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Contribution to the anatomy and evolution of the family Pteronarcidae (Plecoptera).

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CONTRIBUTION TO THE ANATOMY AND EVOLUTION
OF THE FAMILY PTERONARCIDAE (PLECOPTERA)

A Dissertation Presented

By

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CONTRIBUTION TO THE ANATOMY AND PHYLOGENY OF THE FAMILY PTERONARCIDAE (PLECOPTERA)

A Dissertation Presented

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INTRODUCTION

The family Pteronarcidae, consisting of two genera and thirteen species, is one of the smallest groups within the rheophilic order Plecoptera. Yet since this family exhibits many primitive characteristics and is the most plesiomorphic extant group within the suborder Setipalpia, it is important that knowledge of the external anatomy be available as a basis for further work on more recently derived stonefly families.

This present work is an extension of an earlier one (Nelson and Hanson, 1968) which was confined to an examination of the external anatomy of two pteronarcid species, _Pteronarcys_ (_Allonarcys_) _proteus_ Newman and _Pteronarcys_ (_Allonarcys_) _biloba_ Newman. The senior author of that earlier work, now enamored with these insects, decided that since systematic and phylogenetic investigation is based largely on comparative anatomical studies, the external anatomy of all remaining obtainable species in the Pteronarcidae should be considered.

This study consists of two parts. The first part is concerned with descriptions and comparisons of exoskeletal parts of the Pteronarcidae. The second part, utilizing the information gained from the first part as well as that from earlier works, deals with the phylogenetic history and classification of this family.

MUSEUM ABBREVIATIONS

In this study it was found necessary to employ the following abbreviations to designate the collections in which the material utilized in this work is located: American Museum of Natural History (AMNH), Cornell University (CU), John F. Hanson Collection (JFH), Naturhistorisches Museum of Vienna, Austria (NHMV), Charles H. Nelson collection (CHN), and the United States National Museum (USNM).

COMPARATIVE EXTERNAL ANATOMY OF THE FAMILY PTERONARCIDAE

Since Nelson and Hanson (1968) have described and figured in detail the anatomy of the external body parts of two species of the genus *Pteronarcys* and since *Pteronarcella* anatomically is quite similar to *Pteronarcys*, this section is largely restricted to pointing out the structural differences between these two genera. Therefore, a detailed written description of the anatomy of the external parts of the head, thorax and pregenital abdominal segments is omitted. However, the external anatomy of *Pteronarcella* is figured in detail so that the differences as well as similarities of this genus with *Pteronarcys* might be more easily seen. Because genitalic structures have played an important role in phylogeny and classification of most stonefly families, the male and female terminalia of the members of *Pteronarcella* are described as well as figured in detail.

GENERAL APPEARANCE

The two species comprising the genus *Pteronarcella*, *P. regularis* (Hagen) and *P. badia* (Hagen), are the smallest members of the Pteronarcidae. Specimens of both species preserved in ethanol (70%) varied in length from 12 to 18 mm. in the male and from 13 to 20 mm. in the female. Specimens of *Pteronarcys* preserved in the above manner varied in length from 23 to 30 mm. in the male and from 28 to 38 mm. in the female. Although both sexes of *regularis* and *badia* are usually fully winged, a few brachypterous specimens of *badia* were found.

HEAD

Figures 1 to 13

The head capsule and mouthparts of *Pteronarcella* are very similar to those described for *Pteronarcys* (Nelson and Hanson, 1968). However, the flagellum of each antenna of *Pteronarcella* has fewer segments than does that of *Pteronarcys*. In *Pteronarcella* the segments vary from 33 to 43 in number, while in *Pteronarcys* they vary from 55 to 66.

THORAX

Figures 14 to 16

THORACIC TERGA (Fig. 14). The thoracic terga of *Pteronarcella* differ in some details from those of *Pteronarcys*. The lateral margins of the pronotum (pn) are deflected ventrally so as to encroach slightly on the pleural area. The mesothoracic scutum (sct) is crossed by a single, inverted U-shaped transscutal suture (ts) whose posterior lateral extremities extend toward, but do not reach, the posterior notal wing processes. On each side of the metascutum a small oblique suture (ts) is situated close to the mesal posterior margin of the upraised shoulder-like area.

The mesally situated pits (pp) of the meso- and metapostscutellum do not give rise to any noticeable internal apodemes. Each metathoracic posterior notal wing process (pnp) is not detached from the notum, as it is in Pteronarcys (Adams, 1958; Nelson and Hanson, 1968).

THORACIC PLEURA (Fig. 15). The thoracic pleura are similar to those of Pteronarcys. However, the pleural region of each thoracic segment does bear an additional pair of gills not present on Pteronarcys. Thus, there are fourteen pairs of gills situated on the thorax of Pteronarcella, as compared to only eleven pairs found on the thorax of Pteronarcys. The additional propleural gills are situated on each propleuron between the catapleurite (cpl) and the basicoxite. Each gill of the mesopleural pair is situated below the postalar bridge (poa) and just above the meron of the mesocoxa. The third pair of gills is located on the metapleuron in approximately the same relative position as the mesothoracic pair.

THORACIC STERNA (Figs. 16-19). The thoracic sterna of Pteronarcella is like that of Pteronarcys. Nelson and Hanson excluded from their study on Pteronarcys any examination of the internal lateral furcal arms. Newport (1851) in his study of Pteronarcys dorsata (Say) discussed and figured these endoskeletal structures, although not in any great detail. In Pteronarcella these furcal arms are present and are nearly identical to those of Pteronarcys. Each narrow, elongate, arcuate furcal arm (Fig. 17) of the profurcasternum extends dorsolaterally from its base at the furcal pit toward the pleural wall. The wider, straighter furcal arms of the mesofurcasterna (Fig. 18) are similar to those of the metafurcasterna (Fig. 19).

WINGS (Figs. 23-26). The sclerites of the meso- and metathoracic wing bases of *Pteronarcella* are similar to those of *Pteronarcys*. A small, somewhat transversely elongate sclerite (Fig. 14,d), not mentioned by Nelson and Hanson, is situated mesad of the tegula (tg) in the wing bases of the pterothorax. This sclerite, or *myodiscus* (Crampton, 1918), appears to be a consistent feature within the Plecoptera. Although brachyptery (Figs. 25, 26) occurs among some of the males of *P. badia*, the sclerites associated with the wing bases of these individuals do not undergo any modifications.

The wing venation of *Pteronarcella* is basically similar to that of the *Pteronarcys*. However, it differs in that the forewing mesad to the branching of MA does not possess any crossveins between MA and R as well as between MA and RS. Also on the forewing there are fewer crossveins found between 2Va and 3Va. In the hindwing of *Pteronarcella* the number of longitudinal branches of 2Va and 3Va is reduced when compared to that of *Pteronarcys*.

LEGS (Figs. 20-22). The legs of *Pteronarcella* resemble those of *Pteronarcys*. In *Pteronarcys* the number of setae present in each of the two clusters on the arolium (ar) varies from two to twenty-seven. However, in *Pteronarcella* the number varies from none to seven.

ABDOMEN

PREGENITAL ABDOMINAL SEGMENTS (Figs. 16, 27, 35). The pregenital abdominal segments of Pteronarcella, as in Pteronarcys (Nelson and Hanson, 1968), consists of the first eight abdominal segments in the male and the first seven in the female. However, in Pteronarcella the first three abdominal segments each possess a pair of gills (Fig. 16), whereas, in Pteronarcys only the first two abdominal segments have gills. A further difference between the two genera is that in Pteronarcella the hind dorsolateral margins of abdominal tergites 2 through 8 of the male sex are upraised into rounded protuberances (Figs. 27, 35). The protuberances of each tergite are slightly larger than those of the immediately preceding tergite. These upraised tergal areas are not present in Pteronarcys.

TERMINALIA. This section is divided into two parts. The first part deals with the comparative external anatomy of the terminalia of the species within each of the two genera, Pteronarcella and Pteronarcys. The second part of this section is concerned with the comparison of the external anatomy of the terminalia between the genera.

COMPARATIVE EXTERNAL ANATOMY OF THE TERMINALIA OF THE SPECIES OF THE PTERONARCIDAE. It has not been necessary in this study, for reasons previously stated, to include figures of most of the anatomy of *Pteronarcys proteus* and *P. biloba*. However, in this section it has been necessary to duplicate the figures of the terminalia of these species because of the much greater complexity and variety of these structures. Thus, the genitalia of all the available species of both *Pteronarcella* and *Pteronarcys* are figured and described.

Male Terminalia of Pteronarcella regularis (Figs. 27-34). The male terminalia of *P. regularis* involve segments nine, ten, and eleven.

The tergum and the sternum of the ninth segment are involved in genitalic modifications. The posterior half of the ninth tergite is elevated to form a conspicuous broad anteriorly projecting bluntly pointed process (Figs. 27, 29). The dorsal surface of this elevated tergal process is covered with many peg-like setae. The ninth sternite is characterized by a posteriorly produced rounded subgenital plate (Figs. 28, 29) which extends under the tenth segment and covers the genital opening (go). In ventral view a small difficult to discern "plateau" (pl) is situated on the mesal longitudinal region of the ninth sternite.

The tenth tergum is involved in genitalic modification in that it is divided mid-dorsally by the supra-anal process into two hemitergites (Fig. 27). On each side a narrow mesal marginal piece (mhp) is detached, except at its anteriormost extremity, from the rest of the hemitergite. These marginal pieces from the anterior margin of the tenth segment extend posteriorly toward the lateral braces of the supra-anal process. The tenth sternite is not developed and is so greatly narrowed ventrally that it almost disappears.

The supra-anal process and its surrounding cowl, remnants of the dorsum of the eleventh abdominal segment, are present. Smith (1917) cursorily examined the supra-anal process of the closely related species Pteronarcella badia. Needham and Claassen (1925) figured but did not describe the supra-anal process of both P. badia and P. regularis. Unfortunately, the two preceding studies as well as subsequent works did not utilize this taxonomically significant structure. This neglect was probably due to the much more easy accessibility of the highly diagnostic tergal process. However, as in most stoneflies, the supra-anal process of Pteronarcella is useful in species discrimination. In regularis the mesally situated supra-anal process, which from its basal end just in front of the anterior margin of the tenth segment, extends posteriorly between the tenth hemitergites as well as between the subanal lobes (Fig. 27). The process consists of two major regions: the inner part and the free part (Smith, 1917). The very short narrow inner part (Fig. 30,ip) is normally situated between the tenth hemitergites. Its basal end is bluntly pointed and most of its mid-dorsal longitudinal distance is traversed by a broad shallow groove. The inner part serves as an area of muscle attachment and is held to the body by membrane which attaches to its dorsolateral surfaces. At its apex two broad plates, the lateral braces (lb) (Smith, 1917), arise one on each side. Muscles which attach to the apices of these plates may assist the movement of the supra-anal process in a dorsoventral plane. The remaining portion of the supra-anal process, the free part, can be divided into two regions: a ventral section and a dorsal section. The elongate ventral section (vs) when viewed laterally is hook-shaped in appearance (Fig. 32). This structure forks (posterior view, Fig. 31) into two diverging lateral extensions which at their dorsal extremities are connected to each other by a transverse sclerotic bridge. This ventral section is held to the body by membrane from the cowl which attaches to its lateral and posteroapical surfaces. The structurally complex dorsal section can be divided into a smooth basal piece (bds) and a corrugated apical piece (ads). The weakly sclerotized sac-like basal piece is attached posteriorly to the lateral extensions and transverse sclerite of the ventral piece (Fig. 32). When viewed dorsally, this piece is seen to terminate apically in two rounded lobes (Fig. 30). Postero-dorsally the basal piece of the free part of the supra-anal process is connected to the apical piece by a narrow border of very flexible integument. The apical piece is a complex triple-walled (Fig. 41A) sleeve-like structure split along its length like the cuff of a shirt sleeve (Fig. 30). The outer wall of the piece is covered on its lateral and posterior surfaces with elongated transverse grooves (Figs. 30, 31), which basolaterally becomes quite irregular in pattern. The middle wall consists of both a small sclerite and attached membrane. The membrane of this wall attaches the small sclerite to the margins of the outer wall already described as well as to the dorsomesal surface of the basal piece (Fig. 33). The concave surface of the sclerite of the middle layer is loosely covered with a colorless membranous layer (Fig. 41A,mem) which constitutes the third wall of this apical piece. The structural design of both the apical and basal pieces of the dorsal section possibly allows for their expansion upon being filled by body fluids entering through the posterior opening of the basal region. Probably the supra-anal process of regularis is in some manner involved with the mating of this species. However, the exact function of this complex structure is not yet known.

The partly sclerotized and partly membranous cowl (co) surrounds the posterior and lateral sides of the free part of the supra-anal process and lies between the subanal lobes. It is a single unit of integument which is folded double and designed to allow for movement of the supra-anal process. Its membranous infolded mesal surface is attached along the lateral and posteroapical surfaces of the ventral piece of the supra-anal process (Figs. 31, 32). Its outer surface consists chiefly of a narrow basal sclerotic plate (the paragenital plates of Smith [1917]) which when viewed dorsally is a horseshoe shaped sclerite whose anterior lateral ends terminate close to the lateral braces (Fig. 32,pgp). Membrane from the eleventh segment attaching along the entire ventral margin of the basal plate secures the cowl to the body.

The remainder of the eleventh segment is divided into two hook-like subanal lobes (Fig. 29,sbl) or paraprocts. The cerci (ce) are located on the lateral basal extremities of the lobes. Each cercus is composed of 14 to 24 segments. The segments are successively narrower as well as greater in length toward the apex of each cercus. The apical two to three segments are slightly smaller than those immediately preceding.

Female Terminalia of *Pteronarcella regularis* (Fig. 34). The female terminalia of *P. regularis* involves segments eight, nine, ten and eleven.

The anterior lateral margins of the eighth abdominal tergites are provided with a pair of spiracles, as are found on the seven pregenital abdominal segments (Fig. 34). External genitalic modifications occur only on the sternum of the eighth segment. Two short bluntly pointed vaginal projections (vp) arise from the median posterior emargination of the sternum. The projections extend posteriorly beyond the genital opening but do not extend out of the notched area. The mid-sternal region, including each vaginal projection is demarked from the rest of the sternal area by its dark brown coloration.

The ninth tergite is unmodified, but the ninth sternite is a large somewhat shield-like "postgenital" plate. The posterior margin of this sternal plate is covered with many short thick anteriorly pointing setae. This narrow portion, bearing the setae has become membranous and is capable of being infolded dorsally so that it is not visible on the ventral surface.

The tenth segment is nearly as long as the ninth dorsally, but narrows considerably ventrally.

The eleventh segment has undergone some genitalic modifications. The triangularly shaped epiproct (epi) extends posteriorly from under the hind margin of the tenth tergite over the anal opening. The two subtriangular subanal lobes (sbl) or paraprocts are not as large as those of the male. The cerci arise laterad of the lobes and are composed of the same number of segments as in the male.

Specimens of P. regularis Examined. CALIFORNIA, 24 males, 8 females (Shasta Springs, Siskiyou County) (USNM); OREGON, 1 female (Corvallis) (CU), 2 males, 1 female (Nehalem River at Red Bluff Road around 4 miles northeast of Elsie) (USNM), 3 males, 3 females (tributary of Marys River around 5 miles southwest of Philomath) (USNM), 1 male, 1 female (Scio) (CHN); WASHINGTON, 1 male, 1 female (Olympia) (CU).

Male Terminalia of Pteronarcella badia (Figs. 35-41b). The male terminalia of badia although similar to those of regularis do differ in some details. In badia the ninth tergal process is more elevated and its anterior margin is more broadly rounded (Figs. 35, 36). The apical piece (ads) of the free part of the supra-anal process (Fig. 38) when viewed anteriorly is more laterally compressed. The corrugated pattern on the outer wall of the apical piece basolaterally is much less irregular (Fig. 40). The sclerite (sc) of the middle wall of the apical piece in *badia* is much larger than that found in *regularis* (Figs. 33, 41b). This sclerite in *badia* is nearly as large as the outer wall of the apical region.

Female Terminalia of Pteronarcella badia (Fig. 42). The female terminalia of *badia* except for modifications of the eighth abdominal sternite are basically similar to those of *regularis*. The vaginal projections (vp) of the posterior sternal margin are much less pronounced than those of *regularis* (Fig. 42).

Specimens of Pteronarcella badia Examined. ALASKA, 2 males, 12 females (Russian River, Kenai Peninsula) (CHN); COLORADO, 1 female (Boulder) (CU), 1 female (Garland) (CU), 1 male (Gillette) (CU), 1 female (Kenosha Pass) (CU), 2 males, 1 female (Manitou) (CU), 1 female (Platte Canon) (CU), 1 male (South Fork Rio Grand) (CU), 1 male, 1 female (Yampa River) (JFH); MONTANA, 1 female (Bridgewater Mts.) (CU), 1 male, 1 female (Bozeman) (CU), 1 female (Glacier National Park) (CU), 2 males, 2 females (Granite County) (CHN), 6 males, 2 females (Kalispell) (CU), 1 male (Ravelli County) (JFH); NEW MEXICO, 1 female (Holy Ghost Creek, Rero) (USNM), 58 males, 20 females (near Field Tract Campground, Pecos River) (USNM); OREGON, 1 male, 1 female (Austin Junction, Blue Mountain Ranger Station) (USNM), 1 male (Milton) (CU); UTAH, 1 male (Beaver Canyon) (USNM), 1 male, 3 females (Hana) (USNM), 8 males, 7 females (Logan) (CU), 3 females (Logan Canyon) (CU), 27 males, 17 females (Logan River) (CU), 1 female (Old Paper Mill, Salt Lake City) (CU), 1 female (Strawberry Valley) (USNM), 1 female (Uinta National Forest) (USNM); WYOMING, 1 female (Sinks County) (CU), 2 females (Yellowstone National Park) (CU); CANADA, 1 female (Waterton Lakes National Park, Alberta) (USNM), 1 male, 3 females (Revelstoke, Selkirk Mountains, British Columbia) (USNM).

Male Terminalia of Pteronarcys reticulata (Figs. 43-48). The male terminalia of reticulata consist of segments nine, ten and eleven (Figs. 43-45).

Both the tergum and the sternum of the ninth segment are involved with genitalic modifications. The ninth sternite is produced posteriorly into a rounded subgenital plate which extends beyond the genital opening (go) and below the tenth segment (Fig. 45). In ventral view (Fig. 44), the mesal longitudinal area of the sternum is elevated to form a thickened "plateau" (pl) or percussion surface (Ricker, 1952) which from its greatest width anteriorly narrows gradually posteriorly. Perhaps this well developed area, if struck repeatedly against the substratum produces specific vibrations which, as has been observed in other stonefly species (Brink, 1949; Rupprecht, 1968), attract the female for mating. A large light-colored region bordering the "plateau" can be found on each side of the sternum.

The evolutionally important tenth tergite is divided by the supra-anal process (sa) into two hemitergites (Fig. 43). Each hemitergite consists of three transverse hemitergal lobes, which, from their somewhat laterally situated bases on the segment, extend mesally so that their apical margins are closely adjacent to the supra-anal process. On each side the anterior (ahl) and median (mhl) hemitergal lobes are barely separated from each other. However, the median hemitergal lobes, covered on their posterior halves with short thick setae, are readily distinguishable from the anterior lobes. The narrow darkly sclerotized posterior hemitergal lobes (phl) are easily seen and are covered with light thin setae for most of their length.

The well sclerotized tenth sternite is unmodified and ventrally becomes narrowed.

The supra-anal process of the eleventh segment is a narrow elongate structure which from its basal extremity, situated just in front of the anterior margin of the tenth tergite, extends posteriorly between the hemitergites and between the subanal lobes as well as a short distance above them (Figs. 43, 44). The process consists of two principal regions: the inner part and the free part. The inner part (ip) possesses a mid-dorsal longitudinal shallow groove, serves as an area of muscle attachment and is anchored by membrane to the tenth segment (Figs. 46, 47). A well sclerotized lateral brace (lb) arises on each side of the apical end of the inner part. The remaining portion of supra-anal process, the longer free part, in lateral view is S-shaped in appearance. This portion is divided into the following regions: the ventral section (vs), the dorsal section (ds), and the spatula (su). Apically the deep groove of the ventral section is confluent with the sclerotic anterior surface of the tubular interior of the dorsal section. The narrow U-shaped sclerotic loop (u) of the dorsal section arises from the ventral section and supports the membranous part of the opening into the dorsal section (Fig. 48). The sclerotic anterior surface of the dorsal section resembles a long pipe slit along the length of its mid-posterior surface. Apically this sclerotic tube is modified into an anteriorly produced trough-like process (tp) on its exterior surface (Figs. 46, 47). The membranous posterior surface of the apical section attaches along both edges of the slit in the tube over its complete length, and is basally supported by the sclerotic U-shaped loop previously mentioned. Apparently, out of the opening at the loop, body fluids are forced through the dorsal section and into the spatula. The partly sclerotized, partly membranous, dorso-ventrally flattened, hollow spatula (Koponen and Brinck, 1949) arises basally from the extremity of the dorsal section and gradually curves ventrally (Fig. 47). From its greatest width at its base this lobe in posterior view tapers to a broad apex (Fig. 48). Its dorsal surface is almost entirely sclerotic and articulates with the dorsal margin of the trough-like process by two small finger-like extensions (Fig. 46). The remaining membranous area of the spatula is continuous with the membrane of the dorsal section. Since the spatula is hinged as described above it is probably lifted, as a result of turgidity when filled with body fluids, into an upright position so that it lies in the same plane as the dorsal section.

The cowl (co), lying between the subanal lobes, is closely associated with the supra-anal process. It is a single unit of integument folded double and composed of membrane and sclerite. Its outer surface consists largely of the broad sclerotic basal plate (paragenital plates of Smith [1917]) which surrounds the posterior and lateral sides of the free part (Figs. 46-48). Each of the anterior lateral extensions (Figs. 46, 47) of this plate is more darkly sclerotized than the remaining posterior portion. Membrane from the eleventh segment attaching along the entire ventral margin of the plate secures the cowl to the body. A broad membrane most of which is infolded to become the inner mesal membranous surface of the cowl attaches along the ventrolateral sides of the basal region of the supra-anal process as well as to the inverted U-shaped sclerite. Imbedded in this membranous surface, directly behind the apical region and directly above the inverted U-shaped sclerite of the basal region, are three separate elongate sclerites which together form an apically projecting three-pronged fork-like structure (Figs. 47, 48,fls). The medial piece of this structure is divided longitudinally by a mesal narrow light-colored line which may or may not be membranous.

The remainder of the eleventh segment is divided into two lightly sclerotized lobes (Figs. 43, 45,sbl) which in lateral view are somewhat boot-shaped in appearance. Each lobe is provided with a cercus situated at its basal lateral extremity.

Female Terminalia of Pteronarcys reticulata (Fig. 49). The female terminalia of reticulata involve segments eight, nine, ten and eleven.

The eighth segment possesses a pair of spiracles lying within the weakened anterior lateral margins of the tergite (Fig. 49). The eighth sternite is divided mesally by a narrow, elongate ridge connecting the anterior and posterior sternal margins. A narrow, slender vaginal projection (Fig. 49,vp) arises from the medial posterior border of each half of the sternite and extends posteriorly beneath the anterior portion of the ninth sternite.

The ninth tergite is not modified. However, the ninth sternite is modified into a large shield-like "postgenital" plate the posterior margin of which is covered with short, thick anteriorly pointing setae.

The tenth segment ventrally is considerably narrowed from its greatest width dorsally.

The somewhat triangular-shaped epiproct (epi) of the eleventh segment arises beneath the posterior margin of the tenth segment and extends back over the anal opening. The eleventh sternite is divided into two subtriangular subanal lobes (sbl) or paraprocts. The cerci arise laterally from the bases of these lobes.

Specimens of Pteronarcys reticulata Examined. USSR, 2 males, 2 females (Siberia) (NHMV).

Male Terminalia of Pteronarcys excavata (Figs. 50-55). The following discussion concerning the male terminalia of *excavata* is based on specimens collected in Manchuria. Unfortunately, the inadequacy of the available descriptions (Wu and Claassen, 1934; Wu, 1938) of this species and of *sachalina* Klapalek, both described only from the female sex, made it difficult to determine with surety the identity of these specimens. However, the females of these Manchurian specimens do appear to agree, especially regarding the eighth sternite, with Wu's (1934) description and figure of the female holotype of *excavata*. In addition, Zhiltzova (personal communication) compared a figure (Fig. 56) of the female terminalia of these Manchurian specimens to the female terminalia of *sachalina* in the Zoological Institute in Leningrad and was inclined to assign these Manchurian specimens to excavata. Thus, the specimens used in this study will be regarded as members of excavata until the question of identity can be definitely settled.

The terminalia of excavata (Figs. 50-52) closely resemble those of reticulata, differing only in a few details. In excavata the hind margins of the median hemitergal lobes (mhl) are not straight as are those of reticulata, but are posteriorly arcuate (Fig. 52). The spatula (su) of the supra-anal process is greatly reduced in length when compared to that of reticulata (Figs. 54, 55). The medial piece of fork-shaped structure imbedded in the cowl of excavata is a single and undivided structure.

Female Terminalia of Pteronarcys excavata (Fig. 56). The female terminalia of excavata are similar to those of reticulata except for specific modifications of the eighth sternite. The vaginal projections, arising from the posterior border of each half of the sternite (Fig. 56), are much less pronounced than those of reticulata. The mesal posterior border of the eighth sternite, between the vaginal projections, appears "broadly, deeply and roundly excavated" (Wu and Claassen, 1934; Wu, 1938). On each side of the "excavated region" and situated on each vaginal projection is a small darkly colored ovoid spot.

Specimens of Pteronarcys excavata Examined. CHINA, 2 males, 2 females (Kaolingtzu Station, 3200', Kirin Province) (CHN, JFH).

Male Terminalia of Pteronarcys sachalina. No specimen of the undescribed male of this species was available for examination.

Female Terminalia of Pteronarcys sachalina. Unfortunately, as was the case with the male of this species, the female was unavailable for examination. If Klapalek's (1908) description and figures of *sachalina* are correct, this species closely resembles *excavata* in having small vaginal projections and also resembles *excavata* as well as *reticulata* in having the eighth sternite divided by a mesal, longitudinal ridge. However, *sachalina* differs from *excavata* in having the mesal extremities of its smaller vaginal projections turned anteroventrally and the mesal posterior border between the projections only narrowly notched or cleft (Wu, 1938; Zhiltzova [personal communication]). It should be mentioned that the differences between these two species may be the result of distortion possibly due to the drying of the holotype females. The possibility, therefore, exists that *excavata* is a synonym of *sachalina*.

Male Terminalia of Pteronarcys biloba (Figs. 57-62). Although the male terminalia of *biloba* (Figs. 57-59) resemble those of *reticulata* and *excavata*, significant differences do occur.

The ninth tergite is entirely sclerotized and is not divided mesally by a wide longitudinal membranous band (Fig. 57) as in *reticulata* and *excavata*.

On the tenth segment the anterior (ahl) and median hemitergal lobes (mhl) are well separated from each other (Fig. 57). The median lobes, apically covered with short thick setae, are bluntly pointed at their apical margins. The posterior hemitergal lobes (phl), although present and easily seen, are not as well demarked as are those of *reticulata* and *excavata*. The tenth sternite, although narrowed ventrally, is fairly broad for most of its length.

In *biloba* the sclerotic anterior surface (Figs. 60, 61) of the dorsal section (ds) of the supra-anal process is a broad flat piece and does not resemble a pipe with a slit along the length of its mid-posterior surface as is found in *reticulata* and *excavata*. The spatula situated at the apical extremity of the dorsal section in both *reticulata* and *excavata* is not found in *biloba*.

Biloba is similar to *reticulata* and *excavata* in possessing a fork-like structure imbedded in the membranous inner mesal surface of the cowl (Figs. 61, 62). However, the lateral pieces of fork-shaped structure in *biloba*, unlike that of *reticulata* and *excavata* do not diverge apically from each other but are situated very closely together for about half their lengths and then more abruptly diverge from each other.

Female Terminalia of Pteronarcys biloba (Fig. 63). The female terminalia of *biloba*, except for modifications of the eighth sternite, are similar to those of *reticulata* and *excavata*. In *biloba* a narrow, longitudinal mesal ridge dividing the eighth sternite is absent (Fig. 63). The vaginal projections of *biloba* are transversely wider, appearing to arise from almost the entire area of the posterior sternal margin.

Specimens of Pteronarcys biloba Examined. CONNECTICUT, 2 females (Litchfield) (AMNH); MAINE, 1 female (Houlton) (USNM), 3 females (Somerset County) (CHN); MASSACHUSETTS, 1 male (Adams) (CHN), 1 female (Amherst) (CHN), 1 male (Charlemont) (CHN), 1 male (Pelham) (CHN), 1 male (Whately) (CHN), 1 male (Williamsburg) (CHN); NEW HAMPSHIRE, 1 male (Mt. Washington) (JFH), 1 female (Waterville Valley) (JFH); NEW YORK, 1 female (Cranberry Lake) (CU), 1 male, 1 female (Ithaca) (CU), 1 female (Ramapo) (CU), 1 male (Wells) (CHN); NORTH CAROLINA, 1 male (Black Mountains) (JFH), 1 male, 1 female (Valle Crucis) (JFH); PENNSYLVANIA, 1 male (New Milford) (CU); WEST VIRGINIA, 1 male (Forks of Cacapon) (USNM); CANADA, 1 male (Truro, Nova Scotia) (CU).

Male Terminalia of Pteronarcys scotti (Figs. 64-69). The general features of the male terminalia of *scotti* (Figs. 64-66) appear to ally this species closely with *biloba*. However, *scotti* exhibits certain features which serve easily to distinguish this species from *biloba*.

On the tenth tergite the narrow posterior hemitergal lobes (Fig. 64,phl) are less discernible than those of *biloba*.

Ricker (1952) observed that in *scotti* the trough-shaped process (tp) of the sclerotic anterior surface of the dorsal section (Figs. 64, 66,ds) of the supra-anal process has a smoother surface, and is much less anteriorly produced, than that of *biloba*. In addition the process of *scotti* is also smaller and less clearly demarked. The fork-like structure of the cowl (Figs. 68, 69), characteristic of *biloba*, *reticulata* and *excavata*, is not found in *scotti*.

Female Terminalia of Pteronarcys scotti (Fig. 70). The female terminalia of *scotti*, except for minor structural differences involving the eighth sternite, closely resemble those of *biloba*. The vaginal projections (Fig. 70,vp) of *scotti* appear to be slightly more transversely narrower than those of *biloba*. The median area or notch between the projections as noted by Ricker (1952), anteriorly becomes transversely expanded in *scotti*, while this area in *biloba* is straight-sided.

Specimens of Pteronarcys scotti Examined. SOUTH CAROLINA, 4 males, 1 female (Walhalla Federal Fish Hatchery, Oconee County) (CHN, JFH); TENNESSEE, 1 male, 1 female (Gatlinburg) (JFH).

Male Terminalia of Pteronarcys proteus (Figs. 71-76). The male terminalia of *proteus*, although similar to those of the previously mentioned species of *Pteronarcys*, do exhibit certain unique structural features (Figs. 71-73).

The anterior half of the ninth tergite is elevated to form a conspicuous anteriorly projecting and emarginate median process (Figs. 71, 72).

The median hemitergal lobes (Fig. 71,mhl) of the tenth tergite are greatly widened and are broadly rounded at their apical margins. The posterior hemitergal lobes (phl) are similar to those of scotti in that they are pale and difficult to discern. The tenth sternite is well sclerotized and well demarked.

The inner part (Figs. 74, 75,ip) of the supra-anal process is nearly as long as the free part. The trough-shaped process (Figs. 74, 75,tp) of the sclerotic anterior surface of the dorsal section (ds) is very small but is well demarked and noticeably projects anteriorly from the external surface.

Proteus is similar to scotti in lacking the fork-like structure embedded in the cowl.

Female Terminalia of Pteronarcys proteus (Fig. 77). The female terminalia of proteus basically resembles those of the previously mentioned species of Pteronarcys. However, the eighth sternite is modified into a broadly rounded, posteriorly produced subgenital plate which mesally gives rise to two posteriorly projecting long, slender, bluntly pointed vaginal projections (Fig. 77,vp).

Specimens of Pteronarcys proteus Examined. MAINE, 1 female (Rockwood) (JFH); MASSACHUSETTS, 4 males, 2 females (Sunderland) (CHN, JFH); NEW JERSEY, 1 male (Hackettstown)

(CU); NEW YORK, 1 female (West Branch, Ausable) (CU), 1 male (Green County) (CU), 8 males, 17 females (Ithaca) (CU, JFH), 1 female (Oliverea) (JFH), 2 males (Ringwood) (CU), 5 males, 4 females (Slaterville) (CU), 1 female (Wilmington Notch, Adirondacks) (CU); PENNSYLVANIA, 1 female (President) (CU); VERMONT, 1 female (Willoughby Lake) (JFH); VIRGINIA, 1 male (Shenandoah National Park) (USNM).

Male Terminalia of Pteronarcys comstocki. The undescribed male of *comstocki* was not available for this study.

Female Terminalia of Pteronarcys comstocki (Fig. 78). The female terminalia (Fig. 78) of *comstocki*, except for the very short vaginal projections (vp) arising from the posteriorly produced mesal area of the posterior margin of the eighth sternite, are similar to those of *proteus*.

Specimens of Pteronarcys comstocki Examined. MAINE, 1 female (Oxbow, Aroostook County) (CHN); NEW HAMPSHIRE, 1 female (Twin Mountains) (CHN); NEW YORK, 1 female (Tarbel) (CU); VIRGINIA, 2 females (Blowing Springs Camp, 8 miles west of Warm Springs) (USNM).

Male Terminalia of Pteronarcys californica (Figs. 79-84). Although the general features of the male terminalia of *californica* bear resemblance to those of the previously mentioned species of this genus, this species in many of its genitalic features is quite distinct.

The ninth tergite is entirely covered with uniformly short thick setae (Fig. 79). The rounded subgenital plate of the ninth sternite is just barely produced posteriorly (Figs. 80, 81).

On the tenth segment the large median hemitergal lobes (Figs. 79, 81,mhl) are produced noticeably dorsomesally from their bases. The lobes are broadly rounded at their apical margins and are covered apically with short, thick peg-like setae. The apical portions of the posterior hemitergal lobes (phl) are unsclerotized and identifiable only by a small line of long, thin setae. The tenth sternite ventrally is greatly narrowed and poorly demarked.

The supra-anal process is characterized by the elongate inner part which is twice the length of the free part (Figs. 82, 83). The lateral braces, extending ventrolaterally from their bases at the apex of the inner part, are very small, flat sclerotic pieces (Fig. 82). The lightly sclerotized U-shaped sclerotic loop (Fig. 84,u) at the membranous opening into the dorsal section is complete. The free part, in lateral view, can be seen to curve ventrally from its base. The thick anterior sclerotic surface of the dorsal section, when viewed dorsally, midway along its length gives rise to two hollow posteriorly projecting, ventrally curving, bluntly rounded arms (Figs. 82, 83). This sclerotic surface from the base of the arms to its apical extremity is abruptly narrowed as well as abruptly turned ventrally. At its apex the anterior sclerotic surface is expanded into a thin posteriorly projecting plate-like process which is continuous with a small anteriorly situated inverted cup-like process (sperm cup of Smith [1917]).

The anterodorsal area of the inner membranous surface of the cowl (Figs. 80, 84), situated near the U-shaped sclerotic loop, is thickened and deeply recessed to receive the basal portion of the free part of the supra-anal process. The posteroventral area of this membranous inner surface is also thickened and recessed and in some specimens it was noted that the apical extremity of the free part was held within this area. The outer surface of the cowl consists largely of a very broad basal sclerotic plate. The lateral anterodorsal extremities of this plate, as found in those of the previously mentioned species of *Pteronarcys*, are more darkly sclerotized. Smith (1917) mistakenly observed that this plate surrounded the anal opening onto the inner membranous surface of the cowl. However, as in the other members of this family, the anal opening is situated below this plate.

The subanal lobes of *californica* are unusual in that their apical portions are completely membranous.

Female Terminalia of Pteronarcys californica (Fig. 85). The female terminalia of *californica*, except for minor structural differences on the eighth sternite, closely resemble those of *biloba* and *scotti*. However, the vaginal projections of the eighth sternite are not transversely as wide nor as posteriorly produced as those of *biloba* and *scotti*.

Specimens of Pteronarcys californica Examined. CALIFORNIA, 1 male, 1 female (Adobe Creek, Stanislaus County) (USNM), 3 males, 1 female (Dunsmuir, Shasta County) (CU, JFH), 1 male (San Jose) (CU), 1 male (Sonoma County) (CU), 1 male (Wadell County) (CU); COLORADO, 2 males, 2 females (CU), 2 males, 2 females (Gunnison) (CU), 1 male, 1 female (Gunnison River) (CU), 12 males, 3 females (Platte Canon) (CU, USNM), 1 male, 3 females (Steamboat Springs, Yampa River) (CU), 1 male (Truckee) (USNM), 13 males, 5 females (Yampa River) (CU); IDAHO, 1 male (northern Idaho) (JFH), 5 males, 6 females (Rarie) (JFH); MONTANA, 1 male (Bitter Root Valley) (JFH), 1 female (Bozeman) (CU), 2 males, 2 females (Gallatin River) (CU), 2 males, 2 females (Granite County) (CHN), 1 male (Sula, Ravalli County) (USNM); NEW MEXICO, 1 male, 1 female (nr. Field Tract Campground, Pecos River) (USNM); OREGON, 1 female (Alsea) (CU), 1 female (Corvallis) (CU), 1 male (7 miles northwest of Roseburg) (USNM); UTAH, 2 males (Birch Glen, Logan River) (CU), 1 male, 1 female (Cain, Brigham) (USNM), 10 males, 5 females (Logan) (CU), 4 males, 9 females (Logan River) (CU), 1 female (Ogden) (CU); WYOMING, 2 males (National Park) (USNM), 10 males, 4 females (Yellowstone Park) (CU, JFH, USNM), 2 males, 2 females (Upper Falls, Yellowstone River) (JFH); CANADA, 2 males, 1 female (Big Creek, Yukon Territory) (JFH).

Male Terminalia of Pteronarcys princeps (Figs. 86-91). The male terminalia of princeps are very similar to those of *californica*. However, *princeps* exhibits certain unique features which easily distinguish this species from *californica*. The posterior half of the ninth tergite is divided mesally by a broad membranous band which narrows gradually anteriorly from its greatest width at the hind margin (Fig. 86). On each side of the membranous area the posterior portion of the tergite is covered with short thick peg-like setae. On the tenth segment the median hemitergal lobes are narrower along their lengths and much less broadly rounded apically than those of *californica*. The lateral braces of the supra-anal process (Figs. 89, 90) are not present. That region of the sclerotic anterior surface between the basal extremity and the posteriorly projecting arms, in dorsal view, appear to be transversely wider as well as longer than that of *californica*. The anterodorsal region of the inner membranous region of the cowl, as in *californica*, is recessed. However, the mesal portion of this recessed surface is covered by a narrow sclerotic strip, possibly aiding in support, which arises from the narrow U-shaped sclerotic loop (Fig. 91,u). The posteroventral region of the inner surface is not only transversely narrower than that of *californica* but is smooth and not recessed. The darkly sclerotized dorso-anterior lateral extremities of the broad basal sclerotic plate are longer than those of *californica*. A small membranous nipple-like lobe not found in *californica* arises at the posterior basal portion of the membranous apical region of the subanal lobe.

Female Terminalia of Pteronarcys princeps (Fig. 92). The female terminalia of *princeps*, except for the much longer and narrower vaginal projections of the eighth sternite, are basically similar to those of *californica*.

Specimens of Pteronarcys princeps Examined. CALIFORNIA, 1 female (CU), 1 male (Andreas Canon) (CU), 1 male, 1 female (Burney) (CU), 1 male (Cottonwood Creek, Humbug Valley, Plumas County) (USNM), 3 males, 1 female (Dunsmuir, Shasta County) (CU, USNM), 4 males (Shasta, Siskiyo County) (CU); OREGON, 1 male, 1 female (Swim) (JFH); UTAH, 1 male (Logan) (USNM); WASHINGTON, 1 male, 1 female (Mount Adams, West Klickitat) (USNM).

(NOTE: The male specimen of *princeps* from Logan, Utah was collected by G. F. Knowlton on June 23, 1929. This specimen as well as four males and two females collected by E. Gardner and J. A. Rowe on May 6, 1934, are the only records of *princeps* in Utah. Although Gaufin, Nebeker and Sessions (1966) were unable to examine these specimens for their study on Utah stoneflies, they did conclude that, ". . . inasmuch as this species has not been taken in the state otherwise, it is likely that the specimens taken were incorrectly identified and were actually *Pteronarcys californica*, which is very common." Unfortunately, the material collected by Gardner and Rowe was not available for this study either. However, Knowlton's specimen, correctly determined by Frison in 1936, nicely exhibits the numerous distinctive male characteristics of *princeps*.)

Male Terminalia of Pteronarcys dorsata (Figs. 93-98). The general features of the male terminalia of *dorsata* ally this species closely with *californica* and *princeps*. However, certain distinctive features of the genitalic structures readily serve to distinguish *dorsata* from *californica* and *princeps*.

The anterior half of the ninth tergite is covered with a short, thick setae (Fig. 93). The ninth sternite is greatly produced posteriorly into a gradually narrowing elongate subgenital plate (Fig. 94). A distinct median notch is situated in the hind margin of the plate. There is no plateau on the ninth sternite.

On the tenth tergite the median hemitergal lobes (Fig. 93,mhl) unlike those of *californica* and *princeps* apically are greatly produced posteriorly. At their apex the lobes are covered with short thick peg-like setae. The apical portion of the posterior hemitergal lobes (phl) are absent (Fig. 95). Much of the tenth sternite is membranous.

The supra-anal process of *dorsata* is similar to that of *proteus*, *californica* and *princeps* in having an elongate inner part (Figs. 96, 97,ip). The small lateral braces (Figs. 96, 97,lb) at the apex of the inner part extend laterally from their bases. The lightly sclerotized U-shaped sclerotic loop (u) of the dorsal section is present and resembles that found in *californica* (Fig. 98). The anterior sclerotized surface of *dorsata* is not as distended basally or as narrowed apically as is that of *californica* and *princeps* (Figs. 94, 97). The apical extremity of the sclerotized anterior surface of the dorsal section is expanded into a cup-like process (sperm cup of Smith [1917]) containing an eversible, membranous sac (Figs. 96-98). Smith (1917) thought that two tendons, a retractor tendon and a protractor tendon, were responsible for the eversion and retraction of the sac from the cup-like process. However, close examination reveals that no such tendons are present. It is interesting to note that in several specimens this membranous sac could be everted from the cup by squeezing the dorsal section with forceps. When the pressure applied by the forceps was terminated the sac retracted into the cup. Thus, it seems likely that the resulting turgidity caused by body fluids entering into the dorsal section through the opening at the U-shaped sclerotic loop is responsible for the eversion of the sac. Possibly when the body fluids leave the dorsal section the sac retracts into the cup-like process.

The basal external sclerotic plate of the cowl of *dorsata* is much narrower than that found in *californica* and *princeps* (Figs. 97, 98).

Although the apical portions of the subanal lobes of *dorsata* resemble those of *californica* and *princeps*, they differ in being sclerotized medially (Fig. 95).

Female Terminalia of Pteronarcys dorsata (Fig. 99). The female terminalia of dorsata, except for the greatly reduced vaginal projections of the eighth sternite, are similar to those previously mentioned species of this genus. The hind margin of the eighth sternite of dorsata, as noted by Frison (1942), varies from that without any processes to that having two conspicuous medially arising "nipple-like" vaginal projections.

Specimens of Pteronarcys dorsata Examined. GEORGIA, 1 male (Atlanta) (JFH), 1 male (St. College) (CU); INDIANA, 2 males, 3 females (Elkhart) (CU, JFH); MAINE, 1 male (Ashland) (CHN), 1 male, 1 female (Orono) (CU); MINNESOTA, 1 female (CU); MISSISSIPPI, 1 male (Silver Creek) (CU); NEW YORK, 2 females (Binghampton) (CU, JFH), 7 males, 8 females (Ithaca) (CU, JFH); NORTH CAROLINA, 1 female (Asheville) (JFH), 1 female (Burncoat Swamp, Lenoir County) (JFH), 1 male (Raleigh) (CU); PENNSYLVANIA, 1 female (Berwick) (CU), 6 males, 4 females (Harrisburg) (CU, JFH), 1 female (Rockville) (CU); VIRGINIA, 1 male (Rappahannock River, Remington) (JFH); CANADA, 1 male (At'bska Delta, Alberta) (USNM), 1 male (Eagle River, Labrador) (CHN), 1 male (Jack Lanes Bay, Labrador) (USNM), 3 males, 3 females (Lake Freemont, Labrador) (CHN), 1 female (Aweme, Manitoba) (CU), 1 male, 1 female (Churchill, Manitoba) (CU), 1 female (Saquenay County, Quebec) (USNM).

Male Terminalia of Pteronarcys pictetii (Figs. 100-105). The male terminalia of pictetii are nearly identical to those of *dorsata*. However, in *pictetii* the hind portion of the subgenital plate bordering the median notch is strongly decurved ventrally (Figs. 101, 102), while this area in *dorsata* projects posteriorly.

Female Terminalia of Pteronarcys pictetii (Fig. 106). The female terminalia of *pictetii* resemble those of *dorsata*. However, the vaginal projections of *pictetii* are longer as well as transversely wider than those of *dorsata*.

Specimens of Pteronarcys pictetii Examined. ILLINOIS, 1 male (Rock Island) (JFH); IOWA, 1 female (Iowa City) (USNM); KANSAS, 1 female (Manhattan) (CU), 1 male, 1 female (Riley County) (CU); MINNESOTA, 3 males, 1 female (CU), 1 male (Mankito) (CU); TENNESSEE, 1 female (CU), 1 male, 1 female (Nashville) (CHN); WISCONSIN, 1 female (Namekargon River, Spooner) (JFH); CANADA, 2 males (Aweme, Manitoba) (CU).

COMPARATIVE EXTERNAL ANATOMY OF THE TERMINALIA OF THE GENERA OF THE PTERONARCIDAE. Although the male terminalia of *Pteronarcys* and *Pteronarcella* are similar to each other, they do differ in several respects.. The ninth tergite in *Pteronarcys*, which exhibits some species variation, lacks the tergal process found on the posterior half of the tergite in *Pteronarcella*. The ninth sternite of *Pteronarcella* is characterized by a weakly demarked, difficult to discern "plateau." Although this area in most of the species of *Pteronarcys* is well demarked as well as easily seen, it is slightly reduced in *californica* and *princeps* and is absent in *dorsata* and *pictetii*. The subgenital plate in *Pteronarcys* also exhibits some variability. In most of the species of this genus this plate, as in *Pteronarcella*, is moderately produced posteriorly. However, in *californica* and *princeps* it is barely produced posteriorly and in *dorsata* and *pictetii* is greatly produced posteriorly and exhibits a mesal notch in the hind border. The tenth hemitergites of *Pteronarcella* each consist of a narrow longitudinal mesal hemitergal lobe, whereas in *Pteronarcys* each hemitergite consists of three transverse hemitergal lobes exhibiting varying degrees of differentiation within the genus. The tenth sternite, which is greatly narrowed ventrally in *Pteronarcella*, is variously modified in *Pteronarcys*. In most of the species of the latter genus (*reticulata*, *excavata*, *scotti*, *biloba* and *proteus*) it is broad and well developed, but in others (*californica* and *princeps*) it is greatly narrowed ventrally or absent (*dorsata* and *pictetii*). Within *Pteronarcys* an interesting condition occurs involving the inner part of the supra-anal process. This region in *proteus*, *californica*, *princeps*, *dorsata* and *pictetii*, unlike the very short inner part found in the remaining species of *Pteronarcys* and the two species of *Pteronarcella*, is very elongate. The ventral section of the free part of the supra-anal process in *Pteronarcella* is not grooved along its mid-ventral length as it is in *Pteronarcys*. The dorsal section of the free part of the supra-anal process in *Pteronarcys*, essentially a tube-like structure consisting of the U-shaped sclerotic loop and the sclerotized anterior surface and a membranous posterior surface, is structurally less complex than that of *Pteronarcella*. The varied subanal lobes of *Pteronarcys* resemble those of *Pteronarcella* except that apically the former are never hook-like in appearance.

The female terminalia of *Pteronarcys* and *Pteronarcella*, except for modifications of the eighth and ninth sternites, closely resemble each other. The eighth sternite of *Pteronarcys* lacks the darkly colored longitudinal mesal region found in *Pteronarcella*. In most species of *Pteronarcys* the vaginal projections are much longer as well as transversely wider than those of *Pteronarcella*. The anteriorly pointing setae situated at the hind margin of the ninth sternite of *Pteronarcys* are not capable of being infolded when the abdominal segments are telescoped together.

The cerci of both the male and female terminalia of *Pteronarcys* are composed of 26 to 33 segments, whereas those of *Pteronarcella* are composed of 14 to 24 segments.

PHYLOGENY OF THE FAMILY PTERONARCIDAE

This section is concerned with the cladistics of the family Pteronarcidae. In this study the method put forth by Hennig (1965, 1966) is utilized. This method emphasizes that when dichotomic branching occurs in evolution some features undergo little or no change from corresponding features of the ancestor while other features undergo considerable change in one or both branches. Features representing the former condition are referred to as being in the *primitive state* while features representing the latter condition are in the *derivative* or *derived state*. In any particular group a derivative condition of a specific feature, being by definition a state that arose within that group, is never found in all the members, but is more likely found in only a few members or even in just one member of the group. On the other hand, the primitive condition is more likely to be found in all or many members of that group and is also more likely to be found in other related groups. Hence, only derivative and not primitive states, allow the inferring of the branching sequences in the phylogeny of that group.

During this study a large number of species in a wide variety of non-pteronarcid genera was examined. This is necessary for determining the polarity and direction of evolution of attributes within the family Pteronarcidae.

Unfortunately, the determination of the cladogeny of species outside the Pteronarcidae is a formidable task that still lies ahead. Thus, certain attributes of the Pteronarcidae for lack of knowledge concerning their direction of evolution could not be used to construct a cladogram and other attributes that were utilized will have to be made more secure by future investigation. However, it was felt that any reasonable step taken toward constructing the cladogeny of this family was better than taking no step at all. It is hoped that as attention is focused on the cladogeny of the species of other families within the Plecoptera mutual clarification will occur and the phylogeny and classification of the Pteronarcidae will become more fully understood.

Cladistics of the Pteronarcidae

The inferred branching sequence of the genera and species of the family Pteronarcidae is presented in the form of a cladogram (Fig. 107).

Before the determination of the cladogenesis of the genera and species within the Pteronarcidae can be undertaken it must be demonstrated that this family is monophyletic (*sensu* Hennig, 1965, 1966). It is currently thought (Illies, 1965, 1966) that within the suborder Setipalpia the Pteronarcidae is the sister group of the superfamily Sublipalpia. Such a contention cannot be made secure without establishing monophyly for the groups concerned. The following features, because they are found in all the members of the Pteronarcidae and only in the Pteronarcidae and are derivative within the Setipalpia, establish monophyly for this family. The ventropleurites of all three thoracic sterna as well as the postfurcasterna of the pro- and mesothoracic sterna of the Pteronarcidae are quite reduced when compared to the more recently derived Perlidae and Chloroperlidae and the more primitive Eustheniidae and Diamphipnoidae examined in this study. Reduction of these sclerotic plates has also occurred among some of the groups of the subfamily Isogeninae of the family Perlodidae. However, it seems likely that this reduction occurred independently from that of the Pteronarcidae since these areas are well developed in some members of the Isogeninae as well as in the closely related subfamilies Isoperlinae and Perlodinae. Hence, reduction of these plates in the Pteronarcidae is here regarded as an independently derived state of this family. The pretarsus of the leg of the Pteronarcidae is unusual in that the arolium is expanded laterally and is characterized by the presence dorsally on each side of the orbicula of a large sclerotized region. Probably this is a derivative state as no other stonefly exhibits this condition. The ninth sternite of the female terminalia exhibits short thick anteriorly pointed setae situated at its posterior margin. Since this condition is not found in other stoneflies it appears to be a unique and therefore derived state of this family.

The first dichotomic branching within the family Pteronarcidae (1, Fig. 107) gave rise to the sister groups Pteronarcella and Pteronarcys. An analysis of the following anatomical features, utilized in establishing monophyly for Pteronarcella, is presented. The much smaller body size of Pteronarcella as compared to that of Pteronarcys is, perhaps, the most obvious difference between these two genera. Since there are a number of definite evolutionary trends toward reducing the body size within the Plecoptera (Illies, 1965), the smaller body size of Pteronarcella is probably a derivative condition. The flagellum of the antenna of Pteronarcella consists of distinctly fewer segments than does that of Pteronarcys. It appears that antennae with a large number of flagellar segments are usually found among the more primitive members of the Plecoptera. Reduction in the number of flagellar segments has taken place independently many times within the Plecoptera and is usually associated with the more derivative members of this order. Very probably the reduced number of flagellar segments of Pteronarcella is the derived condition. The scutum of the mesothorax as well as that of the metathorax of Pteronarcella is distinguished by well demarked transcutal sutures. This condition, not found in other stoneflies, appears to be a derived feature of this genus. The mesally situated pits of the meso- and metapostscutellum of Pteronarcys give rise to well developed, sharply pointed internal apodemes. These well developed apodemes are also found in the Subulipalpia and in the more primitive Eustheniidae. The small barely developed apodemes of *Pteronarcella* are, therefore, a derived feature. The wings of *Pteronarcella* are distinguished from *Pteronarcys* by having fewer crossveins in the fore and hind wings and fewer longitudinal branches of the vannal veins in the hind wing. However, within the Plecoptera reduction of crossveins and longitudinal branches of veins appear to be correlated with reduction in the size of the wing which in turn is correlated with the reduction in body size. Hence, reduction of veins and crossveins in the wings and reduction in body size are redundant features and will not be treated as independent characters in this study. The dorsolateral margins of abdominal segments 2 through 8 of the male sex of *Pteronarcella* are upraised into rounded protuberances. Since these protuberances are not present in the more primitive Eustheniidae and Diamphipnoidae, it is probable that they are a derivative condition within the Pteronarcidae. Such protuberances have been found on the posteriormost segments of some of the species of *Isogenoides* in the Isogeninae (Perlodidae, Subulipalpia). However, as most of the species and genera of the Isogeninae as well as the species and genera of the closely related subfamilies, the Perlodinae and the Isoperlinae, lack these structures, it appears likely that these abdominal protuberances have arisen independently in *Pteronarcella* and the Isogeninae. The males of both species of the genus *Pteronarcella* have a conspicuous broad anteriorly projecting tergal process arising from the posterior portion of the ninth tergite. This condition is not found in *Pteronarcys* or in other stoneflies and, accordingly, is considered a derivative condition of *Pteronarcella*. The male ninth sternite of the Pteronarcidae is characterized by the presence of a median longitudinal "plateau." This "plateau" is also present in the primitive Diamphipnoidae and in the related and more recently derived Acroneurinae. Very probably the presence of the "plateau" is a primitive condition for the suborder Setipalpia. Within this suborder reduction and loss of the "plateau" appears to have occurred several times independently. The poorly developed "plateau" of the males of the species of *Pteronarcella* is probably, then, a derivative condition. Although most of the species of *Pteronarcys* exhibit a well developed "plateau," loss of this structure has occurred in two species of this genus. The tenth sternite of the males of *Pteronarcella* is greatly narrowed ventrally when compared to that found in most of the species of *Pteronarcys*. Probably a fairly broad tenth sternite, as found in the adult females and the naiads of both sexes, is the primitive condition of the Pteronarcidae. Thus, that condition found in the males of *Pteronarcella* is derivative. The dorsal section of the male supra-anal process of *Pteronarcella* consists of a sac-like basal piece and a triple-walled, sleeve-like apical piece. This condition in *Pteronarcella* is unique within the Plecoptera and deviates considerably from that of *Pteronarcys* which is similar to that found in the Isogeninae and Paraperlinae. The complex dorsal section of *Pteronarcella* is, consequently, considered to be in a derived condition. The restriction of a darkly colored mesal longitudinal region to the female eighth sternite of *Pteronarcella* is very probably a derivative feature of this genus. A well developed subgenital plate homologous to the vaginal projections of the Pteronarcidae and arising from the entire posterior margin of the female eighth sternite is found in most members of the Setipalpia and in the Diamphipnoidae. Very probably this is the primitive condition for the Setipalpia, and reduction of this plate, a derived condition, has occurred several times independently within this suborder. The greatly reduced vaginal projections of *Pteronarcella* situated within a mesal emargination of the posterior margin of the eighth sternite are, therefore, considered as a derived feature. The posterior margin of the ninth sternite of *Pteronarcella* bearing the anteriorly pointed setae is capable of being infolded when the abdominal segments are telescoped together. Since this condition is not found in other stoneflies, it is likely that this feature in *Pteronarcella* is derived. The number of cercal segments of *Pteronarcella* is smaller than the number found in *Pteronarcys*. Within the Plecoptera the number of cercal segments seems to have several times independently undergone reduction from the primitive condition of a large number of segments. Thus, the smaller number of cercal segments found in *Pteronarcella* probably represents the derived condition.

The monophyletic nature of *Pteronarcys* is established by certain anatomical features which are analyzed as follows. The lateral margins of the pronotum of *Pteronarcys* are truncated at the pleural region. This condition differs from that found in *Pteronarcella* and in the subulipalpian families Perlidae and Perlodidae where the lateral margins are deflected ventrally so as to encroach slightly on the pleural region. Thus, it seems likely that the condition found in *Pteronarcys* is a derivative attribute in this genus. The posterior notal wing processes of *Pteronarcys* are detached from the notum to form "fourth axillary sclerites." This condition is apparently derivative; in all other stoneflies these wing processes are part of the notum. The number of thoracic and abdominal gills of *Pteronarcys* is less than that number found in *Pteronarcella*. Within the Plecoptera there have been evolutionary trends toward reduction of the number of gills on the thorax and on the abdomen (Ricker, 1950; Illies, 1965). Accordingly, *Pteronarcys* with fewer gills than *Pteronarcella* exhibits the derived condition. The barely detached mesal hemitergal lobe of each male tenth hemitergite of *Pteronarcella* appears to be less modified than the three pairs of transverse hemitergal lobes of *Pteronarcys*. Yet, transverse hemitergal lobes are found among many subulipalpian groups and it could be argued that the transverse lobes of all the Setipalpia are the result of common ancestry and, therefore, represent a primitive condition. However, the lobes of the hemitergites of the Subulipalpian groups are two in number as compared to three found in *Pteronarcys*. In the Subulipalpia it is the posteriormost portion of the hemitergite which undergoes the greatest development, while in *Pteronarcys* it is the median portion which undergoes the greatest development. Thus, it appears that the transverse lobes of *Pteronarcys* and the Subulipalpia are not homologous. The male subanal lobes of *Pteronarcella* are apically well sclerotized and are hook-shaped in appearance when viewed laterally. This condition is similar to that found in members of the Eustheniidae and Diamphipnoidae and is probably the primitive state. The lobes of *Pteronarcys*, exhibiting various modifications, are considered to be derived. The ventral section of the free part of the male supra-anal process of *Pteronarcys* is grooved along its mid-ventral length. Since this condition is not found in other stoneflies having this structure, it is considered to be derived. The eggs of stoneflies have been studied by various workers (Needham and Claassen, 1925; Frison, 1935; Knight, Nebeker and Gaufin, 1965a, 1965b). However, the evolutionary significance of the eggs of the Pteronarcidae has not been studied. Within the Pteronarcidae the length of the eggs of *Pteronarcella* along the longitudinal axis (the distance from the collar to the opposite pole) is slightly greater than the length of the egg along the transverse axis. This condition is similar to that found in most members of the

Subulipalpia and is probably the primitive state for the Setipalpia. The eggs of *Pteronarcys* have changed from this primitive condition in that the length along the transverse axis is approximately equal to or is greater than the length along the longitudinal axis.

Within *Pteronarcella* a subsequent dichotomy (2, Fig. 107) gave rise to the sister species *badia* and *regularis*. These two species are readily distinguishable from each other on the basis of several genitalic features. However, because there are only two highly modified species in this genus, it is very difficult to determine which of these features are derivative and which are primitive. Since in *Pteronarcella* the presence of a conspicuous anteriorly projecting process arising from the posterior margin of the ninth tergite is a unique feature within the Plecoptera, it would seem more likely that its greater development, as found in *badia*, would be the derivative condition. Reduction of the subgenital plate of the female eighth sternite, as explained previously, has occurred within the Plecoptera several times. Very possibly the smaller size of the vaginal projections of *badia* is the derivative condition in *Pteronarcella*. As the complex triple-walled apical piece of the dorsal section of the supra-anal process is found only in *Pteronarcella*, it seems likely that augmentation in size and complexity rather than reduction of this structure would be the derivative condition. Hence, the larger sclerite of the middle wall of the apical piece in *badia* is probably also a derived state. Since the outer wall of this structure in *regularis* is greatly expanded laterally at its basolateral sides and is also covered with a greater number of grooves arranged in a complex irregular pattern at its basolateral sides, it is also probable that this condition is derivative.

The first dichotomic branching within the genus *Pteronarcys* (3, Fig. 107) gave rise to two groups each centered in one of two geographic regions, Asia and North America. When the species of both the Asian and North American groups are examined they appear to exhibit a morphocline (transformation series of Hennig, 1966) with respect to the three transverse lobes of each male tenth hemitergite. At one extreme of this cline, that found in the Asian species, the anterior and median hemitergal lobes are barely separated from each other and the posterior lobe is darkly sclerotized and easily discerned. At the other extreme of the cline, that found in the North American group, the anterior and median hemitergal lobes are well separated from each other, the median lobe is greatly developed and the posterior lobe is very small and difficult to discern. However, in order to utilize this morphocline in the cladistics of this genus its derivative and primitive extremes must be determined. In some of the North American species the inner part of the supra-anal process is greatly elongated and is equal to or greater than the length of the free part. Since the inner part of all other stoneflies having a supra-anal process is much shorter than the free part, it is likely that this elongated structure found in some of the North American species is a unique derived condition. These species having the elongated inner part also exhibit the greatest development of the median hemitergal lobe and the greatest reduction of the posterior lobe. It is likely that this condition of the hemitergal lobes, being correlated with the derivative condition of the inner part of the supra-anal process, is the derivative extreme of the morphocline of these transverse lobes. In the males of the Asian species of *Pteronarcys* an apparent primitive condition is the presence of a fork-shaped structure in the inner mesal membranous surface of the cowl. The lateral pieces of this structure and the lateral stylets of the Isogeninae and Paraperlinae are situated in very similar positions with respect to the supra-anal process. Thus, it seems likely that the fork-shaped structure and the lateral stylets are homologous structures and that their presence is a primitive condition. Among the North American species of *Pteronarcys* only *biloba* exhibits a fork-shaped structure. However, the lateral pieces of this smaller structure in *biloba*, unlike those of the previously mentioned groups, do not gradually diverge apically from each other but are situated very close together for about half their lengths and then more abruptly diverge from each other. Very probably, therefore, the condition in *biloba* is derivative. Thus, it is likely that the condition of the hemitergal lobes found in the Asian species, correlated with the primitive extreme of the fork-shaped structure of the cowl, is the primitive extreme of the morphocline of these transverse lobes. The dorsal section of the supra-anal process in the males of the Asian species exhibits a narrow tube-like sclerotized anterior region, a well developed trough-shaped process, and an apically situated spatula. In some of the North American species these structures appear to undergo a trend which is correlated with the modification of the hemitergal lobes. This trend is toward flattening as well as expanding laterally the anterior sclerotized surface of the dorsal section, reducing the trough-shaped process and the apical area around it. One result of this trend is the complete absence in the North American species of an apically situated spatula on the dorsal section of the supra-anal process. The ninth tergite of the males of the Asian species is divided mesally by a wide longitudinal membranous band. This condition appears to be derived; a completely sclerotized ninth tergite is found in most stoneflies including the Pteronarcidae. The presence of a narrow longitudinal ridge mesally dividing the female eighth sternite is a condition unique to the Asian species and, therefore, is here regarded as a derivative state. In this study neither the naiads of the Asian species of _Pteronarcys_ nor Zapekina-Dulkeit's (1956) study of the anatomy of _reticulata_ were available for examination. However, if Ueno's (1938) figure of an unknown species of Pteronarcys from Korea is accurate the Asian species lack the "spines" on the abdomen which are characteristic of some of the North American species. Since the presence of "spines" on the abdomen is an unusual condition among stoneflies, their presence in some North American species must be a derivative state. The lack of "spines" in other North American species, in view of the adult attributes which ally all these species of this geographic region is probably the result of their subsequent loss. The North American species lacking "spines" also exhibit the more recently derived condition of large median and reduced posterior lobes, giving further evidence that these species have converged on the primitive condition by loss of "spines." Of course, it is possible that the lack of "spines" in both the Asian and some North American species is the result of independent loss from a primitive "spiny" condition. However, two groups independently losing "spines" is a less probable conclusion than only one group losing "spines." Any further conclusion on this character will have to await examination of the naiads of the Asian species.

Within the Asian branch of Pteronarcys a subsequent dichotomic branching (4, Fig. 107) gave rise to the species reticulata and the group comprising the species sachalina and excavata. In this study the inferring of the cladogenetic relationship between these species is hindered by the fact that the male of sachalina is unknown and that the female of this species was not available for examination. The vaginal projections of the females of *sachalina* and *excavata* are smaller than in *reticulata*. Very probably this reduction in *sachalina* and *excavata*, like that of other stoneflies, is derivative. In the male of *excavata* the posterior margin of the median hemitergal lobes are much more posteriorly arcuate and the posterior lobes are much narrower than those found in *reticulata*. The straight posterior margin of the median lobe and the broad posterior lobe of the latter Asian species is very similar to those of the North American species *biloba*. It is likely, then, that this condition was present in the immediate common ancestor of both the Asian and North American branches of *Pteronarcys*. Thus, the condition of the median and posterior lobes in *reticulata* is derivative. In *Pteronarcys*, as previously mentioned, loss of the spatula of the supra-anal process as well as reduction of the area from which this structure arises is a conspicuous trend. Probably, then, a spatula was present in the common ancestor of both the American and Asian branches. The completely aspatulate condition of the North American branch suggests that the immediate common ancestor had a small spatula. Thus, it is likely that the small spatula present in *excavata*, rather than the greatly elongate spatula of *reticulata*, is the primitive condition. The mesal piece of the fork-like structure of the cowl in males of *reticulata* is medially divided longitudinally by a light colored line. This unique condition is probably derivative since this piece is single and undivided in *excavata* and *biloba*.

If *excavata* and *sachalina* are distinct species (see external anatomy section), they are closely related sister species (5, Fig. 107). Klapalek (1908) shows the mesal extremity of each vaginal projection of *sachalina* projecting anteroventrally from the eighth sternite. This condition is not found in other members of *Pteronarcys* and is probably derivative. The vaginal projections of *sachalina* are more reduced than those of *excavata* and are, therefore, derivative. Each vaginal projection of *excavata* bears on its mesal margin a small darkly colored spot. Probably this spot, not found in other members of *Pteronarcys*, is a derivative attribute in *excavata*.

The first branching within the North American species of *Pteronarcys* (6, Fig. 107) gave rise to the species *biloba* on one branch and the rest of the species of this geographic region on the other. In the latter branch the following advances over those of *biloba* have occurred: further lateral expansion of the dorsal section of the supra-anal process, further reduction of the trough-shaped process as well as the area around it, and of the apical portion of the posterior hemitergal lobes, and complete loss of the fork-like structure of the cowl. The trough-shaped process of the dorsal section of the supra-anal process of *biloba* is covered with large noticeable protrusions. Since in the Asian species as well as the other North American species having this structure these protrusions are considerably smaller, it is likely that the condition in *biloba* is derivative.

A further branching (7, Fig. 107) in the North American group, beyond *biloba*, gave rise to a branch for the species *scotti* and a branch consisting of the remaining species of this group. In the latter line of evolution the anterior sclerotized region of the dorsal section of the supra-anal process has undergone still further lateral expansion, the trough-shaped process as well as the apical area around it and the sclerotization of the posterior hemitergal lobes have become more reduced. The males of this branch also exhibit great development in size and complexity of the median hemitergal lobes and an increase in the length of the inner part of the supra-anal process. The vaginal projections of the females of this branch are transversely relatively narrow at their base and no longer appear to arise from the entire posterior margin of the eighth sternite as in the other species of *Pteronarcys*. In *scotti* the apical trough-shaped process angles only slightly anteriorly from the surface of the dorsal section of the supra-anal process. This structure in the already established more primitive species of *Pteronarcys* is noticeably angled. In *proteus*, in the sister group of *scotti* this structure, although considerably reduced, is also noticeably angled. Very probably, then, the trough-shaped process present in the immediate common ancestor of both *scotti* and its sister group was noticeably angled. Hence, the slight angle of this structure in *scotti* is likely a derivative attribute.

A group comprising the species *proteus* and *comstocki* and a group comprising the species *californica*, *princeps*, *dorsata*, and *pictetii* are the result of the next subsequent branching (8, Fig. 107) in *Pteronarcys*. The species comprising the latter sister group have undergone considerable change, especially regarding the male terminalia. Inferred cladogenetic relationships between the species of both sister groups is somewhat hindered by the fact that the male of *comstocki* is unknown. The males of the *californica*-*princeps*-*dorsata*-*pictetii* branch have undergone continued development of the median hemitergal lobes, reduction and finally loss of the apical portion of the posterior hemitergal lobes, and increase in the size of the inner part of the supra-anal process. In addition to the preceding characteristics, this line of evolution is further distinguished by the following features of the male terminalia. The "plateau" of the male ninth sternite, well developed in all other members of *Pteronarcys*, is slightly reduced or completely lost only in this branch. It is likely, then, that the condition of the "plateau" in the *californica*-*princeps*-*dorsata*-*pictetii* branch is a derivative state. The male subgenital plate of the ninth sternite of the *californica*-*princeps*-*dorsata*-*pictetii* branch, unlike that found in all other members of *Pteronarcys*, is modified by being either barely produced or greatly elongated. Very likely these conditions are derivative. The male tenth sternite in most of the members of *Pteronarcys* is fairly broad ventrally. However, in the *californica*-*princeps*-*dorsata*-*pictetii* branch it is either greatly narrowed or lost ventrally. This condition of the tenth sternite is probably derivative. The lateral braces of the supra-anal process of the *californica*-*princeps*-*dorsata*-*pictetii* branch are either very small or not present. Since large, well developed lateral braces are found in all other pteronarcids as well as in the Isogeninae (Perlodidae) and the Paraperlinae (Chloroperlidae) of the Subulipalpia, it is likely that this condition is primitive. The free part of the supra-anal process in most of the Subulipalpia having this structure as well as in most of the Pteronarcidae is decurved dorsally. Therefore, very proabably this condition of the free part is primitive. In the *californica* - *princeps*-*dorsata*-*pictetii* branch this structure is decurved ventrally and is, therefore, considered a derived attribute of this branch. The small difficult to discern U-shaped sclerotic loop of the dorsal section of the free part of the *californica*-*princeps*-*dorsata*-*pictetii* branch gives rise to a narrow sclerotized mesal projection of varying length. This single projection is situated in the cowl in a position similar to that of the mesal sclerotized piece of the fork-like structure present in some species of *Pteronarcys*. However, the latter when present is never attached to the U-shaped loop as is the single structure. Thus, it is likely that these two structures are not homologous. Probably the single mesal projection of the *californica-princeps-dorsata-pictetii* branch is a unique derived feature developed along with the ventrally decurved free part. The anterior sclerotized surface of the dorsal section of the free part, unlike that found in the other members of *Pteronarcys*, is greatly distended in the *californica-princeps-dorsata-pictetii* branch. It is likely, therefore, that the modification of the anterior sclerotized surface of this branch is the derivative condition. The trough-shaped process of the dorsal section of the supra-anal process as well as the apical area around it are much more greatly reduced in *proteus* than in *biloba*, *scotti*, and the Asian species of *Pteronarcys*. However, it is difficult to determine whether this structure in the preceding species is homologous with that large variable cup-like process of the *californica-princeps-dorsata-pictetii* branch. Although the trough-shaped process and the cup-like process are situated similarly on the free part of the supra-anal process, they do not appear to have any similarities of detailed anatomy and, hence, are probably not homologous. It is possible that the trough-shaped process has been lost in the *californica-princeps-dorsata-pictetii* branch and that the cup-like process is a newly arisen structure on the anterior sclerotized surface, and is, therefore, derivative. The male subanal lobes apically are either largely or completely membranous in the *californica-princeps-dorsata-pictetii* branch. This condition, unique to this branch, is probably correlated with the greater development of the median hemitergal lobes and is, consequently, derivative.

In the proteus-comstocki branch the vaginal projections arise from the mesal region of the eighth sternite. Since in all other members of Pteronarcys these vaginal projections are situated more laterad on the eighth sternite, it is likely that the mesally situated projections of the proteus-comstocki branch are a unique derivative condition. The presence on the male of proteus of an elevated anteriorly projecting tergal process arising from the anterior portion of the ninth tergite, not found in other members of Pteronarcys, is probably a derived attribute of this species. In comstocki (9, Fig. 107) the eighth sternite is distinguished by a mesal posteriorly produced subgenital plate which is slightly notched medially at its posterior border. Since this condition is unique within Pteronarcys, it is likely that this is a derivative attribute for this species. Unfortunately, in this study utilizing female terminalia alone (male unknown) has yielded no derived adult anatomical features for proteus as compared to comstocki.

The californica-princeps-dorsata-pictetii line of evolution subsequently split into the californica-princeps branch and the dorsata-pictetii branch (10, Fig. 107). In the latter branch a median "plateau" is not present on the male ninth sternite. Since the "plateau" is present in all other members of Pteronarcys, its absence in the dorsata-pictetii branch is interpreted as being derivative. In the dorsata-pictetii branch the subgenital plate of the male ninth sternite is greatly produced posteriorly and exhibits a median notch in its hind margin. This condition, not found in other pteronarcids or in other setipalpian stoneflies, is probably derivative. The median hemitergal lobes of the male tenth tergite of both the californica-princeps branch and the dorsata-pictetii branch are greatly developed. However, the median lobes of the californica-princeps branch, exhibiting broadly rounded apical margins, are more like those of the previously discussed proteus (Fig. 107) than they are like the apically posteriorly produced lobes of their sister group, dorsata-pictetii. It is likely, then, that the median lobes of the californica-princeps branch are closer in appearance to those present in the immediate common ancestor of both this branch and the dorsata-pictetii branch. Thus, the condition in the latter branch is probably derivative. The sclerotized apical portion of the posterior hemitergal lobes is absent in both the dorsata-pictetii branch and the californica-princeps branch. In the latter branch this apical area of the posterior lobe is identifiable by a line of long thin setae in the membrane where the posterior lobe would normally lie. This is not found in the dorsata-pictetii branch. Since the apical portions of the sclerotized posterior lobes of the more primitive biloba, scotti and proteus are covered along their lengths by long thin setae, it is likely that the presence of setae in this area in the *californica-princeps* branch is a retention of a primitive attribute. The tenth sternite in the *dorsata-pictetii* branch is not present ventrally, whereas in the *californica-princeps* branch, although greatly narrowed, it is present. In all the other members of *Pteronarcys* the tenth sternite is present and fairly broad ventrally. It is likely, then, that the condition of the tenth sternite in the *californica-princeps* branch is closer to the condition of the immediate common ancestor of both this branch and the *dorsata-pictetii* branch. Thus, the condition of the tenth sternite in the *dorsata-pictetii* branch is derivative. In the *dorsata-pictetii* branch an eversible membranous sac is contained within the cup-like process at the apex of the supra-anal process. This structure is unique within *Pteronarcys* and is probably a newly arisen derived feature of the *dorsata-pictetii* branch. The basal sclerotic plate of the cowl in the *dorsata-pictetii* branch when compared to that of all other members of *Pteronarcys* is greatly narrowed. It is likely then that this condition is a unique derived attribute of the *dorsata-pictetii* branch. The vaginal projections of the female eighth sternite are much smaller in the *dorsata-pictetii* group than in the *californica-princeps* group. The larger projections of the *californica-princeps* branch are more similar than are those of the *dorsata-pictetii* branch to those of the more primitive species *biloba* and *scotti*. Thus, it is likely that the uniquely small vaginal projections of the latter branch are a derivative condition. In the *californica-princeps* line of evolution the lateral braces either are very small structures or are altogether absent. The larger always present lateral braces of the *dorsata-pictetii* branch are more closely similar to the already established primitive condition of large well developed lateral braces. Thus, it is likely that the condition of the lateral braces in the *californica-princeps* branch is a derivative attribute for this group. Since the dorsal section of the supra-anal process of both the *californica-princeps* branch and the *dorsata-pictetii* branch is unique within *Pteronarcys* in having a greatly distended anterior sclerotized surface, it would seem likely that its greater size and complexity of shape in the former branch would be derivative. Its membranous posterior surface in the *californica-princeps* branch, unlike that of the other members of *Pteronarcys*, is rather broad and taut. Very probably this condition in the *californica-princeps* branch is derivative. In the *californica-princeps* branch the apical portion of the subanal lobes are completely membranous, whereas, in the *dorsata-pictetii* branch the apical portion of the subanal lobes, although largely membranous, are sclerotized medially. Very probably the subanal lobes of the *dorsata-pictetii* branch, resembling more than do those of the *californica-princeps* branch the condition of the completely sclerotized apical portion of the lobes of the other members of *Pteronarcys*, is the primitive condition.

In *princeps* (11, Fig. 107) the posterior half of the ninth tergite is mesally divided by a broad membranous band which narrows gradually anteriorly from its greatest width at the hind margin. Since all the other members of the monophyletic North American branch of *Pteronarcys* have a completely or a largely sclerotized ninth tergite, it is likely that the condition of this tergite of *princeps* is a derivative attribute of this species. The lateral braces, present in all the other species of the Pteronarcidae, are absent from the supra-anal process of *princeps*. Very likely this unique condition in *princeps*, as noted earlier, is due to the loss of the lateral braces and is a derived state. The mesal sclerotized projection of the U-shaped sclerotic loop of the dorsal section of the supra-anal process is very elongate in *princeps*. The species *californica*, *dorsata*, and *pictetii* all have a small barely projecting mesal sclerite of the U-shaped loop. Thus, it is likely that this mesal projection was barely extended from the U-shaped loop present in the immediate common ancestor of both the *californica*-*princeps* branch and the *dorsata*-*pictetii* branch and its much greater length in *princeps* is, therefore, derivative. The posterior region of the inner membranous surface of the cowl of *princeps* becomes greatly narrowed posteriorly and is smooth and inflexible. Since this region in other members of *Pteronarcys* is fairly broad as well as flexible, it is likely that the condition of the posterior region of the inner surface of the cowl in *princeps* is derivative. The unique complex anterior sclerotized surface of the dorsal section of the supra-anal process of the *californica-princeps* group, as discussed previously, is derivative within *Pteronarcys*. Very probably in this group enlargement of this surface rather than reduction would be the evolutionary tendency. In *princeps*, as compared to *californica*, the relatively broad as well as elongate region of the anterior sclerotized surface between its basal extremity and posterior projecting arms is probably in the derivative state. The membranous nipple-like lobe situated at the posterior basal portion of the membranous apical region of the male subanal lobes is probably derivative since nothing approaching this somewhat bilobed condition of the subanal lobes is found in other members of *Pteronarcys*. It is interesting to note that in *californica* the vaginal projections of the female eighth sternite are more closely similar than are those of *princeps* to the projections of the already established primitive species *biloba* and *scotti*. Therefore, the vaginal projections present on the immediate common ancestor of both *californica* and *princeps* very probably resembled closely those found in the former species. Hence, the vaginal projections found in *princeps* are derivative. The apically broadly rounded median hemitergal lobes of the male tenth tergite of *californica* are less similar than are those of *princeps* to those of *proteus*. It is likely, then, that the median lobes present on the immediate common ancestor to *princeps* and *californica* more closely resemble those of the former species than those of *californica*. Thus, the larger median lobes of *californica* are considered derivative. The darkly sclerotized dorso-anterior lateral extremities of the outer basal plate of the cowl are very short in *californica*. These dorso-anterior extremities of the basal plate are quite elongate in all other members of *Pteronarcys* and, thus, in *californica* are considered derivative.

In the *dorsata-pictetii* branch dichotomic branching (12, Fig. 107) gave rise to the two unusually closely similar species, *dorsata* and *pictetii*. In *pictetii* the hind region of the elongate male subgenital plate bordering the notch is decurved ventrally. This region of the subgenital plate in all other members of *Pteronarcys* projects posteriorly. Therefore, it is likely that the condition of the subgenital plate in *pictetii* is derivative. The larger vaginal projections of *pictetii* are more similar than are the small variable projections of its sister species *dorsata* to those of the more primitive *biloba* and *scotti*. It is very likely, then, that the vaginal projections of the immediate common ancestor of both *pictetii* and *dorsata* more closely resembled those of the former species. Hence, the smaller projections of *dorsata* are considered to be in the derivative state.

Classification of the Pteronarcidae

The commonly accepted classification used for the Pteronarcidae originated largely from Needham and Claassen's (1925) classic work on North American stoneflies. For the family Pteronarcidae these workers recognized two genera, *Pteronarcella* and *Pteronarcys*, and within *Pteronarcys* they recognized two subgenera, *Allonarcys* and *Pteronarcys*. Ricker (1952) characterized the subgenus *Allonarcys* as containing those members of the genus *Pteronarcys* having a slender dorsally decurved supra-anal process and characterized the subgenus *Pteronarcys* as containing those species of the genus with a massive ventrally decurved supra-anal process. Recently, Illies (1966) elevated both of these subgenera to generic status. However, he mistakenly placed the Asian species of this family in *Pteronarcys* (*s.s.*), although they are clearly members of *Allonarcys* as characterized above.

In this study an examination of the cladistics of the Pteronarcidae has revealed *Allonarcys* as a paraphyletic group. The species *proteus* and *comstocki*, for example, are more closely related to the species of *Pteronarcys* (*s.s.*) than are they to any other member of *Allonarcys*. If a classification is to reflect the cladogeny of any particular group being studied, then it must consist of taxonomic categories the taxa of which are monophyletic. Within *Pteronarcys* (*s.l.*) only two major monophyletic groupings appear to exist, one which comprises the Asian species of this group and one which comprises the North American species. The use of generic or subgeneric categories for each of these monophyletic groups would entail designating a new name for that taxon comprising the Asian species. However, it would probably be more prudent to wait until the cladistics of the Pteronarcidae are more secure. Thus, the possibility of burdening the zoological nomenclature with a name that eventually might have to be abandoned is avoided without causing working difficulties since *Pteronarcys* (*s.l.*) can be nicely divided, informally but yet genealogically, into several distinct natural groups of closely related species.

In an earlier study on this genus Klapalek (1907) utilized the informal category of the species "Gruppe" to subdivide this genus. The use of the species group category has the dual advantage of not introducing new names to the zoological nomenclature for groups separated by only a few minor differences, but yet permits easy recognition of different groups of species within a genus. Klapalek's use of this category almost 40 years ago before its accepted use in the Plecoptera, produced a classification of *Pteronarcys* considerably more detailed and more accurate than that utilized today. The following classification of *Pteronarcys* is adopted, with a few minor modifications, from Klapalek's (1907) study:

Genus *Pteronarcys*

1. group *reticulata*
   P. reticulata
   P. sachalina
   P. excavata

2. group *biloba*
   P. biloba

3. group *scotti*
   P. scotti
4. group *proteus*
   P. proteus
   P. comstocki
5. group *californica*
   P. californica
   P. princeps
6. group *dorsata*
   P. dorsata
   P. pictetii

Thus, the family Pteronarcidae is considered as consisting of two genera, *Pteronarcella* and *Pteronarcys*, the latter with six species groups but without subgeneric divisions.

ABBREVIATIONS

ab-anterior basalare

ads-apical region of dorsal section of supra-anal process

aes-anepisternum

ahl-anterior hemitergal lobe

al-alifer

anp-anterior notal wing process

apc-anapleural cleft

apl-anapleurite

ao-anal opening

ar-arolium

as-antennal suture

asc-antennal sclerites

ata-anterior tentorial arms

atg-acrotergite

1,2,3-axillary sclerites

bc-basicardo

bcx-basicoxite

bds-basal region of dorsal section of supra-anal process

bg-basigalea

bp-basal plates

bs-basisternum

C-costa

ce-cercus

cl-clypeus

co-cowl
cpl-catapleurite
ct-corpotentorium
Cu-cubitus
CuA-anterior cubitus
CuP-posterior cubitus
cx-coxa
d-myodiscus
dc-disticardo
dg-distigalea
dl-dorsal lobes
ds-dorsal section of supra-anal process
dta-dorsal tentorial arm
ecl-ecdysial cleavage line
epi-epiproct
epm-epimeron
eye-compound eye
fa-furcal arms
fcs-frontoclypeal suture
fe-femur
fgr-frontogenal ridge
fgs-frontogenal suture
fls-fork-like structure of supra-anal process
fp-free part of supra-anal process

fr-frons
fs-furcasternum
gl-glossa
go-genital opening
gp-gonopore
hm-hypostoma
hms-hypostomal suture
hp-humeral plate
ip-inner part of supra-anal process
kes-katepisternum
1,2,3,-segments of the labial palpus
la-lacinia
lb-lateral brace
lbi-labiostipites
lc-lateral cervical sclerites
lr-labrum
lsh-lingual sclerites
m-distal median plate
M-media
MA-anterior media
1,2,3,4,5-segments of the maxillary palpus
md-mandible
me-meron
mem-membranous layer of apical piece of supra-anal process
mhl-median hemitergal lobe

mhp-mesal hemitergal lobe
mn-mentum
MP-posterior media
mxp-maxillary palpus
oc-ocelli
occ-occipital condyle
os-ocular suture
osc-ocular sclerite
or-orbicula
p-pedicel
par-parietal
pb-posterior basalare
pfs-postfurcasternum
pgl-paraglossae
pgp-paragenital plate
phl-posterior hemitergal lobe
pl-plateau
pm-pleurostoma
pms-pleurostomal suture
pnp-posterior notal wing process
poa-postalar bridge
poc-postocciput
pocs-postoccipital suture
pra-prealar bridge
pres-pre-episternum

ps-presternum

psc-prescutum

pscl-postscutellum

psi-parastipes

pta-posterior tentorial arm

ptar-pretarsus

R-radius

RA-anterior radius

RS-radial sector

s-scape

sa-supra-anal process

sbl-sub-anal lobe

sc-sclerite of apical piece of supra-anal process

Sc-subcosta

scl-scutellar shield

scl'-scutellar ridge

sct-scutum

si-stipes

sm-submentum

sp-spiracle

ss-spinasternum

st-sternite

su-spatula of supra-anal process

sub-anterior and posterior subalare

sus-hypopharyngeal suspensorium

t-tergite

ta-tarsus

tc-tentorial callosities

tg-tegula

ti-tibia

tn-trochantin

tp-trough-shaped process of supra-anal process

tr-trochanter

u-U-shaped sclerite of supra-anal process

un-unguitractor

unt-unguitractoral tendon

Va-vannal vein

vf-vannal fold

vpl-ventro pleurite

vs-ventral section of supra-anal process

vp-vaginal projections

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EXPLANATION OF PLATES

PLATE I

Fig. 1. Head capsule, dorsal view

2. Head capsule and tentorium, ventral view

3. Head capsule, lateral view

4. Head capsule, anterior view

PLATE II

Fig. 5. Head capsule and mouthparts, ventral view

6. Labium, ventral view

7. Right mandible, biased ventral view

8. Left mandible, biased dorsal view

9. Hypopharynx, ventral view

10. Hypopharynx, lateral view

11. Hypopharynx, biased dorsal view

12. Left maxilla, ventral view

13. Right maxilla, dorsal view

PLATE III

Fig. 14. Thoracic tergum

PLATE IV

Fig. 15. Thoracic pleuron

PLATE V

Fig. 16. Thoracic sternum

PLATE VI

Fig. 17. Prothoracic furcasternum and spinasternum, dorsal (internal) view

18. Mesothoracic furcasternum and spinasternum, dorsal (internal) view

19. Metathoracic furcasternum, dorsal (internal) view

20. Metathoracic leg, anterior view

21. Pretarsus and distitarsus of metathoracic leg, dorsal view

22. Pretarsus and distitarsus of metathoracic leg, ventral view

PLATE VII

Fig. 23. Forewing of *Pteronarcella regularis*

24. Hindwing of *Pteronarcella regularis*

25. Brachypterous forewing of *Pteronarcella badia*

26. Brachypterous hindwing of *Pteronarcella badia*

PLATE VIII

Terminalia of *P. regularis*

Fig. 27. Male genitalia, dorsal view

28. Male genitalia, ventral view

29. Male genitalia, lateral view

PLATE IX

Terminalia of *P. regularis*

Fig. 30. Supra-anal process, anterior view

31. Supra-anal process, posterior view

32. Supra-anal process, lateral view

33. Sagittal section of apical piece of supra-anal process, lateral view

34. Female genitalia, ventral view

PLATE X

Terminalia of *P. badia*

Fig. 35. Male genitalia, dorsal view

36. Male genitalia, ventral view

37. Male genitalia, lateral view

PLATE XI

Terminalia of *P. badia*

Fig. 38. Supra-anal process, anterior view

39. Supra-anal process, posterior view

40. Supra-anal process, lateral view

41a. Frontal section of apical piece of supra-anal process, dorsal view

41b. Sagittal section of apical piece of supra-anal process, lateral view

42. Female genitalia, ventral view

PLATE XII

Terminalia of *P. reticulata*

Fig. 43. Male genitalia, dorsal view
44. Male genitalia, ventral view
45. Male genitalia, lateral view

PLATE XIII

Terminalia of *P. reticulata*

Fig. 46. Supra-anal process, anterior view
47. Supra-anal process, lateral view
48. Supra-anal process, posterior view
49. Female genitalia, ventral view

PLATE XIV

Terminalia of *P. excavata*

Fig. 50. Male genitalia, dorsal view
51. Male genitalia, ventral view
52. Male genitalia, lateral view

PLATE XV

Terminalia of *P. excavata*

Fig. 53. Supra-anal process, anterior view
54. Supra-anal process, lateral view
55. Supra-anal process, posterior view
56. Female genitalia, ventral view

PLATE XVI

Terminalia of *P. biloba*

Fig. 57. Male genitalia, dorsal view

58. Male genitalia, ventral view

59. Male genitalia, lateral view

PLATE XVII

Terminalia of *P. biloba*

Fig. 60. Supra-anal process, anterior view

61. Supra-anal process, lateral view

62. Supra-anal process, posterior view

63. Female genitalia, ventral view

PLATE XVIII

Terminalia of *P. scotti*

Fig. 64. Male genitalia, dorsal view

65. Male genitalia, ventral view

66. Male genitalia, lateral view

PLATE XIX

Terminalia of *P. scotti*

Fig. 67. Supra-anal process, anterior view

68. Supra-anal process, lateral view

69. Supra-anal process, posterior view

70. Female genitalia, ventral view

PLATE XX

Terminalia of *P. proteus*

Fig. 71. Male genitalia, dorsal view

72. Male genitalia, ventral view

73. Male genitalia, lateral view

PLATE XXI

Terminalia of *P. proteus*

Fig. 74. Supra-anal process, anterior view

75. Supra-anal process, lateral view

76. Supra-anal process, posterior view

PLATE XXII

Fig. 77. *P. proteus*, female genitalia, ventral view

78. *P. comstocki*, female genitalia, ventral view

PLATE XXIII

Terminalia of *P. californica*

Fig. 79. Male genitalia, dorsal view

80. Male genitalia, ventral view

81. Male genitalia, lateral view

PLATE XXIV

Terminalia of *P. californica*

Fig. 82. Supra-anal process, anterior view

83. Supra-anal process, lateral view

84. Supra-anal process, posterior view

85. Female genitalia, ventral view

PLATE XXV

Terminalia of _P. princeps_

Fig. 86. Male genitalia, dorsal view

87. Male genitalia, ventral view

88. Male genitalia, lateral view

PLATE XXVI

Terminalia of _P. princeps_

Fig. 89. Supra-anal process, dorsal view

90. Supra-anal process, lateral view

91. Supra-anal process, ventral view

92. Female genitalia, ventral view

PLATE XXVII

Terminalia of _P. dorsata_

Fig. 93. Male genitalia, dorsal view

94. Male genitalia, ventral view

95. Male genitalia, lateral view

PLATE XXVIII

Terminalia of _P. dorsata_

Fig. 96. Supra-anal process, anterior view

97. Supra-anal process, lateral view

98. Supra-anal process, ventral view

99. Female genitalia, ventral view

PLATE XXIX

Terminalia of *P. pictetii*

Fig. 100. Male genitalia, dorsal view

101. Male genitalia, ventral view

102. Male genitalia, lateral view

PLATE XXX

Terminalia of *P. pictetii*

Fig. 103. Supra-anal process, anterior view

104. Supra-anal process, lateral view

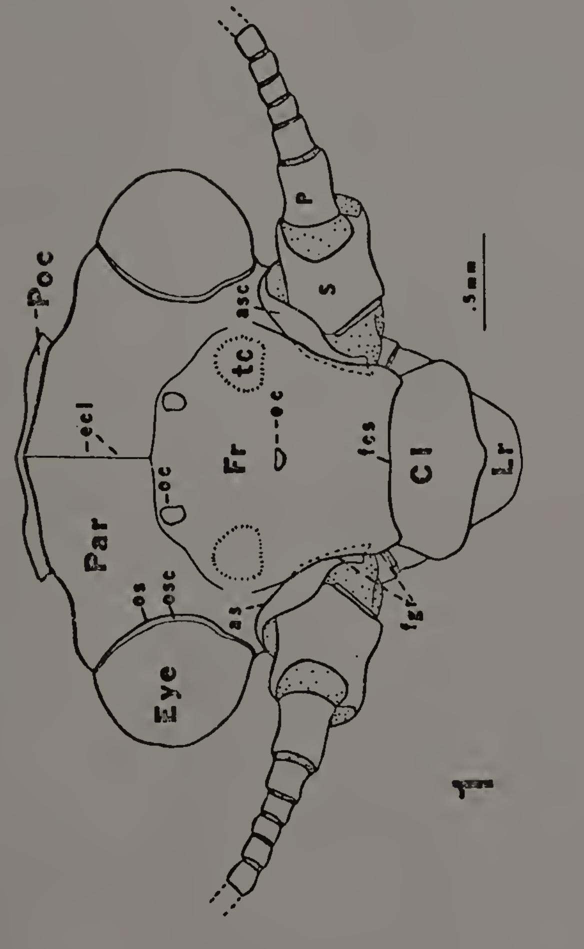
105. Supra-anal process, posterior view

106. Female genitalia, ventral view

PLATE XXXI

Fig. 107. Cladogram of the family Pteronarcidae

PLATE I



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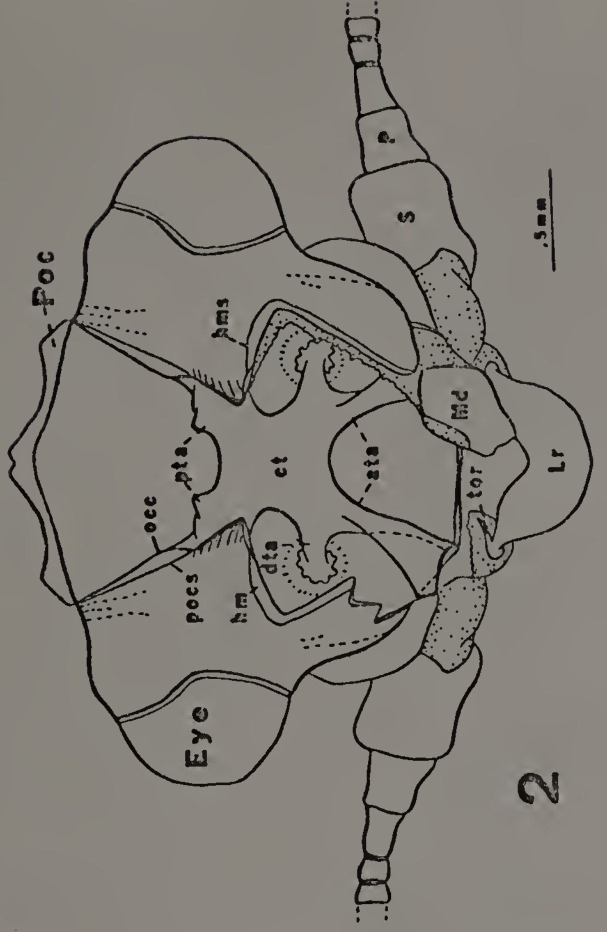

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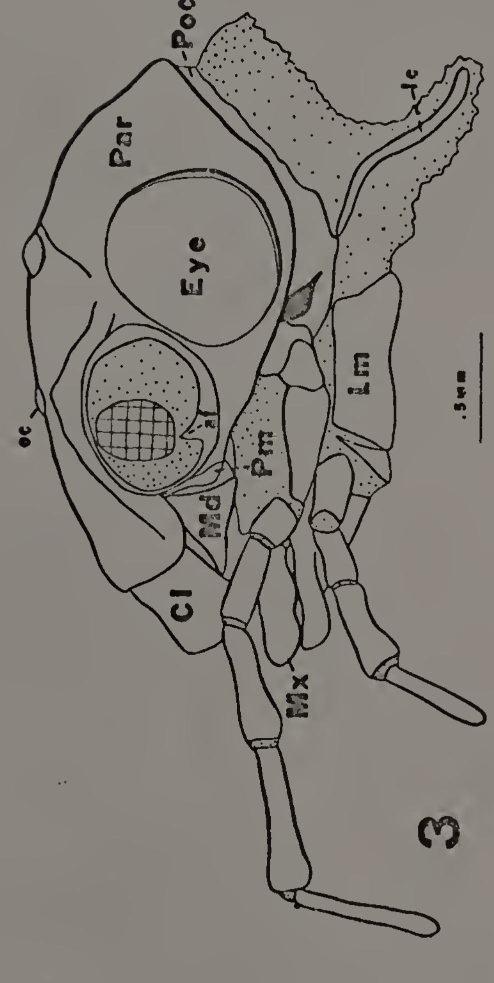

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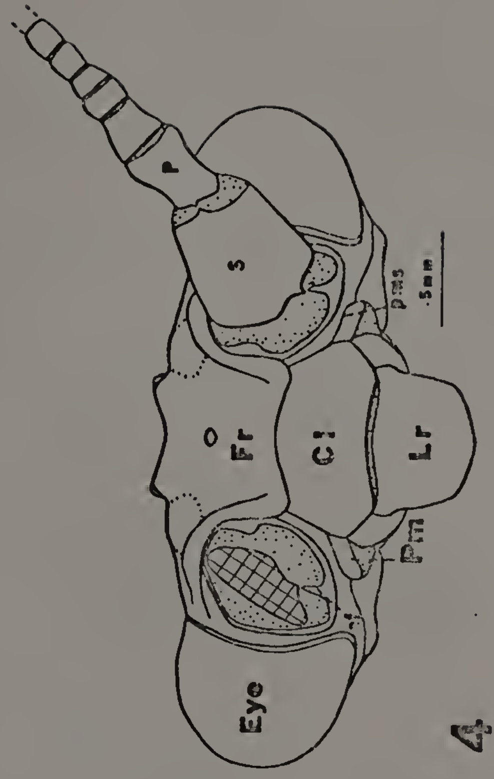

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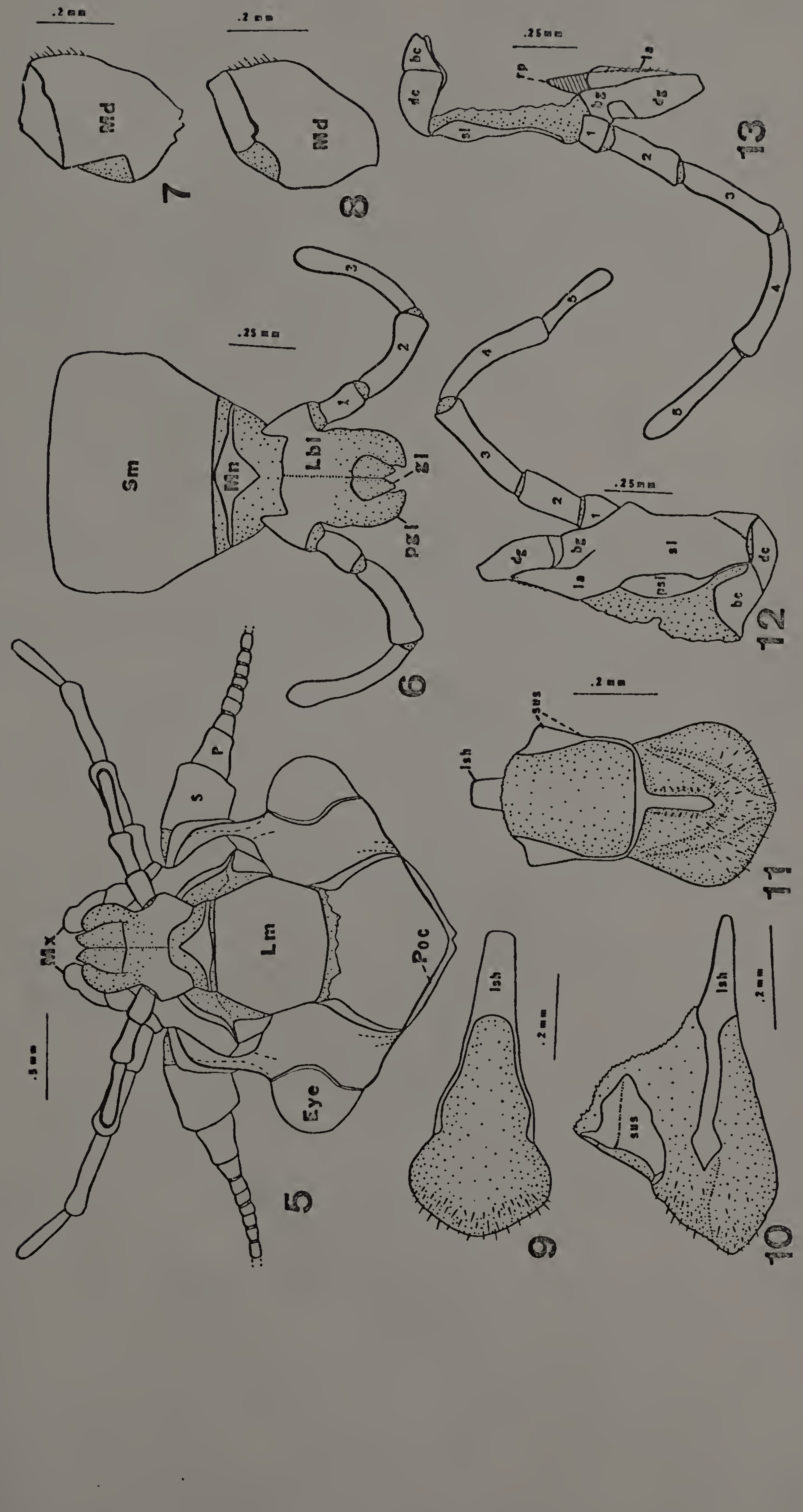
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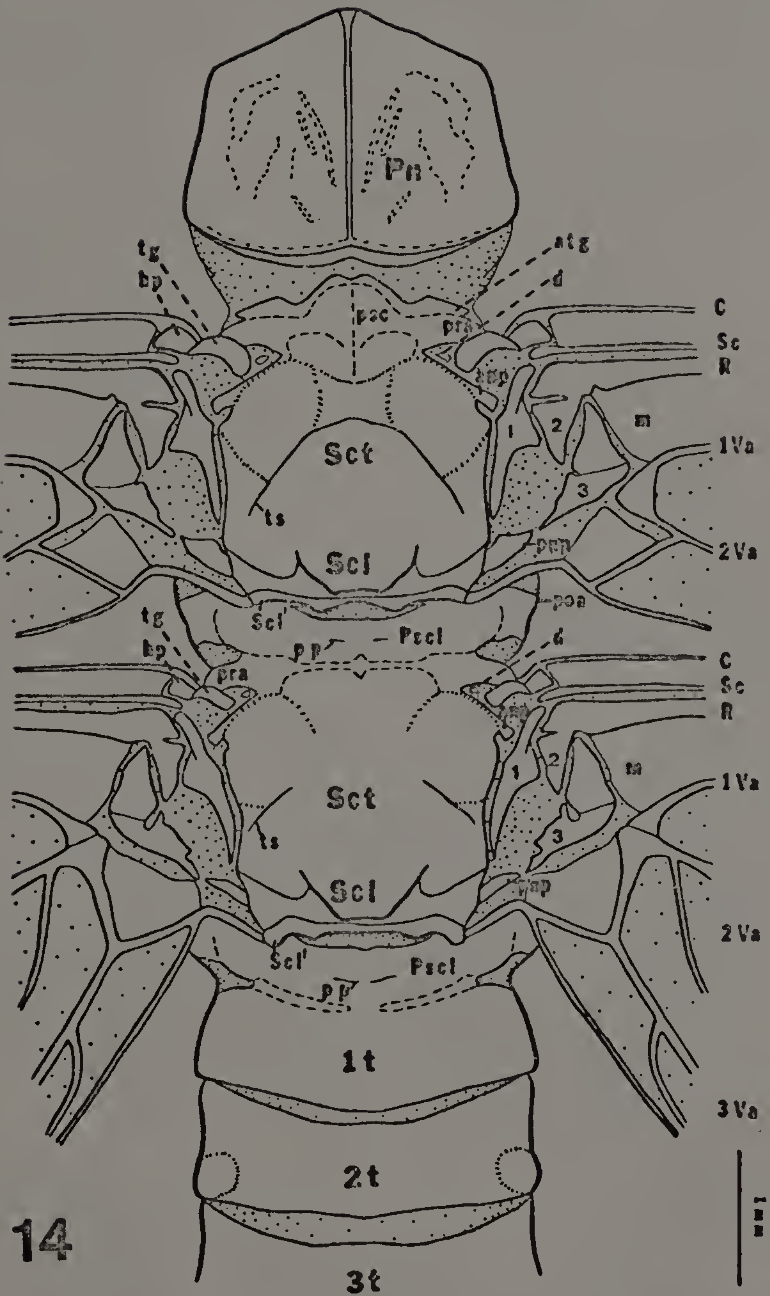
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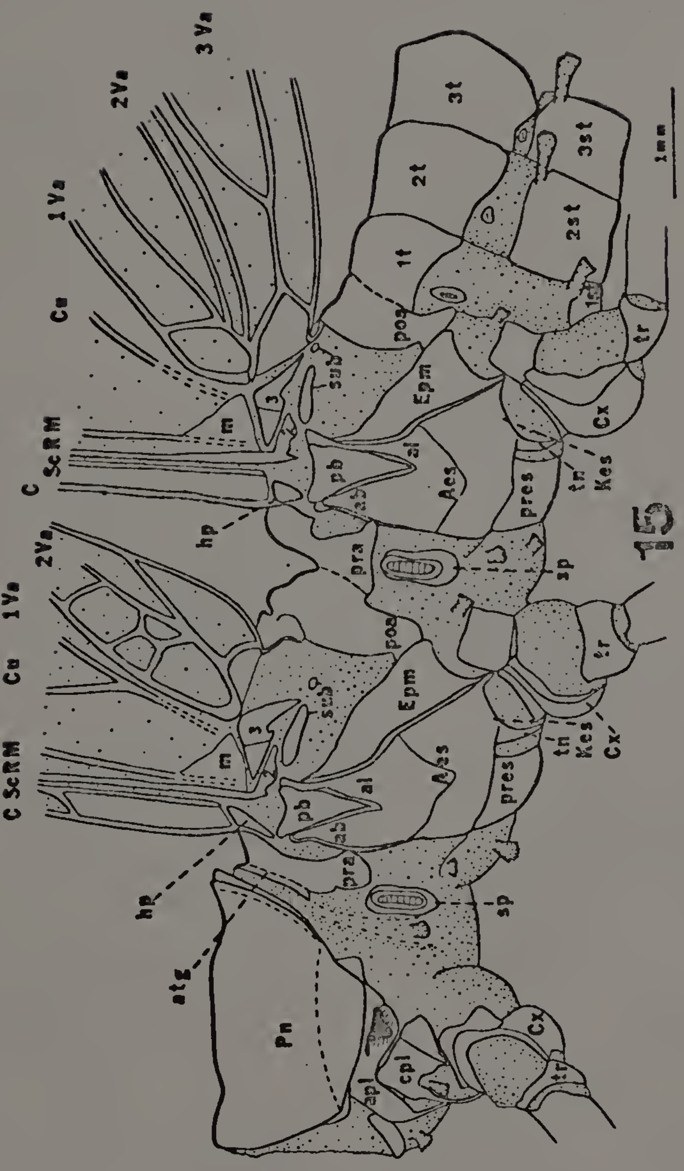
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PLATE V

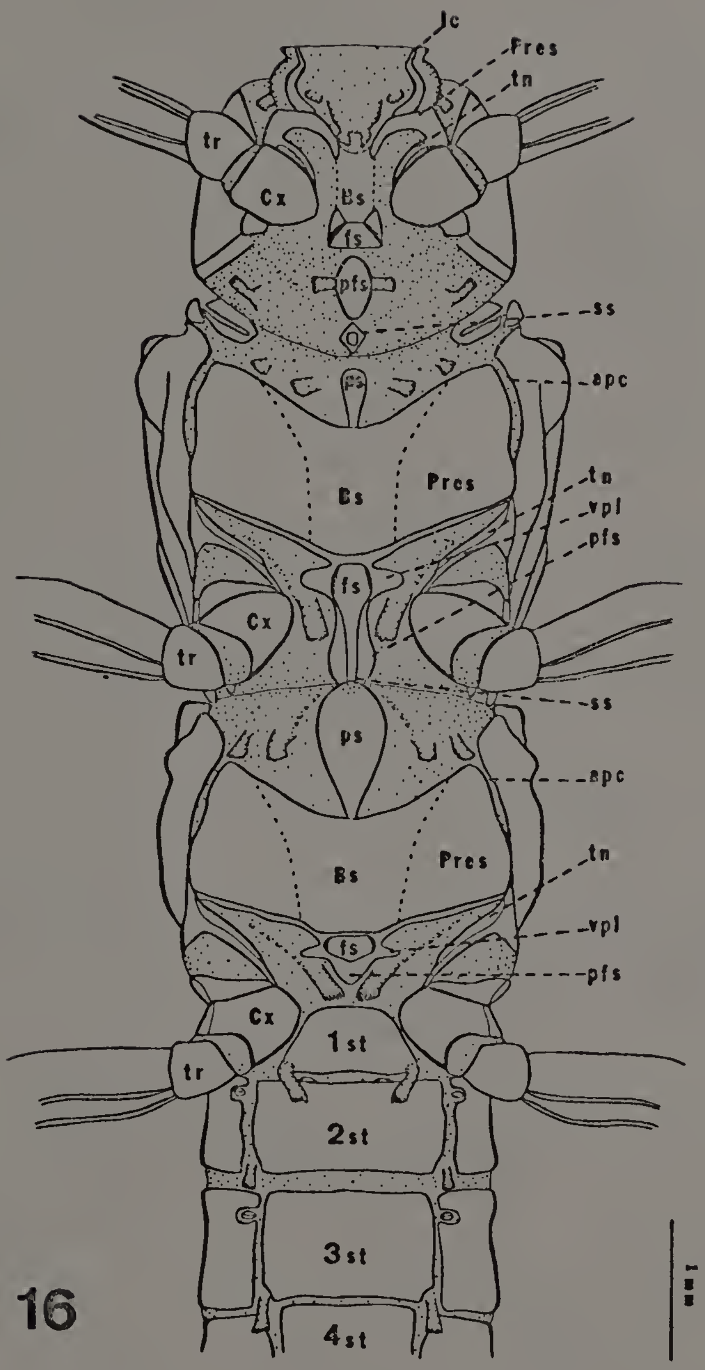
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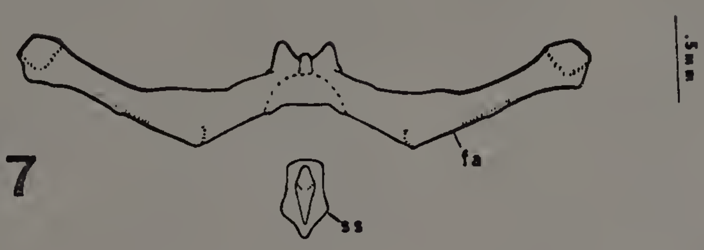
PLATE VI



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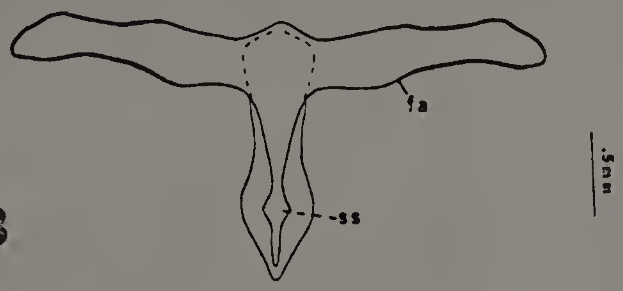

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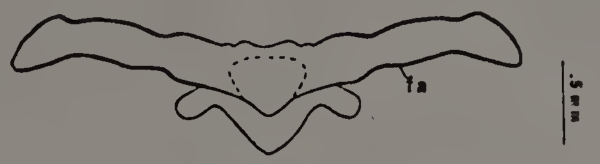

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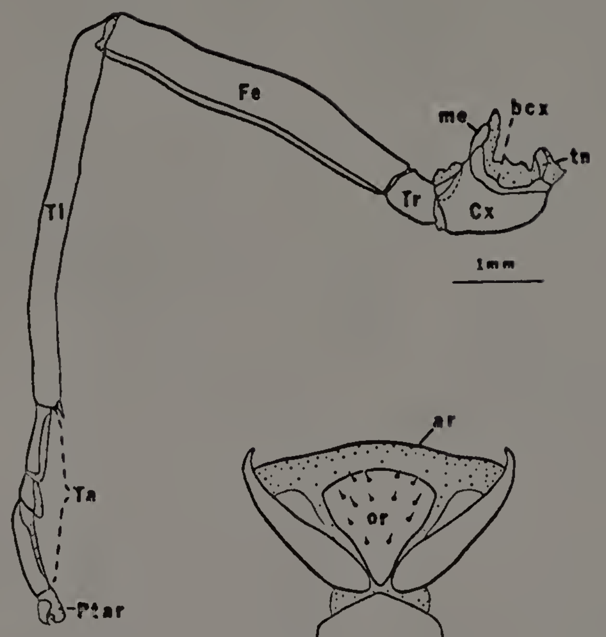

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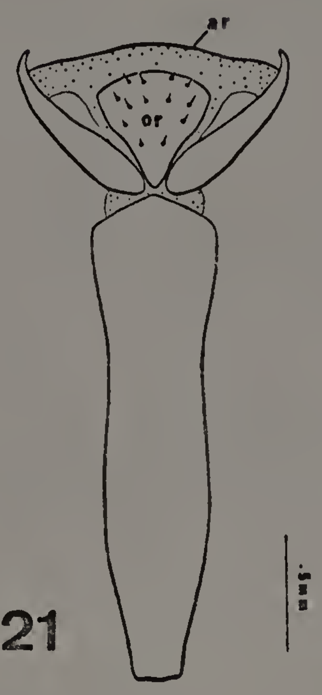

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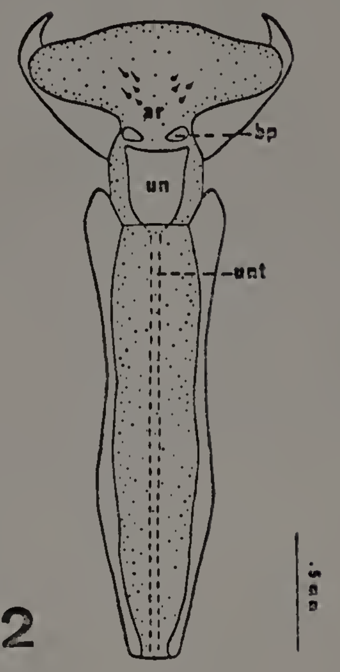

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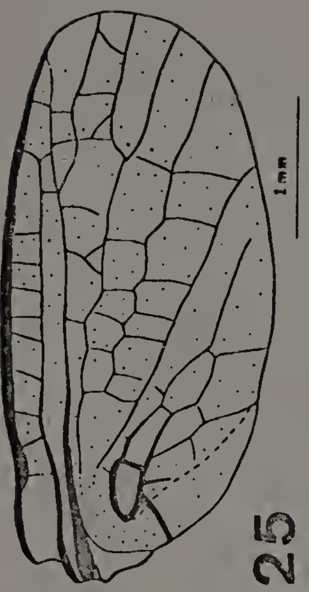
PLATE VII



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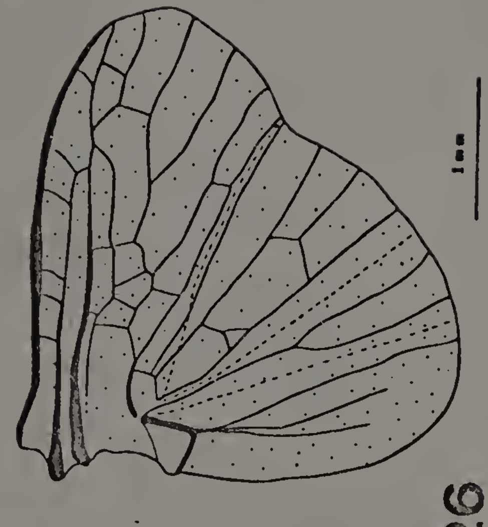

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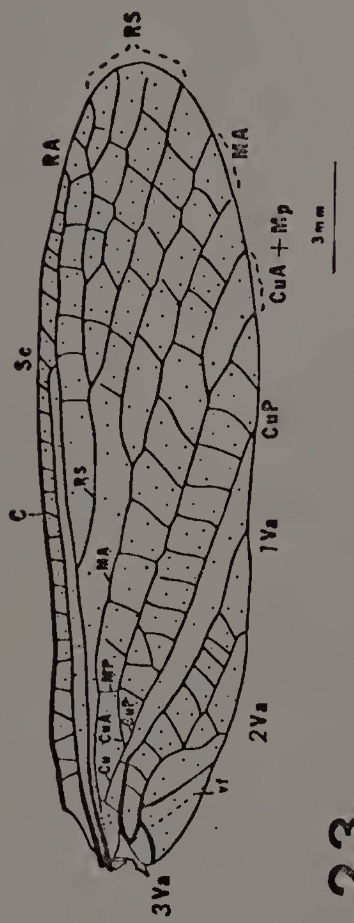

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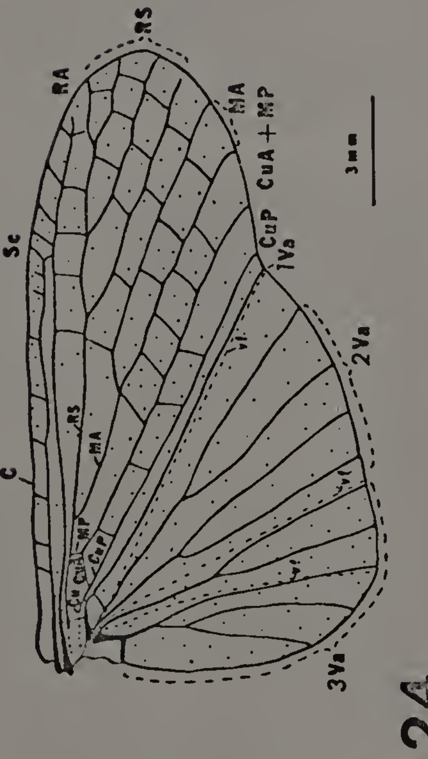

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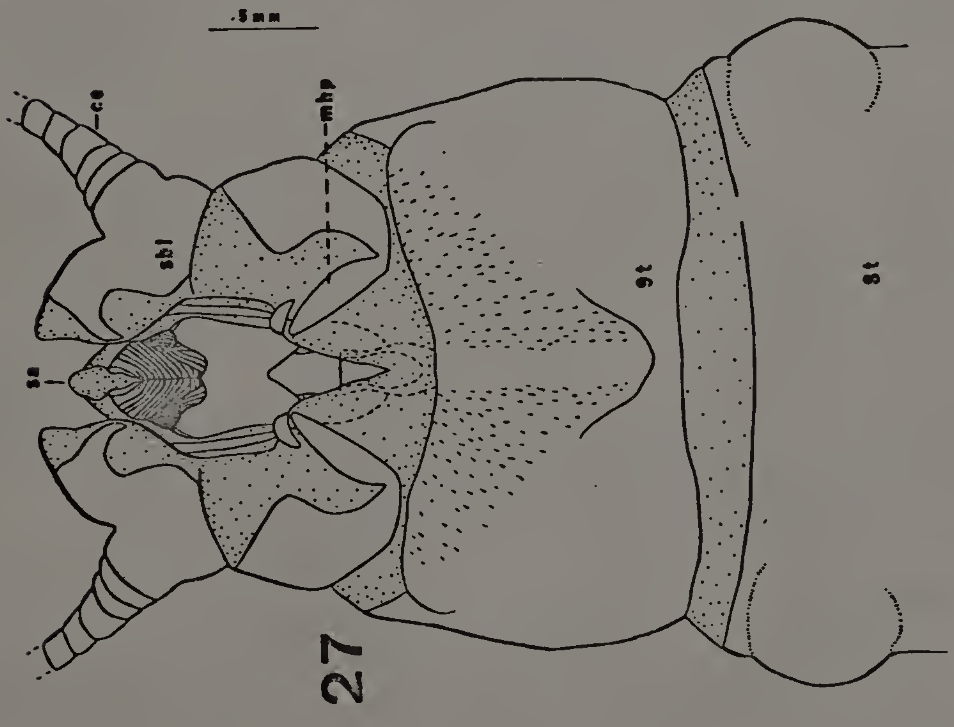

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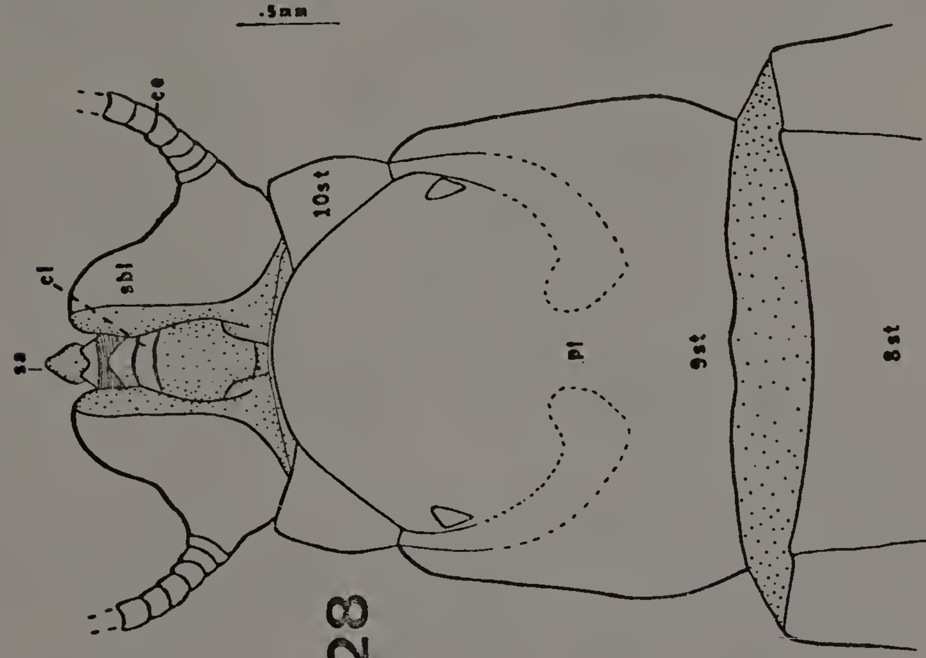

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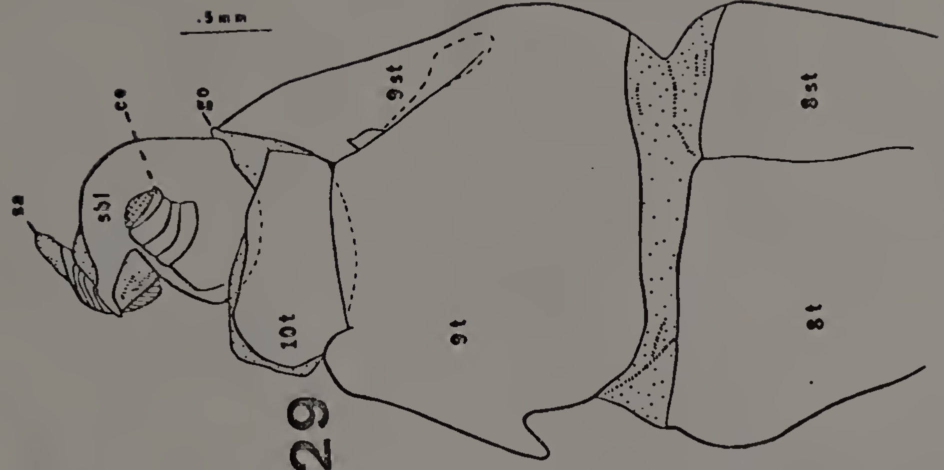

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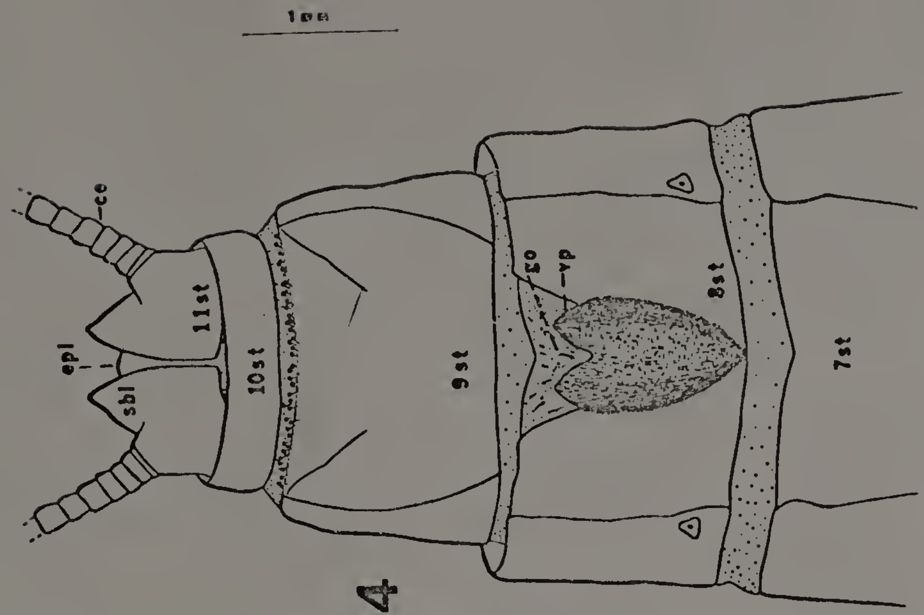

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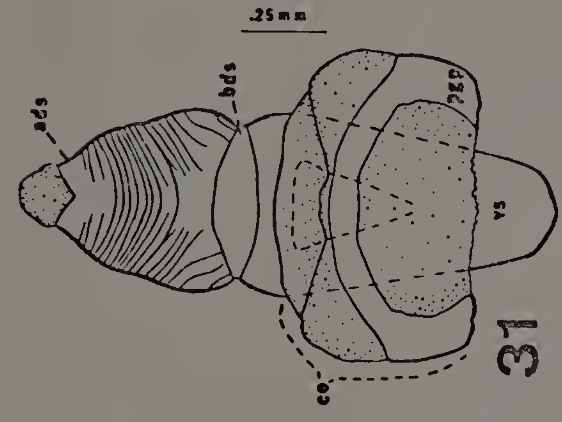

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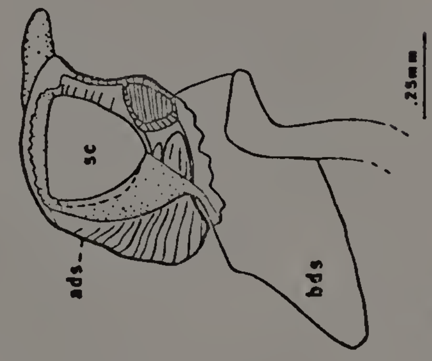

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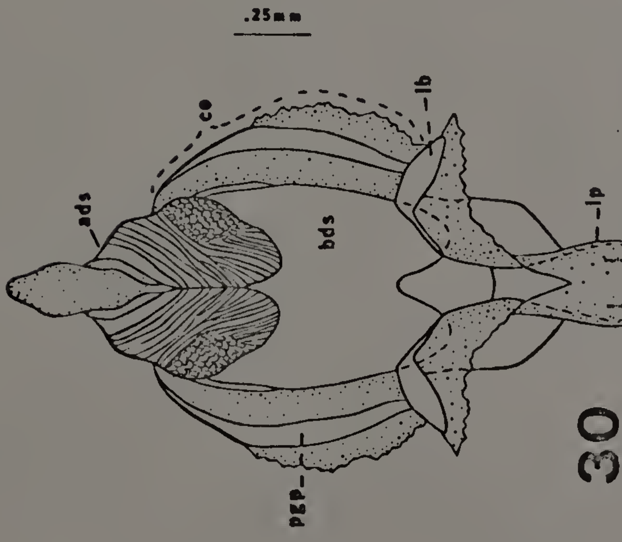

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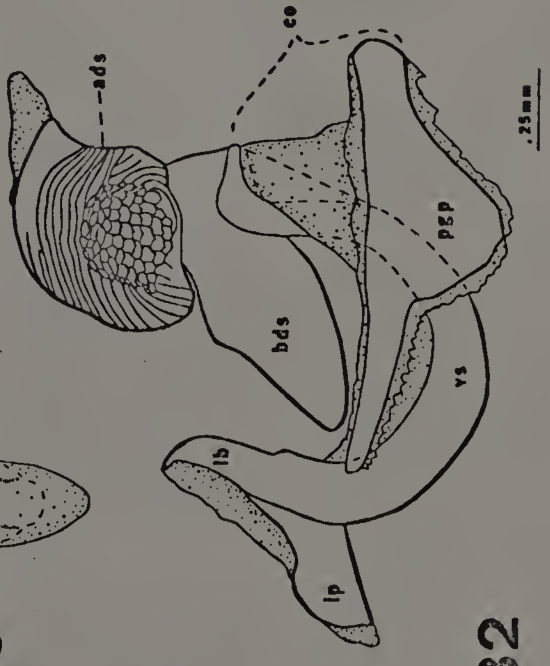

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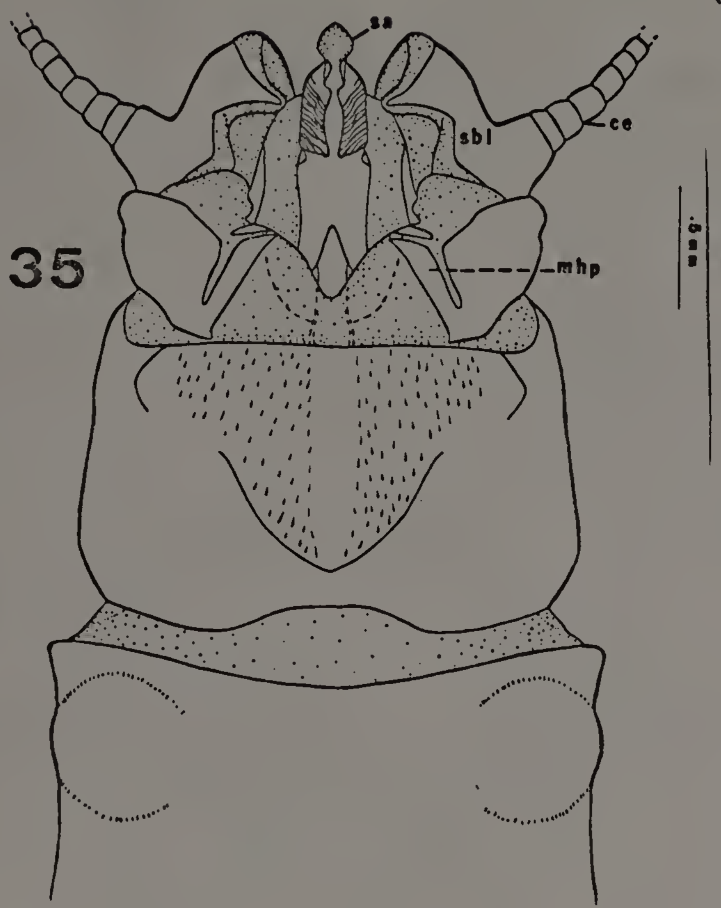

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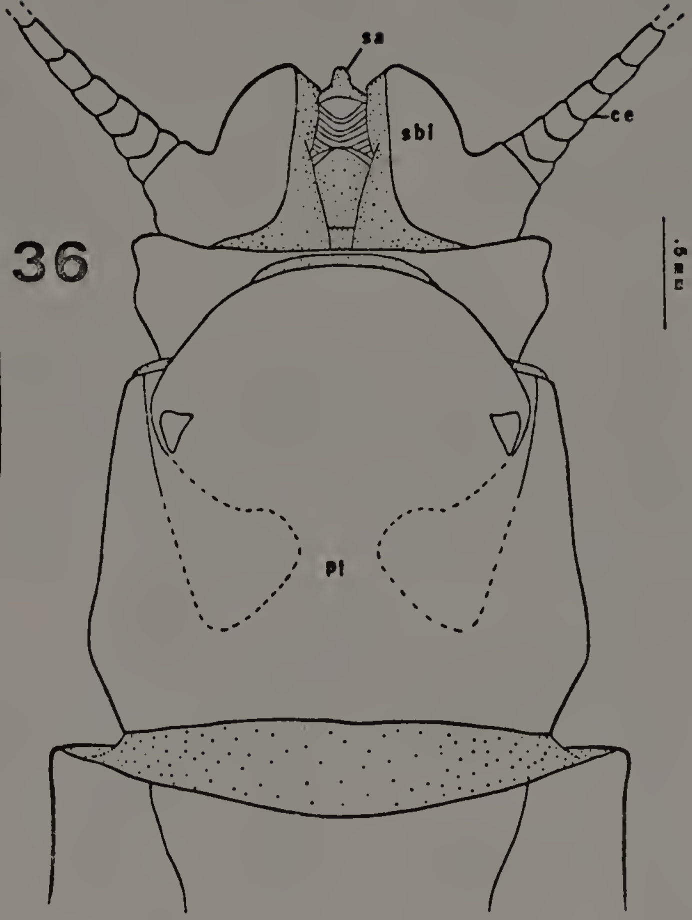

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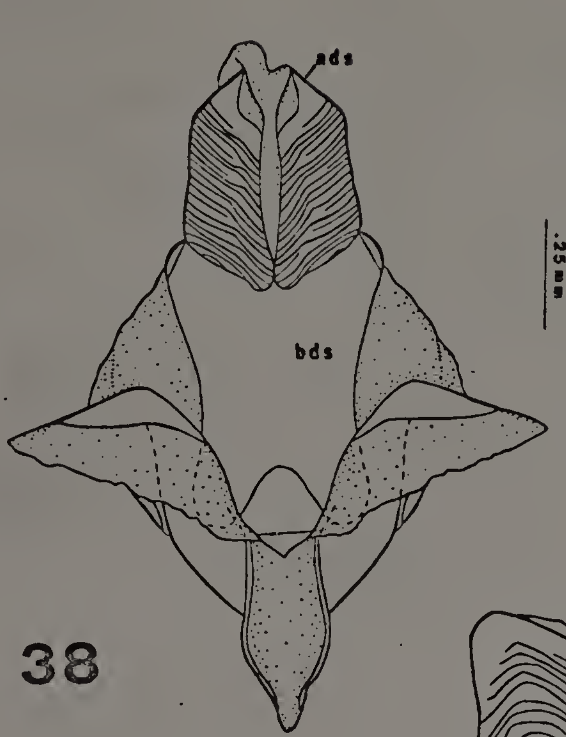

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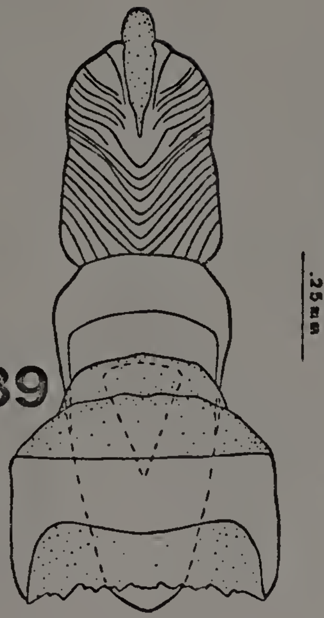

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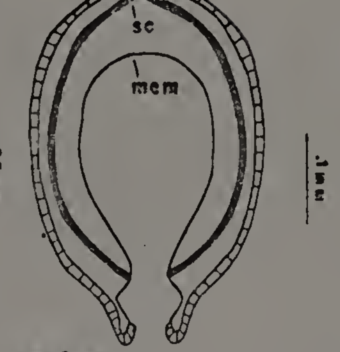

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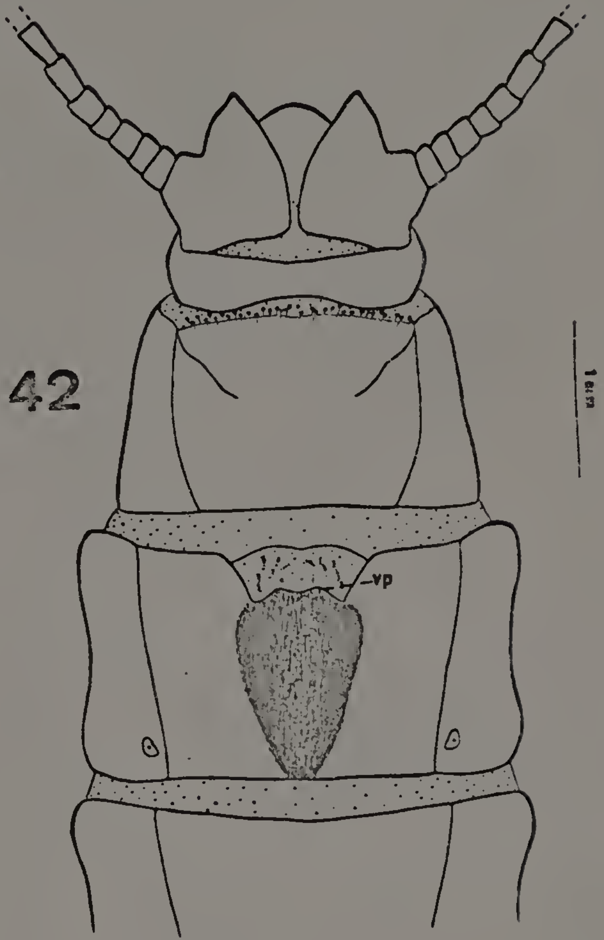

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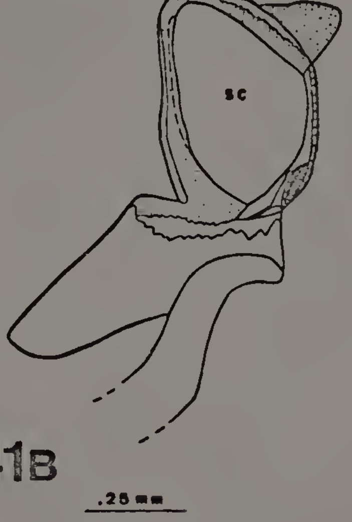

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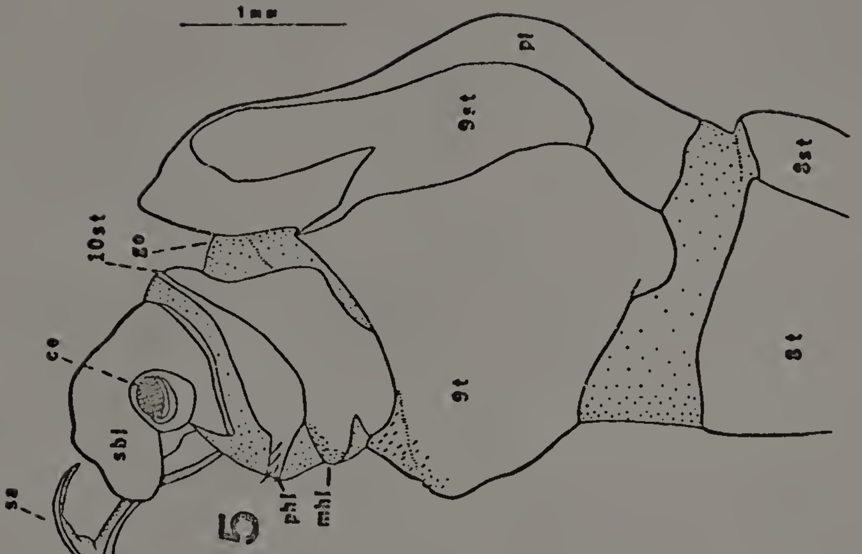

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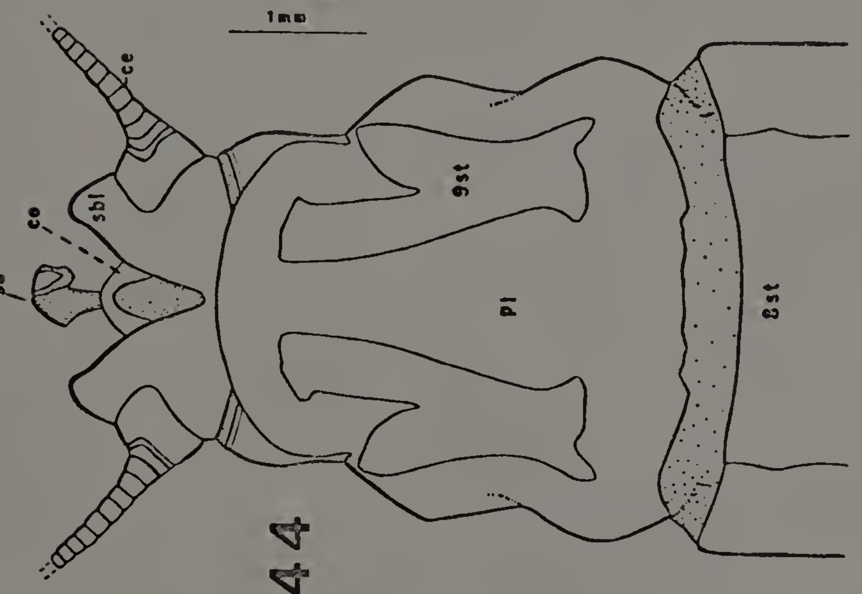

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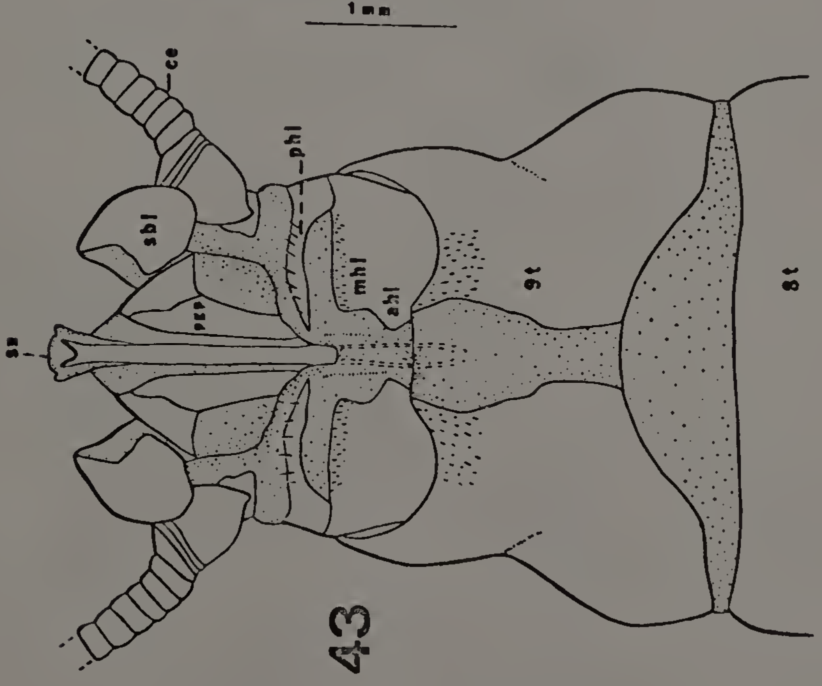

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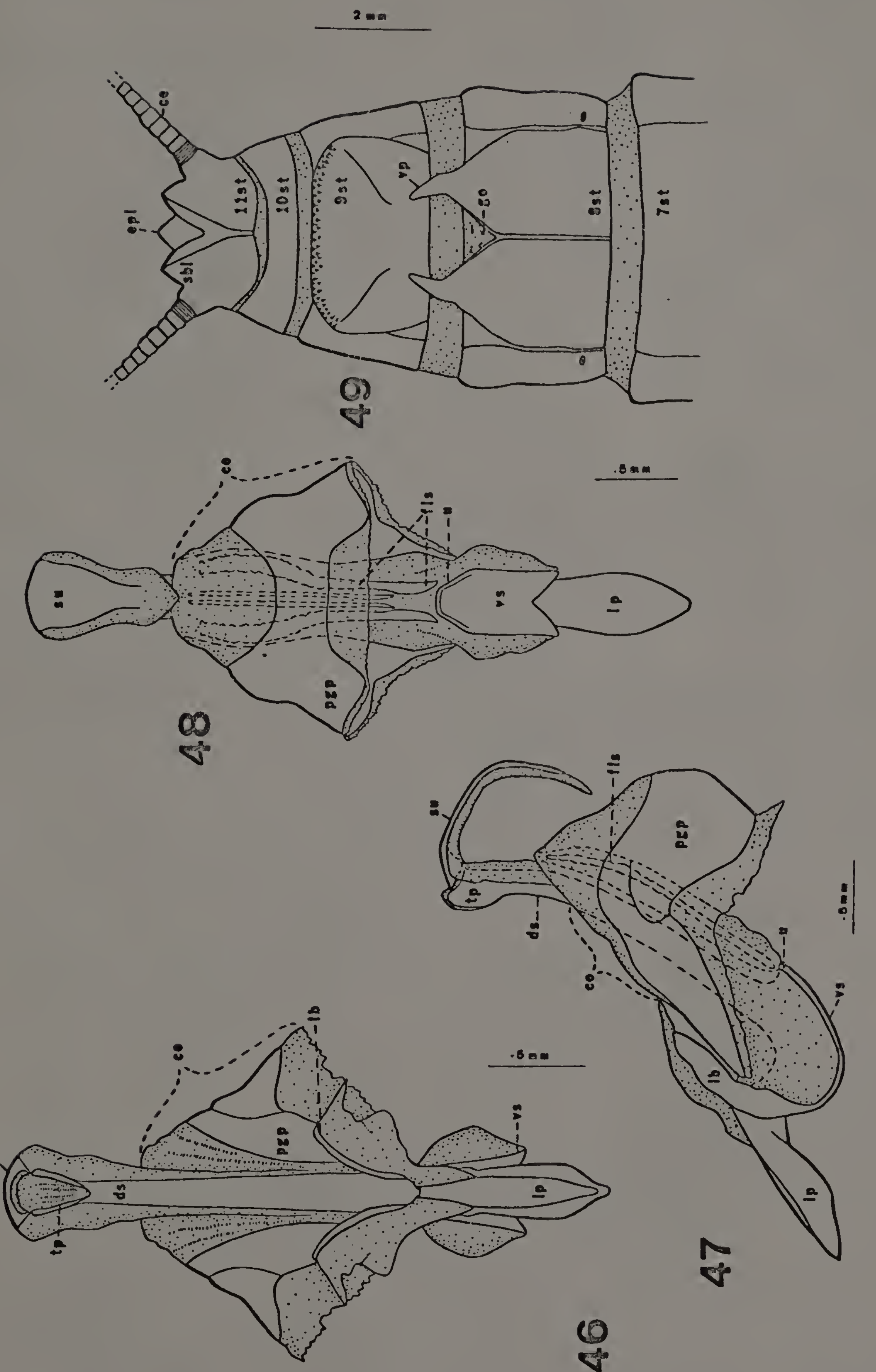

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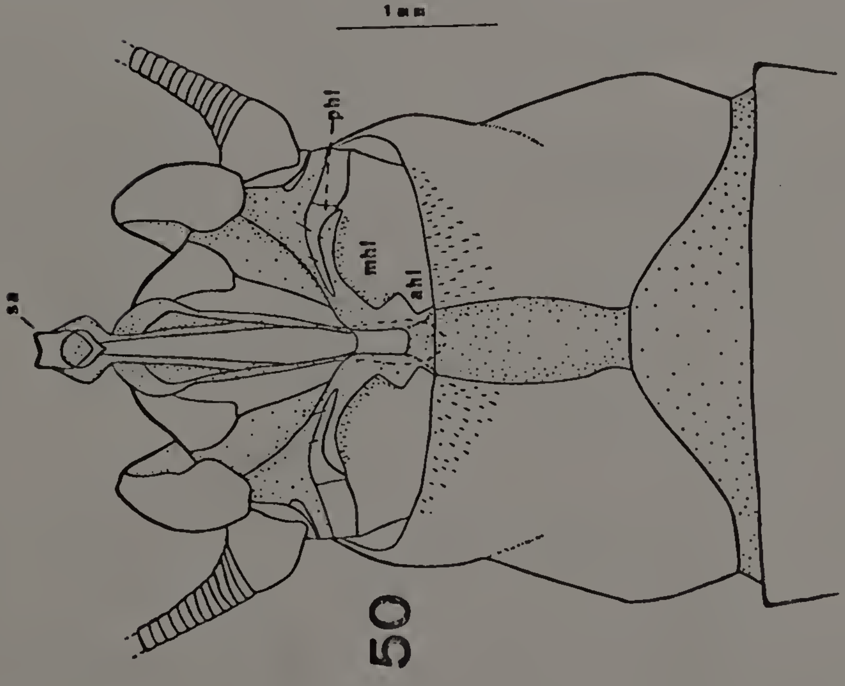

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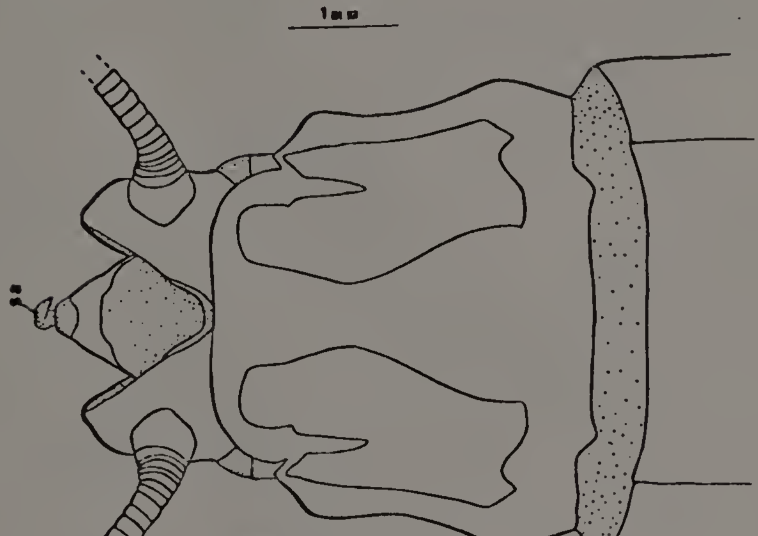

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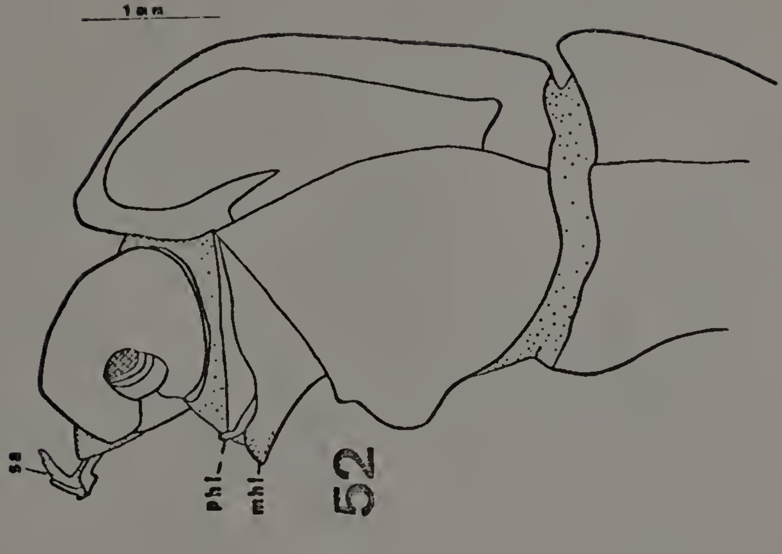

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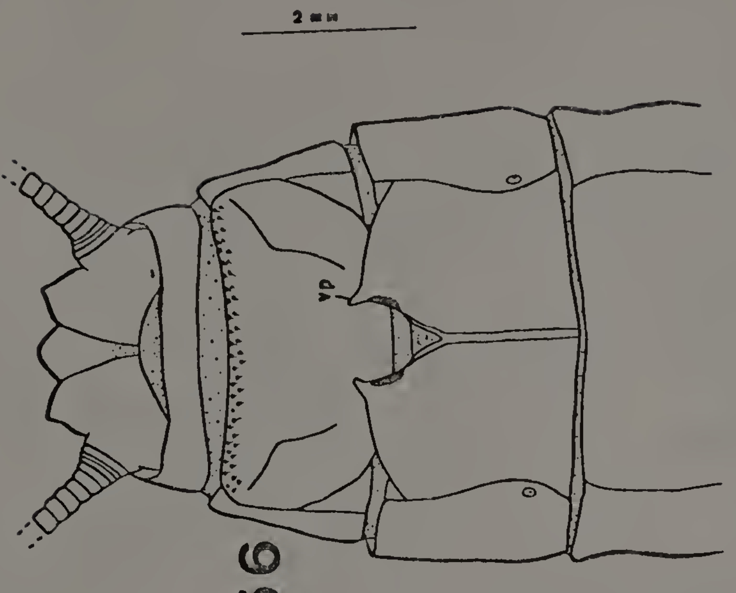

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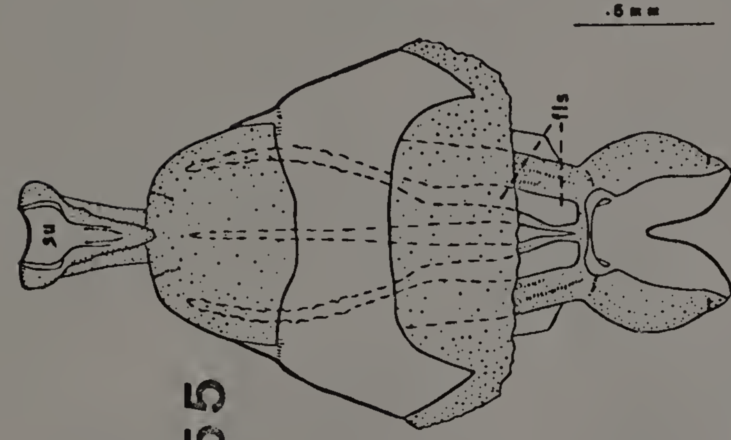

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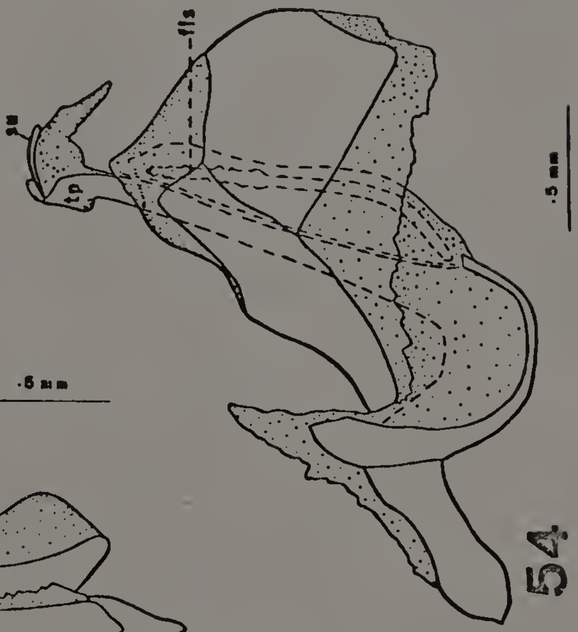

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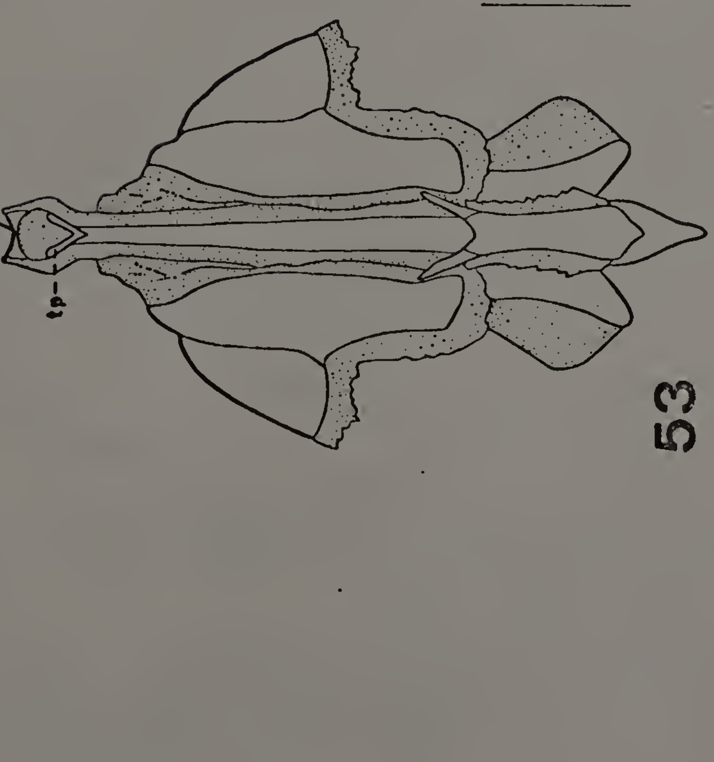

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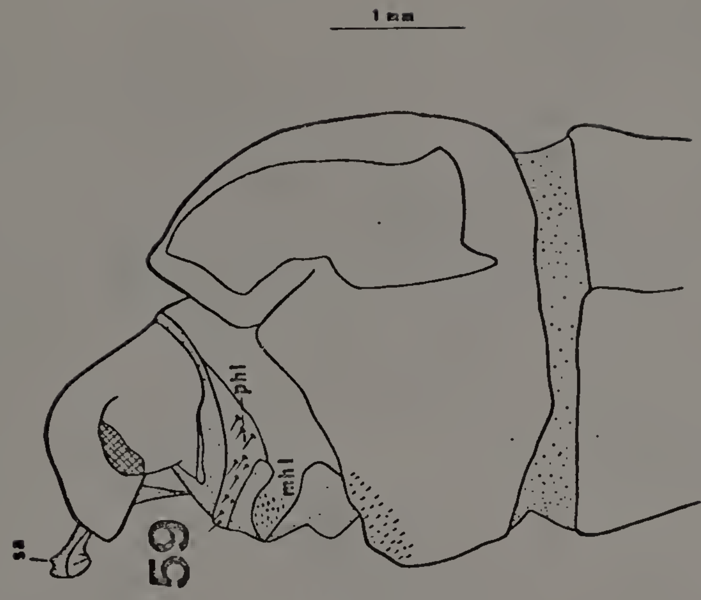

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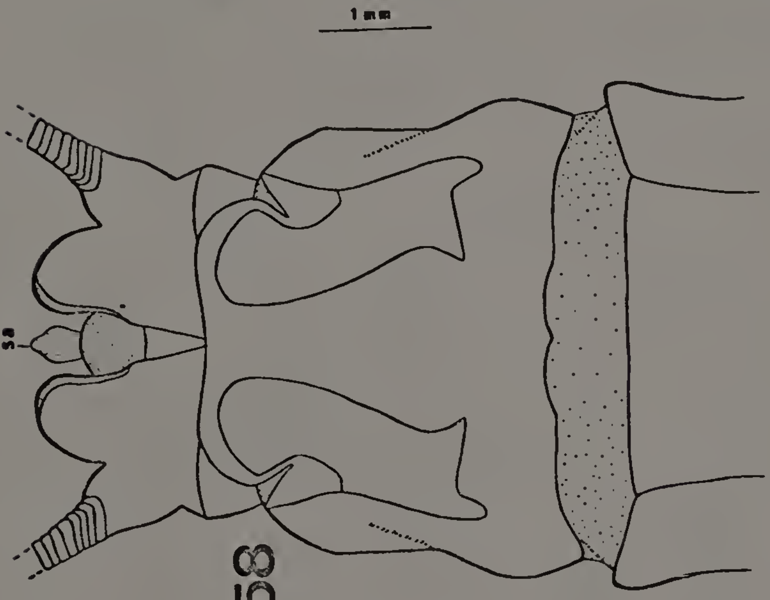

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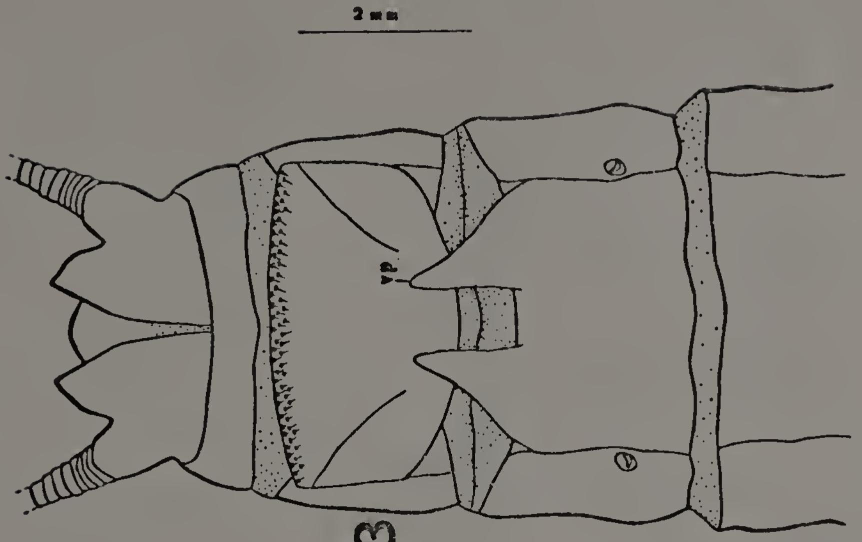

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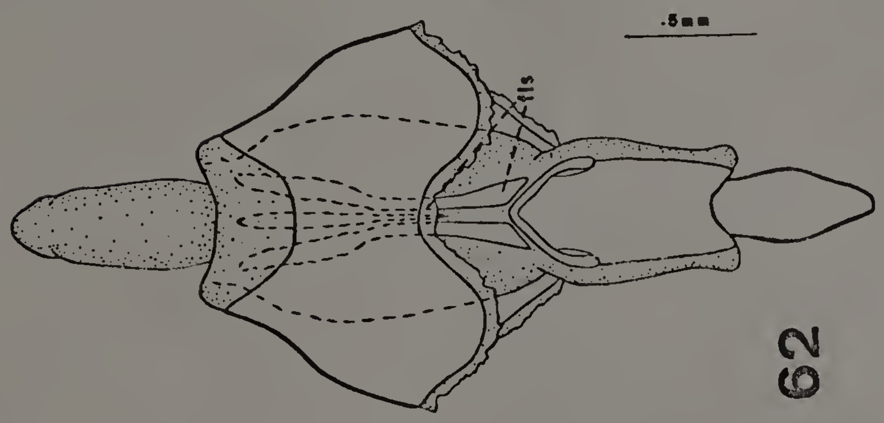

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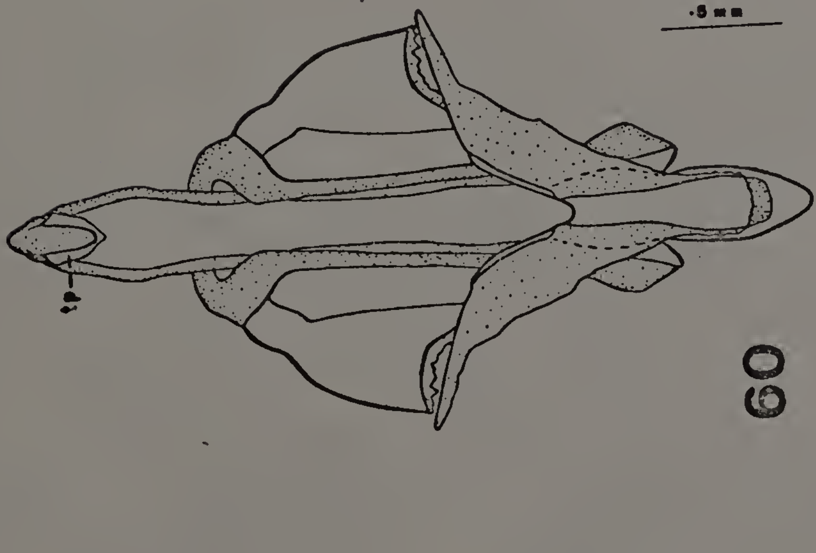

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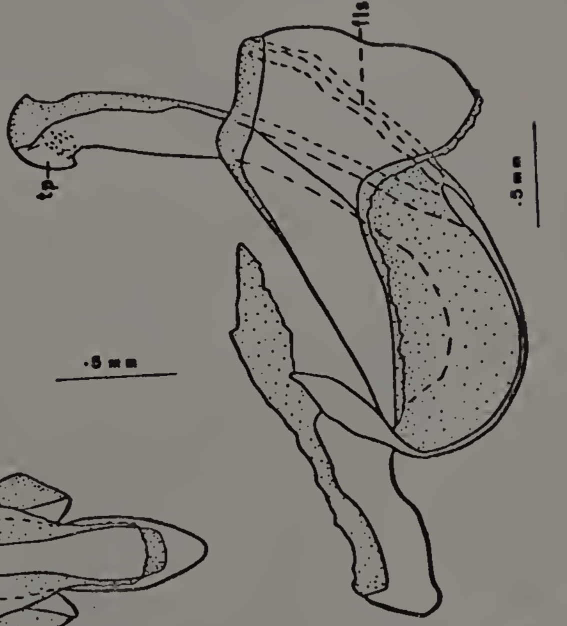

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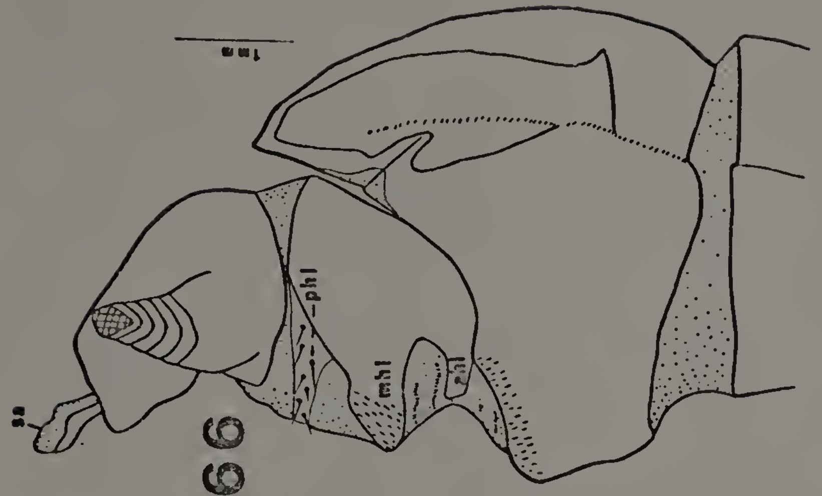

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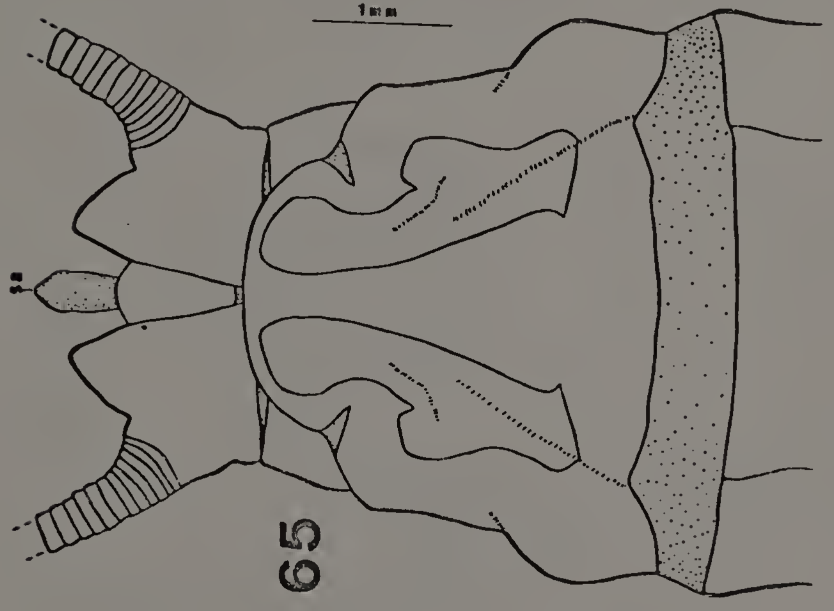

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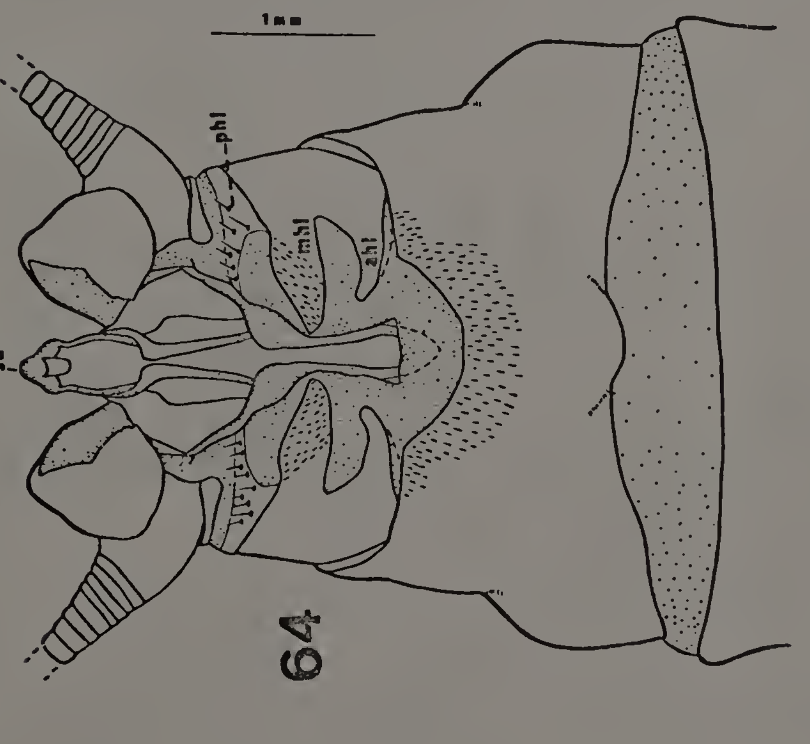

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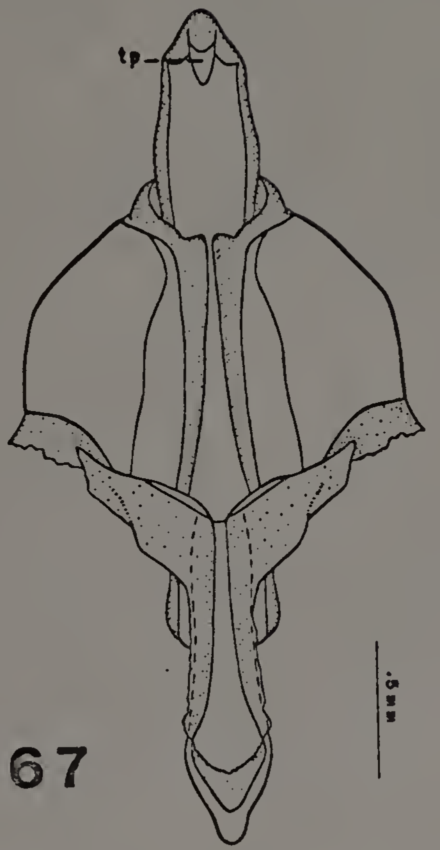

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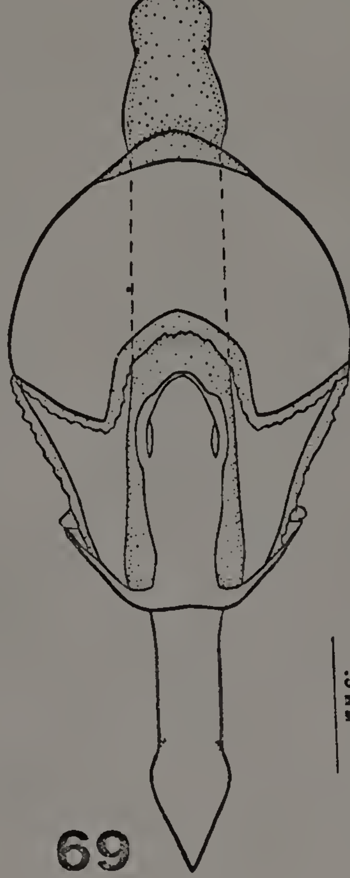

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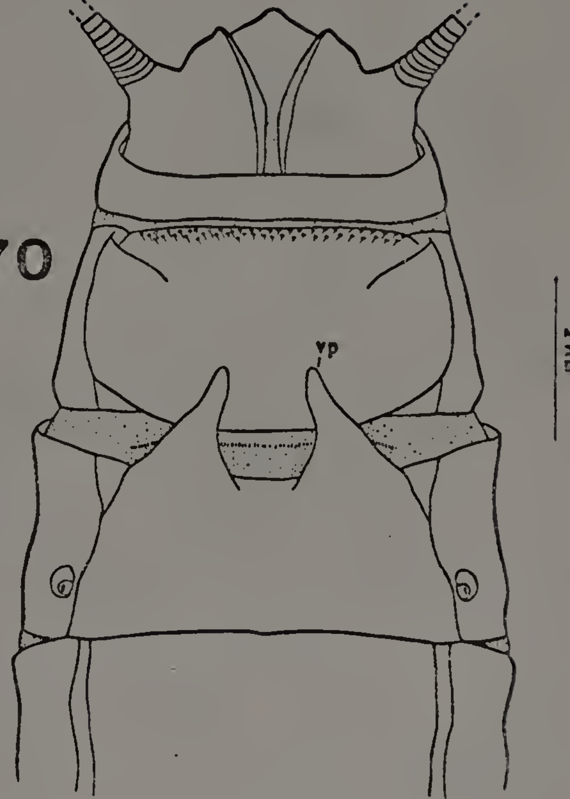

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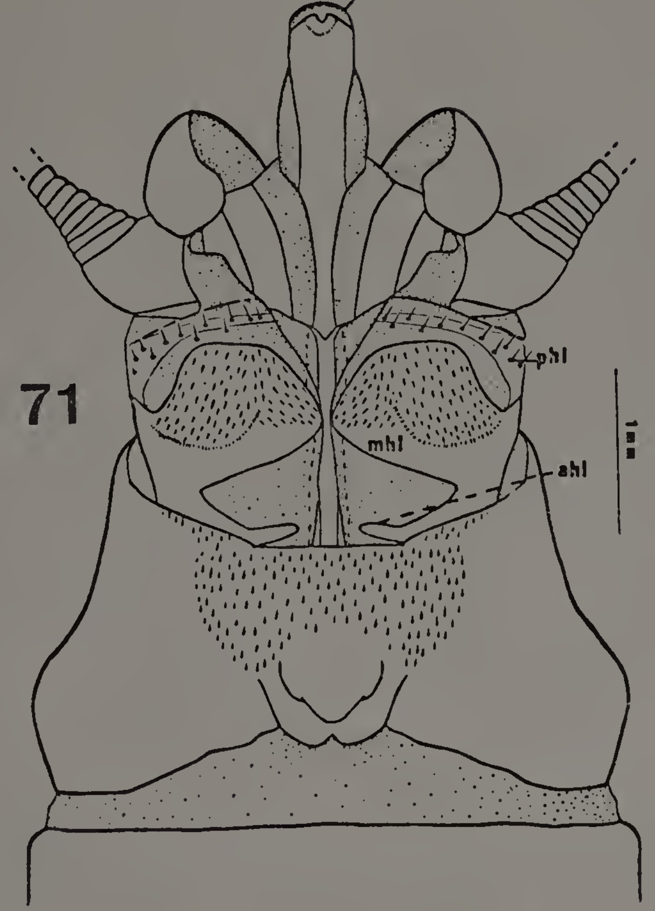
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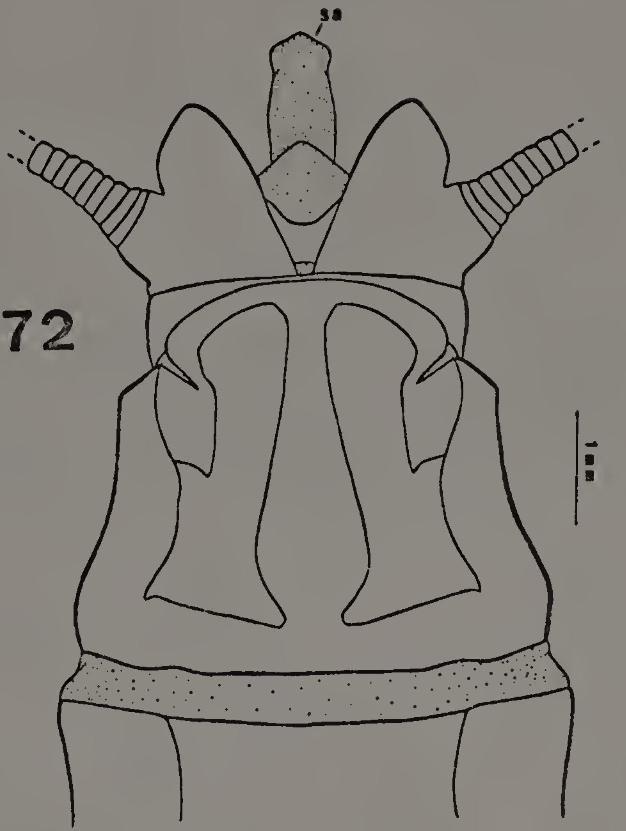
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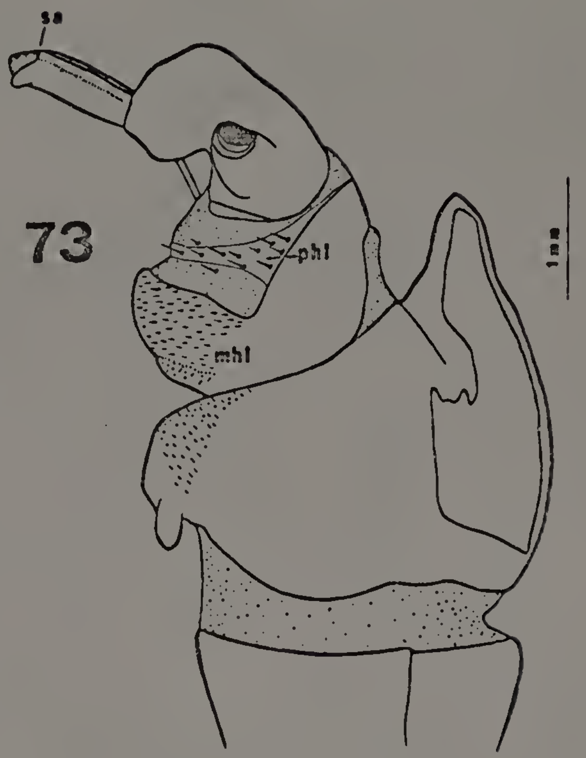
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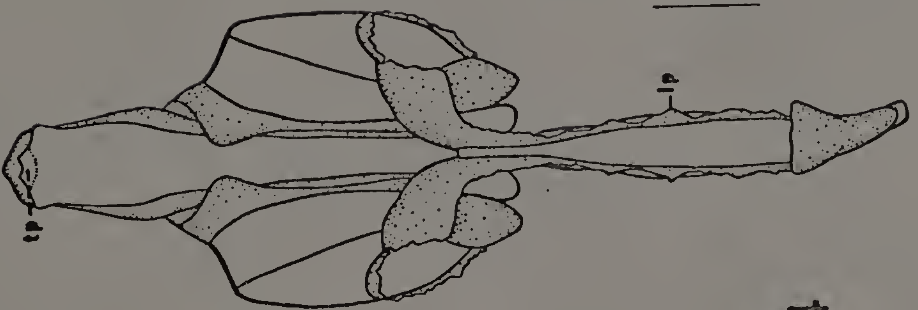

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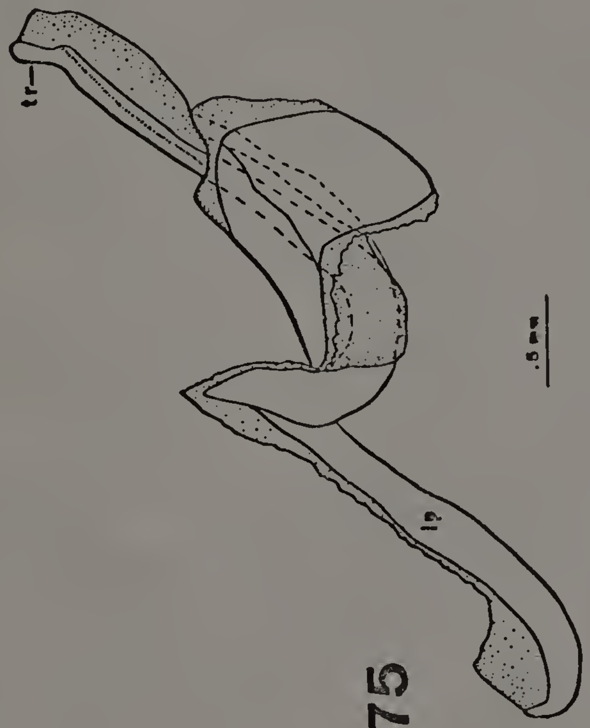

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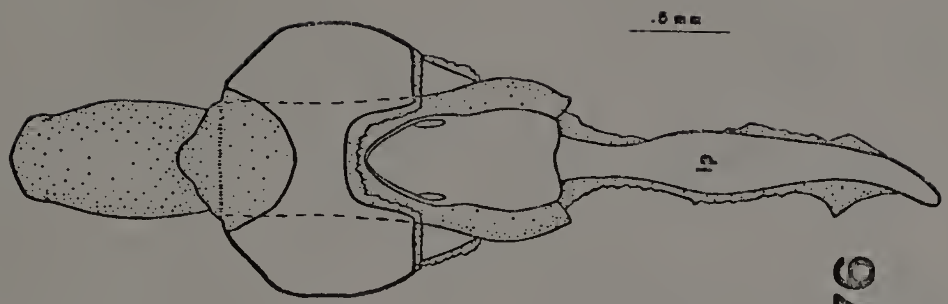

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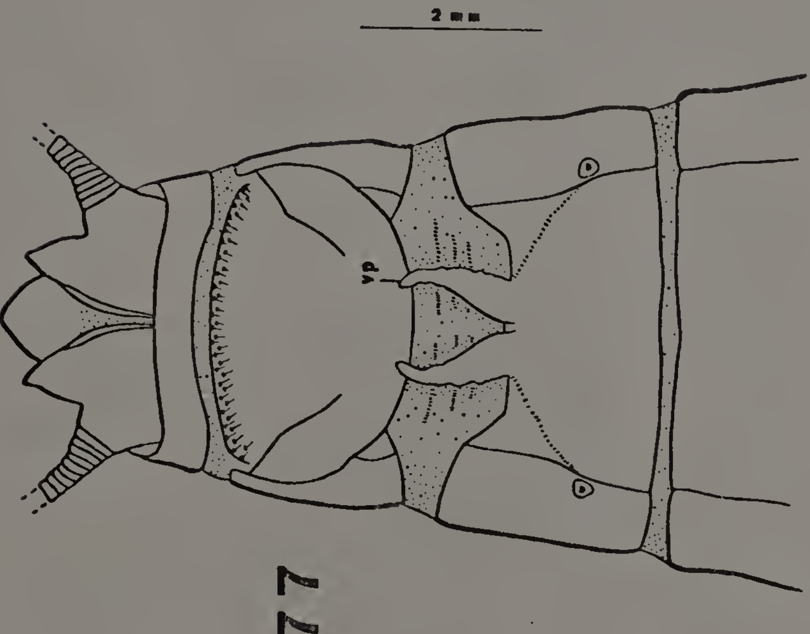

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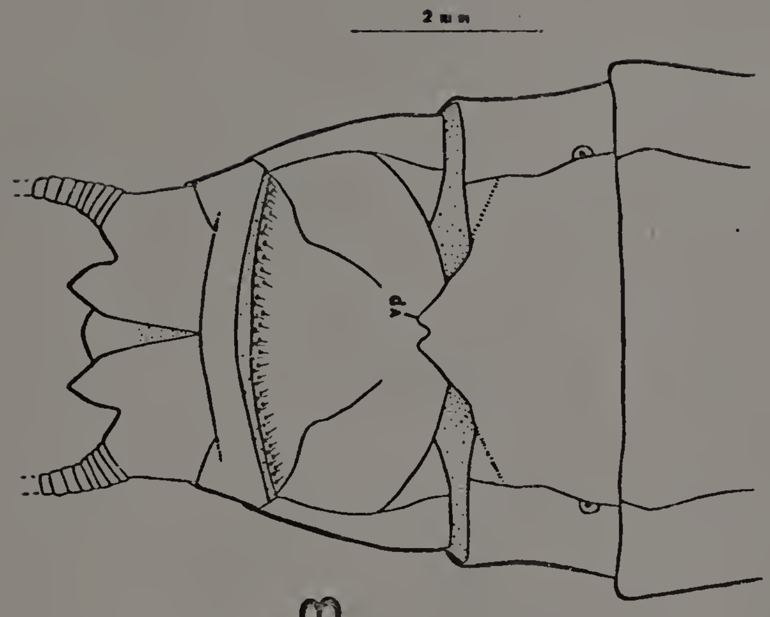

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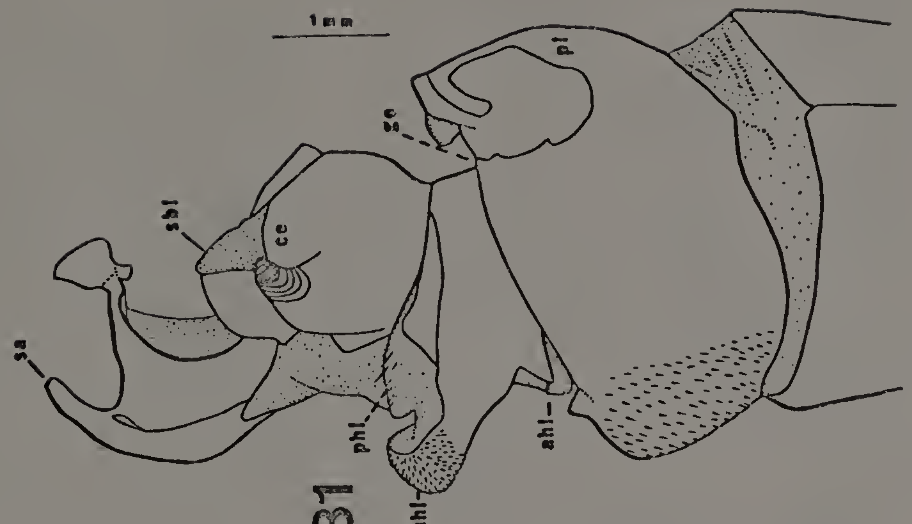

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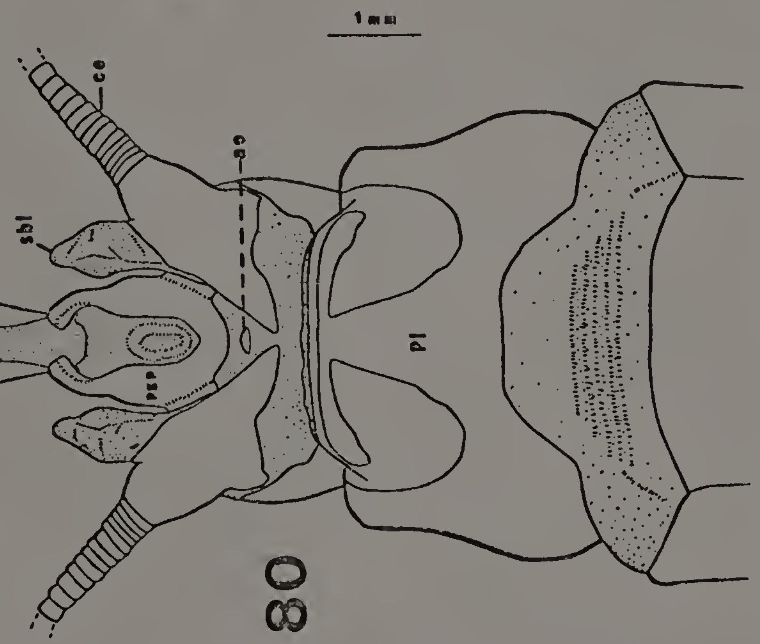

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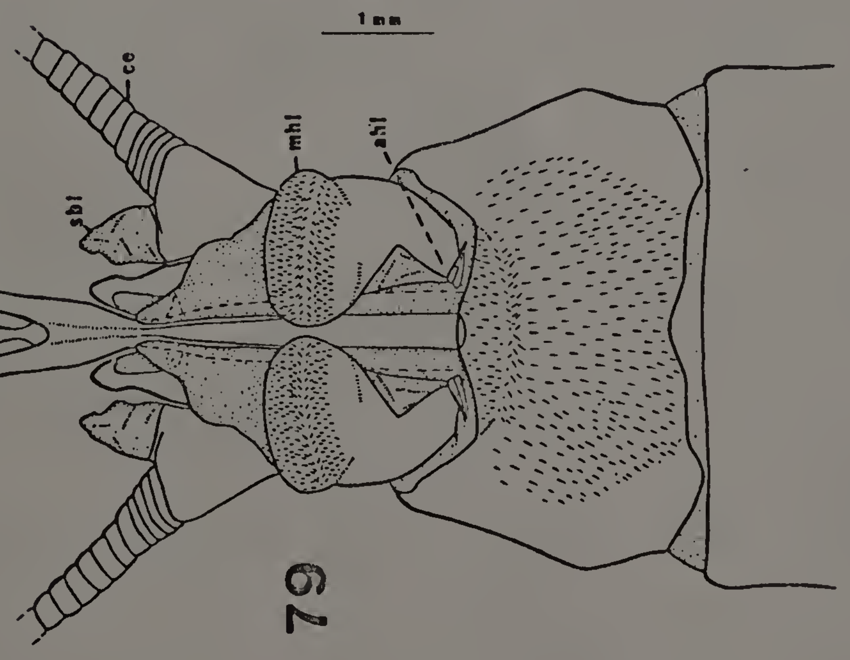

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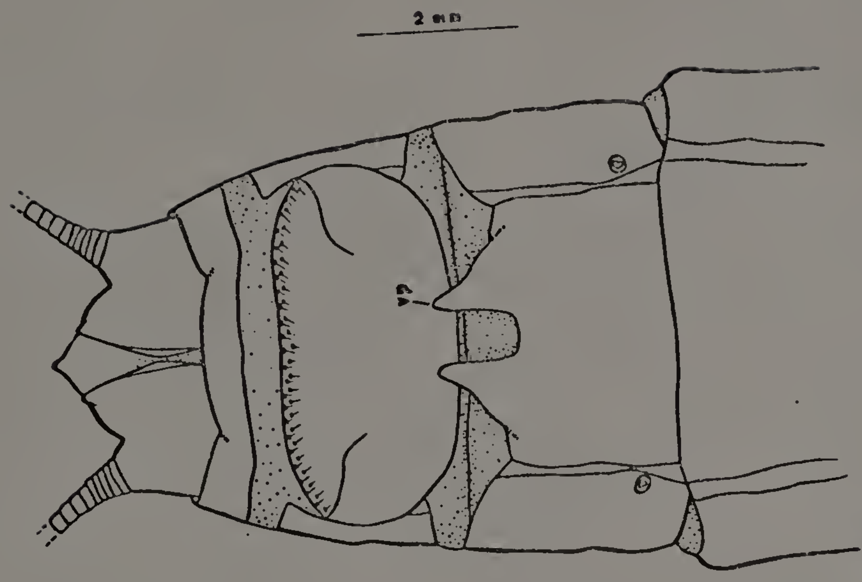

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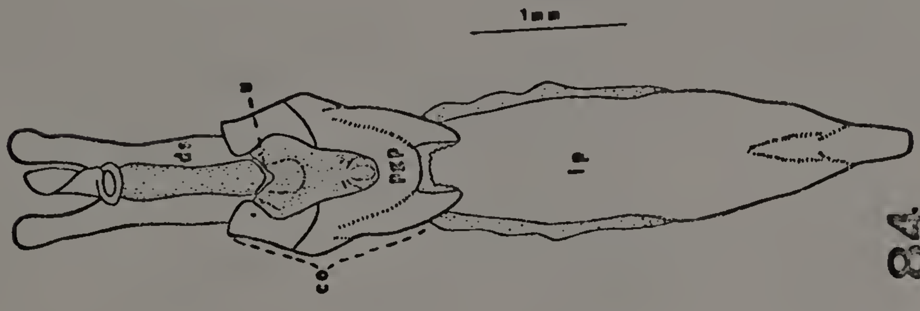

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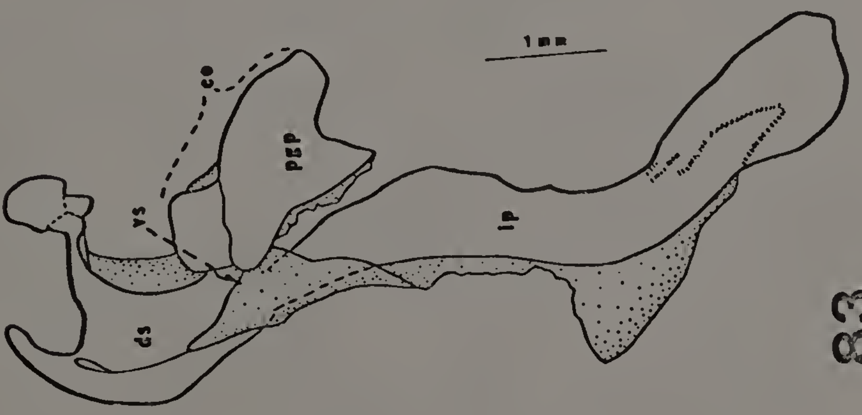

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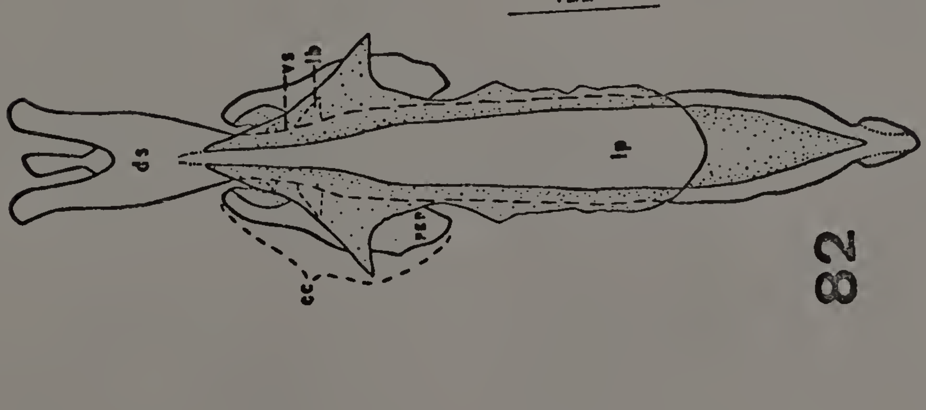

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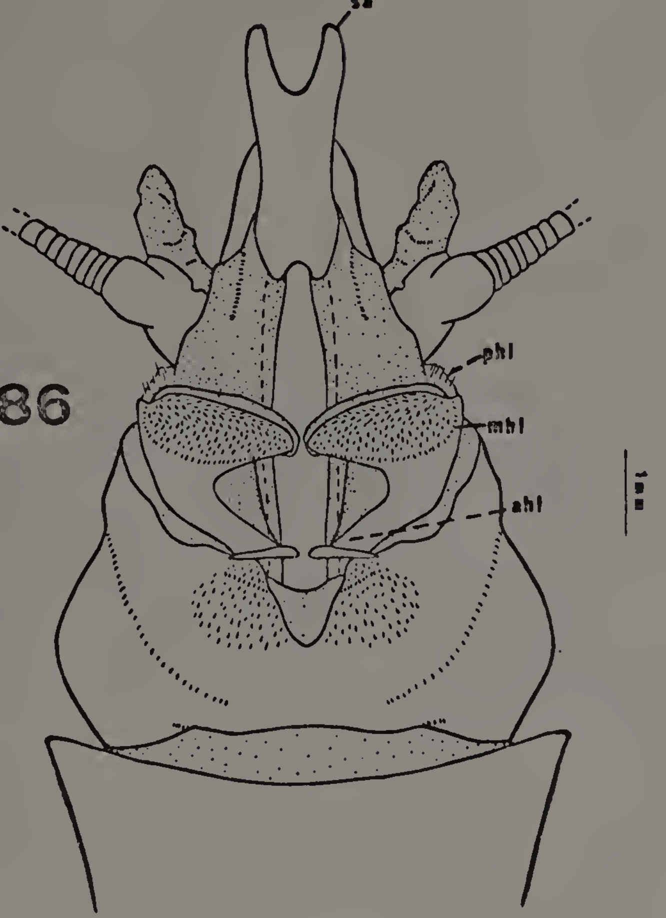

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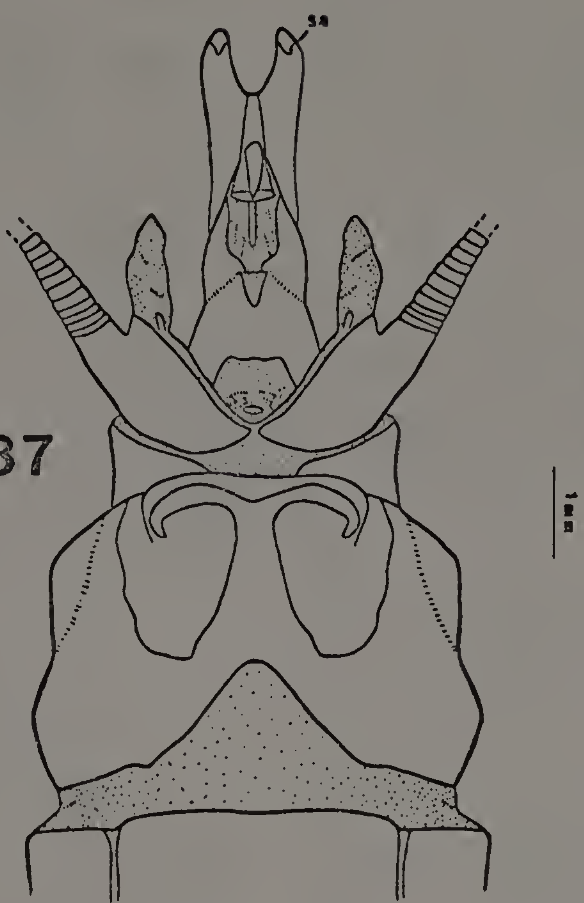

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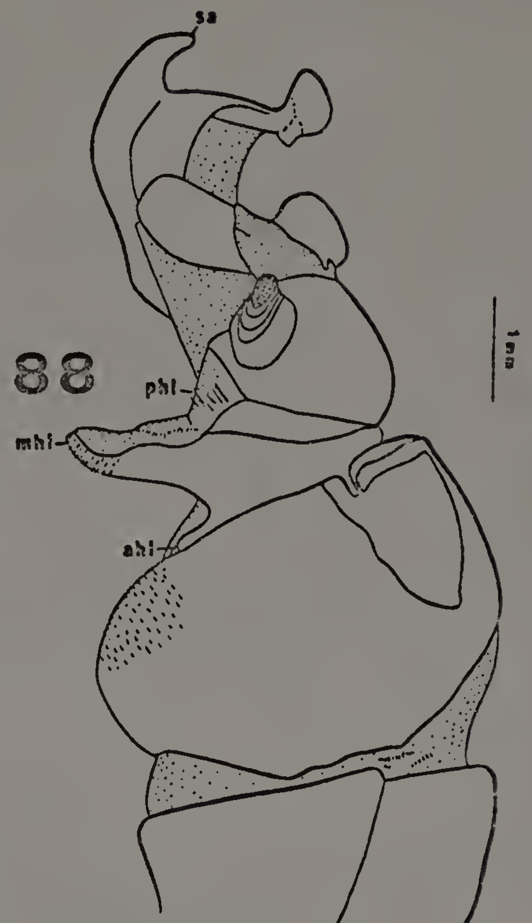

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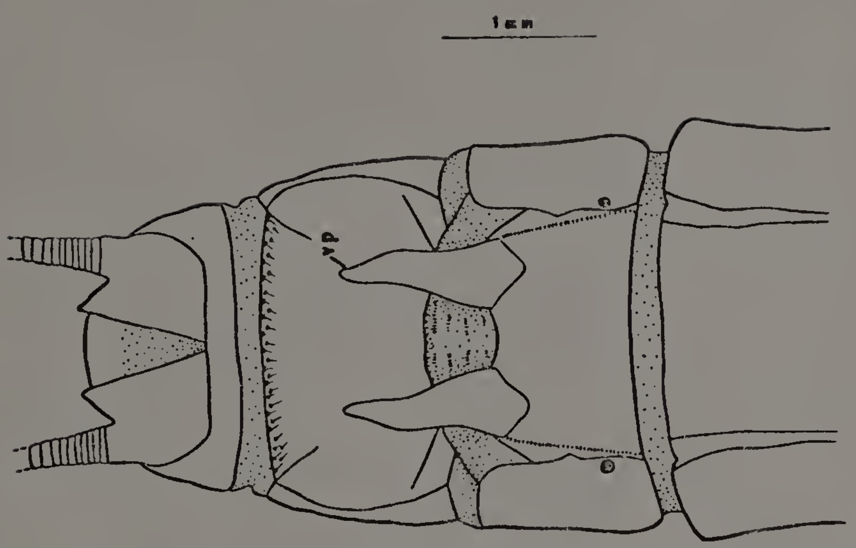

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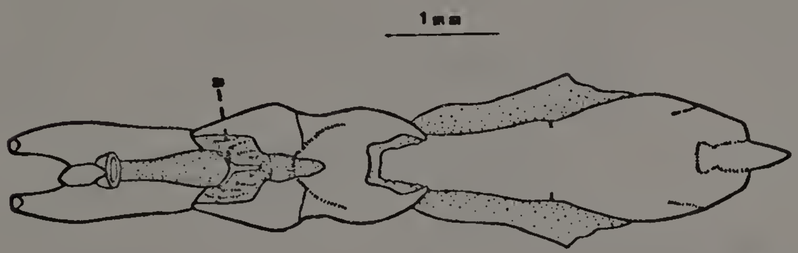

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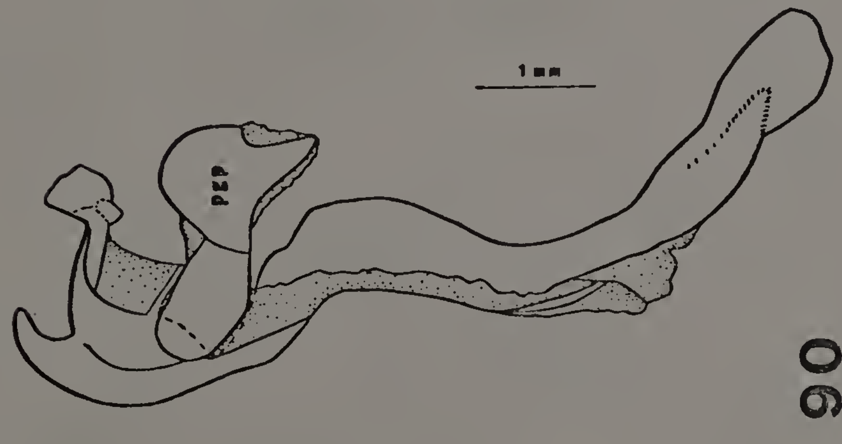

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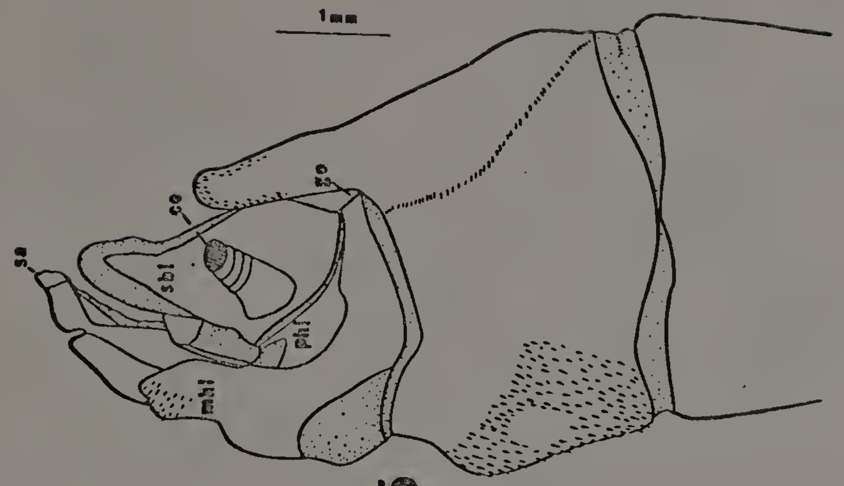

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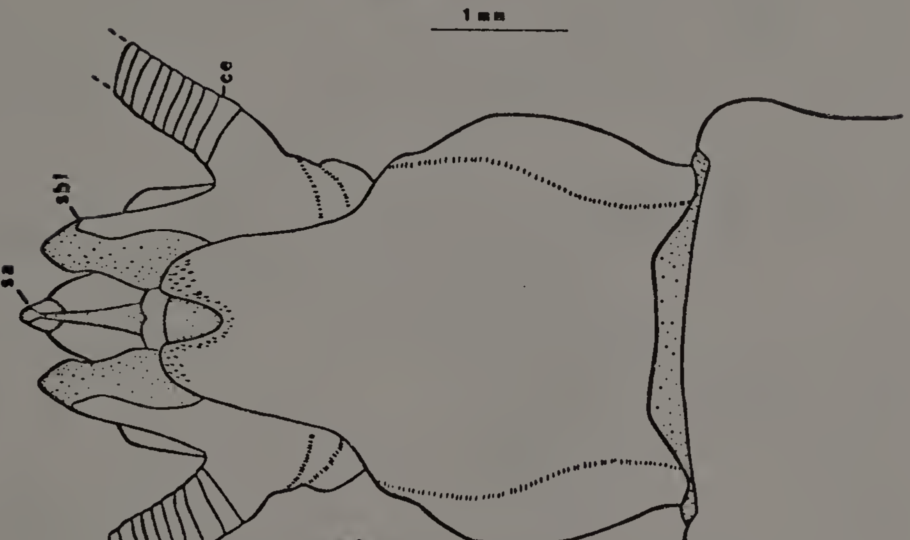

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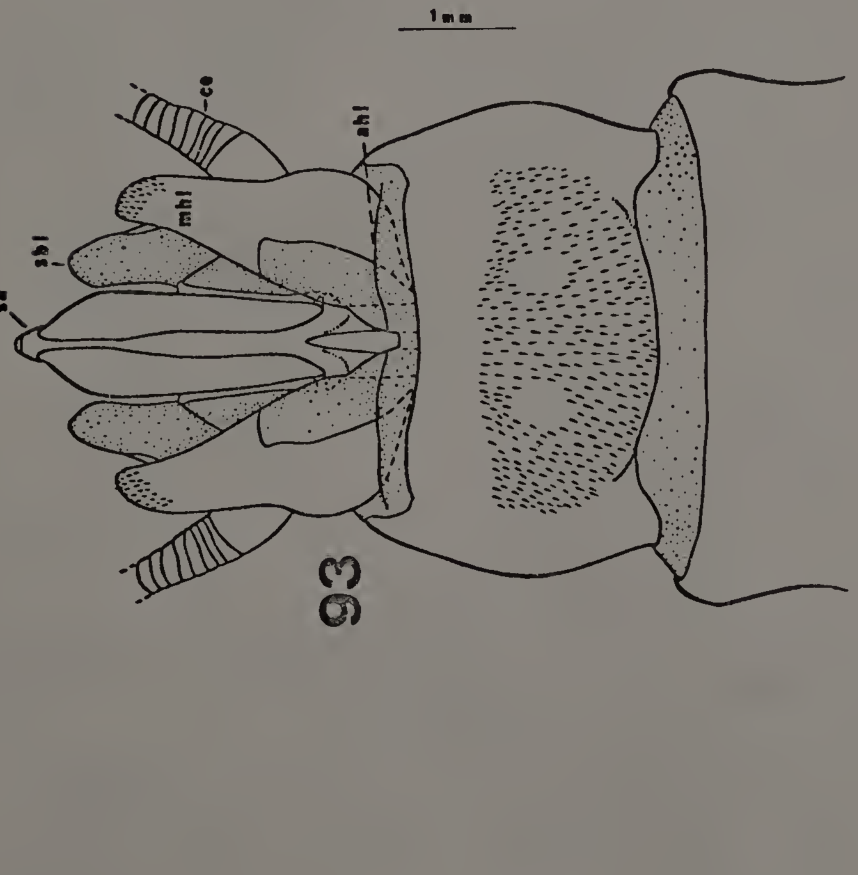

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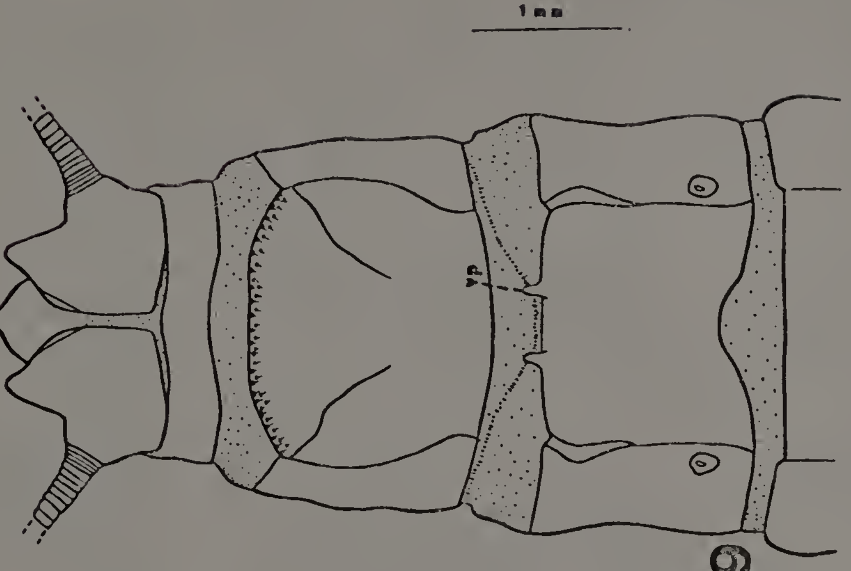

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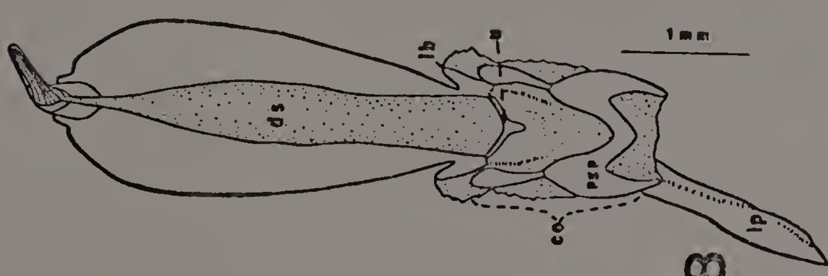

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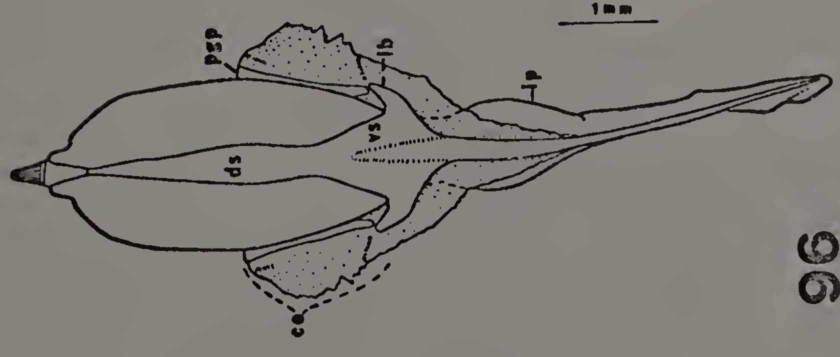

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PLATE XXIX

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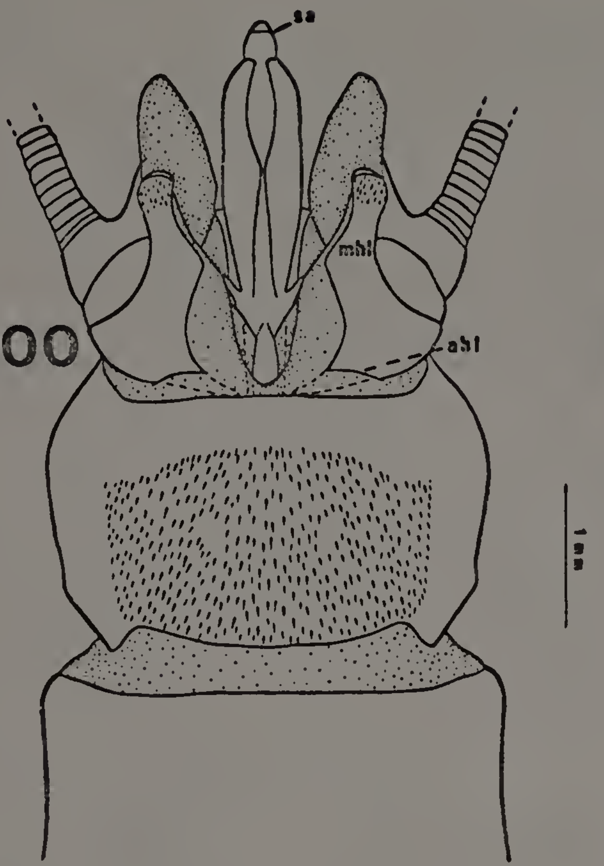

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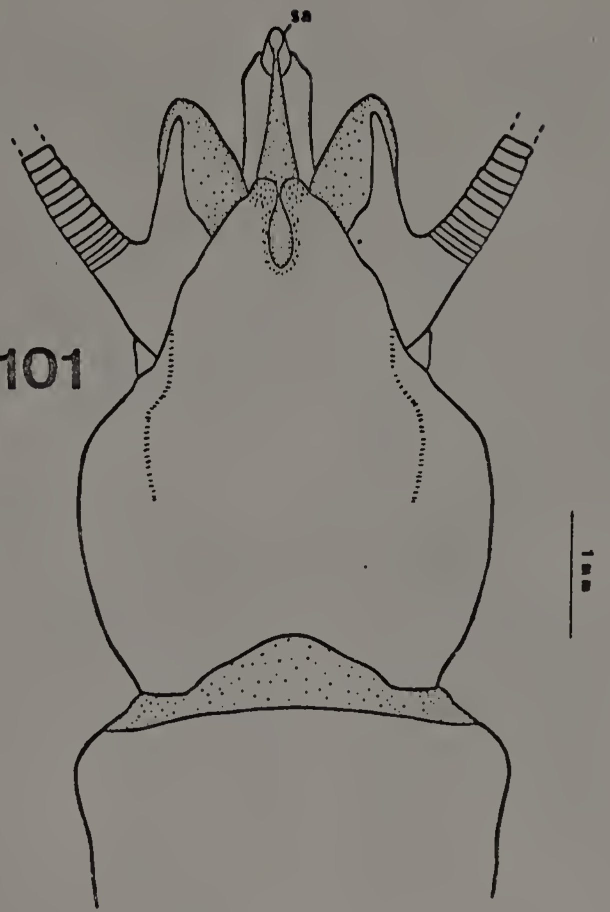

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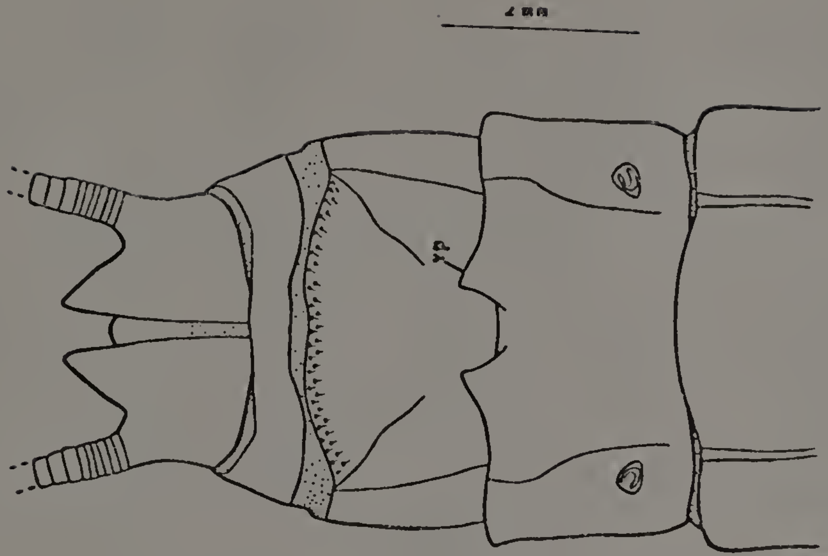

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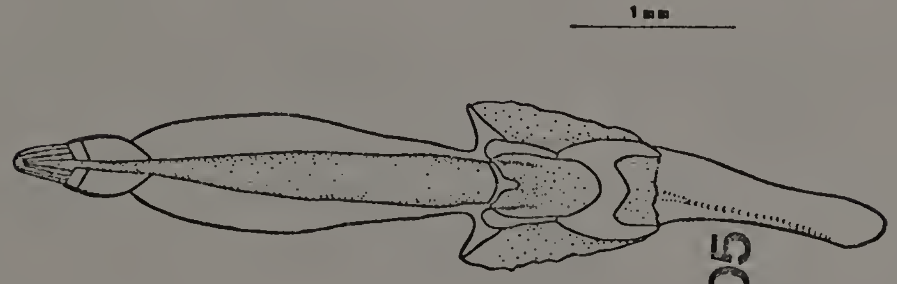

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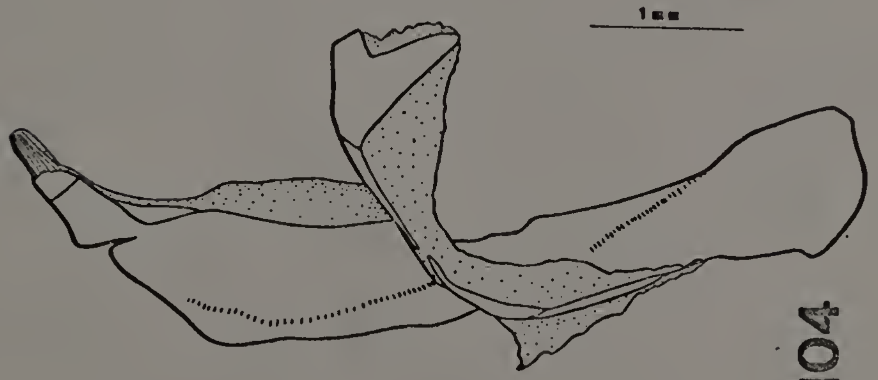

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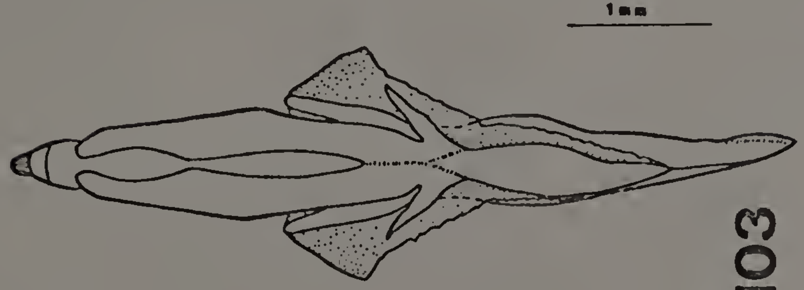

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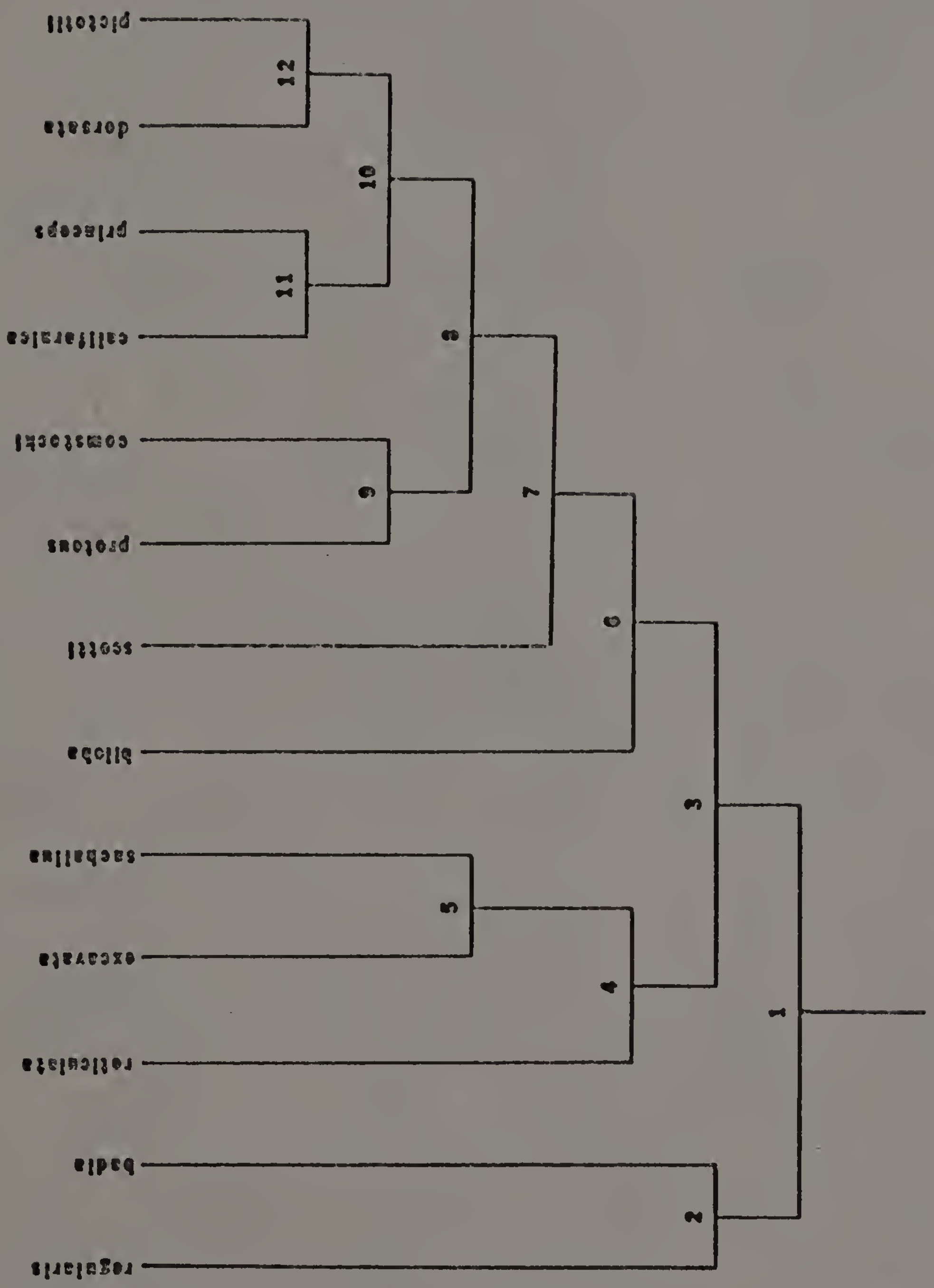
PLATE XXXI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californica
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biloba
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