Gigantism and Variation in *Peringia ulvæ* Pennant 1777, caused by Infection with Larval Trematodes

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With 2 Figures in the Text.

In 1933 an examination of *Peringia ulvæ** for larval trematodes was undertaken at Plymouth (Rothschild, 1936). No actual measurements were made at the time, but there appeared to be a relation between the species of trematode and the size of the individual infected snails. Thus the commonest species, *Cercaria oocysta* Lebour, 1907 (14% infection), and *C. ubiquita* Lebour, 1907 (4% infection), were found in 75% of the largest snails, while the rarer species, such as *C. ephemera* Lebour, 1907 (non Nitsch) (2% infection), and *C. pirum* Lebour, 1907 (0·1% infection), occurred most frequently in medium sized individuals.

Later, random samples of *Peringia ulvæ* were obtained from St. John's Lake, Plymouth. These were measured to procure a rough estimate of the number of individual snails of a given size-group per thousand (Tables I and IA). One hundred snails of each size-group were then selected and examined for cercariæ (Tables II and III, p. 541). Specimens over 5 mm. were rare and only twenty-five individuals of this size were obtained.

Exposure of *Peringia ulvæ* to Infection.

Before examining the result of this investigation it is as well to consider the exposure of snails to infection with miracidia.

TABLE I.

"Random" Sample of *Peringia ulvæ* from Plymouth (June).

Size groups in mm.	Number of snails to each size group.
1 mm.	517
2 mm.	344
3 mm.	451
4 mm.	701
5 mm.	8
5+ mm.	2
Total	2023

* = *Hydrobia ulvæ* (Pennant) of Plymouth Marine Fauna, 1931.

TABLE IA.

THE SAME RANDOM SAMPLE OF *Peringia ulvæ* FROM PLYMOUTH (OF 3 MM. AND OVER) IN SIZE-GROUPS OF $\frac{1}{4}$ MM.

Size groups in $\frac{1}{4}$ mm.	Number of snails to each size group.
3 mm.	114
$3\frac{1}{4}$ mm.	67
$3\frac{1}{2}$ mm.	123
$3\frac{3}{4}$ mm.	147
4 mm.	266
$4\frac{1}{4}$ mm.	216
$4\frac{1}{2}$ mm.	161
$4\frac{3}{4}$ mm.	58
5 mm.	8
$5\frac{1}{4}$ mm.	2
Total	1162

The degree of infection of a population of *Peringia ulvæ*, and the age at which the infection occurs, chiefly depends on the presence and infection of the final host of the Trematode. It is for this reason that practically all workers on larval trematodes, who have carried on their investigations in a particular locality over a long period, have noted the irregular appearance of certain species of cercariæ. In some cases the fluctuations are seasonal. This occurs, for example, when the final host visits the locality regularly, at comparatively long intervals, and when the trematode is common. More often there is no regular seasonal fluctuation ; this applies particularly to marine or brackish water species, where the parasites are either always present to a greater or lesser degree or very sporadic in their appearance. Many other factors, such as climate, the drying up of pools, the concentration of mineral salts in the water, changes in vegetation and the fluctuations in the numbers of the intermediate host can affect the trematode fauna of a snail population, but there is no doubt that the percentage of infection of the snails is more closely linked with the movements of the final host than with any other factor.

A number of authors have agreed with the suggestion put forward by Kemp and Gravely (1919) that immature snails are probably immune to infection. Although this may be true of some species, it does not apply to *Peringia ulvæ*. This species can become infected before it reaches 1 mm. in length and the gonads do not ripen before it attains $2\frac{3}{4}$–3 mm. At this early age (1 mm.) the infections themselves must of necessity be very young and have not had time to develop. They are difficult to find, and doubtless many infections have been overlooked at this stage.

The longer a snail survives, the greater are its chances of becoming infected. Consequently the young stages will be the least heavily parasitised.

Roughly, three types of infections were found in the samples from Plymouth, which departed from the average 0·5 to 2% infection.

(1) Example. *Cercaria oocysta* Lebour, 1907. Common at all times of the year. This indicates an indigenous final host (or hosts), and the final stage of the parasite is probably of frequent occurrence.

(2) Example. Cercaria near *Cercaria lophocerca* Lebour, 1907 (non Fil.). Common in some samples and completely absent in others. This indicates the sudden appearance of the final host in large numbers—a flock of birds or shoal of fish—or possibly the appearance of the second intermediate host in large numbers, and the subsequent infection of the final host, on a large scale.

(3) Example. Cercaria near *C. sagittarius* Sinitzin, 1911. Very rare, 1 per 2,000. This indicates a scarcity of hosts, an accidental infection, or a rare parasite.

The risk of exposure to miracidia is different in all these cases and in consequence affects the percentage of infection per age group. For example, if a random sample of Peringia were examined three weeks after the sudden exposure to a heavy infection of one of the sporadic species, a larger number of small individuals would be found to be infected than is usually the case. If, however, a period of a few months had elapsed, the small individuals of the sample which had metamorphosed and since settled among the population previously exposed, would be quite free from infection.

In the case of one of the very rare species the time factor—i.e. the increasing chances of infection with age—operates more noticeably than in the case of a fairly common species.

Another point which cannot be entirely disregarded is a possible difference in behaviour of young and old snails. Under laboratory conditions no such difference was observed; moreover the cysts of the "Ephemera" group of cercariæ were found equally frequently on the shells of large and small individuals. If, however, in the wild, recently metamorphosed snails were inclined to remain buried in the mud, they would presumably come less into contact with free swimming miracidia, and more frequently with the type of miracidia which never hatches, but is ingested within its egg capsule.

The Types of Trematode infection found in *Peringia ulvæ* at Plymouth.

Almost every group of larval Trematodes differ in some manner in their mode of reproduction within the snail. For the requirements of this study it is only necessary to consider the broad distinctions.

Group 1. Cercariæ requiring a second intermediate host, produced in sporocysts. Primary seat of infection : the gonads.

Example : " Ubiquita " group.

Group 2. Cercariæ encysting within their sporocysts in the first host. Primary seat of infection : the gonads.

Example : " Oocysta " group.

Group 3. Cercariæ developing in rediæ from which they escape directly into the open and seek a second intermediate host. Primary seat of infection : the interlobular spaces of the liver.

Example : " Echinostomum " Group, and " Pleurolophocerca " Group.

Group 4. Cercariæ developing in rediæ, which escape from them into the tissues of the host, where they continue developing before leaving the snail to encyst in the open. Primary seat of infection : the interlobular spaces of the liver.

Example : " Metentera " Group. " Ephemera " Group.

In Group 1, the daughter sporocysts appear to produce cercariæ indefinitely, multiplying themselves meanwhile by transverse fission. No infection was ever found to die down, however long the snail survived. In Group 2, when the infection reaches a certain age the sporocysts degenerate and hundreds of encysted cercariæ remain, packed tightly together, apparently occupying the entire spire of the shell. Only one infection which had actually reached this stage was found, but many have been noted in which the process was clearly taking place.

Group 3 is characterised by very large daughter rediæ which produce large members of cercariæ simultaneously. No dying down of an infection has been noted in this group.

The daughter rediæ of Group 4 are smaller and less numerous, a condition which may have evolved together with post-redial development of the cercariæ in the tissues of the host. Two infections of *Cercaria ephemera* Lebour, 1907 (non Nitsch) have been found which appeared to be waning. Only one old, empty redia was noted and a few cercariæ in the tissues.

Outstanding Features of the infections at Plymouth.

The most striking general features were (1) the lightness (only a few rediæ producing cercariæ) of the infections belonging to Groups 3 and 4,* generally found in medium-sized shells, and absent in the largest size group, (2) the very high percentage of infection of the largest size group of snails (see Tables II and III) with the common species of cercariæ of Groups 1 and 2, and the heaviness of these infections.

TABLE II.

Samples of *Peringia ulvæ* from Plymouth, 1934–1935.

Size group in mm.	Number of snails dissected.	Percentage of infections of cercariæ developing in rediæ (Groups 3 and 4).	Percentage of infections of cercariæ developing in sporocysts (Groups 1 and 2).
1 mm.	200	1	0·5
2 mm.	400	1	1·5
3 mm.	400	1	2·5
4 mm.	400	7	9
5 mm.	100	1	50
5+ mm.	25	0	100

TABLE III.

Sample of *Peringia ulvæ* (of 3 mm. and over) from Plymouth, June, 1935.

Size group in $\frac{1}{4}$ mm.	Percentage of infections of cercariæ developing in sporocysts.	Percentage of infections of cercariæ developing in rediæ.
3 mm.	2	0
$3\frac{1}{4}$ mm.	2	2
$3\frac{1}{2}$ mm.	4	0
$3\frac{3}{4}$ mm.	2	2
4 mm.	6	2
$4\frac{1}{4}$ mm.	4	2
$4\frac{1}{2}$ mm.	8	4
$4\frac{3}{4}$ mm.	18	0
5 mm.	50	1
$5\frac{1}{4}$ mm.	100	0

* Except cercaria near *C. lophocerca*, Lebour. This species, which was common in some samples (3% infection), showed fairly heavy infections and was most frequently found in snails of $4\frac{3}{4}$ mm. size-group. It was also recorded from one snail of 5 mm.

The lightness of the infections of cercariæ of Groups 3 and 4 appears to be due to their age. These species are comparatively rare. The chances of a snail becoming infected in the young stages would be small, and those infections in the older snails would have had a correspondingly short time in which to develop. There are also numerous very young rediæ in the infections. Moreover, if kept for a sufficiently long time, these infections ultimately become very heavy.

A possible alternative explanation was the supposition that a host in an estuarine environment was unsuitable for the development of the trematode, which failed to attain the usual degree of fertility—but comparison with the same species from Scotland proved this to be incorrect.

The heaviness of many of the infections of *Cercaria oocysta* and *C. ubiquita* is likewise accounted for by the incidence of their occurrence. The snails become infected at an earlier age with these common parasites, and the sporocysts have time in which to develop and reproduce.

The incidence of infection, however, cannot account for the peculiar phenomenon mentioned above—that the few snails per thousand which attain a height of 5–5¼ mm. show a 75% infection with these species, and that the infections in question are all of long standing. The evidence suggested that the parasites themselves were closely linked with, and probably responsible for, the size of the snails. This theory was enhanced by the fact that the primary seat of infection of *C. oocysta* and *C. ubiquita* is the gonads. Partial or complete castration which results must seriously affect the metabolism of the host.

Comparison of Infection of Plymouth *Peringia ulvæ* with Samples from Scotland.

Lebour (1911) and Quick (1920) have recorded much higher incidence of infection in *Peringia ulvæ* from Scotland and Swansea Bay. In collected samples the tendency is to select the larger snails which would account for a somewhat higher percentage of infection than that recorded for a random sample which includes very young snails. The discrepancy was too large to be explained in this manner and consequently an effort was made to obtain samples of *Peringia ulvæ* where the proportion infected reached at least 50 per cent, and to compare the size of the snails with those from Plymouth.

Mr. Richard Elmhirst and Dr. Edith Nicol kindly supplied collected samples from different localities in Scotland. With one exception these more or less agreed, both in size and the degree of infection, with *Peringia ulvæ* from Plymouth. The largest snails measured 5 mm. or a little less in height, and the percentage of infection ranged from 10–20%. The sample from Millport, however, displayed a most striking departure from the norm. The percentage of infection was 90 and numerous snails* reached the relatively colossal size of 8–9 mm. in height (Figs. 1 and 2).

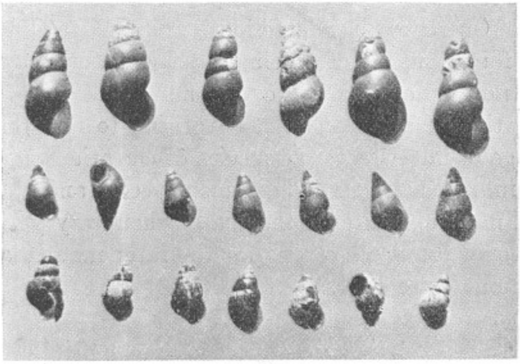

Fig. 1.

Upper row: Living specimens of *Peringia ulvæ* from Millport, showing gigantism and abnormal development of the shell.
Middle row: Living specimens of *Peringia ulvæ* from Plymouth.
Bottom row: Living specimens of *Peringia ulvæ* from near St. Andrews.

All the snails were chosen from the larger size groups of each sample. All × 2.

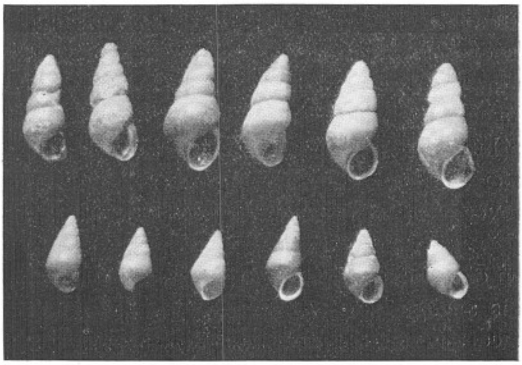

Fig. 2.

Upper row: Living specimens of *Peringia ulvæ* from Millport.
Lower row: Living specimens of *Peringia ulvæ* from Plymouth.

All the snails were chosen from the larger size groups of each sample. All × 2.

The shells in many cases displayed variations and abnormalities such as "ballooning" of certain whorls and asymmetrical development of the spires. The thickness of the shells appeared normal.

* A few of these were kindly submitted to Mr. F. Taylor by Major M. Connolly, who identified them as "varieties of *Peringia ulvæ*." A small series is deposited at the British Museum (Natural History) together with samples from Plymouth.

The infections which included all four groups mentioned on p. 540 were all very heavy and obviously of long standing in the large shells. Thus in the " Echinostomum " group, the rediæ had attained twice the length of those of the same species from Plymouth. Several dozen were present in each snail. On the whole, infections of Group 4 (*Cercaria ephemera* Lebour) were found in smaller specimens than the other groups.

There were no uninfected snails over 5 mm. in height.

Considering these facts it was not surprising to find that despite the high percentage of infection fewer species of cercariæ were found in this sample. The infections were all of common species, and in most cases the miracidia had no doubt entered the snails when very young; thus the competition would prove too strong for the rarer miracidia which would fail to find an uninfected host.*

INFECTED *Peringia ulvæ* IN THE LABORATORY.

Specimens of *Peringia ulvæ*, emitting *Cercaria ubiquita* and cercaria near *C. lophocerca*, Lebour, were isolated and kept well fed on Zostera in the laboratory for six months. They reached a size of 5–5¼ mm. Isolated non-infected individuals kept under similar conditions did not attain these dimensions. A small sample of snails were kept together in one jar, and at the end of six months the surviving individuals were examined. One specimen only measured over 4¾ mm. This proved to be heavily infected with a cercaria of the " Metentera " group. The other snails harboured no parasites.

A few experiments were made to test the effect of starvation on host and parasite. One hundred snails from Millport, all heavily infected, were enclosed in an empty bottle for three weeks, and subsequently placed in water. All proved to be alive and large numbers of cercariæ emerged immediately.

One specimen of *Peringia ulvæ* emitting *C. ubiquita* was kept in water for four months and starved periodically for 2–14 days consecutively. Cercariæ emerged at intervals throughout. The snail measured 5 mm. when it was isolated and increased in bulk and in length by ¼ mm.

A study of the behaviour and external appearance of *Peringia ulvæ* infected with trematodes gives the impression that parasite and host are perfectly adapted to each other. However, examination of the tissues of the host show serious injury and pathological changes like those described by Faust (1920), Agersborg (1924), Dubois (1929) and Rees (1934) in their studies of the histology and cytology of infected snails. In the case of old infections castration is complete and the digestive gland reduced to a remnant. It is difficult to understand how the snail survives at this stage.

* No double infections were ever recorded from *Peringia ulvæ*.

Discussion.

A great number of workers on Trematode larvæ have recorded an apparent relation between the age of the mollusc host and the degree of infection. It is accepted as a general rule that the larger snails, which have been presumed to be the oldest, are more frequently infected than smaller specimens.

To account for this Kemp and Gravely's theory of the immunity of immature snails has been tentatively accepted, and the more rapid growth of gastropod snails after three months of age (Sewell, 1922) is considered a contributing cause to the higher infection of larger individuals.

Only three exceptions to this rule have been recorded (Sewell, 1922; Dubois, 1929) but unfortunately no details of the infections are given.

Wesenberg-Lund (1934) was the first to point out that infected snails are sometimes abnormally large. He receives the credit of originally suggesting that their large size was not indicative of their age, but was due to the presence of the parasites which " cause excessive growth, not the opposite as might perhaps be expected." He also noted ballooning of certain whorls, thinning and corroding of the shells, and colour changes.

He attributed this increase in size to the fact that infected snails ingest abnormally large quantities of food in order to satisfy the demands of the parasites.

The observations on *Peringia ulvæ* strongly support the view of Wesenberg-Lund that parasitism is responsible for an abnormal increase in the size of the host, although it seems more likely that this is brought about by the destruction of the gonads and other glands rather than in the manner suggested by him.

The variation in the shell and asymmetrical development of the spire is probably due to the pressure exerted by the parasites from within.

Such a high percentage infection as displayed by the Millport sample of *Peringia ulvæ*, and the resulting variation in the shells, suggests that the presence of larval trematodes is a factor which cannot be overlooked by conchologists describing local races and " phases " as well as individual varieties.

ACKNOWLEDGMENTS.

My best thanks are due to Major M. Connolly for the great trouble he has taken identifying various samples of snails, to Mr. Richard Elmhirst and Dr. Edith Nicol for sending samples from Scotland, and to Mr. A. E. Lambert for taking the photographs.

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