An abstract of the emended thesis on "The mouth-parts and alimentary canal of Trichopterous larvae in relation to their feeding habits."

A detailed study of the larval habitats, food, feeding and digestive organs of thirty representative genera of Trichoptera has been made. The food has been classified according to the mechanical resistance it would offer to the feeding organs and it has been shown that the degree of carnivorism or vegetarianism is broadly connected with the ~~sha~~ sharpness or bluntness of mandibles. There is a marked adaptation of fore-gut structure to the kind of food ingested, hence in carnivores there is a tendency to develop a gizzard-like structure in the proventriculus. The form of the stomodeal valve is also shown to be related to the food.

Histology and the type of digestive secretion in the gut of about twelve species has been worked out and an attempt has been made to correlate their general features with the food. Histological structure of the mandibular, maxillary and labial glands has been studied in the same twelve species as above. Digestive enzymes of the labial glands & stomach were also examined.

Previous theories concerning the correlation of morphological characters with feeding habits have been discussed.

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"The mouth-parts and alimentary canal of Trichopterous larvae in relation to their feeding habits".

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Introduction

The British Trichoptera comprise 12 families and just over 60 genera. The biology of their aquatic larvae has excited popular interest from a very long time, yet very little attempt has been made in England to study their habitat, food, feeding habits and feeding organs. All the information that one can find is not more than a few scattered accounts of the damage done to weeds in ornamental ponds by these larvae. Slack (1936) has, however, very recently studied the food and some of the feeding organs of twelve species. But on the Continent and in America, studies on the larval food relations have been carried out on a comprehensive scale. The earliest accout of the larval feeding habits, I believe, appears in Reaumur's 'Historyof Insects' begun in 1734 (see Miall, 1912,p.238 and 242). After him there is a long gap, until at the beginning of the present century Ulmer suggested, as a result of his studies, that there might be a connection between the feeding habits and the form of mandibles. Siltala (1907) went into the question more thoroughly, and his theory of the presence or absence of medial brushes on mandibles as indicative of the nature of larval food, is familiar to all students of Trichopterous larvae. In America, the subject of larval feeding has been studied by Lloyd (1921) in a very comprehensive manner. The old family Hydropsychidae has been dealt with by Noyes

(1914-15), and the species <u>Brachycentrus nigrisoma</u> Banks, by Murphy (1919). Branch in 1922 described the morphology of the alimentary canal in three larval forms and towards the close of 1934 Betten edited a magnificent monograph which deals with all aspects of the American Trichoptera.

The purpose of the present paper is to describe the food, feeding organs, head-glands and the alinentary canal of a representative selection of the British species and to see if these several factors are correlated in any way. To facilitate comparison between ~~various~~ different larvae the alimentary system of <u>Hydropsyche</u> larva has been described as the type and descriptions of other larvae have been made with reference to it. <u>Hydropsyche</u> was selected as type because it occupies a middle position with regard to its food and certain features of alimentary canal, and also because no other species was available (for checking some points of anatomy) near Peshawar (India) where this work was finished. After this, an account of food and alimentary canal of each species is given in turn according to its systematic position. This is followed by a description of the general features of feeding and feeding organs. The account of the mouth-parts is deliberately brief since they have been exhaustively treated by Rousseau (1921) and others. Finally, there is a general discussion of the relation of ~~food~~ mouth-parts and gut to the nature of food. Details of food, gut-measurements and enzymes in various species are shown on tables given at the end of this paper.

Material and Methods. Thirty representative genera were selected for study from all the twelve native families. Identification of larval forms is a difficult matter; in many cases, therefore, the attempt to identify them was not carried beyond the genus. Even here, the takk is not always easy. I may quote Orcutt (in Betten, 1934) who concludes that "at present the work has not progressed far enough to admit of thorough classification even to genera".

The larvae were collected from the following localities during different seasons.

1) Hampshire- The river Itchen, round Winchester; the Test near Romsey and Bollington; the Kennet near Newbury.

2) Surrey- Ponds and canals near Wisley, Chobham, Chertsey, Datchet and Virginia water; the Mole.

3) Derbyshire- The Dove near Dove Dale.

4) Westmorland- The lake Windermere and the streams in the district around it.

Hampshire was the district most often visited for collectio of larvae.

The nature of larval food was inferred mainly from the contents of stomach. Since Trichopterous larvae tend to loose their natural preferences and become generally omnivorous in captivity, dissections were made either of freshly captured specimens or of material which was preserved in alcohol directly after capture. At least five specimens were studied in every case though generally a much higher number.

For the study of the form of alimentary canal dissections were made of freshly killed larvae in a late instar. For this purpose larvae had to be kept alive in the laboratory. A tank equipped with the appropriate weeds was set up and a current of air was kept passing through it constantly. The apparatus for forcing the air-current through the tank was devised and perfected by Brett (1936) and it never once failed during two years' constant use. This arrangement also enabled me, on favourable occasions, actually to observed the process of feeding in some larvae. For the study of mouth parts the larvae were boiled in KOH, cleared and preserved in clove oil. Mounts in Canada balsam were also made. For digestive enzymes the larvae were killed by decapitation.

Histology of the gut and head-glands was also studied, and forms the chief addition to the old thesis. Over a dozen species representing all types of feeders (carnivorous, omnivorous, phytophagous and diatom-eaters) were selected for microtomic study, though dissections were also made both for head-glands and alimentary canal. Double-imbedding of Bouin's-fixed material in cloveoil-celloidin and 58 C. Wax gave fairly good serial sections. Since microtomic work was carried out at a time and a place (May-June, Peshawar) where the temperature rose far above 100 F. almost every day, thin sections (below 8 microns) could not be obtained as a rule. Still, the cutting of them was facilitated by working the microtome near a block of ice a few hours just before and after the sunrise.

About 30 new camera lucida drawings have been added and some old ones deleted.

The larval habitat was studied in most cases. An examination, though rather cursory, was made of the flora and fauna ~~kx~~found in connection with it, in a much studied stretch of the Itchen near Winchester. The following plants and animals were recorded from this place during a visit in late summer.

Phanerogams-

1) Ranunculus aquatilis Linn.
2) Nasturtiums sp. (water cress)
3) Hippuris vulgaris Linn.
4) Elodea canadense Michx.
5) Callitriche verna Linn.
6) Veronica beccabunga Linn.

7) *Sium* sp.

8) *Phalaris arundinacea* Trim.

9) *Lemna trisulca* Linn.

Bryophytes-

1) *Fontinalis* sp.

2) *Hypnum* sp.

Filamentous Algae-

1) *Cladophora*

2) *Vaucheria*

3) *Ultothrix*

4) *Oscillatoria*

5) *Bulbochaete*

Diatoms-

1) *Gomphonema constrictum* Ehrenb.

2) *Amorpha ovalis* Kutz.,

3) *Fragilaria capucina* Desmaz.,

4) *Navicula* spp.

5) *Gyrosigma* sp.

6) *Synedra ulna* Ehrenb.,

7) *Diatoma vulgare* Broy,

8) *Trabellaris*,

9) *Cocconema lanceolatum* Ehrenb.,

10) *Melosira arenaris* Moore,

11) *Nitzschia*,

12) *Rhoicosphenia* sp.

Crustacean and Insect fauna-

1) Cladocera,
2) Copepoda,
3) *Gammarus pulex*
4) *Asellus aquaticus*
5) May-fly nymphs,
6) *Sialis* larva,
7) Chironomid larvae,
8) Trichopterous larvae,

Mollusca-

Limnaea sp.

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The Alimentary System of

HYDROPSYCHE sp.

A detailed description of the mouth-parts, head-glands, and the alimentary canal of the selected type - *Hydropsyche*.

The Mouth-parts (figs 8, 37 & 47)

The mandibles

Each mandible is a strongly sclerotized appendage of the head. In form it is like a hollow pyramid, the base of which is triangular and attached to the head-capsule by two condylic joints.

The condyle of the mandible lies on the posterior side of the mandible base and fits into an acetabulum on the head, and, vice-versa, the condyle of the head fits into the acetabulum of the mandible that lies on its anterior edge.

The mandible is primarily a biting organ and since its hinge is dicondylic it is capable of moving only in one plane-- the transverse plane. It develops strong adductor and abductor muscles which originate from the dorsal wall of the head and are inserted on the mandible on the anterior edge of its base through the mediacy of two tendons.

The mandibular teeth are disposed in two rows, anterior and posterior, which lie along the mesal side of the mandible. The anterior row has only a single apical tooth but the posterior row consists of four teeth. Immediately ~~posterior~~ dorsal to these latter teeth is a convex molar surface. There is a fringe of strong hair along the outer edge of the mandible towards its basal half.

The structures described so far have a symmetrical development on the right and left mandibles, but on the mesal edge of the left mandible near its molar surface is a tuft of hair which is not present on the right mandible. The point is rather important since the symmetry of these tufts is considered to furnish an index to the type of food a larva takes.

Labrum

The labrum is essentially a movable pre-oral lobe of the head lying over the mandibles. In form, it is a flat, broad and transversely ellipitical sclerite joined to the front end of the clypeus by a membrane. Growing from the proximal angles of its epipharyngeal surface is a pair of short slender sclerites called the tormae. The exposed surface of the labrum is grown over with some small hairs but each of its distal angles has a tuft of hair which are considerably long.

The labrum is capable of making both up-and-down and forward-and-backward movement. This is undoubtedly the result of muscles that are inserted on it from the frons.

The lower lip

The lower lip is formed by the union of the two maxillae and the labuim, and is articulated to the head behind the insertion of the mandibles. The union of maxillae and labium is complete in the proximal region but distally they remain quite apart from each other.

The base (proximal portion) of each maxilla is divided into two parts by a line of flexture. The more basal of these parts is the cardo and the other is the stipes.

The stipes has a transverse and membranous proximal edge, and bears, besides two groups of very long hairs, a large maxillary palp and a smaller mesal endite which represents the lacinia. The maxillary palp has few hair on it and consists of 5 segments which taper towards the apex.

The labium is a triangular piece formed by the fusi fusion of the two second maxillae. It lies between the first maxillae and is joined to the posterior wall of the head without the mediacy of a gula (which is absent in Hydropsyche). Its basis is formed by the mentum and submentum. The latter is a triangular plate, the apex of which is turned towards the head and whose base is united to the mentum. The mentum has a squarish form with a deeply bipartite distal edge near which long hairs grow sparsely. The apex of the labuim is formed several fused elements-- the prementum, glossae and paraglossae. The palpi of the labium lie at the sides of the aperture for the labial gland and are very short and stumpy.

Glands connected with the mouth-parts (figs. 9-10 + 48-50)

Trichopterous larvae possess certain glands which, since they open on their mandibles, maxillae, and the labium are known respectively as mandibular, maxillary and labial glands. Typically a pair of glands is developed in connection with each pair of the mouth parts but in Hydropsyche the mandibular pair of glands is absent.

Labial glands

These glands are paired, long and tubular. Each lies in the body cavity along-side the gut, and is divided into two major parts:- the secreting part and the conducting part. The secreting portion produces the substance from which the larval net is manufactured. The digestive function of its secretion is more or less completely suppressed.

The structure of the silk gland is quite simple. The greater part of its length consists of the secreting portion whose wall is one cell thick and the lumen wide. The nuclei of the cells composing the gland are not round and compact but appear broken or branched into small irregular pieces. The secretion which fills the lumen of the gland entirely is, as seen in microtomic sections, homogenous and deep-staining.

Each gland passes into its duct in the second thoracic segment. The nuclei in this region are of the ordinary kind being compact and round. The duct becomes progressively narrower as it approaches the head and finally unites with its fellow of the opposite side to form the silk-press in the labium. The structure of the silk-press in Anabolia has been described in detail by Lucas (1893); that of Hydropsyche is not very different. It is essentially an oblong and sclerotized chamber enclosed within the united hypopharynx and prementum. Its dorsal wall is invaginated so that to an external view it appears double. Several muscles which should be able to dilate the lumen of the silk-press run between the press and the walls of the labium. The labial gland finally opens ~~on a spine (the spinneret~~) ~~which is situated~~ on the tip of the labium.

<u>Maxillary gland</u>

The maxillary gland is comparatively a very small gland lying just in front of the sub-oesophageal ganglion. It consists of 4 finger-like lobes, of which the two dorsal lobes are larger than the ventral ones. The ducts carrying secretions from these lobes unite and open at the base of the labium.

The maxillary gland of <u>Hydropsyche</u> has been described by Russ (1910) and Glasgow (1936) but they differ from each other in regarding the gland as double and single respectively. My preparations favour Glasgow's view.

The gland, very roughly, would consist of about 200 cells. The individual cells are very large and cuboid in shape and disposed round a central canal. The cell protoplasm is granular and, in a few cases, is seen to be traversed by a fine intracellular canalicule which runs towards the central canal and probably flows into it. The nucleus is very large and lies to one side of the intracellular canalicule when the latter is present. It seems obvious that the secretion of the cells would pour into the central canals and ultimately reach the mouth through the aperture of the gland which lies near the base of the labium.

Form of gut

The morphology of the gut, in some American and New Zealand species, has been studied by Noyes (1915), Branch (1922) and Glasgow (1936). That of the English forms does not differ from them in any important respect.

The Pre-oral cavity

In front of the true mouth, which is the beginning of stomodaeum, there lies a space partially closed in by the labrum, mandibles and the united maxillae and labrum. This space is termed the pre-oral cavity and serves to hold and orientate a food morsel before passing it into the true mouth. Since the terminal portion of the silk glands forms a silk-press which is completely contained within the body of the united hypopharynx and prementum, and, also, since it opens as far forwards as the tip of the labium, the salivarium forms no part of the pre-oral cavity.

Fore-gut

The fore-gut or stomodaeum extends from the mouth to the front end of the mid-gut which lies in the 3rd thoracic segment. It is divisible into the following more or less well marked rigions: the Pharynx, crop, proventriculus (which is peculiar in Hydropsyche in developing a gizzard), and the stomodeal valve. The last-named region is hidden to view by the fore-gut walls, but is revealed when the latter are dissected away. The tissues which compose the fore-gut walls are, (beginning from the outside):- (1) strands of ~~longitudi-~~ circular muscles (2) a layer of longitudinal muscles (3) epithelium and (4) the intima lining the epithelium.

Pharynx. The portion of the fore-gut which lies in the head is distinguished as the pharynx, and is continuous with the posterior gut-divisions through the fora-men magnum. The brain and the suboesophageal ganglion lie about the middle of the pharynx and the connectives uniting them go round it like a ring. The part of the pharynx in front of the brain is wider than the part which follows it. It is also more heavily supplied with dilator muscles that run between it and the wall of the head. The longitudinal muscles are present but much less strongly developed. The epithelium is flat and the boundaries of its cells are indistinct. The intima which lines the epithelium on the inner side is quite thin, and both the epithelium and the intima are thrown into longitudinal folds which allow for the expansion of the gut-lumen when food is taken in.

The crop extends from the posterior end of the head to where the gizzard becomes visible through the walls of the proventriculus. A proper oesophagus is not distinguishable. The folds of intima which were so conspicuous in the pharynx disappear, but form again as the proventriculu is approached. The epithelium is flat-celled. The circular muscles lie within the longitudinal muscles in this region and gradually attain stronger development towards the more posterior region. The crop is usually regarded as a passive organ for storing food before it is passed on into the stomach, but in view of the strong development of the circular muscles and the intimal folds in the walls of its more posterior portion, it cannot be so regarded in Hydropsyche. The proventriculus appears, to an external view, to form the terminal portion of the fore-gut though actually the terminal portion is formed by the stomodeal valve which lies hidden in the mid-gut. It lies in the meso - and meta-thoracic segments and would be about a fourth of the entire foregut in length.

The Proventriculus in Hydropsyche is characterized by the development of a gizzard mechanism in it. The gizzard is essentially a transformation of the longitudinal folds of the intima into about 38 to 41 sclerotized triangular plates ("teeth") such that their bases lie against the walls of the proventriculus and their apices project into its lumen. The walls of the proventriculus consist of the usual muscle-layers, the longitudinal lying outside the circular. Corresponding with the develop-ment of the teeth, the circular muscles which go round them attain immense proportions and appear like numerous parallel thick rings even to the naked eye. In a longitudinal section of the fore-gut the circular muscles are cut across their breadth and it is then seen that the thickest of them lies opposite to the epices of sclerotized plates. Both in front and behind this level the cross sections of the muscle-rings are seen to reduce ~~thus~~ gradually in size. The longitudinal muscles are not developed so strongly and do not make a uniform layer being cut up into several bands running outside the circular layer. The precise form ~~form~~ of the gizzard is best comprehended by taking a look at figs 2 & 3. . I have just now described it is a triangular plate, but it will be seen that the edges of the triangle are not quite straight but curved gently, and that the apex is not where the two upper sides meet but is formed by one of the sides projecting a little beyond the point of their union. Moreover, the upper sides exhibit abtuse serrations. Except for a small margin along its two upper sides which retain their own brown colour in strained preparations, the main body of the tooth takes the haematoxylin stain quite well. Each tooth, as its height diminishes both in front and behind, and it comes flush with the level of the gizzard-wall, divides and subdivides into several ridges which pursue a linear course till they merge with the background. Of these ridges, those that run backwards (i.e., towards the stomach) are grown over with chitinous spines at two levels so that we get two well-marked annular bands of anteriorly directed spines before the stomodeal valve is reached.

The epithelium is differentiated into a row of specially broad cells which runs beneath the whole length of each tooth.

The stomodeal valve. The stomodeal epithelium, its intima, and some of the associated muscle fibres, instead of stopping short at the beginning of the mid-gut seperate from the outermost muscle-layer, turn in towards the lumen of the foregut, travels forward for a short distance and then turning back pass down into the lumen of the mid-gut. After running down the mid-gut for some length, the whole complex is deflected outward, and then travels up again till it comes to a final end near the anterior extremity of the mid-gut. This cylindrical projection of stomodeal wall into the fore-gut and the mid-gut constitutes the stomodeal valve. It is thus divisible into two parts:- (1), an anterior part, which lies in the fore-gut and (2), a posterior part, which lies in the mid-gut. Neither of these two parts, though described as cylindrical just now, is perfactly cylinderical. The anterior portion consists properly of two discontinuous semicircular folds, and the posterior portion is usually crumpled up and divided by a longitudinal split all along the middle of its vental surface. In virtue of the mode of its formation the valve is double-layered. The space between the two layers is filled up with blood and a few longitudinal muscle fibres, and their free surfaces are covered with the stomodeal intima, The blood space in the two parts of the valve is continuous and it looks very probable that a contraction or expansion of one part would affect the size and the position of the other, and, hence be instrumental in blocking or letting open the aperture between the fore-gut and the mid-gut. The intima of the anterior part of the stomodeal valve is especially thick, and the surface of its semicircular lobes that is turned towards the stomodeal walls is grown over with long chitinous spines pointing anteriorly. Abridging the gap between the two semicircular lobes on the vental side is a small hemispherical protruberance on which can be seen numerous cuticular dots. In section, the epithelial region in the semicircular lobes presents a honeycombed appearance. This is due to the tall epithelial cells being cut accross their breadth.

The walls of the posterior part of the stomodeal valve are generally very much crumpled and never perfectly straight. The presence of muscle fibres in them would indicate that, quite apart from their ability to act on the anterior portion of the valve through pressure of the fluid contained in their cavity, they can contract and obliterate their own inner passages and thus stop the ingress of food from the fore-gut into the mid-gut. On the other hand, they can relax and let the food pass into mid-gut. The free edges of the valve (i.e. edges along the ventral split and the posterior end) are marked by a fairly wide band of cuticular dots running alongside them.

The union of the fore-gut with the mid-gut is marked by the presente of a ring which is only a few cells wide. It is not visible from outside as a distinct region, but in sections it is seen to lie just outside the base of the stomodeal valve. Glasgow (1936) considers this ring to be the terminal portion of the fore-gut and described an intima that lines its inner surface. I have not found on it any intima as described by Glasgow but the cells composing this ring are certainly different in shape and size from those of the vetricular epithelium from which they are also separated by a physical gap.

A structureless membrane passes down from near the posterior-most level of the stomodeal valve well into the posterior region of the mid-gut and envelopes within itself whatever food there is in the mid-gut. The membrane was only seen in some series of sections though in others it was entirely absent. When present, it was never seen to issue from the ring of cells which lies at the front end of the mid-gut. In places, the membrane is seen to consist of several layers. In all this there is nothing which is not reconcilable with the notion of its being the peritrophic membrane. Several authers have described instances of the peritrophic membrane arising from the general surface of of the mid-gut epithelium and its being many-layered. But a more serious difficulty in the way of identifying it as the peritrophic membrane is that here and there along its length it shows the presence of solitary muclei. Unless these muclei have just drifted to the membrane after detaching themselves from the gastric epithelium in the process of holocrine secretion it would be hard to regard the membrane as peritrophic membrane.

Mid-gut

The mid-gut extends from the middle of the metathoracic segment to the beginning of the 6th abdominal segment and is about equal in length to the for-gut. It is composed of four layers. The outermost layer is one of longitudinal muscle, inside it lie here and there the much less powerfully developed circular muscles fibres, then comes the basement membrane, and finally there is the layer of epithelial cells which forms the actual lining of the mid-gut cavity. Glasgow (1936) has not been able to decide whether circular muscle fibres were present in the mid-gut of *Hydropsyche colonica* (a NewZealand species) but in the English species, at any rate, they are clearly demonstrable.

Coming to grosser differences first, the epithelial tissue, which is seen (in longitudinal sections) to run perfectly straight in anterior half of the mid-gut, assumes a wavy outline in the posterior half. The wavy contour is not showed by the outer muscle layers so that, viewed from outside, the posterior half of the mid-gut is be without annulations and appears quite as smooth as the anterior region. This condition of the epithelial tissue in the posterior region of mid-gut though seen in most longitudinal sections, is by no means invariably demonstrable. This would seem to indicate that the wavy appearance was just a phase, due to the contraction of longitudinal muscle fibres. But on the other hand the wavy appearance in the posterior region of the mid-gut is a fairly constant feature of nearly all the Trichopterous larvae studied.

The epithelial cells are of two kinds:- (1) the digestive cells and, (2) the regenerative cells; goblet cells were never seen. The digestive cells are quite tall, being about 8 to 10 times as long as broad. The intercellular walls are not always discernable but differences of shade in the stain which protoplasm takes, easily distinguish one cell from the other. Each cell appears to contain several nuclei. This may be due to several superimposed cells being viewed at-once in thicker sections but this state is also apparent in sections cut at 4 microns. The basement membrane is quite thick and, in a few places in some longitudinal sections, clear square spaces of unknown nature have been seen just below it. Snodgrass (1935, Principles of Insect Morphology) has borrowed a figure of the mid-gut of Ptychoptera contaminator larva from Van Gahushten (1890) which shows such spaces but he does not say anything about them in the text. The upper surface of the epithelial cells is limited by the presence of a striated border. The striatons are very minute and run parallel to the long axis of a cell in section. The striated border is generally continuous over the surface of the epithelial tissue except where secretion products of a cell (in the form of vecicles) escape through it into the lumen of the mid-gut. The protoplasm is generally granular. The nuclei are not confined to any definite level of the epithelial cell, but occur anywhere from the top to the bottom. Occasionally, clear vacuoles are seen near the topmost level od a cell.

A few nuclei of smaller than average size are found scattered here and there near the bases of the epithelial cells. It is presumed that they represent the regenerative cells which by their proliferation continually add to the epithelium as it degenerates in the course of metabolic activity. The tendency of the regenerative cells to collect into nidi seems lacking in Hydropsyche.

Digestive secretions of the epithelium

The evidence of digestive secretion is furnished by the presence of small garnular vesicles that are produced and let loose by the epithelial cells into the lumen of the mid-gut. In certain series of sections they were found to be very abundant, while in others they were hardly noticeable. This would show that the secretion of these ~~diges-tive~~ vesicles, or at least an active secretion of them, was not a continuous process but occoured only at intervals.

There cannot be any doubt that at least some of the secretion-products escape in a perfectly fluid state through the striated border of epithelium into the mid-gut cavity and therefore do not leave any physical traces in histological preparations. For this reason a positive evidence of the histological kind would be difficult to obtain for this process. But other processes that are commonly accepted as digestive processes are not so illusive and leave palpable indications of their occurance. Of such, the various types of vesicular secretion afford an instance.

The commonest method by which the secretion products are discharged into the mid-gut cavity is the production of buds from the upper surface of the epithelial cells. These buds contain deeply staining granular matter and after growing to a certain size get constricted from the parent cells and float away into the lumen of the mid-gut. A much less common method is one in which the separated bud contains a nucleus in it. This latter is evidently not a process of <u>pouring out</u> of secretion from the body of the cell, but of the actual removal of an integral part of the cell itself. The processes described above represent what is generally accepted as holocrine type of digestive secretion but this interpretation has been challenged by many competent workers. Clear vacuoles containing a few dark granules are also seen in certain epithelial cells during the phase of secretion. In a phase of intensive secretion the epithelial cells have often (but not always) been seen to get reduced in size. The mid-gut of Hydropsyche has no differentiated gastric caeca. Even the cells which compose the epithelial tissue are uniform in size and shape (the regenerative cells are, of course, excepted). There are, thus, to all appearance, no specialized regions or even cells set apart for (1) the secretion of digestive juices or (2) the absorption of digested food particles. It may, therefore, be concluded, that in Hydropsyche the same cells perform both functions as the occasion demands.

Hind-gut.

The two major divisions of the hind-gut (which are also the most easily recognised ones) are the anterior intestine and the posterior intestine. The anterior intestine which includes the ileum and the colon is a tube about half as wide as the mid-gut and its passage into the broad, sac-like posterior intestine is marked by a constriction. The walls of the posterior region of the latter are produced into four anal gills which can be

~~pxxxxx~~ protruded outside or drawn into the rectum. Just over their insertion are muscle bands running between the body-wall and rectum. There is much confusion regarding the terms used by various authors to describe the parts of the hind-gut. In my descriptions I follow the terminology adopted by Snodgrass which I find more comprehensive.

Malpighian tubules. There are six malpighian tubules. Two of them originate distinctly separately from the ventral surface of the gut, but the other four appear to arise in two pairs, right and left, although even here the orifice of each remains distinct. The region from where the malpighian tubules open into the hind-gut is not specially distinguished from the adjoining area. It is true that the terminal portion of the ventricular epithelium curves slightly into the lumen of the gut but it would be hard to imagine that a weak curvature like that could act as a valve (cf Glasgow's so called pyloric valve in Hydropsyche). The adjacent proctodeal epithelium is also without an annular fold of any considerable size. A pyloric valve must, therefore, be regarded as definitely absent in Hydropsyche. The opening of each malpighian tubule is limited by the epithelium of the mid-gut on its anterior side and by the epithelium of hind-gut on its posterior side. The latter forms a distinct protuberance on the posterior side of the opening of the malpighian tubules and possibly serves as a valve to it.

The malpighian tubules itself is a long, narrow and wavy tube lying freely in the body-cavity. It travels as far forward as the thoracic region and then turning back ends somewhere in the hinder region of the abdomen. Areas of deep and lighter colour alternate on its body all along its sinuous course. Its wall is composed of a single layer of cells in which the nuclei are fairly large but the inter-cellular walls are not distinguishable There is a striated border on the mesal surface of cells very much like that seen in the cells of ventricular epithelium. Glasgow (1936) regards the malpighian tubules as out-growth of the mid-gut.

The walls of the hind-gut consist of muscle - layers on the outside and a flat epithelium lined mesally by cuticular intima on the inside. The muscularis in general consists of longitudinal muscle fibres lying outside the circular fibres but here and there one or the other kind may be missing.

In the region of ileum the epithelium is somewhat columner but it is not so tall as it is in the mid-gut. At the extreme front end, the cells constituting it are about twice as tall as broad, but very soon the two dimensions become equal and continue thus for a considerable length of the ileum. The intima in the ileum is quite thin. There are six longitudinal folds in the wall of the ileum which are feeble at first but become stronger towards its posterior end.

In the colon the longitudinal folds become very thick and compact. Also, the circular muscles develop considerably and appear to act as a sphincter. The epithelium looses its intercellular walls and nuclei attain a larger size. The rectum broadens out atonce from the point where the colon ends.

A major portion of the rectum forms the rectal sac, the walls of which are irregularly folded. Both circular and longitudinal muscle fibres are present in its walls. The posterior tubular region which is nearly devoid of muscularis, is held to the walls of the last abdominal segment by a pair of lateral muscle bands. In this region the rectal wall is produced into 4 anal gills which has the same histological structure as the rectal tube. There cannot be any doubt that the muscle bands referred to just now serve to draw the rectal tube and the associated gills into the body of the larva.

The anal opening is situated on the posterior edge of the 9th abdominal segment between the bases of anal styles. It is not a definite aperture like the mouth, for it would be surrounded by different regions of the rectal tube according as the gills are extruded, or partially or completely withdrawn.

DETAILED STUDY OF HABITAT, FOOD, AND, STRUCTURE OF GUT AND HEAD - GLANDS IN DIFFERENT TRICHOPTEROUS LARVAE.

RHYACOPHILIDAE

RHYACOPHILA, probably, DORSALIS Curt.

Habitat

The larvae are found in the swiftest parts of Hampshire rivers both in deep and shallow water, most generally on the lower and eroded surfaces of big stones. They do not build any nets and go about in active search for their prey. In summer, 1935 when some weeds in the river Test harboured a host of Chironomid larvae, Rhyacophila larvae were observed crawling about among them, though were also present under stones. It was interesting to discover that they did not show any difference in their food in these two habitats (Table).

The specimens were taken from the fallowing rivers in Hampshire:-

(1) The Itchen near Winchester,
(2) The Test near Romsey,
(3) A tributary of the Test near Bollington,
(4) The Luddon near Basingstoke.

The habitat was similar in all cases with the exception already noted.

Food

The food is mainly furnished by the insect larvae of the streams. The amount of vegetable food taken is negligable; Rhyacophila then is, for all practical purposes a purely carnivorous form. The presence of parasitic protozoa (Gregarinae) was noted in many stomachs.

Form of gut (fig 11-12)

The slender fore-gut ends near the posterior border of the second thoracic segment. The mid-gut also is quite slender and has twice the length of the fore-gut. The hind-gut which begins in fifth abdominal segment, has a nearly uniform calibre throughout its length, the distinction, therefore, between the anterior and posterior intestines is rather difficult to make externally. Six anal gills are present at the end of the gut.

Fore-gut

Distinction into oesophagus, crop and proventriculus is not quite clear. The fore-gut walls have the usual histological structure but the muscularis and intima are very thin except near the posterior end where both of them attain a relatively strong development. The stomodeal valve is double-layered, but is short and leaves a wide aperture. Its intima is quite thick and the epithelium somewhat columnar.

Apparently, there is no special ring of cells joining the fore-gut to the mid-gut.

Mid-gut

In the muscularis, the circular fibres have a very feeble development. The nidi are compact and occour along the whole length of the mid-gut. The digestive cells are columnar but are somewhat pecular in not having a uniform height. Groups of very tall cells (about 12 to 15 times as high as broad) alternate with groups of much shorter cells (about twice as high as broad). The former groups are large but the latter are quite small units of a few cells each. In virtue of the larger and the smaller cell-groups occurring alternately, the epithelium presents a wavy outline in longitudinal sections. The nuclei lie at about middle height in all cells, but, in keeping with the form of each kind, they are either drawn out and elliptical, or just round. The mesal surface of the epithelial cells has an unusually wide light-staining border in which striations are not always very distinct. A peritrophic membrane was never observed. In neither of the two larvae that were sectioned, were the secretion vesicles visible; positive information, therefore, cannot be given on the type of secretion in Rhyacophila. The structure of mid-gut wall as represented in sections presents certain differences in the two larvae studied which I find difficult to understand and reconcile. It is unfortunate that more instances could not be studied to understand the nature of these differences. The differences, however, are stated below:-

(1) In one larva the shorter epithelial cells resemble the goblet cells very much and indeed may be

goblet cells; in the other, no such form is taken by the shorter cells.

(2) Although it is equally difficult to see the basement membrane in either larva, in one of them numerous large clear spaces occur regularly beneath the epithelium the nature of which is not clearly understood. Small nuclei are present here and there in the substance intervening between these spaces which makes one suspect that this is perhaps a peculiar form of connective tissue.

Hind-gut

The malpighian tubules are equidistant at their insertions and open into an annular fold at the beginning of the hind-gut. The fold may be taken as representing the pyloric region of the hind-gut. As in some other forms, the anterior wall of the fold is formed by a slight mesal projection of the ventricular epithelium, and if this projection is to be regarded as the pyloric valve, it must be obvious to any-one that it is a valve of rather ineffective kind. The rest of the hind-gut has the usual kind of flat epithelium, intima and muscularis. The rectum is attached to the body-wall between 8th and 9th abdominal segment by means of muscular strands which would, no doubt, be functional in retracting the anal gills into the hind-gut.

Each labial gland has a pair of accessory glands at the beginning of it discharge duct.

Both mandibular and maxillary glands are present. Both of them are paired but the maxillary pair is much larger then the mandibular.

Each mandibular gland lies in the lateral side of the head capsule near the compound eye. It is a small gland consisting of a few long cells grouped round a central canal. Each cell is pierced by a fine canalicule which is lined by intima and opens into the central canal of the gland. The nucleus of each cell lies near that end of it which is directed away from the central canal. This end of the cell is often curved. The protoplasm surrounding the canalicule shows striations which run at right angles to the length of the canalicule. Each gland opens near the outer articulation of the mandible on the head capsule.

The maxillary gland is also paired. Each gland lies near the sagittal plane of the head just in front of the suboesophageal ganglion, but travels outwards to open near the base of maxilla. It has same essential structure as the mandibular gland but the central canal is much wider and the cells surrounding it are more regularly arranged.

AGAPETUS sp.

Habitat

In certain tracts of the Itchen the larvae are found in very large numbers on the upper surface of stones, in shallows where the current is not very swift. Completely covered ~~with~~ by their relatively huge and dome-shaped cases, they progress in water very slowly and, to a casual observer, would indeed give the impression of being fixed objects. Most of the material was taken from Hampshire streams, though some came from the Lake Windermere.

FoOd

The major bulk of the gut-contents is formed by diatoms, of which the following forms are noted:-

(1) Gomphonema sp.
(2) Navicula sp.
(3) Amorpha ovalis
(4) Trabellaria sp.

Inside the gut, they form compact masses in an unrecognisable medium, which may be the solidified secretions of gut or some extraneous matter but very probably the former. These masses disintegrate on the touch of dissecting instruments, mainly into diatoms. Occasionally bits of branching algae (especially Cladophora) are noticeable.

Form of gut (figs 13 + 14)

The fore-gut has very delicate walls lying in close contact with the nervous system, which makes the dissection of this region rather difficult. The regions of pharynx, oesophagus and proventriculus are fairly distinct. The folds of stomdeal intima are weekly developed. The stomodeal valve is bipartite and thickest, but leaves a fairly wide gap in the centre.

There is nothing of histological interest in the structure of fore-gut except that the posterior-most level of the stomodeal valve develops a disproportionately thick intima.

Mid-gut

The mid-gut is about three times as long as the fore-gut. The ventricular epithelium is broad and short, and better described as square than columnar. The nuclei are large and round and are generally placed near the base of cell than its middle. The striated border is distinct and well developed. The regenerative cells occur after comparatively long intervals and generally lie singally; they do not, as a rule, form groups. Secretion vesicles containing granular products (but not nuclei) are frequently met in the ventricular cavity, and sometimes show a striated border running round them. A membrane enveloping food is present and although its origin form the anterior-most region of the mid-gut is not seen, it is presumed that it is the peritrophic membrane. The secretion vesicles are not to be seen inside the peritrophic membrane, among the food particles. Probably they cannot pass the membrane as vesicles and have to dissolve their individuality first.

Hind-gut

There is nothing unusual in the histology of the hind-gut.

The labial gland is slightly shorter than the gut and without accessory glands.

HYDROPTILIDAE

HYDROPTILA sp.

Habitat

The largest numbers of larvae are found on small-leafed weeds, like Water Ranunculus, Elodea and some mosses. They are difficult to see, because of their small size, but if a weed carrying them is put in a glass jar full of water, the larvae migrate towards the walls and can then be easily caught. They are more usually present on the leaves nearest the water surface and in slow to fairly swift currents. The probable reason why they are not found on broad leaves is that without the protection afforded by the small crevices and turnings of a small-leafed stem, they would be carried away by the force of the stream. They are also frequently found in chinks on stones.

Food

Diatoms, bits of algae, and minute fragments of moss debris form most of the food. A good proportion of the stomachs examined was empty. Others were filled with one solid mass of closely packed diatoms. On a small leaf-cluster of some moss, a larva was seen browsing. An examination of the leaves afterwards showed them minutely bitten here and there. Preference, however, is shown for diatomaceous food.

Form of gut (fig 15)

The fore-gut is delicate and thin-walled and lies in close relation with the anterior part of the nervous system.

Its division into the usual stomodeal regions is not distinct. The longitudinal folds of the intima in the final region of the fore-gut are distinct but weak. The stomodeal valve is very slight, descends only a short distance into the mid-gut and leaves a very wide gap in the centre. The mid-gut, which is nearly twice as long as the fore-gut, begins near the front margin of the second abdominal segment, and ends between the sixth and seventh abdominal segments. The malpighian tubules are compound and arise by two main stems, right and left. The divisions of the hind-gut are not clear, except for the anterior and posterior intestines, the latter showing conspicuous longitudinal folds inside. Histology of the gut was not studied.

The labial gland is about equal to the gut in length and its duct dilates into a comparatively large reservoir in the second thoracic segment. The other head-glands were not studied.

PHILOPOTAMIDAE

PHILOPOTAMUS MONTANUS Donov.

Habitat

Only once in two years did I secure a larva in Hampshire. It had constucted a net on a stone, in one of the swiftest parts of the River Itchen. All the rest of the larvae were sent from Windermere where, I am informed, they dwell in the swiftest streams among stones.

Food

Nothing with certainty could be said about the nature of the gut-contents. Most of the stomachs examined were completely, or almost completely, empty. Debris including minute organic particles and diatoms were seen here and there in the different divisions of the gut, but it is surprising that much the greater part of the gut was always empty. It is certain, however, that the larva does not take in much insect or crustacean food, for otherwise, their remains would surely have been discovered in the stomachs of the dissected larvae. The following are the commonest diatoms found in the food:-

1. *Navicula* (some species)
2. *Gomphonema* ,
3. *Amorpha ovalis*.

Form of gut (figs 16-19)

The alimentary canal is remarkable for its unifrmly slender fore-gut and a very large mid-gut which begins at the anterior border of the 2nd thoracic segment and goes right upto the posterior border of the 6th abdominal segment. There are 5 protrusible anal gills near the posterior end of the hind-gut.

Fore-gut

The muscularis and the longitudinal folds are strongly developed only upto the level of the subesophageal ganglion. Behind that, the folds are hardly noticeable and the muscularis is weak. Oesophagus, crop or even proventriculs is hard to distinguish from other parts. It is remarkable that even that part of the fore-gut where the proventriculus should lie, has a weak musculature and is devoid of longitudinal folds.

The stomodeal valve has no anterior part as in Hydropsyche, but the posterior part (which is all there is of the valve) develops the largest size in Trichoptera. In form and structure it closely resembles the posterior part of the stomodeal valve of Hydropsyche, being formed of a double layer of epithelium and intima, and having a cylindrical body that is split along its mid-ventral line. Longitudinal muscle fibres also enter in its composition. As in Hydropsyche there is a blood space enclosed between the two layers that form its body. The valve can no doubt control the passage of food from the fore- to the mid-gut but the reason for developing all its great proportions is not understood. It may be interesting to note, in passing, that Glasgow (1936) thought that the large size of the stomodeal valve of Hydropsyche was unique among Trichoptera. Evidently he had not studied the case of Philopotamus.

Going round the fore-gut near its posterior end and attached to it is a unique 'bow-necktie' shaped structure which is possibly glandular in nature. The 'bow' lies on the ventral side of the gut and appears to open into it by a very slender duct from each side. In sections, each of it lobes is seen to be composed of just one cell enclosing a relatively large space in it.

Mid-gut

The mid-gut is three times as long as the fore-gut. Its walls are composed of columnar epithelium, a thick basement membrane, a layer of longitudinal muscke fibres and circular fibres. Between the basement membrane and the muscularis clear spaces are sometimes noticeable.

The epithelium is remarakble in being composed of three kinds of cells which are:- (1) the regenerative cells, (2) ordinary digestive cells of columnar form, and (3) clear goblet cells, (seen also by Shinoda 1927).

The regenerative cells which are hardly anything more than their nuclei do not form nidi as a rule, and lie scattered along the basement membrane. In a few instances, however, a tendency for them to come close together is apparent, but this, of course, may be due to a folding of the wall of gut, for these rudimentry 'nidi' seem associated with the folds.

The ordinary digestive cells are columnar, with a striated border on the mesal surface. Their nuclei are large and round, being usually placed at about the middle height of the cells, though sometimes they occur near the base also. The goblet cells are much less numerous than the ordinary digestive cells and occur singly along the whole length of the gut. A goblet cell has a broad, round to oval, upper part which is transparent. The lower part is slender as in the ordinary digestive cell, and it is in this part that a large round nucleus is situated. The upper transparent portion often contains a small quantity of some nonstaining and structureless substance which may be the solidified secretion of the goblet cell.

The basement membrane is quite thick generally, but in a few places it attains extraordinary thickness, and irregular empty spaces come to lie within it. The muscularis consists of longitudinal fibres mainly; the circulars are rare and feebly developed.

Hind-gut:

The malpighian tubules are almost equidistant at their origin, but there is a slightly wider distance between them on the dorsal and ventral surfaces than on the right and left which faintly suggests their being disposed in two groups. The only divisions of the hind-gut that are visible from the outside are the anterior and posterior intestines. Five anal gills are present near the posterior end of the latter. The hind-gut presents nothing uncommon in its histological aspect.

The labial gland is about one and a half times the gut-length.

The situation and the structure of the maxillary ~~and the mandibular glands~~ is very much the same as in Polycentropus and a description of them need not be repeated here. The mandibular glands are absent.

HYDROPSYCHIDAE

HYDROPSYCHE SPP.*

Habitat

Noyes (1914) has given an excellent account of the bionomics of American Hydropsyche larvae. Her account may almost be entirely applied to the English species. Hydropsyche larvae prefer to live in the swiftest parts of rivers, and can be found in all seasons, though in winter, they tend to migrate towards the deeper and more inaccessible regions. Collections were made from the river Mole in Surrey, the Kennet near Newbury, the Itchen and the Test in Hampshire, the Dove in Derbyshire and the streams around the lake Windermere.

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* Foot-note.

It seems almost certain that there are two species of Hydropsyche involved here. I have arbitrarily called them Hydropsyche 'A' and Hydropsyche 'B'. Their distinguishing characters are as follows:-

Hydropsyche 'A'	Hydropsyche 'B'
1) Lighter coloured.	1) Colour very dark.
2) Lateral edges of thoracic tergites margined with thick black lines which are slightly wavy in the last two.	2) Lines on the lateral margins either very thin or absent; more straight.
3) The general appearance of a gill is like a stem on which relatively few branches arise; the stem is more noticeable.	3) The branches are more numerous and form a tuft; the stem is less noticeable.

Food

The gut-contents reveal the presence of both animal and vegetable material, which differ in proportions according to their availability in the particular environment and the preference of the larva. Of the vegetable material, algae and diatoms form a conspicuous part, and naturally so, for they are precisely the sort of vegetation which would lose anchorage in a swift current and be caught in the delicate meshes of a Hydropsyche net. In some cases, the larva also appears to have bitten off small pieces from the leaves and tender stems of the common water weeds, but such instances are comparatively few. Of the animal matter, Chironomid larvae form a large part, though other insect larvae and crustacea are very often included. A comprehensive account of its food is given by Siltala (1907) Noyes (1915), Lloyd (1921), Slack (1936) and Glasgow (1936). On the whole, I would consider Hydropsyche to be omnivorous, taking in more vegetable than animal food. It has, perhaps, a preference for animal food, but the availability of this is strictly limited by the obligation to wait for it behind a web, instead of going out in active search for it.

Form of gut

The form of gut, mouth-parts and the head glands has been described fully before.

Feeding

A hydropsyche Larva was once observed to catch a Chironomid larva and proceed to swallow it. During the whole process the prey was held by the first pair of legs, while the labrum protruded beyond the mandibles hiding them from sight. A dissection of the host revealed, that the prey had been swallowed whole. In another instance a hydropsyche attacked a dead member of its own specices, and bit off a morsal from its abdomen. Probably both methods of ingestion are quite common, as is also evidenced by the examination of stomach contents of a large number of larvae. Noyes (1915) observes, that the size of food fragments becomes smaller after they have passed through the gizzard, which she regards as a grinding organ. This is most probably true of the English forms also.

POLYCENTROPODIDAE

POLYCENTROPUS sp.

Habitat

The larvae spin nets on stones lying in moderately swift to slow streams at a depth of a few inches to two or three feet. An excellent account of the habitat and feeding habits of the American Polycentropodidae is given by Noyes (1914). Her account applies to the English forms also.

Food

Polycentropus is known to be purely carnivorous. A large proportion of the larvae that were dissected were without any contents in their gut. The rest seemed to have fed chiefly on insects, (especially Chironomid larvae).

Form of gut (fig 20-23)

The most striking features of the food canal are:- (1) the extreme length of the ~~mid-gut~~ fore-gut which reaches upto the 3rd abdominal segment, (2) the extreme shortness of the mid-gut, and (3) the presence of a gizzard-like organ (formed by the anterior part of the stomodeal valve) near the end of the fore-gut.

Fore-gut

The fore-gut is divisible into pharynx, an oesophagus which merges insensibly into the crop, and a very short proventriculus which surrounds the anterior part of the stomodeal valve. The homologies of the last two parts are uncertain.

The pharynx is a broad tube which is held to the walls of the head by numerous muscle bands. Its walls have a strong muscularis in which the circular fibres are especially well-developed. The epithelium consists of flat cells the mesal surface of which is lined by an intima of medium thinkness. The walls of the pharynx are thrown into several longitudinal folds.

The pharynx ends behind the level of the suboesophageal ganglion with a distinct constriction which is followed by the oesophagus. The oesophagus has the same histological structure as the pharynx but unlike the latter it has got no attachment with the body-wall by means of muscle bands. Longitudinal folds are present in its walls but they are not so strongly developed as in the region anterior or posterior to it.

There is no line of demarcation between the oesophagus and the crop, but after about a third of the distance between the pharynx and the proventriculus has passed, the longitudinal folds begin to grow strong and become perhaps the most sinuous and complicated in the whole series of fore-guts of the larval Trichoptera. They fill the lumen of the gut completely, and were it not for the distensibility of the muscular walls of the latter, it would be hard to imagine how any food could pass through to the stomach. The epithelium accompanies the intima in all its complicated course and the bundles of circular muscle fibres increase in thickness as the more posterior regions of the crop are approached. Longitudinal muscle fibres are present but they are not developed strongly.

In the 2nd or 3rd abdominal segment, or in both, the crop widens out into a sac-like structure. The intima in it becomes very thin and the longitudinal folds grow faint and all but lose their identity. The muscularis becomes correspondingly weak. If this is to be regarded as forming a definite region by itself, it would be difficult to homologize it with with anything in Hydropsyche.

The preventriculus is a small, narrow and neck-like region connecting the last region with the broad mid-gut. Its epithelium, intima and the muscularis are all very asymmetrically developed. Two of its folds travel horizontally inwards and form the anterior part of the stomodeal valve which is probably homologous with the anterior part of the stomodeal valve of Hydropsyche, though it is also possible that these folds are the homologue of Hydropsyche's gizzard. The anterior part of the stomodeal valve is continuous behind with the posterior part of the stomodeal valve which descends for a much shorter distance into the mid-gut than in Hydropsyche.

The course of longitudinal folds and the arrangement of muscle fibres in the terminal part of the crop, proventriculus and the stomodeal valve is best comprehended, if all of them are considered together: The folds which were so complicated only a little distance before, become straight and simple at the beginning of the sac-like region (fig. 22). Further down, instead of retaining a uniform distribution on the gut-wall, they all converge to one side carrying with them the muscularis (fig. 22). The posterior end of the sac-like chamber is comparatively very narrow, and into the composition of its walls here, only that area from the front enters which carries the intimal folds; the rest of it is cut out (fig. 22). ~~But this condition does not continue for long~~ The proventriculus begins at this point, and the muscularis and the folds again become uniformly ditributed (fig. 22). But this condition does not continue for long, for after travelling for only a short distance, two adjacent folds grow many times their original size and nearly obliterate the lumen of the proventriculus. The associated muscularis develops to a corresponding thickness beneath these folds which at this level are separated by a deep cleft. The epithelium associated with these folds becomes columner, the individual cells growing upto 20 times as tall as broad (fig. 22). The mesal border of the intima becomes sclerotized (spinous plate) and gives rise to long spines ~~opening~~ opposite the epithelial cells. The base of each spine is seen to be imbedded in the intima for some depth.

Further down, the folds become smaller in size and the cleft between them grows deeper; the other folds lose their identity(fig. 22). At a more posterior level the cleft goes still deeper and opens into the mid-gut, for it should be noted that the mid-gut does not begin straight behind the fore-gut but begins rather on one side of the fore-gut's termination. Ultimately the whole stomodeal valve enters the mid-gut and descends into it for a short distance (comparatively, a much shorter distance than in *Hydropsyche*) When the valve has reached its most posterior level the epithelium and the intima turn forward again and come to a final end, near the anterior wall of the mid-gut. The structure of the posterior part of the stomodeal valve is, therefore, essentially the same as in *Hydropsyche*. Another feature of resemblance with *Hydropsyche* is that the free Lower ~~layer~~ edge of the valve is studded with cuticular dots.

Mid-gut

The mid-gut is relatively (to other divisions of the gut) the shortest of Trichoptera larvae, being less than half as long as the fore-gut. The wall of mid-gut is composed of columnar epithelium outside which a very thin basement membrane can be seen occasionally. In the muscularis, both longitudinal and circular muscles are present, though the latter are very feebly developed and would be difficult to demonstrate.

The ventricular epithelium consists of two kinds of cells:- the digestive cells and the regenerative cells. The digestive cells of the ventricular epithelium are very tall though it would be difficult to give an exact ratio of their length and the breadth on account of their very indefinite outline. Their height decreases noticeably towards the more posterior region of the mid-gut. Compact groups of regenerative cells forming nidi lie along the whole length of the stomach, but it is curious that the digestive cells do not occur between them. Contrary to what obtains in most larvae, the digestive cells are confined to the mesal side of the nidi. By virtue of this arrangement empty spaces alternate with the nidi, hence in sections the epithelium is not seen as a continuous layer but appears broken up into as many parts as nidi present in a section.

It is almost impossible to trace the outline of an individual epithelial cell, for it has hardly any outline. Several differentiated nuclei are present in each group of cells over a nidus, and the vacuoles are so numerous in them that their protoplasm presents a frothy appearance. A striated border on the mesal surface is not seen.

Digestive Secretion

That the process of digestive secretion is not always going on is evidenced by the absence of secretion vesicles in some series of microtomic sections. But when the phase of secretion is on, it is always in a very intense form (probably the most intense in the Trichoptera series) judged from the histological preparations.

In the first place, it appears that the cell degeneration as well as cell regeneration is exteremly rapid The regenerative cells are actually more numerous than the digestive cells and seems to be merging into the latter by rapid stages; this would tend to show that there was a heavy demand made on the regenerative cells in trying to keep up with the katabolic processes. The presence of numerous vacuoles in the digestive cells is another indication of the intense pace of the process. And, finally, the "secretion vesicles" not merely take the form of extruded globules of protoplasm which may be nucleated or non-nucleated, but very often it happens that groups of digestive cells get separated off from the general epithelium just above the nidi and float away into the lumen of the mid-gut. All this histological evidence for the rapidity of the digestive processes is corroborated by the fact that the stomach of Polycentropodidae is relatively the shortest in Trichoptera and upon dissection is often found empty of any contents (which means that the latter get through the stomach in a very short time).

Hind-gut

The malpighian tubules are equidistant at their insertion on the front end of the hind-gut. The cells composing them possess a striated border on their mesal surface as in Hydropsyche.

The hind-gut is distinctly divisible into an anterior intestine and a posterior intestine. The division of anterior intestine into ileum and colon is not apparent. In the posterior region of the rectum five gills are present which can be extruded or retrieved into the gut. The composition of the hind-gut wall is essentially the same throughout its length, but the muscularis and the intima attain greater or lesser development in patches.

The epithelial cells lining the hind-gut have cuticular intima on their mesal border and are normally quite flat, but just behind the mid-gut, at the level of the insertion of malpighian tubules, they become somewhat taller and form a distinct region which projects, and even descends, into the gut-lumen for a short distance. This is all there is of the pylorus or the pyloric valve. The longitudinal folds are quite feeble in the anterior intestine but in the posterior intestine they are more compactly developed and almost fill the rectal cavity. The epithelium here is without intercellular walls but has large nuclei. In a limited region just in front of the insertion of the anal gills the epithelial cells grow smaller and more numerous.

The homology of this region is not certain, but apparently it is a part of the rectum. The walls of the gills have the same general structure as the rectum-wall. The anus lies between the anal styles on the posterior wall of the 9th abdominal segment.

Head-glands

It is very curious that in Polycentropus the left salivary gland is considerably shorter than the right one. The length of the right gland is nearly equal to that of the gut.

Both maxillary and mandibular glands (fig. 48) are present, and are composed of similar kinds of cells. The mandibular glands are paired. Each has a short and tubular body and lies in the lateral side of the head capsule near the compound eye. The component cells are arranged round a central canal into which the intracillular canaliculi open. The whole gland opens on the head capsule near the outer angle of the mandible.

The maxillary gland is also paired and has the same essential structure as the mandibular gland though it is built on a much larger scale. Each tube, lies close to the medium line for the greater part of its length but takes an outward course near its discharging end and opens near the base of the maxilla.

PLECTROCNEMIA sp.

HOLOCENTROPUS sp.

~~C~~ CYRNUS sp.

Habitat

Except for one specimen of Holocentropus which was caught from a rather swift tributary of the Itchen, all the material was received from Windermere. I cannot, therefore, say anythying at first hand about the habitat of these genera. It is quite well-known, however, (Noyes, 1914) that they form nets on stones in fairly swift to slow-moving streams and even in lakes.

Food

The larvae of these three genera do not show any great divergence from Poly-centropus in their food. Except for a stray diatom or pollen grain, vegetable matter in any form seems to be completely avoided. Animal food forms almost the entire bulk and consists of various insect larvae (chiefly Chironomus), small Crustacea, and an occasional fish-egg. A look at the tables attached at the end will give a better idea of the larval food.

Form of gut

The form of gut is very similar in all the Polycentropodidae so that the account given for Polycentropus should serve for the other genera as well. There are, however, slight differences among them in the inclination and extent of the spinous plates of the anterior part of the stomodeal valve, and the width of the passage for food running along the vental side of the proventriculus. The left labial gland is shorter than the right one in all of them. It is interesting to note that the specimen of Holocentropus caught from the Itchen, harboured a large Nematode parasite in its body-cavity. The gonads in this individual were very well developed but the alimentary canal was somewhat shrivelled and the left labial gland altogether absent.

PSYCHOMYIDAE

PSYCHOMYA PUSILLA Fabr.

Habitat

The larvae do not make any nets or portable cases. For their dwelling, they construct long, sinuous tubes of sand particles cemented with their salivary secretion on to the upper surface of stones in swift streams. The material here was all collected from the River Itchen, near Winchester.

Food

The greatest volume of gut-contents is made up of sand particles and minute translucent stones, curiously similar to those which form the material of their dwellings and cover the stones on which the dwellings are constructed. This material is very rich in diatoms and small filamentous algae and there seems little doubt that the larvae take it in for what nourishment it may contain in the form of diatoms and algae.

Form of gut (fig 26a)

The divisions of the fore-gut are not very distinct, the oesophagus, crop and proventriculus being almost insensibly continuous. The walls of the fore-gut are weak, the circular muscles being inconspicuous even in the proventriculus region. The longitudinal folds of the intima are more conspicuous in the crop than in the proventriculus. The stomodeal valve is very delicate and leaves a wide gap in the centre. The mid-gut, which is nearly three times as long as the fore-gut, begins in the second thoracic segment and ends near the hinder margin of the fifth abdominal segment. The malpighian tubules are simple and arise in two groups of three each on the right and left, and open on an annular fold on the inside of the gut. The hind-gut divisions are well marked and so are the longitudinal folds in the anterior intestine. The folds continue backwards but become feebler in the rectal sac and disappear in the rectal tube. There are five anal gills.

It is unfortunate that histology of the gut was not studied. In view of the typically diatomaceous food it might have been very interesting.

The labial gland has the usual types of accessory glands near the base of the discharge duct.

TINODES sp.

Habitat

Lake Windermere.

Food

As would be expected of a larva of such small size, Tinodes live mainly on diatoms, particles of debris and very tender (probably because very young) algal filaments. Diatoms show a great variety and are often so numerous that they form solid masses in the gut. The following are their commonest forms:-

(1) *Diatoma vulagre*,

(2) *Synedra ulna*,

(3) *Navicula cryptocephala*,

(4) *Gomphonema constrictum* and

(5) *Cymbella* sp.

Form of gut

The gut is more or less a repetition of Psychomyia's on a miniature scale. The ratio of fore-gut to mid-gut is 1:2.2. The former is very delicate and opens by a very wide aperture, weakly guarded by the stomodeal valve, into the mid-gut. The number of anal gills is five. Histology of the gut was not studied.

ODONTOCERIDAE

ODONTOCERUM ALBICORNE SCOP.

Habitat

The collection was made from the swift streams round the lake Winderemere and the Rivers Itchen and Test in Hampshire. The larvae are most abundant in the swiftest to moderately swift but not very deep parts of the streams. They can be seen crawling about among small pebbles on the river-bed, but I have seldom seen any of them sticking to the water weeds, which are so common in the same environment. In a majority of cases, I have observed numerous rotifers sticking to the outside of their bodies.

Food

Odontecerum is mainly carnivorous with a marked tendency to become cannibalistic in captivity. In nature, it feeds on all sorts of water animals and plants, but the major portion of its food is provided by the larvae of Trichoptera. It would also eat Limnaca-like gastropods.

Form of gut (figs 24-26)

The fore-gut is somewhat longer than the mid-gut and joins the latter in the first abdominal segment. Division of the fore-gut into usual regions is quite distinct in fresh specimens.

The stomodeal wall consists of a muscularis in which the circular muscles lie outside the longitudinal, a flat epithelium and thick intima. Several longitudinal folds run along its inner surface. The circular muscles attain great strength, especially in the posterior half of the fore-gut. Here the longitudinal folds and then intima attain great size and pursue an undulating course. There can hardly be any doubt that the folds can, by the action of the circular muscles, meet in the centre of the gut-lumen and work upon food in the manner of a gizzard.

The stomodeal valve is strong and stout, and leaves only a narrow aperture in the centre. It resembles that of Hydropsyche in developing an anterior part to itself. This anterior part, however, is not a specialized organ as in Hydropsyche, but is merely a collection of folds which rise up slightly above the fore-midgut aperture before passing down into the mid-gut (fig..) . The posterior part of the stomodeal valve descends into the mid-gut for a short distance only. A ring of specialized cells uniting the stomodeal epithelium to the ventricular epithelium is present.

The mid-gut begins in the first abdominal segment and ends near the posterior edge of the sixth. Its wall is composed of the usual layers— the muscularis, basement membrane and the epithelium. The epithelium consists of two kinds of cells, the digestive and the regenerative, the latter forming nidi. The nidi are very numerous and leave little space between them for the digestive cells. The digestive cells are very tall being about 12 times as high as broad. Their nuclei occour at the middle height and there are numerous vacuoles near their mesal edge. The striated broder is not continuous, but seen here and there only.

There are indications of the presence of goblet cells but this could not ascertained due to faulty preparations. I had only one specimen for section-cutting which had remained in cloveoil-celloidin for over two years and had become very brittle. Application for fresh material from England brought wrongly identified larvae, so the matter remains uncertain. A membrane enveloping the food was also present, at least in patches.

Secretion vesicles containing granular material were also seen here and there. They were not very numerous, but their presence indicates holocrine secretion.. This, of course, does not exclude the possibility of other types of secretion processes going on side by side with the holocrine.

The malpighian tubules are equidistant and there is a slight swelling in the gut-wall where they are inserted. Pyloric region is distinct. The ileum and colon appear to have the usual histological structure. The sphincter arround the colon is very strong. The walls of the rectal sac are loose and marked with irregular folds. Its epithelium has broad cells with large nuclei.

Each labial gland has attached to it a pair of small rounded accessory glands near its union with the discharge duct. The glands are remarkable for being white and opaque.

The other head-glands could not be studied.

MOLANNIDAE

MOLANNA sp.

Habitat

The larvae occur on the silt-bed of very slow moving streams, but it is rather hard to spot them because they are almost indistinguishable from their back-ground. The present collection was taken from the Railway Canal near Kingston, and the Itchen near Winchester.

Form of gut (fig 27-28)

A short account of the gut of Molanna cinerea Hagen, was given by Betten in 1922. Nothing has been added to our knowledge of it since then. It is very unfortunate that histology of the gut could not be studied due to scarcity of material.

The fore-gut is quite long and its circular muscles are quite well-developed but become remarkably so in the region of the proventriculus. The latter is a comparatively tough structure and narrows down to a neck before joining the mid-gut. The longitudinal folds of the intima in the fore-gut are very pronounced, but in the proventriculus, they stand out perfectly vertically from their bases and assume a hard, plate-like form, almost meeting in the centre. In one case they even showed a brownish tinge. Molanna has thus made a very near approach to the condition of a hard and six-toothed gizzard. The stomodeal valve descends some length into the mid-gut, is fairly strong and leaves a medium-sized aperture in the centre.

The mid-gut is about three quarters as long as the fore-gut. The ~~malphigian~~ malpighian tubules are coloured reddish brown right from their bases where they are equidistant and open on an annular fold on the inside of the gut. Except for the distinction into anterior and posterior intestine, the divisions of the hind-gut are not well marked.

Food

Rousseau, who studied the species on the continent, regards the genus as mainly carnivorous. Slack, (1936) ~~form~~ from his study of the genus in Hampshire, concludes that it is principally vegetarian, though also feeding on the Entmostraca. My results show that the larva is carnivorous in the main, feeding upon small insects and Crustacea, but also taking in plant food in the form of diatoms. I must confess, however, that my data are very scanty.

LEPTOCERIDAE

LEPTOCRUS SPP.

Habitat

Collected from the Itchem near Alresford in May and July, 1936.

The usual habitat of these larvae is in the bays formed in the banks of the river, which are cut off from the more rapidly moving main stream of water. They are found crawling about on small pieces of flint at a depth of about one foot in the vicinity of the Water Ranunculus or other weeds.

(It is possible that more than one species of Leptocerus is involved here).

Food

Leptocerus shows a queer combination of animal and vegetable food. Siltala and Rousseau regard it as a purely vegetarian form but if that is true, it is probably due to specific environmental and seasonal differences. The common Hampshire form shows, on the one hand, a great partiality for a diet of water mites (Hydracarina) and on the other, for a kind of food which I have nowhere else seen combined with animal diet, namely, sand, diatoms, pollen-grains and various debris. In a fair proportion of the stomachs examined, mites formed about half the amount of total contents, and in one case, a stomach was almost completely filled with them. Most larvae, however, are somewhat more vegetarian than carnivorous, taking in large amounts of sand, debris, diatoms and fine filamentous algae. They are peculiar is not caring for tissues of flowering plants and also in making the Acarina almost their only animal food.

Form of gut (figs 29-30)

The fore-gut is not very long and ends near the hinder margin of the second thoracic segment. The pharynx has well-developed folds in its walls which thin down greatly in the immediately posterior region, but reappear soonin the crop and proventriculus, and attain therein considerable size and complexity. In these regions the circular muscles are quite strong and lie inside the longitudinal muscle fibres which are rather feeble. The stomodeal valve is short and does not descend into the mid-gut for a long distance as in Hydropsyche. Nevertheless, it is quite thickset and leaves a comparatively narrow aperture in its centre.

The mid-gut is almost twice as long as the fore-gut, and tapers towards its posterior end. In it, the epithelial cells are of three kinds; the digestive, the goblet, and the regenerative cells. The latter form compact nidi which lie quite near each other alternating with small groups of digestive cells whose lower surface touches the basement membrane. Not all the digestive cells, however, lie in contact with the basement membrane, for almost half their numbers lie over (mesally to) the nidi. Big vacuoles are present in large numbers near their mesal edge and are very often seen being extruded from the cells. A striated border or the peritrophic membrane is nowhere noticeable. The goblet cells are quite numerous. They have the usual form, being broad and transparent in their mesal half. This part often contains a yellowish substance which does not take stain in sections..

Digestive secretion Both nucleated and non-nucleated vesicles are producedd by the digestive cells but the former kind are somewhat rare to see.

Hind-gut The hind-gut is divided into a pylorus, ileum, colon, rectal sac and a rectal tube and is lined throughout by a flat epithelium and a cuticular intima.

The pylorus is a small but well-defined region into which the malpighian tubules open at equal distance from each other. There are regular rows of small spines on its walls. As in Hydropsyche, the longitudihal folds in the ileum walls are slight, but the ileum is, comparatively speaking, a very long region in Leptocerus. The sphincter between ileum and colon, which is so well-developed in most Trichoptera, is not very strong here. The walls of colon have greatly developed folds which almost fill its lumen. The rectum is broad and has loose walls. Its epithelial cells are not so flat as in colon and have large nuclei and a thick intima. Its walls have strong, sinuous longitudinal folds which disappear completely in the next region, the rectal tube. The rectal tube has six groups of small anal gills just anterior to anus. Muscle bands run between the posterior region of rectum and the body-wall and can, undoubtedly, retract the gill region within the anus, when desired.

The labial gland is rather short, not exceeding the alimentary canal in length.

Both the mandibular and maxillary glands consist of pear-shaped cells with the nuclei and the intracellular canalicules in their usual place.

The mandibular gland is very small consisting of about a dozen cells and lying in the outer part of the head capsule.

The maxillary gland is remarkable in having a structure intermediate between the glands of prognathous larvae and those of the hypognathous ones. It resembles the latter (Limnophilids and and Sericostomatids in general in so far as its cells are broad-based and pear-shaped, but resembles the former (Rhyacophila, Polycentropus and Philopotamus) in these cells forming collectively a compact and tabular body. These tubes are of course, much smaller and have far fewer cells than the maxillary gland tubes of the prognathous forms but the tendency to form a tube in which cells are more compactly arranged is quite obvious. The gland opens in the usual place.

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TRIANODES sp.

Habitat

The larvae are found in fairly swift and shallow streams, attached to the roots of trees, growing from the banks. All specimens were taken from a tributary of the river Test, near Bollington, except one, which was received from Windermere.

Food

The food appears to be chiefly fragments of phanerogamous weeds. Occasionally, Crustacea have been noticed in the gut, but in very small quantities only. Due to the paucity of material, a sufficient number of observations could not be taken, but it is hoped that the data put forward here represents the normal state of things.

Form of gut

Except for the relatively great length of fore-gut there is not much difference in the form of the gut between Triaenodes and Leptocerus. The longitudinal folds of the intima in the fore-gut are not very strong and the stomodeal valve leaves quite a wide gap in the centre.

The labial gland is about equal in length to the gut and carries a pair of accessory glands at its union with the discharge duct. The mandibular and maxillary glands were not studied.

OECETIS Sp.

Habitat

All specimens were received in March from Lake Windermere, where, it is reported, they live in cracks on the under surface of large stones, with a substratum of leaf detritus and mud.

Food

The chief source of food seems to be very small insect larvae and pupae. No trace of vegetable matter was seen. A large proportion of stomachs was void of food, but whenever one contained anything, it was found to be of animal origin.

Form of gut (fig. 31-34)

The extreme length of the fore-gut is remarkable; it has, indeed, to take a zigzag course in order to accomodate itself to the shortness of the body. The circular muscles and the longitudinal folds of the intima which are visible even in dissections, are very strongly developed. The stomodeal divisions are more or less distinct, the crop and proventriculus being relatively large. The stomodeal valve is very stout, descends for some distance into the mid-gut, and leaves a rather narrow aperture in the centre. The epithelium of the fore-gut is flat and is lined by a thick intima throughout its length. The pharynx is comparatively very broad and extremely well supplied with circular and suspensory muscles— an obvious adaptation for swallowing large-sized prey. The longitudinal folds are large and decrease but slightly in the immediately posterior region. In the crop and the proventriculus they attain proportions and a complexity not exceeded, perhaps, by any other Trichopterous larva. Towards the posterior region of the proventriculus the folds stand out straight into the lumen of the fore-gut and in cross sections could easily be mistaken for the teeth of a gizzard (fig..). The stomodeal valve is strong, muscular and double-layed but without any anterior part like that of Hydropsyche. It opens obliquely into the mid-gut which begins rather at its side than directly behind it. It is evident from its form that it should easily be able to close the aperture between the fore- and the mid-gut. There is a ring of special cells uniting the hind extremity of the fore-gut with the anterior end of the mid-gut.

The mid-gut

The mid-gut, which is less than half the length of the fore-gut, is very peculiar in protuding, on one side, beyond the point of its union with the stomodaeum. It begins near the front margin of the second abdominal segment and ends in the fifth. The epithelium of mid-gut has a distinct basement membrane and the nidi are tallish groups of regenerative cells between which there is only little space left for the functional cells, the latter being confined almost solely to the tops of the nidi: The functional cells have very indefinite outlines and their tops which have an abundance of vacuoles protrude very irregularly into the lumen of the mid-gut. In this last respect they resemble the epithelial cells of Polycentropus very much. Numerous goblet cells are also present and have the same form as in Leptocerus.

Digestive secretion

The process could not be studied satisfactorily due to faulty preparations. It seems, however, very probable that the extremely long and irregular processes of digestive cells which nearly meet in the gut-lumen those from the opposite wall would eventually get separated off the parent cells. Also, the very high proportion of nidi seems to suggest that the functional cells degenerate very rapidly— at least more rapidly than in the closely allied Leptocerus. Some actual vesicles were also observed in the gut lumen but on account of their bad stain it could not be decided whether they contained any nuclei in addition to their granular contents. Striated border of the digestive cells or the peritrophic membrane could not be made out.

Hind-gut

The terminal portion of the mid-gut epithelium curves deeply into the hind-gut lumen. The pyloric region is short but distinct and receives the malpighian tubules. Unlike most other Trichoptera, the malpighian tubules are not shortly "waved", but have large undulations and are without the usual reddish pigment. They are equidistant, but give a flase appearance of originating in two groups and go forwards and backwards tracing a very characteristic pattern. As in Leptocerus, the ileum is a [redacted] comparatively large region but without longitudinal folds on its walls. It is continuous behind with a rather small colon which has well-developed longitudinal folds. The sphincter at the begining of colon is much less strongly developed than in the Limnophilidae. The rectal sac has loose folds on its wall but they still retain a general longitudinal direction.

A pair of accessory glands marks the union of the labial gland with its duct. The labial gland is slightly shorter than the gut in length.

The maxillary glands consist of long curved cells ~~and~~ which are more less free from one another but unite near the gland opening.

The mandibular gland is apparently absent in Oecetis.

PHRYGANEIDAE

PHRYGANEA GRANDIS L.

Habitat

The larvae are fairly common in some ponds in Surrey. They like to dwell near the bottom of water, amid thick, submerged vegetation. To obtain them one must delve deep with a net and drag it amongst the roots of water weeds. They pupate early, so that the best time to get them is before the end of May.

A large number of larvae were also obtained from Windermere towards the end of February, 1936.

A detailed account of the Habitat and food of the American species of *Phryganea* is given by Lloyd (1921).

Food

The species is a voracious eater. The average gut-contents of a full-grown specimen would easily exceed twice over that of any other species that I have studied. The food consists of both animal and vegetable matter. In summer when vegetation in its surroundings is more abundant than the animals upon which it preys, plant tissues form a greater part of the contents of its gut. In winter, the proportion is reversed, and it may even become completely carnivorous. The bulk of its vegetable food is furnished by bits of leaves and stems of higher plants. An alga or diatom is rarely included. The animal food consists mainly of insect-larvae, especially the Trichopteraus larvae. On occasions, it has been found to be cannibalistic.

Feeding

I have never actually observed a Phryganea larva feeding, but the character of the fore-gut content shows that it cuts up its food, whether animal or vegetable, into small bits, before taking it in. Small larval prey is, however, devoured whole, sometimes, if not always. It was possible to study the action of the stomodeal valve in fresh dissections. It allowed a brown fluid to pass from the mid-gut into the fore-gut which no doubt helped to soften the fragments of food which were usually protected by the exoskeleton of the prey. In the region just in front of the stomodeal valve, the nature of such fragments was often clear, but behind it, they were reduced in size and their character was generally lost. This would tend to show that the stomodeal valve helps not only in regulating the passage of food from the fore-gut to the mid-gut, but also, to some extent at least, in mechanically breaking down the larger fragments of food.

Form of gut (figs 35-38)

The alimentary canal of Phryganea interrupta Say has been described by Branch (1922) with histological details, yet she omits to mention certain faeture which are significant here. For the rest, the two species are very similar.

Fore-gut

The fore-gut is slightly longer than the mid-gut and its divisions into the pharynx, oesophagus, crop and the proventriculus are quite well-marked. Inside, the stomodeal valve is fairly well developed. The muscularis is not uniform, for the longitudinal muscles which are inside the circulars in the anterior region of the fore-gut, come to lie outside them in the posterior part. Very often the circular and the longitudinal fibres run into each other. Before joining with the mid-gut the broad proventriculus suddenly narrows down into a neck. The gap thus formed between the fore- and the mid-gut is spanned by numerous longitudinal muscle strands which are continuous in the two divisions of the gut. The fore-gut is, of course, lined by a cuticular intima throughout its length.

The pharynx, (particularly that part of it which lies before the brain) has very powerful circular muscles and is attached to the head-capsule by numerous dilator muscles. This is quite in keeping with the very voracious habits of the larva which sometimes swallows its prey whole. The longitudinal folds in its walls are large and should allow great distention of the pharynx. The muscularis thins down considerably in the posterior region of the pharynx and grow feeble in the oesophagus where the longitudinal folds also have a weak development. The epithelium is flat throughout the fore-gut except in certain parts of the stomodeal valve. The crop is comparatively short and thin-walled. The proventriculus forms the posterior two-thirds of the fore-gut and has tough walls due to the strong development of the muscularis, and longitudinal folds with their intima. The circular muscles grow stronger towards the posterior part of the proventriculus but they are particularly well-developed in the 'neck' region just in front of the mid-gut. It appears almost certain that they are capable of powerful sphincter action. The numerous longitudinal muscle bands that span the gap between the fore-gut and mid-gut would seem to help in drawing the stomodeal valve more deeply into the mid-gut and thus help the movement of food into it at the desired moment.

The stomodeal valve is strongly developed but has no counterpart of the anterior part of the valve which is so noticeably developed in the families Hydropsychidae and Polycentropodidae. Essentially, it is the posterior-most part of the stomodeum wall which has descended into the mid-gut. As in all other larvae, it doubles upon itself after travelling a short distance and comes to a final stop near the front end of the mid-gut. The epithelial cells composing it grow very tall just before its termination. As in <u>Hydropsyche</u>

there is a space enclosed between the two layers of the valve.

Mid-gut

The mid-gut extends from the second to the sixth abdominal segment and is somewhat shorter than the fore-gut in length. Its front end is held to the sekeletal parts of the anterior thoracic segments and even head by means of long strands of muscles which lie somewhat loosely in the body cavity. The walls of the mid-gut itself consist of a double muscle layer (longitudinal fibres lying outside the circular) and the epithelium. The basement membrane is very thin and difficult to demonstrate.

The epithelium consists of of two kinds of cells - the digestive and the regenerative. The digestive cells are very tall, being about 10 times as high as broad. For the most part they lie above the regenerative centres but some also lie between them with their bases touching the basement membrane. In the latter kind the nucleus lies at about the middle height of the cell but in others it has no definite position. Vacuoles are present here and there, but the striated border is almost unbroken over most of the mesal surface of the epithelium. The regenerative cells form compact and large nidi which lie very close to each other along the basement membrane. In a nidus the regenerative cells appear to lie above one another in an imbricate manner. The basal regenerative cells are hardly anything more than their nuclei, but, as they grow upwards, they add protoplasm to the nuclei till they assume the form of full fledged digestive cells.

A delicate membrane enveloping the food and lying a short distance from the mesal surface of the ventricular epithelium is present. Its origin could not be traced to the front end of the mid-gut but it is very probable that it is the peritrophic membrane.

Digestive secretion

Only a single mid-gut was sectioned and in this there was no trace of secretion vesicles of any size or form. Their absence, however, does not prove that production of secretion vesicles is not of general occurrance in Phryganea. In keeping with the absence of secretion vesicles the striated border of the ventricular epithelium is unbroken. Here and there parasetic Gregarinae are found cut across in sections of the mid-gut; at first sight they may be mistaken for secretion vesicles but they are really not so.

Hind-gut

The hind-gut is peculiar in being held to the body-wall by numerous well-defined mesentry-like sheets. It is distinctly divided into an anterior intestine and a posterior intestine. The former is subdivided further into an ileum and a colon, the separation being marked by a

W

well developed muscular sphincter. The rectum is a large sac-like organ which occupies the last $2\frac{1}{2}$ segments of the abdomen and opens on the outside at the anus between the paired anal styles. No anal gills are present.

The malpighian tubules are equidistant at their insertion on the hind-gut and open into a distinct ring which, except for its anterior wall, is composed of the hind-gut epithelium (more or less columnar in this region), intima and muscularis. The anterior wall is formed by the deeply in curved ~~in~~ epithelium of the mid-gut. The ring is to be distinguished as the pylorus and behind it lie some strong circular muscles which have probably a sphincter action.

Behind the pylorus the epithelium is more or less flat in whole of the hind-gut. The ileum-wall is thin, being composed of a flat epithelium, thin intima and a feeble musculature in which both kinds of muscle fibres are present. Behind the ileum there is an extremely powerful band of circular muscles which acts as sphincter. The associated intima is also very thick. The colon is short and narrow, but has pronounced longitudinal folds on its inside. Its epithelium is squarish in sections but just behind the sphincter it grows columnar for a very short distance.

The rectum-wall has a muscularis in which the circular fibres are much better developed than the longitudinal. The epithelium is very flat and has a thick intima. The folds in the rectum wall run both lengthwise and crosswise.

GLYPHOTAELIUS PELLUCIDUS Retz

Habitat

A large number of specimens were taken from a shallow and very sluggishly moving canal near Richmond in January 1936 The shed leaves from the surrounding trees had entirely covered the bed of the canal except for a few green plants of Callitriche verna growing here and there. Specimens were also collected from ponds in surrey, where the environment was more or less similar to that of Richmond canal.

Food

Glyphotaelius shows a marked preference for dead leaves and stems, as also for the bark, which it rasps from the dead branches of the higher plants. It is true that most of the specimens were collected in winter but green weeds were not entirely absent at that time. A few specimens collected in June also showed the same preference. Thus, by far the largest bulk of food is formed by raspings from bark and bits of dead leaves and stems. Sticking to the latter are usually a host of epiphytic diatoms and very young algae, which form quite satisfactory food. Only once was animal (Crustacean) material seen included in the gut. The larva should therefore be regarded as one of the purest vegetarian types.

Form of gut (figs 39-42)

The fore-gut is short and thin-walled, the circular muscles being comparatively weak. The distinction between crop and proventriculus is not well marked. The longitudinal folds of the intima are only weakly developed. The stomodeal walve is merely a circular fringe round a very wide gap through wich the fore-gut is continuous with the mid-gut. In structure, the valve is nothing more than the posterior extremity of the stomodeal wall of muscle layers, epithelium and intima, which descends for a short distance into the mid-gut. At its posterior end the epithelium and intima turn outwards and upwards to envelop completely the muscular part on both sides. The mid-gut which begins near the anterior margin of the third thoracic segment is more than three times as long as the fore-gut and relatively very broad. The two ventral malpighian tubules open very near one another, the rest are equidistant. Immediately behind their insertion there is a distinct inward annular fold - the pylorus. The ileum is short, and a strong sphincter divides it from the colon. The latter is marked on its inner surface by six strong longitudinal folds which begin near the level of the spincter and run backwards and become continuous with certain loosely hanging lappets in the rectum. The rectum is much broader than the hinder region of the colon and projects forwards over it for a short distance in the form of of six closely set pouches which are externally held to the colon wall by a few longitudinal muscle bands which span the gap between these two divisions of the proctodaeum. A large proportion of the space inside the rectal sac is filled by the already mentioned lappet-like structures which are continuous with the longitudinal folds of the colon. These are grown over with long processes whose lower extremities reach back beyond the lappets. The rectal pouches which grow over the colon are internally separated from each other by thin septae which are continuous with the lappets. There are loose folds all over the wall of the rectal sac, but the rectal tube is short and without folds.

The labial glands are of the ordinary type. The mandibular and maxillary glands were not studied in _Glyphotaelius_, but it is presumed that they are like those of _Anabolia_.

ANABOLIA NERVOSA (Leach) Curt.

Habitat

This is perhaps the most common Trichoperous larva in the slow to somewhat swift and shallow streams in Hampshire. In some places in early summer, one almost can not see the bed of the stream, for the thick cover of their cases over it. They are usually seen near patches of vegetation.

Food

The food is entirely vegetable. Both dead and living material is made use of but the latter seems to preponderate. Of the vegetable matter, Water Ranunculus appears to form a considerable portion.

Form of gut (fig 42)

All Limnophilid larvae have a very similar gut. The mid-gut in them attains a very large size and is almost always found distended with food. The fore-gut is short, relatively thin-walled and without a gizzard-like Hydropsyche. The stomodeal valve is very short and leaves an extremely wide passage in the centre. The divisions of the hind-gut are always clear and well-developed. A pyloric region is very distinct. The valve between colon and rectum has comparatively enormous proportions. Anal gills are never developed.

Fore-gut

The fore-gut extends upto the anterior border of the 3rd. thoracic segment. Its walls have the usual composition of a flat epithelium lined with cuticular intima plus a supporting muscularis in which the longitudinal muscles lie outside the circular in some regions. The walls are generally very thin, except in the pharynx where both the muscularis and the folds of intima are comparatively thick. The longitudinal folds are feeble generally and do not obtain strong development even in the proventriculus. The terminal portion of the stomodeal wall descends into the mid-gut for a very short distance and forms the stomdeal valve. As in all other Trichoptera the valve is double-layered though very little space is enclosed between the two layers. The outer of these two layers (epithelium and intima) travels up to unite with the epithelium of the mid-gut. The terminal part of the stomodeal epithelium consists of very small cells so that this region appears like a gap between the stomodeal valve and the ventricular epithelium in longitudinal sections.

Mid-gut

The mid-gut is very large and extends upto the 7th abdominal segment. Its walls are composed of a muscularis and an epithelial layer resting on a basement membrane.

The epithelium consists of two kinds of cells:- (1) the digestive cells and (2) the regenerative cells.

Unlike *Hydropsyche*, the regenerative cells form short, compact nidi which occour along the whole length of the mid-gut between larger blocks of the digestive cells. The digestive cells are tall and columnar. They have a striated border on their mesal side and their basal side rests upon the basement membrane. The cell-walls and the nuclei are distinct, the latter lying at about the middle height of the cell. (Histology of the mid-gut was also studied in another Limnophilid species. It agreed with *Anabolia* in all esential respects; only, the columnar epithelial cells were shorter, the nidi broader and the circular muscle fibres better developed).

Digestive secretion

In the few series of sections that were cut of *Anabolia* and the Limnophilid referred to above, digestive secretion was not seen in a very active phase. A few secretions vesicles were noticed here and there just outside the mesal border of the ventricular epithelium in both larvae. In a large number of cases (in both larvae) the vesicles contained nuclei within them, which fact tends to show that this type of 'secretion' vesicle was possibly of general occurance in other Limnophilids also. Vesicles containing granular matter only were also seen, though in much less proportion; this proportion would decrease still further if it is considered that some of them may have contained a nucleus but the section passed across them in a region from which the nucleus was absent.

Malpighian tubules

The divisions of the hind-gut in Anabolia (as in all the other Limnophilids studied) are clear cut and perhaps the best developed in Trichptera.

The Malpighian tubules do not arise from the front end of the hind-gut but from the posterior end of the mid-gut. The reason for believing this is that, in longitudinal sections of the gut, the opening of the tubules is seen to be limited by ventricular epithelial cells on both the anterior and posterior sides. The tubules are inserted singally on the gut-wall, but not at equal distance from one another; they are disposed in 3 pairs, two of which are lateral and one is ventral.

Hind-gut The Pylorus forms a very distinct annular region and is very well developed. Its anterior wall is formed by the inward-projecting posterior extremity of the ventricular epithelium (which also guards the apertures of the Malpighian tubules). The posterior wall of the pylorus is formed by a fold at the anterior extremity of the hindgut. The epithelial cells in this fold are particularly tall and the associated circular muscle fibres are somewhat stronger than those in the immediate neighbourhood.

The ileum is cup-like in form, being very broad in front and tapering sharply behind. Its epithelium is flat, longitudinal folds inconspicuous, and the muscularis thin. The beginning of colon is marked by the most powerful sphincter in the whole of the alimentary canal. Inside it six longitudinal folds attain huge proportions and nearly obliterate the lumen of the colon.

As in *Glyphotaelius*, the posterior part of the colon is covered over on the outside by a forward growth of the rectal sac in the form of six pouches. A gap thus comes to lie between the walls of the colon and the anterior end of the rectal pouches which is spanned by muscle bands running between the two organs. The folds of the colon descend into the rectal sac for some distance and form a kind of valve; after that they become continuous with the 6 septa which separate the rectal pouches from each other. Projections from the valve, referred to above, hang loosely into the cavity of the rectal sac and probably afford the surface for harbouring the host of bacteria that are always present in this region. The walls of the rectal sac consist of a muscularis and large squarish epithelial cells with big nuclei and a thin intima lining their mesal edge. The intima is folded in all directions though principally in the directions of length and breadth. The posterior part of the rectum is distinguishable as rectal tube and is without any folds.

The labial gland is of the usual type.

Both the maxillary and mandibular glands of <u>Anabolia nervosa</u> have been described in great detail by Henseval (1897), I will not, therefore dwell on their structure.

Essentially the mandibular gland consists of big long cells which are quite separate from each other except near the opening of the gland which is near the outer angle of the mandible. Each cell is traversed by a fine canalicule lined by intima but I have not been able to see the striations around the canalicule (as described by Henseval) probably due to the too great thickness of my sections.

The maxillary glands are composed of cells similar to above but they are arranged round a central canal, though not very compactly.. They have a fairly long discharge duct which opens near the base of the maxilla.

COLPOTAULIUS INCISUS Curt.

Habitat

Larvae were collected from ponds near Virginia Water, Wisley and Chertsey at different seasons of the year. They were generally found attached to dead leaves floating near the edges of the ponds. They do not appear to be very common.

Food

The greatest proportion of food is formed by fragments of dead and fresh leaves, especially the former. Diatoms and sand grains are also included, but they do not seem to be deliberately chosen for eating. A Chironomid larva was found in one of the seven stomachs examined and formed only a small proportion of its contents.

Form of gut

The gut does not show any significant difference from that of Glyphotaelius.

LIMNOPHILUS spp.

Habitat

The larvae are found in great abundance during spring and early summer ~~during thus~~ in some of the weedy ponds and slow moving canals of Surrey. They are usually found attached to the weeds, especially grasses, not far from the water surface.

Food

By far the greatest bulk of food consists of fragments cut off from the leaves and stems of the water weeds, both in fresh and rotten condition. Raspings from bark are seldom taken in and that perhaps accounts for the paucity of diatoms (a large proportion of which are epiphytic) in the gut as compared with *Glyphotaelius*. Algae are some times inculded in food, though they form only an infinitesimal part of it. Animal food is taken very exceptionally. The following are the commonest diatom forms:-

(1) *Trabellaria* sp.

(2) *Gomphonema* sp.

(3) *Synedra* sp.

(4) *Melosira* sp.

(5) *Amphineura pellucida*

(6) *Navicula* spp.

(7) *Amorpha ovalis*

Form of gut

Form of gut

This does not differ in any essential respect from that of *Glyphotaelius*. It has been described in detail by Branch (1912) but she does not mention the rectal valve, which attains such enormous development in all the Limnophilidae.

The head glands, except the labial, were not studied.

MESOPHYLAX sp.

Habitat

The larvae are often found aggregated together under stones in shallow and slow to moderately swift streams, though it is by no means uncommon to see them crawling about singly among pebbles on the bed. In the Hampshire rivers, they may be found as late as the middle of October.

Food

Of about a dozen larvae collected at different places and times, only four contained any food in their guts. Such a high proportion of empty guts would tend to show that Mesophylax has strong food preferences. On the other hand, this may be due to their gregarious habits so that if food could not be had by one, the others of the same group would not be likely to have had any. The food consists largely of fragments of fresh leaves, specially of the Water Ranunculus. Some sand grains and diatoms were included, but their total volume was comparatively very small. No animal food seems to be taken.

Form of gut

The form of the gut is not much different from Glyphotaelius except that the mid-gut is relatively short and the valve between colon and rectum less well-developed

STENOPHYLAX spp.

Habitat

The larvae are fairly abundant during the middle and late summer in the moderately swift parts of the River Itchen. They crawl about among the small flints and, since their cases are also made from the same material, they merge well with the back-ground. Some, however, are also to be found sheltering beneath larger stones. A few larvae were also obtained from the Lake Windermere. Stenophylax has often been found to harbour a surprisingly large Nematode parasite within its body.

Food

The food is almost entirely made up of phanerogams. Both dead and living plants are attacked, but the latter, perhaps, more frequently. Some amount of debris is also taken in, probably with the fragments of dead plants. Diatoms are not quite so numerous as in Glyphotaelius. Occasionally pieces of insect skeleton are found in the gut-contents.

The maxillary and the mandibular glands were not studied.

HALESUS sp.

Habitat

The larvae were taken mainly from the River Itchen near Winchester. They inhabit the swiftest parts of the river and are often seen clinging to weeds.

Food

The food is apparently all vegetable. This is interesting, since it is reported (Russeau, 1921, page 791) that the genus is partly carnivorous, and in particular Felber (in Russeau) states that the species *Halesus tesselatus* Rambur is highly carnivorous in aquaria. Slack (1936) dissected twenty stomachs and found only two which incuded any animal food. Of the seven dissected here, only one contained a few bits of insect skeleton. Bits from fresh leaves and stems and even bark are taken in and form the largest proportion of food. Diatoms, though included, are few and do not seem to be selected by the larvae.

Form of gut

The fore-gut seems to be somewhat more strongly developed than in *Glyphotaelius* and *Limnophilus*, and its divisions are usually distinct. The longitudinal folds of its intima and the stomodeal valve also are stronger. In the hind-gut, the rectal valve is not so conspicuous as in *Glyphotaelius*. For the rest the gut is much the same as in other Liminophilidae.

The labial gland has the usual character and is about as long as the gut. The other head glands were not studied.

SERICOSTOMATIDAE

BRACHYCENTRUS SUBNUBILUS Curt.

Habitat

The specimens of Brachycentrus Subnubilus were all obtained preserved in alcohol from the Natural History Museum. I was told that theyr fairly common in the river Test, near Romsey in early summer. I did not chance to see any of them there, though I must confess that I went to look for them rather late. But very young larvae (possibly of this species) were sometimes sticking to vegetation grown from bridges in the swiftest parts of the Itchen, near Winchester, towards the end of July. They make a case which has a different structure from the full grown Brachycentrus subnubilus, but closely resembling that of Brachycentrus nigrisima Banks. These larvae, since they were in the earliest stages, could not very well be compared with the full grown larvae of other Trichoptera. Hence their study was not attempted.

Food

The study of food has been rather unsatisfactory, being based on about 7 specimens, all caught from the same locality and at the same time. The examination of their gut-contents, however, shows that they eat both animal and vegetable food, including in the former kind small insects and Crustacea, and in the latter, leaf - and stem-tissues of the higher plants and diatoms and algae which are probaly taken in with sand.

On the whole, the larva seems to be omnivorous with the vegetable diet exceeding the animal.

A fascinating account is given by Murphy (1919) of the larval habits of the American species, B.nigrisoma, which she regards as becoming mainly carnivorous after the first six weeks of its life.

Form of gut (figs 43-44)

All dissections were made with alcohol preserved larvae, and it cannot be said with certainty that no artificial complication was ~~included~~ induced by this alcoholic preservation. Only seven specimens were available, but all of them showed a uniformity of structure. Histology of the gut was not studied.

The pharynx ends with distinct constriction and the oesophagus passes insensibly into the crop. The relatively large proventriculus is distinct, at least in some cases. Circular muscles though easily seen, are not very strong. The longitudinal folds of the intima are moderately developed. Near the posterior end of the proventriculus, the epithelium and intima turn forwards, independently of the outer gut-wall, and forms a complicated flower-like structure, which is best understood by looking at its diagrams (figs). Its petal-like folds ~~particularly~~ partially cover the narrow aperture of the stomodeal valve. The valve is small in circumference and descends only a little distance into the mid-gut.

The mid-gut begins near the front margin of the third abdominal segment and ends near the hinder margin of the sixth. The malpighian tubules are equi-distant at their insertion. The usual four division of the hind-gut are distinct and there is also a pyloric region, the posterior limit of which is marked by ~~the~~ an annular fold some distance behind the malpighian tubules. There are very conspicuous folds in the ileum.

The labial gland is relatively longer than in the other Sericostomatidae, being 1.7 times the length of the gut. The mandibular and maxillary glands were not studied.

SERICOSTOMA sp.

Habitat

Sericostoma is a case-building form which prefers to live in slow-moving parts of a river that are about a foot deep. The larvae crawl about on small pebbles on the beds of streams, usually in areas which support some vegetation. The present collection was taken from the rivers Itchen and Test in Hampshire, and the wave between shores of Lake Windermere.

Food

In the fifteen cases examined, the greatest proportion of food was made up of cuboid fragments bitten off by from the tender parts of water weeds. Since a good deal of sand is often included in the gut, it is reasonable to suppose that all the diatoms found are not epiphytic. Algae are only rarely taken in and the scarcity of insect or arthropod skeletal fragments would indicate that it is only very slightly carnivorous. The larvae are therefore mainly vegetarian, feeding on the tender portions of the leaves and stems of higher plants.

Feeding

A larva was once seen biting at the stem of Elodea in a laboratory tank. The process was watched under a binocular and it was found that the stem was held between the mandibles, the first and even the second pairs of legs helping in this. When the mandibles were closed tightly over the stem, the head was thrown back with a sudden powerful jerk, and bit of the stem was torn off. The labrum kept touching the twig constantly on its upper side and moving forwards and backwards. The under-lip, which also was moving forwards and backwards as a whole, made a final inward movement and the cut off bit disappeared into the mouth.

Form of gut (fig 45)

The gut of **Sericostoma** resembles the gut of Limnophilidae very closely. The stomodeum is short, pear-shaped and thin-walled, and its divisions are not marked distinctly except for the pharynx and the stomodeal valve. Its epithelium is very flat, the intima very thin, and the muscularis poorly developed though the circular fibres become quite noticeable just before the stomodeal valve is reached. The stomodeal valve is slight, descends a very short distance into the mid-gut and leaves a very large aperture in the centre. A ring of a few small cells joins the fore-gut on to the mid-gut.

The mid-gut is very large, being more than 3 times the length of the fore-gut and extending from the front border of the second thoracic segment up to the hind end of the sixth abdominal segment. Its walls are composed of a muscularis (longitudinal muscles lying outside the circulars), a thin basement membrane and an epithelial layer of cells lining the gut-lumen.

The epithelial cells are of two kinds:- (regenerative cells, and (2) the digestive cells, the former are grouped into nidi, though the latter are not so conspicuous as in the Limnophilidae. In the matter of regenerative cells grouping into nidi, *Sericostoma* comes midway between *Hydropsyche* and the Limnophilidae.

The digestive cells are columnar being about 6-8 times as high as broad. The striated border is well developed and for the most part is unbroken, A peritrophic membrane, though not seen to originate from the ring of cells at the hinder extremity of the stomodeum, is present and envelopes food within itself.

Digestive secretion

Vesicles floated off into the mid-gut cavity were seen here and there in all the series of sections examined. Mostly, they contain granular matter only, but on rare occasions they were also seen to possess nuclei. It should, however, be pointed out that a large number of the parasitic Gregarinae were also present in the mid-gut and in sections they appeared very much like the secretion vesicles and caused much confusion.

The malpighian tubules

The tubules open rather in the terminal region of the mid-gut than at the place where the mid-gut unites with the hind-gut. They are inserted on the mid-gut singally and at equal distance from one another;

the ventral two tubules, however, are exceptional and open close together. Like Hydropsyche, the cells composing the tubules have a striated border on their mesal edge.

The Hind-gut

The hind-gut is lined throughout by cuticular intima and is distinctly divided into an anterior intestine and a posterior intestine. In the anterior intestine a pyloric region is not clearly distinguishable as in the Limnophilidae, but the ileum and colon can be marked out very distictly. The posterior intestine is divisible into a large rectal sac and a short, narrow rectal tube. There are no anal gills.

The ileum is pear-shaped and thin-walled. Its epithelium consists of very small flat cells whose intima is very thin and does not form longitudinal folds of any great size. The passage to colon is guarded by a rather strong circular sphincter. In colon, the longitudinal folds attain prominence and the muscularis also attains better development than in the ileum but the epithelium cells remain quite small.

In the rectal sac, the epithelium consists of larger but still flat cells and folds of the intima obtain quite strong development although they are no longer strictly longitudinal in direction. The rectal tube is without folds.

NOTIDOBIA CILIARIS Steph.

Habitat

Same as *Sericostoma*. The larval case and habits resemble those of *Sericostoma* so closely that it is difficult to tell the difference between the two genera even on a close examination.

Food

This includes a great deal of debris along with the usual cuboid fragments of phanerogamous tissue. Pieces of insect skeleton are also included but they form a minor part of the total contents of gut. The diatoms and algae form an infinitesimal proportion.

Form of gut

The form and the ratio of gut divisions is very much the same as in *Sericostoma*.

The head-glands, except the labial, were not studied.

S I L O sp.

Habitat

The larvae are seen dragging about their flat cases on bare stones in shallow, fairly swift streams. Collections were made from the rivers Itchen and Test and from the Lake Windermere. In both the lake and the rivers, they were commonest near the banks.

Food

The larva taken in large quantities of sand which includes diatoms, tiny particles of decaying organic matter (mostly of vegetable origin) and short bits of algae. It seems to be attracted by bright objects, since the gut frequently contains brilliant, coloured stones and particles of mica. The organic particles and diatoms, of which the following kinds are generally recognisable in the contents of gut, appear to form the main source of nourishment:-

(1) Gomphonema constrictum (2) Diatoma vulgare
(3) Rhoicosphania (4) Navicula spp.
(5) Amorpha ovalis (6) Trabellaria sp.

Occasionally pieces of animal matter are also found in the stomach, but these are probably taken from a dead and decaying host. It appears that the quantity of stomach-contents is much less in March than in August in the Windermere specimens.

Form of gut

The form of gut resembles that of Sericostoma very closely. The fore-gut is short and narrow and its division into the usual parts is not distinct. Histologically it is a replica of the *serlostoma* fore-gut. The mid-gut which begins in the second thoracic segment and ends near the front margin of the seventh abdominal segment, is fully four times as long as the fore-gut. The rectum is broad and its anterior end projects forward in a blind circular pouch, enveloping to a slight extent the ileum, and is held by suspensory muscular strands to the body-wall. The rectal tube is very short.

Both the mandibular and maxillary glands are present though the former is very small and consists of a few cells only.

The cells composing both the glands have a similar form. They are pear-shaped and their nuclei are confined to what would be the base of the pear; the openings of their very conspicuous canalicules lie at the opposite end.

In the maxillary gland the cells remain more or less separate from one another before opening in the central canal. The duct of the gland is fairly long and opens near the maxillary base, (fig).

[redacted]

LEPIDOSTOMA HIRTUM Fab.

Habitat

The larvae live in dark brown wooden cases which are almost quadrangular in section and are found attached to the leaves and stems of water-weeds (especially Nausturtium) growing from the banks of the swiftest to moderately swift streams in Hampshire.

Food

The food is entirely vegetable, consisting mainly of small cuboid fragments, cut off from the higher plants such as, Nausturtium and Water Ranunculus. Diatoms and algae do not seem to be selected itmes of food, though quite a number of them get included in it. The commoner ones are Gomphonema, Navicula and Diatoma vulgare. Sand particles also seem to get mixed with the food. In one case alone was any animal (insect) food detected in the stomach.

Form of gut (fig 46)

The proventriculus is not distinctly marked out and its circular muscles are only feebly developed. The longitudinal folds, though well-defined in the pharynx, almost run out of existence further down, but reappear feebly in the proventriculus. The stomodeal valve is thin, descends for a short distance into the mid-gut and leaves a wide gap in the centre. The mid-gut, which is three times the length of the fore-gut, starts near the front margin of the third thoracic segment and ends near the hinder margin of the sixth abdominal segment. The histological elements of the mid-gut are not very different from those of Sericostoma. The epithelium is composed of digestive and regenerative cells, the latter forming compact nidi between groups of digestive cells. The striated border of the latter is quite distinct. The basement membrane and the muscularis are also well-developed. Some secretion vesicles were noticed in mid-gut sections; most of them were composed of granular protoplasm only but a few contained nuclei also. The latter, ofcourse, are not to be regarded as the result of secretion, and this has been explained before.

The malpighian tubules are disposed in three pairs, one ventral and two lateral, and open between the epithelium of mid-gut and that of the hind-gut. The epithelial cells of the pylorus are most well-developed and assume a columnar form; for the rest of the hind-gut, the epithelium is flat-celled. The arrangement of the muscularis, epithelium and intima is almost identical with that of Sericostoma and a description of it need not be repeated here.

The labial glands are about equal in length to the gut; the other head-glands were not studied.

The glands have a structure which is very similar to that of *Silo*. The intracellular canalicules, however, are much wider and distinctly show a much refracting tube going up them. This is apparently the same structure which Henseval (1897) calls "la paroi du canal", in *Anabolia*.

General features of feeding and digestive organs

Although, in theory, there exists a necessary relation between the form of an organ and the mode of its functioning, that is, between its morphology and physiology, this relation is not always easy to establish. Often, the relation is not very noticdable, but whenever there comes to light a sudden departure from a supposed norm in the one sphere, the logic of the inter-relationship compels one to seek for a correlated deviation in the other. As regards the feeding organs of Trichoptera, several theories have, in the past, been advanced to correlate the differences in feeding habits with modifications in the morphology of feeding organs.

When these larvae first attracted popular attention, it was supposed that they were all phytophagous, but later, when the carnivorous habits of some species were discovered (Siltala 1907), the differences in the sharpness and bluntness of their mandibular teeth assumed significance. Still later, the discovery of the presence or absence of setae on the inner sides of the mandibles suggested another possible adaptation. There are then two main factors which are involved in the problem; on the one hand, there is the food, which may be animal, diatomacous, or phanerogamous, or a mixture of these, offering a wide range of mechanical and chemical resistence to the feeding organs, and on the other is the whole complex of feeding organs formed by the first pair of legs, mandibles, the lower and upper lips, and the various divisions of the alimentary canal. In order to appreciate fully the relation between these two complementary factors the first step would be a proper understanding of the factors themselves, or at least of their significant features. Without attempting, therefore, to go into much detail, a general account of Trichopterous feeding and the alimentary system is given below.

Mouth-parts (figs 8, 37, 47)

The mouth-parts of larval Trichoptera have been described in detail by Rousseau (1921), Krafka (1923) and others. I will not, therefore, go into them exhaustively, but only touch upon their essential or significant features. The mouth-parts comprise:- (1) an upper lip or labrum, (2) a pair of jaws or mandibles and (3) a lower lower lip which is a compound structure, being composed of the maxillae and the labium.

Labrum

The labrum is a transversely elliptical sclerite with a pair of tormae on its clypeal side and a notch on its free edge; its upper surface is more or less covered with hair. It is capable of both up-and-down and forward-and - backward movement.

Mandibles

The mandibles generally have a hollow, pyrmidal body which may become triangular and blade-like in some forms (e.g. Oecetis and Philopotamus), and nearly solid in others (e.g. Silo). They are articulated to the head by their broad and triangular base at points which are, respectively dorsal and ventral. The articulation is of the acetabulum and condyle type, the dorsal articulation being formed by the acetabulum being on the mandible and the condyle on the margin of the head-capsule. In the ventral articulation the positions of the condyle and the acetabulum are reversed. The hinge thus being dicondylic, mandibular movement is possible in one plane only. The power required for the movement is provided by the strong abductor and adductor muscles which are inserted on the mandibles by the mediacy of two tendons.

In those forms which have blade-like mandibles, there is either a single long apical tooth only or it is followed by a few teeth along the single inner edge, e.g. Oecetis, Odontocerum and Philopotamus.

More usually, however, several pointed and sharp teeth lie along two parallel rows, dorsal and ventral in position, and also have the prominent apical tooth. There is a longitudinal depression between the two rows of teeth into which the apex of the opposite mandible works. A tuft of medial hair may be present near the most basal tooth or may be absent e.g. Phryganea and Hydropsyche. In some forms the teeth are not pointed and lie along the thin chisel-like apical edge. Such teeth often have broad molar surfaces and tufts of medial hair. The medial hair may be present on both mandibles or may have an unsymmetrical arrangement and be absent on one of them as shown by Siltala, e.g. Anabolia.

Finally, there are some mandibles which are without any teeth at all. Such are usually very weak and brittle, and break even by a mild working of the dissecting instruments upon them. They have often a hairy inner edge.

The lower lip

The lower lip is formed by the fusion of the basal regions of the maxillae and labium.

The maxilla is formed by a cardo and a stipes which are easily identified, and a large transverse piece beyond the latter, on which are carried an inner lobe and a palpus the homology and precise extent of which are not so certain. The palpus may be regarded as having four or five segments according as the tranverse piece is identified as the palpifer or the first segment of the palpus. The inner lobe may be a united galea and lacinia or lacinia only.

The labium is a median triangular piece, formed by the fused mentum and sub-mentum which is attached by its base to the cephalic margin ~~of the gula~~. Its apex represents the fused prementum glossae and paraglossae on which the labial glands open by a single aperture; the labial palpi are one or two segmented.

According to Das (1936), who has tried to interpret the morphology of the Trichopterous mouth-parts on the basis of their musculature, the mentum and sub-mentum are distinct, the latter corresponding to what has generally been called a gula. Palpifer, according to him, is not developed at all, which makes the number of palpal segments five. The inner lobe is made up of the lacinia only.

The length of the maxillary palp is variable.

The palp may be very long and strong as in Rhyacophila, Cecetis and Polycentropus, or it may be short and weak as in the Limnophilidae and Sericostomatidae. In the former instances it is denuded of hair, but in the latter (especially in Silo) the palp together with the rest of the under-lip may become very hairy. Again, the palp may or may not be capable of moving independently of the rest of the lower lip. The stipes and the labial apex are, however, quite incapable of moving on their own, and must move with the general body of the lower lip. The mentum may consist of a single piece or may be partially or completely divided, showing the primitive condition of the labium (e.g. Hydropsyche and Silo).

Thoracic legs

I can do no better than quote Orcutt (in Better 1934, P. 67) on this subject.

> "Each leg consists of five segments, or of six if one counts, as do Ulmer and some other authors, the additional segment formed between the coxa and the body...
> The first pair of legs is generally the stoutest and shortest. As indicated by Ulmer, this pair of legs is carried alongside of the head and is used not so much for locomotion, as for holding prey and for case-building. In most cases the legs are progressively longer ------ the adaptation of some of these should prove an interesting study".

Head-glands (figs 9-10, 48-50)

Typically one pair of glands is associated with each pair of the mouth-parts, and is named after the particular mouth appendage on which it opens. Their discharge ducts usually remain separate, but the ducts of the glands which open on the labuim (labial glands) always unite before opening on the tip of the labuim.

The labial glands.

The labial glands are a pair of very large glands lying loosely in the body cavity along side the gut. The structure of labial glands has been described in sufficient detail in Hydropsyche and since it is typical of labial glands of almost all Trichopterous larvae, the description need not be repeated here. In some forms, as for example Rhyacophila, Odontocerum and Sericostoma, there is a pair of small globular accessory glands connected with each labial gland where it passes into its duct.

Maxillary and Mandibular glands

The maxillary and mandibular glands are the head-glands proper, for not only their opening but their entire body is situated in the head. Their structure in some forms has been described in great detail by Lucas (1893), Henesval (1897) and Russ (1910), although the first to mention them was Patten (1884) who, according to all subsequent writers on the subject, made the mistake of calling a head-gland of Neophylax "mandibular" while in reality it was the maxillary gland. The glands are just mentioned by Ulmer (in Schulze, 1925), and (1936) the maxillary gland in the larva of Hydropsyche has been described by Glasgow quite recently (1936).

The mandibular glands

They are a pair of very small glands lying in the lateral side of the head capsule near and below the compound eyes. Their occurrence is not constant and they are absent in some forms e.g. Hydropsyche, Oecetis, and Phryganea. Each gland consists of a few cells only, say, from 5 or 6 to 30 or 40 in the different larvae. They take one of the two forms described below: (a) In most larvae the cells do not come together very closely and, in sections, give the appearance of being separate from one another. They are, however, united near the discharge orifice of the gland into which each cell pours its secretion. The cells composing the gland are rather big and each is pierced by a minute canalicule which is lined with intima. Their nuclei are also relatively large and usually lie towards the upper (away from the discharge orifice) end of the cell. In Lepidostoma a fine cuticular tube runs up the canalicule and resembles very much the structure that has been called by Henesval "laparoi du canal" in Anabolia. (b) In prognathous larvae the cells form a more compact and tabular body though they lie in the same situation. The intracellular canaliculi are present but are narrower and open into a central canal which runs through the entire long axis of the gland. The opening of the gland in both types lies near the outer articulation of the mandible on the head capsule.

The form of mandibular gland cells may be different in different species but it always closely resembles the cells of maxillary gland in the same species. In other words, the maxillary and mandibular glands in the same species are formed by similar cell elements.

The maxillary glands

The maxillary glands are paired, each lying close to this or the other side of the sagittal plane between the pharynx and the labial gland ducts, just in front of the suboesophageal ganglion. Each is tubular in form and invariably attains a bigger size than the mandibular gland of the same larva, but becomes especially big in forms, like Rhyacophila, Polycentropus, and Philopotamus probably due to the prognathous condition of the head in them. Their big size makes it easy to demonstrate them even in dissections.

Their structure is essentially the same everywhere. The long axis of the gland is provided by a canal (the central canal) of ectodermal origin (Patten 1884) which is lined by cuticular intima. Going round the centra canal on all sides are large gland cells each of which is pierced by a fine canalicule. These intracellular canalicules are also lined by intima and serve to pour the secretion of the glands cells into the central canal. Henseval has described (in Anabolia) striations in the protoplasm just outside of the canalicules which I could not see in my sections due most probably to their being too thick. Rhyacophila happily was an exception and showed the striations. The nucleus is a large body in all cases and lies near one end of the cell, most usually the end which is directed away from the central canal. There are minor difference, in the various maxillary glands in the number and shape of the components cells, width of the central canal and the granulation in protoplasm but all conform to the essential plan described above.

The secretion of the maxillary and, mandibular glands has been reported (Henseval 1897) to be an oily substance but which was never chemically tested for enzymes. The too minute quantities of available secretion have apparantly been an unsurpassable impediment.

Alimentary Canal

The larval alimentary canal is divided into three main regions, the fore-gut, the mid-gut and the hind-gut.

Fore-gut

The foregut is almost always a straight tube but of very unequal length in different species. It is primarily divided into four regions:- (1) the pharynx, (2) the crop, (3) the proventriculus and (4) the stomodeal valve. The crop, however, may sometimes be preceded by an oesophagus, and, in some forms, the proventriculus or the anterior part of the stomodeal valve may, develop a a gizzard-like organ near the posterior end of the fore-gut. The different regions enumerated above may not be strictly homologous in the different larvae. They are as pointed by Snodgrass (Principles of Insect Morphology, 1935, page 284) "Structural adaptations to functional differences".

Since the terminal part of labial gland is completely enclosed within the hypopharynx and prementum, the salivarium formsno part of the general pre-oral cavity. The mouth leads into the pharynx, which is strengthened by conspicuous circular muscles, and supplied with several dilator muscles, originating from the head capsule and the tentorium (fig. 37). The pharynx may be divided into anterior and posterior regions by the brain but the distinction is arbitrary, since the two parts are continuous and very similar in the composition of their walls and the strength of their longitudinal folds. The posterior pharynx also has inserted upon its dorsal surface vertical muscles originating from the head capsule. An oesophagus is present in some forms but absent in others. It is not so muscular as the pharynx, from which it is also distinguished by the loss of longitudinal folds in its walls. The pharynx is almost always separated from the region following it by a constriction in the gut-wall. The oesophagus passes imperceptibly into the dilated crop, which may or not be quite distinct from proventriculus. The proventriculus is generally a broad chamber in which the folds of the intima and the muscles are fairly strongly developed. In a few extreme instances it has weak walls, but in some cases at the other extreme it develops within it a sclerotized grinding and straining organ, as for instance the gizzard of Hydropsyche and the anterior part of the oesophageal valve of Polycentropus. The terminal portion of the fore-gut may either form a neck before joining the mid-gut or just merge with the latter without break in the curve of the gut-outline. Sometimes, in the former condition, the longitudinal muscles instead of travelling from the fore-gut to mid-gut all along the gut wall, separate from it and span the distance between the two divisions of the gut.

The stomodeal valve is essentially the hinder end of the cylindrical wall of the fore-gut which after descending into the mid-gut for a longer or shorter distance turns up again on the outside and comes to a final end near the anterior extermity of the mid-gut. It is thus a bilamellate structure which is lined by intima on both of its exposed surfaces. It may be a thickset and a powerful organ guarding a narrow aperture and capable of regulating the passage of food from the fore - to the mid-gut, or it m may be just a fringe around a comparatively huge aperture and incapable of exerting any appreciable influence upon the passage of food. In some forms it becomes complicated by the addition to it of a high cuticularized anterior part which lies in the fore-gut lumen, or by gaining an extraordinary length of the original (posterior) part. In some zones of the stomodeal valve the epithelial cells become drawn out and columnar - a rather unusual development in the epithelial cells of the fore-gut.

An intrestitial ring of cells is present in all trichopterous larvae. It is only a few cells wide and marks the union of the fore-gut with the mid-gut. It is regarded as the final part of the fore-gut (Glasgow, 1936) although its intimal lining was not always evident to me. The cell composing it are columnar and well-differentiated but quite different in form from the cells of the mid-gut epithelium from which they are also separated by a physical gap.

The fore-gut wall is composed of the following three layers:- (1) the muscularis which is the outermost layer, (2) the ~~xix~~ epithelium and, (3) the intima which lines the lumen of the fore-gut.

The muscularis of the foregut is double, consisting of a circular and a longitudinal layer. The arrangement of these two layers is by no means uniform throughout the foregut for although the longitudinal muscles generally lie inside the circular muscles, in some regions (for instance - the proventriculus of some forms) the longitudinals lie outside the circulars. Again the same layer has not the same strength in the different ~~xxg~~ regions of the fore-gut. The circular muscles are almost always more strongly developed in the pharyngeal and proventricular regions than in other places; similarly the longitudinal muscles have a tendency to gather beneath the longitudinal folds of the fore-gut. In addition to those muscles which enter the composition of the fore-gut wall, there are suspensory and dilator muscles which run between the pharynx and the skeleton of the head.

The epithelium of the fore-gut is flat throughout with indistinct cell-boundaries. The only exceptions to this rule are provided by (1) certain areas of the stomodeal valve where the epithelial cells come out tall and distinct and (2) the intrestitial ring of cells which follows the valve.

The intima of the fore-gut is continuous with the cuticular covering of the body at the mouth. It has very unequal development in differnt sppecies and in different regions of the fore-gut in the same species. It is usually much better developed in the pharynx and proventriculus than in the crop. Often it is thrown into longitudinal folds that are weak, impermanent sbructures and open out flat when the fore-gut is distended, but in other instances they are tall and powerful, or even sclerotized and spinous so as to form a definite organ of the fore-gut (e.g. the gizzard of Hydropsyche). The degree of development of the longitudinal folds and that of the muscularis seem to be directly related, for wherever the folds grow in size, the muscularis also becomes powerful, and wherever they dwindle in size the muscularis also becomes weak.

Mid-gut

The size of mid-gut varies greatly in different species. In some, it is over three times as long as the fore-gut, while in others it is less than half the length of the fore-gut.

The mid-gut is a straight tube of uniform calibre not differentiated into any specialized regions (such as hepatic caeca) for the manufacture of digestive secretions. Its walls are composed of a muscularis and an epithelium which lines the mid-gut cavity and rests upon a basement membrane.

The muscularis is double, consisting of an outer layer of longitudinal muscle fibres and an inner layer of circular fibres.

The basement membrane is quite thick in most larvae but is especially so in the Limnophilidae. Only in a few larvae is it very thin and difficult to see. It has a peculiar development in some regions of the mid-guts of *Rhyacophila* and *Philopotamus* where it cannot properly be called a membrane. It becomes very broad (as broad as the epithelial layer in sections) in both instances, but in *Rhyacophila* in addition it develops large clear spaces within it and appears to possess nuclei. In *Philopotamus* it shows, in places, a longitudinal split which contains nuclei. All this goes against the accepted definition of a basement membrane, the"basement membrane" of *Rhyacophila* and *Philopotamus* could, therefore, perhaps, be regarded as a connective tissue layer supporting the mid-gut wall in these forms (Snodgrass, 1935, Principles of Insect Morphology, page 366).

The epithelium of the mid-gut consists most usually of two kinds of cells, viz., the digestive cells and the regenerative cells, but in some forms (e.g. *Philopotamus* and *Cecetis*) it includes a third kind - the goblet cells - among its constituents.

The digestive cells are columnar in form and lie above the basement membrane. Their walls may or may not be distinct. There is usually one nucleus in each cell but in a few cases at least the cells appear to be multinucleate. Their mesal ends show a striated border in most cases. The height of a cell varies greatly in relation to its breadth. Usually a cell is 6 to 8 times as high as broad but in some normal instances (*Rhyacophila*) it may become much higher (say, 15 times as high as broad), while in others it is quite short, almost square in sections (*Agapetus*)

The regenerative cells usually form compact groups or nidi between the bases of the digestive cells and lie along the basement membrane. But in some cases such as *Hydropsyche* and *Agapetus*, they occur singally. In *Hydropsyche* they are mere nuclei, while in the other they form proper cells.

The goblet cells occour singly among the digestive cells in some forms only, e.g. Philopotamus and some Leptocerids. They are large cells, the broad upper side of which is transparent and cup-like in form. The basal side is long and narrow, and contains the nucleus. They are large cells, the broad upper side of which is ~~lxmgxamd~~ ~~maxxmax~~ transparent and cup-like in form. The basal side is long and narrow, and contains the nucleus. They are supposed to secrete mucilage for the protection of the digestive cells.

Peritrophic membrane

The peritrophic membrane was noticeable in many larvae but it was particularly clear in the Sericostomidae and the Limnophilidae. According to some authors the identification of the peritrophic membrane rests upon its origi~~mm~~ from the special ring of cells in which the fore-gut terminates and which have come to lie within the mid-gut walls. If that was the only proof of its identity then the membrane which I have described as enveloping the food-mass in the various mid-guts can be regarded as peritrophic only with some doubt, for I could never trace it to the front end of the mid-gut. But according to more recent accounts the peritrophic membrane can also be the product of the general surface of the vetricular epithelium. This latter view is more in conformity with facts as I have been able to see them in microtomic sections. The membrane does not seem to be constantly present even in the same species of larva; very probably it is shed from time to time and goes down the way of food.

Digestive Secretion

It is supposed that the digestive juices which are produced by the vetricular epithelium pass through the striated border of the cells in two ways mainly:- firstly, by oozing out very gradually, in which case they will leave no physical indications of the process in histological preparations (this type of secretion has been called merocrine); secondly, by producing buds from the mesal surface into which digestive secretions of the cell pour out - later, these buds get constricted off from the ~~present~~ parent cells and float away as vesicles into the mid-gut cavity. When these vesicles ultimately break, they pour their contents over the food which is to be digested, (this represents the holocrine type of secretion). The secretion vesicles are most usually without a striated periphery but in Agapetus it is present.

The secretion vesicles can be quite numerous in a single microtomic section. Among them one may sometimes spot a vesicle which is nucleated. This, obviously could not represent a process of secretion, but would result from the physical separation of an integral part of a digestive cell. It is generally believed that such vesicles are the physical indication of a process of cell degeneration and not secretion. Nevertheless, I have included them with the proper secretion vesicles in order to avoid lengthy descriptions. The data referring to digestive secretion as seen in histological preparations got collected just by the way, in the attempt to study the histology of the gut. It should not, therefore, be expected that the data will be all-comprehensive. But it is, at any rate, hoped that whatever conclusions have been drawn are valid within the limits that have been defined more or less implicitly. A study of the process of absorption by the epithelial cells was not even attempted.

Hind-Gut

The hind-gut is held to the body-wall by several suspensory muscles, the most constant of which is a pair inserted between the rectal sac and the rectal tube. The arrangement of the proctodeal muscle-layers is more irregular than in the other parts of the gut, but, speaking generally, the longitudinal layer is outside the circular. The hind-gut is lined throughout by a cuticular intima and its two main divisions are the anterior and posterior intestines. The former is subdivided into pylorus, ileum and colon, and the latter into a rectal sac, and a rectal tube.

The malpighian Tubules

The six malpighian tubules arise in a circle at the junction of the hind - and the mid-gut. They be free or united, and the mode of their insertion on the gut is variable. When free, they may spring from the gut-wall singally, in twos and threes; or some singly and others in a group. After travelling for some distance from their base, they often acquire reddish brown colour and exhibit along their whole sinuous course deeply pigmented and clearer patches alternating with one another. In most species the dorsal pair travels forward and the rest go backwards, and spread round the hind-gut. Most authors regard them as outgrowths of the hind-gut wall, but that could not be universally true even in the Trichoptera. In some Limnophilids that I have studied, their opening is surrounded on all sides by the mid-gut cells. In most cases, however, only the anterior part of their opening is bounded by the mid-gut cells, the posterior part being guarded by cells of the hind-gut. The wall of a tubule is only one cell thick and is lined by a striated border facing the lumen of the tubule. The striated border is very similar to the striated border of the mid-gut cells in shape, but the two have not been found continuous with each other.

The pyloric region is a short annular area into which the malpighian tubules open almost invariably. Its epithelial cells are not quite so flat as in the rest of the hind-gut but occasionally the cells of its most anterior part grow tall and columnar and may constitute what Glasgow (1936) has called the posterior intrestial ring.

The ileum is a broad pear-shaped compartment of the hind-gut which narrows down sharply in the posterior direction. Its epithelial cells are very flat and the longitudinal folds in its walls have only a weak development. A powerful sphincter of circular muscle fibres goes round the posterior end of the ileum and the anterior part of the colon.

The colon is a narrow tube with muscular walls, flat epithelium, and well-developed longitudinal folds which almost fill its cavity. The epithelial cells have large nuclei but their walls are not distinct.

The rectal sac is generally a broad and sac-like region with loose wall on which the folds do not keep any set direction. The walls of the colon or their folds sometimes descend into the rectal sac and constitute a rectal valve (e.g. Limnophilidae). In some forms which have a relatively large rectal sac, the longitudinal proctodeal muscles get separated from the gut-wall and span the arc between the ileum and the rectal sac. The walls of the sac have the same histological composition as the colon. In some forms the rectum is not much broader than the regions preceding or following it.

The rectal tube is quite short and marks the end of the gut. Its walls are composed of elements similar to the rectal sac, but it is without any folds. In most thysanu-reform larvae hollow and finger-like gills grow out into the lumen of the gut from the place where the rectal sac joins the rectal tube. The structure of the rectal gills is the same as the rectum-wall. The gills can be extruded with the evagination of the rectal tube and drawn in, probably, by the action of muscle bands which run between the body-wall and the rectum in the last abdominal segment.

Nature of secretion of the stomach and labial glands

Wigglesworth (1934, Insect Physiology, page 51) states that "Digestive enzymes of insects are such as might be predicted from the nature of their food". Accordingly eight species, including amongst them carnivorous, omnivorous and phytophagous forms were selected for a study of their digestive enzymes to see if these showed any significant differences. Labial glands, fore-guts and mid-guts were tested separately for such enzymes as amylase, invertase, trypsin, pepsin, erepsin, and lipase. The results are given in a more complete form in the table II .

In view of the fact that living British caddis larvae could not be obtained in India, the analysis of the secretion of their mandibular and maxillary glands was not even attempted.

Classification of the Foods

The food of Trichopterous larvae is very diverse. It can be divided into several classes according to the quality of mechanical resistence it would offer to the mouth-parts in catching, tearing, holding, or ingesting it, or dealing with it in any other manner. The classification attempted here, it will be seen, runs more or less closely parallel to a more 'natural' ordering.

Class 1 Food material consisting generally of minute particles, not needing to be torn from a parental body. This includes diatoms, fragments of algae, debris matter, and also sand.

Class II Fragments of plant tissue torn from a parental body. They may be fresh or dead and rotten. In the latter case they often have a host of epiphytic diatoms and algae upon them.

Class III Food material capable of moving away and escaping from the larval organs of ingestion. This includes small-sized animals like insect larvae and pupae, minute crustacea, acarina and the gastropod Limnaea.

Class IV A mixture of classes II and III, and in rare instances of classes 1 and III.

DISCUSSION

(a) General

Slack (1936), investigating the food of caddis larvae comes to the conclusion that they are all more or less omnivorous; that, of the several "nominally" phytophagus types, only a few are "purely" phytophagus. It is somewhat ironical that although I have found even these "purely" phytophagus types to be omnivorous, in his sense, I do not agree with his conclusions. The distinction between carnivorism and vegetarianism in the Trichopterous larvae is a real one and should not be merged into a diffuse omnivorism by quoting isolated instances of phytophagus larvae eating animal diet or vice-versa. Not that there exist any rigid boundaries between the two modes of life. On the contrary, I am inclined to think that it is quite normal for a vegetarian to attack and devour small prey occasionally, and for a carnivore occasionally to eat plant tissues. What defines carnivorism is not an absolute restraint from vegetable diet, but an overwhelming preponderance of animal over plant food in stomachs, when both kinds are available in the environment. It is not so much the exclusion of a certain kind of food as rather a positive. preference in the other direction which determines carnivorism or vegetarianism. It would be confusing, to say the least, if, for instance, Phryganea and Triaenodes were both labelled omnivorous because the latter also takes very small quantities of animal food. Quantitative differences do matter and it is important that they should, in some way, be implied in the definitions. There is, besides, the danger of basing conclusions on too scanty data, or data relating to a restricted locality, or only one season. This I say with the full knowledge that my data also are meagre, too meagre perhaps, in several places. Nevertheless, it is very reasonable to call forms like Stenophylax phytophagus even if they do occasionally feed upon animal material. This is valid because the stomach of Stenophylax shows, in all seasons and environments, a preponderance of vegetable food over the animal. In the same way 'omnivorous' is that type which most often ingests nearly equal amounts of both kinds of food or if there is excess of one kind, in some individuals or seasons, it is approximately balanced by an opposite excess in others. Similarly for the 'carnivorous' types.

Here I would like to make another rather important point concerning the volume of different foods in the gut. When judging their proportions, it should be remembered, that equal volumes of arthropod and phanerogam material would indicate that the amount of the former was much greater to start with. The soft parts of an arthropod dissolve out and the remaining skeletal pieces get compressed into a much smaller volume as they pass along the gut. This does not seem to happen with the cellulose framework of phanerogamous tissues.

(b) The food and the feeding organs

The mandibles show a great variety of form which is often clearly related to the nature of food. In the forms that take in food which is made up of small particles like diatoms and algal fragments, or is mixed with abundant sand grains and debris, (ffod of class I), in short, the forms which utilise food that does not require to be torn from a parental body or sub-divided any further, the mandibles are generally weak, their teeth generally blunt or even absent and /or there are developed prominent combs of setae on their inner sides. The maxillary palpi are very short and stout and/or comparatively very hairy and, apparently incapable of any independent movement. The mouth-parts are adopted more for sifting a generally granular matter and pushing it into the mouth than for anything else. Users of food of this kind include *Silo*, *Agapetus*, *Glossosoma*, *Hydroptila*, *Psychomyia*, *Tinodes*, and, perhaps, *Philopotamus*. The first three agree in having mandibles without teething and extremely short maxillary palpi. Silo has, in addition, prominent hairy fringes to the mandibles, Hydroptila and Psychomyia have just one or two blunt teeth and a very hairy under lip. Tinodes seems exceptional and positive knowledge regarding the food of Philopotamus is so meagre that nothing could really be said about the function of its mouthparts. They closely resemble those of the carnivorous Rhyacophila but it should be seen that their maxillary palpi are relatively more hairy and though quite as long, are definitely weaker.

In the forms that live mainly by tearing morsels from phanerogamous weeds, the mandibles are chisel-shaped, with a few blunt teeth confined to the apex. Below the teeth, the mandible is generally scooped out so that the apex becomes wedge-shaped. Beneath this is the more solid part, the inner side of which acts as a molar surface. A short tuft of hair is usually present on the mesal side of the mandibles as has been pointed out by Siltala (1907). The generally hairy maxillary palpi are short but not stout like those of the first group. A few that were seen in action, appeared capable only of a trembling movement on their own, otherwise they moved with the rest of the underlip. In Sericostoma it was seen that the portion of food intended to be bitten off is held tightly between the mandibles, the head is then thrown back with a powerful jerk and the portion is bitten off. To this group belong Limonophilidae and Sericostomatiae generally.

In the highly carnivorous forms like the Poly-Centropodidae, Rhyacophila and Oecetis, the mandibles are comparatively slender, flat, and more or less blade-like, and the mandibular teeth are very sharp and disposed along the inner edge. The sharpest of the series is usually a long apical one which appears to be better adapted for holding the prey than the teeth which follow it. These latter are usually disposed in two ill-defined rows with a cavity between them and seem to be used rather for cutting and tearing. The thinness of inner edge hardly allows for any molar surface. The maxillae are long, almost without hair and quite capable of independent movement. In a few instances I have seen them actually close over the prey and help to hold it.

Forms like Phrayganea, Hydropsyche, Molanna, Odontocerum and some Leptocerids have an intermediate development as regards the form of mandibles, sharpness of their teeth, the length and mobility of maxillae and the general hairiness of the underlip. The mandibular teeth are usually disposed in two rows for cutting action but a molar surface is also present. The apical tooth may attain extraordinary prominence, as for example, in Odontocerum.

Of course, it has always been known that the

Trichopterous mandibles may be sharp or blunt, according to the nature of larval food. But what was not known or only half known, is the fact that there is, more or less, a complete gradation of forms from the sharpest to the bluntest mandibles which goes nearly parallel with a corresponding gradation of food.s. The function of profusely hairy mandibles or lower lip has not been pointed out except in a very recent paper by Slack (1936). Similarly it was not known what purpose was precisely served by the long maxillae in the carnivorous Trichoptera. Possibly, there is also some difference in the form of teeth between those species which more usually swallow their prey whole and those which cut it up into bits before ingesting. The mandibles of *Rhyacophila*, *Oecetis*, and *Odontocerum* bear only a single long apical tooth, which probably can do nothing more than just catch and hold the prey. It would be interesting to know whether they swalloed their prey whole oftener than do other carnivorous or partly carnivorous forms. I have not got enough data to say anything definite about it, but some Trichoptera (e.g. *Rhyacophila*) do appear to swallow their prey whole very often.

Siltala (1907) has advanced a theory bearing on the relation of food and mandibles. He considers that:-

(a) the larvae with medial brushes of setae on both mandibles are phytophagous,

(b) those with brushes only on the left mandible are either:-

(i) omnivorous, or
(ii) phytophagus, or
(iii) carnivorous and

(c) those with no brushes on either are:-

(i) carnivorous, or
(ii) omnivorous.

But for the single, rather doubtful, instance of <u>Philopotamus</u>, I have come across no exceptions to this rule. However, I have this criticism to offer that when the presence of a certain morphological feature is equally associated with (a) carnivorous (b) omnivorous and (c) phytophagous habits in such a large proportion as six out of twelve families, and with (a) carnivorous and (b) omnivorous habits in the case of another four, its use as an indicator of habits is limited. But the theory has its merits. It holds true in those instances where certain members have deviated from the normal food of their family and have also exhibited a corresponding eccentricity in their mandibular structure. It more than justifies itself there.

Siltala's theory has unjustly been criticised by Slack (1936), mainly, it seems to me, because he has failed to understand it properly. I quote Slack:-

"Silfvenius advances the theory that larvae having brushes on both mandibles are primarily phytophagous, those possessing one on the left mandible only are omnivorous and those without brushes carnivorous". Now that is not exactly what Siltala said; his actual view are quoted above. The root of Slack's misinterpretation seems to be that he does not want to distinguish between an omnivorous group and a group of forms which are severally carnivorous, phytophagous or omnivorous. And what is more, for him, even the slightest deviation from a uniformly pure diet makes a larva omnivorous. I have discussed the matter more fully under the heading of food.

Weisenburg-Lund's theory (1913) which seeks to correlate the more or the less anterior position of eyes with carnivorism or vegetarianism respectively, has been ably discussed by Slack (1936) and I have hardly anything of value to add to his criticism, except that _Philopotamus_ and _Psychomyia_, which are non-carnivorous forms, have an advanced anterior position of eyes on the head capsules and _Odontocerum_ and _Molanna_ which are fairly carnivorous have them as far backward as the Limnophilid _Halesus_. I would venture to suggest here that the position of eyes is perhaps more directly connected with the hypognathous or prognathous condition of the head than with food.

Martynov (1930), in his study of the Trichoptera of China and Eastern Tibet, holds the view that the Annulipalpia are "mainly carnivorous" and that the Integripalpia are "phytophagous by preference". He does not give the data on which he has based this conclusion. But I may point out that his view cannot be held true in the case of British forms, at least. The Annulipalpia in England include the Rhyacophilidae, Polycentropdidae, Hydropsychidae, Philoptamidae, Psychomyidae and the Hydroptilidae. Of these six families the last three are almost purly non-carnivorous. Odontoceridae and Molannidae which he puts under Integripalpia and "Sophytophagous by preference" show a very marked preference for animal food.

<u>The first thoracic legs</u>

Although the study of adaptations of the first legs promised to be interesting, I have not studied them except in a few instances, and even then not in great detail. In <u>Brachycentrus nigrisoma</u>, Murphy (1919) has made a detailed study of the larval food and the way in which the legs help to catch prey. She thinks that the rows of spines on their femora are an adaptation for carnivorous feeding. In <u>Molanna</u> and <u>Odontocerum</u> which are carnivorous in about an equal degree, I find that the powerful spines on the tibiae of the one are similar to those of the other, in the case of the first two legs.

In the non-carnivorous and debris-eating <u>Philopotamus</u>, the legs are without many spines and the claws almost insignificant; in Psychomyia there is a still further degeneration, perhaps, on account of the additional restriction to movement of legs, entailed by life in narrow gallaries. The immophilids, who have to tear food from phanerogamus, have strong legs, but are not provided with as sharp claws as in Phryganca, for instance. Thus, the length and sharpmess of claws can, perhaps, be generally related to the way of obtaining food, but it should be noted that in Rhyacophila, which highly carnivorous, the claws are not particularly long or sharp, and in some phytophagous Leptocerids they are markedly so. The truth is that the legs are put to a greater variety of use and have to be exposed to a more diverse environment than are the mouth-parts, and it may not be very easy to study the effect of the isolated factor of feeding upon them.

(c) The food and digestive organs

Branch (1922) states that "The lack of convolutions as are normal in the alimentary canals of insects which are herbivorous, is unusual - There are a few semi-carnivorous species but even here there is no variation from the above condition". Though she is right about the fact of the alimentary canal being straight in almost all Trichpterous larvae she is far from being so in her implication that the gut of the carnivorous types does not vary in gross characters from that of the herbivorous ones. They differ in many respects but I shall discuss the ratio which the length of the main divisions of gut bear to each other, first.

Friedrich Kruger (1926), shows that in certain Syrphid larvae the ratio between the length of mid-gut and hind-gut has a bearing on the type of food the larvae consume. I too find a similar correlation food and the ratio of mid-gut to fore-gut. More correctly, it is the length of mid-gut relative to the entire alimentary canal which should be our index but I have compared it constantly with the fore-gut because the length of the latter is also significant and I want to bring out certain other relations between the fore - and the mid-guts as well (Table I).

It appears that the mid-gut is relatively the longest in those forms which generally take in such food as would tax the digestive capacity of the larvae to the uttermost. For istance, in Silo, Glyphotaelins, Philopotamus, Agapetus and Psychomyia the mid-gut is nearly three to four times as long as the fore-gut. These genera are mostly diatom-feeders and Glyphotaelius, it should be remembered, subsists chiefly upon decaying vegetable matter besides a relatively large amount of diatoms. Sericostomatinae, Limonophilidae, Rhyacophila, Leptocerus and Hydroptila have a mid-gut from nearly 3 to nearly 2 times as long as the fore-gut, and they are in the main a phanerogam-eating class. It will have been noticed that it includes two very marked exceptions, viz. Rhyacophila and Hydroptila. These two forms placed here so near together should really occupy the two opposite ends of the list, one being the most purely carnivorous form I know and the other being the diatom feeder in the main. The eccentricity of Rhyacophila may partly be explained being its being the most primitive member of the order. I remain unable to account for the other exception. Leptocerus is a case which should, and does, occur a little on this side of the limit of the next, omnivorous, group which includes Brachycentrus, Hydropsyche, Odontrocerum, Molanna and Phyganea. In these latter genera the mid-gut from being slightly longer than the fore-gut, becomes reduced to three quarters as lond. Triaenodes forms the upper limit of this group, though it should have been somewhere near the lower limit of the previous section. In the last group, which includes Oecetis, Polycentro-pus, Plectrocnemia, Cyrnus, and Holocentropus, the mid-gut is reduced still further, becoming from 6/10 to 3/10 of the fore-gut. The larvae included herein are the carnivores par excellence.

Although there are indications that some food is digested in the fore-gut yet the mid-gut must be regarded as the main site where the digestive processes takes place. And since digestion is primarily the function of the epithelial cells, it is reasonable to correlate the differences of their form and differences of the type of food which usually come in contact with them. Accordingly the form of ventricular epithelium in about a dozen larvae, including *Rhyacophila* *Polycentropus* and *Oecetis* among the carnivores; *Odontrocerum*, *Phryganea* *Leptocerus*, and *Hydropsyche* among the omnivorous forms; *Sericostoma*, *Sila*, *Lepidostoma*, *Anabolia* and an unidentified Limnophilid among the phanerogam eaters; and *Agapetus* and *Silo* among the diatom feeders, was examined. *Philopotamus* was also studied though nothing is known about the kind of food it eats. It is unfortunate that specimens of *Molanna*, *Brăchycentrus* and *Odontocerum* (English species of course) could not be had in India inspite of efforts.

The height of a digestive epithelial cell relative to its breadth varies greatly in different larvae and appears to be roughly related to the type of food. It is very short in diatom eaters but increases progressively in phanerogam feeders and the omnivorous and carnivorous groups. In *Agapetus* the height of the functional epithelial cells is so short that they appear squarish in sections while in *Silo* they may be only two to three times as high as broad. In those Limnophilids and Sericostomatids (phanerogam feeders mainly) which were studied, the height of cells was generally about 5 or 6 times their breadth. In the Omnivorous Hydropsyche it rises to nearly 8 times and in Phryganea and Odontocerum even higher than that. The climax is marked by the digestive cells of the carnivorous Polycentropus, ~~and~~ Oecetis and Rhyacophila where they may be 15 times or more as high as broad. It is true that cell walls in Polycentropus and Oecetis are very indistinct and the ratio of height to breadth difficult to fix, but the thickness of ~~different~~ Some cells is visible near the nidi and the point to which the cellular processes reach in the lumen affords a rough measure of their height. The height of cells in the carnivores was sometimes perhaps accentuated due to a phase of secretion being on but even in series of sections which showed that the phase was in abeyance their height remained relatively greater than in the other types. The only serious objection which can be brought against this correlation being generally ~~twice~~ true is that the data are not extensive enough. Nevertheless, the relation holds good in all the studied instances and there is nothing to indicate that it would not stand if the study were extended.

Another difference in the form of digestive cells is that their outline is much more clearly defined in the phytophagous forms than in the carnivorous ones. The omnivorous forms have either intermediate development or lean towards one side or the other.

The regenerative cells are grouped into compact nidi in most cases, but in rare instances (e.g. *Hydropsyche*) they remain separate and lie scattered along the basement membrane. The formation of nidi or its lack does not seem to be related to the type of food. *Hydropsyche*, *Silo*, *Philopotamus* and *Agapetus* may be said to lack nidi (the last 3 possess them in a very rudimentary form), yet their food shows enormous differences of quality.

The relative size and frequency of nidi, however, seems more clearly related to certain types of food. It appears that the larvae with the smallest nidi are diatom feeders. In the diatom eating *Agapetus* and *Silo* for instance, the nidi are very small, only rarely becoming two or three-celled. Most Sericostomatids and all Limnophilids have relatively bigger and broad-based nidi, 4 or 5, or even more cells entering into the composition of a nidus. In the omnivorous groups (*Hydropsyche* excepted) the nidi are bigger and/or more numerous. Cases of *Phryganea* and *Odontocerum* almost border on the next group which includes the highly carnivorous forms. In the carnivorous *Polycentropus*, *Holocentropus* and Oecetus the nidi are most numerous, tallish and quite large sized too. They are so numerous, indeed, that in these forms there is hardly any space left between them for the digestive cells. The case of *Rhyacophila* is somewhat irregular and approximates the omnivorous group more closely.

The pace of degeneration or secretion processes is another character which differs widely in the larvae of different feeding habits. Everything indicates that these processes are very intense in the carnivores but slow down as one passes on to the omnivorous and phytophagus larvae. In _Oecetis_, _Holocentropus_, and _Polycentropus_ the inner margine of digestive cells is so full of vacuoles that it appears like froth on a substratum of nidi; striated border disappears and long, irregular and tongue-like processes of the cell protoplasm project into lumen of mid-gut and nearly meet those from the opposite side; and secretion vesicles grow very abudant and include among themselves large (multinucleate) and small masses which may contain nuclei. Also, the tall imbricate nidi suggest as if the regenerative cells were transforming into the functional cells very rapidly in order to keep pace with the katabolic processes. In short, everything points to the digestive or katabolic processes being very rapid. This conclusion is strengthened by the fact that the stomach of carnivores is very often found empty on dissecting; probably the food gets through it very rapidly.

In omnivorous and phytophagous groups the pace of digestive and/or degenerative processes must be slower than in the carnivores as is evidenced by the smaller number of secretion vesicles and the symmetrical form of digestive cells in them. It might perhaps be argued that the greater speed of these processes in the carnivores was the result of the much smaller size of their stomachs and not of the kind of food they ate, but then it would be remembered that the size of the stomach is directly related to the kind of food, and hence it would be quite right to affirm that the nature of food affects the pace of digestive processes.

Secretion vesicles containing densely granular matter were seen in most of the larvae examined. The presence of such vesicles indicates what is generally called holocrine type of secretion. Their absence in a series of sections, however, is no proof that they are not produced by the sectioned species, for the production of vesicles is known to be a periodic activity, appearing and disappearing with time. When a particular gut was fixed secretion may have been in abeyance. It seems very probable therefore that the holocrine type of secretion is common to all Trichopterous larvae and goes on side by side with the merocrine type of secretion.

No definite relation between the presence or absence of peritrophic membrane and the kind of food was discoverable. The membrane is very delicate and failure to see it any instance may be due to the faulty technique. Still it was found more constantly in the Sericostomatidae and the Limnophilidae which feed mainly on the phanerogamous tissues than in other families.

Perhaps, due to the short length of stomodaeum in them the hard (vascular tissue) fragments of food are not adequately softened before passing into the mid-gut, the delicate epithelium of which would need some protection against their rough edges and corners. Hence in them the peritro- is developed somewhat strongly. The membrane phic membrane was never seen in the highly carnivorous Polycentropodidae, *Rhyacophila* or *Oecetis*. Its absence in *Oecetis*, in common with *Leptocerus* and *Philopotamus* may ~~may~~ perhaps be explained by the compensatory action of goblet cells which are found in the mid-guts of these forms. They are said to secrete mucilage which protects the epithelial cells from injury by mechanical impact.

"The primary function of stomodaeum appears to be mechanical." Snodgrass, (Principles of Insect Morphology 1935). My own impression from the dissections of fore-guts is also more or less the same. It would seem that certain kk kinds of food need greater manipulation than others preparatory to passing into the mid-gut. The structure of mid-gut is delicate and it can best effect a chemical reduction of food if that has previously undergone some physical reduction. Diatoms and broken algal filaments are naturally small enough; the vegetable morsels, I presume are always cut to the optimum size at their very source; it is the mobile, struggling prey threatening to break free till the very last moment, which would often necessitate its being swallowed whole or in excessively large pieces. The stomodeum, therefore, acquires a greater length, and a still greater complexity of its intimal folds in the carnivores to compensate for hurried swallowing and the consequent lack of that thoroughness of molar mastication which is so characteristic of the phytophagous group. Hence, it is in the predacious types that the fore-gut develops the most complicated internal structure in Trichoptera. Every feature in it seems adapted to exert physical pressure on the food and to withhold it for as long as possible. Its great length, the superior development of its circular muscles, the complexity and strength of its folds, the frequent presence of a gizzard, or the anterior part of the stomodeal valve functioning like a gizzard, the thickset form of the stomodeal valve and the narrow aperture it leaves in the centre, all point towards this. It is true that here and there a feature may be incompletely developed, but on the whole, all purely carnivorous types and carnivores of a high degree, tend to realize them to a very great extent.

Take for instance the development of sclerotized apparatus for grinding food situated just above the aperture between the fore-gut and the mid-gut. This may be provided by a true gizzard, or by the sclerotization of the anterior part of the stomodeal valve, or just by a thickening of the proventricular folds. The instance of a true gizzard is met in Hydropsyche, that of the sclerotization of the anterior part of the stomodeal valve in the Polycentropodidae, and while no specific grinding organ is present in Molanna, Odontocerum, and Oecetis, yet in them the longitudinal folds in the region where the gizzard should have been, are developed so strongly and into such definite plate-like structures that they would appear to do almost all that a gizzard could do. Brachycentrus makes up for the deficiency of a gizzard by evolving the complicated structure at the posterior end of its fore-gut that I have already mentioned and which probably is the homologue of the anterior part of the stomodeal valve of Hydropsyche. Thus, the stomodeaum which has to deal with animal food, produces near its posterior extremity, in one form or another, some mechanism for breaking ~~up~~ down food and/or retarding its passage.

In all carnivores the stomodeal valve is very strong and, as shown by Noyes (1914) and some of my own observations on Phyrganea, helps to break down the food still further. The aperture in its centre is always comparatively narrow and would allow only the more finely divided food to get through.

The significance of an extremely long stomodeal valve in larvae of such diverse feeding habits as Hydropsyche and Philopotamus is not quite clear. In Hydropsyche it may, perhaps, be considered to fall in the general scheme of a mechanism which would retard the passage of food from fore-gut to mid-gut, but in Philoptomus its presence seems unaccountable. The glandular structure round the fore-gut of Philopotamus presents another very unusual feature.

The relation of the length of fore-gut ~~with~~ to feeding habits comes out very clearly when the latter differ from those of nearly related species. In Oecetis, which is highly predacious, ~~it~~ fore-gut is so long that it has to be convoluted in order to accomodate itself to the shortness of the Leptoceran body. Again, in the omnivorous Brachycentrus, the fore-gut length is much greater than in the other sericostomatids which are, all of them almost completely vegetarian. Murphy (1919) has recorded some very interesting observations on the feeding of this larva, apparantly without realizing their full significance. She mentions that the larva feeds in its early stages on diatoms and algae and later on changes over to an animal diet. She also states that the length of mid-gut becomes comparatively short in the older larvae. Yet she does not seem to realize that the two changes are mutually related.

Rhyacophila is exceptional throughout, and I can do nothing more to explain its eccentricity than to point out again its extreme primitiveness.

The fore-gut of vegetarian larvae is generally short, without well marked sub-divisions or strong folds of the intima. A weakly developed and fringe-like stomodeal valve which descends only for a very short distance into the mid-gut, leaves the wide aperture between the fore-and mid-gut almost wholly unprotected. Everything here points to the stomodaeum being only indirectly important, being, as a matter of fact, merely an inlet to the stomach. This type is well represented in the Limnophilidae and Sericostomatidae in general.

Between these two extremes are a number of intermediate forms like Phryganea, Leptocerus and Odontocerum etc., in which either all these features obtain a medium development or else they show a few characters from each of the extreme groups. It must, however, be remembered that nowhere in the series is there a sharp boundary where one group finishes and the other begins. Like the range of feeding habits they merge imperceptibly into each other.

The malpighian tubules originate in diverse ways, singly, with compound stems, or in groups. None of these patterns seems to be related with the feeding habits.

The ratio of hind-gut to fore-gut is commonly greatest in the phytophagous larvae, it decreases generally through the omnivorous group and comes to a minimum in the carnivorous Polycentropodidae. The divisions of hind-gut are somewhat better marked in the phanerogam-feeders, and in the Limnophilidae the rectal valve assumes relatively enormous proportions.

The length of labial gland when compared with that of gut does not bring to light any significant relations. As will be shown later, the digestive functions of the labial gland secretions have been suppressed more or less completely in order to give place to the function of the net-spinning and base-building. The presence or absence of accessory glands on them does not seem to be correlated with the nature of food. These are present both in the carnivorous forms like *Rhyacophila* and *Odontocerum* and phytophagous formslike *Sericostoma* and *Psychomyia*, and conversely, they are absent in such diverse feeders as the Limnophilidae, *Hydropsyche* and *Molanna*. It is curious that in the Polycentropodidae the left labial gland is shorter than the right.

With regard to the maxillary and the mandibular glands I must say that I have not been able to discover any correlation between them and the feeding habits.

The mandibular glands are always much smaller than the maxillary glands in size and may be altogether absent in some forms e.g. Hydropsyche and Oectis. They are reported to be lacking in a species of Limnophilus also, (Henseval 1897). Their absence in larvae of such diverse feeding habits as above, would tend to show that they are unrelated to the type of food a larva takes in. Similarly they are present in larvae, far too many to be listed here, who utilize very different kinds of food.

The maxillary glands are present in all larvae except Phryganea, their presence or absence, therefore, could not be related to the type of food. They have, however, a comparatively strong development in prognathous larvae and one is tempted to relate this feature to a carnivorous habit, but prognathous Philopotamus (about the food of which we have no positive information, but which is certainly non-carnivorous) presents a serious exception. Besides, the maxillary gland of Oecetis is not tubular and is weakly developed.

Henseval (1897) regarded them as, in some way, compensating for the general absence of Gilson's glands (Gilson 1896) in the thorax of Trichopterous larvae. He showed that when the thoracic glands were present, as for example in *Phryganea*, the head-glands were totally absent. If the conclusion is true, then the head-glands and their oily secretion must be regarded as aiding the tubicolous habits of the Trichopterous larvae. But, unhappily this can not be regarded as true, for the head-glands are best developed in precisely those forms which go through life without cases.

A chemical analysis of the secretion of the head-glands might settle whether or not they are related with feeding habits, but this has not been attempted by anyone so far; the difficulty of getting the secretion fluid in sufficient quantities being a hitherto unsurpassed difficulty.

Coming to a consideration of the secretion of enzymes I find that there is a marked tendency of all the species examined, to suppress, more or less completely, the digestive functions of the labial glands. This may be explained by the importance of its secretion in net-spinning and case-building, which seems to occupy this gland so entirely as to leave no room for the digestive functions. The only digestive secretion found in the labial gland of a carnivore is in Polycentropus. There a very weak amylase was found, but no invertase. In this connection, it may be significant that Polycentropus shows a marked morphological eccentricity in its labial glands, the right one being much longer than the left. Whether or not there is also a functional difference between the two, I am unable to say at present.

The vegetarian Trichoptera generally show a weak secretion of amylase and invertase in the labial gland. I assume that a vegetarian's food contains more Carbohydrates than a carnivore's. But this alone would not account for the lack of this secretion in the carnivore's labial glands as can be seen from the case of the omnivorous net-spinning Hydropsyche, which shows no labial gland enzymes, and the case-building Odontrocerum, which has a weak amylase.

Another very interesting difference between the carnivorous and vegetarian forms is that the former possess a pepsin which, though generally weak, is quite strong in Rhyacophila. As this secretion seems to be very rare in insects, the result was verified by two methods, which yielded identical results, and it seems therefore, quite safe to conclude that pepsin does occur in the carnivorous Trichoptera. No pepsin was ever found in the vegetarians.

Speaking broadly, it would appear that there is a transition from vegetarian forms whose labial glands secrete amylase and invertase but whose gut lacks pepsin to carnivorous forms with no enzymes secreted by the labial glands but a strong pepsin by the gut. (Table II)

All tests were carried out at a constant pH value

It is perhaps significant that the gut of carnivorous larvae is more often found to be empty than in vegetarian forms. This suggests that digestion is much quicker in the former. Also, the gut in vegetarians is generally broader, which may mean that they have to eat a greater quantity of food than the carnivorous larvae for normal living, but on the other hand, it may only be the result of the first condition, viz., the retention of food in the stomach for longer periods.

"It has sometimes been said that the forms which live in rapid water are largely carnivorous and those in standing water phytophagous" Davis (in Betten, 1934, P. 96). I do not know who made this statement originally but I find several notable exceptions to this, and my observations on habitat are confirmed by those of Sleight (1913). Thus, *Lepidostoma*, *Silo*, *Halesus*

Psychomyia, and *Philopotamus*, which are all non-carnivorous forms live in very swift streams. Conversely *Phryganea*, *Molanna* and *Polycentropus* live in still or slow-moving water, yet they are carnivorous to a very considerable degree. I would, therefore, conclude with Siltala that the feeding habits are connected more with distinctions of natural relationship than those of habitat.

Summary and conclusions.

(1) A detailed study has been made of the larval habitat, food, feeding and digestive organs of thirty genera taken from all the twelve British families of Trichoptera.

(2) A classification of food, according to the mechanical resistance it offers to the feeding organs, is attempted.

(3) The degree of carnivorism or vegetarianism is broadly connected with the sharpness or bluntness of the mandibles, and the greater length and mobility or the shortness and immobility of the maxillary palpi.

(4) There is some indication that the form of first legs is related to the nature of the food.

(5) The mandibular, maxillary and labial glands have been studied. Their form does not appear to be related with the larval feeding habits.

(6) There is a strong tendency to suppress the digestive functions of the labial glands in both the carnivorous and vegetarian forms, though there are some minor differences between the two types.

(7) The mid-gut is very long in the purest vegetarians and short in the purest carnivores. Between these two extremes there is a series of intergradations which runs more or less parallel to the series of food-classes.

(8) The epithelial cells seem related to the

kind of food. In carnivores they are much taller than in others; the nidi are also bigger in them. When goblet cells are present the peritrophic membrane is absent.

(9) Almost all studied larvae show a holocrine type of digestive secretion. In the carnivores, however, the pace of this process is much quicker than in others.

(10) The fore-gut, the function of which appears to be predominantly mechanical, is very long in the purest carnivores and its intima is thrown into stout and complicated folds; often a "gizzard-like" structure is present. In the purely vegetarian larvae the fore-gut is short and weak. Between the two extremes there are intermediate forms.

(11) The stomodeal valve is generally stout in the carnivores and the aperture it guards is narrow. Its anterior part sometimes forms a "gizzard-like" structure in the fore-gut. In the vegetarians the aperture is very wide and the stomodeal valve generally weak.

(12) Previous theories concerning the correlation of morphological characters with feeding habits are discussed.

REFERENCES.

Betten, C. (1902) "The larva of the Caddis Fly, Molanna cinerea Hagen". Jour. N.Y.Ent. Soc., 10: 147-~~54~~ 154.

Betten, C. (1934) "The Caddis Flies or Trichoptera of New York State". N.Y.St. Mus. Bull.,292: 1-576.

Branch, H.E. (1922) "A Contribution to the knowledge of the Internal Anatomy of Trichoptera". Ann.Ent. Soc. Amer., 15: 256-72.

Brett, G.A. (1836) "Some Breeding Experiments with Hemerophila abruptaria, Thunb". Proc. S.Lond.Ent. and Nat. Hist. Soc. (1935-36) : 84-92.

Das, G.M. (1936) "The Musculature of Mouth-parts of Insects larvae in Relation to Classification".

Glasgow, J.P. (1936) "INternal Anatomy of a Caddis (Hydropsyche colonica Mcl.)". Quart. Journ. Micr. Sci., 79: 1-29

Henseval,M. (1895) "Les glandes Buecales des Larves de Trichopteres" La Cellule, Vol. 12.

Krafka,J. Jr. (1923) "Morphology of the Head of Trichopterous Larvae as a Basis for the Revision of the Family Relationships" Jour.N.Y.Ent.Soc.,31: 31-52.

Kruger, F. (1926) "Biologie and Morphologie Einiger Syrphidenlarven". Zeitschrift fur Morphologie und Okologie der Tiere, 6:

Loyd, J.T. (1921) "The Biology of the North American Caddis Fly Larvae" Lloyd Library of Botany, Pharmacy, and Materia Medica Bull., 21: 1-124, Cincinnati, Ohio.

Lucas, R. (1893) "Beit. Zur Kennt. der Mundwerkzeuje der Trichoptera." Arch. f. Naturg. 1893 in 1-47.

Martynow, A.B. (1930) "On the Trichopterous Fauna of China and Eastern Tibet". Proc. Zool. Soc. London, No. 5: 65-112.

Miall, L.C. (1912) "The Natural History of Aquatic Insects".

Murphy, H.E. (1919) "Observations on the Egg-Laying of the Caddis-Fly, Brachycentrus nigrisoma and on the Habits of Young Larvae". Jour. N.Y. Ent. Soc., 27: 154-159.

Noyes, A.A. (1914) "The Biology of Net-Spinning Trichoptera of Cascadilla Creek". Ann. Ent. Soc. Amer., 7: 251-271.

Noyes, A.A. (1914) "The Proventriculus of Hydropsyche Larva". Jour. Ent. and Zool., 7: 34-44.

Patten, W. (1884) "The development of Phryganids." Quart. Ji. Micros. Science. P. 1-54.

Roussenu, E. (1921) "Les Larves et Nymphes Aquatiques des Insects d' Europe". 543-964. Bruxelles.

Ruzz, E.L. (1910) "Beit. zur. kennt. der Kopfdruzen der Trichopterenlarven". Arch. Zool. Exp. Gen. Vol. V. 61-67.

Schulze, P. (1925) "Trichoptera (by G. Ulmer) in Biologie den Tiere Deutschlands". Lief, 13 Part 36.

Shindo, O. (1927) "Contributions to the Knowledge of intestinal secretion in insects. II. A comparative Histocytology of the mid-intestine in various orders of insects". Zeit. f. Zellforsch. u. Mikeo, Anat., 5.

Sitala, A.J. (1897) "Uber die Nahrung der Trichopteren" Acta. Soc. Fauna et Flora Fenn., No. 5, 34 p.

Slack H.D. (1936) "The food of Caddis Fly (Trichoptera) Larvae" Jour. Animal Ecol. 5: 105-115.

Sleight, C.E. (1913) "Relations of Trichoptera to their Envirornment" Jour. N.Y. Ent. Soc., 21: 4-8.

Snodgrass, R.E. (1935) "Principles of Insect Morphology" London.

Vorhies, C.T. (1905) "Habits and Anatomy of the larva of the Caddis fly <u>Platyphylax designatus</u> Walker" Trans. Wis. Acad. Sc., Vol. XV.

Wesenburg-Lund, C. (1913) "Wohnungen und Gehausebau der Susswasserinsekten" Fortschr. Naturw. Forsch. 9: 55-132.

Wigglesworth, V.B. (1934) "Insect Physiology" London.

TABLES OF FOOD ANALYSIS.

RHYACOPHILA, probably, DORSALIS

	Date	Locality	Contents of gut
1.	28.4.35	River Kennet Near Newburry.	Legs of insects and other chitinous pieces only.
2.	29.5.35	The Itchen near Winchester.	Empty.
3.	29.5.35	"	"
4.	15.4.35	"	Unrecognisable whitish jelly-like substance; no plant tissues evident.
5.	25.12.35	The Test near Bollington.	Limbs, mandibles and other chitinous plates from the bodies of insects form the bulk; one small bit of leaf-tissue and a few diatoms forming an infinitesimal part of the whole.
6.	24.3.36	The Itchen near Winchester.	Entire body of a Chironomid worm; a few bits of insect skeleton; the rest unrecognisable.
7.	"	"	Whole bodies of insect ~~larvae~~ larvae; no vegetable particles.
8,9,10 (3 specimens)	"	"	Empty.
11.	21.6.36	The Ludden near Basingstoke.	Empty.
12.	"	"	Mainly animal, including limbs of Crustacea.
13.	"	"	Empty.
14-33 (20 specimens)	24.3.36	The Itchen near Winchester	Almost entirely animal, including Trichopterous larvae (mainly Agapetus), Chironomid larvae, Dipterous pupae and small Crustacea; diatoms and sand grains in negligible amount; no bits of phanerogams or filamentous algae.

(Continued)

Comparison of gut-contents from two different habitats. (1. The weeds covered with Chironomid larvae, and 2. the under surface of stones).

	Date	Habitat	Contents of gut
1.	2.6.35	Upon weeds.	Not recognisable, but vegetable tissues definitely absent.
2.	"	"	Heads and limbs of Chiromid larvae in large numbers; one bit of alga and numerous diatoms, infinitesimal as compared with animal food.
3.	"	"	Heads, limbs and cuticular shields from the bodies of insects; diatoms not very numerous.
4.	"	"	"
5.	"	"	" plus sand grains.

....

1.	"	Under stones.	Mainly skeletons of heads and limbs from insects.
2.	"	"	A bit of leaf-tissue; a few diatoms.
3	"	"	Unrecognisable but no plant tissues.
4.	"	"	Animal matter including a whole chironomid larva.

AGAPETUS Sp.

	Date	Locality	Contents of gut
1.	4.8.35	The Itchen near Winchester.	Diatoms and sand grains.
2.	25.12.35	The Test near Bollington	Diatoms; the commoner ones were:- (1) Gomphonema sp. (2) Navicula sp. (3) Amorpha ovalis (4) Trabellaria sp, and sand grains.
3.	25.12.36	"	Greater part unrecognisable; a branching alga; some diatoms.
4.	31.3.36	The Itchen near Winchester	Diatoms and the mass in which they are entangled; a few short bits of algae; numerous very bright siliceous particles; Tabellaria flocculosa.
5.	"	"	" " "
6.	"	"	Diatoms and the mass in which they are embedded; a few short bits of algae.
7.	"	"	The greatest bulk is formed by the mass in which the diatoms are enmeshed; diatoms; a few bits of algae.
8.	"	"	Very numerous diatoms forming the major portion of contents; a few bits of algae.

HYDROPTILA Sp.

No.	Date	Locality	Contents of gut
1.	11.5.35	The Itchen near Winchester.	Unrecognisable, (probably the coagulated secretions of stomach).
2.	"	"	Nothing recognisable except a few diatoms.
3.	5.8.36	"	A solid mass of closely packed diatoms formed the entire bulk (*Amorpha ovalis* and *Gomphonema constrictum* are the commonest forms).
4.	"	"	"
5.	"	"	"
6.	17.8.36	"	Diatoms; minute bits of moss leaves; fragments of algae.
7.	26.8.36	"	Empty.
8.	"	"	"
9.	"	"	Nothing recognisable except for a few diatoms.

PHILOPOTAMUS MONTANUS

No.	Date	Locality	Contents of gut
1.	March, 36	Windermere (Streams)	Empty, except for some sand, mud and diatoms
2.	"	"	"
3.	"	"	"
4.	"	"	"
5.	"	"	Empty for the greater part, numerous diatoms forming a solid mass with sand: commonest diatoms are (1) *Gomphonema*. (2) *Navicula* and (3) *Amorpha ovalis*.
6.	28.4.36	"	Empty.
7.	"	"	Empty.
8.	"	"	Empty, except for some corky matter and mud.
9.	"	"	Empty, except in one small region which is filled with sand and diatoms.
10.	May, 36	"	Empty, except for some mud and diatoms.
11.	"	"	"
12.	"	"	"
13.	"	"	"

HYDROPSYCHE spp.

No.	Date	Locality	Contents of gut
1.	9.4.35	River Mole near Kingston.	A Chironomid larva; small pieces of cuticle; a bit of green alga.
2.	28.4.35	River Kennet near Newbury	Animal matter forming more than half the bulk; algae; Diatoms; sand grains.
3.	"	"	Algae and diatoms preponderate over animal matter.
4.	"	"	Algaeand diatoms preponderate over crustacean and insect matter.
5.	"	"	"
6.	"	"	Insect and algal material in almost equal proportions.
7.	"	"	"
8.	"	"	"
9.	"	"	Crustacean and vegetable material about equal.
10.	2.6.35	River Test near Romsey.	Sand grains form the major bulk; insect and crustacean material; numerous diatoms; a bit of stem-tissue.
11.	"	"	Empty.
12.	"	"	Insect material formed the bulk; branching algae and diatoms numerous.
13.	9.6.35	River Itchen near Winchester.	Insect material predominent; about 3 small bits of stem-tissue.
14.	"	"	Chiefly insect and C~~h~~rustacean matter; one small bit of alga.

(Continued)

No.	Date	Locality	Contents of gut
15.	9.6.35	River Itchen near Winchester	Mainly insect and crustacean material.
16.	24.8.35	a small river near Ashbourne	Bits of phanerogam tissue formed the bulk; next in order of magnitude come diatoms, and sand particles.
17.	28.8.35	Ambleside	Insect material formed the bulk; several kinds of branched and unbranched algae; bits of phanerogam leaf- and stem-tissue.
18.	"	"	Empty except for a few bits of leaf-tissue.
19.	25.10.35	The Itchen near Winchester	Fragments of insect limbs formed the bulk; several kinds of algae; bits of phanerogam tissue; diatoms.
20.	28.11.35	Wisley pond Surrey	Phanerogam ~~[illegible]~~ tissues form the bulk; ~~xx~~ debris.
21.	26.11.35	A tributary of the Test near Bollington	Phanerogam leaf-and stem-tissues preponderate; insects and crustacean material; a few diatoms.
22.	"	"	Phanerogam leaf-and stem-tissues form by far the largest part; insect material; diatoms; sandgrains.
23.	"	"	"
24.	4.36	Scotland	"
25.	18.5.36	The Itchen near Winchester	Algae form the bulk; fragments of insect skeleton; diatoms.
26.	"	"	"
27.	"	"	Bits of phanerogam tissue; algae; diatoms.

HWDROPSYHE 'A'

No.	Date	Locality	Contents of gut.
1.	26.8.35	Ambleside	Pieces of ibsect skeleton form the bulk; branched and unbranched algae, afew bits of leave and stems of higher plants; some diatoms.
2.	"	"	Algae (mainly unbranched) form the bulk; chironomid heads; some diatoms; and particles.
3.	"	"	Phanerogam bits form the bulk; unbranched and branched algae; sand particles.
4.	"	"	Pieces of insect skeleton form the bulk; algae; some diatoms.
5.	"	"	Algae and pieces of insect skeleton in about equal proportions.

A good deal of sand is included in all.

HYDROPSYCHE 'B'

No.	Date	Locality	Contents of gut.
1.	26.8.35	Ambleside	Phanerogamous bits form the bulk; diatoms; sand particles.
2.	"	"	Unbranched algae of several kinds form the bulk; several chironomid heads; bits of phanerogam-tissues; sand particles.
3.	"	"	Algae; pieces of insect skeleton in nearly equal volume; diatoms; sand grains.
4.	"	"	Pieces of insect skeleton form the major bulk; algae; bits of phanerogamous leaves and stems; diatoms; sand grains.
5.	"	"	"

POLYCENTROPUS sp.

No.	Date	Locality	Contents of gut
1.	5.8.35	The Itchen near Winchester	Fragments of insect skeleton especially chironomid heads form the bulk; sand grains.
2.	?	Lake Windermere	Fragments of insect skeleton entirely.
3.	?	"	Some bits of animal tissue form bulk; sand grains; one diatom.
4.	20.8.36	The Itchen near Winchester	Empty.
5.	"	"	"
6.	"	"	Fragments of insect skeletons including chironomid heads.
7.	"	"	Empty.

~~PLECTROCNEMIA~~

PLECTROCNEMIA sp.

No.	Date	Locality	Contents of gut
1.	March, 1936	Windermere	Meagre and unrecognisable.
2.	"	"	Fragments of insect skeleton form the entire bulk.
3.	"	"	Meagre and unrecognisable.
4.	"	"	"
5.	"	"	Eggs, (of some fish presumably)
6.	"	"	Body of a may-fly nymph seems to form the entire bulk.
7.	"	"	Broken pieces of insect limbs formed the entire bulk.
8.	"	"	Meagre and unrecognisable.
9.	"	"	"
10.	"	"	Broken pieces of insect limbs form the major bulk; some unrecognisable matter.

CYRNUS sp

No.	Date	Locality	Contents of gut
1.	March 1936	Windermere	A few Chironomid heads; an egg of some fish; unrecognisable matter.
2.	"	"	Empty.
3.	"	"	Unrecognisable whitish matter, most probably of animal origin.
4.	"	"	"
5.	"	"	Empty.
6.	"	"	Unrecognisable whitish matter forms the bulk; a Chironomid head, sand grains.
7.	"	"	Empty.
8.	"	"	"
9.	"	"	Unrecognisable whitish matter forms the bulk; Crustacean skeletons; a chironomid head.
10.	"	"	"

HOLOCENTROPUS sp

No.	Date	Locality	Contents of gut
1.	March 1936	Windermere	Heads of Chironomid larvae form the bulk; skeletons of small Crustacea.
2.	"	"	Empty.
3.	"	"	Skeletons of insects (including a number of Chironomid heads) form the major bulk, Crustacea; sand grains.
4.	"	"	"
5.	"	"	"
6.	"	"	Empty.
7.	"	"	"
8.	"	"	Pieces of Chironomid larvae; small Crustacea; sand grains; diatoms.
9.	"	"	"
10.	"	"	Empty.
11.	10.8.36	The Itchen near Winchester	A few Chironomid heads are the only recognisable objects.

PSYCHOMYIA sp.

No.	Date	Locality	Contents of gut
1.	25.7.36	The Itchen near Winchester	Sand forms the bulk; diatoms - Navicula sp., Gamphonema, Frakilaria, Capucina; very fine colourless and short filamentous algae.
2.	"	"	"
3.	"	"	"
4.	"	"	Sand mixed with debris forms the bulk; Two small fragments of phanerogamous leafe-tissue; Diatoms, several kinds; Algae; Unrecognisable dark brown particles of organic matter.
5.	"	"	Sand forms the bulk; algae diatoms; short and slender /
6.	"	"	"

TINODES sp.

No.	Date	Locality	Contents of gut
1.	March, 1936	Lake Windermere	Unrecognisable.
2.	"	"	Diatoms form almost the whole of bulk and include the following forms:- (a) Synedra ulna (b) Navicula cryptocephala (c) Gamphonema constrictum (d) Diatoma vulgare (e) Cymbella sp.; a few strands of the tenderest septate algae.
3.	"	"	Diatoms form the bulk; debris matter; a few very tender (young) strands of green septate algae.
4.	"	"	Debris form the bulk; diatoms especially Fragilaria capusina; few stands of very tender algae.
5.	"	"	"
6.	"	"	Diatoms form the bulk; debris.
7.	"	"	" plus some fragments of algae.

ODONTOCERUM ALBICORNE

No.	Date	Locality	Contents of gut
1.	28.8.35	Ambleside	Head capsules of several kinds of insects including Trichopera; Limbs, anal styles and chitinous shields which definitely belong to Trichopera; bits of a limnaea-like gastropod; bits of hard stem tissue, almost wooden; sand grains. The bulk of first and second items exceeds by far all other items put together.
2.	"	"	Broken bits of insect skeleton form almost the entire bulk; sand grains.
3.	"	"	Bits of a limnaea-like gastropod form by far the major bulk; bits of hard wooden stem tissue; parasitic protozoa (Gregarinae); sand particles but no diatoms.
4.	22.3.36	Winchester	Bits of Limnophilid larva filling the fore-gut completely; a few bits of the skeletons of insects; grains of sand in the hind-gut.
5.	17.5.36	"	Bits of insect limbs and bodies which progressively lose their form as they travel backwards.
6.	10.6.36	"	Heads of insect larvae; bits of leaf tissue; bits of chalk stones; other inorganic particles.
7.	"	"	"
8.	"	"	"

<u>MOLANNA</u> sp.

No.	Date	Locality	Contents of gut
*.	~~*).£.%£~~		
1.	10.5.35	The Itchen near Winchester	Unrecognisable matter formed the bulk; a few pieces of ~~ixxx~~ insect skeleton; diatoms.
2.	25.11.35	Canal near Wisley	Pieces of insect skeleton form the bulk; sand also included.
3.	6.6.36	The Itchen near Winchester	Unrecognisable white loose mass, probably secretions of stomach, form the entire bulk.
4.	"	"	Pieces of insect skeleton formed by far the greatest bulk; sand grains; diatoms.
5.	"	"	"
6.	"	"	A few pieces of Crustacean skeleton lying in a whitish unrecognisable mass; numerous diatoms.

LEPTOCERUS spp.

No.	Date	Locality	Contents of gut
1.	31.5.36	The Itchen near Winchester	Debris matter forms the bulk; pollen grains; diatoms.
2.	"	"	Tissues from phanerogams; a few strands of algae; diatoms.
3.	"	"	Debris forms the bulk; diatoms the common ones are Navicula and Gomphonema.
4.	"	"	Unrecognisable.
5.	17.7.36	"	Sand containing a large proportion of unrecognisable organic matter forms the bulk; bodies of 2 or 3 acarina; diatoms; fine algal strands.
6.	"	"	"
7.	"	"	Bodies of acarina form almost the entire bulk; sand; diatoms.
8.	"	"	Bodies of acarina form the bulk; debris; diatoms; fine short algal filaments.
9.	"	"	Sand, with a large proportion of deep brown organic matter mixed with it, forms the bulk; diatoms; algal plants.
10.	"	"	Sand with organic matter forms the bulk; bodies of acarina; diatoms.
11.	"	"	"

TRIAENODES sp.

No.	Date	Locality	Contents of gut
1.	August '35	Lake Windermere	Bits of phanerogam tissues form the bulk; limbs of some Crustacean
2.	17.7.36	Tributary of the Test near Bollington	Bits of phanerogam-tissues form the entire bulk.
3.	"	"	"
4.	"	"	Bits of phanerogam-tissues form the bulk; limbs of some crustacean.

OECETIS sp.

No.	Date	Locality	Contents of gut
1.	August 1935	Lake Windermere	Empty.
2.	March 1936	"	Pieces of insect skeleton formed the entire bulk.
3.	"	"	A whole Chironomid larva without the head formed the entire bulk.
4.	"	"	Empty.
5.	"	"	Pieces of insect skeleton formed the entire bulk.
6.	"	"	Entirely animal, included the anal hooks of an oecetis larva.
7.	"	"	Empty.
8.	"	"	"

PHRYGANEA GRANDIS

No.	Date	Locality	Contents of gut
1.	26.5.35	Chobham, Surrey	Empty.
2.	"	"	Vegetable entirely - mainly small brown bits of dead leaves and stems among which are scattered bits of green tissue. Parasatic greagaimae are also present.
3.	?.35	Windermere	Limbs, plates of exoskeleton and tracheal tubes of insects form the major bulk; sand grains.
4.	10.11.35	Surrey	Fragments of Trichopterous bodies entirely fill the fore-gut; the contents of the mid-gut semi-liquid and unrecognisable; in the hind-gut they are hardened but still unrecognisable.
5.	24.11.35	Wisley, Surrey	Limbs, skeletal plates, gills, lateral line fringes and anal styles of Trichopetous larvae form the entire bulk of the fore-gut contents; fragments of a Phryganea larva are also recognisable.
6,7,8.	?.3.36	Windermere	Mainly animal tissues - some chironomid larvae swallowed whole; amount of vegetable matter very small; parasitic gregarinae.
9.	?.3.36	"	Both animal and vegetable matter but the former (mainly insect larvae) preponderates.

GLYPHOTAELUS PELLUCIDUS

No.	Date	Locality	Contents of gut
1.	15.1.36	Canal near Richmond	Raspings from bark of dead twigs and bits of dead leaves form the largest bulk; numerous strands of *Oscillatoria*; several diatoms - *Gomphonema*, *Cymbella*; a deep brown fluid pervading the fore- and mid-guts; some living protozoa; large number of *Cladophora* fragments carrying epiphytic *Gomphonema*.
2.	"	"	Raspings from the bark of dead twigs and fragments of dead leaves and stems form the largest bulk; spiral thickenings of vascular cells detached from the cells fairly numerous; a colony of *Volvox*, algal filaments; diatoms; a few living protozoa.
3.	"	"	Raspings from bark of dead twigs, bits of dead leaf and stem-tissues form the largest bulk; sand particles; diatoms - a few; algal filaments - a few; a few living protozoa.
4.	"	"	Rasping from bark, bits of dead leaves and stems form the largest bulk; very numerous diatoms, probably epiphytic, *Cymbella*, *Ceratoneis arcus* etc.; a few green algae, growing from bits of dead leaves.
5.	5.1.36	Canal near Richmond	Raspings of bark and bits of vascular tissue form the largest bulk; bits of green algae; numerous diatoms seen sticking to other kinds of vegetation, mostly *Cymbella* and *Gomphonema*.
6.	"	"	Raspings of bark, bits of leaf- and stem-tissue form the largest bulk; a few diatoms; pollen grains; fragments of *Cladophora* carrying epiphytic *Gomphonema*.
7.	"	"	"

(Continued)

No.	Date	Locality	Contents of gut
8.	2.2.36	Pond near Chertsey	Bits of dead phanerogams and of duck weed leaves form the largest bulk; young algae; diatoms; numerous Gregarinae.
9.	"	"	Bits of dead phanerogam tissues form the bulk; body of a crustacean; debris.
10.	"	"	Bits of phanerogam tissue from bark, stem and dead leaves form bulk; debris.
11.	"	"	Bits of bark, leaf and stem tissue form the bulk; numerous Gregarinae; epiphytic <u>Gomphonema</u> on fragments of <u>Cladophora</u>.
12.	"	"	" plus a few diatoms.
13.	"	"	Bits from dead leaves, stems and bark form the bulk; a few bits of green tissue; pollen grains; a few diatoms.
14.	"	"	Bits from dead leaves; steams and bark form the major bulk; epiphytic <u>Gomphonema</u> on fragments of <u>Cladophora</u>.
15.	9.2.36	"	Bits of dead leaves, stems and barks form the bulk; few bits of green duck-weed; bits of green algae; diatoms - Desmids and <u>Cymbella</u>, mostly epiphytic.
16.	"	"	Bits of dead leaves, stem and barks form the largest bulk; strands of <u>Vaucheria</u>; diatoms; <u>Oscillatoria</u>.
17.	27.5.36	Pond near Datchet	Bits of dead leaves, stems and bark form the largest bulk; bits of algae; diatoms; spores; sand particles.
18.	"	"	"

COLPOTAULIUS INCISUS

No.	Date	Locality	Contents of gut
1.	18.5.35	Lake near Virginia Water	Fragments of fresh and dead leaves form the bulk; a few strands of algae; a few diatoms - (*Amorpha ovalis* mainly).
2.	"	"	"
3.	"	"	"
4.	10.11.35	Pond near Wisley	Fragments of fresh and dead phanerogam-tissue form the bulk; pieces of a Trichopterous larva; a few strands of *Vaucheria*.
5.	"	"	Fragments of fresh and dead leaves form the entire bulk.
6.	24.2.36	Pond near Chertsey	Fragments of dead and fresh phanerogam-tissues form the bulk; an entire chironomid larva; a few sand grains; a few diatoms.
7.	"	"	Fragments of dead phanerogam-tissues form the bulk; some diatoms.

LIMNOPHILUS spp.

No.	Date	Locality	Content of gut
1.	10.4.35	Pond near Wisley	Discoloured fragments of leaves and stems of phanerogamous weeds.
2.	"	"	"
3.	1.6.35	"	Both green and discoloured bits of leaf-and stem-tissues form the bulk; a Chironomid head.
4-7.	15.4.35	The Itchen Winchester (a very slow moving side stream)	Bits of phanerogam-tissue, both green and discoloured form, the bulk; a few algae and diatoms.
8.	9.6.35	"	Bits of leaf-and stem-tissues; numerous diatoms, a few strands of algae; sand grains.
9.	?.5.35	Pond near Wisley	" except algae.
10.	"	"	" "
11.	25.2.36	Pond near Chertsey	Both green and discoloured bits of leaf- and stem-tissues form the bulk; bits of insect organs; diatoms.
12.	"	"	Bits of leaf-and stem-tissues form the bulk; a few diatoms.
13.	"	"	" plus some algal fragments.
14.	"	"	Bits of dead leaves and stems mostly but some green also; numerous diatoms.
15-34. (20 specimens)	18.3.36	Windermere	Fragments of fresh and old phanerogamous leaf-and stem-tissues formed almost the entire bulk; body of a single lepidostoma larv diatoms are numerous and of consid-erable variety but would form an infinitesimal proportion of the first item, the following are the

(Continued)

No;	Date	Locality	Contents of gut
			commonest forms:- (a) Tabellaria (b) Gomphonema (c) Synedra (d) Melosira (e) Amphineura (f) Navicula (g) Amorpha ovalis (h) Cymbella.

ANABOLIA NERVOSA

1.	31.5.35	The Itchen near Winchester	Fragments of green leaf-and stem-tissues form almost entire bulk; a few diatoms.
2.	9.6.35	"	Fragments of green leafe-tissues form the bulk; debris; sand particles; diatoms.
3.	"	" near Alresford	Fragments of green and discoloured leaf and stem-tissues form the entire bulk.
4.	17.5.35	The Itchen near Winchester	Sand forms the bulk; fragments of dead leaves over-grown with algae green bits of the water Ranunculus leaves; a few diatoms.
5.	27.5.35	"	Fragments of discoloured and green leaf-and stem-tissues form almost the entire bulk; some diatoms.
6.	April,36	Scotland	Fragments of leaves and stems; some diatoms.
7.	"	"	"

MESOPHYLAX sp.

No.	Date	Locality	Contents of gut
1.	Aug. 1935	Stream in Derbyshire	Empty.
2.	"	"	"
3.	"	"	Fragments of leaves (*Ranunculus aquatilis*) form the greatest bulk; a few sand grains; a few diatoms.
4.	"	"	A few bits of leaf-tissues form the entire bulk.
5.	July, 1936	The Itchen near Winchester	Empty.
6.	"	"	Fragments of leaf-and stem-tissues form the entire bulk.
7.	Aug. 1936	"	Empty.
8.	"	"	"
9.	"	"	"
10.	"	"	"
11.	"	"	Some fragments of leaves (*Ranunculus aquatilis*) formed the bulk; a few sand grains.

STENOPHYLAX sp.

No.	Date	Locality	Contents of gut
1.	16.11.35	The Itchen near Winchester	Bits of leaf-and stem-tissue form the bulk; sand grains; a few diatoms.
2.	"	"	"
3.	"	"	Bits of leaf-and stem-tissues from weeds which include Ranunculus aquatilis and moss; diatoms; sand grains.
4.	"	"	Fragments of bark, stems and leaves of phanerogams; diatoms; sand grains.
5.	1.3.36	Lake Windermere	Bits of leaf-and stem-tissues; sand grains, diatoms.
6.	"	"	Discoloured and green fragments of leaves and stems of phanerogams form bulk; debris matter; pieces of insect skeleton; numerous diatoms.
7.	"	"	Discoloured fragments of phanerogam tissue form the bulk; debris; diatoms.
8.	"	"	Discoloured fragments of phanerogam tissues form the bulk; debris; mandibles of a Limnophilid larva; diatoms.
9.	4.36	Scotland	Fragments of leaf-and stem-tissues form bulk; pieces of insect skeleton; sand grains.
10.	"	"	"

HALESUS sp.

No.	Date	Locality	Contents of gut
1.	Summer 1934	Kent	Fragments of phanerogam leaves and stems form the bulk; a few diatoms
2.	"	"	"
3.	July 1936	The Itchen near Winchester	Bits of bark stem-and leaf-tissues especially the last, form the bulk diatoms - including Amorpha ovalis Gyrosigma, Cacconema lanceolatum, and Fragilaria capucina.
4.	"	"	"
5.	"	"	"
6.	"	"	"
7.	"	"	" plus a few pieces of insect skeleton.

BRACHYCENTRUS SUBNUBILUS

1.	?	The Test near Romsey	Bits of stem-and leaf-tissues form bulk; sand; diatoms.
2.	"	"	"
3.	"	"	Limbs of insects and Crustacea form bulk; a few bits of phanerogam tissue; a few parasitic Gregarinae
4.	"	"	Bits of phanerogam-tissues form the bulk; sand particles.
5.	"	"	Sand particles; fragments of insect and Crustacean bodies; bits of phanerogam tissues; a few diatoms.
6.	"	"	Bits of phanerogam tissues; bits of insect or Crustacean bodies, equal in bulk to previous item; diatoms; Cladophora - one strand.

SERICOSTOMA sp.

No.	Date	Locality	Contents of gut
1.	11.5.35	The Itchen near Winchester	Cuboid bits of leaf-and stem-tissues form the bulk; a few fragments of insect skeleton; sand grains.
2.	9.6.36	"	Bits of leaves and stem only.
3.	"	"	Bits of leaf-and stem-tissues form the bulk; a few fragments of insect skeleton.
4.	4.8.35	"	Cuboid bits of leaf-and stem-tissue form the bulk; sand grains; a few diatoms.
5.	"	"	Sand grains; bits of leaf-and stem-tissue; algal filaments; a few diatoms.
6.	26.12.35	A tributary the Test, Bollington	Bits of leaf-stem-tissues and bark form the bulk; diatoms; a few algal strands; sand grains.
7.	"	"	Bits of leaf-, stem-and bark-tissues form bulk; a few fragments of insect skeleton; sand grains; diatoms.
8.	7.3.36	Lake Windermere	Cuboid bits of leaf-and stem-tissues form the bulk; a few algal strands.
9.	"	"	Cuboid bits of leaf-and stem-tissues of higher plants form the entire bulk.
10.	"	"	Bits of phanerogam-tissues form almost the entire bulk; a few sand grains.
11.	"	"	"
12.	"	"	Bits of phanerogam-tissue form the whole bulk; parasitic Gregarinae.
13.	"	"	Bits of leaf-and stem tissues form the whole bulk.

(Continued)

No.	Date	Locality	Contents of gut
14.	?.3.36	Lake Windermere	Bits of leaf-and stem-tissues form the whole bulk.
15.	"	"	"

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NOTIDOBIA CILIARIS

1.	March 1936	Windermere	Broken skeleton pieces of insects form the major bulk; debris phanerogam tissue; diatoms.
2.	"	"	Bits of phanerogam tissues form the bulk; debris; diatoms.
3.	"	"	" plus sand grains.
4.	"	"	Bits of phanerogam tissues form the bulk; pieces of insect skeleton; debris; broken algal filaments; sand grains; a few diatoms.
5.	"	"	Bits of phanerogam tissues form the bulk; debris; diatoms; sand grains.
6.	"	"	"
7.	"	"	"

SILO sp.

No.	Date	Locality	Contents of gut
1.	5.5.35	The Itchen near Winchester	Sand forms the bulk; Algae; diatoms.
2.	"	"	Sand forms the bulk; Diatoms; organic particles.
3.	"	"	Sand forms the bulk; diatoms very numerous.
4.	28.8.35	Lake Windermere	A single strand of alga only.
5.	"	"	Unrecognisable.
6.	"	"	Diatoms make the bulk; Alga filaments; organic particles.
7.	"	"	Bulk is formed by unrecognisable matter; possibly of animal origin; sand.
8.	"	"	Fine particles of organic matter form the bulk; Skeleton of an insect head; sand, diatoms.
9.	"	"	Flesh of some animal; pieces of insect - skeleton; diatoms, chiefly Gomphonema, Navicula and Diatoma vulgare; a few strands of Ulothrix.
10.	"	"	Sand mixed with particles of debris and diatoms form the bulk.
11.	28.8.35	"	Sand; Diatoms - Rhoicosphenia, Gomphonema constrictum, Diatoma vulgare.

(Continued)

No.	Date	Locality	Contents of gut
12.	7.3.36	Lake Windermere	Amount of contents meagre, very small bits of phanerogam-tissue form the bulk; very numerous algal filaments; diatoms; particle of mica.
13.	"	"	Amount of contents is meagre; Diatoms embedded in brittle masses form the bulk; organic matt-er, small bright stones, sand grains and particles of mica; a few algal filaments.

LEPIDOSTOMA HIRTUM

No.	Date	Locality	Contents of gut
1.	2.6.35	The Test near Romsey	Fragments of green leaves form the bulk; a few limbs of insect.
2.	9.6.35	The Itchen near Itchen Abbas	Brown fragments of leaf-and stem-tissues form the entire bulk.
3.	3.36	Lake Windermere	"
4.	"	"	Empty.
5.	14.5.36	The Itchen near Winchester	Bulk formed by bits cut off from the leaves of water Ranunculus; a few diatoms.
6.	17.7.36	"	Fragments of phanerogamous leaf-and stem-tissues form the bulk; diatoms; sand grains.
7.	"	"	"
8.	"	"	"
9.	"	"	"
10.	"	"	"

TABLES SHOWING RATIO OF GUT-DIVISIONS.

RHYACOPHILA, probably, DORSALIS

No.	Fore-gut	Mid-gut	Hind-gut
1.	13.5	32	13
2.	14	37	19
3.	13.5	31	16
4.	11	12	17
5.	19	32	19
6.	12	18	7
Total	~~77~~ 83	162	91
Ratio	1	2	1.2

AGAPETUS sp

No.	Fore-gut	Mid-gut	Hind-gut
1.	10.5	23	12.5
2.	22	4	32
3.	14	42	23
4.	4	12	7.5
Total	50.5	14~~4~~1	75
Ratio	1	2.9	1.8

HYDROPTILA sp

No.	Fore-gut	Mid-gut	Hind-gut
1.	5	9	4.5
2.	6	10.5	4
3.	6.5	10.	3
4.	5	8	3
5.	3.5	6.5	2.5
6.	3.5	7.5	3
Total	29.5	51.5	20
Ratio	1	1.7	.7

PHILOPOTAMUS MONTANUS

No.	Fore-gut	Mid-gut	Hind-gut
1.	11	36	8
2.	9	34	6.5
3.	9	32	6.5
4.	9	32	6.5
5.	23.5	86	21.5
6.	15	32	12
7.	16.5	51.5	16
8.	18	38	11
Total	111	341.5	88
Ratio	1	3	.8

HYDROPSYCHE 'A'

No.	Fore-gut	Mid-gut	Hind-gut
1.	12	9	8
2.	13	11	9
3.	12	10.5	8
4.	14.5	13.5	8
Total	51.5	44	33
Ratio	1	.9	.7

HYDROPSYCHE 'B'

No.	Fore-gut	Mid-gut	Hind-gut
1.	10.75	11	6.5
2.	7.75	5	4.25
3.	7	7	4.5
4.	8.75	7.75	6.
Total	34.2	30.8	21.2
Ratio	1	.9	.6

POLYCENTROPUS sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	44.	21	19
2.	25	9.5	10.5
3.	15	6.5	10.5
Total	84	37	40
Ratio	1	.47	.5

PLECTROCNEMIA sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	21.	9	9
2.	61	25	22
3.	24	12	6
4.	24	11	6.5
Total	130	57	43.5
Ratio	1	.44	.33

HOLOCENTROPUS sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	43	13.5	19
2.	45	15	18
Total	88	28.5	37
Ratio	1	.32	.4

CYRNUS sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	34	14	15
2.	65	20	27
3.	42	16.5	18
4.	35	10	12
Total	176	60.5	72
Ratio	1	.34	.4

PSYCHOMYIA PUSILLA

No.	Fore-gut	Mid-gut	Hind-gut
1.	6.	19	7.5
2.	22	59	27
3.	6	15	7.5
Total	34	93	42
Ratio	1	2.7	1.2

TINODES sp.

No	Fore-gut	Mid-gut	Hind-gut
1.	15	28	15
2.	5	16.5	8.5
3.	4.5	9.5	4
4.	3	6.5	3.5
5.	19	38.5	18
6.	3.5	8	4
7.	6	13	7.5
8.	3.5	9	4
9.	5	10	5.5
Total	64.5	139	70
Ratio	1	2.2	1.1

ODONTOCERUM ALBICORNE

No.	Fore-gut	Mid-gut	Hind-gut
1.	23	19	18
2.	19	18	15
3.	50	34	31
4.	28	32	18
5.	22	16	14
Total	142	119	96
Ratio	1	.84	.7

MOLANNA sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	21	15	22
2.	29	31	24
3.	47.5	28.5	33
Total	97.5	74.5	79
Ratio	1	.76	.8

LEPTOCERUS spp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	8	15	7
2.	7	13	5.5
3.	10	19	6.5
4.	7	13	6
Total	32	60	25
Ratio	1	1.9	.8

TRIAENODES sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	12	16	8
2.	16	20	12.5
Total	28	36	20.5
Ratio	1	1.3	.7

OECETIS sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	9.5	3.5	3.5
2.	9	4	3.5
3.	21	10	8
4.	48	24	18
5.	12.5	5	4.5
Total	100	46.5	37.5
Ratio	1	.46	.37

PHRYGANEA GRANDIS

No.	Fore-gut	Mid-gut	Hind-gut
1.	15	6	10
2.	13.5	6	8
3.	10.5	9.5	10
4.	12.5	8.5	8.5
5.	14	14.5	11
6.	21.	17	15
7.	40	33	28
Total	126.5	94.5	90.5
Ratio	1	.75	.7

GLYPHOTAELIUS PELLUCIDUS

No.	Fore-gut	Mid-gut	Hind-gut
1.	14	47	12
2.	15	61	19
3.	14	46	20
4.	18	48	20
5.	17	56	20
Total	78	258	91
Ratio	1	3.3	1.2

COLPOTAULIUS ICISUS

No.	Fore-gut	Mid-gut	Hind-gut
1.	16	40	14
2.	15	32	16
3.	9	26	9
Total	40	98	39
Ratio	1	2.5	1

LIMNOPHILUS spp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	23	59	14
2.	9	19	8
3.	9	20	7
4.	11	26	10
Total	52	124	39
Ratio	1	2.4	.75

ANABOLIA NERVOSA

No.	Fore-gut	Mid-gut	Hind-gut
1.	10	30	10
2.	10	25	14
3.	10	32	9
4.	10	26	13
5.	13	31	17
Total	53	144	63
Ratio	1	2.7	1.2

MESOPHYLAX sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	13	22	12
2.	14	22	16
3.	10.5	21	11
4.	12	28	13
5.	9.5	20	9.5
Total	59	113	61.5
Ratio	1	2	1

STENOPHYKAX sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	31	55	28
2.	15	27	13
3.	13	25	10
4.	13	29	13
5.	16	28	20
Total	88	164	84
Ratio	1	1.9	1

HALESUS sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	20	42	20
2.	19	44	15
3.	14	24	16
4.	36	63	40
5.	16	29	13
Total	105	202	104
Ratio	1	2	1

BRACHYCENTRUS SUBNUBILUS

No	Fore-gut	Mid-gut	Hind-gut
1.	20	24	16
2.	20	23	18
3.	19	19	18
4.	25	22	22
5.	23	20	16
Total	107	108	90
Ratio	1	1	.8

SERICOSTOMA sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	17	57	17
2.	3.5	10.5	3
3.	5	11	4.5
4.	5	19	5.6
5.	5	16	5
6.	5.25	17	5
Total	40.75	130.5	40.1
Ratio	1	3.2	1

NOTIDOBIA CILIARIS

No.	Fore-gut	Mid-gut	Hind-gut
1.	12	35	13
2.	7.5	22	7
3.	14.5	46	16
Total	34	103	36
Ratio	1	3	1

S I L O sp.

No.	Fore-gut	Mid-gut	Hind-gut
1.	5	19	7.5
2.	4.5	22	9
3.	5.5	20	7
4.	5.5	22.5	6.5
5.	6	24	8
6.	6	23	7
Total	32.5	130.5	45
Ratio	1	4	1.4

LEPIDOSTOMA HIRTUM

No.	Fore-gut	Mid-gut	Hind-gut
1.	6	17	6
2.	5.5	15.5	5
3.	6	18	9
4.	6	21	7
5.	6	18	8.5
6.	8	24	9.5
7.	8	21	7
Total	45.5	134.5	52
Ratio	1	3	1.1

TABLE I

No.	Larva	Fore-gut	Mid-gut	Hind-gut
1.	Silo	1	4	1.4
2.	Glyphotaelius	1	3.3	1.2
3.	Sericostoma	1	3.2	1
4.	Notidobia	1	3	1
5.	Philopotamus	1	3	.8
6.	Lepidostoma	1	3	1.1
7.	Agapetus	1	2.9	1.8
8.	Psychomyia	1	2.7	1.2
9.	Colpotaulius	1	2.5	1
10.	Anabolia	1	2.7	1.2
11.	Limnophilus	1	2.4	.75
12.	Tinodes	1	2.2	1.1
13.	Mesophylax	1	2	1
14.	Halesus	1	2	1
15.	Stenophylax	1	1.9	1
16.	Rhyacophila	1	2	1.2
17.	Leptocerus	1	1.9	.8
18.	Hydroptila	1	1.7	.7
19.	Triaenodes	1	1.3	.7
	Brachycentrus	1	1	.8
21.	Hydropsyche (A)	1	.9	.7
22.	Hydropsyche (B)	1	.9	.6
23.	Odontocerum	1	.84	.7
24.	Molanna	1	.76	.8
25.	Phryganea	1	.75	.6

No.	Larva	Fore-gut	Mid-gut	Hindgut
26.	Polycentropus	1	.47	.5
27.	Oecetis	1	.46	.37
28.	Plectrocnemia	1	.44	.33
29.	Cyrnus	1	.34	.4
30.	Holocentropus	1	.32	.4

TABLE II

TABLE OF ENZYMES FOUND IN THE LARVAE

Species.	Secreting organ	Amylase	Invertase	Trypsin	Pepsin	Erepsin	Lipase.
PHYACOPHILA	LABIAL gland	−	−	−			
	fore-gut	?	?	+			
	Mid-gut	+	+ +	+	+ +		
POLYCENTROPUS	Labial gland	$\underline{\pm}$	−	−	−	−	
	Fore-gut	±	+	+	?	±	
	Mid-gut	+	+ +	+	±	+	
HYDROPSYCHE	Labial gland	−	$\underline{\pm}$	−	−		
	Fore-gut	+		+	±		
	Mid-gut	+	$\underline{\pm}$	+	±		
ODONTOCERUM	Labial gland	$\underline{\pm}$	−				
	Fore-gut	+	±				
	Mid-gut	+	±				
STYNOPHYLAX	Labial gland	−		−			
	Fore-gut	?		+			
	Mid-gut	+		+			
MESOPHYLAX	Labial gland	$\underline{\pm}$	$\underline{\pm}$	−	−		
	Fore-gut	+	?		−		
	Mid-gut	+	+ +	+	−		
ANABOLIA	Labial gland	$\underline{\pm}$		−			
	Fore-gut	?		?			
	Mid-gut	+		+			
GLYPHOTAELTUS	Labial gland			−			−
	Fore-gut			?			?
	Mid-gut			+			+

Asymmetrical lab. gland. The right gland which is much longer than the left contain amylase but it is not certain whether the left contains any or none.

The fore-gut itself probably does not secrete enyzmes in any of the larvae.

Explanation of signs:

+ = present

++ = strong

± = weak

$\underline{\pm}$ = very weak

− = absent

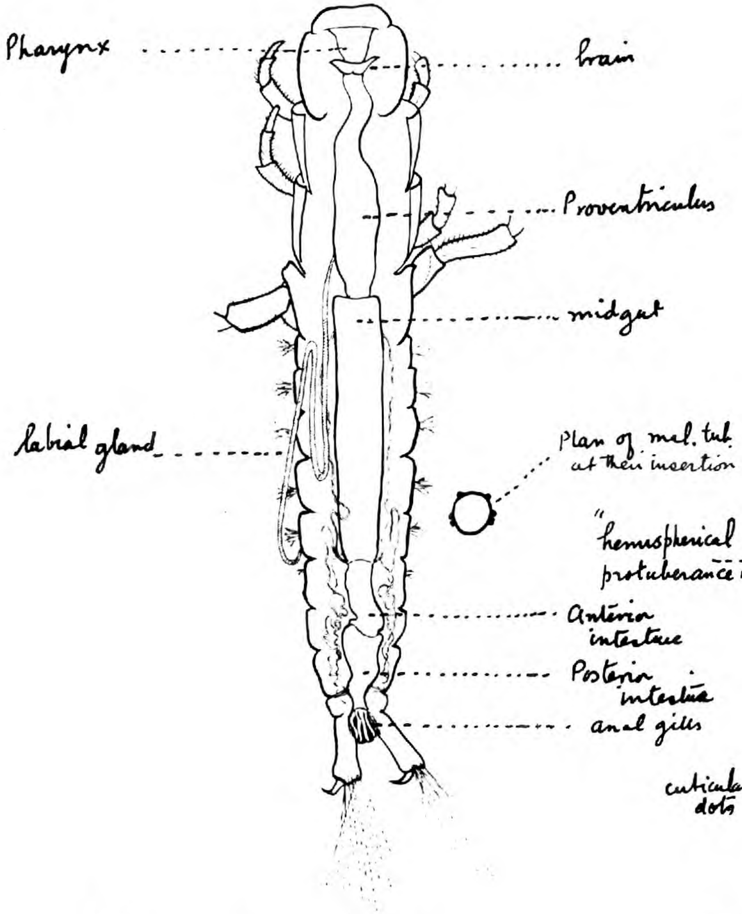
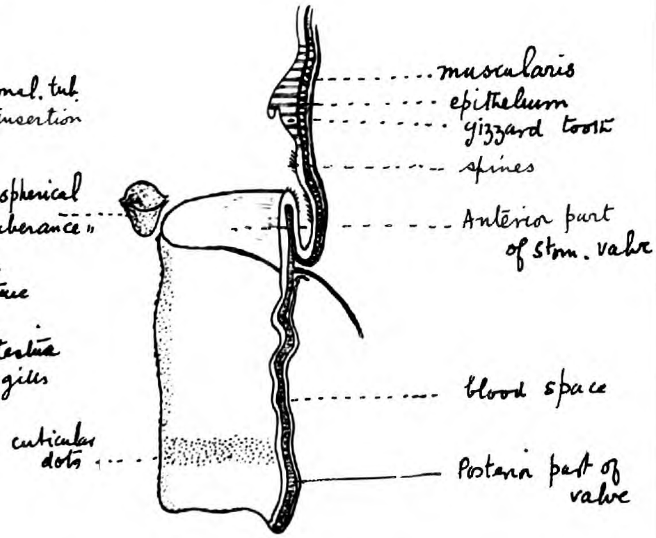


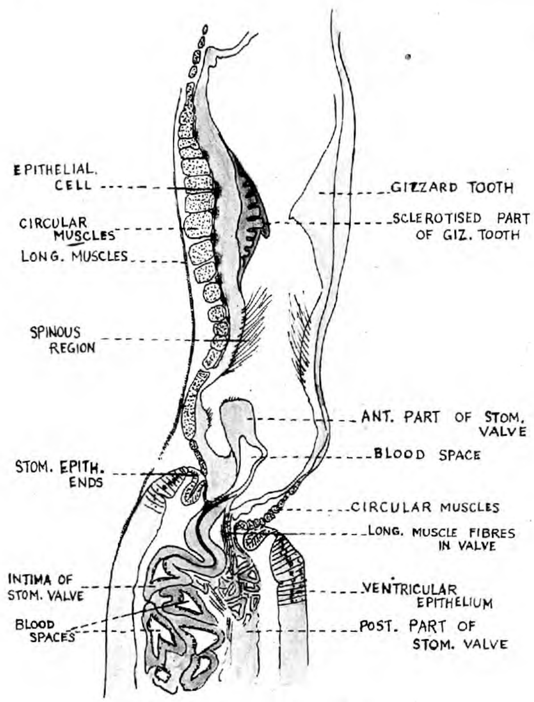
fig 1 ENTIRE GUT

HYDROPSYCHE



SECTIONAL VIEW OF GIZZARD AND STOMODEAL VALVE.

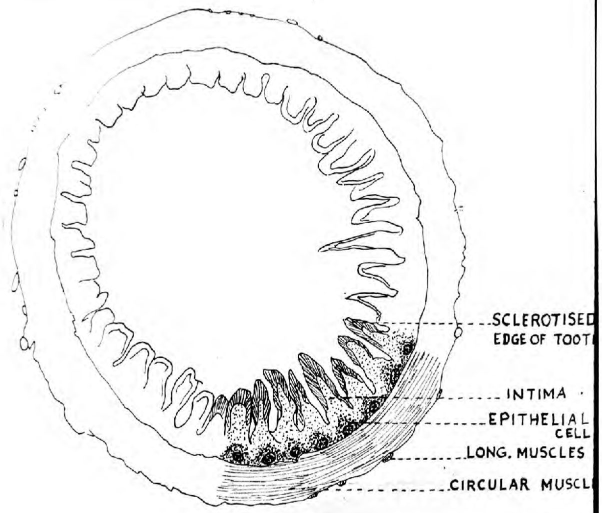
fig 2.



HYDROPSYCHE

PROVENTRICULUS, L.S.

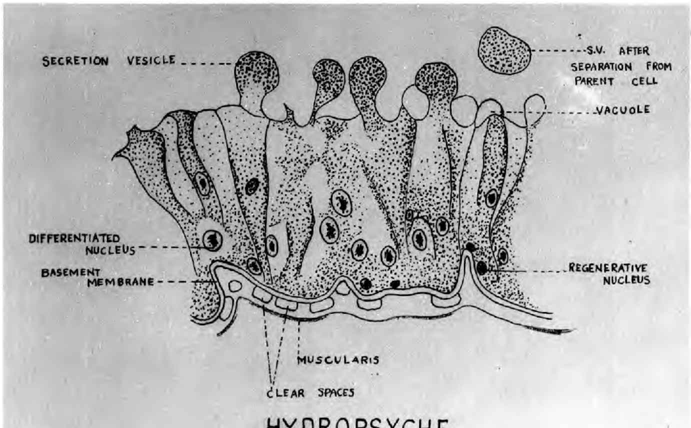
fig 3



HYDROPSYCHE

GIZZARD, T.S.

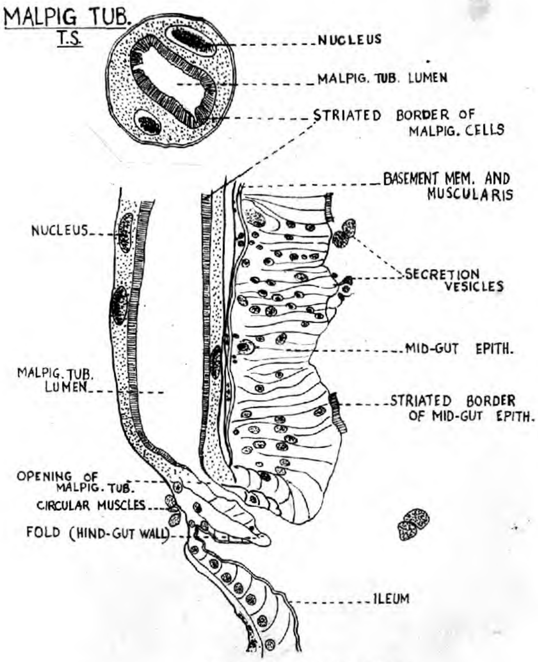
fig 4



HYDROPSYCHE

MID-GUT, L.S.

fig 5



HYDROPSYCHE

L.S. OF PYLORIC REGION

fig 6

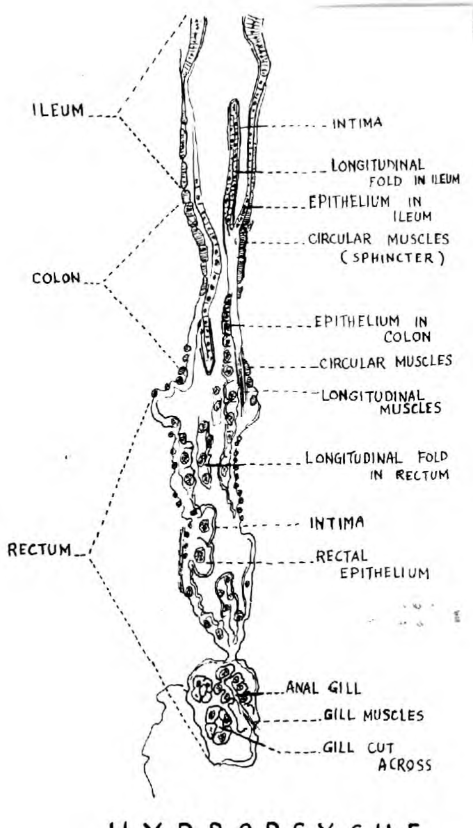
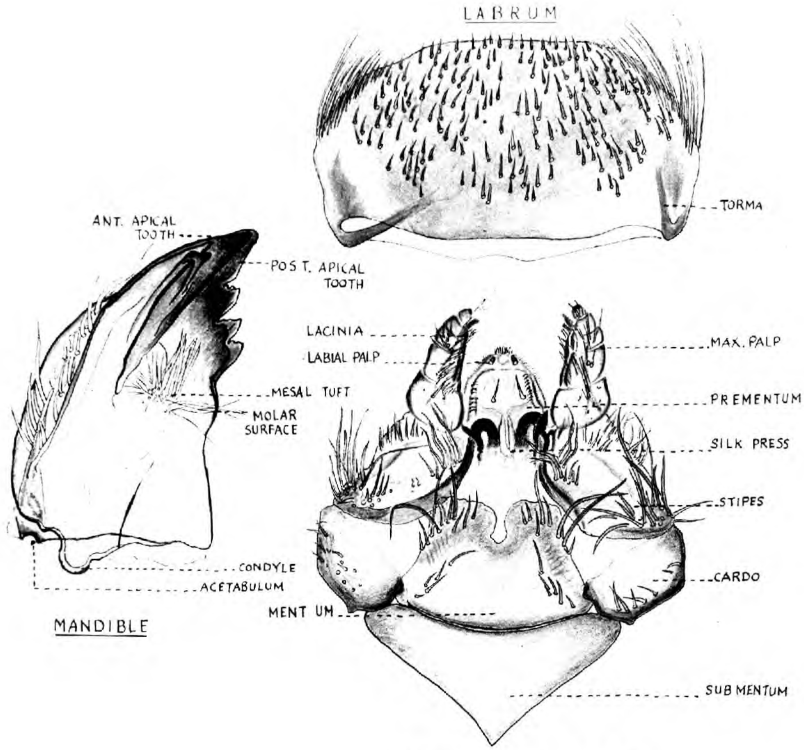


fig 7

HYDROPSYCHE

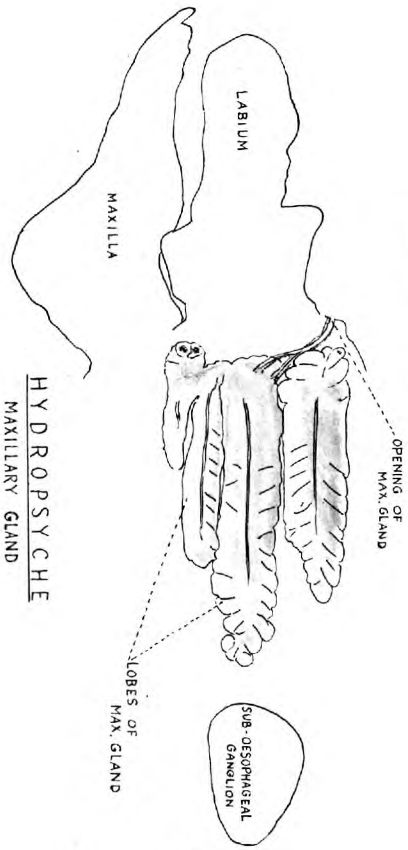
HIND-GUT, L.S.

(DETAIL SHOWN IN PLACES)



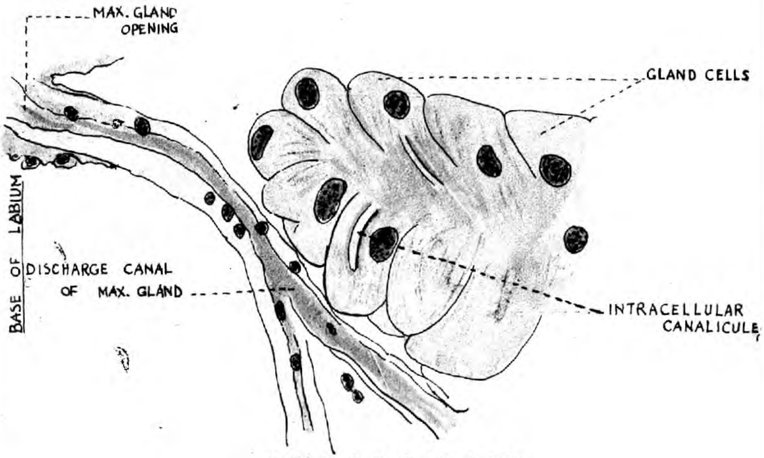
HYDROPSYCHE
MOUTH-PARTS

fig 8



HYDROPSYCHE
MAXILLARY GLAND

fig 9



HYDROPSYCHE
DETAIL OF MAXILLARY GLAND

fig 10

RHYACOPHILA

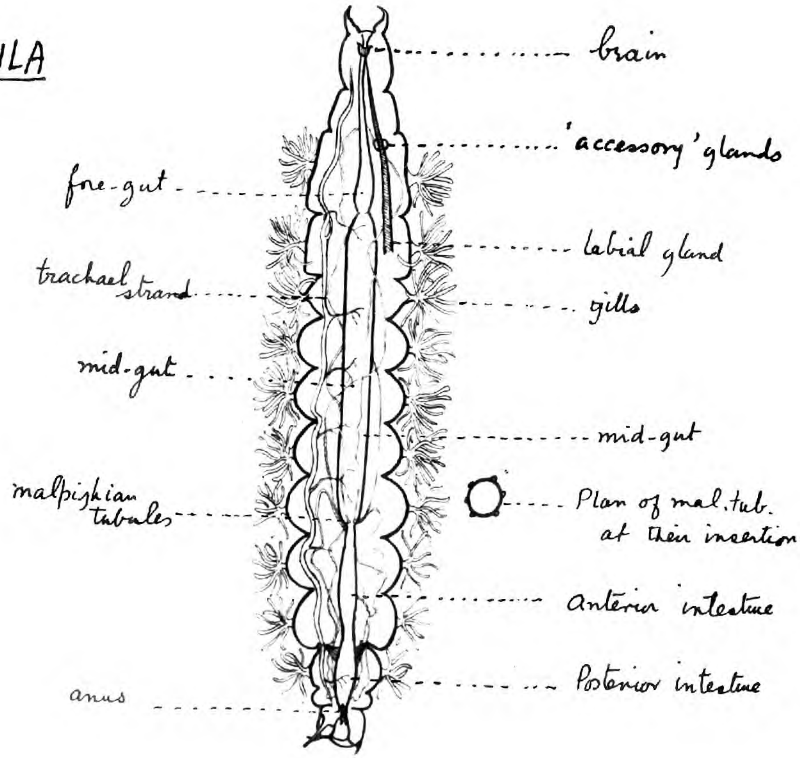
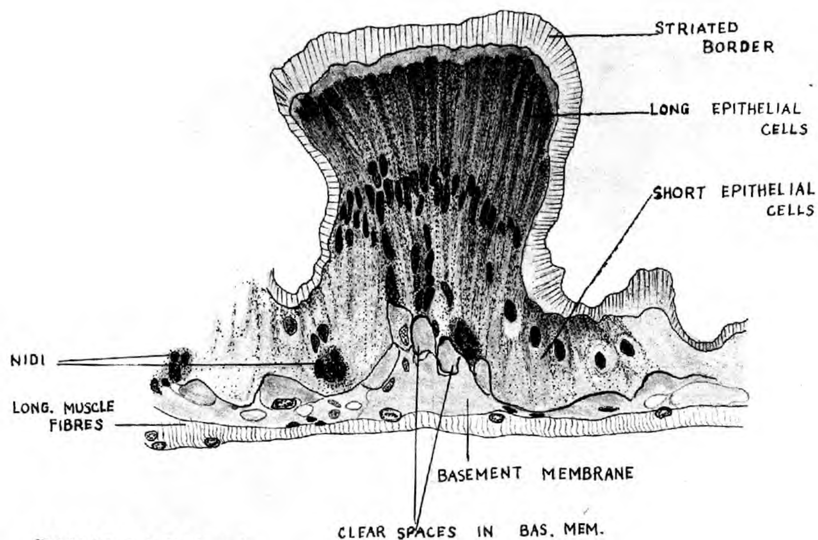
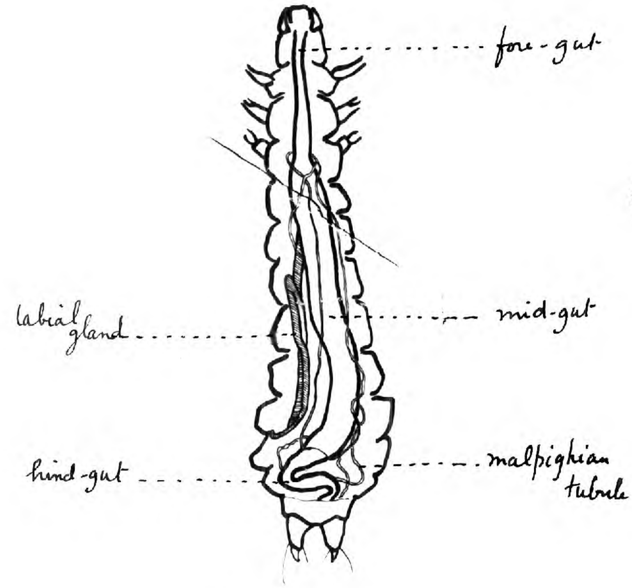


fig 11



RHYACOPHILA
MID-GUT, L.S.

fig 12



AGAPETUS

fig 13

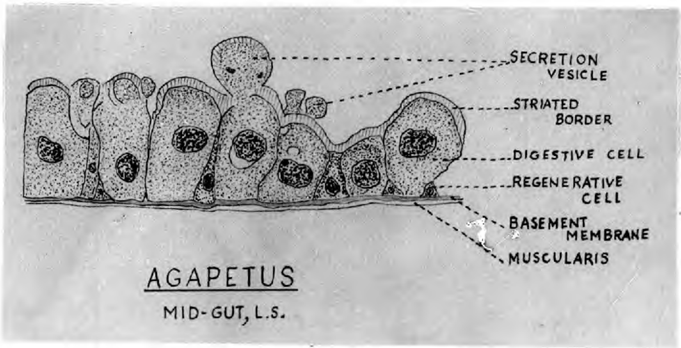


fig 14

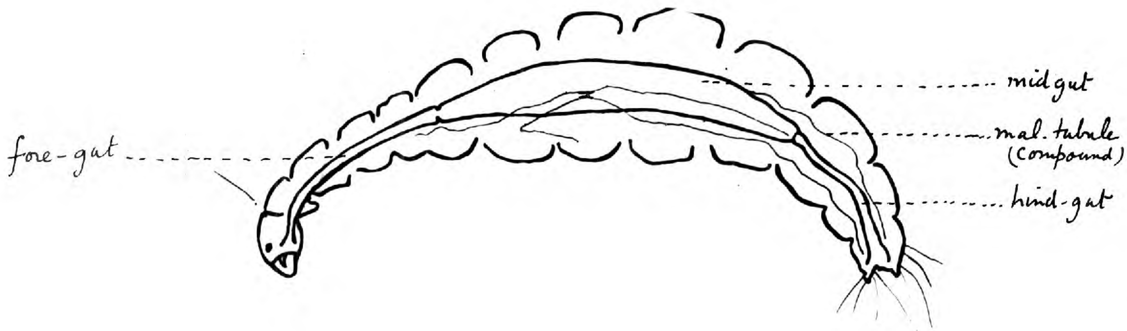
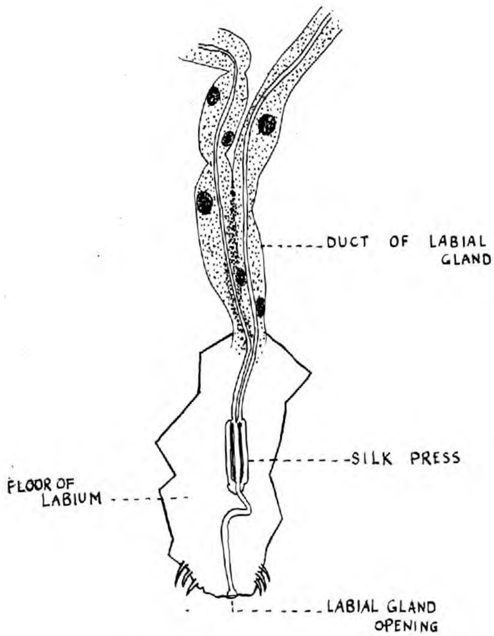


fig 15

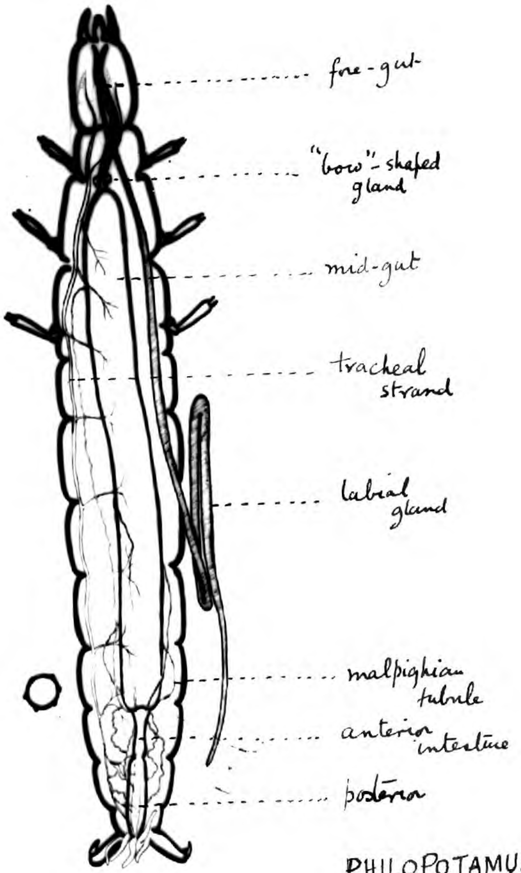
HYDROPTILA



PHILOPOTAMUS

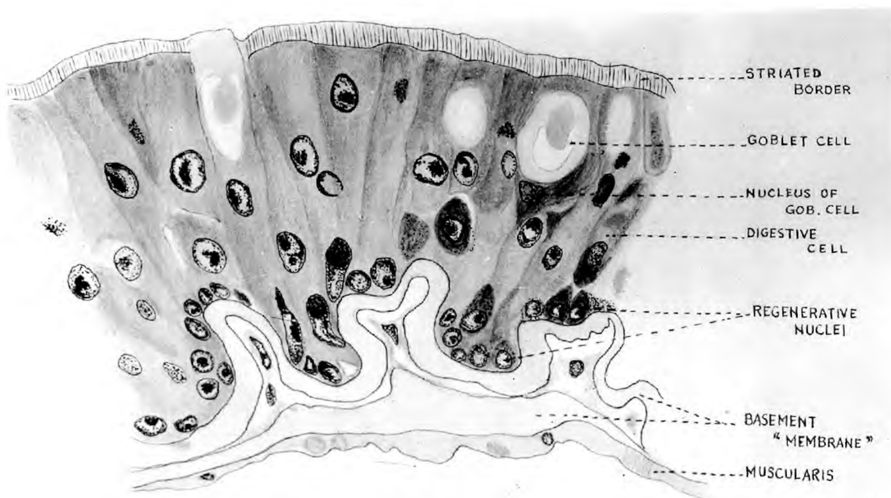
LABIAL GLAND OPENING

fig 17



PHILOPOTAMUS

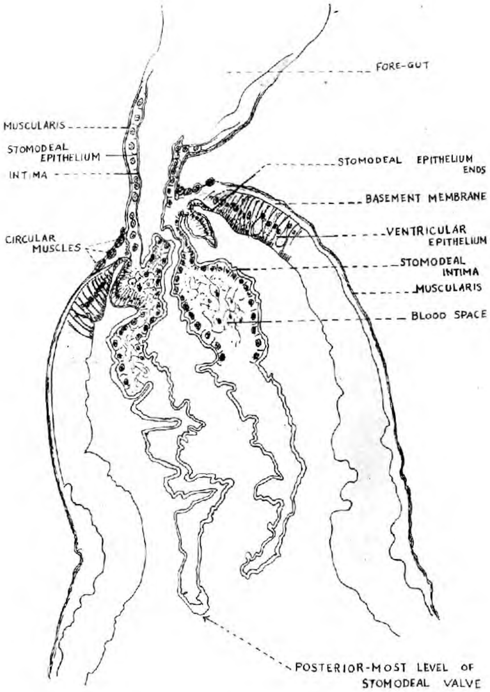
fig 16



PHILOPOTAMUS

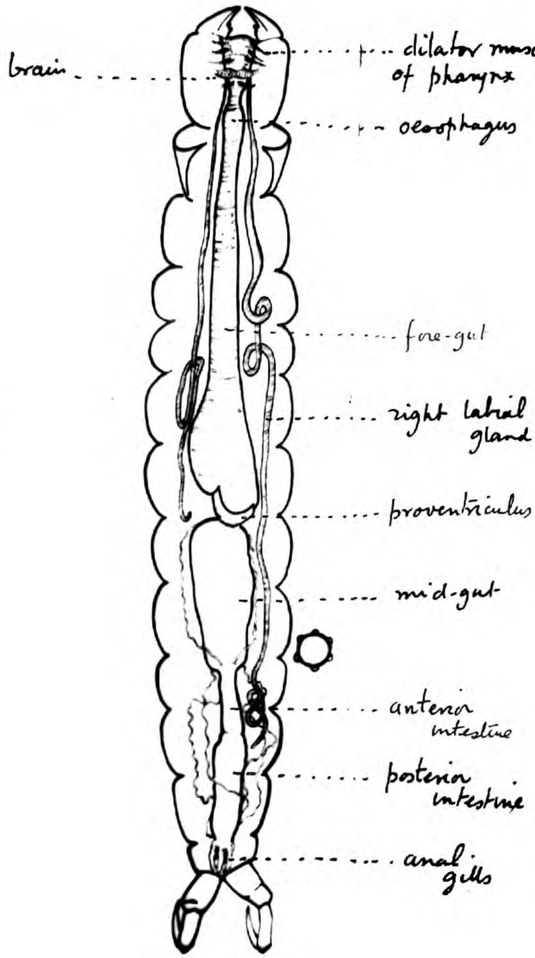
MID-GUT, L.S.

fig 18.



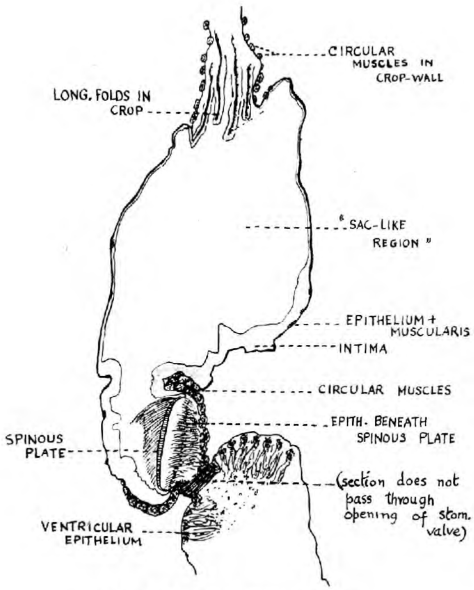
PHILOPOTAMUS
STOMODEAL VALVE
(SEMI-DIAGRAMMATIC)

fig 19



POLYCENTROPUS

fig 20



POLYCENTROPUS
GUT, L.S.

fig 21

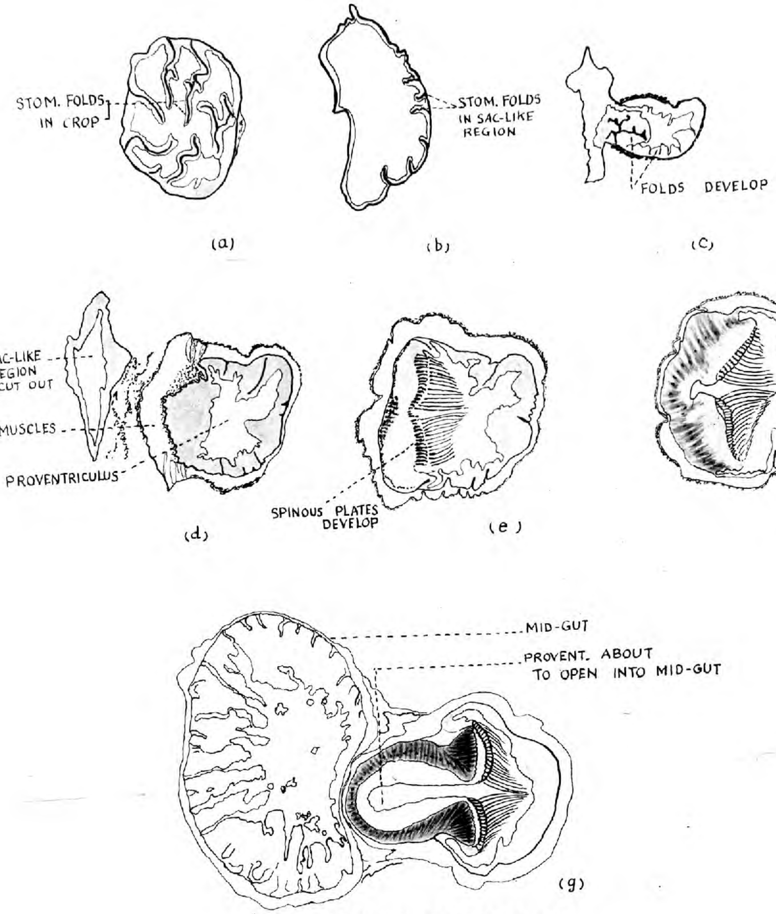
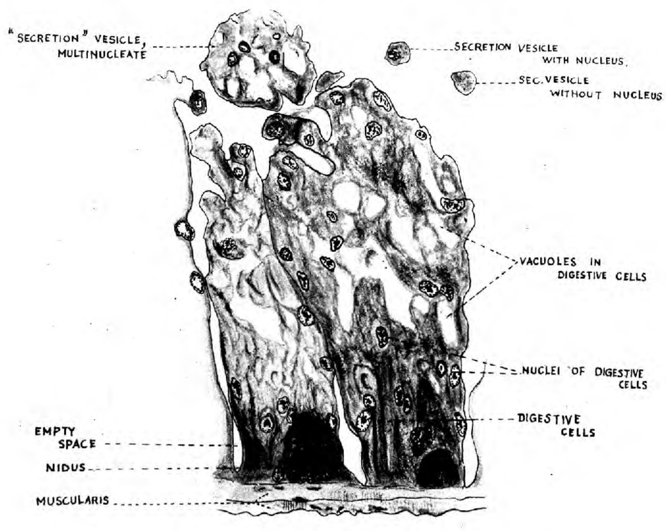


fig 22

POLYCENTROPUS

PROVENTRICULUS
T.SS. AT DIFFERENT LEVELS



POLYCENTROPUS

MID-GUT, L.S.

fig 23

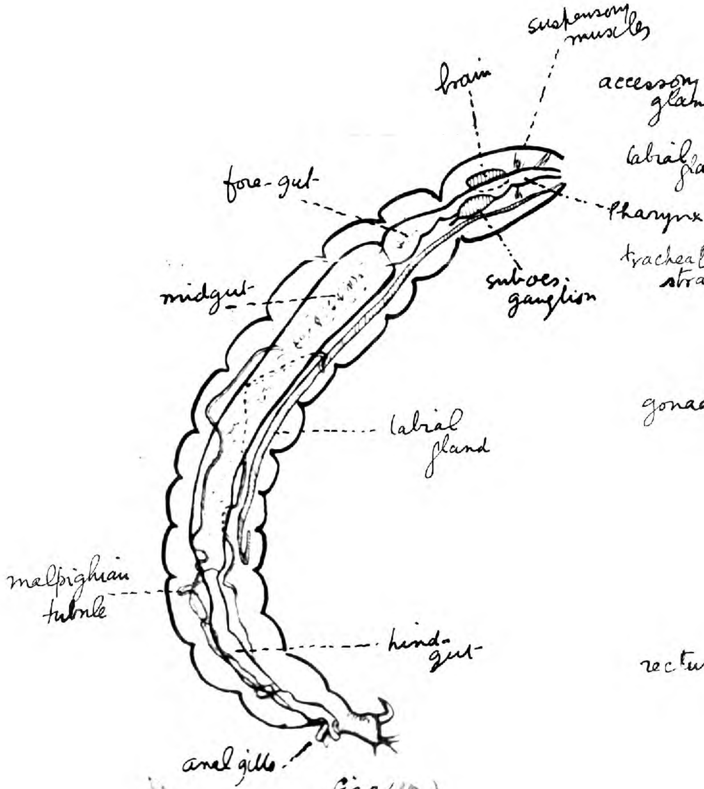


fig 26 (a)

PSYCHOMYIA

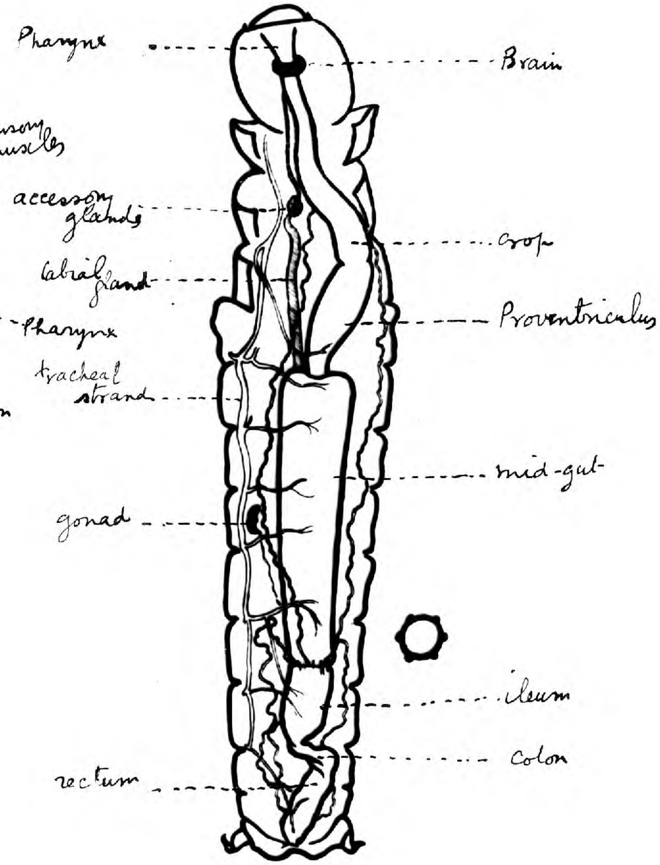
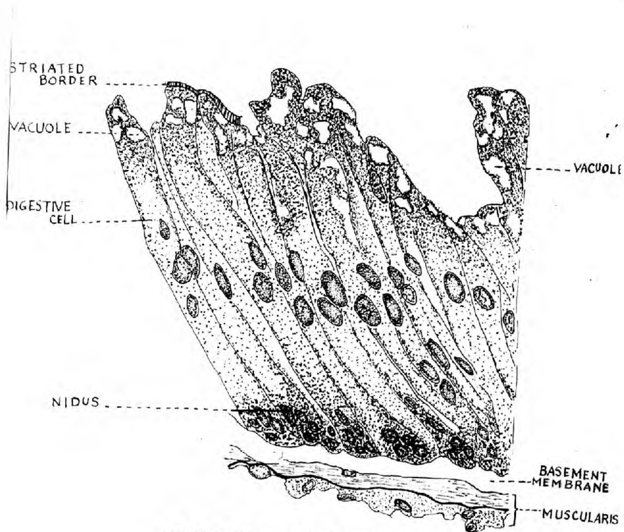


fig 24

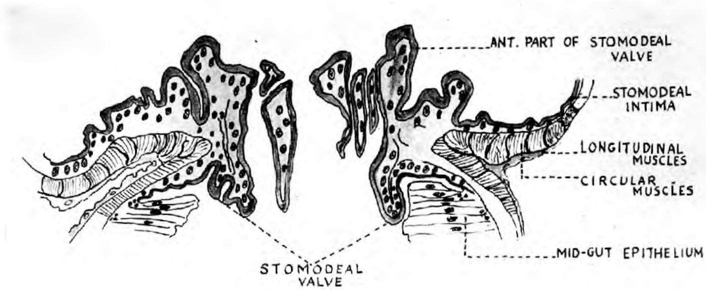
ODONTOCERUM



ODONTOCERUM

MID-GUT, L.S.

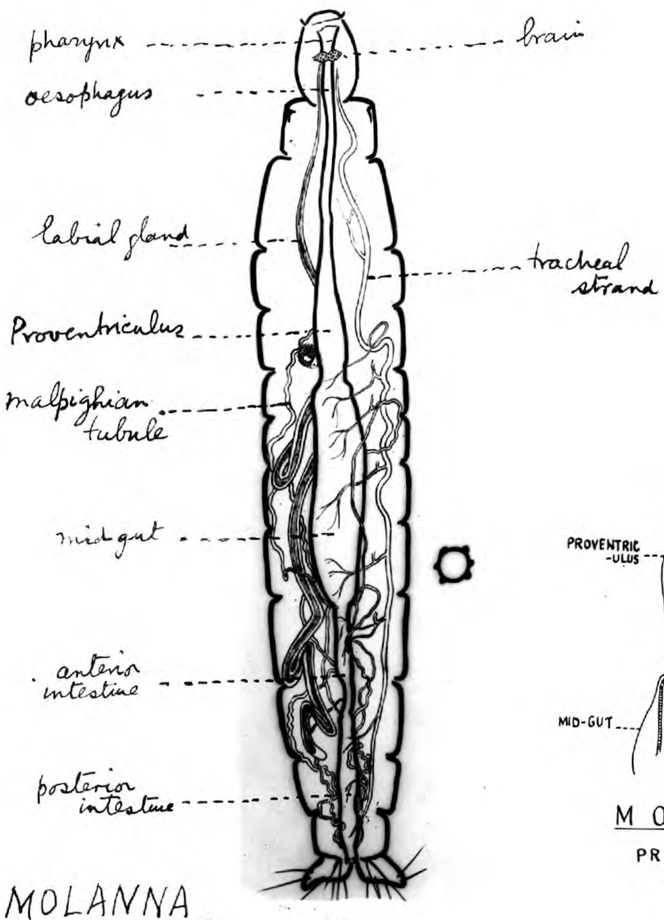
fig 25



ODONTOCERUM

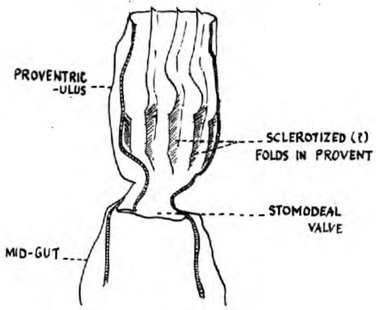
STOMODEAL VALVE, L.S.

fig 26



MOLANNA

fig 27



MOLANNA

PROVENTRICULUS

fig 28

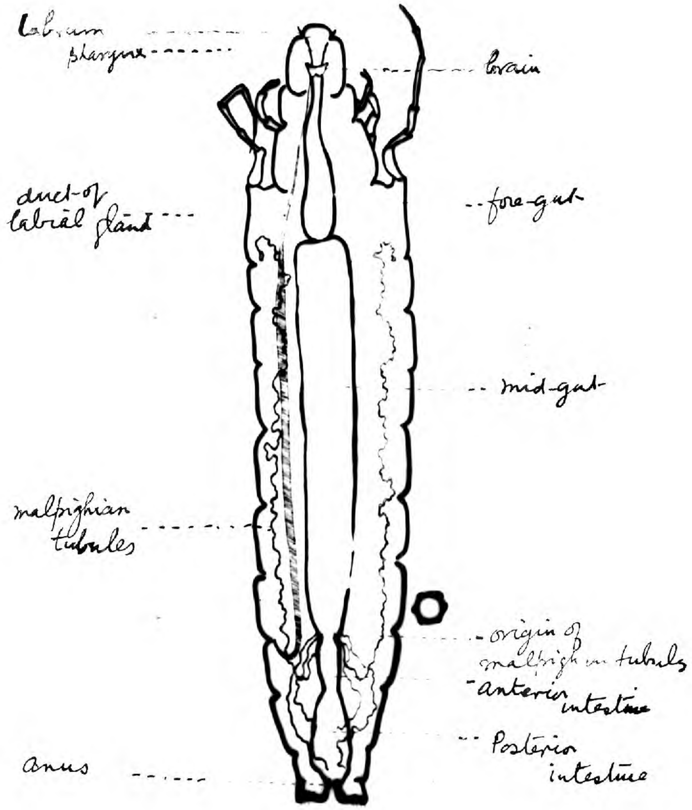


fig 29

LEPTOCERUS

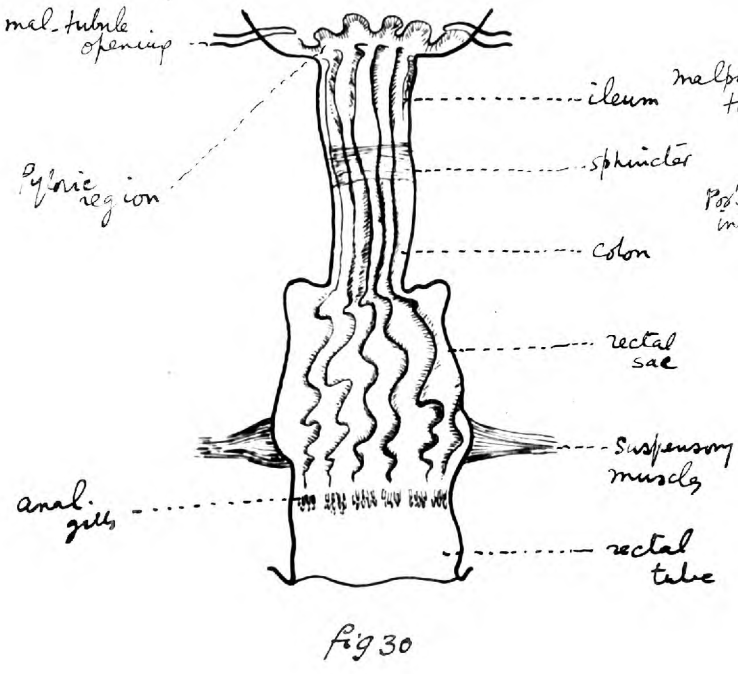


fig 30

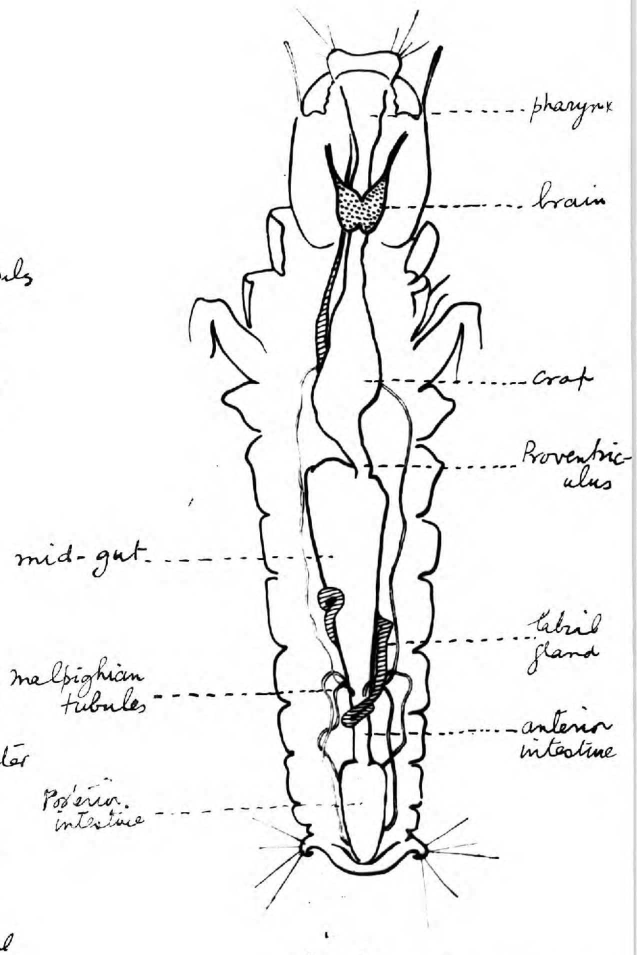
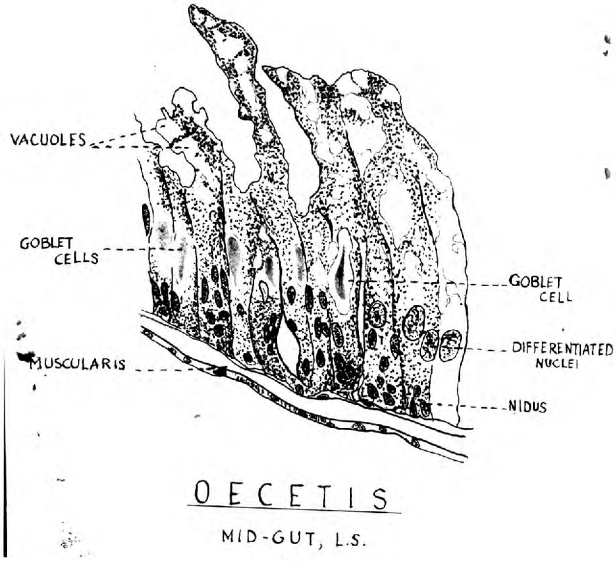


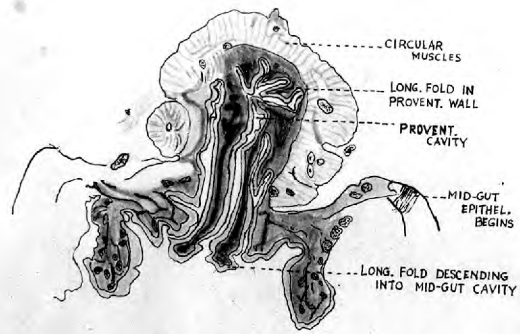
fig 31 OECETIS



OECETIS

MID-GUT, L.S.

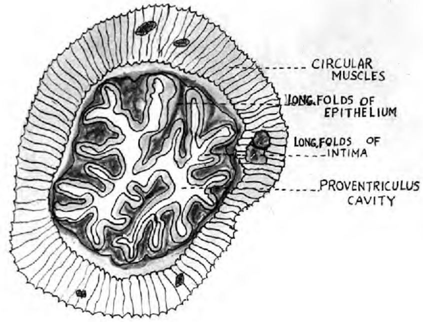
fig 32



OECETIS

PROVENT. JOINING MID-GUT, T.S.

fig 33



OECETIS

PROVENTRICULUS, T.S.

fig 34

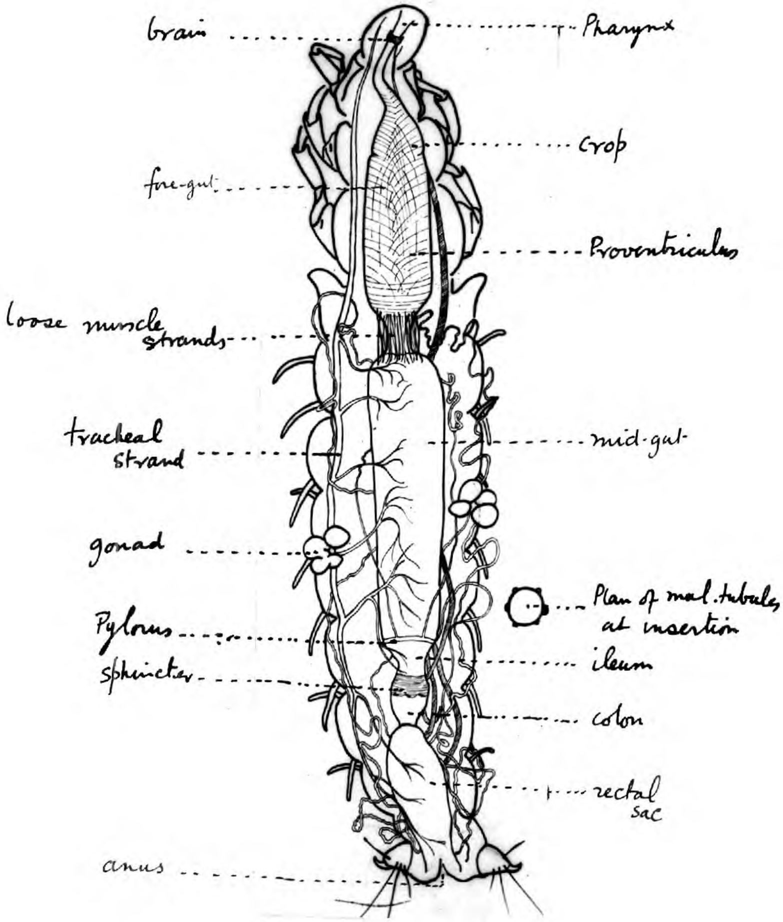
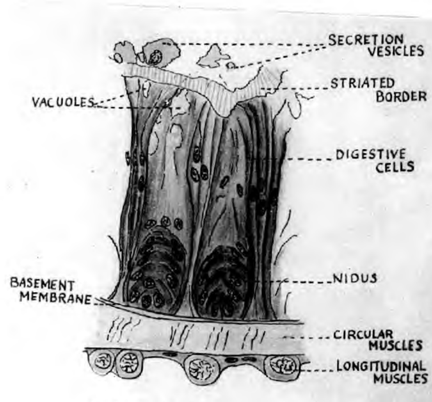


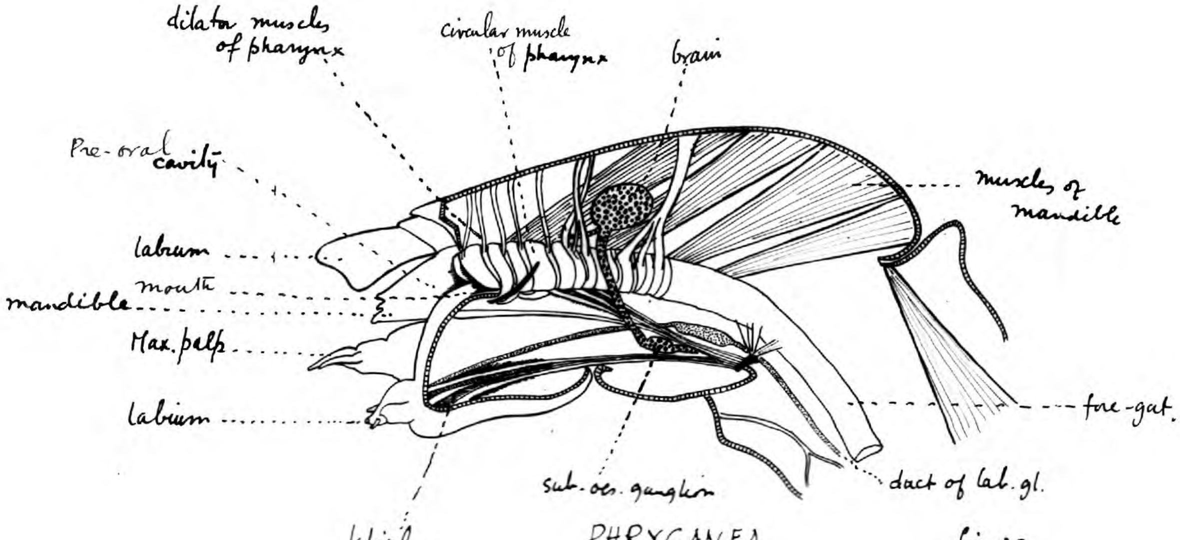
fig 35

PHRYGANEA



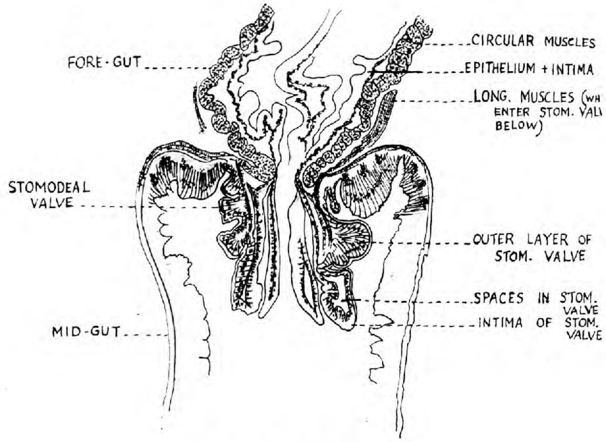
PHRYGANEA
MID-GUT, T.S.

fig 36



PHRYGANEA

fig 37



PHRYGANEA
- STOMODEAL VALVE, L.S.

fig 38

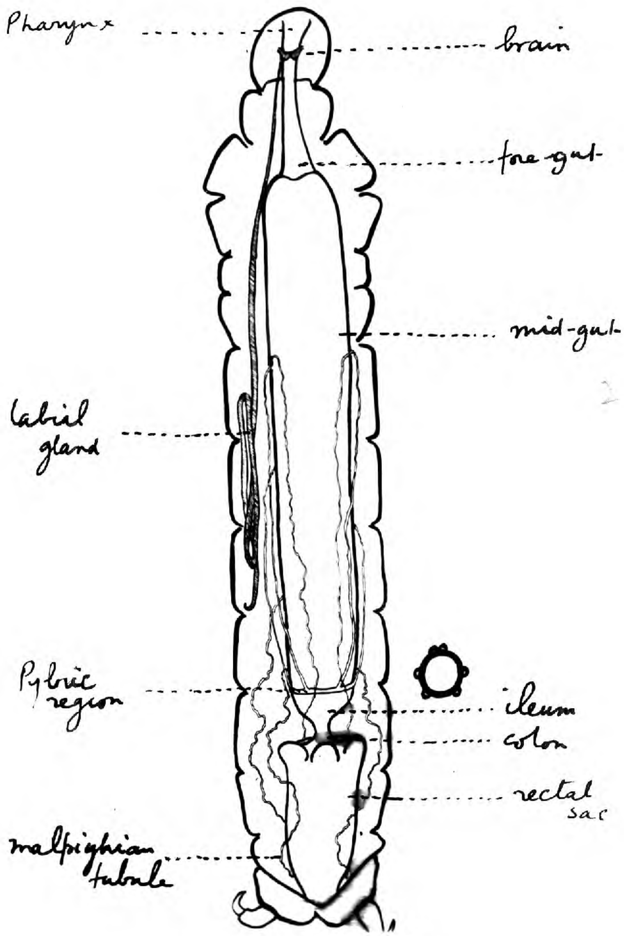


fig 39

GLYPHOTAELIUS

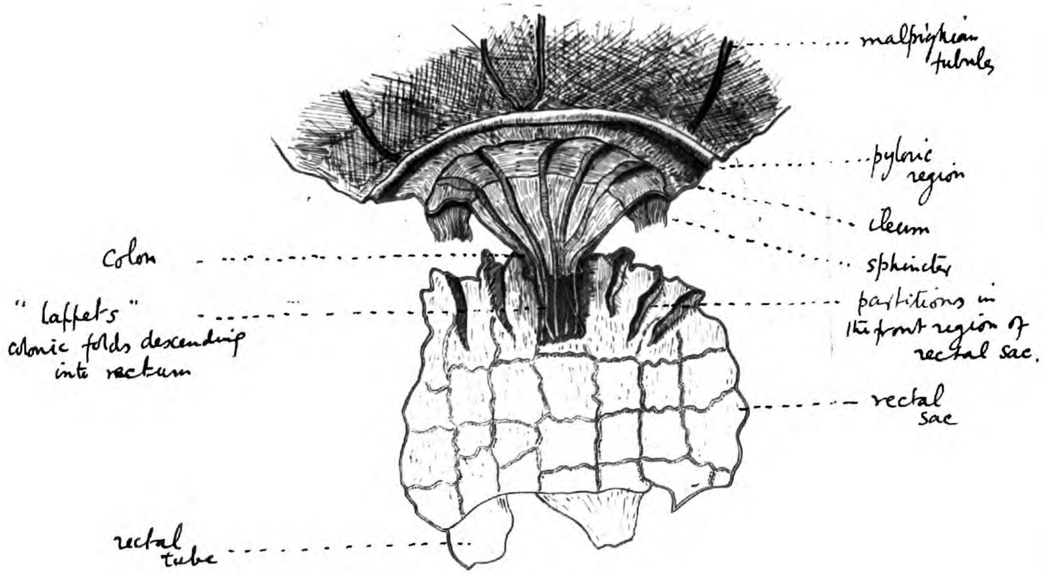
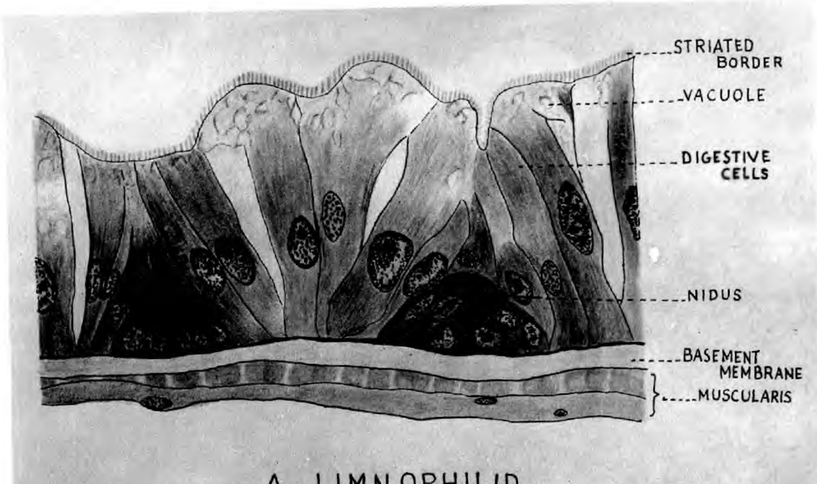


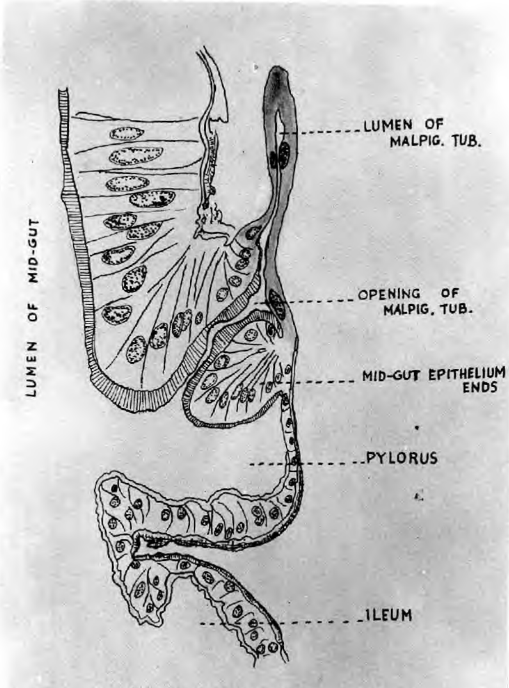
fig 40

GLYPHOTELIUS
Hind-gut dissected open



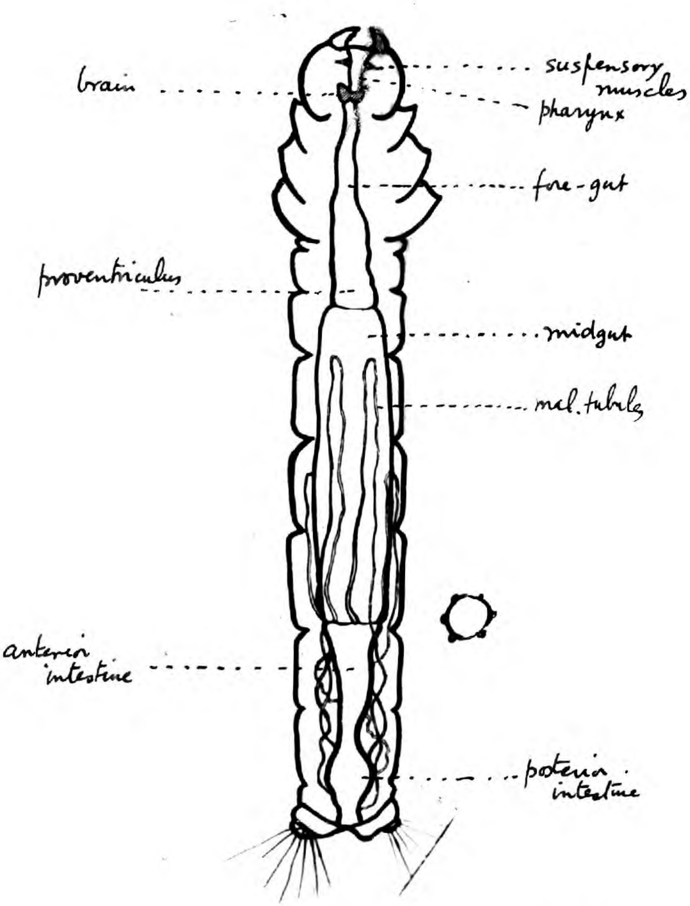
A LIMNOPHILID
MID-GUT, L.S.

fig 41



ANABOLIA
PYLORUS, L.S.

fig 42



BRACHYCENTRUS fig 43

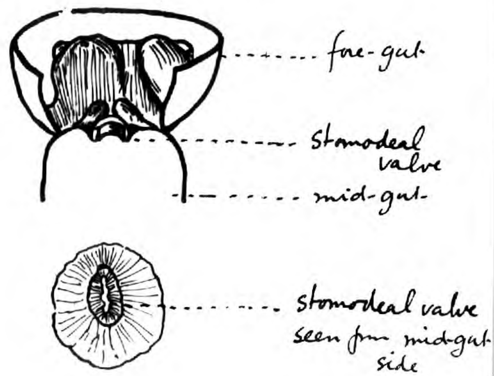


fig 44

BRACHYCENTRUS
proventriculus dissected open

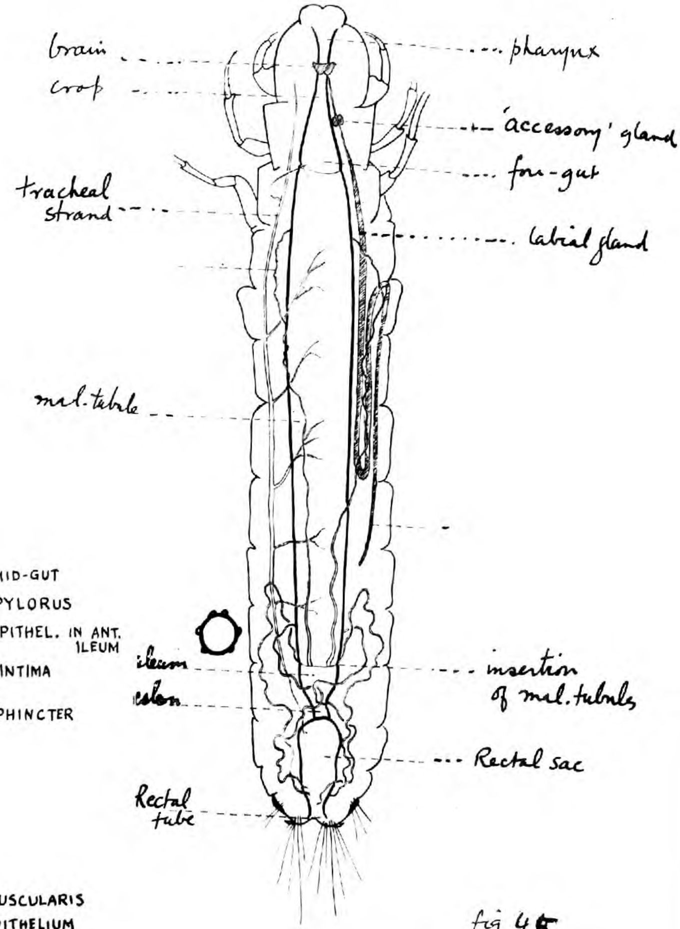
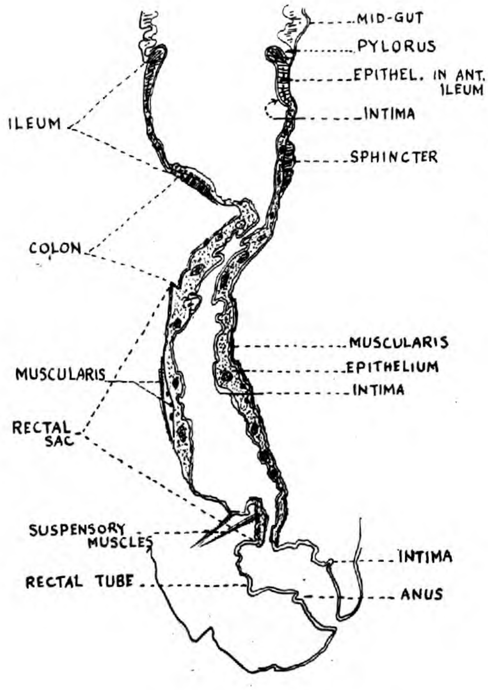


fig 45

SERICOSTOMA



LEPIDOSTOMA

HIND-GUT, L.S.

fig 46

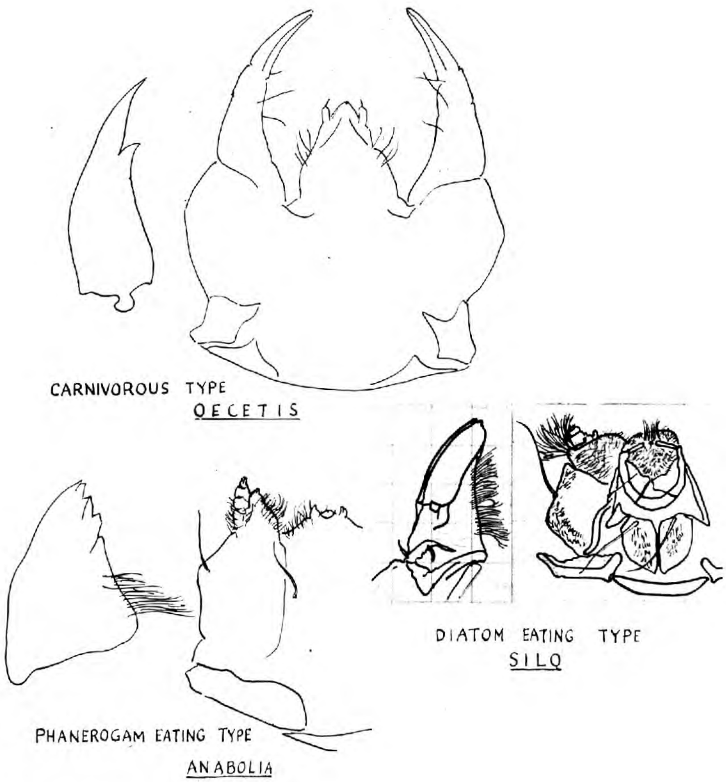
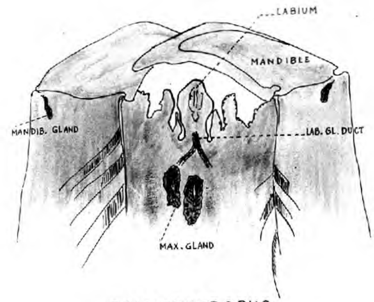
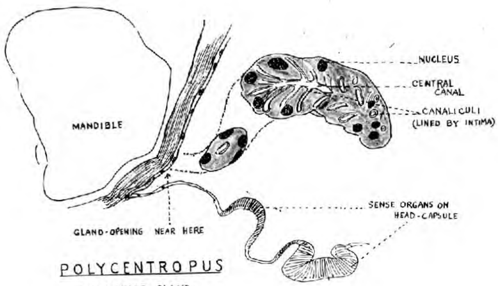


fig 47

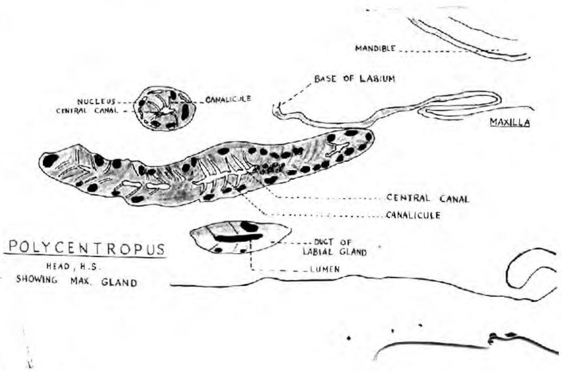
MOUTH-PARTS OF TRICHOPTERA



POLYCENTROPUS
SITUATION OF
HEAD-GLANDS
IN H.S.



POLYCENTROPUS
MANDIBULAR GLAND

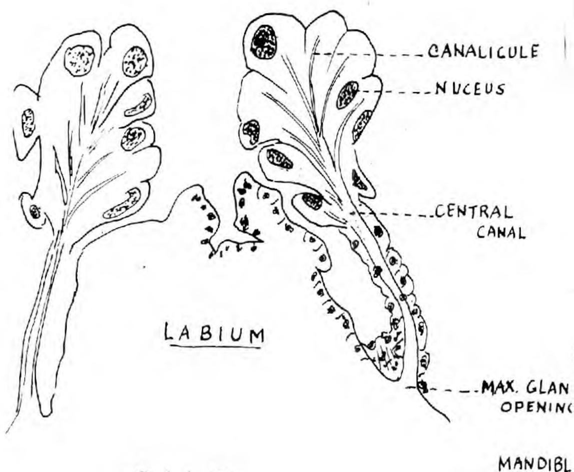


POLYCENTROPUS
HEAD, H.S.
SHOWING MAX. GLAND

fig 48

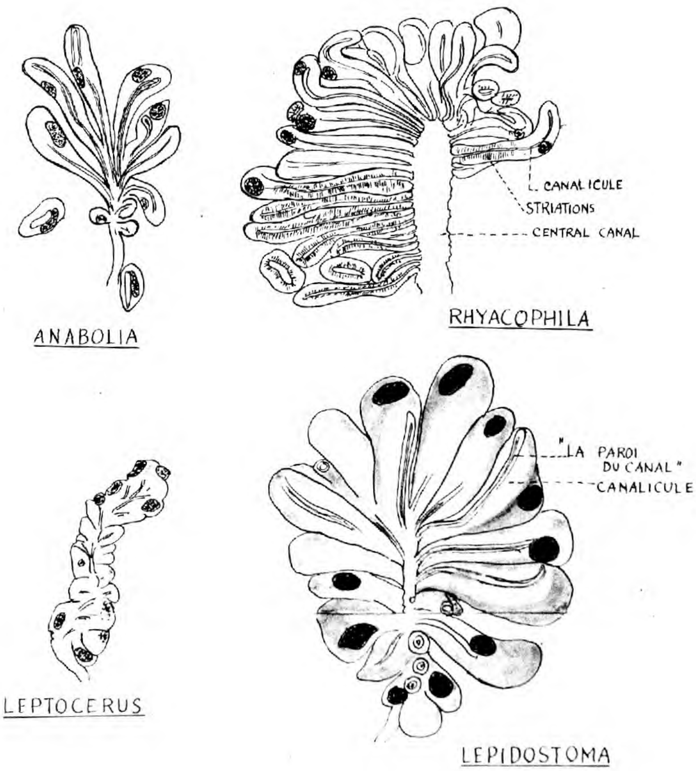
POLYCENTROPUS

MOUTH-PARTS



SILO
MAXILLARY GLAND

fig 49



MAXILLARY GLANDS

Fig. 50