

A CHANGE IN THE CHROMATOPHORE PATTERN OF CRUSTACEA AT SEXUAL MATURITY

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(With One Text-figure)

I. INTRODUCTION

WHILE studying the chromatophores of the prawn, *Leander serratus*, it was noticed that the ovigerous females possessed certain groups of white chromatophores which were absent in the males or immature females of this species. These chromatophores appeared on the egg-bearing segments after the "breeding-moult", when the pleopods of the females became structurally modified. It has not been previously suggested that the chromatophore pattern of Crustacea becomes modified at sexual maturity, and an investigation was therefore undertaken to determine the occurrence and behaviour of these chromatophores. *Leander serratus*, *L. squilla*, *L. adspersus* and *L. xiphias* were examined at Naples; *Palaemonetes varians* from Plymouth was also examined. In all these species the additional white chromatophores were found in ovigerous females.

II. STRUCTURE AND DISTRIBUTION OF THE WHITE CHROMATOPHORES IN THE PALAEMONIDAE

(a) *Immature males and females.* The structure and behaviour of the normal white chromatophores of shrimps and prawns has already been described (Knowles, 1939). Two main types were observed: The first type is polychromatic and contains red and yellow pigments in addition to the white pigment. This type responds as an independent effector to a change of illumination and is not affected by an injection of eye-stalk extract. It is found distributed at regular intervals along the posterior edges of the body segments of *Leander serratus* and *L. squilla*, and assists in the production of the bars of colour found in these species. The second type responds to an injection of eye-stalk extract by contracting. It contains only a white pigment and is found irregularly scattered in the epidermis of *L. adspersus*, *L. xiphias* and *Palaemonetes varians*, influencing the shade of the body colour, but not assisting in the formation of a body pattern.

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(b) *Ovigerous females*. The additional white chromatophores which are found in ovigerous shrimps and prawns appear gradually during the early spring as the female approaches the breeding condition. They are situated on the sides of the pleura, at the basal joints of the first four pleopods, and on the expanded external posterior margins of the basipodites of the first three pleopods. The full development of these chromatophores occurs after the "breeding-moult" when the female acquires a number of structural modifications of the pleopods. Thus the precoxae of

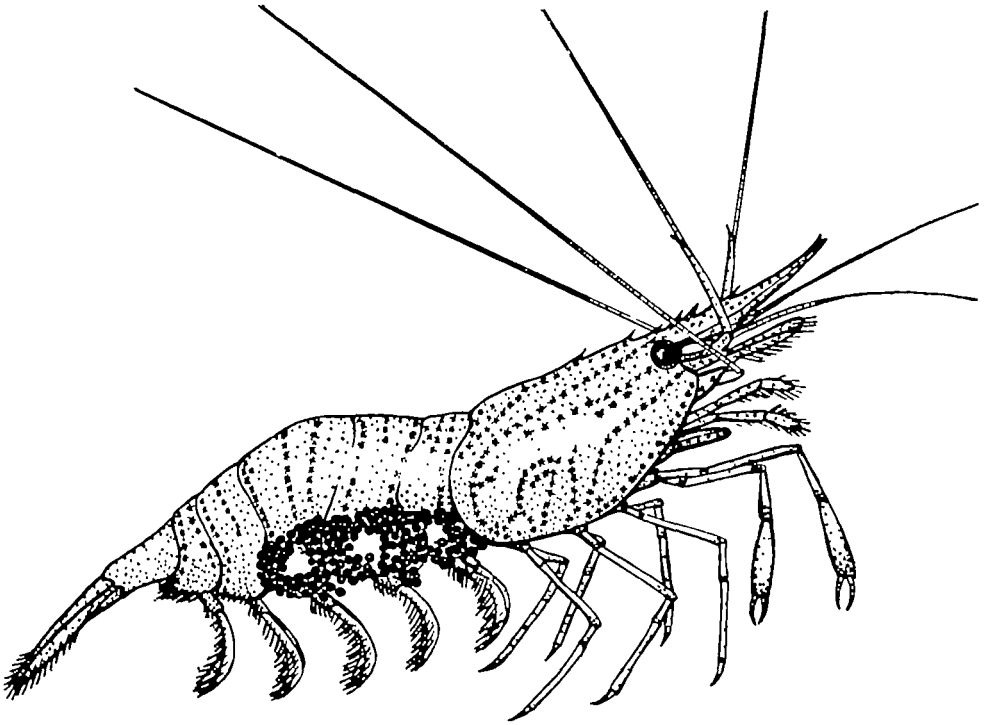


Fig. 1. An ovigerous *Leander serratus*, showing the position of the patches of white chromatophores which appear on the egg-bearing segments during the breeding season. These chromatophores restore the protective pattern which is upset by the presence of eggs.

the first three pairs of pleopods become elongated, the external posterior margins of the basipodites become expanded posteriorly, and a number of new setae tracts, for the protection of the eggs, appear on the first four pleopods (Sollaud, 1923).

Only a white pigment can be seen in these expanded white chromatophores of *Leander serratus*, *L. squilla*, *L. adspersus* and *Palaemonetes varians* although traces of a red pigment can be seen when they are contracted. The white chromatophores of *Leander xiphius*, however, all possess a central patch of red pigment.

III. FACTORS INFLUENCING THE DEVELOPMENT AND CONDITION OF THE ADDITIONAL WHITE CHROMATOPHORES OF OVIGEROUS FEMALES

(a) *Normal conditions.* The secondarily developed white chromatophores of all the species studied are more sensitive to changes of illumination than to changes of background. They contract sharply in darkness and expand in light, but behave in a more erratic manner on illuminated black or white backgrounds. On an illuminated white background they are always maximally expanded, whereas on an illuminated black background the majority of the white chromatophores on the egg-bearing segments contract. This contraction, however, does not prevent the appearance of the white patches over the eggs formed by these chromatophores (Fig. 1), but tends to minimize their effect.

In their normal behaviour therefore, the secondary white chromatophores of ovigerous females resemble more closely the normal white chromatophores found in *Leander adspersus*, *L. xiphias* and *Palaemonetes varians* than those of *Leander serratus* and *L. squilla*.

(b) *Injection experiments.* The white chromatophores situated over the eggs of ovigerous females responded to the injection of an eye-stalk extract in all the species studied. In this respect they differ from the normal white chromatophores of *Leander serratus* and *L. squilla*, but behave in a comparable fashion to the normal white chromatophores of *L. adspersus*, *L. xiphias* and *Palaemonetes varians*.

One-twentieth of a millilitre of an aqueous extract of the eye-stalk of *Leander serratus* was injected into individuals of *L. serratus* and *L. squilla*, from which both eye-stalks had previously been removed. Each injection, which corresponded to one-twentieth of an eye-stalk, was followed by a marked contraction of the white chromatophores situated over the eggs, although the main white chromatophores of the body were not affected by the injection. Therefore, the secondarily developed white chromatophores seen in ovigerous females of *L. serratus* and *L. squilla* are distinct from the normal white chromatophores of these species both in their structure and in their physiological behaviour. However, they resemble the normal white chromatophores of *L. xiphias* and *L. adspersus* and *Palaemonetes varians*, although they are more sensitive to the injection of the eye-stalk extract than are the normal white chromatophores of these species.

(c) *Castration experiments.* Females of *Leander xiphias* and *L. squilla* were examined after their ovaries had been prevented from maturing by X-rays or parasites. The largest available individuals were chosen as experimental animals, i.e. in the case of *L. xiphias*, those which had an overall length from the tip of the rostrum to the extremity of the uropods of approximately 6 cm. In *L. squilla* the largest animals obtainable had an overall length of approximately four and a half centimetres.

The ovarian oocytes of a number of these animals were destroyed by X-ray irradiation, some 1-3 months before the breeding season. It was found that one dose of 6800 r. units was sufficient to inhibit vitellogenesis. Post-mortem examination by sections of the gonads of females which had been treated in this way showed that

the oocytes had almost without exception been destroyed, and that the gonads consisted simply of a connective tissue stroma. The mortality of experimental animals was high, but about thirty significant results were obtained for each species. These irradiated animals moulted normally, and survived during the breeding season. The irradiated animals and controls were kept living until the first week in May, by which time the controls had all developed the white chromatophores, passed the "breeding-moult", and laid their eggs. In the irradiated animals, however, no ova were laid, and the white chromatophores did not appear.

Females, the maturation of whose gonads had been inhibited by parasites, were also examined. *Leander xiphias* is parasitized by *Bopyrus xiphias* (Giard & Bonnier) and *Leander squilla* by *Bopyrus Hellier* (Giard & Bonnier). These Bopyrid parasites interfere with the general metabolism of their hosts by withdrawing blood from the circulation. Very large parasitized females are rare. However, twenty individuals of each species of, or exceeding the sizes given above for the average egg-laying females, were examined. These females did not develop the white chromatophores which are found in the normal ovigerous females; a postmortem examination of their gonads showed that the ovaries of parasitized animals are similar to those found in immature females, consisting entirely of small oocytes without any deposition of yolk.

It was noticed that in females castrated, whether by X-rays or parasites, the suppression of the development of the white chromatophores was not due to a prevention of moulting. The parasitized animals moult much more frequently than normal individuals, while in the case of X-rayed females only individuals which had moulted were considered.

IV. DISCUSSION

It is clear that the white chromatophores which appear on the egg-bearing segments of the female prawn's body are developed in immediate relation to the presence of maturing ovaries, since the suppression of the normal development of the ovaries will prevent the appearance of these chromatophores. This dependence of the appearance of a secondary sexual character on the presence of a normal gonad is a striking and unusual phenomenon for a Crustacean. The change cannot, however, be taken as demonstrating the existence of a "female sex hormone" in these animals, since it is very probable that it is related simply to the metabolic conditions which obtain during yolk deposition. It is not surprising to find that nuptial colorations due to pigment modifications should appear during the internal modifications which accompany sexual maturity. It is probable that the white pigment contained in the chromatophores of Crustacea is guanin, a purine derivative which is found widely distributed in the integument of vertebrates and invertebrates. This substance is known to augment at maturity, and it plays an important part in the nuptial colorations of many fishes, batrachians and reptiles (Verne, 1930). The male of *Triton alpestris* develops a nuptial pattern at maturity due to an accumulation of guanin on the back. *Lacerta viridis* and the teleostean fishes *Gasterosteus aculeatus*, *Perca fluviatilis*, and *Phoxinus laevis* all develop at sexual maturity nuptial colorations of

which guanin is an important constituent. It is probable that elaboration of guanin in these forms is due to the violent nucleo-protein movements which occur at gametogenesis.

It is not clear, however, why certain regions of the body in prawns and shrimps are particularly sensitive to the disturbances in metabolism which lead to guanin accumulation, as indicated by the constancy in position of the white chromatophores. The white chromatophores nearest to the eggs are the most affected, and only a small increase is observed in the number of white chromatophores in other parts of the body. Probably sexual maturity leads to a general disturbance of the body metabolism in female shrimps and prawns, but the chromatophores on the egg-bearing segments have developed a greater sensitivity to guanin augmentation because of the special protective coloration which they give. Such groups of white chromatophores situated directly over the gonads serve to mask the eggs and to render males and females less easily distinguishable, besides breaking the continuous line of shadow under the body due to the presence of the eggs (Fig. 1). Since the egg-bearing females are less agile than the males, the development of these white chromatophores at maturity may thus help to protect the females from possible predators.

It is difficult to determine the origin of the white chromatophores on the egg-bearing segments. Possibly they may replace red chromatophores by a substitution or transformation of the red pigment. This suggestion is supported by the behaviour of these chromatophores, which in *Leander serratus* and *L. squilla* function in a manner different from the normal white chromatophores of these species.

SUMMARY

1. White chromatophores appear on the egg-bearing segments of female prawns and shrimps at sexual maturity.
2. Such chromatophores do not appear in the females whose gonads have been destroyed by X-rays or by parasites.
3. It is probable that this appearance of white chromatophores at sexual maturity is correlated with the metabolic changes occurring at yolk deposition in the ovaries.

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