ECOLOGICAL STUDY OF AQUATIC MIDGES AND SOME RELATED INSECTS WITH SPECIAL REFERENCE TO FEEDING HABITS.

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CHIRONOMIDÆ.

INTRODUCTION.

The insects belonging to the family Chironomidæ, commonly known as midges, constitute an obscure group of Diptera which, on account of their small size and inoffensive habits, have very largely escaped notice except as they may have been mistaken for mosquitoes, which they resemble only in general appearence. They are, however, very common in every community from the polar region to the Tropics. The adults are often seen on moist evenings flying in dense swarms near the ground, over sidewalks, or under trees by the roadside, and it is in this brief period of their existence, consisting of from 5 to 10 days, that they are most familiar to the general public.

Closely related to the Chironomidæ are the Orphnephilidæ, a family of semiaquatic insects as scarce as the Chironomidæ are common, the only known habitat in this country being in the environment of Ithaca, N. Y. The larval stages of the Chironomidæ, which extend over a period varying from all winter to 25 or 30 days, according to food and weather conditions, are only infrequently observed, chiefly because of the small size and secluded habits of the larvæ. They are aquatic, mainly fresh-water, insects living in burrows which they construct by fastening together the débris found at the bottom of ponds with silk secreted by their salivary glands. The great abundance of these larvæ and their relation to other aquatic organisms were the fundamental considerations that gave impetus to this study. It was hoped that an investigation of their feeding habits would give a clue to the chief adaptations which have given rise to their numerical dominance and widespread distribution.

That they do subsist in great numbers has been called to the author's attention not alone by his own observations, but by various published and unpublished works of students who have recorded them as forming an important part of the food of trout, suckers, and various other fish, and of salamanders, dragonflies, mayflies, and a variety of other predacious aquatic organisms. Herein lies the chief interest of these observations from the fish-cultural point of view, that a careful study is made of a particular group of animals which are engaged in converting vegetable detritus and other organic materials existing in fishponds into a form suitable for consumption by fish. How useful they are as a direct medium in transforming and conserving the food supply furnished by the microorganisms found in small quantities in all habitats will be shown in greater detail in the subsequent discussion.

In beginning this work the larvæ of many species were examined in order to determine their stomach contents. The organisms found were so similar, both in number and variety, to those available in a given locality that there seemed to be little or no sorting in their method of feeding. Consequently, attention was directed more to their method of capturing food than to the substances eaten, and it was here that the fundamental adaptations were found which enable the different genera and species to live in a similar environment with a minimum amount of competition. The small size of the larvæ and their great power of tiding over periods of food shortage, together with their capacity to live in habitats containing a scanty supply of oxygen, readily enable them to subsist where a larger animal would find the food supply insufficient or the environment unsuited to its manner of life.

In this study of the feeding habits the author has endeavored to associate into groups those larvæ which obtain their food in an essentially similar manner. An attempt has been made to cover the entire family. The subfamily Chironominæ has been divided into six groups, while the subfamilies Tanypinæ and Ceratopogoninæ each constitute but a single group. The number of these divisions shows in a somewhat graphic way the relative size and amount of specialization of the three subfamilies. It is to be hoped that these groups will be found sufficient to accommodate all the various species of the family, although the two consecutive seasons devoted to this work, in the absence of any considerable literature on the feeding habits of the larvæ, are all too short a time to exhaust a study involving such small and relatively obscure organisms.

This work was done in the entomological laboratory of Cornell University, under the direction of Prof. J. G. Needham, to whom the author is greatly indebted for much counsel, assistance, and encouragement in the prosecution of the work. The author wishes to acknowledge his appreciation of the assistance rendered by Prof. O. A. Johannsen in the identification of specimens, general suggestions, and sympathetic interest and encouragement in every phase of the work. He is also greatly indebted for many favors from the various members of the Department, to whom he wishes to express his appreciation for the thoughtfulness that prompted such generous cooperation.

TECHNIQUE.

In order to carry on the laboratory experiments with various chironomids it was found desirable to keep a number of living larvæ always on hand. For most larvæ very simple containers proved most satisfactory. Those that live in the manner described under Group III were brought home, together with a small mass of the débris in which

they were living, and placed in shallow agateware trays. The débris containing the larvæ was usually spread out, so as not to be more than one-fourth of an inch deep, and was then covered to a depth of half an inch with tap water. After a day or so, when the larvæ were especially numerous, as a rule they used all the loose débris in constructing rather long U-shaped tubes, where they usually succeeded in maintaining themselves for weeks at a time. The shallow agateware trays were rather generally used for the various forms of larvæ that could be collected in numbers. They are especially to be recommended on account of the large amount of water surface exposed to the air, thus facilitating aeration.

In breeding the various species collected a considerable number of individual receptacles were required. In the early experiments square watch glasses with covers were used successfully. They were later discarded in favor of medium-sized test tubes. Such a tube with a cotton wool plug has numerous points of advantage over a watch glass. First, the cotton plug permits a free exchange of gases. This circulation prevents the accumulation of moisture on the inside of the test tube, so that the newly immerged fly is not so liable to be caught in a water film and drowned. Second, the cotton plug makes a very satisfactory surface to which a freshly immerged fly may cling. Third, a number of test tubes may be placed together in a slanting position, so that the water which they contain will expose a proportionally large surface to the air, thus insuring perfect aeration. Fourth, a considerable number of tubes may be placed in a tray and a uniform temperature maintained either by flowing water or by evaporation from the surface of standing water. Fifth, the data concerning the larva may be written on a small piece of paper and inserted with the cotton in the mouth of the test tube.

Mectriocnemus knabi larvæ were kept for several weeks by bringing in the leaves of the pitcher plant and placing them so that they would remain in an upright position. They were kept full by the occasional addition of small amounts of water. The larvæ were also kept for weeks at a time in petri dishes containing the water and insect remains obtained by emptying the leaves of the pitcher plant. They do not appear to be so exacting in their environmental requirements as most chironomid larvæ and can doubtless be reared in most any sort of a container.

Chironomus lobiferus were brought into the laboratory in water-soaked Sparganium stems, which were allowed to float freely in trays filled with water. In this condition the larvæ maintained themselves for considerable periods at a time. Upon removing them from their burrow they were found to adjust themselves to various artificial receptacles. The most satisfactory glass preparations for the observation of the habits of *Chironomus lobiferus* larvæ were constructed so as to give flat horizontal surfaces. This was accomplished by cementing two rectangular strips of glass cut from cover slips to either side of parallel capillary glass tubes. The size of the capillary tubes used was slightly larger than the full-grown larva.

It was found that King's "Microscopical Cement" is more satisfactory than a cement made by dissolving asphaltum in turpentine or xylol, especially when it is desired to make permanent mounts of the silken tubes. It is necessary to dehydrate rapidly in order not to dissolve this cement, but even with this defect it is more satisfactory than other cements soluble in xylol. Because of the uniform thickness and the

flatness of the surfaces (fig. 26) this type of glass preparation is more satisfactory than any flattened tube the author was able to manufacture.

Ehrlich's acid hematoxlin was found to be the most satisfactory of any stain used for bringing out the silk structures. "Licht green" and "eosin" were also used but were not found satisfactory. The licht green, while staining the silk glands and the silk within the silk duct, did not stain the silk outside of the body. The eosin, while staining the silk slightly, was found unsatisfactory because of the ease with which it was removed in dehydration.

There are few animals that lend themselves more readily to a laboratory or lecture demonstration than do these stem-dwelling larvæ. They seem to differ decidedly from other chironomids, especially those that characteristically live in a mud burrow, in their reactions to strong light. Their greater tolerance of light enables one to demonstrate the silk-spinning movements and the general behavior of the larvæ by means of a stereopticon. The only requirements are that the larvæ shall have recently built a fresh, clean silk tube in a glass preparation, and that the temperature of the water be kept down to normal room temperature. The reason for requiring that the silken tube be a fresh one is that after a week or two the silk becomes much discolored by the lodgment of fine particles as well as by the deliberate attachment of masses of castings to the ends of the burrow. It is only necessary to remove the larva by a jet of water and then the tube can be removed by a needle. A few hours will usually suffice to enable them to again replace the silken tube. The temperature is easily controlled by having a specially constructed lantern slide through which a current of water can be made to pass. A type used with considerable success was constructed as follows:

Two pieces of sheet brass the size of a lantern slide were cut so as to give a symmetrically placed rectangular opening 1¼ by 2 inches near their center. These two brass strips were drilled and fitted with screw bolts. Two sheets of transparent celluloid and a single sheet of rubber packing material about an eighth of an inch in thickness were punched so that the holes coincided with those in the brass plates. The rubber packing was cut so as to give a rectangular opening which coincided with that in the brass plates, and the parts were assembled in the following order: Sheet brass, celluloid, rubber packing, celluloid, and brass. Two one-eighth-inch rubber tubes were connected with the inclosed chamber by openings at diagonally opposite corners. It was found easier to make this connection through one of the sheets of celluloid than through the rubber packing material. These tubes were fused in with beeswax and their ends weighted and put into separate jars. The tube opening at the bottom of the lantern slide was used as the intake tube and the jar to which it was connected was filled with cold water. Then by gravity the water was made to flow through the chamber. Two adjustable pinchcocks were provided and the flow of water stopped while the glass preparations containing the larvæ were being placed in the chamber. Then by regulating the flow of water by means of the pinchcocks the preparation was used as long as desired. When the water had all been passed through, the jars were changed and it was sent through a second time. It was found desirable to have the water removed from the top of such a chamber on account of air bubbles which tend to accumulate when well-aerated water is heated slightly.

STRUCTURE AND FUNCTION OF HEAD OF Chironomus braseniæ WITH REFERENCE TO FEEDING HABITS.

The head of the chironomid larva, while so constructed as to be wonderfully adapted for feeding upon a large variety of foods in diverse environmental conditions, nevertheless shows a wide range of variations. These variations, while especially well marked in the subfamilies, are also to be found among the different genera and to a lesser extent within the genus. They have been taken advantage of by the systematists, who have figured the structures that best lend themselves to their purposes. Miall and Hammond (1900) and more recently Goetghebuer (1911) have made more careful studies of these structures, with special consideration of their morphology. The object in this discussion is therefore to consider the special adaptation of the mouth parts, with particular reference to their function in the feeding habits. As certain of these structures have already been treated more fully than others, only those parts whose function appears to the author to be either poorly or inadequately discussed elsewhere will be considered in great detail here.

In this study the head parts of *Chironomus braseniæ* n. sp. are figured, and an attempt is made to point out the more conspicuous differences between this species and the larger and better known species upon which Miall and Hammond (1900) worked. The most noticeable feature about the head of the larva of *C. braseniæ* is its great width relative to the length. The labrum is also unusually narrow and the head has a roughly triangular outline (fig. 10).

The labrum undergoes a remarkable amount of variation in minor details, such as the presence or absence of a thin triangular labral comb, variously arranged pectinate hairs, and paired lobular bodies. The structures located on the ventral surface of the labrum are commonly assigned to the epipharynx and consist of a three to many toothed epipharyngeal comb located on the anterior border, a thickened chitinized horseshoe-shaped area just posterior to it, within which are attached a variable number of claws or spines, and just outside of these spines a pair of peculiarly mandiblelike structures, known as premandibles (Goetghebuer) or lateral arms (Johannsen). The corresponding structures of *C. braseniæ* are peculiar in being reduced in number, larger in size, and more strongly chitinized as an adaptation to its leaf-eating habits. The function of the labrum is that of a very complexed scraping organ, and the degree of specialization of its various parts is usually found to be correlated with the nature of the food and its method of collection.

The labrum is rather less specialized in this species than in *Chironomus cayugæ* and the others included by Goetghebuer (1911) in his Group I. The pectinate hairs are fewer in number and simpler (figs. 1 and 2, *s*). The epipharyngeal comb (figs. 1 and 2, *co*) consists of three large rounded teeth with smooth inner surfaces. The horseshoe-shaped chitinous area (figs. 1 and 2, *h*) on the ventral surface of the epipharynx is in this species much less horseshoe shaped than usual. It is here represented by two chitinous bars which articulate in front with the thickened anterior border of the labrum and posteriorly with a median caudad projecting process (fig. 1) within this horseshoe area. There are four pairs of chitinous hooks (figs. 1 and 2, *e*), rather blunt in outline in *Chironomus braseniæ*, but often very much specialized and developed as minutely serrate plates. Just lateral to the posterior end of the horseshoe-shaped chitinous area are the "lateral arms" of Johannsen or "premandibles" of Goetghebuer (figs. 1 and 2, *a*). These are provided

with a mesad projecting process, which loosely articulates which the central chitinous structure (figs. 1 and 2). These arms are provided with muscles and are capable of a wide variety of movements.

The lateral arms, while figured for a considerable number of species, do not seem to have been treated at all from a functional standpoint. From the author's experience it seems possible that the small size of the head and the constant activity of the larva have served to vitiate many attempts in this direction. It is easy to see from the study of a large number of dead larvæ that the arms are to be found in a variety of positions, the most frequently observed position being that found when the labrum is drawn in between the maxillæ. When the labrum is in this position, the arms project posteriorly down into the pharynx, just above the surface of the hypopharynx. When the labrum is raised somewhat, they are seen to lie just above the labium. When the labium is elevated, as in the normal feeding, the ends of the arms are farther forward.

Several times while examining the labium of living larvæ the author has observed what he considers the normal movements of these appendages. They are moved forward and toward each other when the labrum is elevated, so that their setigerous anterior margins (fig. 2, a) scrape the chitinous claws (figs. 1 and 2, e) attached within the horseshoe area, removing any food material that they may have collected. They are then swung backward in close proximity to each other as the labrum is pressed down. From these occasional observations, together with the structure of associated parts of the pharynx, it seems reasonable to conclude that the lateral arms have an important function, as they convey the food down the alimentary tract to such a level that the circular muscles of the esophagus can act upon it in the swallowing process. They would, therefore, appear to supplement the mandibles and maxillæ, which may have lost something of their primitive functions as an adaptation to their present manner of life.

The mandibles have been figured by a large number of authors, especially from the systematic standpoint. The author has tried to show in detail the method of articulation of the mandibles with the head because of the restricted movements of these appendages resulting from their method of attachment. The anterior median margins of the epicranial plate (fig. 5) carry on their inner surfaces special internal chitinous processes (figs. 4 and 5, i) upon which the mandibles articulate. These processes alone would give the mandibles a considerable freedom of movement. This movement, however, is somewhat restricted by the process q (figs. 3 and 6) and the plate st (figs. 4, 11, and 12). Their chief movements are consequently confined to plains approximately at right angles to each other. In this motion they oppose the labium rather than each other. The complexity of the adductor muscles, however, enables the mandibles to oppose each other when elevated. The external process of the mandible (fig. 3, q), which projects beyond the point of articulation out over the thickened margin of the epicranial plate (fig. 12, pr), adds considerable firmness and rigidity. The function of the mandibles is of especial interest, because they, next to the labium, limit the range of adaptability of the chironomids. This is especially emphasized in the discussion of the adaptability of *Chironomus braseniæ* and *C. lobiferus*.

The maxilla (fig. 11) has been the object of considerable speculation especially as regards its homologies. Mundy (1909) figures vibrissæ, which he considers as replacing the striated structures shown in figures 11 and 12, c. This structure Goetghebuer (1911) considers a part of the labium. The attachment of the movable parts of the

maxilla is especially interesting in this connection. The structures below *p* (fig. 11) are attached to the chitinous plate *st* (fig. 11) along its outer margin. The parts marked *l* and *g* (fig. 11) are attached to the part beneath the letter *p* (fig. 11) and are capable of being folded over it. They articulate at *w* (fig. 11) and swing inward. In attempting to homologize these structures the plate *st* (figs. 11 and 12) is considered as representing the stipes, which is fused to the anterior margin of the epicranial plate *p*. Evidently *p* (fig. 11) represents the palpus and the structures below it (*p*) the palpifer; *l* and *g* represent the combined lacinia and galea and *c* the two cardos, one beneath the other.

The movements of the maxillæ are restricted by their attachment to a fixed plate outside the plane of movement of the mandibles. It seems probable that their function has been largely taken over by the labrum and especially the lateral arms. The anterior part (fig. 4, *g* and *l*) is capable of a considerable movement in a lateromedial direction and although rather thin is doubtless an important factor in the concentration of the food particles. This part of the maxilla, as well as the palpifer, carries a number of sense papillæ which doubtless have more or less well-developed taste cells, as it is easy to see that the larvæ have very acute taste organs in this part of the head. It therefore seems probable that as the function of the maxilla has decreased the maxilla itself has become very much modified.

The labium in the family Chironomidæ is very important in the determination of the larva and consequently is a familiar structure in the systematic literature. This structure is developed as a thickened plate with an anterior toothed margin. It is so closely fused with the lower surface of the epicranial plate that in many species it seems to be only a modification of the anterior border of this part of the head. This is especially noticeable in those species which show a suture between these plates in the labial region. This structure is, however, capable of being removed as a separate plate, and more complete study will doubtless show a similar arrangement throughout the subfamily. Its function is that of a scraping and cutting edge, and it is next to the mandibles in its importance in governing the range of adaptability of the species.

The hypopharynx (figs. 7 and 8) is furnished with chitinous plates *th* and a variety of spines and setæ. This anterior portion is separated from the posterior by a cavity *z* (fig. 7), which is continuous with the salivary ducts *d* (fig. 8). It is supported by a chitinous ring *f* (fig. 8). The posterior part is furnished with a large number of backward pointing setæ on its dorsal surface and is supported by a chitinous skeleton shown in figure 8, *k* and *f*. The arms (fig. 7, *k*) of the hypopharynx form a point of attachment for the upper end of the pharynx and hold this part extended.

The function of the hypopharynx is doubtless sensory to a large extent, as its rôle of guarding the entrance to the alimentary tract and the exit of the salivary ducts would naturally demand. It seems probable that the backward projecting setæ (fig. 7, *e*) at the entrance of the pharynx may also serve to disentangle the food material brought in by the lateral arms. The structure of the anterior and posterior borders of the cavity in the hypopharynx through which the silk escapes is of special interest in connection with the study of the silk structures spun both by this and other species of Chironomidæ, although the part which it plays is still uncertain.

SUBFAMILY CHIRONOMINÆ.

Group I.—Chironomus lobiferus Say.

In this first group the author wishes to consider as a type one of the chironomid larva that seems to have departed most widely from the more familiar examples. This species, however, is capable of living in a loose mud burrow and of collecting and eating its food directly from the surface of the accumulated débris about it, but this is not its most characteristic method of feeding when living in competition with other species.

HABITAT.

The burrows of *Chironomus lobiferus* may be found on floating logs, at the bottoms of ponds, or attached to stems, stumps, and other perpendicular surfaces. In these habitats the larvæ live by straining the fine particles from the water which passes through their burrows. A still more unique mode of life is shown by *C. lobiferus* in the readiness and frequency with which it penetrates the stems of aquatic plants. A list of the plants attacked includes so nearly all the submerged aquatics that it is concluded that the structure of the epidermis is the important limiting factor.

The presence of larvæ within a stem is easily recognized by two small round openings through the epidermis which they make at either end of that portion of the tissue occupied by their burrows. These openings enable the larvæ to set up a current through their burrows by throwing their bodies into an undulatory motion. In this way the larvæ are able to obtain food and carry on their respiratory processes at the same time. The general behavior of *Chironomus sparganii* Kieffer [*lobiferus*(?)] larvæ has been observed and well described by Willem (1908).

The general facts are as follows: The larvæ are found in both dead and living stems of Sparganium, in the softer tissue where the chlorophyll is lacking. They are commonly located some 8 or 10 inches below the surface of the water. In the dead and especially the well water-soaked stems of Sparganium they are to be found in abundance. Their burrows communicate with the exterior by two small openings from one-quarter to one-half millimeter in diameter. The openings are at varying distances from each other, but usually measure in a rough way the relative lengths of the larvæ, the average distances being about 15 millimeters.

The method by which the larvæ penetrate these stems seems not to have been observed nor questioned so far as the literature is concerned. In Group IV is discussed the adaptation of the head of *Chironomus braseniæ* for burrowing, and evidence is given that the penetration of the uninjured epidermis is a matter of very considerable difficulty. The larvæ of *C. braseniæ*, however, show a unique adaptation to this procedure by spinning a special silken arch by which they are able to apply pressure more advantageously to their mouth parts. This phenomenon was not seen in a considerable series of *C. lobiferus* larvæ that were kept under observation for this purpose, and it is concluded that this species has not yet developed such an adaptation.

The experiments set up for the purpose of testing out the ability of a larva to enter an uninjured stem were of two kinds: First, outdoor experiments with uninjured stems fastened together as rafts and placed among the infested stems; and, second, small sections of infested stems taken into the laboratory and placed in watch glasses, in which

several larvæ removed from similar stems were placed.   In the outdoor experiments the rafts were made of freshly cut stems about 2 feet long and were left to float freely in an infested portion of a pool where similar larvæ could be taken at any time during the year.   These stems were observed at intervals for two months, and none showed any signs of the presence of the larvæ.   In this relatively short period they showed but slight signs of decay and practically no accumulation of diatoms.

In the laboratory experiments with sections of similar stems in a more advanced stage of decay only such stems as had already been infested were used.   It was soon found that the larvæ would readily accept these stems, which they usually entered by creeping into the openings at the ends.   The sections cut to fit into a Syracuse watch glass could ordinarily be entered from the ends and were usually short enough to enable the larvæ to maintain their water current without penetrating the epidermis.   In order to make it necessary for the larvæ to penetrate the epidermis, the cut ends were coated with melted paraffin.   The result in many cases was that they simply crawled under the stems and spun their silken tubes, fastening them to the stem above and the glass below.   In only one instance did a larva penetrate the stem from the side.   In this case the opening was rough and jagged in outline and was located near one of the lower corners of the stem, where it seems fair to assume that the larva might have gained some advantage (by catching its posterior end under the edge of the stem) from the sharpness of the angle that would in a way compensate for its light weight in bringing pressure to bear on the mouth parts.   This seems especially possible when it is observed that the claws of the posterior prolegs point forward and are capable of holding the posterior end of the body in place while the muscles of the body are used in flexing the body and holding the mouth parts of the larvæ in contact with the epidermis.

Observation on a series of stems selected at random from among a considerable number dipped up from the bottom of a pool where the larvæ were abundant showed a greater number of larvæ near the ends of the stems.   In some cases a larva was so located that one end of its tube opened at the end of the stem and the other by an opening bored through the epidermis.   Several stems were found to have openings along their entire length, but all were confined to what had been the inner or upper surface of the leaf where the epidermis was thinnest.   In other cases the larvæ had an opening on one side of the leaf with a long vertical tube leading to its gallery which was on the opposite side, where it opened to the surface through a thickened epidermis. Old Typha stems were occasionally found with larvæ located near the broken ends, but in no case was there noticed a larval-made opening penetrating the epidermis. When the Typha stems were tested with a sharp point, the epidermis was found to be very much tougher than that of Sparganium which is most frequently inhabited by the larvæ.

The thickness and texture of the epidermis of a stem is an especially important factor, as the above observations indicate.   This, however, is not the only source of evidence, but when considered in connection with the fact that two larval molts out of six examined had one of the lateral teeth of the labial plate broken (fig. 28) it becomes evident that the larvæ exert themselves to the limit in penetrating the various plants in which they construct their galleries.   That the larvæ more frequently penetrate the epidermis from the inside than from the outside seems to be shown from the greater

abundance of openings near the broken end of stems, and that the penetration is more easily accomplished in a small gallery, where the larva is able to brace its body against a somewhat resistant parenchymous tissue, is obvious when the nature of the larval mouth parts is understood.

These structures have been fully discussed in connection with *Chironomus braseniæ*, and it is only necessary to consider them very briefly here. The labium is used as a cutting edge and is applied at an angle of about 45° to the surface. Pressure is brought to bear upon it by the mandibles, which on a flat surface have to be widely extended in order to bring their pointed tips into use. This pressure is therefore applied very largely as a sidewise pull and has the effect of using the labium more or less like a scraper. Hence, the strength of the larva and the toughness of its labial plate are important factors limiting its attack on plant tissue.

USES MADE OF SILK.

The fact that the larva of *Chironomus lobiferus* lives as it does in a burrow which communicates with the exterior by two small openings, too small to allow the larva within to extend its body, naturally makes one curious to know how it is able to obtain food. The natural conclusion, of course, would be that it ate the plant tissue, but this is not found to be the case when the stomach content of the larva is examined. Willem (1908) observed this and stated that the stomach content was composed of organic débris analogous to that which floats in the water—"desmids, diatoms, Pediastrum, Clathrocystis, spicules of Spongilla, carapace of hydrachnids, rotifers, together with grains of sand and sometimes the fragments of plant diaphragms." The author's study of stomach contents fully corroborated the above observations, although at the time the author was not acquainted with Willem's work.

In the author's study of the behavior of the larvæ a number of burrows were cut from the stems with just enough tissue to prevent disturbing the silk lining. These preparations were placed in Syracuse watch glasses and observed under a binocular microscope. Considerable difficulty was encountered in seeing through the epidermis,[1] so it was cut away and replaced with a cover glass. The larvæ readily readjusted themselves by making their burrows open at the ends of the section of tissue instead of up through the epidermis. In this way the behavior could be watched much more exactly, but it was not until one of the most characteristic performances, over an area where the underlying tissue had been entirely removed, was observed that a clew to the method by which the larvæ obtain their food was discovered. Willem (1908) dismisses this subject by stating that the food is removed by adhering to the walls of the burrow near the end at which it enters. The following statement, translated from the same source, seems to refer to the movement that gave this clue:

Sometimes the larva is fixed posteriorly retracting and elongating in the act of going and coming rhythmically, its body playing the rôle of a piston for renewing the water in the tube.

This movement, so well described by Willem, the author has been able to demonstrate is concerned in the spinning of a thin conical net across the end of the burrow. This net is used to strain the floating organisms out of the water which the larva forces through it by the rhythmic undulatory motion of its body. In this process the larva

clings to the silk with which its burrow is lined by means of the hooked claws on the anterior and posterior prolegs.

The current of water which is driven through the burrow by the undulating motion of the body of the larva serves the double function of bathing the branchial gills, thus renewing the oxygen supply, and of bringing in whatever particles may be floating in the adjacent water that are of use to the larva as food. The normal undulations move from the head backward, and the larva always turns about after spinning its net, so that the current is driven into the open end of the conical net. The position assumed by the larva places the caudal filaments in such proximity to the net that they are able to serve a more or less important tactile function. When the larva has maintained this current for about 10 minutes (the time element appearing more uniform than the amount of food actually present in the net at any one time), it turns about in its burrow quickly and gathers in and swallows the catch, net and all.

The net is "hauled" in a very characteristic way. The larva seizes that portion of the rim with which it first comes in contact. The mandibles, the labrum, and probably the lateral arm of the epipharynx are brought into use, and the flimsy net is torn away from the silk of the burrow and crowded down the throat of the larva by the labrum. Then the larva rotates its body and seizes the other side, which is swallowed at once. Then the remainder of the net is swallowed while the larva rotates its body first to one side and then to the other as if to wring out or twist up the net, so that it can be more easily swallowed. The conical tip of the net usually contains a considerable variety of plankton organisms ranging from bacteria, which are either stuck to the net or caught in its meshes, to crustaceans and various rotifers, which sometimes succeed in escaping but are nevertheless often captured. The entire process of "hauling" the net and eating it takes only about six seconds.

The most striking and fundamental use made of silk by *Chironomus lobiferus* is in the construction of a net by means of which the larva obtains its entire food supply. Silk has, however, other uses of very great adaptive importance even in this unusual habitat. Many burrows are found where old openings have been entirely sealed up by its use. The regular openings through the epidermis are usually made round and smaller in size by the addition of a silk margin, and the burrow itself is lined with silk which is uniformly made of such a diameter that the movements of the larva are especially effective. This ability to spin a thin, flexible, and at the same time practically water-tight lining enables the larva to adapt itself to cavities of varying sizes.

The small size of the openings at the ends of the burrow seems to be a special adaptation, for when the larvae live under the very different conditions afforded by glass tubes they retain this same habit. It seems probable that the narrow openings increase the speed of the current and so prevent Protozoa, Crustacea, and other small organisms from swimming against it. Large particles are also prevented from entering the burrow. In case these small openings are plugged by an accumulation of particles the larva stops its rhythmic undulatory movements and suddenly throws its body into several much shorter waves which move in the reverse direction. This sets up a strong countercurrent which usually dislodges the obstruction, although the contents of the net are usually lost. In case an obstruction is not readily dislodged the larva creeps forward and brings its mandibles and labrum into play.

METHOD OF SPINNING SILK.

The method by which *Chironomus lobiferus* larvæ spin or spread out the silk used in the construction of their burrows and in the formation of the little conical nets mentioned above is very simple. The anterior pair of prolegs is the chief implement employed and so far as can be observed the only part of the body used for this purpose. The structure of these appendages takes on a new significance when function is suggested, and we at once notice the difference in structure between the anterior and posterior prolegs.

The chitinous claws of the posterior pair are widened at their base (fig. 33), are few in number, and are arranged around the front and lateral margins of the prolegs (fig. 15). The muscles of the prolegs are so arranged as to set these hooks into the silken lining of the burrow, and thus hold the larva firmly in place. The hooks point outward and are so attached that by the contraction of the muscles of the proleg they are all brought close together in the center. When extended, the hooks all move outward in different directions, with the result that the prolegs are hooked fast to the silk lining of the burrow. Their function is preeminently that of an attachment, and it is to this specialization of the posterior appendages that the anterior prolegs owe their greater freedom of movement.

The anterior prolegs are often mistaken for a part of the head because of their position just posterior to the chitinized portion of the head proper. They commonly appear as a mass of bristles radiating in all directions. From the side they appear as one, because they are always moved together and are so completely covered by relatively long spines that it is hard to see how they are attached. A sagittal view shows them to be made up of two rounded lobes separated by a narrow depression. The spines are graded in length from mere tubercles in front to long narrow hooked and barbed spines in the centre and again decreasing in size on the posterior surface. Here the short spines have rather wide bases and the tips are deeply serrate and somewhat hooked (fig. 34). The spines are obviously arranged in rows which diverge somewhat from the mid line laterally (fig. 35). The spines located near the centre of the prolegs are the best developed and are probably the most used in silk spinning. They are curved backward and hooked at their tips. Near the end there are a number of barbs on both the anterior and posterior edges. They are flattened laterally and are capable of being condensed into a very compact mass by the contraction of the muscles of the proleg. The hooks at the end of the spines point backward, and all the long spines are hooked except a few of the very outer spines, which seem to be slimmer and more hairlike.

The actual process of silk spinning is much more easily studied by observing the construction of the conical net mentioned above than in any other way. It is constructed out free from other substances and is consumed and replaced every 10 minutes night and day until the activities of the larva are slowed down by the approach of the pupal stage. The larva begins the spinning by extending its body well forward and making several fairly rapid passes with its anterior prolegs in various radial directions. These movements place the silk strands that form the attachment for the apex of the net. Then, withdrawing its body somewhat and attaching the silk to the place where these radiating strands fuse with each other, the larva retracts its body, drawing out a ribbon

of silk spread by the prolegs. During this retraction the prolegs are held pointing forward at an angle of about 45 degrees with the body, and their exact use can only be surmised, but from their position and the speed of the movements it seems possible that the semifluid silk is spread either by the short spines in front or what seems more probable by the carding effect of variously hooked and serrate spines located farther back on the prolegs. When the larva reaches the end of its backward movement, the prolegs are spread and rapidly touched to the silk lining of the burrow at two nearby points. Then the forward movement is carried out. In this movement the prolegs are extended slightly forward and are more or less spread out. When the end of this movement is reached, the thread is attached either by the contact of the head or the prolegs to this central point of attachment and the process repeated. It is impossible to tell whether the head takes part in the process of attachment or not, because both the head and the prolegs are so close together at this point. It would seem probable from the small size of the apex of the finished structure that at some point in its construction the head occupying such an advanced position would be the only possible part of the body that could accomplish the attachment of the fibers. It is obvious, however, that the head does not touch the wall in the process of attaching the silk at the rim of the net, for the head is held projecting straight out and the movements of the prolegs are unmistakable.

The forward and backward movements of the body are accomplished largely through the instrumentality of the posterior prolegs. These are held attached to the silk, and the last three or four segments of the body are flexed on them as axes. On the forward movement the body is straightened and the prolegs extended forward; on the backward stroke the prolegs point backward according to the degree with which the body is flexed.

The silk net (figs. 26 and 27) is too long to be spun from one place by the simple flexing of the body. This means that it has to be spun in two sections. The overlapping of the sections gives the appearance of a continuous sheet of silk extending from the apex to the base of the net, and the original posterior attachments of the first section appear as radiating strands from the sides of the net.

The entire process of constructing the net requires less than half a minute and involves the spinning of 42 to 44 ribbons or sheets, as determined by counting the movements. When this process is completed and the larva turns about and begins forcing the water into the net, it can readily be made visible by adding a few drops of water containing powdered carmine.

The method by which the silk lining of a burrow is spun is not so easy to observe as the process of spinning a net. It takes longer, and the number of movements is so great that it is almost impossible to correlate them with any definite structure later observed. But even here, if proof were lacking that the prolegs are the one necessary factor to explain the entire process, there are structures that bear unmistakable evidence of their use. The lining, as the silk net, is spun in sections which, while not of uniform length all the way around the tube, are nevertheless approximately so.

The exact way in which the first section is constructed is not so easily understood, but from this on the process involves a considerable repetition of the method employed in the construction of the net. The body is extended and retracted in the process of attaching the sheets of silk to the first section, to each other, and to whatever support

there may be available. These silken sheets are held extended by the thin branching threads of silk (figs. 36 and 37). The whole aggregation of silk sheets and threads is held under tension by silk layers attached in a spiral position. The supporting threads are then originally used as attachment fibers to hold a section of the tube extended and are later pulled into a position nearly at right angles to the lining by the tension exerted by the addition of another section. In this way the lining or tube appears slung in the centre of a cavity with numerous threads radiating in various directions (fig. 26).

SILK STRUCTURES.

The completed silk lining shows relatively little structure as far as the tube itself is concerned, but the supporting lines thrown out when the larva fastens this lining between two parallel glass surfaces are quite interesting. In studying the structure the tube is seen to be of a fairly uniform diameter and to be composed of a thick layer of silk, which shows no definite layers or strands. At intervals the silk is pulled out into conical enlargements. At these points the tube is seen to be made up of more than one layer, for the lining continues straight on leaving a space. The lining is held extended in the form of a cylinder by very interesting branched threads. These threads are often more or less sheetlike next to the tube, but divide and subdivide toward their point of attachment where they are much more widely spread out than at their origin (fig. 37). These structures show unquestionably the use of the prolegs, for it is inconceivable that such fine threads often ending in more than one plane could have been attached in any other way.

The structure of the conical net is not easily made out even under high powers of the microscope, but the addition of powdered carmine to the water passing through the net gives it such a uniform coat that the author is inclined to think the entire structure porous. At times Protozoa and other relatively large organisms are seen to be forced into one of these nets and to escape by a circuitous route, which would suggest a breach between ribbons or sheets of silk. In other cases relatively large gaps, opening directly through one side of the net, are indicated by the escape of particles. When the net is collapsed, as it always is when the larva is not forcing water through it (the condition always existing in stained material), none but the grosser structures are visible (fig. 27).

The net, as explained above, is spun in sections, but the position of the threads attached to its sides, as well as the observed behavior of the larva, shows these sections to be less regular than one might infer from the previous description. The arrangement of the net in sections in a manner similar to that of the lining of the gallery suggests the possibility of narrow slits in its surface of the same nature as those in the attachments of the tube (fig. 36). It is probable, however, that the impact of the current is necessary to open them wide enough to allow water to pass through.

The conical net is spun exceedingly thin, as one would expect from the frequence with which it is consumed and replaced. This is doubtless correlated with the speed of the movements involved in its construction. In fact, it seems reasonable to conclude that the nature of the silk rather than the psychology of the larva dictates the speed of its movements. The spinning of one part of the net upon another in such rapid

succession indicates that the silk hardens very quickly on contact with the water. The quickness with which the silk hardens determines the speed at which the larva must work in order to spin silk of a given thickness. Hence, the thinner the structure the greater the speed required, because of the greater surface relative to the volume exposed. Thus it appears that the very rapid movements of the larvæ are dictated by considerations of economy in the silk used.

RELATED FORMS.

Goetghebuer (1911) in a special examination of the external structures of the larvæ of the genus Chironomus established three groups, as follows:

Group I.—Containing those species possessing two pairs of branching filaments on the eleventh segment; a thickened oval area on the labrum; an epipharyngeal comb composed of a row of regular teeth; the antennæ with five segments; and the abdominal segments of the pupa without spinose protuberances.

Group II.—Branchial filaments of the eleventh segment lacking; the median anterior piece of the labrum simple without the thickened oval area; the comb of the epipharynx not composed of a regular row of teeth; the antennæ with five segments without Lauterborn's organs; and the pupa without spinose protuberances.

Group III.—Agrees with Group II except in the presence of small granulations on the labrum of the larva and the presence of spinose protuberances on the posterior abdominal segments of the pupa.

The specimens upon which the last two groups were founded all live in the parenchyma of submerged leaves of numerous aquatic plants and are as follows: *Chironomus sparganii* Kieffer, *C. viridis* Macquert, *C. niverpennis* Fabricus, *C. tendens* Fabricus, and *C. dispar* Meigen. The list of plants in which these larvæ were found as given by Goetghebuer is as follows: *Stratiotes aloides*, *Sparganium ramosum*, *Butomus umbellatus*, and *Alisma plantago*.

In addition to this list the author has bred *Chironomus lobiferus* Say, *C. pedellus* Deger and *Tanytarsus obediens* Johannsen, from Sparganium stems, and Needham (1908) reports *Chironomus albistria* Walker from Nymphæa stems. While, of course, only the bred specimens have actually been observed to build conical feeding nets, yet the similarity of their external structures and the nature of their habitat give a considerable justification for including them in this group, especially when it is observed that *Tanytarsus obediens*, a member of another genus, possesses this habit.

A bit of information regarding the similarity of the larvæ of *Chironomus sparganii* Kieffer is contained in a paper by Willem (1908). He finds the uniform punctations of the abdominal tergites, the posterior teeth of the lateral plate of the eighth segment, and especially the peculiar process carried by certain abdominal segments would suggest *C. lobiferus* Say, the description of which was found in Johannsen's monograph. He finds his most striking difference in the fact that Johannsen says that these processes occur on all the segments, while he finds them on segments two to six only. Upon examining his own material the author finds this to be also true for *C. lobiferus* Say, as well as *C. sparganii*. Dr. O. A. Johannsen has also observed the author's material and agrees with him in the identification of this species. While it is not known how great weight this observation had with Kieffer in establishing the species *C. sparganii*,

yet there is no doubt whatever that the two species will be found to resemble each other very closely, as it is difficult to find any satisfactory distinctions between them from their descriptions.

Group II.—Tanytarsus pusio Meigen.

For this group *Tanytarsus pusio* Meigen has been selected as a type, because Mundy (1909) has already studied it so completely that there is relatively little new material to be added. The only larva whose feeding habits he describes is the species given above, but he designates "Larva No. 1" and apparently "Larva No. 18" as also feeding in a similar manner. "Larva No. 18," he says, "builds a still more elaborate case, composed of long stalks to which is attached a short tube with three long arms given off at the free end. The case is not quite so opaque as that of *T. pusio* and is of a light brown color." The author has bred *T. exiguus* from similar tubes and observed its habits, which resemble very closely those of *T. pusio*, as described by Mundy.

CONSTRUCTION OF TUBE.

The following description is taken from Mundy's work (1909). The latter part is condensed from a more complete description.

The first thing the larva does is to gather a number of particles of mud together and form them into a short strap or band passing across the body and fixed to the dish on each side. Using this band as a starting point the larva sets about building a simple straight tube closely applied to the dish and open at both ends. At first the band is merely broadened so as to cover more of the body, but soon it is shortened as well until length and breadth change places and a real tube is formed. * * *.

Anchored, as it were, to the strap by its anal feet it rapidly sweeps through an angle of about 60°, touching the surface here and there with its mouth as it passes. Then, firmly grasping a particle by means of the labial armament and the anterior appendages, it powerfully contracts its body, thus drawing the particles toward the centre of operations; but not only do the above mentioned particles move, but all those touched during the sweeping movement follow in its wake, having been united together by silk threads or mucus during the first action. In this way abundance of material is collected and the building of the case proceeds rapidly.

According to Mundy (1909) *Tanytarsus pusio* and "Larva No. 1," which builds a stalk case, begin their tubes and construct them to a large extent exactly alike. When the tube of "No. 1" is 3 millimeters long, it begins to build it up horizontally, removing material from the opposite end of the old tube for this purpose. This is carried on until there is only a narrow stalk projecting up from one side of the original burrow supporting on its top end a short tube. This tube is later strengthened by the addition of saliva especially at the attachment. Then three arms are provided and the web attached.

In strengthening an arm the larva twists its head right around it, describing thereby a complete circle, completing the forward and return movements with the greatest rapidity. [Mundy, 1909.]

Tanytarsus pusio makes a dark-brown mud tube fastened together with saliva but not lined with a distinct silk lining.

The tube is attached for a variable length to rock or moss stem in the bed of a river, but it gradually curves away from its support, so that the anterior end projects freely in the water. This end is the widest, from which it gradually tapers toward the base.

VARIATIONS IN TUBES.

The tubes, as explained above, are composed of débris fastened securely together with silk. Taylor (1905) and Lauterborn (1905) have described other closely related larvæ, living in similar situations, that spin tubes of nearly pure silk. In texture the tubes of *Tanytarsus pusio* Meigen and *T. exiguus* Johannsen are intermediate between those of pure silk, such as are spun by *Chironomus lobiferus* when living within a stem, and those composed of a mass of débris only loosely fastened together with silk, such as are characteristic of the group that is represented by *C. cayugæ*.

The tubes figured by Mundy for *Tanytarsus pusio* are rather different in structure and proportions from those of *T. exiguus*. The substance of the tubes gives them a gray, slatey appearance that closely resembles the general color of the bottom. The arms are proportionally stouter and are represented on the sides of the burrow by elevated ridges. The tubes are as often fastened flat down to the surface upon which they rest as elevated at the end, apparently depending upon the convexity of such surfaces.

The arrangement of the tubes is not to any great extent dependent upon the direction of the current. Small stones having from 8 to 10 tubes on their undersides usually showed such a variety in the arrangement of those tubes that it would seem that free space was of more importance than the direction of the current.

Johannsen (1905) says of the tubes of *Tanytarsus exiguus:*

During the early summer most of the cases will be found attached by the stems alone, but later in the season most of them lie flat on the rocks and are attached on one side like Simulium pupal cases.

It seems evident that this species varies considerably in the type of tube which it builds. The author's observations on this species in nature are confined to small streams which were not very rapid, and in these localities the food supply has been fairly abundant, as shown by the number and variety of the population. In such habitats the predominance of the attached type of tube would seem to indicate that the strength of the current and perhaps the food supply are the governing factors. Since the writer's observations were made both in the fall and in the spring, the effect of seasonal changes should be eliminated unless these tubes were able to persist throughout the winter, which seems improbable in most cases considering the erosion to which such small streams are subjected.

THE NET.

The arms, as before mentioned, are connected by webs so as to form a net to retain all passing objects; but even with a high-power lens I have been unable to detect single threads. The network seems only to be made up of irregular bands of slime or mucus passing between the neighboring arms, so probably it issues from the creature's mouth in this form. [Mundy, 1909.]

NET MAKING.

To build its net the larva proceeds as follows: Running up one of the arms for some distance it swings across to the next arm, carrying with it a thread of silk, then quickly back again, at the same time retreating somewhat into its case. This zigzag movement is repeated two or three times until the base of the arms is reached, when the whole process may be repeated over again until a sufficient number of threads have been stretched across to make a rude network which, whatever its workmanship compared with that of a spider, is at any rate good enough for its purpose and effectually stops all objects

floating by. In the case of larva No. 1 this has only to be done twice, but in *Tanytarsus pusio* from four to seven times, according to the number of arms present. From time to time the larva pulls down the net between two arms, using the labrum and thoracic feet to collect the particles together into a compact mass, which may then be used for further building operations or may be pressed into the mouth to be consumed. [Mundy, 1909.]

SILK SPINNING.

This process has not been treated in any considerable detail by Mundy except that he rightly inferred that the silk was made up of bands of slime or mucus instead of threads. The author has followed the activities of *Tanytarsus exiguus* in its silk-spinning movements and finds it a very difficult species to observe in this particular. Its chief silk-spinning activities consist of the rapid movements of its head and anterior prolegs in such close proximity to the surface that in spite of the numerous repetitions of the same movement, while applying layer after layer of silk to the rim of its burrow, the author was unable to determine that the head did not play an equally important part in this process. It was more nearly possible to distinguish the use of the prolegs in the work of reinforcing the arms. Here the most characteristic movements were upward, in which movements the head was held somewhat away from the arm as the body encircled it.

The most satisfactory movements in this process were those concerned in the construction of the web mentioned above. The specimen studied in this particular had a tube fastened to the bottom of a glass vessel. This tube had two radiating arms on which the larva spun a single thread. This web was attached to the glass as far out as the larva could reach, then to the nearest arm, and from this arm to the second and down to the glass again on the opposite side. In this process the larva in swinging from one arm to the other repeatedly struck the end with its prolegs while its head projected well beyond.

The silk is especially viscous, and the particles swept against it by the current readily stick fast. By this means the single thread spun by *Tanytarsus exiguus* was very effective in catching particles. At intervals this thread was pulled down and consumed, the labrum and maxillæ playing the important part in the process. The prolegs were not seen to be employed in the pulling down or rather pulling in of this single thread, as stated by Mundy.

ADAPTABILITY.

The *Tanytarsus pusio* larvæ were taken from flowing water and placed in dishes containing only about a quarter of an inch of water with relatively few fatalities, considering the crude methods employed in removing their burrows. The dead larvæ were removed and a small amount of organic débris added. This the larvæ raked together in masses near the ends of their burrows and consumed in what seemed tremendous amounts for such small larvæ. They simply placed their heads against one side of a mass, and by the motion of the appendages of the head alone the food was passed down their throats in a steady stream. It was apparently fastened together by the silk spun during the process of collecting it together. In this connection Mundy's observation,

quoted above, on the method of collecting particles in the construction of their tubes seemed to be related phenomena.

Perhaps the most remarkable change in the behavior of these larvæ was that exhibited by a specimen which, after living a week in quiet water, suddenly found its food swept out of reach by a current. This larva in less than 15 minutes raked away a part of the rim that it had spun between the radiating arms and after reinforcing these outrakers spun a web upon them. The current was set up by a pipette operated by hand, and gave a very satisfactory means of testing the reactions of the larva, for the strength and direction of the current could be changed at will. A complete reversal in the direction of the current seemed to alter the behavior of the larva not at all in regard to its web or any other observed activity.

It would seem feasible to demonstrate the behavior of this larva in such a special lantern slide as recommended for this purpose with *Chironomus lobiferus*. The larvæ, while sensitive to a jar, do not seem to notice the light particularly, and the adhesive nature of the silk makes it possible to use powdered carmine or India ink to make the strands visible. The current recommended to keep the temperature down could be adjusted to answer for the natural flow of a stream.

Group III.—Chironomus cayugæ Johannsen.

This group is based upon a recently described species which, so far as can be judged from direct observation as well as indirect references, will prove to be one of the most widely distributed species of the family. It is on this account, as well as upon its unique habit of living in watering troughs where it is easily accessible, that *Chironomus cayugæ* Johannsen has been selected for the purposes of this study. It is a type of a very large group which is included in Goetghebuer's first group and characterized by the presence of two pairs of branchial filaments on the eleventh segment, a thickened oval area on the labrum, an epipharyngeal comb composed of a row of regular teeth, antennæ with five segments, and the pupa without spinose protuberances on the abdominal segments. The division includes most of the bigger red chironomid larvæ and is probably of greater economic importance than any other group in the family. At this point it may be of interest to recall that most, if not all, of the species of Group I under stress of circumstances adopt the habitat and behavior of this group.

HABITAT.

These larvæ are fitted by their extra branchial filaments and red blood for life in the débris at the bottom of lakes, ponds, and stagnant pools. The larvæ of the species selected as the type, while living in various other habitats, are especially common in horse troughs, having been taken by the author from troughs in Orrington, Me.; Woods Hole, Mass.; Ithaca, N. Y.; Dayton, Ohio; Greencastle, Ind.; Evanston, Ill.; and Milwaukee, Wis. The troughs most carefully studied are those in Woods Hole, Mass., Ithaca, N. Y., and Greencastle, Ind. In none of these troughs was the author able to find any other species belonging to this group represented, and it seems that by some special adaptation this species has succeeded in adjusting itself to conditions different from those common to the group. It is also found associated with *Chironomus decorus* and others in the débris at the bottoms of larger bodies of water, and it is obvious that it

is not only capable of living in the same conditions as they, but, as can be shown by a simple experiment, both are able to live on the débris found in a watering trough.

It seems possible, then, that the difference may consist in such a simple adaptation as in the manner of depositing eggs. Needham (1906) has referred to the habit of *Chironomus annularis* Degeer of extruding its eggs while in flight and depositing them free in the water. Mundy (1909) has referred to the fact that *Tanytarsus pusio* eggs were found attached to leaves several centimeters below the surface. J. T. Lloyd informs the author that he has observed masses of chironomid eggs of considerable extent blown upon the shore of Cayuga Lake. The author has observed *Chironomus hyperboreus* Staeger depositing its eggs upon the surface. Some of these females were caught in flight and found to have a considerable mass of eggs ready to be deposited. On the other hand, *Chironomus cayugæ* females were observed just at dusk to light upon small stones which projected slightly above the water level and to thrust the tips of their abdomens beneath the surface of the water and there deposit egg masses attached to the stones. All the eggs taken from troughs have been found attached, and it seems possible that by this habit alone *C. cayugæ* may be especially adapted to such a singular habitat.

It is interesting to note that troughs fed from flowing streams where a considerable amount of silt is constantly present have in every case been found to contain but few or no larvæ, and it seems probable that the choking out or covering up of the food supply is the controlling factor.

Other members of this group are found in streams, ponds, reservoirs, and lakes, even at very great depths, as in Lac Leman. Here Mlle. Zebrowska (1914) found specimens designated as *Chironomus "B"* abundant to a depth of 20 meters and rare to the extreme depth of 100.

THE BURROW.

The process of building a burrow has probably been observed in this group more frequently than in any other, because the larvæ when out of their burrows are very restless and at once begin to rake particles together. The pectinate hairs and comb of the labrum and the epipharyngeal comb are used in this work. The anterior prolegs usually form the limit of the backward stroke of the head, and it is difficult to say for certain that they remove the accumulated débris; but it is clear that this débris is fastened together with silk, and it seems possible that they may be instrumental in spreading it.

When a certain amount of débris is accumulated, it is raked back by a looping of the body, so that the posterior prolegs hook into the silk that holds the particles together. When a sufficient amount has been so accumulated, the larva seizes the mass adhering to its posterior prolegs by means of its head and anterior prolegs and fastens it over the posterior end of the body in such a manner as to form a narrow band or strap, which is referred to in Group II of Mundy's description. This narrow band has the dimensions of a cross section of a burrow, and with this as a beginning the construction work consists of a direct application of building material to either side of the strap. From this stage on the behavior is the same as that observed in the ordinary lengthening of the burrow. The larva now reaches out and grasps by means of its labrum, mandibles, and prolegs a mass of débris and draws it in and puts it in place at the edge of the burrow.

Then silk is spun by the obvious use of the prolegs, as in the case of *Chironomus lobiferus.*
Each addition of débris is fastened in place by silk which is attached to the older parts
of the burrow and spun out and part way around this material. In this way the larvæ
construct long tubes that give them protection from enemies and at the same time
help support them on the surface of the soft débris where they are usually found. The
tubes are often U-shaped, and thus serve to bring in fresh water from which the larvæ
are able to carry on their respiration while living among decaying organisms at the
bottom.

<center>FEEDING HABITS.</center>

The author has found it exceedingly difficult to satisfy himself that the members
of this group are not really similar in habit to those included in Group I, but repeated
experiment has convinced him that their habits are distinct. When a large number
of these larvæ are scraped up together with a mass of the surrounding débris and then
spread out in a shallow dish, they literally spin every bit of the débris into loose inter-
woven U-shaped burrows. When one tests the current in these burrows, the water is
found to be flowing through them in a definite direction.

Methods have been repeatedly tried to get these larvæ to adapt themselves to glass
tubes of the sort used so successfully with *Chironomus lobiferus*, but in no case have
these experiments succeeded except when sufficient débris was present to make it possible
for the larva to completely conceal itself.

Several larvæ were put upon pure sand with the hope that it would furnish pro-
tection, if that was what was desired, and at the same time fail to serve as food. The
larvæ were obviously not well satisfied with their surroundings and moved about over
the surface apparently in search of more suitable conditions. In removing the larvæ
from their burrows a small piece of the organic débris of which their tubes are character-
istically composed was left adhering to one of them. This the larva kept clinging to
and trying to roll up into a burrow. The other larvæ as soon as they encountered this
débris attempted to get possession of it; after a few hours they all made burrows out
of sand. The current was tried by means of powdered carmine but without satisfactory
results.

In another experiment several larvæ which had well-constructed tubes were
removed, tubes and all, to a flat dish. These larvæ were keeping a strong current of
water flowing through their burrows. After being removed they were placed in shallow
water. The tubes were well separated from each other, and the bottom was lightly
sprinkled with loose débris similar to that from which the tubes were constructed.
After a few hours the larvæ ceased to maintain so strong a current and in most cases
maintained it only spasmodically. The débris sprinkled over the surface was not
disturbed even after being left over night. The current was repeatedly tested and
found to be insufficient to furnish any considerable amount of food.

The tubes were then dissected under a microscope and their inner surfaces were
found to be eaten full of rounded holes and enlarged in places. From this it was de-
termined that the larva ate away the substance of its burrow from within. While the
larva is in such a tube it would probably not be possible to maintain a sufficient current
through the burrow to bring in much food on account of the number of openings through
its wall. It seems possible, nevertheless, that the current would at times bring in and

deposit substances that could be used as food. This seems especially possible, because the larvæ of Group I are known to eat and replace certain parts of the silk composing the wall of their burrows at irregular intervals.

The larvæ, on the other hand, are known to have the habit of scraping up substances to be eaten directly as food. The author has observed this behavior in the case of well-soaked pieces of cracked corn. These the larvæ seemed to have eaten exclusively, for their stomachs were full of the starch grains. The larvæ frequently reached out for some distance and unless the fragments were easily moved did not seem to attempt to drag them in. Once a piece of corn was found it was usually eaten out until nothing but the hull remained.

An examination of the débris at the bottom of the Greencastle (Ind.) troughs showed the greatest number of larvæ per square foot yet found, which by count of a smaller area was estimated to be 500 to the foot. Here an abundance of diatoms, interspersed with corn and oats brought in the mouths of the horses from a near-by livery stable, formed a layer about an inch and a half in depth. The flowing water and the undulating motion of the larvæ kept the conditions suitable to favor the development of diatoms, as was indicated by the great abundance of a relatively few species. The presence of a considerable amount of horse champings did not seem to upset the balance, as a too liberal addition of corn has been found to do in laboratory cultures. Miss Tilbury (1913) found it possible to rear the larvæ of this species from egg to adult on *Potamogeton crispus* alone. This she grated up and fed to them in small amounts.

It will be seen from the above observations that *Chironomus cayugæ* is well suited to experimental culture methods, and it seems probable that the group as a whole is equally hardy. Their large size and overlapping broods offer considerable encouragement to the hope that they may sometime be an important factor in fish culture.

Group IV.—Chironomus braseniæ, n. sp., a leaf-eating chironomid.

INTRODUCTION.

While on a lymnological trip to North Spencer, N. Y., the author's attention was called by Dr. Needham to the work of an insect larva that was cutting burrows in the floating leaves of the water shield, *Brasenia schreberi*, and to a lesser extent in the leaves of the sweet-scented water lily, *Castalia odorata*. The larvæ were found to be those of a midge of the genus Chironomus and apparently an undescribed species, although this or a species with similar habits seems to have been observed by workers in several different parts of the country. Mr. Isley, of the U. S. Bureau of Entomology, informs the writer that he has seen larvæ of this genus with similar habits in the vicinity of Washington, D. C. Dr. R. H. Pettit has referred to a species which he bred from the leaves of both *Nuphar advena* and *Nymphea odorata* in the Wild Gardens, Forest Hill, Mass. He also observed this same species at Pine Lake, Ingham County, Mich. The author has seen specimens from Fair Haven and North Spencer, N. Y. Dr. Pettit's note on an undescribed species published in the first report of the Michigan Academy of Science (1900) is the only reference the writer has found in the literature, however, to a species of Chironomus with similar habits, although the closely related genus of Cricatopus, according to a brief note by C. W. Johnson published in the Entomological News (vol.

12, p. 30) apparently contains a leaf-eating species, as Mr. Johnson states that *Crica-topus sylvestris* was bred by Prof. Smith from the leaves of *Victoria regia*. These two species, so far as the author knows, are the only ones that feed directly on living plant tissue. Other larvæ, however, are found in the large air spaces of dead and living aquatic plants, where they maintain themselves in the same way as while living in a burrow made of trash.

Dr. Pettit's note gives only a brief explanation of the nature of the damage done and a general description of the larva and pupa based on the color characters. He bred the adults and states that they belong to the genus Chironomus and are probably a new species. Since the above quoted studies are substantially in agreement with the writer's observations it would seem probable that all the above chironomid records refer to this species. The unusual food habits and other unique adaptations seem to justify a rather more comprehensive study of this species.

GENERAL HABITS.

The larvæ of *Chironomus braseniæ* from a superficial examination would appear to be true leaf miners. The straight or winding galleries are covered with a green ridge, which closely resembles the epidermis in color, and the lower epidermis is left intact. Closer examination, however, shows that the cover of the larval burrow is not the upper epidermis but rather an artificial cover made up of plant fragments fastened together with silk and moistened with a film of water which floods the entire burrow and spreads out in a thin film a little way on each side of the burrow. The larvæ can also be seen when at work to actually project their body out onto the surface of the leaf at times. They are completely immersed in the water which constantly floods their burrows, and they breathe by blood gills. Their burrows are lined with silk, which is also used in constructing the coverings of the burrows. The larvæ of the typical representatives of this genus do not carry their cases about with them as was erroneously stated in his discussion of this species by Dr. Pettit. On the contrary, this larva resembles the other members of the genus except in the method of obtaining and the nature of its food.

LIFE HISTORY.

The life history differs in several important particulars from that of the typical species of the genus Chironomus. The eggs are laid on the surface of partially submerged leaves of both the water shield and the sweet-scented pond lily (fig. 19). They are laid in strings which tend to show a double arrangement of the eggs, due doubtless to an egg coming from each ovary simultaneously. These egg strings are wound about and crisscrossed in such a way that they form a somewhat disklike mass which tends to be only one layer deep, the gelatinous coating fusing to unite the whole into a single mass. In the limited area where the eggs were found most abundantly the leaves of Castalia were selected rather more frequently than those of Brasenia, although the latter is clearly preferred by the larvæ. It seems probable that the chief factor governing the selection of these leaves is their partial submergence, as the eggs are laid on the top surface of the leaf and are unable to endure desiccation.

The young larvæ obtained from these eggs were placed on sections of Brasenia leaves and confined there in drops of water. These preparations were placed in watch glasses

and the normal conditions maintained for several days. Careful observations showed no signs of the larvæ having begun burrows. They were then allowed to enter the water beneath the leaf where they lived for several weeks, but failed to develop, even though a miscellaneous supply of aquatic organisms was furnished. Several of the larvæ died and the experiment was abandoned after two months' observation.

Just how the very young larvæ maintain themselves is still undetermined. A thorough search in the early spring before the leaves of Castalia or Brasenia had reached the surface failed to reveal the presence of any of the larvæ on the roots, stems, or leaves of these, their characteristic host plants, or of any of the other near-by aquatic vegetation. From the facts that none of the small larvæ succeeded in penetrating the leaves under laboratory conditions, that only large larvæ were found in all the burrows opened, and that the burrows are of a uniform width in practically all cases, it seems probable that the larvæ do not enter the burrows before mid-larval life (figs. 20, 21, 22).

The author has been unable to make any direct observations on the length of time spent in feeding on the leaves, as the larvæ are not to be found in any of the apparently similar aquatic situations about Ithaca and when brought into the laboratory on leaves frequently leave their old burrows and start new ones. This confusion, together with the writer's inability to rear the young under laboratory conditions, forced him to use indirect means in determining the length of time spent in feeding on the leaf tissue. Late in the season a dozen leaves containing active larvæ were each labeled by pinning a square piece of paper so that a marked corner came opposite the end of the burrow. The label carried the number of the larva, and the rate of progress was measured daily. These results showed that not more than 10 days on the average would be required to construct a burrow of average length, while the larva that made the greatest progress would not have required more than seven days. Subsequent examination of these larvæ showed 100 per cent infested with a Gordian worm, so the results are doubtless inaccurate, although all larvæ that ceased burrowing after a day or two were omitted in making up the average.

The larva transforms to a pupa on the leaf where it has been feeding. The pupal chamber can often be seen at the end of a burrow 2 inches in length on the leaves of Brasenia and somewhat shorter on the leaves of Castalia. A burrow of this length represents the work as a rule of a single individual. The pupal chamber can be easily picked out because of its club-shaped appearance (fig. 24), the big portion being at the end of the burrow. The pupal chamber is, however, often completely separated from the ordinary burrow, suggesting a vagrant tendency on the part of the larva just before pupation. When separated from the larval burrow it has the same general shape and appearance as when attached. It is but little longer than the pupa and is in rough agreement with it in general outline. The pupa lies in this burrow with the head next to the large open end. When ready to transform it wriggles through this opening and the imago escapes. The pupal molt is usually ˙ ft with the thoracic part projecting from the pupal chamber (fig. 24). The length of ime spent as a pupa is about five days, varying considerably with the temperature and the condition of the individual pupa and the larva from which it transforms.   ˙

The adults, both males and females, were found among the bushes and underbrush along the banks, and several were shaken from the tops of trees 6 to 8 feet high. The

leaves found with egg masses on them were near these trees and were shaded during a part of the day. Mating and egg laying probably takes place in the early evening, as is the habit of the family.

When infested leaves are brought into the laboratory, the adults begin to emerge in a day or so and continue to transform a few at a time until they have all completed their development. This lack of uniformity in the time of transforming is characteristic of the Chironomidæ and is an important factor in their adaptation to the dominant position that they hold in the life of the fresh waters. In the case of *Chironomus braseniæ* this adaptation makes it a worse pest.

Dr. Pettit bred his first specimens about the middle of May while at Forest Hill, Mass., and in his note before the Academy of Science he states that a second brood was seen on August 1 at Pine Lake, Ingham County, Mich. It seems probable that the term "brood" is here rather loosely applied.

PENETRATING THE EPIDERMIS.

The author has given evidence above to show that the leaf-mining method of feeding seems not to be adopted before mid-larval life, and hence is doubtless a less primitive habit than that of the young larvæ.

That this method of feeding is probably impossible for the young larvæ seems borne out by observations made upon the behavior of the half-grown larvæ in penetrating the epidermis of aquatic leaves. In attempting to induce the larvæ to start new burrows the writer removed them from their old ones and placed them on leaves where there were no unoccupied burrows. This work was for the most part rewarded only by observing the larvæ searching vainly for their original burrows. If by chance one encountered the burrow of another larva it crept boldly in, only to be met by the owner, who usually administered a sharp nip by means of its mandibles. Since the members of the genus are chiefly herbivorous and therefore for the most part peaceably inclined, the intruder usually retires quickly. It often repeats its attempt to enter the same burrow several times in succession, each time more cautiously, until it finally gives up or in some cases enters an unused part of the burrow and begins feeding. In this case it extends its burrow as a continuation of the original burrow or as a side branch, showing that it finds a decided advantage in using a burrow already started.

In case the larva gives up the attempt to enter an already formed burrow it begins a new one. The first requisite is the spinning of an arch formed of many thicknesses of silk about the size of an ordinary burrow. This, from the author's laboratory observations, is preferably located near another burrow, perhaps because of the water film that always accompanies the burrow. The larva next enters this silken arch, which is about as long as wide, turns itself on its back, and bends its head backward. This position enables the larva to brace its anterior prolegs against the underside of the silken arch and so bring pressure upon its head, which is at such an angle to the surface that the mandibles and the labrum are in contact with the surface of the leaf. In this position, with the head bent backwards a little more than at right angles, it extends its mandibles and rasps its way slowly through the epidermis. The spinning of the arch and the penetrating of the epidermis take over an hour and are doubtless severe tests on the strength of so small a larva.

Chironomids labor under greater handicaps than other gnawing larvæ in not having strong legs provided with claws for holding them in position and in not having mandibles that are opposable for cutting the tissue. Instead they have to depend upon indirect methods, of applying pressure to their mouth parts, and the utilization of their labial plates in conjunction with their mandibles for cutting the tissue.

THE BURROW.

The method of penetrating the epidermis in the beginning of the burrow is the same for the leaves of *Brasenia schreberi* as for *Castalia odorata*, but from this point on it differs markedly, due to differences in the texture of the plant. That chironomids show adaptability in their feeding habits is well shown by the differences in their burrows in *B. schreberi* and *C. odorata*, resulting from a difference in the thickness and texture of the leaves of these two plants.

We will take up first the nature of the burrow made on the leaves of Brasenia, since they are thinner, more easily penetrated, and where equally available more seriously attacked. This shows an evident selective power on the part of the larva. The writer is, however, aware that the softness of texture may be the deciding factor. When the larva has penetrated the epidermis of a leaf, it is able to bring pressure to bear more directly on the labial plate. The mandibles are hooked under the edge, and they, together with the pressure derived from the anterior prolegs, readily force the labial plate down through the epidermis. Then the larva moves a little to one side and repeats the operation. In this way the epidermis and parenchymatous tissue are removed from under the silken arch. Then the larva commences in the mid line and makes a cut as explained above from the center of the burrow to the outside edge. The larva during this operation is inverted, with its head turned backward. It next assumes an upright position, grasps the strip near its free end between its mandibles and labial plate, and pulls the strip backward, raising it upward at the same time. Then by bending its body to one side in its burrow it gets under the loose end and scrapes it clean of the green parenchymatous cells that adhere to it and fastens it in place against the silken arch (fig. 23). It next rakes this exposed area free of all the parenchymatous cells down to the lower epidermis. This removal of tissue usually results in the admission of water, probably through the mucous gland, as no openings are visible; at any rate the burrow becomes flooded and capillarity keeps it wet both inside and out.

The larva continues to cut slabs and to extend its burrow as long as it cares for food. These slabs are twisted backward and fastened in an upright position and their tips bound together with silk secreted by the salivary glands. The bottom as well as the sides and top are lined with silk. In the leaves of Brasenia the bottom and sides of the burrow have a very thin layer of silk which is closely applied to the surrounding tissue. When castings are to be extruded, the larva turns about in its burrow and the partially digested material is fastened to the arched top of the burrow by silk in such a way as to serve as sort of a porch. It is held extended by silk threads which are fastened out on the surface of the leaf. This porch or canopy serves a threefold purpose, being a shelter from the sun, a means of retaining a film of water over the area that is being excavated, and an entanglement in which the free end of the slab of epidermis becomes lodged so as to be held up while the tissue is being removed from its underside.

Later it becomes a part of the roof.   Figure 23 is a diagram representing the nature of the burrow and an area with the top removed to show the general appearance of the lower epidermis, which forms the floor of the burrow.

In the case of the leaves of *Castalia odorata* the larva is obliged to bite the epidermis to pieces and remove it by sections because of its thickness.   The head is applied at different angles and pieces of varying sizes are removed.   Those that are small enough are swallowed and the rest are used in the construction of the sides and top of the burrow. The large spines are also removed and woven into the burrow with silk.   On account of their relatively large size they greatly tax the strength of the larva.   The thickness of these leaves is considerably greater than that of Brasenia leaves and the work of excavating greater.   This necessitates a much greater thickness in the layer of silk making up the bottom of the burrow, especially as its bottom is at a higher level than the lower epidermis of the leaf.   The castings are utilized in the same way as explained above for Brasenia, and the parenchymatous cells are eaten as food.   The above changes in the method of procedure show a marked contrast to the habits of many other insect larvæ.   This ability to adapt themselves to a variety of conditions has doubtless been an important factor in the adoption of their present unusual feeding habits.   The pupal burrow is essentially similar to the larval burrow in structure, but is made up more largely of silk, is larger in diameter, and persists longer than the larval burrow (fig. 24).

RESPIRATION.

The larva breathes by means of four blood gills located on the posterior part of the last segment.   These gills are longer and more pointed than in the species having red blood (fig. 15).   The water in the burrow while small in amount is kept in circulation by an undulating motion of the body during the intervals while the larva is not feeding. The current flows from the head backward over the gills and out through the chinks in the sides of the burrow, passes forward over the surface of the leaf in thin films on either side, and again enters the open end of the burrow.   The water should be well aerated, since it is exposed in thin films both to the air and to the surface of the leaf while flowing forward outside of the burrow.   It is also exposed to favorable conditions for the desired exchange of gases while within the burrow, as it comes in contact with the air in the air-containing spaces of the parenchyma which is rich in oxygen and poor in carbon dioxide.   That the oxygen supply is rich seems to be demonstrated by repeated accidental experiments where leaves were submerged overnight with the result that the larvæ died in the submerged leaves but lived in those on the surface.

The pupa is active and continues to aerate its burrow by occasional undulations of its abdomen.   The repiratory filaments consist of several much-branched tufts located on each side of the thorax.

FEEDING HABITS.

The larvæ feed intermittently.   They find an abundant food supply at hand, and the only limit set them is the rate at which digestion can be carried on.   They are yellowish white in color, their blood lacking the hæmoglobin which gives the characteristic color to the other chironomid larvæ which are known as bloodworms.   The green food material can be readily seen through the translucent body.   It is seldom that the

stomach is allowed to become more than half empty, and often the larva resumes its feeding operations when the stomach is practically full.

An attempt was made to determine the length of time that the food remained in the alimentary canal, but the small size of the larvæ and the acute discrimination in their feeding habits prevented the use of any coloring substances to mark any portion of their food. Direct observation was resorted to but proved too tedious to afford accurate data. The larvæ often withdraw from the end of their burrows and remain almost motionless for an hour or so at a time. Then they will begin feeding again, working for a half or three quarters of an hour at a time with only occasional short intermissions for the purpose of renewing their air supply by setting the water in circulation. By noting the intervals between feeding and resting it seems doubtful if the food remains in the body for more than two hours.

There is no special masticating apparatus present, and the result is that a very large per cent of the parenchymatous cells swallowed pass through the body entirely unaltered. The use of the castings for roofing material in connection with the burrow places these cells in a position which, while artificial, nevertheless offers conditions under which the carrying on of their life processes should be partially possible. These cells are held suspended in a silken mesh, bathed in water rich in the mineral salts, resulting from the digestion of similar cells, and favorably placed for the obtaining of carbon dioxide. That the covering of a larval burrow remains green for a considerable time is readily observed, and it seems possible that the larvæ have in this matter hit upon a favorable adaptation.

ECONOMIC IMPORTANCE.

The aquatic conditions of life required by *Chironomus braseniæ* larvæ confine their attacks to leaves at or beneath the surface where their burrows may be flooded with water. This requirement limits their attacks to a restricted variety of plants. The writer's observations on the injury done aquatic plants by *C. braseniæ* are confined to the one place where they occur within a reasonable distance of Ithaca, N. Y., which is Spencer Lake. Here the conditions seem to be excellently adapted to the growth of aquatic plants. The lake is shallow and *Brasenia schreberi* is the dominant plant with floating leaves, while *Castalia ordorata* is present in various parts of the lake and is next in abundance. Observations made on July 22 show a very considerable proportion of the leaves of Brasenia infested, while only one or two doubtful cases of the infestation of Castalia were observed. On October 7 the entire pond was examined, and a leaf of Brasenia which had not been injured by this larva was so rare as to make it difficult to explain how it escaped. The leaves of Castalia showed a greater percentage of infestation later in the season than at the time of the author's earlier visit, but they were not badly injured. Dr. Pettit says of the damage to water lilies:

The pads of both *Nuphar advena* and of *Nymphea odorata* were furrowed by some miner. The pads had been badly eaten in some places and many contained living larvæ and pupæ.

CONTROL.

The injury done by these larvæ in parks and private gardens may some time become so great that methods of control will be necessary. At first thought it would not seem feasible to spray for an aquatic larva, but, as shown above, the water is kept circulating

through the burrow and out on the surface of the leaf again. This use of the same water over and over, except as it is removed by evaporation and replaced by a fresh supply drawn in by capillarity through minute openings, prevents the dilution of any poison that may be added. Any arsenical spray should be effective. There is, however, an important difficulty encountered by the lack of uniformity in the rate of development of the larvæ. They are present in increasing numbers from the first of the season to late in September and infestation is taking place constantly.

Where feasible the larvæ may be destroyed in the early part of the season by draining the pond and allowing the bottom to become dry for a few days. The larvæ are unable to breathe unless immersed in water and are, therefore, easily destroyed by a relatively short period of drying. In small pools the mechanical removal and destruction of eggs and larvæ should be effective.

DESCRIPTION OF CHIRONOMUS BRASENIÆ, N. SP.

Larva.—Light green in color, the chitinized areas such as the head and claws reddish brown; antennæ slender, about three-quarters as long as the mandibles, the basal joint four-ninths of the whole length; a small spine on the apex of the basal joint and another at the apex of the second joint probably represent Lauterborn's organ. Each eye consists of two black spots in such close contact as to appear as one on superficial examination. The labrum much narrowed anteriorally, with a few setæ and four pectinate hairs. The epipharynx with three blunt teeth on its anterior border, the usual chitinized horseshoe area laterally compressed with the usual pectinate setæ, a posteriorly projecting median process and the two lateral arms articulate with the posterior margin of this area. The lateral arms also have dorsally projecting portions for the attachment of muscles. They are furnished with a median projecting membraneous flap. Maxilla with short palpus, several setæ, and two mesad projecting lobes. Mandibles with blackened teeth, the two median and outermost teeth not much blackened. Labrum with blunt-pointed margin, the teeth with rounded outline. Posterior prolegs with bilobed claws. Anal blood gills long and somewhat pointed. The posterior dorsal tufts of setæ are each placed upon a papilla, which is about as broad as long (fig. 15). There is also a pair of setæ just dorsal to the anal gills. Length, 7 millimeters.

Pupa.—Light green in color, the chitinized parts somewhat infuscated. Respiratory organs consist of a pair of tufts of white filaments. Dorsal surface of the second to sixth abdominal segments with a well-developed anterior band of brown setæ, the second and third segments with a posterior row of coarse spines, the entire surface covered with minute setæ, which are slightly smaller on a few irregularly placed areas, thus giving the surface a slightly mottled appearance. The lateral fin of the eighth segment with the usual set of four filaments and a brownish slightly toothed chitinized portion seen best in the pupal molt (fig. 16). The caudal fin has the usual fringe of filaments. Length, 5 millimeters.

Male.—Head, proboscis, palpi, and basal joint of antennæ yellow, tubercle slightly developed, eyes black. Antennal shaft and verticils brown. Antennæ with 14 joints, the terminal two-thirds as long as the rest of the antennæ. Pronotum projecting laterally, but not reaching the level of the mesonotum dorsally. Mesonotum greenish yellow, translucent, somewhat pruinose; vittæ of a light buff color; scutellum and

halteres yellow; metanotum and sternopleura buff colored. Wings white, longitudinal veins and cross veins not infuscated. Cubitus forking distinctly beyond the cross vein; third and fourth veins ending about equally distant from the apex of the wing. Abdomen light green, densely clothed with long yellow hairs. Segments without distinct fascia. Hypopygium as in figure 17. Legs whitish, fore tarsus not bearded, second and third joints densely bearded for their entire length. Tibial comb darkened on all legs; basal segments of fore tarsus more than one-half longer than the tibia, proportions as 47 : 30. Pulvilli well developed, empodium, narrow. Length, 4 millimeters.

Female.—Antennæ yellow, apical joint slightly infuscated, seven jointed; posterior margins of the abdominal segments with a narrow whitish fascia. Otherwise like the male. Length, 3.5 to 4 millimeters.

Group V.—Trichocladius nitidellus Malloch.

To this group belong those larvæ which feed directly and apparently by preference on filaments of Spirogyra. *Trichocladius nitidellus* Malloch, a species described in 1915, is the only species that the author has thus far found which properly belongs here, although Lyonet (1832) described the habits of a species which obviously belongs to this group. Miall and Hammond (1900) state that this species has been rediscovered and studied by T. H. Taylor. They give in considerable detail the habits and behavior of this larva based on Taylor's observations. But it seems to the writer that there is a considerable difference between the two species and that the larva studied by Taylor agrees more nearly with that of *Trichocladius nitidellus*, which the author has studied, than with that observed by Lyonet. This difference will be more readily understood after the feeding habits of Trichocladius have been outlined.

FEEDING HABITS.

The description of the habits of this group has been well given by Miall and Hammond (1900, p. 11–17) based on Taylor's studies. *Trichocladius nitidellus* differs only in a few details. Filaments of Spirogyra are eaten exclusively by the older larvæ. There seems to be some selective ability exercised in the choice of filaments when more than one species of Spirogyra is present. This selection favors the smaller filaments. The larva often seizes a filament near the middle and forces the loop down its throat two fibers abreast. The same thing is often done with the larger filaments, and only occasionally are they bitten off completely. In this respect the author's observations differ from those of Taylor, who says: "A filament of Spirogyra is seized by the mandibles and bitten in two."

Taylor also states: "The labrum beginning at one end of the filament draws it into the gullet by a stroking action." The labrum is not so well adapted to meet the requirements of this method of feeding as the lateral arms which are located on the epipharynx. This will become more obvious when it is understood that the filaments are only crushed a little between the mandibles and possibly also between the labrum and the labium. This leaves the filaments in so natural a condition that when evacuated they immediately straighten out into their original shape. The stroking action of the labrum on a smooth filament, it would seem, is a far less effective method of forcing such a filament down into the stomach than the contact on either side by a well-developed pair of lateral arms

which can be swung through an especially wide angle due to their position on the under-side of the labrum. The movements of the lateral arms are so correlated with those of the labrum that the apparent stroking action observed by Taylor might well have been misinterpreted. The correctness of this line of reasoning has been confirmed by the author by direct observation with the low power of the compound microscope on a larva which was feeding with the ventral side up.

Digestion in *Trichocladius nitidellus* as in *Chironomus braseniæ* is incomplete, many cells appearing to be unaltered in the course of their passage through the body.

THE BURROW.

The burrow, as far as the author has been able to observe, is quite variable. In the older species it is made up of filaments of Spirogyra which have already passed through the body, as Taylor has also observed. In the case of the very young larva the burrow seems to be made up of dark-colored débris due to a different type of food eaten by the young larva. It is found to be made up of organic débris in which diatoms figure very largely. The writer is not sure at what stage the larvæ begin to feed upon Spirogyra, but it is certain that specimens not more than one-fourth the size of the mature larvæ do feed upon Spirogyra. These larvæ have been observed to drag their burrow after them in a manner similar to that described by Lyonet. His observations when translated are approximately as follows:

Its activity in transporting itself from one region to another is very great and its behavior is peculiar. It extends its head for this purpose, seizes in its teeth all objects which it encounters, retiring quickly without relaxing its hold. The claws of the anterior prolegs hook themselves into the object seized by the teeth, loosening them it elongates itself again in order to seize some more distant object and draw itself forward.

Taylor does not seem to have noticed this habit, for he states under the heading of "locomotion":

As the case is not fixed the larva can travel without leaving it. It does not creep like a caddis larva, but jerks itself forward by a few powerful undulations, in which the flexible case participates.

The older larvæ, however, according to repeated observations made on *Trichocladius nitidellus* both in the laboratory and out of doors, show so wide a range of behavior that it is impossible to confirm or disprove any of the above statements. Larvæ of this species found living on the algæ near the surface in a watering trough were placed in watch glasses and fed diatomaceous débris, which they ate and from which they con-structed tubes in no way different from those characteristic of *Chironomus cayugæ*, as described above. Others, fed on a scant amount of Spirogyra, built no tube at all. About 30 larvæ were found at the bottom of a small pool clinging to an old and partly decayed table leg. These had no tubes. It is not difficult to find all intermediate stages between the attached, the free tube, and the larvæ without any tubes.

The food supply seems to be a controlling factor in the nature of the tube built. Since the larva lives on Spirogyra by preference, it eats away all the filaments in its immediate vicinity unless they are very abundant and closely matted. In that case it selects out the filaments which it prefers and simply extends the case. When the food becomes scarce, the larva is able to feed upon whatever débris it finds available, and when feeding in this manner it constructs the tube characteristic of larvæ feeding in this manner.

Taylor's observation upon the use of evacuated Spirogyra filaments in the construction of the tube is quite correct for *Trichocladius nitidellus*, as is also his observation of the use of silk to fasten the fragments together. "Fibrous structure," which Taylor saw only "faintly," was not noticed.

The larva carries on its respiration in the usual way; but since it habitually lives in a well-aerated environment it lacks hæmoglobin in its blood and simply takes the color of the food contained in its stomach. Such larvæ characteristically have much better-developed tracheal systems than those provided with hæmoglobin. This fact, together with Taylor's drawing (Miall and Hammond, 1900, p. 15, fig. 8), which shows a well-developed tracheal system, tends to corroborate his identification to the genus Orthocladius to which all the species of Trichocladius were formerly referred.

The available literature on the feeding habits of all the Orthocladius larvæ is so limited that it is impossible to tell whether any considerable number feed upon different filamentous algæ or not. It seems probable that the specimen observed by Taylor and assigned to this genus is either identical or closely related to *Trichocladius nitidellus*.

Group VI.

This group or subdivision of the Chironominæ is erected to include several species known to live throughout the larval stage without building any semblance of a tube. Since there are several genera represented by these forms which have relatively little more in common than their free living manner of life, the author has divided them into subgroups based upon the structure of their mouth parts and the nature of their habitats.

Group VI: Subgroup A.—Metriocnemus knabi Coquillett.

These larvæ are quite unique in their habitat, food, and manner of life. They were apparently first studied in the larval condition by Knab (1905), who made a number of observations on the larvæ and pupæ. He found them in the pitchers of the pitcher plant (*Sarracenia purpurea*), and, so far as known, the larvæ are not found in any other habitat. Although confined apparently to a single limited habitat, they are evidently widely distributed, for Knab found them at Westfield, Springfield, and Wilbraham, Mass., and at Cedar Lake, Ill. The writer has found them at McLean, N. Y., and they are doubtless to be found wherever *Sarracenia purpurea* occurs.

The larvæ of the present species live at the bottom of the water-filled leafcups of *Sarracenia purpurea*, burrowing in the closely packed débris composed of the fragments of decomposing insects. Evidently their food is from this source. [Knab, 1905.]

HEAD STRUCTURES.

The head structures for this subfamily have already been discussed, but this particular species and doubtless the entire genus (for the larval stage of very few are known) show decided modifications in their mouth parts. These modifications are well adapted to the present mode of life of the larvæ.

The labrum has the usual epipharyngeal comb well, though not strongly developed. It also has the labral comb well developed, very wide, and finely toothed. The usual hooks, pectinate hairs, and spines are present, but somewhat modified. The pectinate hairs are here quite broad at their tip and furnished with a straight and uniformly

toothed margin. There are two pairs of these pectinate hairs, which, together with the other spines and processes, make quite a formidable and closely set array of scraping implements. The labium is, on the whole, not very different from the one figured for *Chironomus braseniæ* except in the number and relative lengths of the teeth. In *Metriocnemus knabi* the teeth of the labium are of nearly uniform length.

The maxillæ are quite remarkably different. The inner mesad projecting portion has a number of long close set spines which lie in the same plane as the labium and doubtless are of great assistance in supplementing it and the hypopharynx in their scraping action. The basal portion labeled for *Chironomus braseniæ* is in *Metriocnemus knabi* narrower and less firmly united to the epicranial plate. The fan-shaped structure marked *c* (figs. 11 and 12) is entirely lacking in this species.

The hypopharynx is long and well supplied with short, blunt processes. Its margin lacks the chitinized plates shown for *Chironomus braseniæ* and is obviously specialized as a delicately sensitive scraping structure. Its general appearance is that of a soft and somewhat flexible tonguelike structure covered with processes that are doubtless tactile in function. The epipharynx is provided with the usual pair of lateral arms which are here similar but less strongly developed than is the case with *Chironomus braseniæ*.

FEEDING HABITS.

Knab's remark that the larvæ burrow among the fragments of decayed insects and evidently obtain their food from this source is true as far as it goes. It leaves one in doubt, however, as to the actual food of the larvæ. Several times the author saw larvæ with broad chitinous bands around their bodies, evidently segments of insects' legs. Other observations have shown the larvæ with considerable parts of their bodies extending into these narrow insect appendages where the larvæ were apparently feeding. This would lead one to think that the larvæ feed upon the decaying tissues found there. This is doubtless true, for they are quite adaptive in their habits; but from other observations it would seem that they were, perhaps, even here feeding indirectly on the insect structures by devouring the large numbers of bacteria that in turn break down the insect tissues. This conclusion has been reached after considerable experience with these larvæ under artificial conditions.

Larvæ were removed from the pitcher plants and placed in petri dishes, together with the insect débris in which they were living. They were found to be perfectly well fitted to live in this manner. It was also found that they could live on beef broth, smoked beef, and decaying plant material. It is obvious, therefore, that insects are not the only source of food for these larvæ.

The question at once arises, Why is this species found so universally in the pitcher plant and nowhere else if it can live upon so wide a range of food? The answer is obviously given in the adaptation of this larva to a particular kind of food. In this adaptation the mouth parts are doubtless most fundamental. As explained above, they are fitted with a number of combs, spines, and fingerlike processes. The structure and length of the hypopharynx also indicate that it, too, is used as a delicate scraping organ, which is of prime importance in assembling the scattered bacteria. In this connection the presence of well-developed silk glands in close association with the hypopharynx suggests the possible function of their secretion in assembling the bacteria upon which the larva largely subsists.

That the larvæ prefer bacteria to the more solid tissues can be observed by their behavior in a petri dish, where they move about in a very characteristic manner. The head is carried at an angle of about 45° to the bottom, and the anterior prolegs are the chief organs of locomotion. They alternate with the head in supporting the body and are provided with about three rows of strong coarse spines. The larva moves along by a rapid alternate depression of the head and backward stroke of the anterior prolegs. The posterior prolegs are little used, and the larva curves its body up first on one side and then on the other, thus aiding the head and anterior prolegs in their forward movement. The larvæ always move forward, and the spines on the inner border of the maxillæ and hypopharynx are doubtless of prime importance in collecting the fine organisms, in correlation with this progressive method of feeding.

The pitcher plant seems to be the chief natural environment where such food substances are available. While its inner surface is covered with closely placed spines which all point inward, it nevertheless offers a favorable environment to such small larvæ, for they are able to move about among these spines and collect the bacteria and mold spores which accumulate there. That these larvæ may find conditions at least imperfectly suited to their method of feeding in other environments would seem to simplify the explanation of their distribution. The swamps are widely separated, and the pitcher plants are not numerous, and if a few larvæ could live in other environments the distribution would be more readily accounted for.

Group VI: Subgroup B.—Orthocladius sp. (?)

These larvæ have not been bred, but are abundant and will doubtless be found to be one of the common species. They are found in flowing streams about Ithaca and were collected the first part of June among the débris resulting from the disintegration of Cladophora. They were at that time very numerous, but the writer has been unable to find them on several occasions during the last of July and the first part of August. As forms found in flowing water are hard to rear, none of those taken early in the season were reared.

LARVAL CHARACTERS.

The larvæ are bluish green in color and have several rows of coarse black claws both on the anterior and posterior prolegs. The caudal filaments are placed on very small short papillæ, and the filaments themselves are very short, scarcely extending beyond the anal gills. The head parts are rather stout (figs. 29 and 30), and the fan-shape membranes are entirely absent.

The larvæ apparently do not make use of their well-developed silk glands for the purpose of building tubes. It seems probable that they would not be so well developed unless they had some important function. The author has concluded therefore that their development is correlated with the nature of the food eaten.

FEEDING HABITS.

The larvæ creep about on the surface of submerged stones and even out of the water where the rocks are only moist. A very noticeable feature in the behavior of these larvæ is the frequency with which they turn over. This habit of rolling over every few

minutes while creeping over moist stones seems to be an adaptive measure. The upper portion of the body would become dry and the surface film would break away from the larva if it were not for the frequent moistening of the entire surface of the body. This revolving of the body about on its long axis the larva accomplishes by bending its head and the first two or three segments of its body off to one side, then, by relaxing the underneath muscles and stressing the upper muscles, this angle is made to revolve about the body until the larva again reaches an upright position.

These larvæ feed upon the organic débris to be found on the ledges in flowing water. Those whose stomach contents were studied had eaten Cladophora almost exclusively, and both the cell contents and the cell walls could be recognized. There were also a few diatoms, several filaments of Oscillatoria, and a few spherical cells, possibly of Aphano-capsa sp. The well-developed silk glands are doubtless used by the larvæ as digestive glands, and their development may be due to the coarse organic nature of their food.

Group VI: Subgroup C.—Prodiamesa sp.

The genus Prodiamesa was established by Kieffer in 1906. In the "Genera Insectorum" he refers six European species to this genus, and the writer has found only one South American species which has subsequently been referred to it. There is therefore no record of the occurrence of the species of this genus in this country. The species upon which these observations are based has been bred, and, from the larval mouth parts figured by Kieffer and Thienemann (1908), it is found to resemble *Prodiamesa præcox* very closely. The adult description, however, does not agree with that of *P. præcox*, and it seems probable that it will be found to be a new species.

The larvæ are yellowish white with reddish-brown heads and brownish claws on the prolegs. They, as well as the larvæ of the genus Diamesa, are characteristically found in flowing streams. The larvæ of Prodiamesa were found burrowing through the coarse débris that had accumulated in a roadside watering trough which was fed by a rapidly flowing stream from a near-by hillside. The trough was nearly full of sticks, grass, and leaf mold in various stages of decay, and it was through this rather loosely aggregated material that the larvæ were seeking their food.

BODY STRUCTURES.

This genus as represented by the writer's material (which is essentially in agreement with the larva of *Prodiamesa præcox*) is structurally quite similar to the burrowing forms. This is especially true of the anterior prolegs which are made up of several rows of fine spines. The branchial gills of the eleventh segment are absent in this genus. The caudal filaments are well developed.

MOUTH PARTS.

The most characteristic modifications in the mouth parts are to be observed in connection with the maxilla, the hypopharynx, and another structure the homology of which has not yet been satisfactorily established.

The maxilla is capable of a great deal of free movement, as the basal portion (as in the other species in this group) is not fused to the adjacent epicranial plate (fig. 31). Its inner mesad projecting process (fig. 31, *l*) is provided with numerous fingerlike

processes resembling those observed in *Metriocnemus knabi.* The hypopharynx also suggests that of *M. knabi* and doubtless shows a close generic relationship.

The structures referred to above as not having their homologies well established are those to be found on the ventral side of the head (fig. 32, *c*), and suggest at once the fan-shaped membrane which the writer has labeled *c* in figure 11. Mundy (1909) has observed and mentioned these structures. He also gives a figure (Pl. V, fig. 18) and states that it is his opinion that the long filaments which the author has shown in figure 32 doubtless fuse and form the fanlike membrane which is so characteristic of the genus Chironomus. The author has been unable to establish the connection between these structures and the articulation of the maxilla shown in figure 11 and is therefore doubtful about their identity. The other mouth parts are very similar to those given for *Chironomus braseniæ* and therefore need no special mention.

FEEDING HABITS.

The feeding habits, judging from the food found in the stomach, involve a process of selection. The larvæ, as indicated above, creep along through the trash at the bottom of streams and consume whatever they encounter that seems most edible. Those examined had a considerable quantity of plant fragments and some soft, brown unrecognizable substance in their alimentary canal, but no diatoms were found. It was suggested by Mundy that the vibrissæ on the ventral side of the head of this larva might serve as the vibrissæ on the sides of a cat's head. It seems probable to the writer that their function is a tactile one. They doubtless enable the larva to distinguish the different substances which are more or less edible and in this way supplement the more delicate sense structures within the head of the larva.

The group as a whole contains larvæ with mouth parts that allow greater freedom of movement, especially in connection with the maxillæ, than in any of the other groups. Associated with this modification of the maxillæ is the entire lack or slight development of the fanlike membrane on each side of the labrum. The hypopharynx seems to be developed as a more efficient organ of sense and doubtless serves an important function in the selection of the food. The other structures of the head are in general similar to those characteristic of the previously discussed groups. It seems probable from the structure of the mouth parts that this is the more primitive group, as Goetghebuer has also suggested. The free-living habits of the larvæ seem also to supplement this conclusion.

SUBFAMILY TANYPINÆ.

This subfamily contains seven genera, and at least 45 species are known to occur in North America; but in spite of the number of known adults the author has failed to find any considerable literature bearing on the larval habits. Fr. Meinert (1886) made a number of observations upon a Tanypus species which he figures. These observations have been followed quite closely by Miall and Hammond (1900) and Johannsen (1903). This literature while good as a general treatise fails to give any very adequate idea of the feeding habits beyond the statement that the larvæ are predacious. Miall and Hammond, however, state:

Bloodworms are preyed upon by many aquatic insects as well as by fishes. Caddis worms, Perla larvæ, Sialis larvæ, and Tanypus larvæ devour them greedily. A number of empty heads of the bloodworms may often be seen in the stomachs of a single Perla or Tanypus larva.

The behavior of the larvæ belonging to this subfamily is quite similar for the members of the group but very different from that of the larvæ of the other subfamilies. The Tanypinæ differ from the Chironominæ in the length and structure of the head and the function and arrangement of the mouth parts. The anterior prolegs are less strongly developed in Tanypus and are capable of being entirely retracted, so as not to give even a protuberance on that part of the body. The posterior prolegs are more strongly developed, are longer, and are furnished with claws of greater length than those of the Chironominæ. In other respects they differ less from the Chironominæ in appearance than in structure. They are not all nearly colorless, as Miall (1895) states, but there are a few which are blood red in color. These differ in their behavior as will be explained below. They also differ from all the aquatic members of the subfamily *Ceratopogoninæ* in the possession of both anterior and posterior prolegs.

In his study of this group the author has observed as many different species as he could find, but his chief attention has been given to *Tanypus carneus, T. hirtipennis, T. monilis,* and *T. dyari,* which have also been bred in the course of this work.

Tanypus hirtipennis differs from the other species mentioned in having red blood with which is correlated a burrowing habit. The presence of hæmoglobin in the blood seems to enable this species to live in a less well-aerated environment in the same way that it does in the case of certain members of the subfamily Chironominæ. They do not build tubes as so many of the true bloodworms, however, but simply prowl around pushing their inquisitive heads here and there among the organic débris at the bottom. On this particular point Meinert (1886) states that the Tanypus larvæ construct tubes where they remain concealed. Dr. Johannsen tells the writer that in no case has he observed them to behave in this manner. Since the salivary glands are much smaller in proportion to the rest of the body, since the larvæ live upon tube-dwelling larvæ, and since the pupæ are active like those of Culex, it seems probable that they are only found in tubes where they have gone in pursuit of their normal food. This also seems most likely from the fact that the Tanypus larvæ when disturbed flap themselves out of the tube or débris where they are, as readily as otherwise, which is not the case with the tube-building larvæ. This species, except for its adaptation to a lower level where it is more protected from bottom-crawling enemies as well as impeded in its locomotion, differs but little from the surface-dwelling forms.

Tanypus carneus is perhaps the best representative of a surface-dwelling member of this subfamily. It is slim, has a head about three times as long as wide, and its anterior proleg is long and slim and shows its double nature only toward the tip, where it is divided into two rounded branches provided with a few rather delicate claws. This proleg is capable of being completely withdrawn and thus adapts the larva to life among filamentous algæ where it seems most at home. The long posterior prolegs enable the larvæ to glide along snakelike through the filaments. When an enemy approaches, they are able to withdraw by a backward flexing of these prolegs and the posterior end of the body. Their behavior when sufficiently stimulated resembles that of the crayfish. So rapid is their movement that whether their prolegs catch on any solid particles or not they shoot backward far out of danger. When at rest on the débris beneath the surface, the stimulation of their caudal setæ causes them to give a little flip to their bodies which brings their heads almost exactly at the point where their posterior ends had been. This power to rapidly right about face, while especially characteristic of all

the Tanypinæ, is not confined to this subfamily, but is a common reaction in all free-living species of the Chironominæ.

The author's chief justification for considering the feeding habits of this entire subfamily together is the similarity in the structures of the head and the mouth parts. The figures and the discussion of these parts found chiefly in systematic works have misinterpreted the homology of these parts. On this account, as well as the fact that the mouth parts in this group are of prime importance in any discussion of their feeding habits, they will be discussed in considerable detail.

MOUTH PARTS.

The hypopharynx of the larva of the subfamily Tanypinæ has commonly been called the labium. But it seems probable from figures 42 and 43, *th*, that what has hitherto been called the labial plate is really an especially well chitinized anterior border of the hypopharynx. Its strong development is here associated with its very much greater functional importance in this species. The strong muscles attached to this part of the head swing the plate upward and backward, the entire chitinized framework of the hypopharynx taking part in this movement. The toothed border of the upper chitinized bar also serves a similar scraping and cutting function (figs. 42 and 43, *hy*). The labium proper is double and has been labeled hypopharynx. From its position it seems more properly called the labium, and its double nature finds a partial counterpart in the labium of *Chironomus digitatus* Malloch (Malloch, 1915, pl. 30, fig. 13).

In the latter species the central part of the labium is a large rounded light-colored process, while the two sides are black and toothed in a manner very similar to the two-toothed areas in the Tanypinæ. The central area appears to be homologous to the "labial papillae" of Malloch, 1915 (pl. 25, figs. 4 and 9; see also fig. 41 in this work). This centrally arranged flap is soft and muscular and has a band of roughened scales on its dorsal surface. The mandibles are opposable and very pointed. They are also able to be used in opposition to the labium. In *Tanypus dyari* they are furnished with a row of seven lateral teeth (fig. 41, *md.*), the first of which is especially well developed in practically all species, as is the case in *T. dyari*. It seems possible that this long-pointed tip, together with the first well-developed tooth, are structures homologous to the double tip so common in the Chironominæ, which is frequently mentioned as of specific value.

The maxilla in the Tanypinæ (fig. 40) is very different from the homologous structure in the Chironominæ. Here instead of being attached to a flattened plate (figs 11 and 12) it is capable of a considerable movement. It consists of a flattened appendage with a roughly circular chitinous supporting structure made up of several partially fused sclerites (fig. 40). This freedom of movement and increased functional importance of the maxilla have an important bearing on the freedom of the movement of the mandible, as one can readily appreciate who is familiar with the restricted movement of the latter in the genus Chironomus due to the fusion of the maxilla to the sides of the head. Correlated with this freedom of movement of the maxilla one is able to note that the mandibles may be employed either above or below the maxilla. The anterior portion of the maxilla (fig. 40) is furnished with a large number of thin plate-like processes which doubtless have a tactile function.

The labrum (fig. 39) is thin and but slightly developed compared to the labrum in the Chironominæ. It is furnished on its anterior border with several processes apparently possessing sensory functions. These processes seem to be of more or less specific value and may sometime be of use, as this group is lacking in really good larval characters of systematic value. The chitinous processes (cp) may be homologous to the lateral arms of the hypopharynx of the Chironominæ.

The head structure of Tanypus is quite unique, being developed for a special manner of life, and the constant recurrence of this structure throughout the group, together with the great similarity in the habits of these species, seems to abundantly justify the placing of all the species in one group. From the ventral side of the head one is able to distinguish longitudinally arranged muscles which are attached at one end to the chitinous framework of the hypopharynx and at the other end to the posterior border of the head. From the dorsal surface, however, one sees a very different muscular arrangement. Here the muscles in the anterior part of the head radiate anterio-laterad from the mid-dorsal line, and in the posterior part of the head they radiate posterior-laterad from this same mid-dorsal line. Here in the center of the head is an area which doubtless serves as a sort of pump and to which are attached long muscles which radiate anteriorly and posteriorly. This pump is a structure present throughout the subfamily so far as the author has observed.

Another unique feature of the head is the presence of retractile antennæ, which Meinert (1882) has figured and described in detail. He does not seem to have observed their functional significance, however, but considers them only from the standpoint of their anatomy and homology. It will, therefore, be sufficient to state that the antennæ are withdrawn into the head capsule itself where there are special chitinous sheaths to receive them. They are withdrawn by special well-developed muscles and are said to be extended by blood pressure. They are of great functional importance in that they enable the larvæ to actually measure the distance from their prey. A few easily made observations enable one to see how constantly they are used. The larvæ prowl about with their antennæ partially extended, and upon encountering an active object they withdraw them as they approach, thus keeping in touch until near enough to seize the object.

FEEDING HABITS.

The larvæ are all predacious as far as the author has been able to determine, although it is very difficult to actually observe them feeding. Numerous studies of the stomach contents of the larvæ have shown such an array of diatoms and desmids as to entirely mislead one looking for proof of their predacious habits. Meinert (1886) states that he has observed a living Simocephalus in the intestine of a Tanypus larva, while Miall and Hammond (1900) have apparently observed indubitable evidence that they were predacious on bloodworms from the presence of the heads of these larvæ in their stomachs.

It was not, however, until the author had starved a Tanypus carneus larva for a week that he was able to observe the actual feeding habits. This larva when put in a dish containing a number of large Cyprididæ would apparently strike at them when they came in contact with its head. The striking seemed to be a more or less involuntary reaction, for when the nature and size of these crustaceans were discovered they were

allowed to go uninjured. One of these crustaceans was killed and placed near the head of the hungry larva, but it was left undisturbed until movement was imparted to it by the aid of a needle. From repeated observations it seems apparent that the larvæ of this subfamily will not touch anything which is not moving. When movement was imparted artificially to dead pyschodid larvæ they were attacked, but before the skin was broken the larva abandoned them. When tried a day or so later on this larva it would not touch it, thus showing that decaying or dead material is not eaten even when the larva is very hungry, a fact in decided contrast with the behavior of a number of Chironomus larvæ, especially *Chironomus lobiferus*. The Tanypus larva to which was offered a freshly killed crustacean, however, ate it readily. It nevertheless showed a preference for small recently hatched bloodworms. These were swallowed whole and were apparently uninjured, as they were capable of moving for a time after being swallowed.

The method of attack and the defensive attitude of the larvæ of this subfamily were well shown in an encounter which occurred between two larvæ which the author was keeping on short rations preparatory to making observations on their feeding habits. The larvæ were of different species, one having a smaller and longer head than the other. The encounter was a head-on collision, each apparently striving to defend itself. They were taken under the compound microscope and their behavior observed. The head of the smaller larva was apparently not much within that of the larger one, but it was easy to see that the muscles within its head were being sucked toward the anterior tip of the head. The result was that the smaller larva was killed, although it was not consumed nor were any of the muscles of the head actually sucked out. The survivor, although unprovided with food from any other source, left its victim undisturbed as a result, doubtless, of its lack of movement.

An observation on *Tanypus carneus* well illustrates the function of the head as a sucking organ. A specimen that had been without food for four or five days was placed in a watch glass with a very active bloodworm (Chironomus sp.?) which was about the same size as the Tanypus larva. The Tanypus larva attacked the bloodworm just back of the head, employing its sharp mandibles to hold the larva. Very soon a reddish color could be observed in the head of the attacking larva, showing that it was beginning to suck the blood of the other. Then the alimentary canal was cut off, probably by the mandibles, and with its contents (diatoms, etc.) sucked into the body of the Tanypus. This left only the collapsed body wall of the larva to be consumed. This was accomplished by the use of the same powerful sucking apparatus. The body wall was drawn into the mouth while the hypopharynx rasped a hole through it, then the continued squeezing and sucking action of the head removed the muscles of the body wall. This method of treatment was repeated on different parts of the body until finally all the muscles of the body wall were removed. In this case the head was not swallowed and the muscle fragments of the bloodworm were in such a broken state that they would almost defy identification.

Miall and Hammond have remarked on the presence of red coloring matter in the body of Tanypus larvæ which they consider due to the bloodworms they have eaten. It is easy to confuse a natural red color with the color due to the food eaten, but a little experience will enable one to see a difference in the intensity of the color that is unmistakable.

The silk glands (fig. 44) are small and egg-shaped in general outline. Their ducts fuse some little distance posterior to their opening, which is situated just dorsal to the anterior border of the hypopharynx. The shape, relative size, and transparency of these salivary glands, together with the very different functions of the head and mouth parts in the Tanypinæ, at least suggest that their function is more exclusively that of a digestive gland than it is in the Chironominæ.

The alimentary canal is developed rather differently in the Tanypinæ than in the Chironominæ. Miall (1895) figures the alimentary tract for *Tanypus maculatus* but does not label the parts. In comparing these structures with the drawings of the alimentary canal of Chironomus sp.? given by Miall and Hammond the croplike enlargement so easily distinguished in the Tanypinæ (fig. 44, *cr*) is represented only by a narrow esophagus. The cardial chamber (fig. 44, *c*) is narrow and sharply marked off, and its surface is covered with longer coeca than in the Chironomus, but, on the whole, not so very different from it. The stomach proper (fig. 44, *st*) is proportionally shorter and of less functional importance. The remainder of the alimentary canal is quite similar in both subfamilies.

The food is retained in the crop (fig. 44, *cr*) part of the alimentary canal when first consumed and is constantly being stirred about by a peristaltic motion. When specimens are starved for a considerable time, the food is retained in this part of the alimentary tract often for the greater part of a week, which would seem to indicate its relative importance.

The peritrophic membrane, if present, is very thin and inconspicuous. The author has been unable to discover its presence by gross dissection and has consequently concluded that in this respect the Tanypinæ are decidedly modified as a result of their carnivorous habits. From the length of time that the diatoms are retained in the alimentary canal it would seem probable that they also are as well digested as they are in the stomach of the Chironominæ. As stated above, the digestion in this latter group is quite incomplete and any comparative statement must be relative in its nature.

It will be clear from the above considerations that the fundamental structures of this subfamily are closely correlated with its peculiar manner of life. It seems probable that this subfamily represents a more primitive type of insect than those included in the Chironominæ. This conclusion is based not alone on the free-living active behavior of the larvæ, but also upon the pupæ, which resemble the pupæ of Culex in their manner of life, as well as upon the primitive venation of the wings of the adults.

SUBFAMILY CERATOPOGONINÆ.

This is a widely distributed group. Many of the adults are known as blood-sucking insects, some attacking other insects exclusively and some turning their attention to the higher animals including man, while others appear not to take any food in the adult condition.

In the larval condition their habits are also variable. Guérin (1833) found the larvæ of *Ceratopogon geniculatus* Guérin and *C. flavifrons* Guérin under the bark of dead trees in a humid environment. Dufour (1845) found larvæ of a species which he identified as *Ceratopogon geniculatus* Guérin in decomposing onions. Perris (1847) found the larvæ of *Ceratopogon brunnipes* Perris in decomposing mushrooms at the

base of a poplar tree. He also found *Ceratopogon lucorum* Mirgen in a heap of decomposing elm leaves and succeeded in rearing them indoors in this same material. Laboulbène (1869) found the larvæ of an unidentified species of Ceratopogon in the ulcers or injured places in elm trees where they were living in what Dufour (1845) calls "la marmelade de l'Orme." These larvæ were reared and the species named *Ceratopogon dufouri* in honor of Léon Dufour by Laboulbène. Long (1902) found *Ceratopogon brumalis* Long in great numbers on the underside of nearly dry cow dung. He also found several hundred larvæ of all ages on the undersurface of a piece of moist rotting elm wood. He found similar larvæ and pupæ in the nests of the common foraging ants (*Eciton coecum*). The larvæ of *Ceratopogon specularis* Coquillett were found by Long to live gregariously in cow dung. Larvæ of *Ceratopogon stenomatis* Long were found by Dr. W. M. Wheeler in an ant nest, where they were moving about in the refuse heaped up by the ants in certain portions of their nests.

The larvæ of *Ceratopogon taxanus* Long (Long, 1902) were found beneath the bark of old dead trees in moist places or on the underside of very damp rotting wood. The only other habitat so far as known where the larvæ are commonly found is a strictly aquatic one. This latter environment according to Johannsen (1905) is occupied by the species having smooth wings. An examination of Malloch's (1915) keys, which cover only the Illinois species of this subfamily, shows 4 genera and 22 species with hairy wings to 9 genera and 72 species with smooth wings. It would appear, therefore (granting the supposition that smooth wings and aquatic habitat for the larvæ are correlated characters), that the greater number of the species are aquatic, but so few species are known in the immature stages that it is impossible to say whether the greater number undergoes development in water or in some more distinctly terrestrial environment.

BODY STRUCTURES.

The bodies of the aquatic larvæ are long and tapering, and their heads are proportionally longer and slimmer than those of the semiaquatic and terrestrial forms. The aquatic larvæ are entirely devoid of walking appendages, and the only external body structures that link them up with their near allies are the caudal filaments. These have either been considered homologous with claws of the posterior prolegs or left without any attempt at a comparison. In a permanent preparation of the larva of a Culicoidies sp.? the author has discovered that these filaments are arranged in two groups (figs. 45 and 48), which clearly suggest that they are homologous with the caudal filaments of the Chironominæ. Several authors have suggested that these structures, since they can be made to point either forward or backward, function as locomotor appendages. This observation is apparently correct. The great relative size and length of these caudal filaments seem to be functional modifications, for they are sense organs in other genera of the family.

The semiaquatic species (fig. 49) found in the sap flows of injured elms here at Ithaca, N. Y., resembles the one described by Laboulbène (1869), which he named *Ceratopogon dufouri*. These larvæ differ from the aquatic forms in having only poorly developed caudal setæ and in the presence of very short and contractile posterior prolegs, which are fused together and provided with a circle of hooked claws (fig. 50). This

form was not bred, but from the mouth parts it seems possible that this is a myceto-philid and not a chironomid at all.

The typically terrestrial forms have well-developed anterior and posterior prolegs. Perris's (1847) observations on *Ceratopogon brunnipes* and *C. lucorum*, together with a study of the aquatic species already mentioned, would indicate a series of intermediate stages between those with both anterior and posterior prolegs and those without either. The author has indicated one stage of this series above. The first stage has caudal filaments which replace the posterior prolegs. The other stages are represented by the two species described by Perris. The first, *Ceratopogon brunnipes*, he found in decaying mushrooms at the foot of a poplar tree. Of this species he says the anterior prolegs are deeply dilobed and each lobe is furnished with a few claws. These are completely retractile, but those of the posterior prolegs are not. The other species, *Ceratopogon lucorum*, he says, appears to have a proleg formed of two pieces united by a suture, each of which is feebly bilobed. The exterior lobe is bare, and the inner lobe is furnished with fine spines. The last species, found in decaying elm leaves, resembles the typically terrestrial forms in general; besides possessing both anterior and posterior prolegs it has a spiny body.

In considering the terrestrial nature of these larvæ Laboulbène (1869) says that stigmates certainly exist but that he has not been able to count the openings. His opinion that they really do exist seems to be due to his observations on the arrange-ment of the tracheæ. The authors quoted in regard to the variety of habitats occupied by the larvæ of the Ceratopogoninæ all emphasize the humid condition of the habitat, and in the absence of any direct observations on the presence of spiracles it seems probable that in this respect at least the group is a unit.

HEAD STRUCTURES.

To understand the feeding habits of any insect, the structure of the mouth parts lends an important clue. This is equally true of the mouth parts of the larvæ of the Ceratopogoninæ. The frequency with which the early students complain of the diffi-culties of such a study is a sufficient justification for a somewhat incomplete consideration of these structures here.

In the aquatic larvæ Culicoides sp.?, probably *C. guttipennis*, the head is long and slim, about four times as long as wide. The antennæ, so conspicuous and useful in the other subfamilies, are here very slightly developed, scarcely reaching to the anterior border of the head. Their location (fig. 45) on the dorso-lateral border of the head, together with their slight development, fits them to serve as a sense organ with only a very limited function. This slight development of the antennæ is characteristic of the entire subfamily and is doubtless associated with the nature of the food consumed.

The mandibles, in Culicoides sp.?, possibly *guttipennis*, are quite characteristic structures (figs. 46, 47, *md*). They are so hinged as to be capable of being extended beyond the head and are opposable. They are also often observed within the head with their tips pointing backward, showing that they have a wide range in their move-ments. The fact that the mandibles are capable of being swung through such a wide angle shows that they are doubtless very essential to the feeding habits of the larvæ.

The larvæ resembling Laboulbène's larvæ which the author found in the sap flows on elm trees about Ithaca have mandibles with teeth resembling those on the typical

Chironomus mandibles (fig. 51). These were used by the larvæ for the purpose of locomotion. They move alternately, and the head is tipped down slightly, so that their motion in a dorso-ventral direction enables them to function as feet. In this species the anterior prolegs are entirely lacking, and the larva moves by a gliding eel-like motion aided by the mandibles, which also help to clear the way. A similar function of the mandibles in Culicoides sp. is suggested (figs. 46 and 47).

The labium has several times been figured showing a strongly chitinized central tooth and in some species a single pair of lateral points on the otherwise smooth, somewhat thickened lower margin of the head. This central tooth appears to be the hypopharynx. Its probable function as a piercing organ would doubtless be suggested to everyone by its shape.

The epipharynx in Culicoides sp. seems to be located near the middle of the head and, so far as it is possible to tell from drawings, what the author considers as the epipharynx (figs. 46 and 47, *ep*) is what has been called the hypopharynx by Malloch (1915). Its function seems to be that of a strainer or comb, coupled doubtless with a tactile function.

The ventral half of the head seems to be fitted with long muscles which doubtless operate the mouth parts. The dorsal half of the head posterior to the epipharynx seems to be filled with radiating muscles, as described in the case of the Tanypinæ, which doubtless serve a similar function, namely, that of a pump or sucking organ.

FEEDING HABITS.

Culicoides (guttipennis?) larvæ, which were under observation for some time, were extremely hard to observe while feeding. The only case actually seen was that of a larva feeding within the dead body of a pupa. This pupa was of the same species as the larva. When observed, the body of the larva was thrust deep into the nearly empty shell. The larva was revolving its head and first two segments about, and of course could not bring pressure upon its mouth parts because of its lack of prolegs. It seems probable that the mandibles came into use at this time, as they are the only mouth parts adequate to the purpose. It was impossible to observe the activity of the mouth parts on account of the thickness of the chitinous wall.

The author's experience in trying to study the stomach contents of these species is exactly parallel to that of Miall and Hammond (1900), who were unable to identify the small particles occasionally found in the stomach. According to these same authors ''The digestive system is straight and simple and apparently adapted to the wants of a carnivorous animal.''

From the obvious specialization of these aquatic larvæ, as shown by their relatively great length and slight breadth, it seems fair to assume that they are adapted to an environment where they are able to reach food inaccessible to thicker and more chubby larvæ. During the winter larvæ of an aquatic species were found deep in various decaying stems, especially those of Typha and Sparganium. The following summer the writer was unable to find them in connection with these stems, but by dipping up masses of floating green algæ in the same pool he found them in considerable numbers.

What then is the nature of the food upon which the larvæ of the Ceratopogoninæ live? It seems probable that larvæ living under decaying bark, in rotting onions, among decaying elm leaves, or under cow dung would have but little choice in the food

which they obtain, especially when we learn that these larvæ do not burrow but simply wiggle and creep along through the moist and semifluid portions of their environment. That they in all probability live on decaying organic matter, together with the bacteria and mold which are always present in such substances, seems obviously a case of necessity. That an aquatic environment offers a greater opportunity for larvæ adapted to such a life to select their food is readily seen from the study of even a limited habitat.

The fact that aquatic larvæ kept in confinement will eat animal material is well shown by the observations mentioned above of a larva found eating the tissue of a dead pupa of its own kind. Their presence among filamentous algæ suggests that they may also eat out the protoplasmic contents of the larger filaments. It seems probable that various other organisms might become entangled in these filaments and be used as food by these larvæ.

In conclusion, it may be said that the larvæ of this group as a whole show a specialization of the mouth parts which fit them to live on soft substances. The various habitats in which the larvæ are found seem to bear testimony to the organic nature of the food consumed. The uniform failure of all attempts at microscopic analysis of the stomach contents of these larvæ suggests the structureless nature of the food taken. It seems apparent, therefore, that, since all decomposing organic matter offers a very similar food supply, the larvæ of this subfamily are capable of adapting themselves to a wide range of food substances. The humidity more than any one other factor doubtless limits this adaptability, since moisture not only aids decay, thus making hard inedible substances available as food, but also serves as a factor of prime importance from the standpoint of respiration to a larva lacking spiracles.

SUMMARY.

In the following groups the author has tried to show the more striking differences in the feeding habits of the Chironomidæ. In each group the mouth parts and general behavior have been made use of in determining the feeding habits. The stomach contents have been depended upon only as a confirmation of activities actually observed, thus avoiding several errors in connection with the predacious forms. The family as a whole shows a wide range of structural variations and a wider range, if possible, of special adaptations.

In Group I the larvæ, although somewhat variable in habits, can and do live to a very considerable extent upon bacteria, Protozoa, diatoms, small Crustacea and other free-floating aquatic organisms, which they strain from the current driven through their burrows by means of delicate silken nets.

In Group II the larvæ utilize the natural flow of the stream and subsist on the plankton organisms found there. The individuals of this group are usually very numerous, but as Group I consists of forms characteristic of quiet water, Group II does not compete with it.

Group III contains the greater number of the typical Chironomus larvæ, known as bloodworms. They are found wherever any considerable accumulation of diatoms and plant débris occurs. In laboratory experiments they were found to be able to subsist for considerable periods upon a very scanty supply of food material. Thus, we find them to be a group capable of utilizing and conserving whatever amount of diatoms, algæ, and plant débris may chance to fall upon the bottoms of fresh-water ponds. Their

large size and overlapping broods indicate their possible importance to fish life and in fish culture.

Group IV contains an aberrant species that feeds directly upon floating aquatic leaves and is noteworthy chiefly for its direct injury to those plants.

Group V contains at least one species (*Trichocladius nitidellus*) that promises to be of considerable importance, as it is able to subsist entirely upon filamentous algæ, chiefly Spirogyra.

Group VI includes a number of free-living forms that occupy somewhat unique habitats but constitute a group of minor importance.

The entire subfamily Tanypinæ consists of predacious forms, which as a group apparently do not contribute anything of economic importance to the Chironomidæ as a whole. They, however, do occasionally feed upon small Crustacea and the more rapidly moving diatoms and in this way help to counteract their otherwise well-merited position as an economically undesirable group, from the standpoint of the fish-culturist.

The subfamily Ceratopogoninæ are scavengers as a group and as such fulfill a useful function.

From the consideration of these rather arbitrary divisions, as well as the natural subdivisions of this large family, it becomes evident that there is a wide range in the adaptations of its different members. Some of these adaptations are of generic value, while others seem to vary within the genus, as in *Tanytarsus obediens*, which is included in Group I, although the other members of the group belong to the genus Chironomus. In a similar manner the red color of the larvæ seems to occur with little or no relation to the genus or subfamily but is rather more closely associated with the nature of the environment.

It is obvious from the above that the family has become specialized for different habitats. While the author has tried to point out what seems to be the behavior normally characterizing each group, it is easily apparent from a few observations that the great adaptability of all these species when under the stress of adverse conditions reduces them to what is probably the primitive habit of the group, namely, that of direct feeding on the débris about them.

The degree of departure from the primitive method of feeding, however, varies considerably. In the Tanypinæ we have a form that is strictly predacious, while in the Ceratopogoninæ we have a form that is adapted to live on dead and even decaying organic matter. The latter group seems to be about as abundantly represented in semiterrestrial environments as in those that are strictly aquatic, and it is this group that doubtless contains the most or perhaps the least primitive representatives of the family. The Tanypinæ doubtless come next and then the Chironominæ.

In the Chironominæ it would seem that from direct feeding by the use of silk to attach together the particles fed upon the use of silk in entangling particles in a stream would be but a simple step. Then, from this beginning an artificial current, made necessary by the poor supply of air, might readily lead up through a series of stages, from the entanglement of particles in the lining of their burrows to the present highly specialized silk net, which characterizes Group I.

The small size of these larvæ and their adaptability to such a wide range of habitats enable them to take possession of an environment where the food supply would be

insufficient for a larger form with similar food requirements.   It is this factor that seems most readily to explain the wide range and great numerical dominance of the family. It is this fact, too, which seems best to account for their numerous enemies among the aquatic animals.

ORPHNEPHILIDÆ.

This family is included here because of its close kinship with the Chironomidæ, as shown by the structure of the adult.   It is also of considerable interest on account of the unique and little known habits of the larva, which lives on the surface of ledges covered by only a thin film of water (fig. 38) and breathes by means of a trachea, rendering it entirely unable to live submerged for any considerable time.   As might be inferred from these two conditioning factors this family is not likely to occur in many parts of the country.   That it is really scarce is well illustrated by the fact that the record for the family in this country prior to 1916, so far as known, was based on three specimens found by Dr. O. A. Johannsen at Ithaca, N. Y.   Dr. V. L. Kellogg (1902) states that he has examined specimens of every family of the Nematocera except Orphnephila.   References in the literature to this family are so infrequent as to make it almost unknown except to a specialist in Diptera.   Thienemann (1909), however, found and described the larva which he obtained from mountain streams in Europe. His paper considers the nature of the habitat, the distribution, and the method of locomotion of the larvæ of *Orphnephila testacea*.   According to Kellogg (1905, p. 327) this species is the only one representing the family in this country and as far as the author is aware the only species known, if the American and European forms are actually identical.

The three adult flies found by Dr. Johannsen referred to above were taken in sweeping for insects, and none were taken in a manner to reveal the whereabouts of their immature stages.   It was therefore a very pleasant surprise to the author to accidentally run across the habitat of this most unique semiaquatic insect in the environment of Ithaca, the only place in this country where this species is known to occur.

As the interests of the author centered about the ecology of the species, especially as it concerns the feeding habits of the larvæ, he several times attempted to take specimens into the laboratory that the necessary conditions of their environment might be more readily studied.   Several of these attempts were failures because the larvæ were drowned while en route, but by lining test tubes with moist cheesecloth it was found very easy to carry any number of the larvæ considerable distances under perfectly normal conditions.

HABITAT.

While Thienemann's description is in substantial agreement with the writer's own observations, it seems best to summarize the conditions under which the larvæ were found.

The horizontal strata of the rock, so characteristic of all the gorges and "hanging valleys" in the environment of Ithaca, together with the usually rather irregular vertical cleavage, frequently gives rise to a stair-stepped bottom to the streams that enter the deeper valleys.   The only habitat in which these larvæ were found was on a series of "giant steps" (fig. 38), where a small stream spreads out over these broad and nearly horizontal stones in its precipitous descent to the valley of Six Mile Creek.   Here the larvæ were found rather more frequently on the vertical than the horizontal surfaces of

the ledges... They also seemed to select those parts of the rocks which were free from any vegetable growth, a selection probably closely correlated with their method of locomotion.

That the larvæ are unable to live on the surface of any other than perfectly quiet water was discovered by repeated attempts, as above stated, to carry living larvæ home in bottles half filled with water. The result was nearly 100 per cent fatalities. This does not mean that they can not move over quiet water, for they are very much at home in such conditions; but as soon as the surface film rises above the ventral third of the body, which is distinguished by being somewhat flattened and white in color, the result is total submergence. Total submergence is, of course, only fatal in larvæ which breathe by means of tracheæ and have no special means of escaping from the water. The larvæ of Orphnephila do breathe by tracheæ, and, while they are very well adapted to move rapidly on the surface of moist ledges, their very peculiar sidewise movement of the body is not at all suited to locomotion beneath the surface film. In fact, they depend very largely upon the surface film which holds them so closely in contact with the rock's surface that with the claws of their anterior and posterior prolegs they are able to anchor one end while the other is being swung around in a horizontal plane. This zigzag sidewise movement is sufficiently rapid to enable them to move four or five times as fast as a chironomid can crawl and gives them the appearance of being very sprightly.

This poor adaption to an aquatic environment is one of the factors that doubtless makes for their infrequent occurrence, next to the nature of their habitat, which is of itself rather unique. In several laboratory experiments in which the author attempted to duplicate natural conditions the larvæ were observed leaving the moist stones upon which they had been placed and voluntarily subjecting themselves to the current which swept them over the edge of the dish. So far as it is possible to judge, the same thing is liable to occur in nature, and the results are doubtless fatal, for the bigger streams are constantly agitated by swirls and cross currents which would submerge and drown the larvæ.

In order to try to eliminate the nonessentials in the environment of the larvæ, the author began searching for suitable methods of rearing them in captivity. At first an experiment, referred to above, was set up in which rocks taken from the natural habitat were placed in a tray through which a stream of gently flowing water was maintained. The result was that the larvæ allowed themselves to be carried over the edge and were lost down the sink spout. At Dr. Johannsen's suggestion a cheesecloth pocket was used and resulted in the successful completion of the transformation of some five or six adults.

This pocket was made by placing a double thickness of cheesecloth over the top of a wide lamp chimney and pressing it down so that it would hang in a conical sort of a pocket. This was covered with two thicknesses of cheesecloth after the larvæ and a fair supply of food had been placed within. Then both the cover and the pocket were made fast by successive coils of white thread, which were wound about so tightly that the larvæ were unable to creep out between the layers of the cheesecloth. The pocket was moistened by water which was kept dripping slowly over its surface. To insure the more uniform distribution of the water to all parts of the receptacle, a mass of cotton wool was placed on the cheesecloth cover. That this sort of an artificial environment seemed to meet their every need was demonstrated by the fact that the larvæ lived under

these conditions for several weeks with very few fatalities, even though the water ceased dripping several times for a number of hours, thus causing a considerable drying out. The pupæ, which seem never to have been found in nature, were observed to be located in a fold in the pocket where the water supply was more uniform and where greater security of position was doubtless possible.

The author was unable to find a pupa out of doors even after he had bred the pupæ in an artificial environment. The larvæ, while quite abundant in the one habitat in which the author succeeded in finding them, either do not live to transform to pupæ in any considerable numbers or else they possess some unusual habits which entirely escaped the writer's notice, for repeated search for pupæ in the most likely places and at such widely separated intervals was made that it does not seem possible that they could have been abundant in the environment occupied by the larvæ. That the pupa can live under the same conditions in which the larvæ are found is amply demonstrated by the author's laboratory experiments, where upwards of 50 per cent of the nearly mature larvæ transformed to adults. Another source of information which seems to corroborate the notion that the pupæ are not abundant was the fact that repeated sweeping over these rocks and in the adjoining region failed to give even a single adult specimen. The eggs so far as is known have never been found, and nothing is known of the mating habits of the adults.

FEEDING HABITS.

The feeding habits of Orphnephila are no less unique than its other environmental adaptations. Let us first take up the structure and arrangement of the mouth parts, as a knowledge of their nature and position is fundamental to all ecological considerations.

Thienemann (1909), as mentioned above, has figured the more commonly observed mouth parts of Orphnephila, but the separate drawings give no adequate notion of the relative position of each part. The author has found it necessary to draw the mouth parts as they appear in position and then for the sake of comparison several of them separately. The assembled mouth parts (figs. 53 and 54) show that the mandibles, instead of moving from the outside inward toward the mid line, as described in the case of the chironomids, are so hinged as to move outward from the mid line when in use for the purpose of scraping food from the rocks. This arrangement of the mandibles in Orphnephila, so far as the author is aware, is unique among Arthropoda. Correlated with the mandibles are the maxillæ which are furnished with a border of spoon-shaped plates which are opposable to the mandibles. This arrangement makes their function as collecting baskets, for gathering in the particles scraped free from the stones by the mandibles, quite obvious. The rods shown in figure 54, rd are supporting structures which fuse with the clypeal plate and extending beneath the mandibles form a partial support for the articulation of the maxillæ. The very marked development of the labrum suggests at least its probable function, and while the writer has not been able to observe this particular mouth part in use it is probably brought into play in connection with the mandibles in such a way as to scrape an intermediate area not touched by them.

The rather narrow labrum is provided with a considerable number and variety of spines at its terminal end and, together with the somewhat similarly clothed hypopharynx, is doubtless instrumental in collecting the food scraped loose by the labrum, as well as in the removal of the food particles assembled by the maxillæ (fig. 53, lb).

The food itself consists almost exclusively of diatoms, and as the number of kinds of diatoms in such streams is few and as those found on exposed ledges where the larvæ feed are even less varied the variety is not great. Figure 57 shows a typical selection of the food from the stomach of one of these larvæ. The many unique features in the habits of this insect seem to limit its life and activities to a very restricted environment to which it seems but poorly adapted, if the infrequent capture of adults and the evident scarcity of pupæ can be taken as criterions. From the above observations it might readily be considered as a species which had only recently acquired the aquatic habit.

EXPLANATION OF FIGURES.

CHIRONOMUS BRASENIÆ.

FIG. 1.—Ventral aspect of the epipharynx; a, lateral arm; co, epipharyngeal comb; e, chitinous claws; h, horseshoe-shaped chitinized area; p, lateral process; s, pectinate hairs; t, thickened border of the labrum; x, chitinous process.

FIG. 2.—Lateral view of the strongly chitinized structures somewhat diagrammatic; p, lateral process; s, setæ and pectinate hairs; u, clypeus; (other structures as above).

FIG. 3.—Lateral aspect of the mandible (md); j, pectinate setæ; q, external process; m, portion of the adductor muscle and its thickened exteria; v, extensor muscle.

FIG. 4.—Median aspect of the left side of the head; c, cardo (position indicated); g, galea; i, internal chitinous process; j, pectinate setæ; l, lacinia; la, labium; m, adductor muscle; md, mandible; p, maxillary palpus; st, stipes; u, clypeus; v, extensor muscle; w, center of articulation of the galea and lacinæ.

FIG. 5.—Ventral aspect of a portion of an epicranial plate; i, internal chitinous process; r, antenna; u, clypeus.

FIG. 6.—Dorsal aspect of mandible; j, pectinate setæ; o, articular surface of mandible; q, external process.

FIG. 7.—Dorsal aspect of hypopharynx; b, posterior lobe; e, backward pointing setæ; k, arm or chitinous process; th, chitinous plate; z, exit of the salivary ducts.

FIG. 8.—Dorso-ventral aspect of the hypopharynx; d, salivary duct; f, chitinous ring; k, arm or chitinous process; th, chitinous plate.

FIG. 9.—Antenna, lateral aspect; l, Lauterborn's organ; n, sensory spine.

FIG. 10.—Ventral view of the head; c, cordo; d, salivary duct; e, epicranial plate; la, labium; md, mandible; mx, maxilla; r, antenna; u, clypeus.

FIG. 11.—Lateral aspect of the maxilla; c, cardo or striated membrane; g, galea; l, lacinia; p, palpus; pf, palpifer; st, stipes; w, center of articulation of the galea and lacinia.

FIG. 12.—Lateral aspect of a portion of the epicranial plate; c, cardo or striated membrane; la, labium; pr, chitinous process limiting the movement of the mandibles; st, stipes.

FIG. 13.—Ventral aspect of the anterior margin of the labium.

FIG. 14.—Labium of young larva.

FIG. 15.—Posterior segments of the larva; b, branchial gills; ca, caudal filaments; c, claws.

FIG. 16.—Lateral fin on the 8th segment of the pupa; ca, chitinized area.

FIG. 17.—Hypopygium of the imago, dorsal aspect.

FIG. 18.—Wing.

FIG. 19.—Portion of an egg mass.

FIG. 20.—Tracings of the larval burrows in the leaves of Brasenia.

FIG. 21.—The same as fig. 20.

FIG. 22.—The same as fig. 20.

FIG. 23.—Diagrammatic drawing of the larval burrow greatly enlarged; a, silk supporting threads; b, section of the epidermis cut out by the larva; c, canopy composed of larval castings; d, epidermal slab used as the sides of the larval burrow; e, edge of epidermis and the underlying parenchyma; f, vein of the leaf; g, mucus gland.

FIG. 24.—Pupal chamber on the leaf of Castalia odorata; c, idioblast; p, anterior portion of pupa molt.

FIG. 25.—Cross section of a Castalia odorata leaf showing its general structure; a, stomata; b, upper epidermis; c, idioblast; d, lower epidermis; e, air space.

CHIRONOMUS LOBIFERUS.

FIG. 26.—Diagram of a glass preparation showing the position occupied by the larva in its burrow; lc, lower glass; nt, conical net; t, glass tube; u, upper glass; v, larva.

FIG. 27.—Diagram of the contracted conical net.

FIG. 28.—Broken labial plate.

ORTHOCLADIUS SP.

FIG. 29.—Labium.

FIG. 30.—Mandible.

PRODIAMESA SP.

FIG. 31.—Maxilla; ar, articular process; c, vibrissæ; l, lacinia; la, labium; p, palpus; st, stipes.

FIG. 32.—Ventral aspect of a portion of the head; ar, articular process; c, vibrissæ; la, labium.

CHIRONOMUS LOBIFERUS.

FIG. 33.—Claw of posterior proleg.

FIG. 34.—Spines of anterior proleg; a, serrate spine; b, c, hooked spines; d, hairlike spine.

FIG. 35.—Left anterior proleg; a, hairlike spines; b, hooked spines; c, serrate spines.

FIG. 36.—An enlarged silken holdfast attached to a glass surface; g, a process on the side of a larval burrow.

FIG. 37.—Silken network between two larval burrows (g, h); i, interlacing silk fibers.

ORPHNEPHILA AMERICANA.

FIG. 38.—View of habitat where larvæ were found, west bank of Six Mile Creek, Ithaca, N. Y.; F, water level of the main stream; l, ledges kept moist by water flowing in a small stream shown just above; w, water flowing over ledges.

TANYPUS DYARI.

FIG. 39.—Labrum; ch, chitinous plate; cp, chitinized process; se, sensory process.

FIG. 40.—Chitinous structures of the maxilla; l, lacinia; p, palpus.

FIG. 41.—Ventral aspect of the head; hy, hypopharynx; la, labial papilla; md, mandible; mx, maxilla; p, maxillary palpus; r, antenna.

FIG. 42.—Dorsal view of the labium and hypopharynx; ar, articular plate; cb, chitinous band; hy, hypopharynx; la, labial process; lp, lateral hypopharyngeal process; pr, sensory process; th, chitinous plate of the hypopharynx.

FIG. 43.—Lateral view of the same.

FIG. 44.—Dorsal view of the entire larva; br, branchial gill; c, cardiac chamber; cr, crop or proventriculus; g, salivary gland; m, malpighian tubule; r, retractile antenna; st, stomach or ventriculus.

CULICOIDES SP.

FIG. 45.—Dorsal view of entire larva; f, caudal filaments; g, branchial gills.

FIG. 46. Lateral view of the head; d, salivary duct; ep, epipharynx; ey, eye spot; hy, hypopharynx; la, labium; lb, labrum; md, mandible; mx, maxilla.

FIG. 47.—Ventral view of the head; structures the same as shown in fig. 46.

FIG. 48.—Dorsal view of the posterior end of the larva considerably enlarged; f, caudal filaments; ff, accessory caudal filaments; g, branchial gills. Larva from sap flow in elms resembling *Culicoides hieroglyphicus*.

FIG. 49.—The entire larva, dorsal view; ch, chitinous rod.

FIG. 50.—Posterior end of the same greatly enlarged; c, caudal processes; g, branchial gills; s, setæ resembling caudal filaments.

FIG. 51.—Mandible.

ORPHNEPHILA TESTACEA.

FIG. 52.—Side view of entire larva showing characteristic color pattern.

FIG. 53.—Side view of the head and proleg; ey, eye spot; la, labium; lb, labrum; md, mandible; mx, maxilla; pr, proleg; r, antenna; sp, spines.

FIG. 54.—Frontal view of the head; cl, clypial plate; la, labium; lb, labrum; md, mandible; mx, maxilla; rd, rod attached to the mandible.

FIG. 55.—Ventral aspect of the mandible.

FIG. 56.—Dorsal-lateral aspect of the hypopharynx.

FIG. 57.—Miscellaneous diatoms from the stomach of Orphnephila.
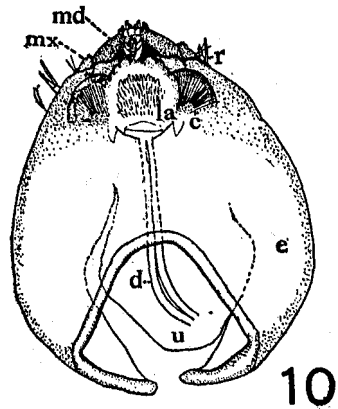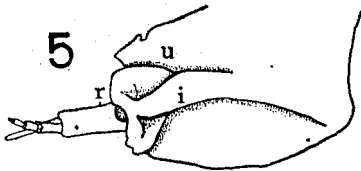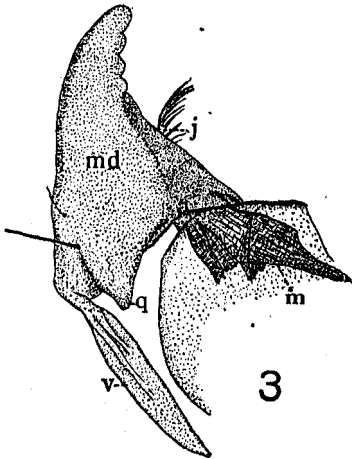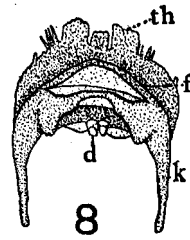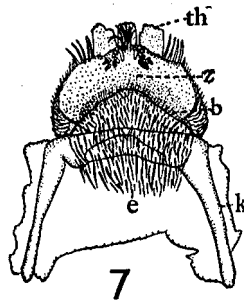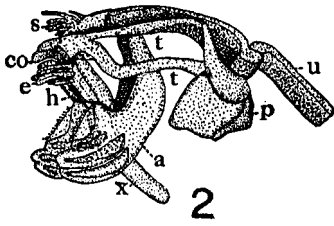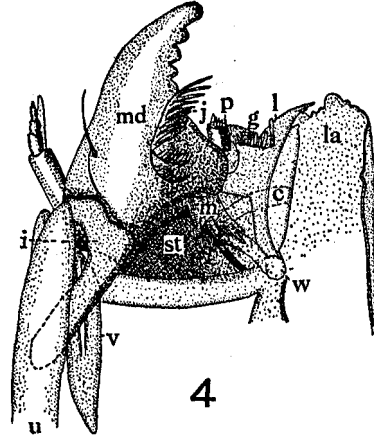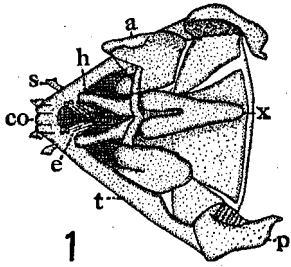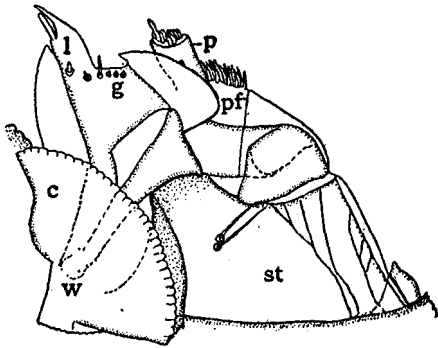
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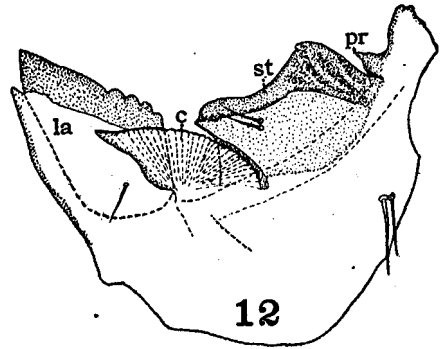
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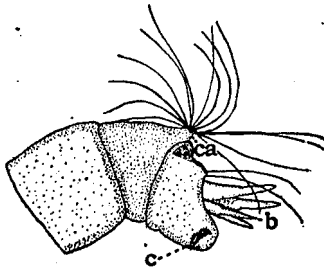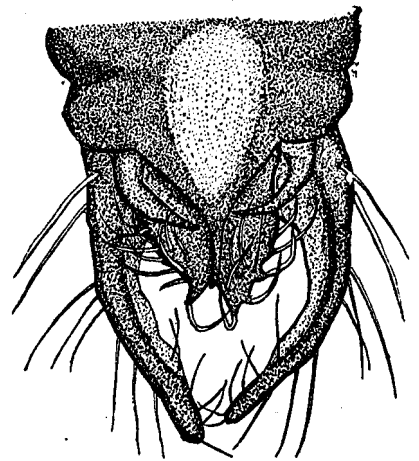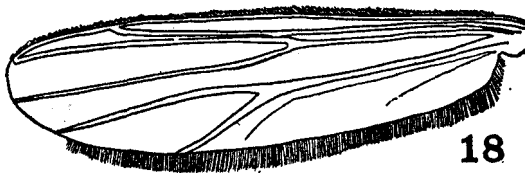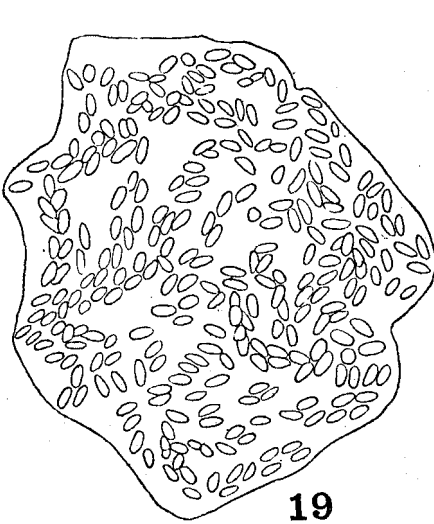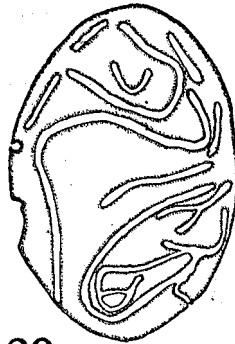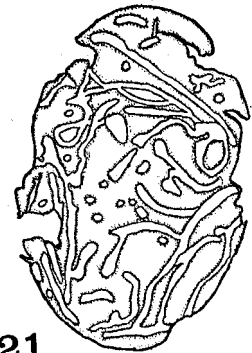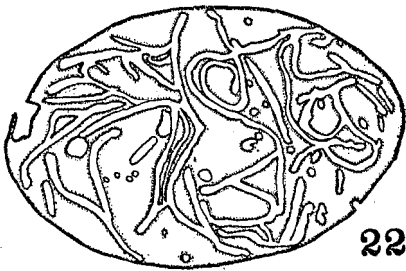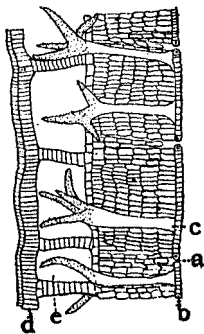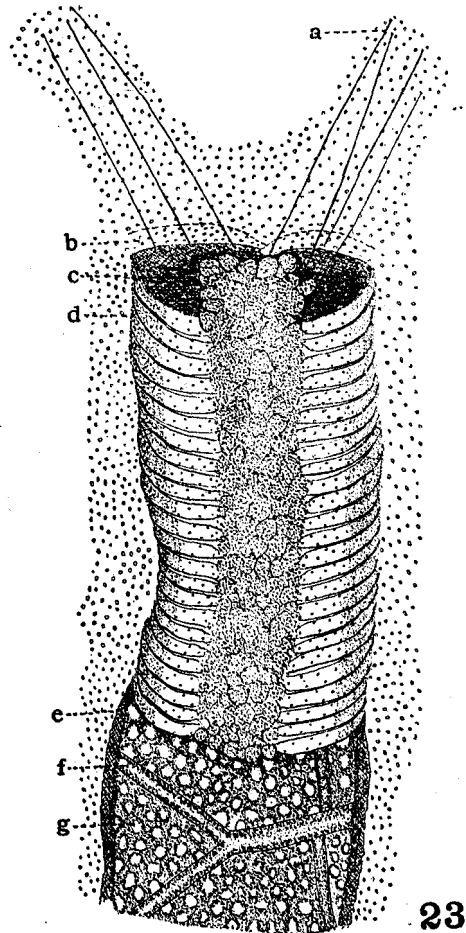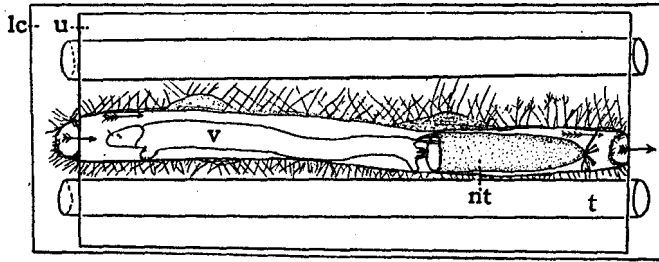
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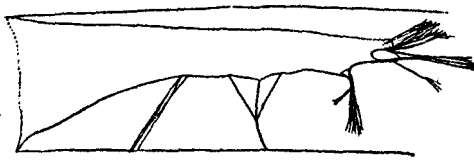
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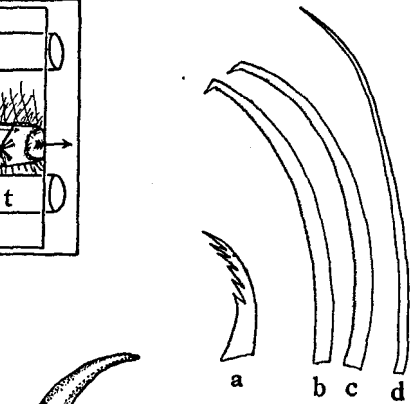
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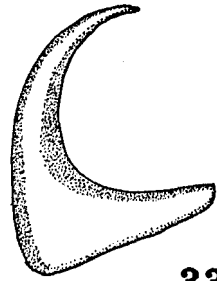
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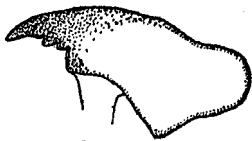
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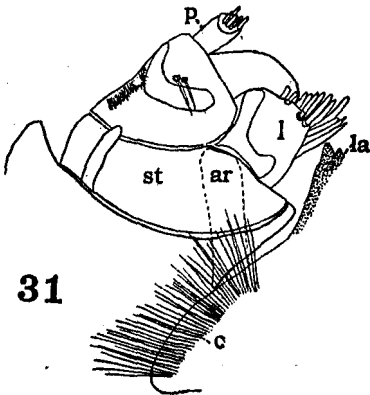
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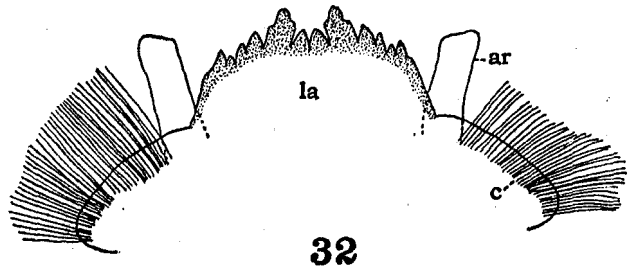
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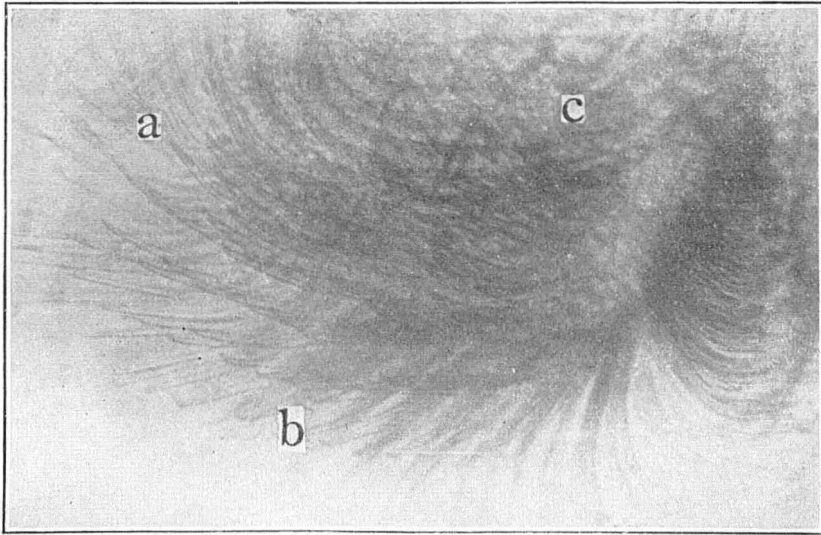
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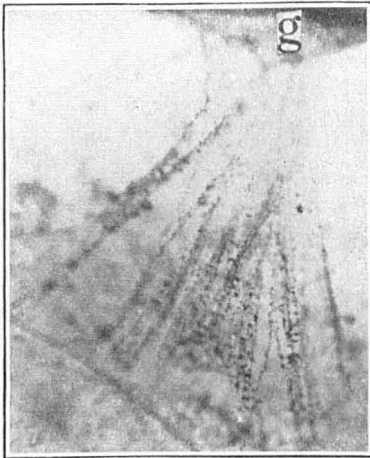
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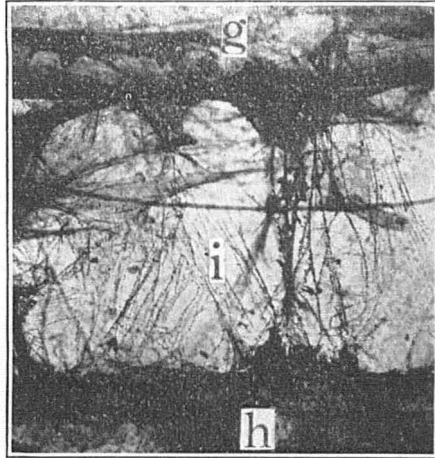
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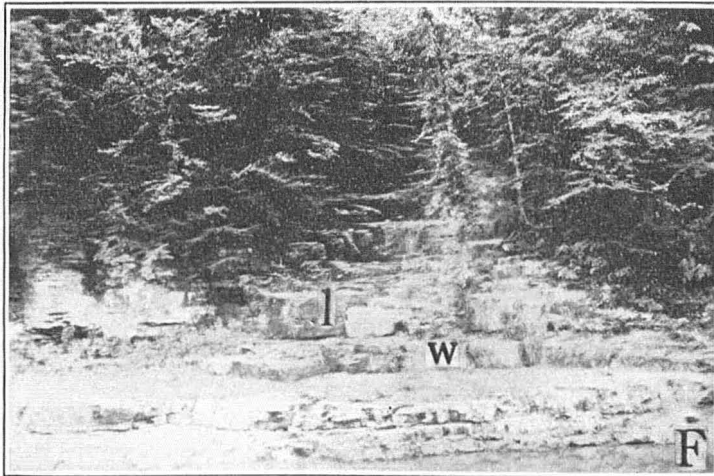
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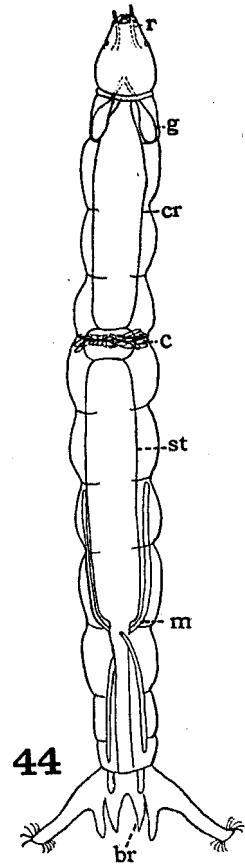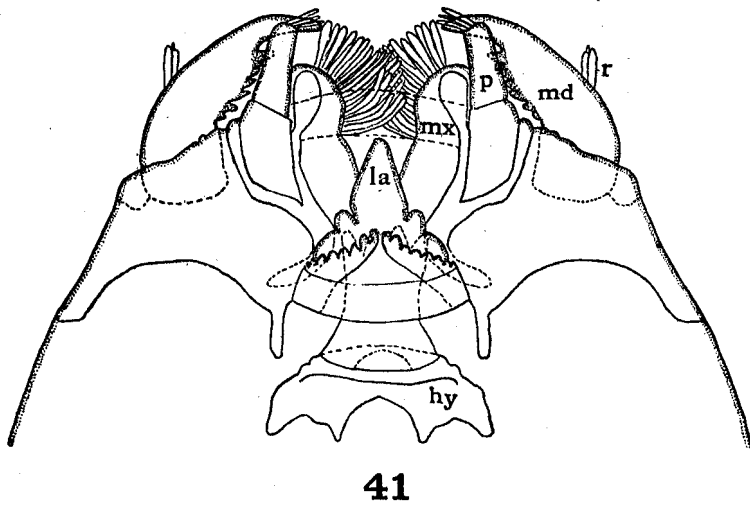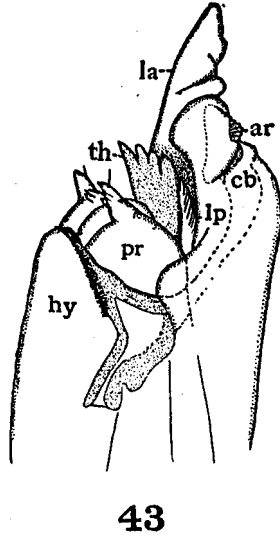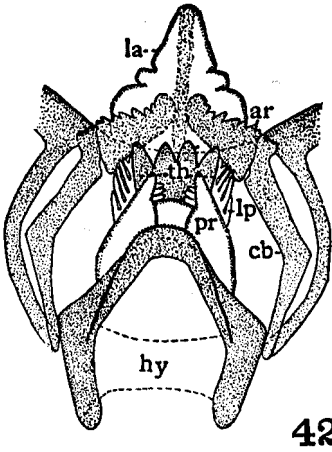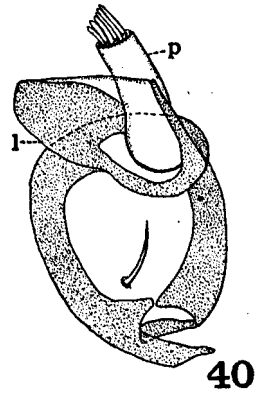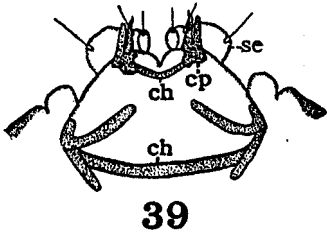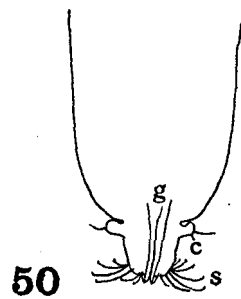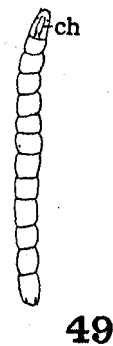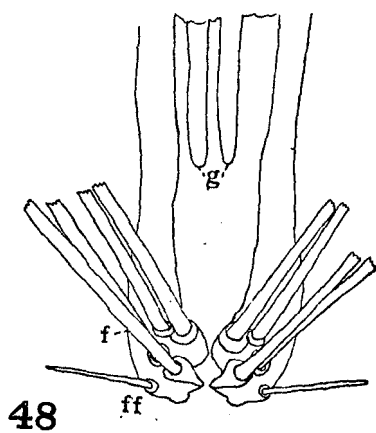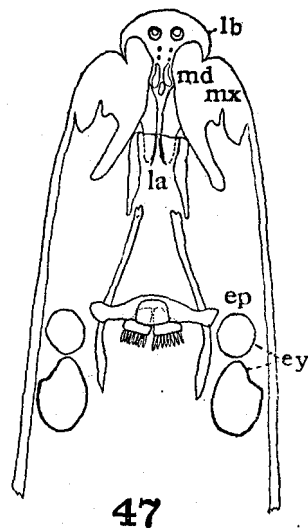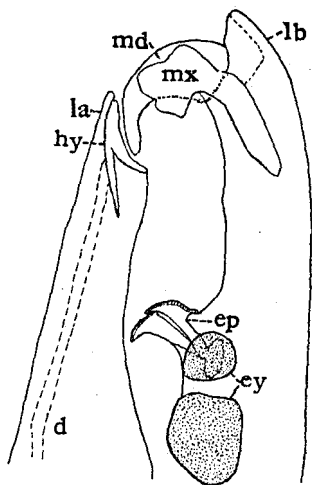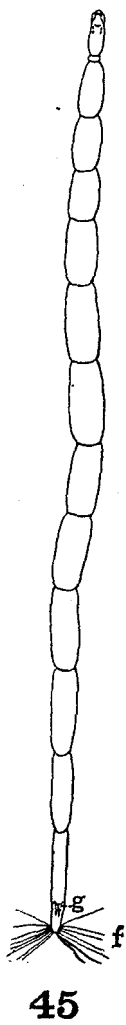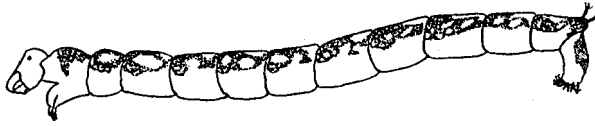
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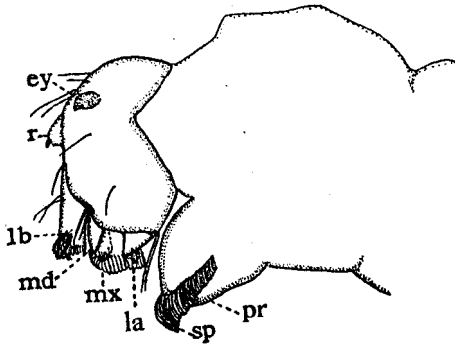
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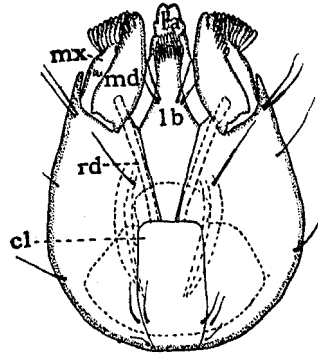
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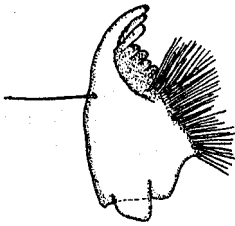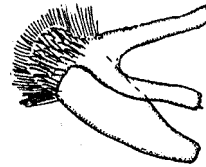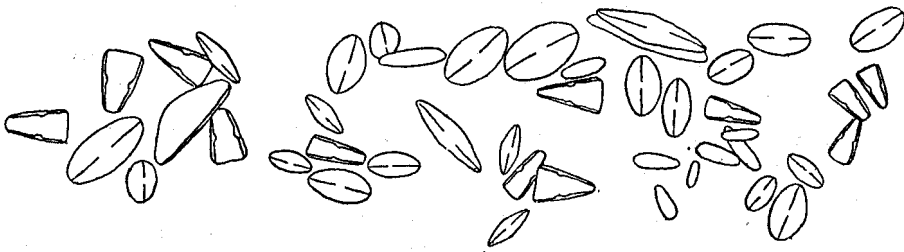
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