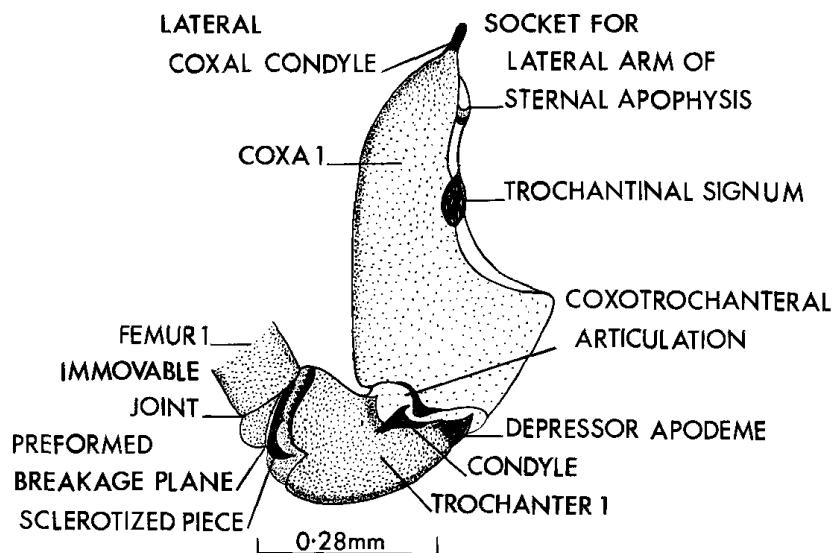


Fig. 12 Anterior view of coxa 1, trochanter, and base of femur in *Culiseta inornata*. Note the preformed breakage plane and sclerotized piece in the trochanter.

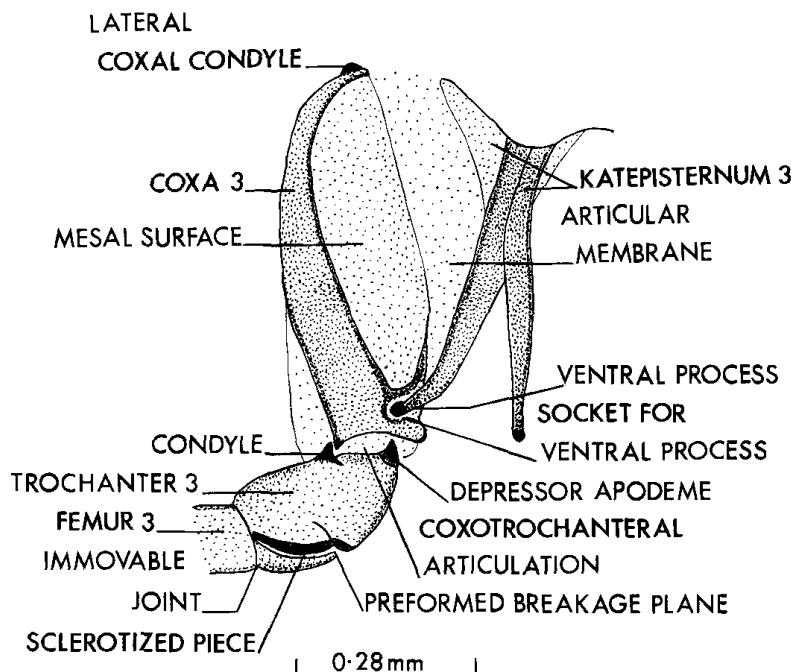


Fig. 13 Anterior view of articulation of coxa 3 with katepisternum 3 in *Culiseta inornata*. Note the pre-formed breakage plane and sclerotized piece in the trochanter.

nized five points of contact between the scutal margin and the axillary sclerites of the Tetrigoniidae and Acrididae. These processes are developed to varying degrees among the species he studied. Four of them in the anterior position articulate with the first axillary sclerite while the fifth is attached to the third axillary. Matsuda ('70) has changed La-Greca's names, with the result that the terms

applicable to the mosquito are the anterior notal wing process and postmedian notal wing process. Both of these articulate with the first axillary sclerite. The anterior notal wing process is the same as that of long usage and is formed from a sclerotized cuticular projection from the scutal margin, the suralare of Crampton ('42). The lateral margin of this process is heavily sclerotized and in contact

with the basal part of the first axillary sclerite (fig. 8). The postmedian notal wing process is caudad and slightly ventrad of the anterior. This process is formed from the adanal process of Crampton ('42) and is the modified distal end of the anterior scutellar ridge. The lateral margin of the postmedian notal wing process is sclerotized and articulates with the mesal face of the posterior part of the first axillary sclerite (fig. 8). The two ventral points of articulation are with the posterior anepisternum 2 and represent the pleural articulations. The pleural wing process is formed from the dorsal head of posterior anepisternum 2. This head fits into a socket on the ventral surface of the proximal end of subcosta, forming a ball and socket union (fig. 10). The distance from this point to the notal wing processes represents the short end of a fulcrum during activity of the indirect wing muscles. The second pleural articulation is between a process on the anterior surface of the third axillary sclerite and a socket on the posterodorsal surface of the posterior anepisternum 2 (fig. 10). This point of articulation apparently provides support during wing movements. There is no evidence of a pleural structure articulating with the subepaulet (humeral plate) in *Anopheles*, *Culex* and *Theobaldia*, as stated by Prashad ('18). The sabroid of Prashad is a sclerotized saber-shaped bar connected to the base of cubitus. His conoid is a cone-shaped area with the apex sclerotized and located in the membrane posterior to radius (figs. 8, 11).

Basal sclerites. There are three well-developed axillary sclerites at the base of the wing of a mosquito. This is contrary to a statement by Snodgrass ('59) that mosquitoes were specialized by the elimination of these sclerites. The integument of the dorsum above the wing base must be removed to expose these structures for a mesal view. In this study, each axillary sclerite was examined *in situ* with the wing attached. These sclerites are very similar in *Aedes flavesiensis*, *Anopheles quadrimaculatus*, *Culex tarsalis*, and *Culiseta inornata*.

The first axillary, dens of Christophers ('60), is the largest of the articulatory sclerites of the wing. It is somewhat club-shaped, with the base directed slightly dorsad (figs. 8-11). The base is slightly enlarged and its mesal surface articulates with the anterior notal wing process (fig. 8). The enlarged body has three parts, a smaller area on the mesal

surface which articulates with the postmedian notal wing process, a lateral arm, and an apical area that tapers to a point (figs. 8, 10, 11). This is the only axillary in the mosquito that has a muscle attached to it. The second axillary is the smallest of the three and fits like a cap over the proximal end of radius and along its caudal surface. It has a concavity forming a socket for the enlarged head of the first axillary (figs. 8, 11). The second axillary was called the epaulet by Christophers ('60) and Prashad ('18). The third axillary has four arm-like protuberances with one arm in contact with the second axillary along the caudal surface of the radius (figs. 8, 11). A second process articulates with the first axillary (fig. 11); a third arm fits into a socket on the posterior anepisternum 2 (fig. 10); and a fourth process points ventrad. The third axillary was called unguiculus by Christophers ('60) and Prashad ('18). Christophers thought his dens and unguiculus might be homologous with the first and third axillaries and that the epaulet was possibly the second.

The wing base. The wing base is the proximal end of the wing where the veins originate. The humeral plate of Snodgrass ('35) is a small triangular sclerite at the proximal end of costa (figs. 8, 10, 11). This is the subepaulet of Christophers ('60). Costa is the most anterior of the wing veins. Subcosta and radius are partially united in the basal area with a groove on the ventral surface (fig. 10). The line of union between these veins is clearly visible after treatment with 10% KOH. The term remigium was used for this section of the subcosta and radius by Prashad ('18), Christophers ('60), and Belkin ('62). Snodgrass ('59) called it a jointed bar that supports the radial vein and bends at the joint when the vein is flexed. The proximal end of subcosta has become modified into a socket to accommodate the pleural wing process (fig. 10). Costa and subcosta support the wing at its base and do not bend during flexure. Although attached to the subcosta, the radius may be bent at the flexible zone. As the wing is drawn backward during flexure it is rotated ventrad on the pleural wing process, forcing the radius to bend at the flexible zone and the membrane to become folded (figs. 8, 11). The sclerotized processes on the ventral surface of the united subcosta and radius represent points of contact during flexure movements. The posterior membrane of the wing base bears the basal and distal calypters and axil-

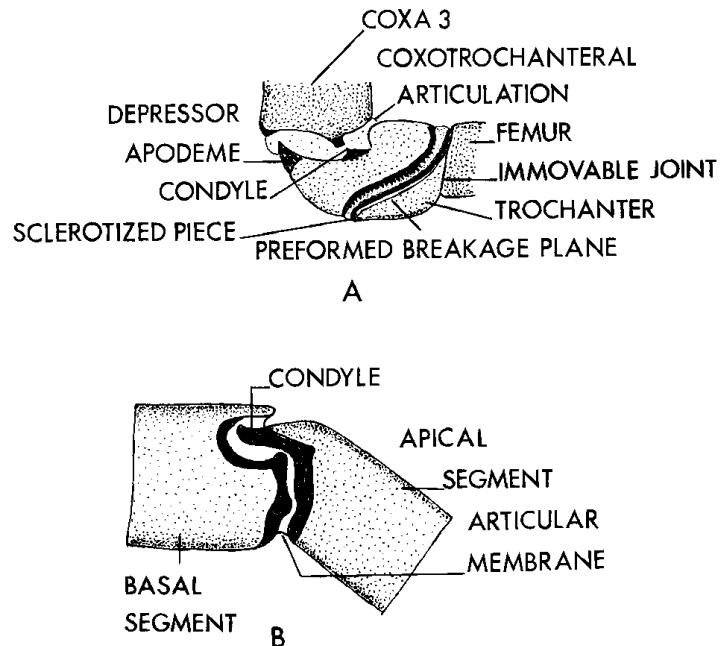


Fig. 14A Posterior view of the articulation of coxa 3 with trochanter 3 in *Culiseta inornata*. Note the pre-formed breakage plane and sclerotized piece.
B Lateral view of a tarsal joint.

lary cord (figs. 8, 10, 11). A special sclerotized area on the upper calypter serves as a point for insertion of wing muscles numbers 61 and 62 (figs. 11, 23).

The halters

The halters are the modified metathoracic wings in the Diptera and consist of three principal divisions. The basal area is the scabellum, the constricted middle part the mid-halter, and the distal half the capitellum (Crampton, '42) (fig. 6). Wing veins in the halter of the mosquito cannot be identified with certainty. The halter pivots on the pleural wing process by a socket that may be the modified base of subcosta (fig. 6). The halter articulates dorsally with the anterior and postmedian notal wing processes (fig. 8). The tegula and basalar are present, but the axillary sclerites are not recognizable.

The legs

The prothoracic leg

The coxa. Coxa 1 is somewhat club-shaped, being small at its proximal end and enlarged distally. There is a socket on the mesal surface at the base for the lateral arm of the sternal apophysis (figs. 5B, 12). The lateral articulation of coxa 1 is by means of two condyles which embrace the pleurocoxal process on the episternum 1 (figs. 1, 12). On the anterior face

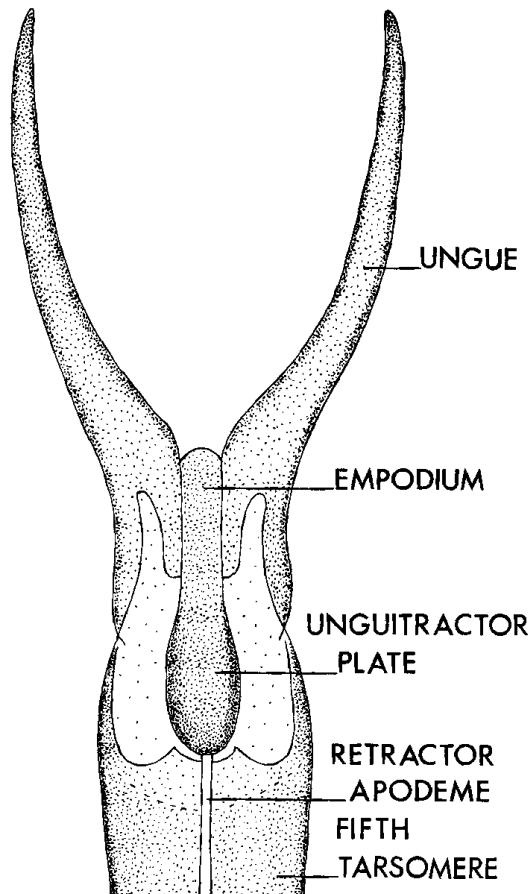


Fig. 15 Ventral view of pretarsus and distal end of fifth tarsomere in *Culiseta inornata*.

is a minute sclerotized area that appears to be the trochantinal signum, as illustrated by Rees and Ferris ('39) for *Tipula reesi*. Articulation with the trochanter is dicondylic with a pair of condyles for contact with those on the trochanter. The points of articulation are in the anterior mesal and posterior lateral positions (fig. 12).

The trochanter. The trochanter is smaller than the coxa, oblong in shape, with the preformed breakage plane near the distal end. A slight pull on the leg of a living mosquito may result in detachment of the limb at this level (fig. 12). The preformed breakage plane appears as a suture with a heavily sclerotized piece basal to it in a flexible membrane. The muscle responsible for breakage is inserted on the sclerotized piece. After breakage the sclerotized piece remains attached to the basal part of the trochanter (fig. 25A). The heavily sclerotized depressor apodeme that connects with the depressor tendon is at the proximal end of the trochanter. The distal end of the trochanter is united with the femur by an immobile joint (fig. 12).

The femur. The femur is uniform in diameter for about two-thirds of its length and then slightly smaller at the apical end. The femur and tibia are united by a dicondylic hinge joint. At the apex of the femur there is a socket on each side for contact with the condyles at the base of the tibia (fig. 24).

The tibia. The tibia is slightly longer than the femur, uniform in size except for a smaller distal end. At the basal end is the prominent median levator apodeme with a condyle on each side (fig. 24). The articulation with the first tarsomere is by a dicondylic hinge joint. At the apex of the tibia are paired sockets for reception of the condyles on the base of the first tarsomere.

The tarsus. A tarsus has five tarsomeres united by hinge joints. The first tarsomere is the longest, and the second, third, and fourth are progressively shorter. The fifth is longer than the fourth (fig. 24). The articulation between all tarsomeres is basically dicondylic. There is a prominent median condyle at the base of each tarsomere, which fits into a socket at the apex of the preceding segment. The areas on each side of this condyle are heavily sclerotized and function as lateral condyles, making contact with similar areas on the adjoining tarsomere (fig. 14b). The pretarsus is attached to the distal end of the fifth tarsomere (figs. 15, 16). This highly special-

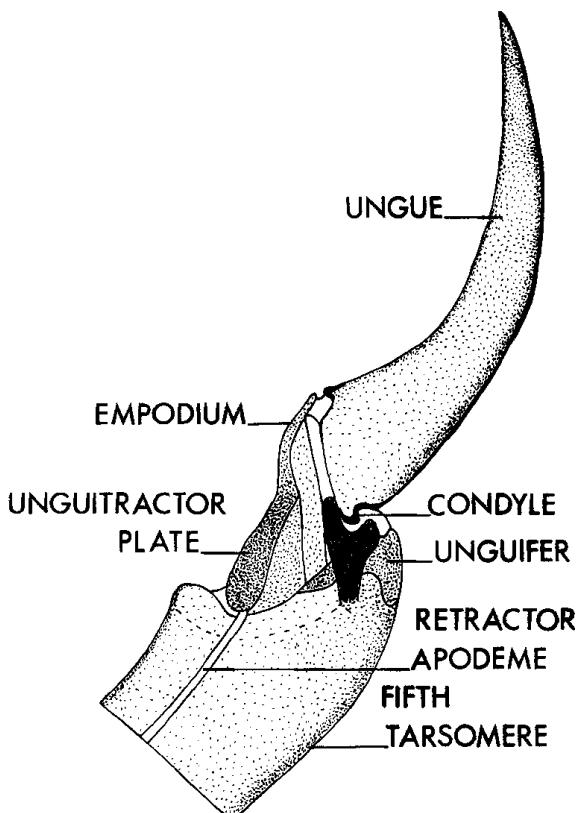


Fig. 16 Lateral view of pretarsus and distal end of fifth tarsomere in *Culiseta inornata*.

ized structure is composed of unguifer, unguitractor plate, empodium, and ungue. The retractor apodeme is attached to the unguitractor plate. This apodeme functions as the depressor tendon of both the tarsus and pretarsus.

The mesothoracic leg

The coxa. Coxa 2 is somewhat wedge-shaped, with its lateral articulation at the anterodorsal angle. At this point its condyle is in contact with a condyle on katepisternum 2 (figs. 1, 2). Ventrad of this condyle is a conspicuous spine. The ventral articulation of coxa 2 is with the ventral process on katepisternum 2 (fig. 2). Coxa 2 is rather firmly attached, which limits its movement in all directions.

The trochanter. The trochanter of the mesothoracic leg has a preformed breakage plane similar to trochanter 1 (fig. 12), and is united to the femur by an immovable joint. Other segments of the mesothoracic leg are similar to the prothoracic leg.

The metathoracic leg

The coxa. Coxa 3 is rectangular in shape.

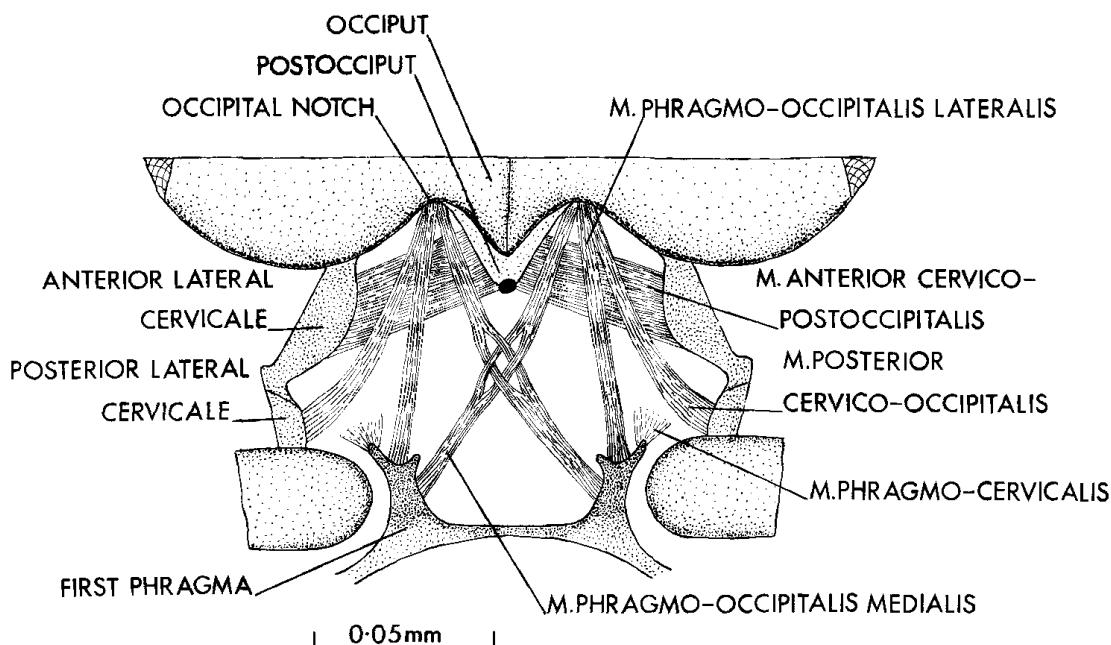


Fig. 17 Dorsal view of the cervical muscles on the dorsal side of the neck in *Culiseta inornata*. M, musculus (muscle).

The lateral articulation is with a condyle on the anteroventral angle of katepisternum 3 (figs. 1, 2, 13). The mesal surface is covered with a membrane, except for a sclerotized area at the apex. The ventral articulation is between a condyle on the ventral process of katepisternum 3 and a socket on the mesal surface at the apex of the coxa (fig. 13). Coxa 3 can be pivoted freely along its anteroposterior axis.

The trochanter. Trochanter 3 is short, joined to coxa 3 by a dicondylic hinge joint, and united with the femur by an immobile joint. At the base of trochanter 3 is a prominent depressor apodeme. The preformed breakage plane is similar to those in the other trochanters. The coxotrochanteral articulation and other features of trochanter 3 are illustrated in figures 13, 14A.

The femur, tibia, and tarsomeres of the metathoracic leg are similar to those of the other legs, except for minor differences in size.

Muscles of the thorax and its appendages

Muscles of the neck

Dorsal muscles (fig. 17)

1. M.² phragmo-occipitalis medialis (29³). The fibers of this pair of muscles cross or decussate on the mid-line. The origin is on the anterior mesal surface of the arm of the first phragma and the insertion is on the occipital notch lateral to the postocciput and dorsal to

the occipital condyle. This pair of muscles is a levator of the head and may also rotate the head.

2. M. phragmo-occipitalis lateralis (29). The origin is on the anterior surface of the arm of the first phragma and the insertion is on the occipital notch lateral to muscle number 1. This muscle is a levator of the head.

3. M. phragmo-cervicalis (35). The origin is at the apex of the arm of the first phragma and the insertion is on the dorsolateral surface of the cervical membrane. This is a levator muscle of the neck.

4. M. posterior cervico-occipitalis (28). The origin is at a dorsomesal point at the caudal end of the posterior lateral cervicale. The insertion is on the occipital notch lateral to muscle number 2. This is a remotor muscle turning the head caudad.

5. M. anterior cervico-postoccipitalis (27). The origin is on the mesal surface of the anterior lateral cervicale near the cephalic end. The insertion is on the lateral surface of the postocciput. This muscle is a rotator and abductor of the head.

Ventral muscles (fig. 18)

6. M. sternal apophyso-tentorialis medialis (25?). This muscle originates on the mesal surface of the mesal arm of the sternal

² M, musculus (muscle).

³ The number after each name is that of Christophers ('60).

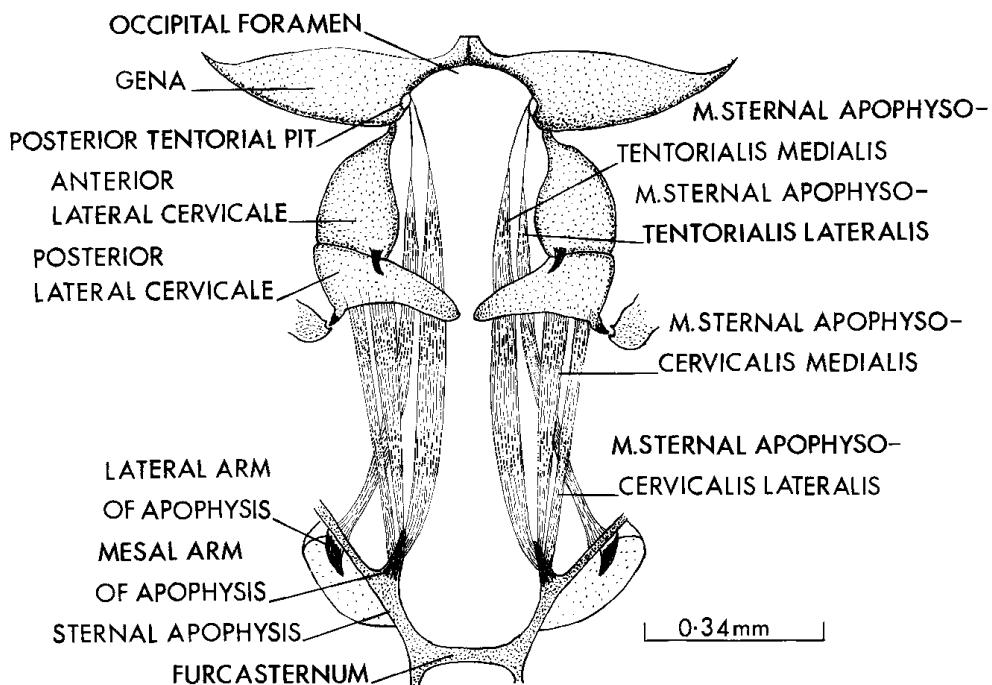


Fig. 18 Ventral view of the cervical muscles on the ventral side of the neck in *Culiseta inornata*. Skeletal structures are illustrated in figure 2.

apophysis and enters the occipital foramen dorsad and mesad of the tentorial pit. The insertion is on the tentorium. This is a depressor muscle of the head.

7. M. sternal apophyso-tentorialis lateralis (26?). The origin is on the anterior surface of the sternal apophysis opposite the lateral arm. It enters the occipital foramen along with muscle number 6 and the insertion is on the tentorium. This muscle is a depressor of the head.

8. M. sternal apophyso-cervicalis medialis (32). The origin is near the apex of the mesal arm of the sternal apophysis and the insertion is on the mesoventral surface of the posterior lateral cervicale. The action is to depress the head and neck.

9. M. sternal apophyso-cervicalis lateralis (?). The origin is on the lateral surface of the mesal arm of the sternal apophysis and the insertion is laterad to muscle number 8 on the mesoventral surface of the posterior lateral cervicale. This is a depressor muscle of the neck and head.

Muscles of the prothorax (fig. 19)

10. M. anterior pronoto-katepisternalis (38). The origin is on the interior surface of the anterior pronotum. The fibers pass ventrad to insert on the apex of katepisternum 1.

This is apparently a stator muscle antagonistic to muscle number 12.

11. M. posterior pronoto-trochanteralis (63). The origin is on the dorsal suture of the posterior pronotum with no fibers attached to the scutum. This is a broad, fan-shaped muscle at its origin, but tapers as it passes mesad of the episternal apophysis. It unites with the depressor tendon which in turn is inserted on the depressor apodeme of the trochanter. This is one of the depressor muscles of the trochanter and femur.

12. M. episternal apophyso-trochanteralis (62?). The origin is on the anterodorsal part of the episternal apophysis and the apex of katepisternum 1. This muscle tapers as it runs parallel with muscle number 11 to join the depressor tendon. The action is to depress the trochanter and femur.

13. M. sternal apophyso-trochanteralis (64). The origin, which is not illustrated, is at the base of the mesal arm of the sternal apophysis. It tapers to join the depressor tendon along with muscles numbers 11 and 12. The action is to depress the trochanter and femur. The combined action of muscles numbers 11, 12 and 13 is to depress or extend the trochanter and femur. Thus, Christophers ('60) described this action as extending the femur and leg.

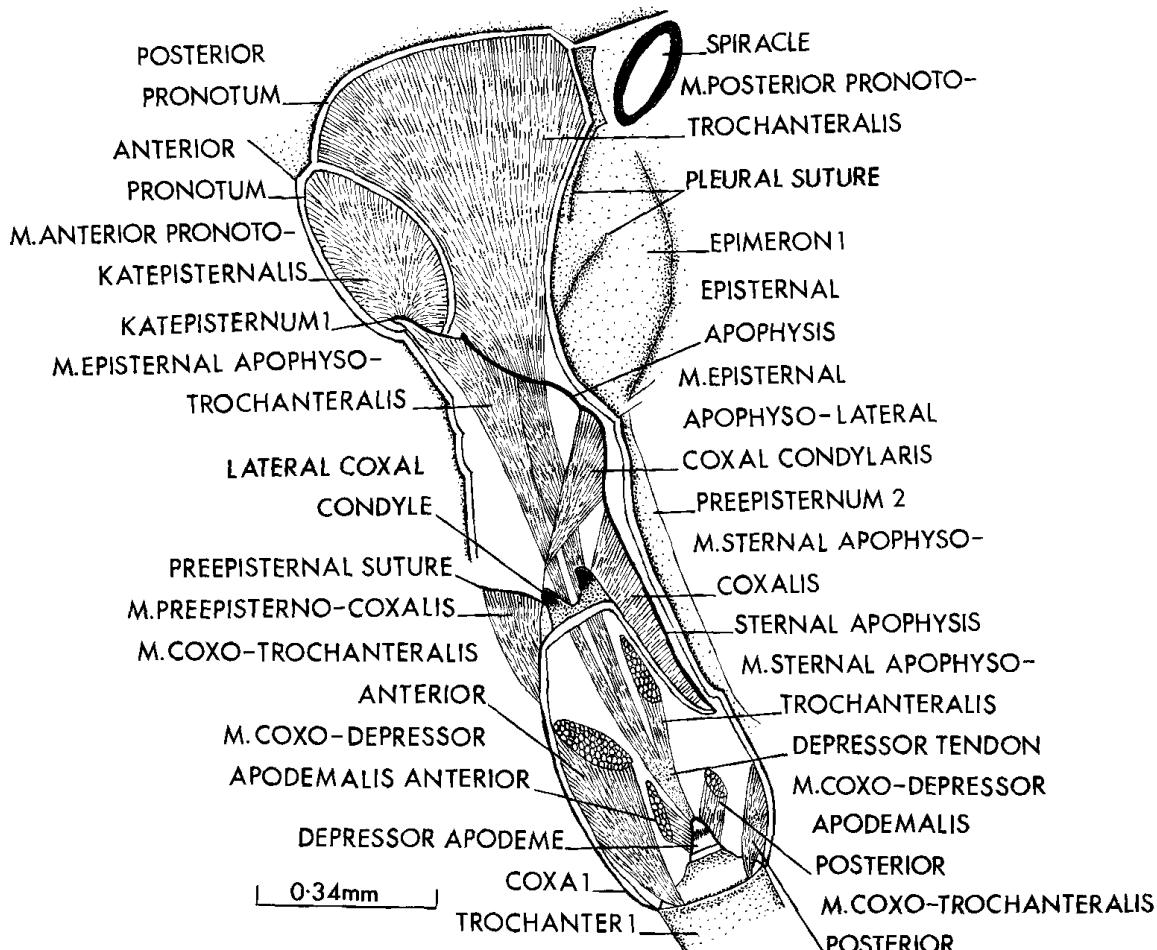


Fig. 19 Lateral view of the prothoracic muscles on the left side in *Culiseta inornata*. Anterior is to the left. Skeletal structures are illustrated in figures 3, 4.

14. M. episternal apophyo-lateral coxal condylaris (69). The origin is along the anterior surface of the episternal apophysis. This muscle tapers to a point and is inserted on the anterior bifurcate of the lateral coxal condyle. This is probably a stator muscle of the coxa 1.

15. M. preepisterno-coxalis (70). This muscle originates along the preepisternal suture and extends laterocephalad beneath the preepisternum to insert on the anterior margin of coxa 1. The action is to serve as a promotor of the coxa.

16. M. sternal apophyo-coxalis (71). The origin is on the anterior margin of the sternal apophysis. This is a thin, sheet-like muscle which is inserted on the posterior margin of the coxa. It acts as a remotor of the coxa and is antagonistic to muscle number 15.

17. M. coxo-trochanteralis anterior (65). This is the largest muscle attached to coxa 1. Its fibers originate on the anterior lateral and basal surfaces of the coxa. The insertion is on

the anterolateral base of the trochanter opposite the depressor tendon. This is the major levator muscle of the trochanter and femur.

18. M. coxo-trochanteralis posterior (68). This is a small muscle originating on the posterior wall of the coxa and inserting on the posterolateral base of the trochanter. It is a levator of the trochanter and femur.

19. M. coxo-depressor apodemalis anterior (67). The origin is on the anterior surface of the coxa and the insertion is on the anterior surface of the depressor apodeme of the trochanter. It is probably a stator muscle.

20. M. coxo-depressor apodemalis posterior (67). The origin is on the posterior surface of the coxa and the insertion is on the depressor apodeme of the trochanter opposite muscle number 19. It is probably a stator muscle.

Some muscles of the mesothorax (fig. 20)

21. M. posterior pronotum, epimero-spirac-

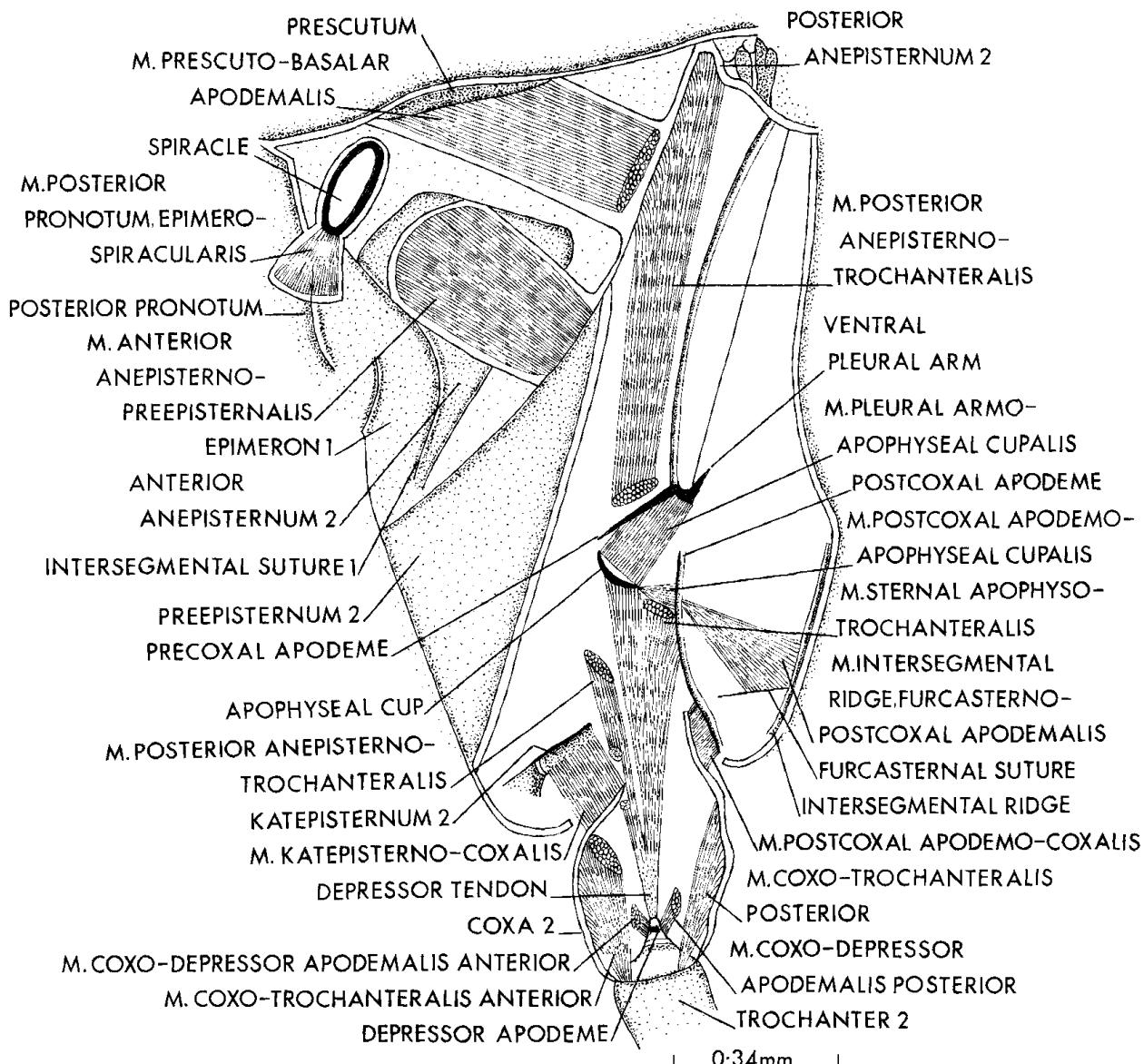


Fig. 20 Lateral view of some mesothoracic muscles on the left side in *Culiseta inornata*. Anterior is to the left. Skeletal structures are illustrated in figures 3, 4.

ularis (58). The origin is on the caudal area of the posterior pronotum and the apex of epimeron 1. The insertion is on the ventral margin of the mesothoracic spiracle. This is an occlusor muscle closing the spiracle with contraction. When it relaxes, the caliper and lids regain their former position by virtue of their own elasticity and that of the surrounding body wall, thus opening the spiracle (Hassan, '44).

22. M. anterior anepisterno-preepisternalis (59). The origin is on the anterior margin of anterior anepisternum 2. This muscle extends across the basalar cleft and is inserted on the anterior margin of preepisternum 2. It is not

the dilator muscle of the spiracle, as stated by Christophers ('60). Contraction of this muscle results in compression of the basalar cleft. This movement of posterior anepisternum 2 depresses the costal margin of the wing. This is an indirect wing muscle listed here because of its location.

The prescuto-basalar apodemalis muscle is illustrated with its insertion in figure 21 and is described with the direct wing muscles.

23. M. posterior anepisterno-trochanteralis (72). The origin is on the anterior apical margin and apex of the posterior anepisternum 2. This is a long, slender muscle passing ventrad to join the depressor tendon that is

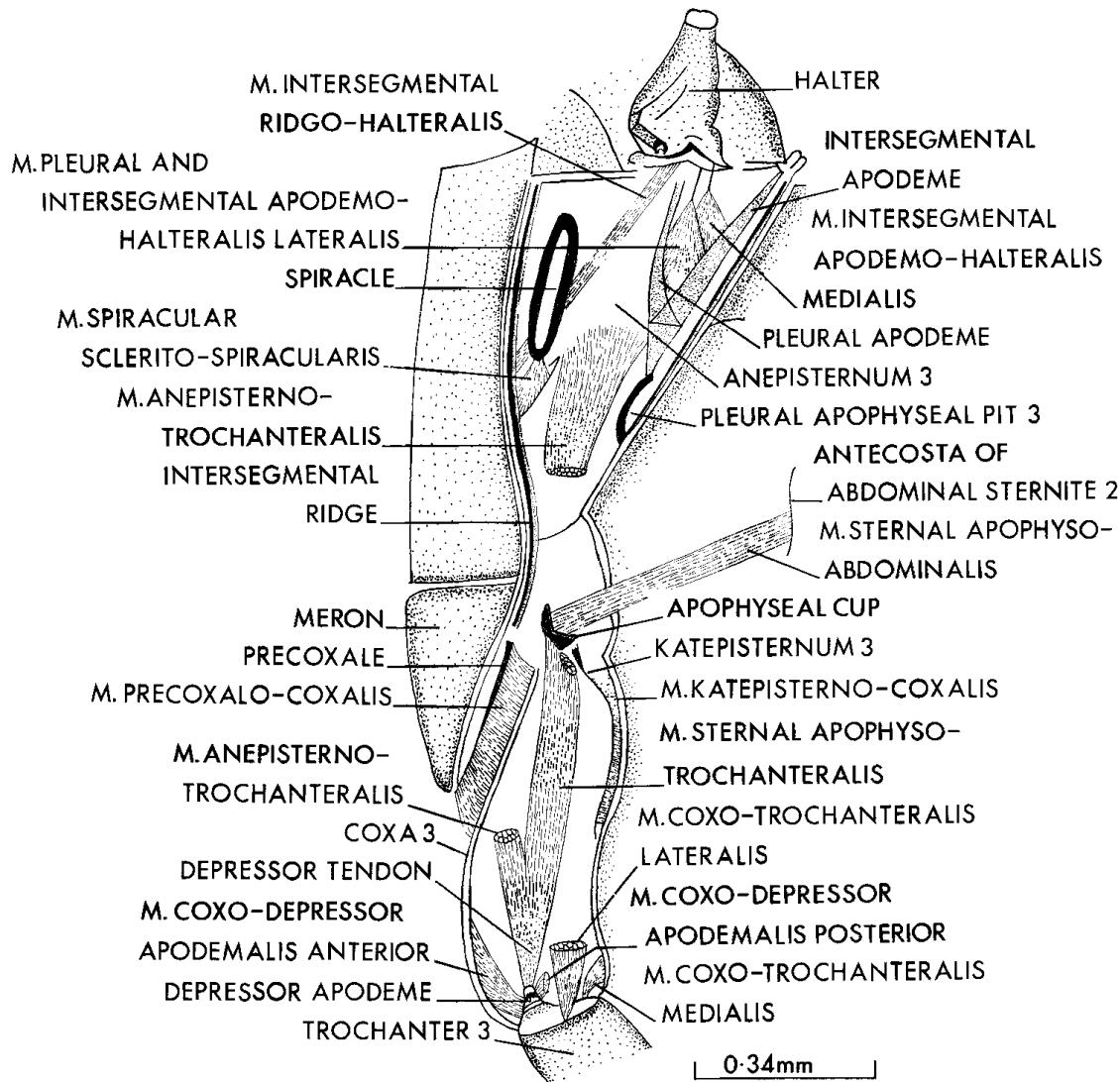


Fig. 21 Lateral view of some metathoracic muscles on the left side in *Culiseta inornata*. Anterior is to the left. Skeletal structures are illustrated in figures 3, 4, 7.

attached to the depressor apodeme of the trochanter. The action is to depress the trochanter and femur. This appears to be the muscle that Smart ('59) called the tergal depressor of the trochanter and stated that it was absent in the Culicidae.

24. *M. sternal apophyso-trochanteralis* (73). This muscle originates on the ventral surface of the apophyseal cup and dorsal anterior margin of the postcoxal apodeme. From this rather broad base it passes ventrad to join the depressor tendon and inserts with muscle number 23 on the depressor apodeme of the trochanter. The action is to depress the trochanter and femur.

25. *M. pleural armo-apophyseal cupalis* (54). The origin is on the ventral pleural arm and along the mesal surface of the precoxal

apodeme. The insertion is on the apophyseal cup. This is probably a stator muscle for the sternal apophysis.

26. *M. postcoxal apodemo-apophyseal cupalis* (?). This is a small muscle with the origin on the postcoxal apodeme and the insertion on the apophyseal cup. The action is probably to serve as a stator muscle for the sternal apophysis.

27. *M. intersegmental ridge, furcasterno-postcoxal apodemalis* (?). This muscle has its origin on the intersegmental ridge and furcasternal suture. It tapers from a broad base to the point of insertion on the postcoxal apodeme. It is probably a stator muscle for the postcoxal apodeme.

28. *M. katepisterno-coxalis* (78). The origin is on the discriminial line of katepisternum 2.

This is a broad sheet-like muscle that is inserted on the anterior basal margin of coxa 2. It is the promotor muscle of the coxa.

29. M. postcoxal apodemo-coxalis (79). This small muscle originates on the postcoxal apodeme and is inserted on the posterior basal margin of coxa 2. It is the remotor muscle of the coxa 2.

30. M. coxo-trochanteralis anterior (74). The origin of this muscle is over the entire anterior surface of coxa 2 and the insertion is on the anterolateral margin of the base of trochanter 2. This is the levator muscle of the trochanter and femur.

31. M. coxo-trochanteralis posterior (77). This muscle arises on the posterior surface of coxa 2 and is inserted on the posterolateral basal margin of trochanter 2. It is a levator muscle for the trochanter and femur.

32. M. coxo-depressor apodemalis anterior (?). This is a small muscle originating on the anterior surface of coxa 2 and inserting on the depressor apodeme at the base of trochanter 2. It is probably a stator muscle.

33. M. coxo-depressor apodemalis posterior (76). The origin of this small muscle is on the posterior surface of coxa 2 and the insertion is on the depressor apodeme at the base of trochanter 2. This is probably a stator muscle.

Some muscles of the metathorax (fig. 21)

34. M. anepisterno-trochanteralis (80). The origin is on the surface of anepisternum 3 near the ventral level of the metathoracic spiracle. From this area it extends ventrad, joining muscle 35 and the depressor tendon which is attached to the depressor apodeme at the base of trochanter 3. The action is to depress the trochanter and femur.

35. M. sternal apophyo-trochanteralis (81). The origin is on the ventral surface of the apophyseal cup. From here it passes ventrad to unite with muscle number 34 and the depressor tendon. The insertion is with number 34 at the base of trochanter 3. The action is the same as number 34.

36. M. precoxalo-coxalis (86). This is a broad short muscle with its origin on the posterior surface of the precoxale. The insertion is along the anterior basal margin of coxa 3. It is a promotor muscle of the coxa.

37. M. katepisterno-coxalis (87). The origin is along the ventral and posterior margins of katepisternum 3, where the sclerite tapers to form the precoxale, figure 4. The insertion is on the posterior basal surface of coxa 3. It is a remotor muscle of the coxa.

38. M. coxo-trochanteralis lateralis (82). The origin is on the lateral surface of coxa 3 and the insertion is on the laterobasal margin of trochanter 3. It is a levator muscle of the trochanter and femur.

39. M. coxo-trochanteralis medialis (83). The origin is on the posterior mesal surface of coxa 3 and the insertion is on the posterior mesobasal margin of trochanter 3. This is a levator muscle of the trochanter and femur.

40. M. coxo-depressor apodemalis anterior (?). The origin is on the anterior lateral surface of the coxa and the insertion is on the anterior margin of the depressor apodeme. This is probably a stator muscle.

41. M. coxo-depressor apodemalis posterior (84). This is a small muscle, with the origin on the mesal surface of the coxa and the insertion is on the posterior surface of the depressor apodeme. This is probably a stator muscle similar to muscle number 40.

42. M. sternal apophyo-abdominalis (?). The origin is on the posterior margin of the apophyseal cup. It extends caudad across the first abdominal segment to insert on the antecosta of the second abdominal sternite. This is a homologue of muscle number 112, as illustrated in *Tabanus* by Bonhag ('51). It probably depresses the abdomen.

43. M. spiracular sclerito-spiracularis (60). This small muscle originates on the spiracular sclerite and is inserted on the ventral margin of the spiracle. It is the occlusor muscle of the metathoracic spiracle.

44. M. intersegmental ridgo-halteralis (56). This is a long, strap-like muscle originating on the intersegmental ridge near the ventral margin of the spiracle. It extends dorsad, inserting on the mesal surface of the halter at the level of the postmedian notal wing process. Traction on this muscle elevates the halter. Christophers ('60) assumed that it was a depressor of the halter.

45. M. pleural and intersegmental apodemo-halteralis lateralis (55). The origin is on the posterior margin of the pleural apodeme and the anterior margin of the intersegmental apodeme. The insertion is in the mesal position on the integument dorsal to the postmedian notal wing process. Pressure at the point of insertion or traction on the muscle elevates the halter. It may also modify the upward movement of the halter.

46. M. intersegmental apodemo-halteralis medialis (?). This muscle originates on the intersegmental apodeme and about half of its

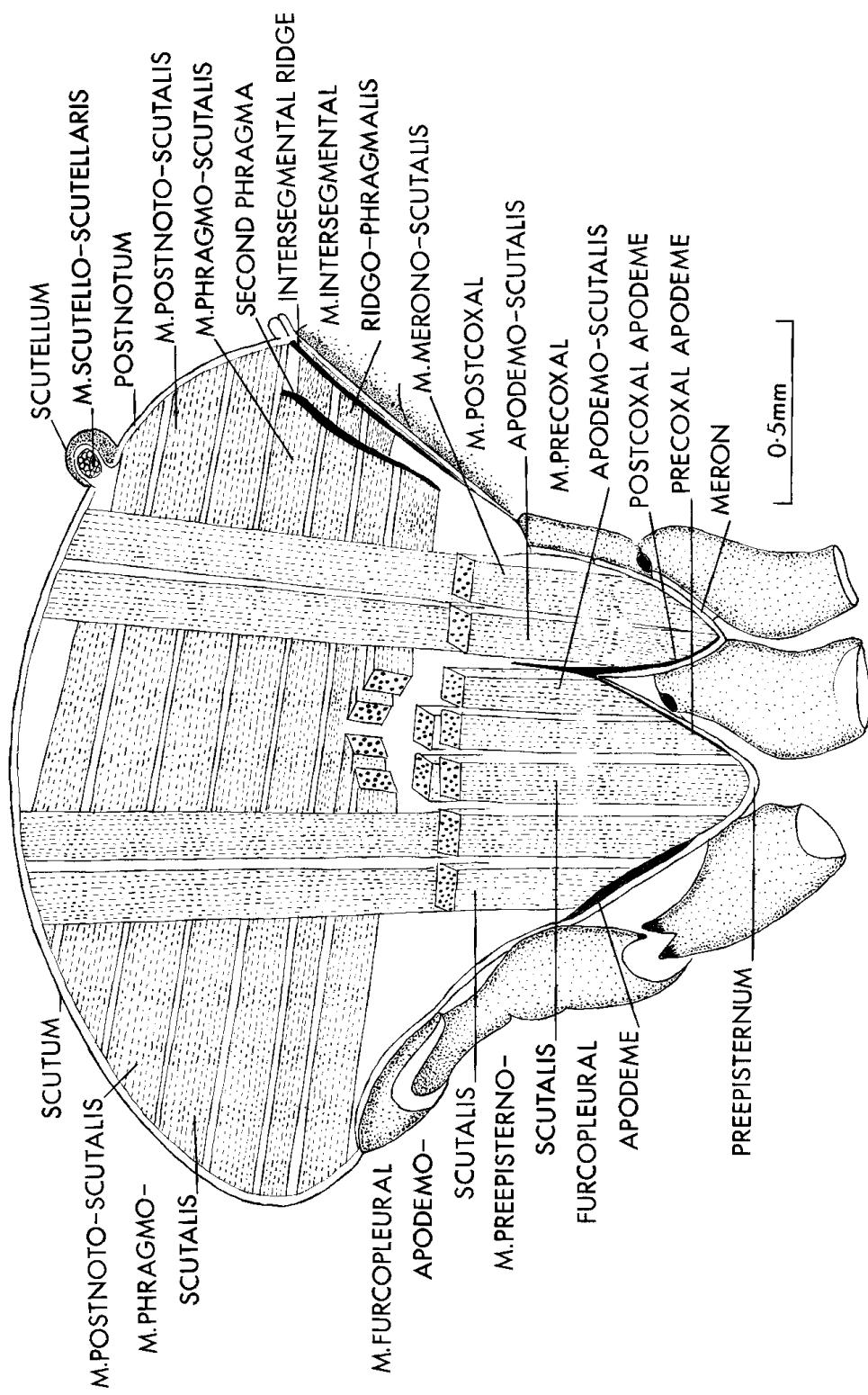


Fig. 22 Lateral view of the indirect wing muscles in *Culiseta inornata*. Anterior is to the left. Skeletal structures are illustrated in figures 3, 7.

body is mesad of muscle number 45. Traction on the muscle depresses the halter.

Indirect wing muscles (fig. 22)

The indirect wing muscles are vibrators and, in terms of histology, they belong to the fibrillar type (Tiegs, '55). The fibers of *Culiseta* are rectangular in cross-section and are usually arranged in pairs on each side of the mid-line.

Longitudinal. The total number of longitudinal muscle fibers in *Culiseta* is usually 14 on each side of the mesothorax. Beckett ('74) has found that these numbers vary among species of mosquitoes and also among individuals of the same species.

47. M. phragmo-scutalis (39). There are four pairs of fibers in this muscle on each side, i.e., four tiers with two fibers each. The origin of these fibers is on the second phragma and the insertion is on the anterior surface of the scutum. The action is to depress the wings by arching the mesonotum.

48. M. postnoto-scutalis (39). There are three pairs of fibers on each side of the mesothorax in this muscle. The origin is on the mediotergite of the postnotum and the insertion is on the anterodorsal surface of the scutum. This is a depressor muscle of the wings, acting in unison with muscle number 47.

Dorsoventral. The total number of dorsoventral muscle fibers is usually 13 on each side of the mesothorax. As a rule, one fiber is unpaired.

49. M. furcopleural apodemo-scutalis (41). There are two pairs of fibers on each side in this muscle. The origin is on the caudal surface of the furcopleural apodeme and the insertion is on the scutum. This muscle is a levator of the wing. Its direct action is to draw the scutum downward.

50. M. preepisterno-scutalis (41). This muscle has one pair of fibers on each side of the mesothorax. Its origin is on the ventral surface of the preepisternum and the insertion is on the scutum. The action is to elevate the wing in conjunction with muscle number 49.

51. M. precoxal apodemo-scutalis (41). There are usually three fibers on each side of the mesothorax in this muscle. The origin is on the precoxal apodeme and the insertion is on the scutum. The action is the same as numbers 49 and 50.

52. M. postcoxal apodemo-scutalis (41). This muscle has one pair of fibers on each side

of the mesothorax. It arises on the postcoxal apodeme and is inserted on the scutum. The action is to elevate the wing.

53. M. merono-scutalis (42). There is one pair of fibers on each side in this muscle. The origin is on the caudoventral surface of the meron and the insertion is on the scutum. The action is to elevate the wing.

54. M. intersegmental ridgo-phragmalis (40). There are three pairs of fibers on each side of the metathorax in this muscle. The origin is on the anterior margin of intersegmental ridge 3 (fig. 7). The insertion is on the posterior lateral surface of the second phragma. This is a stator muscle supporting the second phragma.

55. M. scuto-scutellaris (43). This muscle extends in a transverse manner the full width of the scutellum. Christophers ('60) listed it as a possible indirect wing muscle that could assist in deformation of the scutum. Jones ('54) called it the "scutellar pulsatile organ" and considered it an accessory pulsatile organ of the heart.

Direct wing muscles (fig. 23)

Culiseta inornata has only three muscles attached directly to the wing. Several which act as indirect wing muscles are considered here with those inserted on the wing proper.

56. M. prealar apophyo-pleural ridgalis (45). The origin is over the entire ventral surface of the prealar apophysis. This muscle tapers to a point and is inserted on the anterior surface of the pleural ridge near the apex. Its action draws the pleural ridge and pleural wing process forward, deflecting the costal margin of the wing downward.

57. M. anepimeral ridgo-parascutellaris lateralis (?). The origin is on the anepimeral ridge at the union of the meron and anepisternum 2. This muscle tapers to a point as it extends dorsad to terminate in a tendon that is inserted on the parascutellar process. The action is to extend the wing from the flexed position and to depress the anal margin. These motions can be achieved by downward pressure on the parascutellar process.

58. M. anepimeral ridgo-parascutellaris medialis (?). This muscle is mesad of number 57 and of approximately the same size and shape. About one-third of its width is posterior to number 57. It has the same origin, insertion, and action as number 57.

59. M. pleural ridgo-parascutellaris ventralis (?). The origin is on the caudal surface

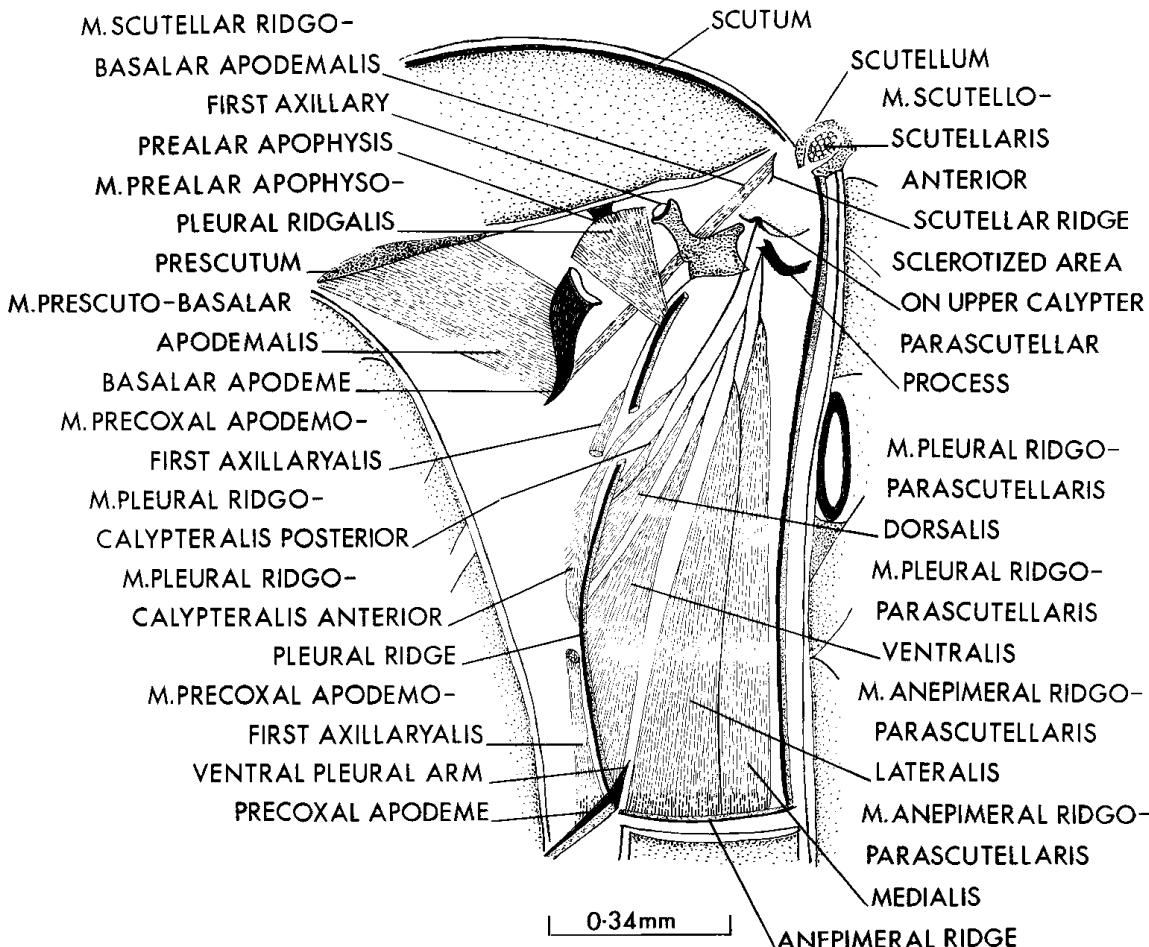


Fig. 23 Lateral view of the direct wing muscles and others with functions related to flight in *Culiseta inornata*. Anterior is to the left. Skeletal structures are illustrated in figures 3, 8, 11.

of the pleural ridge with some fibers attached to the ventral pleural arm. It passes dorsad and tapers to a point, forming a tendon that unites with the tendon of number 57. The action is the same as number 57.

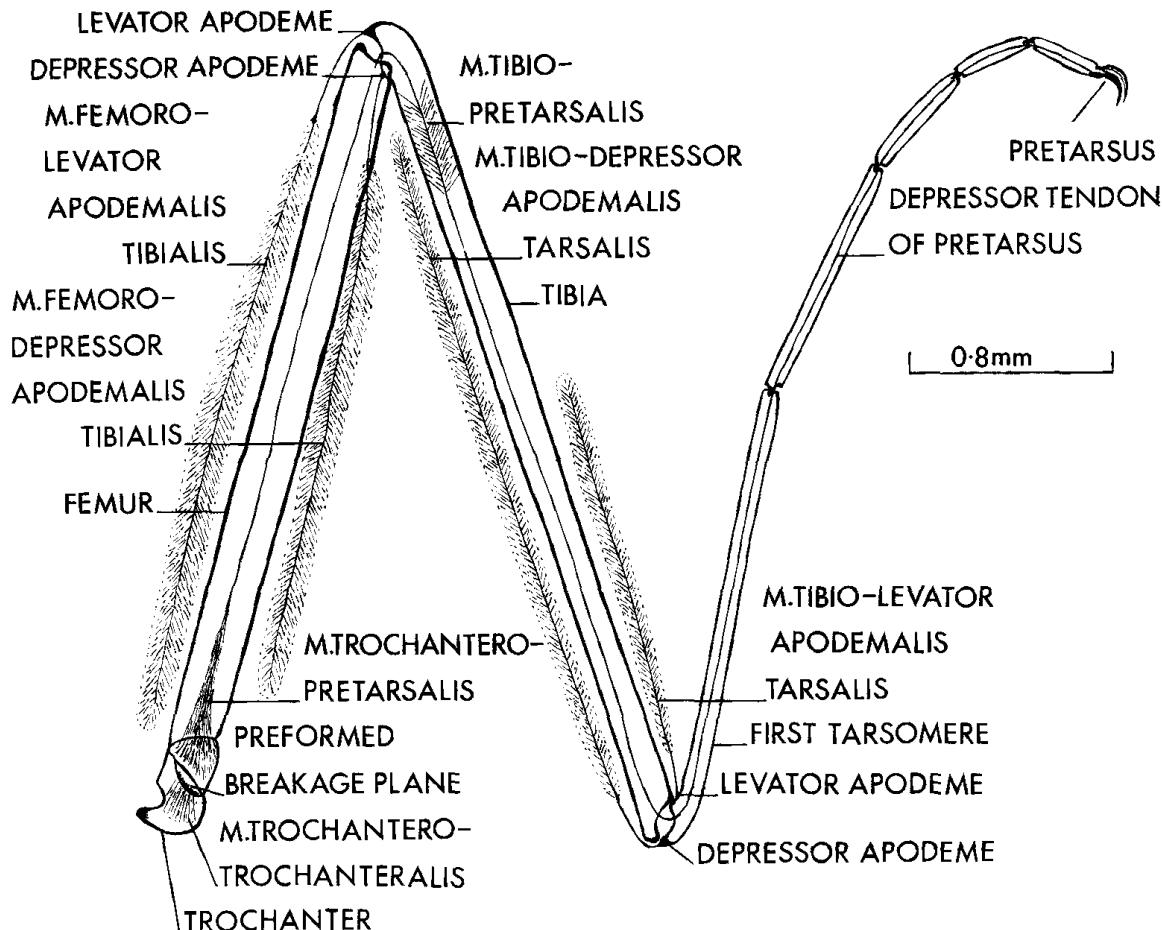
60. M. pleural ridgo-parascutellaris dorsalis (52?). The origin is on the posterior surface of the pleural ridge dorsal to number 59. It is smaller than number 59 and tapers to a tendon that unites with the tendon of 59. Consequently, muscle numbers 57, 59 and 60 are inserted via a common tendon on the parascutellar process and have the same action.

61. M. pleural ridgo-calypteralis posterior (48). The origin is on the caudal surface of the pleural ridge mesad of and almost completely overlapped by number 60. It extends dorsad, joining a large tendon that is inserted on a sclerotized area on the ventrobasal margin of the distal calypter. The action is to flex the wing.

62. M. pleural ridgo-calypteralis anterior (49). The origin is on the anterior surface of the pleural ridge; from here it extends dorsad, passing mesad of the pleural ridge and pleural thread. Its tendon joins the tendon of number 61, giving the two muscles the same insertion. The action is to flex the wing.

63. M. precoxal apodemo-first axillaris (47). The origin is on the base of the precoxal apodeme. From here it extends dorsad anterior to the pleural ridge and mesad of muscle number 62. It has a long tendon that is inserted on the ventrolateral protuberance of the first axillary sclerite of the wing. The action is to extend the wing after flexion.

64. M. prescuto-basalar apodemalis (44). The origin is along the entire ventral surface of the prescutum. From here it extends caudad across the basalar cleft to insert on the anterior surface of the basalar apodeme. The action deflects the costal margin of the wing during the downward stroke. Bonhag

Fig. 24 Lateral view of leg muscles in *Culiseta inornata*.

('49) stated that the anterior tergal muscle of the basalare in *Tabanus*, a homologue of number 64, acts to extend the wing. Muscle number 64 of *Culiseta* is a homologue of number 44 in *Tipula vernalis* of Mickoleit ('62).

65. M. scutellar ridge-basalar apodemalis (46). This is a narrow strap-like muscle originating on the anterior surface of the anterior or scutellar ridge. It passes at a ventrocephalad angle mesad of the wing base and is inserted on the caudal surface of the basalar apodeme. It is antagonistic to number 64 and probably acts as a stator muscle for the basalar apodeme. This muscle is a homologue of number 46 of Mickoleit ('62) in *Tipula vernalis*.

Muscles of the leg (fig. 24)

66. M. trochantero-trochanteralis (fig. 25B) (?). The origin of this muscle is on a wide area at the base of the trochanter and the insertion is on the sclerotized piece within the pre-

formed breakage plane. This is the autotomizer muscle in the mosquito's leg. Contraction draws the sclerotized piece toward the base of the trochanter, resulting in separation along the preformed breakage plane. Autotomy may be induced in the living mosquito by tension on the leg.

67. M. femoro-levator apodemalis tibialis (100). The origin is on the dorsal wall of the femur for almost the entire length. The tendon of this muscle is attached to the levator apodeme at the base of the tibia. This is the levator muscle of the tibia.

68. M. femoro-depressor apodemalis tibialis (101). The origin is on the ventral wall of the femur opposite number 67, and the insertion is on the depressor apodeme at the base of the tibia. Contraction of this muscle depresses or flexes the tibia.

69. M. tibio-depressor apodemalis tarsalis (102). The origin of this muscle is on the entire ventral surface of the tibia. Its tendon

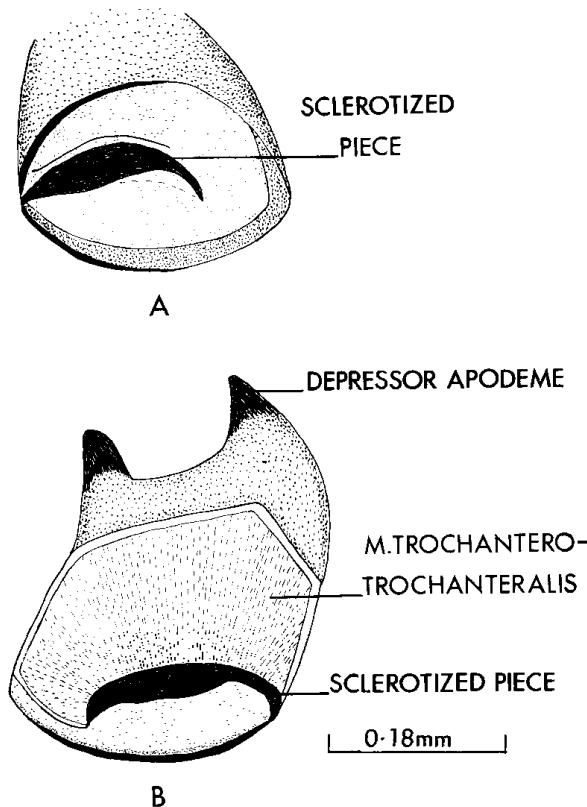


Fig. 25A Free end of trochanter illustrating position of sclerotized piece after autotomy in *Culiseta inornata*.

B Lateral view of trochanter illustrating position of autotomizer muscle in *Culiseta inornata*. Skeletal structures are illustrated in figures 12-14, 24.

is inserted on the depressor apodeme at the base of the first tarsomere. This is the depressor muscle of the tarsus.

70. M. tibio-levator apodemalis tarsalis (103). This is a short muscle originating on the dorsal surface of the tibia. The insertion is on the levator apodeme at the base of the first tarsomere. This is the levator or flexor muscle of the tarsus.

71. M. trochantero-pretarsalis (?). The origin is on the apical half of the trochanter beyond the preformed breakage plane. This muscle tapers to a tendon that passes through the femur, tibia, and tarsomeres, to become the retractor apodeme and insert on the unguiractor plate (figs. 15, 16).

72. M. tibio-pretarsalis (?). This is a small muscle at the base of the tibia whose fibers originate on the wall of this segment and unite with the tendon of number 71. The action of muscle numbers 71 and 72 is to depress or flex the tarsomeres. Extension of the tarsomeres is automatic with relaxation

of these muscles because of the elasticity of the joints.

DISCUSSION

The prothoracic skeleton

Preepisternum 1. The preepisternum 1 of *Culiseta* is homologous with this sclerite in *Dixa brevis*, as illustrated by Nowell ('51). It is also a homologue of the sclerite in *Chaoborus americanus*, labeled katepisternum 1 by Cook ('56). Ferris ('50) used preepisternum 1 for this sclerite in *Drosophila*.

Autotomy. Autotomy, or self amputation of appendages, is known in several groups of insects. It is the result of stress and always occurs at a definite breakage point (Brousse-Gaury, '58; Legrand, '74). There seems to be no description of this response in mosquitoes, although living adults are frequently observed to lose their legs. The anatomical provisions for breakage are not uniform in insects. In the mosquito, there is a preformed breakage plane in the trochanter with an autotomizer muscle having its origin at the base of this segment and the insertion on a sclerotized piece in the breakage plane. Owen ('63) erroneously stated that this break occurred at the union of the trochanter and femur. According to Brousse-Gaury ('58), this type of breakage in the leg of the cricket *Acheta domesticus* occurs at the articulation of the trochanter and femur. This joint is immobile and has a natural weakness. Stress on this union is produced by three large muscles that arise on the thoracic body wall and insert on the trochanter. Hemorrhage at the point of amputation in the cricket is prevented by a fibrous diaphragm which closes the wound. A similar mechanism for closing the wound after autotomy in Odonata larvae was described by Legrand ('74). Since there is no loss of blood at the breakage site in the mosquito, it is assumed that the wound is closed in like manner with a diaphragm of some type.

Lateral arm of sternal apophysis 1. The lateral arm of sternal apophysis 1 and the socket on the coxa into which it can engage appear to be limited to the Culicinae. These two structures are present in *Aedes*, *Anopheles*, *Culex*, *Culiseta*, *Psorophora*, *Uranotaenia* and *Wyeomyia*. They were not depicted for *Chaoborus americanus* by Cook ('56), nor by Bonhag ('49) for *Tabanus sulcifrons*. These parts are also absent in the Neuroptera (Fer-

ris, '40a; Ferris and Pennebaker, '39; Kelsey, '57) and the Mecoptera (Ferris and Rees, '39). This may be significant because members of these two orders are considered the immediate ancestors of the Diptera. The presence of these two structures in both sexes may indicate a general function. Snodgrass ('12) noted that the anterior coxae of *Psorophora ciliata* were not articulated firmly to the prothorax, but were connected by the rather broad pre-coxal and postcoxal membranes. The lateral arm and socket appear to compensate for this loose attachment. Action of the forelegs in lifting the thorax upward would engage the arm in the socket, resulting in a firm union. This mechanism may also assist the female in withdrawal of the stylets from the skin of a host after feeding.

Furcopleural apodeme. The furcopleural apodeme was found in seven genera of mosquitoes. It provides surface for attachment of a dorsoventral indirect wing muscle. It is not present in *Chaoborus americanus*, as represented by Cook ('56), and it is also absent in *Tipula reesi* (Rees and Ferris, '39). One figure by Mickoleit ('62) suggests that it may be very small in *Tipula vernalis* without a muscle attached. Bonhag ('49) does not show it in *Tabanus sulcifrons*.

The mesothoracic skeleton

Acrotergite 2. Acrotergite 2 of *Culiseta* is clearly homologous with this sclerite in *Corydalus cornutus*, *Tipula reesi*, and *Tabanus*, as represented by Matsuda ('70). It is also a homologue of the acrotergite 2 in *Agulla adnixa*, as depicted by Ferris and Pennebaker ('39) and *Panorpa nuptialis*, as shown by Ferris and Rees ('39).

Prescutum. The prescutum of the mosquito is known to taxonomists as the paratergite (Knight and Laffoon, '70a). Belkin ('62) first suggested that the paratergite was homologous with the mesoprescutum of *Tabanus sulcifrons*, as depicted by Bonhag ('49). The prescutum of *Culiseta* is delimited by the prescuto-scutal suture in the same manner as shown in *Tipula reesi* and *Bittacus pilicornis* by Matsuda ('70). In *Tipula reesi* this sclerite is elongate and lateral to the scutum. In *Culiseta* it is in the same position, but more compact in outline.

Parapsidal suture. The parapsidal suture is the same as the prescutal suture of Knight and Laffoon ('70a). According to Matsuda ('70) this suture arises from near the middle

of the prescutoscutal suture in *Tipula reesi*, and is homologous with the same suture in *Bittacus pilicornis*. The similarity between this suture in *Culiseta* and in these two species seems clear.

Posterior anepisternum 2. The posterior anepisternum 2 is separated from preepisternum 2 by the anapleural suture in *Tipula reesi* (Matsuda, '70). Cook ('56) called this suture the pleural cleft in *Chaoborus americanus*. This suture is usually present in the mosquito tribe *Uranotaeniini* (Belkin, '62). In this study it was observed in the American species *Uranotaenia sapphirina*. Since the anepisternum 2 is demarcated by a suture in some true mosquitoes and in their relatives, this designation seems justified. A term taken from comparative morphology here replaces prealar knob, a descriptive term used by taxonomists (Knight and Laffoon, '70; Belkin, '62).

Preepisternum 2. The preepisternum 2 of *Culiseta* is homologous with this sclerite in *Tipula reesi* as depicted by Rees and Ferris ('39). These authors analyzed the homologies between the pleura of *Tipula reesi* and the neuropteran *Agulla adnixa* and concluded that although preepisternum was not the ideal term homologies were maintained with its usage. The term preepisternum 2 replaces sternopleuron and mesepisternum of taxonomists, as listed by Knight and Laffoon ('70a).

Subalifer. The subalifer is present in many Diptera. Crampton ('25) recognized it in six families of the Nematocera, of which the Chironomidae and Psychodidae are near relatives of the mosquitoes. In the illustration of *Chaoborus americanus* by Cook ('56), there is a small unlabeled sclerite in the position of the subalifer. This sclerite in *Culiseta*, shown in figure 10, seems to meet the description by Crampton ('42). This interpretation is supported by the view that the suture demarcating the subalifer from epimeron 2 is not the transepimeral.

Basalare and basalar apodeme. The basalare is labeled second parapterum in the diagram of *Psorophora ciliata* by Snodgrass ('12). Since then, it either has been omitted from illustrations of the mosquito thorax or included without a label. The basalare of *Culiseta* is homologous with this sclerite in *Tipula reesi*, as depicted by Rees and Ferris ('39), *Corydalus cornutus* as illustrated by Kelsey ('57), and *Panorpa nuptialis* of Ferris

and Rees ('39). The basalar apodeme of *Culiseta* is a homologue of this structure in *Corydalus cornutus*, as depicted by Kelsey ('57), and the pleural apophysis of *Agulla adnixa*, which Matsuda ('70) interprets as being the same as the basalar apodeme in other insects. Although absent in *Tipula reesi*, the basalar apodeme is represented in *Tipula vernalis* by Mickoleit ('62) as having three muscles attached to it. His muscle number 44 is a homologue of the prescuto-basalar apodemalis in *Culiseta*, and his number 46 may be a homologue of the scutellar ridge-basalar apodemalis. The basalar apodeme of *Aedes aegypti* was called the ungoid process by Prashad ('18) and Christophers ('60).

Parascutellar process. The parascutellar process of the mosquito is here described for the first time. Its functional relationship to the wing was established by the discovery that four direct wing muscles were inserted on it (fig. 23). It was also observed that downward pressure on it resulted in movement of the wing. Some of the muscles which are inserted on this process in *Culiseta* are probably homologous with the three muscles in *Tipula vernalis* that are attached to the fourth axillary, as illustrated by Mickoleit ('62). If these homologies are correct, it implies that the parascutellar process and the fourth axillary of *Tipula vernalis* are also homologous. According to Rees and Ferris ('39) there is no fourth axillary in *Tipula reesi* and the third axillary is closely associated with the postmedian notal wing process. Matsuda ('70) interpreted Bonhag's figure of *Tabanus sulcifrons* as showing the fourth axillary formed by detachment from the terminal part of the postmedian notal wing process. In *Culiseta* the postmedian notal wing process is associated with the first axillary, and the parascutellar process is caudad of this level and attached only to the wall of the parascutellum near the posterior scutellar ridge (fig. 8). If the parascutellar process is the fourth axillary of the mosquito, this question arises: How far can a structure depart from the generalized condition and yet be known by the original name? Crampton ('42) pointed out that a morphological term is a designation, not a description, and he thought it would lead to a needless multiplicity of terms if homologous structures were called by different names every time they happened to vary in nonessential details. However, the parascutellar process is so unlike the other axillaries in both shape and

location that it is here given a name and regarded as a homologue of the fourth.

Mesosternum. Evidence for invagination of the sternal elements in certain holometabolous insects was first presented by Weber ('28). This condition, resulting in a cryptosternum, is now known to occur in many insect groups (Ferris, '40a). The two halves of the katepisternum 2 of *Culiseta* are infolded, forming the discrimin or discrimin line of Ferris ('40a). In specimens of this species treated with a 10% KOH solution the katepisternum may be separated along the discrimin line, revealing the furcasternum and furcasternal suture. This is similar to the mesosternal area of *Tipula reesi*, as reported by Rees and Ferris ('39). These authors proposed that, in keeping with the subcoxal theory for the origin of the pleuron in the Diptera, Mecoptera, and Neuroptera, the apparent sternal elements of the pterothorax are the ventral portions of the original subcoxal segments of the leg. This view was apparently more inclusive than justified by the evidence. Chen ('29) has found that, at the end of the larval period in *Drosophila*, the imaginal buds on the thorax giving rise to the legs are also centers for the origin of the pleura. Development is similar to this in the mosquito where each limb bud gives rise to a part of the thoracic body wall of the adult (Bodenstein, '45). These results appear to support the view of Matsuda ('70) that the pleuron does not arise from the subcoxa in the higher holometabolous insects.

Paracoxal suture. Matsuda ('70) proposed the term paracoxal suture for the line separating the pleural wall into anapleural and katapleural rings. Therefore, evidence of this suture should be found in all groups of insects. He interpreted the figures of Crampton ('25) as showing this suture in the following Nematocera: *Simulium*, *Eucorethra*, *Dixa*, *Ceratopogon*, *Johannsenomyia*, and *Psorophora*. This suture is also present in *Culiseta*, separating katepisternum 2 from preepisternum 2.

Prealar apophysis. According to Ferris and Pennebaker ('39) the prealar apophysis is a constant feature of the neuropteran thorax being present in all families. Cook ('56) illustrated it in *Chaoborus americanus*, but it is absent in diagrams of *Tipula reesi* by Rees and Ferris ('39). It was not shown in *Tabanus* by Bonhag ('49). This apophysis in *Culiseta* has an important flight muscle attached to it, the

prealar apophysal-pleural ridgalis. Christophers ('60) suggested that the prealar apophysis may be the basalare, although it has no relationship to either the basalare or basalar apodeme.

Precoxal and postcoxal apodemes. The precoxal and postcoxal apodemes of *Culiseta* are adaptations for attachment of indirect wing muscles. These apodemes are not shown in the diagrams of *Chaoborus* by Cook ('56), *Tipula reesi* by Rees and Ferris ('39), and *Tipula vernalis* by Mickoleit ('62). They are also not present in the thorax of *Tabanus* (Bonhag, '49).

Upper and lower laterotergite apodemes. The shape of these apodemes and their location suggests that their primary function is to reinforce the wall of the postnotum. There are no muscles attached to them. There seems to be no mention of these apodemes in publications on the dipteran thorax.

The metathoracic skeleton

Metapostnotum. The metapostnotum was called postnotum 3 by Snodgrass ('12). In a later paper ('59), he illustrated it in *Aedes aegypti* and *Psorophora ciliata* and changed the name to metapostnotum. He noted that the longitudinal tergal muscles of the first abdominal segment were attached to it and used this as one criterion for the designation. Young ('21) represented it without a label in diagrams of *Anopheles quadrimaculatus* and *Culex canadensis*. The part labeled postnotum II, by Peters and Cook ('66) in *Dixella indiana*, may be the metapostnotum. Morphologically, the metapostnotum is the acrotergite of the first abdominal segment (DuPorte, '59). In *Culiseta* it has expanded laterally to cover the anterior margin of the first abdominal segment.

Intersegmental cleft. The intersegmental cleft is a prominent feature on the caudal margin of the metapleuron of several genera of mosquitoes. This cleft results from a bifurcation of the intersegmental suture (fig. 6). The suture on its caudal margin gives rise internally to the intersegmental ridge, and, for this reason, is considered the cephalic margin of the first abdominal segment (fig. 7). The intersegmental cleft seems to occur only in the true mosquitoes.

Pleural and intersegmental apodemes. In *Culiseta inornata* two of the halter muscles are attached to these apodemes. The three halter

muscles of *Tipula vernalis* originate on the episternum, ventral pleural arm, and pleural ridge, respectively, rather than on apodemes of this type (Mickoleit, '62). The halter muscles of *Tabanus* likewise are not attached to apodemes as in the mosquito (Bonhag, '49). The pleural and intersegmental apodemes appear to be limited to the mosquitoes.

Wing muscles

The indirect wing muscles are the vibrators and vary rather widely in their numbers and attachments in different species of insects; yet, regardless of these variations, they all perform the same function. The action of the more direct wing muscles differs among species more than is generally recognized. Snodgrass ('35) pointed out that homologous muscles may have different functions owing to differences in skeletal parts of separate species. For this reason, he believed that it was impossible to name insect muscles in all cases on the basis of their functions. He noted that a muscle attached to the first axillary is known only in the Diptera and that in a syrphid fly it acts to flex the wing. Bonhag ('49) listed a muscle attached to the first axillary of *Tabanus* that is also a flexor of the wing. In contrast with these observations, Tiegs ('55) reported that in the tipulid *Plusiomyia* there is a small muscle attached to the first axillary that extends the wing. A homologue of this muscle in *Culiseta*, number 63, is inserted on the first axillary and, likewise, extends the wing after flexion. Tiegs ('55) noted that in *Plusiomyia* there are two muscles inserted on the alula which seem to rotate the wing by tilting the costal margin upward. The two homologues of these muscles in *Culiseta*, numbers 61 and 62, are clearly flexors of the wing. Christophers ('60) found two muscles attached to the membrane at the base of the wing of *Aedes aegypti* that are also flexors of the wing.

Mosquitoes are an exception to several statements in the literature regarding muscles of insects. Snodgrass ('35) stated that all wing-flexing insects have a muscle inserted on the third axillary. In *Culiseta* there is no muscle attached to this sclerite and this is true for *Aedes aegypti* (Christophers, '60). Snodgrass ('35) also stated that a large muscle from the outer margin of the coxa to the basalare is a constant feature of winged insects. This muscle was not found in *Culiseta*.

inornata, *Culex tarsalis*, or *Psorophora confinis*. It is also absent in *Aedes aegypti* (Christophers, '60). Tiegs ('55) reported that a coxosubalar muscle was present in the Culicidae. Knight and Laffoon ('70a) listed a posterior pleural muscle of the wing as being inserted on the subalare. There is no muscle attached to the subalare of *Culex tarsalis*, *Culiseta inornata*, or *Psorophora confinis*. This is also true in *Aedes aegypti* according to Christophers ('60).

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