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# THE COMPARATIVE LARVAL MORPHOLOGY OF REPRESENTATIVE NEW WORLD DRYOPOID BEETLES

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EDWIN ALFRED GREEN

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THE COMPARATIVE LARVAL MORPHOLOGY OF REPRESENTATIVE NEW WORLD DRYOPOID BEETLES

APPROVED BY

Harley P. Brown

Cluff E. Hopla

Frank J. Sonleitner

George J. Goodman

DISSERTATION COMMITTEE

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## INTRODUCTION

With the publication of Leng's checklist (1920), taxonomists became aware of the need for a more natural system of classifying the Coleoptera. Such a system could only be developed when an adequate consideration of larval features is taken into account along with adult features.

In spite of general recognition of the need for studies of larvae, our present knowledge of the morphology of immature dryopoid beetles results from the work of a very limited number of investigators. The classical work by Böving and Craighead (1931) represents the largest single publication concerned with the larvae of beetles. This work, which included a number of dryopoids, caused Leng and Mutchler (1933) to make significant changes in their subsequent classification scheme.

West (1929), preserving the family name of Dryopidae, studied the external morphology of larval structures in selected genera. Later studies by other investigators have necessitated changes in most of the names used by West, but his work represented a great contribution to our knowledge of the taxonomic relationships suggested by the larvae of dryopoid beetles.

Sanderson (1938) noted in chronological sequence many changes in the classification scheme since the work of Boving and Craighead. In addition, he presented a revision of the nearctic genera of elmids (Sanderson, 1953-54). His identification of the larvae was based on a process of association and elimination.

Bertrand (1955) attempted to show phylogenetic relationships using many external larval characters. His work represented another step in the attempt to understand whether natural relationships may be correlated with purely external features of dryopoid beetle larvae.

Hinton (1939) was of the opinion that no valid phylogenetic system could be based only on selected external features. He was the first to attempt to establish family and generic relationships based on a correlation of external and internal morphological features of dryopoid beetle larvae (Hinton, 1940).

A few other workers have made contributions to our knowledge of the internal morphology of immature dryopoids. Their work has been confined to specific internal systems. Beier (1927) carried out a study of the central nervous system of some selected beetle larvae, including the dryopoids. Susskind (1936) published a study of the respiratory system in various instars of Stenelmis sulcatus (a synonym of Stenelmis quadrimaculata).

My objective was to expand our knowledge of the comparative morphology of dryopoid beetle larvae by describing in systematic detail the external and internal morphology of larvae of New World genera representing various body forms or types. This has involved examination of external features, both intact and dissected, and internal features, by dissection and serial sections, in order to describe characters which mightbe useful in establishing natural relationships among families and among genera.

## MATERIALS AND METHODS

Twenty-four genera belonging to three families of dryopoid beetles were used in this study. Most of the specimens were from the H. P. Brown collection in the Stovall Museum of Science and History at the University of Oklahoma in Norman. Other specimens were collected from the Blue River, Clear Boggy Creek and Pennington Creek in southern Oklahoma. The specimens obtained from the museum were preserved in 80% alcohol. Those collected were preserved in KAAD solution.

Preparation of the larvae for external study was carried out by placing a larva in a depression made in tissue mat (paraffin) contained in a centerwell Petri dish. Tissue mat (melted at 52-54°C.) was poured over the specimen, affixing it in place. Using a Bausch and Lomb Stereo-Zoom dissecting microscope, the labium, maxillae, mandibles, head, thoracic segments, abdominal segments, and operculum were dissected. Dissecting tools were constructed from insect pins, dissecting needle holders, disposable hypodermic needles, and razor blades. Each dissected part was placed on a microscope slide which contained Hoyer's medium. The dissected part was covered with the medium and both were covered with a cover slip. The dissected parts were allowed 2 - 5 days to clear. When cleared, they were studied with a compound microscope and sketched with the aid of a camera lucida.

The intersegmental membranes of the specimens used for internal study were perforated with a No. I insect pin. Each specimen was placed in enough Mayer's paracarmine to cover it. Specimens were allowed to remain in the stain for two hours. At the end of this time, the specimens were rinsed in tap water. Each specimen was placed, with the ventral side up, in a depression within the paraffin. It was affixed there by pouring melted paraffin over it. After the paraffin cooled, the specimens were exposed by removing a portion of the paraffin. With the aid of the stereoscopic microscope and dissectiong tools, sternal plates were removed from the eighth abdominal segment forward. Internal parts were observed, studied, sketched, and removed from the body. Additional sketches were made of the internal organs, then all body parts were mounted on microscope slides in Hoyer's medium. All dissections were made under water to prevent desiccation of the larval parts.

Preparation of the larvae for sectioning met with difficulty using the paraffin method. The following procedure adapted from Woodring and Cooke (1962) yielded moderate success.

1. Larvae were transferred from the preservation fluid to Bouin's fixative.
2. Specimens were kept in Bouin's for 12 hours.
3. Each specimen was transferred to a 50-50 mixture of phenol and chloral hydrate.
4. Each larva was passed through three changes of the above and allowed to remain in the last change for one week.
5. Each larva was returned to Bouin's solution for 1-2 hours.
6. Specimens were placed in a 50-50 mixture of dioxan and distilled water for 24 hours.

7. They were transferred to a pure solution of dioxan.

8. Each larva was transferred to a 50-50 mixture of dioxan and N-butyl methacrylate, from which the hydroquinone inhibitor had been removed. (The inhibitor was removed by washing the N-bm with 30% sodium hydroxide in a separatory funnel until the sodium hydroxide was no longer turned brown by the hydroquinone. After two washes with distilled water and several passes through anydrous calcium sulfate, the N-bm was ready for use.)

9. Specimens were transferred to the pure monomer of N-bm and allowed to infiltrate for 4-8 hours in an oven at 52-54°C in Stender dishes.

10. A mixture of 2 grams of N-bm, 3 grams of benzoyl peroxide, and 5 grams tissue mat was prepared. A small amount of the mixture was placed in a small gelatin capsule. The capsule was placed in the oven at 52-54°C for 4-8 hours, or until the mixture partly polymerized. This prevented the sinking of the specimen to the bottom of the mixture in the capsule.

11. A larva was placed in the gelatin capsule and enough of the unpolymerized mixture was added to keep the specimen near the middle and perpendicular to the surface of the mixture.

12. The larva-containing mixture was allowed to polymerize for 12 hours in an oven at 52-54°C, with the capsule affixed to the side of a beaker by cellophane tape.

13. After polymerization, the gelatin capsule was removed by softening in water and the specimen-enclosing tissue mat-plastic mixture was trimmed away close to the body of the

specimen.

14. Specimens were placed in molten tissue mat for two hours in an oven at 52-54$^{\circ}$C.

15. Specimens were embedded in tissue mat, the mat was prepared for sectioning, and the sections were cut at 8-10 microns. Various techniques were used to combat static electricity.

16. Sections were affixed to microscope slides with egg albumen and stained with Mallory's triple stain following the procedure of Galigher and Kozloff (1964).

All hand illustrations were done by the writer and the lines next to the figures represent a length of 0.20 mm unless otherwise indicated.

Gut contents of the larvae were identified by the writer with the aid of works by Smith (1950), Prescott (1954), Thompson (1959), Patrick (1959), and Weber (1966).

## PSEPHENIDAE (Lacordaire, 1854)

This family of water beetles and others related to it have undergone a number of name changes (Murvosh, 1960). The old family name Parnidae included three subfamilies: Psepheninae, Parninae, and Elminae. Leng (1920) raised each of them to family rank, but used the name Dryopidae instead of Parnidae and Helmidae instead of Elmidae. West (1929), in a study of larval morphology, retained the family name Dryopidae and included in it the subfamilies Psepheninae, Dryopinae, and Elminae.

Leech and Sanderson (1959) listed five nearctic genera as belonging to this family. Species of <u>Psephenus</u> occur widely over eastern, central, and western parts of the United States, and south through Central America. <u>Eubrianax</u> occurs in California, Oregon, western Nevada, and the Orient. <u>Acneus</u> has been recorded from California and Oregon. <u>Ectopria</u> has been found in eastern and central United States and Canada (Florida to Maine and Canada then west to Iowa, Missouri, and Oklahoma). <u>Dicranopselaphus</u> has been found in a few eastern states and in Central America.

Adults are small, depressed, black or brown and sometimes variegated, riparian or terrestrial beetles. Eggs (of <u>Psephenus</u>) are laid on the undersides of stones in streams. Eggs hatch into flat-bodied, broadly oval larvae which may or may not have a series of ventral gills.

Pupation occurs beneath the last larval integument. Pupation may occur in or out of the water. According to Hinton (1939) larvae have maxillae with very large articulating surfaces. Maxillary palps may be of 2, 3, or 4 segments. In all genera with well developed gills, spiracles are present, but are closed. Those without ventral gills have retractile anal gills and spiracles are rudimentary or absent.

Three genera were considered in this investigation, Psephenus Ectopria, and the Neotropical genus Psephenops.

Psephenus (Haldeman, 1853)

According to Brown (1970b) this genus is represented in the eastern United States and adjoining Canada by a single species, P. herricki (Dekay, 1844), in the western states by three different species: P. haldemani (Horn, 1870) in California, Oregon, and Idaho, P. texanus (Brown and Arrington, 1967) in southern Texas and P. murvoshi (Brown, 1970) in central Arizona. Two additional new species from Arizona will soon be described by Brown and Murvosh.

As described by West (1929), larvae of Psephenus herricki have flattened, elliptical bodies. The larva proper is concealed beneath an arched carapace formed by the extension of the pleurites of the first ten body segments. The entire peripheral margin is bordered by a row of long hairs and is capable of being closely appressed to rocks. Lateral lobes of the eleventh body segment (which is the eighth abdominal segment) tend to be obliterated. The ninth abdominal segment is composed of a broad, flat, rectangular dorsal sclerite and a small ventral one, between which is located the anal opening.

The head, which is visible only in ventral view, bears three-segmented, elongated antennae. The first segment is about equal in length to the distance between the ocelli, the second, three-fourths the length of the first, the third minute and composed of two small segments lying side by side. The larger of the latter bears distally a tiny spine. The first antennal segment usually bears six hairs along its posterior margin. Ocelli are in two groups of six each.

Labrum broad, anterior margin straight or slightly rounded, lateral margins convex, each bearing a row of rather coarse spines. Mandible large, heavily sclerotized, especially near the tips, bearing at about mid-point of inner margin, a brush or tuft of bristles (the prostheca), evidently sensory in function. Outline of mandible usually subtriangular. Maxillae large, complex, and with palpi of four segments. Lacinia with papilla-like prominences which taper into short, thick spines. Galea more or less covered with short hairs. Stipes, first, and second segments of palp bearing 1, 2, and 2 stout bristles, respectively. Labium short, broad, not heavily sclerotized, and bearing a pair of three-segmented palpi. Tip of third segment, like fourth segment of maxillary palp, beset with tiny tubercles evidently tactile in function. Basal segment of palp bearing three-branched spines. Mentum quadrangular and broad.

Legs all similar and stout. Each leg thickly beset with hair and bearing a single strong claw with a short interior spine.

Gills ventral, arranged in five pairs and taking origin from the posterior margin of abdominal segments 2-6. Each gill tuft composed on the average of ten filaments arranged in a somewhat comb-like fashion.

Length of mature larva 8.4 mm. Width 5.75 mm.

I have studied the external and internal morphology of six larvae of _Psephenus texanus_, collected in Del Rio, Texas on August 26, 1967. The specimens measured 7.20-9.04 mm in length and 4.1-5.61 mm in width at the first abdominal segment. Two specimens were used for histological study.

_Psephenus texanus_

## External Morphology

Many of the characteristics outlined above by West (1929) were observed. Additions and differences are noted below.

Dorsum: cuticular nodules in pattern of interlocking circles dispersed over the carapace. Dichotomous suture on anterior tergo-pleural junction of prothoracic carapace (Fig. 1). Proximal arm of suture passes toward mid-dorsal line, then assumes a subparallel direction with mid-tergal suture. An antero-lateral section of first abdominal tergite is subtriangular in outline (Figs. 1, 2). Anterior nodules on second and third thoracic pleura and first 7 abdominal segments of carapace run subparallel to anterior margins of pleura.

Head: bearing 3-segmented antennae as described by West (1929), but no tiny spine was observed on the larger member of the third segment. The first member bears 6-7 hairs along its antero-lateral border instead of six only as described by West (1929). There are 5-6 ocelli just laterally to the base and 8-10 spinous setae at the base of each antenna (Fig. 3). Labrum broad, anterior margin rounded, and a transverse row of tubercles, containing multibranched setose bristles, are present (Fig. 3). Clypeus with anterior margin emarginate and convex lateral borders (Fig. 3). Lacinia with distinct prominence on antero-medial surface. Maxillary palp consisting of four segments, with suggestions of a palpifer (Fig. 4). Lateral spines on palpi vary in number. Cardo slipper-shaped and articulating with stipes. Chisel-shaped incisor of mandible adjacent to slanting molar surface (Fig. 5). Ligula wide, with slightly irregular anterior periphery. First segment of labial palp club-shaped, twice as long as segment two and slightly less than twice as long as the palpiger (Fig. 6).

Each leg consists of a coxa, trochanter, femur, tibiotarsus, and tarsal claw. The internal tarsal claw spine was observed to be blunt in all cases. The tibiotarsus is slightly flattened on inner and outer proximal surfaces. Prothoracic and mesothoracic legs bear a distinct depression at coxa-trochanter junction. First and second legs are approximately the same length. Each segment of third leg (except for the trochanter) is longer than the corresponding segment of first and second legs (Figs. 7A, B, C).

Spiracles located on mesothoracic and first 7 abdominal pleurites. Eighth abdominal spiracle located on lateral margin of 8th abdominal tergite of carapace (Figs. 1, 2).

## Internal Morphology

The material is divided into gross internal morphology and histological morphology. The condition in Psephenus texanus is taken as a basis of comparison and where other members of the family differ from the above this is noted and illustrated with figures.

### Digestive System

The alimentary tract (Fig. 8), revealing no distinctive external features, consists of a stomodeum (a short buccal cavity, an esophagus, an expanded crop, and a short proventriculus), a mesenteron (ventriculus), and a proctodeum (anterior intestine and posterior intestine). The stomodeum shows no constrictions externally which suggest all of the divisions listed. Evidence for listing such zones will be given below. The mesenteron and proctodeum are approximately the same length, but the stomodeum is shorter. The mesenteron tapers as it joins the proctodeum. A fold in the proctodeum causes it to lie along the posterior one-fourth of the mesenteron. Posteriorly the proctodeum terminates at the anus.

Respiratory System

The tracheal system is amphipneustic (with only the first pair and one or two pairs of posterior spiracles open). Paired lateral vessels represent main lateral trunks. From them arise vessels which pass to the head, gills, spiracles, and other parts of the larval body (Fig. 10). According to Hinton (1955) functional spiracles in *Psephenus* (those of the mesothorax and 8th abdominal segment) lack a functional closing apparatus. The openings of the spiracles are guarded by atria largely filled with tiny cuticular processes. In addition, the spiracles are biforous (spiracles having two pouches of the atrium originally supposed to open separately to the exterior).

Paired ventral gills arise between adbominal segments 2 and 3, 3 and 4, 4 and 5, 5 and 6, and 6 and 7. As indicated by Hinton (1955), the gills of *Psephenus* are branched prolongations of the body surface. A tracheal branch extends into each gill filament, of which there are about eleven in each gill of Psephenus texanus.

## Excretory System

Six malpighian tubules arise at the junction of mesenteron and proctodeum (Fig. 8). They pass anteriorly over one-half the length of the mesenteron and then posteriorly, following the folds of the gut. They terminate within the space between the posterior end of the mesenteron and the posterior intestine of the proctodeum.

## Central Nervous System

Psephenus texanus has a bilobed, pyriform supraesophageal ganglion which is located within the posterior part of the head capsule and anterior one-fourth of the prothorax (Fig. 9). Anteriorly it is drawn out into nerve tracts which send branches (optic) to the simple eyes. Circumesophageal connectives (the crura cerebri) connect the supraesophageal ganglion with the subesophageal ganglion. There are three enlarged thoracic ganglia and seven abdominal ganglia. The first abdominal ganglion appears to be fused to the metathoracic ganglion and the 7th is the longest due to fusion of the 7th and 8th. Extending beyond this last abdominal ganglion are nerves which arise from its lateral borders (Fig. 9).

# Histological Morphology

## Integument

The exocuticle takes up acid stain and averages 18 microns in thickness. The endocuticle averages 40 microns in thickness and takes up basic stain. The endocuticle consists of layers or bars which appear to form rectangules. The epidermis is formed by a thin layer of cells resting on a basement membrane.

Scattered dorsally over the carapace are multicellular nodules. The nodules are 11 microns higher than the epicuticle surface and within each nodule is a sensory bristle (Fig. 36). The nodules are not present on the ventral surface of the carapace, nor on other parts of the larva. Protruding from the exocuticle on the ventral side of the carapace are flabellate setae. On the legs are spinous setae which pass from the endocuticle through the surface.

## Digestive System

The external mouth parts are composed of paired mandibles, maxillae and the labium. The mandibles are hinged to the head by firm atriculations allowing only transverse movements of abduction and adduction produced by respective muscles.

There is no observable differences between the wall of the buccal cavity and that of the esophagus. The innermost layer is a heavy cuticular intima; external to this is a thin layer of low epithelial cells, then a rather thin muscle layer. No distinction can be made between inner longitudinal and outer circular muscle layers. Posterior to the esophagus is a dilated crop. The crop proper takes up one-half of the dilation. The wall of the crop is made up of a strong cuticular intima, a very low epithelial layer and a basement membrane on which it rests, then inner longitudinal and outer circular muscle layers which are covered by a connective tissue layer. Following the crop is the proventriculus. The anterior wall contains proventricular pads and teeth. The teeth are subrectangular and triangular and form a complete ring around the gut lumen (Fig. 11). In cross-section the teeth appear acute at the apex. Just behind or posterior to them, epithelial cells are massed, forming scattered subtriangular organelles. On the surfaces of the organelles are spines which project anteriorly toward the foregut (Fig. 11). Esophageal invaginations extend from the foregut into the midgut. The form of the invaginations suggests a sphincter or a valve.

The midgut represents the most dilated part of the alimentary tract. Surrounding the lumen is a peritrophic membrane. The epithelium consists of tall columnar cells resting on a very thin basement membrane. A striated border is not very evident. The muscles consist of a thin, inner layer of circular and several bands of outer longitudinal muscles.

The hindgut exhibits a slightly different appearance. The epithelial cells are at first shorter than those of the midgut, then they are thrown into six wide folds. The folds decrease to finger-like villi which disappear toward the anus. The muscle layers of the anterior hindgut are thicker than those of the midgut, but they decrease in thickness posteriorly. The peritrophic membrane is replaced here by a cuticular intima.

## Respiratory System

Structurally the vessels do not differ from the description given by Snodgrass (1935). The matrix layer of the trachea is an epithelium of flat polygonal cells continuous with the epidermis around the spiracle. Outside is a basement membrane and inside is a strong cuticular intima. The characteristic feature of a trachea is the closely-ringed appearance resulting from the presence of thickenings of the intima to form minute circular or spiral ridges called taenidia.

The ventral gills are pale filaments. In cross-section, their penetration by branching tracheal vessels was evident.

## Excretory System

Cellular components of malpighian tubules do not differ from the description by Patton (1953). They are long, narrow tubes composed of a single layer of epithelial cells. The cells are limited externally by a coat which often contains muscle fibers and internally by a delicate membrane. Cross-sections of Psephenus texanus revealed that each tubule appears as a ring of six large cells having prominent nuclei. A brush border exists on the inner apices of the cells.

## Central Nervous System

A complete neural sheath surrounds the brain, subesophageal, thoracic, and abdominal ganglia. There apparently is a medullary and a cortical zone in each of the ganglia. Basophilic material is abundant. Neuroglial nuclei are scattered throughout the tissue. Observations did not reveal fibers identifiable as giant axons. All of the axons appeared to be of the same size.

Examination of the sections revealed the brain, subesophageal, thoracic, and abdominal ganglia to be connected transversely. Interganglionic membranes are present between all abdominal ganglia except numbers seven and eight.

## Sense Organs

These organs are the ocelli, sensory setae of the legs, antennae, palps, and the prosthecae. The ocelli consist of an aggregation of light sensitive cells resembling the retinular cells of the compound eye, covered by a simple corneal lens of transparent cuticle. Multicellular tactile setae of the legs consist of cuticular bristles articulated in cuticular sockets and innervated by sensory cells. Associated with such a sensillum, according to Snodgrass (1935), are trichogen and tormogen cells. On the antennae are spines with a bulbous base. Attached to the mandibles and extending into the buccal cavity are brush-like prosthecae. These, along with the palpi and associated spines or hairs are postulated to bear chemoreceptors. Chemoreceptors can be determined as such only by physiological means. All of the above are considered to be primary sense organs by the writer. They will be referred to as such throughout this work.

Study of vertical sections through the cuticular nodules suggests that they apparently are campaniform organs. Workers have suspected that they are sensitive to water pressure changes in aquatic insects.

## Fat Bodies

Each fat body consists of several spherical masses of fat cells within a meshwork. Associated with them are uric acid granules and glycogen globules. The bodies fill the coelomic space and extend into the tips of the carapace between the upper and lower epidermis.

## Gut Contents

Cross-sections of the gut revealed in the lumen diatoms (*Rhopalodia*, *Navicula*, *Meridion*, *Cocconeis*, *Synedra*, and *Nitzschia*), other algae (*Chlorococcus*, *Coccochloris*, and *Hormidium*), sand, etc.

Ectopria (LeConte, 1853)

The larva of Ectopria has been mistakenly described in several publications as that of Helichus (Dryopidae), as pointed out by Leech and Chandler (1959). Specimens have been collected from Florida to Maine and Canada west to Iowa, Missouri, and Oklahoma (Brown, in press).

The following features identify the larva of Ectopria, as described by West (1929) under the genus Helichus.

Body: form elliptical-ovate, flattened; lateral lobes of the carapace are not closely joined together. The portion of the carapace derived from the prothorax is characterized by backward-projecting postero-lateral angles. Dorsal surface bearing many small tubercles scattered irregularly over the prothorax and lateral lobes. Mid-dorsally they are arranged in six longitudinal rows, the outer four joining up anteriorly in the pattern of a broken W. Lateral lobes of eighth abdominal segment morphologically similar to those of preceding segment. Junction of pleura with sternum not in line with base of lateral lobes, but at a considerable distance nearer the mid-line. Posterior abdominal segment flattened and subrectangular. Dorsal sclerite slightly longer than broad, ventral sclerite two-thirds as wide and nearly as long as the dorsal one. Entire margin of animal ciliate with tufted hairs. Ciliation tending to disappear on anterior and posterior borders of most antero-lateral lobes.

Head: large, concealed beneath the carapace, usually directed forward, capable of partial withdrawal into a rather elaborate collar composed of a reflected portion of the integument of the neck. Antennae composed of three segments, the first stout and barely twice as long as broad, second somewhat more slender and of slightly greater diameter at the middle than at either end, and the third duplicate, composed of similar members side by side. Basal segment of antennae usually bearing three strong spines and the second segment, one strong spine.

Labrum nearly two-thirds as long as broad. Anterior margin regularly convex with slight antero-medial expansion and antero-lateral angles heavily ciliate with hair. Mandibles large, elongate or short, subtriangular, heavily sclerotized, with stout interior sensory filament (prostheca) covered with distally directed setae, and surrounded at the base with a considerable mass of sensory hairs. Maxillae complex, rather membranous, bearing small four-segmented palpi, the distal segment of which is very minute. Hairs on stipes and basal segments of palp noticeably branched. Galea without characteristic form, being roughly cuboidal, bearing distally about six, stout, curved spines, together with many lesser hairs which cover a large portion of its surface. Lacinia simulates a truncate sleeve open along the free margin and bordered distally with many fairly stout spines. Labium membranous and twice as long as broad. Anterior margin heavily ciliate. Ventral surface morphology suggests differentiation into glossa and paraglossae. Palpi of two segments each in addition to a palpiger.

Ventral surface of femur characterized by the presence of several modified spines. Each spine short, considerably thickened, and bearing many tiny processes. Each tarsal claw with a slender interior spine.

Anal gills arranged in three tufts and capable of extrusion between the ventral and dorsal sclerites of posterior abdominal segment. Spiracles confined to pleurite of eighth abdominal segment.

Length of mature larva 5.5 mm. Width 3.3 mm.

I have studied the external and internal morphology of five larval specimens of Ectopria nervosa, collected near Bunch, Adair County, Oklahoma on May 4, 1963 and from the Mountain Fork River, McCurtain County, Oklahoma on June 19, 1962. The larvae measured 4.84 mm. to 5.98 mm. in length and 2.96 to 3.51 mm. in width. Two specimens were used for histological study.

Ectopria nervosa

## External Morphology

Many of the features of the structure (Figs. 12, 13, 16A, B, 17, 18A, B) described by West (1929) for Ectopria (referred to as Helichus) are illustrated by Ectopria nervosa, which is presumably the species with which he worked. Some additional or different features are described below.

Dorsum: Interpleural setae cuneate. Setae along pleural margin spinous. Ninth tergite slightly truncate to rounded posteriorly and slightly emarginate on lateral margins (Figs. 12, 13). Operculum with non-sclerotized postero-lateral margin giving concave appearance. Parted cuneate setae on ventral surface of operculum and linear spines along posterior border (Fig. 19).

Head: clypeus wedge-shaped posteriorly (Fig. 17). Six or more spines on first segment of antenna. Maxillae (Fig. 15) differ slightly from the structure illustrated by West (1929). Cardo suboblanceolate. Distinct protuberance at junction of lacinia and stipes (Fig. 15). Labium (Fig. 14) bears two-segmented palpi and mental palpigers are suggested. Palpigers are suggested by an emargination below the outer lateral base of the first palp segment. Antero-internal surface of second member bears a secondary appendage and a pair of incrassate bristles on the apex, but emargination on antero-lateral surface of second palp segment contains a tuft of setae. Anterior margin of labium bears a transverse row of subspherical tubercles from which arise subobconic setae. Posteriorly to the subobconic setae are irregularly arranged setae tufts arising from small punctures. Setae on mental and submental surfaces as figured (Fig. 14).

Legs: (Figs. 18A, B) articulating surfaces distinct between coxa and trochanter and between femur and tibiotarsus; tarsal claw spine long and sharp, one-half as long as claw.

## Internal Morphology

### Digestive System

The alimentary canal is divided into the same divisions and is folded as in *Psephenus texanus*. It differs in that the hindgut is longer than the foregut as well as the midgut (Fig. 20).

### Respiratory System

The main tracheal vessels are paired lateral trunks. They pass posteriorly to terminate in distinct spiracles on the internal part of the 8th abdominal pleurite. Prior to the point of termination of the vessels, internal ventral and dorsal branches arise (Fig. 21). These branches communicate with dorsal and ventral gill tufts. As in *Psephenus texanus*, the spiracles are biforous.

### Excretory System

This system is as that in *Psephenus texanus*.

Central Nervous System

The brain and subesophageal ganglia are as they are in Psephenus texanus. Three thoracic ganglia are present. The metathoracic ganglion is distinctly larger than the others in contrast to all three ganglia being of the same size in Psephenus texanus. Eight discrete abdominal ganglia occur in a series (Fig. 22). There is no evidence of a very close association or fusion.

## Histological Morphology

Integument

Exocuticle and endocuticle average 14 and 25 microns in thickness, respectively. Exocuticular and endocuticular relationships are as in P. texanus.

Digestive System

The longitudinal and circular muscles of the buccal cavity are thicker than in P. texanus. The crop is not unlike that in Psephenus texanus, but there is a distinct difference in the proventriculus. There are apparently no triangular teeth at the anterior of this zone, but there is a circle of rectangular teeth (formed as a result of longitudinal folds along this region of the gut) which are covered by small sclerotized tubercles (Fig. 23). Posteriorly irregular folds bearing blunt villi with a sclerotized intima line the inner wall of the proventriculus. Esophageal invaginations extend backward into the midgut, the epithelium of which contains many folds (Fig. 24). The morphology of the folds suggests that they have a secretory function. No such folds are present in the wall of the proventriculus of Psephenus texanus.

Goblet cells of the midgut are rather distinct in Ectopria, in contrast to the opposite condition in Psephenus. Hindgut muscle layers are as figured (Fig. 25).

Respiratory System

Histologically, the tracheal system is not different from that of Psephenus. Anal gill filaments are greater in number in comparison with those of ventral gills, but do not appear to differ histologically. Examination of serial sections revealed that each of the three gills receives two tracheal vessels (Fig. 26), but a single vessel terminates in the functional spiracle on the 8th abdominal pleurite.

Excretory System

The cellular components of the malpighian tubules do not differ from the description for Psephenus.

Central Nervous System

The cellular components are not different from those found in Psephenus.

Sense Organs

Primary sense organs do not differ histologically from those in Psephenus. The tubercles on the carapace are apparently campaniform organs as found on Psephenus.

Fat Bodies

These bodies are similar to those found in Psephenus. An apparent difference is that each fat cell has an eccentrically placed flat nucleus.

Gut Contents

The nature of the gut contents suggests two possibilities, either a more efficient grinding system than in *Psephenus* or the ingestion of large amounts of debris and broken cell parts. The gut lumen contained diatoms (*Rhopalodia*, *Coscinodiscus*, and *Cocconeis*), filamentous algae (*Spirogyra*), other algae (*Coccochloris* and *Protococcus*), miscellaneous cell fragments, seeds, sand, and grit.

## *Psephenops* (Grouvelle, 1898)

When described, this genus was based on a single species, *P. smithi* Grouvelle, of which only the male was known (Champion, 1913). A female collected from the same site (the Antillean Islands of Grenada and St. Vincent) as *P. smithi* and named *Xexanchorinus latus* by Grouvelle was later postulated to be the female of *P. smithi* (Darlington, 1936). This genus is represented in Guatemala, Haiti, Colombia, and the Antillean Islands of Grenada and St. Vincent (Blackwelder, 1944).

I have studied the external and internal morphology of three larvae believed to be *Psephenops smithi* from Bocono, Trujillo, Venezuela, collected on June 4 and 6, 1968, and from Tinaco, Venezuela, collected on June 1 of the same year. The specimens ranged from 2.5 to 5.2 mm in length and 2.5 to 3.0 mm in width. Two larvae were studied histologically.

### *Psephenops smithi*

#### External Morphology

Dorsum: flattened, as in *Psephenus*, concealed beneath a protective arched carapace. Pleurites of first through tenth segments elongate.

Pleurite of 11th body segment (eighth abdominal segment) absent or rudimentary. Ninth abdominal tergite is rectangular and slightly less than twice as wide as it is long. Entire peripheral margin bordered by cilia-like hairs (Figs. 27, 28). Dichotomous suture on anterior tergo-pleural junctions of the carapace. Proximal arm of suture passes toward mid-dorsal line and assumes a direction subparallel with mid-dorsal suture (Fig. 28). An antero-lateral section of first abdominal tergite is subtriangular in outline (Figs. 27, 28). Sensory organelles on second and third thoracic segments form a wing-like design adjacent to mid-tergal suture. Sensory nodules on dorsal surface of all pleurites and ninth abdominal tergite.

Head: visible only from ventral view and covered by extended anterior carapace; capable of the same movements as in Psephenus (Fig. 29). Ocelli in two groups of six. Clypeus emarginate; labrum slightly emarginate on mid-anterior margin, and covered with sensory bristles (Fig. 29). Antenna elongate; first segment almost three times as long as second; third consists of two small segments lying side by side, the inner member with a spine projecting from its distal end. Five to six setae on distal end of first segment and one small spinous bristle on head lateral to anterior margin of frontal suture and parallel with first segment of antenna (Fig. 29). Mandibles subtriangular, with two apical teeth (Fig. 30). Prostheca short, bristles parted, not compact. Cardo slipper-shaped (Fig. 31), lacinia elongated, and convex on medial surface distally, with an apical row of clavate spines. Galea with many spines of short and intermediate length. Maxillary palp four-segmented; fourth segment bears several sensory bristles on distal end, and a palpifer is suggested. Labium membranous and contains a medial cleft (Figs. 32A, B). Many tubercles bearing parted cuneate setae cover margin of labium.

Legs all rather similar but differing in length (Figs. 33A, B, C). Tarsal claw with a short, blunt internal spine. A slender spine as long as the claw projects from outer base of claw.

Gills ventral and emerging from between the same segments as in _Psephenus_. Functional spiracles on mesothorax and 8th abdominal pleurite.

## Internal Morphology

### Digestive System

The outline of this system differs slightly from that of _Psephenus texanus_ (Fig. 34).

### Respiratory System

This system does not differ from that of _Psephenus texanus_ (Fig. 10).

### Excretory System

This system is similar to that found in _Psephenus_ and _Ectopria_.

### Central Nervous System

This system is similar to that present in _Psephenus texanus_, except that in gross view fusion of the third thoracic and first abdominal ganglia is not suggested (Fig. 35).

## Histological Morphology

### Integument

Exocuticle and endocuticle average 14 microns in thickness. From the surface of the exocuticle arise tubercles as in Psephenus and Ectopria. The tubercles attain a height of 9 microns above the surface of the exocuticle. The serial sections revealed a groove along the mid-dorsal line (mid-tergal suture) with a width of 10 microns (Fig. 36).

Digestive System

The dilated buccal cavity differs from that of Psephenus and Ectopria in being lined with a very thick cuticular intima which decreases the diameter of the lumen. The esophagus, which is not different from that of Psephenus texanus, expands posteriorly into a crop. There is a ring of flat sclerotized plates which encircle the lumen (Fig. 37). The presence of these plates designates approximately one-half of the crop as proventriculus.

Subcolumnar cells lining the wall of the midgut are covered by a distinct peritrophic membrane. These tall cells are very close together, reducing the lumen as in the buccal cavity (Figs. 36, 38).

Anteriorly the hindgut epithelium is thrown up into irregular folds. A thick cuticular intima covers the epithelia, decreasing the lumen as in the midgut and buccal cavity.

Respiratory System

The histology does not differ from that given for Psephenus.

Excretory System

This system is similar to that observed in Psephenus and Ectopria.

Central Nervous System

The components of this system differ from those of Psephenus and Ectopria only in that an abundant number of fat cells are concentrated around them.

Sensory Organs

Sensory components observed on Psephenops smithi are similar to those observed on Psephenus and Ectopria.

Fat Bodies

The body cavity is very full of fat cells with the cytoplasm drawn out into star-shaped processes. Associated with the above are many urate and glycogen granules.

Gut Contents

Serial sections revealed identifiable material in the buccal cavity and in the esophagus. In the remaining part of the gut, the substance appeared as a bolus.

Organisms identified were diatoms (Nitzschia), cell fragments of filamentous algae, wood particles, sand granules, and debris.

## EXPLANATION OF FIGURES

Figure 1. Psephenus texanus, dorsal view of carapace.

Figure 2. Psephenus texanus, ventral view of carapace.

Figure 3. Psephenus texanus, dorsal view of head.

Figure 4. Psephenus texanus, right maxilla.

Figure 5. Psephenus texanus, right mandible.

Figure 6. Psephenus texanus, ventral view of labium.

Figure 7. Psephenus texanus, legs.
A. Metathoracic leg
B. Mesothoracic leg
C. Prothoracic leg

Figure 8. Psephenus texanus, digestive tract. MT-malpighian tubule

Figure 9. Psephenus texanus, central nervous system.

Figure 10. Psephenus texanus, lateral tracheal vessel, eighth spiracle, and ventral gill of abdominal sclerites 6 and 7. TV-tracheal vessel; GF-gill filament; ES-eighth spiracle.

Figure 11. Psephenus texanus, longitudinal section through proventriculus. PPS-proventricular pad spine; PP-proventricular pad; ST-sclerotized tooth; LM-longitudinal muscle; PO-proventricular organ or structure; CM-circular muscles; POS--proventricular organ spine; Es.V-esophageal invagination.

Figure 12. Ectopria nervosa, dorsal view of carapace.

Figure 13. Ectopria nervosa, ventral view of carapace.

Figure 14. Ectopria nervosa, ventral view of labium.

Figure 15. Ectopria nervosa, ventral view of maxilla.

Figure 16. *Ectopria nervosa*, right mandible.
A. Inner view
B. Dorsal view

Figure 17. *Ectopria nervosa*, dorsal view of head.

Figure 18. *Ectopria nervosa*, legs.
A. Prothoracic leg.
B. Metathoracic leg.

Figure 19. *Ectopria nervosa*, operculum.

Figure 20. *Ectopria nervosa*, digestive tract.

Figure 21. *Ectopria nervosa*, right posterior half of lateral tracheal vessel with branches to gill and eighth spiracle.

Figure 22. *Ectopria nervosa*, central nervous system.

Figure 23. *Ectopria nervosa*, transverse section through anterior of proventriculus. CM-circular muscles; LM-longitudinal muscles; PT-proventricular tooth; PS-proventricular spine.

Figure 24. *Ectopria nervosa*, transverse section through base of foregut. Es.V-esophageal invagination.

Figure 25. *Ectopria nervosa*, transverse section through region of hindgut. FM-fatty mass; Exo-exocuticle; Endo-endocuticle; TM-transverse muscle; FB-fat body; CM-circular muscle; P-section of a pleurite; Ep-epithelium; Ci-cuticle intima.

Figure 26. *Ectopria nervosa*, transverse section through eighth abdominal segment. FM-fat mass; FB-fat body; TV-tracheal vessel; TM-transverse muscle; $TV_8$-tracheal vessel in eighth abdominal pleurite.

Figure 27. *Psephenops smithi*, dorsal view of carapace.

Figure 28. *Psephenops smithi*, ventral view of carapace.

Figure 29. *Psephenops smithi*, dorsal view of head.

Figure 30. *Psephenops smithi*, ventral view of right mandible.

Figure 31. *Psephenops smithi*, ventral view of right maxilla.

Figure 32. *Psephenops smithi*, labium.
A. dorsal view
B. ventral view

Figure 33. *Psephenops smithi*, legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

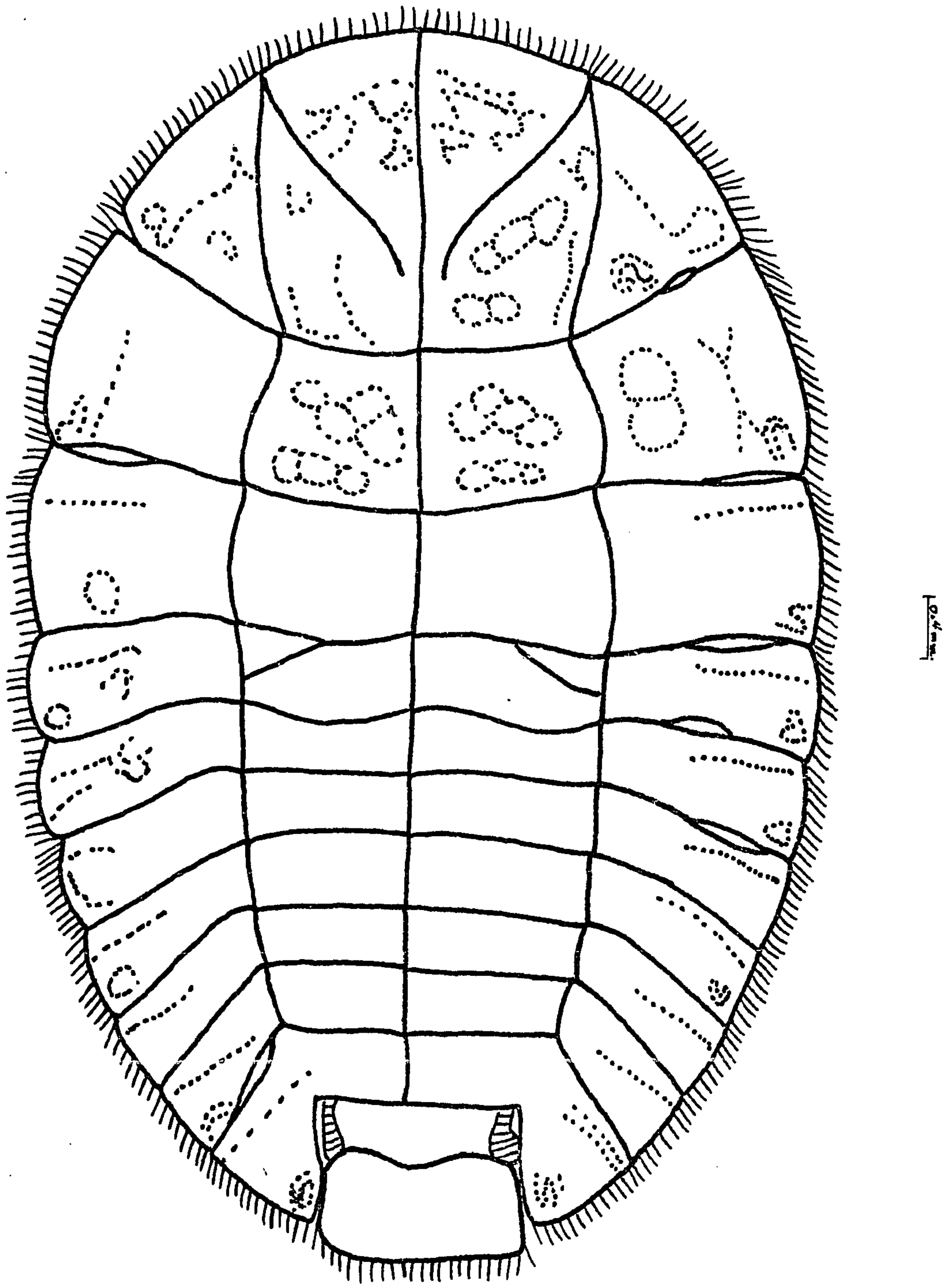
Figure 34. *Psephenops smithi*, digestive tract.

Figure 35. *Psephenops smithi*, central nervous system.

Figure 36. *Psephenops smithi*, transverse section through region of the midgut. MG-midgut; MTG-mid-tergal groove; VM-ventral muscle; FB-fat body.

Figure 37. *Psephenops smithi*, longitudinal section through the proventriculus revealing proventricular plates.

Figure 38. *Psephenops smithi*, transverse section through the midgut. LM-longitudinal muscle; CM-circular muscle; L-lumen of gut.



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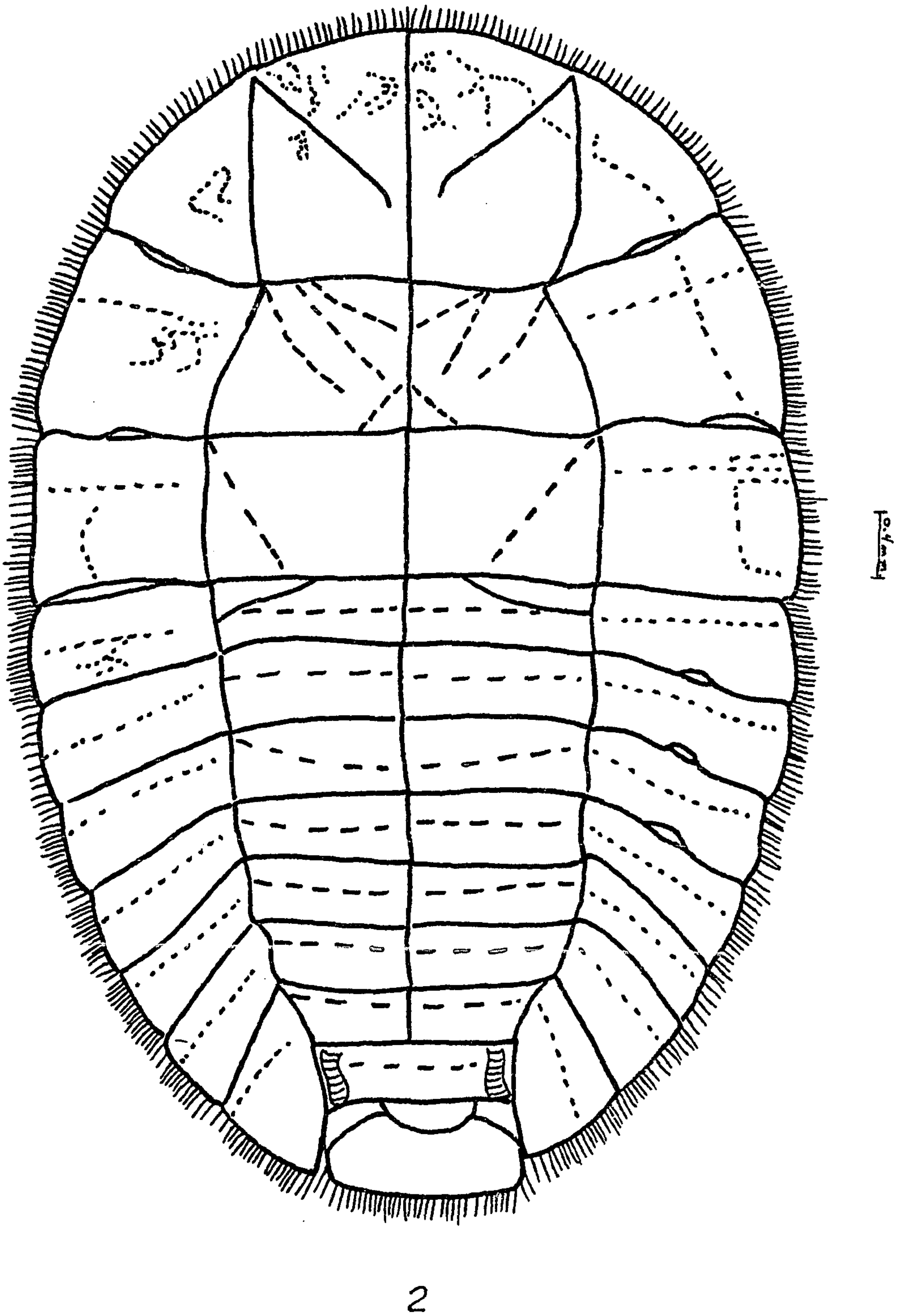

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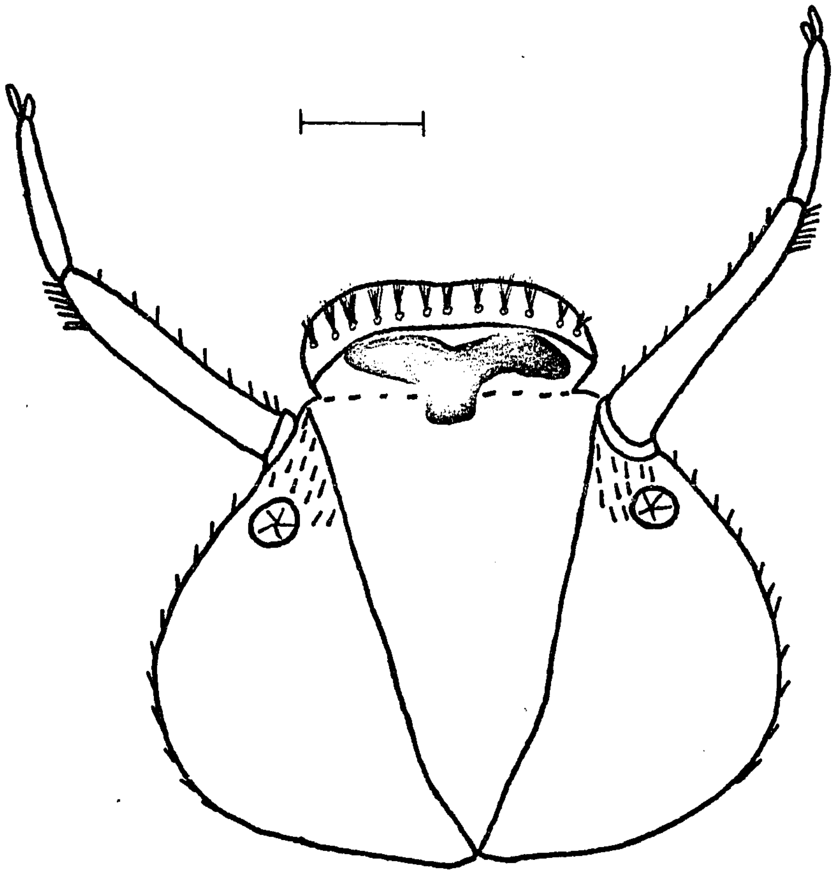

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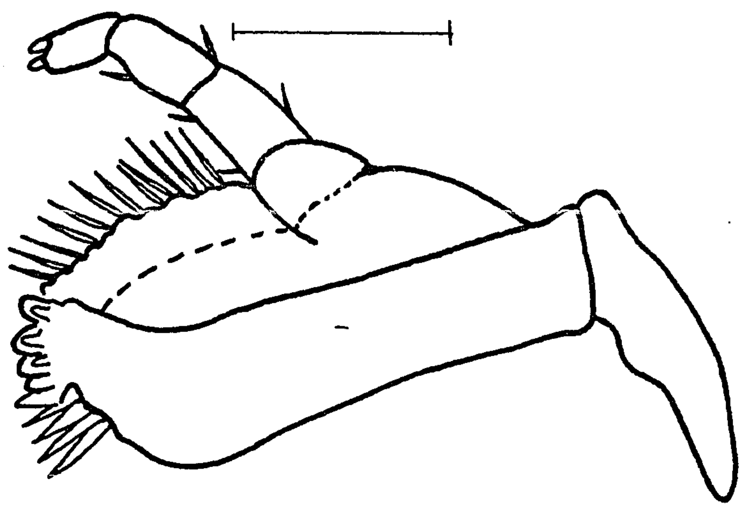

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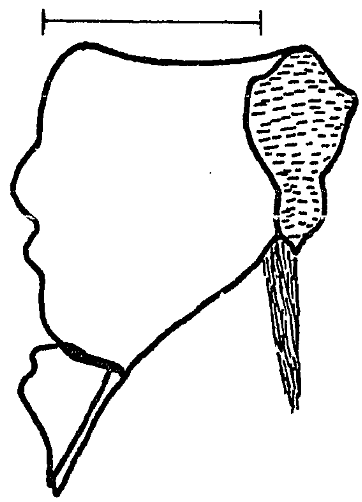

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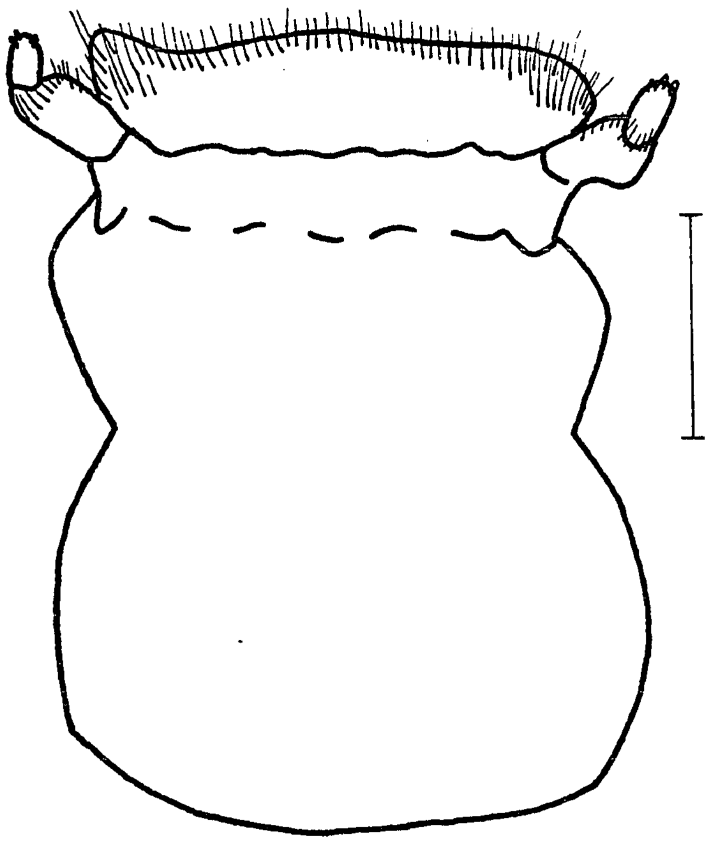

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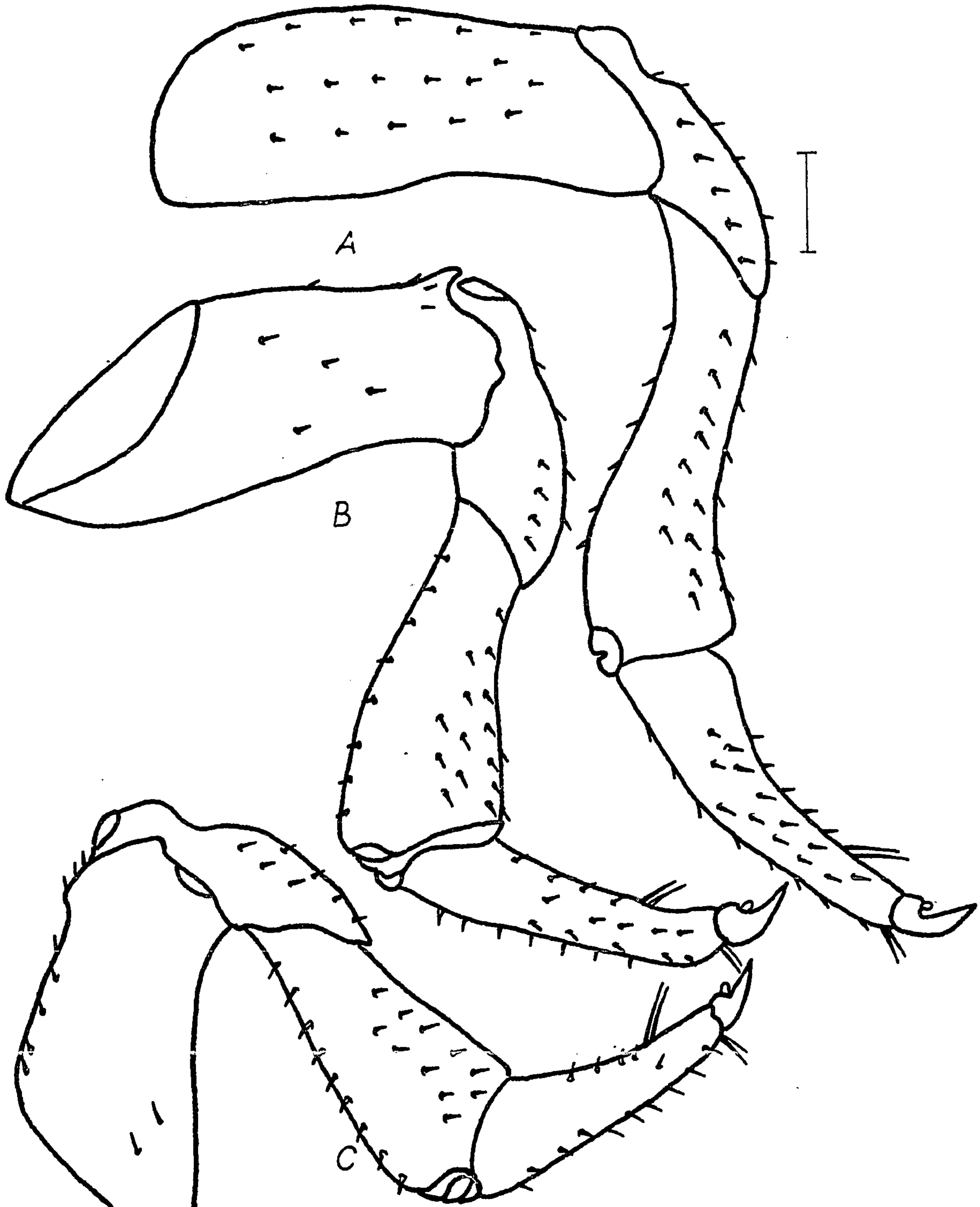


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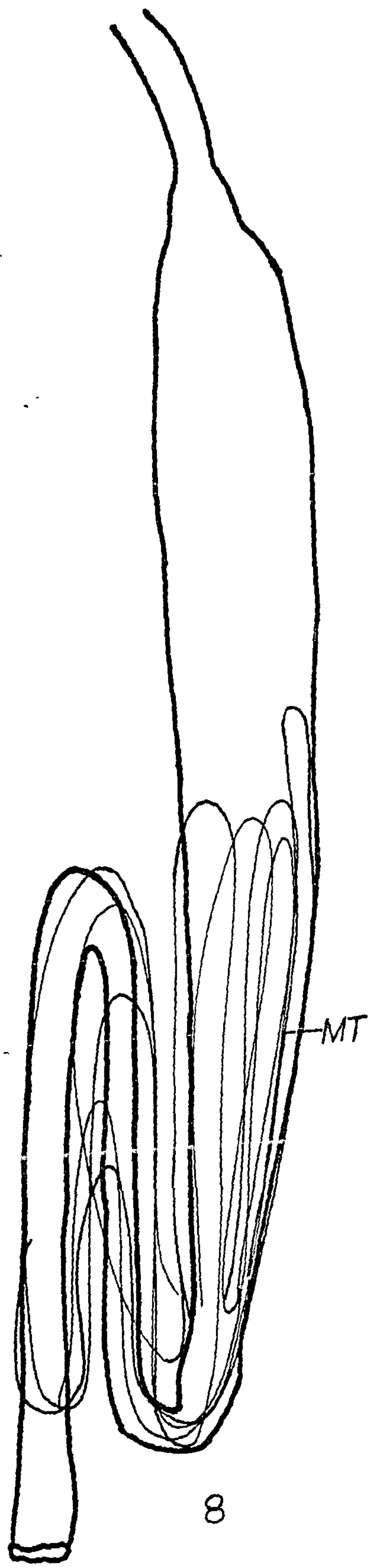


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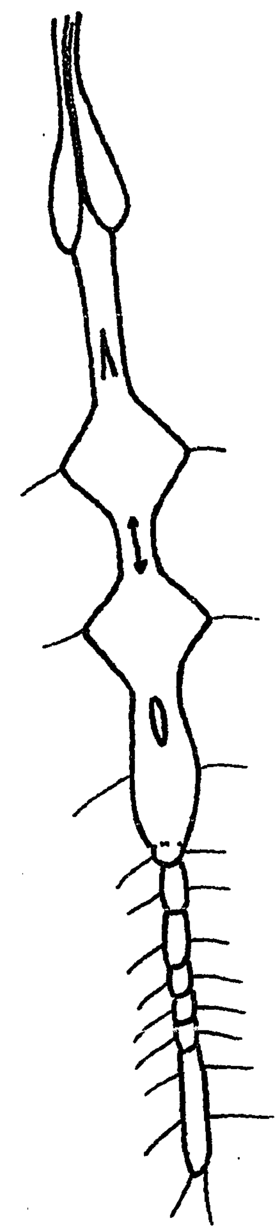

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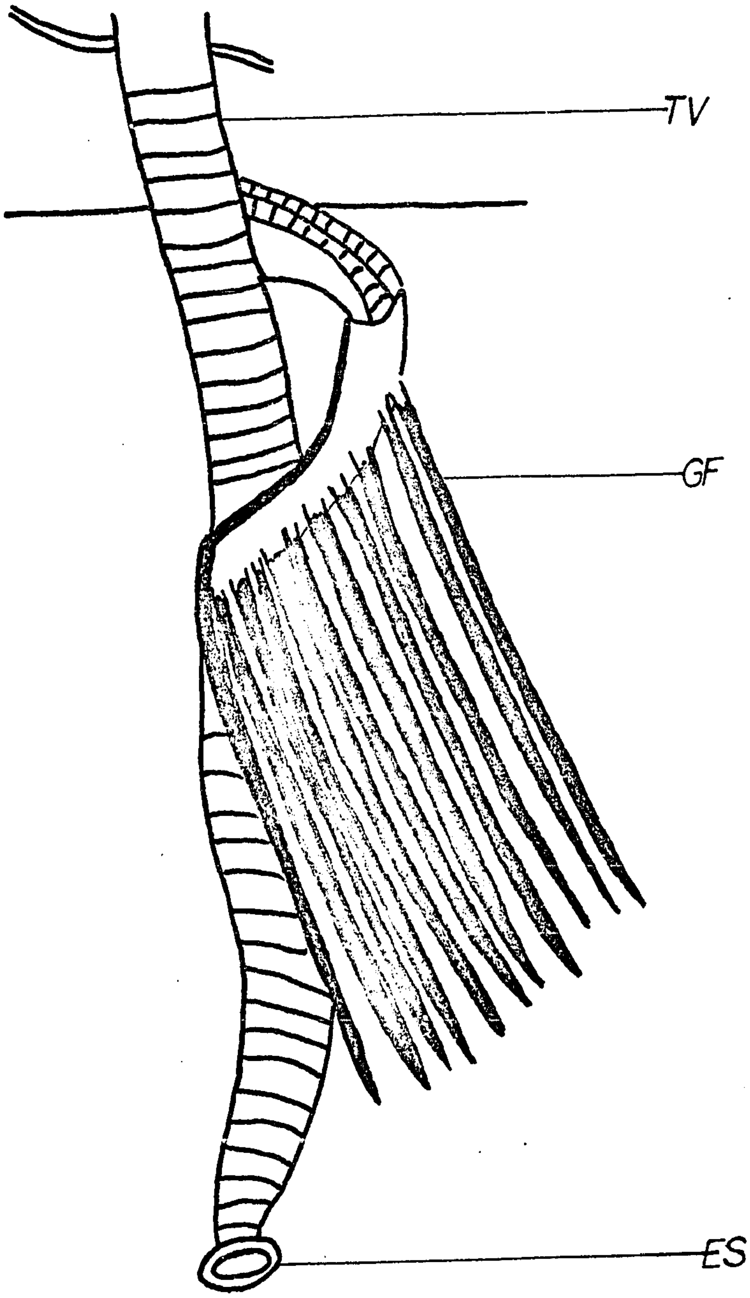


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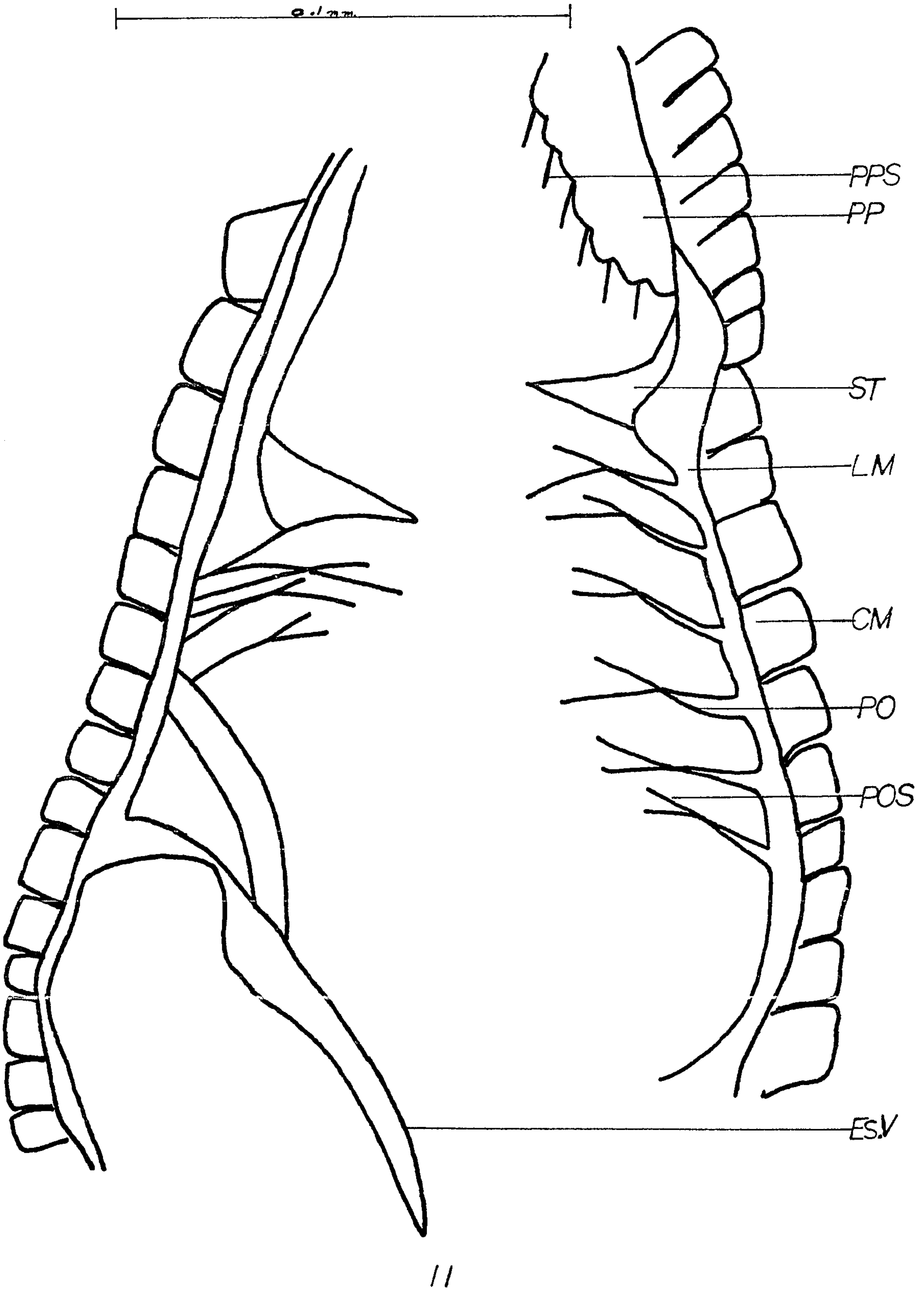


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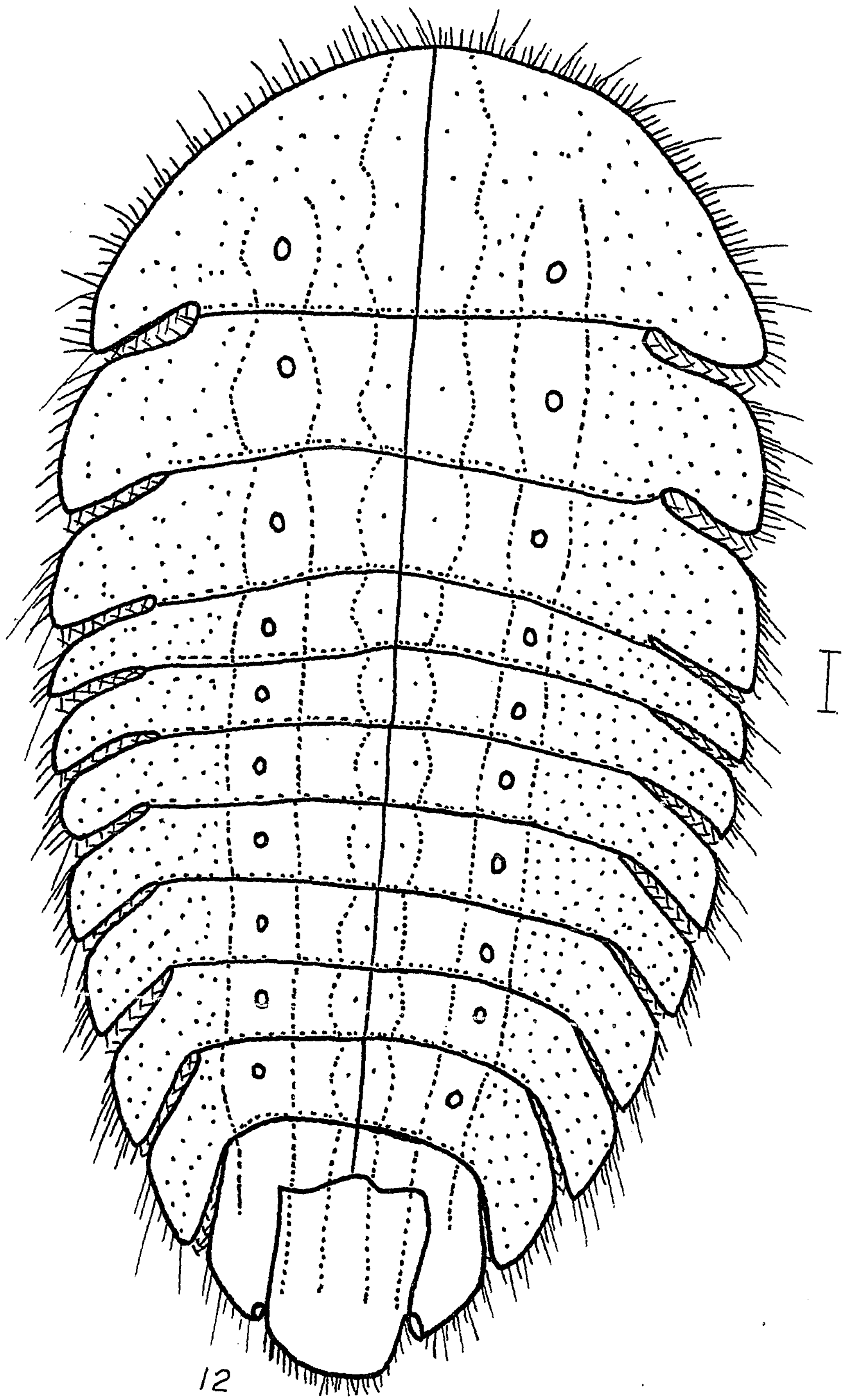


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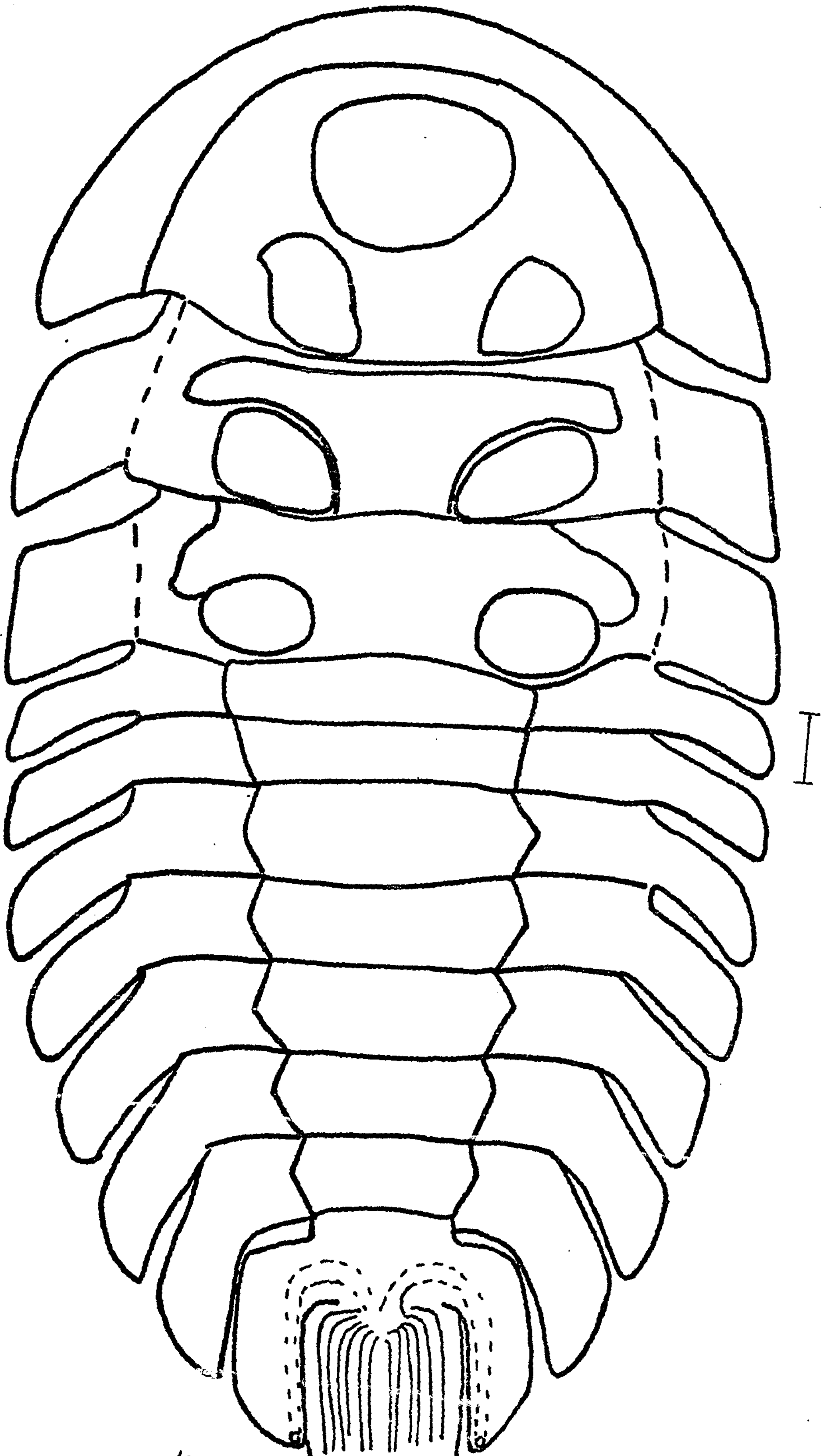


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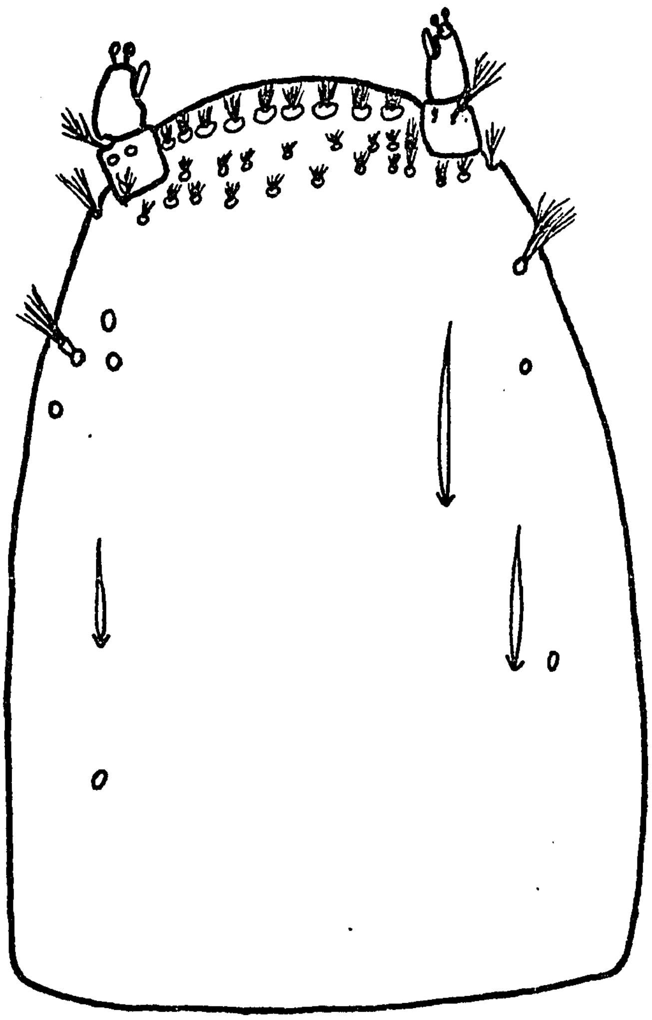

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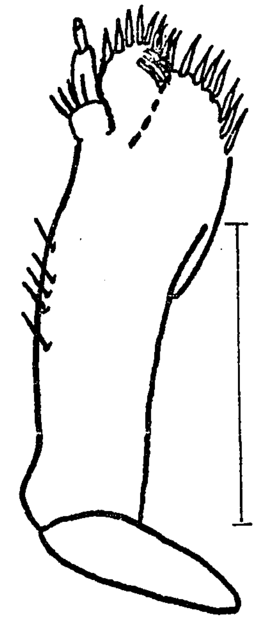

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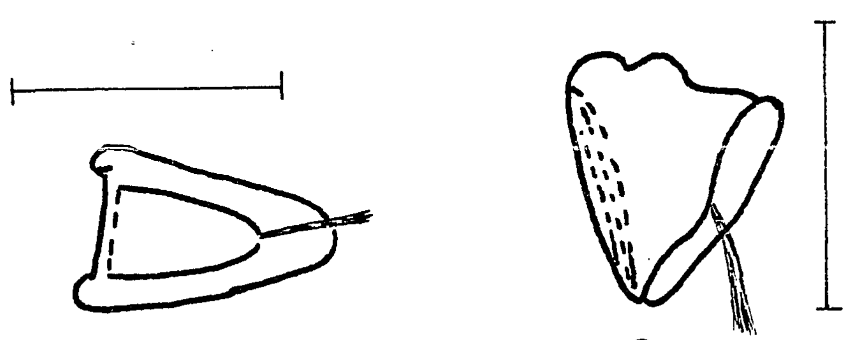

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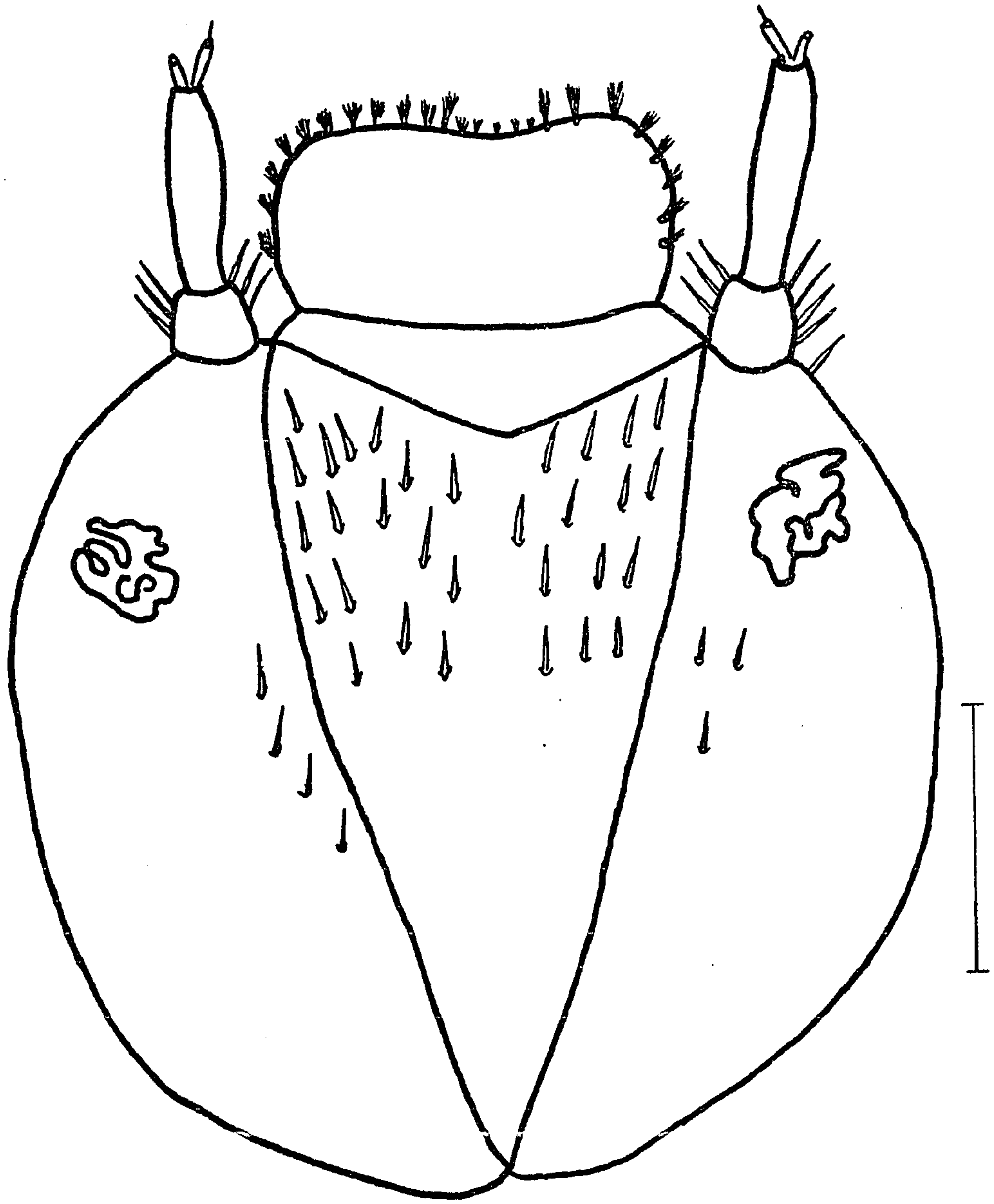

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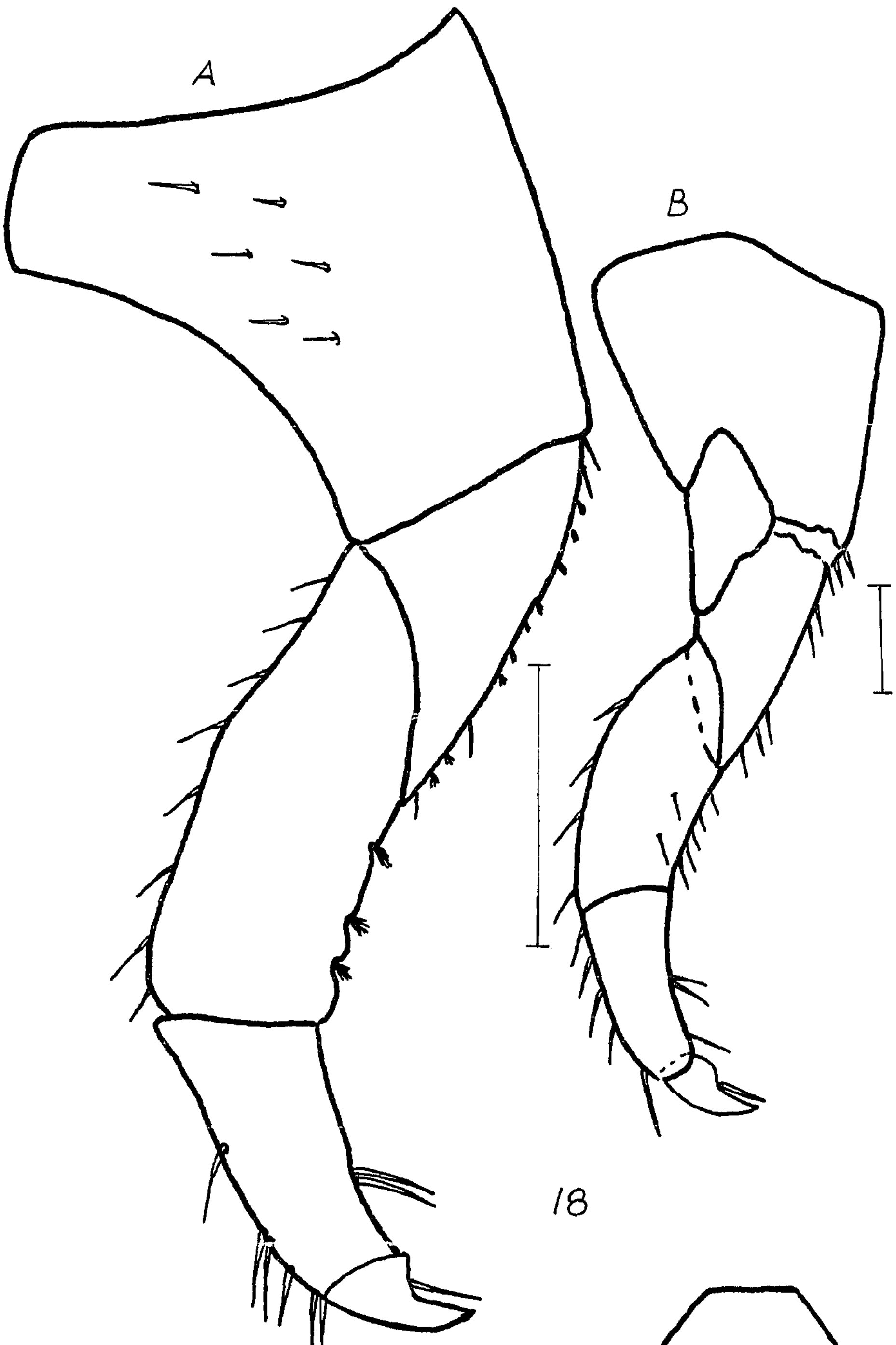

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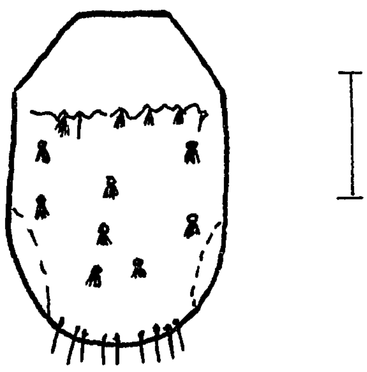
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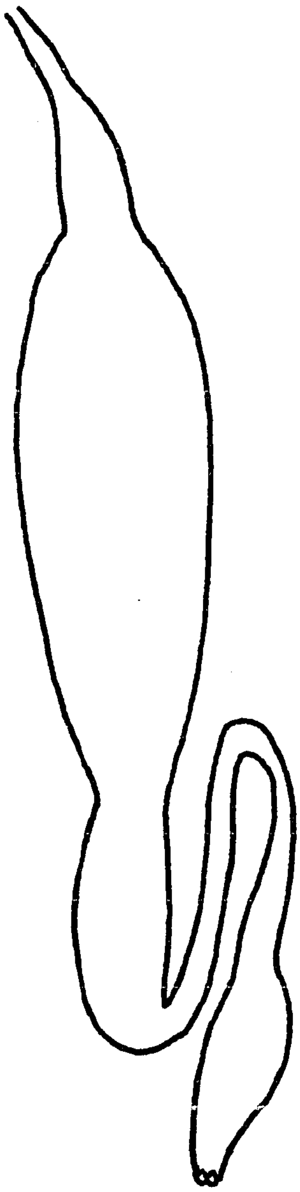

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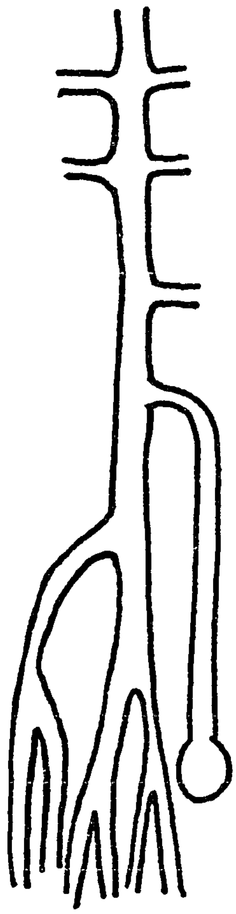

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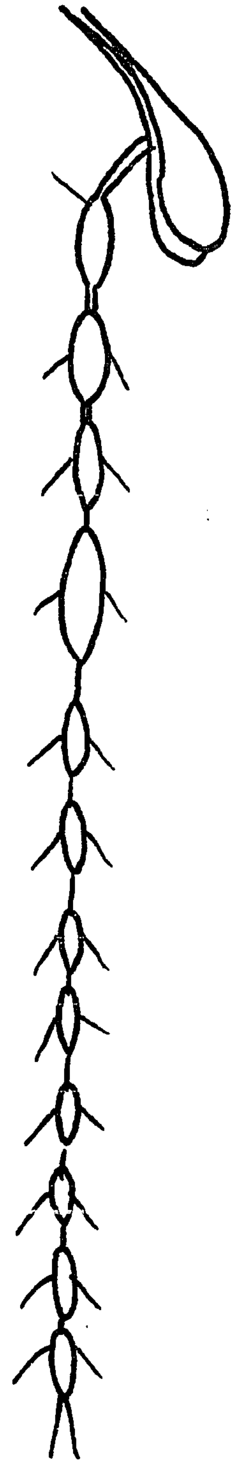

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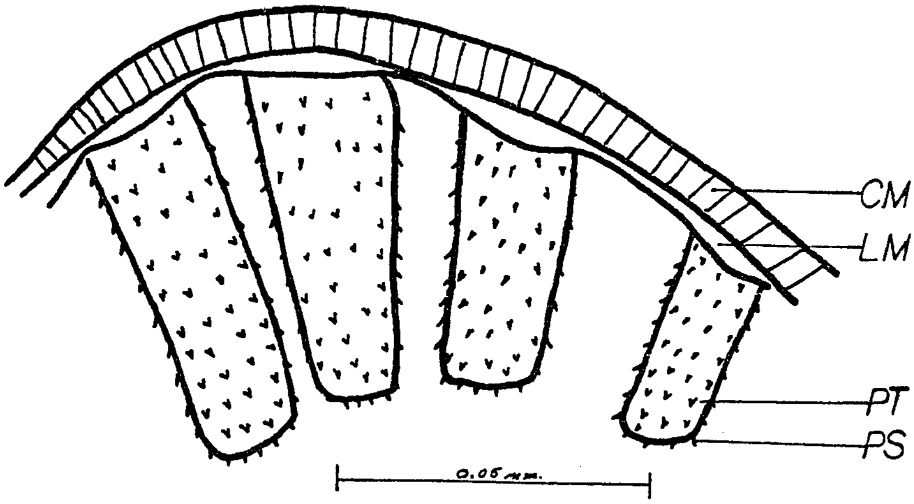


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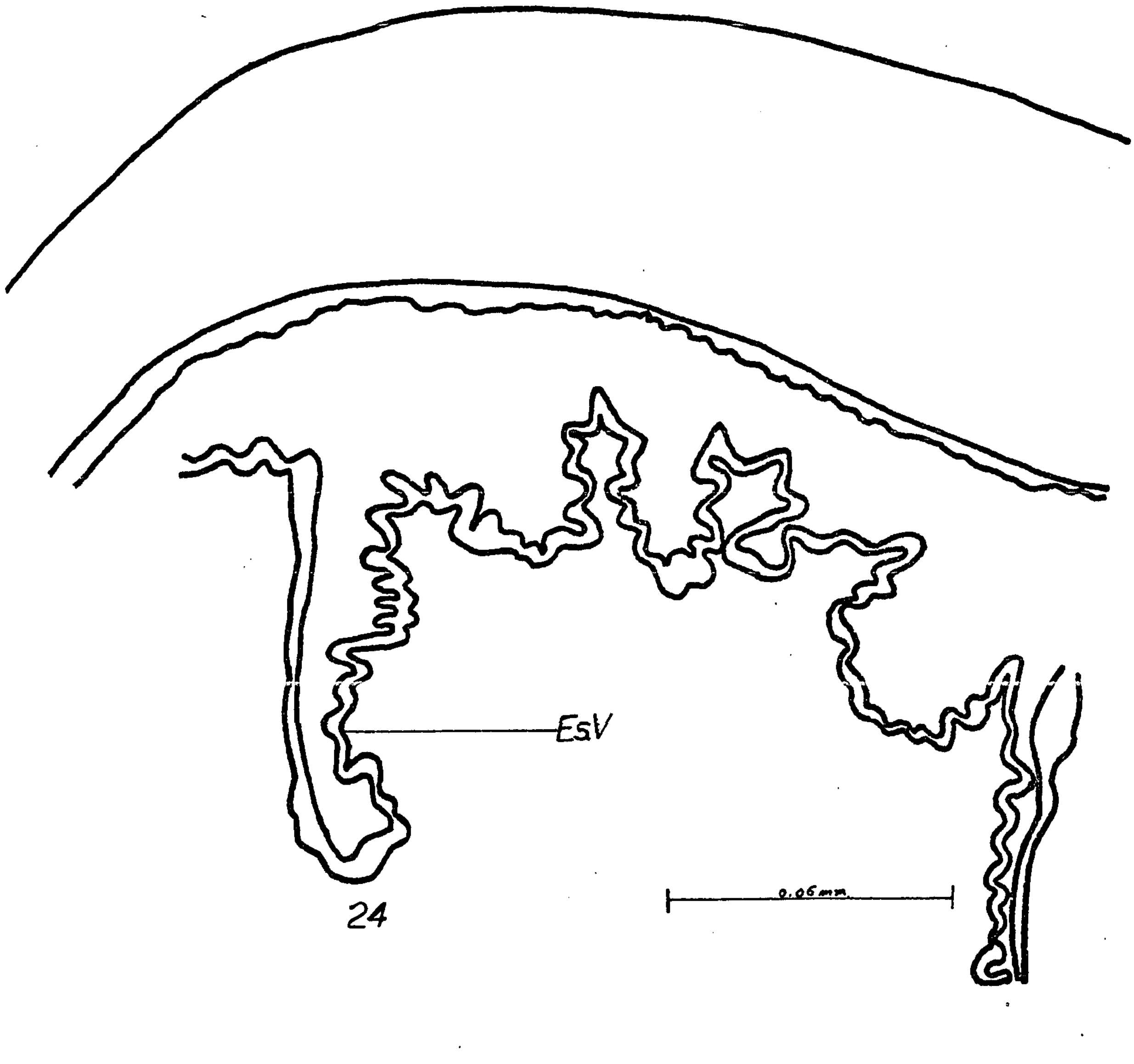


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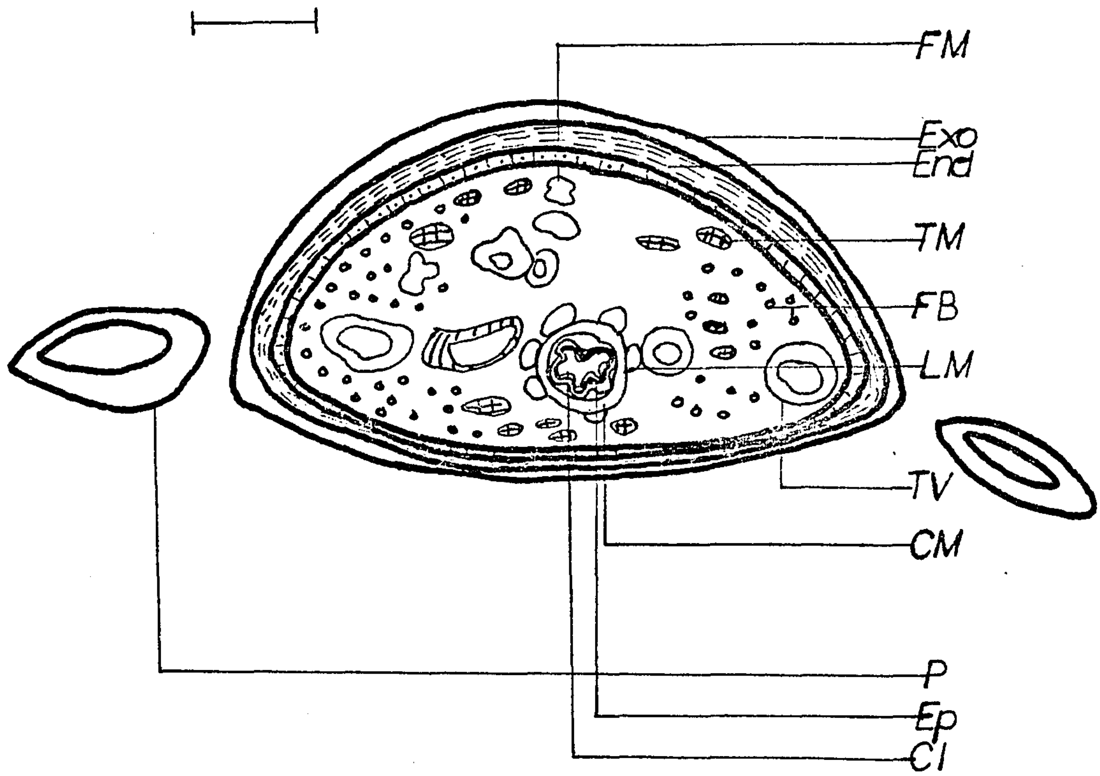


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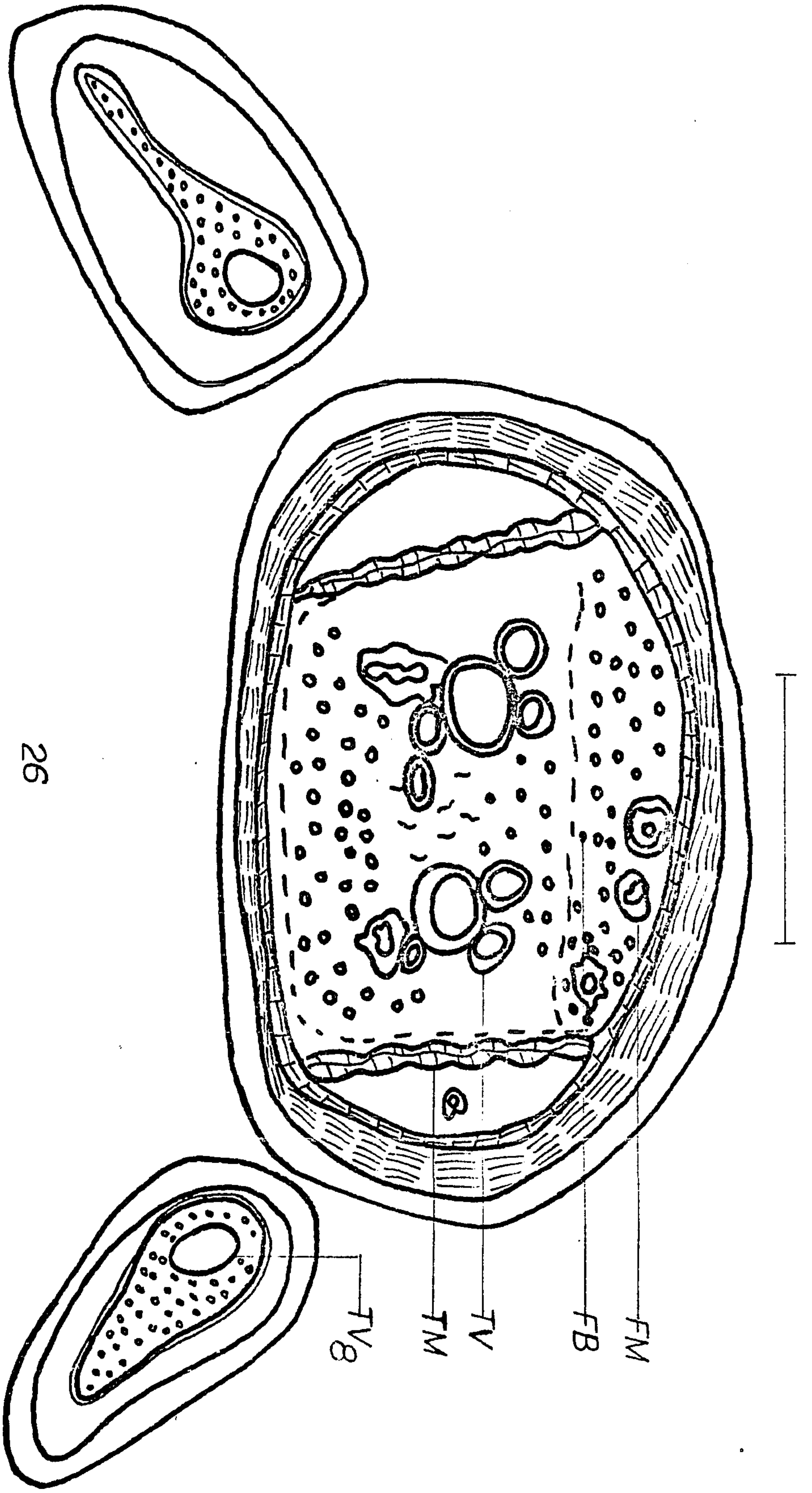

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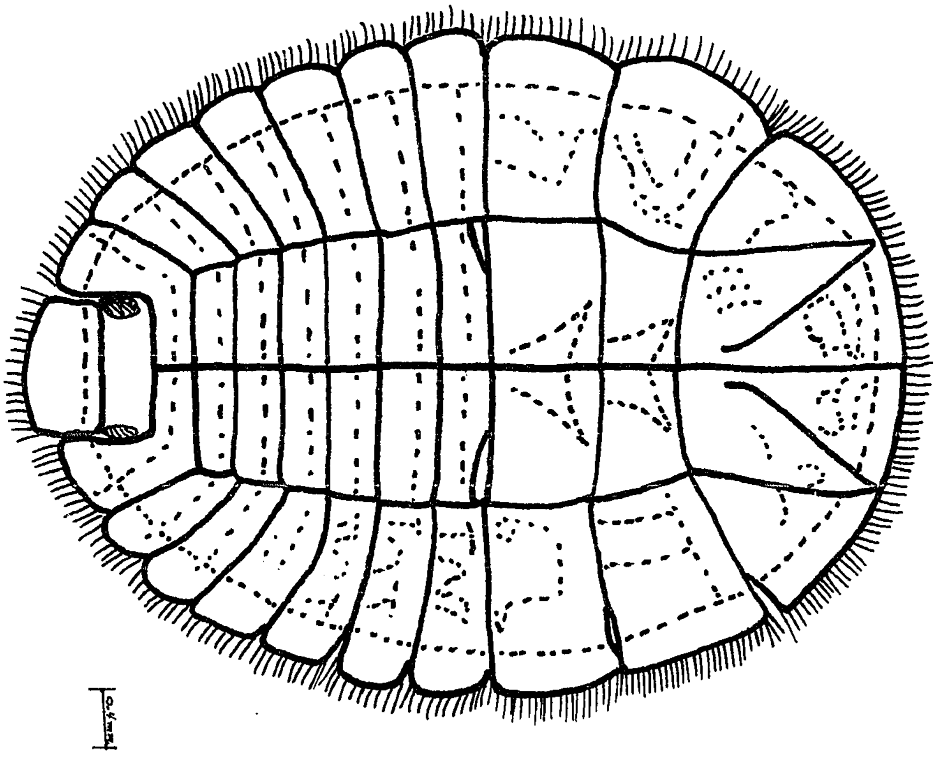

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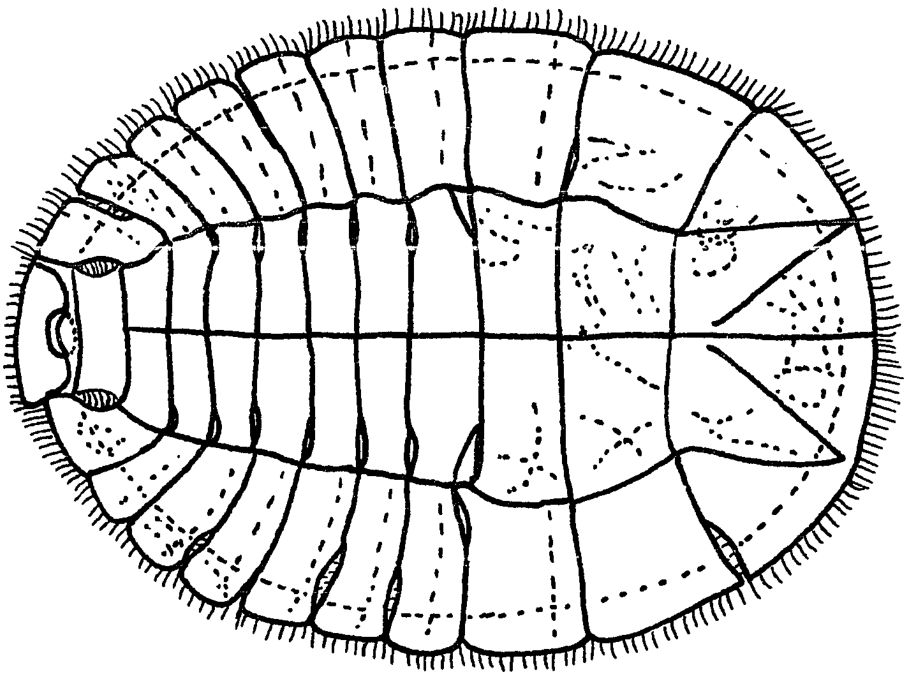

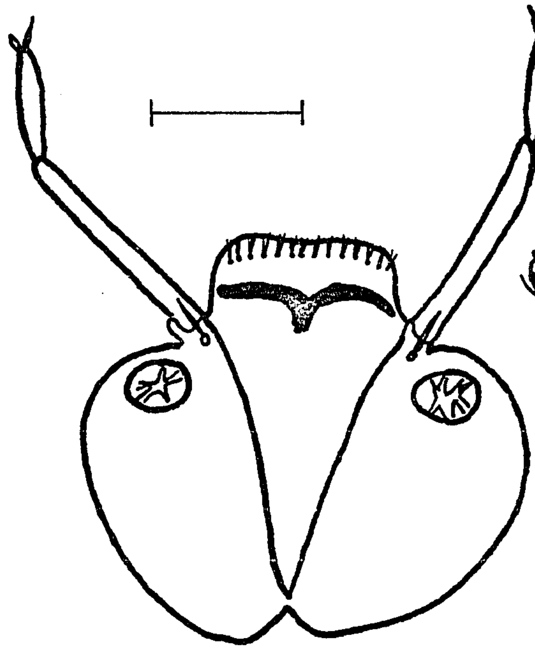

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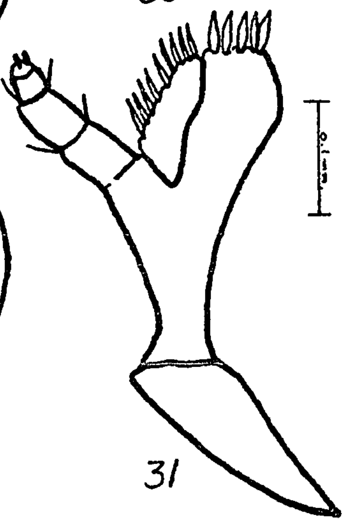

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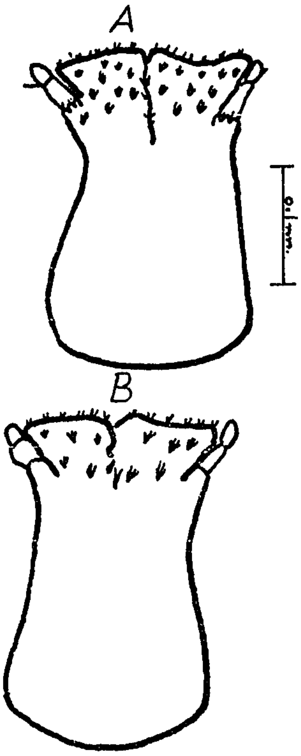


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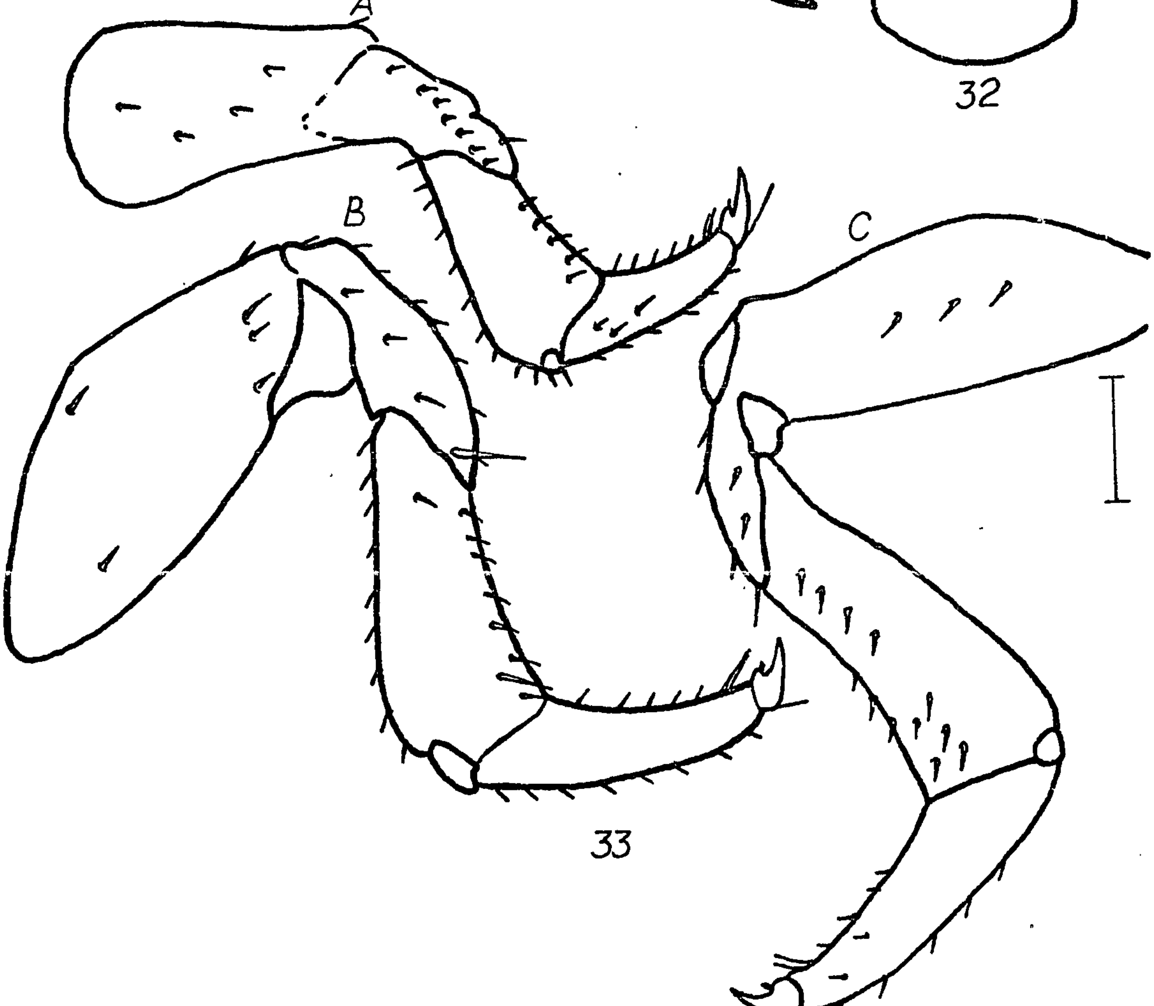


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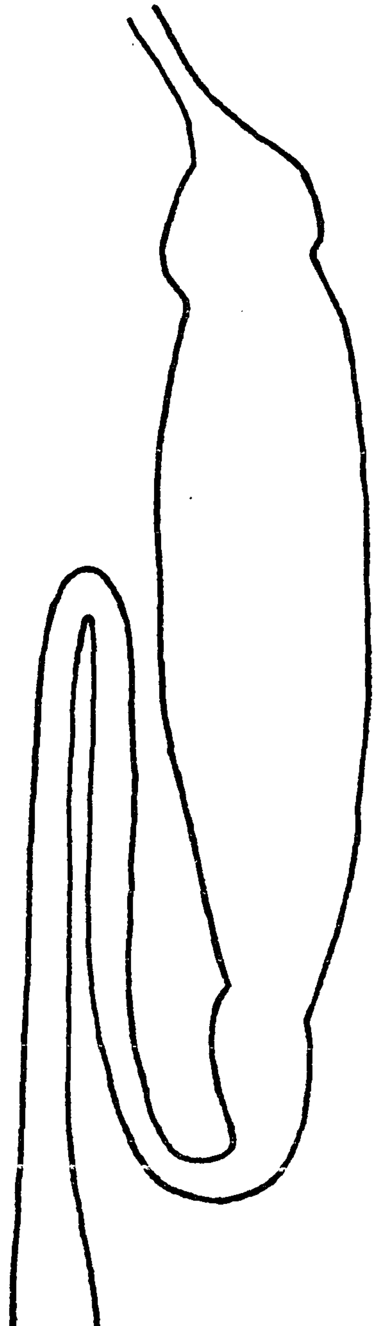

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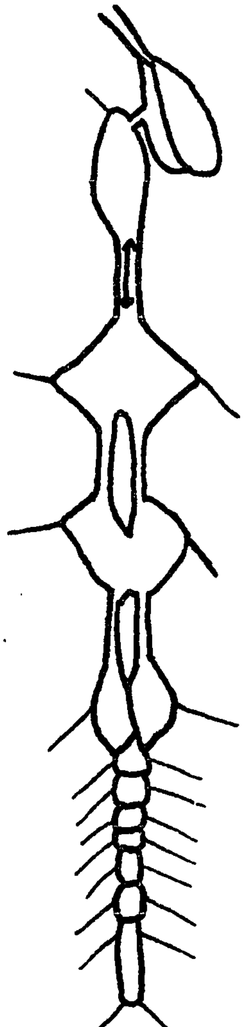

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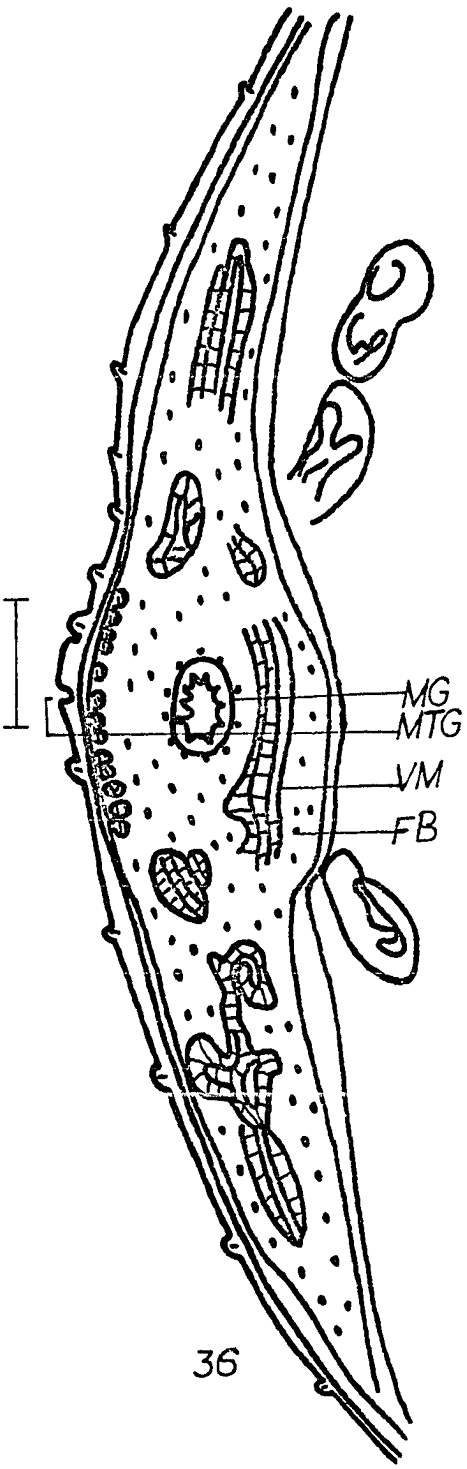


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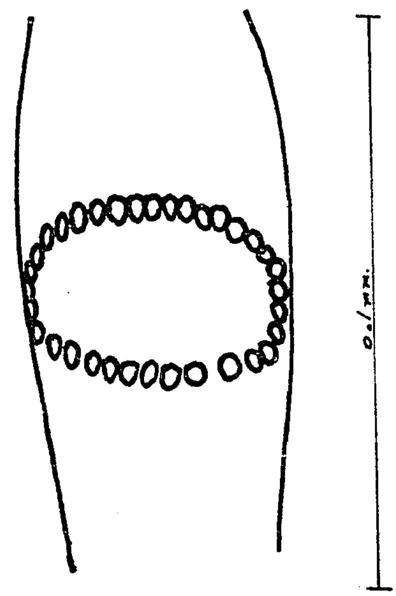

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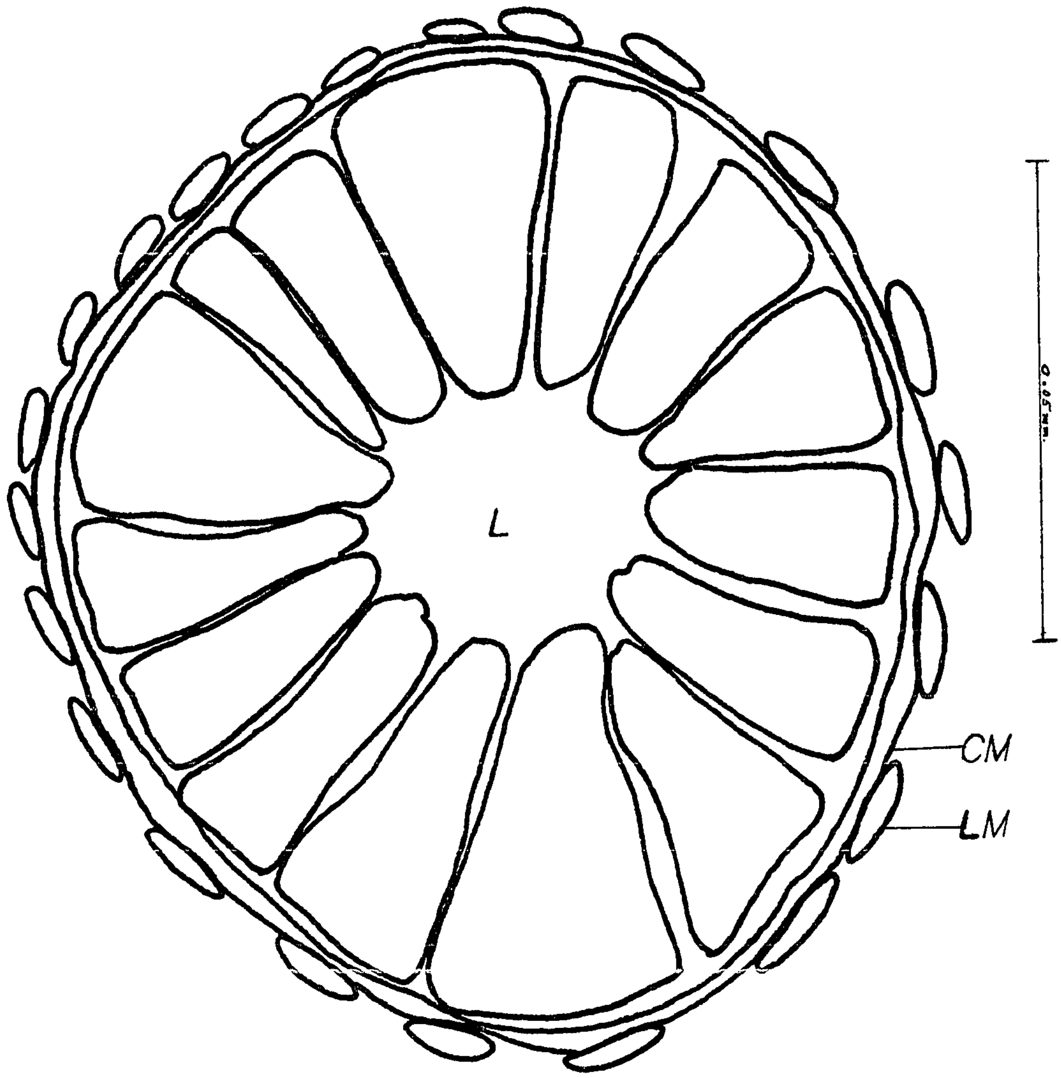


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## LIMNICHIDAE (Erichson, 1845)

Erichson in 1845 erected the tribe Limnichini to include a few genera of Byrrhidae--*Limnichus* and allied genera. Jacquelin du Val 1857-59 considered *Limnichites* to be one of three groups of the Byrrhidae (Hinton, 1939). Thomson in 1860 gave Limnichini family rank and placed it near the Dryopidae. This arrangement was not followed in subsequent classifications because some later workers considered the Limnichidae to constitute only a tribe (Hinton, 1939).

Hinton (1939) compared internal and external features of specimens of Limnichidae and Byrrhidae. As a result of his finding Limnichidae was given family rank and was transferred from the superfamily Byrrhoidea to the superfamily Dryopoidea.

Arnett (1968) lists four genera as belonging to the Limnichidae. Species of *Limnichus* are generally distributed over the United States. *Lutrochus* occurs in eastern, central, and southwestern United States and southward. *Physemus* contains a single species found in southwestern United States, and *Throscinus* occurs on intertidal mudflats of Texas and southern California.

As described by Hinton (1939), larval features of family importance are: mandibles without a series of long hairs on their margins, postmentum undivided, submento-mental muscles absent, articulating mandibular surface absent, abdomen with only nine segments, and biforous spiracles are on mesothorax and first eight abdominal sclerites.

The genus Lutrochus was studied in this investigation.

Lutrochus (Erichson, 1847)

With the description of Lutrochus arizonicus from central Arizona there are presently three species of this genus known within the United States, including L. luteus LeConte (1852) from central Texas and Oklahoma to eastern New Mexico, and L. laticeps Casey (1893) from Maryland to Michigan and eastern Oklahoma (Brown and Murvosh, 1970). Species have also been described from Cuba, Guatemala, Bolivia, Peru, and other South American countries (Blackwelder, 1944).

Some generic features of Lutrochus larvae agreed on by Hinton (1939) and Bertrand (1955) are given below.

Body: parallel-sided, cuticle colored dorsally with variations of brown and many pale spots forming a pattern. Cuticle ventrally unicolor except for operculum.

Head: large, rounded, slightly broader than long, and cuticle sparsely pubescent. Ocelli in groups of six and separated from each other. The sixth ocellus is located and directed ventrally near the vicinity of the mandibles. Antennae three-segmented, first segment massive and long, second short, third small, and flanked by a small lateral segment. Maxillae with four-segmented palpi and stipes fused to postmentum.

Sterna of thoracic segments mostly membranous, but with narrow, moderately sclerotized pleura. Pleura of first two abdominal segments bounded by sutures, third segment without a tergo-pleural suture, but with a distinct sterno-pleural suture, and segments four to eight forming complete sclerotized rings. Posterior sternal region of ninth abdominal segment with a suboval operculum which bears well-developed claws that are serrated on concave margin.

Legs short and robust, increasing in length posteriorly.

I have studied the external and internal morphology of larvae of two species of Lutrochus:

Lutrochus luteus, collected in Turner Falls, Oklahoma on April 16, 1960 and November 21, 1961. The specimens measured 4.3-5.1 mm in length and 1.0-1.15 mm in width. Four specimens were used for the above study and two were used for histological study.

Lutrochus "B", collected in Porto Franco, and in Ria Chim, Goias, Brazil on June 10, 1964 and June 17, 1968 respectively. Three specimens were used in the above study and two were studied histologically.

Lutrochus luteus

## External Morphology

The above features agreed on by Hinton and Bertrand were observed. Some additions and differences are given below.

Dorsum: cuticle pubescent; straight long hairs (spines) extend from ostia along posterior one-fourth of dorsal sclerites, along posterior borders, and on ventral surface (Figs. 42, 43, 45). Many tubercles are dispersed among hair-like spines on dorsal surface. Branched membranous setae over anterior three-fourths of each dorsal sclerite (Fig. 43) and short posteriorly-projecting spines are dispersed over abdominal sternites (Fig. 42).

Head: clypeus truncate and epistomal suture not very distinct

(Fig. 39). Labrum broad, twice as wide as long, with transverse row of thick tufted hairs near anterior margin (Fig. 48). Antero-lateral borders of frons elevated forming cavities into which antennae are inserted. Mandibles (Fig. 46) of both sides similar, bearing five apical teeth, and a prostheca which is not obvious from ventral or dorsal view. Sensory prosthecal brush at anterior base of molar surface, and outer margin with spinous setae (Fig. 46A). Maxilla with multibranched setae at internal base of palp and no differentiation of a palpifer. Galea and lacinia separate, galea robust with convex anterior margin, and anterior border covered with bristles. Lacinia small, cylindrical, and with a few bristles (Fig. 48) arising from apex. Stipes elongate and not fused with postmentum. Cardo absent or membranous. Labium almost twice as long as broad, palpi two-segmented, with a well-defined palpiger, mentum emarginate, and submentum undivided.

Thorax dorsally sculptured as cuticle. Pronotum (Fig. 44) wider than long, sides subparallel, and wider at base than at apex. Mesonotum wider than long and length one-half that of pronotum. Metanotum and tergites of eight abdominal segments similar to mesonotum except for tapering. Ninth abdominal segment slightly flattened, tapering posteriorly, and with a rounded posterior margin (Fig. 40). Operculum as figured (Fig. 41).

Legs (Figs. 47A, B, C) composed of four segments, each segment with spinous setae on all surfaces. Hooked tarsal claw on each leg bears long and short internal spines. Long spine one-half as long as tarsal claw.

## Internal Morphology

## Digestive System

The alimentary tract (Fig. 49) is an elongated tube with no apparent surface marking except slight constrictions which serve to indicate the divisions between the foregut, midgut, and hindgut.

The foregut is a short tube, approximately equal in length to the hindgut. It consists of a narrow tube which constitutes the buccal cavity and esophagus, and the dilated crop and proventriculus.

The midgut is the longest and most dilated part, without any constrictions. It is separated from the foregut by an anterior constriction and from the hindgut at the point of origin of the malpighian tubules.

The hindgut is dilated near its junction with the midgut, but it tapers for a short distance then dilates to form the anus. In comparison, it is second to the midgut in lumen diameter.

## Respiratory System

Lateral trunks are the primary tracheal vessels. They lie parallel to the gut and send branches to the head, gut, and other internal organs. Posterior to the mesothoracic zone the vessels form four dilations which apparently function as air sacs (Fig. 50). Posteriorly the dilations are absent and each gill tuft receives two secondary vessels.

## Excretory System

Six malpighian tubules arise at the midgut-hindgut junction. They pass anteriorly over two-thirds or more of the midgut, turn posteriorly and end free in the posterior body cavity (Fig. 49).

## Central Nervous System

The brain consists of a pair of pyriform ganglia with nerves passing toward the ocelli, antennae, and labrum. Circumesophageal connectives pass ventrally from the brain and connect with the subesophageal ganglion. This ganglion supplies fibers to the mandible, hypopharynx, labium, and maxillae. Three spherical thoracic ganglia are evident, the third being the largest of the three. Eight spherical abdominal ganglia were observed in all cases except one. Examination of the peripheral nerves of this specimen revealed that ganglia 7 and 8 had fused.

## Histological Morphology

### Integument

Exocuticle and endocuticle average 18 and 64 microns in thickness, respectively. Exocuticle takes up acid stain and endocuticle takes up basic stain. Scattered over dorsal and ventral surfaces are spinous setae. Multicellular nodules are scattered over the dorsum. The setae are set in depressions within the exocuticle (punctures).

### Digestive System

A folded cuticular intima lines the buccal cavity as it rests on a flat layer of epithelial cells. A basement membrane separates the epithelia from an underlying indistinct layer of longitudinal muscle which is surrounded by circular muscle. The lumen is constricted in the narrow esophagus, which does not differ histologically from the buccal cavity. Posteriorly the esophagus dilates and becomes the crop (Fig. 51). The epithelial cells are flattened to dome-shaped, lie close together, and bear spines which project toward the lumen. The anterior one-third of the crop (proventriculus) bears triangular teeth with a sclerotized intima. Along the wall posteriorly are subrectangular cells with chitinized margins which are drawn out into many spines (Fig. 52). Each of the foregoing cells contains an oval nucleus at its base and rests on a basement membrane (Fig. 53). A thin longitudinal muscle layer lies beneath the basement membrane, and a thick circular muscle layer follows. Behind the proventriculus, esophageal invaginations project into the midgut and appear as elongated folds or masses of secretory cells (Fig. 24).

A peritrophic membrane replaces the cuticular intima and lines the midgut lumen, apparently to protect the underlying brush-bordered cells. These columnar cells and the goblet cells among them rest on a distinct basement membrane. The circular muscles lie outside this membrane, forming a closely united ring around the midgut. Longitudinal muscle fibers are found in many groups outside of the circular muscle layer.

An intima of chitin lines the hindgut, taking the shape of the underlying epithelial layer. The epithelium is composed of low cells forming villi, then six distinct folds extending posteriorly to the rectum. The order of the muscles is as in the foregut. The circular muscle layer is thicker than in the midgut, but it becomes thinner posteriorly. The longitudinal muscle layer contains larger fibers, but the number of bundles is less than in the midgut.

## Respiratory System

Histologically the tracheae do not differ from the description given by Snodgrass (1935). Serial sections revealed lateral vessels with an increase in diameter followed by a decrease posteriorly. This corresponds to the conclusions reached from gross study.

Excretory System

The morphology does not differ from the description given by Patton (1953).

Central Nervous System

Serial sections revealed nerve cells of different sizes and neuroglia cells. Each ganglion consists of a medullary and a cortical zone.

Sense Organs

Primary sense organs are present which do not differ from the description given for similar structures in the above genera. The setae in punctures over the cuticle of this genus are suggestive of the setal sensilla described by Snodgrass (1935).

Fat Bodies

Individual masses consist of fat globules enclosed in closely meshed membranes. Uric acid and glycogen granules are associated with the fat bodies. The masses lie alongside the brain and esophagus, dorsally and laterally, along the gut, and along the margin of the peritoneum.

Gut Contents

Serial sections of the gut revealed in the lumen diatoms (Rhopalodia, Cocconeis, Meridion, and Synedra), cell fragments of filamentous algae, fungal spores, and debris.

_Lutrochus_ "B"

## External Morphology

Dorsum: body subparallel, slightly cylindrical, and tapering slightly at the ninth abdominal segment. Cuticle medium brown or brownish dorsally with well-defined spots or lines on head, thorax, and abdomen, but differing in pattern from _L. luteus_. Pale line along lateral surface from first abdominal segment to anterior margin of ninth. Pale zigzag lines lateral to mid-tergal suture extend from pronotum to posterior margin of eighth abdominal tergite, forming a diamond-backed design. Cuticle ventrally pale or flavotestaceous except for operculum which is brownish with pale spots on postero-lateral surface. Most of cuticular surface, dorsally and laterally, bears low tubercles (Figs. 54, 58, 60); in addition, the dorsal anterior margin of all segments except prothorax bears a transverse row of flat, posteriorly-projecting tubercles (Fig. 55).

Head: retracted into anterior projection of prothorax and with epicranial and frontal sutures as shown (Fig. 58). Antenna as figured (Fig. 57) and may be retracted as in _L. luteus_. Clypeus short with anterior margin slightly rounded. Labrum covered with fine straight hairs of different lengths and with anterior margin slightly lunate (Fig. 58). Mandible with four rounded apical teeth (Fig. 62), instead of five. A short tuft of sensory bristles (prostheca) is located on the medial surface, and branched setae are on outer lateral surface (Fig. 56). Galea and lacinia separate with apex of each densely covered with setae (Fig. 61). Stipes fused to postmentum, in contrast to condition in _L._

luteus, and cardo not evident or membranous. Labium with two-segmented palpi, a palpiger, and emarginate anterior margin.

Pronotum wider (Fig. 54) than long, sides subparallel, and broader at base than at apex. Mesonotum (Fig. 55) broader than long, but length and width of metanotum are approximately equal. Ninth (Fig. 67A) abdominal segment hemispheric in dorsal view. In lateral view, cylindrical at junction with eighth abdominal segment and flattened posteriorly on dorsal and ventral surfaces (Fig. 60).

Sterna of thoracic segments mostly membranous (Fig. 63, 64, 65). Pleura of first two abdominal segments with tergo-pleural and sterno-pleural sutures, third segment with only a sterno-pleural suture (Fig. 66); abdominal segments 4-8 (Fig. 66), and basal part of ninth (Fig. 67B) form complete sclerotized rings. Claws attached to inner surface of operculum (sternum of ninth abdominal segment) appearing serrate because of dentate setae on internal surface (Fig. 59).

Legs divided into coxa, trochanter, femur, tibiotarsus, and tarsal claw (Fig. 68). Internal spine half as long as claw to which it is attached; usually with long spines at inner apex of femur and outer apex of tibiotarsus.

Spiracles located on mesothorax and first through eighth abdominal segments, all spiracles biforous. Three tufts of gills extend from anal chamber.

## Internal Morphology

### Digestive System

Morphologically this system (Fig. 69) is similar to that of L. luteus.

Respiratory System

The tracheal vessels differ from those in L. luteus in that the dilation is uniform from the midgut toward the posterior intestine (Fig. 70). If one can designate any enlargement of the vessel as an air sac, then this species exhibits them, but they are not as distinct as in L. luteus.

Excretory System

The number of malpighian tubules, point of origin, and their location along the gut are as in L. luteus.

Central Nervous System

The number and arrangement of the ganglia does not differ in the two species, but abdominal ganglia are slightly larger in L. "B" (Fig. 71).

## Histological Morphology

Integument

Exocuticle and endocuticle respectively average 11 and 54 microns in thickness. Tubercles scattered over dorsum differ from those on L. luteus as illustrated (Fig. 54, 60). Ventrally the tubercles are similar to those on L. luteus.

Digestive System

The buccal cavity, esophagus, and crop are as in L. luteus, but the proventriculus reveals some differences. In contrast to the condition in L. luteus, longitudinal folds (primary and secondary) are present and their margins bear many small tubercles. The tubercles bear on their apices sclerotized spines (Fig. 72). There apparently are no distinct columnar cells with sclerotized, serrated margins. Arising from the wall is an anvil-shaped sclerite.

No significant difference in the midgut and hindgut (Fig. 73) of the two species was obvious.

## Respiratory System

No difference between the two species was obvious.

## Excretory System

The description given by Patton (1953) applies here as in *L. luteus*. The tubule wall is cross section consists of 4-5 cells in both species.

## Central Nervous System

No significant difference between the two species was obvious.

## Sense Organs

The histology is similar to that in *L. luteus*.

## Fat Bodies

The nature and disposition of fat bodies in the two species are similar.

## Gut Contents

Serial sections of the gut revealed in the lumen diatoms (*Rhopalodia*, *Cocconeis*, and *Meridion*), cell fragments of filamentous algae, and debris.

EXPLANATION OF FIGURES

Figure 39. Lutrochus luteus, dorsal view of head.

Figure 40. Lutrochus luteus, ventral view of ninth abdominal sclerite.

Figure 41. Lutrochus luteus, dorsal view of operculum.

Figure 42. Lutrochus luteus, ventral view of 4-6 abdominal sclerites.

Figure 43. Lutrochus luteus, dorsal view of 4-6 abdominal sclerites.

Figure 44. Lutrochus luteus, ventral view of thoracic region.

Figure 45. Lutrochus luteus, marginal spine.

Figure 46. Lutrochus luteus, right mandible.
A. Dorsal view
B. Inner view

Figure 47. Lutrochus luteus, legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 48. Lutrochus luteus, ventral view of maxilla and labium.

Figure 49. Lutrochus luteus, digestive tract.

Figure 50. Lutrochus luteus, right lateral tracheal vessel.

Figure 51. Lutrochus luteus, longitudinal section through crop and anterior margin of proventriculus.

Figure 52. Lutrochus luteus, longitudinal section through proventriculus. PO-proventriculus organ or cell structure; S-sclerite or proventricular tooth; LM-longitudinal muscle; CM-circular muscle.

Figure 53. Lutrochus luteus, transverse section through base of

proventriculus. N-nucleus; CM-circular muscle; LM-longitudinal muscle.

Figure 54. Lutrochus "B", pronotum.

Figure 55. Lutrochus "B", mesonotum.

Figure 56. Lutrochus "B", dorsal view of left mandible.

Figure 57. Lutrochus "B", antenna.

Figure 58. Lutrochus "B", dorsal view of head.

Figure 59. Lutrochus "B", dorsal view of operculum.

Figure 60. Lutrochus "B", lateral view of ninth abdominal sclerite.

Figure 61. Lutrochus "B", ventral view of maxillae and labium.

Figure 62. Lutrochus "B", inner view of mandible.

Figure 63. Lutrochus "B", ventral view of prothorax.

Figure 64. Lutrochus "B", ventral view of mesothorax.

Figure 65. Lutrochus "B", ventral view of metathorax.

Figure 66. Lutrochus "B", 2-4 abdominal sternites.

Figure 67. Lutrochus "B", ninth abdominal sclerite.
A. Dorsal view
B. Ventral view

Figure 68. Lutrochus "B", legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 69. Lutrochus "B", digestive tract.

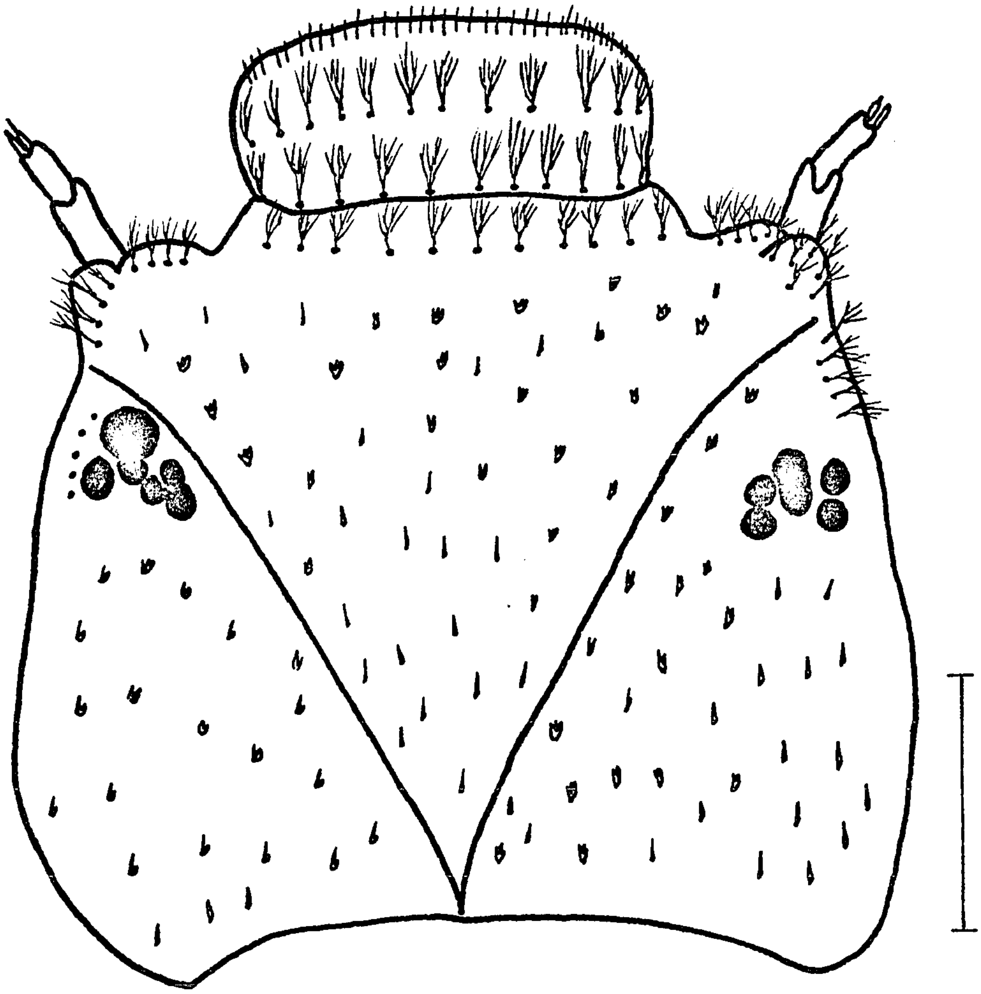
Figure 70. Lutrochus "B", right lateral tracheal vessel.

Figure 71. Lutrochus "B", central nervous system.

Figure 72. Lutrochus "B", transverse section through proventriculus. H-hair of spine; S-sclerite; PF-primary fold; SF-secondary fold; LM-longitudinal muscle; CM-circular muscle; Ep-epithelium.

Figure 73. Lutrochus "B", transverse section through anterior intestine. DM-dorsal muscle; FB-fat body; CM-circular muscle; LM-longitudinal muscle; CI-cuticle intima;

Ep-epithelium; VM-ventral muscle; VNC-ventral nerve cord; TV-tracheal vessel; BV-blood vessel; MT-malpighian tubule.



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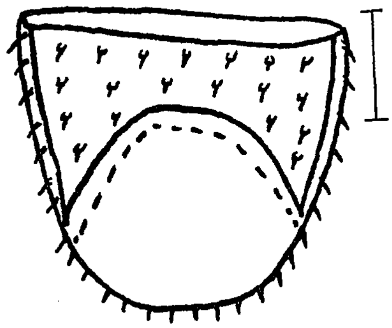

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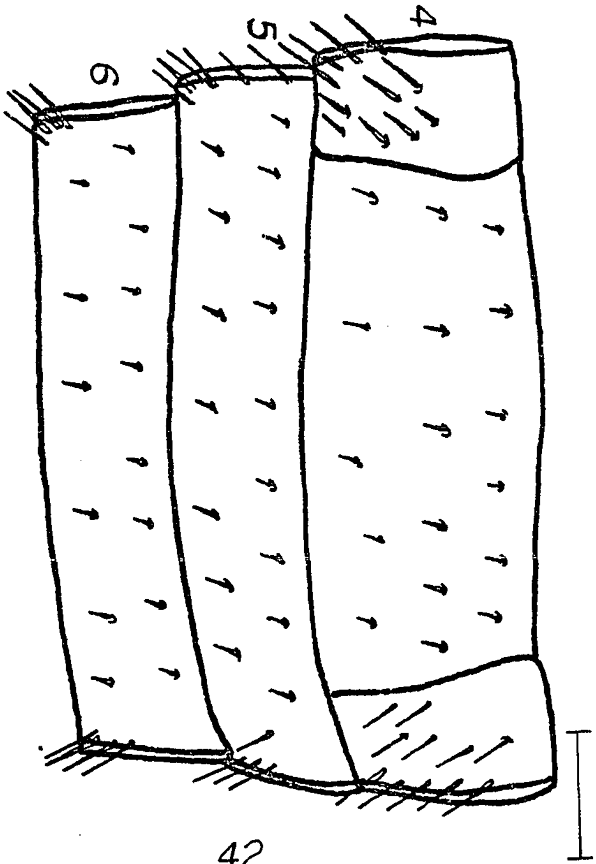


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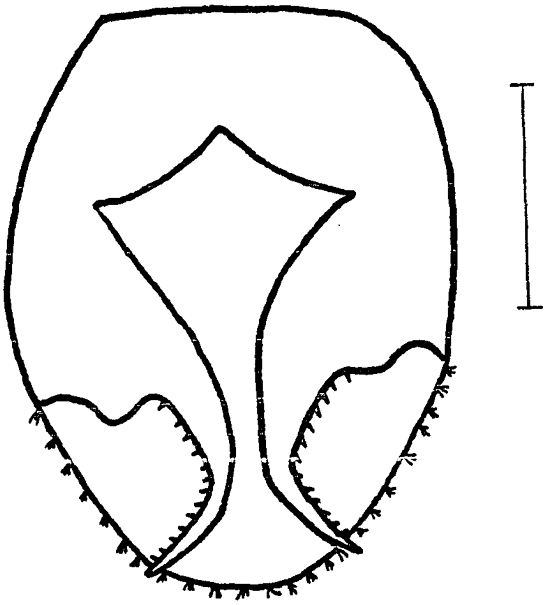

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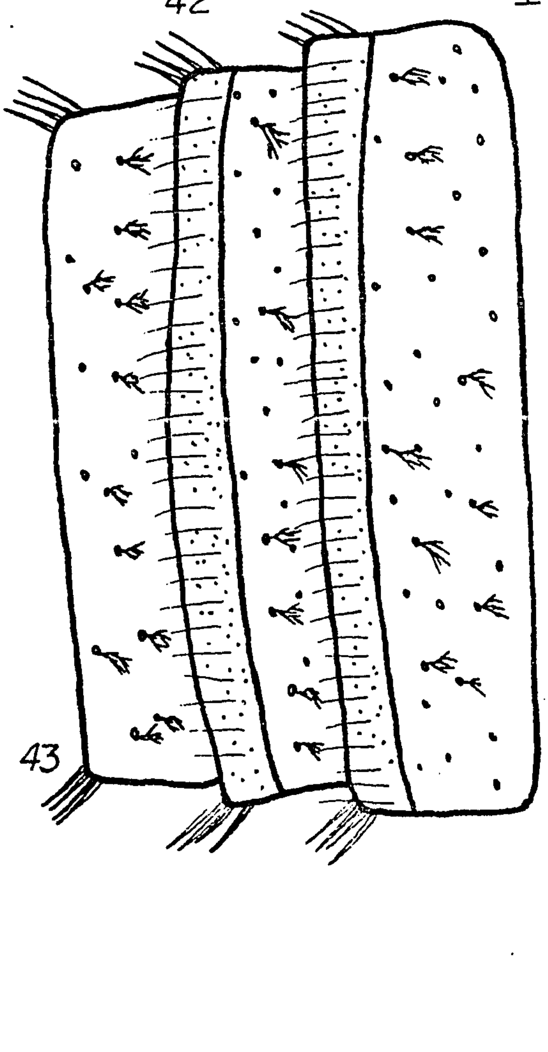

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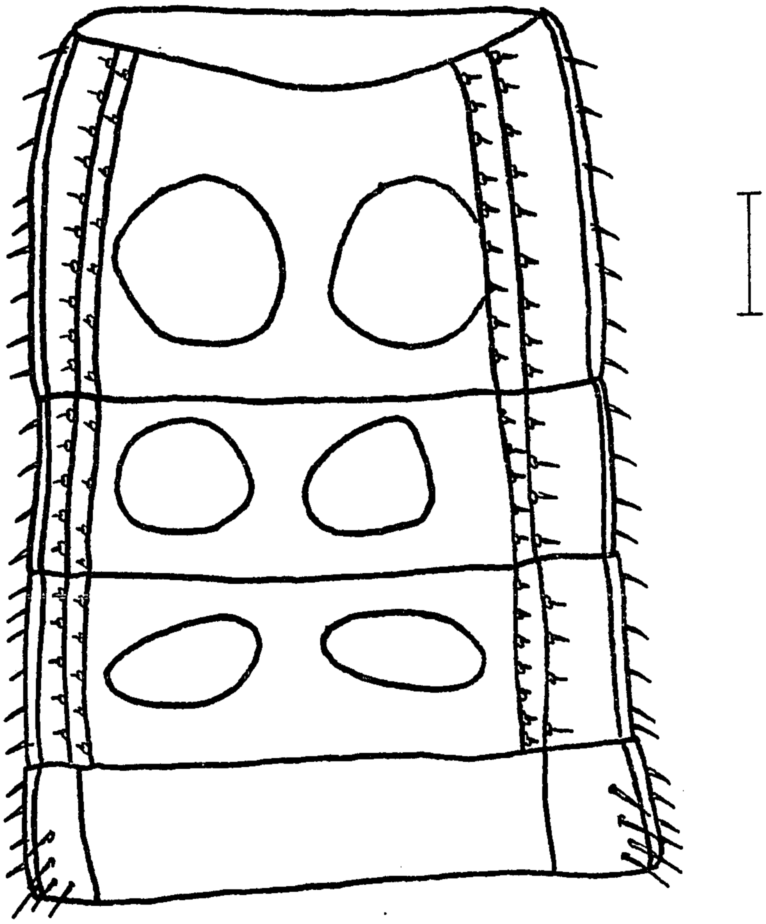

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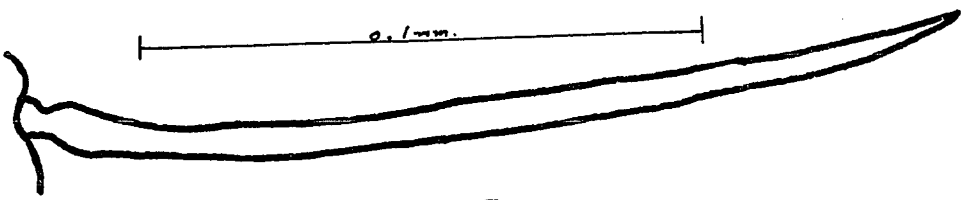


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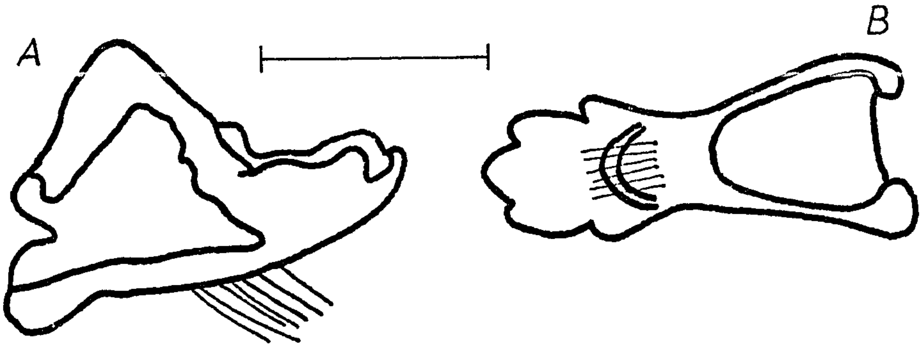


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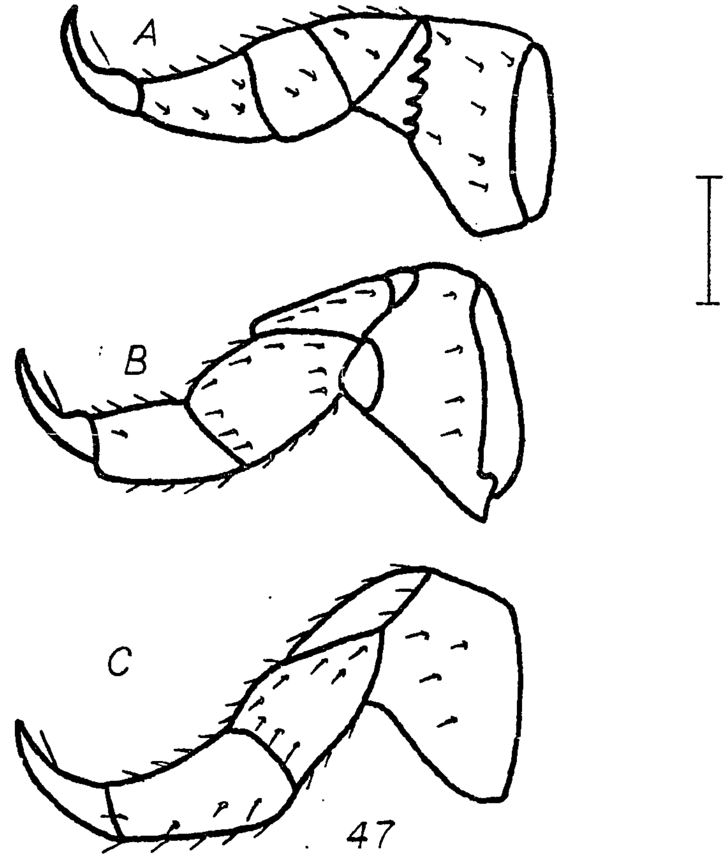


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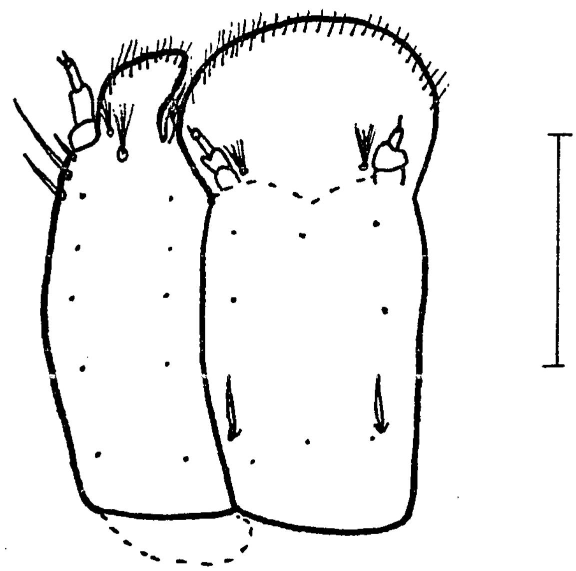

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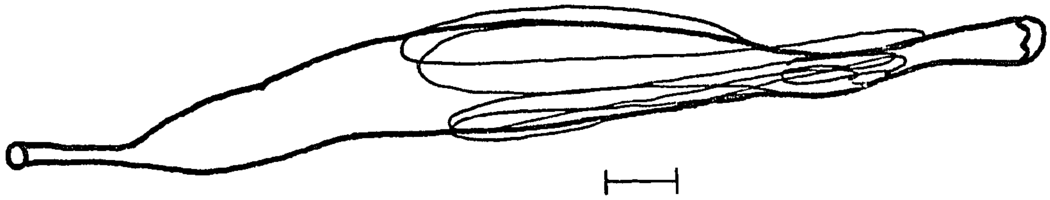

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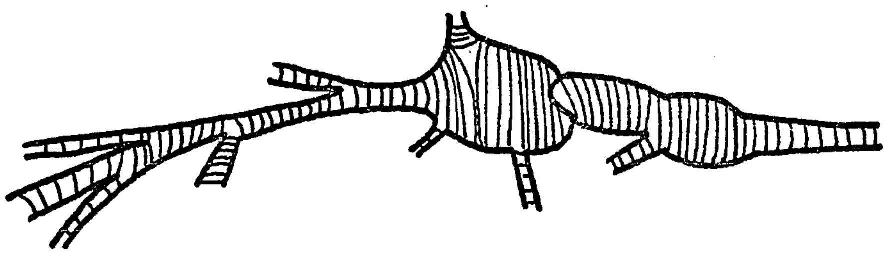

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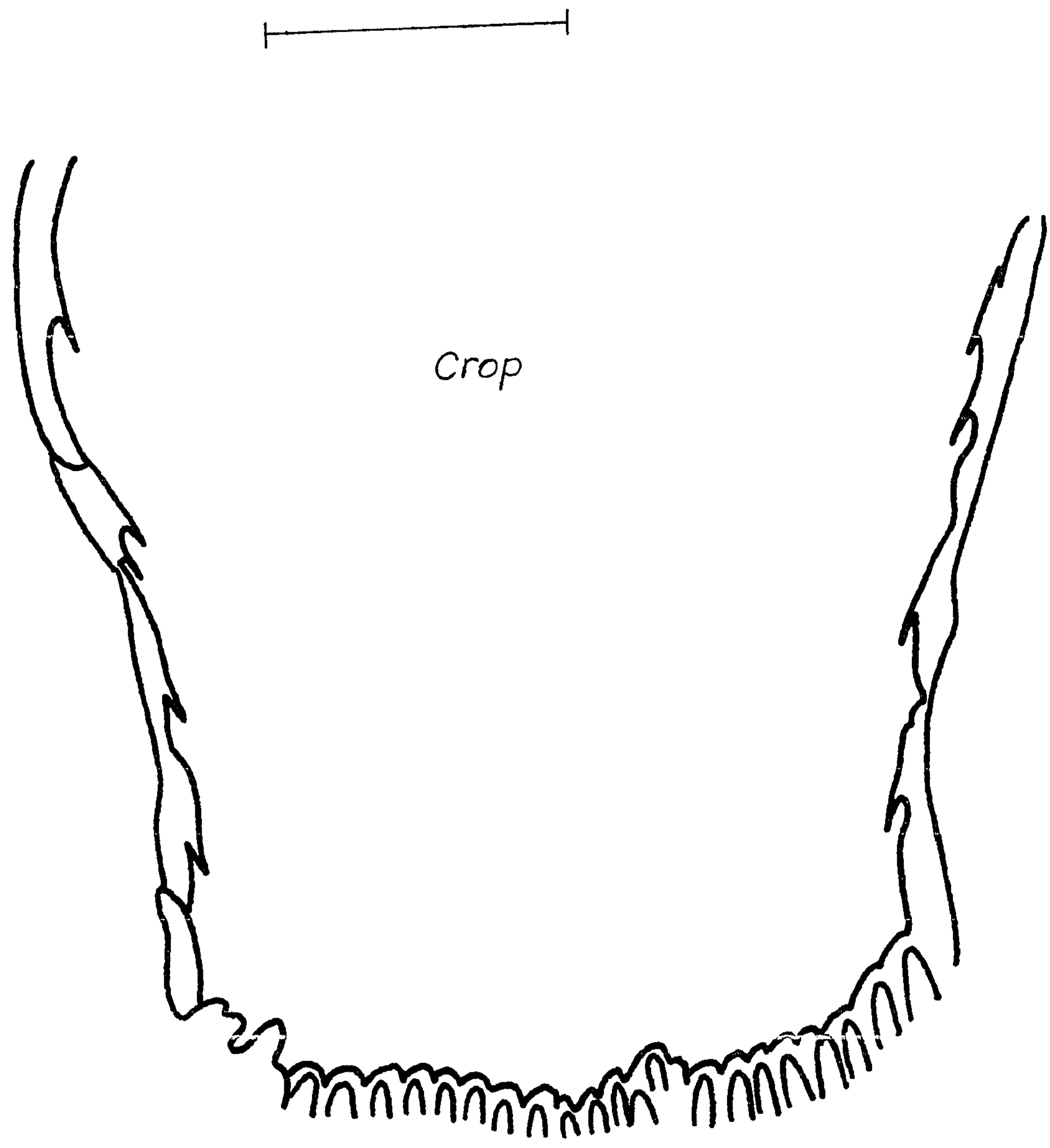


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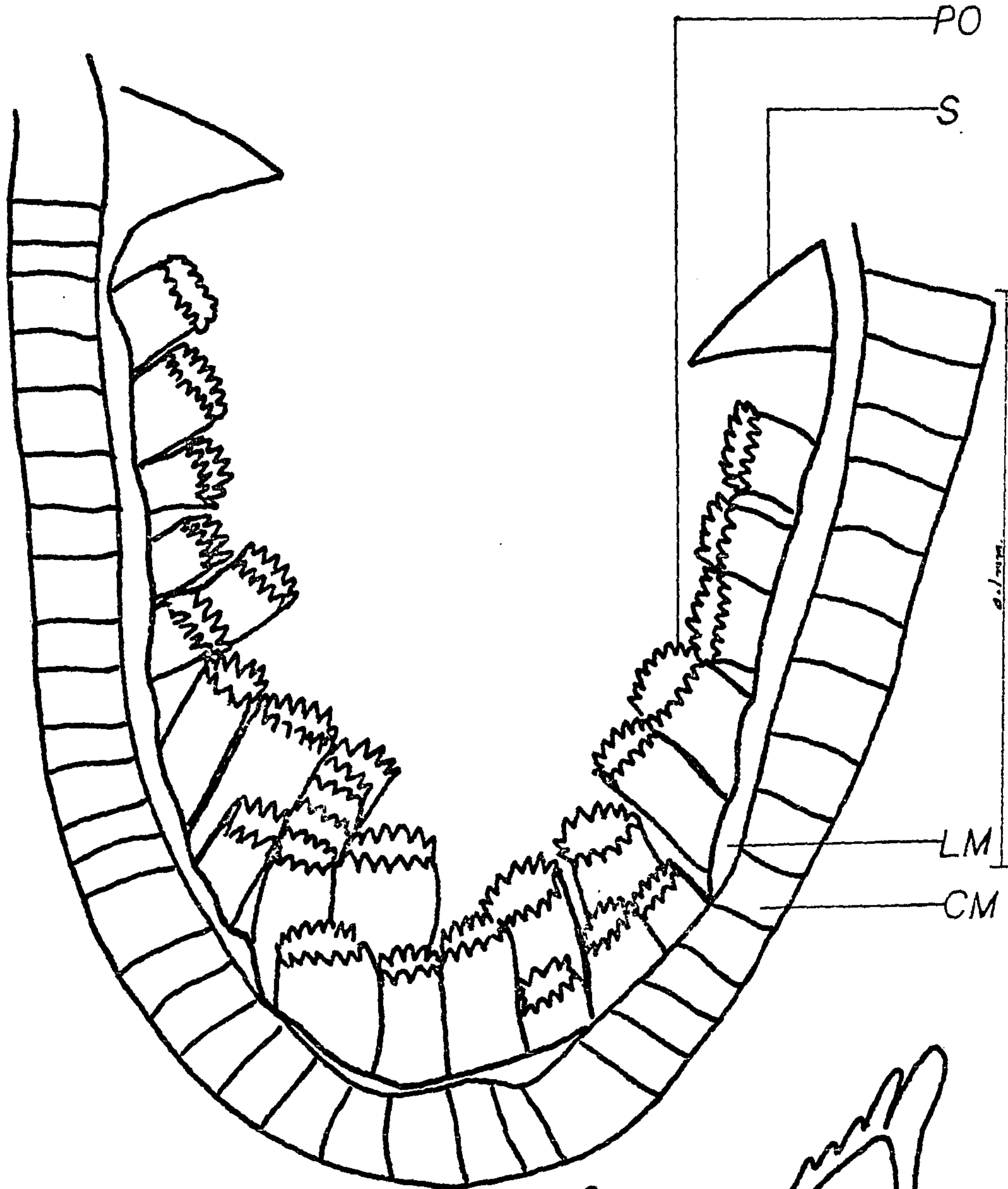


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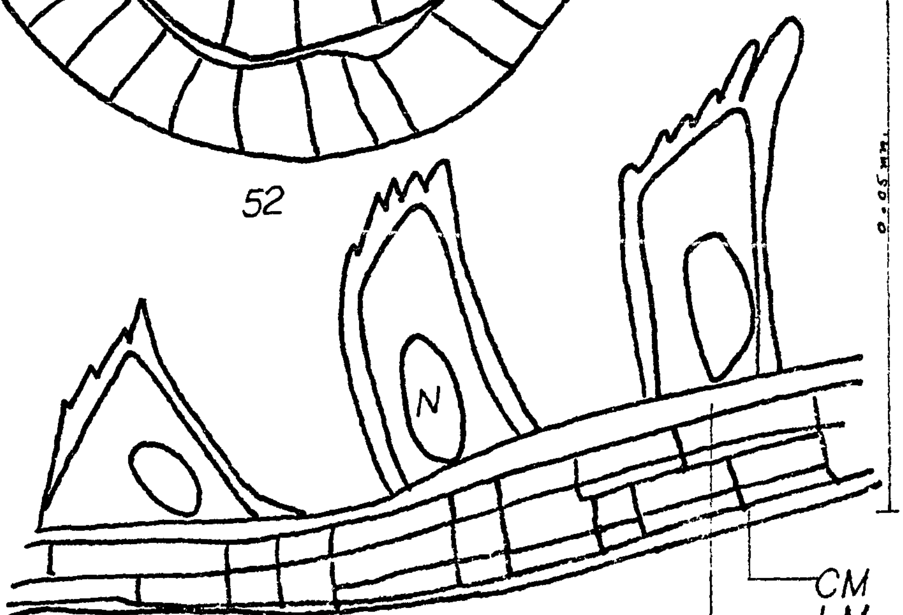


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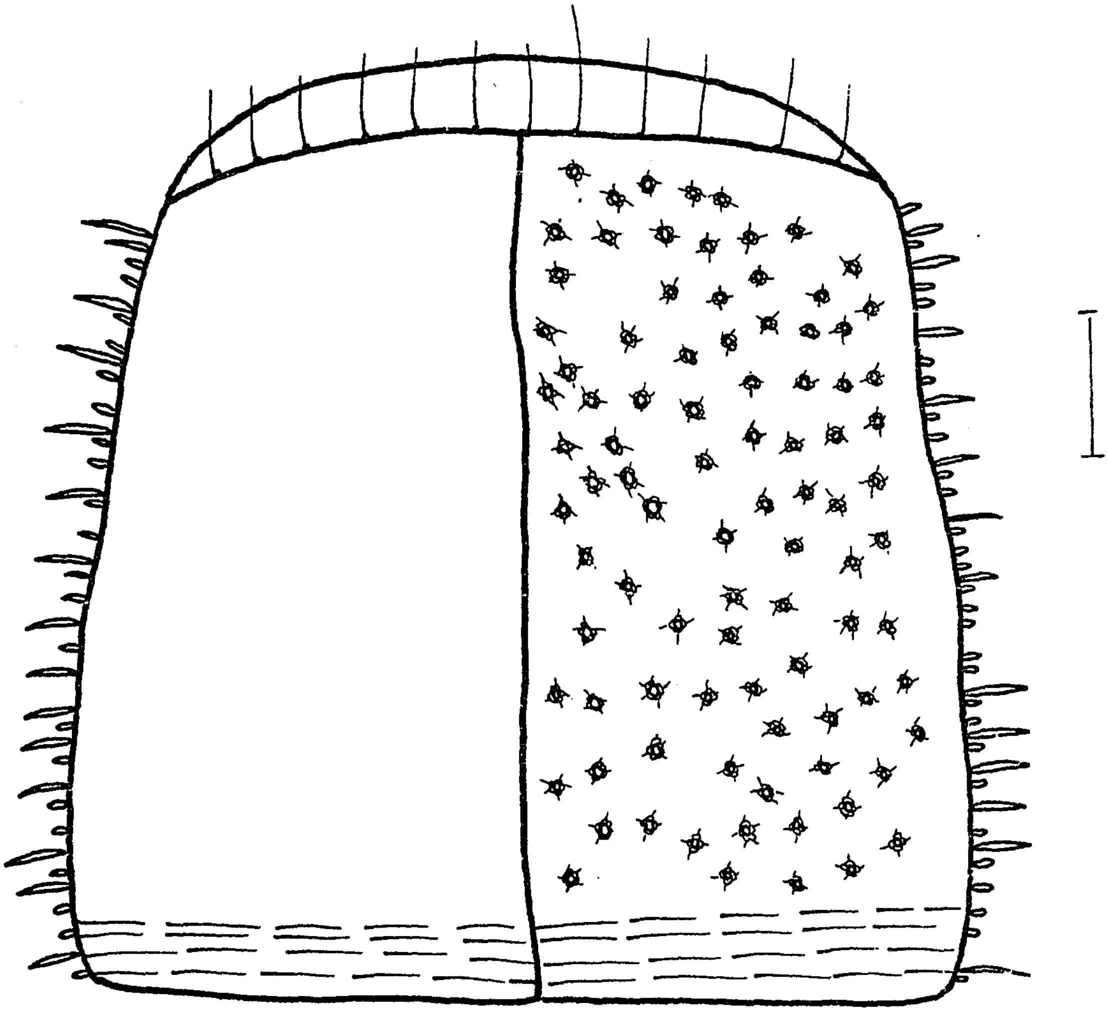

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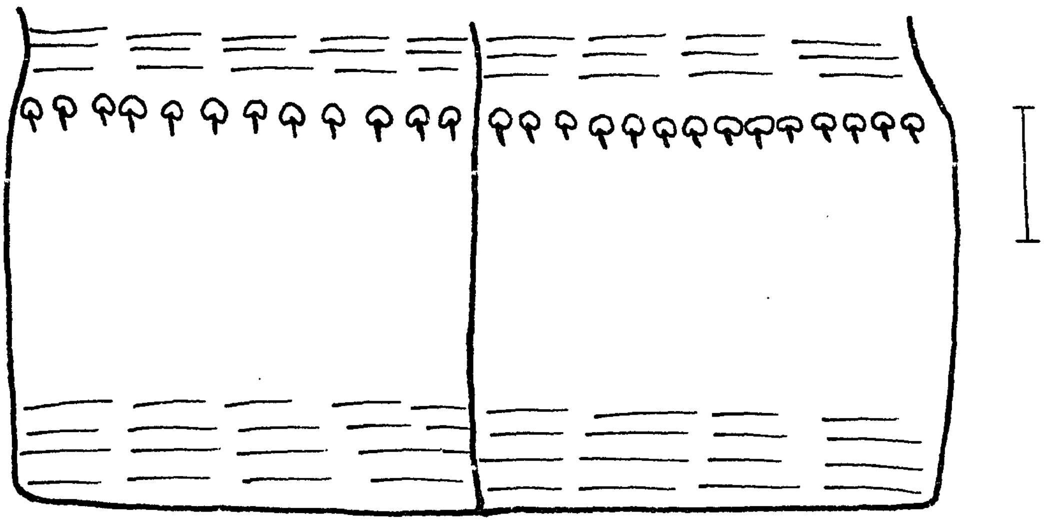

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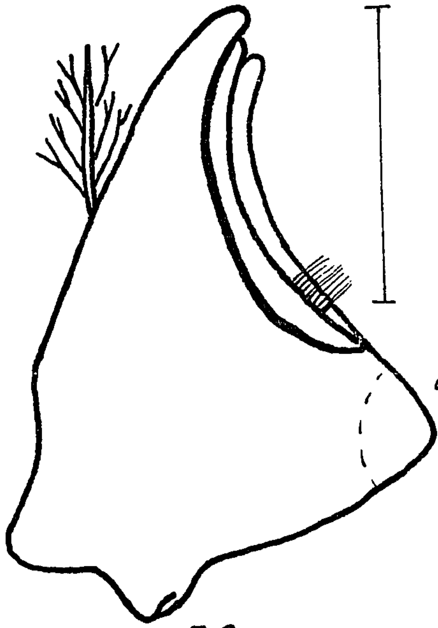

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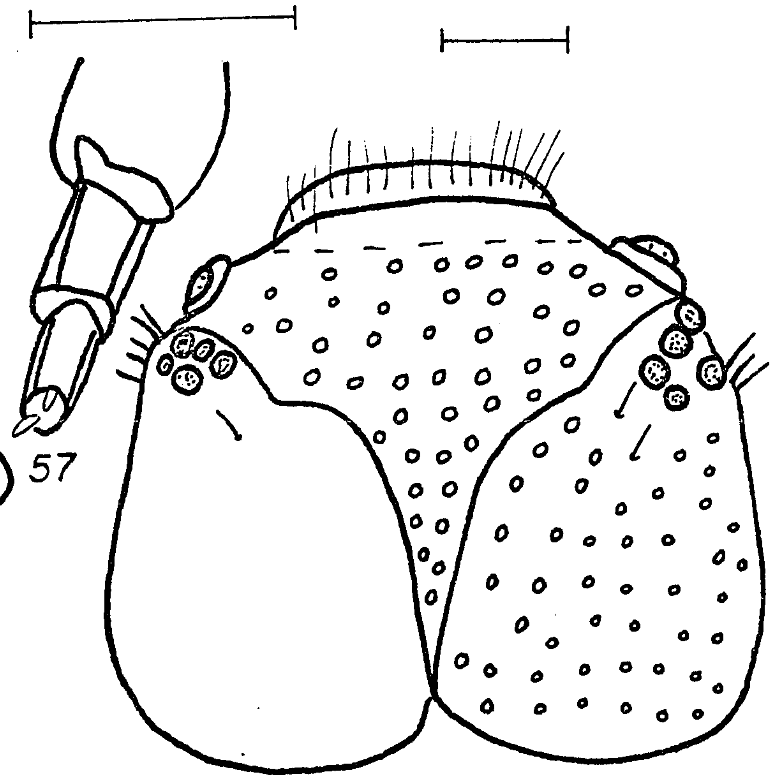

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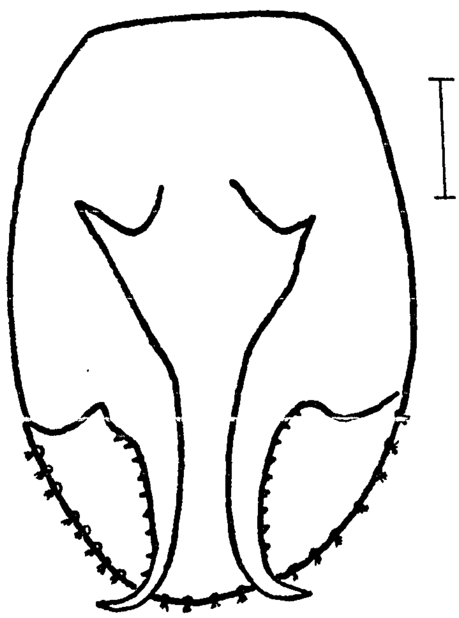

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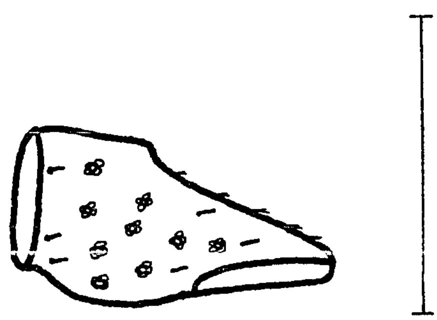

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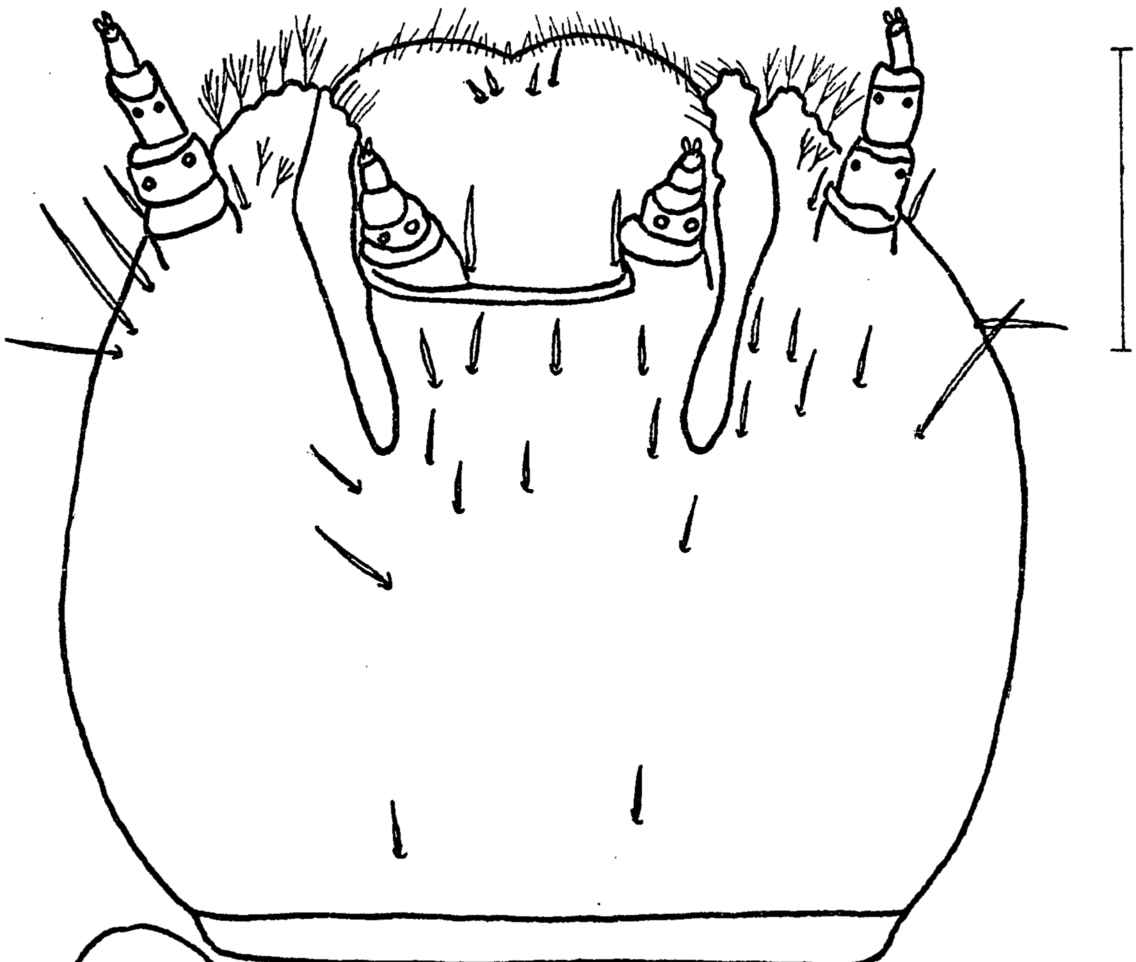

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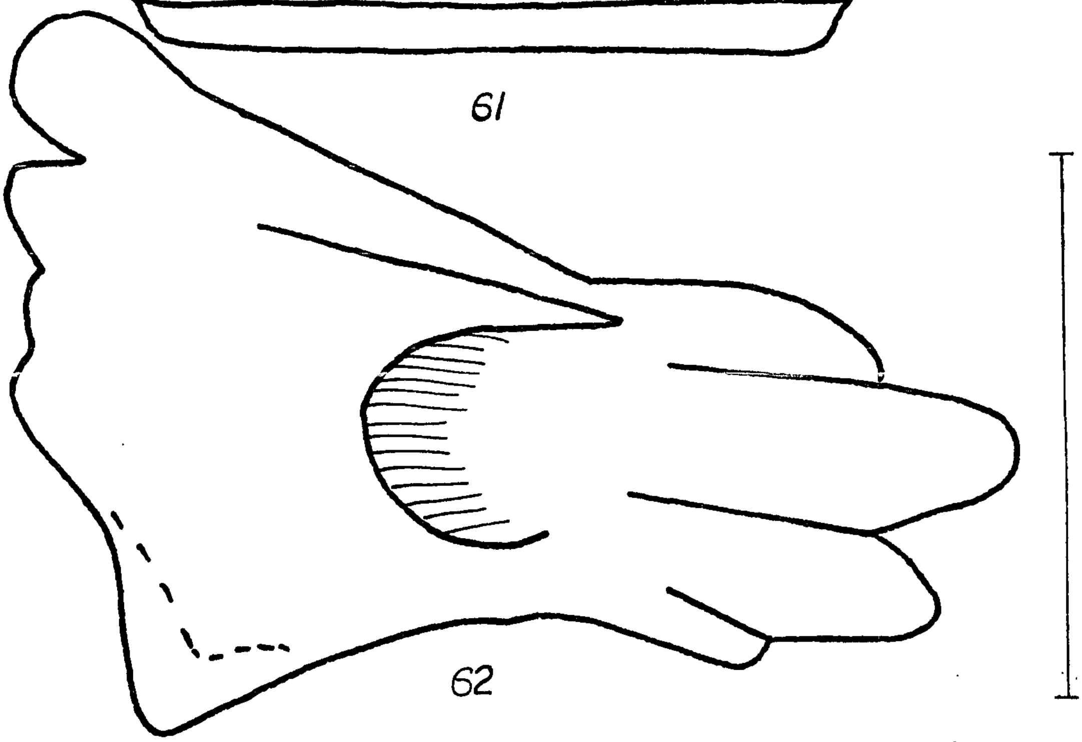

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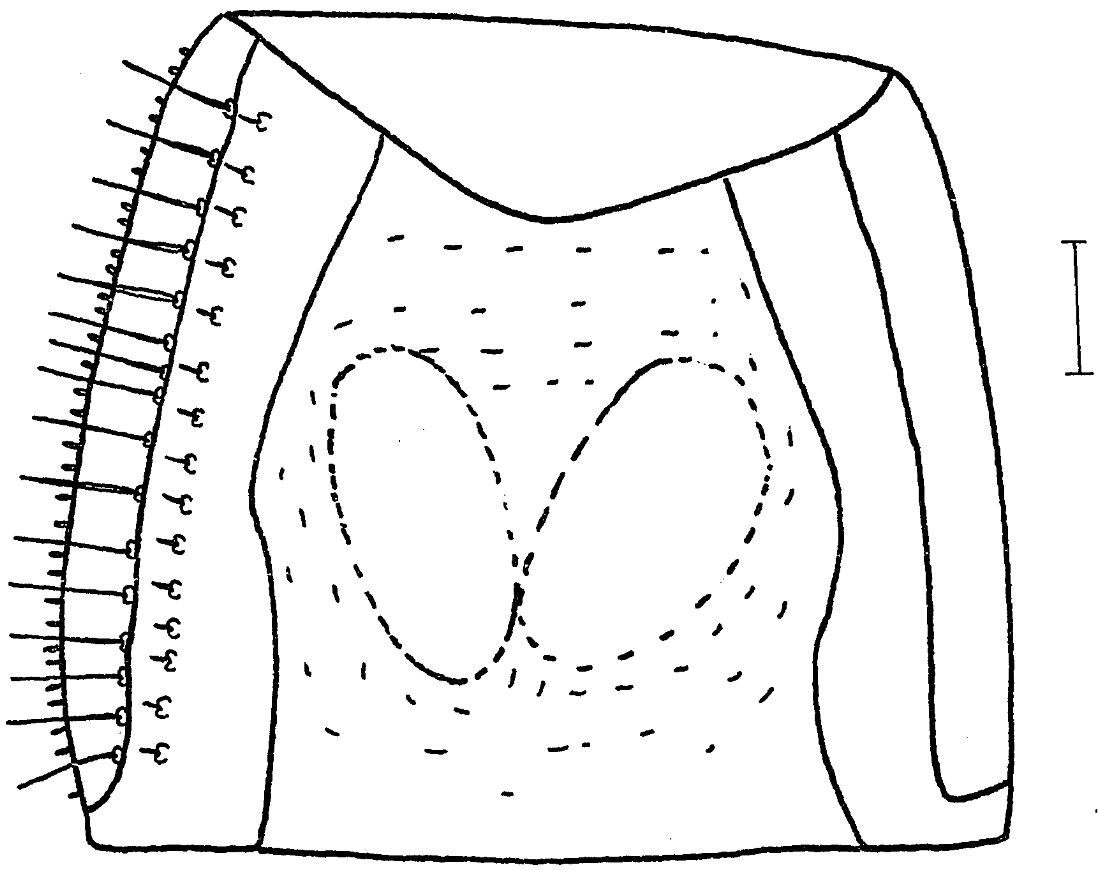

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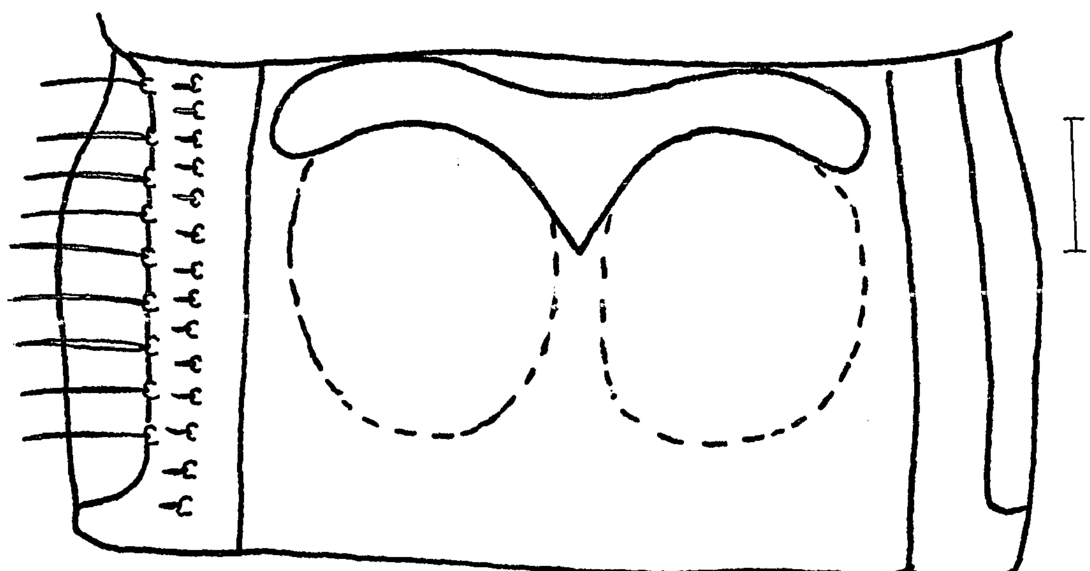

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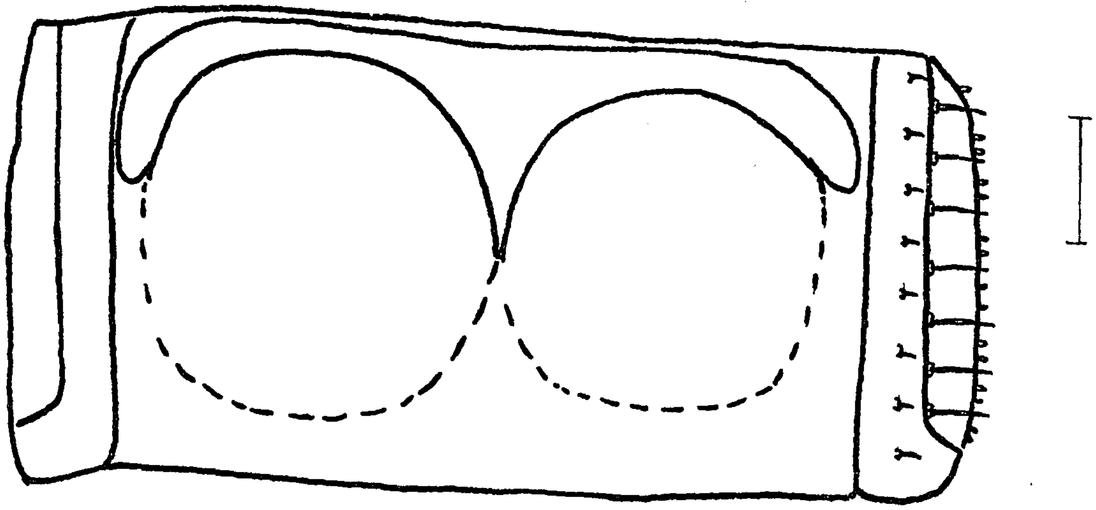

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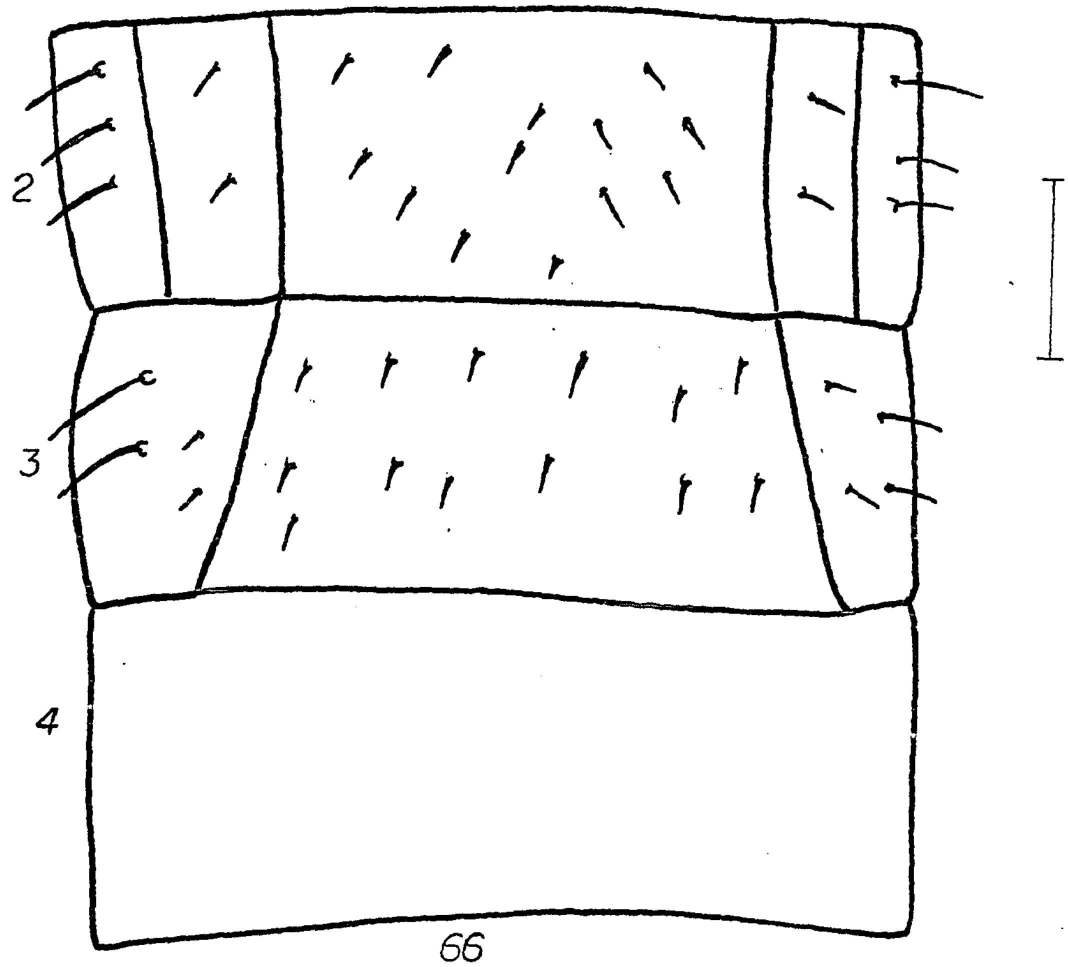


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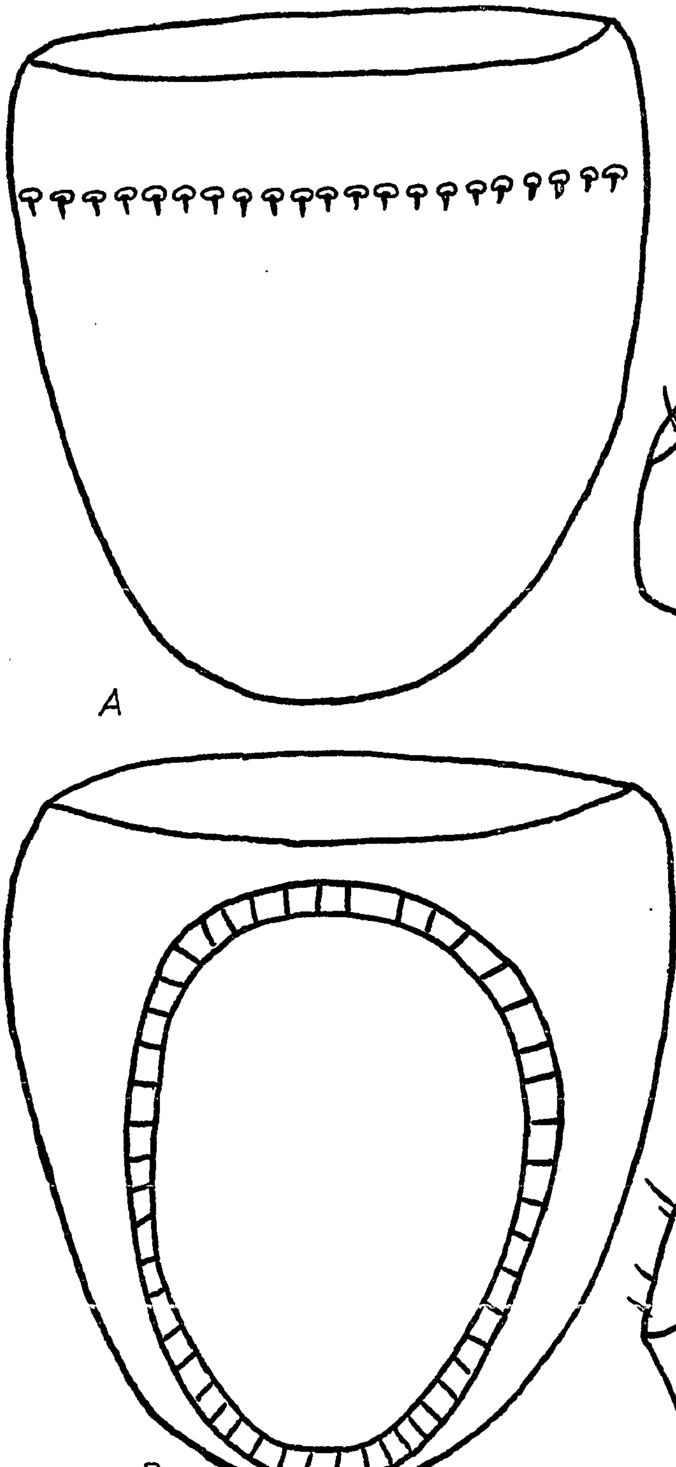


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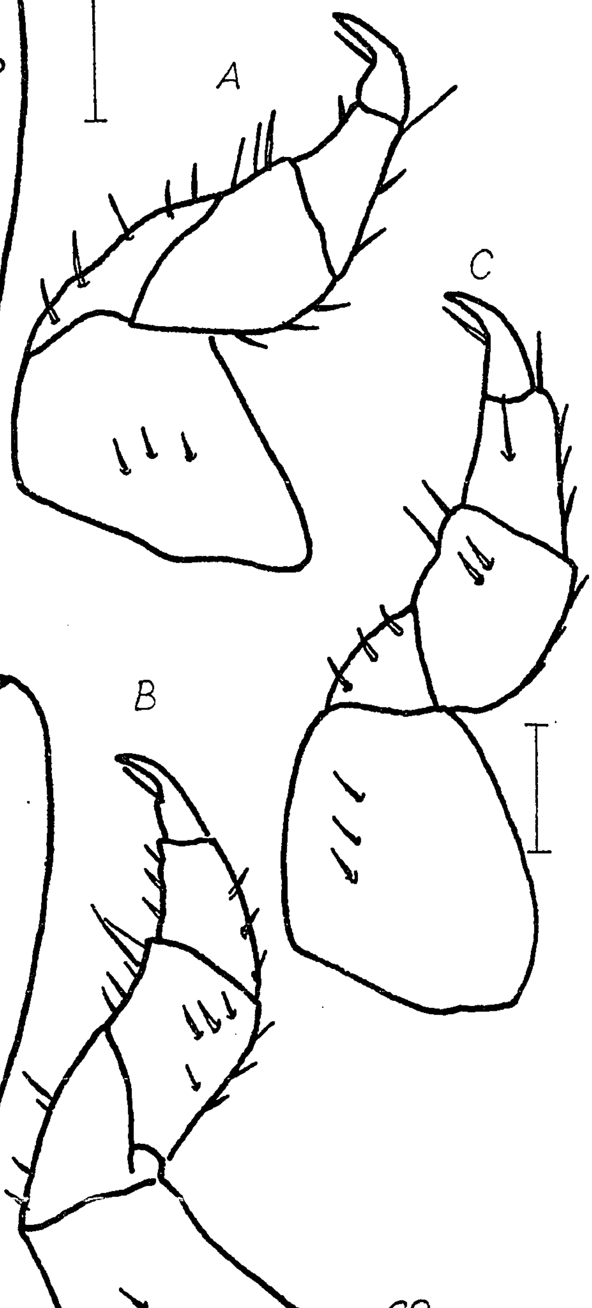


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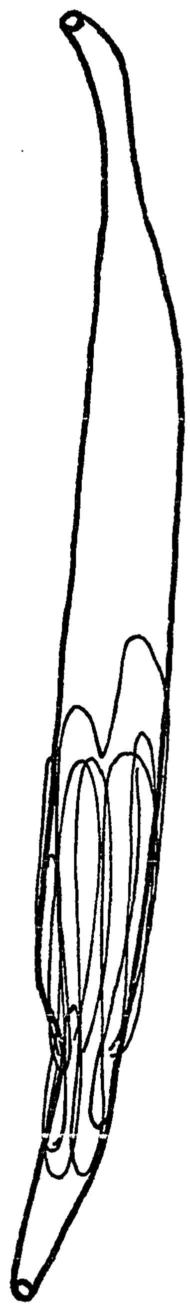

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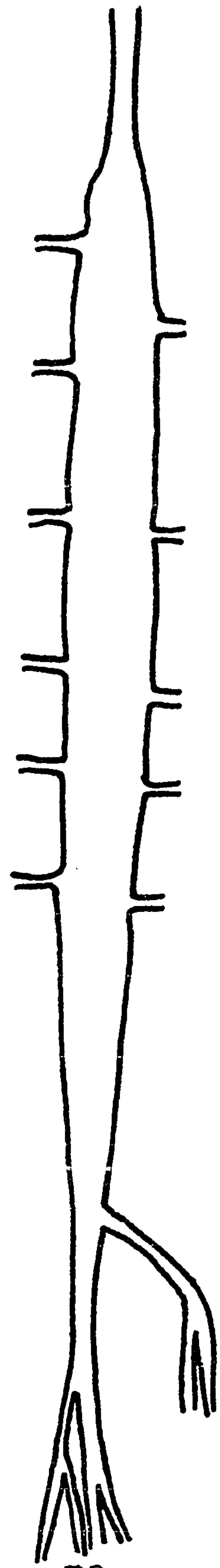

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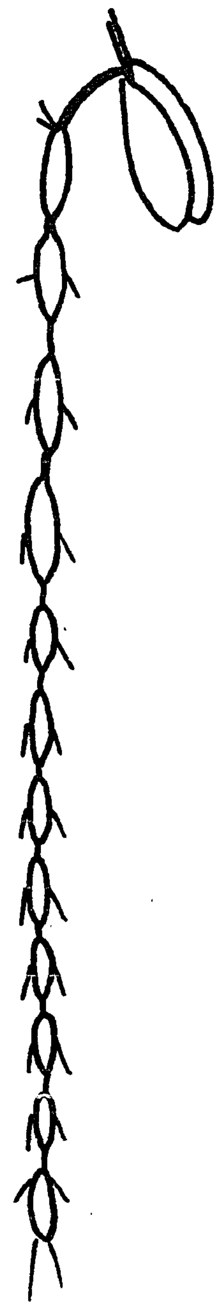

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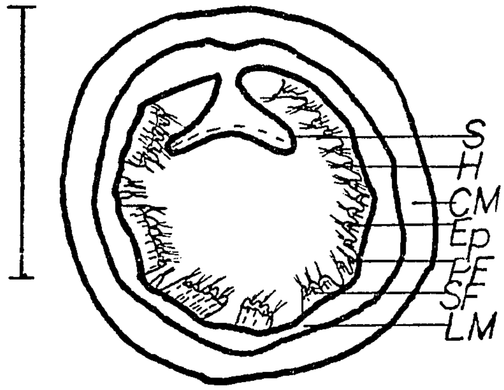


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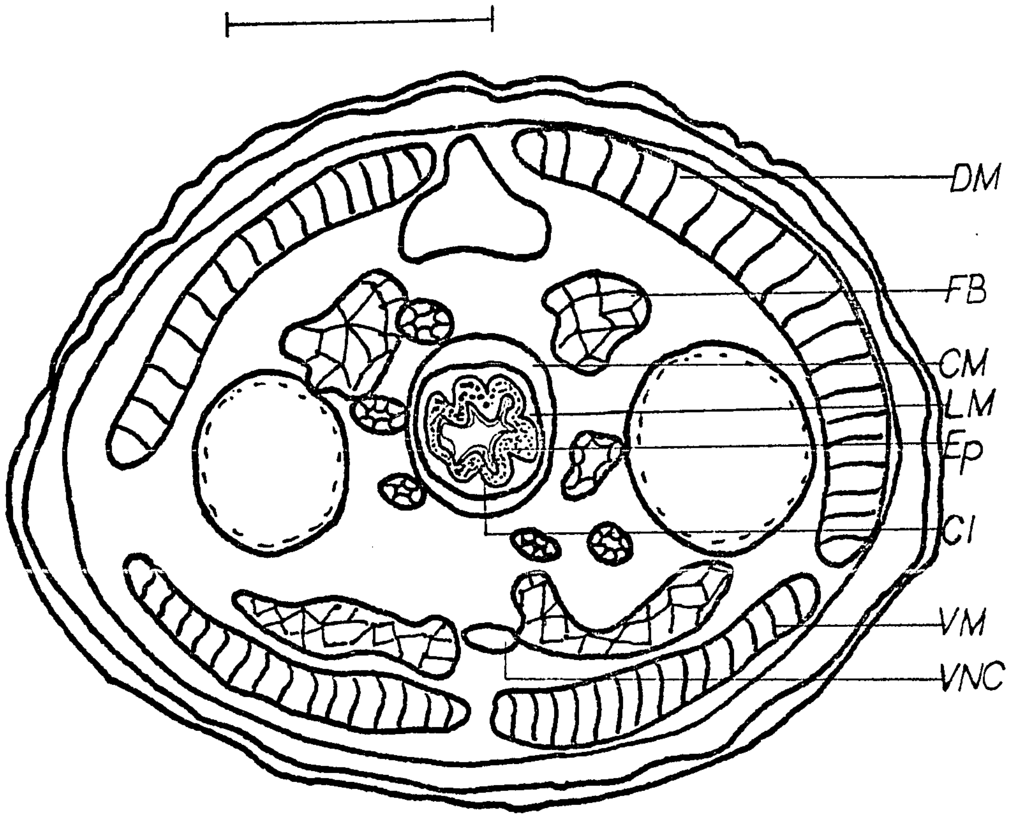


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## ELMIDAE (Westwood, 1838)

This, the largest family of Dryopoidea in North America, was earlier known under the family name Parnidae which was created in 1825 by McLeay. Westwood in 1839 preferred Elmidae as a subfamily under Parnidae (Sanderson, 1938). Blatchley in 1910 considered the family Parnidae as containing three distinct subfamilies, Psepheninae, Parninae, and Elminae (Sanderson, 1938). Leng (1920) raised Elminae to family rank but used the name Helmidae instead of Elmidae, and Parninae were given family rank under the name Dryopidae. Hinton in 1935 recognized three subfamilies of Dryopidae: Larinae, Dryopinae, and Elminae. After later concluding that the Elmidae are not closely related to the Dryopidae, Hinton (1939) separated the two into separate families. He demonstrated that the Larinae do not belong to the family Dryopidae, but to the Elmidae, and that tribal rank for this group is only justified when dealing with adult beetles. Only one character separates Larini from Elmini, that being the presence of tomentose tracts in all Elmini and their absence among the Larini (Hinton, 1939).

Brown (in press) lists 24 North American genera as belonging to this family, two in the tribe Larini and twenty-two in the tribe Elmini. Elmidae are distributed throughout North America, north to British Columbia, the Great Slave Lake, and eastern Canada, and south throughout Central and South America, and the West Indies.

In his synopsis, Sanderson (1953-1954) describes elmid larvae as having three tufts of retractile anal gills bearing slender filaments, one pair of hooks attached to an abdominal operculum, one to three thoracic pleura, six to eight abdominal pleura, and the last abdominal segment slightly to deeply emarginate. The larvae are aquatic and live submerged.

In addition to the above, Arnett (1968) lists the following larval features: body convex, cylindrical or depressed, or onisciform with lateral projections, and size five to twelve mm long; head exserted, prognathous, epicranial suture distinct or absent, antennae two-segmented, labrum arcuate, mandibles dentate or acute, and one pair of ocelli.

Hexanchorus (Sharp, 1882)

According to Bertrand (1955) this genus is widespread in Mexico, Central America and much of South America. It is represented in Martinique and Guadeloupe in the West Indies.

As described by Hinton (1940) the head of the Hexanchorus larva is exposed when viewed dorsally. Anterior margin between base of antennae and clypeus toothed and head bearing one to six ocelli on each side. Antennae three-segmented, not retractile, mandibles on both sides similar with three obtuse teeth and bearing a long, slender and densely spinose prostheca. Maxillae with four-segmented palpi and stipes showing no differentiation into a palpifer. Galea and lacinia separate with apex of each densely spinose. Labial palpi two-segmented and prementum with a palpiger.

Prothoracic pleura divided into three parts on each side, but mesothoracic and metathoracic pleura divided into two parts. Prosternum divided into an anterior and posterior sclerite. First six abdominal segments with pleura bounded by tergo- and sterno-pleural sutures, segments seven and eight forming complete sclerotized rings.

I have studied the external and internal morphology of five larval specimens of Hexanchorus caraibus collected in Rio Monsieur, Saint Joseph, Martinique on May 5, 1965. The specimens averaged 3 mm in length and 1 mm in width. Two specimens were used for histological study.

Hexanchorus caraibus

## External Morphology

The generic features as described by Hinton (1940) were observed. Several additional features are given below.

Body. subcylindrical and subparallel. Cuticle dorsally a mixture of light and pale brown with dark brown spots scattered over thorax. Thoracic and abdominal segments are covered with spherical to oval tubercles from which project stiff setae (Figs 79, 83). At posterior margins of above segments are tetra-spined tubercles which bear branched setae (Figs. 79, 83). From lateral surface project heavy tubercles which bear subflabellate (flabellate = the appearance of an open fan), highly branched, membraneous (Figs. 76, 79, 83) setae. They cover the margins of thoracic segments, but are confined to posterior portions of first eight abdominal segments. Cuticle sculpture of ninth segment as anterior segments. Cuticle ventrally, from thorax to ninth abdominal segment, sculptured as dorsum.

Head: subcircular, slightly longer than broad, with epicranial and frontal sutures as illustrated (Fig. 75). Cuticle pubescent; tubercles spherical to oval, serrated at base, and concave at point of emergence of hairy setae. Six ocelli per mass, the two masses connected by a transverse band of tubercles. Clypeus slightly truncate, bordered laterally by a fronto-clypeal tooth on each side. Antennae not retractile and with longer distal member bearing a hook-shaped organelle (Fig. 77). Labrum slightly emarginate along anterior margin, with a transverse line of stiff setae to each side of emargination. Mandible as shown (Fig. 85) with short sensory brush in addition to a prostheca. Labium as figured (Fig. 84). Galea and lacinia separate and apex of each densely spinose. Stipes and postmentum separate, but elongate and closely appressed; cardo as illustrated (Fig. 84), and prementum without a well-defined palpiger.

Pronotum, mesonotum, and metanotum wider than long (Fig. 83). First through seventh abdominal segments similar, whereas eighth is modified dorsally to form triangular tubes on apices of which are the eighth tracheal spiracles (Figs. 79, 80). Apparently only segment eight and anterior part of ninth form complete sclerotized rings.

Sterna of thoracic and first eight abdominal segments are sclerotized (Fig. 74). Posterior sternal region of ninth forms operculum as figured (Figs. 78, 81, 82). Claws attached to ventral surface of operculum serrate with setae on inner margin (Figs. 82, 86) of curvature.

Legs all similar and as figured (Fig. 87). Each segment slightly increasing in length posteriorly.

## Internal Morphology

Digestive System

The alimentary tract (Fig. 88) consists of three divisions: the stomodeum, mesenteron, and proctodeum. The stomodeum or foregut is the shortest division and consists of the buccal cavity, esophagus and proventriculus. A distinct constriction divides the foregut from the midgut. The longest division, the mesenteron or midgut, is a straight tube without any constrictions along its length. The proctodeum is shorter than the midgut, but longer than the foregut, and begins behind the point of origin of the malpighian tubules.

Respiratory System

The main tracheal vessels are lateral trunks, which lie alongside the gut. Between the gut and lateral trunks lie spherical air sacs which are connected to the lateral trunks and abdominal tracheal vessels supplying the midgut (Fig. 90). Short transverse tracheal vessels in the mesothorax and first through eighth abdominal segments communicate with spiracles of the above segments.

Excretory System

Six malpighian tubules arise at the junction of midgut and hindgut. The tubules pass anteriorly over half of the midgut, then pass posteriorly to end free near the middle of the hindgut.

Central Nervous System

H. caraibus has a pyriform bilobed brain from which nerve tracts pass anteriorly to the ocelli and antennae. It is connected by circumesophageal connectives to an oval subesophageal ganglion which supplies larval mouth parts. The three thoracic ganglia are relatively large and discrete; there are 8 discrete abdominal ganglia, the last being largest (Fig. 89).

## Histological Morphology

### Integument

The exocuticle averages 5.2 microns in thickness and is tuberculate. The tubercles rise 16 microns above the epicuticle surface. The endocuticle averages 16 microns in thickness and is laminated. Sensory cells which communicate with the spines and tubercles of exocuticle are situated here.

### Digestive System

An irregular cuticular intima lines buccal cavity and esophagus, followed by a single layer of dome-shaped epithelial cells resting on an indistinct basement membrane. Below the membrane are indistinct longitudinal muscle bands which are surrounded by a well-developed circular muscle layer. The dilated crop which follows posteriorly is very short; most of the dilation is taken up by the proventriculus. A thin intima lines the crop and covers a layer of flattened epithelial tissue. The muscle layers are as in the esophagus. Anteriorly and laterally the proventriculus contains cylindrical to rectangular-shaped cells which bears spinous or serrate processes. All of the cells project posteriorly toward the midgut (Fig. 91). At the base of the proventriculus, these small cells have their apices drawn out to form spinous processes. No proventricular pads were observed and no large basal proventricular cells. Esophageal invaginations extend posteriorly from the wall of the proventriculus into the midgut giving the appearance of a distinct sphincter.

The cuticular intima of the foregut is replaced by a heavy peritrophic membrane which overlies a distinct layer of columnar cells bearing brush borders. These cells have interspersed among them distinct goblet cells. Both cell types rest on a distinct basement membrane. Surrounding the membrane is an internal layer of circular muscle and several bundles of longitudinal muscle externally.

Anteriorly the cuticular intima is thick and closely associated with the epithelial cells, but posteriorly it becomes rather irregular. The epithelial cells are cuboidal to flat and are thrown up into six folds which are very pronounced toward the rectum. Near the anus the folds become irregular as the lumen of the gut increases. The muscles of this zone correspond to those of the foregut in respect to order or position.

Respiratory System

The histological morphology of the trachea and air sacs present in H. caraibus appears to correspond to the description given by Snodgrass (1935).

Excretory System

The structure of the malpighian tubules is similar to the description given by Patton (1953). Each tubule consists of a cylinder of cells limited externally by a basement membrane. The inner margin of the cells facing the lumen of the tubule appears to have a brush border. Heavy granulation of the cytoplasm makes individual cell boundaries indistinct.

Central Nervous System

A distinct neurilemma covers each neural compent of this system. Each component is basophilic and fat cells are very abundant on the margins. Neuroglia cells are abundant, large fibers are concentrated near the periphery, and small fibers are centrally situated.

Sense Organs

Sensory organs are primary (ocelli, antennae, palps, setae of dorsum, venter, palps, and mouth parts), sensilla campaniforma, and sensilla basiconica. The sensilium basiconicum described by Snodgrass (1935) is apparently an unspecialized form of the organ observed here.

Fat Bodies

These organs consist of closely associated bunch-like masses which lie along the gut from the region of the esophagus to hindgut. The masses increase in size posteriorly and contain many uric acid and glycogen granules.

Gut Contents

Serial sections revealed in the gut lumen plant fragments, fragments of filamentous algae, sand, and various types of unidentifiable debris.

## *Lara* (LeConte, 1852)

This genus contains our largest species of Elmidae and occurs only in western North America (Sanderson, 1953). Specimens have been collected from British Columbia to southern California and eastward through Idaho and Utah to Wyoming and Colorado (Brown, in press). The larva of the type species, Lara avara LeConte, was illustrated by West (1929) and Boving and Craighead (1931). Darlington (1929), using adult characters, revised the genus. Presently there are two species and one subspecies: Lara avara avara, L. avara amplipennis, and L. gehringi.

I have studied external and internal morphological features of eight larval specimens of Lara avara, collected from Soap Creek, Tehama County, California on November 20, 1952 and near Alta Sierra, California July 14, 1969. The specimens averaged 12 mm in length and 3 mm in width. Two specimens were studied histologically.

Lara avara

## External Morphology

The larval features observed by the writer correspond to those described by West (1929) and Bertrand (1955), with minor changes and additions.

Body: elongate, subparallel, subcylindrical, and tapering caudally. Cuticle on dorsal side dark greenish-brown. Ornamentation of all segments elaborate, consisting of tubercles and papillae arranged in an irregular pattern from anterior to posterior (Figs. 96, 98). Lateral margins of each tergite bear a complex row of backward-projecting processes (papillae) which are also adorned with fine spines. The arrangement of the ornamentation gives the effect of four (quadrangular) longitudinal rows (two subdorsal and two lateral) of backward-projecting processes extending the length of the dorsum. Cuticle ventrally only slightly lighter than dorsum.

Head: length and width are approximately equal and epicranial and frontal sutures as figured (Fig. 92). Cuticle pubescent, most of surface covered by oval tubercles, but near clypeus tubercles are replaced by a transverse line of branching membranous setae. Eyes consist of five small ocelli on each side clustered near base of antenna. Antennae conspicuous and hairy; first segment short and robust; second elongate and tapering, surrounded at base by prominent blade-like setae; third minute and duplicate, consisting of two subequal, setose members. Labium three times as broad as long, with a basal transverse row of small tubercles, each bearing a large, branched seta; angles broadly rounded, and anterior margin straight. Clypeus narrow and bears two indistinct submedial depressions. Small frontal spines adjacent to base of antennae bearing branched setae (Fig. 92). Mandibles of both sides similar, each with three apical teeth, long prostheca, short internal tuft of sensory bristles, and on outer lateral margin several multi-branched setae (Figs. 94A, B). Maxillae (Fig. 95) with four-segmented palpi, stipes showing no differentiation into a palpifer, galea and lacinia separate, each bearing short apical spines, but those on lacinia are more robust. Palp with first two segments subequal, short, broader than long; third segment slender, slightly longer than broad, and expanded apically; fourth segment smaller and rounded, with a pair of stubby terminal spines. Situated between palp and galea are many straight setae. Stipes separate from postmentum and bearing along lateral margin numerous multi-branched, membranous setae. Labium (Fig. 93) subrectangular, twice as long as broad, and bearing two-segmented palpi and a palpiger. Postmentum with numerous multi-branched setae.

Pronotum broader than long with transverse anterior groove (Fig.

96) outlining receptacle for head. Mesonotum, metanotum, and first eight abdominal segments ornamented as pronotum except that setal masses are concentrated on posterior half of each abdominal segment. Ninth tergite (Fig. 98) tapering posteriorly with apex curved dorsally and strongly emarginate.

Sterna of thoracic segments mostly sclerotized. Prosternum present, poststernum absent, and coxal cavities open posteriorly (Figs. 100, 101). Pleura consisting of two parts in prothorax and one part in mesothorax and metathorax. Pleura of first eight abdominal segments bounded by sutures. Sternal region of first eight abdominal segments sculptured similarly. Posterior sternal (Fig. 97) region of ninth segment forms operculum as figured (Fig. 99). Attached to operculum on dorsal surface are two long, curved spines or claws.

Legs (Figs. 102A, B, C) all similar, increasing in size posteriorly. Internal spine on tarsal claw three-fourths as long as claw. Outer margin of trochanter with branched setae. Tibiotarsus with several large, spinous setae on inner margin and a prominent seta at outer apex.

With nine spiracles, the first is located on a postero-lateral protuberance at outer base of mesothoracic segment and each of the remaining eight communicates with a protuberance above heavy setae on lateral margin of each of the first eight abdominal segments. All spiracles are biforous.

## Internal Morphology

### Digestive System

The gross morphology of this system is like that of Hexanchorus (Fig. 103). In one specimen the foregut was folded, causing the ventral surfaces of the crop and proventriculus to lie adjacent to each other (Fig. 107). The midgut is the most robust division, but the hindgut is slightly longer and a fold brings the upper posterior intestine forward almost to the lower midgut region (Fig. 103).

Respiratory System

This system is similar to that in Hexanchorus. The main tracheal trunks are lateral ones and there are spherical air sacs lying between the trunks and gut in the ventricular region.

Excretory System

This system does not differ from that of Hexanchorus.

Central Nervous System

There was no difference observed between the central nervous systems of this genus and Hexanchorus.

## Histological Morphology

Integument

Generally the morphology is similar to that of Hexanchorus. It differs in that the exocuticle averages 14 microns in thickness and endocuticle averages 43 microns in thickness. Serial sections revealed the posterior-projecting tubercles to have a core which extends down into the endocuticle (Fig. 104). Scattered over the surface of them are membranous setae and spinous setae. Ventral setae are as figured (Fig. 105).

Digestive System

The buccal cavity is the only areas of the foregut which is similar to that in Hexanchorus. The esophageal wall is thrown up into six folds and there is a well-developed cuticular intima. The crop is longer, wider, and bears a very thick cuticular intima. The muscular layers are thicker in comparison, but this could be correlated with the size of the organism. The proventriculus is very unlike that found in Hexanchorus. Apparently there are no cylindrical to columnar cells as in Hexanchorus. At the most anterior part of this zone are subtriangular cells with the apex drawn out into sclerotized spines. Posteriorly there are longitudinal folds which are modified laterally to form helical cords bearing sclerotized borders (Fig. 106). This gives the appearance of rows of beads within the proventriculus. Cells on the wall of this area are like those in the anterior zone, except that they are more dome-shaped. At the posterior of this region are cells identical to those located in the anterior zone (Fig. 107).

The histology of the midgut and hindgut (Fig. 108) is similar to that of Hexanchorus.

## Respiratory System

The histological morphology of this system does not differ from that of Hexanchorus.

## Excretory System

This system does not differ from the description given by Patton (1953). The tubules have a smaller lumen than Hexanchorus and six cells may be distinguished in cross section.

## Central Nervous System

This system differs from that of <u>Hexanchorus</u> in that nerve fibers within ganglia apparently are uniform in size.

<u>Sense Organs</u>

These organs are primary and typical for both genera. There apparently is a specialization of setae sensillae. Comparison of the club-shaped tubercle with the sensilla trichodea (Snodgrass, 1935) suggests that they may be similar.

<u>Fat Bodies</u>

These bodies appear as irregular masses of cells enclosed by a limiting membrane and dispersed around the gut from the esophagus posteriorly. Peripherally the fat forms mesh-shaped masses and distinct fat globules are evident. As in <u>Hexanchorus</u> there are uric acid and glycogen granules.

<u>Gut Contents</u>

Serial sections revealed in the gut lumen plant fragments, wood fibers, cell wall components of filamentous algae, and debris.

<u>Potamophilops</u> (Grouvelle, 1896)

This genus was formed by Grouvelle to include <u>Potamophilops cinereus</u> (Blanchard), which was collected in Corrientes Province of Argentina by d'Orbigny and described in 1842. Adults are 5-7 mm in length, thorax anteriorly with deep transverse groove, and posteriorly with two triangular depressions separated at ends by a medial narrow longitudinal ridge (Brulle, 1842). Hinton (1940) considered <u>Potamophilops</u> synonymous with <u>Hexanchorus</u>, but he did not get to examine specimens in detail.

Larvae have not previously been described.

I have studied external and internal morphological features of five larval specimens of Potamophilops collected in the Rio Bananal near Agua Azul, Para, Brazil on June 9, 1968. The specimens averaged 8.7 mm in length and 2.3 mm in width at the level of the meso- metathorax. Two specimens were studied histologically.

Potamophilops sp.

## External Morphology

Body: parallel and cylindrical to level of third abdominal segment and posteriorly subparallel and tapering. Cuticle dark brown dorsally and densely tuberculate with bundles of polysetae (Figs. 112, 117) from pronotum to ninth abdominal tergite. Scattered sparsely among the bundles are filiform setae (Fig. 112), the base of each surrounded by a double row of scales. Tergal sutural line pale from first to eighth abdominal segment. First eight abdominal tergites on each side with a feeble submedial and sublateral carina composed of posteriorly-directed tubercles reinforced with heavy masses of setae. Ninth tergite with strong posteriorly-curved spines and similar but less prominent sub-lateral carina on each side. Cuticle slightly lighter ventrally, with small spines on thorax, and larger spines on abdomen as illustrated (Figs. 116, 118).

Head: nearly round, slightly broader than long; epicranial and frontal sutures as shown (Fig. 109). With tubercles on central portion of head and medially along central portion of head and laterally along frontal suture (Fig. 109). Tubercle-like spines at anterior margin of frons. Each eye with six fused ocelli. Antennae with three segments, the first short and tubular, the second slender and longer than first, and the third very small, with a small apical seta; alongside minute segment is a much larger spine extending from apex of second segment (Fig. 109). Clypeus short, anterior margin slightly truncate, and dorsal surface bears minute punctures (Fig. 109). Labrum bearing tufts of slightly branching setae arising from a transverse row of cup-shaped tubercles. Mandibles with four apical teeth, a long prostheca, and an adjacent sensory brush consisting of several close erect setae (Fig. 119); outer margin bearing a tuft of setae (Fig. 119). Maxillae (Fig. 113) with four-segmented palpi and stipes showing no differentiation into a palpifer. Galea and lacinia separate, cardo with a posteriorly directed spinous part, and stipes with a number of large, branching, membranous setae on antero-ventral surface. Labium (Fig. 120) with postmentum undivided, erect bristles covering ligula, palpi three segmented, and no differentiation into a palpiger. Solitary mental seta below third segment.

Pronotum wider than long, slightly rounded anteriorly, with a transverse groove on anterior one-fourth of tergal surface, and head recessed into projection of pronotum as in <u>Hexanchorus</u> and <u>Lara</u>. Very dark band along postero-lateral surface of pronotum intersecting the transverse groove anteriorly. A rather slight carina connects the dark bands. Lateral margins bordered by pedicellate tubercles bearing large spines clothed with many secondary setae (Fig. 115). Posterior margin with a row of pedicellate tubercles, each bearing a pair of two-segmented lateral spines and a terminal, fringed globule or disk (Fig.

111). Illustrated (Fig. 112A) are only four of the foregoing organs or organelles per segment, but 18-20 of them are located on each side lateral to the mid-tergal suture. Mesonotum broader than long, sides parallel, otherwise similar to pronotum. Lateral C-shaped bands on anterior two-thirds of mesonotum and metanotum connected by a slight carina. Metanotum and first eight abdominal tergites similar to mesonotum in ornamentation (Fig. 112B).

Ninth tergite longer than wide, apex strongly emarginate; pentagonal in cross section, with mid-dorsal and ventro-lateral carinae more prominent than mid-lateral carinae (Fig. 122). Posterior projecting pedicellate tubercles bearing small spines covered with setae along ventro-lateral and mid-dorsal lines, decreasing in size posteriorly. The mid-dorsal tubercles have an obconic appearance from dorsal view. Other ornamentation similar to that of previous tergites.

Sterna of thoracic segments sclerotized (Fig. 114). Prosternum present, poststernum absent or membranous; coxal cavities open posteriorly. Three pleura on prothorax, two on mesothorax and metathorax, and pleura of first six abdominal segments bounded by sterno-pleural and tergo-pleural sutures (Figs. 110, 114). Segments seven and eight form complete sclerotized rings except for mid-tergal suture (Fig. 110), and anterior part of ninth forms complete sclerotized ring. Sterna of first five abdominal segments similar and sixth slightly tapered. Posterior sternal region of ninth forms an operculum to which two claws are attached (Fig. 121). Abundant spinous setae are attached to the claws (Fig. 121).

Legs (Figs. 123A, B, C) are similar, slightly differing in length.

Tarsal claw spine longer than tarsal claw.

## Internal Morphology

### Digestive System

This system is not unlike that of *Hexanchorus* and *Lara* (Fig. 124).

### Respiratory System

This system is similar to that of *Hexanchorus* and *Lara*. The air sacs are ovoid in this genus (Fig. 125).

### Excretory System

The morphology of this sytem corresponds to what was observed in *Hexanchorus* and *Lara*.

### Central Nervous System

The gross form of this system resembles that of *Hexanchorus* and *Lara*.

## Histological Morphology

### Integument

Exocuticle averages 14 microns and endocuticle 54 microns in thickness. As in other Larini, the exocuticle is adorned with elaborate sensilla which involve the exo- and endocuticle (Fig. 126). Such sensilla are almost as complex ventrally (Fig. 127) as they are dorsally. Their morphology suggests that they are of at least three types: trichodea, chaetica, and basiconica (Snodgrass, 1935).

### Digestive System

The foregut is unlike that in Hexanchorus in that there are folds of the esophageal wall, an esophageal sclerite (Fig. 128), and cells in the anterior proventriculus are dome-like and triangular in sectional view. In addition, cells in the posterior region are columnar-shaped and bear many sclerotized spines on their apices (Fig. 129). There are no specializations of longitudinal folds as in Lara and apparently Lara bears no columnar cells at the base of the proventriculus.

The mid- and hindguts do not differ from those of Hexanchorus and Lara.

Respiratory System

There is no difference in this system among the Larini considered.

Excretory System

The diameter of the tubules appears to be smaller than in the above genera of Larini and granular concentrations in the cytoplasm prevented determination of cell boundaries. Generally the tubules correspond to the description given by Patton (1953).

Central Nervous System

No significant difference in this system could be determined.

Sense Organs

These organs are primary, many are complex externally, but they are histologically alike in all genera of Larini treated thus far.

Fat Bodies

They are very sparse and are located near lateral and ventral margins of the sclerites internally. Here they form thin meshes.

Gut Contents

Serial sections revealed in the gut lumen diatoms (*Cocconeis*), filamentous algae, hydrophyte fragments, wood fibers, and debris.

## *Phanocerus* (Sharp, 1882)

This genus is widespread in the neotropical region (Bertrand, 1955). One of the species (*Phanocerus clavicornis* Sharp, 1882) is found from Central America and Mexico northward to Val Verde County, Texas (known in the United States only from Devil's River and San Felipe Creek in Del Rio, Texas).

Hinton (1940) presented a generic description of the larval form and described the larva of *P. clavicornis*. His description is given below.

Head when viewed dorsally exposed and not concealed from above by pronotum. One ocellus on each side, antennae three-segmented, clypeus fused with frons, maxillae with four-segmented palpi, and stipes showing no differentiation into a palpifer.

Prothoracic pleura divided into two parts with anterior parts meeting on mid-line. Meso- and metathoracic pleura divided into two parts. First eight abdominal segments with pleura bounded by tergo- and sterno-pleural sutures.

Spiracles annular and biforous, present on mesothorax and first eight abdominal segments, opening at cuticle level or on apices of small tubercles.

I have studied external and internal morphological feature of five larvae of *Phanocerus clavicornis* collected near Izucar de Matamoros, Puebla, Mexico and Bocono, Trujillo, Venezuela on October 25, 1964 and June 4, 1968 respectively. The specimens averaged 4.1 mm in length and 1.5 mm in width. Two specimens were used for histological study.

Phanocerus clavicornis

## External Morphology

The generic description given below is the same as that described by Hinton (1940) with some minor modifications.

Body: flattened, subparallel, and slightly tapering posteriorly. Cuticle yellow-brown, and rather translucent, bearing punctures on head, pronotum, posterior two-thirds of mesonotum and metanotum, and first eight abdominal tergites. Arising from (Fig. 145) each puncture (average diameter 10 microns) is a stiff spinous seta (average diameter 3 microns). Anterior one-third of mesonotum and metanotum and first eight abdominal tergites bear flat, posteriorly projecting tubercles from which arise flat, oval setae. Anterior to the above are several rows of scales with serrated posterior margins. Cuticle ventrally, same color as dorsum, punctures few generally, but many on lateral pleural expansions. Multi-spinous bristles adorn the margins of the coxal cavities (Fig. 134).

Head: subcircular in outline, longer than wide, with epicranial and frontal sutures as figured (Fig. 133). Punctures end anteriorly on frons at base of a transverse line of long setae. Each eye composed of five or six ocelli in a fused mass. Antennae with three segments: first segment short and robust, second slender and longer than first or third, and third consisting of a slender, setiform shaft subequal in length to

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Head: subcircular in outline, longer than wide, with epicranial and frontal sutures as figured (Fig. 133). Punctures end anteriorly on frons at base of a transverse line of long setae. Each eye composed of five or six ocelli in a fused mass. Antennae with three segments: first segment short and robust, second slender and longer than first or third, and third consisting of a slender, setiform shaft subequal in length to the basal segment and bearing a terminal spine (Fig. 133); also arising from the apex of the second segment is a small spine medial to the apical segment. Clypeus truncated and slightly rugose at anterior margin. Labrum with anterior margin slightly emarginate and angles broadly rounded; anterior one-third bears a transverse row of multibranched setae. Interspersed among the setae, on both sides of emargination and along rounded border are thick bristles averaging 46 microns in length. Mandibles (Fig. 141) of both sides similar, bearing three apical teeth, a long prostheca, and a short tuft of sensory setae anterior to prostheca; outer lateral margin bearing two large, multibranched setae, not without, as Hinton (1940) apparently thought. Maxillae as shown (Fig. 139). Galea and lacinia fused (a line can be seen on a cleared specimen). Labium with two-segmented palpi, ligula round on lateral margins and slightly emarginate anteriorly. In Hinton's diagram, it appears that the ligula might have been lost during dissection.

Thoracic and first eight abdominal tergites broader than long (Figs. 130, 131) with dorsal ornamentation as described above. Laterally expanded pleurites of mesothorax, metathorax, and first eight abdominal segments bear on antero-lateral and postero-lateral surfaces flattened, dome-shaped, membranous tubercles, each bearing a long, stiff seta (Fig. 135). The above are only on postero-lateral margin of expanded prothoracic pleura. Ninth tergite flat with proportions as figured (Fig. 132), dorsal and ventral punctures, and postero-lateral setae arise from short tubercles.

Sterna of thoracic segments and pleura sclerotized (Fig. 136, 137). Pleura of first eight abdominal segments bounded by sutures. Posterior sternal region (Fig. 138) of ninth forms operculum (Fig. 140). Attached to operculum on inner side are two claws which bear a few elongated, spinous setae on inner and outer surfaces.

All legs similar, segments decreasing in width, but increasing in length posteriorly, the metathoracic legs being long and narrow (Fig. 142C).

Spiracles on mesopleurite and first eight abdominal pleura.

## Internal Morphology

### Digestive System

This system is not unlike that in *Lara*, *Hexanchorus*, or *Potamophilops* (Fig. 143).

### Respiratory System

The structure of this system does not differ in comparison with other members of Larini. The air sacs here are more ovate in outline as in *Potamophilops*.

### Excretory System

The number and morphology of the malpighian tubules are similar in all members of this tribe.

### Central Nervous System

As in *Hexanchorus*, *Lara*, and *Potamophilops*, this system consists of supraesophageal, subesophageal, thoracic, and abdominal ganglia in the same numbers, but the three thoracic ganglia are proportionately larger in *Phanocerus* (Fig. 144).

## Histological Morphology

### Integument

Exocuticle and endocuticle average 9 and 29 microns in thickness respectively. Both layers are histologically similar to those of other members of the tribe, differing only in respect to cuticle sculpture. Serial sections revealed setae within the punctures along dorsal surface to have an average length from base of puncture to tip of setae of approximately 28 microns (Fig. 145).

### Digestive System

The buccal cavity is typical for the tribe, but the esophageal wall is thrown up into folds as in *Lara* and *Potamophilops*. The crop is typical, but the proventriculus differs from that of other tribe members. Near the anterior there are large and irregular villi (resulting from modification of longitudinal folds) which bear small secondary lobes (Fig. 146). Covering the above is a cuticular intima. Posteriorly the secondary lobes become larger (Fig. 147). At the base of the folds are columnar cells which bear sclerotized spines on their apices only. Just anterior to where esophageal valves project into the midgut, these spine-adorned cells reach their greatest dimensions (24 microns in length and 14 microns wide). A subrectangular sclerite projects from the dorsal foregut wall into the lumen.

The mid- and hindgut do not differ among members of this tribe.

### Respiratory System

The histological morphology does not differ among members of the tribe.

Excretory System

This system is similar to that found in other members of the tribe.

Central Nervous System

No significant histological difference could be determined between Phanocerus and other members of the tribe.

Sense Organs

Primary organs are present. Cuticular appendages are not as elaborate or as varied as in other members of the tribe, but examination of the serial sections revealed no unique generic features for Phanocerus.

Fat Bodies

The masses exist without any specific design. There are scattered particles packed around the esophagus, very abundant beneath the midgut, and on the lateral walls of the body cavity.

Gut Contents

Serial sections revealed in the gut lumen a large concentration of debris, some sand granules, and a few wood fragments.

Ancyronyx (Erichson, 1847)

Sanderson (1953) gave some diagnostic features of larval forms he considered to belong to this genus. He described the larva as being broad, the posterior angles of first eight abdominal segments conspicuously produced, opercular hooks less curved than those in many elmid genera, and the last abdominal segment broadly emarginate at apex with angles not produced.

Bertrand (1955) considered this genus as being represented by several species in the Oriental and Ethiopian Regions, but by only two species in America: _A. perfectus_ Grouvelle in northern South America and _A. variegatus_ Germar in the United States. To Sanderson's features for the larval form, he added several features. He described the larval as having closed coxal cavities, only one epipleurite on the prothorax, but two on the remaining thoracic segments.

The first antennal segment is short and transverse and the second more or less twice the length of the first. Maxillary palpi consist of four segments.

The head integument exhibits some rather large cuticular scales. Cuticular tubercles are rounded, globular, now and then slightly bicuspid, and those on pleura and sternal surfaces are very reduced. Tubercles on posterior borders of tergites are, on the contrary, large and compact and such tubercles are usually present on the lateral prolongations.

Dorsal and ventral hairs are single and reduced. There are no marginal hairs; hairs on lateral prolongations are the longest, and hairs on posterior borders of tergites are wide and palmate.

Bertrand (1965) postulated that many larvae which were considered to belong to this genus prior to 1963, in fact, did not belong to this genus. He also compared adults of Grouvelle's collection in the Entomological Laboratory of the Paris Museum and noticed differences between the types species (_A. variegata_) and other species of this genus. He concluded that this genus should be reduced to include only one species, the type, and all others previously included in this genus should be placed in another genus, for which he proposed the name Pseudancyronyx.

Ancyronyx variegata, according to Brown (in press), is found in the United States in streams from Maine to Florida, westward to Wisconsin, and in eastern parts of Kansas, Oklahoma, and Texas.

I have studied external and internal morphological features of four larval specimens of Ancyronyx variegata collected from Flint Creek in Delaware County, Oklahoma, July 23, 1963. The specimens averaged 4.5 mm in length and 1.0 mm in width. Two specimens were studied histologically.

Ancyronyx variegata

External Morphology

Body: subparallel, subcylindrical, and tapering posteriorly. Cuticle slightly pubescent, dorsal side medium brown, with many pale spots mixed with brown along anterior one-third of mesonotum, metanotum and lateral surface of first eight abdominal tergites. Distinct pale spot on mid-tergal suture at head-pronotal junction and every segment posteriorly to the rear of 6th abdominal tergite. Each spot is connected by a line along mid-tergal suture. Seventh, eighth, and ninth tergites do not bear a mid-tergal suture. Body tuberculate (Figs. 149, 152, 153, 155) from base of head to posterior margin of eighth abdominal tergite. Ninth tergite slightly darker than other tergites and also tuberculate. Cuticle ventrally, pale yellow, except for operculum which appears slightly darker. Ventral tubercles smaller and fewer than those of dorsum.

Head: colored as tergites, but pale on postero-lateral parietal surface; slightly broader than long, with epicranial and frontal sutures as figured (Fig. 149). Eye likely composed of five fused ocelli. Antennae three-segmented, first segment robust, second cylindrical, third minute and setiform, bearing a small terminal seta. As in some other elmids, the spine arising from the apex of the second segment is situated beside the third segment, lateral to it and subequal to it in size (Fig. 149). Cylpeus truncate anteriorly and with lateral margin slightly emarginate (Fig. 149). Labrum longer than length of antennae, with anterior margin slightly emarginate, angles broadly rounded, and anterior surface covered with spinous setae and tufts of branched setae. Fronto-clypeal suture distinct, emarginate, crenate (bordered by tubercles). Mandible of both sides similar (Fig. 148), with three apical teeth, an elongate, comb-like prostheca, a line of adjacent sensory setae, and outer lateral surface with four multi-branched bristles. Maxillae (Fig. 151) with four-segmented palpi and stipes showing no differentiation into a palpifer. Galea and lacinia separate and apex of each densely spinose. Stipes not fused to postmentum and cardo distinct and suboval. Labium (Fig. 150) subrectangular, with three-segmented palpi, and no differentiation of a premental palpiger (the presence of mental seta below the base of the palp instead of at the base suggests no palpiger). Ligula divided along midline, with anterior medial margin not covered by setae, and setae on prementum as figured (Fig. 150).

Pronotum (Fig. 155) wider than long, sides subparallel, and broader at base than at apex. Cuticle ornamented as frontal region of head. Bordered laterally with emarginate tubercles bearing elongate spinous setae. Mesonotum (Fig. 155) broader than long and similar to pronotum except that lateral tubercles are confined to posterior two-thirds of lateral margin behind spiracular protuberance. Metanotum and tergites of first eight abdominal segments similar in sculpture and proportions to mesonotum, but tubercular prolongations on abdominal sclerites confined to posterior one-third of lateral margin and spiracular protuberances moved backwards to one-half the length of the sclerites. Ninth tergite with proportions as figured (Fig. 154), tubercles small, lateral spines small, postero-lateral margins not drawn out into spines, and apex slightly emarginate.

Sterna of thoracic segments sclerotized with pre- and poststernites on prothorax. One pleurite on prothorax and two on meso- and metathorax (Figs. 157, 158). Pleura of abdominal segments 1-7 (Fig. 159) bounded by sterno-pleural and tergo-pleural sutures; segment 8 and anterior part of 9 form complete sclerotized rings. Sternites of first five abdominal segments are similar, but the 6th and 7th taper posteriorly (Fig. 160).

Sternum (Figs. 161, 162) of ninth segment forms an operculum which bears weakly curved claws on its dorsal surface. Each claw bears long setae on its internal and external margins (Figs. 156, 162).

Legs as figured (Fig. 163). Each segment of each leg increases in length posteriorly.

## Internal Morphology

### Digestive System

The gross morphology of this system does not differ from that in other elmids (Fig. 164).

### Respiratory System

This system differs from all members of the Larini in that no air sacs are present.

Excretory System

This member of the tribe Elmini is not different from any of the Larini in respect to this system. There are six malpighian tubules and their relations with the gut are similar.

Central Nervous System

The morphology of this system (Fig. 165) is similar to that of the other elmids described above, but the three thoracic ganglia are ovoid in *Ancyronyx*, diamond-shaped in *Phanocerus*, and spherical in *Lara*, *Hexanchorus*, and *Potamophilops*.

## Histological Morphology

Integument

Exocuticle and endocuticle average 11 and 28 microns in thickness, respectively. In longitudinal section dorsal tubercles appear as posteriorly-projecting spines. A few bear associated setae (Fig. 167). Ventrally there are only a few long tubercles, but large spines emerge from the cuticular surface and project backwards (Fig. 166).

Digestive System

The buccal cavity has the same basic morphology as that of the genera of Larini studied, but the esophagus has a lumen somewhat constricted by the irregular nature of the cuticular intima, its folds and elevations. The low epithelium which is thrown up into folds, is like that in *Lara*, *Phanocerus*, and *Potamophilops*. The crop is typical, thin-walled, dilated, and lined with an irregular cuticular intima. The proventriculus differs from the conditions in members of Larini in several ways. A ring of distinct sclerites surrounds the anterior of this region (proventricular teeth), just below are elevations bearing dome-shaped serrations (proventricular pads) which also encircle the lumen. Peripheral cells bearing sclerotized spines line the wall of this region and at the base are columnar cells bearing many sclerotized spines on their apices (Fig. 168). The basal cells in Ancyronyx (Fig. 169) are similar to those in Potamophilops, but they differ in that the cells in this genus are closer together, are more abundant, and the crypts are very narrow in contrast to the opposite conditions observed in Potamophilops.

The mid- and hindguts are similar in all elmids considered so far.

Respiratory System

This system does not differ from the conditions found in other elmids.

Excretory System

This system as described by Patton (1953) does not differ among the elmids considered so far.

Central Nervous System

The neural structures are similar to those of other elmids.

Sense Organs

Some of the organs are elaborate externally as in the Larini, but primary sensilla types are alike histologically.

Fat Bodies

They lie along the gut from the head region posteriorly. In head and thoracic areas they are compact, in the abdomen the masses are loose globules enclosed within a limiting membrane. In addition, fat cells line surfaces of organs and walls of cavities.

## Gut Contents

Serial sections revealed in the gut lumen debris, wood fibers (fragments), and hydrophyte body fragments.

## *Austrolimnius* (Carter and Zeck, 1929)

Carter and Zeck erected this genus to contain two species described by King in 1865 (Hinton, 1940). Fifty-two species have been described from Australia (Hinton, 1965) and at least 17 species are known from North and South America. Of these, three species (*A. formosus*, *A. halffteri*, and *A. sulcicollis*) have been collected as far north as Mexico (Hinton, 1971).

I have studied external and internal morphological features of five larval specimens of *Austrolimnius formosus* Sharp, collected June 4, 1968 at Bocono, Trujillo, Venezuela and April 4, 1969 near Saucito, Guerrero, Mexico. The specimens averaged 3.48 mm in length and 0.47 mm in width. Two specimens were studied histologically.

### *Austrolimnius formosus*

### External Morphology

Body: parallel-sided, cylindrical, and tapering at seventh abdominal segment. Dorsal view tectiform. Cuticle light brown, concolorous. Ninth tergite colored like other tergites. Cuticle ventrally like dorsal surface.

Head: (Fig. 172) slightly longer than broad, frontal suture as shown (Fig. 172), and clypeal suture represented by a thin line suggesting fusion of clypeus and frons. Cuticle pubescent; spinous and flabellate bristles (Figs. 172, 182) arise from scattered tubercles over frons, but scales clothe most of this surface. Ocelli single and confined to an ocellar zone. Antennae three-segmented, first segment robust, second slender, and third small, consisting of a short segment bearing a short spine and medial to a much longer slender spine arising from apex of second segment. Clypeus short with anterior margin truncate. Labrum (Fig. 172) with a transverse row of flabellate setae near base, many small hairs along apex, and sides broadly rounded. Mandibles of both sides similar (Fig. 185), with three apical teeth, a long, spinous prostheca, and short, medially-directed sensory hairs. Maxillae (Fig. 175) with four-segmented palpi, galea and lacinia separate, apex of each densely spinose, stipes not fused with postmentum, and cardo as figured (Fig. 176). Labium (Fig. 177) with postmentum undivided and palpi two-segmented. Prementum with a well-defined palpiger. Mentum (Fig. 177) with a long, movable spine postero-lateral to each palpiger. Ligula arcuate, undivided.

Pronotum (Fig. 174) broader than long, subparallel, slightly broader at base than at apex, and with a transverse groove near anterior one-third. Cuticle ornamented as frons. With flabellate bristles along lateral margins (Figs. 173, 174), scattered among dorsal scales, and arising from each member of a row of tubercles along the posterior margin. Mesonotum broader than long, similar to pronotum but without transverse groove; with submedial and sublateral rows of tubercles.

Metanotum and tergites of first eight abdominal segments similar in sculpture to mesonotum, but tapering posteriorly, with tubercles on posterior margins becoming fewer (Fig. 170). Ninth tergite (Fig. 171) subcylindrical with proportions as figured; tubercles parallel subdorsally and sublaterally. Posterior apex sharply tapered, with row of flabellate setae along shallowly emaringate posterior margin (Fig. 171).

Sterna of thoracic segments mostly membranous (Figs. 178, 179). Pleura sclerotized and divided into two pleurites on each thoracic segment (Figs. 178, 179). Pleura of first seven abdominal segments delimited by sutures (Figs. 180, 181). Eighth and ninth abdominal segments without distinct pleura. Sternites of first eight abdominal segments are similar (Figs. 180, 181) and posterior region of ninth forms an operculum (Figs. 183, 184). Attached to operculum on inner side are two feeble claws bearing a few straight setae (Fig. 184). Dorsal posterior margin of operculum bears a row of flabellate bristles (Fig. 186).

Legs (Fig. 187A, B, C) sparsely setose and sculptured as figured.

Spiracle on each lateral surface of mesothorax and first eight abdominal segments.

## Internal Morphology

### Digestive System

This system is not unlike the same system in other elmids studied.

### Respiratory System

This system is similar to that in *Ancyronyx*, but is unlike that found in the Larini in not having air sacs as a part of the tracheal system.

Excretory System

This system is similar to the one found in *Ancyronyx* and the Larini.

Central Nervous System

This system resembles that of *Ancyronyx*.

## Histological Morphology

Integument

Exocuticle and endocuticle average 5 and 18 microns in thickness respectively. Tubercles which bear the flabellate setae are distinct in serial section (Fig. 188). Histological morphology of endocuticle is not different from that in other elmids.

Digestive System

Buccal cavity, esophagus, and crop are similar to those in *Ancyronyx*. The proventriculus differs in that its anterior end contains long sclerotized spines which project posteriorly, almost closing the gut lumen (Fig. 189). At the base of this zone are flat sclerotized plates which do not bear spines (Fig. 190).

The mid- and hindguts do not differ from those observed in other elmids.

Respiratory System

The description given by Snodgrass (1935) can be applied here as in other elmids.

Excretory System

In serial section malpighian tubules were not observable due to a high concentration of fat cells (fat bodies). Presumably they are not histologically different from those in other elmids.

Central Nervous System

Serial sections did not reveal anything unusual in the neural histological morphology.

Sense Organs

These organs are similar to those in all elmids considered.

Fat Bodies

They exist in irregular shapes and sizes and are not enclosed by a limiting membrane. They tend to fill the coelom and prevent clear observation of internal organs (Fig. 191).

Gut Contents

No material other than debris could be identified.

*Elsianus* (Sharp, 1882)

This is a genus of the neotropical region which extends into the nearctic region where it is presently represented in the United States by three species. *Elsianus moestus* (Horn, 1870) is found beneath rocks in Arizona streams, *E. texanus* (Schaeffer, 1911) is found in gravel or under rocks in streams with a high calcium content from Austin, Texas to southeastern New Mexico and southward into Mexico, and *E. shoemakei* Brown 1971 is found in gravel or beneath rocks in San Felipe Creek in Del Rio, Texas and the upper Rio Salado in Coahuila, Mexico (Brown, 1971a).

Hinton, who is presently making a revision of this genus, remarked that *Elsianus* will probably end up second to *Cylloepus* in number of species.

He indicated in 1940 that 18 species had been described and over 20 more were in his collection from South America (Hinton, 1940).

I have studied external and internal morphological features of five larval specimens of E. texanus collected in Del Rio, Texas on July 19, 1968. The specimens averaged 7.1 mm in length and 1.2 mm in width. Two specimens were studied histologically.

Elsianus texanus

## External Morphology

With a few differences and additions this description corresponds to that given for this genus by Hinton (1940).

Body: parallel-sided, hemi-cylindrical, and crescent-shaped in cross-section. Cuticle dark brown on head, one-third of thorax through eighth abdominal tergite, and posterior two-thirds of ninth abdominal tergite. Medium brown on all areas not included above. Cuticle pubescent, with scales on anterior one-third of all segments except pronotum. Complex setae arise from posterior margin of each segment (Fig. 193), among the scales (Fig. 201) and from within punctures (Fig. 200). Scattered among the punctures and scales are a few spinous bristles arising from punctures which are surrounded by a rosette of punctures (Fig. 194). Cuticle ventrally, colored as dorsum.

Head: longer than broad, epicranial and frontal sutures as figured (Fig. 192). Cuticle covered with punctures 7 microns in diameter, except on posterior. Punctures are approximately an equal distance apart and bear flabellate bristles. Punctures are replaced by tubercles on anterior margin of frons. Eye consists of 5-6 ocelli forming a fused mass.

Antennae three-segmented and capable of being retracted (the morphology of the gena-antennal junction is as in Lutrochus); first and second segments subequal in length, third minute and setiform, with a small apical seta, beside third segment is a bristle of equal length. Clypeus with rounded anterior and lateral margins. Distinct frontal tooth on each side between base of antenna and clypeus. Labrum (Fig. 192) with anterior margin rounded and slightly irregular, resulting from the origin of many large bristles along anterior margin; two large bristles arise subdorsally amid a transverse row of flabellate bristles. Mandibles (Fig. 195) of both sides similar, with three apical teeth, an elongated prostheca, and a wide mass of short sensory setae. Maxillae (Fig. 196) with four-segmented palpi and stipes showing no differentiation into a palpifer. Galea and lacinia separate, apex of each densely spinose, stipes and postmentum separate, and cardo subtriangular. Labium (Fig. 196) with postmentum undivided, labial palpi two-segmented, and prementum with a palpiger. One club-shaped seta is adjacent to outer base of each palpiger and four are along anterior of prementum, below the base of ligula (Fig. 196).

Pronotum broader than long, sides parallel, slightly broader at base than at apex, with spinous setae along lateral margin. Mesonotum broader than long. Metanotum and first eight abdominal tergites similar to pronotum and mesonotum in ornamentation. Abdominal tergites 2-6 with a sublateral longitudinal suture on each side. Ninth tergite with rounded basal angles, tapering, and with apex strongly emarginate (Fig. 206).

Prosternum reduced and poststernum (Fig. 197) distinct. Pleurites of prothorax, mesothorax, and metathorax divided into two parts each (Figs. 197, 198, 199). Pleura of first seven abdominal segments bounded by sterno-pleural and tergo-pleural sutures. Eighth and anterior of ninth segments form complete sclerotized rings (Figs. 204, 205). Sternal region of first abdominal segment not like sterna of segments 2-8 (Fig. 202). Posterior sternum of ninth forms an operculum (Fig. 207A, B) which bears distinct claws on its inner surface. Claws with relatively short bristles on antero-lateral and long bristles on internal posterior margins.

Legs all similar (Fig. 208A, B, C) distinctively long and slender in relation to the size of the specimen.

Spiracles, as in other elmids, present on lateral surface of mesothorax and first eight abdominal sclerites, but there is a small area suggestive of a spiracle on lateral surface of metathorax.

## Internal Morphology

### Digestive System

The gross morphology of this system is similar to that in other elmids (Fig. 210).

### Respiratory System

This system is similar in all respects to what has been observed in other Elmini. There are no air sacs, but there is a pair of tracheal tubes which lead to possible rudimentary metathoracic spiracles. (Fig. 199).

### Excretory System

This system is similar in all respects to what has been observed in other elmids.

## Central Nervous System

There are no significant (Fig. 209) morphological differences between this genus and other elmids in respect to this system.

# Histological Morphology

## Integument

Exocuticle 11 microns and endocuticle 25 microns in thickness. Exocuticle dorsally in serial section as illustrated (Fig. 211). Ventrally there is a decrease in the number of punctures and an increase in the number of tubercles (Fig. 212).

## Digestive System

Differences from other elmids are seen in the high, irregular folds of the esophageal wall (Fig. 213) and the villi covered by a loose cuticular intima in the crop (Fig. 214). An esophageal sclerite is present and there are many narrow folds along the foregut wall in the proventricular zone. Arising from the folds anteriorly are many sclerotized spines which line the gut lumen (Fig. 215). Along the wall posterior to the base of this zone the spines are replaced by columnar cells bearing sclerotized multispinous apices (Fig. 216). the above corresponds somewhat to the condition in Ancyronyx, but proventricular pads are not apparent and basal cells are more robust (Fig. 217). Other features of this region are typical for the elmids.

The midgut (Fig. 218) and hindgut morphology corresponds to that of other elmids.

Respiratory System

This system does not differ from the description given by Snodgrass (1935).

Excretory System

As in other elmids, the description is similar to the one given by Patton (1953).

Central Nervous System

This system is generally similar to that in other elmids, differing only in that the ganglia appear in serial section to be divided into cortical and medullary areas.

Sense Organs

No distinct differences in the histological makeup of the sensilla were observed in this genus.

Fat Bodies

The concentration of these bodies is low. They exist as thin masses along the lateral gut wall and contain large fat globules in an irregular chain. Each globule is separated from its neighbor by a thin cytoplasmic strand and all members are contained within a sac-like membrane. The bodies are most abundant around the midgut.

Gut Contents

Serial sections revealed in the gut lumen diatoms (Cocconeis and Navicula), fragments of filamentous algae, many wood fragments, and much debris.

Respiratory System

This system does not differ from the description given by Snodgrass (1935).

Excretory System

As in other elmids, the description is similar to the one given by Patton (1953).

Central Nervous System

This system is generally similar to that in other elmids, differing only in that the ganglia appear in serial section to be divided into cortical and medullary areas.

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Gut Contents

Serial sections revealed in the gut lumen diatoms (Cocconeis and Navicula), fragments of filamentous algae, many wood fragments, and much debris.

Macronychus (Muller, 1806)

This genus is found in the New and Old World. Currently it contains three species: Macronychus quadrituberculatus Muller, in Europe and North Africa, M. glabratus Say, in the United States, and M. simplex Hinton, from the Malayan Peninsula. Macronychus glabratus, according to Brown (in press), is found on submerged wood and debris in streams of the eastern and central states of the United States, from Florida to Maine and eastern Texas and Oklahoma to Wisconsin.

I have studied external and internal morphological features of five larval specimens of Marcronychus glabratus, collected from the Illinois River in Cherokee County, Oklahoma on July 23, 1963. The specimens averaged 6.5 mm in length and 1.4 mm in width. Two specimens were studied histologically.

Marcronychus glabratus

External Morphology

This description is like that given by West (1929) for this genus (which he called Stenelmis, type 4) with some additions and some slight changes.

Body: parallel-sided and hemicylindrical to level of fifth abdominal segment, then tapering posteriorly. Cuticle on dorsal side brownish-testaceous to brown. Mid-tergal suture ends posterior to fifth abdominal tergite. Cuticle tuberculate, pubescent, and with long bristles on lateral and posterior margins of all tergites from pronotum to ninth abdominal segment. The last segment also bears a large number of hairs and small tubercles.

Head: nearly round; broader than long, with epicranial and frontal sutures as figured (Fig. 219). Cuticle brownish, pubescent; most of surface with tubercles bearing short, thick and irregular bristles (Figs. 222, 231) and scattered among the tubercles are long spinous bristles (Fig. 230). Along lateral and posterior margins are scales which are rounded to irregular anteriorly. Each eye apparently composed of 5 ocelli. Antennae three-segmented as figured (Fig. 219). Clypeus subtruncate anteriorly with rounded margins. Labrum slightly emarginate, with broadly rounded margins, and with a basal transverse row of long, branching, membranous bristles. Near antero-lateral margin of frons are multibranched setae (Fig. 221). Mandibles (Fig. 220) of both sides similar with three apical teeth, a long prostheca, short erect sensory bristles, and branching, membranous bristles on outer lateral margin. Maxillae (Fig. 224) with four-segmented palpi, terminal element bearing a distinct pair of sensory papillae, stipes showing no differentiation into a palpifer, and galea and lacinia separate with apex of each densely spinose. Stipes separate from postmentum and cardo (Fig. 223) subtriangular. Labium (Fig. 225) with postmentum undivided, labial palpi three-segmented, and prementum without a well-marked palpiger (based on the criterion of the location of premental seta).

Pronotum (Fig. 228) broader than long, anterior rounded, subparallel, and slightly broader at base than at apex. Slight transverse groove along anterior third; anterior lateral margin very slightly explanate. Cuticle ornamented as on frons. Mesonotum broader than long and similar to pronotum. Metanotum and first eight abdominal tergites similar in structure to mesonotum, but thoracic tergites do not have posteriorly-located setae bearing expansions as lateral margins of abdominal segments.

Ninth abdominal tergite as figured (Fig. 235), highly tuberculate, and with lateral setae (Fig. 237); apex with strong spinous projections and strongly emarginate.

Poststernum absent, coxal cavities open posteriorly, and prosternum fused with prepleurite (Fig. 226). Thoracic segments bearing 3, 2 and 2 sclerotized pleurites respectively (Figs. 226, 227, 232). Pleura of first six abdominal segments bounded by sutures (Figs. 232, 233). Sternites of first six abdominal segments similar in form and sculpture (Fig. 232). Abdominal segments seven, eight, and anterior of ninth form complete sclerotized rings (Figs. 234, 239). Posterior region of ninth forms an operculum as figured (Figs. 236, 238); with apex distinctly triangular; attached to its inner surface are feebly curved spines bearing many bristles.

Legs (Fig. 40A, B, C) are robust, heavily sculptured, and increasing in length posteriorly. Internal tarsal spine extends to tip of tarsal claw.

Spiracles on protuberances on lateral surfaces of metathorax and abdominal segments one through eight.

## Internal Morphology

### Digestive System

This system is similar to what was observed in other elmids (Fig. 241).

### Respiratory System

The main tracheal vessels are lateral ones as in other elmids and this genus is similar to the Larini in having air sacs. They are oblong

(Fig. 242) and extend lengthwise in the body cavity. They are attached to the lateral vessels and visceral vessels by long, thin tracheal vessels.

Excretory System

This genus exhibits six malpighian tubules as in most other elmids considered.

Central Nervous System

The gross morphology does not differ from the conditions in other Elmini.

## Histological Morphology

Integument

Exocuticle and endocuticle 11 and 22 microns in thickness, respectively (Fig. 243). The endocuticle does not differ from that in other elmids.

Digestive System

The buccal cavity is similar to that found in other elmids, but there are six high irregular folds (Fig. 246) of the esophagus as in Elsianus. Along the gut wall to the proventriculus there are six low folds of the epithelial layer and the muscles (Fig. 244). The cuticular layer is highly folded and bears fine spines (Fig. 244). Near the base of the proventriculus, the folds become high and wide and crypts develop between them. The apices of the folds become transformed into or replaced by sclerotized, multi-spinous, columnar organs (Fig. 245). Posteriorly the above cells yield to folds, an esophageal sclerite is present, and esophageal invaginations extend backward toward the midgut (Fig. 247). The morphology here is similar to that observed in Elsianus, but the spines along the lumen are smaller and the basal cells appear slightly different apically.

The basic components of the midgut are present as in all elmids, but the epithelial cells are packed very close together, resulting in a spindle-shaped appearance (Fig. 248). The lumen is very constricted and a peritrophic membrane is not distinct, but it is assumed to be present.

The six folds of the hindgut are generally subtruncate, thus not as round as in other elmids. Other structures are similar to those of other elmids.

## Respiratory System

Neither the histology of the air sacs nor that of the tracheal vessels differs from the conditions found in other elmids.

## Excretory System

The morphology does not differ from the description given by Patton (1953).

## Central Nervous System

Generally this system is similar to the conditions found in other elmids, but medullary and cortical zones are apparent.

## Sense Organs

No fundamental difference could be noted in these organs in comparison with other elmids.

Fat Bodies

All along and around the gut they occur in spherical to oval masses, closely packed against the gut wall. They appear to be enclosed by a limiting membrane.

Gut Contents

Serial sections revealed within the gut lumen diatoms (*Diatoma*) and debris.

## *Neocylloepus* (Brown, 1970)

This genus was formulated to include certain elmid species which previously were placed in the genus *Cylloepus*. Presently there are seven known species, all in the New World: *Neocylloepus petersoni* from Chiapas, Mexico, *N. arringtoni* from Rio Axtla, Mexico, *N. hintoni* from the highlands of Central Mexico, *N. sculptipennis* from western Mexico to Nicaragua, *N. championi* (Sharp) from Panama, *N. sandersoni* from Costa Rica and Panama, and *N. boeseli* from Arizona, Texas and northern Mexico (Brown, 1970a).

I have studied external and internal morphological features of seven larval specimens of *Neocylloepus sandersoni* collected in Canoas, Costa Rica and Pacora, Panama on November 10, 1966 and June 26, 1968 respectively. The specimens averaged 4.8 mm in length and 0.82 mm in width. Two specimens were studied histologically.

*Neocylloepus sandersoni*

### External Morphology

This description corresponds to that given by Brown (1970a) with slight modifications and additions.

Body: parallel-sided, cylindrical, and slightly tapering at seventh abdominal segment. Cuticle dorsally, ferruginous, bearing scales and bicuspid tubercles from which emerge spinous bristles. Mid-tergal suture extends from anterior of pronotum to two-thirds the length of eighth abdominal tergite. Ninth abdominal tergite tuberculate (Fig. 256), similar in color to anterior tergites, robust, tectiform in dorsal view, and bearing mid-dorsal, lateral, and sublateral carinae which are accented by abundant tubercles. Posterior lateral margins of tergites not elongated except by the enlargment of bicuspid tubercles. Cuticle ventrally a pale brown and bearing fewer tubercles.

Head: (Fig. 251) longer than broad and frontal suture as shown; distinct teeth between base of antennae and clypeus. Fronto-clypeal suture covered by anteriorly-projecting tubercles along anterior margin of frons. Eye consists of 5-6 fused ocelli; antennae three-segmented (Fig. 251). Clypeus truncate and with slightly rounded margins. Labrum with strongly rounded lateral margins and anterior margin broadly arcuate to straight; antero-lateral margins adorned with long spines; with a transverse row of small tubercles crossing middle portion (Fig. 251). Mandibles (Fig. 253) on both sides similar, bearing three apical teeth, a long prostheca, a brush or row of sensory setae on the inner margin, and apparently no bristles on outer lateral margin. Maxillae (Fig. 249), with four-segmented palpi and no differentiation into a palpifer. Galea and lacinia separate, densely spinose on apices, and rather elongate in comparison with other elmids studied (Fig. 249). Stipes not fused to postmentum and cardo (Fig. 250) subtriangular. Labium (Fig.

252) with postmentum undivided, two-segmented palpi, and a distinct premental palpiger. Adjacent to the external margin of palpiger is a mental seta and lateral to this is a tooth-like elongation of anterior margin of mentum.

Pronotum wider than long, sides subparallel, slightly wider at base than at apex. Mesonotum and metanotum similar in proportions and ornamentation to pronotum. First eight abdominal tergites (Fig. 255) similar in sculpture and ornamentation to metanotum. Ninth tergite subcylindrical, slightly tapered, and truncate apically (Fig. 256).

Posternum (Fig. 257) suppressed, poststernum present; coxal cavities partly separated by a thin sclerotized rod. Prothoracic, mesothoracic, and metathoracic pleura consist of two parts (Figs. 257, 258, 259). Pleura of first seven abdominal segments bear tergo-pleural and sterno-pleural sutures. Eighth abdominal segment with only the mid-tergal suture (Fig. 260). Anterior part of ninth abdominal segment forms a complete sclerotized ring (Fig. 262). Sternal region of first seven abdominal segments sculptured and ornamented similarly. Posterior sternal region of ninth forms an operculum (Fig. 261), attached to inner surface of which are two weakly-curved claws which bear a protuberance on outer lateral margins and setae on dorsal surface as figured.

Legs (Fig. 254) elongate as in Elsianus and Neoelmis and increasing in length posteriorly. Internal tarsal spine rather small in comparison with other elmids.

Spiracles on protuberances on lateral surfaces of mesothorax and first eight abdominal segments.

## Internal Morphology

### Digestive System

The morphology of this system is not unlike that in other elmids.

### Respiratory System

This system is similar to that of other elmids which lack air sacs.

### Excretory System

Three pairs of malpighian tubules arise at the midgut - hindgut junction as in all elmids considered.

### Central Nervous System

Generally there are no gross differences in this system in comparison with other elmids.

## Histological Morphology

### Integument

Exocuticle and endocuticle average 5.4 and 10 microns in thickness. An outline of the tubercles is illustrated (Fig. 263), but no distinctly different generic features are present.

### Digestive System

The anterior buccal cavity is like that found in other elmids. The esophagus differs from that of Hexanchorus only in that no distinct esophageal folds are apparent. The crop (Fig. 263) is dilated and bears villi, but they are not as elaborate as in Elsianus. Anteriorly the proventriculus contains elongated organelles with serrated posterior margins; posteriorly, there is a row of triangular organelles with sclerotized apices. Just posterior to this region is a circle of dome-shaped cells with serrated margins, followed posteriorly by cylindrical cells (Fig. 264) with irregular apical serrations and distinct nuclei. Posterior to these proventricular cells is an anvil-shaped sclerite (Fig. 265). The structure of the proventriculus in this genus is similar to that in Hexanchorus.

The features of the midgut and hindgut are generally similar to those of all elmids considered except Macronychus.

## Respiratory System

There are no air sacs and the primary tracheal vessels are lateral ones. Histologically they do not differ from those of other elmids.

## Excretory System

This system is similar to that in other elmids studied.

## Central Nervous System

No distinct features distinguish this genus from the other elmids.

## Sense Organs

The serial sections did not reveal any distinct internal difference in the morphology of these organs.

## Fat Bodies

Small capsules and spherical bodies, united in oval masses in serial section, are found along the gut. The bodies are very abundant along the midgut.

## Gut Contents

Serial sections revealed in the gut lumen diatoms (Navicula, Diatoma and Cocconeis), filamentous algae fragments, debris, and wood filaments.

Neoelmis (Musgrave, 1935)

This genus was created to contain a new species of elmid from Puerto, Rico and to it Musgrave added *Elmis apicalis* Sharp, *E. caesa* LeConte, and *E. minima* Darlington (Hinton, 1940). Hinton (1940) also referred to this genus *Elmis simoni* Grouvelle from Venezuela. Hinton is presently revising the genus and describing many new neotropical species. Only *N. caesa* has been collected within the United States. This species is found in gravel and under rocks in riffles of clear streams with a high calcium content in south-central and southwestern Texas and rarely in the Arbuckle Mountain region of south-central Iklahoma (Brown, in press).

I have studied external and internal morphological features of five larval specimens of *Neoelmis* collected in Bocono, Trujillo, Venezuela on June 4, 1968 and Coahuila, Mexico, on August 17, 1970. The specimens averaged 4 mm in length and 0.47 mm in width. Two specimens were studied histologically.

*Neoelmis* sp.

External Morphology

The generic description given here is like that given by Hinton (1940) with some additions and slight modifications.

Body: parallel-sided, cylindrical, and tapering at the ninth abdominal segment. All segments from mesothorax posteriorly to the eighth abdominal are approximately the same length and width. Cuticle on dorsal side, tan in color and bearing very low, bicuspid tubercles from which arise flabellate bristles (Fig. 271). Anterior and posterior margins of prothorax and posterior margins of all segments posteriorly to ninth abdominal tergite bear subrectangular, membranous scales which are emarginate along their apices (Fig. 270). The mid-tergal sutural line passes from anterior margin of prothorax to posterior margin of the sixth abdominal segment. Ninth abdominal segment colored and tuberculate as the anterior tergites. Ventral surface like the dorsum except that tubercles are replaced by scales from which arise flabellate setae.

Head (Fig. 266) slightly longer than wide and epicranial and frontal sutures as figured. Without tooth between base of antenna and clypeus. Cuticle covered by scale-like tubercles centrally, but posteriorly and laterally the tubercles become high. Spinous and flabellate bristles arise from the above tubercles. Ocelli (5 ?) on each side fused into a single mass. Antennae consist of three segments each; following Bertrand's usage (1955), the third segment consists of two components which are identical except for a spine on apex of inner member (Hinton considers the piece bearing the spine as the true segment). Clypeus with anterior margin truncate and slightly rounded lateral margins. Labrum with antero-lateral margin bearing a serrate or crenate appearance resulting from the presence of spine sockets (Fig. 266); with a rounded median marginal protuberance; crossing posterior third of labrum is a transverse row of small flabellate bristles. Mandibles (Fig. 268) of both sides similar, with three apical teeth, and suggestions of a fourth on the middle tooth; with distinct elongate prostheca and sensory bristles on inner surface whereas several small spinous bristles or tufts are on the outer lateral margin. Maxillae with four-segmented palpi and stipes showing no differentiation into a palpifer (Fig. 267); galea and lacinia separate, apices densely spinose, stipes separate from postmentum, and cardo suboval. Labium (Fig. 267) with two-segmented palpi and a distinct palpiger. Ligula bearing only minute ornamentation. Mentum bearing a large club-shaped palp on each antero-lateral margin.

Pronotum wider than long, sides subparallel, slightly wider at base than at apex. Mesonotum broader than long and similar to pronotum except that rectangular bristles are only on posterior margin of tergite. Metanotum and tergites of first eight abdominal segments similar in ornamentation (Fig. 269) and general proportions to mesonotum. Ninth abdominal segment subconical, not emarginate at apex.

Prosternum suppressed in mid-ventral line, poststernum distinct, and coxal cavities closed (Fig. 273). Pleura of prothorax, mesothorax, and metathorax consisting of two parts each. Pleura of first seven abdominal segments (Figs. 273, 274) bounded by sterno-pleural and tergo-pleural sutures. Segment eight and anterior of ninth form complete sclerotized rings. Posterior sternal region of ninth (Fig. 275) forms an operculum which bears weakly curved claws (Fig. 276).

Legs (Fig. 272) rather slender, with segments increasing in length and decreasing in width posteriorly; covered with few spines; apparently no internal tarsal claw spines are present.

Tracheal spiracles on lateral surface of mesothorax and first eight abdominal segments.

## Internal Morphology

### Digestive System

This system is similar to that in other elmids.

Respiratory System

The primary vessels, apparently, are lateral ones which communicate with transverse vessels and subdivide as in other elmids not containing air sacs.

Excretory System

With only four malpighian tubules, two less than the number found in other elmids.

Central Nervous System

The morphology of this system is similar to that of other elmids.

## Histological Morphology

Exocuticle and endocuticle average 4 and 18 microns in thickness, respectively. the bicuspid tuberculate nature of the exocuticle is very obvious in serial section.

Digestive System

The buccal cavity, esophagus, crop, and anterior of proventriculus are like those in Neocylloepus in that there are present: columnar organelles bearing sclerotized serrated apices; proventricular teeth (triangular organelles which surround the anterior of the proventriculus); dome-shaped, sclerotized folds (proventricular pads) bearing serrations; and, posteriorly, subcolumnar cells which are serrated and sclerotized (Fig. 277). This genus differs in that the basal cells appear to bear a neck beneath the sclerotized apex.

The midgut and hindgut do not differ from these regions in other elmids.

Respiratory System

Histologically these vessels fit the description given by Snodgrass (1935).

Excretory System

The nature of the tubules fits the description given by Patton (1953).

Central Nervous System

This system is similar to that observed in other elmids.

Sense Organs

Only primary organs are present and they do not differ from those in other elmids.

Fat Bodies

They exist as clump-like masses which appear to have no specific order within the body wall. As in other elmids they are most abundant around the midgut.

Gut Contents

Serial sections revealed in the gut lumen wood fibers, debris, and diatoms (*Cocconeis*).

*Optioservus* (Sanderson, 1954)

This genus was created by Sanderson to include numberous species formerly included within the genus *Heterlimnius* (Bertrand, 1955). In the United States there are 13 species which have been collected from the south, northeast to Canada, central midwest, southwest, and northwest to British Columbia. This genus and *Microcylloepus* have the widest distribution within the United States, but no members of Optioservus have yet been collected from Mexico (Sanderson, 1954).

I have studied external and internal morphological features of five larval specimens of Optioservus ovalis (?), collected from Grover Creek near West Union, Iowa on July 8, 1968 and near Berlin, Pennsylvania on July 7, 1970. Specimens averaged 4.74 mm in length and 0.42 mm in width. Two specimens were studied histologically.

Optioservus ovalis (?)

## External Morphology

This generic description of larval morphology is similar to that given by Sanderson (1954) with slight modifications and some additions.

Body: subparallel-sided, cylindrical, and tapering at level of fifth abdominal segment. Cuticle pubescent, dorsum brownish and tuberculate. With scales at posterior of head and anterior of all tergites except pronotum. Mid-tergal suture extends from anterior margin of pronotum to posterior of sixth abdominal segment and is accented by a slight submedian carina on each side. Cuticle ventrally brownish and ornamented as dorsum, but tubercles are fewer.

Head: slightly longer than broad, with epicranial and frontal sutures as figured (Fig. 278). Cuticle pubescent, with scales on posterior of head and tubercles centrally which bear flabellate bristles are dispersed around each of the ocellar zones. Antennae as figured (Fig. 278). First segment slightly wider than long; second about four times longer than wide; third slender and setiform with a small bristle; spine alongside third segment equal in length to segment. Antero-lateral margins of frons bear blunt tooth-like tubercles which bear flabellate bristles. Clypeus truncate anteriorly with angles on each side rounded. Labrum (Fig. 278) with margin arcuate and densely setose; angles rounded; with a transverse row of irregular, flabellate bristles which extend beyond the anterior margin. Labium (Fig. 279) with postmentum undivided, palpi two-segmented, mental setae at lateral base of a distinct palpiger, and a short ligula which is rounded anteriorly. Maxillae (Fig. 280) with four-segmented palpi, no differentiated palpifer, galea and lacinia separate with apices densely spinose, stipes separate from postmentum, and cardo suboval in outline. Mandible (Fig. 281) with three apical teeth, a prostheca, oral setae anterior to prostheca, and three slender setal tufts on outer lateral margin.

Pronotum wider than long, wider at base than at apex, and bears a W-shaped furrow (Fig. 282). Margin explanate and bears large tubercles. Mesonotum broader than long; margin explanate; cuticle ornamented as pronotum. Metanotum and first eight abdominal segments ornamented as pronotum, margins explanate only on posterior third of each abdominal segment. Ninth tergite tectiform, with median and lateral carinae accented with tubercles, and posterior margin emarginate (Fig. 283).

Prosternum fused with propleurite and postpleurite divided into two parts (Fig. 284). Poststernum absent or membranous. Mesothoracic and metathoracic pleura consist of one part each. Abdominal pleura of first seven segments delimited by sterno-pleural and tergo-pleural sutures. Eighth and anterior of ninth abdominal segments form complete sclerotized rings. Sternal region of ninth forms an operculum (Fig. 286). Attached to operculum on inner surface are two strongly curved claws which bear slender setae.

Legs (Fig. 287) all similar, segments increasing in length posteriorly and decreasing in width. Each tarsal claw bears a distinct internal spine.

## Internal Morphology

### Digestive System

The morphology of this region is not unlike that of other elmids (Fig. 288).

### Respiratory System

The primary vessels are the lateral ones, but they are supplemented with air sacs (Fig. 289), as present in the Larini.

### Excretory System

There appear to be four malpighian tubules as in *Neoelmis*.

### Central Nervous System

The morphology of this system does not differ from that of other elmids.

## Histological Morphology

### Integument

Exocuticle and endocuticle average 18 and 54 microns in thickness. In serial section the tubercles (Fig. 290) are distinct, but generally the histology is not unlike that of other elmids.

### Digestive System

The buccal cavity and esophagus are generally similar to those in other elmids. There are folds in the esophagus; the esophagus leads into a dilated crop, which continues into the proventriculus. Folds in the wall of the proventriculus terminate in apices which are sclerotized and serrated, are followed by proventricular teeth, pads (Fig. 291), and columnar cells with multi-spinous margins. Many of the cells, near the base of the proventriculus, are drawn-out as illustrated (Fig. 292). The above morphology is similar to the conditions found in Neocylloepus and Neoelmis. At the posterior of the foregut are an anvil-shaped sclerite and esophageal invaginations which project toward the midgut.

The midgut and hindgut zones are not different from those in other elmids, but the midgut is constricted due to the presence of air sacs.

## Respiratory System

Histologically the tracheal vessels and air sacs are in accord with the description given by Snodgrass (1935).

## Excretory System

The malpighian tubules are not unlike those of other elmid larvae studied.

## Central Nervous System

No distinct histological feature is present.

## Sense Organs

No organs are revealed other than the primary ones.

Fat Bodies

Along the surface of the foregut the fat bodies are thin and cord-like, but the masses become enlarged around the midgut. These masses appear to be enclosed within a membrane.

Gut Contents

Serial sections revealed in the gut lumen diatoms (*Opephora*, *Cocconeis*, *Nitzschia*, *Navicula*, and *Diatoma*), debris, and algal fragments.

## *Oulimnius* (Des Gozis, 1886)

Berthélemy (1965) considered *Oulimnius* Gozis the same as *Limnius* Erichson and *Oulimnius rivularis* Rosenhauer 1856 the same as *Limnius variabilis* Ganglbauer 1904. In his treatment of the genus he considered critical generic characters of the antennae, operculum, and integumental ornamentation.

Bertrand (1955), considering Erichson's *Limnius*, noted that this genus is best represented in the Old World, with only one or two species in the New World. Bertrand (1955) and Brown (in press) recognize one species in the United States. According to Brown (in press), *Oulimnius latiusculus* may be collected in gravel or under rocks in riffles of clear streams from Alabama, eastern Tennessee, and South Carolina, north-east to Canada, ranging from cool lowland streams to elevations higher than any of the other local elmids.

I have studied external and internal morphological features of three larval specimens of *Oulimnius latiusculus* collected in Watauga County, North Carolina, 1966. The specimens averaged 2.4 mm in length and 0.5 mm in width. Two specimens were studied histologically.

Oulimnius latiusculus

## External Morphology

Under the genus name Limnius, Bertrand (1955) gave several larval features of Oulimnius. I have attempted to expand his work with additions and some modifications.

Body: parallel, cylindrical, and tapering at fifth abdominal segment. Cuticle dorsally light brown to reddish-brown with numerous sub-bicuspid tubercles arranged along tergal surface in submedian, sublateral, and lateral incomplete lines from pronotum to eighth abdominal tergite. Similar tubercles are also located along the posterior margin of each tergite posteriorly to the same level. Mid-tergal suture extends from anterior margin of pronotum to posterior of sixth abdominal segment. Seventh to ninth abdominal tergites tectiform. Ninth tergite brownish and tuberculate. Cuticle ventrally light brown to pale, tubercles small and few.

Head: slightly longer than broad, epicranial and frontal sutures as figured (Fig. 293). Scale-like tubercles, from which arise flabellate setae over central, posterior, and dorso-lateral surfaces. Anterior of frons bears scattered flabellate setae. Eyes composed of 5 (?) fused ocelli on each side. Antennae three-segmented; basal segment broader than long; second segment about four times as long as wide; third segment small and setiform with a terminal bristle; spine alongside third segment about three times longer than segment (Fig. 293). Clypeus with straight anterior margin, rounded lateral margins. Labrum with anterior margin weakly emarginate and broadly rounded lateral margins; with a transverse row of long and short bristles and many short setae bordering anterior margin. Mandibles of both sides similar, with three blunt apical teeth, posteriorly projecting prostheca, and a tuft of sensory setae (Fig. 295A, B). Apparently there are no bristles along outer lateral margins of mandibles. Maxillae (Fig. 294) with three-segmented palpi and stipes showing no differentiation into a palpifer. Galea and lacinia appear separate at anterior and apex of each densely spinose. Stipes not fused to postmentum and cardo as figured (Fig. 294). Labium (Fig. 294) with postmentum undivided, palpi two-segmented, prementum without a distinct palpiger, and mental seta below base of labial palp.

Pronotum rounded, slightly wider than long, slightly broader at base than at apex, slightly explanate laterally. Mesonotum and metanotum similar to pronotum in ornamentation, but subrectangular in shape. First eight abdominal segments (Fig. 297) similar to metanotum in proportions except that lateral expansions and associated tubercles are smaller. Ninth tergite (Fig. 296) tectiform and tapering posteriorly. Submedian tubercles form a double row which merges posteriorly to form a single row. Posterior margin not drawn out into spines, the slightly emarginate appearance being due to the enlargement of terminal tubercles which bear elongate flabellate setae.

Posterior sternum absent, coxal cavities open posteriorly, prosternum and propleurite fused, and postpleurite divided into two unequal components (Fig. 298). Pleura on mesothorax and metathorax each divided into two units and pleura of first seven abdominal segments bounded by tergo-pleural and sterno-pleural sutures (Figs. 298, 299). Eighth and anterior of ninth (Fig. 300) form complete sclerotized rings. Sternal region of first eight abdominal sclerites sculptured similarly.

Posterior sternal region of ninth forms an operculum which bears strongly curved claws on its inner surface (Fig. 301). Setae on anterior surface of claws are few in comparison with other elmids.

Legs (Fig. 302) bearing many spines and bristles. Internal tarsal spine very distinct. Segments of each member increasing in length posteriorly.

Spiracles occur laterally on mesothorax and first eight abdominal segments.

## Internal Morphology

### Digestive System

The components and arrangement of this system are as in other elmids.

### Respiratory System

There are no air sacs and the main vessels are the lateral ones.

### Central Nervous System

This system is not unlike that found in other elmids.

## Histological Morphology

### Integument

Exocuticle and endocuticle averaged 4 and 7 microns in thickness, respectively. Tubercles on dorsum are dome-shaped in cross-section and bear small spinous processes (Fig. 303).

### Digestive System

This system (Fig. 304) is similar to that of *Neocylloepus*, *Neoelmis*, and *Optioservus*.

### Respiratory System

This system does not differ from that of other elmids with no air sacs.

### Excretory System

The description is the same as that given by Patton (1953).

### Central Nervous System

The neural components are like those present in other elmids.

### Sense Organs

The primary sense organs are as those in other elmids.

### Fat Bodies

They consist of follicle-like masses enclosed within a meshwork of connective tissue.

### Gut Contents

Serial sections revealed in the gut lumen diatoms (*Fragilaria*, *Navicula*, and *Cocconeis*), debris, wood filaments and filamentous algal fragments.

## *Promoresia* (Sanderson, 1954)

This genus was created by Sanderson to include some elmids which were previously placed under the genus *Heterlimnius* and earlier in *Limnius* or *Helmis*. Two species are included within this genus: *Promoresia elegans* LeConte and *P. tardella* Fall. *Promoresia elegans* is found in gravel and under rocks in riffles of cool streams from the Great Smoky Mountains northeast to lower New England and *P. tardella* is found in gravel and among moss and rocks of cool streams in the Great Smoky Mountains, in New England, and in eastern Canada (Brown, in press).

I studied external and internal morphological features of three larval specimens of Promoresia tardella collected from the Ellis River, north of Jackson, New Hampshire on July 5, 1966. The specimens averaged 3.5 mm in length and 0.5 mm in width. Two specimens were studied histologically.

Promoresia tardella

## External Morphology

Descriptions of Promoresia larvae have been given by West (1929), as Elmis quadrinotatus Say, Sanderson (1954), and Bertrand (1955). The following description is similar to those given by the above with additions and some slight modifications.

Body: parallel-sided, subcylindrical, and slightly tapering posteriorly. Cuticle dorsally light to medium brown. Head, thorax, and ninth abdominal tergite are darker than other body parts. Mid-tergal suture extends to base of sixth abdominal segment. Cuticle ventrally, similar to tergum, unicolor, but with a darker brown operculum.

Head: slightly broader than long and epicranial and frontal sutures as figured (Fig. 305). Cuticle pubescent with scales bearing flabellate bristles on posterior portion of gena and frons. Anteriorly on frons there are short flabellate bristles and laterally on frons and gena short and long setae arise from dorsal punctures. Ocelli with apparently four units in each group. Antennae three-segmented; basal segment longer than broad; second segment almost four times as long as wide, third segment small and setiform with a terminal bristle; spine alongside third segment slightly shorter than segment. Clypeus with anterior margin feebly truncate, rounded on each side, and fronto-clypeal margin adorned with a transverse row of membranous branching bristles. Labrum slightly emarginate at mid-anterior margin, slightly rounded laterally, and bearing a transverse row of flabellate bristles. Mandibles (Fig. 306) of both sides similar, with three apical teeth, a slender, elongated prostheca, and two or three large membranous spinous bristles on outer lateral margin. Maxillae (Fig. 308) with four-segmented palpi, stipes showing little or no differentiation into a palpifer, galea and lacinia separate, and both are densely spinose at apex. Stipes not fused to postmentum and cardo suboval. Labium (Fig. 307) with three-segmented palpi and a premental palpiger is only suggested. Twin spinous setae arise from anterior margin of prementum medial to palpi; mental setae or palpi at base of suggested palpiger.

Pronotum slightly longer than broad, wider at base than at apex, and with distinct submedian and postero-lateral carinae. Submedian carina is broad along anterior margin, but tapers posteriorly. A distinct U-shaped groove separates the carinae, which are accented by numerous tubercles as on posterior margin of the head. The posterior explanate lateral margins bear bicuspid tubercles from which arise brush-like bristles. Mesonotum broader than long, similar to pronotum except that dorsal and lateral carinae are more pronounced. Depressions which separate dorsal and lateral carinae are also more evident. Metanotum (Fig. 310) similar to mesonotum except that dorsal carinae are slightly lower. First through eighth abdominal tergites sculptured as metanotum except that dorsal carinae increase in length posteriorly to form a flattened ridge. Lateral carinae low, but in proportion to the segments. Lateral carinae on eighth abdominal tergite indistinct and lateral expansion of tergite feeble. Ninth tergite with pronounced mid-dorsal carina accented with spinous bristles, which decrease in height posteriorly. Apex slightly emarginate and adorned with a row of setae. Cuticle tuberculate (Fig. 316) as on anterior segments, but tubercles are arranged as figured.

Prosternum present (fused with prepleurites), poststernum absent, and coxal cavities open posteriorly (Fig. 313). Pleura consist of three divisions on prothorax and one piece on each side of mesothorax (Fig. 314) and metathorax (Fig. 315). Pleura of first seven abdominal segments delimited by sterno-pleural and tergo-pleural sutures (Fig. 315). Eighth and anterior of ninth sclerite form complete sclerotized rings. Sternal region of first eight abdominal segments sculptured similarly; posterior region of ninth forms an operculum which bears weakly curved claws on its inner margin (Fig. 311).

Legs (Fig. 312) all similar, increasing in length posteriorly, and heavily invested with spinous bristles. Tarsal claw spines are present and are approximately one-half the length of the tarsal claw.

Number and location of spiracles as in other elmids.

## Internal Morphology

### Digestive System

This system is not unlike the same system in other elmid larvae.

### Respiratory System

The morphology of this system is typical for those elmids not bearing air sacs.

Excretory System

The morphology is typical for those elmids with six malpighian tubules.

Central Nervous System

The components of this system are similar to those present in other elmids studied.

## Histological Morphology

Integument

Exocuticle and endocuticle 11 and 18 microns in thickness, respectively. Distinct spines which arise from the tubercles are evident from the serial sections (Fig. 318).

Digestive System

The conditions found in the foregut (Fig. 317), midgut, and hindgut (Fig. 318) of this genus are similar to those found in *Neocylloepus*, *Neoelmis*, *Optioservus*, and *Oulimnius*.

Respiratory System

The histology does not differ from the description given by Snodgrass (1935).

Excretory System

The histology does not differ from the description given by Patton (1953).

Central Nervous System

The histology does not differ from that of other elmids.

Sense Organs

The primary organs are similar histologically to those present in other elmids.

Fat Bodies

They are sac-like masses of spherical bodies enclosed by a limiting membrane and lying along the gut wall.

Gut Contents

Serial sections revealed in the gut lumen diatoms (Cocconeis), debris, and massive amounts of filamentous algal fragments.

Tolriolus (Hinton, 1940)

This genus was formed by Hinton to include specimens which he had earlier placed in the genus Limnius in 1934 and the asiatic genus Macronychoides Champion in 1936. A comparative study of the specimens and members of the latter genus revealed that his specimens should not be included within the genus Macronychoides (Hinton, 1940). This work by Hinton was supported by Bertrand (1955) when he compared the larvae of Hinton's specimens with the larvae of Macronychoides.

According to Hinton (1940) Tolriolus has been collected in Mexico from the districts of Temascaltepec, Tejupilco, Real de Arriba, and Rio Verde. Brown has also taken it in the highlands of Guatemala.

I have studied external and internal morphological features of three larval specimens of Tolriolus ungulatus collected near Antonio, Mexico, on October 12, 1966. The specimens averaged 4.00 mm in length and 0.7 mm in width. Two specimens were studied histologically.

Tolriolus ungulatus

## External Morphology

The following description is like that given by Hinton (1940) with slight modifications.

Body: subparallel-sided, cylindrical. and tapering posteriorly. Cuticle ferruginous with tubercles concentrated on prominent lateral and dorsal carinae producing dark brown V-shaped designs on mesothorax, metathorax, and first eight abdominal tergites. Pronotum also bears the V-shaped design or the outline of merging parallel lines. Ninth tergite colored as anterior of body and subdorsal carina accented by cubical tubercles which bear posteriorly-projecting setae. Cuticle ventrally slightly paler than color of dorsum. Operculum darker than sternites. Margins of coxal cavities bordered with tubercles as figured (Fig. 326).

Head: (Fig. 321) slightly longer than broad, fronto-clypeal sutures as figured. Anterior two thirds of frons covered with bicuspid tubercles bearing spinous setae and posterior third bears low scales. Each side of head bears eye composed of fused ocelli. Antennae consist of three segments as figured (Fig. 321). First member broader than long; second segment about four times as long as wide; third segment small and setiform with a terminal bristle; spine alongside third segment same length as segment. Clypeus with straight anterior margin, and with rounded lateral margins. Labrum broad, slightly emarginate anteriorly and strongly rounded laterally. The lateral margins are covered with poly-branched setae and the anterior margin bears thin bristles. Mandibles on each side similar, bearing three apical teeth, a long prostheca, short inner bristles, and one to three brush-like bristles on outer lateral margin. Maxillae (Fig. 319) with four-segmented palpi, stipes showing no differentiation into a palpifer, galea and lacinia separate, and apex of each densely spinose. Stipes not fused with postmentum and cardo subtriangular in outline. Labium (Fig. 322) with three-segmented palpi, prementum with a short palpiger, and postmentum undivided. Small premental seta located at internal base of labial palp and similar large seta located below base of palpiger. Lateral to palpi are four to five spinous bristles and postmental setae as figured (Fig. 322).

Pronotum longer than broad, wider at base than at apex, and lateral margin explanate. Cuticle with signet-shaped tubercles over dorsal surface and bicuspid ones laterally and posteriorly. Dorsal carinae are broad anteriorly and posteriorly, but slightly constricted medially. Accented tubercles give the dorsum a crescent shape at the base of the carina. Below the carina is a distinct protuberance. Mesonotum tuberculate, ornamented as pronotum, lateral expansions confined to posterior two-thirds of lateral margin. Metanotum and first eight abdominal tergites (Fig. 323) sculptured as mesonotum, except that mid-dorsal carinae are more pronounced and lateral expansions are more narrowed and confined to posterior half of lateral margins. Ninth tergite tectiform; dorsal carina distinct; lateral margin slightly explanate; apex notched (Fig. 331B).

Prosternum suppressed or fused with prepleurites and poststernum present, coxal cavities closed, medially separated by a rod-shaped sclerite (Fig. 326). Pleura on prothorax, mesothorax, and metathorax are divided into two plates (Figs. 326, 327, 328). Sterno-pleural and tergo-pleural sutures on first seven abdominal segments, but eighth and anterior of ninth form complete sclerotized rings. Sternal regions of first eight abdominal segments sculptured similarly (Figs. 329, 330). Posterior sternal region of ninth (Fig. 331A) forms an operculum as figured (Fig. 323).

Legs all similar to mesothoracic leg (Fig. 325). Each segment increases in length posteriorly on each pair of legs.

Spiracles situated on distinct protuberances of lateral surfaces of mesothorax and first eight abdominal segments.

## Internal Morphology

### Digestive System

The outline of this system does not differ from that of other elmids (Fig. 332).

### Respiratory System

The morphology of this system does not differ from other elmids lacking air sacs.

### Excretory System

There are six malpighian tubules which originate and terminate as those in other elmids bearing the same number of tubules.

### Central Nervous System

As in other elmids, there are a pyriform, bilobed brain, a subesophageal ganglion, three thoracic ganglia, and eight abdominal ganglia.

## Histological Morphology

### Integument

Exocuticle and endocuticle are 7.2 and 28.8 microns in thickness. Histologically the endocuticle is similar to that observed in other elmids.

### Digestive System

The conditions found in the foregut, midgut, and hindgut of this genus (Fig. 333) are similar to those found in *Neocylloepus*, *Neoelmis*, *Optioservus*, *Promoresia*, and *Oulimnius*.

### Respiratory System

The histology fits the description given by Snodgrass (1935).

### Excretory System

The histology fits the description given by Patton (1953).

### Central Nervous System

The histology does not differ from the conditions observed in other elmids.

### Sense Organs

The primary sense organs are similar histologically to those found in other elmids.

### Fat Bodies

In serial section they appear as mesh-like masses along the external wall of the gut. Within the masses are fat globules, glycogen, and urate granules.

Gut Contents

Serial sections revealed in the gut lumen diatoms (*Diatoma*, *Navicula*, *Nitzschia*, and *Cocconeis*), debris, and filamentous algal fragments.

### *Zaitzevia* (Champion, 1923)

Insects of this genus, though primarily Asiatic (Sanderson, 1953), are found in various parts of the western United States. Of the presently known species in the United States, *Zaitzevia parvula* and *Zaitzevia thermae*, the former is usually found in gravel or under rocks in fast mountain streams of western states from New Mexico to California, north to South Dakota, Montana, and Bristish Columbia. *Z. thermae* was described from a warm spring in Montana and may be only an ecological variant of *Z. parvula* (Brown, in press).

I have studied external and internal morphological features of three larval specimens of *Zaitzevia parvula* collected near Boulder, Colorado on August 27, 1964 and Piercey, California on July 7, 1969. The specimens averaged 3.1 mm in length and 0.49 mm in width. Two specimens were studied histologically.

*Zaitzevia parvula*

External Morphology

The description given below supplements and slightly changes the work on this larva by Bertrand (1955) and West (1929), who described it as larval type 6.

Body: very elongated, parallel-sided, cylindrical, and suboval in cross-section. Cuticle dorsally, brownish-testaceous to a slightly dark brown. Pale parts include labrum, ocellar areas, and circular pale areas on the lateral surfaces of the pronotum. Central areas of head and pronotum are slightly darker than the surrounding areas. Mid-tergal suture extends from anterior margin of pronotum to posterior of seventh abdominal segment. Lateral suture extends from anterior of first to posterior of seventh abdominal segment. Ninth abdominal tergite colored as other abdominal tergites and subtriangular in shape. Cuticle ventrally, colored as posterior of dorsum, except for sternum of ninth sclerite which is dark brown.

Head: slightly longer than broad, epicranial and frontal sutures as figured (Fig. 334). Cuticle sparsely pubescent with long, scattered hairs; with scale-like tubercles posteriorly and punctures anteriorly and medially. Arising from the punctures are spinous and flabellate bristles. Anterior margin of frons bordered with bicuspid tubercles from which arise spinous bristles. Margin between base of antennae and clypeus toothed and bearing subflabellate bristles. Eyes apparently composed of 5 fused ocelli on each side. Antennae (Fig. 334) three-segmented and appear to be capable of being retracted. Basal segment longer than broad, second segment slightly more than three times as long as wide, third segment small and setiform with a terminal bristle, and spine alongside third segment about three times as long as segment. Clypeus with straight anterior margin and rounded lateral margins. Labrum feebly emarginate along anterior margin and angle on each side broadly rounded. A transverse row of flabellate setae adorns the anterior half of the labrum and along the apex are fine setae. Mandibles (Fig. 348) on each side similar with three apical teeth (not two), oral sensory bristles, a prostheca; thin bristles are along outer lateral margin. Maxillae (Fig. 338) with four-segmented palpi and stipes showing no differentiation into a palpifer. Galea and lacinia short and spinose, but spines are slightly larger on lacinia. Stipes not fused with postmentum and cardo as figured. Labium (Fig. 337) with postmentum undivided, labial palpi three-segmented, premental palpi or setae on antero-lateral margin of prementum and ligula covered with fine hair. Postmental palps or setae in sockets on antero-lateral margin of postmentum.

Pronotum (Fig. 335) broader than long, anterior margin with small, irregular bicuspid tubercles bearing spinous bristles, posterior margin with large bicuspid tubercles; discoidal scales which lie along the lateral and dorsal surfaces bear flabellate bristles. In between the tubercles and scales are many small punctures. Mesonotum broader than long, ornamentation similar to pronotum, except that bicuspid tubercles are more abundant and around their margins are many scale-like tubercles. Metanotum and first eight abdominal tergites similar in sculpture and proportions to mesonotum. Ninth tergite with proportions as figured (Fig. 339), expanded anterior two-thirds tapering posteriorly. Sculpture differs from other sclerites in that mid-dorsal tubercles form two rows which merge near apex into a single row which forms a slightly accented mid-dorsal carina. Apex of emarginate tergite with enlarged marginal apical tubercles forming lateral spines, from which arise brush-like bristles (Fig. 347).

Prosternum fused in mid-ventral line or divided by a mid-ventral suture; poststernum absent; coxal cavities open medially and posteriorly. Prothoracic pleura (Fig. 341) divided into three parts, not two as stated by Bertrand (1955), and pleura of mesothorax (Fig. 342) and metathorax

(Fig. 343) consists of two parts each. Pleura of first seven abdominal segments (Figs. 344, 346) bounded by tergo-pleural and sterno-pleural sutures. Posterior sternal region of ninth (Fig. 349) forms an operculum (Figs. 336, 345) which bears strongly curved setae-bearing claws. Segment eight and anterior of ninth form complete sclerotized rings.

Legs (Fig. 340) spinose and setose. The tibiotarsal segment of each member increases slightly in length posteriorly and the proximal segments remain approximately the same length.

Spiracles on lateral surfaces of mesothorax and first eight abdominal segments. Lateral and dorsal gill filaments are present as in all other elmids.

## Internal Morphology

### Digestive System

This system in gross outline is not unlike that found in other elmids.

### Respiratory System

The basic vessels are similar to those in other elmids not bearing air sacs (Fig. 349).

### Excretory System

There appear to be four malpighian tubules as in *Neoelmis* and *Optioservus*. Their positions are as in other elmid larvae.

### Central Nervous System

This system is not unlike that found in other elmids studied (Fig. 350), with the exception that the thoracic ganglia are not much larger than abdominal ganglia.

## Histological Morphology

### Integument

Exocuticle and endocuticle 11 and 14 microns in thickness, respectively. The endocuticle is not histologically different from that in other elmid larvae.

### Digestive System

The features of the foregut (Fig. 351), midgut, and hindgut are similar to those present in *Neocylloepus*, *Neoelmis*, *Optioservus*, *Promoresia*, *Oulimnius*, and *Tolriolus*, except that the chitinized intima within the hindgut is very thick in comparison with the same area in other elmid larvae.

### Respiratory System

This system is not unlike that found in other elmid larvae studied.

### Excretory System

As in other elmid larvae studied.

### Central Nervous System

Histologically, this system is similar in all elmid larvae studied.

### Sense Organs

Primary organs are present and under the conditions of this investigation they do not differ from such organs in other elmid larvae studied.

### Fat Bodies

These bodies consist of thin mesh-like masses of cytoplasm which surround fat globules and urate granules.

## Gut Contents

Serial sections revealed in the gum lumen diatoms (*Navicula* and *Cocconeis*), debris, and filamentous algal fragments.

## *Xenelmis* (Hinton, 1936)

This genus includes species of small water beetles found from Central Mexico through much of South America. The larva was not described until 1971 (Brown, 1971b).

I have studied external and internal morphological feature of five larval specimens of *Xenelmis bufo*, collected in Tierra Colorada, Guerrero, Mexico on March 3, 1969. The specimens averaged 2.34 mm in length and 0.74 mm in width. Two specimens were studied histologically.

### *Xenelmis bufo*

#### External Morphology

This description is similar to that given by Brown (1971b) with slight modifications.

Body: robust, cylindrical, and tapering from fifth abdominal segment posteriorly. Cuticle dorsally brownish-testaceous to brown with well-defined pale zones on head, subdorsal and lateral surfaces of pronotum and first abdominal tergite. Contrasting dark areas are on pronotum. Mid-dorsal tergal line runs from anterior margin of pronotum to posterior of fourth abdominal tergite and sublateral suture extends from second to fifth abdominal sclerite. Anterior half of ninth abdominal tergite pale, but posteriorly it is brownish. Cuticle ventrally, light brown and unicolor. Operculum pale anteriorly and brownish posteriorly.

Head: nearly round, partly withdrawn beneath pronotum, and with accented epicranial and frontal sutures as figured (Fig. 352). Cuticle slightly pubescent with short, fine hairs over central area which arise from apices of scale-like tubercles. Each eye appears to consist of irregular pigmented masses (probably about 5 fused ocelli). Antennae three segmented: first segment short and robust; second about four times as long as wide; third segment small, setiform, and bears a terminal bristle; spine next to third segment over twice as long as segment. Clypeus short with anterior margin straight and rounded lateral margins. Labrum (Fig. 352) feebly emarginate anteriorly and with lateral margins strongly rounded; a transverse row of spinous bristles project from dorsal surface and dense shorter bristles project from the anterior margin. Mandibles (Fig. 353) on both sides similar, bearing three rounded to blunt apical teeth; an elongate prostheca and short sensory bristles emerge from inner surface. Apparently no outer lateral bristles are present. A slightly ridged zone is located posterior to the prostheca which suggests the existence of a molar surface (Fig. 353A). Maxillae (Fig. 354) with four-segmented palpi and no differentiation of a palpifer. Galea and lacinia separate and densely spinose, but spines on lacinia larger than those on galea. Stipes not fused to postmentum and cardo oval and separate. Labium (Fig. 354) with postmentum undivided; ligula short, slightly emarginate, and bears short bristles over outer surface. Prementum as long as labial palp and bears thin scale-like tubercles. Each palp consists of three segments and differentiation of a palpiger is suggested. Such appears to be likely since the mental seta is not at the base of the first segment of the palp. In other genera where a palpiger is obvious I have observed mental setae at the base (internal or outer) of the palpigers. Setal arrangement on postmentum as figured.

Pronotum (Fig. 355) suboval, wider than long, and bears bicuspid tubercles from which arise flat, spine-shaped bristles (Figs. 362, 363). Mid-anterior and postero-lateral margins emarginate and lateral margin broadly rounded. A very slight lateral extension of pronotal tergum is present at postero-lateral margin. Mesonotum broader than long, sculpture similar to pronotum, but lateral tergal extension more defined, crescent shaped, and densely spinose. Metanotum and first eight abdominal tergites sculptured like mesonotum. Lateral extensions on terga similar in proportion to size of segments. Ninth tergite (Fig. 356) sculptured like anterior tergites with distinct lateral apical spines, and with slight plateau between spines. With a bristle situated on inner base of each apical spine (Fig. 359).

Prosternum with suture in mid-ventral line. Poststernum absent and coxal cavities open posteriorly. On each side there are two prothoracic pleurites (including those which meet mid-ventrally), three on mesothorax and three on metathorax (Fig. 357). Pleura of first six abdominal segments are bounded by tergo-pleural and sterno-pleural sutures (Fig. 360). Seventh and eighth (Fig. 361) abdominal segments bear no sutures and form complete sclerotized rings. Sternal region of first six abdominal segments similar in sculpture and proportions.

Posterior sternal region (Fig. 358) of ninth forms operculum (Fig. 364) which bears strongly curved claws on innner surface, adorned with membranous bristles.

Legs (Fig. 365) heavily ornamented. Each leg increasing in length posteriorly with distinct internal spines on the tarsal claws.

Spiracles on lateral surface of mesothorax and first eight abdominal sclerites. Three tufts of gill filaments extend from opercular opening as in other elmids.

## Internal Morphology

### Digestive System

The morphological outline is not different from that found in other elmids (Fig. 366).

### Respiratory System

The main tracheal vessels are the lateral ones, as in other elmids. There is no evidence of air sacs.

### Excretory System

Six malpighian tubules arise near the junction of midgut and hindgut as in other elmids.

### Central Nervous System

A brain, subesophageal ganglion, three thoracic, and seven abdominal ganglia constitute the primary components (Fig. 367). Abdominal ganglia 5, 6, and 7 are enlarged. Ganglion seven is larger than 5 and 6. Its state results from the fusion of 7 and 8.

# Histological Morphology

## Integument

Exocuticle and endocuticle are 11 microns and 29 microns in thickness, respectively. Distinct emarginate tubercles are well illustrated by the serial section.

## Digestive System

The general morphology is similar to that of *Zaitzevia*, *Neocylloepus*, *Optioservus*, *Promoresia*, *Oulimnius*, and *Tolriolus*. This genus differs in that the proventriculus does not appear to be differentiated or is more advanced due to fusion of the columnar cells in comparison with the above genera. This is seen in the posteriorly located cylindrical cells which bear sclerotized serrated apices in the above genera; in this genus they are smaller and much less differentiated (Fig. 368).

## Respiratory System

This system is not unlike that found in other elmids and there are no air sacs.

## Excretory System

The morphology fits the description given by Patton (1953).

## Central Nervous System

The morphology does not differ from the conditions observed in all elmids studied.

## Sense Organs

As in the other elmids studied, primary sense organs are present and they are similar histologically in serial section, differing only in the complex nature of their external processes.

## Fat Bodies

They lie along the gut wall and form mesh-like masses consisting of many fat globules and urate acid granules.

## Gut Contents

Serial sections revealed in the gut lumen diatoms (*Navicula*, *Diatoma*, *Nitzschia*, *Cocconeis*, *Coscinodiscus*, *Synedra*, *Rhopalodia*, and *Melosira*), filamentous algal fragments, and debris. Many gregarines were observed within the foregut.

### *Microcylloepus* (Hinton, 1935)

According to Bertrand (1955) there are approximately twenty species in this genus and it is represented in the United States by about twelve species. Brown (in press) lists 10 species and subspecies which have been described from the United States; these occur from Mexico east to Florida, west to California, north to Oregon, eastward to Idaho, Missouri and Tennessee, then along the east coast to Maine. Hinton (1940) noted that species have been collected from southern Brazil, the British West Indies (Trinidad, Tobago), Mexico, and Guatemala.

I have studied external and internal morphological features of four larval specimens of *Microcylloepus pusillus* collected from Pennington Creek, Johnston County, Oklahoma on September 21, 1968 and the Agua Fria River in Arizona on July 10, 1969. The larvae averaged 3.3 mm in length and 0.40 mm in width. Two specimens were studied histologically.

Microcylloepus pusillus

External Morphology

Hinton (1940) gave a generic description of the larval form of this genus. I have slightly modified his description and pointed out additional descriptive features.

Body: cylindrical and parallel-sided. Cuticle flavotestaceous with pale spots at the base of each tergite along the mid-tergal sutural line which terminates at posterior of seventh abdominal tergite. In additon, there is a distinct sublateral suture which passes along the first seven abdominal segments and which is covered with small tubercles. There also appears to be sublateral suture on the eighth abdominal segment. Ninth tergite with a dark brown apex. Cuticle ventrally, unicolor, except for margins around coxal cavities.

Head: slightly longer than broad; epicranial and frontal sutures as figured (Fig. 369). Margin of frons bears widely spaced serrated tubercles from which emerge flabellate bristles. Cuticle with rectangular tubercles from which emerge small flabellate bristles over anterior two-thirds of head. Posterior and lateral to ocelli are elongated bristles; along lateral margin are anteriorly-projecting setae, and on posterior third are low scale-like tubercles. Antennae consist of three segments: first short and robust; second almost four times longer than wide; third bearing a thin spine on apex; seta next to third segment slightly longer than segment. Clypeus short, anterior margin straight with angle on each side rounded. Labrum broad at base; anterior margin slightly irregular with flabellate bristles aligned transversely along dorsal surface; lateral apex with spinous setae, and angle on each side broadly rounded. Mandibles (Fig. 371) of both sides similar, with three apical teeth, an elongated prostheca, a number of erect oral setae, and two large multi-branched bristles on outer lateral margin. Maxillae (Fig. 372) with four-segmented palpi and stipes not differentiated into a palpifer. Galea and lacinia separate, apex of each densely spinose, stipes separate from postmentum, and cardo subtriangular. Labium (Fig. 374) with three-segmented palp on each side and prementum not differentiated into a palpiger. At ventro-lateral base of first palp segments are mental setae and at the dorso-lateral margin are multibranched membranous bristles. At base of ligula near internal apex of first palp member are long spinous bristles, along the anterior margin are many short bristles, and postmental setae are as figured.

Pronotum (Fig. 370) broader than long, sides subparallel, and slightly broader at base than at apex. Transverse groove on anterior one-third denotes the point where head is inserted into prothorax. Protuberance on postero-lateral surface extending from subdorsal to sublateral surface. Bicuspid tubercles scattered over dorsal and lateral surfaces of tergum and along the tergal margin are small flabellate bristles. Mesonotum broader than long, cuticle tuberculate as pronotum, but tubercles are more oriented, forming four subdorsal irregular rows which become more irregular from mid-tergal suture laterally. From anterior to posterior these rows diverge slightly. Metanotum and first eight abdominal tergites are similar in sculpture and general proportions to mesonotum except that the orientation of the tubercles becomes less distinct posteriorly. Ninth tergite (Fig. 373) tectiform and tapers posteriorly with a very feeble lateral expansion in basal third of tergite. Apex feebly emarginate, but without pronounced spinous elongations of lateral apex. Tubercles aligned as on other tergites, but differing in that subdorsal rows merge into a single mid-dorsal row near the apex.

Prosternum suppressed, with prepleurites continguous along mid-ventral line, poststernum distinct, and coxal cavities closed, being separated medially by a thin, rod-shaped sclerite. Prothoracic, meso-thoracic, and metathoracic pleura consist of 2, 3, and 3 parts respectively (Figs. 375, 376). Pleura on first seven abdominal segments bounded by sutures (Figs. 377, 378). Eighth segment (Fig. 378) forms a complete sclerotized ring except for sublateral tergal suture. Sternal region of first eight abdominal segments tuberculate as tergites, but tubercles are without a linear pattern and are fewer in number. Posterior sternal region of ninth forms operculum with a truncated apex (Fig. 379). Claws strongly curved toward apex, and bearing many setae.

Legs all similar to prothoracic leg (Fig. 380A). A proportional increase in length of each segment occurs posteriorly.

Spiracles on lateral surface of mesothorax and first eight abdominal segments as in other elmid larvae.

## Internal Morphology

### Digestive System

The outline (Fig. 381) of this system is like that in other elmid larvae.

### Respiratory System

This system is like that found in other elmid larvae without air sacs.

Excretory System

There are six malpighian tubules along the gut of this genus as in all genera considered except Neoelmis, Optioservus, and Zaitzevia.

Central Nervous System

This does not differ from the general plan of other elmid larvae.

## Histological Morphology

Integument

Exocuticle and endocuticle 4 microns and 14 microns in thickness, respectively. The endocuticle is not different histologically from that in other elmid larvae.

Digestive System

The general histology of this larval system is similar to that in Zaitzevia, Neocylloepus, Neoelmis, Optioservus, Promoresia, Oulimnius, and Tolriolus. The proventriculus (Fig. 382) differs from Xenelmis in the same respects as do the above genera.

Respiratory System

The description does not differ from the one given by Snodgrass (1935).

Excretory System

The description does not differ from the one given by Patton (1953).

Central Nervous System

The histological nature of this system is not unlike that of other elmid larvae considered.

## Sense Organs

No unique features of the primary sense organs were revealed in the serial sections.

## Fat Bodies

These bodies occur as mesh-like masses of fat globules. They lie, as in other elmid larvae, from the esophagus posteriorly to the anterior hindgut and they are more concentrated around the midgut.

## Gut Contents

Serial sections revealed in the gut lumen only sand and debris. No identifiable plant material was evident.

## Dubiraphia (Sanderson, 1954)

Dubiraphia larvae have been known for a long time, but their identity has been completely misunderstood. It was under the name of Ancyronyx variegatus that the larva was figured by Boving and Craighead (1931). Later Peterson described it under the genus Simsonia, which, at the time, was appropriate (Bertrand, 1955). Sanderson (1954) showed upon comparison of adult morphology that the Australian genus Simsonia should not include the New World species previously assigned to it. He created the genus Dubiraphia to include most of them. This genus, which presently contains five species, is being revised by Dr. William Hilsenhoff. The genus is represented in eastern, central, and western parts of the United States (Brown, in press).

I have studied external and internal morphological features of three larval specimens of Dubiraphia sp. collected in Sulphur, Oklahoma on November 9, 1968. The specimens averaged 6 mm in length and 0.38 mm in width. Two specimens were studied histologically.

Dubiraphia sp.

## External Morphology

To the larval description given by Sanderson (1954) I am adding additional features.

Body: slender and tapering posteriorly. Cuticle on dorsal side pale unicolor. Ninth tergite colored as other abdominal tergites. Cuticle ventrally colored as dorsum, except that operculum is dark.

Head: (Fig. 383) slightly longer than wide; with scattered punctures, from each of which arises a spinous seta, and along the lateral margins are long spinous and short irregular flabellate bristles (Fig. 391). Eyes composed of fused ocelli. Antennae with first segment broader than long; second segment elongate and tapering; third segment minute and setiform; being much shorter than spine which is lateral to it. Clypeus with anterior margin straight and rounded on lateral margins. Labrum fully arcuate anteriorly, rounded laterally, and with a transverse basal row of tubercles bearing flabellate setae. Mandibles (Fig. 386) of both sides similar, with three apical teeth, a distinct elongated prostheca, thin hair-like setae on outer lateral margins. Maxillae (Fig. 385) with four-segmented palpi and stipes showing no differentiation of a palpifer. Galea and lacinia separate and apex of each densely spinose. Stipes not fused with postmentum and cardo suboval. Labium with two-segmented palpi, a well developed palpiger, and undivided, subcircular postmentum. Ligula with submarginal row of small bristles. Mental setae or palpi (Fig. 392) are at the outer base of the palpiger and mental bristles are as figured (Fig. 387).

Pronotum wider than long, sides rounded; slightly broader at base than at apex. Cuticle pubescent, with many small tubercles, many of which are bicuspid. Lateral margins with flabellate bristles. Mesonotum broader than long and cuticle similar to pronotum.

Metanotum and tergites of first eight abdominal segments similar in sculpture and proportions to mesonotum (Fig. 389). Posterior margins of abdominal tergites bordered with distinct bicuspid tubercles bearing flabellate bristles. Ninth abdominal segment sculptured as other abdominal sclerites, five times as long as wide, tapering posteriorly; apex drawn out into lateral spinous projections and emarginate.

Prosternum (Fig. 394) with prepleurites meeting at mid-ventral line. With median triangular accesory (?) sclerite which may represent displaced prosternum. Poststernum absent or membranous, coxal cavities open posteriorly and separated only by a membranous partition; postpleurite consists of one isolated piece. Pleuron on each side of mesothorax consists of two unequal non-contiguous pieces (Fig. 394). Pleura of metathorax rather like those of mesothorax. Pleura on first eight abdominal segments are delimited by sterno-pleural and tergo-pleural sutures (Fig. 388). Sterna ventrally sculptured like terga, but with fewer tubercles and the punctures are shallow. Posterior sternal region of ninth (Fig. 393) forms an operculum (Fig. 390), which bears on its inner side two strongly curved claws.

Legs (Fig. 384) all similar, increasing in length posteriorly, and tarsal claws and spines are distinct. Tarsal claws are large and strongly curved as figured.

Spiracles occur on lateral surface of mesothorax and first eight abdominal segments. Each abdominal spiracle is located on a distinct protuberance.

## Internal Morphology

### Digestive System

The gut resembles that of other elmids, but is rather narrow.

### Respiratory System

There are no air sacs and the tracheal vessels are like those in other elmids.

### Excretory System

There are six malpighian tubules which originate as in other elmids and terminate free around the hindgut (Fig. 395).

### Central Nervous System

The basic morphology (Fig. 396) is like that of other elmid larvae.

## Histological Morphology

### Integument

Exocuticle and endocuticle are 4 microns and 11 microns in thickness, respectively, the punctures are very distinct in serial section and the endocuticle is not different from that of other genera.

Digestive System

The foregut, midgut, and hindgut of this genus are similar to these areas in *Microcylloepus*, *Tolriolus*, *Optioservus*, *Neoelmis*, *Oulimnius*, *Neocylloepus*, and *Promoresia*. This genus differs from *Xenelmis* in the same manner as the above genera.

Respiratory System

The morphology is not unlike that found in other elmid larvae.

Excretory System

No distinguishing histological feature is present.

Central Nervous System

The morphology is not unlike that found in other elmids.

Sense Organs

No organs other than the primary ones are obvious and histologically they do not differ appreciably from those of other genera except in degree of development of the processes.

Fat Bodies

They are mesh-like masses near the periphery of the body wall and closely associated with the midgut wall. Associated with them are urate and glycogen granules.

Gut Contents

Serial sections revealed in the gut lumen diatoms (*Diatoma* and *Navicula*), wood fragments, debris, and sand.

Heterelmis (Sharp, 1882)

According to Bertrand (1955) three of the 15 New World species of this genus are found within the United States. Larvae have been collected in association with adults in Mexico, Peru, Bolivia, Brazil, French Guiana, and Trinidad (B.W.I.) (Hinton, 1940). The three species mentioned above: H. glabra Horn, which occurs in lowland streams from southern Nevada, through Arizona, much of Mexico, and into the Rio Grande River along the Texas border; H. obesa Sharp occurs in cold, fast, high-elevation streams of Arizona and New Mexico, and H. vulnerata LeConte, in streams of Oklahoma and Texas (Brown, in press).

I have studied external and internal morphological features of twelve larval specimens of Heterelmis vulnerata collected from Clear Boggy and Blue Rivers in Johnston County, Oklahoma on September 21, 1968. The specimens averaged 3.6 mm in length and 0.49 mm in width. Four specimens were studied histologically.

Heterelmis vulnerata

External Morphology

This description is similar to that by Hinton (1940) with slight modifications.

Body: parallel-sided, hemicircular in cross-section, and tapering from seventh to ninth abdominal segments. Cuticle on dorsal side brownish-testaceous to brown. Five distinct rows or carinae accented by heavy setiferous tubercles on each side of distinctly accented mid-tergal suture. These rows or lines pass from anterior of pronotum to posterior of eighth abdominal tergite. Carinae more linear on posterior than on anterior tergites. Setae and carinae reduced on ninth abdominal tergite to four rows laterally and a double mid-dorsal row which becomes fused into a single row at posterior of the tergite. Cuticle ventrally pale yellow and unicolor except around the edges of sterna, coxal cavities, and on surface of operculum.

Head: slightly longer than wide, epicranial and frontal sutures as figured (Fig. 397), anterior two-thirds of cuticle heavily tuberculate with small, scale-like bicuspid tubercles (Fig. 400), and scattered among them are a few spinous setae. On posterior third and along lateral margins are rounded tubercles and spines. Eye on each side small, composed of 5 (?) fused ocelli. Antennae three-segmented; first segment about as broad as long; second segment about half as wide and twice as long as first; third setiform and subequal to spine beside it, bearing a minute apical spine or hair. Clypeus short, with anterior margin straight and angle on each side slightly rounded. Labrum broadly arcuate anteriorly (Fig. 397), and with a transverse row of branching setae. Small frontal teeth are adjacent to basal antennal segment and small flabellate setae are along anterior margin of frons. Mandibles on both sides similar, with three apical teeth, a sensory brush anteriorly, a long spinous prostheca, and a large multibranched bristle on lateral margin (Fig. 399). Maxillae with four-segmented palpi and stipes shows no differentiation into a palpifer; galea and lacinia separate, their apices densely spinose; stipes separate from postmentum, and cardo subtriangular. Lablum with three-segmented palpi and an indistinct labial palpiger. Club-shaped mental palp posterior to basal member of labial palp and anterior to spinous and flabellate bristles as figured (Fig.

398). Ligula hemi-circular and bears short flabellate bristles along anterior margin.

Pronotum (Fig. 401) broader than long, with a slight transverse groove on anterior third, sides subparallel, bearing rectangular marginal tubercles from which arise curved bristles (Fig. 407); slightly broader at base than at apex. Mesonotum, metanotum, and first eight abdominal tergites similar to pronotum except that curved lateral bristles are confined to posterior two-thirds of abdominal sclerites. Ninth tergite strongly tectiform, apically emarginate, tubercles drawn out at apex and bearing spinous setae which give the appearance of a posterior lengthening of the lateral apices.

Prosternum suppressed, prepleurites fused medially; poststernum present; coxal cavities closed and separated by a rod-shaped sclerite (Fig. 402). Sterna of first eight abdominal segments similar in sculpture and proportions. Prothoracic, mesothoracic, and metathoracic pleura divided into 2, 3, and 3 plates respectively (Figs. 402, 403, 404). Pleura on first seven abdominal segments bounded by tergo-pleural and sterno-pleural sutures. Eighth sclerite forms a complete sclerotized ring. Posterior of ninth (Fig. 406) forms an operculum which bears strongly curved claws and setae as figured (Fig. 405).

Legs (Fig. 408) all similar. Each segment increases in length posteriorly, but decreases in width.

Spiracles on protuberances on lateral surfaces of mesothorax and first eight abdominal segments. Suggestion of a spiracle on lateral surface of metathorax was noted.

## Internal Morphology

### Digestive System

The gross morphology is similar to that present in all elmid larvae studied.

### Respiratory System

There are no air sacs and the gross morphology is like that found in all elmids except the Larini, Macronychus, and Optioservus.

### Excretory System

There are six malpighian tubules and their organization does not differ from what was observed in other elmids.

### Central Nervous System

Examination of several specimens revealed a bilobed brain, subesophageal ganglia, three thoracic ganglia, and seven or eight abdominal ganglia (Fig. 412), depending on the degree of fusion of ganglia 7 and 8.

## Histological Morphology

### Integument

Exocuticle and endocuticle 7 microns and 17 microns in thickness, respectively. Tergal setae of carinae enter large canals through exocuticle and endocuticle to underlying sensory cells.

### Digestive System

This system (Figs. 409, 410, 411, 412) is similar to that present in Microcylloepus, Toiriolus, Optioservus, Neoelmis, Oulimnius, Promoresia, Neocylloepus, and Dubiraphia. It differs from that of Xenelmis in the same manner as does that of Dubiraphia.

Respiratory System

The histology of the tracheal vessels of this elmid does not differ from that of others.

Excretory System

This system is like those of the genera considered earlier.

Central Nervous System

Serial sections through the brain and ganglia revealed that there are large cells around the periphery and smaller ones internally, suggesting a medullary and a cortical zone. In addition, there is a distinct neurilemma. both the latter and former have been observed in other genera and represent no unique features.

Sense Organs

Primary sense organs are present as in other elmids and histologically they do not differ greatly from other genera except in the development of external setal processes.

Fat Bodies

Oval and rod-shaped organelles are formed into sac-like crescent-shaped masses around the gut. The mass is most prominent in the region of the midgut.

Gut Contents

Serial sections revealed in the gut lumen only dirt and debris.

<u>Stenelmis</u> (Dufour, 1835)

This genus was formed by Leon Dufour in 1835 to include <u>Elmis canaliculata</u> Gyllenhall, a species described from Europe in 1808. The genus is widely distributed in the Old and New Worlds, and includes over 70 species. In the new World, <u>Stenelmis</u> appears to be confined to North America. It represents the largest genus of North American Elmidae, containing about 28 species (Sanderson, 1953). Brown (in press) lists 27 species within the United States, but indicated that a number of new species await description.

The initial description of pupa and larva of a North American species was given by Matheson in 1914 (Sanderson, 1938). This was followed by a detailed description of the larva by West (1929).

I have studied external and internal morphological features of 20 specimens of <u>Stenelmis</u> sp. collected from Clear Boggy and Blue Rivers in Johnston County, Oklahoma on September 21, 1968. The specimens averaged 5.1 mm in length and 0.52 mm in width. Four specimens were studied histologically.

<u>Stenelmis</u> sp.

<u>External Morphology</u>

This desctiption is similar to that given by West (1929) as his "Type 5" larva, with slight modifications and additions.

Body: subparallel-sided and hemicylindrical. Cuticle on dorsal side brownish-testaceous to brown with numberous small irregularly arranged and poorly defined spots on head and tergites. Scattered among the above are paler areas which are scarce on the head and ninth abdominal tergite.

Cuticle ventrally, pale yellow and unicolor except for operculum which bears dark spots.

Head: slightly longer than broad, epicranial and frontal sutures as figured (Fig. 413). Cuticle sparsely pubescent, tuberculate, and from tubercles arise branching setae (Fig. 417). One eye composed of fused ocelli on each side. Antennae three-segmented and as figured. Clypeus with straight anterior margin and rounded lateral margins. Labrum with irregular anterior margin which bears spinous bristles; rounded lateral margins. Frontal tooth on each side at junction of clypeus and first antennal segment. Just behind fronto-clypeal suture lies a row of thin flabellate bristles. Mandibles (Fig. 414) of both sides similar, with three apical teeth, an elongated prostheca, a row of oral bristles, and at least one branched bristle on outer lateral margin. Maxillae (Fig. 415) with four-segmented palpi and stipes showing no differentiation into a palpifer. Galea and lacinia separate and apex of each densely spinose. Stipes not fused to postmentum and cardo subtriangular. Labium with postmentum undivided, bearing two-segmented palpi, and prementum with a well-marked palpiger. Ligula emarginate and bearing long spines on infero-lateral margin. Mentum bearing tufts of bristles and mental palp at outer base of palpiger.

Pronotum wider than long, wider at base than at apex. Cuticle sculptured as frontal region of head. A slight groove on anterior third which outlines posterior of head; short tubercles along posterior and lateral margins. Mesonotum broader than long and similar to pronotum in ornamentation except that tubercles are slightly fewer in number. Metanotum and first eight abdominal tergites similar in sculpture and general proportions to mesonotum. Ninth abdominal tergite subtectiform; hemicircular in cross-section, slightly tapering, widely emarginate at apex, with lateral apices drawn out into spines (Fig. 418).

Prosternum suppressed, the prepleurites meeting at midline. Poststernum distinct and coxal cavities closed. Prepleurite not separated from postpleurite by distinct suture. Mesopleura and metapleura each divided into two plates (Fig. 416). Abdominal pleura bounded by tergopleural and sterno-pleural sutures on first seven segments. Eighth abdominal segment forms a complete sclerotized ring. Sternal region of first seven abdominal segments similar. Posterior sternal region of ninth forms operculum which is suboval in ventral view. Attached to dorsal surface of operculum are heavy, strongly curved claws; with setae as figured (Fig. 419) on lateral margins of operculum and claws.

Sculpture of all legs similar (Fig. 420). Prothoracic legs robust and with short segments. Posterior legs more slender and segments longer.

Spiracles were observed only on the lateral margins of mesothorax and first eight abdominal segments. No spiracles were observed on metathorax, but based on the observations made while studying Heterelmis and Neocylloepus, I am inclined to agree with Susskind (1936) that tracheal connections do pass toward possible (?) metathoracic spiracles. Hinton (1939) seems to be in error in stating that her figure and description are in error.

## Internal Morphology

### Digestive System

The morphology of this tract is not unlike that present in other elmids

Fig. 421). The hindgut may or may not be folded. The presence of a fold tends to be correlated with the size and age of the larva.

Respiratory System

The main vessels are lateral ones and the morphology does not differ from that of other elmids and the description given by Susskind (1936).

Excretory System

There are six malpighian tubules existing in three groups of two each. As in all elmids considered, they arise at the midgut-hindgut junction. After passing anteriorly along the posterior two-thirds of the midgut they pass posteriorly and may or may not become closely associated with the hindgut.

## Histological Morphology

Integument

Exocuticle and endocuticle are 4 microns and 7 microns in thickness, respectivley. Serial sections revealed low, subtriangular integumental tubercles, the cores of which penetrate into the endocuticle.

Digestive System

This system is similar to that in other elmids such as Heterelmis.

Respiratory System

Histologically this system does not differ from the description given by Snodgrass (1935).

Excretory System

The histology does not differ from the description given by Patton (1953).

Central Nervous System

Serial sections revealed the brain and ganglia to be similar to those present in other elmids.

Sense Organs

The primary organs have the same internal histology as those in other elmids.

Fat Bodies

The bodies are distinctly like those present in *Heterelmis*.

Gut Contents

Serial sections revealed in the gut lumen diatoms (*Diatoma* and *Navicula*), dirt, sand, and debris.

## EXPLANATION OF FIGURES

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Figure 75. *Hexanchorus caraibus*, dorsal view of head.

Figure 76. *Hexanchorus caraibus*, seta from lateral margin.

Figure 77. *Hexanchorus caraibus*, lateral view of head showing ocelli and antenna.

Figure 78. *Hexanchorus caraibus*, ventral view of ninth abdominal segment.

Figure 79. *Hexanchorus caraibus*, dorsal view of abdominal segments 5-8.

Figure 80. *Hexanchorus caraibus*, ventral view of abdominal segments 5-8.

Figure 81. *Hexanchorus caraibus*, ventral view of operculum.

Figure 82. *Hexanchorus caraibus*, dorsal view of operculum showing opercular claws.

Figure 83. *Hexanchorus caraibus*, dorsal view of thorax and abdominal tergites 1-4.

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Figure 85. *Hexanchorus caraibus*, ventral view of left mandible.

Figure 86. *Hexanchorus caraibus*, opercular claw.

Figure 87. *Hexanchorus caraibus*, mesothoracic leg.

Figure 88. *Hexanchorus caraibus*, digestive tract and associated malpighian tubules.

Figure 89. *Hexanchorus caraibus*, central nervous system.

Figure 90. *Hexanchorus caraibus*, air sac.

Figure 91. *Hexanchorus caraibus*, longitudinal section through the

proventriculus. AO-anterior proventricular organ or fold; LO-longitudinal or peripheral organ; Es.V-esophageal invagination; L-lumen.

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Figure 94. Lara avara, right mandible
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B. Dorsal view

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Figure 96. Lara avara, dorsal view of pronotum.

Figure 97. Lara avara, ventral view of ninth abdominal segment.

Figure 98. Lara avara, dorsal view of ninth abdominal segment.

Figure 99. Lara avara, ventral view of operculum with hooks.

Figure 100. Lara avara, ventral view of prothorax and mesothorax.

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A. Prothoracic leg
B. Mesothoracic leg
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Figure 103. Lara avara, digestive tract and associated malpighian tubules.

Figure 104. Lara avara, longitudinal section through dorsal cuticular seta.

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Figure 106. Lara avara, longitudinal section through proventriculus showing the cord-like structures along the wall of this organ.

Figure 107. Lara avara, longitudinal section through the proventriculus illustrating the masses (cells ?) with posteriorly projecting spines. S-spine; C-crop; Es.V-esophageal invagination.

Figure 108. Lara avara, cross section through the hindgut revealing six folds and the thick cuticular intima. CM-circular muscle; Ep.-epithelial; LM-longitudinal muscle; CI-cuticular

intima.

Figure 109. *Potamophilops* sp. dorsal view of head.

Figure 110. *Potamophilops* sp., ventral view of abdominal segments 3-8.

Figure 111. *Potamophilops* sp., stalked organ found at posterior margin of tergites.

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Figure 117. *Potamophilops* sp., tubercle on frons.

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Figure 120. *Potamophilops* sp., ventral view of labium.

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Figure 122. *Potamophilops* sp., lateral view of ninth abdominal segment.

Figure 123. *Potamophilops* sp., legs.
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B. Mesothoracic leg
C. Metathoracic leg

Figure 124. *Potamophilops* sp., digestive tract and associated malpighian tubules.

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Figure 126. *Potamophilops* sp., cross section of a tergal tubercle.

Figure 127. *Potamophilops* sp., cross section of ventral cuticle. Exo-exocuticle; End-endocuticle.

Figure 128. *Potamophilops* sp., cross section of proventriculus illustrating

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Figure 134. *Phanocerus clavicornis*, multispinous seta from margin of coxal cavity.

Figure 135. *Phanocerus clavicornis*, seta from between adjacent pleural expansions.

Figure 136. *Phanocerus clavicornis*, ventral view of thorax and abdominal segments 1-2.

Figure 137. *Phanocerus clavicornis*, ventral view of abdominal segments 3-8.

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Figure 139. *Phanocerus clavicornis*, ventral view of labium and maxillae.

Figure 140. *Phanocerus clavicornis*, dorsal view of operculum.

Figure 141. *Phanocerus clavicornis*, right mandible.

Figure 142. *Phanocerus clavicornis*, legs.
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B. Mesothoracic leg
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Figure 143. *Phanocerus clavicornis*, digestive tract and associated malpighian tubules.

Figure 144. *Phanocerus clavicornis*, central nervous system.

Figure 145. *Phanocerus clavicornis*, cross section through the dorsal cuticle illustrating cuticular spines and punctures.

Figure 146. *Phanocerus clavicornis*, cross section through anterior third

of proventriculus. CM-circular muscle; LM-longitudinal muscle; S-spine; CI-cuticular intima; Ep.-epithelia.

Figure 147. Phanocerus clavicornis, cross section through middle of proventriculus. PF-primary fold; SF-secondary fold.

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Figure 149. Ancyronyx variegata, dorsal view of head.

Figure 150. Ancyronyx variegata, ventral view of labium.

Figure 151. Ancyronyx variegata, ventral view of left maxilla.

Figure 152. Ancyronyx variegata, pronotal tubercle.

Figure 153. Ancyronyx variegata, pronotal tubercle.

Figure 154. Ancyronyx variegata, ninth abdominal tergite.

Figure 155. Ancyronyx variegata, pronotum and mesonotum.

Figure 156. Ancyronyx variegata, ventral view of operculum.

Figure 157. Ancyronyx variegata, ventral view of prothorax.

Figure 158. Ancyronyx variegata, ventral view of mesothorax and metathorax.

Figure 159. Ancyronyx variegata, ventral view of first abdominal segment.

Figure 160. Ancyronyx variegata, ventral view of abdominal segments 6-7.

Figure 161. Ancyronyx variegata, ventral view of ninth abdominal segment.

Figure 162. Ancyronyx variegata, dorsal view of operculum.

Figure 163. Ancyronyx variegata, legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 164. Ancyronyx variegata, digestive tract and associated malpighian tubules.

Figure 165. Ancyronyx variegata, central nervous system.

Figure 166. Ancyronyx variegata, cross section through ventral cuticle.

Figure 167. Ancyronyx variegata, cross section through dorsal cuticle.

End-endocuticle; Exo.-exocuticle; Ap-apodeme.

Figure 168. *Ancyronyx variegata*, longitudinal section of proventriculus. PS-proventricular sclerite (tooth); SP-sclerotized pad; PT-proventricular tooth; CM-circular muscle; LM-longitudinal muscle.

Figure 169. *Ancyronyx variegata*, cross section through base of proventriculus. PT-proventricular tooth, cell or organ; PS-proventricular spine; LM-longitudinal muscle; MM-muscular mass.

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Figure 173. *Austrolimnius formosus*, lateral seta.

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Figure 176. *Austrolimnius formosus*, cardo.

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Figure 178. *Austrolimnius formosus*, ventral view of prothoracic and mesothoracic segments.

Figure 179. *Austrolimnius formosus*, ventral view of metathorax.

Figure 180. *Austrolimnius formosus*, ventral view of first abdominal segment.

Figure 181. *Austrolimnius formosus*, ventral view of abdominal segment 6-7.

Figure 182. *Austrolimnius formosus*, tergal tubercle bearing flabellate seta.

Figure 183. *Austrolimnius formosus*, ventral view of ninth abdominal segment.

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Figure 186. *Austrolimnius formosus*, apex of operculum.

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Figure 190. Austrolimnius formosus, cross section of posterior third of proventriculus.

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Figure 194. Elsianus texanus, tergal spine.

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Figure 197. Elsianus texanus, ventral view of prothorax.

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Figure 199. Elsianus texanus, ventral view of metathorax.

Figure 200. Elsianus texanus, sternal tubercle and seta.

Figure 201. Elsianus texanus, sternal tubercle and seta.

Figure 202. Elsianus texanus, ventral view of first abdominal segment.

Figure 203. Elsianus texanus, ventral view of seventh abdominal segment.

Figure 204. Elsianus texanus, ventral view of eighth abdominal segment.

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Figure 206. Elsianus texanus, ninth abdominal tergite.

Figure 207. Elsianus texanus, operculum.
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B. Ventral view

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B. Mesothoracic leg
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Figure 210 <u>Eisianus texanus</u>, central nervous system.

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Figure 214. <u>Eisianus texanus</u>, cross section through crop. CM-circular muscle; LM-longitudinal muscle; Ep.-epithelium; CI-cuticle intima.

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Figure 217. <u>Eisianus texanus</u>, basal part of proventriculus. CM-circular muscle; SSA-sclerotized serrated apparatus or proventricular organ.

Figure 218. <u>Eisianus texanus</u>, cross section of body through region of midgut. Ep.-epithelium; LM-longitudinal muscle; CM-circular muscle; FB-fat body; DM-dorsal muscle; TV-tracheal vessel; End.-endocuticle; Exo.-exocuticle; PM-peritrophic membrane; VNC-ventral nerve cord.

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Figure 228. _Macronychus glabratus_, prothoracic, mesothoracic, and metathoracic tergites.

Figure 229. _Macronychus glabratus_, seta of the type on lateral and posterior margins of thoracic and first eight abdominal segments.

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Figure 231. _Macronychus glabratus_, seta from dorsum of head.

Figure 232. _Macronychus glabratus_, ventral view of metathoracic and first abdominal segments.

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Figure 237. _Macronychus glabratus_, seta from lateral margin of ninth tergite.

Figure 238. _Macronychus glabratus_, dorsal view of operculum.

Figure 239. _Macronychus glabratus_, ventral view of ninth abdominal segment.

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B. Mesothoracic leg
C. Metathoracic leg

Figure 241. _Macronychus glabratus_, digestive tract.

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Figure 243. Macronychus glabratus, cross section of tergal cuticle. Exo.-exocuticle; End.-endocuticle.

Figure 244. Macronychus glabratus, cross section through the crop. CM-circular muscle; Ep-epithelium; LM-longitudinal muscle; Cl-cuticular intima.

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Figure 247. Macronychus glabratus, cross section through lower region of proventriculus near junction with midgut. S-sclerite; Ep-epithelium.

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Figure 250. Neocylloepus sandersoni, cardo.

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Figure 252. Neocylloepus sandersoni, ventral view of labium.

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Figure 254. Neocylloepus sandersoni, legs.
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B. Mesothoracic leg
C. Metathoracic leg

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Figure 256. Neocylloepus sandersoni, dorsal view of abdominal segment.

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Figure 260. Neocylloepus sandersoni, ventral view of abdominal segments 7-8.

Figure 261. Neocylloepus sandersoni, dorsal view of operculum.

Figure 262. Neocylloepus sandersoni, ventral view of ninth abdominal segment.

Figure 263. Neocylloepus sandersoni, cross section of body through region of crop. DM-dorsal muscle; FB-fat body; Ep.-epithelium; Cl-cuticular intima; VNC-ventral nerve cord; VM-ventral muscle

Figure 264. Neocylloepus sandersoni, basal portion of proventriculus. PO-proventricular organ; LM-longitudinal muscle; CM-circular muscle

Figure 265. Neocylloepus sandersoni, cross section through region of posterior proventriculus. FB-fat body; S-sclerite; PO-proventricular organ (base); CM-circular muscle; TM-transverse muscle; VNC-ventral nerve cord

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B. Mesothoracic leg
C. Metathoracic leg

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Figure 274. Neoelmis sp., ventral view of seventh abdominal segment.

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Figure 279. Optioservus ovalis (?), ventral view of labium.

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Figure 282. <u>Optioservus ovalis</u> (?), dorsal view of pronotum.

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Figure 284. <u>Optioservus ovalis</u> (?), ventral view of prothorax.

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A. Prothoracic leg
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Figure 290. <u>Optioservus ovalis</u> (?), cross section of tergal cuticle.

Figure 291. <u>Optioservus ovalis</u> (?), cross section of anterior third of proventriculus. CM-circular muscle; LM-longitudinal muscle; PP-proventricular pad; CI-cuticular intima

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Figure 308. Promoresia tardella, ventral view of left maxilla.

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Figure 310. Promoresia tardella, dorsal view of metanotum.

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Figure 315. Promoresia tardella, ventral view of metathorax and first abdominal segment.

Figure 316. Promoresia tardella, lateral view of ninth abdominal segment.

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Figure 318. Promoresia tardella, cross section of body through region of hindgut. Exo.-exocuticle; DBV-dorsal blood vessel; End.-endocuticle; FB-fat body; TV-tracheal vessel; VNC-ventral nerve cord; MT-malpighian tubule

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Figure 320. Toirioius unguiatus, right mandible.

Figure 321. *Toiriolus ungulatus*, dorsal view of head.

Figure 322. *Toiriolus ungulatus*, labium.

Figure 323. *Toiriolus ungulatus*, dorsal view of first abdominal segment.

Figure 324. *Toiriolus ungulatus*, dorsal view of operculum.

Figure 325. *Toiriolus ungulatus*, mesothoracic leg.

Figure 326. *Toiriolus ungulatus*, ventral view of prothorax.

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Figure 328. *Toiriolus ungulatus*, ventral view of metathorax.

Figure 329. *Toiriolus ungulatus*, ventral view of first abdominal segment.

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Figure 331. *Toiriolus ungulatus*, ninth abdominal segment.
A. Ventral view
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Figure 332. *Toiriolus ungulatus*, digestive tract and malpighian tubules.

Figure 333. *Toiriolus ungulatus*, longitudinal section of proventriculus. PT-proventricular tooth; PP-proventricular pad; PO-proventricular organ; LM-longitudinal muscle; CM-circular muscle

Figure 334. *Zaitzevia parvula*, dorsal view of head.

Figure 335. *Zaitzevia parvula*, dorsal view of pronotum.

Figure 336. *Zaitzevia parvula*, ventral view of operculum.

Figure 337. *Zaitzevia parvula*, labium.

Figure 338. *Zaitzevia parvula*, left maxilla.

Figure 339. *Zaitzevia parvula*, dorsal view of ninth abdominal segment.

Figure 340. *Zaitzevia parvula*, legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 341. *Zaitzevia parvula*, ventral view of prothorax.

Figure 342. *Zaitzevia parvula*, ventral view of mesothorax.

Figure 343. *Zaitzevia parvula*, ventral view of metathorax.

Figure 344. *Zaitzevia parvula*, ventral view of first abdominal segment.

Figure 345. *Zaitzevia parvula*, dorsal view of operculum.

Figure 346. *Zaitzevia parvula*, ventral view abdominal segments 6-7.

Figure 347. *Zaitzevia parvula*, ventral view of ninth abdominal segment.

Figure 348. *Zaitzevia parvula*, mandible.

Figure 349. *Zaitzevia parvula*, one branch of lateral tracheal vessels.

Figure 350. *Zaitzevia parvula*, central nervous system.

Figure 351. *Zaitzevia parvula*, longitudinal section through proventriculus. PT-proventricular tooth; PP-proventricular pad; PO-proventricular organ

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Figure 353. *Xenelmis bufo*, mandible.
A. Internal view
B. Dorsal view

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Figure 356. *Xenelmis bufo*, dorsal view of abdominal segments 8-9.

Figure 357. *Xenelmis bufo*, ventral view of thoracic and first abdominal segments.

Figure 358. *Xenelmis bufo*, ventral view of ninth abdominal segment.

Figure 359. *Xenelmis bufo*, seta internal to postero-lateral spine.

Figure 360. *Xenelmis bufo*, ventral view of ninth abdominal segment.

Figure 361. *Xenelmis bufo*, ventral view of abdominal segments 6-7.

Figure 362. *Xenelmis bufo*, tergal seta.

Figure 363. *Xenelmis bufo*, tergal seta.

Figure 364. *Xenelmis bufo*, dorsal view of operculum.

Figure 365. *Xenelmis bufo*, legs.

A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 366. Xenelmis bufo, digestive tract and malpighian tubules.

Figure 367. Xenelmis bufo, central nervous system.

Figure 368. Xenelmis bufo, longitudinal section of proventriculus. CM-circular muscle; LM-longitudinal muscle; PT-proventricular tooth; PP-proventricular pad; PO-proventricular organ; FPO-fused proventricular organs

Figure 369. Microcylloepus pusillus, dorsal view of head.

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Figure 371. Microcylloepus pusillus, left mandible.

Figure 372. Microcylloepus pusillus, right maxilla.

Figure 373. Microcylloepus pusillus, dorsal view of ninth abdominal segment.

Figure 374. Microcylloepus pusillus, labium.

Figure 375. Microcylloepus pusillus, ventral view of prothoracic and mesothoracic segments.

Figure 376. Microcylloepus pusillus, ventral view of metathoracic segment.

Figure 377. Microcylloepus pusillus, ventral view of first abdominal segment.

Figure 378. Microcylloepus pusillus, ventral view of abdominal segments 7-8.

Figure 379. Microcylloepus pusillus, dorsal view of operculum.

Figure 380. Microcylloepus pusillus, legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 381. Microcylloepus pusillus, digestive tract and malpighian tubules.

Figure 382. Microcylloepus pusillus, longitudinal section through proventriculus. PT-proventricular tooth; PF-proventricular fold; PO-proventricular organ; PP-proventricular pad;

LM-longitudinal muscle; CM-circular muscle; Es.V-esophageal invagination

Figure 383. Dubiraphis sp., dorsal view of head.

Figure 384. Dubiraphia sp., legs.
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B. Mesothoracic leg
C. Metathoracic leg

Figure 385. Dubiraphia sp., ventral view of right maxilla.

Figure 386. Dubiraphia sp., right mandible.

Figure 387. Dubiraphia sp., labium.

Figure 388. Dubiraphia sp., ventral view of first abdominal segment.

Figure 389. Dubiraphia sp., dorsal view of abdominal segments 4-8.

Figure 390. Dubiraphia sp., dorsal view of operculum.

Figure 391. Dubiraphia sp., thoracic tergal seta.

Figure 392. Dubiraphia sp., thoracic tergal spine.

Figure 393. Dubiraphia sp., ventral view of ninth abdominal segment.

Figure 394. Dubiraphia sp., ventral view of thoracic segments.

Figure 395. Dubiraphia sp., digestive tract and malpighian tubules.

Figure 396. Dubiraphia sp., central nervous system.

Figure 397. Heterelmis vulnerata, dorsal view of head.

Figure 398. Heterelmis vulnerata, ventral view of left maxilla and labium.

Figure 399. Heterelmis vulnerata, mandible.

Figure 400. Heterelmis vulnerata, tergal scale.

Figure 401. Heterelmis vulnerata, dorsal view of pronotum.

Figure 402. Heterelmis vulnerata, ventral view of prothorax.

Figure 403. Heterelmis vulnerata, ventral view of mesothorax.

Figure 404. Heterelmis vulnerata, ventral view of metathorax and first abdominal segment.

Figure 405. Heterelmis vulnerata, dorsal view of operculum.

Figure 406. Heterelmis vulnerata, ventral view of ninth abdominal segment.

Figure 407. Heterelmis vulnerata, tergal marginal seta.

Figure 408. Heterelmis vulnerata, legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 409. Heterelmis vulnerata, cross section through crop. CM-circular muscle; LM-longitudinal muscle; CS-cuticular spine; Ep.-epithelium.

Figure 410. Heterelmis vulnerata, cross section through hindgut. CM-circular muscle; LM-longitudinal muscle; Ep.-epithelium; CI-cuticular initma

Figure 411. Heterelmis vulnerata, cross section through midgut. LM-longitudinal muscle; CM-circular muscle; Ep.-epithelium; PM-peritrophic membrane; RC-regenerative cell (?) or goblet cell.

Figure 412. Heterelmis vulnerata, longitudinal section, with cross sections as follows:
A. cross section through brain.
B. cross section through crop.
C. cross section through proventriculus
D. cross section through proventriculus
E. cross section through proventriculus
F. cross section through base of proventriculus and anterior of midgut.
G. cross section through midgut.
H. cross section through anterior intestine
I. cross section through posterior intestine.
J. cross section through anus gills.

Figure 413. Stenelmis sp., dorsal view of head.

Figure 414. Stenelmis sp., right mandible.

Figure 415. Stenelmis sp., labium and left maxilla.

Figure 416. Stenelmis sp., ventral view of thorax.

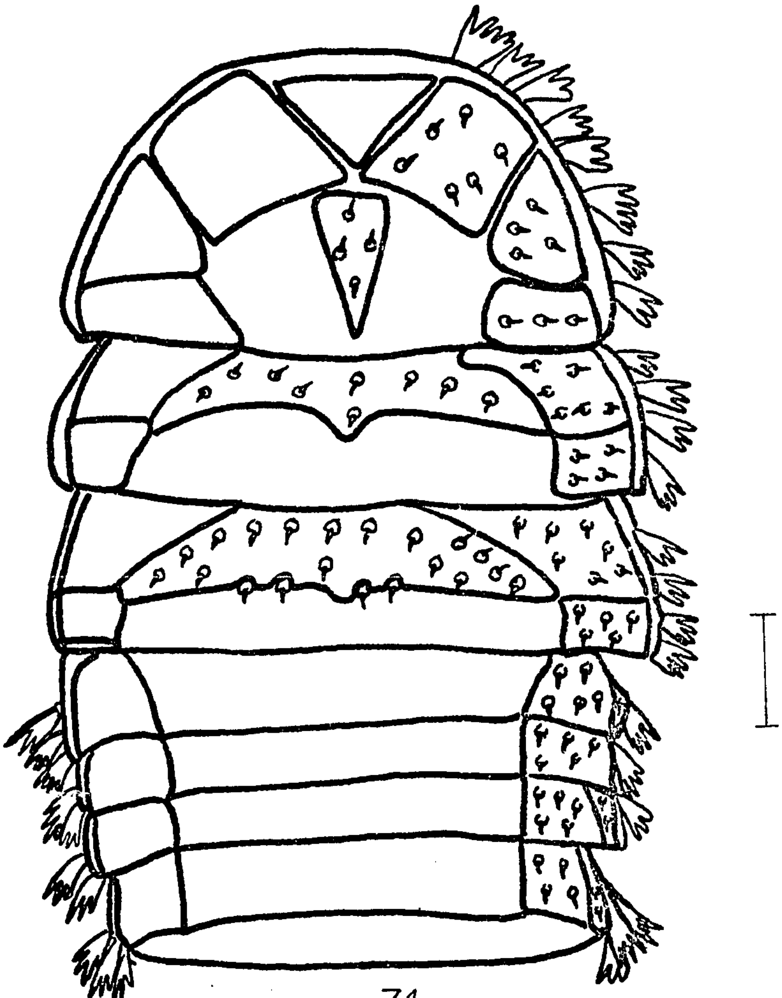
Figure 417. Stenelmis sp., tergal scale and seta.

Figure 418. Stenelmis sp., dorsal view of ninth abdominal segment.

Figure 419. <u>Stenelmis</u> sp., dorsal view of operculum.

Figure 420. <u>Stenelmis</u> sp., legs.
A. Prothoracic leg
B. Mesothoracic leg
C. Metathoracic leg

Figure 421. <u>Stenelmis</u> sp., digestive tract and malpighian tubules.



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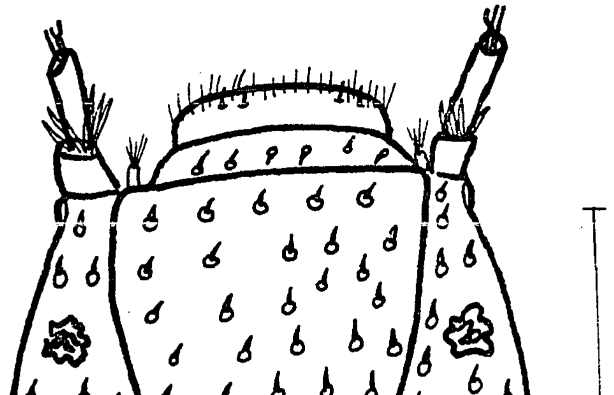

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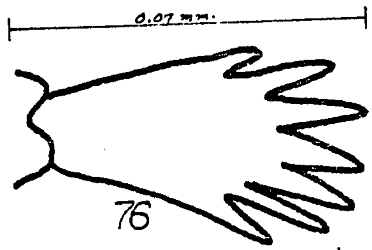


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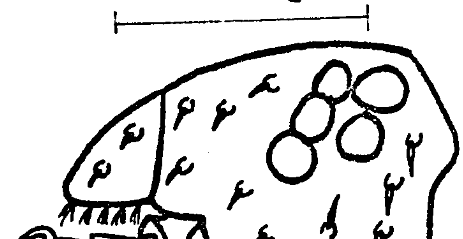

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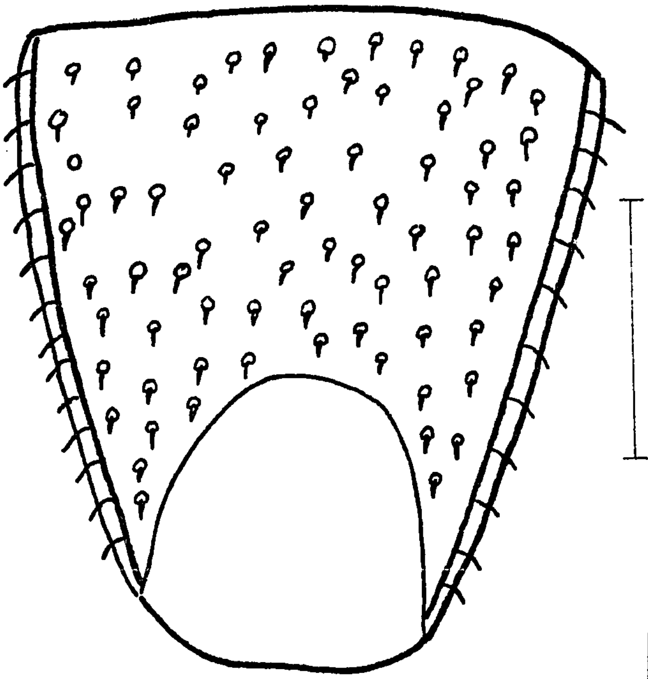

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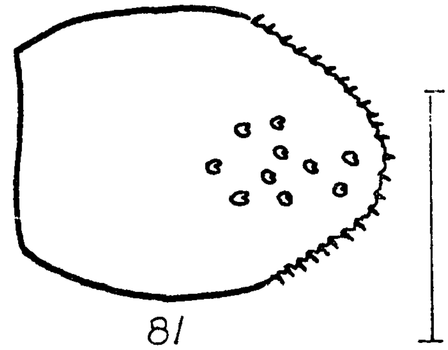

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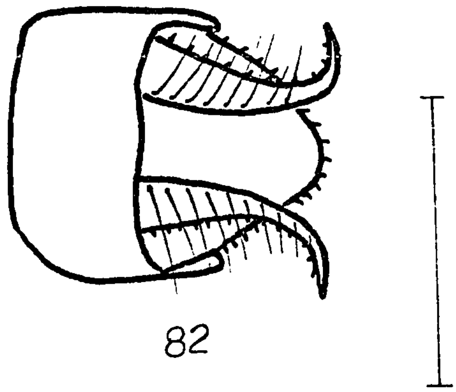

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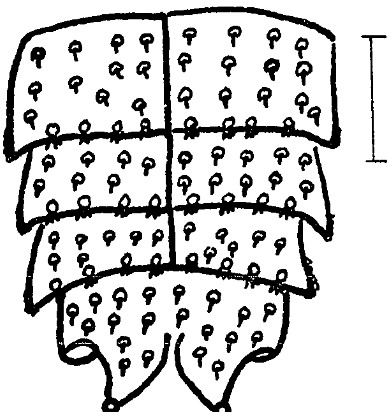

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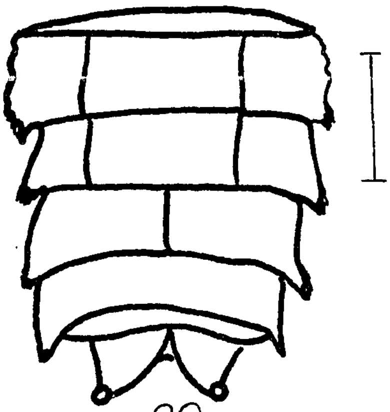

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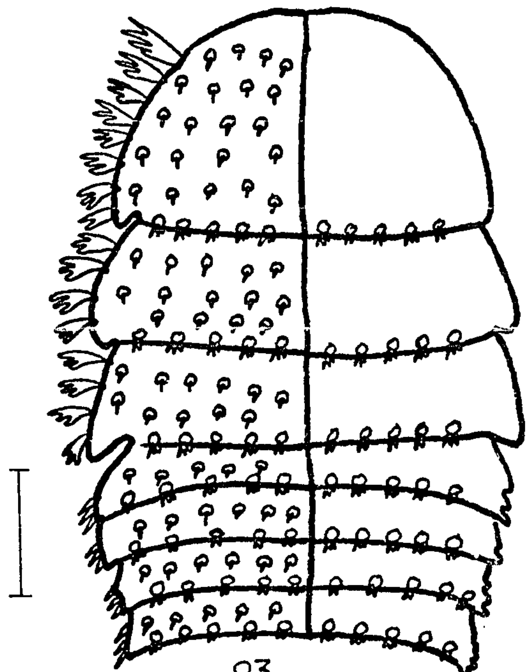

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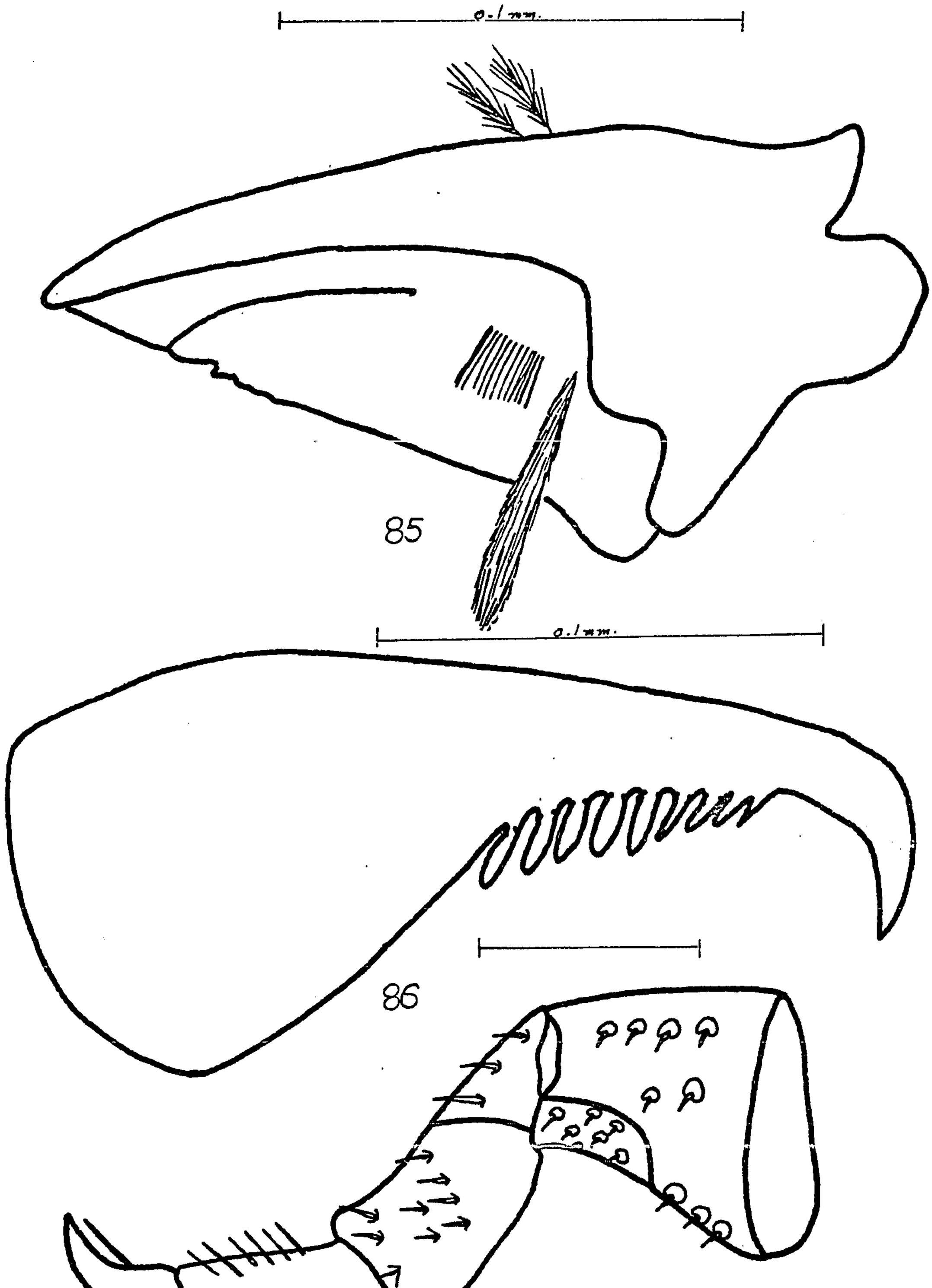
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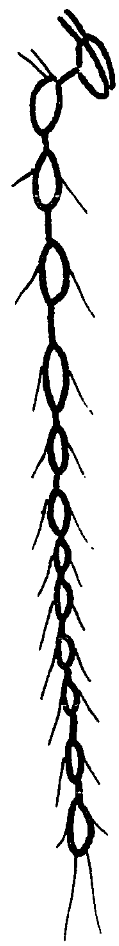

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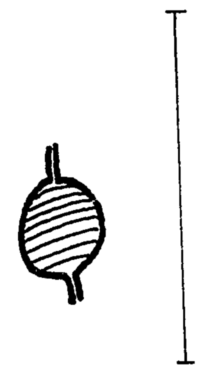

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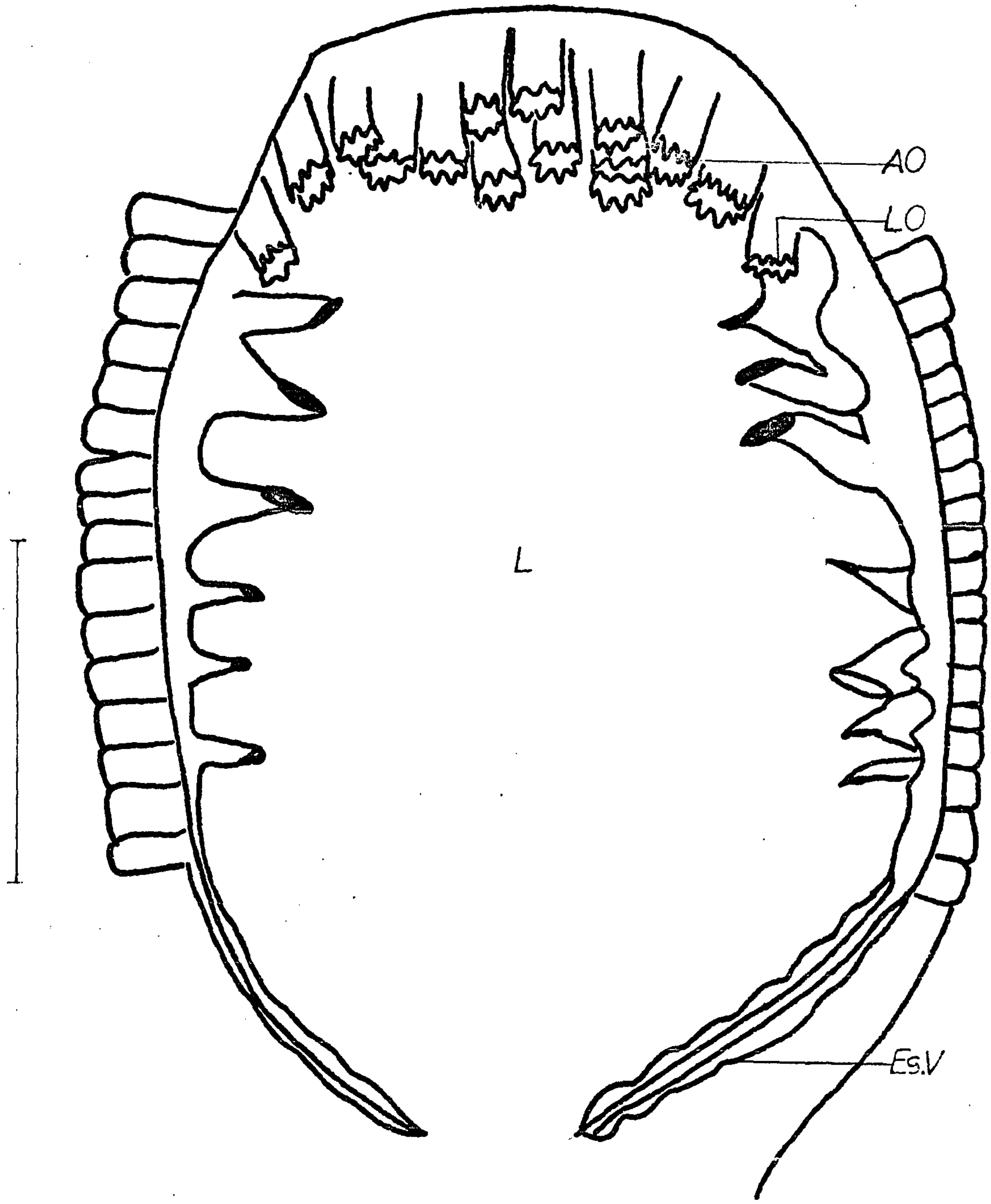


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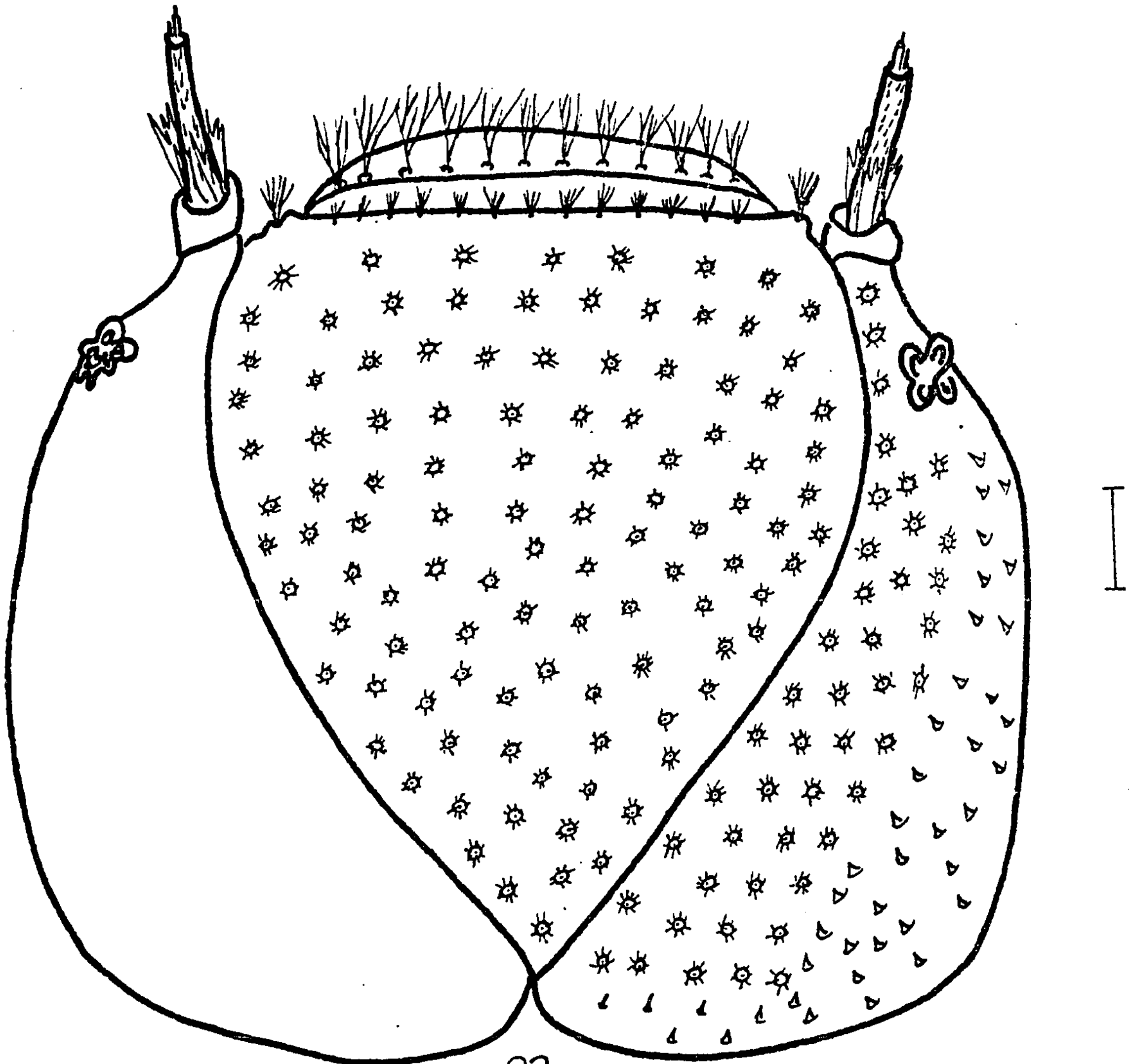

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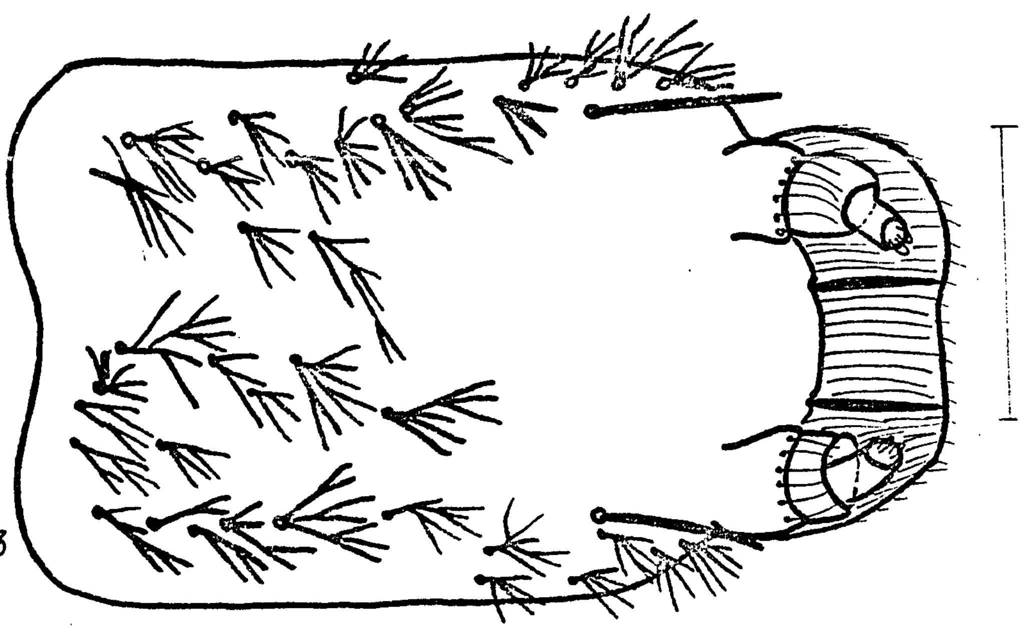

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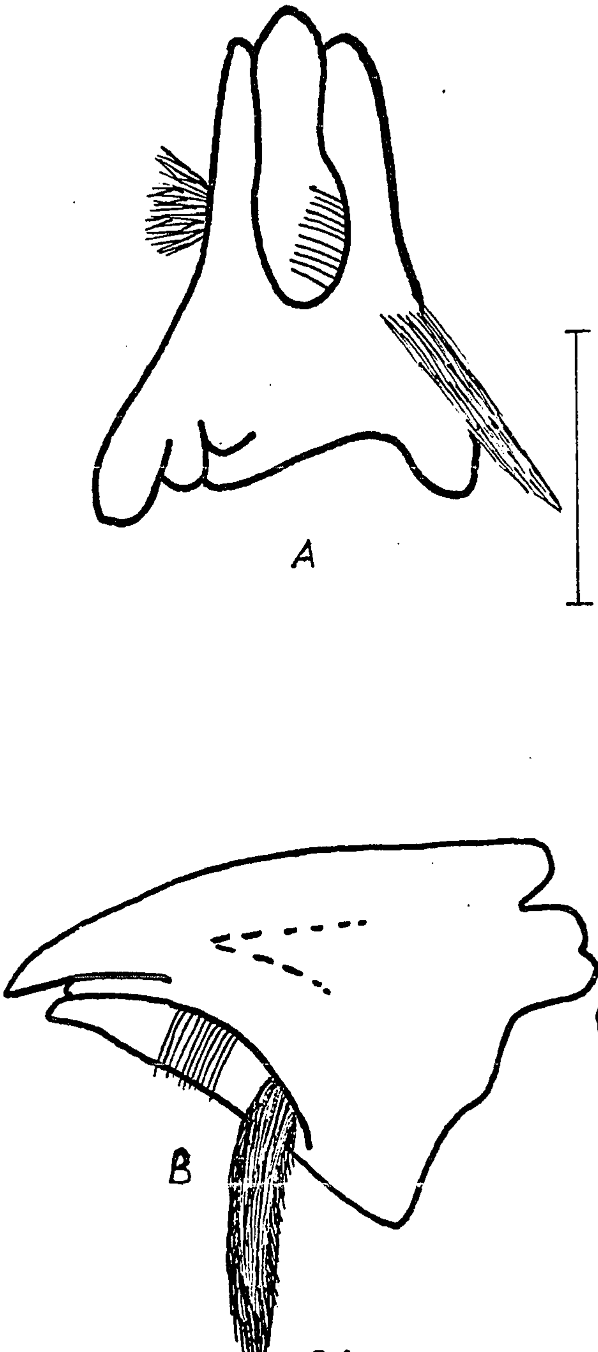

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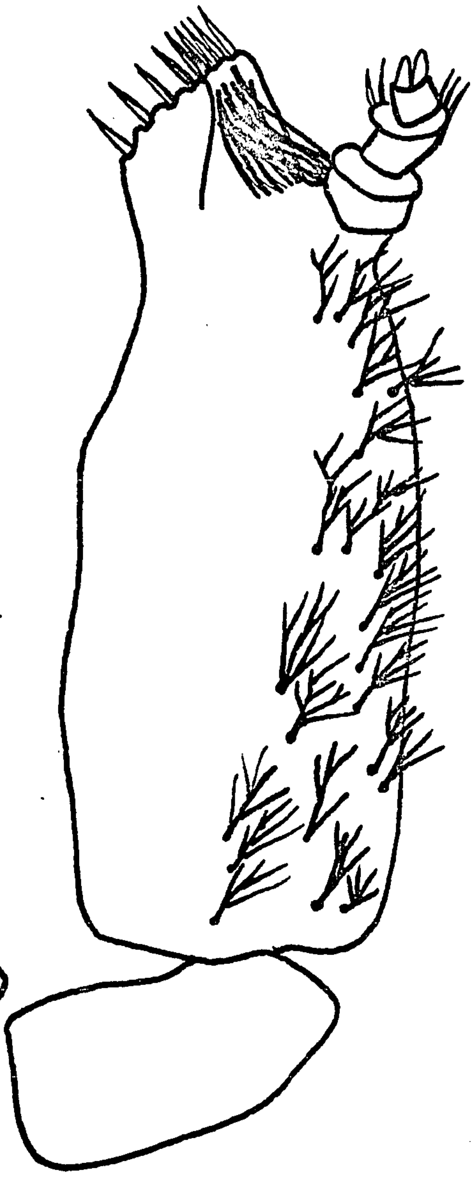
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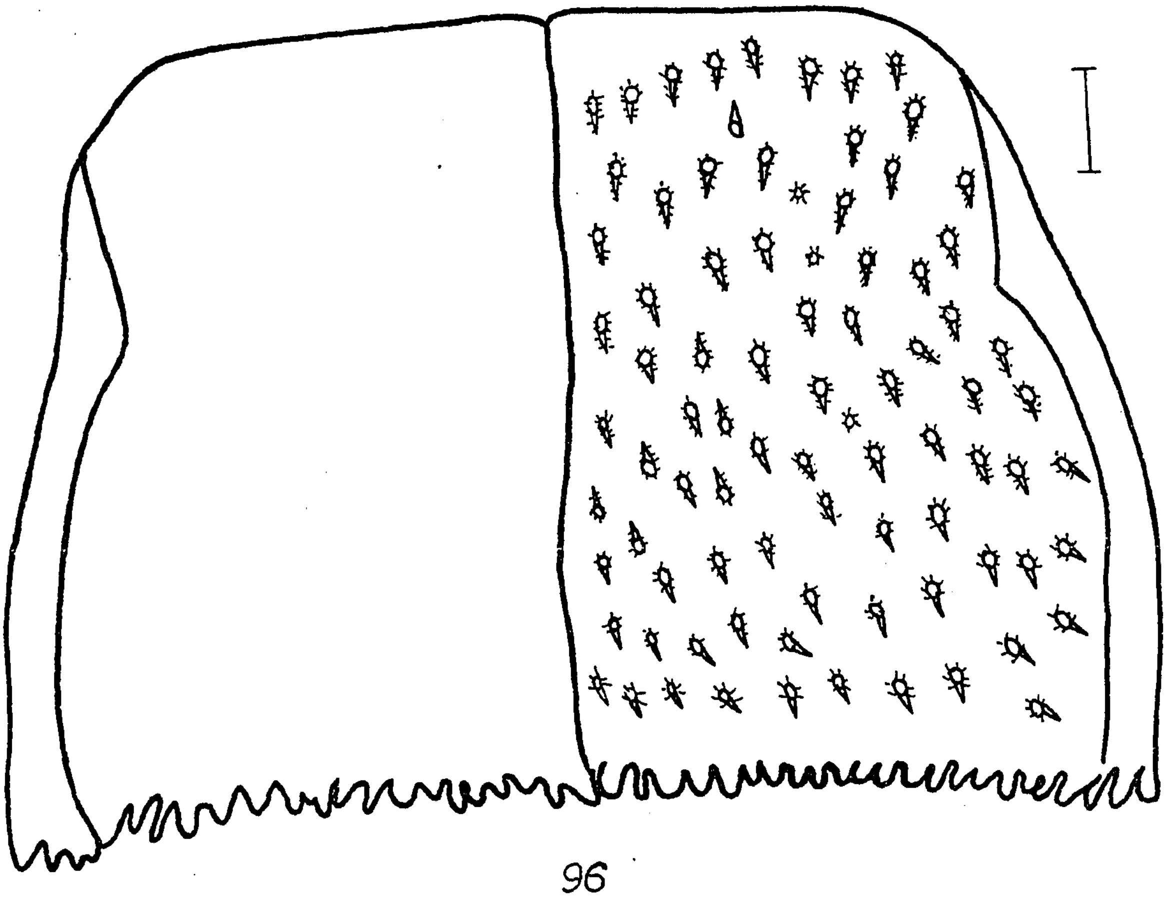

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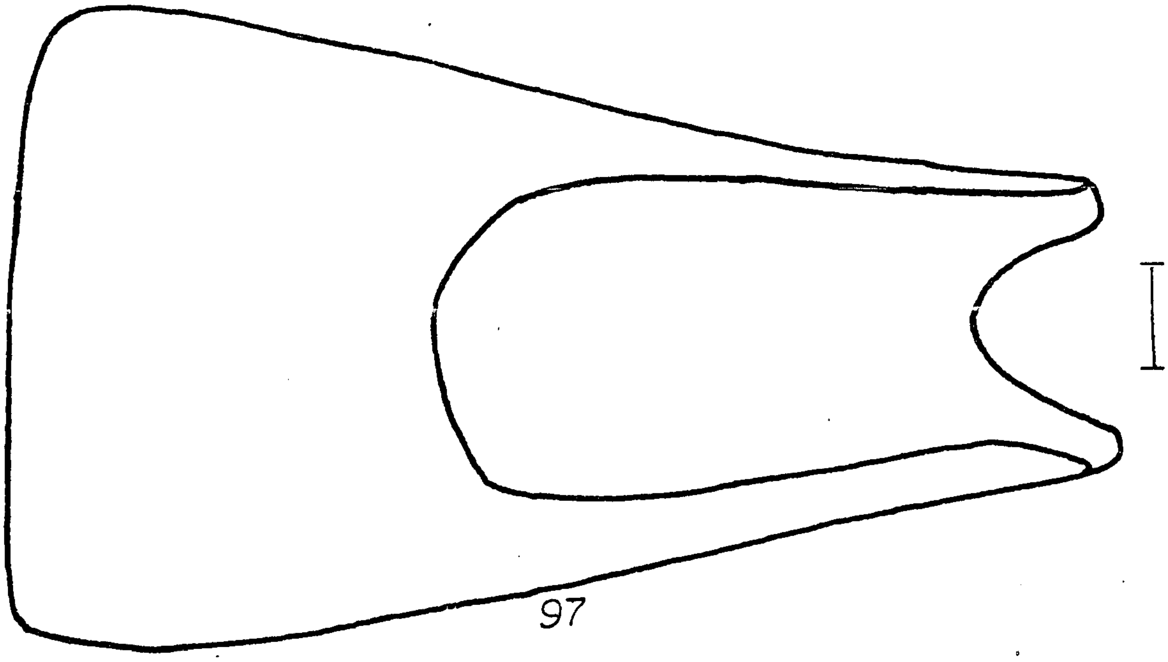

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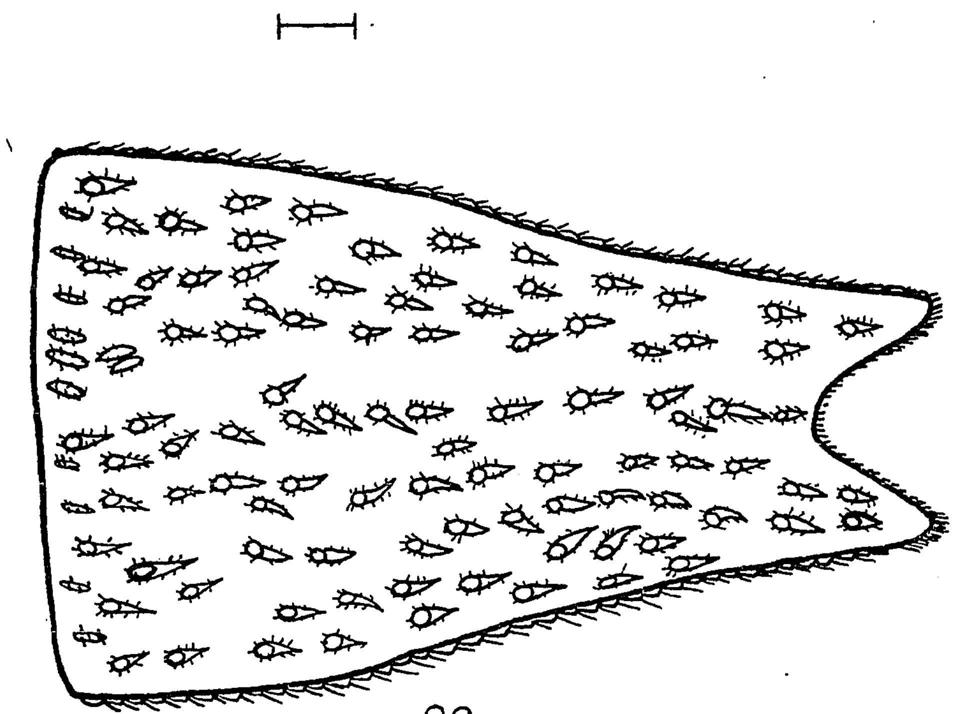

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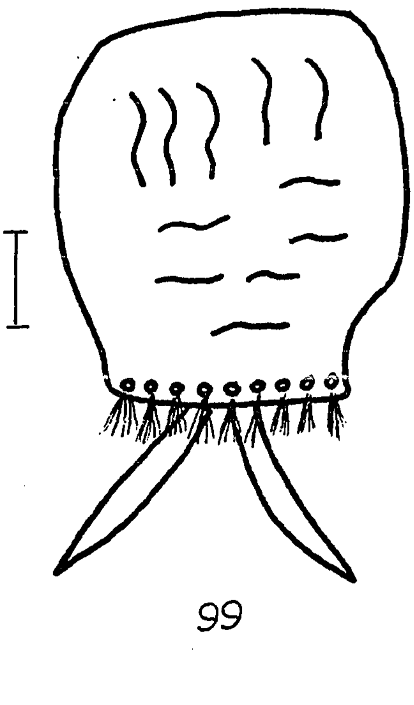

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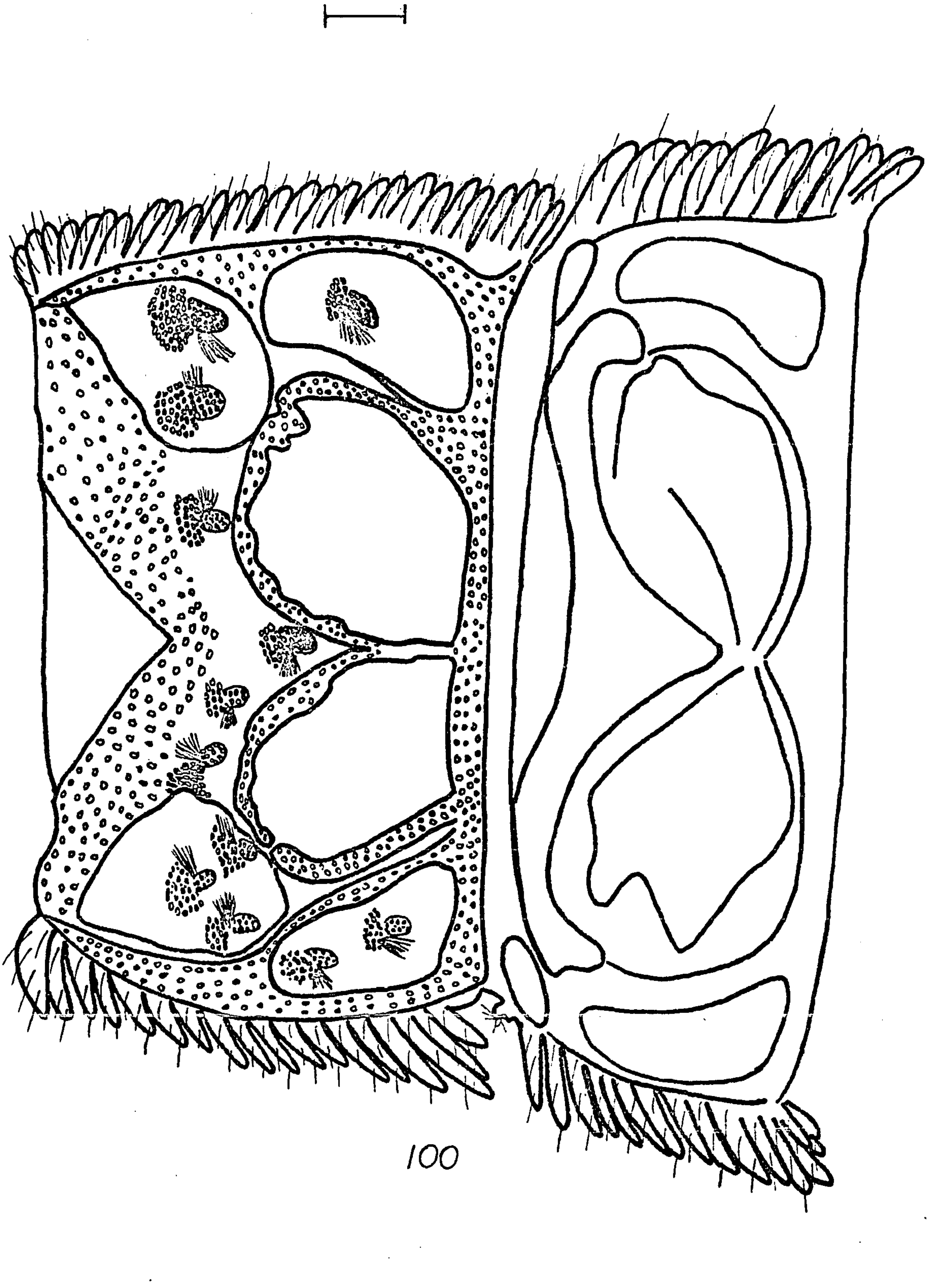

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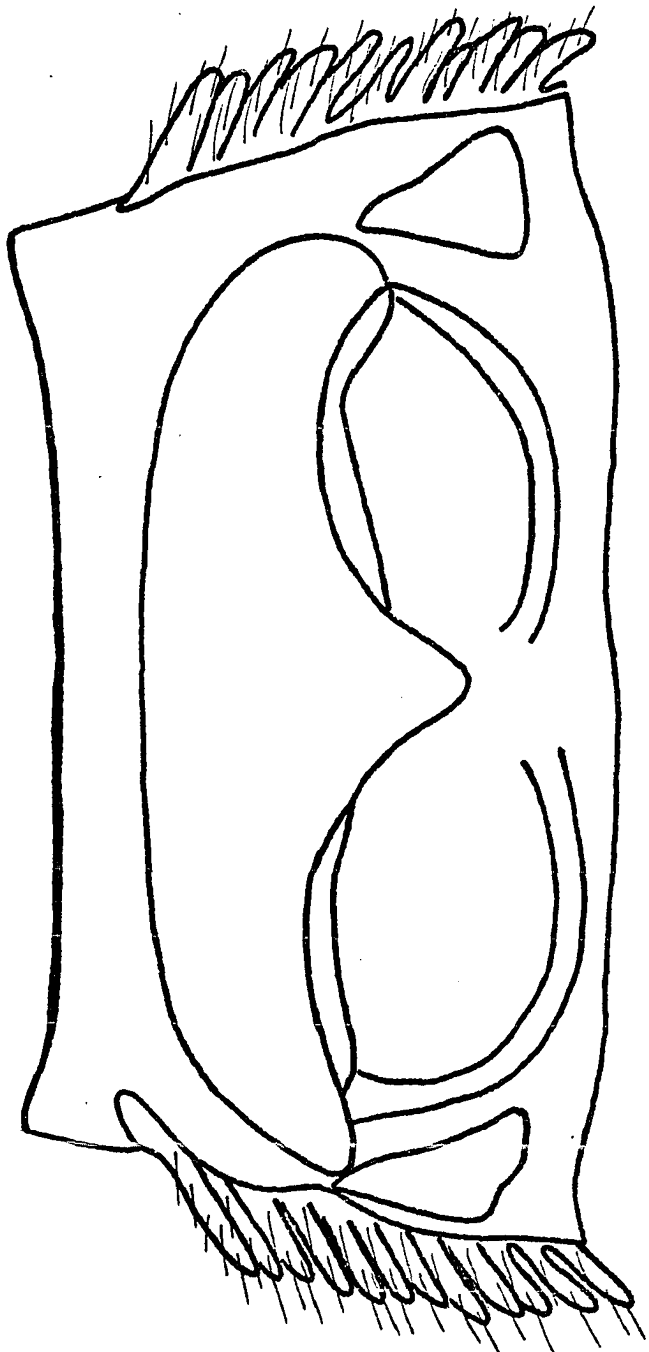

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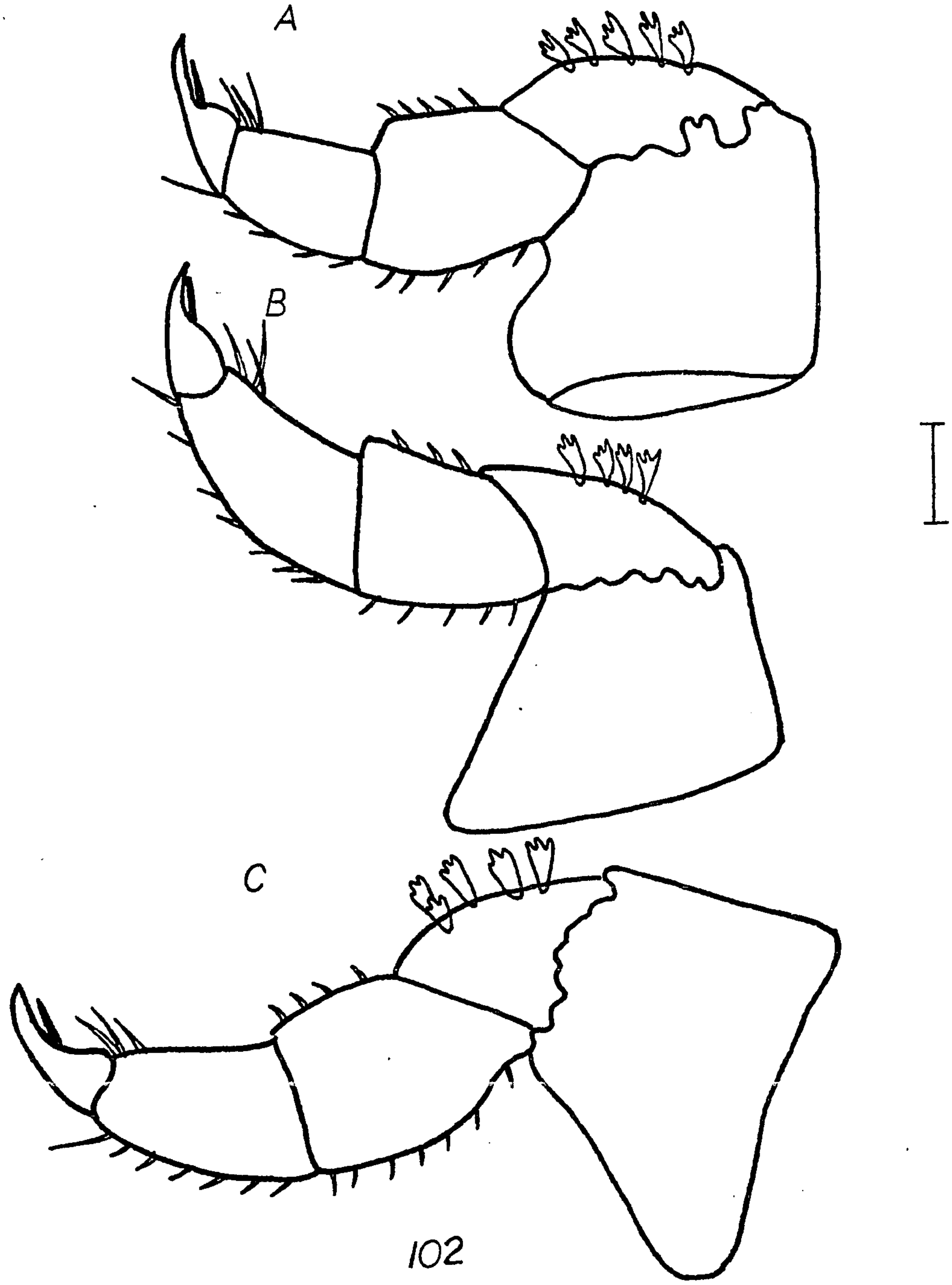

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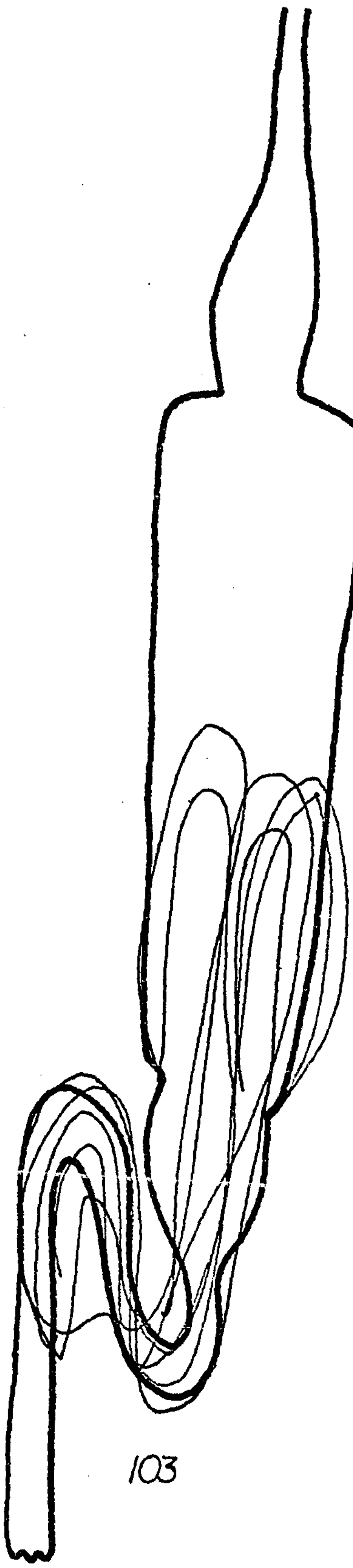

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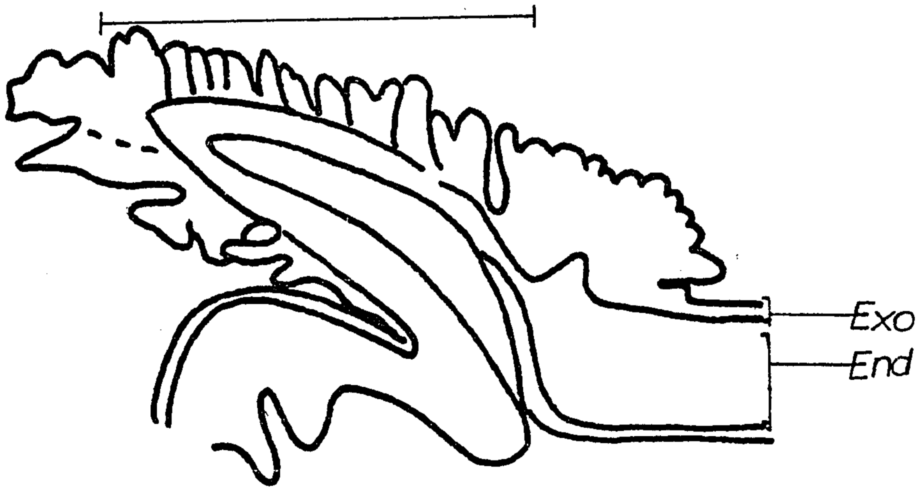


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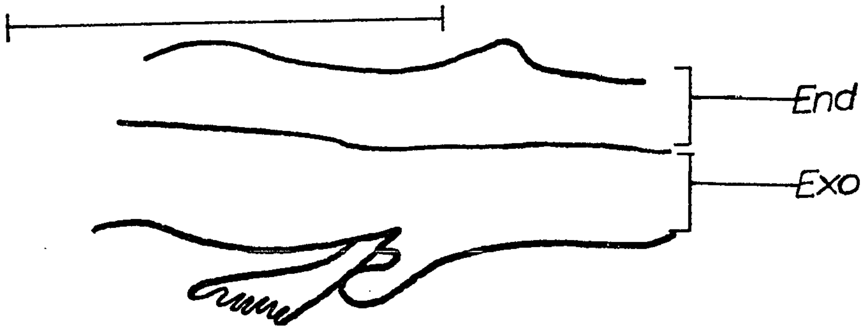


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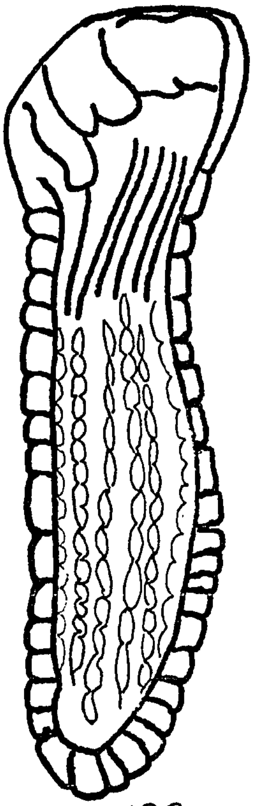

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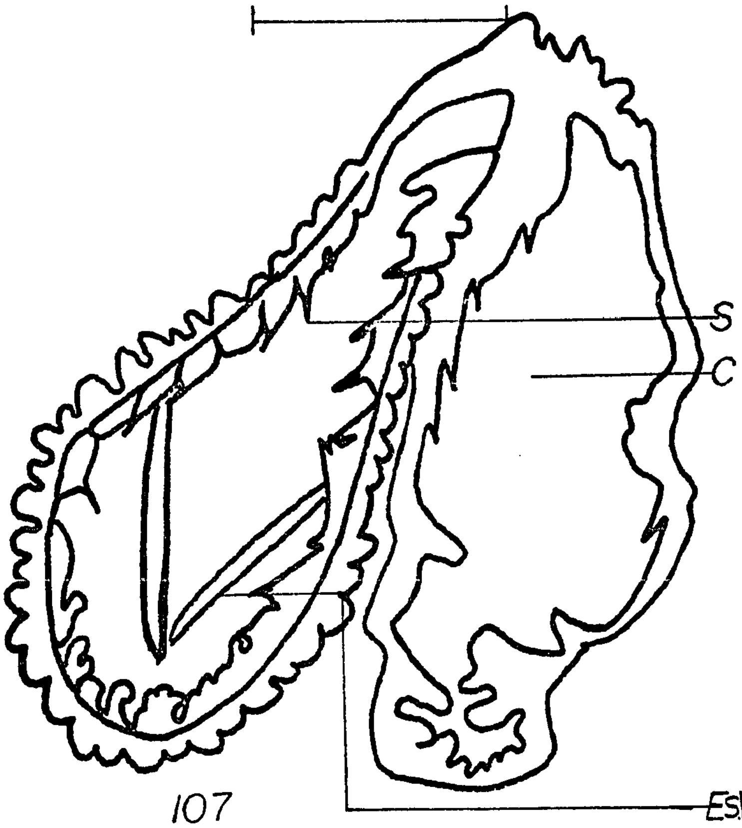


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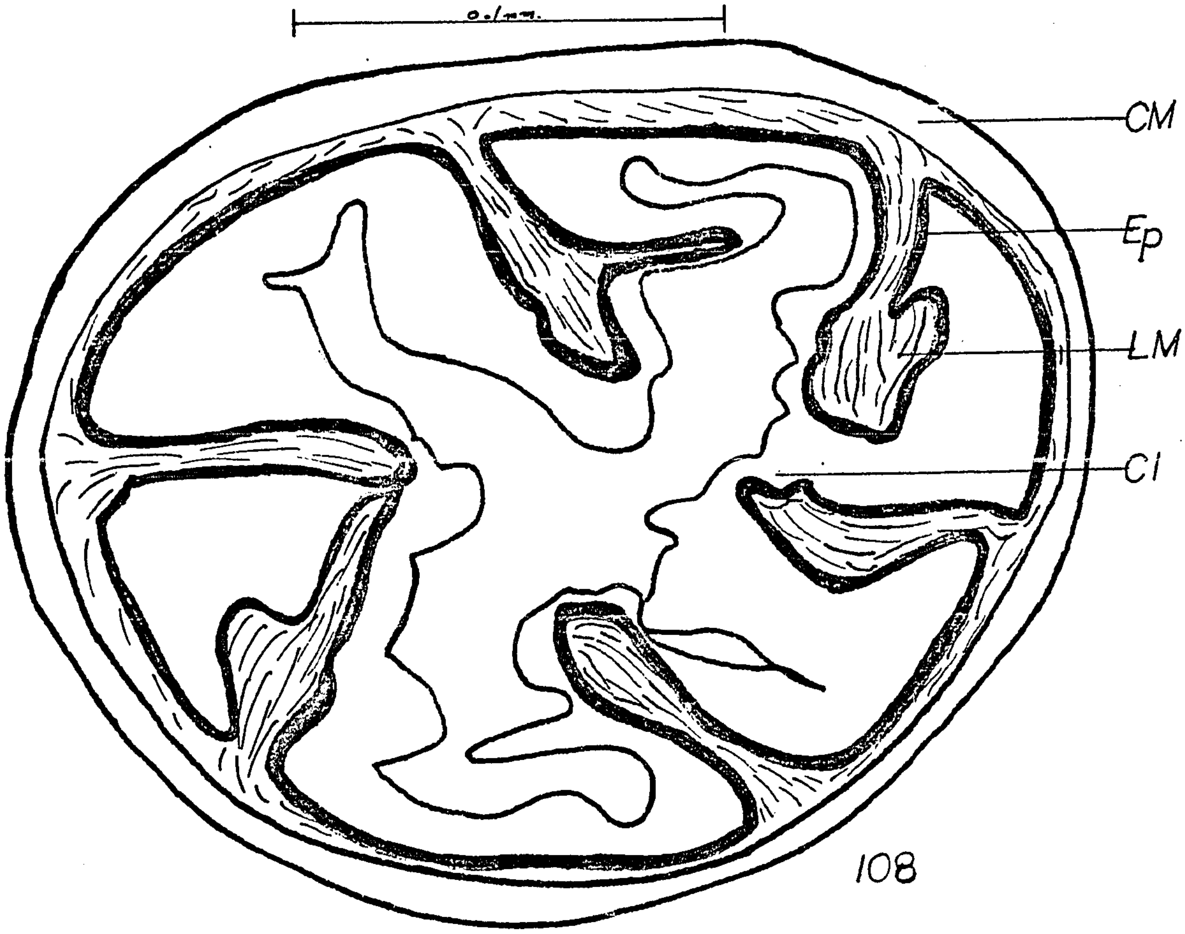


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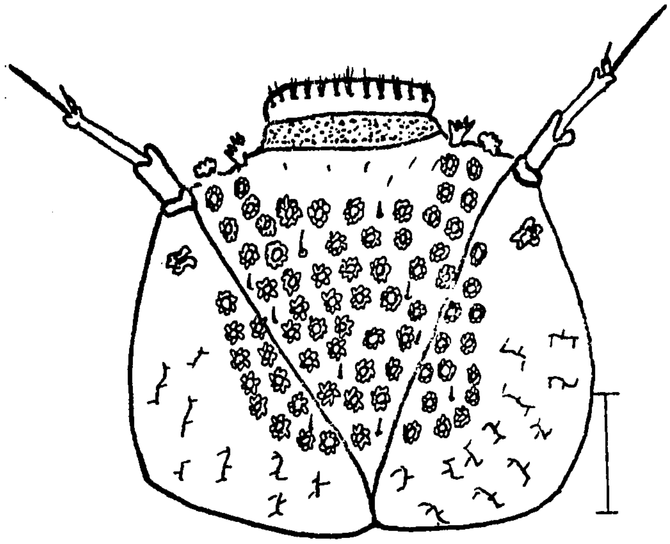

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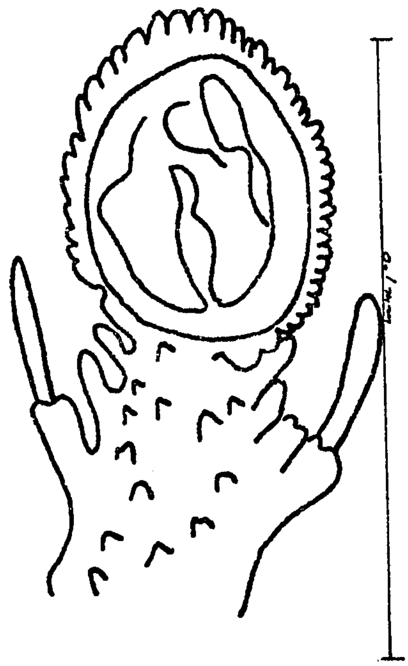

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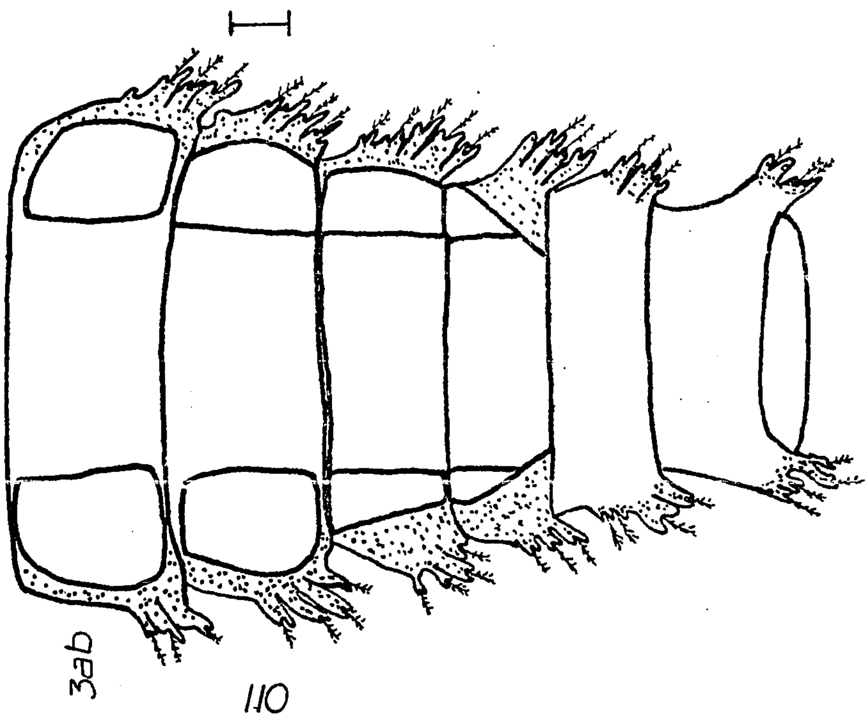


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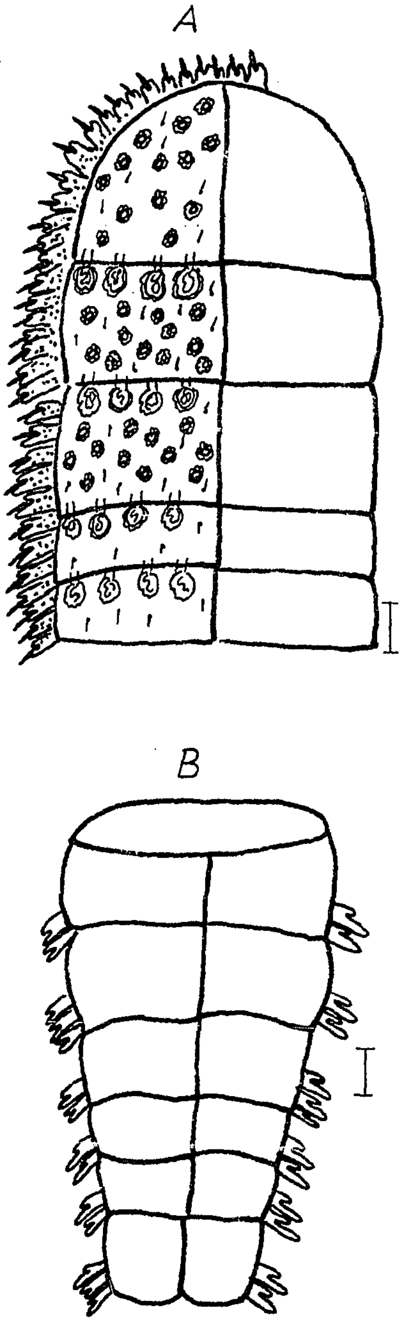


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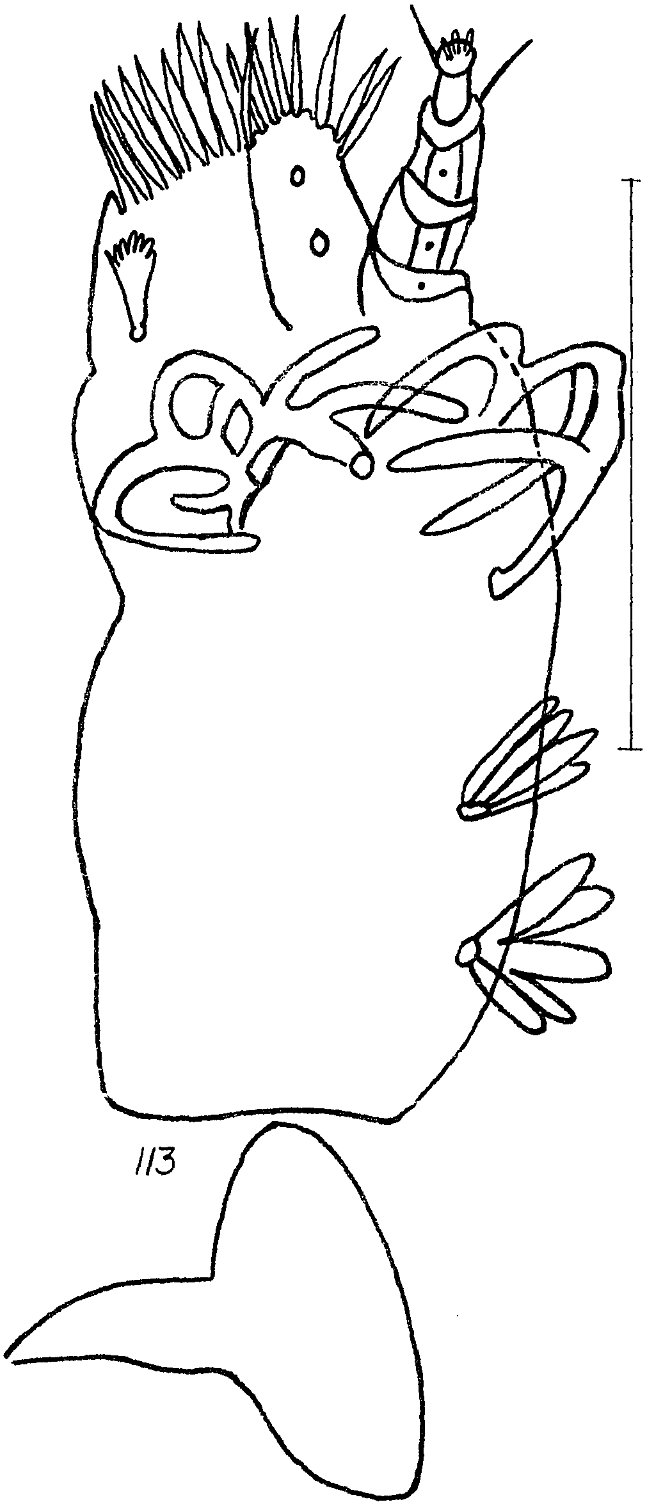

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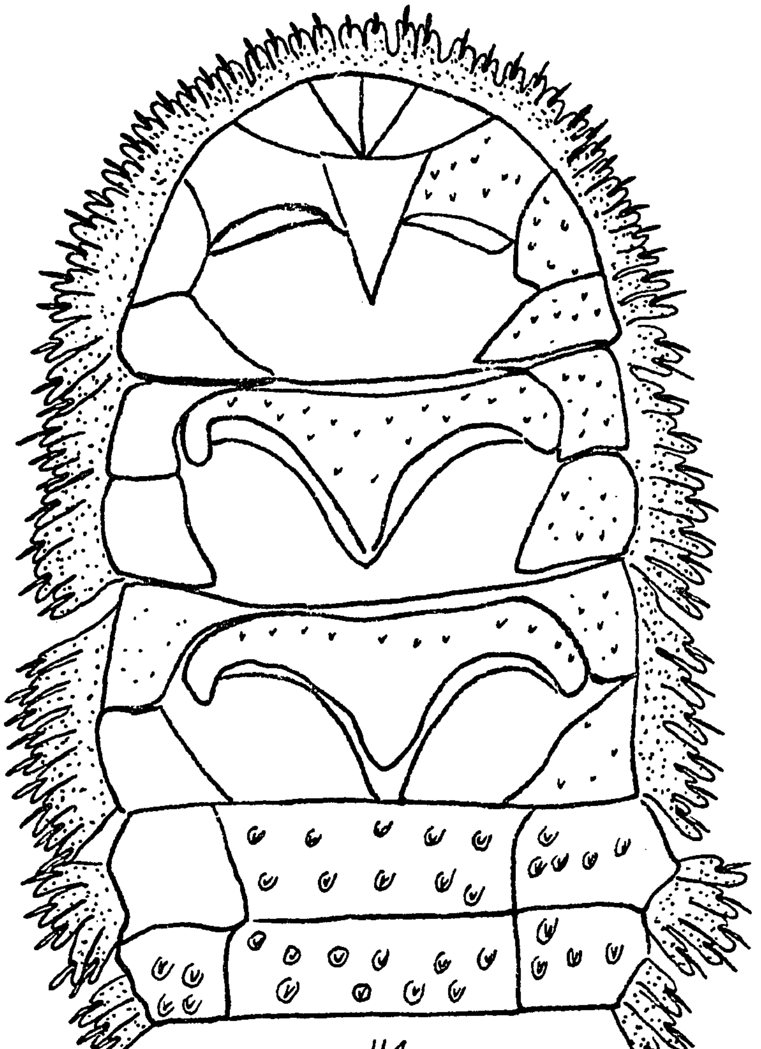

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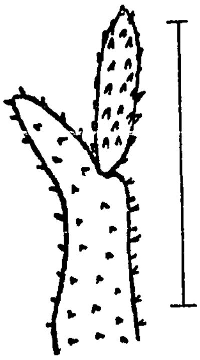

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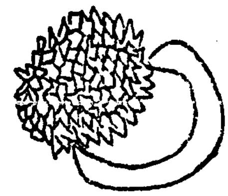

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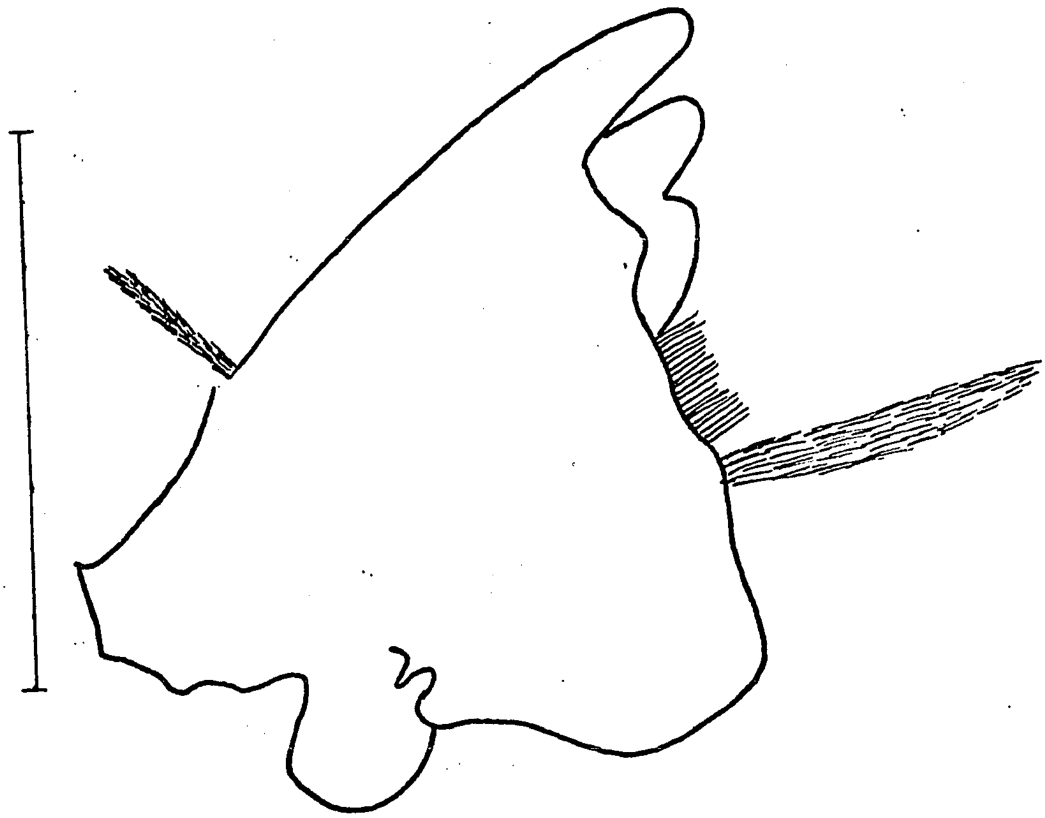

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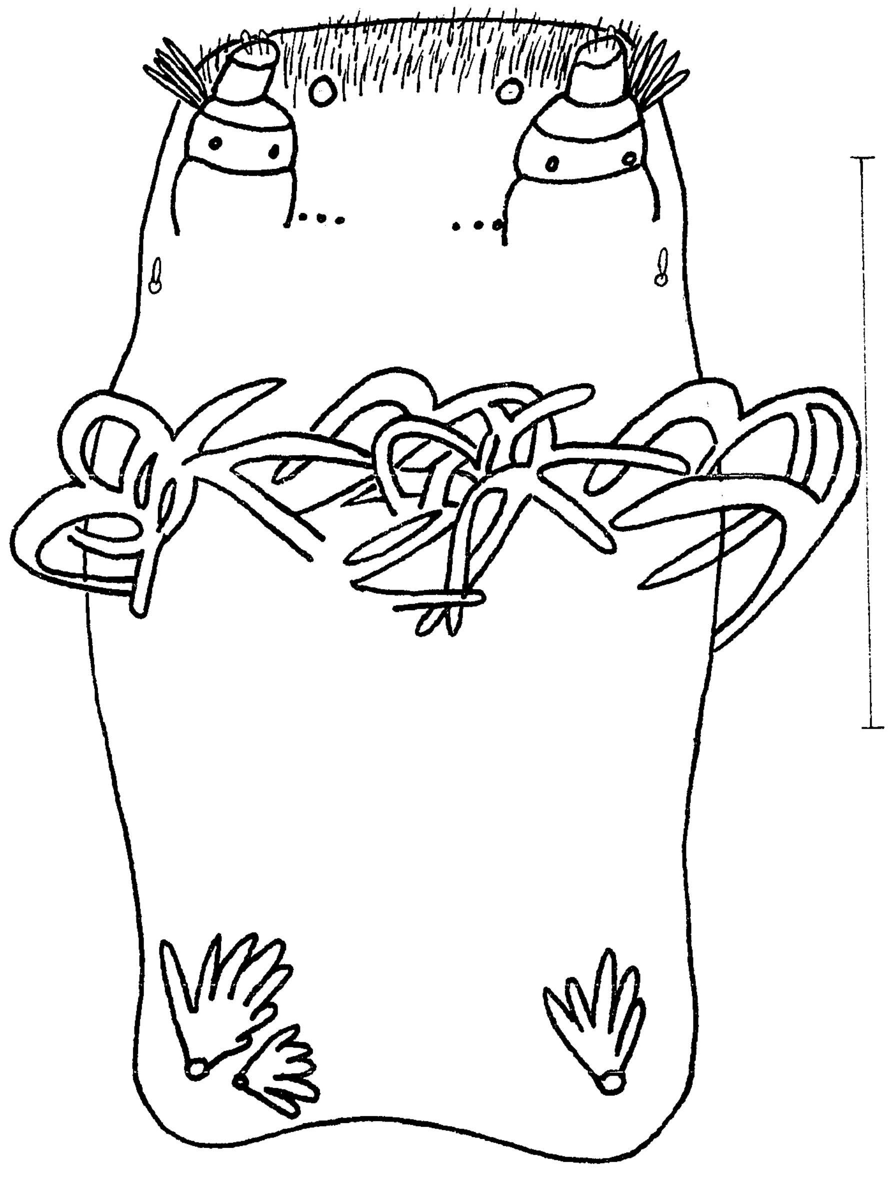

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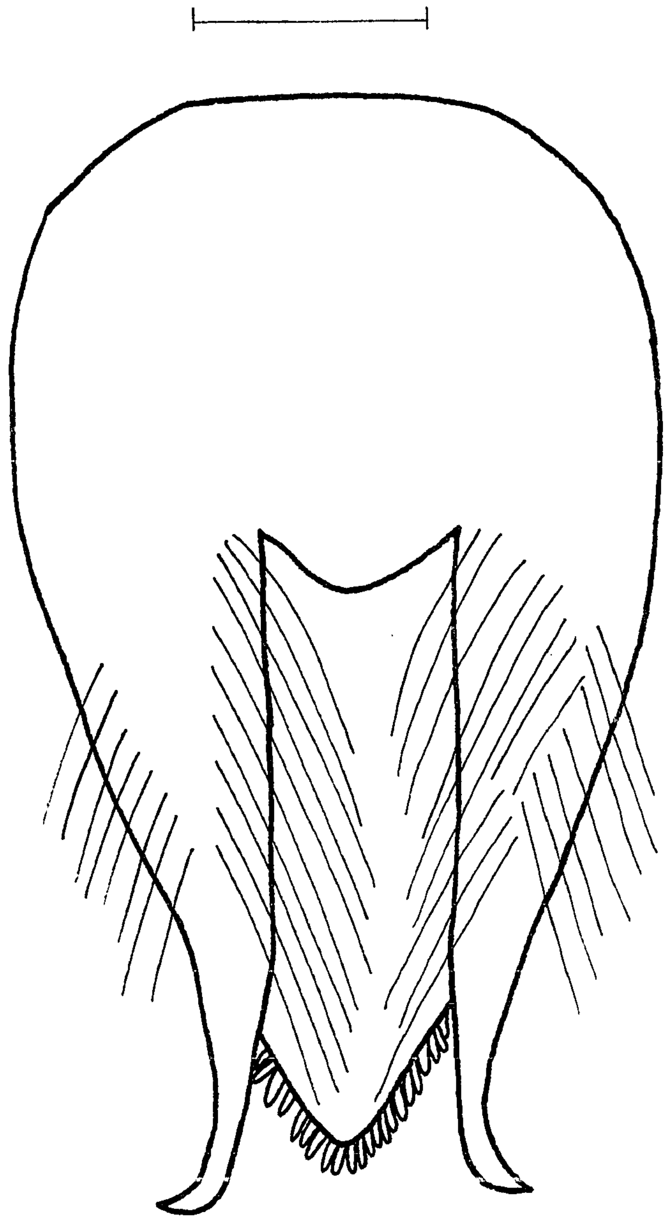

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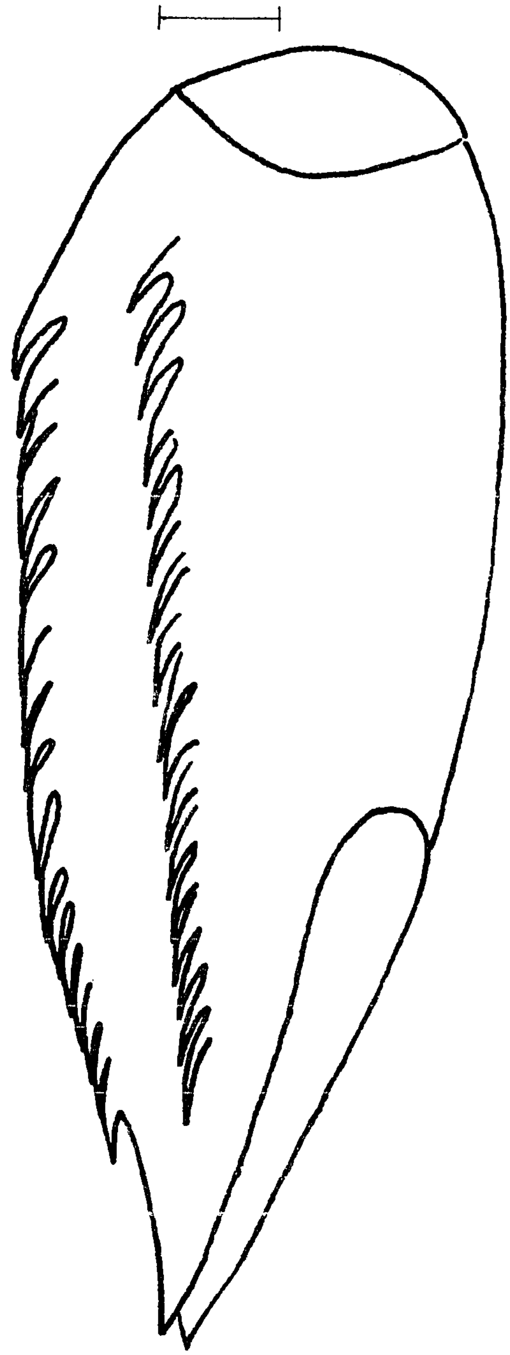

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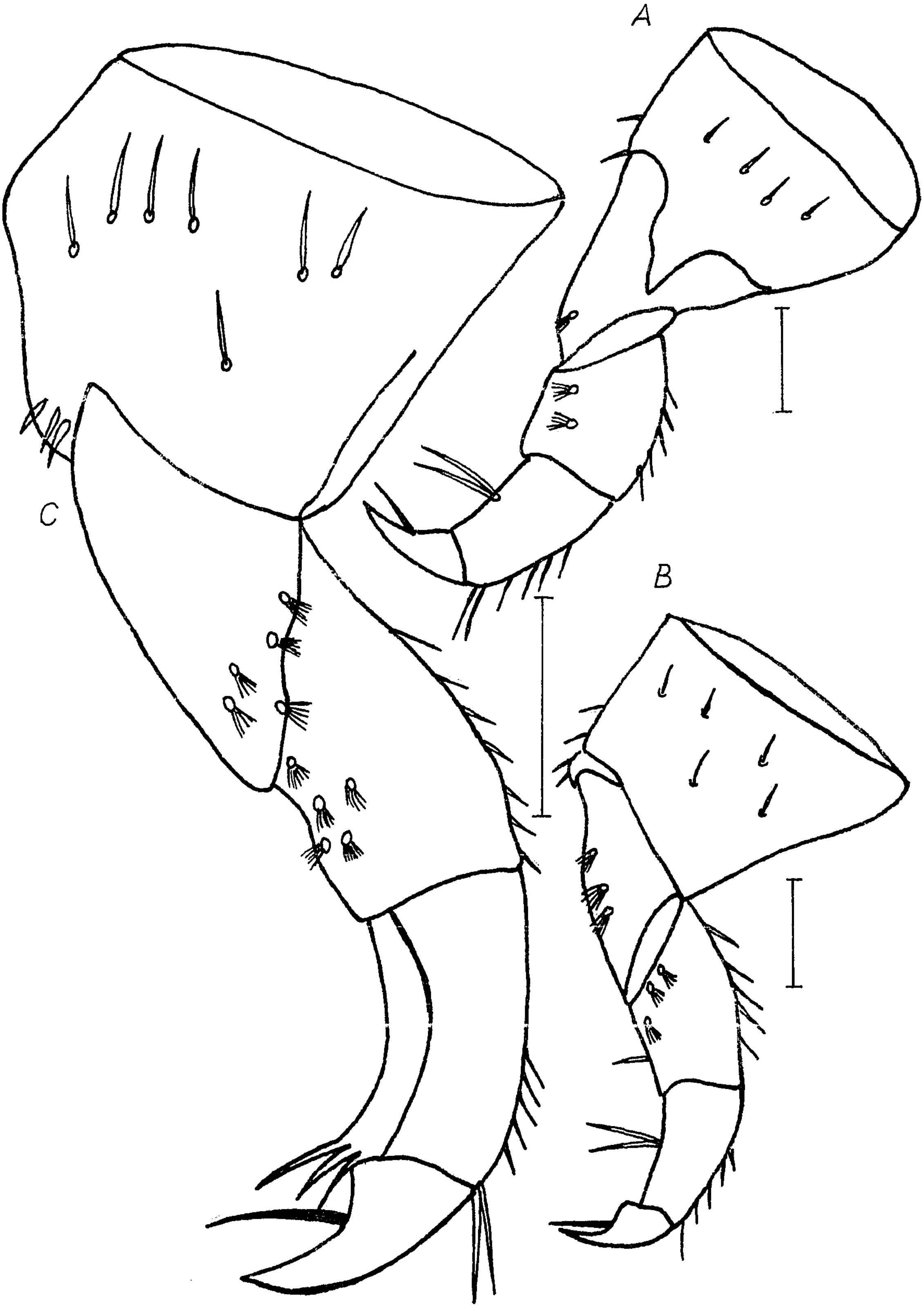


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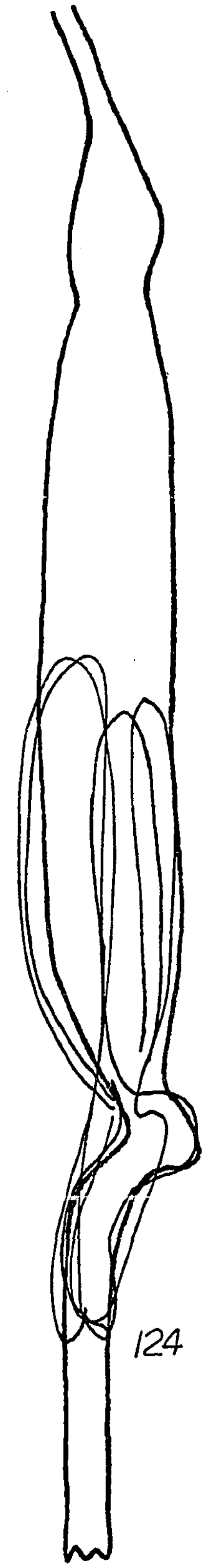
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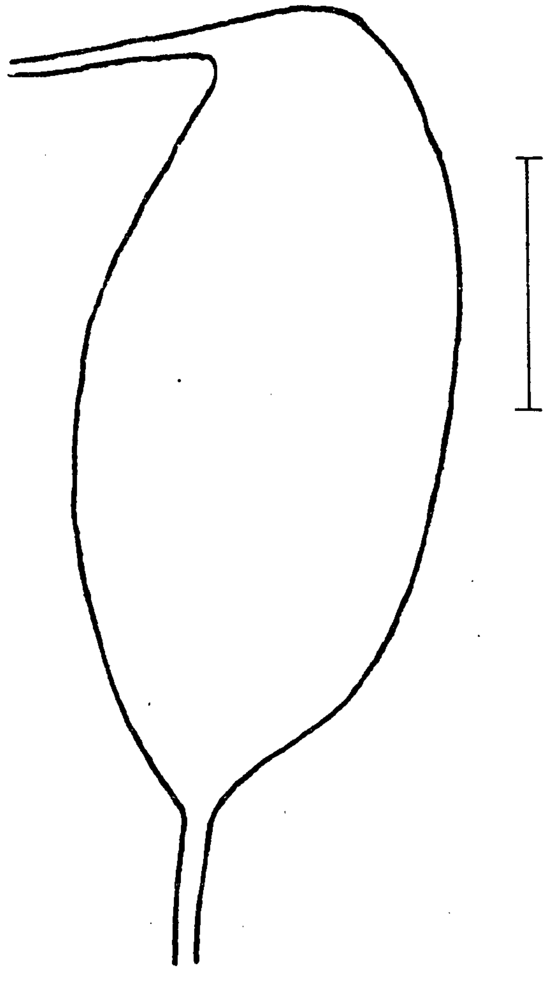
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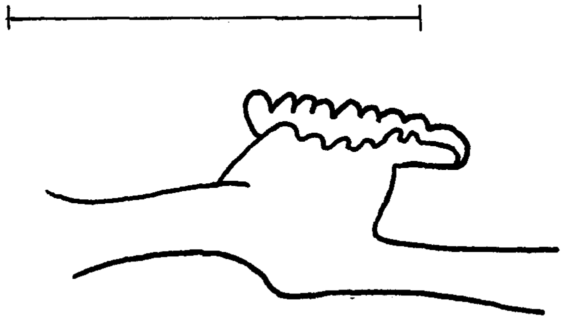

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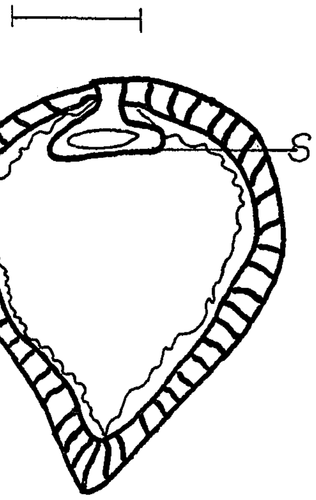


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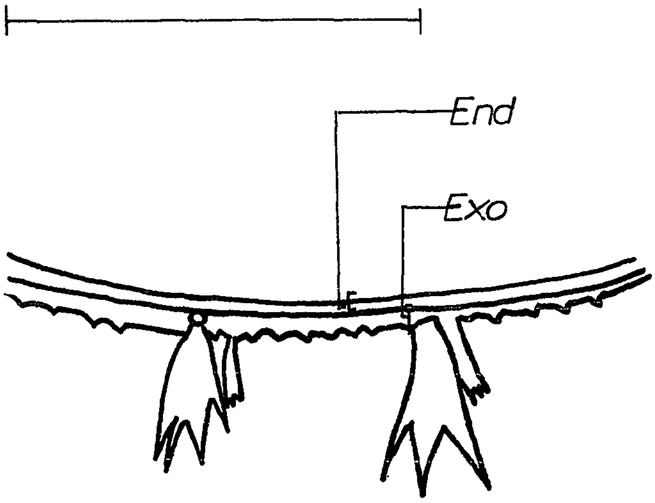


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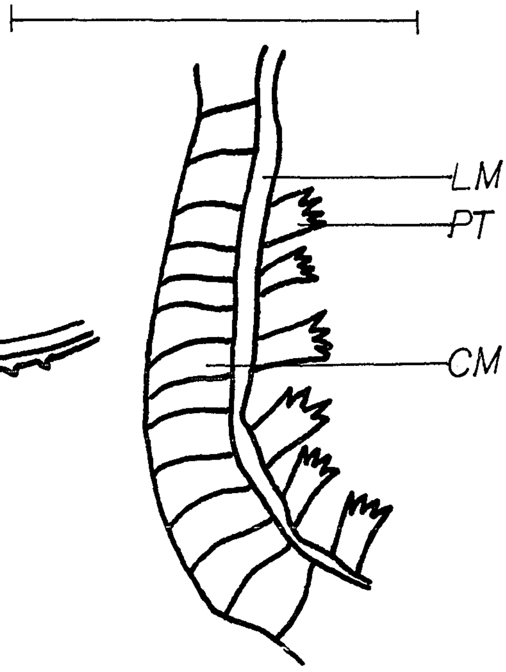


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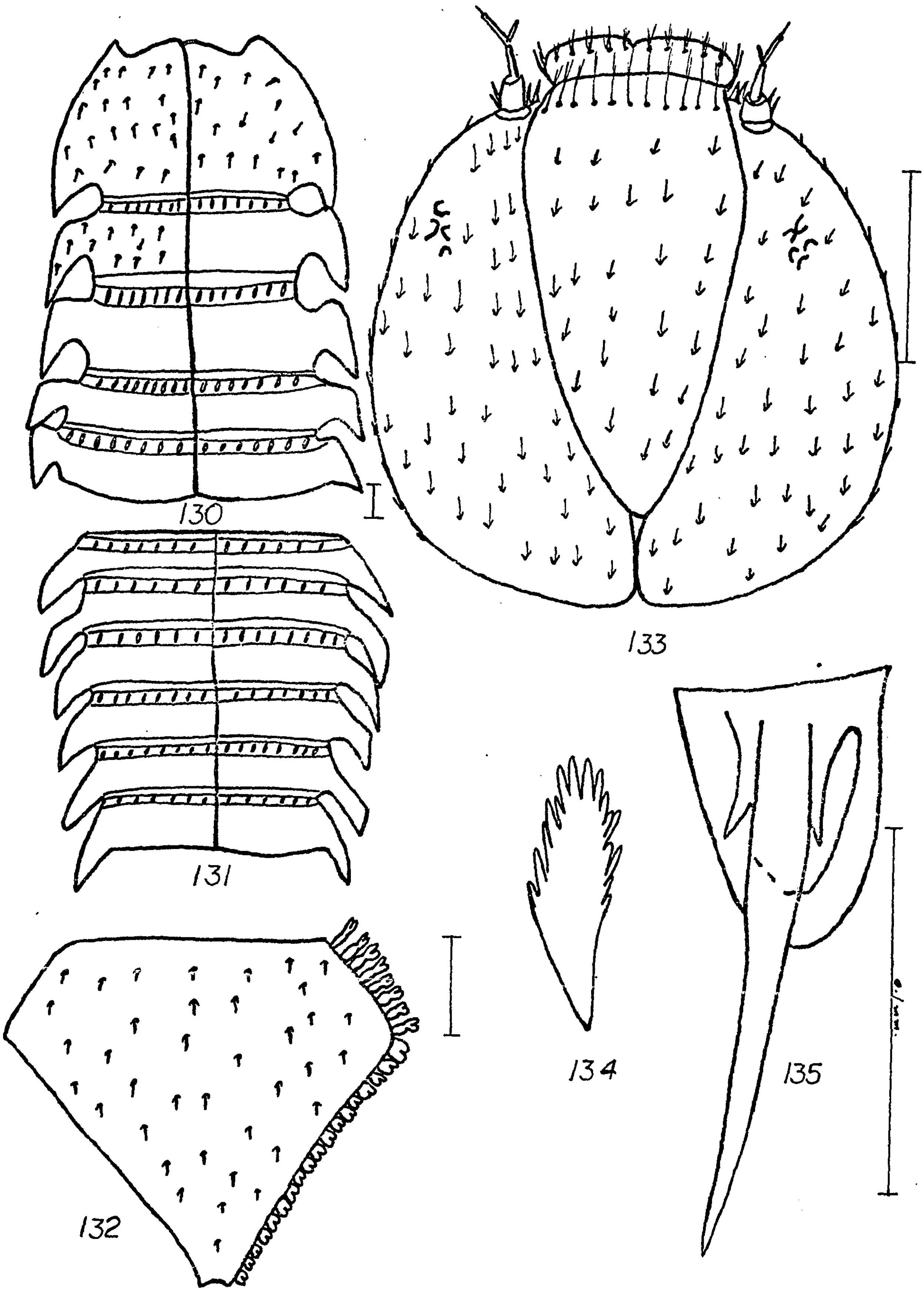
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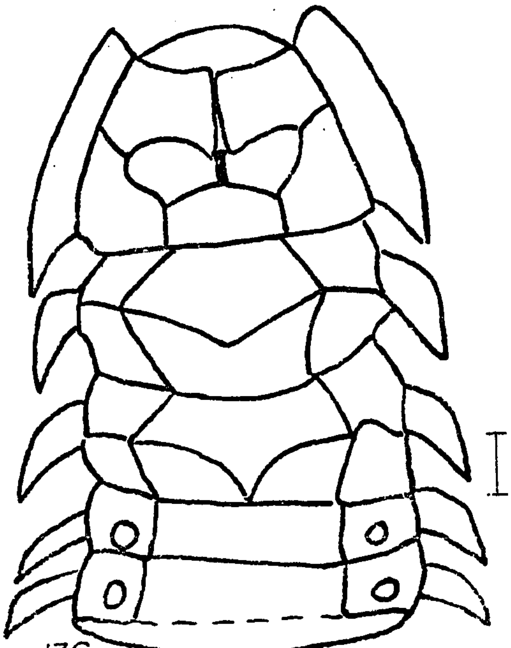

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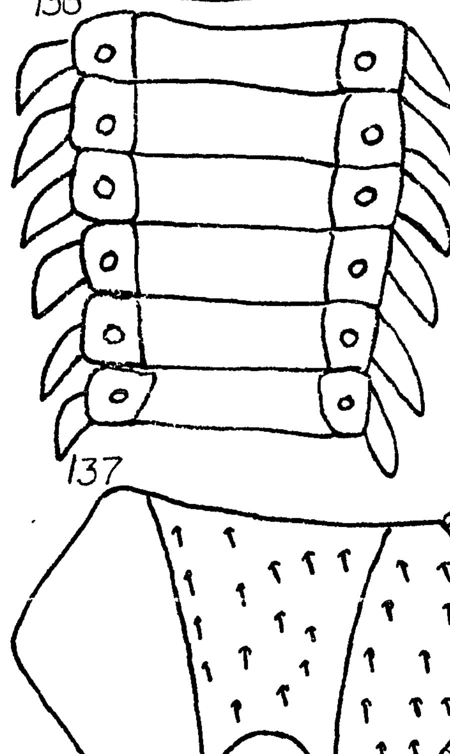

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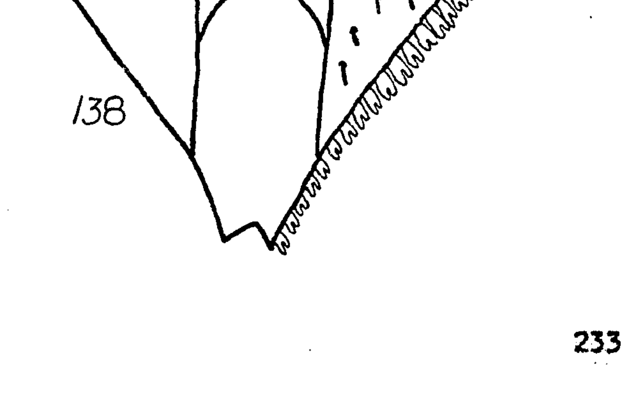

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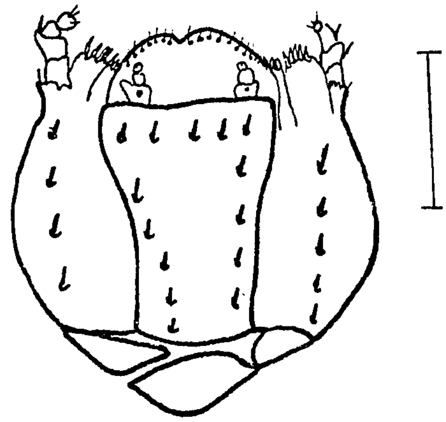

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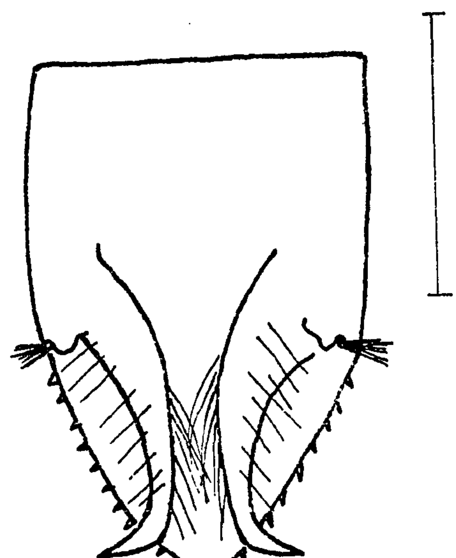

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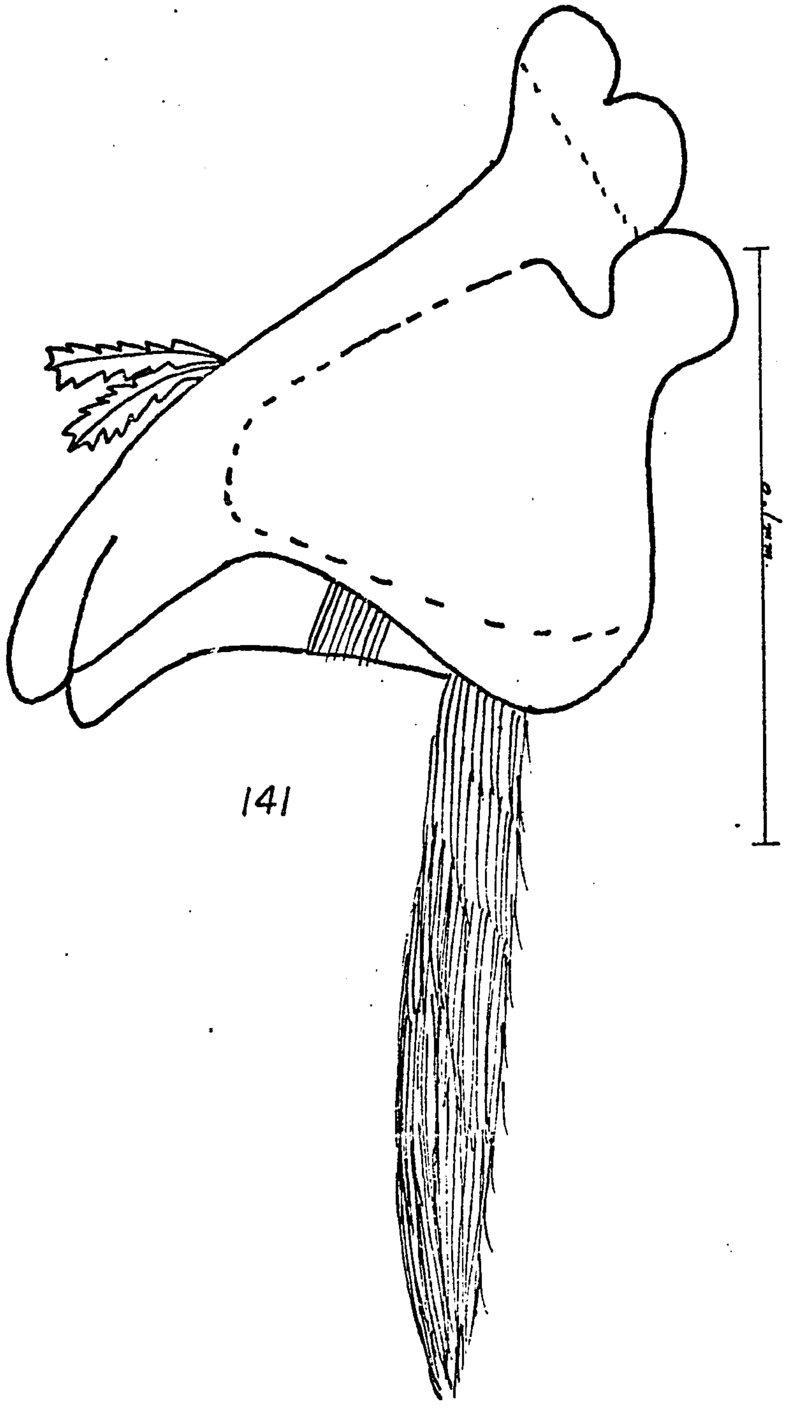

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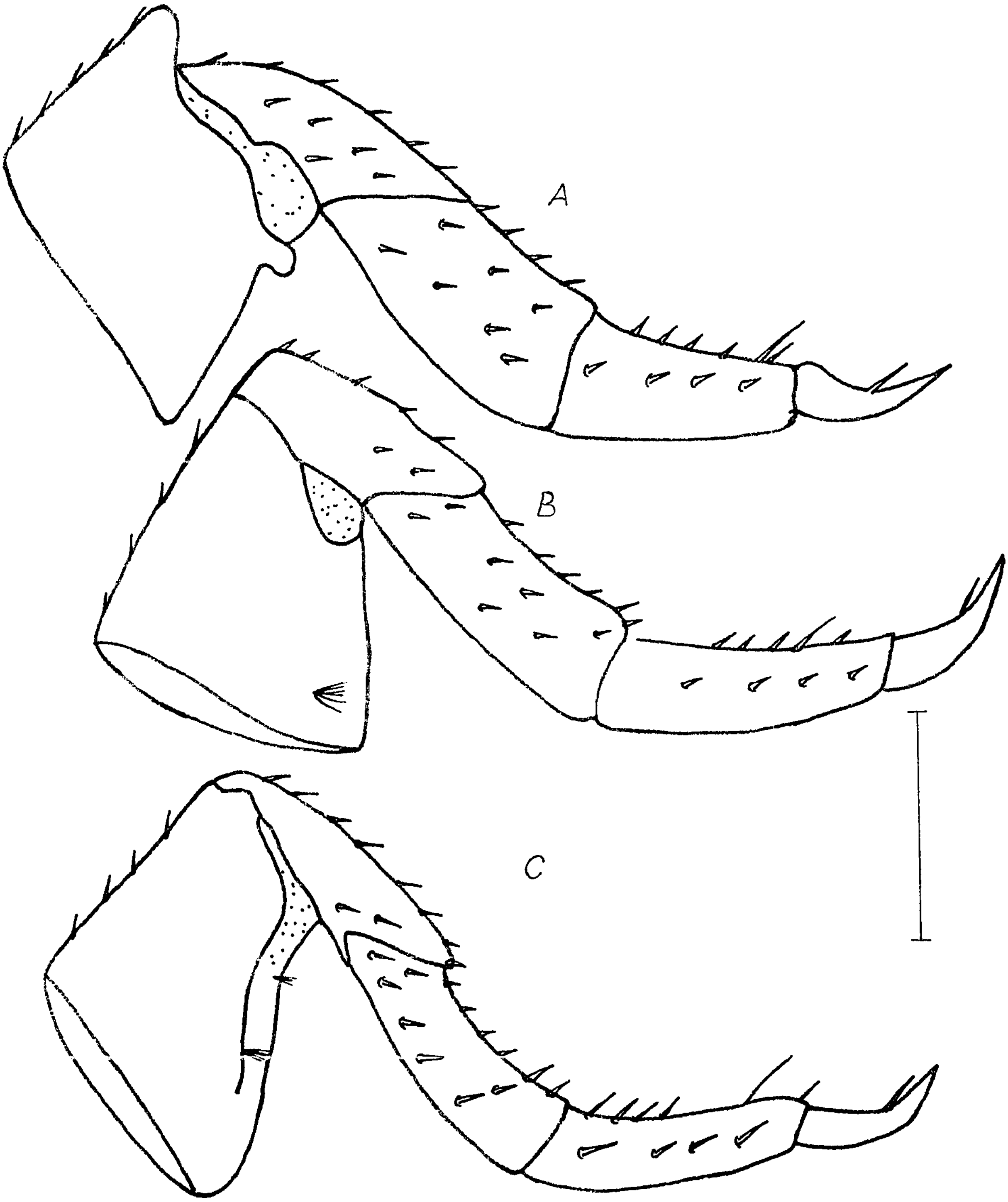


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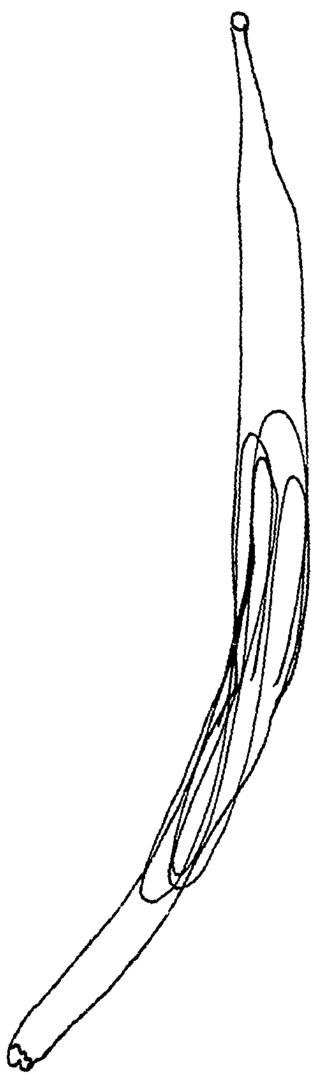

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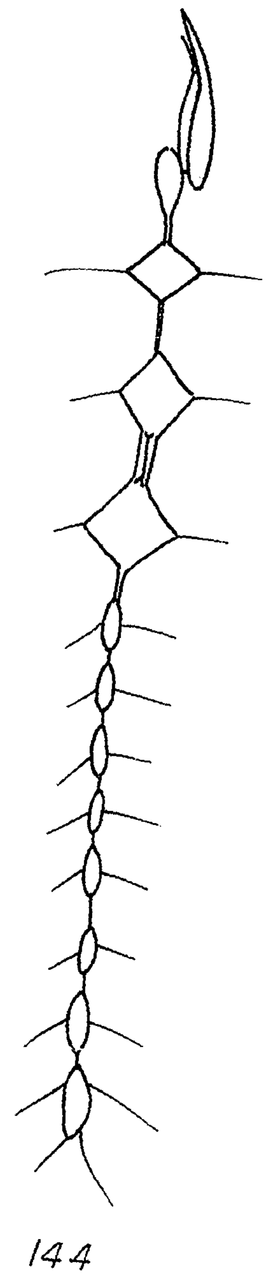

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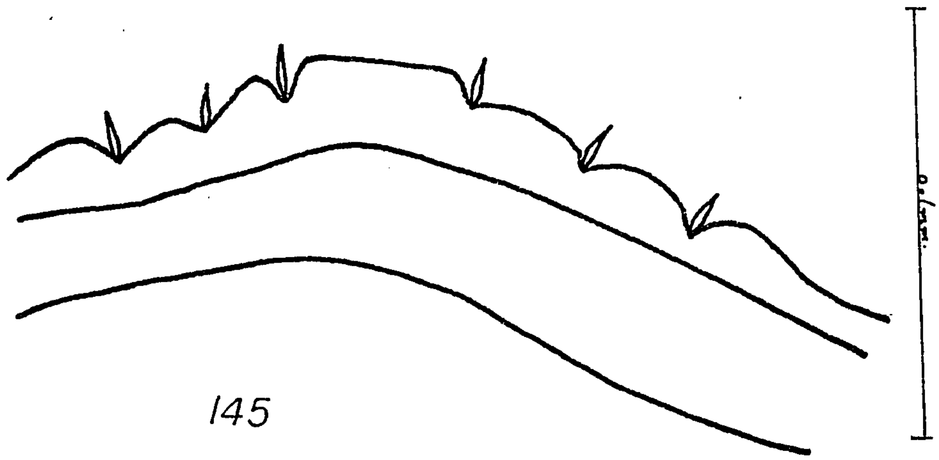

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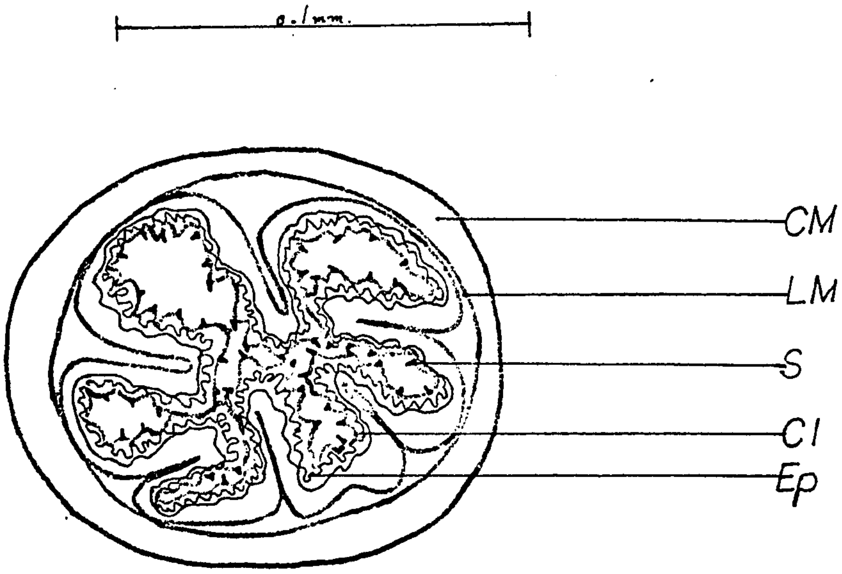


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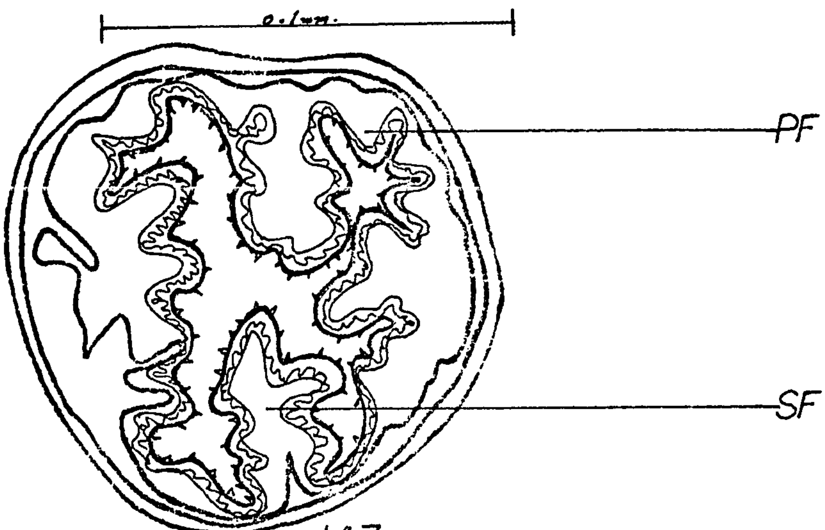


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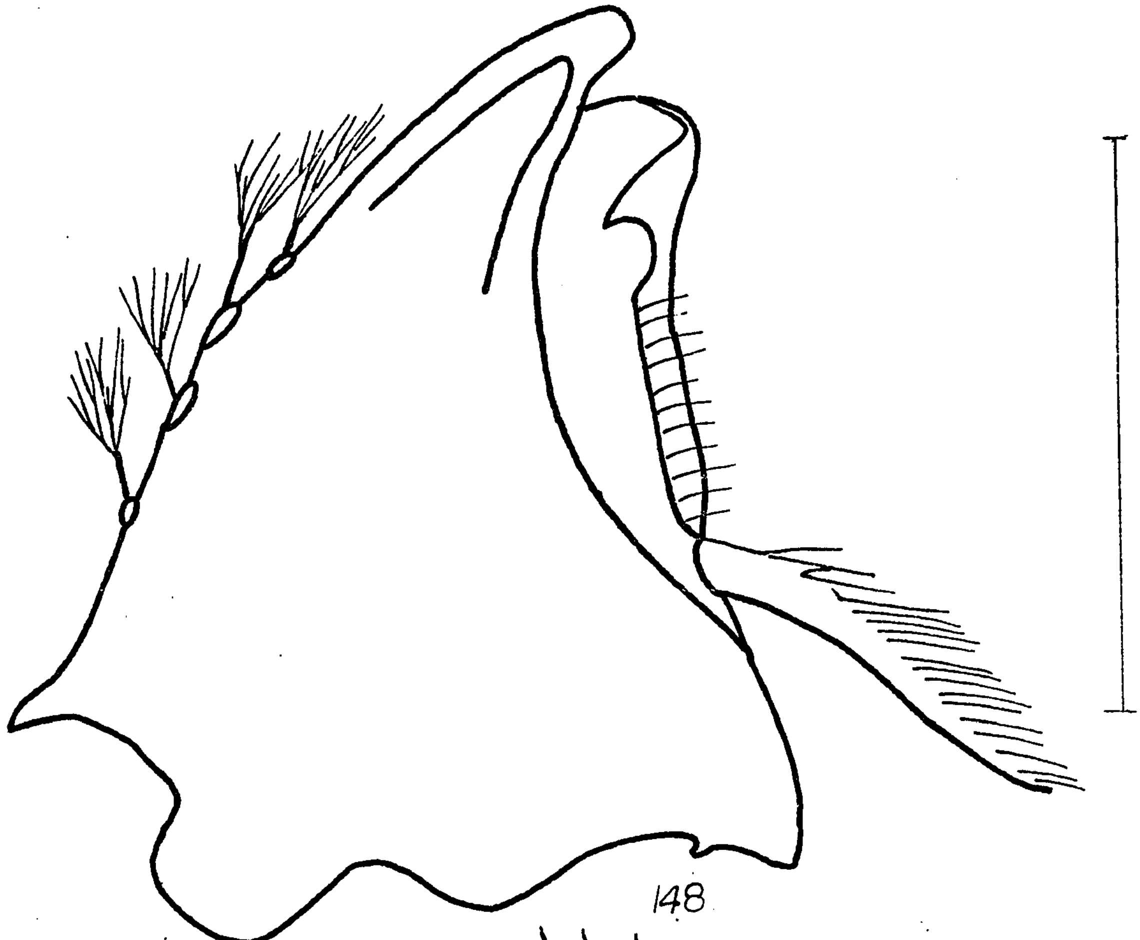

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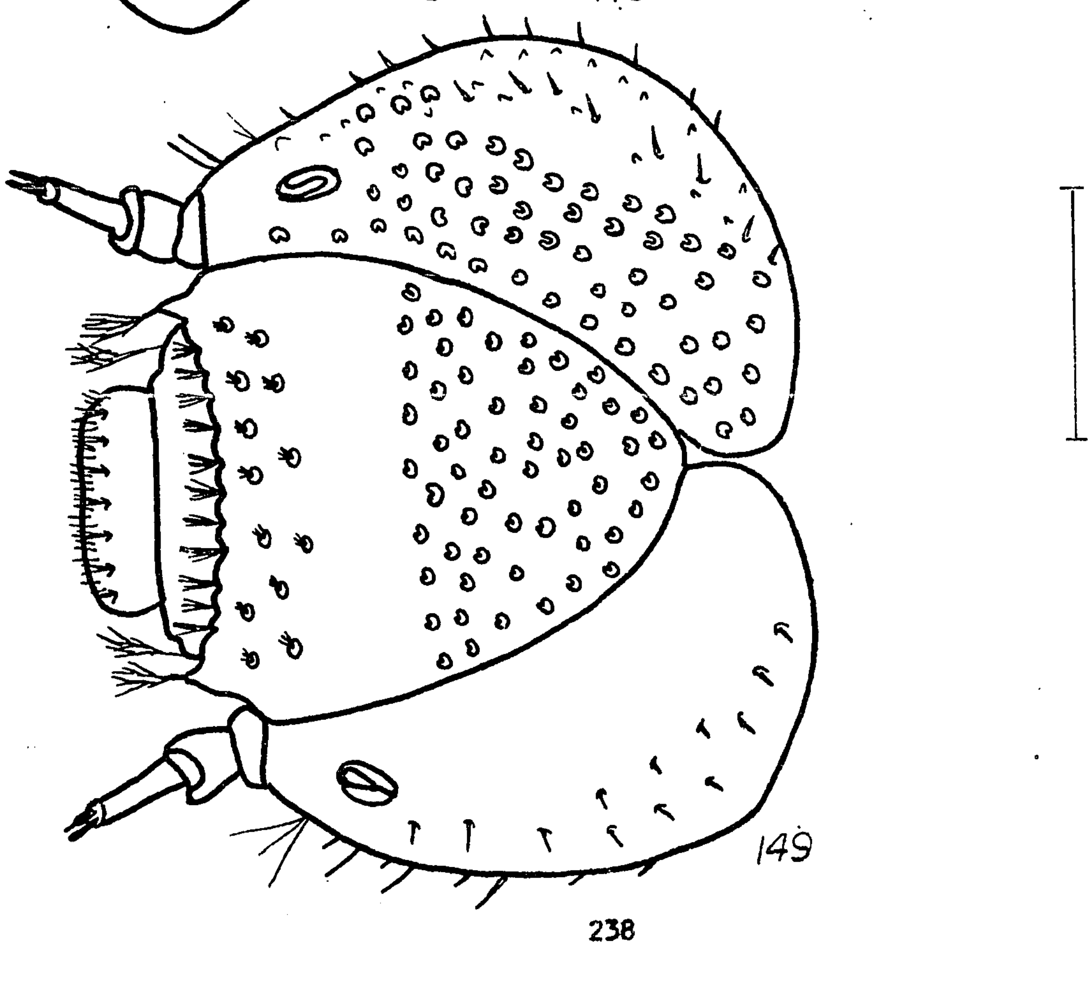

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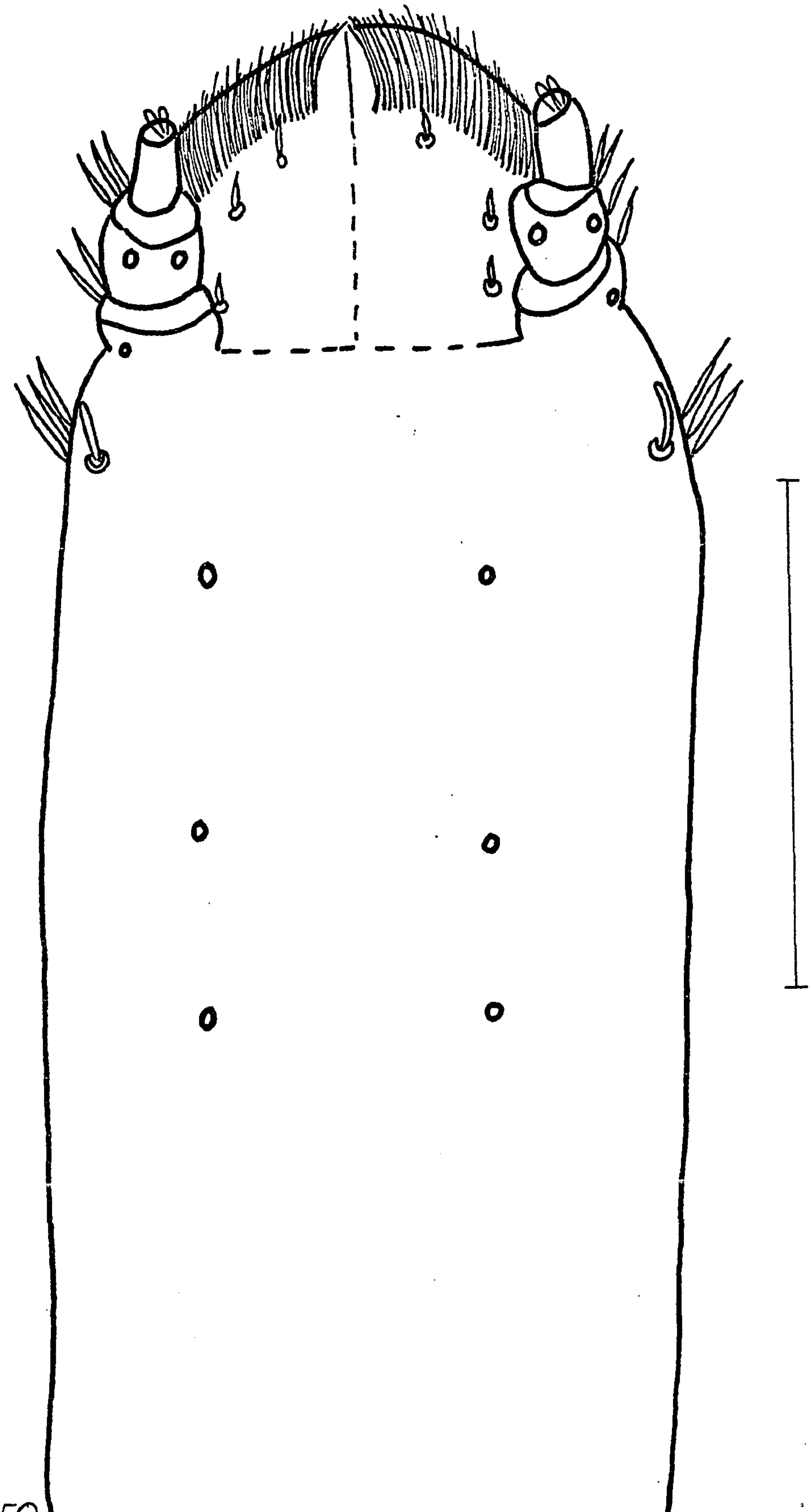

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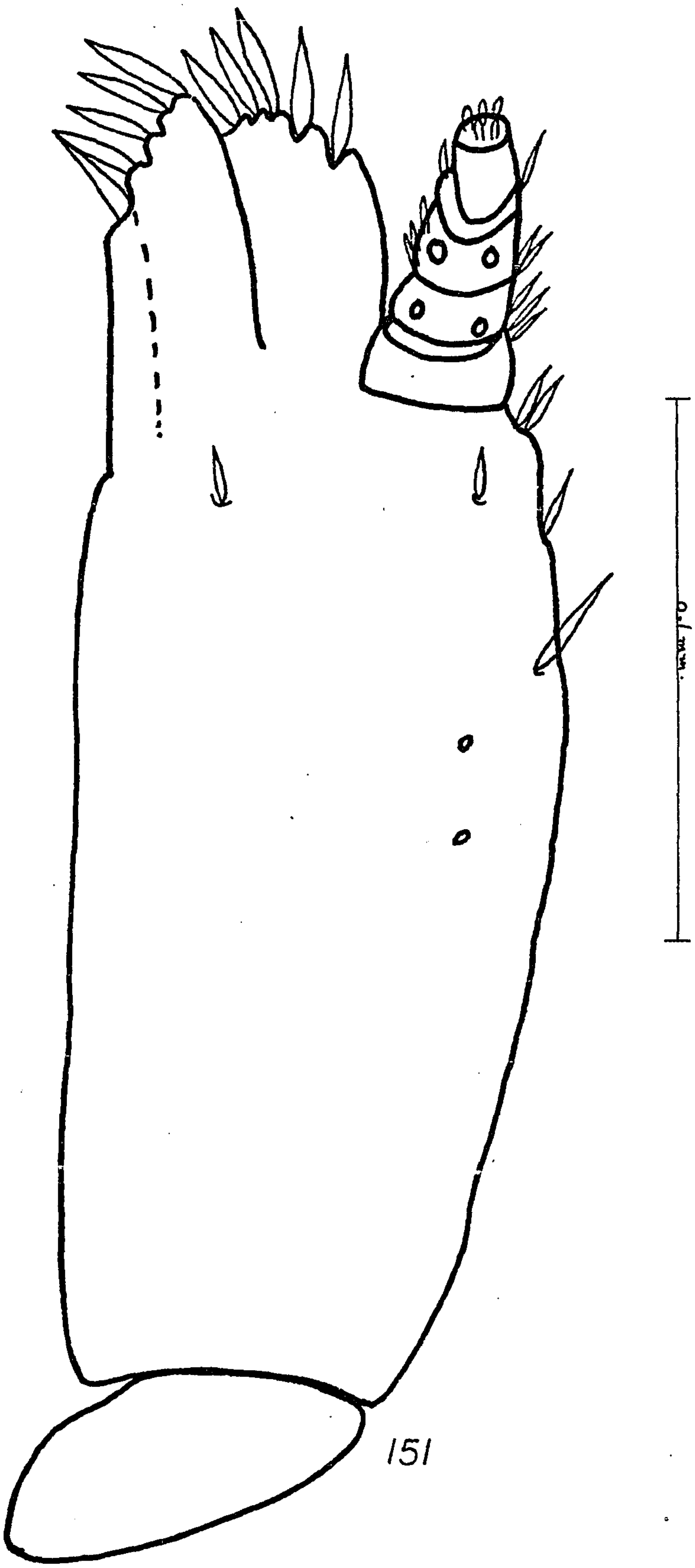


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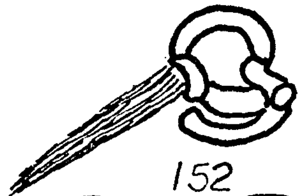

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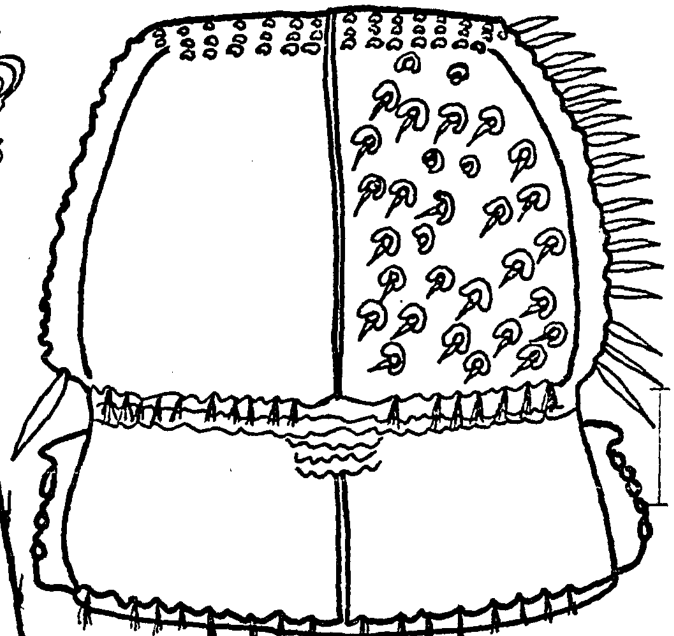

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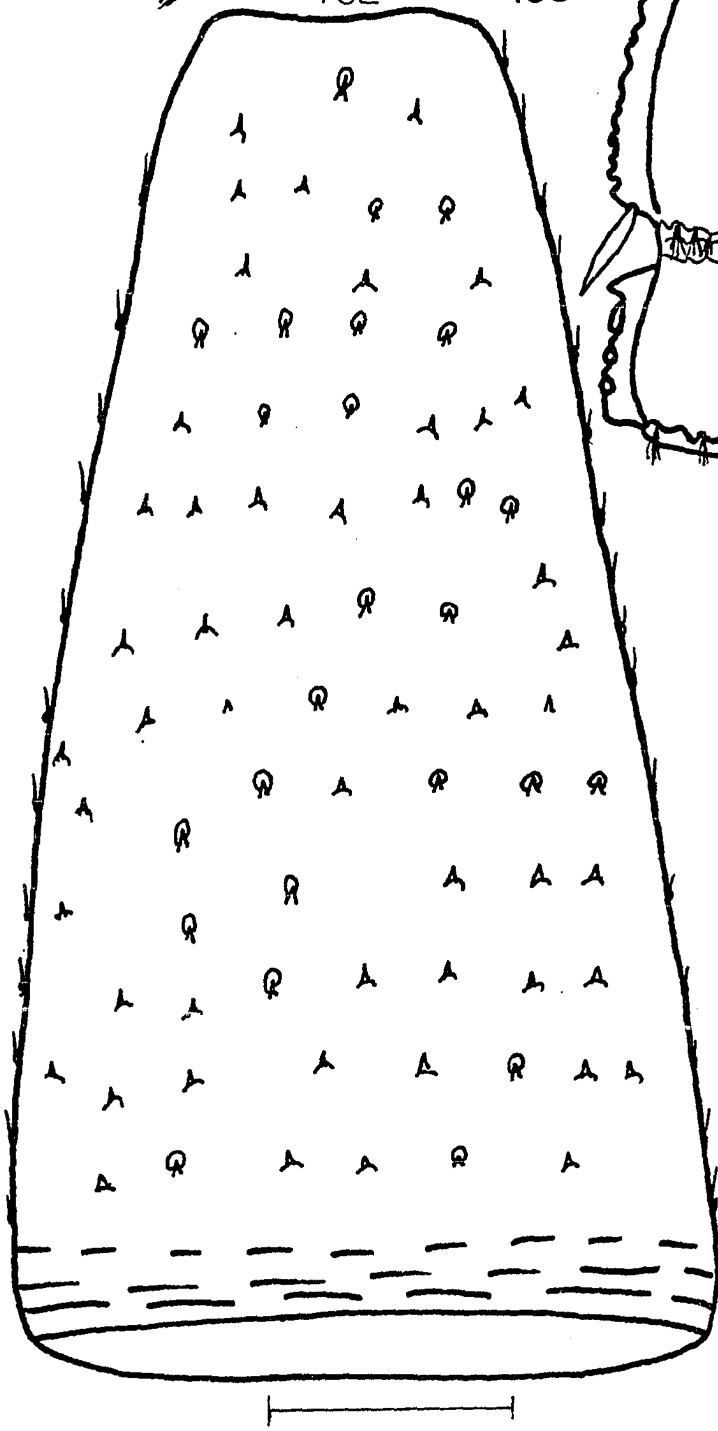

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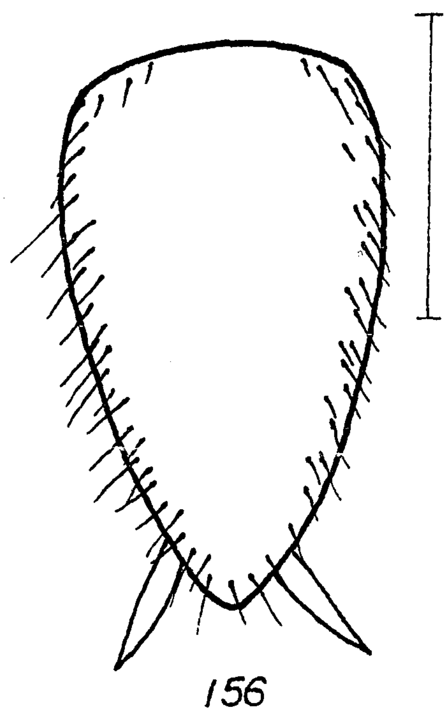

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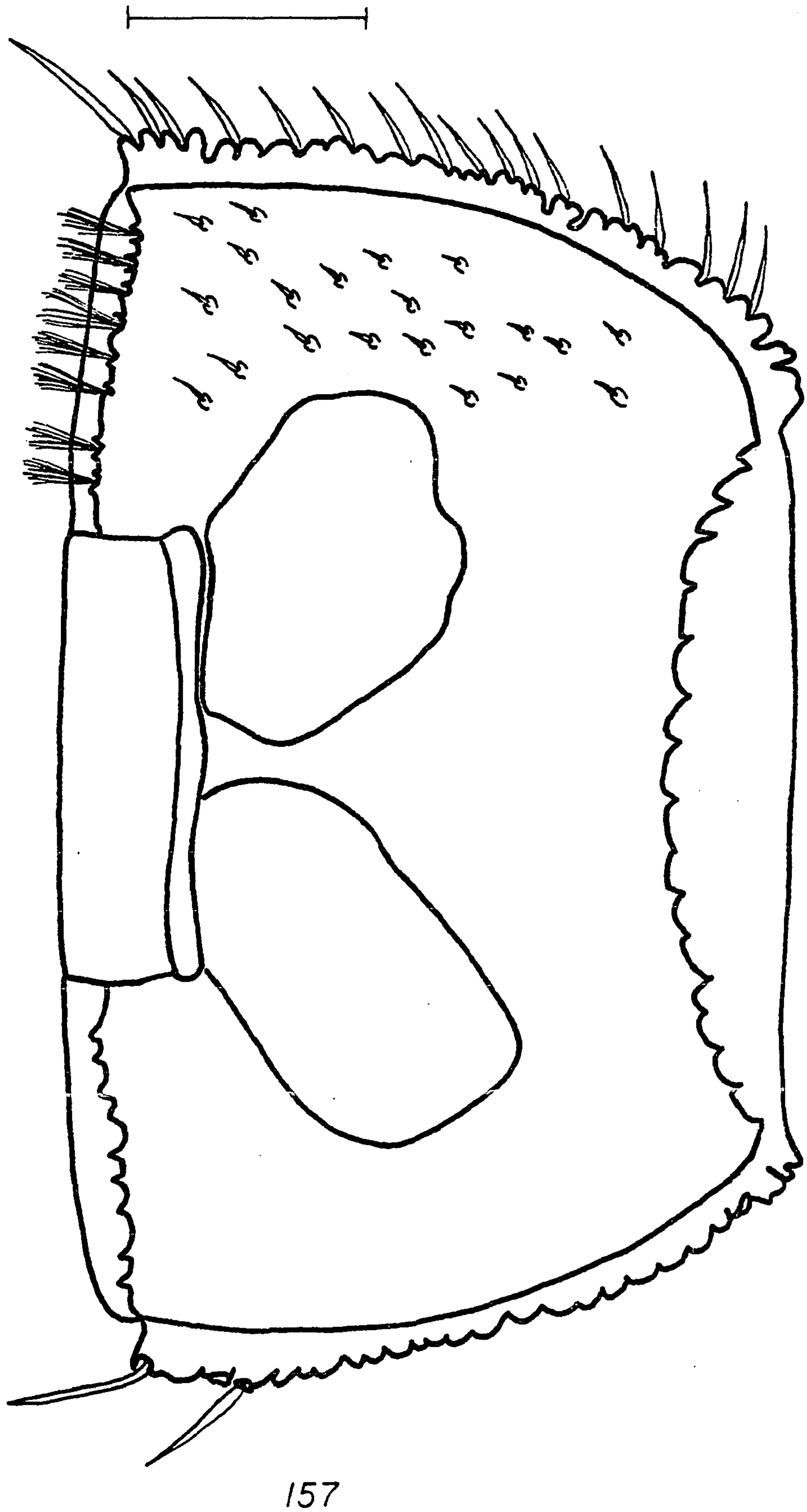

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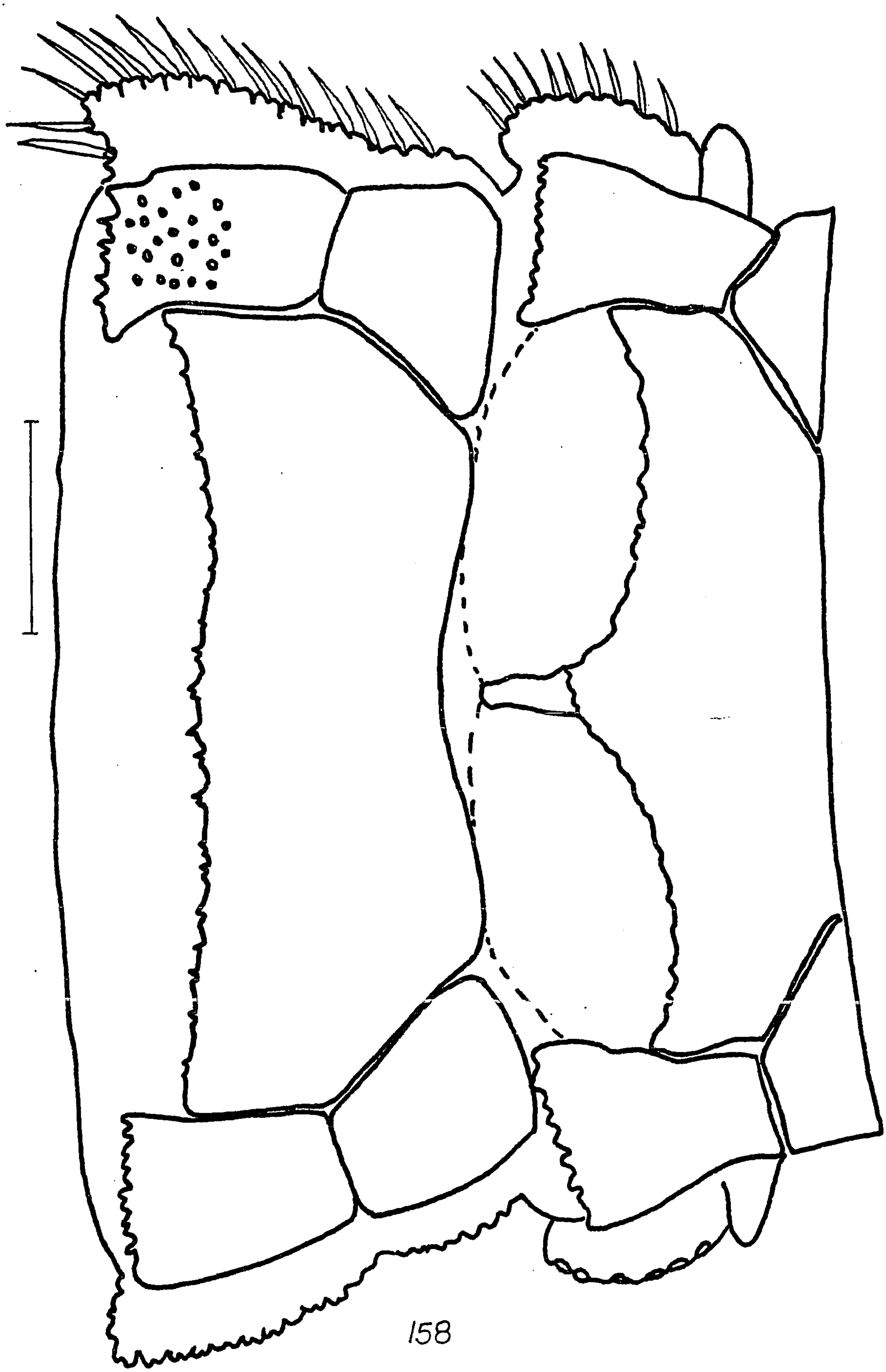

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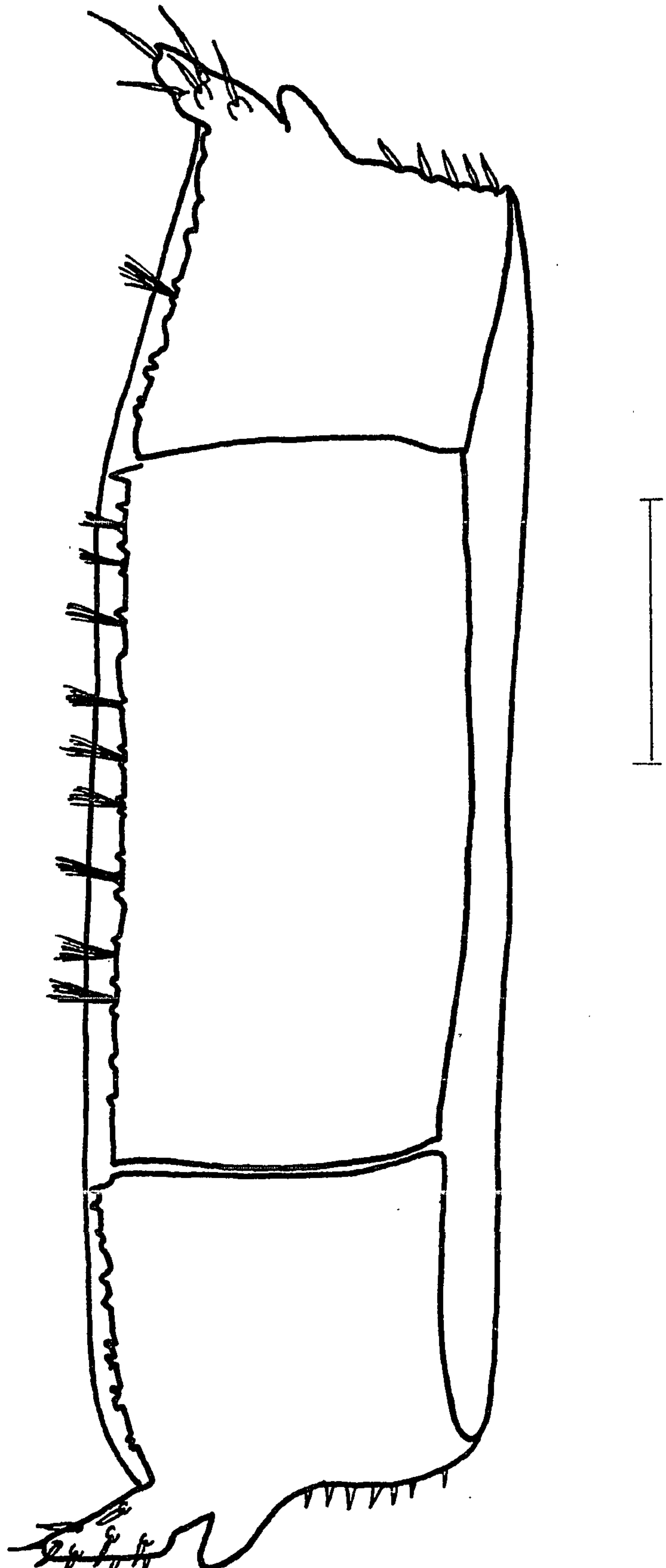

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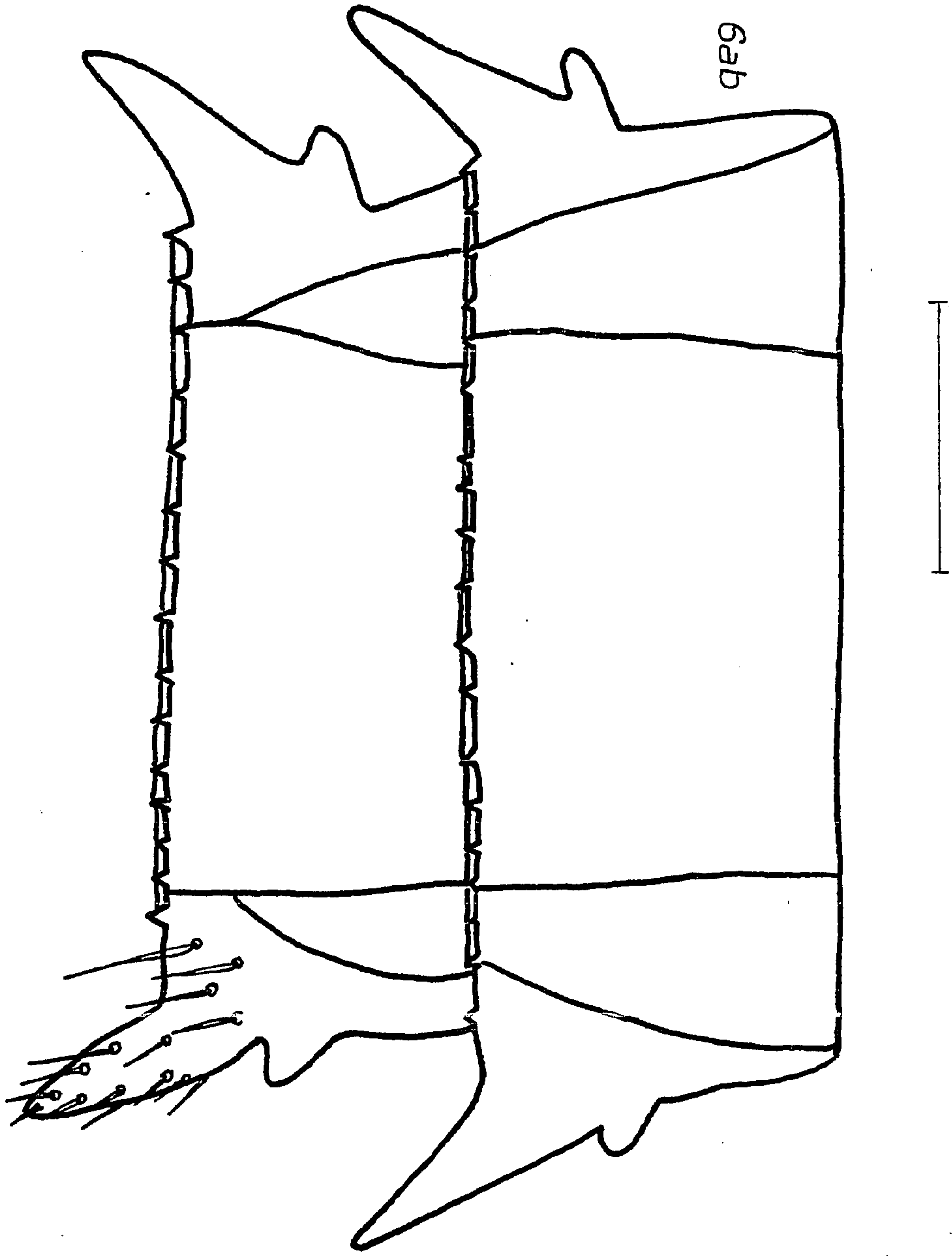

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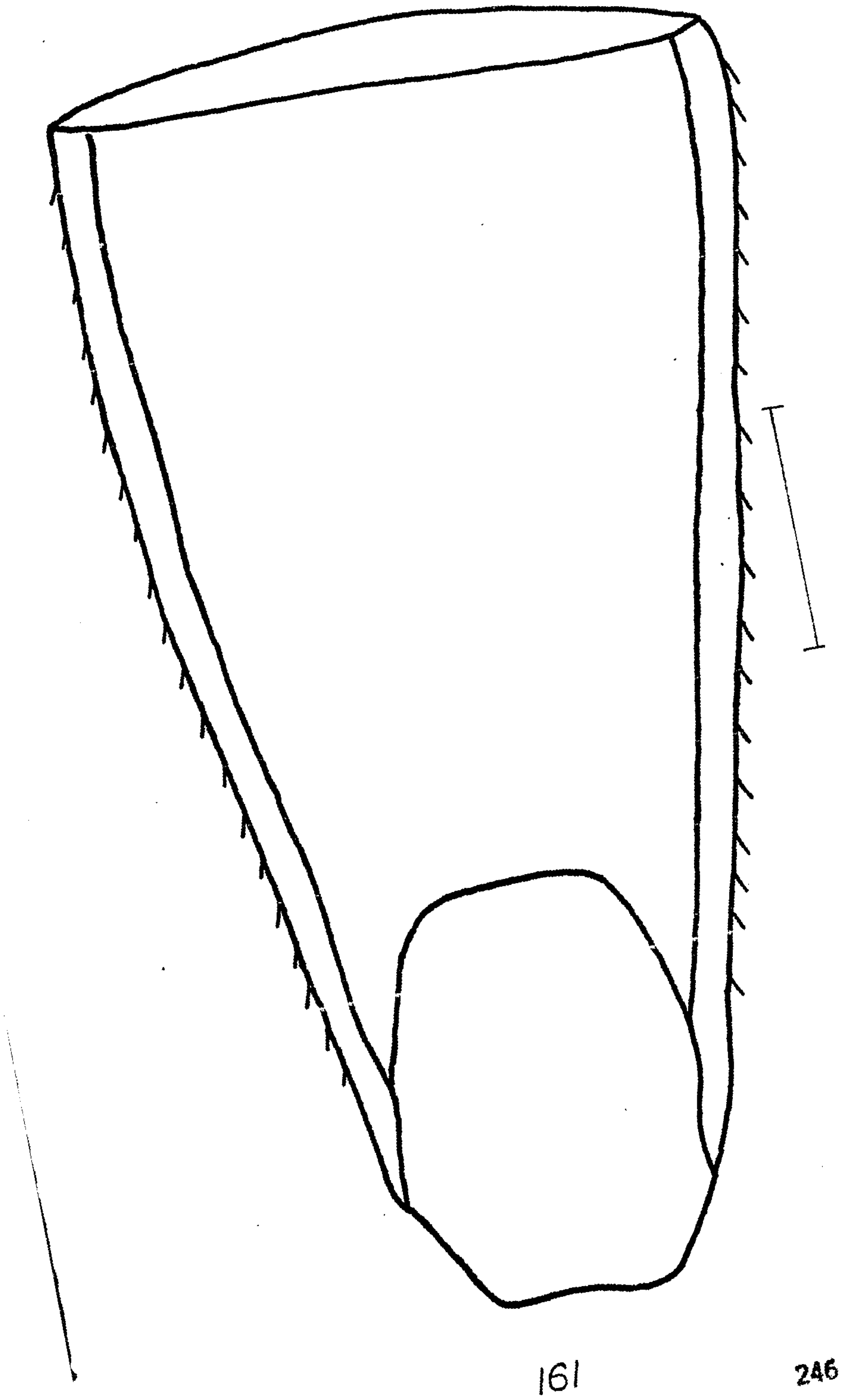

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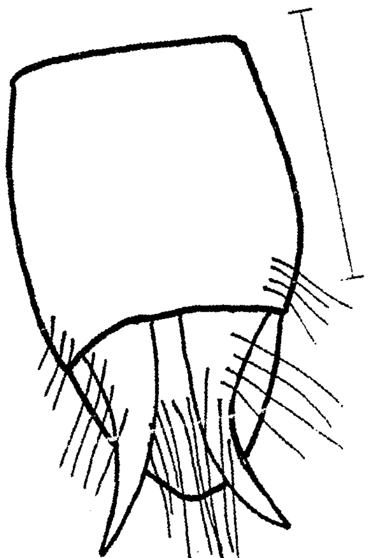

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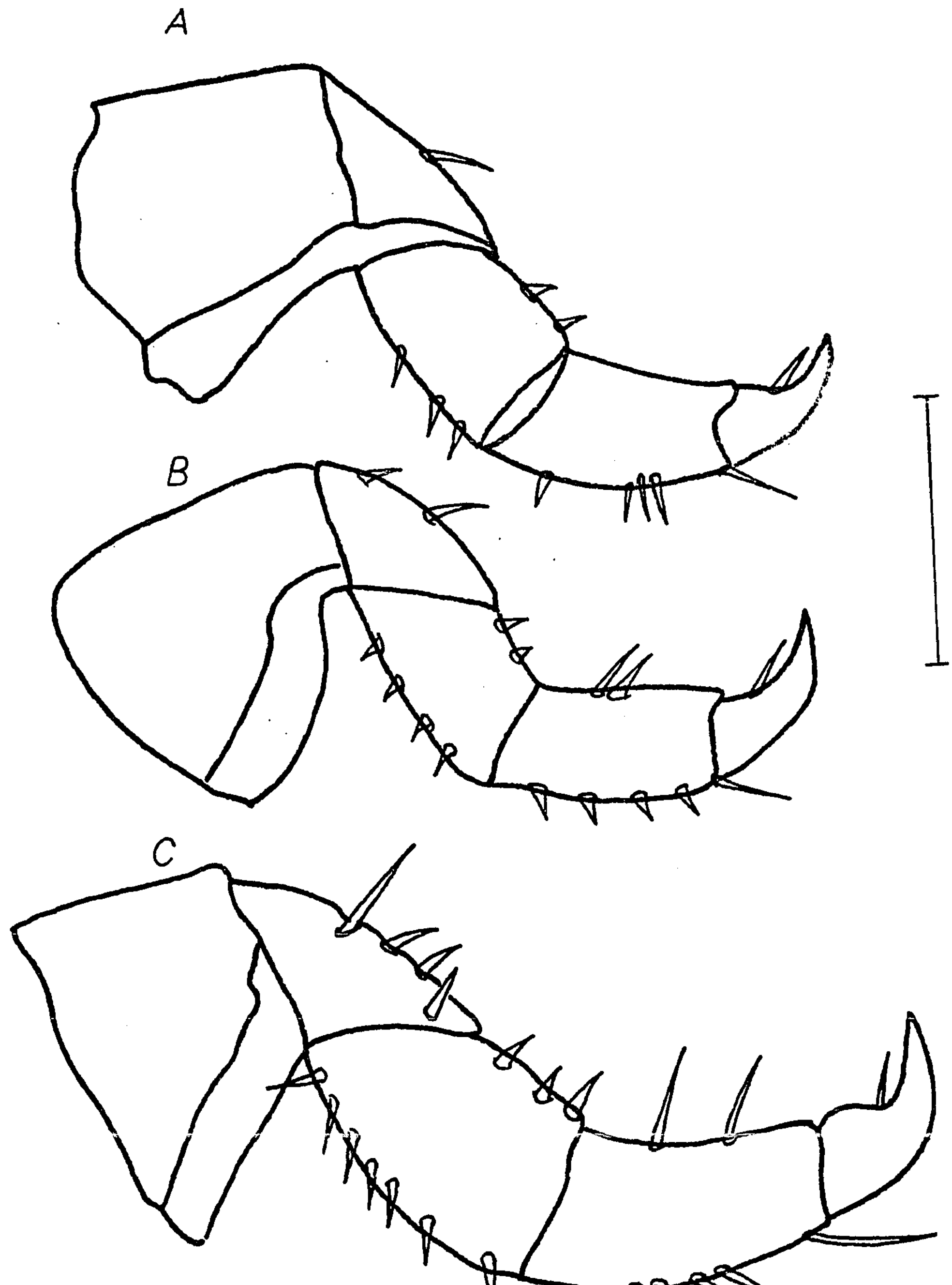


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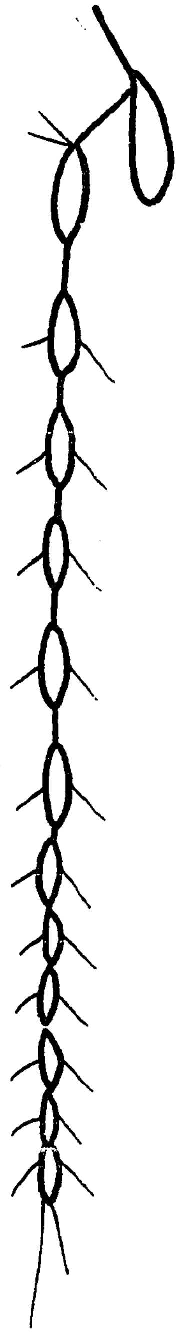

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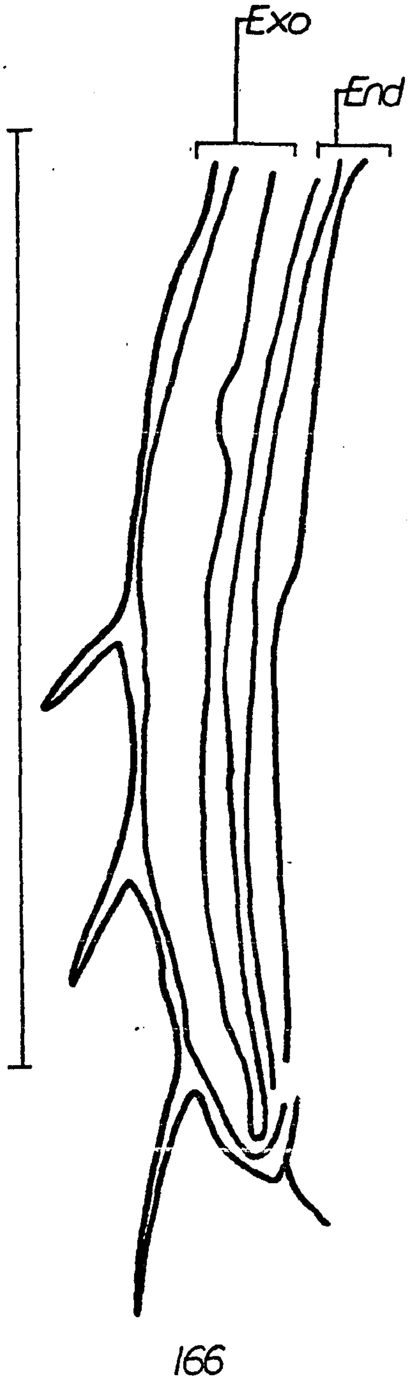


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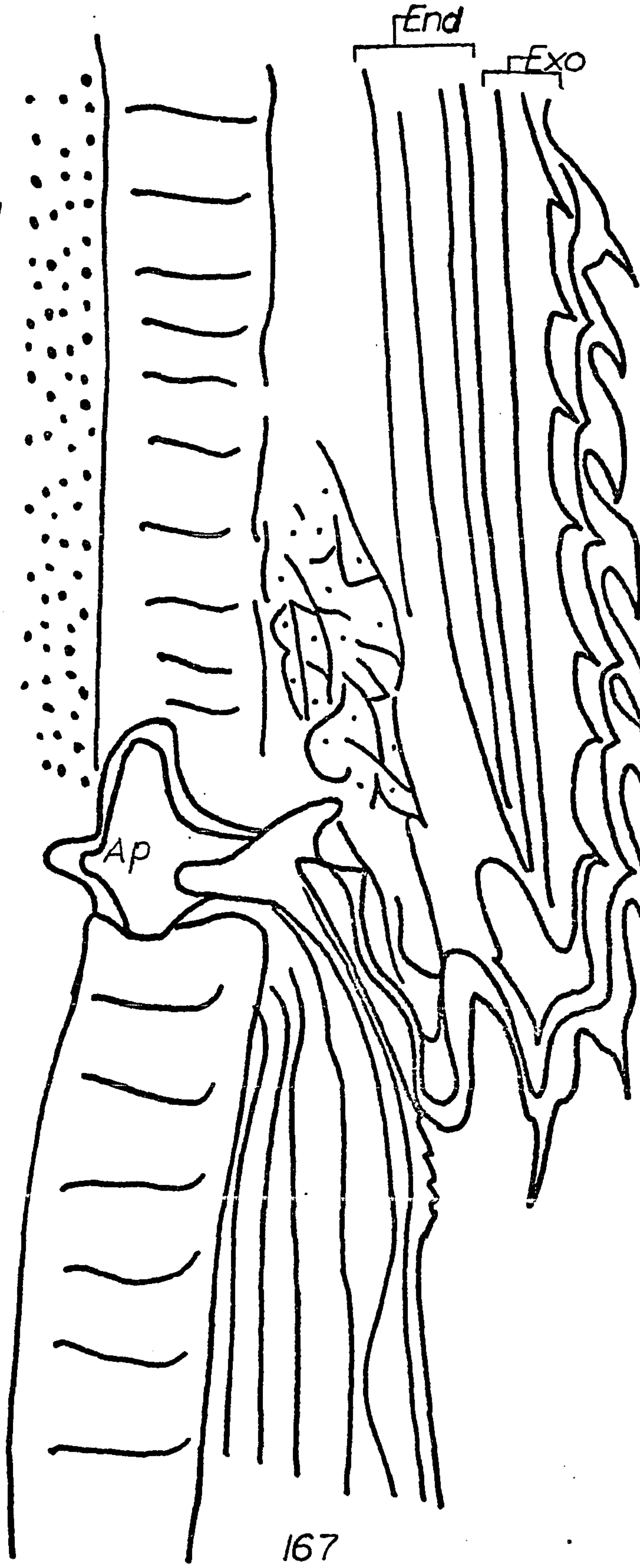


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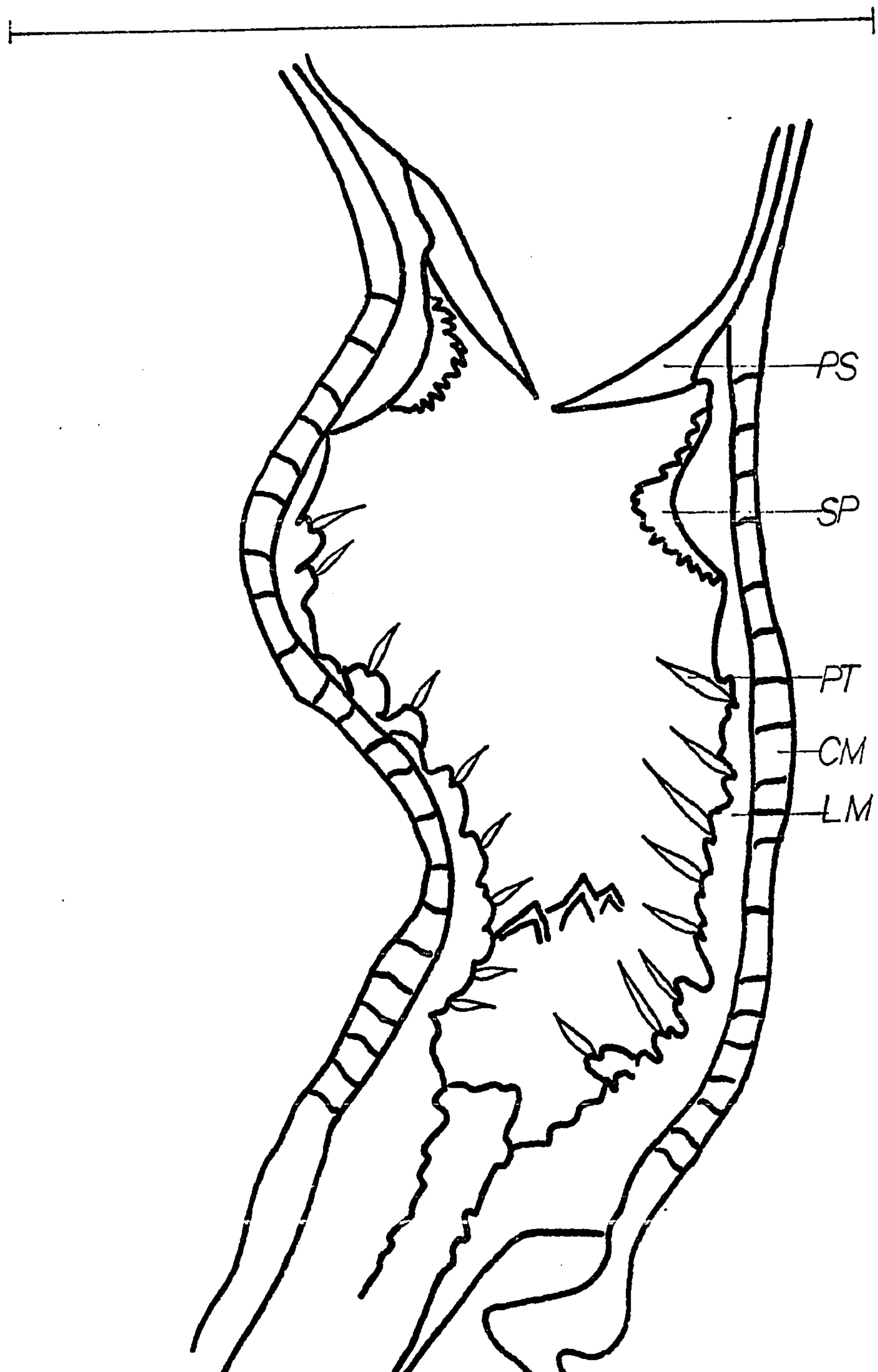


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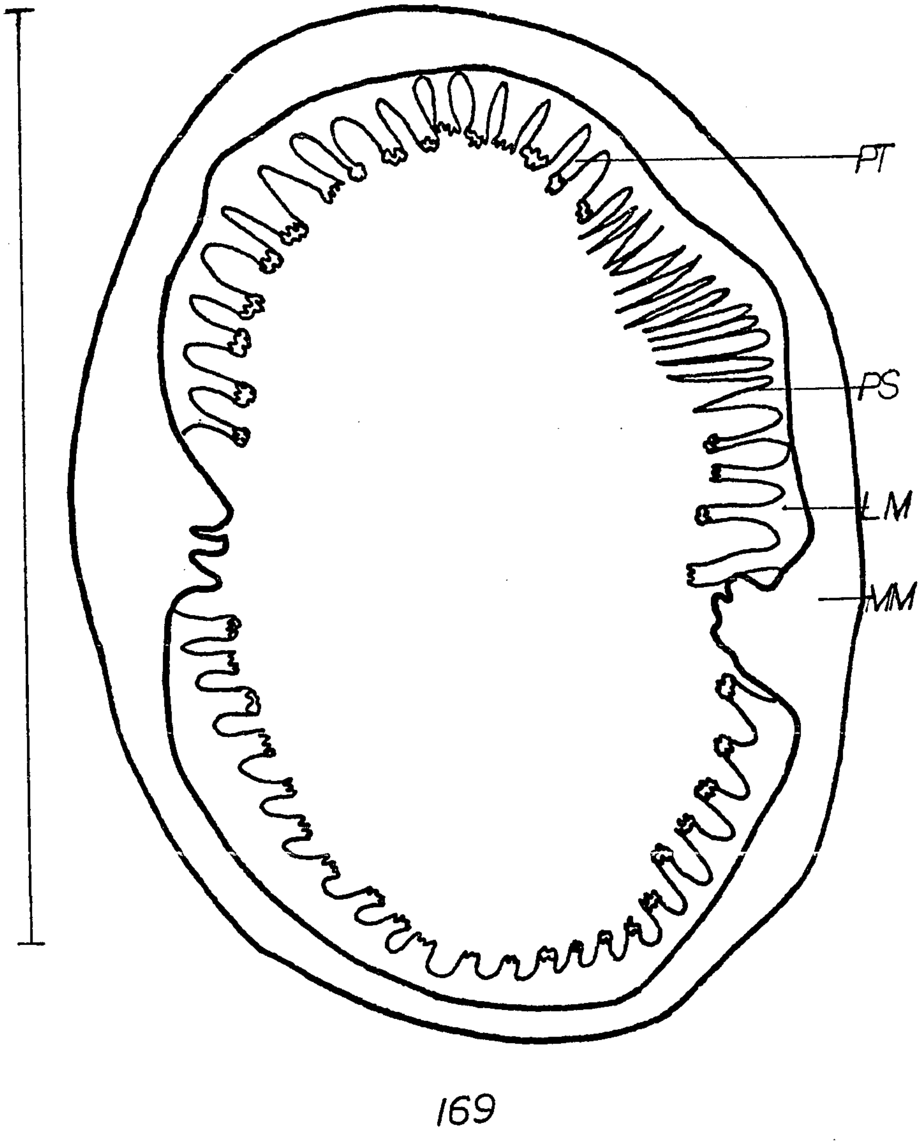


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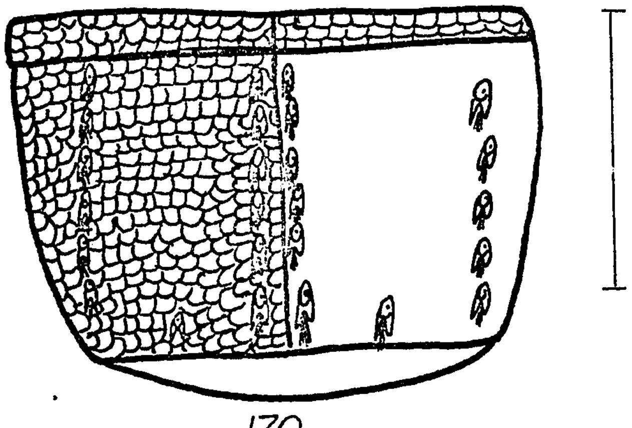

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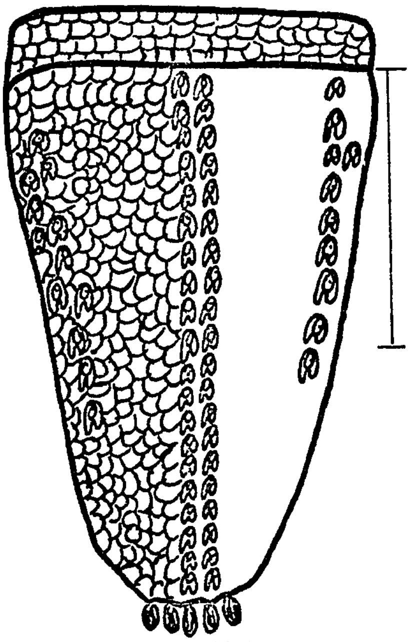

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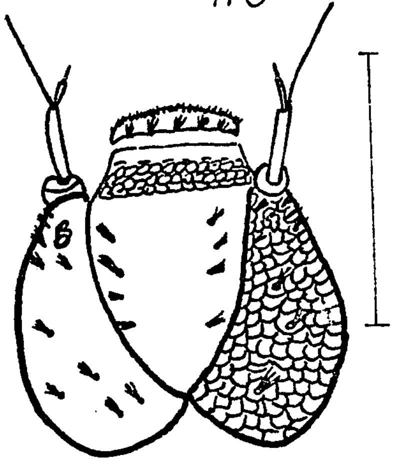

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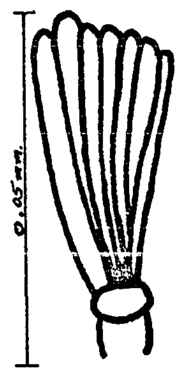

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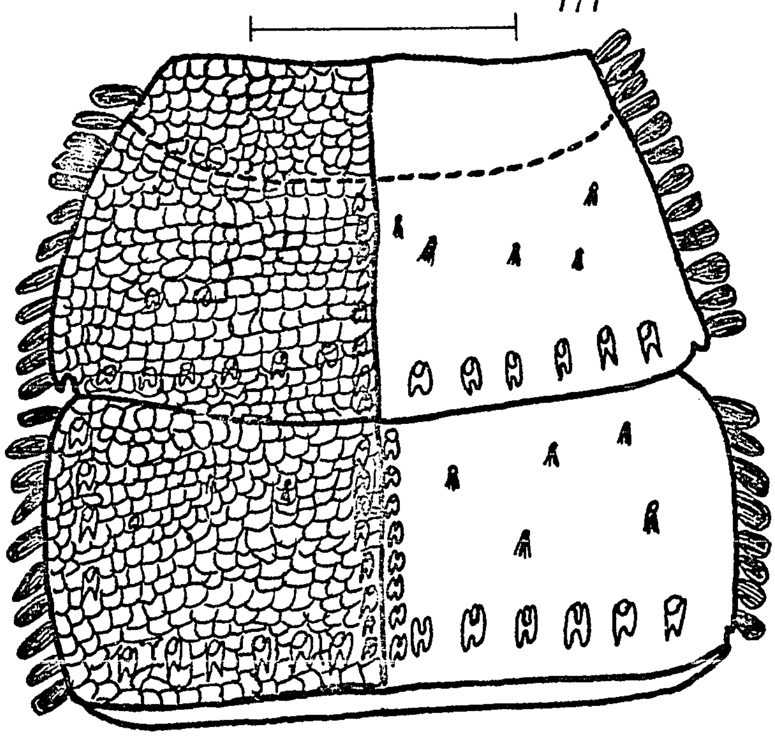

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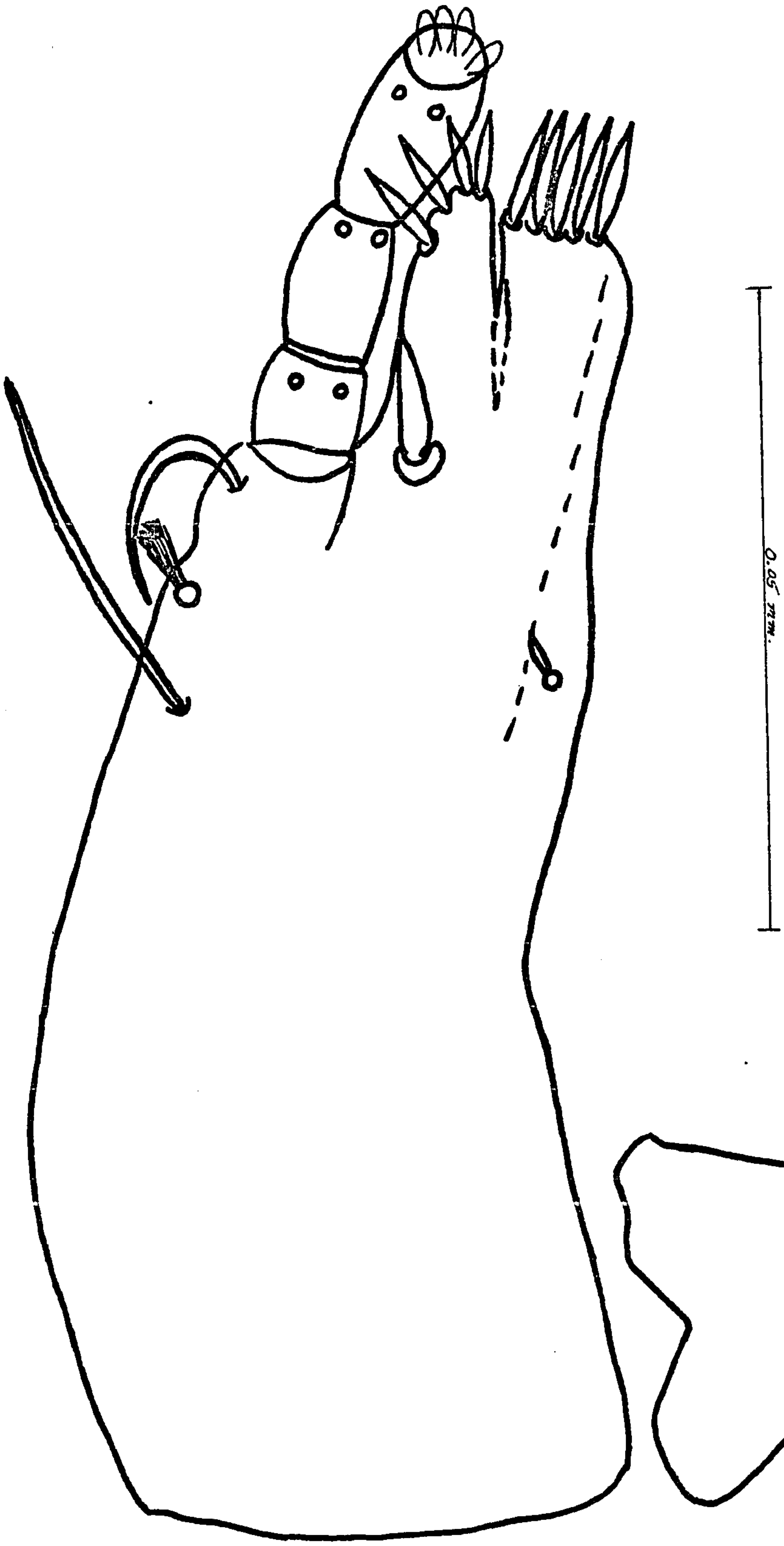


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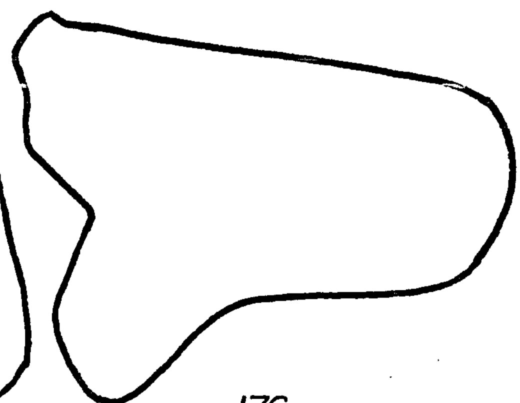

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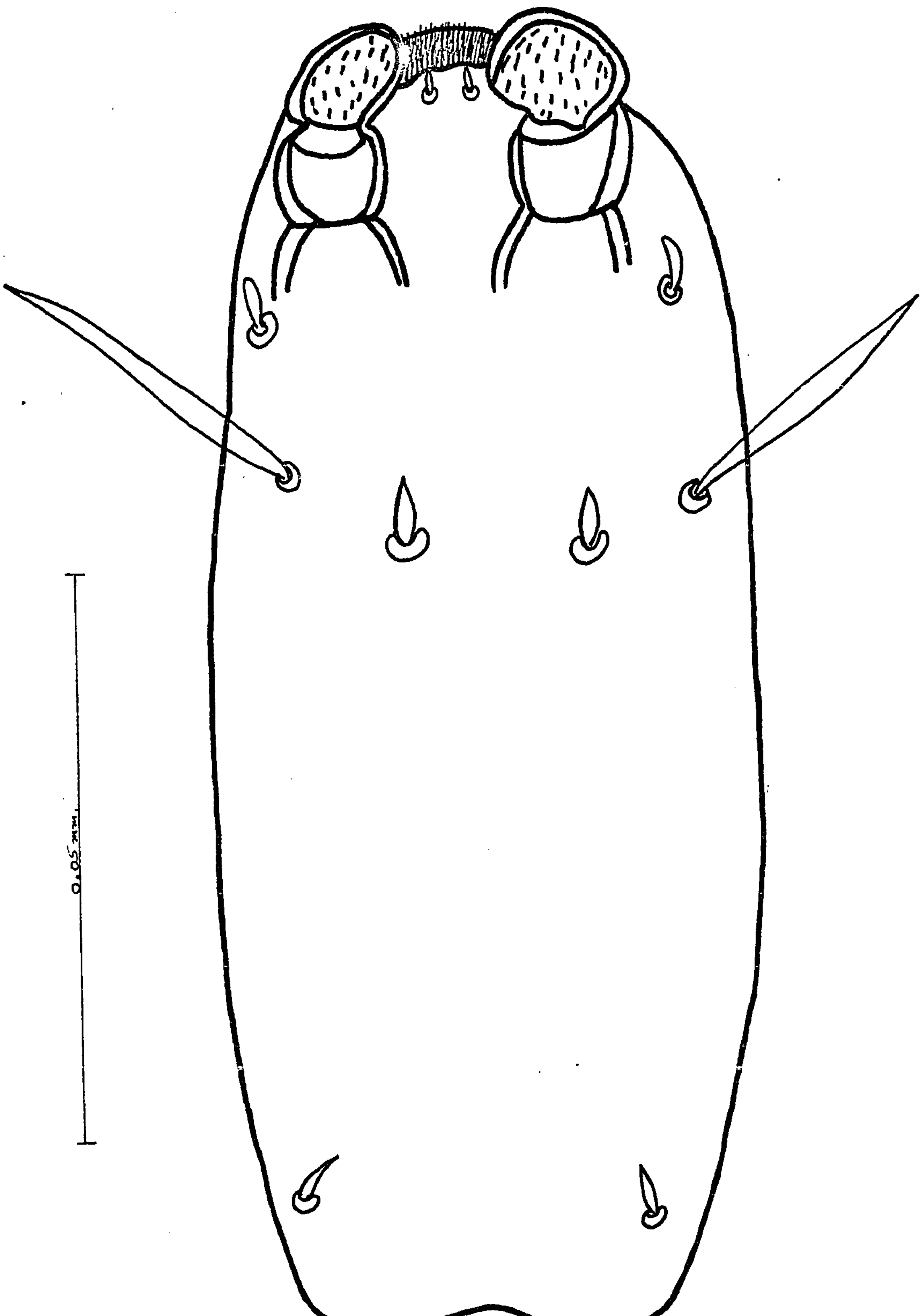


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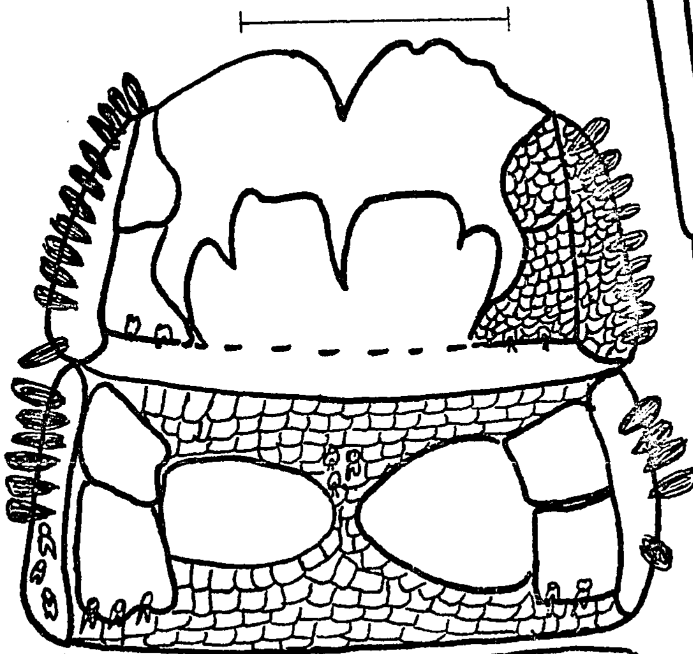

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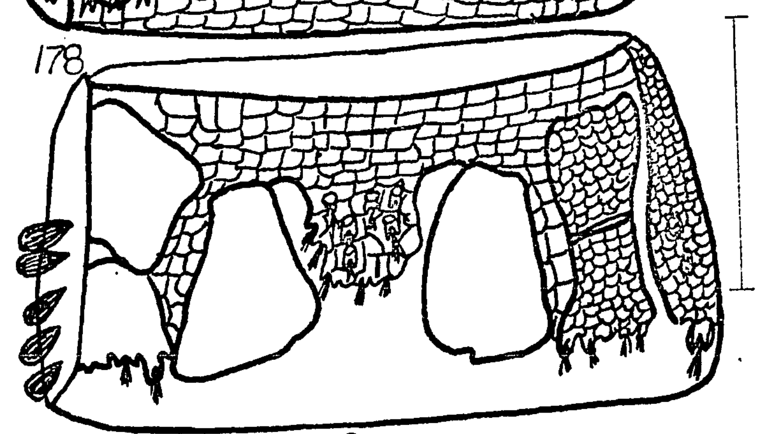

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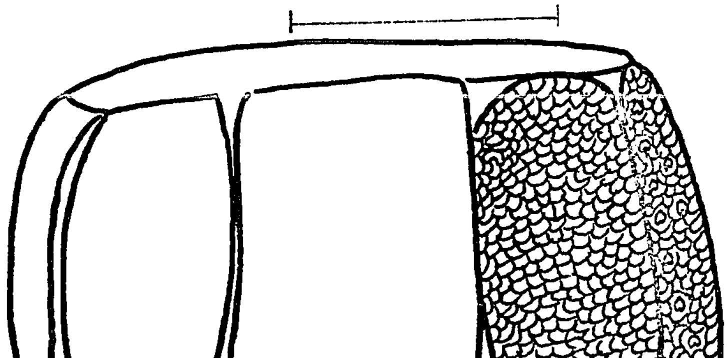

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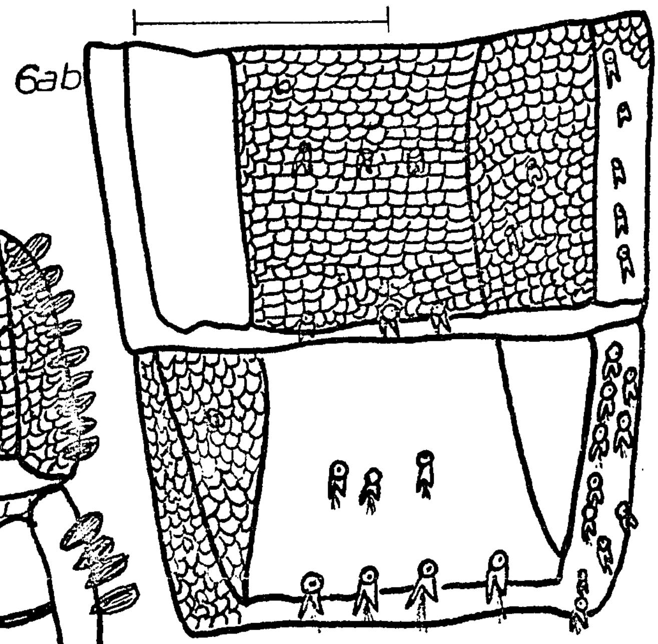


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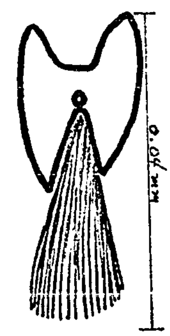

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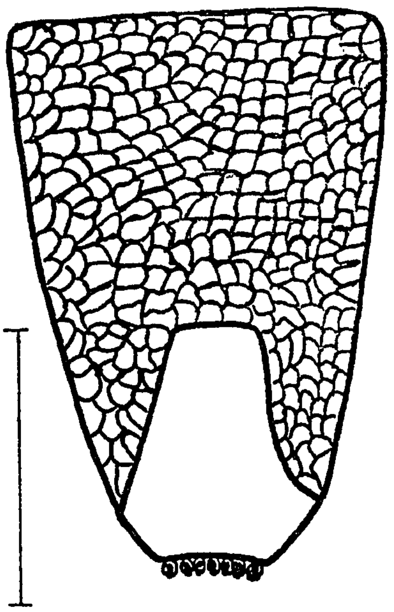

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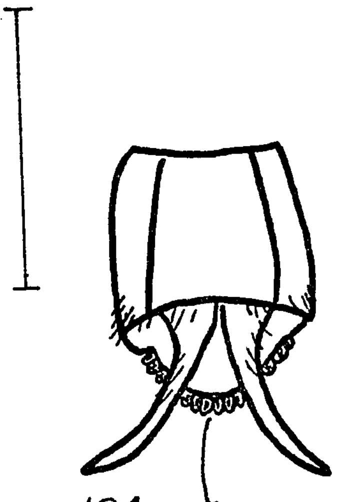

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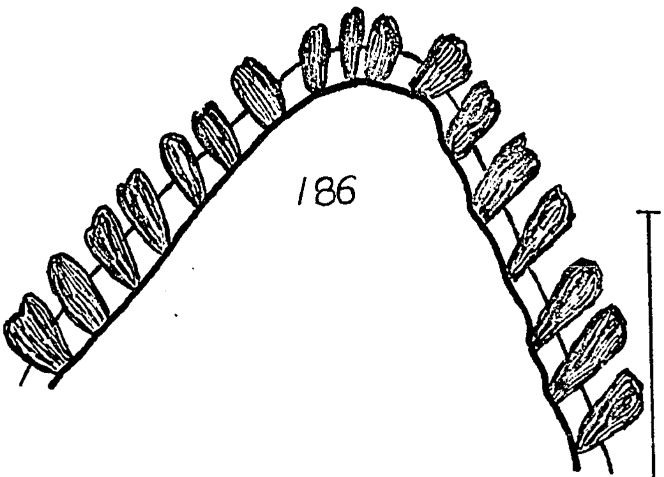

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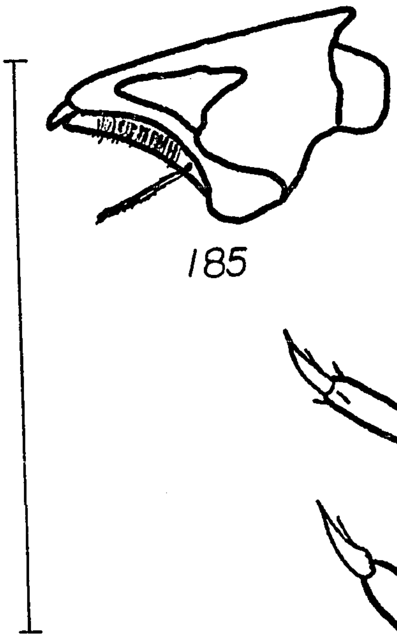

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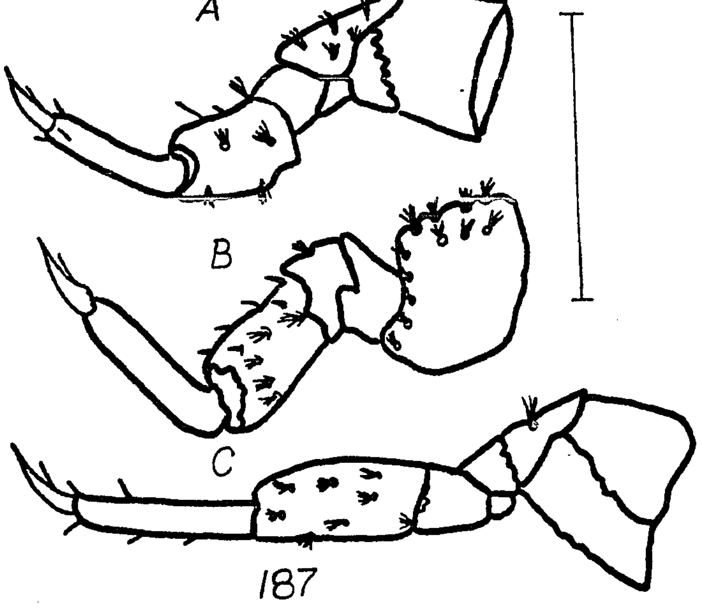


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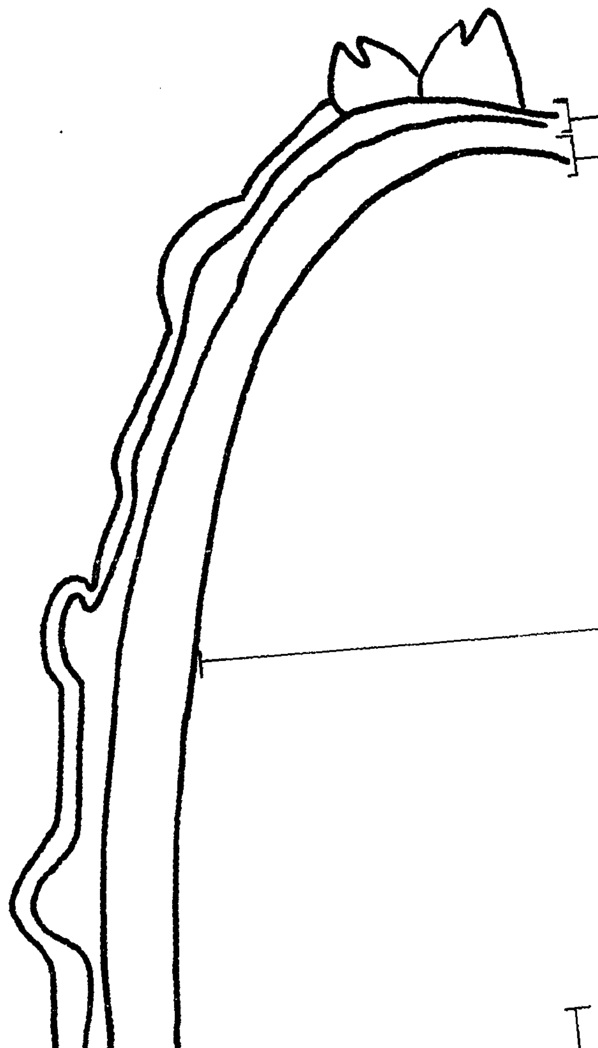


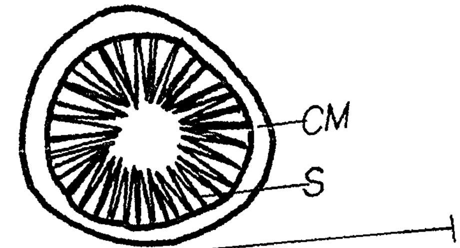


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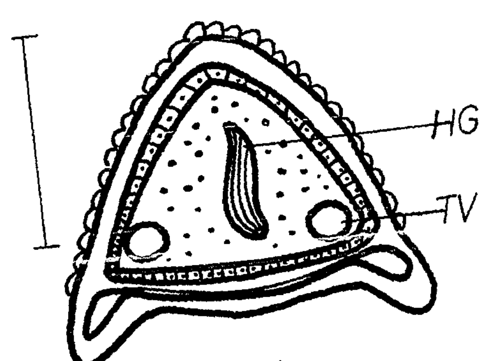


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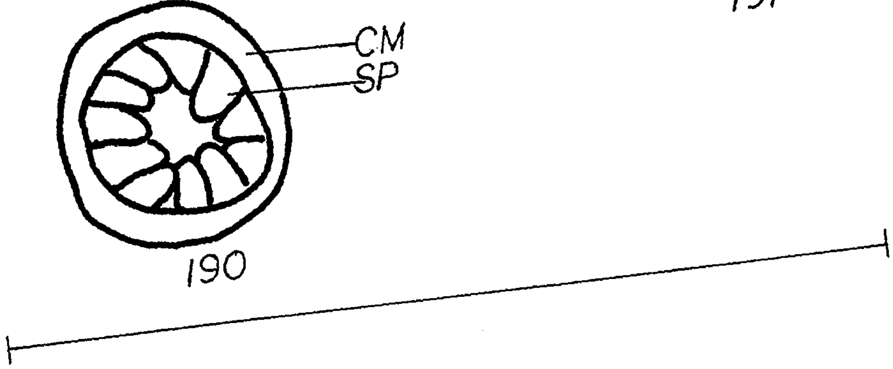


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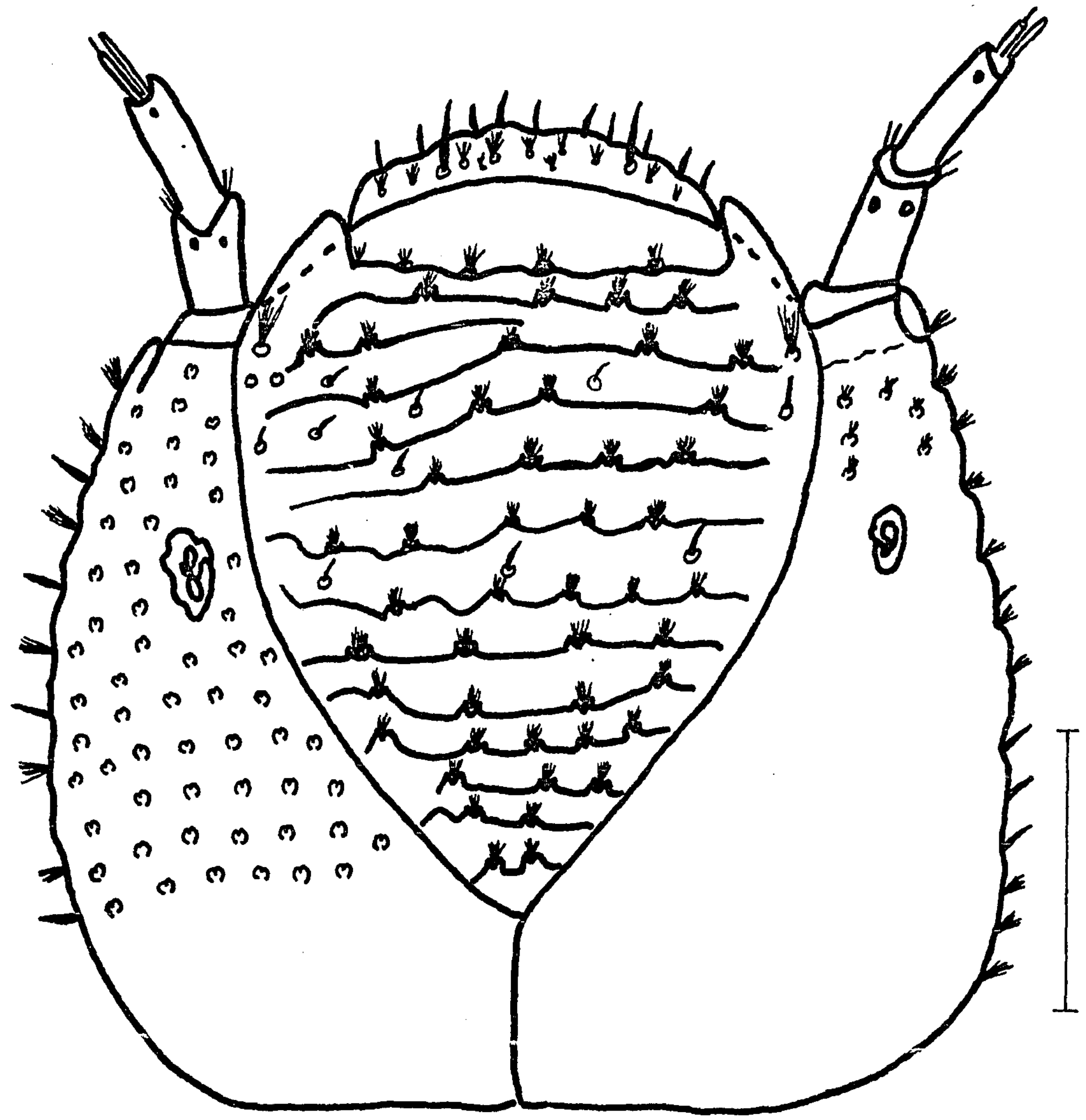

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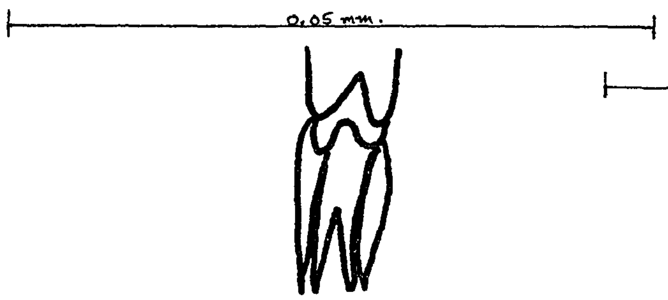


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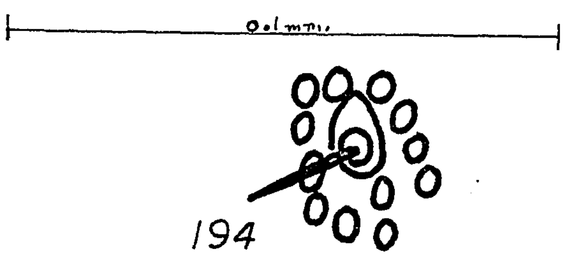


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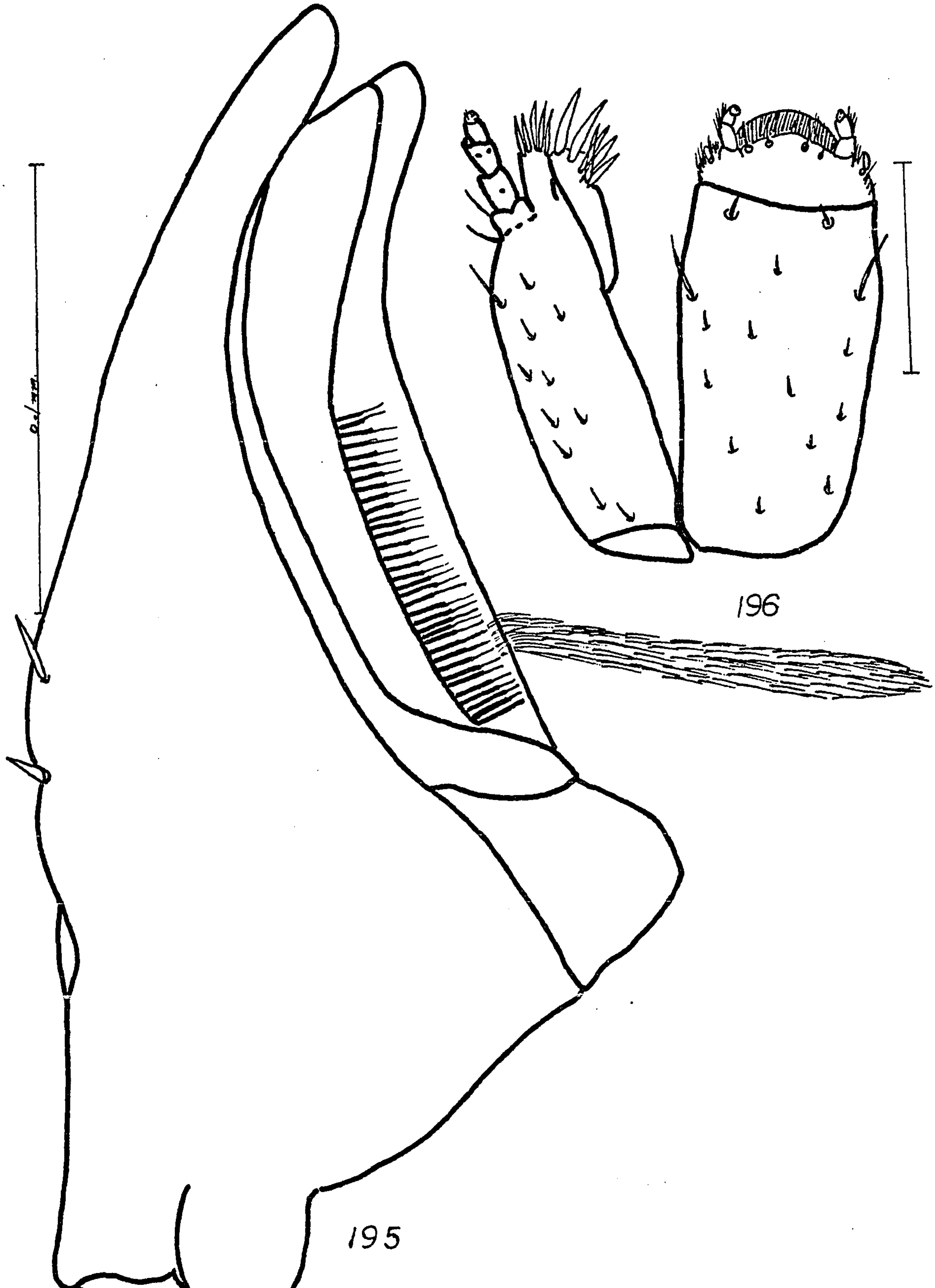

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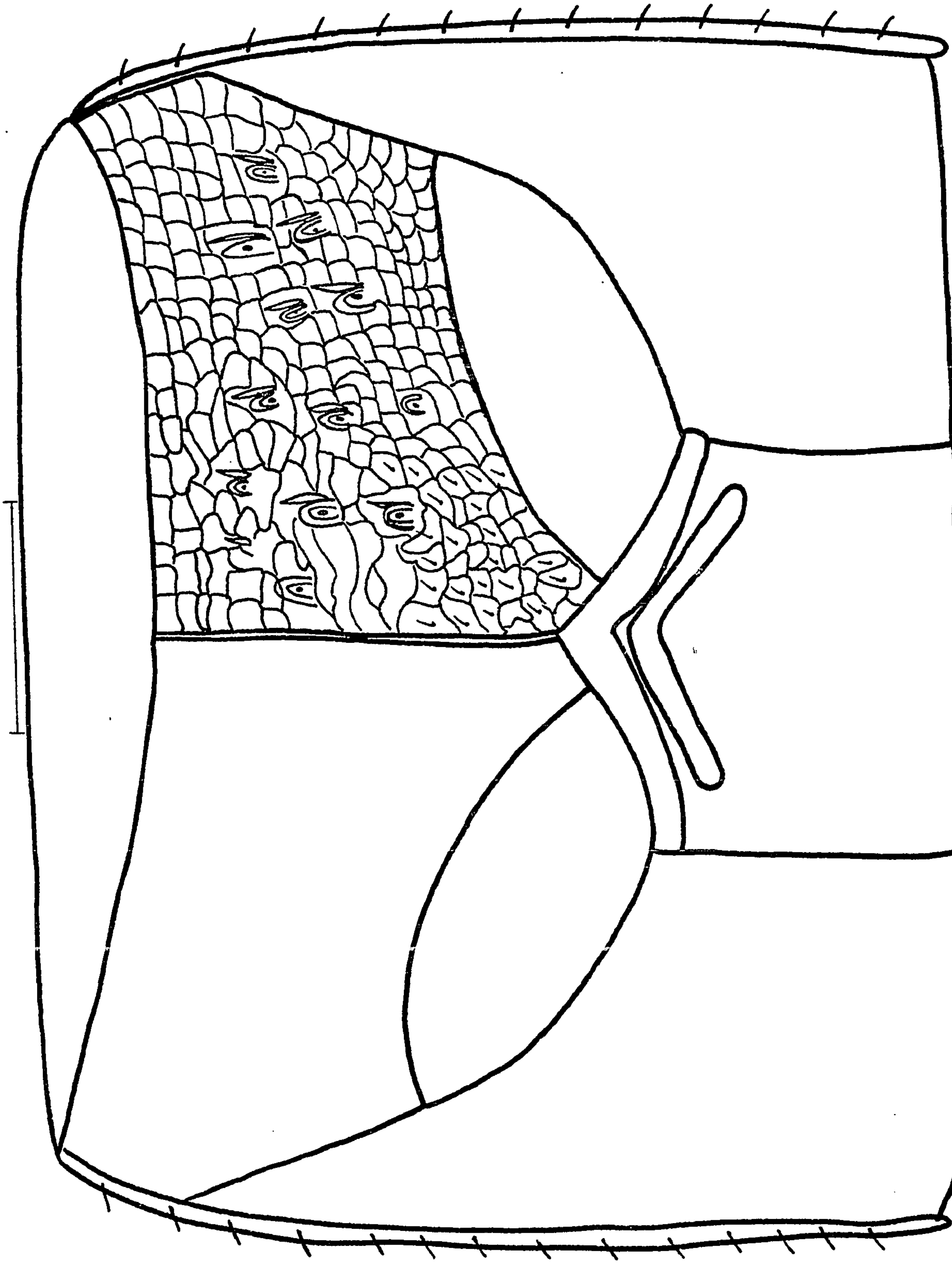

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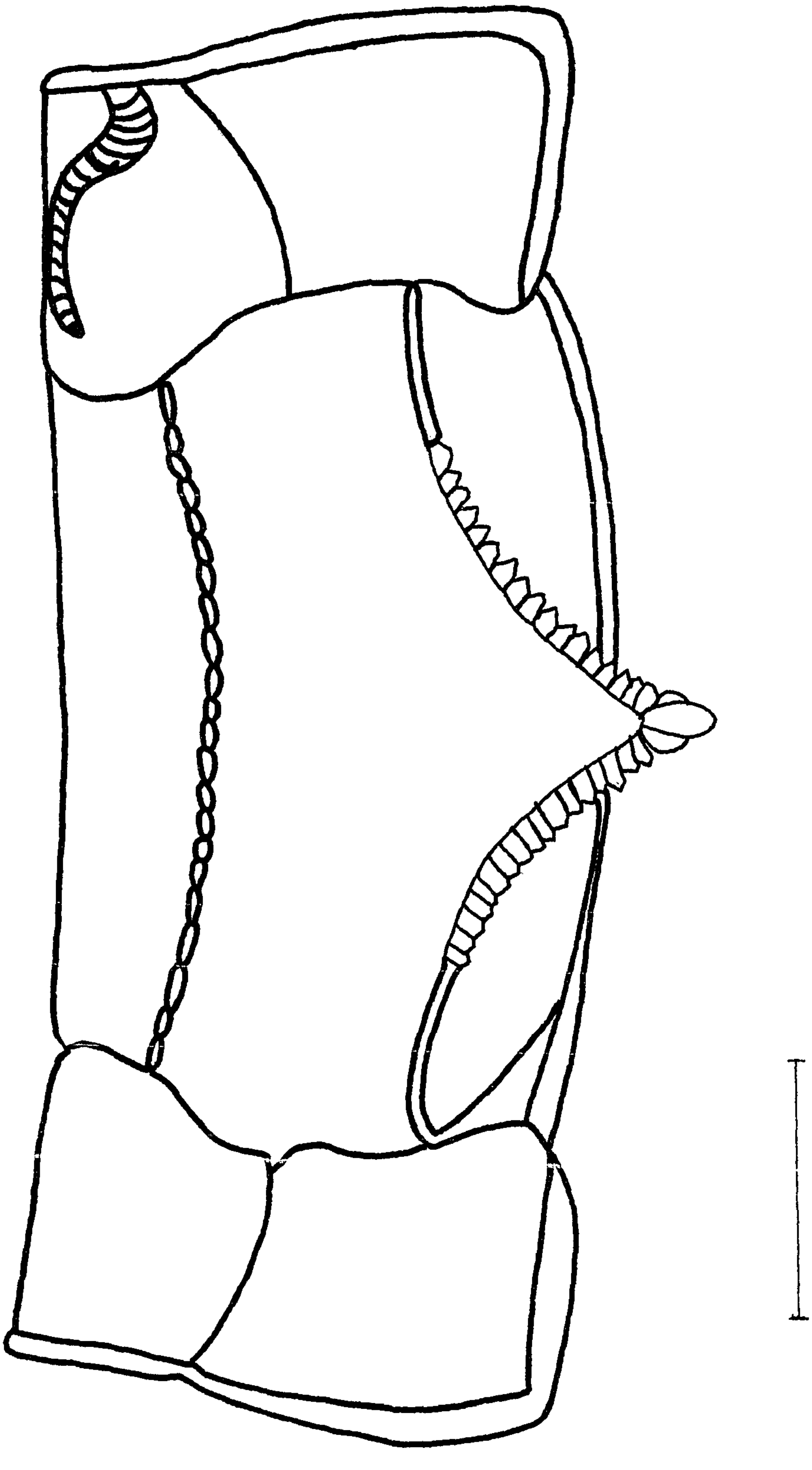

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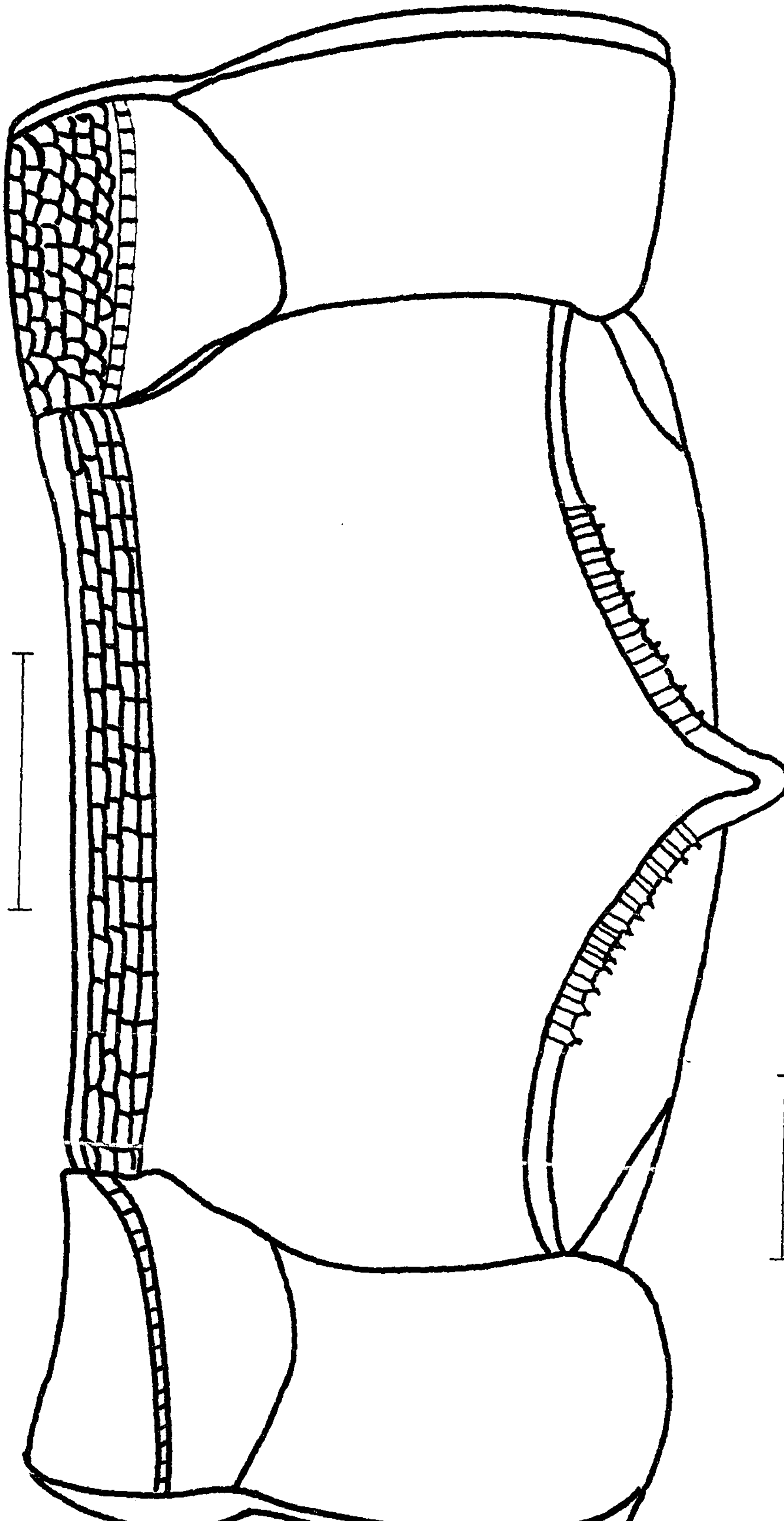

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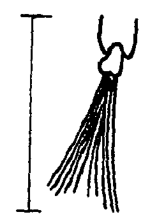

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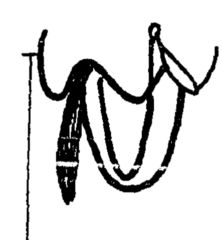

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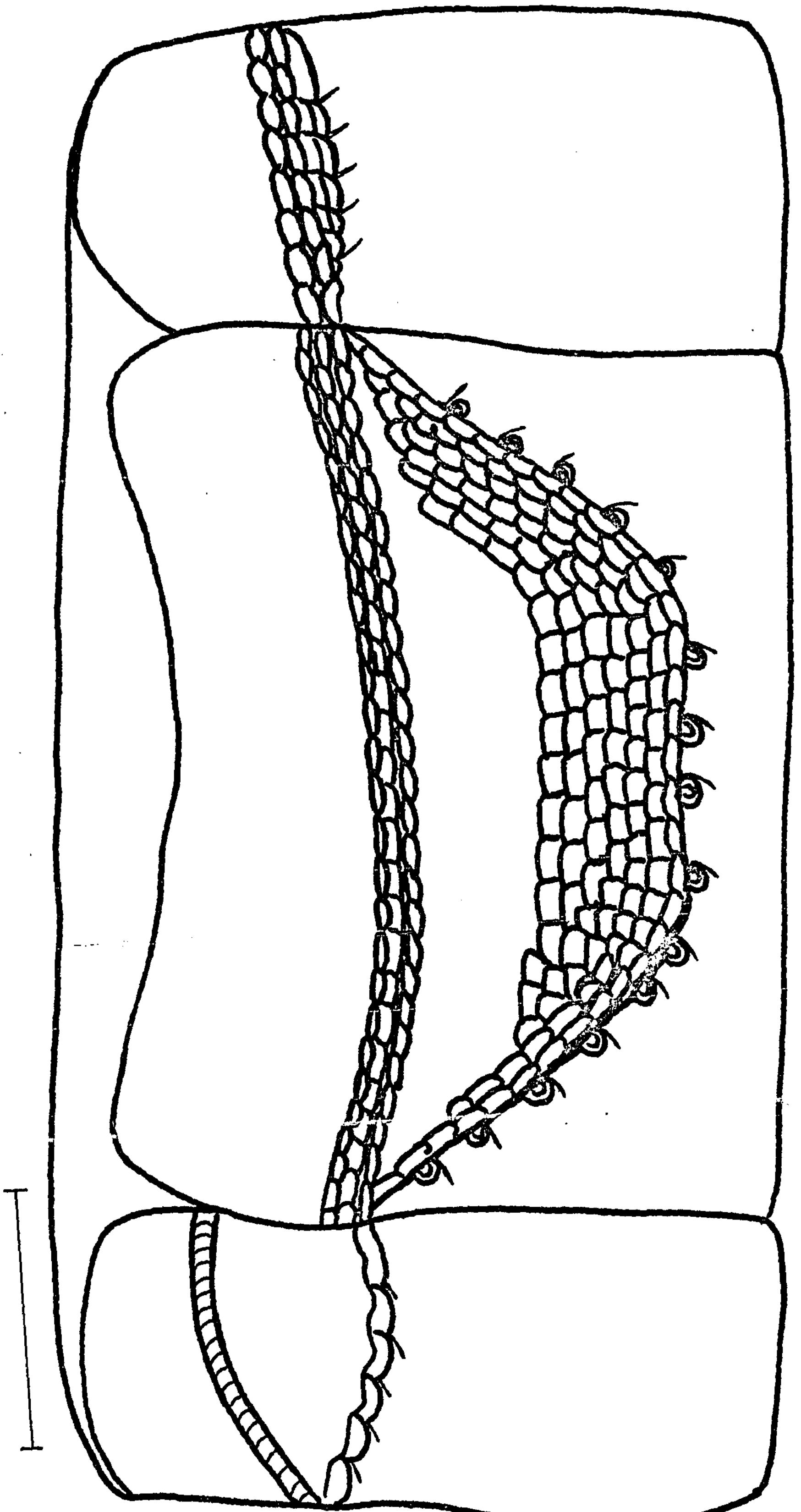

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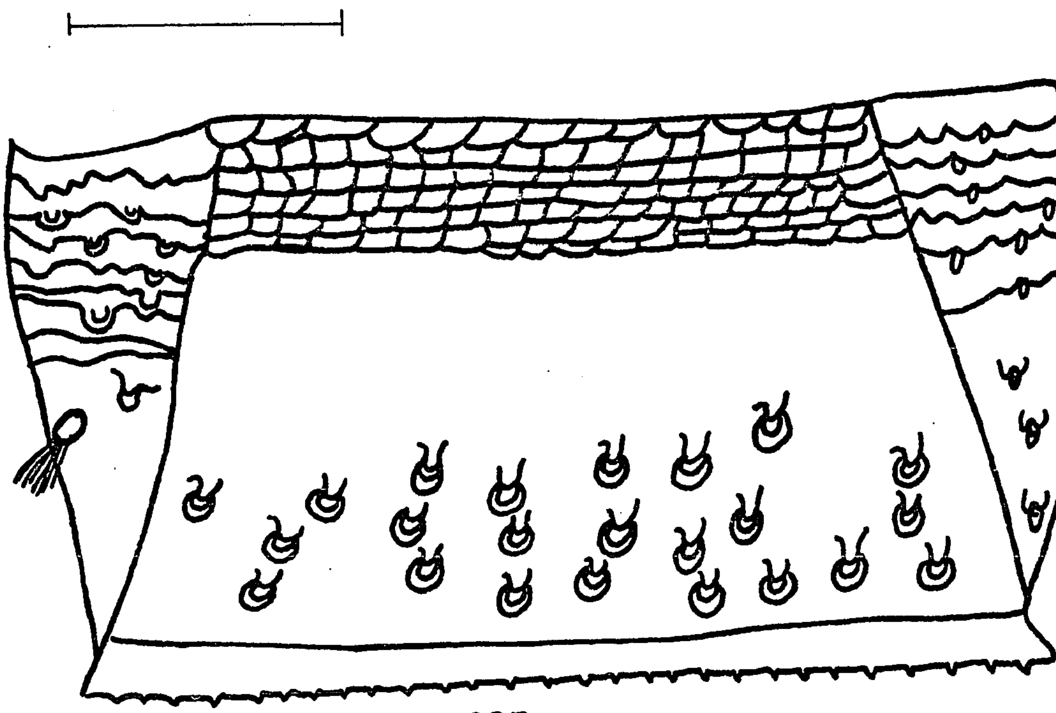

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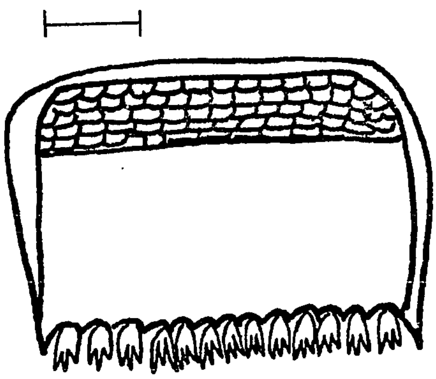

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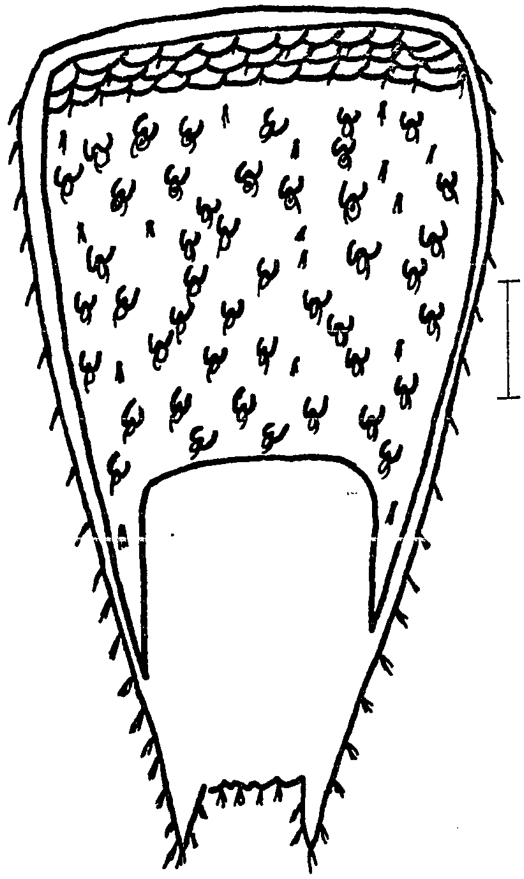

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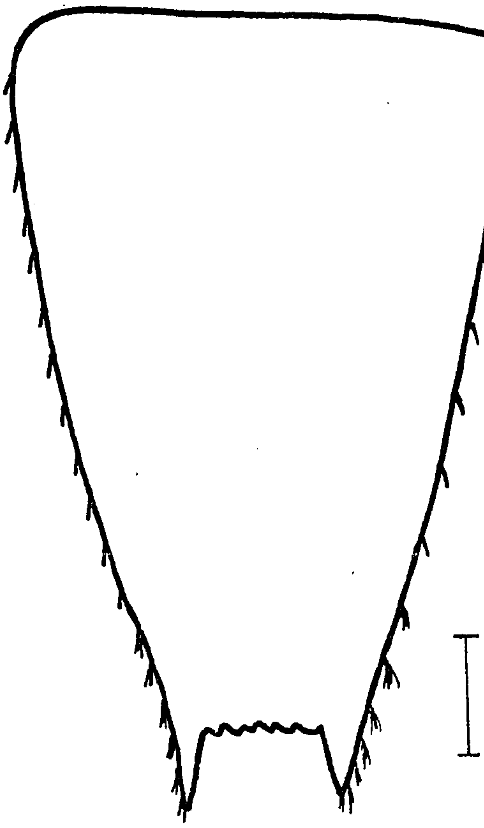

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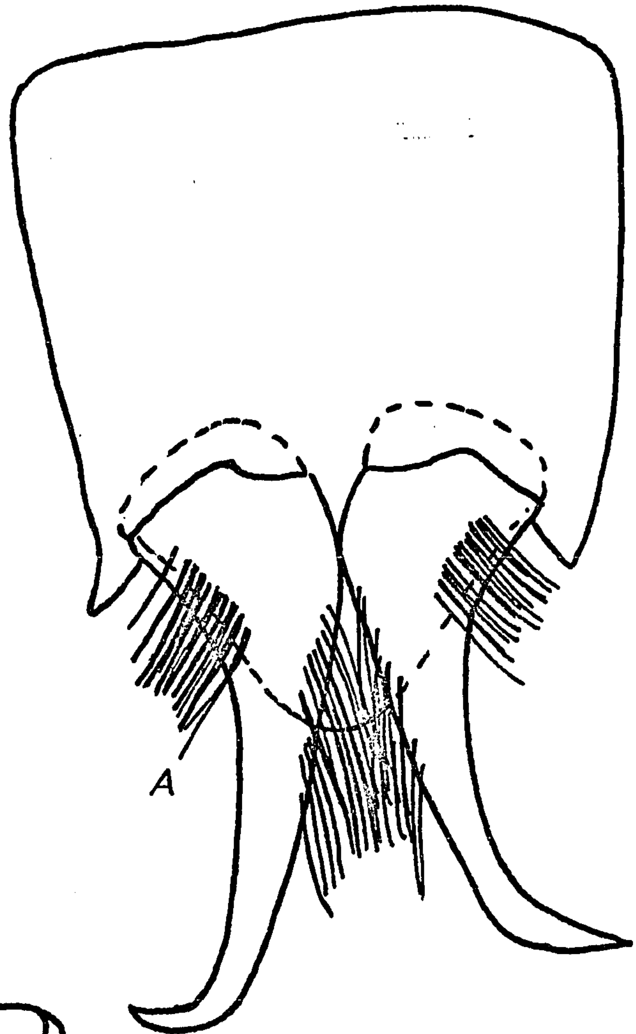


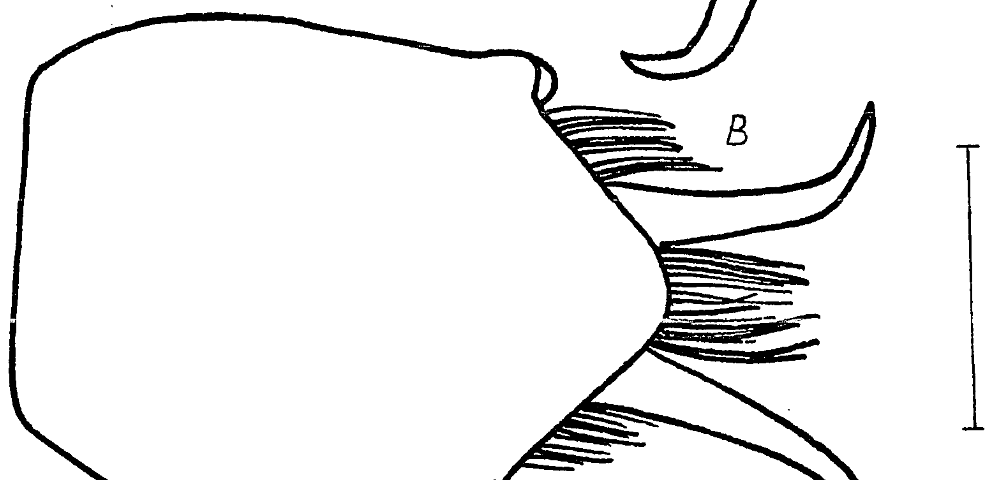


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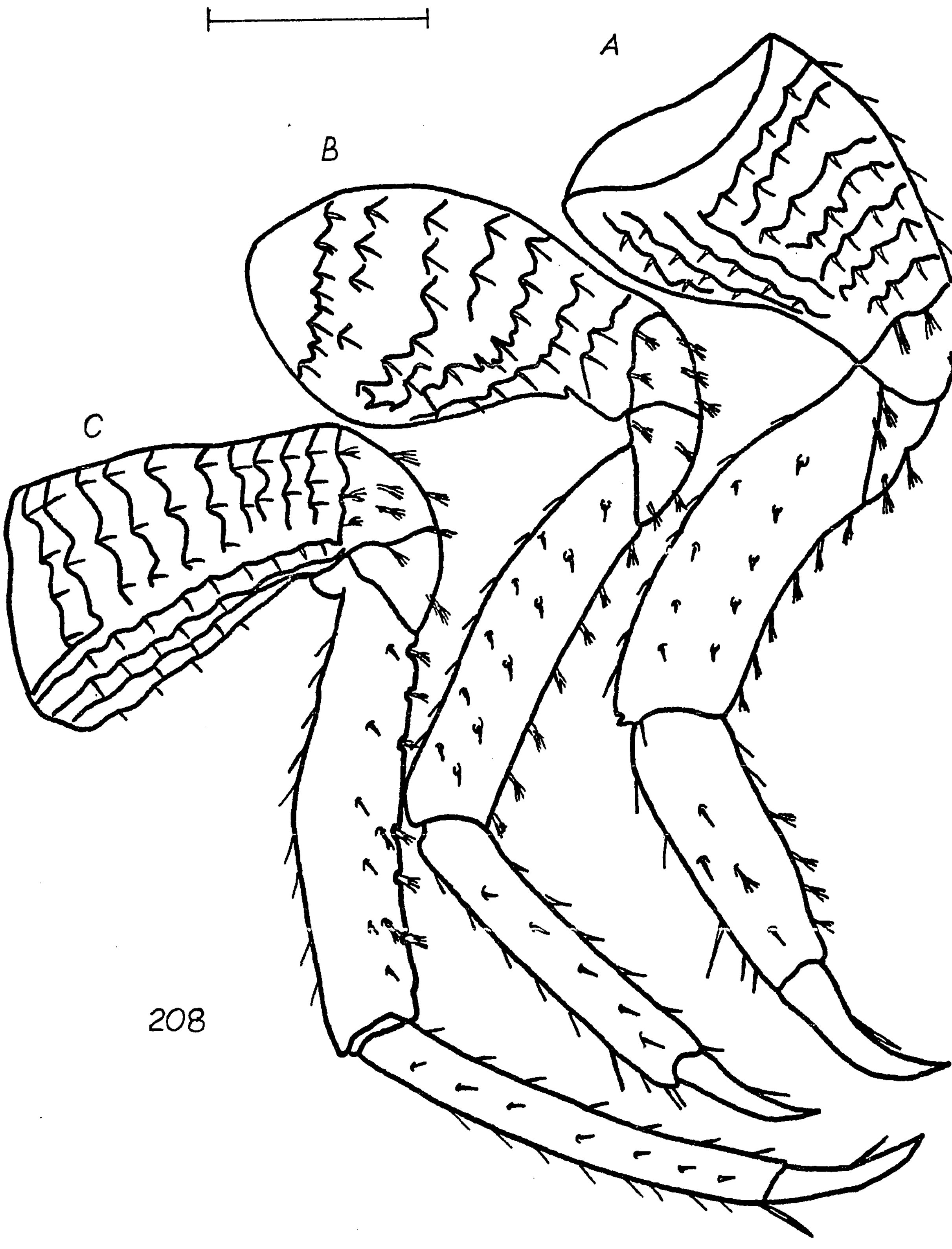
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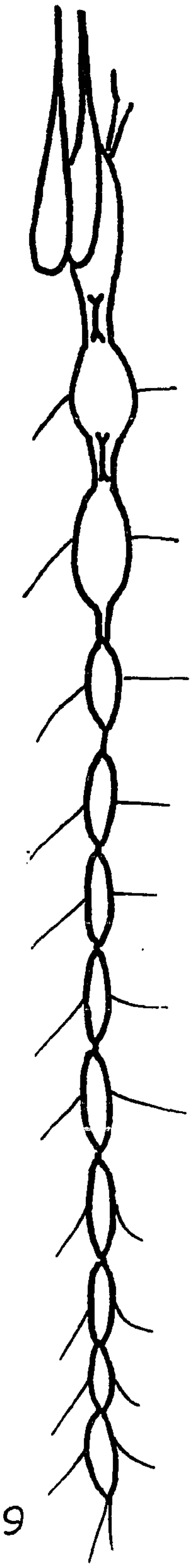

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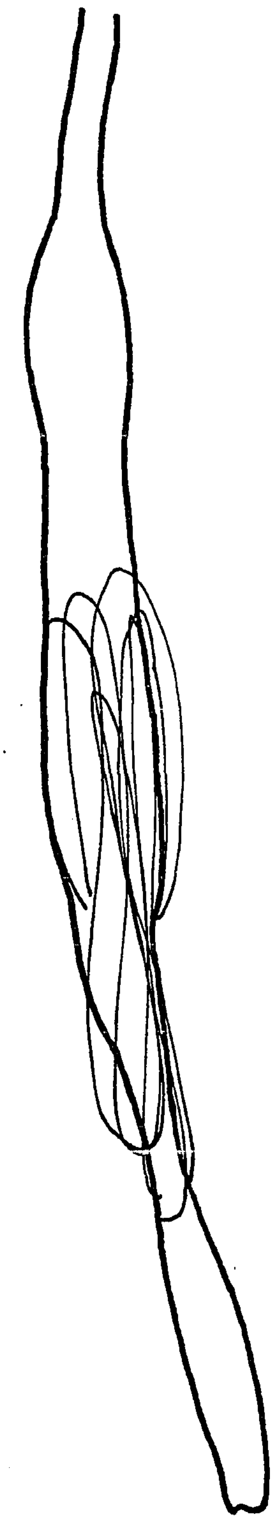

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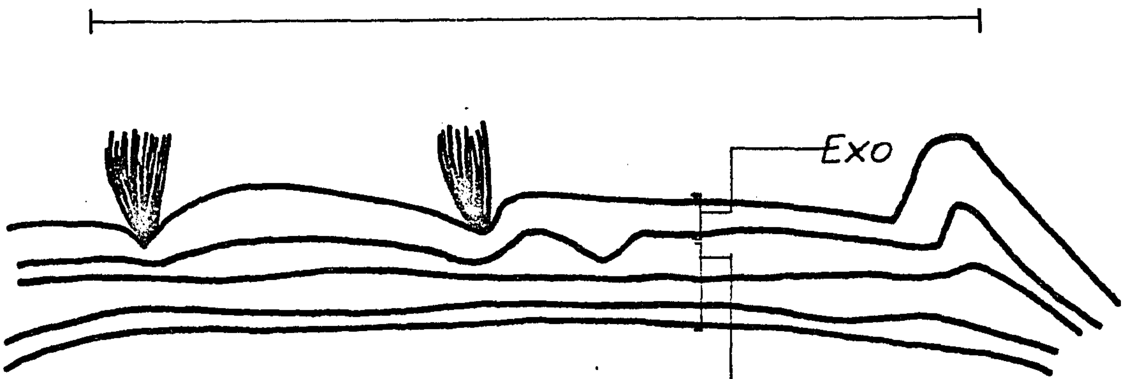


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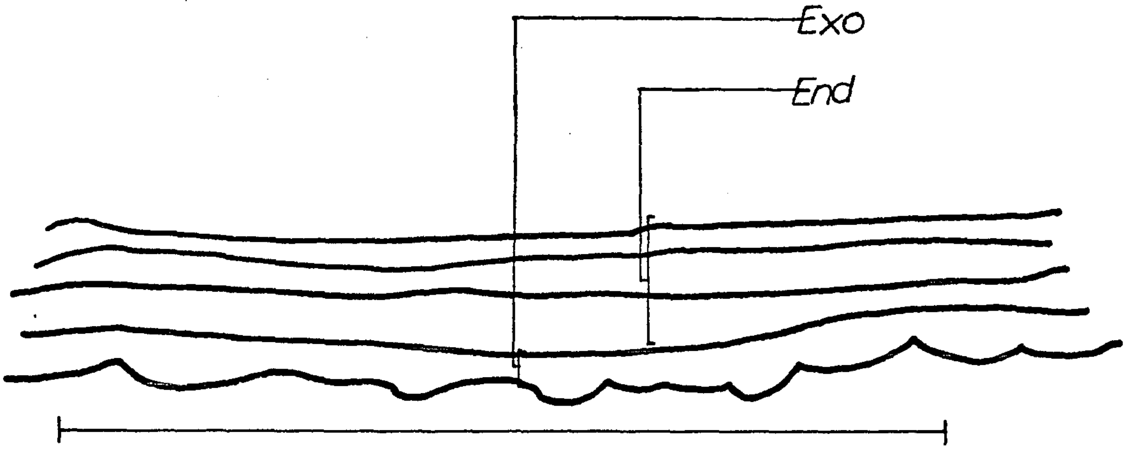


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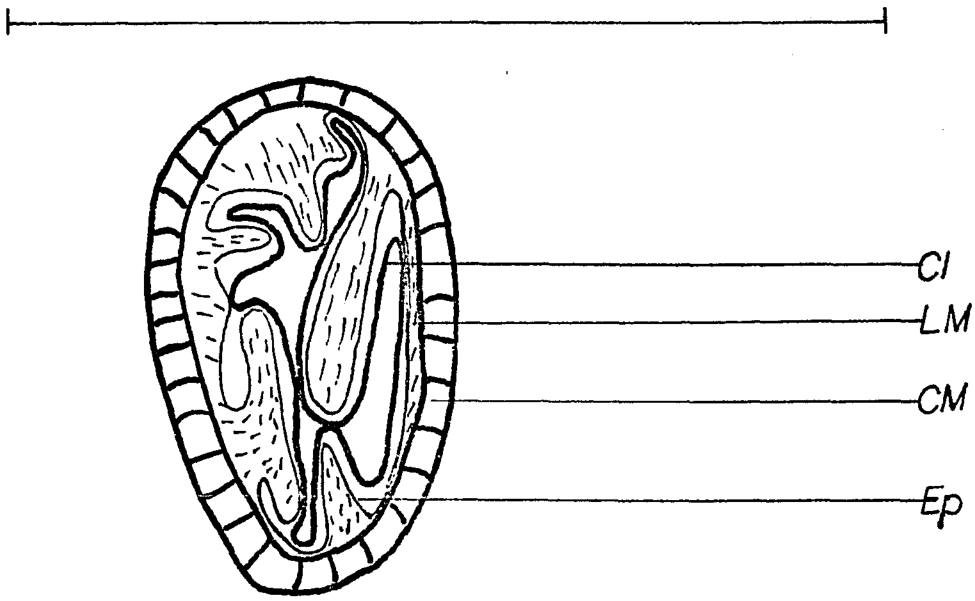


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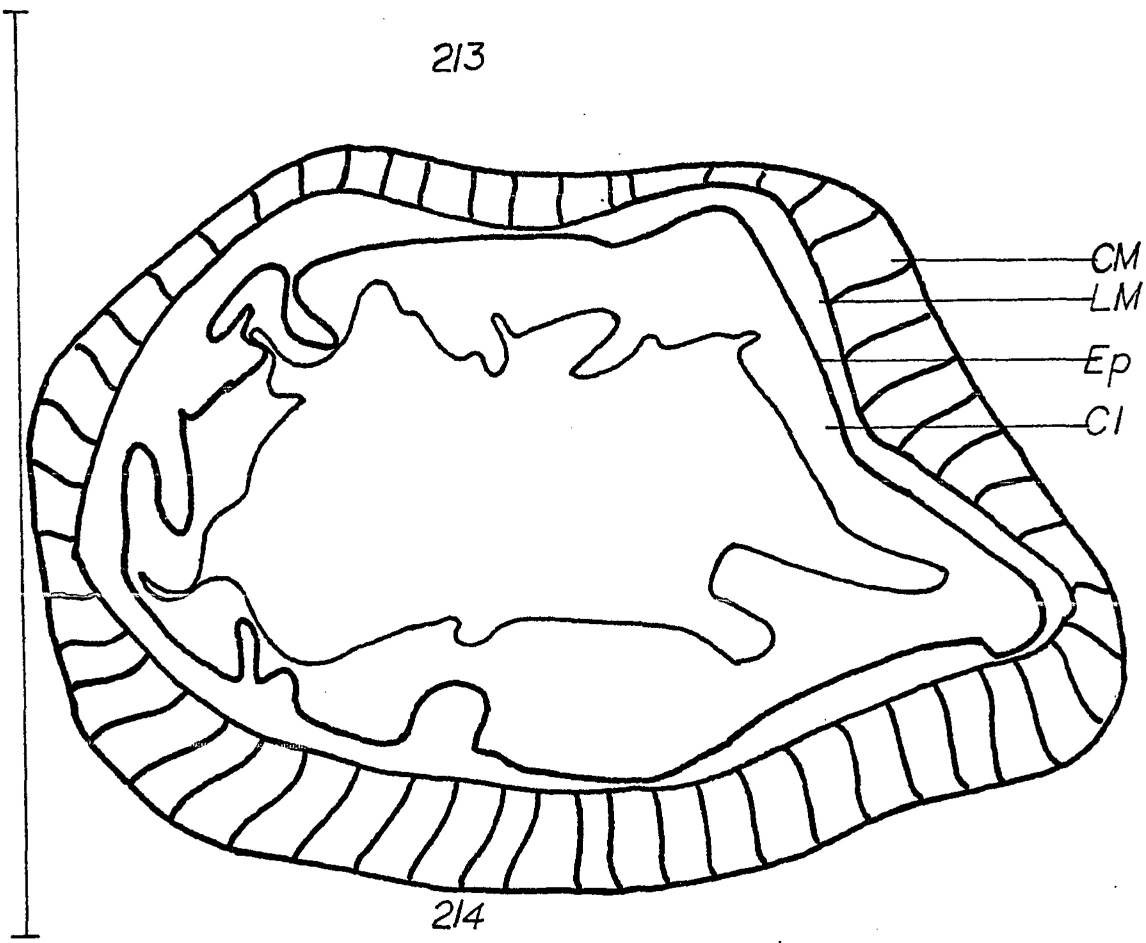


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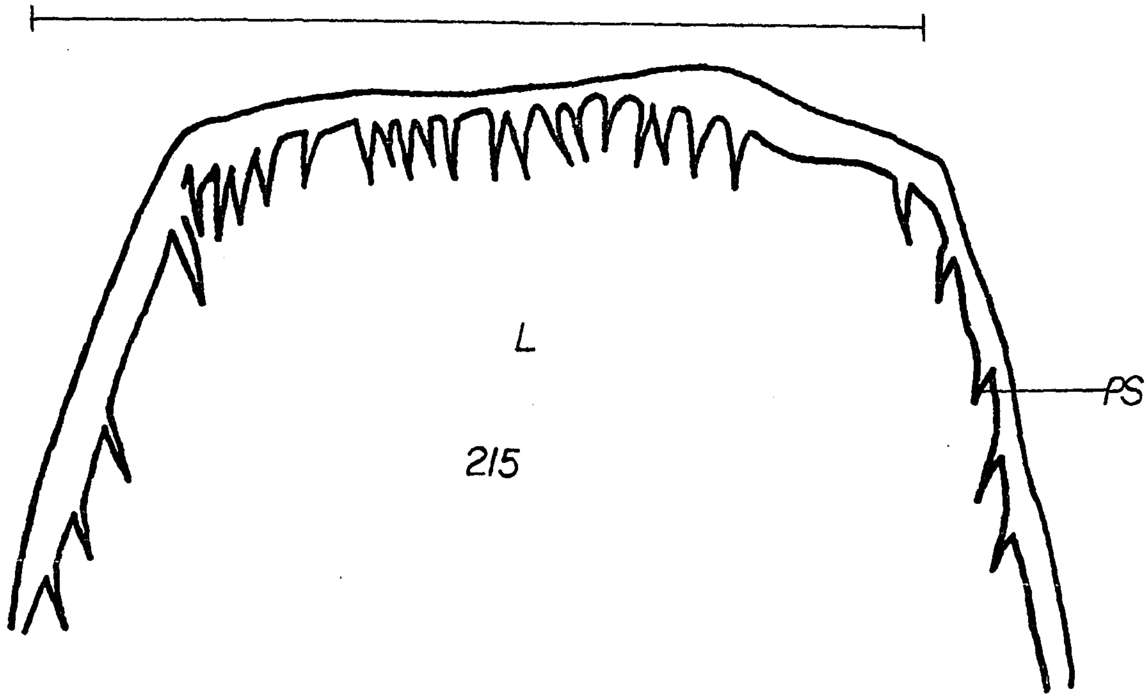


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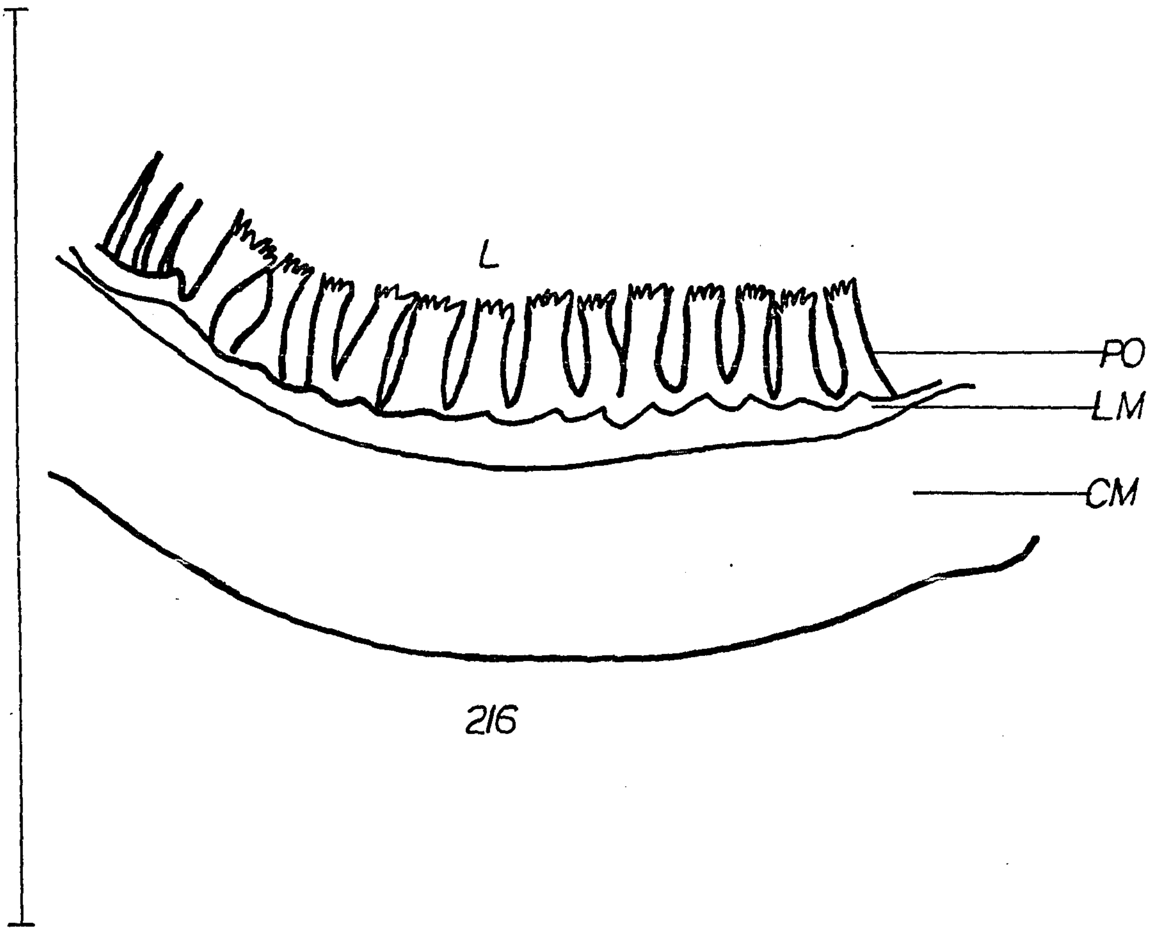


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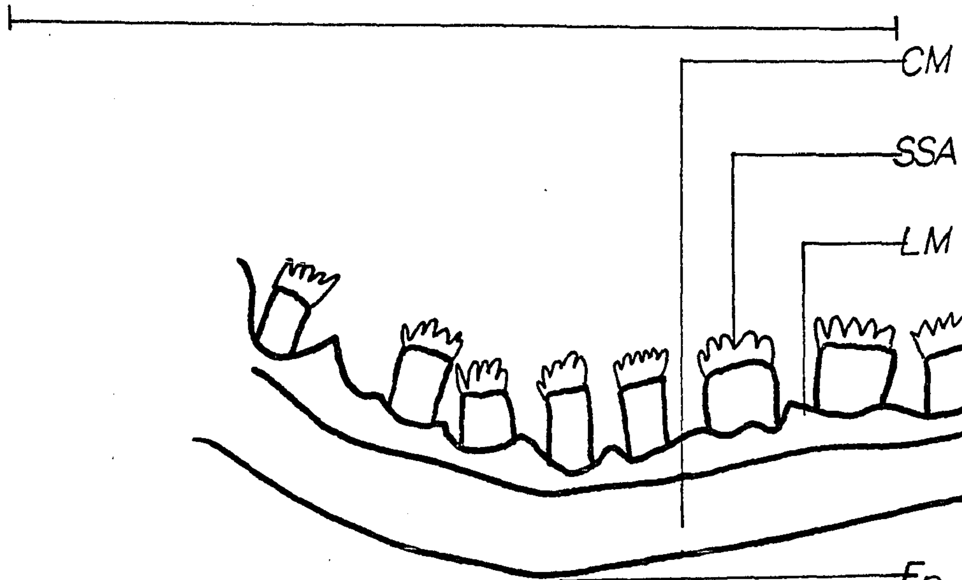


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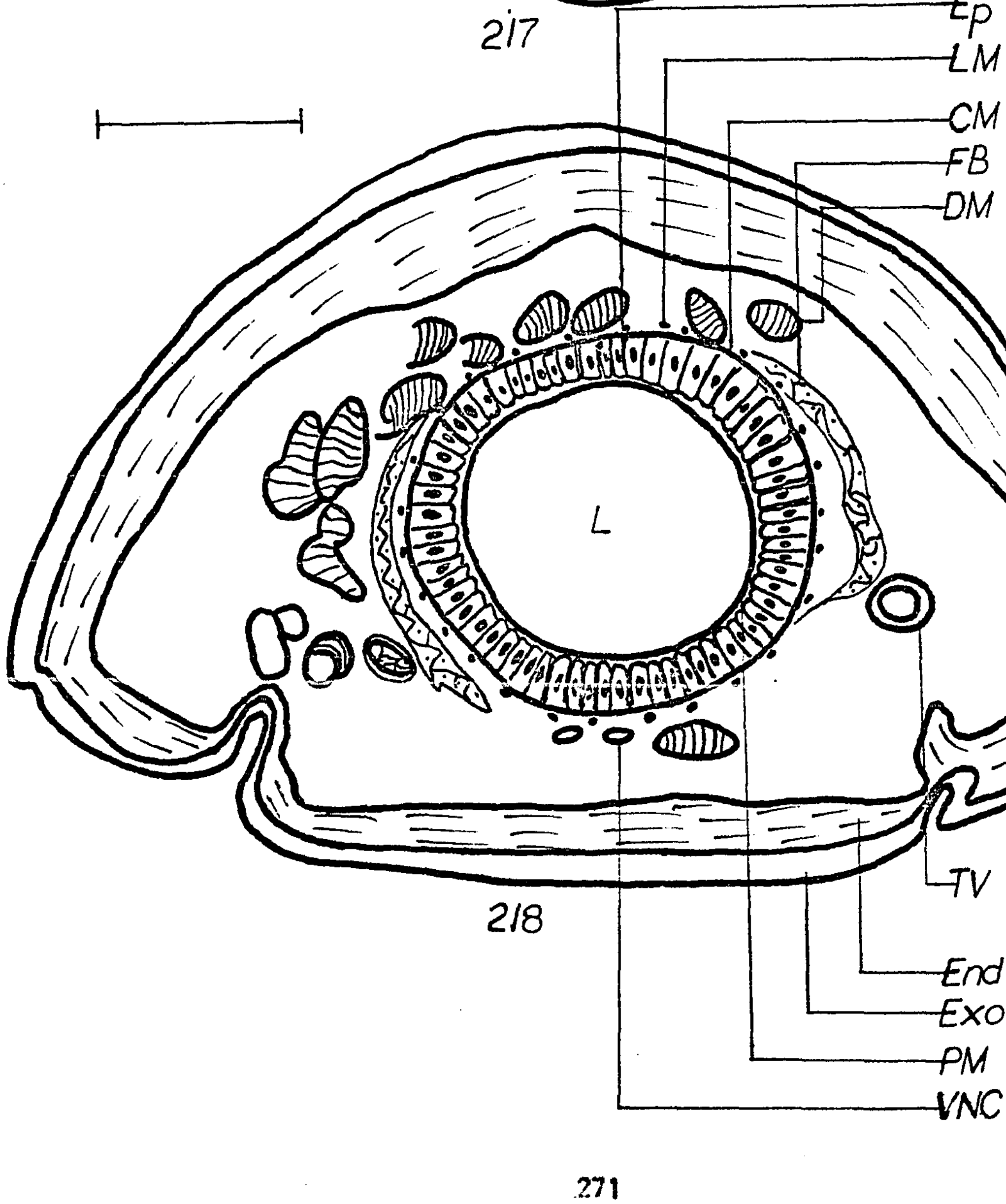


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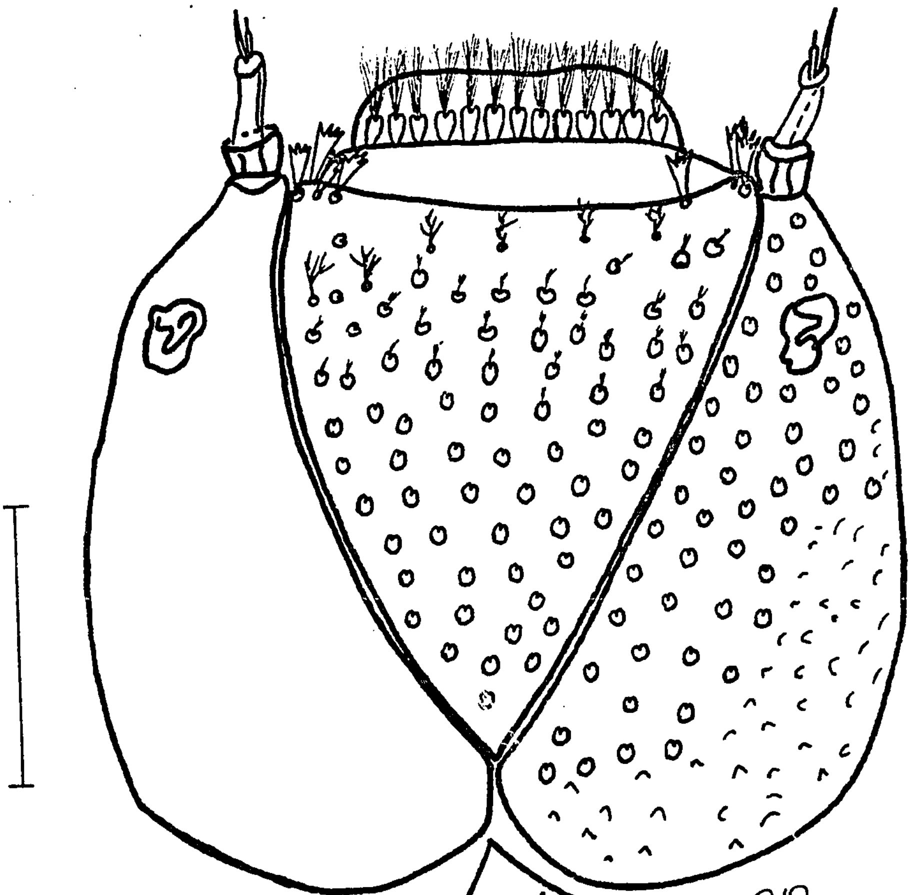

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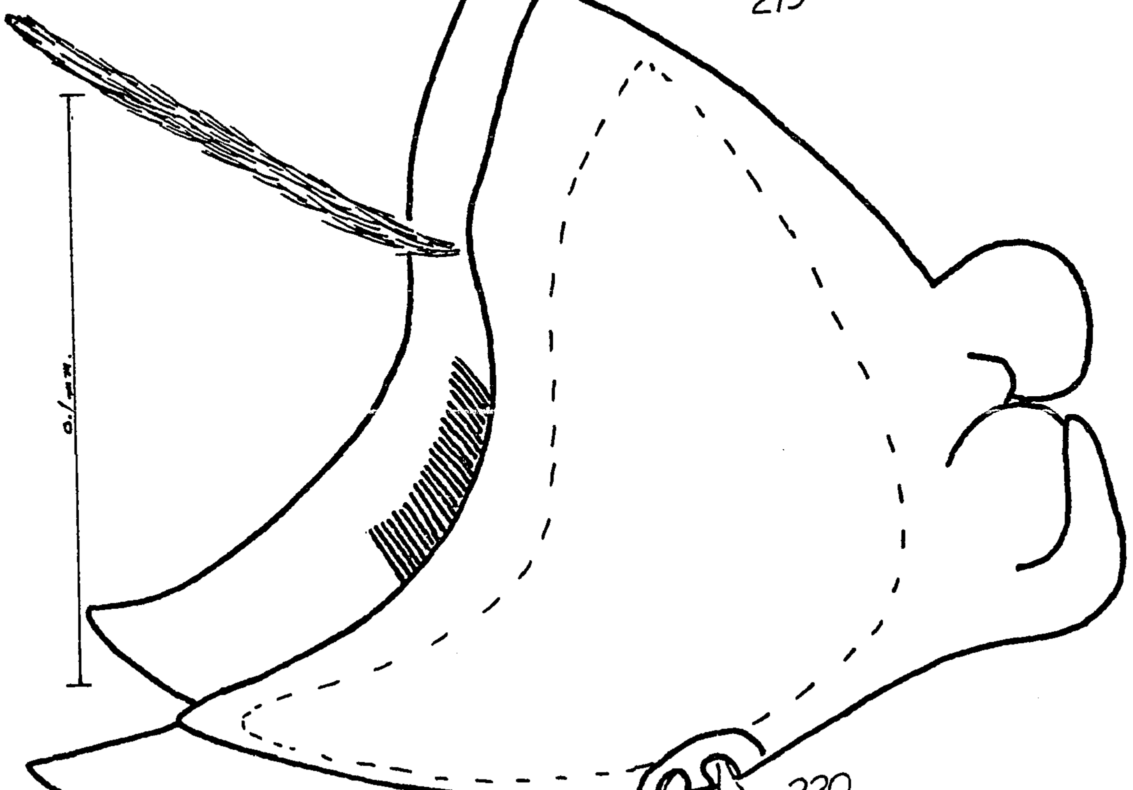


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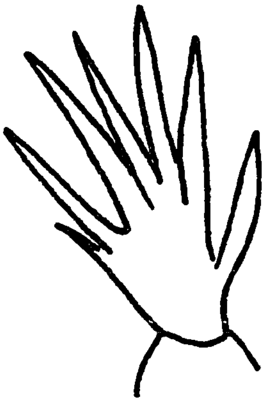


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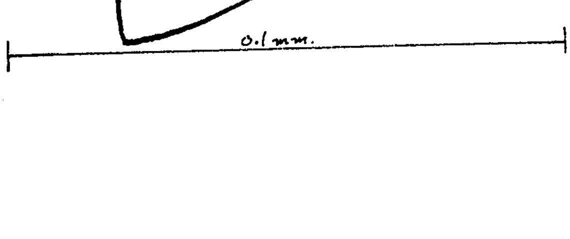


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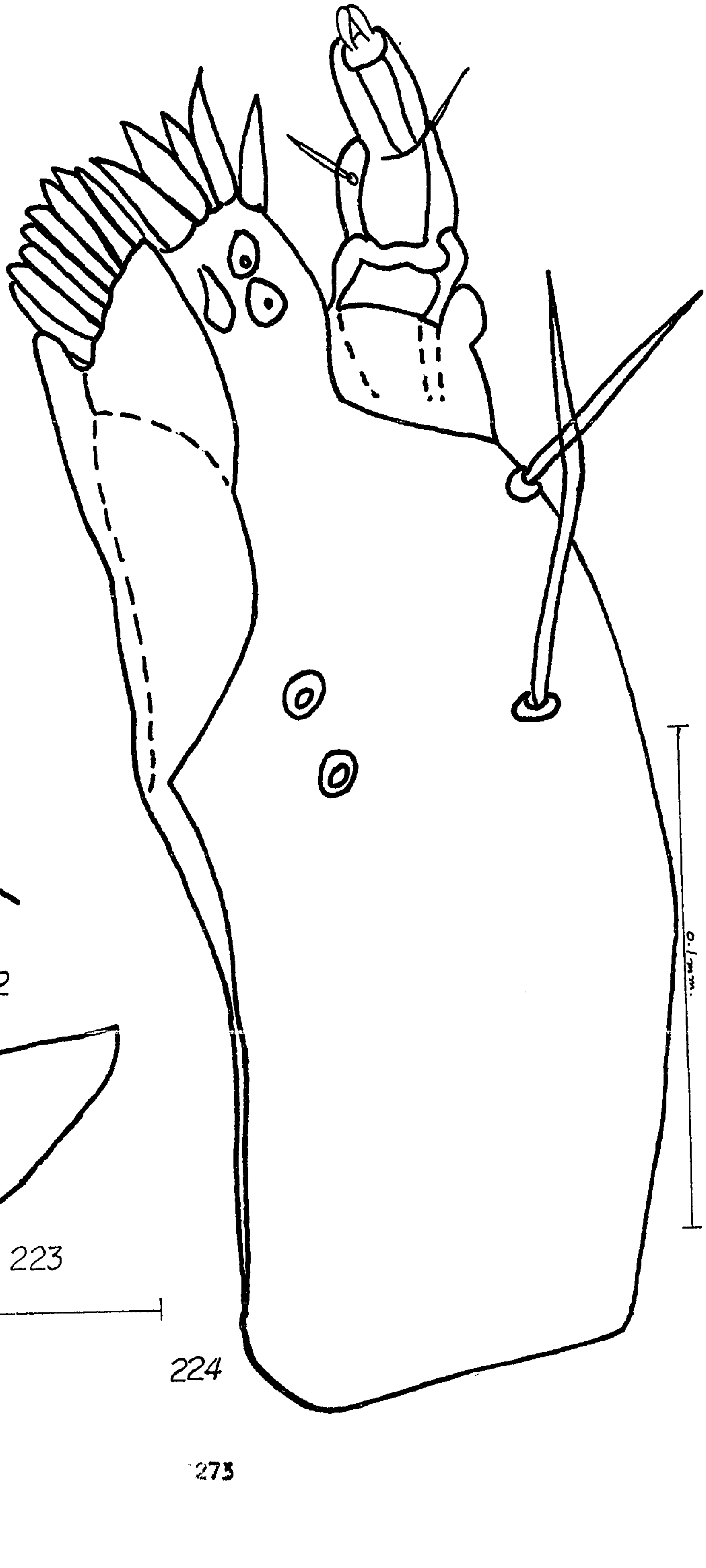


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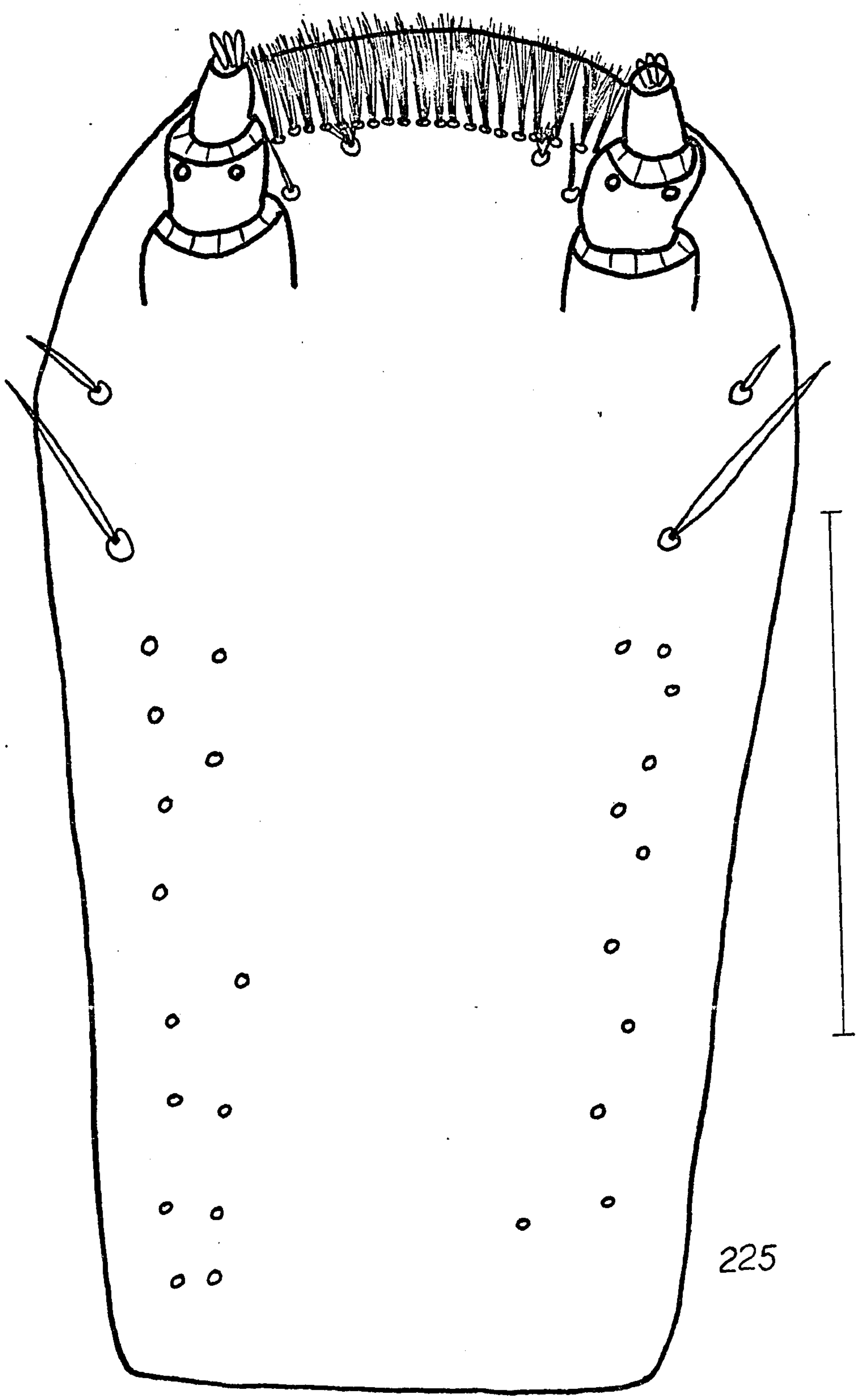

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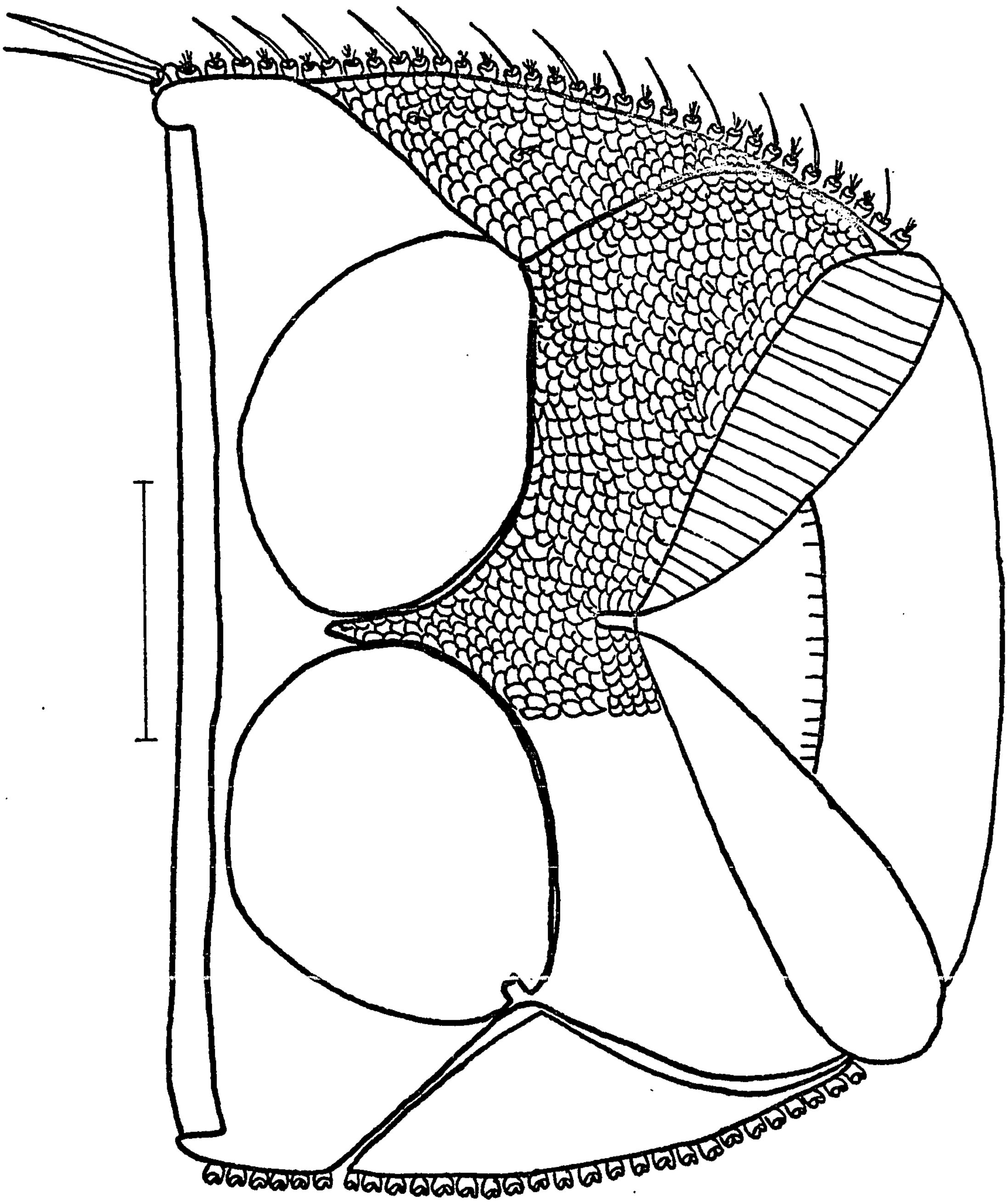

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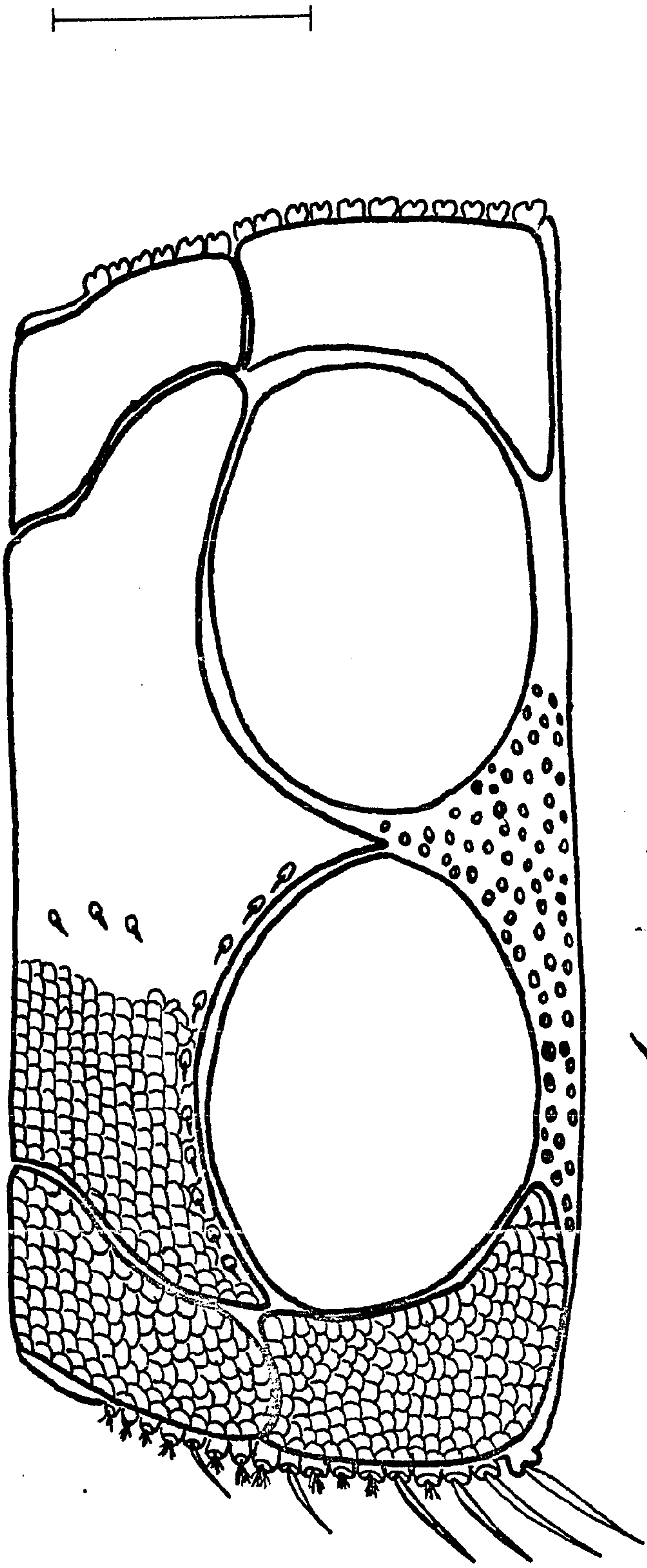

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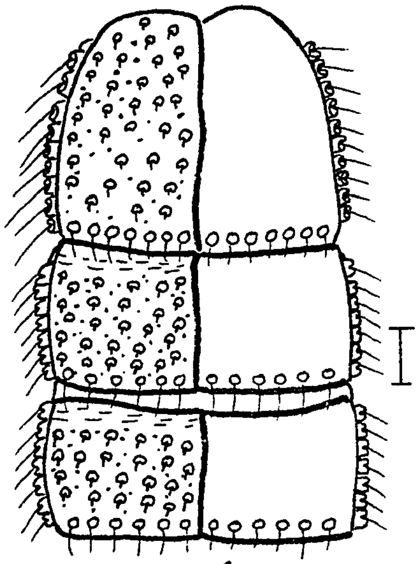

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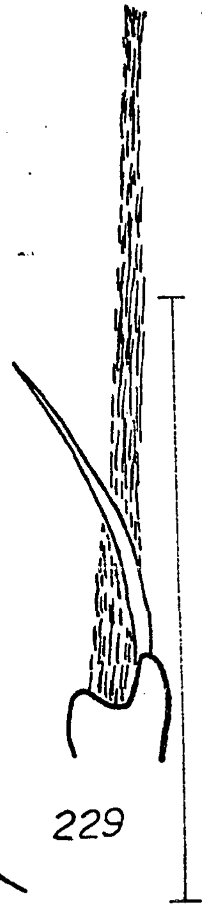

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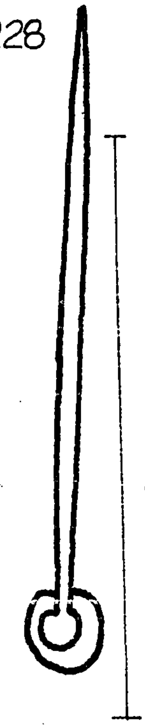

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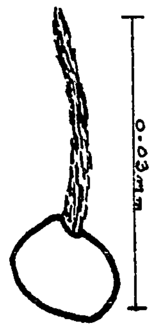


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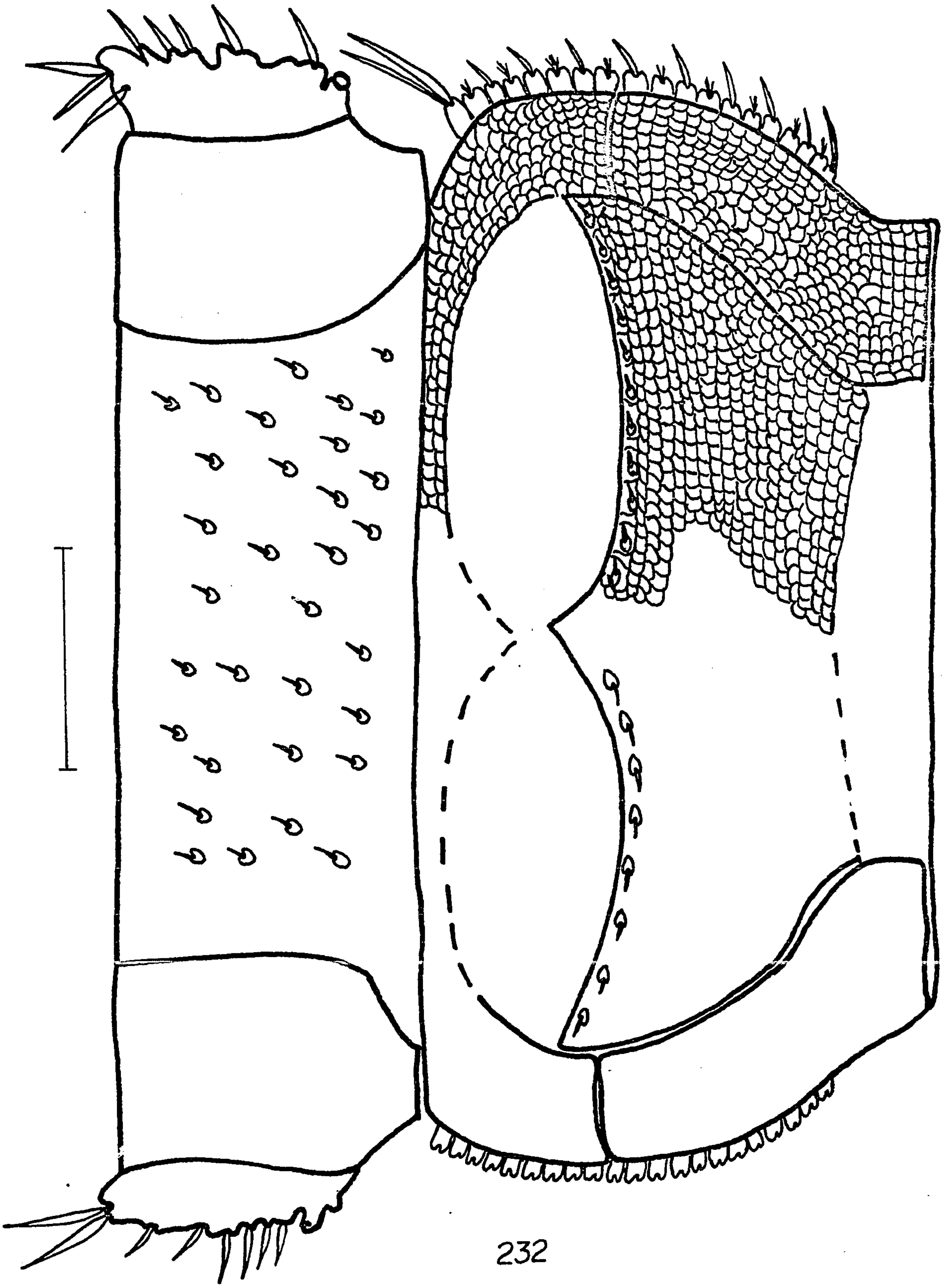

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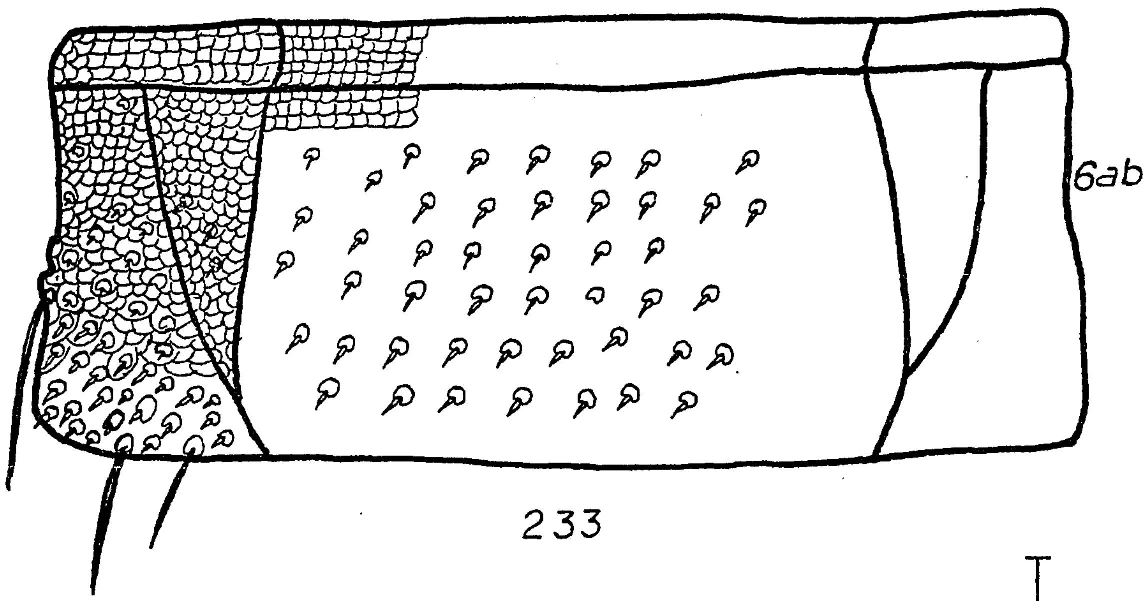


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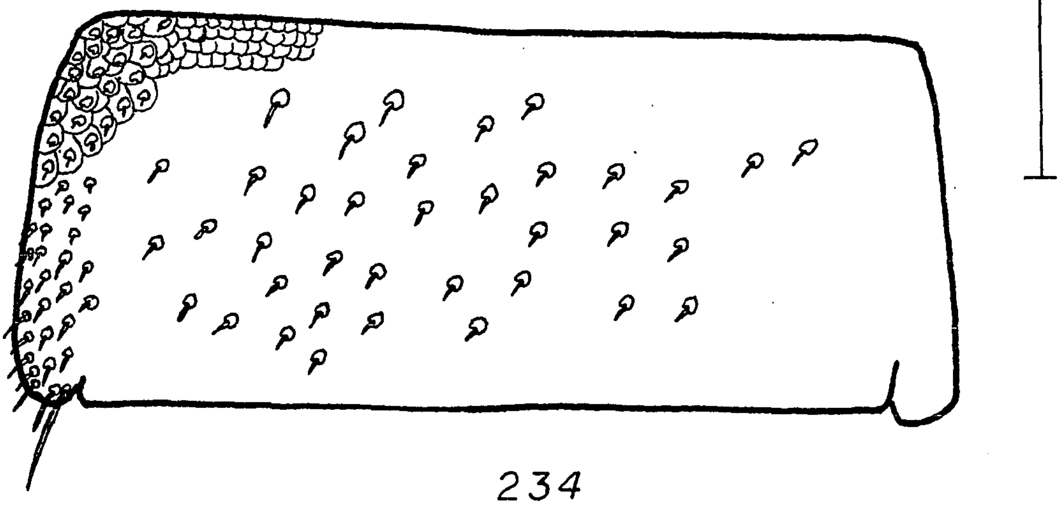

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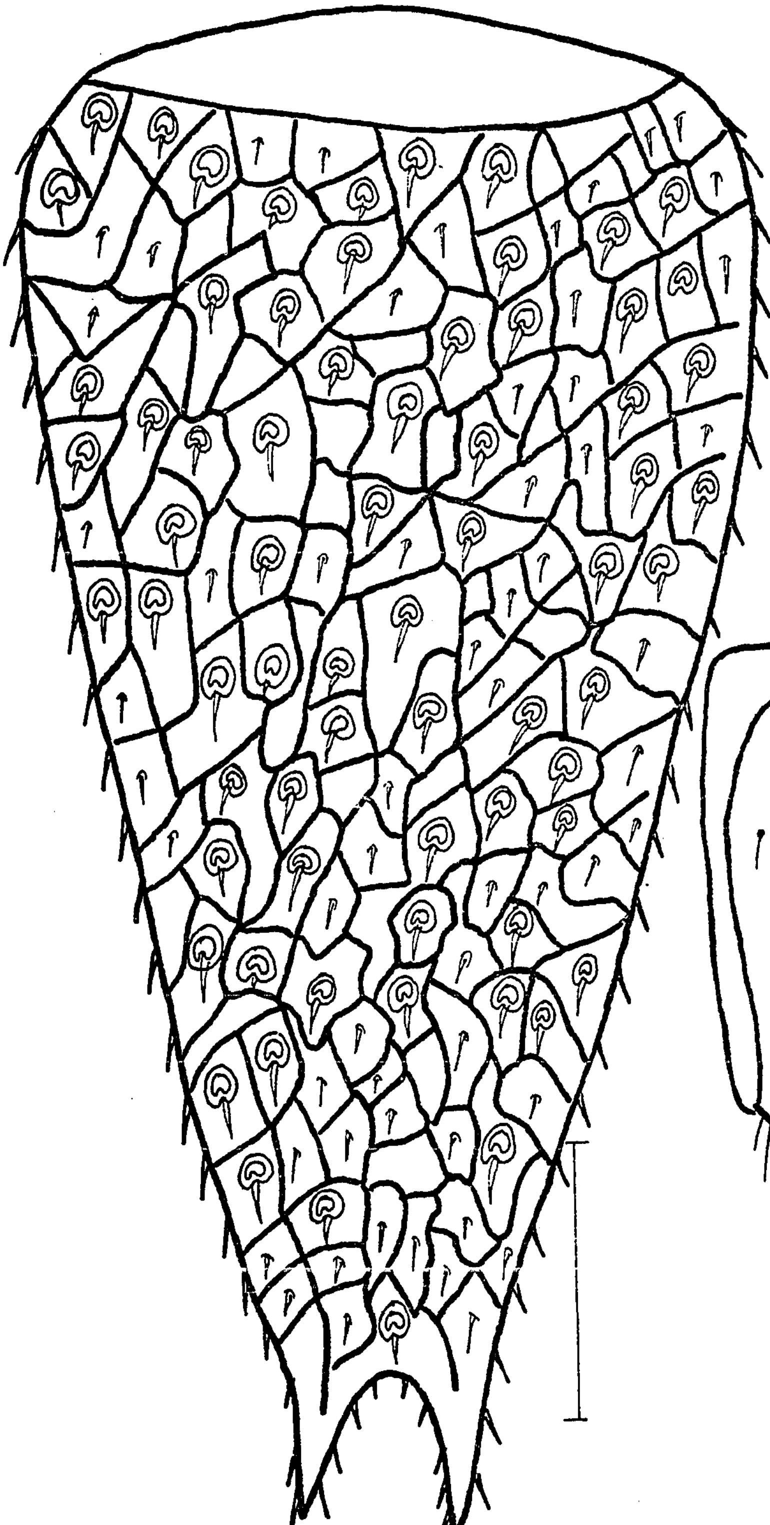

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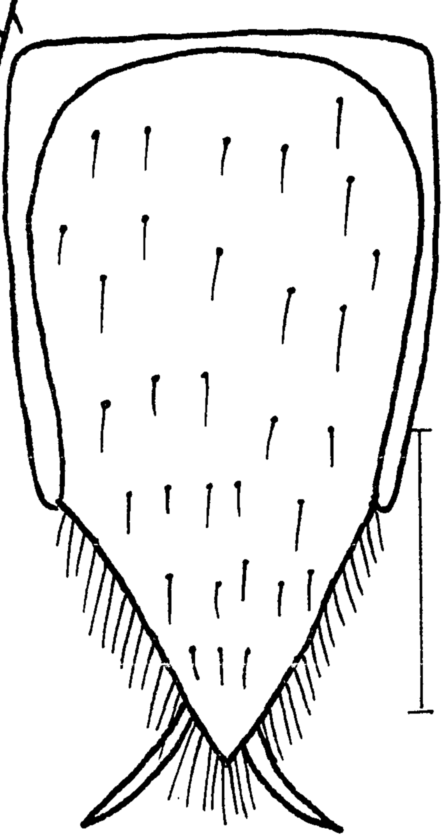

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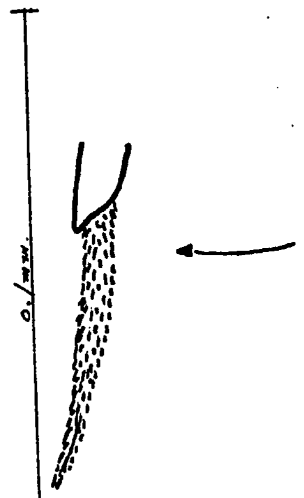

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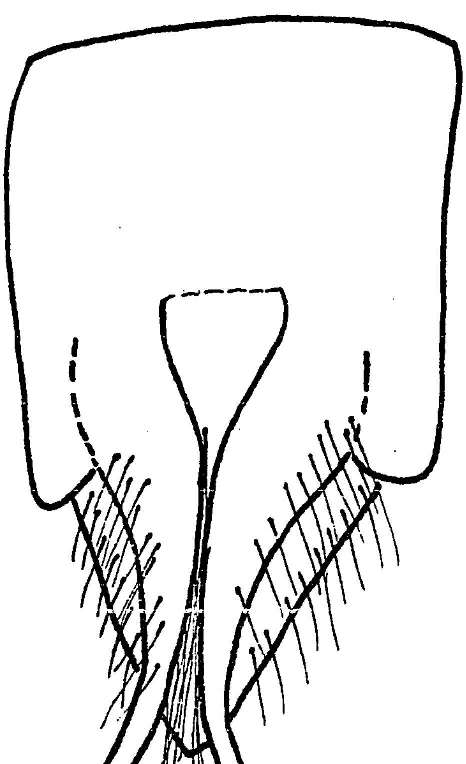

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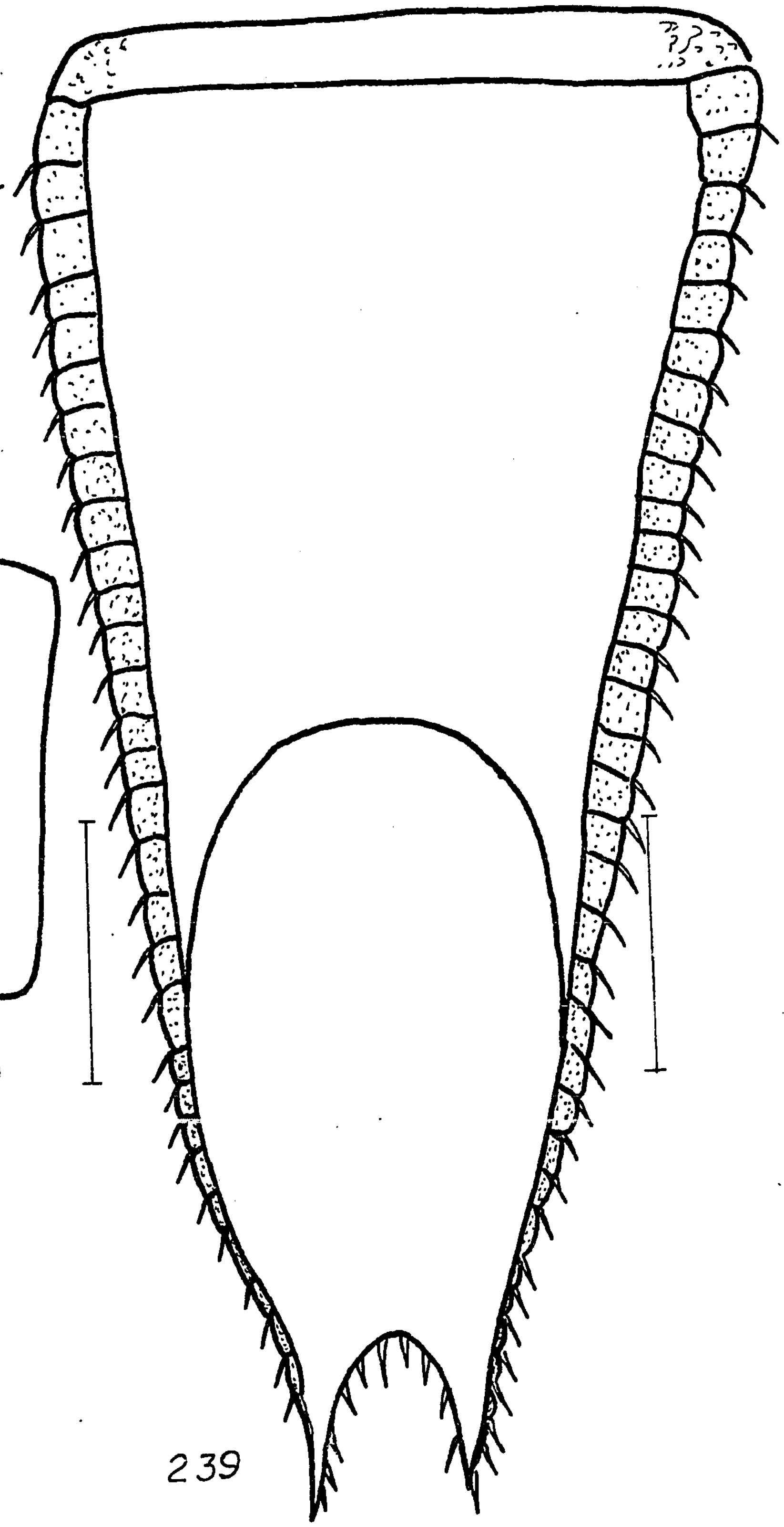

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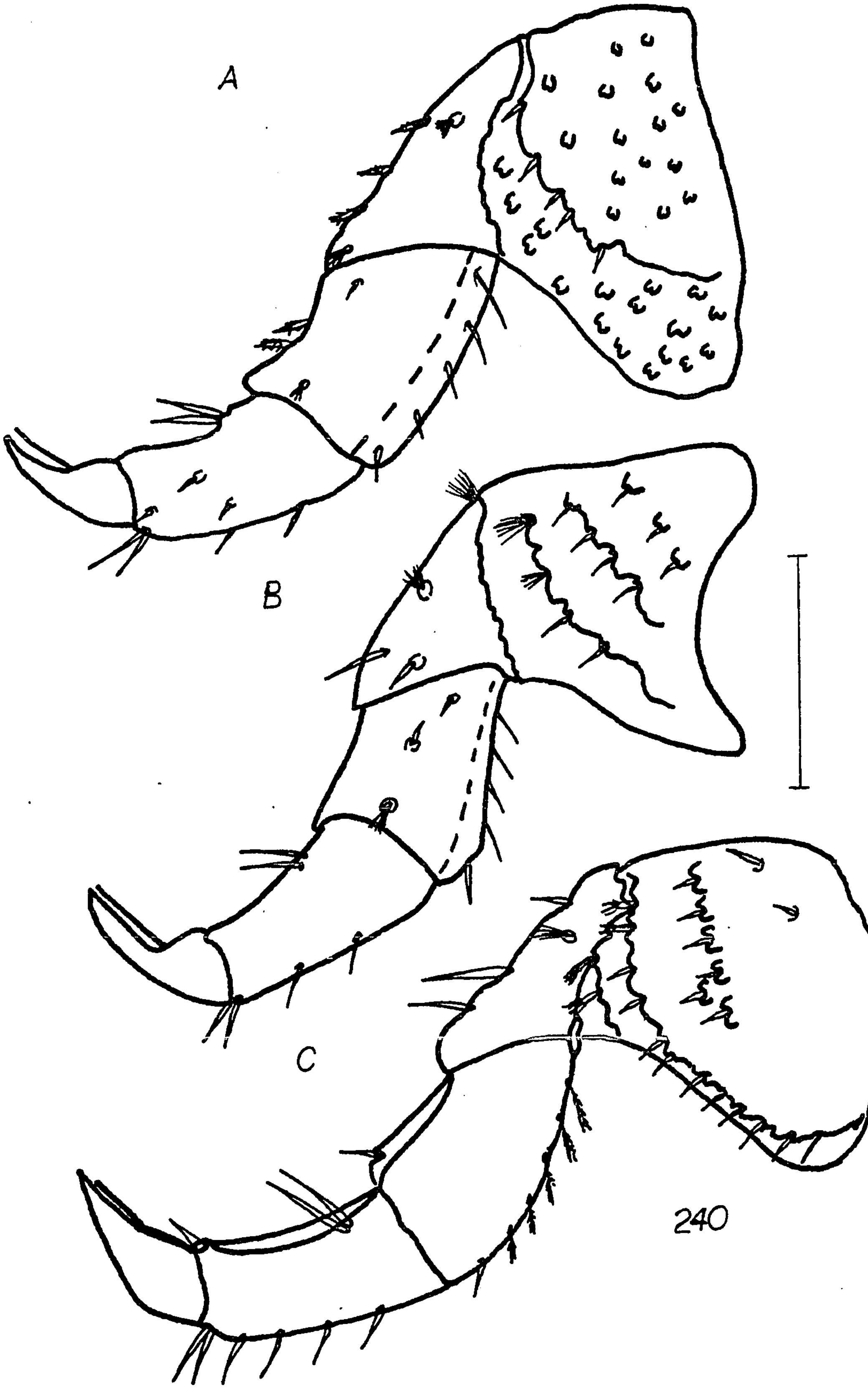

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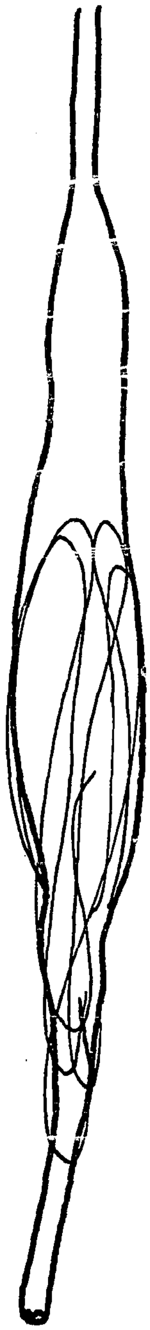

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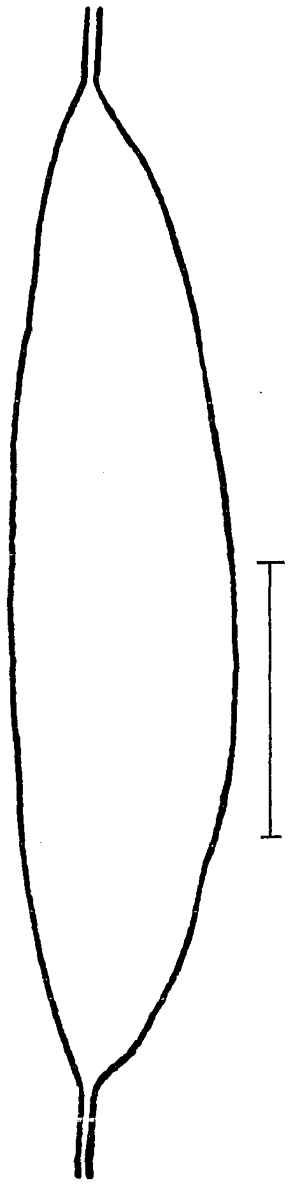

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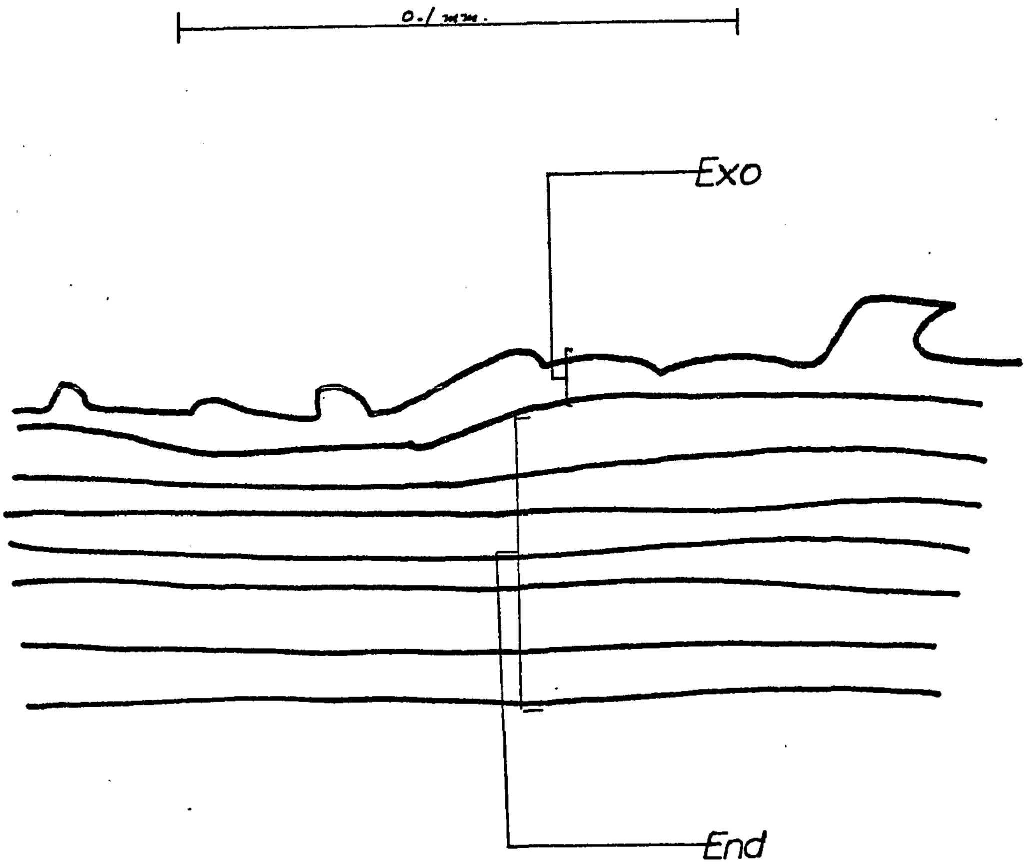


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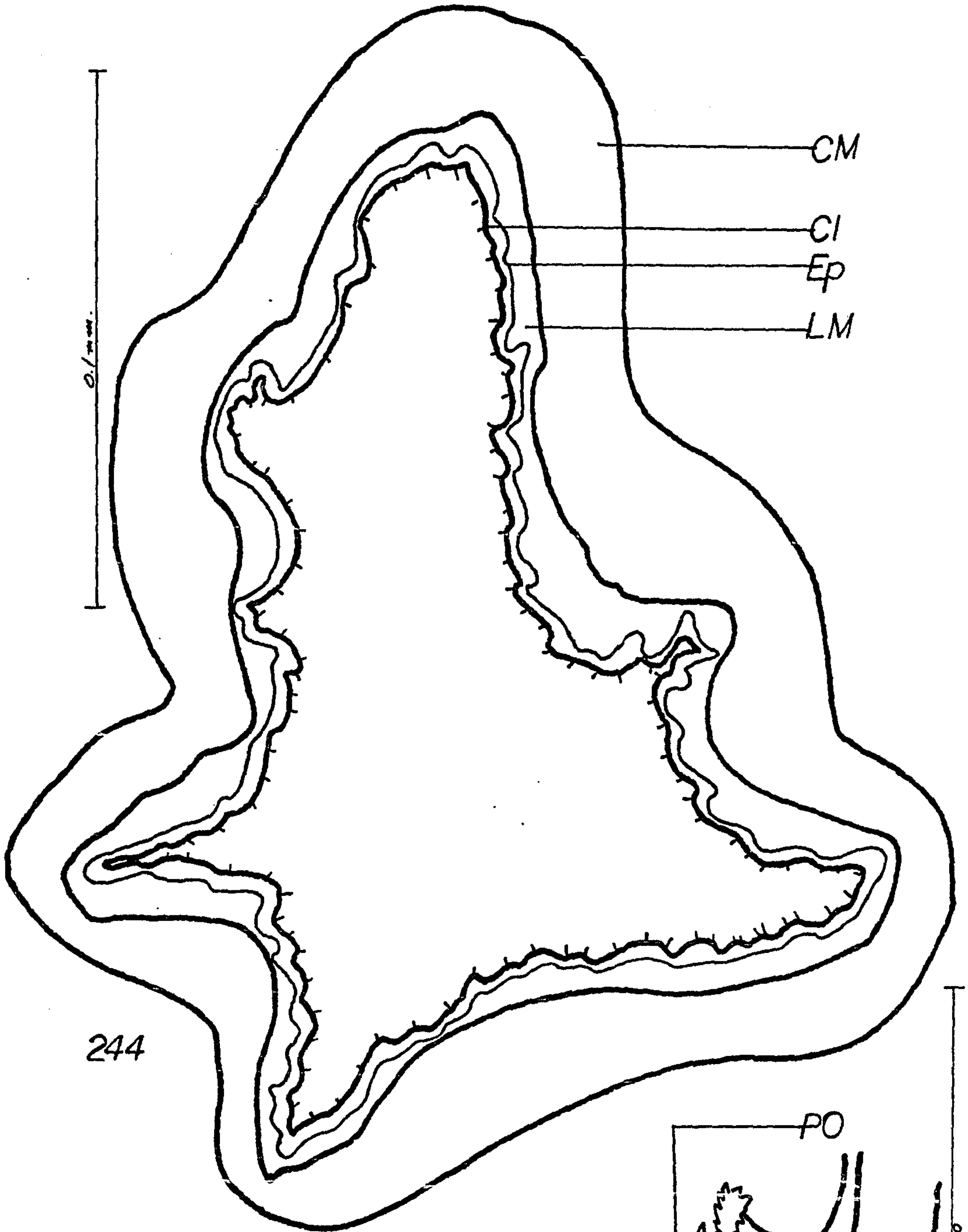


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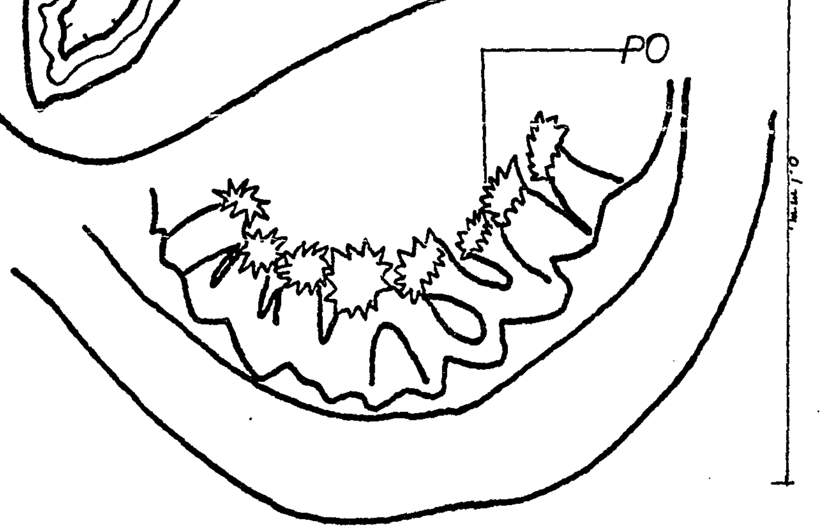


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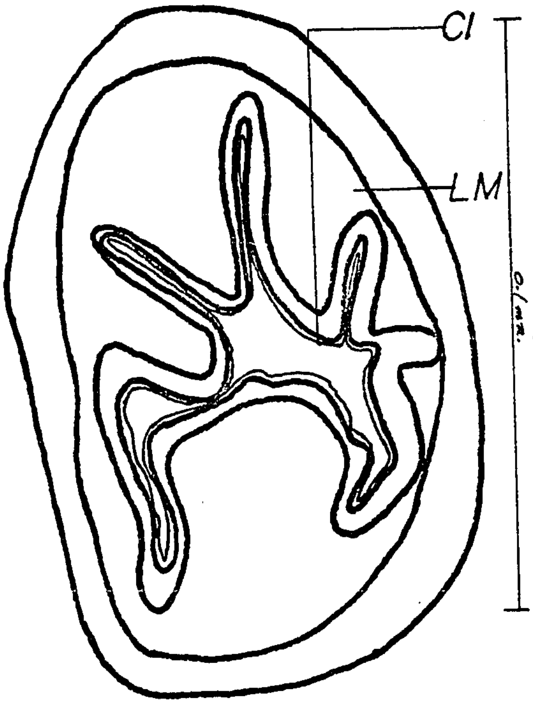


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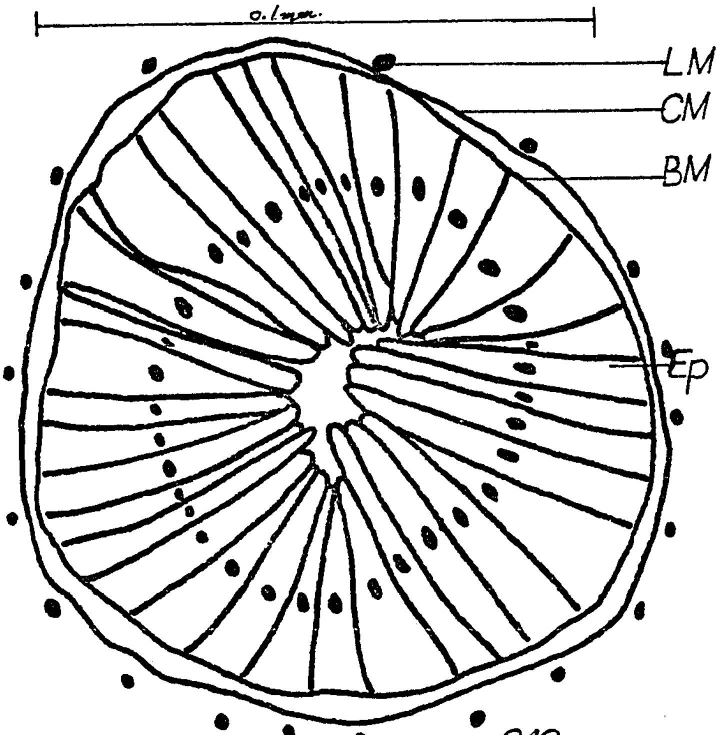


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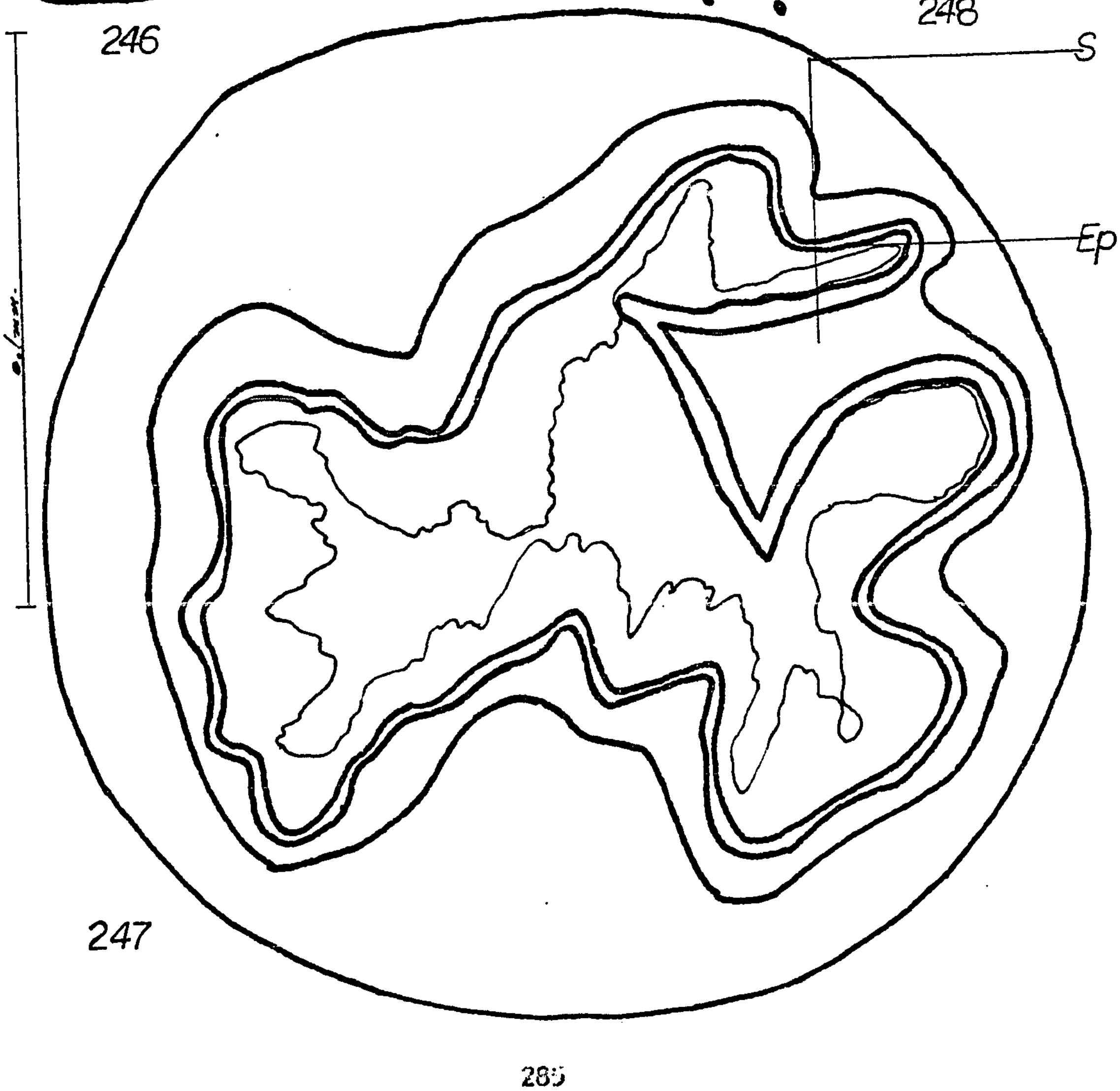


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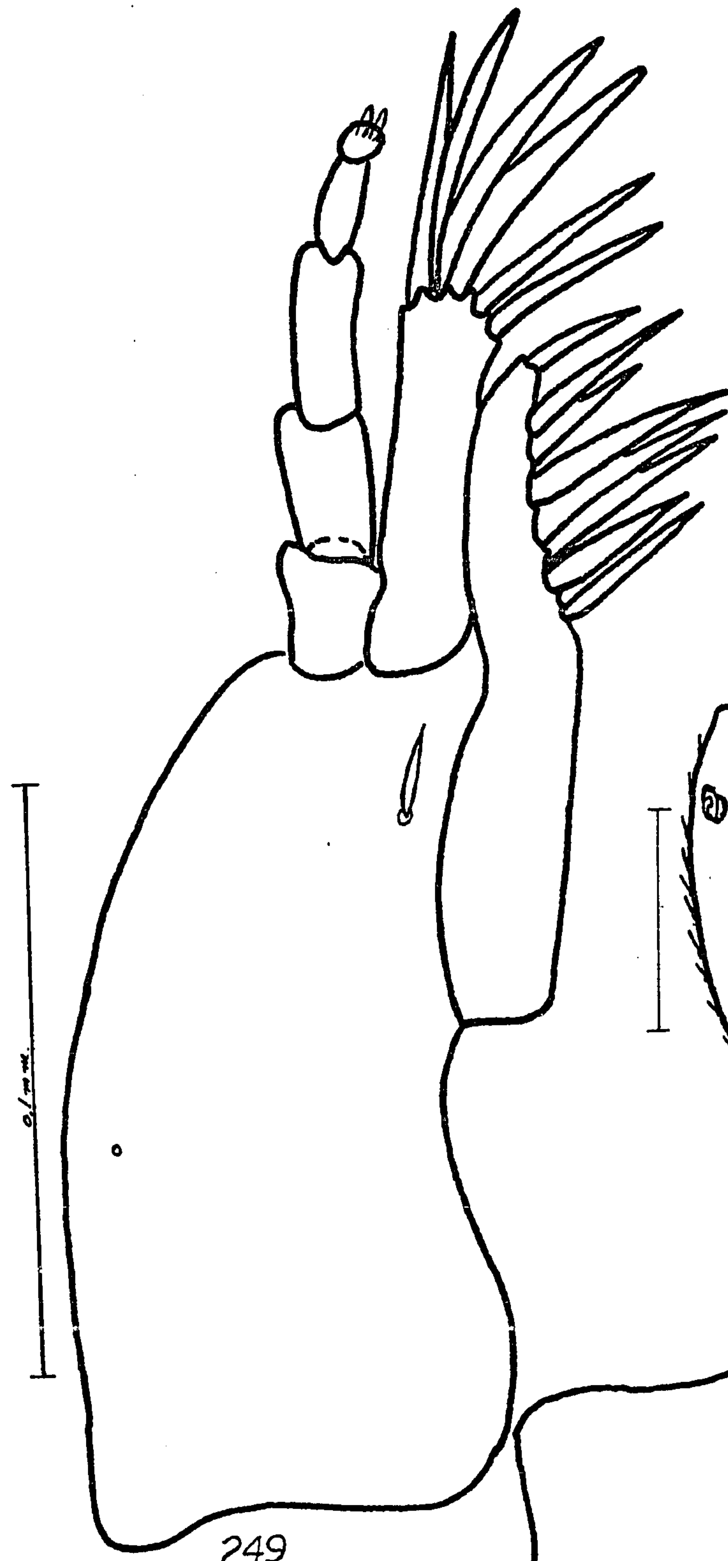

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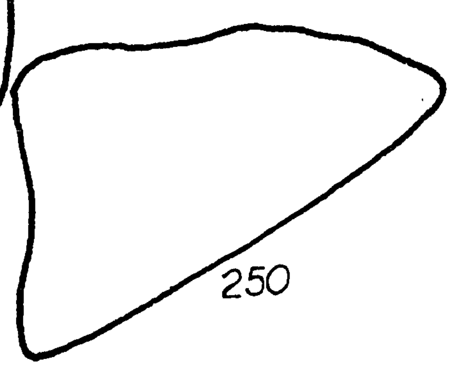

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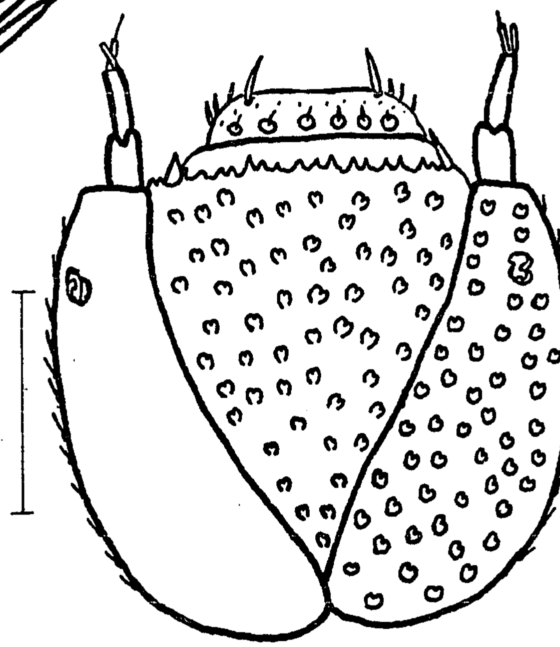

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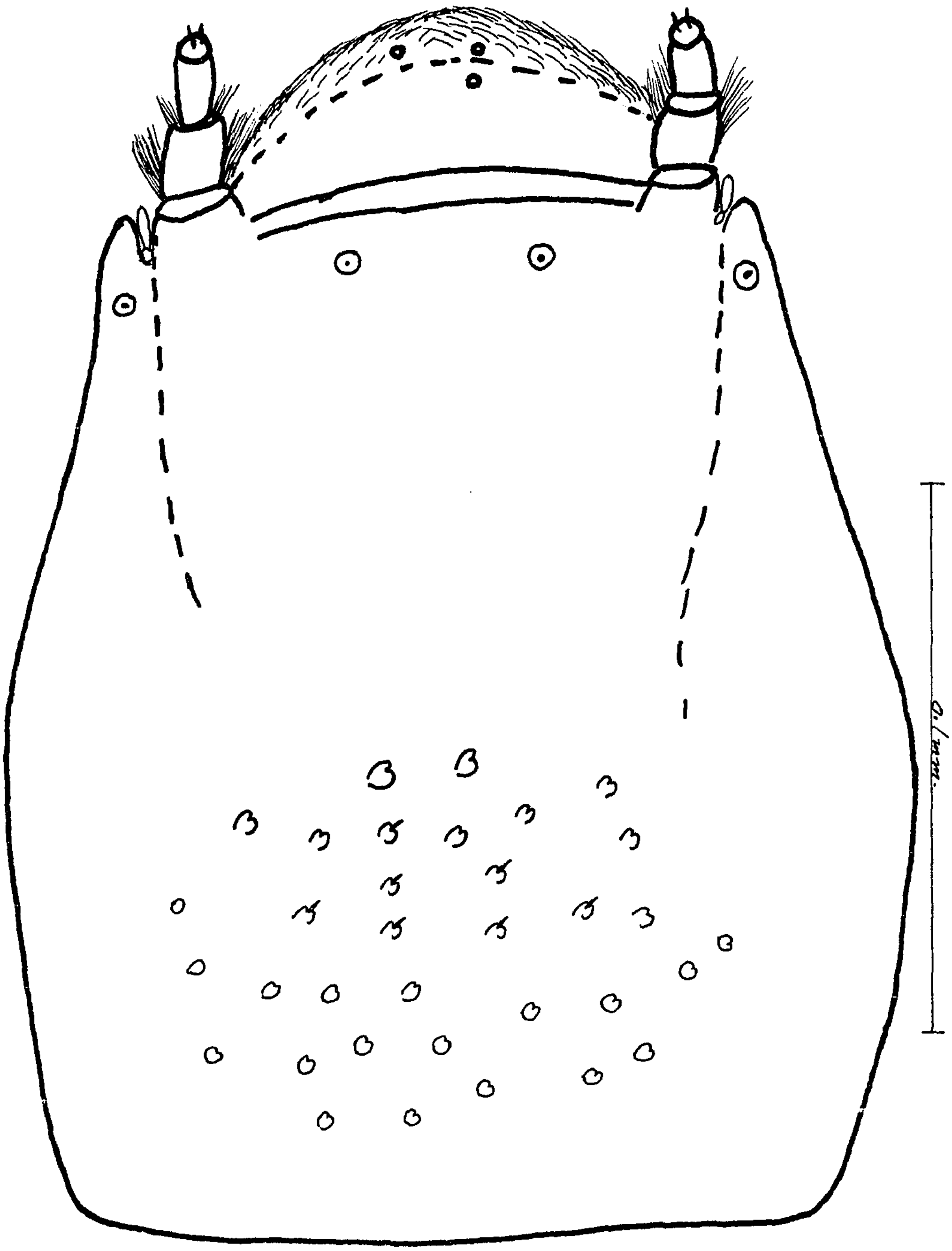


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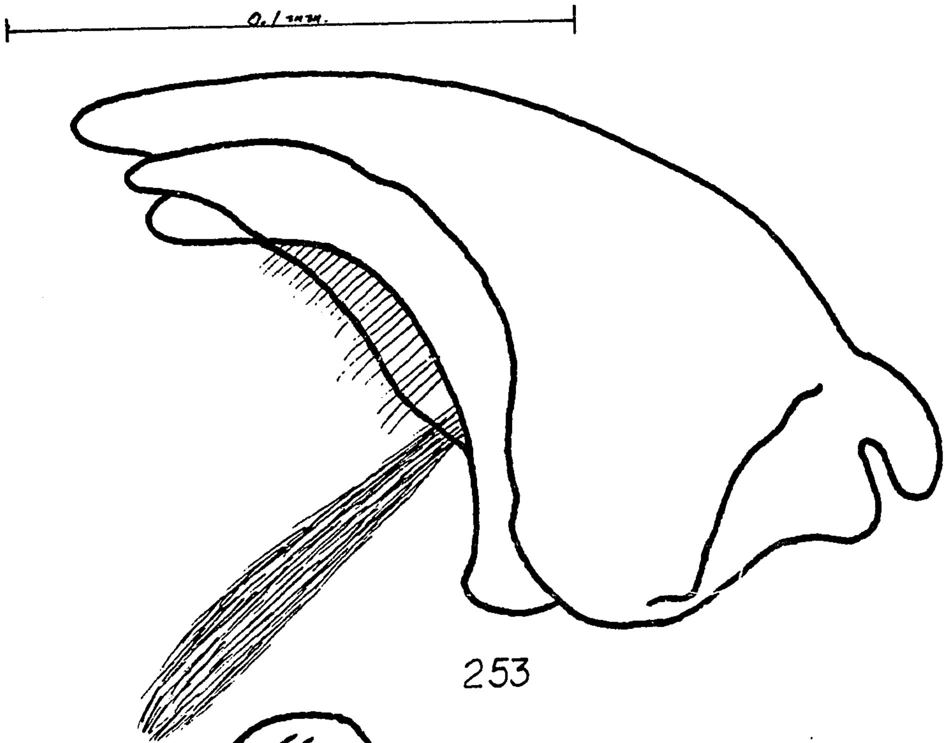


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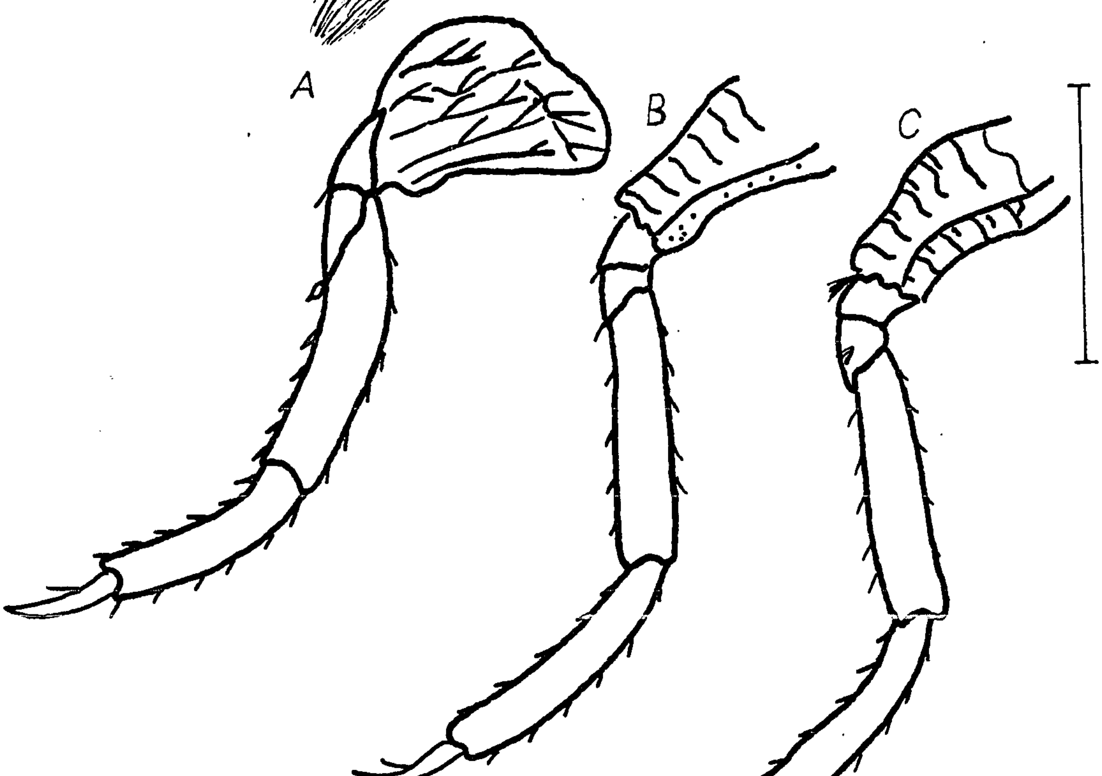


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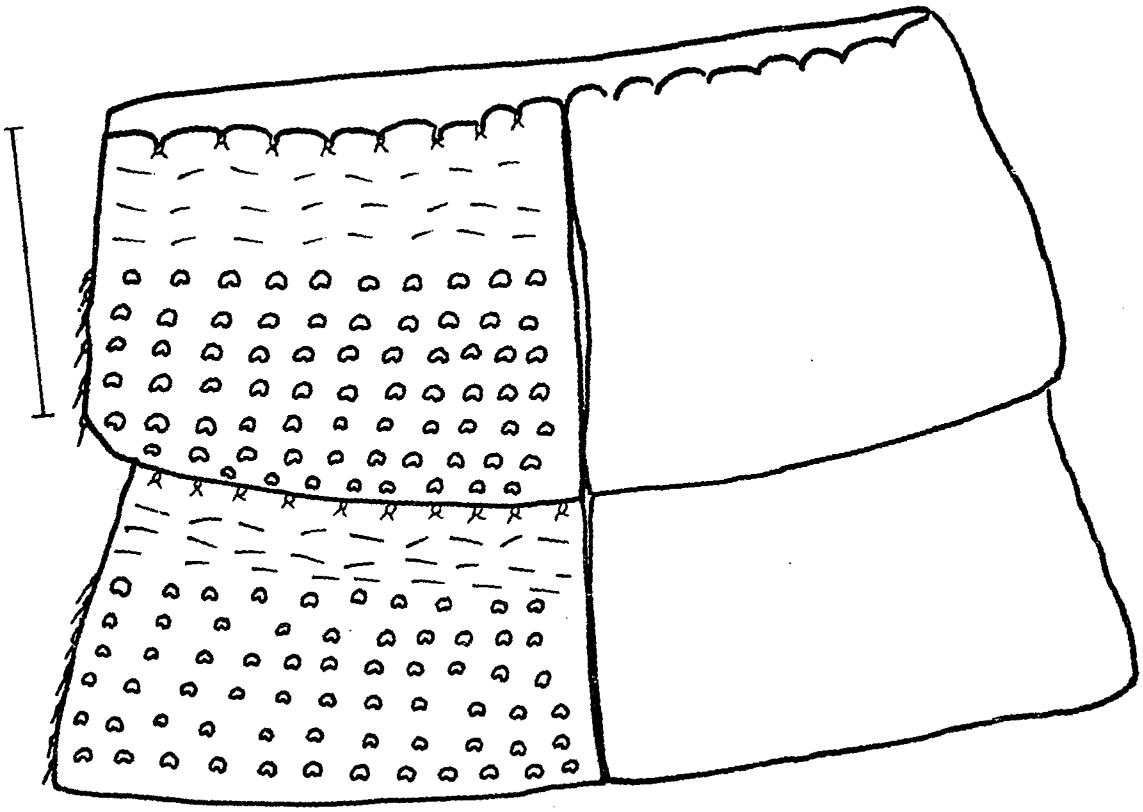

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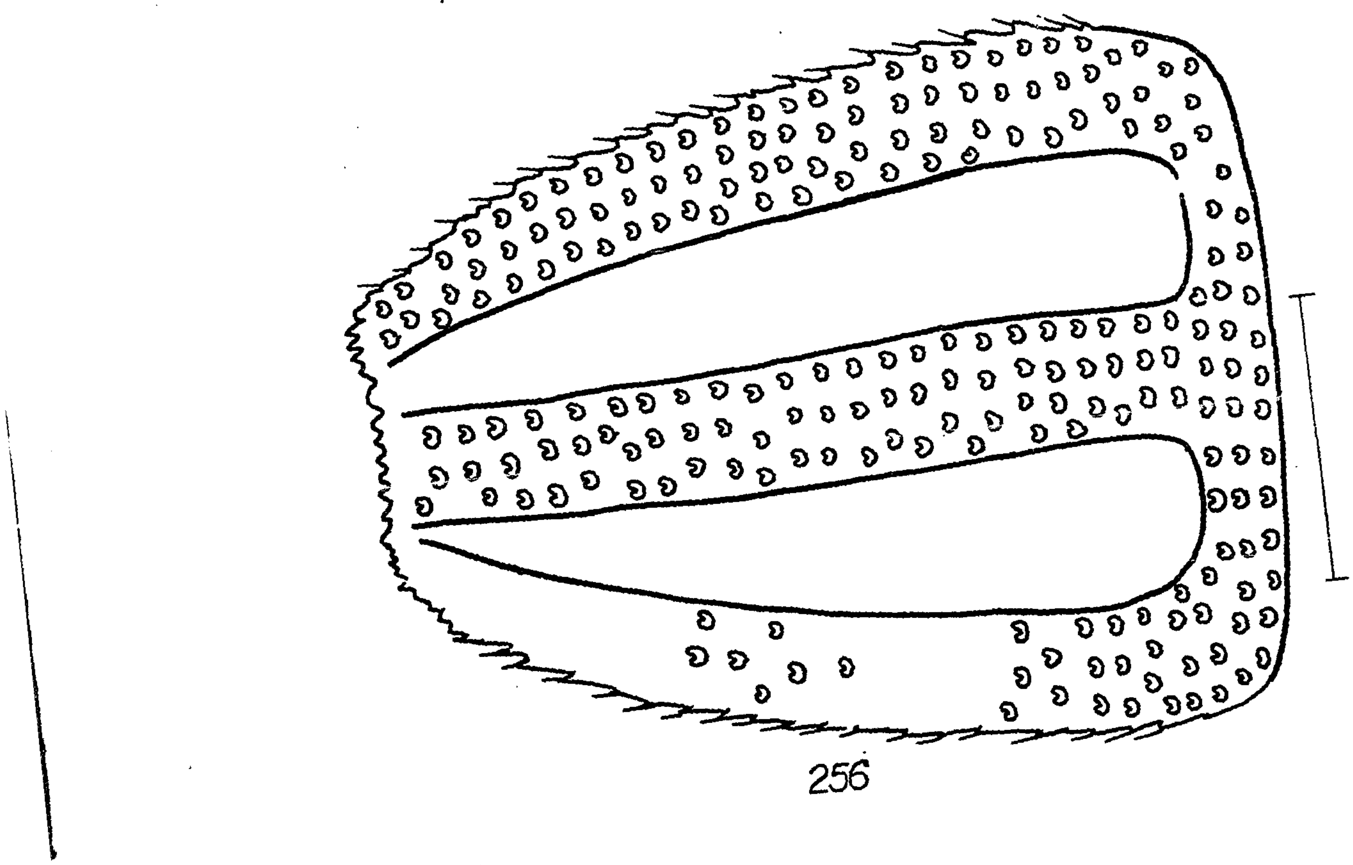

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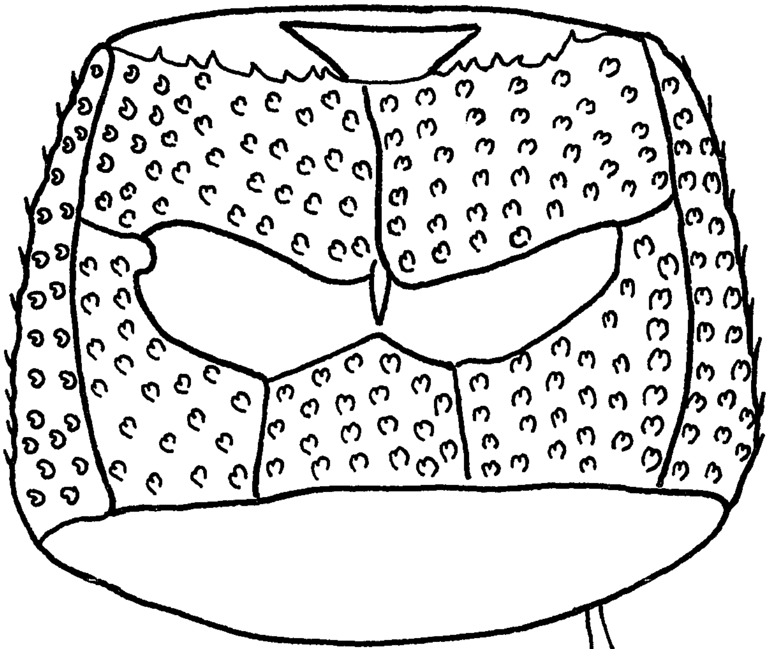

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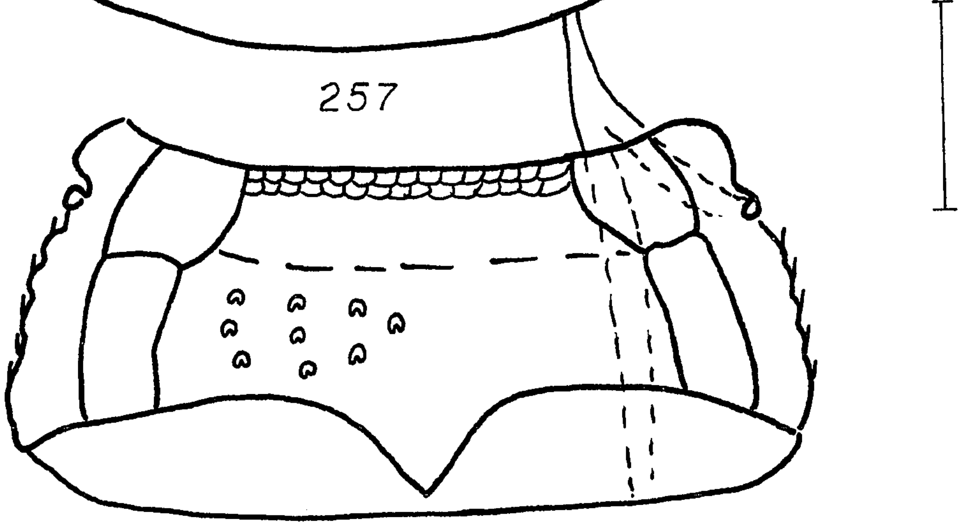

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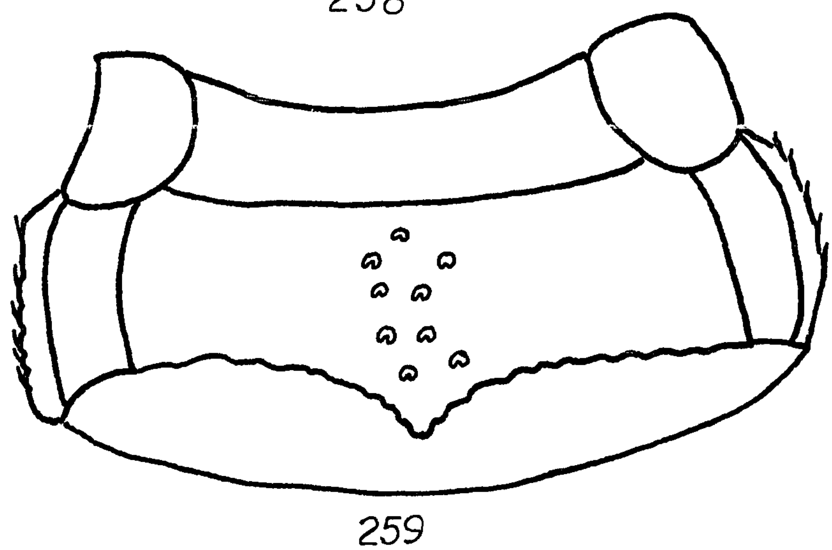

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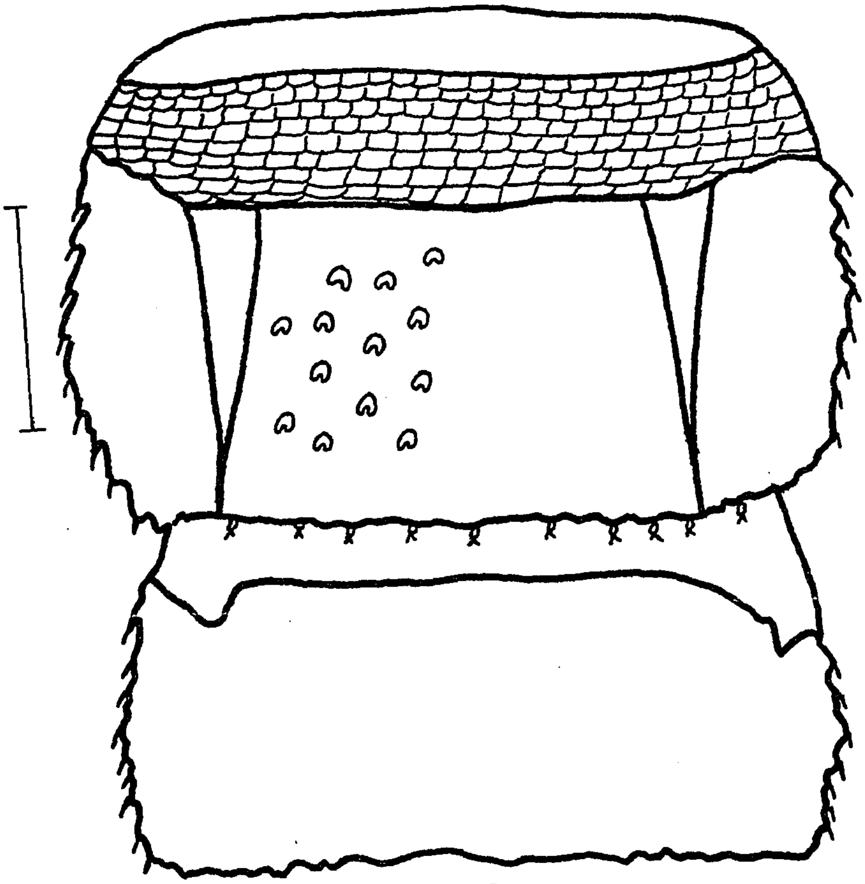

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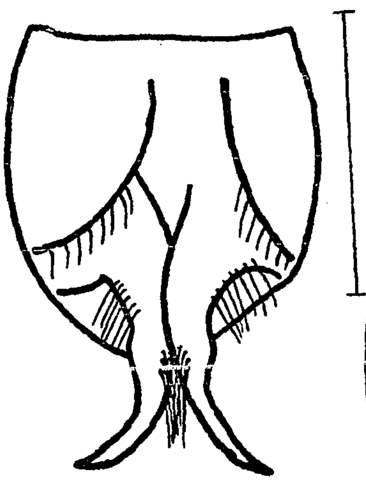

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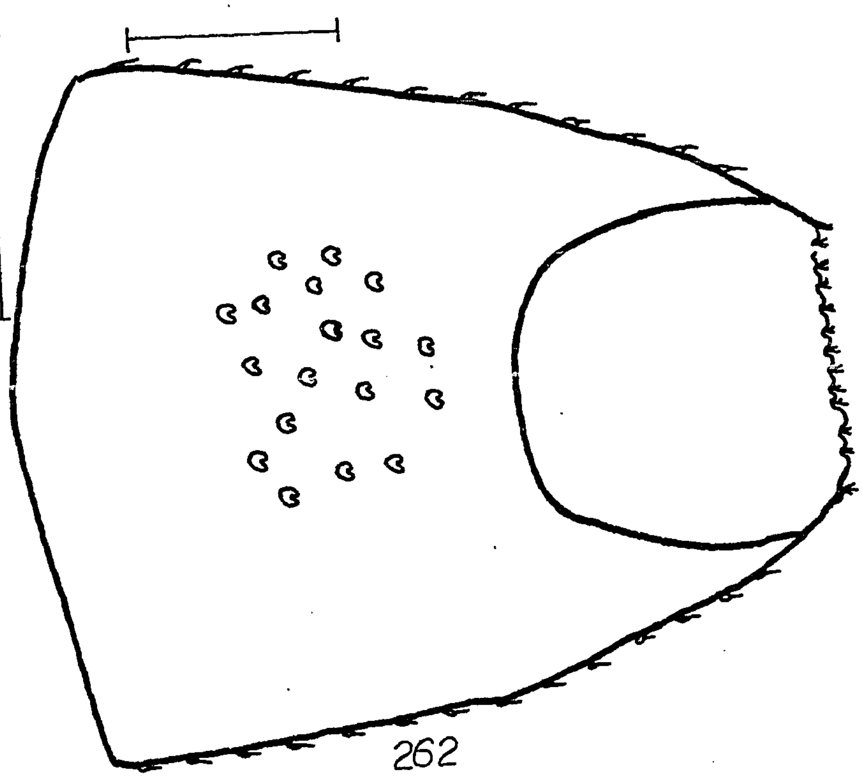

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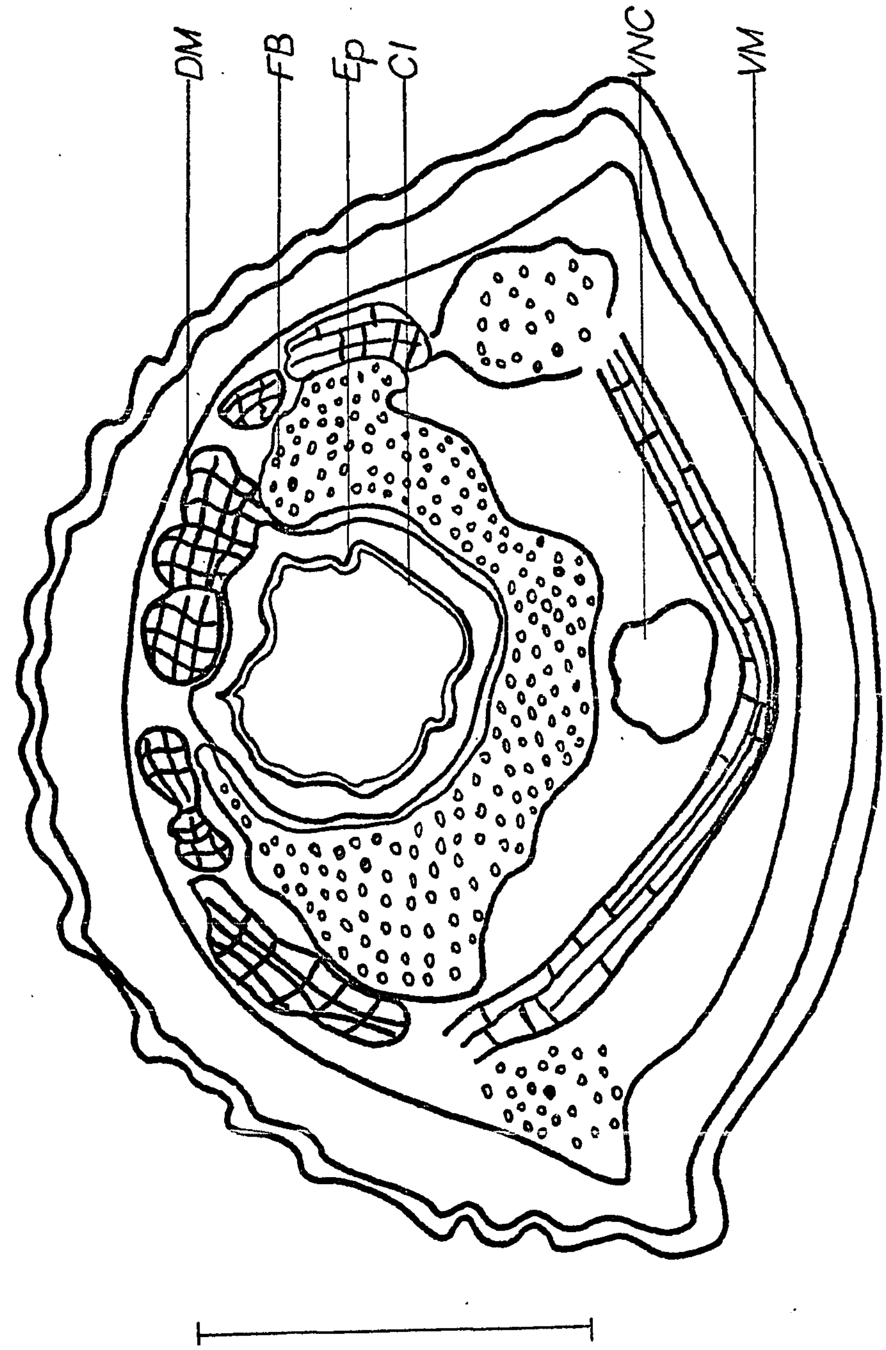


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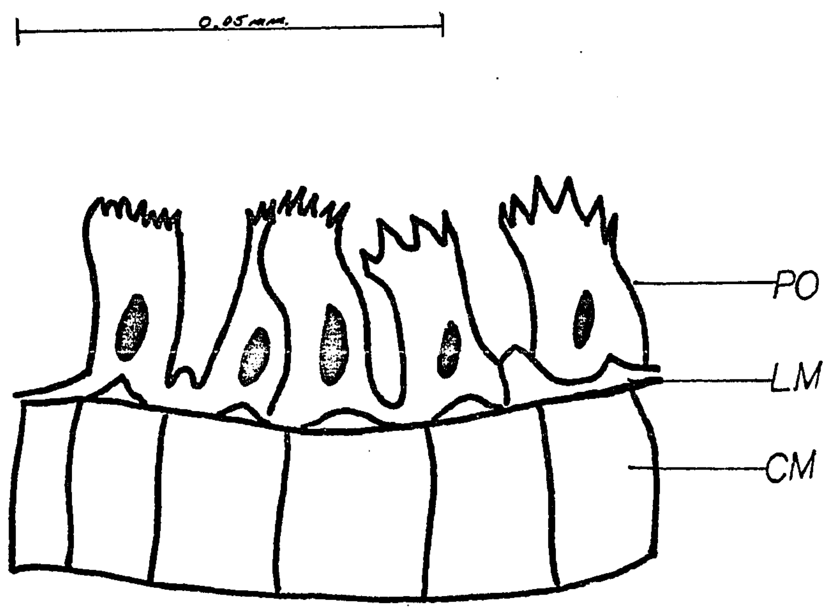


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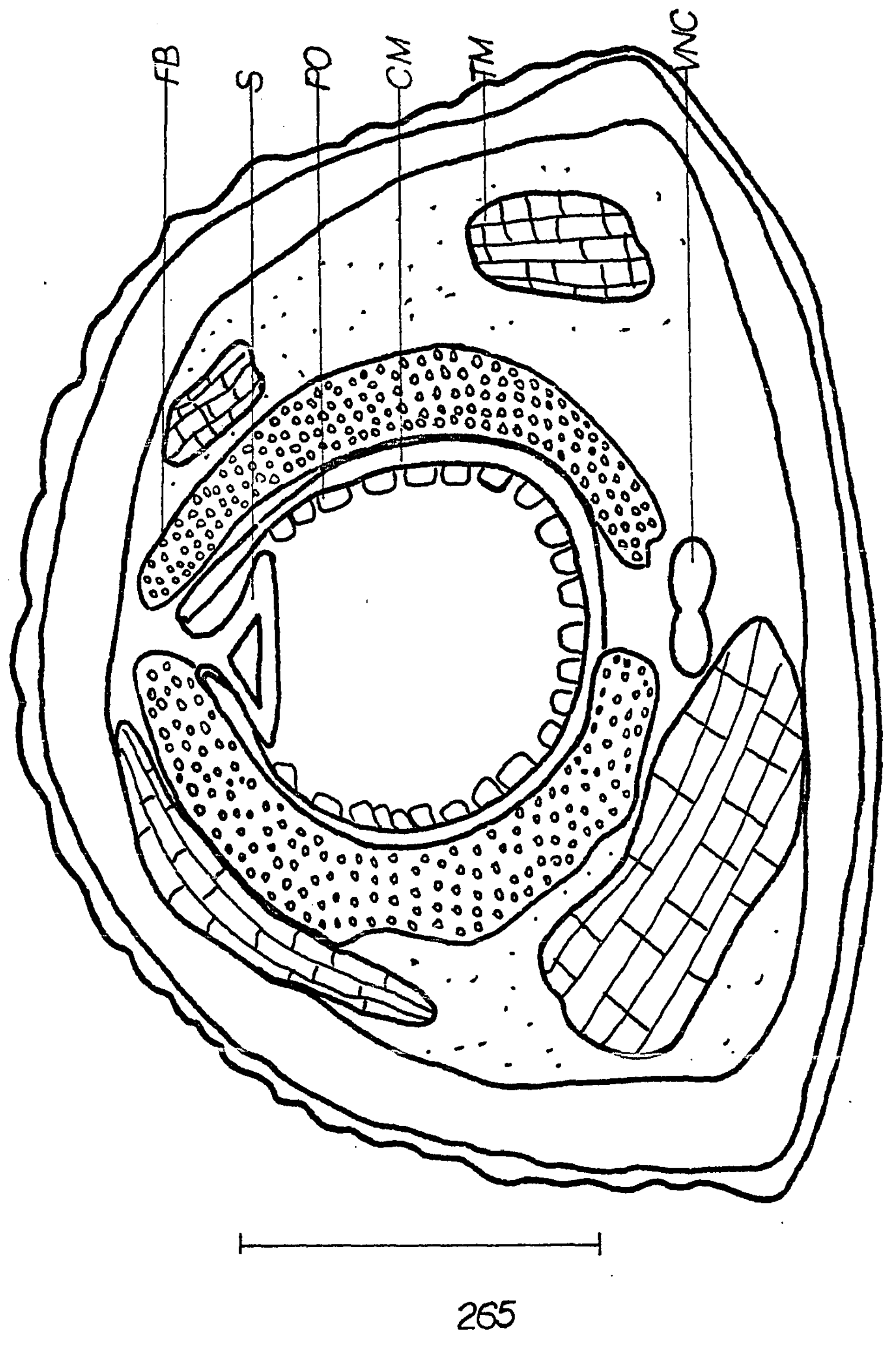


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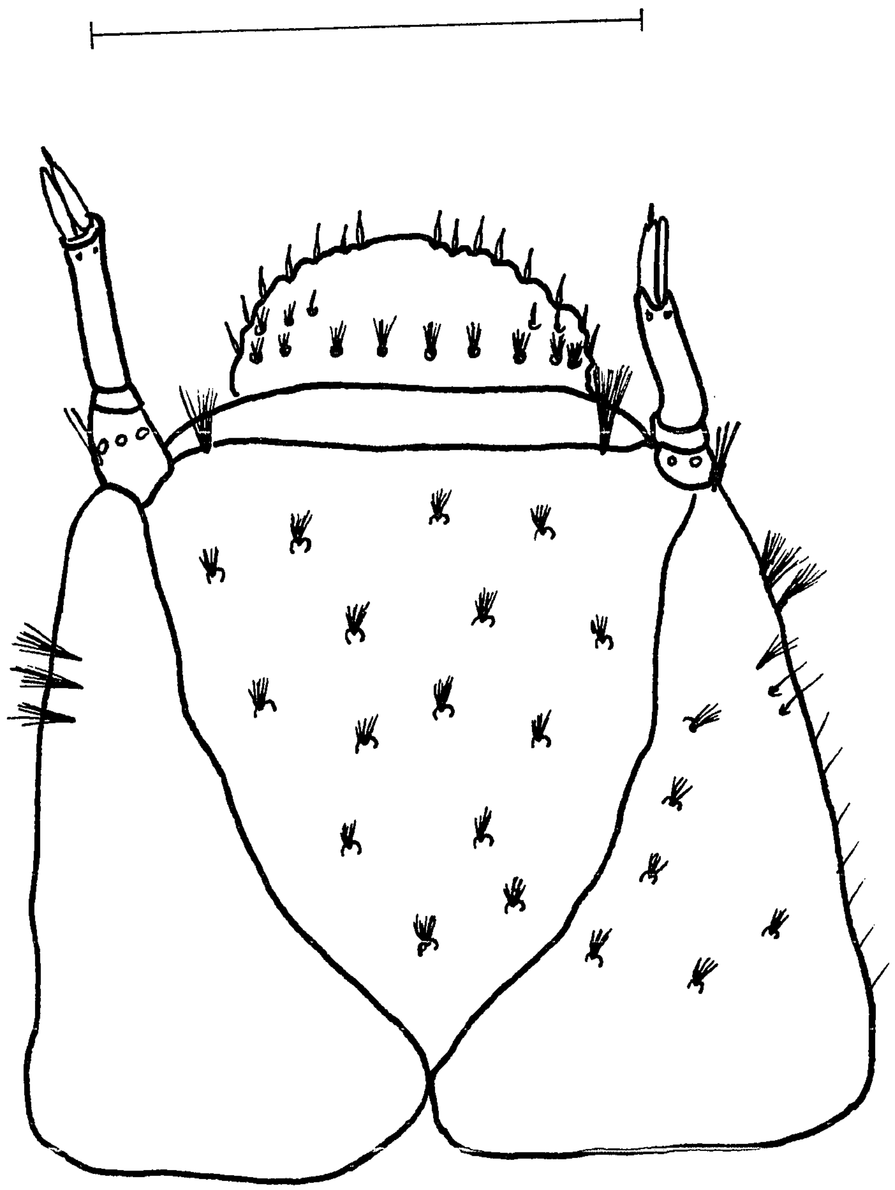

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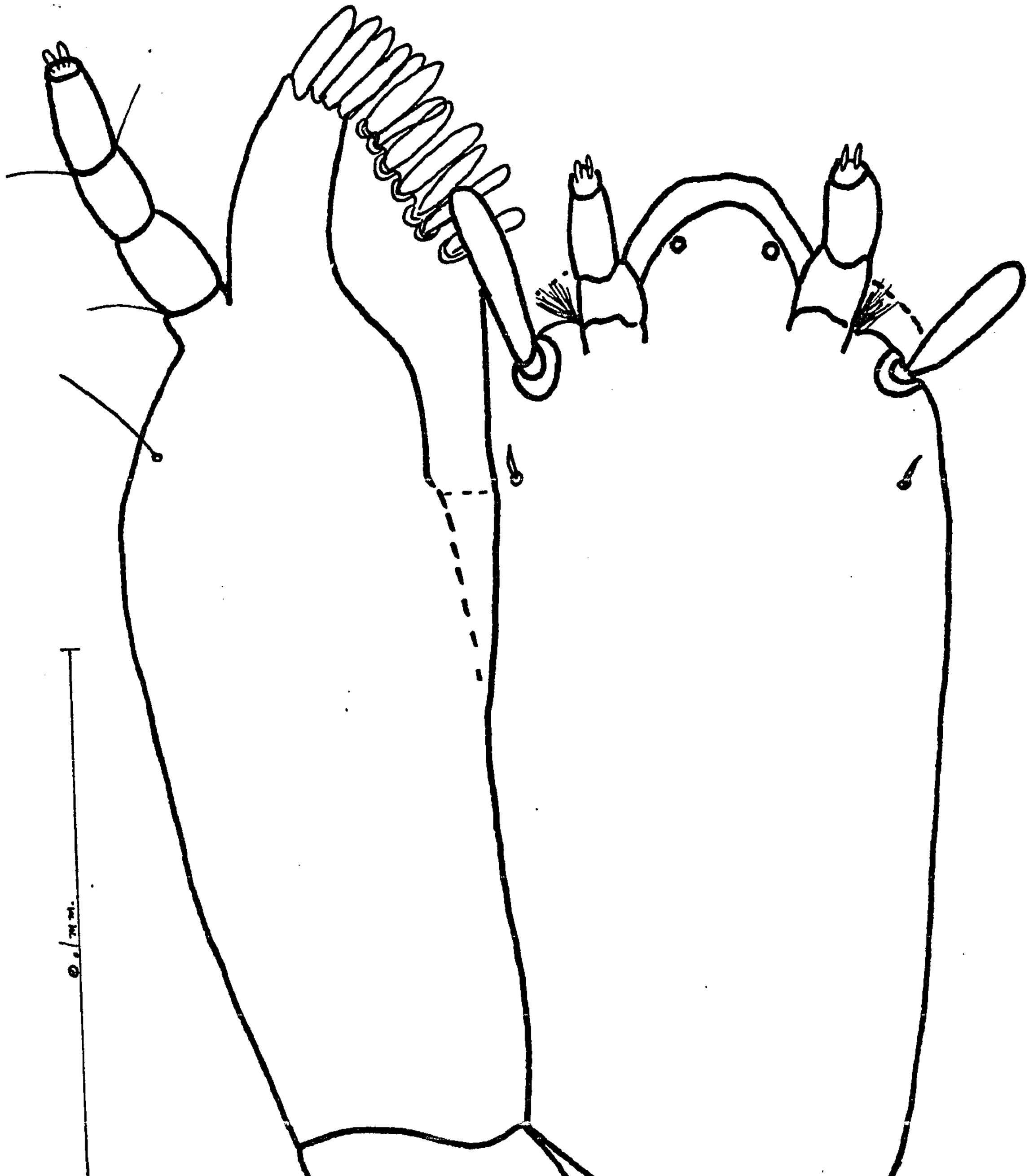

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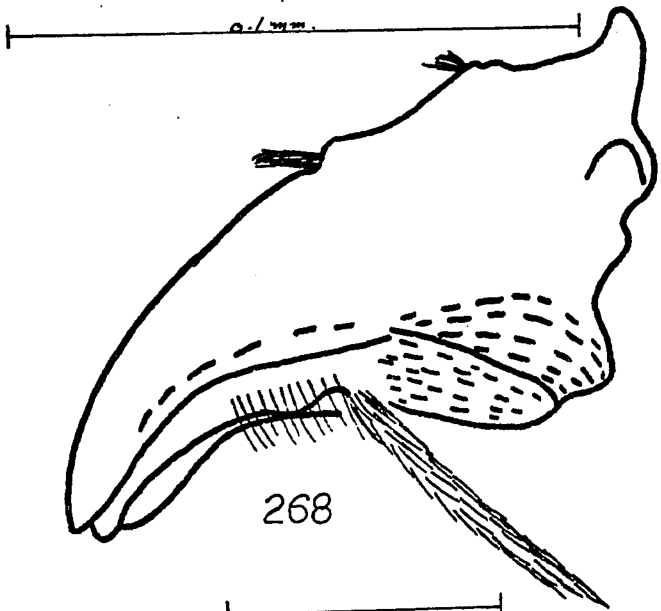


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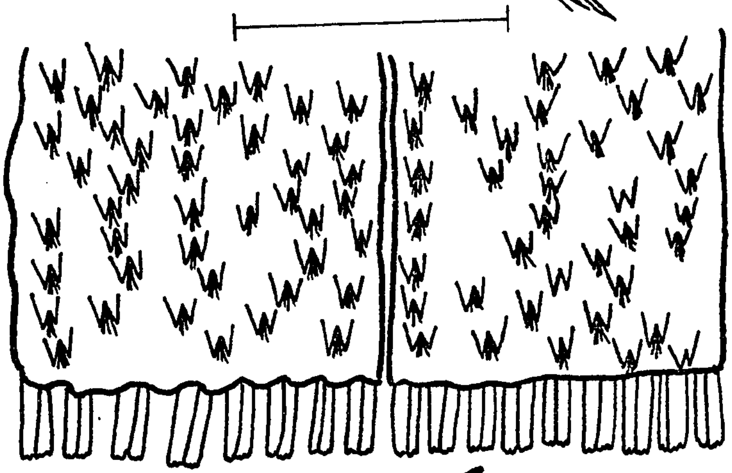

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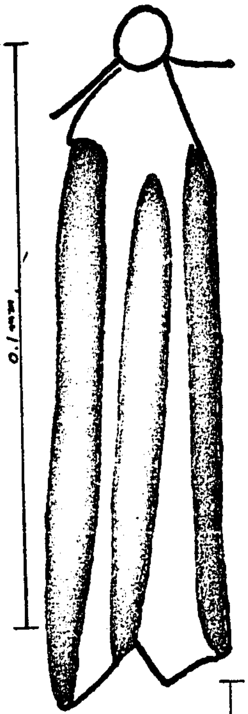


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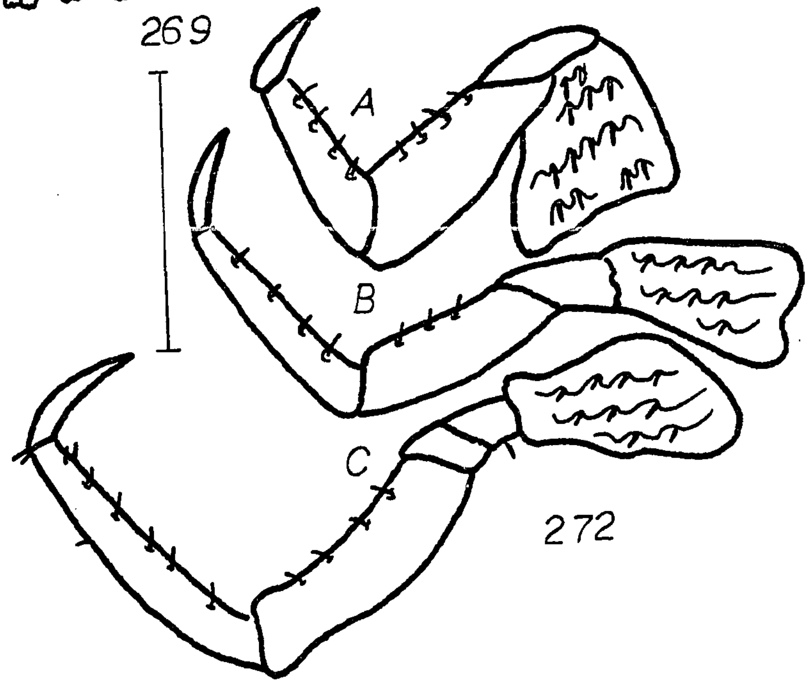


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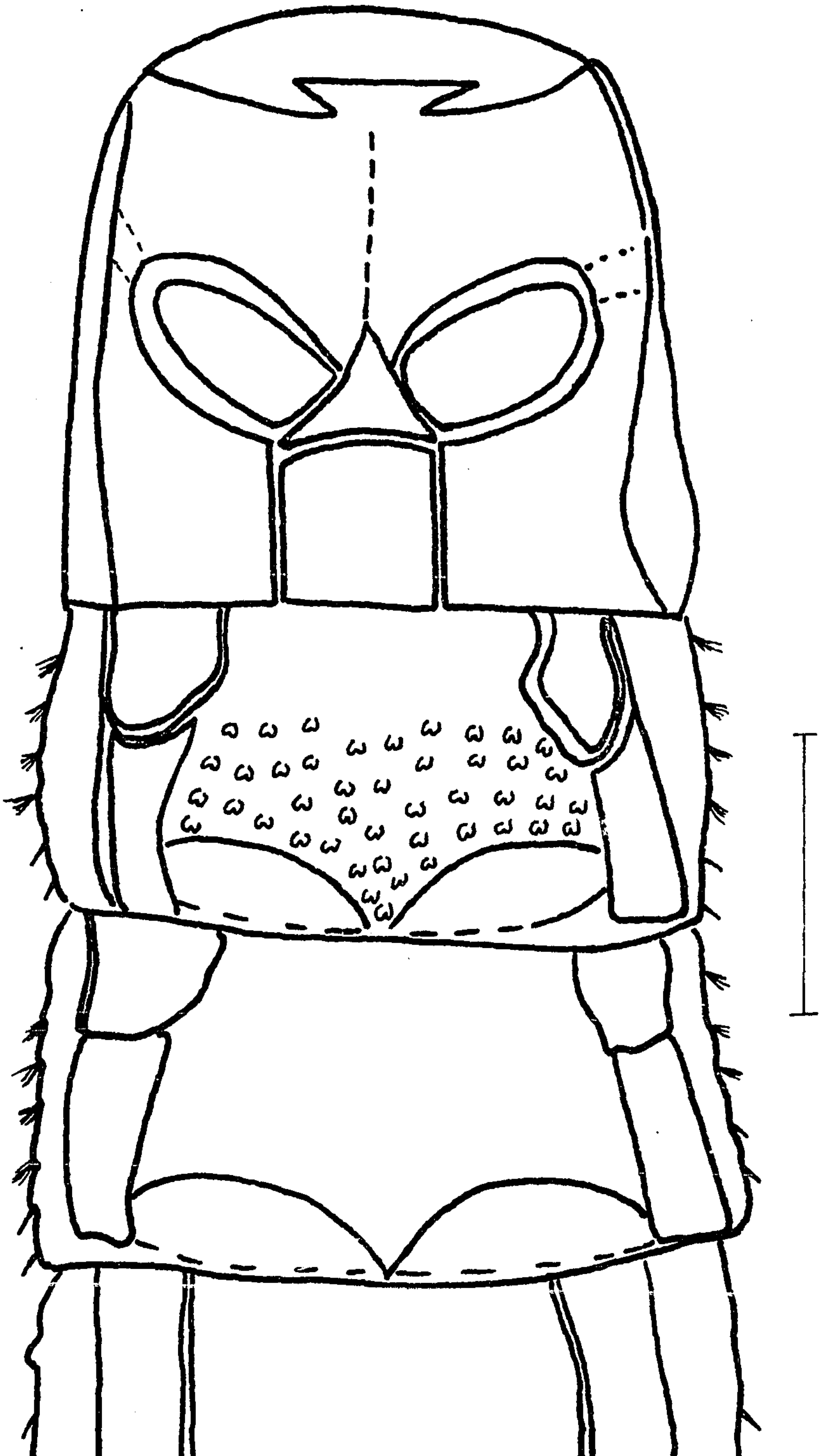

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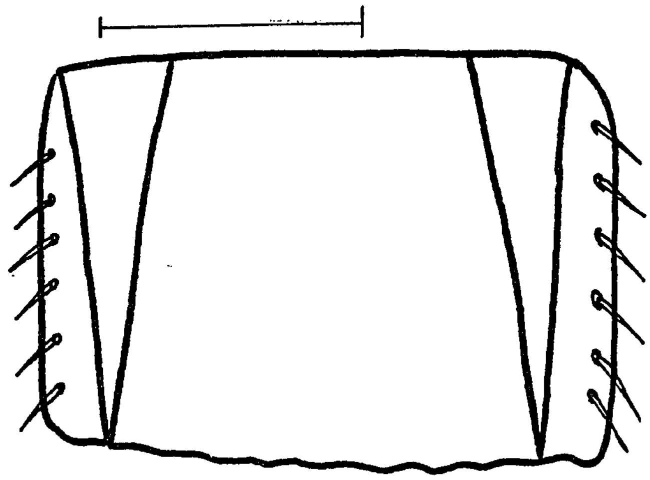

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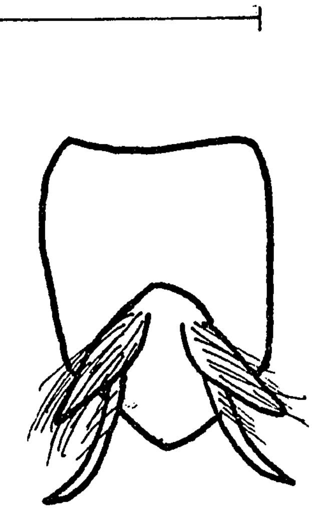

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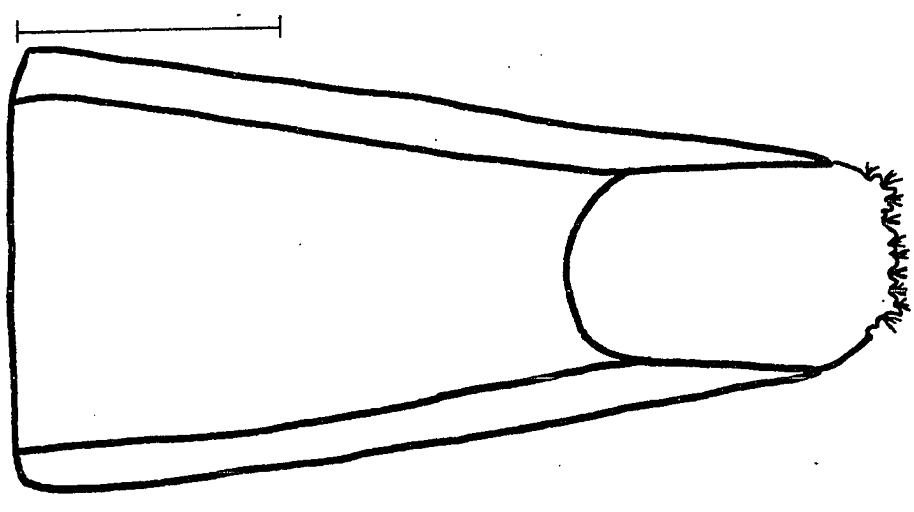

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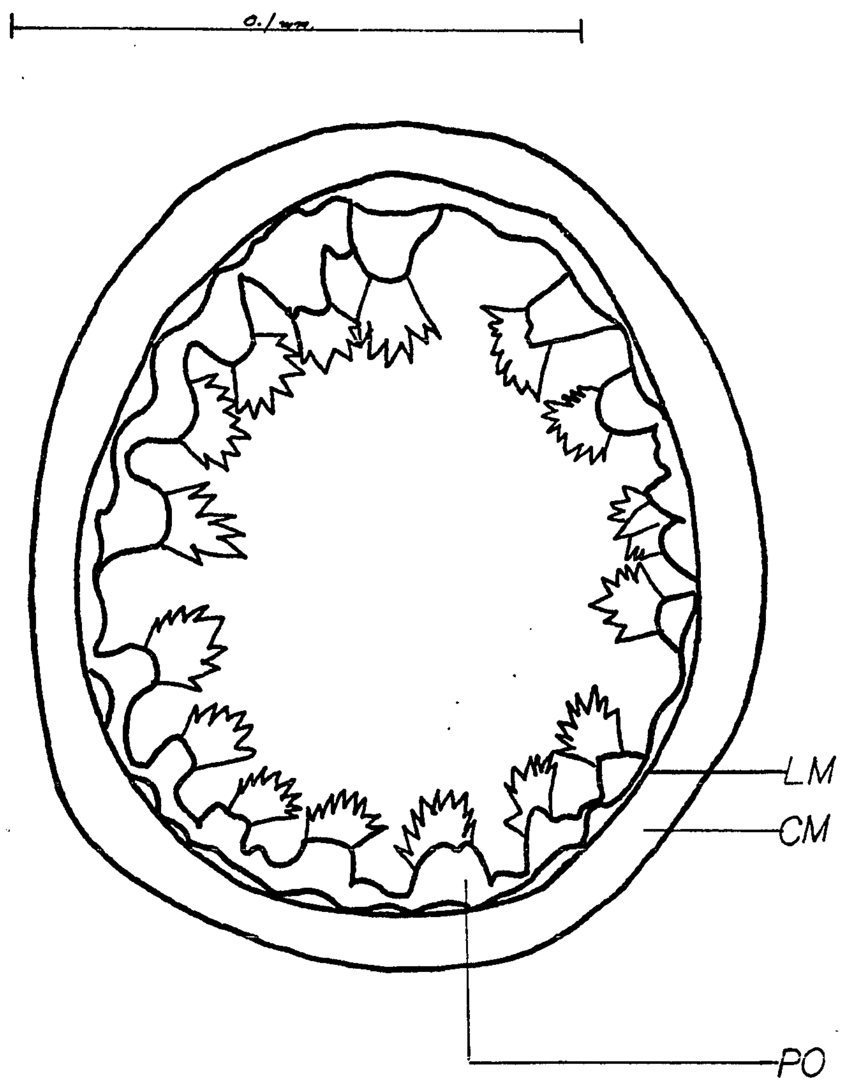


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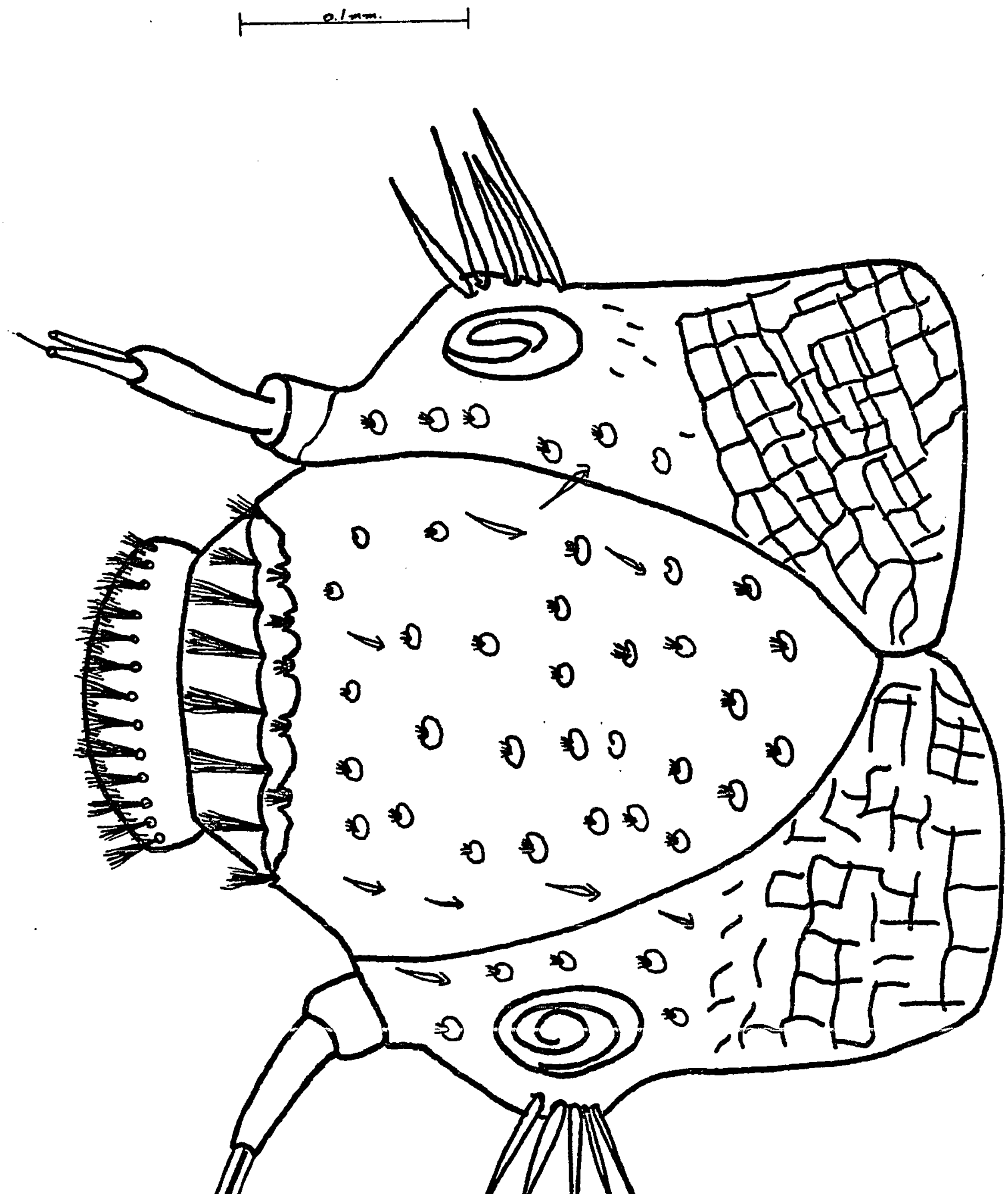


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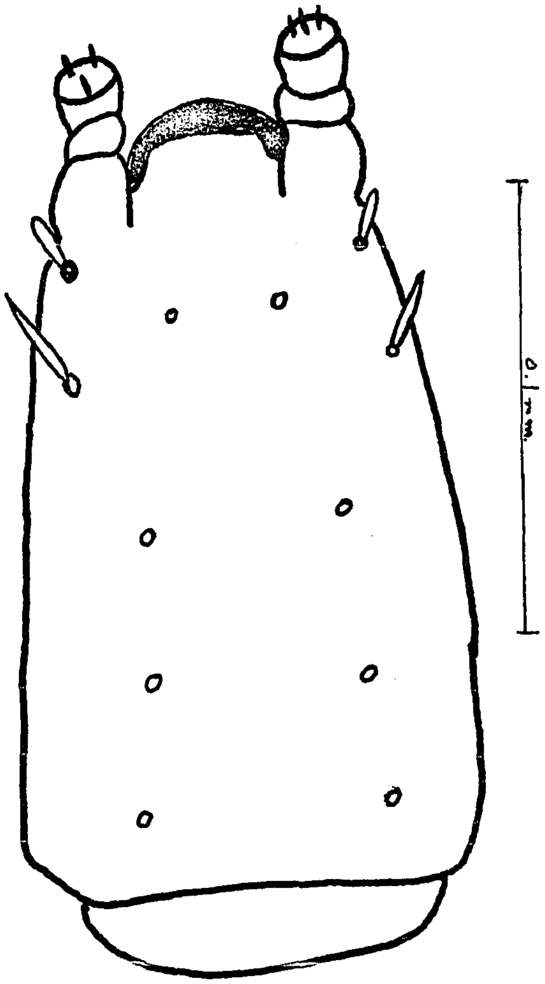


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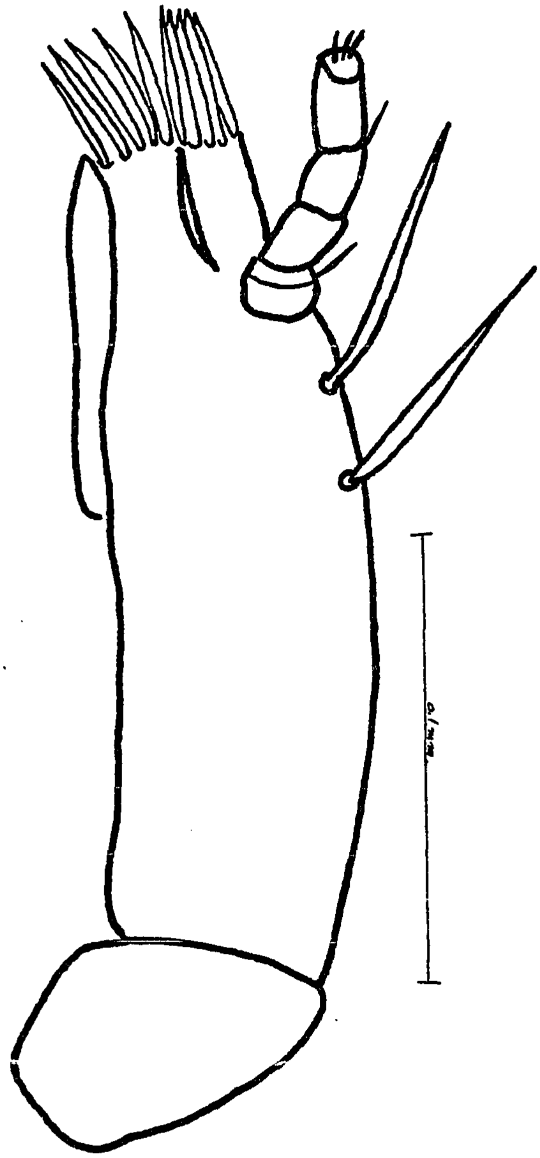


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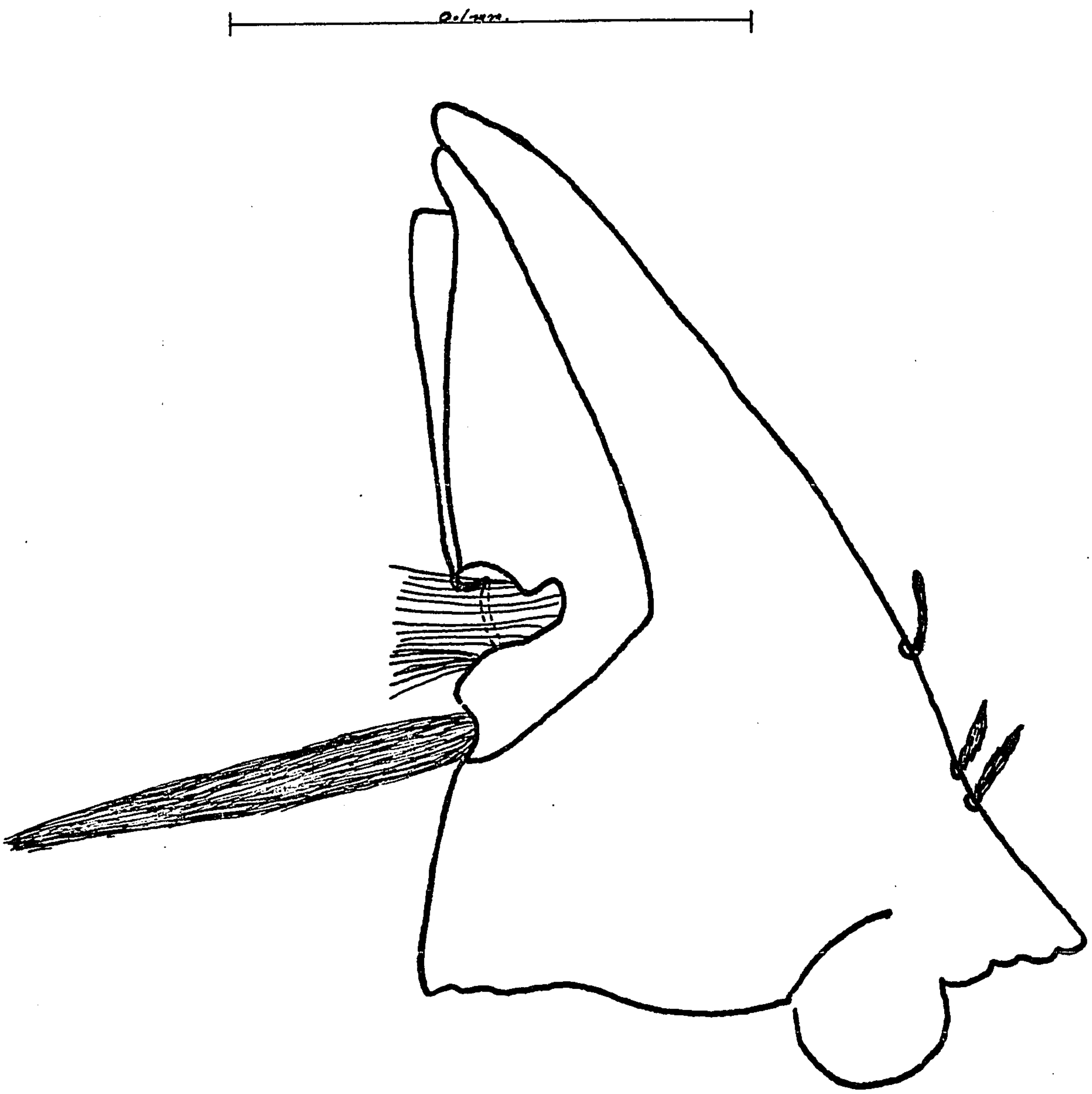


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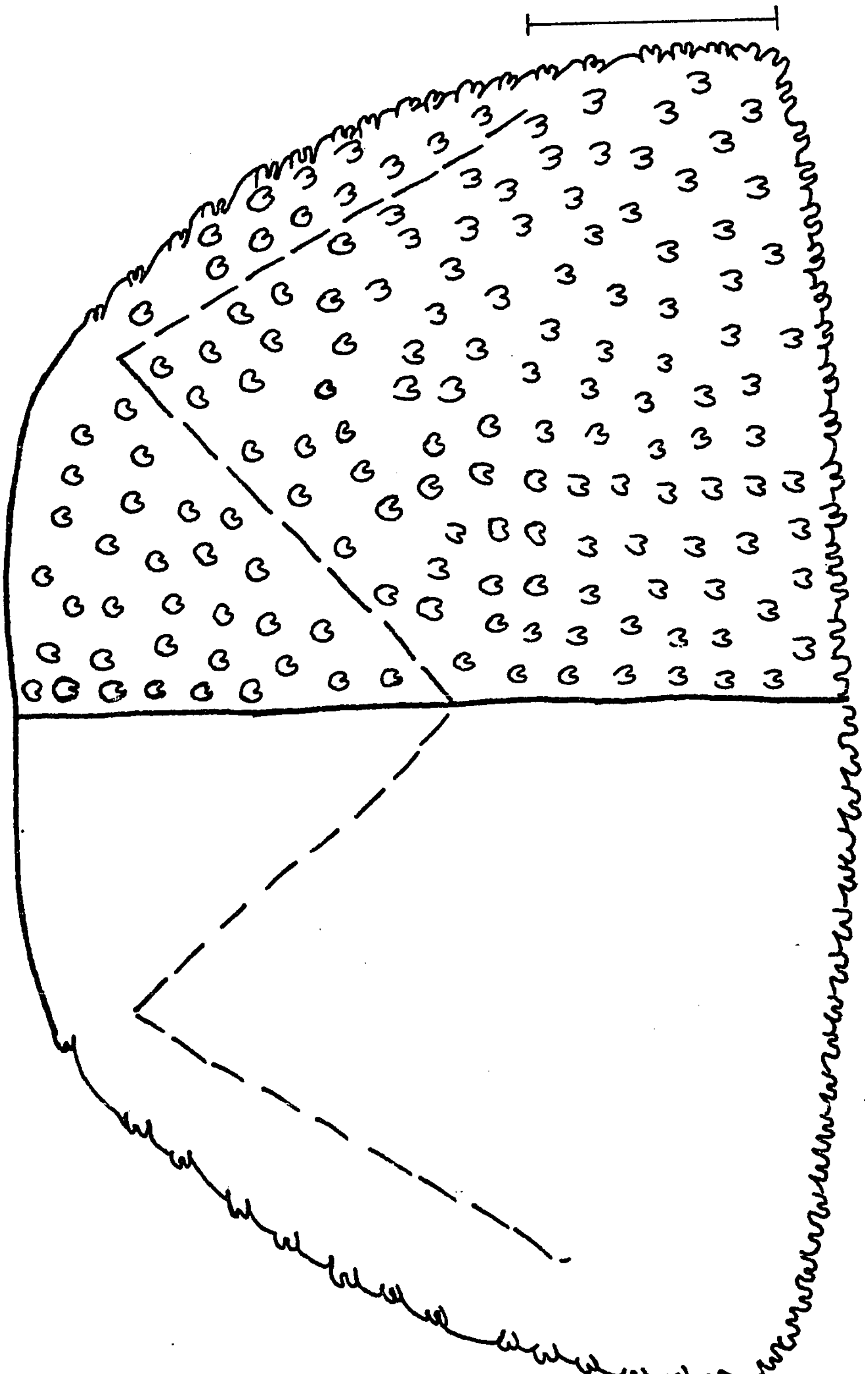

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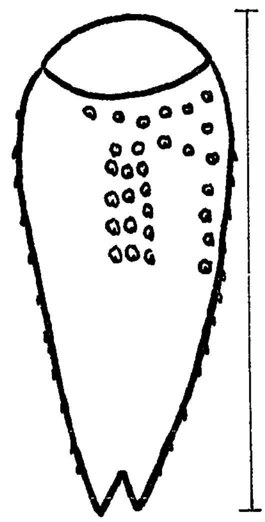

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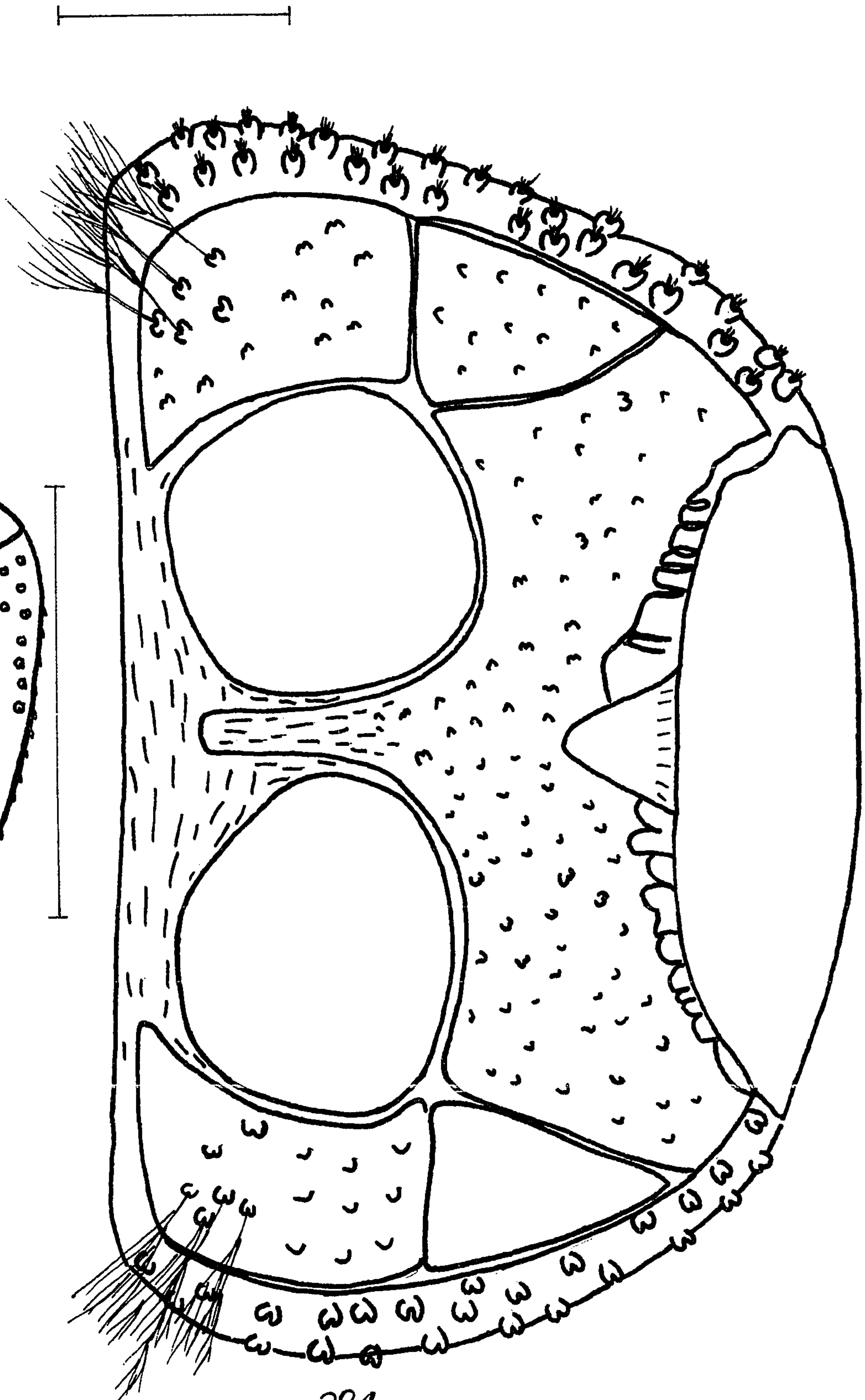

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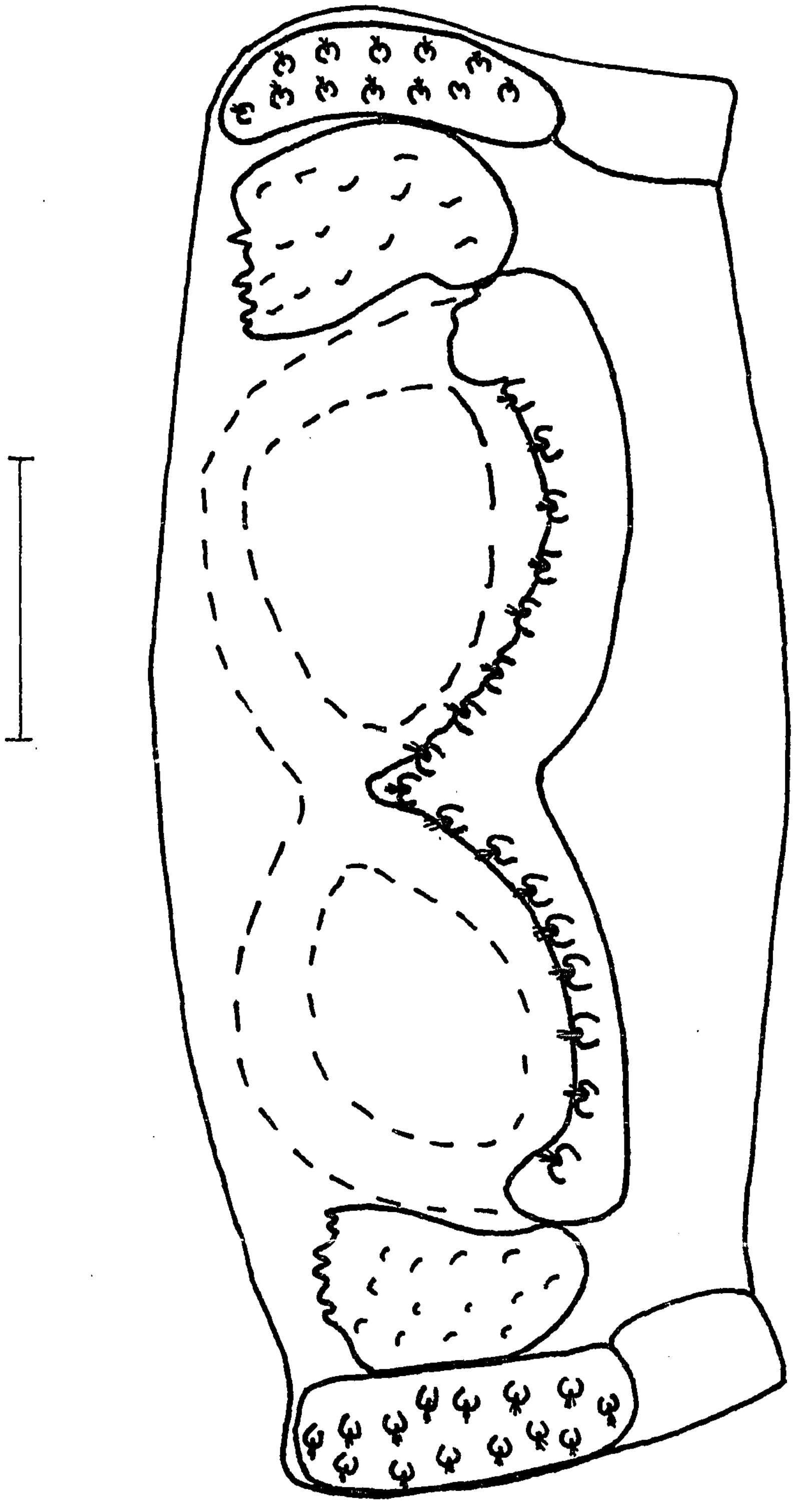

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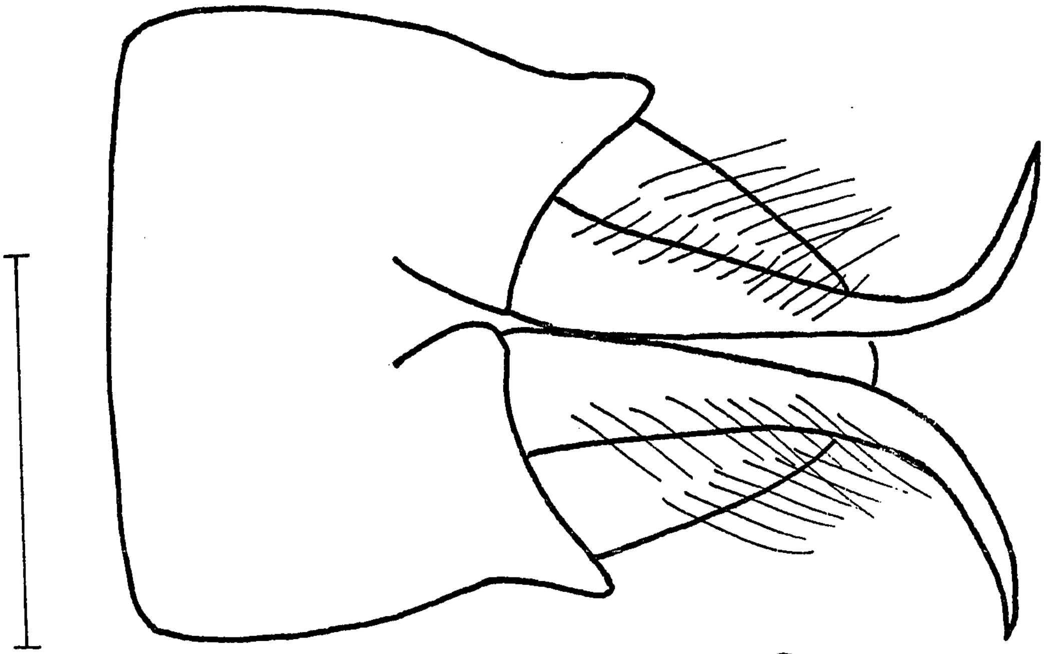

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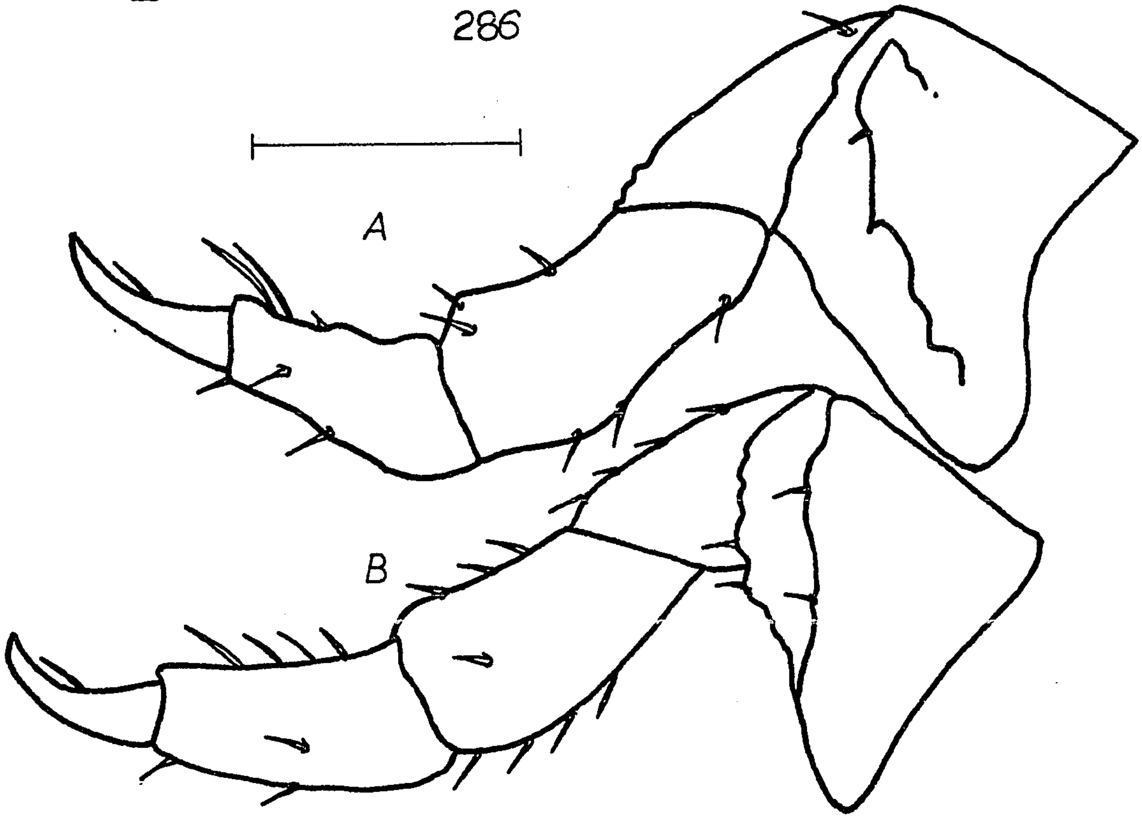


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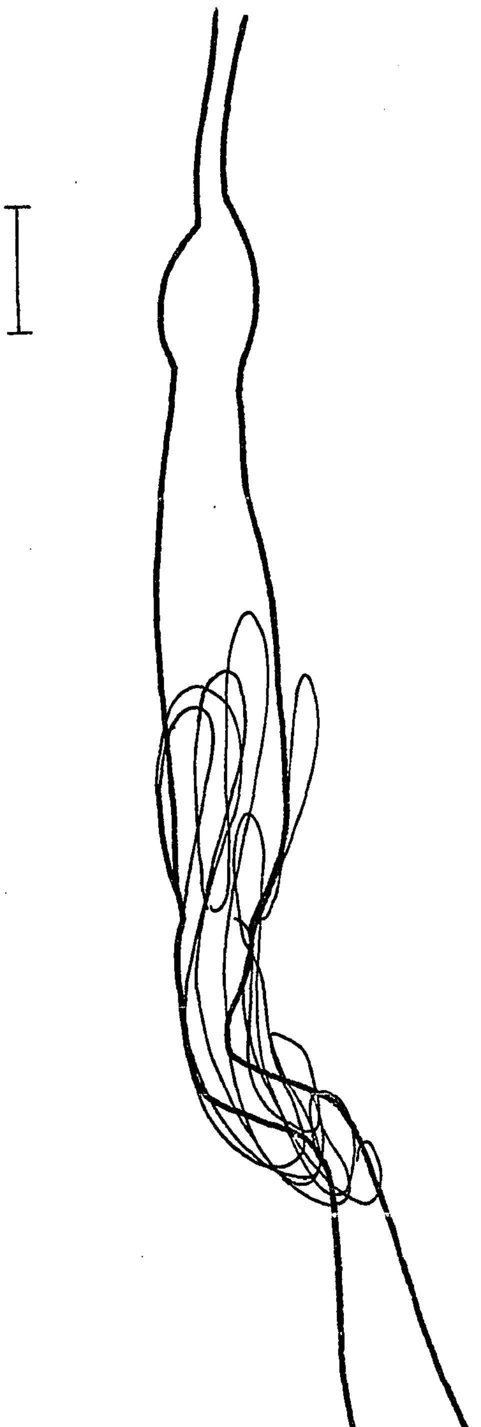

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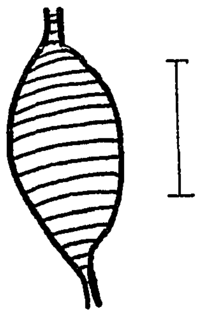

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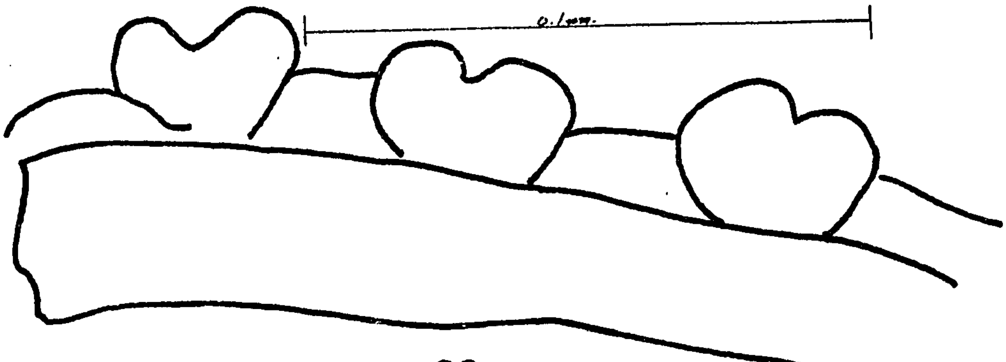


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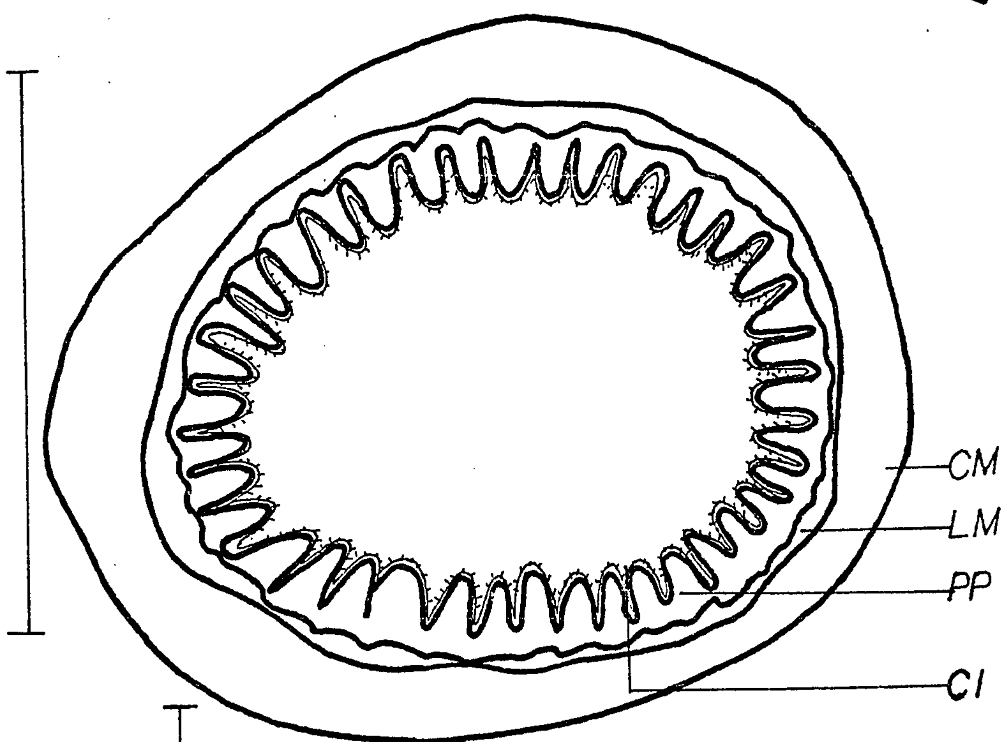


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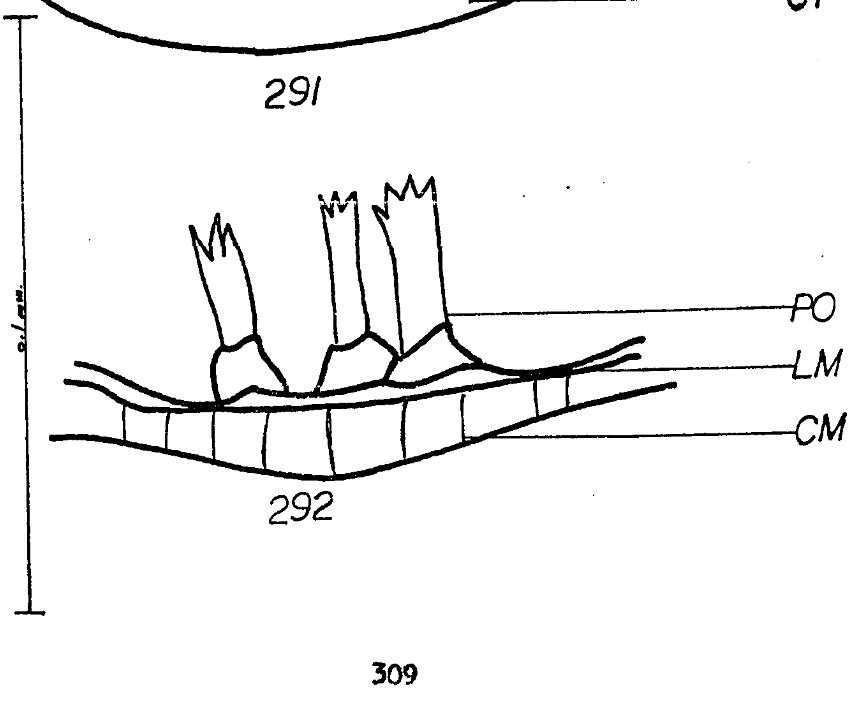


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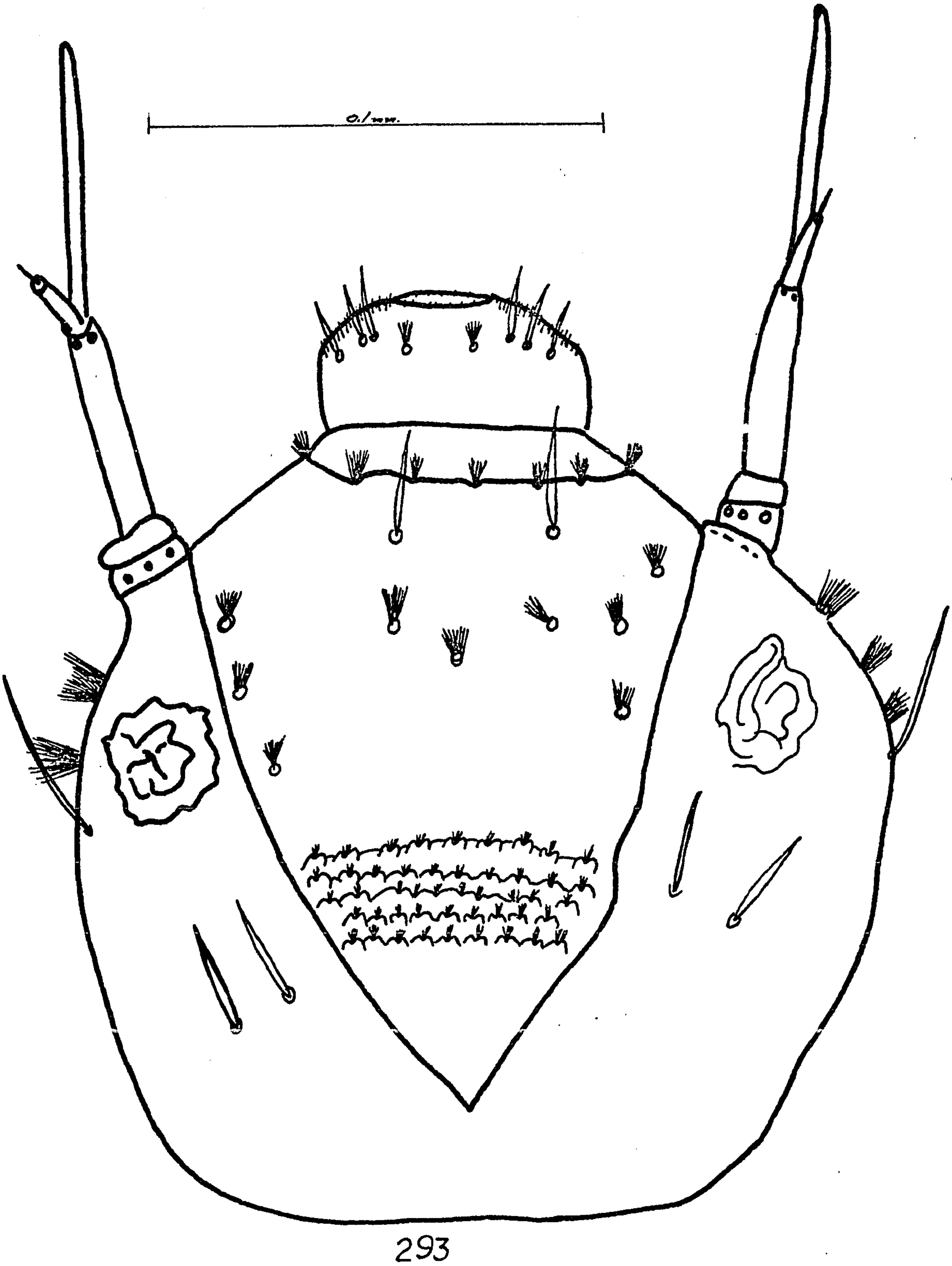


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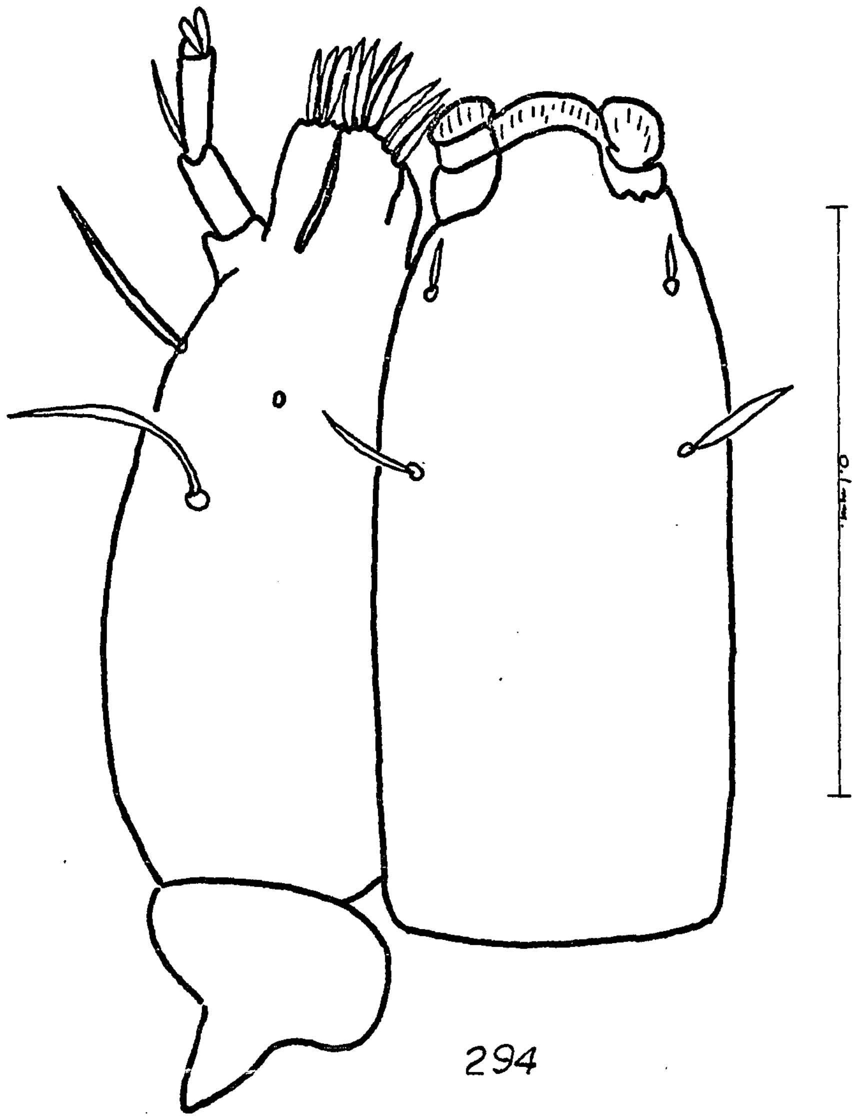

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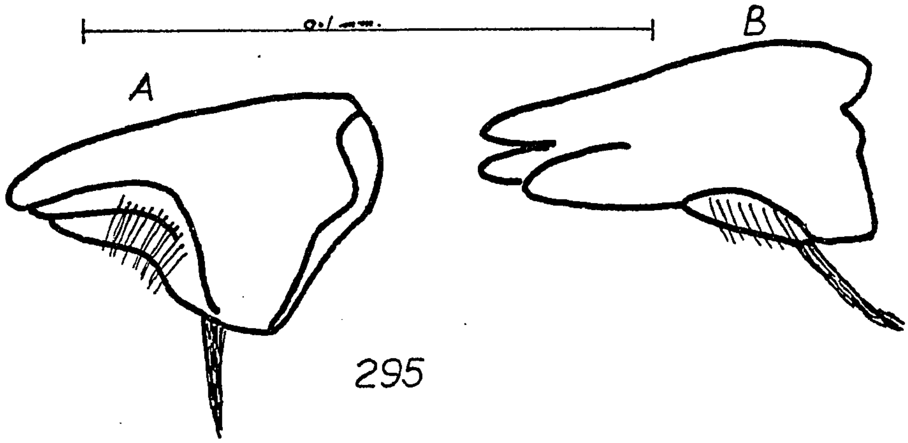

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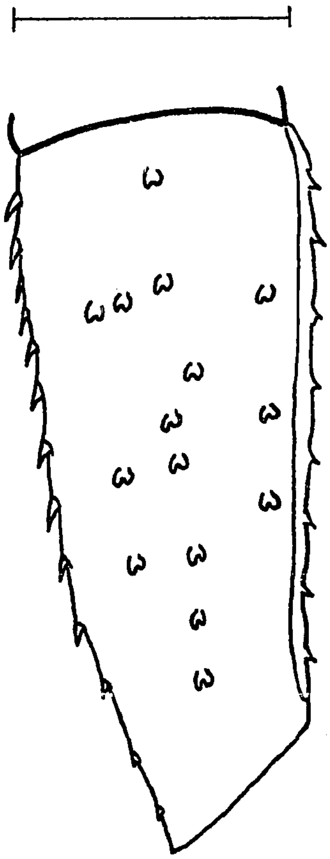
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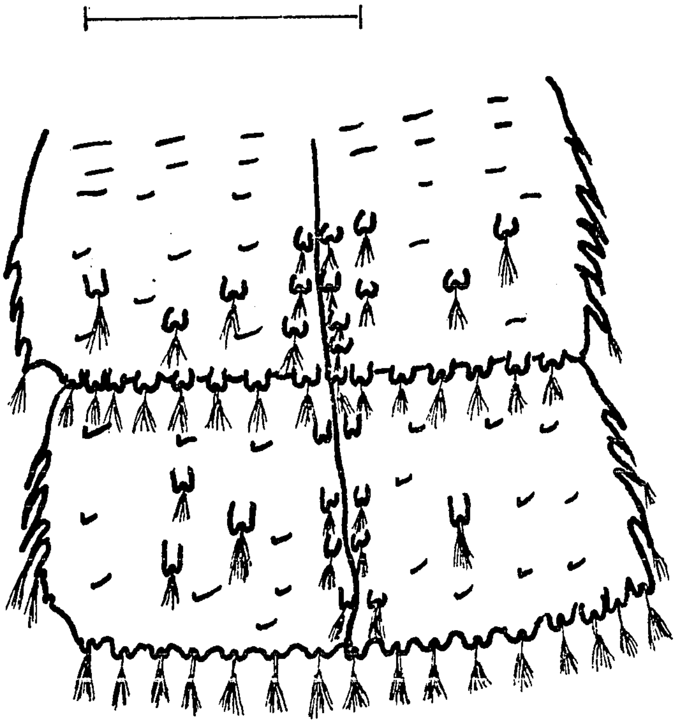
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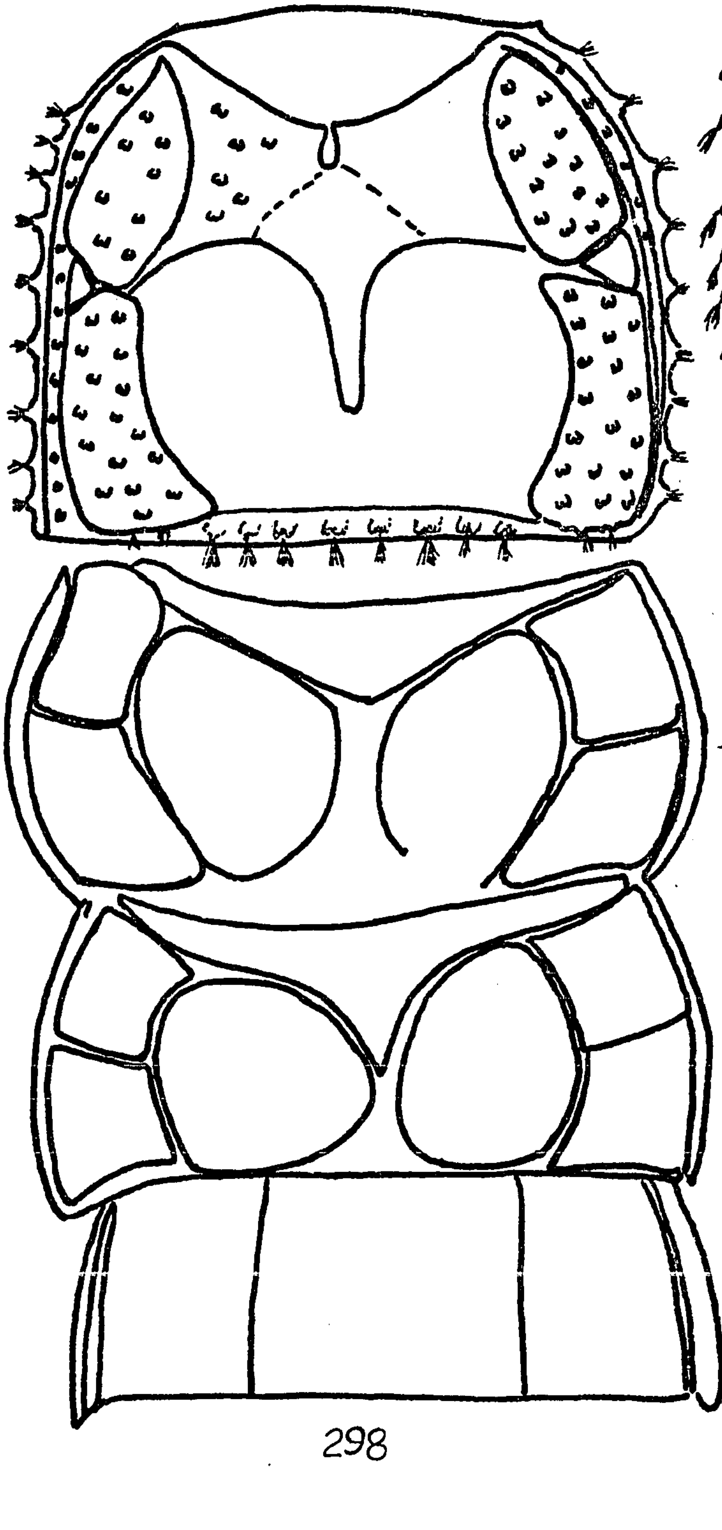

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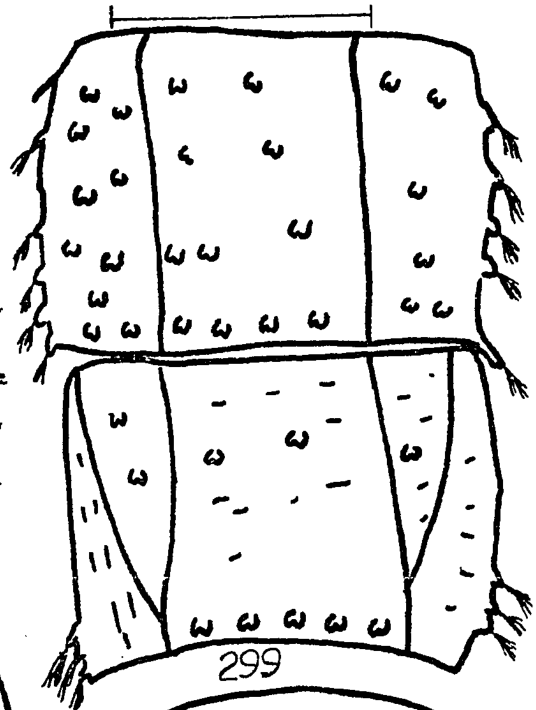

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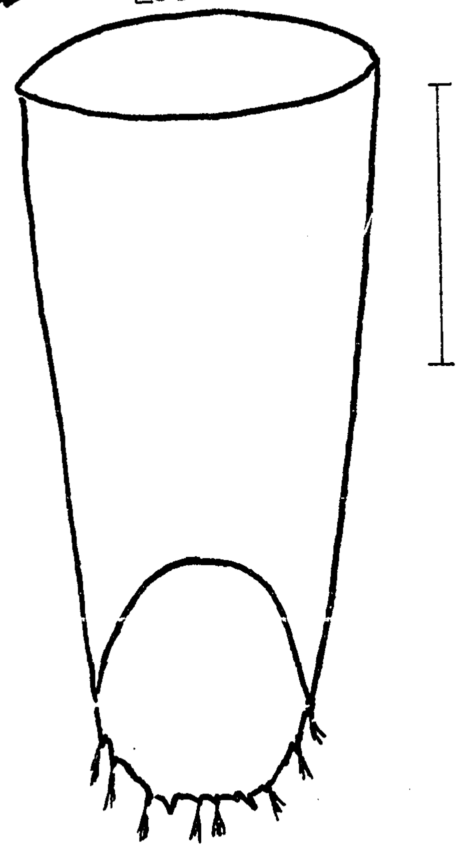

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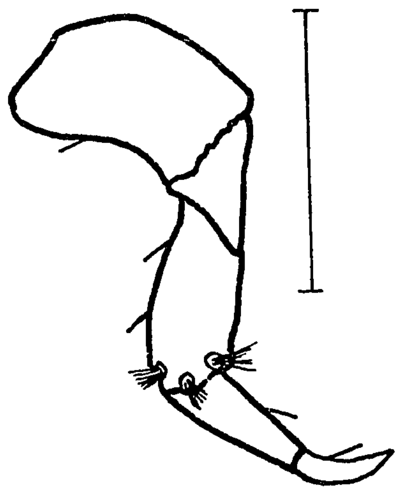

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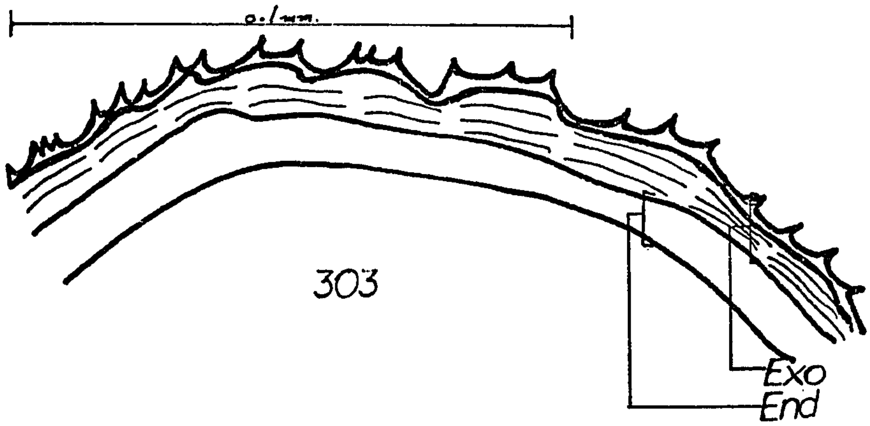

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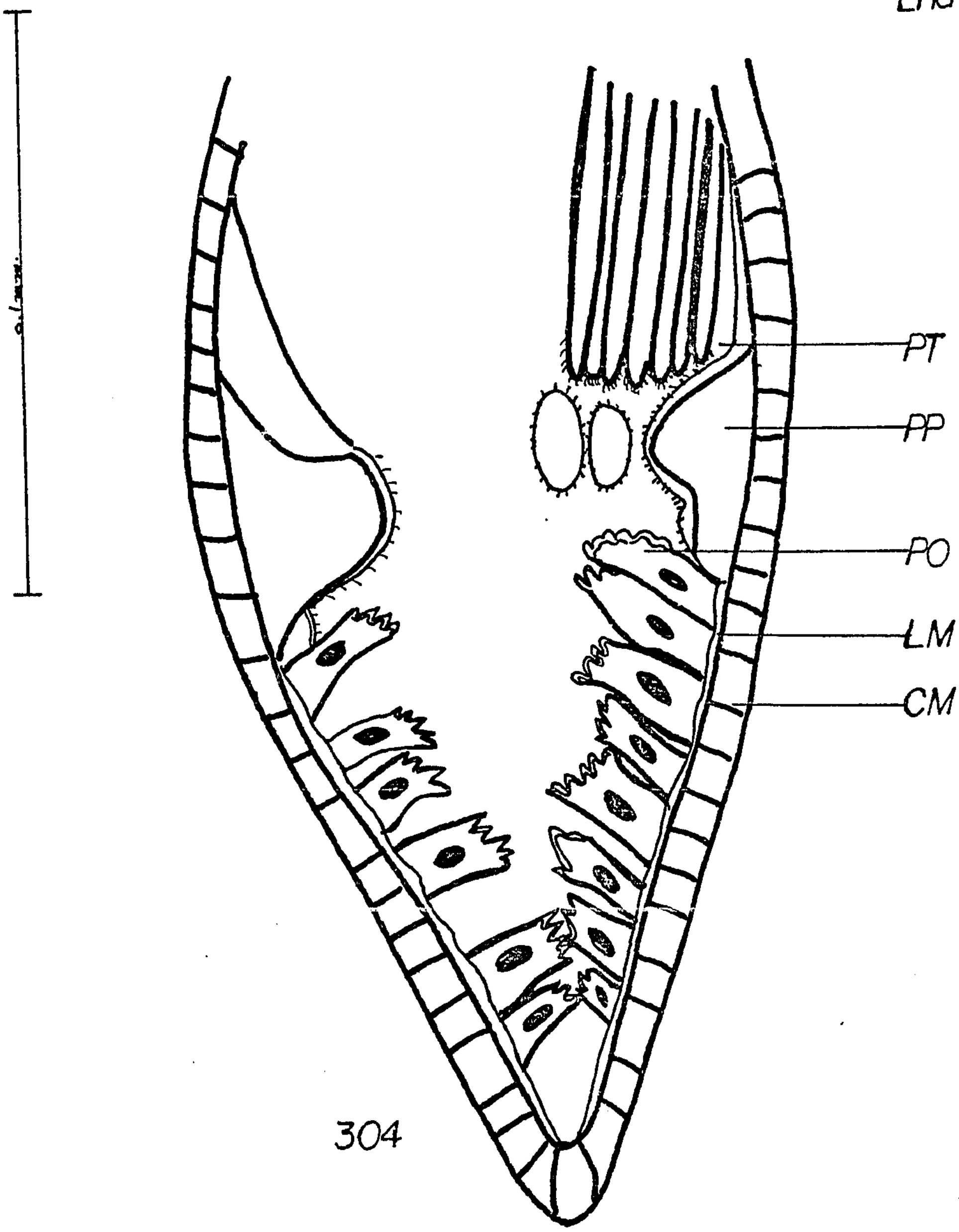

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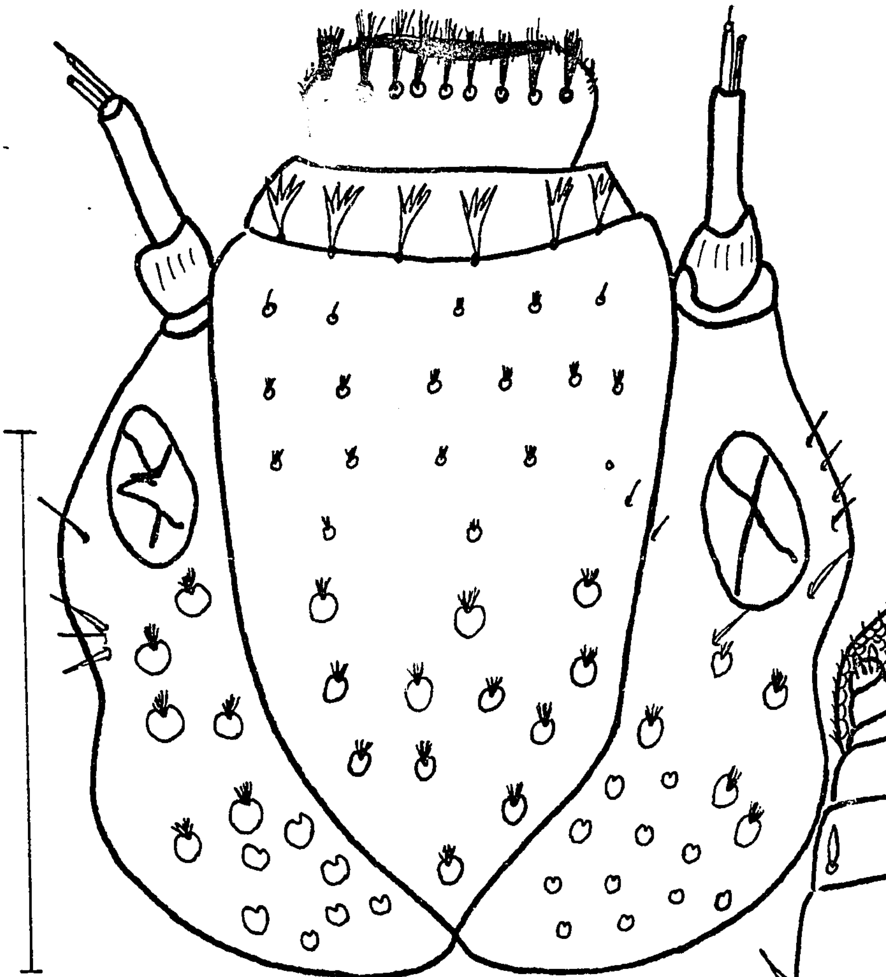

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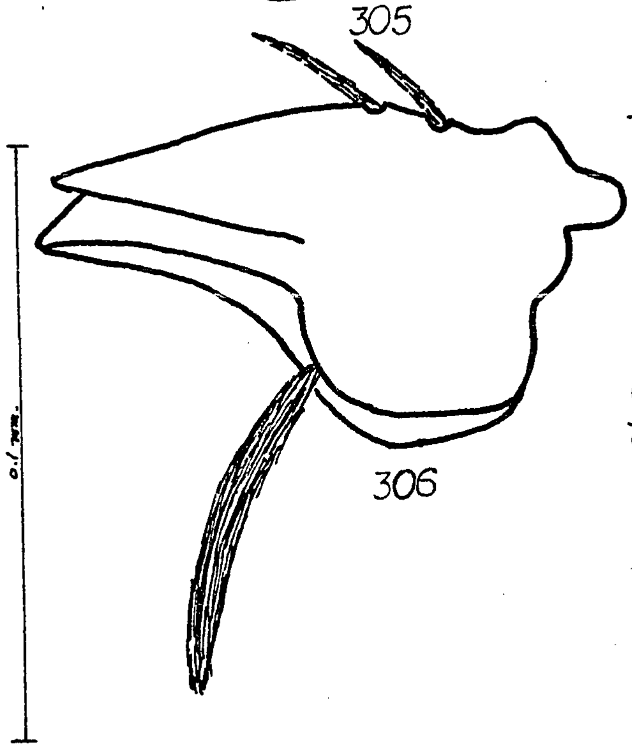


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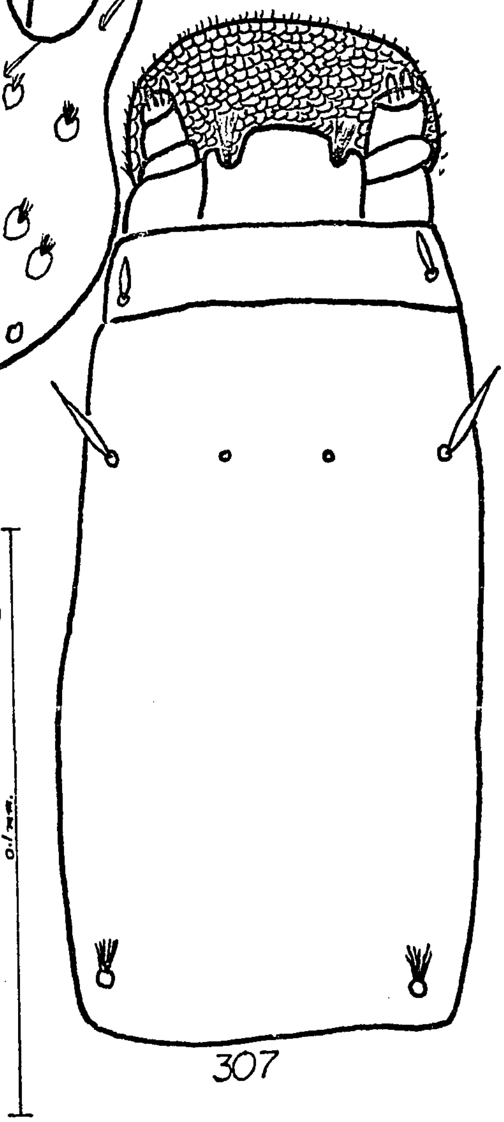


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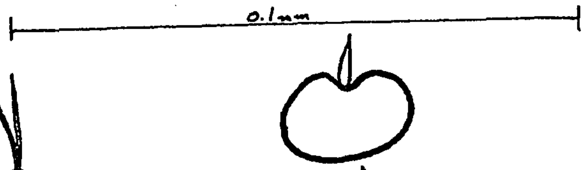

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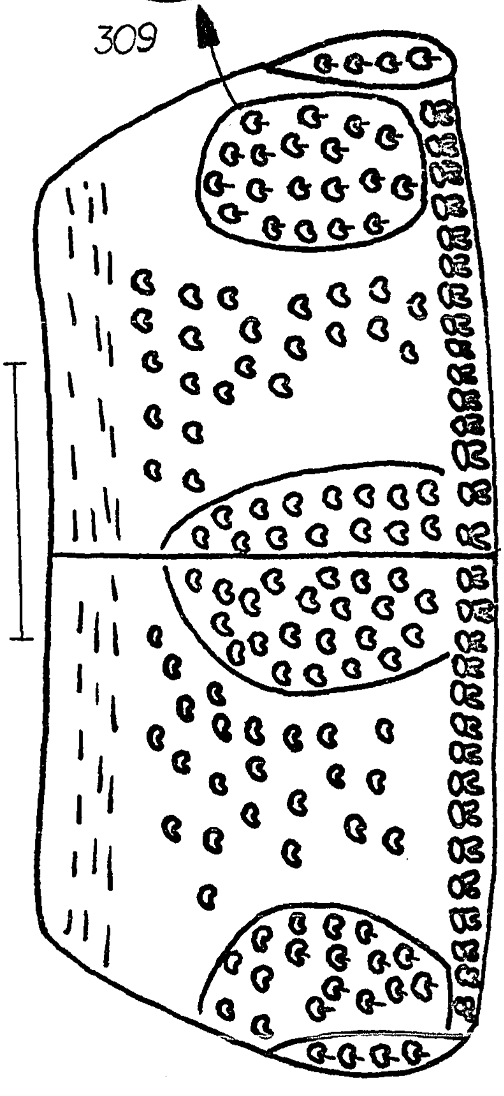

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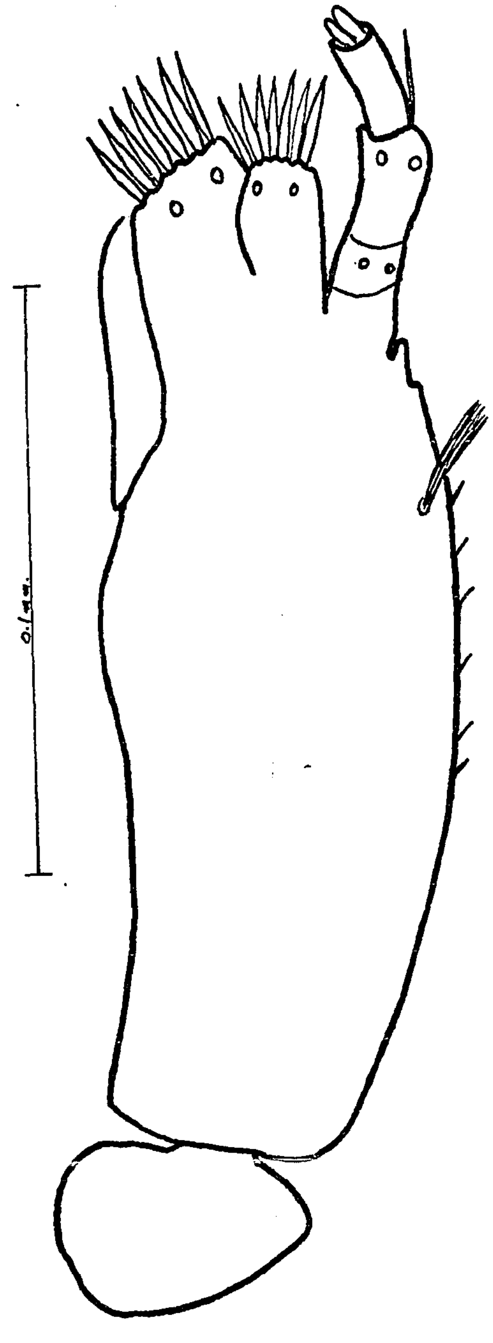

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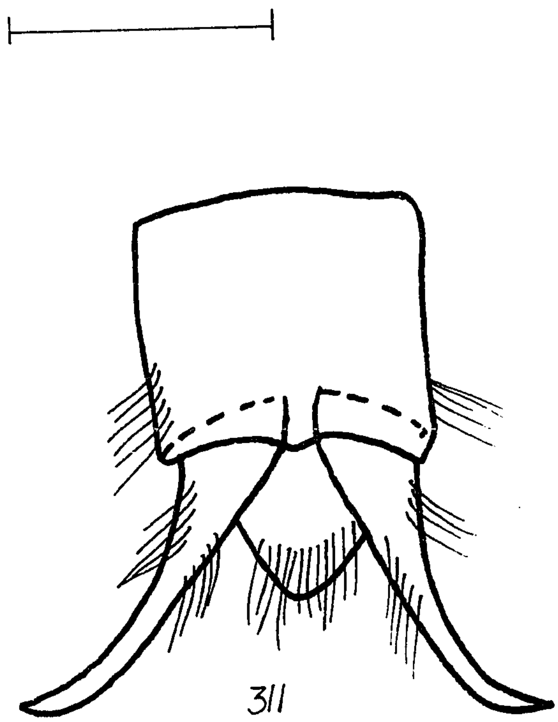

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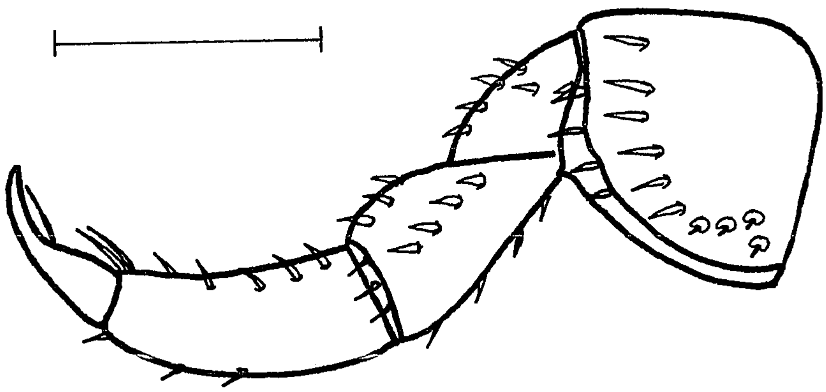

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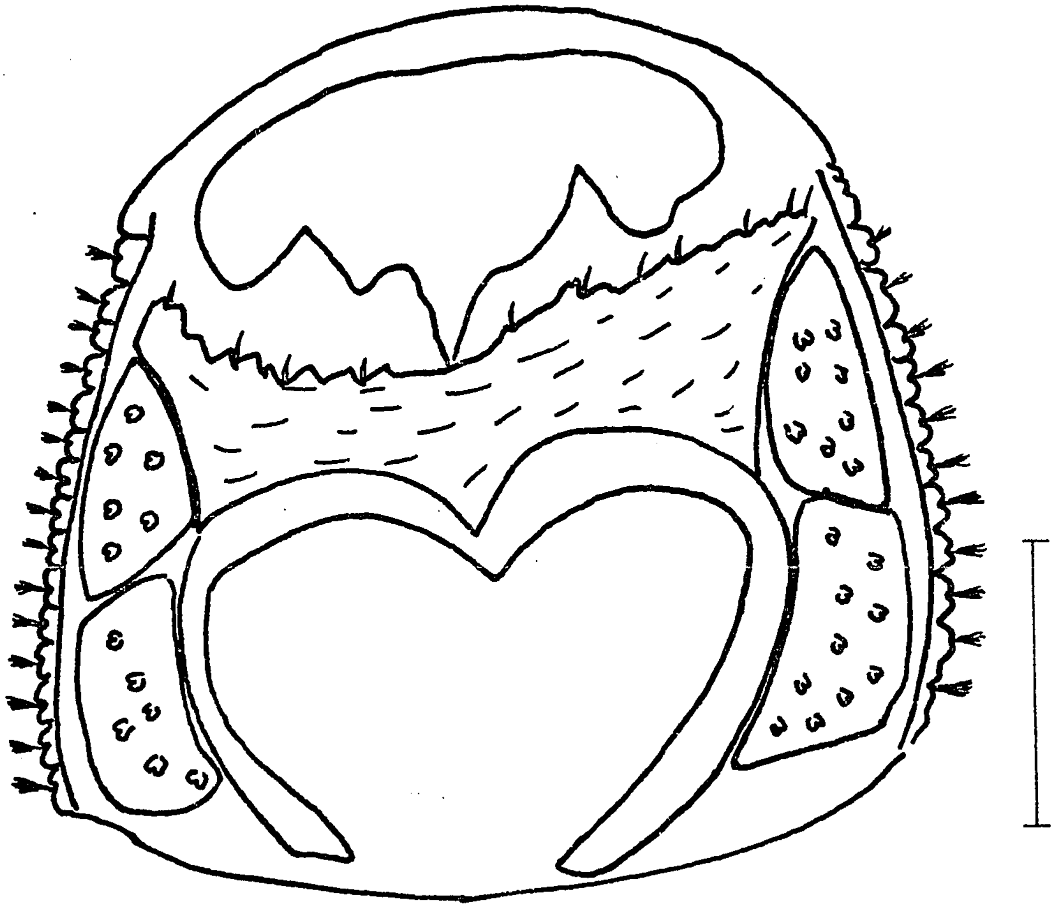

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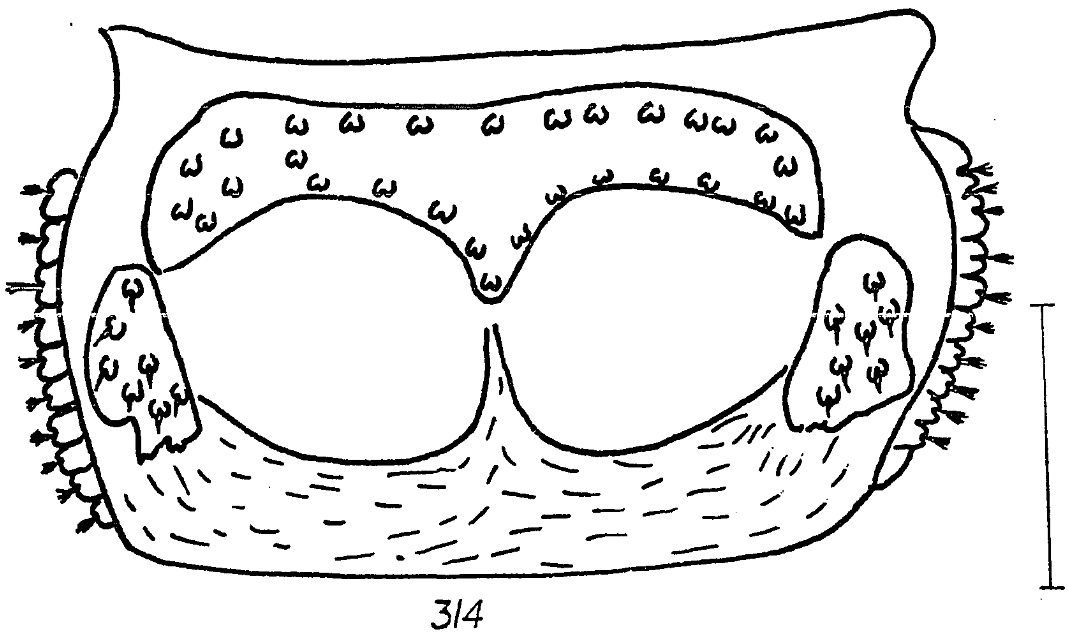

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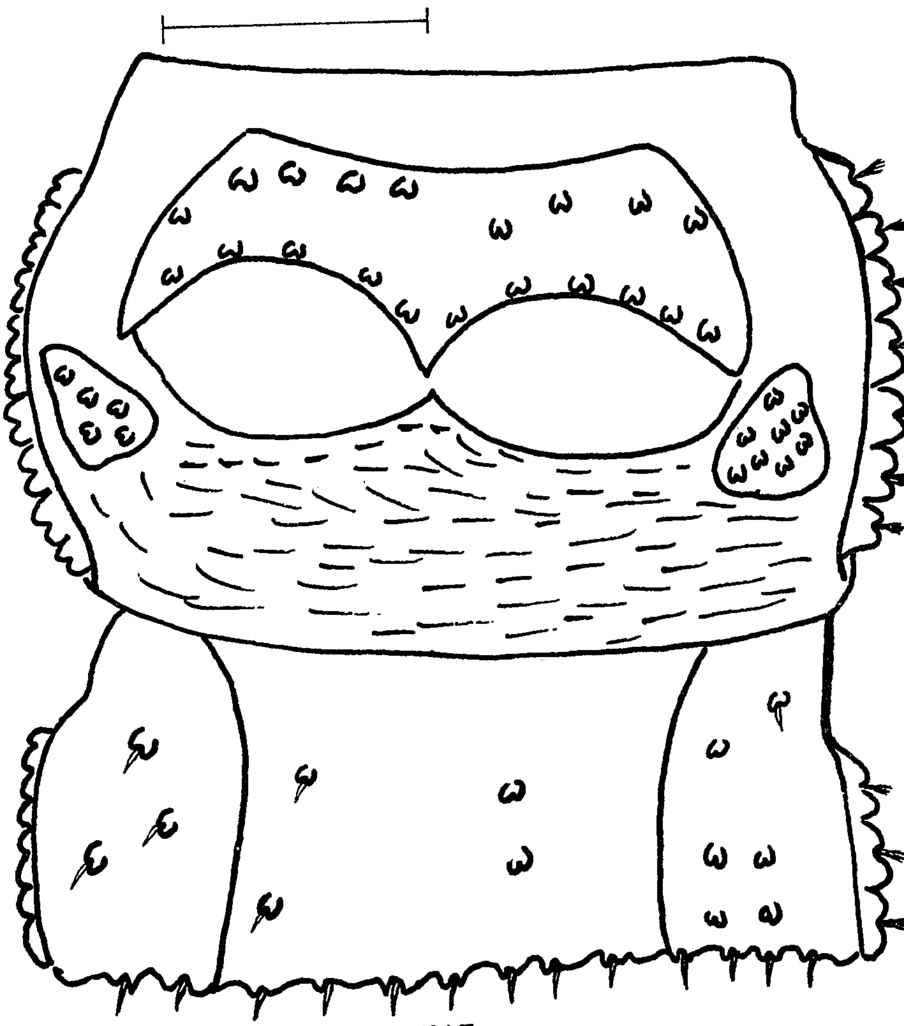

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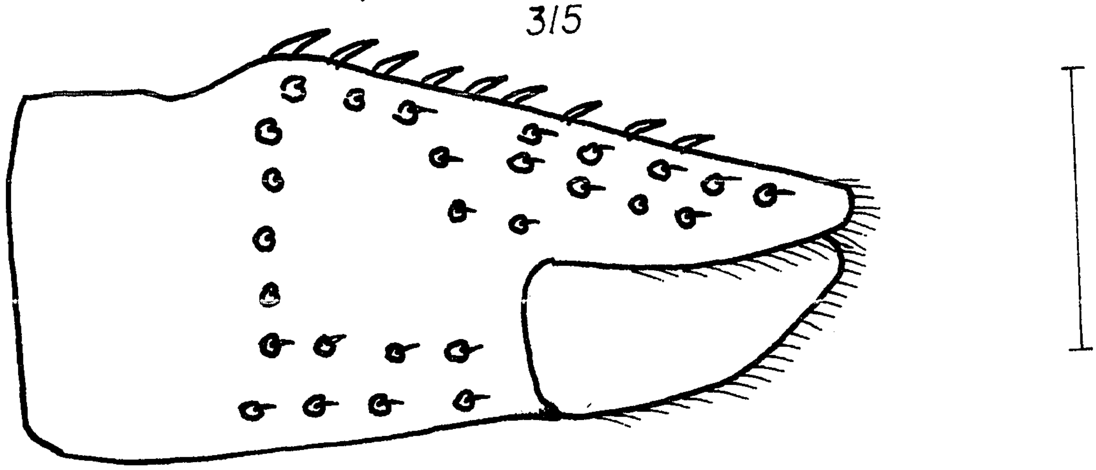

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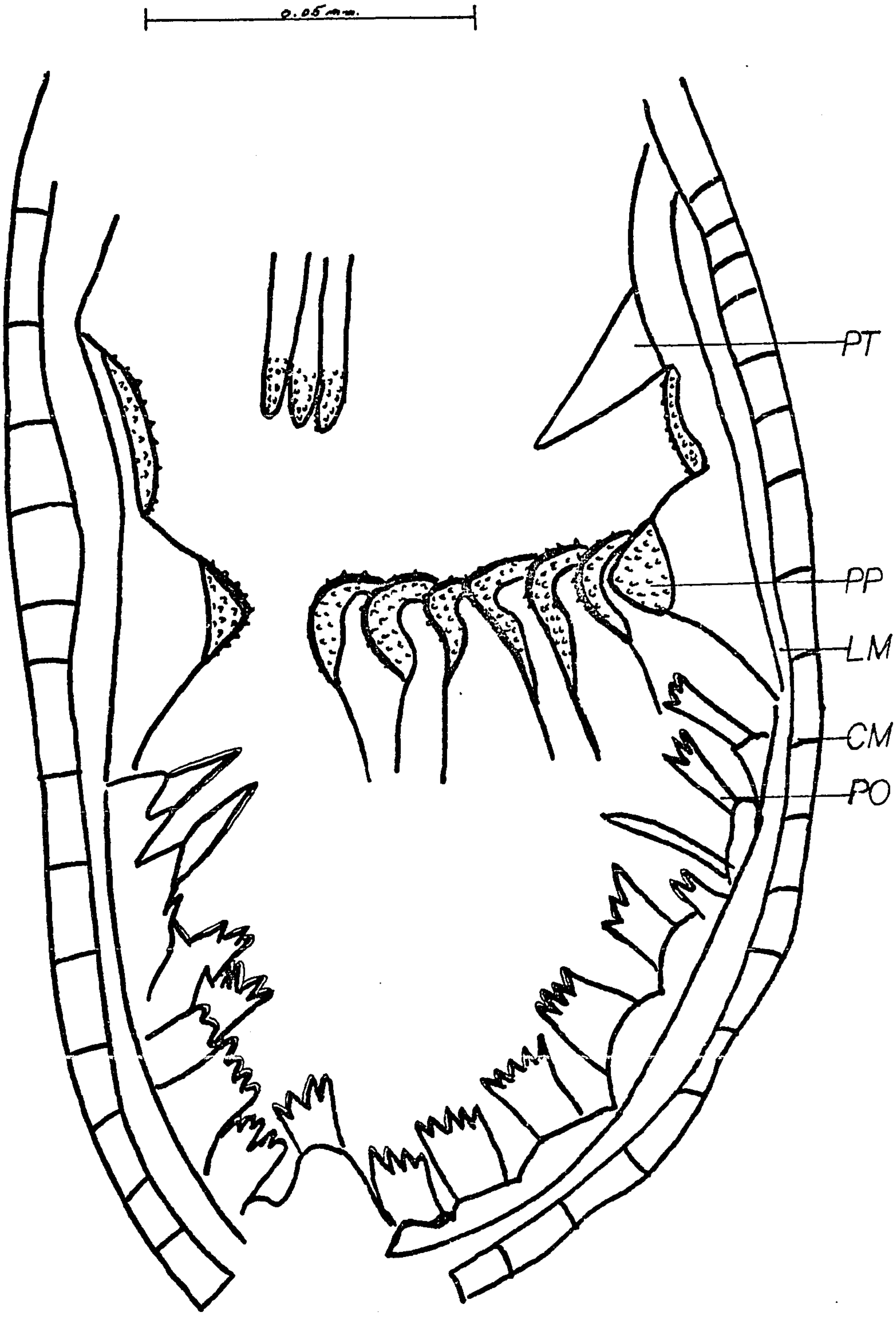


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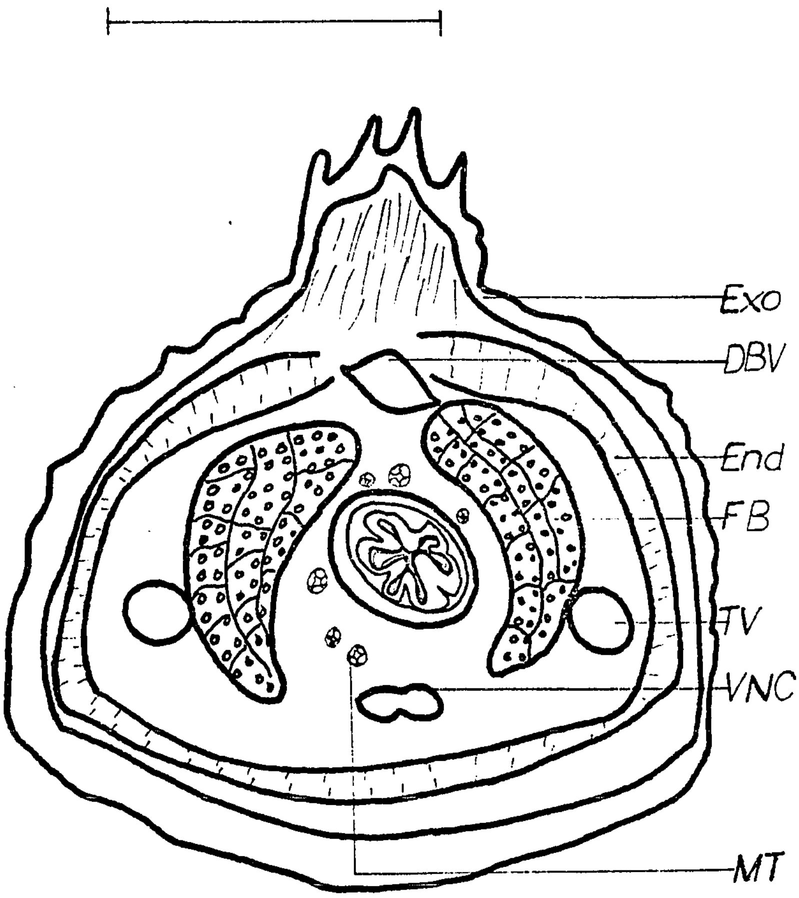


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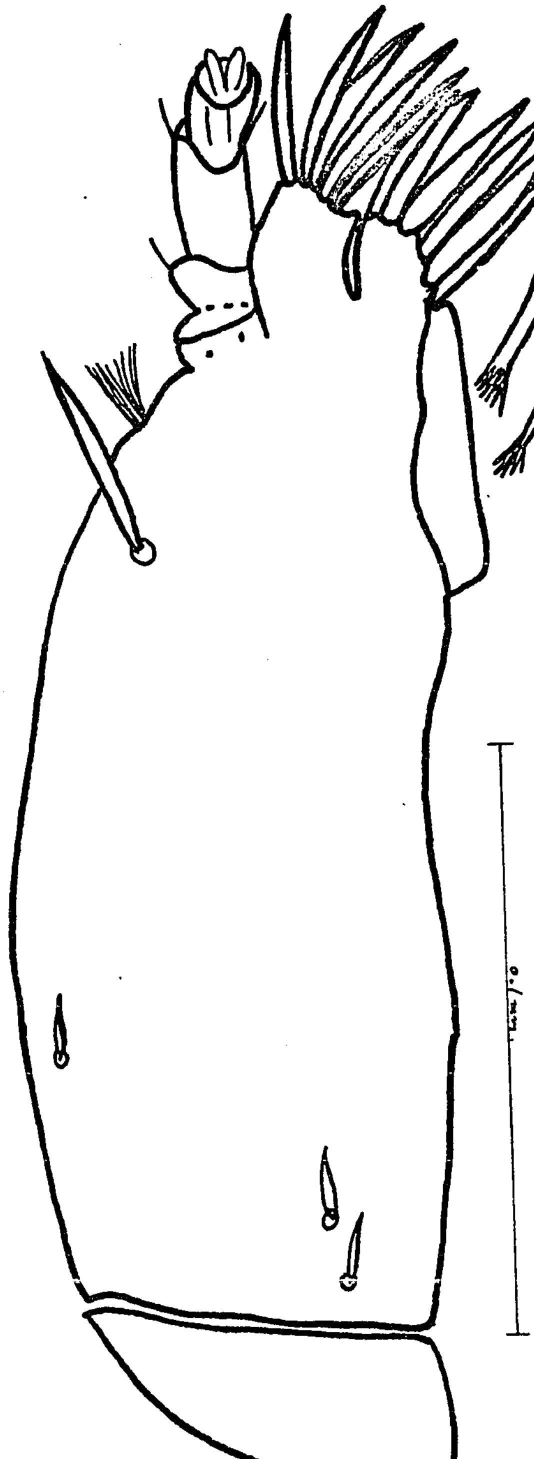


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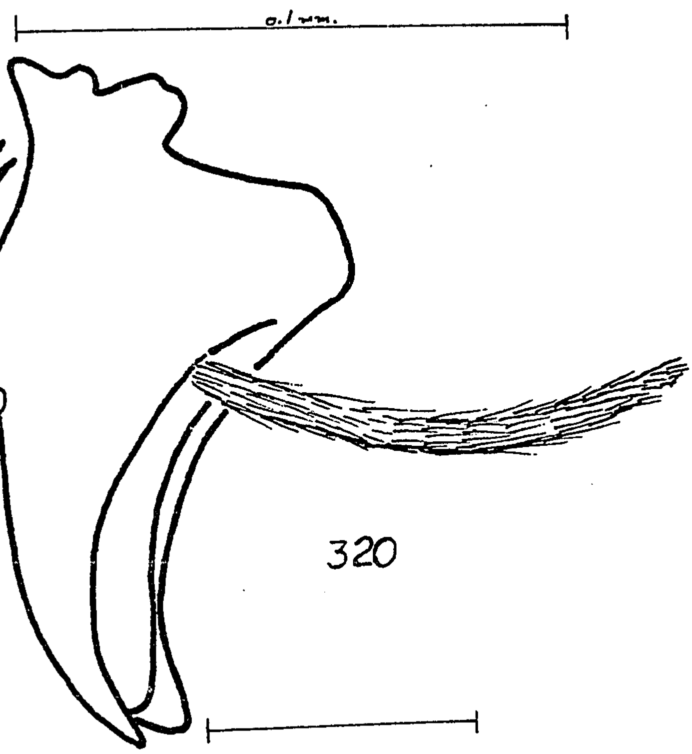


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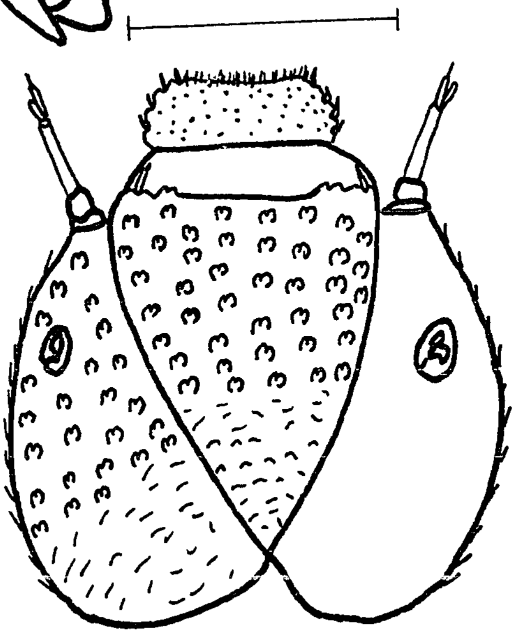

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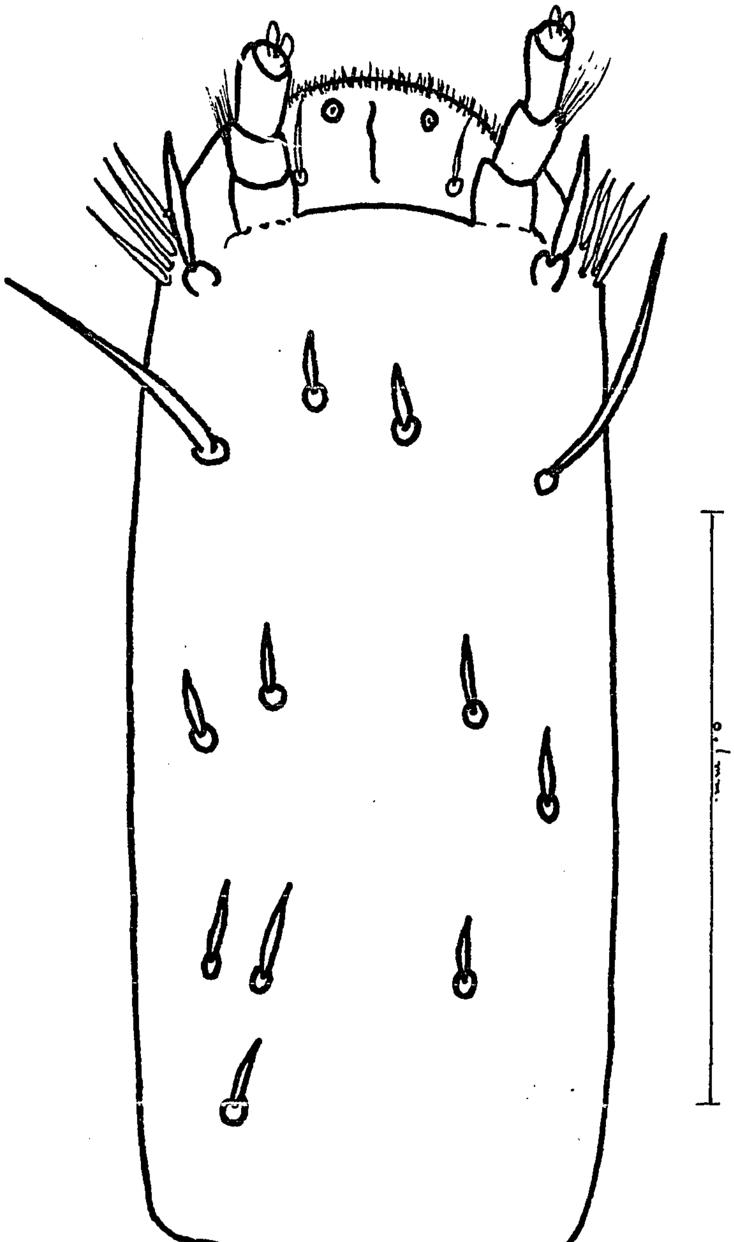


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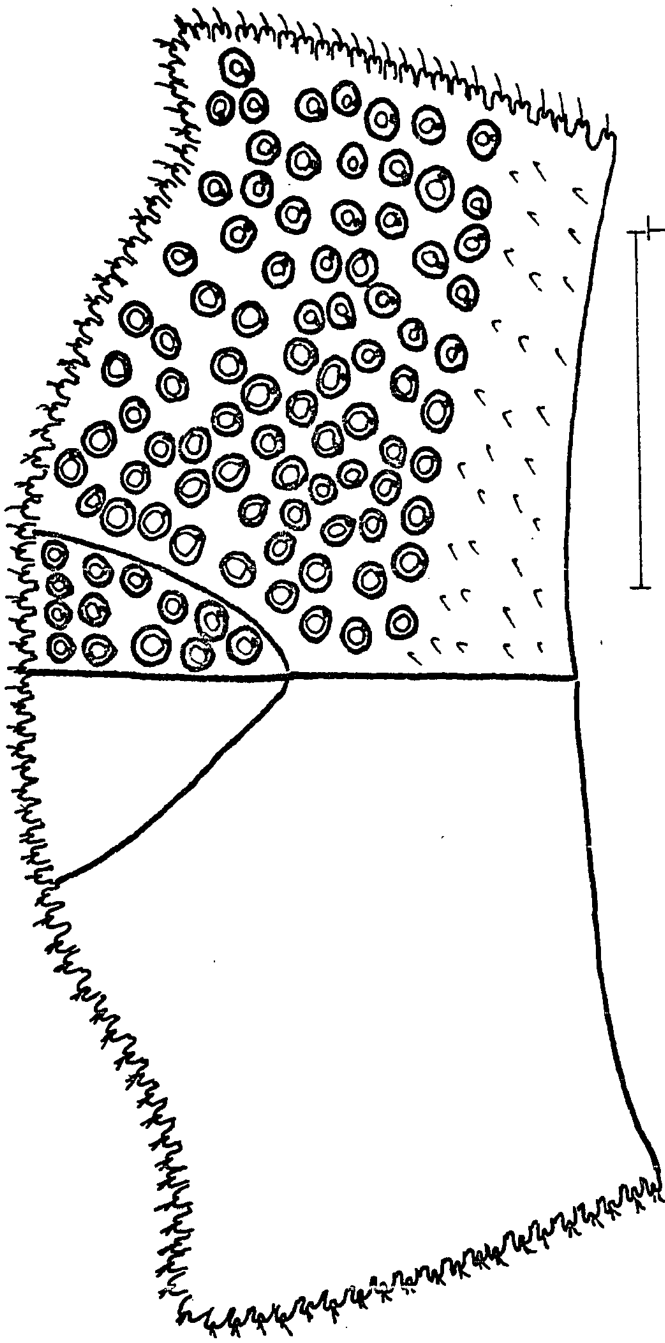

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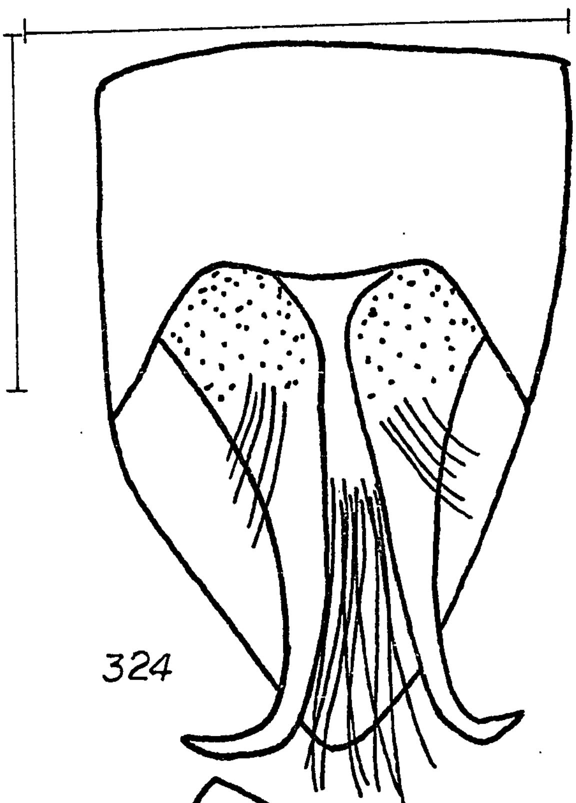

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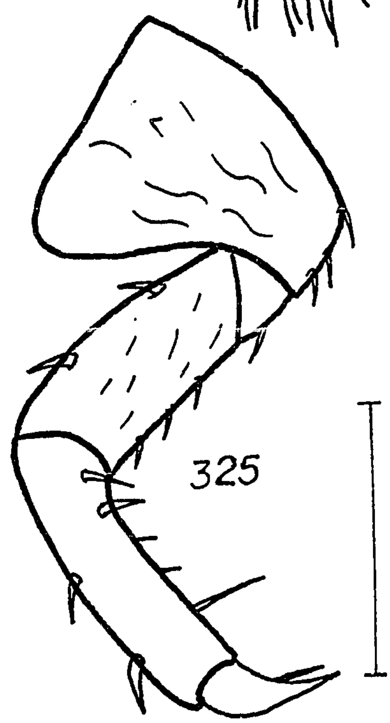

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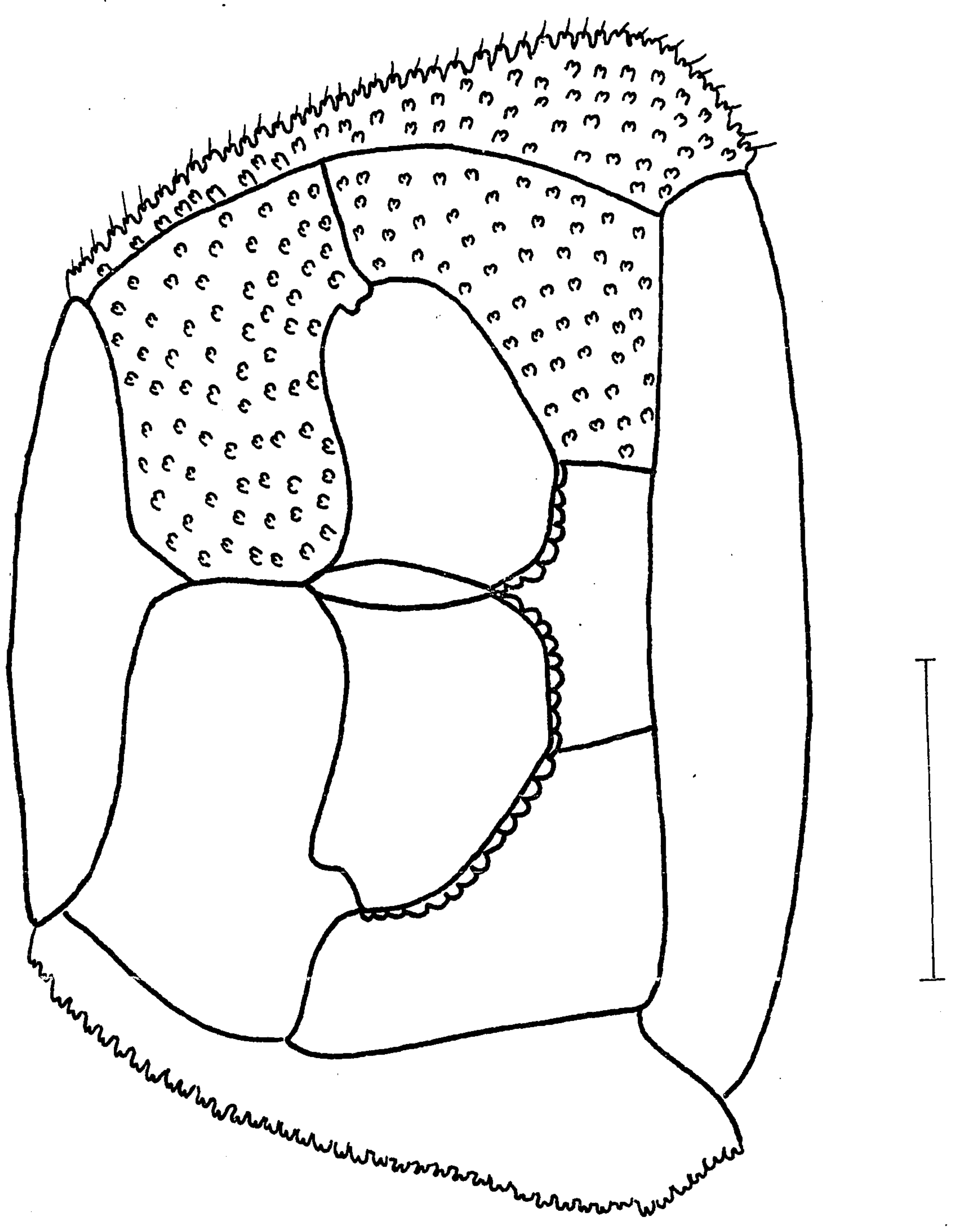

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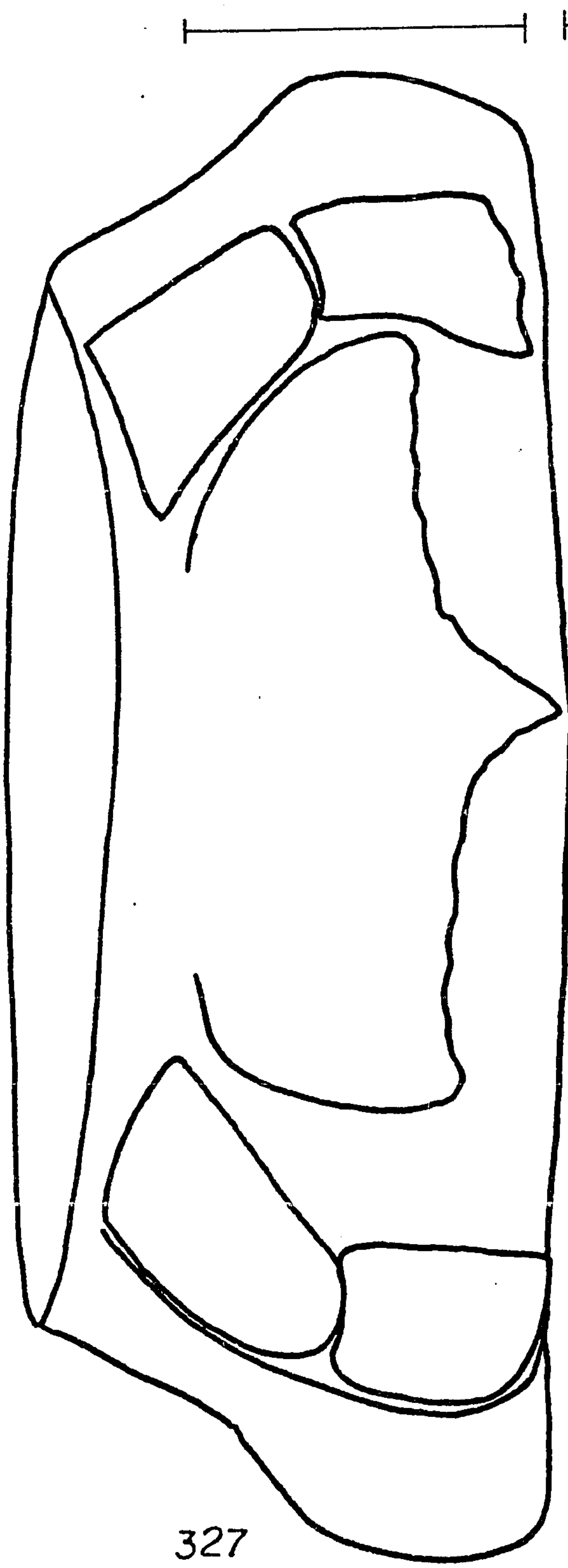

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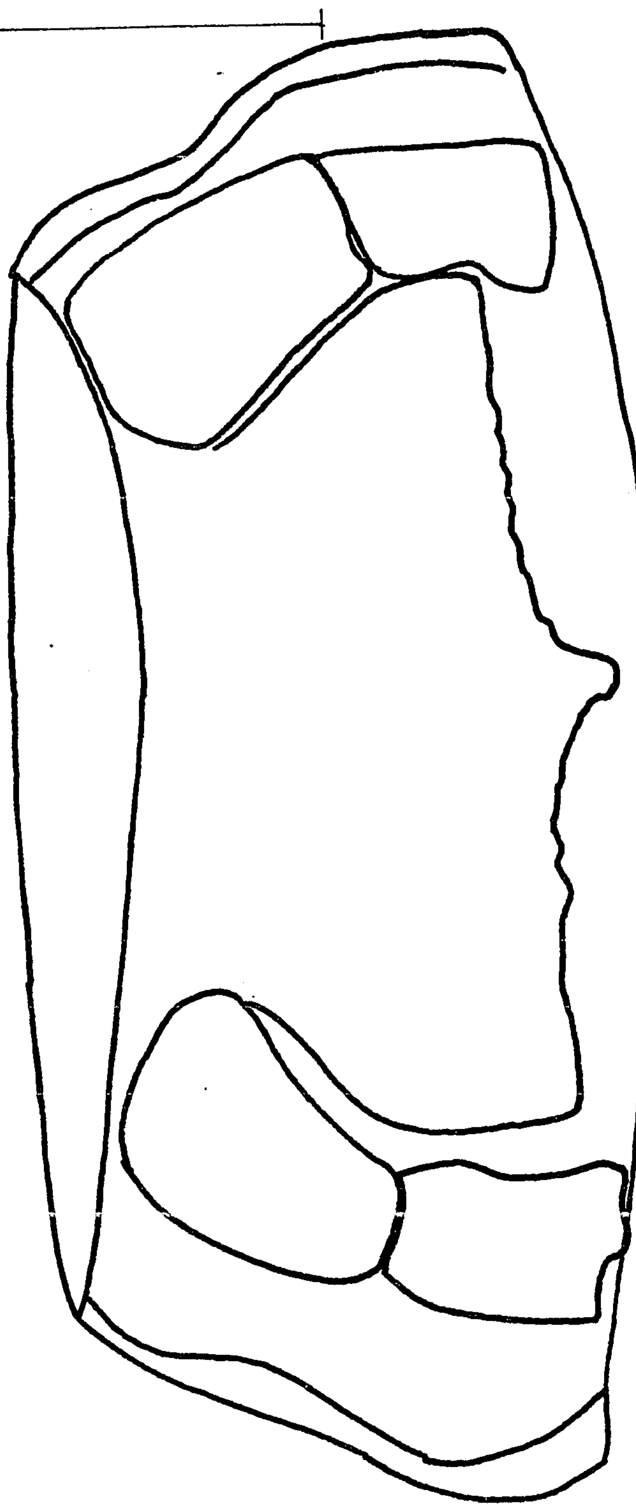

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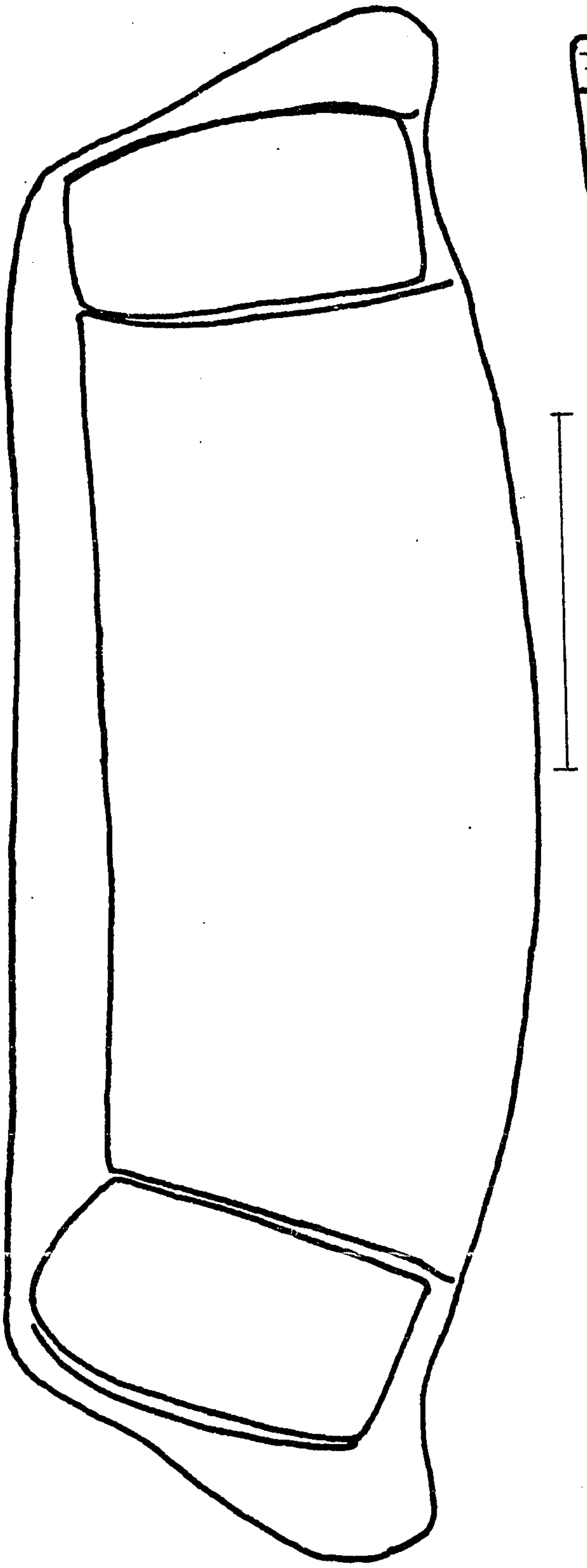

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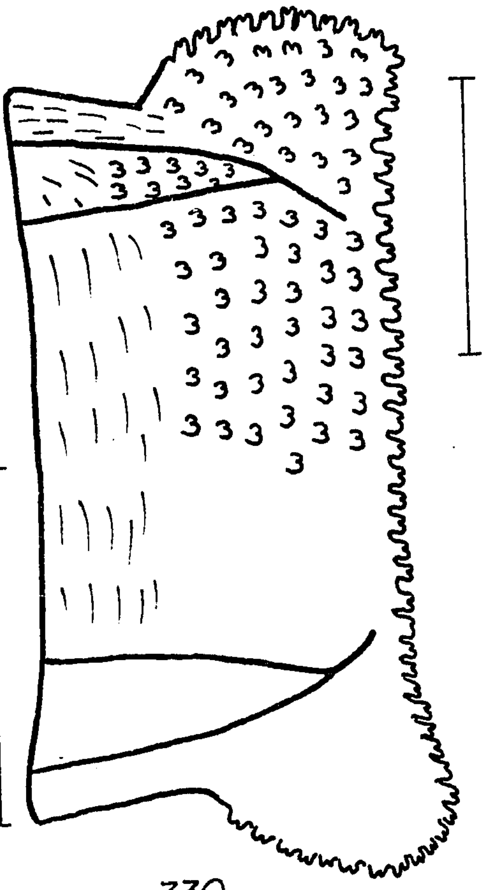

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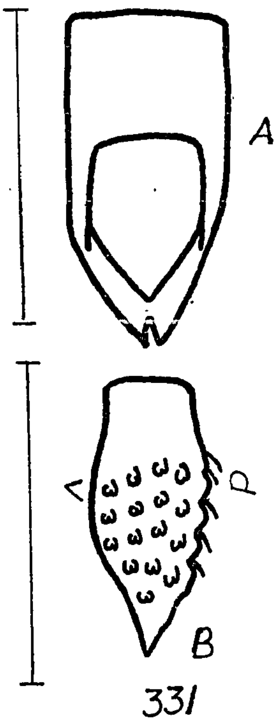


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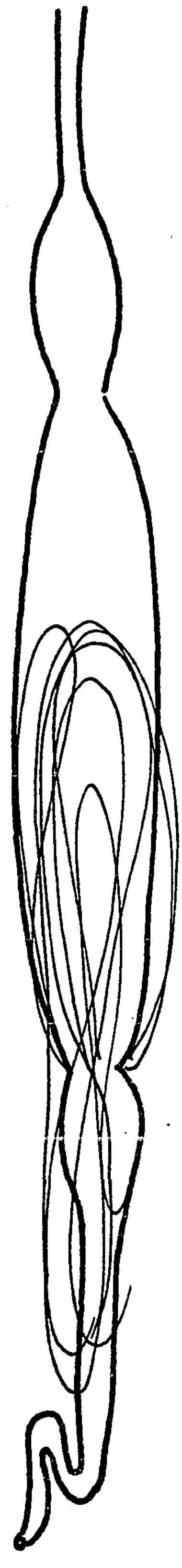

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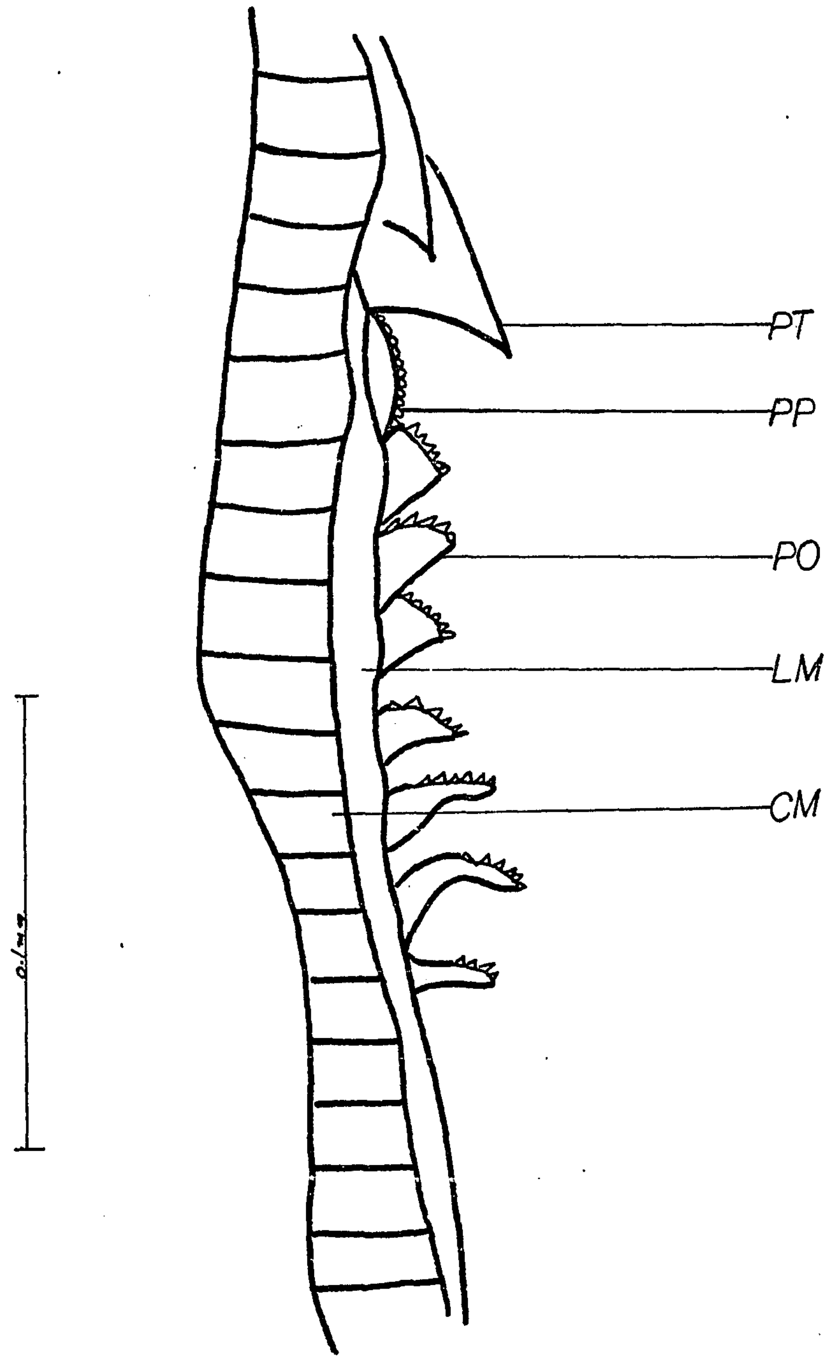


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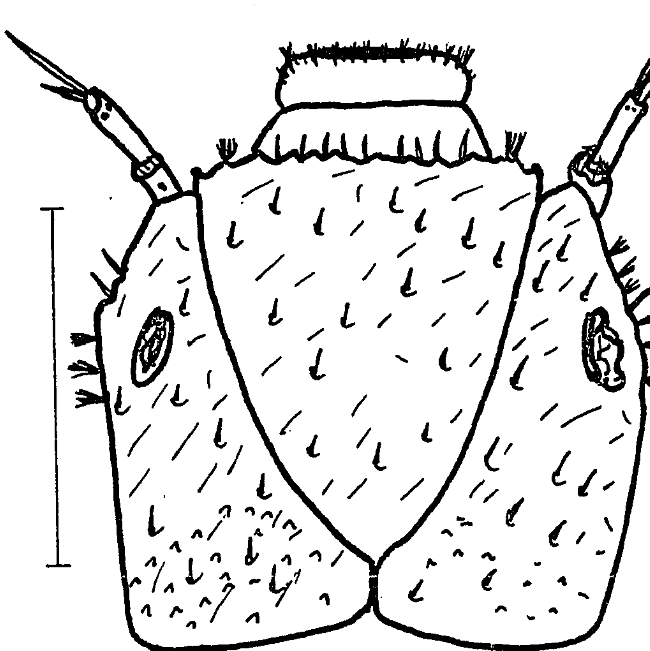

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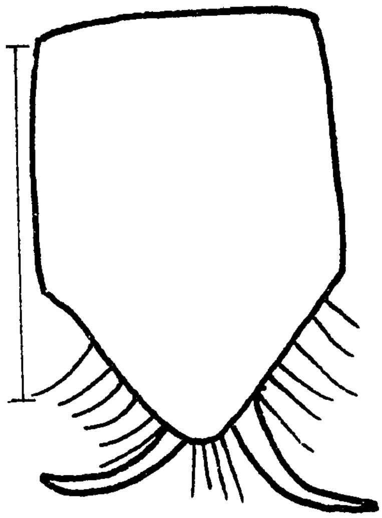

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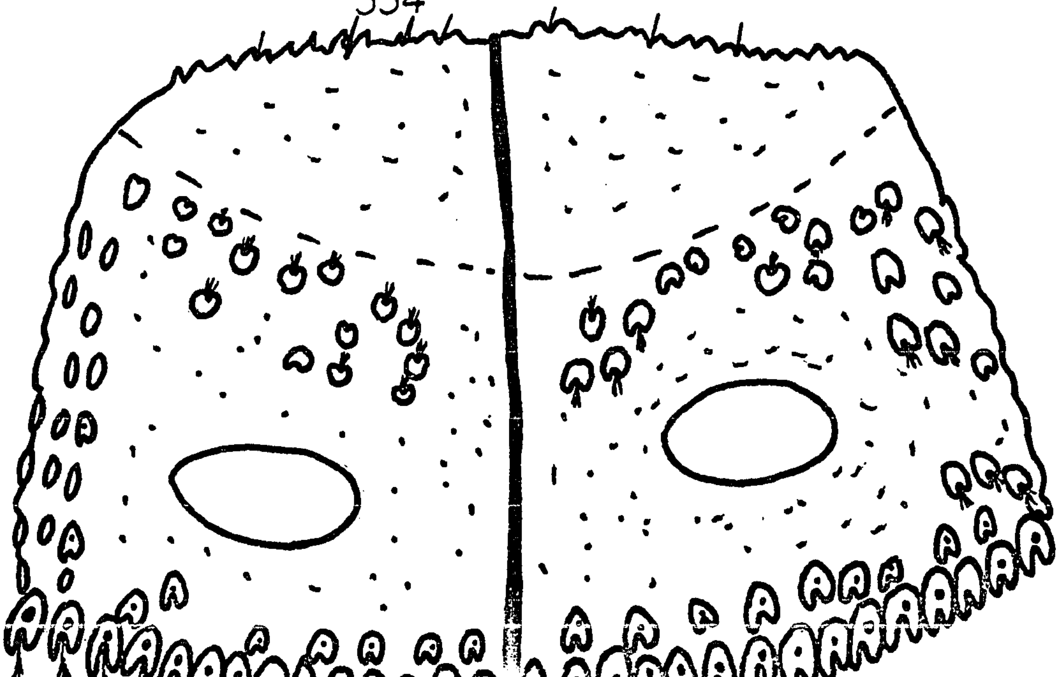

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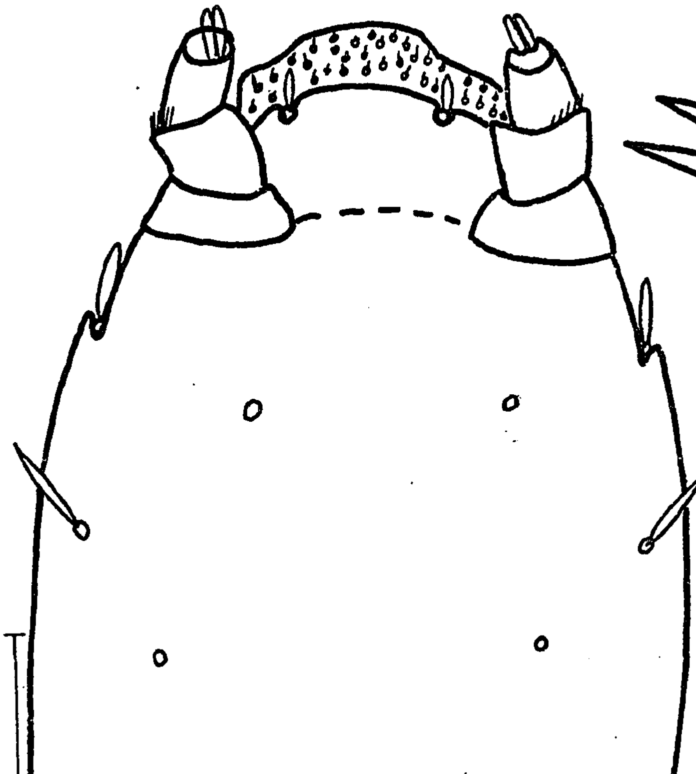

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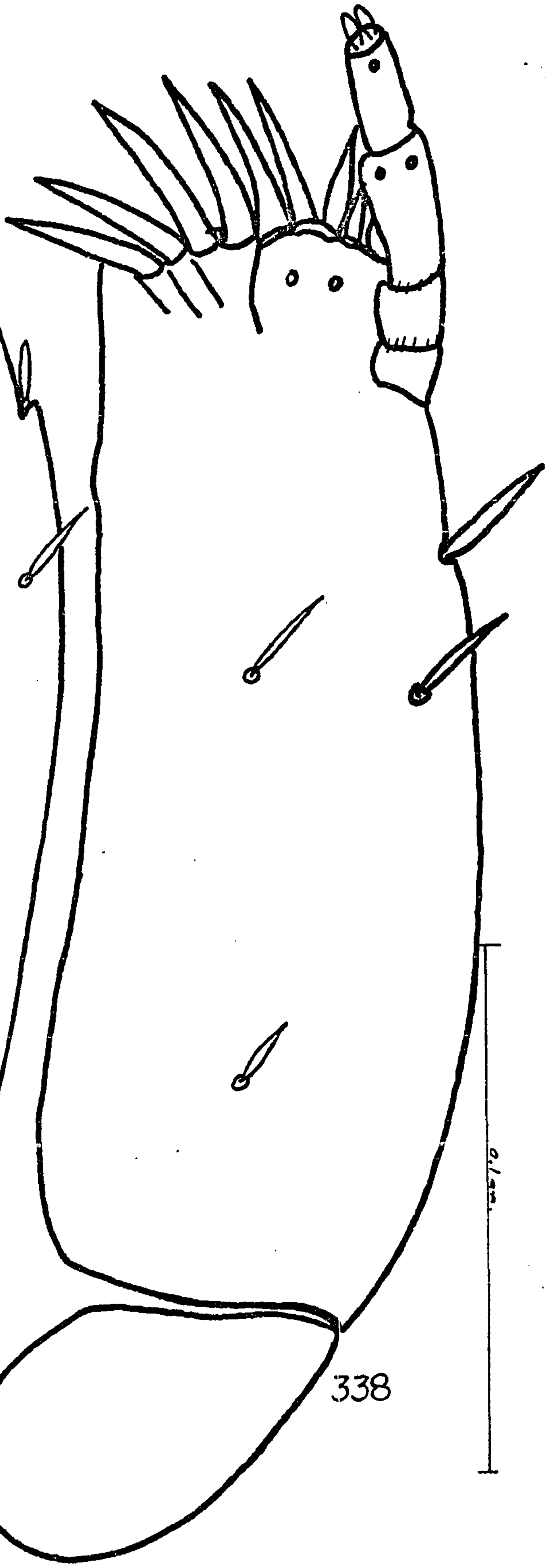

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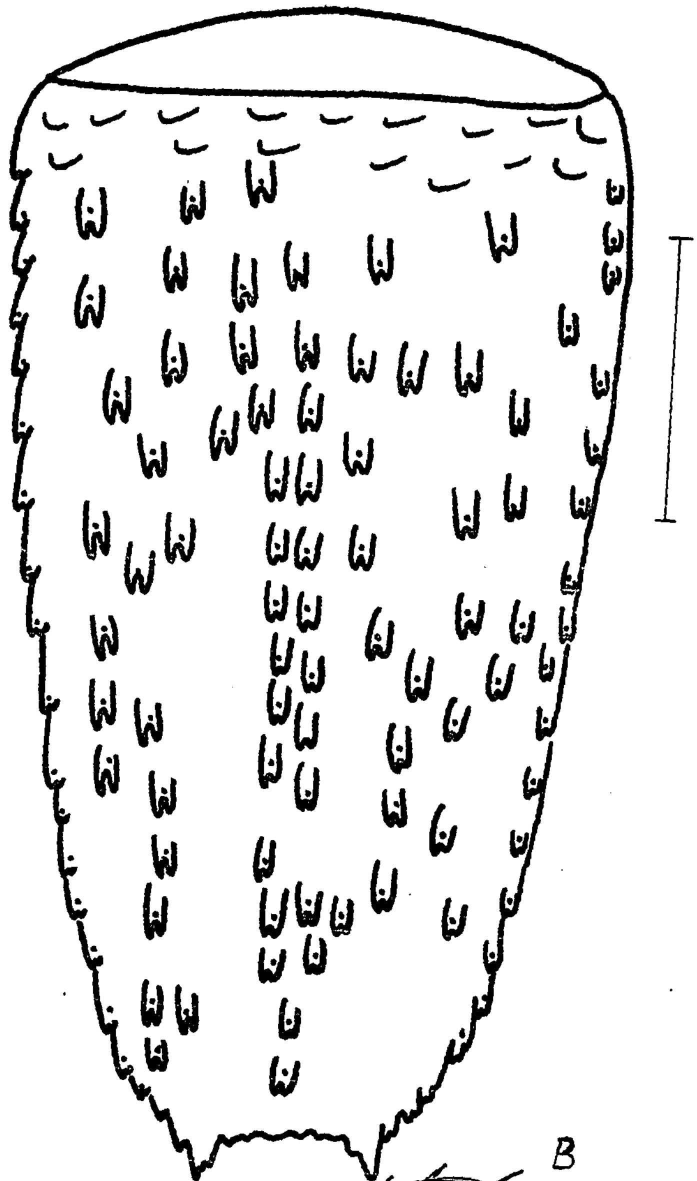

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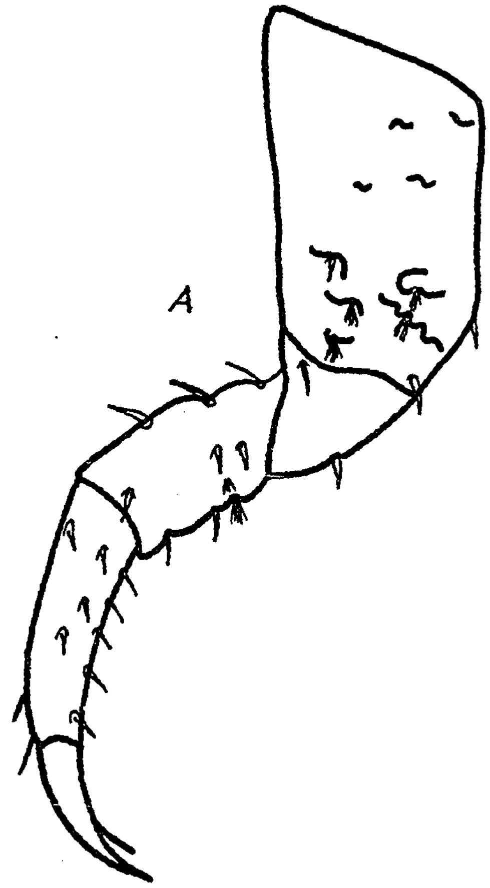


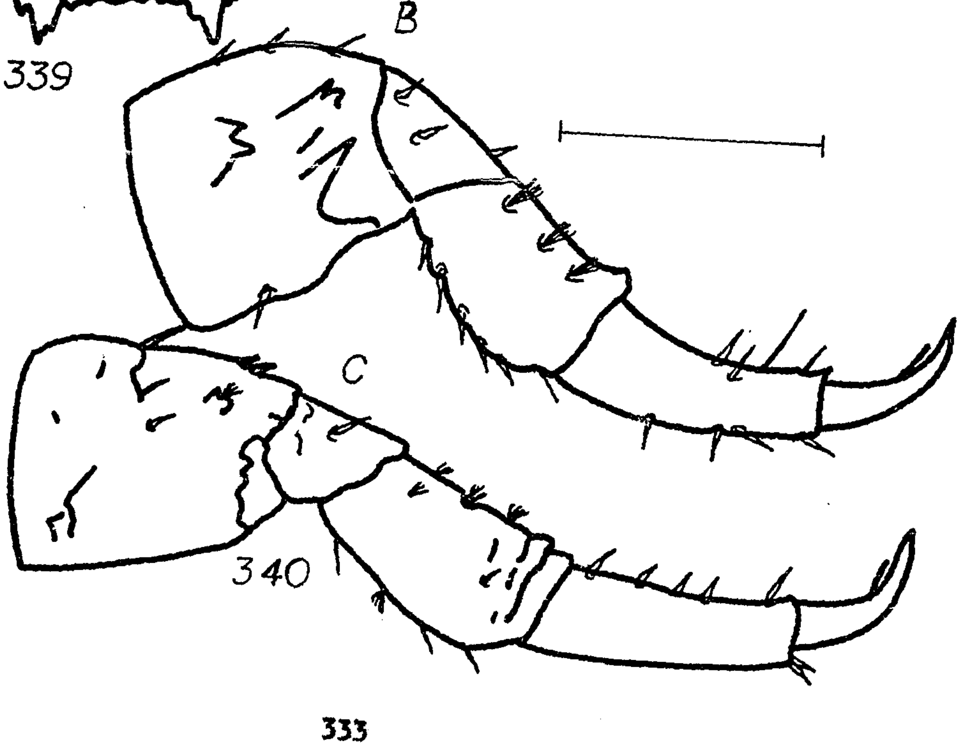

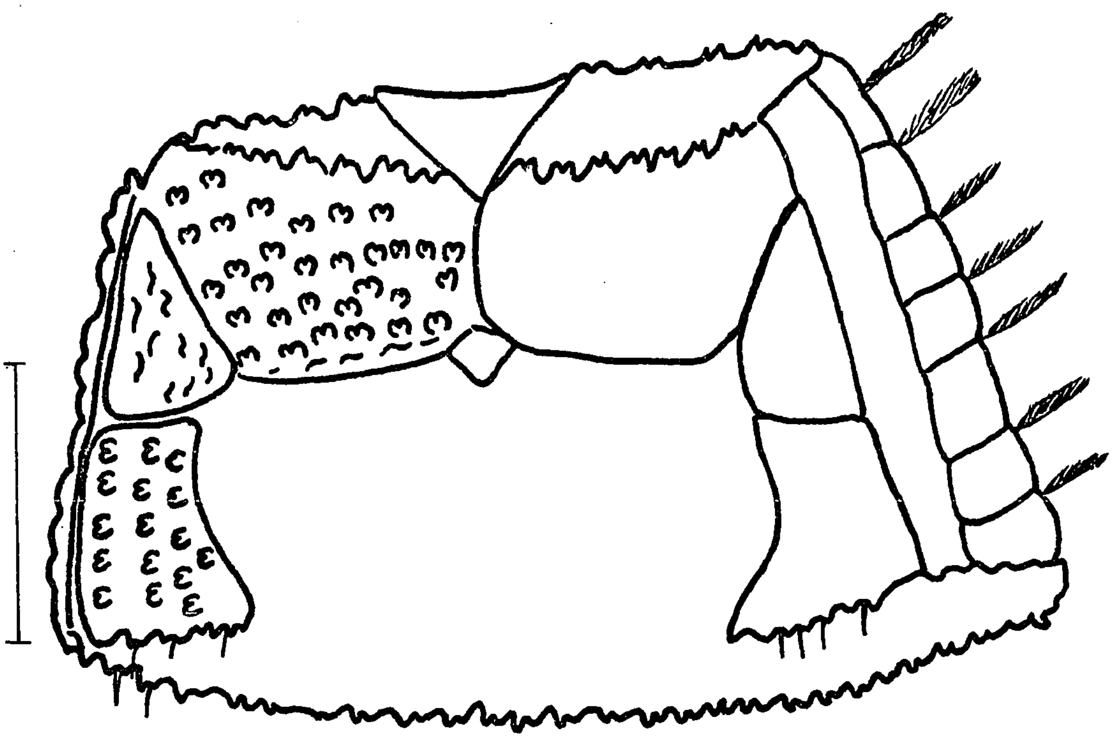

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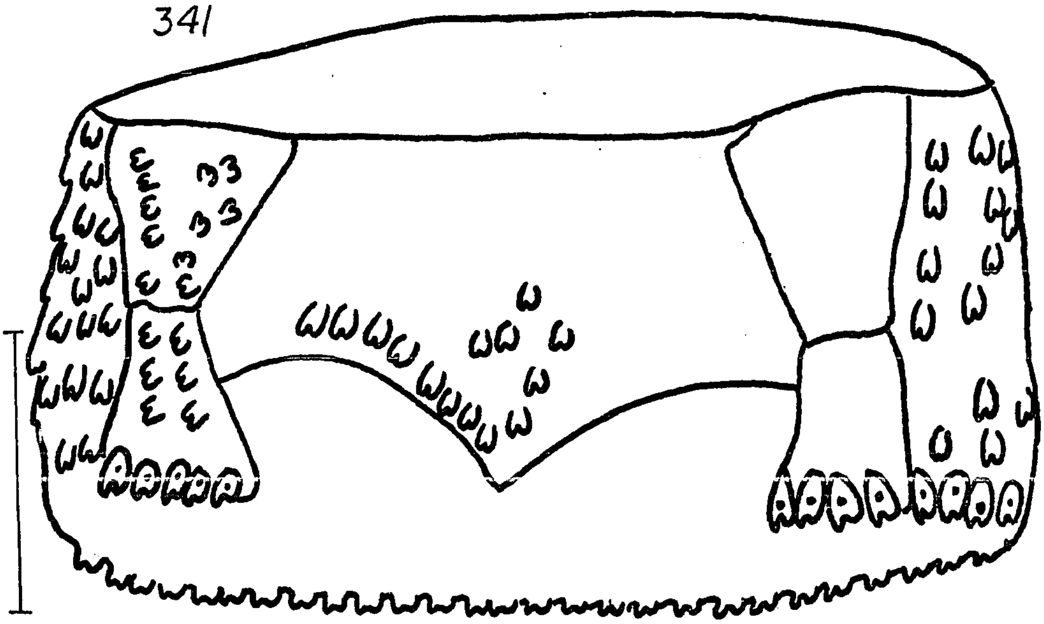

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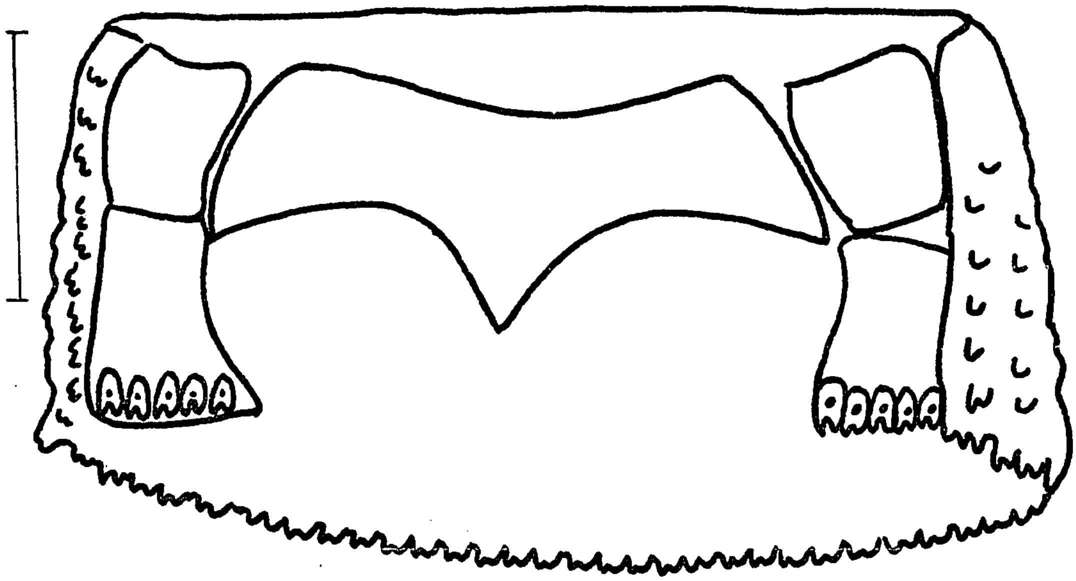

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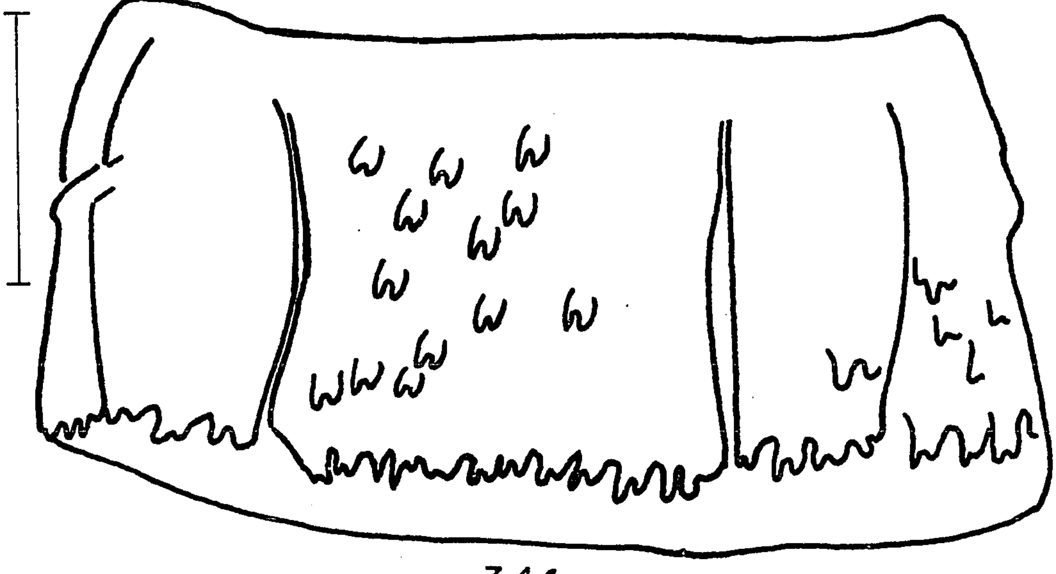

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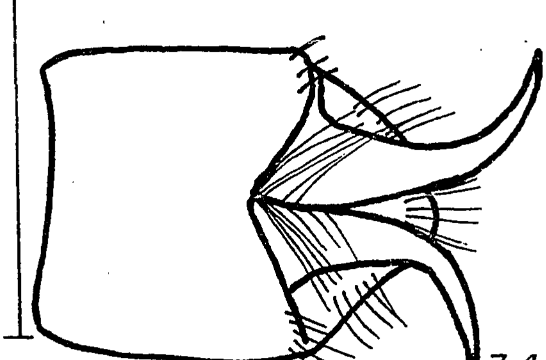

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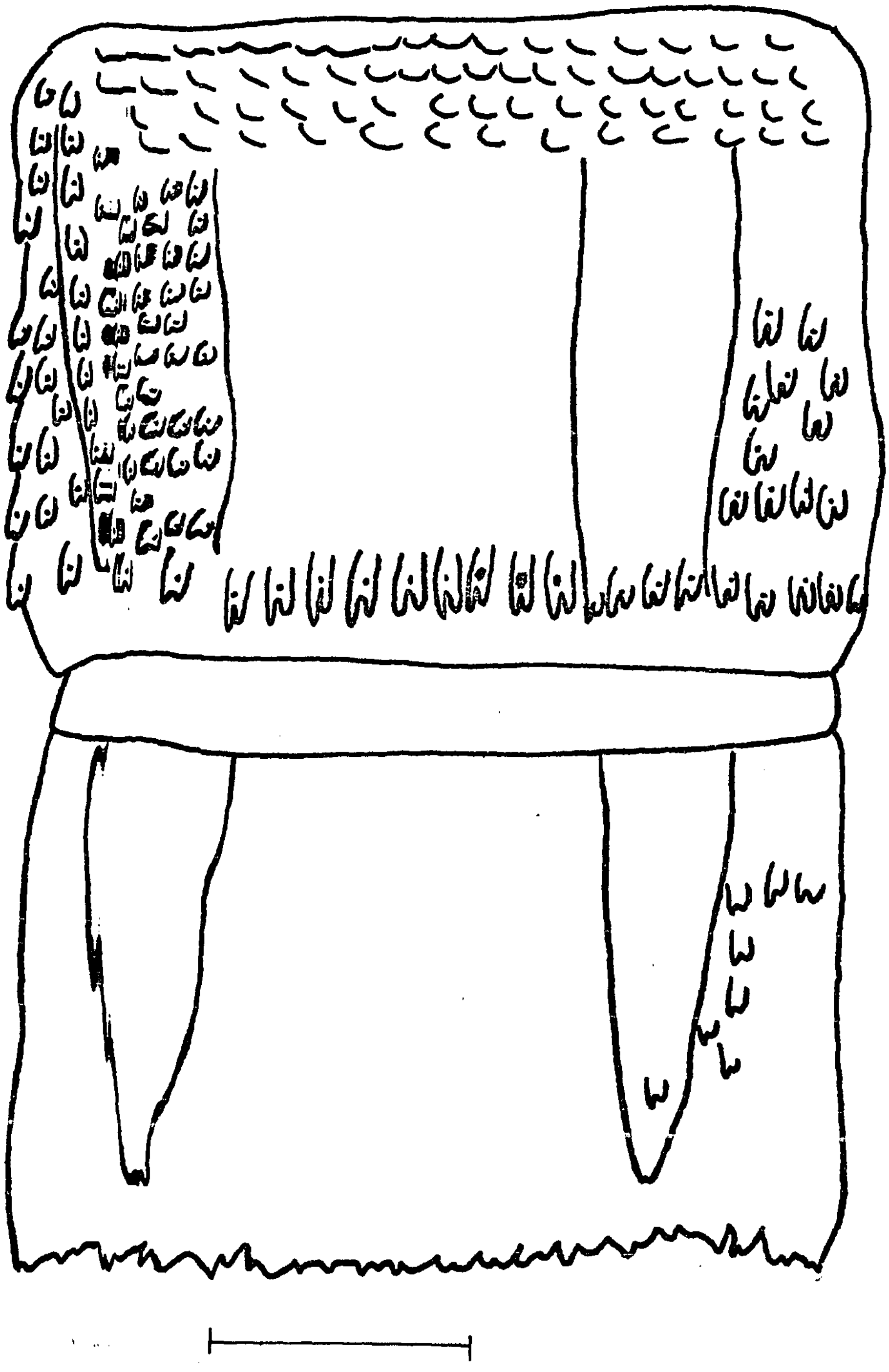

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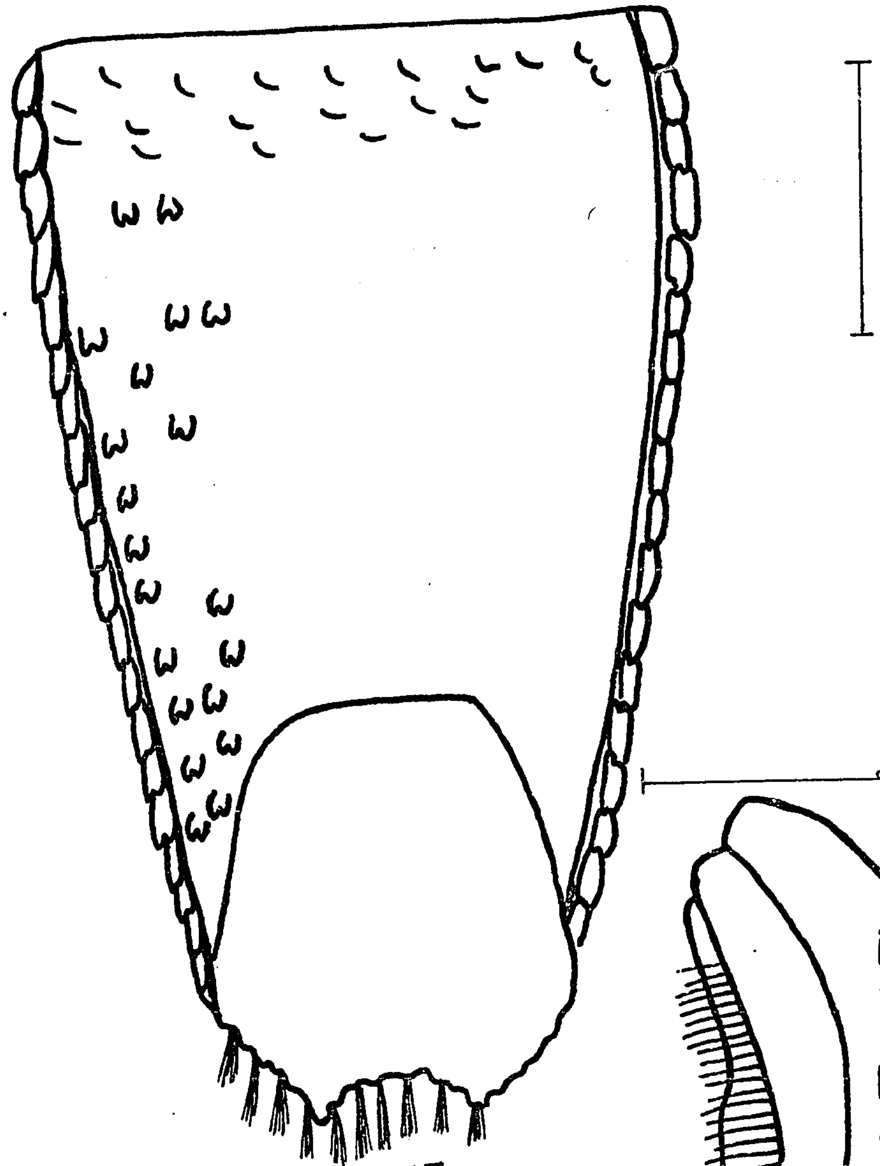

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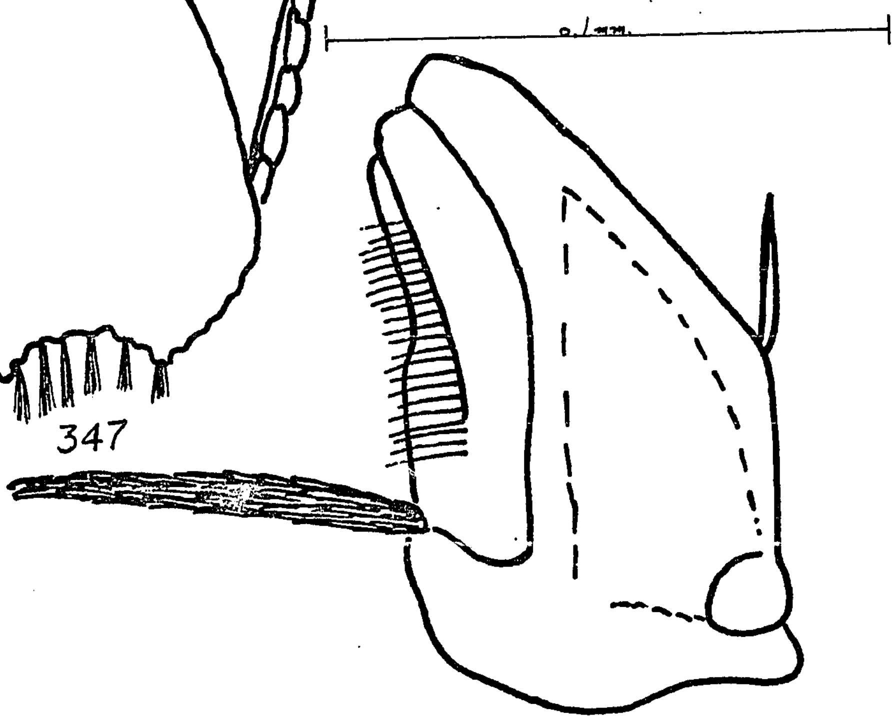


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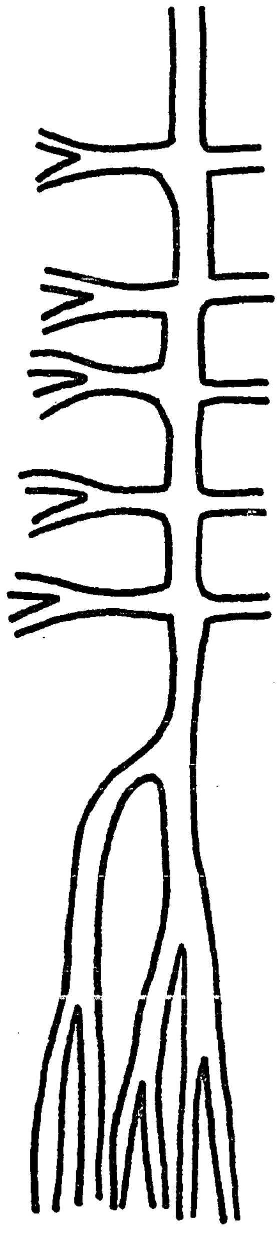

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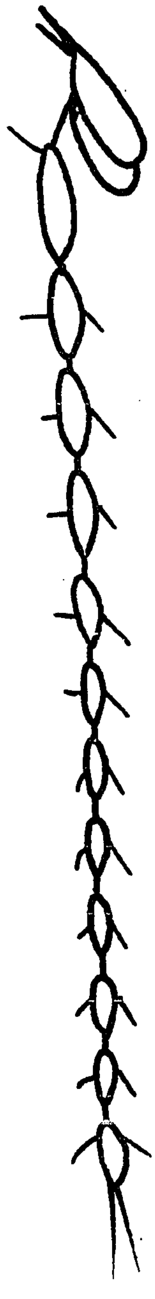

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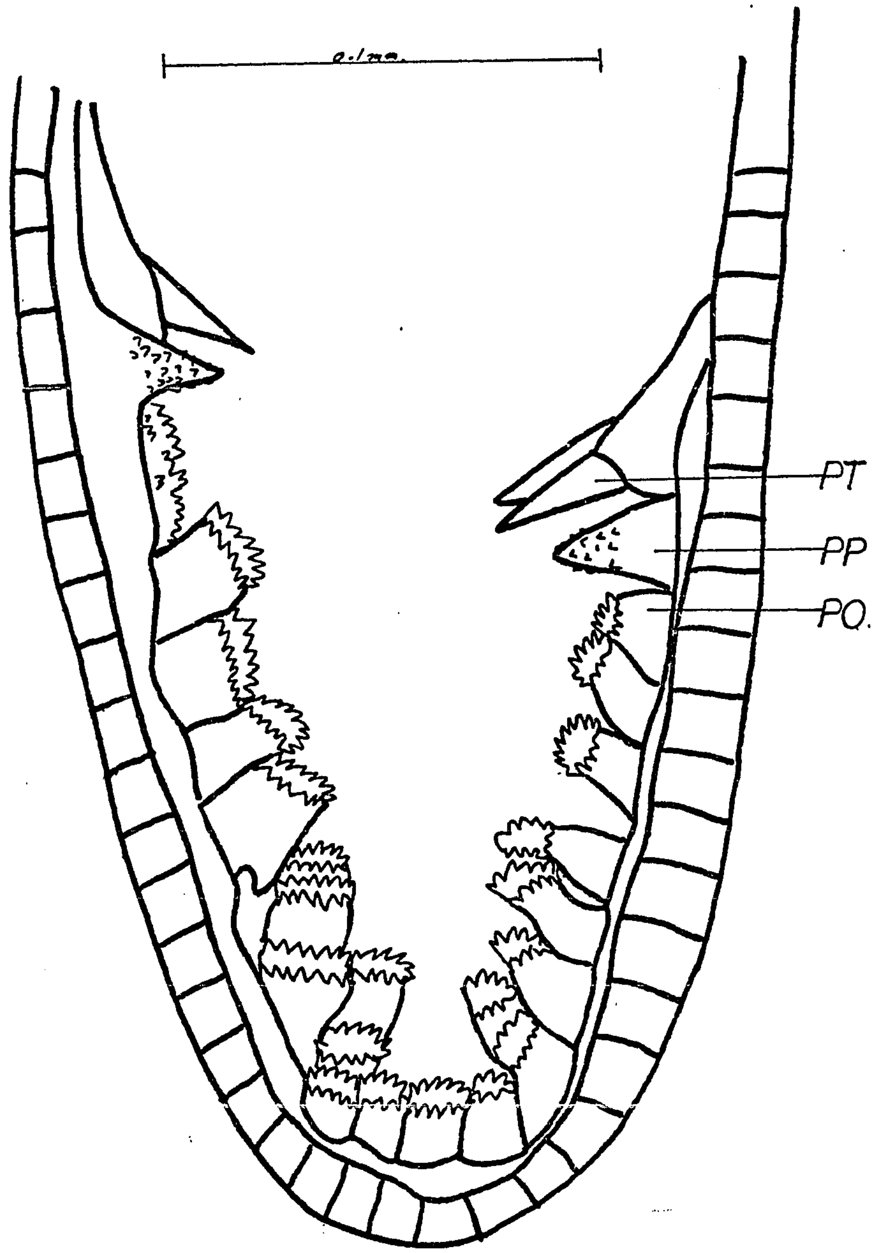


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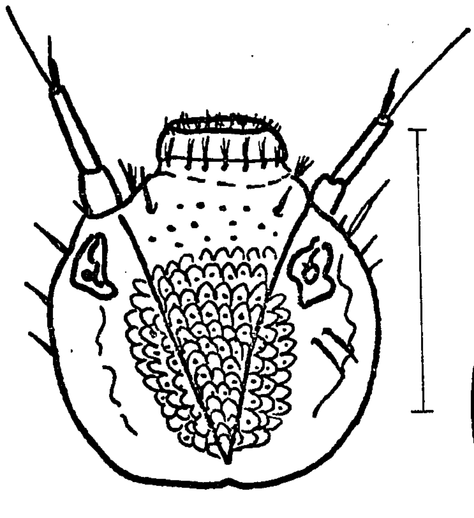

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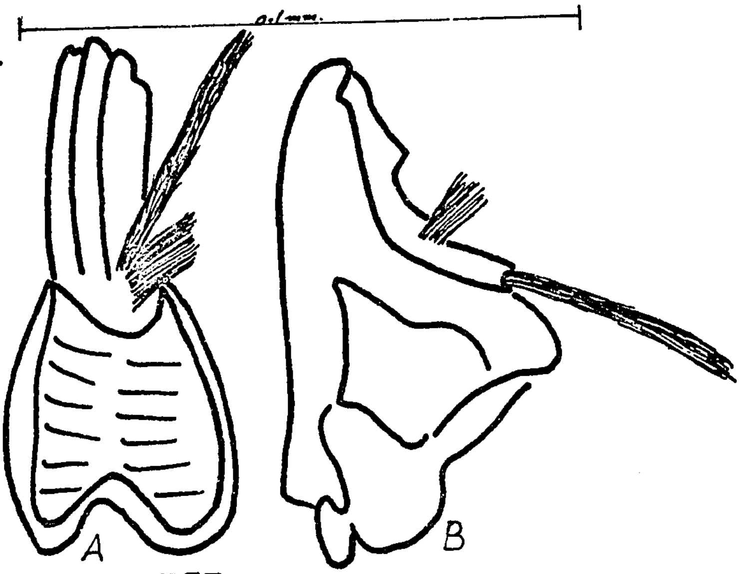


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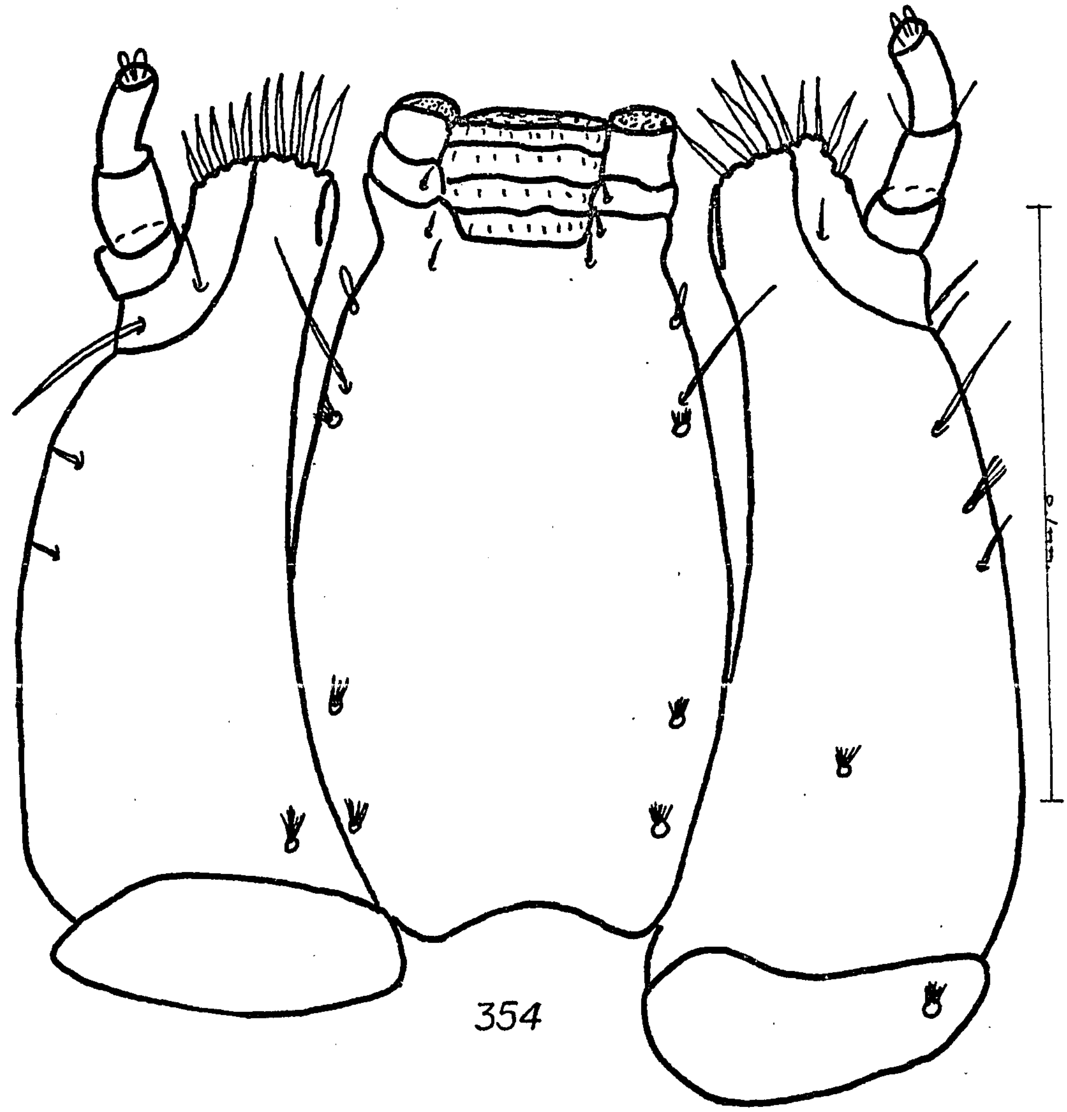

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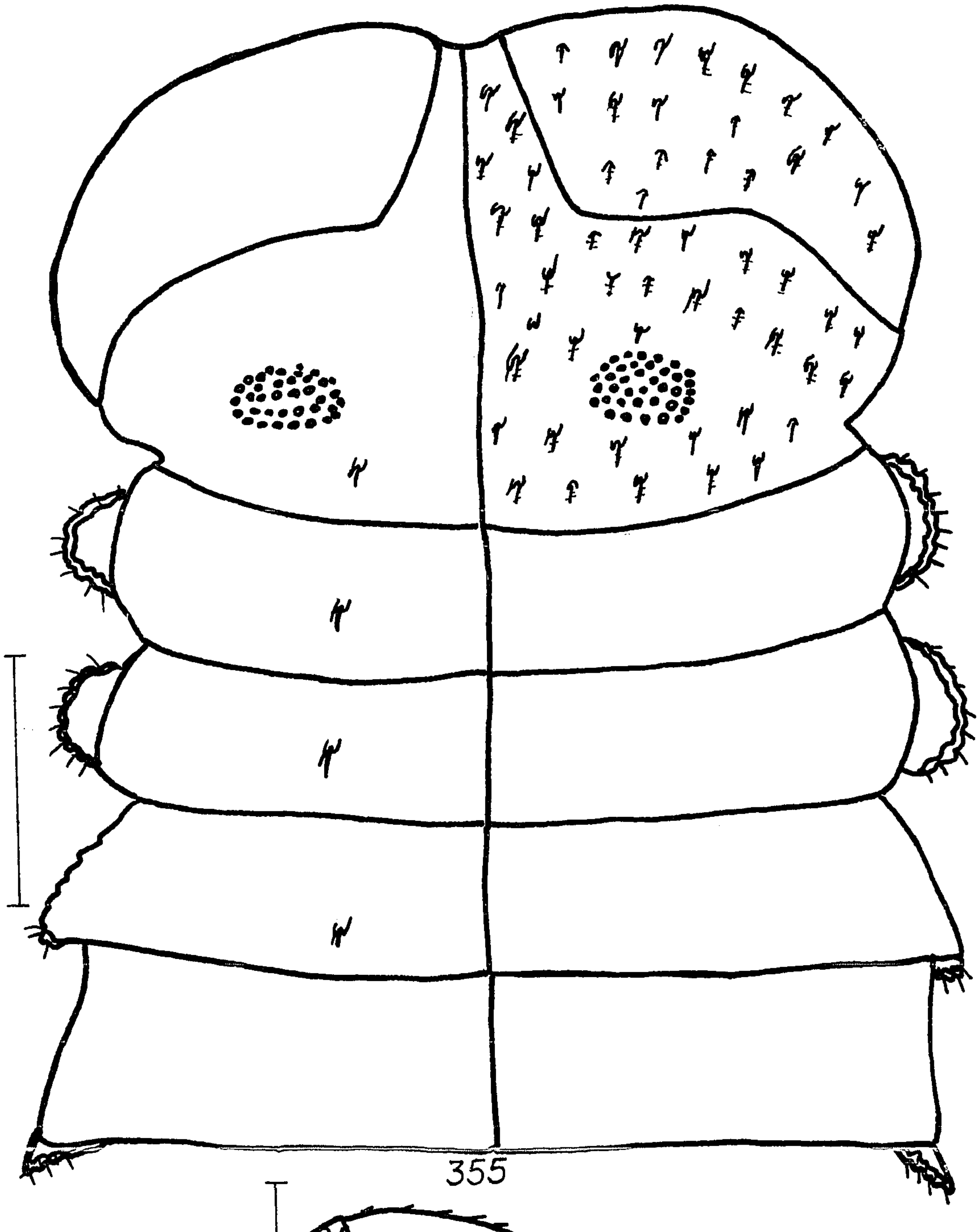

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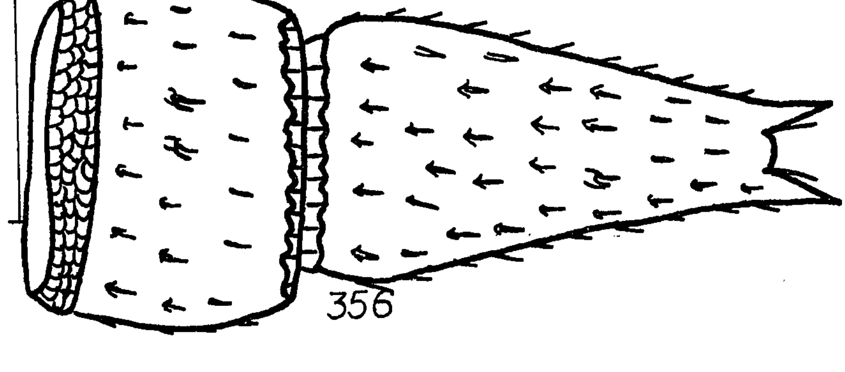

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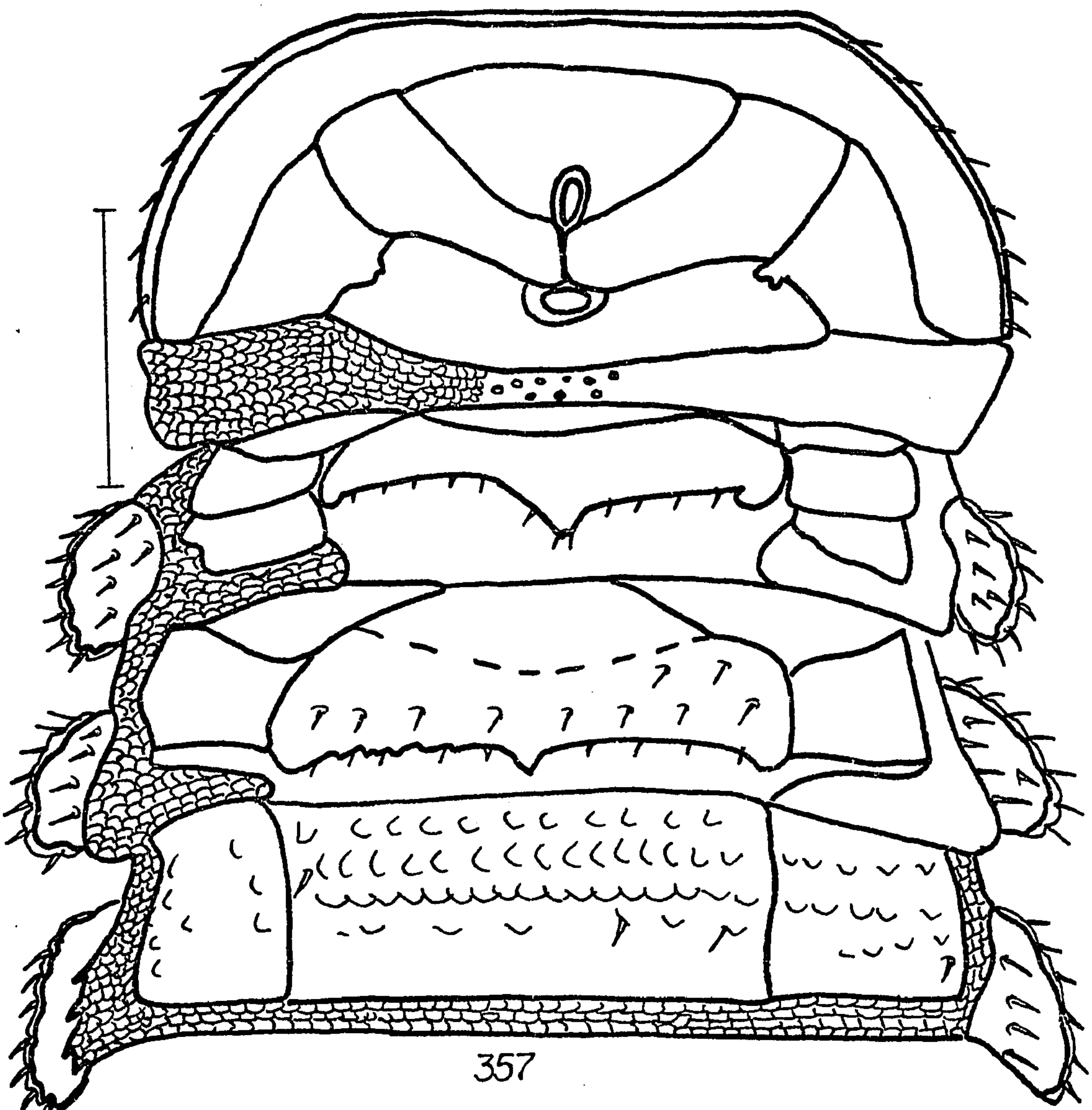

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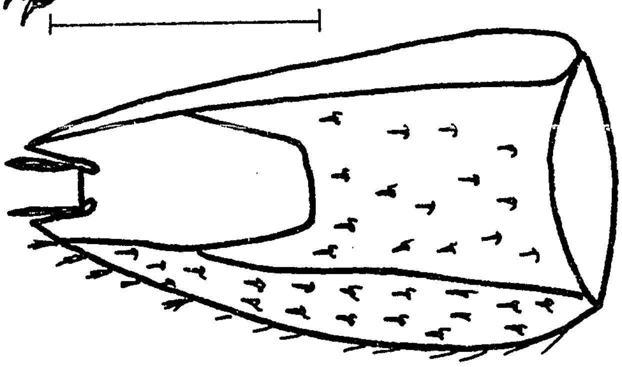

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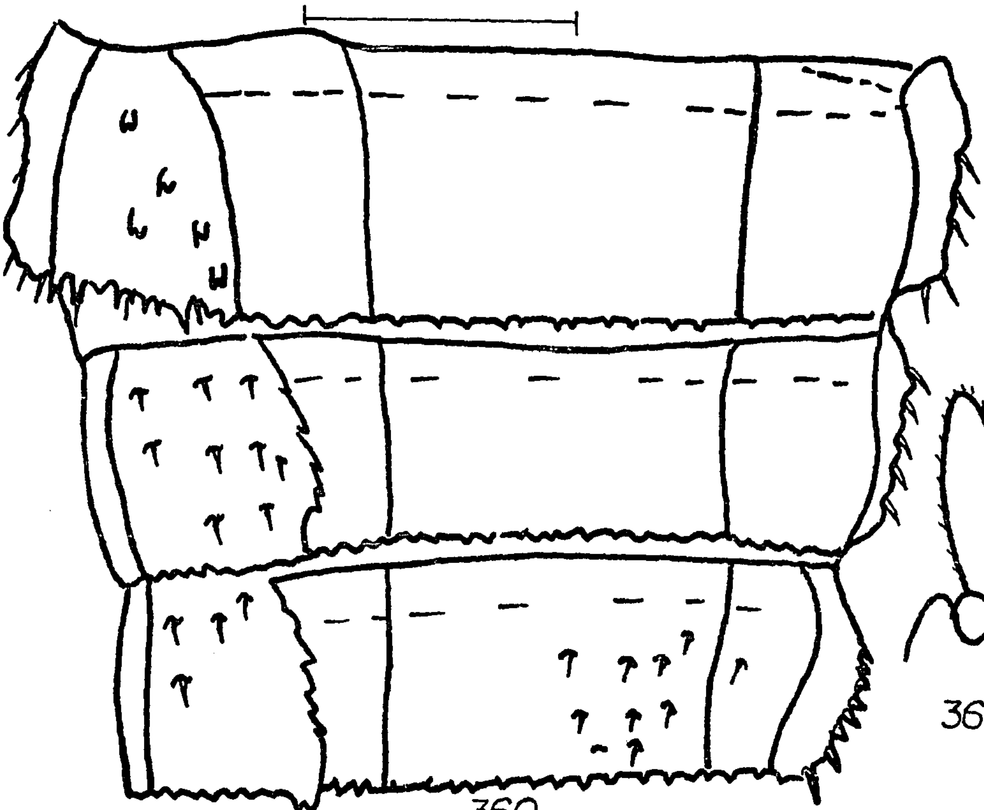
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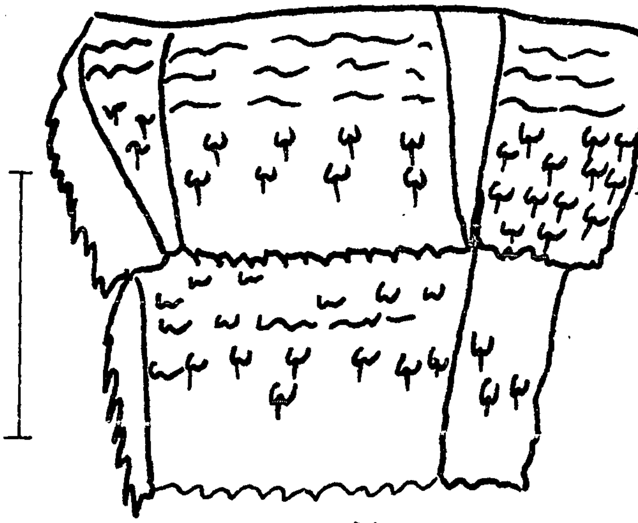
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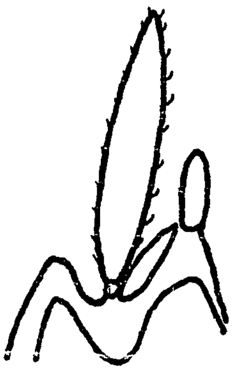
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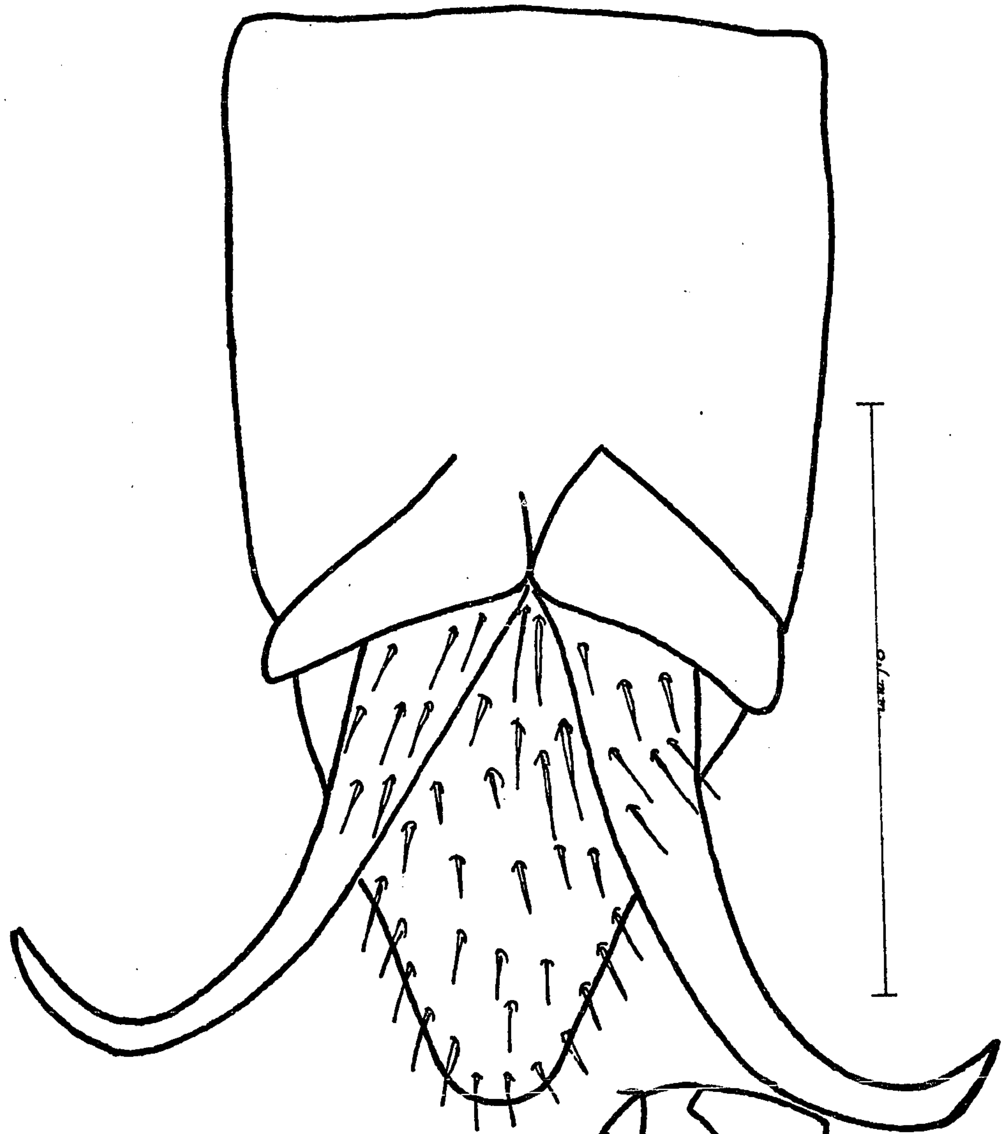

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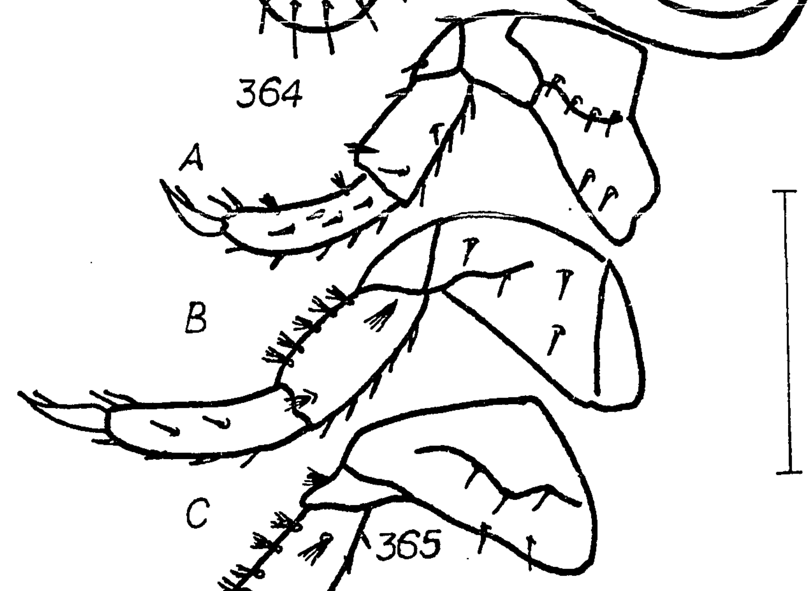


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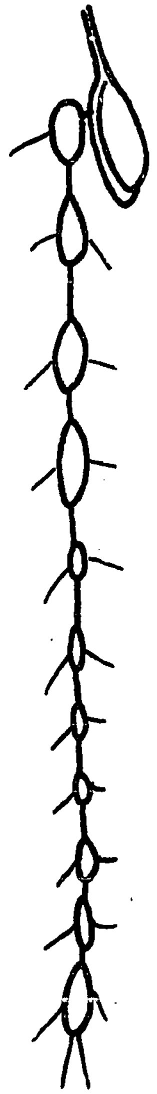

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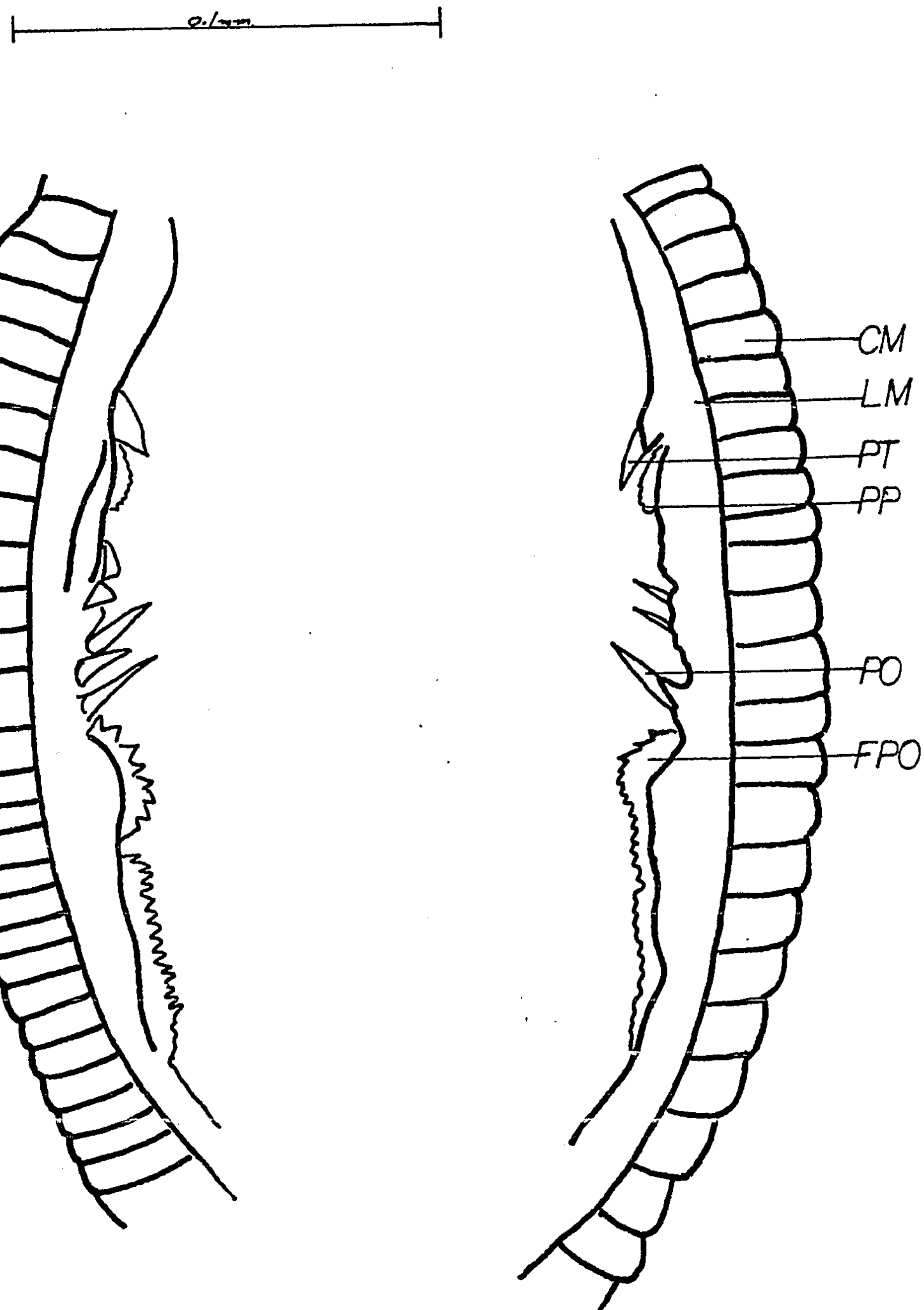


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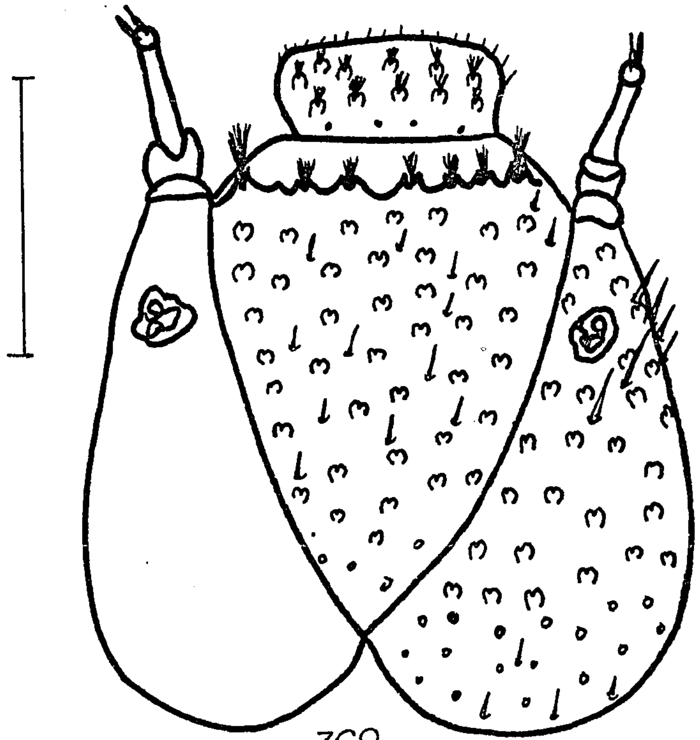

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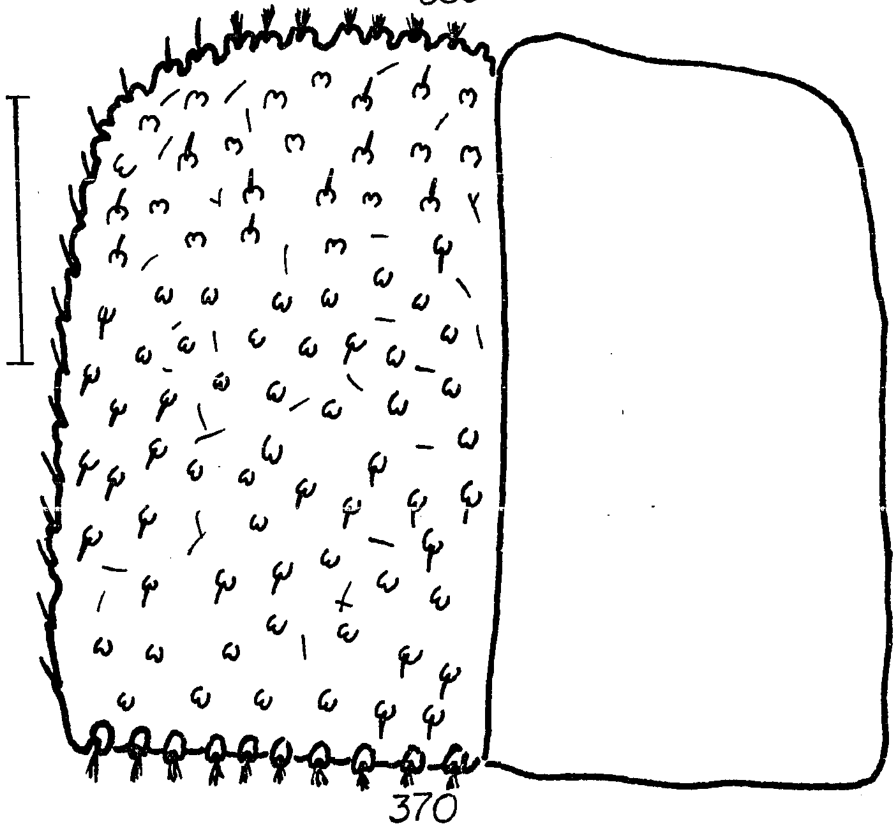

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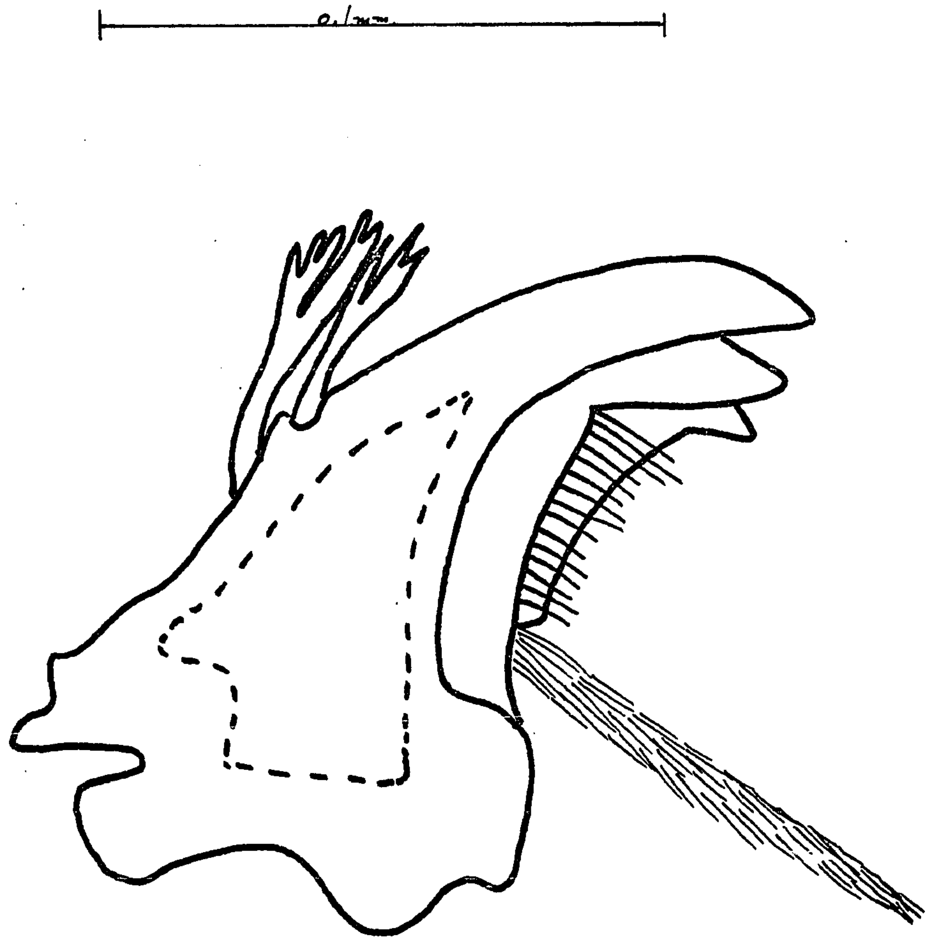


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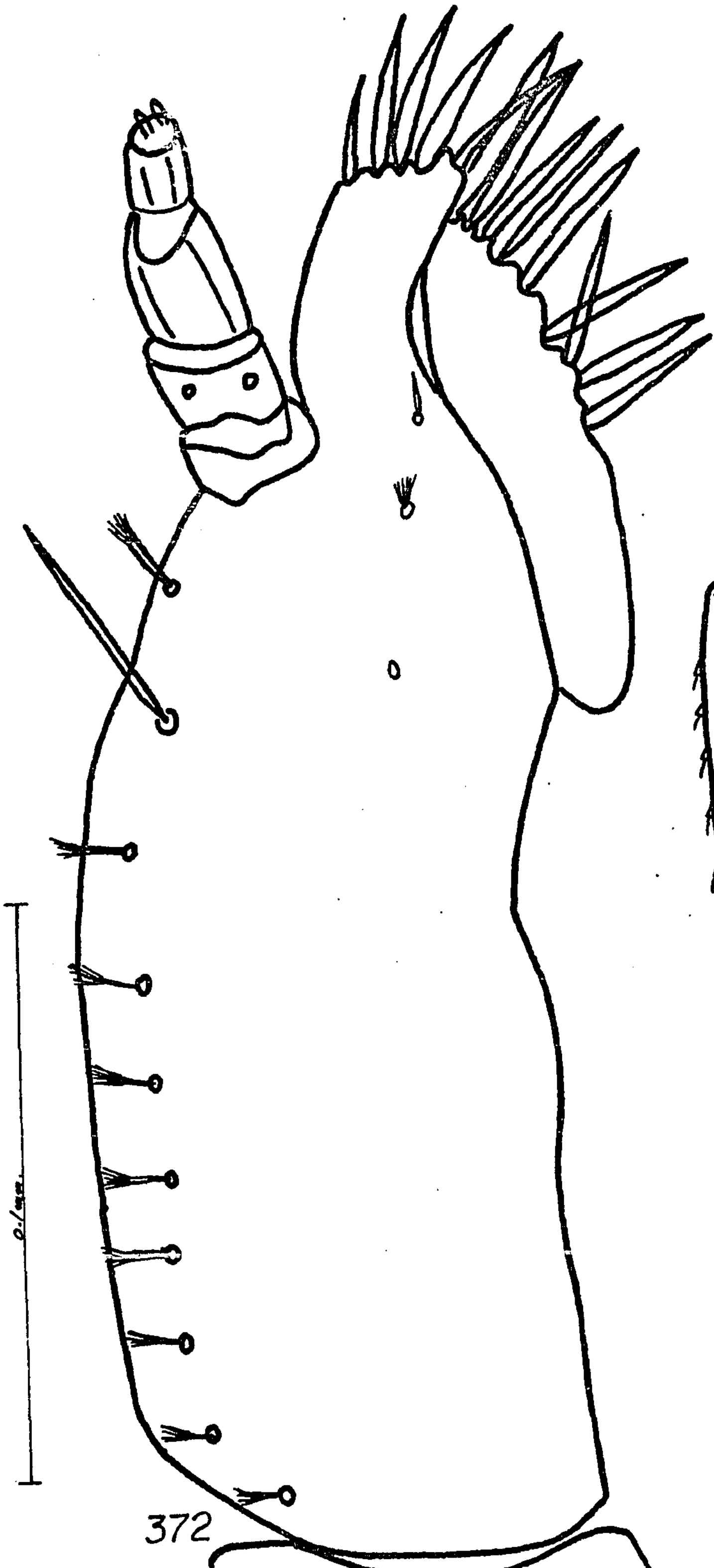


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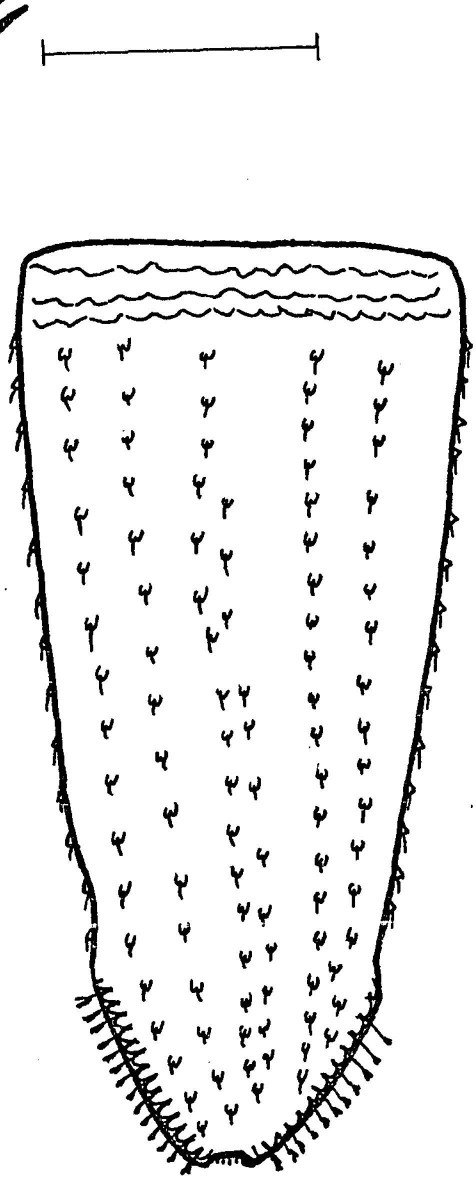

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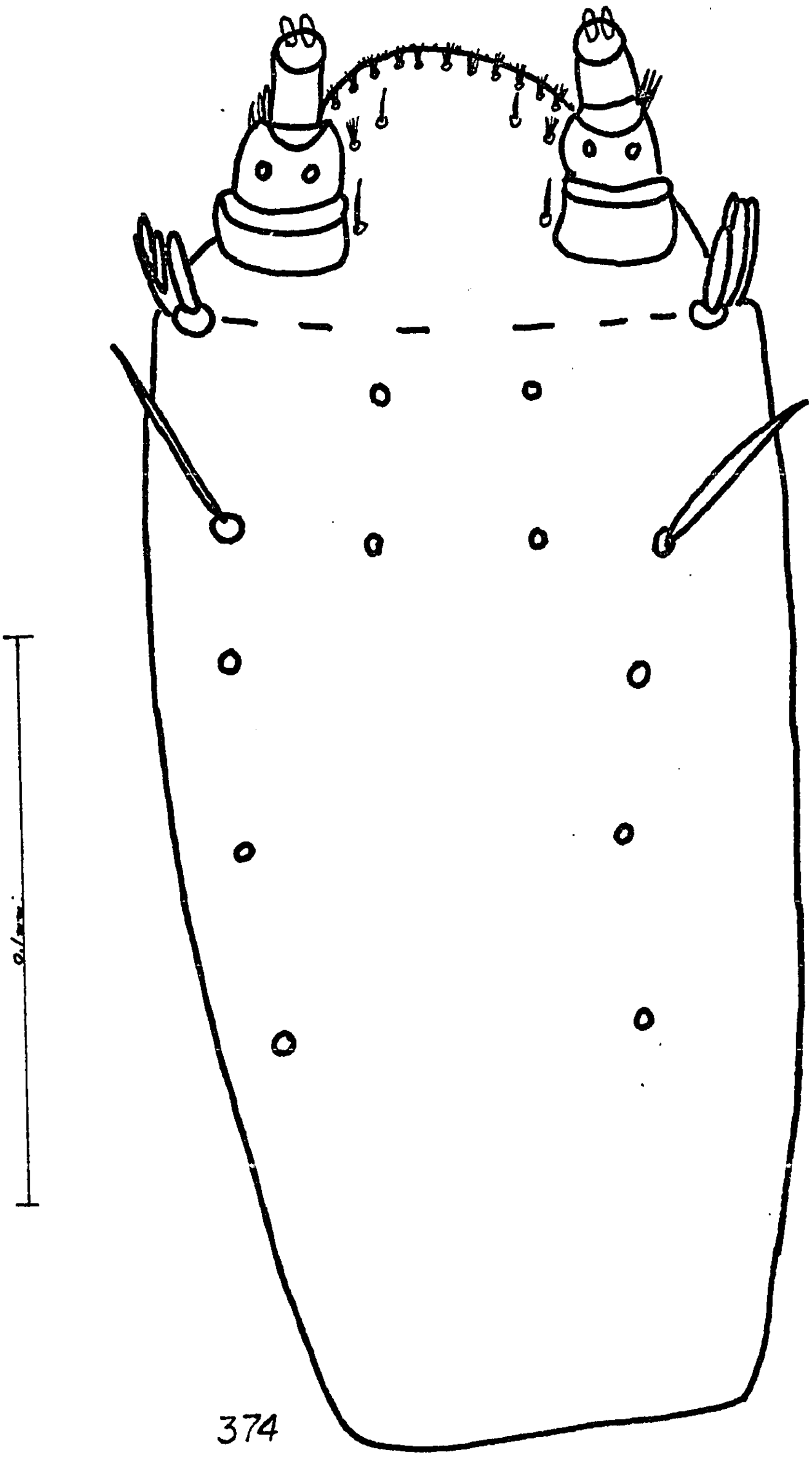

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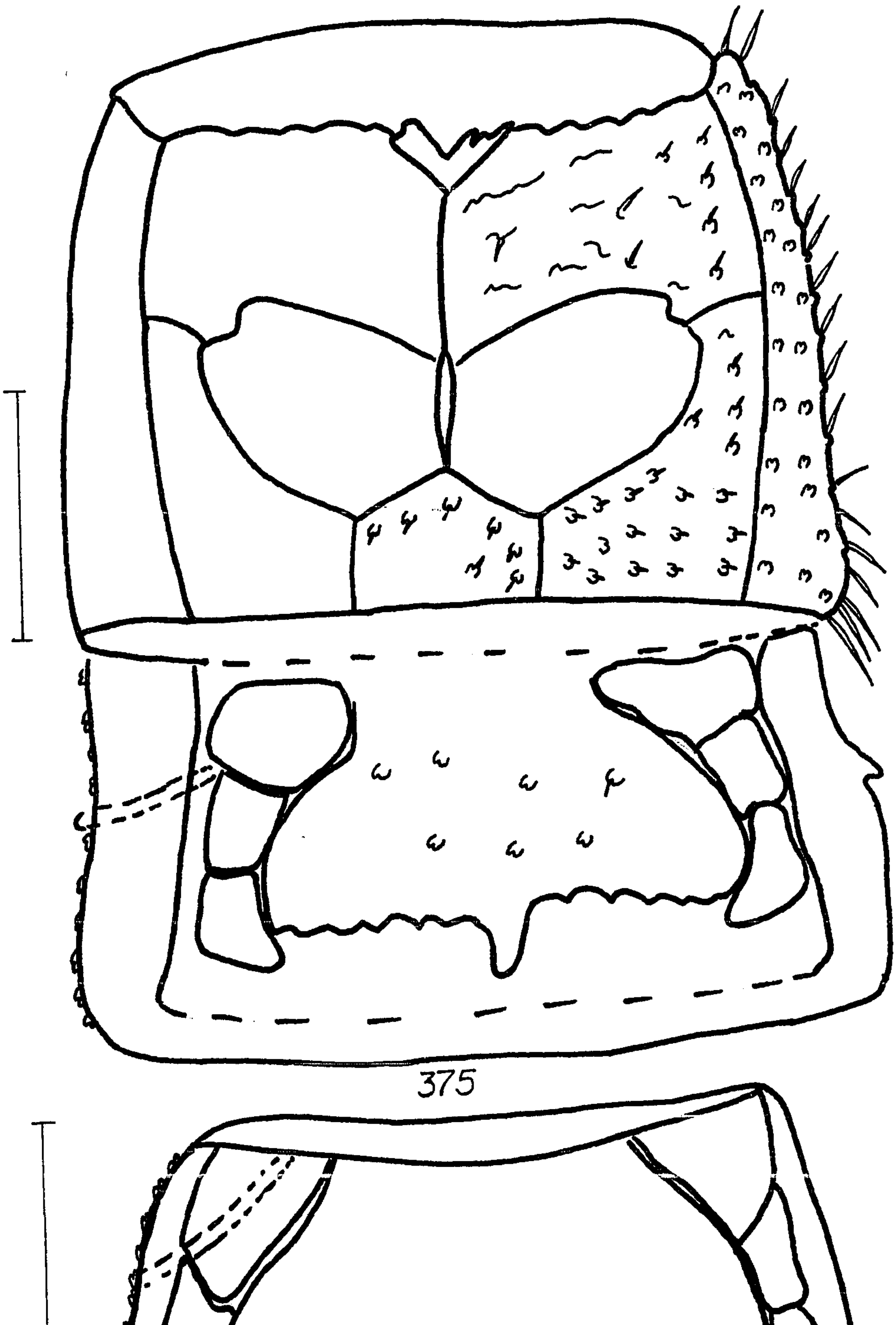

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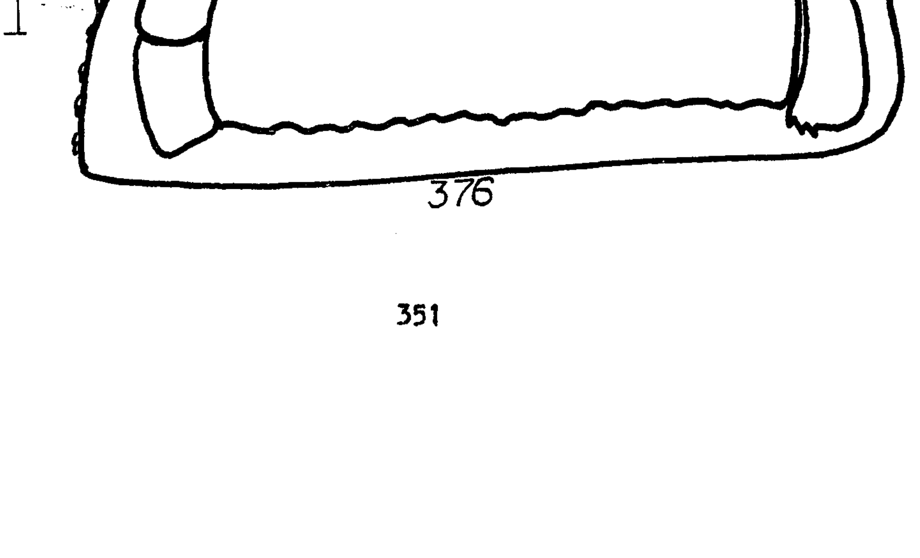

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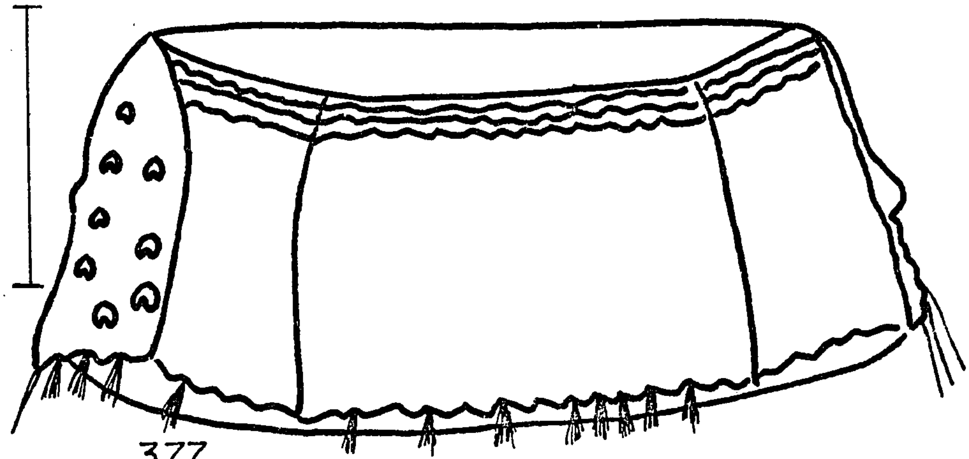

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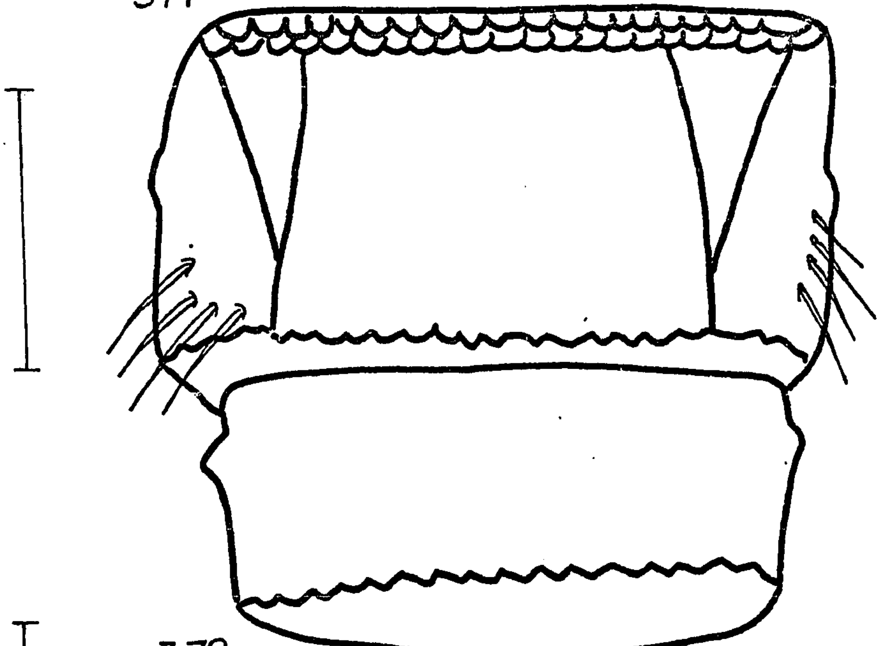

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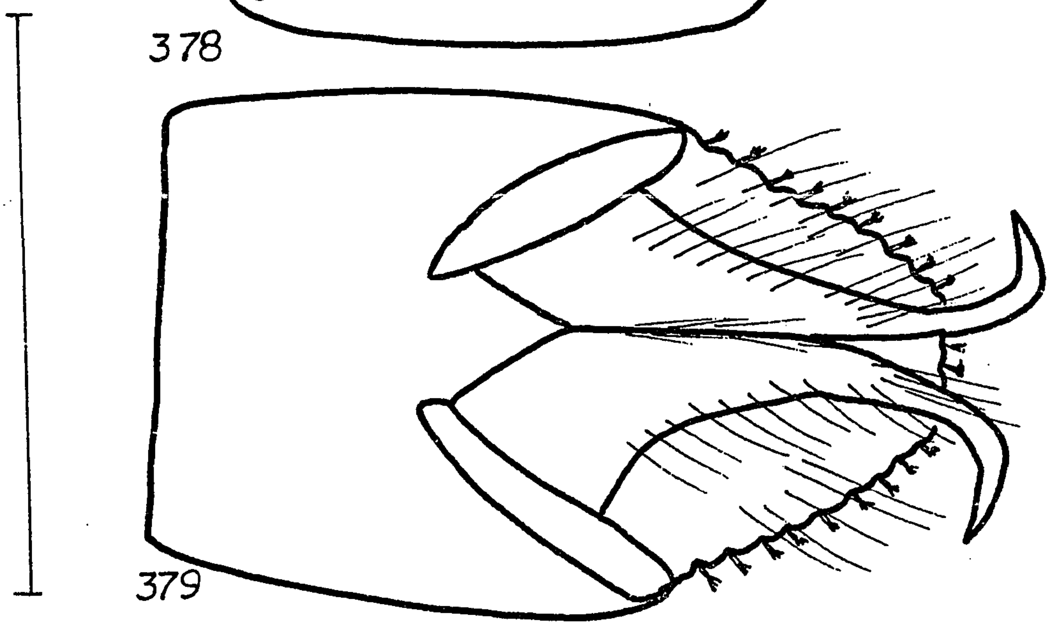

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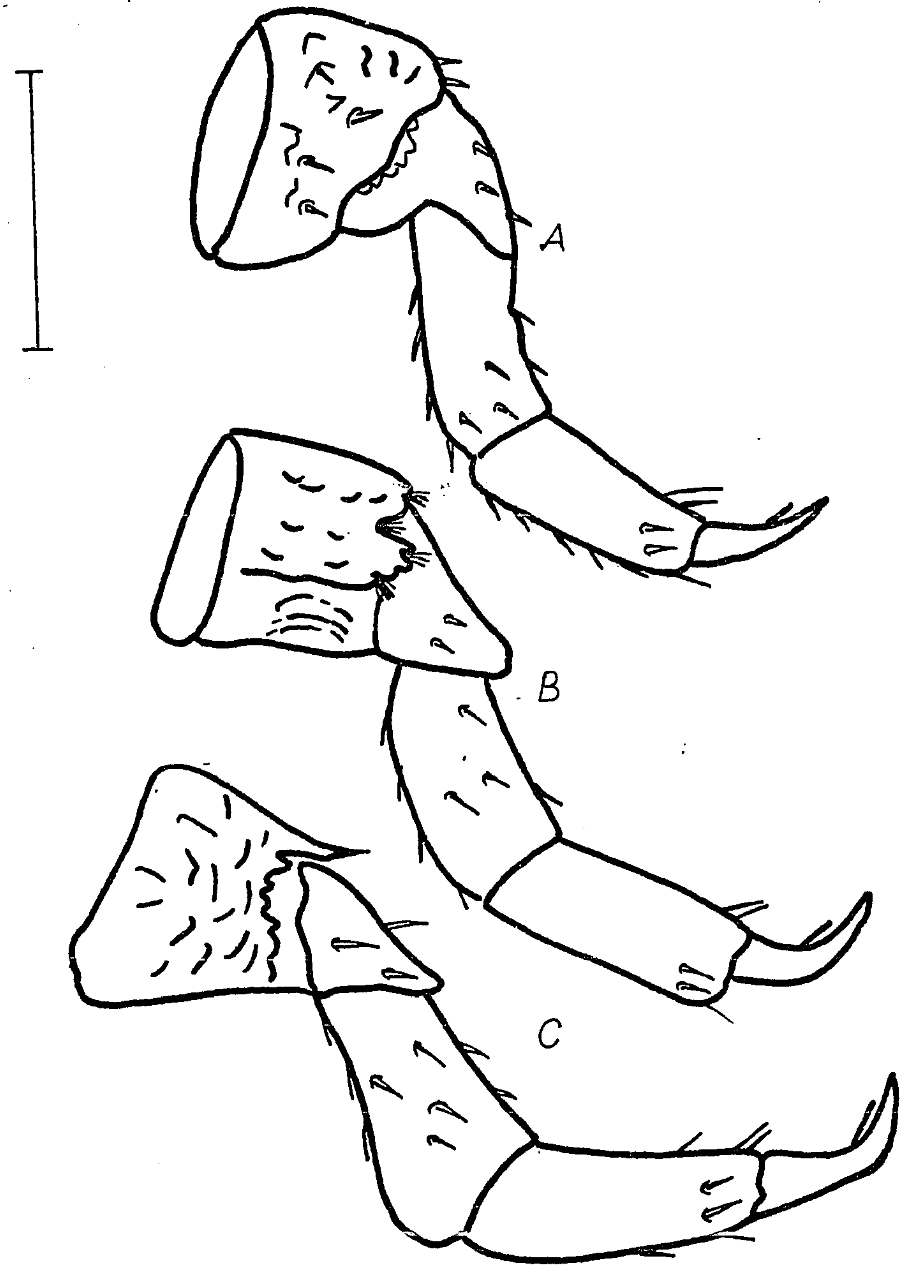


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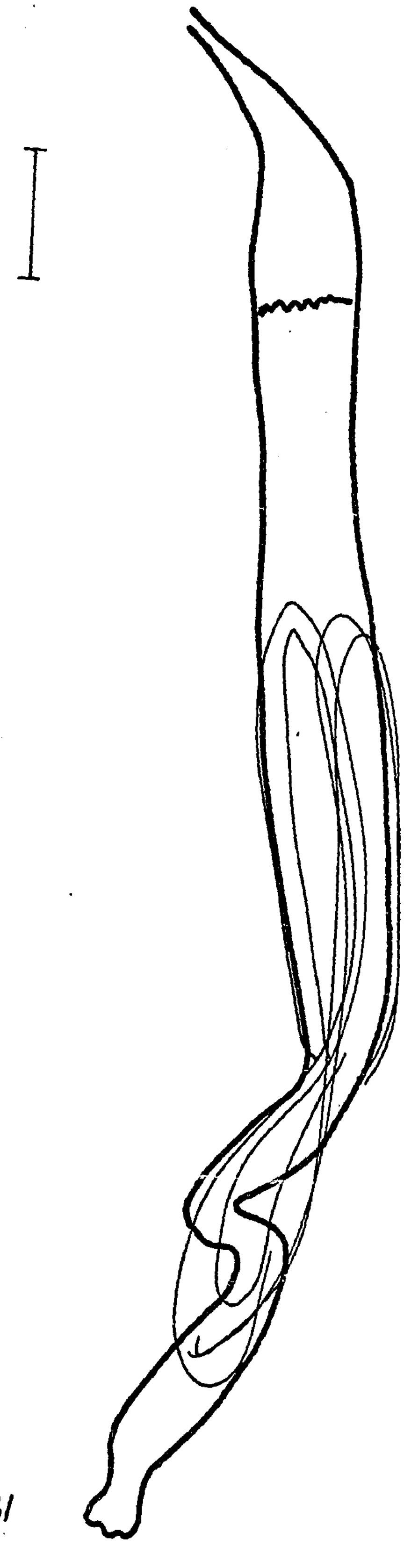

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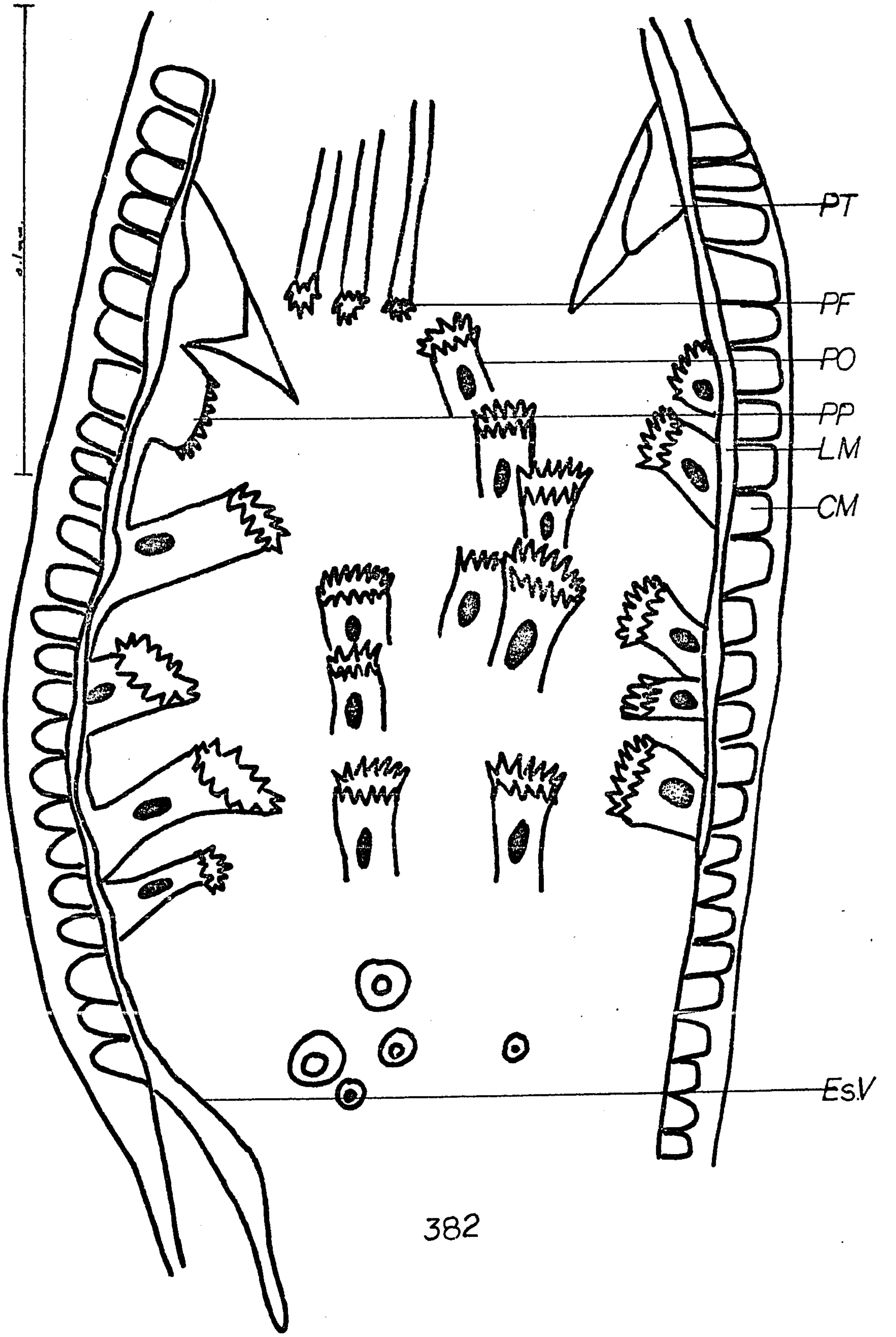


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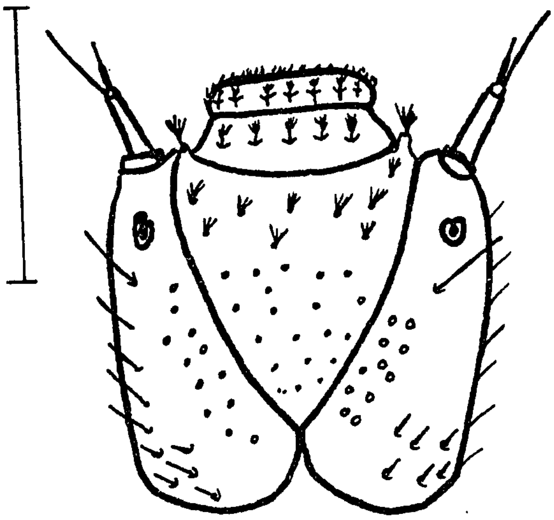

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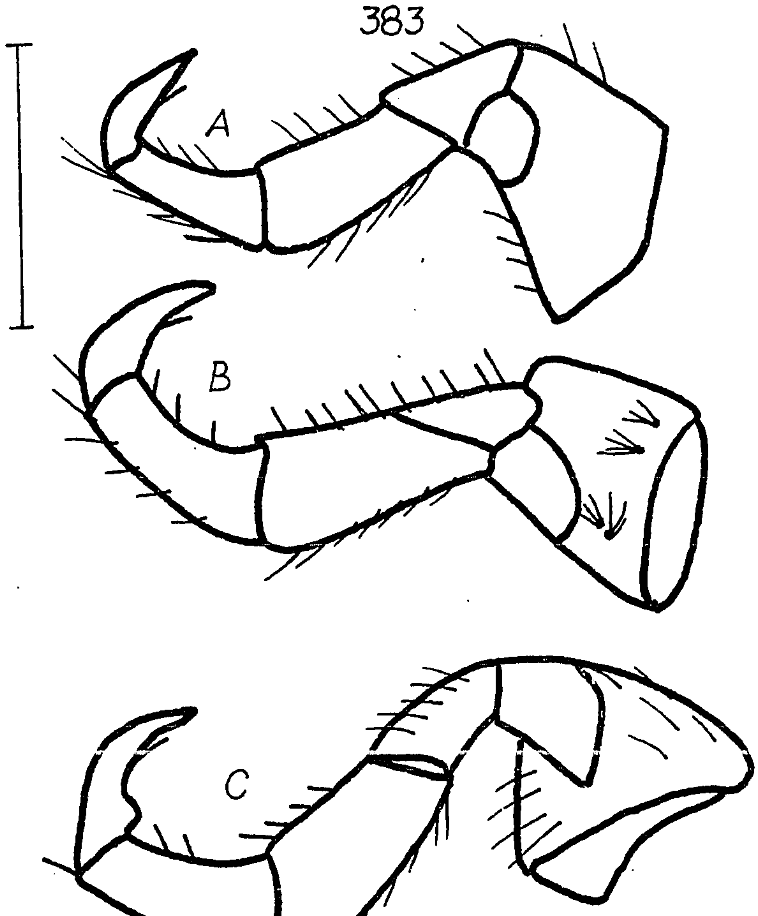


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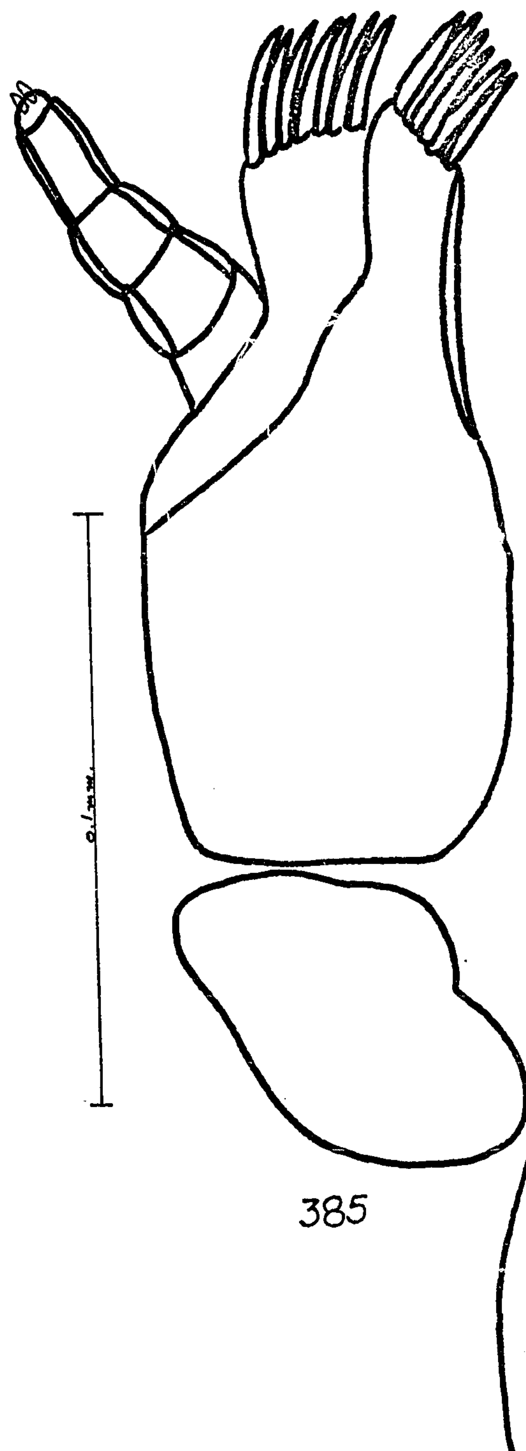


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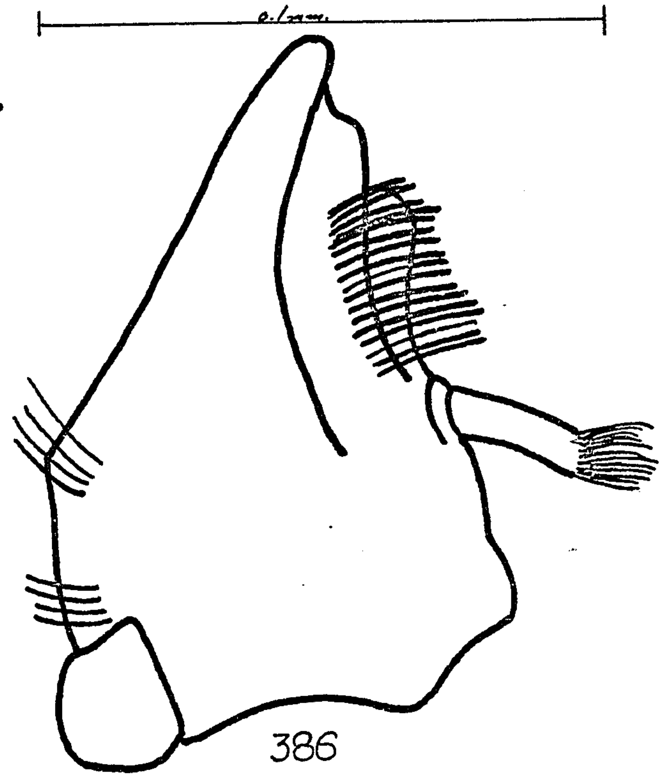


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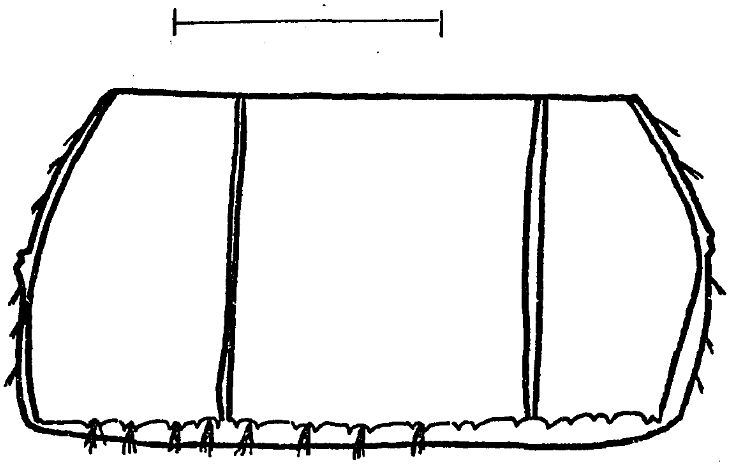

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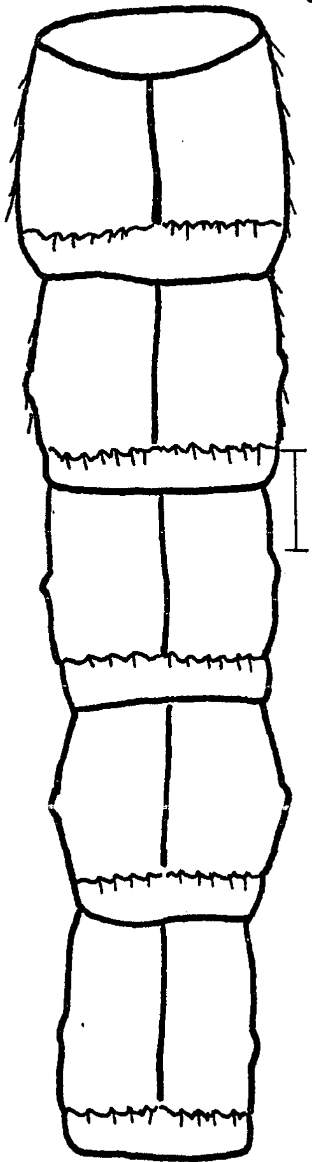

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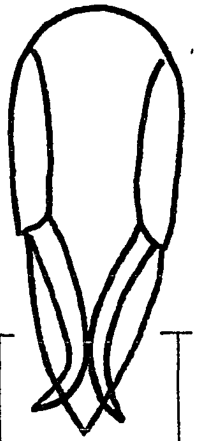

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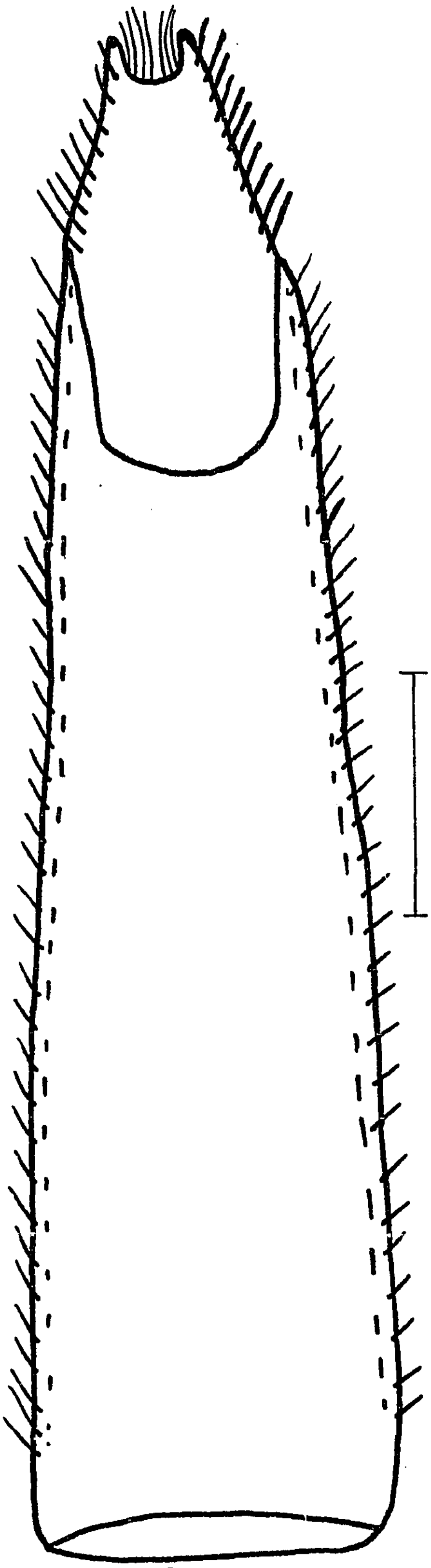

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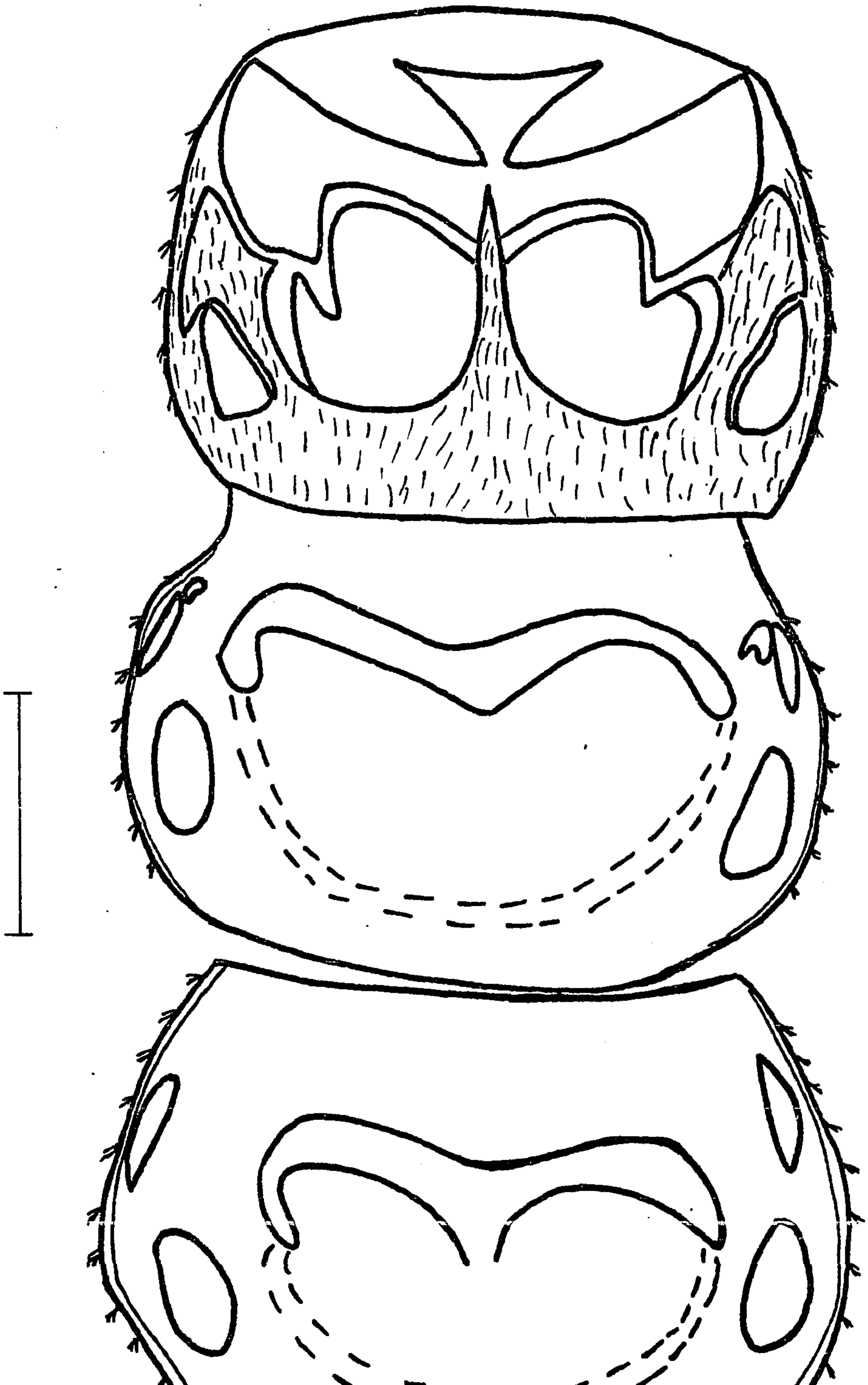

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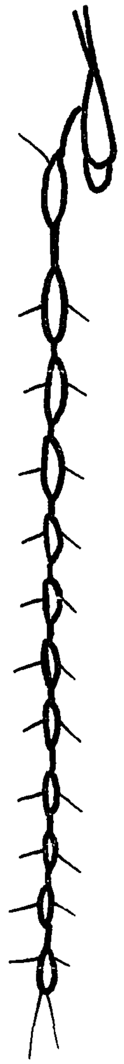

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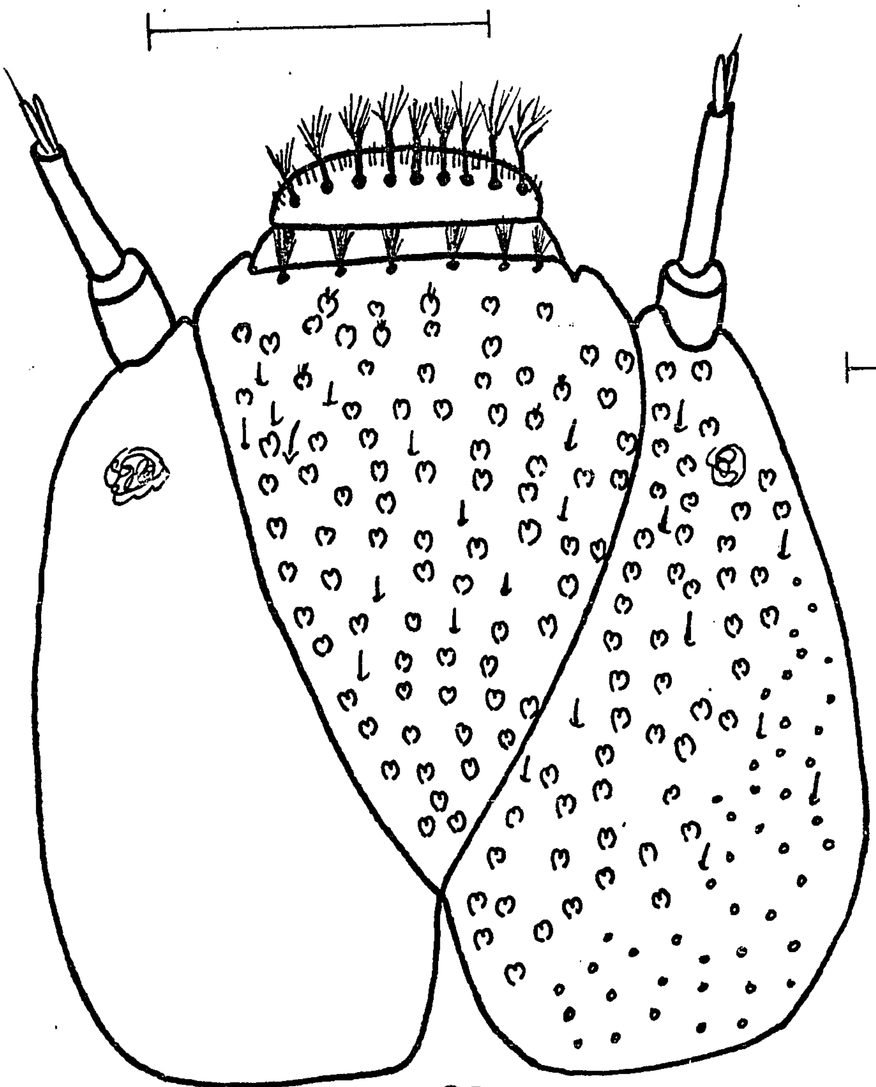

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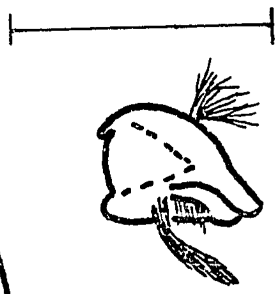

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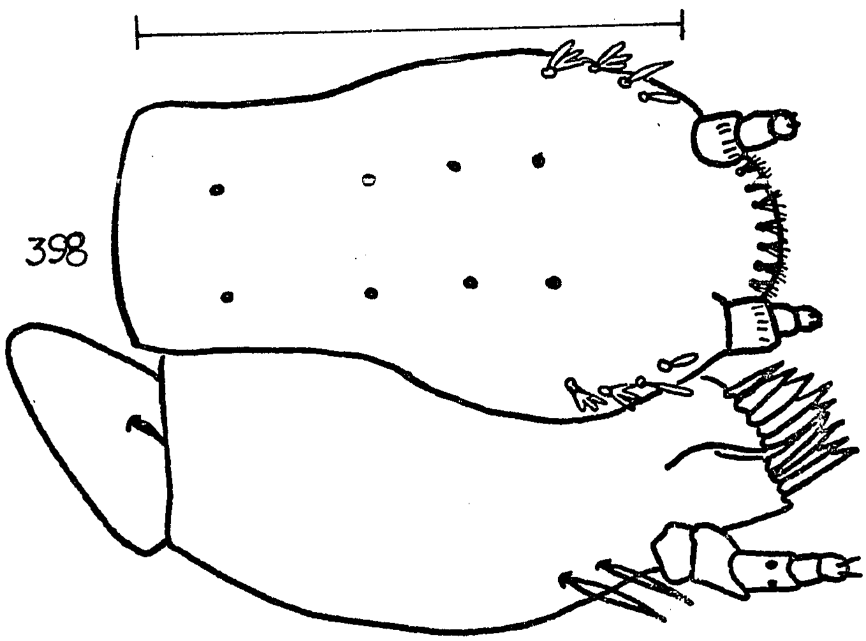

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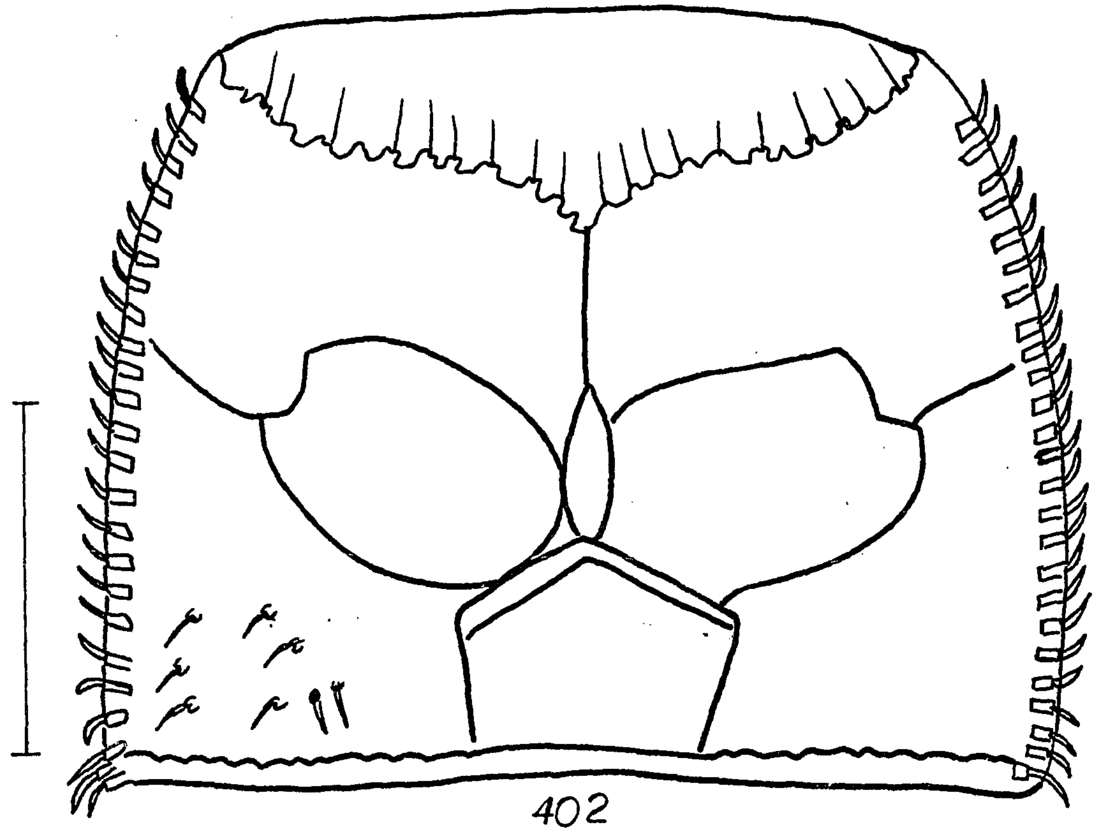

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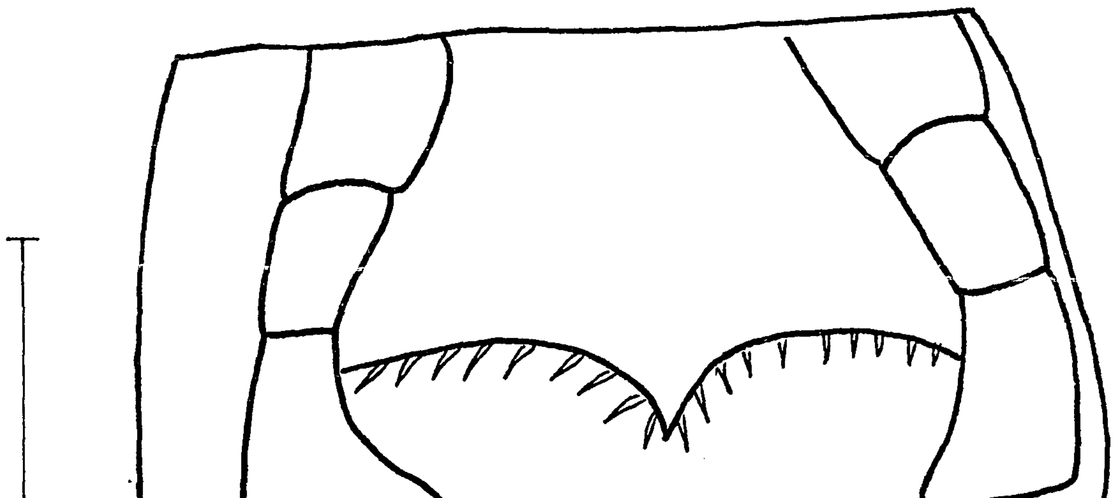

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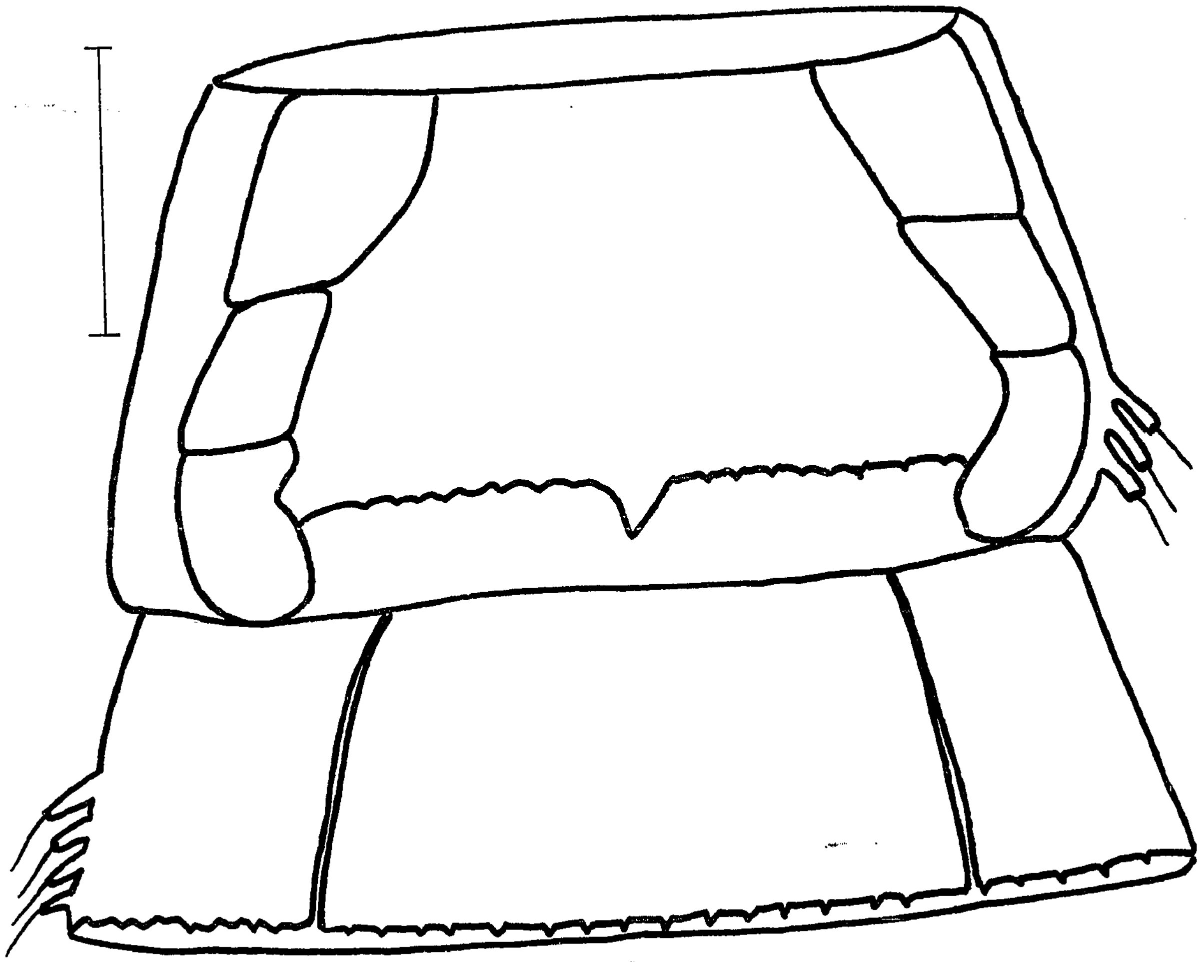

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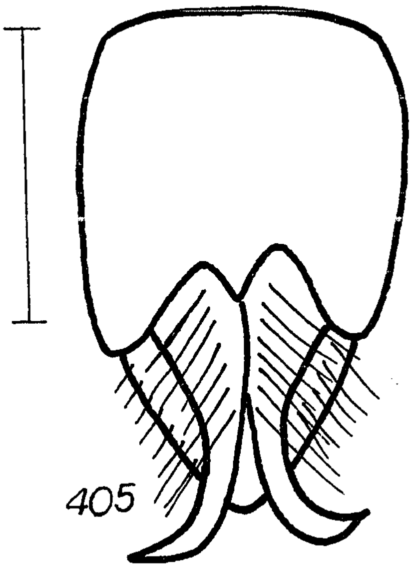

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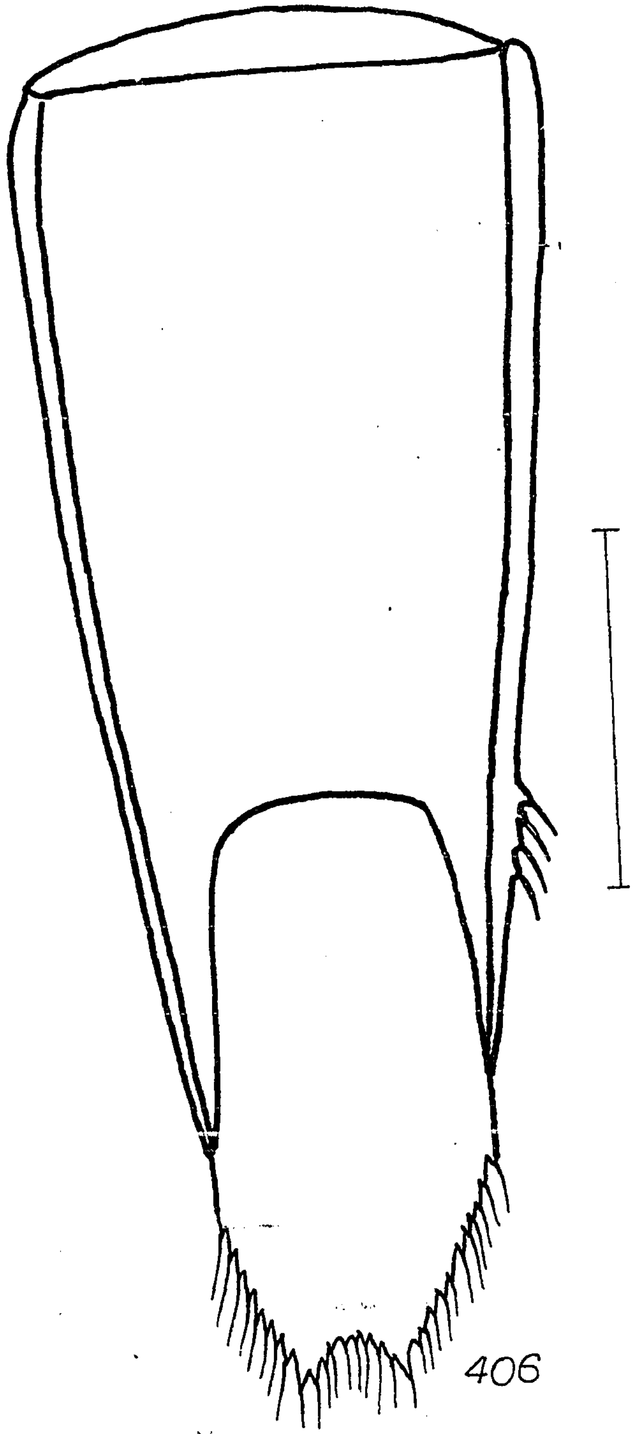

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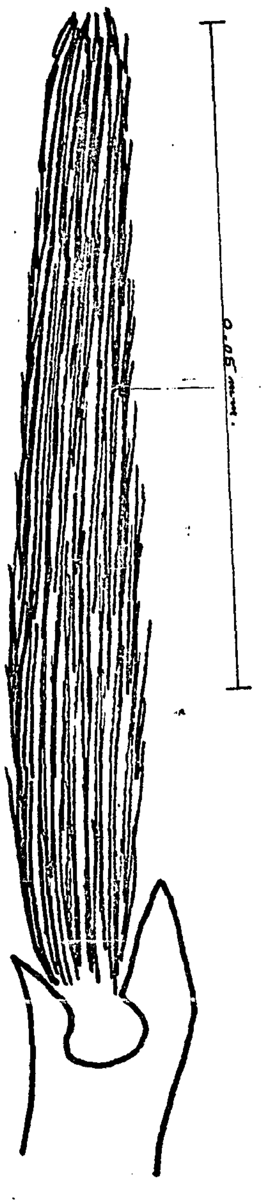


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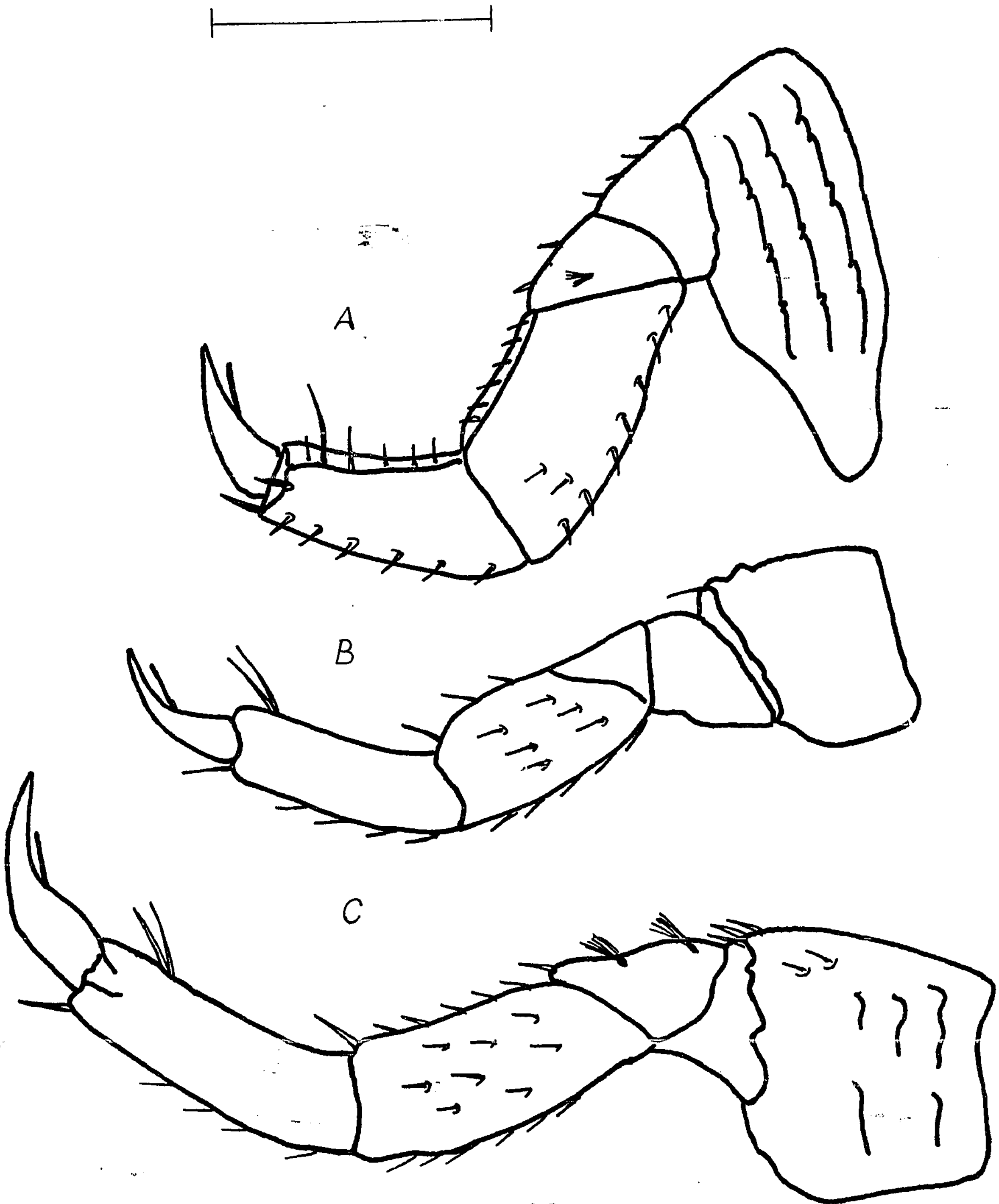


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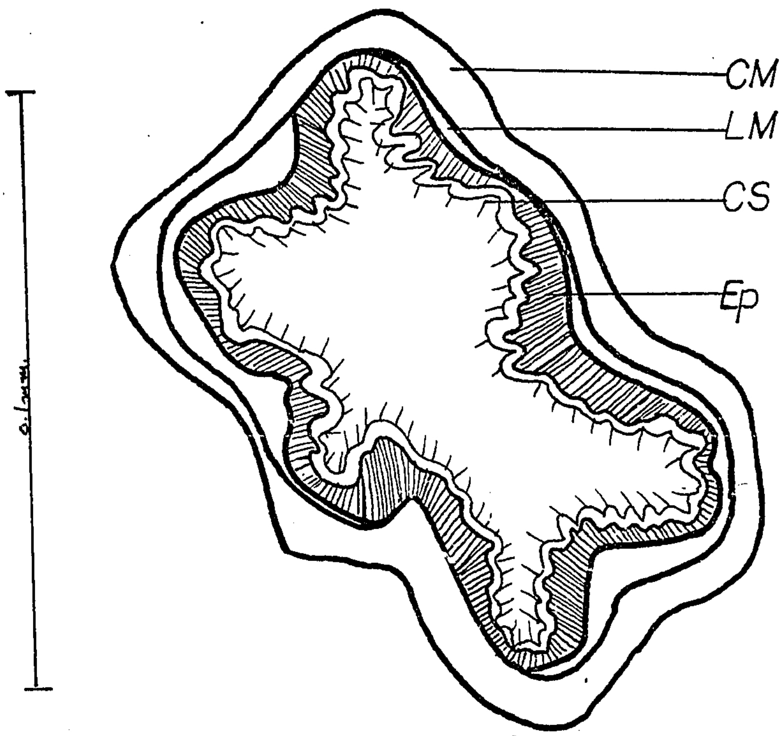


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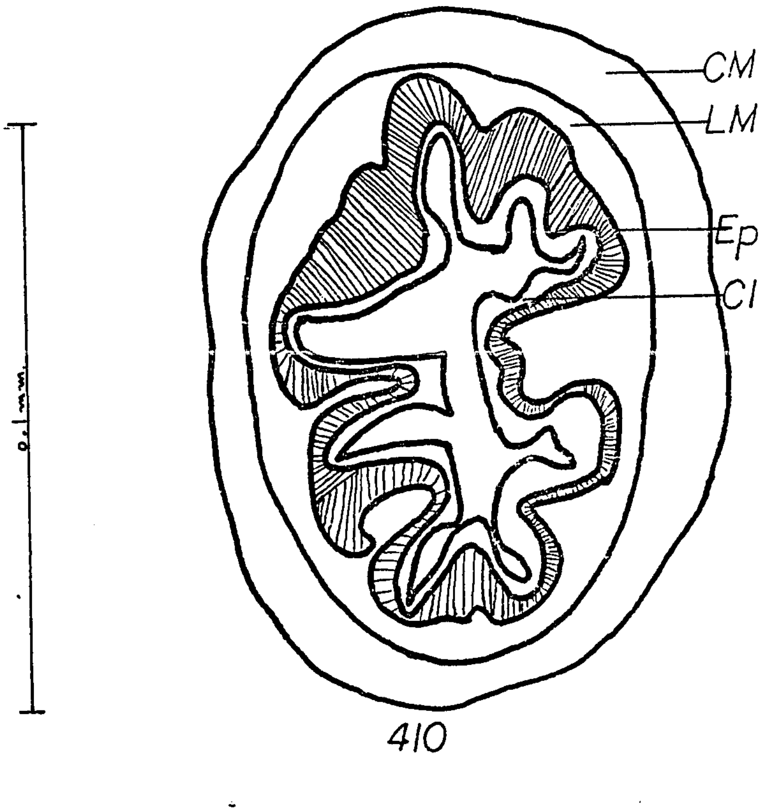


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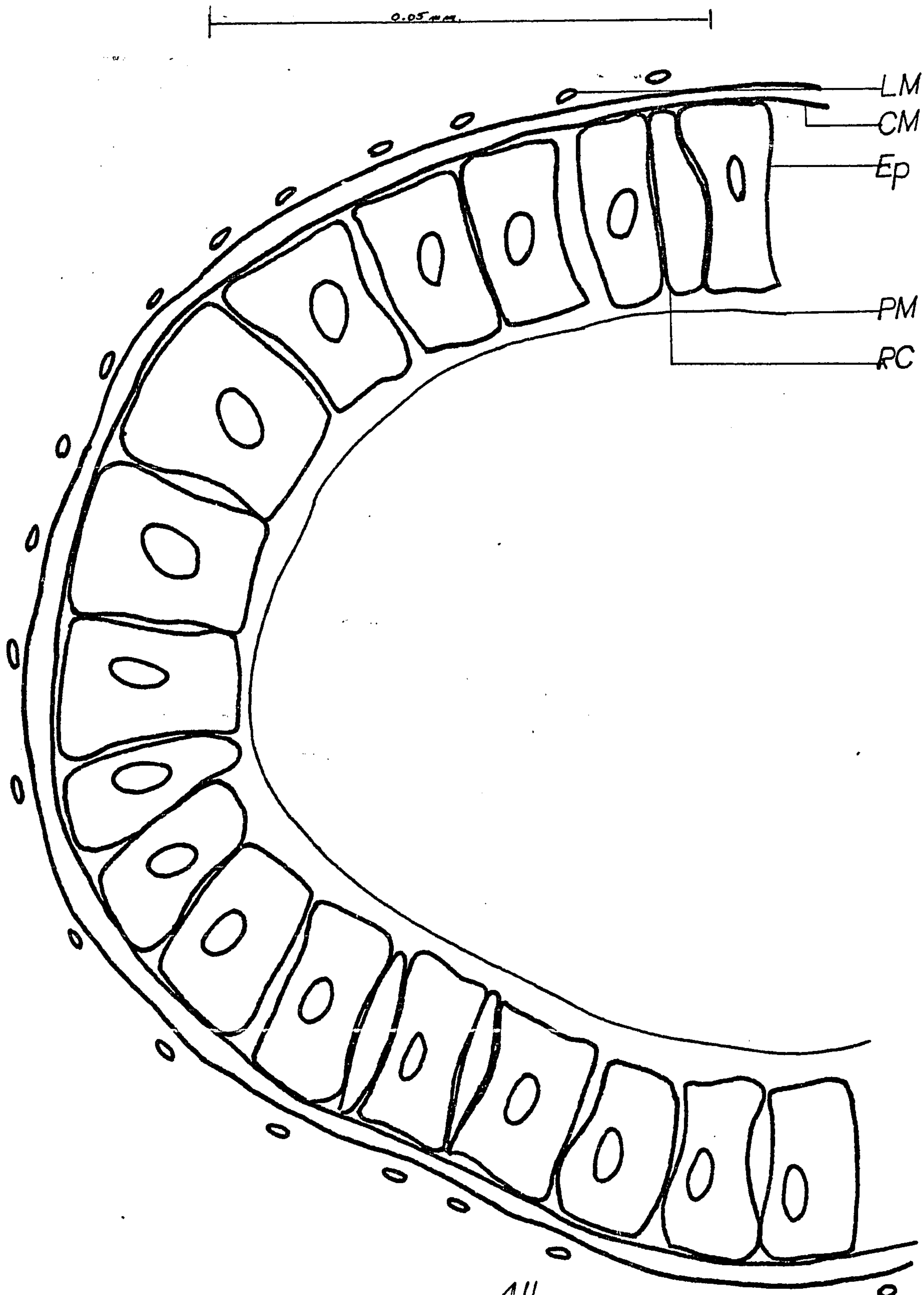


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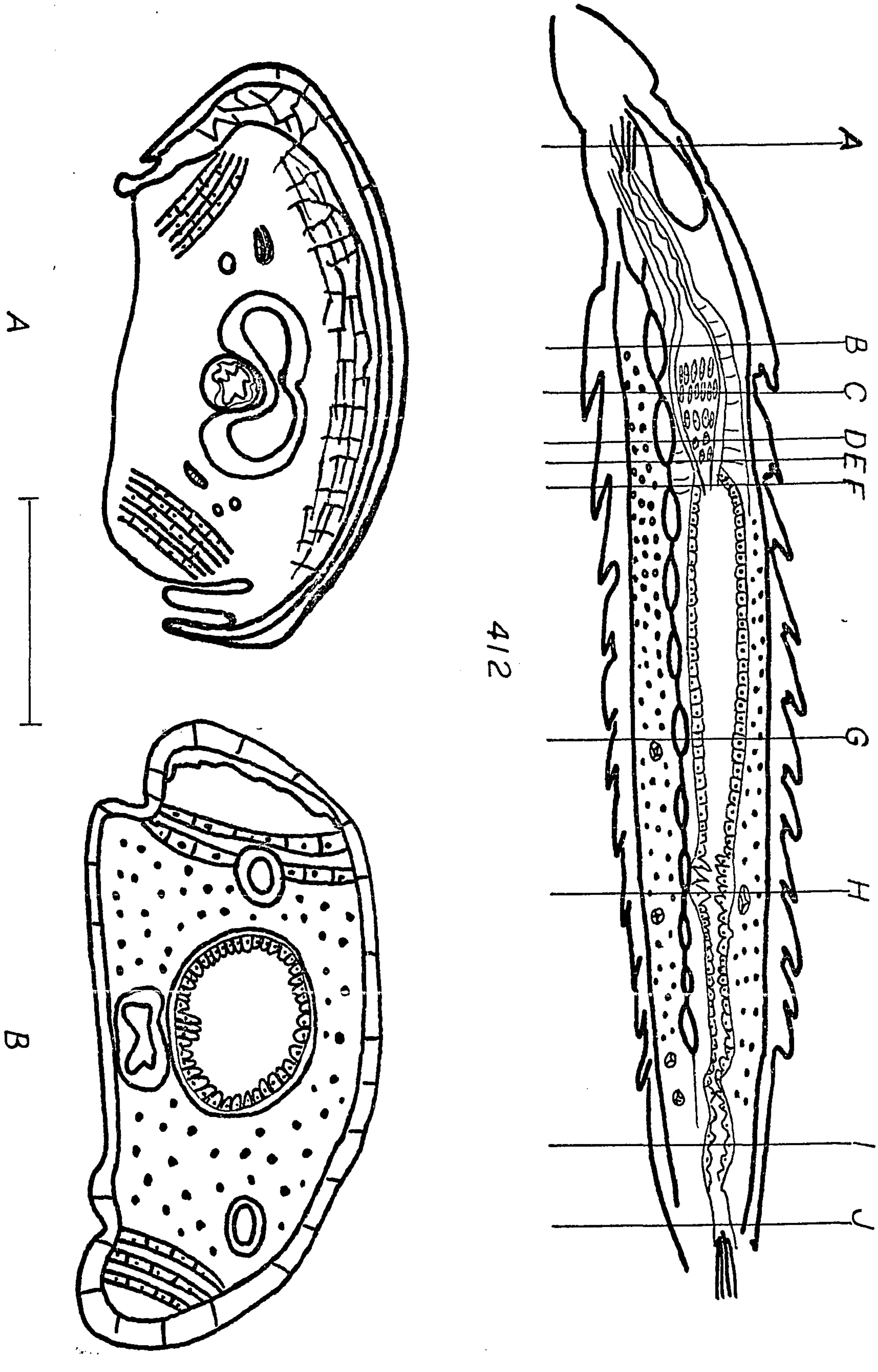
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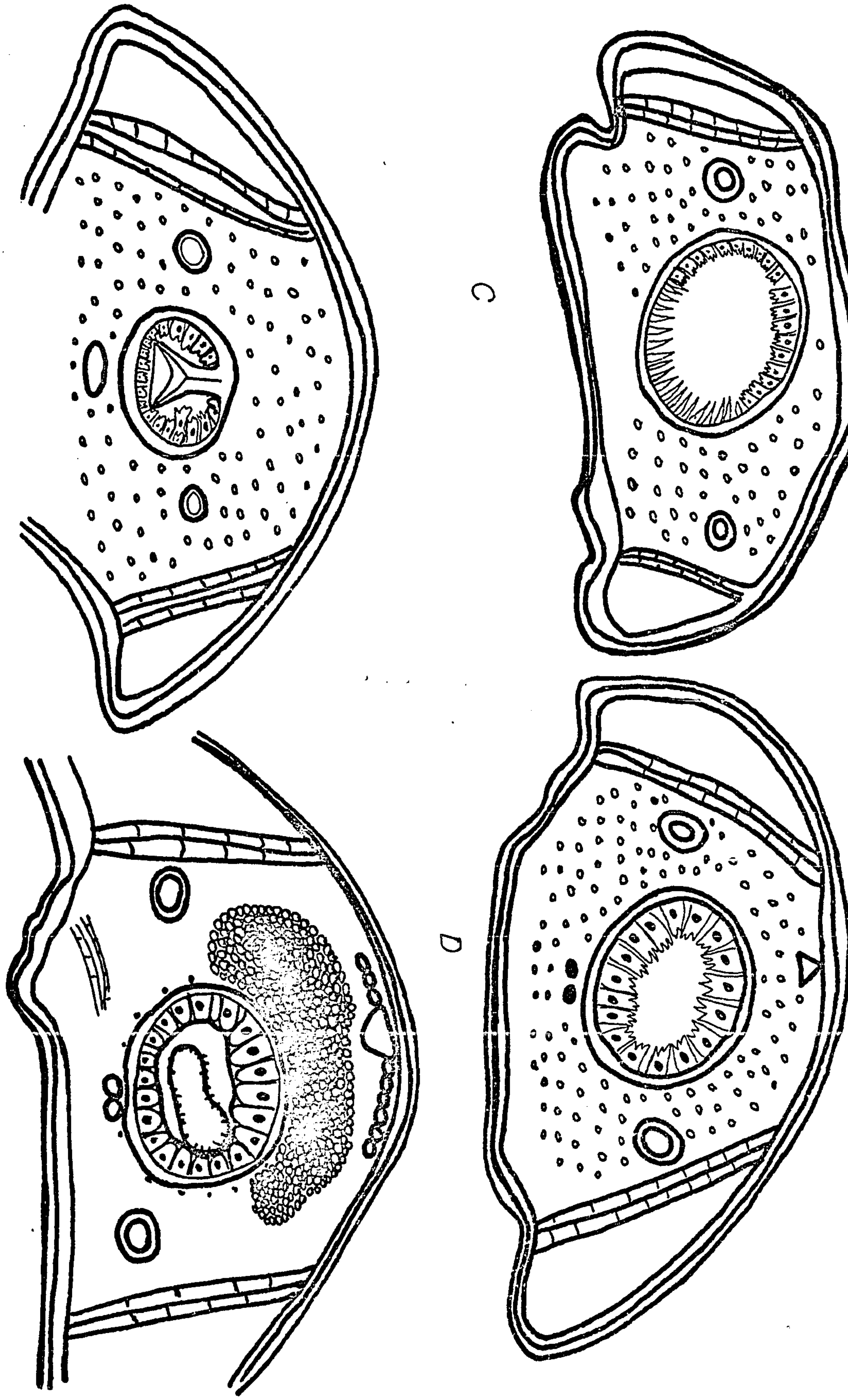
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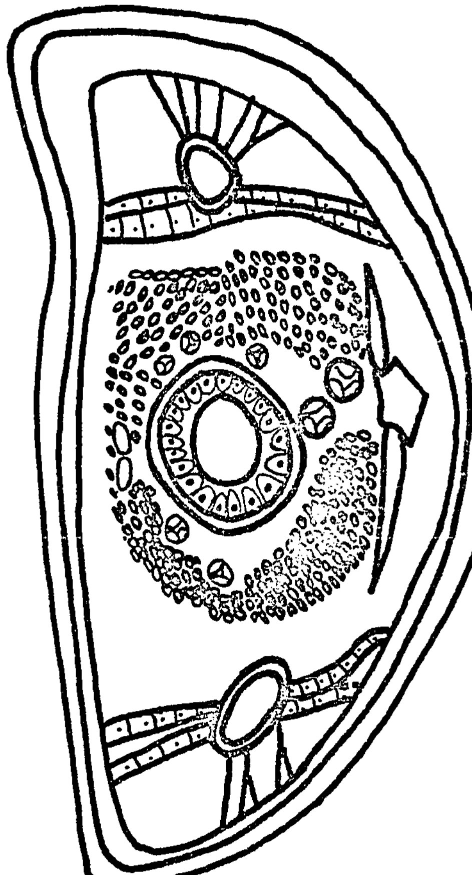

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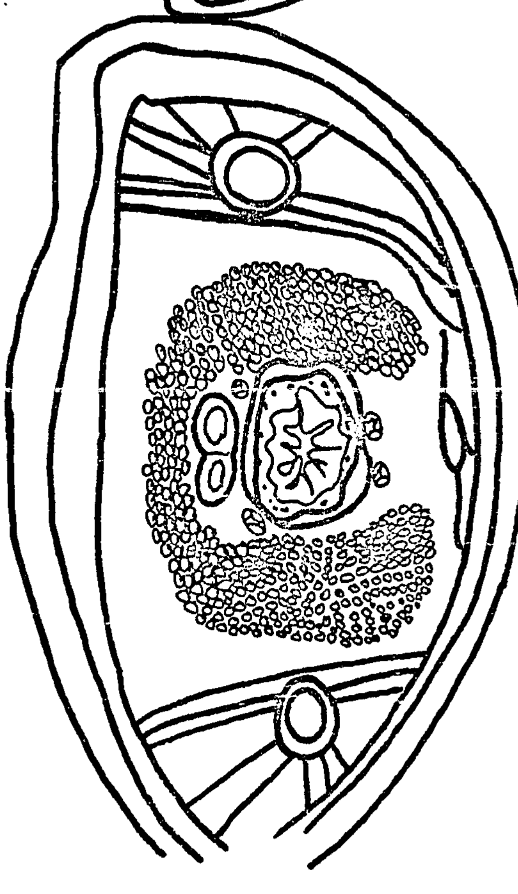

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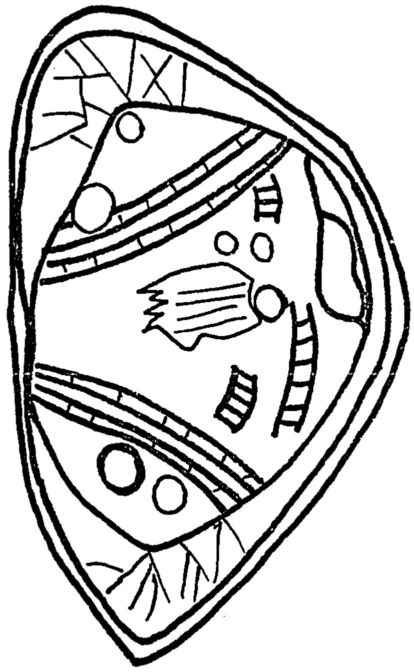

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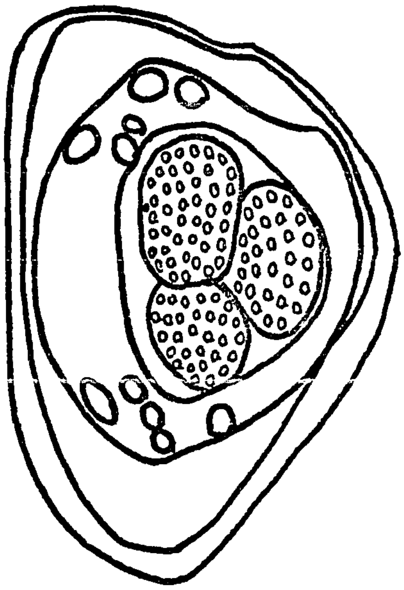

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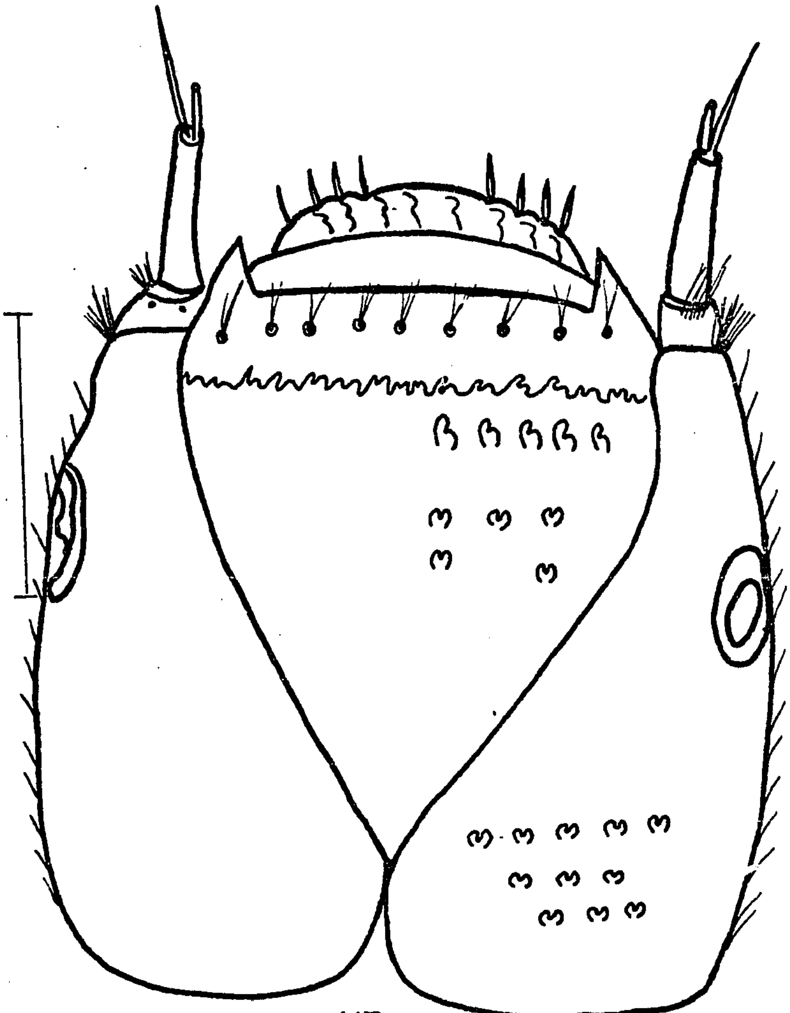

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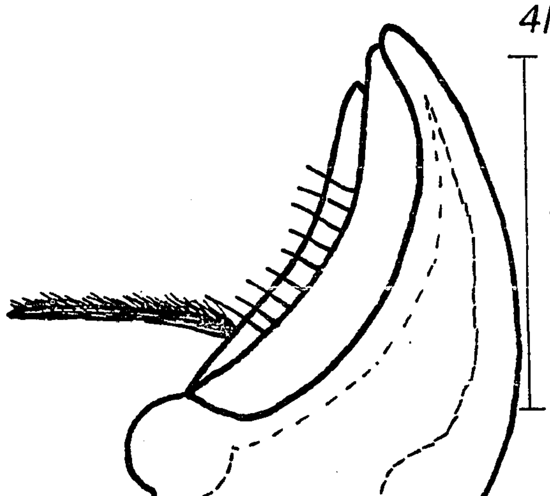

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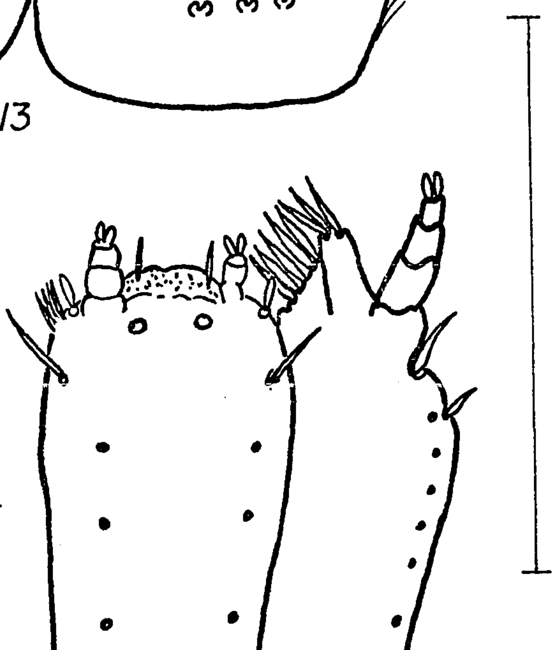

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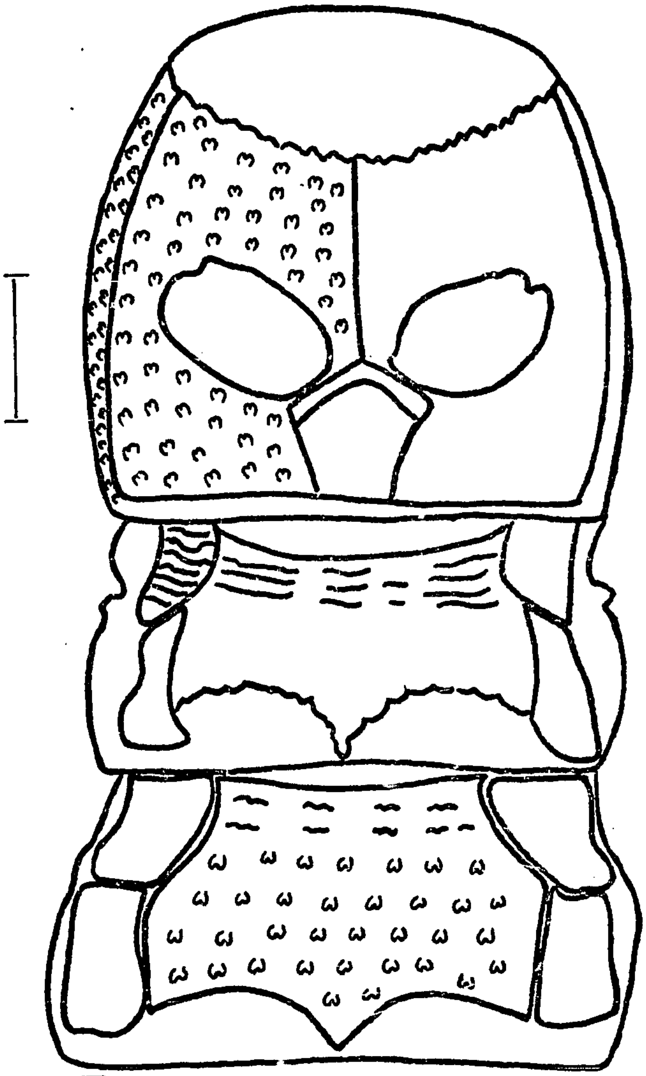
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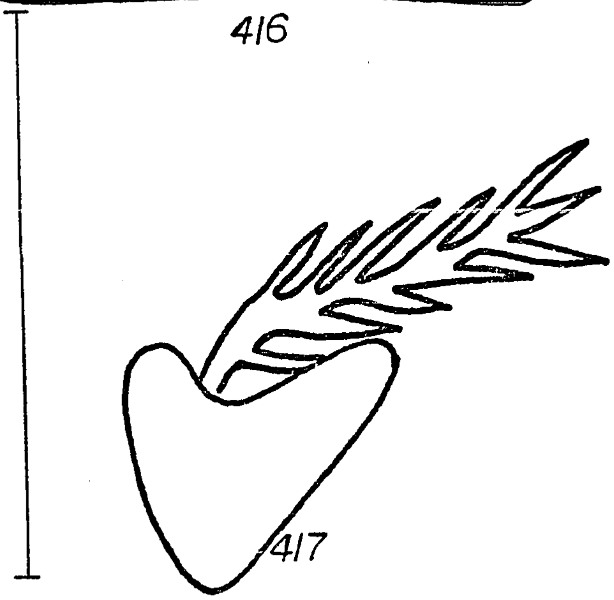
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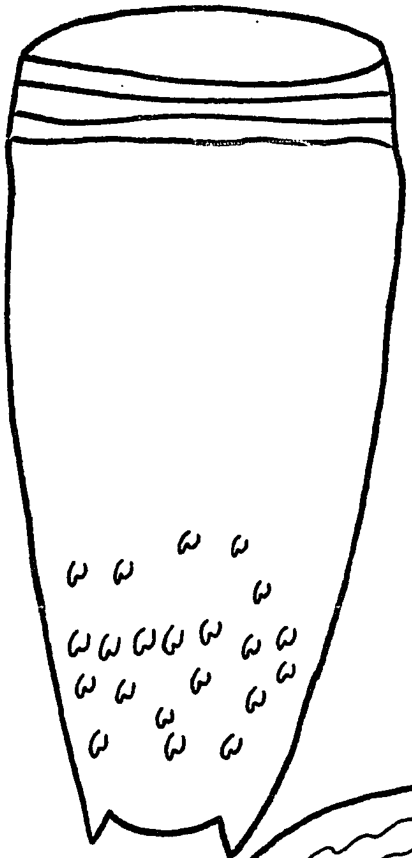

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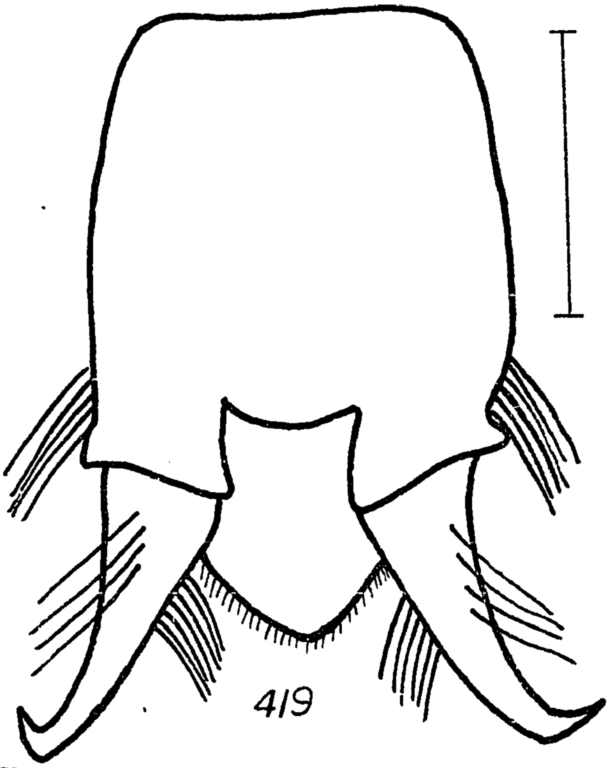

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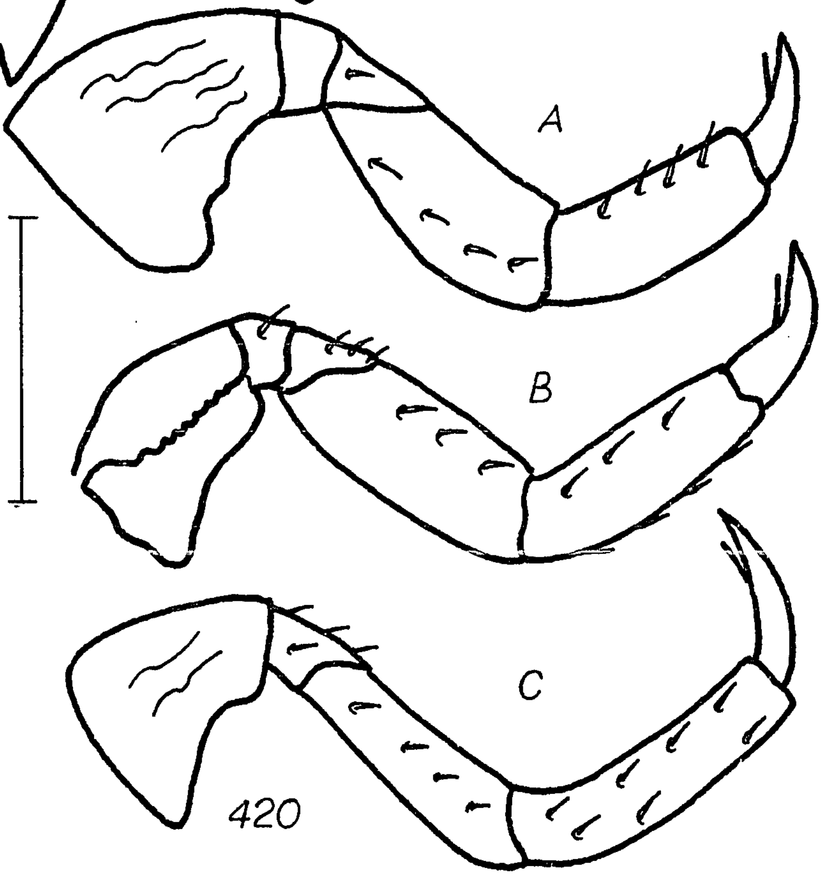


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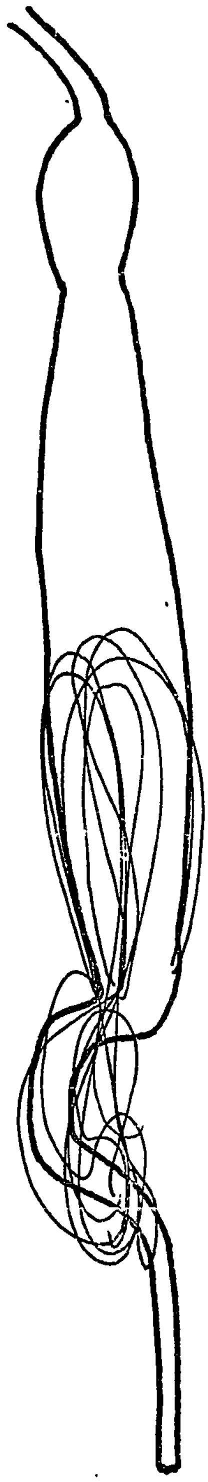

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# DISCUSSION

This work brings out the need for taking into account total larval morphology in order to insure sound phylogentic reasoning. I have cited several investigations concerned only with external larval structures. Only Hinton's works of 1939 and 1940 reveal a concentrated effort to correlate external and internal morphology in order to establish true phylogenetic relationships between dryopoids.

My efforts were to expand present knowledge by delimiting some diagnostic characters of dryopoid beetle larvae. Since there are many features which might be subject to variations associated with age, I had to distinguish such characters from valid general characters. According to Davis and Heywood (1963), a good character is one which has a narrow range of expression and can be easily recognized. Characters used to group genera into a family are many. Using my findings, I shall attempt to correlate specific external and internal features which support or oppose the presently accepted taxonomic scheme.

One character which has not been used to establish phylogenetic relationships between dryopoids is the structure of the proventriculus. Work by Felt in 1906 and Swaine in 1918 led them to conclude that the proventriculus has taxonomic value (Judd, 1947). The diversity of structure displayed by the proventriculus of insects has led several authors to base keys for identification of genera on the characters of this organ.

Balfour-Browne (1935) concluded that the proventriculus in Dytiscidae exhibits a very interesting process of evolution. In an earlier paper he formulated a key using this structure to separate 22 genera and noticed that it compared equally with a key formed using tarsal claw morphology (Balfour-Browne, 1934).

## External Morphology

### PSEPHENIDAE

Psephenus, Psephenops, and Ectopria, as indicated in the descriptions, exhibit different features which clearly define them as separate genera, but a flattened, elliptical body form with the entire peripheral margin bordered by rows of long hairs suggests a specific morphological relationship between Psephenus and Psephenops. Concealment of the larva proper beneath an arched carapace formed by extensions of the pleurites is a common feature of all three genera. Features of Ectopria, such as an elliptical, flattened-ovate body with expanded pleura which are not joined together marginally as in Psephenus and Psephenops revealed one difference between Ectopria and the above.

The head, which is only visible in ventral view, bears three-segmented antennae in all three genera. In contrast to the slender nature of this structure on the head of Psephenus and Psephenops, it is thick and robust on the head of Ectopria. Segments one and two are long and short respectively on Psephenus and Psephenops, but both are robust on Ectopria.

There is a similarity between the ligulae of Psephenus and Psephenops which is not present in Ectopria. This structure is not broad, but much reduced and the labial outline is more rectangular in Ectopria (Fig. 14). Neither Psephenops nor Psephenus bears a distinct transverse row of setae along the ventral margin of the ligula.

Maxillae reveal the same degree of difference between Psephenus, Psephenops, and Ectopria as the above characters. Maxillary palps arise along the mid-lateral margin of the stipes in the former genera, but at the antero-lateral margin of the stipes in the latter genus.

Legs of Psephenus and Psephenops are similar in sculpture and proportions, tarsal claws are emarginate on inner antero-lateral margins, and each bears a blunt internal tarsal spine. This is in contrast to the absence of emargination and the presence of a long internal tarsal claw spine in Ectopria.

## Internal Morphology

Serial sections revealed differences within the foreguts of the above genera. Some of the differences apparently are generic. I feel that the spinous organelles which line the posterior of the proventriculus in Psephenus (Fig. 11) are probably also present in Psephenops, but they are smaller or were not revealed by the histological preparations. Contrasting Ectopria with Psephenus and Psephenops, the proventricular teeth are blunt and bear peripheral spines or nodules. Such features are not evident on the proventricular teeth of Psephenus or Psephenops.

As noted by the figures (9 and 22) there is a contrasting difference in the size of the metathoracic ganglia and in Ectopria there are eight distinct abdominal ganglia which are not closely associated or fused posteriorly as in Psephenus or Psephenops. This is in direct conflict with the opinion of Hinton (1939) that an elliptical flattened body is correlated with fusion of the abdominal ganglia.

## Comments

It is obvious that Ectopria bears a few features which are shared by Psephenus and Psephenops but there are many which are not. If one places emphasis on a single stage of development in an attempt to establish natural relationships (Hinton, 1939 states that no natural system of classification can be established from a consideration of a single stage of development) one might be inclined to separate Ectopria and Psephenus into separate families.

Leech and Chandler (1963) are of the above opinion. Arnett (1968) places Ectopria in a separate family, the Dascillidae, based on adult morphology. Leng (1933) recognized the different and similar features of these two genera and placed them in separate subfamilies, Psepheninae and Eubriinae. Crowson (1967), who notes a need for a revision of the family Psephenidae, states that Psephenus, Eubria, and its allies belong in Psephenidae according to both adult and larval characters.

## External Morphology

### LIMNICHIDAE

Limnichid larvae are different from psephenid larvae in not having the flattened, elliptical body form. They are parallel-sided, cylindrical, and the ninth abdominal sclerite bears a rounded apex. The general body outline is similar to that of the Elmidae. The above features are illustrated by both species of Lutrochus, but several described features distinguish between them.

The most obvious difference is the arrangement of the frontal suture (Figs. 39, 58). There are four apical mandibular teeth in L. "B", but five in L. luteus; the outer lateral margin of the mandible bears spinous setae in L. luteus, but branching ones in L. "B"; fusion of stipes and postmentum occurs in L. "B", but not in L. luteus, and the anterior margin of the ligula is emarginate in L. "B", but not in L. luteus.

Legs are robust in both species. The proportions of ornamentation of each pair of legs are similar.

A family trait for limnichids postulated by Hinton (1939) is fusion of the stipes and postmentum, but such is not obvious in L. luteus. His description of larval Lutrochus sp. in the same paper illustrates some of the features of L. "B". I have not seen Hinton's specimens, but based upon his description I conclude that they are different species.

## Internal Morphology

There are obvious differences between foreguts of these species. In L. luteus, the peripheral and basal proventricular armature consists of large cylindrical structures (cells) with serrated margins. In Lutrochus "B" the proventricular armature consists of small cells (?) which are in the form of primary folds. The fusion of them results in forming secondary folds. From the apices of the folds arise hair-like spines.

Modifications of tubular tracheal vessels are also evident in both species. The dilations do not represent air sacs as observed in Larini and some Elmini. As defined by Snodgrass (1935), "An air sac is any conspicuous enlargement in the course of a tracheal vessel."

The number of malpighian tubules (6) does not vary in the two species, but it was noted that their distal ends did not always fuse with the wall of the hindgut as postulated by Hinton (1939).

## Comments

The work with Lutrochus has pointed out the errors in the list of family traits for limnichids set forth by Hinton (1939) (fusion of the stipes and postmentum in limnichid larvae, no air sacs, and fusion of the distal ends of the malpighian tubules to the hindgut). The errors I have pointed out have obviously become clear to him. This would explain the intention of R. A. Crowson and Hinton to create a new family (Lutrochidae), separating it from the family Limnichidae on the basis of adult as well as larval characters.

Sanderson (1953) suggests that limnichids are close to elmids in retaining three-branched anal gills, but they are toward the dryopid line. Comparing the morphology of Lutrochus to the elmids which I have considered, I have reached the conclusion that the limnichids are close to the elmids, but just how near they are to the dryopid line I do not care to speculate at this time. It is apparent that the degree of closeness between Limnichidae and Dryopidae should be investigated further.

ELMIDAE

Good characters of taxonomic merit for diagnosing elmid larvae have been confined to a consideration of the shape, sculpture, and morphology of the head, thoracic sclerites, abdominal sclerites, and ninth abdominal segment. Some of the workers who have made contributions have been cited in this paper.

## External Morphology

In my attempt to expand the above list, I have looked for external features which might show some correlation and thus suggest some evolutionary trends. Following Davis and Heywood's (1963) definition of a good character, I decided on the following: number of abdominal pleurites, the presence or absence of a poststernum and the number of thoracic pleurites.

## Comments

Data from the descriptions for each genus studied have allowed me to speculate that the ancestral form of all elmids probably contained membranous thoracic pleura and sterna and eight abdominal pleurites. From the ancestral form arose two main lines, one with partial sclerotization of the thoracic pleura and sterna (this line arose first) and later a line with total sclerotization of the thoracic pleura and sternites. Genera with partial sclerotization of the pleura and sterna never developed poststerna and the most unspecialized genera contain few thoracic pleura.

Consideration of the genera studied in respect to these characters divides them into two main groups. Genera not conforming to the pattern may be considered to be independent lines of evolution.

*Lara* would be the most unspecialized genus (8 abdominal pleurites) with a 2-1-1 thoracic pleurite pattern. *Dubiraphia* (8 abdominal pleurites) and *Austrolimnius* (7 abdominal pleurites) could follow with a 2-2-2 thoracic pleurite sequence, *Austrolimnius* being slightly more specialized than *Dubiraphia* as is evident by the loss of one abdominal pleurite. *Xenelmis* could represent an independent line with 6 abdominal pleurites and a 2-3-3 thoracic pleurite sequence. On the main line could be *Promoresia* (7 abdominal pleurites) and *Optioservus* (7 abdominal pleurites) with a 3-1-1 thoracic pleurite sequence, followed by *Zaitzevia* (7 abdominal pleurites), *Oulimnius* (7 abdominal pleurites), *Macronychus* (6 abdominal pleurites), *Potamophilops* (6 abdominal pleurites), and *Hexanchorus* (6 abdominal pleurites) with a 3-2-2 thoracic pleurite sequence. The last three genera are more specialized than *Zaitzevia* and *Oulimnius*.

From the second line; (and based on the general outline of the ventral thorax *Macronychus* could be closer to it than I speculate) arose *Stenelmis* (7 abdominal pleurites) and *Ancyronyx* (7 abdominal pleurites) with a 0 (no division of the prothoracic pleurite) -2-2 thoracic pleurite sequence. Unlike the first major line, each member of this line developed a poststernum. Following could be *Tolriolus* (7 abdominal pleurites), *Neocylloepus* (7 abdominal pleurites), *Elsianus* (7 abdominal pleurites), *Neoelmis* (7 abdominal pleurites), and *Phanocerus* (8 abdominal pleurites) with a 2-2-2 thoracic pleurite sequence. I suspect that *Phanocerus* represents an independent line of evolution. Finally there could follow *Microcylloepus* (7 abdominal pleurites) and *Heterelmis* (7 abdominal pleurites) with a 2-3-3 thoracic pattern sequence.

## Internal Morphology

Two internal components appear to fit the criteria set forth by Davis and Heywood. They are the presence or absence of air sacs and the histological morphology of the proventriculus.

## Comments

It is my opinion that air sacs in a larva represent an unspecialized condition. They are found in larvae which are not far from the ancestral form or those bearing several unspecialized features. This might explain their presence in larvae both with and without a poststernum. They are present in all larvae studied possessing eight abdominal pleurites except _Dubiraphia_. _Dubiraphia_ could belong on the ancestral line which gave rise to non-air sac bearing forms which do not contain a poststernum.

Using the histological morphology of the proventriculus as a criterion. The genera can be placed into five groups, as follows:

1. (a) _Stenelmis_
   (b) _Dubiraphia_
   (c) _Microcylloepus_
   (d) _Neoelmis_
   (e) _Elsianus_
   (f) _Heterelmis_
   (g) _Optioservus_
   (h) _Ancyronyx_
   (i) _Zaitzevia_
   (j) _Promoresia_
   (k) _Hexanchorus_
   (l) _Tolriolus_
   (m) _Neocylloepus_
   (n) _Oulimnius_
   (o) _Potamophilops_
2. (a) _Lara_

3. (a) Phanocerus

4. (a) Austrolimnius

5. (a) Xenelmis

The histology of the proventriculus of each genus in group one (1) illustrates several features in common as outlined in the descriptions. The histological morphology of the proventriculus of each member of groups 2, 3, 4, and 5 is specific for the genus (as evident from the descriptions). The results here could support the idea of independent evolution for these groups.

There is a correlation between the external morphology of Lara, Phanocerus, Austrolimnius and Xenelmis and the structure of the proventriculus of each genus. Each genus seems to bear external features which set it aside from the members in group (1) and the same applies in the case of the proventriculus. None of the genera in groups 2, 3, 4, or 5 illustrate proventricular features which suggest that they are closely realted. Dubirapha has a proventriculus similar to the members in group (1), but it is the only member of that group with eight abdominal pleurites. This might suggest that it is primitive but is not far from the line(s) which gave rise to most of the present elmids.

## Relationships

In respect to the above features, I feel that the limnichids arose at a point during the evolution of one or several of the present elmid lines. They could have arisen from a branch which maintained membranous thoracic pleura and undergone a reduction in the number of abdominal pleurites. This correlates with the morphlogy of the proventriculus in that this organ in L. luteus is similar to that in elmids (group 1). The proventriculus in L. "B" is not identical to that in L. luteus, but it falls within the same realm. I cannot logically suggest a point where psephenids probably arose, but I know that the proventriculus in Psephenus texanus bears characteristics similar to that in elmids (group 1).

The point of view proposed is not in conflict with Sanderson (1954), who considers Elmidae more primitive than Limnichidae. He does not mention elmid-psephenid relationships, but I feel a closer relationship exists between the families than can be determined from their external morphology alone.

Correlation of internal morphology with habit.

The results did not reveal any striking features which could support a suggestion or a conclusion concerning the relationship between the internal morphology and known habits. Only in Psephenus and Xenelmis did I find a large variety of organisms which might suggest a euryphagic tendency on the part of the larvae. In general aspects, the gut morphology within these two genera bears similar characteristics. No correlation could be determined between the xylophagous tendency and the structure of the proventriculus.

## SUMMARY AND CONCLUSIONS

1. External and internal morphology of larvae is described for representatives of 24 genera of dryopoid beetles as follows:

   Psephenidae--Eubriinae--Ectopria

   Limnichidae--Limnichinae--Lutrochus (2 species)

   Elmidae--Larini--Hexanchorus, Lara, Phanocerus, Potamophilops

   Elmini--Ancyronyx, Austrolimnius, Dubiraphia, Elsianus, Heterelmis, Macronychus, Microcylloepus, Neocylloepus, Neoelmis, Optioservus, Oulimnius, Promoresia, Stenelmis, Tolriolus, Xenelmis, Zaitzevia

2. On the basis of this investigation it is clear that the psephenids Psephenus and Psephenops are much more closely related to each other than to Ectopria.

3. The limnichid larvae studied are more similar to the elmids than to the psephenids, and could be derived from primitive elmid stock.

4. Among the elmid genera studied, no patterns of relationship are suggested by some of the systems, since all genera are essentially alike, but other systems appear to offer promise. Of the internal organs, the proventricular region of the gut and the major tracheal vessels of the respiratory system (with respect to air sacs) provide means of grouping genera in a significant manner. Of external

features, the number and nature of pleurites can provide a rationale for phylogenetic speculation.

5. Upon the morphological evidence here described, I suggest that some of the elmids such as Lara could be the least specialized of all dryopoid larvae studied, that the limnichids studied are more specialized than such elmids, and that the elmid-psephenid relationship is still a question despite the similarity between the proventriculi of these two groups.
6. This work points up the need for more detailed study of the complete dryopoid larva--internally as well as externally--before an adequate phylogenetic picture can be drawn.
7. I suggest additional research on the problem of dryopoid evolutionary relationships which should include a consideration of development prior to the larval stage, a comparative study of larval enzymes, an application of numerical taxonomic methods to larval characters, and the use of such biosystematic methods as karyotyping.

# LITERATURE CITED


Arnett, R. H. 1968. The beetles of the United States. The Amer. Ent. Institute, Ann Arbor, Michigan

Balfour-Browne, F. 1934. The proventriculus in the Dytiscidae (Col.) as a taxonomic character. Stylops 3:241-244.

______. 1935. The proventriculus in Dytiscidae (Col.) as a taxonomic character. Stylops 4:191.

Beier, M. 1927. Vergleichende Untersuchungen über der Centralnervensystem der coleopteren Larven. Zeitschr f. wissenschaft. Zool. 130:174-250.

Berthélemy, C. et M. Ductor. 1965. Taxonomie larvaire et cycle biologique de six espèces d'Esolus et d'Oulimnius européen. Annales de Limmologie t. 1. fasc. 2:257-276.

Bertrand, H. 1955. Notes sur les premiers états des dryopides d'Amérique (Col.). Ann. Soc. Ent. France 124:7-139.

______. 1965. Notes sur les premiers états des dryopides d'Amérique (Col.). Bull. Soc. Ent. France 70:163-166.

Blackwelder, R. E. 1944. Checklist of the Coleopterous Insects of Mexico, Central America, the West Indies, and South America. part 2. United States Nat. Mus. Bull. 185:189-341.

Böving, A. G. and F. C. Craighead. 1930-31. An illustrated synopsis of the principal larval forms of the order Coleoptera. Ent. Amer. 11:1-351.

Brown, H. P. 1970 (a). Neocylloepus, a new genus from Texas and Central America (Coleoptera: Dryopoidea: Elmidae). Coleopt. Bull. 24(1): 1-28.

________. 1970 (b). A new species of Psephenus from Arizona (Coleoptera, Psephenidae). Coleopt. Bull. 24:34-38.

________. 1971 (a). A new species of Elsianus from Texas and Mexico, with records of other species in the United States (Coleoptera: Dryopoidea: Elmidae). Coleopt. Bull 25(2): 55-58.

________. 1971 (b). Neotropical dryopoids III. New records of Xenelmis, with a description of the larva (Coleoptera: Elmidae). Coleopt. Bull. 25(3): 95-101.

________. (In press). Biota of freshwater ecosystems. Identification manual No. ____. Aquatic dryopoid beetles of the United States. Environmental Protection Agency. Water Pollution Control Research Report, 18050 ELD.

Brown, H. P. and Chad Murvosh. 1970. Lutrochus arizonicus, new species, with notes on ecology and behavior (Coleoptera: Dryopoidae: Limnichidae). Ann. Ent. Soc. Amer. 63(4): 1030-1035.

Brullé, G. A. 1842. Insects de l'Amérique meridionale recueills par Alcide d'Orbigny. In Voyage dans l'Amérique Meridionale par Alcide d'Orbigny 2(2):57-88.

Champion, G. C. 1913. Notes on various Central American Coleoptera with descriptions of new genera and species. Trans. Ent. Soc. Lond. 58-169.

Crowson, R. A. 1967. The Natural Classification of the Families of Coleoptera. E. W. Classey Ltd., Middlesex, England.

Darlington, P. J. 1929. On the dryopid beetle genus Lara. Psyche 36:328-331.

_____. 1936. A list of the West Indian Dryopidae (Col.) with a new genus and eight new species including one from Colombia. Psyche. 43: 66-83.

Davis, P. H. and V. H. Heywood. 1963. Principles of Angiosperm Taxonomy. Oliver and Boyd, Edinburgh, Scotland.

Galigher, A. E. and E. N. Kozloff. 1964. Essentials of Practical Microtechnique. Lea and Febiger, Philadelphia, Pennsylvania.

Hinton, H. E. 1939. On an inquiry into the classification of the Dryopoidea. Trans. R. Ent. Soc. Lond. 89(7):133-184.

_____. 1940. A monographic revision of the Mexican water beetles of the family Elmidae. Nov. Zool. 42(2): 217-396.

_____. 1955. On the respiratory adaptations, biology, and taxonomy of the Psephenidae, with notes on some related families (Col.). Proc. Zool. Soc. Lond. 125 (3/4): 543-565.

_____. 1965. A revision of the Australian species of Austrolimnius (Coleoptera: Elmidae). Australian Jour. Zool. 13(1): 97-172.

_____. 1971. Some American Austrolimnius (Coleoptera: Elmidae). Jour. of Entomol. (B) 40(2): 93-99.

Judd, W. W. 1947. A comparative study of the proventriculus of orthopteroid insects with reference to its use in taxonomy. Can. Jour. of Res. 26(D): 93-161.

Leng, C. W. 1920. Catalogue of the Coleoptera of America, north of Mexico. The Cosmos Press. Cambridge, Massachusetts.

Leng, C. W. and A. J. Mutchler. 1933. Second and third supplements

1925-1932 (Inclusive) to Catalogue of Coleoptera of America, north of Mexico. The Cosmos Press. Cambridge, Massachusetts.

Leech, H. B. and H. P. Chandler. 1963. Aquatic Coleoptera, chapter 13, pp. 293-371. In R. L. Usinger, Aquatic Insects of California. University of California Press, Berkeley.

Leech, H. B. and M. W. Sanderson. 1959 Coleoptera. Chapter 38, pages 981-1023. In W. T. Edmondson, Fresh-water Biology, 2nd ed. John Wiley and Sons, Inc. New York.

Murvosh, C. M. 1960. An ecological study of the riffle beetle, Psephenus herricki (Dekay) (Coleoptera: Psephenidae) Ph.D. dissertation The Ohio State University, Columbus, Ohio.

Patrick, R. 1959. Bacillariophyceae. Chapter 7 pages 171-189. In W. T. Edmondson, Fresh-water Biology, 2nd ed. John Wiley and Sons, Inc. New York.

Patton, R. L. 1953. Insect Physiology. John Wiley and Sons, Inc., New York, New York.

Prescott, G. W. 1954. How to Know the Freshwater Algae. Wm. C. Brown Co. Dubuque, Iowa.

Sanderson, M. W. 1938. A monographic revision of the North American species of Stenelmis. Uni. Kan. Sci. Bull. 25: 635-717.

______. 1953. A revision of the Nearctic genera of Elmidae (Col.). J. Kan Ent. Soc. 26(4): 148-163.

______. 1954. A revision of the Nearctic genera of Elmidae (Col.). J. Kan. Ent. Soc. 27(1): 1-11.

Smith, G. M. 1950. The Freshwater Algae of the United States. McGraw-Hill Inc., New York, New York.

Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Inc., New York, New York.

Susskind, M. E. C. 1936. A morphological study of the respiratory system in various larval instars of Stenelmis sulcatus (Blatchley) (Dryopidae: Coleoptera). Pap. Mich. Acad. Sci., Arts, and Letters 21: 679-714.

Thompson, R. H. 1959. Algae. Chapter 6, pages 115-170. In W. T. Edmondson, Freshwater Biology, 2nd ed. John Wiley and Sons, Inc. New York 1248 pages.

Weber, C. I. 1966. A Guide to the Common Diatoms of Water Pollution Surveillance System Stations. United States Depart. of Interior. Federal Water Pollution Control Administration, Washington, D.C.

West, L. S. 1929. A preliminary study of larval structure in the Dryopidae. Ann. Ent. Soc. of Amer. 22: 691-727.

Woodring, J. P. and E. F. Cook. 1962. Internal anatomy of Ceratozetes cisalpinus. Ann. Ent. Soc. Amer. 55: 164-181.