THE EFFICIENCY OF ADAPTIVE STRUCTURES IN THE NYMPH OF *RHITHROGENA SEMICOLORATA* (CURTIS) (EPHEMEROPTERA)

BY A. M. STUART
*Department of Zoology, University of Glasgow**

(*Received* 23 *February* 1957)

INTRODUCTION

Rhithrogena semicolorata (Curtis) (Fig. 3) has long been known to inhabit fast-flowing streams, but there have been hardly any critical observations on its clinging properties in torrents. It is remarkable in that all of its seven pairs of gill lamellae overlap one another and form what has been regarded as a sucker (Percival & Whitehead, 1929) or an adhesive organ functioning on the principle of a 'Venturi' tube (Hora, 1930). If the gills act as a sucker they could only be effective on a fairly smooth surface. It thus seemed reasonable to expect that the animal would tend to have an optimal substrate on which it would obtain the best hold using both sucker and claws. It was in order to find this postulated optimal surface and to attempt to assess the true value of the gills as a structural adaptation to currents that the experiments described below were carried out. In order to obtain a comparison with a mayfly nymph of similar structure and same habitat, yet not possessing overlapping sucker-like gills, *Ecdyonurus* sp. was chosen for further experiments.

Previous work on *R. semicolorata* has been scanty. Percival & Whitehead (1929) and Harker (1951, 1953) are the only ones to have made any first-hand observations on its behaviour. Harker (1953) states that the sucker-like arrangement of the gills of *R. semicolorata* gives a greater adhesive power than is found in other British species of mayfly nymphs. Hora (1930), whilst not having any live *Rhithrogena* at hand, offers some views on the sucker-like arrangement of the gills, based mainly on a similar ephemerid nymph *Iron* sp. from India. His 'Venturi' tube theory, however, could not be upheld as by direct observation under a lens *Rhithrogena* was seen to keep all its gills overlapping. Two American species of *Iron* are described by Dodds & Hisaw (1924) who put forward an explanation of the clinging properties of these species. Of the above workers, however, only Harker has made a serious attempt to examine critically the current-resisting properties of *Rhithrogena* in the laboratory.

METHODS AND MATERIALS

Nymphs were collected from the Craigton Burn, Dunbartonshire, and were kept alive in an artificial cascade similar to that used by Hynes (1941).

* Present address: The Biological Laboratories, Harvard University.

In order to examine the current-withstanding powers of the nymphs, special apparatus was designed and constructed (Fig. 1). A reservoir situated in a room above the laboratory maintained a constant head of water of sufficient magnitude. From it water flowed through a rubber hose to a glass tube 1 in. in diameter, 10 in. long and having a 1 × 1 in. side arm almost midway along its length. A Perspex slide, to which strips of Perspex had been cemented to form a cell, was placed midway along this tube, and the water inlet was so arranged that the water flowed directly along the surface of the slide, this surface being the experimental

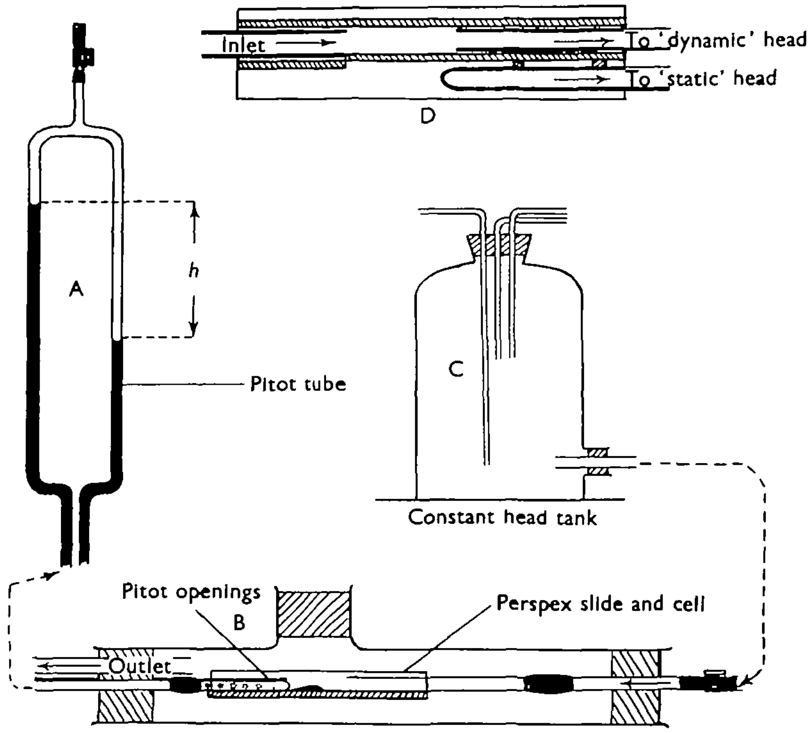


Fig. 1. Diagram of apparatus (not to scale). A, Pitot tube. B, tube containing Perspex cell. C, constant head tank. D, detail plan view of Perspex slide and cell.

substrate. Four such slides were prepared with different surfaces. The tops of two were softened with chloroform, covered evenly with sand, and allowed to dry. Thus, surfaces simulating those found in natural conditions were obtained. Sand passing through a 20-mesh/in. sieve, but stopped by a 30-mesh/in. (i.e. with an average diameter of 0·04 in.) formed surface A, and sand passing through an 80-mesh/in., but stopped by a 90-mesh/in. (approximate diameter being 0·01 in.), formed surface B. One slide was left smooth, surface C, and another was left slightly scratched, the scratches being criss-crossed and approximately 2·0 mm. apart, surface D.

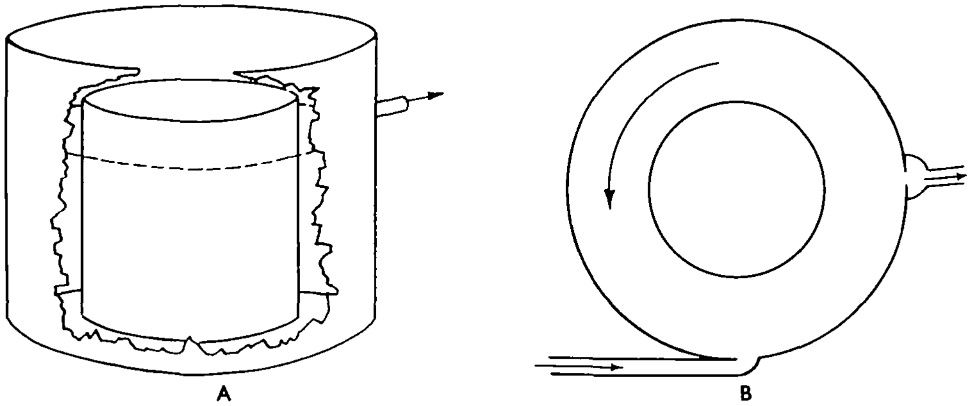
Table 1. *Experimental surfaces*

Surface	Type
A	Sand grains, of average diameter 0·04 in.
B	Sand grains of average diameter 0·01 in.
C	Smooth Perspex
D	Perspex with scratches approximately 2·0 mm. apart

The current was measured by means of a Pitot tube. The opening of the tube to the dynamic head was placed immediately behind the animal so as to obtain as true a reading as possible of the current passing immediately over the nymph; the opening to the static head lay to one side.

The difference in height between the two levels of the Pitot tube was measured initially by means of a reading microscope with a scaled eyepiece, but later a steel rule was used, as the degree of fluctuation of the head (± 2 mm.) did not warrant the more accurate method.

The height in cm. was converted to a current in metres per second by the formula $V = K\sqrt{gh}$, where for the purposes of these experiments K was taken as 1·0, $g = 981$ cm./sec.^{2} and h = difference in height in cm. between the two columns.



A B

Fig. 2. Adapted print washer. A, cut-away diagram. B, plan view.

In a final experiment use was made of an adapted photographic print-washer (Shelford, 1930, p. 74). This (Fig. 2) was fitted with a central cylinder and so formed an annular trough. The bottom and sides were of pitted metal and enamel, thus providing a surface not quite smooth.

EXPERIMENTAL

The effect of current velocity and degree of roughness of the substrate on *Rhithrogena* and *Ecdyonurus* nymphs has been investigated by means of the above apparatus. Unfortunately, it was impossible in winter to obtain *Rhithrogena* of reasonable size, and those used initially were of 4·0–5·0 mm. in length. Later, larger nymphs 7·0 mm. long were used.

The experiments were carried out at room temperature 16·7° ± 2·2° C. Each nymph was first examined to make sure that all the gills were intact, measured for length, and then inserted through the side arm on to a prepared slide by means of a camel-hair brush. The animal was restricted by the small cell on the slide, and was compelled to remain there with its head facing the inlet tube. The flow of water was then turned on, increased gradually and as far as possible at a constant rate. At a certain current the animal could no longer maintain a hold on the substrate and was washed off to be collected later. The difference in heights of the Pitot arms was read quickly and noted.

The above procedure could not always be carried out successfully owing to various technical difficulties. Some animals refused to keep themselves orientated with their heads pointing against the flow, others refused to settle and persisted in swimming, while most attempted to avoid the current.

To obtain results in which conditions were as constant as possible, animals which did not face upstream were not included in the calculation of a mean for a specific surface. It was noticed, however, that it did not make a great deal of difference to their holding powers which way they faced. One which faced downstream in Exp. 2 withstood a current of 1·58 m./sec. which compared favourably with most of those which faced upstream. Nymphs which were knocked off the slide by air bubbles originating from airlocks in the water system were also disregarded.

Table 2. *Summary of experiments*

Exp.	Animal under observation	Remarks	Length of nymph (mm.)	No. in sample	Experimental surface	Average difference in heights of Pitot heads in cm. (h)	S.D. of (h)	Average current in m./sec. at which nymphs lost hold of substrate
1	*R. semicolorata*	—	4·0–5·0	20	B	10·35	1·58	1·43
2	*R. semicolorata*	—	4·0–5·0	20	A	7·15	1·81	1·18
3	*R. semicolorata*	Refused to settle	4·0–5·0	—	C	—	—	—
4A	*R. semicolorata*	—	7·0	5	D	11·98	5·96	1·53
4B	*R. semicolorata*	Clawless; note selection of results	7·0	5	D	4·86	1·96	0·98
5	*Ecdyonurus* sp.	—	6·0–7·5	5	D	12·56	2·53	1·57
6A	*R. semicolorata*	—	6·0–7·0	5	B	15·98	2·62	1·77
6B	*Ecdyonurus* sp.	—	7·0–7·5	5	B	15·42	2·66	1·74
7	*Ecdyonurus* sp.	—	6·0	5	A	7·82	1·63	1·24
8	*R. semicolorata*, *Ecdyonurus* sp.	—	Print washer experiment					

In Exp. 1 it was noticed that even at moderate currents the nymphs used their claws rather than their gills for adhesion. The sand grains on this surface B would not be big enough to interfere with the action of a sucker.

Table 3. '*T*' *test for significance of results*

Comparisons (Exp.)	D.F.	*T*	Significance	*T* 5 %
1 and 2	38	5·84	S	1·96
4A and 5	8	0·50	NS	2·31
*4B and 5	8	6·55	S	2·31
6A and 1	23	5·31	S	2·07
6A and 6B	8	0·50	NS	2·31
7 and 6B	8	5·99	S	2·31

NS = not significant. S = significant

The grains of sand on surface A in Exp. 2 were so big that any sucker formed by the gills would be useless. The lower average current required to sweep the nymph off the slide is probably due to the larger grains providing less suitable holds than the finer grains. It should be noted that the claws can maintain a strong grip, even if only a very minute hold is available.

In Exp. 3 readings could not be taken satisfactorily, since the insect refused to remain on the slide if no holds could be obtained for its claws. The claws of several were amputated, and they were again placed on this slide, it being thought that they would use their suckers, being unable to use their claws. They again refused to settle.

Exp. 4A was set up as it had been thought that perhaps the nymphs, as they showed a disinclination to settle on a smooth surface, would prefer a slightly scratched surface to a smooth one, and would so be persuaded to use gills as a sucker. The animals were placed on the slide in the usual manner and watched under a $\times 8$ lens. None of the nymphs used their gills as a sucker though the scratches were not of sufficient depth or number to make a suction device inoperative.

Differences in the figures obtained would seem to depend merely on how the insect was positioned relative to the scratches. One which stayed on till a current of 2·01 m./sec. was reached had all its six claws in good holds, whilst the others had one or more of their claws out of action due to there being no convenient scratches in which to place them.

In Exp. 4B the nymphs' claws were amputated in an attempt to compel the animals to use their gills as suckers. Though these nymphs were eventually persuaded to settle by leaving them in still water for some time, great difficulty was experienced in keeping them in one position. They were easily swept away and few could be persuaded to stay on the slide. So far as could be seen, the nymphs which could be persuaded to settle did use their gills for adhesion. It should be noted that the number of nymphs rejected as unsuitable in this experiment was very much greater than in the other experiments due to the refusal of almost all the nymphs to settle once the claws had been amputated. The readings, however, despite this greater selection, are still smaller than in Exps. 4A and 5.

* The significant difference in this comparison is very much greater than indicated as the animals used in Exp. 4B were more highly selected than those in Exp. 5 and the other experiments (see text).

Since normal *Rhithrogena* did not appear to use its gills as a sucker on the scratched slide (surface D) and persisted in using its claws, it appeared reasonable to predict that *Ecdyonurus* would also be able to maintain a hold under the same conditions. In Exp. 5, therefore, *Ecdyonurus* sp. was placed on the same slide as used in Exp. 4A.

Since *Ecdyonurus* has no suction device it has no alternative other than to use its claws, and as can be seen from the above results it compares favourably with *Rhithrogena*, though the animals used were slightly larger than in the previous experiment. There is no significant difference between the readings obtained in this experiment and in Exp. 4A.

Exps. 6A and 6B were carried out to ascertain whether there was much difference in the current-resisting powers of *Rhithrogena* and *Ecdyonurus* when placed on what would seem to be an optimal surface. There is no significant difference in the holding powers of the animals tested in these experiments though this conclusion should perhaps be qualified by pointing out that the *Ecdyonurus* nymphs used were slightly larger than those of *Rhithrogena*. The sizes of the nymphs do make a difference at least in *Rhithrogena*, since by comparing the figures obtained in Exp. 6A with those obtained in Exp. 1 it can be seen that significantly higher current speeds can be withstood by nymphs of 7·0 mm. than by nymphs of 4·0 or 5·0 mm.

The readings in Exp. 7 were taken in order to provide a comparison with *Ecdyonurus* and *Rhithrogena* in Exps. 6A and 6B. The average figure is significantly lower than in Exp. 6B, and may be again accounted for by considering that the holds available are fewer and more widely spaced.

For Exp. 8 the adapted print washer was used instead of the usual apparatus. Clawless *Rhithrogena* nymphs, 7·0 mm. long, were introduced along with similar sized clawed *Rhithrogena* and *Ecdyonurus* nymphs. It was seen that, even at quite gentle currents, the clawless *Rhithrogena* were unable to settle, whilst the *Ecdyonurus* and *Rhithrogena* with claws quite easily caught hold of the bottom or the sides by means of their claws. This experiment, while not so critical as the previous experiments in that no currents were measured, nevertheless, confirms the previous results more graphically.

DISCUSSION

Various workers at various times have noted the sucker-like arrangement of the gills of *Rhithrogena* and of the similar genus *Iron*. They seem, however, to have placed more emphasis on the gills of *Rhithrogena* as an organ of attachment than is really warranted. The animal appears to use its gills for adhesion only when it finds itself on a surface so smooth that it can get no grip with its claws, or experimentally when its claws have been amputated and it is again on a smooth surface. The gills, however, do not appear to be efficient, and even if there are only minute scratches available as holds the nymphs will use their claws rather than their gills at currents above the most gentle (Exp. 4A).

Percival & Whitehead (1929) have stated that *R. semicolorata* can easily attach itself to smooth surfaces when the claws are removed. It was found here that while a clawless nymph could be persuaded to settle and use its gills for adhesion when placed on a smooth surface in still water, yet if it was placed in the print washer (Exp. 8) where there was a current it was unable to settle even when the flow of water was comparatively gentle. A similar nymph with claws, when placed in the print washer under similar conditions, obtained holds with its claws on minute scratches in the same manner as did *Ecdyonurus* sp. Percival & Whitehead (1929) have also stated that 'The power of the sucker is very great as it will withstand a powerful jet of water a couple of millimetres away.' As was shown above (Exps. 4A and 4B), however, the figures obtained for animals with claws and animals without claws on a surface which would not render a sucker inoperative indicate that the claws are of greater value to the animal. It should be noted that many nymphs obtained from the stream had one or more gills lost and thus the gills could no longer act as a sucker.

Harker (1951) has carried out a more critical investigation into the current-resisting properties of *R. semicolorata* than Percival & Whitehead (1929). Her results disagree with those obtained in the present experiments in respect of the clinging properties of *Rhithrogena* and *Ecdyonurus*, and in the maximum current required to make a nymph lose hold of the substrate. Harker used a beeswax-lined trough of 56 × 4 in. and with a constant depth of water of 2 in. She found that 50% of the nymphs of *R. semicolorata* are swept away at a current of 5·2 m./sec. while the greatest current withstood by a *Rhithrogena* nymph of 7 mm. in the present experiments was 2·01 m./sec. The discrepancies in the results are probably due to what is considered a less accurate measurement made by her of the current actually acting on the animal, and to the fact that her nymphs may have been of a different size from the ones in the present experiment. The substrate used, of course, was different and beeswax must provide an excellent, if somewhat unnatural substrate to which nymphs can cling. Apart from absolute discrepancies, however, Harker found that *Rhithrogena* was more successful in resisting currents than either *Ecdyonurus* or *Baetis*. In the stream where the present nymphs were collected, *Baetis* with its torpedo-shaped body always greatly outnumbered *Rhithrogena* and *Ecdyonurus* and appeared to be the most successful of the three genera as was also noted by Dodds & Hisaw (1924) in America. Unfortunately, Harker's paper and thesis were not seen until after the present experiments were completed.

As was shown above, the actual current-withstanding powers of *Ecdyonurus* and *Rhithrogena* are not very different; nor, as will be discussed later, should they be expected to differ.

It was found in the above experiments that the general form of *Rhithrogena* and *Ecdyonurus* could not be described as a current-resisting form, in the same sense as that of *Baetis* which is streamlined and torpedo-like. Hora (1930) considers *Rhithrogena, Iron* and other similarly flattened forms to present an ideally streamlined form to the current. He states that the shape (Fig. 3) is streamlined on all sides, and compares it to an aeroplane strut section of what is known as the 'Baby' type (Fig. 3). He does not comment on the fact, however, that the shape of such nymphs as *Iron* and *Rhithrogena* is really more of an aerofoil, i.e. half a torpedo-shaped form. A body of this shape held stationary in a current in the position shown in the diagram (Fig. 3) experiences a lifting force on the downstream half. This lifting force can be observed in the laboratory, when with increasing current first the body of *Rhithrogena* rises, and then the tail, till the insect finally loses hold and is swept away (Fig. 3). So while the form of *Rhithrogena* is streamlined, this is not considered a current-withstanding adaptation. Dodds & Hisaw (1924) do not mention a dorsal lifting force of the current acting on *Iron* sp. and in fact only mention a lesser downwards force.

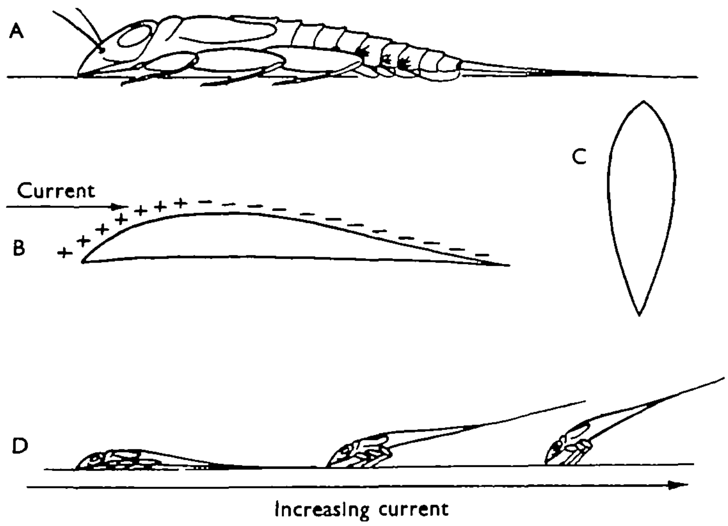


Fig. 3. A, lateral view of nymph of *Rhithrogena semicolorata* (Curtis). B, aerofoil section, + = positive pressure; − = negative pressure. C, 'Baby' strut section. D, diagram showing the result of the lifting effect of increasing current on *Rhithrogena semicolorata* (Curtis).

It was noted on several occasions in the laboratory and in the field that *Rhithrogena* will evade a strong current by sheltering among obstacles and in cracks, rather than face it as is commonly supposed. This, indeed, was one of the main causes of difficulty in forcing nymphs to remain in the current during experiments. If, in the experimental cell, a nymph settled just in front of the water inlet, it was almost impossible to sweep it off the substrate by increasing the current. The thickness of the glass composing the tube was sufficient to shield the nymph from the full force of the current, a current greatly in excess of that normally required to sweep away the nymph.

It is, therefore, postulated here from the above observations and experiments that the form of *Rhithrogena* and *Ecdyonurus* is not designed to withstand currents in the way a torpedo-shaped body does (Hora, 1930; Dodds & Hisaw, 1924), but is designed to enable these animals to utilize cracks and crevices for avoiding the current. It should be noted that in nature the chances are that the currents meeting the animal will not come strictly in the direction of its long axis (Fig. 3), nor will it be on a perfectly flat surface.

I wish to express my thanks to Dr H. D. Slack, who supervised this work, for much helpful encouragement and criticism.

I am indebted to Prof. C. M. Yonge, C.B.E., F.R.S., for facilities made available in his department, and to Dr P. Whittle of the Applied Mathematics Laboratory, Wellington, New Zealand, for statistical analysis of the results.

My thanks are also due to Prof. E. Percival and to Mr B. B. Given who have both read the manuscript of this paper.

SUMMARY

1. The current-resisting powers of *Rhithrogena semicolorata* Curtis have been investigated and measured, and compared with those of *Ecdyonurus* sp.

2. The part played by the gills as organs of adhesion is considered, and they are found to contribute little to the current-resisting powers of the nymph. The claws are regarded as being of more importance to the animal in clinging than the gills.

3. The dorso-ventral flattening of the animal is considered to be a crevice-seeking adaptation, and not a current-resisting one.

REFERENCES

DODDS, G. S. & HISAW, F. L. (1924). Ecological studies of aquatic insects. I. Adaptations of mayfly nymphs to swift streams. *Ecology*, **5**, 140–3.

HARKER, J. E. (1951). Unpublished thesis in Manchester University Library.

HARKER, J. E. (1953). An investigation of the distribution of the mayfly fauna of a Lancashire stream. *J. Anim. Ecol.* **22**, 1–13.

HORA, S. L. (1930). Ecology, biology and evolution of torrential fauna with reference to organs of attachment. *Phil. Trans.* **218** B, 172–282.

HYNES, H. B. N. (1941). The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. *Trans. R. Ent. Soc. Lond.* **91**, 459–557.

PERCIVAL, E. & WHITEHEAD, H. (1929). A quantitative study of the fauna of some types of stream bed. *J. Ecol.* **17**, 282–314.

RAWLINSON, R. (1939). Studies on the life history and breeding of *Ecdyonurus venosus* (Ephemeroptera). *Proc. Zool. Soc. Lond.* B, **109**, 377–450.

SHELFORD, V. E. (1930). *Laboratory and Field Ecology*. Baltimore.

APPENDIX 1

Experiment 1

Rhithrogena of 0·4–0·5 cm. in length on surface B.

	Length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·40	11·5	1·50
2	0·40	10·0	1·40
3	0·40	8·6	1·30
4	0·40	12·4	1·56
5	0·40	10·3	1·42
6	0·40	10·5	1·44
7	0·40	8·0	1·25
8	0·40	10·4	1·43
9	0·40	8·9	1·32
10	0·45	7·7	1·23
11	0·40	9·0	1·33
12	0·50	12·1	1·54
13	0·50	13·3	1·62
14	0·40	8·7	1·31
15	0·50	12·0	1·53
16	0·50	10·2	1·42
17	0·50	10·6	1·44
18	0·50	12·5	1·57
19	0·50	10·6	1·44
20	0·40	9·6	1·37

Approximate mean, 1·43 m./sec.

APPENDIX 2

Experiment 2

Rhithrogena of 0·4–0·5 cm. in length on surface A.

	Length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·45	4·9	0·98
2	0·40	7 7	1·23
3	0·45	6·8	1·15
4	0·45	6·7	1·15
5	0·40	6·6	1·14
6	0·55	6·8	1·15
7	0·60	10·0	1·40
8	0·45	6·0	1·08
9	0·50	8·4	1·28
10	0·45	5·5	1·04
11	0·40	5 8	1·07
12	0·50	4·1	0·90
13	0·45	9·8	1·39
14	0·40	8·7	1·30
15	0·50	7·8	1·24
16	0·40	9·4	1·36
17	0·40	9·3	1·35
18	0·40	5·4	1·03
19	0·40	4·7	0·96
20	0·40	8·5	1·29

Approximate mean, 1·18 m./sec.

APPENDIX 3

Experiment 4A

Rhithrogena of length 0·70 cm. on surface D.

	Size—length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·70	6·5	1·13
2	0·70	6·5	1·13
3	0 70	20·5	2·01
4	0·70	14·3	1·67
5	0·70	12·1	1·54

Approximate mean, 1·53 m./sec.

APPENDIX 4

Experiment 4B

Rhithrogena of 0·70 cm. length, without claws on surface D.

	Length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·70	8·1	1·26
2	0 70	4·5	0·93
3	0·60	3 0	0·77
4	0·70	3·8	0·86
5	0·70	4·9	0·98

Approximate mean = 0·98 m./sec.

APPENDIX 5

Experiment 5

Ecdyonurus 0·6–0·75 cm. on surface D.

	Length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·75	14·4	1·68
2	0 75	14·9	1·71
3	0·60	13·5	1·63
4	0 70	8·9	1·32
5	0·75	11·1	1·48

Approximate mean = 1·57 m./sec.

APPENDIX 6

Experiment 6A

Rhithrogena 0·6–0·7 cm. on surface B.

	Length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·60	14·7	1·70
2	0·70	14·6	1·69
3	0·70	16·2	1·78
4	0·70	20·5	2·01
5	0·75	13·9	1·65

Mean = 1·77 m./sec.

APPENDIX 7

Experiment 6B

Ecdyonurus 0·6–0·75 cm. on surface B.

	Length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·75	16·3	1·79
2	0·60	14·7	1·70
3	0·75	13·0	1·60
4	0·75	18·5	1·91
5	0·75	14·6	1·61

Mean = 1·74 m./sec.

APPENDIX 8

Experiment 7

Ecdyonurus of 0·6 cm. on surface A.

	Length (cm.)	Pitot head (cm.)	Velocity of current (m./sec.) ($V=\sqrt{2gh}$)
1	0·60	8·1	1·26
2	0·60	9·3	1·35
3	0·60	6·4	1·12
4	0·60	5·9	1·08
5	0·60	9·4	1·36

Mean = 1·24 m./sec.