ON THE LARVAL STAGE OF PEDICIA RIVOSA, L.

by

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During the Spring of 1923 Dr. R. Stewart MacDougall suggested to me that a study of the larva of *Pedicia rivosa*, L. would form a very interesting piece of work, and with this in view I accordingly went north into Argyllshire to collect larvae and to observe their environment and mode of living.

This paper deals with the fully-grown larva, its structure and anatomy, together with records of observations made on the habitat, life, etc. of living specimens.

I wish to take this opportunity of thanking Dr. R. Stewart MacDougall for his kindness in assisting me during the course of the investigation with information regarding literature and general technique, and also in supplying me with several specimens of the larva from his private collection and through the agency of Miss D.J. Jackson who very willingly sent me several examples of living larvae. I am also indebted to Mrs. R. S. MacDougall for showing me the exact location of the animals, in Argyllshire. To Mr. Percy H. Grimshaw, of the Royal Scottish Museum, Edinburgh, I owe my thanks for his having placed at my disposal his records of the distribution of the insect. Professor J.H. Ashworth also gave me some help with a protozoan parasite of the larva, and I desire to acknowledge my thanks to him. The work has been carried in the Department of Entomology, the University of Edinburgh.
INTRODUCTION.

In agreement with the method generally used by systematists in zoological work the following short note on the systematic position of the insect under consideration is as far as possible in accordance with the generally accepted theory of evolutionary development in the arrangement of the Diptera. Malloch's (11) arrangement has been taken as the basis.

Pedicia rivosa, L. belongs to the suborder Orthorrhapha, division Nematocera, and according to Brauer's grouping is contained in the Section or Tribe of Brauer Polyneura. Its inclusion in the Limnobiidae is justified amongst other characteristics by the short antennae - shorter than the maxillary lobe, the labium subdivided into two lobes, the mandibles having more than two teeth, and the apical segment with less than six processes.

The subfamily Pedicinae in which the insect is placed has, as one definite character, the possession of pseudopods or elevated transverse areas on some of the abdominal segments, which fact is easily recognisable in the species under discussion. These remarks naturally refer to the larval stage.

Genus PEDICIA, Latreille. (Gr. a field).

This genus was first introduced by Latreille (9) who placed it among the Tipulidae longipalpi. It is, according to Alexander (2:899-900, and 3:568), a small one and contains only six described species, one of them occurring in Europe, four in North America and one in Japan. Of the four North American species two are eastern and two western in distribution. These species include the largest and most handsome of the Limnobiidae.

Needham (15 and 16) was the first to describe and figure the larva of the commonest eastern American species, Pedicia albivitta, Walk.

The European species, Pedicia rivosa, Linn. was found by Beling who described the larva and pupa (4).
DISTRIBUTION.

*Pedicia rivosa*, L. is a European species but according to the literature does not occur in America. Beling (4) found it in Germany where he described it. Schiner (13) also quotes it as being a German species. Dr. MacDougall tells me that it occurs in Ross-shire, and records(10) his having been given both adult and larva by Miss L.H.Huie, F.E.S. from various parts of Argyllshire. Rennie (17) notes species of Tipulidae occurring in the district surrounding Aberdeen and says "*Pedicia rivosa*, L. widely distributed in the northern area, but not common". Other locality records are:

(a). Gibside, 1 ♂; Healeden, 2 ♂, 31-7-00. Rev. W.J.Wingate in *A Preliminary List of Durham Diptera*, etc. Fam. XII, Genus 128, Species 783.


(c). Near Evanton, Ross-shire, Scotland. vii and viii.1924. Specimens were kindly sent to me from this locality by Miss D.J.Jackson.


Mr. Percy H. Grimshaw kindly supplied me with the following localities which have been recorded for *Pedicia rivosa*, L.:


The following records have hitherto been unpublished, and I have to thank Mr. Grimshaw for allowing me to include them in this paper.

Specimens in the Museum from Glen Falloch (Loch Lomond), Levisham (Newtondale, Yorkshire), and Bonhill (Dunbartonshire).
THE EGG.

Information regarding the egg is lacking. It is not known how many eggs are laid nor can a description of the egg be found. As the insect is decidedly aquatic it would be natural to expect that the eggs are deposited at the water surface as is the case in the majority of the aquatic forms of Crane-flies, and especially so in Dicranota bimaculata which is a closely allied form and which Miall suspected of having eggs "enveloped in a slimy mass, or egg-ropes, and laid in water." (12).

THE EARLY LARVA.

I have not been able to find any published accounts of any stages other than that of the full-grown larva. Fortunately I was able to examine three specimens which were similar in size and which I concluded were the second last larval stage, one of the larvae being a living specimen which ultimately moulted to grow to the size of the full-grown larva which is described later.

As far as I can ascertain this second last stage larva differs very slightly from the full-grown one, the chief points of difference being in size and in the head-capsule. From external appearance this younger form is a replica of the final stage larva but it measures about 24 mm. and has a diameter of 2-2.5 mm. The head-capsule when compared with the length is narrower in the younger larva than in the older larva, and the median chitinous septum which gives origin to the muscles and which projects downwards from the dorsal shield of the capsule is continued into a distinctly long pointed process, whereas, in the mature larval capsule, this septum ends almost flush with the sides of the capsular shield. The mandibles also are more slender and their sickle-shape is very apparent.

Whilst in captivity, as already stated, one larva moulted,
the entire operation being completed in about 80 hours. The head-capsule was first shed and then the body was removed from the old skin which split down the dorsal surface. Towards the end of the moult the cast skin became turned inside-out and the hind end of the body was quite easily withdrawn. The larva was almost colourless after the moult being very difficult to distinguish in the water. After about three days the head-capsule and posterior spiracles assumed their natural dark brown-black colour.

THE FULL-GROWN LARVA.

(a) External Form.

1. Body.

The larva is acephalous with a well formed retractile mandibular capsule, metapneustic, soft-skinned and cylindrical, 12-segmented with scarcely discernible secondary segmentation - i.e. each segment is divided into an anterior and a posterior half by a very slight constriction. In length it may measure 40-45 mm., being 5-5.5 mm. in diameter. The larva is very contractile, and when contracted may measure only 20-25 mm. long, being then 6-7 mm. in diameter. The general colour is creamy-white, the thoracic and first few abdominal segments being somewhat greyish-brown above, and paler at the sutures; the posterior half of the body is quite pale, almost transparent, the internal organs, and very specially the tracheae being distinctly seen through the cuticle. The entire ventral surface is paler but more greyish. In the water the larva appears as a gleaming object with a smooth skin, but the body is covered with a very short microscopic adpressed dusky pubescence. The three thoracic segments each bear a pencil of very small setae on the pleural region. The abdominal segments have a few - two or three at the most - small delicate individual setae borne laterally about the midlength of each segment, and, as
a rule, are situated just posterior to the inconspicuous depression or crease which marks off the posterior from the anterior annulus.

On segments 4 to 7 of the abdomen (i.e. segments 7 to 10 from the anterior end) are situated, ventrally, transverse creeping pads or raised areas on the anterior annulus of each segment. Each pad is prolonged ventro-laterally into a somewhat indistinct pseudopod which is unarmed but which is covered by a microscopic roughness. This roughness is present only on the pseudopods of the anterior pad, but proceeding backwards, the roughness spreads until the posterior pad is wholly covered both on transverse ridge and on pseudopods. The pseudopods increase very slightly in size from before backwards. These practically naked pseudopods thus differ from the distinct paired prolegs, armed with circlets of chitinised hooks, which are present in Dicranota (12). Again in Dicranota 5 pairs of prolegs are found on segments 6 to 10, while in this case only 4 pairs exist. Miall says: "In many of its external features the larva of Dicranota resembles that of the nearly allied Pedicia rivosa, L. Both belong to the same section (Amalopina) of the Tipulidae brevipalpi, and they are similar in size, colour, and habitat. The chief difference observed in comparing Beling's description of the larva of Pedicia rivosa with the larva of Dicranota was that the abdominal feet of Pedicia are said to be borne upon segments 8, 9, 10, and 11; while those of Dicranota are borne upon segments 6, 7, 8, 9, and 10." Beling's description of the larva of Pedicia rivosa (4) though not very full is useful, but he makes an error in stating that the pseudopods occur on segments 8 to 11 since they exist on segments 7 to 10.

At times the 10th and 11th segments may be expanded into a cone-like form, the apex being occupied by the terminal 12th segment. This expanded portion may attain a diameter of 7 mm. This phenomenon was also noted by Beling in Pedicia and in Limnophila lineola, Meig. as Grünberg (6) states: "In the case of the craw-
ling larvae (i.e. *L. lineola*, Mg.), as with the larva of *Pedicia rivosa*, the penultimate segment is wont at times to be strongly thickened."

Segments 1, 2, 3, and 8 of the abdomen are devoid of any appendages. The terminal segment, which is the smallest one and may only be half the length of the other abdominal segments, bears on its dorsal surface the two very conspicuous black hind spiracles. The spiracles are circular, separated by a distance about equal to the diameter of one, and are situated on a slightly protuberant elevation facing postero-dorsally.

More ventrally, but median in origin, are two spiracular lobes which are naked and slender, each bearing about 6 setae at the tip. These lobes are comparatively short but distinctly project behind the body being fairly thick-walled and enclosing fair-sized tracheae. In the insect under consideration the spiracular disc is by no means so salient when compared with that of *Tipula* larva.

Ventrally placed on the last segment are two pairs of anal tracheal gills which are constricted into two segments, the apical ones being more or less telescopic into the basal ones, while the whole gill is almost entirely retractile within the body. The anal gills, which are unbranched, are short, stout at the base, with an elongate conical segment, comparatively thin-walled, and are well supplied with tracheae and muscles used in contracting these appendages. The anus opens between the two pairs of gills in the mid-line.

2. **Head-capsule.**

The head-capsule is massive, shining black-brown and elongated, four-sided and flattened. The labrum is broadly transverse, with the lateral parts a little enlarged and projecting anteriorly into blunt lobes, with a long seta near the inner margin and a small papilla just internal to this. The median anterior region of the labrum has two shorter widely separated setae each of which has a small papilla placed laterally to it. The epipharynx reaches almost to the edge of the labrum; its
sides being subparallel. Anteriorly it is roughened into a narrow transverse band of small spines, which is succeeded posteriorly by a broader band of hairs.

The mentum (labium of Beling; pharyngeal plate of Meinert; submentum of Miall) is completely divided by a median cleft, each half being continuous with a ventral plate of the same side. The anterior margin of each half bears three slender flattened teeth, the middle one of which is slightly the shortest. Just lateral to the base of each half of the mentum is situated a single long seta which reaches to the tip of the teeth. The hypopharynx (labium of Meinert; mentum of Miall) is fairly conspicuous and resembles the shape of the labrum. The anterior margin has a deep notch to form distinct lobes at the lateral angles. It bears on its dorsal surface several rows of small chitinised plates or spines. The common salivary duct opens dorsally from it at about one-third of the total length from the anterior edge.

The mandibles are elongate, sickle-shaped and powerful, the ventral cutting inner edge bearing a row of about four teeth which are successively enlarged from tip to base, the basal tooth being very broad and flat with the outer margin truncate or slightly concave. The remaining teeth are also more or less truncate. The teeth on the dorsal cutting edge are indistinct. On the scrobal region of the mandible is situated a pencil of moderately delicate setae, while a second pencil is found on the prosthecal region.

The maxilla is elongate, with distinct outer and larger and inner smaller lobes, which are chitinised. The base which probably represents the cardo and stipes is feebly chitinised and shows no distinct form. The inner lobe is narrow and elongated, with several isolated small setae near the tip and a long powerful seta on the ventral face, a short distance from the apex. The outer lobe bears, near the tip, a few small setae, while the actual apex is occupied by the palp which is flat and circular with a few disc-like papillae around its margin, and a few sensory papillae or pegs scattered over the pale apex.
The antennae are borne on the anterior lateral margin of the head-capsule at the sides of the labrum. They are small, thin, and cylindrical, the basal segment being elongated and slightly curved with a circular auditory plate near the base. Numerous papillae are present at the tip, two of which are very long being nearly as long as the segment itself. The other papillae are tiny cylindrical pegs and number only three or four.

The top of the head-capsule consists of a protecting chitinous shield which is very strong behind. From this descends, in the posterior half of the capsule, a median chitinous septum which serves as an origin for muscles. At the anterior part of this shield, just behind and internal to the bases of the antennae are two darker patches which are devoid of structure and which may represent eye-spots. The whole of the head-capsule is occupied by muscles which consequently displace the brain.

(b) Internal Structure.

1. The Body-wall and Coelom.

The cuticle is fairly stout and has attached to it at several points the very numerous annular muscles. Internal to these are the longitudinal muscles which are less numerous and which are grouped into definite tracts. A broad band occurs on either side of the dorsal vessel, while another traverses the whole ventral surface. A narrow band runs down each side.

The fat-body, which envelopes the alimentary canal and extends almost throughout the whole body of the larva, consists of two much-folded semicylindrical masses.

2. The Digestive System.

The alimentary canal in this carnivorous type of Crane Fly is a nearly straight tube of unequal diameter running from the front of the head-capsule to the last segment, with a minimum of appendages such as caeca and diverticula. It is divided into
Fore-gut, Mesenteron or Mid-gut, and Hind-gut, and is provided with salivary glands and Malpighian tubes.

The Fore-gut extends from the mouth to the posterior part of the metathorax but, owing to the contractions and relaxations of the muscles of the head-capsule, the junction of the fore- and mid-gut may be displaced considerably from the normal position. The mouth is formed by the labrum and epipharynx above, the mandibles and maxillae at the sides, and the mentum and hypopharynx below. The ventral inner surface of the epipharynx bears numerous short setae and spines which are directed backwards and which probably may be sensory and also may assist in holding and cutting the food. The mandibles are mostly used for taking the food into the mouth, and these are moved in almost the same plane. Immediately behind the mouth the dilated fore-gut forms the pharynx from whose walls muscles radiate to the walls of the head-capsule. Circular muscle fibres are present in the wall of the pharynx. The pharynx quickly narrows to form a tube of nearly uniform calibre and simple structure. This part, the oesophagus, is lined by a chitinous intima which is much folded longitudinally. Outside the epithelium lies a muscular coat which consists of a layer of circular fibres forming a series of transverse rings. About the middle of the mesothorax the oesophagus dilates somewhat and may at times be folded slightly on itself. Just where the oesophagus joins the stomach a constriction occurs which may function as an oesophageal valve.

The Stomach which follows is yellowish in colour and extends from the metathorax to the middle of the 9th segment, while in diameter it exceeds that of the fore-gut and hind-gut. The stomach is broadest in front gradually narrowing to a slight constriction about two-thirds of its length where it again slightly dilates to meet the hind-gut. The widest portion of this mid-gut is almost twice that of the narrowest part. Owing to the fact that preserved specimens do not give satisfactory sections I was unable to study the structure of the walls. The preparations show, however, close-set internal annular muscles overlaid by longitudinal mus-
The Hind-gut commences at the 9th segment and extends to the anus, the wall being lined with longitudinally folded cuticle. Here the position of the muscles is reversed the longitudinal muscles being internal to the annular muscles. Near the anus, which is situated between the two pairs of anal gills, the intestine dilates somewhat and the annular muscles become close-set. This probably forms the rectum but no sharp distinction between ileum and colon exists.

The Salivary Glands are fairly large and lie on either side of the oesophagus, occupying the first three segments. They are much folded and twisted on themselves. The glands are fairly long stretching to the end of the first abdominal segment when pulled out straight. They are comparatively narrow in diameter, the lumen being quite narrow. The end of each gland is flattened into an elongate lobe which is in intimate connection with the abundant fat tissue. The epithelium of these glands is characterised by the large nuclei as are seen in the glands from the larvae of Chironomus and Musca. The paired salivary ducts are very slender tubes passing from the anterior end of each gland to unite into a common duct which, passing ventrally to the fore-gut, enters the hypopharynx and there ends. The ducts are comparatively short and slender and show distinct striae making them very similar in appearance to tracheae.

The Malpighian tubes are four in number, being very long and bent back upon themselves and intertwined with each other. They are given off from the beginning of the intestine separately and not by a short common duct as in the case of Bibio and Dilophus larvae (14). The tubes are uniform in diameter, except for a very slight dilation where each enters the alimentary canal. The tubes are covered on the outside with a delicate membrane inside of which is a lining of protoplasm containing numerous large nuclei which bulge into the cavity of the tube. The protoplasm is very granular. The Malpighian tubes are yellow to orange-brown and
are very distinct in the living animal.

As Miall (12) remarks in the case of Dicranota, the straightness of the alimentary canal and the absence of the large diverticulum of the vegetable-feeding Tipula and Ctenophora larvae are adaptations to the carnivorous diet.

3. The Nervous System.

The nervous system of the Pedicia rivosa larva consists of a brain or supra-oesophageal ganglion, a sub-oesophageal, three thoracic, and eight abdominal ganglia. The brain is two-lobed and lies in the fore-part of the mesothorax or rear part of the prothorax according to the position of the very retractile head-capsule. As pointed out by Miall (12) in the case of Dicranota, a considerable shifting of the anterior ganglia is caused by the protraction and retraction of the head-capsule, and the nerve cord is very loosely attached and mobile. The two lobes of the brain are distinct but closely connected.

The sub-oesophageal ganglion lies directly below the brain and is connected with it by short fine oesophageal connectives which connect its anterior end with the anterior end of the lobes of the brain. The above-named organs form a complete ring or collar around the alimentary canal. The head-capsule is so completely filled with large muscles used in its movements that the brain is considerably displaced.

The first thoracic ganglion immediately follows the sub-oesophageal one being almost as large and occupying the middle of the mesothorax. At the rear of this segment lies the second thoracic ganglion, while the third thoracic ganglion occupies the fore part of the metathorax.

The abdominal ganglia are slightly smaller and are situated in segments 4 to 10. The first abdominal ganglion is in the fore-part of the first abdominal segment, ganglia 2 to 6 of the abdomen occupy the middle of each segment, while in segment 10 the last two ganglia (i.e. 7 and 8) lie close together, the terminal ganglion
being slightly larger and occupying the middle of the segment. From this terminal ganglion two main branches are given off posteriorly which run into segments 11 and 12. The connectives between the ganglia are double throughout, whilst each ganglion sends off four large lateral nerve trunks - two to each side - the exact distribution of which was not studied.

4. The Circulatory System.

The dorsal vessel occupies 10 segments of the body running from the posterior end of the penultimate segment to the brain which is in the anterior part of the second thoracic segment. It is enclosed in a wide pericardium which increases in size from before backwards, appearing to be, in the last abdominal segments, flatly quadrilateral in section. Attached to the pericardium are thirteen pairs of alary muscles the bases of which are joined to extensions of the pericardial cavity. Their distribution is as follows - segments 5 to 10 each with two pairs, and one pair in segment 11. In each segment which contains two pairs of alary muscles, the anterior pair is situated immediately posterior to the slight constriction marking off the segmentation, while the posterior pair occupies the middle of each segment. The pericardium ends at the rear of segment 11 in an oval opening which looks ventrally and allows blood to enter from the body cavity.

The wall of the pericardium appears to be fibrous in nature, but is much obscured by the very numerous small cells, spherical or oval in outline, which almost completely cover it.

The vessel, which can hardly be termed a heart, increases in diameter towards the hind end. Though very slightly constricted at intervals no distinct chambers are visible. At the rear end is an inlet, median in position, with two prolongations, probably valves, at each side. At the anterior end of segment 11 the dorsal vessel shows a distinct constriction, which may mark the position of a pair of ostia, but I cannot say definitely that ostia occur in this position. The wall of the vessel is of transverse
fibres. The blood is colourless.

5. The Respiratory System.

The larva, like the great majority of other Tipulid larvae, has only one pair of spiracles which are borne on a slightly protruberant elevation of the dorsal surface on the last body segment, facing upwards and backwards. The spiracles are very conspicuous being fairly large and black, and almost circular. The external opening is surrounded by a rim, or radially folded margin - the stigmal ring - which is composed of numerous scale-like pieces. Descending into the vestibule is a plug or cone of chitin which appears to be an imperforate chitinized plate. Many authors have the view that respiration takes place through the stigmal ring, and this, to me, seems the only way. Alexander (2:747), however, adds an interesting note on this and says: "Gerbig (in 'Über Tipuliden-Larven mit besonderer Berücksichtigung der Respirationsorgane,' Zool. Jahrb., Syst. 35:127-184. 1913.), however, shows that the middle piece is split across the disk, the cleft being closed by two overlapping membranes." I have searched for this in Pedicia but cannot determine its existence.

Outside of this cone the vestibule occurs being a chamber crossed by many chitinous fibres which radiate from the outer wall, branch, and become intermixed. Some of the fibres are very short, others quite long reaching the central cone. From this 'network-chamber', which is the first enlarged part of the trachea, with its apparently anastomosing branches of chitin, the attached tracheae lead away to the body.

From the spiracles two fairly large tracheae run along the dorsal surface of the body to the second segment where they divide and form several branches to supply the muscles controlling the head-capsule, the oesophagus, brain and other closely connected nervous ganglia. Secondary tracheal trunks run from the spiracles in a ventro-lateral position along the body ending in fine branches
in the second segment. These secondary trunks are in fairly close connection with the body-wall being overlaid by the muscles. These communicate directly with the main tracheal trunks by short transverse connections which occur in the anterior part of segments 3 to 10 inclusive. Close to where the connections leave the secondary tracheal trunks, a branch is given off from each connective which runs inwards and forwards and supplies the alimentary canal and surrounding fat tissue. This branch is fairly long and loose, probably so to allow of the forward and backward movement of the canal during the retraction and protrusion of the head-capule. About the middle of the same segments a ventral branch arises from the secondary trunk and runs inwards to supply the nerve cord.

In the anterior part of the penultimate segment two thick short branches arise from the main tracheae, run inwards in a transverse direction and unite. From this cross-connection smaller branches are given off anteriorly and supply the dorsal vessel. In the posterior half of the same segment three small branches from the main tracheae arise ventrally to supply the hind-gut.

In the extreme anterior part of the last segment two short trunks from the main tracheae are given off in a transverse direction and meet and unite in the mid-line. From this short connection two branches arise which soon fork into two, each fork supplying and descending into one of the anal gills. Each fork in its course forks again into a smaller and a larger branch, and from these finer branches arise. Given off from the spiracles and running in a posterior direction are two small tracheae. These enter the spiracular lobes where they repeatedly divide up into a fine network of tracheae.

In the foregoing account of the respiratory system the gills have been spoken of as being anal tracheal gills in preference to anal blood gills on account of their enclosed tracheae and tracheoles. Imms (8) suggests that they are probably blood gills and says: "In certain Chironomids two pairs of blood gills are situated on the 11th segment, and a similar number of smaller
blood gills are present around the anus. The caudal retractile processes of *Pedicia*, and other aquatic Tipulid larvae are probably of a similar nature. It is, of course, well known that blood gills derive their name from the fact that they contain blood and not as a general rule any tracheae or tracheoles, although these latter may exist at times. Further, in some instances blood gills and tracheal gills show but little real distinction. It seems, however, from a close examination of the gills of this larva that they really function principally as tracheal gills and much less so as blood gills.

My own observations on the habit of respiration coincides very closely with those of Hiall with *Dicranota* (12). The larva comes to the surface of the water at intervals which vary greatly in length, and thrusts the hind end above the water, lying for quite a long time in this condition. When the hind segments are withdrawn below the water an air-bubble has frequently been observed attached to each spiracle. When in the water the larva has a habit of holding the last few segments up, almost at right-angles to the rest of the body, especially so when the water is shallow, so that the tail-end is only a very short distance below the surface. On the other hand, in deeper water they can live quite normally without any visible signs of inconvenience, although they again seek shallower water after some hours have elapsed.

In considering the network of tracheae present in the thin-walled anal gills and spiracular lobes and their probable assistance in respiration, in order to ascertain if breathing could be accomplished by these structures only experiments were carried out. Vigorous healthy larvae, chosen for the purpose, were taken from the water, had their hind spiracles only varnished over, and were then returned as soon after as possible to the water when their natural environment was simulated as closely as possible. All showed, after a longer or shorter period - for example from ten minutes to half an hour or more - signs of discomfort and attempted to breathe atmospheric air directly through their varnished over
hind spiracles by thrusting the hind end above the water surface. As each animal found this an impossibility it proceeded to crawl about the foot of the containing vessel, only to renew its efforts after about ten to fifteen minutes had elapsed in an attempt to get air directly through the spiracles. This process was repeated many times in every case until very apparent discomfort produced much crawling which resulted in the animal getting gradually weaker until all movement ceased. After periods ranging from 7½ to 11 hours the larvae died. Similar experiments were carried out in which the spiracles were left free, while the anal gills and spiracular lobes were varnished over. No appreciable difference was noted except that the animals appeared to be uncomfortable. These larvae remained alive for two or three weeks and appeared quite unaffected. From these experiments, and other observations, one is led to believe that respiration is carried out principally by the two posterior spiracles which take in air directly, while the anal gills and spiracular lobes, which take in dissolved air, although co-existing with open spiracles, are accessory in function and merely assist in the respiratory process which cannot be accomplished by these latter organs alone.

During the examination of the tracheal system I looked carefully for the presence of lateral spiracles, or vestiges of these, but I cannot claim to have found their existence. Their unusual occurrence in the larva of Bibio (14) is well known, and Carpenter and Pollard (5) demonstrated the presence of vestigial lateral spiracles in Hypoderma, with a solidified spiracular tube arising from them to merge into a short stretch of open trachea with the normal spiral thickening. In the examination of Pedicia no such formations were observed, and this along with the total absence of anything which might remotely resemble spiracles leads me to conclude that none exist. In connection with this Carpenter and Pollard note "in the maggot of the bluebottle and in other dipteran larvae - that of Tipula, for example - we thought that we had detected them (ie. lateral spiracles), only to find later that we
were examining cuticular bristle-bearing pits from which the bristles had been broken off."

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**THE PUPA.**

I was not successful in finding either any pupae or empty pupal cases, or in breeding any of the larvae to the pupal stage. Several full-grown larvae, when they seemed to be ready for pupation by showing a disinclination to feed and becoming sluggish and contracted, were given every opportunity to pupate but in no case did this happen, and the larvae all died. It seems very difficult to rear this strictly aquatic form which survives in rapidly flowing and well-aerated water, as it is a difficult matter to imitate this condition successfully. Alexander states (2:743) that, in general, he "found species of the tribe Pediciini the most difficult to rear", and also that "species from rushing torrents are at the opposite extreme (from mud-inhabiting species) and it is almost an impossibility to bring some of these species thru to the adult condition."

Grüenberg's description (5:61) of the pupa is as follows:

"Pupa (after Beling) up to 34 mm. long, at the thorax 4.5 mm. thick, slender and smooth, contracted behind. Frons with 2 oval, button-shaped, fairly large, widely separated, downwardly directed, dark brown, coarsely pitted and strongly shining between the pits, loop-shaped projections showing processes. Thorax chestnut brown, strongly arched, with fine dense transverse grooves. Wing- and leg-cases shining yellow-brown, the first reaching up to the hind edge of the 5th, the last up to the middle of the 6th abdominal segment. Abdomen dorsally a shining brown-yellow, ventrally dirty-white, laterally with broad, flat, longitudinal channels and very fine pilose bands. Pupal period 1 to 2 weeks. Pupae in vertical burrows, up to a finger-length long."
in which they move up and down."

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THE ADULT.

The fly is well known to systematists who are acquainted with its large size and handsome appearance. According to Grünberg (6:60) they fly in woods in moist swampy places and also in high mountains being found from June to September, particularly in August and September. Schiner (18) also points out that it is very rare and that it occurs in woods, and there particularly at boggy places, rich in vegetable matter. He also observed it in high mountainous parts, on willows, so high that they were not attainable with a net. On the other hand Malloch (11:218) says of Pedicia that "their flight is slow and heavy, and they seldom rise much above the level of the rank vegetation in the marshy or wet situations in which they normally occur."

From the information I have regarding the insect I suspect the generation to be a biennial one.

There is no record of any species of the Pedicinae being preserved as fossils.

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HABITS, FOOD, ETC.

The material on which this paper is based was collected from July 11th to 28th, 1923, in the region of Loch Awe in Argyllshire, at an average altitude of 300 feet. After a thorough examination of the district I found that the larvae were restricted to very small streams, merely rivulets, which flowed down the hillsides very rapidly. All the animals were found in small collections of water where the progress of the stream was somewhat retarded, these pools,
strangely enough, all occurring at the roadside. No larvae were taken from parts of the streams higher up the hill-side. The surrounding country was well wooded, but on one occasion I took two or three specimens from a pool in very open heather moorland.

At this point I perhaps, however, ought to state that the period of collecting was very wet, rain falling almost every day. In consequence the rivers and "corries" of the district were very much swollen beyond their normal size, and it is possible that the large amount of water found in these streams washed all the larvae down from higher altitudes to the natural checks which were found at the road-side ditches. Not only was this true of the larvae under consideration but also of other aquatic forms.

The larvae were found, in the majority of cases, resting underneath fairly large flat stones, and, owing to their comparatively rapid movements and semi-transparency, were by no means easy to detect and catch. They swim about in the water with a looping or snake-like movement which is not so pronounced as in Chironomus however. A few specimens were taken from the edges of pools, the majority being taken from depths of six inches and over up to fourteen inches. In captivity these animals lived in shallow water in an ordinary soup plate with apparent comfort. They seem, however, to avoid light and welcome as a hiding and shelter place pieces of moss, etc. Several times larvae were placed on moist soil but sooner or later they found their way back to the neighbouring water, although whilst out of their natural environment they showed no signs of discomfort, respiration being apparently quite normal.

Beling (4) describes the larvae as living in brooks and springs also in wet places in mud and soil or under wet leaves and other débris, sometimes associated with the larvae of Tipula lutescens, Fabr. Schiner (18) states that according to Scheffer's observations they live in spring-water. Alexander (2:716) gives as the haunts of Pedicia the following situations: "1. In very rapid water (lotic) or in submerged mosses (hygro-petric association). 2. In cold springs."
From larvae living in captivity I have observed that the sense of small seems to be very poorly developed. These carnivorous forms would pass and repass large pieces of raw meat placed beside them for feeding purposes as close as almost to touch them. On the other hand they are possessed of a very delicate sense of touch throughout the whole body surface. By gently touching any part of the body with a very fine pencil of hairs the larva would at once respond by twisting the head-end round and gripping the hairs tenaciously between the powerful mandibles, only letting go when it was discovered that the object fastened on to was not food.

In food habits the larva is decidedly carnivorous, even cannibalistic, so much so that it was only by keeping living specimens in separate receptacles that they could be prevented from eating one another. In two preparations which were made for microscopic examination it was by no means difficult to observe that the last meal of the animal had been one of its companions - identification of this was simple since the chitinous parts of the head-capule which had been swallowed entire had scarcely been damaged. In Argyllshire I supplied captive larvae with Caddis-, May-, and Stone-fly grubs. All were devoured. They seemed to be especially fond of small Blood-worms which were very plentiful. In one case a larva of Pedicia overcame and partly ate a small dragon-fly larva. Malloch (11) states that the food of the larvae consists of algae, diatoms, and small crustaceans. Alexander (2:710) notes that Pedicia usually feeds on the larvae of small insects especially Chironomidae, but that the larger species are capable of capturing almost any insect of a size equal to their own.
PARASITES.

Information regarding parasitic natural enemies is very scanty. During the course of the investigation I found no external parasites, but in two larvae which were dissected I found, in the mid-gut, several specimens of a large gregarine, one case being a very heavy infection. Professor J.H. Ashworth of the Department of Zoology, University of Edinburgh, was kind enough to verify the protozoa as being gregarines, but owing to the lack of the cysts and spores further determination was not possible. Alexander (2:733) mentions that he "found a large gregarine very abundant in the alimentary canal of the larva of Pedicia albivitta, many of the individuals being very heavily infested."

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COMPARISON WITH THE LARVAE OF OTHER DIPTERA.

Of the two most nearly related species to Pedicia rivosa, namely P. albivitta and P. contermina which occur in America, only the former is described in Alexander's Memoir (2:900), and this description has largely to do with the head-capsule, which resembles that of P. rivosa very closely, so closely in fact, that no good distinctions are possible. Little help is found from the figures.

The allied form, Dicranota, resembles Pedicia very closely in almost all its aspects, the chief differences being in the number of pseudopods borne by these two animals and their structure, and in the size and structure of the anal gills. I have endeavoured throughout, in the descriptions, to use Dicranota for comparison purposes.

While no other order of insects presents so great a diversity of larval habits as the Diptera the truly aquatic larvae belong to
the Orthorrhapha, particularly to the Nematocerous families. Exceptions of course are found in some Sciomyzidae and Ephyridae. Pedicia is singular, however, in living in quick flowing water and few species are found in such haunts as this animal inhabits.

A well developed head is present only in a small number of families. It is fully formed in many Nematocerous larvae, except in Cecidomyiidae, Tipulidae and Limnobiidae. In the two last named families the larvae are in a "hemi-cephalous" condition, the head-capule being incomplete posteriorly and permanently imbedded within the thorax. The reduction of the head-capule is in the form of a breaking up of the fusion of the component parts posteriorly, the caudal portion of the head thus having the appearance of several slightly diverging pieces, the membrane of the prothorax being attached to the head just anterior to the point of divergence. These larvae may be distinguished from those of the higher families of the Brachycera by their opposed, instead of parallel, mandibles. The mouth-parts, especially amongst Orthorrhaphous larvae, are variable in character and in certain families of Nematocera are in their least modified condition. Of the mouth-parts of Pedicia, the most noteworthly is the labium or mentum which is modified in a similar way to that of Dicranota, Chironomus, Bibio, and species of Tipula.

Although, generally speaking, dipterous larvae are apodous, pseudopods occur in some genera such as Eristalis, Chironomus, Simulium, Dicranota, and Orphnephila. The pseudopods, however, vary in number and structure and the condition in Pedicia is characteristic.

With respect to the alimentary canal the absence of caeca is noteworthy. It conforms to the general dipterous character of having four Malpighian tubes, all entering the canal separately. The oesophageal valve is very primitive and in this it resembles Bibio and Dicranota.

While in the Nematocera the position of the brain varies it lies, as a rule, in the head and its occurrence in the front part
of the thorax of Pedicia is of remark.

While the primitive or peripneustic type of tracheal system is practically confined to Hematocera, the amphipneustic condition is most prevalent in dipterous larvae, although in some cases - e.g. Hyponema, to which reference has been made - indications of a former peripneustic condition are observable. In Pedicia, however, the truly metapneustic condition occurs, and, while present in Cyclorrhaphous larvae, is mostly lost in the later instars, except in those forms which are physiologically metapneustic owing to the non-functioning of the prothoracic spiracles. Gills, as accessory respiratory organs, occur in several aquatic forms but their position and nature, however, vary. Pedicia is a more or less generalized form of the Tipulidae possessing, as it does, four gills which are segmented, the apical segment being telescopic into the preceding one. More specialized Tipulids have six or eight gills.

The spiracular disc is peculiar and lacks the characteristic form such as in Tipula paludosa, for example, where the stigmatic area is expanded on its border into six conical papillae of definite form and arrangement. Even in the Limnobiidae, to which it belongs, the possession of only two spiracular lobes separates it from all other genera except those of the subtribe Pedicaria as defined by Alexander (2:699).
Pedicia rivosa, L. (Limnochilidae, Diptera) is a member of a small genus whose larvae are strictly aquatic. Records of its distribution in Britain are given.

The paper deals principally with the full-grown larva. A description of the external morphology and internal anatomy of this stage is detailed, special attention being given to the respiratory system. A particular feature of the larva is its possession of four anal gills which, although co-existing with two posterior spiracles, are concluded - from respiration experiments which were carried out - to be accessory in function, merely assisting in the respiratory process, which cannot be accomplished by these organs alone.

Brief mention is made of the pupa and habits of the adult. Observations made on larvae in captivity and also in their natural environment are given with reference to their occurrence, mode of life, and food habits.

A protozoan (Gregarine) parasite was encountered in the larval alimentary canal.

A short comparison of the species with the larvae of other Diptera is included.
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EXPLANATION OF FIGURES.

(All the figures are original and relate to the full-grown larva.)

Fig. 1. - Five larvae photographed from nature. Specimens A and C from dorsal side show the segmentation, head-capsule, posterior spiracles, and spiracular lobes. B side view. E ventral view to show pseudopods and anal gills. D is a second-last stage larva. (Natural size.).

Fig. 2. -- A living specimen photographed in a dish of water to show the appearance of the animal. Photo. in strong sunlight. (Reduced).

Fig. 3. -- Habitat of the larvae. The photograph is of a small pool at the roadside, in Argyllshire, at Loch Awe region. A represents the end-half of a walking stick and B a 3-inch collecting tube - for comparison of size.

Fig. 4. -- Larva of Pedicia rivosa, side-view, x 4. The setae on the body are exaggerated in size so as to show their position.

Fig. 5. -- Twelfth segment, dorsal view, showing spiracles, spiracular lobes and anal gills, x 30.

Fig. 6. -- Twelfth segment, ventral view, showing spiracular lobes and anal gills, x 30.

Fig. 7. -- Above - Pseudopods and creeping pad on 8th segment, ventral aspect, x 10. Below - Cross-section of same segment to show projection of creeping pad.

Fig. 8. -- Roughness on pseudopods. x 480.

Fig. 9. -- Pubescence on cuticle. x 480.

Fig. 10. -- Head-capsule, dorsal aspect. x 30. a - antenna; lbr - labrum; m - mandible; ms - median chitinous septum; mx - maxilla.

Fig. 11. -- Head-capsule, ventral aspect. x 30. h - hypopharynx; m - mentum; or - cephalo-thoracic orifice occupying the posterior ventral surface of the capsule.
Fig. 12. - Labrum and epipharynx, ventral aspect. x 80.
Fig. 13. - Hypopharynx. x 80.
Fig. 14. - Mentum, ventral aspect. x 80.
Fig. 15. - Right maxilla, ventral aspect. x 80. il - inner lobe; ol - outer lobe; p - palp.
Fig. 16. - Right mandible and its muscle apodemes, dorsal aspect. x 80.
Fig. 17. - Right antenna, dorsal aspect. x 300. ap - auditory plate.
Fig. 18. - Alimentary canal, ventral aspect. x 4. oes - oesophagus; ag - salivary gland; st - stomach; Mp - Malpighian tubes; i - intestine.
Fig. 19. - Nervous system, head retracted. The brain is folded forwards. x 4.
Fig. 20. - Circulatory system, dorsal aspect. x 4. br - brain.
Fig. 21. - Respiratory system (partly diagrammatic). x 5. mt - main trunk; st - secondary trunk; c - connective; al - branch to alimentary canal and fat tissue; nc - branch to nerve cord.
Fig. 22. - Spiracular vestibule of right side with its tracheal branches. x 80.
Fig. 23. - Hind end of body, showing tracheae distributed to the anal gills, spiracular lobes and their connections with the spiracles. x 15.
Fig. 24. - Posterior spiracles. x 300.