THE BIOLOGY OF ASTERIAS RUBENS L. II. PARASITIZATION OF THE GONADS BY THE CILIATE ORCHITOPHRYA STELLARUM CÉPÈDE

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(Plate I)

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INTRODUCTION

The astomatous holotrich ciliate, Orchitophrya stellarum, was originally described and named by Cépède (1907a, b), who found it in the gonads of only three males out of a total of over 6000 Asterias rubens of both sexes. These starfishes were taken by him from the Boulogne and Wimereux area. There was no trace of the parasite in any ovaries, but he noticed that it caused a partial and direct castration of its male host. Orchitophrya was found by Piatt (1935) in the testes of Asterias forbesi in Long Island Sound, where Burrows (1936) observed that the percentage of parasitized males varied from 1 to 20% according to the locality. Burrows also found that a small number of the female starfishes (about 1%) were infected. Smith (1936) recorded the parasite in the ovaries of about 25% of the females of A. vulgaris from oyster beds in Malpeque Bay, Prince Edward Island. Eggs taken from these infected ovaries appeared normal and were fertilizable.

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DISTRIBUTION OF THE PARASITE OFF PLYMOUTH

During the years 1946–50 large numbers of A. rubens have been trawled from different localities in the Plymouth area. In the course of investigations on the reproductive cycle in these localized populations, smears have been taken

from the gonads of each starfish and transverse sections cut of a number of selected gonads. In March 1947 trawling was commenced on the Outer Grounds, to the south and south-west of Eddystone. The differences between the starfish from this area and those from the more northerly Rame-Eddystone Grounds have already been described (Vevers, 1949). Orchitophrya stellarum was found in a varying percentage of the males from all the six trawl hauls taken in spring 1947 on the Outer Grounds. In the early months of the years 1948, 1949 and 1950 the parasite was again found in male starfishes from these Grounds and also in a population of Asterias rubens trawled from Asia Shoal, Plymouth Sound. The parasite has never been found in starfishes from the geographically intermediate Rame-Eddystone Grounds. The significance of this

Table I. Analysis of Parasite Occurrences in Starfish from Hauls from Outer Grounds and Plymouth Sound

Ι	Date	Total in haul	Total males	No. of males parasitized	Approx. percentage of males parasitized	
		(a) Out	er Grounds			
9. i 17. i 18. i 25. i 15. i 14. i 13. i 15. i	iii. 47 iv. 48 iii. 48 iii. 48 iii. 49 iiii. 49	33 29 44 50 175 57 29 38 103 231 63 46	12 11 17 25 66 17 15 15 50 87 26	3 3 4 7 16 2 1 1 6 1 2	25 27 24 28 24 12 7 7 7 12 1 8	
	ii. 50 iii, 50	41 79	23 32	3	9	
		(b) Plymouth S	Sound (Asia	Shoal)		
20.	iv. 48 iv. 49 iii. 50	100 25 80	52 10 37	3 1 1	6 10 3	

distribution will be discussed later. Table I gives a synopsis of the occurrences of *Orchitophrya stellarum* in *Asterias rubens* from the Plymouth area.

The occurrence of the parasite is strictly seasonal. It has only been found near Plymouth during January to May (inclusive) when the host's testes are either ripe or nearly ripe. Smith (1936) and Burrows (1936) both record it as occurring during 'summer'.

The absolute number of parasitized starfishes caught in any one haul is necessarily small and so it is difficult to obtain a figure representing the true percentage of males infected. However, the data given in Table I show clearly that the percentage infected was much greater in 1947 than in any of the three succeeding years. The catches taken from the Outer Grounds in March and April 1947 gave very constant percentages of infected males. A month later

(23 May 1947) the percentage infected had dropped to half; probably because most of the males had spawned in the meantime, leaving fewer ripening testes available for the parasites. In January-April 1948 the percentage infected was, on the average, 10, and again there was a sharp drop in percentage to less than 2 in May. There were only two infected catches in 1949 from the Outer Grounds, one in February and one in March, and the percentage with parasites was less than 10. The same was found in the two catches for 1950.

In the Plymouth Sound starfish population *Orchitophrya* has been found only in small numbers in one catch in each of the years 1948, 1949 and 1950.

The percentage of males infected was proportionately much greater in the size classes 10·0–19·9 cm. than in the size classes 5·0–9·9 cm. and 20·0–25·9 cm. (Table II). In the lower-size classes (5·0–9·9 cm.) the scarcity of parasitized individuals is understandable, since some, at least, of these starfishes were definitely juvenile with testes which showed no signs of ripening at the time of observation.

Table II. Size Distribution of Infected Males in the Population (Outer Grounds)

Total males	Infected males	Percentage infected
35	2	6
162	29	18
181	19	II
35	I	3
	35 162 181	Total males males 35 2 162 29 181 19

The very low percentage of infections in the highest size classes (20·0-25·9 cm.) suggests that there may be a certain resistance to the parasites with increased host size. There is, however, no direct evidence for this interpretation.

DISTRIBUTION OF THE PARASITE WITHIN THE HOST

Burrows (1936) noted variation in the amount of parasites within the individual, including cases where some gonads were parasitized and others were normal. Similar conditions were found in the present investigation, thus in starfish 3076 (16 April 1948) there was a very heavy infection of the testes in arm II/interradius 2/3, while all the rest of the testes showed mobile spermatozoa and no parasites. In starfish 3087 (16 April 1948) there were medium infections in two testes in non-contiguous arms and no parasites in the other eight gonads. At the time these starfishes were caught, in mid-April, most of the starfishes on the Outer Grounds were ripe, but few had spawned. In the previous year larger catches of starfishes were made, and among these were a few in which ripe, spawned and parasitized testes were

found in the same animal. Thus in starfish 998 (23 May 1947) the condition of the gonads was:

Arm	Interradius	Condition of gonad
I	5/I I/2	Spawned, re-ripening Spawned
II	Arm missing	Charles and Charle
III	2/3 3/4	Spawned Mobile sperm distally, rest spawned
IV	3/4 4/5	Few parasites Few parasites
V	4/5 5/1	Mobile sperm distally, rest spawned Spawned

There is no doubt that the main centre of infection is in the testes, although the parasites can sometimes be found in other organs. In starfish 640, for instance, *Orchitophrya* was found in the gut and coelomic fluid as well as in the testes, but not in the digestive coeca or tube feet. These are probably chance infections from lesions in the testis and are not considered to be of any importance.

EFFECT OF THE PARASITE ON THE TESTES OF ASTERIAS RUBENS

Cépède (1910) gives a good description of the morphology and life cycle of the parasite, and he noted that it caused partial or direct castration of the host. His material was very limited and neither he nor subsequent workers have recorded the histological changes which occur in testes infected with *Orchitophrya*. With the large number of infected males available from the Plymouth grounds, it has now been possible to obtain further information on this subject.

In the early stages of infection the testes still have well developed spermatogonial ridges, with numerous spermatocytes and spermatids filling the lumen of each tubule. As the parasites increase in number, the sexual products in the lumen disappear and a transverse section then shows that each tubule has distinct spermatogonial ridges and its lumen is filled with parasites. The ridges become progressively smaller and the parasites increasingly crowded (Pl. I, fig. 1). The nutrient medium in which the parasites are living is that of the ripening germ cells, and as the latter disappear so does the food supply of the parasites. When this happens the parasites start to decrease in numbers and the gonad tubules show only a very thin layer of genital epithelium (Pl. I, figs. 2 and 4). In this stage the connective tissue sheath begins to thicken, probably due to a shrinking of the whole tubule, as it becomes less distended with parasites.

Finally, very few parasites are left in the tubule lumina, there is little or no trace of genital epithelium and all that remains are the thick shrunken sheaths of the original testis tubules (Pl. I, fig. 3).

DISCUSSION

The spread of the parasite would appear to be greater in starfish populations which are relatively crowded, for the largest percentages of infected males occurred on the Outer Grounds in 1947. During this year the number of starfishes caught on these grounds in comparable hauls was larger than in subsequent years, and in addition the values for their mean individual body and testes sizes and available food supply were also higher. It has already been found (Vevers, 1949) that a numerically rich population, with abundant food supply, has a large mean body and gonad size. From the present observations it appears that rich and 'successful' populations (as on the Outer Grounds and on Asia Shoal, Plymouth Sound) were also characterized by the presence of a varying percentage of males with ciliate-infected testes. Conversely, a starfish population with small numbers, and low mean body and gonad size (as on the Rame-Eddystone Grounds) showed no trace of the parasites, although many starfishes from these grounds were examined.

Testes containing Orchitophrya never showed mobile sperms, even when the infection was relatively light, and there is little doubt that once it has been infected a testis ceases to function as a reproductive organ during that season. Although sometimes ripe, spawned and infected testes were found in the same starfish, it was more common to find all the testes of a starfish infected in some degree. In a population where over 20% of the males were infected (as in the Outer Grounds in March-April 1947) the intensity of reproduction, measured as the number of potential gametes, would necessarily be reduced by at least a similar amount, since the same number of predators and adverse factors would be preying on a reduced number of gametes. On theoretical grounds this check to reproduction should be reflected in a reduced population in subsequent years. There was, in fact, an observed reduction in the population of Asterias rubens on the Outer Grounds in 1948, 1949 and 1950 as compared with 1947 (Vevers, unpublished data). As it is not possible to follow the fate of broods which go through a pelagic phase one cannot gather direct evidence to show the causes of such a population reduction. On the Outer Grounds any reduction in population following on a year of heavy testis parasitization could easily be masked by immigration from neighbouring areas. There are also other factors, such as movement of food supply, which might reduce the population in numbers and mean body size. The observed population reduction since 1947 is probably the result of many factors, but it is considered that the parasitic castration of over 20% of the males in this population during 1947 must have played a definite part, and that it did, in practice, act as a natural check to a crowded population, a view which is supported by the observations of Galtsoff & Loosanoff (1939) on A. forbesi.

SUMMARY

The parasitic astomatous holotrich ciliate, Orchitophrya stellarum Cépède, has been found in the testes of starfishes (Asterias rubens) in the Plymouth area. It was found only in starfishes from numerically rich and well-fed populations, which also showed large gonad growth. In such populations it occurred in up to 28% of the males during March-April 1947, and in lower percentages during the spring of the three following years. The parasite was never found in a geographically adjacent population containing smaller numbers of poorly fed starfishes. The parasite was found to be relatively more common in the testes of medium-sized starfishes than in those of large and small starfishes.

Presence of the parasite causes a complete breakdown of all the germinal tissue of the testes, so that most of the infected starfishes suffer complete castration. This involution of the testicular tissue has been studied, and photomicrographs are given which show a number of stages in the process.

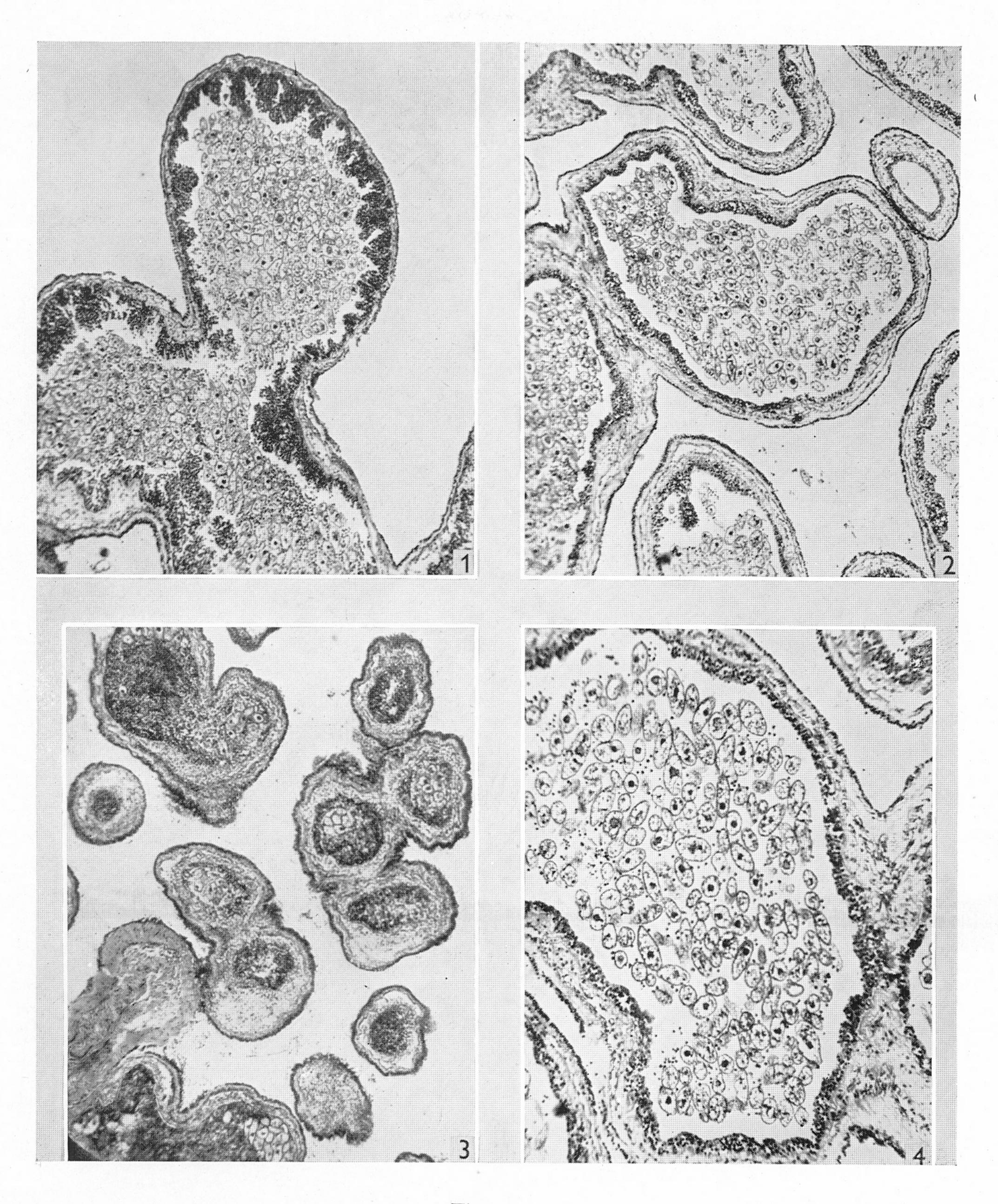
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EXPLANATION OF PLATE I

Photomicrographs of transverse sections of Asterias rubens testes showing stages of infection by Orchitophrya stellarum.

- Fig. 1. Numerous parasites free in the lumen of a gonad tubule. Spermatogonial ridges still distinct.
- Fig. 2. Parasites starting to decrease; spermatogonial ridges have disappeared. Fig. 3. Final stage in the involution of the testis, with genital epithelium destroyed and gonad only represented by the thick shrunken connective tissue sheath. Very few parasites
- Fig. 4. Enlargement of part of fig. 2 to show parasites (cut at different angles) completely filling the lumen of the testis tubule. Very few germinal cells remain among the parasites.



Figs. 1-4.