OBSERVATIONS ON THE OVA AND OVIPOSITION OF CERTAIN EPHEMEROPTERA AND PLECOPTERA

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REPRINTED FROM THE
PROCEEDINGS OF THE LEEDS PHILOSOPHICAL SOCIETY
(SCIENTIFIC SECTION)
VOL I. PART VI. Pages 271—288

Observations on the Ova and Oviposition of Certain Ephemeroptera and Plecoptera. By E. PERCIVAL, B.Sc., Lecturer in Zoology, The University, Leeds, and H. WHITEHEAD, B.Sc., Lecturer in Biology, City Training College, Leeds (communicated by Professor Garstang).

(*Received* 25th February 1928)

It is well known that mayflies and stoneflies provide a considerable proportion of the fauna of running water. The former in the aquatic stages are found under widely different conditions and exhibiting a variety of adaptations. The stonefly nymphs are very much less varied in structure and visible adaptations but have a very wide range of habitable conditions.

Observations made on the form of the eggs of some *Ephemeroptera*, especially by Morgan (11) and Bengtsson (1), show that the remarkable variety of structure is not limited to the body of the nymph, but is also seen in the eggs of many species. These workers have described remarkable mechanisms for the attachment of eggs to the substratum and have given detailed descriptions of the structures. Relatively few observations, however, have been made on oviposition in this order. Miall (10) has translated the accounts of observations made by Swammerdam, Reamur, and de Geer. Gros (6) gives a short account of oviposition in *Ecdyonurus forcipula* and we (13) have described the conditions in which the eggs of *Ephemera danica* may be deposited. Eaton (4) has made some incomplete observations on the oviposition of *Baëtis* sp.

Regarding the *Plecoptera*, there is a shortage of information on the matter of ova and oviposition. Imhof (7) has described the egg of *Perla maxima* and Rousseau (14) has a description of the egg of *Perla abdominalis* which does not agree with that given by Samal (15). The last-named worker has given an account of the oviposition of *Perla abdominalis* and has described the post-embryonic development with many excellent figures.

The observations here recorded have been made chiefly on rivers and streams in the west of Yorkshire. We are greatly indebted to the Leeds Philosophical Society for grants to cover expenses.

PLECOPTERA

Perlodes mortoni Klp.

The egg-mass is held by the sub-genital plate and the ventral side of the post-genital segments. A large depression is formed into which opens the oviduct. The mass of ova has a treacly appearance, being dark brown with a very faint greyish sheen, and contains

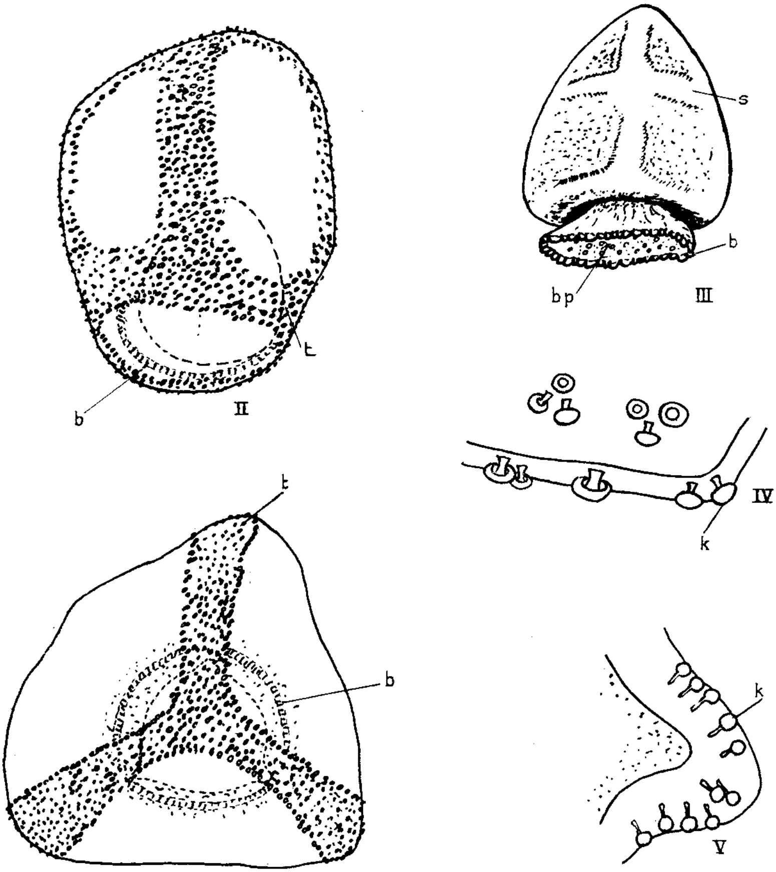

FIG. 1

Perlodes mortoni—(i.) Swollen egg-membrane seen from apex, *t*—tract of adhesive knobs, *b*—brown ring round basal plate. (ii.) Swollen egg-membrane seen from side, *t*—tract of adhesive knobs, *b*—brown ring round basal plate. (iii.) Egg removed from membrane, *b*—brown ring, *b.p.*—basal plate, *s*—position of splitting on hatching. (iv.) Portion of membrane with adhesive knobs *k*. (v.) Portion of edge of basal plate with adhesive knobs *k*. (All camera lucida drawings.)

three hundred to four hundred eggs. It is not sticky to the touch nor does it adhere to a dry surface. The mass very quickly separates from the female on coming into contact with water and proceeds slowly to disintegrate. Observations made in the laboratory showed that the eggs began to move from the outer part of the mass in five seconds, while the whole mass swelled. The outer eggs fell away and ultimately disintegration was complete.

The egg is roughly tetrahedral in shape, having the base slightly smaller than the sides, while the basal angles are rounded (see Fig 1, iii.). The colour of the hard chorion is chestnut brown with faint sepia spots. On each side, about two-fifths down from the apex, is a paler transverse band with darker edges marking the position of a split to be formed to allow of the escape of the larvule, the apex making a lid which may completely break away.

The base bears a circular white patch, the basal plate, whose edge is continuous with the thin transparent membrane which completely includes all the egg except the circular area. Before coming into contact with water this membrane closely invests the egg. When examined dry the covering is seen to bear a large number of small, more or less hemispherical bodies arranged in definite order. These are adhesive knobs and are present on the surface of the basal plate.

Close examination of the egg-mass placed in water shows that the disintegration is brought about by the passage of water through the membrane, causing swelling and the solution of the substance which causes the eggs to cohere as a whole. This substance is coagulable in 70% alcohol. When the membrane is turgid, being then more or less spherical, it is seen that the egg is attached to one side with the apex pointing to the centre. The white patch is very striking in appearance, it being opalescent. The small hemispherical bodies absorb water within the first minute, swelling slightly. They lie in tracts running in the same direction as the edges of the egg, i.e. there are three bands converging on the side of the sphere towards which the egg apex points, and three tracts running parallel with the sides of the base connecting the proximal ends of the other tracts (see Fig. 1, i., ii.).

The hemispherical bodies are mushroom-shaped or club-shaped, the stalks being set in the membrane with the heads on the surface.

The function of the structure described above is seen when the egg-mass disintegrates in water under the microscope. The spheres roll down to the floor of the capsule and the small stalked bodies adhere to the substratum with a tenacious grip. In falling, it usually happens that the base of the egg is lowermost and attachment is made by the adhesive knobs of the basal plate, a region limited by a ring of brown cell-like structures, but a grip may be taken by the knobs of any other portion. Shaking the capsule usually results in bringing round the basal plate to the substratum. The significance of this is seen in the fact that the membrane is easily torn away from the brown border leaving the plate. At the same time the apex of the egg is brought upwards, no doubt to facilitate the exit of the larvule. The neck of the basal plate is very tough, since it can be stretched to five or six times its length without rupture and without breaking the hold of the adhesive knobs from the substratum. On release it immediately resumes its original length.

Attachment is apparently due entirely to the knobs since no other portion of the membrane showed any tendency to adhere.

The dimensions of the egg are as follows—

Height from attachment of peduncle	0·44 mm.
Diameter at widest part	0·37 mm.
Diameter of opalescent patch	0·27 mm.

The diameter of the swollen membrane is about 0·8 mm. to 0·9 mm. Swelling and disintegration of an egg-mass after 18 hours' drying in ordinary summer weather took place on treatment with water and the eggs adhered normally to the substratum.

The membrane is semi-permeable, a shrinkage to half size taking place in 0·75% salt solution. Dehydration is also brought about by 70% alcohol. There is apparently, between the membrane and the chorion, a substance which absorbs water rapidly and which can be dehydrated, the extent to which swelling takes place being dependent upon the concentration of the external solution.

The egg-mass fell through a column of still water at 15·5° C. at the rate of 3·46 cm. per second. Disintegration was not obvious during a 16-inch fall. Separate eggs with swollen membrane fell at 0·6 cm. per second at 16° C.

Adult *Perlodes mortoni* taken in the field and kept captive readily copulated under cover.

Five females deposited seven egg-masses in seven days and produced eleven egg-masses in eleven days. Thus a female may extrude at least two egg-masses.

The insects readily drank water after being deprived of it for some time. The labrum and labium are moved similarly to lips. In the case of three females allowed to drink after seven days, the egg-masses which they carried were seen to increase in size, apparently by further extrusion. The insects always show increased activity after imbibing. Some were kept for 24 days, during which time they had drunk twice and produced eggs.

Incubation at about 15·5° C took 91 days (21/3/27 to 20/6/27).

Perla carlukiana Klp.

Klapálek (8) has regarded *Perla maxima* Scop., as found in Britain, to differ from those found on the continent and has given the British type specific rank. The egg-mass of the British species is carried in as *Perlodes*. Schoenemund (16) figures the female of *Perla cephalotes* with eggs. Imhof (*loc. cit.*) has described and figured a micropylar apparatus in the egg of *Perla maxima* and Samal (*loc. cit.*)

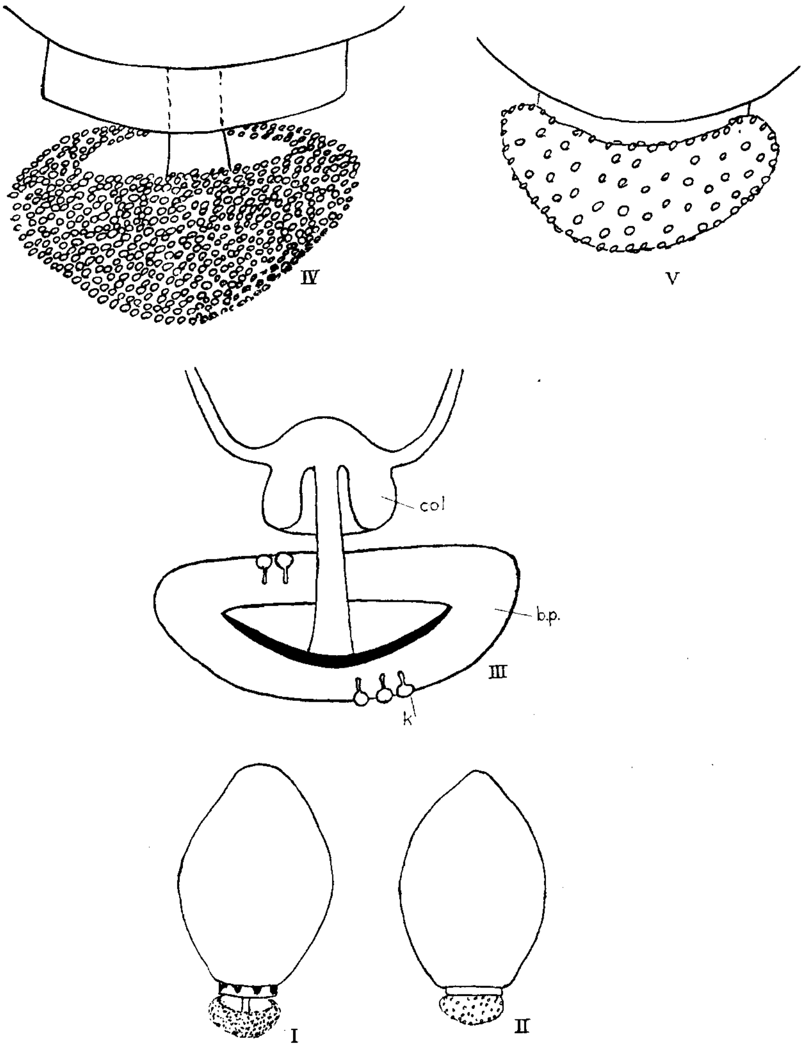

FIG. 2

(i.) Egg of *Perla cephalotes* (note rounded apex). (ii.) Egg of *Perla carlukiana* (note rather pointed apex). (iii.) Diagram of anchoring apparatus of egg of *Perla*, *b.p.*—basal plate, *col.*—collar, *k*—adhesive knob. (iv.) basal plate of egg of *P. cephalotes*. (v.) basal plate of egg of *P. carlukiana*.

has also given a description with figures of the same for *Perla abdominalis*. The latter gives a figure of the female ovipositing and the following account—"Elles immergent leur abdomen en plein vol, toujours tournée contre le courant ou un peu vers l'un des bords. Les œufs reunis en sac au sommet de l'abdomen, sont, pour ainsi dire, arrachés par le courant et tombent au fond où ils restent parmi le sable."

The eggs of *Perla carlukiana* and *Perla cephalotes* are very similar, differing in only slight details. That of *Perla abdominalis* is rugose on the surface of its shell, presenting a markedly different appearance from that of the previously named species, which is smooth.

The ovoid eggs of the two British species (Fig. 2, i., ii.) carry at one end a short collar, into the canal of which is set a stalk carrying a concavo-convex basal plate. The proximal end is continuous with the chorion to which also belongs the collar (Fig. 2, iii.). The chorion is chestnut-brown in colour and tough. The peduncle is elastic, returning to its original length after being stretched four times its length. The distal end is continuous with a middle lamella in the crown which is milk-white by reflected light and brownish by transmitted light. The outer convex surface of the plate is provided with a number of adhesive knobs similar to those of *Perlodes*, their stalks being embedded in the outer transparent lamella.

The eggs in mass cohere by means of a thick transparent slime which is rapidly soluble in water and coagulable in 70% alcohol. On the solution of this material in water, the eggs fall apart basal plate downwards and the adhesive knobs, behaving as in *Perlodes*, grip the substratum almost immediately they touch it. The cohering fluid appears to prevent the action of the knobs, since they do not adhere until it is dissolved. Adhesion is so strong that the peduncle may be stretched to breaking point without the hold being broken. These anchored eggs were able to withstand a very strong current of water (this adhesion persisted in the dry condition for several weeks after attachment; attached shells were found in water over seven months after oviposition).

While the egg-mass is disintegrating, the thick slime, on becoming more mobile acts as a lubricant allowing the falling eggs to slide rapidly over one another, at the same time appearing to control their movement so that they fall close together. Probably this has significance in nature since it would tend to prevent a too rapid scattering.

The egg-mass carried by a female, which ran on the water surface, on coming into contact with the water commenced to break up, the eggs falling separately. In ten seconds the whole mass had broken up. This is not invariable, since a mass allowed to fall through a column of water 42·5 cm. high reached the bottom in ten seconds (4·25 cm. per second), and only shortly before the end of the fall did disintegration become evident. In a capsule an egg-mass broke up completely in ten seconds and formed a more or less flat layer. Probably when the female runs over the water surface, the surface tension of the water will tend to force the loosened eggs apart. Individual eggs fall at about 0·8 cm. per second at 14° C.

Oviposition takes place in the manner described by Samal (*loc. cit.*) and also when the egg-bearing female runs on the water surface.

In the laboratory copulation took place immediately after the removal of an egg-mass (*Perla carlukiana*) and within half an hour more eggs were extruded.

Eggs of *Perla carlukiana*, deposited 27/5/27, hatched 25/7/27 at 17° C. (59 days). The emergence of the larva is facilitated by a transverse split about one-quarter of the distance from the apex of the chorion. The split in the chorion of the egg of *Perla abdominalis* is vertical across the apex (Samal, *loc. cit.*).

	Measurements of the eggs of	
	Perla cepholotes	*Perla carlukiana*
Body of egg—length	0·44 mm.	0·46 mm.
diameter	0·30 ,,	0·30 ,,
Collar—length	0·02 ,,	0·015 ,,
diameter	0·10 ,,	0·10 ,,
Basal plate—diameter	0·12 ,,	0·12 ,,
height	0·07 ,,	0·07 ,,
Adhesive knobs—diameter	0·003 ,, (numerous)	0·004 ,, (relatively few)

The collar of the egg of *Perla cephalotes* has externally six vertical thickenings equidistant from each other. The egg of *Perla carlukiana* does not appear to bear such structures.

We have not been able to detect either a micropylar opening or a canal in this adhesive apparatus. In our opinion the structure is present mainly for the purpose of attaching the deposited egg. Samal (*loc. cit.*) mentions the adhesive knobs of the egg of *Perla abdominalis*, but believes that they belong to the agglutinating mass which keeps the eggs together at the top of the abdomen. We have shown that this is carried out by other means.

Smith (18), describing *Perla immarginata*, says that the eggs separate as soon as they touch water and become attached to the substratum by a glutinous cap round the micropylar apparatus.

Leuctra hippopus Kpny.

McLachlan (9) states that *Leuctra geniculata* St. carries its egg-mass of many hundreds of eggs extending "from the upcurved last segment to the base of the posterior wings, all along the dorsal surface of the abdomen." He also noted a similar habit in the female of *Leuctra fusciventris* St.

In *Leuctra hippopus* the cream coloured egg-mass is carried as in *Perla* and *Perlodes*, in a recess formed by the subgenital plate and the post-genital sternites and extends upwards. Here, as McLachlan says, the tip of the abdomen turns upwards, but we have not, out of hundreds of females noted, seen the eggs extending along the dorsal surface of the abdomen. When at rest the wings form a cover for the egg-mass.

From 250 to 300 eggs may be extruded at once.

The egg measurements are—Length 0·175 mm.—0·180 mm., breadth 0·146 mm.—0·148 mm. The shape is ovoid with smooth, thin, transparent chorion, through which can be easily seen the contained yolk granules. The latter vary very much in size from 0·07 mm. diameter to much less in some eggs, while in others they are fairly uniform in diameter, being about 0·012 mm.

In contact with water the mass disintegrates owing to the solution of a binding slime which is less viscous than that of *Perla* and *Perlodes*. It is also coagulable in 70% alcohol. After separation, the eggs still possess a thick coat of transparent gelatinous material, having a depth equal to three times the egg diameter. It is not adherent to the substratum and finally completely dissolves. When this layer disappears a further definite transparent adhesive coat appears and attaches the egg after a few hours from oviposition.

Oviposition was observed several times (1/6/27 and 1/8/27). The females fly strongly in the bright sunshine with absence of wind. The body is held almost upright with the egg-mass carried as described. The latter may become detached in mid-air, as was observed on two occasions, when it reached the water as a solid mass, or the insect may come down to touch the water surface with the egg-mass, repeating this in a series of short flickering flights until the eggs have separated from the abdomen. Further, as in *Perla*, a female was observed to run on to the water from its perch on a stone at the bank and on the egg-mass touching the water it commenced to break up, the individual eggs falling independently to the stream bed. This took place in a small, calm bay formed by a group of emergent stones. The eggs were watched on their way to the bottom where they fell among a short algal growth.

It is probable that oviposition takes place shortly after extrusion, as females carrying ova are not commonly found except during warm sunny weather when they are very active.

Protonemura meyeri Pict.

The egg-mass of this species has the same appearance and is carried in the same way as that of *Leuctra hippopus*. Also during rest the wings form a dorsal and lateral covering.

The eggs are white with granular contents, ovoid, with dimensions—Length 0·18 mm., breadth 0·16 mm., or spherical with diameter 0·144 mm. The surface of the chorion is finely granular.

The mass separates from the female on touching water and disintegration is rapid. This action is due to the solution of a binding substance which is coagulable in 70% alcohol. The eggs adhere to the substratum within a few seconds of touching, due to the formation of an adhesive layer outside the chorion which is apparently produced from a pre-existing layer by absorption of water.

Individual eggs fall through still water at the rate of 0·15 cm. per second at 18° C.

Oviposition is similar to that in *Leuctra*.

Nephelopteryx nebulosa L.

The white egg-mass is carried as in *Leuctra* and contains about 200 eggs. Detachment is brought about as in *Leuctra* and *Protonemura* but disintegration is less rapid; the mass tends to fall a short distance as a solid body. The processes of detachment and disintegration appear to be the same as in the other insects mentioned.

The eggs vary from ovoid to spherical, in the former case having dimensions—Length 0·18 mm., breadth 0·15 mm., in the latter case, diameter 0·17 mm. The chorion is smooth.

In water each egg develops an extremely adhesive gelatinous coat, the process being similar to that already described. Detached eggs immediately adhere again on contact with the substratum. The process of oviposition is probably similar to that described for *Leuctra*.

Incubation at 15° C. occupied 20 days, the eggs being laid 1/3/27.

Taeniopteryx risi Mort.

The white egg-mass is carried as in *Leuctra*.

Here again disintegration comes about on wetting and is complete in two to three seconds. The egg adheres firmly to the substratum in less than a minute. In their general behaviour the eggs resemble those of *Nephelopteryx*.

A point of interest in connection with this species is that an egg-bearing female taken and preserved in alcohol was found to have carried eggs which were in various stages of development, in fact some of the embryos were almost ready to hatch out (16/5/27).

Chloroperla grammatica Scop.

Schoenemund (*loc. cit.*), speaking of *Perla*, *Chloroperla*, and *Isopteryx*, describes "wie die Tierchen heranflogen (on quiet running water) sich auf die Oberfläche niederliessen und halb laufend, halb flatternd die Berührung mit dem Wasser herstellten und dann die Eier abstiessen. In den weitaus meisten Fällen kriechen jedoch die Weibchen an den Ufersteinen herum und tauchen dabei ihren Hinterlieb in das Wasser. Sobald die Eierklumpen benetzt werden, lösen sie sich auf."

We have seen the females carrying egg-masses which are borne in the same manner as in *Perlodes*. In contact with water they disintegrate, the eggs falling separately.

The dimensions of the eggs are—Length 0·30 mm., breadth 0·25 mm. The colour is brownish and at a magnification of 90 diameters the chorion appears small and granular. After immersion in water a few fine filaments appear, which attach the egg to the solid substratum.

Ephemeroptera

As already stated, the eggs of many *Ephemeroptera* present remarkable structures which are said to be employed in anchoring them to the substratum. Morgan (*loc. cit.*) has described and figured the eggs of 13 species which show a sculptured chorion or sticky threads with or without adhesive terminal knobs. She states that the eggs of *Heptagenia interpunctata* when shaken out into water containing Chara gave out threads which became entangled in the weed. "The anchors of *Ephemeralla rotundus* and *Tricorythus allectus* hang the eggs on sticks and stems and prevent them from being buried in the mud. The many viscid threads upon those of *Leptophlebia* and *Ecdyurus maculipennis* accomplish the same result in a different fashion." She also determined the number of eggs produced by different species and found a considerable variation, some species producing as many as 3,700. It was pointed out that the eggs of closely related forms may be very different. This would be expected if the habits of the species differed in any marked degree. Bengtsson (*loc. cit.*) appears to have confined his attention to the form of the egg and examined a considerable amount of preserved material. Grenacher (5), who described the egg of "Ephemera s. str." (*Potamanthus luteus, vide* Rousseau (14), Fig. 43), believed "dass diese Fäden dazu bestimmt sein möchten, die Eier die bekanntlich ins Wasser gelegt werden, dem Einfluss der Strömung zu entziehen, indem sie sich mit benachbarten Gegenständen verwickeln und so gewissermaassen als Anker dienen."

Siphlurus armatus Eaton

The ripe female of this species has a bluish-green colour in the middle of the abdomen, which disappears after oviposition. Females captured in copulation extruded all the eggs at once about 24 hours afterwards (in the evening).

The individual eggs have contents of a beautiful green colour with a very faint tinge of blue. The chorion is transparent and unsculptured. In oviposition (under laboratory conditions) the eggs were passed out in a mass and, no doubt, fell to the bottom, where they eventually spread out forming a more or less flat layer. They remained coherent owing to the swelling by the absorption of water, of a cohering substance, and formed a roughly circular patch about 0·6 cm. in diameter and about 0·7 mm. thick. The eggs lay near the lower side, somewhat separated from each other and in roughly parallel rows. Although the act of oviposition was not seen, the fact that some egg-masses were observed to swell and change from approximately spherical masses to flattened form, also becoming adherent to the substratum, allows of strong presumption that the female did not enter the water but dropped the mass in. The flat mass was firmly attached inside two hours and did not readily adhere after being removed.

The matrix is opaque to the naked eye and whitish, but with relatively low magnification the eggs may be seen.

In this species copulation takes place in the evening during flight about 6 feet from the ground, the pair continuing in uninterrupted horizontal flight with separation at the end of a couple of minutes. The relations of the parts were observed to be as described by Eaton (3).

Incubation of eggs deposited 14/6/26 in the laboratory took place on or about 29/9/26 (about 15 weeks). Water temperature about 18° C.

Drenkelfort (2) stated that the female of *S. lacustris* held its body vertically during oviposition and touched the water surface. Two egg-masses were produced and were carried away by the water, becoming attached to grass, etc., after sinking.

Ephemerella ignita Poda

It is well known to observers of aquatic insects that females of this species carry the greenish, spherical egg-mass at the genital aperture. That the mass is not dry is indicated by the fact that when the insects are swept into a net it becomes dislodged and may be found adhering to the wings or any other portion of the body. It will stick to the fingers on being picked up.

Swarming for oviposition takes place in the evening commencing, in June–July, about 7 p.m. (G.M.T.). This occurrence is very striking, since in the space of a quarter of an hour there may be thousands of females where previously there were ones and twos. In the warm evenings of late June and early July these swarms occur regularly and last until shortly after sunset. They are influenced very much by the weather, being inhibited by wind, low temperature, rain, and overcast skies.

The females ultimately descend to the water-surface where probably the egg-mass is detached. What takes place is difficult to discover owing to the waning light. In the laboratory the mass separates immediately on becoming wet. Here again is probably a substance which brings about adhesion of egg-mass to abdomen, and is soluble in water. The sphere is about 1·2 mm. in diameter and falls rapidly through a column of water. The eggs which have been described by Bengtsson (*loc. cit.*) are bound together by a stiff substance which absorbs water, swelling to about three times its original size and, becoming gelatinous, adheres firmly to the substratum. By this swelling the individual eggs are separated from each other fairly uniformly throughout the mass.

The nymphs of *Ephemerella ignita* are very abundant in moss in many of our rivers. The probability is that they were born in the same locality. Confirmation was obtained when pieces of moss, caught in a coarse net during November floods, were found to carry, adhering strongly to them, the gelatinous egg-masses of this insect. At this time some of the eggs had hatched while others were on the point of breaking.

Moseley (12) states that incubation of the eggs of this species took six months in a London greenhouse.

Ecdyurus venosus Fab.

Gros (*loc. cit.*) states that the bright green egg-mass of *Ecdyonurus forcipula* is brought into contact with the water at the end of a sharp downward flight, which may be repeated. The eggs detach immediately and fall separately. The egg of this species has a rugose chorion and has apparently no adhesive structures.

The egg-mass of *Ecdyurus venosus* is whitish and readily breaks up on being placed in water probably, again, by the solution of a cohering medium. The individual eggs fall separately and shortly after immersion give rise to a number of thin filaments, about 0·26 mm. long, which attach themselves to the substratum, thus playing the part of anchors. The egg dimensions are, length 0·18 mm., breadth 0·13 mm.

Incubation at about 16° C. occupies about 15 days (eggs deposited 5/6/26, hatched 20/6/26).

Bætis spp.

Bengtsson (*loc. cit.*) gives the measurements of the egg of *B. pumilus* as being length 0·147—0·241 mm., breadth 0·09 mm. Eaton (4) observed females of *Bætis sp.* creeping down the sides of stones, when the wings were folded over the abdomen enclosing a mass of air. They were able successfully to emerge from the water on the upward journey. Our friend, Mr. L. Eastham, of Cambridge, has given us the following account of his observations on *Bætis sp.* relating to oviposition—

"The egg-masses of the species observed take the form of a single layer of eggs closely packed together, the whole being glued to the underside of stones in fast flowing streams. The shape of the mass is fairly constant and resembles that of the palmar surface of the hand excluding digits. Two sides are nearly parallel, one end, generally the broader, being convex, the other slightly concave. Each mass measures about $\frac{3}{16}$ inch in diameter. The constant shape is of interest and one naturally is glad of an opportunity to explain how it arises.

"The first observation, made in June, was in finding the mayfly attached to the underside of a stone when the latter was lifted from a stream bed. The stone carried several egg-masses, one lying with its concave end close to the tip of the abdomen of the fly.

"The insect came out high and dry with its wings erect and appeared not to have been wet at all. Since it made no attempt to escape I gently returned the stone to the water, turning it so that the fly met the water head first and pointing upstream. The insect willingly suffered the immersion and, as the wing-bearing segments reached the water, it folded the wings over its back in the form of a tent, so enclosing a considerable volume of air between them and the dorsal surface of the body. The stone was again removed after a few minutes and the fly reappeared quite dry.

"Two flies were seen to enter the water from half-covered stones, facing upstream the while. Further observation proved that this was the normal manner of entering the water.

"I was fortunate in inducing a female to oviposit in captivity. The immersion experiment was carried out on a gravid female in a glass bowl of water. A small stone on which the *Bætis* was resting was immersed and almost immediately she began to oviposit. A single egg was laid attached to the stone by a gelatinous substance, another placed on one side, a further one on the other, and so on, until five were laid. The abdomen was then withdrawn sufficiently to allow the fly to lay a second more proximal row of seven which it did, starting from the middle and putting more alternately on each side. A third row of eight and a fourth of ten followed, but not with the same regular alternation. It will be seen that if this be continued the row of eggs will increase in length, so producing a semi-circular patch. The maximum diameter of the egg-mass (or length of rows) will be determined by the lateral movement of the abdomen, a limit to which is set by the length of the latter, and its power of lateral movement while the thorax is stationary.

"Once the maximum is reached the rows will be of about the same length and the mass will, in the region under consideration, have parallel sides. The last rows of eggs are usually shorter than the maximum. Each row is curved because the tip of the abdomen moves along the arc of a circle whose radius equals the length of the abdomen. This explains why one end of the mass is convex, i.e. where oviposition commences, and the other concave, where the last eggs are laid.

"The *Bætis* which I had under observation laid eggs readily in captivity, one specimen actually producing a fairly typical egg-mass on the wet side of a wide glass tube."

We have watched females of *Bætis pumilus* Burm. enter strongly running water in the way described, and have identified a number of females of *B. binoculatus L.* which were captured from the underside of stones.

The folding back of the wings during submergence is not a voluntary movement on the part of the insect but is due to the surface tension of the water. The whole of the body of the insect is encased in air which thus gives an atmosphere in which the animal may breathe for a considerable period.

A mature nymph of *Bætis rhodani* Pict. was taken on March 13th and the subimago emerged the following day. After four days the imago appeared and in about 20 hours unfertilised eggs were deposited on the slightly damp cork of a specimen tube. The method of oviposition was not observed but a flat layer was formed, the eggs being loosely attached to the substratum. On the cork being submerged in water a gelatinous matrix arose in about a minute, which swelled slightly, causing the eggs to separate further and cementing them to the cork. These unfertilised eggs were ovoid with a brownish tinge in transmitted light and whitish in reflected light. The contents were granular. The chorion was uniformly thin with a smooth surface. The dimensions were, length 0·17 mm., breadth 0·11 mm.

The Œcological Significance of the Recorded Facts

In a general way the eggs which we have described may be divided into three types, (*a*) those which are deposited separately on the bed of the stream, (*b*) those which are attached directly to solid bodies, (*c*) those which are liberated as persistent masses and are deposited as such on the substratum. The second type is well-known among the *Trichoptera*, many being described by Silfvenius (17), where the females creep down the surface of stones or plant stems and deposit either gelatinous masses or cement-like layers of eggs. At present the third type does not appear to be well known. We have seen only one other case where a gelatinous egg-mass was liberated freely as in the case of *Ephemerella*. This happened when a female, afterwards identified as the Caddis Fly, *Stenophylax stellatus* Curt., flying over a smooth pool, allowed itself rapidly to fall through about 2½ feet tail down so as to strike the water with the greenish egg-mass. After six repetitions of this fall the insect flew away without the mass which was finally dislodged.

As we have seen, oviposition in these insects is not brought about by the tearing away of the egg-mass, but is an ordered process dependent on certain well-marked conditions which have each their own importance at appropriate times. Common to all is the substance which causes the egg-mass to remain attached to the female. This is seen to be readily water-soluble. In the stone-flies, and in *Ecdyurus* and *Ephemera*, this substance appears to be the same as that which causes the eggs to cohere in mass. It is not, however, the same material as that which produces the adhesive surface by means of which the eggs are anchored. Again there are the peculiar binding materials of the egg-masses of *Ephemerella*, *Bætis*, and *Siphlurus*, which prevent the disintegration of the mass and play a part in the process of final egg deposition.

TABLE

Perla egg-mass	4·25 cm./sec.	Coarse sand above 1 cm./sec.
Perlodes egg-mass	3·46 ,,	
		Fine sand 1 cm./sec.
Perla egg	0·8 cm./sec.	down to
Perlodes egg	0·6 ,,	
**Chloroperla* egg 0·3×0·25mm.	?	
Protonemura egg 0·18×0·16 mm. ...	0·15 ,,	
**Leuctra* egg 0·18×0·14 mm. ...	? (Perhaps similar to *Protonemura*)	
**Ecdyurus* egg 0·18×0·13 mm. ...		
**Nephelopteryx* egg 0·17 mm. ...		0·1 cm./sec.

Eggs and egg-masses arranged according to their known and probable* rates of fall to indicate their relations with the various portions of the coarse and fine sand fractions.

In a previous paper (*loc. cit.*) we have shown that the eggs of *Ephemera danica* are deposited under similar conditions to those required for fine quartz sand grains (diameter of 0·25 mm. to 0·05 mm.). In the fine sand fraction the particles fall through still water at from 1 cm. per second for the coarsest to 0·1 cm. per second for the finest. The speeds include those determined for *Perla carlukiana* (0·8 cm./sec.), *Perlodes mortoni* (swollen membrane, 0·6 cm./sec.), and *Protonemura meyeri* (0·15 cm./sec.). These figures show such differences that we can assume that the more rapidly falling eggs of *Perla* and *Perlodes* come into the coarser portion of the fine sand fraction and the less rapidly falling egg of *Protonemura* comes into the finer portion. Thus the eggs would be variously sorted out by a given rate of flow, the heaviest egg falling first, the lightest last. The eggs of *Leuctra, Nephelopteryx,* and *Ecdyurus* are about the same size as that of *Protonemura* and probably they have about the same velocity through a column of still water.

The large, heavy eggs of *Perla* are attached to stones and moss. We have found them on boulders among which was practically no fine material less than fine sand, this indicating that the current was usually fairly swift.

We may consider the stream as a screen which sorts out the different eggs passing into it in the same way as it sorts out other transported material. Boulders, roots, variations in depth and in the form of the bank produce changes in the transporting force of the water, bringing about deposition or erosion, and doubtless they act similarly indirectly on the eggs. The slight slackening of current in the shelter of stones on the bed no doubt causes many eggs to come to rest in the shelter of such objects. Fine sand and coarser grades collect behind and beneath them. We have taken from such places nymphs of *Perla, Chloroperla, Perlodes, Protonemura, Amphinemura, Leuctra,* and *Ecdyurus* varying in length from 1·25 mm. upwards. Similarly small organisms have been taken from moss. This suggests that many of the transported eggs finally come to rest in such places which also offer shelter for the growing animal and provide surfaces on which they may cling and browse.

It is striking that stones which do not shelter fine material have no appreciable fauna; a typical example, consisting of rounded pebbles of 1 in.—4 in. diameter, harboured a population of 1·5 per square decimetre, held by a sieve of 0·5 mm. mesh. The poverty in fine detritus is determined by the transporting power of the water which probably plays an important part in preventing egg deposition here.

Regions in which egg deposition takes place act as centres from which migration of immature forms takes place. It is probable that many of the heavily washed regions obtain their scanty fauna from these sources.

Regarding the structure of the eggs of *Perla* and *Perlodes* it is to be noticed that the larvule emerges from the shell near the end opposite to the anchoring portion. The investing membrane, in the case of *Perlodes*, may be torn off, but attachment is finally brought about at the basal plate, thus the apex, which ultimately forms a lid, is free from the substratum.

As has been seen, the egg-masses of *Perlodes* easily become detached on dry land. It is quite probable that this happens in nature when the females are hiding under stones. Since 18 hours' drought in the laboratory had no ill-effects on the disintegration of the mass and the anchoring of the separated eggs, it is probable that the rather damp conditions under the stones of a bed of shingle will have no effect. It may happen then, that, should the egg-mass become detached, the eggs would remain fertile for some time and would be dispersed at the next flood.

A female *Perlodes mortoni* was taken in flight within the City of Leeds over a mile from the nearest stream. It is quite possible for females from one stream to fly over considerable distances, thus bringing about the population of other streams.

Oviposition in the *Plecoptera* appears to be dependent largely on sunshine, calm atmospheric conditions and smoothly flowing water. In our experience the females fly most abundantly in these circumstances and it is easy for them to descend to the water surface without being drowned. Small streams with fairly rapid flow, containing many emergent boulders and having stony banks usually have an abundant fauna of the smaller species.

The egg-masses of *Ephemerella ignita* are caught by patches of moss. We have taken several from samples of *Fontinalis* and *Eurhynchium* and it is probable that large numbers are held up, since the population of this species in moss may be as much as 200 per square decimetre, while among stones without moss it may be as high as 7 per square decimetre or absent. Among filamentous algæ (*Cladophora*, etc.) the numbers vary between 30 and 60 per square decimetre. This indicates a definite relation between vegetation and the abundance of this species.

The case of *Bætis* presents certain interesting features. The method of entering the water and of egg-laying suggests a necessity for the presence of emergent bodies for the successful population of a stream by this genus. The species *B. pumilus*, *B. binoculatus*, and *B. rhodani*, on which observations are recorded in this paper, are more abundant, as nymphs, in such streams than where emergent bodies are few or absent.

The deposition of eggs as recorded here bears some relation to the occurrence of very young stages. The earliest stages of *Plecoptera* which we have obtained do not occur in large numbers grouped together, but tend to be found more evenly distributed throughout the region in which they occur, indicating that the eggs from which they came were strewn broadcast rather than dropped in clusters. On the other hand the very small nymphs of *Ephemerella* e.g. 2 mm. in length, are found in large numbers in small samples of moss, a condition due, without doubt, to the clustering of eggs in considerable quantities.

The *Ephemeroptera* as a whole, like the *Plecoptera*, are most active in oviposition during pleasant open weather, but we have several times observed *Bætis pumilus* engaged in entering the water during cold, dull and rather windy conditions. There is, no doubt, a correlation between its mode of oviposition and its disregard for the quality of the weather.

It will be gathered from the foregoing account that the distribution of eggs is an orderly process in which several factors come into operation. Among these are the cohering water-soluble substance holding the unwetted eggs together, the solution of which leads to their separation, the adhesive substance which is the means of anchoring them, and the rate of fall of the egg or egg-mass which, acting against the flowing stream, is largely responsible for determining the region in which deposition will take place.

The rate of flow of a stream can be modified with a consequent production of changes in the nature of the bed. These changes, both in current and in bed, would have a direct effect on the distribution of the eggs of *Ephemeroptera* and *Plecoptera* and consequently on the ultimate population of these insects in the stream. These orders provide quite a substantial portion of the food of fish (a 10-inch trout contained over 1,000 recognisable subimagines of *Ephemerella ignita*) so that changes affecting their numbers would, no doubt, be reflected on the nutrition of fish living in the vicinity.

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