# THE BIOLOGY AND MORPHOLOGY OF *HYDROMETRA MARTINI* KIRKALDY

by

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# INTRODUCTION

The purpose of this investigation is the correlation of form and function in a single species of insect, *Hydrometra martini* Kirkaldy. For this, the internal and external structures of the adults were examined and the post-embryonic development of the nymphs was followed. The behavior of both nymphs and adults was observed in the laboratory and in the field throughout the year.

This species is a representative of a small family, the Hydrometridae. Of its six genera, four are monotypic: *Limnobatodes paradoxus* Hussey (Hussey, 1925), *Trichometra robusta* Hungerford and *Dolichocephalometra pacifica* (VanDuzee) (Hungerford, 1939), and *Hydrobatodes schoutedeni* China and Usinger (China and Usinger, 1949). Another genus, *Bacillometra*, includes three species: B. *ventralis* Esaki, B. *woytkowskii* Hungerford and B. *mulfordi* (Hungerford) (Hungerford, 1935). *Hydrometra*, the only widely distributed genus in the family, now includes 81 species, 47 from the Eastern and 34 from the Western Hemisphere.

The biology and anatomy of the hydrometrids is known almost entirely from the studies of the European *H. stagnorum* (Linnaens) and the North American *H. martini* Kirkaldy. Arrow (1895), Teyrovsky (1920), Poisson (1924), Ekblom (1926), Jordan (1931) and Schumann (1934) have reported on various phases of the life history of *Hydrometra stagnorum*; Martin (1900), Hungerford (1920) and Bueno (1926) have discussed *Hydrometra martini*. Anatomical studies of *Hydrometra* consider mainly the head with its mouthparts and the genitalia. Ekblom (1926) described both, Singh-Pruthi (1925) discussed and illustrated the male genitalia and Spooner (1938) the head capsule in their comparative works on hemipterans. Larsen (1945a, 1945b) used a tropical macropterous hydrometrid in his very careful investigation of the thorax of Heteroptera.

As in many genera of hemipterans, *Hydrometra* occurs in both a long and a short winged form. The micropterous form of *H. martini* is notably more abundant in the areas in which observations were made than is the macropterous form. However, males and females of both are found throughout the year. This dimorphism has been noted by Bueno (1926) and others for *H. martini* and by various workers for *H. stagnorum*.

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## MORPHOLOGY

The extremely slender, elongate form of the genus Hydrometra, its most outstanding characteristic, is especially pronounced in the adults. Males which average 8 mm in length are about 0.5 mm wide in the region of the metathorax, the widest part of the body. Females tend to be 1 to 2 mm longer. The abdomens of those which are laying eggs are as much as 0.2 mm wider than the metathorax.

The exoskeleton of adult hydrometrids is both hard and inflexible. The antennae, mouth parts and legs have motility because of their membranous connections and muscular attachments. The head has rather limited movement but the thoracic and pregenital abdominal segments are completely fused ventrally. The genital segments, especially those of the male, have considerable flexibility.

### Methods

Adults were killed for morphological study in 80% ethyl alcohol or in hot Dietrich's fluid, made according to directions in Kingsbury and Johannsen (1927) and stored in 80% alcohol. For skeletal structures, the insects were boiled in 10% potassium hydroxide, washed overnight in tap water and stored in 80% alcohol.

For studies of internal structures, freshly killed or fixed insects were dissected with fine needles. Muscle and nervous tissue could be demonstrated best in preserved material which was stained with eosin during the dissection. Tracheae were visible only when air-filled and the other internal structures tended to adhere to each other after storage in alcohol. These were examined in freshly killed material.

Relationships of internal structures, especially those of the head region and the nervous system, were checked in serially sectioned nymphs or recently molted adults. These were fixed in hot Dietrich's fluid, dehydrated in dioxane, infiltrated in 53° paraffin and imbedded in Tissuemat. Sections cut at 7.5u with a Spencer rotary microtome were stained with Delafield's hematoxylin and eosin and mounted in Canada balsam.

## The Head

### External structure

The head of the adult hydrometrid is extremely slender, those of the nymphs, especially in the early instars, are much less so. The progressive changes in proportions of the head, antennae and beak, as well as those of other regions are considered in the section on growth and differentiation (see pp. 93-98). Almost as remarkable as the elongation of the head is its lack of clearly defined sclerites. Except for the eye, the head capsule is a heavily sclerotized tube for most of its length. The dark red, hemispherical eyes are on the more posterior part of the head. The antennal sockets form the widest part of the head. Each is set off by a suture which is best seen in lateral view (fig. 5). The antennae are four segmented (fig. 8). The basal part of the first segment is a rounded knob which fits into the antennal socket. This segment is shorter than the second. The third segment is long and slender; the fourth is subequal to the second.

The most conspicuous sclerite in the anterior part of the head is the anteclypeus, which in lateral view (fig. 5) projects above the surrounding areas. The other sclerites associated with the mouth parts are lateral and anterior to it.

The broad labrum (figs. 3, 6) is attached to the anterior border of the anteclypeus. A median ridge of the epipharyngeal surface of the anteclypeus and labrum is produced distally to form a slender epipharynx (figs. 6, 7). The labrum forms a dorsal cover for the anterior part of the labium; the epipharynx lies within the labium, dorsal to the mandibular and maxillary stylets (fig. 18).

Ventro-lateral to the anteclypeus are two pairs of sclerites which aid in the formation of the cranium. The more dorsal pair are the so-called lora, lateral extensions of the hypopharynx (figs. 3, 10). The ventral pair are the maxillary lobes or plates (figs. 3, 16). Deep sutures separate the lora from the postclypeus and from the maxillary plate (figs. 3, 5). The outer parts of the latter are lightly sclerotized and, in younger adults, unpigmented. Ventral projections of the maxillary plates, the buccalae, partially surround the base of the beak and prevent its lateral movement (figs. 5, 16). The membranous proximal part of the labium inserts on the inner surface of the maxillary plates.

In the resting position, the beak is parallel to the head and lies close to it (fig. 5). Of the four labial segments, the third is by far the longest. It is marked, except at either end, with dark striations. The first and second segments are short and broad. The fourth, another short segment, terminates in a point. The labium is slightly flexible but the intersegmental sutures are not movable.

The edges of the labium fit together tightly. Cross sections of a fifth instar nymph show variations in the closure at different levels, as well as differences in width of the labium. At both the proximal and distal ends, the sides merely meet each other (figs. 18, 20), whereas in the middle portion they are grooved (fig. 19). The epipharynx, the most dorsal structure within the labial furrow, extends only through its proximal segment (fig. 18). The hollow mandibular stylets are lateral to the maxillary stylets throughout their length (figs. 18, 19, 20). Both pairs extend to the tip of the labium and protrude from it when the animal feeds. The tips of the mandibles are spear-shaped and bear rows of recurved barbs (fig. 13).

A ridge on the right maxillary stylet fits into a groove on the left one; thus, the maxillae are locked together to form a single tube. The distal end of each maxilla bears a row of minute setae. On the left stylet these are spaced evenly (fig. 12) but on the right, they are arranged in groups of three or four which fasten together so that they appear to be heavier teeth (fig. 11).

## Internal structure

Two slender apodemes extend posteriorly from the basal segment of each antenna. A feather-like muscle attaches each of these to the side of the cranium (fig. 8). The muscle of the outer apodeme is slightly larger and is lateral to that of the inner apodeme.

Figure 9 shows the mandible and its associated structures. As the stylets pass between the anteclypeus and the body of the hypopharynx, they are slightly lateral and dorsal to the maxillae. Within the head, a membranous fold attached a vertical bar of the mandibular stylet to the rectangular mandibular lever. A second heavy membrane extends from the lower anterior corner of the lever to the lorum. A slender apodeme continues posteriorly from the mandibular lever to the occipital region of the head. The posterior part of this process is surrounded by a retractor muscle which originates on the lateral cranial wall from the posterior margin of the eye to the occiput. The protractor is a prominent fan-shaped muscle which attaches by a short, slender ligament-like apodeme to the lower posterior corner of the lever. This muscle originates on the cranium behind the antennal socket, near the origin of the muscles of the antenna.

Each maxilla is held in place by a membranous sheath, the anterior end of which attaches to the posterio-lateral edge of the body of the hypopharynx (fig. 10). The sheath extends a half of the length of the stylet. Both it and the stylet itself are enveloped by the heavy protractor which has its origin on the maxillary plate. Since the stylet becomes wider posteriorly, its forward movement is limited by the sheath. The retractors, which insert on the posterior part of the stylet, originate on the occipital regions of the head capsule. The protractors insert just anterior to the retractors and pass under the hypopharynx to attach to the posterior border of the maxillary plate or lobe.

The hypopharynx consists of a medial bridge which is internal and a pair of lateral wings, the lora, which form a part of the head capsule. The maxillary sheaths and salivary syringe (figs. 10, 14) are derived from the hypopharyngeal bridge. The salivary syringe, a lightly sclerotized funnel-shaped structure, opens by a duct on the hypopharyngeal bridge just ventral to the opening of the food tube. The plunger, fitting closely into the funnel, has a very delicate apodeme which extends posteriorly near the ventral surface of the head. A heavy muscle originates on the ventral wall of the head capsule and inserts on the base of the plunger and along the length of its apodeme.

The pharynx (figs. 15, 17) is a lightly sclerotized, slender tube which extends the length of the head. Anteriorly its floor flattens to form a narrow lip which rests on the body of the hypopharynx. The mouth opening is closely associated with the tube formed by the maxillae as they emerge from their sheaths and unite to make the sucking tube. A series of strap-like muscles which originate on the cranial wall and insert on the pharynx operate the pharyngeal pump. Since the origin of these muscles identifies the frons, this area extends two-thirds of the length of the head to the interocular region.

### Function of the mouth parts

A description of the food finding process and of the kinds of food used by *Hydrometra martini* is given in the section dealing with behavior. In general, hydrometrids feed on living or recently killed animals by inserting their mandibular and maxillary stylets and sucking out the fluid content.

In preparation for spearing its prey, the animal swings its beak forward, and thrusts it toward the victim with the whole body. When this is a dark, shiny insect, a minute drop of saliva glistens on the exoskeleton at the point at which the stylets begin to penetrate. The saliva, secreted by the paired salivary glands located in the thorax, enters the salivary syringe through on the ventral side of the head, and is pumped by the syringe through its medial duct to the groove of the maxillary stylets.

The spear-like tips of the mandibles pierce the prey and hold it so securely with their retrorse barbs that small animals can be lifted and carried considerable distances. Extension of the mandibles is effected by contraction of their protractors. This action tips the entire mandibular lever and the attached stylet forward. The mandibles retain their position while the maxillae protrude between them in feeding. The contraction of the retractor muscles withdraws the mandibular stylets.

The slender maxillary tube not only injects saliva into the prey but also carries the fluid food into the mouth. Quick thrusts of the maxillae result from alternating contractions of the protractor and retractor muscles within the head. The tips of the maxillae have a tongue-like action, lashing and gouging within the soft tissues. The actual sucking seems to result from the dilation of the food tube through muscular action of the pharyngeal dilators which originate in the anteclypeus and frons.

## Discussion

The most thorough study of the structure of the hydrometrid head is that reported by Ekblom (1926). He worked out the relationships not only of the mouth parts but also of their musculature. Severadei (1950) added a description of the salivary syringe. Spooner (1938) included drawings of three views of the head and one of the mandibular lever of *H. martini* in his comparative study of the head capsules of Hemiptera. Other papers concerning the homologies of the hemipterous head are those of Snodgrass (1938, 1944), Butt (1943), DuPorte (1948) and Kramer (1950).

In *Hydrometra*, as in all Hemiptera, there has been much confusion as to the homologies and hence the names of the various sclerites. This has been especially true of the two pairs of sclerites at the anterior end of the head. Ekblom (1926) called the more dorsal pair the lamina maxillaris and the structures which surround the base of the labium, the lorae. Many taxonomists have called the dorsal pair the juga in Hemiptera. In drawings of *Oncopeltus*, Butt (1943) labeled the external portion of the corresponding lobe the juga but he referred to its internal extension as the lorum. Spooner (1938) considered the more dorsal pair of plates to be the paraclypeus and the more ventral pair, the maxillary plates.

In a paper published later in the same year, Snodgrass (1938) discussed the homologies of these sclerites. His conclusion, that the dorsal sclerites are lateral extensions of the hypopharynx was based on the facts that: 1) although the plates adjoin the postclypeus, they are continuous with the hypopharynx in the area ventral to the anteclypeus, and 2) the protractor muscles of the mandibles originate on it. The ventral pair, Snodgrass (1944) called maxillary lobes.

In the only hemipteran which he illustrated, DuPorte (1946) designated the dorsal sclerites discussed above as the hypopharynx. Kramer (1950) working with representative auchenorhynchous Homoptera called it "lorum" and pointed out the relationship with the hypopharynx.

Both Ekblom (1926) and Severadei (1950) correlated the elongation of the head and that of the mandibular and maxillary apparatus. Ekblom (1926, 1930) described the attenuated mouth parts, especially maxillae, in several relatively shortheaded semiaquatic hemipterans. In these forms, the stylets and their associated muscles extend deep into the thorax. The maxillae and mandibles of Hemiptera, like those of mandibulate insects, arise embryologically from paired evaginations of the head (Johannsen and Butt, 1941). Newcomer (1948), who investigated the development of the mouth parts of Oncopeltus, found that the maxillary plates (= maxillary lobes) differentiate from the bases of the maxillary processes before blastokinesis. This corroborated the homology established by Snodgrass (1944), who, working with *Magnicicada* adults, identified the maxillary lobe as the stipes. Snodgrass also found that the stylet is homologous with the lacinia, and a lateral distal process of the maxillary lobe as the galea. The latter, which is present in the adult homopterans figured by Spooner (1938), is reduced or absent in his drawings of hemipterans.

In *Oncopeltus* (Newcomer, 1948), the maxillary and mandibular evaginations elongate at blastokinesis and their proximal ends sink deeply into the head. The ectoderm surrounding the base of each developing stylet invaginates to form a sac or pouch. The levers and sheaths of the maxilla and the mandibular levers are derived from the corresponding sacs.

The origin of the protractors of the maxillae on the maxillary lobe seems to be quite constant. Kramer (1950) reported this relationship in the homopterans which he examined. Ekblom (1926, 1930) described it in a variety of hemipterans. Butt (1943) and Newcomer (1948) found that in the milk weed bug, *Oncopeltus fasciatus*, the protractors also originate on the maxillary lobe. Griffith (1945) stated that in *Ramphocorixa acuminata* the protractor muscles of the maxillary stylets attach on the margins of the labial wall and on the attenuated hypopharyngeal processes.

The insertion of the protractor is typically on the maxilla near its base but below the attachment of the retractor.

This is the case in *H. martini* and in all of the hemipterans discussed by both Ekblom and Butt with the exception of *Notonecta* (Butt, 1943). Here the protractor inserts on the end of the maxilla and the retractor on the side of the stylet, anterior to the attachment of the protractor.

The retractor of the maxilla extends in both homopteran and hemipteran forms from its insertion on the end of the stylet to the posterior part of the head capsule. In those forms combining unusually long maxillae with head capsules of the normal length (*Gerris*, *Velia* and *Mesovelia*) a pair of projections of the head capsule extend into the thorax and serve as places of attachment for the retractors (Ekblom, 1926, 1930).

A maxillary lever which is found in the Homoptera (Kramer, 1950) as well as in *Oncopeltus* (Newcomer, 1948) is lacking typically in the Homoptera (Kramer, 1950) and in some Hemiptera (Ekblom, 1926, 1930). In the homopterans, this lever is associated with the posterior tentorial bridge. In some, the cicada, for example, it is retracted by a muscle which arises on the tentorium and is protracted by one from the maxillary lobe. According to Ekblom (1926), when a maxillary lever is present in hemipterans, it lacks independent muscular attachments and seems to serve as a guide.

Another structure closely associated with the maxilla is the maxillary sheath. Earlier workers (Ekblom, 1926, 1930 and Hamilton, 1931) considered this to be the tentorium. Spooner (1938) in his discussion of the homologies of the head capsule, reported that a true tentorium appears in the

Homoptera together with the sheaths which serve as guides for the maxillary stylets. Although in the Hemiptera, the tentoria are lacking, the sheaths, which he considered to be hypopharyngeal evaginations, remain.

The mandibular apparatus of *H. martini* seems to be typical of the group of semiaquatic Hemiptera. In all described homopterans and hemipterans this consists of the paired stylets each of which is supported by a lever, protractor muscles which insert on the lever and a retractor muscle which inserts on an apodeme extending posteriorly from the stylet.

There is considerable variation in the place of origin of the protractor. According to Kramer (1950), in the auchenorhynchous Homoptera it originates on the ventral and anterior margins of the lorum. In some of the Hemiptera a muscle with these attachments is also the only mandibular protractor. Butt (1938) reported this to be the case in *Notonecta*, *Oncopeltus* and *Benacus*, as well as in the homopterans *Tibicina* and *Cephisus*. In the pentatomid *Acrosternum* he found an additional protractor which inserts on the mandibular lever but originates on the hypopharynx.

Ekblom (1930) described two protractor muscles of the mandible in only one hemipteran, the corizid *Myrmus miriformis* Fall. Both of these muscles insert on the mandibular lever; one on the lorum and the other on the head capsule. In the other species which he studied, the only protractor is the fan-shaped muscle arising on the cranium.

In *Hydrometra martini* the salivary syringe and its duct are similar in form, position and function to those found in the homopterans and in other hemipterans (Butt, 1943, Weber, 1930). The fact that Hydrometra has only one groove in the maxillary tube has interested various authors since it was first described by Ekblom (1926). He and Severadei (1946) associated this with the fact that Hydrometra eats dead or nearly dead insects. Since the salivary glands as well as the salivary syringe are well developed, it seems likely that the single maxillary channel serves to transport both saliva and food.

The pharyngeal pump in some predacious Hemiptera (for example in Gerris and Reduvius, according to Weber, 1930) is operated by muscles which form two or three groups. In Hydrometra these are spread along the very long pharynx but the muscle fibers bear the usual relationship to it and to the cranium, making a V-pattern in cross section.

## The Thorax

The thorax of the wingless hydrometrids is slenderer and less flexible than that of the winged forms. Figures 23 through 27 show the thorax of the wingless and figures 21, 22, 28 and 29 that of the long winged form. In both, only the metathorax is notably elongate. In addition to the muscles of the appendages, the thorax contains the esophagus, the salivary glands, the fused thoracic and abdominal ganglia, the anterior part of the heart and the thoracic tracheae. Both the adults and the nymphs lack scent glands. The skeleton and its musculature will be considered here; the other internal structures will be discussed later. Comparisons of the nymphs of macropterous and apterous forms, as well as a consideration of the progressive changes in proportion and differentiation through the nymphal instars, are also presented later (pp. 99, 100).

## Thoracic exoskeleton

### Prothorax

The anterior margin of the prothorax is a heavy rim formed by the inflection of its border. The cervical membrane, continuous with this inflection, is short so that the occiput telescopes slightly into the prothorax. This arrangement limits the movement of the head in any direction.

Punctations surround the anterior margin of the prothorax in an irregular ring and also mark the dorsal part of the pronotum (figs. 21, 23). A similar punctation marks each of the supracoxal lobes, except that of the metathoracic epimeron (figs. 22, 24).

The pronotum is continuous laterally with the pleura and forms a posterior lobe which covers the mesonotum and the anterior part of the metanotum. The large size of this posterior lobe in the winged individuals corresponds with the general difference in the size of the two forms. A fissure separates the episternal and epimeral supracoxal lobes. The first thoracic (mesothoracic) spiracle lies just behind the supracoxal lobe of the epimeron. Depressions of the sternum form the inner walls of the coxal cavities. The small furca are medial to them.

### Mesothorax

The mesothorax of the wingless forms (figs. 26, 27) not only is smaller but also shows less differentiation than that of winged individuals (figs. 28, 29). The tergal area, which is completely covered by the posterior lobe of the pronotum, is reduced to a delicate membrane in wingless hydrometrids. In these animals the phragmata are not developed. Neither the prealare bridge nor the prealare membrane is differentiated; apparently they are incorporated in the tergal membrane. The wing pads, the bases of which are covered by the pronotal lobe, are small strap-like processes near the midline of the notum.

In winged forms, the tergum is less heavily sclerotized than the rest of the exoskeleton but it is differentiated into clearly marked sclerites. The tongue-shaped first phragma projects anteriorly and somewhat ventrally from the antecostal suture. The acrotergite (precosta) is narrow. The prescutum is set off from the scutum both laterally and posteriorly by the parapsidal sutures. The posterior angles of the scutum form the tergal wing process. A wide membrane connects the scutum and scutellum laterally. The anterio-lateral angles of the scutellum are extended to form the axillary cords of the first pair of wings. Ventrally the wing bases are supported by the pleural processes. A pair of short processes of the scutellum articulates with the postnotum, which is represented by a pair of lateral sclerites; medially the sclerite is lacking. Neither a basalare nor a subalare is present.

Although the pleural region is similar in the two forms, it is larger in winged individuals. The pleural wing processes, which are more developed in the macropterous hydrometrids, extend dorsally and obliquely anterior from the mesothoracic-metathoracic juncture. A fissure, which is continuous with the lower part of the pleural suture, separates the anterior supracoxal lobe, formed by the episternum, from the posterior supracoxal lobe, formed by the epimeron. Each epimeron bears a second (metathoracic) spiracle. There is no separation of the mesothoracic sterna from either the pleura or the metasterna. Deep depressions of the sterna form the inner walls of the coxal cavities. The furcae, which lie just medial to these cavities, are much larger in the long winged animals.

### Metathorax

The extremely long metathorax forms an almost inflexible cylinder which is continuous ventrally with the mesothorax and abdomen. The large episterna are fused with the sternum (fig. 27). Posteriorly these sclerites form the anterior supracoxal lobes which are separated from the small posterior (epimeral) lobes by fissures continuous with the pleural suture. The epimera are not differentiated from the abdominal pleura.

The metanotum consists of three areas. For most of its length it is a narrow internal ridge, compressed by the episterna. The second phragma, well developed in winged individuals, adheres along the ridge and expands into a broad, concave vertical plate anterior to the metapostnotum. The latter, a small triangular sclerite, lies between the episterna in the mid-dorsal line.

The most conspicuous structure in the anterior part of the metatergum is the heavy ridge on which the posterior pronotal lobe rests. This forms an arch whose arms are medial to the mesopleural wing processes. This ridge is especially pronounced in the macropterous individuals. A less heavily sclerotized portion of the metanotum extends forward from the ridge and articulates with the mesopostnotum. Laterally a pair of triangular sclerites, evidently fragmenta of the notum, extend medially to the wing bases.

## The Legs (figs. 30, 31, 32)

The legs of Hydrometra martini are extremely slender. The lengths of the various segments are given in Table 1; the total length of the legs in each nymphal instar is included in Table 7, p. 94. The paired claws of each leg are inserted at the apex of the third tarsal subsegment. The distal end of each tibia and the tarsal subsegments are covered with short stiff setae which are used in grooming.

Table 1. Average lengths in millimeters of the leg segments of 10 Hydrometra martini males. Coxal lengths include the coxal processes.

| Segment | Leg<br>Prothoracic | Mesothoracic | Metathoracic |
|---|---|---|---|
| Coxa | 0.5 | 0.5 | 0.6 |
| Trochanter | 1.4 | 1.4 | 1.5 |
| Femur | 8.1 | 9.7 | 12.0 |
| Tibia | 8.4 | 11.0 | 14.6 |
| Tarsus (1) | 0.4 | 0.4 | 0.6 |
| (2) | 1.2 | 1.5 | 1.3 |
| (3) | 1.3 | 1.3 | 1.2 |

Each coxa is almost completely enclosed in the cavity formed by the supracoxal lobes and the sternum. At rest, the prothoracic and mesothoracic legs extend anteriorly; the metathoracic legs, posteriorly. In each, the very large coxal process articulates with the supracoxal lobes just dorsal to the fissure between them. This articulation is lateral in the first and second pairs of legs and nearly posterior in the third.

Two small sclerites, the basicoxa and the trochantin, are associated with the articulation of the coxa. Both are present at the base of each leg and are considerably smaller in the wingless than in the winged forms. The trochantin is attached to the proximal coxal margin, anterior to the coxal process. The basicoxal sclerite, which lies behind this process, is associated with the tendon of the principal coxal retractor.

### The Wings (figs. 33 and 34)

The base of the mesothoracic wing lies between the scutal wing process and the lateral arm of the scutellum. The metathoracic wing attaches just posterior to it. Figure 35 shows the articular region in side view; the wings are lifted to show the basal sclerites.

The third axillary sclerite of the mesothoracic wing can be identified positively since the direct flight muscle (M 38), which arises on the episternum, inserts on this sclerite. Its distal projection articulates with the posterior margin of the wing. A short thick sclerite, which extends distally from the pleural wing process, articulates with the scutal wing process, the pleural wing process, the third axillary sclerite and another elongate sclerite. A heavy sclerite, which articulates also with the scutal wing process, extends along the anterior margin of the wing. Distally this sclerite makes contact with the base of a heavy vein which seems to be the proximal part of the media, since it serves as the pivot of the wing. A long arm of the first axillary sclerite extends between the second and third axillary sclerites. This sclerite is not closely associated with any of the wing veins.

Except for the base of the media, the veins of the mesothoracic wing are not clearly differentiated. Immediately beyond the base there are five longitudinal veins. The costa runs along the anterior margin of the wing. Parallel to it is a vein which represents the fused subcosta and radius. This joins the costa and a single vein extends from the junction toward the distal margin of the wing. The media extends to the end of the wing. The vestiges of two veins, one extending anteriorly and the other posteriorly, are visible in most wings. Two cross veins connect the main longitudinal veins in the posterior part of the wing. The short cubitus and postcubitus arise together and run to the edge of the wing.

The base of the metathoracic wing articulates with two small sclerites. One abuts on the heavy anterior vein and the other extends from the lateral arm of the notum toward the media. A heavy vein supports the base of the posterior edge of the wing.

## Thoracic Musculature

Larsen (1945a, 1945b) in his comprehensive studies of the hemipterous thorax included a winged South American form. The winged Hydrometra martini resembles it closely, while wingless individuals lack the flight muscles except M. furca-pleuralis (M 39). The differences, together with specific information as to the origins and insertions of the muscles, are given here with the names and numbers used by Larsen. Although they were not studied, the leg muscles distal to the coxa are listed according to Larsen's findings.

### Prothoracic muscles (figs. 36, 37).

M 1. M. pronoti primus. Levator of head. Arises on pronotum and inserts by apodeme on postoccipital ridge near mid-dorsal line.

M 2. M. pronoti secundus. Rotator and depressor of head. Arises on pronotum and inserts on ventro-lateral part of postoccipital ridge.

M 3. M. pronoti tertius. Levator of head. Origin from first phragma in winged form and from anterior margin of mesonotum in wingless form. Insertion on dorsal part of postoccipital ridge.

M 5. M. pronoti quintus. Depressor of prothorax. Arises on lateral margins of first phragma and inserts on lateral part of pronotum. Not present in wingless forms.

M 6. M. prosterni primus. Depressor of head. Arises on furca and inserts on ventral margin of postoccipital ridge.

M 7. M. prosterni secundus. Levator of head. Arises on sternum and inserts on lateral part of postoccipital ridge near insertion of M 2.

M 10. M. proepisterno-postoccipitalis. Rotator and depressor of the head. Arises on the episternum and inserts on the postoccipital ridge above insertion of M 6.

M 13. M. noto-trochantinalis. Rotator of coxa and elevator of leg. Arises on the posterior part of pronotum and inserts by apodeme on the trochantin.

M 14. M. noto-coxalis primus. Rotator of the coxa and elevator of leg. Arises on the notum and inserts with M 16 and M 17 on a tendon.

M 16. M. *noto-coxalis tertius*. Rotator of coxa and elevator of leg. Arises on notum. Insertion on apodeme associated with basicoxal sclerite.

M 17. M. *pleura-coxalis*. Rotator of coxa and elevator of leg. Arises on episternum and inserts on apodeme with M 14.

M 19. M. *furca-coxalis posterior*. Retractor of leg. Arises on furca and inserts on medial proximal border of coxa.

M 20. M. *noto-trochanteralis*. Depressor of trochanter. Arises on notum medial to M 16. Inserts by a long apodeme with M 21 and M 23 on the posterior process of proximal part of trochanter.

M 21. M. *pleura-trochanteralis*. Depressor of trochanter. Arises on episternum. Inserts with M 20 and M 23.

M 23. M. *coxa-trochanteralis medialis*. Depressor of trochanter. Arises on posterior wall of coxa and inserts with M 20 and M 21.

M 24. M. *coxa-trochanteralis lateralis*. Levator of trochanter. Arises on anterior and lateral wall of coxa and inserts on anterior process of the trochanter.

M 25. M. *reductor femoris*. Arises on anterior wall of the trochanter and inserts on proximal part of femur.

M 26. M. *depressor tibiae*. Arises on ventral part of the femur and inserts by apodeme on the ventral part of tibia.

M 27. M. *levator tibiae*. Arises on dorsal part of femur and inserts by tendon on dorsal part of tibia.

M 28. M. *depressor tarsi*. Arises on tibia and inserts by apodeme on ventral part of first tarsal segment.

M 29. M. *depressor praetarsi*. Arises on tibia and inserts on the unguitractor apodeme.

## Mesothoracic muscles

M 30. M. *mesonoti primus*. Indirect flight muscle; depressor of forewings. From ventral surface of first phragma and prescutum to anterior surface of second phragma. Lacking in apterous forms.

M 34. M. *dorsoventralis primus*. Indirect flight muscle; elevator of the forewings. Attaches to scutum lateral to parapsidal suture. Lacking in apterous forms.

M 38. M. *episterno-alaris*. Direct flight muscle; flexor of forewing. Arises on episternum near its upper edge, lateral M 34. Not present in apterous forms.

M 39. M. *furca-pleuralis*. Regulates position of the pleural process. Inserts on this process and arises on furca. Reduced in apterous forms.

M 40. M. *noto-trochantinalis*. Rotator of coxa and extensor of leg. In winged forms, arises on posterior part of scutum; in wingless individuals, on mesonotal membrane. In both, inserts by apodeme on trochantin.

M 41. M. noto-coxalis. Rotator of coxa and elevator of leg. Arises on scutellum in winged forms and on notal membrane in wingless forms. Inserts by long apodeme on lateral part of coxal margin. Insertion associated with small sclerite, free basicoxa.

M 42. M. episterno-coxalis. Rotator of coxa and extensor of leg. Arises on the episternum and inserts on anterio-medial margin of coxal margin.

M 45. M. furca-coxalis posterior. Extensor of leg. Arises on furca and inserts on medial margin of coxa.

M 46. M. noto-trochanteralis. Depressor of trochanter. Origin on scutellum posterior to that of M 40 in winged individuals; in wingless forms on notal membrane. Inserts on a long apodeme with M 47 on ventral edge of trochanter.

M 47. M. pleura-trochanteralis. Depressor of trochanter. Arises on pleura and inserts on apodeme with M 46.

M 48. M. furca-trochanteralis. Depressor of trochanter. Arises on furca and inserts on trochanter apodeme.

M 49. M. coxa-trochanteralis medialis. Arises on medial coxal wall and inserts on trochanteral apodeme.

M 50. M. coxa-trochanteralis lateralis. Arises on lateral coxal wall and inserts on lateral wall of trochanter.

M 51. M. reductor femoris. Like M 26 of prothorax.

M 52. M. depressor tibiae. Like M 27 of prothorax.

M 53. M. levator tibiae. Like M 28 of prothorax.

M 54. M. depressor tarsi. Like M 29 of prothorax.

M 55. M. depressor praetarsi. Like M 30 of prothorax.

## Metathoracic muscles

M 57. M. metanoti secundus. Indirect flight muscle. Extensor and levator of the hindwing. Arises on third phragma and inserts on small anterior sclerite of notum. Not present in apterous forms.

M 62. M. furca-pleuralis. No apparent function. Arises on furca and inserts on episternum. Reduced in wingless individuals.

M 63. M. noto-trochantinalis. Rotator of coxa and promotor of leg. Arises on anterior part of notum and inserts on trochantin.

M 64. M. noto-coxalis. Rotator of coxa and retractor of leg. Arises on notal ridge. In winged forms, insertion on medial coxal margin is associated with free basicoxal sclerite.

M 66. M. episterno-coxalis. Rotator of coxa and extensor of leg. Arises on intersegmental line and inserts by an extremely long, slender apodeme which is pateral to other muscles and their tendons on lateral part of trochantin.

M 69. M. furca-coxalis posterior. Arises on furca and inserts on median coxal margin. Rotator and adductor of coxa.

M 70. M. noto-trochanteralis. Depressor of trochanter. Arises on notal ridge posterior to origin of M 64. Inserts with M 71 and M 72 by a long apodeme on posterior margin of trochanter.

M 71. M. pleura-trochanteralis. Depressor of trochanter. Arises on pleura and inserts with M 70 and M 73.

M 73. M. coxa-trochanteralis medialis. Depressor of trochanter. Arises on anterior wall of coxa and inserts with M 70 and M 72.

M 74. M. coxa-trochanteralis lateralis. Levator of trochanter. Arises on posterior and lateral wall of coxa and inserts on posterior (dorsal) margin of trochanteral margin.

M 75. M. reductor femoris. As M 25 and M 51.

M 76. M. depressor tibiae. As M 26 and M 52.

M 77. M. levator tibiae. As M 27 and M 53.

M 78. M. depressor tarsi. As M 28 and M 54.

M 79. M. depressor praetarsi. As M 29 and M 55.

## Discussion of the thorax

Little was reported on the hemipterous thorax prior to the thorough studies of Larsen in 1942 and 1945. Both Gulde (1902) and Brindley (1930) called attention to the fact that Hydrometra lacks scent glands. In early comparative work on the thoraces of both Homoptera and Hemiptera, Taylor (1918) considered the cicada in detail. Among the other forms, he included a gerrid. Differences in the interpretation of the homologies of the various sclerites and lack of detail in the drawings make this paper and others, that on the stink bug by Tower (1913) for example, less valuable than Larsen's work in present investigations. The structure of numerous homopterans have been investigated by Kramer (1950). The thoraces in this group are markedly different from those of the Hemiptera.

In 1942, Larsen described the metathorax of a number of insects, a few of which he figured. Gerris was discussed in considerable detail and Hydrometra was compared with it briefly. In the later, more comprehensive papers (1945a, 1945b), he discussed the thoracic structure and its musculature in 26 species from 25 families of hemipterans, including a macropterous gerrid, an apterous veliid, and a macropterous hydrometrid. He illustrated the latter with two figures, one of the thoracic musculature and the other of the second phragma.

The present study compares the winged and wingless forms of Hydrometra martini with the macropterous South American Hydrometra, the macropterous Gerris rufoscutellatus and Velia currens which were described by Larsen.

The prothorax of Hydrometra martini is apparently very similar to that of other hemipterans. The length of the pronotal lobe varies with the size of the mesonotum which it covers; both are markedly larger in macropterous than in apterous individuals.

Well developed supracoxal lobes (the acetabular caps of taxonomists) are usually found in Hemiptera (Larsen, 1945b). The leg articulation with the trochantin imbedded in the anterio-lateral portion of the coxal membrane and the free basicoxal sclerite associated with the tendon of the coxal retractor (M 16) is also typical (Larsen, 1945a). Both of these sclerites are small in Hydrometra.

The prothoracic muscles in the wingless and winged forms are the same and like those of Larsen's species except that the apterous individuals lack the prothoracic depressor (M 5), which inserts on the base of the first phragma. Although most of the leg movement is in a horizontal plane, some elevation and depression is possible. Both the prothoracic and mesothoracic legs can swing from a nearly anterior position to a nearly posterior one.

The mesothorax of both *Gerris* and *Hydrometra* closely resembles that of other Hemiptera. It is characterized by a single scutal process for each wing, rather prominent parapsidal sutures, a well developed first phragma and a scutellum which articulates with the postnotum laterally. In many of the forms studied by Larsen, as in *Hydrometra*, the postnotum consists of lateral sclerites, the median section being lacking. Laterally the scutum and scutellum in *Gerris* and *Hydrometra* are separated by a wide lightly sclerotized band, called by Larsen the "tergalspalt." The flight muscles in *H. martini* appear to be identical with those of the species described by Larsen.

The mesonotum of the apterous form of *Hydrometra martini* shows interesting similarities to that of the wingless *Velia currens* studied by Larsen (1945a). In both, the tergal sclerites are reduced to an undifferentiated membrane. The phragma is reduced in *Velia*; in *H. martini* it seems to be lacking. In both species there is a correlated loss of the large indirect flight muscles (M 30 and M 34) and the direct flight muscle (M 38). *Musculus furca-pleuralis* (M 52) which is lacking in *Velia* is reduced in *H. martini*.

The leg articulation in the winged individuals differs from that in the wingless individuals only in having larger basicoxal sclerites and larger trochantins. The muscles and leg movement are similar to those of the prothorax.

The metathorax of *Hydrometra* is markedly different from that of other hemipterans which have been investigated. In the reduviid, Emesa, which also has an extremely elongate body, both the mesothorax and metathorax are long and both have clearly defined tergal sclerites (Taylor, 1918). Hydrometra has not only a metathorax which is much longer than the mesothorax, but also a reduced tergum. That the narrow mid-dorsal line with its corresponding internal ridge is the notum is shown by the origin of the leg muscles (M 63, M 64 and M 70) on it.

The metapostnotum, which according to Larsen (1942) can be distinguished from the metanotum by the absence of notal leg muscles, is small. M. metanoti secundus, an indirect flight muscle, takes its origin on it in winged animals but is lacking in apterous hydrometrids. This muscle is present in Gerris rufoscutellatus and absent in wingless specimens of Velia currens.

It is difficult to interpret the homologies of the anterior part of the metathorax. The heavy ridge which characterizes this area in apterous as well as macropterous forms of Hydrometra martini is not mentioned by either Taylor (1918) or Larsen (1945a) in any of the insects which they described. It seems to be a secondary development which gives rigidity to the area. No other differentiation is found in the wingless H. martini.

Larsen (1942) pointed out that in Hydrometra as well as in Gerris, the anterio-lateral angles of the metanotum are separated to form small independent sclerites above the wing bases. These serve as places of insertion for a pair of indirect flight muscles (M 57) which originate on the third phragma. He found homologous structures in a number of terrestrial hemipterans which also have a direct flight muscle (M 61) which inserts on the third axillary sclerite. Neither Gerris nor Hydrometra has this muscle. Three other landmarks of the typical thoracic region are missing: the basalare which is never found in Hemiptera as an independent sclerite, the subalare which is not found in many aquatic or semiaquatic bugs and the metapleural wing process which all hemipterans lack.

Two sclerites are present in the base of the hindwing. One, which acts as a fulcrum and extends toward the media, is probably the second axillary sclerite. The other sclerite articulates with the anterior margin of the wing and is probably the humeral plate. If this is so, the first and third axillary sclerites are missing. This area is not described by Larsen in Hydrometra or in any form which shows such a marked reduction of sclerites.

The extremely large size of the second phragma is made possible by the elongation of the metathorax. It has the same relative position in Hydrometra that it has in other hemipterans. Another effect of this elongation is the manner in which the leg muscles insert. The origins of all of the muscles are anterior to the leg base and each inserts with a long apodeme. These connections limit the horizontal movement of the hindlegs. Because of the comparatively larger size of the metepisternum, the distance between the middle and hind coxae is much greater than that between the fore and middle coxae.

Wing venation in the Hemiptera has not been the subject of recent investigation. Comstock and Needham (1898) studied a number of nymphs and figured a nymphal pentatomid wing. They found that the subcosta and radius coalesced. Two papers published in 1926, one by Hoke and one by Tanaka, described the venation in a large number of hemipterous nymphs and adults. In general, the nymphal wing includes the typical veins; the adult wing shows considerable reduction. Of those described, the wing of <u>Hydrometra</u> most closely resembles those of <u>Mesovelia</u> and <u>Merragata</u>, which were figured by Hoke. However, both of these wings have a small but clearly developed anal region which <u>Hydrometra</u> lacks. Unfortunately, neither of these papers included results of a study of positions of the wing sclerites. A thorough review of the wing venation with consideration of the basal sclerites would be interesting from the point of view of phylogenetic relationships.

## The Abdomen

The abdomen of the female hydrometrid consists of seven pregenital segments, two genital segments (VIII and IX) (fig. 39) and a postgenital region, the anal tube or proctiger. In the male, there are eight pregenital segments the last of which is cylindrical and partially encloses the ninth (fig. 40). The latter, the genital segment, forms the capsule which bears the external genitalia. As in the female, the postgenital area is an anal tube. The female abdomen is both longer and wider than that of the male (figs. 42, 43). The almost complete sclerotization of the adult abdomen prevents variation in total body length which is characteristic of the nymphs. This, and other aspects in the differentiation of the region, especially of the genital segments will be considered below (pp. 100-101).

Pregenital region (figs. 41, 42, 43)

In both sexes, the first abdominal segment is reduced to a tergal plate. Its rounded anterior end fits closely behind the metapostnotum; in winged individuals the small third phragma arises between them. Ventrally the first segment is indistinguishable from the metathorax and the rest of the abdomen.

The ventral fusion of the definitive sterna of the pterothorax and abdomen makes flexion of the body as a whole impossible. Variation in the diameter of the abdomen is possible because of the arrangement of the dorsal sclerites. In the typical pregenital segments (II through VII) these consist of a pair of lateral plates (paratergites or laterotergites) and segmentally arranged tergites. Each of the latter is further subdivided into a broad ridged median and a pair of narrow, flat lateral sclerites. The fused laterotergites of each side form long dorso-lateral plates which taper to a point anteriorly and posteriorly. The junctions of the sclerites on the dorsum are membranous and allow for variation in size of the abdomen. In an unexpanded abdomen, the fused laterotergites cover the lateral part of the medial tergite of each segment. In a distended abdomen, they are raised (fig. 43).

The ventral part of the abdomen is marked laterally by a pigmented band (fig. 41). The spiracles, a pair on each segment from II through VII, lie between this line and the margin of the fused laterotergites. Segments I and VIII, which in the nymphs bear spiracles (see p. 100), lack them in the adult. The spiracles of the second segment are near the metepisterna and are more dorsal than the others. The midventral line is very slightly carinate. The intersegmental lines are indicated on either side by pigmented lines. In the males, a pair of ridges project from the sternum of segment VII (fig. 41).

The pregenital region of the mature adult lacks intersegmental longitudinal muscles. In fifth instar nymphs and in very recently molted adults, five or six heavy muscle fibers run from one intersegmental ridge to another on either side of the mid-dorsal and mid-ventral lines. In both nymphs and adults, each abdominal segment has a series of strap-like dorso-ventral muscles which attach to the laterotergites dorsally and ventrally to the sternum at the level of the pigmented band.

Female external genitalia (Figs. 44, 45, 46, 47)

The terminal segments of the female hydrometrid are covered dorsally by the eighth tergum and ventrally and laterally by the first valvifers. The first valvifers hinge on the lateral margins of the triangular eighth tergite (fig. 46) and extend ventral nearly to the midline (fig. 45). The ventro-lateral portions of these sclerites are partially telescoped into the seventh segment, which extends back to form a subgenital plate. The proctiger, bearing the anal opening, and the tips of the second valvulae project posteriorly between the first valvifers (fig. 46).

Figure 47 is a diagram of the region with the left anterior valvifer and the left side of the seventh segment removed to expose the other structures. The retractor muscles of the valvifer which arise on the seventh sternum and the membranous lining of this valvifer are also removed. The first valvula hinges on the inner surface of the first valvifer. The vagina passes between the first valvulae which nearly surround the wide vulva. The second valvifers are dorsal and medial to the first. Together they form an egg guide rather than a true ovipositor. The second valvulae, or gonapophyses, either are lacking or are incorporated in the valvifers.

Two pairs of muscles originate on the seventh sternum. One pair attaches to the anterior margin of the first valvifer; the other inserts by a long apodeme on the first valvula. The protractors of the first valvulae arise on the eighth tergum and attach dorsally. The two muscles of the second valvifer arise on the lateral margin of the small ninth tergum. The anal muscle takes its origin on the seventh tergum and inserts by a slender apodeme which extends under the ninth tergum to the posterior part of the proctiger.

Male external genitalia (figs. 48, 49, 50, 51, 52)

In the male hydrometrid, the membrane which attaches the eighth abdominal segment is extensible enough to allow flexion of approximately 60° (fig. 48). Its movement is produced by two pairs of muscles which arise on the seventh segment, one laterally and one ventrally. The ninth segment, the genital capsule, is partially telescoped into the eighth. The connecting membrane here too allows for movement; the capsule can twist laterally about 90°. Two pairs of intersegmental muscles, originating laterally and ventrally on the eighth segment, insert on it.

The outer surface of the entire capsule is rigid but the dorsal margin, and particularly its lateral angles, are extremely heavily sclerotized. The portions usually enclosed by the eighth segment are lighter in color and less heavily sclerotized. The ventral wall of the genital chamber, formed by the concave inner lining of the capsule, is lightly sclerotized.

The proctiger, or anal tube, projects from the basal part of the ninth segment and forms a partial cover for the genital chamber (fig. 50). The large basal plate which articulates with the capsule posteriorly is nearly concealed (fig. 51). This plate is a sclerotized ring with a median dorsal projection. The tubular phallosoma or phallobase extends from it and the genital claspers (parameres, harpagones, gonoforceps, genitalhaken) articulate with it laterally. The aedeagus is telescoped within the phallobase.

When the genital apparatus is evaginated, the phallobase and the aedeagus extend perpendicular to the capsule. The lightly sclerotized valves of the aedeagus are imbedded in its ventral wall. The tip of the aedeagus is elongate (fig. 52). The claspers are paddle-shaped and each bears four or five setae on its anterior margin (fig. 49).

The musculature of the genital capsule is shown in figure 49. Two small muscles, one of which arises anteriorly and the other posteriorly on the genital capsule, insert on the base of each clasper. Protraction and retraction of the phallobase are caused by two pairs of muscles arising anteriorly and laterally on the genital capsule and inserting on the basal plate. The protractors are broad flat muscles which originate on the ventral part of the capsule, extend under the lining of the genital chamber and attach broadly to the medial part of the basal plate. The retractors are fan-shaped muscles which arise on the lateral walls of the capsule and insert by a tendon on the lateral projections of the plate.

## Discussion

Work on the hemipterous abdomen has been concerned especially with the genitalia. Some studies have included the number of abdominal segments and others have dealt with patterns of sclerotization of this region. The most detailed paper considering all the aspects of the abdomen and the genitalia is that of Larsen (1938).

Typically, the first abdominal segment of hemipterans is reduced as it is in _Hydrometra_ (Larsen, 1938). In the adult the first tergum is separated from the second by a faint line. Also, the presence of eight pregenital segments, the second through the seventh bearing spiracles and the others lacking them, is typical of this order (Snodgrass, 1935). In adult hemipterans, the postgenital region always consists of a small sclerotized tube which is considered to represent the fused tenth and eleventh abdominal segments (Snodgrass, 1935, Larsen, 1938). This region has been referred to as the proctiger (Snodgrass, 1935), Analkonus (Larsen, 1938), anal lid (Ekblom, 1926), Analkegel (Weber, 1930). Eleven abdominal segments develop embryologically in Naucoris, Nepa and Notonecta (Heymons, 1899) and in Pyrrhocoris (Seidel, 1924). The embryological development of Hydrometra is not known but the nymphs as well as the adults have only ten distinct segments.

The arrangement of the dorsal and ventral intersegmental muscles of Hydrometra shows clearly the nature of the primary segmentation of the pregenital region. Although the loss of these muscles is not reported in hemipterans it correlates with the loss of flexibility, since these muscles, essential for the final molt, have no function in the adult insect.

The lateral margin of each abdominal segment in many hemipterans is differentiated into a laterosternite as well as a laterotergite (Snodgrass, 1935, Larsen, 1938). These lateral sclerites are considered together as the connexivum (Torre-Bueno, 1937), a structure which is frequently mentioned in taxonomic descriptions (Blatchley, 1926, Hungerford and Evans, 1934). Only the laterotergites are formed in Hydrometra, and in most species of the genus, each of these is independent of the others. However in a number of species, including *H. ambulator* Stål, *H. albolineata* Scott, *H. butleri* H. & E. and *H. greeni* H. & E., which Hungerford and Evans (1934) figured in dorsal view, as well as in *H. martini*, the laterotergites of each side form fused lateral plates.

According to Snodgrass (1935), the spiracles of the insect abdomen lie in the tergum. Their location in *Hydrometra* indicates the incorporation of a part of the tergum into the definitive sternum, which Snodgrass illustrated as a variation in the pattern of abdominal sclerotization. The origin of the dorso-ventral abdominal muscles on the wall of the definitive sternum ventral to the spiracles shows that this region is a part of the sternum. If any pleural area is present, it must, therefore, be incorporated in the narrow band between the spiracles and this line of muscle insertion.

By far the most thorough comparative work on hemipterous genitalia is that by Larsen (1938) mentioned previously, who reported on the reproductive systems of several aquatic species. The earlier papers of Ekblom (1926, 1930) described the male and female genitalia as well as head structures in a variety of hemipterans, including *Hydrometra stagnorum*. Comparisons of the male external genitalia in a large number of species were figured and discussed by Singh-Pruthi (1925). Snodgrass (1933) included descriptions of female genitalia of a coreid, *Anasa tristis*, and a saldid, *Pentacora ligata*.

According to Larsen (1938), the female genitalia of Hemiptera typically include two pairs of valvifers (gonapophysistrager), the anterior bearing the first valvulae (gonapophyses) associated with the eighth segment and the posterior, associated with the ninth segment, bearing the medial (second) and lateral (third) valvulae (gonapophyses). The lateral gonopophyses do not part in the formation of the ovipositors in Hemiptera. Snodgrass (1938) and Michener (1944) homologized the third valvulae with the gonostyli of primitive insects. Larsen (1938) found that in typical Hemiptera the muscles of the first valvifer include one from the seventh sternum and two others from the eighth tergum; those of the second valvifer arise on the ninth tergum. In the corixids, the only family which he considered in which the female genitalia are greatly reduced, the valvulae are small and incorporated in the valvifers. This may be true also in Hydrometra. The relationships of the sclerites correspond with the description by Snodgrass (1933) of hemipterans.

Ekblom (1926) found that although the ovipositor in Hydrometra was greatly reduced, it resembled those of Gerris and Velia. In the species which he studied of all three genera, the anal tube bent ventrally covering the genitalia. This is not the case in H. martini. There are other minor differences between H. stagnorum as described by Ekblom and H. martini. In the former, the ninth tergum and proctiger are larger and the sternum of the seventh segment extends much farther posteriorly.

The origins and insertions of the various muscles help to establish the homologies of the sclerotized parts. These have been investigated by Snodgrass (1933) and Larsen (1938). The muscles of the ninth segment are typically, as they are in Hydrometra, two pairs arising on the tergum and inserting on the second valvifer. Usually two ventral muscles which originate on the seventh sternum insert on the first valvifer. In Hydrometra, only one was found both in this study and in that of Ekblom (1926). The position of the dorsal muscle, arising on the eighth tergum and inserting on the dorsal part of the first valvula is typical.

The hemipteran male genitalia consistently include a genital capsule, formed from the ninth segment, which bears the intromittent organ and a pair of articulated appendages (Snodgrass, 1935, Larsen, 1938). The species studied by Ekblom (1926, 1930) and Larsen (1935) have intromittent organs consisting of a sclerotized proximal portion (phallobase or phallosoma) and a rather membranous distal portion (aedeagus). The aedeagus is extremely variable in shape; in H. stagnorum it is long and tapering (Singh-Pruthi, 1925).

In Hemiptera, the phallobase attaches to the basal plate. The retractor and protractor muscles which arise on the genital capsule, insert on this plate rather than on the phallobase or the aedeagus. Both the position and the musculature of the genital claspers in Hydrometra are of the typical hemipterous pattern.

Although the male external genitalia in Hemiptera are consistent in their form, the homologies of the various structures are not yet clearly understood. Snodgrass stated that "concerning the origin of the insect phallus, we can say only that the facts at present known about the development of the organs are not sufficient to warrant any definite statement, but that they appear to favor the view that the phallus is an independent genital structure" (1941, p. 8). However, Michener (1944) was able to work out the homologies of male and female structures by using gyandromorphs and intersexes of a number of species of Hymenoptera and Orthoptera. Assuming that his conclusions were correct and that these homologies also apply to the Hemiptera, the basal plate represents the fused proximal portions of the gonopophyses and the genital claspers represent either the gonocoxite alone or a fusion of the gonocoxite and the gonostylus.

An interesting report by Wygodzinsky (1947) suggested that the male claspers of the cryptostemmatid, Trichotonannus, are serially homologous with ventro-lateral, spiracle-bearing extensions (which he termed "parasternites") found on abdominal segments seven and eight. Wygodzinsky proposed the theory that this is a primative condition retained by the cryptostemmatids which he believed to be more closely related than most other families to generalized Hemiptera.

## Internal Anatomy

### The Digestive System (figs. 53, 54)

The pharynx of Hydrometra martini is readily identified in cross section by its characteristic U-shape and dilator muscles. It extends nearly to the posterior margin of the head. Here the digestive tube is surrounded by nervous tissue and changes to the esophageal pattern, which is round in cross section. In the prothorax, the alimentary canal emerges from the circumesophageal ring and continues posteriorly, margined on either side by the principal salivary glands. These are composite structures with lobules of four types (fig. 53). Those of the most anterior group are transparent, small and vesicular. The others are translucent and of variable shapes; one group is elongate, the next, ovate. The posterior part of the gland is a single large, round acinus. The accessory gland consists of a median, a lateral and a posterior lobe, each of which is elongate and thin-walled. A duct connects this gland with that of the primary gland and a second duct leads anteriorly to join that from the opposite side. The common duct extends anteriorly just ventral to the digestive tube.

At the level of the mesothorax, the esophagus widens to form the broad anterior part of the ventriculus, which extends back to the fourth abdominal segment (fig. 54). The next section of the ventriculus, a narrow tube, continues posteriorly to the middle of the fifth segment, loops back to the level of the fourth segment and then turns posteriorly again. At the level of the sixth abdominal segment, the ventriculus enters the thick-walled intestine. The Malpighian tubules, two on each side, enter the alimentary canal at this level. These twisted, white tubules extend into the fifth and seventh segments.

The intestine continues to the posterior part of the seventh abdominal segment, where it joins the rectum, a short, thin-walled tube. A large diverticulum, which is an evagination of the ventral wall of the rectum, extends under the intestine. The rectum passes through the proctiger and opens to the exterior at its tip.

The female reproductive system (figs. 55)

The ovaries of Hydrometra martini, consisting of seven ovarioles or egg tubes, extend from the thorax through the sixth abdominal segment (fig. 55). Each egg tube has an anterior terminal filament, a group of undifferentiated cells and a series of eggs of which the most posterior is the most nearly mature.

The combined terminal filaments join dorsally between the digestive tube and the metathoracic leg muscles and hold the ovaries in place. The ovarioles of each ovary open into a short oviduct which joins with that of the other side to form the common oviduct. The wall of the common oviduct is thickened anteriorly and leads posteriorly to the vagina. The seminal receptacle, which also enters the anterior part of the vagina is made of two parts, a slightly twisted duct and a flat gland which contains long, coiled and very slender tubules. Posterior to the base of the seminal receptacle, the vagina is enlarged to form a muscular bursa copulatrix. On its dorsal surface is a heavily sclerotized evagination. The vaginal opening, the vulva, lies between the valvifers of the eighth and ninth abdominal segments.

Recently molted or overwintering females have inactive ovaries which are small and compact. The females which are reproductively active may have tremendously enlarged ovaries with as many as seven mature or nearly mature eggs. Those females which have mated may have masses of sperm in both the dorsal evagination of the bursa and the seminal receptacle.

## The male reproductive system (fig. 56)

The internal reproductive organs of the male are simple (fig. 56). The elongate testes of the sexually active male extend from the first through the fifth abdominal segments. In immature and in over-wintering individuals these may be less than half the size of the active testes. A slender duct, the vas deferens, leads from the anterior end of each testis along its median margin to the seminal vesicle. These vesicles have rather muscular walls and large lumina. In living males which are dissected, masses of sperm are moved back and forth in the vesicles by contractions of the walls. The narrow duct of each seminal vesicle joins that of the other side to form a common ejaculatory duct which enters the genital capsule. There are no accessory glands.

## Organs of conservation, respiration and distribution (figs. 58, 59, 60)

Layers of cells, many of which are fat-ladened, lie between the exoskeleton and the internal organs. In many individuals, especially those dissected in the early spring, these cells are bright green, while in other animals, they are white. The ventral and lateral walls of the abdomen are lined with a continuous double-layered sheet of this tissue through which numerous tracheal tubes spread (fig. 60). A double layer of cells spreads under the tergal area of the abdomen and both tracheae and a part of the dorsal blood vessel are imbedded in it.

The positions of the spiracles were described above (see p. 33 and fig. 41). Of the eight pairs, only the first has a closing apparatus (fig. 58). The short atrium lies between the external opening and a valve consisting of a process on one side which closes against the opposite wall. The other spiracles open directly into spiracular trunks.

Figure 60 shows the arrangement of tracheae in the right side of the fourth abdominal segment. The short spiracular trunk gives off three main tracheae: one which sends branches ventrad and obliquely caudad, another which aupplies the viscera and the third which goes to the dorsal layer of cells. Branches of the dorsal tracheae, which join corresponding tubes of the adjacent body segments, form a dorso-lateral trunk. These large trunks extend anteriorly and posteriorly to the body segments which lack spiracles. Branches from them supply the various tissues. There are no vessels which connect the tracheae of the left and right sides.

The dorsal blood vessel extends from the seventh abdominal segment to the level of the deutocerebrum. In the abdomen, it lies in the dorsal diaphragm. In the thorax and head it parallels the anterior portions of the ventriculus and the esophagus. There is no bbvious variation in diameter in the anterior and posterior parts of the vessel. The fine structure of the vessel was not studied but in stained whole amounts of the dorsal body wall and blood vessel, two cell layers are evident. The inner layer consists of flat epithelial cells with flattened nuclei and non-granular cytoplasm. The cells of the outer epithelium are cuboidal; the nuclei are round with large nucleoli and the cytoplasm is granular. Many of the surrounding cells have large flat droplets. Others are smaller with centrally placed nuclei and granular cytoplasm.

Nervous system (fig. 57)

The ganglia of the central nervous system are concentrated in the posterior part of the head capsule and the prothorax. Their fusion is nearly complete but there are indications of the original ganglia in both dissected and sectioned material. The optic nerves extend from the protocerebral ganglia. These and the deutocerebrum are not contiguous medially since the pharynx with its dilator muscles lies between them. The dorsal blood vessel opens between the bases of the deutocerebral lobes. The large tritocerebral ganglia are fused and, together with the circumesophageal connectives and the subesophageal ganglia, make a heavy ring of nervous tissue through which the esophagus and the dorsal blood vessel pass. In the thorax the esophagus emerges from this concentration of nervous tissue and continues posteriorly dorsal to it. The thoracic concentration consists of four ganglia. Since nerves of the first, second and third ganglia innervate the legs, these are clearly thoracic. The last ganglion gives off two pairs of nerves, one directed obliquely and the other posteriorly, and represents the fused abdominal ganglia.

## Discussion

In general, the structure of Hydrometra seems to be similar to that of other hemipterans described in the literature. Among the studies on the internal anatomy of the group, that of Dufour (1833) remains the most comprehensive. Weber (1930) and more recently Poisson (1951) have brought together information on morphology in their general works on the Hemiptera. Other than the papers mentioned earlier on the structure of the head, thorax and external genitalia, only two mention original work on the anatomy of Hydrometra. One by Gross (1901) concerns the number of ovarioles in the female _H. stagnorum_ and the other by Mammen (1912) deals with the spiracles in the same species. _Hydrometra martini_ will be compared here for the most part with Gerris, which has been studied by numerous morphologists.

The digestive system of Hydrometra is very similar to that of _Gerris canalium_ as described by Dufour (1833). In _Gerris_, the ventriculus is figured as being constricted anteriorly and having a prominent pouch just before its entrance into the intestine; in _Hydrometra_, it is a simple sac. Both kinds are figured for various hemipterans by Elson (1937) who also found forms in which the extremely long ventriculus had four subdivisions and others in which there were numerous gastric caeca. In this study in which he compared the length of the alimentary canal with the total body length of hemipterans with different feeding habits, Elson found that the predatory forms, _Belostoma_ and _Notonecta_, had digestive tracts three times the body length, the phytosuccivorous forms, twice the body length and the algophagous forms, one and a half times the body length. In Gerris, as well as in Hydrometra, the alimentary canal is about one and a half times the body length (Dufour, 1833).

Dufour showed three pairs of salivary ducts entering the head in Gerris. In Hydrometra, as in the coreid, corixid and belostomatid examined by Elson (1937), a single duct is present on each side. Dufour mentioned the possibility that the accessory salivary glands serve as reservoirs. Certainly their thin walls and large lumina have the appearance of storage rather than of secretory activity.

The posterior part of the digestive tract in all of the described Hemiptera consists of a short intestine into which open four Malpighian tubules and a thin walled rectum with a large ventral diverticulum (cul-de-sac or sac stercorale) (Elson, 1937). According to Poisson (1951) this structure may serve as a hydrostatic or a respiratory organ in the aquatic hemipterans. Its function in other insects is not known.

The internal organs of reproduction of Hydrometra have not been described except that Gross (1901) reported that each ovary of H. stagnorum consists of four ovarioles. This is the minimum number found in hemipterans, whereas seven, the number found in H. martini, is the maximum (Weber, 1930). Besides the differences in numbers of ovarioles, variations in the female pattern seem to involve the vaginal region. Both Dufour (1833) and Wilke (1908) included figures of the female Gerris but neither showed this area. Of the aquatic hemipterans considered by Larsen (1938) only in *Micronecta minutissima* is the vaginal cuticule modified as it is in *Hydrometra martini* to form a chamber in which sperm can be stored. In both species, sperm are found here as well as in the seminal receptacle.

The male reproductive system of Hydrometra is similar to that of *Gerris lacustris*, as described by Wilke (1908) and of *Velia currens* as described by Dufour (1833). In Gerris, the testes are U-shaped; the ducts and the seminal vesicles are broader than those of Hydrometra. In *Velia*, the testes are shorter and the vasa diferentia emerge from nearly the middle rather than at the anterior end of the gland. In all three species, the ejaculatory duct is straight and lacks accessory glands.

The tracheae of the abdominal segments of *Hydrometra* follow the general pattern described by Snodgrass (1935). The structure of the spiracles, the first pair having a closing apparatus and the others lacking it, was found in both *Gerris* and *Hydrometra stagnorum* by Mammen (1912). Dufour (1833) commented on the sparcity of tracheal tubes in the gerrids which he examined and correlated this with their low rate of activity and their less frequent flight. Dufour noted also the relationship of the tracheae with the tissues under the exoskeleton which serve in fat storage.

The dorsal blood vessel is usually divided into an abdominal region which bears ostia and is heavier walled than the anterior part, or aorta (Snodgrass, 1935). In the stink bug, *Nezara*, there are three pairs of ostia in the abdominal section (Malouf, 1933). These structures were not seen in *Hydrometra*.

The comparative study of the nervous systems of Hemiptera published by Brandt in 1878 continues to be the most comprehensive work in the field. The nervous system in this group is characterized by a concentration of ganglia. Various combinations of ganglia occur in the different species. In *Gerris*, as in *Hydrometra*, the subesophageal ganglia are connected broadly with both the circumesophageal commisures and the combined thoracic and abdominal ganglia. However, in *Gerris* the eyes are relatively close to the central nervous system and the optic nerves are correspondingly short. In other species, the ganglia may be fused in other patterns; there may be two or three concentrations joined by relatively long connectives.

## BIOLOGY

*Hydrometra martini* was collected in and near South Hadley, Massachusetts from 1948 through the spring of 1952 and in the vicinity of Douglas Lake, Cheboygan County, Michigan in the summers of 1948, 1949, 1951 and 1952. In both areas, it was abundant in pasture ponds, in small lakes and in other still or slow-moving waters having plant-lined shores supporting abundant animal life.

### Descriptions of habitats

In the South Hadley area, hydrometrids were found most readily in and on the shores of spring-fed pasture ponds at Lithia Springs in South Hadley and at Whately Glen in the town of Whately. They were also taken at Upper and Lower Lakes on the Mount Holyoke College campus, Paradise Lake in South Hadley, Aldrich Lake in Granby and the Old Mill pond in Hadley.

The Whately Glen pond, which is approximately 40m long and 30m wide, is fed throughout the year by springs at its northeast end. On the north and west sides of the bank, the banks slope gradually. The bottom, which is covered here with a thick flocculent ooze, becomes sandy near the southern end where the outlet has been dammed. Cattails (*Typha latifolia*) are the principle vegetation of the spring fed area. Bur-reeds (*Sparganium americanum*) emerge from the bottom mud and through the summer and fall, a thick scum of algae fills the spaces between their bases and lies over the decaying leaves. *Myriophyllum* is rooted in the deeper water.

From late spring to early fall the shore and the matted vegetation supports a varied population of animals. Among them are collembolans, gerrids, lycosid spiders, mesoveliids, hebrids and *Microvelia* as well as hydrometrids. Large numbers of entomostracans, hydrachnids and dipterous larvae swim through the shallow water. Dragonfly and damselfly naiads, corixids, notonectids, naucorids and larval and adult beetles dart through the open water or crawl over the submerged vegetation. Larger animals, *Rana clamitans*, *Triturus viridescens* and *Chrysema picta* also live in the pond.

In the autumn, the leaves of the oak and maple trees and the needles of the white pines which surround the pond, drop into the water. The bur-reeds turn brown and fall, making a floating raft before they sink to the bottom. In this period the hydrometrids migrate to land; gerrids and gyrinids disappear from the surface. Spotted newts become more abundant as the red efts return to the water and change to their green and yellow colors. On the land, arachnids, cicadellids and staphylinid beetles crawl among the grass hummocks and dead leaves with the hydrometrids. Until snow falls in the early winter, marsh treaders are found on the moist earth in protected places, depressions among clumps of grass and under dead leaves. In most years, the snow- and ice-covers last until the spring rains in late March.

The pasture pond at Lithia, which is also spring fed, is nearly round with a maximum diameter of approximately 10m. It lies in a hilly pasture surrounded by *Tsuga*, *Chamaecyparis*, *Juniperus* and *Kalmia*. *Iris* and *Typha* surround the margin of the pond and *Vallisneria* and *Myriophyllum* cover its floor.

In the early spring as the ice melts, fairy shrimp, *Eubranchipus vernalis* and larvae of the limnophilid caddis fly, Platycentropis, appear. *Rana sylvatica* and *Ambystoma maculatum* come in to lay their eggs. Tadpoles of *R. catesbiana* and *R. clamitans* are present through the year as are *Triturus viridescens* adults. Many species of water beetles and a variety of hemipterans (*Ranatra*, *Notonecta*, *Belostoma* and corixids) are to be found in the water and gerrids and gyrinid beetles, on its surface. In late summer, if there has been little rain, the pond shrinks to about a tenth of its maximum size; the animal population is concentrated. With the fall rains, the water level rises so that the pond is well filled before the ice forms. This pond, too, is covered with snow from late December until March.

In the Douglas Lake area, hydrometrids occur in varying numbers in many habitats, bog lakes, beach pools, slow moving side waters of creeks and man-made pools. Among these are Nichol's, Smith's and Bryant's bogs, Bessey Creek, Nigger Creek, Fontinalis Run, the beach pools at Sedge Point on Douglas Lake and at Black Lake, Nelson Lake and the gravel pit pools near Pellston. Collections and observations were most frequently made at the gravel pit pool near Pellston and at Nelson Lake because they were more accessible and hydrometrids were relatively abundant there.

The gravel-pit pools are four miles north of Pellston on the east side of highway 31. Irregular in shape and in depth, they occupy an area approximately 25m long and 16m wide.

They were made by the removal of gravel to a depth of two to three meters at least 15 years ago. The sources of water are springs on the north side and drainage from the adjacent area; there is no outlet. The water level fluctuates greatly. In each of the years in which collections were made, the pools were well filled during the early summer. In 1951 and 1952, rains were frequent through the summer and the water level remained rather high in August. Even in these years, the shallowest place dried completely. In the drier years, 1948 and 1949, the deepest depressions held only about 0.5m of water by mid-August. Emergent vegetation, consisting mainly of *Typha*, is limited to these deeper areas in which decomposing material has formed a deposit. *Chara* beds cover the bottom and *Juncus* with some *Carex* grows in the shallow water and along the shores. Clumps of *Cornus stolonifera*, *Salix lucida* and *Salix subsericea* overhang the north banks. A great variety of aquatic and semiaquatic hemipterans, notonectids, corixids, *Belostoma*, *Lethocerus*, *Ranatra*, *Gerris*, *Hebrus*, saldids as well as *Hydrometra*, abound here. Other insects include bettle larvae, soldier fly larvae, damsel fly, dragon fly and mayfly naiads. Amphibian tadpoles and metamorphosing frogs and toads are present in numbers.

Nelson Lake lies on either side of a gravel road separating sections 15 and 22 in Hebron township (Row 3W, Tier 38N), Cheboygan County. The lake is a low marsh about 8000m long and 3000m wide. Earth was thrown up to make a causeway on which the road runs. The ditches thus made are considerably deeper than the rest of the area. In dry years, in 1948 and 1949 for example, the water evaporated from the entire area, except the roadside ditches, causing concentrations of animals here. The soil is yellowish sand except for the detritus which accumulates in the deeper water. *Spirea* and *Salix* grow along the road and the willows extend to the edge of the water. The marsh is covered with a mixture of *Juncus* and *Scirpus* with some *Carex* and *Dulichium*. *Potomageton* and *Polygonum* grow in the deeper water. The animals here are of the same groups represented at Pellston. However, *Spongilla* is common and the amphibious snails, *Succinea*, are extremely abundant.

### Collecting methods

Adult hydrometrids were caught easily by hand or with a small tea-strainer and were transferred to an aspirator. They survived transportation best either in a dry container or in one which was lined with paper to absorb excess moisture. The nymphs were collected with a strainer and an aspirator with damp paper in the bottom. The nymphs were subject to death by desiccation if they were left too long in dry containers and by drowning if caught in condensation of moisture on the glass. They survived best when kept in containers which were lined with moist paper.

Both in the field and in the laboratory, cannibalism was prevalent among the nymphs. The harder bodied adults seemed invulnerable.

### Rearing methods

In the laboratory, hydrometrids lived well in aquaria with plants extending to or above the surface or in dishes partially filled with wet sand. They lived equally well in covered containers lined with several layers of moist towelling paper. This method has several advantages; the eggs could be removed and the nymphs and their molted skins were easier to see. These containers could be cleaned by removing the top layer of paper. The eggs were removed and placed on moist paper in containers. Because of cannibalism, the mortality rate was high unless the hatching nymphs were isolated and reared separately.

Hydrometrid nymphs and adults feed on any recently-killed insects. Because of the ease with which they can be handled, fruit flies having vestigal wings were used to a large extent.

## Behavior of the Adults

### Locomotion

Hydrometrids are equally at home on slowly moving water, on floating or emergent vegetation or on moist earth. In warm weather they are most active near aquatic vegetation but sometimes individuals venture 4.5 or 6.0m on the open water. On cool or cloudy days, hydrometrids most often seek the shore vegetation, sometimes climbing 25 or 30cm on the cattails or sedges.

Their typical gait is the deliberate walk that has given them both their common names, marsh treader and water measurer. They do not glide or hop as do the gerrids, but a disturbed animal runs rapidly from danger.

As a hydrometrid walks it typically swings its antennae from side to side. Both in the laboratory and in the field, the adults and nymphs characteristically elevate and lower their bodies by the rapid bending of the legs at the femero-tibial junction either when the animal is moving or stationary.

A frequent activity is the grooming of the appendages. The insects repeatedly draw their antennae or beak between the setose tarsi of the front legs or rub their legs against each other. Resting insects often raise one leg while standing on the others. This may also hasten evaporation of water from the tarsi.

Complete cessation of activity occurs only during cold weather; the animal takes a flattened position in which the antennae and legs are outstretched, the front and middle legs anteriorly and the hind legs postero-laterally.

Under water activity is limited to accidental incidents since hydrometrids never seem to submerge themselves deliberately. An experimentally immersed adult is lighter than water because of the air film held by body pubescence. It sucks air into its digestive system either from this film on the ventral side of the body or, if its body touches the water surface, by extending the beak through the film and drawing in air. The insect then swims or sculls along the surface to emergent vegetation or the shore and walks out. By intensified grooming, the insect soon dries its appendages.

Macropterous individuals exhibit the same behavior patterns as the micropterous forms. However they can fly well. Twice animals kept in the laboratory flew from their containers. The flight, which was preceding by fluttering of the wings as the animal walked, was almost vertical for about a meter. One animal flew to the window; the other disappeared in a few seconds and was not recovered. Flight was not observed in the field.

### Feeding

When food is available continuously under laboratory conditions, the adults begin to feed not sooner than three hours but usually not longer than five hours after the molt.

In the laboratory, hydrometrids appear willing to eat any sort of freshly killed or inactivated insects. Small living insects, such as nymphal hydrometrids are devoured readily.

They take plankton animals and aquatic larvae, mosquito wigglers and blood worms, for example, spearing them under the surface film. In the field they were observed to eat adult midges, mosquito wigglers, cladocerans, ostracods and collembolans. Usually a feeding insect was seen only after it had impaled its victim and was carrying it. On seven occasions, most of them during the summer of 1950, adults hydrometrids were observed to spear living aquatic forms (3 cladocerans, 2 mosquito larvae and 2 ostracods). No field records were made of hydrometrids feeding on large insects or of several individuals sharing a victim.

In seeking food, the insect stalks with its lowered antennae swaying from side to side, as though they were helpful in locating the prey. As the animal approaches food, it swings its beak forward and with a movement of the whole body, impales its victim.

The process of securing and holding the prey with the retorsely barbed mandibles and probing out the juices with the maxillary stylets has been described in the section dealing with function of the mouth parts (p. 10).

The use of saliva in feeding was brought out in the discussion of the head structure. The size and degree of differentiation of the salivary glands and the drop of fluid which can be seen occasionally as the beak of the hydrometrid touches its prey indicate the activity of the glands. In addition, the victim is paralyzed quickly; one which is attacked and almost immediately released soon dies.

In the laboratory, the imbibing of water by adults was observed only when the animals were changed from a dry container to one with water. Those kept in a damp situation probably obtained enough with their food.

## Overwintering

In Massachusetts the hydrometrid population in late September and October consists of adults, apparently young, and fifth instar nymphs. The females are sexually immature; the abdomen is slender and the ovaries are small. When the temperature approaches 15°, usually in mid-October, the land-ward migration starts. In the warm fall of 1951, this movement was delayed until October 25th. At the beginning of the migration at Lithia, a few individuals can be seen walking up the gently sloping north bank. Within ten days of the onset of migration, all of the individuals are off the water. Nymphs are rarely found; those taken into the laboratory at this time molt in one to three days.

Through the winter, when the ground is not snow-covered, adult hydrometrids are found singly or in small groups on the moist ground near the ponds at Lithia and at Whately. Usually they are among the decaying vegetation or in depressions among the grass roots. In the coldest weather, the animals which are completely inactive assume the resting position described above (see p. 57). Their inactivity combined with their earth-like coloration renders them nearly invisible. If these animals are touched, they arouse themselves and walk away slowly.

Further evidence of their dormancy inactivity is the lack of food in the digestive tubes of the animals taken after the land migration has begun.

The emergence from hibernation in the spring occurs at about the time the surface temperature of the water reaches 15°. The date differs with the year and with the locality. In 1950, a typical year, early March was very cold and snowy. On March 19th, when the air temperature was 13°, the snow at Whately Glen was 0.6m deep on the northwest slope of the pond. Only the spring fed area at the north-east part of the pond was free of snow; a few grass hummocks rose above the snow. The water temperature in the ice free area was 6°. A week later the air temperature had risen to 17° and much of the snow and ice had melted. The water temperature at the north east end of the pond was 10°. About 20 hydrometrids which were crawling on the grass roots and on the water-filled depressions between them, were taken. That they had not yet started to eat was indicated by the completely empty digestive systems of the five that were killed immediately and dissected. On April 1st, the air temperature was 15° and the water, 13°. Hydrometrids were near the shore but none was on the water. April fourth was a warm day with the air temperature 21° and the surface water near the shore, 17°. Hydrometrids were both on the water and on the vegetation near it. The five insects examined had not eaten. On April 8th, when the air temperature was 19° and the water temperature 16°, most of the hydrometrids seen were on the water; of the ten examined, nine had partly filled digestive tracts.

In the same year, open water appeared later at Lithia.

On March 19th the pond here was completely covered with snow and ice. On the 25th, a sunny day with an air temperature of 14°, the ice had melted but the water temperature was only 3° and there were snow banks on the south and west slopes. No hydrometrids were found. Ten days later, on April 4th the water temperature was 15°, the air temperature 21° and dozens of hydrometrids were stalking on the water. Three of the ten examined had eaten recently.

The earliest spring collection of *Hydrometra* was March 16, 1949, when two wingless females were found on the water at Whately. This was a rather warm day with an air temperature of 17° and the water in the place where the insects were taken was 13°. However, there were large snow patches on the ground and most of the pond was ice-covered.

In 1951, warm spring weather was late. On April 3rd, the pond at Whately was almost completely covered with ice and the snow cover was between 0.5 and 1.0 deep. Hydrometrids were not collected until April 20th.

## Reproduction

The mating of *Hydrometra* can be observed in the laboratory or in the field in the spring and summer. Typically, as he approaches the female, the male protracts the eighth abdominal segment to lower the genital capsule. He may come toward her from any direction but usually he approaches from the side and, swinging his body parallel to hers, the male mounts the female and holds her prothorax with one or both of his forelegs. The seventh abdominal processes rest on the eighth tergite of the female; the other pregenital segments do not touch. The eighth segment of the male projects obliquely ventrad and the ninth segment (genital capsule) is directly under the ninth segment of the female. The phallobase extends to the vulva while the aedeagus with its process are within the female reproductive tract. The short parameres do not make contact with the female.

During copulation, the female walks, elevating and depressing her body, carrying the male on her back. Not infrequently she feeds in the process. The male remains mounted on the female for as long as 15 minutes but actual mating seems to last not more than six minutes. After the male releases the female, she may push him aside with her middle and hind legs.

Males were never observed to copulate with a second female immediately after a successful mating. However, if the male failed to mate with the first female he approached, he usually sought another.

The preoviposition time in <u>Hydrometra</u> <u>martini</u> is variable; in the first spring generation, this period seems to be from 9 to 17 days in Michigan. Table 2 summarizes the preoviposition times and egg laying records of ten animals brought into the laboratory on June 29, 1949, as fifth instar nymphs. As these animals molted to the adult stage, each was placed in a 3" stender dish with a sexually mature male. Each dish was examined every other day; the eggs were counted and removed. In the observation period, five males died and were replaced. There was no apparent pattern of numbers of

### Table 2

Egg laying records of 10 Hydrometra martini females collected as 5th instar nymphs on June 29th and kept in the laboratory until August 15, 1949. ($x$ = death of   and replacement with another, d = death of  ).

| | date of first molt | date of first egg | 7/12 | 7/14 | 7/16 | 7/18 | 7/20 | 7/22 | 7/24 | 7/26 | 7/28 | 7/30 | 8/1 | 8/3 | 8/5 | 8/7 | 8/9 | 8/11 | 8/13 | 8/15 | total no. | average per day |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 6/30 | 7/12 | 1 | 2 | 0 | 0 | 4 | 4 | 8 | 9 | 6 | 14 | 9 | 6 | 5 | 8 | 8 | 1 | 6 | 4 | 95 | 5.3 |
| 2 | 6/30 | 7/17 | - | - | - | 1 | 3 | 4 | 4 | 3 | 8 | 6 | 4 | 9 | 8 | 8 | 6 | 4 | 3 | 2 | 73 | 4.9 |
| 3 | 6/30 | 7/16 | - | - | 1 | 2 | 4 | 2 | 6 | 1 | 5 | $7^x$ | 12 | 12 | 10 | 6 | 11 | 5 | 6 | 6 | 96 | 5.4 |
| 4 | 7/1 | 7/18 | - | - | - | 1 | 3 | 6 | 7 | 8 | 4 | 10 | 5 | $7^x$ | 4 | 12 | 6 | 10 | 6 | 0 | 89 | 5.9 |
| 5 | 7/2 | 7/17 | - | - | - | 1 | 2 | 0 | 4 | 6 | 5 | 5 | 9 | 4 | 6 | 2 | 0 | 11 | 8 | 4 | 67 | 4.5 |
| 6 | 7/2 | 7/18 | - | - | - | 1 | 6 | 8 | 9 | 4 | 12 | 11 | $3^x$ | 6 | 6 | 3 | 1 | d | - | - | 70 | 5.8 |
| 7 | 7/3 | 7/20 | - | - | - | - | 1 | 4 | 0 | 3 | 6 | 2 | 5 | 9 | 6 | 4 | 9 | 8 | 3 | 5 | 65 | 4.6 |
| 8 | 7/4 | 7/19 | - | - | - | - | 1 | 5 | 2 | 4 | 9 | 6 | 6 | 13 | 8 | $14^x$ | 5 | 8 | 0 | d | 81 | 6.2 |
| 9 | 7/4 | 7/16 | - | - | 2 | 3 | 5 | 5 | 4 | 2 | 3 | 5 | 5 | 3 | 8 | 1 | 0 | d | - | - | 46 | 3.5 |
| 10 | 7/6 | 7/17 | - | - | - | 2 | 4 | 4 | 3 | 5 | 9 | 8 | 4 | 8 | 13 | 6 | 6 | 3 | 3 | 1 | 79 | 5.3 |

eggs laid. The greatest number laid by any individual in the two day period was 14 while the average number laid in two days varied between 3.5 and 6.2. The longest lived individual (#4) in this series continued to lay eggs until September 5th, and died on September 12th. Between August 15th, and September 9th, she laid 72 more eggs making a total of 161. Number 5, which lived until September 2, laid a total of 118 and Number 8 laid 121 before she died on September 3rd.

Fifteen females reared from fifth instar nymphs collected later in the same summer, matured more rapidly. This group was collected on July 21st and completed the final molt between that date and July 26th. The average preoviposition time was 8 days, the minimum 7 days and the maximum 10 days.

In the field, females which undergo their final molts at the end of the summer or in the early fall seem ordinarily not to lay eggs until the following spring. However, young females brought into the laboratory in September and October of 1950 began to lay eggs after November 20th. The average preoviposition time of six females collected in September was 69 days with a variation of from 59 to 81 days; that of five females taken in October was 65 days with a range of 53 to 73 days. Females collected from hibernacula in mid-December of the same year laid eggs about 4 weeks later.

Hydrometrids collected in the early spring mature more rapidly than those brought into the laboratory in the fall and winter. A group of five animals taken at Whately, Massachusetts on March 26, laid their first eggs between

April 13th and April 18th; the average interval between collection and egg laying was 19 days. Ten others taken at Whately two weeks later began laying eggs within 5 to 13 days with an average of about 10 days. All of the females brought in after April 25th of that year laid eggs within a day or two of their collection.

Because observations of the previous year had indicated that *Hydrometra* mates before going into hibernation, all of the females collected for this study in 1950 were isolated. Since the eggs of all but two females (these were of the group collected on March 26th) were fertile, copulation must occur normally in the early fall when the females have small ovaries with no well developed eggs.

The egg laying process is an extremely simple one. In the laboratory, a female walks about the container slowly, dragging or touching her abdomen to the floor. Then she stops and raises the anterior part of her body. Her front legs are almost straight, her middle legs extend laterad and her hind legs are bent at the femero-tibial junction. After the female has tapped the supporting surface with her abdomen for two or three minutes, a small drop of fluid is expelled from the genital opening.

The base of the egg follows the fluid, and as the egg emerges, the female lifts her body. In so doing, she draws the egg perpendicular to the support. The whole process may be completed in four to five minutes although it may take as long as 15 minutes.

If the hydrometrid is disturbed in oviposition, she moves to another place and starts the process anew. Some may choose a vertical instead of a horizontal support. In this case, the female with her head downward, holds her body parallel to this surface.

Discussion

The measured gait of Hydrometra was noted by Arrow (1895) and by numerous later authors (Kirkaldy, 1899, Martin, 1900, Bueno, 1905, Weber, 1930, Jordan, 1931). That the movement of the legs is principally on a horizontal plane was mentioned by Weber (1930). This is correlated with the articulation of the coxae deep within the supracoxal cavities which was mentioned previously (pp. 20, 27). The front and middle legs can swing in a wide arc but the hind legs with its coxal process articulating with the posterior part of the supracoxal wall, is limited in its forward movement.

The elevation and depression of the body by a curious swinging movement which is characteristic of hydrometrids was reported by Jordan (1931). No function can be ascribed to this behavior pattern, but the equally characteristic grooming movements, which Jordan also noted, seem to be important in the animals in keeping their appendages dry. Both Jordan and Weber believed that waxy or oily secretions distributed by this action, as well as the fine setae, help in making the body surface hydrofuge. The distribution of weight of this slender-bodied insect on its six widely separated legs and the hydrofuge nature of the exoskeleton (especially of the tarsi) are sufficient adaptations to enable it to walk on the surface film.

Flight in gerrids in the laboratory has been reported by Wilke (1908), who found that although recently caught gerrids did not fly, those which had been kept in tight containers for about ten hours flew away as soon as they were released. From observations on gerrids on the field, he concluded that they flew only at night since pools, in which there had been none in the evening, would have a large population the next morning. Tevrovsky (1920), also reporting on gerrids, observed that flight also occurs during the day.

Flight in Hydrometra is not reported in the literature. Beamer (1949), however, found that Hydrometra as well as many other water bugs were attracted to lights. A South American species, *Hydrometra mensor*, was described by White from a specimen labeled "Manaos on board at light VIII, 1875" (Hungerford and Evans, 1934).

An additional record of attraction to light is that of Hungerford and Spangler (1952) who collected two first instar and one fourth instar nymphs of *H. martini* in a light trap set at the surface of Nichol's Bog, Cheboygan County, Michigan on the night of August 11, 1952.

Other investigators have mentioned many kinds of insects which serve as food for Hydrometra. *Hydrometra stagnorum* has been reported to feed on springtails (Arrow, 1895) and on dead or nearly dead insects such as dipterans and mayflies (Ekblom, 1926), and dead flies (Jordan, 1931).

Martin (1900) and Bueno (1905) emphasized the use of aerial insects caught in the surface film as food for *H. martini*, while Hungerford (1917, 1920) observed that *Hydrometra* eats a great variety of animals in the field. These include: mosquito wigglers and pupae, emerging midges, nymphal corixids, ostracods and small terrestrial insects. Riley (1918) fed hydrometrids with entomostracans in the laboratory.

The methods by which *Hydrometra* obtains these food animals are typical of the predacious Hemiptera which lack raptorial forelegs. The securing and holding of prey with the mandibular stylets and the probing and sucking by the maxillae were mentioned specifically by Hungerford (1920) for this genus. The carrying of small insects on the beak was seen by Arrow (1895) and Ekblom (1926) as well as by Hungerford (1920). Although more than one hydrometrid was never seen to feed on a single victim in the field in the present study, this sharing of an individual food insect has been cited for both *Hydrometra stagnorum* (Ekblom, 1926) and *H. martini* (Martin, 1900).

Because *Hydrometra* lacks a separated salivary channel in the maxillary tube, the use of saliva in the feeding process has been questioned (Ekblom, 1926, Weber, 1930). However, the evidence seems overwhelming that saliva is injected by hydrometrids into their victims and that it is effective in paralyzing them. Bueno (1905) also thought that living victims were paralyzed by hydrometrids, although according to Baptist (1941) the saliva of Hemiptera is principally digestive in function and only secondarily toxic.

The hard exoskeletons of the adults seem to render them invulnerable to other insects of the same or larger sizes. This is probably the advantage of the fusion of body parts and the lack of thin intersegmental membranes. Cannibalism was never seen in adults nor were adults observed to be eaten by other animals in the field although large lycosids and gerrids roam the surface film with them and Ranatra, Dytiscus and other large carnivorous insects lurk beneath it.

When Hydrometra leaves the water to hibernate, feeding ceases. Both H. martini and H. stagnorum have long been known to hibernate as adults in the decaying vegetation around the banks of the waters which they inhabit. This was reported for H. stagnorum by Wesenburg-Lund (1913), Stichel (1926), Jordan (1931) and Schumann (1934). Schumann also found a wingless pair in the woods far from water. Jaczewski (1936) mentioned finding very few nymphs of H. aegyptia in collections made from September to March in Egypt and concluded that here, as well as in Central Europe, most Hydrometras winter as adults. Both Martin (1900) and Hungerford (1920) saw Hydrometra martini coming out of hibernation during the first warm days of spring. Bueno (1905) found hundreds in May at Staten Island.

Although female hydrometrids are able to lay fertile eggs prior to mating in the spring, proof that they do so in nature is lacking. Jordan (1931) observed that H. stagnorum and H. gracilenta mate at the end of April and early May in Germany; he did not mention whether egg laying preceded copulation in these species. Martin (1900) who worked on Hydrometra at Ithaca, New York, collected females which were laying eggs as early as May 1st, but whether or not these animals had mated was not reported. Bueno (1905) bred virgin females with captured males on May 26th, and found that they had deposited eggs two or three days later.

The first report of mating in Hydrometra is that by Palumba (1891). According to this account, the female is pursued by as many as eight males which battle ruthlessly. The victor mates with the female, but dies a few days later; the female lays her eggs and then dies. This process of selection, which Palumba believed to lead to the strengthening of the species, has not been confirmed.

Both Ekblom (1926) and Jordan (1931) included accounts of copulation of H. stagnorum. Mating pairs were never seen on the surface film by Ekblom but Jordan mentioned the depression of the female by the added weight of the male. They both found that sometimes, immediately after mating with a female, a male would mate again with the same or another female. These two authors agreed in finding the duration of copulation highly variable.

In the northern part of the United States, the egg laying period, like the mating period, is continuous from April through August. This is the case in New York (Martin, 1900, Bueno, 1905) and Kansas (Hungerford, 1920), as well as in Michigan and Massachusetts, as shown in the present study. Jordan (1931), working in Germany, found that the egg laying periods for H. stagnorum and H. gracilenta last for at least six weeks in April and May.

The length of the egg laying period and the number of eggs laid by a single *Hydrometra* have been recorded most completely by Hungerford (1920). One female which had molted to the adult stage in the laboratory on July 25th, had mated and laid 28 eggs by August 4th. She had deposited a total of 173 eggs by August 31st, and continued to lay eggs after that date. In part of the period, she averaged 7.8 eggs per day and on one day, laid 11. This indicates a production of an egg by almost every ovariole each day.

The only reports on numbers of eggs laid by European species are those of Jordan (1931) who found that average number of eggs laid by *H. stagnorum* was 47 and that a single *H. gracilenta* deposited 53 eggs.

The simple expulsion of the egg by the female and its attachment by a sticky disc to a support has been observed by other investigators for several species: *H. martini* by Martin (1900) and Hungerford (1920), *H. stagnorum* and *H. gracilenta* by Jordan (1931) and *H. vittata* (probably *H. albolineata*) by Takahashi (1921).

## Number of Generations and Longevity

There seem to be three full generations and a partial fourth generation of Hydrometra martini in both Michigan and Massachusetts. The over-wintering generation begins reproductive activity in late April or early May in Massachusetts. Some of these individuals live and lay eggs as late as the second week of July. In both places, the first nymphs of the spring generation molt to the adult state about June 20th. In the laboratory and probably in the field, these females begin to lay eggs in about ten days and live, laying eggs, until nearly the end of the summer. The first offspring of this generation, arising from eggs laid about July 1st, are the summer generation. They complete the nymphal instars and reach their final molt in three to four weeks. After a preoviposition period of a week to ten days, the females begin to lay eggs. Eggs of the summer generation, then, appear as early as August 1st and they are laid continuously until late summer. Some animals arising from this generation may also reproduce in the same season, and therefore give rise to the fourth generation. Most of them, however, do not lay eggs until the following spring but they do mate before going into hibernation.

Because of the long life and extended oviposition period of the females, members of various generations are sexually active simultaneously during the summer. In the laboratory the animals that lived longest were those of the summer generation; they lived from late August until the following June or July, having attained an age of about ten months.

## Discussion of Longevity and Number of Generations

The record for the longest life in Hydrometra martini is that reported by Bueno (1905) who found that an individual taken in May overwintered and lived until the following August. Neither in the present study nor in others in the literature has a span longer than from September or October to the following June or July been reported.

Bueno (1905) gave an average life cycle of 25 to 35 days and three to five broods per summer in Staten Island, New York. Martin (1900) implied that there were several generations in Ithaca, New York. In Kansas and farther south, the number of generations may well be more than five. Hungerford (1920) reported an optimum life cycle of 15 days from egg to egg although the average in the summer was about 21 days. With reproductive activity beginning earlier in the year and continuing until fall, there are conceivably as many as eight or nine generations in a season.

Workers in northern Europe (Wesenberg-Lund, 1913, Ekblom, 1926) found only one generation per year of Hydrometra stagnorum which Ekblom found to reach the adult state at the end of July but in England according to Arrow (1895) and in Germany according to Jordan (1931) there are two broods. Jordan supported his field observations with laboratory rearings; one generation matured in late June and the other, the over wintering generation, approximately seven weeks later.

The number of generations produced in different areas varies greatly. Temperature probably is the factor responsible for reproductive activity in *Hydrometra*.

## The Egg

### Appearance

The spindle-shaped and beautifully sculptured egg of Hydrometra martini is comparatively large, about 2.0mm long and 0.2 to 0.28mm wide. The egg shell or chorion consists of two layers. The leathery outer exochorion protects the embryo and is responsible for the shape and surface pattern of the egg (fig. 61). The central portion of the inner layer, or endochorion, is a delicate sheath which surrounds the embryo proper. From it extend two slender projections: a spicule leading through the stalk into the basal attachment disk and a delicate tube terminating in the micropyle at the free end of the egg (fig. 62).

The sculpturing of the exochorion indicates the intricate arrangement of the air spaces within it. Each of the larger divisions, the basis of which abut on the micropylar tubule, is subdivided into a myriad of minute alveoli. Their outer surfaces make a diamond pattern on the exochorion. A cross section of this region shows the arrangement of these compartments (fig. 64), and the proximal part of the basal stalk has a similar pattern. Here large air chambers surround the spicule of the endochorion. The distal part of the stalk, adjoining the gummy basal disk, consists of simple and rather transparent air cells which lack internal partitions (fig. 63).

The sculptured pattern of the wider middle area gradually merges with that of the two ends. In most of the eggs the sculpturing of that part consists of crests separated by furrows extending from one end of the central area to the other. In some of the less typical eggs, transverse ridges connect the longitudinal ones making a more or less extensive network. The raised surfaces are spongy with a vast number of minute air spaces. In a few eggs a hexagonal pattern takes the place of longitudinal grooves.

All of the air-filled spaces in the exochorion make the hydrometrid egg look opaque and give it excellent flotation. Dry eggs dropped in water rest on the surface film or float just beneath it. Those which are submerged, so that some of the air is replaced by water, soon sink and the outer chorion becomes translucent.

When they are laid, hydrometrid eggs are pearly white. They darken quickly if dampened either by being attached to wet surfaces or by being exposed to moist air. Within five minutes they turn to a light tan color and fifteen minutes later they are brown. No further color change occurs during the development of the embryo. On the other hand, eggs that are completely submerged in water immediately after they are laid, darken slowly. After 24 hours they are only slightly colored and within the next few days, they become cream colored.

Eggs of Hydrometra martini vary between 1.8 and 2.2mm long and between 0.20 and 0.22mm wide when they are laid. The length does not change but the width increases notably during development. During the third day of incubation (at 25$^{o}$), the eggs expand to their maximum diameters; some reach

0.28, others only 0.25mm. The size of the egg remains constant from this time until it hatches.

Development

Some features in the development of the embryo can be seen in living hydrometrid eggs and can be followed only if the eggs are moist enough to be translucent. Eggs for this study were incubated at 25° in stender dishes lined with moist towelling paper.

The first change that can be seen as the living embryo develops is the appearance of small red eye spots on the third day after the egg is laid. These are near the posterior end of the egg where they remain for four to eight hours (fig. 65). During the next two hours blastokinesis or inversion of the embryo, occurs and the eyes shift to the apical part of the egg (figs. 66, 67 and 68). The eyes remain in this position, enlarging rather gradually for the next five days (figs. 69 through 73). The egg burster, a conspicuous black cross between the eyes, becomes apparent on the 8th day. On the 8th and 9th days, the margins of the embryonic cuticle surrounding the labrum begin to darken (figs. 70 and 71). By the eleventh day, the labrum is clearly outlined and the appendages of the head and thorax are pigmented enough to be seen (fig. 73). The antennae and first and second pairs of legs extend posteriorly and then loop upwards on the embryo's left side before they continue backward. The antennae and beak lie ventral to the legs. The claws of the first and second pairs of legs are close together posterior to the tips of the antennae. The metathoracic legs extend caudad almost to the end of the abdomen, and then bend upward on the opposite side so that the claws are lateral.

Some of the eggs incubated at 25° hatch on the 11th day, some on the 13th and a few on the 14th, but the highest percentage hatch on the 12th day of incubation. Table 3 gives data on eclosion of 68 eggs laid on July 22, 1950, by wingless hydrometrids in the laboratory. About 70 per cent hatched on the 12th day and 17 per cent on the 13th day of incubation. Eleven other eggs laid on July 22nd failed to hatch. Of these, five did not show any signs of development and may have been infertile. Three failed to complete blastokinesis, and in each the eyespots and egg burster developed in abnormal positions. Three other embryos, which had appeared to be normal, turned black without beginning to emerge.

Table 3. Hatching of 68 eggs laid by wingless hydrometrids on July 22, 1950 and incubated at 25°.

|  | Date of hatching |  |  |  |
|---|---|---|---|---|
|  | 8/2 | 8/3 | 8/4 | 8/5 |
| Number | 6 | 48 | 12 | 2 |
| % of total | 8.8 | 70.6 | 17.6 | 2.9 |

Of the 50 eggs collected in the field on July 28 and July 30, 1950, only three failed to develop. The others hatched between July 31st and August 9th.

Hatching

The hatching of a hydrometrid egg follows a fixed pattern. Table 4 is a time schedule of the procedure in a series of five nymphs which hatched on the morning of August 5, 1949. These eggs of unwinged adults were laid in the laboratory on July 24th and were kept on moist towelling paper. The process of eclosion is essentially the same in eggs which are submerged or rest on the surface film.

The young hydrometrid begins the hatching process by sucking in the fluid within the egg shell. With the increased pressure from the enlarging animal, the egg burster moves against the chorion and splits it. The vertical part of the egg burster is knife-like, hard and slightly raised from the surface of the rest of the embryonic cuticle. The nymph pushes its head through the slit in the egg shell until the inner margins of its eyes begin to show. It continues sucking and swallowing the fluid still surrounding it within the chorion. Within six minutes of the time the chorion splits, the eyes are half exposed (fig. 74). Then it is completely quiet for four to seven minutes. As air replaces the fluid within the chorion, the continued sucking brings bubbles of air into the digestive system. Within the next minute the nymph pushes its head outward, frees its labrum and thrusts its thorax out of the chorion (figs. 76 and 77). It then continues to extend its its body from the egg shell by movements in a dorso-ventral plane. As the nymph arches its body, it lifts its head, holding its antennae and beak rigid (fig. 78). Straightening the body, it bends its head down (fig. 79), pushes the thorax out, unfolds and draws out its legs. The tarsal segments and the tips of the antennae and beak as well as the end of the abdomen remain in the chorion and support the rest of the body. With its body perpendicular to the egg shell, the nymph rests and completes the process of filling its entire abdomen with air.

By muscular contractions that start in the metathorax and pass forward to the base of the head, the nymph now increases the pressure on the embryonic exuviae and these break along the conspicuous dark sutures of the head (fig. 80). The animal pushes its head out of the embryonic cuticle rapidly, the egg burster and the membrane attached to it pass backward over the thorax, the bases of the legs and the abdomen, (figs. 81 and 82) and within three minutes frees its legs. During this process, the femora bend at a number of points as well as at the articulations. After it extricates its last leg, the nymph pulls the antennae and labium out. The tip of the abdomen remains for a short time within the molted skin and within the chorion. This anchor gives support to the nymph while it struggles to bring its feet into contact with a surface. When the animal begins to walk, it finally pulls the abdomen free.

The hatching process takes between 20 and 30 minutes. If eclosion is prolonged or if any part of it is out of proper sequence, the nymph dies. Death may occur at the beginning of hatching or when the nymph has started to molt its embryonic cuticle. But the greatest number of

Table 4. Intervals of time in minutes taken in eclosion by 5 *Hydrometra martini* nymphs on August 5, 1949.

| Activity | | | | | |
|---|---|---|---|---|---|
| First split | | | | | |
| "Egg burster" exposed | 1 | 1 | 1 | 1 | 2 |
| Inner margin of eye exposed | 3 | 2 | 4 | 2 | 1 |
| Half of eye exposed | 2 | 2 | 2 | 1 | 2 |
| Eyes entirely exposed | 6 | 5 | 4 | 4 | 7 |
| Labrum freed | 1 | 1 | 2 | 1 | 1 |
| Thorax entirely exposed | 1 | 3 | 1 | 3 | 4 |
| Exuviae split | 2 | 3 | 2 | | |
| Head and thorax out of exuviae | 2 | 3 | 3 | 3 | 1 |
| 1st leg freed of exuviae | 1 | | | | 3 |
| 2nd and 3rd leg free | 2 | 2 | 1 | 1 | 1 |
| Antennae free of exuviae | 2 | 1 | 1 | 1 | 2 |
| Legs on support | 1 | 2 | 1 | 2 | |
| Abdomen lifted from exuviae | 3 | 2 | 1 | 2 | 2 |

fatalities comes as the nymphs free themselves from the chorion. The legs are hopelessly caught if they do not molt before the labium and antennae do.

A hydrometrid hatching from an egg floating on or immediately under the surface of the water lifts its head above the surface film so that it swallows air. The chorion, lying parallel to the water, acts as a platform until the nymph can lower its legs to the surface film and walk away.

When a nymph emerges from a completely submerged egg, it sucks in water instead of air to distend the digestive system. A nymph can live only an hour under water; after that its exoskeleton becomes permeable and the tissues become hypotonic. A nymph which approaches the surface with one side uppermost cannot lift its body for most of its movement is parallel to the film.

Any nymph which maneuvers in such a way that its dorsum comes in contact with the surface film quickly raises itself out of the water. For an instant it lies with its body outstretched, the first and second pairs of legs extending diagonally forward, its hind legs stretching parallel to the abdomen. First it lifts its head and antennae out of the water, next its thorax, then its first and second pairs of legs and finally its abdomen and hind legs. Then it dries its appendages by lifting them in the air and by rubbing the various parts together.

## Discussion of the egg stage

The eggs of _Hydrometra_ have been described and illustrated by a number of workers. The earliest description of a hydrometrid egg was that published in 1855 by Leuckart whose careful drawing showed the basal shaft with the attachment disc as well as the micropyle. Some of the information from the literature on the eggs of three species of Hydrometra is summarized in Table 5.

Table 5. Summary of information on hydrometrid eggs in the literature

| Species | Author | Length in mm | Width | Color |
|---|---|---|---|---|
| H. stagnorum | Brocher ('11) | 1. | - - | grayish, opaque |
| | Jordan ('31) | 1.66 | .25 | white when laid; yellow-brown later |
| | Schumann ('34) | - - | - - | dark brown |
| H. gracilenta | Jordan ('31) | 1.5 | .23 | yellow |
| H. martini | Martin ('00) | 2.0 | - - | - - - - - - - |
| | Hungerford ('20) | 2.07 | .277 | white when laid; brown later |

The eggs of Hydrometra stagnorum are less elongate but otherwise similar to those of H. martini. Some illustrations in the literature, like that of Leuckart (1885), show a basal shaft only slightly shorter than that of H. martini, but others (Tevrovsky, 1920, Schumann, 1934) indicate a short base. Brocher (1911) pictured and described an egg in which the basal air cells are broken and referred to the egg as being mobile as the clapper of a bell. This part of his description, as well as his figure showing longitudinal grooves within an oval outline, were criticized by Jordan (1931). The illustration of the egg by Jordan shows deep grooves arranged longitudinally and oval granules at either pole. Schumann (1934) indicated grooves extending from one end of the egg to the other, and a little papilla near the micropyle. Tevrovsky (1920) included two drawings of the egg of H. stagnorum, one of its external appearance and one as it looked after being cleared in cedar wood oil. The latter shows the micropylar tube and the basal shaft, which in this drawing is very short. The egg of H. gracilenta, which was described by Jordan (1931), was not illustrated.

The drawing of the egg of H. martini by Martin (1900) is well known because it has been used in text books (Comstock, 1936, Wesenburg-Lund, 1943). As he mentioned in his text, Martin overemphasized the hexagonal pattern at the expense of the longitudinal furrows. Hungerford (1920) showed these clearly in his figure. His photographs of hydrometrid eggs with sprouting cattail seeds showed their similarity to one another.

The considerable variation of colors mentioned in the descriptions of the eggs of each species correlates with the actual differences in eggs of a large series. Eggs of H. martini, which are grayish and iridescent when they are dry, become a dark or light brown when they are wet. That newly laid eggs are white and that they darken quickly was mentioned by Hungerford (1920) and by Jordan (1931).

Poisson (1924) stated that eggs of a variety of water bugs are white when they are laid and that a secretion of the reproductive tract is responsible for their darkening. This is certainly true of the eggs of H. martini. The change in color must be the result of an interaction of the secreted substance with air and water since all three are necessary for the color. Eggs dissected from the female do not darken, those which are submerged as soon as they are laid darken slowly and those kept dry do not change color at all.

*Hydrometra stagnorum*, as well as *H. martini*, lays eggs on any convenient object. Jordan listed a large number of plants on which he found eggs and both he and Schumann (1934) described eggs being laid on the sides of containers in the laboratory. Bueno (1905) found the aquarium in which he kept two female hydrometrids studded with eggs by the end of the summer. Both Martin (1900) and Hungerford (1919) said that the females placed eggs on any firm object. Jordan (1931) found the eggs always laid high above the water surface on dry leaves but he did not discover any on Nymphaea or on emergent reeds. Brocher (1911) however collected hydrometrid eggs on floating vegetation and debris; all of these were covered with water or resting on its surface. Takahashi (1921) working with a Japanese species stated that these insects deposited their eggs on grass or twigs on the water, but that the eggs were often found under water.

The length of the developmental period varies considerably. According to Arrow (1895), eggs of *H. stagnorum* laid on May 23, hatched three weeks later. Schumann (1934), working with this species, found nymphs on June 11th which had hatched from eggs laid on May 29.

Martin (1900) gave 17 days as the developmental period for H. martini. According to Hungerford (1920), eggs laid in May took 23 days to hatch while those laid in July hatched after only seven days. Bueno (1905) noted that embryonic development took nine to ten days in midsummer.

Hungerford (1920) in Kansas in July and Bueno (1905) on Staten Island, New York in summer, found the incubation period to be less than 11 days. The temperatures probably were higher than 25°. The incubation periods observed by me were 11 to 13 days.

Of the numerous authors who have worked with Hydrometra, only Hungerford (1920) has discussed the hatching process in detail. He described the bulging of the head with the eyes and the egg burster appearing, the pushing of the body at right angles to the shell followed by the breaking and shedding of the embryonic cuticle and finally the unfolding of the appendages. He provided three figures - two of the emergence of the head and the other of the exuviae.

Brocher (1911), who referred to the role of the egg burster and the post-natal molt in H. stagnorum, included a drawing of the shed cuticular skin caught in the opening of the egg shell. Schumann (1934) observed a nymph of this species escape from its shell and mentioned that the process took 5 minutes. His figures are of the late stages of hatching. In each, the egg is on its side and the emerging nymph is twisted with its head close to the base of the egg. With H. martini, this does not occur. Schumann also showed a torn opening in chorion rather than a simple slit which has been described by other investigators.

Takahashi (1921) described the hatching of *Hydrometra vittata* (probably = *H. albolineata*) from submerged eggs. This species seems to be better adapted to life underwater than *H. martini* for none of the animals he observed died underwater or while emerging from it. The nymphs that hatched under water walked or swam until they came to rest with their backs against the surface film. A nymph in this position bent its head and abdomen until it had lifted its head above the water. Then the thorax, first and second pairs of legs and finally its hind legs and abdomen were raised. This procedure is essentially the same as that followed by the successful nymphs of *Hydrometra martini*.

## The Activities and Structure of the Nymph

### Activities of nymphs

The bright red eyes of the hatching hydrometrid nymph are conspicuously set off by the paleness and delicate green of its head and body. Its legs and antennae are transparent. The abdomen is expanded and through the translucent body wall the anterior part of the ventriculus can be seen filled with air. At this time the nymph is 1.5mm long. If the nymph is undisturbed, it will remain close to the egg shell from which it hatched. However, if it is disturbed, it can easily walk or run. Within 15 minutes after hatching, the abdomen contracts, forcing the air from the gut of the abdominal region into that of the second and third thoracic segments. The contracted abdomen appears a darker green and, by this time, there is a darkening of the legs and head. The body-length decreases to about 1.2mm.

Before the nymph is an hour old, it lowers its rostrum to the moist substratum to obtain water. The stylets extend beyond the tip of the last labial segment and water is pumped up through them by the muscles of the head. The fluid passes into the pharynx and through the narrow esophagus into the ventriculus. The first water that enters the stomach seems to absorb the air there so that after the animal has been drinking for 10 minutes or so, the size of the air bubble is greatly reduced. Peristaltic contractions of the wall of the gut, some of which start anteriorly and others, posteriorly, churn the contents.

When food is available, the nymph may begin to eat about an hour and a half after it has hatched. Some nymphs observed in the laboratory, however, did not feed for as long as 12 hours after hatching although food was available. When the nymph begins to eat, the juices of the prey pour into the ventriculus and mix with the water there. After 24 hours, the curved posterior ventriculus which lies in the abdominal segments is distended with dark residual substances. An animal to which food and water is available stretches out to about 1.6mm, nearly its maximum length.

The locomotion and feeding of first instar nymphs, as well as those of the older nymphs, are essentially those of the adults. They walk on the surface film, on damp earth or on vegetation, their antennae swaying from side to side. The nymphs continually groom their appendages and display the up and down movement characteristic of the adults. The flexibility and longitudinal intersegmental muscles of the abdomen make possible its curvature; nymphs often carry the posterior end of the abdomen arched over the body.

Submerged nymphs regain the surface rather quickly. Such an animal swims up so that its back makes contact with the surface film. By flexion of the head and prothorax, the anterior part of the body, including the forelegs, breaks through the film. The nymph then swims until it reaches an emerging leaf or other support, and crawls up on it. If no suitable substrate is available, the nymph arches its back, pushes its forelegs close together to raise the thorax until the middle legs and finally the hind legs and abdomen are elevated. Since hydrometrid nymphs are usually near land and hurry to it when they are disturbed, complete emersion probably is not a frequent occurence.

In the laboratory, hydrometrids which are not isolated have a strong tendency toward cannibalism throughout their nymphal stadia. Hatching nymphs may be devoured by others which have emerged only a short time before. The victims are not necessarily the weaker animals; unwary nymphs of the fourth and fifth instars may be eaten by smaller nymphs. As with the adults, subsurface Entomostraca and other small animals form the chief food sources, but any sort of recently-killed or slow-moving living insect may be used as food. Nymphs, carrying midges or ostracods with their beaks, walk on the surface film. In the present study, nymphs in the field were not seen to feed on organisms too large for them to carry, but in the laboratory they fed on flies such as <u>Musca</u> and <u>Drosophila</u>.

The interval between molts is highly variable even in series of animals kept under similar laboratory conditions. Table 6 presents the data for a series of animals reared in the laboratory during the summer of 1949. Nymphs hatching from eggs laid from June 28th to July 8th were isolated and kept in stender dishes lined with paper towelling. Each animal was fed one or more fruit flies a day and the exuviae were removed as they appeared.

Table 6. Record of intervals in days between molts of Hydrometra martini in the summer of 1949.

| No. | Egg Laid | Nymph hatch | 1st molt | 2nd molt | 3rd molt | 4th molt | 5th molt | Sex | Length of development in days |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 6/28 | 15 | 3 | 2 | 3 | 4 | 5 | o | 32 |
| 2 | 6/30 | 13 | 4 | 3 | 3 | 4 | 4 | o | 31 |
| 3 | 6/30 | 13 | 3 | 3 | 4 | 3 | 6 | o | 32 |
| 4 | 7/1 | 8 | 4 | 4 | 2 | 2 | 4 | o | 24 |
| 5 | 7/1 | 8 | 5 | 3 | 3 | 2 | 4 | o | 25 |
| 6 | 7/1 | 8 | 5 | 3 | 2 | 5 | 4 | o | 27 |
| 7 | 7/1 | 8 | 6 | 2 | 3 | 5 | died<br>- | o | - |
| 8 | 7/6 | 8 | 3 | 2 | 2 | 3 | 4 | o | 22 |
| 9 | 7/6 | 8 | 2 | 3 | 3 | 2 | 4 | o | 22 |
| 10 | 7/6 | 8 | 3 | 3 | 2 | 2 | 4 | o | 22 |
| 11 | 7/8 | 9 | 3 | 2 | 2 | 3 | 3 | o | 22 |
| 12 | 7/6 | 8 | 3 | 2 | 2 | 3 | 4 | o | 22 |

As a nymph approaches the time of molting, it reaches nearly maximum length for its instar. The pigmentation of the cuticle, which gives a grayish cast to its exoskeleton, is lacking along the ecdysial line which extends in the mid-line from the metathorax anteriorly to the middle of the head where the ecdysial line forks and forms an arm on either side of the frontal region.

In the hour before molting, the nymph imbibes water more frequently than before. As the gut is distended, the nymph becomes a little longer than it had been previously and its entire body appears turgid. As water is taken in, small droplets of fluid are emitted through the anus. During the early part of the period, the animal walks about as much as usual. Then it becomes less active; if it is undisturbed it moves but little, although it continues to imbibe water.

The actual molting process takes place rather rapidly. For a minute or two, the nymph seems to be inactive. Then it resumes the intake of water and moves backward as it lowers its body. It pushes its hind legs into the substrate, arranging them so that they are parallel with the long axis of the abdomen. The middle legs are planted firmly at right angles with the body and the front legs extend forward.

When the nymph has placed its legs securely, it lifts its body and starts to suck air rather than water. As the sucking continues, the cuticle of the mesothorax begins to cleave. The head bends so much that the antennae almost touch the front legs. Air, in small bubbles, passes through the narrow esophagus into the ventriculus. With the distention of the digestive tube, the body lengthens. Alternate waves of contraction and dilation move up and down the body.

Since the head is bent ventrally, the prothorax is the most anterior part of the body at this time. With the posterior end close to the supporting surface, the long axis of the body forms an angle of about 45° with the substratum. As the body stretches upward the proximal parts of the legs emerge from the exuviae and begin outward movements, which help to pull the trunk forward. First the prothoracic and then the mesothoracic and metathoracic legs pull away from the exuviae. The legs touch the substrate; the antennae and finally the beak pull free. The nymph begins to walk away and the tip of the abdomen slides out from the molted skin.

The color of recently-molted hydrometrids resembles that of the hatching nymphs. The body is pale green and the appendages are transparent. There is a touch of red on the pleura of the mesothorax, metathorax and, in the region of the spiracles, on the abdominal segments. The brownish contents of the posterior ventriculus make it distinct. The abdomen of fifth instar nymphs is marked by an opaque white mid-dorsal stripe and two more translucent lateral lines. The lora are white and conspicuous.

Within thirty to forty-five minutes a recently molted nymph again begins to suck up water. When food is available, the nymphs begin to feed about two hours after they have molted.

## Growth and Differentiation

The increases in size of the head, beak, body and appendages progress at rather constant rates with each nymphal molt (Table 7, fig. 1). The total body length increases most rapidly, especially after the third and fourth molts. Of the structures measured, the width of the head increases most slowly. The relative length of the beak decreases in the older instars. In the first instar nymphs it reaches to the mesothorax and in the adult, only to the middle of the head. The lengths of the head, the antennae, and the legs increase at about the same rates; the increment is smaller in the early molts than after the fourth and fifth molts.

The remarkable variation in the total body-length during a nymphal stadium is the result of a partial telescoping of the abdominal segments and depends mainly upon the degree of distension of the digestive system (cf. figs. 82 and 83). The minimum length, which is approximately that of the maximum in the previous instar, is reached about an hour after the molt is completed. At this time the air which filled the digestive tube during the molt has not been replaced by water or food. Later in the stadium, if the nymph does not maintain a distended gut by feeding frequently, the body length may decrease again. Of the nymphs taken in the field, most had bodies of nearly maximum length. Food seems usually to be available to them there.

## Table 7

Measurements of nymphs of Hydrometra martini in millimeters. (Average of 10 animals)

|  | Head |  | Antennal length | Leg length |  |  | Total body length (interval after hatching) |  |  | Beak length |
|---|---|---|---|---|---|---|---|---|---|---|
| Instar | length | width |  | 1 | 2 | 3 | immed. | 1 hr. | 2 days |  |
| 1 | 0.5 | 0.17 | 1.4 | 1.2 | 1.3 | 1.8 | 1.5 | 1.2 | 1.6 | 0.7 |
| 2 | 0.7 | 0.18 | 1.8 | 1.7 | 1.8 | 2.4 | 2.1 | 1.5 | 2.3 | 0.9 |
| 3 | 1.0 | .2 | 2.2 | 2.1 | 2.2 | 3.3 | 3.0 | 2.3 | 3.3 | 1.1 |
| 4 | 1.3 | 0.22 | 2.7 | 3.2 | 3.6 | 4.6 | 4.2 | 3.1 | 4.6 | 1.5 |
| 5 | 2.0 | 0.3 | 3.4 | 3.6 | 4.2 | 6.3 | 6.2 | 5.1 | 6.5 | 1.7 |
| adult | 2.8 | .4 | 4.0 |  |  |  | 8.0 | - | - | 2.2 |

Figure 1

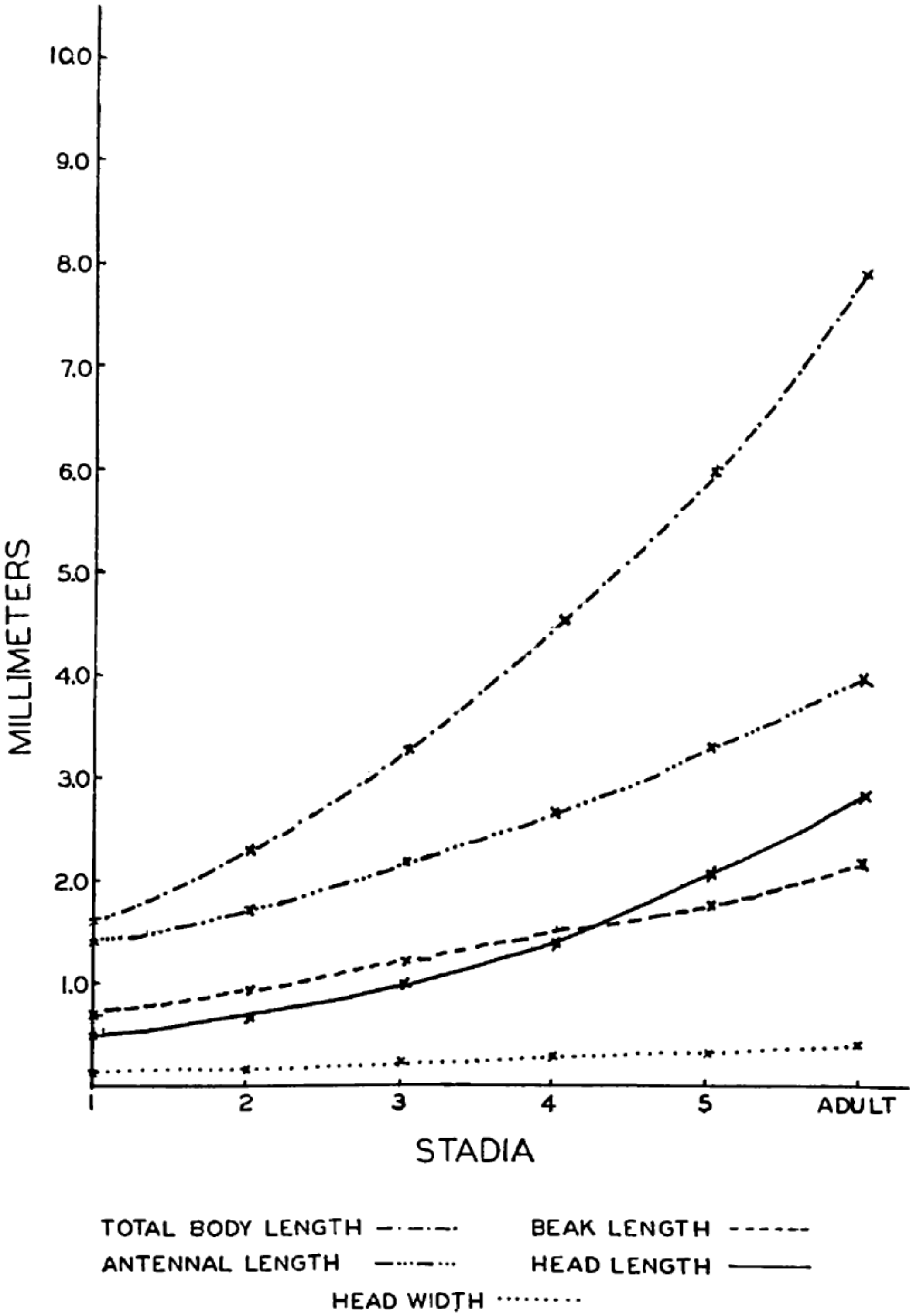

Fig. 1. Graph showing measurements of nymphs and adults of Hydrometra martini in millimeters. Each figure represents the average of 10 animals. In the 4th and 5th instars and in the adult stage, only males were used. (Data are presented in Table 9.)

The nymphal head, like that of the adult, shows little differentiation into sclerites. The dorsal and lateral parts are more heavily sclerotized and more deeply pigmented than is the ventral part. In the later instars the ventral surface becomes increasingly setose. The prominent setae, a pair near the posterior end of the head and a pair lateral to the anteclypeus, remain constant in position.

In the first and second instars (figs. 85 and 88) the lora and maxillary plates are difficult to see. During the later stadia, the maxillary plates are white and conspicuous. Their ventral projections, the bucculae, appear in the fourth instar nymphs as narrow rims which are directed anteriorly (fig. 93). In the fifth instar these lobes are larger (fig. 102) but they do not cover the basal segments of the rostrum, until the final molt.

The proportions of the head change with successive molts (table 8, fig. 2). The eye increases in size at a very slow and regular rate. The preocular part of the head increases much more rapidly than the postocular part from the first through the fifth instars. The ratio of the preocular to the postocular length is 1.43:1 in the first instar, 1.86:1 in the fifth instar and 1.83:1 in the adult. Within the preocular region, the length between the part containing the mandibular protractors and the eye increases most (cf. figs. 83, 87, 91, 94, 101).

Table 8. Comparisons of the sizes of the eye, and the preocular and postocular portions of the head of Hydrometra martini nymphs and adults. Each figure represents an average for 10 animals in millimeters.

| Instar | 1 | 2 | 3 | 4 | 5 | adult |
|---|---|---|---|---|---|---|
| Preocular | 0.25 | 0.35 | 0.53 | 0.71 | 1.19 | 1.65 |
| Eye | 0.07 | 0.1 | 0.125 | 0.14 | 0.17 | 0.2 |
| Postocular | 0.18 | 0.25 | 0.35 | 0.45 | 0.64 | 0.95 |
| Total length | 0.5 | 0.7 | 1.0 | 1.3 | 2.0 | 2.8 |

Figure 2

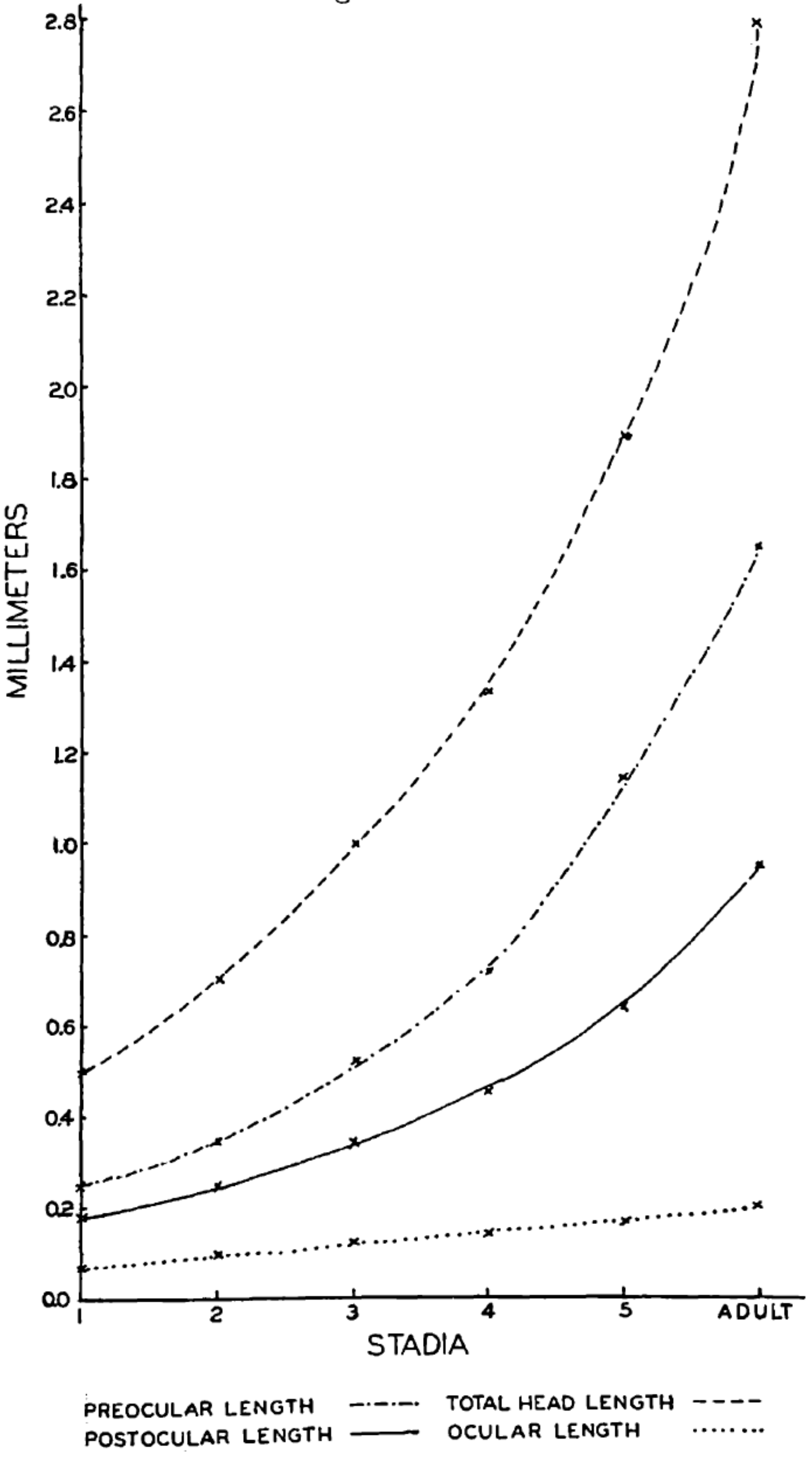

Fig. 2. Graph showing measurements in millimeters of the head, the eye, and the preocular and postocular parts of the head in nymphal and adult *Hydrometra martini*. (Data are presented in Table 10.)

The thorax of the hydrometrid nymph shows much less fusion than that of the adult. In the first instar, the tergum of each segment is a rather flat broad plate (fig. 83). In the second instar the posterio-lateral angles of the mesotergum and metatergum are produced, indicating the formation of wing pads (fig. 87). The metatergum is much smaller than the mesotergum in the third instar nymphs (fig. 91). The wing pads of those individuals which will become macropterous are much more conspicuously developed than those of animals which will give rise to apterous adults (cf. figs. 110 and 111 with figs. 89 and 91). These differences are emphasized in the fourth and fifth instar nymphs. In the fourth instar nymphs, the wing pads reach the second abdominal segment; those of the metathorax are slightly longer than those of the mesothorax (figs. 112 and 113). The metathoracic wing pads of the fifth instar nymph extend to the middle of the third abdominal segment and the mesothoracic wing pads are slightly shorter (figs. 114 and 115). The mesothoracic wing anlage of the fourth instar nymphs which will become apterous adults extend over the bases of those of the metathorax (fig. 94). In the fifth instar the wing pads of the metathorax are not developed further, but those of the mesothorax extend posteriorly as broad lobes (figs. 101 and 102). The posterior lobe of the pronotum develops gradually; in the fourth instar it projects over the anterior margin of the mesonotum (fig. 94) and in the fifth over about a third of it (fig. 101).

The episternum and epimeron are of about the same size in the prothorax and mesothorax of the first instar (fig. 85). During the succeeding stadia, the proepimeron and the mesepisternum increase in size more, relatively, than do the proepisternum and the mesepimeron, so that in the fifth instar there are marked differences (cf. figs. 85, 89 and 102). In all of the nymphs, the metepimeron is a small posterior lobe, set off by a suture from the metepisternum. The latter lengthens the most rapidly of any part of the thorax and by the fifth instar extends toward the mid-dorsal line. The supracoxal lobes develop gradually and even in the fifth instar nymphs are relatively small. The legs of all nymphs articulate with two processes, one near the plural suture and one on the sternum (fig. 103).

The thoracic spiracles lie in the membrane between the prothorax and mesothorax and in that between the mesothorax and metathorax in the first, second and third instars (figs. 85, 88, 89). In the fourth and fifth the second spiracle becomes associated with the posterior part of the mesepimeron and the first, with that of the proepimeron (figs. 93 and 102).

The abdomen of the first and second instar nymphs is marked by intersegmental lines which are especially noticeable if the abdomen is contracted. The spiracles of the first segment are more dorsal than those of the second through the eighth segments (figs. 82 and 86). The tenth segment is separated from the ninth by a ventral groove (figs. 84 and 88). The dorsal surfaces of the seventh, eighth and the terminal segments bear more heavily sclerotized setose plates. In the third and succeeding instars, the dorsal intersegmental boundaries are marked by dark lines (fig. 91). Well developed intersegmental muscles run between these dark lines on the dorsal body wall and between the ventral intersegmental lines, indicating that these lines mark the primary segmentation of the abdomen.

Differentiation of the external genitalia begins to become apparent in the fourth instar. In the female, a small dorsal projection of the eighth tergum extends over the reduced ninth segment and the proctiger (figs. 98 and 99). A pair of lobular sclerites represent the sternum of the ninth segment (fig. 100). In the female fifth instar nymph the dorsal projection of the eighth tergum is larger (figs. 104, 106); ventrally the sclerotized plates which are the anlage of the first valvifers of the adult female, are joined by a membrane. The ventral sclerites of the ninth segment are partially covered by the eighth segment (fig. 105).

In the male fourth instar nymphs, the eighth abdominal tergum also has a dorsal projection (figs. 95 and 96). Caudad to this the terminal segments are differentiated, forming a dorsal sclerotization which will become the proctiger and a ventral sclerotization, the anlage of the genital capsule (fig. 97). In the fifth instar nymph, tergal projection at the eighth segment is relatively longer but not as long as the proctiger. The genital capsule is larger (fig. 108) and the ninth tergum appears as a dorso-lateral lobe (figs. 107, 109).

Discussion of the nymph

Although several papers consider the nymphal instars of Hydrometra stagnorum, comparatively little work has been done on the post-embryonic development of H. martini. The nymphs of only two other species are mentioned in the literature, those of H. vittata (= H. albolineata) by Takahashi (1921) and those of H. gracilenta by Jordan (1931).

The first description of the complete life history of a hydrometrid was that of Hungerford (1920). Working in Kansas, he found that the nymphal stadia lasted on the average two days, with some taking three to four days. Jordan (1931) found that the nymphal stadia of H. stagnorum lasted from four to six days. The average length of the instars of 11 H. martini nymphs reared in Michigan in the summer and reported in Table 8 is 3.2 days, with variations of two to five days. In these animals, the first and last stadia were, on the average, longer than the others. The rapid post-embryonic development of H. martini reported by Hungerford probably is correlated with the warm Kansas temperatures. There is great variation, however, not only in the length of time of development (from egg to adult) of the various individuals, but also in the period that each nymph spends in the different instars.

In an earlier paper Bollweg (1915) described only four nymphal instars in Hydrometra stagnorum, but Tevrovsky (1920) and Lundblad (1921a, 1921b) as well as Jordan (1931) found five nymphal instars.

By far the most detailed description and drawings of the hydrometrid nymph are those of Lundblad (1921a, 1921b), who was particularly interested in the proportional growth. He found that the lengthening of the head, which had also been mentioned by Arrow (1895), was especially the result of growth of the "präokularen parallelseitigen Partie". In *H. martini*, also, this region grows most rapidly (see Table 10, fig. 2). Jordan (1931) found, however, that this region is less elongate in nymphs of *H. gracilenta* than in those of *H. stagnorum*.

The observations made by Lundblad (1921b) on the development of the wing pads in the apterous form were also confirmed in the present work. In both species, these are apparent first in the second and third instar nymphs as slightly produced corners of the terga. In the fourth instar these tergal angles are differentiated as wing pads and in the fifth continue to elongate. Lundblad did not include descriptions of the nymphs of the winged form, nor has any subsequent paper.

Lundblad was concerned also with the segmentation of the abdomen. He identified nine segments including the first which Bollweg (1915) seems not to have found in the late instars because of the overgrowth of the metathorax and small size of the first segment. Lundblad mentioned the sclerotization of the dorsal plates of the terminal abdominal segments but he did not consider the differentiation of the external genitalia.

One of the most interesting features in the development of the hydrometrid nymph is the extreme variation in the total body-length. This was recognized by Hungerford (1920) who used the length of the animal from the tip of the head rather than the length of the body as a criterion for the recognition of the various instars. The lengths of the appendages, which were tabulated by Lundblad for *H. stagnorum* and by Hungerford for *H. martini*, are constant throughout each stadium. The body-lengths of the nymphs of *H. stagnorum* as given by Jordan and Lundblad, both of whom found that this measurement varied during each stadium, are presented in table 9. The measurements given by Bollweg (1915) are also included. Since the instar which he omitted from his description was obviously the second, the measurements are arranged accordingly.

None of these investigators correlated the differences in size in a given stadium with the expansion of the abdomen which results from distention of the gut with air or food and water. Both Tevrovsky (1920) and Lundblad (1921a) figured first instar nymphs with extremely contracted abdomens. In *Hydrometra martini*, the abdomen is of minimum size approximately a half hour after eclosion and later in the stadium if the nymph does not eat or becomes dry. The larger size of adult females was mentioned by Jordan (1931) but he did not correlate variation of size of the nymphs with sex.

The head and appendages in successive instars of *Hydrometra* demonstrate allometric growth, that is, "growth of a part at a different rate from that of the body as a whole or of a standard" (Huxley and Tessier, 1936, p. 380). This pattern of growth is usual in insects.

The similarities in behavior, locomotion and feeding habits of the nymphs to those of the adults which are reported in the present study in general confirm the observations of other investigators. Arrow (1895) stated that nymphs reared in the laboratory fed only on springtails until the last instar when they took aphids. Hungerford (1920) observed that the nymphs as well as the adults eat entomostracans and a variety of insects, including weaker hydrometrids. Both Jordan (1931) and Schumann (1934) also mentioned cannibalism.

Investigators working with both *Hydrometra stagnorum* (Arrow, 1895, Jordan, 1931, Schumann, 1934) and *H. martini* (Martin, 1900) have found that the nymphs stay closer to land and are more susceptible to drowning than are the adults. On the other hand, Takahashi (1921) described the nymphs of *H. vitatta* (= *H. albolineata*) as swimming under the water and crawling from it to the surface film. Certainly, under laboratory conditions, *H. martini* nymphs are capable of this type of locomotion.

Two curious habits of the nymphs, the elevation-depression movements which were observed also in the adults and the carrying of the abdomen curved over the back, have been noted by Schumann (1934) and Jordan (1931).

Table 9. Measurements of nymphs of <u>Hydrometra stagnorum</u> in millimeters.

| Instar | Bollweg | Lundblad | Jordan | Tevrovsky |
|---|---|---|---|---|
| I | 2.0 | c 1.0 | 1.5-1.8 | 1.6-2.0 |
| II | --- | c 2.0 | 2.4 | 2-4 |
| III | 2.5-3.2 | c 3.0 | 3.5 | 1.5-5.5 |
| IV | 3.7-4.1 | c 4.5 | 5.4 | 5-7 |
| V | 5.0-7.1 | c 6.0 | 7.5 | 7-9 |

## Dimorphism

### Observations

Dimorphism in Hydrometra martini is evidenced by two patterns of wing development; an apterous form which has vestigial wing pads projecting just beyond the pronotum and a macropterous form in which the two pairs of wings extend beyond the middle of the sixth abdominal segment. In the field, the adults of these categories are differentiated easily and the wing pattern of the fourth and fifth instar nymphs can be identified with good light. Third instar nymphs have been separated only with the aid of a binocular microscope.

Hydrometrids with long wings are scarce and those without wings are abundant in both Massachusetts and Michigan. In the four summers in Michigan, an average of about six adults or nymphs of the macropterous form were taken whereas hundreds of apterous animals were seen. The ratio was perhaps one winged to 100 or more wingless hydrometrids. In Massachusetts a higher percentage of winged forms were collected; it was estimated that one in 45 was macropterous. In the autumn of 1950, collections at the Lithia pond yielded a ratio of about one winged individual to ten of the wingless type. At that time, the pond had little water and the animals including the hydrometrids, were concentrated. Twenty-seven winged forms were taken.

Apterous and macropterous males and females have been collected through the year. At least four mating pairs of which one individual was winged and the other wingless have been collected in the field. In the laboratory they mate readily and produce fertile eggs.

Studies in the laboratory have been directed toward gaining an understanding of the cause of development of long wings in some individuals and of only vestiges in others. In the summer of 1949, a series of nymphs, 26 of which lived to or beyond the fourth instar, were reared from eggs of apterous females crossed with apterous males, under constant light with a temperature of about 30°. All of the 26 individuals which lived to or beyond the fourth instar were apterous. In the summer of 1950, a group of similar nymphs were reared at 30° in a constant temperature oven. The glass door of this incubator allowed normal daylight to enter. The 31 animals of this series were also wingless. Of the hundreds of nymphs reared from eggs of apterous individuals under normal laboratory conditions during all seasons of the year, none were macropterous.

Offspring of other crosses (winged ♀ x winged ♂, wingless ♀ x winged ♂, winged ♀ x wingless ♂ ) have been reared in the laboratory. Since female hydrometrids store sperm for long periods of time, only those which emerged from isolated fifth instar nymphs or teneral individuals were used. Winged females produced fewer eggs and were shorter lived in the laboratory than wingless individuals. Because of the small numbers of animals, the results of my studies are not conclusive but they suggest that some form of inheritance governs wing form. These results are as follows:

winged ♀ x wingless ♂ gave 16 wingless offspring; wingless ♀ x winged ♂ gave 9 wingless offspring; winged ♀ x winged ♂ gave 21 offspring of which 19 were wingless and 2 winged.

Some information on the distribution of winged and wingless forms of Hydrometra martini has been assembled from the series in the Snow Entomological Museum at the University of Kansas. Of the 277 insects of this species, taken from 11 localities in Florida, in July and August of 1930, 54 or 24.2 per cent were winged. The collection includes also 140 specimens taken from three localities in Kansas in the autumns of 1924, 1925 and 1926, of which 3 or about 2 per cent are macropterous. A third series of 104 hydrometrids taken from Sedge Point Pool, Douglas Lake, Michigan in June and July of 1923 is made up of 101 apterous and 3 or approximately 3 per cent of macropterous individuals.

## Discussion

The presence or absence of wings, as well as variations in their length, has been of interest to investigators of many groups of Pterogota. In relatively few species are the causes of these variations well understood. Poisson (1946) summarized the problem of apterism in the Hemiptera. Ford (1940) reviewed polymorphism and taxonomy of insects.

In an earlier review article, Larsen (1930) discussed the loss of flight by reduction of wing musculature and also variation in types of wings found in the aquatic and semiaquatic Hemiptera. Of the insects in these groups, the mechanism of wing development is best understood in

*Aphelocheirus aestivalis*, a true aquatic bug. Larsen (1931) found in the laboratory that individuals reared in aquaria with running water were winged whereas wing development was suppressed in animals kept during their last nymphal instar in aquaria equipped with air pumps.

As many as six distinct wing types are known in some European species of *Gerris* (Ekblom, 1927, Jordan, 1947). All of these may occur in one locality. Some species, however, are known only from macropterous and others only from apterous or macropterous specimens. Observations in Finland of distribution of polymorphism in *Gerris najas* and *G. lacustris* led Sahlberg (1868) to believe that brachypterous forms were significantly more abundant in the north, and macropterous forms in the south. This was substantiated by Lindberg (1929) who found that brachypterous *Gerris lacustris* was the common form in the coastal areas of the outer archipelago as well as in northern Lappland. Lindberg also correlated the collection of a larger ratio of winged to wingless forms of *G. najas* in Finland with the warm temperature in 1917-1925. Jordan (1943) has found that *Gerris odontogaster* is also found most often in the brachypterous form in the north and the macropterous form in the south of Finland.

Another worker, von Mitis (1937), correlated temperature with wing form. Working with Gerris in Germany, he found that the spring generation was brachypterous but the generation which developed during the warm summer weather was macropterous. Similarly, Ekblom (1927) found fewer winged animals at Piteå than at colder Stockholm.

The only studies reported in the literature of crossing the winged and wingless forms of gerrids are those of Ekblom (1927) and those of Poisson (1924). Poisson found that in some crosses of *G. lacustris* macropterous x macropterous gave about 92 per cent macropterous and 8 per cent brachypterous; in others this cross yielded only macropterous individuals. In the same species, brachypterous x brachypterous gave about 80 per cent brachypterous and 20 per cent macropterous. Poisson also varied environmental conditions in some of the rearings but he found that the variations of food and temperature which he used did not influence the expression of wings. In 1927, Ekblom working with *Gerris asper* crossed apterous x apterous and micropterous x macropterous forms. Both yielded only macropterous offspring. Four macropterous females which had resulted from the micropterous x macropterous cross were mated with an apterous male. Most of the offspring of these crosses were macropterous but a few were micropterous and a few, apterous.

Poisson (1924) has also described sexual dimorphism which is correlated with wing dimorphism in *Gerris odontogaster*. Micropterous males of this species have lateral teeth on the sixth abdominal segment, which never occurs in macropterous individuals.

Comparatively little work has been done on variations of wing form in Hydrometra. In contrast to the dimorphic *Hydrometra martini*, both of the European species, *H. stagnorum* and *H. gracilenta*, are polymorphic. Poisson (1924) and Walton (1938) have found that the apterous form of Hydrometra stagnorum is the most common in France and England, respectively, but that macropterous and brachypterous forms are also found. Polymorphic forms like those of H. stagnorum have been described in H. gracilenta by Walton (1943) from animals taken in England. Both there and in Germany H. gracilenta is less frequently collected than is H. stagnorum. That the brachypterous and macropterous forms are rare in Germany is obvious from the report of Schumann (1934) who collected only one winged H. stagnorum and from that of Jordan (1931) who collected only two winged forms, one of each species.

Poisson (1924) reported that the offspring of wingless individuals was always wingless in his rearings and that only winged offspring resulted from two pairs of macropterous individuals, which he crossed in the laboratory. Although he attempted to cross winged ♀ x wingless ♂ and wingless ♀ x winged ♂, these animals did not mate. This condition, which he termed "amixie", he believed important in the origin of new species.

However, Jordan (1931) reported collecting mating pairs in the field in which one individual was winged and the other wingless. Such a pair of H. gracilenta continued to mate after they were brought into the laboratory. Jordan, realizing that the female might have sperm stored from a previous mating, destroyed the eggs laid during the first ten days. Those deposited after that time were fertile.

No study of the length of time which females may retain viable sperm has been reported for Hydrometra stagnorum. If, like H. martini, this species can retain sperm for a period of months, the eggs observed by Jordan possibly were fertilized by a previous impregnation.

The occurrence of winged and wingless individuals in a relatively constant ratio indicates that this is a balanced population. Balanced populations are defined by Ford (1940, p. 493) as being those in which "two or more forms of the same species are maintained in optimum proportions, a departure from which, in either direction, constitutes a disadvantage". In Hydrometra, the most apparent advantage of the winged condition is motility; these individuals can escape an unfavorable environment by flying to different areas. Laboratory studies indicate lower reproductive and survival rates which, if they occur in nature, would be disadvantageous. The higher proportion of winged to wingless individuals in the southern part of the range of this species suggests that lower reproductivity of winged individuals may be no serious disadvantage in the south, possibly because there are more generations there or for other reasons. The possibility exists that the winged condition is inherited with a lethal factor in some parts of its range. The inheritance of a recessive lethal factor with a factor for color occurs in dimorphic females of some species of the pierid genus Colias (Ford, 1937). The lower reproductive capacity of winged hydrometrids might result from the greater demands for nourishment by the thoracic muscles and the subsequent deficiency for optimum ovarian growth.

## SUMMARY AND CONCLUSIONS

Hydrometra martini is the only species of the family Hydrometridae in the northern part of the United States. Water measurer and marsh treader are vernacular names applied to insects of this family and indicate their characteristically deliberate gait. Adults of H. martini are slender; they measure approximately 9mm in length and 0.5mm in width. The exoskeleton is heavy and, because of the fusion of the sternal area, rigid. Most individuals are apterous, the wings being represented by small strap-like processes; a few have well devèloped wings which extend to the sixth abdominal segment. The nymphs, especially those of the early instars, are proportionately less elongate and their exoskeletons are light sclerotized.

These insects are found throughout the spring and summer on still or slowly moving waters and on the banks. They walk on the surface film and crawl over the floating and emergent vegetation, preying upon recently dead or living insects. Reproductive activity is continuous from early spring until late summer. There are three generations and a partial fourth generation per year in both Michigan and Massachusetts. In the fall, when the water temperature approaches 15°C, the adults of the overwintering generation crawl on land and seek shelter in depressions of the earth or under decaying plants. Here they remain until spring when the migration to water takes place. Since females collected in the winter and early spring lay fertile eggs in the laboratory, viable sperm must be stored from copulation in the fall.

The elaborate sculpturing of the egg of <u>Hydrometra martini</u> results from the subdivision of the exochorion into minute air chambers. The length of time of development of the embryo depends upon the temperature; at 25° this period is 11 to 14 days. The hatching process, which is rapid and uniform in nature includes the molting of an embryonic cuticle.

From the time the nymph walks away from the egg shell, its activities closely resemble those of the adult. This is especially true of its locomotion, its grooming and its feeding.

The morphological changes are more marked and involve both proportional growth and differentiation. With each molt, the head increases in length to a much greater extent than in width. This growth is especially marked in the preocular region. The head capsules of the nymphs are lightly sclerotized, but in them, as in the adults, there are differentiated sclerites associated with the mouth parts.

The mouth parts, like those of all hemipterans, consist of a labium which forms a sheath enclosing the mandibular and maxillary stylets. The labrum partly covers the base of this sheath and the elongate epipharynx extends into it. The maxillae form a single channel through which saliva passes to the prey and food materials are pumped back to the pharynx. The complex musculature of the mouth parts is contained entirely within the elongate head capsule. The well-developed salivary glands lie in the anterior part of the thorax.

Changes in the developing thorax involve the fusion of sclerites and the differentiation of the tergum associated with wing formation. The fusion in the thorax includes the union of the pleura with the sterna which occurs only in the adult and also the reduction of the membranes joining the regions of the thorax in the nymphs to the sutures found in the adults. The development of the supracoxal lobes of the episterna and epimera begins in the fourth instar nymphs. The articulation of the legs of both the nymphs and adults is such that movement of the coxae is on a horizontal plane. The legs are slender and especially in the adults, elongate. The setae of the tarsi and the distal parts of the tibiae are used in the almost continuous grooming motions which help in keeping these surfaces hydrofuge.

Differentiation of the tergum is especially associated with wing formation. The pronotum, which completely covers the mesotergum in the adults, is not markedly developed even in the fifth instar nymphs. The mesoterga and metaterga of the first instar nymphs are rectangular plates; the posterior angles of these sclerites indicate the development of wing pads in the second and succeeding instars. In the third instar, the wing pads of individuals which will become macropterous are somewhat larger and in the fourth and fifth instar nymphs these are conspicuously larger than the wing pads of potentially apterous individuals. The mesonota of macropterous nymphs are not differentiated into sclerites as are those of adults. The metanotum is progressively compressed by the upward growth of the metaepisterna. In the fifth instar nymph, the metanotum is a rather wide membrane but in the adult, it is represented by an external line and an internal fold on which the metanotal leg muscles take their origin.

The mechanisms regulating wing growth in Hydrometra are not known. The possible influence of environmental factors is indicated by the occurrence of about 24 per cent winged individuals in series in the University of Kansas collection taken from Florida and only 2 to 3 per cent in those from Michigan and Kansas. Genetic control is suggested by crosses made in the laboratory. The offspring of two apterous individuals are always apterous. In the small numbers of crosses involving macropterous individuals, only a few of the offspring of two macropterous parents and none of those having one apterous and one macropterous parent, were macropterous.

The first pair of thoracic spiracles lies in the posterior border of the proepimera and the second, in that of the mesoepimera in the nymphs. Each pair shifts anteriorly to lie just behind the supracoxal lobe of the adult epimera. In the nymph each of the abdominal segments I through VIII bears a pair of spiracles. Those of segments I and VIII are lost in the adult. The tracheal system consists of two independent dorso-lateral trunks which extend into the head, tracheae to the viscera, and tracheae to the ventral body-wall.

The nymphal abdomen consists of ten segments. In the first three instars, each of these, except the reduced tenth segment, is a simple cylinder separated from adjacent segments by secondary segmentation. In the third and succeeding instars the dorso-lateral parts of the intersegmental boundaries are marked by heavy dark lines, and in the fourth and fifth instar nymphs the terminal segments are modified with the differentiation of the external genitalia.

In the adult, the first abdominal segment is greatly reduced and all of the pregenital segments are fused ventrally and laterally; segmentation is indicated only by the terga and by the positions of the abdominal spiracles.

The external genitalia of the female consist of broad plates which serve as a guide in the deposition of the egg; they show considerable reduction in comparison with the oviposition apparatus of more nearly typical hemipterans. The male external genitalia closely resemble those of related insects; a genital capsule formed from the ninth abdominal segment bears a telescoped aedeagus and a pair of claspers or parameres.

The internal organs follow the pattern of other hemipterans although these organs are attenuated, following the body form. The female reproductive system includes a pair of ovaries each of which consists of seven ovarioles. Under optimum conditions, each ovariole can produce an egg per day. The ducts from the ovaries are simple; the seminal receptacle associated with them may store sperm for a period of months. The male reproductive system consists of a pair of elongated testes, each of which is connected by a vas deferens with a seminal vesicle, and a common ejaculatory duct. The digestive system is a simple tube; the ventriculus is especially long. The salivary glands lie in the thorax and open at the junction of the maxillae by a single duct. Their secretion has a toxic effect on the prey. The compact central nervous system is composed of the fused ganglia of the head, thorax and abdomen and is found in the posterior part of the head and the anterior part of the thorax. The dorsal blood vessel extends from the seventh abdominal segment to the posterior part of the head.

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## PLATE I

Description of figures

3 Dorsal view of the head.

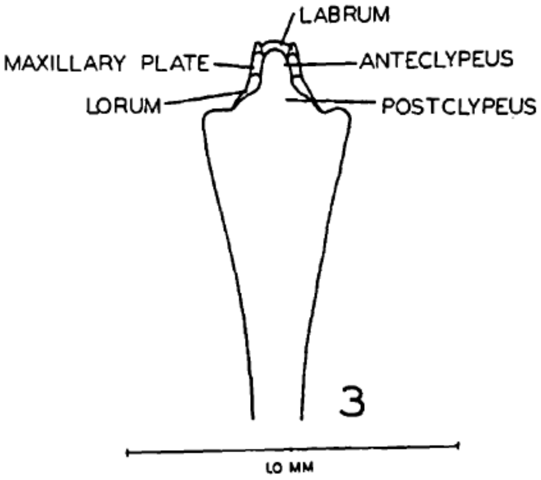
4 Ventral view of the head.

5 Lateral view of the head.

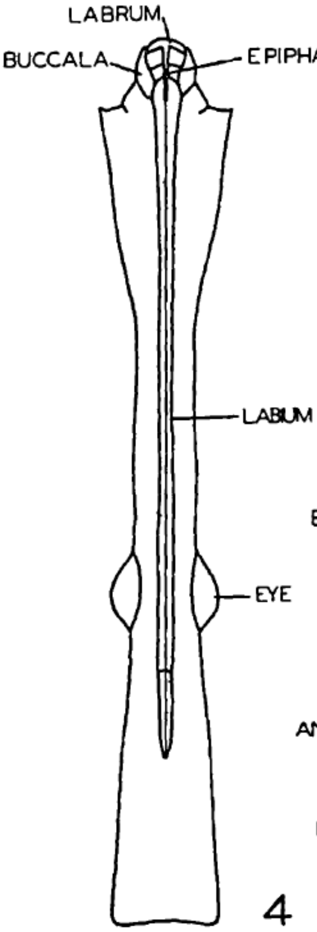
6 Anteclypeus, labrum and epipharynx in lateral view.

7 Anteclypeus, labrum and epipharynx in ventral view.

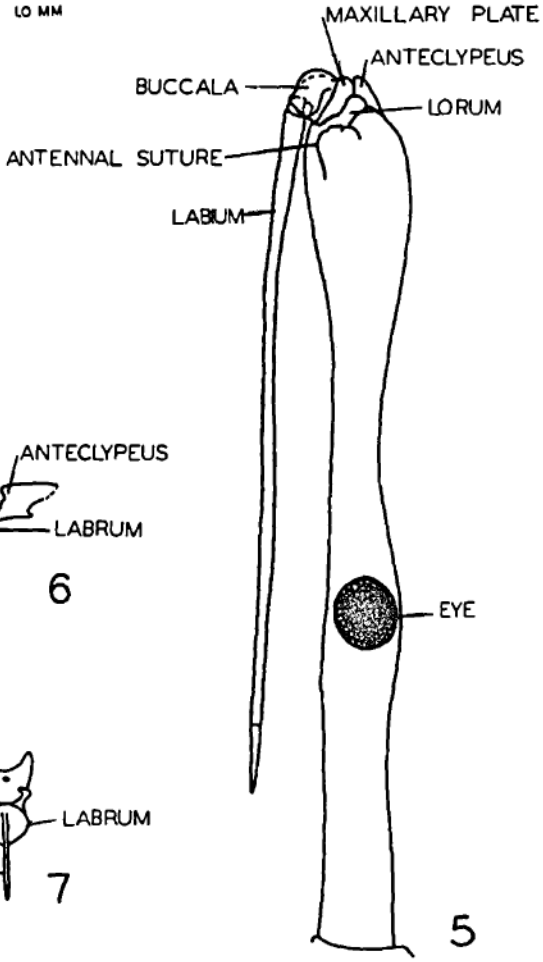
I


LABRUM
MAXILLARY PLATE
ANTECLYPEUS
LORUM
POSTCLYPEUS
10 MM

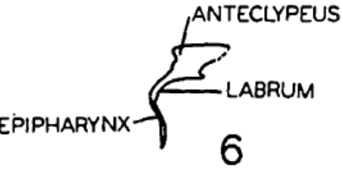
3


LABRUM
BUCCALA
EPIPHARYNX
LABIUM
EYE

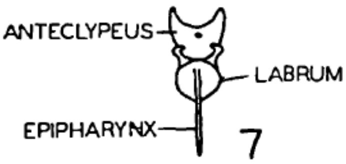
4


MAXILLARY PLATE
ANTECLYPEUS
BUCCALA
LORUM
ANTENNAL SUTURE
LABIUM
EYE

5


ANTECLYPEUS
LABRUM
EPIPHARYNX

6


ANTECLYPEUS
LABRUM
EPIPHARYNX

7

# PLATE II

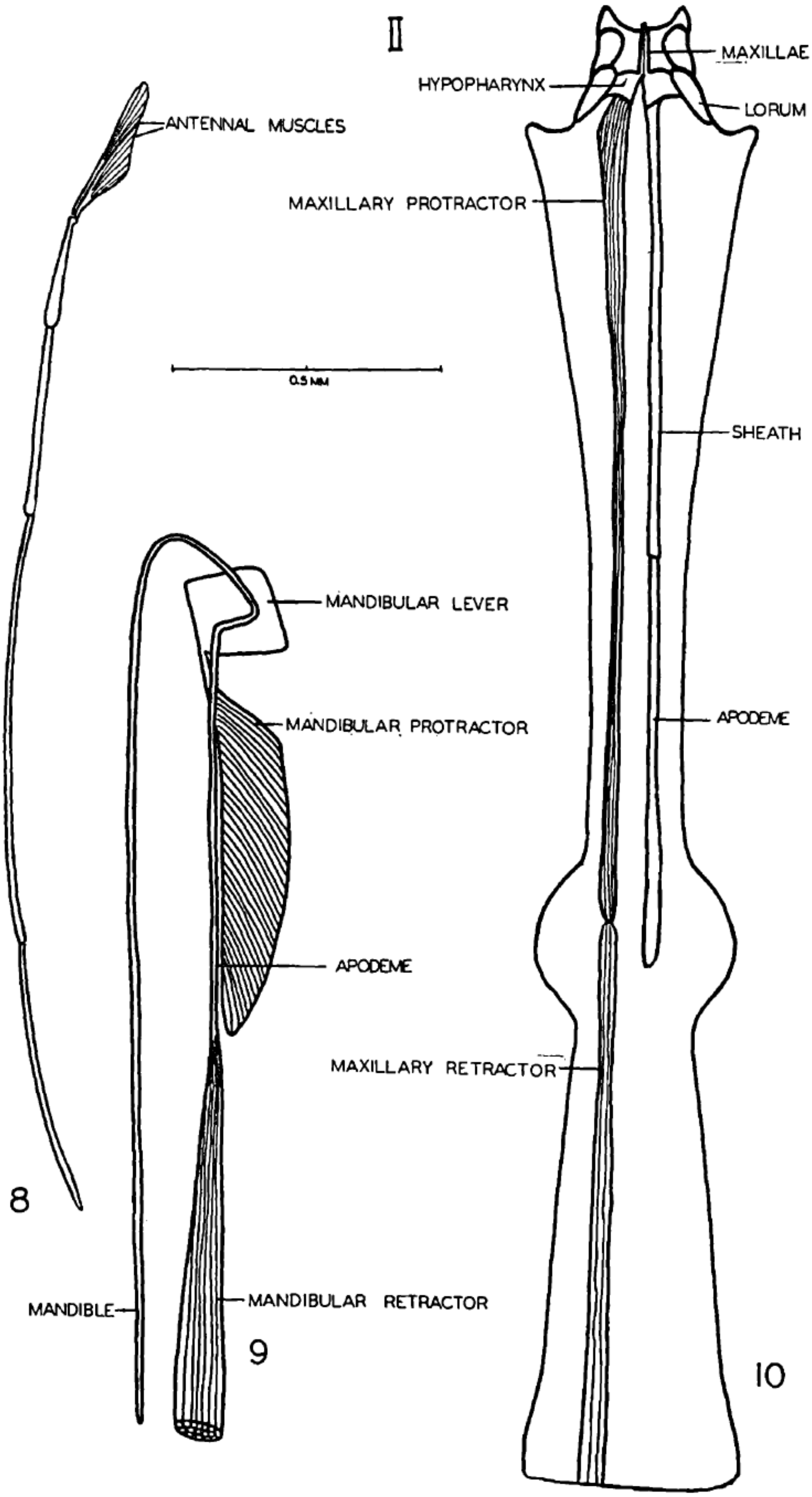
Description of figures

8 Right antenna in medial view.

9 Mandibular apparatus. Right mandible in median view.

10 Maxillary apparatus. Dorsal view with protractor and retractor muscles of the right maxilla removed to show the maxillary sheath.

II


ANTENNAL MUSCLES
0.5 MM
8
MANDIBULAR LEVER
MANDIBULAR PROTRACTOR
APODEME
MANDIBLE
MANDIBULAR RETRACTOR
9
MAXILLAE
HYPOPHARYNX
LORUM
MAXILLARY PROTRACTOR
SHEATH
APODEME
MAXILLARY RETRACTOR
10

## PLATE III

Explanation of figures

11 Tip of right maxilla.

12 Tip of left maxilla.

13 Tip of mandible.

14 Salivary syringe.

15 Cross section of head at the level of the mandibular lever.

16 Frontal view of the head.

17 Anterior part of the head dissected to show the mandibular apparatus and the pharynx.

18 Cross section of the labium through the second segment.

19 Cross section of the labium through the third segment.

20 Cross section of the labium through the fourth segment.

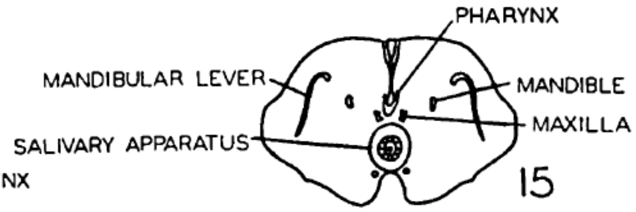
III


11


12


13


14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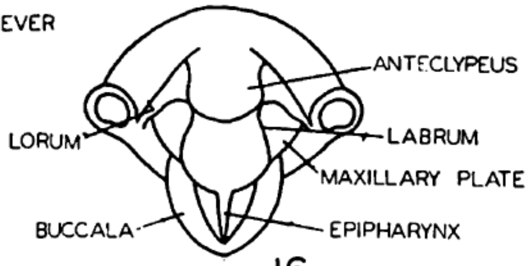
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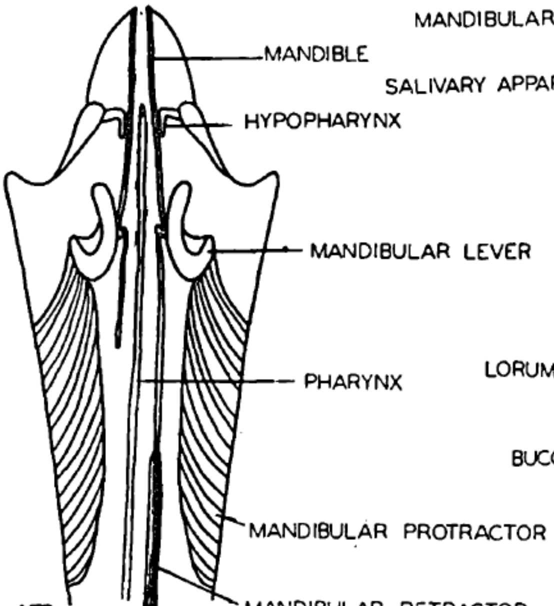
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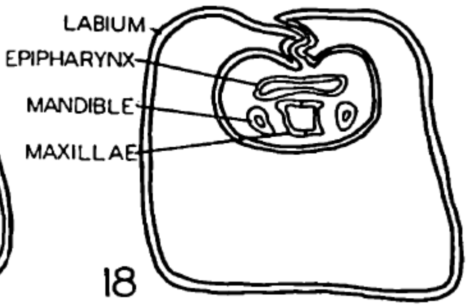
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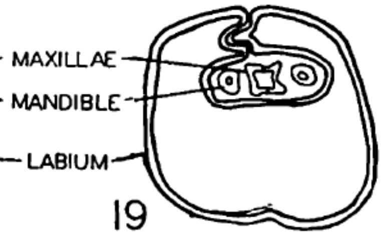
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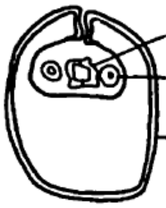
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## PLATE IV

Description of figures

21 Pronotum of winged adult. Dorsal view.

22 Pronotum of winged adult. Lateral view.

23 Pronotum of wingless adult. Dorsal view.

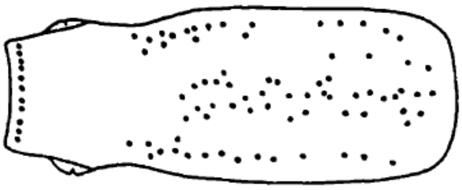
24 Pronotum of wingless adult. Lateral view.

25 Thorax of wingless adult. Ventral view.

26 Pterothorax of wingless adult. Dorsal view.

27 Pterothorax of wingless adult. Lateral view.

IV



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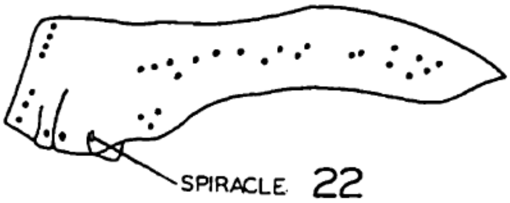

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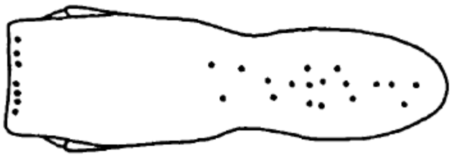

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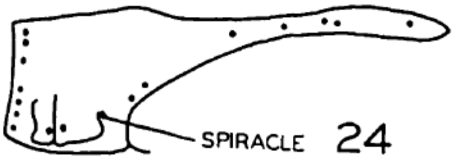

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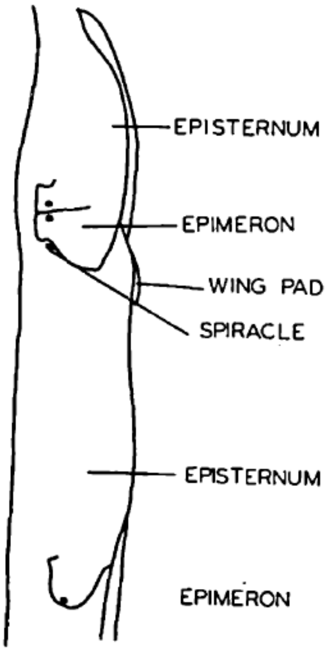

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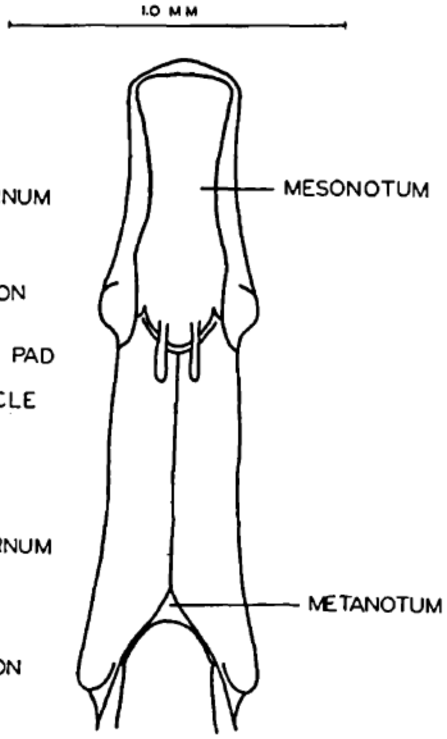

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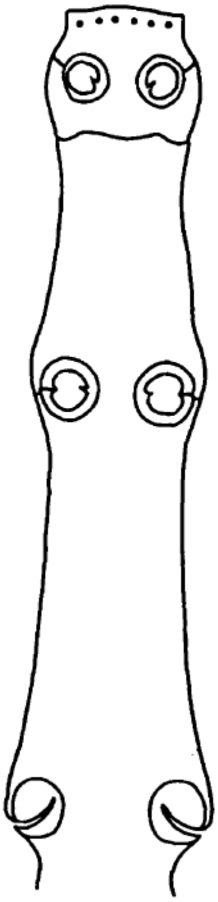


27

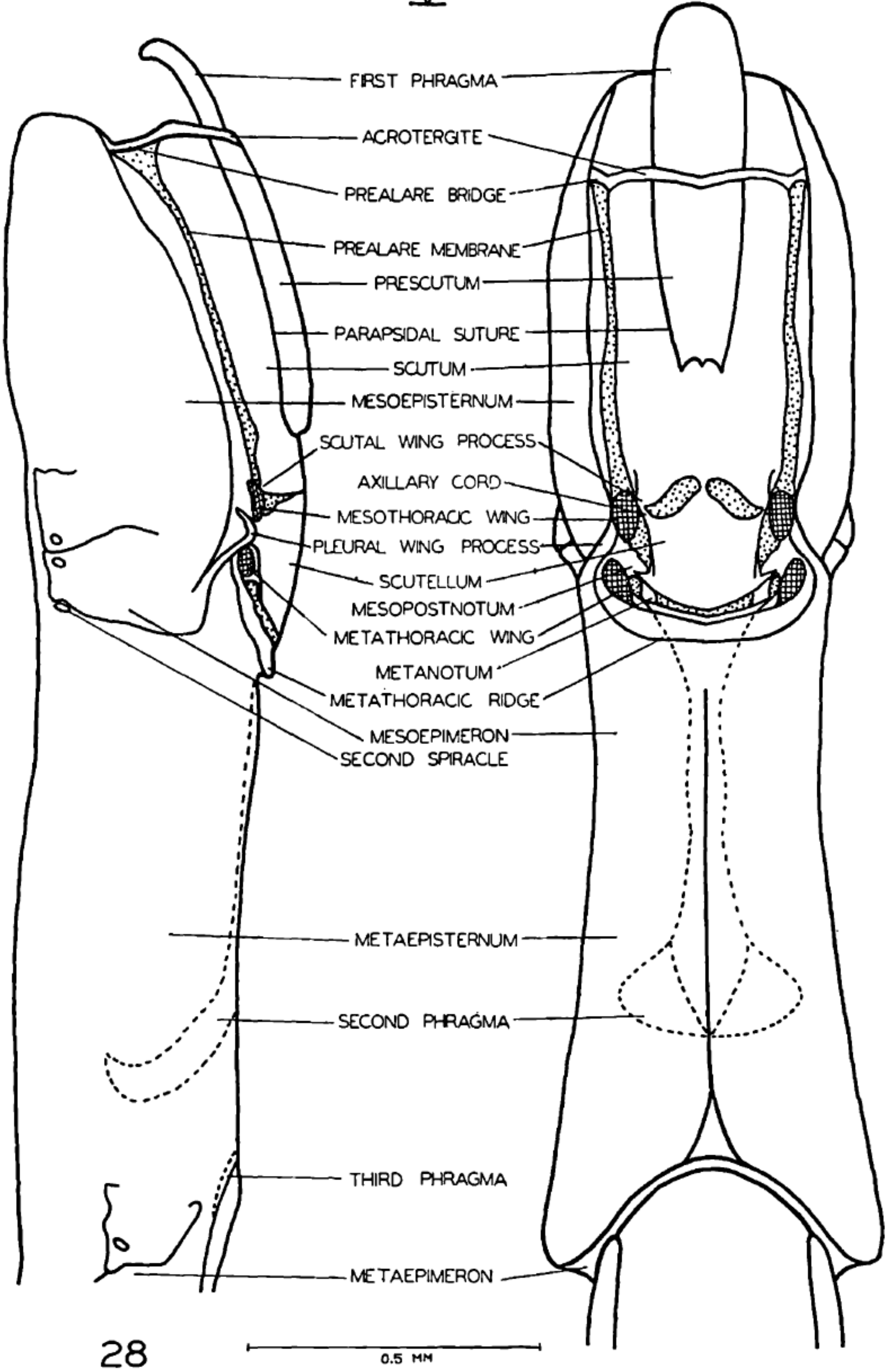
## PLATE V

Description of figures

28 Pterothorax of winged adult in lateral view.

29 Pterothorax of winged adult in dorsal view.

V


FIRST PHRAGMA
ACROTERGITE
PREALARE BRIDGE
PREALARE MEMBRANE
PRESCUTUM
PARAPSIDAL SUTURE
SCUTUM
MESOEPISTERNUM
SCUTAL WING PROCESS
AXILLARY CORD
MESOTHORACIC WING
PLEURAL WING PROCESS
SCUTELLUM
MESOPOSTNOTUM
METATHORACIC WING
METANOTUM
METATHORACIC RIDGE
MESOEPIMERON
SECOND SPIRACLE
METAEPISTERNUM
SECOND PHRAGMA
THIRD PHRAGMA
METAEPIMERON
0.5 MM

28

29

## PLATE VI

Description of figures

30 Right prothoracic leg in median view.

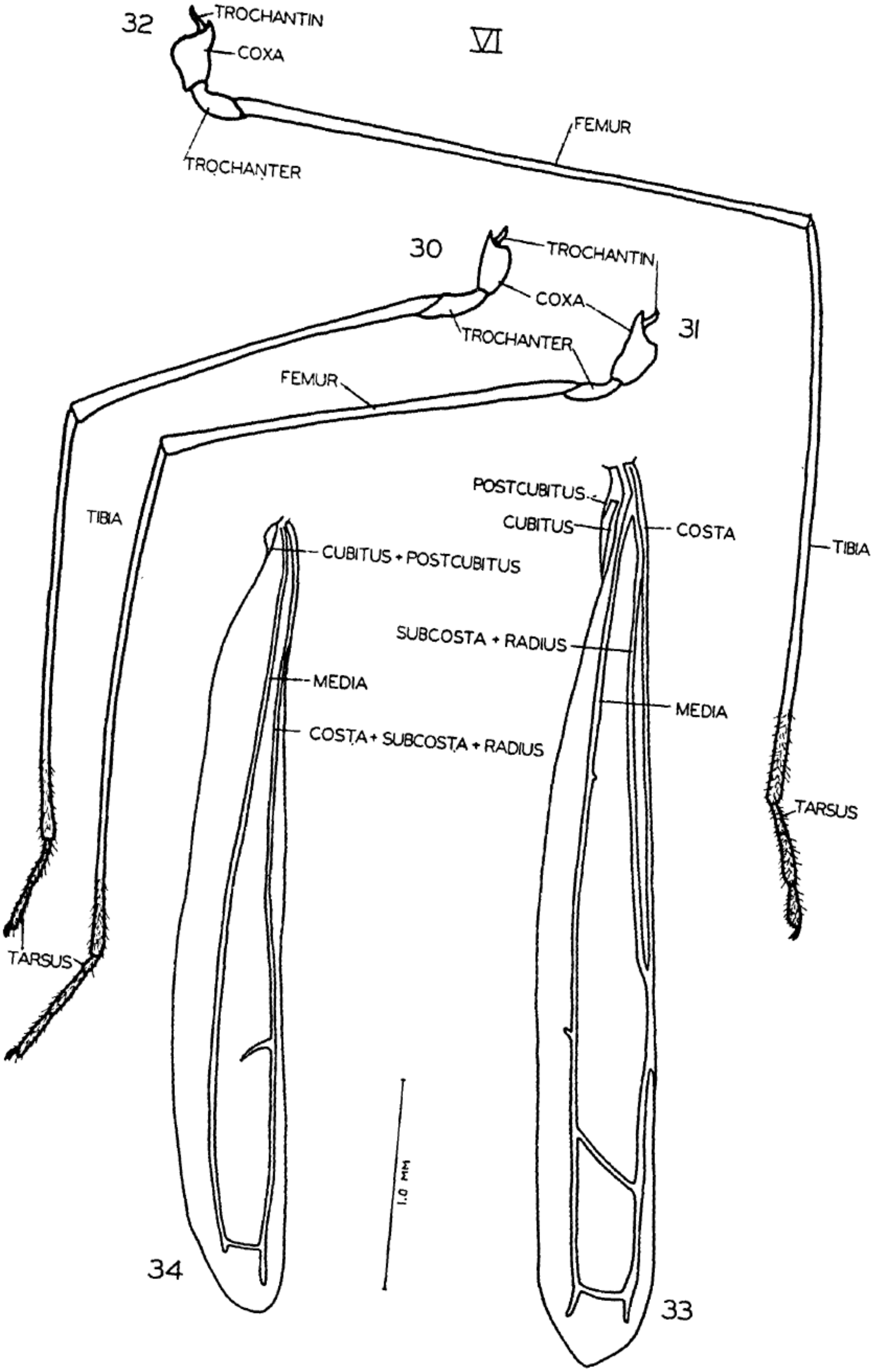
31 Right mesothoracic leg in median view.

32 Right metathoracic leg in median view.

33 Right mesothoracic wing.

34 Right metathoracic wing.

VI

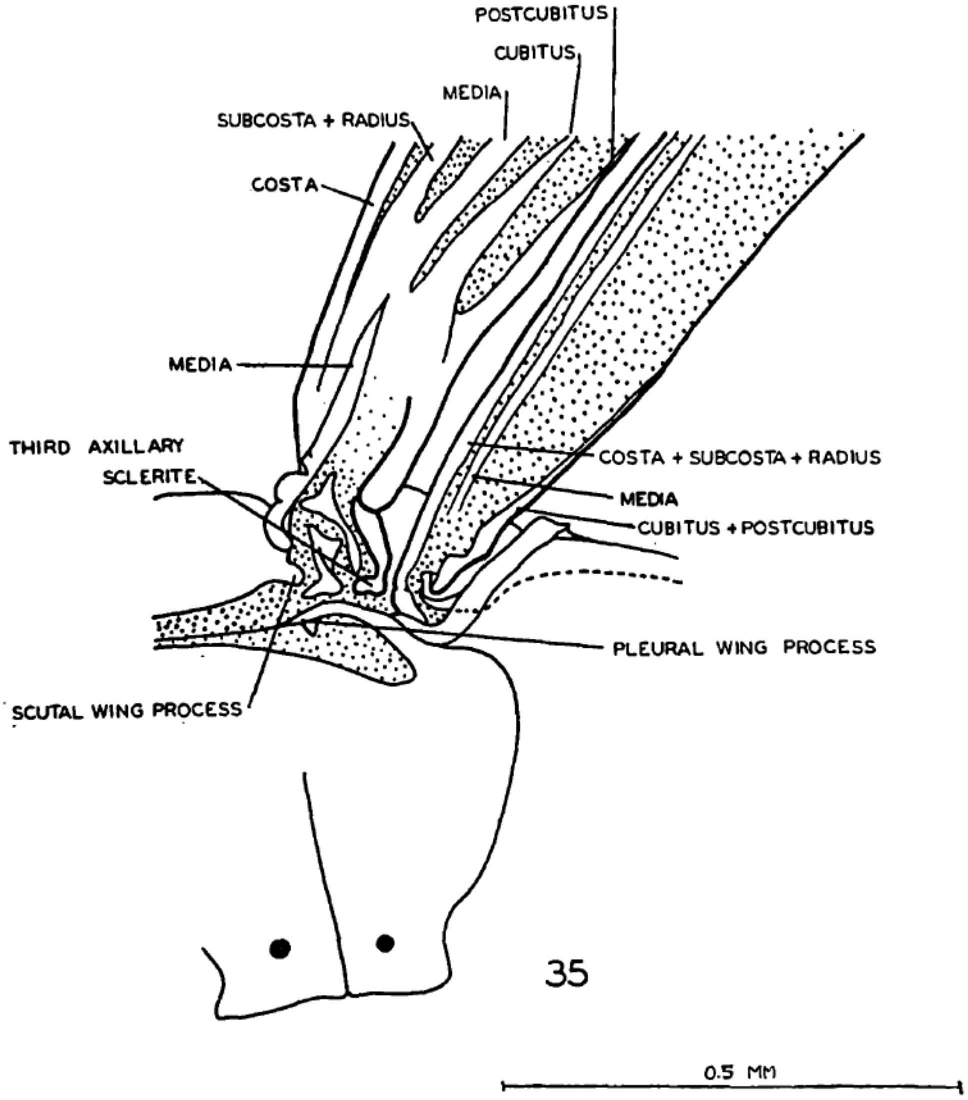

32
TROCHANTIN
COXA
TROCHANTER
FEMUR
TIBIA
TARSUS
30
TROCHANTIN
COXA
TROCHANTER
31
FEMUR
TIBIA
TARSUS
POSTCUBITUS
CUBITUS
COSTA
CUBITUS + POSTCUBITUS
SUBCOSTA + RADIUS
MEDIA
MEDIA
COSTA + SUBCOSTA + RADIUS
1.0 MM
34
33

## PLATE VII

Description of figures

35 Wing bases of the mesothoracic and metathoracic wings. Both wings are lifted to show the basal sclerites. Lateral view.

VII


POSTCUBITUS
CUBITUS
MEDIA
SUBCOSTA + RADIUS
COSTA
MEDIA
THIRD AXILLARY SCLERITE
COSTA + SUBCOSTA + RADIUS
MEDIA
CUBITUS + POSTCUBITUS
PLEURAL WING PROCESS
SCUTAL WING PROCESS
0.5 MM

35

## PLATE VIII

Explanation of figures

36 Prothoracic muscles of the head. Base of the head and muscles of the right side in lateral view.

| | |
|---|---|
| M 1 | M. pronoti primus |
| M 2 | M. pronoti secundus |
| M 3 | M. pronoti tertius |
| M 6 | M. prosterni primus |
| M 7 | M. prosterni secundus |
| M 10 | M. proepisterno-postoccipitalis |

37 Lateral view of the coxa and trochanter of the right prothoracic leg showing notal and pleural muscles.

| | |
|---|---|
| M 13 | M. noto-trochantinalis |
| M 14 | M. noto-coxalis primus |
| M 16 | M. noto-coxalis tertius |
| M 17 | M. pleura-coxalis |
| M 20 | M. noto-trochanteralis |
| M 21 | M. pleura-trochanteralis |

38 Lateral view of the coxa and trochanter of the right mesothoracic leg showing notal and pleural muscles.

| | |
|---|---|
| M 40 | M. noto-trochantinalis |
| M 41 | M. noto-coxalis |
| M 42 | M. episterno-coxalis |
| M 46 | M. noto-trochantinalis |
| M 47 | M. pleura-trochanteralis |

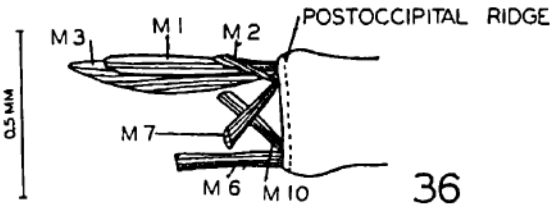
39 Lateral view of the coxa and trochanter of the right metathoracic leg showing notal, pleural and trochanteral muscles.

| | |
|---|---|
| M 63 | M. noto-trochantinalis |
| M 64 | M. noto-coxalis |
| M 66 | M. episterno-coxalis |
| M 70 | M. noto-trochanteralis |
| M 71 | M. pleura-trochanteralis |
| M 73 | M. coxa-trochanteralis medialis |
| M 74 | M. coxa-trochanteralis lateralis |

40 Pterothorax dissected to show the principal flight muscles of the right side. Lateral view. The leg muscles are removed.

| | |
|---|---|
| M 30 | M. mesonoti-primus |
| M 34 | M. dorso-ventralis primus |
| M 38 | M. episterno-alaris |
| M 39 | M. furca-pleuralis (mesothoracic) |
| M 57 | M. metanoti-secundus |
| M 62 | M. furca-pleuralis (metathoracic) |

# VIII



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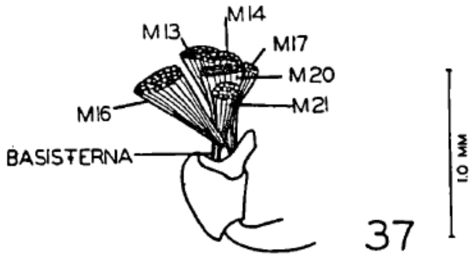

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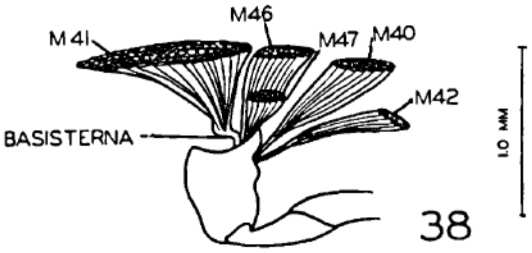

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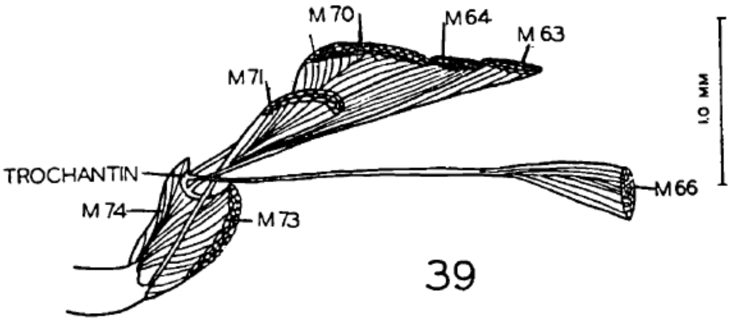

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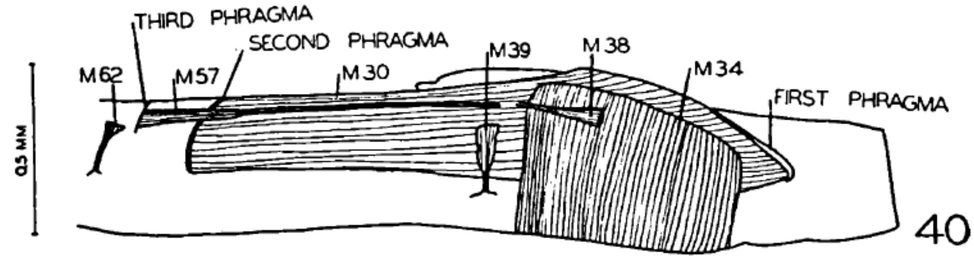


40

## PLATE IX

Description of figures

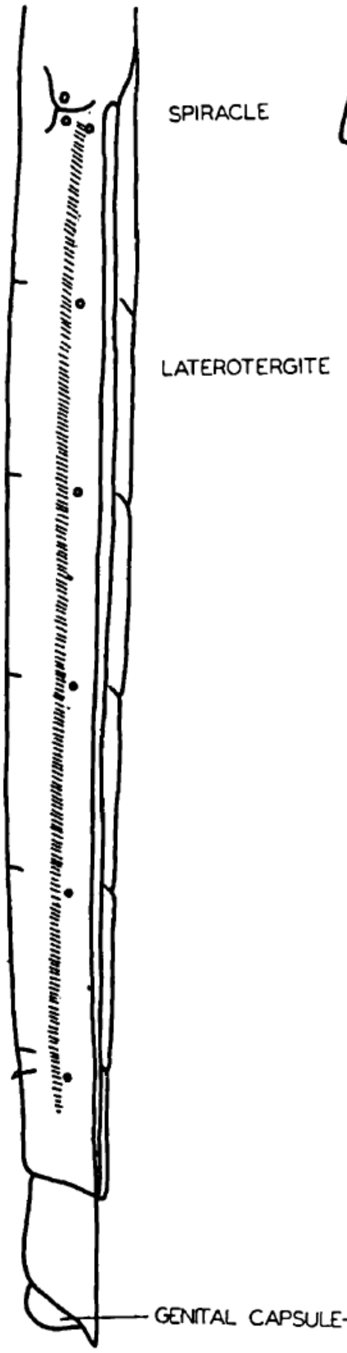
41 Abdomen of adult male. Lateral view of left side.

42 Abdomen of adult male. Dorsal view.

43 Abdomen of adult female. Dorsal view.

IX

1.0 MM



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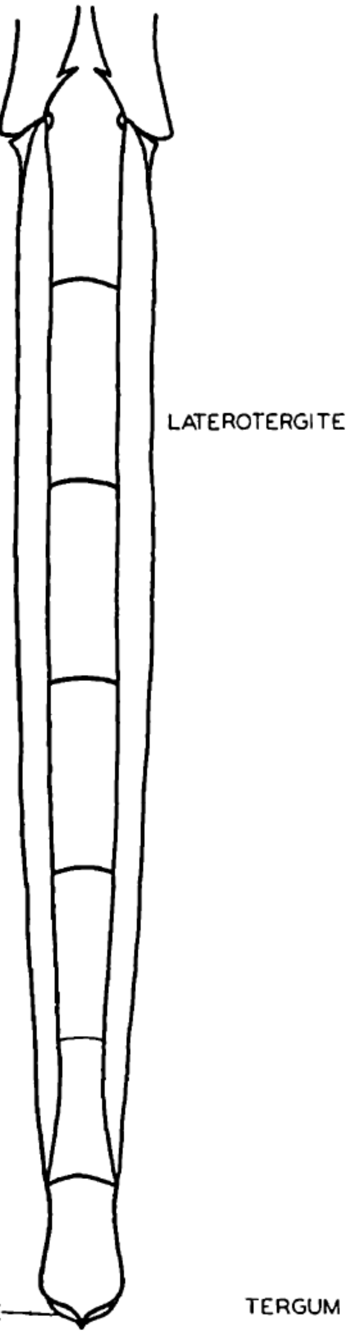

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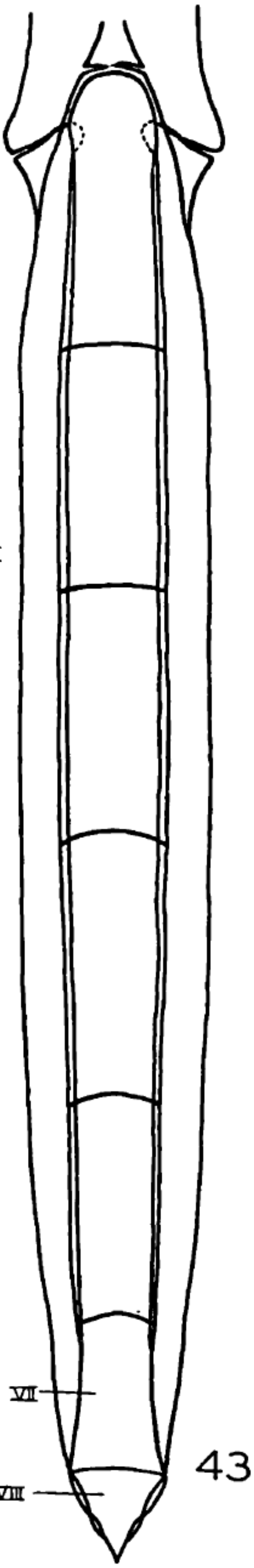


43

## PLATE X

### Description of figures

### Terminal segments of the adult female

44 Dorsal view.

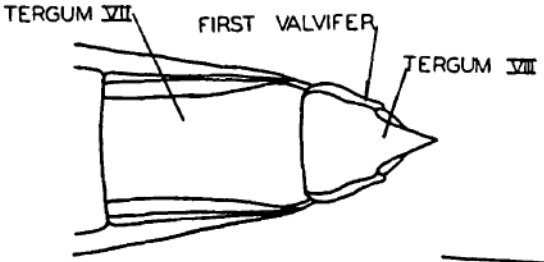
45 Ventral view.

46 Lateral view.

47 Lateral view. Left half of exoskeleton of the seventh segment and the left parasternite of the eighth segment have been removed to expose the genitalia and the musculature of the region. (Diagrammatic)

X

10 MM



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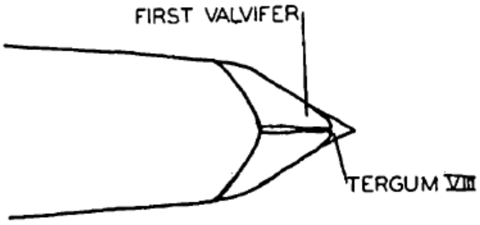

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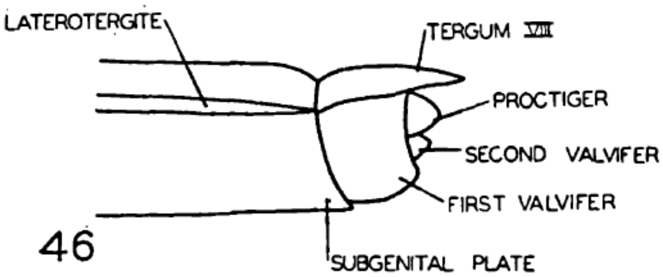

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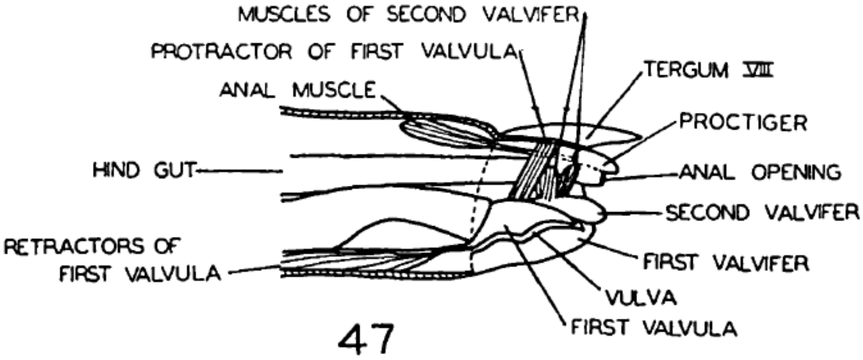


47

## PLATE XI

### Description of figures

### Terminal segments of the adult male

48 Lateral view of the left side. The eighth segment is deflected ventrally.

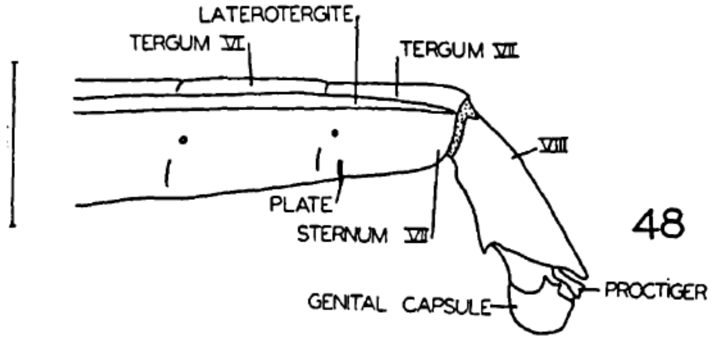
49 Genital capsule in lateral view. The left side of the capsule is removed to demonstrate the muscles of the basal plate and the parameres. The proctiger and the phallobase are partially protracted.

50 Dorsal view of the ninth segment.

51 Dorsal view of the ninth segment, the proctiger removed.

52 Lateral view of the ninth segment, with the intromittent apparatus everted.

# XI



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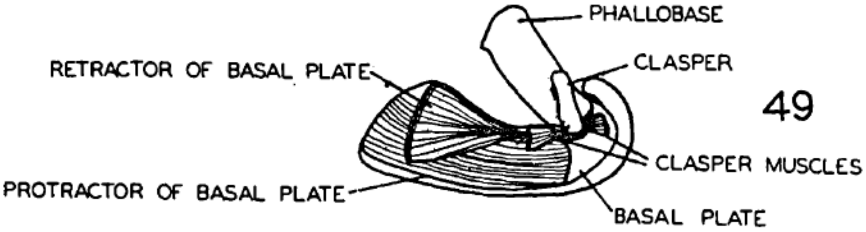

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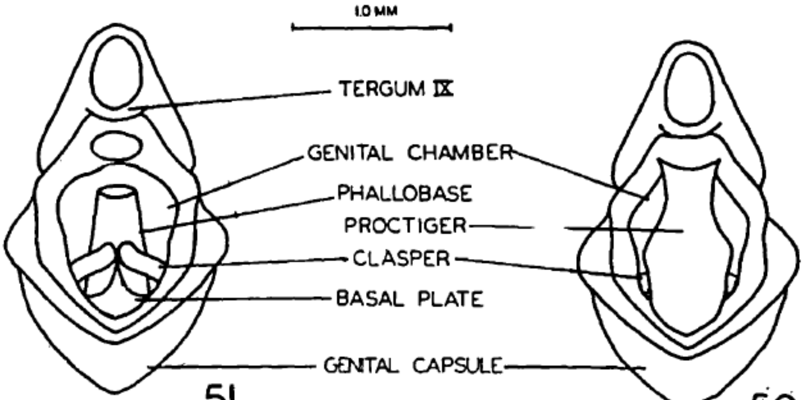

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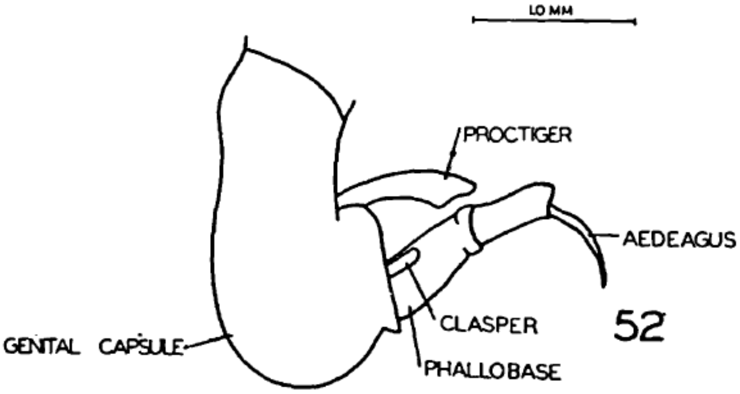


52

## PLATE XII

Explanation of figures

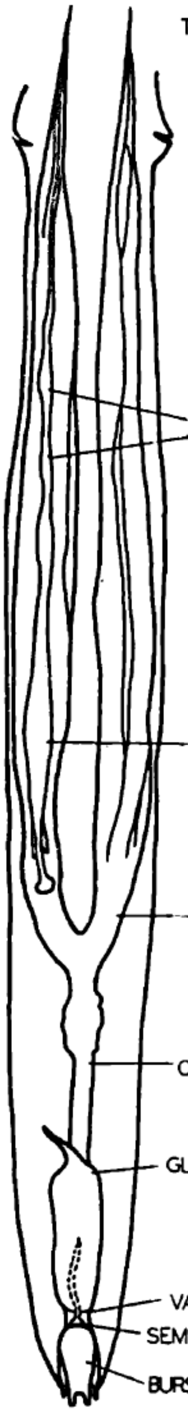
53 Salivary glands of the left side in dorsal view.

54 Digestive system in dorsal view.

55 Female reproductive system in dorsal view.

56 Male reproductive system in dorsal view.

XII



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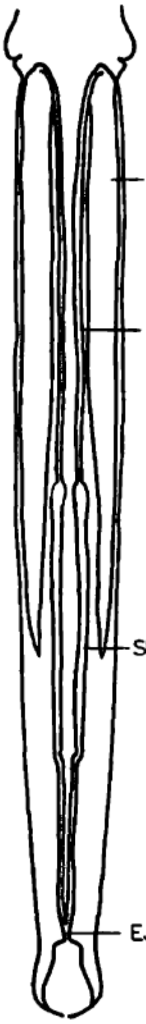
53

1.0 MM



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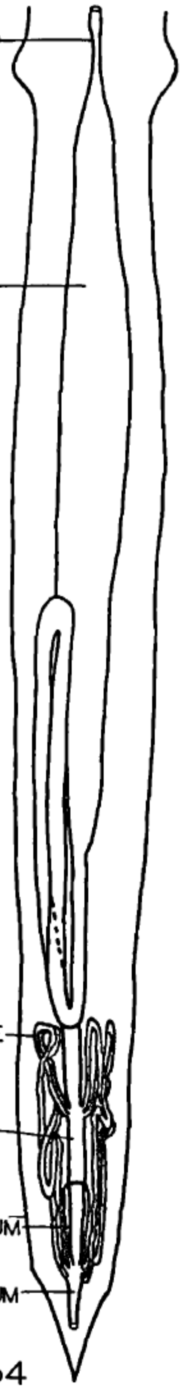


54

## PLATE XIII

Explanation of figures

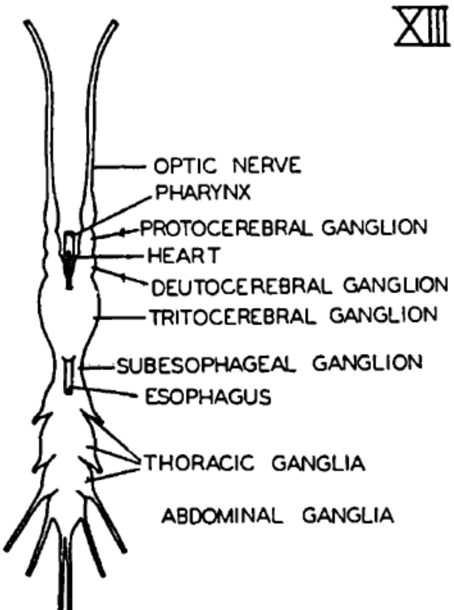
57 Ganglia of the central nervous system.

58 First thoracic spiracle. Diagrammatic side view.

59 Portion of the dorsal blood vessel and surrounding cells.

60 Tracheae of the fourth abdominal segment.

XIII



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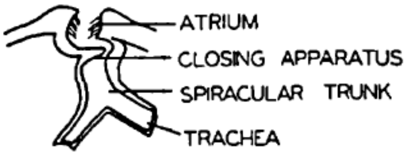

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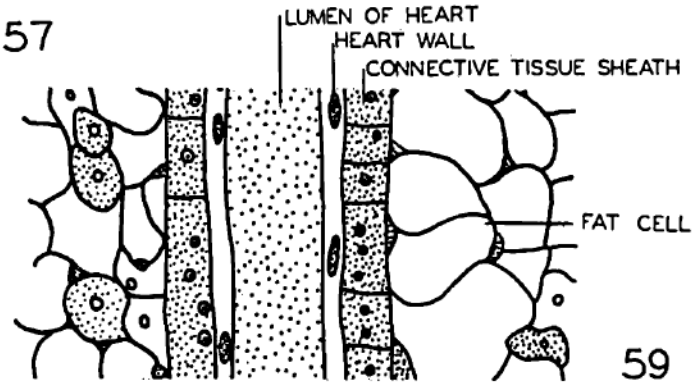

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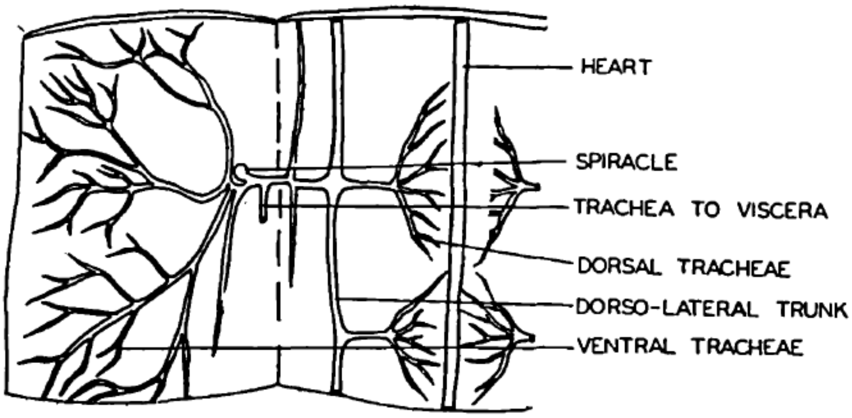


60

## PLATE XIV

Explanation of figures

61 External view of an egg of *Hydrometra martini*, showing the sculpturing of the exochorion.

62 Cleared egg, showing the endochorion, micropylar tube and basal spicule.

63 Cross section through the basal region of the egg, above the basal disc.

64 Cross section through the apical region of the egg, below the micropyle.

Series of diagrams showing the development of living eggs from the 6th through the 11th day of incubation at 25°.

65 Egg showing the position of the eyes at 9:30 and 10:30 AM on the 6th day of incubation.

66 Egg showing the position of the eyes at 11:30 AM on the 6th day of incubation.

67 Egg showing the position of the eyes at 12:00 noon on the 6th day of incubation.

68 Egg showing the position of the eyes at 12:15 and 12:45 on the 6th day of incubation.

69 Egg showing the development on the 7th day of incubation.

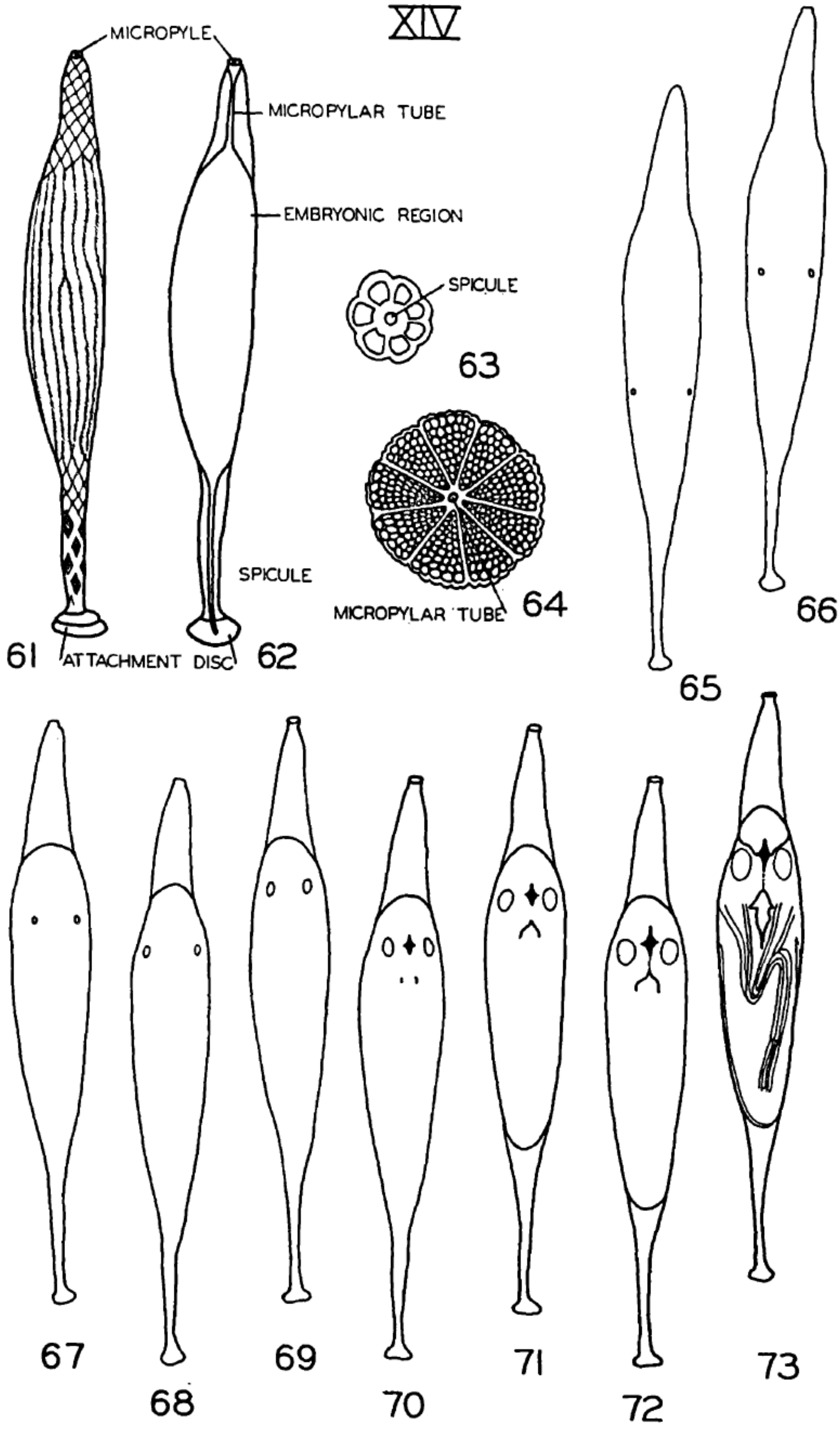
70 Egg showing the development on the 8th day of incubation.

71 Egg showing the development on the 9th day of incubation.

72 Egg showing the development on the 10th day of incubation.

73 Egg showing the development on the 11th day of incubation.

XIV


MICROPYLE
MICROPYLAR TUBE
EMBRYONIC REGION
SPICULE
63
SPICULE
MICROPYLAR TUBE
64
61
ATTACHMENT DISC
62
65
66
67
68
69
70
71
72
73

## PLATE XV

Explanation of figures

Series of sketches to show the hatching process in Hydrometra martini.

74 Head pushing through split in chorion; half of eyes exposed.

75 Head exposed; eyes and labrum free of the chorion.

76 Thorax nearly exposed.

77 Thorax exposed.

78 Nymph arching back, pulling legs, antennae and beak out.

79 Nymph straightening back and flexing head.

80 Exuviae split; beginning of "prenatal molt".

81 "Prenatal molt" nearly complete.

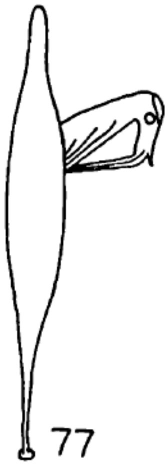
82 Nymph approaching supporting surface; antennae, beak and tip of abdomen still within exuviae.

XV


74


75


76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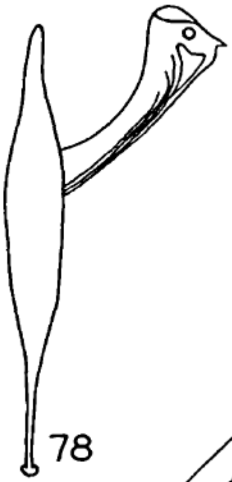
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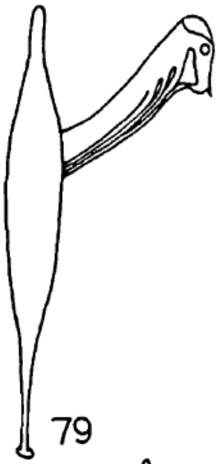
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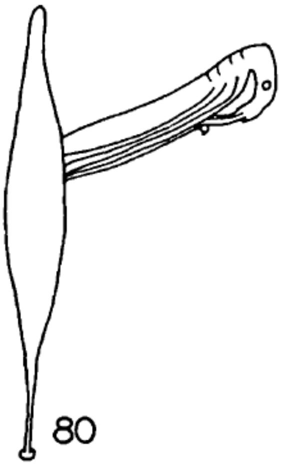
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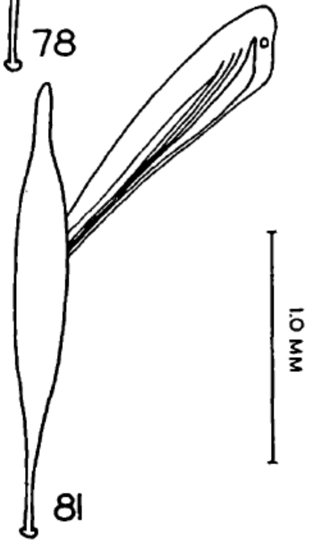

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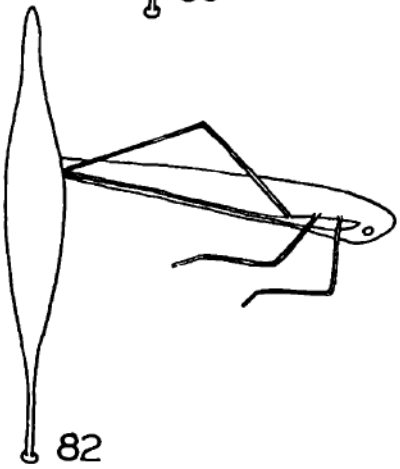

82

## PLATE XVI

### Explanation of figures

Drawings of first and second instar nymphs

83 Dorsal view of first instar nymph with an extremely contracted abdomen.

84 Dorsal view of first instar nymph.

85 Ventral view of first instar nymph.

86 Lateral view of first instar nymph.

87 Ventral view of second instar nymph.

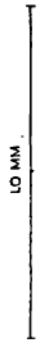
88 Dorsal view of second instar nymph.

89 Lateral view of second instar nymph.

XVI


83


84

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89

## PLATE XVII

### Explanation of figures

### Drawings of third instar nymphs

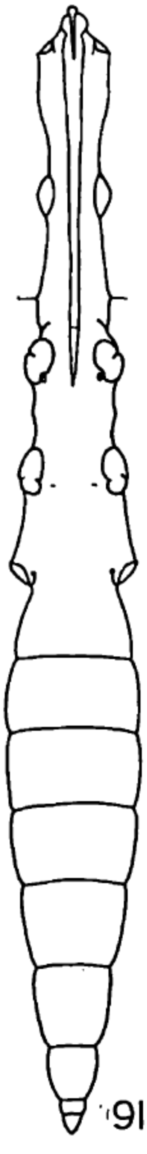
90 Lateral view.

91 Ventral view.

92 Dorsal view.

XVII

90



91

1.0 MM

92

# PLATE XVIII

## Explanation of figures

## Drawings of fourth instar nymphs

93 Ventral view of head and thorax of apterous form.

94 Lateral view of head and thorax of apterous form.

95 Dorsal view of head and thorax of apterous form.

96 Dorsal view of terminal segments of the male.

97 Lateral view of terminal segments of the male.

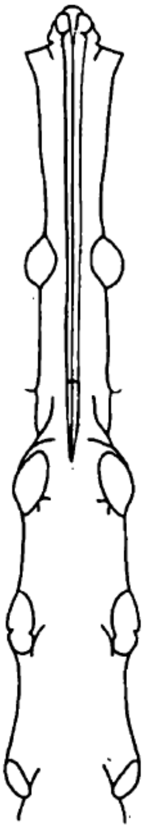
98 Ventral view of terminal segments of the male.

99 Dorsal view of terminal segments of the female.

100 Lateral view of terminal segments of the female.

101 Ventral view of terminal segments of the female.

XVIII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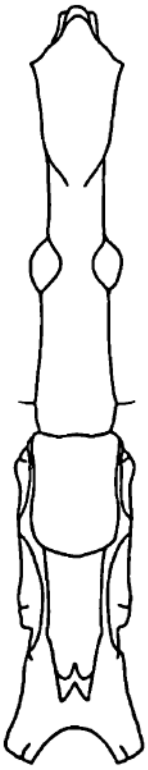
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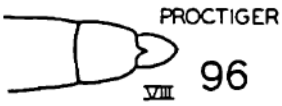
0.5 MM



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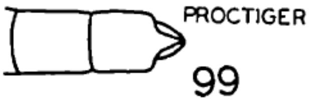

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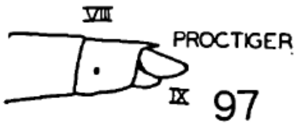

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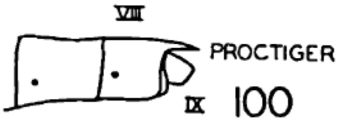

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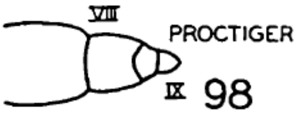

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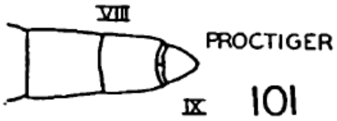


101

## PLATE XIX

### Explanation of figures

### Drawings of fifth instar nymphs

102 Dorsal view of head and thorax of apterous form.

103 Lateral view of head and thorax of apterous form.

104 Ventral view of head and thorax of apterous form.

105 Lateral view of terminal segments of the female.

106 Ventral view of terminal segments of the female.

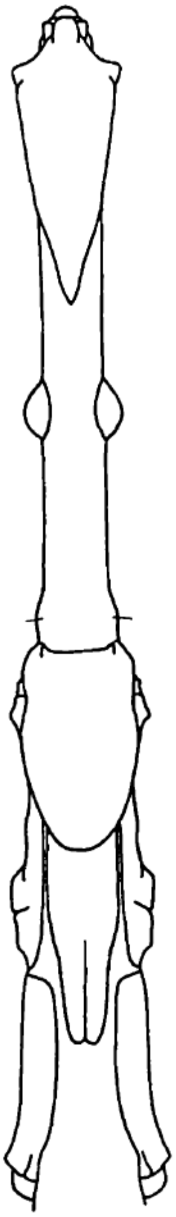
107 Dorsal view of terminal segments of the female.

108 Lateral view of terminal segments of the male.

109 Ventral view of terminal segments of the male.

110 Dorsal view of terminal segments of the male.

# XIX



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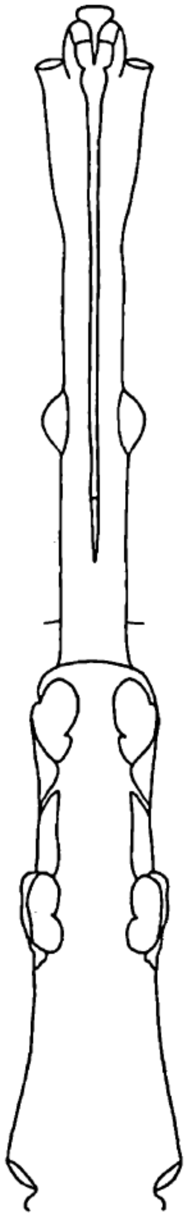

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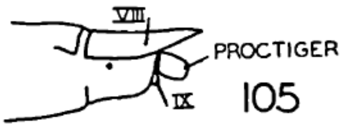

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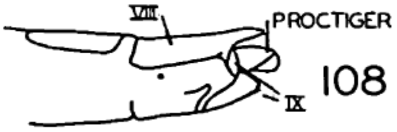

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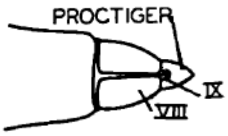

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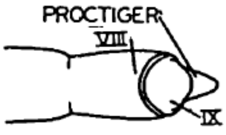

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110

## PLATE XX

### Explanation of figures

Drawings of the thoraces of nymphs of the macropterous form.

111 Dorsal view of the third instar nymph.

112 Lateral view of the third instar nymph.

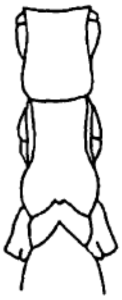
113 Lateral view of the fourth instar nymph.

114 Dorsal view of the fourth instar nymph.

115 Lateral view of the fifth instar nymph.

116 Dorsal view of the fifth instar nymph.

# XX



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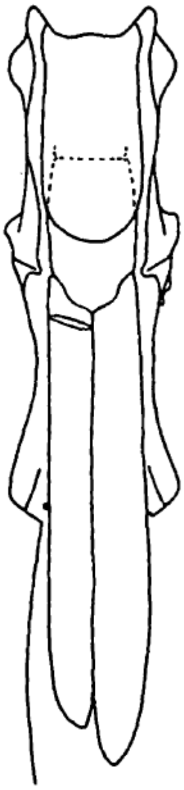

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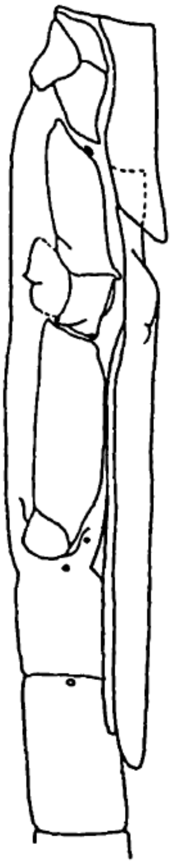

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