FURTHER OBSERVATIONS ON THE EFFECT OF TREMATODE PARASITES ON *PERINGIA ULVAE* (Pennant) 1777

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(With Plates I and II and text-figures 41–47.)

INTRODUCTION.

THROUGHOUT the investigations on the trematode parasites of *Peringia ulvae* an attempt has been made to establish various points regarding the relationship of parasite and host. Those noted here concern the relative changes of growth in male and female snails, and the probable " sex-reversal " of the host.

Experimental evidence is required to prove both these phenomena, but as this is not at present available the discussion is based on the results of examining and sampling large collections of *P. ulvae* from different localities. Each collection has necessarily been dealt with separately and a comparison made between the infected and uninfected portions of the sample.

One of the major difficulties is the lack of a suitable method for estimating the age of the snails. As will be seen later, size is no criterion and so far has not proved useful in this respect.

Pelseneer (1928) first drew attention to the fact that the males of gastropod molluscs are more frequently infected than the females. He noted one exception, *Turritella communis* Lamark 1785, but Rothschild (1936) found that at Plymouth this species conformed to the rule. Pelseneer (1906 and 1928) also originally pointed out the reduction of the penis in infected snails, due in his opinion to the partial or complete castration of the host by the parasites. Wesenberg-Lund (1931) was, however, the first to put forward the view that changes in sex might be directly due to the effect of trematode parasites. He found that in the hermaphrodite snail *Succinea putris* (L.) 1758 the female organs are totally destroyed, but the production of spermatozoa continues after this for some time—although greatly decreased—before castration is complete. " With some right it may be maintained that many parasitized snails pass through a male stage, or in other words that the parasite alters a hermaphrodite organism into a male."

Krull (1935), apparently unaware of either Pelseneer's or Wesenberg-Lund's observations, published an interesting paper on the morphology of various snails, including *Peringia ulvae* (= *Paludestrina ulvae*), in which he suggests that those infected specimens showing a reduced penis are in reality " sex-reversed " females. He bases his belief on the discovery of specimens in which the internal organs were only partially destroyed and which he considered were unquestionably female, while a small functionless penis had also been developed. He does not suggest that these snails ever function as males. " Sex-reversal " is therefore a rather unsatisfactory term to employ. In default of a better one it is used by the author of this paper.

The change in relative size of parasitized male and female snails has not received any attention until now. In view of the gigantism produced in *P. ulvae* and various other snails by trematode parasites (Rothschild 1936) it was

thought probable that the normal differences in size between the sexes might be noticeably altered, irrespective of whether the males are more frequently infected as appears to be the case with most species, or whether a certain proportion of the infected " males " are in reality sex-reversed females.

The Normal Sex Ratio of *P. ulvae*.

In nature the relative number of males and females of *P. ulvae* seem to vary considerably, according to both size (age) and distribution, and other unknown factors, and therefore each sample must be examined separately. Pelseneer (1926) states that in the Mollusca as a whole, it is usual to find the males outnumber the females in the whole population—their numbers being greatly in excess of the females in the young stages, approximately equal when they become sexually mature, and somewhat fewer in the older stages.

Pelseneer himself examined 115 specimens of *P. ulvae* from the mouth of the River Slack (Port d'Ableteuse) and a further 663 collected from the mouth of the Canche (Étaples). Sixty-eight per cent. of the former and 58 per cent. of the latter were females. This surprised Pelseneer, who thought that some of the females might be in reality males—the penis having regressed after the breeding season as happens with *Littorina littorea* (L.) 1758, and various other species. He records trematode parasites, but we can infer from his remarks that the rate of infection was low.

TABLE I.

Snails between 1 and $2\frac{1}{2}$ mm. in Length.

	♂♂	♀♀	Total
Tamar Saltings, February 1938 . .	17	33	50
Tamar Saltings, March 1938 . .	23	51	74
St. John's Lake, February 1938 . .	63	137	200
St. John's Lake, June 1937 . .	13	36	49

Although the females do appear to outnumber the males in numerous samples examined, yet my observations in no way support the theory of a seasonal regression of the penis. Only four uninfected males have been noted with a reduced penis, although numbers have been looked at during all seasons of the year. These four specimens can be regarded as abnormal examples, just as a few individual snails were found with a split or reduced tentacle.

It is very doubtful, however, if the sex of specimens under $2\frac{3}{4}$ mm. can be determined with certainty. Among these very small snails specimens without a penis greatly outnumber those with one. The penis is then found in all stages of development, and it is quite probable that many of these very small snails are males in which the penis has not developed. In comparing the sex ratio it has been found safer to ignore all snails under $2\frac{3}{4}$ mm. in size. Figures for the small size groups are given in Table I. It will be seen that apparent females regularly outnumber recognizable males by about 2 to 1.

The distribution of *P. ulvae* is patchy, but when it is present it is often found in enormous numbers. As many as 28,400 per square metre are recorded [1]

[1] Mr. G. M. Spooner supplied this figure in a private communication.

from St. John's Lake, Plymouth. It is not at all unusual to find a considerable difference in the sex ratio for random samples collected a few feet apart, or at the same ground on different occasions. Thus from the same area of St. John's Lake, Plymouth, collections of snails gave the following results: 39 per cent. ♂♂ (6 per cent. infection), 38 per cent. ♂♂ (3 per cent. infection), 60 per cent. ♂♂ (4 per cent. infection), 26 per cent. ♂♂ (2 per cent. infection), 48 per cent. ♂♂ (3 per cent. infection). Similar variation was discovered in samples from Millport (West Scotland), Holbeach (Lincoln), Wittering (Sussex), Poole Harbour (Dorset), and Blakeney (Norfolk). Extensive sampling would be necessary for an exact estimate of the sex ratio of the whole population of any given area. If infection is high it is very important to record the number of uninfected males and females of each sample. Krull unfortunately completely ignores this point, and does not record the sex ratio of the uninfected specimens which he examined.

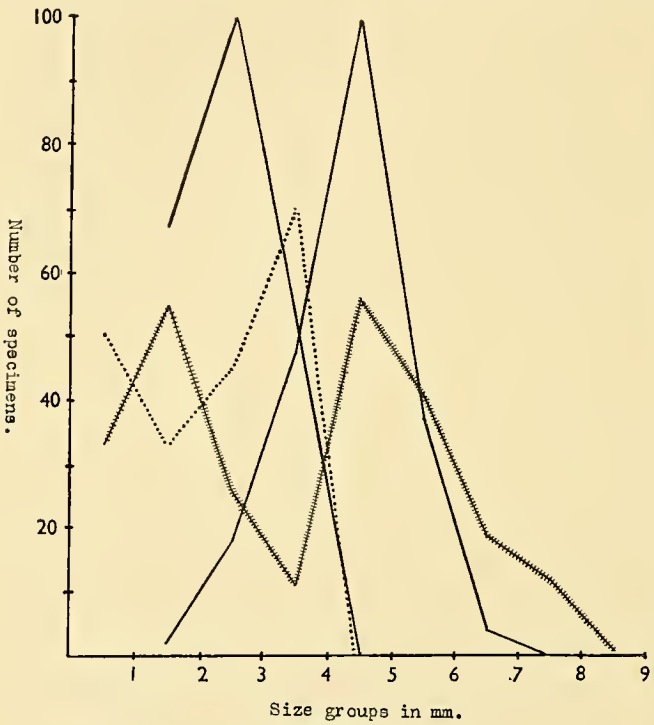


Fig. 41: Samples showing uneven spat fall.
——— Holbeach Saltings, August.
..... St. John's Lake, September.
–·–·–·– Tamar Saltings, March.

The Varying Growth of *P. ulvae* and the Relative Size of Males and Females.

Examination of samples of *P. ulvae* from various habitats shows that their size varies greatly irrespective of the age of the snails and the degree of parasitism (Pl. I). On the whole those populations of *P. ulvae* commonly found in saltings attain a larger size than the populations on mud flats (Pl. II, figs. 1, 2). In addition, the size of the snails varies in a most remarkable manner from one permanent pool in the saltings to another. This must partly be due to irregularity of spat fall, which is a feature of this type of habitat and accounts for those pools which contain hundreds of thousands of tiny specimens—generally fringing the edge—none of which exceed 2–3 mm. in length, and other pools in which it is difficult to find any small snails at all, and a third type in which there are large and small specimens, but few or no intermediate stages (fig. 41).

Apart from this there are strong indications that the growth-rate itself varies from one pool to another. The variation in growth referred to above is generally associated with a difference in shell texture, a difference in shell colour and shape and, somewhat surprisingly, in extreme cases with a definite difference

in the consistency of the soft parts of the body. It seems likely that it is dependent on environmental conditions, since both extremes of growth and of shell texture are found in different types of pools in the same saltings. On the mud flats the largest shells are not found at all; it is unusual to discover a specimen exceeding $5\frac{3}{4}$ mm. in samples from this habitat.

The difference in growth greatly complicates the study of the effect of parasitism on the various populations, as it makes it almost impossible to gauge the age of the snails. It is difficult to say with certainty, unless observations are made over a long period, whether a pool is populated with all comparatively young specimens or whether growth conditions in the pool are particularly poor.

Irrespective, however, of whether the environmental conditions tend to produce large or small snails, those individuals infected with trematode parasites are relatively larger. Thus, in certain areas of the saltings of the River Tamar, Plymouth (higher up the estuary than St. John's Lake), very large-sized uninfected samples are found with snails ranging up to $6\frac{1}{2}$ mm. in length. In this area heavily infected pools are stocked with *P. ulvae* displaying super-gigantism, where shells of 10–$10\frac{3}{4}$ mm. are found quite frequently (Pl. I, rows G and K).

With many uncertain factors such as age, growth rate, uneven spat fall, etc., to take into account, it is difficult to decide whether there is a true difference in the size and growth-rate of the sexes, such as is demonstrated for *Littorina littorea* (H. B. Moore, 1937) or whether the difference in size between the largest males and females of *P. ulvae* is due to the longer life of the latter. Pelseneer (1926) believes that this accounts for the greater size of the females in many species of molluscs—the males dying off before they attain the dimensions of the largest females.

It appears to be a fairly general rule with *P. ulvae* that, whatever the relative number of the sexes of the whole sample may be, the largest uninfected specimens are females, and that the uninfected females outnumber the uninfected males in the largest size groups.

The three following examples are typical. A random sub-sample of 530 from a collection of 10,000 snails from St. John's Lake, Plymouth (June 1937), showed 332 (62 per cent.) females and 198 (38 per cent.) males. Forty-six of the largest specimens were selected. Twenty-eight were uninfected. Of these 24 (85 per cent.) were females and 4 (15 per cent.) males. This 6 : 1 ratio considerably exceeds the 1·7 : 1 ratio for the whole sample and the difference proves statistically significant. A random collection of several hundred snails from Wittering showed that in the largest size groups, $6\frac{1}{4}$–5 mm., there were only 35 per cent. males, but among the smaller snails ($4\frac{3}{4}$–$3\frac{1}{2}$ mm.) males outnumbered females by 6 to 1. Several hundred specimens from Millport displayed 68 per cent. males for the whole sample: of the 30 largest uninfected snails opened, 22 (73 per cent.) were females.

In a collection of several thousand snails from Poole Harbour Zostera-beds (August 1937) the uninfected females outnumbered the uninfected males by 3 : 1 in the largest size groups. Several hundred snails from a pool in Burnham Saltings (August 1937) showed a 4 : 1 excess of females among the largest uninfected snails. A similar figure was shown for a Holbeach sample (August 1937) from grass sweepings. It is perhaps worth noting two exceptions. A collection of snails from a pool at Blakeney (August 1937) showed 16 males and 15 females among the largest size group. The ratio of the rest of the sample was unfor-

tunately not recorded. In the sample from the Tamar Saltings, with 100 males and 80 females, 12 uninfected males and 11 females were found in the largest size groups.

Thus even in pools in saltings, a habitat where the irregularity of spat fall might well produce some inconsistency in the results, the largest uninfected females were usually larger than the uninfected males. As will be seen in these instances the mean size of uninfected specimens of the whole sample, or of the largest size groups, was sometimes approximately equal.

ANALYSES OF SAMPLES OF *P. ULVAE*.

The samples described below were selected for the following reasons. They were collected from different parts of Britain, and somewhat different habitats. In addition they showed the greatest contrast in the degree of parasitism by the various groups of cercariae.

The snails were collected by scooping them up with the mud from the pools in the saltings or off the mud flats. Collections from the plant roots on the saltings were made by sweeping the grass, and from *Zostera* by washing the snails from the plant in fresh water. Snails below $2\frac{3}{4}$ mm. in length were subsequently discarded for the reasons given above. Fig. 41 includes the measurements of entire sub-samples from single pools in the saltings. These were obtained by sieving the mud from permanent pools with a fine-mesh sieve. It illustrates the irregularity of spat fall in this habitat—the intermediate, large, or small sizes being sometimes absent.

Hunterdon Sands (Sample C) (Pl. I, Row D).

This sample was collected in May 1937 from the edge of the sands, along a rather extended front, and not from one small pool. The various sizes were found mingled together. After discarding the smaller snails, 239 living specimens remained for examination. The mean size of the snails was not great (4·58 mm.), but a number of them attained dimensions and variation in shape only associated with heavy infections and good growth conditions. The shells were of the hard grey type. Eighty-four specimens (34 per cent.) were infected, and of these no less than 57 proved to be harbouring Echinostome cercariae (see Appendix). Almost all these infections were very heavy and many cercariae were emitted. There was a striking difference in the size of infected and uninfected snails, the former ranging between $7\frac{1}{2}$–$3\frac{3}{4}$ mm., with a mean length of 5·62 mm., the latter between $5\frac{1}{4}$–$2\frac{3}{4}$ mm. with a mean length of 4·02 mm. This suggests that the infections were acquired at an early age.

Sixteen of the infected snails were required for life-history experiments and were put aside after their infections had been identified. The rest of the sample was dissected and it was found that 153 were males (i.e. snails with a penis) and 70 females. Most of the females were gravid and some laid eggs before they were killed. The size of the uninfected males and females showed the usual difference referred to above. The largest specimens were females, no uninfected males reaching $5\frac{1}{4}$ mm. in length. The mean length of the females was also larger, 4·26 mm. compared with 3·82 mm.

Of the 68 infected snails which were dissected 64 proved to be males and only 4 females. When the mean lengths of the males and females of the whole sample are compared it will be seen that the males are larger (4·5 mm. for ♂♂,

4·2 mm. for ♀♀). This sample therefore displays a complete reversal of the difference in size generally exhibited by the sexes. Yet if the uninfected snails alone are considered it is perfectly normal in this respect.

Another suggestive feature was the comparative lightness of the female infections ; eggs were present, indicating that these were of comparatively recent origin—the destruction of the gonads not being far advanced. In three out of four of these infections the rediae and sporocysts had not reached the cercariae-producing stage. This, taken into consideration with the fact that the rest of the infections were heavy, inevitably leads one to suspect that some of the snails with a penis were in the first place females which had " reversed " as the infection developed.

In all these infected males, the penis was more or less reduced—a feature which is discussed in a later portion of this paper.

Summary of Hunterdon Sands (Sample C).

(Mean size with standard error of the mean given in brackets.)

Total 239 (4·58 mm.)

- Uninfected 155 (4·02 ± 0·051 mm.)
  - ♂♂ 89 (3·82 ± 0·063 mm.)
  - ♀♀ 66 (4·26 ± 0·074 mm.)

  Larger size of ♀♀ significant.

  153 ♂♂ with 64 infections = 42 per cent.
- Infected 84 (5·62 ± 0·111 mm.)
  - ♂♂ 64 (5·65 ± 0·125 mm.)
  - ♀♀ 4 (ca. 4·44 mm.)

  70 ♀♀ with 4 infections = 6 per cent.
- Not examined 16 (5·80 mm.)

Marked difference in size. *Numbers of ♀♀ too small for adequate estimate of mean size.* *Very marked difference in infection-rate of the two sexes.*

Holbeach Saltings (Sample A) (Pl. I, Row J).

This sample contained a very high percentage of the Pleurolophocerca group of cercariae. It was collected from a permanent pool on the extreme upper edge of the saltings at Holbeach (Lincoln) in August 1937. Two scoops of mud were made from the centre of the pool. The sample contained 326 living snails over 2½ mm. in length ; 33 of these died before the dissections were completed.

The shells were very dark reddish brown with the spires well preserved. There was a certain amount of individual variation in shell texture. The growth conditions were obviously good on the whole, the mean length of the snails being large (5·40 mm.) and the maximum length attained 8½ mm. The contrast, however, between the uninfected and infected portions of the sample was not so great as in the collection from Hunterdon Sands. The percentage of infection was about 50. Of the 148 infections 90 pertained to the Pleurolophocerca group of cercariae (see Appendix). Fifty-five of the largest specimens were spared for experiments. The remaining snails of the whole sample revealed on dissection 104 males and 134 females. The uninfected females outnumbered the males by 91 : 54, and, as is usually the case, the largest snails of this portion of the sample were females. No male attained a greater length than 6¼ mm., whereas females reached 6½ mm., and the five largest size groups contained 31 females compared with 14 males.

The disproportion in infected females is slight compared with the sample from Hunterdon Sands. Also no reversal of the normal size of the sexes is shown in this case and both the individual and mean sizes of infected female snails are greater than those of the males. However, not much importance should be attached to this, owing to the fact that the sex of 55 of the largest infected snails was not determined.

SUMMARY OF HOLBEACH SALTINGS (SAMPLE A).

(Mean size with standard error of the mean given in brackets.)

Total 293 (5·40 mm.)

- Uninfected 145 (5·20 ± 0·060 mm.)
  - ♂♂ 54 (5·19 mm.)
  - ♀♀ 91 (5·20 mm.)
  - *Difference in size not significant.*
  - 104 ♂♂ with 50 infected = 48 per cent.
  - 134 ♀♀ with 43 infected = 32 per cent.
- Infected 148 (5·60 ± 0·063 mm.)
  - ♂♂ 50 (5·32 mm.)
  - ♀♀ 43 (5·36 mm.)
  - *Difference in size not significant.*
  - Not examined 55 (6·05 mm.)

Larger mean size of infected significant.

Difference in percentage infection significant (even though largest specimens not examined).

Holbeach Saltings (Sample C) (Pl. I, Row L).

A collection of about 800 snails was made from a permanent pool in the middle zone of the saltings, alongside another pool in which very large specimens had been found. This sample contained only relatively small shells, and their friable nature and shape, together with the condition of the soft parts of the bodies of the snails, suggested poor growth conditions rather than a collection of young snails only. Twenty-five of the largest specimens were selected and examined. These ranged in size from 5½–3¾ mm. Ten were not infected and of these 8 were females and 2 males (see Appendix). The largest uninfected specimen was as usual a female.

Of the fifteen infected snails ranging between 5½–4 mm. in length, 8 were females and 6 males. The sex of one specimen was not determined. Thus considerably more males were infected than would be expected from a comparison of the sex ratio. The mean size was 4·73 mm. as against 4·38 mm. for infected examples.

Holbeach Saltings (Sample E) (Pl. I, Row F).

This collection of about 1,000 snails was made by sweeping the grass round a permanent pool in the middle zone of the saltings, where the percentage of infection had been found to be high, and growth conditions favourable. The snails obtained from the grass sweepings were of the same type, but not so large. This habitat does not favour a high infection-rate and the snails rarely, if ever, reach the dimensions of those found in many of the pools.

Twenty-five of the largest snails, ranging between 6½–5½ mm. in length, were selected. Four only were infected. Of the 21 uninfected specimens 16 were found to be females and 4 males. The sex of one snail was not determined.

Three of the infected specimens were males and one female. It will thus be seen that although the females in the largest size groups outnumber the males by 4 : 1, yet the infected males outnumber the females by 3 : 1.

Uninfected females reached a size of $6\frac{1}{2}$ mm., but the only males to reach these dimensions were infected.

Burnham Saltings (Sample A) (Pl. I, Row E).

A collection of about 1,000 snails was made in August 1937 from a permanent pool in the middle zone of the saltings near Burnham (Norfolk). Populations of *P. ulvae* from this area showed an exceptionally low incidence of infection.

The growth conditions of this pool appeared favourable and the shells were of the hard grey type, with very well preserved spires. Twenty-five of the largest were selected, of which two were empty. The range of the remaining 23 was $7\frac{1}{4}$–$5\frac{1}{4}$ mm. Two specimens, one male and one female, were infected. Seventeen of the uninfected snails were females, with a mean length of 6·76 mm., and only 4 males, with a mean length of 5·75 mm. Here again the females outnumber the males by over 4 : 1, yet there was one male among the two infected specimens.

Tamar Saltings (Samples A1 and A) (Pl. I, Rows G and K; Pl. II, fig. 1).

It was discovered in October 1937 that growth conditions were very favourable for *P. ulvae* in certain pools in the upper levels of the saltings on a stretch of ground locally known as "Egypt" (see Map, Hartley & Spooner, 1938). Here uninfected snails reached $6\frac{1}{2}$ mm. in length. The shells were of the very hard type, red in colour with blunted spires. A search was made for a highly infected sample, and this was ultimately found in a permanent pool with a very soft muddy bottom. Here large specimens, ranging up to $10\frac{3}{4}$ mm. in length, were discovered lying on the surface of the mud. About fifty of these were collected by hand and all proved to be infected. Scoops were made round the edges of the pool, but there appeared to be a complete absence of the smaller sizes of snails. In March 1938 a larger and strictly random collection was made in the same pool, and on this occasion a number of smaller specimens were found, but there was a marked absence of intermediate sizes (fig. 41).

The total collection (March 1938) numbered 2,200 specimens. The shells were red, exceptionally hard, with blunted spires and corroded surface in the larger sizes. Some of the smaller shells were grey with well-preserved spires. A random sub-sample of 254 specimens was dissected (see below). After the sub-sample had been taken, 33 of the largest snails were selected from the rest of the collection and opened (Sample A1). They ranged in size from $10\frac{1}{2}$–7 mm. in length, with a mean of 8·24 mm. All were infected (see Appendix). Twenty-five were males and 8 were females. Two of the females contained developing eggs.

Seventy-four of the sub-sample were under $2\frac{3}{4}$ mm. and were discarded. Details of these smaller specimens are given in Table I. The mean size of the remaining 180 specimens, ranging between 9–$2\frac{3}{4}$ mm., was 5·48 mm. One hundred were males (mean length 5·86 mm.) and 80 females (mean length 5·00 mm.). The uninfected females, however, outnumbered the uninfected males in the ratio 69 : 55.

The sample displayed a 31 per cent. infection. Forty-five of the infected specimens were males (mean length 6·96 mm.) and only 11 were females (mean

length 7·36 mm.). The difference in the proportion of the sexes infected is clearly significant. The gigantism displayed by infected snails (mean 7·04 mm. compared with 4·77 mm.) is very marked, but on the other hand there is no evidence regarding the reversal of the normal differences in size displayed by the sexes.

Attention should here be drawn to a unique and peculiar feature of the samples from this area. With one exception (see p. 93) no hermaphrodite examples of *P. ulvae* have been found by me. However, among the largest size groups from this pool and a neighbouring uninfected pool, a few gravid females were discovered with a swelling or papilla in the region of the penis, sometimes to the left of the body. No trace of such a swelling is generally visible. It was therefore thought safer to regard 50 per cent. of infected specimens with a papilla as females. Ten specimens fell into this category.

SUMMARY OF TAMAR SALTING (SAMPLE A).

(Mean size with standard error of the mean given in brackets.)

Total 180

- Uninfected snails 124 (4·77 ± 0·12 mm.)
  - ♂♂ 55 (4·96 ± 0·17 mm.)
  - ♀♀ 69 (4·63 ± 0·16 mm.)
- Infected snails 56 (7·04 ± 0·125 mm.)
  - ♂♂ 45 (6·96 ± 0·14 mm.)
  - ♀♀ 11 (7·34 ± 0·20 mm.)

100 ♂♂ with 45 infections (45 per cent.)

80 ♀♀ with 11 infections (13 per cent.)

Difference in size clearly significant. *Difference in each case not significant.* *Difference in proportion of sexes infected significant.*

St. John's Lake (Sample A) (Pl. I, Row B, Pl. II, fig. 2).

This collection contained approximately 10,000 snails and was obtained from the mud flats of St. John's Lake (Trevol Range), Plymouth, in June 1937. Of these 530 were examined to determine the sex ratio. There were 332 females and 198 males. The percentage of infection was low (3 per cent.), and in order to avoid the dissection of a large number of specimens 46 of the largest snails of the whole sample were selected. Eighteen, about 40 per cent., were found infected (see Appendix). As usual the females outnumbered the males among the largest uninfected specimens of the sample : on this occasion in the proportion 6 : 1, as compared with under 2 : 1 for the whole sample (see p. 87).

Twelve of the infected snails were females and 4 males. The sex of one specimen was not recorded. In this sample therefore the proportion of infected males is only slightly more than would be expected if infection was governed solely by chance, and indeed is not statistically significant.

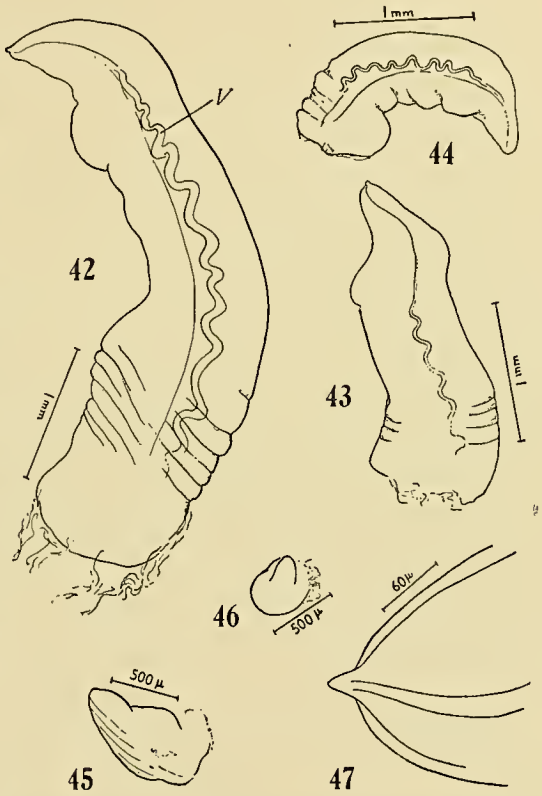
The majority of the infections (11) pertained to the Oocysta group of cercariae.

THE EFFECT OF PARASITISM WITH TREMATODES ON THE PENIS OF *P. ULVAE*.

Very little attention has hitherto been paid to the effect of trematode parasites on the external sex organ, although the destruction of the gonads has been described constantly. I have found that the penis of infected *P. ulvae* is invariably abnormal. It is almost always possible to recognize an infected

specimen by the casual examination of this organ. However, in light infections, or young infections, this is much less marked.[1]

The abnormality consists of reduction in size, which may be slight, or so pronounced that the penis is replaced by a small, almost shapeless papilla. (Figs. 42–47 show both normal and abnormal penis). In advanced stages of reduction the vas deferens cannot be distinguished, although in a penis less than half the normal size (fig. 44) it is still functional. Change of shape is also quite common. On one occasion an abnormally large penis was developed, with a highly sculptured border. The heavier the infection the greater the reduction in size. In those cases in which some of the seminal vesicles are still producing sperm the organ is generally of fair dimensions. One gravid female containing many eggs was found to be lightly infected with *C. ubiquita* Lebour 1907. A small penis had been developed. This was the only definitely hermaphrodite specimen found.



It is highly improbable that all the snails displaying small or abnormal penis are "sex-reversed" females as Krull suggests. Some are almost certain to be males in which the normal growth has been inhibited, or in which the tissue has atrophied. In fact it is quite possible and indeed probable that certain specimens devoid of a penis, in which the gonads are also destroyed, are not females but totally castrated males. It is only when the gonads are recognizable that one can be certain of the sex of the parasitized specimens.

General Remarks.

It will be seen from the samples of *P. ulvae* described above that the males were found to be more frequently infected than the females. This is invariably so if the sex ratio of uninfected snails is taken into consideration. Several causes may be suggested to account for this. The miracidia may exercise sex selection in their free-swimming stage, or, having either penetrated from without or been ingested within their egg capsule, they may only develop further in a male host. Infected females, on the other hand, may have a much higher rate of mortality than the males. On the whole, however, what little evidence

[1] Krull considers that these infected specimens with a "normal" (= large) penis showing a vas deferens are probably true males. He also notes these snails are not so large and the infections less heavy. The specimens with a reduced and often functionless penis without a vas deferens he suggests were originally female. It should be noted that in the author's experience the unusually small penis is not only associated with the heaviest infections, but also with the most marked gigantism and shell variation.

we have tends to support the view that a certain number of snails with a penis are in reality sex-reversed females. Both Krull and the author have found infected females which have developed a penis. Moreover the altered condition of the penis of all infected snails emphasizes the profound effect these parasites exert on the sexual organs.

It will be noticed that the ratio of infected males and females differs considerably in the different samples. Several explanations may be offered to account for this, but here again no proof is available.

P. ulvae, particularly in the saltings, is exposed to infection very sporadically, for most of its trematode parasites are found in the sexually mature stage in birds. This is well illustrated by the populations of adjacent pools in the saltings, which will often harbour a completely different trematode fauna. This fact, together with the irregularity of the spat fall so characteristic of this habitat, suggests that the age at which the snails of any given pool become infected is also likely to vary. It is quite possible that changes in the sex of the host are only brought about by infections which enter the snail at an early age and are of long standing.

Another factor which may be of importance in this respect is the effect of the snail's environment upon the parasites. If conditions are somewhat unfavourable the parasites are few in number, small in size, and the output of cercariae is greatly reduced. Often the infections are moribund. The parasites react surprisingly quickly to loss of vigour or sluggishness on the part of the host, and, for example, in the laboratory (Pl. II, figs. 3 and 4) fare much worse than the snails themselves. In habitats where growth conditions are poor it is possible that a number of infections do not develop sufficiently to produce sex-reversal. It is also possible that the tendency to grow a penis is more pronounced in female snails living under maximum growth conditions.

Whatever is ultimately proved to be the cause of the excess of parasitized males over females, it seems certain that this phenomenon in conjunction with the gigantism produced by infections is capable of disturbing or reversing the normal differences in size displayed by the sexes. It is therefore necessary to employ great caution when studying this aspect of sexual dimorphism in *P. ulvae*, and probably the same applies to any heavily infected species of snail.

TABLE II.

PERCENTAGE OF THE DIFFERENT GROUPS[1] OF CERCARIAE FOUND IN INFECTED *P. ULVAE* FROM THREE TYPES OF HABITAT.

Groups of Cercariae	Infected specimens examined		Specimens from mud flats		Specimens from saltings		Specimens from Hunterdon and Fairlie Sands	
	Number	per cent.	Number	per cent.	Number	per cent.	Number	per cent.
Pleurolophocerca .	246	29·6	20	8·2	167	56·4	59	20·2
Echinostome . .	197	23·8	11	4·5	15	5·0	171	58·5
Ubiquita . . .	154	18·6	58	24·0	16	22·6	30	10·2
Oocysta . . .	127	15·3	115	47·7	9	3·0	3	1·0
Notocotylid . .	26	3·1	6	2·9	6	2·0	14	4·7
Metentera . .	10	1·2	4	1·6	—	—	6	2·0
Sagittarius . .	3	0·4	2	0·8	—	—	1	0·3
Undescribed or unidentified . .	66	7·9	25	10·3	33	11·1	8	2·7
Total .	829	—	241	—	296	—	292	—

[1] The term " group " indicates a collection of related cercariae, but whereas one group may include an entire superfamily (Pleurolophocerca), another may contain only a few related genera (Oocysta or Ubiquita).

The numerous groups, and even species of cercariae, probably exert both a different and varying degree of influence on the host. In the laboratory, for example, the Echinostome infections are by far the most lethal. The impression is also gained that the penis is altered to a greater extent in these infections than in any other, and that sex-reversal occurs most frequently in snails parasitized by Echinostomes. Further investigations are being carried out on this aspect of the problem.

The relative degree of parasitism by the various groups of cercariae is given in the Appendix and Table II. It is clearly shown that the Oocysta group is commonest on mud flats, and is in fact comparatively rarely found in *P. ulvae* from saltings, despite the higher percentage of infection met with in this habitat. The adult worm of *Cercaria oocysta* is nevertheless a bird parasite and develops in the Black-headed Gull into an undescribed species of *Maritrema* Nicoll 1907 (Rothschild 1936). The Ubiquita group is found commonly in both habitats, but relatively more frequently on the mud flats. The heaviest infections of Echinostome larvae are met with in the samples from Hunterdon and Fairlie Sands, where they have always proved the most numerous group, while the Pleurolophocerca cercariae which develop into Heterophyid flukes are found in highest numbers in the saltings. The rarer species, such as the Notocotylid and Metentera groups of cercariae, are sparsely but more evenly distributed.

It is perhaps worth noting that in *P. ulvae*, as in many other species of molluscs, the larger the individual snail, the greater the number of cercariae produced by an infection. Apart from the environmental changes already referred to, it would appear that the amount of cercariae produced is directly controlled by the amount of food available. The gigantism of the host, which involves an increase in the soft parts of the body as well as the shell, is thus of great advantage to the parasite. The faculty of producing this increase in size is a character which is presumably most susceptible to selection and its widespread occurrence among the Trematoda is therefore not surprising.

SUMMARY.

(1) The normal sex ratio of *P. ulvae* varies from sample to sample irrespective of age and size.

(2) The growth of *P. ulvae* is also very varied and the size of the shell is no criterion of the age of the snail. The variation in growth, shell texture, shell shape and shell colour, and the consistency of the soft parts of the body, are probably closely linked with environmental factors.

(3) Female specimens attain a larger size than do males, and usually outnumber them in the largest size groups of any given sample.

(4) *P. ulvae* conforms to Pelseneer's rule that more male than female snails are infected with larval Trematodes. In some samples the ratio of infected males to females is as high as 16 : 1.

(5) The higher rate of infection among males, together with the gigantism produced by the parasites, can combine to obscure or even reverse the normal difference in size generally displayed by the sexes.

(6) The penis of all infected *P. ulvae* is abnormal, and usually more or less reduced in size. It is possible that some specimens without a penis are totally castrated males. An infected gravid female, with a small penis, was discovered.

(7) There is some evidence to support Krull's suggestion that infected females of *P. ulvae* grow a penis. This would explain satisfactorily the excess of parasitized males over females. It is, however, highly improbable that all infected snails with reduced penis are sex-reversed females.

(8) There are indications that the metabolism of the snail is more seriously disturbed by some species of cercariae than by others.

(9) The parasites are extremely sensitive to the condition of the host. Under favourable growth conditions the parthenitae increase in size, number, and fertility. The larger the snail the greater the number of cercariae emitted. It is therefore of considerable advantage to the parasites to produce gigantism in the host.

ACKNOWLEDGMENTS.

I would like to express my gratitude to Miss Anne Rothschild for her assistance with the measurement and collection of samples of snails and to Mr. G. M. Spooner for his invaluable help and advice.

APPENDIX.

Hunterdon Sands (*Sample A*), September 1935.

Hard grey type shell. Spires well preserved.

	Range.	*Mean.*
Total, 101 specimens	9 –4 mm.	5·97 mm.
89 infected specimens	9 –4¼ ,,	6·16 ,,
12 uninfected specimens	5¼–4 ,,	4·50 ,,

Group.		*Range.*	*Mean.*
Echinostome	48	9 –4¾ mm.	6·37 mm.
Pleurolophocerca	20	7½–5½ ,,	6·05 ,,
Ubiquita	12	6½–4¼ ,,	4·83 ,,
Notocotylid	7	7 –5 ,,	5·57 ,,
Undescribed	2	6 –5 ,,	—

Hunterdon Sands (*Sample B*), March 1936.

Hard grey type shell. Spires well preserved.

	Range.	*Mean.*
Total, 131 specimens	8¾–4¼ mm.	6·27 mm.
119 infected specimens	8¾–4½ ,,	6·40 ,,
12 uninfected specimens	6 –4¼ ,,	4·92 ,,

Group.		*Range.*	*Mean.*
Echinostome	66	8¾–4¾ mm.	6·77 mm.
Pleurolophocerca	35	7½–5½ ,,	6·17 ,,
Ubiquita	9	5¾–4¾ ,,	5·22 ,,
Notocotylid	4		
Metentera	2		
Oocysta	2	7½–5¼ ,,	6·56 ,,
Unidentified	1		

Hunterdon Sands (*Sample C*), May 1937 (see p. 88).

	Range.	Mean.
Total, 241 specimens	$7\frac{1}{2}$–$2\frac{3}{4}$ mm.	4·57 mm.
84 infected specimens	$7\frac{1}{2}$–$3\frac{3}{4}$,,	5·63 ,,
157 uninfected specimens	$5\frac{1}{4}$–$2\frac{3}{4}$,,	4·00 ,,

Group.			Range.	Mean.
Echinostome	57	(54♂♂, 1♀, 4 unopened)	$7\frac{1}{2}$–$4\frac{3}{4}$ mm.	5·98 mm.
Ubiquita	9	(5♂♂, 4 unopened)	$6\frac{1}{4}$–4 ,,	4·89 ,,
Pleurolophocerca	4	(not opened)	$6\frac{1}{2}$–$4\frac{1}{2}$,,	6·00 ,,
Metentera	4	(1♂, 3 unopened)	$5\frac{1}{4}$–4 ,,	4·75 ,,
Notocotylid	3	(3♂♂)	5 –$4\frac{1}{4}$,,	4·67 ,,
Oocysta	1	7 (3♂♂, 3♀♀, 1 unopened)	$5\frac{1}{2}$–$3\frac{3}{4}$,,	4·57 ,,
Sagittarius	1			
Undescribed	1			
Unidentified sporocysts and rediae	4			

Holbeach Saltings (*Sample A*), August 1937 (see p. 89).

	Range.	Mean.
Total, 288 specimens	$8\frac{1}{2}$–$2\frac{3}{4}$ mm.	5·42 mm.
148 infected specimens	$8\frac{1}{2}$–4 ,,	5·63 ,,
145 uninfected specimens	$6\frac{3}{4}$–$2\frac{3}{4}$,,	5·20 ,,

Group.			Mean.
Pleurolophocerca	90	(22♂♂, 19♀♀, 49 not opened for sex determination)	5·66 mm.
Ubiquita	18	(6♂♂, 8♀♀, 4 not opened)	5·79 ,,
Oocysta	6	(3♂♂, 3♀♀)	6·00 ,,
Notocotylid	2	—	—
Echinostome	3	—	—
Not identified [1]	29	(14♂♂, 13♀♀, 2 unopened)	5·28 ,,

Holbeach Saltings (*Sample B*), August 1937. Hard grey type shell.

A hand-picked selection of 12 of the largest snails from a very small sample from a permanent pool in the middle zone of the saltings. One snail dead. One female ($5\frac{3}{4}$ mm.) not infected. Range of infected specimens $6\frac{3}{4}$–5 mm. Mean : 5·82 mm.

Group.		Range.	Mean.
Pleurolophocerca	6	$6\frac{3}{4}$–$5\frac{1}{2}$ mm.	5·92 mm.
Ubiquita	3	$6\frac{1}{4}$–5 ,,	5·58 ,,
Echinostome	1	6 ,,	—

[1] A number of these snails were kept under cold conditions in the laboratory for several months before dissection. Consequently numbers of these infections showed only rediae containing germ balls, but no cercariae. Many were of the Pleurolophocerca type.

Holbeach Saltings (*Sample C*), August 1937 (see p. 90).

Total, 800 specimens. 25 of the largest selected.

	Range.	Mean.
15 infected specimens	$5\frac{1}{2}$–$4\frac{1}{4}$ mm.	4·73 mm.
10 uninfected specimens	5 –$3\frac{3}{4}$,,	4·38 ,,

Group.			Range.	Mean.
Pleurolophocerca	8	(3♂♂, 5♀♀)	5 –4 ,,	4·50 mm.
Echinostome	5	(2♂♂, 2♀♀, 1 unopened)	$5\frac{1}{4}$–$4\frac{1}{2}$,,	5·00 ,,
Ubiquita	1	(♀)	$5\frac{1}{4}$,,	—
Oocysta	1	(♂)	$5\frac{1}{2}$,,	—

Holbeach Saltings (*Sample D*), August 1937.

Red medium-hard shells. Spires blunted. A selection of 15 of the largest [1] snails hand picked from a permanent pool in the middle zone of the saltings. All infected. Range: 7–$5\frac{1}{2}$ mm. Mean: 6·38 mm.

Group.		Range.	Mean.
Ubiquita	7	$6\frac{3}{4}$–$5\frac{1}{2}$ mm.	6·25 mm.
Pleurolophocerca	6	7 –$6\frac{1}{4}$,,	6·50 ,,
Echinostome	2	$6\frac{3}{4}$–$6\frac{1}{4}$,,	—

Holbeach Saltings (*Sample F*), August 1937.

Very hard grey type. Spires perfectly preserved. A selection of 12 of the largest snails hand picked from a dried-up pool in the lower zone of the saltings, around which sweeps were made and Sample E (see p. 90) collected. All infected. Range: 8–$5\frac{3}{4}$ mm. Mean: 7·19 mm.

Group.		Range.	Mean.
Ubiquita	8	8 –$6\frac{1}{2}$ mm.	7·41 mm.
Echinostome	3	$7\frac{1}{2}$–$6\frac{1}{2}$,,	7·08 ,,
Pleurolophocerca	1	$5\frac{3}{4}$,,	—

Tamar Saltings (*Sample A*1), March 1938 (see p. 91).

Total, 1,946 specimens. 33 of the largest snails selected; all infected. Range: $10\frac{1}{2}$–7 mm. Mean: 8·57 mm.

Group.			Range.	Mean.
Pleurolophocerca	21	(17♂♂, 4♀♀)	$10\frac{1}{2}$–7 mm.	8·62 mm.
Ubiquita	6	(3♂♂, 3♀♀)	9 –$7\frac{1}{4}$,,	8·50 ,,
Echinostome	2	(2♂♂)	$8\frac{3}{4}$–$8\frac{1}{2}$,,	—
Notocotylid	2	(1♂, 1♀)	9 ,,	—
Undescribed	2	(2♂♂)	$8\frac{3}{4}$–7 ,,	—

Tamar Saltings (*Sample A*), March 1938 (see p. 91).

	Range.	Mean.
Total, 180 specimens	9 –$2\frac{3}{4}$ mm.	5·47 mm.
56 infected specimens	9 –$4\frac{3}{4}$,,	7·04 ,,
124 uninfected specimens	$8\frac{1}{4}$–$2\frac{3}{4}$,,	4·77 ,,

[1] The large specimens were lying on the mud in the middle of the pool. Around the edges which were not under water were hundreds of thousands of very small specimens. A scoop from the middle and the edge gave completely different size groups.

Group.			*Range.*	*Mean.*
Pleurolophocerca . .	35	(27 ♂♂, 8 ♀♀)	$8\frac{3}{4}$–$5\frac{1}{2}$ mm.	7·23 mm.
Ubiquita	17	(14 ♂♂, 3 ♀♀)	9 –$5\frac{1}{2}$,,	6·88 ,,
Oocysta	1			
Notocotylid . . .	1	(4 ♂♂)	$7\frac{3}{4}$–$4\frac{3}{4}$,,	6·00 ,,
Undescribed . . .	2			

Tamar Saltings (*Sample B*), October 1937.

Hard red type shell. Spires blunted.

Total, 1,000 specimens, 16 of the largest selected.

	Range.	*Mean.*
7 infected specimens	8 –$6\frac{1}{2}$ mm.	7·71 mm.
9 uninfected specimens	$6\frac{1}{2}$–6 ,,	6·33 ,,

Group.		*Range.*	*Mean.*
Ubiquita	6	8 –$6\frac{1}{2}$ mm.	7·83 mm.
Oocysta	1	$7\frac{1}{4}$,,	—

St. John's Lake (*Sample A*), June 1937 (see p. 92).

Total, 10,000 specimens. 46 of the largest selected.

	Range.	*Mean.*
18 infected specimens	$5\frac{1}{4}$–$4\frac{1}{4}$ mm.	4·89 mm.
28 uninfected specimens	$5\frac{1}{4}$–$4\frac{1}{4}$,,	4·88 ,,

Group.			*Range.*	*Mean.*
Oocysta . . .	11	(7 ♀♀, 3 ♂♂, 1 unopened)	$5\frac{1}{4}$–$4\frac{1}{4}$ mm.	4·82 mm.
Ubiquita	2	(2 ♀♀)	$4\frac{3}{4}$,,	—
Pleurolophocerca . .	2	(2 ♀♀)	$5\frac{1}{4}$–5 ,,	—
Echinostome . . .	1	(1 ♂)	5 ,,	—
Undescribed . . .	2	(2 ♀♀)	5 –$4\frac{1}{4}$,,	—

St. John's Lake (*Sample B*), December 1933.

Red hard shell type. Several thousand shells selected, of which 182 of the largest were taken and roughly divided into two groups, one containing the largest specimens.

1st Group.

100 largest shells. 42 infections.

Group.	
Oocysta	25
Ubiquita	7
Pleurolophocerca . . .	5
Notocotylid	2
Metentera	2
Too young to identify . .	1

2nd Group.

82 of the smaller shells. 23 infections.

Group.	
Ubiquita	7
Oocysta	6
Pleurolophocerca . .	6
Notocotylid . . .	1
Metentera	2
Echinostome . . .	1

St. John's Lake (*Sample C*), December 1934.

	Range.	*Mean.*
Hard type grey shells. A random sub-sample of 206 shells over $2\frac{3}{4}$ mm. . . .	$5\frac{1}{2}$–3 mm.	4·27 mm.
18 infected specimens	5 –$3\frac{1}{2}$,,	4·42 ,,

Group.		*Range.*	*Mean.*
Oocysta	8	5 –3½ mm.	4·37 mm.
Ubiquita	5	5 –4½ ,,	4·60 ,,
Pleurolophocerca	3	4½–3½ ,,	4·17 ,,
Echinostome	1	4½ ,,	—
Unknown.	1	4½ ,,	—

St. John's Lake (*Sample D*), January 1935.

Hard type grey shells. 35 of the largest shells of 5¼–5 mm. selected. 16 infected specimens.

Group.		
Oocysta	10	No measurements taken.
Ubiquita	4	
Pleurolophocerca	1	
Notocotylid	1	

St. Andrews, Esturine Mud (*East Scotland*), 1935.

Very soft grey type shell. Several thousand shells, of which 83 of the largest selected.

	Range.	*Mean.*
24 infected specimens	4½–3½ mm.	4·07 mm.
61 uninfected specimens	4½–2½ ,,	3·70 ,,

Group.		*Range.*	*Mean.*
Oocysta	12	4½–3¾ mm.	4·17 mm.
Ubiquita	5	4 –3½ ,,	3·90 ,,
Echinostome	3	4¼–3¾ ,,	4·00 ,,
Notocotylid	1	4 ,,	—
Too young for identification	3	—	—

St. John's Lake (*Sample E*), July 1935.

Hard grey type shell. About 10,000.

A certain number of each size group were dissected.

Total 1,385. Range: 5½–1 mm. Mean: 3·09 mm.

100 infected specimens. Range: 5½–1 mm. Mean: 3·85 mm.

Size Group in mm.	Number examined	Total infections	Oocysta Group	Ubiquita Group	Echinostome Group	Pleurolophocerca Group	Sagittarius Group	Notocotylid Group	Undescribed Groups	Too young for identification
5 mm.	47	19	10	6	—	—	—	1	1	1
4 mm.	574	59	27	17	3	2	2	—	2	6
3 mm.	335	12	5	2	—	1	—	—	—	4
2 mm.	321	8	1	3	—	—	—	—	1	3
1 mm.	108	2	—	—	—	—	—	—	—	2
Total	1,385	100	43	28	3	3	2	1	4	16
Range in mm.	5½–1	5½–1	5½–2	5¼–2	4	4–3	4	5	5–2	5–1
Mean length in mm.	3·09	3·85	4·07	3·93	4	3·67	4	5	3·75	3·06

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EXPLANATION OF PLATES AND TEXT-FIGURES.

Plate I. *Peringia ulvae* from various habitats (× 2).

Row A. Some of the largest specimens, black, soft-shelled type about four years old, from a collection bred in the laboratory. The eggs were obtained from a typical red hard-shelled sample of snails from the mud flats, St. John's Lake.

Rows B and C. The largest snails from two collections of several thousand snails from the mud flats, St. John's Lake.

Row D. Some of the largest snails from Hunterdon Sands (Sample C).

Row E. Ditto, Burnham Saltings (Sample A).

Row F. Ditto, Holbeach Saltings (Sample E) (grass sweepings).

Row G. Ditto, Tamar Saltings (Sample A1).

Row H. Ditto, Poole Harbour.

Row I. Ditto, Estuarine Mud, St. Andrews (see Appendix).

Row J. Ditto, Holbeach Saltings (Sample A).

Row K. Ditto, Tamar Saltings (Sample A).

Row L. Ditto, Holbeach Saltings (Sample C).

Plate II.

Fig. 1. A portion of sample A from the Tamar Saltings (× 2).

Fig. 2. A portion of sample A from St. John's Lake (× 2). Note the contrast in size between the specimens of the two samples.

Fig. 3. Longitudinal section of very heavily infected *P. ulvae* (× 18) killed after it had been kept some time in the laboratory, showing the reduction in number, size, and fertility of the Echinostome rediae.

Fig. 4. Section of infected *P. ulvae* (× 18) killed soon after it had been collected, showing the vigorous condition of the Echinostome rediae.

Text-fig. 41. Irregularity of spat fall in samples of *P. ulvae*.

Text-fig. 42. Normal penis of a specimen of *P. ulvae* measuring 6 mm. in length.

Text-fig. 43. Somewhat reduced penis of a specimen measuring $6\frac{3}{4}$ mm. in length, infected with *Cercaria oocysta*.

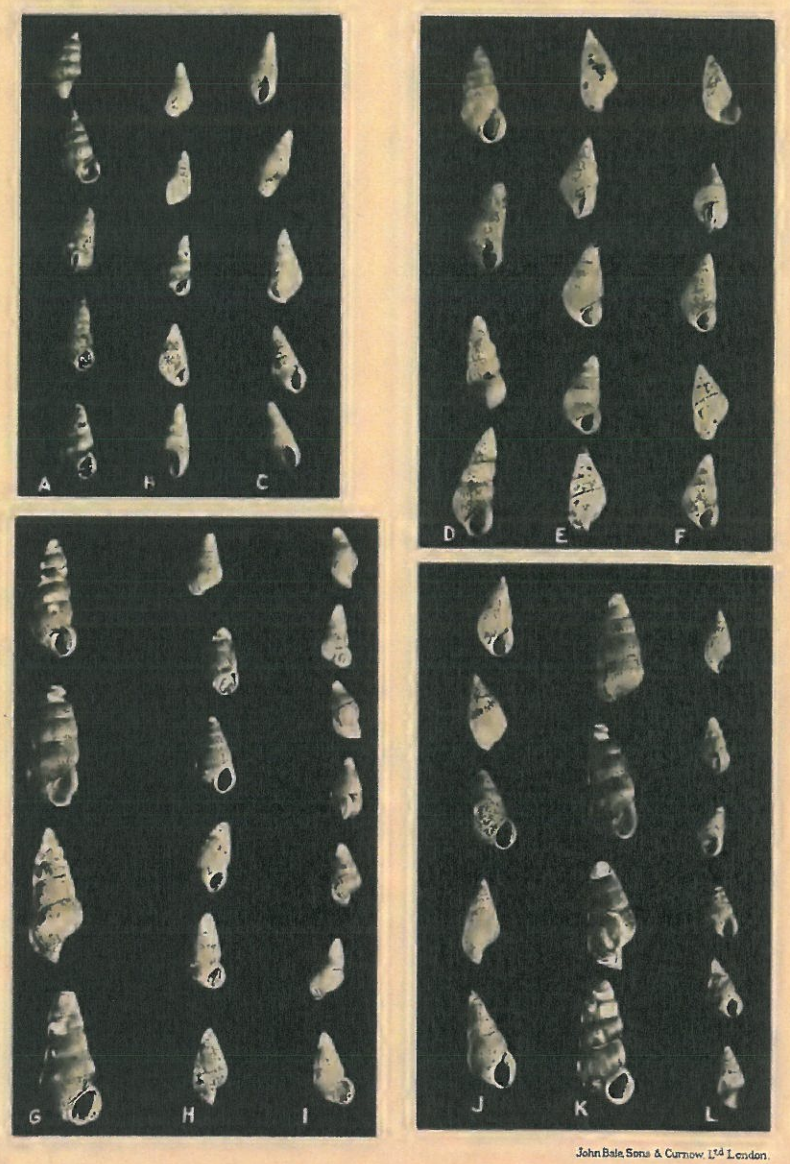
Text-fig. 44. Reduced penis of a specimen measuring $8\frac{1}{2}$ mm. in length, infected with the cercaria of *Cryptocotyle jejuna* Nicoll 1907.

Text-fig. 45. Greatly reduced penis of a specimen measuring 8 mm. in length, infected with an Echinostome cercaria.

Text-fig. 46. Papilla-like penis of a specimen measuring $8\frac{1}{4}$ mm. in length, infected with the cercaria of *C. jejuna*.

Text-fig. 47. Papilla at the terminal portion of a normal penis of *P. ulvae*. This is lost in most reduced examples.

EXPLANATION OF PLATES I AND II (see pp. 101 and 102).



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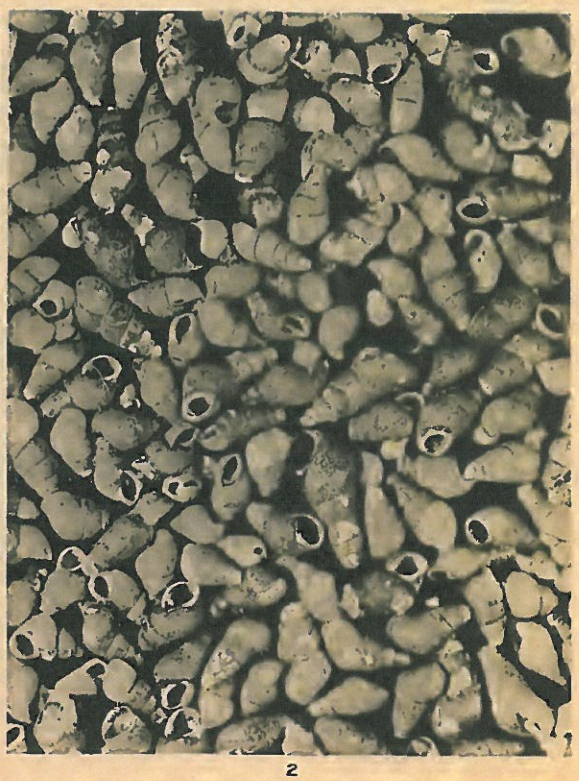

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