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THE undersigned, acting as a committee of the Graduate School, have read the accompanying thesis submitted by George H. Childs for the degree of Master of Arts. They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts.

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X

Some Observations on the
Life History of the Water Springtail
(Podura Aquatica - 1758)

A Thesis Submitted to the Faculty
of the Graduate School of the University
of Minnesota

By George H. Childs,

In partial fulfillment of the re-
quirements for the degree of Master of
Arts.

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I N T R O D U C T I O N .

The present work aims at no more than a simple presentation of conclusions drawn from observations covering a period of nine months on the ecology, external structure, and ontogeny of the water spring-tail (*Podura aquatica*-Linne' 1758). These are all of a general nature, far from final, and serve more to outline rather than cover the three fields on which they are based. Thus they do not tend toward the solution of any one problem, but merely offer suggestions for future investigation.

From the literature which I have consulted it would appear that, at the present time, very little is known about *Podura aquatica*, despite the fact that it is one of the first-named, commonest and most widely distributed of the Collembola; and that, with the exception of systematists like Fabricius, Reuter, Schäf-

fer and Packard who have helped to determine its distribution, De Geer, Linnaeus and Nicolet are the only writers in whose works this meager knowledge is contained. Of the latter, De Geer in his "Memoires pour Servir a l' Histoire des Insects" (1778) records the following observations:

1. That the insects live in large clusters on the surface of stagnant ponds.
2. That they are blackish in color, one twelfth of an inch long, with the nine segments of the body similar, the segments of the antennae four in number and the legs short and hairy.
3. That they leap only when disturbed and, in leaping, extend the furcula caudad but never flex it back to its normal position until after they have alighted.
4. That in structure the furcula is paired, bowed and somewhat flattened.
5. That the moults are complete and white in color.

6. That the Poduras cannot live long in dry places, can neither sink nor swim but may live for several days under the water if forcibly submerged. In addition to the above, De Geer noted the ocelli but was unable to determine their exact number, and also the ventral tube to which he ascribed an adhesive function.

The next writer, Linnaeus, shows in his "Systema Natura" (1758) that he found the ocelli to be sixteen in number, eight on each side of the head. Also, in his "Fauna Suecica" (1746) he refers to the insects' habit of congregating together in large numbers when the weather is cold. In the same work he mentions some smaller globular, reddish insects interspersed among the Poduras, and regards these as another sex or form of the same species. But among the specimens which I collected in the spring were a number of small, immature Sminthurids which corresponded so closely to Linnaeus' description that it is probable these were what he mistook for another form of

Podura.

Finally, Nicolet in his "Recherches pour Servir a' l' Histoire des Podurelles" (1842) mentions the prominent transverse ridges of the body, the convexity and distinctness of the eye patches, the absence of anal horns from the abdomen, and the fact that the frons (vertex as he calls it) is very pronounced and bears three pits so arranged as to form a triangle. Furthermore, he claims that Podura lays its eggs on the surface of the water and presents a drawing which figures the egg as dark brown and elliptical in shape. But, as will be shown later, both statement and figure are apparently incorrect.

Although I know of no subsequent literature which contributes any further observations on the species, it is evident from Tullberg's figures in the "Sveriges Podurider" (1872) that the granular character of the cuticula, the segments of the legs, and the structure of the catch and mucrones have been determined.

ECOLOGICAL RELATIONSHIPS.

HABITAT.

The water springtail is holarctic^c in distribution and has always been found, either on the surface of fresh water or in very close proximity to it. Occasionally this has been near the shores of lakes and streams, but usually on stagnant ponds, rife with decaying plant matter and well protected from the wind. Such a pond is the lagoon immediately west of the Minnesota State Fair Grounds, the only location in Hennepin County where I have found this species and one which bountifully provides all the conditions necessary for its existence. Hence, in describing the habitat of the water springtail, I shall refer particularly to this lagoon.

There are two characteristics which the habitat must possess, and one which is highly advantageous but not indispensable. In the first place, it must contain an abundance of moisture, since dryness in the surround-

ing air will cause these insects to shrivel up and die within a short time, even when resting on the water's surface. Indeed, it is extremely doubtful if any part of their bodies, save the mouth-parts when feeding, comes into direct contact with the liquid water, for every specimen that I immersed was completely enveloped by a film of air sufficient to keep it from drowning for at least a day. This is probably due to the presence of an oily secretion on the cuticula, inasmuch as the hairs of the body are far too few and too short to be effective in holding air bubbles. Also the solid objects upon which they walk must be damp, for otherwise they will stick to them and tear themselves to pieces in attempting to get free. In the second place, the habitat must maintain at least an even balance between plant growth and plant decomposition. There should be, however, an excess of plant detritus, either near the shore or scattered over the surface of the pond in question. This is of the utmost importance, since it forms the springtail's food, which I shall

consider in detail later. In the third place, a smooth, unruffled body of water is a valuable asset, since it enables this species to cover a relatively great distance in search of food. Lacking wings and well developed legs, its progress over uneven surfaces is slow and difficult. Of course, it has its leaping abdominal appendage, the furcula; but this, though effective in saving the insect from immediate danger and leading him in a given general direction, is not calculated to land him on the exact spot where his instincts prompt him to go. On the contrary, it often lands him in very unfavorable places and is much more likely to do so on land than on the surface of a pond. Nevertheless, water springtails can persist in damp places apart from standing water since I have kept a large number of them in a thriving condition merely on moist filter paper containing a little dead algae.

The lagoon near the State Fair Grounds fulfills all three of these requirements. It is surrounded on all sides by high clay banks which protect the water

pretty well from the wind, thereby insuring moisture and calmness. It has no outlet and consequently no currents which would carry the springtails away from their natural environment. Furthermore, it has no inlets and thus depends wholly upon melting snow and local rains for its water. Its aquatic plant life is very luxurious, particularly the green algae, Spirogira and Hydrodictyon, Potamogeton and the duck weed (*Lemna minor*) which completely covers the surface of the water in a good many places. There is a great deal of evaporation during the summer and early fall which reduces the depth to an average of from two to three feet, and therefore a great deal of decay. Though the whole lagoon seems favorable as a habitat for the springtails, I have found them only at its most easterly end where its banks are steepest and its width narrows down to only eight or nine feet from shore to shore. Here they occur in such great numbers that it is hard to find a square inch of pond surface that does not contain some thirty or forty individuals. With the advance

of the season come marked changes in habitat. Thruout the summer and early fall they are very active and well distributed over the surface of the water, feeding particularly on the plant scum which adheres to the ubiquitous duck weed pads; but toward the latter part of October, when the weather gets markedly colder and the plant life has died down, they congregate in large, dense clusters upon the undersides of damp, dead leaves which accumulate on the shores, or in the protected crevices of water soaked bark and wood. Then they are relatively inactive, feeding only on the plant scum which lies in their immediate vicinity, and never changing their locations unless disturbed or tempted forth by unusually warm weather. Shortly before freezing temperature is reached, the springtails burrow down into the mud near the shores, but rarely, if ever, go beneath the water line which is hardly more than four or five inches below the surface of the ground. Thus they survive the winter. In the middle of January I visited the lagoon and procured some chunks of frozen

mud from above the water line, and also some unfrozen mud from beneath it. Upon examining both kinds indoors, I found that the former contained a great number of springtails, the vast majority of which were alive; while in the latter were very few and most of these dead. This fact fails to support Miall's belief that these insects pass the winter below the water's surface on the stems of aquatic plants. It is doubtful if they hibernate in large masses, since all the chunks which I broke open revealed only isolated individuals and small groups of from ten to twelve. While the mud remains frozen, they are dormant and have the furcula extended backwards as in death; but with the first spring thaw they become active once more, and begin to emerge from their winter quarters. As early as March 18th, when snow and ice still covered the lagoon's surface, I found a few clusters of them on small puddles of water near the shore.

BEHAVIOR.

REACTIONS TO LIGHT. The water springtail reacts positively toward light, and in this respect differs markedly from most Collembolans, which, according to Lubbeck, avoid the light. But my own observations on this species have brought me to the following conclusions:

1. In the first place, the active response to light is of short duration, usually lasting from one to five minutes, and longer if the temperature is very high. This occurs only when the insects are disturbed or suddenly exposed to the sun's rays.

2. The passive response is relatively permanent unless the insects are in a dormant condition, since those which I kept over winter remained congregated on the light side of the glass aquaria in which they were confined.

3. When first made aware of the presence of light, the springtails first circle about with the middle of their bodies as axes, until they directly

face the rays. Then they leap forward by snapping the furcula free of the catch on the ventral side of the abdomen, and forcibly extending it caudad. The distances covered in these leaps are extremely variable, but I have found none to exceed four inches horizontally or three vertically. Upon alighting, they immediately flex the furcula back to its normal position beneath the abdomen and veer about to face the light as before.

4. In every instance that I observed, there was always a small minority which failed to respond, probably because these individuals were dying or physically impaired in some way or other.

5. Finally, I am convinced that this reaction is not a simple response to light alone but to heat also, since the temperature proved an important factor in determining the eagerness with which the insects acted as well as the duration of the activity. On the other hand it cannot be claimed that sun light is the sole stimulus, since I have seen them respond to electric lights as well. One of my largest glass aquaria was

so situated that the rays from the electric light in the room struck it on the side directly opposite to that on which the sun light shone during the day. On several December evenings after nightfall, I observed that the majority of the springtails had assembled on the side of the aquarium facing the electric lights, and that a number of them were actively leaping in that direction. The heat from this source could not have been great enough to elicit a reaction.

REACTION TO WATER CURRENTS. The water springtail evinces a strong negative reaction toward currents of water which tend to carry him away from his place of abode. In this case he orients his body parallel to the direction which the current takes and leaps against it, probably repeating this operation as long as he is aware that the water is in motion and has strength to resist it. I have found that, when the current stimulus and the light stimulus operate antagonistically, the former proves the determining factor. At various

times thruout the winter, I kept a large number of the springtails on water contained in tin pails. Whenever I slowly tipped these toward the light and the water commenced to run out, the insects invariably turned toward the interior of the pails and leaped in that direction. But when I stopped pouring and allowed the water to become stationary, they faced about and hopped toward the light. Sometimes, however, I met with one or two apparently normal individuals that passively allowed themselves to be poured out, thus appearing unaffected by either stimulus.

REACTIONS TO HEAT AND COLD. These insects are very susceptible to heat. Even the slightest rise in temperature will accelerate their activity to a marked degree. On several occasions, I placed some of my covered aquaria on a hot steam radiator. At the same time, I was careful not to disturb the insects while moving the aquaria or to change their positions in reference to the light. Once on the radiator, they

immediately commenced a rapid succession of leaps toward the light, to which stimulus they were not actively responding before the experiments. Upon removing the aquaria, the former state of quiescence was resumed within a very few seconds. In no instance did I take the glass covers from the vessels, or subject the insects to the heat for over a fraction of a minute. Thus the temperature of the enclosed water and air must have been raised only very slightly. The same increased activity was noticeable, though to a less extent, whenever I removed the covers from the aquaria and exposed the springtails to the warm, dry air of the room in which I kept them; but here air currents as well as heat had to be taken into consideration. Nevertheless, these experiments would indicate that heat, while it elicits no characteristic responses as do the other stimuli, is instrumental in starting, sustaining and intensifying the general activity of the insect.

Under the influence of cold, the springtails congregate together in compact masses (a fact noted by

Linnaeus), and the density of the masses appears to be in some degree proportionate to the intensity of the cold. On chilly mornings, I found the individuals of my aquaria gathered within narrow limits, but never so closely that all were in contiguity. One day near the close of November, I placed a glass aquarium containing twenty springtails out doors on a window sill. The thermometer, which hung within a foot or two of the aquarium recorded a temperature of 19 degrees above zero Fa., and the aquarium itself was uncovered, thereby exposing the insects to the full effect of the cold. For one whole hour I left them thus, and upon examining them afterwards, found all the twenty congregated on the surface of the ice in so dense a cluster that I was unable to discern any spaces between the individuals. None of them appeared in any way injured by the cold. Such facts point to the existence of an inter-relationship, which enables the individuals to secure sufficient warmth to withstand lower temperatures than would otherwise be possible. This is the only respect in which

I have found them truly gregarious, since their occurrence in large numbers can readily be explained by the fact that the species is incapable of a wide dispersion within a single generation.

WALKING. In walking, the springtails fail to show a distinct reaction to light or water currents, since they rarely follow a straight course. An increase in temperature causes them to walk more rapidly; but, inasmuch as they are always slow movers in this respect, the difference is not very noticeable. They seldom appear to be going in any definite direction but move hither and thither as though in search of food, which is undoubtedly the chief underlying cause of this form of activity. They walk on vertical surfaces with as much ease as on horizontal, provided that both are equally moist and even; and in so doing, fail to exhibit any geotactic orientation or sense of balance. With every step, the body wobbles from side to side and backward and forward. At the same time, the antennae are moved in unison with the prothoracic legs

and usually touch the walking medium alternately with their tips, as though they were a fourth pair of walking appendages. The mutilation or removal of the antennae has a marked effect on their walking. Sometimes it causes them to travel about in a circle, but very often prevents them from walking at all. It would thus seem that the springtails depend more upon touch than sight in finding their food; a conclusion which the small size and number of the ocelli tend to bear out.

FOOD AND FEEDING HABITS.

As I have already intimated, the water springtails feed on decayed plant matter, preferably the scum which is the product of decomposed algae, duck weed pads and dead leaves. All my observations in this connection go to show that this is their sole means of nourishment. Many times thruout the year, I offered my specimens decayed animal matter, particularly snails flesh which, according to Davenport, it is believed at least one species of Collembolan, the *Anurida maritima* eats; but every individual that I saw approach

the flesh, turned away without so much as touching it with his antennae. Also, decayed apples, grapes and mushrooms were apparently rejected by all, though I finally succeeded in getting a few to feed on a piece of decayed banana. Furthermore, I examined under the microscope a great deal of the insects' excretia, which takes the form of elliptical brown pellets about one tenth of a millimeter in length, but these revealed nothing save dead water plant tissue.

By carefully observing a number of individuals that were feeding on a moist, vertical glass surface, I was able to ascertain the exact method of procedure. I thus found that the mouth-parts were alternately retracted and extended, and that, when retracted, the water containing the dead plant matter was forced up into the mouth cavity. To increase this effect, the head was bent downward during each extension and upward during each retraction. Only when the water that was being swallowed contained a relatively large amount of solid material, did I observe any lateral movements in-

dicative of chewing. These were always slight and of short duration, but while going on, the other movements were suspended. This observation leads to the conclusion that, since the food is ingested in a semi-liquid form, there is very little occasion for mastication, and that consequently, thru disuse, the mouth-parts have become too weak to chew anything but the softest kind of material. The process of digestion is evidently very rapid, inasmuch as my specimens were continually voiding excreta. One that I particularly noted voided three dung pellets within one minute, and these were shot out from the anal aperture to a distance of one half a millimeter.

HABITAT ASSOCIATES.

At the lagoon I was able to find only two species of animals which mingle with the water spring-tails in the same habitat and are not hostile toward them. These were the plant louse (*Rhopalosiphum nymphaeae*) which, thruout the summer and early fall, was very abundant on the duck weed pads; and the Collembolan

(*Isotoma palustris*) which can readily be distinguished from *Podura* by its larger size, its light greenish grey color marked by a broad, middorsal black band and a narrow white transverse streak for every segment of the thorax and abdomen, its proportionately longer antennae and prominent black eye patches. Of the two, the plant louse deserves no special mention, since it has no inter-relationship with the water springtail at all; but the *Istoma* has. Beginning with the middle of October, I found it in all the locations where the *Poduras* were present, though never as abundant. Later on, when the weather grew colder and the latter species began to form in clusters on the under sides of dead leaves, I rarely failed to find a few *Istomas* interspersed among them. This fact may indicate a primitive state of commensalism, in which the *Isotomas* depend upon the more abundant *Poduras* for protection against the cold; but whether this relationship is general or merely local I have as yet been unable to ascertain. This species also survives the winter in frozen mud, since

all the pieces which I examined contained it in common with the water springtail.

ENEMIES.

Whether the water springtail has any enemies which prey upon it exclusively is not clearly known, nor do my own observations contribute any data on this point. Miall, however, in his "Natural History of Aquatic Insects", says that the imagoes of one species of Dolichopodid flies are known to be habitual enemies of this insect. Suffice it to say, that I noted no Diptera at the lagoon which I recognized as belonging to this family. But there are a large number of animals which, despite the Podura's ability to leap away, occasionally succeed in capturing a few individuals. In my aquaria, I have seen them siezed and devoured by *Hydra fusca* and *Corethra* larvae, and know of a few instances in which individuals that were stuck to a dry surface or in a dying condition, were eaten by Limnaeid pond snails. Their most inveterate enemies were immature water striders (*Hydrobatidae*), a great number of which

hatched out in one of my aquaria. These, though they were rarely able to spear the Poduras with their beaks, were constantly attempting to do so. Oddly enough, when approached by the water striders, the springtails never hopped away immediately but first remained perfectly motionless, evidently feigning death. At that, the water striders usually moved away, but when they did not, their prey was either caught or escaped by means of its furcula.

GENERAL EXTERNAL STRUCTURE.

FORM. *Podura aquatica* is a relatively small Collemolan, the body of the adult being usually one millimeter in length and rarely, if ever, exceeding one and one half millimeters. The length is approximately four times as great as the average width, while the head is about one third and the thorax two thirds as long as the abdomen. In general, the body is sub-cylindrical, greatly wrinkled and with the segments of the thorax

and abdomen so similar that these two regions cannot be sharply differentiated. Post-antennal organs and anal horns which characterize some of the Podurids are entirely lacking. (See Figs. 1, 2.).

The coloration is almost uniform over the entire body, and the predominating color, a deep, dull blue with a more or less definite approach toward purple. Usually the antennae and legs are distinctly purplish, while the mouth-parts, furcula and terminal abdominal segment rarely fail to show a marked reddish tinge. But the tarsi, tarsal claws and distal tips of the mucrones are invariably colorless. (See Figs. 1, 2.).

In texture, the Podura's body is soft and larval-like, and is capable of great contraction and expansion. Consequently the exoskeleton is reduced to a thin cuticula which is very porous and distinctly furrowed. It is probable that these furrows are not indicative of the margins of former sclerites but due simply to muscle attachments, since in the newly hatched larvae, moults and long preserved specimens, little or nothing save the

simple outline of the segments is discernible. The cuticula is thicker on the antennae and legs than on the body, and thickest of all on the dentes of the furcula, where it is folded into a series of rings which undoubtedly serve to give this structure its necessary rigidity. Distributed evenly over the surface of the cuticula are minute papillae which lend a decidedly granular appearance and which are absent only from the tarsi, tarsal claws, mucrones and mouth-parts. In cross section, these appear as merely slight elevations surmounted by single, short bristles and without any noticeable variation in size or structure. On the dorsal side of the thorax and abdomen are a series of segmentally arranged pits, each of which consists of a smooth, flat sub-triangular surface which is slightly sunken, and surrounded by a ring of seven or eight papillae similar to those just described. It is highly probable that these structures are sensoria, since they seem too shallow for glandular pits. In general appearance they suggest post-antennal organs, and La Boulbene (1864),

who noted similar pits in forms like *Anurida* and *Lipura* which possess such organs, concluded that both are homologous, rather than that the latter are derived from ocelli as Nicolet and Schioedte believed. (For the papillae of the cuticula see Fig. 3 in particular).

Besides the minute bristles, which I have already noted, the cuticula presents setae which are much larger, but so few in number that they hardly affect the general appearance of the insect. These are simple, colorless, slightly curved and with conspicuous circular bases which are always well elevated. They are apparently similar in external structure but quite variable in size, and are more abundant on some individuals than on others. On certain parts of the body they show a fairly well defined arrangement; since on the most anterior ridge of the vertex, they usually appear in a row of four, and in rows of eight or more on the two posterior ridges and all the thoracic and the first five abdominal segments. Also, the lateral margin of each dens bears a row of from ten to twelve

(See Fig. 21). Their greatest profusion is on the labrum, the terminal segment of the abdomen and the pleural tubercles along the lateral and ventro-lateral aspects of the body; while from the midventral region they are almost entirely absent. The fact that they are more abundant on the tips of the antennae and legs than on the remaining parts of these appendages would suggest that at least some of the setae are sensory in function. (See Fig. 3 in particular).

HEAD. The head of Podura bears a rather close resemblance to that of a locust. Its longest axis is dorso-ventral, while its greatest width is at its caudal border midway between its dorsal and ventral extremities. From this point, it narrows cephalad and tapers ventrally, ending with the mouth-parts at the extreme ventral tip. The vertex and genae merge into one another, and are thus distinguishable only as areas of the head. The former bears three transverse ridges, of which the foremost is much narrower than the others, while the last takes the form of a blunt crest. Both

genae unite caudo-ventrally to form a midventral suture, and envelope the mouth-parts laterally in three folds; an outer one which becomes continuous anteriorly with the apical margin of the clypeus, a middle one which unites laterally with the base of the labrum, and an inner one which is overlapped anteriorly by the other two. (See Figs. 6, 7.). The frons is small but very prominent and distinct from the remainder of the head. It is sub-triangular in shape with its base dorsal and its apex ventral, and bears three conspicuous pits, a pair of wide dorsal ones and a V shaped ventral one which appears to consist of three small depressions connected by furrows. In arrangement, these pits correspond very closely to the imaginal ocelli of other insects and, could it be shown that these once contained ocelli, there would be strong evidence for regarding the Collembolans as derived from a true Pterygote stock of insects. The clypeus is widest at its apical margin and is separated laterally from the genae by deep furrows in which the antennae rest, while the

labrum is bluntly rounded distally. It overlaps the mouth-parts anteriorly and can be bent back ventrally so as to completely close the oral aperture. (See Fig. 3.).

THORAX. Dorsally, the thoracic segments show a series of very distinct transverse ridges. The prothorax, which is as long but somewhat narrower than the meso- and metathoraces, bears three; of which the first is small, collar-like and almost completely overlapped by the last ridge of the vertex, while of the remaining two, both present a prominent tubercle at each lateral extremity but the second slightly overlaps the third. On the mesothorax, two ridges are distinguishable; a slender fusiform anterior, and a broad, flat posterior one which is laterally joined to the former by two pairs of very short longitudinal ridges. The posterior ridge presents a narrow transverse suture at each end of which is a pit, identical with those already referred to in connection with the cuticula. At each extreme lateral

side of the mesothorax both ridges unite in a common tubercle, while immediately posterior to this is a second, dorsally flattened tubercle bearing a pit similar to the others. The metathorax differs from the mesothorax only in being slightly wider and shorter. Ventrally, the thoracic segments are distinct and similar, but divided by a prominent midventral suture. Each presents a pair of folded, conical projections, which form the bases for the attachment of the legs. In these structures, the folds run obliquely dorsolaterad, are inclined to vary somewhat in distinctness, but are usually so well marked laterally, that they appear to constitute distinct segments. On account of this resemblance, one might be justified in regarding these projections as the basal segments of the legs rather than evaginations of the body proper. But the following observations have led me to take the latter view and, in so doing, I have the support of Lubbock and Tullberg.

1. These projections are soft like the re-

mainder of the body and are capable of being extended and retracted to a considerable degree; thus making their function that of elevating the head when the insect is walking, since the legs alone are too short and too widely spread to do this.

2. They are much thicker than the segments of what I regard as the true legs, and the long axes of the former are dorso-ventral while those of the latter run ventro-laterad.

3. When the insect walks, these structures act as pivots upon which the proximal segments of the true legs rotate, and have only a distinctive backward and forward movement of their own.

4. Finally, in most of the moults they show no folds at all and cannot be marked off from the body proper, while the true legs are very distinct and their segments clearly marked. (See Figs. 1, 2, 12, 20.).

ABDOMEN. The abdomen tapers distally to a blunt point and is composed of six segments. Dorsally,

the first three are so similar to the meso- and meta thoraces that they require no special mention; while the fourth differs only in being distinctly longer, in lacking the short longitudinal ridges which connect the anterior and posterior transverse ridges, and in possessing a prominent tubercle at each side which slightly overlaps the fifth segment and bears a number of pits similar to the symmetrically arranged ones before noted. The fifth segment is narrower but just as long as the fourth and bears three transverse ridges of equal breadth, of which the first is always prominent while the last two are sometimes indistinguishable.

Much smaller than the preceding and partly overlapped by it, is the sixth or terminal segment which consists of a thin, distally rounded supra-anal area which unites proximally with a pair of ventro-laterally placed anal papillae to form the anal aperture. Ventrally, the abdominal segments cannot be very clearly differentiated. The first, second and third are depressed midventrally, but bear at each side a conspicuous tubercle. On the

fourth segment is a well elevated ridge which envelopes the base of the manubrium caudally and laterally. Two transverse ridges are distinguishable on the fifth segment; a broad flat anterior and a narrow posterior one which almost completely overlaps the former when the furcula is flexed. Lying midventrally between the fifth and sixth segments and partly concealed by the anal papillae, is a small, round eminence which, in the Sminthuridae where it is larger and more prominent, is known as the genital papilla. In Podura this structure has a minute genital pore on its summit and can be expanded laterally, thereby greatly enlarging the opening. Neither on the genital papillae nor on any other part of the body have I been able to note external sexual differences. (See Figs. 1, 2, 20, 23, 24, 25.).

EYE PATCHES. Closely opposed to the sides of the frons are a pair of convex, reniform bodies bearing ocelli which appear to be peculiar to Collembolans, and have thus been distinctly termed eye patches. In Podura, these are small relative to the size of the head,

very prominent and well separated from the vertex and genae by deep furrows. A conspicuous sulcus extends down the center of each from the dorsal extremity half way to the ventral, where it unites with a less conspicuous one which transversely bisects the mesial half. Each eye patch bears eight small ocelli which are of almost equal size, of a decidedly reddish color and sunk in shallow pits. Of these, one occurs near the junction of the sulci while the remaining seven are distributed about the periphery. Nicolet figures the left eye patch of this species but shows, in addition to the eight ocelli, fourteen distinct areas bordered by white lines which are not mentioned in his text. I have been unable to observe any structures corresponding to these, but have noticed in specimens which are about to moult, freed parts of the cuticula which stand out as white streaks against the dark blue of the body. In no other way can I account for the white lines on his figure. (See Figs. 3, 4.).

ANTENNAE. The antennae of Podura are short, drooping and originate at the sides of the frons directly below the eye patches. They are composed of four segments, of which the first three are usually equal in length, while the fourth is somewhat longer and bluntly rounded at its tip. In some individuals the basal segment is much broader and shorter than the others, and often the distal one presents a transverse crease on its ventral side which is probably the vestige of a former joint and, if so, indicates that the segments are undergoing a reduction in number. In spite of the fact that injuries to the antennae are of very common occurrence, the Podura's ability to regenerate lost parts seems very limited. On March 11th, an individual that I kept under observation had two segments broken off from his left antenna. Fifteen days later the third segment had been partly regenerated (as shown on Fig. 5.), but there was no subsequent change. From two individuals which had three segments missing, I obtained no results whatever. (See Figs. 3, 5.).

MOUTH PARTS. In general, the mouth-parts may be described as mandibulate, weak for chewing but not reduced. As has already been noted, they are retractile and capable of drawing up liquid food into the mouth cavity. It is thus probable that, as Meinert suggests in referring to the group as a whole, they are in the process of becoming truly suctorial. The mandibles are elongate, colorless, and supported on massive fulcra which divide proximally to form two slender apodemes. Each consists of a narrow apical part which bears five teeth on its mesial side, and a broad basal part which presents minute bidentate eminences arranged in a series of transverse rows and, along its posterior margin, a number of large teeth. (See Figs. 8, 9.).

In the maxillae, three parts are distinguishable; a small colorless apical lobe made up of five curved teeth proximally united, a long, thick, light reddish brown stipe, and a broad, short fulcrum partly divided off from the latter and with a number of very long apodemes extending from its base. (See Fig. 10.). The

labium is composed of a pair of superior hypopharyngeal laminae and a median inferior lamina, which envelope a thin walled hypopharynx. Branching ventrolaterally from the base of the labium, are a pair of long palps which appear to consist of only one segment. The tips of these are dark blue in color, extremely bristly and externally visible at the sides of the labrum near its base. (See Figs. 6, 7, 11.).

LEGS. All three pairs of legs are very similar in structure and size, and made up of five segments which, according to Lubbock and Tullberg, represent the coxa, trochanter, femur, tibia and tarsus. Of these, the first four are of nearly equal length, while the fifth is very much reduced and bears a single, slightly curved claw which is almost one fourth as long as the entire leg.

In walking, the Podura supports himself on the tips of these claws and thereby greatly minimizes his chances of sticking to objects. Herein, he resembles the spiders rather than typical insects which have

plantigrade tarsi. Functionally as well as structurally, the three pairs cannot be sharply differentiated; but, since the metathoracic are more posteriorly inclined than the other two, it is probable they are of more service in shoving the body forward. (See Fig.12).

VENTRAL TUBE. The ventral tube is situated midventrally on the first abdominal segment. It consists of a tubular basal part which inclines anteriorly and envelopes a pair of laterally placed valves, the distal ends of which project well beyond it. These are capable of being opened and shut, and, when shut, appear ventrally as two semi-circular bodies separated by a longitudinal suture. Their inner surfaces are slightly concave and apparently glandular, since, when the valves are opened, a globule of light yellowish or sometimes colorless fluid is plainly visible between them. (See Figs. 13, 14, 15, 16, 20.).

This structure is possessed by all Collembans but by no other insects, and has therefore been made the basis for their classification as a separate order.

Its function, however, is still a mooted question. Latreille regarded it as a reproductive organ but this view is now discredited, since the genital organs have been found to be opisthogeneate as in other insects. At the present time there are three theories in vogue which no one has yet been able to prove or disprove. I shall outline these and attempt to show how closely my observations on *Podura* accord with them. In the first place, Reuter regarded it as an organ for introducing moisture into the body cavity. He claimed that the body hairs of Collembolans are hygroscopic or moisture absorbing, and that, by means of the tarsal claws, the moisture is transferred from the hairs to the ventral tube. But I have already noted that *Podura* lives under very moist conditions, eats liquid food and possesses a porous cuticula. It would thus appear that the insect is fully capable of absorbing moisture without the aid of such a highly specialized structure. In the second place, Davenport suggests that its function is respiratory on the grounds that in *Anurida maritima*, *Xenylla humicola* and *Isotama besselsii*, it appeared as thin walled and

X

filled with blood. In *Posura*, however, the cuticula is perceptibly thicker on the ventral tube than on the body proper where its thinness and porosity would indicate that an exchange of gases could readily take place thru it. Moreover, external respiratory organs should be so situated that they can receive a maximum amount of air, and the ventral side of the body would seem to be the least likely place of any. Finally, Lubbock recognized it as an adhesive organ; a view which is perhaps less far afield than any yet proposed. Such an organ, however, is certainly not much needed by *Podura*, which cannot only rest on the smoothest vertical surfaces without the use of the tube, but has great difficulty in preventing himself from becoming permanently stuck to them if they are the least bit dry. Therefore it seems evident that what *Podura* really needs is, not a specialized adhesive organ, but a specialized lubricating organ; and the following observations have led me to conclude that the ventral tube functions as such in this species. On several

occasions thruout the year, the filter paper in two of my aquaria became so dry that the Poduras experienced great difficulty in walking over it. At such times, a number of them turned over on their backs by bending their abdomens dorsally and anteriorly. Once over, they opened the valves of their ventral tubes, thus exposing the globule of fluid previously mentioned. Then they dipped their tarsal claws into this globule (first the fore pair and then the middle and hind pairs together), which, when withdrawn, had minute drops of the fluid clinging to them. Next, they rubbed their legs together; and, with the forepair, the antennae and mouth, while, with the hind pair, the furcula and terminal abdominal segments- parts which most readily come into contact with the walking media. Finally, they righted themselves by bending head and thorax posteriorly, and walked off unhindered by the filter paper. Also I observed one individual that had his antennae stuck together, free them by going thru similar operations.

CATCH (TENACULUM). Situated midventrally on the second abdominal segment is a small structure designed to hold the furcula back when flexed and known as the catch. It inclines posteriorly, and in *Podura* three parts are clearly distinguishable; a paired corpus which is retracted and hidden from view when the organ is not in use, a stout, terminal cone-like structure which might properly be called the conus, and a pair of lateral rami somewhat notched on their lateral sides. The conus shows a slight midventral furrow at its base, thus making it seem likely that the whole structure was distinctly paired at one time, and giving it a resemblance to a fused pair of biramus appendages. (See Figs. 17, 18.). When the catch is not in operation, the rami are extended laterally; but when the furcula is flexed, are first drawn tightly against the sides of the conus, and then once more extended so as to act as clamps against the mesial sides of the dentes. Immediately after the furcula is snapped free, they are often moved laterally and

mesially a few times in rapid succession while the corpus is being retracted. The action of the catch and furcula is clearly under the direct control of the organism. (See Figs. 19, 20.).

FURCULA. Last of all comes the furcula which is born on the ventral side of the fourth abdominal segment. It is almost as long as the abdomen and, when flexed, extends as far cephalad as the prothorax. Thruout the greater part of its length, it is paired and each furculum consists of three parts; a short, thick manubrium which is fused proximally with its fellow, a long slender dens, and a small, almost colorless mucro bearing a short tooth (Unguiculus superior) at its tip and at its lateral side a distinct lobe (pseudonychia) which may be the vestige of a second tooth. From the manubrium, the dens extends obliquely lateral to a point midway between its proximal and distal extremities where it bends abruptly mesiad at an obtuse angle, thus forming two halves. Of these, the proximal half is relatively

thick and almost circular, while the distal half is tapering and somewhat flattened at its extremity. Often a transverse crease is noticeable on the ventral side of the dens near its bend and it is probable that this is the remnant of a former joint. (See Figs. 21, 22.).

ONTOGENY.

General Considerations.

My observations on the development of Podura reveal characteristics which are primitive, not only as compared with Pterygote insects but even with Arthropods in general. The newly hatched larva is structurally similar to the adult, save in a few minor details which I shall point out later, and the intermediate changes so gradual that, from the standpoint of growth alone, it is impossible to tell just where the larval stage ends and the adult begins. Like the Decapods, Podura moults thruout life, but, unlike them, has no well defined larval instars. It thus has imaginal moults and, in this respect, resembles no Pterygote

insects with the exception of certain species of Ephemera which are known to have one. In having a decidedly incomplete metamorphoses, its development is in harmony with that of the spiders (Araneida), but the latter, according to Comstock, cease moulting when the adult state is reached. Another primitive character is to be seen in the tendency toward variability in the development, which I shall now consider in detail.

1. The adult Poduras tend toward individual variations in the number of moults within a given time. Between December 9th and March 20th, nine specimens in one of my filter paper jars had an average of twenty two moults a piece, while four which lived on the water's surface in a small aquarium averaged only seventeen. Of the two vessels, the former contained an abundance of decayed plant matter but the latter very little. This, together with the fact that two groups of individuals in two similar aquaria each averaged exactly eleven moults apiece between February 20th and April 15th, would indicate that the available food sup-

ply is instrumental in determining the rate of moulting.

2. The intervals between moults may be variable in duration with the same adult individuals. One specimen under record was twelve days without moulting in December, while toward the close of January he moulted twice in forty-eight hours. Usually, however, the intervals were within a more limited range of time, being between eight and four days thruout the winter months and five and three in March and April.

3. In the larvae, both the time and the number of moults between hatching and maturity are susceptible to individual variations. One *Podura*, in growing from one third to seven ninths of a millemeter long, took fifty-four days and had ten moults, while a second needed only twenty-four days and seven moults. Of two other individuals which grew from one half to one millemeter long, one required twenty-nine days and five moults and the other fifty days and eight moults.

4. In the same larvae, the changes in size and pigmentation between moults may be variable. In

the case of one specimen, which was one third of a millimeter in length and still light reddish brown on his dorsal side when I first put him under record, were no noticeable changes between the first, second and third moults. Between the third and fourth, however, he grew to half a millimeter in length and his back took on the dark blue color of the adult; but the three succeeding moults marked only very slight changes. Moreover, the interval between the third and fourth was shorter than any save that between the first and second.

The foregoing facts contribute to the conclusion that, in this species, ecdysis is not a primary factor in growth, and further evidence points the same way. It has already been noted that the cuticula is so elastic as to allow the body great freedom in contraction and expansion. Consequently, if moulting were essential to grow, very few moults would be necessary. But their great frequency is one of Podura's most outstanding characteristics. After reaching ma-

turity, a number of my specimens had an average of thirty-two apiece between October 30th and April 20th, during which time there was only a very slight increase in size. Thus it is probable that here, as among the lower Arthropods, the chief function of moulting is excretory.

ECDYSIS.

The process of moulting consists of five distinct acts.

1. In the first place, the insect becomes motionless and remains so a long while, often several hours, before the actual moulting begins.
2. Then the old cuticula becomes loosened from the tips of the antennae, legs and furcula and, at the same time, the furcula is extended caudad.
3. Next the abdomen and thorax are gently wiggled laterally and dorso-ventrally, with the result that the cuticula becomes detached almost at once from the remaining parts of the body.

4. This accomplished, the head is inclined and the thorax humped up, thus causing the freed cuticula to split middorsally from the head to about the middle of the fourth abdominal segment.

5. In very short order, the thorax, proximal half of the abdomen, head and legs emerge from the moult; but though, up to this point, the four last acts require from five to seven minutes, the furcula is not withdrawn from the exuvia until at least half an hour afterwards, probably because the thick cuticular rings of the dentes tend to hold it back. Contrary to Miall's statement that the newly moulted Poduras are white, the process is attended by no apparent changes in coloration.

In appearance the moults are white and without the slightest vestige of coloring matter, save on ocelli which are very light reddish. Under moist conditions they retain the general shape of the Podura, and often the middorsal slit becomes so completely closed up that its presence is hardly recognizable; but dryness causes them to shrivel up in a very short time.

Usually the eye patches, segmentation of the body, antennae and legs, and outlines of the ventral tube, catch and furcula are quite distinct. (See Fig. 26.).

BREEDING.

At the lagoon the Poduras commenced their breeding activities in April. How many generations they have thruout the year I do not know, but am inclined to believe there is only one. In the fall I found a surprisingly small number of immature individuals and in the early spring practically none at all. Moreover, in my search for eggs at these times, I failed utterly, nor did I observe any behavior suggestive of copulation or oviposition either at the lagoon or among the specimens I kept over winter. Nevertheless, in February five eggs, hidden away in some pond scum taken in the early fall, hatched. It is probable these had been there ever since that time, and were retarded in their development by lack of exposure to sun light and heat. But individuals collected in the middle of April layed

a vast quantity of eggs from which larvae hatched in great numbers. From such limited data, it would thus seem likely that the Poduras breed only in the spring, and that, of the eggs layed, the majority hatch in a short time, while the remainder, because of less favorable conditions, wait until summer, fall or even the succeeding spring before hatching.

Hardly more conclusive is my evidence regarding the method of copulation. In the early part of April clusters of from about twenty to one hundred Poduras were very abundant on the water's surface at the lagoon. Also, specimens which I collected formed similar clusters on the water of my aquaria. Upon examining these closely I noted the following facts. All the individuals which composed them were of mature size. Approximately one third of these were dead or dying. The others were actively engaged in crawling over one another, and occasionally a pair would turn over on their sides and remain for a short interval with the ventral surfaces of their abdomens touching. From time to time

individuals hopped or walked away from the groups. Since it is obvious they were not feeding nor seeking protection from the cold, it is possible they were copulating; and, if so, would further indicate that the dead and dying were the males and those which left the groups the females.

EGGS.

The eggs are layed either singly or in groups of three or four among the filaments of decaying water plants, on dead leaves and within the interstices of moist mud near the shore. Nicolet, the only writer who claims to have seen the eggs of this species, says they are layed on the surface of the water. But I doubt if this is true, since all that I examined refused to float and sank to the bottom, while the newly hatched larvae appeared unable to rise to the surface when once submerged. In ovipositing, the females drop the eggs as they walk along. I observed two individuals, however, which became stationary, extended the furcula caudad, and with the vagina extruded a considerable distance

from the genital opening, layed a string of three very small eggs. This may indicate that the females first distribute their well developed eggs, and then forcibly eject all those remaining in their oviducts. At all events, both of these individuals died shortly after laying, and further evidence tends to show that this is true of the females in general. In one of my aquaria where eggs were layed, every adult died within two days after the larvae began to hatch out. Since the latter were unaffected, it is doubtful if unfavorable conditions caused the deaths. Also in my other aquaria a large proportion of deaths followed the ovipositing.

In being very thinned shelled, opaque, and subspherical, the eggs fail to accord with Nicolet's figure which represents them as elliptical and dark brown. When first layed, they are approximately one eighteenth of a millemeter in diameter and of a distinctly yellow tinge which is due to the presence of yellow oil globules in the yolk. (See Figs. 27, 29.). They depend on moisture for their preservation; and apparently sun

light is a very important factor in determining the rate of the embryo's development, since specimens which I kept in the dark remained unchanged for a whole week. It would thus seem that the time between laying and hatching is at least somewhat variable, but it is probably never less than three or four days under the most favorable conditions. During this interval the eggs increase in size until they have attained a diameter of from one ninth to one sixth of a millimeter. The embryological development commences after they are laid, and in its later stages the embryo is clearly distinguishable through the transparent chorion. (See Fig. 28.). Pigmentation begins shortly before the time of hatching; first on the eye patches which receive the dark blue color of the adult at the start, and then on the dorsal side of the head, thorax and abdomen which become light yellow. In its final stage, the embryo lies curled up inside the egg, with its distal abdominal segment elongated and attached to the egg shell by means of a thread or cord. (See Fig. 30.). The process of hatching is simple and

of short duration. First the body is extended. By means of the thread, the egg shell is drawn tightly against the dorsal side of the head and thorax, and the resulting tension causes a breakage at this point. Once broken, it is quickly torn free of the whole body, save the last abdominal segment, and thrown back. (See Fig. 31.). Almost immediately afterwards, the young larva begins to walk about trailing the crumpled chorion behind him. At odd intervals, he thrashes his abdomen about in his attempt to get rid of this encumbrance, but some time elapses before he finally succeeds. Then the last abdominal segment becomes retracted until it is proportionally no longer than that of the adult.

SUBSEQUENT DEVELOPMENT.

In the subsequent development of the larvae, all my observations tend to show that the relation between size and pigmentation is, with a very few exceptions, constant thruout the whole species. It is thus possible, despite the variability of the moulting

and the gradualness of the growth, to recognize four distinct stages. The first stage represents the larva shortly after the chorion has been freed from the tip of the abdomen. Then it is one sixth of a millimeter long, with the eye patches dark blue and the dorsal side of the body light yellow, but the remaining parts still colorless. It is structurally different from the adult only in the following respects; the head, thorax and abdomen are of equal length, the head is considerably broader than the remainder of the body and the prothorax broader than any of the succeeding segments, the segments are smooth and without any vestige of furrows, the segments of the antennae are equal in length and the furcula very little longer than the legs. (See Fig. 32.). In the second stage, the larva has attained a length of one third of a millimeter and has become proportionally similar to the adult, though the ridges and folds of the body are yet only faintly discernible. The dorsal side is now dull reddish or reddish brown, and the under side and appendages light yellow. Also dark

blue pigment has assembled in a middorsal band down the back, beginning at the posterior margin of the head and ending at the fourth abdominal segment. This always begins on the thorax, and first spreads longitudinally and then laterally. (See Fig. 33.). Five specimens under record had an average of four moults apiece between the first and second stages. When the third stage is reached, the *Podura* has increased its length to two thirds of a millimeter. Then the ridges and folds are as well defined as in the adult and the dorsal surface of the body, dark blue, save the tip and sides of the abdomen which are still reddish as are also the other parts of the body. Between this and the final or adult stage, the only changes are an increase in length to one millimeter and the completion of the process of pigmentation. When the dark blue pigment has fully distributed itself on the dorsal side, it next assembles on the distal segments of the antennae and tibiae of the legs. Thence it spreads proximally until these organs as well as the whole ventral surface of the insect has received

the color. The last parts to receive it are the folds of the mouth-parts, the furcula and the ventral side of the last abdominal segment; but often these remain distinctly reddish thruout life. Both larva and adult have essentially the same ecology, save that the furcula does not come into use until after the first or second moult. During the entire larval period the number of moults may be as many as sixteen, and the time of development is probably never shorter than one month. How long the adults usually live, I was unable to determine, but I do know that they can remain in an active state for at least six months. It is therefore not unlikely that individuals hatched in April, reach maturity in May, survive the summer and fall as adults, hibernate over winter and die in the succeeding April after breeding; while those hatched later complete their life cycle within a shorter range of time.

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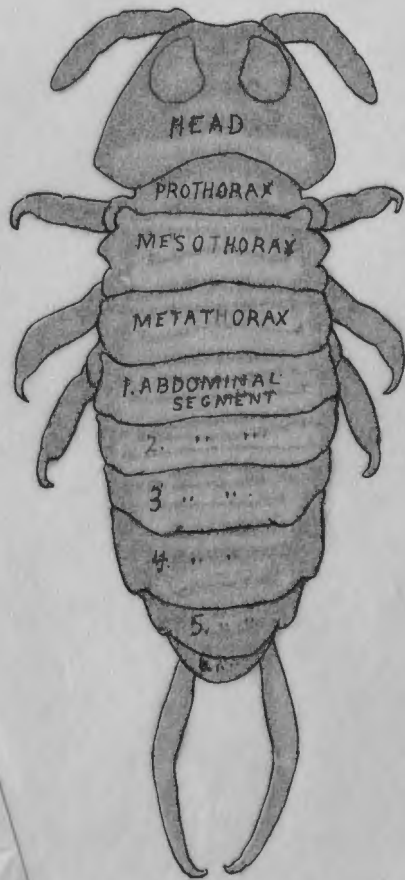
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FIGURES.

Fig. I. Dorsal view of adult
Podura with furcula extended.



G.I. (X86-DEAD)

Fig. 2. Lateral view of adult
Podura with furcula extended.

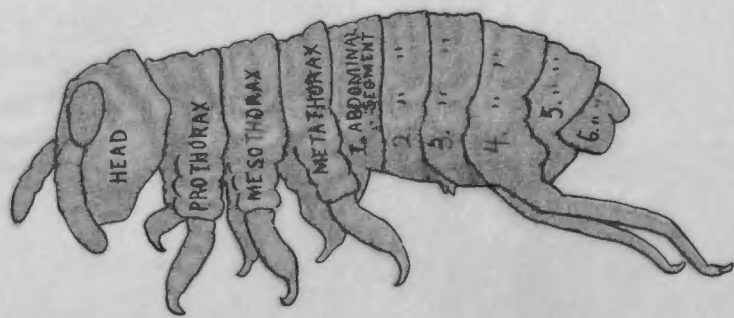


FIG. 2 (X76-DEAD).

Fig. 3. Anterior view of head with labrum extended (proximal three segments of antennae similar in this individual).

Fig. 4. Right eye patch.

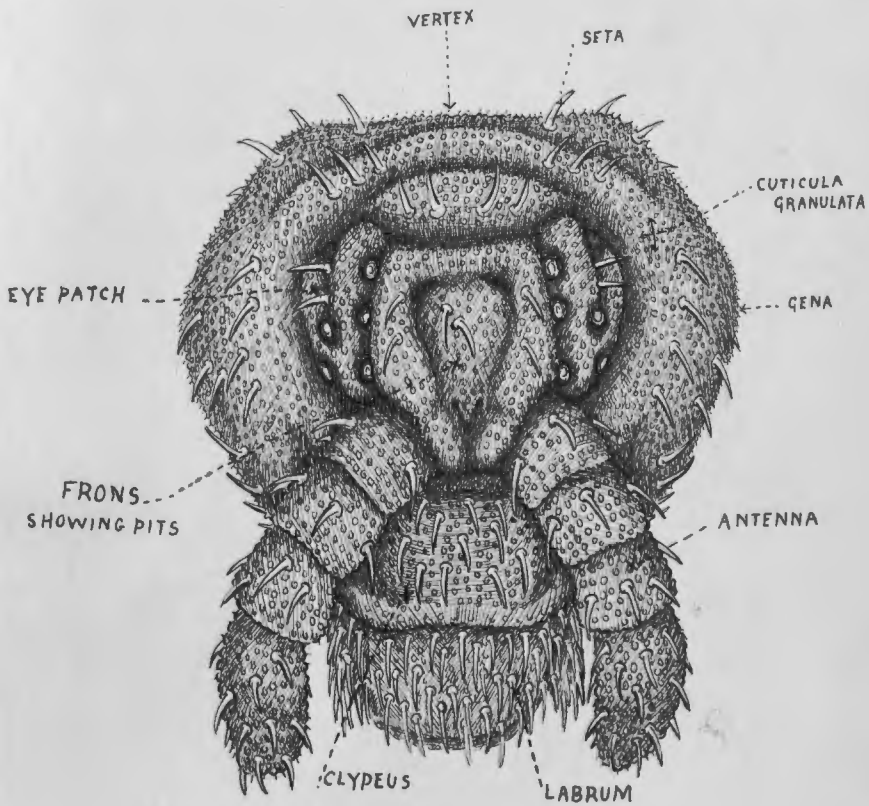


FIG. 3.

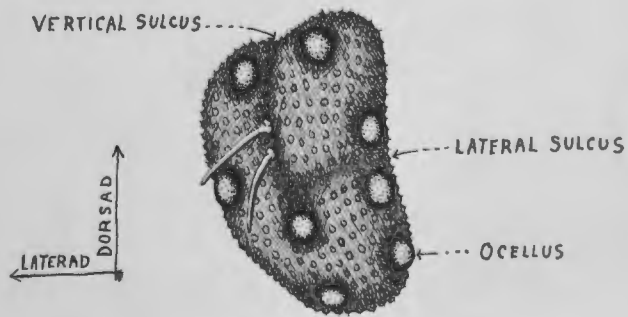


FIG. 4.

Fig. 5. Figures showing regeneration of third segment of left antenna in one individual.



A. LEFT ANTENNA MUTILATED-
MARCH 11TH.

COLORLESS



B. REGENERATION BEGUN-
MARCH 16TH - AFTER ONE MOULT.

REDDISH



C. REGENERATION CONTINUED-
MARCH 23RD - AFTER SECOND MOULT.

DARK BLUE



D. REGENERATION COMPLETED-
MARCH 26TH AFTER THIRD MOULT.

FIG. 5.

Fig. 6. Ventral view of head,
showing genal folds, oral aperture
and palps in situ.

Fig. 7. Lateral view of distal
extremity of head, showing genal
folds, oral aperture and palps in situ.

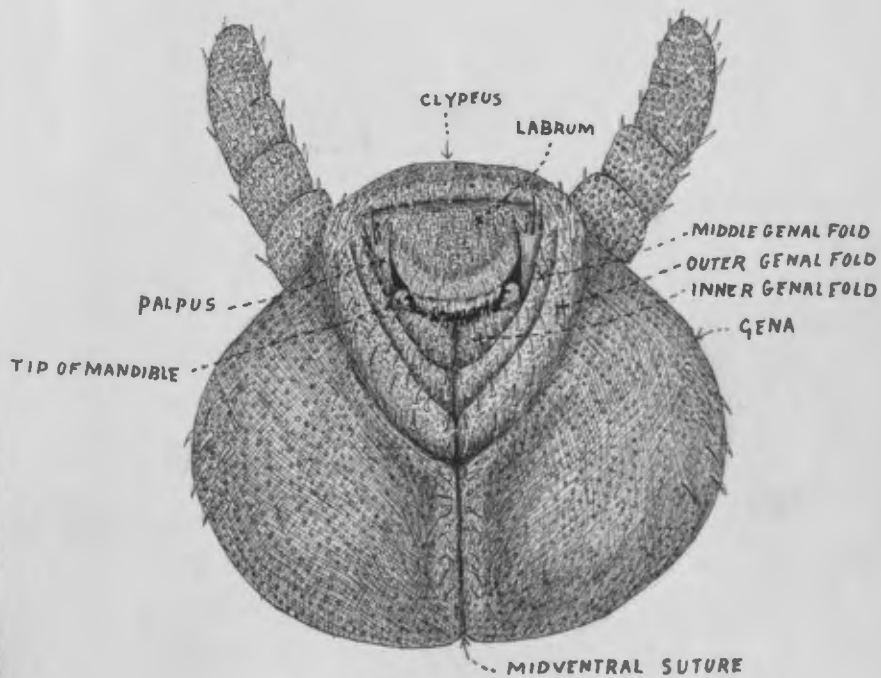


FIG. 6.

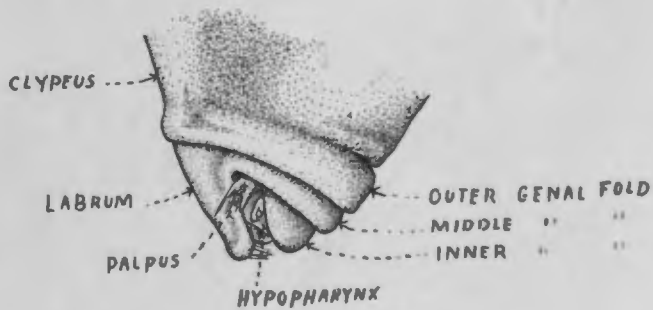


FIG. 7.

Fig. 8. Left mandible - posterior side when in situ.

Fig. 9. Distal (ventral) surface of left mandible.

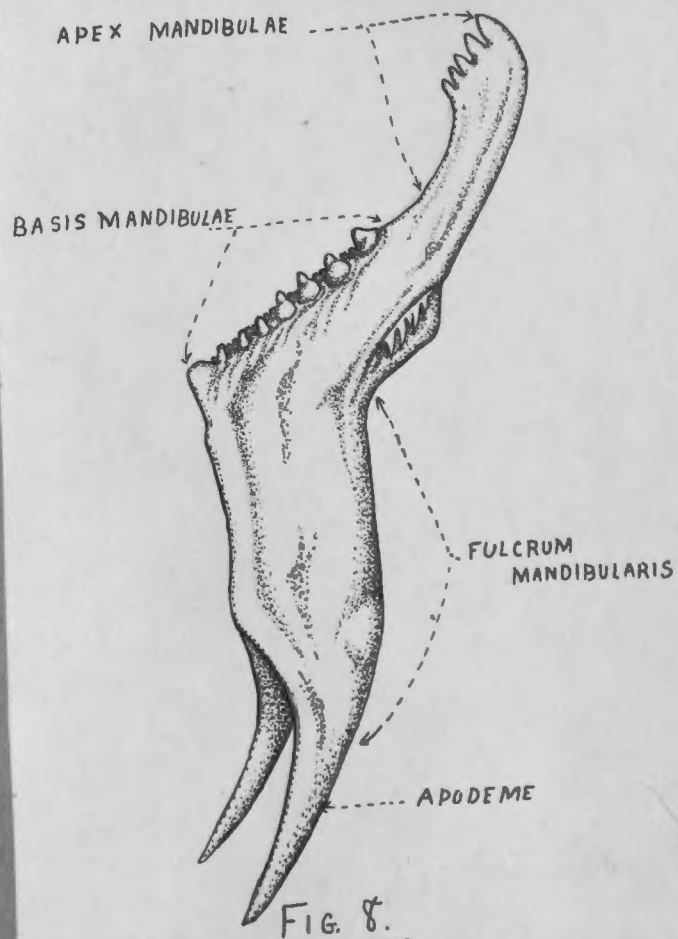


FIG. 8.

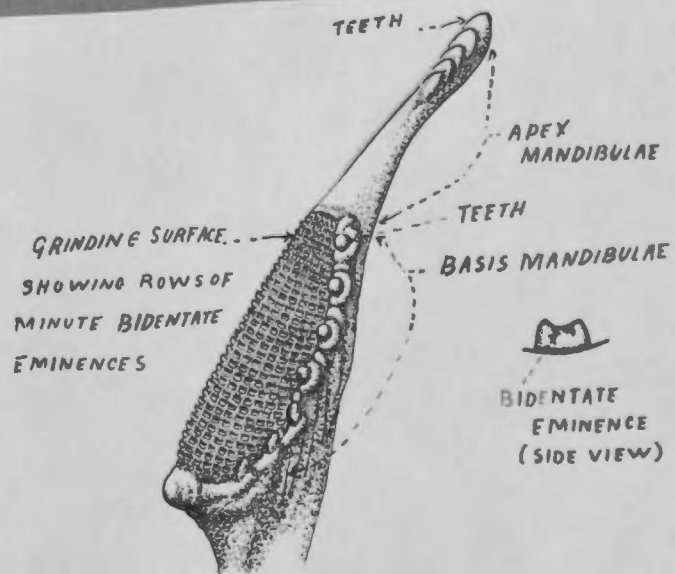


FIG. 9.

Fig. 10. Right maxilla - posterior
side when in situ.

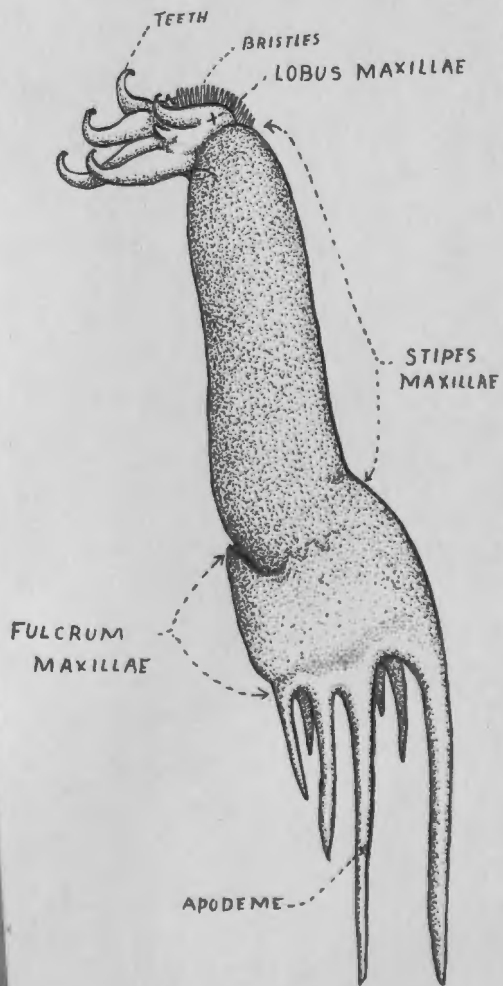


FIG. 10.

Fig. 11. Labium showing palps
and hypopharynx.

Fig. 12. Anterior view of prothoracic
legs, showing ventral protuberances
(coxa is usually retracted and partly
concealed by distal fold of protuberance)

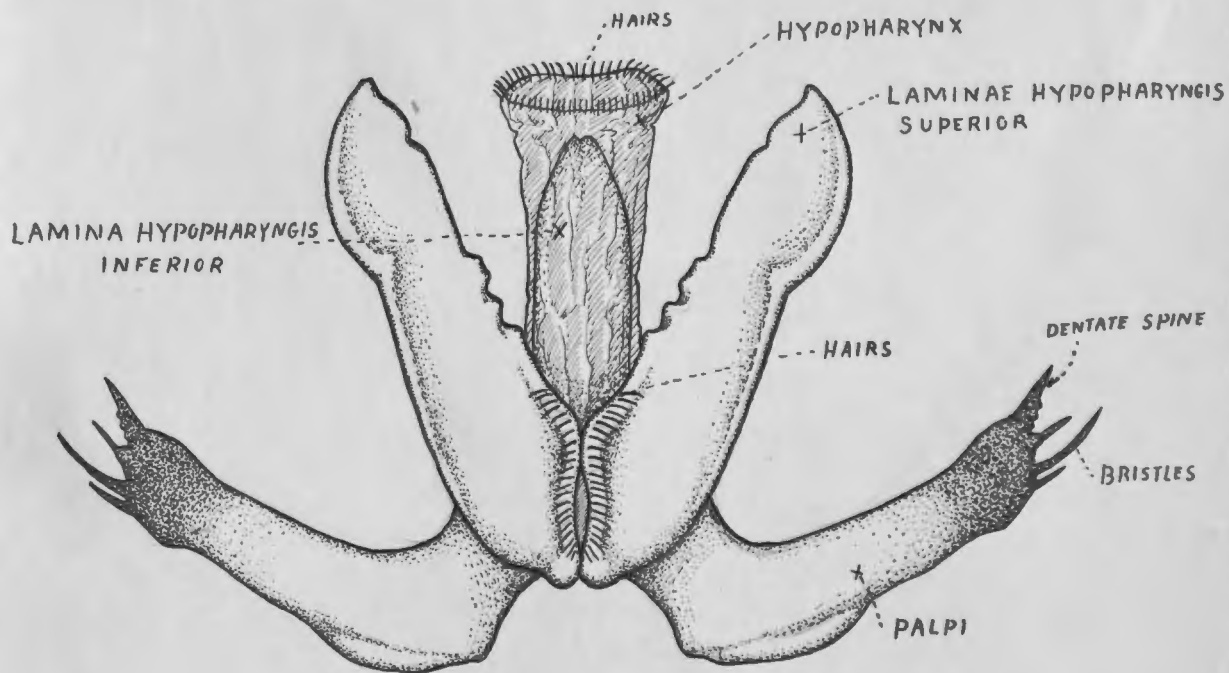


FIG. 11.

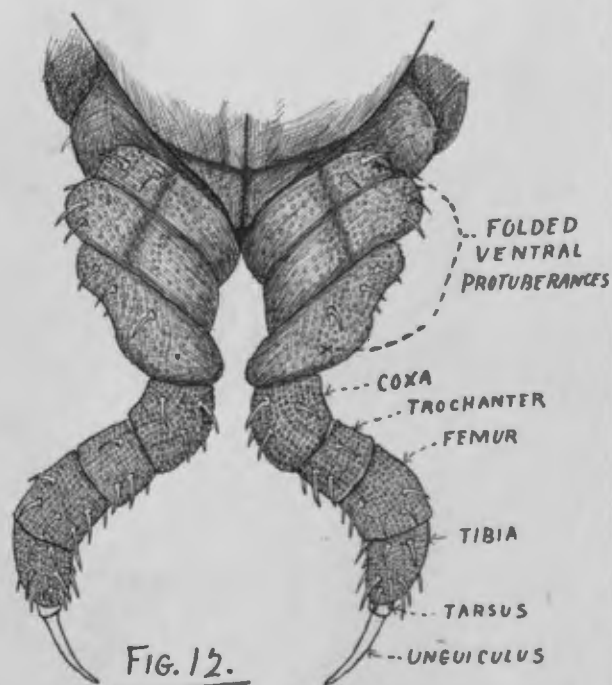


FIG. 12.

Fig. 13. Ventral view of ventral tube
with valves closed.

Fig. 14. Ventral view of ventral tube
with valves open.

Fig. 15. Posterior view of ventral tube
with valves closed.

Fig. 16. Posterior view of ventral tube
with valves open.

Fig. 17. Anterior view of catch when
retracted.

Fig. 18. Anterior view of catch when
extended.

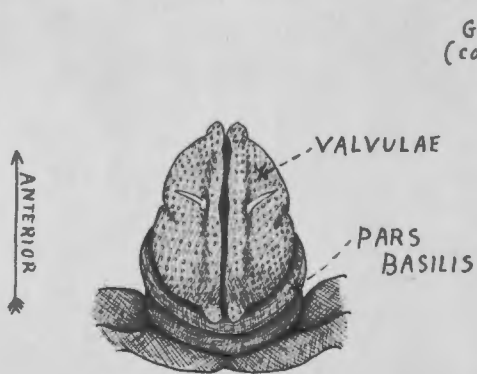


FIG. 13.

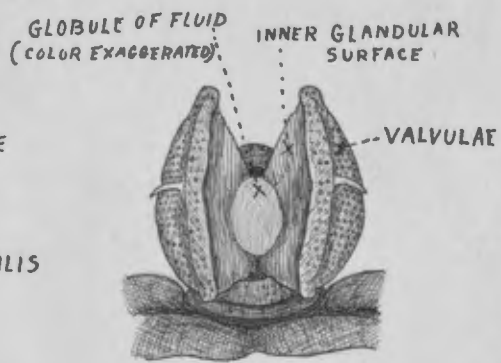


FIG. 14.

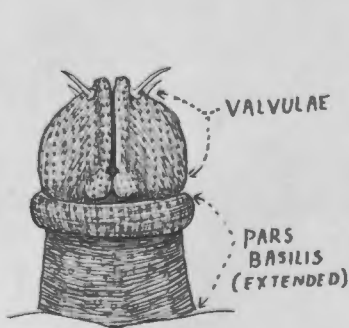


FIG. 15.

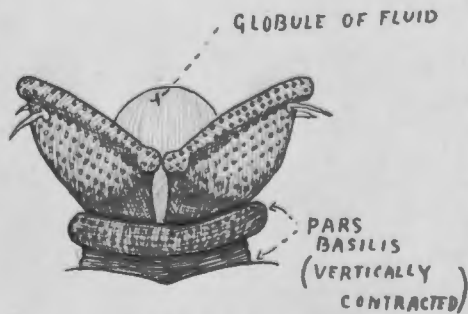


FIG. 16.

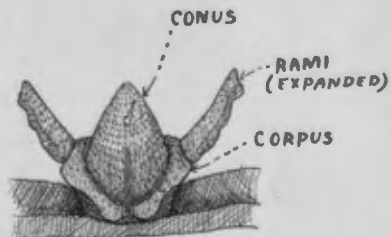


FIG. 17.

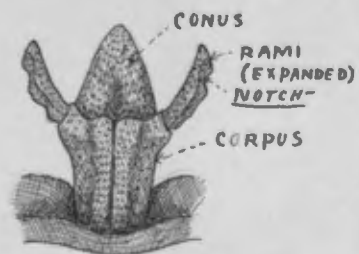


FIG. 18.

Fig. 19. Diagram showing catch in the act of holding the furcula when the latter is flexed-anterior view.

Fig. 20. Diagram of ventral side of Podura, showing furcula flexed.

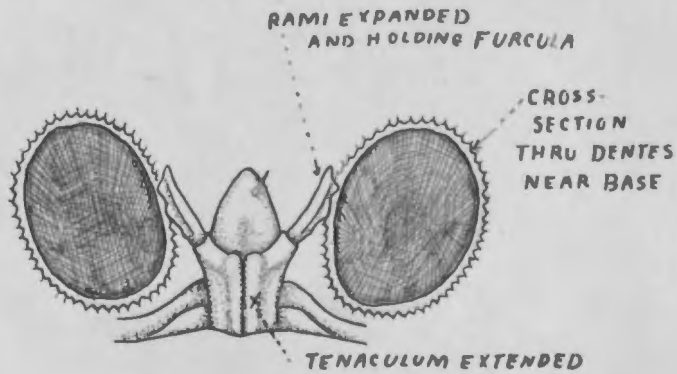


FIG. 19.

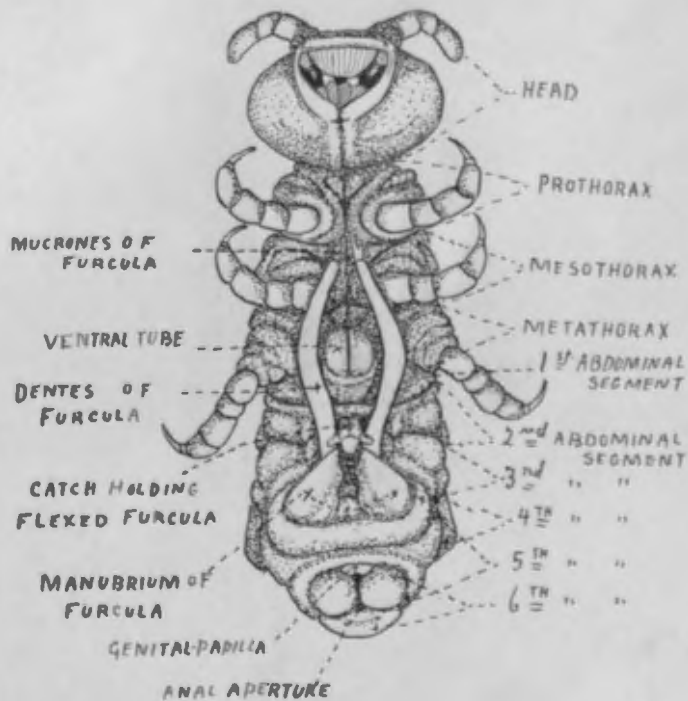


FIG. 20.

Fig. 21. Ventral view of furcula when extended.

Fig. 22. Lateral view of right micro-furcula extended and Podura in a supine position.

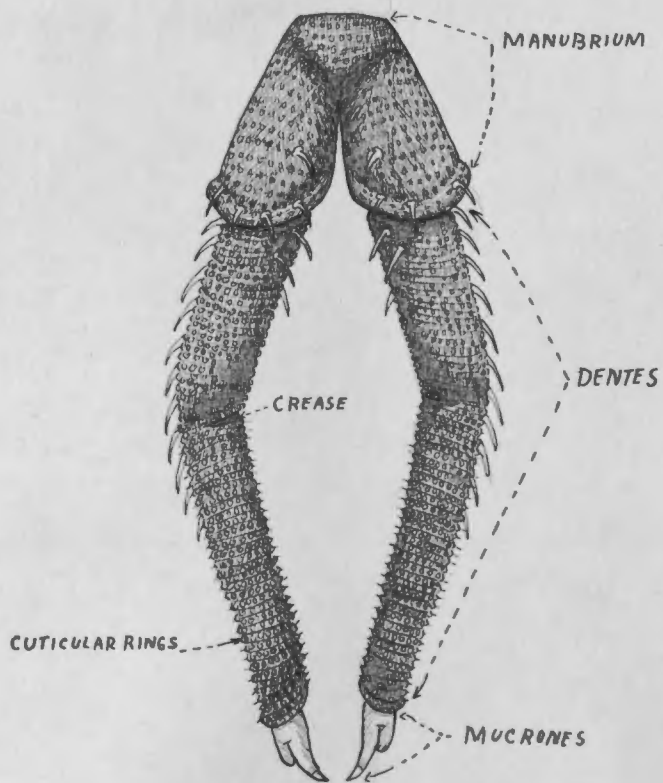


FIG. 21.

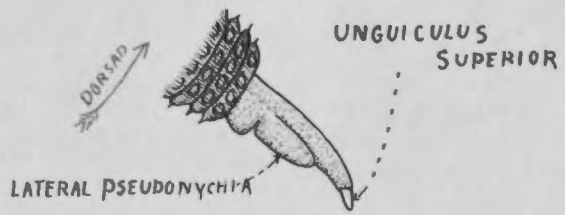


FIG. 22.

Fig. 23. Posterior view of distal extremity of abdomen, showing genital papilla.

Fig. 24. Ventral view of genital papilla when contracted.

Fig. 25. Ventral view of genital papilla when expanded.

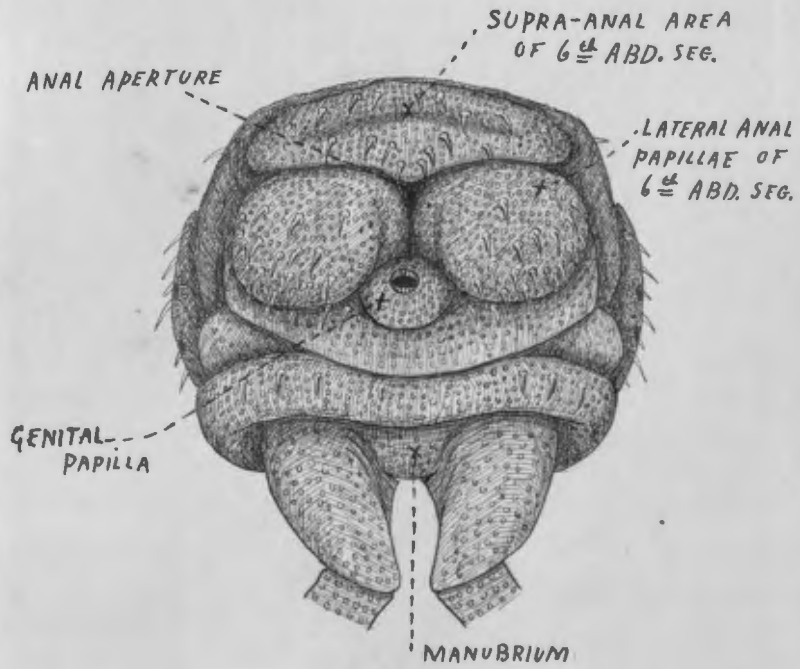


FIG. 23.

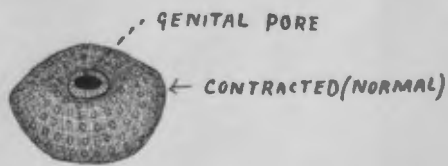


FIG. 24.

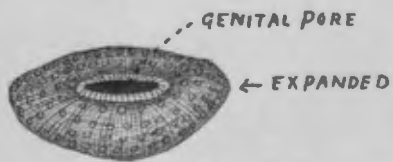


FIG. 25.

Fig. 26. Dorsal view of a typical
moult.



FIG. 26. (MID-DORSAL SLIT
EXAGGERATED)

Fig. 27. Egg of *Podura* immediately after oviposition.

Fig. 28. Egg showing embryos in an advanced stage.

Fig. 29. Egg immediately after oviposition.

Fig. 30. Egg about one day before hatching.

Fig. 31. Larva in the act of hatching.

Fig. 32. Larva one sixth of a millimeter long - first stage.

Fig. 33. Larva one third of a millimeter long - second stage.

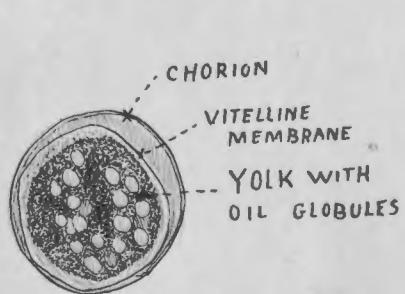


FIG. 27.

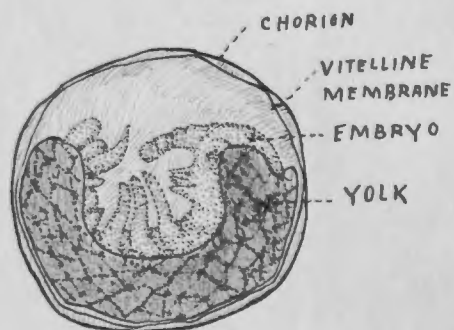


FIG. 28.



FIG. 29. x102



FIG. 30. x102



FIG. 31. x102



FIG. 32. x102



FIG. 33. x102