# The Functional Anatomy of *Hemimerus vosseleri* Rehn, 1936 (Dermaptera: Hemimeridae)

By

Edwin V. Beylerian

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Department of Biology
American University of Beirut
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Beylerian

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## ABSTRACT

The external anatomy, muscular system, digestive tract, reproductive organs and elements of the nervous system of *Hemimerus vosseleri* are described. *H. vosseleri* presents structural modifications illicited by its parasitic mode of existence. The exoskeleton is compact. The muscles are mainly designed to increase structural unity and the leg muscles are highly developed. The digestive, reproductive and nervous systems do not differ greatly from those of forficulid dermapterans.

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# INTRODUCTION

Some 900 species of dermapterans are known with the great majority included in the suborder Forficuloidea, Bolivar 1893, known commonly as the earwigs (Chopard, 1949). The two other sub-orders are Arixenoidea, a poorly known, aberrant group of earwigs, and the Hemimerina, Burr 1911 (Rehn, 1936), a group comprising a single family (Hemimeridae) and genus (*Hemimerus*) of 8 species. The Hemimeridae are all specific ectoparasites of various species of the Giant Gambian Banana Rat, a murid of the genus *Cricetomys*, Waterhouse 1840 (Ellerman *et al*. 1953). The distribution of *Hemimerus* probably coincides fully with that of its host, which extends from East through Equatorial Africa, south to the northeastern Transvaal (Ellerman *et al*., 1953). *Hemimerus vosseleri* has been reported by various authors from the Amani, Tanganyika territory and from Mt. Mbololo, Teita District, Kenya. This species seems to be a strict parasite of *Cricetomys gambianus enguvi* Heller (Rehn, 1936).

The members of this group of insects are blind, apterous and measure about 13 mm in length. They live in close association with their host and seemingly feed on its hair and epidermal derivatives (Jordan, 1910, Rehn 1936, Chopard 1949). The offspring are born viviparously (Jordan, 1910) and maintained through a pseudo-placental formation in each ovariole (Chopard, 1949 after Heymons, 1911).

Most of publications dealing with Hemimerus species focus on ethological, taxonomical and geographical considerations. After the description of Hemimerus talpoides by Walker in 1871 (Rehn, 1936), its external anatomy was studied by Hansen in 1894 (Rehn, 1936).

In 1910, Jordan published the first series of internal anatomical notes on the genus. His paper includes a review of Hansen's taxonomic approach and of the accepted theories on the food habits of Hemimerus. The anatomical section contains a full description of the digestive tract and the excretory tubules, the nervous and the reproductive systems of H. talpoides. The findings of Hansen pertaining to the viviparity of the insect are reviewed, and the similarity in the method of attachment and the nourishment of the eggs with the method used in forficulids is pointed out.

In 1909 and 1911, Heymons (in Rehn, 1936) published his findings relatively to the various embryonic stages and viviparity of Hemimerus. In 1912 (in Rehn, 1936), he published an anatomical study on the genital apparatus and the growth of H. talpoides. A subsequent study of the hemimeroid genital apparatus was made by Burr in 1915 (Rehn, 1936).

The extensive study of the genus by J. A. G. and J. W. H. Rehn (1936) is a synthesis of previously published papers and of data collected by the authors, either from museum material or in the field. The diagnostic features of the family are given as follows:

> "Apterous, eyes absent, viviparous, cursorial; head narrow cephalad, broad caudad; thoracic tergites laterally expanded, tibiae compressed, in outline expanded subtriangular, extensor surface of tibiae, in distal half, concavely excavate for reception of tarsi when flexed; distal portion of parameres asymmetrical, with one penis and two praeputial sacs, elongate cerci not segmented, nor modified into forceps, ectoparasites on mammals."

The work includes a generalized taxonomic morphology of Hemimerus species and a thorough study of their geographical distribution. The eight known species are described individually, and a taxonomical key, based on the morphology of the terminal abdominal segments in both sexes is given. Four new species are described (including H. vosseleri), together with information on their distribution.

Chopard (1949), reviewed the morphological and diagnostic features of the genus, and presented an ethological study and a summary of the embryonic development.

In 1962, C. A. Hubbard of the Malaria Institute of Amani, Tanga, Tanzania, informed possible investigators about the availability of Hemimerus specimens and supplied the writer with the materials used in this study.

This anatomical work has for its object the elucidation through *Hemimerus vosseleri*, of some structure-to-function relationships developed for the specific ectoparasitic existence of this highly specialized group of dermapterans.

## MATERIALS AND METHODS

Adult *Hemimerus vosseleri* specimens were collected from *Cricetomys gambianus* captured at Amani, Usambara, Tanzania (Western Equatorial Africa) and preserved in 70% Ethanol.

The internal configuration of the cuticle was studied after boiling specimens in 15% aqueous KOH for 15 minutes. The digestive tract, reproductive organs and nervous system, were studied following microdissection of the organism. The musculature was studied in specimens stained *in-toto* in Grenacher's Borax-Carmine, and cleared. Dissections were performed using a stereomicroscope with incident lighting for the external anatomy, digestive, nervous and reproductive systems and with a substage lighting for the muscles.

## RESULTS

### I. EXTERNAL ANATOMY

#### The Head

The head capsule of *Hemimerus* is triangular and prognathous.

On the average it measures 3 mm transversely, 1.5 mm longitudinally and 1 mm dorsoventrally. Compound eyes and ocelli are lacking (Fig. 1, A and B).

The cranium shows very little division. It consists of a large trapezoidal vertex (Fig. 1, A, B, Vx) occupying the entire dorsal surface and extending ventrad to the boundaries of the gnathocephalon. The occipital plate (Fig. 1, B) is sharply deflected ventrad at the posterior margin of the vertex and is shallowly concave. No occipital suture is present. The occipital foramen (Fig. 1, B; OF) is dorsally overhung by a mesally notched and a distally carinate nuchal plate (Fig. 1, A. B.; Nch) which serves as an attachment for the prothoracic tergal muscles. Laterad, the occipital foramen is bordered by the posterior tentorial arms (Fig. 1, B.; TAP) and ventrally by the labial submentum (Fig. 1, B. Pmt).

The dorsal cephalic margin of the vertex extends mesally as a short, anteriorly arcuate, frontoclypeal platform (Fig. 1 A, F-C), articulating with a convex, dorso-ventrally situated labrum (Fig. 1, A. B.; Lr) the labrum bears no epipharynx entally. Laterad to the frontoclypeal platform the anterior tentorial maculae (Snodgrass 1935) (Fig. 1 A; TMA) border the cephalic margin of the parietal vertex. The antennal sutures (Fig. 1 A, B; PAS) lie laterad in the parietal region of the vertex, caudad to the anterior tentorial maculae. On the ventral aspect of the parietals a sub-antennal suture (not illustrated) extends caudad to a distance and is inflected in the wall of the cranium.

Internal Skeletal Components

The head is equipped with a large tentorium consisting of a broad rectangular corporo-tentorium with two pairs of anterior arms: the mesal anterior pair is inserted dorsally in the anterior boundary of the fronto-parietal region, determining externally the anterior tentorial maculae (Fig. 1 A, TMA). The distal anterior pair of arms branch off from the median arms and attach to the roof of the cranium directly mesad of the antennal sclerites. The posterior tentorial arms are short and stout. They delimit laterally the occipital foramen and fuse ventrally with the labial postmentum (Fig. 1 B, TAP).

The Head Appendages

The antennal sockets are located in the parietal region of the vertex (Fig. 1 A). The antennal suture delimits an ellipsoidal antennal sclerite, ventrally provided with an articular condyle around which pivots the acetabulum of the scape (Fig. 1, A, B, PAS). The scape (Fig. 1, A, B, Scp) is long, cylindrical and ventrally concave. The pedicel (Fig. 1, A, Ped) is half the length of the scape. The flagellum (Fig. 1, A, Fg) when depressed, extends down to the level of the mesothorax. It is filiform and composed of nine subsegments. The two proximal subsegments are short and the ultimate subsegment is acuminate.

The mandible (Fig. 1, B, 6, Md) bears on its base, a dorsal acetabulum (Fig. 6, x") and a ventral articular condyle (Fig. 6, x') inserted in the subgenal acetabulum of the head. This condition is due to a 90° cephalad rotation of the pleurostomal region. The abduction-adduction of the mandibles is thus in a plane parallel to the body axis, in contrast to the perpendicular plane of hypognathous insects. Two apodemes (Fig. 6, Apd 1 and Apd 2), inserted on the mandibular base, serve as attachments for the abductor and adductor muscles. The mandible is slightly convex dorsally and deplanate to concave ventrally. The mesal margin is thin and transparent. The apex bears sharp, black dentes.

The cardo of the maxilla (Fig. 1 B, Cd) articulates cephalad to the junction between the posterior tentorial arms and the postmentum. Proximally, it bears a cardinal ridge (Fig. 1 B, CdR) marking an inflection of the cuticle. The stipes (Fig. 1 B, St) forms a right angle with the cardo. Mesally, the stipes is marked by a sutural groove (Fig. 1 B, StR), serving for muscle attachment similarly to the blattid maxilla (Snodgrass, 1935).

The telopodite of the maxilla, consists of a distal galea (Fig. 1 B, 7A, Ga) and a mesal lacinia (Fig. 1 B, Lac), cephalically bearing a mesally directed concavity, fringed with a row of fine undulating hairs. The maxillary palpus (Fig. 1 B, MP) consists of two short hemispherical basal segments and three elongated subcylindrical distal segments. The hypopharynx is dorsoventrally flattened and consists of a central lobe with a pointed anterior margin, and two lateral superlinguae. The stomodaeum opens on the dorsal margin of the hypopharynx. The dorsal stomodaeal wall is continuous with the cibarium which lines the labrum.

The labial postmentum (Fig. 1 B, Pmt) is an arched structure fused caudally with the posterior tentorial arms (Fig. 1 B, TAP) and set off from the mentum (Fig. 1 B, 10, Mt) which is large and quadrate, acting as a floor for the preoral cavity. The two prementum lobes (Fig. 1 B, 10, Prm) are separated by a medial cleft. The glossae and paraglossae are fused. The labial palpi (Fig. 1 B, Lp) are reduced and three-segmented.

## The Cervical Region

The cervix is a narrow, flexible, membranous junction between the head and the prothorax, dorsolaterally bordered by the nuchal plate and laterally by a pair of lateral cervical sclerites (Fig. 2, A, B, CvSL), lodged at the cephalic pleurosternal corner of the prothorax. The proximal lateral cervical sclerite and the distal lateral cervical sclerite are joined by a narrow intersegmental membrane. The internal surface of the proximal sclerite bears a longitudinally directed keel assisting in cervical muscle attachment. The cervix is bordered ventrad by a large triangular ventral cervical sclerite (Fig. 2 A, B, 15, CvSV) joining the postmentum to the prosternum.

## The Thorax

This region is slightly greater than 40 per cent of the total body length. The nota are large and extended laterally as definite scutella. The sterna are narrow and deplanate. There is a strong tendency toward dorso-ventral flattening.

Prothorax.- The scutellum is the largest of the thoracic terga. It is broadly convex, flexing ventrally at its anterior margin. The caudal margin is concave and overlays part of the mesonotum. (Fig. 2 A, Scl) The pleuron is diagonally transected by the pleural suture (Fig. 2 A, A) bearing in its center an apophyseal pit. The anterior margin of the episternum (Figs. 2 A, B, Eps 1) is flexed entad. The extensive precoxal ridge (Fig. 2 A) bears internally, near the pleurosternal junction, a long sclerotized and flexible bar (Figs. 2 A, B PB) articulating anteriorly with a ventral extension of the internal ridge corresponding to the anterior marginal flexure of the Episternum (Fig. 2 B). Posteriorly the pleural bar articulates with the anterior ventral margin of the coxa. The prosternum (Figs. 2 A and B, Stl) narrows sharply caudad to the precoxal ridge.

It overlaps the prothoracic spinasternum and part of the mesonotum posteriorly. Its posterior margin is slightly convex.

A depression in the caudo-mesal region of the sternal surface marks the sternal apophysis externally. Internally, the sternal apophysis and the pleural apophysis fuse into a single pleurosternal brace (Fig. 2 B, PSA 1) the internal ridge of the pleural suture flexes ventro-cephalically, thus internally reinforcing the anterior marginal flexure of the Episternum. The first spiracle lies deep in the intersegmental membrane between pleuron 1 and 2 (Fig. 2 A Spr).

Mesothorax.- Transversely, tergum 2 forms the broadest scutellum of the thorax (4.5 mm average). Longitudinally it is smaller than scutellum 1. The antecostal element forms a slight phragma where tergal muscles are inserted. The episternum (Figs. 2 A, B, Eps 2) is entally deflected along a line extending from the caudal margin of the precoxale to the anterior pleurotergal margin. The flexure is sharp, reaching $90^0$ dorsally where the episternal surface faces cephalad. The epimeron (Figs. 2 A, B, Epm 2) is flexed entally on its caudal margin along a line extending from the coxopleural articulation to the posterior tergopleural corner. A large arcuate trochantin (Figs. 2 A, B, Tn 2) fringed with long setae, articulates with the ventral coxal margin. The prothoracic spinasternum (Fig. 2 B, Sp 2) is free and bears a heavy spina. The mesosternum is rectangular, with uplifted anterior corners (Figs. 2 A, B, St 2). Its posterior, slightly convex margin, covers the anterior region of the metasternum. The mesothoracic spina (Fig. 2 B, Sp3) is fused in the caudal region of the mesosternum. It is situated on an internal ridge which curves cephalad joining the base of the sternal apophysis (Fig. 2 B, SA2), an extensive chitinous structure with a long anterior arm. The cephalic end of the internal pleural ridge flexes ventrally along the inner episternal margin (Fig. 2 B, PA2). The triangular pleural apophysis is externally marked by a narrow apophyseal slit along the pleural suture (Fig. 2 A, B). The second thoracic spiracle is situated in the intersegmental membrane between pleurites 2 and 3 (Fig. 2 A, Spr).

Metathorax.- The metathoracic scutellum (Fig. 2 A, Sc3), is the smallest of the thoracic nota. The cephalic margin is inflected as a small phragmal ridge. The lateral margins are inflected laterally, covering part of the pleurite (Figs. 2 A, B, St3) the pleurite is small and externally undifferentiated. The pleural suture (Fig. 2 A, C) is a broad, sparingly sclerotized band. The precoxale found in the preceding two segments is replaced by an upward extension of the anterior lateral margins of the metasternum, ending entally a small distance beyond the margin of Episternum 3. The metasternum (Figs. 2, A, B, St3) is a short, trapezoidal and slightly convex segment its posterior margin overlaps partly the first abdominal sternum. The metathoracic coxa (Fig. 2 A, Cx3) articulates with a coxopleural condyle and ventrally with a large trochantin (Fig. 2 A, B, tn3) fringed with long setae. Internally the sternal apophysis (Fig. 2 B, SA3) is subquadrate and distally bifurcate. The internal ridge of the pleural suture (Fig. 2 B, PA3) flexes at the cephalic dorsal angle of the episternum, reinforcing its margin. It does not give rise to a pleural apophysis.

The thoracic legs are short, homonomous, unspecialized and compressed (Fig. 4) the coxae are large, with a caudal meron, extending cephalad to a pointed sclerotized lobule limiting the anterior rotation of the leg. The trochanters are unspecialized. The femur and tibia are equal in size. The latter is triangular in outline, with a ventral excavation bordered on both sides with a row of long setae. The tarsal segments can be reflexed within the tibial excavation. The first two tarsal segments are short, heavy with large fleshy pads. The unguiferous segment is provided with two claws and a central arolium. The sizes increase and the proportions are somewhat altered from the prothoracic to the metathoracic legs.

The Abdomen

This region is about one-half of the total body length, with a number of sexually dimorphic characters.

In the female, eight tergites and six sternites are visible. Five pairs of abdominal spiracles are located in the intersegmental membranes along the dorsopleural line, between the metapleurite and abdominal segment II, and between the abdominal segments II-III, III-IV, IV-V and V-VI. Tergite I overlays epimeron 3 and has no corresponding sternum (Fig. 2 A, Tg1). The first complete abdominal set, is tergite II and sternite II (Fig. 2 A, Tg2, ASt2). Rehn (1936) describes the tergites as "extending mesad on (the) ventral surface" and the sternites as "extending almost the full width of (the) venter". Present material shows clearly however, that the two abdominal components are equal in size and both extend laterad up to the dorsopleural line. The last complete abdominal segment is the sixth. Tergite VII extends caudad and ventrad, overlapping the eighth and the ninth tergites. The posterior margin of tergite VII partially covers tergite X, which fuses with the dorsal surface of tergite XI, a large, trigonal and caudally pyriform sclerite, with a deep ventral concavity (Fig. 5, XI Tg). The antero-ventral margin is supplied with a flange interlocking with sternite VII.

The seventh sternite is a broad, rectangular plate (Fig. 3, A) with a caudal submarginal carina and a rather deep submarginal groove, covering the abdomen posteriorly and protecting the anus and the external vaginal opening (Rehn, 1936). The eighth tergite (Fig. 5, VIII Tg) is a small lateral sclerite situated immediately caudad to the sixth sternite (VI st). Sternite VIII (VIII st) is divided into a pair of rectangular sclerites. The ninth tergite (IX Tg) is immediately caudal to tergite VIII. Sternite IX is modified into a pair of fleshy lobes, sclerotized on their distal margins and limiting the vaginal opening (IX st). Tergite X (X tg) is directly caudal to the ninth and extends dorsad to fuse with the eleventh segment. The eleventh and tenth tergites encircle a socket into which the bases of the cerci are inserted. The cercus is a hollow unsegmented extension, provided with deeply embedded setae. The ventral part of the socket is covered by the Xth sternite (X st) with which the cercus articulates.

In the male, the abdomen consists of eleven visible tergites and nine visible sternites. The segments I and II are similar to those of the female in their relationship with the thorax. Segment VIII constitutes the last undifferentiated set. The tergites proceed to XI, which occupies a position similar to that of the female, except that its posterior end is broadly arcuate rather than trigonal. Sternite IX, which is the last visible abdominal sternite (Fig. 3 B, 22 A, IX St), can be considered as the Xth actual sternite, if the two laterally inserted processes (Fig. 22 A, B, Br) which serve for the attachment of the penis retractor muscles are considered to be vestiges of a ninth sternite. The caudal margin of the ninth visible sternite (Fig. 3 B, 22 A) is divided into two caudally convergent lines. The dextral line is more sclerotized than the sinistral, and it terminates with a sinistrally curved finger-like process. The cerci are inserted on tergum XI along a cephalo-lateral notch.

## II. INTERNAL ANATOMY

### The Muscles

Although the muscles of Hemimerus seem to be generalized in the majority of cases, there is an important fraction of muscles showing interesting modifications and adaptations. The muscles of dermapterans having not been studied significantly so far (Chopard, 1949), it was not possible to establish useful parallels between hemimerids, forficulids, arixenoids and other orders.

### The Muscles of the Head Region

(The stomodaeal and pharyngeal muscles will be considered with the digestive tract).

The muscularization of the labrum provides it with an extensive production-reduction movement (Fig. 9). The compressor of the labrum (53) is a single median muscular bundle connecting the walls of the labrum. The dorsal labral productor (51) originates centrally on a ridge of the anterior epicranial region directly cephalad to the anterior margin of the corporotentorium. It inserts on the posterior dorsal margin of the labrum and corresponds to the anterior labral muscles in hypognathous insects as described by Snodgrass (1932). A pair of elongate ventral labral reductors (52) corresponding to the posterior labral muscles of hypognathous insects as described by Snodgrass (1932) inserts on either side of the posterior ventral labral margin and originates distally to the dorsal labral productor.

The muscles of the mandible (Fig. 6) comprise two categories classified as adductors and abductors. The adductor of the mandible (26) originates in a mesal concavity of the occipital surface, directly distal to the occipital foramen and inserts on a slender mesal apodeme (Apd 1), fused with the mandibular base. The abductor of the mandible (27, a and b) consists of two fiber trunks inserted on a filiform apodeme of the mandible (Apd 2) and originating on the lateral dorsal margin of the occipital plate.

The hypopharynx is provided with a retractor muscle (not illustrated) inserted in the center of its median lobe and originating on the center of the corporotentorium (ventral surface).

The basal muscles of the maxilla (Fig. 7, A) are prominently strong in accordance with the large size of this appendage. The adductor of the cardo (21) is a broad and flat muscular bundle arising on the ventral lateral margin of the tentorium and inserting distad to the cardinal ridge. A massive stipital adductor (20) arises immediately ventrad to the adductor of the cardo and inserts on the stipital ridge (Fig. 1 B, StR). The posterior rotator of the maxilla (22) is a large, fan-shaped fiber bundle inserting on a marginal lip of the cardo and originating from the occipital plate proximad and ventrad to the mandibular adductor. A slender and prominent cranial flexor of the lacinia (23) flexes the lacinia proximally. It originates on the occipital plate, directly distad to the posterior rotator of the maxilla and inserts on the internal margin of the lacinia.

The maxillary telopodite contains two large muscles: A thin stipital flexor of the lacinia (24) which flexes the lacinia distad, originates on the stipital ridge and inserts on the basis of the lacinia and a flexor of the galea (25) arising directly cephalad to the stipital flexor of the lacinia and inserting on the ental margin of the galea.

The maxillary palpus is provided with three types of muscles (Fig. 7 B): Arising on the stipital wall, the levator of the palpus (104) inserts on the external basal margin of the second palpal segment. The depressor of the palpus (105) originating on the ventral side of the stipital ridge, inserts on the proximal margin of the second palpal segment. The small palpal flexors (106 and 107) arise on the third and fourth palpal segments respectively and insert on the proximal margins of the segment following their origin.

The caudal fusion of the postmentum to the tentorium dispells the necessity of suspensorial labial muscles which are lacking. The other labial muscles (Fig. 10) are present following the limited range of motility of this appendage. A pair of short and stout labial adductors (46), inserted on the wall of the mentum, originates from the ventral surface of the tentorium. The flexors of the postmentum (45) originate on the caudal margin of the postmentum and insert on the anterior sutural ridge separating the mentum from the prementum. A pair of flexors of the prementum (50) connects the anterior labial suture to the dorsal wall of the premental lobes.

Although the labial palps are reduced (Rehn 1936, Chopard 1949), their basal musculature is complete (Fig. 10). The adductors of the labial palpi (47) originate dorsad to the caudal margin of the palpifer lobe and insert on the proximal caudal margin of the first labial palpal segment. The tiny abductors of the labial palpi (48 and 49), both arising ventrally on the mento-premental suture, insert respectively on the caudal margins of the labial segments 1 and 2.

The antennal muscles (Fig. 8) permit a variety of movements to the antennal base. The anterior rotator of the scape (28) is a slender triangular muscle inserted on the ventral margin of the scape and connected cephalad to the distal anterior pairs of tentorial arms. The posterior rotators of the scape (29 and 30) originate caudad to the distal anterior pairs of tentorial arms and converge to insert on the proximal dorsal margin of the scape. A bifurcate anterior rotator of the pedicel (31 and 32) inserts on the proximal margin of the pedicel and originates on two points of the scape. Its function is to reduce and rotate slightly the pedicel. The origin of the levator of the pedicel (33) is the proximal submarginal ridge of the scape and its insertion is on the proximal margin of the pedicel. The short depressor of the pedicel (34) connects the ventral proximal margin of the pedicel to the ventral wall of the scape.

The Muscles of the Thorax

The thoracic muscles are closely related to the general pattern of insect muscles. The main characteristics are of pterygote thoracic muscles. However the tergosternal muscles are lacking, the tergal muscles are reduced and the alar components of the tergopleural muscles are absent.

The tergal longitudinal median muscles (Fig. 15) consist in the prothorax of a pair of slender fiber tracts originating from the first phragma and inserting on the posterior margin of the nuchal plate (Fig. 1 B, Nch). These muscles serve as levators of the head capsule (Fig. 15, 55). In the mesothorax (93), these muscles are flattened and extend medially as a pair from the second phragma to the caudal surface of the first phragma. In the metathorax (95) they are developed into two broad bands joining the third phragma to the caudal surface of the second phragma and they cover the notal region, leaving two lateral zones of attachment for the coxotergal muscles.

The oblique lateral muscles of the tergum (Fig. 15) show various degrees of development. In the prothorax a large fan-shaped muscle (54), extends from the first phragma where it originates distal and dorsal to the longitudinal muscle and inserts on a prominent medial ridge of the pronotum. Similarly, the mesothoracic oblique muscle (92) arises on the second phragma and inserts mesally on a slight notal inflection, but it is considerably narrower than the prothoracic oblique and restricted to the caudal region of the dorsum. The oblique lateral muscle of the metathorax (94) is confined to a thin and narrow bundle of fibers arising on the third phragma and inserting caudally on the medial notal region, directly on the inner scutellar surface.

In the prothorax, the anterior and posterior tergopleural muscles (Fig. 11 B, 68 and 66) are two relatively thick muscular sheets connecting the dorsal surface of the pleural ridge to the anterior distal portion of the pronotum. In the mesothorax (Fig. 12 B and C), the broad and massive posterior tergopleural muscle (87) connects the posterior half of the pleural ridge to the distal margin of the mesonotum. The sheet-like anterior tergopleural muscle (89) connects the cephalic surface of the pleural arm (PA2) to the anterior distal portion of the mesonotum.

The category of tergosternal muscles (Snodgrass, 1935) (Fig. 15) has been used to classify the two muscles of the lateral cervical sclerite. Their origin, however, was not ascertained.

The posterior adductor of the lateral cervical sclerite (59) originates partly on the surface of the proximal sclerite and partly on its keel (see above, thorax external anatomy) and inserts cephalad and proximad to the anterior tergosternal muscle of the prothorax (Fig. 11 B, 68). The anterior cranial reductor (58) arises on the distal lateral cervical sclerite and inserts on the ventro-caudal margin of the nuchal plate.

The prothorax is devoid of pleurosternal muscles. From the posterior surface of the mesothoracic pleural arm, a triangular pleurosternal bundle (Fig. 12 B, 88), extends to attach on the anterior arm of the sternal apophysis (SA2). A thin ligament joins the anterior sternal flexure of the metathorax (Fig. 13C, 103) to the internal episternal surface.

The ventral intersegmental muscles are numerous and large, providing a strong intersegmental linkage for the thoracic segments. In the prothorax, the two longitudinal ventral muscle pairs are inserted on the posterior margin of the tentorial bridge, directly mesad to the posterior tentorial arms. The long pair of sterno-cranial reductors (Fig. 11 A, 15, 56) extends from the sternal arm of the pleurosternal brace (PSA 1) to the tentorium. The cervico-cranial flexor (Fig. 11 A, 15, 57) originates on the caudal margin of the ventro-cervical sclerite (Fig. 2 A, B, CvSV) and inserts on the tentorium, directly mesad to the sterno-cranial reductor.

The mesothoracic longitudinal ventral muscles (Figs. 12 A, 15) consist of a single median interspinal muscle (78) connecting the prothoracic and mesothoracic spinae and of a pair of interapophyseal muscles (80) joining the prothoracic and mesothoracic sternal apophyses. The metathorax (Fig. 13 A, 15) is provided with two longitudinal ventral muscles: The interapophyseal muscle (83) connects the mesothoracic and metathoracic sternal apophyses. The broad, massive thoraco-abdominal muscle (96) connects the posterior margin of the metathoracic sternal apophysis to the first abdominal sternite (Sternite II). The oblique ventral muscles are represented in the mesothorax by a ligament (Fig. 15, 79) establishing the junction between the mesosternal apophysis and the prothoracic spina and by a short ligament (81) connecting the mesosternal apophysis to the mesothoracic spina. In the metathorax, (Fig. 13, 15) the oblique ventral muscle (82) connects the spina of the mesothorax to the metasternal apophysis.

The muscles of the leg base are prominent and outstanding in the thorax. The tergal promotor of the leg rotates the coxa cephalad (Snodgrass, 1927). This muscle is enlarged in the prothorax (Fig. 11 B) where it consists of two large fiber bundles (62, 63) inserting on the anterior coxal margin and originating in the caudal lateral corner of the tergum. The distal bundle (63) arises distal to the posterior tergopleural muscle. In the mesothorax, the tergal promotor of the leg (Fig. 12 A, 85) is single and occupies a similar position although originating more caudally. The same is true for the metathoracic tergal promotor (Fig. 13 A, 98). The tergal remotor of the leg, rotates the coxa caudad. In the prothorax, it consists of two, rather large fiber masses, (Fig. 11 A, 60 and 61) originating on the cephalo-lateral corner of the tergum and inserting on the caudal coxal margin. It occupies a similar position in the mesothorax (Fig. 12 A, 84) and in the metathorax (Fig. 13 A, 97) although it is not branched in those two segments. The pleurocoxal muscles of the prothorax include two bundles inserted on the anterior pleurosternal coxal margin and aiding in the promotion (or anterior rotation) of the leg. The proximal branch (Fig. 11 B, 64) originates on the posterior facet of a flange extending from the junction of the pleural apophysis to the sternal apophysis. The distal branch (65) passes distally to the sternal arm and originates on the anterior surface of the episternum. In the mesothorax (Fig. 12 C) this muscle category comprises two discrete muscular bundles, both originating on the anterior episternal flexure. The pleural promotor of the leg (90) is inserted on the anterior pleural margin of the coxa and the trochantinal promotor of the leg (91) inserts on the anterior trochantinal margin. In the metathorax the pleural promotor (102) and the trochantinal promotor (101) are similar to the mesothoracic correspondents, the origin of the latter being more ventral. The adductor muscle of the coxa connects the ventral coxal margin to the sternal apophysis. In the mesothorax

(Fig. 12 B, 86) it is single. In the metathorax, it is double-branched, with an anterior element inserting on the trochantin (100) and a posterior one, inserting on the ventral coxal margin (99).

Three muscles of uncertain origin connecting various parts of the prothoracic pleurite (Fig. 11, B, C) have been classified under the category of pleural muscles. Two of those muscles connect the anterior facet of the pleurosternal flange to the posterior surface of the episternal flexure (67 and 69). The third muscle (70) tiny, fan-like, originates distad to the second branch of the pleurocoxal promotor (65) and inserts on a filiform apodeme fused caudally with the pleural rod (Fig. 11 C, 70).

The description of the muscles of the leg telopodite is centered on the muscles of the mesothoracic leg. The telopodite musculature of the hemimerid leg follows closely the generalized musculature pattern of an insect leg as described by Snodgrass (1935). The trochanter is provided with two muscles: A depressor of the trochanter (43) arising ventrally from the coxal base and inserting on the proximal dorsal trochanteral margin, and a levator of the trochanter (44) arising on the dorsal coxal margin and inserting on the dorsal proximal trochanteral margin. The femur, is provided with a stout femoral reductor (41) occupying all the trochanteral cavity, originating on the proximal peripheral margin of the trochanter and inserting on the proximal femoral lip. The origin of the tibial depressor (38) is the proximal dorsal margin of the femur; its insertion is the proximal ventral rim of the tibia. The tibial levator (39-40) has a ventral branch which originates along the proximal dorsal wall of the femur and inserts on the lateral proximal margin of the tibia (39) and a dorsal branch (40) originating along the crest of the femoral wall and inserting directly dorsad to the preceding levator. The tarsus is supplied with a depressor (37) and a levator (36) originating in the tibia and inserted on its proximal margin. The tarsal retractor (35) arises in the posterior femoral surface and inserts on the unguitractor plate (utr) of the ultimate tarsal segment (Ps), through a long tendon (O) which passes through the femur, tibia and the penultimate tarsal segments.

Abdominal Muscles

The muscularization of the abdominal segments is simple and generalized. Each segment possesses paired interno- and externo-dorsal, interno- and externo-ventral and lateral muscles, with only a single compressor element per segment. The spiracular muscles could not be seen. The predominance of retractor and compressor muscles (Snodgrass, 1935) indicates a high degree of cohesion between the abdominal segments. The terminal portion of the abdomen in the female contains a set of four muscles that move the cerci transversely and longitudinally. These muscles all insert on an apodeme extending from the proximal margin of the cercus (Fig. 19). These muscles have various origins: The cercal abductor (71) is the largest cercal muscle and it arises from the caudal wall of the eleventh tergite. The origin of the cercal levator (72) is on the anterior margin of the sixth sternite. The cercal adductor (73) originates on the anterior margin of the seventh tergite. The origin of the cercal depressor (74) is on the posterior margin of the seventh tergite.

The Digestive Tract (Fig. 16)

The food of Hemimerus is still in doubt. The type of digestive tract found seems to indicate an omnivorous diet. There is a large absorptive and storage surface but no definite clue indicating some specialization.

The stomodaeum opens on a buccal cavity situated caudad to the cibarium and ventrally delimited by the hypopharynx. Caudally, the stomodaeum extends as a pharynx lying on the dorsal surface of the tentorium. The walls of the pharynx consist of a series of longitudinal and circular muscles. The pharyngeal dilators can be divided into two groups: The dorsal dilators anchored at various points of the epicranium and comprising three pairs of anterior muscles inserted directly caudad to the buccal opening and one pair of posterior muscles originating from the epicranium somewhat cephalad to the posterior tentorial margin. The ventral dilators comprise one pair of muscles connecting the anterior ventral pharyngeal wall to the anterior margin of the tentorium, another pair linking the pharynx to the center of the corporo tentorium and a third caudal pair connecting the pharynx to the posterior tentorial margin at the level of the last dorsal dilator.

Caudally the pharynx expands as a large crop (Oe) occupying the whole thorax. The ingluvial intima is finely plicate. The crop abruptly narrows down to a short proventriculus (PrV) at the level of the first abdominal segment. The proventriculus has six longitudinal folds, each with a row of minute teeth. The stomach (Sm) occupies the abdominal cavity, to the level of the fourth tergite, where it loops dextrad and continues as the rectum (Rt). The malpighian tubules (MT) arise from this site and they are grouped in two pairs of bunches, one dorsal and one ventral, each containing five tubules.

At the level of the last two abdominal segments, the rectum expands to a small bulbous tube with four rectal pads. The anus opens caudad to the vagina in the female (Fig. 5).

The Reproductive System (Fig. 17)

In the female, the ovaries occupy the anterior two thirds of the abdomen and may extend anteriorly to the level of the meta-thorax. Each ovary has seven ovarioles (Or) connected by an egg duct (Ovd). The eggs develop in-situ (Chopard, 1949), the posterior-most being the most developed. One or two advanced nymphs can be found in the posteriormost ovarioles. The two oviducts expand caudad and meet mesally to form a vagina (Vag) which passes ventrally to the rectum and opens cephalad to the anus beneath the paired lobes of the ninth sternite (Fig. 5).

In the male, paired testes (Ts) lie at the base of the thorax. Each testis consists of two densely coiled follicles opening jointly into a vas deferens (VD) which extends to the anterior of the stomacal loop and then curves upward to the level of the testes where it expands as a seminal vesicle (SV) (Jordan, 1910). The two seminal vesicles open into a coiled reservoir (Fig. 18, 21 A, Res), the ventral part of which gives rise to an ejaculatory duct (Fig. 21 A, ED) connected to the copulatory organ, a sheath-like tube comprising two peripheral layers of circular muscles and a central layer of longitudinal muscles (75, 76 and 77), the core of which is traversed by the ejaculatory duct. The muscular tube has a thin, chitinous dorsal lever (Lev) inserted at the base of the ejaculatory duct. The borders of the lever are heavily sclerotized and continuous with the internal surface of the parameres (Par 1 and 2), two long sclerites ensheathing the ejaculatory tube and strongly united ventrad. The caudal end of each paramere is curved sinistrad, the left paramere is longer (Par 2) than the right one (Par 1). Anteriorly, the parameres separate into two lobes serving for the insertion of the copulatory muscles. The two large protractors of the penis (79) arise on the posterior portion of the ninth sternite (IX St) and insert on the dorsal surface of the anterior lobe of each paramere. (Fig. 22, Band C) A pair of retractors of the penis (78) arising on the hemisternites preceding sternum IX (Br) inserts on the lateral ventral surface of the anterior lobe of each paramere. Through the interparameral space, the muscular copulatory tube proceeds caudad and bifurcates as an eversible penis provided internally with a bifurcated sperm duct, continuous with the ejaculatory duct, (Fig. 20) a condition also found in members of the order Dermaptera *s. str.*

## The Nervous System

In the female, the nervous system consists of two cephalic supraoesophageal and suboesophageal ganglia, three thoracic ganglia and six abdominal ganglia. The possibility of the male having a larger number of ganglia due to its more numerous segments, was not investigated, due to the lack of material.

## DISCUSSION AND CONCLUSIONS

The relationship of Hemimerids to Dermaptera is unquestionable. The number of tarsal segments is the same, the abdomen has the same number of tergites and sternites. The mouthparts are similar except for the increase of size of the mentum and the stipes in Hemimerus sp. and for the reduction of the labial palpi. The digestive systems between hemimerids and dermapterans are essentially comparable. The male reproductive organs are disposed along the same pattern and are also provided with parameres. Both forficulids and Hemimerids are viviparous. Finally the nerve cord has the same number of ganglia (Chopard, 1949). The Hemimerids, however are extremely specialized. This obscures their relationship with the group and sets them apart.

The main trends of this specialization connected with the ectoparasitic life of Hemimerus vosseleri are a better structural unity and compactness and an improved motility due to strong and abundantly muscularized legs.

The structural uniformity of Hemimerus is reflected by the streamlined body outline with the head and ultimate tergite tapering off smoothly. The lateral margins of the abdomen also taper off, thus reducing peripheral friction.

Although the head is relatively mobile on its flexible cervix, its margins do not exceed the lateral limits of the thorax.

The lateral outline of the head makes a single continuous line with the first notum. The labrum, situated frontally, is convex, presenting a rounded angle of attack and efficiently protecting the mouthparts. The antennae can be depressed along the body line. The eyes and ocelli, too delicate for the environment of Hemimerus, are lacking. The head capsule is light and flexible due to the suppresion of nearly all the sutural ridges. The tentorium however, greatly reinforces it through its oblique orientation (dorsal, anteriorly ventral posteriorly) and by supporting the flexure points.

The posterior overlapping of the nota, protects the delicate intersegmental membranes. The lateral extension of the first two nota deflects the coarse hair of the host from the pleuron, thus allowing the free movement of the legs. The thoracic spiracles are sunken deep in the intersegmental membranes. The abdominal spiracles are concealed by the lateral tergal extensions.

The role of the seventh sternite in the protection of the vaginal entrance and of the anus, and the correlation of the tightness of the closure with the coarseness of the host's hair has already been discussed by Rehn (1936). This is extremely accurate as a taxonomical means and points also to the host specificity of Hemimerus.

The intersegmental muscles are strong and extensively developed such as the extensiveness of the tergal and ventral thoracic muscles and the predominance of retractor and compressor muscles in the abdomen.

The legs of Hemimerus are stout and offer large surfaces of attachment for the muscles of the telopodite. The coxal muscles, especially promotors and remotors are the most prominent in the thorax and occupy the largest volume. The remotors are larger than the promotors, and the promotion movement is limited by the meron of the coxa which bumps anteriorly on the pleurocoxal articulation. The pleurocoxal muscles allow a variety of movements and their extensive development has promoted the development of anterior episternal flexures. An interesting point is also the fact that the tarsi can be flexed within the concavity of the tibia.

The internal organs do not differ basically from the forficulids. The most significant modifications are encountered in the muscles and the exoskeletal features of Hemimerus.

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## List of Abbreviations

### Figure 1

| | | |
|---|---|---|
| Cd | = | Cardo |
| CdR | = | Cardinal Ridge |
| F-C | = | Fronto-Clypeal Region |
| Fg | = | Flagellum |
| Ga | = | Galea |
| Lac | = | Lacinia |
| LP | = | Labial Palp |
| Lr | = | Labrum |
| Md | = | Mandible |
| Mp | = | Maxillary Palp |
| Nch | = | Nuchal Plate |
| OF | = | Occipital Foramen |
| "OP" | = | Occipital plate |
| PAS | = | Antennal Sclerite |
| Ped | = | Pedicel |
| Pmt | = | Postmentum |
| Prm | = | Prementum |
| Scp | = | Scape |
| St | = | Stipes |
| StR | = | Stipital Ridge |
| TAP | = | Posterior Tentorial Arm |
| TMA | = | Anterior tentorial Macula |
| Vx | = | Vertex |

### Figure 2

| | | |
|---|---|---|
| A | = | Pleural Prothoracic Suture |
| Ast | = | Abdominal sternile |
| B | = | Pleural Mesothoracic Suture |
| C | = | Pleural Metathoracic Suture |
| CvSL | = | Lateral Cervical Sclerites |
| CvSv | = | Ventral Cervical Sclerite |
| Cx | = | Coxa |
| Epm | = | Epimeron |
| Eps | = | Episternum |
| PA | = | Pleural Apophysis |
| PB | = | Pleurosternal Bar |
| PsA | = | Pleurosternal Brace |
| SA | = | Sternal Apophysis |
| Sc | = | Scutellum |
| Sp | = | Spina |
| Spr | = | Spiracle |
| St | = | Sternum |
| Tg | = | Abdominal Tergite |
| Tn | = | Trochantin |
| 1 | = | Prothorax |
| 2 | = | Mesothorax |
| 3 | = | Metathorax |

Figure 5

| | | |
|---|---|---|
| Ci | = | Cercus |
| St | = | Sternite |
| Tg | = | Tergite |

Figure 6

| | | |
|---|---|---|
| Apd 1 | = | Mesal Apodeme |
| Apd 2 | = | Distal Apodeme |
| X' | = | Articulation Condyle of Mandible |
| X" | = | Acetabulum of Mandible |

Figure 7

| | | |
|---|---|---|
| Pl | = | Palp |
| Sp | = | Spina |

Figure 14

| | | |
|---|---|---|
| Cx | = | Coxa |
| Fe | = | Femur |
| O | = | Unguitractor Tendon |
| Ps | = | First tarsal segment |
| Ti | = | Tibia |
| Tr | = | Trochanter |
| Un | = | Claw |
| Utr | = | Unguitractor plate |

Figure 16

| | | |
|---|---|---|
| MT | = | Malpighian Tubules |
| Oe | = | Crop |
| Prv | = | Proventriculus |
| Rt | = | Rectum |
| Sm | = | Mesenteron |

Figure 17

| | | |
|---|---|---|
| Or | = | Ovariole |
| Ovd | = | Oviduct |
| Vag | = | Vagina |

Figure 18

| | | |
|---|---|---|
| Lev | = | Lever |
| Par 1 | = | Dextral Paramere |
| Par 2 | = | Sinistral Paramere |
| Pen | = | Penis |
| Res | = | Sperm Reservoir |
| Sv | = | Seminal Vesicle |
| Ts | = | Testis |
| VD | = | Vas defereus |

Figure 21

| | | |
|---|---|---|
| ED | = | Ejaculatory Duct |
| Res | = | Reservoir |
| SE | = | Dorsal sperm chamber |

Figure 22

| | | |
|---|---|---|
| Br | = | Hemisternites for attachment of Retractor muscles |

Figure 1. External Anatomy of the Head, 26x.

A. Dorsal View

B. Ventral View

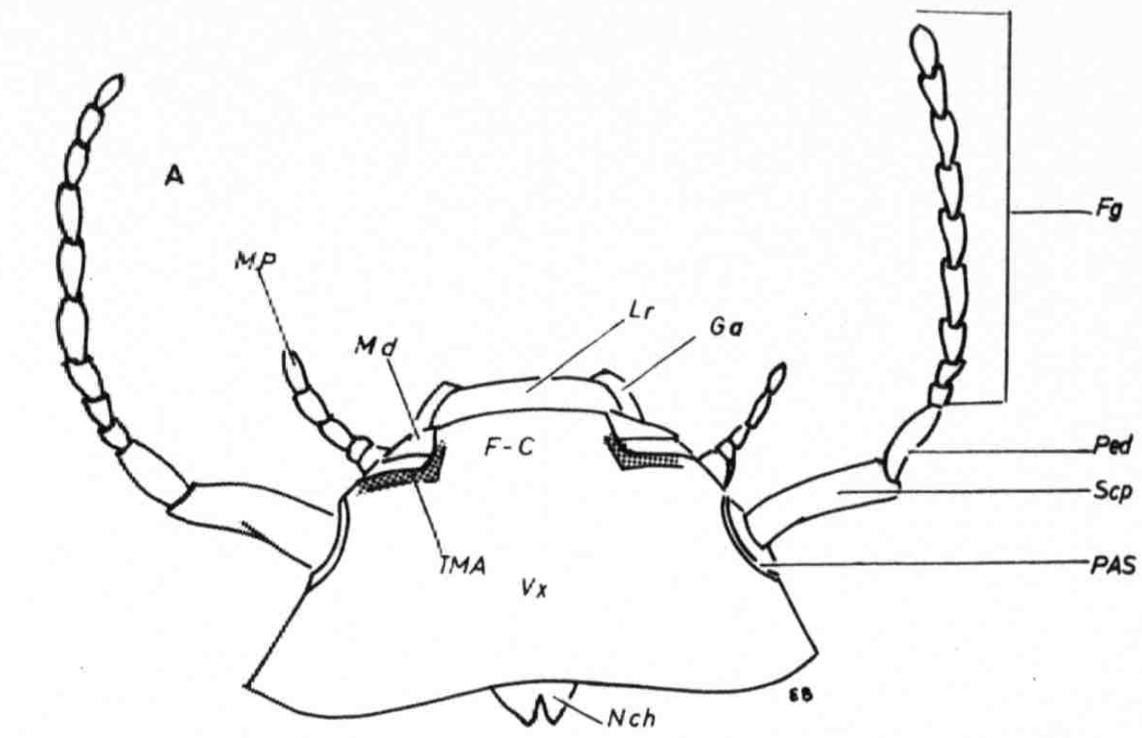



FIG.1

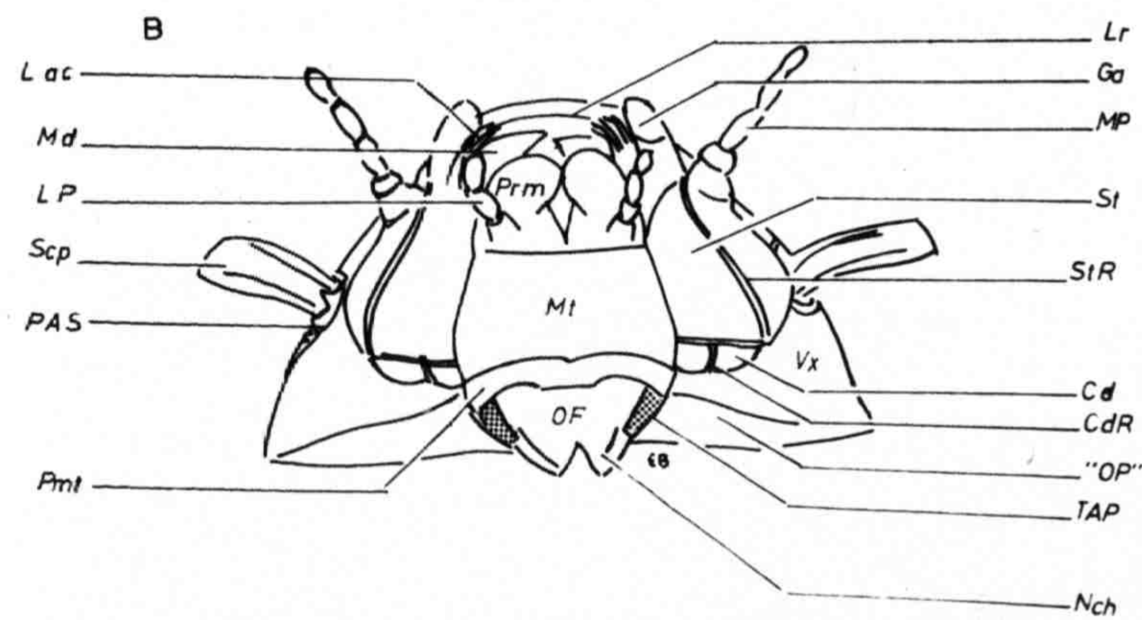


Figure 2. Anatomy of the Thorax, 28x.

A. Lateral View

B. Ental View

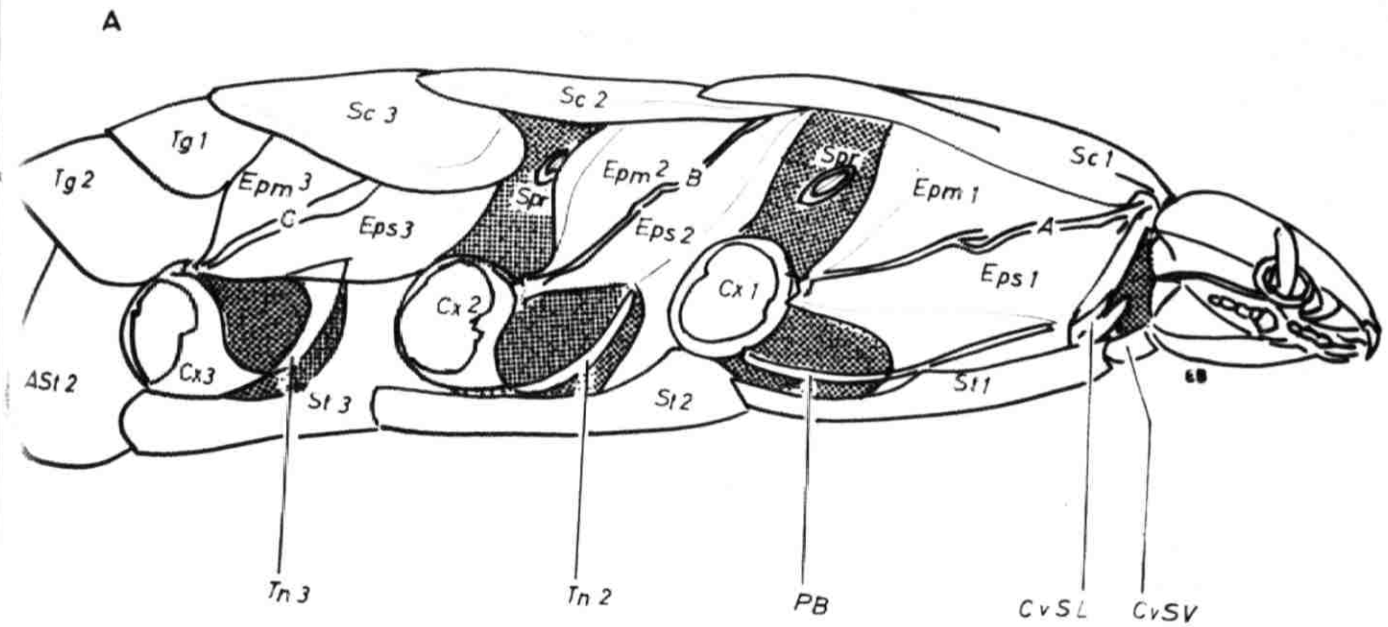



FIG.2

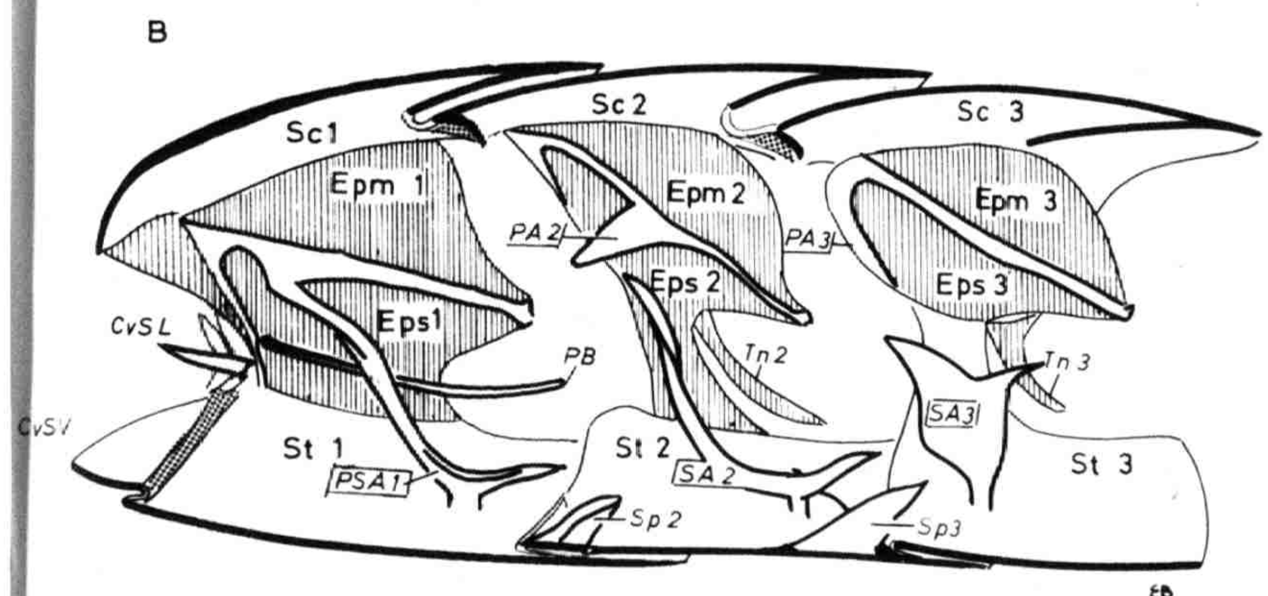


Figure 2. Anatomy of the Thorax, 28x.

A. Lateral View

B. Ental View

A

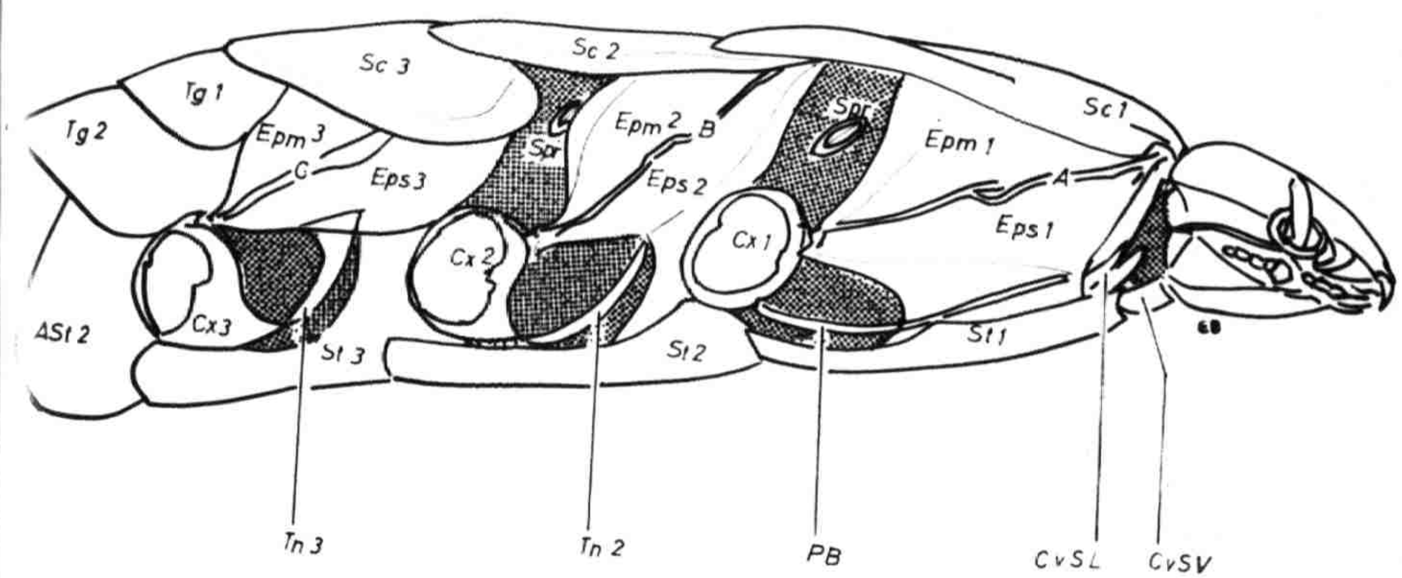



FIG.2

B

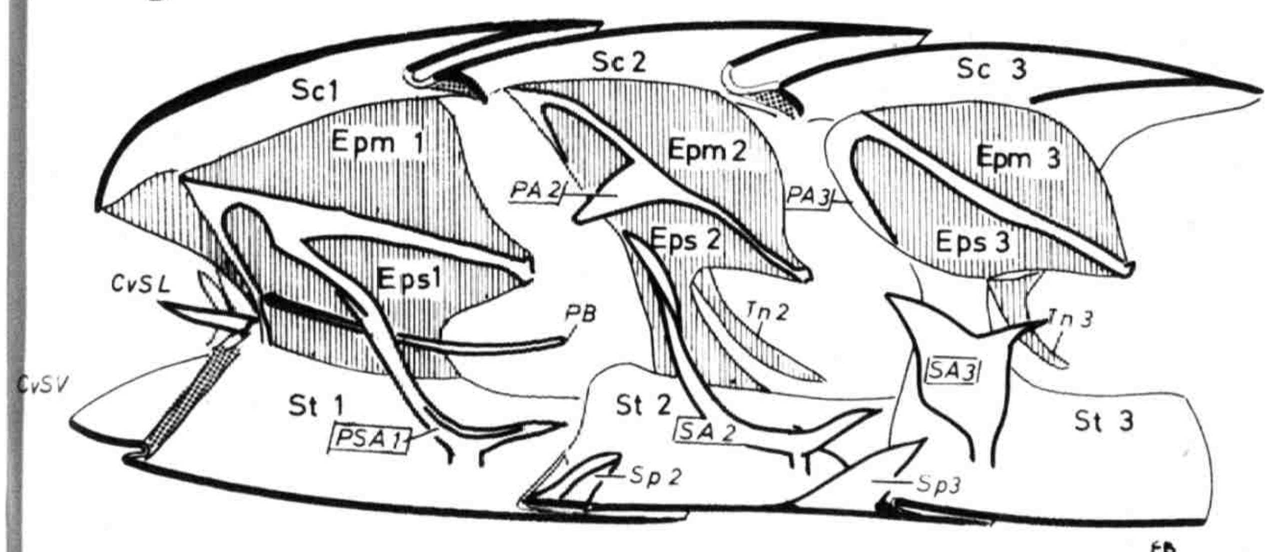


Figure 3. Ultimate Abdominal Segments, Ventral View, 23x.

A. Female

B. Male

Figure 4. Left Prothoracic Leg, 80x.

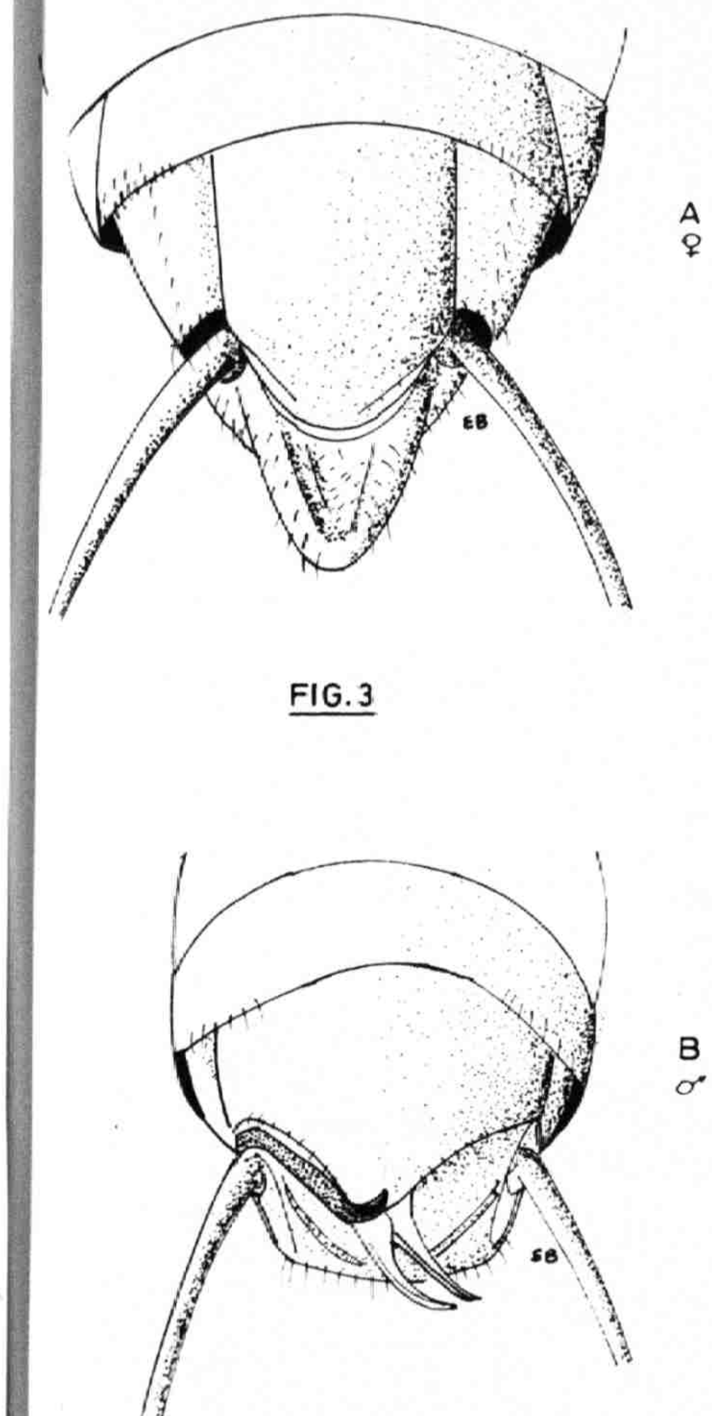



FIG. 3


FIG. 4

Figure 5. Internal Ventral View of the Ultimate Abdominal Segments of the Female, with the VIIth Sternite Removed, 46x.

FIG. 5

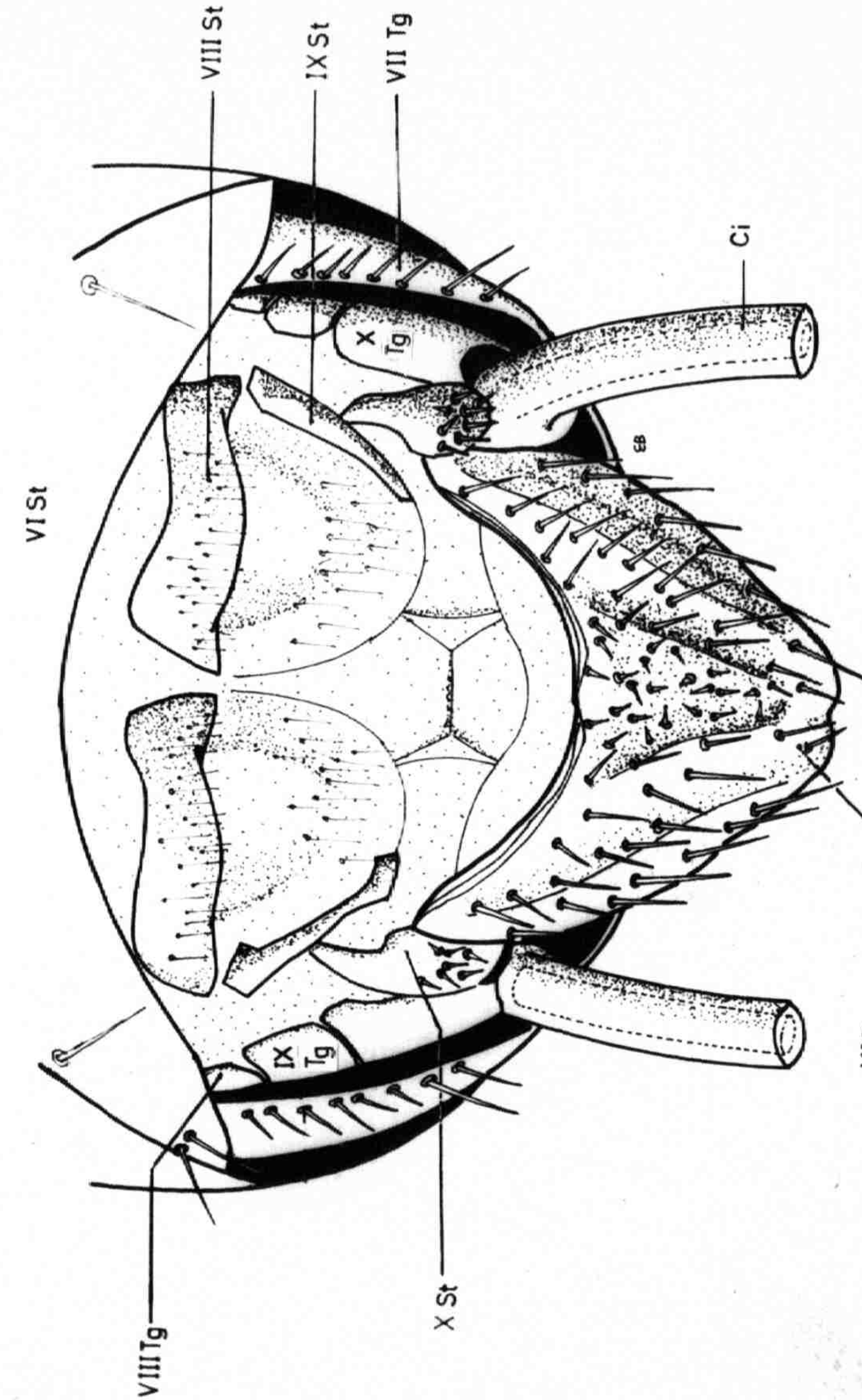


FIG.6

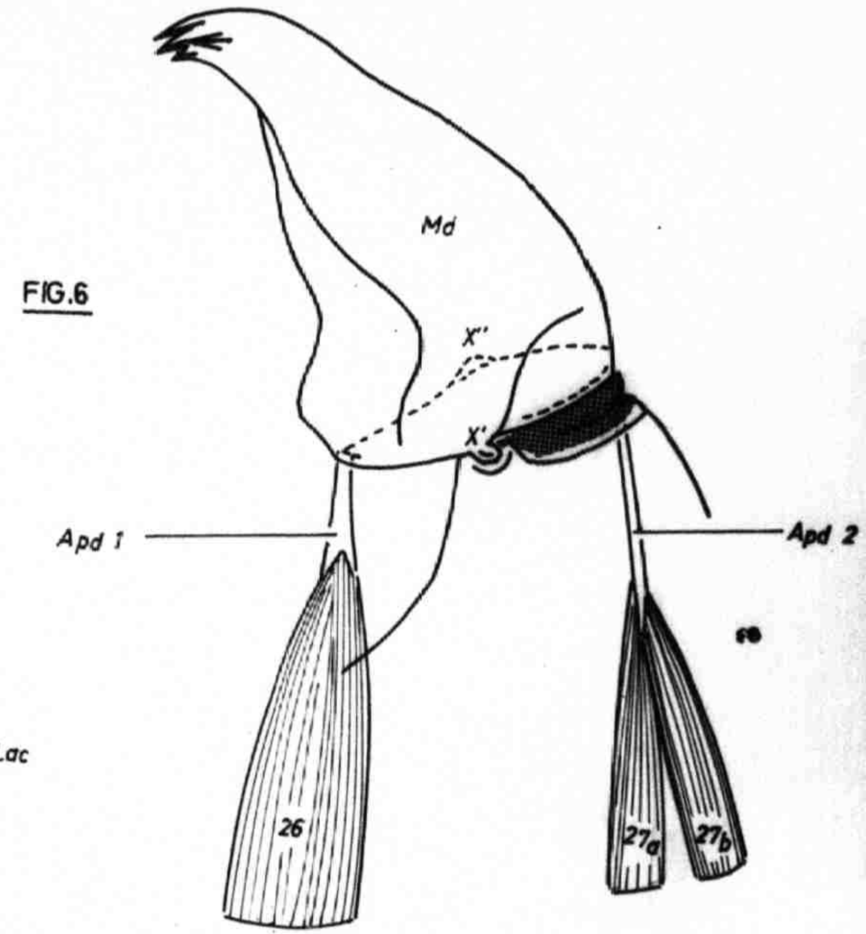



Figure 6. Muscles of the Left Mandible, Ventral View, 160x.

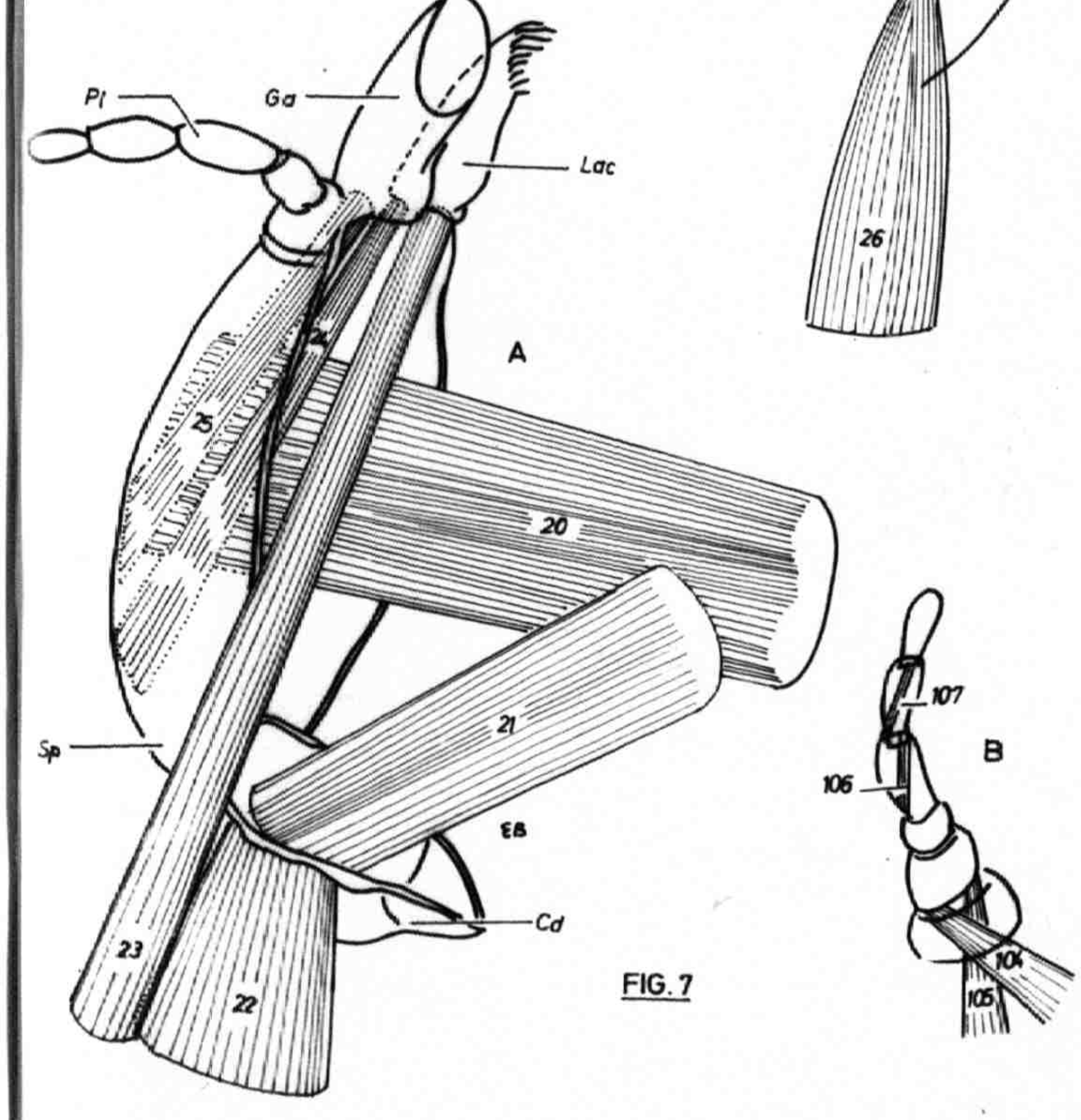



FIG. 7

Figure 7. A. Muscles of the Left Maxilla, Dorsal View
B. Muscles of the Maxillary Palpus, 150x.

Figure 8. Muscles of the Right Antennal Scape, 100x.

Figure 9. Muscles of the Labrum, Ventral View, 60x.

Figure 10. Muscles of the Labium, Dorsal View, 55x.

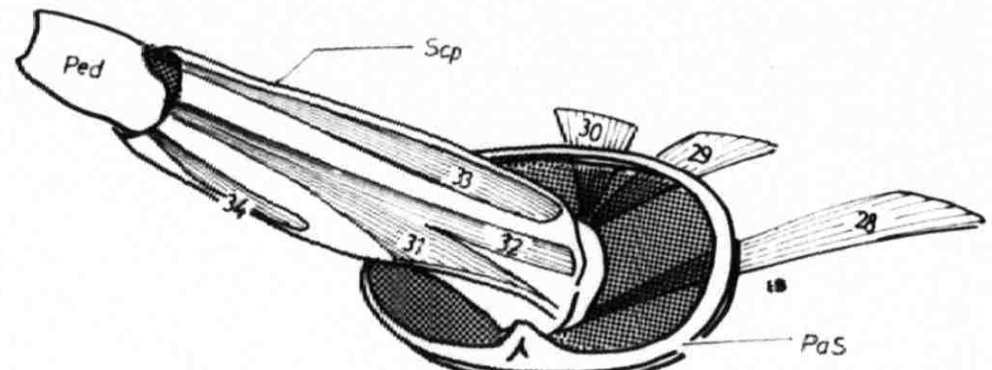



FIG.8

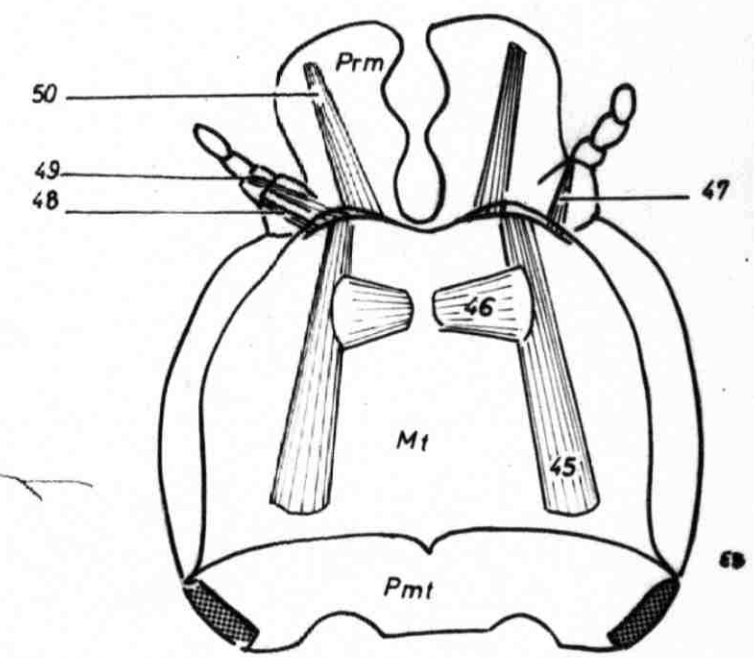



FIG.10

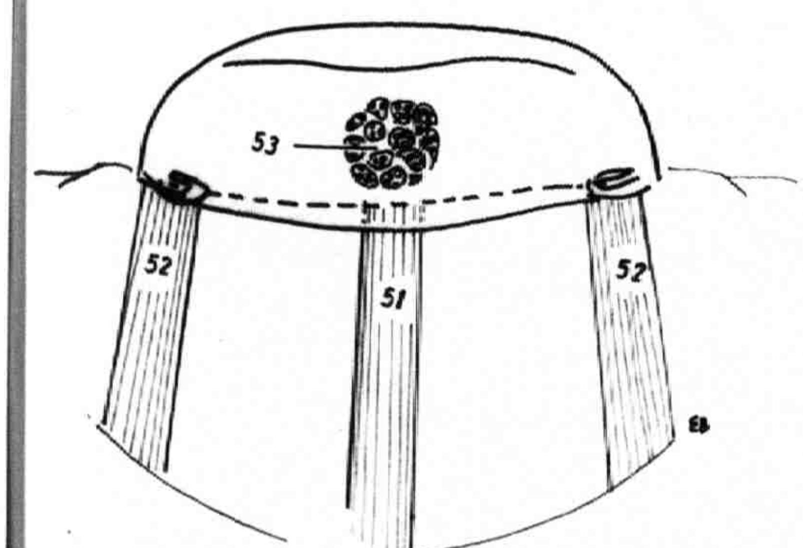



FIG.9

Figure 11. Muscles of the Prothorax, from Mesal to Distal, 50x.

FIG.11

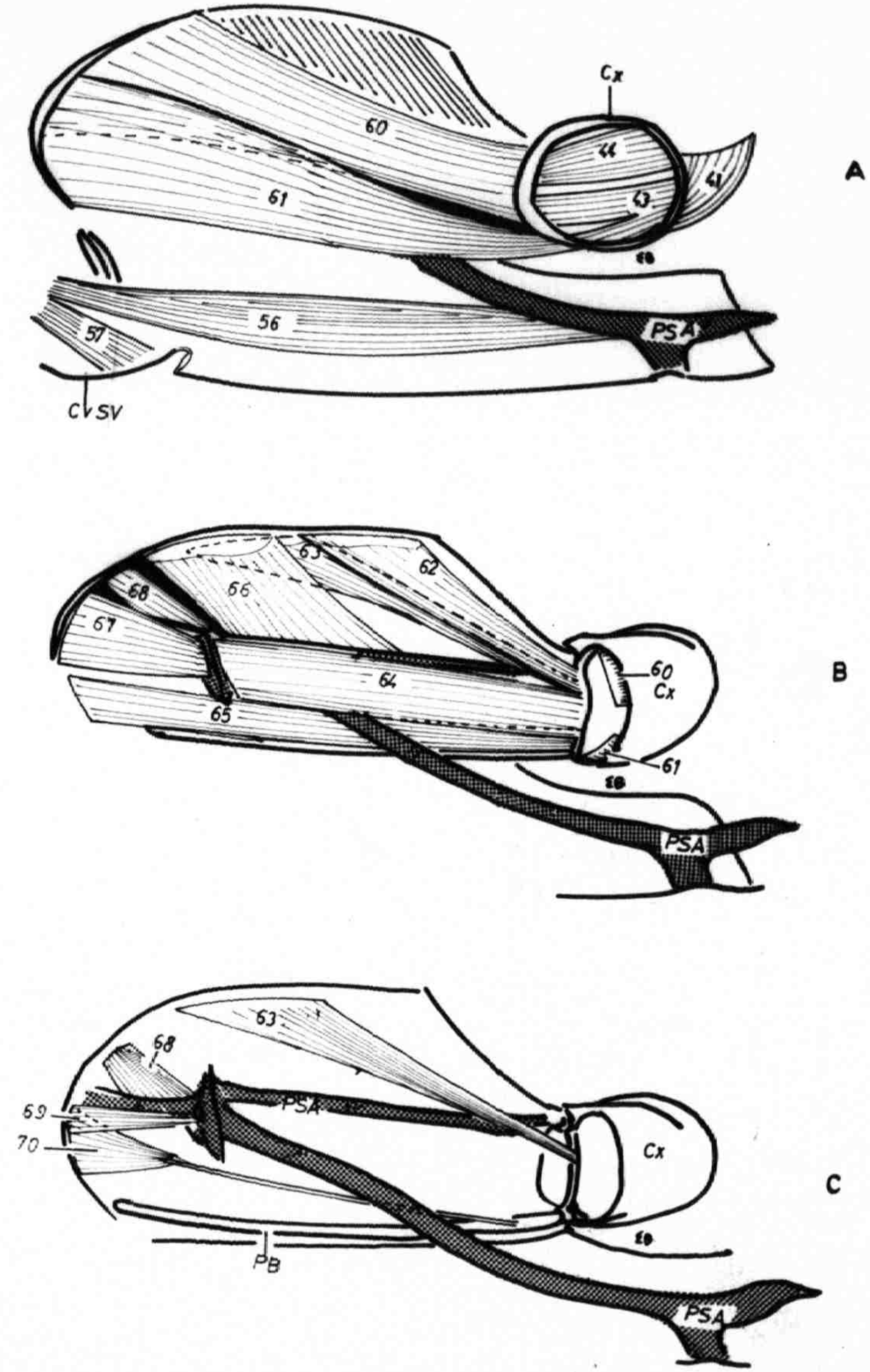


Figure 12. Muscles of the Mesothorax, from Mesal to Distal, 33x.

**FIG.12**

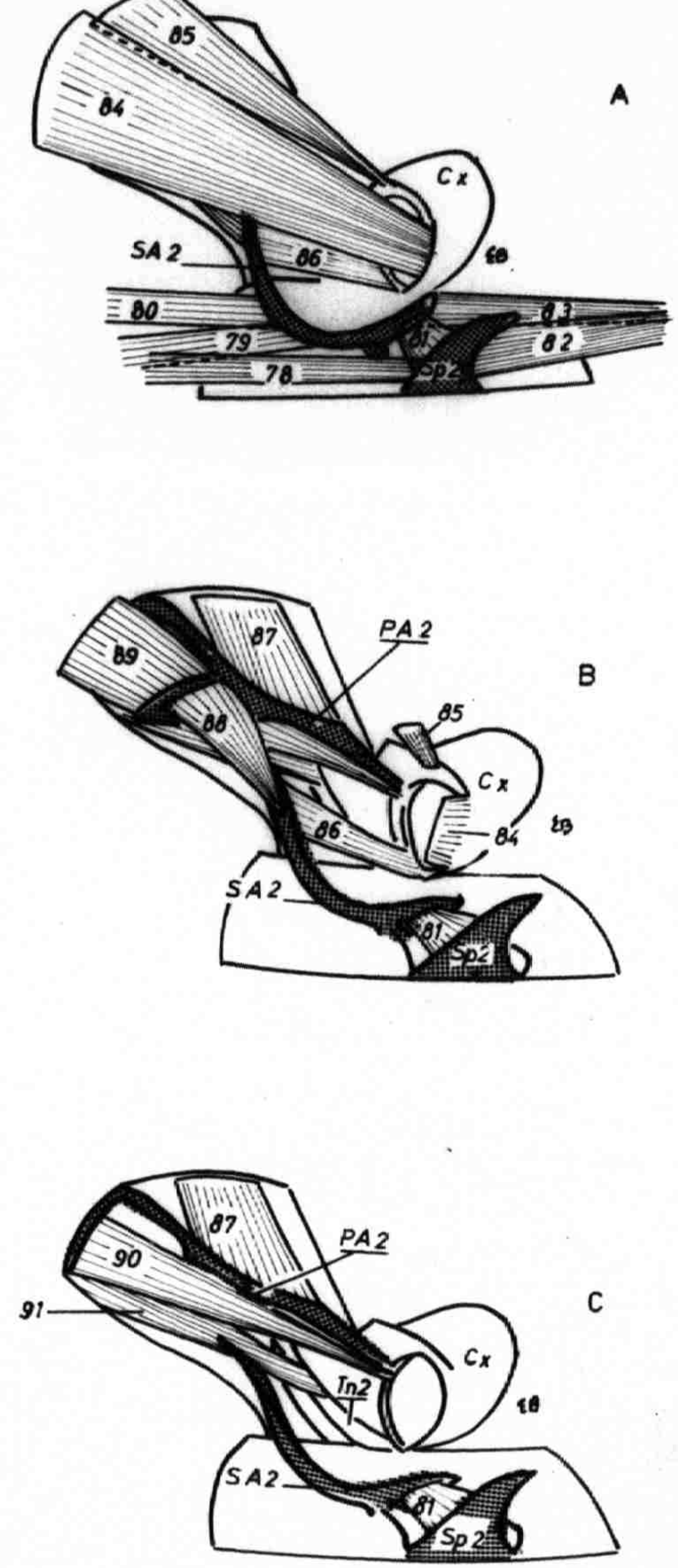


Figure 13. Muscles of the Metathorax from Mesal to Distal, 33x.

FIG.13

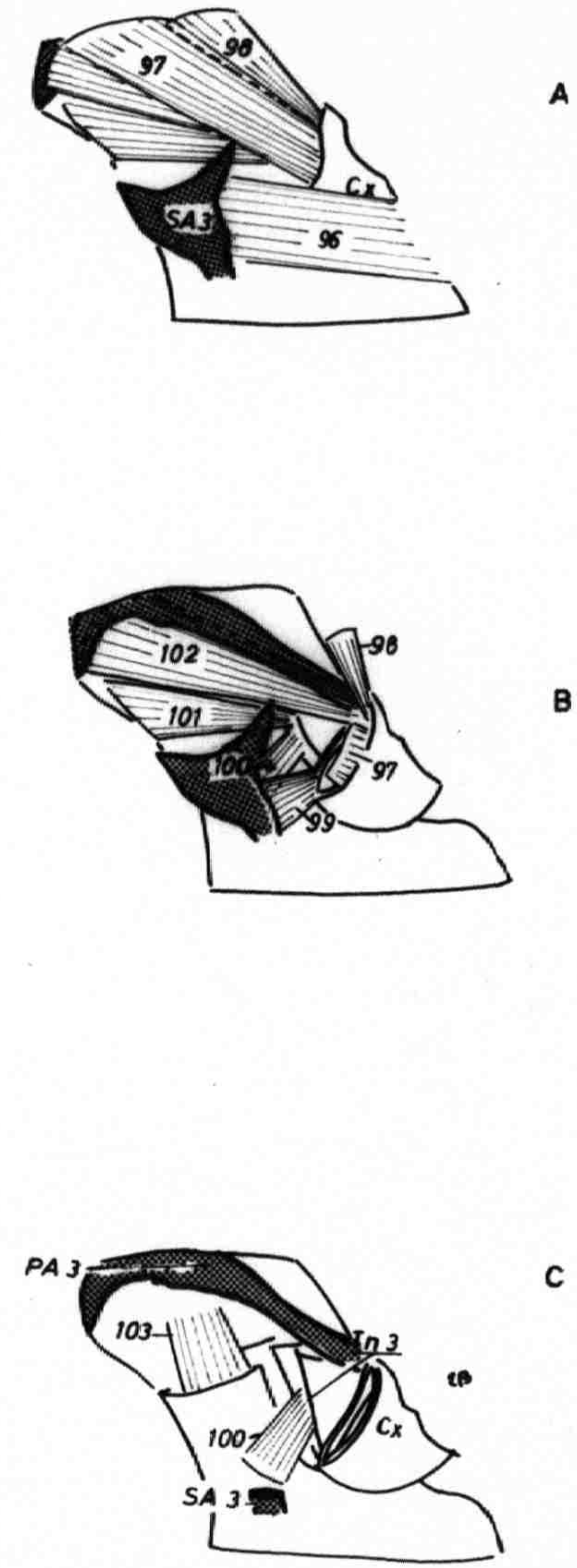


Figure 14. Muscles of the Right Mesothoracic Leg, 50x.

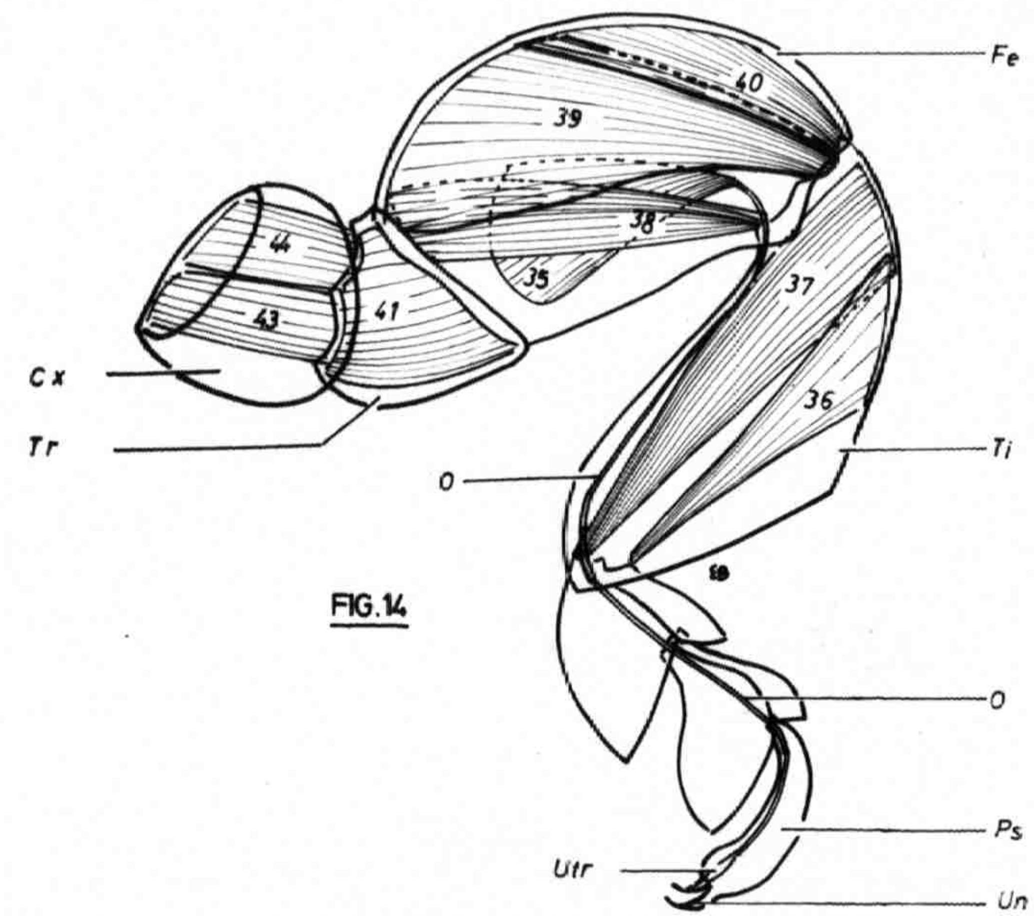
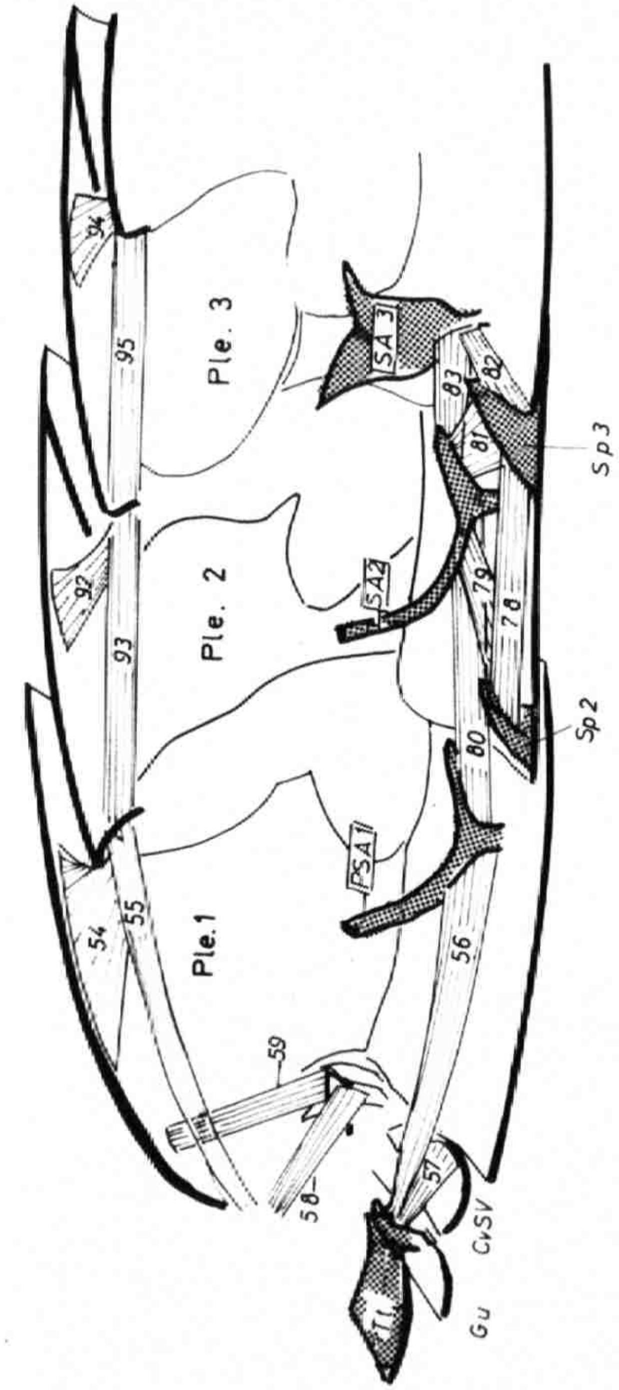


Figure 15. Ental View of the Tergal, Ventral and Cervical Muscles of the Thorax, 28x.

Figure 16. Dorsal View of the Digestive Tract, 11x.

FIG. 15



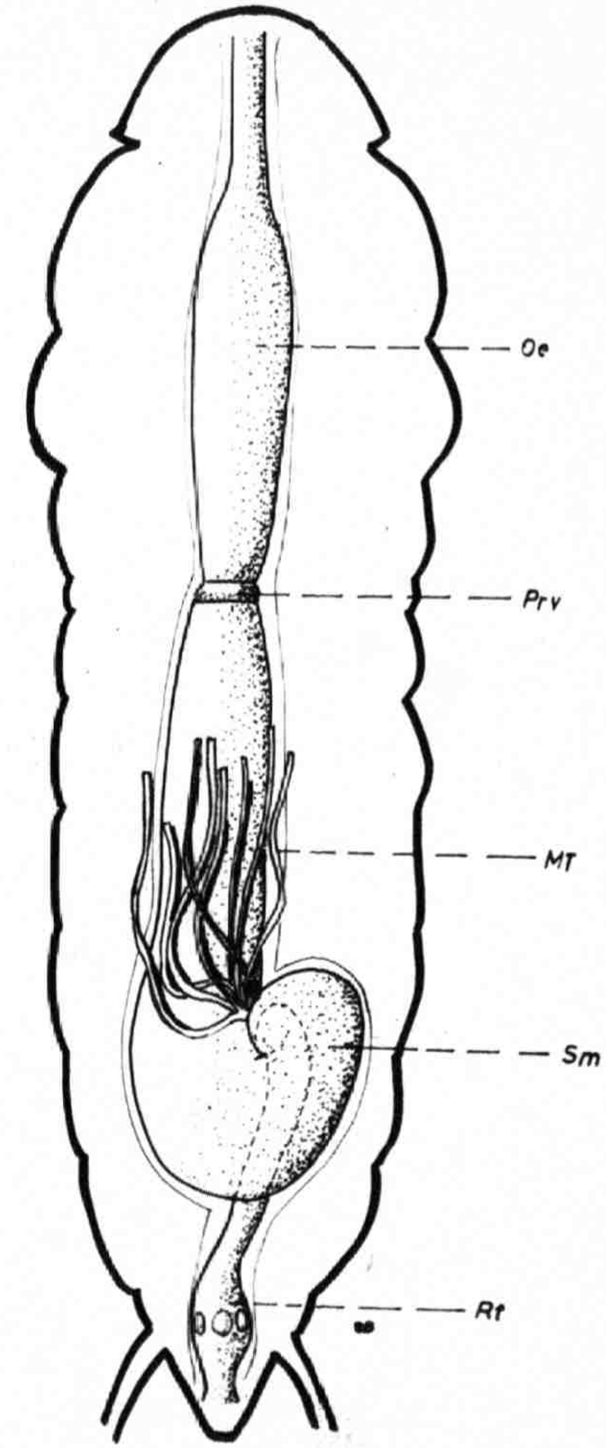




FIG.16

Figure 17. Female Reproductive System, Right Branch, Dorsal View, 11x.

Figure 18. Male Reproductive System with Left Testis Removed, Dorsal View, 14x.

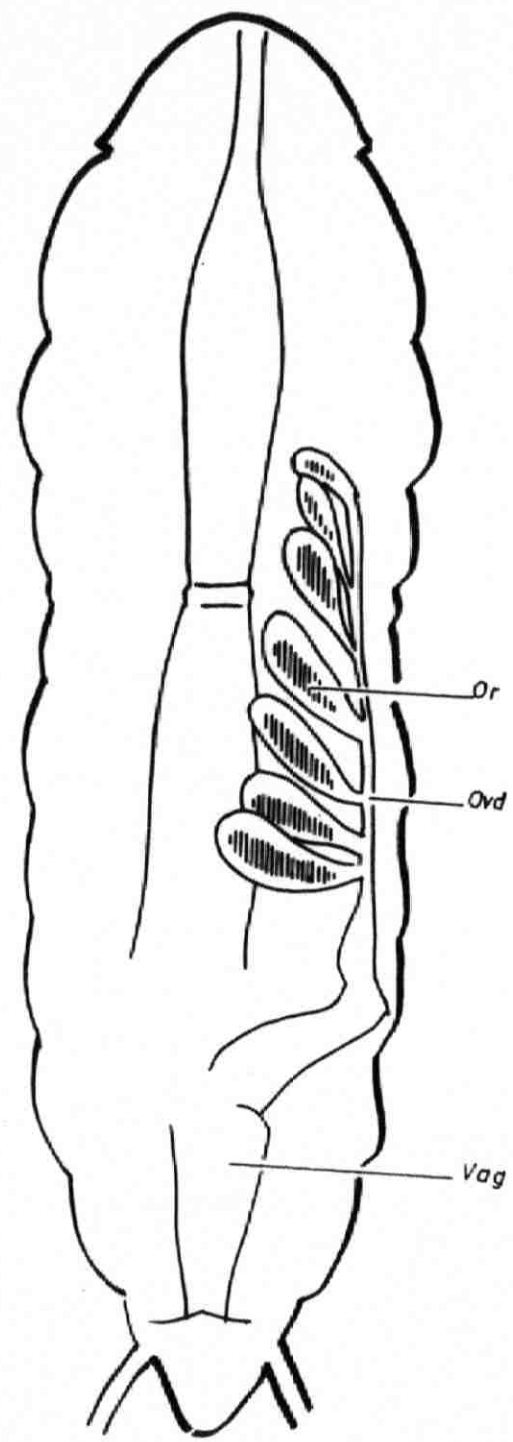



FIG. 17 ♀

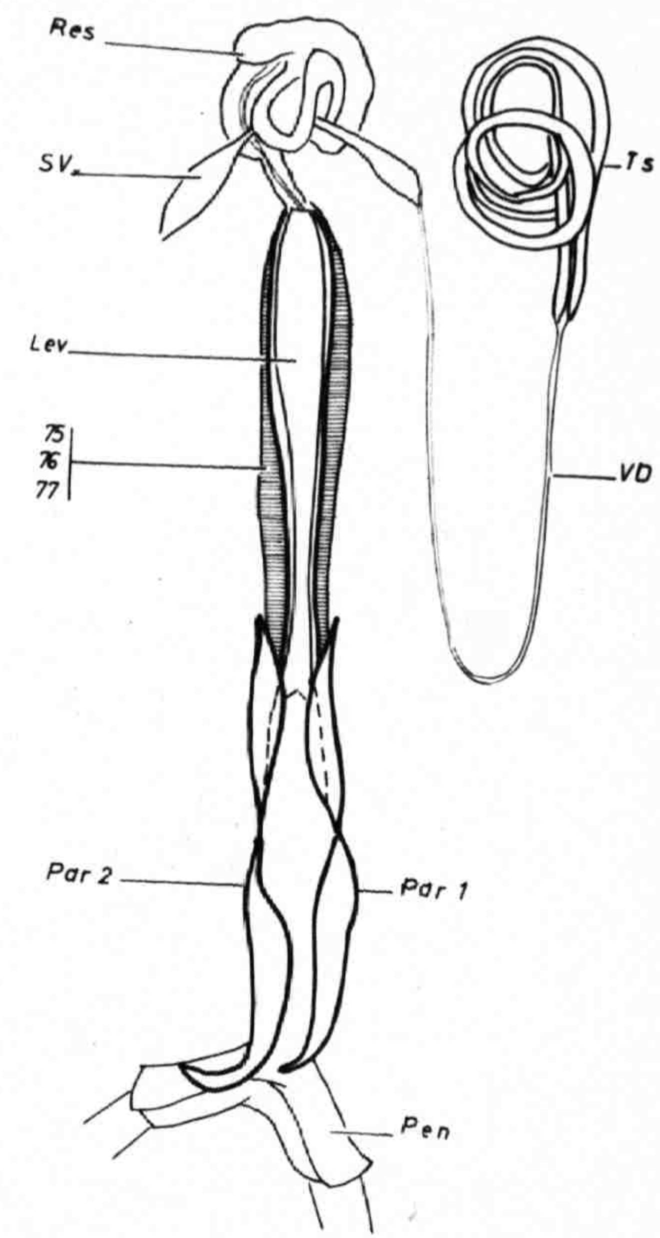



FIG. 18 ♂

Figure 19. Muscles of the Left Cercus, Dorsal View, 35x.

Figure 20. Penis, Ventral View, 30 (approx.)

Figure 21. Sperm Reservoir, 42x.

A. Ventral View

B. Dorsal View

Figure 22 Retractor and Protractor Muscles of Penis

A. Origins on IX Sternite, 20x

B. Insertion on Parameres, Dorsal View.

C. Insertion on Parameres, Ventral View .

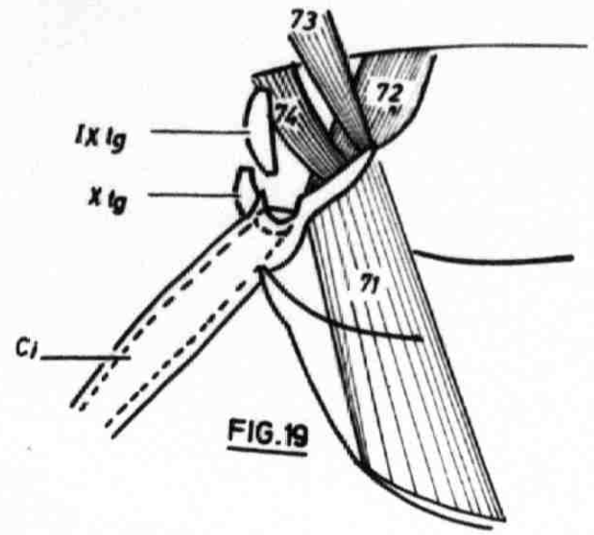



FIG.19

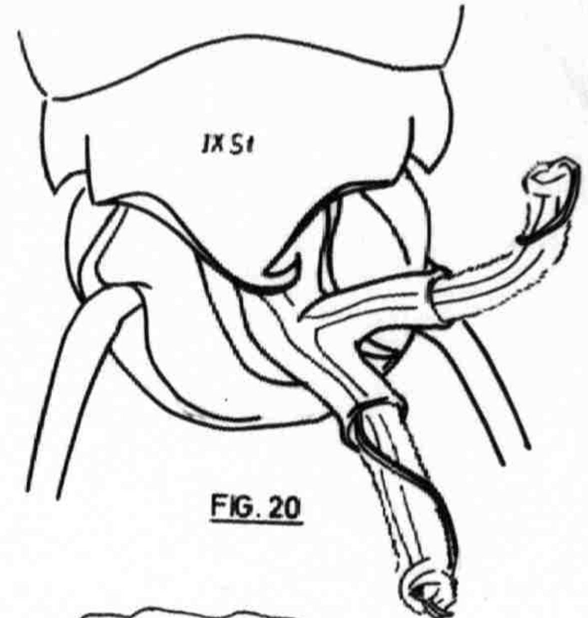



FIG. 20

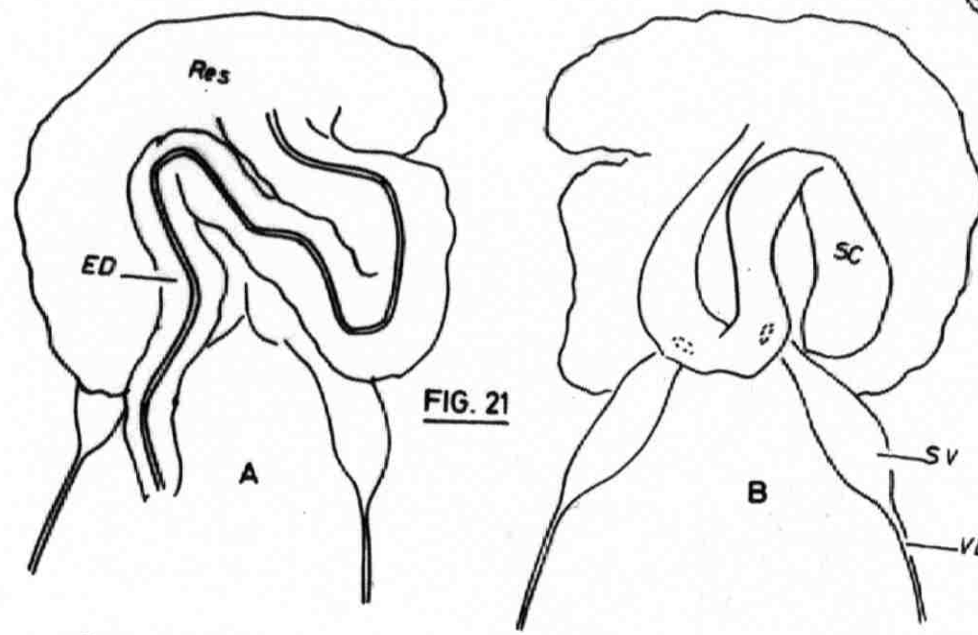



FIG. 21

FIG. 22