The external anatomy of the horse-fly (Tabanus atratus Fab. diptera; tabanidae)

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THE EXTERNAL ANATOMY OF THE HORSE-FLY

(TABANUS ATRATUS FAB. DIPTERA; TABANIDAE)

STANLEY W. BROMLEY

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science

MASSACHUSETTS AGRICULTURAL COLLEGE

AMHERST, MASS.

1924
THE EXTERNAL ANATOMY OF THE HORSE-FLY

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INTRODUCTION

The marvelous advances made during the last decade in discovering the part played by insects in the transmission of disease have naturally lead to a more detailed investigation of the structure of the insects themselves. The Diptera, containing so many forms implicated in this activity, have afforded a rich field for research, and considerable attention has been given in recent years to the detailed morphology of many forms, the culicid and muscoid flies in particular. Progress on the interpretation of the external anatomy of these insects has been made principally on the mouthparts in the case of the blood-sucking flies and on the genitalia for specific differentiations in the case of the mosquitoes. Work on other structures has been neglected to a certain extent.

In other groups careful work has been done on the genitalia in the case of the Syrphidae (Metcalf '21), and there have been recent works in which certain structures of Dipterous insects have been homologized with the corresponding structures of lower insects. Important contributions have been made in this country by Peterson ('16)
in homologizing the head structures throughout the order; by Comstock and Needham (1898-1899) and Comstock (1918) in homologizing wing structure and venation throughout all orders, and by Young (1921) in homologizing parts of the thorax and abdomen, while the works of Crampton and Snodgrass have been of great value in homologizing the thoracic sclerites, legs, and genitalia of the Diptera with those of other orders.

Nowhere, however, has a single species been considered and treated fully in the light of the most recent morphological interpretations. Hence it appeared desirable that a paper dealing with the complete detailed external anatomy of a large, common, characteristic, and at the same time rather generalized member of the order should be at hand and with that end in view the following paper was prepared.

While this paper is essentially a study in morphology an effort has been made to broaden its application into a reference for taxonomic study of the family to which the species under consideration belongs. The terms used in taxonomic work on this group have therefore been given in comparison with the terms used by morphologists.

MATERIAL AND METHODS

The Dipteron selected for this work was the common black horse-fly (*Tabanus atratus* Fab.), chosen because of its large size, availability and wide distribution.
Dissections were made from both dried and alcoholic specimens. In the case of a dried specimen, boiling for two or three minutes in water brought about sufficient softening of membrane to allow manipulation and to bring out differentiation of plates and membrane. Further softening was necessary in some cases and was obtained by just bringing the specimen or parts to a boil in 10% potassium hydroxide. Boiling should not be allowed to continue as it causes distortion. The potassium hydroxide causes fading out of chitin if the specimen is left in too long, hence care must be taken to prevent this.

The action of the potassium hydroxide solution on the chitin will continue if there is a trace left on the specimen after it is placed in alcohol. To avoid this, the material was washed in water after removing from potassium hydroxide and placed in 70% alcohol to which a few drops of glacial acetic acid were added. The acid neutralizes whatever traces of potassium hydroxide may have been left in the specimen and thus arrests further dissolution of the chitin.

A strong illumination was found necessary for examining the dissections. This was furnished by a Spencer high power Mazda Microscope Lamp (400 watt - 100 volt). This threw a powerful light which was focused on the specimen.
by a converging lens.

TERMINOLOGY

Terms applied by the taxonomist to structures in the Diptera, as in every other order, have in many cases been morphologically inaccurate in that they have been previously applied to other structures or to structures which they really are not. An example of the latter case is the term "metanotum" in use among systematists for the post-scutellum of the mesothorax. Many of these terms, however, have persisted in literature until they have become well established. Since this is the case, it has been the policy in this work to retain any term of long standing use as preferable, except where the terminology is too flagrantly in error, at the same time presenting the term in use among morphologists. In this way it is hoped that a little may be contributed toward a closer relationship between the actual homology of the structure and its employment as a taxonomic character.

The development of a uniform terminology must of necessity be of slow growth but the gradual acceptance of such a terminology for the fundamental structures in all groups of insects is certain. Different terms for different group modifications are necessary and acceptable, but homologous structures throughout the class and even the phylum should bear the same names.
ACKNOWLEDGMENTS

The preparation of this paper was undertaken under the direction of Dr. G. C. Crampton, to whom the author is very grateful for the many valuable suggestions and various helps that he has given, and for the use of his excellent library of works on insect morphology. To Dr. H. T. Fernald the writer is deeply indebted for the obtaining of material for study, for many helpful criticisms and suggestions pertaining to the drawings, and for the careful going over of the manuscript resulting in a smoother terminology.

THE HEAD

The head of Tabanus atratus is large and disc-like, the anterior or cephalic aspect being roughly convex and the posterior or caudal aspect being slightly concave. The differences exhibited between the heads of the two sexes, particularly in the eyes and mouthparts as well as in general contour, are quite marked. The structures of the head will be considered under two groupings; those forming a part of the head capsule and those belonging to the mouthparts.

The head capsule.

The large compound eyes (c.e.) are fixed structures of the head capsule. They occupy a dorso-lateral position in the head and form about three-fourths of its cephalic aspect. They are dichoptic or quite distinctly separated in the female and are holoptic or contiguous in the male.
In the latter sex, the facets on the upper portion are much larger than those on the lower while in the female all facets are of uniform size. The ocelli are absent in both sexes. Furthermore, there is no indication of an ocellar tubercle such as is present in many Dipterous insects.

The antennae (a) are movable isolated appendages of the head capsule. They consist of seven segments and are inserted in the membranous antennal fossae (a.f.). The segments differ in size and shape. The proximal segment is termed the scape (sc.), the second the pedicel (pd.), while the five remaining segments compose the flagellum (fl). The first segment of the flagellum is greatly modified and enlarged. In fact, it is the largest segment of the antenna. It is bifurcate, the lower lobe bearing four small segments or "annuli", closely approximated, so that they appear to be one.

The external sclerites of the head capsule are the vertex, fronto-clypeus, genae, post-genae, gula, occiput and labrum. [Although a true sclerite of the head capsule, the labrum will be discussed with the mouth-parts because of its close association with them. The limits of many of the sclerites of the head are indefinite and the names have been applied to general regions rather than to clearly defined areas.]
The vertex (v) is a dorsal area of the head between the compound eyes. It is divided into an anterior and a posterior portion. The anterior portion is divided by a vertical suture into two areas in which the antennal fossae are located. This vertical suture, which is not visible in the posterior vertex, is the stem of the epicranial suture. The anterior vertex (a.v.) also bears a prominence at the base of each antenna which is known as the subcallus (sbc). The posterior vertex (p.v.) extends backward between the compound eyes far onto the posterior aspect of the head. Near the line demarking the anterior vertex is a prominence known as the frontal callosity (frc) which has been frequently used as a taxonomic character. In the male, the close approximation of the eyes has limited the posterior vertex on the frontal aspect of the head to a small triangular piece termed the vertical triangle (vtr) while the anterior vertex has been termed the frontal triangle (f.t.).

The frontal aspect of the head ventrad of the arms of the epicranial suture not including the labrum and torae is designated the fronto-clypeus (frc). It is composed of the frons (fr) and the clypeus (cl) but the absence of the clypeo-frontal suture indicates the fused condition of the two, although the clypeus is partly demarked laterally.
The front has been termed the "face" by systematic workers. There is a triangular membranous area, larger in the male than in the female, adjoining the labrum, which may allow partial mobility of this sclerite.

The *genae* (*ge*) or "cheeks", are the areas on each side of the head below the compound eyes, between the frons and the postgenae. The *post-genae* (*pge*) are indefinite areas of the lower caudal aspect of the head merging with the occiput. The term *occiput* (*occ*) has been used for the general region of the upper half of the posterior aspect of the head behind the compound eyes, into which the vertex extends. There is a cervical projection of the occiput around the dorsal border of the *occipital foramen* (*oc. f.*) This was termed the *parocciput* (*pocc*) by Peterson.

In the *gular* (*gu*) region of the female is a weakly chitinized ridge below the ventral border of the occipital foramen. This area in the male is strongly chitinized and merges with the postgenae.

Pits and sutures are generally external indications of internal structures. The external manifestations of the large internal tentorium are the *frontal pits* (*f.p.*) which mark the invaginations of its two anterior arms; the grooves (*i.d.*) between the bases of the antennae and the compound eyes, which mark the invaginations of its two dorsal arms; and the *gular pits* (*g.p.*) which mark the invaginations of its two posterior arms.
The epicranial suture is a prominent land-mark of the head region. The arms (a.ep.) of this suture separate the vertex from the frons, while the vertical stem (s.ep.) is visible only in the anterior vertex. The frontal pits are located in the arms of the epicranial suture one on each side.

The clypeo-labral suture (c.l.su.) demarks the clypeus from the labrum.

The mouth-parts.

The mouthparts in both sexes are produced into a prominent proboscis, projecting downward and slightly forward from the head capsule. In the female the parts are strong and modified for piercing and sucking, whereas in the male they are weaker and are not modified for piercing.

The labrum-epipharynx (lr-ep) forms the anterior protective covering of the more delicate mouthparts, while the fleshy labium (li) forms the posterior covering. The rigid, highly chitinized labrum (lr) is a fixed sclerite of the head connected with the clypeus. The epipharynx (ep) forms a roof-like extension over the buccal opening forming with the hypopharynx (hyo) a sucking tube leading into the basispharynx (bp). The epipharynx is joined by a membranous connection to the caudal aspect of the labrum. The tormae (to) are small pharyngeal sclerites, the exposed portions of which are visible as hinge-like
thickenings between the clypeus and labrum, and form a part of the epipharynx.

The mandibles (md) lie immediately beneath the labrum-epipharynx, but are present only in the female. They are hard chitinized thin blades with five sharp points fitted for piercing and lacerating the skin of the host. They operate like a pair of scissors, producing the "bite" which draws the blood.

Beneath the mandibles lie the maxillae (mx). The basal portions of the maxillae are embedded in a membranous region which is connected with the caudal portion of the hypopharynx. Each maxilla is composed of the cardo (car) or basal segment, the stipes (stp) or the second segment which bears the maxillary palp or "palp" (mx.p.) and the galea (ga.) or distal segment. The stipes and cardo are firmly imbedded in the membranous area below the gular region. In the male this whole region is chitinized and the cardines are fused with this chitinization. The maxillary palpi (mx.p.) in both sexes are 2-segmented. The galea (ga) is a slender delicate structure at the tip of which are borne minute projections which may indicate a sensory function. Imbedded in the membrane joining the basal portion of the maxilla, at the juncture of the galea and the stipes, with the hypopharynx is a small chitinous plate, the interlora (il.) Rterson (1916) considered this plate homologous with the lacinia of other insects.
Crampton (1923), however, proved its homology with the interloca found in certain hymenoptera.

The hypopharynx (hyp) is a delicate unpaired structure arising partly from the mandibular and partly from the maxillary segment and forms the lower lip of the pharyngeal opening. The basal portion of the caudal aspect of the hypopharynx is connected with the labium and the stipes by a membrane. The cephalic aspect of the hypopharynx is grooved, forming a trough leading into the basipharynx (bph). Through the basipharynx the liquid food is pumped by the oesophageal pump (o.p.) into the oesophagus. Through the hypopharynx runs the salivary canal (s.c.) opening at its distal end. Through this canal pass the secretions of the salivary glands which are injected into the wound by the salivary pump, composed of a thin distensible sac (s.s.) demarked from the salivary duct (s.d.), and the salivary bulb (s.b.).

The labium (li) is largely membranous and consists of the trunk or mediproboscis, and two distal oval lobes, the labella (l.p.) which compose the distiproboscis. The labium of the male is slightly more elongate and slender than in the female. A large chitinous plate, the theca of Peterson (1916), occupying a position on the caudal aspect of the trunk, represents the united palpigers (u.p.). The labella represent the fused and modified labial valni. On
the lateral portions of the distiprobooscis are small chitinizations, termed by Peterson Kappa, Sigma, and Furca (1, 2, and 3), which may represent vestiges of the segments of the fused palpi. On the inner surfaces of the labella are the so-called pseudo-tracheae (pt) bearing minute chitinous projections ostensibly of rasping function.

THE THORAX

The thorax consists of three segments, the prothorax, the mesothorax, and the metathorax, and bears the wings and legs. For the operation of these organs of locomotion the interior of the thorax is filled chiefly with muscles. The muscles are attached to invaginations of the integument, and to these invaginations different terms are applied depending on their position. A tergal projection for muscle attachment is termed a phragma; a pleural projection, an apodeme; and a sternal projection; an apophysis. The external manifestations of the internal structures for muscle attachment are found in sutures, fissures, etc., which are of importance in demarking the sclerites. That considerable stress is brought to bear upon the thoracic integument by the action of the wing and leg muscles is indicated by the presence of strongly chitinized plates in some places and areas of membrane in others where movement of the body walls is necessary. The dorsal sclerites are termed tergites; those on the sides, the
pleurites; and the ventral plates, the sternites. The principal membranous areas are those in the neck region; at the articulation of the legs, wings, and halteres; at the attachment of the abdomen; and around the spiracles.

There are two pairs of spiracles present on the thorax, one on the meso and one on the metathorax. They are designated the mesothoracic or anterior spiracle (a.sp.) and the metathoracic or posterior spiracle (p.sp.) Each consists of an opening, through the body wall, of a main tracheal branch. Around this opening is a narrow encircling rim of chitin termed the peritreme (pr) which bears a row of bristles protecting the opening against the entrance of foreign particles.

The Cervix

The cervix or neck region (cx) is intersegmental. It is membranous for the most part, but possesses lateral and ventral sclerites. The lateral sclerites have been termed the lateral cervical plates (lcp). The anterior margins of these articulate with posterior condyles of the parocciput. The posterior portion of the lateral plate is large and bears a callosity beset with long hair. Its posterior apex is contiguous with the prothorax at the region of demarkation of the pronotum and proepisternum. Ventrally there is a deposition of chitin in the membrane to form a weak sclerite which probably corresponds to the presternum (prs), a definite intersegmental plate in the lower insects.
Fused with the lower extremity of the anterior pronotum, and closely approximating the ventral margin of the lateral cervical plate is a narrow strip of chitin, which normally is concealed from view by the callosities of the sclerites bordering it. As shown by Crampton (1924), this strip in the lower Diptera was part of the lateral cervical plate but has split off and migrated toward the pronotum with which, in the present species, it has fused.

The Prothorax

The great development of the meso-thorax has resulted in the crowding of the prothorax into a small portion of the anterior-ventral region of the thorax. The propleuron is also greatly reduced but the prosternum is retained in a more primitive condition than in the two remaining thoracic segments. There is no spiracle in the prothorax.

The tergum.

There are two tergal plates; the anterior pronotum (a.p.) and the posterior pronotum (p.p.)

The anterior pronotum consists of a dorsal band of chitin which becomes broader in its development lateral until it fuses with the episternum. At the base of this lobe just above the indistinct point of fusion with the episternum is a large rounded callosity bearing long hairs.

The posterior pronotum is divided into two lateral portions known as the pronotal lobes (plo), by the anterior
development of the mesonotum, the dorsal connecting band being obsolete. Each of these lobes bears a callosity, the so-called humeral callus (h.c.) The pronotal lobes are closely associated with the prescutum of the mesonotum of which in fact they have been figures in literature as being a part. In some of the more primitive Diptera such as certain Tipulids these lobes are connected dorsally forming a continuous notal plate.

The pleuron.

The pleuron is divided by a distinct suture, the propleural suture (p.su.), into episternum (es.) and epimeron (em.). The episternum fuses with the lower lobe of the anterior pronotum. The posterior portion is produced ventrally into a coxal process (c.p.) which articulates with the procoxa (c₁). Fused with the anterior portion of the episternum is a large lobe, the ventral margin of which closely approximates the basisternum (bs₁). This is a relic of the precoxal bridge (prx), which is a connecting strip of chitin between the episternum and sternum in certain of the lower groups.

There is a distinct line of demarkation between the epimeron of the prothorax and the anepisternum of the mesothorax, but the lower and upper portions of the proepimeron have undergone such modifications through fusion with other sclerites and secondary deposition of chitin that its
boundaries in these regions are very vague. In the upper region there has been an invasion of the posterior pronotum and in the lower region there has been a secondary deposition of chitin bringing about a very nearly complete fusion with the sternopleurite.

**The sternum.**

The ventral region of the pro-thorax is divided into two sclerites, a large anterior basisternum (the true or eusternum) (ba1) and a smaller posterior furcaisternum (fca2).

The basisternum lies caudad of the intersegmental presternum and separates the coxae. The furcaisternum is a triangular sclerite between the anterio-ventral apices of the sternopleura of the mesothorax and the basisternum. On either margin close to the coxal membrane is a depression. These two depressions are the furcal pits (fp) and are the external manifestations of the invaginations of the furca, an internal forked structure, the apophysis for muscle attachment.

**The Mesothorax**

The mesothorax or middle segment is much the largest of the three divisions of the thorax. The great development of its external sclerites is in keeping with its great internal muscular development for the operation of the wings. The mobility of the wings is insured by the large
membranous area on each side at the articulation of the wings. As there is more or less motion of the integument in the region of the spiracles, these areas are also membranous.

The tergum.

The mesonotum comprises most of the dorsum of the thorax. It is composed of two large tergal plates, the *scuto-scutellum* (*S*) and the *postscutellum* (*Ps*), both of which are divided into subregions.

The *scuto-scutellum* is the large anterior plate and is divided into three portions; the *prescutum* (*prc*), the *scutum* (*sc*), and the *scutellum* (*set*). The transverse suture (*ts*) is here regarded as demarking prescutum and scutum, although the true division is anterior to this suture, being internally manifested by heavy integumental folds of which no external evidence is given. On each side of the prescutum is a lobe projecting caudad toward the base of the wing. These are the *antealares* (*ant*) or posterior lobes of the prescutum. The *scutum* bears a projection at the articulation of the wing, the *suralare* (*sl*) or anterior notal wing process, one of the wing pivots. Cephalad of this process is a narrow strip of chitin, the *prealarbridge* (*pre*) connecting the scutum with the anterior basalar.

The *scutellum* is the conspicuous elevated plate immediately caudad of the scutum. It consists of two elevations, the anterior or *prescutellum* (*prsc*) being much smaller than the second to which the term *scutellum* is generally restricted. On either side of the scutellum there is demarked a
depressed region, the _parascutellum_ (pac). This bears the adanal or posterior notal wing process which is the posterior pivot of the wing (pwp). Immediately behind this process lies the axillary cord (ax.c.) which is a differentiated continuation of the parascutellum encircling the calypteres, as a thickened margin.

The _postscutellum_ is the second tergite on the mesothorax and is composed of a notal plate, the _meditergite_ (mp); the _anapleurotergite_ (a.pl) immediately behind the axillary cord; and the large _katapleurotergite_ (k.pl.) just below the wings and above the metathoracic spiracle. The latter sclerite bears a large callosity, the _postalar callus_ (pac). The ana- and katapleurotergites together form the _pleurotergite_ of the postscutellum.

**The pleuron.**

The large _mesothoracic_ or anterior spiracle marks the anterior terminus of the lateral membranous area extending through the articulation of the wings and separating the notum from the pleuron. The spiracle is borne in membrane but a secondary deposition of chitin has been laid down around the periphery of this membrane.

The meso-pleuron is composed of two large divisions, the _meso-episternum_ (es2) and the _meso-epimeron_ (em2) demarked by the _meso-pleural suture_ (p.su2). (The meso-pleural suture in primitive Diptera is straight). The
zig-zag in this suture here and in the higher Diptera is a modification due to the specialization and the great development of the meso-episternum. Hence this is a group landmark of value in the interpretation of the phylogeny of the different families of the order.

The meso-episternum is divided into an upper sclerite, the anepisternum or mesopleurite (a.es₂), and a very large lower sclerite, the sternopleurite or katepisternum (k.es₂). The dorsal posterior portion of the anepisternum has undergone considerable modification. The hypodermal cells have not laid down chitin in parts of this area, and detached plates have therefore been left partly or wholly surrounded by membrane. The anterior basalare (abl) is one such sclerite partly demarked from the anepisternum. On the other hand the posterior basalare (pbl) is wholly demarked. The pleural wing process or alifer (alf) is a narrow strip of chitin produced dorsally to form the ventral pivot of the wing.

The sternopleurite (spl) is the large lower sclerite formed from katepisternum and sternum. The sternopleurites of either pleuron extend into the ventral region where fusion with the sternal sclerites has taken place.

The meso-epimeron consists of an upper pteropleurite (a.em₂) or anepimeron, and a lower mesopleurite or katepimeron (k.em₂). The pteropleurite is closely asso-
ciated with the pleurotergite of the postscutellum, and is also partly subdivided by a zig-zag suture, the pteropleural suture (pt.s.). Demarked from the dorsal region of the pteropleurite by a deep groove is the subalare or subalar plate (sbl).

The meropleurite is a clearly demarked region ventrad of the pteropleurite and cephalad of the meta-episternum. The sternum.

The anterior portion of the meso-sternum has become fused with the meso-episternum forming the sternopleurite, and the furcasternum the only plate that can be clearly homologized is very much reduced due to the close approximation of the coxae.

The wing and its articulation.

The wings are long and the venation strong fitting the heavy-bodied fly for sustained flight. The costal vein in particular is strengthened as the stress due to the resistance of the air is greatest on this part of the wing during flight. The venation is very easily followed and the wing of Tabanus has served as an illustration of venation in the Diptera in many text-books.

In the Diptera the mesothoracic wings alone are functional in flight; the metathoracic wings have degenerated into mere knobbed threads, the halteres (h.).
The meso-thoracic articulation.

The wings are joined with the meso-thorax by means of a membranous connection, known as the axillary membrane (ax.m.), in which are embedded the axillary sclerites or pteralia (alar ossicles) of definite form and number.

The axillary membrane is a thick, heavy membrane continuous with the notum.

The supporting wing-pivots on the thorax are three in number, two dorsal and one pleural. The two dorsal pivots are designated the suralare (sl) or anterior notal wing process and the adanal or posterior notal wing process (pwp). The pleural pivot is the alifer (alf).

The axillary sclerites are four in number. The first or notopterale (n) is a triangular goose-necked plate hanging upon the suralare of the thorax on the one side and upon the second axillary sclerite or medinterale (m) and the base of the radius on the other. The third or basanal pterale (bsa) hinges upon the fourth or adanal pterale (adc) and the thickening at the base of the alula (al). The fourth or adanal pterale hinges upon the posterior notal wing process (pwp) which is a projection partly detached from the parascutellum.

The posterior margin of the scutellum is prolonged into a corrugated axillary cord (ax.c.) extending around the calypteres. Embedded in the membrane at the anterior
attachment of the wing just opposite the mouth of the transverse suture is a thickened bristle-bearing pad, known as the tegula or epaulet. The term squama has been incorrectly applied to the Dipterous tegula, which is homologous with the tegula in Hymenoptera and should bear that name. A portion of the base of the thickened costa is demarked into a small plate. This is the basicosta (bse) or paratetgula.

The venation.

In Fig. 7, the Comstock-Needham system for the venational terminology has been followed with slight modification. This is found in the interpretation of the radius, where a change recently proposed (Shannon and Bromley 1924) is shown. A few years ago, Tillyard (1919) proposed quite radical modifications in the nomenclature, particularly that concerned with the medial, cubital and anal branches. These changes have been presented as there seems to be some evidence for his views.

The Principal Veins

COSTA. (C) The costa or costal vein is thickened at its base. It encircles the entire margin of the wing to the axillary excision. It is setose, bearing macrotrichiae from its base to slightly beyond the juncture of R3+4. The extension of the costa around the posterior margin of the wing has been termed the ambient vein.
SUBCOSTA (Sc.) The *subcosta* or auxiliary vein fuses basally with the stem-vein of the radius and joins with the costa at about three-quarters the distance to the apex of the wing. The subcosta is partly setose. *Macrotrichiae* are present on the vein in a region between the humeral cross-vein and the meeting of the costa and subcosta.

RADIUS (R). The great *radius* vein arises at the notopterale and gives rise to several large branches. It consists of a large basal *stem-vein*, demarked at the arculus by the *stem-vein* suture; and the continuation of this stem-vein beyond the arculus into a main axis giving rise to the remaining branches. The continuation of the main axis to the margin of the wing is designated the *radius-one* (R₁). This is first longitudinal vein of Williston. The posterior branch of the first dichotomy of the radial axis gives rise to a series of veins which constitute the *radial sector*. The anterior branch of the radial sector or the second longitudinal vein (R₂) according to Comstock is R₂⁺³, (assuming that it is composed of a fusion of the second and third branches of the radius). There is evidence to show, however, that in most of the Brachycera R₃ fuses with R₂, and the basal portion of R₃ is lost. Therefore the second longitudinal vein is simply R₂ and the third longitudinal vein is composed of the two branches R₃⁺⁴ and R₅. The portion of R₁
from the stem-vein suture to the costa is setose.

**MEDIA** (M). The media after branching off from the arculus divides into two main branches the anterior of which is the fourth longitudinal and the posterior, a portion of the fifth longitudinal. The anterior branch divides into M₁ and M₂ and the posterior branch is the single M₃. Tillyard considers Comstock's Cu₁ to be the branch M₄ of the media.

**CUBITUS** (Cu). The cubitus is the large fifth longitudinal vein arising at the base of the arculus and dividing into two branches Cu₁ and Cu₂. Cu₂ joins the second anal near the margin of the wing. According to Tillyard's revision Cu₂ is Cu₁, and the 1st anal is Cu₂.

**ANAL** (A) veins. The anal furrow is a vestigial vein and represents the First Anal. The Second Anal is the sixth longitudinal vein and fuses with Cu₂ near the margin of the wing. The Third Anal is abortive, not reaching the margin of the wing. Tillyard interprets the anal furrow as cubitus-two; the second anal as the first anal; and the third anal as the second.

**The Crossveins**

**HUMERAL** (h). The humeral is a heavy crossvein connecting the costa and subcosta near their bases.

**RADIO-MEDIAL** (r-m). The radio-medial or anterior cross vein connects the posterior branch of the radius with the
first branch of the media, forming the distal margin of first basal cell (R).

MEDIAL (m). The medial or posterior cross vein connects M₂ with M₃.

MEDIO-CUBITAL (m-cu). The medio-cubital or discal cross vein connects M₃ and Cu₁. According to Tillyard this is not a cross vein but a part of the vein M₄. He considers the small vein at the basal margin of the cell Cu₁, the medio-cubital cross vein.

ARCULUS (ar). The arculus is a heavy oblique thickening connecting the radius, media and cubitus near their bases.

The cells

The areas of the wings between the veins are known as cells. Here the membrane is more or less transparent, although pigmented to appear dark brown in the present species. The following table gives a comparison of the two terminologies in general use.

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<thead>
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<th>1st C and 3rd A parts of Costal and Axillary, respectively.</th>
</tr>
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<tr>
<td>2nd C .........Costal             2nd M ............ 2nd basal</td>
</tr>
<tr>
<td>Sc ............Subcostal          M₁............ 2nd posterior</td>
</tr>
<tr>
<td>R .............1st basal           1st M₂......... discal</td>
</tr>
<tr>
<td>R₁ .............marginal          2nd M₂......... 3rd posterior</td>
</tr>
<tr>
<td>R₃ .............1st submarginal    M₃............ 4th posterior</td>
</tr>
</tbody>
</table>
The posterior lobes

The posterior lobes of the wing are three in number; the alula (al) and the distal (d.ca.) and proximal calypteres (p.ca.). The alula is more closely associated with the wing proper than the others. It is attached to the thickening at the base of the anal veins and is demarked from the posterior margin of the wing by the axillary excision (ax.c.). The calypteres are heavy leathery membranous lobes with thickened margins. A fringe of flattened hairs, the squamal fringe (s.f.), encircles the margins of the calypteres. The distal calypter or upper squama has been referred to in literature as the squamula and more incorrectly as the antitegula. The proximal calypter or lower squama has been termed the squama and more incorrectly the tegula, a term which should be restricted to the epaulet.

The leg.

A discussion of the meso-thoracic leg alone will be presented, but the differences between it and the others will be cited. The trochantin is absent in all. The meso-coxa (c2) is closely associated with the pleural region.
As if to compensate for this and insure the mobility of the limb, there has occurred a breaking away of the distal portion of the coxa to form a separate piece, the distitarsus (dt). The membranous depression into which the trocanthecae or basal portion of the trochanter is set, is the coxathecæ or coxal cup (cc). The trochanter (tr) is firmly associated with the femur (fc) of which it is a portion demarked by a construction. The basal portion of the tibia (ti), termed the tibia caput, articulates with the femur at the femur cup (fc). Projections of the femur at this point, the gonylegial lobes (gl) prevent the tibia from moving sideways. Two heavy tibial spurs (tsp) are borne at the tip of the tibia.

The tarsus (ta) is composed of five segments or tarsomerae, the basal segment of which is the longest and is designated the basitarsus (bt). The tarsocaput (tsc) or basal portion of the tarsus is received into the tibiathecæ (tt) the socket in the tibia for its reception. The fifth tarsomere is known as the distitarsus (dt) and bears the claws or unguæ (u), the pulvilli (pv) and the arolium (ar).

The unguæ are connected ventro-basally with a movable plate on the ventral side of the distal portion of the distitarsus, and are flexed when this plate is retracted by the unguitor (u.t.)
There are three pad-like structures borne on the distal portion of the distitarsus. The two lateral pads are the pulvilli. At the basal portion of each pulvillus is a small plate, the basipulvillus (bp)[the arolium.] The median pad between the claws[.] The arolium although generally termed the pulvilliform empodium is not a true empodium as shown by Crampton (1923).

In the structure of the coxae, the three legs differ.

The pro-coxa (c₁) is elongate and freely movable.
The meta-coxa (c₃) is also movable but less so than the pro-coxa (c₁). Furthermore the meta-coxa is compact rather than elongate. There is no disti-coxite to provide for greater mobility as occurs in the meso-thoracic leg.

The Metathorax

The metathorax, particularly its notal portion, has been restricted by the great development of the mesothorax to a small posterior region more or less concealed by the abdomen.

The tergum.

When the insect is in a natural position, the notal region is concealed by the postscutellum of the meso-thorax and the first abdominal segment. The tergum is composed of two plates, the scuto-scutellum and the postscutellum.

The scuto-scutellum (S₃) is a narrow band of chitin extending over the notum on either side to the halteres (h).
The postscutellum (PS₃) is continuous with the epimeron, extending over the notum as a narrow strip of chitin.

The pleuron.

The pleuron is composed of episternum (es₃) and epimeron (em₃) demarked by the metapleural suture (p.su₃).

Below each halter is a membranous area in which the metathoracic or posterior spiracle (p.sp.) is located. Embedded in this membrane are a number of small chitinous areas and there is also a chitinized zone around the periphery of the membrane surrounding the spiracle. A small raised papilla-like structure which may be sensory in function is located in this region, just below the halteres. The upper portion of the episternum fades into membrane below the halteres but is clearly demarked from the epimeron by the meta-pleural suture. A narrow strip of chitin extends from the episternum to the sternum forming the pre-coxal bridge (prx₃).

The epimeron is the largest sclerite of the metathorax and is closely applied to the abdomen. It bears sculpturings or sense-pits similar to those found on the abdominal plates. There are two rows of these; one near the postero-sternal margin and one at the meeting of the postscutellum and epimeron. The name hypopleura has been loosely applied to the meta-pleuron, including the meropleurite and the meta-episternum and sometimes to the pleurotergite of the postscutellum.
The sternum.

Due to the apposition of the coxae, the sternal region is much reduced, although it is more in evidence than that of the mesothorax. The furcasternite, indicated by the presence of the furcal pit is the only sternite which can be clearly homologized in this species but there has undoubtedly been a fusion here with the other plates of the sternum. The ventral chitinization may really be the basisternum and furcasternum combined.

THE ABDOMEN

The Preabdomen

The term preabdomen was introduced by Metcalf (1921) in describing the external anatomy of the Syrphidae. It is used here to include the seven visible segments of the abdomen, or those in which spiracles are located.

Sculpturings or the so-called sense-pits are present in definite areas on both tergites and sternites. Their significance is not clearly understood. A row of particularly large pits according to Young (1921) mark the fusion point of the first and second sternites.

The abdomen as well as the occiput of the head and anterior part of the thorax is covered with a plum-colored "bloom", consisting of very fine scales lightly adhering to the integument.
The dorsum of the abdomen presents a series of tergites, seven of which are visible in a dried specimen. The first is narrow and overlaps the corresponding sternite to a much greater extent than do the others. The second tergite is the largest and the others diminish in size to the seventh, which is overlapped by the sixth and part of the fifth tergites due to the telescoping of the segments, so that only the posterior third is visible. Counting from the seventh back to the first, each of the other tergites visible in the dried specimen is overlapped by the one preceding it in a diminishing degree until we reach the second, the anterior margin alone of which is covered by the first.

The pleuron.

The pleuron consists of the membranous region between the tergites and sternites. As the tergites overlap the sternites this region is visible only when the plates are pulled apart. The spiracles are found in this membrane but are concealed by the tergites and consequently difficult to locate from the exterior. Their position, however, can be determined by an internal examination, tracing the main branches of the tracheae to their orifices in the membrane. There are seven pairs of spiracles present, a pair to each visible segment. The telescoping of the seg-
ments mentioned in the paragraph on the tergum has resulted in the crowding together of the spiracles, so that the third segment appears to bear two pairs of spiracles.

The sternum.

The first sternite is much the largest and according to Young (1921) represents the fusion of the first two normal sternites. The remaining sternites occupy positions opposite the corresponding tergites and decrease in size to the seventh.

The postabdomen.

The term postabdomen was proposed by Metcalf (1921) in referring to the Syrphidae. It is used for that part of the abdomen in which the segments have undergone modifications and are without spiracles.

The male terminalia.

The term hypopygium has been applied collectively to the terminal structures of the abdomen of the male in the Diptera, more particularly to the genitalia and accessory structure but has also been used for the female terminal structures. Hence it is of little morphological significance.

The genitalia proper consist of modifications of the ninth sternite, and are composed of a pair of gonostyles or "claspers" (gs) and the chitinous aedeagus (ae) or intermittent organ. The gonostyles consist of two segments, the
strong proximal basistylus (bs) and the movable dististylus (ds). These clasp the female during copulation, while the aedeagus is applied to the genital opening. The aedeagus possibly represents the fused penis valves of lower insects, while the term "penis" (p) refers to the internal terminal portion of the ejaculatory duct which is eversible.

The proctiger (pr) or anus-bearing structure consists of the segments beyond the ninth. These have undergone fusion and modification to such an extent that their homologies are not clear. The paraprocts (pp) or parapodial plates may represent sclerites of the tenth segment fused with those of the ninth which persist as lateral lobes of the paraprocts. The paraprocts are fused at the dorsum but the line of demarkation is not pigmented. A pair of cerci (c) are present. There is a small triangular membranous suranal area which may represent the vestigial epiproctal region of the eleventh segment. The ventral supports of the anus are two narrow chitinous plates side by side which may be called the sub-terminal plates (Vp). They may be homologous with the so-called "ventral plates" of mosquitoes. At any rate they probably represent the fused tenth and eleventh sternites.

The female terminalia.

The term ovipositor has been used to designate the modified terminal portions of the female abdomen particularly the genital portion, to which it should be restricted.
The eighth sternite projects posteriorly beyond the eighth tergite but the membranous connections indicate that it belongs to this segment. It is modified into a large plate known as the infra-anal plate (iap) which is of taxonomic significance in this group. What may represent the ninth sternite is a weak chitinization folded back into the venter of the genital opening.

The structures of the female proctiger are similar to those of the male, except that the plates considered in the discussion of the male genitalia as the lateral lobes of the paraprocts are detached in the female and form distinct sclerites. This is evidently a more primitive condition, and the plates probably represent lateral vestiges of the ninth tergite.
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Wesche, W.  


Westhoff, F.  

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<thead>
<tr>
<th>Abbreviation</th>
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<td>a.</td>
<td>antenna</td>
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<tr>
<td>abl.</td>
<td>anterior basalare</td>
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<tr>
<td>adl.</td>
<td>adanale</td>
</tr>
<tr>
<td>ac.</td>
<td>aedeagus</td>
</tr>
<tr>
<td>a. emg</td>
<td>pteropleurite</td>
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<td>a. ep.</td>
<td>arm of epicranial suture</td>
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<tr>
<td>a. cs₂</td>
<td>mesopleurite</td>
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<td>a. f.</td>
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<tr>
<td>al.</td>
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<td>antecalare</td>
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<td>a. pl.</td>
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<tr>
<td>ar.</td>
<td>arolium</td>
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<tr>
<td>a. sp.</td>
<td>mesothoracic spiracle</td>
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<td>a. v.</td>
<td>anterior vertex</td>
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<td>ax. c.</td>
<td>axillary cord</td>
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<td>ax. e.</td>
<td>axillary excision</td>
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<td>bt.</td>
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<tr>
<td>c₁, c₂, c₃</td>
<td>pro, meso, and metacoae</td>
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<td>car.</td>
<td>cardo of maxilla</td>
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<td>c. e.</td>
<td>compound eye</td>
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<td>cr.</td>
<td>cercus</td>
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<td>ex.</td>
<td>cervix</td>
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<td>d, ca.</td>
<td>distal calypter</td>
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<td>de.</td>
<td>dixticoxite</td>
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<td>ds.</td>
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<td>fcs.</td>
<td>furcasternum</td>
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<tr>
<td>fe.</td>
<td>femur</td>
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<tr>
<td>fl.</td>
<td>flagellum of antenna</td>
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<td>f. p.</td>
<td>frontal pits</td>
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fr. - frons
frcl. - fronto-clypeus
f.t. - frontal triangle
gla. - galea of maxilla
gc. - genae
gl. - gonythecal lobes
g.P. - gular pits
gs. - gonostyles
gu. - gula
h. - halter
h.c. - humeral callus
hyp. - hypopharynx
ia.p. - infr-anal plate
i.d. - dorsal invagination of tentorium
il. - interlora
k. cm2 - meropleurite
k.cs. - sternopleurite
k.pl. - katapleurotergite
l.c.p. - lateral cervical plate
li. - labium
l.p. - labial palpi or labella
lr. - labrum
lr-cl. - labrum-epipharynx
m. - medipterale
md. - mandible
mp. - meditergite of post-scutellum
mx. - maxillae
mx.p. - maxillary palpus
n. - notopterale
occ. - occiput
oc.f. - occipital foramen
o.p. - oesophageal pump
p. - penis
pac. - post-alar callosity
pb. - proboscis
pbl. - posterior basalare
p.ca. - proximal calypter
p.ch. - precoxal bridge
pd. - pedical of antenna
per. - peritreme
pge. - post-genae
plo. - pronotal lobe
pocc. - parocciput
pp. - paraprocts
p.pr. - posterior pronotum
pr. - proctiger
prc. - prescutum
pre. - prealare or prealar bridge  
sl. - suralare  
prs. - presternum  
s.p. - salivary pump  
prsc. - prescutellum  
spl. - sternopleurite  
prx. - precocal bridge  
s.s. - salivary sac  
PS. - postscutellum  
stp. - stipes  
psc. - parascutellum  
t. - tegula  
p.ap. - metathoracic spiracle  
ta. - tarsus  
p.su. - pleural suture  
tac. - tarsocaput  
ptr. - pseudotracheae  
tbc. - tibiaceput  
pt.s. - pteropleural suture  
ti. - tibia  
pv. - pulvillus  
to. - torax  
p.vr. - posterior vertex  
tr. - trochanter  
pwp. - posterior pivot of wing  
ts. - transverse suture  
S. - scuto-scutellum  
tap. - tibial spurs  
s. - sigma  
tac. - tarsocaput  
s.b. - salivary bulb  
tt. - tibiatheca  
sbc. - subcallus  
u. - ungues  
sbl. - subalare  
u.p. - united palpigers  
scc. - scape of antenna  
u.t. - ungirtractor tendon  
S. - scutellum  
v. - vertex  
sct. - scutum  
vp. - sub-terminal plates  
s.d. - salivary duct  
vtr. - vertical triangle  
s.ep. - stem of epicranial suture  
s.f. - squama fringe

NOTE. The subscripts 1, 2, and 3 indicate the segment of the thorax on which the structures are borne. For example, e1 - pro-epimeron.
EXPLANATION OF PLATES

Plate I

Fig. 1. Head of female— anterior aspect.
Fig. 2. Head of female— posterior aspect.
Fig. 3. Head of male— anterior aspect.
Fig. 4. Head of male— posterior aspect.

Plate II

Fig. 5. Mouth parts of female, labrum and right maxilla removed— posterior aspect.
Fig. 6. Head of female— ventro-lateral aspect.

Plate III

Fig. 7. Right wing, upper surface, showing articulation with thorax.
Fig. 8. Thorax of female— left lateral aspect.
Fig. 9. Meso-thoracic leg of female showing ventral aspect of tarsus.
Fig. 9a. Dorsal aspect of tarsus, showing appendages of disti- tarsus partly withdrawn to show unguitractor tendon.

Plate IV

Fig. 10. Abdomen of female— lateral aspect.
Fig. 11. Terminalia of female— posterior aspect.
Fig. 12. Terminalia of male— lateral aspect.