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The external and internal morphology are considered and important morphological characters are found which relate Macrovelia to the family Mesoveliidae.

Both Macropterous and Brachypterous forms occur throughout the western half of the United States. The adults and nymphs are restricted to the margins of springs and streams during the reproductive period, but the adults are able to withstand quite dry conditions during the summer. Copulation and oviposition apparently take place only in the spring. Nymphs, whose behavior closely follows that of the adults, normally finish their development by May. Nymphs, reared in the laboratory, reached maturity in four instars.

THE MORPHOLOGY AND BIOLOGY OF *MACROVELIA HORNII* UHLER (HETEROPTERA:MESOVELIIDAE)

by

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TABLE OF CONTENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF FIGURES

LIST OF FIGURES

THE MORPHOLOGY AND BIOLOGY OF *MACROVELIA HORNII* UHLER (HETEROPTERA:MESOVELIIDAE)

INTRODUCTION

Little is known about the morphology, habits and life history of *Macrovelia hornii* Uhler. The exact taxonomic position of this annectant species has been in question since it was described by Uhler (44, p. 422) as a veliid in 1871. At this time he erected the genus *Macrovelia* to contain this species. Kirkaldy (25, p. 154; 26, p. 205), in two different catalogs of the Hemiptera, listed *Macrovelia* in the Veliinae under the Gerridae. He did not consider the taxonomic position in any more detail than Uhler did in his original description.

The taxonomic position was first discussed in detail by McKinstry (31, p. 94) when he reviewed the characters of *Macrovelia* and considered the possibility of its relationship to the Veliidae. He concluded that a new family, Macroveliidae, should be erected to contain this taxon. McKinstry (31, p. 95) stated that the family Macroveliidae is much closer to the Hebridae than to any other family. He did not include it in the Hebridae since they have exposed mesothoracic and metathoracic scutelli, different wing venation, a prominent rostral groove and bucculae.

China and Usinger (9, p. 348), in their classification of the Veliidae, erected a new genus, *Ocellovelia*,

which they considered to be closely related to Macrovelia. They included these two genera in the Macroveliinae of the family Veliidae. Macrovelia and Ocellovelia, along with Hebrovelia, were placed in the Veliidae on the basis of the median longitudinal suture on the vertex of the head and the concealment of the mesonotal scutellum by the backward extension of the pronotum. They are considered to be primitive veliids because of the presence of ocelli in Ocellovelia and Macrovelia, the generalized nature of the wings and the apical and preapical claws. Macrovelia and Hebrovelia have apical claws and Ocellovelia has preapical claws. Pendergrast (32, p. 7), in a study on the internal reproductive organs of the Heteroptera, noted that the female fecundation canal was similar to that found in Mesovelliidae. Scudder (34, p. 441), in his work on the external female genitalia of the Heteroptera, agreed with China and Usinger. He described the morphology of the anal tube in the veliids and found that it was reduced in Microveliinae and absent in Rhagoveliinae, while present in Macrovelia as in the Veliinae. He stated that if these three subfamilies are retained within the Veliidae, there appeared no reason not to include Hebroveliinae and Macroveliinae in the Veliidae. China and Miller (8, p. 36), on information supplied by Usinger, placed the Macroveliinae in the Mesoveliidae. Usinger has noted that the nymphs

of the two groups are very similar.

MORPHOLOGY

The study of the morphology of this monotypic species may aid in the correlation of the relationships between the families contained in the Gerroidea. Macrovelia and the near relative, Ocellovelia, are relicts and their taxonomic position is not clear at the present time. An attempt will be made to interpret the characters of Macrovelia hornii on a phylogenetic basis and to place it in the most logical taxon.

External Morphology

The Head

The head of the adult is neither strongly compressed nor extremely slender. The antennal sockets form the widest part of the head and are separated by the antennal suture. The antenna is four-segmented; the first segment is club-shaped. The proportions of antennal segments I to IV are 5:5:6:8.

The epicranial arms are distinct and form a V-shaped suture between the compound eyes and the base of the neck. An ocellus and an apodemial pit are located within the anterior curve of each epicranial arm. The apodeminæ are pits in the head and are present in both nymphs and adults. They are located just anterior to the ocelli (Figs. 1, 2)

in the adults. The three pairs of sensory setae on the head form a distinct pattern as shown in Figures 1 and 2.

The anteclypeus is located centrally on the head and demarks the base of the rostrum. The labrum is a broad plate below the anteclypeus. The epipharynx is long and pointed (Fig. 21). The maxillary plates extend laterally around the base of the beak. The bucculae and lora are absent in Macrovelia. The labium contains four segments, the first being reduced and invisible. The second segment is short and just visible below the maxillary plates. The third and fourth segments are the predominate segments of the rostrum.

Internal Structure of the Head. The hypopharyngeal wings extend through the center of the head, extending from the base of the anteclypeus to the neck. It contains the cibarium and the cibarial dilators. The dilators project into the dorsal area of the head and originate on the frons. Underneath the cibarium the salivary pump joins the alimentary canal or the pharynx near the base of the internal rods of the maxillary plates (Fig. 20). Two very strong dilators extend posteriorly from the salivary pump and run parallel to the maxillary stylets, supported by the hypopharyngeal evagination, to the base of the neck whence these muscles have their origin. Two slender apodemes

extend posteriorly from the base of the inner edge of each antennal socket. Antennal muscles are attached here. A long narrow muscle extends from the antennal socket to the cranium and originates on the apodemina.

The mandibular lever sits along the inner side of the paraclypeus. The lever is quadrangular in shape and the rod-shaped base of the mandibular stylet articulates with the lever on the middle upper edge and rests on what appears to be the fulcrum for the structure. The mandibular rod terminates in the middle of the plate. A muscle is attached to this end. A second muscle is attached to the lower posterior corner of the quadrangular lever. These muscles operate the mandibular lever, which increases the action of the stylets. They originate on the frons near the base of the compound eye. The mandibular stylets form a curved loop above the lever and extend down to the anteclypeus, joining the maxillary stylets and continuing into the beak.

Discussion of the Head. The head of Macrovelia contains some characters which have a strong bearing on its taxonomic position. The precence of ocelli in Macrovelia suggests that it should not be included in the Veliidae. The mandibular lever may be of use in the classification of the Heteroptera. According to Spooner (39, p. 35), the semiaquatic Hemiptera fall into a group that has a

quadrangular-shaped mandibular lever. The variation between the illustration of different families given by Spooner is not great, however the mandibular levers of Macrovelia and Mesovelia seem to be almost identical.

The presence of the apodemina in Macrovelia is unusual for the only other occurrence of this structure is found in the Saldidae (39, p. 36). This character suggests a common ancestry.

The Thorax

The thorax of the brachypterous form of Macrovelia is slightly smaller than that of the macropterous form. This is due to the larger area for muscle attachment in the macropterous form. There is little difference in morphological structure between the two forms. Generally, the macropterous thorax will be illustrated and discussed here.

The Prothorax (Figs. 4-6). The anterior margin of the prothorax is a heavy rim formed by the inflection of its borders. The head telescopes into the prothorax and is held in place by the short cervical membrane. The head movement is slightly limited by this arrangement. Heavy punctation, apparently arranged randomly, covers the dorsal and ventral surface of the prothorax. There are two laterally enlarged and extended areas that are

characterized by very fine pits. These areas are the widest points on the pronotum. Located between these areas are two large, deep, crescent-shaped pits. Behind the enlargements there appears to be a constriction that divides the thorax into two parts. The anterior part contains the large dorsoventral muscles that operate the front legs. The posterior portion is prolonged over the mesonotum and metanotum. Internally, the constriction contains a phragma which serves as a site for muscle attachment (Fig. 6). There is no evidence that the constriction may be the fusion of a suture. The coxae are inserted ventrally, close together, thus restricting the sternal area. The epimeron and the episternum are continued over the coxal bases to form the supracoxal flange. The pleuron is continued posteriorly, overlapping the mesonotum and fitting into grooves in the mesopleuron. Below the grooves there are sockets in the anterior portion of the mesopleuron that contain the lateral posterior projections from the pronotum (Figs. 5, 9). The pronotum is held rigid by these projections to the mesonotum. Above the sockets, on the mesothorax, are the mesothoracic spiracles. They are located similarly in the Gerridae (Fig. 9).

The Mesothorax (Figs. 7, 9). The lightly sclerolized mesonotum lies under the pronotal lobe. The first

sclerite in the mesonotum is the acrotergite that bears the phragma. Next to the acrotergite is the large scutum which is divided into the medium scutal area and two lateral scutal areas by the parapsidial sutures. A median suture may be more or less developed in some individuals (Fig. 7). Matsuda (30, p. 35), working on gerrid taxonomy, refers to this as the median longitudinal sulcus. On each latero-anterior corner of the scutum there are knob-like projections which hold the pronotum down over the mesonotum. The scuto-scutellar suture, which separates the scutum from the scutellum is absent. The tergal split interrupts the scutum and forms the antero-lateral boundary for the scutellum. A wide membrane connects the scutum and scutellum laterally. The posterior portion of the mesonotum is continuous with the scutum and this is called the scutellum (Fig. 23). The scutum and scutellum extend dorso-laterally to the wing base. These areas are called the anterior and posterior notal wing processes. The postnotum is a narrow sclerite compressed to the latero-posterior borders of the scutellum. The inner corner of the postnotum joins with the anterior extension of the metanotal phragma (Fig. 7).

The pleural region is divided latero-ventrally by the supracoxal ceft which extends from the lateral edge of the coxal cavities into the pleural area and partially

separates the episternum from the epimeron. The pleural wing process and pleural suture are absent. The wing bases are supported ventrally by an epipleurite, the subalare sclerite, and posteriorly by the prealare sclerite. The subalare sclerite serves as a fulcrum for the front wing. Internally this sclerite carries an apodeme which, when moved, will carry the wing away from the body (Fig. 11). The prealare sclerite is a long narrow plate extending between the prealare bridge and the subalare sclerite. These two sclerites join at the base of the wing along with the anterior and posterior notal wing processes (Fig. 7). The metathoracic spiracle is located in the dorso-posterior corner of the epimeron.

The mesosternum is fused with the mesopleural region. Only a small invaginated area between the coxal cavities may suggest an earlier condition. This may be a reduced spinasternum. The spinasternal pits are found in the coxal cavities and are assumed to have migrated there. The eusternum is undivided but is heavily sculptured and pitted along the antero-lateral edges.

The Wing Bases (Figs. 40-47, 50). The forewing base contains the first axillary sclerite (Fig. 43) that articulates with the anterior notal process and the prealary sclerite. It fits around the broad basal end of the triangular shaped second axillary sclerite (Fig. 44). The

narrow pointed end of the second axillary sclerite extends into the wing between the anal and the cubital vein. The third axillary sclerite (Fig. 45) is the largest of the three and articulates with the posterior edge of the second sclerite. It joins with the anal vein distally and with the subalare sclerite and the posterior notal wing process proximally (Figs. 46, 48). The tegula and the median plates are absent or poorly defined. The base of the hind wing is difficult to interpret because of the reduction of the axillary sclerites (Fig. 50).

The Metathorax (Figs. 7, 8, 23). The metanotum is short, U-shaped, and extends antero-laterally up to the wing bases. Medially it borders and joins the scutellum and postnotum of the mesonotum. The metatergum is divided by the metanotal costa. The costa extends diagonally from the antero-lateral corner of the tergum to a point midway between the median line and the edge of the tergum. It runs parallel to the meta-abdominal suture across the median line to the midpoint and up to the opposite corner. The inner area enclosed by this costa is called the meta-scutum and the two lateral areas are the divided scutellum. Above the lateral edge of the costa, on both sides, are two areas called the latero-scutal extensions (Fig. 7). They are connected to the scutum by subdorsal sclerites found between the mesopostnotum (Figs. 7, 23) and the scutum.

This may be the "Gelenkkopf" of Larsen as noted by Matsuda (30, p. 36). The true relationship of this sclerite with the tergal composition is unknown. The sclerite appears to be involved in the phragmal plate (Fig. 23) found under the metatergum. This plate consists of the fused second and third phragma and may be the metapostnotum. The phragma is associated with the metanotal costa. Invaginated pits are found near the antero-lateral ends of the costa and extend into the metathoracic segment joining at the base of the mesocoxal cavities (Figs. 11, 23).

The metatergal wing bases are supported by the anterior edge of latero-scutal extension and the lateral extension of the scutellum. (Figs. 7, 23)

The metapleural area is similar to the mesopleural area except that the coxal cavities are projected more posteriorly and the supracoxal cleft does not divide the coxal cavity but runs between the pleural wall and the coxal cavity. The first abdominal spiracle is located in the dorso-lateral corner of the pleuron. The sternal area is characterized by the presence of the metathoracic scent gland. It is located in the mid line and slightly posterior of the center in the metasternum.

Wing Venation (Figs. 12-14). The forewing is not well differentiated into the corium, clavus and membrane as in

other Heteroptera. The C (costa) and Su (subcosta) are absent from the forewing. The anterior vein is made up of R (radius) and M (media) vein. The two separate and join again a short distance from the base to form a narrow enclosed area. M branches off from the radius at the end of the enclosed strip (i.e., the hamus). M continues to the end of the wing but joins R near the tip. Cu (cubitus) interrupts M in two places, forming two cells, and later joins with the Pcu+1stA (postcuibitus and first anal) vein at the wing tip. The Pcu+1stA vein is connected to the cubital by a cross vein creating two posterior cells. A cross vein between the radius and the median creates two cells anteriorly and two cells are formed by the median and the cubitus in the middle of the wing. This gives the forewing a total of six enclosed cells. The number of enclosed cells in the forewing is used to compare the wing venation of the semiaquatic Hemiptera by McKinstry (31, p. 95). It is not a good character because of the variation of cell numbers.

The hind wing is simpler than the forewing. The subcosta is a very short vein at the base of the radial medial vein. The medial dip (i.e., the hamus) of the forewing is lost and M appears to be a diagonal cross vein between the cubital and radial veins. C extends medially through the hind wing and is only interrupted by M. The cubital

furrow is bifurcated, the anterior arm runs parallel to C and the posterior runs parallel to Pu (post-cubitus) for a short distance. Pu branches off from the first anal vein and continues along the posterior portion of the wing. The first anal vein is ahead of the anal fold in the post-cubital sector and it denotes the distal margin of the lobe. The anal lobe contains the second anal vein. Particular areas are set off by the cubital furrow. The area between the anterior arm and the posterior arm is called the cubital sector. The area of the wing between the posterior cubital furrow and the anal fold is called the post-cubital sector.

The Thoracic Legs (Figs. 15-19). The legs of Macrovelia are slender. They are covered with short stiff setae which are used in grooming. Each coxa is almost completely enclosed in the cavity formed by the supracoxal lobes and sternum. A slight collar on the coxa holds it in the coxal cavity. Muscles from the main part of the coxa enter the thorax and are attached there. A small plate is located near the dorsal articulation of the coxa with the supra-coxal lobes. This plate is called the basicoxa (Fig. 18) and is associated with a muscle from the thorax. The trochantin is fused to the coxa or absent. The distal end of each tibia and tarsal subsegment has a few short

bristles projecting from the apex (Figs. 15-17). The paired claws of each leg are inserted at the apex of the third tarsal subsegment. There are two claws and a pair of leaf-like arolial bristles at the apex of the last tarsal segment (Fig. 19).

Discussion of Thorax. A comparison of the thoracic region of Macrovelia hornii with the Gerridae, Velliidae, and Mesoveliidae is necessary for complete understanding. The prothorax of Macrovelia is apparently very similar to some of the other groups of Hemiptera. The pronotum covers all of the dorsal area of the thorax not covered by the wings. Macrovelia resembles the Veliidae in this respect, but the Gerridae and Hydrometridae also possess a long pronotum. In Mesovelia the pronotum is extended to the metathorax and covers only the wing bases. The metascutum is left exposed (Fig. 22).

The mesotergum of Gerridae, Mesovelia and Hydrometridae closely resembles that of Macrovelia. They are characterized by rather prominent parapsial sutures, a well-developed first phragma and a scutellum that articulates with the postnotum laterally. The postnotum of Macrovelia compares with other forms studied by Larsen as being lateral sclerites with the median section absent. Laterally the scutum and scutellum are separated by the tergal split

which is common in Macrovelia as well as in other groups. It would be expedient to study the flight muscles of Macrovelia and Mesovelia for similarities. The metathorax of Macrovelia differs considerably from that of the other Hemiptera that have been investigated. The segment is prolonged and reduced in Hydrometridae. The segment is compressed and extended laterally in the Rhagovelinae. In Gerris, the segment is similar but the metanotal costa is absent and the phragma is arranged differently. In Mesovelia, the metascutum is produced out over the first abdominal tergum. However, the metascutum of Mesovelia appears to resemble the metanotal costa of Macrovelia (Figs. 7, 22), and may very well be related to it. The phragmata of the two bugs also suggests a relationship. Further comparison should be made between these two bugs. The sclerites of the wing bases are difficult to interpret. The metapleural wing process is absent, a process which all hemipterans lack. However, two sclerites are found in the pleural region that may be epipleurites. For the purpose of this paper they are called the prealary-basalar sclerite and the subalary sclerite. The musculature of the thorax must be known before these names may be correctly applied to these sclerites.

Davis (10, p. 342) reconsiders the wing venation of the Heteroptera. He supports the ideas of Tanaka on the

absence of C (costa) from the wing. He points out that principal veins on the Heteroptera hemelytra are Sc, R, M and Cu extending through the anterior portion of the wing and the Pcu+1A through the posterior portion. The Sc vein is usually reduced and found only in the base of the wing.

In the hind wing, the jugal lobe is called the anal lobe and the vein inside the lobe is called 2A (second anal) by Davis (10, p. 342). He points out that the cubital furrow is bifurcated in many cases and the posterior arm is not the anal fold. The anal lobe constitutes that portion on the wing which is turned under when the wing is folded over the back. The anal fold extends from the anterior edge of the third axillary sclerite and generally lies just in front of the first anal vein.

In Macrovelia the proximal portion of M (the hamus) is absent and the remainder of M forms a vein extending diagonally between R and Cu. This is also the case for the veliid wing as described by Hoke (22, p. 32). The hind wing venation for the two families is identical except for the origin of Pcu on the first anal vein. There is no apparent similarity of wing venation in the Mesoveliidae.

The Abdomen

The abdomen of the female is made up of seven pregenital segments. The ovipositor is situated on segments VIII and IX. The post-genital region, the anal lobe, is the tergum or the ninth segment. The male abdomen is made up of eight pregenital segments, the last of which is cylindrical and partially contains the ninth segment. The post-genital area, as in the female, is the anal tube. The female abdomen is wider and considerably more rounded ventrally than is the male. The generally larger abdomen of the female helps to distinguish the sexes in the field.

The Pregenital Region. In both sexes, the first abdominal segment is reduced to a tergal plate. Its anterior end fits closely behind the metanotum. Ventrally the first segment is indistinguishable from the metathorax and the rest of the abdomen. The abdomen and thorax are strongly fused and flexion is impossible. The dorsal sclerites allow for variation in the abdomen because of their arrangement. The pregenital segments (II through VII) consist of a pair of lateral plates, paratergites or laterotergites, and segmentally arranged median tergites. The laterotergites of the second, third and fourth segments are fused together forming a large triangular plate in the anterior lateral corner of the abdomen. The remaining

latero-tergites are free. They all contain one pit which seems to serve as a place of attachment for tracheae and muscles. The junctions of the sclerites on the dorsum are membranous and allow for variation in the size of the abdomen. The second and third dorsal abdominal segments are provided with paired longitudinal carinae arising from the median elevated area of the first segment (Fig. 37).

The ventral part of the abdomen is marked laterally by a pigmented band. The spiracles, a pair on each segment from segments II through VII, lie between this line and the margin of the fused latero-tergites. Below the spiracles and the lateral pigmented band there is a suture that extends from the base of the metacoxal cavities to the sixth and slightly into the seventh segment. This suture sets off the latero-sternites from the venter. In the ventral mid-line there is a carina that extends from the anterior edge of the seventh segment to the base of the thorax.

Female Genitalia (Figs. 27, 29-32). The terminal segments of the female are covered dorsally by the eighth tergum and ventrally and laterally by the fused eighth latero-tergite and the first gonacoxa. The first gonapophysis is elongate, slender and sclerotized laterally and is carried by the first gonacoxa ventrally and caudally.

The dorsal edge of the gonapophysis is sclerolized and forms the first ramus. The first ramus interlocks with the second gonapophysis. The second gonapophysis is slender, elongate, and subapical to the first gonapophysis. It is partially sclerotized laterally and joins with the first gonacoxa by a membrane that forms an egg guide rather than a true ovipositor. The second gonapophysis is attached to the second gonacoxa which is supported by the ninth latero-tergite. The ninth latero-tergite is fused to the posterior edge of a triangular-shaped plate called the gonangulum which in turn is fused to the internal part of the first gonapophysis. The gonangulum articulates with the dorsal edge of the second gonacoxa which forms the fulcrum on which the second gonacoxa pivots (Fig. 29). The spermatheca is median and has an accessory canal (Fig. 32).

Male Genitalia. The ninth urite is the genital segment and is modified to hold the phallus. The anal tube is the ninth tergum according to Bonhag and Wick (1, p.181), and it is narrow at the base, but broader at the apex. It extends out over the phallus and forms a partial cover. When the phallus es expanded, the anal tube is lifted up and away from the mid-line of the ninth urite. The saber-shaped claspers articulate below the base of the anal tube

and lie parallel to it, extending to the posterior midline of the urite. Internally, the claspers articulate with the lateral portions of the basal plates near the remnants of the capitate processes. The basal plates are collar-shaped structures that support the phallus. They are strongly sclerotized and are fused together forming one plate (Fig. 26). The phallus, according to Dupuis (43, p. 158), is made up of the phallosoma and the endosoma. The endosoma is divided into the anterior conjunctiva and the posterior vesica. In the resting position the phallosoma surrounds and encloses the vesica and conjunctiva, its base is attached to the basal plates and communicates with the body cavity through the basal foramen. The phallosoma is cylindrical and scleritized dorsally and is membranous ventrally and is open at the distal end, through which the endosoma is extruded. The conjunctiva is characterized by two lobe-like conjunctival processes located dorsally near the phallosomal opening. Ventrally the conjunctiva contains a sclerotized plate that lies flat against the inner portion of the phallosoma when not erect. The endosoma has two lobe-like processes at the apex that extend ventro-laterally away from the phallus. The paired titillators are located opposite the endosomal processes near the dorsal edge. They contain two chitinous rods which seem to support the secondary gonopore and the

titillators. Below the titillators, the dorsal aspect of the endosoma is enlarged and extends out over the conjunctiva. This extension is characterized by striations and grooves located near the junction of the endosoma and the conjunctiva. The processes of the conjunctiva and the vesica hold the phallus in the vulva of the female.

According to Dupuis (43, p. 163), in the Hemiptera the ejaculatory tube is made up of the ductus ejaculatorius (proximal) and the ductus seminis (distal). The ductus ejaculatorius runs into the body cavity between the distal end of the mesodermal part of the genital tract and the basal foramen. The junction with the ductus seminis, between the basal plates, is called the primary gonopore. This has not been observed in Macrovelia. The ductus seminis runs into the phallus from this junction and ends at the secondary gonopore in the titillators. It is unmodified in Macrovelia and remains a simple tube.

Discussion. The abdomen of Macrovelia hornii is typical of most Hemiptera. In the adult the first tergum is separated from the second by a faint line. Also typical of this order is the presence of seven pregenital segments, the second through the seventh bearing spiracles, the others lacking them. Snodgrass (37, p. 254) considers the small sclerotized tube (the anal tube) to represent the

fused tenth and eleventh abdominal segments in the male. Bonhag and Wick (1, p. 181) consider the anal lid to be the ninth tergum in both sexes. Matsuda (30, p. 44) points out the advantages of this interpretation stating that the homology of the male and female genitalia would become more compatible if the anal lid was considered the ninth tergum.

Little or no discussion of the genitalia of Macrovelia appears in the literature. Scudder (36, p. 443) mentions that the female genitalia of Macrovelia and Ocellovelia are similar to the Hebroveliidae. He points out that the Veliinae have tergum IX forming an anal lid, and the Macroveliinae have the termination only partially obscured by tergum IX and the Rhagovelinae are without an anal lid. He states that if these three subfamilies are within the Veliidae, then there is no reason not to include the Hebroveliidae and the Macroveliidae as subfamilies. Scudder (36, p. 440) considers the Mesoveliidae and relates them to the Saldoidea. He points out that the fecundation canal, which Pendergrast (32, p. 3) uses to support a monophyletic group containing the Hydrometridae, Hebridae, Gerridae and Veliidae, may have arisen independently in the Mesoveliidae and the other families mentioned. Since the female genitalia of Mesovelia is similar to

that of the Saldidae and different from the Veliidae, he places them within the Saldoidea.

The male genitalia of the Macrovelia is difficult to compare. It is simple in construction and appears to be in a group of its own. The basal plates and the phallosoma of the Mesoveliidae are similar in construction to Macrovelia. But the ductus seminis (Fig. 25) of Mesovelia is modified into what may be an ejaculatory reservoir as in the Pentatomidae. In Macrovelia the ductus seminis is a simple tube. Two chitinous rods appear in the titillators of Macrovelia but it is impossible to correlate them with the chitinous rods of the Gerridae.

Internal Morphology

The Digestive System

The pharnyx of Macrovelia is identified by its characteristic U-shape and dilator muscles. It is supported along with the maxillary stylets by the hypopharyngical wings which extend nearly to the posterior margin of the head. The digestive tube, or oesophagus, passes through the brain near the posterior base of the eye. In the prothorax the alimentary canal enlarges and forms the first chamber of the ventriculus. The paired salivary glands are located along the anterior end of the ventriculus. The gland is

made up of the salivary gland proper which is divided into an anterior and posterior gland. The anterior gland is small, nearly spherical and sits above the posterior gland. They are connected by a short duct. The posterior gland is larger and is divided into two lobe-like areas. The anterior lobe is crenulate and internally divided. The posterior lobe is slightly longer and not divided internally. The accessory gland is also divided into a median and posterior lobe. The median lobe is granular and thick walled while the posterior lobe is transparent and thin walled. The accessory gland is connected to the main salivary gland by a narrow duct (Fig. 28). A duct from the main gland runs into the head and connects with the salivary syringe. The first chamber of the ventriculus is a large sack-like structure which seems to vary in shape. It extends to about the fourth abdominal segment where it narrows and forms the second chamber. This chamber is often dark in color due to food held in the tube. The canal folds back on itself once and becomes the third chamber which enters the intestine. The malpighian tubules mark the beginning of the intestine and also the pyloric collar. There are two pairs of tubules which are coiled around the chambers of the ventriculus. The apecies of the tubules are attached to the pyloric collar and give the impression

that they are continuous tubules. The intestine is short and joins the rectum, which is a bag-like structure. The rectum narrows and passes through the anal tube and opens to the exterior at the tip (Fig. 38).

The Female Reproductive Organ

The paired ovaries of Macrovelia, consisting of six ovarioles or egg tubes, extend from the base of the abdomen to about the fourth segment. Each egg tube has an anterior terminal filament, a group of undifferentiated cells and a series of eggs. The terminal filaments combine together from each ovary to form one large mass of filaments. They are attached to the base of the abdomen under the first chamber of the ventriculus. Tracheae are found around the terminal filaments and ovarioles. The ovarioles appear to have only one egg developing at a time in pregnant females. The body cavity may contain as many as eight large eggs during the egg laying period.

The ovarioles of each ovary open into a large oviduct, which in turn joins with the opposite oviduct to form a common oviduct. The oviduct is large and the wall is thickened anteriorly and leads into the vagina posteriorly. The spermatheca rests on the vagina wall and extends from the junction of the oviduct to the posterior end of the vagina. It consists of a heavily scleritized, tightly

coiled tube, folding back on itself and gradually enlarging in area from a narrow fused tube to the width of the vagina at its base. The tube enlarges and terminates in the spermathecal bulb (Fig. 32). Anterior to the spermathecal bulb the spermatheca is less coiled and the apical tube branches off from the main canal. The apical tube is thin-walled and coiled in a random manner. The vaginal opening, the vulva, lies between the gonapophsis of the female genitalia (Fig. 32).

The Male Reproductive Organ (Fig. 33)

The internal organs of the male are simple in structure. The testes of Macrovelia are long tubes that are lightly coiled around the lower chambers of the ventriculus and intestine. It is difficult to uncoil or dissect out the testes of this species. There are two testes and their bases are near the posterior end of the first ventriculus. A narrow duct, the vas deferens, leads from the testes to the paired vesiculae seminales. The vesiculae seminales are large lobe-like structures joined at their bases to form a common tube. One accessory gland is attached under each vesicula seminalis. The ductus ejaculatoris is attached between these glands to the vesicula seminalis. The ductus ejaculatoris is a fine tube running between the primary gonopore, in the genital capsule and the vesicula

seminalis. The tube is tightly coiled into a ball near the base of its attachment to the vesicle.

The Nervous System (Figs. 34-36)

The ganglia of the central nervous system are concentrated in the posterior part of the head and the prothorax. The fusion of the ganglia is almost complete making interpretation difficult. The short optic nerves extend from the protocerebral ganglion (Fig. 36). These nerves and the fused deutocerebral-tritocerebral ganglia are not contiguous medially since the pharynx, with its dilator muscles, lies partially between them. The right and left sides of the brain (deutocerebral-tritocerebral ganglia) are connected by a small sphere internally. The function of this structure is not known. The circum-oesophageal connectives are lost between the brain and the sub-oesophageal ganglion. Together these ganglia make a heavy ring of nervous tissue through which the oesophagus and other tubes pass. The thoracic concentration consists of four ganglia. The first ganglion is partially covered by the sub-oesophageal ganglion. It is easily picked out if viewed from the venter (Fig. 34). The meso- and meta-ganglia are distinct along with the larger last ganglion. The last ganglion gives off two pairs of nerves, one directed obliquely and the other posteriorly, and

represents the fused abdominal ganglion.

Discussion of the Internal Morphology

The internal organs of Macrovelia are generally similar to the other Hemiptera. DuFour's (12, p. 243) work remains the most comprehensive one on internal anatomy of the Hemiptera. He illustrates two genera of semiaquatic Heteroptera, Gerris and Velia. The alimentary canal of Macrovelia is quite similar to these genera and is also comparable to Nepa as described by Hamilton (18, p. 1091). In all cases the alimentary canal is simple and without gastric caeca. Elson (15, p. 579) compared the length of the alimentary canal with total body length of hemipterans. In Macrovelia it is one and one-half times the length of the body as it is in Gerris and Hychometria.

Southwood (38, p. 77) considers the taxonomic importance of the salivary glands in the terrestrial Heteroptera. No such work appears in the literature for the aquatic or semi-aquatic Heteroptera. DuFour illustrated the salivary glands of Gerris and points out that three pairs of salivary ducts enter the head. In Macrovelia and Hydrometra only one duct enters the head from each gland. Phylogenetic similarities in the salivary glands are difficult to point out because of the lack of related information. The posterior part of the digestive track in all of the described

Hemiptera, according to Sprague (40, p. 609), cosists of a short intestine, into which open four Malpighian tubules, and a thin-walled rectum. Four Malpighian tubules are found in Macrovelia.

The internal organs of reproduction have not been described except for a consideration of the spermatheca by Pendergrast (32, p. 7). He points out that the fecundation canal of Macrovelia is close in form to Mesovelia. There is also a similarity in the nature of the spermathecal bulb and the apical tube.

The male reproductive organs of Macrovelia were not considered by Pendergrast. However, he does illustrate the male organs of Mesovelia. According to Pendergrast (32, p. 27), Mesovelia differs from the others in this group (Gerridae, Veliidae, Hydrometridae and Hebridae) in possessing two pairs of accessory glands which enter the dorsal aspects of the vesicula siminalis. Macrovelia possess one pair of accessory glands located in a position similar to Mesovelia. The presence of accessory glands in both families relates them very closely.

The nervous system of Macrovelia, as well as most hemipterans, is characterized by a concentration of the ganglia. The optic nerves are small. The deutocerebral and tritocerebral ganglia appear to be fused and for simplicity are termed the brain. The circum-oesophageal

commisures and the sub-oesophogeal ganglia are truly fused and form the nerve mass around the oesophagus. The thoracic ganglia are also fused but the boundaries are easily recognized. The abdominal ganglion is larger than the thoracic ganglia but strongly joined to them.

BIOLOGY

Description of Habitats

Macrovelia hornii may be found along the edges of most fresh water situations. Collecting is generally good among mosses and grasses along the margins of streams, springs and ponds. A description of two study sites will illustrate the habitat of this bug. The site at Pinehurst, Oregon, a spring, has a northern exposure and the direct sun does not reach the site until late afternoon. The spring is located on the side of a gently sloping hill. Below the spring the area is swamp-like and is commonly termed a seepage area. The ground is covered with only mosses and grasses. A pine tree, at the base of the spring, shades the area. The spring forms a small pool at the head of the seepage area. This pool is very cold and the bugs are not found near its edge. The water is quite warm in the seepage area and the bugs are found in this niche.

Macrovelia appears to thrive in the high humidity and moisture conditions found in the moss "plants." Adults and nymphs may be found deep in the protonema of the mosses.

In late May, when the flow of the spring begins to decrease, the nymphs seek the moistened portions of the seepage area. The adults may be found at the bottomsof dried out depressions in the mud. These depressions

appear to serve as chambers for the quiescent adults during the dry period. As many as fifteen or twenty individuals may be found in one of these depressions. The population at Pinehurst is predominantly made up of macropterous forms.

The second study site is located at Corvallis, Oregon (Fig. 5). A small temporary stream flows through a grove of deciduous trees. The sunlight filters through the trees and the area is generally cool. The greater part of the site is covered with decaying leaves. Patches of moss are found along the stream's edge. Macrovelia is readily captured in these mossy areas. In the late spring, camas and pond grasses cover the edges of the stream. Snowberries and wild roses are the main shrubs at this site. The stream flow is slow and gradually decreases as the days become warmer. By the middle of June the stream is completely dry. The population of Macrovelia may drop to only a few adults and these adults are not active. The adults find protection from the dry conditions in between the moss protenema and the soil air spaces. Adults reared in the laboratory under relatively similar conditions of temperature and relative humidity followed this general pattern of activity. The individuals of Macrovelia in the Willamette River Valley undergo a definite period of quiescence during the dry summer months. In the laboratory,

adults are able to go without food and live under quite dry conditions from four to five months. However, when disturbed, they show definite signs of life during this period.

The adults are not surface feeders, and are particularly helpless when found on the water surface. The legs are not covered with hydrofuge pile and the claws are apical, reducing the efficiency of the bug on the water. When the bugs are caught in the surface film they draw their legs up over the dorsum, exposing the pile-covered venter to the water and drift along until beached. This type of behavior is referred to as "boating." Perhaps this is a means of transportation for the brachypterous forms. The nymphs are found more frequently running on the surface film. Stagnant water seems to support their light weight easily. Actual flight of macropterous individuals was not observed. One record of a macropterous adult, taken in a light trap, would suggest that flight is possible. It was not possible to induce flight of individuals in the laboratory.

Collecting Methods

Adults and nymphs in the field are readily collected with an aspirator. Samples of mosses and grasses taken from the edges of streams and run through Berlese funnels provide the best method of collection. Transportation to the laboratory was accomplished in cottage cheese cartons.

The bottom was partially filled with a moistened mixture of plaster of paris and lamp black.

Rearing Methods (Figs. 52, 53)

A special rearing cell was developed for the life history studies. Plastic tubes, one inch in diameter, were cut into one-inch segments. One end was filled with a mixture of plaster of paris and lamp black to a depth of about three-eighths of an inch. The vial was placed on wet paper towels in aluminum trays, which in turn were placed in plastic, refrigerator boxes partially filled with water. The plaster of paris served as a wick and the moisture was held fairly constant by adding a few drops of water to the paper towels each day. Temperature and humidity were held relatively constant by the water bath in the refrigerator boxes.

In rearing studies, mated females were placed in cells containing moss protonema. Eggs were laid on the moss and were removed before hatching.

Nymphs and adults will feed on any recently killed insect of comparable size. Because of the ease of handling, small annelids, called white worms, were used as a food source. They are commonly used by tropical fish fanciers and can be reared in moist sand to which oatmeal or dry tropical fish food is added as a food source.

Feeding

In the laboratory, Macrovelia will eat a wide variety of insects. Small living insects, such as Collembola, are devoured readily. They are known to feed on aphids, spittle bugs, various lepidopteran larvae, and fruit flies. In the field the insect probably feeds on various larvae, Collembola and worms.

The insect moves about with its lowered antennae moving from side to side while seeking food. When prey is located, the insect appears to become more excited as the antennae move more rapidly and the insect lifts its rostrum and feels about with it. As the bug approaches food, it swings its beak forward and with a movement of the whole body, impales its victim. The victim usually reacts violently, and the bug withdraws its rostrum until the victim dies. The bug then re-approaches its victim and feeds. It is presumed that saliva, secreted by the salivary gland, has a toxic effect on the prey. During feeding the stylets are seen lashing and gouging within the soft tissues with a tonguelike action.

Adults were observed to carry their prey for considerable distances by means of the recurved barbs on their mandibles.

Hibernation

Quiescence of the adult continues throughout the summer and probably into late winter. During this period, collecting is sparse. Active adults, along with a few copulating pairs, may be collected in January and February. This depends on the weather during these months for a cold January and February will keep the adults inactive. Eggs usually appear around the first of March when the adults are the most active.

Mating (Figs. 55, 56)

The mating of Macrovelia was observed during the spring months. Typically, as the male approaches the female, the male protracts the eighth abdominal segment to lower the genital capsule. The male quickly mounts the female, grasping the female with his front legs at the corners of her pronotum. The middle legs of the male fit behind the front legs of the female and grasp the thorax. The hind legs are either placed on the abdomen of the female or used to stabilize the male. During copulation, the female may move about and even feed. After the male has mounted the female, the male genitalia and accompanying abdominal segments are projected down towards the female genitalia. The phallosoma extends into the vulva while the

endosoma extends into the female reproductive tract. During copulation, the male moves the anal tube up and down. The male claspers are used to locate and guide the aedeagus during copulation.

Mounting without copulation was observed and was quite common. Pairs remained in this position for long periods of time. Actual copulation may last for only fifteen to thirty minutes. After the male releases the female, she may push him aside with her middle and hind legs.

Fecundity and Oviposition

Copulating pairs were taken from the field and allowed to lay eggs on moss protonema in the rearing cells. On March 6, 1962, one such pair was introduced into a rearing cell. Copulation was observed the next day together with two new eggs. Supposed copulation was observed ten days later and by this time, a total of sixteen eggs had been laid by the female. At that time some of the earliest laid eggs were about to hatch. Copulation of the pair was again observed on March 23, and a total of 20 eggs was recorded for this female over a 25-day period. Twenty eggs per female was found to be the average, with a maximum of 24 and a minimum of 16. The number of eggs laid per day varied from one to six.

When given a choice, moss was the preferred egg-laying site. Otherwise, eggs were laid at random. Each egg was usually placed on a moss scale with the anterior end (eye spot end) pointing outward and downward, and the ventral side (rounded side) up. The eggs have a sticky covering and adhere to one another.

Number of Generations and Longevity

There appears to be only one generation per year of Macrovelia in the Willamette Valley. The winter is spent in the adult stage. There is evidence that more than one generation per year may occur on the coast. Records from the Oregon coast show that nymphs may occur in late July. Generally, reproductive activity begins in late February and early March. Egg laying may continue until late May. The nymphs normally reach maturity between May and June. These adults then go into a quiescent state for the summer.

Egg Appearance (Figs. 57, 58)

The eggs are spheroid and are about 1.1 mm long and .42 mm wide. They are slightly pointed at each end, with the anterior end slightly more pointed than the posterior end. The flattened dorsal side is attached to the substrate. The ventral side is rounded (Fig. 57). The surface of the egg does not have hexagonal sculpturing but is

shagreened, visible only under very high power. When the eggs are laid they are pearly white. No definite color change occurs within the egg until development of the embryo starts. No evidence of an operclum or of a micropylar apparatus was found.

Development. As the embryo matures, various color changes may be observed within the egg. The egg gradually changes from a pearly white to yellow. The transition from white to yellow begins as a yellow blotch in the middle of the egg and progresses towards the ends until the egg is completely colored. This process takes from four to five days. Sterile eggs may be detected after a few days by the absence of this yellow coloring. On the eighth day of development, the faint reddish eyespots appear at the anterior end. At first they are small in size, later they develop into large black spots. The eyespots reach their maximum development on the fourteenth day. Blastokinesis or inversion apparently does not occur in this species. A few days before hatching, the antennae and legs appear under the transparent chorion of the egg. The visible antennae are held along the venter of the developing nymph. The small egg burster is not visible under the egg shell.

The average incubation period of the egg is about 15 days, with a minimum period of 11 days and a maximum period

of 19 days. The rate of development of the egg is related to the temperature. An increase in four to five degrees in temperature will speed up development by about six days.

Hatching. When hatching, an egg burster is employed to split the egg shell. The egg burster is a cap-like structure with two scleritized ridges that support two spines (Fig. 49). This fits over the head of the embryo. The shell is split either by the nymph pushing against the egg burster or by the change in pressure caused by the nymph sucking in embryonic fluid and enlarging within the egg. The egg burster is pushed through the shell and out over the egg shell as the nymph moves out of the egg. Slow, back and forth movements, together with a swelling of the body move the nymph forward and out. When the thorax is out of the egg shell the legs and antennae are still held to the body by embryonic fluids. First one limb is pulled forward and freed, and then another, until all the legs and the antennae are free. After a period of rest the nymph will clean itself of the embryonic fluids. During the cleaning period the nymph will rest from time to time. When resting the legs are drawn up alongside the head and held there. After the cleaning period the nymph pulls the abdomen free from the egg. The newly hatched nymph is pearly-white and gradually begins to darken. The legs and

head are the first to turn brown. The abdomen develops a yellowish cast.

The hatching process requires approximately twenty to forty minutes. Mortality during hatching was not common. Only one case of death during eclosion was observed.

Nymphs

The newly emerged Macrovelia nymph is pearly-white. The legs and antennae are transparent. The abdomen is compressed with the anus drawn up under the body. If undisturbed the nymph will stay close to the egg shell from which it hatched. However, if it is disturbed, it can easily walk or run. Thy nymph seems to prefer to stay motionless during this early period.

When food is available the nymph will feed within an hour and a half after hatching; but some nymphs may not feed for over a 24-hour period. Failure to feed causes some mortality in the first instar. Cannibalism is found only in special cases, when food is not available or when the nymphs are in overcrowded conditions. Nymphal feeding is similar to adult feeding but they are limited in the size of food they are able to take.

The nymph is ready for molting when it reaches its maximum length and maturity. The pigmentation of the cuticle is lacking along the ecdysial line that extends

along the mid-line from the abdomen to the base of the head where it bifurcates and forms an arm on either side of the frontal region.

Just before molting a site is selected and the nymph then becomes less active. An elevated position such as a moss or grass stem is usually selected. The head is pointed downward with the hind legs anchored to the substrate and parallel with the long axis of the body. The middle legs are planted firmly at right angles with the body and the front legs extend forward. The beak is held between the front legs and below the body. When the nymph is secure, the cuticle of the mesothorax begins to cleave. The nymph begins a series of swelling movements that push the emerging body forward, out and over the cast skin. The head emerges first with the bases of the antennae and the legs next. The legs begin outward movements which help to pull the trunk forward. First the prothoracic legs and then the mesothoracic and metathoracic legs pull away from the exuvia. Finally the antennae and the beak pull away and are free.

The free nymph will rest and clean itself by rubbing the legs together and over the body. The color of the newly hatched nymph is similar to the hatching nymph, that is, a pearly-white color with transparent legs. The mortality rate during molting is quite high. Moisture

in the cell may be too low, causing desiccation. Also the molting fluids in the legs may be deficient and the nymph may be caught in the cast skin. Nymphs that break away from the substrate during the molt are unable to attach themselves again and eventually die. In rearing studies the most common cause of death was excessive humidity.

Description of the Nymphal Stages and Development.

The body and limbs of the first instar nymph are covered with hairs and bristles. There is one stout bristle located on the first segment of the antennae while the other three segments are covered with short hairs. The antennae are four-segmented and stout. The legs are stout and have a one-segmented tarsus. The abdominal scent gland is just visible on the fourth segment after the abdomen is extended. It is easily seen on the abdomen of the other three instars.

The average development period for the first instar is about five to six days with a minimum of four days and a maximum of eight days. The size of this stadium ranges from .75 mm to 1.12 mm in total body length. The increase in size is due to the extension of the abdomen by feeding. The thoracic sclerites do not show wing pad development (Fig. 42).

The second nymphal instar is larger in size, measuring 1.40 mm in length. The wing pads are not visible but the

thoracic sclerites are larger than those of the first instar. The developmental period for the second instar is approximately five to six days with a minimum of four days and a maximum of seven. The third instar has an average body length of 2.06 mm. The wing pads are present and lap over onto the next segment. Development for this instar takes from five to six days with a minimum of four days and a maximum of eight days. The fourth instar's average body length is 2.59 mm. The wing pads are well developed, extending across to the second abdominal segment. The nymph reaches maturity in an average of ten days.

The average time for development from the abandonment of the egg to the mature adult is about forty days. Nymphal development is completed in about 26 days.

Dimorphism

Dimorphism of Macrovelia is characterized by two patterns of wing form. The brachypterous form has vestigial wings projecting just behind the pronotum and the macropterous form has fully developed wings, reaching the apex of the abdomen. The brachypterous form may vary in length and in venation. Wing length may extend to the middle of the abdomen or to any length between this and the normal short wing condition. The longer wings may have

a normal vein complement but in the shorter wing forms the veins are reduced to two thick veins.

The two conditions of alarary polymorphism exist together in some localities, although one form is dominant over the other. Specimens from Pinehurst, Oregon are mainly macropterous but an estimated 10 per cent were brachypterous. At Corvallis, macropterous forms are unknown but intermediate wing forms are found. Matings in the laboratory with brachypterous forms produce only brachypterous forms. Rearing and mating studies should be made before this condition can better be evaluated.

Discussion of Biology

Macrovelia seems to need a special type of habitat. Important characteristics of the habitat are moisture, a moderate temperature and "moss plants." Moisture is important to the developing immature insect. Lack of moisture during the period of growth would be fatal. Temperature is important because of its effect on moisture and on the rate of development of the immature stages. Low temperatures retard the growth rate and high temperatures are fatal to the nymphs. The moss plants are important as a place for oviposition. Moss is apparently preferred because of its moisture-holding capacity.

Adult quiescence is a protective mechanism to insure the continuance of the species. However, the adult remains active in moist situations. On the Oregon coast, nymphs and adults remain active into July and August.

The number of generations per year appears to be restricted to one. However, Sprague (40, p. 624) reports the different species of Hydrometra have different numbers of generations per year. She also notes that temperature is probably the factor responsible for reproductive activity in Hydrometra. This is probably the case with Macrovelia.

There are four nymphal instars in Macrovelia and this is unusual for the Hemiptera. Hoffmann (14, p. 94) notes that Microvelia borealis Bueno and M. buenoi Drake are water bugs having less than five instars. The average length of nymphal development of these species is similar to Macrovelia. True relationships cannot be made from this because other species of these genera have five instars.

The condition of dimorphism in Macrovelia is different from that of Gerris sp. and Hydrometra martini Kirkaldy. According to Brinkhurst (3, p. 223) polymorphism is controlled by two factors, temperature and a genetic system that produces a winged, winter generation and a

wingless summer generation. Sprague (40, p. 648) concludes that the condition of polymorphism in Hydrometra is termed a balanced population, that is, both winged forms are in the same optimal proportions in a population. Macrovelia differs and the proposed explanation of polymorphism is purely genetic. Genetic data at this time are incomplete which makes speculation difficult, however matings with only brachypterous forms has produced only brachypterous adults in rearing studies. However, a genetic mechanism such as the multiple gene hypothesis may be involved. The pure population of one wing form may be the result of environmental conditions selecting for the homozygous (41, p. 314).

DISTRIBUTION

Two biotic provinces, the Oregonian and the Californian, are found to contain a habitat suitable to this species. The foothills of the coastal ranges, the Cascade and the Sierra Nevada mountains afford a more specific habitat. Relic populations appear in the Saskatchewan, Coloradan and Navahonian biotic provinces. Additional collecting is needed to provide a more accurate picture of the distribution of Macrovelia.

Location of Types

Uhler described the genus and species, Macrovelia hornii, in 1871 (44, p. 420). Uhler gives the type locality as Ft. Defiance, Arizona. Most of the material collected at that time is in the National Museum in Washington, D. C. It is assumed that the type specimen is located there.

List of Localities (Map I)

Data on distribution: ARIZONA: Pima Co., Mt. Lemmon, April, 1949 (K.U.), 70 brachyp.; Catalina Mt., May 22-25, 1958, L. O. Brien (P.D.A.), brachyp.; Coconino Co., Oak Creek Canyon, Oct. 1935 (K.U.) 2 brachyp.; Yavapai Co., Granite Dells, July 1950 (K.U.) 91 brachyp., 1 macrop.;

Apache Co., Ft. Defiance, type locality.

CALIFORNIA: Marin Co., Inverness, May 29, 1958, P. D. Ashlock (U.B.C.), 1 2 brachyp.; Corte Madera, May 1928, Hungate, (R.L.U.) 1 brachyp.; Woodacre, Sept. 1930 (C.A.S.) 4 macrop.; Lagunitas, May 1924 (C.A.S.) 5 brachyp., 7 macrop.; Fairfax, Oct. 1911 (C.A.S.) 14 macrop.; Napa Co., Pope Valley, April 14, 1955, Lattin (U.B.C. & O.S.U.) 9 macrop., 1 1 brachyp.; Monticello, August 15, 1942, McKinstry (C.I.S.) 9 13 macrop.; St. Helena, July 1912, L. R. Reynolds (C.N.H.M.) macrop., same place, October 1910 (C.A.S.) macrop.; Tehama Co., Mineral, June 26, 1954, Schuster (P.D.A.) 1 macrop.; Nevada Co., Grass Valley, July 19, 1936 (C.I.S.) 2 macrop.; Riverside Co., Palm Canyon, June 14, 1952 (J.D.L.) (P.D.A. & O.S.U.) 2 1 macrop.; Whitewater, April 13, 1948, J. W. MacSwain (C.I.S.) 1 brachyp.; Calaveras Co., Mokelumne Hill, May 21, 1931, Usinger (R.L.U.) 3 3 macrop.; Murphy's, May 1937 (C.A.S.) 3 macrop.; Madera Co., Bass Lake, July 1, 1946, R. L. Usinger (R.L.U. & C.I.S.) 4 3 macrop.; Placer Ry. Sta., June 1920 (K.U.) 1 brachyp.; San Diego Co., Santee, April 3, 1952, R. D. Lee (R.L.U.) 1 1 macrop., 1 brachyp.; Santa Barbara, Davy Brown Camp, April 18, 1953, W. McDonald (R.L.U.) 1 brachyp.; Tulare Co., Wood Lake, April 30, 1947, N. W. Frazier (C.I.S.) 1 9 macrop.; Sequoia National Park, June 1929 (C.A.S.) 1 macrop.; Humboldt Co.; Fort

Seward, June 5, 1935, Essig (C.I.S.) 3 10 macrop.; Willow Creek, July 1929, C.A.S.) 18 macrop.; Mendocino Co., Hopland, May 28, 1950, L. W. Quate (C.I.S.) 1 macrop.; Yorkville, April 1928 (K.U.) 3 macrop.; Willits, June 1948 (C.A.S.) 2 macrop.; Santa Clara Co., Morgan Hill, May 23, 1922 (C.I.S.) 1 macrop.; Santa Clara Co.; Eldorado Co., Camino, June 23, 1948, J. W. MacSwain (C.I.S.), 1 macrop.; Nashville, May 1954 (K.U.) 1 macrop.; Tuolumne Co., Yosemite, May 22, 1931, E. O. Essig (C.I.S.) 1 brachyp.; Sonora, May 1930 (C.A.S.) 1 macrop.; Sonoma Co., Cazadero, Sept. 1918 (K.U.) 52 macrop.; Mark West Sp., May 1930 (C.A.S.) 1 macrop.; Butte Co., Richardson Spr., May 1944 (C.A.S.) 27 macrop.; Oroville, May 1928 (C.A.S.) 1 macrop.; Contra Costa Co., Redwood Cn, May 1905 (C.A.S.) 3 macrop.; Madrone, April 26, 1952, Lattin (O.S.U.) 1 macrop.; Alameda Co., Leona Hyts, August (C.A.S.) 3 brachyp. 19 macrop.; Monterey Co., Carmel, July 1938 (C.A.S.) 1 macrop.; Bryson, May 1920 (C.A.S.) 7 macrop.; Sacramento Co., Michigan Bar, April 1922 (C.A.S.) 1 macrop.; Folsom, May 1935 (C.A.S.) 1 brachyp.; Ingo Co., Darwin Falls, May 1954 (K.U.) 3 macrop.; other counties without localities are Los Angeles Co., Monterey Co., Siskiyou Co., Sonoma Co., Santa Clara Co., and Trinity Co.

COLORADO: Routt Co., Steamboat Springs, Aug. 15, 1944, Bryant (P.D.A., K.U. & C.I.S.) 17 brachyp.; same

place, Sept. 1941 (K.U.) 4 brachyp.; other records show three state records only from Colorado in the Philadelphia Academy of Science Museum and one record from Colorado in the Chicago National History Museum.

NEW MEXICO: Otero Co., Mescalero, May 1949 (K.U.) 9 brachyp.; San Miguel Co., Las Vegas, July 1950 (K.U.) 2 Brachyp.; Torrance Co., Tajugue, June 1947 (K.U.) 1 brachyp.

OREGON: Yamhill Co., Bald Mountain, July 28, 1957, McKay-Fender (U.B.C.) 2 macrop., 12 brachyp.; Peavine Ridge, Sept. 1959, Fender (O.S.U.) 1 macrop.; Lake Co., Lakeview, June 1951 (K.U.) 1 macrop.; Josephine Co., O'Brien, May 1930, Roth (O.S.U.) 1 brachyp.; Selma, May 1960, Anderson (O.S.U.) 1 brachyp.; Benton Co., Corvallis, May 12, 1950, Roth (O.S.U.) 2 brachyp.; Corvallis, June 9, 1950, Lattin (O.S.U.) brachyp.; Nashville, Feb. 4, 1960, F. Lewis (O.S.U.) 1 brachyp.; McDonald Forest, Oct. 29, 1958, Lattin O.S.U.) brachyp.; Berry Creek, June 18, 1959 (O.S.U.) brachyp.; Jackson Co., Pinehurst, May 24, 1958 (O.S.U.) macrop., brachyp.; Central Point, April 1959, Lattin (O.S.U.) macrop.; Dead Indian Soda Springs, May 21, 1950, J. D. Lattin (O.S.U.) 3 brachyp.; Tubb Springs, May 19, 1960, Lattin (O.S.U.) macrop.; McLeod State Park, May 20, 1960, Lattin (O.S.U.) macrop. and brachyp.; Camp White, May 22, 1960, Lattin (O.S.U.) macrop.; Touvelle State Park, May 21,

1960 (OSU), macrop.; Lane Co., Washburn State Park, November 2, 1957, McKay-Fender, (OSU), brachyp.; Lincoln Co., Waldport, March 13, 1937, Chamberlin, (OSU), brachyp.; same place, March 16, 1956, (OSU), brachyp.; Yacquina Head Lighthouse, August 31, 1961, Lattin, (OAU), brachyp.; Douglas Co., Roseburg, June 15, 1960, P. O. Ritcher, (OSU), macrop.; Marion Co., Silverton, April, 1962, Anderson, (OSU), brachyp.; Tillamook Co., Sand Lake, July 7, 1962, Lattin, (OSU), brachyp.; Coos Co., Bandon, August, 1961, Lattin, brachyp.

SOUTH DAKOTA: Pennington, Black Hills, August 17, 1954, William Sanderson, (I.N.H.S.), 9 brachyp.; Custer Co.; Custer, August, 1937, (KU), 20 brachyp.

Discussion of the Distribution

Two factors which control habitat, and subsequently the distribution of a species, are climate and geological barriers. Any climatic or geographical change in the past will be a factor in discussing the present distribution of a species (Good 17, p. 267). Climatic changes will produce migrations and some species become extinct and others decimate, leaving behind relic colonies (Cain 6, p. 169). The main climatic change possibly affecting the distribution of Macrovelia hornii would be the glacial advances during the Pleistocene. Perhaps the distribution of

Macrovelia was more widespread in the western biotic provinces during active glaciation because of cooler temperatures and more precipitation. If this is so, the present distribution in these biotic provinces are examples of relict populations. The present distribution, chiefly in the coastal biotic provinces may be due to climatic conditions similar to those of the Pleistocene.

THE TAXONOMIC POSITION OF *MACROVELIA HORNII*

The author has placed *Macrovelia* under the Mesoveliidae as the subfamily Macroveliinae. This has been done on the basis of the new characters found in this study. The presence of accessory gland in the male reproductive organ along with a similar spermatheca seems to relate *Macrovelia* with the Mesoveliidae. The general characters of the presence of ocelli, the median thoracic scent gland, apical claws, and tarsal segment number also has been used to relate this group.

The male external genitalia can not be compared with the genitalia of *Mesovelia*. The genitalia of *Macrovelia* seems to be similar to the Pentomoidea.

The female genitalia seems to differ from both the Mesoveliidae and the Veliidae in that the Mesoveliidae have a gonoplacs and a serrate gonapophysis while the Veliidae have feathery projections on the gonapophysis. *Macrovelia* does not contain these modifications of the gonapophysis. Perhaps these differences have developed by convergent evolution.

The hind wing venation is definitely similar to the Veliidae, however the forewing venation is characteristic only to *Macrovelia*.

The presence of similar characters within *Macrovelia*

suggest that it may be a connecting link between the two families and that the Mesoveliidae and the Veliidae are more closely related than originally thought.

SUMMARY AND CONCLUSIONS

Macrovelia hornii is the only species of the genus, and is restricted in its range to the western half of the North American continent. Its nearest relatives, Ocellovelia and Hebrovelia, are found in South Africa. All of these are considered as annectent species and considered to be primitive veliids.

The exoskeleton is heavy, and because of fusion of the sternal area, rigid. Alary polymorphism is common and both brachypterous and macropterous forms are found. Intermediate winged forms are also present. The nymphs are proportionately smaller and the exoskeleton more lightly sclerotized. These insects are found readily only in the spring near the edges of ponds, springs, or streams. They are found hiding among moss and preying on small arthropods and annelids. Reproductive activity is restricted to late winter and spring. There is only one generation per year in the Willamette Valley. In the summer, these insects become increasingly difficult to find. They are thought to go into a period of quiescence during the dry summer months. The period of quiescence is not interrupted by fall. Winter is spent in the adult stage.

The egg is not sculptured and is simple in form. Development takes from 12 to 15 days, depending on the

temperature. The eggs are usually laid on moss. The hatching process is rapid and uniform in nature.

From the time the nymph hatches, its activities closely resemble those of the adult. This is especially true of feeding and grooming. Molting is a dangerous process and mortality is high during this time.

The general morphology of Macrovelia has aided in establishing relationships with the Gerroidea. In the cranium the apodemina is thought to be common only to the Saldidae. The mandibular levers of Macrovelia are comparable to Mesovelia. The thoracic segments are generally similar within the Gerroidea. However, the metatergum of the Gerroidea is modified considerably between families. The projected metascutum of Mesovelia appears to be a modification of the metanotal costa of Macrovelia. The hind wing venation of Macrovelia is identical to that found in the Veliidae. The external female genitalia is also typical of the veliids. The male genitalia is definitely unrelated to the Veliidae or to the Mesoveliidae. Internally, the male and female reproductive organs are found to be similar to that found in Mesovelia. The fecundation canal in the female is similar in construction and the presence of accessory glands on the vesicula seminalis is unique among the semiaquatics.

McKinstry (31, p. 95) includes a chart summarizing the family characters for the semiaquatic bugs, Amphibiocorisae. A revision of his chart is given together with additional information in Table I.

The balance of characters seems to point to the inclusion of Macrovelia under the Mesoveliidae as the subfamily Macrovelliinae. Perhaps this annectant family is truly a connecting link between the Saldoidea and the Gerroidea.

Table I. A summary of the characters from selected families of the Amphibicorisae.

Winged forms	Hebridae	Meso-veliidae	Macro-veliidae	Hebro-veliidae	Hydro-metridae	Gerri-dae	Veli-dae	Saldi-dae
Apodemina	absent	absent	present	absent	absent	absent	absent	present
Claws	apical	apical	apical	apical	apical	pre-apical	pre-apical	apical
Thoracic scent gland	median	median	median	median	none	median	lateral	none
Abdominal scent gland	present	present	present	absent	absent	absent	absent	present
Ocelli	present	present	present	absent	absent	absent	absent	present
Female spermatheca fecundation canal	short and straight	heavily sclero-tized & fused	heavily sclero-tized & fused	?	short simple and sinuous	complex narrow & heavily sclero-tized	rudi-mentary	fecunda-tion canal absent
Male accessory gland	absent	two pairs	one pair	?	absent	absent	absent	present but as mesadene glands
Number of tarsal segments	222	333	333	122	333	222	122 & 333	333
Oviposition for piercing tissues	none	present	none	none	none	none	none	present

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APPENDIX

Figure 1. Dorsal view of the head.

AC	Anteclypeus
AP	Apodeme
AT	Antennal Tubercle
EA	Epicranial arm
FR	Frons
LBR	Labrum
MP	Maxillary plate
O	Ocellus
PAC	Paraclypeus
PC	Postclypeus
V	Vertex

Line scale equals 1 mm.

Figure 2. Lateral view of the head.

AC	Anteclypeus
AP	Apodeme
AT	Antennal tubercle
EA	Epicranial arm
FR	Frons
LBR	Labrum
LB	Labium
MP	Maxillary plate
O	Ocellus
PAC	Paraclypeus
V	Vertex

Figure 3. Mandibular lever.

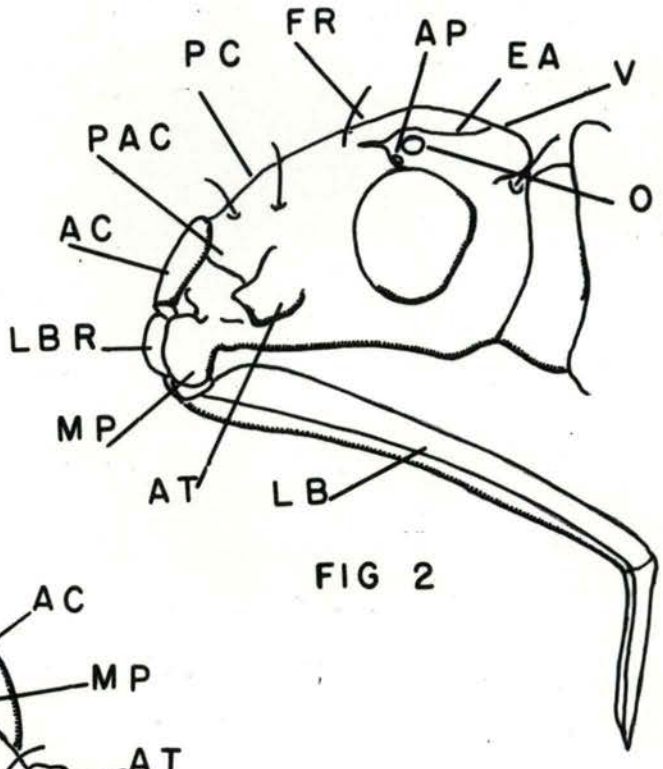

FIG 2

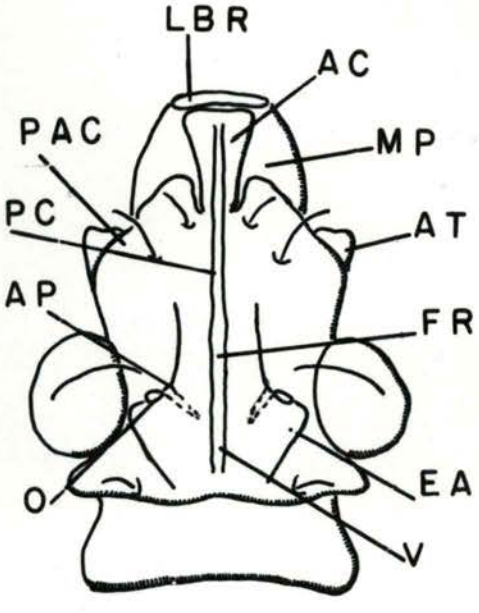

FIG 1

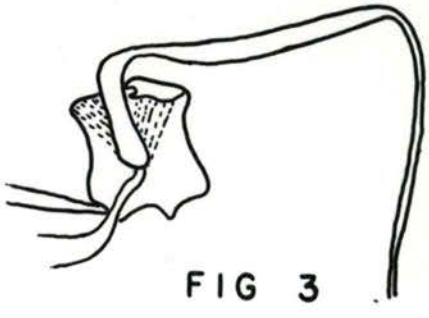

FIG 3

Figure 4. Dorsal view of the prothorax.

Figure 5. Lateral view of the prothorax.

LPP Lateral posterior projection.

Figure 6. Ventral view of the prothorax.
Line scale equals 1 mm.

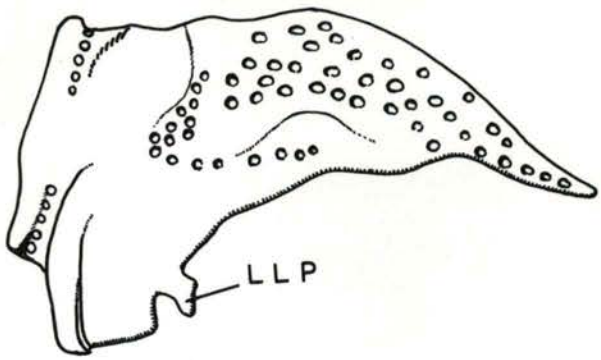

FIG 5

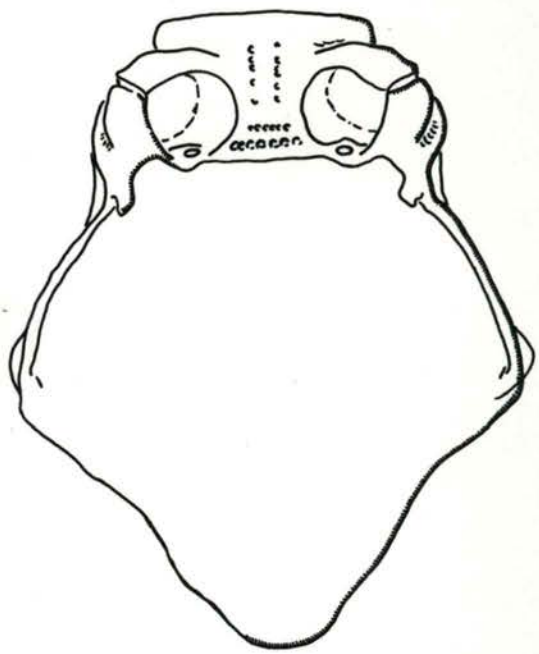

FIG 6

FIG 4

Figure 7. Dorsal view of the pterothorax.

P	Phragma
PAS	Parapsidial suture
MS	Median scutual area
LS	Lateral scutual area
TS	Tergal split
ANP	Anterior notal wing process
PNP	Posterior notal wing process
SCL	Scutellum
PN	Postnotum
MPG	Meso-pleural grooves
SCT	Scutum - 3
SCL	Scutellum - 3
SCE	Latero-scutal extention
SCIE	Latero-scutellar extention
MC	Metanotal costa

Figure 8. Lateral view of the pterothorax.

P	Phragma
PAS	Parapsidial suture
PRB	Prealare bridge
PRA	Prealare
TS	Tergal split
SA	Subalare
SCT	Scutum - 3
MNS	Metathoracic spiracle
EM	Epimeron
ES	Episternum
S	Supracoxal cleft
MPL	Metapleuron
SF	Supracoxal flange
1 AS	First abdominal spiracle

Line scale equals 1 mm.

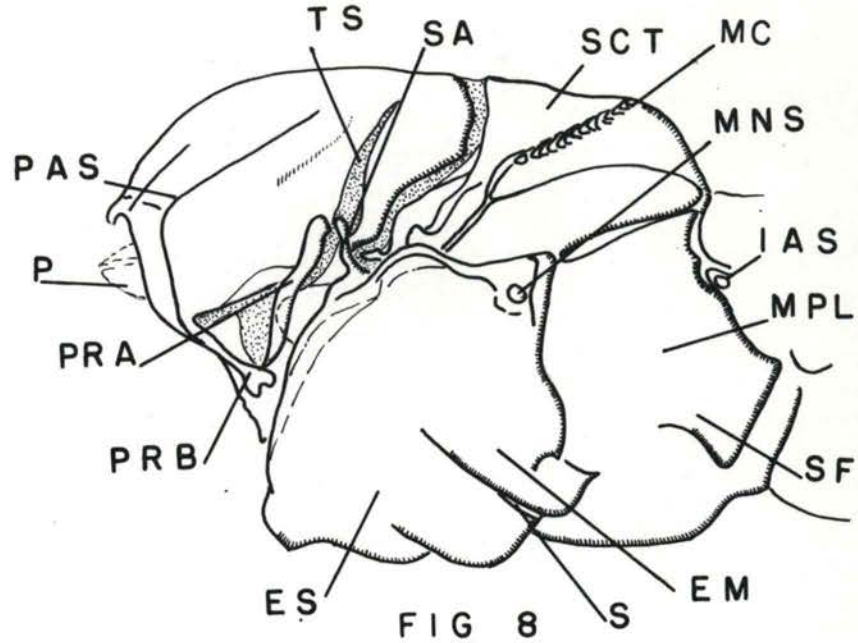
TS
SA
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FIG 8

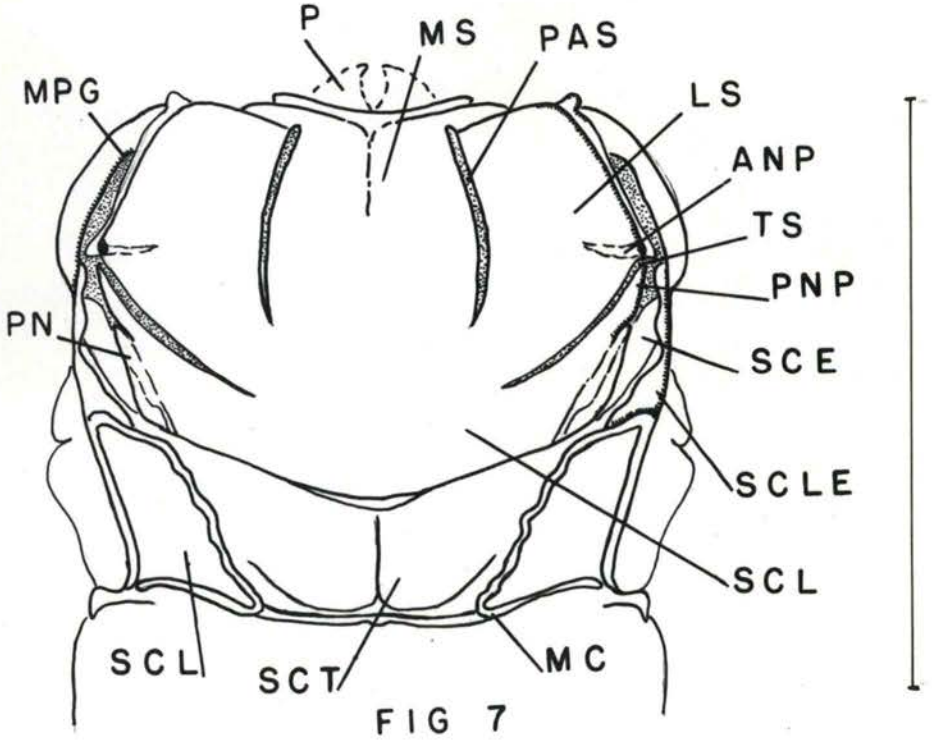

P
MS
PAS
MPG
LS
ANP
TS
PNP
PN
SCE
SCLE
SCL
SCL
SCT
MC

FIG 7

Figure 9. Anterior view of the mesothorax.

P	Phragma
PAS	Parapsidial suture
PRB	Prealary bridge
PRA	Prealare
MPG	Metapleural groove
S	Spiracle
SK	Socket

Figure 10. Cross section of metathorax showing meso-metaphragma.

Figure 11. Longitudinal cross section of the Pterothorax.

P	Phragma
MMP	Meso-meta phragma
SAA	Subalare apodeme

Line scale equals 1 mm.

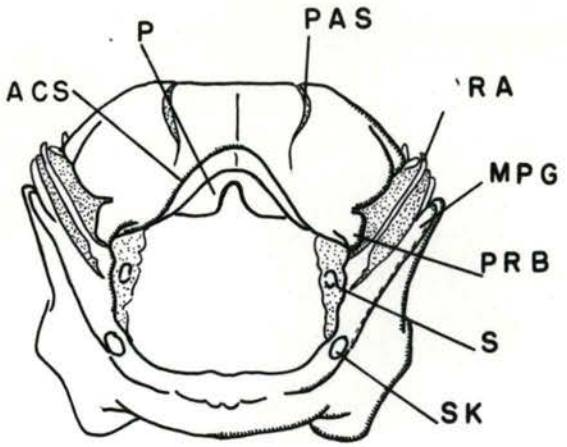


FIG 9

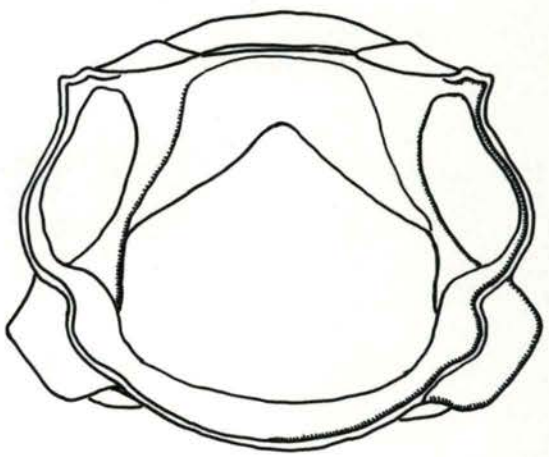


FIG 10

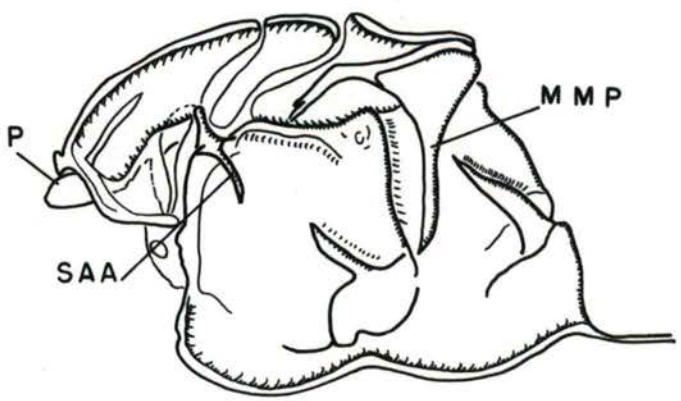


FIG 11

Figure 12. Intermediate wing forms.

Figure 13. Forewing.

R	Radius
M	Media
CU	Cubitus
PCU+1A	Postcubitus and first anal

Figure 14. Hind wing.

SC	Subcosta
R	Radius
M	Media
CU	Cubitus
PCF	Cubital furrow. Posterior arm.
ACF	Cubital furrow. Anterior arm.
1 A	First anal
2 A	Second anal
CS	Cubital sector
PCS	Postcubital sector

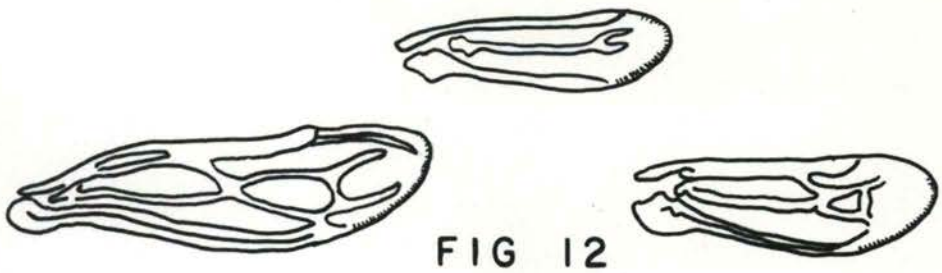


FIG 12

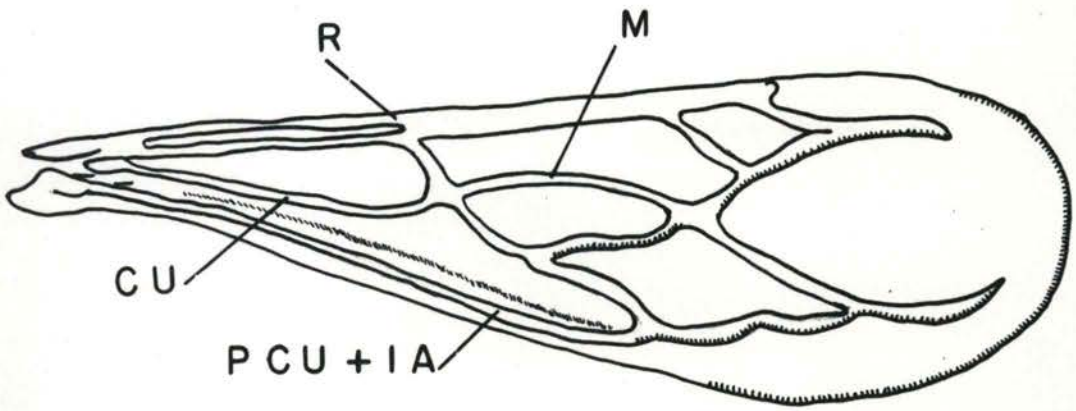


FIG 13

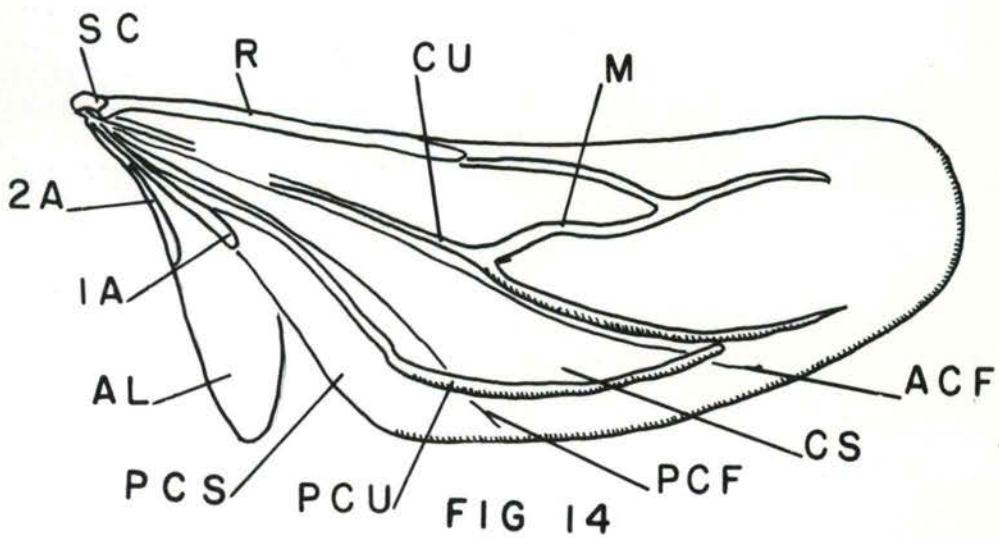


FIG 14

Figure 15. The prothoracic leg.

Figure 16. The mesothoracic leg.
Line scale equals 1 mm.

Figure 17. The metathoracic leg.
Line scale equals 1 mm.

Figure 18. Coxa showing basicoxa

Figure 19. Tarsus and claws.

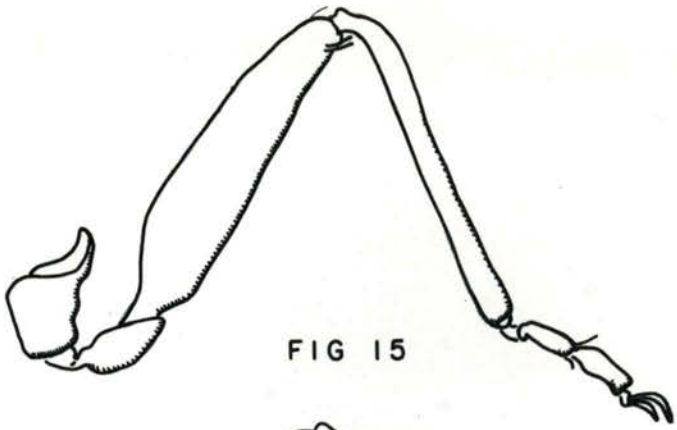


FIG 15

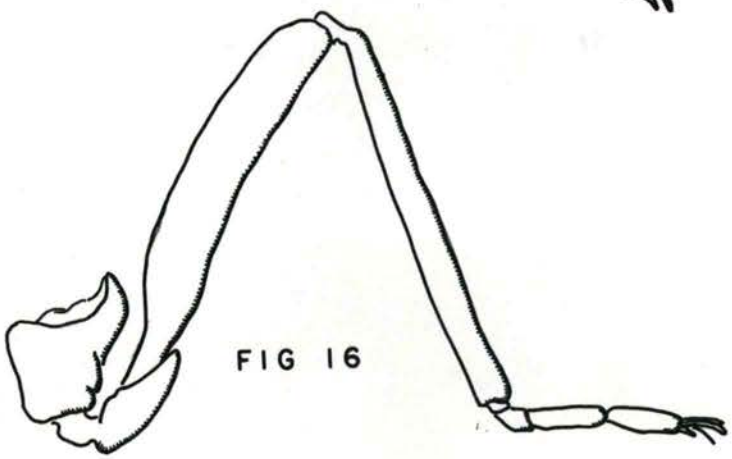


FIG 16

FIG 18

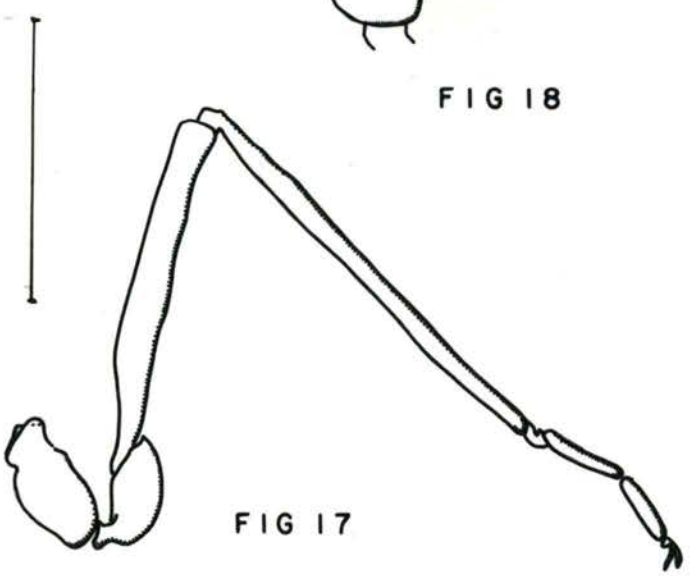


FIG 17

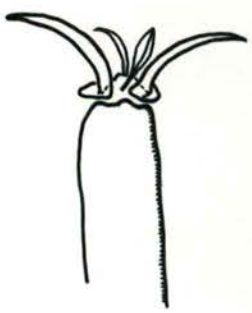


FIG 19

Figure 20. Internal rods of the maxillary plates. Anterior view.

AT	Antennal tubercle
MP	Maxillary plates
MIR	Maxillary internal rods

Figure 21. Epipharynx. Ventral view.

AC	Anteclypeus
LBR	Labrum
EP	Epipharynx

Figure 22. Metathorax of Mesovelia mulsanti White.

Figure 23. Metathorax of Macrovelia hornii Uhler.

MC	Metanotal costa
SCE	Latero-scutal extention
MMP	Meso-meta phragma
PT	Pit

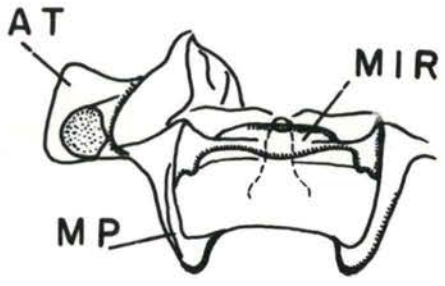


FIG 20

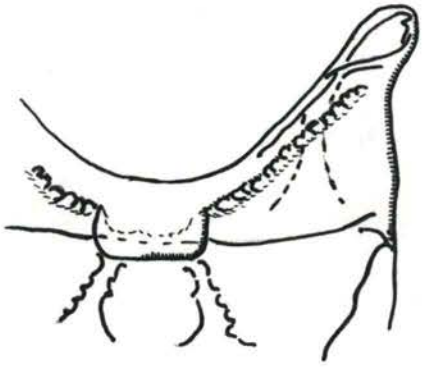


FIG 22

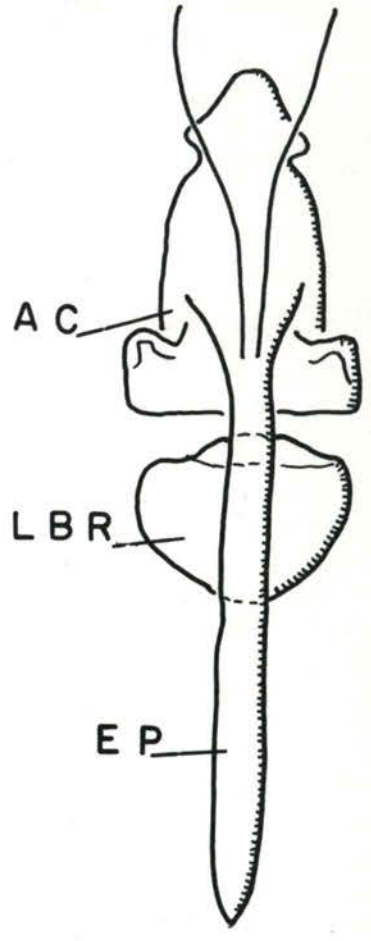


FIG 21

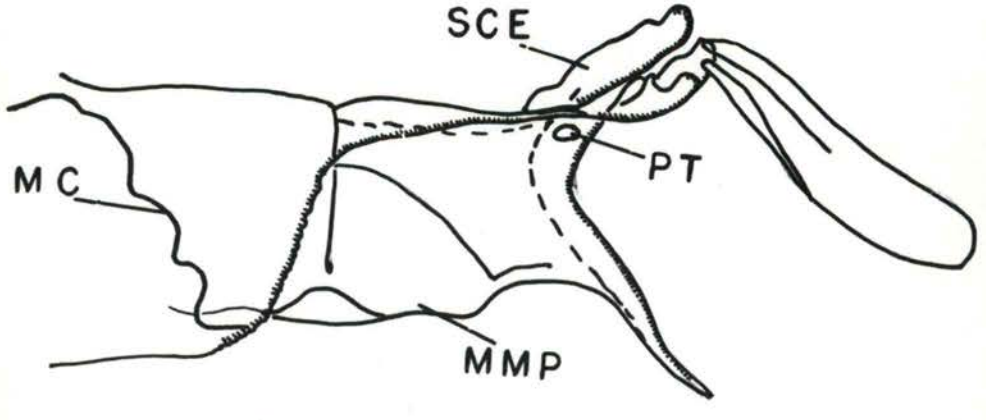


FIG 23

Figure 24. Male genitalia of Macrovelia hornii Uhler.

T	Titillator
ED	Vesica
CJ	Conjunctiva
CJP	Conjunctival plate
PS	Phallosoma
TR	Titillator rods
EP	Vesical process
CP	Conjunctival process
DUS	Ductus seminis

Figure 25. Male genitalia of Mesovelia mulsanti White.

Figure 26. Male genitalia in resting position. Dorsal view.

CL	Claspers
PS	Phallosoma
BS	Basal plates
CP	Remnants of capitate processes

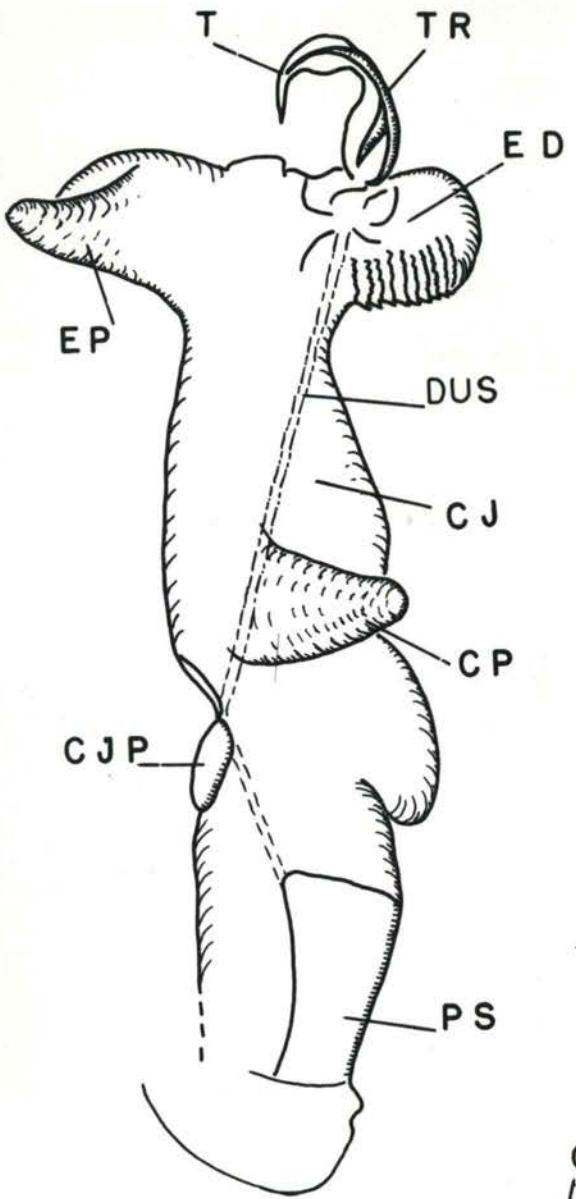


FIG 24

FIG 25

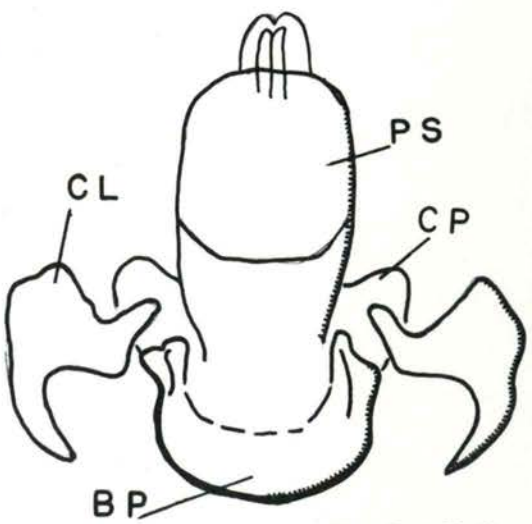


FIG 26

Figure 27. Female genitalia.

1 GPO	First gonapophysis
2 GPO	Second gonapophysis
1 GX	First gonacoxa
2 GX	Second gonacoxa
T8'	Laterotergite VIII
AT	Anal tube

Figure 28. Salivary gland.

AG	Anterior gland
PG	Posterior gland
MAG	Median accessory gland
PAG	Posterior accessory gland

Figure 29. Female genitalia with 1 GX and T8' removed.

1 GPO	First gonapophsis
2 GPO	Second gonapophysis
2 GX	Second gonacoxa
T 9	Tergum IX
GA	Gonangulum
AN	Anal tube

Figure 30. First gonapophysis.

Figure 31. Second gonapophysis and second gonacoxa.

Figure 32. Female reproductive organ.

TF	Terminal filament
UC	Cells
OVL	Ovarioles
OV	Ovary
OD	oviduct
SP	Spermatheca
VA	Vagina
SB	Spermathecal bulb
AT	Apical tube

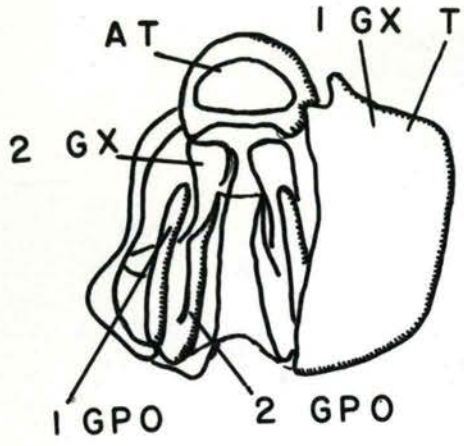


FIG 27

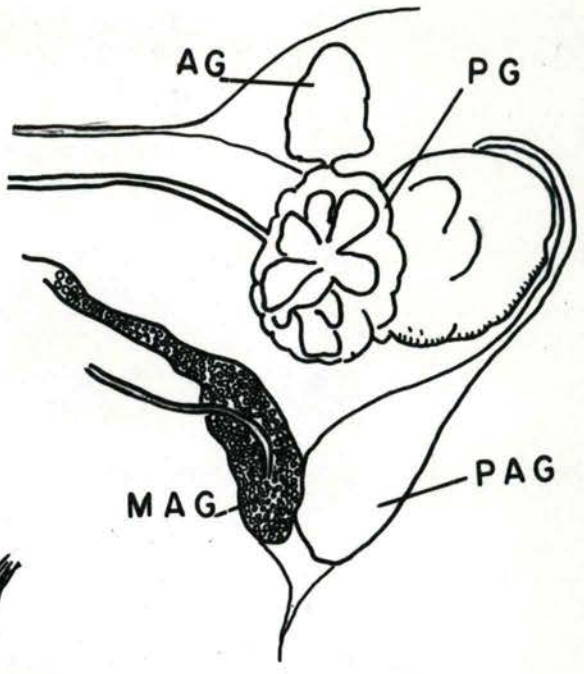


FIG 28

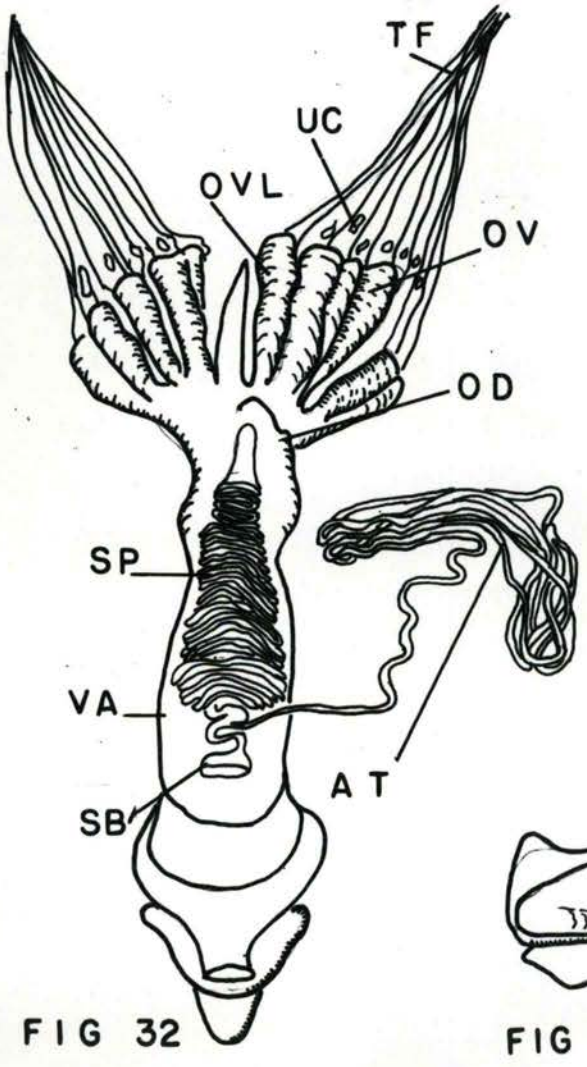


FIG 32

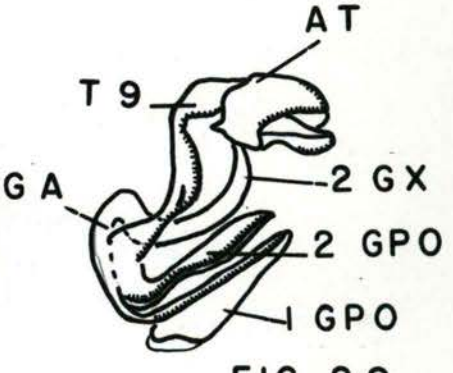


FIG 29

FIG 30

FIG 31

Figure 33. Male reproductive organ.

T	Testis (cut off)
VS	Vesicula seminalis
G	Accessory gland
D	Ductus ejaculatorus
VD	Vas deferens

Figure 34. Ventral view of the brain.

B	Brain
TG	Thoracic ganglia
AG	Abdominal ganglia

Figure 35. Dorsal view of the brain.

ON	Optic nerve
PRG	Protocerebral ganglion
B	Brain
MSG	Mesothoracic ganglion
MTG	Metathoracic ganglion
AG	Abdominal ganglia

Figure 36. Lateral view of the brain.

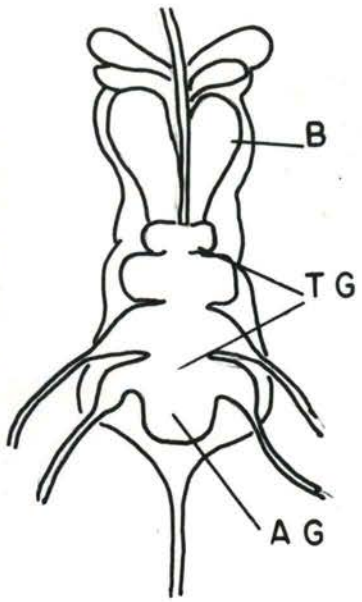


FIG 34

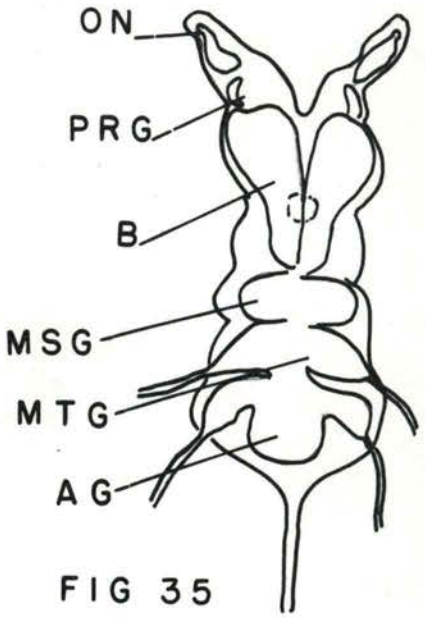


FIG 35

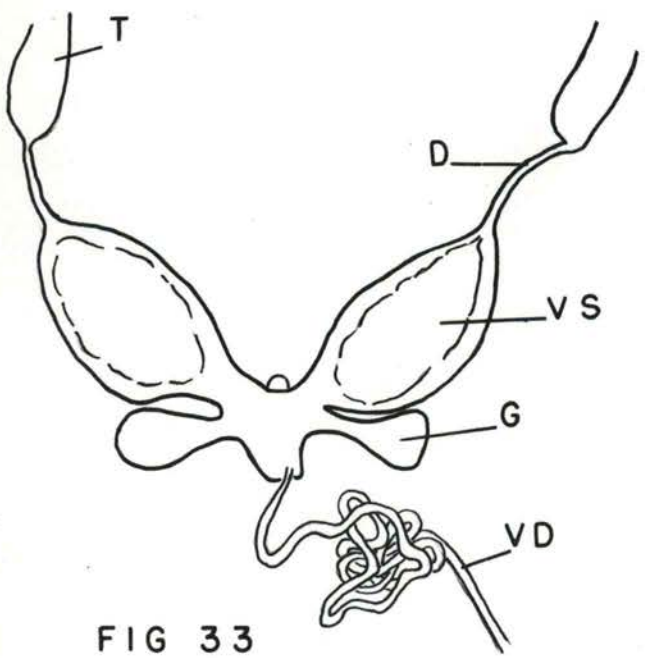


FIG 33

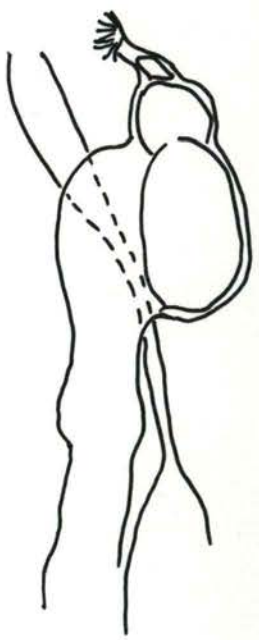


FIG 36

Figure 37. Dorsal view of the abdomen.

LC	Longitudinal carina
LT	Laterotergit

Figure 38. Alimentary canal.

1 CH	Ventriculus, first chamber
2 CH	Second chamber
3 CH	Third chamber
MT	Malpighian tubules
PC	Pyloric collar
RC	Rectum

Figure 39. Fourth instar nymph.

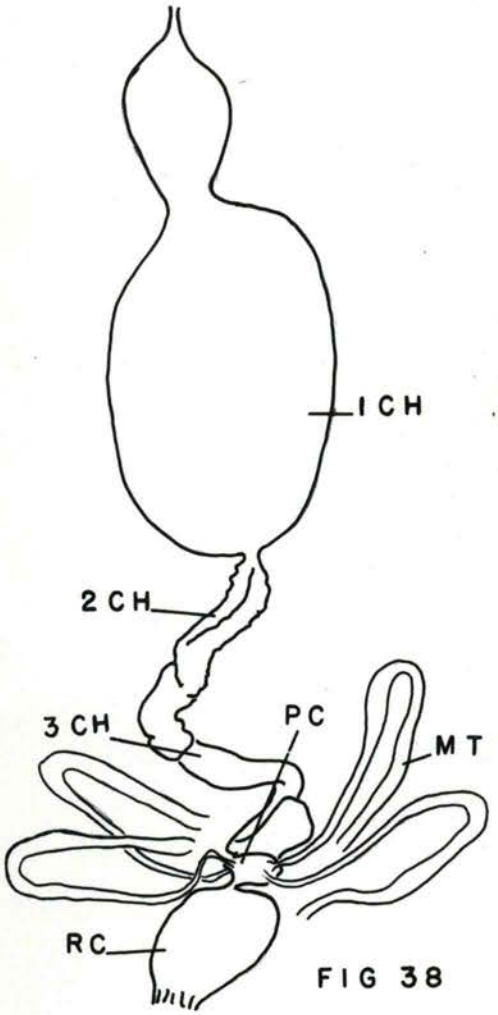


FIG 38

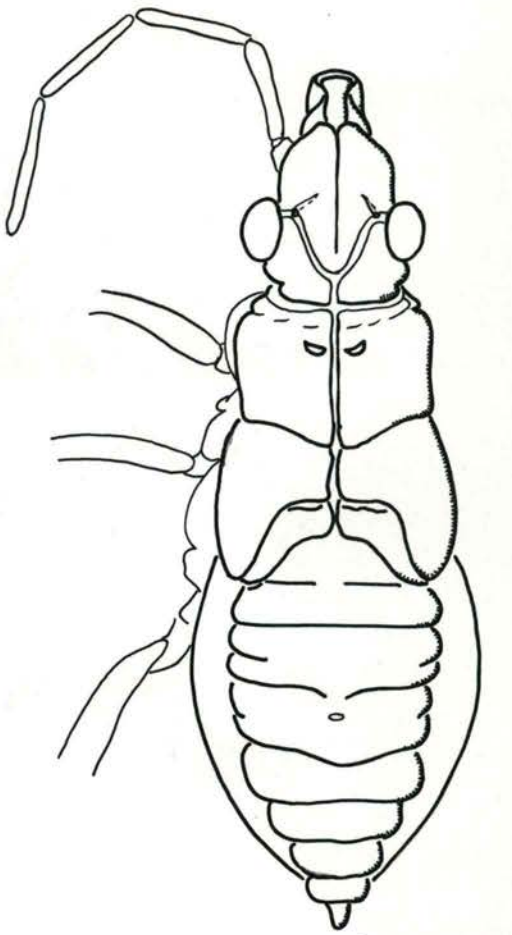


FIG 39

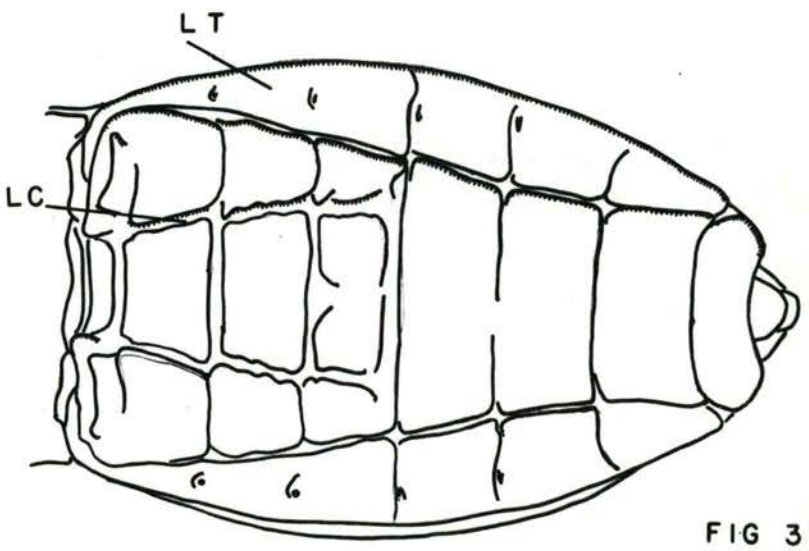


FIG 37

Figure 40. Third instar nymph.

Figure 41. Second instar nymph.

Figure 42. First instar nymph.

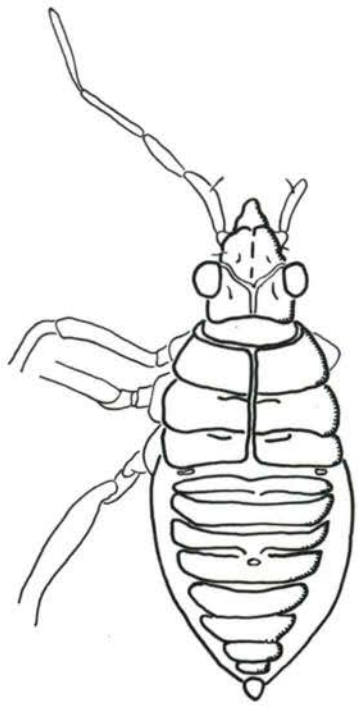


FIG 41

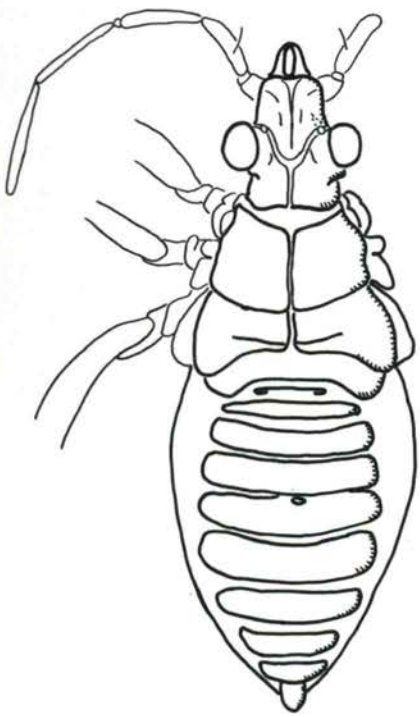


FIG 40

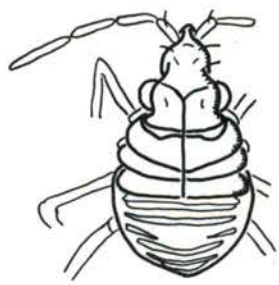


FIG 42

Figure 43. First axillary sclerite.

Figure 44. Second axillary sclerite.

Figure 45. Third axillary sclerite.

Figure 46. Wing base

1. First axillary sclerite
2. Second axillary sclerite
3. Third axillary sclerite

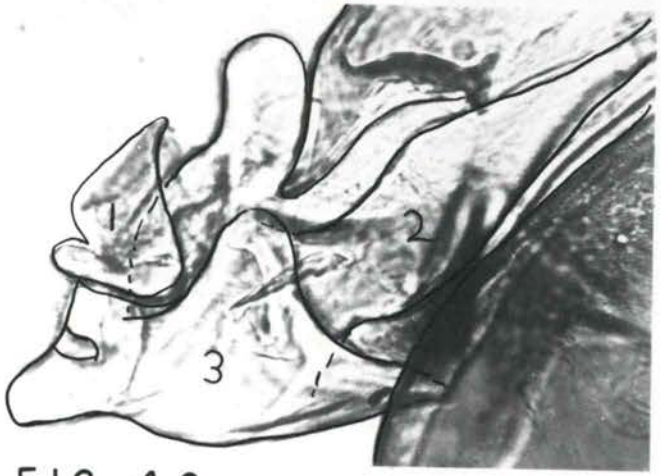


FIG 46

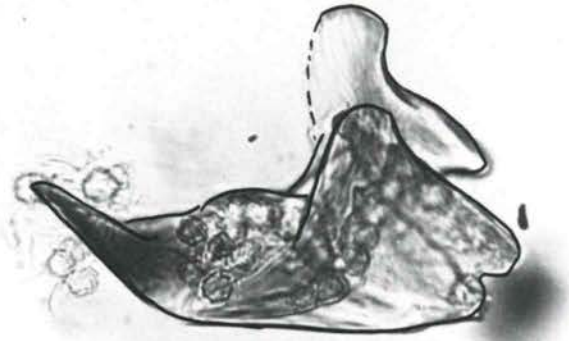


FIG 45

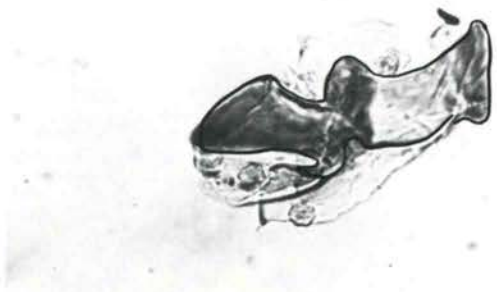


FIG 43

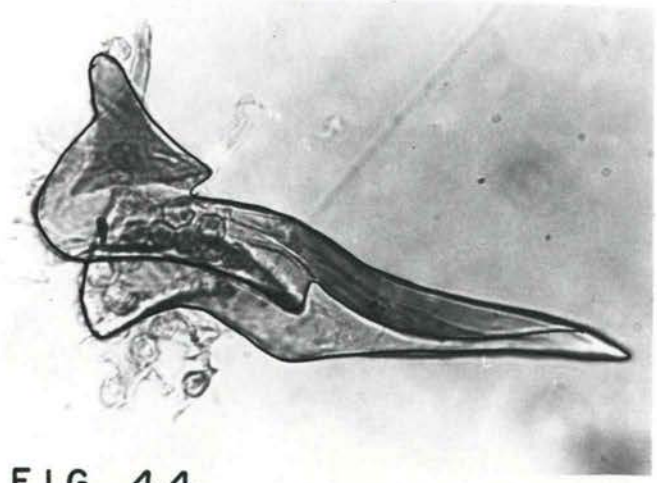


FIG 44

Figure 47. Wing base.

Figure 48. Wing base showing prealare and anterior notal wing process.

Figure 49. Egg burster.

Figure 50. Hind wing base.

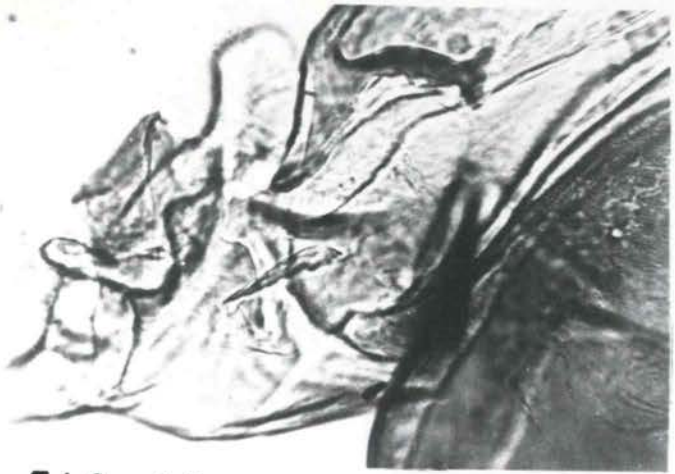


FIG 47

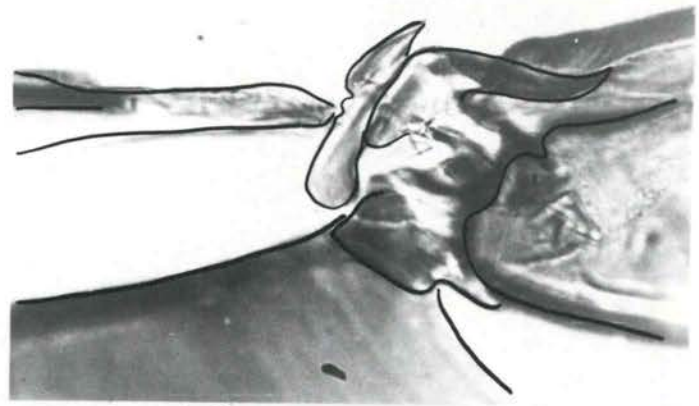


FIG 48

FIG 49

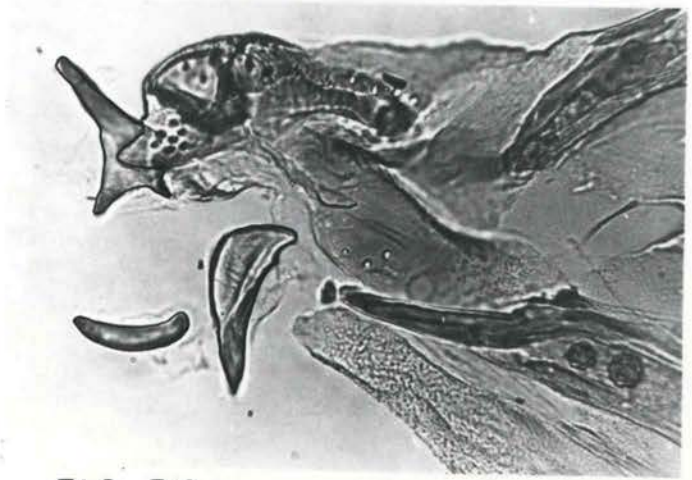


FIG 50

Figure 51. Collecting site at Corvallis.

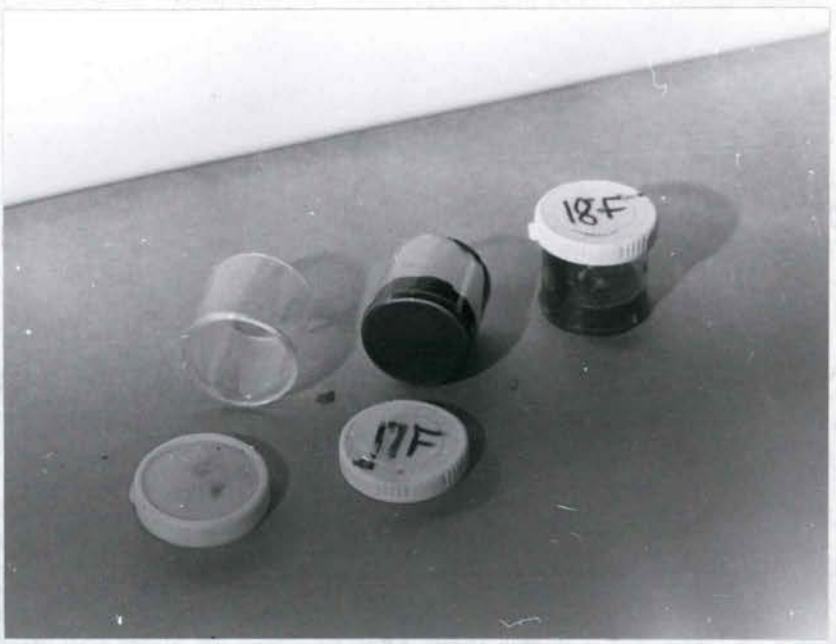


Figure 52. Methods--the cell construction.

Figure 53. Methods--Refrigerator box.

Figure 54. Adult

Figure 55. Copulation--lateral view.

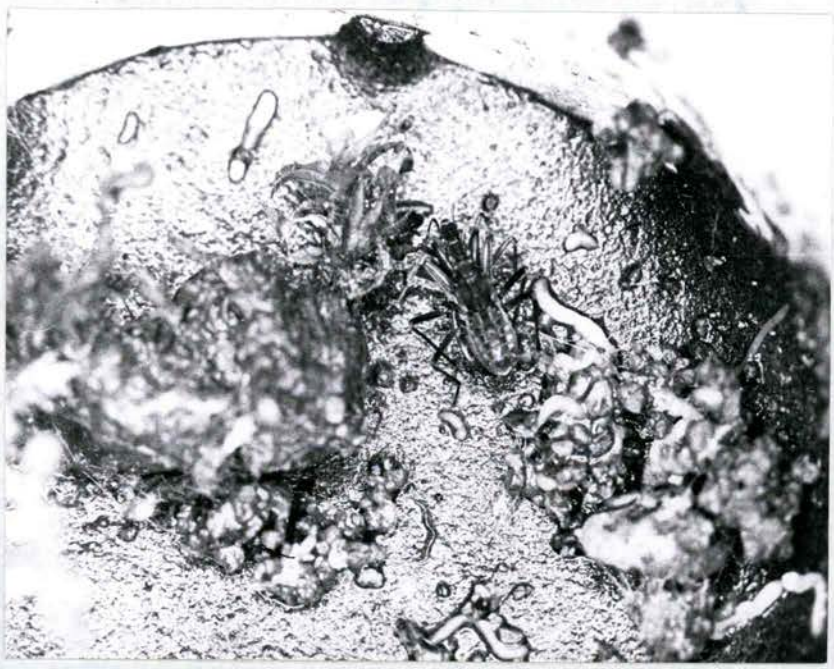


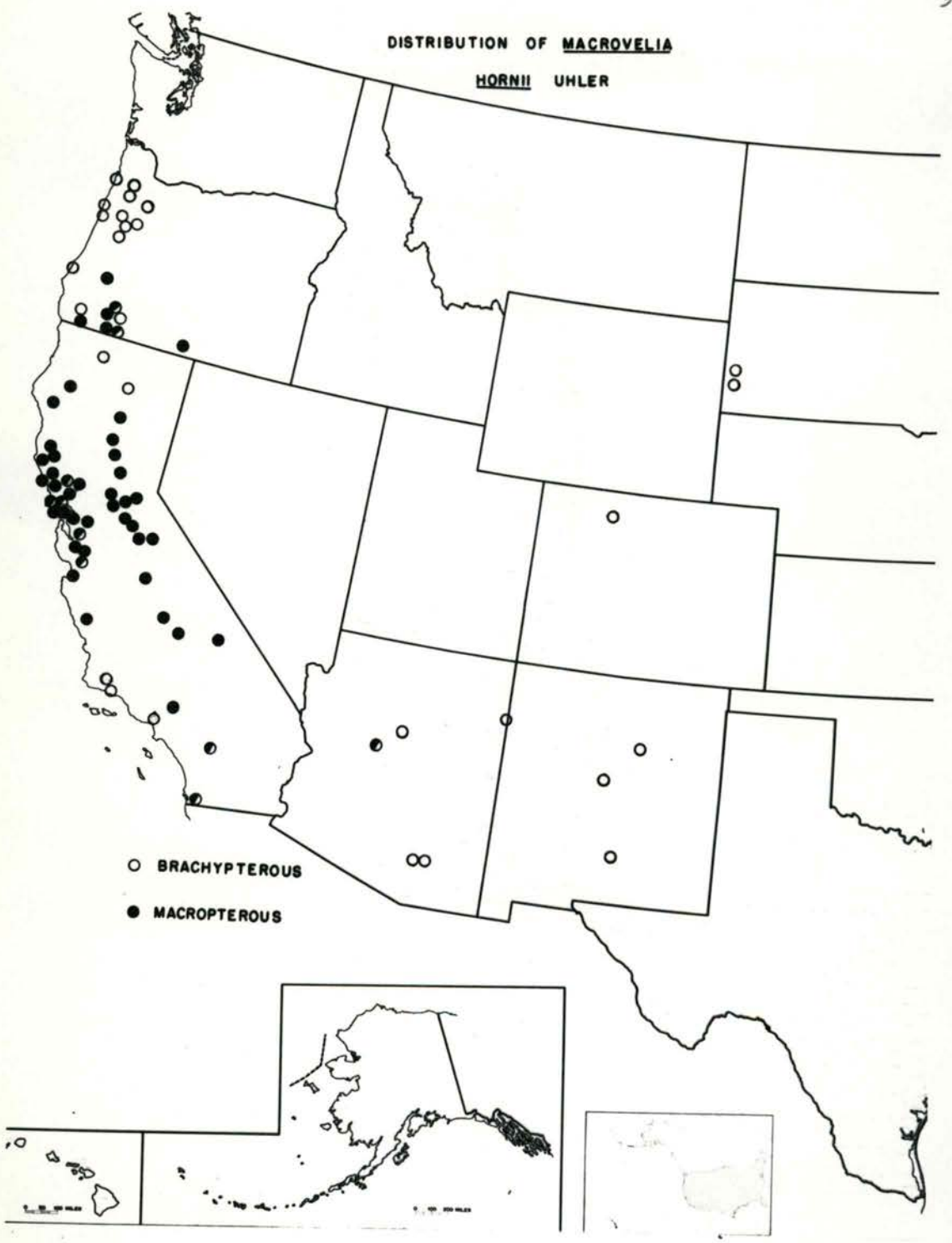
Figure 56. Copulation--dorsal view.

Figure 57. A single egg.

(Photo by Victor Duran)

Figure 58. Eggs on moss.

Figure 59. Molting.



Map I. Western United States with distribution of Macrovelia hornii Uhler.