

THE COMPARATIVE EXTERNAL MORPHOLOGY OF TRICHOBIUS  
CORYNORHINI COCKERELL, I. MAJOR COQUILLET  
AND I. SPHAERONOTUS JOBLING  
(DIPTERA, STREBLIDAE)

By

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## PREFACE

Because of the author's interest in morphological studies and the intriguing biological relationships existing between parasitic organisms and their hosts, the following study was initiated.

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## INTRODUCTION

In recent years considerable attention has been given to the study of bats and their possible public health importance. Since 1954, Dr. B. P. Glass and associates have been conducting extensive research on bats in Oklahoma. This research included studies on the occurrence and distribution of bats and extensive banding activities to determine their migratory habits in the western part of the state. In addition to these studies, collections were made of the parasites of several species of bats.

During the summer of 1958 the author participated in these field studies and became familiar with the identification of Oklahoma bats, methods for their capture, and the host-parasite relationships. As a result of reviewing the cooperative work carried on by Drs. Glass and Twohy under research grants E-819 and E-1041 (C1) respectively from the National Institute of Allergy and Infectious Diseases, United States Public Health Service, it was apparent that the extensive arthropod fauna of bat caves merited further investigation. A survey of the literature revealed that while some taxonomic studies had been conducted on the arthropod fauna, practically nothing was known on their morphology, histology or anatomy.

Because of the recognized disease-vector relationships of the Pupipara, and the reported finding of trypanosomes in Oklahoma bats (Twohy 1959) the need for more detailed information on the Streblidae became apparent.

The purpose of this investigation is to present a detailed account of the comparative external morphology of the species of Trichobius occurring in bat caves in western Oklahoma.

## LITERATURE REVIEW

The Streblidae or bat flies (Fig. 1) belong to the order Diptera, suborder Pupipara, which includes two additional families, the Nycteribiidae and Hippoboscidae. These Diptera are referred to as pupiparans because of their unique reproductive habit. Unlike most insects which produce several eggs or larvae, these flies produce one larva which is retained in the female and nourished until fully mature. When the larva is deposited, on the host or substrates, it is incapable of locomotion or feeding and within a few moments develops into a pupa. This mode of reproduction differs from other larva-producing Diptera because in other groups, such as the African tsetse flies of the genus Glossina, the larva is capable of movement, and more than one is produced at a time. In other groups, for example the genus Sarcophaga, the larvae are quite immature at the time of deposition but are capable of movement and feeding.

The Nycteribiidae and Streblidae are parasites of bats, while the Hippoboscidae parasitize birds and various mammals.

The family Streblidae was established by Kolenati (1863) and for the most part is ectoparasitic with both sexes feeding on blood. Muir (1912) described an Old World species in which the female assumed an endoparasitic stage encysted in the skin of the host, while the male remained entirely ectoparasitic. Further accounts of this group including their life history, have been published by Jobling (1939b, 1940).

The genus Trichobius was erected by Gervais (1844) and now contains

17 species of which four have been recorded for North America. Three of these species, Trichobius corynorhini Cockerell, T. major Coquillett, and T. sphaeronotus Jobling were found on bats in Oklahoma during this investigation, but T. adamsi Augustson was not encountered. According to Ross (1959), T. adamsi is most often collected in association with the leafnose bat, Macrotus californicus Baird. This bat was not collected during this study and it appears that its range does not include Oklahoma.

Most of the literature dealing with Trichobius is concerned with taxonomy, distribution and host-parasite relationships. Inasmuch as any taxonomic discussion involves the morphology of the species, it seems useful to present the following review of publications. Individual distribution records for T. corynorhini, T. major and T. sphaeronotus were contributed by Townsend (1893), Coquillett (1899), Jobling (1939a) and Brues (1904). Cockerell (1910) described T. corynorhini and included some notes on the general morphology of the species. Kessel (1925) later published a synopsis of the Streblidae of the world and in this publication he described a new subspecies, T. major quadrisetosus. This species was later referred to by Smith (1934) who published records of bat flies from southern Kansas and northern Oklahoma. In his excellent revision of Trichobius, Jobling (1938) compared T. major quadrisetosus with T. corynorhini and found the former subspecies to be synonymous with the latter. From specimens collected from the bat, Leptonycterus nivalis (Saussure), Jobling described T. sphaeronotus. In the late summer of 1940, Kohls and Jellison (1948), collecting in Texas bat caves, obtained numerous specimens of this species in association with the Mexican free-tailed bat, Tadarida



brasiliensis mexicana (Saussure). More recently Ross (1960) recorded T. sphaeronotus from Arizona.

In addition to the previously mentioned publications, other distributional records of these parasites may be found in Stiles and Nolan (1930), Jobling (1949), Kessel (1952), Kohls (1954), and Jameson (1959).

Information concerning the distribution, observations on the biology and external morphological variations within species of Trichobius were presented by Zeve (1959). Recently Zeve (1960) presented additional records of ectoparasitic insects, including Trichobius, on bats in Oklahoma.

Although these dipterans are widespread very little is known of their life history and general morphological makeup. This fact is not surprising when the habitat and host availability are considered. Some aspects of the morphology of these flies are included in the publications concerning the taxonomy and distribution of the genus. Specifically, there has been very little work done on the detailed morphology of Trichobius, or on the Streblidae as a whole, in North America.

The structure of the head and mouthparts in the Streblidae was briefly described by Speiser (1900) and subsequently by Muir (1912). The treatment of the subject by the latter author was brief and lacked sufficient illustrations. Jobling (1929) published a comparative study of the head and mouthparts in the Streblidae in which he included both external and internal aspects. This and other earlier works (Jobling 1926, 1928), dealing with the same areas in the Hippoboscidae and Nycteribiidae respectively, served in the present study as invaluable guides to the examination of the head and its appendages.

Little information has been published on the thoracic region of

the Streblidae. In a brief discussion, Jobling (1939b) described the thorax of Ascodipteron africanum Jobling, an Old World streblid, but the thoracic region of this species is quite unlike that of Trichobius.

Some external descriptions of the thorax in hippoboscids have been published by Roberts (1927), Crampton (1942) and Bequaert (1953).

No studies were found concerning the internal structures of the thorax except for one publication of Hennig (1941) that deals mainly with the sclerotized processes of the sternal region in the hippoboscids.

The external structure of the abdomen was briefly described for the Pupipara by Speiser (1900) and by Cole (1927). Jobling (1951), in a comparative study of the subfamilies Nycteriboscinae, Streblinae and Trichobiinae, described the external features of the abdomen from representative species of each group.

In the Streblidae there appears to have been no detailed examination of the internal anatomy of the abdomen.

Most of the embryological investigations in the Pupipara have dealt primarily or exclusively with the sheep tick, Melophagus ovinus Linnaeus. A very thorough discussion of the embryology of this species was compiled by Hagan (1951). Many individual papers have been published on the internal anatomy of the Hippoboscidae. Among the earlier workers describing both gross anatomical and histological examinations of the genital tracts were Dufour (1825, 1845), Pratt (1899), Falcoz (1926) and Hase (1927). An excellent study of the respiratory system and musculature of the abdomen in M. ovinus was presented by Webb (1945).

The structure of the genitalia in the Streblidae was described by Jobling (1951) and it appears that this is the only work appearing in the literature which deals specifically with the Streblidae in this

respect. In the Nycteribiidae, Cole (1927) mentioned these structures briefly but did not describe them in detail. Karaman (1936, 1939, 1948) described and illustrated numerous structures of the genital area of many species of Nycteribiidae but did not give a complete description of the overall genital apparatus. Hennig (1941) presented a diagrammatic drawing of the male genitalia but it was not until later (Theodor 1953), that a complete and well illustrated presentation of the genitalia appeared.

Due to the scarcity of external or internal morphological studies on the Streblidae several publications warrant mention here which served as excellent references throughout the present investigation. The publications of Weber (1933), Imms (1948), Snodgrass (1935) and Bonhag (1949, 1951) were found to be extremely useful when drawing analogies and homologies in areas of great complexity.

## METHODS AND MATERIALS

Numerous adult specimens were required for this study. This necessitated a thorough survey of possible hosts which might yield specimens sufficient for study. Although collection of streblids had occurred in Oklahoma, little information was available as to their distribution and life history. Early in this study it became quite apparent that collecting of streblids required some knowledge of their life history and for this reason the following discussion necessitates the inclusion of some aspects of the life history of these dipterans.

### Location of Caves.

Specimens utilized in this investigation were collected from several caves in western Oklahoma. Nineteen caves were examined for streblids but only 17 were found to contain these parasites. On many occasions flies were found in caves where bats were not present. In all caves where streblids were found in the absence of their host, evidence in the form of guano deposits and ectoparasites of bats were collected which would indicate the presence of bats in these caves during other periods of the year. The caves are listed below by their established name or by the name of the landowner and for each, the approximate and legal description is included. One or more species of Trichobius were found in the following caves.

Alabaster Caverns: Sec. 33, T. 26N., R. 18 W. of Indian Meridian,  
5 miles W., 3 miles S. of Freedom, Woodward County.

Anderson Creek Caves: Sec. 17, T. 27N., R. 17 W. of I.M., 3 miles E. of Camp Houston, Woods County; two caves.

Conner's Cave: Sec. 30, T. 22N., R. 15 W. of I.M., 5 miles E. of junction of U. S. Highway 281 and State Highway 15, Major County.

Corn Caves: Sec. 5, T. 11N., R. 15 W. of I.M., 5.5 miles N., 2 miles W. of Corn, Washita County; three caves.

Griever Creek Cave: Sec. 30, T. 22N., R. 15 W. of I.M., 3 miles E., 4 miles S. of junction of U. S. Highway 281 and State Highway 15, Major County.

Icebox Cave: Sec. 33, T. 27N., R. 19 W. of I.M., 6 miles S., 7.5 miles W. of Freedom, Woodward County.

Lake Cave: Two hundred yards east of Conner's Cave.

Merrihew Cave (Merehew Cave): Sec. 17, T. 29N., R. 17 W. of I.M., 13 miles N., 3 miles E. of Camp Houston, Woods County.

Owl Cave: Sec. 33, T. 26N., R. 18 W. of I.M., 5 miles S., 2 miles W. of Freedom, Woodward County.

Reed Caves 1 and 2: Sec. 28 and 29, T. 15N., R. 24 W. of I.M., 2 miles W., 1.5 miles S. of Reed, Greer and Harmon Counties.

Selman's Cave: Sec. 33, T. 26N., R. 19 W. of I.M., 4 miles S. 7 miles W. of Freedom, Woodward County.

Vickery Caves 1 and 2: Sec. 5, T. 22N., R. 16 W. of I.M., 2.5 miles W. of junction of U. S. Highway 281 and State Highway 15, Major County.

In addition to the above list, other known bat caves in Oklahoma are given by Glass and Ward (1959).

### Collection of Specimens.

With the aid of a head lamp and a large flashlight, the walls, ceilings, and floors of caves were inspected for streblids and bats. Bats were netted with a long-handled insect net, placed in screen-wire cages and taken to the entrance of caves for inspection. Specimens were collected from bats with forceps and from cave walls and ceilings with an aspirating tube. On many occasions, when conditions were satisfactory, adult flies were collected directly from bats in caves. On one occasion I. major was collected from guano deposits in Selman's Cave.

Bats were also collected with Japanese mist nets (Dalquest, 1954) which were placed across the entrance to caves shortly after sunset. This method made possible the examination of bats for parasites which do not normally inhabit caves.

Six species of bats, Antrozous pallidus (Le Conte), Eptesicus fuscus pallidus (Young), Lasiuris borealis borealis (Müller), Myotis velifer incautus (Allen), Plecotus townsendi pallescens (Miller) and Tadarida brasiliensis mexicana (Saussure) were examined for streblids. The last three species of bats were found to be parasitized.

The host-parasite relationships as shown in Table 1, are as follows:

Myotis velifer incautus (Allen), the cave bat.

Because this species of bat occurs in large aggregations while hibernating in caves during the winter months their collection is greatly facilitated. Very few streblids were collected from this host during the summer months, due to the inaccessibility of roosting colonies of M. velifer. Jobling (1951) stated, "The Streblidae cannot exist on

hibernating bats." Observations of T. major from November through March show that this species overwinters as an adult on M. velifer at least in Oklahoma, as over one thousand specimens were removed from the outer ears, and to a lesser extent from other body regions of this host. No matings of flies were observed nor were any pupae observed during this period. Serial sections of the alimentary tract revealed that these populations of T. major continued feeding during this period. Infestations ranged from 1 to 4 per bat.

Trichobius corynorhini Cockerell was taken from this host on one occasion at Reed No. 2 Cave.

Trichobius major Coquillett was collected from this host in Alabaster Caverns, Anderson Creek, Griever Creek, Icebox, Reed No. 2, Vickery No. 1 and No. 2 Caves.

Trichobius sphaeronotus Jobling was not found in association with this bat.

Plecotus townsendi pallescens (Miller), the western longeared bat.

This bat was referred to in an earlier work (Zeve, 1959) as Corynorhinus rafinesquei pallescens (Miller). Handley (1959) now places Corynorhinus as a subgeneric name under the genus Plecotus. Strebliids were collected from both hibernating and active hosts. Due to the solitary nature of this bat very few were examined. Trichobius corynorhini was collected from this host at Alabaster Caverns, Anderson Creek, Corn, Griever Creek, Icebox, Lake, Merrihew, Reed No. 2 and Vickery No. 1 Caves. This streblid, when taken from hibernating bats, was found only in the region of the interfemoral membranes. On other occasions there was no specific area infested. A total of 292

specimens were collected with infestations ranging from 2 to 12 flies per bat.

Trichobius major and T. sphaeronotus were not found in association with this host.

Tadarida brasiliensis mexicana (Saussure), the Mexican free-tailed bat.

Free-tails were extremely abundant in some caves during the summer months with populations reaching the millions. This bat is not present in Oklahoma from late October to early May, as it spends this period in southern Texas and Mexico. Collecting in caves inhabited by this species was greatly hampered by the large bat populations and by the annoyance of the large arthropod fauna. Due to the lack of free air circulation, high ammonia content and high temperatures prevailed throughout the summer. Open-flame lanterns as a light source were abandoned due to insufficient amounts of oxygen. It was noted that incomplete combustion produced fumes which had a tendency to drive bats from the caves.

Several known ectoparasites of bats inhabit these caves but it appears that many of these only cling to their host while feeding. This phenomenon was also reported by Smith (1934) and Jameson (1959). Numerous free-tailed bats were examined in caves but no streblids were found when bats were handled. Observations of roosting bats revealed that streblids feed on this host but leave as soon as the bat is disturbed by light, netting or handling. On one occasion, one specimen of T. major was taken directly from this host which had been netted during October 1960, the approximate time of the hosts southern migration.

As further evidence of this phenomenon, streblids have been



collected on other occasions from bats taken in mist nets. In July and October 1960, I. corynorhini was taken from Plecotus townsendi pallescens at Alabaster Caverns and Owl Caves. Examination of caves during the summer months, which are used as sites for hibernation by M. velifer during the winter, did not reveal streblids. Myotis velifer does use these caves for brief periods of time during the summer months but they were not found to harbour flies at this time. As indicated previously, M. velifer is parasitized during the winter months, which indicates that these dipterans cling to the host during periods of host dispersal and migration.

Trichobius major in association with this host was taken from cave walls and ceilings from Conner's, Merrihew, Reed No. 1, Selman's, and Vickery No. 1 Caves. In addition to these sites the fly, as indicated previously, was taken on one occasion from Tadarida at Alabaster Caverns.

The largest collections of I. major parasitizing this host were collected in Selman's Cave. This cave was more easily accessible and housed a large Tadarida population. Both adults and pupae were easily collected as a result of low ceilings in this cave. Trichobius major was quite abundant during the summer months. Populations increased steadily until the bats left the caves, and flies could be taken from the cave, well after the southern migration of Tadarida. Collections made in October, November and December contained both newly emerged and fully developed adults. In October 1960, when it was estimated that this cave had been free from bats for approximately 2 weeks, over one hundred I. major were collected within a period of 30 minutes. The majority of this large population were newly emerged flies.

Collecting was hampered by excessive attacks by these flies on the face, neck and arms of the collector. This circumstance was also reported by Kohls and Jellison (1948). On the same date numerous newly emerged flies were collected from guano deposits. No specimens collected from cave floors were alive. No other species of streblids were seen at this time.

Trichobius sphaeronotus Jobling was taken exclusively from cave walls and ceilings in Conner's, Merrihew, Reed No. 1, Selman's and Vickery No. 1 Caves. This fly was seldom taken during the interval in which bats occupied the caves and never directly from its host. Upon examination of Selman's Cave in early October 1959, it was found that large numbers of viable pupae and newly emerged adults were present. Over one thousand specimens were collected in a period of 90 minutes from ceilings and walls. In comparison, only three specimens of T. major were collected at this time. It was estimated that the cave had been free of bats for approximately 3 weeks. Periodic examinations of this cave during the winter months revealed that both pupae and adults were present. Examination of Conner's Cave in early May 1958, prior to the return of free-tail colonies, revealed large numbers of newly emerged T. sphaeronotus. This observation suggests that newly emerged, unfed adults overwinter or, more likely, that the pupae are capable of overwintering. This observation was also recorded in Selman's Cave in April, 1959. With these observations in mind, many pupae were collected from Conner's Cave in the Spring, and from Selman's Cave during the winter months. These pupae were placed in gauze-covered ice cream cartons and kept in a shallow pan of water held at approximately 82°F. A total of 153 flies were reared in this manner.

This procedure established the viability of the pupae and also served as another means of obtaining adult flies. It is quite possible that both adults and pupae are capable of overwintering simultaneously although some experimental evidence indicates that the latter may be more successful.

Direct light had a tendency to repel streblids. This reaction was more profound in cases where specimens were collected from cave substrates and to a lesser extent on those taken directly from the host. In areas of lower light intensity, around the main beam of light, no repelling effect was noted upon these dipterans.

Trichobius corynorhini was not taken in association with this host.

#### Fixation and Preservation of Materials.

All specimens collected were placed in a killing fixative. A fixative in this case is defined as a substance which is used to preserve the cytological, histological and gross morphological anatomy of the entire tissue, as closely as possible to its natural living state. Numerous fixatives were screened initially for speed of penetration and ability to preserve. In addition to these basic requirements, further observations were made with regard to their shrinking and swelling properties, and their subsequent effect on staining. Due to the size of these flies and the lack of laboratory facilities in the field, a fixative was needed which did not require an incision to insure rapid penetration.

Specimens used for the study of external morphological structures were drawn from those collections which had been inadequately fixed for sectioning of internal structures. Three fixatives were used in this

study. A modified Bouin's fixative was used for the majority of specimens used for sectioning. Salthouse (1958) introduced the use of tetrahydrofuran (tetramethylene oxide) as a histological reagent for insect tissues. This compound was found to penetrate the insect cuticle very rapidly and to reduce hardening of the sclerotized areas, unlike conventional reagents such as chloroform, xylene and toluene. Tetrahydrofuran was incorporated into Bouin's fixative as follows:

Picric Acid, saturated aqueous solution	- 75 ml
Formalin	- 25 ml
Glacial Acetic Acid	- 5 ml
Tetrahydrofuran	- 10 ml

The amount of tetrahydrofuran was established at 10 milliliters as the greatest amount that could be used without causing substantial swelling or shrinkage. This evaluation could be made only on the appearance of stained sections.

Live specimens were placed directly into unheated solution and allowed to remain for 12 hours. After this period of time the flies were removed and washed in a mixture of equal parts tetrahydrofuran and distilled water, to which lithium carbonate had been added to remove the picric acid. Tissues remained in this mixture for 30 minutes and were then washed in three changes of tetrahydrofuran for 10 minutes per change. If tissues were to be stored for further use they were placed in 95 percent ethanol. Tissues washed in tetrahydrofuran may be infiltrated, embedded and sectioned in paraffin without further dehydration. After several months of storage, materials fixed in this solution showed no additional hardening; however, tetrahydrofuran, like other isoparaffins, dissolves lipid structures.

Approximately five hundred specimens were collected and quick-frozen in the field by placing living flies in an ice cream carton surrounded by dry ice. This carton was prepared with a 1" X 1/2" flap in the lid to receive specimens and two 1" X 4" gauze-covered openings on the side to insure rapid freezing. This material was then transported to the laboratory and separated as to sex. One hundred flies were retained in a deep-freeze for future gross dissection. The remaining flies were fixed in boiling Kahle's fixative as follows:

95% Ethyl Alcohol	- 17 ml
Formalin	- 6 ml
Glacial Acetic Acid	- 2 ml
Distilled Water	- 28 ml

Frozen flies were fixed in boiling Kahle's fixative for 5 minutes after which they were immediately transferred to an oven for 16 hours at 60° C. Following this treatment they were then washed several times in fresh solutions of 70 percent ethanol and stored in 95 percent ethanol.

Tissues fixed in Kahle's fixative were used for dissection only. Internal structures, including lipids, were well preserved and retained a high degree of resilience. This fixative was not satisfactory for tissues which were to be sectioned as the application of heat tends to harden sclerotin. Further, heat in conjunction with alcohol and formalin increases the major difficulty encountered in the preparation of arthropod sections, that of hardening of the exoskeleton which results in shattering of the body wall upon contact with the microtome blade.

If Kahle's fixative is used unheated, an incision must be made in the body wall to insure penetration, otherwise fixation is too slow and damage to internal structures by proteolytic enzymes results.

A third fixative, tetrahydrofuran sublimate, (Salthouse, 1958), was modified and incorporated into this study. This solution consists of:

Tetrahydrofuran	- 95 ml
Mercuric Chloride	- 8 g
Glacial Acetic Acid	- 5 ml
Formalin	- 12 ml

It was found that the basic formulation, consisting of only the first three compounds, caused considerable swelling of the entire specimen. To correct this, the amount of tetrahydrofuran was reduced without decreasing the effectiveness of the mixture as a fixative. Varying concentrations of formalin were added to the basic formula in several vials and then taken to the field. That solution which contained 1 percent formalin was found to reduce swelling within normal limits. By altering the amount of formalin, varying degrees of swelling could be obtained. This swelling aided in the dissection of smaller external morphological structures and greatly aided the study of the external features of the abdomen and membranous articulating areas.

Materials fixed in this solution for 6 hours were then washed in several changes of tetrahydrofuran to insure complete removal of the mercuric chloride. These were then stored in 95 percent ethanol until needed. For the most part, this fixative was used primarily for external study. Mallory's triple connective tissue stain was unsatisfactory for specimens fixed in tetrahydrofuran sublimate, although it produced satisfactory results following Bouin's tetrahydrofuran fixative.

### Mounting Techniques.

Specimens which had previously been fixed in one of the three fixatives and subsequently preserved in 95 percent ethyl alcohol were cleared in 10 percent KOH. Flies were hydrated in a series of decreasing concentrations of ethyl alcohol and thoroughly washed in distilled water prior to clearing. After sufficient clearing at a temperature of 60° C. specimens were then washed in 3 to 4 changes of distilled water and prepared for mounting in one of two mounting media, Hoyer's or Permount. Hoyer's mounting medium consists of the following materials mixed in the order given below:

Distilled Water	-	50 ml
Gum Arabic	-	30 g
Chloral Hydrate	-	200 g
Glycerine	-	20 ml

For convenience and speed of mounting, Hoyer's medium was used. Materials which had been cleared and washed were mounted directly on slides to which Hoyer's medium had been added. In many instances, small amounts of a saturated aqueous solution of picric acid and basic fuchsin were added directly to the medium as a stain. Heavily sclerotized areas were more easily differentiated by the addition of picric acid, while basic fuchsin greatly facilitated the study of both membranous and sclerotized structures.

The second material employed, Permount, a synthetic resin, required complete dehydration prior to its use. Specimens which had been cleared and washed were subjected to increasing concentrations of ethyl alcohol. Upon completion of dehydration, they were then placed in equal amounts of 95 percent ethyl alcohol and beechwood creosote for approximately 20 minutes or until sufficient clearing had taken place. They were then

washed in xylol and mounted directly in Permount. Basic fuchsin was employed when a stain was desired. This staining procedure was inserted in the dehydration process when tissues had reached the 70 percent ethyl alcohol concentration. A 0.5 percent solution of basic fuchsin in 70 percent alcohol was used for staining. Body areas were placed in this solution and observed until adequate staining was obtained. The staining period varied depending on the structure being stained. Specimens were then washed in fresh 70 percent alcohol to remove excess stain and dehydration was then continued.

In many cases particular structures required dissection prior to mounting in order to facilitate their study. Sharpened insect pins and sewing needles were used in these dissections. Jewelers forceps were utilized to handle small structures and for subsequent manipulation of materials on slides prior to applying the coverslip.

The axillary sclerites, genitalia, halteres and mouthpart regions were dissected from hydrated specimens, imbedded in wax dishes and immersed in Hoyer's medium. The use of Hoyer's medium prevented the loss of these small structures as was the case when water was utilized. All dissections were made under a stereoscopic microscope.

#### Sectioning, Mounting and Staining.

The sectioning of insect tissues has long been a difficult task. The major problem has been one of cutting sclerotized body regions. Sclerotin, due to its peculiar chemical properties, is hard and rendered even more so by the addition of heat and many standard reagents used in imbedding procedures.

Two imbedding methods were employed in the preparation of serial sections. All specimens to be sectioned were placed in a petri dish



of 95 percent ethyl alcohol and the legs were removed at the coxal cavity. This permitted a more positive site for infiltration of reagents. They were then placed directly in several changes of tetrahydrofuran until dehydration was insured. Following dehydration specimens were imbedded in paraffin or doubly embedded in celloidin (Pyroxylin) and paraffin.

Procedure 1. Tissues to be embedded in paraffin (Tissuemat) were transferred from tetrahydrofuran to a mixture of equal parts of tetrahydrofuran and 60° C. paraffin in a tightly capped 50ml bottle. This bottle was placed in a 60° C. oven for 30 minutes after which materials were transferred to 60° C. paraffin in an open beaker for 30 minutes. Tissues were then removed and oriented in paper containers containing fresh paraffin and hardened in a refrigerator. Embedded tissue was held under these conditions for future sectioning.

Tetrahydrofuran is highly volatile at room temperatures. Materials placed in tightly capped vials containing a solution of tetrahydrofuran and paraffin were rapidly infiltrated by positive vapor pressure created by this reagent. This method greatly reduced the time tissues were exposed to the harmful effects of heat. Attempts to infiltrate at room temperatures without utilizing the embedding oven were unsatisfactory as evidenced by the lack of paraffin inside the body capsule.

The single embedding method was employed for the abdominal region only. This area is almost entirely membranous, thus does not require maximum internal support as is necessary in more heavily sclerotized regions.

Procedure 2. A double embedding procedure was utilized when the internal anatomy of the head and thorax were of main interest. Tissues were washed in several changes of tetrahydrofuran following dissection of the legs. These were then placed in a series of increasing concentrations of celloidin solution. Two solutions were employed.

The first solution employed the use of tetrahydrofuran as the solvent for concentrations of 2, 4, 6, 12, and 16 percent celloidin at 50° C., oven temperatures. Tissues were permitted to remain in tightly capped half-pint Mason jars at these concentrations for 12 hours each. Upon completion of infiltration, tissues were removed with forceps and embedded in fresh 16 percent celloidin. These were placed under a bell jar containing volatilized chloroform to create a firm block. In order to maintain such a saturated chloroform atmosphere an open container of chloroform was employed. Celloidin blocks containing tissues were exposed to chloroform vapors for at least 8 hours to insure uniform firmness. It was found that blocks exposed to chloroform vapors were more porous than those immersed directly in this reagent. This increased porosity aided greatly in the penetration of paraffin. These blocks were then trimmed and celloidin embedded tissues were immersed in terpeneol until cleared, which often required from 48 to 72 hours. After sufficient clearing, the blocks were briefly washed in tetrahydrofuran to remove excess terpeneol. These blocks were infiltrated for 10 minutes in equal parts of tetrahydrofuran and paraffin, and then transferred to 60° C. paraffin for 30 minutes. These tissues were then blocked in 60° C. paraffin in the usual manner.

Procedure 3. The second celloidin infiltration solution utilized equal parts of ethyl alcohol and ethyl ether as the solvent. All other techniques were identical to those given in procedure 2.

Embedded specimens were sectioned with a rotary microtome at from 5 to 15 microns. The sharpness of the microtome blade was of ultimate concern in that any imperfection in the cutting edge caused considerable shattering of the sclerotized areas. A knife blade angle of from 60° to 75° was found to be most satisfactory. All sections were prepared in serial form for ease of handling.

Microscope slides were cleaned in dichromate cleaning solution and thoroughly rinsed in distilled water. Sections were affixed to slides with the following gelatin fixative as given by Sass (1940).

Solution A

Gelatin	1.0 g
Sodium Benzoate	0.5 g
Distilled Water	100.0 ml

Solution B

Chromium Potassium Sulfate	1.0 g
Distilled Water	90.0 ml
Formalin	10.0 ml

Prior to sectioning, cleaned slides were flooded with a mixture of 1 part solution A to 9 parts solution B. Sectioned ribbons were cut to a desired length and floated on the slide. These were manipulated into position with a small camel's-hair brush. Slides were placed on a 45° C. warming table to flatten ribbons. After a period of time sufficient to evaporate all visible liquid, the slide was removed and permitted to cool at room temperatures. Slides were then

blotted under finger pressure with dampened filter paper and placed in a 45° C. oven to dry. A period of 48 hours was then allowed to elapse to insure complete drying of slides. In addition to heat, an open beaker of concentrated sulphuric acid was inserted in the oven as a desiccant. Very often tissues became loosened or fell off the slides during staining procedures when albumin and other standard affixatives were used, but this seldom occurred when gelatin fixative was properly employed. Two factors were of uppermost importance to insure proper adherence of sections to the slides. Slides had to be thoroughly cleaned and those containing sectioned material had to be completely dried prior to staining.

Two procedures for staining sectioned material were utilized. The first procedure involved the combined use of Delafield's hematoxylin stain for nuclei and Eosin Y stain for cytoplasm and cell walls. The second staining procedure employed Mallory's triple connective tissue stain. This stain was valuable for the differentiation of gross internal structures. The procedures for the use of these stains as given by Kennedy (1949), were followed throughout this study.

Upon completion of staining, all tissues were cleared in beechwood creosote. They were then washed in xylol, flooded with Permount and coverslips applied.

#### Illustrations and Measurements.

Illustrations were made in various ways. The basic outline of structures was projected on tracing paper using a Bausch and Lomb Triple-Purpose Micro-Projector. Further details were added freehand using the compound microscope equipped with a Whipple disc for

verification of position and measurement. Entire structures, such as the abdomen, which collapse when mounted on slides, were drawn from cleared, stained unmounted specimens. By use of a compound microscope equipped with a Whipple disc, these structures were drawn on grid paper. Microscopic mounts were prepared for particular structures or areas of a membranous nature which required increased magnifications.

Drawings were transferred to extra-heavy Ross board and inked. All specimens and their corresponding structures were measured with a calibrated ocular micrometer disc from materials preserved in 95 percent ethyl alcohol. All observations and counts of morphological variations were made from both mounted and unmounted specimens.

## OBSERVATIONS AND COMPARISONS

### The Head

#### Dorsal View.

When viewed dorsally the head (Figs. 2,3,4) is oval, longer than wide and tapers gradually to its posterior margin. The anterior border of the head capsule shows a medial concavity which becomes progressively deeper in T. major, T. corynorhini and T. sphaeronotus respectively.

The head of Trichobius is almost entirely occupied by the vertex dorsally. There are no sutures with which to subdivide this area, but on the basis of chaetotaxy and the degree of sclerotization, relative boundaries may be defined. The vertex extends from the ptilinal membrane (Pt.m.) (Fig. 12) anteriorly and to the occiput (Oc.) posteriorly. The middle part of the vertex, the mediovertex (Mvx.), is represented by a narrow, membranous depression along the dorsal midline. This is continuous with the ptilinal membrane anteriorly and occupies the anterior third of the head in T. major and T. corynorhini and approximately half the anterior portion of T. sphaeronotus. The mediovertex merges with the heavily sclerotized head capsule posteriorly and when observed in cross section is free of setae.

The greater part of the vertex is made up of the laterovertices (Lvx.) which are separated medially by the mediovertex. The surface of the laterovertices is highly convex, forming two dorsal elevations anteriorly. The entire dorsal surface of the vertex, with the

exception of the mediovertex, is covered with numerous microsetae. In *T. major* the laterovertices bear many long setae which are most numerous on the posterior half of the anterior elevations. These setae are longest centrally and diminish in length toward the lateral borders of the vertex. In *T. corynorhini* these setae are more evenly distributed while in *T. sphaeronotus* there is a marked reduction in total number. The setae rarely overlap the mediovertex in *T. major* and *T. sphaeronotus* but it is not uncommon for this to occur in *T. corynorhini*. On the anterolateral margins of the vertex, the eyes (E.) are readily visible in all species and extend beyond the lateral border of the head.

The remainder of the dorsal head capsule is occupied by the occiput. The anterior border of this region is not clearly delineated morphologically, but based on the position of this area in other calypterate flies, the following interpretation was made. The anterior limits of the occiput extend to the posterior border of the vertex. This point of reference is marked by a single longitudinal row of short spines. There is a total of four such spines in *T. major* and *T. corynorhini* and two in *T. sphaeronotus*. The arrangement of these spines is often asymmetrical but their numbers appear to remain constant within each species. Posteriorly the occiput terminates with the postocciput (Poc.) (Fig. 13). The lateral limits of the occiput are defined by the theoretical dorsal limits of the postgenae (Pg.) (Fig. 5). The entire surface of the occiput is smooth which is apparently due to its close association with the prothorax.

The further subdivision of the vertex into a well defined post-vertex, as described by Jobling (1929) for the Nycteriboscinae, is not

recognizable in the species of Trichobius involved in this study. In the latter case the mediovertex does not bifurcate posteriorly to form a triangular postvertical region. The absence of this area becomes an interesting taxonomic character which could be used to separate the Nyteriboscinae of the Old World from the Trichobiinae of the New World. Although this was not mentioned specifically by Jobling (1936), it further supports the systematic separation of the two subfamilies based, in part, on the structure of the head.

#### Lateral View.

In lateral view (Figs. 5,6,7) the heads of all three species are slightly longer vertically than anteroposteriorly, excluding the length of the maxillary palpi (Mx.plp.), with the anterodorsal areas of the laterovertices dome-shaped.

The laterovertices are convex and extend anterolaterally to the frontoclypeus (Frclp.) and ventrally to the membranous cleft (M.c.) arising dorsal to the anterior limits of the genae (Ge.). Posteriorly, the laterovertices extend to the occiput. The lateral limits of the laterovertices and occiput must be defined arbitrarily due to the lack of external and internal morphological landmarks. If a hypothetical line is drawn from the anteroventral margin of the membranous cleft (M.c.) to the lateral midpoint of the postocciput (Poc.), it separates the laterovertices and occiput dorsally from the genae and postgenae ventrally. The chaetotaxy of the laterovertices is similar in T. major and T. corynorhini for in both they bear long setae dorsal to the eyes while those bordering the anterior and posterior margins are considerably shorter. Those setae located ventral to the eye are



directed anteroventrally in T. corynorhini and T. sphaeronotus while those of T. major are directed for the most part posteriorly.

The faceted eyes (E.) are situated in the anterodorsal portion of the laterovertrices in all species. They are comparatively large and are surrounded entirely by the dorsal extension of the membranous cleft. This membranous area is less conspicuous in that region contiguous to the anterior border of the eyes. Individual eye facets are arranged within a lightly sclerotized ring, with the greater number forming a circle and varying numbers found within. The total number of facets varies considerably in T. major and T. corynorhini but to a lesser extent in T. sphaeronotus. When increase or decrease in the total number of facets occurs in T. major and T. sphaeronotus this usually occurs on the perimeter. In T. corynorhini increases generally occur in those facets centrally located and decreases occur perimetrically.

Facets usually appear spherical but numerous variations in shape occur frequently when there is a variation in facet number.

All species show some degree of asymmetry in the number of facets in the right and left eyes. This variation in number of facets within a species was recorded by Jobling (1938) but no data were presented. In the original description of T. major, Coquillett (1899), established the number of facets in each eye at eight. Zeve (1959) presented data showing variations in the number of facets in two populations of T. major represented by a total of 829 specimens. As a result of further investigation, a total variation count has been determined for over two thousand specimens of T. major taken in association with M. velifer

and T. mexicana (Table 2). These data show that the combination of eight facets in both eyes represents the highest percentage of each sample. Less than 3 percent of each population of this species showed other combinations of eye facet number. These ranged from 5 to 11 facets in the right eye and from 5 to 10 in the left.

Variations in the number of eye facets observed in male and female T. corynorhini are presented in Table 3. This species was originally described by Cockerell (1910) as exhibiting sexual dimorphism with regard to eye facet number.

Males of this species were described as having 14 facets whereas females had 11 in each eye. A total of 135 male flies was examined during this study. Of this number, 70 contained 14 facets distributed symmetrically, while 28 showed 13 facets. Other combinations ranging from 11 to 16 in the right eye and 12 to 17 in the left eye were represented in the remainder.

A total of 157 females was examined with 103 exhibiting 11 facets in each eye. In addition to combinations of from 11 to 14 facets in the right eye and 11 to 18 in the left, 12 females had 14 facets in each as did the highest percentage of males.

The least variation in eye facet number was encountered in T. sphaeronotus (Table 4). A total of 1064 specimens was collected and examined. Of these 1054 showed eight facets in the right and left eyes. Three specimens had seven on each side, while seven exhibited a seven and eight combination. In those having eight facets, seven form the periphery and one is located centrally.

The genae (Ge.) are contiguous with the frontoclypeus anteriorly and the rostral membrane (R.m.) ventrally. The genae bear many short anteriorly directed setae.

The postgenae (Pg.) occupy parts of the posterolateral and ventral surfaces of the head and extend posteriorly to the postocciput. Dorsally they fuse with the occiput to form the occipital arch. The posterior one-third of the postgenae are smooth, the remainder being clothed with short anteroventrally directed setae.

The chaetotaxy of the lateral aspect of the head of all three species is quite similar as to position, but with regard to density, T. sphaeronotus shows the greatest overall reduction in number.

#### Ventral View.

The ventral surface of the head capsule (Figs. 8,9,10) is formed posteriorly by the postgenae (Pg.). The postgenae extend posteriorly to the postocciput (Poc.) (Fig. 13) and dorsally to the occiput. Anteriorly they fuse with the genae (Ge.) but the exact point of fusion is not marked externally or internally. These structures are slightly convex with the posterior areas smooth and lacking setae. Anterolaterally directed setae are evenly distributed over the remainder of the postgenal surface in T. major while those of T. corynorhini are to a greater extent directed posteriorly. Only the extreme anterior limits of the postgenae contain setae in T. sphaeronotus and these are anterolaterally directed.

The remainder of the anteroventral surface of the head is formed by the genae (Ge.). These are separated by the broad rostral membrane (R.m.) medially. Posteriorly they fuse with the postgenae. Along the

border of the rostral membrane there is a single line of long, stout setae, which, in all species, are directed anteroventrally.

In ventral view, only the eyes of I. sphaeronotus can be seen projecting beyond the lateral margins of the head.

#### The Antennae.

The structure of the antennae may be seen in dorsal, lateral or anterior views (Figs. 2,3,4,5,6,7,12).

The antennae consist of two segments which project anteriorly from their base on the dorsal surface of the frontoclypeus (Frclp.). The first movable segment, the pedicel (Pd.), is triangular in anterior and lateral view but more spherical in dorsal view. The pedicel bears a distinct furrow, the pedicellar furrow (Pdc.f.), which extends from the anterior margin dorsoposteriorly for two-thirds of its length and divides the segment into two unequal parts. The pedicel is completely sclerotized and is covered with numerous microsetae which become more numerous and slightly longer toward the anteroventral margin. The medial halves of the pedicel bear a single short spine located anterodorsally in all species.

The flagellum (Fl.) consists of two parts, the flagellum proper and the arista (Ar.). The flagellum is spherical in shape and is covered with a dense pile of microsetae over its entire surface. On the anteroventral surface there are several shallow olfactory pits (O.p.) which are surrounded by heavier olfactory setae (O.s.) (Fig. 11). In addition to these pits, there is one deeper pit extending well into the flagellum. This has its external opening

on the dorsolateral surface. The structure of the olfactory pits is more easily studied in sectioned material.

Dorsally the flagellum of all species is produced into a finger-like projection inside the ventral concavity of the pedicel. Just posterior and contiguous to the dorsal projection of the flagellum, the pedicel bears a ventrally directed projection to form the articulation of the two segments. Both articulating surfaces bear short spiny setae which interlock the segments. At the point of entrance of the antennal nerve, innervating the flagellum, there is a thin enclosing membrane between the two segments which is the only connecting membrane.

The second segment of the flagellum, the arista (Ar.), arises from the dorsolateral margin. It is approximately twice as long as the greatest width of the flagellum and projects anterolaterally with its apical limit recurving posteriorly. In I. major and I. corynorhini the tines of the arista consist of from 3 to 4 branched extensions. Those of I. sphaeronotus are not subdivided except for those at the apex.

#### Mouthparts.

The structure of the mouthparts in Trichobius greatly resemble those of the nycteribiidae as described by Jobling (1928). As in the Nycteribiidae and Hippoboscidae (Jobling, 1926), the general area of the mouthparts is divided into the rostrum, haustellum and labella.

Externally (Figs. 5,6,7) only the rostral membrane (R.m.) and maxillary palpi (Mx.plp.) are distinguishable in the rostrum. The rostral membrane is thick and appears fibrous in sectioned material. Its surface is striated horizontally with numerous microsetae through-

out. The membrane is bordered laterally by the genae and genae-postgenal complex posteriorly. Anteriorly it is contiguous with the frontoclypeus. Within the rostral membrane the theca (Thc.) arises anteromedially. When the labium is retracted the membrane invaginates within the head capsule while in the hypognathus condition it appears cone shaped.

The maxillary palpi (Mx.plp.) consist of one segment each. Their dorsal surface is membranous, concave, and bears numerous short microsetae over their entire surface. Ventrally the palpi are sclerotized, convex and clothed with short stout setae. The arrangement and density of these setae vary considerably among species. In I. major and I. corynorhini they are evenly distributed over the ventral surface, but in I. sphaeronotus only the posterior one-half is sparsely clothed. The anterior margin of each palpus bears one long stout bristle which is equal in length to the palpus bearing it. The setae arising from the lateral margins of the palpi are directed anteroventrally as are those of the ventral surface. The palpi of all species are ovate as seen from dorsal and ventral view with rounded anterior margins in I. major and I. corynorhini whereas in I. sphaeronotus they are sinuate. The palpi are attached to the ventral border of the frontoclypeus by the rostral membrane and when viewed laterally are carried slightly elevated.

The theca (Thc.) and the labella (Lbl.) (Figs. 8,9,10) which make up the combined structure of the labium are the only remaining mouth-part structures which may be differentiated externally. The dorso-lateral surface of the theca is attached to the rostral membrane (R.m.).

The labium is held in the prognathus position when retracted and hypognathus when feeding. Ventrally the theca is convex turning sharply dorsal at its lateral and posterior margins. With the exception of the dorsal surface and a narrow ring of membrane at the point of insertion of the labella, the theca is entirely sclerotized. The ventral shape and chaetotaxy of this structure varies in the three species. In I. major (Fig. 8) it is cordiform and approximately equal in length and width. Its surface is sparsely but evenly set with short setae directed anteroventrally, except for two setae on the posterior margin which point posteroventrally. The theca in I. corynorhini (Fig. 9) exhibits a scutiform shape and is a third longer than wide. Just lateral to the ventral midline of the theca there is a single row of anteriorly directed setae on each side which overlap each other. The remainder of the setae are directed anteroventrally, and the posterior third of the theca is bare. The shape of the theca in I. sphaeronotus (Fig. 10) is pyriform, with the posterior margin sinuate, and one-fourth longer than wide. Unlike I. major and I. corynorhini the theca of this species bears very few setae. These are restricted to its ventrolateral margins. Like I. major, those setae located posteriorly are directed posteroventrally while the remainder point anteroventrally. In I. sphaeronotus there are six long, thin, blunt setae arising at the junction of the labella and theca laterally. These are quite constant in number, and in length they approximate the width of the theca.

The labella (Lbl.), which forms the distal portion of the labium, varies slightly in length in I. major and I. corynorhini, averaging

0.07mm and 0.06mm respectively. That of T. sphaeronotus is much longer, averaging 0.13mm in length and extending well beyond the anterior limits of the maxillary palpi. Measurements were made from a sample of one hundred mounted specimens of each species, made up equally of males and females. Variations in length never exceeded 0.01mm plus or minus.

#### Anterior View.

When viewed anteriorly the head of all three species (Fig. 12) is oval in shape with the dorsal margin depressed medially in the region of the mediovertex (Mvx.). Dorsally the mediovertex separates the laterovertices (Lvx.) which bear the eyes (E.), and merges anteriorly with the ptilinal membrane (Pt.m.). The ptilinal membrane projects laterally and fuses with the lateral membranous cleft at the approximate ventral limits of the pedicel (Pdc.). The membranous cleft is bordered laterally by the genae (Ge.) and merges ventrally at the level of the maxillary palpi (Mx.plp.) with the rostral membrane (R.m.). As illustrated the labium, composed of the theca (Thc.) and labella (Lbl.), is figured in the prognathus condition and is suspended ventrally from its attachment to the rostral membrane.

The frontoclypeus (Frclp.) is a lightly sclerotized structure and occupies a more vertical position on the front of the head. The attachments of the frontoclypeus to the other structures on the head are as follows. From its dorsal border the ptilinal membrane arises and is continuous with the membrane of the mediovertex posteriorly. This extends ventrolaterally along the lateral border of the frontoclypeus separating it from the anterior borders of the laterovertices. The frontoclypeus is also bordered laterally by the lateral membranous



cleft while ventrally it is attached to the rostral membrane. The ventral part of this region is projected anteriorly and in dorsal view is more or less spherical in shape. At its dorsal angle the frontoclypeus has fused with the antennal scapes. These regions cannot be morphologically defined except by the attachment of the pedicel and the apertures through which the antennal nerves pass. The regions of the scapes have, by their fusion with the frontoclypeus, formed the antennal pits in which the pedicel and flagellum rest. The entire surface of the frontoclypeus is clothed with a dense pile of microsetae which gives the initial impression of being membranous when observed in unmounted material. The general appearance in frontal view, with reference to basic structural positions and texture, is similar in all three species.

#### Posterior View.

Posteriorly the head (Fig. 13) exhibits the same outline as it does in anterior view. Dorsally the laterovertices fuse medially and posteriorly with the mediovertex. The major part of the posterior head capsule is made up of the occiput (Oc.) dorsally and the postgenae (Pge.) ventrally. Laterally the occiput and postgenae fuse at about the level of the vertical midline of the postocciput (Poc.). The postocciput has no postoccipital suture marking its limits, but is differentiated by a raised and heavily sclerotized rim surrounding the foramen magnum (For.). Dorsally the postocciput bears a process on each side, the occipital condyles (Oc.c.), to which are articulated the lateral cervical sclerites. From the dorsomedial, interior border of the postocciput there is produced a postoccipital apophysis (Poc.a.).

This structure is directed posteroventrally and serves as a point of muscle attachment. With the exception of size and chaetotaxy the posterior aspect of the head capsule is similar in all species.

## The Thorax

Dorsal View.

In dorsal view the thorax (Figs. 14,15,16) appears circular in outline in all three species. The anterior margin is depressed medially at the anterior limits of the median suture (Md.s.). This suture extends posteriorly to the transverse suture (Tr.s.) and is complete in all three species. The median suture subdivides the mesoprescutum (Prsc.2.) into two equal halves which are bounded laterally by the longitudinal membranous cleft (L.m.c.) and posteriorly by the transverse suture. The mesoprescutum fuses with the pronotum (P.1.) anteriorly (Figs. 21,22,23) and the proepisternum (Eps.1.) anterolaterally (Fig. 17).

Posterior to the transverse suture, the mesoscutum (Sct.2.) an undivided plate, extends laterally to the longitudinal membranous cleft and posteriorly to the trans-scutellar suture (Trscl.s.). On the anterolateral border of the mesoscutum the anterior notal wing process (ANP.) projects laterally while posteriorly the mesoscutum bears a smaller projection, the posterior notal wing process (PNP.). These processes are concerned with the articulation of the wing base and will be discussed in more detail later.

The posterior surface of the notum consists of a shield-shaped plate, the mesoscutellum (Scl.2.), which is bounded anteriorly by the trans-scutellar suture (Trscl.s.) and posteriorly by the longitudinal membranous cleft (L.m.c.). The trans-scutellar suture is continuous medially only in I. major. In I. corynorhini the medial portion of this suture is weak and often lacking while in I. sphaeronotus it is completely obliterated.

The extreme lateral limits of the mesoscutellum are fused with the metanotum (P.3.) and the dorsoposterior limits of the laterotergites (T.3.) bearing the axillary cord (Ax.c.).

The chaetotaxy of the dorsal thorax has been used as a means of species determination and, except for the mesoscutellar bristles, is usually constant within each species. In T. major the posteromedially directed setae of the mesoprescutum (Prsc.2.) are denser toward the midline while in T. corynorhini these setae are more evenly distributed over the entire surface. There are 10 posteromedially directed setae to each side of the median suture (Md.s.) on the mesoprescutum of T. sphaeronotus, and these are located on the anterior and lateral margins.

The setae of the mesoscutum (Sct.2.) and mesoprescutum (Prsc.2.) are more dense medially in T. major and more evenly distributed in T. corynorhini. A row of longer setae is located along the posterior border of the mesoscutum of T. major and T. corynorhini. These setae overlap the trans-scutellar suture with those of T. corynorhini twice as long as those of T. major. This row of setae continues along the lateral margin of the mesoscutum to approximately the position of the posterior notal wing process (PNP.) of T. corynorhini and to the lateral limits of the transverse suture (Tr.s.) in T. major. The setal pattern on the mesoscutum of T. sphaeronotus consists mainly of a number of short setae forming a W-shaped, single row following the lateral and posterior margins of this plate. In addition to this row of setae, four longer ones are seen on the lateral margin of the mesoscutum.

The number of bristles on the mesoscutellum (Scl.2.) has been used in conjunction with other morphological structures as a key character-

istic to separate species of Trichobius. The scutellar bristles are long and overlap the posterior limits of the thorax considerably. The number of scutellar bristles shows a surprising variation in T. major (Table 5) and to a lesser extent in T. corynorhini and T. sphaeronotus.

Of the 851 T. major collected in association with the Mexican free-tailed bat, Tadarida brasiliensis mexicana, 15.5 percent of the males had 6 scutellar bristles, 26 percent had 7, 51 percent had 8, 7 percent had 9, and 0.5 percent had 10. From the same population of T. major, 6 percent of the females had 6 scutellar bristles, 17 percent had 7, 66 percent had 8, 8 percent had 9, and 3 percent had 10.

Of the 1,387 T. major, collected from the cave bat Myotis velifer incautus, 0.3 percent of the males had 5 scutellar bristles, 14 percent had 6, 27 percent had 7, 53 percent had 8, 3 percent had 9, and 2 percent had 10. The females of this sample had 4 percent with 6 bristles, 12 percent with 7, 74 percent with 8, 7 percent with 9, and 3 percent with 10.

The number of scutellar bristles was extremely constant in T. corynorhini with only one male having three scutellar bristles and the remaining 291 flies having four.

In T. sphaeronotus the number of scutellar bristles was likewise nearly constant. In this case only two females had three bristles and one had five while the remaining 1,061 specimens of both sexes had four.

The arrangement of the scutellar bristles was not always bilaterally symmetrical nor did they occupy the same position on the meso-scutellum. Very often they formed an irregular transverse line which was not necessarily at right angles to the longitudinal midline of the notum.

As indicated by stippling, there is a narrow band of dense micro-pile on the extreme lateral margins of the mesoprescutum (Prsc.2.), mesoscutum (Sct.2.) and posterior margin of the mesoscutellum (Scl.2.) in all three species.

Although the metathoracic calypters (Ca.3.) are not part of the notum, they are more easily viewed from the dorsal aspect. The calypters are seen as posteriorly projecting lobes arising medially from the base of the halteres (Hlt.).

#### Lateral View.

In lateral view the thorax of all three species presents the same basic plan and is figured separately (Fig. 17) without chaetotaxy for clarity of presentation.

The pleural elements of the mesothorax are separated by the pleural suture (Pls.2.) into an anterior episternum and a posterior epimeron. This division, marked by the pleural suture, serves as a landmark when determining the position of the pleural plates of wing-bearing insects. The pleural suture is expressed externally at its dorsal limits but does not visibly extend ventrally as a definite suture to the dorsal rim of the mesothoracic coxal cavity in Trichobius as it does in most Diptera. As indicated in the figure of the pleural wall, the ventral extension of the pleural suture is shown by a dotted line. This line represents the path of the internal pleural apophysis which is continuous with the pleural suture dorsally and points directly to the pleural wing process (WP.).

Dorsally the longitudinal membranous cleft (L.m.c.) for the most part marks the termination of the pleural complex. In the anteroventral

projection of the longitudinal membranous cleft the anterior thoracic spiracle (A.sp.) occupies a nearly vertical position. Anterior to the prothoracic spiracle the proepisternum (Eps.1.) is continuous with the mesoprescutum (Prsc.2.) dorsally and anteromedially fuses with the pronotum (P.1.) (Fig. 21). The ventral limits of the proepisternum are delineated by a heavily sclerotized triangular region ventral to the anterior spiracle. This area represents a fusion of the proepisternum anteriorly and mesoanepisternum (Aeps.2.) posteriorly. Anteriorly the lateral thorax is composed of a large plate, the mesoanepisternum (Aeps.2.) which extends to the longitudinal membranous cleft dorsally and anteriorly. Posteriorly the mesoanepisternum extends to the pleural suture (Pls.2.) and is fused ventrally with the mesokatepisternum (Keps.2.). There is no anepisternal suture marking the termination of the mesoanepisternum but on the basis of muscle attachment, the ventral limits of this plate may be placed at the approximate longitudinal level of the dorsal rim of the mesothoracic coxal cavity. The mesoanepisternum is divided posteriorly by the vertical membranous cleft (V.m.c.) which is continuous dorsally with the longitudinal membranous cleft (L.m.c.). The pleural wing process (WP.) which lies posterior to the dorsal origin of the vertical membranous cleft, serves as the ventral support of the wing and is produced by the extreme posterodorsal limits of the mesoanepisternum. Anterior to the pleural wing process two small sclerites are found within the membranous cleft regions. The most anterior sclerite, the basalare (Ba.), lies in close contact with the mesoanepisternum from which it is derived. This sclerite bears an internal apodeme for muscle attachment and is associated with wing

movements. The small sclerite anterior to and in close association with the pleural wing process was referred to by Snodgrass (1909) as the parapterum (P.). When first examined, the parapterum appeared to be fused with the pleural wing process but closer study proved its independence. This sclerite does not contain an internal apodeme for muscle attachment and appears to be a displaced fragment of the pleural wing process with no apparent function.

Dorsal and posterior to the pleural suture the mesoanepimeron (Aepm.2.) appears as a V-shaped plate ventral to the subalare (Sa.) lying within the posterior extension of the longitudinal membranous cleft. The surface of the mesoanepimeron is highly concave except for an anterior plate projecting posterolaterally. The mesoanepimeron is bounded ventrally by the mesokatepimeron (Kepm.2.) and posteriorly by the laterotergite (T.3.). The mesokatepimeron is continuous with the laterotergite dorsally while anteriorly it is separated from the episternal plates by the pleural suture (Pls.2.). Upon careful examination of heavily stained specimens the mesokatepimeron (Kepm.2.) may be seen to terminate with a thickened area in the body wall that represents the primitive suture between it and the ventral meron (Mer.2.). The thickenings in the body wall have been figured as intermittent dot-dash lines. This line continues dorsoposteriorly to the base of the haltere (Hlt.) and represents the posterior boundary of the mesokatepimeron.

Three plates, located in the ventroposterior aspect of the laterothorax may be delineated by thickenings in the body wall. The most anterior of these, the meron (Mer.2.), forms the dorsoposterior margin



of the mesothoracic coxal cavity and fuses posteriorly with the anterior limits of the metepisternum (Eps.3.). The ventral extension of the metepisternum forms the anterodorsal rim of the metathoracic coxal cavity and fuses posteriorly with the metepimeron (Epm.3.). The metepimeron completes the dorsolateral rim of the metathoracic coxal cavity posteriorly.

The remaining plate, the laterotergite (T.3.) turns medially at its posterior extension and joins the metanotum (P.3.) which composes most of the posterior thoracic capsule. Arising on the anterodorsal rim of the laterotergite the axillary cord (Ax.c.) extends from the point of connection of the notum and pleuron to the posterior wing margin.

The pleural chaetotaxy of T. major and T. corynorhini (Figs. 18,19) is quite similar. Both species bear numerous evenly spaced setae on the dorsal areas of the mesoanepisternum (Aeps.2.). An additional patch of setae positioned posterior to the vertical membranous cleft (V.m.c.) on the posterior limits of the mesoanepisternum is found in both species, but in T. major they are more dense and for the most part are directed anterodorsally. In the same area of T. sphaeronotus (Fig. 20) the number of setae is greatly reduced and these are directed more dorsally. There are three posterodorsally directed setae on the anterior portion of the mesoanepimeron (Aepm.2.) in T. major and T. corynorhini, and either two or three on the same area in T. sphaeronotus. In all species these short setae are directed posterodorsally and extend over the longitudinal membranous cleft (L.m.c.). Ventrally there are numerous posteroventrally directed setae arising from the mesokatepisternum (Keps.2.)

in T. major and T. corynorhini. In T. sphaeronotus these setae are located only on the anterior and posterior limits of this plate and are considerably less dense. In all three species a dense micropile, indicated by stippling, covers the posterior half of the laterotergite (T.3.) and continues ventrally to include the posterior margin of the meron (Mer.2.), the entire surface of the metepisternum (Eps.3.), metepimeron (Epm.3.) and metanotum (P.3.).

The halteres (Hlt.), which represent the greatly modified metathoracic wings, are entirely covered with a dense micropile. In all species the stalk is annulated and the knob bears two short spines.

#### Ventral View.

Primitively, the sternum consists of the pro-, meso-, and metasternal plates. In the three species of Trichobius only the meso-, and metasternal plates remain.

In T. major and T. corynorhini the entire sternal region (Figs. 21,22) is divided along the longitudinal midline into equal halves by the furcasternal suture (Fu.2.) while in T. sphaeronotus (Fig. 23) this suture is not complete posteriorly on the metasternum (Stn.3.).

The mesosternum (Stn.2.) extends laterally and fuses with the mesokatepisternum (Keps.2.) (Fig. 17) while anteriorly it forms the ventral margin of the prothoracic coxal cavity. The mesosternum is separated from the metasternum by the V-shaped sternacostal suture (Stc.s.) which continues to the lateral margin of the sternum in T. major and T. corynorhini but terminates shortly before the mesothoracic coxal cavity in T. sphaeronotus.

The shield-shaped metasternum deserves considerable attention

because it is extremely definitive in species determination. This plate is produced in a short, blunt posteromedial projection in T. major. In T. corynorhini it is more elongate but is rounded in T. sphaeronotus. The metasternum of all three species fuses laterally with the metepisternum (Eps.3.) (Fig. 17) to complete the posteroventral rim of the mesothoracic coxal cavity.

Anteriorly the pronotum (P.1.) may be viewed conveniently from the venter when the head is removed. The pronotum bears a single blunt projection ventrally on each side of the midline. These processes serve as articulating surfaces for the lateral cervical sclerites which articulate the head with the pronotum. The cervical membrane (Cvx.) is attached to the pronotum and ventrally is continuous with the membrane of the prothoracic coxae (Cx.1.).

With the exception of the anterolateral areas of the mesosternum, the entire surface of the sternal region in all species is clothed with evenly spaced setae. Those setae located on the anterior periphery of the mesosternum of T. major and T. sphaeronotus are directed anteriorly, while only an occasional one assumes this direction in T. corynorhini. A series of longer setae on the posterolateral border of the mesosternum overlaps the mesothoracic coxa (Cx.2.) of T. corynorhini. Other notable characteristic setal patterns are found on the posterior limits of the metasternum. A series of three long setae is found on the lateral limits of the metasternum of T. corynorhini only.

In T. major and T. sphaeronotus there is a continuous single row of long posteriorly projecting setae over the entire length of the posterior margin of the metasternum. In addition to the characteristic

shape of the posteromedial projection of the metasternum, that of T. major is evenly clothed while that of T. corynorhini is bare. As in other body regions the chaetotaxy of T. sphaeronotus is sparse in comparison with T. major and T. corynorhini.

#### Posterior View.

The elements of the metathorax are figured in posterior view (Fig. 24) with the right haltere, left metathoracic coxa, and chaetotaxy omitted to describe more clearly the structures of this greatly modified region.

The metanotum (P.3.) occupies a medial position posteriorly and extends dorsally to the longitudinal membranous cleft (L.m.c.) which separates this plate from the mesoscutellum (Scl.2.). The surface of the metanotum is extremely convex, curving anterolaterally to join the laterotergites (T.3.). This junction is marked by a definite vertical suture. On the ventral extension of this suture, the posterior thoracic spiracle (P.sp.) occupies a vertical position in the body wall just lateral to the base of the haltere (Hlt.). The base of the haltere is represented by a series of fused plates that theoretically represent the axillary sclerites of the greatly reduced and modified metathoracic wing. One component of this area, the metathoracic calypter (Ca.3.), is clearly defined and is of key interest in that its retention strongly suggests that the Streblidae evolved from the calypterate flies. The base of the haltere is surrounded by the metanotum dorsally and by the metepisternum (Eps.3.) ventrally. As in the mesothoracic wing articulating areas, the metanotum would theoretically produce the anterior and posterior metanotal wing processes while the

metepisternum would produce the ventral, or metapleural wing support. These areas and the axillary sclerites of this segment have undergone considerable fusion and are not distinguishable either externally as definite sclerites or internally by musculature. The latter statement is not intended to suggest complete atrophy of the haltere as a functioning structure in Trichobius. The haltere does contain musculature, but the muscles do not insert on definite axillary sclerites.

The ventral surface of the metathorax is greatly modified to connect the abdomen to the thorax. Two lateroposteriorly projecting plates arise from the ventrolateral surface of the metepimeron and insert on the fused first and second tergites (1+2T.) (Fig. 61) of the abdomen. Dorsally the tergum of the abdomen connects with a heavily sclerotized, horizontal ridge on the metanotum which forms a bridge between the two lateral projecting plates. The ventral thickening on the metasternum, forming the limits of the foramen (F.), is connected by membranous cuticle to the abdomen. Dorsal to the foramen the metathoracic phragma (Ph.3.) is surrounded by the lateral plates, and the dorsal ridge of the metanotum. The metathoracic phragma serves as a site for muscle attachment.

#### The Wings.

The wings of Trichobius (Figs. 25,26,27) have six longitudinal veins and three cross-veins. In many respects the basic structure of all three species is similar. The leading edge of the wing is formed by the proximal basicosta (Bac.) and costa (C.) which continues to the apex of the wing and terminates with the distal extension of the third longitudinal vein ( $R_4+5$ ). Between the basicosta and costa there is a weakened area, referred to by some authors as a "fracture". The

subcosta has fused with the proximal end of the radius to form a combined structure (Sc.+R.). The fused portion of the subcosta terminates distally with the humeral cross-vein (H.) that connects with the costa. The humeral cross-vein connects with the costa at the approximate level of the heavily sclerotized fracture line on the basal portion of the radius. Distally the radius (R<sub>1</sub>.) continues as the first longitudinal vein and terminates at the costa. Posterior to the radius the radial sector (Rs.) produces the second and third longitudinal veins, R<sub>2</sub>+3 and R<sub>4</sub>+5 respectively. The fourth longitudinal vein is the media (M<sub>1</sub>+2.). Between this vein and the third longitudinal, the first cross-vein (radio-medial, Rm.) occupies a position in the proximal one-third of R<sub>4</sub>+5 and corresponds to the anterior cross-vein of other Diptera, separating the first basal cell from the submarginal cell.

The fifth longitudinal vein (Cu<sub>1</sub>.) is formed by the third and fourth medial and first cubitus veins. The second cross-vein (M<sub>3</sub>+4.) is located distally between the fourth and fifth longitudinal veins and corresponds to the posterior cross-vein of other Diptera. At the terminal extension of the fifth longitudinal vein (Cu<sub>1</sub>.) a short spur is produced and, like the distal ends of the last three longitudinal veins, does not reach the wing margin.

The sixth longitudinal vein has been termed the second anal (2a.) because in the higher Diptera there is a tendency for the first anal to be lost. This vein originates at the wing base and extends to the third cross-vein, (Cu<sub>2</sub>.) and combines with the latter to form a short spur (Cu<sub>2</sub>+2a.) distally.

The third anal vein (3a.) is rudimentary and remains in the proximal vannal area. The trailing edge of the wing in all species is fringed alternately by short and long hairs which extend from the distal end of the costa to the posterior base of the wing. At the posterior base of the wing the anal fold (Vf.) is well developed and is represented by a darker pigmented membranous area in all three species.

In cross section the six longitudinal veins of all species do not exhibit dorsal sclerotization as they do ventrally. These veins are closed dorsally by the wing membrane which is clothed in a dense even micropile.

The chaetotaxy of the wings in all three species is quite similar. The basicosta (Bac.) and proximal third of the costa (C.) bear long setae which become gradually shorter as they progress toward the apex of the wing. The six longitudinal veins contain a single row of evenly placed setae that are directed anteroapically in T. corynorhini and T. sphaeronotus. On some areas of the third through the sixth longitudinal veins of T. major these setae are quite often posteroapically directed. In all species the distal areas of the radial and medial veins bear longer setae approximating the length of those found on the basicosta. There are no setae on the three lightly sclerotized cross-veins or the humeral cross-vein in any of the three species.

The wings of T. major (Fig. 25) vary from 3.6 to 4.3 mm in length and are approximately twice as long as wide. In this species the distal part of the basal cell narrows slightly near the first cross-vein (Rm.) while the discal cell is slightly enlarged distally near the third

cross-vein ( $Cu_2$ ). This widening is a result of a pronounced curvature in the fifth longitudinal vein ( $Cu_1$ ).

The wings of *T. corynorhini* (Fig. 26) vary from 3.5 to 4.2 mm in length and are three times longer than wide. The basal cell of this species is widest near the first cross-vein. The fifth longitudinal vein ( $Cu_1$ ) is more nearly straight basal to the third cross-vein and, therefore, does not cause a definite enlargement of the distal part of the discal cell as it does in *T. major*.

The wings of *T. sphaeronotus* (Fig. 27) are much shorter, varying from 2.2 to 2.8 mm in length. The fifth longitudinal vein of this species is diagnostic in that just distal to the third cross-vein a definite curvature occurs which is not present in *T. major* or *T. corynorhini*.

Several interesting wing anomalies were noted in *T. major* and to a lesser extent in *T. corynorhini* and *T. sphaeronotus*. In *T. major* the anomalies were mainly a part of the wing venation and were not always bilaterally symmetrical. A series of figures shows a wide diversity of deviations including remnants of the subcosta (Figs. 28,29) and often complete doubling and tripling of cross-veins (Figs. 29,30,31, 32,33). In addition to these involvements several incomplete spurs may be seen arising from the fourth, fifth, and sixth longitudinal veins (Figs. 28,29,33,34,35,36,37). No specimens were encountered with deviations from the basic pattern that included the costa, the first two longitudinal veins and the third anal vein. Data are presented (Table 5) to show the frequency of occurrence of these deviations in relation to the number of scutellar bristles in two



populations of T. major. From the sample of T. major collected in association with the Mexican free-tailed bat, Tadarida brasiliensis mexicana, 8 males (2.2 percent) and 28 females (6.0 percent) showed one or more venation anomalies. This represents 4.2 percent of the total number of males and females collected.

Collections of T. major from the cave bat, Myotis velifer incautus, had almost the same percentage of flies exhibiting wing variations. Twenty-seven (5 percent) of the males and 36 (4 percent) of the females showed some form of venation anomaly. In this case 4.5 percent of the specimens collected were anomalous.

Only one type of venation anomaly occurred in T. corynorhini and this involved a bifurcation of the third cross-vein (Fig. 38). This was found in 6 males (4 percent) and 8 females (5 percent). No other anomalies in the wing structure of this species were noticed.

Three types of wing variations occurred in T. sphaeronotus. The most common of these was the condition in which a double radio-medial vein occurs (Fig. 39). One specimen exhibited a distally projecting spur arising from a single radio-medial vein (Fig. 40), and another had an irregularity in the costa between the first and second longitudinal veins (Fig. 41). Only two males and three females were involved which represents less than 1 percent of the specimens collected.

#### The Wing Articulation.

The wings articulate with the mesothorax by an arrangement of axillary sclerites. The articular sclerites and their relation to the thorax and wing veins are figured diagrammatically (Fig. 42) representing all three species.

The tegula (Tg.) is a small sclerite overlapping the anterior margin of the wing base and positioned anterior to the first axillary (1.Ax.). In all three species this sclerite bears several long setae that equal the length of those found on the closely associated basicoستا (Bac.).

The first axillary (1.Ax.) forms the anterior hinge of the wing base. Proximally it articulates with the anterior notal wing process (ANP.) while posteriorly it is limited by a laterally projecting lobe on the mesoscutum (Sct.2.). The anterior limit of this sclerite is produced as a thin arm, the apex of which points to the anterior portion of the radius (R<sub>1</sub>.). Posteriorly the first axillary articulates laterally with the second axillary (2.Ax.).

The proximal half of the second axillary (2.Ax.) articulates with the first axillary. Its anterior projection points to the intermediate axillary (In.Ax.) at the base of the radius (R<sub>1</sub>.). The ventral surface of this sclerite rests upon the pleural wing process (WP.) (Fig. 17) while posteriorly it lies closely associated with the anterior margin of the third axillary (3.Ax.).

In the three species of Trichobius examined, an intermediate sclerite (In.Ax.) was present at the base of the radius (R<sub>1</sub>.) which appears to be a detached portion of this vein. Distally the intermediate sclerite articulates with the radius by a finger-like projection inserted into a basal indentation of this vein. Proximally this sclerite lies in close contact with the anterior portion of the second axillary (2.Ax.).

The third axillary (3.Ax.) lies posterior to the second axillary and median plates (M.,M<sup>r</sup>.). It is triangular, and articulates proximally

with the posterior end of the second axillary. Distally it is associated with the third anal vein (3a.) while its posterior projection lies close to the fourth axillary (4.Ax.).

The fourth axillary (4.Ax.) lies posterior in the wing base and articulates with the posterior extension of the third axillary. Proximally this sclerite is drawn out into a long, narrow process which articulates with the posterior notal wing process (PNP.) forming the posterior hinge of the wing.

The median plates (M., M'.) are not as easily differentiated as the four principal axillaries but with sufficient staining their outlines may be determined. As indicated by their name they lie in the median area of the wing base. The proximal plate (M.) is closely associated with the anterior portion of the third axillary and the distal surface of the second axillary. The distal plate (M'.) lies anterior to the proximal plate and posterior to the intermediate axillary and proximal end of the radius.

#### The Legs.

Due to the structural similarity exhibited by the legs of I. major and I. corynorhini, only those of the latter species have been figured (Figs. 43,44,45,49,50,51,55,56,57). The legs of I. sphaeronotus warrant separate figures (Figs. 46,47,48,52,53,54,58,59,60) mainly on the basis of chaetotaxy. For descriptive purposes the legs are considered as oriented at right angles to the main axis of the body; thus the surface of the leg resting on the substratum is referred to as the ventral surface, the upper surface as dorsal, the surface facing cephalad as anterior and the surface directed caudad as the posterior surface of the leg or any of its segments.

The prothoracic coxae (Cx.1.) of all species are represented by a single segment vertical to the long axis of the body. In lateral view (Figs. 43,46) they are fusiform in all three species. Dorsally the posterior angle of the coxa articulates with the prothoracic pleuro-coxal process (Plcx.p.1.) (Fig. 17) which projects internally from the ventral margin of the heavily sclerotized triangular area formed by the fusion of the proepisternum (Eps.1.) and mesoanepisternum (Aeps.2.). The pleuro-coxal process articulates in a pit on the dorsolateral rim of the coxa. The ventral articulation of this segment is more easily viewed from the ventral aspect (Fig. 21). This articulation consists of a coxal condyle (Cx.c.1.) projecting internally from the anterolateral rim of the mesosternum (Stn.2.) and inserts in a pit located in the posteroventral surface of the coxa (Cx.1.). The chaetotaxy of the prothoracic coxal segments is sparse in all three species. There are a few long evenly spaced setae on the anterior margin in T. major and T. corynorhini while in T. sphaeronotus (Fig. 46) these are restricted to the anterodorsal and ventral margins. The posterodorsal angle of the coxa in T. sphaeronotus has a small patch of microsetae that are not present in the other two species. The mesothoracic coxae (Cx.2.) consist of two articulating sclerites in all three species (Figs. 44,47). Together these two sclerites form a vertically split, ringed segment consisting of a coxite (Cxt.a.) anteriorly and another coxite (Cxt.b.) posteriorly. From the base of the meron (Mer.2.) the mesothoracic pleuro-coxal process (Plcx.p.2.) (Fig. 17) articulates with the dorsal extension of the posterior coxite. The sternal articulation of this segment (Fig. 21) is expressed by a condylar

process (Cx.c.2.) projecting from the posterolateral margin of the mesosternum (Stn.2.). This condyle articulates with the mesothoracic coxa at a point where the two coxites meet ventrally. A few short setae are present on the mesothoracic coxa of I. sphaeronotus but in I. major and I. corynorhini several long, ventrally directed setae cover the surface of both coxites. The metathoracic coxae (Cx.3.) lie in a longitudinal plane in relation to the body axis. In lateral view (Figs. 45,48) it appears broadest anteriorly, narrows posteriorly, and is slightly longer than broad in all three species. In I. sphaeronotus there is a definite indentation on the anterodorsal angle. The metathoracic coxa (Cx.3.) articulates with the pleuron (Fig. 17) by means of the third pleuro-coxal process (Plcx.p.3.) that originates on the ventral margin of the metepimeron (Epm.3.). Ventrally the metasternum (Stn.3.) (Fig. 21) bears the coxal condyle (Cx.c.3.) on its posterolateral margin. This condyle likewise articulates with a shallow indentation on the anteroventral margin of the metathoracic coxa. In all three species the metathoracic coxae have several posteriorly directed setae laterally and ventrally (Figs. 45,48). On the ventroposterior margin (Figs. 57,60), all three species bear several longer marginal setae that project well over the trochanter (Tr.). The dorsal surface of the third coxa is bare in I. major and I. corynorhini but bears a dense micropile anterior to the posterior articulating membrane in I. sphaeronotus (Fig. 54). Anterolaterally there is an additional patch of longer microsetae on the coxa of this species which is not present on the others.

The pro-, meso-, and metathoracic trochanters (Tr.) are small, single segments located at the distal end of the coxae. The prothoracic

trochanter articulates with the ventral end of the prothoracic coxa (Cx.1.) and is produced as a small condylar process (a.) (Figs. 55,58). There is an additional process (f.) directed laterally on the posterior rim of the coxa which completes the articulation. The surface of the prothoracic trochanter is clothed with several anteroventrally directed setae which in I. major and I. corynorhini (Fig. 55), are more dense than in I. sphaeronotus (Fig. 58). The mesothoracic trochanter of all three species articulates proximally with the mesothoracic coxa (Cx.2.) at point (g.) ventrally (Figs. 56,59) and point (s.) dorsally (Figs. 44, 47). The mesothoracic trochanter is sparsely set with short ventrally directed setae in all three species. The metathoracic trochanter is articulated to coxa 3 at points (c.) and (b.) dorsally, (Figs. 51,54) and at point (p.) ventrally (Figs. 57,60). The trochanters of the metathoracic legs are set with several posteriorly projecting setae on the lateral and ventral surfaces in I. major and I. corynorhini (Figs. 45,57). These setae are less dense in I. sphaeronotus (Figs. 48,60).

The pro-, meso-, and metathoracic femurs (Fm.) are fused to their respective trochanters at points (l.) and (m.) in all three species (Figs. 55,56,57,58,59,60). The metathoracic femurs are slightly longer than those of the pro-, and mesothoracic legs in all three species. This segment is expanded medially and for the most part, where setae occur they are dense in I. major and I. corynorhini and less so in I. sphaeronotus. A series of longer setae is present in all species on the dorsolateral areas of each leg. In all three species the metathoracic femur is bare where it is in close contact

with the abdomen (Figs. 51,54). The tibia (Tb.) or fourth segment of the leg is slender. Those of the metathoracic leg are slightly longer than those of the other segments. The articulation of the tibia with the femur occurs at the lateral points (x.) and (n.) on the pro-, meso-, and metathoracic legs of all three species (Figs. 55,56,57,58, 59,60). The tibiae of the pro-, and metathoracic legs are clothed with evenly spaced, short setae in all three species. In T. major and T. corynorhini the mesothoracic tibia bears a group of slightly longer setae on its anterodorsal margin (Fig. 44). The only difference between the legs of T. major and T. corynorhini is the presence of from 1 to 3 ventral, long, weak setae at the posterior end of the metathoracic tibiae in the former species. The position of these setae is indicated by a dotted line (Fig. 57).

The tarsi (Tar.) consist of five segments with the fifth or pretarsus (Ptar.) bearing the claws and associated structures (Figs. 43, 46). The tarsal segments of each leg are almost identical within each species. The segment nearest the tibia, commonly referred to as the basitarsus, is slightly longer than each of the next remaining three, and in all three species bears short setae. The pretarsus (Ptar.) or terminal segment, bears a pair of stout curved claws (ungues, Un.). At the base of each claw there is a pad-like structure, the pulvillus (Pv.), that bears a dense pile of tenent hairs. Between the bases of the two pulvilli a tapering empodium (Emp.) (Figs. 55,58) projects to the terminal margin of the pretarsus. The empodium of T. major and T. corynorhini is membranous and set with very fine microsetae over its surface (Fig. 55). The empodium of T. sphaeronotus is sclerotized and surrounded with numerous spines (Fig. 58). In all three

species the pretarsus bears many short proximal setae and several long terminal ones.



## The Male Abdomen

Dorsal View.

The dorsal aspect of the male abdomen (Figs. 61,62,63) shows for the most part a membranous nature and therefore assumes different shapes according to the extent of previous blood meals. The anterior border in all species is occupied by the dorsal extension of the fused first and second tergites (1+2T.), which are represented by a narrow sclerotized rim terminating posterolaterally where the abdomen begins to taper posteriorly. The posterolateral margins of the abdomen exhibit a narrow sclerotized rim made up of the fused seventh and eighth tergites (7+8T.) anteriorly and the ninth tergite (9T.) posteriorly. The ninth tergite is notched medially. This notch is deeper in I. corynorhini than in I. major and I. sphaeronotus. The proctiger (Pr.) projects from the apex of the abdomen and bears the anal opening. It is lightly sclerotized laterally and membranous medially. The proctiger of I. major characteristically bears four short setae on both sides of the midline as opposed to four short and one longer one in I. corynorhini. The short, posteriorly projecting setae of the proctiger in the latter species equal the length of the organ. The chaetotaxy on the proctiger in I. sphaeronotus is variable but in this species short setae arise laterally and dorsally as well as terminally.

The entire dorsal surface of the membranous portions of the abdomen is set with microsetae in all three species. This micropile is dense in I. sphaeronotus as compared with I. major and I. corynorhini. In addition to this micropile, each species bears characteristic patches of short setae on each side of the midline. These setae are quite constant

in number and position. In I. major there is a lateral band of posteriorly directed setae that is continuous with those on the lateral aspect of the abdomen. From this band, five single lines of setae radiate toward the midline. It appears that these setae indicate the obsolete dorsal areas of the tergal plates. This opinion is substantiated by the position of the spiracles on the lateral aspect of the abdomen (Fig. 64). These setae are represented by isolated patches lateral to the midline in I. corynorhini. In this species the setal patches are located on the obliterated dorsal limits of the third, fourth, fifth, and seventh tergites. In I. sphaeronotus there are five patches of setae that also lie in the obliterated dorsal tergal plates. As in I. corynorhini, the anterior group of setae are positioned slightly anterior to the obliterated third tergal plate. Posteriorly these setae lie within the dorsal limits of the fourth, fifth, sixth and eighth tergal plates. There are no internal indications that would delineate areas to which these setae correspond.

#### Lateral View.

The lateral aspect of the male abdomen (Figs. 64,65,66) also varies in shape according to the extent of feeding. Anteriorly the fused first and second tergites (1+2T.) extend around the anterior margins of the abdomen and fuse medially on the anteroventral surface. This syntergite (1+2T.) fuses with the metanotum and forms the dorsal part of the connection of the abdomen to the thorax. The ventral part of the connection is membranous, and completes the attachment of the abdomen to the thorax in both sexes of all three species.

The syntergite is drawn out to posterolateral projections which terminate just anterior to the third abdominal spiracles in all three

species. This plate contains two heavily sclerotized ridges in I. major and I. corynorhini. The posterior ridge lies in a vertical plane and projects dorsoanteriorly to meet the anterior ridge. The anterior ridge originates on the anteroventral margin of the syntergite and progresses in a posterodorsal line. This ridge weakens as it turns anteromedially over the dorsal surface of the abdomen. The subdivisions of the syntergite of I. sphaeronotus are much weaker and do not resemble those of the other two species. Dorsally there is a weak ridge projecting anteriorly from the dorsoposterior margin to meet the anterodorsal margin of this plate. On the anterodorsal margin a weak ridge is present where the segment turns medially. Additional lines of thickening occur in the anteromedial portion of the syntergite and are represented by three lines radiating from a common central area. The first two abdominal spiracles are located in the syntergite (1+2T.) of all three species. The first spiracle (Sp.1.) is situated in the anteroventral margin while the second spiracle (Sp.2.) occupies a marginal position posteroventrally. The second spiracle of I. major lies in line between the first and third abdominal spiracles while in the other two species the first three spiracles are not in line.

Ventral to the syntergite (1+2T.) a small triangular plate, the first sternite (1S.), remains as fragmentary evidence of the once continuous plate on the venter of the abdomen. The first sternite lies in close proximity to the anterior margin of the abdomen in I. corynorhini and I. sphaeronotus and posterior to this margin and the first abdominal spiracle in I. major.

Posterior to the first sternite a larger plate, the second sternite (2S.), occupies a position ventral to the syntergite (1+2T.). Dorsally

this plate approximates the posteroventral limits of the syntergite (1+2T.) and extends ventrally as a continuous sclerotized plate to the opposite side of the abdomen. Posteriorly the second sternite extends beyond the posterior margin of the syntergite (1+2T.) in T. major and T. corynorhini but terminates before this boundary in T. sphaeronotus.

Posterior to the syntergite (1+2T.) and the second sternite (2S.) the abdomen is membranous except for the sclerotized plates of the post-abdomen. The third through the sixth abdominal spiracles lie in this membranous area dorsal to the lateral longitudinal line. The third spiracle is near the posterior margin of the syntergite (1+2T.) and the sixth spiracle lies close to the anterodorsal margin of the fused seventh and eighth tergites (7+8T.). The distance between the third and fourth spiracles of T. corynorhini is almost twice as great as that between the fourth and fifth. The third through sixth abdominal spiracles of T. sphaeronotus and T. major are more evenly spaced.

The fifth sternite (5S.) is separated from the syntergite (7+8T.) by a membranous area in all three species. The fifth sternite extends dorsally to just below the lateral longitudinal line, and continues ventrally where it terminates medially on the venter of the abdomen.

The seventh and last spiracle (Sp.7.) is situated in the anterodorsal margin of the syntergite (7+8T.). In T. major and T. corynorhini this plate is fused with the ninth tergite (9T.), but is divided by a membranous cleft in T. sphaeronotus. The fusion in T. major is indicated externally by a strong suture but in T. corynorhini this line (indicated by a broken line, Fig. 65) is weak and requires heavy staining to establish this boundary.

The lateral aspects of the male abdomen in all three species present several characteristic setal patterns which are less dense in T. sphaeronotus. The syntergite (1+2T.) bears several long, stout bristles on its posterior limits in T. corynorhini and T. sphaeronotus and weaker ones in T. major. In T. major and T. corynorhini these bristles extend anteriorly along the dorsal margin and diminish in length medially. The remainder of the syntergite bears short setae in all three species, except for a patch of short spines dorsal to the first abdominal spiracle (Sp.1.) in T. major.

The first sternites (1S.) of all three species bear several posteriorly directed setae on the posterior margins.

In T. major and T. corynorhini the second sternite (2S.) is set with short setae forming a narrow band extending from the anterodorsal surface ventrally, while in T. sphaeronotus only the posterior two-thirds is clothed.

The major portion of the membranous abdominal cuticle in the lateral and ventral areas in all three species bears numerous densely set, short setae. Along the mid-lateral line of T. major and T. corynorhini these setae are directed horizontally and continue posteriorly as a narrow band terminating before the fused seventh and eighth tergites. The setae above this band continue dorsally well above the spiracles in T. major but terminate just above the spiracles in T. sphaeronotus and T. corynorhini. Posterior to the second sternite (2S.) in T. major, there is a wide band of posteroventrally directed setae that terminate in line with the fifth abdominal spiracle. The setae posterior to this band and anterior to the fifth sternite (5S.) are posteriorly oriented. The posteroventrally directed setae behind the second sternite of T. corynorhini

form a narrower band than is found on the same area in I. major. This band terminates on a line half-way between the third and fourth abdominal spiracles. Posterior to this band the setae are posteriorly directed. All the setae of the membranous cuticle of I. sphaeronotus are postero-ventrally directed except for occasional ones dorsal to the fourth and fifth spiracles.

Several long stout bristles are found on the syntergite (7+8T.) of all three species. These bristles occupy the dorsal and dorsoposterior margins of this plate in I. major. Heavier bristles are found on the anterodorsal areas of I. corynorhini. Still heavier bristles line the dorsal margin of the syntergite of I. sphaeronotus. The remainder of the syntergite surfaces are clothed with setae which are approximately half the length of the corresponding bristles in I. major and I. corynorhini. The ventral projection of the syntergite in I. sphaeronotus is free of setae.

The chaetotaxy of the ninth tergite (9T.) is variable in all three species and is limited to the posterior two-thirds. In I. major the setae are of equal strength but in I. corynorhini and I. sphaeronotus stronger setae are present on the dorsoposterior area. The chaetotaxy of this plate is sparse in I. sphaeronotus as compared with the other two species.

#### Ventral View.

In ventral view the sclerotized areas of the abdomen quite often assume varying positions in relation to one another according to the degree of distention following feeding. Several representative specimens were examined with this phenomenon in mind and the figures presented (Figs. 67,68,69) exhibit the general position of the sclerotized plates.

Along the anterior and anterolateral margins the syntergite (1+2T.) may be visible in all species as figured in I. corynorhini. The first sternite (1S.) is represented by a patch of setae on either side of the midline in I. major and I. sphaeronotus and by a well-developed, narrow U-shaped plate in I. corynorhini. The anterior projections of this plate extend anteriorly to meet the anteroventral projection of the syntergite (1+2T.) on the frontal surface of the abdomen. Posteriorly the second sternite (2S.) assumes a characteristic shape in all three species. This plate is rounded laterally and the posterior margin is sinuate in I. major and I. corynorhini but the anterior margin is sinuate only in the latter species. The posterior margin of the second sternite is straight in I. sphaeronotus and the anterior margin is only slightly curved.

In freshly preserved specimens the membranous cuticle posterior to the second sternite often exhibits a fold that extends to the lateral aspects of the sternum. In the accompanying illustrations this fold is indicated by a solid line. Posterior to this fold the membranous cuticle is interrupted by the divided fifth sternite (5S.) which continues laterally and dorsally. The fifth sternites approximate each other medially in all three species.

The ventral extensions of the syntergites (7+8T.) are pointed medially and approximate the longitudinal midline in I. major and I. sphaeronotus. In I. major the triangular complex formed by the syntergite (7+8T.) and ninth tergite (9T.) contains a cleft ventrally between the two components which is not present in I. corynorhini.

Between the anteromedial limits of the ninth tergite the external male genitalia (Gon., Aed.) may be seen projecting anteriorly. These will be discussed separately.

For the most part the ventral chaetotaxy has already been discussed. The setae found on the membranous cuticle are directed somewhat posteriorly depending on the degree of abdominal distention.

#### The Male Genitalia.

The following account, unless specifically excepted, pertains to all three species. In lateral view (Figs. 64,65,66) the external male genitalia are seen projecting ventrally from a membranous extension below the ninth tergite. The cuticle forms a pocket from which protrude the aedeagus (Aed.) and gonapophyses (Gon.). This membranous pocket surrounding the external genitalia is more readily seen when viewed ventrally (Figs. 67,68,69). The entire structure of the genital apparatus of *T. major* is figured separately in anterolateral view (Fig. 70).

The genitalia are theoretically derived from the modified ninth sternite. The ninth sternite is trough-shaped and is represented by the gonapophyseal sheath (Gon.s.) producing the apodeme of the gonapophyses (Gon.a.) dorsally. Ventrally the ninth sternite bifurcates to produce the paired gonapophyses (Gon.). Surrounding the bases of the gonapophyses there are two U-shaped sclerites (S.) attached to the gonapophyseal sheath; only one is figured in its entirety. These sclerites and the lateral margin of the forked sheath attach to the external membranous cuticle forming an inverted pocket through which the aedeagus and gonapophyses protrude.

The term "gonapophyses" was first coined by Lowne (1893-1895) and was later referred to as the "parameres" (Patton and Cushing 1934). The terminology of the genitalia is confused but it appears that the majority of workers prefer the term "gonapophyses".



Dorsal to the aedeagal sheath (Aed.s.) the aedeagal apodeme (Aed.a.) projects anterodorsally. On the posterodorsal border of the aedeagal sheath there is an opening through which the ejaculatory duct passes. From this opening the duct progresses dorsally, as indicated by a dotted line, and turns ventrad where it opens on the distal end of the aedeagus (Aed.) or intromittent organ. The entire structure of the aedeagus lies posterior to the gonapophyseal sheath. The dorsal half of the aedeagus lies in the posterior trough of the gonapophyseal sheath.

The gonapophyses bear one long and one short seta on each fork in all species (Figs. 64,65,66).

#### The Female Abdomen

##### Dorsal View.

The female abdomen becomes greatly distended as the larva develops internally. The shape also varies considerably in correlation with the amount of blood consumed. For the purpose of illustrating the external features of this body region, only non-gravid specimens were used. The female abdomen in dorsal view (Figs. 71,72,73), presents the same outline anteriorly as that of the male. Posteriorly, in the region of the sixth spiracle, all three species bear a characteristic lateral lobe which contains the seventh abdominal spiracle (Sp.7.).

Anteriorly the syntergite (1+2T.) occupies a similar marginal position as seen in the male but is longer anteroposteriorly in the female.

The cuticle posterior to the syntergite (1+2T.) is membranous and contains the third through seventh spiracles. The seventh spiracle lies in the sclerotized tergite in the male but is located in the membranous

cuticle in the female. In I. corynorhini a varying number of membranous cuticular folds anterior to the seventh tergite (7T.) are present in non-distended specimens. These folds are also figured in lateral view (Fig. 75).

The seventh tergite (7T.) is represented by a small, single, median plate anterior to the supra-anal plate (S.a.p.) in I. corynorhini and I. sphaeronotus. The seventh tergite of I. major is represented by a pair of small oval plates located lateral to the midline. Posterior to the seventh tergite the well-defined scutiform, supra-anal plate (S.a.p.) projects posteriorly over the terminalia in I. major and I. corynorhini. This plate is considerably weaker in I. sphaeronotus and, unlike the other two species, bears a dense micropile.

Extending posteriorly from the lateral margins of the supra-anal plate a pair of long heavily sclerotized cerci (Cer.) project over the proctiger (Pr.) in I. major and I. corynorhini. The cerci are greatly reduced in I. sphaeronotus where they are represented by very small terminal rods. Ventral to the cerci the proctiger is membranous dorsally in all three species. The sclerotized areas of the terminal segments are quite constant in shape for each species.

The dorsal chaetotaxy of the female abdomen differs slightly from that of the male. On the posterior margin of the syntergite (1+2T.) the number of short, posteriorly directed setae is quite constant for each species, being five setae on each side of the midline in I. major, eight in I. corynorhini and two in I. sphaeronotus. On the membranous cuticle of I. corynorhini there are five patches of setae lateral to the midline. The first and second patches do not correspond to the obsolete second

and third tergal plates. Posteriorly the third, fourth and fifth patches lie well within the boundaries of the fourth, fifth and seventh tergites respectively. In I. sphaeronotus there are two anterior and two posterior setae lying in close association with the sixth spiracle. The setae of the membranous cuticle of I. major extend from the lateral aspects as medially tapering bands representing the obsolete third through sixth tergites (3,4,5,6,T.).

The reduced sclerotized plates of the seventh tergite (7T.) of I. major bear several posteriorly projecting setae that continue antero-laterally and surround the seventh spiracle (Sp.7.). In I. corynorhini the reduced median plate of the seventh tergite bears two short posteriorly directed setae on the anterolateral margins. In addition to these setae, corresponding pairs arise from the adjacent membranous cuticle anteriorly. The seventh tergite of I. sphaeronotus bears, on each side of the midline, two stout setae that extend over the supra-anal plate (S.a.p.).

The supra-anal plate of I. major bears a row of short anteriorly projecting setae on the anterior margin. This row of setae extends posterolaterally and terminates on the anterior third of the plate. The posterior half of the plate bears several short setae medially and four longer, lateral setae that project beyond the apex of the proctiger (Pr.). The supra-anal plate of I. corynorhini bears two long posteriorly directed setae which extend beyond the ends of the seventh sternal setae. The chaetotaxy of the supra-anal plate in I. sphaeronotus is somewhat variable, but usually six short setae lie anteriorly while four marginal setae project beyond the distal limits of the proctiger.

Lateral View.

The anterior sclerotized segments of the female abdomen (Figs. 74, 75, 76) represent the same segments as those previously described for the male.

The syntergite (1+2T.) in I. major is more triangular in the female and, like the male, bears anterior and posterior ridges. In I. corynorhini this plate exhibits a pronounced posterior elongation. The syntergite of I. sphaeronotus is narrower in the female and bears anterior and posterior ridges that are not present on this area in the male.

The shape of the first sternite (1S.) is variable in the female of all three species. It is usually triangular with rounded angles in I. major and I. sphaeronotus. In I. corynorhini this plate assumes many shapes depending on the degree of sclerotization. The first sternite always lies ventral to the syntergite (1+2T.) and anterior to the second sternite (2S.).

The second sternite of the female in I. major is shorter antero-posteriorly than in the male while that of I. corynorhini is similarly shaped in both sexes. The anterodorsal border of the second sternite is not well defined in the female of I. sphaeronotus but its overall shape appears similar to that of the male. In all three species this plate extends ventrally as a continuous segment to the opposite side of the abdomen.

On the posteroventral areas a large seventh sternite (7S.) is present in all three species. This segment is oval in I. major, triangular in I. sphaeronotus and anteroposteriorly elongated in I. corynorhini. The seventh sternite lies ventral to the seventh spiracle (Sp.7.) and extends posteriorly around the distal end of the abdomen

in all three species. Anteriorly the seventh sternite approximates a vertical line drawn through the sixth spiracle in all three species.

The chaetotaxy of the first abdominal sternite in T. corynorhini is similar to that of the males of all three species. The first sternite bears several short setae over its medial regions in T. major while in T. sphaeronotus they are on the dorsal half of the segment.

The setal patterns of the membranous abdominal regions of T. corynorhini and T. sphaeronotus are quite similar to those of the corresponding males but in T. major the female has setae of two different lengths. In the latter species shorter setae occupy regions above a midlateral line with heavier setae below. A band of dense setae extends in a continuous line that is limited dorsally by the third through sixth spiracles. These setae continue as tapering, sparse, triangular patches dorsally beyond the spiracles.

The seventh sternite of T. major bears evenly spaced posteriorly directed setae over its entire surface. Several longer setae occupy the dorsal margin while posteroventrally only two of these setae are present. In T. corynorhini the posterior third of the seventh sternite bears long setae while those on the remaining surface of this plate are shorter. The chaetotaxy of this sternite in T. sphaeronotus is characterized by long, stout, setae which arise on the posterior half of the plate dorsally while posteroventrally they extend anterior to the vertical midline. Except for three anteriorly directed setae on the anterior margin, the remainder are directed posteriorly. On the membranous area adjacent to the anterior margin of this sternite, a single, long seta is present and points posteroventrally.

### Ventral View.

Ventrally the first sternite (1S.) is represented in all three species (Figs. 77,78,79) by a patch of setae near the anterior margin of the abdomen. These setae lie lateral to the midline. They arise from small plates in I. corynorhini, but in I. major and I. sphaeronotus they are set in the membranous cuticle. An additional plate, that is free of setae, represents the medial fragment of the first sternite in I. corynorhini.

The seventh sternites (7S.) are separated into two identical plates in all three species. These plates in I. major are cleft posteromedially while those of the other species are entire.

Between the seventh sternal plates, the vulva (Vul.), or external opening of the reproductive tract, appears as a transverse slit in the membranous cuticle of all three species. The position of this opening varies with the degree of abdominal distention but it always lies ventral to the proctiger (Pr.).

The heavily sclerotized areas of the proctiger are quite distinctive in I. major and I. corynorhini but these areas are completely membranous in I. sphaeronotus. In I. major this area is in the form of a U-shaped bar while that of I. corynorhini is scutiform. Posteriorly the proctiger continues as a tapering membranous extension in I. major and I. corynorhini.

For the most part the ventral chaetotaxy has already been discussed. The setae appearing on the membranous cuticle are directed posterolaterally and are evenly spaced. In I. corynorhini and I. sphaeronotus these setae extend over the entire ventral surface from the second

sternite to the anterior margins of the seventh sternites. In the figure of I. major (Fig. 77) a membranous fold has been indicated by a solid line posterior to the second sternite. The fold may be present or absent in all three species, depending on the degree of abdominal distention. When present, this fold marks the anterior limits of the setae present on the membranous cuticle. A single longer seta is present on the membranous area adjacent to the anterolateral margin of each of the seventh sternites in all these species.

## DISCUSSION

This study indicates that several morphological changes have occurred in Trichobius which appear to be a result of their adaptations to a parasitic mode of life. These include a highly modified feeding apparatus, loss of sutures in the head and extensive reduction of sclerotized areas in the abdomen. Variations were found within all three species and the author wishes to emphasize that these variations may be geographical. Although a long series of specimens was examined no attempt has been made to revise the taxonomy of Trichobius.

Cockerell (1910), described I. corynorhini as having 14 eye facets in the male and 11 in the female. This statement implies that sexual dimorphism exists in this species. A majority of the specimens collected in this study (Table 3) showed these eye facet combinations, but often the females contained the same number of facets as the males. These data do not suggest sexual dimorphism in this species. No cephalic or thoracic characters of the three species serve to separate the sexes.

The number of scutellar bristles has been used to separate I. major from other species of Trichobius. Jobling (1938), stated that there are eight bristles in I. major and only four in I. corynorhini. In the present study, variations in the number of scutellar bristles in I. major ranged from 5 to 10 (Table 5). In both samples, collected in association with M. velifer and I. brasiliensis, a higher percentage of males showed five, six and seven scutellar bristles. The majority of



both sexes in both samples had eight bristles. It is interesting to note the similarity of variations that occur in the two sample populations of T. major.

In addition to the number of scutellar bristles, Jobling (1938) utilized the setal patterns of the mesoprescutum (Prsc.2.) and mesoscutum (Sct.2.) to separate T. major and T. corynorhini. In all three species (Figs. 14,15,16) the setal patterns of these plates are usually constant. These setal patterns serve as a more reliable character than the number of scutellar bristles for making species determinations.

The occurrence of wing venation anomalies has been recorded by Dybas and Wenzel (1947) as appearing in the streblid Joblingia schmidti Dybas and Wenzel. In their description of this species they recorded that the cross-veins were variable in number and position. It was further stated that these anomalies were asymmetrical. Similar anomalies in T. major and T. sphaeronotus were encountered in the present study. The occurrence of venation anomalies in T. sphaeronotus involved a small segment of the sample. The number and percent of anomalous wings are presented for both sample populations of T. major (Table 5). The total number of individuals with venation anomalies represents 4.2 percent of the specimens collected in association with T. brasiliensis and 4.5 percent of those associated with M. velifer. In both samples there was no correlation between the number of scutellar bristles and anomalous wings. These data suggest that the host-parasite relationships have had no apparent phenotypic effect on the occurrence of anomalous wing venation. Trichobius major has become associated with two very different hosts, M. velifer and T. brasiliensis. Myotis velifer lives under cooler conditions and hibernates during the winter

months. In contrast, T. mexicana lives under much warmer conditions and migrates south during the winter months. It is not uncommon for M. velifer and T. brasiliensis to occupy the same caves during some periods of the year. This may explain the occurrence of similar variations in both samples of T. major. The author is of the opinion that individuals of T. major may transfer from one bat species to the other, thereby establishing gene flow between the gene pools of the two fly populations. This hypothesis is further substantiated by the occurrence of similar eye facet combinations and scutellar bristle numbers in both sample populations of T. major.

The abdomen of Trichobius has undergone considerable modification. Unlike most Diptera, the major portion of this body region is membranous. The reduction, and often complete obliteration, of the tergal and sternal plates permits extensive distention of the membranous cuticle. In both sexes of all three species the anterior sclerotized plates of the preabdomen are similar.

There are great differences of opinion among leading insect morphologists concerning the abdominal segmentation in male Diptera. These differences of opinion have resulted in confused terminology, especially in the postabdominal area. The basic problem appears to lie with the theories concerned with the rotation or torsion of the seventh, eighth and ninth segments. Proponents of these theories state that these segments rotate from  $180^{\circ}$  to  $360^{\circ}$  around the longitudinal body axis from left to right. A comparative study of the abdomen in the Streblidae was presented by Jobling (1951). In this work he stated that the postabdominal segments rotate  $180^{\circ}$ . The evidence submitted for this phenomenon was based on the fact that in adult specimens the

ejaculatory duct was looped over the rectum from left to right. A similar observation was recorded by Crampton (1941) as observed in a comparative study of the Cyclorrapha. In the species of Trichobius examined in this study the ejaculatory duct does loop over the rectum. The ejaculatory duct descends from the dorsum of the abdomen and must loop over the hind-gut in order to join the aedeagus which lies ventrally. It appears that stronger evidence is needed to establish the theory of rotation in the Streblidae. Assuming that a rotation had occurred, Jobling referred to the fused seventh and eighth segments as sternites. The seventh abdominal spiracle lies in the anterodorsal border of these fused segments in all three species (Figs. 64,65,66). Jobling accounted for the presence of the seventh spiracle in this region by stating that the area of the seventh tergite, had become segregated and that this fragment fused with the seventh and eighth segments after the latter had completed the 180° rotation. The fused seventh and eighth segments are herein regarded as tergites (7+8T.) (Figs. 64,65,66) because there are no conclusive external or internal indications of rotation in the adults of the three species examined. If the seventh spiracle comes to lie in a sternite, then it appears that the Streblidae occupy the unique position as being the only recorded example where a spiracle is not in the tergal or pleural area.

In the males of I. major and I. corynorhini (Figs. 64,65) the syntergites (7+8T.) are fused with the ninth tergites (9T.). In the former species the fusion is marked by a strong suture but in the latter it is weak. In I. sphaeronotus (Fig. 66) these plates are divided by a membranous cleft. These conditions are quite constant within each species and serve as valuable aids to species determination.

In the females of all three species the distinctive shapes of the seventh sternites (7S.) (Figs. 74,75,76), cerci (Cer.) and supra-anal plates (S.a.p.) (Figs. 71,72,73) have not been employed in taxonomic works. The shapes of these structures do not vary with the degree of abdominal distention and therefore it is suggested that these characters be utilized in taxonomic keys.

In the present investigation it was necessary to study the internal morphology in order to delineate several external boundaries. These data are being prepared for presentation under separate cover.

## SUMMARY AND CONCLUSIONS

Three species of Trichobius: major Coq., corynorhini Cock., and sphaeronotus Job., were collected. Several caves were inspected in western Oklahoma but only 17 were found to contain streblids. Three species of bats: Myotis velifer incautus (Allen), Plecotus townsendi pallescens (Miller) and Tadarida brasiliensis mexicana (Saussure) were found to be parasitized by these Diptera. For each of these species of flies the host-parasite relationship and distribution is presented. Methods employed to collect parasites and hosts are discussed in detail.

The Streblidae are viviparous and the larvae are retained within the female until fully developed. Only one larva matures at a time and it is deposited on cave substrates where it remains immobile. Within a few moments the larva develops into a pupa. On the basis of these findings, the name Pupipara, which infers the deposition of pupae, is considered misleading.

A detailed comparative morphological examination of the adult species of Trichobius corynorhini, major and sphaeronotus shows that these Diptera have undergone extensive modifications as a result of their adaptations to a parasitic mode of life. The head and abdomen show the greatest amount of change while the thorax has retained most of the structures usually found in wing-bearing insects. The presence of the metathoracic calypters strongly suggests that the Streblidae evolved from calypterate ancestors. No sexual dimorphism was noted in the head or thorax of the three species. Illustrations showing the

details of the external morphology are included for all three species.

Variations within each species and populations of the same species were studied intensively. All three species show variations in the number of eye facets and scutellar bristles. In addition to these variations several wing vein anomalies were found in all three species. Data are presented to show these variations in 2,238 specimens of T. major, 292 T. corynorhini and 1,064 T. sphaeronotus. Comparable numbers of individuals showing the same variations in two populations of T. major appear to indicate gene flow between gene pools of the populations.

Several external morphological structures have been suggested which will aid in the determination of the three species. On the basis of the data presented it is concluded that the three recognized species are morphologically distinct.

Although no unusual microfauna or flora have been recognized in these flies to date, it is suggested that future investigators continue the survey of streblid populations.

#### LITERATURE CITED

- Bequaert, J. C. 1953. The Hippoboscidae or louse flies (Diptera) of mammals and birds. Part I. Entomol. Americana 32: 1-209.
- Bonhag, P. F. 1949. The thoracic mechanism of the adult horsefly (Diptera, Tabanidae). Cornell Univ. Agri. Expt. Sta. Mem. 285: 1-39.
- Bonhag, P. F. 1951. The skeleto-muscular mechanism of the head and abdomen of the adult horsefly (Diptera, Tabanidae). Trans. Am. Entomol. Soc. 77: 131-202.
- Brues, C. T. 1904. Notes on Trichobius and the systematic position of the Streblidae. Am. Museum Nat. Hist. 20: 131-134.
- Cockerell, T. D. A. 1910. A new dipterous parasite of bats. Canad. Entomol. 42: 59-60.
- Cole, F. R. 1927. A study of the terminal abdominal structures of male Diptera. Proc. Calif. Acad. Sci. 16: 397-499.
- Coquillett, D. W. 1899. New genera and species of Nycteribiidae and Hippoboscidae. Canad. Entomol. 31: 333-336.
- Crampton, G. C. 1941. The terminal abdominal structures of male Diptera. Psyche 48: 79-94.
- Crampton, G. C. 1942. The external morphology of the Diptera. Guide to the insects of Connecticut. Part VI, First Fascicle: 10-165.
- Dalquest, W. W. 1954. Netting bats in tropical Mexico. Trans. Kansas Entomol. Soc. 57: 1-10.
- Dufour, L. 1825. Recherches anatomiques sur l'Hippobosque des chevaux. Ann. d. Sci. Nat. 6: 299-322.
- Dufour, L. 1845. Etudes anatomiques et physiologiques sur les insectes Diptères de la famille des Pupipares. Ann. d. Sci. Nat. 3: 49-95.
- Dybas, H. S. and R. L. Wenzel. 1947. A new genus of batflies from Guatemala (Diptera Acalypterae, Streblidae). Fieldiana Zool. 31: 149-154.
- Falcoz, L. 1926. Diptères Pupipares. Faune de France. 14: Paris. 64 p.

- Gervais, P. M. 1844. Atlas de Zoologie, Paris.
- Glass, B. P. and C. M. Ward. 1959. Bats of the genus Myotis in Oklahoma. J. Mamm. 40: 194-201.
- Hagan, H. E. 1951. Embryology of the viviparous insects. Ronald Press Co., New York. 472 p.
- Handley, C. O. 1959. American bats of the genera Euderma and Plecotus. Proc. U. S. Nat. Museum. 110(3417): 95-246.
- Hase, A. 1927. Beobachtungen über das Verhalten des Hirschschlagers sowie den stech- und saugakt der pferdelausfliege Hippobosca equina L. (Diptera, Pupipara). Z. Morphol. Oekol. Tiere, Berlin 8: 187-237.
- Hennig, W. 1941. Die verwandtschaftsbeziehungen der Pupiparen und die morphologie der sternalregion des thorax der Dipteren. Arb. Morph. Taxon. Entomol. Berlin - Dahlem 8: 231-249.
- Imms, A. D. 1948. A general textbook of entomology. E. P. Dutton and Co., New York. 607 p.
- Jameson, D. K. 1959. A survey of the parasites of five species of bats. Southwestern Nat. 4: 61-65.
- Jobling, B. 1926. A comparative study of the head and mouth-parts in the Hippoboscidae (Diptera, Pupipara). Parasitol. 18: 319-349.
- Jobling, B. 1928. The structure of the head and mouth-parts in the Nycteribiidae (Diptera, Pupipara). Parasitol. 20: 254-272.
- Jobling, B. 1929. A comparative study of the head and mouth-parts in the Streblidae (Diptera, Pupipara). Parasitol. 21: 417-445.
- Jobling, B. 1936. A revision of the subfamilies of the Streblidae and the genera of the subfamily Streblinae (Diptera Acalypterae) including a redescription of Metelasmus pseudopterus Coquillett and a description of two new species from Africa. Parasitol. 28: 355-380.
- Jobling, B. 1938. A revision of the species of the genus Trichobius (Diptera Acalypterae, Streblidae). Parasitol. 30: 358-387.
- Jobling, B. 1939a. On some American genera of the Streblidae and their species, with the description of a new species of Trichobius (Diptera Acalypterae). Parasitol. 31: 486-497.
- Jobling, B. 1939b. On the African Streblidae (Diptera Acalypterae) including the morphology of the genus Ascodipteran Adens, and a description of a new species. Parasitol. 31: 147-165.



- Jobling, B. 1940. Description of the young female and of the male of Ascodipteron africanum Jobling (Diptera, Streblidae). Parasitol. 32: 399-404.
- Jobling, B. 1949. Host-parasite relationship between the American Streblidae and the bats, with a new key to the American genera and a record of the Streblidae from Trinidad, British West Indies (Diptera). Parasitol. 39: 315-329.
- Jobling, B. 1951. A record of the Streblidae from the Philippines and other Pacific Islands, including morphology of the abdomen, host-parasite relationship and geographical distribution, and with descriptions of five new species (Diptera). Trans. Roy. Entomol. Soc. London 102: 211-246.
- Karaman, Z. V. 1936. Die Nycteribien Jugoslaviens. Bull. Soc. Sci. Skoplje 17: 9-15.
- Karaman, Z. V. 1939. Beitrag zur Kenntniss der Nycteribien. Bull. Soc. Sci. Skoplje 20: 131-138.
- Karaman, Z. V. 1948. Beitrag zur Kenntniss der Nycteribien. Radjug Acad. Jugoslav. 273: 117-127.
- Kennedy, C. H. 1949. Methods for the study of the internal anatomy of insects. Mimeographed. Univ. of Michigan, Dept. of Zoology, Ann Arbor. 103 p.
- Kessel, E. L. 1952. New host records for Trichobius corynorhini (Diptera, Streblidae). Wasmann J. Biol. 10: 7-8.
- Kessel, Q. C. 1925. A synopsis of the Streblidae of the world. J. New York Entomol. Soc. 33: 11-34.
- Kohls, G. M. 1954. New distributional records for Trichobius corynorhini (Diptera, Streblidae). Wasmann J. Biol. 12: 27-28.
- Kohls, G. M. and W. L. Jellison. 1948. Ectoparasites and other arthropods occurring in Texas bat caves. Nat. Speleological Soc. Bull. 10: 116-117.
- Kolenati, F. A. 1863. Beiträge zur Kenntniss der Phthiriomyiarien. Horae Soc. Entomol. Rossicae 2: 9-109.
- Lowne, B. T. 1893-1895. The anatomy, physiology, morphology, and development of the blowfly (Calliphora erythrocephala). R. H. Porter, London. 778 p.
- Muir, F. 1912. Two new species of Ascodiptera. Bull. Museum Comp. Zool. 54: 351-366.

- Patton, W. S. and E. C. Cushing. 1934. Studies on the higher Diptera of medical and veterinary importance. A revision of the subfamily Calliphorinae based on a comparative study of the male and female terminalia. *Ann. Trop. Med. Parasitol.* 28: 107-314.
- Pratt, H. S. 1899. The anatomy of the female genital tract of the Pupipara as observed in Melophagus ovinus. *Z. für Wiss. Zool.* 66: 16-42.
- Roberts, J. I. 1927. The anatomy and morphology of Hippobosca equina. *Ann. Trop. Med. Parasitol.* 21: 11-22.
- Ross, A. 1959. A redescription of Trichobius adamsi Augustson (Diptera, Streblidae). *Wasmann J. Biol.* 17: 69-74.
- Ross, A. 1960. Distribution records for Trichobius sphaeronotus Jobling, with a first report for Arizona (Diptera, Streblidae). *Pan-Pacific Entomol.* 36: 81-82.
- Salthouse, T. N. 1958. Tetrahydrofuran and its use in insect histology. *Canad. Entomol.* 90: 555-557.
- Sass, J. E. 1940. Botanical microtechnique. McGraw-Hill Book Co., New York. 222 p.
- Smith, H. M. 1934. Notes on some bat-flies of southern Kansas and northern Oklahoma. *J. Kansas Entomol. Soc.* 7: 62-64.
- Snodgrass, R. E. 1909. The throax of insects and the articulation of the wings. *Proc. U. S. Nat. Museum* 36: 511-595.
- Snodgrass, R. E. 1935. Principles of insect morphology. McGraw-Hill Book Co., New York. 667 p.
- Speiser, P. 1900. Über die Strebliden, Fledermausparasiten aus der gruppe der Pupiparen Dipteren. *Arch. Naturgesch.* 66: 31-70.
- Stiles, C. W. and M. A. Nolan. 1930. Key catalogue of parasites reported for the Chiroptera (Bats) with their possible public health importance. *Bull. Nat. Inst. of Health. U. S. Treasury Dept.* 155: 603-742.
- Theodor, O. 1953. On the structure of the genitalia in the Nycteribiidae (Diptera, Pupipara). *Trans. Ninth Intern. Congr. Entomol.* 2: 27-33.
- Townsend, C. H. T. 1893. Notes on Trichobius. *Entomol. News* 3: 177-178.

- Twohy, D. W. 1959. Final technical report on National Institute of Health Grant E-1041 (C1) studies on the blood Protozoa of Oklahoma bats September 1, 1955 - August 31, 1958. Multilithed. Research Foundation, Oklahoma State University, Stillwater.
- Webb, J. E. 1945. On the respiratory mechanism of Melophagus ovinus L. (Diptera). Proc. Zool. Soc. London 115: 218-250.
- Weber, H. 1933. Lehrbuch der Entomologie. Jena. 726 p.
- Zeve, V. H. 1959. Notes on the biology and distribution of Trichobius in northwest Oklahoma. Proc. Oklahoma Acad. Sci. 39: 44-49.
- Zeve, V. H. 1960. Additional records of ectoparasitic insects on bats in Oklahoma. Proc. Oklahoma Acad. Sci. 40: 52-56.

APPENDIX

Table 1. The host-parasite relationships and distribution of Trichobius from Oklahoma Bat Caves, 1958-1961.

HOSTS	*T.c.	T.m.	T.s.	LOCATIONS
<u>Myotis velifer incautus</u> (Allen)		x		Alabaster Caverns
		x		Anderson Creek Cave
		x		Griever Creek Cave
		x		Icebox Cave
	x	x		Reed Cave No. 2
		x		Vickery Cave No. 1
<u>Plecotus townsendi</u> <u>pallescens</u> (Miller)		x		Vickery Cave No. 2
		x		Alabaster Caverns
		x		Anderson Creek Cave
		x		Corn Caves
		x		Griever Creek Cave
		x		Icebox Cave
		x		Lake Cave
		x		Merrihew Cave
		x		Owl Cave
	x		Reed Cave No. 2	
	x		Vickery Cave No. 1	
<u>Tadarida brasiliensis</u> <u>mexicana</u> (Saussure)		x		Alabaster Caverns
		x	x	Conner's Cave
		x	x	Merrihew Cave
		x	x	Reed Cave No. 1
		x	x	Selman's Cave
	x	x	Vickery Cave No. 1	

\*T.c.=Trichobius corynorhini, T.m.=T. major, T.s.=T. sphaeronotus.

Table 2. Occurrence of eye facet combinations in Trichobius major Coq., taken in association with Tadarida brasiliensis mexicana (Saussure) and Myotis velifer incautus (Allen) from Oklahoma Bat Caves, 1958-1961.

FACET COMBINATIONS		NUMBER OF FLIES	
Right Eye	Left Eye	<u>T. mexicana</u>	<u>M. velifer</u>
11	9	2	0
10	10	1	3
9	9	6	3
9	8	5	5
8	10	8	0
8	9	5	5
8	8	795	1356
8	7	6	2
8	6	2	4
8	5	4	0
7	9	3	0
7	8	3	3
7	7	2	2
6	8	3	4
6	7	2	0
5	8	4	0

Table 3. Occurrence of eye facet combinations in male and female Trichobius corynorhini Cock., taken in association with Plecotus townsendi pallescens (Miller) from Oklahoma Bat Caves, 1958-1961.

FACET COMBINATIONS		NUMBER OF FLIES	
Right Eye	Left Eye	Male	Female
17	18	0	3
16	17	1	0
16	16	2	0
15	15	6	0
15	14	3	0
14	15	5	0
14	14	70	12
14	13	7	0
14	12	3	1
13	16	4	0
13	14	4	2
13	13	28	3
12	15	1	0
12	14	0	2
12	12	0	10
11	14	1	12
11	10	0	9
11	11	0	103

Table 4. Occurrence of eye facet combinations in Trichobius sphaeronotus Job., taken in association with Tadarida brasiliensis mexicana (Saussure) from Oklahoma Bat Caves, 1958-1960.

FACET COMBINATIONS		NUMBER OF FLIES
Right Eye	Left Eye	
7	7	3
7	8	1
8	8	1054
8	7	6





PLATE I

Fig. 1. Trichobius major Coq., dorsal view of female.

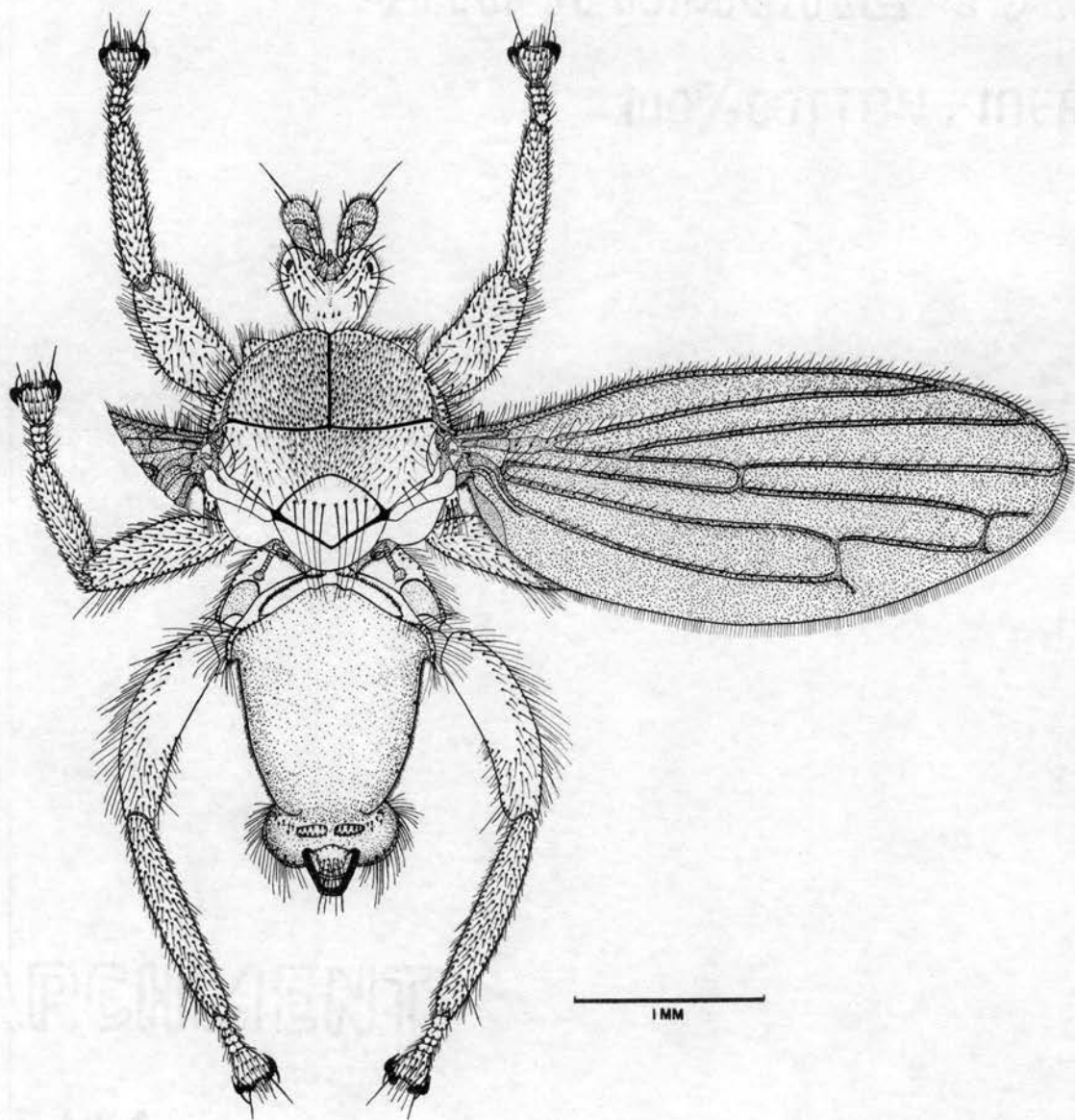


Fig. 1

PLATE II

Fig. 2. Trichobius major Coq., dorsal view of head.

Fig. 3. Trichobius corynorhini Cock., dorsal view of head.

Ar. -----	Arista
E. -----	Eye
Fl. -----	Flagellum
Frclp. -----	Frontoclypeus
Lbl. -----	Labella
Lvx. -----	Laterovertex
Mvx. -----	Mediovertex
Mx.plp. -----	Maxillary palpus
Oc. -----	Occiput
Pdc. -----	Pedicel
Pdc.f. -----	Pedicellar furrow

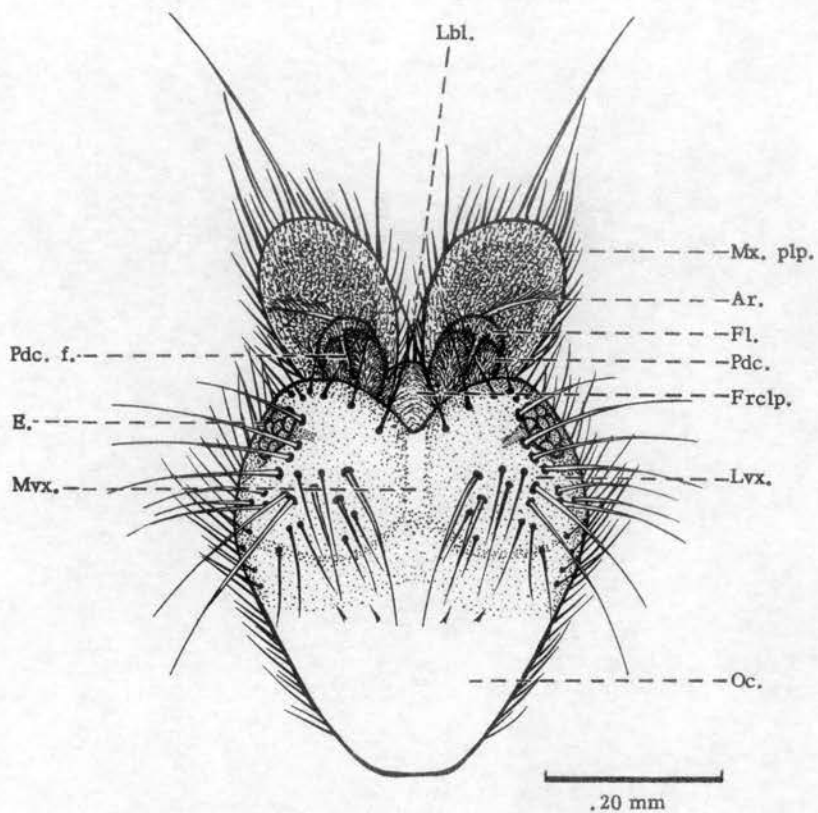


Fig. 2

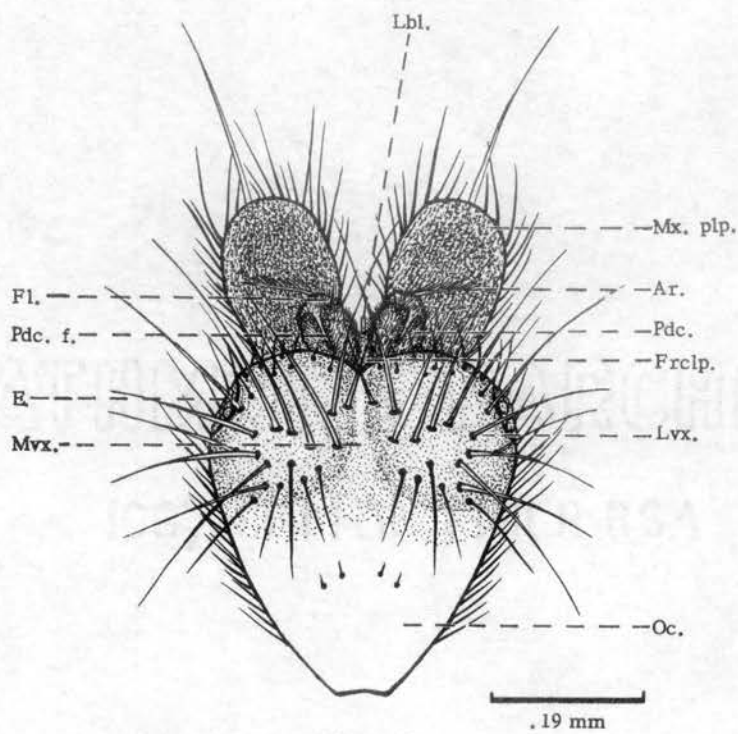


Fig. 3

PLATE III

Fig. 4. Trichobius sphaeronotus Job., dorsal view of head.

Fig. 5. Trichobius major Coq., lateral view of head.

Ar. -----	Arista
E. -----	Eye
Fl. -----	Flagellum
Frclp. -----	Frontoclypeus
Ge. -----	Gena
Lbl. -----	Labella
Lvx. -----	Laterovertex
M.c. -----	Membranous cleft
Mvx. -----	Mediovertex
Mx.plp. -----	Maxillary palpus
Oc. -----	Occiput
Pdc. -----	Pedicel
Pdc.f. -----	Pedicellar furrow
Pg. -----	Postgena
Poc. -----	Postocciput
R.m. -----	Rostral membrane
Thc. -----	Theca

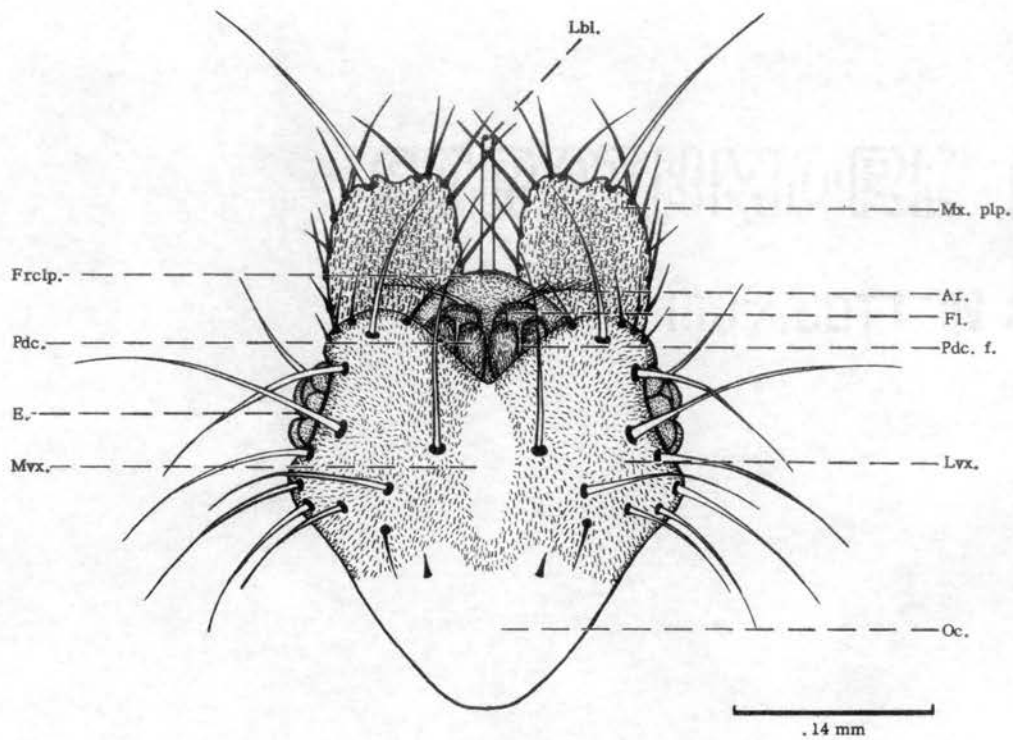


Fig. 4

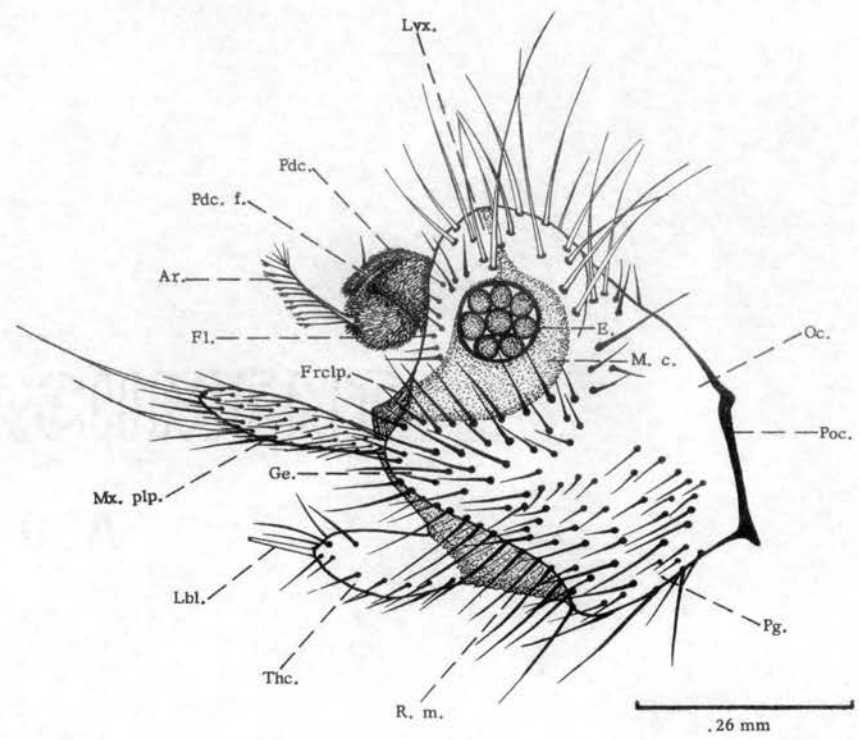


Fig. 5

PLATE IV

Fig. 6. Trichobius corynorhini Cock., lateral view of head.

Fig. 7. Trichobius sphaeronotus Job., lateral view of head.

Ar. -----	Arista
E. -----	Eye
Ge. -----	Gena
Fl. -----	Flagellum
Frclp. -----	Frontoclypeus
Lbl. -----	Labella
M.c. -----	Membranous cleft
Mx.plp. -----	Maxillary palpus
Lvx. -----	Lateroververtex
Oc. -----	Occiput
Pdc. -----	Pedicel
Pdc.f. -----	Pedicellar furrow
Pg. -----	Postgena
Poc. -----	Postocciput
R.m. -----	Rostral membrane
Thc. -----	Theca

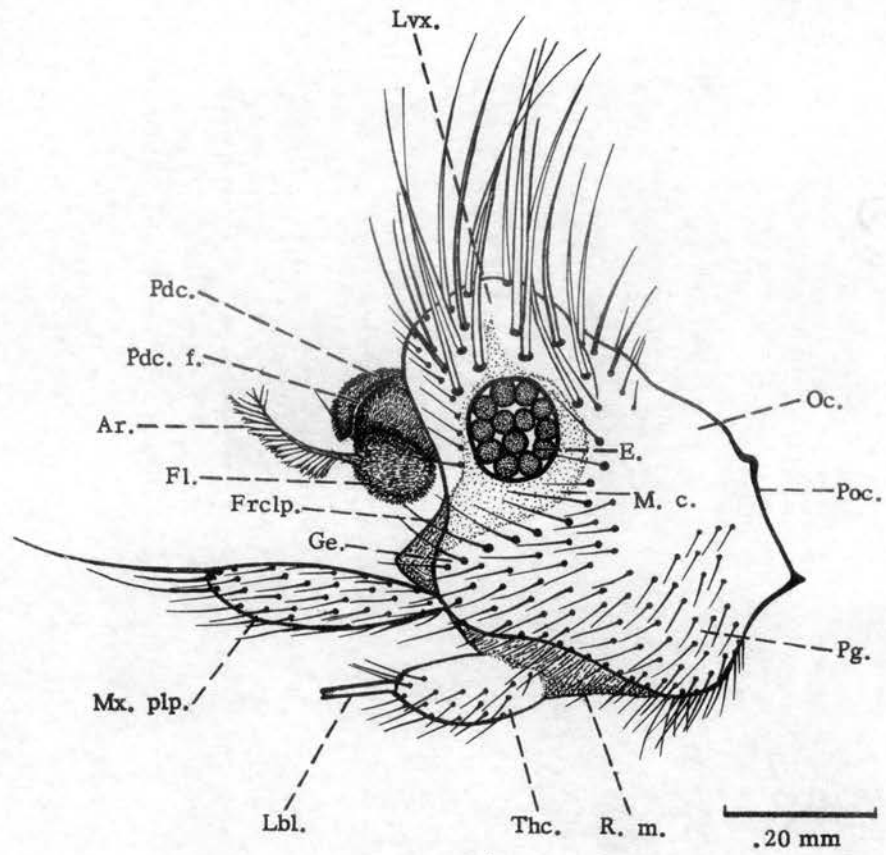


Fig. 6

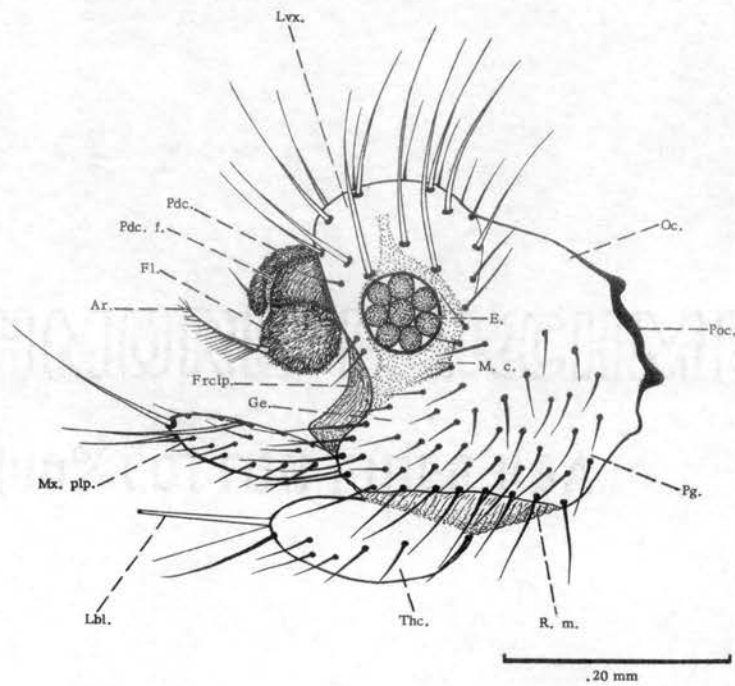


Fig. 7



PLATE V

Fig. 8. Trichobius major Coq., ventral view of head.

Fig. 9. Trichobius corynorhini Cock., ventral view of head.

Frclp. -----	Frontoclypeus
Ge. -----	Gena
Lbl. -----	Labella
Mx.plp. -----	Maxillary palpus
Pg. -----	Postgena
R.m. -----	Rostral membrane
Thc. -----	Theca

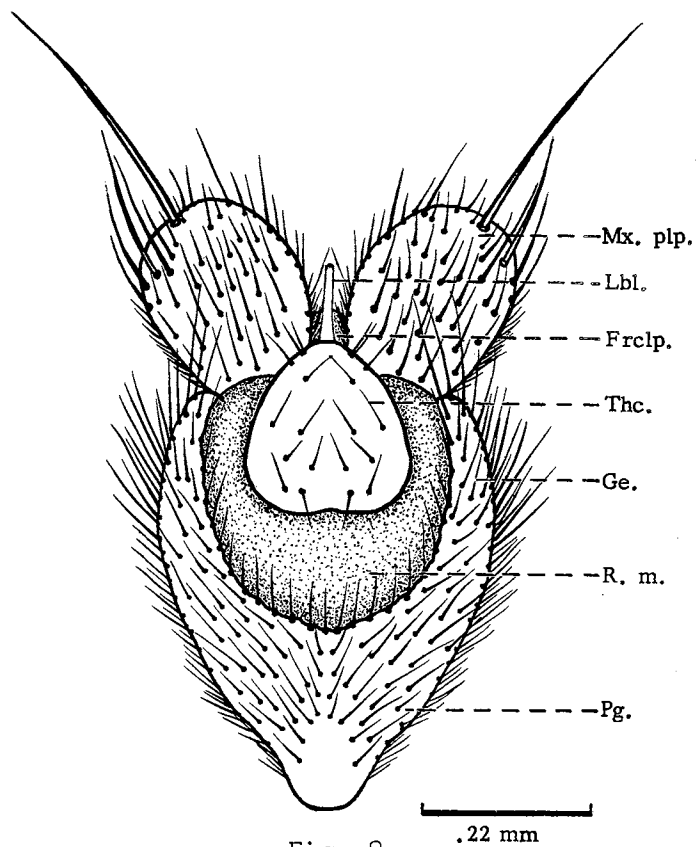


Fig. 8

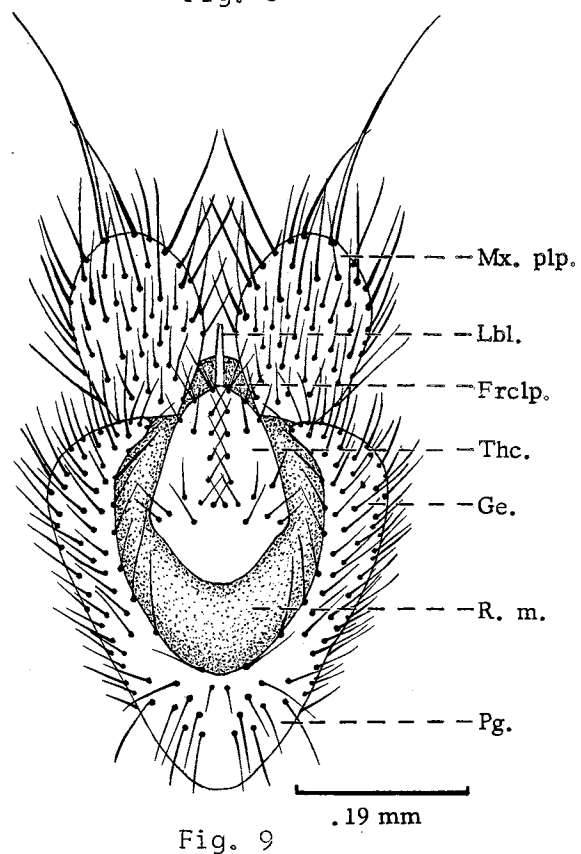


Fig. 9

PLATE VI

Fig. 10. Trichobius sphaeronotus Job., ventral view of head.

Fig. 11. Trichobius spp., sagittal view of antenna.

Ar. _____	Arista
E. _____	Eye
Fl. _____	Flagellum
Frclp. _____	Frontoclypeus
Ge. _____	Gena
Lbl. _____	Labella
Mx.plp. _____	Maxillary palpus
O.p. _____	Olfactory pit
O.s. _____	Olfactory seta
Pdc. _____	Pedicel
Pg. _____	Postgena
R.m. _____	Rostral membrane
Thc. _____	Theca

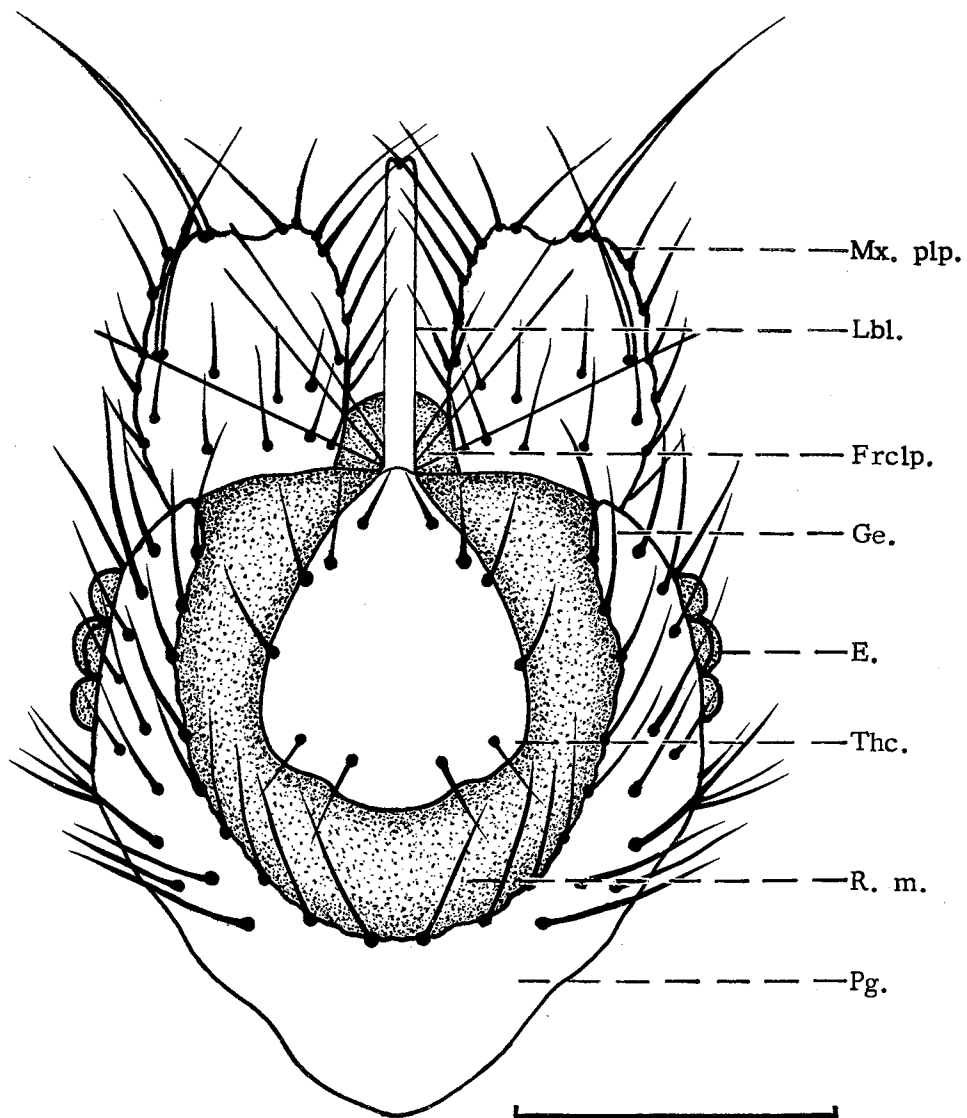


Fig. 10

.15 mm

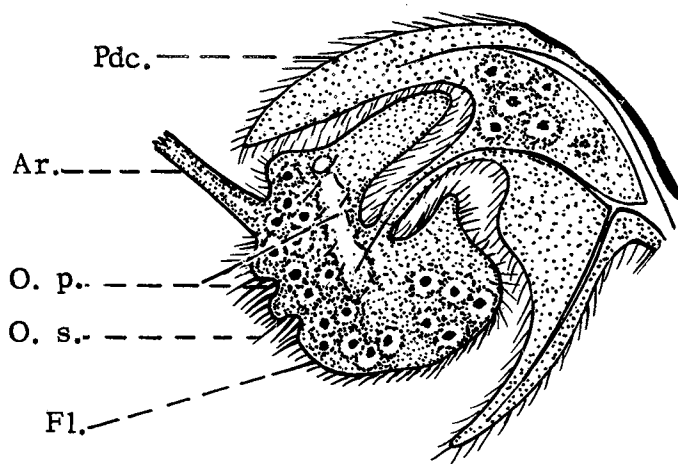


Fig. 11

PLATE VII

Fig. 12. Trichobius spp., anterior view of head.

Fig. 13. Trichobius spp., posterior view of head.

Ar. -----	Arista
E. -----	Eye
Fl. -----	Flagellum
For. -----	Foramen magnum
Frclp. -----	Frontoclypeus
Ge. -----	Gena
Lbl. -----	Labella
Lvx. -----	Laterovertex
Mvx. -----	Mediovertex
Mx.plp. -----	Maxillary palpus
Oc. -----	Occiput
Oc.c. -----	Occipital condyle
Pdc. -----	Pedicel
Pdc.f. -----	Pedicellar furrow
Pg. -----	Postgena
Poc. -----	Postocciput
Poc.a. -----	Postoccipital apophysis
Pt.m. -----	Ptilinal membrane
Ri.m. -----	Rostral membrane
Thc. -----	Theca

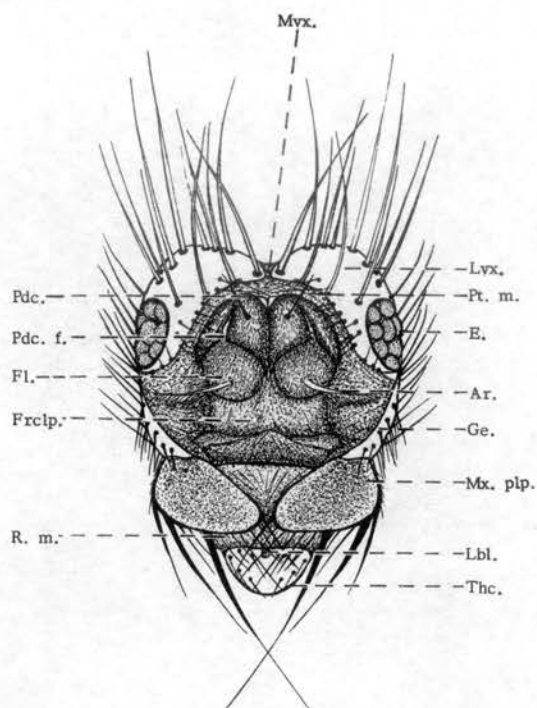


Fig. 12

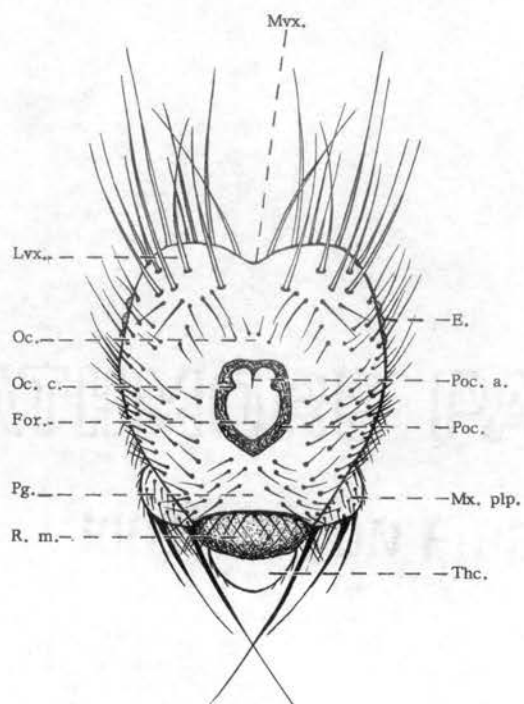


Fig. 13

PLATE VIII

Fig. 14. Trichobius major Coq., dorsal view of thorax.

Fig. 15. Trichobius corynorhini Cock., dorsal view of thorax.

ANP. -----	Anterior notal wing process
Ax.c. -----	Axillary cord
Ca.3. -----	Metathoracic calypter
Hlt. -----	Haltere
L.m.c. -----	Longitudinal membranous cleft
Md.s. -----	Median suture
P.3. -----	Metanotum
Pl.2. -----	Mesopleuron
PNP. -----	Posterior notal wing process
Prsc.2. -----	Mesoprescutum
Scl.2. -----	Mesoscutellum
Sct.2. -----	Mesoscutum
T.3. -----	Laterotergite
Tr.s. -----	Transverse suture
Trscl.s. -----	Trans-scutellar suture

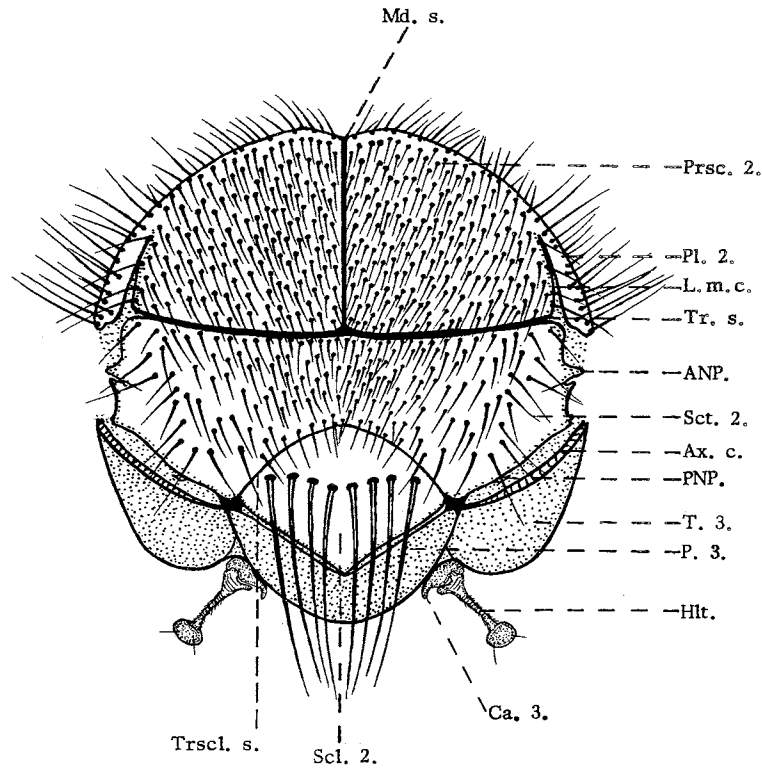


Fig. 14

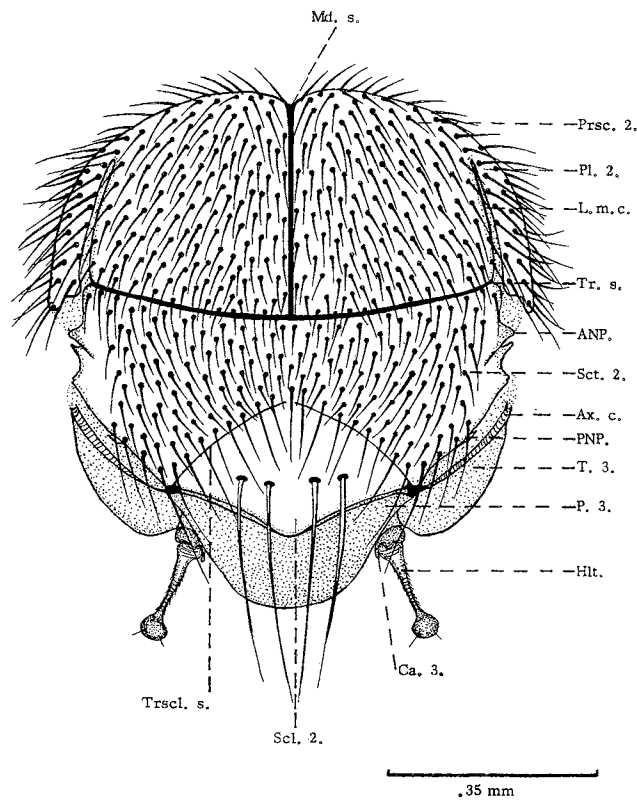


Fig. 15



PLATE IX

Fig. 16. Trichobius sphaeronotus Job., dorsal view of thorax.

Fig. 17. Trichobius spp., diagrammatic lateral view of thorax.

A.sp. -----	Anterior thoracic spiracle
Aepm.2. -----	Mesoanepimeron
Aeps.2. -----	Mesoanepisternum
ANP. -----	Anterior notal wing process
Ax.c. -----	Axillary cord
Ba. -----	Basalare
Ca.3. -----	Metathoracic calypter
Cx.1.,2.,3. -----	Pro-, meso-, and metathoracic coxae
Cxt.a.,b. -----	Meso- and metathoracic coxal coxites
Epm.3. -----	Metepimeron
Eps.1. -----	Proepisternum
Eps.3. -----	Metepisternum
Hlt. -----	Haltere
Kepm.2. -----	Mesokatepimeron
Keps.2. -----	Mesokatepisternum
L.m.c. -----	Longitudinal membranous cleft
Md.s. -----	Median suture
Mer.2. -----	Meron
P. -----	Parapterum
P.3. -----	Metanotum
Pl.2. -----	Mesopleuron
Plcx.p.1.,2.,3. -----	Pleuro-coxal processes
Pls.2. -----	Pleural suture
PNP. -----	Posterior notal wing process
Prsc.2. -----	Mesoprescutum
Sa. -----	Subalare
Scl.2. -----	Mesoscutellum
Sct.2. -----	Mesoscutum
Stc.s. -----	Sternacostal suture
Stn.2. -----	Mesosternum
Stn.3. -----	Metasternum
T.3. -----	Laterotergite
Tr.s. -----	Transverse suture
Trscl.s. -----	Trans-scutellar suture
V.m.c. -----	Vertical membranous cleft
WP. -----	Pleural wing process

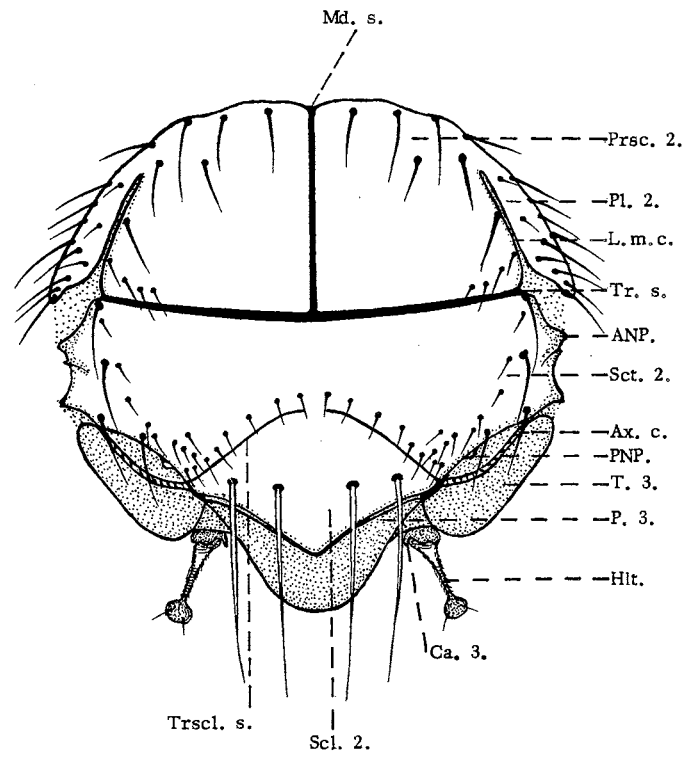


Fig. 16

.27 mm

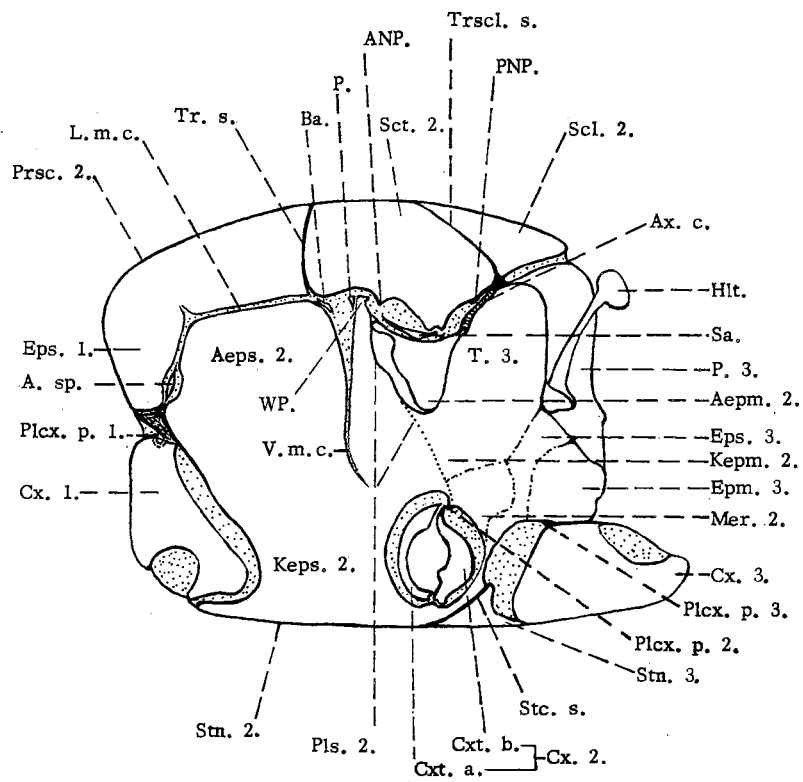


Fig. 17

PLATE X

Fig. 18. Trichobius major Coq., lateral view of thorax.

Fig. 19. Trichobius corynorhini Cock., lateral view of thorax.

A. sp. -----	Anterior thoracic spiracle
Ba. -----	Basalare
Aepm.2. -----	Mesoanepimeron
Aeps.2. -----	Mesoanepisternum
ANP. -----	Anterior notal wing process
Ax. c. -----	Axillary cord
Cx.1.,2.,3. -----	Pro-, meso-, and metathoracic coxae
Cxt.a.,b. -----	Mesothoracic coxal coxites
Epm.3. -----	Metepimeron
Eps.1. -----	Proepisternum
Eps.3. -----	Metepisternum
Hlt. -----	Haltere
Kepm.2. -----	Mesokatepimeron
Keps.2. -----	Mesokatepisternum
L.m.c. -----	Longitudinal membranous cleft
Mer.2. -----	Meron
P. -----	Parapterum
P.3. -----	Metanotum
Pls.2. -----	Pleural suture
PNP. -----	Posterior notal wing process
Prsc.2. -----	Mesoprescutum
Sa. -----	Subalare
Scl.2. -----	Mesoscutellum
Sct.2. -----	Mesoscutum
Stc.s. -----	Sternacostal suture
Stn.2. -----	Mesosternum
Stn.3. -----	Metasternum
T.3. -----	Laterotergite
Tr.s. -----	Transverse suture
Trscl.s. -----	Trans-scutellar suture
V.m.c. -----	Vertical membranous cleft
WP. -----	Pleural wing process

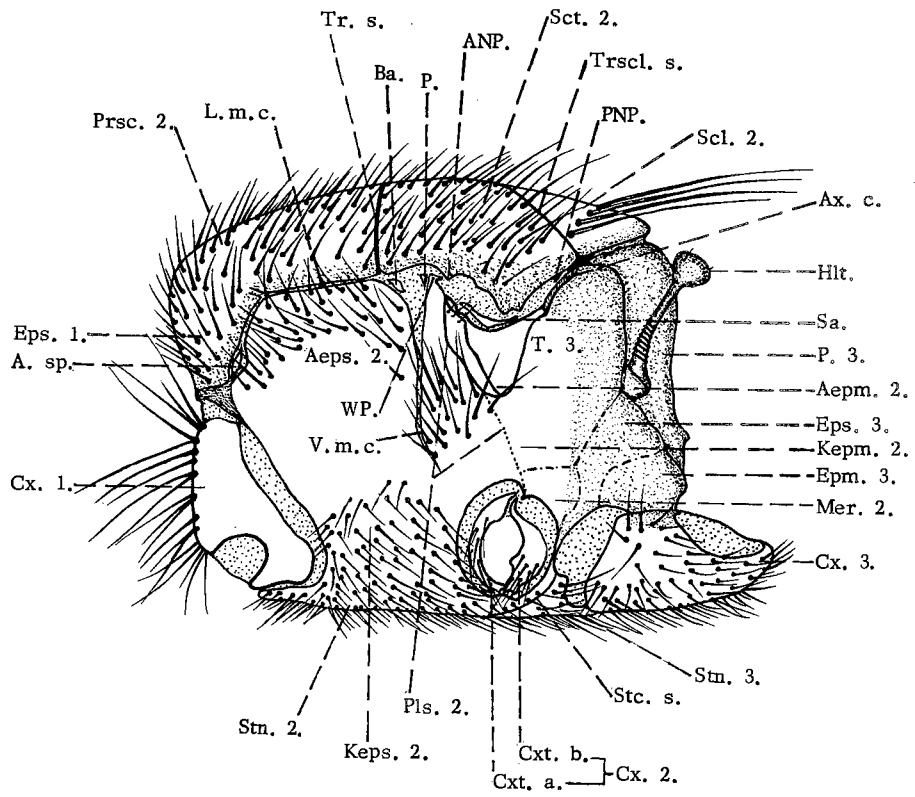


Fig. 18

.35 mm

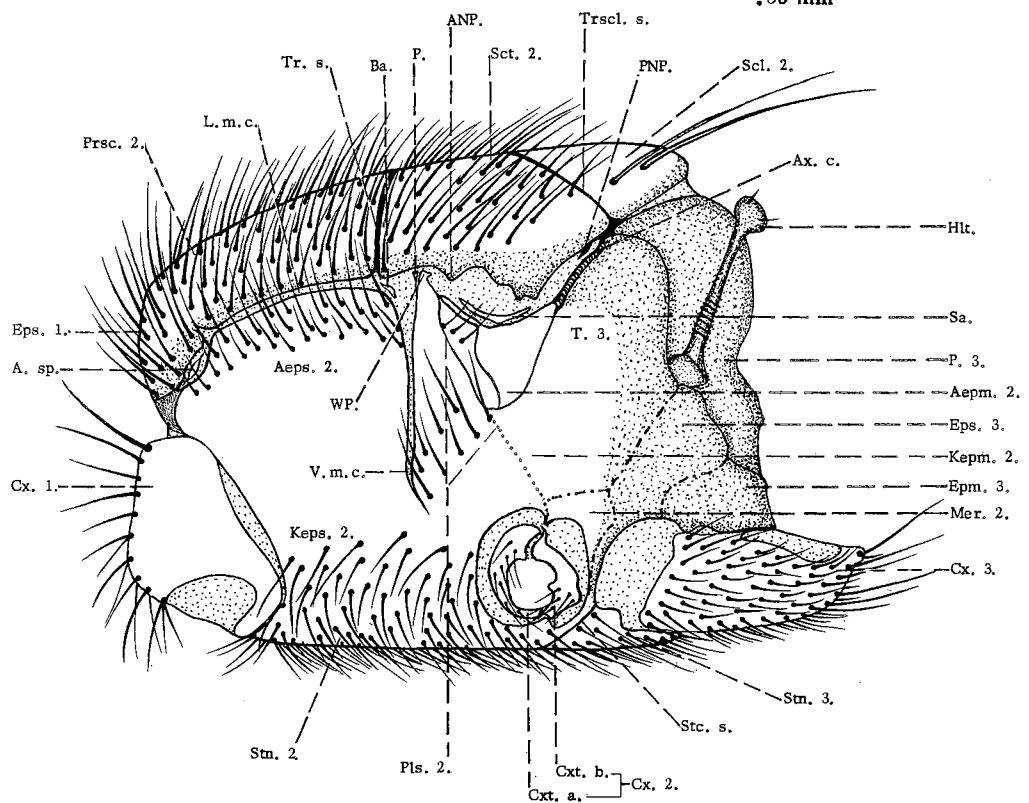


Fig. 19

.27 mm

PLATE XI

Fig. 20. Trichobius sphaeronotus Job., lateral view of thorax.

Fig. 21. Trichobius major Coq., ventral view of thorax.

A.sp.	-----	Anterior thoracic spiracle
Ba.	-----	Basalare
Aepm.2.	-----	Mesoanepimeron
Aeps.2.	-----	Mesoanepisternum
ANP.	-----	Anterior notal wing process
Ax.c.	-----	Axillary cord
Cvx.	-----	Cervix
Cx.1.,2.,3.	-----	Pro-, meso-, and metathoracic coxae
Cx.c.1.,2.,3.	-----	Coxal condyles
Cxt.a.,b.	-----	Mesothoracic coxal coxites
Epm.3.	-----	Metepimeron
Eps.1.	-----	Proepisternum
Eps.3.	-----	Metepisternum
Fu.2.	-----	Furcasternal suture
Hlt.	-----	Haltere
Kepm.2.	-----	Mesokatepimeron
Keps.2.	-----	Mesokatepisternum
L.m.c.	-----	Longitudinal membranous cleft
Mer.2.	-----	Meron
P.	-----	Parapterum
P.1.	-----	Pronotum
P.3.	-----	Metanotum
Pls.2.	-----	Pleural suture
PNP.	-----	Posterior notal wing process
Prsc.2.	-----	Mesoprescutum
Sa.	-----	Subalare
Scl.2.	-----	Mesoscutellum
Sct.2.	-----	Mesoscutum
Stc.s.	-----	Sternacostal suture
Stn.2.	-----	Mesosternum
Stn.3.	-----	Metasternum
T.3.	-----	Laterotergite
Tr.	-----	Trochanter
Tr.s.	-----	Transverse suture
Trscl.s.	-----	Trans-scutellar suture
V.m.c.	-----	Vertical membranous cleft
WP.	-----	Pleural wing process

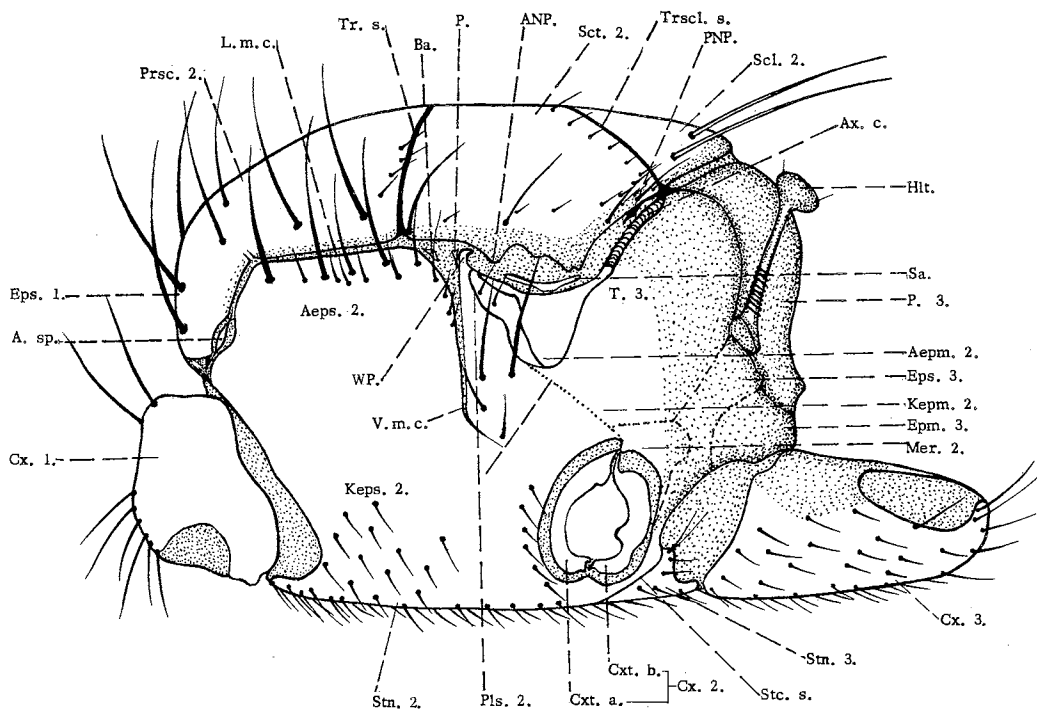


Fig. 20

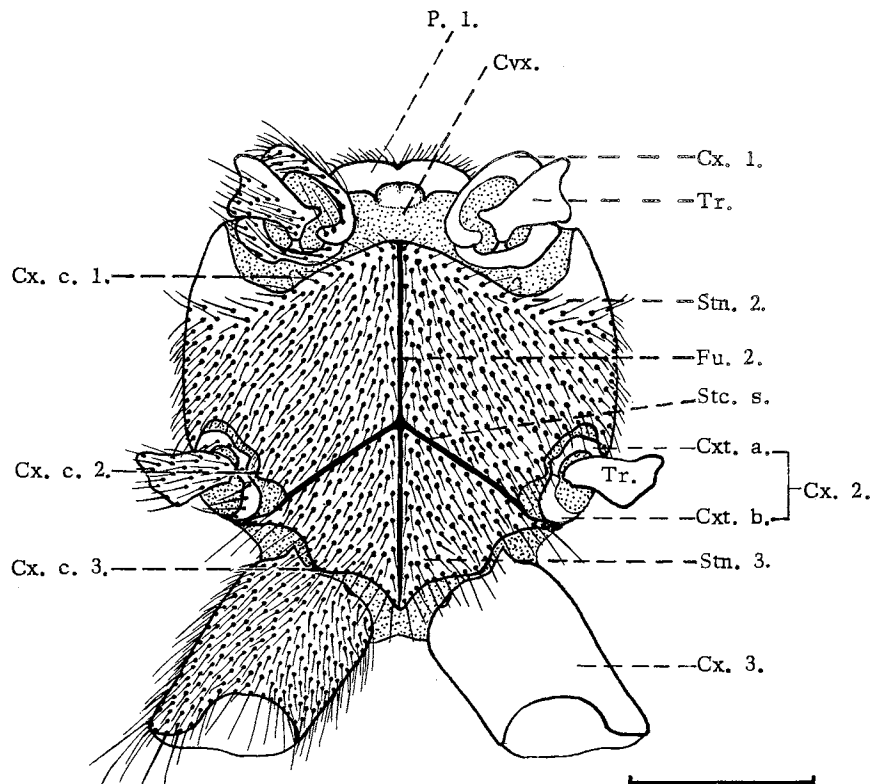


Fig. 21

PLATE XII

Fig. 22. Trichobius corynorhini Cock., ventral view of thorax.

Fig. 23. Trichobius sphaeronotus Job., ventral view of thorax.

Cvx. -----	Cervix
Cx.1.,2.,3. -----	Pro-, meso-, and metathoracic coxae
Cxt.a.,b. -----	Mesothoracic coxal coxites
Fu.2. -----	Furcasternal suture
P.1. -----	Pronotum
Stc.s. -----	Sternacostal suture
Stn.2. -----	Mesosternum
Stn.3. -----	Metasternum
Tr. -----	Trochanter

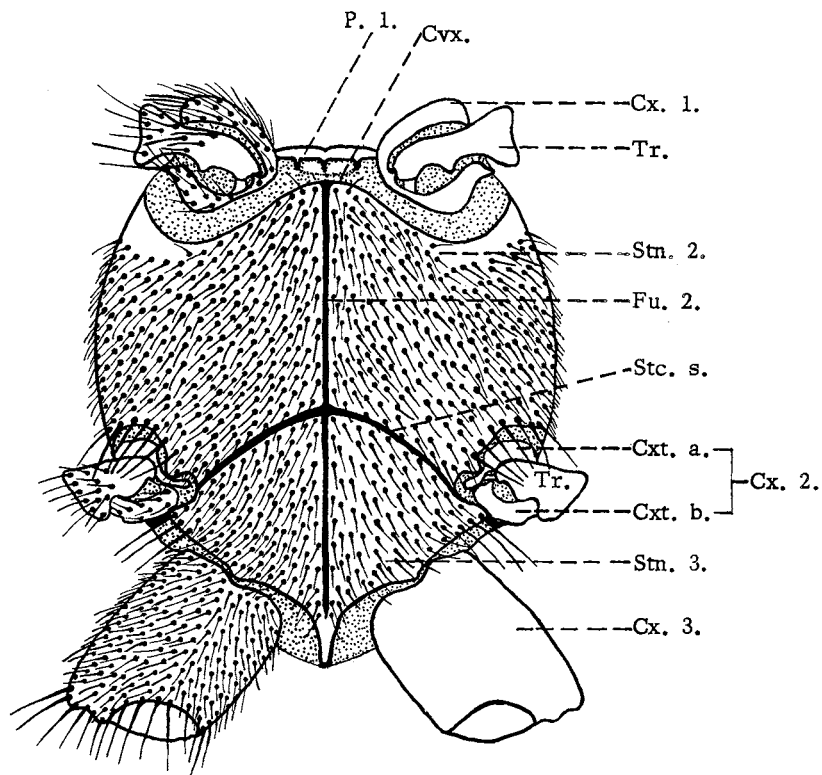


Fig. 22

— .40 mm

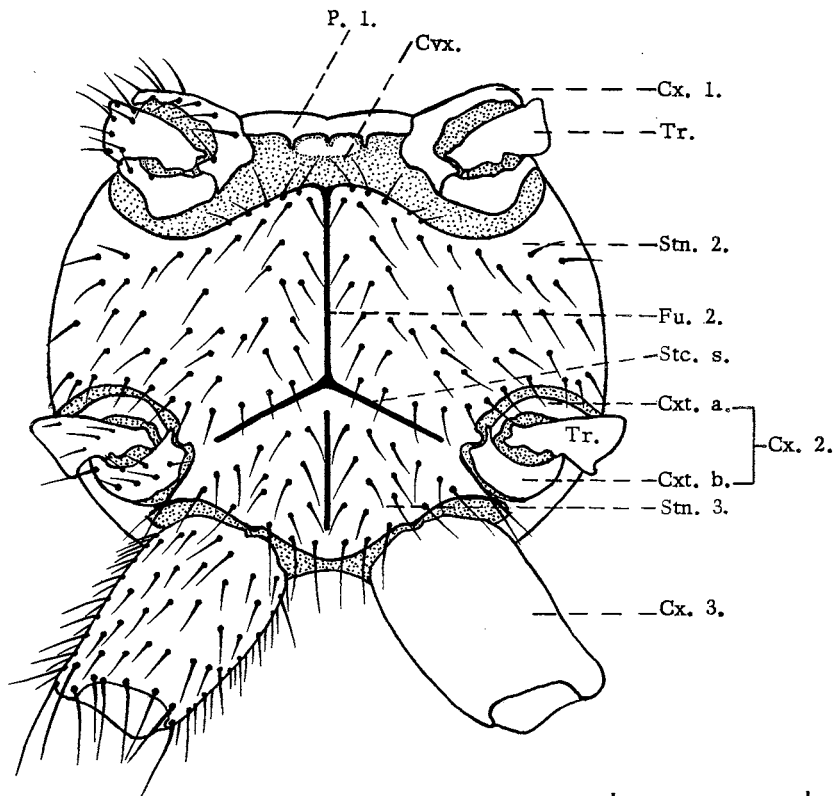


Fig. 23

— .27 mm



PLATE XIII

Fig. 24. Trichobius spp., diagrammatic posterior view of thorax.

Fig. 25. Trichobius major Coq., wing.

Aepm.2.	-----	Mesoanepimeron
Ax.c.	-----	Axillary cord
Bac.	-----	Basicosta
C.	-----	Costa
Ca.3.	-----	Metathoracic calypter
Cu <sub>1</sub> .	-----	Cubitus one
Cu <sub>2</sub> .	-----	Cubitus two
Cu <sub>2</sub> +2a.	-----	Cubitus two plus second anal
Cxc.	-----	Coxal cavity
Cx.3.	-----	Metathoracic coxa
Epm.3.	-----	Metepimeron
Eps.3.	-----	Metepisternum
F.	-----	Foramen
Fu.2.	-----	Furcasternal suture
H.	-----	Humeral
Hlt.	-----	Haltere
L.m.c.	-----	Longitudinal membranous cleft
Mer.2.	-----	Meron
M <sub>1</sub> +2.	-----	Media one plus two
M <sub>3</sub> +4.	-----	Media three plus four
M <sub>3</sub> +4+Cu <sub>1</sub> .	-----	Media three plus four plus cubitus one
P.3.	-----	Metanotum
P.sp.	-----	Posterior thoracic spiracle
Ph.3.	-----	Metathoracic phragma
Plcx.p.3.	-----	Pleuro-coxal process
PNP.	-----	Posterior notal wing process
R <sub>1</sub> .	-----	Radius one
R <sub>2</sub> +3.	-----	Radius two plus three
R <sub>4</sub> +5.	-----	Radius four plus five
Rm.	-----	Radio-medial
Rs.	-----	Radial sector
Sc.+R.	-----	Subcosta plus radius
Scl.2.	-----	Mesoscutellum
Sct.2.	-----	Mesoscutum
Stn.3.	-----	Metasternum
T.3.	-----	Laterotergite
Trscl.s.	-----	Trans-scutellar suture
Vf.	-----	Anal fold
2a.	-----	Second anal
3a.	-----	Third anal

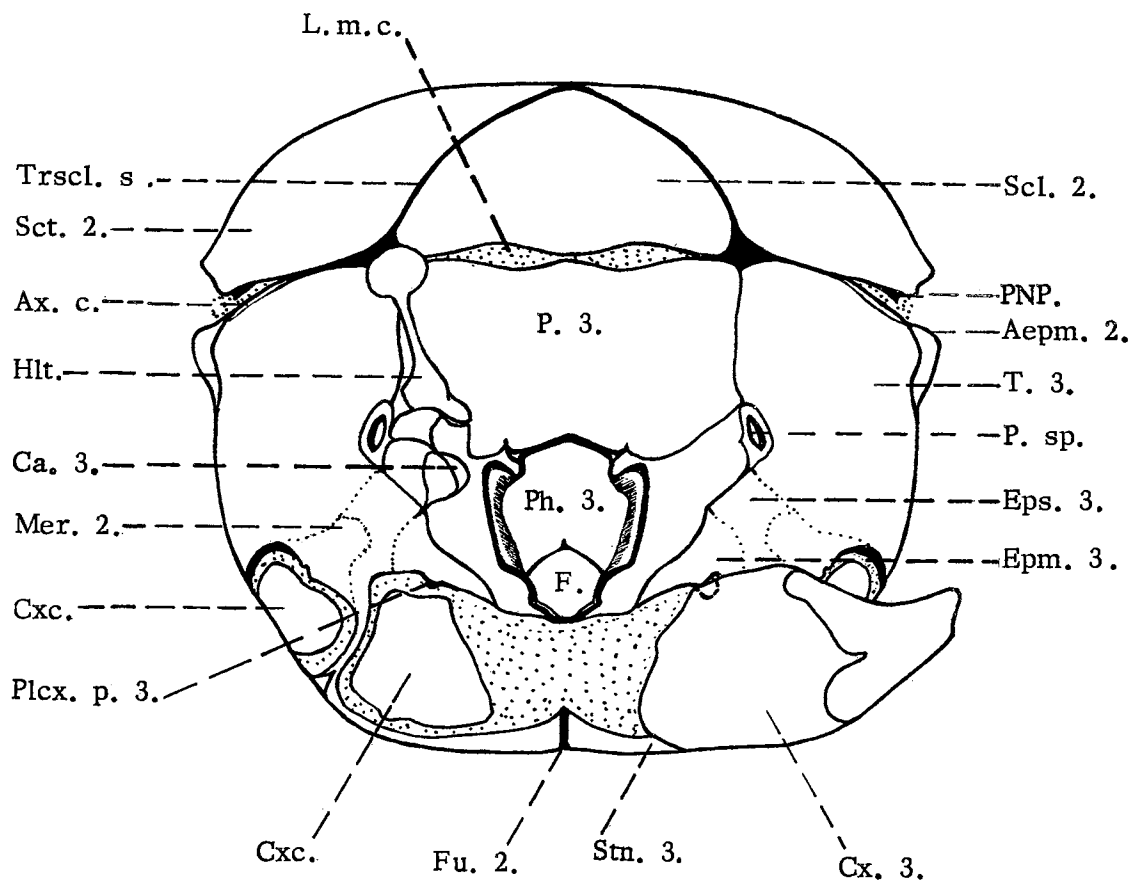
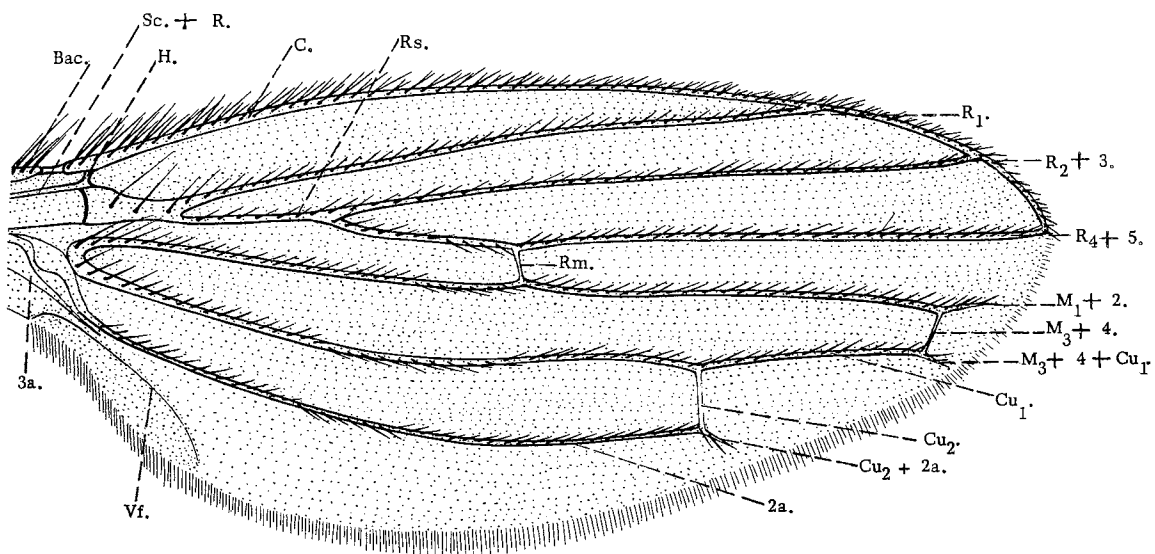


Fig. 24



.64 mm

Fig. 25

PLATE XIV

Fig. 26. Trichobius corynorhini Cock., wing.

Fig. 27. Trichobius sphaeronotus Job., wing.

Fig. 28. Trichobius major Coq., wing showing a remnant of the  
subcosta and a spur on the second anal vein.

Bac. -----	Basicosta
C. -----	Costa
Cu <sub>1</sub> . -----	Cubitus one
Cu <sub>2</sub> . -----	Cubitus two
Cu <sub>2</sub> +2a. -----	Cubitus two plus second anal
H. -----	Humeral
M <sub>1</sub> +2. -----	Media one plus two
M <sub>3</sub> +4. -----	Media three plus four
M <sub>3</sub> +4+Cu <sub>1</sub> . -----	Media three plus four plus cubitus one
R <sub>1</sub> . -----	Radius one
R <sub>2</sub> +3. -----	Radius two plus three
R <sub>4</sub> +5. -----	Radius four plus five
Rm. -----	Radio-medial
Rs. -----	Radial sector
Sc. -----	Subcosta
Sc.+R. -----	Subcosta plus radius
Vf. -----	Anal fold
2a. -----	Second anal
3a. -----	Third anal

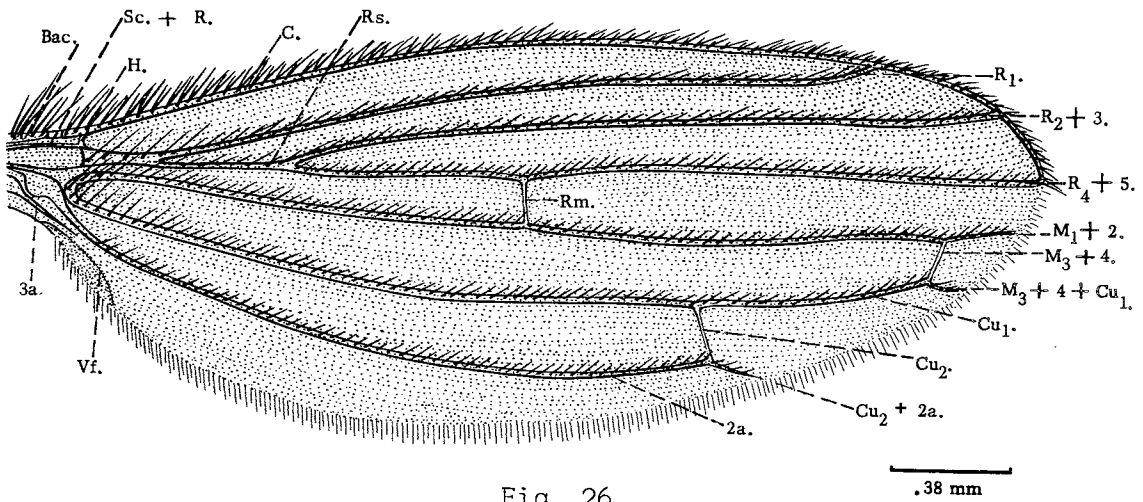


Fig. 26

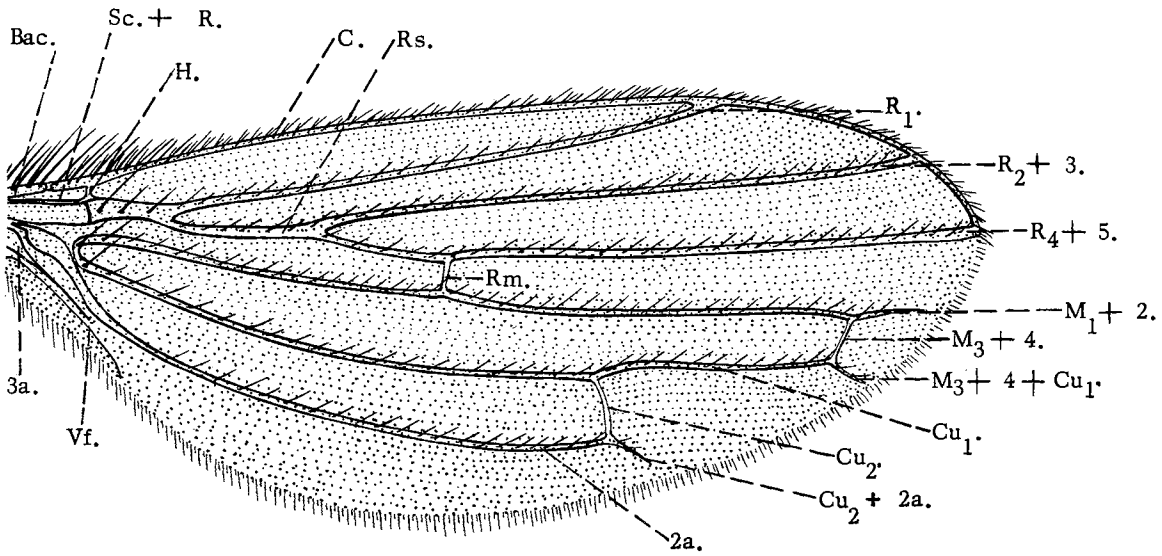


Fig. 27

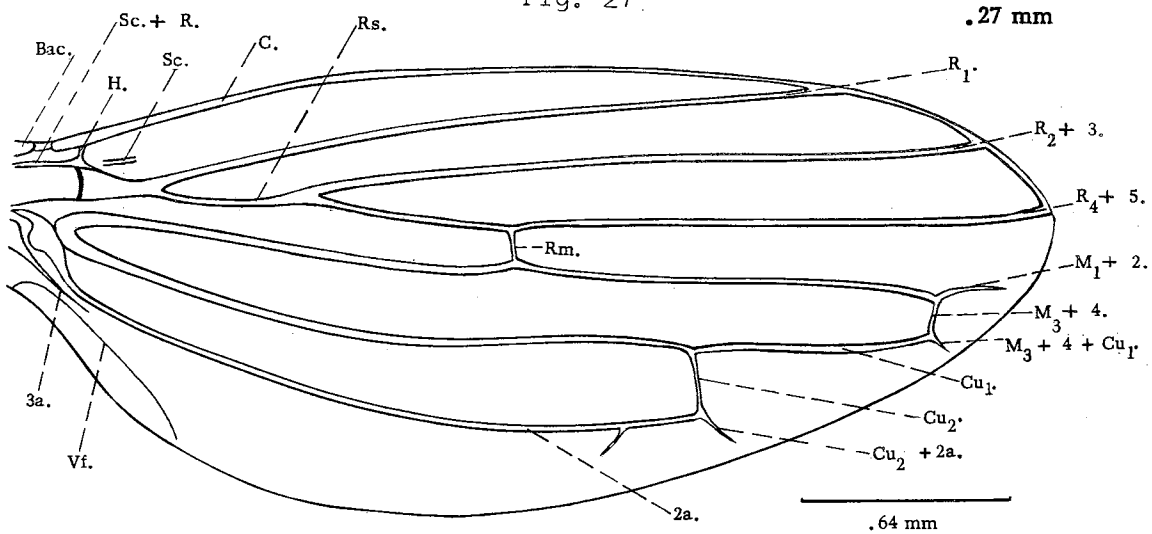


Fig. 28

PLATE XV

Fig. 29. Trichobius major Coq., wing showing a remnant of the sub-  
costa, additional cross-veins, and spurs.

Fig. 30. Trichobius major Coq., wing showing additional cross-veins.

Fig. 31. Trichobius major Coq., wing showing additional cross-veins.

Bac.	-----	Basicosta
C.	-----	Costa
Cu <sub>1</sub> .	-----	Cubitus one
Cu <sub>2</sub> .	-----	Cubitus two
Cu <sub>2</sub> +2a.	-----	Cubitus two plus second anal
H.	-----	Humeral
M <sub>1</sub> +2.	-----	Media one plus two
M <sub>3</sub> +4.	-----	Media three plus four
M <sub>3</sub> +4+Cu <sub>1</sub> .	-----	Media three plus four plus cubitus one
R <sub>1</sub> .	-----	Radius one
R <sub>2</sub> +3.	-----	Radius two plus three
R <sub>4</sub> +5.	-----	Radius four plus five
Rm.	-----	Radio-medial
Rs.	-----	Radial sector
Sc.	-----	Subcosta
Sc.+R.	-----	Subcosta plus radius
Vf.	-----	Anal fold
2a.	-----	Second anal
3a.	-----	Third anal

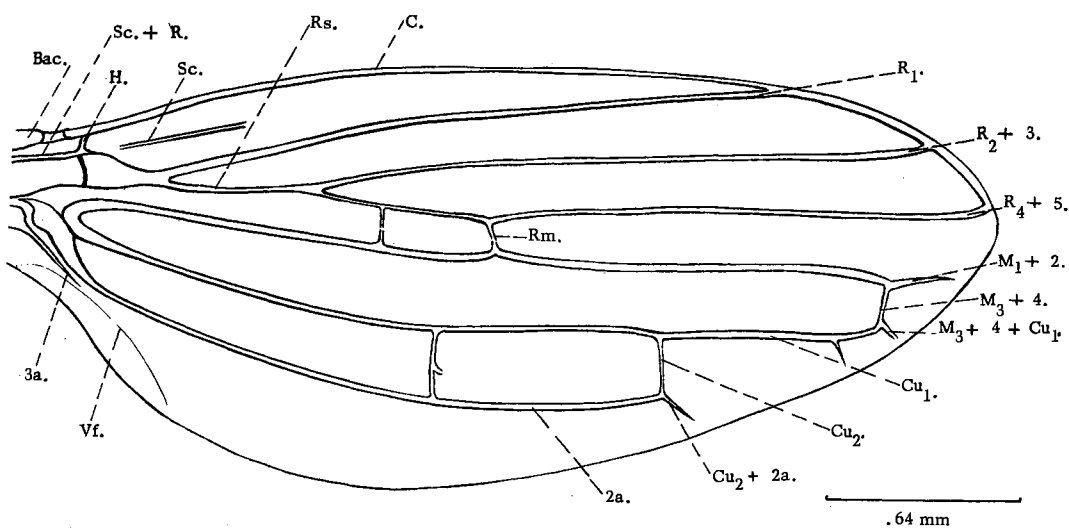


Fig. 29

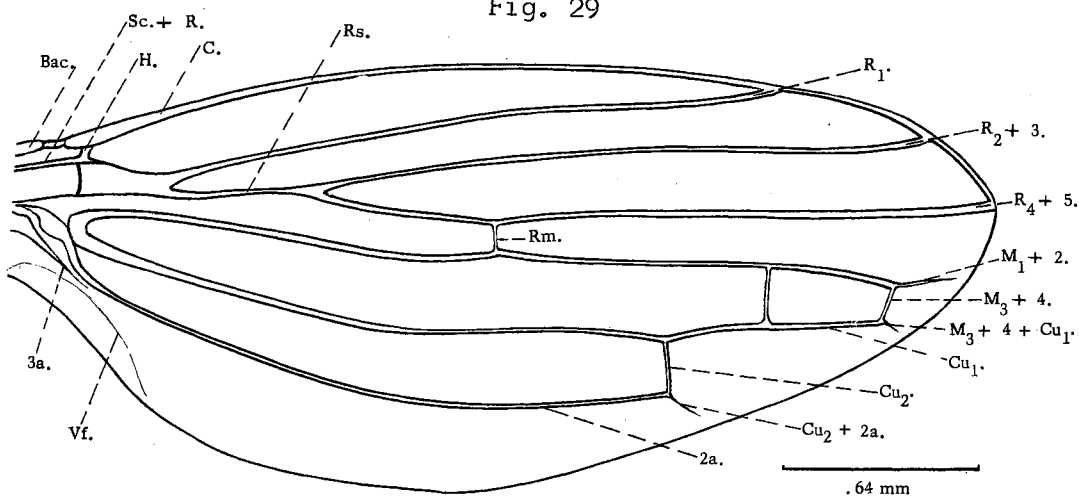


Fig. 30

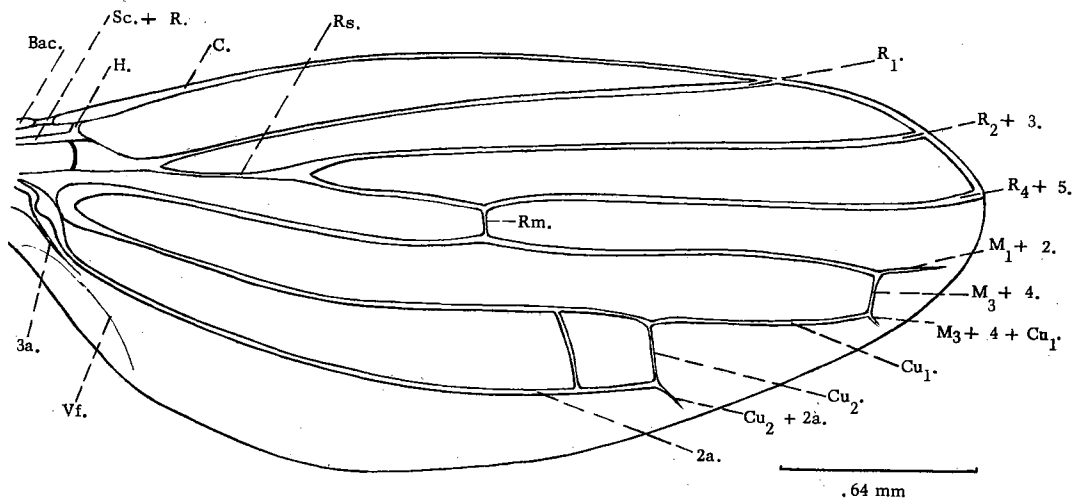


Fig. 31

PLATE XVI

Fig. 32. Trichobius major Coq., wing showing additional radio-medial cross-veins.

Fig. 33. Trichobius major Coq., wing showing additional radio-medial cross-veins and spurs on other veins.

Fig. 34. Trichobius major Coq., wing showing additional spurs.

Bac.	-----	Basicosta
C.	-----	Costa
Cu <sub>1</sub> .	-----	Cubitus one
Cu <sub>2</sub> .	-----	Cubitus two
Cu <sub>2</sub> +2a.	-----	Cubitus two plus second anal
H.	-----	Humeral
M <sub>1</sub> +2.	-----	Media one plus two
M <sub>3</sub> +4.	-----	Media three plus four
M <sub>3</sub> +4+Cu <sub>1</sub> .	-----	Media three plus four plus cubitus one
R <sub>1</sub> .	-----	Radius one
R <sub>2</sub> +3.	-----	Radius two plus three
R <sub>4</sub> +5.	-----	Radius four plus five
Rm.	-----	Radio-medial
Rs.	-----	Radial sector
Sc.+R.	-----	Subcosta plus radius
Vf.	-----	Anal fold
2a.	-----	Second anal
3a.	-----	Third anal

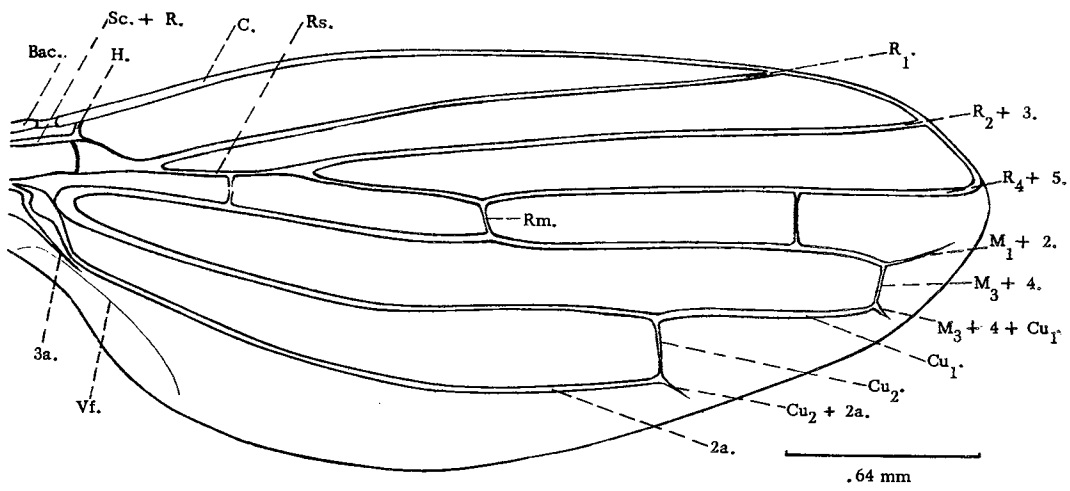


Fig. 32

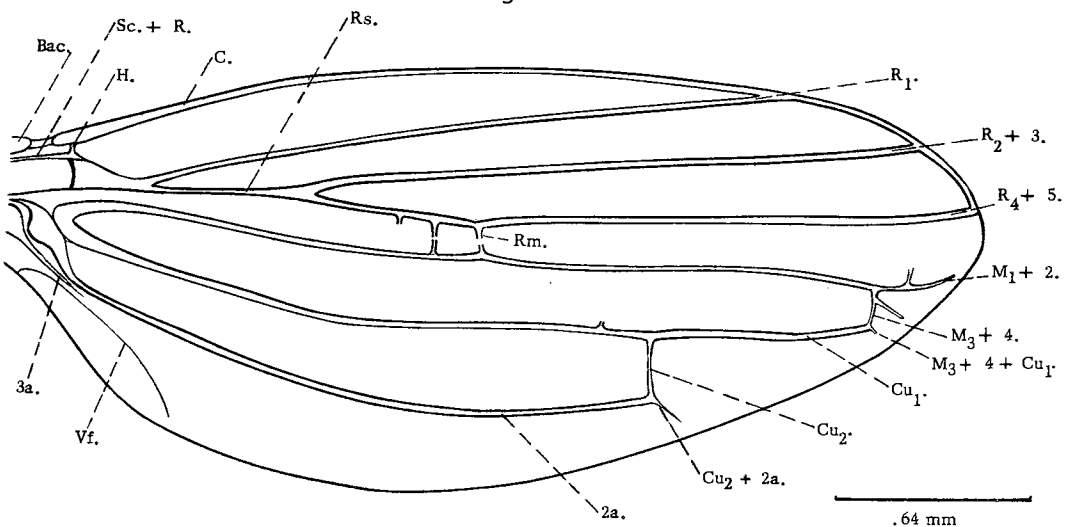


Fig. 33

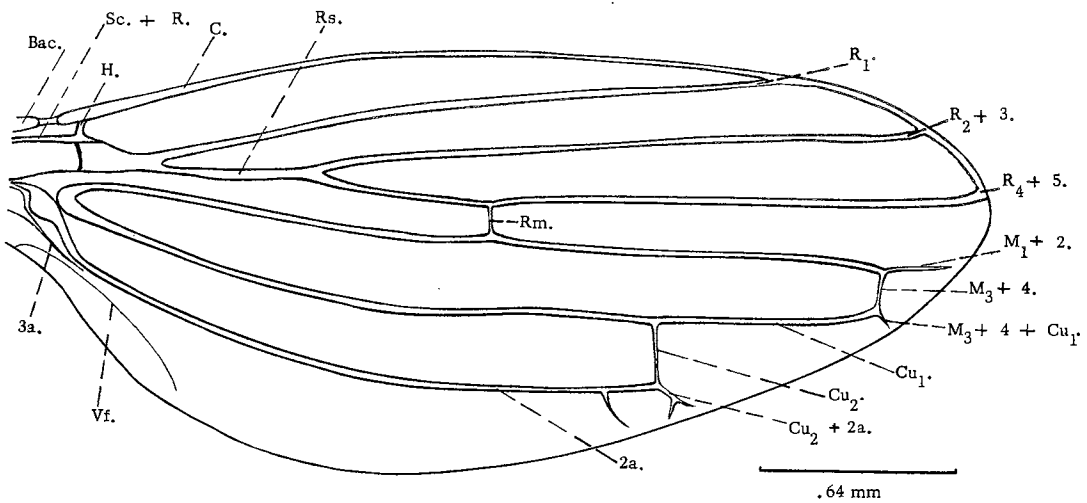


Fig. 34



PLATE XVII

Fig. 35. Trichobius major Coq., wing showing additional spurs.

Fig. 36. Trichobius major Coq., wing showing additional spurs.

Fig. 37. Trichobius major Coq., wing showing additional spurs.

Bac. -----	Basicosta
C. -----	Costa
Cu <sub>1</sub> . -----	Cubitus one
Cu <sub>2</sub> . -----	Cubitus two
Cu <sub>2</sub> +2a. -----	Cubitus two plus second anal
H. -----	Humeral
M <sub>1</sub> +2. -----	Media one plus two
M <sub>3</sub> +4. -----	Media three plus four
M <sub>3</sub> +4+Cu <sub>1</sub> . -----	Media three plus four plus cubitus one
R <sub>1</sub> . -----	Radius one
R <sub>2</sub> +3. -----	Radius two plus three
R <sub>4</sub> +5. -----	Radius four plus five
Rm. -----	Radio-medial
Rs. -----	Radial sector
Sc.+R. -----	Subcosta plus radius
Vf. -----	Anal fold
2a. -----	Second anal
3a. -----	Third anal

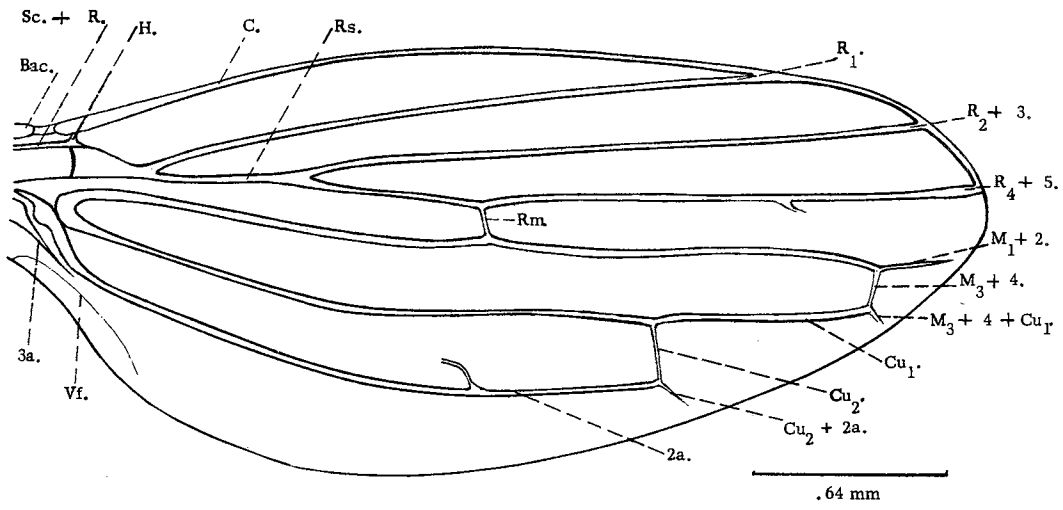


Fig. 35

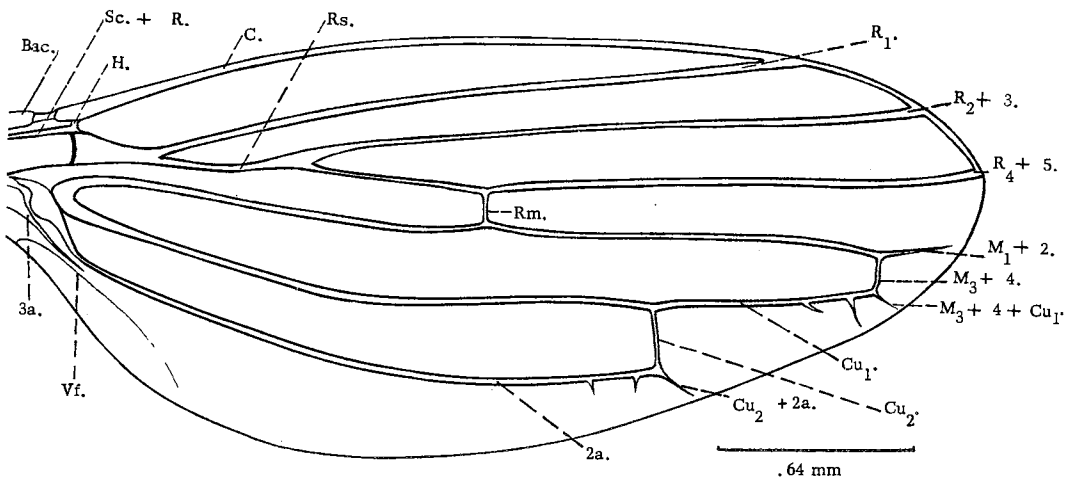


Fig. 36

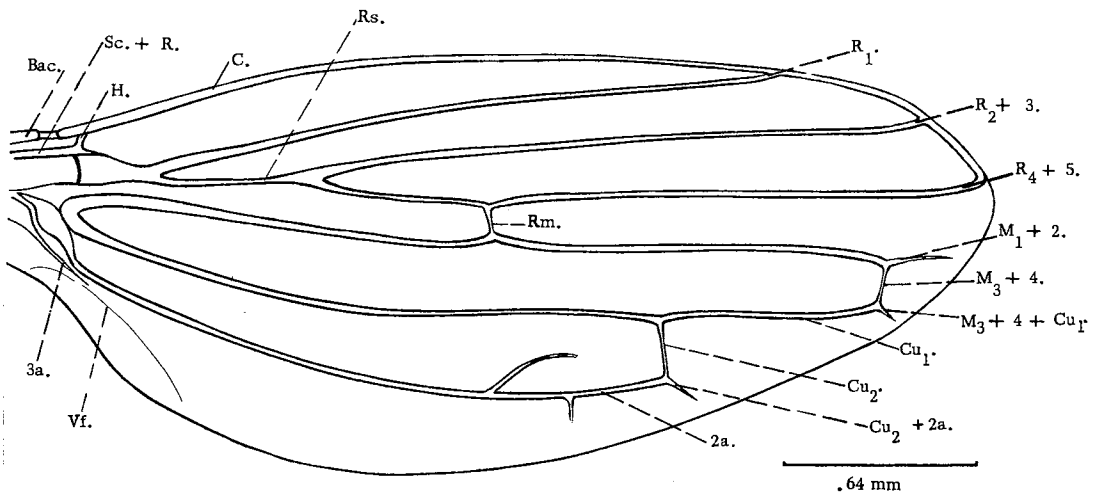


Fig. 37

PLATE XVIII

Fig. 38. Trichobius corynorhini Cock., wing showing a bifurcation of cubitus two.

Fig. 39. Trichobius sphaeronotus Job., wing showing an additional radio-medial cross-vein.

Fig. 40. Trichobius sphaeronotus Job., wing showing a radio-medial spur.

Bac.	-----	Basicosta
C.	-----	Costa
Cu <sub>1</sub> .	-----	Cubitus one
Cu <sub>2</sub> .	-----	Cubitus two
Cu <sub>2</sub> +2a.	-----	Cubitus two plus second anal
H.	-----	Humeral
M <sub>1</sub> +2.	-----	Media one plus two
M <sub>3</sub> +4.	-----	Media three plus four
M <sub>3</sub> +4+Cu <sub>1</sub> .	-----	Media three plus four plus cubitus one
R <sub>1</sub> .	-----	Radius one
R <sub>2</sub> +3.	-----	Radius two plus three
R <sub>4</sub> +5.	-----	Radius four plus five
Rm.	-----	Radio-medial
Rs.	-----	Radial sector
Sc.+R.	-----	Subcosta plus radius
Vf.	-----	Anal fold
2a.	-----	Second anal
3a.	-----	Third anal

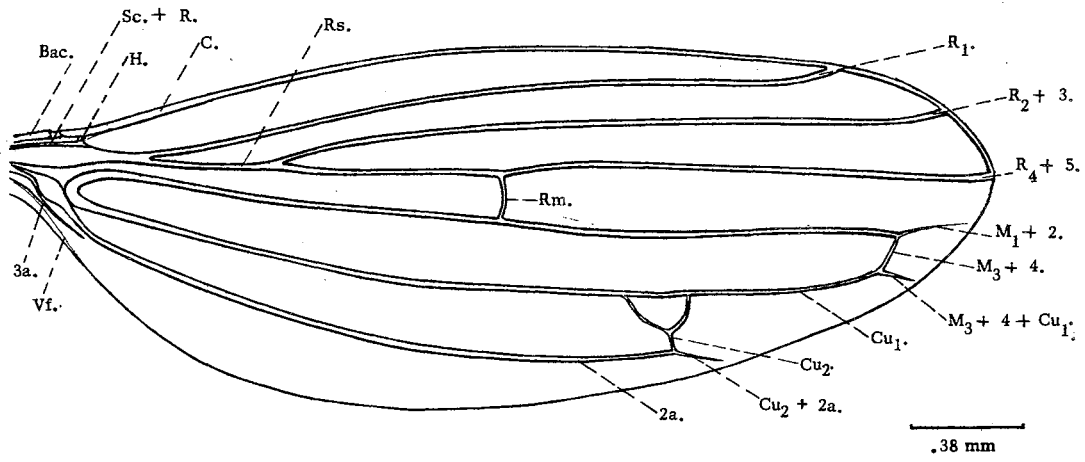


Fig. 38

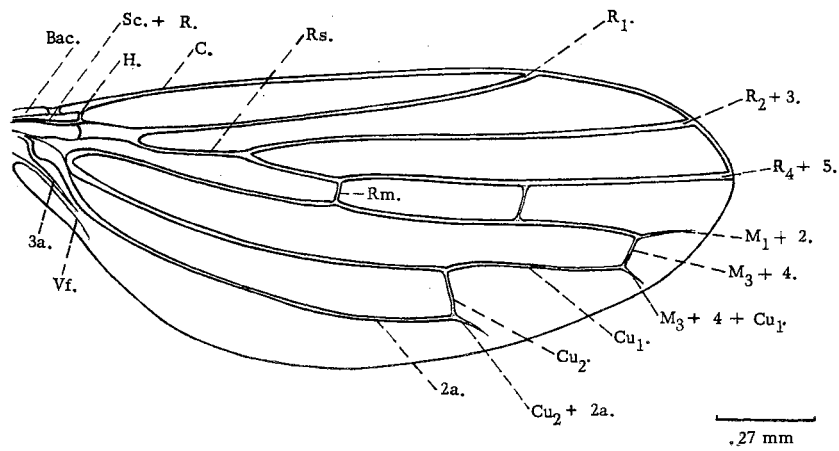


Fig. 39

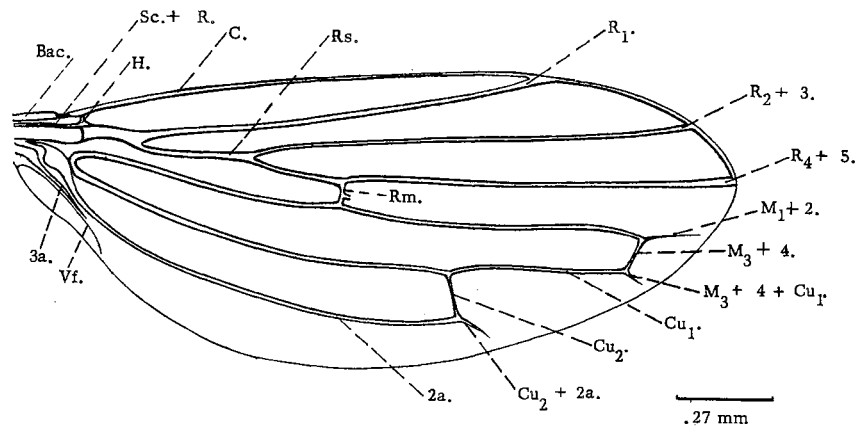


Fig. 40

PLATE XIX

Fig. 41. Trichobius sphaeronotus Job., wing showing an irregular costa.

Fig. 42. Trichobius spp., diagrammatic dorsal view of wing base.

ANP.	-----	Anterior notal wing process
Ax.c.	-----	Axillary cord
Ba.	-----	Basalare
Bac.	-----	Basicosta
C.	-----	Costa
Cu <sub>1</sub> .	-----	Cubitus one
Cu <sub>2</sub> .	-----	Cubitus two
Cu <sub>2</sub> +2a.	-----	Cubitus two plus second anal
H.	-----	Humeral
In.Ax.	-----	Intermediate axillary sclerite
L.m.c.	-----	Longitudinal membranous cleft
M.	-----	Proximal median plate
M*	-----	Distal median plate
M <sub>1</sub> +2.	-----	Media one plus two
M <sub>3</sub> +4.	-----	Media three plus four
M <sub>3</sub> +4+Cu <sub>1</sub> .	-----	Media three plus four plus cubitus one
Pl.2.	-----	Mesopleuron
PNP.	-----	Posterior notal wing process
Prsc.2.	-----	Mesoprescutum
R <sub>1</sub> .	-----	Radius one
R <sub>2</sub> +3.	-----	Radius two plus three
R <sub>4</sub> +5.	-----	Radius four plus five
Rm.	-----	Radio-medial
Rs.	-----	Radial sector
Sc.+R.	-----	Subcosta plus radius
Sct.2.	-----	Mesoscutum
T.3.	-----	Laterotergite
Tg.	-----	Tegula
Tr.s.	-----	Transverse suture
Vf.	-----	Anal fold
1.Ax.	-----	First axillary sclerite
2.Ax.	-----	Second axillary sclerite
3.Ax.	-----	Third axillary sclerite
4.Ax.	-----	Fourth axillary sclerite
2a.	-----	Second anal
3a.	-----	Third anal

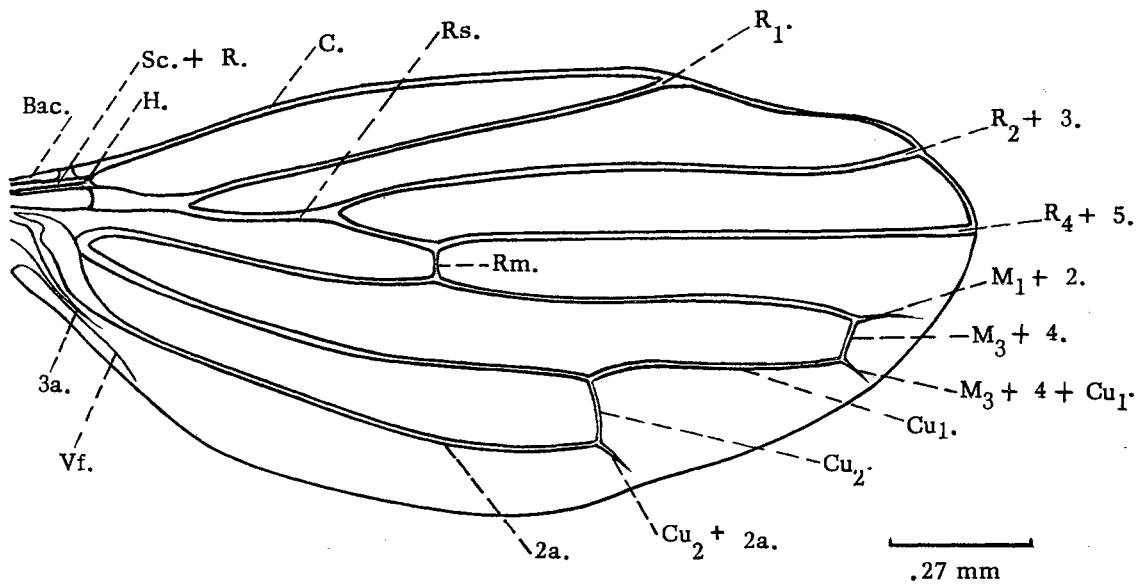


Fig. 41

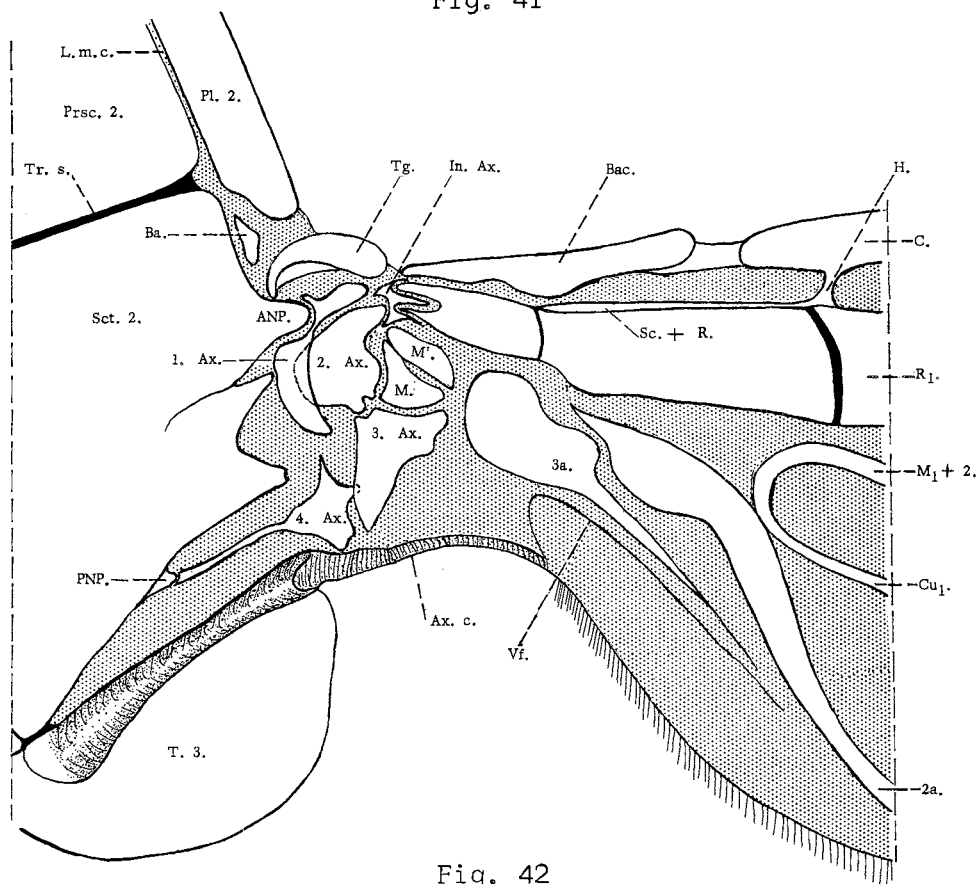


Fig. 42

PLATE XX

Fig. 43. Trichobius corynorhini Cock., lateral view of prothoracic leg.

Fig. 44. Trichobius corynorhini Cock., lateral view of mesothoracic leg.

Fig. 45. Trichobius corynorhini Cock., lateral view of metathoracic leg.

Cx.1.,2.,3.	-----	Pro-, meso-, and metathoracic coxae
Cxt.a.,b.	-----	Mesothoracic coxal coxites
Emp.	-----	Empodium
Fm.	-----	Femur
Ptar.	-----	Pretarsus
Pv.	-----	Pulvillus
Tar.	-----	Tarsi
Tb.	-----	Tibia
Tr.	-----	Trochanter
Un.	-----	Unguis
s.	-----	Point of articulation, trochanter with mesothoracic coxa

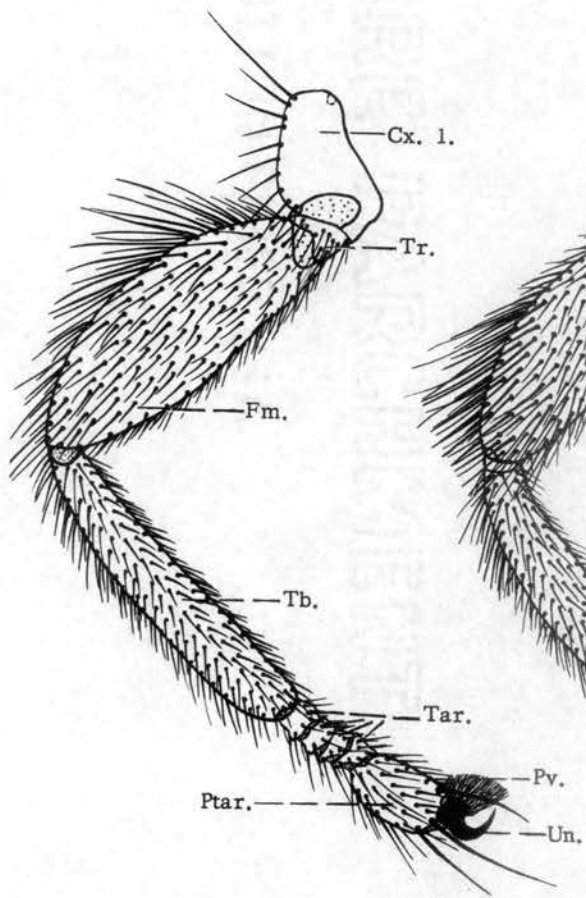


Fig. 43

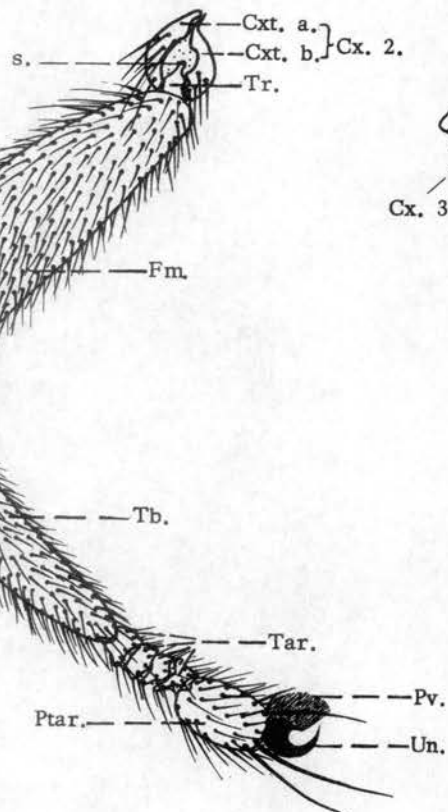


Fig. 44

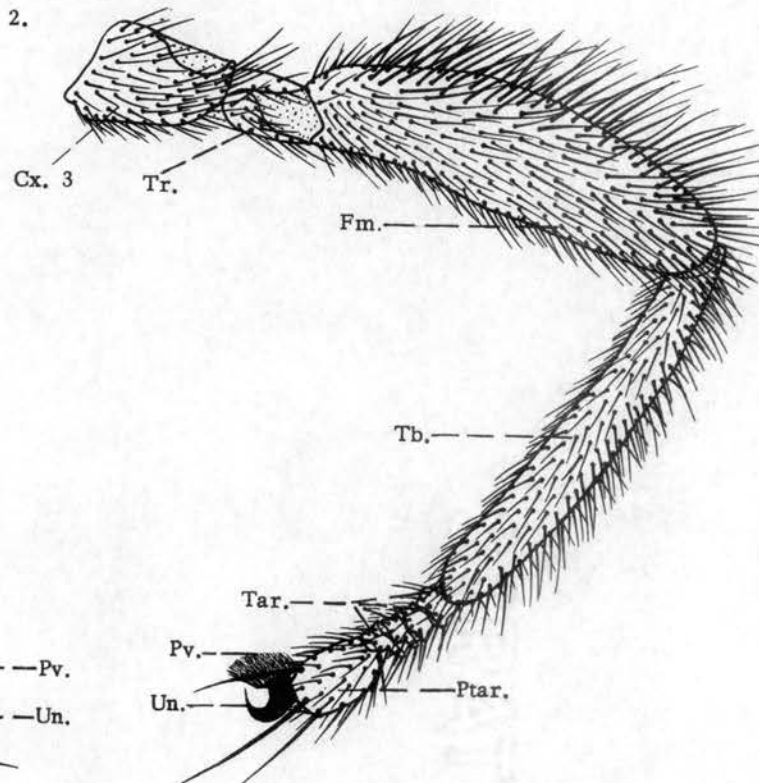


Fig. 45

.46 mm



PLATE XXI

Fig. 46. Trichobius sphaeronotus Job., lateral view of  
prothoracic leg.

Fig. 47. Trichobius sphaeronotus Job., lateral view of  
mesothoracic leg.

Fig. 48. Trichobius sphaeronotus Job., lateral view of  
metathoracic leg.

Cx.1.,2.,3. ----- Pro-, meso-, and metathoracic coxae  
Cxt.a.,b. ----- Mesothoracic coxal coxites  
Emp. ----- Empodium  
Fm. ----- Femur  
Ptar. ----- Pretarsus  
Pv. ----- Pulvillus  
Tar. ----- Tarsi  
Tb. ----- Tibia  
Tr. ----- Trochanter  
Un. ----- Unguis  
s. ----- Point of articulation, trochanter with  
mesothoracic coxa

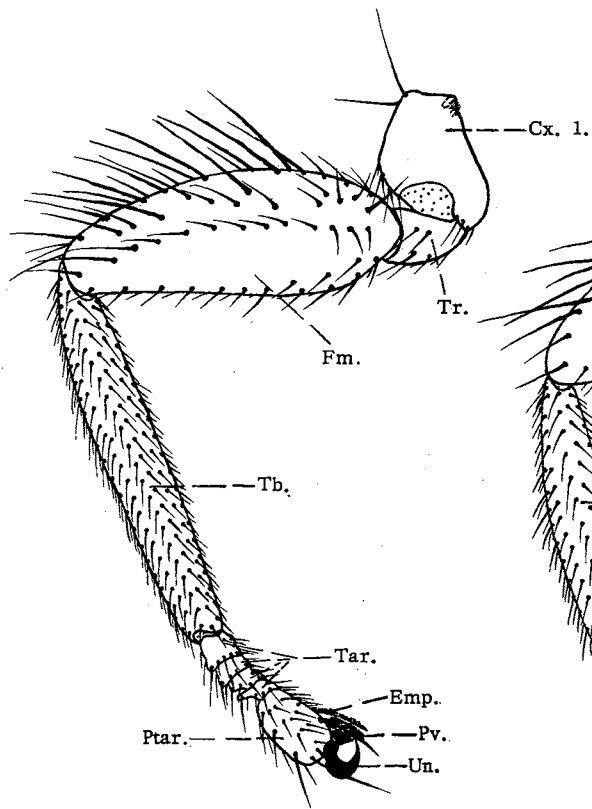


Fig. 46

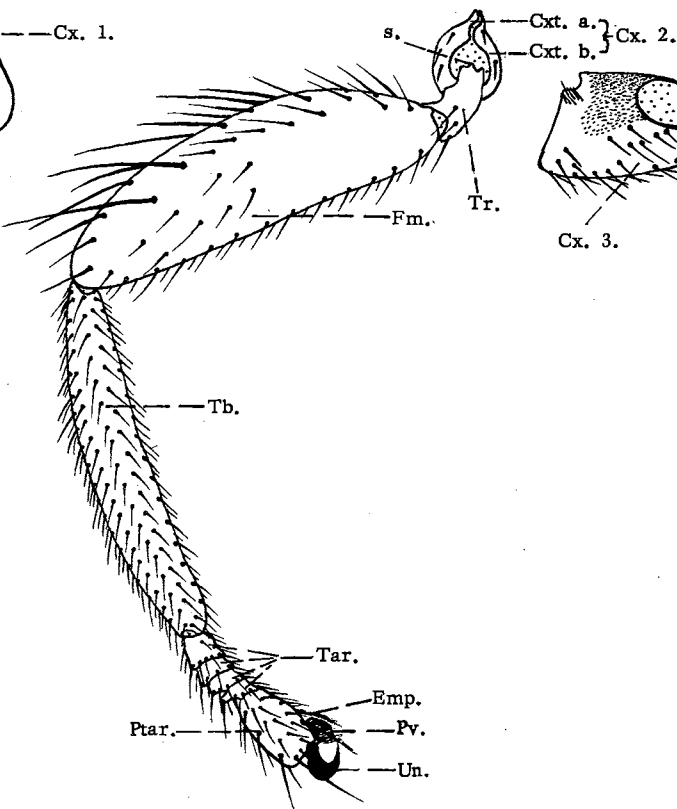


Fig. 47

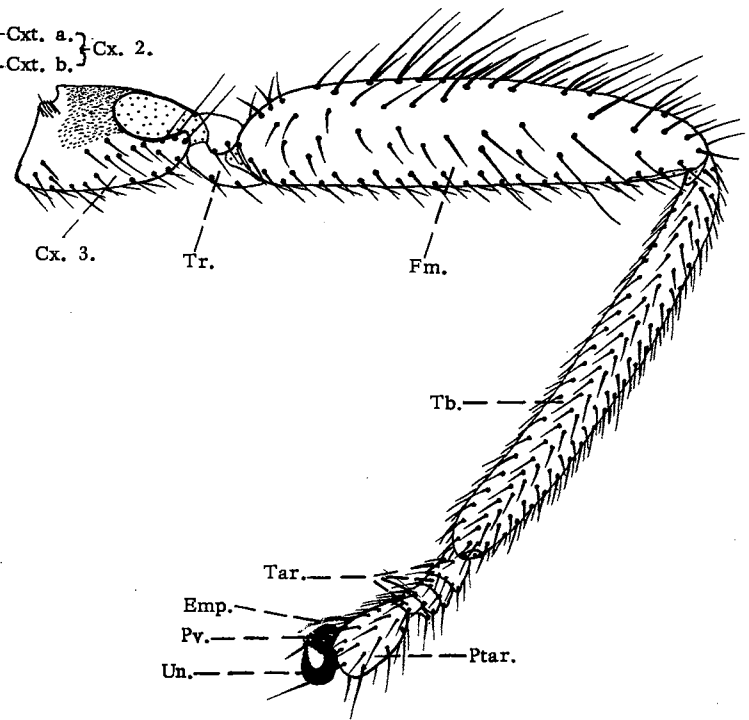


Fig. 48

.25 mm

PLATE XXII

Fig. 49. Trichobius corynorhini Cock., dorsal view of prothoracic leg.

Fig. 50. Trichobius corynorhini Cock., dorsal view of mesothoracic leg.

Fig. 51. Trichobius corynorhini Cock., dorsal view of metathoracic leg.

Cx.1.,2.,3. ----- Pro-, meso-, and metathoracic coxae  
Cxt.a.,b., ----- Meso- and metathoracic coxal coxites  
Fm. ----- Femur  
Ptar. ----- Pretarsus  
Pv. ----- Pulvillus  
Tar. ----- Tarsi  
Tb. ----- Tibia  
Tr. ----- Trochanter  
Un. ----- Unguis  
b.,c. ----- Points of articulation, trochanter with metathoracic coxa

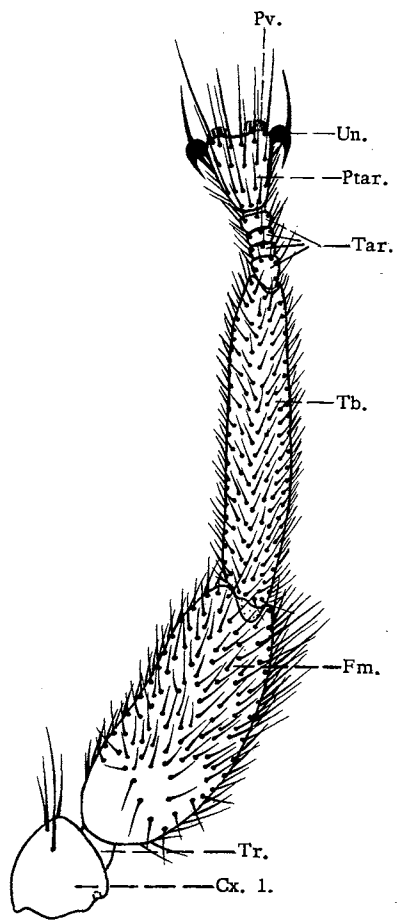


Fig. 49

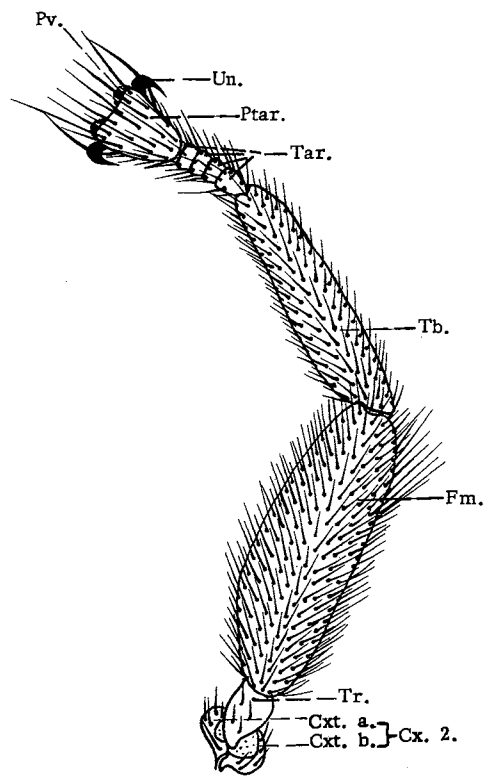


Fig. 50

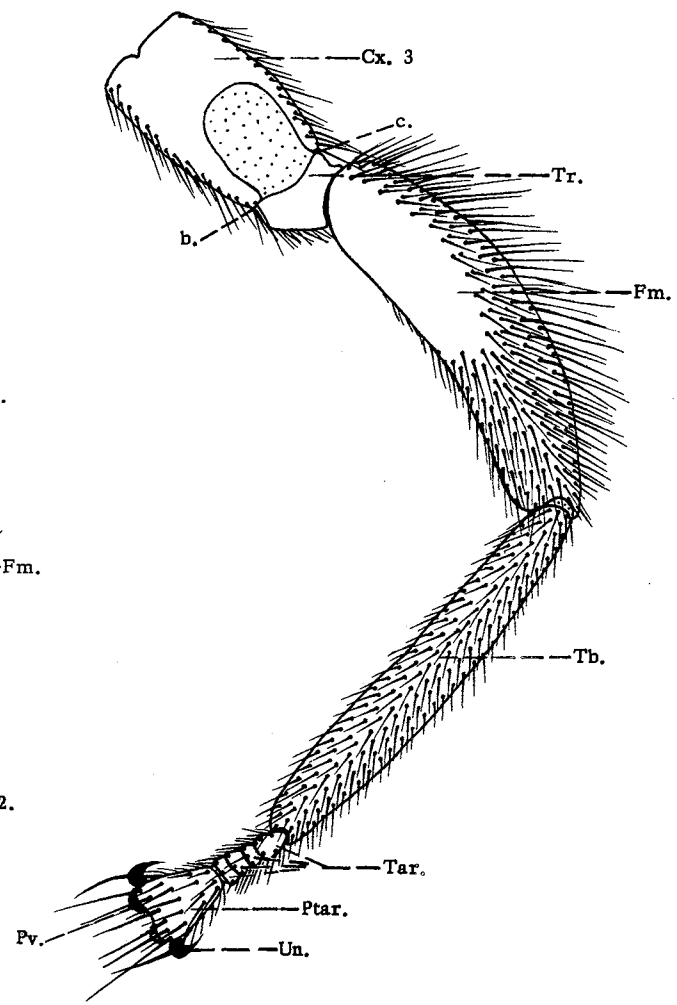


Fig. 51

.46 mm

PLATE XXIII

Fig. 52. Trichobius sphaeronotus Job., dorsal view of prothoracic leg.

Fig. 53. Trichobius sphaeronotus Job., dorsal view of mesothoracic leg.

Fig. 54. Trichobius sphaeronotus Job., dorsal view of metathoracic leg.

Cx.1.,2.,3. ----- Pro-, meso-, and metathoracic coxae  
Cxt.a.,b., ----- Mesothoracic coxal coxites  
Fm. ----- Femur  
Ptar. ----- Pretarsus  
Pv. ----- Pulvillus  
Tar. ----- Tarsi  
Tb. ----- Tibia  
Tr. ----- Trochanter  
Un. ----- Unguis  
b.,c. ----- Points of articulation, trochanter with  
metathoracic coxa

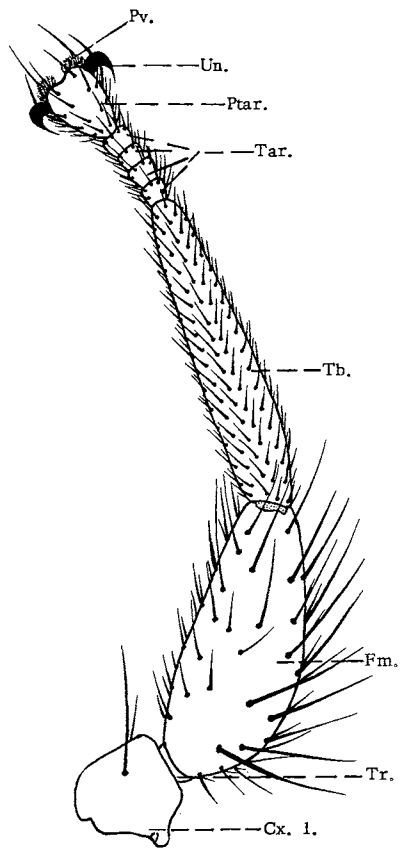


Fig. 52

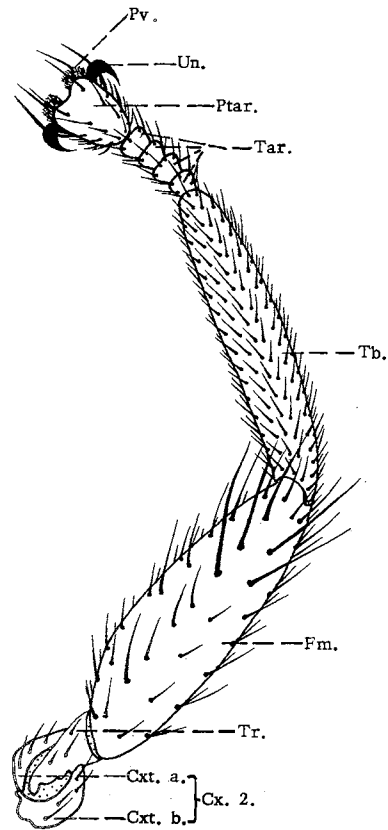


Fig. 53

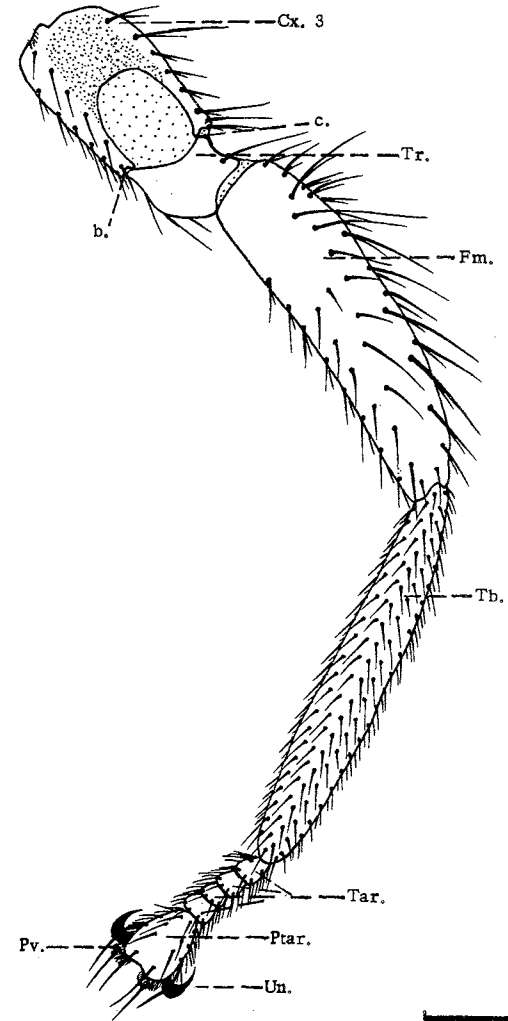


Fig. 54

.25 mm

PLATE XXIV

Fig. 55. Trichobius corynorhini Cock., ventral view of prothoracic leg.

Fig. 56. Trichobius corynorhini Cock., ventral view of mesothoracic leg.

Fig. 57. Trichobius corynorhini Cock., ventral view of metathoracic leg.

- |             |       |  |
|-------------|-------|--|
| Cx.1.,2.,3. | ----- | Pro-, meso-, and metathoracic coxae                                      |
| Cxt.a.,b.   | ----- | Mesothoracic coxal coxites   |
| Emp.        | ----- | Empodium   |
| Fm.         | ----- | Femur  |
| Ptar.       | ----- | Pretarsus  |
| Pv.         | ----- | Pulvillus  |
| Tar.        | ----- | Tarsi  |
| Tb.         | ----- | Tibia  |
| Tr.         | ----- | Trochanter   |
| Un.         | ----- | Unguis   |
| a.,f.       | ----- | Points of articulation, trochanter with prothoracic coxa                 |
| g.          | ----- | Point of articulation, trochanter with mesothoracic coxa                 |
| l.,m.       | ----- | Points of fusion, trochanter with metathoracic femur                     |
| n.,x.       | ----- | Points of articulation, femurs with pro-, meso-, and metathoracic tibiae |
| p.          | ----- | Point of articulation, trochanter with metathoracic coxa                 |

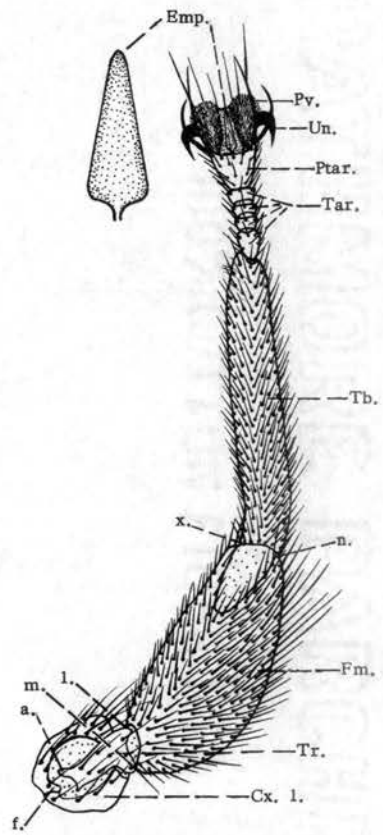


Fig. 55

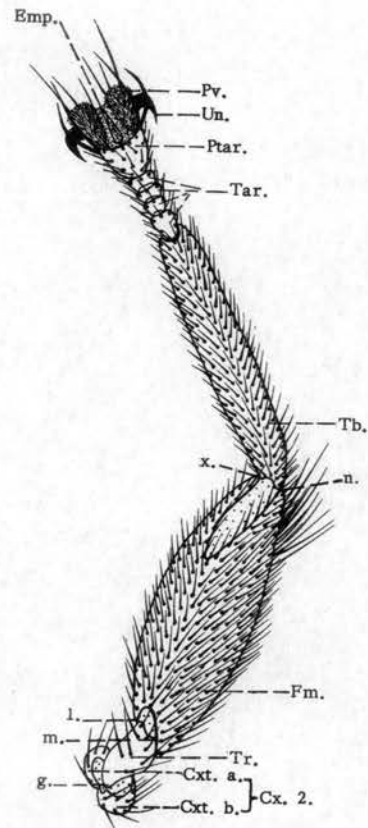


Fig. 56

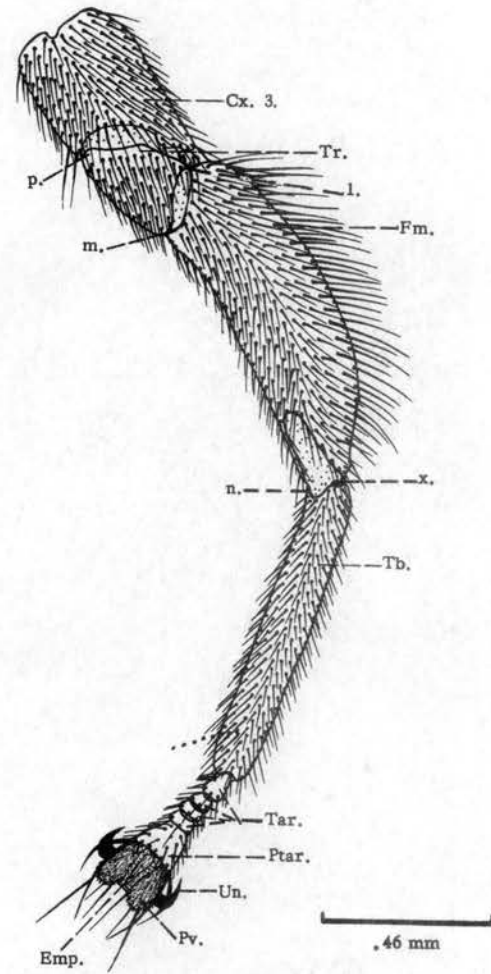


Fig. 57



PLATE XXV

Fig. 58. Trichobius sphaeronotus Job., ventral view of prothoracic leg.

Fig. 59. Trichobius sphaeronotus Job., ventral view of mesothoracic leg.

Fig. 60. Trichobius sphaeronotus Job., ventral view of metathoracic leg.

Cx.1.,2.,3.	-----	Pro-, meso-, and metathoracic coxae
Cxt.a.,b.	-----	Mesothoracic coxal coxites
Emp.	-----	Empodium
Fm.	-----	Femur
Ptar.	-----	Pretarsus
Pv.	-----	Pulvillus
Tar.	-----	Tarsi
Tb.	-----	Tibia
Tr.	-----	Trochanter
Un.	-----	Unguis
a.,f.	-----	Points of articulation, trochanter with prothoracic coxa
g.	-----	Point of articulation, trochanter with mesothoracic coxa
l.,m.	-----	Points of fusion, trochanter with metathoracic femur
n.,x.	-----	Points of articulation, femurs with pro-, meso-, and metathoracic tibiae
p.	-----	Point of articulation, trochanter with metathoracic coxa

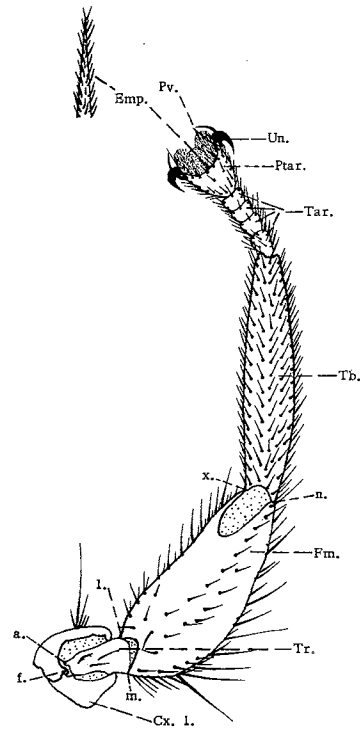


Fig. 58

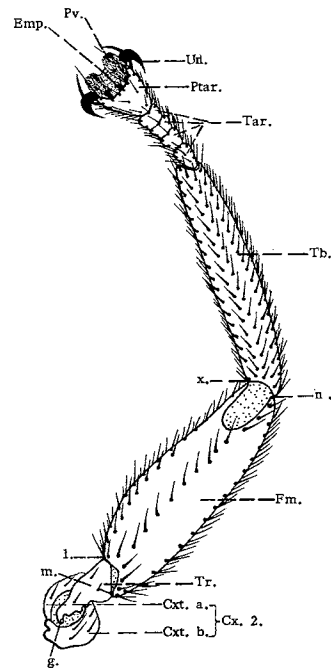


Fig. 59

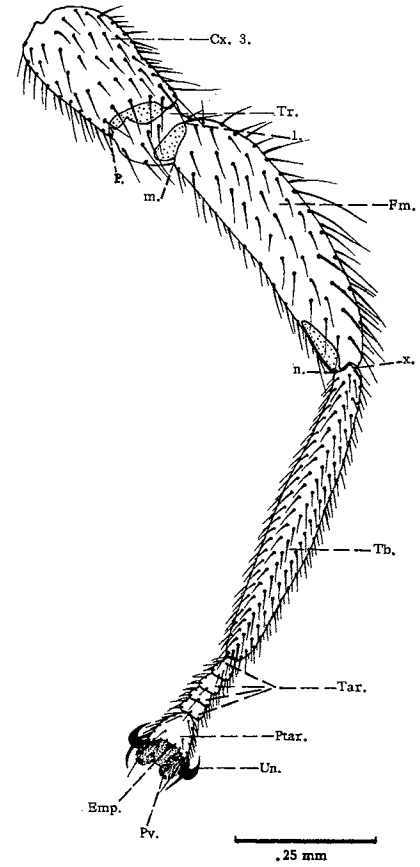


Fig. 60

PLATE XXVI

Fig. 61. Trichobius major Coq., dorsal view of male abdomen.

Fig. 62. Trichobius corynorhini Cock., dorsal view of male abdomen.

Pr. ----- Proctiger  
1+2T. ----- Fused first and second tergites  
3T. ----- Third tergite  
4T. ----- Fourth tergite  
5T. ----- Fifth tergite  
6T. ----- Sixth tergite  
7+8T. ----- Fused seventh and eighth tergites  
9T. ----- Ninth tergite

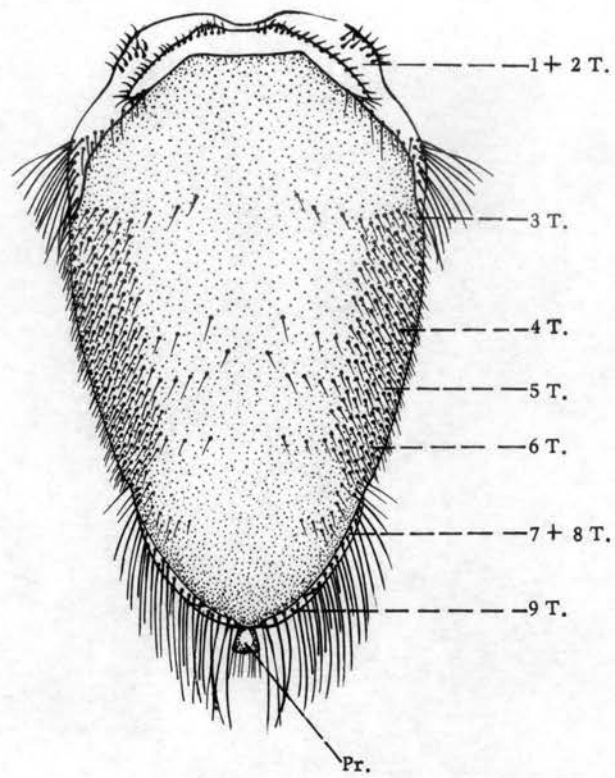


Fig. 61

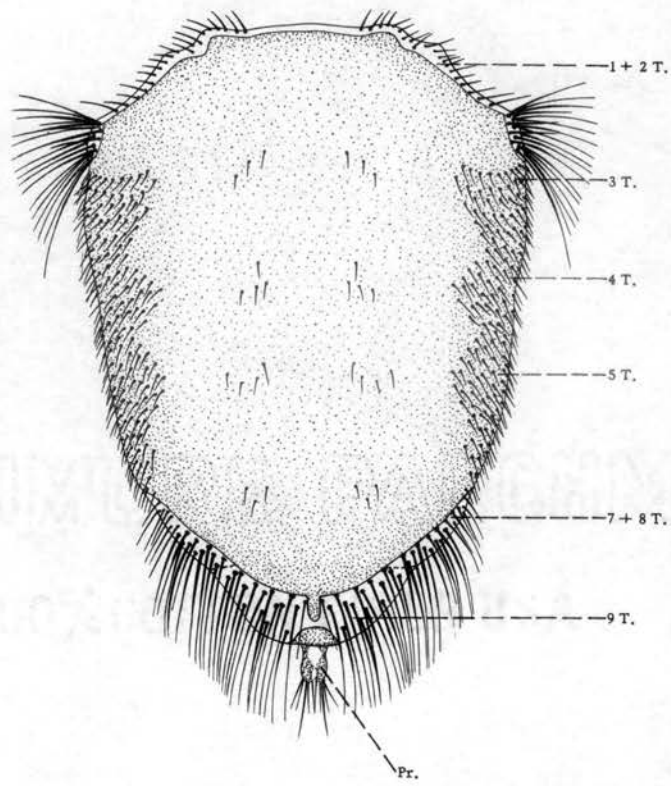


Fig. 62

PLATE XXVII

Fig. 63. Trichobius sphaeronotus Job., dorsal view of male abdomen.

Fig. 64. Trichobius major Coq., lateral view of male abdomen.

Aed. ----- Aedeagus  
Gon. ----- Gonapophyses  
Pr. ----- Proctiger  
Sp.1.,2.,7. ----- First, second, and seventh abdominal spiracles  
1+2T. ----- Fused first and second tergites  
3T. ----- Third tergite  
4T. ----- Fourth tergite  
5T. ----- Fifth tergite  
6T. ----- Sixth tergite  
7+8T. ----- Fused seventh and eighth tergites  
9T. ----- Ninth tergite  
1S. ----- First sternite  
2S. ----- Second sternite  
5S. ----- Fifth sternite

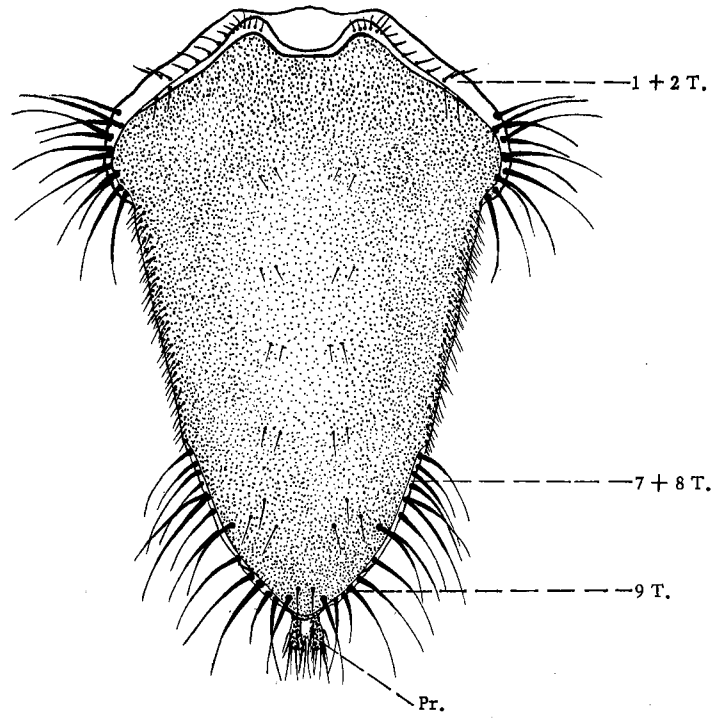


Fig. 63 .23 mm

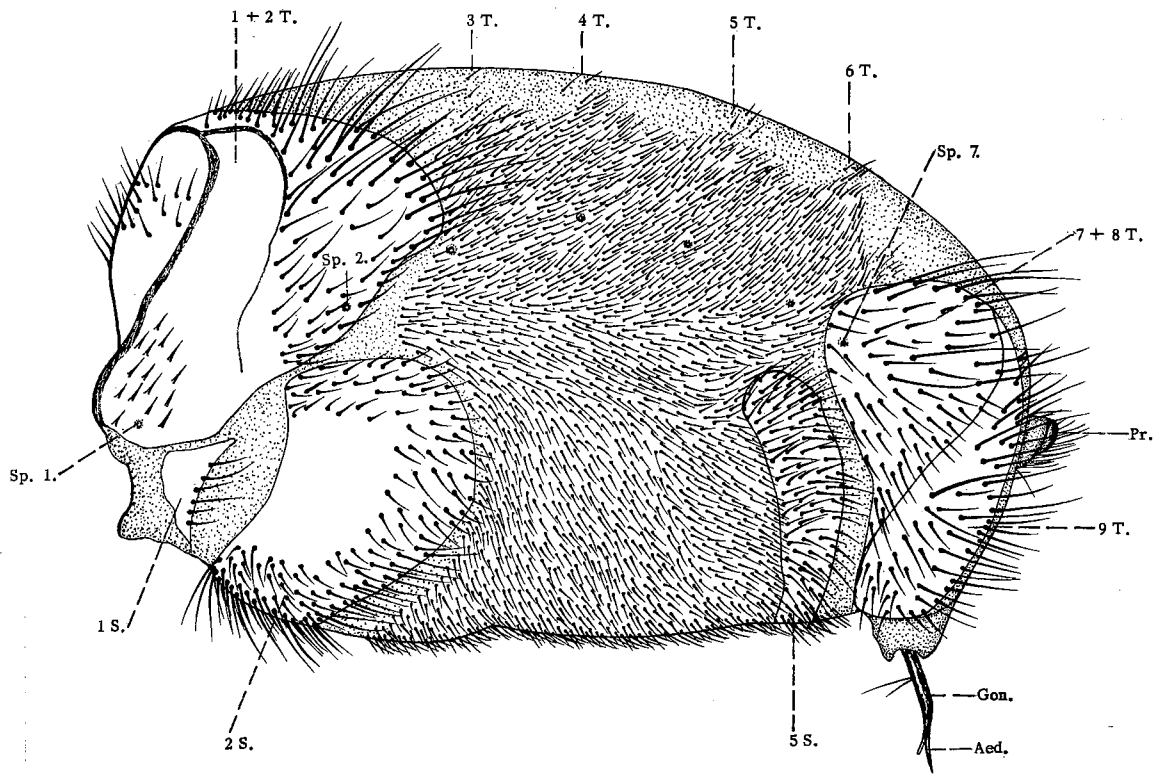


Fig. 64 .40 mm

PLATE XXVIII

Fig. 65. Trichobius corynorhini Cock., lateral view of male abdomen.

Fig. 66. Trichobius sphaeronotus Job., lateral view of male abdomen.

Aed. ----- Aedeagus  
Gon. ----- Gonapophyses  
Pr. ----- Proctiger  
Sp.1.,2.,7. ----- First, second, and seventh abdominal spiracles  
1+2T. ----- Fused first and second tergites  
3T. ----- Third tergite  
4T. ----- Fourth tergite  
5T. ----- Fifth tergite  
7+8T. ----- Fused seventh and eighth tergites  
9T. ----- Ninth tergite  
1S. ----- First sternite  
2S. ----- Second sternite  
5S. ----- Fifth sternite

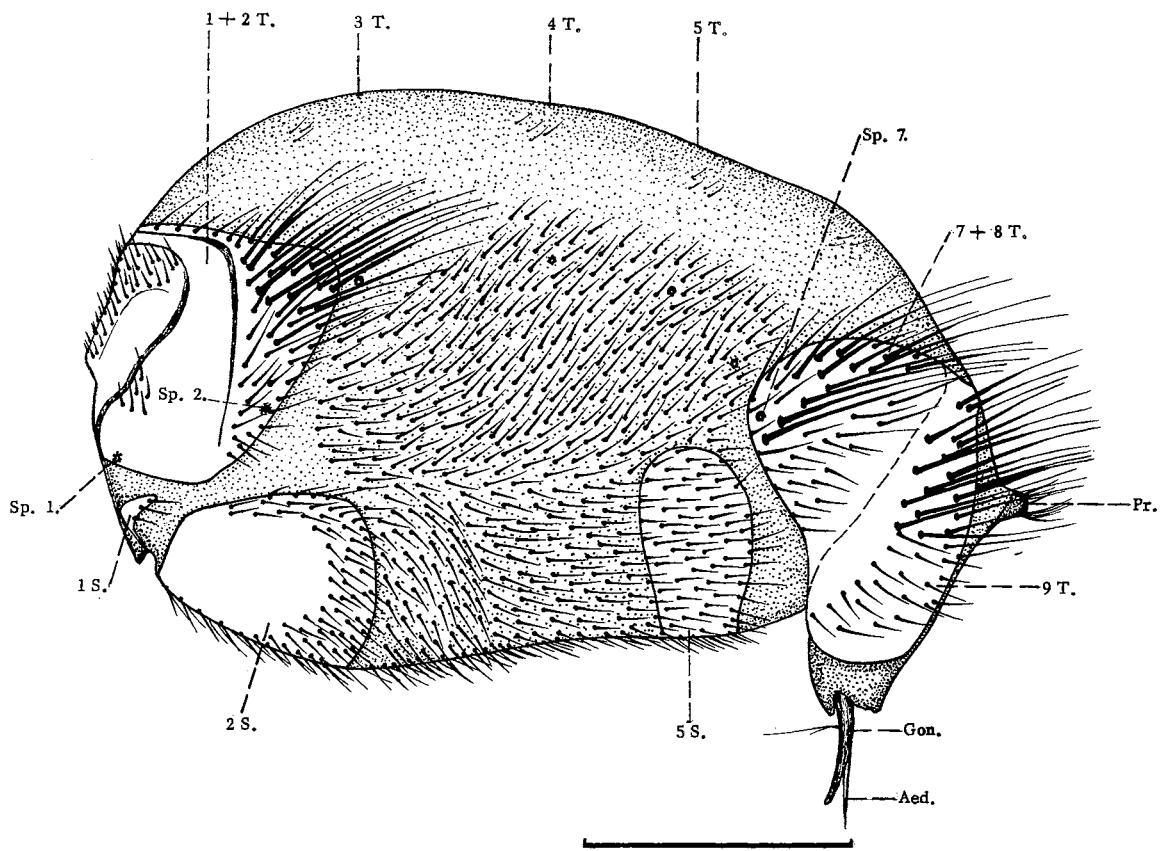


Fig. 65

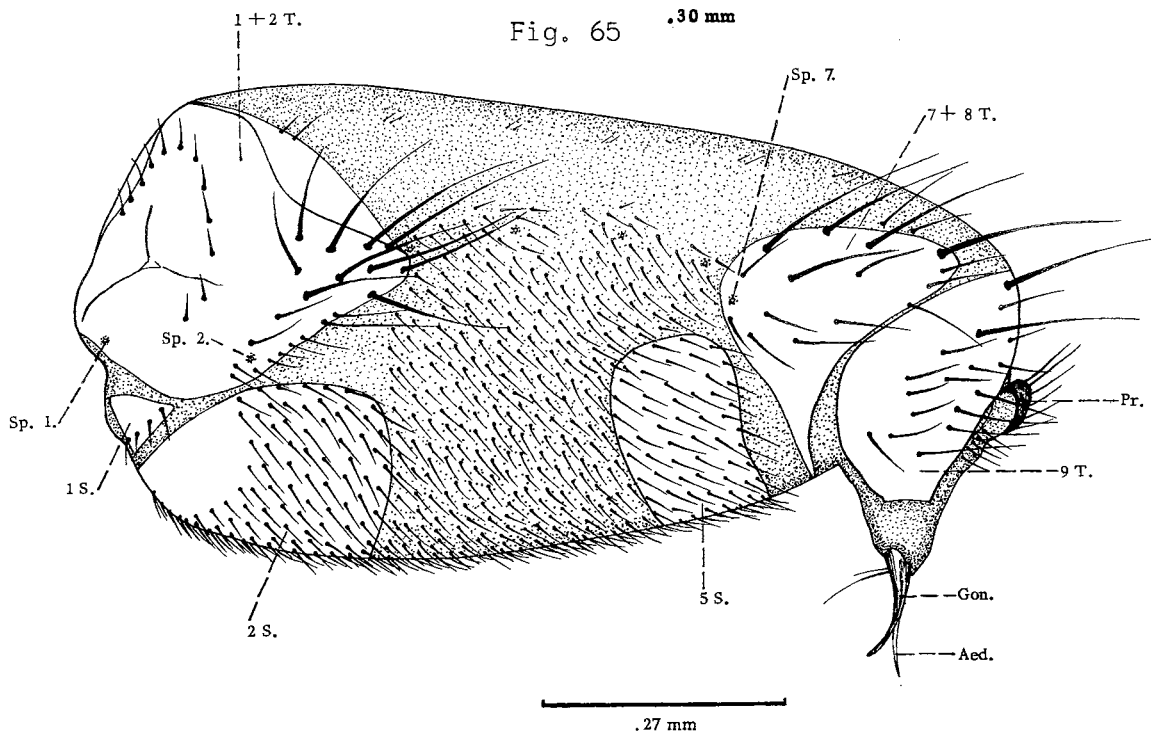


Fig. 66



PLATE XXIX

Fig. 67. Trichobius major Coq., ventral view of male abdomen.

Fig. 68. Trichobius corynorhini Cock., ventral view of male abdomen.

Aed. ————— Aedeagus  
Gon. ————— Gonapophyses  
Pr. ————— Proctiger  
1+2T. ————— Fused first and second tergites  
7+8T. ————— Fused seventh and eighth tergites  
9T. ————— Ninth tergite  
1S. ————— First sternite  
2S. ————— Second sternite  
5S. ————— Fifth sternite

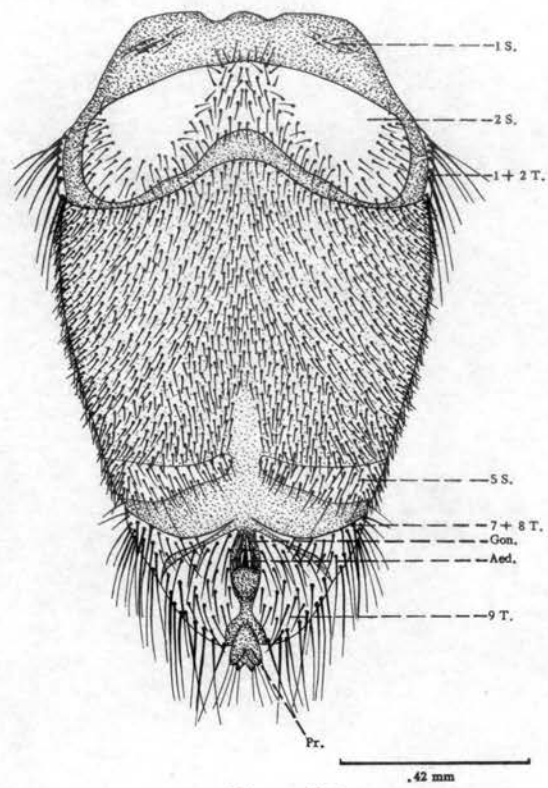


Fig. 67

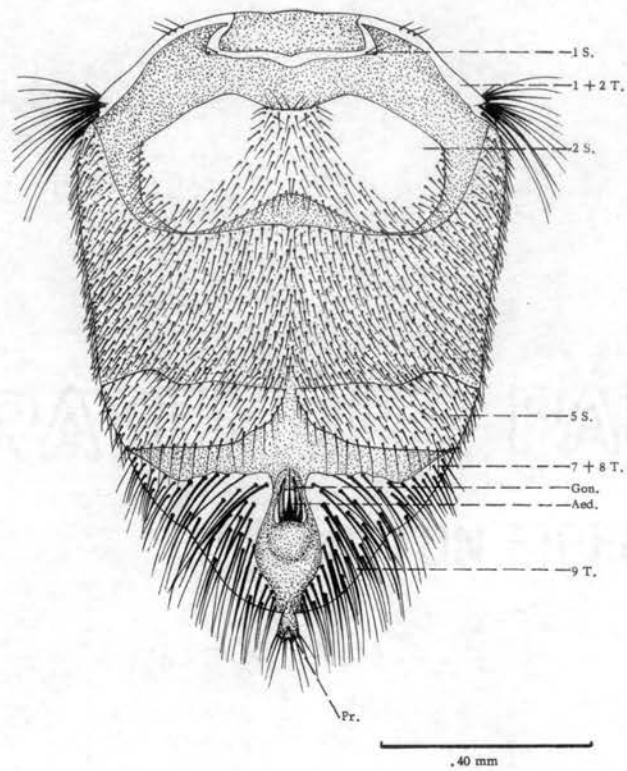


Fig. 68

PLATE XXX

Fig. 69. Trichobius sphaeronotus Job., ventral view of male abdomen.

Fig. 70. Trichobius major Coq., anterolateral view of male genitalia.

Fig. 71. Trichobius major Coq., dorsal view of female abdomen.

Aed.	—————	Aedeagus
Aed.a.	—————	Aedeagal apodeme
Aed.s.	—————	Aedeagal sheath
Cer.	—————	Cercus
Gon.	—————	Gonapophyses
Gon.a.	—————	Gonapophyseal apodeme
Gon.s.	—————	Gonapophyseal sheath
Pr.	—————	Proctiger
S.	—————	U-shaped sclerites
S.a.p.	—————	Supra-anal plate
Sp.3.,7.	—————	Third and seventh abdominal spiracles
1+2T.	—————	Fused first and second tergites
7T.	—————	Seventh tergite
7+8T.	—————	Fused seventh and eighth tergites
9T.	—————	Ninth tergite
1S.	—————	First sternite
2S.	—————	Second sternite
5S.	—————	Fifth sternite
7S.	—————	Seventh sternite

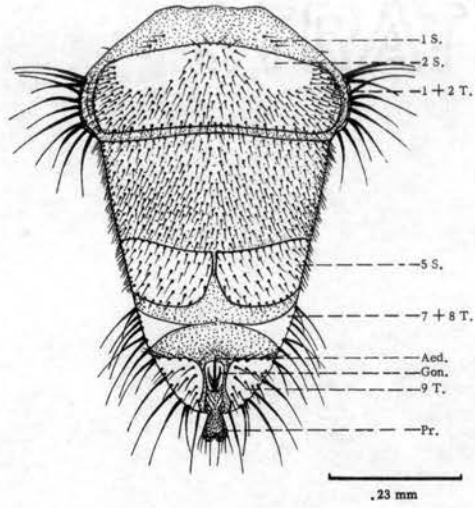


Fig. 69

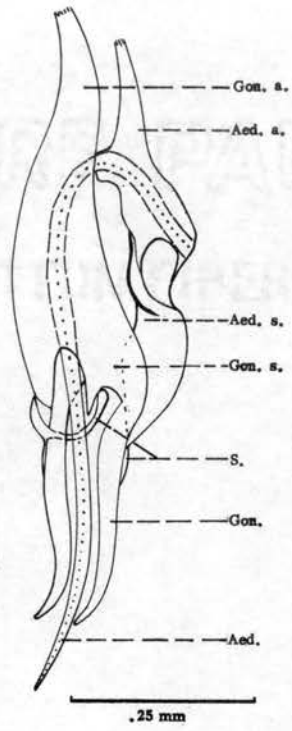


Fig. 70

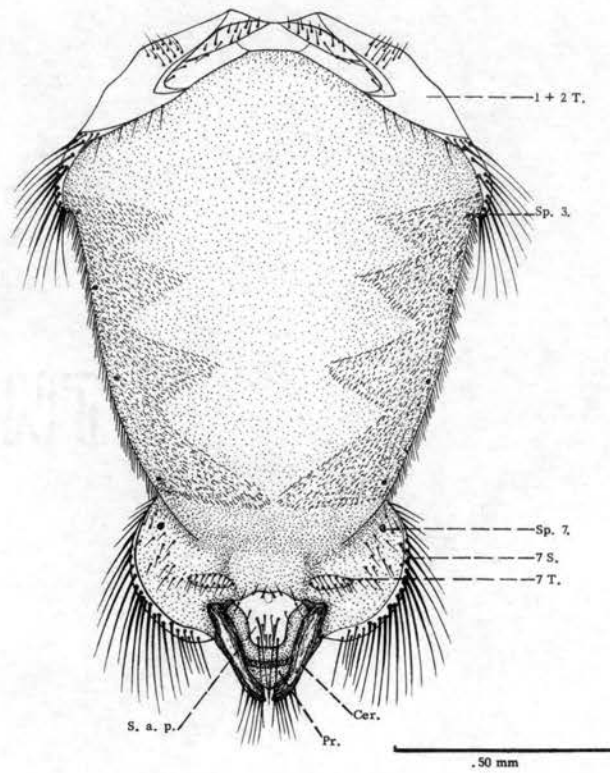


Fig. 71

PLATE XXXI

Fig. 72. Trichobius corynorhini Cock., dorsal view of female abdomen.

Fig. 73. Trichobius sphaeronotus Job., dorsal view of female abdomen.

Cer. ————— Cercus  
Pr. ————— Proctiger  
S.a.p. ————— Supra-anal plate  
Sp.3.,7. ————— Third and seventh abdominal spiracles  
1+2T. ————— Fused first and second tergites  
7T. ————— Seventh tergite  
7S. ————— Seventh sternite

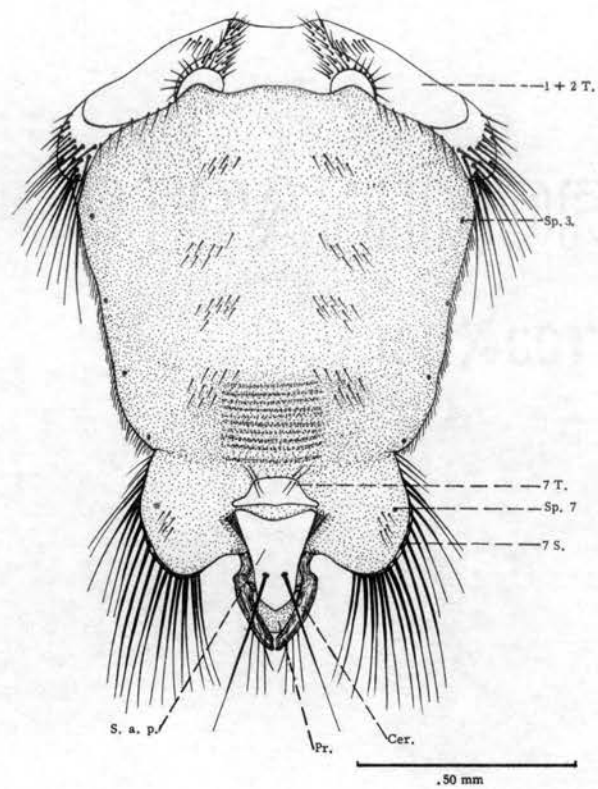


Fig. 72

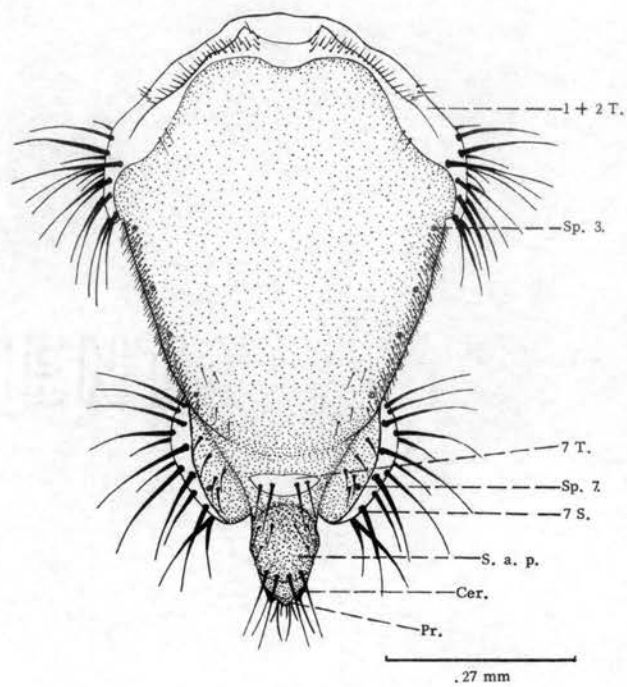


Fig. 73

PLATE XXXII

Fig. 74. Trichobius major Coq., lateral view of female abdomen.

Fig. 75. Trichobius corynorhini Cock., lateral view of female abdomen.

Cer.	—————	Cercus
Pr.	—————	Proctiger
Sp.1.,2.,7.	—————	First, second, and seventh abdominal spiracles
1+2T.	—————	Fused first and second tergites
3T.	—————	Third tergite
4T.	—————	Fourth tergite
5T.	—————	Fifth tergite
6T.	—————	Sixth tergite
7T.	—————	Seventh tergite
1S.	—————	First sternite
2S.	—————	Second sternite
7S.	—————	Seventh sternite

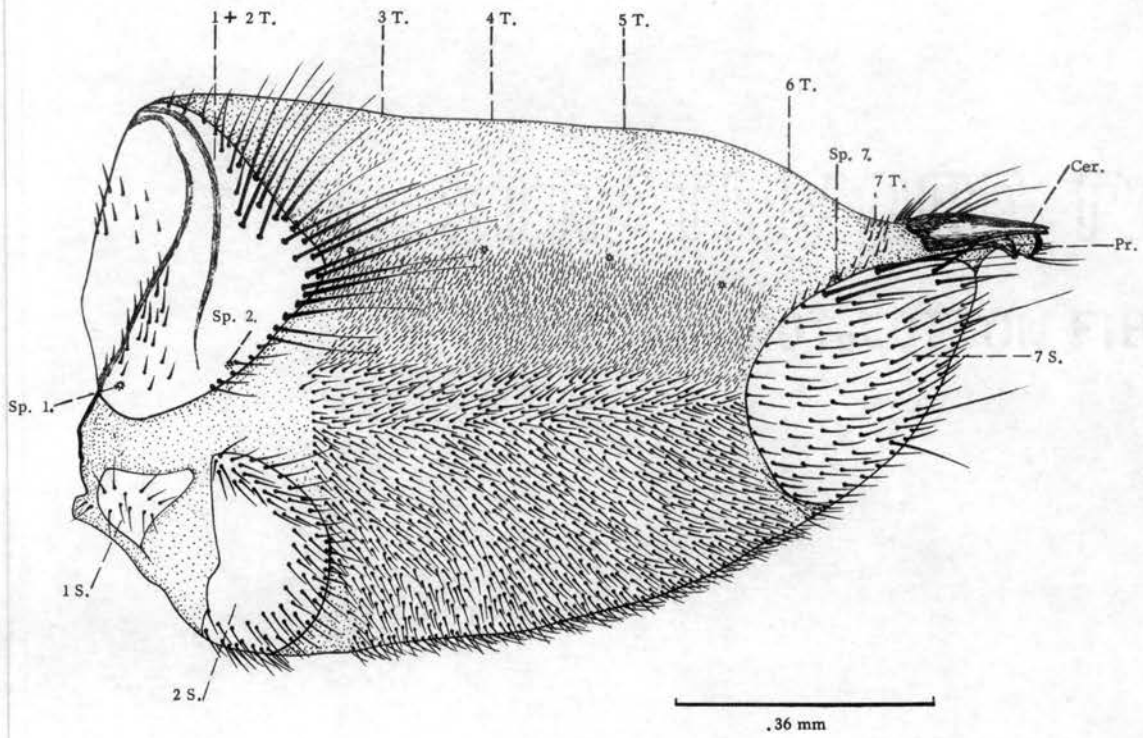


Fig. 74

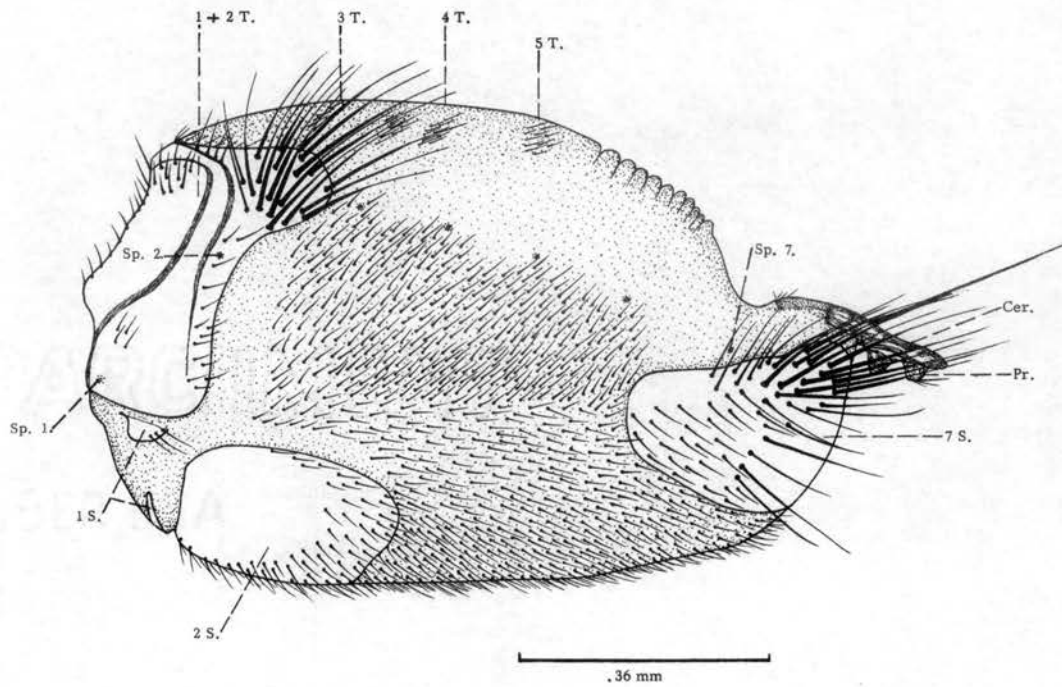


Fig. 75



PLATE XXXIII

Fig. 76. Trichobius sphaeronotus Job., lateral view of female abdomen.

Fig. 77. Trichobius major Coq., ventral view of female abdomen.

Cer. ————— Cercus  
Pr. ————— Proctiger  
Sp.1.,2.,7. ——— First, second, and seventh abdominal spiracles  
Vul. ————— Vulva  
1+2T. ————— Fused first and second tergites  
1S. ————— First sternite  
2S. ————— Second sternite  
7S. ————— Seventh sternite

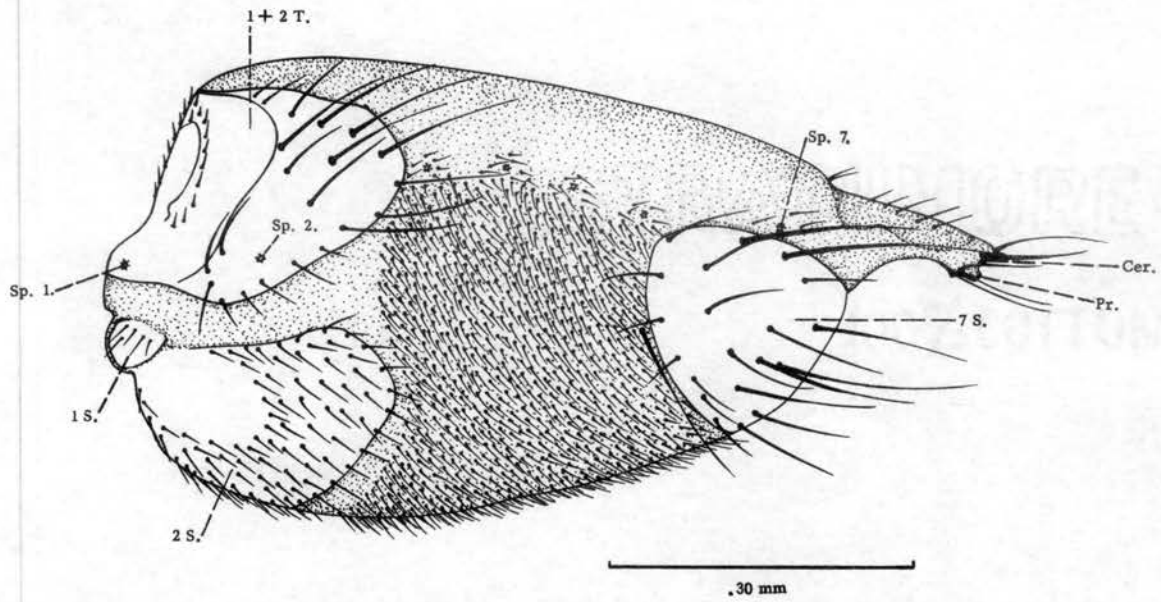


Fig. 76

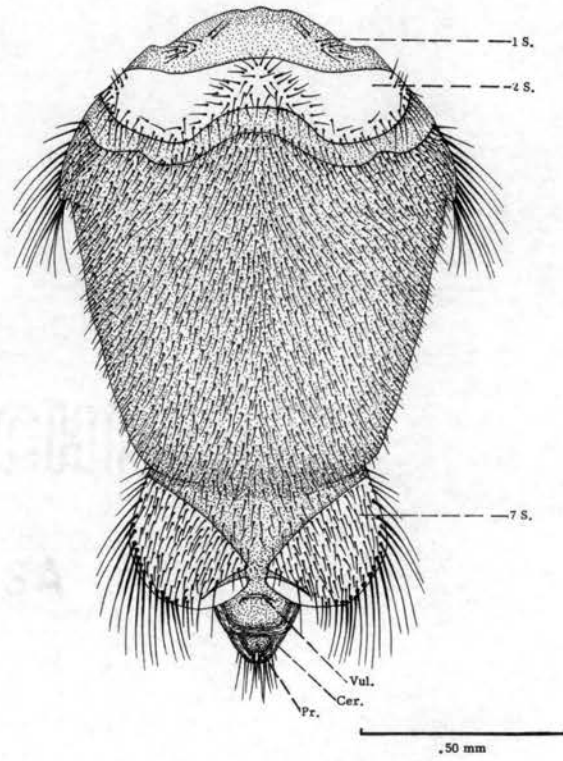


Fig. 77

PLATE XXXIV

Fig. 78. Trichobius corynorhini Cock., ventral view of female abdomen.

Fig. 79. Trichobius sphaeronotus Job., ventral view of female abdomen.

Cer.	-----	Cercus
Pr.	-----	Proctiger
Vul.	-----	Vulva
1S.	-----	First sternite
2S.	-----	Second sternite
7S.	-----	Seventh sternite

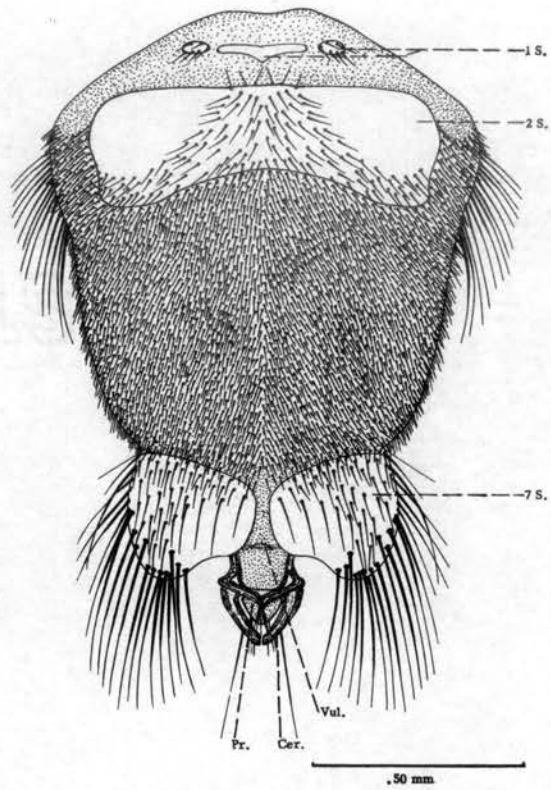


Fig. 78

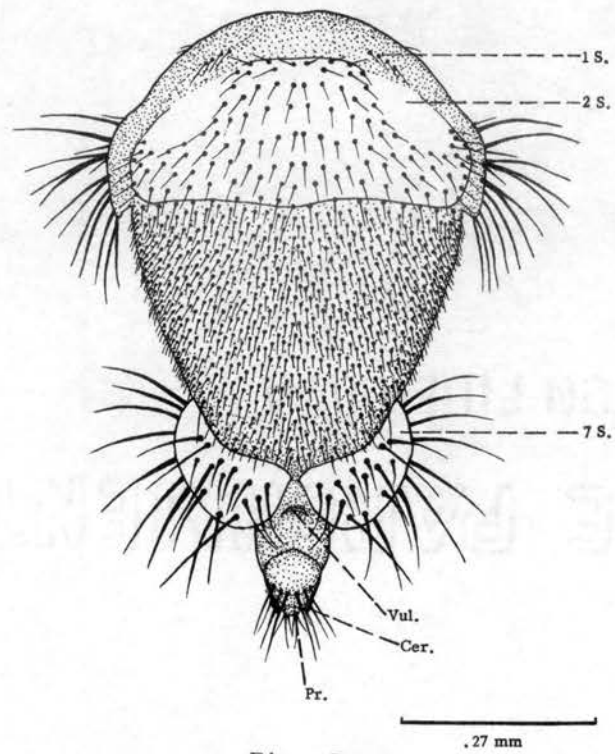


Fig. 79

VITA

VICTOR HENRY ZEVE

Candidate for the Degree of

Doctor of Philosophy

Thesis: THE COMPARATIVE EXTERNAL MORPHOLOGY OF TRICHOBIUS CORYNORHINI  
COCKERELL, T. MAJOR COQUILLET AND T. SPHAERONOTUS JOBLING  
(DIPTERA, STREBLIDAE)

Major Field: Entomology

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