THE GENERATIVE ORGANS OF THE PARASITIC ISOPODA.

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IN the following pages are recorded some observations on the generative organs of some of the parasitic Isopoda. My investigations were carried on last spring in Dr Dohrn's Zoological Station, and my best thanks are due to him for his help and advice, as well as to Dr Eisig for his kind assistance during my stay at Naples.

The species investigated are the following:—

Cymothoa æstroides (Risso).
Nerocila maculata (M. Edw.).
Nerocila bivittata (Risso).
Anilocra physodes (Lin.).
Anilocra mediterranea (M. Edw.).

With the exception of the last they were kindly determined for me by Prof. Heller. They are all hermaphrodite. The generative organs are essentially alike in all. To avoid future confusion it may be well to state at once that the organs are paired, and those of the two sides quite distinct. The animals during the development of the generative products pass through three distinct stages, which may be distinguished by the following characters.

In the first stage[1] they have externally the appearance of males. There is a double penis (Pl. IV. fig. 4 P.), situated in the median line of the ventral wall of the last thoracic segment. The internal parts of the generative organs on each side consist (Pl. IV. fig. 1) of the ovary and the testes and their ducts. The ovary and testes form a continuous gland, of which the ovary is the posterior simple tubular portion, while the testes appear anteriorly as three cæcal diverticula at its outer border. The oviduct, a widish tube continuous with the wall of the ovary, arises from the outer border of the ovary behind the testes, and runs to the anterior edge of the sixth thoracic segment, where, at this stage, it ends

[1] C. æstroides and A. mediterranea are the only species which I have obtained in this stage.

blindly. The vas deferens is continued from the posterior end of the ovary; it is much narrower than the oviduct; after running straight backwards for a short distance it turns outwards and downwards, and opens externally at the extremity of the penis of its side.

Between the first and second stage a moult takes place, and the penis being part of the skin is thrown of, and in the second stage there is no penis. Neither the vas deferens nor oviduct have an external opening.

In the third stage the vas deferens still remains closed, but the oviduct has acquired a slit-like aperture at the anterior edge of the sixth thoracic segment, just at the base of the posterior flap of the brood-pouch, which is present at this stage.

I will now describe each stage more fully.

In the first stage the generative gland is always comparatively small, owing to the incompletely developed state of the ovary. This may be very small, containing only a few young ova, or it may contain more numerous ova, some of a considerable size. Except in the case of the very youngest ovaries it is easily seen that the formation of the fresh ova takes place only along the outer border of the organ (Pl. IV. fig. 2).

The testes (Pl. IV. fig. 1 T.) at this stage are fully developed; they often contain numerous spermatozoa.

The spermatozoa are arranged in bundles (Pl. IV. fig. 6) with their heads all pointing one way, and are so disposed that the anterior end of the bundle is wedge-shaped. Each spermatozoon (Pl. IV. fig. 6) consists of a very long thin filament tapering to a point at the posterior extremity. The anterior extremity is thicker, and here a peculiarly twisted leaf-like appendage is attached to it (Pl. IV. fig. 6). The spermatozoa are perfectly motionless. Their average length is 1.15 Mm., and that of the appendage .04 Mm.

The bundles of spermatozoa may be seen in the act of making their way from the testes down the outer side of the ovary to the vas deferens. They always pass downwards head foremost.

The vas deferens (Pl. IV. fig. 1 VD.) is usually filled with spermatozoa, and, except at a very early stage, presents a fusiform enlargement near its lower end, which is crowded with spermatozoa. The outer surface of this enlargement is generally covered with branched pigment-cells.

In the second stage the skin has been changed, and, as stated above, the oviduct and vas deferens are both closed externally.

The ovary has increased considerably in size, and frequently many of the ova are completely developed. Young ova are also being formed along the outer margin of the ovary.

The wall of the ovary is an exceedingly fine membrane, lined internally with a single layer of large flattened epithelium-cells (Pl. IV. fig. 5), each of which contains generally four, but sometimes three or two conspicuous nuclei. Both the protoplasm and nuclei of the cells are very granular, the latter usually containing one or more larger granules. As the young ova increase in size they move away from the germinal part of the ovary, pushing out its wall where they come in contact with it to suit their shape, so that at this stage the wall of the ovary loses its primitive even outline. Owing to these changes each ovum, when examined with a high power, appears to be surrounded by a ring of cells, but by careful focussing, it can be easily seen that these are the lining cells of the wall of the ovary.

The oviduct is lined internally with a single layer of flattened epithelium-cells, continuous with those lining the wall of the ovary, but differing from them in being smaller and in containing only a single nucleus. The oviduct is provided with an external layer of longitudinal muscular fibres, which are continued on each side along the outer border of the ovary. There are apparently no circular fibres.

The testes have not increased in size. They contain, as before, spermatozoa.

The vas deferens is also filled with spermatozoa, the enlargement at its lower end being usually crowded with them.

At this stage the skin of the ventral surface can, with care, be separated like a blister from the body wall, and beneath it the flaps of the brood-pouch are seen arising as small oval buds from near the bases of the legs. At first they are quite soft and flat, but as they increase in size they become thrown into numerous small wrinkles, and at the same time it becomes more and more easy to remove the outer skin. While the brood-flaps are being developed a very delicate chitinous skin is formed over the ventral surface beneath them. The brood-flaps reach their full development in size before the loose outer skin is thrown off.

The hardening of the brood-flaps by the formation of an outer chitinous layer is probably a quick process, for in individuals in which, as sometimes happens, half the outer skin is shed at a time the uncovered flaps are quite hard, while those remaining covered are still soft. Probably the hardening of the brood-flaps helps to burst the outer skin.

The young flaps are covered externally by a flattened epithelium. The chitinous layer is formed subsequently, and is quite structureless.

In the third stage, which is attained on the shedding of the outer skin, described in the last stage, the animal possesses a completely developed brood-pouch, formed by the overlapping flaps. The skin of the ventral surface is exceedingly delicate, and is now protected by the brood-pouch. The ovaries at the first part of the stage are very large, and fill nearly the whole of the body-cavity, causing the ventral wall to protrude considerably.

Very soon, however, the eggs are laid, and it is therefore a rare thing to find an individual of this stage with the eggs still in the ovary. When the eggs are laid the shape of the body is altered, the ventral wall being now pressed close up to the dorsal surface.

The testes (Pl. IV. fig. 3 T.) still remain; they have not increased in size, and look withered and dry, though they occasionally contain a few bundles of spermatozoa.

The vasa deferentia (Pl. IV. fig. 3 VD.), especially their enlargements, are still filled with spermatozoa.

The manner in which the ova are fertilised is a point which I have not as yet been able to determine satisfactorily. The oviduct only opens externally at the time when the brood-pouch is present, and as its opening is situated inside the brood-pouch it seems quite impossible that spermatozoa could be introduced into it by another animal.

There is often not more than one individual on a fish, and as these solitary individuals may have embryos in their brood-pouches, they must either have fertilised their own ova, or be parthenogenetic, for they cannot be imagined to pass from one fish to another; indeed for one species at least, C. æstroides, which cannot swim, this is impossible.

Now self-impregnation, if it occurs, must be internal, for the vas deferens becomes closed before the eggs are laid, and remains so until after their development is complete.

Of course if self-impregnation occurs in these cases it occurs always. We have already seen that from the position of the external opening of the oviduct, the ova of one animal cannot be impregnated by another before they are laid. Therefore the only way in which we can imagine that a cross occurs is by supposing that self-fertilisation does not act until after the eggs have been laid, and that the spermatozoa of another individual are introduced by some means, at present unknown, into the brood-pouch, and have a prepotent effect.

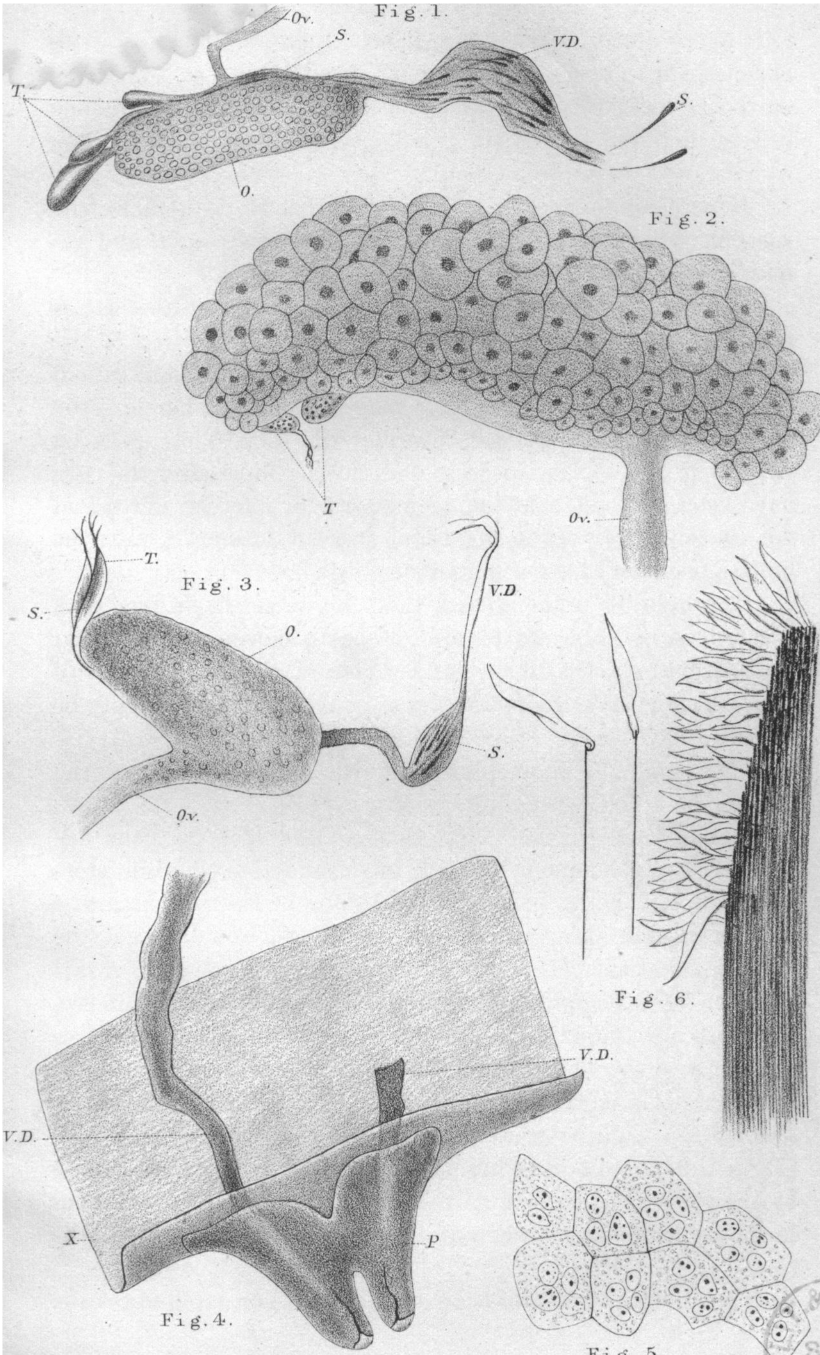
It should be remembered that the brood-flaps overlap a great deal, and are not capable of being moved, and also that the spermatozoa are immoveable. These facts make it difficult to understand how the spermatozoa could by any possibility be introduced.

These animals show perhaps better than any others the manner in which hermaphroditism is acquired.

I think no one can doubt that all the Isopoda have descended from a common bisexual stock, and that the ancestors of the present parasitic species when they began to be parasitic were bisexual. It is evident that their hermaphroditism is the effect and not the cause of their habits. If a free form varied so as to be hermaphrodite, it would have, as far as we can see, no advantage over the bisexual forms, and would not therefore tend to be preserved. On the other hand, it is of such immense advantage to a parasitic animal to be hermaphrodite that such a variation would be almost certain to be preserved.

In the present case hermaphroditism was probably gained by the occurrence of a sport. The following considerations seem to show clearly that it was not the result of gradual modification.

The internal generative organs of the hermaphrodites re-



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semble exactly the combined male and female organs of the free forms, such as Assellus aquaticus, described by G. O. Sars (*Crust. d'eau douce*). It is hardly credible that this would be the case if gradual modification either in the males or females had taken place.

The same argument applies to the external brood-pouch and penis, which are identical with those found in the free forms.

From the analogy of vertebrates it is reasonable to conclude that every embryo contains parts capable of developing into the generative organs of both sexes, and it is conceivable that from these parts both sets of organs may in certain cases become developed and functional. If we imagine such a sport to have been developed in one of the parasitic ancestors of the present animals, and to have produced some individuals like itself, it is all that is required to account for the hermaphroditism of the existing parasitic Isopoda.

DESCRIPTION OF THE FIGURES.

T. Testes. V.D. Vas deferens. S. Spermatozoa. O. Ovary. P. Penis.

Fig. 1. Generative organs of A. mediterranea. First stage. The whole of the vas deferens and oviduct are not shewn.

Fig. II. Generative organs of C. æstroides. First stage. The vas deferens and one of the testss are not shewn.

Fig. III. Generative organs of A. physodes. Third stage—after the eggs have been laid.

Fig. IV. Penis and part of ventral wall of last thoraic segment of C. æstroides.

Fig. V. Cells from wall of ovary. First stage.

Fig. VI. Spermatozoa of A. mediterranea; only the anterior parts are represented.